Taxonomy and systematics of nonmarine Late Jurassic and Early Cretaceous ostracods: their phylogeny and application to biostratigraphy with emphasis on the Early Cretaceous of the North American Western Interior foreland basin

Taxonomie und Systematik nichtmariner Ostrakoden des Oberjura und der Unterkreide: Ihre Phylogenie und biostratigraphische Anwendung mit Hauptaugenmerk auf die Unterkreide des nordamerikanischen Western Interior Vorlandbeckens

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Dedicated to my parents,
whose skills and enthusiasm for scientific discourse
have guided my journey.

Meinen Eltern gewidmet,
die mir die Fähigkeit und die Begeisterung für den wissenschaftlichen
Diskurs mitgegeben haben.

Declaration of Authenticity

I hereby certify sole authorship of the thesis "Taxonomy and systematics of nonmarine Late Jurassic and Early Cretaceous ostracods: their phylogeny and application to biostratigraphy with emphasis on the Early Cretaceous of the North American Western Interior foreland basin" as submitted to the Department of Earth Sciences of the "Freie Universität Berlin" for the conferral of a doctorate, and that no sources other than those indicated have been used in its preparation. Parts of this thesis that have been drawn on the work of others with regard to contents or by literal quotation have been appropriately marked through indication of source. Where any collaboration has taken place with other researchers, I have clearly stated my own personal share in the investigation.

This work in the same or a similar form has not been submitted to any other examining body.

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Hiermit versichere ich an Eides statt, dass ich die der Fachrichtung Geowissenschaften der Freien Universität Berlin zur Promotion eingereichte Arbeit „Taxonomie und Systematik nichtmariner Ostrakoden des Oberjura und der Unterkreide: Ihre Phylogenie und biostratigraphische Anwendung mit Hauptaugenmerk auf die Unterkreide des nordamerikanischen Western Interior Vorlandbeckens" selbstständig verfaßt und keine anderen als die angegebenen Hilfsmittel verwendet habe. Teile der vorliegenden Arbeit, die anderen Werken wörtlich oder inhaltlich entnommen sind, wurden durch Angaben der Quellen gekennzeichnet. In allen Fällen einer Zusammenarbeit mit anderen Forschenden habe ich meinen persönlichen Arbeitsanteil klar dargestellt.

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This doctoral thesis is produced for the purpose of a public examination only. Systematic names introduced or nomenclatural acts herein will not become available until they are going to be formally published within the meaning of the valid International Code of Zoological Nomenclature, ICZN (Article 8.3.).

Extended Abstract

Taxonomy and systematics of nonmarine Late Jurassic and Early Cretaceous ostracods: their phylogeny and application to biostratigraphy with emphasis on the Lower Cretaceous of the North American Western Interior foreland basin

The taxonomic revision of some important nonmarine ostracod groups with emphasis on selected taxa from Lower Cretaceous deposits of the Western Interior foreland basin (Lakota Formation, South Dakota and Wyoming, and Cedar Mountain Formation, Utah) conducted from the perspective of application, resulted in a breakthrough in the consideration of their utility. Inconsistent taxonomy was determined to have been the main reason hampering their application. The understanding and verification that the Early Cretaceous nonmarine ostracods of North America are not as endemic as erstwhile believed in combination with an upgraded taxonomic concept, is the key to their successful multifaceted application and the interpretation of their paleobiology, evolution, paleobiogeography, and paleoecology. The results of the revision signify considerable progress in the taxonomy and systematics of these ostracod groups, the supraregional correlation and Early Cretaceous North American biostratigraphy based on their representatives, and the assessment of the further application potential of the latter in the foreland basin.

Representatives of the genus *Theriosynoecum* Branson 1936 of the Subfamily Timiriaseviinae (extant, Cytheroidea) and the genus *Cypridea* Bosquet 1852 of the Family Cyprideidae (extinct, Cypridoidea) are important taxa in nonmarine Lower Cretaceous deposits of the world, which have great regional utility in biostratigraphy. As to representatives of *Theriosynoecum*, this also applies to the Upper Jurassic.

With respect to the Timiriaseviinae, the species *Theriosynoecum forbesii* (Jones 1885) and *T. verrucosa* (Jones 1885) are considered separate and not subspecies of *T. forbesii*. *Theriosynoecum verrucosa* occurs in the uppermost Morrison Formation of the southern Black Hills margin (South Dakota, U.S.A.), *T. fittoni* (Mantell 1844) in the Lakota Formation of the southern and eastern Black Hills margin (South Dakota), and *T. pahasapensis* (Roth 1933) in the Lakota Formation of the eastern Black Hills margin. The latter is, to the present state of knowledge, endemic to North America. It is proposed to consider and test whether *Theriosynoecum fittoni* (Mantell 1844) and *T. alleni* (Pinto and Sanguinetti 1962) are synonymous because of their many striking similarities. Fossil representatives of several genera of the Timiriaseviinae (*Theriosynoecum*, *Metacypris*, *Cytheridella*, *Timiriasevia*) are well distinguishable by their carapace characters. Aptian–Albian taxa of the extinct genus *Theriosynoecum* are clearly distinct from contemporaneus ones of *Metacypris* Brady and Robertson 1870.

The emended Family Cyprideidae Martin 1940 includes the genera *Bisulcocypridea* Sohn 1969, *Cypridea*, *Mongolocypris* Szczechura 1978, *Paracypridea* Swain 1946, and *Praecypridea* gen. nov. Representatives of *Praecypridea* gen. nov. have been described from the Middle to Upper Jurassic of Europe, North America and Africa, and are considered ancestral to *Cypridea*. As to the North American Lower Cretaceous representatives, the genus *Longispinella* Sohn 1979 is now considered a subgenus of *Cypridea*. *Cypridea (Guangdongia)* Guan 1978 is allocated to *Bisulcocypridea*. *Cypridea (Ulwellia)* (Anderson 1939) is rejected, and *Cypridea (Sebastianites)* Krömmelbein 1962 and *Cypridea (Yumenia)* Hou 1958 questioned to belong to the Cyprideidae. With regard to the subgeneric taxonomy, the North American species *Cypridea (Pseudocypridina) inornata* (Peck 1951) is now considered a junior synonym of *Cypridea (P.) setina* (Anderson 1939), *Cypridea (P.) laeli* Sohn 1979 considered an ecophenotype of *Cypridea (P.) piedmonti* (Roth 1933), and *Cypridea (Longispinella) asymmetrica* Sohn 1979 designated synonymous (sexual dimorph) to *C. (L.) longispina* Peck 1941. *Cypridea? minuta* (Peck 1951) most probably represents an early representative of *Bisulcocypridea* Sohn. Sexual dimorphism is presumed in several species of *Cypridea* and mixed reproduction is corroborated to be the most likely reproductive mechanism among taxa of this genus with according consequences for their dispersal mechanisms and distributional patterns. The evidence for a substantial overestimation of the species diversity in *Cypridea* but underestimation of the quantity of possible phenotypes of different origin is confirmed, and, therefore, the Latest Jurassic to Early Cretaceous faunal dominance of the Cyprideidae in nonmarine Purbeck/Wealden-like environments becomes strongly arguable. The upgraded taxonomic approach facilitates an improved general application of taxa of *Cypridea* and constitutes a good basis for future research in phylogeny, evolution, and distribution of the biostratigraphically most important representatives of the Cyprideidae in the nonmarine Lower Cretaceous of North America.

Representatives of the Trapezoidellidae Sohn 1979 (extinct, Cypridoidea) are known from the Upper Jurassic and Cretaceous of North America, Central Asia, and East Africa. These (particularly the North American taxa) are in need of detailed revision and, provided that, are considered for further application.

Early Cretaceous species of *Theriosynoecum* are not yet applicable biostratigraphically in North America as they are in Europe, but this is mainly due to the lack of data from the former area. In contrast, taxa of *Cypridea* proved to be of great utility in improving the biostratigraphic age determination for, and correlation of, relevant formations of the Western Interior foreland basin.

The timespan represented by the hiatus between nonmarine Upper Jurassic (to Early Berriasian?) and unconformably overlying Lower Cretaceous deposits throughout the North American Western Interior foreland basin has been under discussion for the entire 20th century and remains controversial to date. Ostracod correlations to well dated western European strata (Purbeck/Wealden of England and "German Wealden" of NW-Germany), mainly based on representatives of *Cypridea*, strongly suggest a much higher maximum age for some Lower Cretaceous formations of the Western Interior foreland basin (Lakota Formation, South Dakota and Wyoming, and Cedar Mountain Formation, Utah), i.e., Berriasian to Early Valanginian instead of Barremian or Aptian. These biostratigraphic results affect the correlatable formations as well and, therefore, have considerable consequences on a wide scope of basin-related geologic and paleontologic topics. The central issue hampering an integrated synthesis of the Western Interior foreland basin is its yet imprecise chronostratigraphic framework and inadequate documentation. Temporal relationships between the basins geologic processes and their control factors are still insufficiently calibrated or controversial. Detailed ongoing revision of North American Early Cretaceous nonmarine ostracods demonstrates their applicability, utility, and excellent further potential as a tool for the improvement of the chronostratigraphy of the Western Interior foreland basin at smaller and larger scale. Thereby, these ostracods also help to expedite our understanding of animal (e.g. early mammals and dinosaurs) and plant (angiosperms) evolution on the North American continent.

The first major step as to the multifaceted application of North American Early Cretaceous nonmarine ostracods has been made by their utilization through taxonomic revision. This marks the advent of a refined ostracod-based biostratigraphy in the nonmarine Lower Cretaceous of the Western Interior foreland basin. An application of ostracod biostratigraphy to other Lower Cretaceous formations of the basin in conjunction with other stratigraphic methods is expected to considerably improve the Lower Cretaceous nonmarine stratigraphy in the Western Interior by facilitating a better chronologic framework and providing additional correlating ties, potentially even for nonmarine-marine correlation in the northern and southern parts of the basin. Based on a refined biostratigraphy, ostracods are also expected to support the identification and justification of stratigraphic unconformities and provide age determinations of single sample horizons. Considering the present state of ongoing research regarding the ostracod taxonomy and stratigraphic distribution, an aspired ostracod biozonation of the North American nonmarine Lower Cretaceous seems to be within reach.

Erweiterte Kurzfassung

Taxonomie und Systematik nichtmariner Ostrakoden des Oberjura und der Unterkreide: Ihre Phylogenie und biostratigraphische Anwendung mit Hauptaugenmerk auf die Unterkreide des nordamerikanischen Western Interior Vorlandbeckens

Die anwendungsorientiert durchgeführte taxonomische Revision einiger wichtiger nichtmariner Ostrakodengruppen mit Schwerpunkt auf ausgewählte Taxa aus unterkretazischen Ablagerungen des Western Interior Vorlandbeckens (Lakota-Formation, South Dakota und Wyoming, und Cedar-Mountain-Formation, Utah) hat zu einem Durchbruch bezüglich der Einschätzung ihrer Brauchbarkeit geführt. Als Haupthindernis für eine Anwendung dieser Ostrakoden wurde ihre uneinheitliche Taxonomie ermittelt. Das Verstehen und der Nachweis, dass die nichtmarinen Unterkreide-Ostrakoden Nordamerikas nicht so stark endemisch sind, wie früher angenommen, verbunden mit einem verbesserten taxonomischen Konzept, sind der Schlüssel zu ihrer vielfältigen Anwendung und der Interpretation ihrer Paläobiologie, Evolution, Paläobiogeographie und Paläoökologie. Die Ergebnisse der Revision bedeuten erhebliche Fortschritte in Taxonomie und Systematik dieser Ostrakodengruppen, überregionaler Korrelation und unterkretazischen Biostratigraphie Nordamerikas, basierend auf ihren Vertretern und der Beurteilung deren weiteren Anwendungspotentials im Vorlandbecken.

Vertreter der Gattung *Theriosynoecum* Branson 1936 (Unterfamilie Timiriaseviinae, existent, Cytheroidea) und der Gattung *Cypridea* Bosquet 1852 (Familie Cyprideidae, ausgestorben, Cypridoidea) sind weltweit wichtige Taxa in nichmarinen Ablagerungen der Unterkreide, die regional eine hohe Bedeutung für die Biostratigraphie haben. Für Vertreter von *Theriosynoecum* trifft dies ebenfalls im Oberjura zu.

Hinsichtlich der Timiriaseviinae werden *Theriosynoecum forbesii* (Jones 1885) und *T. verrucosa* (Jones 1885) als getrennte Arten betrachtet und nicht als Unterarten von *T. forbesii. Theriosynoecum verrucosa* wurde im obersten Bereich der Morrison-Formation im südlichen Randgebiet der Black Hills (South Dakota, USA) nachgewiesen, *T. fittoni* (Mantell 1844) in der Lakota-Formation der südlichen und östlichen Randgebiete der Black Hills (South Dakota) sowie *T. pahasapensis* (Roth 1933) in der Lakota-Formation des östlichen Randes der Black Hills. Letztere Art ist, soweit derzeit bekannt, endemisch in Nord Amerika. Es wird vorgeschlagen, *Theriosynoecum fittoni* (Mantell 1844) und *T. alleni* (Pinto und Sanguinetti 1962) aufgrund markanter Ähnlichkeiten als synonym zu betrachten beziehungsweise dahingehend zu überprüfen. Die fossilen Vertreter mehrerer Gattungen der Timiriaseviinae (*Theriosynoecum*, *Metacypris*, *Cytheridella*, *Timiriasevia*) können anhand ihrer Carapax-Merkmale gut voneinander unterschieden werden. Taxa der ausgestorbenen Gattung *Theriosynoecum* aus dem Aptium bis Albium sind von zeitgleich auftretenden Vertretern der Gattung *Metacypris* Brady and Robertson 1870 deutlich zu unterscheiden.

Die überarbeitete Familie Cyprideidae Martin 1940 schließt die Gattungen *Bisulcocypridea* Sohn 1969, *Cypridea* Bosquet 1852, *Mongolocypris* Szczechura 1978, *Paracypridea* Swain 1946 und *Praecypridea* gen. nov. ein. Vertreter von *Praecypridea* gen. nov. wurden aus dem Mittleren und Oberen Jura Europas, Nordamerikas und Afrikas beschrieben und werden als Vorfahren von *Cypridea* erachtet. Hinsichtlich der Vertreter der Unterkreide Nordamerikas wird die Gattung *Longispinella* Sohn 1979 als Untergattung zu *Cypridea* gestellt. *Cypridea (Guangdongia)* Guan 1978 wird der Gattung *Bisulcocypridea* zugeordnet. *Cypridea (Ulwellia)* (Anderson 1939) wird als ungültig betrachtet und die Zugehörigkeit von *Cypridea (Sebastianites)* Krömmelbein 1962 sowie *Cypridea (Yumenia)* Hou 1958 zur Familie Cyprideidae in Frage gestellt. Bezüglich der Taxonomie unterhalb des Gattungsniveaus ergeben sich folgende Änderungen: Die nordamerikanische Art *Cypridea (Pseudocypridina) inornata* (Peck 1951) ist ein jüngeres Synonym von *Cypridea (P.) setina* (Anderson 1939), *Cypridea (P.) laeli* Sohn 1979 wird als Ökophänotyp von *Cypridea (P.) piedmonti* (Roth 1933) interpretiert und die Art *Cypridea (Longispinella) asymmetrica* Sohn 1979 als synonym (sexualdimorph) zu *C. (L.) longispina* Peck 1941 betrachtet. *Cypridea? minuta* (Peck 1951) ist mit hoher

Wahrscheinlichkeit ein früher Vetreter der Gattung *Bisulcocypridea*. Für etliche Arten von *Cypridea* wird das Auftreten von Sexualdimorphismus vorausgesetzt, und „gemischte Reproduktion“ (*mixed reproduction*) als wahrscheinlichster Reproduktionsmechanismus für die Vetreter dieser Gattung bekräftigt, mit entsprechenden Auswirkungen auf deren Verbreitungsmechanismen und Verbreitungsmuster. Anhaltspunkte für eine erhebliche Überbewertung der Artvielfalt bei *Cypridea*, verbunden mit einer Unterschätzung der Anzahl von möglichen Phänotypen verschiedenen Ursprungs, haben sich bestätigt, und deshalb wird die oberjurassische bis unterkretazische Faunendominanz der Cyprideidae in nichtmarinen Purbeck/Wealden-artigen Lebenswelten zweifelhaft. Die modernisierte taxonomische Vorgehensweise ermöglicht eine verbesserte allgemeine Anwendung von Taxa der Gattung *Cypridea* und stellt eine gute Basis für zukünftige Untersuchungen bezüglich der Phylogenie, Evolution und Verbreitung der biostratigraphisch äußerst wichtigen Vertreter der Cyprideidae in der nichtmarinen Unterkreide Nordamerikas dar.

Vertreter der Trapezoidellidae Sohn 1979 (ausgestorben, Cypridoidea) sind aus dem Oberjura und der Unterkreide Nordamerikas, Zentralasiens und Ostafrikas bekannt. Diese (insbesondere die nordamerikanischen Taxa) bedürfen einer gründlichen Revision und hätten, darauf basierend, weitere Anwendungspotentiale.

Unterkretazische Arten von *Theriosynoecum* sind in Nordamerika bisher noch nicht so gut biostratigraphisch anwendbar wie in Europa, was allerdings durch den Mangel an Datenmaterial in Nordamerika bedingt ist. Hingegen erwiesen sich Taxa von *Cypridea* als sehr gut geeignet für die biostratigraphische Verbesserung der zeitlichen Einstufung und Korrelation von entsprechenden Formationen im Western Interior Vorlandbecken.

Über die Dauer der Zeitspanne, die im gesamten nordamerikanischen Western Interior Vorlandbecken durch einen Hiatus zwischen oberjurassischen (bis Unter-Berriasium?) und diskordant überlagernden unterkretazischen Ablagerungen repräsentiert ist, wurde durch das gesamte zwanzigste Jahrhundert debattiert, und sie ist bis heute umstritten. Auf Ostrakoden basierende Korrelationen mit gut datierten westeuropäischen Schichten (Purbeck/Wealden von England und „Wealden“ von Nordwestdeutschland), hauptsächlich mittels Vertretern von *Cypridea*, deuten nachhaltig auf ein wesentlich höheres Maximalalter einiger Unterkreideformationen des Western Interior Vorlandbeckens hin (Lakota-Formation, South Dakota und Wyoming, und Cedar-Mountain-Formation, Utah), das heißt, Berriasium bis frühes Valanginium anstatt Barremium oder Aptium. Diese biostratigraphischen Ergebnisse betreffen ebenfalls Formationen, die mit diesen korreliert sind, und haben somit erhebliche Auswirkungen auf eine große Bandbreite von beckenbezogenen geologischen und paläontologischen Themenbereichen. Haupthindernis für eine ganzheitliche Synthese des Western Interior Vorlandbeckens sind dessen noch immer unpräzises chronostratigraphisches Gerüst und eine unzulängliche Dokumentation. Die zeitlichen Beziehungen zwischen den geologischen Prozessen im Becken und den beeinflussenden Faktoren sind nach wie vor unzureichend abgeglichen oder umstritten. Laufende ausführliche Revisionen von nichtmarinen Ostrakoden der Unterkreide zeigen deren Verwendungsmöglichkeiten, Eignung und ausgezeichnetes weiteres Potential als Werkzeug zur Verbesserung der Chronostratigraphie des Western Interior Vorlandbeckens in kleinräumigem und großräumigem Maßstab. Damit helfen diese Ostrakoden zusätzlich, unser Verständnis der Evolution von Tieren (z.B. Mammalia und Dinosauria) und Pflanzen (Angiospermen) auf dem nordamerikanischen Kontinent zu verbessern

Der erste Schritt hinsichtlich vielfältiger Anwendung von nichtmarinen Ostrakoden der nordamerikanischen Unterkreide ist vollzogen: das Erschließen ihrer Nutzbarkeit durch taxonomische Revision. Dies begründet das Aufkommen einer weiterentwickelten Ostrakoden-Biostratigraphie in der nichtmarinen Unterkreide des Western Interior Vorlandbeckens. Von der biostratigraphischen Anwendung der untersuchten Ostrakoden auf weitere Formationen des Beckens ist, in Verbindung mit anderen stratigraphischen Methoden, eine erhebliche Verbesserung der nichtmarinen Unterkreidestratigraphie im Western Interior zu erwarten und zwar, weil die Ostrakoden ein verbessertes chronostratigraphisches Gerüst ermöglichen sowie zusätzliche Anknüpfungspunkte für Korrelationen bereitstellen, möglicherweise sogar für nichtmarin-marine Korrelationen in den nördlichen und südlichen Randbereichen des Beckens. Ausgehend von einer verbesserten Biostratigraphie ist auch zu erwarten, dass Ostrakoden die Identifizierung und Begründung von stratigraphischen Diskordanzen unterstützen und die zeitliche Einstufung einzelner Probenhorizonte ermöglichen werden. Unter Berücksichtigung des derzeitigen Forschungsstandes sowie laufender Forschungen bezüglich Taxonomie und stratigraphischer Verbreitung der Ostrakoden scheint eine angestrebte Ostrakoden-Biozonierung der nichtmarinen Unterkreide Nordamerikas in Reichweite zu geraten.

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I thank many people from the Insitut für Geologische Wissenschaften, Fachrichtung Paläontologie of the Freie Universität Berlin (Berlin, Germany) for varied support and help: I am grateful to Ulla Schudack with whom I have exchanged ideas and materials on the topic of Early Cretaceous ostracods for years and who effectively became my unofficial third dissertation advisor. I thank Nadine Siegling who patiently processed and picked most samples and served as a field assistant in 2004. My gratitude is extended to Constanze Stehr (Geoscience Library) who provided me with many important original references and infallibly supported me in finding specific sources of literature. I also thank Gerd Schreiber (now Universität Münster) for essential support concerning work in the lab, sample processing and more, and uncountable servings of delicious coffee. Anne Beck (Administration) is thanked for considerable help in English corrections and for improving my English skills. Many thanks go to Rolf Kohring, who has always been one of my mentors and has given me motivation in scientific and cultural matters of all kinds of fields. He introduced me to the art of Flamenco guitar and to Flamenco music. Our classic guitar sessions on the weekends will always be remembered. I am also grateful to my office mates Britta Bookhagen and Michael Kramer for their collegiality, friendship and emotional support; and many other colleagues in Berlin as well.

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I would like to thank Gene Hunt and Carlita Sanford (The National Museum of Natural History, Smithsonian Institution, Washington, DC, U.S.A.) for hosting and assisting me during my work with the ostracod collection of I.G. Sohn. I also appreciate the assistance of Scott Whittaker (same institution) with SEM work.

It is with pleasure to express my gratitude to the Institut für Paläontologie, Universität Wien (Wien, Austria) for giving me the opportunity to make this huge task possible by providing me with the position of an assistant, which enabled me to put two more years of essential effort into this thesis and to complete it. This was possible due to the wholehearted support of many colleagues, particularly, among others, Johann Hohenegger, Peter Pervesler, Martin Zuschin, Doris Nagel and Andrey Ostrovsky. It has been an instructive time and, besides scientific matters, I have been introduced to the Austrian, or Viennese, way of life. My deepest thanks go to my office mate Antonino Briguglio, who has been an invaluable friend, challenging discussion partner, and an amazing genial and tolerating colleague. Antonino withstood my times of frustration, shared both good times and bad with me, and supported me in a most varied manner. I am likewise grateful to Jennifer A. Sawyer for her cordial friendship, camaraderie, and collegiality. Jennifer also has an important part in this thesis for, over the years and upon its completion, having read, corrected and improved the English of major sections of it with thankworthy critical power.

I would like to thank all of my friends in Berlin and elsewhere, for the good times and for keeping me out of trouble, including Pedro el Marinero and the Berlin Flamenco community. I am grateful to Sabine Horvath (Berlin) for having been a kind and helpful neighbor and looking after my apartment during my many extensive travels.

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"I cannot say whether things will indeed get better, should they change; what I can say, however, is that they have to change if they are to get better."

Georg Christoph Lichtenberg (1742-1799, German author, satirist, mathematician and the first German professor of experimental physics)

(translation Kathleen Kleinhenz)

„Ich kann freilich nicht sagen, ob es besser werden wird, wenn es anders wird; aber soviel kann ich sagen: es muß anders werden, wenn es gut werden soll."

Georg Christoph Lichtenberg (1742-1799, deutscher Autor, Satiriker, Mathematiker und erster deutscher Professor für experimentelle Physik)

Preamble

This thesis deals with the taxonomy and systematics of Late Mesozoic (latest Jurassic and Early Cretaceous) nonmarine ostracods (microcrustaceans with a calcified, bivalved shell) from the North American Western Interior foreland basin and their utilization and application, within the scope of the German Science Foundation (DFG) project "Ostracoden und Charophyten aus der nichtmarinen Unterkreide der westlichen USA: Biostratigraphie, Paläoökologie, Biogeographie und Phylogenie" (Ostracods and charophytes from the nonmarine Lower Cretaceous of the U.S.A.: Biostratigraphy, paleoecology, biogeography and phylogeny), projects DFG Schu 694/14-1 and 14-2 to Michael E. Schudack (Freie Universität Berlin, Berlin, Germany). This thesis focuses on the ostracods and implications of the first results of the taxonomic revision of some important taxa on a wide array of ostracod-related, as well as basin-related geologic and paleontologic, topics.

Structure

The thesis presented is written in a cumulative style and comprises five chapters including six scientific papers:

- **Chapter 1: Introduction**
- **Chapter 2: Scientific Papers (Publications Nos. 1–6)**
- **Chapter 3: Discussion and Synopsis**
- **Chapter 4: Conclusions and Perspectives**
- **Chapter 5: References**
- **Appendix**

Chapter 1 is subdivided into nine subchapters and presents an introduction to ostracods, the area under investigation and its geology, the scientific background and development of the project, aims and working hypotheses, an overview of the publications comprised and their interconnection, and information concerning the methodology of the thesis.

Chapters 2.1–2.6 cover the scientific papers which have been published or submitted for publication. The author of this thesis is the first author, or single author (3 of 5), for five of these, and is second author in the one remaining. None of the publications has more than three contributors. Papers Nos. 2, 3 and 4 make up the major component of the thesis. The origin and publication history/plans of these papers are outlined in the following and in case of a multi-authored paper, the personal work input and percentage of contribution of the author of this thesis are given:

Chapter 2.1., Publication No. 1

SAMES, B., WHATLEY, R. and SCHUDACK, M. E., accepted. *Praecypridea*: A new nonmarine ostracod genus from the Jurassic and Cretaceous of Europe, North and South America, and Africa. *Journal of Micropalaeontology*.

This paper had been conceptualized by Robin C. Whatley (Aberystwyth, UK) and Michael E. Schudack (Berlin, Germany) between 1997-1999 in a first detailed draft, and then was set aside for some years. As a consequence of ongoing research concerning the taxonomic revision of the genus *Cypridea* and its evolution in context with its close relatives within the family Cyprideidae, Benjamin Sames took the manuscript over in 2004. It underwent considerable emendation, restructuring and supplementation (integration of additional data). It is in review and considered for publication in "Journal of Micropalaeontology" after some additional changes. Based on new results, the species *Praecypridea? anomala* (Peck 1941) will be assigned to a new genus, *Kegelina*, a paper for the description of which is in preparation including B. Sames as a co-author.

The personal work input of B. Sames for this publication makes up more than 50%, including some parts of the non-taxonomic chapters, most of the taxonomy as well as the discussion, conclusions, figures, plates and editing in their entirety.

Chapters 2.2. and 2.3., Publications Nos. 2 and 3

Chapter 2.2., Publication No. 2
SAMES, B., submitted. Revision of the genus *Theriosynoecum* Branson 1936 (Ostracoda, Crustacea) and some of its species from the Lower Cretaceous of the U.S. Western Interior (Lakota Formation, Black Hills) and the European 'Purbeck/Wealden'. *Micropaleontology.*

Chapter 2.3., Publication No. 3
SAMES, B., submitted. Revision of the genus *Cypridea* Bosquet (Ostracoda, Crustacea), with emphasis on representatives from the nonmarine Lower Cretaceous Lakota and Cedar Mountain formations of the U.S. Western Interior and the European 'Purbeck/Wealden'. *Micropaleontology.*

These two papers have been conceptualized and written by B. Sames. They are similar in their structure and extent and have been submitted to "Micropaleontology". Upon proposal of the chief editor, John van Couvering (The Micropaleontology Project Inc., New York) and in agreement with the author, these shall be published in a special issue of "Micropaleontology", but have been submitted as separate articles to be harmonized and edited for a special issue after the review process. The proposed date for publication is special issue No. 1, 2010, coming out February 15th, 2010 (E-mail from John van Couvering from 30-06-2009).

Chapter 2.4., Publication No. 4

SAMES, B., CIFELLI, R. L. and SCHUDACK, M. E, 2010. The nonmarine Lower Cretaceous of the North American Western Interior foreland basin: New biostratigraphic results from ostracod correlations and early mammals, and their implications for paleontology and geology of the basin—an overview. *Earth-Science Reviews*, 101: 207-224.

This article was conceptualized by B. Sames upon invitation of Claudia Schröder-Adams (Carleton University, Ottawa, Canada) and James W. Haggart (Geological Survey of Canada, Vancouver) at the "2008 Joint Annual - GSA | SSSA | ASA | CSSA | GCAGS | GCSSEPM" in Houston, Texas, October 5-9, who had planned to edit an SEPM (Society for Sedimentary Geology) Special Publication "From the Forearc to the Foreland: Contrasting Tectonics, Paleogeography, and Paleoenvironments of the North American Cretaceous". Having been one of the very few at this meeting with a contribution to the nonmarine Cretaceous of the Western Interior foreland basin, the author of this thesis was asked to contribute an overview paper concerning the nonmarine Early Cretaceous stratigraphy of the basin for a broader geoscientific audience, including ongoing research and his own results. The Special Publication had to be cancelled because the majority of the proposed papers were not delivered; however, the interdisciplinary synopsis, including new biostratigraphic results and their implications, is long overdue and considered to be of broad interest. Thus, this paper underwent minor supplementation and changes and has been submitted to the journal "Earth-Science Reviews".

The concept is by B. Sames, and his work input makes up more than 85% of the paper with regards to content (except for the two sections on North American Vertebrata), writing and editing.

Chapter 2.5., Publication No. 5

KHAND, Y., **SAMES, B.** and SCHUDACK, M. E., 2007. New ostracod species from the non-marine Cretaceous of Mongolia. *Revista Española de Micropaleontología*, 39(1-2): 71-80.

This paper is based on data and a rough draft of the first author but has been largely written and supplemented by B. Sames (work input about 70%). This includes parts of the introduction and the taxonomic section as well as most of the figures and the complete remaining sections (Chapters 3 and 4 therein).

Chapter 2.6., Publication No. 6

SAMES, B., 2010. To correlate or not to correlate—That is not the question anymore! Nonmarine Late Jurassic to Early Cretaceous supraregional correlation based on ostracodes (Palaios-Spotlight). *Palaios*, 25: 3-5.

This short article arose out of a talk the author gave at the "2008 Joint Annual - GSA | SSSA | ASA | CSSA | GCAGS | GCSSEPM" in Houston, Texas, October 5-9, to introduce the work and some results presented in this thesis. Upon invitation of the co-editors of the journal *Palaios*, Stephen T. Hasiotis and Edith L. Taylor (E-mail from January 2009), the author was asked to present his ongoing research and its implications in the "Spotlight"-column of *Palaios*. It has been accepted and is scheduled to be published in the January 2010 issue of the journal (E-mail from Jill Hardesty, Managing Editor, 17-07-2009).

Chapter 3 discusses approaches, scientific progress, and results of the thesis as a whole, including the critical examination of the results achieved in relation to the aims and working hypotheses, and gives an overall synopsis.

Chapter 4 provides the conclusions and gives perspectives based on the findings achieved within the scope of this thesis.

Chapter 5 consists of the full reference list of all citations appearing in parts of this thesis, regardless of whether these appear in text, tables, figures, or taxonomic names of all hierarchy levels. Works published until June 2009 were considered and integrated.

The Appendix includes all abstracts published in the context of this project.

1. Introduction

"A problem well stated is a problem half solved."

Charles Franklin Kettering (1876-1958)

1.1. What Is an Ostracod?

Ostracods are principally aquatic microcrustaceans with a bivalved shell (the carapace, see Fig. 1.1) that today inhabit virtually all aquatic environments, e.g. all marine depths and freshwater to highly saline waters, permanent and temporary waterbodies, even "extreme" environments such as the water filled leaf base of bromeliads, hot springs, or even live interstitial in groundwater aquifers (stygobiotic life mode). Ostracods are known from Ordovician to recent (up to 65.000 fossil and 40.000 recent species are known), typically are around 1 mm in size and mineralize their carapace with (low-Magnesium) Calcite, thus having excellent fossilization potential and fossil record. The ostracod's small size, morphologic variability, ecology, fossilization potential and long geologic history renders them excellent candidates for a wide array of applications: biostratigraphy, paleoecology, paleogeography, paleoceanography, paleolimnology, paleoclimate reconstructions, and others.

The history of nonmarine ostracods goes back to the Carboniferous, potentially Devonian (e.g. Horne 2003 for comprehensive overview). The majority of recent nonmarine ostracods are representatives of the Superfamily Cypridoidea, the modern diversity of which largely results from a major evolutionary radiation in Later Jurassic to Early Cretaceous, highly improving their application potential from Late Jurassic onwards. This Late Mesozoic major radiation of the Cypridoidea is mainly attributed to a global diversification of its subfamily Cyprideidae, namely the genus *Cypridea*, whose revision and its implications make up a crucial part of this thesis.

Nonmarine ostracods in general—and representatives of the Cypridoidea in particular—have developed different strategies and mechanisms facilitating their (passive) short- and long-distance dispersal between different waterbodies and their adaption to temporary habitats. Considering the high fossilization potential, frequency of occurrence in high numbers, high Late Jurassic-Early Cretaceous diversity and their distribution mechanisms facilitating a passive long-distance transport even overcoming migration barriers, these ostracods have the potential to be an excellent tool for many applications, even supraregional and intercontinental correlation.

It is, therefore, not surprising that ostracods are quite common in nonmarine Lower Cretaceous deposits of the North American Western Interior foreland basin, the majority of which have been regarded as being widely inapplicable in the past. There are several reasons for this that will have to be elucidated herein. Demonstrating the utility and application potential of nonmarine ostracods to improve the age determination, biostratigraphic correlation, and paleoenvironmental interpretation of Lower Cretaceous North American formations is one of the main objectives of this thesis and project.

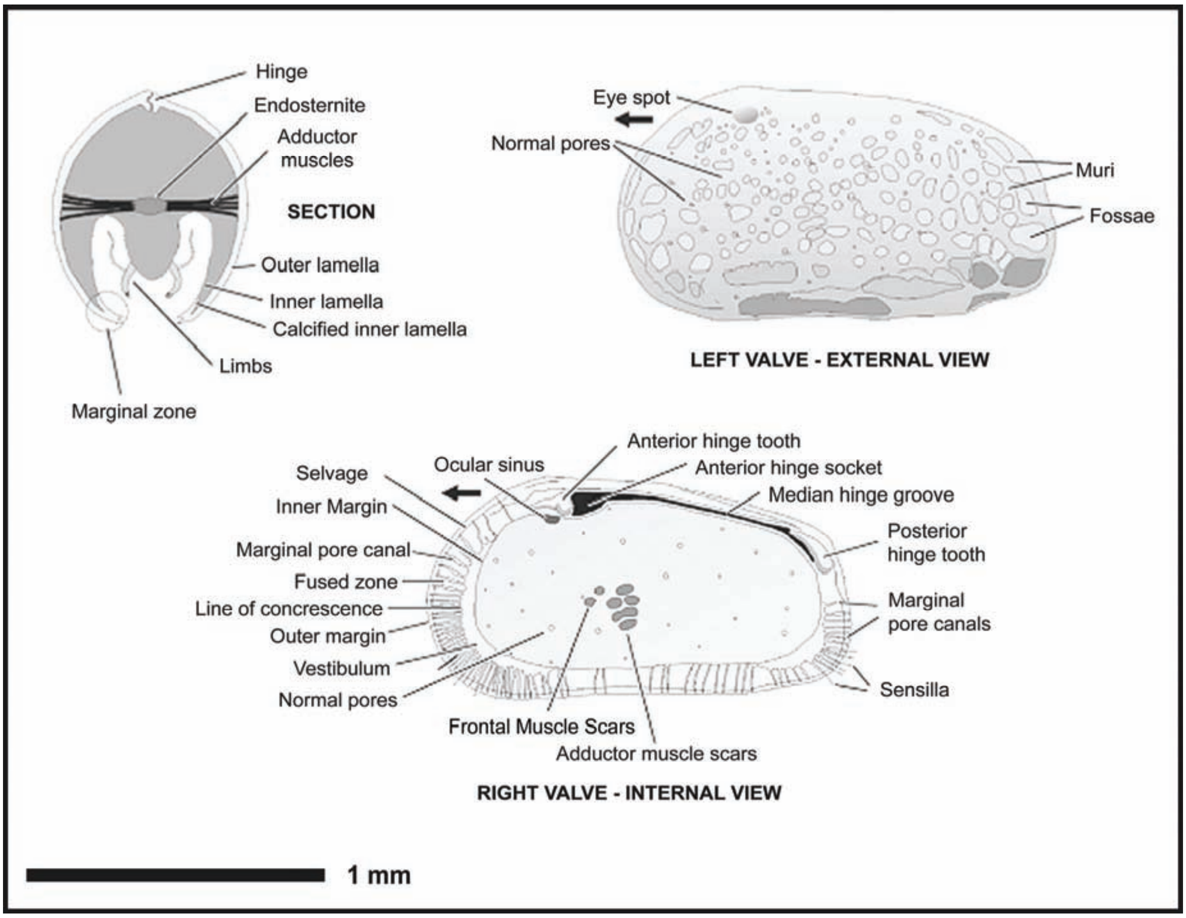

Fig. 1.1. Schematic illustration of an ostracod carapace (modified after Horne 2004). Illustrated are different views of a representative of the family Cytheroidea with typical characters.

1.2. Geographic and Geologic Overview of the Study Area

The main working areas are located in the "Mid-West" of the U.S.A., in the Black Hills area of South Dakota and the San Rafael Swell of Utah (Fig. 1.2), and are part of the Western Interior foreland basin. This basin, also the "North American Cordilleran foreland basin", is the largest of its type known. It extends from northeast Canada to central Mexico (Fig. 1.2) and occupies an area of more than five million square kilometers (e.g. Kauffman and Caldwell 1993). The basin began to develop in the Late Jurassic between the North American Cordilleran orogenic belt to the west and the North American craton to the east in response to the subduction of oceanic plates of the Pacific domain (Kauffman and Caldwell 1993; DeCelles 2004). The orogenic belt and the foreland basin evolved contemporaneously (for about 100myr) until the Eocene in various types of process-response and feedback relationships. This includes the Sevier orogeny ("Middle" to Late Cretaceous) and the Laramide orogeny (Late Cretaceous to Eocene). According to DeCelles and Giles (1996) and DeCelles (2004), the basin's subsidence was caused by flexural thrust-loading—a combination of the flexure of the lower crust due to overthrust of the evolving Cordillera, sediment load and longer wavelength (>400km) dynamic subsidence. The question when this system initially developed is controversial. Age ranges given are from Bajocian (~170 Ma, Fuentes et al., 2009) to Tithonian (e.g. Miall, 2009, and references therein). Sediment deposition during the Late (Middle?) Jurassic to Early Cretaceous period was strongly connected with the tectonic coevolution of both the proto-Cordillera and its associated foreland basin causing alternating source, supply rate and depozones of the nonmarine sediments (e.g. Kaufmann and Caldwell, 1993). The Laramide event (Late Cretaceous to Eocene) later led to fracturing of the craton and partitioned a part of the foreland basin into a mosaic of smaller foreland basins and uplifts (DeCelles 2004; Dickinson 2004), such as the easternmost of these, for example, the Black Hills uplift (Wyoming and South Dakota).

Nonmarine Late Jurassic deposits of the basin are represented by the Morrison (Fig. 1.4) Formation (U.S. part) and the Kootenay Formation (Canada; not to confuse with the geologically younger, Lower Cretaceous Kootenai Formation of Montana and Wyoming, U.S.A.). These are unconformably overlain by several lower Cretaceous formations of more limited lateral extension (see Miall et al. 2008 and references therein for overview), such as the Cedar Mountain and Lakota formations (Fig. 1.4). Both formations are strongly different in their paleogeographic position within the basin as well as their geology: the Cedar Mountain Formation was deposited in the proximal part of the basin that was affected by the Laramide orogeny, whereas the Lakota Formation was deposited distal to the Cordilleran orogenic belt (Fig. 1.2; also Sevier orogenic belt of some authors). This implies different depositional environments of the two formations.

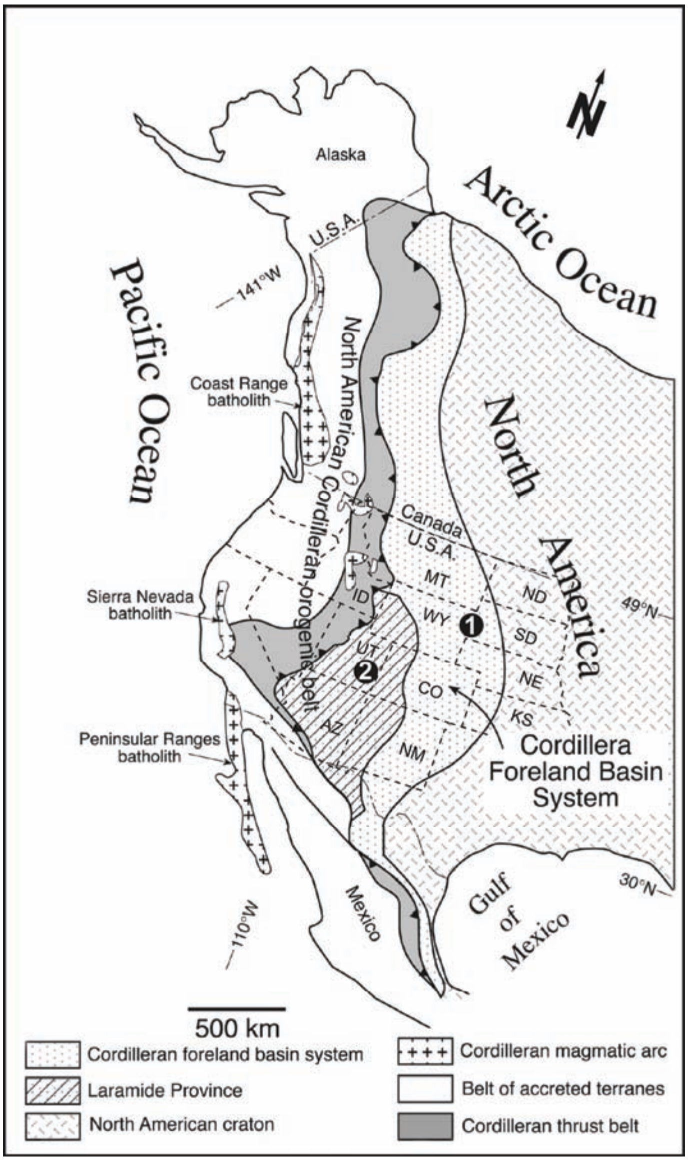

Fig. 1.2. Generalized tectonic map of western North America (modified after DeCelles 2004), showing the Cordilleran foreland basin system and the geographic position of the Black Hills uplift, South Dakota (1), as well as the distal position of the Lakota Formation within the foreland basin, and the position of the San Rafael Swell, Utah (2), with the more proximal position of the Cedar Mountain Formation within the foreland basin and in relation to the Cordilleran orogenic belt. Abbreviations for indicated states within the U.S.A.: ID–Idaho, ND–North Dakota, SD–South Dakota, MT–Montana, WY–Wyoming, UT–Utah, CO–Colorado, NE–Nebraska, KS–Kansas, AZ–Arizona, NM–New Mexico.

The Lakota Formation and the overlying Fall River Formation (together forming the Inyan Kara Group) crop out around the Black Hills uplift (Fig. 1.3; see Zaleha 2006 and references therein for geologic overview; Elliot et al. 2007, and references therein for facies description and interpretation).

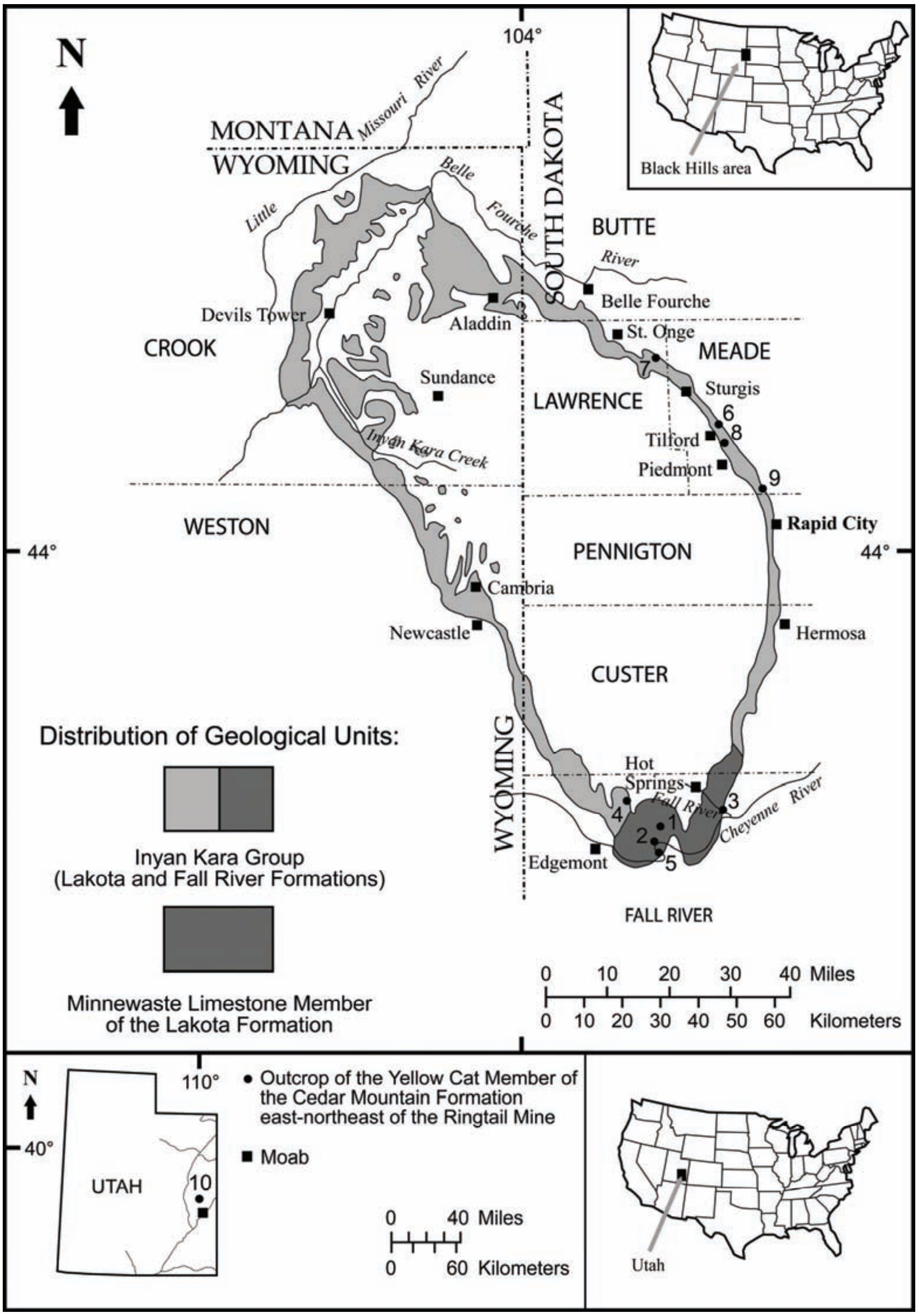

Fig. 1.3. Maps of the sample localities. Upper part: Black Hills area of South Dakota and Wyoming showing the distribution of the Inyan Kara Group (Lakota and overlying Fall River formations) deposits (modified after Waagé 1959, and Sohn 1979), and the sample localities discussed herein (Nos. 1–9). Lower part: San Rafael Swell area of Utah with the sample locality in the Cedar Mountain Formation (No. 10).

The Lakota Formation typically is between 15-140m thick and has been subdivided into three Members by Waagé (1959), the Chilson, Minnewaste Limestone, and Fuson members, or three informal lithostratigraphic intervals, the L1, L2, and L3 intervals, by Way et al. (1998), as illustrated in Fig. 1.4.

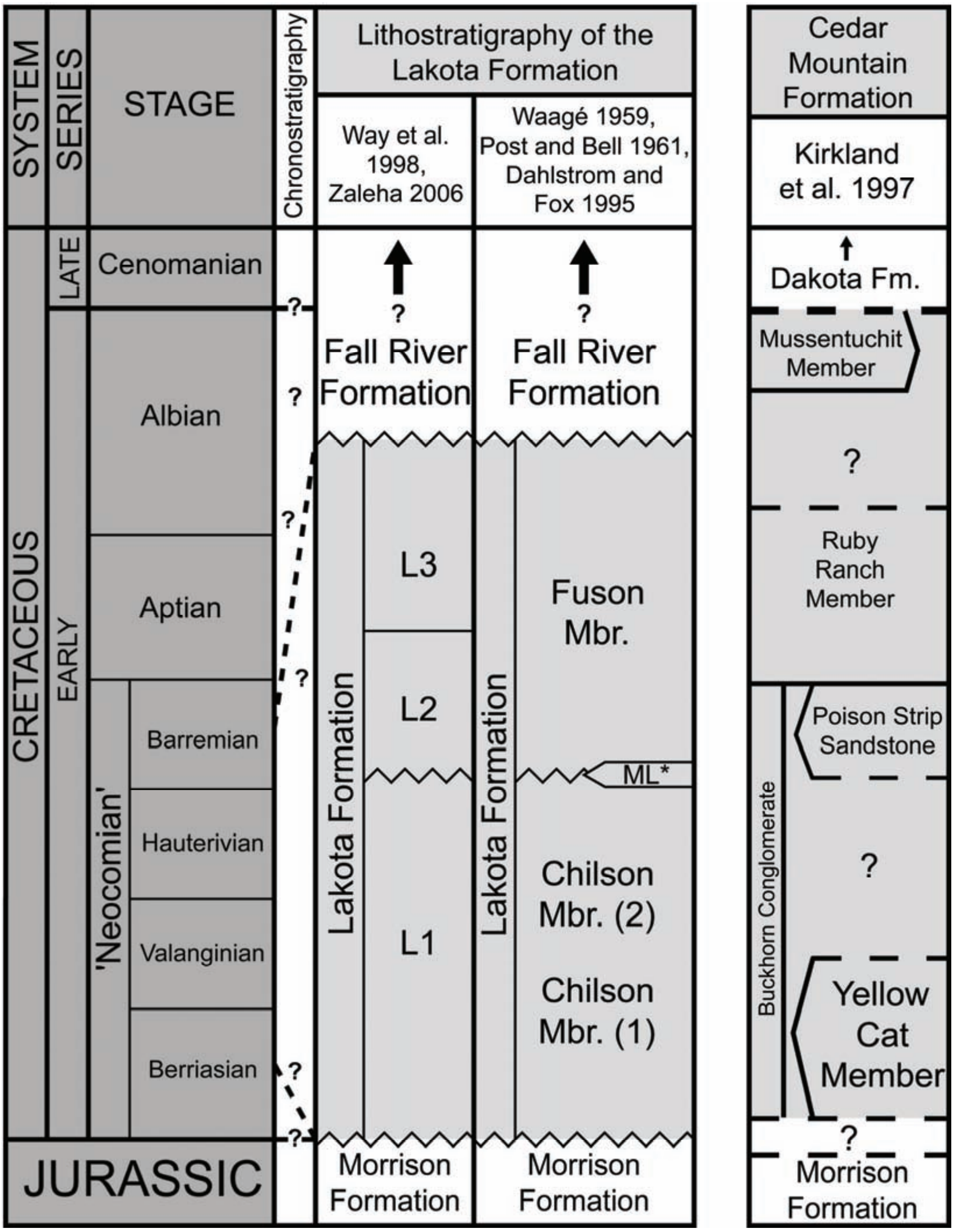

Fig 1.4. Lithostratigraphic subdivision of the Lakota Formation (Black Hills margin, south Dakota and Wyoming) and Cedar Mountain Formation (San Rafael Swell, Utah). No litho- and chronostratigraphic correlation implied between the two formations. Chronostratigraphy of the Lakota Formation according to results derived from ostracod correlations presented herein (Publication No. 3, Chapter 2.3). * ML: Minnewaste Limestone Member of the Lakota Froamtion. As to the chronostratigraphy of the Cedar Mountain Formation, see Kirkland et al. (1997, 1999) and Kirkland and Madsen (2007), for example. Results presented herein only concern a part of the Yellow Cat Member of the Cedar Mountain Formation.

In general, the dominant lithologies of the Lakota Formation (mudrocks, sandstones, and limestones) indicate a deposition on floodplains and/or wetlands adjacent to rivers (e.g. Elliot et al. 2007, and references therein), and the latter are represented by fluvial sandstones (particularly well developed in the southern Black Hills). The Minnewaste Limestone is lacustrine and restricted to the southern Black Hills (see Fig. 1.3), nearly pure limestone with a maximum thickness of 24m but typically between 3-6m thick (Gott et al. 1974) and top part of the L1 interval (Zaleha 2006). L1 and L2 intervals are separated by an unconformity which locally is developed as a strong angular unconformity (Way et al. 1998, Zaleha et al. 2001). Lithostratigraphic correlation within the Lakota Formation throughout the Black Hills margin is still under discussion, in part resulting from the strong lateral facies and thickness changes and particularly where single members are missing, e.g. the Minnewaste Limestone Member is restricted to the southern Black Hills and L1 strata (Chilson Member) are absent throughout much of the northern Black Hills (e.g. Zaleha 2006, and references therein).

The Cedar Mountain Formation is exposed in eastern Utah to western Colorado (Fig. 1.3) "in nearly continuous outcrops around the San Rafael Swell, the north end of the Henry Basin, and south of the Book Cliffs eastward to the Colorado River" (Kirkland and Madsen 2007, p. 31). It has been defined by Stokes (1952), comprising the Cedar Mountain Shale and the Buckhorn Conglomerate as its basal member. Based on the distribution of specific dinosaur faunas in relationship to distinct rock types, Kirkland et al. (1997, 1999) defined four additional members of this formation: the Yellow Cat Member, the Poison Strip Sandstone, the Ruby Ranch Member and the Mussentuchit Member (see Fig. 1.4). The Cedar Mountain Formation is composed dominantly of fluvial silt and mud, channel sandstones and lacustrine and pedogenic limestone. The Yellow Cat Member, where the samples dealt with herein derive from (see Publication No. 3, Chapter 3), has been interpreted as lacustrine and marginal lacustrine deposition including debris-flows (Eberth et al. 2006), or fluvial hyperconcentrated-flow deposits (Greenhalgh and Britt 2007).

The ostracod samples mainly derive from limnic/lacustrine deposits of either permanent or temporal waterbodies of highly variable lateral extension and thickness. Although certain lithologies are more promising to yield (more or less) well-preserved ostracods and charophytes, there barely is a rule of thumb, except that the rock or sediment has to be calcareous and been deposited under water coverage. Ostracods and charophytes have been retrieved from sand- and siltstones, limestones, marls and mudstones.

1.3. Age Determination Problems in Nonmarine Lower Cretaceous Formations of the North American Western Interior Foreland Basin

Precise age determination of Lower Cretaceous nonmarine formations of the North American Western Interior foreland basin as well as the state of knowledge regarding their faunas and floras are still in need of improvement. Most formations are just known to be of pre-middle Albian Early Cretaceous age (i.e., the minimum age given by well-dated deposits of the first major of the so called mid-Cretaceous marine transgressions in North America leading to the through-going Cretaceous Western Interior Seaway from Canada to the Gulf of Mexico established by mid-Albian time, e.g. DeCelles 2004 and references therein). The lower boundary of nearly all Lower Cretaceous nonmarine deposits in the Western Interior foreland basin is given by an (synchronous or diachronous?) unconformity separating the Lower Cretaceous formations from the underlying Morrison Formation (late Oxfordian to early Tithonian, lowermost Cretaceous?). However, there are some major problems associated with the contact of the top Morrison Formation and the base of the overlying Lower Cretaceous formations:

A) The exact age of the uppermost Morrison Formation, that is to say the age of the unconformity surface, is uncertain because these parts rarely contain fossils, and existing magnetostratigraphic or geochronometric data derive from few isolated and geographically widely-scattered samples.

B) Resulting from a relatively consistent lithology, most Upper Jurassic nonmarine deposits throughout the U.S. part of the Western Interior are designated as Morrison Formation but may (and most probably do) strongly vary in the timespan they comprise, particularly in their maximum and minimum ages. The unconformity surface of the top Morrison Formation is not isochronous in different areas, on a larger as well as smaller regional scale.

C) The existence of a strong erosional unconformity between the Morrison and Lower Cretaceous formations, representing a hiatus of unknown time period, led to strongly conflicting maximum ages of the latter formations (Aptian mostly, or Barremian, Hauterivian?), mostly much too young in the view of the author of this thesis.

D) Lower Cretaceous sediments that deeply incise into the upper part of the Morrison Formation additionally complicate the situation.

E) In contrast to the wide spatial extent of the Late Jurassic Morrison Formation, Lower Cretaceous deposits are characterized by numerous different formations with a lateral extension partially well under 500 km diameter that are not easy to correlate and—owing to their different relative paleogeographic positions within the foreland basin and the syndepositional intra- and extrabasinal tectonics leading to different separated intrabasinal depositional evironments—of highly variable composition and thickness.

Taking these arguments into account when discussing the Morrison Formation, a minimum age of lowermost Cretaceous seems to be probable for some parts of the Morrison Formation, at least in some areas, as has already been suggested by some authors (e.g. Currie 1997, 1998).

Despite an integration of different geologic, geophysical, and paleontologic methods, no major breakthrough regarding the age determination—particularly the maximum age—of Lower Cretaceous nonmarine formations in the U.S. Western Interior has been achieved during the last thirty years. Time intervals ranging from at least 15–20 up to 35 Ma have been given for the nonmarine Jurassic-Cretaceous hiatus, according to assumed maximum ages of Middle Albian to Barremian (Hauterivian?) for the Lower Cretaceous formations.

The minimum age of the nonmarine Lower Cretaceous formations is given by overlying well dated Albian marine sediments of the North American "Cretaceous Western Interior Seaway" (e.g. the Mowry/Thermopolis and Mancos shales overlying the Fall River and Dakota formations, see Fig. 1.4) that are of middle Albian age and younger (Cenomanian), depending on the paleogeographic position of the depositional area of the particular formations within the Western Interior foreland basin (the transgressions entered the basin from the north, e.g. DeCelles 2004, Yang and Miall 2009).

Lithostratigraphic correlations of nonmarine Lower Cretaceous formations of the U.S. Western Interior have proven to be difficult in the past due to strong lateral facies change, although there has been some progress during the last two decades through the application of different correlation methods or an integration of several of these. As Ostrom (1970) aptly put it when referring to the Upper Jurassic Morrison-Lower Cretaceous Cloverly formation sequence in Wyoming: the extreme degree of lateral variability is perhaps the most distinguishing characteristic of these rock units. Geochronometric methods (magnetostratigraphy, radiometric dates) failed to produce ages with satisfactory accuracy in many cases, are mostly isolated, or give ages that seem too young. Therefore, the existing chronostratigraphic framework of the Western Interior foreland basin is insufficiently calibrated to a large extent.

With respect to biostratigraphy as a chronologic tool, this method has been of limited use due to the scarcity of fossils within these nonmarine Lower Cretaceous sediments and their recognition as being endemic. There is much inconsistency between age estimates based on different paleontologic works. This problem is additionally increased by the fact that publications of different time periods during the 20th century reflect stage definitions and determinations that have changed over time. Correlation attempts to Europe were made during a time when Early Cretaceous stage definitions in Europe and North America were in flux.

At the same time there has been continual, major scientific interest in the North American nonmarine Early Cretaceous formations for several reasons. First, these formations are relevant to the development of both the basin and the coevolving eastern Cordillera as well as their chronostratigraphic framework. Second, the Lower Cretaceous formations are famous for their vertebrate fossil content, amongst others dinosaurs and early mammals in particular. Regarding the latter, the question of maximum ages of nonmarine Early Cretaceous formations is of particular interest. In most cases, ages older than Early Aptian (rarely Barremian) have been rejected by various authors and, consequently, a 15-20 Ma minimum duration was assumed for the time span represented by the Jurassic-Cretaceous hiatus. This would, for example, imply that the chance to find vertebrate remains of lower Early Cretaceous age (pre-Aptian, Barremian) in North America has to be ruled out to a large extent, if not completely. However, the Early Cretaceous is a time during which an important event in the evolution within major mammal groups (australosphenidans, eutriconodontans, multituberculates, metatherians and eutherians) took place, the "Early Cretaceous Diversification" (cf. Kielan-Jaworowska et al. 2004), and is thus of particular interest in this field of research.

With respect to the geology of the basin, older maximum ages and better inter- and intraformational correlations of Lower Cretaceous formations also considerably affect a wide scope of geologic and paleontologic topics in the context of the basin's structural and chronostratigraphic framework.

1.4. Starting Point of the Project

Despite comprehensive works during the second half of the 20th century, especially those of Raymond Elliot Peck (1904-1984, ostracods and charophytes) and Israel Gregory Sohn (1911-2000, ostracods), the nonmarine Early Cretaceous ostracods of North America were considered endemic and therefore inapplicable to supraregional correlation and application. It was not until the 1990s that Michael E. Schudack disproved a considerable endemism of North American Late Jurassic nonmarine ostracods of the Morrison Formation (e.g. Schudack 1995, 1996, Schudack et al. 1998). Therefore, this likewise appeared to be true for the ostracods of the nonmarine Lower Cretaceous formations unconformably overlying the Morrison Formation throughout most areas of the Western Interior foreland basin.

The idea to the project on which this thesis is mainly based was initiated through an inquiry of Richard L. Cifelli (Sam Noble Oklahoma Museum of Natural History and University of Oklahoma, Norman, OK, U.S.A.), who had found ostracods during a field campaign in 2001, when he and his team were searching for early mammals within the Lakota Formation of the eastern Black Hills area. Being aware of Schudack's (1995, 1996, Schudack et al. 1998) publications about nonmarine ostracods of the Morrison Formation, Cifelli sent a sample of these ostracods to Michael E. Schudack (Freie Universität Berlin, Germany) in Summer 2001 asking him for identification and age determination. However, this was not easily possible at that time because the Early Cretaceous nonmarine ostracod fauna of the U.S. Western Interior is much, if not totally, different from the Late Jurassic one. Resulting from their assumed endemism at that time, it was also not possible to correlate the Lower Cretaceous ostracods to other continents, and consequently no improvement in age determination could be given thus far. On this account, Michael Schudack had the idea to conceive a project in cooperation with R.L. Cifelli and his team, dealing with the taxonomic revision of these ostracods, thereby disproving their assumed endemism to the North American continent and to render their correlation and application possible as well as to support biostratigraphic data by associated charophytes, if possible. The author of this thesis was dealing with Late Jurassic/Lower Cretaceous marine and nonmarine ostracods of the Tendaguru formation, SE Tanzania, East Africa, in his Diploma thesis (about equivalent to Master's) at that time, and thus gained some expert knowledge in taxonomy of late Mesozoic ostracods. Funding was provided by the German Science Foundation (DFG Schu 694/14-1 and 14-2).

As to the possibilities of a supraregional correlation of North American nonmarine latest Jurassic to Early Cretaceous (Tithonian to Barremian) ostracods and those of other continents, the key role to the solution of biostratigraphic problems plays the ostracod biozonation of the NW-European Purbeck/Wealden, particularly that of the English type area (Anderson 1985 and references therein, synopsis; zonation revised by Horne 1995, see Horne 2009 also). This is the most detailed and high resolution data available and derives from numerous boreholes. Moreover, these data have been lately integrated into the correlation chart of Hoedemaeker and Herngreen (2003), a chart which is based on the International Geoscience Programme (IGCP) project 362 "Tethyan-Boreal Cretaceous Correlation". Combining biostratigraphic, magnetostratigraphic and sequence-stratigraphic data-sets, this chart correlates the Berriasian to Barremian marine Tethyan standard sections of Spain and France with the Boreal successions of southern England (type area for the Purbeck/Wealden), The Netherlands (subsurface) and NW Germany, including the nonmarine ostracods.

To come back to North America, this study acts on the assumption that—based on older ostracod publications (e.g. Sohn 1958, 1979) and new developments in nonmarine ostracod evolution, biology and stratigraphy—at least a few, if not most of the nonmarine Lower Cretaceous formations of the Western Interior foreland basin are considerable older than has been indicated in the past, with their oldest parts reaching well into the Valanginian and Berriasian.

1.5. Aims

Starting from the primary object to improve the biostratigraphic age determination of nonmarine Lower Cretaceous formations of the U.S. Western Interior foreland basin, ostracods and charophytes of selected formations (most notably the Lakota Formation, Black Hills area, South Dakota and Wyoming) should be revised and analyzed biostratigraphically, paleoecologically and paleogeographically. Fundamentals of these analyses are comparisons to the classic area of ostracod biostratigraphy of the nonmarine Early Cretaceous: the Purbeck/Wealden of southern England and other European areas with Purbeck/Wealden-like deposits (e.g. NW-Germany, France, Spain, Poland and others).

Based on a detailed taxonomic revision of relevant taxa, the following results were aspired at the beginning:

1) an improvement of the age determination of some important formations of the North American nonmarine Lower Cretaceous (Lakota Formation, South Dakota and Wyoming; Cloverly Formation, Wyoming; Bissett Formation, Texas) exemplary for other formations,

2) contributions to their paleoecologic interpretation,

3) a methodic acquisition of relevant ostracod faunas and charophyte floras necessary for it, and the paleobiogeographic analysis and interpretation of these faunas and floras in a supraregional context,

4) resultant contributions to the evolution of particular taxonomic groups (primarily Ostracoda: Cypridoidea–Cyprideidae, Cytheroidea–Timiriaseviinae, Charophyta–Clavatoraceae) in the context of plate tectonic and paleoclimatic developments with the respective reproduction and dispersal mechanisms.

Owing to the development of the project that is considerably different from what was originally planned (see Chapter 1.6 right below), aims and working hypotheses (Chapter 1.7 below) have been modified.

1.6. Development of the Project

According to the aims given above (Chapter 1.5), the main objective of the project was a revision of the faunas and floras based on existing and new data and to apply the calcareous microfossils to improve the biostratigraphic age determination of selected formations. With further progress in the taxonomic work on the ostracod material and familiarization with the literature, however, several problems occurred that had to be dealt with to enable a biostratigraphic utilization of the ostracods:

1) For a general utilization of the North American ostracods, and even more so for a supraregional (global) approach of biostratigraphic correlation, a new major revision of stratigraphically important taxa—representatives of the genera *Theriosynoecum* Branson 1936 and *Cypridea* Bosquet 1852—had to be conducted beforehand (see also introduction of these two papers, Chapter 2.2 and 2.3 herein). This included a revision of the genera as well. Different usage, interpretation and evaluation of morphologic terminology has resulted in relatively restrictive and inconsistent, and partially incorrect, taxonomic concepts, having led to a large quantity of new taxa that, consequently, were regarded and treated as being endemic mostly, thus hampering a stratigraphic application.

2) The numerous samples taken from sections of the Cloverly Formation in southern Wyoming (southern Bighorn Basin) during the first field campaign in summer 2003 were all barren.

3) The charophyte flora from the samples from the Lakota and Cedar Mountain formations proved to be of low diversity and stratigraphic value after a preliminary analysis.

Resulting from these problems, a completely modified approach became necessary and, therefore, has been developed and conducted by the author. The most important genera, stratigraphically, *Cypridea* and *Theriosynoecum*, have been thoroughly revised with emphasis on their North American Early Cretaceous representatives, leading to two comprehensive single-authored publications (Nos. 2 and 3, Chapters 2.2 and 2.3). Owing to the effort necessary therefor and because the main purpose was an improvement of the biostratigraphy of certain formations, other ostracod groups, such as representatives of the Trapezoidellidae, have been excluded thus far. These are of no stratigraphic use at the current state of knowledge (few taxa are known, see Publications No. 5, Chapter 2.5), and they have to be thoroughly revised as well prior to any potential application.

The modified approach includes an elaborate revised morphologic terminology of the ostracods, which has been combined into an illustrated glossary, a consistently structured and comprehensive taxonomic description based on and supported by that glossary, and extensive synonymy lists combined with detailed analyses and discussions. The revision was only possible within a global context (or a larger supraregional view, i.e., northern hemisphere, at least) and has been integrated with newer insights into ostracod physiology, ecology, dispersal, and reproduction. In view of the focus on application, emphasis has been put on the elaboration of the type of significance of the morphologic characters, i.e., whether these be taxonomically, ecologically, ontogenetically, or otherwise significant. A differentiation and better attribution of such carapace features facilitates a targeted application. Based on this concept (see Publications Nos. 2 and 3, Chapters 2.2 and 2.3), as well as the adoption and an up-to-date modification of the species-group concept with respect to *Cypridea* (Wolburg 1959, see Publication No. 3, Chapter 2.3), a biostratigraphic application of the nonmarine Early Cretaceous ostracods of the Western Interior foreland basin has been rendered possible. With that, one of the main aims of the project has been achieved. The concept, moreover, provides a solid basis for ongoing (other taxonomic groups) and future research, and it led to considerable progress in taxonomy and systematics of the studied groups. The results, as well as the long overdue detailed examination of the topic (as a basis and starting point for further research), justify the comprehensiveness of the taxonomic revisions of *Theriosynoecum* and *Cypridea*.

Since the samples from the Cloverly Formation of Wyoming were barren (see above) and the fieldwork plans of the cooperating partners from the Sam Noble Oklahoma Museum of Natural History (Richard L. Cifelli, and his team) changed, additional samples were taken from the Yellow Cat Member of the Cedar Mountain Formation of Utah in 2004. Attempts to sample additional outcrops in the northern and northwestern Black Hills during fieldwork in 2004 failed because access to private property was not granted.

The field campaigns in summer 2003 and 2004 were followed by several research stays. In 2005, the collection of Thomas Rupert Jones at The Natural History Museum (formerly The British Museum, Natural History) in London (UK) was examined, the Purbeck/Wealden type sections in southern England were visited, and the collection (more than 4000 slides) of Frederick W. Anderson at the British Geological Survey in Keyworth (near Nottingham, UK) was pre-inspected. The collection of Raymond Elliot Peck at the University of Missouri, Columbia, turned out to be incomplete (visit of the author in summer 2005). All the type and most of the figured materials are missing and their whereabouts unknown. However, available parts of this collection were examined, SEM-photographed and included in the analysis. SEM-work of Peck's and the author's own material was conducted at the Sam Noble Oklahoma Museum of Natural History (Norman, OK, U.S.A.). Owing to the vacancy of the position of a curator responsible for the ostracod collection at the National Museum of Natural History, Smithsonian Institution (Washington, DC, U.S.A.) in 2005, the examination of the collections of Israel G. Sohn and Frederick M. Swain was made up in 2006. These turned out to be complete, and relevant parts could be SEM-photographed free of charge. To conclude, despite several necessary modifications regarding localities/formations and schedules, the project could be successfully conducted because of the considerable support of the cooperating partners in the U.S.A. (particularly Richard L. Cifelli, Sam Noble Oklahoma Museum of Natural History and University of Oklahoma, Norman, OK, U.S.A.) and the UK (particularly David J. Horne, Queen Mary University of London, London, UK).

With respect to the charophytes, these have been excluded from the thesis and will be dealt with and published separately since they are considered of no major stratigraphic value at the moment. The results will be combined into detailed biostratigraphic, paleoecologic and paleobiogeographic papers.

Since the papers on the ostracod taxonomy and their biostratigraphic application (Publications Nos. 2–4, Chapters 2.2–2.4) already are of considerable comprehensiveness, and central issues with regards to the main aims have been successfully dealt with (demonstration of the biostratigraphic utility of the ostracods, improvement of age determination of selected formations and contributions to the evolution of major groups in context of their reproductive and dispersal mechanisms, see Chapter 1.5 above), the review and publication of the detailed stratigraphic and paleoecologic/paleoenvironmental results (including the charophytes) have been excluded from the thesis as well. This is due to the new approach (see Chapter 4.1 also) which has been strongly modified from the initial plans, and because the latter analyses require quantitative data of entire assemblages, taxa other than *Cypridea* and *Theriosynoecum* of which remain to be taxonomically revised afore.

1.7. Working Hypotheses

Based on the aims as given in Chapter 1.5 and the development of the project as given in Chapter 1.6 above, the following working hypotheses were formulated as guidelines for the project and thesis and to be tested during their progress. The results in relation to these hypotheses are given and discussed in Chapter 3: Discussion and Synopsis.

A) The nonmarine latest Jurassic to Early Cretaceous Ostracoda of the North American Western Interior foreland basin are applicable to supraregional biostratigraphy and improvement of the age determination of certain Lower Cretaceous formations.

B) It is possible to use ostracod faunas for the improvement of inter- and intraformational correlations (example: Lakota Formation, Black Hills, South Dakota and Cedar Mountain Formation, San Rafael Swell, Utah).

C) It is possible to establish a chronostratigraphy (biostratigraphy) of certain formations, that is complementary to, or even better than, the existing chronostratigraphic and geochronologic results.

D) The application of recent findings in ostracod biology, physiology, reproductive and dispersal mechanisms, genetics, ecology and evolution improve the taxonomy of these, partially extinct, ostracods.

E) The results obtained from ostracods can improve the paleoecologic/paleoenvironmental interpretation of the respective geological units.

F) The "explosive" radiation and faunal domination of representatives of the family Cyprideidae Martin 1940 (*Cypridea* s.l. in particular) during the Late Jurassic/Early Cretaceous is either a function of their particular anatomy (e.g. the rostrum, alveolus and cyathus etc.) or rather a function of the combination of intrinsic and extrinsic factors, i.e., their reproduction mode (mixed reproduction: parthenogenesis and sexual reproduction), distribution mechanisms, and habitat characteristics.

G) The results of this thesis as elaborated by means of ostracods can possibly improve our understanding of the latest Jurassic/Early Cretaceous widely distributed nonmarine Purbeck/Wealden-like deposits.

H) Ostracod correlation and age determination improvements are expected to have considerable implications on a wide scope of geologic and paleontologic topics (e.g. early mammal, dinosaur and angiosperm fossil record and evolution) in the context of the Western Interior foreland basin's Early Cretaceous structural and chronostratigraphic framework.

1.8. Interconnection and Overview of the Scientific Papers

In the following, an overview of the incorporated publications is given. These consist of six scientific papers, four papers (Nos. 1-3, 5) mainly emphasizing ostracod taxonomy, and two others (Nos. 4 and 6) focusing on the application aspect. Papers Nos. 2, 3 and 4 are the major components of the thesis. Paper No. 1 provides the wider taxonomic setting of one of the main ostracod groups dealt with here (the genus *Cypridea*, Paper No. 3), papers Nos. 2 and 3 comprise the major revisions of the stratigraphically most important ostracod taxa of Early Cretaceous Purbeck/Wealden-like deposits, with emphasis on North American species. Based on this new data, Paper No. 4 gives an up-to-date survey of the Late Jurassic to Early Cretaceous chronostratigraphy and age determination in the North American Western Interior foreland basin, and the first major implications of the ostracod correlations on its geology and paleontology. Paper No. 5, the only publication where the thesis' author is neither first nor single author, deals with some new nonmarine ostracods from the Cretaceous of Mongolia, some groups of which were first described from the Lower Cretaceous of North America and are hoped to become applicable in various ways in the future, once more data are available. Paper No. 6, finally, is a short introduction of the author's ongoing research and its background for a broader scientific audience.

Publications Nos. 1–6:

Chapter 2.1, Publication No. 1: **SAMES, B.**, WHATLEY, R. and SCHUDACK, M. E., in review. The origin and early evolution of the nonmarine Cypridoidea—*Praecypridea*: A new nonmarine ostracod genus from the Jurassic and Cretaceous of Europe, North America and Africa. *Journal of Micropalaeontology*.

The paper gives a comprehensive overview and synopsis of the current state of research concerning the early Cypridoidea, the representatives of which are believed to dominate nonmarine ostracod faunas of the world since the latest Jurassic. The new genus, *Praecypridea*, introduced therein is presumed to be a member of the most important extinct family Cyprideidae Martin 1940, and the ancestor of the genus *Cypridea* Bosquet 1852. Representatives of the latter are important index taxa in the latest Tithonian to the earliest Aptian Purbeck/Wealden-like deposits of the world, particularly those of western and northwestern Europe (which are the best documented, dated and correlated to date). The revision of *Cypridea*, with emphasis on some Early Cretaceous North American representatives, including an update of the taxonomy of its closer relatives as well as an emendation of the family Cyprideidae Martin 1940, is a major part of this thesis (Publication No. 3, Chapter 2.3). The paper provides the wider scope of the early evolutionary history of today's most diverse group of nonmarine ostracods, the Cypridoidea, leading to the particular success of the group starting in latest Jurassic times and spanning most of the Early Cretaceous. This differential success is mainly attributed to representatives of *Cypridea*.

The paper has been submitted to *Journal of Micropalaeontology* and is in review. It will undergo some changes based on new results from the revision of some Early Cretaceous ostracods of North America. The Cretaceous taxon *Praecypridea? anomala* (Peck 1941), that has initially been considered a potential representative of *Praecypridea*, will be assigned to a new genus, *Kegelina*, based on ongoing research and discussions with one of the reviewers. A paper regarding the taxonomy of this genus and its representatives is in preparation including B. Sames as one of the co-authors.

Chapter 2.2, Publication No. 2: **SAMES, B.**, submitted. Revision of the genus *Theriosynoecum* Branson 1936 (Ostracoda, Crustacea) and some of its species from the Lower Cretaceous of the U.S. Western Interior (Lakota Formation, Black Hills) and the European 'Purbeck/Wealden'. *Micropaleontology*.

This major, single-authored manuscript comprehensively revises one of the most important genera of nonmarine deposits of the Middle Jurassic to Early Cretaceous, *Theriosynoecum* Branson 1936, the Tithonian to Barremian representatives of which are used for the biozonation (three zones) of the English Purbeck/Wealden (see Horne 1995, 2009). Not only does this work emphasize the taxonomic revision of some Early Cretaceous North American representatives, but also deals with the taxonomy, systematics and morphologic terminology of the genus in general and its closer fossil to recent relatives. Effectively being a "sister" of the Publication No. 3, Chapter 2.3 herein, regarding methodology and structure, it comprises revisions and redefinitions of important carapace characters present in all representatives of *Theriosynoecum*, which have been combined into an extensive glossary and are supplemented by many newly created illustrations by the author. Although the biostratigraphic utility of the North American *Theriosynoecum* species is not yet very good (in contrast to representatives of *Cypridea*, this is mainly a problem of the insufficient stratigraphic record) and far from an aspired biozonation, this revision provides the basis for future research and demonstrates their application potential. Moreover, the outcome is a considerable step towards a distinction of characters of taxonomic significance and those of paleoecologic significance, thus widening the options of application of the genus' representatives.

As a by-product, a differentiation of five important fossil to recent genera of the subfamily Timiriaseviinae Mandelstam 1960 including *Theriosynoecum* has been elaborated. These genera had been confusingly used by different authors over time and can now be better distinguished based on their carapace characters.

This article has been submitted to the journal "Micropaleontology". Upon proposal of the chief editor, John van Couvering (The Micropaleontology Project Inc., New York), it shall be published in a special issue together with its "sister" article (Publication No. 3, Chapter 2.3). The proposed date for publication is special issue No. 1 in 2010, coming out February 15th 2010 (E-mail from John van Couvering from 30-06-2009).

Chapter 2.3, Publication No. 3: **SAMES, B.**, submitted. Revision of the genus *Cypridea* Bosquet (Ostracoda, Crustacea) and some of its species from the nonmarine Lower Cretaceous Lakota and Cedar Mountain formations of the U.S. Western Interior and the European 'Purbeck/Wealden'. *Micropaleontology*.

This second major, single authored manuscript is a revision of *the* most important genus of the Purbeck/Wealden-like and other contemporaneous (latest Tithonian to earliest Aptian) nonmarine deposits of the world. Representatives of *Cypridea* are used, for example, for the biozonation of the English Purbeck/Wealden (type area, eight subzones, e.g. Horne 1995, 2009) or the "German Wealden", NW-Germany (e.g. Elstner and Mutterlose 1996). Focusing on some North American representatives, the article effectively is a "sister" of the Publication No. 3, Chapter 2.3 herein, regarding methodology and structure. It comprises revisions and redefinitions of important carapace characters of the genus, which have been combined into a comprehensive glossary and are supplemented by many new illustrations by the author, including the newly defined term "alveolar ridge". These are used as a basis for a comprehensible detailed description and discussion of the species as well as a revision and update of the family Cyprideidae Martin 1940. In contrast to the genus *Theriosynoecum* (although revisions are between 30-50 years old), no major broad revision of the genus *Cypridea* has been published for over 50 years, but an overwhelming amount of specific taxonomic and stratigraphic articles in multiple languages exists (English, German, Russian, French, Spanish, Portuguese, Chinese etc.), distributed among multiple journals. Therefore, a larger historic overview and synopsis of relevant publications, regarding taxonomy and stratigraphy of *Cypridea* and the context of the subject, is given and partially commented upon.

The biostratigraphic utility of representatives of *Cypridea* in Lower Cretaceous formations of the Western Interior foreland basin is good and promising, and first results have been included in Publication No. 4, Chapter 2.4 of this thesis. A biostratigraphic application of *Cypridea* taxa is made possible through an updated taxonomy: some taxonomic problems are solved by the identification of, and differentiation between, taxonomically significant and insignificant characters, the latter, i.e., characters of ecophenotypic and ontogenetic origin, or intraspecific variation, are in part otherwise applicable. This is possible based on new insights into recent ostracod biology, ecology, and reproduction. Since the application-oriented aspect was one primary objective of the project, some taxonomic problems can be avoided, quasi circumnavigated, by the application of morphogroups, as to *Cypridea*, species groups in particular (see Chapter 5.4.1). This concept has largely been developed by Wolburg (1959), who successfully applied it to the biozonation of the "NW German Wealden" as based on representatives of *Cypridea*. As discussed in this article (Chapter 6.1) in the context of new insights into reproductive modes of nonmarine ostracods and their implications, this concept is particularly useful for the application of *Cypridea* taxa, and is taken on and refined therein. The central point in doing so is the fact that well-defined species groups facilitate a biostratigraphic application without the distracting and unresolved, or disputed, details of an inconsistent taxonomy.

The main biostratigraphic implication concerning the Western Interior foreland basin is the higher maximum age derived from ostracod correlations: Berriasian to Valanginian (~ 142-138 Ma) for the lower part of the Lakota Formation (Black Hills area, South Dakota) and the Cedar Mountain Formation (Utah) instead of Barremian to Albian (see Publication No. 4, Chapter 2.4 of this thesis). Results of the revision of *Cypridea* also have important implications on our understanding of the diversity and distribution of representatives of the Cyprideidae Martin 1940 and future approaches in taxonomy and application of this genus (Chapters 6.1-6.4 and 7). With respect to ornamentation (local ornamentation elements) in its representatives, noding in *Cypridea* is clearly identified as being ecophenotypic and, therefore, taxonomically insignificant but of high potential utility in paleoecology (rapid salinity changes and their paleoenvironmental interpretation).

Chapter 2.4, Publication No. 4: **SAMES, B.**, CIFELLI, R. L. and SCHUDACK, M. E, submitted. The nonmarine Lower Cretaceous of the North American Western Interior foreland basin: new biostratigraphic results from ostracod correlations and their implications for paleontology and geology of the basin – an overview. *Earth-Science Reviews*.

The publication has a bifocal intention: 1), to give a historic overview of the development of the chronostratigraphy and geochronology of the Western Interior foreland basin, also introducing particular approaches and problems involved, and 2), to introduce the first results and revival of ostracod biostratigraphy and new discoveries of early mammals plus the implications— particularly of much higher maximum ages of some Lower Cretaceous formations—of these new data on a wide scope of geologic and paleontologic topics in the context of the basin's structural and chronostratigraphic framework. At the same time, it is a comprehensive up-to-date survey for a broader geoscientific audience of both geologists and paleontologists/paleobiologists, and is meant to provide starting points as the basis for fruitful future research and discussions. With regard to "working hypothesis H" (given in Chapter 1.6 above), this article gives a synopsis of the first major implications of the results of the taxonomic revision of representatives of *Theriosynoecum* and *Cypridea* (Publications Nos. 2 and 3, Chapters 2.2 and 2.3 of this thesis) and shall serve as guideline for more specific upcoming publications by author.

The central issue hampering an integrated synthesis of the foreland basin is its yet imprecise chronostratigraphic framework and documentation. Temporal relationships between the basins geologic processes and their control factors are still insufficiently calibrated or controversial. The new results in ostracod biostratigraphy strongly suggest a maximum age of Late Berriasian to Valanginian (~ 142-138 Ma) for the lower part of the Lakota (Black Hills area, South Dakota) and Cedar Mountain (Utah) formations. These biostratigraphic results affect the correlative formations as well and, therefore, have considerable consequences on a wide scope of basin-related geologic and paleontologic topics that are overviewed and discussed.

Chapter 2.5, Publication No. 5: KHAND, Y., **SAMES, B.** and SCHUDACK, M. E., 2007. New ostracod species from the non-marine Cretaceous of Mongolia. *Revista Española de Micropaleontología*, 39(1-2): 71-80.

This published, multi-authored article introduces four new species of nonmarine Cretaceous ostracods of two important families, the Trapezoidellidae Sohn 1979 and the Cyprididae Baird 1845. Of these, the Trapezoidellidae have been first described from the Lower Cretaceous Lakota Formation of the Black Hills area (South Dakota, U.S.A.) and few representatives are known thus far. For that reason, these are not applicable to biostratigraphy to date and have been excluded from the thesis for the time being.

Based on the material from Sohn (1958, 1979; collection of the National Museum of Natural History, Smithson Institution, Washington, DC, U.S.A.) and the senior author's own material, however, a future revision of the Trapezoidellidae is hoped to utilize representatives of this family for biostratigraphic and paleoecologic application by resolving its phylogeny and affinities to modern ostracods. In the context of the Late Mesozoic to recent evolution and distribution of representatives of the superfamily Cypridoidea and their potential application, the extinct families Cyprideidae Martin

1940 and Trapezoidellidae Sohn 1979 are of particular interest: representatives of the Cyprideidae Martin 1940 as closest relatives and ancestors of the extant Cyprididae Baird 1845 and the Ilyocyprididae Kaufmann 1900(a) as well (details in Publication No. 3, Chapter 2.3 herein), and representatives of the Trapezoidellidae as potential closest relatives and ancestors of the extant highly diverse Candonidae (research in progress). It is not clear yet whether representatives of the Trapezoidellidae have closer affinities to either the Cyprididae Baird 1945 or the Candonidae Kaufmann 1900(b). As pointed out by K. Martens (Brussels, written communication, May 2008) *Trapezoidella hornei* Khand, Sames and Schudack 2007 bears striking resemblance to *Pseudocandona gajewskajae* Bronshtein 1947. Since the frontal scar of representatives of the eponymous genus *Trapezoidella* Sohn 1979 is relatively distant from the central adductor muscle scar field as typical for the Candonidae Kaufmann 1900(b), this could point towards a closer affinity of the Trapezoidellidae to the Candonidae, a hypothesis to be looked into in the future.

Altogether, this article is a small but important contribution as to the documentation of Late Mesozoic nonmarine ostracod faunas of the northern hemisphere, representatives of which have potential to become applicable in various ways once more data will be available.

Chapter 2.6, Publication No. 6: **SAMES, B.**, in press. To correlate or not to correlate—That is not the question anymore! Continental Late Jurassic to Early Cretaceous supraregional correlation based on ostracodes. *Palaios*. (Palaios-Spotlight)

This short article arose out of a talk the author gave at the "2008 Joint Annual - GSA | SSSA | ASA | CSSA | GCAGS | GCSSEPM" in Houston, Texas, October 5-9, to introduce the work and some results presented in this thesis. Upon invitation of the co-editors of the journal *Palaios*, Stephen T. Hasiotis and Edith L. Taylor (E-mail from January 2009) the former of which was the convener of the session in which the talk had been given, the author was asked to present his research and its implications in the "Spotlight"-column of *Palaios*. As given in the guidelines of this column, this is a 2-3 pages article giving an overview of the respective's author research relevant and timely for *Palaios'* audience of paleontologists, sedimentologists and other geoscientists. Hence, this article gives a résumé of the background of the author's research, introduces into the problems and approaches as well as gives some results, implications, and perspectives of broader interest. The column also includes a short biography to introduce the author. It is scheduled to be published in the January 2010 issue (E-mail from Jill Hardesty, Managing Editor, 17-08-2009).

1.9. Material and Methods

Detailed descriptions of material and methods are given in Chapter 4 of Publications Nos. 2 and 3 (Chapters 2.2 and 2.3 of this thesis) in each case. At this point, some additional information mainly concerning general methodology, approaches and concepts (philosophy) of the thesis as a whole are noted (also refer to Chapters 3 and 4 of the thesis).

In matters of the quotation at the very beginning of this chapter, comprehensibility and traceability were considered essential, partially at the (necessary) expense of brevity. Whether agreeing or disagreeing on it, the reader has to understand the statement of a problem and suggested solutions first, and that requires a common language, i.e., terminology. An application of any group of organisms requires a well justified and comprehensible taxonomy, which is fundamental therefor. However, with respect to the general and specific morphologic terminology of the ostracod carapace, many relevant publications are rather old (e.g. Kesling 1951, Moore 1961, van Morkhoven 1962, Sylvester-Bradley 1956, Sylvester-Bradley and Benson 1971), and the new "Ostracod Treatise" (Treatise of Invertebrate Paleontology) is long overdue. That does not necessarily imply that these publications are dated, but the usage and definition of some terms has become rather inconsistent over time and some terms have proved not to be suited for all ostracod groups. Other terms have to be redefined in the context of new insights into the (ultra-)structure, origin and genesis of the characters they describe and the respective significance of these (taxonomic, ecologic, ontogenetic etc.). Independent from whether the definition of terms presented is accepted by the readers, the definitions given make the context in which each term is used clear and comprehensible and, even more important, criticizable. Therefore, the comprehensive taxonomic glossaries in the revisions of *Theriosynoecum* and *Cypridea*, including the supporting graphics and some discussions and additional remarks, are essential in works of such extent.

The thesis at hand is a qualitative work on purpose. It has been written with the intent to provide a well-founded basis for upcoming quantitative analyses and applications. As the example of *Cypridea* clearly demonstrates (Publication No. 3, Chapter 2.3), i.e., particularly the new estimation that the diversity of its representatives has been grossly overestimated in the past, the worth and meaning of a quantitative analyses of ostracod taxa is strongly dependent from the quality of the data it is based on. More precisely, in the cases of the revision of *Theriosynoecum* and *Cypridea*, the qualitative analysis and clear differentiation of carapace characters, as well as respective taxa, facilitates meaningful quantitative analyses (assemblages, diversity, paleoecology, paleobiogeography etc.) in the first place (see Chapter 3.1 also).

Another intention concerning the major components of the thesis (particularly Publication Nos. 2 and 3, Chapters 2.2 and 2.3) was the consideration and integration of important literature in languages other than English (and German). Some of these are difficult to obtain and, therefore, have not been considered or have been overlooked in the past. Others have not been considered due to language barriers. Important parts of these references were partially translated, summarized and commented, wherever necessary. Publications until June 2009 have been considered for the thesis.

Altogether, 33 samples from the Lakota Formation covering the whole section (southern and eastern Black Hills area, Fig. 1.3) yielded ostracods, 7 of these also charophytes. Six samples from the Yellow Cat Member of the Cedar Mountain Formation produced ostracods and charophytes.

Since the publication of specific biostratigraphic correlations—integrating charophytes, geologic sections, detailed taxon-based (ostracods and charophytes) supraregional as well as inter- and intraformational correlations—is not part of the thesis, but in preparation to be published in the near future, its elements have not been integrated in the Appendix here.

In contrast to many micropaleontologic publications, SEM-photographs have been taken in backscatter mode throughout (4 quadrant backscatter detector). This mode turned out to be perfect to distinctly illustrate significant carapace features, such as ornamentation elements and their distortions, pores, ridges, and sulci. Some structures were even not clearly identified until application of this mode. In addition, the various possibilities to highlight important carapace features by applying different modes of lighting (enabling different quadrants and numbers of quadrants of the detector) is very helpful for an illustration of these.

Because of the fact that most articles of this thesis are or will be published in U.S American Journals, American English orthography and grammar (Merriam-Webster Dictionary) is used throughout the thesis (except Publications Nos. 1 and 5, Chapters 2.1 and 2.5, which have been or will be published in European journals). An exception is the usage of “ostracod”, which is preferred to the commonly used term “ostracode” in North American publications (the discussion “ostracod vs. ostracode” will not be picked up here).

As common and practical for the presentation of a cumulative thesis, reference lists have been removed from the single scientific papers and a collective reference list (Chapter 5) for the thesis as a whole has been compiled. Since Publications Nos. 2 and 3 (Chapters 2.2 and 2.3) make up the main part of the thesis and have been formatted for “Micropaleontology”, the citation style of this journal (author and year not separated by a comma) is used throughout the thesis except for the other Publications (Nos. 1, 4, 5, and 6, Chapters 2.1, 2.4, 2.5, and 2.6).

2. Scientific Papers

2.1. Publication No. 1

SAMES, B., WHATLEY, R. and SCHUDACK, M.E., accepted. *Praecypridea*: A new non-marine ostracod genus from the Jurassic and Early Cretaceous of Europe, North and South America, and Africa. *Journal of Micropalaeontology*.

The article will be available online via the Lyell Collection http://jm.lyellcollection.org/

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2.2. Publication No. 2

Revision of the genus *Theriosynoecum* Branson 1936 (Ostracoda, Crustacea) and some of its species from the Lower Cretaceous of the U.S. Western Interior (Lakota Formation, Black Hills) and the European 'Purbeck/Wealden'

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Abstract

The revision of *Theriosynoecum* Branson 1936, a common ostracod genus of Middle Jurassic to Early Cretaceous nonmarine deposits worldwide, demonstrates that its representatives—particularly the Early Cretaceous North American ones—are not as endemic as hitherto assumed. The taxonomic concept, as developed and applied herein and supported by an extensive glossary of taxonomic terms as well as new complemental illustrations, resolves many problems resulting from an overestimation of the taxonomic significance of ornamentation (particularly local ornamentation elements as defined herein) in the genus as well as the too regional view of the faunas during the second half of the 20th century. This is the first step to a supraregional biostratigraphic and improved paleoecologic application of representatives of the extinct genus *Theriosynoecum* (Cytheroidea, Limnocytheridae, Timiriaseviinae).

It is proposed to consider and test *Theriosynoecum fittoni* (Mantell 1844) and *Theriosynoecum alleni* (Pinto and Sanguinetti 1962) for being synonymous in the future because of their many striking similarities. The species *Theriosynoecum forbesii* (Jones 1885) and *T. verrucosa* (Jones 1885) are considered separate and not subspecies of *T. forbesii*. *Theriosynoecum verrucosa* occurs in the uppermost Morrison Formation of the Black Hills area, South Dakota, U.S.A., *Theriosynoecum fittoni* in the Lakota Formation of the same area. *Theriosynoecum pahasapensis* (Roth 1933) is, thus far, endemic to North America. A key to the described species is presented.

Early Cretaceous species of *Theriosynoecum* are not yet as well biostratigraphically applicable in North America as in Europe, but this is due to the lack of data from the former area and considered to be promising once more data are available. Nevertheless, the "classic" taxonomic approach provides a considerable step towards better application of these taxa as well as future analysis and robust discussion regarding the phylogeny, evolution and distribution of the limnocytherid subfamily Timiriaseviinae.

Keywords: Western Interior foreland basin, nonmarine Ostracoda, taxonomy, Lower Cretaceous, Lakota Formation, Black Hills

1. Introduction

Ostracods (aquatic microcrustaceans with a calcified bivalved shell) are among the most common fossils in Mesozoic nonmarine deposits of the world. Because of their small size, good fossil record and preservation, as well as their ecology and dispersal strategies they have a high potential to be good index fossils with at least moderate resolution in these deposits. *Theriosynoecum* (Greek for "living with the monsters", i.e. dinosaurs) is a fossil (Late Bajocian?/Bathonian to Albian/early Cenomanian?) nonmarine genus of the family Limnocytheridae (Cytheroidea, Ostracoda). Representatives of *Theriosynoecum* are common in Middle Jurassic to Lower Cretaceous nonmarine deposits virtually worldwide, except for Australia and Antarctica. Several species of *Theriosynoecum* have successfully been used for biozonation in nonmarine deposits, especially in those of Late Jurassic and Early Cretaceous age (Purbeck/Wealden-like facies). Hitherto, it has seemed barely possible to apply species of this genus to supraregional biostratigraphy. Major revisions published during the last 50 years have summarized and discussed important data in a global view, linked the extinct genera to recent successors but in part also complicated the taxonomy, and increased the assumed factor of endemism by the erection of new genera and species. A biostratigraphic application was not the main object of these revisions, and many aspects remained controversial.

In the view of the present author, the central issue inhibiting the harmonization of taxonomy and supraregional correlations has been the different usage, interpretation and evaluation of the morphologic terminology (notably local ornamentation elements as defined herein, see glossary) resulting in relatively restrictive taxonomic concepts of species and genera (i.e., based on very few or even single characters). Therefore, to render a wider and global utilization possible, a new revision that places emphasis on specifying, redefining and harmonizing the morphologic terminology of *Theriosynoecum* and its representatives became necessary, also including and discussing new discoveries in ostracod biology that were published in the last two decades (e.g., new insights into the influence of ecologic parameters on some ornamentation elements, reproduction and dispersal mechanisms, intraspecific variation and hybridization, etc.).

Within the scope of a project carried out in cooperation with a research group from the Sam Noble Oklahoma Museum of Natural History, Norman, Oklahoma (led by Richard L. Cifelli), dealing with early mammals, the taxonomy of an important genus (*Theriosynoecum* Branson 1936) of nonmarine Lower Cretaceous ostracods of the U.S. Western Interior and other contemporaneous deposits of the world is revised herein. The main object of this project and cooperation was an examination of the ostracods retrieved from some Early Cretaceous formations of the U.S. Western Interior where vertebrate remains (particularly early mammals) had been found, and to improve the age determination of such formations, if possible. During the project, it soon became clear that, within the frame as given above, a comprehensive revision of the most important nonmarine ostracod index genera/species in Western Europe during Latest Jurassic-Early Cretaceous times (i.e., *Theriosynoecum*, and *Cypridea* Bosquet 1852, the latter to be dealt with in another paper) was necessary to apply these to the biostratigraphy of North American formations of Early Cretaceous age. Many of these formations are poorly dated, often just known to lie above the Upper Jurassic Morrison Formation and to be of Early Cretaceous (pre-middle Albian) age. In addition, a lowermost Cretaceous age of some top parts of the Morrison Formation seems to be probable.

Consequently, this work focuses on selected *Theriosynoecum* species of the Lower Cretaceous U.S. Western Interior and closely related ones, their comparison to the most adjacent faunas in Western Europe at that time (English Purbeck/Wealden, German 'Wealden', Spain) as well as parts of other continents, and their potential usability for supraregional and regional biostratigraphy, and paleoecology. The detailed implications and consequences of the taxonomic results for paleobiogeography, biostratigraphy and paleoecology of selected formations (top Morrison Formation and Lakota Formation, South Dakota and Cedar Mountain Formation, Utah) of the U.S. Western Interior and other areas will be published elsewhere, including the author's results of the revision of the genus *Cypridea*, as well as the analysis of other taxa. Owing to the lack of the author's own data from the

Lakota and Cedar Mountain formations regarding the "Aptian-Albian fauna" of Peck (1956, 1959; informally designated as "Fauna C", see Chapter 6.4. herein) deriving from partially younger formations (Bear River Fomation and upper Cloverly Formation, Wyoming; upper Gannett Group (Peterson, Bechler and Draney Limestone formations, Wyoming and Idaho; Kootenai Formation, Montana; upper Cedar Mountain Formation, Utah), this fauna has been mostly excluded thus far. Important taxa closely related to those analyzed herein are discussed, however.

2. Previous work and aims

A comprehensive historical overview about the development of the taxonomy of the *Theriosynoecum* group as well as synonymous and related taxa, the problems associated therewith, and synonymy lists can be found in Pinto and Sanguinetti (1962, p. 12-33, 77-84). Schudack (1994, p. 64-66) gives an updated synthesis of publications dealing with the problem and discusses the diagnostic characters and arguments quoted by the different authors through time. Of particular interest and influence on taxonomy is the paper of Colin and Danielopol (1980), who linked the fossil and recent taxa of the limnocytherid subfamily Timiriaseviinae.

The taxonomy of the genera *Bisulcocypris* Pinto and Sanguinetti 1958, *Dryelba* Sohn 1982, *Gomphocythere* Sars 1924, *Metacypris* Brady and Robertson 1870, and *Theriosynoecum* Branson 1936 (including the genus *Cytheridella* Daday 1905), all belonging to the family Limnocytheridae (subfamily Timiriaseviinae), has been discussed controversially for a long time. Names such as *Metacypris* and *Gomphocythere*, which have been used for Mesozoic representatives of this group, should properly be applied to (sub-)recent taxa (*Gomphocythere*), or restricted to fossil to recent lineages (*Metacypris*), respectively. Mandelstam (in Schneider et al. 1956, p. 139) had already suggested assigning the bisulcate Mesozoic representatives of *Metacypris* and *Gomphocythere* to *Theriosynoecum*, a concept also supported by Sohn and Anderson (1964). *Metacypris* was commonly applied in general for Mesozoic species in North and South America as well as in Africa, whereas *Gomphocythere* has often been used for such species by European authors (see also Table 1 and Chapter 6.4 for more information and discussion).

The genus *Metacypris* is now restricted to an Aptian to recent lineage of the Timiriaseviinae, smaller than 0.6mm, relatively compact (with a low length/height coefficient) with absent or one very weakly developed anterolateral sulcus (monosulcate) in each valve as well as strongly developed brood-pouches in the females.

The name *Gomphocythere* Sars 1924 (Late 'Quaternary' to recent) is not applicable to fossil or recent representatives of the '*Metacypris*'-*Bisulcocypris*-*Theriosynoecum* group because representatives of the former possess sieve pores. In addition, *Gomphocythere* also has a normal LV>RV overlap but combined with an inverse lophodont hinge: the teeth and the hinge groove are situated in the larger LV, whereas the hinge bar and the sockets are in the smaller RV, and it has a narrow calcified inner lamella.

This leaves *Bisulcocypris* Pinto and Sanguinetti 1958 and *Theriosynoecum* Branson 1936 as available names for the older (Albian and older, questionably early Cenomanian and older) fossil representatives, as well as *Dryelba* Sohn 1982. In the past, the arguments for the differentiation of *Bisulcocypris* and *Theriosynoecum* were mainly based on some ornamentation elements (tubercles or node-like tubercules sensu Sames herein), the occurrence of an accommodation groove and a bipartite median hinge element (cf. Branson 1966, Pinto and Sanguinetti 1958, 1962, 1984, Sohn 1982). Several other authors, e.g. Colin and Danielopol (1978, 1980, Colin and Dépêche 1997, Do Carmo et al. 2004), have regarded the two as synonymous, and thus *Bisulcocypris* to be invalid, a concept that is adopted, discussed and explained herein. The genus *Dryelba* Sohn 1982 is considered invalid as well (see discussion of the genus *Theriosynoecum*, Chapter 5.2).

At species level, ornamentation—particularly the development of tubercles and nodes or node-like tubercles—has been (and still is) the main taxonomic problem in *Theriosynoecum*. There is some evidence now, however, that the occurrence (not the position!) of tubercles and nodes in *Theriosynoecum* is mostly an ecophenotypic feature, and possibly induced by increasing salinity (Do Carmo et al. 1999). This concept has particular influence on the validity of many species and subspecies.

When trying to apply Early Cretaceous nonmarine ostracods to supraregional biostratigraphy, it became apparent to the present author that, despite major revisions in the past (e.g. Colin and Danielopol 1980, Pinto and Sanguinetti 1962), a new taxonomic revision under certain aspects (taxonomic terminology and interpretation of characters in particular) as well as a synopsis of remaining problems would be essential to communicate and confirm the arguments for taxonomic and biostratigraphic correlations. The present paper specifies, (re-)defines and discusses the terminology for carapace morphology, which, in part, is particularly adapted to and clarified for *Theriosynoecum*, and assesses the taxonomic significance of certain characters. On this basis, an emendation of the diagnosis and differentiation of *Theriosynoecum* from other genera of the Timiriaseviinae is presented, as well as an inclusion/validation of some others. This is also a revision of several species of this genus (*T. alleni*, *T. fittoni*, *T. forbesii*, *T. pahasapensis* and *T. verrucosa*).

The main purpose of this paper is to provide sufficient arguments for new taxonomic hypotheses that led to a somewhat wider concept of some (potential) index species that have erstwhile been considered different and endemic to certain areas in the world. On the one hand, the approach followed herein is, therefore, to provide and discuss many traceable arguments and terms to support and communicate the author's taxonomic hypotheses that, on the other hand, should be readily criticizable if desired. It is also hoped that this revision will provide the basis for more global approaches in nonmarine late Mesozoic ostracod biostratigraphy in general, and for multifaceted regional and supraregional applications in different areas of the world.

The endemism of Early Cretaceous North American nonmarine ostracods became strongly doubtful when Schudack published his results about taxonomy and paleobiogeography of ostracods from the famous nonmarine Late Jurassic Morrison Formation in the late 1990s (Schudack 1995, 1996, Schudack et al. 1998). Schudack (1996) showed that the grade of endemism at species level for the Morrison fauna in comparison to that of Europe is below 50%, and thus this also became very probable for most of the Lower Cretaceous formations of the U.S. Western Interior overlying the Morrison Formation that have, in part, similar paleoenvironmental settings.

While dealing with the taxonomy of these Early Cretaceous ostracods, the present author recognized strong similarities between North American, European, South American and West African species. Representatives of the '*Metacypris*'-*Bisulcocypris*-*Theriosynoecum* group have been found in many ostracod-bearing samples of the Lakota Formation collected by the author and a field party from the Sam Noble Natural History Museum of Oklahoma (led by Richard L. Cifelli, Sam Noble Oklahoma Museum of Natural History) during field campaigns in summer 2003 and 2004. As assumed before, and due to detailed inspection of original material, some North American species appeared to be nearly identical with well-known index species from the Purbeck and Wealden of England and other contemporaneous deposits of the world, except for their ornamentation (local ornamentation elements sensu Sames herein). Scrutiny became necessary and promising, particularly for representatives of the '*Metacypris*'-*Bisulcocypris*-*Theriosynoecum*-group, because these seemed not to have been considered as potential index fossils for supraregional biostratigraphy in North America before.

There are several eventualities to explain this: First, nonmarine Early Cretaceous ostracods of the U.S. Western Interior were believed to be strongly endemic in the past, which became apparent through the designation of numerous new species just described from North America during the 20th century. Second, one of the U.S. American pioneers for nonmarine Early Cretaceous Charophyta and Ostracoda, Raymond E. Peck, published most of his works prior to the establishment of a good biostratigraphy of Purbeck/Wealden deposits in Western Europe in the 1960s and 1970s, especially the comprehensive stratigraphic works of Frederick W. Anderson on the British Purbeck and Wealden. Thirdly, it remains unknown why Israel G. Sohn, the second famous specialist for nonmarine Lower Cretaceous ostracods of North America, does not even mention—let alone describe—representatives of the '*Metacypris*'-*Bisulcocypris*- *Theriosynoecum* group in his comprehensive publication about ostracods from the Lakota Formation of the Black Hills area, South Dakota and Wyoming (Sohn 1979). Instead, he later establishes the new family Dryelbidae (Sohn 1982) including the genera *Dryelba* Sohn 1982 and *Theriosynoecum*, thus enhancing the complexity of the problem. The only specimen mentioned in Sohn (1958, p. 123, figs. 19-20), *Theriosynoecum* sp., is *T. wyomingensis* (Branson 1936) and derives from the Late Jurassic Morrison Formation underlying the Lakota Formation in the Black Hills area (South Dakota and Wyoming). Sohn (1979, p. 1) also states that in contrast to the Morrison Formation "... the Lower Cretaceous sedimentary rocks do not contain *Theriosynoecum* ...". The reason is taxonomic problems within the group. Representatives of '*Metacypris*' were frequently reported in sections of USGS mapping reports of the Black Hills, particularly in the southern and eastern area (e.g. in Pillmore and Mapel 1963, Bell and Post 1971; the reported specimens having been identified by Sohn himself). Sohn had received samples from the field campaigns beginning in 1953 and joined the field party in 1957 for additional collections (Sohn 1979). Nevertheless, for unknown reasons he (Sohn op. cit.) neither describes nor mentions representatives of '*Metacypris*' either, although his 1979 publication is based on these collections, and thereby Sohn inhibited a potential biostratigraphic application of the taxa in question in North America.

Another reason why representatives of *Theriosynoecum* may not have been stratigraphically important is their relatively rare occurrence in contrast to *Cypridea.* For example, samples from the lower Cedar Mountain Formation, Utah, revealed not even a single specimen of *Theriosynoecum,* whereas several samples of the Lakota Formation, South Dakota did. This is most probably related to paleoecology (in contrast to *Cypridea*, *Theriosynoecum* is believed to require permanent water bodies, not temporary/semi-temporary ones).

Altogether, the reasons given might explain why no attempt at a supraregional correlation of Early Cretaceous nonmarine ostracods of the U.S. Western Interior was made in the second half of the 20th century. Hitherto, the supraregional nonmarine ostracod biostratigraphy of Lower Cretaceous rocks of North America is still poorly developed, a gap to be partially filled with the results of this paper.

The comprehensiveness of this paper, including long synonymy lists, descriptions and discussions, derives—in the view of the author—from the need for:

A) compiling large amount of information scattered throughout hundreds of publications in many different languages, in part hardly available,
B) a detailed review of the definition of specific taxonomic terms, supported by illustrations in conjunction with progress in research of ostracod phylogeny, biology and ecology (this led to the detailed glossary at the end of this paper),
C) describing and figuring as many carapace features as possible as well as discussing their taxonomic significance,
D) a global approach to the comparison of the taxa, a matter often neglected in the past owing to language barriers, the partial unavailability of references in pre-Internet times and because of the fact that potential long-distance distribution mechanisms were either unknown or not considered.

One aim of this paper is to provide a synopsis within one publication that is hoped to be a good basis for future research regarding *Theriosynoecum* – its taxonomy, phylogeny, and its stratigraphic and paleobiogeographic distribution worldwide. For the purpose of a global approach, this work attempts to include as many references as possible in non-English languages and from continents other than North America and Europe, specifically South America (Spanish, Portuguese, German) and Asia (Russian, Chinese), as well as Africa in part (French, German; altogether, the state of knowledge about Upper Jurassic to Cretaceous nonmarine ostracods in Africa is not yet good, except for central West Africa). As for the Central Asian ostracods, luckily there are some comprehensive newer publications, practically taxonomic atlases, summarizing and refiguring the hitherto published species: Hou and Gou 2007, Nikolaeva and Neustrueva 1999, and Neustrueva et al. 2005.

3. Geologic overview, stratigraphy and localities

The North American Cordilleran foreland basin (U.S. Western Interior Basin) is the largest of its type known, reaching from northeast Canada to central Mexico and occupying an area of more than five million square kilometers (e.g. Kauffman and Caldwell 1993, see Fig. 1 herein). During Late Jurassic times, the basin began to develop between the North American Cordilleran orogenic belt to the west and the North American craton to the east in response to the subduction of oceanic plates of the Pacific domain (Kauffman and Caldwell 1993, DeCelles 2004). Contemporaneously, and in various types of process-response and feedback relationships, the orogenic belt and the foreland basin evolved together until Eocene times. Altogether, this evolution lasted for about 100myr, including two main orogenic phases: the Sevier orogeny ("Middle" to Late Cretaceous) and the Laramide orogeny (Late Cretaceous to Eocene). Basin subsidence was caused by flexural thrust-loading – a combination of the flexure of the lower crust due to overthrust, sediment load and longer wavelength (>400km) dynamic subsidence (e.g. DeCelles and Giles 1996, DeCelles 2004). Deposition during Late Jurassic to Early Cretaceous times was strongly connected with the tectonic coevolution of both the proto-Cordillera and its associated foreland basin, which affects source, supply rate and depozone of the nonmarine sediments (Kauffman and Caldwell 1993). DeCelles and Giles (1996, p. 117) point out that in their expanded definition for foreland basin systems "… a depozone is defined in terms of its position during deposition, rather than its eventual position with respect to the thrust belt", which is important to understand the interaction of tectonics and syndepositional stratigraphic architecture, and its regional differences.

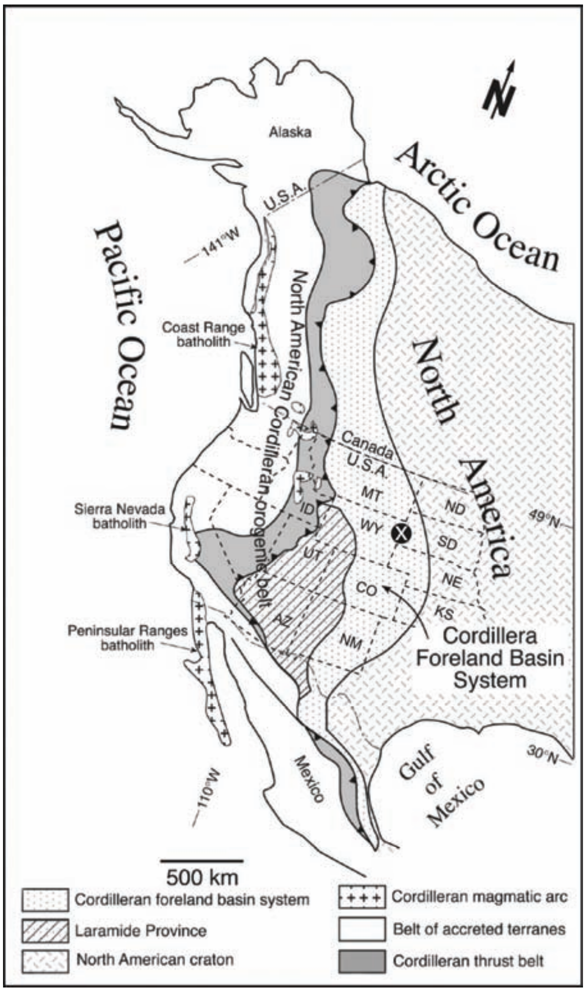


Fig. 1. Generalized tectonic map of western North America (modified after DeCelles 2004), showing the Cordilleran foreland basin system and the geographic position of the Black Hills uplift (white "x" in black circle) as well as the distal position of the Lakota Formation within the foreland basin. Abbreviations for indicated states within the U.S.A.: ID – Idaho, ND – North Dakota, SD – South Dakota, MT – Montana, WY – Wyoming, UT – Utah, CO – Colorado, NE – Nebraska, KS – Kansas, AZ – Arizona, NM – New Mexico.

Stratigraphic correlation and refined dating of Upper Jurassic to Lower Cretaceous Western Interior nonmarine strata, which had been problematic throughout the 20th century, improved after integrated stratigraphy was applied (e.g. Currie 1997, 1998, Way et al. 1998, Zaleha 2006). Dating such formations is still a problem, however, and especially the maximum age of the Lower Cretaceous formations or rather the hiatus between their base and the underlying Morrison Formation is under controversial discussion, a problem hoped to be solved by improving age estimations due to combined ostracod/charophyte biostratigraphy.

The Lakota Formation (Black Hills, South Dakota and Wyoming) was deposited in the distal part of the foreland basin (Fig. 1). The Laramide event led to fracturing of the craton and partitioned a part of the foreland basin into a mosaic of smaller foreland basins and uplifts (e.g. De Celles 2004, Dickinson 2004), such as the Black Hills uplift, the easternmost of the Laramide foreland uplifts.

The Inyan Kara Group, consisting of the Lakota Formation in its lower part and the overlying Fall River Formation, crops out along the flanks of the Black Hills uplift, South Dakota and Wyoming (Fig. 2). In most areas, the Morrison Formation unconformably underlies the Inyan Kara Group except for the southeastern area, where it is substituted by the locally occurring Unkpapa Sandstone. In his revision of the Lakota Formation, Waagé (1959) subdivided the Lakota Formation into "the Lakota formation below [the] Minnewaste limestone member" (op. cit., p. 86), the "Minnewaste limestone member" and the "Fuson member". Furthermore, Waagé (1959) restricted the term Inyan Kara Group and its formations to the Black Hills area, differentiated several sequences of the Lakota Formation in the Black Hills (the northwestern, the coal-bearing, the eastern, and the southern sequence, whereas the southern is the stratigraphically most complex and probably most complete) to illustrate some of its principal variations, and also defined a new reference section for it in the Fall River Canyon (Fig. 2, No. 3). Post and Bell (1961) designated the lower part of the Lakota Formation as Chilson Member, particularly in the southern Black Hills.

Way et al. (1998) subdivided the Lakota Formation in the northern Black Hills into three informal intervals (L1, L2 and L3), L1 corresponding to the Chilson Member including the Minewaste Limestone Member restricted to the southern Black Hills (Zaleha 2006, see Fig. 2 herein also), L2 correlating with the lower part of the Fuson Member as defined for the western Black Hills by Post and Bell (1961), and L3 with the upper part of the Fuson Member of workers such as Post and Bell (1961) or Dahlstrom and Fox (1995). Zaleha (2006) correlates these informal intervals with Lower Cretaceous rocks of central and western Wyoming, thereby giving a Barremian to Aptian (112.2 Ma) age for the Lakota Formation, possibly Hauterivian and even Valanginian for some deposits of the L1 interval.

The ostracod samples dealt with in this paper derive from the Lakota Formation in the eastern and southern sequence of South Dakota (Fig. 2). As mentioned before, the detailed implications and consequences of the taxonomic results for biogeography, biostratigraphy, and paleoecology will be analyzed and discussed elsewhere.

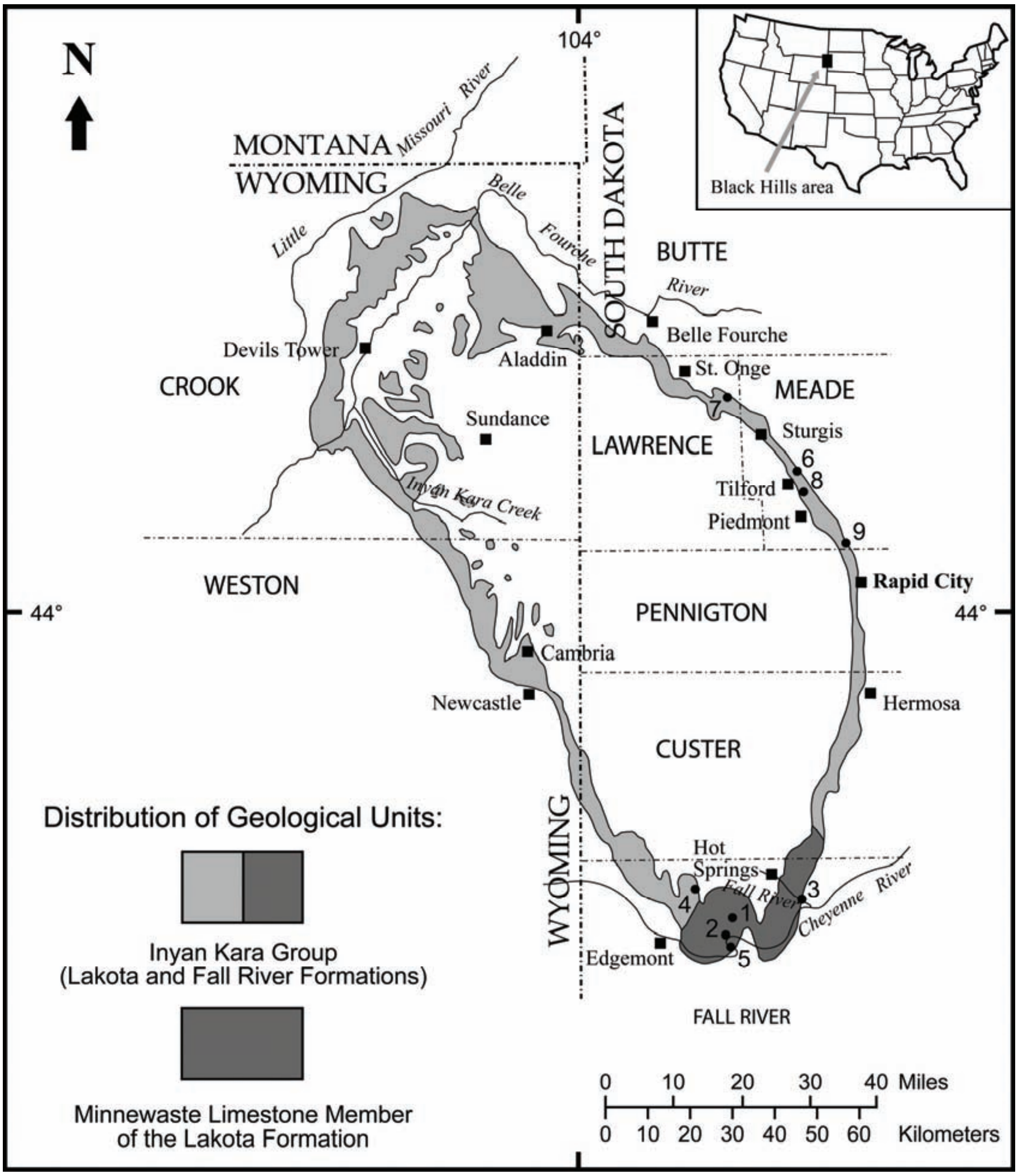


Fig. 2. Map of the Black Hills area showing the distribution of the Inyan Kara Group (Lakota and Fall River formations) deposits (modified after Waagé 1959, and Sohn 1979), and the sample localities discussed herein, SD: South Dakota. GPS coordinates UTM projection (NAD27): **1.** Buck Canyon, Lakota Formation, section label BC (BCB, BCE; loc. 17 of Sohn, 1979), section of Post and Bell (1971, p. 530-531), northeastern Flint Hill Quadrangle, UTM: 13 T 611329E 4800660N. **2.** Horse Sanctuary/Devil's Canyon, Lakota Formation, section label HSDC, section of Post and Bell (1971, p. 538-539), eastern Flint Hill Quadrangle. **3.** Fall River Canyon, Lakota Formation, section label FRCA (close to loc. 12 of Sohn, 1979), SE of Hot Springs, southeastern Hot Springs Quadrangle, UTM: 13 T 625855E 4807594N. **4.** Red Canyon, Morrison Formation, section label RCS (loc. 9? of Sohn, 1979), southeastern Edgemont NE Quadrangle, Fall River County, UTM: 13 T 598799E 4804793N. **5.** Angell Ranch/Cheyenne River, section label ARCR, southeastern Flint Hill Quadrangle, Fall River County, UTM: 13 T 611226E 4792665N. **6.** Little Elk Creek, Lakota Formation, section label LEC, NE of Tilford, Meade County, UTM: 13 T 629259E 4901379N. **7.** East of road to Belle Fourche, Lakota Formation, north of Whitewood, section label EBF (close to loc. 2 of Sohn, 1979), Hot Springs Quadrangle, Lawrence County, UTM: 13 T 608929E 4928509N. **8.** Stage Barn Canyon Road, Lakota Formation, section label SBCR, SE of Tilford, Rapid City Quadrangle, Meade County, Roth's (1933) type locality (?), UTM: 13 T 633461E 4894622N. **9.** Boxelder Creek east of Blackhawk, Lakota Formation, section label REKO04, southeastern Black Hawk Quadrangle, Meade County, UTM: 13 T 638901E 4887800N.

4. Material and methods

Surface bulk samples from promising lithologies (calcareous claystones, marls and calcareous silt- and sandstones) were taken from several sections of the Lakota Formation in the southern and eastern Black Hills (South Dakota, Fig. 1). Processing followed standard methods, treating the samples with warm water, and 2-8% hydrogen peroxide (0.5-3 hours), if necessary (i.e. if samples did not disperse in warm water only). The samples were then washed through sieves (500, 250, and 125m), picked and scanned uncoated with a LEO 1450 VP Scanning Electron Microscope at the Sam Noble Oklahoma Museum of Natural History (Norman, Oklahoma) in variable pressure mode using the four-quadrant backscatter detector. The backscatter mode proved to be ideal for displaying and analyzing different large- and small-scale types of ornamentation.

The specimens were mounted using needle and wax, which, without coating, may appear as small black grains on the specimens, because the contrast between organic (dark, very low conductivity) and inorganic (bright, stronger conductivity) matter is very strong then.

For purposes of clarity, the taxonomic descriptions follow a consistent scheme as far as possible, maintaining the same succession of terms within the paragraphs. To enable the reader to better evaluate the hypotheses and results presented herein, the discussion section of each species reviewed herein is detailed and deals successively with nearly all species listed in the synonymy that required further comments.

Every now and then, specific terms that the author considers in need of clarification in the context of their usage, are highlighted by an arrow (=>) in combination with *italic type*, especially when they occur for the first time. This refers to the glossary at the end of this paper where these terms are elucidated and discussed whenever necessary.

The size parameters used are as follows: Very small: 0.20-0.60mm; Small: 0.60-1.00mm; Medium: 1.00-1.50mm; Large: 1.5-5mm (in relation to maximum length parallel to the base line). For better readability and intelligibility, abbreviations are mostly avoided. The few common abbreviations used are: LV for left valve, RV for right valve, L for length, H for height and W for width as well as L/H for length/height coefficient, L/W for length/width coefficient. For better accuracy, measurements were obtained digitally from the SEM pictures by using the CANVAS program (by ACD Systems).

The measured parameters to describe the carapace are illustrated in Fig. 4. In lateral view, the carapace is oriented in relation to the => *base line*. Maximum length, height, and width include all protrusions that overreach the outline but not the very variable and environmentally influenced => *local ornamentation elements* as defined herein (see Fig. 4, dorsal view: the width of the male carapace is measured excluding => *tubercles*). Thus, the carapace outline is significant prior to the outer margins where applicable (dorsal and ventral margins mostly).

The abbreviations for "plate(s)" and "figure(s)" are given in upper case (Pl. and Fig.) when referring to those in this publication, whereas lower case (pl. and fig.) indicates those of cited references.

Concerning salinity (sensu lato) tolerances, the classification of brackish waters follows the Venice System according to Oertli (1964).

The item "faunal association" in the taxonomic description refers to North American assemblages only. Species belonging to other genera than *Theriosynoecum* will be dealt with in other papers; concerning *Cypridea* refer to Sames (submitted).

Correlation and age determination of NW European Purbeck/Wealden deposits follow the correlation chart of Hoedemaeker and Herngreen (2003). Although there are still a few details to be discussed, this is the most recent and comprehensible dataset available and is also very useful because of its practical format and the detailed information given therein. Accordingly, if any future changes in this chart prove necessary, it will be easy to retrace and correct any data in the publication at hand that have been adopted from the chart and might be affected by such changes.

Abbreviations and symbols used in the synonymy list follow the established biologic nomenclature (cf. Granzow 2000, for example).

Remarks: Concerning the carapace margin, a recent publication by Yamada (2007) revises some widely used terms based on new findings in its ultrastructure. This has more or less stronger effects regarding the definition, usage, usability and interpretation of morphologic terms such as flange, selvage, duplicature, (calcified) inner lamella, outer lamella, (inner) list, contact margin etc. For reasons of usefulness, to avoid confusion, and because Yamada's (op. cit.) concept has not yet been tested on many taxa (especially fossil ones), the "classical" terminology is used herein. Nevertheless, wherever applicable, the new terminology and its effects on particular terms and interpretations are integrated and discussed in the definition of the carapace terminology of the taxonomic glossary herein.

5. Systematic section

5.1. Repositories and their abbreviations

The specimens figured herein will be deposited in the collections of the National Museum of Natural History, Smithsonian Institution, Washington, DC, USA (USNM) under the numbers given. Abbreviations for repositories cited are as follows:

- BfB – Bundesanstalt für Bodenforschung, Han(n)over, Germany.
- BMNH – The Natural History Museum (formerly The British Museum, Natural History) London, UK.
- BGS – British Geological Survey Palaeontological Collections, BGS Headquarters Keyworth, Nottingham, specimen numbers: Mik(M) xxxx.001 (".001" is the suffix of earlier citations).
- M.P., U.R.G.S. – Museo de Paleontologia da Universidade do Rio Grande do Sul, Porto Alegre, Brazil.
- SJCC – Sir John Cass College (London Metropolitan University), London, UK.
- SMF – Forschungs-Institut Senckenberg, Frankfurt/Main, Germany.
- U.M. – University of Missouri Collection, Columbia, Missouri, USA. Unfortunately, the disposition of the ostracod type material and many of the figured specimens is unknown, although it is listed in the catalog (visit of the author May, 2005; pers. comm., R.L. Ethington, University of Missouri).
- USNM – The National Museum of Natural History, Smithsonian Institution, Washington, DC, USA.

5.2. Taxonomy

Class **Ostracoda** Latreille 1802
Order **Podocopida** Müller 1894
Suborder **Podocopina** Sars 1866
Infraorder **Cytherocopina** Gründel 1967

Superfamily **Cytheroidea** Baird 1845

Remarks: According to the International Code for Zoological Nomenclature and as suggested by Martens et al. (1998, p. 41) the ending "-oidea" is used for superfamily level (e.g., Cypridoidea instead of Cypridacea), thereby avoiding confusion with plant taxa.

Family **Limnocytheridae** Klie 1938

Remarks: Systematics of this family has been under continuous and, in part, confusing discussion, particularly its subdivision into subtaxa (subfamilies and tribes) and the genera to be included. The family Limnocytheridae (Permian to recent) comprises three subfamilies (Whatley and Moguilevsky 1998), the solely Permian Tomiellinae *sensu* Whatley and Moguilevsky (1998) as well as the Limnocytherinae Klie 1938 (Sars 1925 of some authors, late Permian to recent) and the Timiriaseviinae Mandelstam 1960 (late Permian to recent). The most important "classical" carapace characters to differentiate both latter subfamilies are the sieve pores present in the Limnocytherinae, while the female brood pouches (and brooding behavior of living representatives) are absent in this subfamily, whereas it is the other way round in the Timiriaseviinae, i.e. the latter have no sieve pores and strong brood pouches (and brooding behavior of living representatives). Exact phylogenetic relationships of the subfamilies have yet to be determined, however. Particularly the separate tribe Cytheridellini (including *Gomphocythere* Sars, *Cytheridella* Daday and *Gomphodella* De Deckker, see also Table 1), having originally been placed within the subfamily Limnocytherinae by Danielopol et al. (1990) because of the fact that its representatives possess (true) sieve pores, has been transferred to the subfamily Timiriaseviinae by Martens (1995) on the basis of several other morphologic characters (hard and soft parts: hinge structure, mandibular palp, position of the furca on the hemipenis). Admittedly, Martens recently described the Cytheridellini "… as a transitionary group between the Limnocytherinae and the Timiriaseviinae, although they share most characters with the latter subfamily" (in Park et al. 2002, p. 16).

Unfortunately, a recent substantial synopsis regarding the systematics of the Limnocytheridae and its subdivision, as well as included fossil and recent representatives, is still lacking and cannot be given herein. In addition, the subdivision in tribes and species is, in part, mostly based on soft parts, making it difficult to assign it to fossil species. Therefore, attention is invited to refer to other publications (e.g., Chen 1965, Colin and Danielopol 1978, 1980, Colin et al. 2000, Danielopol et al. 1990, De Deckker, P. 1981, Gidó et al. 2007, Karanovič 2006, Mandelstam 1960, Martens 1995, McKenzie et al. 2004, Park et al. 2002, Pinto and Sanguinetti 1962) and references therein. It is noteworthy that McKenzie et al. (2004) described a new representative of the Timiriaseviinae, *Progomphocythere mawsontalenti*, which has a corneous-chitinous carapace and lacks calcification.

However, the taxonomic revision resulted in a concept to distinguish selected fossil and recent genera of the Limnocytheridae based on carapace morphology (as given in Table 1, see Chapter 6.4 for discussion).

Subfamily **Timiriaseviinae** Mandelstam 1960
syn. Metacypridinae Danielopol 1965 emend. Colin and Danielopol 1980

Remarks: The morphologic peculiarities in the carapace and, if applicable, in the soft parts of representatives of the Timiriaseviinae are discussed in detail by Colin and Danielopol (1980), who successfully linked fossil and recent taxa of this subfamily. For elucidation of the assignment and redefinition of the subfamilies Limnocytherinae Sars 1924, and Timiriaseviinae Mandelstam, as different lineages within the family Limnocytheridae and their phylogenetic relationships or that of the included taxa, see Colin and Danielopol (1978, 1980), Colin et al. (2000), Danielopol (1965), Danielopol et al. (1990), Mandelstam (1960) Martens (1995), McKenzie et al. (2004), Park et al. (2002), Savatenalinton et al. (2008), for example, and references therein.

Fossil representatives of the Timiriaseviinae have the following hard part characters making them members of this subfamily: presence of simple pores but absence of sieve pores, the female brood pouches are always present and mostly strongly developed (broadly inflated), and the carapace can either show one, two or no anterior dorsolateral sulcus(-i).

Genus ***Theriosynoecum*** Branson 1936 **emend.**

1935 *Morrisonia* Branson, p. 521 – non *Morrisonia* Grote 1874

1936 *Theriosynoecum* nom. nov., nom. subst. pro *Morrisonia* Branson 1935 – Branson, p. 323

1955 *Theriosynecum* Mandelstam in Galeeva [error in spelling and author attribution]

1958 *Bisulcocypris* gen. nov. – Pinto and Sanguinetti, p. 77

1982 *Dryelba* gen. nov. – Sohn, p. 313

Remarks: In 1935 Branson established the new genus *Morrisonia* with the type species *M. wyomingensis*. Because the name *Morrisonia* was preoccupied by a living species of the Lepidoptera (butterflies, Hexapoda), Branson (1936) retracted the name and replaced it with *Theriosynoecum*. For the reasons given above (see Chapter 2), *Theriosynoecum* Branson 1936 is the oldest valid genus name and therefore preferable.

Type species: *Morrisonia wyomingensis* Branson 1935

Diagnosis: A representative of the Limnocytheridae/Timiriaseviinae with the following specifications: small to medium sized (typically around 1mm), LV>RV, rarely inverse, subequivalve. Carapace moderately thick. Anteriorly with two dorsolateral sulci. Subrhomboidal to oblong in lateral view, dorsal margin straight. Cardinal angles well defined, especially the posterior one. Strong sexual dimorphism. Females piriform in dorsal view (brood pouches), node-like tubercles common; males elliptic to diamond-shaped in dorsal view, and nearly always tuberculate. Ventrally with carinae. Surface punctate to reticulation-like punctate. Hinge merodont and of lophodont type, all elements being smooth, posterior tooth roundish and anterior tooth developed as narrow ridge, both inclined downwards.

Description: Small to medium sized. LV>RV in general, occasionally inverse (e.g. "*Bisulcocypris*" *pricei* Pinto and Sanguinetti 1958, recte *Theriosynoecum pricei*). Carapace subrhomboidal, rounded-oblong in lateral view. Irregularly ovate or elliptic (♂), piriform or cordiform (♀) in dorsal view. Strong sexual dimorphism - females more compact and rounded in lateral view, very broad with large posterior brood pouches, males more elongate and oblong, usually with strong tubercles/spines. Carapace thick-walled. Valve overlap weak, except for a stronger overlapping, convex, tongue-like segment ventrally, at about 2/5 of length (below position of S2-sulcus, Fig. 6/A). Cardinal angles well marked in most cases. Hinge margin somewhat incised forming a narrow and shallow dorsal furrow between the cardinal angles. Ventral margin straight to slightly convex, ventral lateral outline of females moderately convex due to overreaching brood pouches or ventrolateral extensions in both sexes. Two lateral sulci anterior of half length, separated from each other by a ridge ending below the dorsal margin. The posterior and larger one (sulcus no. 2 or "S2") is well defined extending from the dorsal margin down to about half height. Front sulcus (sulcus no. 1 or "S1", see Fig.6/A) generally much shorter, located at about 1/4 of carapace length (at about anterior cardinal angle) and extending downwards to about 2/3 of carapace height at maximum. Beginning of both sulci on the smaller valve always noticeably closer to the hinge line than on the larger valve. With variably broad anterior marginal zone.

Surface punctate, sometimes with very large and deep puncta, which can approximate a reticulation. Ventrally, sometimes also ventrolaterally, these puncta form longitudinal rows separated by moderately projecting carinae. Strong tubercles and/or node-like tubercles very common. Node-like tubercles either with or without surface characters, true tubercles always without surface characters, displacing the latter at the base instead. Position of these => *local ornamentation elements* fixed in almost all cases. Males with at least four characteristic posterior tubercles (see Fig. 6/E, Nos. 1-4 and Pl. 2, Fig. 2 for illustration) in most cases. Several simple pores, generally outside of the puncta.

Sinuous hinge line in dorsal view caused by overlap change from LV over RV at the cardinal angles and overlap of the RV's flange over the LV along hinge margin.

Hinge merodont and of lophodont type, with or without accommodation groove, all elements being smooth (Fig. 8). Median hinge element forming a ridge/bar in the larger valve and a groove in the smaller, with or without a small constriction at about half of its length separating it into two parts. If the latter is the case, then the posterior part of the hinge bar bears a sharp edge (Fig. 8) towards its anterior end. Anterior tooth narrow with sharp edge, posterior tooth broad, ovate and well rounded - both in the smaller valve, fitting into an appendant socket of the larger valve.

Inner lamella moderately broad. Line of concrescence and inner margin only coinciding towards dorsum. Fused zone of both valves narrow with strong and sharply edged selvage (Fig. 7). The selvage of the larger valve fits into a groove between the selvage and the outer margin of the smaller valve, thus enveloping the selvage of the smaller valve. Flange developed along the carapace's margin below half height, posteriorly reaching somewhat higher in the larger valve, formed by the inwards contorted outer margin and enveloping the selvage of the smaller valve if carapace is closed. Selvage of the smaller valve not so sharp-edged and more weakly developed, often slightly enveloping and overreaching the selvage of the larger valve anteriorly and posteriorly. Ventrally with tongue-like projection of the valve at 2/5 of length, formed by the outer margin in the larger valve, overlapping that of the smaller valve, here being a protrusion of the selvage.

Anterior => *inner lamella* moderately broad, crescent, forming a small vestibulum; posterior free inner lamella narrow, extending posteroventrally up to 2/3 of height, and with very narrow vestibulum. Free inner lamella sometimes with very narrow and just slightly prominent ridges running parallel to the inner margin.

Adductor muscle scars (AMS) central to centroventral (Fig. 3), below S2-sulcus and consisting of a vertical row of four closely placed elongate scars (cf. Fig. 6/B also). The upper and lowermost ones of these are smaller than the longer, elongated-elliptical ones in the middle. Frontal scar small, situated slightly above and relatively distant to AMS-field. Two mandibular scars situated slightly below AMS-field, a distal one, strongly incising and thus easy to notice, is placed directly below the frontal scar, the second proximal one, being shallow and often barely recognizable, is situated about half way between the latter and the AMS-field.

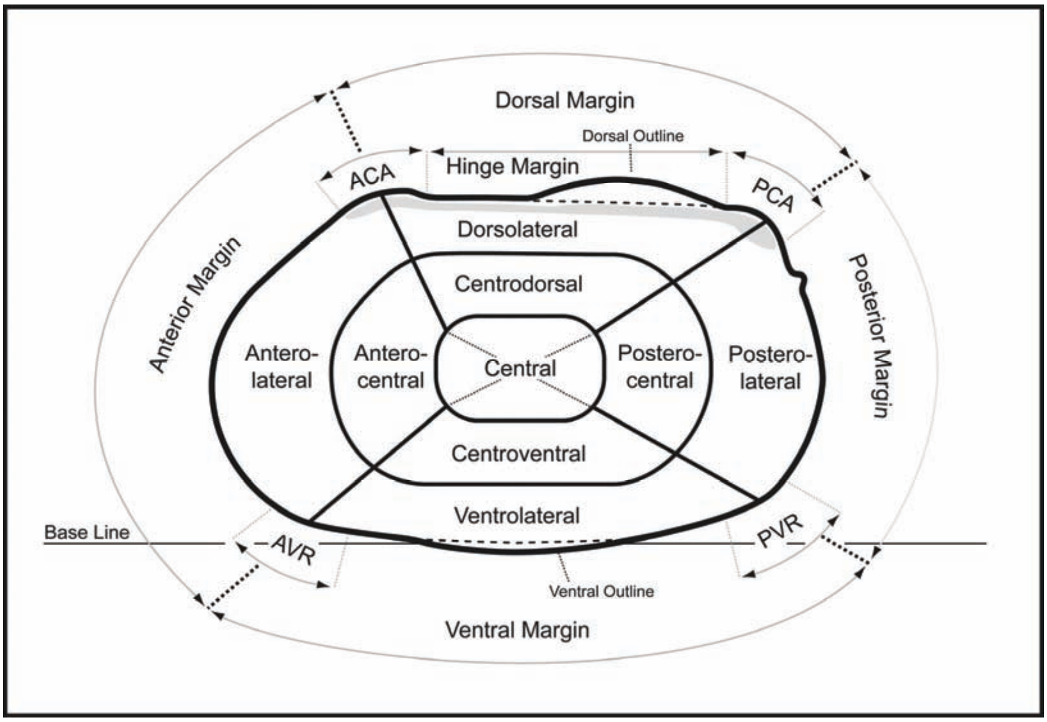


Fig. 3. Terminology for outline, outline regions, margins and carapace regions of the genus *Theriosynoecum* (exemplified on *T. fittoni*) as proposed and defined in this paper. Carapace regions modified based on Kesling (1951). ACA: Anterior Cardinal Angle. AVR: Anteroventral region. PCA: Posterior Cardinal Angle. PVR: Posteroventral region.

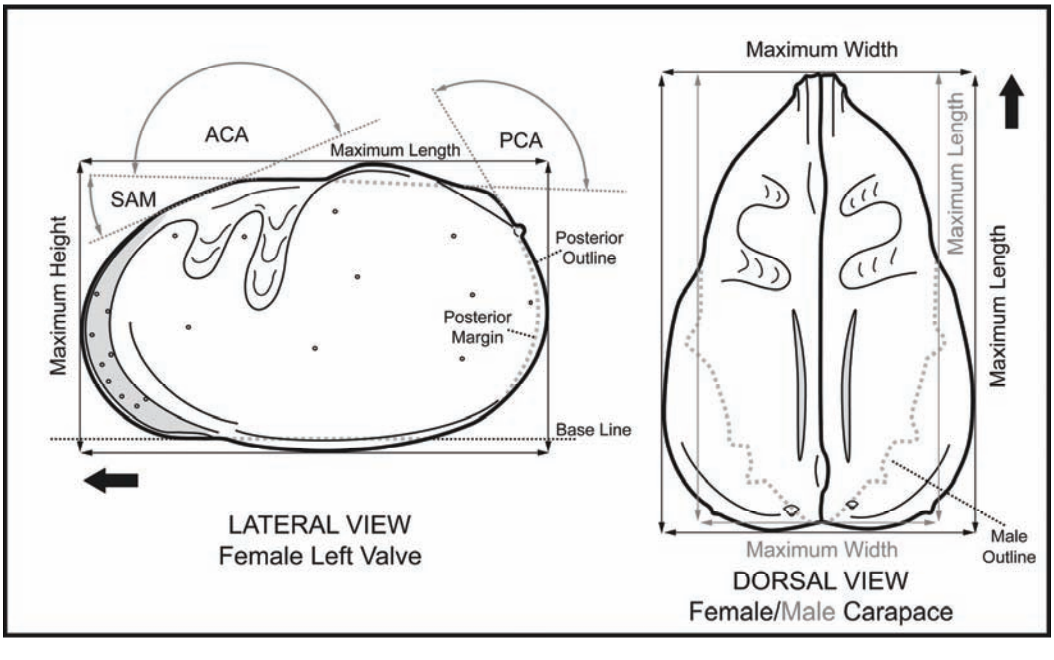


Fig. 4. Illustration of methods of measurement in relation to the carapace orientation. Note that parameters of length/height/width exclude ornamentation elements but include carapace protrusions, i.e. where not congruent, the outline defines the outer delimitation prior to the margins. The ventral margin is oriented along the base line. ACA: Anterior Cardinal Angle. PCA: Posterior Cardinal Angle. SAM: Inclination of the Straight dorsal part of the Anterior Margin.

Dimorphism: Strong sexual dimorphism, => *precocious sexual dimorphism* (see glossary and item directly below) also occurs. Males almost always tuberculate, with a posterolateral tuberculation pattern (Fig. 6/E) that sometimes can be diagnostic at species level. Males more elongate in lateral and more elongate-elliptical in dorsal view than the females. Also, the overall length of males usually tends to be somewhat bigger in comparison to females, but the maximum size is subject to high variability and partially controlled by environmental factors. Adult females usually with moderate to strong posterolateral inflation (brood pouches).

Precocious sexual dimorphism: It has to be considered that "precocious sexual dimorphism" (sensu Whatley and Stephens 1977) or "preadult sexual dimorphism" (sensu Rohr 1979) may occur in A-1 and A-2 or earlier instars, even though not as strongly as in adults. Following Whatley and Stephens (1977, p. 89), "... the term precocious sexual dimorphism as used here, does not in any way imply precocious sexual maturity". The authors (op. cit.) give examples for fossil (Bathonian of Oxfordshire, England) and recent podocopid (Cytheroidea) taxa and differ between 'protomales' and 'protofemales' as well as male and female lineages back to the A-5 stage in some cases.

Rohr (1979) demonstrated "preadult sexual dimorphism" in the cytheroid fossil species *Bisulcocypris aveyronensis* Rohr 1976 (recte *Theriosynoecum aveyronensis*) from the Bathonian of the Grands Causses, southern France, and the recent species *Cyprideis torosa* (Jones 1850), based on and supported by statistical analyses of the length-width (L/W) and length-height (L/H) coefficients. For *B. aveyronensis*, Rohr (op. cit.) showed high size variabilities, strongest in adults, and distinct sexual dimorphic features in the A-1 and A-2 instars: besides the higher L/W and lower L/H relation of 'protomales' (sensu Whatley and Stephens, 1977), i.e. that they are more elongate in lateral and dorsal view than 'protofemales', representatives of the male lineage generally have a stronger ornamentation (local ornamentation elements, particularly => *tuberculation* as defined herein) as well as a more strongly developed 'reticulation' (reticulation-like => *punctation* as defined herein, area-wide ornamentation elements). Rohr (1979) also states that, in contrast to his own earlier considerations (Rohr 1976), preadult sexual dimorphism is not connected with the environmental setting (salinity sensu lato in particular).

In summary, precocious/preadult sexual dimorphism is common in *Theriosynoecum* (e.g. *Theriosynoecum pahasapensis* herein, Pl. 3, Figs. 11-19) and often easily noticeable because of the strong differences in tuberculation and lateral as well as dorsal outlines. It seems possible to distinguish the male and female lineages, from the A-2 instar onwards definitely, possibly much more earlier. The maximum size of ontogenetic stages can vary to a great extent, particularly in adult stages (Rohr 1979), related to environmental factors. Thus, in contrast to the statement of Sohn and Anderson (1964, p. 82) the size of an individual alone does not seem to be a proper parameter to recognize certain (later) growth stages of representatives of *Theriosynoecum* Branson, especially when there are not enough specimens available. Other characters to determine instars or growth stages with adequate accuracy are given right below (see item "general trends in ontogeny"). Emphasis is placed on their applicability to single specimens also.

General trends in ontogeny: Instars of *Theriosynoecum* can be identified by several characteristic features and trends. The younger the instars, the thinner is the shell, the lesser is the development of the sulci and the narrower is the free inner lamella. The carapace outline and margins are coincident in younger instars of both sexual lineages (see discussion of precocious sexual dimorphism above), because of the lesser lateral inflation, especially apparent in females. Also, the surface characters seem to be coarser and more towards a reticulation (sensu Sames herein). This is an optical illusion caused by the fact that the diameter of the single elements of the surface characters (puncta) is the same as in adults, but they are fewer in number and closer to each other since the carapace surface is much smaller.

Moreover, the dorsal and ventral margins are not parallel, because the posterior end is lower than the anterior one and thus, starting from the ventral margin as base line orientation, the dorsal margin is inclined towards posterior end. Therefore, the maximum height is shifted to a position well anterior of half the carapace length. This is probably the most easily recognizable feature for the identification of juveniles in *Theriosynoecum*.

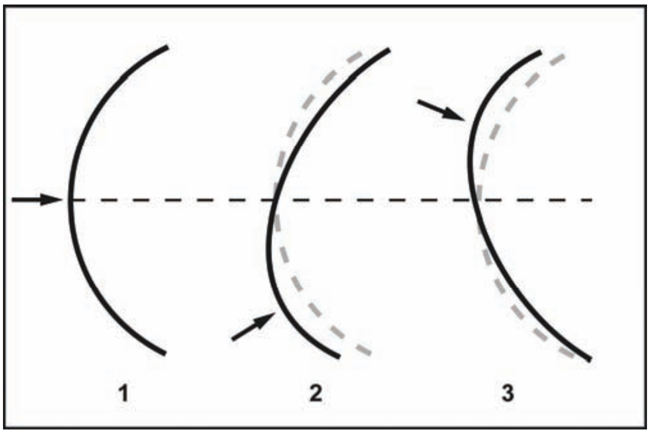


Fig. 5. Terminology of curvature of anterior and posterior ostracod carapace margins after Lüttig (1962), arrows indicate the area of maximum curvature. These very useful terms are adopted here and translated into English: **1.** equicurvate (in German "äquikurvat") means equally rounded, **2.** infracurvate (in German "infrakurvat") stands for narrower rounded towards venter, **3.** supracurvate (in German "suprakurvat") defines a dorsally narrower rounded margin.

Relative valve size: The valve size relation of *Theriosynoecum*, and the genera synonymized with it herein, is 'normal' (LV>RV, for elucidation see also => *inverse* in the glossary). The fact that the flange of the RV can overlap the LV along the hinge margin, together with the complex structure of the anterior and posterior margins, may have led some authors to conclude an inverse valve size relation in *Theriosynoecum*, when they were analyzing the dorsal view and had no single valves or internal views available.

The true valve size relation can be determined with certainty by the hinge elements (the hinge bar and the anterior and posterior sockets are situated in the larger valve, the anterior and posterior teeth are in the smaller valve—but there might be exceptional forms with => *inverse hinge*, e.g. "*Bisulcocypris*" *pricei* Pinto and Sanguinetti 1958, recte *Theriosynoecum pricei*)—or, if no internal view is available, by the tongue-like convex section of the ventral margin below the S2-sulcus, overlapping the smaller valve (there is also a similar element in the smaller valve at the same position, but it lies internally due to being totally enveloped by that of the larger valve!). On the larger LV, the tongue-like lateral projection (convex overlap) is formed by the flange; on the smaller RV it seems to be a prolongation of the selvage (Fig. 6/C and F).

Hinge: The hinge in *Theriosynoecum* (see Fig. 8, ad Pl. 1, Fig. 14 herein by way of example) is tripartite in general: merodont and of lophodont type. All elements are smooth; the anterior element is a more or less long tooth-like ridge in the larger LV, with a corresponding groove (socket) in the RV, not necessarily wider than the median element; the posterior element is a swollen, elliptic to ovate knob-like tooth which is much shorter than its anterior counterpart, fitting into the posterior socket of the smaller RV. Both terminal elements are inclined downwards (20-45°) in relation to the median element. The median hinge element is developed as a smooth => *hinge bar* in the smaller RV, being either simple or bipartite, that fits into a corresponding groove in the LV.

The designation of the hinge applied here follows the terminology of the ostracod Treatise (Scott 1961), Hartmann (1966-1989, p. 95-96) and Gründel (1974): the hinge in *Theriosynoecum* belongs to the merodont group of hinges (i.e., the main teeth of the terminal elements are located in one valve only), and is of lophodont type (i.e., the larger valve with the terminal sockets and the hinge bar, the smaller valve with the terminal teeth and a median groove).

The bipartition of the median hinge element in some species, used as one characteristic feature to distinguish *Bisulcocypris* (with simple median element) from *Theriosynoecum* (with bipartite median element) by some authors, e.g. Helmdach 1974a, p. 228 (see also discussion directly below), seems to be caused by a contortion of the posterior part of the hinge bar (see anterior and posterior position of the edge in Fig. 8). The inner margin in that area looks like being rotated upwards, thus forming an edge on the posterior hinge bar. With the hinge bar being rotated by 90°, its broad flanks now define its height, not its width, and, therefore, it is considerably narrower. This structure might be connected with the extension of height on the posterior end of the carapace, often associated with stronger ventrodorsal overreach of the carapace, and therefore an effect of alteration in the anatomy of the viscera and/or reproductive organs.

As for the anterior hinge element, its shape and extension causes and defines the length of the straight dorsal part of the anterior margin.

Discussion: The separation of the genera *Bisulcocypris* Pinto and Sanguinetti, *Dryelba* Sohn and *Theriosynoecum* Branson based on either the ornamentation (Pinto and Sanguinetti 1962 base their diagnoses and differential diagnoses of otherwise similar forms mainly or explicitly on some => *local ornamentation elements* sensu Sames herein), or the bipartite median hinge element as well as the existence of an accommodation groove (e.g. Pinto and Sanguinetti 1962, Sohn 1982, Schudack 1994), is no longer considered reliable (refer to Chapter 2 herein also). Moreover, the type species chosen by Pinto and Sanguinetti (1962), "*Bisulcocypris*" *pricei* Pinto and Saguinetti 1958 (recte *Theriosynoecum pricei*) is the only known representative of this group with an => *inverse hinge* and therefore not adequate as type species for the genus.

Since all mentioned genera share most other carapace characters and occur virtually worldwide with about the same stratigraphic range and none of them geographically isolated, they are synonymized herein under the oldest valid name *Theriosynoecum* Branson 1936. *Theriosynecum* Mandelstam in Galeeva 1955 is just an error in spelling.

The genus *Dryelba* Sohn 1982 is considered to be invalid for the following reasons: Sohn (op. cit.) erected the new family Dryelbidae, including *Theriosynoecum* as well as his new genus *Dryelba*. He again based his differentiation between these two on local ornamentation elements (sensu Sames herein), nor does he differentiate between true => *nodes* (following the definition herein, only appearing in *Theriosynoecum* after Sohn's 1982 concept) and => *node-like tubercles* or discuss the taxonomic position of *Bisulcocypris* as well. Moreover, he (op. cit.) lists many taxa either belonging to *Theriosynoecum* or *Dryelba* in his view, but most of these are marked as "to be restudied". At the very end of his paper Sohn (op. cit.) also states that his concept disagrees with that of Colin and Danielopol (1980), a paper which he had received after the completion of his manuscript, and that "... only time will tell as to who is on the right track" (Sohn 1982, p. 315). From the current point of view, the arguments, i.e. diagnostic characters chosen by Sohn, justify neither the erection of a new family nor the erection of an additional genus separated from *Theriosynoecum* anymore. All these characters are either ecophenotypic, ontogenetic or intrageneric variations (see discussion of => *ornamentation* in the glossary herein).

Stratigraphic range: Middle Jurassic (Upper Bajocian?, Bathonian) to Early Cretaceous (middle? Albian), questionably Late Cretaceous (Cenomanian).

Remarks: The oldest known report of *Theriosynoecum* is that of *T. tenuimarginata* (Oertli), Oertli in Bizon et al. (1956), from the 'Bathonian' of the Paris Basin near Poitou, France. The horizon from which this material came is now dated as (or older than) Late Bajocian on ammonite evidence, in that it is overlain by a level containing *Parkinsonia parkinsoni* (Colin and Carbonel 1996, and Colin pers. comm., October 1998).

In North America, an occurrence up to at least the Aptian to Albian of Alberta, Canada (Loranger 1951, 1954; geochronologic age of the Blairmore Group is 115-103 Ma following Ross et al. 2005) is given by true representatives of *Theriosynoecum*: i.e. *T. angularis* (Peck 1941), *T. persulcata* (Peck 1941), *T. provostensis* (Loranger 1951), *T. crossfieldensis* (Loranger 1951) and *T. ramriverensis* (Loranger 1951). These taxa were formerly designated as representatives of *Metacypris* or of '*Bisulcocypris*' or '*Dryelba*' by different authors (e.g. Loranger 1951, 1954, Pinto and Sanguinetti 1962, Swain 1999) but are integrated in *Theriosynoecum* here instead of *Metacypris* due to their strongly developed (two pairs of) sulci and => *surface characters* (sensu Sames herein), whereas *Bisulcocypris* Pinto and Sanguinetti 1958 as well as *Dryelba* Sohn 1982 are considered junior synonyms of *Theriosynoecum* Branson 1936 (for details see Chapter 2 'Previous works and aims' and the discussion for *Theriosynoecum* above). However, some taxa (particularly *Theriosynoecum angularis*) might be closely related to—or even be—the ancestor of the *Metacypris* lineage.

The stratigraphic distribution of representatives of *Theriosynoecum* Branson 1936 on other continents is as follows (supported by recent references): A distribution up to Aptian-Albian times is known for South America (e.g. Do Carmo et al. 2004), (West-)Africa (e.g. Bate 1999, Colin and Dépêche 1997), in Europe up to early Aptian (Wilkinson 2008). A lower Cenomanian occurrence is given by Pojarkova (1984) for northeastern Central Asia (Fergana Depression, near Kokand and Osh, former USSR, now partially Tadzhikistan, Uzbekistan and Kyrgyzstan), but the article lacks pictures or descriptions of the ostracods, and thus it cannot be verified taxonomically whether the species mentioned really belong to *Theriosynoecum*. These might be representatives of *Metacypris*. However, a longer occurrence of such taxa does not seem impossible in Central Asia because of the longlasting continental paleoenvironment in large areas of this continent during the Mesozoic.

Concerning the successive Aptian/Albian extinction of Timiriaseviinae within the North American Western Interior foreland basin, *Theriosynoecum* in particular, the major causes seem to have been "Mid-Cretaceous" marine transgressions and climatic changes. For a more detailed discussion, see chapter 6.2 of this paper.

Geographic distribution: Worldwide, except for Australia and Antarctica.

Paleoecology: Salinity: (Classification of brackish waters according to the Venice System as published by Oertli 1964): Freshwater (Kilenyi and Allen 1968), freshwater, oligo- to mesohaline (0 to ~7‰) after Brenner (1976), freshwater (Neale 1988), limnic to mesohaline (up to ~7‰) according to Carbonel et al. (1988), freshwater (0-0.5‰) after Mette (1997), indicative for higher alkalinity (15-30mEq/L) by tentative analogue comparison with related modern representatives of *Gomphocythere* and *Metacypris* (Colin and Dépêche 1997), freshwater – more alkaline (carbonate + bicarbonate) waters (Horne 2002).

Habitat/life mode: Nonmarine permanent water bodies. Benthic, crawling and burrowing, without swimming capability (e.g. Horne 2002).

Fig. 6. (see following page): Terminology of the valve and carapace characters of the genus *Theriosynoecum* (exemplified on *T. fittoni*) as proposed and defined in this paper. Lateral view given of left valve only, because it is very similar to right valve. LV: left valve, RV: right valve, S1: front sulcus, S2: back sulcus. **A:** left valve in lateral view, dotted line: valve margins. **B:** Internal view of left valve, AMS: Adductor muscle scars, FS: frontal scar, MS: mandibular scar(s), FIL: Free inner lamella, IM: inner margin. **C:** ventral view of female carapace, dotted line: ventral outline of male dimorph. **D:** dorsal view of female carapace, dotted line: dorsal outline of male dimorph. **E:** valve ornamentation patterns (as used and defined herein). Dotted circles: small posterodorsal tubercles regularly occurring in most species, also on female dimorphs. Nos. 1 to 4 (black circles): main posterior tubercles (rarely node-like tubercles), nearly always occurring on male dimorphs, sometimes on female dimorphs also, 1-3: posterolateral row, 4: posterocentral tubercle, often less strongly developed than 1-3. 5-6: additional main tubercles, more infrequently developed. A1 to A3: anterior main tubercles, if occurring, then mostly swollen and developed as node-like tubercles. Small grey circles: anterolateral minor tubercles on or at the marginal area of the anterior laterally flattened marginal zone, typical for both sexes if occurring (see also Pl. 2, Fig. 2 herein). **F:** anteroventral margin internally, IM: inner margin, FIL: free inner lamella, LC: line of concrescence.

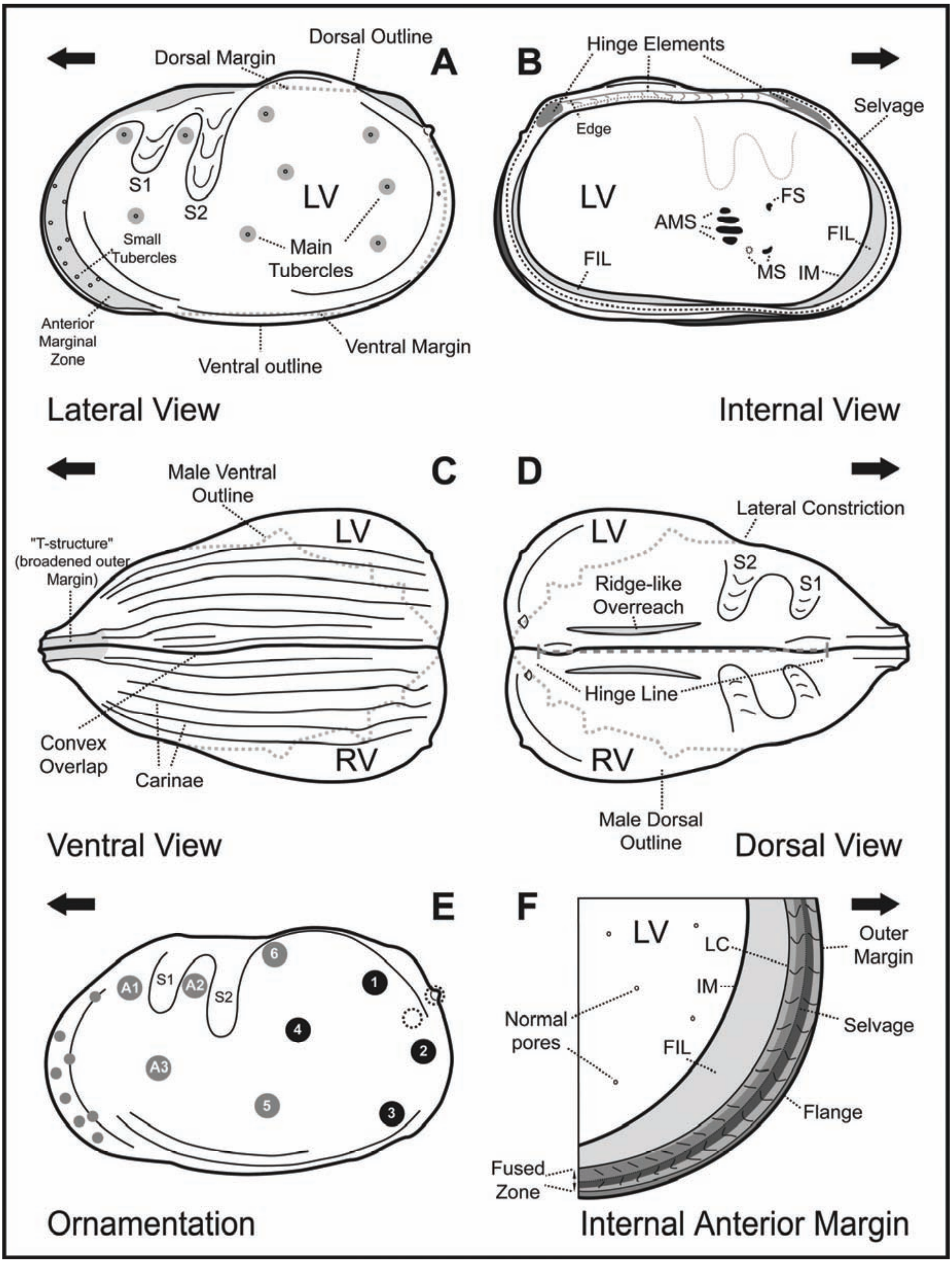

A
Dorsal Outline
Dorsal Margin
S1
S2
LV
Small Tubercles
Main Tubercles
Anterior Marginal Zone
Ventral outline
Ventral Margin
Lateral View
B
Hinge Elements
Selvage
Edge
LV
FS
AMS
FIL
FIL
MS
IM
Internal View
C
Male Ventral Outline
LV
"T-structure" (broadened outer Margin)
Convex Overlap
Carinae
RV
Ventral View
D
Lateral Constriction
LV
S2
S1
Ridge-like Overreach
Hinge Line
RV
Male Dorsal Outline
Dorsal View
E
S1
A1
A2
S2
6
1
4
2
A3
5
3
Ornamentation
F
LV
LC
Outer Margin
IM
Normal pores
Selvage
FIL
Flange
Fused Zone
Internal Anterior Margin

Fig. 6

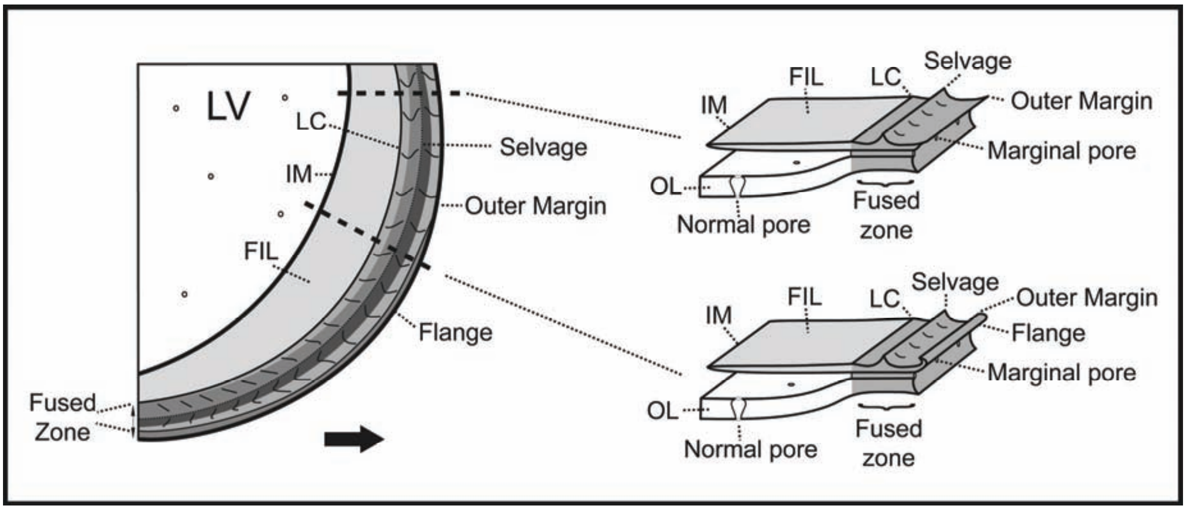


Fig. 7. Section through anterior marginal area of a left valve of *Theriosynoecum*. The more anteroventral section shows the inwards contorted outer margin that forms a flange in this lower part of the valve. FIL: free inner lamella, IM: inner margin, LC: line of concrescence, OL: outer lamella.

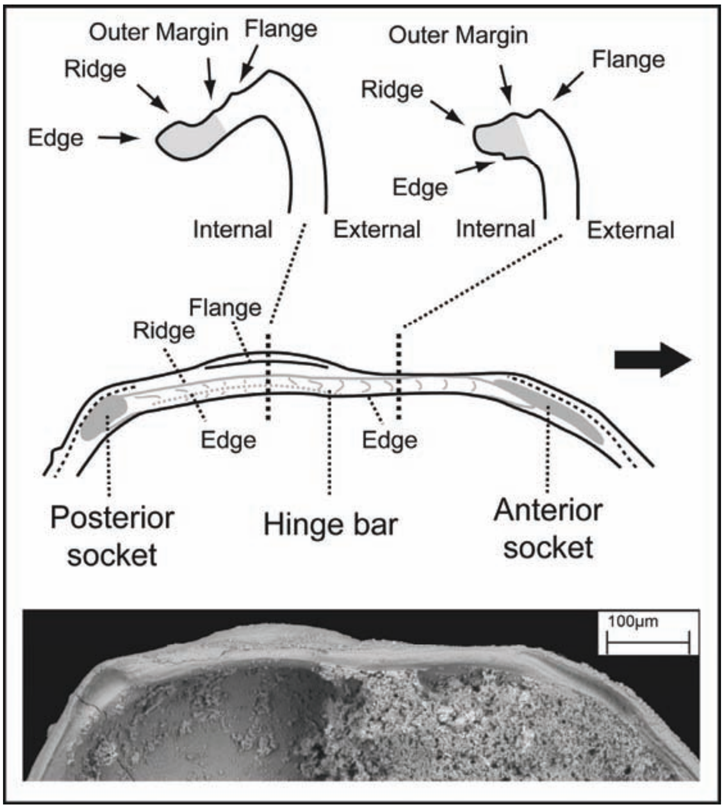


Fig. 8. Section through hinge area of a left valve of *Theriosynoecum fittoni* with bipartite median hinge element. The posterior part of the hinge bar is contorted upwards about 90°.

5.3. Key to the described species in *Theriosynoecum*:

Females:

1a	Lateral outline piriform, anterior marginal zone barely developed	2
1b	Lateral outline not piriform, broad anterior marginal zone	3
2a	Posterior cardinal angle almost covered in lateral view, broad S2-sulcus	4a
2b	Posterior cardinal angle visible, S1- and S2-sulcus moderately wide	4b
3a	Strong, ridge-like posterior dorsolateral overreach	5a or 5c
3b	Posterolateral cusp, weak posterior dorsolateral overreach, elongate	5b

4a	Strong posteroventral overreach, strongly cordiform in dorsal view	*T. forbesii*
4b	Weak posteroventral overreach, elogated piriform in dorsal view	*T. verrucosa*
5a	Dorsal part of anterior marginal zone inclined about 45° or more, maximum height at 3/4 of length	*T. fittoni*
5b	Dorsal part of anterior marginal zone inclined less than 40°, around 35°	*T. pahasapensis*
5c	Maximum height at 4/5 of length	*T. alleni*

Males:

6a	Anterior marginal zone barely developed	7
6b	Anterior marginal zone well developed and broad	8
7a	Long straight dorsal part of anterior margin, inclined with about 35°	9a
7b	Moderately long straight dorsal part of anterior margin, inclined about 35-40°	9b
8a	Strong, ridge-like posterior dorsolateral overreach	10a or 10c
8b	Weak posterior dorsolateral overreach, elongate in lateral view	10b

9a	Strong ventrolateral overreach, broad S2-sulcus	*T. forbesii*
9b	Weak ventrolateral overreach, S1- and S2-sulcus moderately wide	*T. verrucosa*
10a	Moderately long and about 45° inclined dorsal part of anterior margin, maximum height at 3/4 of length	*T. fittoni*
10b	Long dorsal part of anterior margin inclined less than 40°, around 35°	*T. pahasapensis*
10c	Maximum height at 4/5 of length	*T. alleni*

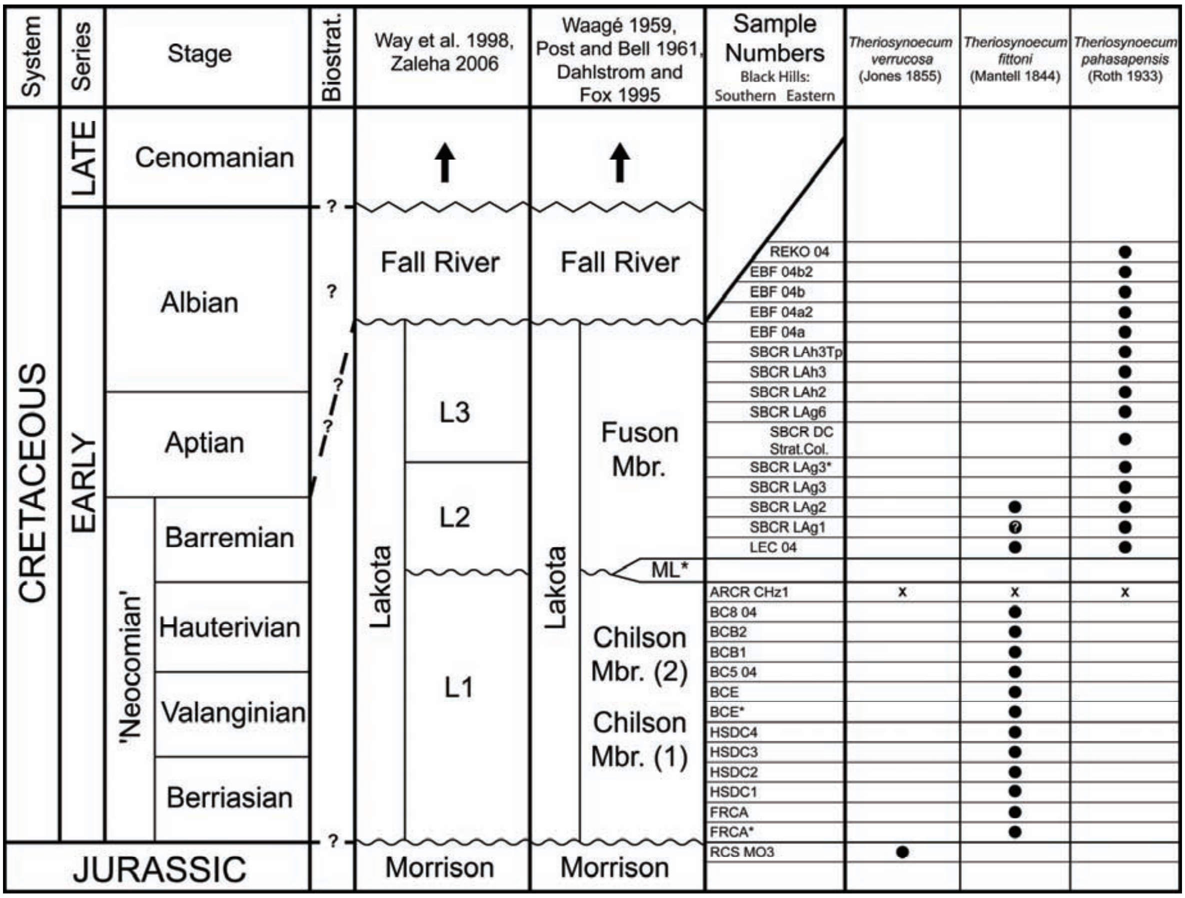


Fig. 9. Sketch and overview of the stratigraphic distribution and occurrence of representatives of *Theriosynoecum* in the Lakota Formation, eastern and southern Black Hills area, South Dakota. Preliminary overview—no true correlation intended here! The stratigraphic succession of samples from different localities is only an approximation and may be subject to change when all faunal elements have been analyzed. A biostratigraphic interpretation and correlation based on several taxa is beyond the scope of this paper and will be given in a separate publication. As for the geographic distribution of the Minnewaste Limestone Member (ML*) refer to Fig. 2 herein. For elucidation of the lithostratigraphic correlation of the newer and older terminology refer to Zaleha 2006, p. 888-889. Section labels: RCS: Red Canyon Section (Fig. 2, loc. 4); HSDC: Horse Sanctuary/Devil's Canyon (Fig. 2, loc. 2); BC (BCE, BCB): Buck Canyon (Fig. 2, loc. 1); ARCR: Angell Ranch/Cheyenne River (Fig. 2, loc. 5); LEC: Little Elk Creek (Fig. 2, loc. 6; SBCR: Stage Barn Canyon Road (Fig. 2, loc. 8); EBF: East of road to Belle Fourche (Fig. 2, loc. 7), REKO: Boxelder Creek east of Blackhawk (Fig. 2, loc. 9, sample taken by Reko Hargrave 2004). Black circle: taxon present, black circle with question mark: taxon questionable in this sample, X: taxon absent.

5.4. Description and taxonomy of the species

Theriosynoecum alleni (Pinto and Sanguinetti 1962)

(Pl. 5, Figs. 1-3)

?	1940	*Gomphocythere pahasapensis* (Roth) – Martin, p. 340, pl. 6, figs. 95-97; pl. 7, figs. 98-100
pars*	1962	*Bisulcocypris alleni* sp. nov. – Pinto and Sanguinetti, pl. 9, figs. 1-8, 11-16; pl. 16, figs. 4a-d
?	1962	*Bisulcocypris alleni* sp. nov. – Pinto and Sanguinetti, pl. 9, figs. 9a-b, 10
non	1981	*Theriosynoecum alleni* (Pinto and Sanguinetti) – Colin et al., pl. 11.6, fig. 1
	1985	*Theriosynoecum alleni* (Pinto and Sanguinetti) – Anderson, p. 37, pl. 7, fig. 15

Material: No own material from North America. Specimens discussed comprise material from BGS (F.W. Anderson collection) and from the literature.

Dimensions: Overall length: 0.87-1.20
As given in the literature (various references):

Females	L: 0.87-1.10	H: 0.55-0.58	W: n/a
Males	L: 0.98-1.20	H: ~0.60	W: n/a

Type locality and horizon: Lower Wadhurst Formation, Hastings Group, Wealden Supergroup, Lower Cretaceous, Valanginian(?), Gate Wood, Beckley, near Rye, East Sussex, UK.

Holotype: M.P., U.R.G.S., No. MP-0-50A, complete male carapace [with atypically developed (swelling?) anterior cardinal angle].

Diagnosis: Lateral outline rounded subrhomboidal, relatively short anterior part in front of posterolateral inflation. Maximum height at 4/5 of length. Posterior half of hinge margin hidden in both sexes in lateral view, covered by moderately to strongly overreaching ridge-like dorsal part of the carapace's postero-lateral inflation. Weak convex overreach of ventrolateral carapace inflation over ventral margin. Dorsal straight part of anterior margin short to moderate, inclined about 45°, with continuous transition into anterior cardinal angle. Cardinal angles distinct. Broad anterior marginal zone. With or without anterolateral node-like tubercles. Males usually with posterolateral tubercles (Nos. 1-4, sometimes also Nos. 5 and 6 developed, see Fig. 6/E), females usually without, rarely with tubercles Nos. 1 and 6 only (Fig. 6/E).

Description: Carapace shape: Small to medium sized. Carapace rounded subrhomboidal in lateral view. Maximum length at or slightly below half height, maximum height at 4/5 of length, maximum width in females at 4/5 of length, somewhat more anterior in males, at 3/4 of length. LV>RV, subequivalve. LV barely recognizable overlapping the RV along entire margin, except for the somewhat stronger overlap of the LV's tongue-like ventral segment and the hinge margin, where the flange of the smaller RV's hinge margin overlaps the LV (see also Fig. 8 for illustration). LV very weakly or not overreaching the RV.

Anterior margin infracurvate with a short straight to slightly concave dorsal part passing into the anterior cardinal angle, inclined about 45°. Anterior marginal zone moderately broad with up to 80µm. Posterior margin slightly supracurvate and straightly passing into posterior cardinal angle in males, in females being not coincident with posterior lateral outline—due to overreaching brood pouches—which is thus more convex, about equicurvate and slightly concave passing into the posterior cardinal angle. Both anterior and posterior margins of about equal width. Dorsal margin nearly straight, slightly wavy, i.e. concave anteriorly and convex posteriorly, cardinal angles slightly elevated above it. Dorsal lateral outline differing in being strongly convex on the posterior half of hinge margin, hiding it in both sexes through a ridge-like overreaching dorsal part of the carapace's posterolateral inflation. Ventral margin generally straight with a small concave segment just in front of half length, below the S2-sulcus (i.e., also below the adductor muscle scar field), the concavity incising more deeply in the smaller RV. Ventral lateral outline straight to weakly convex in both sexes through overreaching ventrolateral parts of the carapace, somewhat stronger as well as also affecting the posteroventral region in the female dimorph. Dorsal and ventral margins nearly parallel. Both cardinal angles usually well noticeable, but not always completely visible and mostly not exactly in line with the hinge margin. Anterior cardinal angle broad and well rounded, about 135°-140°. Posterior cardinal angle more conspicuous and moderately rounded, more distinctive on the LV, about 120°, in females weakly exposed in lateral view because of the strong posterolateral inflation.

Anteriorly with the characteristic two dorsolateral sulci and a resulting lobe in between, all moderately developed; expressed internally with very slight valve deformations only. S2-sulcus somewhat deeper and longer, extending from slightly below dorsal margin downwards to about half maximum height. On the smaller RV (visible in dorsal view) its beginning is considerably closer to the hinge line than on the larger LV. S1-sulcus shorter than the S2 one, extending from slightly below dorsal margin downwards to somewhere between 3/4 and 2/3 of maximum carapace height. S1-sulcus not as deeply incising as S2-sulcus. Like the S2-sulcus, the S1-sulcus on the smaller RV begins closer to the hinge line than its counterpart on the larger LV.

Carapace of males in dorsal view oblate-elliptic, slightly flattened and concave laterally at position of the S2-sulcus, rounded posteriorly and acute anteriorly. Anterior end also flattened laterally. Female dimorph piriform in dorsal view with moderately strong inflated posterior end (brood pouches) and constricted laterally at the position of the S2-sulcus. Shape of anterior end same as in males. Both sexes with distinct angularity in outline at position of the S1-sulcus, obtuse-angled with about 145° (Pl. 5, Fig. 1a, 2a). The posterior dorsolateral ridge-like protrusion forms a groove around the posterior part of the hinge margin. Both sexes showing a slight convex overlap of LV over RV at both cardinal angles. Along hinge margin, the flange of the RV slightly overlaps the LV fitting into a shallow accommodation groove. Therefore, the hinge line is sinuous.

Moderate overlap of the larger LV in ventral view with a more or less distinct convex segment at about 2/5 of length—below the S2-sulcus. Anterior fifth ventrally forming a broad flat outer margin with sharp lateral edges and a lateral furrow above it (a "T-structure"), running parallel to the margin.

<u>Ornamentation:</u>

<u>1. Area-wide ornamentation elements/surface characters:</u> Carapace of both sexes regularly punctate, puncta more or less shallow, between 20 and 40µm in diameter. Puncta closer to the outline arranged in concentric rows running more or less parallel to the anterior, posterior and ventral margins. In marginal areas, ventrally, as well as in anteroventral and posterocentral regions up to about half height, the rows of puncta are separated by carinae. Puncta in between the carinae elongated in lateral direction and their margins deformed, thus ventrally being rectangular to quadrate. Punctation always seems to cover the anterior marginal zone.

<u>2. Local ornamentation elements:</u> Tuberculation common, especially in male dimorphs the posterolateral tubercles are often well developed, as well as in instars. Main tuberculation pattern in males consisting of four posterolateral tubercles (Fig. 6/E, Nos. 1 to 4). One posterocentral tuberculum

(No. 4), not always developed, the other three (Nos. 1, 2, 3) being located along the virtual line separating the posterocentral and posterolateral (Fig. 3) carapace area. Tuberculum No. 2 always below No. 4, if developed. Two additional larger tubercles occurring regularly but not always: a dorsolateral one (No. 6, see Fig. 6/E) and a centroventral one (No. 5, cf. Fig. 6/E), both at about half length of carapace. Females usually without posterolateral tubercles except No. 2. Both sexes usually with two pairs of small posterolateral tubercles, one directly behind the posterior cardinal angle the other at half height (dotted circles in Fig. 6/E).

Three anterior tubercles can occur in both sexes (Fig. 6/E, Nos. A1 to A3), often developed as node-like tubercles below (A3), on (A2) the lobe between the sulci, and in front of the S1-sulcus (No. A1). Both sexes also bearing anterolateral rows of poorly developed tubercles parallel to the anterior margin (Fig. 6/E, small grey circles), most of them in the anteroventral part of anterolateral part of carapace.

<u>Internal characters:</u> (Not well known and given here as partially incorrectly (i.e. hinge) figured but not described in Pinto and Sanguinetti 1962, pl. 9, figs. 8a, 9a). All hinge elements smooth. Median element forming a ridge on the larger LV (it is impossible to deduce from the figures with certainty if the median element is divided into two parts, see discussion of the species below). Anterior tooth on smaller RV narrow with sharp edge, posterior tooth broad, ovate and well rounded, both fitting into a matching socket of the larger LV.

Free inner lamella of moderate width anteriorly, narrower posteriorly, vestibuli developed accordingly. Line of concrescence and inner margin only coinciding dorsally. Outer margin displaced inwards and thus forming a flange along anterior, posterior and ventral margins, particularly strong at posteroventral region, somewhat more in the smaller RV. Selvage (cf. Fig. 7) of larger LV fitting into a matching groove between selvage and outer margin/flange of the smaller RV and enabling the animal to close the valves tightly. Ventral margin of both valves with a convex tongue-like excrescence below the adductor muscle scars/S2-sulcus and above a concavity of the ventral margin, the one of the larger LV overlapping the one of the RV and fitting into the stronger ventral margin's concavity of the RV.

<u>Muscle scar pattern:</u> (Not well known and given here as figured but not described in Pinto and Sanguinetti 1962, pl. 9, figs. 8a, 9a) as diagnostic for the genus. Central muscle scar field consisting of four more or less elongated-elliptic scars, the upper- and lowermost being about half the size of the middle ones.

<u>Morphologic variation:</u> (not much data available) Variation mainly concerns occurrence and intensity in development of local ornamentation elements, especially nodes and node-like tubercles which are also very common in juveniles. Specimens of both sexes can develop strong anterior node-like tubercles (A1 to A3, cf. Fig 6/E). The anterior cardinal angle can be swollen (see holotype, Pinto and Sanguinetti 1962, refigured here in Pl. 5, Fig. 1a, b).

<u>Ontogenetic variation:</u> The general outline of instars of *Theriosynoecum alleni* (cf. Pinto and Sanguinetti 1962, pl. 9, figs. 2-5, 10-16) rounded-oblong, slightly tapering towards posterior end, and ventral and posterior lateral outlines and margins mostly coincident. Posteror margin lower than the anterior one and slightly infrarcurvate. Hinge margin inclined towards posterior end and thus, ventral and dorsal margins not parallel. Dorsal margin nearly coinciding with dorsal lateral outline except for a slight overreach of the elevated ridge-like area ventrodorsally, behind mid-length. Unlike most other species but similar to *T. fittoni*, this overreach remains noticeable also in earlier instars (A-3 to A-5?).

Dorsolateral sulci become the weaker with decreasing instar stage, and become covered by distorted surface characters, the latter then also being the case for the lobe in between the sulci. The anterior marginal zone becomes less noticeable with decreasing instar stage. Carapace of younger instars elliptic in dorsal view, only slightly more acute anteriorly than posteriorly.

Surface punctate, the pattern and size of puncta being the same as in adults, just fewer in number. Therefore, the pattern of the surface characters appears to be more coarse because of the smaller valve size, and also tends towards reticulation.

Precocious sexual dimorphism present. Tubercles and/or node-like tubercles present (although in part weakly developed) in both dimorphs, protomales as well as protofemales, but not as strong in their maximum development as known from some instars of *T. fittoni* (based on the few data available). Mostly, the pattern of tuberculation follows that of the male adults, sometimes anterior tubercles/node-like tubercles (Fig. 6/E, Nos. A1 to A3) occur.

Dimorphism: Strong sexual dimorphism. Lateral outline of both sexes similar except for posterior and posteroventral regions where the outline of the female strongly differs from its margins. Males more elongate-subrhomboidal in lateral view. Posteroventral region in females completely covered through extreme inflation (brood pouches). Females with slightly concave transition of posterior lateral outline into posterior cardinal angle (overreach of brood pouches). Female dimorphs posteriorly much broader in dorsal view (piriform) with distinct constriction at the position of the posterior sulci caused by the brood pouches, males being more elliptic in dorsal view and laterally flattened. Males usually with at least tubercles Nos. 1-4 (Fig. 6/E).

Precocious sexual dimorphism occurring (at least to A-2 stage). Protomales with node-like tubercles, more elliptic in dorsal outline and with maximum width at 3/5 of length, protofemales also with node-like tubercles but the posterior ones usually not as strongly developed as in males, and subpiriform with maximum length at 4/5 of length (see Pinto and Sanguinetti 1962, pl. 9, figs. 10-16).

Discussion: General taxonomic remarks: *Theriosynoecum alleni* (Pinto and Sanguinetti 1962) is tentatively considered synonymous with *Theriosynoecum fittoni* because of the striking morphologic similarity (except for some local ornamentation elements). Yet the reason why the two species are not synonymized herein, although difficult to distinguish morphologically, is that there are some considerable problems remaining to be solved:

1) As far as documented, *T. alleni* is relatively endemic, only known from the Wealden Supergroup of England and questionably the 'NW German Wealden' of Europe.
2) *T. alleni* and *T. fittoni* are stratigraphically separated in the Wealden Supergroup of England, i.e. *T. alleni* reaches from Anderson's Hastings to Philpots faunicycles (cycles No. 41 to 61), then there is a gap (Anderson's Copyhold, No. 62, to Cuckfield, No. 67, faunicycles, and *T. fittoni* starts to appear with Anderson's Sevenoaks faunicycle No. 68 (Anderson 1985, fig. 4; Horne 1995, figs. 4 and 5). Note that in the zonation scheme of Horne (1995, fig. 4) his *T. alleni*-zone is longer than the actual range of the latter species!
3) Making *T. alleni* a junior synonym of *T. fittoni* would imply that the latter species lived for about 15 Ma; for an ostracod species, this is a long lifetime that has to be justified with good arguments.
4) Information about the internal features is sparse. Although Pinto and Sanguinetti (1962, pl. 9, figs. 8a and 9a) figure two internal views (retouched photographs?), they give no description of these, and the information that can be deduced from the figures is sparse, precise and partially conflicting, particularly regarding the median hinge element. In their generic description for '*Bisulcocypris*', Pinto and Sanguinetti (1962, p. 38) describe the hinge bar as being straight, which seems also to be the case in their illustration of an internal view of a LV of *T. alleni* (op. cit., pl. 9, fig. 9a). However, the illustration of the right valve (op. cit., pl. 9, fig. 8a) shows a strong bipartition and, strangely, a complete separation of the anterior and posterior part of the median groove.
5) It should be noted that the lithostratigraphy given by Pinto and Sanguinetti (1962) for the occurrence of *T. alleni* is most probably right, but cannot be retraced since the specimens were

not collected by the authors themselves (but by its eponym instead: Prof. P. Allen, University of Reading, England, UK), and no stratigraphic section is given or cited.

For the moment, the taxonomic and stratigraphic data available are not sufficient (and partially conflicting) to legitimize a synonymization of the two species. Notwithstanding, both taxa are considered here to be closely related.

The hypothesis that both are synonymous should be tested in the future as follows: More material of *Theriosynoecum alleni* from the Hastings Group of the English Wealden Supergroup should be photographed in high-quality SEM pictures and compared to similar SEM pictures of specimens of *T. fittoni*. Morphometric methods (outline analysis, and landmarks for pore and tubercle position) may be used to support the visual taxonomic hypothesis and have only failed so far owing to the lack of sufficient measurable specimens. Some major problems arise from the fact that figures of specimens in older publications are of poor quality in part and certain features such as dorsal and hinge margins, straight dorsal part of anterior margin, and ventral margin are difficult to position due to overreaching ornamentation elements or carapace protrusions. Resulting from the poor quality of some figures in older literature, it is sometimes not possible to see whether the view of specimens is perpendicular to the lateral surface or dorsally or whether the specimens are somewhat inclined, which also influences the outline shown (see also Chapter 6.1 herein).

In summary, more taxonomically significant characters are needed to clearly define both species morphologically to support either a synonymization or separation of the two. Finding a section where *T. alleni* and *T. fittoni* either overlap in their stratigraphic occurrence or even finding them in one assemblage of the same layer/sample would be a strongly convincing argument for the synonymization of the two species. If *T. alleni* can be well defined morphologically and thus clearly separated from *T. fittoni*, its identification and stratigraphically separate occurrence outside the area where it is known (NW European Wealden Basin, England, UK, and NW Germany) would also support the hypothesis of separate species.

Discussion of the synonymy list: *Gomphocythere pahasapensis* (Roth) in Martin (1940, p. 340, pl. 6, figs. 95-97; pl. 7, figs. 98-100) from the Wealden of NW Germany is questionably included. Pinto and Sanguinetti (1962) include this species in *T. alleni* without explanation. Other authors (Wicher 1957, Grekoff 1958, Wolburg 1962) designate it as a subspecies of *T. fittoni*. The arguments of the latter authors are based on the occurrence and development of tubercles/node-like tubercles only. To the current author, a designation as *T. fittoni* seems to be the best solution. However, because of the taxonomic problems discussed above and for stratigraphic reasons, this species is (very) questionably included in *T. alleni* herein. The reason is that *G. pahasapensis* in Martin 1940 is reported to be distributed in the whole 'German Wealden' 4 by Wolburg 1962, the upper boundary of which correlates to the upper boundary of Anderson's Battle faunicycle (e.g. Anderson 1985, Horne 1995) following Hoedemaeker and Herngreen (2003). This would imply that the German species occurs below Horne's (1995) *T. alleni* subzone and demonstrates the taxonomic and/or stratigraphic problems remaining to be solved.

Two specimens of *Bisulcocypris alleni* figured in Pinto and Sanguinetti (1962, pl. 9, figs. 9a-b, 10) probably do not belong to *T. alleni*. These two specimens are much more elongate and have a very weak posterior dorsolateral overreach. Those specimens should more likely be designated as *T. angularis* Peck 1941, but this is not certain from the pictures.

T. alleni of Colin et al. (1981, pl. 11.6, fig. 1) is a juvenile (shortened posterior margin and distinctly unparallel ventral and dorsal margins, relatively coarse surface characters) of either *T. alleni* or *T. fittoni*, because it matches the diagnostic features, having distinct cardinal angles, the posterior dorsolateral elevation and overreach and the short straight dorsal part of the anterior margin, inclined about 45°. However, it is indicated with a question mark here because, based on the taxonomic information available, this specimen cannot be distinguished from juveniles of *T. fittoni*.

Theriosynoecum alleni in Anderson (1985) is an untypical, strongly nodose and reticulate specimen. However, in all other respect it matches the diagnostic characters of *T. alleni* and also matches the stratigraphic distribution in the English Wealden Supergroup. More specimens are necessary for a better assessment of the intraspecific variation.

Differential Diagnosis: The morphologic differentiation of *T. fittoni* and *T. alleni* is, as already mentioned (see general taxonomic remarks above), difficult to determine from the data available. In contrast to *T. fittoni*, the maximum height of *T. alleni* as defined by the posterior dorsolateral overreach lies more posteriorly, i.e. at 4/5 of length (instead of 3/4 in *T. fittoni*). In addition, the anterior marginal zone in *T. alleni* seems to be always covered by distinctly developed surface characters, whereas in *T. fittoni* these are very weak or the marginal zone is smooth. This, however, is not considered to be very significant taxonomically.

Female representatives of *T. forbesii* differ from those of *T. alleni* in their strongly piriform outline in *lateral* view and the elongated (but distinct) cordiform outline in dorsal view resulting from the more anterior (at 3/5 of length, instead of 4/5 or 5/6 like in the other representatives discussed) position of the maximum width. Both sexual dimorphs of *T. alleni* also have a broad anterior marginal zone, unlike *T. forbesii* which has a weak and narrow laterally flattened anterior marginal zone. *T. alleni* shows the strong posterior dorsolateral overlap being almost totally absent in *T. forbesii.*

T. pahasapensis is more elongate in lateral outline than *T. alleni*, its straight dorsal part of the anterior margin is longer and less inclined, and females of *T. pahasapensis* have the characteristic posterolateral cusp.

T. verrucosa has a very narrow anterior marginal zone, the dorsal straight part of the anterior margin is much less inclined. Moreover, *T. verrucosa* shows a weak posterior dorsolateral overreach, and the posterior cardinal angle is almost or completely covered in lateral view.

Paleoecology: As for the genus.

Faunal association: Not applicable here since the species is not known from North America thus far.

Stratigraphic and geographic distribution (Stratigraphic terms follow the most recent terminology available):

Europe:
+ Upper Ashdown Formation, Wadhurst and Tunbridge Wells formations, Hastings Group, Wealden Supergroup of England, most part of *T. alleni*-zone of Horne (1995) as equivalent to Anderson's (1985) Hastings to Philpots faunicycles (cycles Nos. 41 to 61, the whole *T. alleni*-zone of Horne 1995 is longer and reaches up to Anderson's Cuckfield faunicycle, cycle No. 67), Lower Cretaceous, Valanginian (after Hoedemaeker and Herngreen 2003), England, UK

Questionable occurrence:

Europe:
+ 'Wealden', Lower Cretaceous, NW Germany (Martin 1940); 'Wealden' 4, Lower Cretaceous (upper Berriasian to lowermost Valanginian after Hoedemaeker and Herngreen 2003), NW Germany (Wicher 1957, Wolburg 1962)—depending on the inclusion of '*Gomphocythere pahasapensis*' (Roth) of Martin (1940)

Stratigraphic range in North America: Not applicable.

Stratigraphic range outside North America: Europe: Valanginian, most parts of the *Theriosynoecum alleni*-zone (Horne 1995), equivalent to Anderson's (1985) Hastings to Philpots faunicycles (cycles Nos. 41 to 61), England, UK; questionably late Berriasian to earliest Valanginian, 'Wealden 4', NW Germany.

Theriosynoecum fittoni **(Mantell 1844)**

(Pl. 1, Figs. 1-10; Pl. 2, Figs. 1-15; Pl. 5, Figs. 1-16)

pars	1836	*Cypris tuberculata* Sowerby – in Fitton, p. 345, pl. 21, fig. 2a [non figs. 2b, c]
*	1844	*Cypris fittoni* Mantell, p. 545, pl. 119, fig. 2
	1878	*Cypridea*? *Fittoni* (Mantell) – Jones, p. 277
	1885	*Cythere fittoni* (Mantell) – Jones, p. 333
	1888a	*Metacypris fittoni* (Mantell) – Jones, p. 539
	1888b	*Metacypris fittoni* (Mantell) – Jones in Prestwich, p. 263, fig. 137a
	1940	*Gomphocythere berwickensis* sp. nov. – Martin, p. 344, textfigs. 1, 2, pl. 12, figs. 176-181
?	1955	*Theriosynoecum krystofovichi* sp. nov. – Mandelstam *in* Galeeva, p. 57, textfigs. 4a-e
	1957	*Gomphocythere fittoni fittoni* (Mantell) – Wicher, p. 270, pl. 2, figs. 2a-c, 3a-c
?	1957	*Gomphocythere fittoni berwickensis* (Martin) – Wicher, p. 270, pl. 2, figs. 4a-c, 5a-c
	1958	'*Metacypris*' *fittoni* (Mantell) – Grekoff, p. 26, pl. 2, fig. 19
	1962	*Bisulcocypris fittoni* (Mantell) emend. – Pinto and Sanguinetti, p. 70, pl. 2, figs. 6a-e; pl. 9, figs. 1-14; pl. 17, figs. 3°-d
	1962	*Bilsulcocypris fittoni* "*germanica*" – Wolburg, p. 222, pl. 32b, figs. 14a-b, 15
•	1962	*Bisulcocypris martini* sp. nov. – Pinto and Sanguinetti, p. 69, pl. 10, figs 5-9; pl. 17, figs. 2a-d
•	1962	'*Metacypris*' sp. 1 – Krömmelbein, p. 490, pl. 62, fig. 64a, b
	1964	*Theriosynoecum fittoni* (Mantell) – Sohn and Anderson, p. 73, pl. 15, figs. 1-35, text-figs. 1(part), 3
v	1966	*Gomphocythere fittoni* (Mantell) – Kneuper-Haack, p. 191, pl. 46, fig. 25
	1967	*Theriosynoecum fittoni* (Mantell) – Anderson, p. 258, pl. 18, fig. 78
?	1968	'*Metacypris*' sp. B – Krömmelbein, p. 262, pl. 45, figs. 6a, b
•	1971	*Theriosynoecum papillaris americanum* ssp. Nov. – Krömmelbein and Weber, 1971, p. 53, pl. 10 figs. 44a-c
non	1973	*Theriosynoecum fittoni* (Mantell) – Salomon, p. 133, pl. 1, figs. 1-13

? 1975 *Bisulcocypris variabilis* sp. nov. – De Klasz and Uliczny, p. 195, pl. 2, figs. 2, 3 [juveniles]

1976 *Theriosynoecum fittoni* (Mantell) – Brenner, p. 161, pl. 15, figs. 17-19

1978 *Theriosynoecum fittoni* (Mantell) – Kilenyi and Neale, p. 312, pl. 5, figs. 9-10

1980 *Theriosynoecum fittoni* (Mantell) – Colin and Danielopol, pl. 11, figs. 1, 3, 5-8

? 1980 *Theriosynoecum* sp. 5 – Colin and Danielopol, pl. 15, fig. 5

? 1981 *Theriosynoecum alleni* (Pinto and Sanguinetti) – Colin et al., pl. 11.6, fig. 1

1981 *Theriosynoecum fittoni* (Mantell) – Colin et al., pl. 11.6, fig. 2

• 1982 *Dryelba fittoni* (Mantell) – Sohn, p. 314, pl. 4, figs. 1-12

1985 *Theriosynoecum fittoni* (Mantell) – Anderson, p. 38, pl. 9, figs. 12, 13

? 1999 *Theriosynoecum krystofovichi* Mandelstam – Nikolaeva and Neustrueva, pl. 17, figs. 2-4

? 2005 *Theriosynoecum krystofovichi* Mandelstam – Neustrueva et al., pl. 28, figs. 3, 4a-b, 5-7

Material: Lakota Formation, South Dakota, many hundred carapaces and valves, samples FRCA? (questionable due to bad preservation), HSDC1, HSDC2, HSDC3, HSDC4, BCE*, BCE, BC5 04, BCB1, BCB2, BC8 04, LEC 04, questionably SBCR LAg2 (cf. Fig. 9 for details).

Dimensions (in mm): Overall length: 0.87-1.20
Own specimens:

Females	L: 0.88-1.01	H: 0.53-0.62	W: 0.57-0.62
Males	L: 0.88-0.93	H: 0.54-0.64	W: 0.45-0.47

As given in the literature (various references):

Females	L: 0.87-1.10	H: 0.55-0.58	W: n/a
Males	L: 0.98-1.20	H: ~0.60	W: n/a

Type locality and horizon: Top of the Weald Clay Group, Lower Cretaceous (Barremian), Punfield Cove, Swanage Bay, Dorset, UK.

Lectotype (designated by Sohn and Anderson 1964): GSM Mik(M) 1905.001 (British Geological Survey, Keyworth, *ex* Geological Society of London Collection, No. 2479), complete carapace, adult female.

Diagnosis: Lateral outline rounded subrhomboidal, anterior part in front of posterolateral inflation relatively short. Posterior half of hinge margin hidden in both sexes in lateral view, in adults as well as in juveniles, covered by moderately to strongly overreaching ridge-like dorsal part of the carapace's posterolateral inflation. Moderate convex overreach of ventrolateral carapace inflation over ventral margin. Dorsal straight part of anterior margin short, inclined about 45°, with continuous transition into anterior cardinal angle. Cardinal angles distinct. With broad anterior marginal zone. Both sexes always with a pair of tiny tubercles close to posterior cardinal angle. With or without anterolateral node-like tubercles. Males usually with posterolateral tubercles (Nos. 1-6, Fig. 6/E), females usually without, rarely with tubercles Nos. 1 and 6 only (Fig. 6/E).

Description: Carapace shape: Small to medium sized. Carapace rounded subrhomboidal in lateral view. Maximum length at half height, maximum height at 3/4 of length, maximum width in females at about 4/5 of length, somewhat more anterior in male dimorphs, at about 3/4 of length. LV>RV, subequivalve. LV slightly to barely recognizable overlapping the RV along entire margin, except for the stronger overlap of the LV's tongue-like ventral segment, and the hinge margin, where the flange of the smaller RV's hinge margin overlaps the LV. Larger LV very weakly or not overreaching the RV.

Anterior margin infracurvate with a short straight dorsal part passing into the anterior cardinal angle, inclined about 45°. Anterior marginal zone moderately broad, up to 80μm. Posterior margin slightly supracurvate and straightly passing into posterior cardinal angle in males, in females not coincident with posterior lateral outline, which is more convex, and slightly concave passing into the posterior cardinal angle through overreach of the brood pouches. Both anterior and posterior margins of about equal width. Dorsal margin nearly straight and slightly wavy, i.e. concave anteriorly and convex posteriorly, with posterior cardinal angle slightly elevated above it. Dorsal lateral outline differing in being strongly convex on the posterior half of hinge margin, hiding the dorsal margin in both sexes through a ridge-like overreaching dorsal part of the carapace's posterolateral inflation. Ventral margin generally straight with a small concave segment just in front of half length, below the S2-sulcus (i.e. also, below the adductor muscle scar field), the concavity incising more deeply in the smaller RV. Ventral lateral outline convex in both sexes through overreaching ventrolateral parts of the carapace, somewhat stronger and also affecting the posteroventral region in the female dimorph. Dorsal and ventral margins nearly parallel. Both cardinal angles usually well noticeable but not always completely visible and sometimes not in line with the hinge margin. Anterior cardinal angle broad and well rounded, about 135°-140°. Posterior cardinal angle more conspicuous and moderately rounded, more distinctive in the LV, about 120°, in females weakly exposed in lateral view because of the strong posterolateral inflation.

Anteriorly with the two characteristic dorsolateral sulci and a resulting intermediate lobe in between the sulci in both valves; expressed internally with very slight valve deformations only. S2-sulcus somewhat deeper and longer, extending from slightly below dorsal margin downwards to about half maximum height. In the smaller RV (visible in dorsal view) its beginning is considerably closer to the hinge line than in the larger LV. However, the S2-sulcus in the smaller RV is slightly shallower than its counterpart in the LV and not so strongly inclined.

S1-sulcus shorter than the S2 one, extending from slightly below dorsal margin downwards to somewhere between 3/4 and 2/3 of maximum carapace height. S1-sulcus not as deeply incised as S2-sulcus. Like the S2-sulcus, the S1-sulcus on the smaller RV begins closer to the hinge line than its counterpart on the larger LV.

Carapace of males in dorsal view elliptic and slightly flattened and concave laterally at position of the S2-sulcus, rounded posteriorly and acute anteriorly. Anterior end also flattened laterally. Female dimorph piriform in dorsal view with strongly inflated posterior end (brood pouches) and strongly constricted laterally at position of the S2-sulcus. Shape of anterior end same as in males. Both sexes with distinct angularity in dorsal outline at position of the S1-sulcus (Fig. 10B, letter "1"), being obtuse-angled with about 145°. The posterior dorsolateral ridge-like protrusion forms a groove around the posterior part of the hinge margin. Both sexes showing a slight convex overlap of LV over RV at both cardinal angles. Along hinge margin, the flange of the RV slightly overlaps the LV fitting into a shallow accommodation groove. Therefore, the hinge line is sinuous.

Moderate overlap of the larger LV in ventral view with a distinct convex segment at about 2/5 of length – below the S2-sulcus. Anterior fifth ventrally forming a broad flat outer margin with sharp lateral edges and a lateral furrow above it (a "T-structure"), running parallel to the margin.

Ornamentation:

1. Area-wide ornamentation elements/surface characters: Carapace of both sexes regularly punctate, puncta more or less shallow, between 20 and 40µm in diameter. Puncta closer to the outline arranged in concentric rows running more or less parallel to the anterior, posterior and ventral margins. Unlike in males, puncta on the posterocentral carapace region in females also concentric and skew, i.e. slightly elongated and shallower towards area center (=maximum lateral extension of the inflation, i.e. brood pouches). Dorsolateral sulci in adults in general nearly smooth, rarely with extremely vertically elongated puncta, the lobe in between without or with puncta, but then these are alleviated and distorted.

In marginal areas, ventrally as well as in anteroventral and posterocentral regions up to about mid-height, the rows of puncta are separated by carinae. Puncta between them elongated in lateral direction and their margins deformed, thus ventrally rectangular to quadrate.

A few larger simple lateral pores (about 4µm in diameter), occurring unevenly distributed over the carapace and always between the puncta. Their position is fixed, and the main tubercles, if present, develop around them/from them. These pores often form very flat tubercle-like pore conuli. Several very small lateral pores (about 1-2µm diameter) occurring, with relatively unfixed position and situated independently from the punctation, i.e. lying either between or inside the puncta, in all possible positions from marginally to centrally. Each valve with a regular row of surfacing radial pore canals along the whole outline except for hinge line and cardinal angles (see frontal views, Pl. 1, Figs. 7 and 9), about 1µm in diameter.

2. Local ornamentation elements: Tuberculation common, especially in male dimorphs the posterolateral tubercles often being well developed, and also in instars. Males with very weak tuberculation uncommon but present (Pl. 1, Fig. 5; in part possibly A-1 instars). Main tuberculation pattern in males consisting of four posterolateral tubercles (Fig. 6/E, Nos. 1 to 4) of about 50-65µm diameter at the base and 10µm at the apex with an enlarged pore of about 4µm diameter in center. One posterocentral tuberculum (No. 4, Fig. 6/E), not always developed, the other three (Nos. 1, 2, 3, Fig. 6/E) being located along the virtual line separating the posterocentral and posterolateral carapace area. Tuberculum No. 2 always below No. 4, if developed, or its corresponding pore; the upper tuberculum (No. 1) being mostly less developed than the middle and lower ones (Nos. 2, 3). Two additional larger tubercles occurring occasionally: a dorsolateral one (No. 6) and a centroventral one (No. 5), both at about half length of carapace (e.g. Pl. 2, Figs. 8). Tubercles Nos. 1 and 6 (Fig. 6/E) can be strongly developed in females also (e.g. the specimen figured by Kilenyi and Neale, 1978, pl. 5, fig. 9).

Three anterior tubercles can occur in both sexes (Fig. 6/E, Nos. A1 to A3, e.g. Pl. 2, Figs. 7, 12), often developed as node-like tubercles below (A3) or on (A2) the lobe between the sulci, or in front of the S1-sulcus (A1), almost never developed in the North American specimens, but typical in other specimens (e.g. English Wealden species) and then considered to be related to elevated salinities (Do Carmo et al., 1999, see discussion below also). Both sexes usually with two pairs of small posterolateral tubercles, one directly behind the posterior cardinal angle, the other at mid-height (dotted circles in Fig. 6/E; cf. Pl. 1, Figs. 1-2, 4-5, 8, 10).

Either sex also bearing two main anterolateral rows of poorly developed tubercles parallel to the anterior margin (Fig. 6/E, small grey circles and Pl. 2, Fig. 2), most of them in the anteroventral part of anterolateral part of carapace. The outer row consisting of 5-6 tubercles, situated in the anterior marginal zone; the inner, less marginal one, consisting of 3 (rarely 4) tubercles situated along the transition between the flattened marginal zone and the laterally convex part of carapace (e.g. Pl. 2, Fig. 7).

Internal characters: All hinge elements smooth. Median element forming a ridge in the larger LV with a small constriction at about mid-length dividing it into two parts, the posterior part being narrower than the frontal one and having a sharp edge. LV's median hinge element with adjoining weak accommodation groove. Anterior tooth in smaller RV narrow with sharp edge, posterior tooth broad, ovate and well-rounded – both fitting into a matching socket of the larger LV.

Free inner lamella of moderate width anteriorly, narrower posteriorly, vestibuli developed accordingly. Line of concrescence and inner margin only coinciding dorsally. Outer margin displaced inwards and thus forming a flange along anterior, posterior and ventral margins, particularly strong at posteroventral region, somewhat more in the smaller RV. Selvage of larger LV fitting into a matching groove between selvage and outer margin/flange of the smaller RV and enabling the animal to close the valves tightly. Ventral margin of both valves with a convex tongue-like excrescence below the adductor muscle scars/S2-sulcus and above a concavity of the ventral margin, the one of the larger LV overlapping the one of the RV and fitting into the stronger ventral margin's concavity of the RV.

Internal bulge of external dorsolateral sulci only slightly recognizable, in most cases just the one from the deeper S2-sulcus. Lobe in between the dorsolateral sulci internally expressed as shallow sulcus. Hollow tubercles, if present, visible internally as conical pits.

Muscle scar pattern: Muscle scar pattern as diagnostic for the genus. All adductor muscle scars (AMS) more or less elongated-elliptic, the upper- and lowermost ones having about half the size (30µm) of the middle ones, which are of equal size (60µm length, 20µm width). The latter may also be more or less constricted at about half their length.

Morphologic variation: Variation mainly concerns occurrence and intensity in development of ornamentation elements. Females sometimes show posterodorsal main tubercles (Nos. 1 and 6, Fig. 6/E). In elevated salinity environments (e.g. the English Wealden) the specimens of both sexes can develop strong node-like tubercles in the anterior region (3 tubercles around the sulci, see Fig. 6/E, Nos. A1 to A3), that may totally subdue the sulci and lobe in between them. Only very minor variations in lateral outline and shape occur, the anterior cardinal angle may be swollen and/or elevated above the hinge line. However, specimens with strong tuberculation/noding (as defined herein; often the case in specimens from the English Wealden, e.g. Pinto and Sanguinetti 1962, specimens on pl. 11, figs. 3-14) can have strongly different outlines that may completely distort and superimpose the true outline (Fig. 3, Fig. 6/A), specifically in dorsal/ventral views (Fig. 6/C-D). In this case, the dorsal outline then shows strong zigzag trends. Strong node-like tubercles (A3 especially) also increase the anterior and posterior maximum width, and in dorsal view the females show posterolateral angularities that are caused by tubercles in *T. fittoni*, in contrast to *T. pahasapensis* where this is a result of the typical posterolateral cusp that is a diagnostic character, not ecophenotypic.

A special feature that may occur is a lateral node at both sides of the anterior cardinal angle. These nodes occur every now and then (e.g. '*Bisulcocypris*' *fittoni* in Pinto and Sanguinetti 1962, pl. 11, fig. 4 or '*Gomphocythere berwickensis*' of Martin 1940, pl. 12, fig. 176, refigured here in Pl. 5, Fig. 12) and distort the shape of the lateral outline. In this case, the anterior cardinal region is elevated above the hinge line and the otherwise straight posterior part of the anterior margin is concave. In addition, the posterodorsal lateral outline may deviate strongly, caused by nodes or an additional dorsolateral node-like tuberculum (e.g. Pl. 5, Figs. 4, 6a-b, 7a-b, also refer to discussion under item 6.1 herein).

Ontogenetic variation: The ontogeny of *T. fittoni* specimens from the Wealden of England has been analyzed and described in detail by Sohn and Anderson (1964). However, the material used by these authors only comprises heavily ornamented (noded/tuberculate) material which has some influence on the outline of the instars (overreach of ornamentation elements, partial deformation of the outline). In addition, these authors were not yet aware of precocious sexual dimorphism and variation of absolute size for the growth stages, but based their recognition of instars mainly on the carapace size and size of tubercles.

During ontogeny (cf. also Sohn and Anderson 1964), the general outline of the instars is more rounded-rectangular, and the ventral and posterior lateral outlines and margins are coincident. The posterior margin is lower than the anterior one and yet slightly infarcurvate. The hinge margin is inclined towards posterior end; thus, the ventral and dorsal margins are not parallel. The dorsal margin nearly coincides with the dorsal lateral outline except for a slight overreach of the elevated ridge-like area ventrodorsally behind half length. Unlike in other species, this overreach is also noticeable in earlier instars (A-3 to A-5?). The dorsolateral sulci are more weakly developed the younger the instar is, and always covered by distorted surface characters, as well as the lobe in between them. The anterior marginal zone is less noticeable the younger the individual is. The carapace of younger instars is elliptic in dorsal view, only slightly more acute anteriorly than posteriorly.

Surface punctate, the pattern and size of puncta the same as in adults, just fewer in number. Therefore, the pattern of the surface characters appears to be more coarse because of the smaller valve size and also tends towards reticulation.

Ornamentation present to nearly absent, some instars may have strong tubercles which can be either conical or hemispherical. Mostly, the pattern of tuberculation follows that of the male adults, sometimes anterior tubercles/node-like tubercles (Fig. 6/E, Nos. A1 to A3) occur.

Free inner lamella very narrow in juveniles, having the same width along anterior, ventral and posterior margins.

Regarding the ontogeny of *T. pahasapensis*, a differentiation of its juveniles and those of *T. fittoni* might be difficult where both species occur together due to the similarity of both species. Further research is necessary.

Dimorphism: Strong sexual dimorphism. Lateral outline of both sexes very similar except for posterior and posteroventral regions where the outline of the female strongly differs from its margins. Posteroventral region in females completely covered through extreme inflation (brood pouches). In contrast to other representatives of *Theriosynoecum*, the males are not distinctly elongated in comparison to the female dimorphs. Females with slightly concave transition of posterior lateral outline into posterior cardinal angle (overreach of brood pouches). Female dimorphs posteriorly much broader in dorsal view (piriform) with distinct constriction at position of the posterior sulci caused by the brood pouches, males being more elliptic in dorsal view and laterally flattened. Males usually with at least tubercles Nos. 1-4 (Fig. 6/E).

Precocious sexual dimorphism occurring (at least to A-2 stage) but barely recognizable in earlier instars to similarity of both morphs in lateral outline. For later preadult stages (at least A-1 to A-2), the dorsal outline is more significant. Protomales with node-like tubercles, more elliptic in dorsal view and with maximum width at 3/5 of length, protofemales usually lacking node-like tubercles and piriform with maximum length at 4/5 of length.

Regarding precocious sexual dimorphism in *T. fittoni*, further research is necessary. From the figured specimens of Sohn and Anderson (1964), although this material is from strata of approximately the same age from four widely separated localities of the English Wealden, it is impossible to differentiate sexes because these specimens all bear very strong nodes and node-like tubercles. Following Do Carmo et al. (1999), such heavy (local) ornamentation points to a paleoenvironment with (strongly) elevated salinity.

More North American specimens with weak ornamentation and without nodes have to be examined. Where *T. fittoni* and *T. pahasapensis* occur together, a differentiation between their juveniles of early ontogenetic stages may be difficult.

Discussion: The specimens from the Lakota Formation assigned to *Theriosynoecum fittoni* (Mantell), including other North American species integrated as given in the synonymy list, lack strong => *local ornamentation elements*, especially the anterolateral node-like tubercles (A1-A3) very common to the Wealden specimens of NW Europe, for example. As these are most certainly ecophenotypic characters, this results from the different paleoenvironmental conditions of the NW European Wealden Basin and the Western Interior foreland basin (refer to Chapter 6.2 for more details). In all other morphologic aspects, the North American specimens are very similar to, almost identical to the NW European ones and thus assigned to *T. fittoni* (cf. Chapter 6.1.2 for detailed discussion also).

The specimens of *Gomphocythere berwickensis* Martin 1940 are strongly nodose and in part instars of *Theriosynoecum fittoni* (cf. also Sohn and Anderson 1964, p.75). Martin's (1940) specimen on pl. 12, fig. 176 (herein refigured on Pl. 5, Fig. 12) also has a node on the anterior cardinal angle (e.g. also in the holotype of '*Bisucocypris*' *alleni* Pinto and Sanguinetti 1962), a character occurring every now and then that distorts the shape of the lateral outline. In this case, the anterior cardinal region is elevated above the hinge line and the otherwise straight posterior part of the anterior margin is concave.

Gomphocythere fittoni fittoni in Wicher (1957) is a *Theriosynoecum fittoni* (Mantell) by matching the diagnostic features as illustrated in Wicher's figures, although his argumentation is insufficient.

Gomphocythere fittoni berwickensis Martin in Wicher (op. cit) is most probably a strongly nodose variation of *Theriosynoecum fittoni*, the former having been synonymized with *Bisulcocypris martini* Pinto and Sanguinetti 1962 (therein), a species also considered a synonym of *T. fittoni* (see below) herein. However, some uncertainty remains because Wicher (1957) gives neither a good description nor good figures (and, of the ventral view, just line drawings). Sohn and Anderson (1964, p. 75) refer this species to instars of *T. fittoni*.

Grekoff (1958) places '*Metacypris*' *fittoni* into the genus *Gomphocythere* (Sars), gives a short redescription and figures some line drawings.

Bisulcocypris fittoni "*germanica*" given by Wolburg (1962) is also just an ornamentation-based ecophenotypic variation, and is, as he indicates in the synonymy (op. cit., p. 222), equivalent to *Gomphocythere pahasapensis* (Roth) in Martin (1940), as discussed before (see discussion of *T. alleni* above). According to the recommendations of the International Code of Zoological Nomenclature, this subspecies would be invalid anyway, because it has only been figured without any description.

Another synonomous species is *Bisulcocypris martini* Pinto and Sanguinetti 1962 from the Wealden of Germany. Again, the species diagnosis is based only on ornamentation, i.e. the anterior lateral node-like tubercles (A1-A3). In their remarks Pinto and Saguinetti (op. cit., p. 70) already state that *B. martini* "… is quite similar to *Bisulcocypris fittoni* …" and only different in form and disposition of the node-like tubercles. Except for its ornamentation *B. martini* is identical to *Theriosynoecum fittoni* (Mantell) and therefore synonymized with the latter herein.

'*Metacypris*' sp. 1 of Krömmelbein (1962, refigured on pl. 5, fig. 9 herein) matches *T. fittoni* very well in outline; it also has the strong posterior overreach, the well-defined anterior marginal zone and the 45° inclined dorsal part of the anterior marginal zone. Exceptional in this specimen is, however, that it seems to bear node-like tubercles with coarse undeformed net-like puncta.

The West African (Ghana) '*Metacypris*' sp. B of Krömmelbein (1968) is, as already stated by Krömmelbein himself, very similar to *T. fittoni*, but certain designation is not possible due to its poor preservation (op. cit.). However, Krömmelbein (op. cit.) based the similarity just on the pattern of nodes (node-like tubercles herein), a character herein considered to be of insufficient taxonomic expressiveness. Based on the short description and figures in Krömmelbein (op. cit.) and apart from the similarity of both taxa in lateral and dorsal outlines, no certain taxonomic statement is possible.

Theriosynoecum papillaris americanum Krömmelbein and Weber 1971 (refigured on Pl. 5, Fig. 8a-c) is very similar to *T. fittoni* in lateral and dorsal outlines and also shows the 45° inclined straight dorsal part of the anterior margin, the broad anterior marginal zone, and the strong posterior dorsolateral overreach as well. The only difference is that *T. papillaris americanum* shows true nodes (sensu Sames herein) in combination with node-like tubercles and a strongly developed reticulation-like punctation pattern, all ecophenotypic characters insufficient for species differentiation. In the lower posterolateral carapace region, the tubercles No. 2, 3 and 5 (see Fig. 6/E) are more or less completely fused, thus forming a curved ridge. However, the synonymy with *T. fittoni* is only true for the Brazilian taxon designated as subspecies *americanum* by Krömmelbein and Weber (1971). The species *T. papillaris* Krömmelbein 1965 from the Congo Basin, Democratic Republic of the Congo (formerly Zaire), is a different taxon with a nearly right-angled posterior cardinal angle and very weak posterior dorsolateral overreach.

Bisulcocypris variabilis De Klasz and Uliczny 1975 can only be questionably referred to *T. fittoni*. It shows similarities in outline and has a (weak) posterior dorsolateral overreach, a 45° inclined dorsal part of the anterior margin as well as a distinct anterior marginal zone. However, the figures (drawings) in De Klasz and Uliczny (op. cit.) are very insufficient and do not show many important features, and only one specimen (the holotype) is illustrated. Additionally, outline and the weak lateral inflation point to the fact that the specimen chosen therein is a juvenile (A-2? Instar).

Theriosynoecum sp. 5 of Colin and Danielopol (1980, pl. 15, fig. 5), a female carapace with node-like tubercles, is probably a *T. fittoni.* The figured specimen, however, although showing the typical broad anterior marginal zone and the posterior dorsal overrreach, is somewhat too elongate and the dorsal part of the anterior margin inclines less than 45°. This might be due to the fact that the specimen is laterally compressed (see posterolateral crack and strong overreach of the LV).

T. alleni of Colin et al. (1981, pl. 11.6, fig. 1) is a juvenile (shortened posterior margin and distinctly unparallel ventral and dorsal margins, relatively coarse surface characters) of either *T. fittoni* or *T. alleni*, because it matches the diagnostic features, having distinct cardinal angles, the posterior dorsolateral elevation and overreach and the short straight dorsal part of the anterior margin, inclined about 45°. However, it is indicated with a question mark here because, based on the taxonomic information available, this specimen cannot be distinguished from juveniles of *T. alleni.*

The specimens of *Theriosynoecum fittoni* figured in Anderson (1985) are strongly ornamented (local ornamentation elements, not diagnostic!) and the specimen designated as male (op. cit., pl. 9, fig. 13) is considered a juvenile A-1 (or A-2) instar with precocious sexual dimorphism, and not characteristic in some aspects. In Anderson's figure, the specimen is also not aligned in relation to the base line and has to be rotated (see Fig. 10, specimen 4 herein). Particularly conspicuous in this specimen is the posterior margin which is distinctly less high than the anterior. Therefore, the ventral and dorsal margins are not parallel and the dorsal margin inclines towards the posterior end, which points to a juvenile (see also item 'general trends in ontogeny' in description of the genus above) according to what Sohn and Anderson (1964, p. 82, fig. 3g, pl. 15, fig. 12) refer to as "growth stage 9" which is equal to an A-1 instar in commonly used terminology. The adult males figured by these authors (op. cit., pl. 82, figs. 32 and 35) have roughly parallel dorsal and ventral margins.

Theriosynoecum krystofovichi Mandelstam as figured in Nikolaeva and Neustrueva (1999, pl. 17, fig. 2-4) matches the diagnostic features relatively well but is only tentatively synonymized for the time being due to the lack of detailed data.

T. krystofovichi Mandelstam as figured in Neustrueva et al. (2005) matches *T. fittoni* in many characters (strong posterior dorsolateral overlap, broad anterior laterally flattened marginal zone, development and inclination of the straight dorsal part of the anterior margin), but the figured specimens are strongly ornamented and some (op. cit., pl. 28, figs. 5 and 7) have considerably inclined dorsal/hinge margins (juveniles?). Thus, their affiliation to *T. fittoni* remains uncertain for the present.

Differential Diagnosis: The morphologic differentiation of *Theriosynoecum fittoni* and *T. alleni* is difficult to determine from the data available (see discussion of *T. alleni* herein). In contrast to *T. fittoni*, the maximum height of *T. alleni* as defined by the posterior dorsolateral overreach lies more posteriorly, i.e. at 4/5 of length (instead of 3/4 in *T. fittoni*). In addition, the anterior marginal zone in *T. alleni* seems to be always covered by distinctly developed surface characters whereas in *T. fittoni* these are very weak or the marginal zone is smooth. This, however, is considered not to be very significant taxonomically.

Theriosynoecum fittoni (Mantell) differs from *T. forbesii* (Jones 1885) (also *T. forbesi*, *Bisulcocypris forbesi[i]* or *Theriosynoecum forbesi[i] forbesi[i]* of some authors) in appearing more elongate (male) or piriform (female) in lateral outline because it lacks the ridge-like posterior dorsolateral elevation of the carapace. Therefore, it also lacks the dorsal groove along the posterior part of the hinge line. In addition, compared to *T. fittoni* the cardinal angles of *T. forbesii*, as well as the anterior marginal zone, are very indistinct. *T. forbesii* also has a strong ventrolateral overreach in both sexes. Finally, in *T. forbesii* the dorsal part of the anterior margin is less strongly inclined (only about 35°) towards the anterior end than in *T. fittoni.*

T. pahasapensis (Roth) is more elongate in outline than *T. fittoni*, and its dorsal part of the anterior margin is longer and less inclined. Especially the females of *T. pahasapensis* also have the typical strong posterolateral cusp and posterodorsal lateral flattening of the carapace which creates posterior angularities in the dorsal outline. It must be noted, however, that strongly ornamented female specimens of *T. fittoni* also may show the latter character (Pl. 5, Fig. 7a, refigured from Pinto and Sanguinetti 1962).

T. verrucosa barely has an anterior marginal zone, the dorsal straight part of the anterior margin is less strongly inclined (about 35° instead of 45° in *T. fittoni*) and the posterior dorsolateral overreach is weak in females, but almost completely covers the posterior cardinal angle in lateral view.

Paleoecology: As for the genus.

Faunal association (North America): With representatives of the Cypridoidea: Cyprideidae, i.e. *Cypridea (Pseudocypridina) piedmonti* (Roth 1933) syn. *Cypridea (Pseudocypridina) henrybelli* Sohn 1979), *Cypridea (Longispinella) longispina* Peck 1941 syn. *Cypridea (Pseudocypridina) asymmetrica* Sohn 1979, *Cypridea (Pseudocypridina) setina* var. *setina* (Anderson 1939), *Cypridea (Pseudocypridina) setina* (Anderson) var. *rectidorsata* Sylvester-Bradley 1949, *Cypridea* ex. gr. *tuberculata* cf. *C. tilleyi* Loranger 1951; Trapezoidellidae, i.e. *Trapezoidella rothi* Sohn 1979, *Trapezoidella trapezoidalis* (Roth 19333), *Limnocypridea? morrisonensis* (Roth 1933); Cyprididae, i.e. *Paracypris*?; and some Darwinuloidea

Stratigraphic and geographic distribution (Stratigraphic terms follow the most recent terminology available):

North America:

+ lower Lakota Formation (Chilson Member corresponding to: L1 informal interval after Way et al. 1998), southern Black Hills, South Dakota, USA

Europe:
+ Oncala Group (?Upper Tithonian to ?Lower Berriasian), Cabreton Beds of the Urbion Group (?Berriasian), Enciso Group (?Hauterivian-Barremian), Late Jurassic to Lower Cretaceous "Wealden" of northern Spain (Kneuper-Haack 1966)
+ Enciso Group (Hauterivian-Barremian), "Spanish Wealden", northern Spain (Brenner 1976)
+ Weald Clay Group (Lower and Upper Weald Clay), Wealden Supergroup, uppermost Valanginian to Barremian, *T. fittoni*-zone of Horne (1995) as equivalent to Anderson's (1985) Sevenoaks to Earlswood (cycles Nos. 68 to 98) faunicycles, England, UK
+ Uppermost Weald Clay Formation and Sheperd's Chine Member of the Vectis Formation, Barremian to early Aptian, Wessex Basin, southern England, UK (Wilkinson 2008)

South America:
+ São Sebastião Formation, Upper Bahia Series, "NE Brazilian Wealden", upper Lower Cretaceous, Brazil (*T. papillaris americanum* ssp. nov. Krömmelbein and Weber 1971)

Questionable occurrence:

Africa:
+ Moundounga Member (formerly "Schistes Noires") of the Cocobeach Formation, Lower Cretaceous, Gabon, West Africa (De Klasz and Uliczny 1975)

Asia:
+ Dzunbain Formation, Lower Cretaceous (Barremian), Mongolia (Mandelstam in Galeeva 1955)
+ Dushiulin Formation, Lower Cretaceous (Aptian-Albian?), Mongolia (Neustrueva et al. 2005)

+ Zazin Formation, Lower Cretaceous (Hauterivian-Barremian?), Transbaikalia, Russia (Nikolaeva and Neustrueva 1999)

<u>Europe:</u>
+ "Wealden", Lower Cretaceous, NW Germany (Martin 1940); 'Wealden' 4, Lower Cretaceous (upper Berriasian to lowermost Valanginian after Hoedemaeker and Herngreen 2003), NW Germany (Wicher 1957, Wolburg 1962) – depending on the possible inclusion of '*Gomphocythere pahasapensis*' (Roth) of Martin (1940), which is included in *T. alleni* herein for now

Stratigraphic range in North America: As inferred from England and Spain and excluding *T. alleni* from being synonymous with *T. fittoni* herein: latest Valanginian to early Aptian.

Stratigraphic range outside North America: <u>Europe:</u> latest Valanginian to early Aptian (Valanginian to Barremian *Theriosynoecum fittoni* Zone sensu Horne 1995, England, UK; Late Jurassic?, Hauterivian – Barremian, Spain. 'Wealden' 4, late Berriasian after Hoedemaeker and Herngreen 2003, Germany; Barremian to early Aptian, Upper Weald Clay Formation and Sheperd's Chine Member of the Vectis Formation, Wessex Basin, England, Wilkinson 2008). <u>South America:</u> Late Early Cretaceous (pre-Middle Albian). <u>Asia (questionable):</u> Early Cretaceous of Russia, Transbaikal, and Early Cretaceous, Barremian, Mongolia.

Theriosynoecum forbesii **(Jones 1885)**

(Pl. 3, Figs. 1-10)

v* 1885 *Metacypris forbesii* sp. nov. – Jones, p. 345, pl. 8, figs. 11-13, 15-16

v 1886 *Metacypris forbesii* Jones – Jones, pl. 4, figs. 1a-c

1940 *Metacypris forbesii* Jones – Martin, p. 336, pl. 6, figs. 89-94

1953 *Metacypris forbesii* Jones – Hoare, p. 40, pl. 2, figs. 14-16 [unpubl.]

? 1956 *Theriosynoecum defensum* sp. nov. – Lyubimova, p. 141, pl. 25, figs. 4a-c

1957 *Gomphocythere forbesii forbesii* (Jones) – Wicher, p. 270, pl. 1, figs. 3a-c

non 1957 *Gomphocythere forbesii* (Jones) *planiverrucosa* Klingler – Wicher, p. 269, pl. 1, figs. 1a-c, 2a-c

non 1957 *Gomphocythere forbesii* (Jones) *silvana* – Wicher, p. 270, pl. 1, figs. 6a-c; pl. 2, figs. 1a-c

non 1957 *Gomphocythere forbesii* (Jones) *striata* Martin – Wicher, p. 270, pl. 1, figs. 4a-c, 5a-c

non 1959 *Gomphocythere forbesii* subsp. Wicher – Moos in Wicher, p. 47, pl. 7, fig. 8; pl. 8, fig. 9, pl. 9, fig. 7

non 1962 "*Gomphocythere forbesii* (Jones)" sensu Wicher 1959 – Krömmelbein, p. 492, pl. 62, fig. 66

1962 "*Metacypris*" *forbesii* (Jones) – Klingler et al., p. 174, pl. 25, fig. 14

? 1962 "*Metacypris*" sp. 2 – Krömmelbein, p. 490, pl. 62, fig. 65

? 1962 "*Metacypris*" sp. 3 – Krömmelbein, p. 490, pl. 62, figs. 67a, b

1962 *Bisulcocypris bradyi* Jones – Pinto and Sanguinetti, p. 55, pl. 6, figs. 5-7; pl. 14, figs. 4a-d

1962 *Bisulcocypris forbesii* (Jones) emend. – Pinto and Sanguinetti, p. 39, pl. 3, figs. 1-4; pl. 12, figs. 1a-d

1966 *Theriosynoecum forbesii* (Jones) – Barker, p. 480, pl. 7, fig. 6; pl. 9, figs. 11, 12

v 1966 *Metacypris forbesi* Jones, 1885 – Kneuper-Haack, p. 199, pl. 47, fig. 36

? 1971 *Bisulcocypris dilatata* sp. nov. – Anderson, p. 124, pl. 19, figs. 4, 5 [juvenile *T. forbesii*?]

1971 *Theriosynoecum forbesii forbesii* (Jones) – Anderson, p. 128, pl. 22, figs. 8, 9

? 1971 *Theriosynoecum forbesii* (Jones) – Ramalho, pl. 24, fig. 16

1976 *Theriosynoecum forbesii* (Jones) – Brenner, p. 160, pl. 15, figs. 12-16

1978 *Bisulcocypris forbesii* (Jones) – Kilenyi and Neale, p. 312, pl. 5, figs. 1-4

1980 *Theriosynoecum forbesii* (Jones) – Colin and Danielopol, pl. 11, figs. 9-10

1981 *Theriosynoecum forbesii* (Jones) – Colin et al., pl. 11.6, fig. 4

1985 *Theriosynoecum forbesi forbesi* (Jones) – Anderson, p. 38, pl. 2, fig. 9

? 1985 *Theriosynoecum* gr. *forbesii* (Jones) – Colin and Oertli, pl. 39, fig. 11

? 1986 *Bisulcocypris*? *dilatata* Anderson – Ainsworth, p. 166, pl. 13, fig. 16

? 1986 *Theriosynoecum forbesii* (Jones) – Ainsworth, p. 167, pl. 13, fig. 17

1991 *Theriosynoecum forbesi forbesi* (Jones) – Sztejn, pl. 4, fig. 7

1994 *Bisulcocypris forbesii* (Jones) – Schudack, p. 66, pl. 10, figs. 1-2

1997 *Theriosynoecum forbesi* (Jones) – Horne, pl. 1, fig. 12

• 2002 *Bisulcocypris dilatata* Anderson – Mojon, pl. 30, figs. D1-D6

2002 *Theriosynoecum forbesii forbesii* (Jones) – Mojon, pl. 30, figs. A1-3, B1-3

2004 *Bisulcocypris forbesii* (Jones) – Schudack, fig. 10/M

2004 *Theriosynoecum forbesii* (Jones) – El Albani et al., p. 198, fig. 3/10

? 2005 *Theriosynoecum defensum* Lyubimova – Neustrueva et al., pl. 29, figs. 1a, b

2008 *Theriosynoecum forbesi* (Jones) – Arp and Mennerich, fig. 7a

Preceding remarks: Unless species are cited in the spelling used by other authors, the name '*forbesii*' is used in the spelling as given originally by Jones (1885), i.e. with double "i", because T.R. Jones chose to latinize the name of Edward Forbes to *Forbesius* and then correctly added the "I" to the stem of the word (*Forbesi*) for naming the species after a male person.

The taxa *forbesii* and *verrucosa* (designated mostly as variations or subspecies of *T. forbesii* by various authors) are separated and described as two different species herein for the reasons given below (refer to the discussion/differential diagnosis of the respective species).

None of the present author's own material is described regarding *T. forbesii*, because his own samples from selected formations in the U.S. Western Interior yielded no specimens of *T. forbesii* so far, but one sample of the uppermost Morrison Formation in the southern Black Hills, South Dakota yielded representatives of *T. verrucosa.* However, in the opinion of the present author these are two species with remarkably different features and therefore, a revision and clear distinction of both taxa became necessary. A detailed analysis of *T. forbesii*, especially with SEM documentation of its internal characters, is still lacking. Most probably, *T. forbesii* does occur in North America (Jones 1886, Hoare 1953), but thus far, the publications are more than 50 years old, localities and stratigraphy are arguable, the material is lost or badly preserved, and these reports have to be confirmed by new samples and revision.

Altogether, the taxonomy of *T. forbesii* and closely related taxa is the most elusive one in comparison to the other taxa dealt with herein.

Material: No own material from North America. Specimens discussed are type specimens and additional material from the BMNH (Jones), BGS (Anderson) and from the literature.

Dimensions (in mm): Overall length: 0.80-0.98
As given in literature (various references):

Females	L: 0.80-0.98	H: 0.50-58	W: 0.60
Males	L: 0.81-0.87	H: 0.50-0.55	W: 0.49-0.53?

Type locality and horizon: Ridgway Bay, Dorset, Middle Purbeck Beds

Lectotype (designated by Anderson 1971): *Metacypris forbesii* Jones 1885, female right valve, BMNH In. 39021 (Jones 1885, slide 123A-3, pl. 8, fig. 16; refigured in Kilenyi and Neale 1978, pl. 5, fig. 1).

Diagnosis: Small sized. Lateral outline of females piriform, strong posteroventral overreach over ventral margin. Males rounded subrhomboidal to elliptic. Strong sexual dimorphism. S2-sulcus shallow but broad and distinct, reaching downwards to somewhat below mid-height. Anterior marginal zone narrow and weakly developed, therefore specimens in dorsal view barely or not constricted close to the anterior apex. Females elongated-cordiform in dorsal view with strong posterior overreach of the brood pouches with maximum width at 3/5 of length. In lateral view with moderate dorsolateral overreach between 3/5 and 4/5 of length, somewhat stronger in females. Both sexes with strong ventrolateral overreach with its maximum at 3/4 of length in males, at 4/5 of length in females. Surface finely punctate, without tuberculation.

Description: Carapace shape: Small sized. Carapace piriform (♀) or ovoid-elliptic (♂) in lateral view. Males usually somewhat longer and less high than females. Maximum length at half height, maximum height at about 2/3 of length (♀), slightly more anterior in males, maximum width at about 3/5 of length in both sexes. LV>RV, subequivalve, LV very weakly or not overreaching the RV. LV very slightly overlapping the RV along entire margin except for the somewhat stronger overlap of the tongue-like ventral segment below the S2-sulcus, and the hinge margin, where the flange of the RV's hinge margin overlaps the LV.

Anterior margin slightly infracurvate in both sexes with slightly convex dorsal part, inclined around 35°. Anterior marginal zone barely developed. Posterior margin and outline coincident (♂) or strongly discordant (♀). Posterior margin equicurvate to slightly supracurvate with a moderately long straight (♂) or slightly convex (♀) dorsal segment, inclined about 60°. Posterior lateral outline in females equicurvate and noticeably more broadly rounded than anterior end, completely covering the posterior cardinal angle. Dorsal margin straight, cardinal angles not prominent, nearly but not completely coincident with dorsal lateral outline. Dorsal lateral outline in both sexes slightly convex posteriorly, due to a very slight overreach of the dorsolateral protrusion. Ventral margin straight, in males with moderately convex ventral lateral outline due to ventrolateral overreach having its maximum extension at about 3/5 of length; in females having a strongly convex posterior ventral outline with maximum extension at 4/5 of length (overreaching brood pouches), overreach intensified by strongly developed carinae forming an angularity. Dorsal and ventral margins parallel to each other. Both cardinal angles in line with the hinge margin. Anterior cardinal angle broadly rounded, especially in females less distinct, obtuse-angled with about 140°. Posterior cardinal angle more narrow and less rounded, masked in females, about 120°.

Dorsolateral sulci weakly incising, S2-sulcus somewhat more than S1-sulcus, the latter about 3/4 the length of the former. S2-sulcus broad, reaching downwards to about 3/5 of height. RV's dorsal beginning of the sulci closer to the hinge line than on LV (lateral offset, cf. Fig. 6/D).

Carapace elongated-cordiform (♀) or elongated-elliptic (♂) in dorsal view, in both dimorphs slightly acute towards anterior end and with faint lateral constriction close to it, somewhat more distinct in males. Females showing strong posterolateral overreach and having a slight lateral constriction at position of S2-sulcus. Anterior angularity in front of S1-sulcus strongly rounded. Hinge line slightly sinuous, LV overlapping RV at cardinal angles with a convexity, flange of RV's hinge margin overlapping the LV.

Ventrally, the tongue-like overlap (Fig. 6/C) below S2-sulcus is very weakly developed.

<u>Ornamentation:</u>

<u>1. Area-wide ornamentation elements/surface characters:</u> Carapace of both sexes punctate to finely reticulate in no specific pattern except towards anterior, ventral and posterior margins, where concentric rows are formed. No or much more weakly developed surface characters in the S2-sulcus area, but definitely occurring in the area of the weak S1-sulcus (Fig. 6/A). Puncta relatively small, about 15µm in diameter. Ventrally, posterolaterally, but especially anterolaterally, the pattern tends to be more coarsely reticulate, showing larger meshes (20-25µm in diameter) elongated parallel to the anterior and ventral margins. In marginal areas, ventrally as well as in antero- and posteroventral areas up to about half height, puncta or meshes elongated and separated by carinae.

A few typical larger simple pores of about 5µm as characteristic for the genus, mostly in between the puncta, with relatively fixed positions. One row of such pores anterolaterally, close to and parallel to the anterior margin; a second inner row, more distal to the margin is hardly noticeable (subdued by reticulation/carinae).

Several small (1-2µm) lateral simple pores, unfixed in their position and independent from surface character pattern.

<u>2. Local ornamentation elements:</u> So far, no node-like tubercles or nodes were observed or are reported, except for a weak A2 (Fig. 6/E) node-like tuberculum in Jones' (1885) specimen.

<u>Internal characters:</u> Not seen.

Muscle scar pattern: Not seen.

Morphologic variation: Some variation in the intensity of the surface characters. A few female specimens figured in the literature (e.g. the lectotype of *T. forbesii* as refigured by Kilenyi and Neale, 1978, pl. 5, fig. 1) show a very strong 'false' angularity in the posteroventral region of the carapace, which is caused by high carinae situated on the overreaching ventrolateral inflation (brood pouches).

Ontogenetic variation: Not observed in detail or often reported in the literature. However, precocious sexual dimorphism occurs in females at least in A-1 instars with the characteristic maximum width at 3/5 of length but less strong posterior overreach in dorsal view. Brenner (1976, pl. 15, figs. 15-16) figures juveniles of *T. forbesii*, and because these do not co-occur with other species of *Theriosynoecum* a wrong designation is improbable. These specimens are A-4 or A-5 instars and show a coarse reticulation-like punctation, no overreach, no sulci (yet), have a slightly concave ventral margin and the anterior margin is distincly higher than the posterior one and thus, the dorsal margin is inclined with about 15° towards posterior end.

Dimorphism: Sexual dimorphism very strong. Females with large brood pouches that strongly overreach the posterior and ventral margins, therefore strongly differing from male dimorphs in lateral (♀ piriform, ♂ ovoid-elliptic) and dorsal (♀ cordiform, ♂ elongated-elliptic) outline. Males always(?) with tubercles, females with or without tubercles. Posterior cardinal angle of females almost not visible or completely masked in lateral view. Males without strong posterolateral inflation and elongated posterior end.

Precocious sexual dimorphism distinct, protomales elongate, protofemales more compact-rectangular (Pl. 3, Figs. 7-10).

Discussion: As already proposed by other authors (e.g. Pinto and Sanguinetti 1962), the taxa *forbesii* and *verrucosa* are accounted as two species herein, not as subspecies or variations of *T. forbesii.* One reason that may have led many authors to the conclusion that both taxa are variations or subspecies of *T. forbesii* is the fact that both taxa always seem to co-occur, at least in the well-documented Purbeck/Wealden deposits of western Europe. However, the arguments given herein are based not just on ornamentation (tuberculation sensu Sames herein) but on several other carapace features differing in both species (see differential diagnosis below). In addition, one sample from the top Morrison Formation of the Red Canyon, southern Black Hills, South Dakota (sample RCS MO3) contained specimens of *T. verrucosa* only and is therefore one of the few examples where both taxa do not occur together.

Nearly all specimens of *T. forbesii* Jones, including the males, are reported and diagnostically defined as showing hardly any ornamentation in both sexes. This case shows that it could be possible that also the male dimorphs in *Theriosynoecum* may be attributed back to a morphotype without ornament. However, it may otherwise be considered that the lack of tuberculation (especially tubercles 1-6) in males of *T. forbesii* is a fixed feature. Together with the extremely strongly developed female brood pouches causing a cordiform dorsal view, the weak development of the S1-sulcus, the very small anterior marginal zone and the relatively small overall size in comparison to other species of *Theriosynoecum*, these features make *T. forbesii* an ideal candidate for a possible ancestor of the genus *Metacypris* and related genera.

Jones (1886) reported *Metacypris forbesii* from the "Atlantosaurus Beds" (lower Morrison Formation) near Cañon City, Colorado, after having erected this species on English representatives in 1885, and states that the American specimens "... do not show the ornament seen in their English representatives; but some that have been beaten out (not separated by acid) show the characteristic ornament …" (Jones 1886, p. 146). Most probably, the 'ornament' that Jones was talking about refers to the surface characters (sensu Sames herein). His figures (op. cit., pl. 4, figs. 1a-c) do not show any local ornamentation elements as defined herein (i.e. tubercles or node-like tubercles). From Jones' (op. cit.) short description and figures, no taxonomic statement is possible. A personal examination (short visit of BS, March 2007) of Jones' (1886) slides at the British Museum of Natural History, London (slides Nos. I. 2453, I. 2452) revealed that there are specimens in slide I. 2453 that are at least very similar to *Theriosynoecum forbesii*. Detailed research (SEM pictures) and new material are necessary.

The figures of *Metacypris forbesii* Jones in Martin (1940) show female representatives of *T. forbesii*, A-1 instars in part (op. cit., pl. 6, fig. 90) and probably younger. The specimen No. 89 (op. cit., pl. 6), designated as male, is most probably an A-2 or A-3 instar (protofemale?).

Metacypris forbesii Jones in Hoare (1953, unpubl. MA thesis, University of Missouri) is one of the few reports of this species from North America following that of Jones (1886). He describes specimens from the Morrison Formation near Cañon City, Colorado and north of Fort Collins, Colorado. Unfortunately, the material figured is indeed in the catalogue, but was no longer in the University of Missouri collection. A further inquiry revealed that Hoare (pers. comm., March 2007) has not seen the material since he finished his thesis, and has no further information about its whereabouts. However, on the basis of the figures and description in his thesis, the specimens are very similar to *Theriosynoecum forbesii*. New samples from Colorado are necessary to accurately reappraise this matter, especially the stratigraphy.

Metacypris planiverrucosa Klingler 1955[b] nom. nov. subst. pro *Metacypris verrucosa* Klingler 1955[a] is, as already stated by Klingler (1955b) not identical to *T. forbesii* var. *verrucosa* (Jones), thus neither identical with *T. forbesii* nor to *T. verrucosa* following the taxonomic concept applied herein.

Theriosynoecum defensum Lyubimova 1956 is very similar to *T. forbesii* in lateral and dorsal outlines as well as the development of the anterior marginal zone and the sulci. The dorsal view of a female shown in figure 4b (drawing) in Lyubimova (1956, pl. 25) incorrectly reproduces the valve size relation and overlap, which is shown as RV>LV but is the opposite instead (LV>RV, cf. photo of the same specimen in Neustrueva et al. 2005, pl. 29, fig. 1b). However, because no original material could be personally studied and because the females are not considerably piriform in lateral view, the affiliation must remain slightly tentative.

Gomphocythere forbesii subsp. *planiverrucosa* in Wicher (1957) differs from *T. forbesii* in a broader anterior marginal zone (therefore with a distinct anterior constriction in dorsal view), the weak ventrolateral overreach and a longer anterior half of the carapace.

Gomphocythere forbesii subsp. *silvana* of Wicher (1957) certainly represents a juvenile morphotype of a species other than *T. forbesii* (as therefore does *Gomphocythere silvana* Martin 1940). Besides the not necessarily diagnostic fact that the specimens of these two species are relatively small, they show weak sexual dimorphism, tending to the male morphotype in overall shape. Moreover, the anterior margin is higher than the posterior one and the dorsal margin inclines towards the posterior end. Therefore, there can be no doubt that these are juveniles. Because of the characteristic ventrolateral velate projection posteriorly ending in a "thorn" which Martin (1940) and Wicher (1957) mention (not present in juveniles of *T. forbesii*) and the fact that *T. forbesii* and the species or subspecies *silvana* appear in different stratigraphic levels, it seems almost improbable that these species are related, not to mention synonymous.

Gomphocythere forbesii subsp. *striata* in Wicher (1957) does not belong to *T. forbesii* because it has a distinct and broad anterior marginal zone that in dorsal view forms a strong anterior constriction close to the apex. In addition, the maximum width of the females is at about 4/5 of length (piriform in dorsal view), whereas that of *T. forbesii* is more anterior, at about 3/5 of length (elongated cordiform in dorsal view).

Gomphocythere forbesii subsp. Wicher (Moos in Wicher 1959) is much different from *T. forbesii* in having a velate posteroventral extension of the carapace and a broad and distinct anterior marginal zone. This species is more likely to be *Theriosynoecum striata* (Martin 1940) instead. This applies to Krömmelbein's (1962) *Gomphocythere forbesii* (Jones) sensu Wicher (1959) as well.

"*Metacypris*" sp. 2 of Krömmelbein (1962), a male carapace as figured on pl. 62, fig. 65 therein, has the same outline and narrow, weakly developed anterior marginal zone as *T. forbesii*. Since the material was not studied personally and no description is available, the synonymy with *T. forbesii* is indicated with a question mark. "*Metacypris*" sp. 3 of Krömmelbein (op. cit, pl. 62, figs. 67a, b) seems to be the female dimorph of the aforementioned species.

Metacypris forbesi (Jones) of Kneuper-Haack (1966) is only figured in a dorsal view (drawing) without description, but the material (Micropalaeontologic collection of the Fachrichtung Paläontologie, Freie Universität Berlin) was studied personally and the designation confirmed.

Bisulcocypris dilatata Anderson 1971 is most certainly a juvenile *Theriosynoecum*, probably a *T. forbesii*, but it may also be a *T. striata* (Martin) or *T. verrucosa*, which occur in the same horizons. Since documentation of an ontogenetic line of *T. striata* is lacking, some uncertainty remains.

Ramalho (1971) reports *T. forbesii* from the Purbeckian of Portugal, but only had one specimen (a female carapace). Since the figure is of moderate quality, an affirmation is impossible. However, the specimen is very similar to *T. forbesii* in lateral outline (piriform) and lacks a well defined anterior marginal zone, and therefore the designation is most likely to be correct.

Brenner's (1976) specimens are *T. forbesii* without doubt, he also figures some juveniles (op. cit., pl. 15, fig. 15-16).

For *Bisulcocypris*? *dilatata* Anderson 1971 in Ainsworth (1986) see comments on the corresponding species (see this paragraph above).

Theriosynoecum forbesii in Ainsworth (1986) probably does not belong to this species. The case must remain questionable because Ainsworth (op. cit.) gives no description and there is only one figured specimen, a female carapace. This specimen seems to have an anterior marginal zone, shows no posterior dorsolateral overreach, and the ventral striae continue upwards to the dorsoventral region at the posterior end. Accordingly, this specimen has more similarities to *Theriosynoecum planiverrucosa* (Klingler 1955[b]). Since a dorsal view is lacking and the original material was not studied, a certain designation is not possible here.

Colin and Oertli (1985, pl. 39, fig. 11) figure a moderately well preserved (female) specimen that has some similarities with *T. forbesii* in its general shape and the poorly developed anterior marginal zone but does not have the typical piriform outline in lateral view. However, if the specimen figured belongs to the species *forbesii*, it is an (A-1?) instar with precocious sexual dimorphism, a protofemale whose posterolateral inflation is not yet fully developed.

The *T. forbesi forbesi* specimen figured in Sztejn (1991, pl. 4, fig. 7) is a female, not a male, as indicated in the plate description.

Regarding *Bisulcocypris dilatata* Anderson 1971 in Mojon (2002), these specimens are most probably juveniles of *T. forbesii*, since they show the typical ontogenetic characters and occur together with the latter species (op. cit.)

Theriosynoecum defensum Lyubimova as figured in Neustrueva et al. (2005, pl. 29, figs. 1a, b) matches *T. forbesii* well in lateral and dorsal outlines as well as the development of the anterior marginal zone and the sulci. However, the lateral outline of the female carapace figured is not distinctly piriform, and therefore its inclusion in the latter is conditional herein.

Differential diagnosis: The adult females of *Theriosynoecum forbesii* differ from most other female dimorphs of representatives of the genus through their strongly piriform outline in lateral view and the (elongated) cordiform outline in dorsal view because of the more anterior position (3/5 instead 4/5 or 5/6 of length) of the maximum width. Additionally, both sexual dimorphs of *T. forbesii* have nearly no developed anterior marginal zone, which is most distinctive in dorsal view because there is no lateral constriction visible close to the anterior end. Additionally, both dimorphs show only a weak tongue-like ventral overlap below the S2-sulcus.

T. fittoni differs from *T. forbesii* in the features listed right above, but also in the strong posterior dorsolateral overreach. Yet, the posterior cardinal angle in adult females is visible in *T. fittoni*, whereas it is masked in *T. forbesii*.

T. pahasapensis differs in the long straight dorsal part of the anterior margin and the typical posterolateral cusp of the females. The posterior cardinal angle is not masked in adult females in ventral view, and both sexes have a broad and distinct anterior marginal zone.

T. verrucosa has narrower sulci than *T. forbesii*, and the S1-sulcus of the former is also better defined. In contrast to *T. forbesii*, the males barely show any ventrolateral overreach; the ventral lateral outline and margin, although not coincident, are both straight. The females are piriform in dorsal view, the posterior flanks evenly rounded, and they have a very weak posterolateral overreach or none at all.

Paleoecology: As for the genus.

Faunal association (North America): Not applicable here since the species is not known from North America thus far.

Stratigraphic and geographic distribution (Stratigraphic terms follow the most recent terminology available):

North America:
+ "Atlantosaurus Beds" (lower Morrison Formation), Upper Jurassic(?), Colorado, USA (Jones 1886); Morrison Formation(?) near Cañon City, and Fort Collins, Upper Jurassic(?), Colorado, USA (Hoare 1953)

Europe:
+ Serpulit Subformation, Berriasian, Lower Cretaceous; NW Germany (Martin 1940); Upper Münder Formation and Serpulit Subformation, Lower Cretaceous, NW Germany (Klingler et al. 1962); Upper Münder Formation including Katzberg Subformation (lower Berriasian) to Bückeberg (upper Berriasian), Lower Cretaceous, NW Germany (Schudack 1994); Portland 6, Serpulit Subformation, Berriasian, N Germany (Schudack 2004)
+ Bohrberg Member of the Münder Formation, Berriasian, Lower Cretaceous, Hils Syncline, NW Germany (Arp and Mennerich 2008)
+ Lulworth Formation (Lower Purbeck Group, Portlandian) to Ashdown Formation (lower Hastings Group, lower Wealden Supergroup, Valanginian), Upper Jurassic to Lower Cretaceous of England, UK (Anderson 1971, 1985, Horne 1995, 1997, Kilenyi and Neale 1978)
+ upper unit (U2), (?upper) Berriasian, Aquitaine Basin, Lower Cretaceous, SW France (El Albani et al. 2004)
+ Lower Berriasian to basal Middle Berriasian, Jura Mountains of NE and West Switzerland France (Mojon 2002)
+ 'Purbecko-Wealden' of the North Celtic Sea Basin, Upper Jurassic/Lower Cretaceous (Tithonian? To Valanginian?), offshore southern Ireland (Colin et al. 1981)
+ Cabreton Beds of the Urbion Group (?Berriasian), Lower Cretaceous, Spanish "Wealden", Spain (Kneuper-Haack 1966); Berriasian, Spain (Brenner 1976)
+ Purbeckian (and Portlandian?) Upper Jurassic?, central Poland (Sztejn 1991)

Questionable occurrence:

Europe:
+ Lower Purbeckian, Berriasian?, Lower Cretaceous, Portugal (Ramalho 1971)
+ Purbeckian (sensu gallico: Berriasian), Lower Cretaceous, France (Colin and Oertli, 1985)
+ Lower Cretaceous, Portlandian?, Fastnet Basin, North Atlantic, offshore SW Ireland (Ainsworth 1986)
+ Lower Cretaceous (Top venegated marl, Purbeck), Ile d'Oleron, France (Pinto and Sanguinetti 1962, p. 40, the source of this information is unknown)

South America:
+ lower Bahia Series, "NE Brazilian Wealden", Uppermost Jurassic?/Lower Cretaceous, Brazil (Krömmelbein 1962)

Africa:
+ Lualaba Series, upper Stanleyville Formation, Uppermost Jurassic?/Lower Cretaceous, Democratic Republic of the Congo (Grekoff 1957)

Asia:
+ Dzunbain Formation, Lower Cretaceous (Barremian?), eastern Mongolia (Lyubimova 1956, Neustueva et al. 2005)

Stratigraphic range in North America: Tithonian?, lower to upper Berriasian as inferred from Europe.

Stratigraphic range outside North America: Lower Cretaceous, Berriasian, of Europe (Germany, France, Spain, Portugal). Uppermost Jurassic?/Lower Cretaceous (Portlandian to Valanginian) of England, UK. 'Purbecko-Wealden' offshore southern Ireland. Portlandian?, Purbeckian of Poland, uppermost Jurassic?/Lower Cretaceous of Poland. Questionably: uppermost Jurassic?/Lower Cretaceous of Brazil and Democratic Republic of the Congo, and Lower Cretaceous of the People's Republic of Mongolia.

Theriosynoecum pahasapensis **(Roth 1933) comb. nov.**

(Pl. 1, Figs. 11-14; Pl. 3, Figs. 11-19; Pl. 4, Figs. 1-14)

v*	1933	*Jonesina pahasapensis* sp. nov. – Roth 1933, p. 401, pl. 48, figs. 2a-g
	1933	*Jonesina minnekahtensis* sp. nov. – Roth, p. 399, pl. 48, figs. 1a-g [a female *J. pahasapensis* Roth]
?	1935	*Metacypris minnekahtensis* (Roth) – Branson, p. 521, pl. 57, figs. 15, 16
	1935	*Metacypris pahasapensis* (Roth) – Harper and Sutton, p. 624, pl. 76, figs. 3-11
non	1940	*Gomphocythere pahasapensis* (Roth) – Martin, p. 340, pl. 6, figs. 95-97; pl. 7, figs. 98-100
?	1946	*Metacypris?* sp. aff. *M. pahasapensis* – Swain 1946, p. 543
	1953	*Metacypris pahasapensis* (Roth) – Hoare, p. 46, pl. 2, figs. 25-31, pl. 3, figs. 1-9 [unpubl.]
?	1956	*Metacypris pahasapensis* (Roth) – Peck, fig. 24
?	1958	'*Metacypris*' *pahasapensis* (Roth) – Grekoff, p. 28, pl. 1, figs. 12-14
	1962	*Bisulcocypris pahasapensis* (Roth) – Pinto and Sanguinetti, p. 64, pl. 8, figs. 13-19; pl. 16, figs. 3a-d

non	1974b	*Bisulcocypris* cf. *pahasapensis* (Roth) – Helmdach, p. 18, Fig. 6
pars	1976	*Theriosynoecum castellana* (Kneuper-Haack) – Brenner, p. 161, pl. 15, fig. 1
non	1998	*Bisulcocypris pahasapensis* (Roth) – Schudack, pl. 1, fig. 15

Material: Lakota Formation, South Dakota, many hundred carapaces and valves, samples SBCR LAg1, SBCR LAg2, SBCR LAg3, SBCR LAg3*, SBCR LAg6, SBCR LAh2, SBCR LAh3, SBCR LAh3Tp, LEC 04, EBF 04a, EBF 04a2, EBF 04b, EBF 04b2, REKO 04 (cf. Fig. 9 for details).

Dimensions (in mm): Overall length: 0.86-1.05
Own specimens:

Females	L: 0.98-1.03	H: 0.55-0.58	W: 0.57-0.60
Males	L: 0.94-1.11	H: 0.52-0.57	W: 0.48-0.54

As given in literature (various references):

Females	L: 0.90-1.10	H: ~0.64	W: 0.54-0.64
Males	L: 0.86-1.10	H: ~0.64	W: ~0.44

Type locality and horizon: Roth's (1933) locality, sec. 28, T. 4 N., R. 6 E. (cf. Sohn 1979, p. 7, Fig. 2, Map loc. 8, USGS Mesozoic collection locality no. 30997), Chilson Member? - Unit 2? of the Lakota Formation, 3 miles north of Piedmont, Meade County, South Dakota, USA.

Holotype: USNM No. 74 468, male carapace.
Remarks: Unfortunately, Roth's female holotype of *Jonesina minnekahtensi*s (USNM No. 74 467) is not in its slide in the USNM collection (lost?, USNM visit, BS 2006), but was figured by Pinto and Sanguinetti (1962, pl. 8, fig. 15, dorsal view). A new neotype remains to be designated.

Diagnosis: A species with distinct posterolateral flattening of the carapace and a weaker posteroventral flattening, thereby forming an acute posterolateral cusp at half height, much more strongly developed in females. Posterolateral cusp almost overreaching the posterior margin in adult females. Lateral outline rounded subrhomboidal to rounded rectangular, and elongate. With long straight to slightly convex dorsal part of anterior margin, inclined less than 40° with about 35° usually. Broad anterior marginal zone. Posterolateral inflation of carapace not or very slightly overreaching the posterior margin. Anterior cardinal angle strongly rounded, indistinct. Females with or without posterolateral node-like tuberculum (No. 2, cf. Fig. 6/E, cf. Pl. 4, Figs. 1, 2 and 6) at top of posterolateral projection, males usually with node-like tubercles Nos. 1-4 (Fig. 6/E), both sexes with or without anterior node-like tubercles (A1-A3, as defined herein, see Fig. 6/E).

Description: Carapace shape: Small to medium sized. Carapace moderately rounded subrhomboidal and elongate in lateral view. Maximum length at about half height, maximum height at 3/4 of length, maximum width at about 3/5 of length in both sexes. LV>RV, subequivalve. LV barely recognizable overlapping the RV along entire margin, except a convex, tongue-like overlap ventrally (at about 2/5 of length); and hinge margin, where the flange of the RV's hinge margin overlaps the LV. Weak overreach of the LV at dorsal part of anterior margin.

Anterior margin infracurvate with moderately long, straight to slightly concave dorsal part passing into the anterior cardinal angle and inclined about 35-40°. Anterior marginal zone moderately broad. Posterior margin and outline coincident in both sexes, being weakly infracurvate (♂) or supracurvate (♀), with a short straight dorsal segment passing into the posterior cardinal angle, strongly inclined around 60°. Dorsal margin nearly straight with a very slight concave segment somewhat anterior to its half length (where the middle hinge element is divided), not coincident with dorsal lateral outline. The latter one is straight with a convex segment between 3/5 and 4/5 of carapace length, caused by dorsolateral overreach of the carapace's lateral inflation. Ventral margin slightly convex with a concave segment at about 2/5 of carapace length (below S2-sulcus), where the tongue-like projection is located, not coincident with ventral lateral outline. Ventral lateral outline convex between 1/3 and 2/3 of carapace length due to ventrolateral overreach. Dorsal and ventral margins about parallel. Both cardinal angles in line with the hinge margin, not overreaching. Anterior cardinal angle indistinct and well rounded, strongly obtuse-angled, about 145-150°; posterior cardinal angle well exposed in both dimorphs, moderately obtuse-angled, about 120°, area around it laterally flattened.

Dorsolateral sulci moderately deep incising, the S2-sulcus more than the S1-sulcus (cf. Fig. 6/A), S1-sulcus of about 3/4 length of the S2 one. S2 sulcus reaching downwards to 3/5 of height. Beginning of both sulci in the smaller RV only slightly closer to the hinge line than in the larger LV. Carapace's posterolateral inflation posterodorsally and posteroventrally flattened, more distinctly recognizable in females, thereby forming a posterolateral cusp in both female valves. Cusp coincident with position of—and usually covered by—the middle posterolateral tubercle (see Fig. 6/E, node No. 2), but not caused by the latter. Because of the posterodorsally flattening, the posterior cardinal angle is not covered by the posterior inflation in the female dimorph (brood pouches) at all.

Carapace piriform (♀) or elongated-ovate (♂) in dorsal view, with acute anterior end. Females with slight lateral constriction at position of S2-sulcus and angularity at posterior end due to posterolateral cusp. Both sexes with angular transition to anterior carapace at posterior end of S1-sulcus, more strongly developed in females. Posterior dorsolateral ridge-like protrusion forming a shallow furrow along the posterior hinge margin, extending between position of S2-sulcus and posterior cardinal angle. Hinge line sinuous, LV convex overlapping the RV at cardinal angles, flange of the RV slightly overlapping the LV along hinge margin.

In ventral view slight overlap of the larger LV over the RV with the stronger, tongue-like overlap below the S2-sulcus, at about 2/5 of carapace length.

<u>Ornamentation:</u>

<u>1. Area-wide ornamentation elements/surface characters:</u> Carapace of both sexes regularly punctate. Puncta between 20 and 30μm in diameter, towards outline (ventral view) arranged in more or less concentric rows. Puncta much smaller, more shallowly developed within the sulci and partially distorted (vertically elongated mostly). In marginal areas, ventrally, and in antero- and posteroventral areas up to about half height, punctae arranged in rows separated by carinae. In between the carinae, the punctae are elongated in lateral directions.

A few larger simple lateral pores of about 5μm diameter, as typical for the genus, mostly between, rarely within the puncta. Position of these pores relatively fixed, possible tubercles or tubercle-like nodes originating from them. Two rows of such pores in the anterior marginal zone, parallel to the adjoining margin (see Fig. 6/A). The outer, more marginal row consisting of six (five) pores with shallow tubercles around them of about 20μm diameter, five (four) of them at or below half height and close together, one above half height and distant from the lower ones. The inner row consisting of three to four widely spaced pores, also with shallow tubercles, located at the transition of the anterior flattened zone and the lateral inflated part of the carapace. Several small lateral pores (1-2μm diameter), independent of the punctation in their distribution and with unfixed position.

Regular row of surfacing radial pore canals close to and parallel to the valve's margin, also following the stronger convex tongue of the LV.

<u>2. Local ornamentation elements:</u> Tuberculation common, mainly at posterior end. Females less tuberculate, usually only showing the middle posterolateral tubercle (No. 2, Fig. 6/E) on top of the posterolateral inflation's cusp. Males usually having the posterior tubercles 1-3, sometimes also no. 4, developed (cf. Fig. 6/E), rarely additionally nos. 5 and 6. Both sexes may have the anterolateral node-like tubercles A1-A3 and if this is the case, A3 is more strongly developed (larger) than A1 and A2

(Fig. 6/E). Two rows of shallow and small tubercles around the pores in the anterior marginal zone, parallel to the anterior margin. The lower, more lateral pair of the two pairs of small posterodorsal tubercles (Fig. 6/E, dotted circles) very weakly or not developed, the one close to the margin more or less strong but always recognizable.

Internal characters: Hinge without accommodation groove, all elements being smooth. Significant bipartition of the median hinge element, the posterior part being much narrower than the anterior one (Pl. 1, Figs. 11, 12, 14). Posterior tooth moderately developed, relatively small and narrow. Anterior tooth narrow, even somewhat narrower than the anterior part of the hinge bar. Because of the small size of the terminal hinge elements, the area of the cardinal angles in outer lateral view is not elevated above the hinge margin. Internal bulge of the sulci very weak, barely recognizable. Internal bulge of posterolateral cusp (♀) shallow, but visible.

Inner lamella developed as diagnostic for the genus, anterior free inner lamella slightly striated (1-2 main striae).

Muscle scar pattern: Four adductor muscle scars (AMS) in a vertical row, the upper- and lowermost ones of about the same size (about 30µm), small and ovate; the two middle ones longer and of elongated-elliptic shape, the lower of these is the largest one (about 60µm) about twice as long as the uppermost/lowermost scar. Frontal scar (FS) small, roundish to kidney-shaped, slightly higher than upper AMS. Two mandibular scars (MS) situated slightly below the lowermost AMS. The anterior one lying at a distance from the AMS, below the FS, being distinct, kidney-shaped and deeply incising into the valve; the other being proximal to AMS, indistinct, often barely or not recognizable, and rounded.

Above the AMS, on the internal bulge of the S2-sulcus, a zigzag row of 4-5 round muscle scars of about 40µm diameter occur, and some others in the anterodorsal area (Pl. 4, Fig. 3).

Morphologic variation: Variation mainly in occurrence and development of => *ornamentation* (sensu Sames, herein). Posterolateral tuberculum in female may be present or not. Males usually with the three posterolateral tubercles (Nos. 1-3, Fig. 6/E), the centrolateral one (No. 4, Fig. 6/E) not always present. Weak A3 node-like tuberculum (Fig. 6/E) occasionally developed. Slight variations in height of dorsolateral ridge-like protrusion.

In some male dimorphs, especially when diagenetically flattened laterally, the ventrolateral part of the carapace's lateral inflation mimics a ridge, just because of the flattening and the presence of carinae.

Ontogenetic variation (see Pl. 3, Figs. 11-18): Dorsal margin nearly coinciding with dorsal lateral outline, except for a slight overreach of the elevated ridge-like area ventrodorsally, behind half length. The carapace outline is more elongate and in earlier instars, the maximum height lies anteriorly. Dorsal and ventral margins are not parallel, the dorsal margin is inclined towards the posterior end. The dorsal part of the anterior margin is not yet long and inclined less than 40°, but short and inclined about 45° instead! In addition, the anterior cardinal angle tends to be less obtuse-angled (between 120° and 130° instead of the 150° in adults), and the sulci are more weakly developed the younger the specimen is, which is also the case for the anterior marginal zone that becomes less to barely noticeable. The carapace of younger instars is elliptic in dorsal view, only slightly more acute anteriorly than posteriorly (Pl. 3, Fig. 15).

The surface character in instars tends towards reticulation and is relatively coarser, i.e. the puncta have the same diameter as in adults (~20µm), but the carapace is much smaller. Distortion effects of the surface ornament (e.g. within and around the sulci) are strong. Ornamentation present or nearly absent, some instars may have strong tubercles which may be either conical or hemispherical. Mostly, the pattern of tuberculation follows that of the male adults, sometimes anterior node-like tubercles (Fig. 6/E, Nos. A1 to A3) occur additionally (Pl. 3, Fig. 14). Free inner lamella very narrow, having the same width along anterior, ventral and posterior margins.

Regarding the ontogeny of *T. pahasapensis*, a differentiation of its juveniles and those of *T. fittoni* may be difficult where both species occur together. Further research is necessary.

Dimorphism: Strong sexual dimorphism. Females with fewer local ornamentation elements, strong posterolateral inflation being flattened posterodorsally and posteroventrally, thereby forming a posterolateral cusp with mostly a tuberculum (No. 2) on its top. Piriform in dorsal view with moderate lateral constriction behind S2-sulcus and strong posterior angularity because of the lateral cusp. The latter can slightly overreach the posterior margin which therefore appears to be slightly acute in lateral view.

Males without posterolateral inflation, and usually having posterolateral tubercles (Nos. 1-4) more or less strongly developed, elongated-ovate in dorsal view. Posterior margin almost evenly rounded. Ventrolateral overreaching part of carapace tending to form a narrow ridge curving towards venter and most distinct in its posterior part.

Precocious sexual dimorphism recognizable, protomales somewhat more elongate and usually with posterolateral tubercles.

Discussion: Roth's type material is from the Lakota Formation (not the Morrison Formation, as he formerly believed) and has been studied personally by the present author (USNM collection, June 2006; the holotype of *Jonesina minnekahtensis* syn. *pahasapensis* Roth 1933, USNM No. 74 467 is missing and a neotype remains to be designated). By reason of taxonomic uncertainty, Roth (1933, pl. 48, figs. 1a-g, 2a-g) also mistakenly inverted the orientation of his specimens in that he confused anterior and posterior end and therefore also LV and RV, although he (op. cit., p. 400) points out that "… if they [both species *pahasapansis* and *minnekahtensis*] are truly Jonesinas, then a reversal in orientation is necessary". All features match the diagnosis and description given herein. Although Roth's type locality could not be revisited, the specimens are identical to those recovered by the recent author from the Lakota Formation nearby (eastern Black Hills) and also derive from a coquina at about (exactly?) the same stratigraphic level. Representatives of *T. pahasapensis* are only reported from North America to date. It is possible that this lineage is endemic to North America. However, an occurrence in other continents (especially Asia and South America) is not unlikely.

It is noteworthy that *Theriosynoecum angularis* (Peck 1941), except for its very prominent anterior cardinal angle, is otherwise very similar to *T. pahasapensis* (Roth 1933). As stated before, much of Peck's type and figured material is not in his collection at the University of Missouri anymore (BS visit 2005), and therefore certain confirmation based on the original material is not possible. However, some specimens figured (good drawings) in Peck (1941, pl. 44, figs. 5, 10, 14) strongly resemble *T. pahasapensis.* A close relation of both species is very likely, and bearing in mind that the species *angularis* mainly occurs in upper Lower Cretaceous (Aptian to lower Albian?) formations of Wyoming and Idaho, it is probably a younger relative that evolved from the species *pahasapensis.* This has already pointed out by Hoare (1953, p. 49) who presumed an evolutionary trend from *T. pahasapensis* to *T. angularis* (Peck 1941) and *T. persulcata* (Peck 1941).

Metacypris minnekahtensis (Roth) of Branson (1935, p. 521, pl. 57, figs. 15, 16) seems to match the outline but lacks a description, and due to the insufficient quality of the figures its designation as *T. pahasapensis* (Roth) must remain arguable.

The descriptions and figured specimens of Hoare (1953) fit the diagnosis very well and thus, the identification is doubtlessly considered correct although Hoare's specimens are not in the collection at the University of Missouri (its whereabouts are unknown, R.L. Ethington, pers. comm., BS visit 2005; Hoare, pers. comm. 2007).

Swain (1946, p. 543) mentions a species identified by I.G. Sohn showing some similarities to '*Metacypris*' *pahasapensis* (recte *Theriosynoecum pahasapensis*) from a core sample (Bahia beds, Bay of Todos os Santaos, Brazil). However, there is no other information available and this identification cannot be confirmed.

Metacypris pahasapensis (Roth) in Peck (1956, fig. 24) is most probably a *T. pahasapensis*. Peck's collection includes several species which definitely belong to this species, but due to missing type and some figured material, some uncertainty remains because it is not possible to definitively confirm the identification from the drawings in Peck's publication .

Grekoff (1958) redescribes and refigures some specimens of "*Metacypris*" *pahasapensis* (Roth) after Roth (1933).

Helmdach (1974b) figures (drawing) and describes *Bisulcocypris* cf. *pahasapensis* (Roth) from the Upper Jurassic "*Cetacella armata* Beds" (stratigraphic range of *Cetacella armata*: Late Oxfordian to Late Tithonian), Porto Pinheiro and Porto das Barcas, Portugal and, in addition to his indication of the species, states that "There is little, but existing doubt, that the studied material belongs to the species *pahasapensis*" (op. cit., p. 19). The species of Helmdach is similar to the species *pahasapensis*, but more probably a Late Jurassic ancestor of this species for the following reasons: Original SEM photographs of Helmdach's specimens in his collection at the Fachbereich Paläontologie, Freie Universität Berlin (Berlin, Germany) indeed show strong similarities in outline, i.e. the elongated carapace, the long dorsal part of the anterior margin, the weak posterior dorsolateral overreach and other features, such as the broad anterior marginal zone. However, the diagnostic cusp-forming strong posterodorsal and less stronger posteroventral lateral flattening of the female carapace is not developed in Helmdach's specimens. Additionally, the A1 and A2 sulci are weakly developed and the surface characters in Helmdach's specimens are much stronger developed, forming a distinct reticulation pattern, which is very likely a typical character of this Jurassic representative (see remarks on *Bisulcocypris pahasapensis* of Schudack 1998 below).

One specimen of *T. castellana* (Kneuper-Haack) in Brenner (1976, pl. 15, fig.1, proto(?)female carapace, A-1? Instar) from the Enciso Group of the Celtiberian Chains, Spain, strongly resembles *T. pahasapensis* in outline, general shape and development of the anterior marginal zone and is thus included here.

Bisulcocypris pahasapensis (Roth) of Schudack (1998) is no *T. pahasapensis* (Roth) for the reasons given for Helmdach's (1974b) species (see above). Moreover, the specimens of Helmdach (op. cit.) and Schudack (1998) look identical; both share the reticulation and are believed to be of about the same age (Kimmerdigian). Thus, both latter species are considered not to belong to *T. pahasapensis* (Roth) but to another undetermined (new?) species of Late Jurassic age instead.

Differential Diagnosis: Despite some details in shape (as follows below) *Theriosynoecum pahasapensis* is relatively similar to *T. fittoni* (as described herein), by trend younger than the latter, and thus considered to be closely related and possibly deriving from the North American lineage here designated as *T. fittoni.*

Theriosynoecum pahasapensis differs from *T. alleni* and *T. fittoni* in being more elongate in outline, having a distinctly weaker posterior dorsolateral overreach, and in the long dorsal part of the anterior margin, which is also less strongly inclined (below 40°). The anterior marginal zone of *T. pahasapensis* is also broader and appears more strongly flattenend in dorsal view, especially in the male dimorphs.

Unlike *T. pahasapensis*, *T. forbesii* has no or a very weakly developed anterior marginal zone and thus in dorsal view no distinct constriction behind the anterior apex. The adult female dimorphs of *T. forbesii* are cordiform in dorsal view with a strong posterolateral overreach of the brood pouches, which is not the case in *T. pahasapensis*. The male dimorphs of *T. forbesii* have a weak posterior dorsolateral overreach in lateral view that covers the posterior cardinal angle, whereas in *T. pahasapensis* this overreach is somewhat more distinct and leaves the posterior cardinal angle visible.

In contrast to *T. pahasapensis*, *T. verrucosa* does not have a well-developed anterior marginal zone and therefore no distinct anterior lateral constriction in dorsal view; the posterior cardinal angle is visible in both sexes in lateral view, and both sulci are well defined. In dorsal view, the females of *T. verrucosa* are well rounded posteriorly and elongate piriform, whereas those of *T. pahasapensis* show a posterior angularity and appear more longitudinally jolted.

Paleoecology: As for the genus.

Faunal association (North America): *Cypridea (Pseudocypridina) piedmonti* (Roth 1933), *Cypridea (Pseudocypridina) laeli* Sohn 1979 (!! in samples SBCR LAh3 und LAh3Tp), and representatives of the Cypridoidea: Trapezoidellidae Sohn 1979, i.e. *Trapezoidella rothi* Sohn 1979, *Trapezoidella trapezoidalis* (Roth 19333); Cyprididae, i.e. *Mantelliana*?; the Cytheroidea, i.e. *Stenestroemia*?(known only from sample REKO 04 thus far) and some Darwinuloidea.

Stratigraphic and geographic distribution (Stratigraphic terms follow the most recent terminology available):

<u>North America:</u>

+ Lakota Formation (erroneously designated as Morrison Formation), South Dakota, USA (Roth 1933; Harper and Sutton 1935)

+ upper? Lakota Formation (Chilson Member to Fuson? Member, corresponding to: L1 to L2? informal intervals after Way et al. 1998), eastern Black Hills, South Dakota, USA

+ Cloverly Formation (erroneously designated as Morrison Formation in part), Bighorn Basin, Wyoming, USA (Branson 1935)

+ Draney Limestone (Sub-?)Formation, Lincoln County, Wyoming and Kootenai Formation near Drummond (east of Helena), Granite County, Montana (Hoare 1953)

Stratigraphic range in North America: Lower Cretaceous, upper Berriasian??/Valanginian? [depending on stratigraphic range of *Cypridea (Longispinella) longispina*] to Barremian (questionably up to middle? Albian).

Stratigraphic range outside North America: Not applicable, because the species is thus far unknown outside North America.

Theriosynoecum verrucosa **(Jones 1885) emend.**

(Pl. 3, Figs. 1-10)

v*	1885	*Metacypris forbesii*, and var. *verrucosa* sp. et var. nov. – Jones, p. 345, pl. 8, fig. 14
non	1955a	*Metacypris verrucosa* sp. nov. – Klingler, p. 206, pl. 12, fig. 17a; pl. 13, fig. 17b-d [nom. inval.]
non	1955b	*Metacypris planiverrucosa* nom. nov. subst. pro *Metacypris verrucosa* Klingler 1955a
?	1956	*Theriosynoecum praetuberculata* sp. nov. – Lyubimova, p. 139, pl. 25, figs. 1a-c, 2a-c, 3a, b [recte *T. praetuberculatum*]
non	1957	*Gomphocythere forbesii* (Jones) *planiverrucosa* Klingler – Wicher, p. 269, pl. 1, figs. 1a-c, 2a-c
?	1957	*Metacypris cornuta* sp. nov. – Grekoff, p. 79, pl. 6, figs. 93-95

? 1957 *Metacypris* sp. 390 – Grekoff, p. 84, pl. 6, figs. 93-95

? 1957 *Metacypris trinodosa litokoensis* subsp. nov. – Grekoff, p. 77, pl. 5, figs. 88-92

1962 "*Metacypris*" *verrucosa* (Jones) – Klingler et al., p. 174, pl. 25, fig. 13

1962 *Bisulcocypris verrucosa* (Jones) – Pinto and Sanguinetti, p. 61, pl. 8, figs. 1-4; pl. 16, figs. 1a-d

1971 *Theriosynoecum forbesii verrucosa* (Jones) – Anderson, p. 128, pl. 22, figs. 10, 11

1978 *Bisulcocypris verrucosa* (Jones) – Kilenyi and Neale, p. 312, pl. 5, figs. 5-7, 8[?]

? 1982 *Dryelba pustulosa* sp. nov. – Sohn, p. 314, pl. 3, figs. 1-13; pl. 4, figs. 13-30

1985 *Theriosynoecum forbesi verrucosa* (Jones) – Anderson, p. 38, pl. 2, fig. 8

v 1998 *Bisulcocypris pahasapensis* (Roth) – Schudack, pl. 1, fig. 15

v? 1998 *Bisulcocypris pustulosa* (Sohn) – Schudack, pl. 1, fig. 14

? 1999 *Theriosynoecum praetuberculata* Lyubimova – Nikolaeva and Neustrueva, pl. 17, fig. 10 [recte *T. praetuberculatum*]

2002 *Theriosynoecum forbesii verrucosa* (Jones) – Mojon, pl. 30, fig. B4

? 2004 *Theriosynoecum verrucosa* (Jones) – El Albani et al., p. 198 [not figured]

? 2005 *Theriosynoecum praetuberculata* Lyubimova – Neustrueva et al., pl. 28, fig. 8 [recte *T. praetuberculatum*]

Preceding remarks: The taxa *forbesii* and *verrucosa* (designated mostly as variations or subspecies of *T. forbesii* by various authors) are separated and described as two different species herein for the reasons given (refer to the discussion of the respective species).

The author's own specimens of the North American taxon designated as *T. verrucosa* herein are more or less well preserved but strongly deformed (compressed). Hence, a designation of the North American specimens as *T. verrucosa* is considered preliminary and needs to be confirmed by more data and better preserved specimens.

Material: Over hundred strongly deformed carapaces and valves, upper Morrison Formation, South Dakota, sample RCS MO3 (cf. Fig. 9 for details).

Dimensions (in mm): Overall length: 0.72-0.82 (1.24?)
Author's own specimens (few data, specimens strongly deformed mostly, probably somewhat too long and high due to lateral compression):
Females L: ~1.16 H: ~0.68 W: n/a
Males L: ~1.24 H: ~0.63 W: n/a

As given in literature (various references):
Females L: 0.72-0.76 H: ~0.47 W: n/a
Males L: 0.75-0.82 H: 0.47 W: n/a

Type locality and horizon: Ridgway Bay, Dorset, Middle Purbeck Beds.

Lectotype (designated by Anderson, 1971): *Metacypris forbesii* var. *verrucosa* Jones 1885, male carapace, BMNH In. 39020 (Jones, 1885, slide 61-2, pl. 8, fig. 14).

Diagnosis: Carapace in lateral view rounded subrhomboidal in both sexes, posterior dorsolateral and ventrolateral overreach weak. Long straight dorsal part of anterior margin, inclined about 35-40°. Surface with net-like punctation, especially anterolateral, node-like tubercles occurring in both sexes, in males always present, sometimes in females also. With narrow anterior marginal zone. Sulci moderately developed.

Description: Carapace shape: Small to medium(?) sized. Carapace rounded subrhomboidal in lateral view, males somewhat less high, females somewhat higher due to slight posterior dorsolateral overreach lacking in males. Maximum length at half height, maximum height at or slightly in front of half length (♂) or at 2/3 of length (♀), maximum width at 3/5 of length. LV>RV, subequivalve. LV very slightly overlapping the RV along entire margin except for the tongue-like ventral segment below the S2-sulcus, and the hinge margin where the flange of the RV's hinge margin overlaps the LV. LV very weakly or not overreaching the RV.

Anterior margin infracurvate in both sexes, having a long straight dorsal part inclined around 35-40°. Anterior marginal zone narrow. Posterior margin and outline coincident (♂) or moderately different (♀). Posterior margin slightly supracurvate with a moderately long straight, dorsal segment, inclined about 60°. Posterior lateral outline in females equicurvate, nearly but not completely covering the posterior cardinal angle. Dorsal margin straight, cardinal angles not prominent. Dorsal lateral outline straight and coincident with dorsal margin (♂) or slightly convex posteriorly (♀), due to a very slight overreach of dorsolateral ridge-like protrusion. Ventral margin straight and nearly coincident with ventral lateral outline in males, somewhat differing in females that have a slightly convex posterior ventral margin, between 3/5 and 4/5 of length (overreaching posterior inflation—brood pouches). Dorsal and ventral margins parallel to each other. Both cardinal angles in line with the hinge margin. Anterior cardinal angle broadly rounded and obtuse-angled with about 135-140°. Posterior cardinal angle narrower and less rounded, in lateral view mostly masked in females, about 120°.

Anterior dorsolateral sulci weakly incising, S2-sulcus somewhat more than S1-sulcus, better visible in dorsal view, the latter having about 3/4 the length of the former. S2-sulcus reaching downwards to about 3/5 of height. RV's dorsal beginning of the sulci closer to hinge line than on LV.

Carapace elongated-piriform (♀) or elongated-elliptic (♂) in dorsal view, in both sexes acute towards anterior end with slight lateral constriction close to the apex. Females showing weak posterolateral overreach and having a slight lateral constriction at position of S2-sulcus. Anterior angularity in front of S1-sulcus strongly rounded. Hinge line slightly sinuous, LV overlapping RV at cardinal angles with a convexity, flange of RV's hinge margin overlapping the LV. Ventrally, the tongue-like overlap below S2-sulcus is very weakly developed.

Ornamentation:

1. Area-wide ornamentation elements/surface characters: Carapace of both sexes punctate to finely reticulation-like punctate in no specific pattern except towards anterior and anteroventral margins, where concentric rows are formed. Surface characters in S2 area absent or weakly developed, but definitely occurring in the area of the weak S1-sulcus. Puncta relatively small, about 15µm in diameter. Ventrally, posterolaterally, but especially anterolaterally, the pattern tends to be more coarsely reticulation-like punctate, showing larger puncta ("meshes", 20-25µm in diameter) that are elongated parallel to the anterior and ventral margins. In marginal areas, ventrally as well as in antero- and posteroventral areas up to about half height, puncta or "meshes" elongated and separated by carinae.

A few typical larger simple pores of about 5µm as characteristic for the genus, mostly in between the puncta, with relatively fixed positions.

2. Local ornamentation elements: Main lateral tubercles regularly occurring in males, common in juveniles but also in females. The common tubercle pattern for both sexes, if also occurring in females, is tubercles Nos. 4, 5, 6 plus A3, more seldom No. 2 in addition (cf. Fig. 6/E). The small posterodorsal tubercles close to the posterior cardinal angle are common but may be absent, e.g. in the females without tuberculation.

Internal characters: Not observed, unknown.

Muscle scar pattern: Not observed, unknown.

Morphologic variation: Variation mainly in occurrence of tuberculation especially in females, and in the intensity of its development. The pattern of the occurring main tubercles (lacking the posteroventral tubercles Nos. 1 and 3, Fig. 6/E) is relatively consistent in both sexes, except for tubercle No. 2 (same figure). Additional tubercles not belonging to the main pattern may occur in strongly tuberculate specimens. The node-like tubercles A1 and A2 (Fig. 6/E), adjoining the sulci, never seem to occur. Some variation in the intensity of the surface characters. The female specimen figured by Kilenyi and Neale (1978, pl. 5, fig. 8) seems to have a moderately well defined anterior marginal zone, and it is neither clear whether this is somewhat related to the stronger carapace calcification intensity nor whether this specimen is indeed a representative of *T. verrucosa*.

Ontogenetic variation: Not reported in the literature. However, precocious sexual dimorphism occurs in some of the author's own specimens from the Morrison Formation (see below). In the instars the anterior margin is higher than the posterior one and the dorsal part of the anterior margin more strongly inclined. Surface characters of the same size as in adults. Sulci absent or weakly developed.

Dimorphism: Sexual dimorphism strong. Females with large brood pouches that do not, or only slightly, overreach the posterior and ventral margins, therefore strongly differing from male dimorphs in dorsal outline (♀elongate piriform, ♂ elongated-elliptic). Males always(?) with, females with or without tubercles. Posterior cardinal angle of females almost not visible or totally masked in lateral view. Males without strong posterolateral inflation and with elongated posterior end.

Precocious sexual dimorphism distinct, protomales elongate, protofemales more compact-rectangular (Pl. 3, figs. 7-10).

Discussion: *Metacypris planiverrucosa* Klingler 1955[b] nom. nov. subst. pro *Metacypris verrucosa* Klingler 1955[a] is, as already stated by Klingler (1955b), not identical to *T. forbesii* var. *verrucosa* (Jones), thus neither identical to *T. forbesii* nor to *T. verrucosa* following the taxonomic concept applied herein. *M. planiverrucosa* differs from *T. verrucosa* in having a broader anterior marginal zone (therefore a distinct anterior constriction in dorsal view), and having the maximum width in females at about 4/5 of length instead of 3/5 in the latter. The same applies to *Gomphocythere forbesii* subsp. *planiverrucosa* in Wicher (1957).

The species *Theriosynoecum praetuberculata* Lyubimova 1956 must correctly be named *T. tuberculatum*, following the International Code of Zoological Nomenclature (International Commission on Zoological Nomenclature - ICZN 1999). According to this, "a species-group name, if it is or ends in a Latin or latinized adjective or participle in the nominative singular, must agree in gender with the generic name with which it is at any time combined" (op. cit., article 31, paragraph 31.2. - Agreement in gender). As the gender of *Theriosynoecum* is neuter and *praetuberculatus* (-a, -um) a Latin adjective, the species name must become neuter (i.e. *tuberculatum*), too. This species matches the diagnostic characters, but is only questionably included in *T. verrucosa* due to unavailability of better data (more photographs) for the moment, and the present author could not examine any original material. The specimens figured (drawings) by Lyubimova (1956) are probably juveniles (op. cit., pl. 25, figs. 1a-c, 2a-c).

Grekoff (1957) described *Metacypris cornuta* sp. nov. from the uppermost Stanleyville Formation, northern Congo Basin, Democratic Republic of the Congo. This species is very similar to *Theriosynoecum verrucosa* except for its surface characters (reticulation rather than punctation), which is considered not to be taxonomically significant herein. Because the material could not be personally studied, Grekoff's descriptions are short and his pictures small (op. cit.) and with low contrast, the synonymy has been given with a question mark.

Another species of Grekoff (1957), *Metacypris* sp. 390, is most probably a male *T. verrucosa*. The diagnostic features are present, only the surface characters tend to reticulation rather than punctation. The synonymy is given a question mark because of the small pictures with low contrast and the short description (op. cit.).

Metacypris trinodosa litokoensis subsp. nov. Grekoff 1957 also seems to fit into *T. verrucosa* very well. The characteristic features, especially the weakly defined anterior marginal zone and the faint posterior dorsolateral overreach, are present. The synonymy remains questionable for the same reasons as for *Metacypris cornuta* Grekoff 1957 above.

Bisulcocypris verrucosa (Jones) in Pinto and Sanguinetti (1962) is synonymous with *Metacypris forbesii* var. *verrucosa* Jones 1885 (see above), which is also the case for "*Metacypris*" *verrucosa* (Jones) in Klingler et al. (1962). Pinto and Sanguinetti (1962) already distinguished between the species *forbesii* and *verrucosa* based on the presence of node-like tubercles, but also stated that some specimens lack them. Following Pinto and Sanguinetti (1962, p. 62), these specimens should be differentiated from the species *forbesii* by the absence of the posterolateral expansion, less deeper-reaching sulci and "not [being] 'kritheform' …".

Theriosynoecum forbesii verrucosa (Jones) in Anderson (1971) is designated as species *verrucosa* here for the reason given above, and not a subspecies of *T. forbesii.*

Kilenyi and Neale (1978) also separate *T. verrucosa* (although they use *Bisulcocypris* instead of *Theriosynoecum*) from *T. forbesii* and show good photographs. The specimen shown on pl. 5, fig. 8 (op. cit.) is most probably a female *T. verrucosa* with strong node-like tubercles, the synonymy of which is slightly questionable because this specimen seems to have an unusual broad anterior marginal zone.

Dryelba pustulosa Sohn 1982 [recte *Theriosynoecum pustulosa*] is a strongly ornamented form showing similarity to the author's own specimens of *T.* verrucosa from the upper Morrison Formation of the Red Canyon, southern Black Hills (Fig. 2, loc. 4), except that the latter only have weak tubercles (males) and no nodes or node-like tubercles. Sohn (1982) based his diagnosis solely on (optional) => *ornamentation* elements and therefore just described a strongly ornamented ecophenotype. His (op. cit.) species also shows a strongly developed reticulation-like punctation with deep puncta, even at the node-like tubercles and strong calcification pointing to a high calcium availability. Leaving aside the ornamentation and the intensity of the surface characters, *T. pustulosa* has the same outline (also in juveniles), position and development of sulci as well as the narrow laterally flattened anterior marginal zone (covered by distinct surface characters) as *T. verrucosa*. Therefore, it is included in the North American taxon preliminarily designated here as *T. verrucosa*.

The identification of *Bisulcocypris pahasapensis* [recte *Theriosynoecum pahasapensis*] by Schudack (1998) is considered wrong because this species does not show the diagnostic characters of *T. pahasapensis*, such as the broad anterior marginal zone, the distinctly below 40°(around 35°) inclination of the dorsal part of the anterior margin, the posterolateral cusp, the weak posterior dorsolateral overreach, and the highly rounded anterior cardinal angle. In fact, Schudack's (op. cit.) species is identical with the North American species assigned here to *Theriosynoecum verrucosa*.

For *Bisulcocypris pustulosa* (Sohn 1982) in Schudack (1998), the same arguments as to *Dryelba pustulosa* Sohn 1982 (see above) apply.

The specimen of *Theriosynoecum praetuberculata* [recte *T. praetuberculatum*] figured in Nikolaeva and Neustrueva (1999, pl. 17, fig. 10, male dimorph) matches the diagnostic characters but is only questionably included in *T. verrucosa* due to unavailability of more information for the moment. This specimen also has a strong reticulation-like punctation, atypically also covering the A2 node-like tuberculum.

Theriosynoecum forbesii verrucosa figured in Mojon (2002, pl. 30, fig. B4) is a female *T. verrucosa* because of the distinct anterior marginal zone and the piriform (not cordiform) dorsal outline.

Theriosynoecum verrucosa in El Albani (2004) is only mentioned, without description or figure, and therefore indicated with a question mark.

The affiliation of the *Theriosynoecum praetuberculata* [recte *T. tuberculatum*] specimen as figured in Neustrueva et al. (2005, pl. 28, fig. 8) is difficult to judge and therefore given tentatively. The specimen has a narrow anterior marginal zone as typical for *T. verrucosa* but seems to be a juvenile and shows moderate nodes covered by puncta.

Differential diagnosis: *Theriosynoecum verrucosa* differs from *T. alleni* and *T. fittoni* in having almost no anterior marginal zone, a less strongly inclined dorsal part of the anterior margin (35-40° instead of 45°) and a very weak posterior dorsolateral overreach which almost completely covers the posterior cardinal angle.

In contrast to *Theriosynoecum verrucosa*, *T. forbesii* has broader sulci, but these are not well-defined. The males of *T. forbesii* show a strong ventrolateral overreach, whereas in *T. verrucosa* the ventral lateral outline and margin are nearly coincident and straight. The female representatives of *T. verrucosa* are piriform in dorsal view, not cordiform, and thus have little or no posterolateral overreach and evenly rounded posterior flanks and only show a weak ventrolateral overreach in lateral view as well.

Representatives of *T. pahasapensis* have a strongly developed laterally flattened anterior marginal zone and therefore a distinct anterior lateral constriction in dorsal view. They also show very distinct sulci; the posterior cardinal angle is always well visible in both sexes in lateral view. Females of *T. pahasapensis* appear longitudinally jolted in dorsal view and show their characteristic posterior angularity.

Paleoecology: As for the genus.

Faunal association (North America): with representatives of the Darwinuloidea and some Cypridoidea (*Paracypris*?)

Stratigraphic and geographic distribution (Stratigraphic terms follow the most recent terminology available):

North America:
+ uppermost Morrison Formation, Red Canyon (Fig. 2, loc. 4), southern Black Hills area, South Dakota, USA

Europe:
+ Lulworth Formation (Lower Purbeck Group, Portlandian), lower Berriasian, to Ashdown Formation (lower Hastings Group, lower Wealden Supergroup), Valanginian (equals the Warren to Eastbourne faunicycles of Anderson 1985), Upper Jurassic to Lower Cretaceous of England, UK (Anderson 1971, 1985, Horne 1995, 1997, Kilenyi and Neale 1978)
+ Upper Münder Formation and Serpulit Subformation, Lower Cretaceous, lower to middle Berriasian, NW Germany (Klingler et al. 1962, Schudack 1994, Gramann et al. 1997)
+ Lower Berriasian to basal Middle Berriasian, Jura Mountains of NE and West Switzerland France (Mojon 2002)

Remark: Concerning the detailed stratigraphic distribution and range of *T. verrucosa* in the English Purbeck Group and Wealden Supergroup, Anderson (1985) gives *T. verrucosa* as subspecies of *T. forbesii*, and thus it is not possible to differ between the two. An occurrence in the uppermost Tithonian might be possible.

Questionable occurrence:

Africa:
+ Ruiki and Lilo members(?) of the Stanleyville Formation, Lualaba Series, northern Congo Basin, uppermost Jurassic, Democratic Republic of the Congo (formerly Zaire), West Africa

Europe:
+ upper unit (U2), (?upper) Berriasian, Aquitaine Basin, Lower Cretaceous, SW France (El Albani et al. 2004)

Asia:
+ Dzunbain Formation, Lower Cretaceous (Barremian?), Mongolia (Lyubimova 1956)
+ Zazin Formation, Lower Cretaceous (Hauterivian-Barremian?), Transbaikalia, Russia (Nikolaeva and Neustrueva 1999)

Stratigraphic range in North America: Lower to middle Berriasian as inferred from Europe. Questionably uppermost Tithonian to lower Valanginian (if considered subspecies of *Theriosynoecum forbesii*.

Stratigraphic range outside North America: Europe: Uppermost Jurassic?/Lower Cretaceous, lower Berriasian to middle Berriasian, possibly up to lower Valanginian (upper Tithonian?/Berriasian *Theriosynoecum forbesi* Zone sensu Horne 1995 and Warren, No. 2, to Eastbourne, No. 43, faunicycles of Anderson 1985, lower Berriasian to lowermost Valanginian after Hoedemaeker and Herngreen 2003, England, UK; Katzberg Member of the Münder Formation and Serpulit Subformation, lower to middle Berriasian, Germany; lower Berriasian to basal middle Berriasian of NW France and Switzerland). Africa (questionable): Uppermost Jurassic (Tithonian), Democratic Republic of the Congo. Asia (questionable): Lower Cretaceous of Mongolia and Russia.

6. Discussion

6.1. Outline comparisons and discussion of the assignment of North American species to *T. fittoni*

6.1.1. Discussion of outline comparisons

Remark: The discussion under this item and the given indices refer to Fig. 10 herein if not otherwise identified. The specimens used in Fig. 10 are not to scale. They have been scaled to sizes as appropriate for best graphic illustration of the text (i.e. the white specimens were scaled down mostly to fit them into the dark grey ones for the purpose of making the differences more visible).

As already stated in the discussion of *T. alleni* (see Chapter 5.4), the validity of this species may have to be challenged and tentatively considered a possible junior synonym of *T. fittoni* (Mantell 1844). Besides the fact that the species *T. alleni* was only established based on few => *local ornamentation* elements (particularly the => *node-like tubercles* A1 and A3, see Fig. 6/E) that are ecophenotypic and optional, Pinto and Sanguinetti (1962) already pointed out in their discussion that this species is very similar to '*Bisulcocypris*' *fittoni*, '*Bisulcyocypris*' *martini* Pinto and Sanguinetti 1962 (considered to be synonym of *T. fittoni* herein, see discussion of this species in taxonomy section), and *Theriosynoecum praetuberculata*

Lyubimova 1956 (most probably another synonym of *T. fittoni* as well). Moreover, the types of both taxa derive from the English Wealden deposits.

By visually comparing the lateral and dorsal outlines of specimens of *Theriosynoecum alleni* (Pinto and Sanguinetti 1962) with *T. fittoni* (Mantell 1844) from Europe (English Wealden) as well as European specimens of *T. fittoni* with own specimens from North America (Lakota Formation, Black Hills, South Dakota), strong similarities can be demonstrated, e.g. in the positions and development of diagnostic characters, such as the cardinal angles (b, c), the position of the posterior dorsolateral overreach (d) or antero- and posteroventral regions (i, j), the anterior lateral constriction (anterior marginal zone, k), the lateral constriction at the S2-sulcus (m), and the maximum width (n). However, there are also some differences to be discussed in the following.

Example A in Fig. 10 shows that the superimposed lateral outlines of a male paratype of *T. alleni* (3) and a specimen of *T. fittoni* (8) are very similar to each other except for the dorsal region directly in front of the posterior cardinal angle. However, the figure of the former specimen is of moderate quality and has been rounded when the photo was cut out with scissors to mount the plate (this also can affect the ventrolateral overreach usually straightened then).

A comparison of female specimens of *T. alleni* (paratype) and *T. fittoni* (lectotype) given in example C in Fig. 10 shows differences in the position of the posterior dorsolateral overreach/position of maximum height (d), one of the few more or less significant morphologic characters allowing a differentiation between both species thus far. Only to some extent do these differences result from—and are amplified by—the strong development of local ornamentation elements in this region, particularly connected with an additional dorsolateral node and/or node-like tuberculum in some specimens (see, for example, Pl. 5, Figs. 6b, 7b, and Fig. 10, specimen 6 and 7 herein), which leads to an atypical stronger posterior dorsolateral overreach (d) and outline deviation.

The comparison of female lateral outlines (Fig. 10/E) of a specimen from North America designated as *T. fittoni* herein with one of the same species from the UK shows some stronger differences anteriorly, especially in the inclination of the straight dorsal part of the anterior margins (a) and the position of the anteroventral region (i). However, in general the outlines match relatively well and the specimens intentionally chosen differ in that the North American one (12) has almost no local ornamentation elements, whereas the British one (7) is strongly ornamented (also showing the additional dorsolateral tubercle at position of maximum height). This example is to demonstrate the difficulties that can occur while dealing with the literature and having to rely on figures, if the descriptions are not detailed enough (or one does not understand the language in which the paper is published). The original figure of specimen 7 in Fig. 10/E (see also Pl. 5, Fig. 7b herein) is unfortunately not of adequate quality to show important details clearly. It seems that the A3 node-like tuberculum (cf. Fig. 6/E) is accompanied by another one directly behind and slightly below it, the border area of which overreaches the ventral margin and causes an angularity in the outline that gives the impression of a more posteriorly lying anteroventral region. The same applies to example F in Fig. 10 – the conformity of both male specimens, however, is even better with exception of the anteroventral region again.

By comparing dorsal views (Fig. 10, examples B and D, comparing North American species assigned to *T. fittoni* with types of *T. alleni*), many conformities can be demonstrated. Although there seem to be some distinct differences due to the absolute size of adults or an inclusion of an ontogenetic stage (specimen 11 is a preadult A-1 specimen), the important characters match quite well: In both examples, the anterior lateral constriction (k), the angularity at the position of the S1-sulcus (l), the lateral constriction at the S2-sulcus (m), the position of the maximum width (n), as well as the posterior angularity in males (o) and position of tubercle pair No. 4 in females (p) are at the same position. Example B even shows that such comparison based on diagnostic characters also works with late preadults (specimen 11; specimen 1a is slightly inclined to the right), whereas example D shows the same with specimens of different maximum size (length of specimen 2a: 1.05mm, length of specimen 13: 0.89mm).

The previous discussion and comparison would imply that: a) as already stated, *Theriosynoecum alleni* and *Theriosynoecum fittoni* are morphologically very similar, especially when the lateral views and outlines are compared, b) the North American specimens designated as *T. fittoni* herein show somewhat stronger differences to the types of *T. alleni* in lateral view and outline but match the latter quite well in dorsal view, and c) the males seem to match somewhat better.

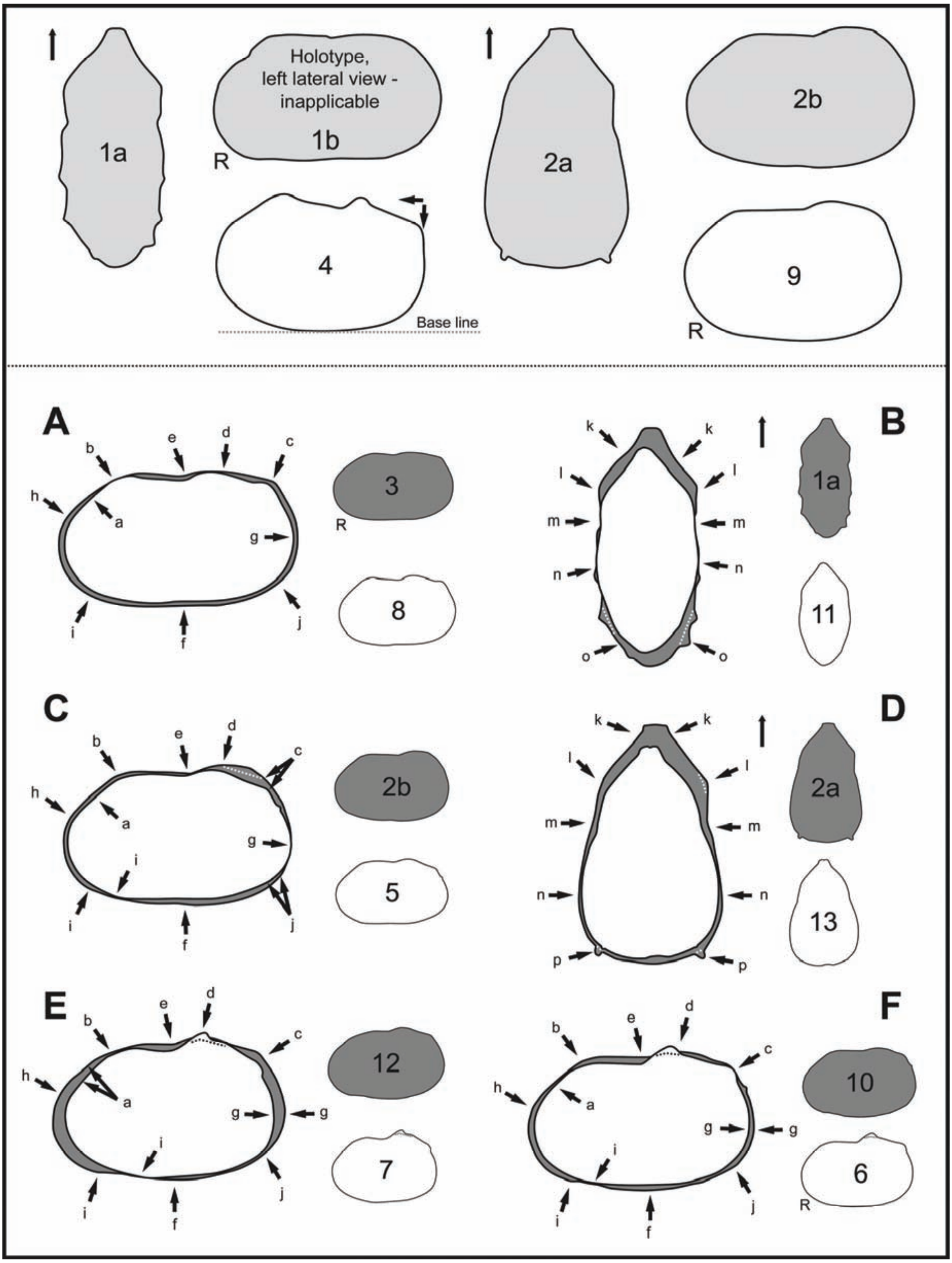
However, it has to be pointed out that the selection of some type specimens (especially the holotype) of *Theriosynoecum alleni* is disadvantageous, and the quality of the figures as well as the diagnosis is insufficient. The specimen of a female *Theriosynoecum alleni* as figured by Anderson (1985, pl. 7, fig. 15) shows an atypical feature, namely the strongly developed area-wide ornamentation elements/surface characters: almost a reticulation (instead of reticulation-like punctation) that even covers the anterolateral sulci and is also prominent at the anterior marginal zone as well as on the node-like tubercles.

Fig. 10. (see following page): Outline comparisons (lateral and dorsal outlines) of representatives of *Theriosynoecum alleni* (Pinto and Sanguinetti 1962) and *Theriosynoecum fittoni* (Mantell 1844) – all lateral views from the left, i.e. anterior ends left. Specimens not to scale but transformed to about same size for better comparison. Since the valves in *Theriosynoecum* are subequal (subequivalve), the outlines of some specimens (if not available in left lateral view) have been reversed (indicated with "**R**") to achieve the lateral left view in all specimens for reasons of better comparison. Types of *T. alleni* in light grey.

Description (upper case): A) Outline comparison of left lateral views of males of *T. alleni* and *T. fittoni*. B) Outline comparison of dorsal views of males of *T. alleni* (holotype) and *T. fittoni*. C) Outline comparison of left lateral views of females of *T. alleni* (paratype) and *T. fittoni*. D) Outline comparison of dorsal views of females of *T. allleni* (paratype) and *T. fittoni*. E) Outline comparison of left lateral views of females of *T. fittoni* from North America and the UK. F) Outline comparison of left lateral views of males of *T. fittoni* from North America and the UK.

Character index (lower case): a) Straight dorsal part of anterior margin. b) Anterior cardinal angle. c) Posterior cardinal angle. d) Posterior dorsolateral overreach. e) Concave transition from anterior part of dorsal outline into posterior dorsolateral overreach. f) Ventral lateral outline, in part coincident with ventral margin. g) Posterior margin, position of maximum length. h) Transition from curved part of anterior margin into its straight dorsal part. i) Anteroventral region. j) Posteroventral region. k) Anterior lateral constriction at transition from anterior marginal zone to anterocentral area. l) Angularity at position of S1-sulcus. m) lateral constriction, position of S2-sulcus. n) Position of maximum width. o) Posterior angularity in dorsal view of males. p) Position of tubercle pair no. 4 (see Fig. 6/E herein).

Specimen index: 1a) *Theriosynoecum alleni* (Pinto and Sanguinetti), holotype M.P., U.R.G.S. MP-0-50A, length: 1.06mm, dorsal view of male, Pl. 5, Fig. 1a herein. **1b)** *Theriosynoecum alleni* (Pinto and Sanguinetti), holotype M.P., U.R.G.S. MP-0-50A, length: 1.06mm, reversed right lateral view of male, Pl. 5, Fig. 1b herein. **2a)** *Theriosynoecum alleni* (Pinto and Sanguinetti), paratype M.P., U.R.G.S. MP-0-50B, length: 1.05mm, dorsal view of female, Pl. 5, Fig. 2a herein. **2b)** *Theriosynoecum alleni* (Pinto and Sanguinetti), paratype M.P., U.R.G.S. MP-0-50B, length: 1.05mm, left lateral view of female, Pl. 5, Fig. 2b herein. **3)** *Theriosynoecum alleni* Pinto and Sanguinetti, paratype M.P., U.R.G.S., M.P.-0-51A, length: 1.10mm, reversed right lateral view of a male, Pl. 5, Fig. 3a herein. **4)** *Theriosynoecum fittoni* (Mantell) as figured by Anderson (1985), BGS Mik(M) 4498, length 1.00mm, male(?) left lateral view, extremely strong ornamentation, probably an A-1 or A-2 instar with precocious sexual dimorphism, Pl. 5, Fig. 4 herein. **5)** *Theriosynoecum fittoni* (Mantell) as figured by Anderson (1985), lectotype BGS Mik(M) 1905, length 0.95mm, lateral left view of a female, Pl. 5, Fig. 5 herein. **6)** '*Bisulcocypris*' *fittoni* (Mantell) as figured in Pinto and Sanguinetti 1962, M.P., U.R.G.S., M.P.-0-24A, length: 1.20mm, reversed right lateral view of male carapace with strong tuberculation, Pl. 5, Fig. 6b herein. **7)** '*Bisulcocypris*' *fittoni* (Mantell) as figured in Pinto and Sanguinetti 1962, M.P., U.R.G.S., M.P.-0-24B, length: 1.10mm, left lateral view of female carapace with strong tuberculation, Pl. 5, Fig. 7b herein. **8)** *Theriosynoecum fittoni* (Mantell) as figured in Kilenyi and Neale (1978), SJCC 68/28.5, length: 1.04mm, left lateral view of male left valve (designated as female specimen by Kilenyi and Neale), Pl. 5, Fig. 10 herein. **9)** *Theriosynoecum fittoni* (Mantell) as figured by Kilenyi and Neale (1978), SJCC 68/28.6, length: 0.96mm, reversed right lateral view of female carapace, Pl. 5, Fig. 11 herein. **10)** *Theriosynoecum fittoni* (Mantell), length: 0.95mm, lateral view of male left valve with weak tuberculation, Pl. 2, Fig. 12 and Pl. 5, Fig. 13 herein. **11)** *Theriosynoecum fittoni* (Mantell), length: 0.86mm, dorsal view of preadult (A-1) male carapace, Pl. 1, Fig. 5 and Pl. 5, Fig. 14 herein. **12)** *Theriosynoecum fittoni* (Mantell), length: 0.96mm, lateral view of female left valve, Pl. 12, Fig. 1 and Pl. 5, Fig. 15 herein. **13)** *Theriosynoecum fittoni* (Mantell), length: 0.89mm, dorsal view of female carapace.


1a
Holotype,
left lateral view -
inapplicable
1b
R
2a
2b
4
Base line
9
R
A
b
e
d
c
h
a
g
i
f
j
3
R
8
B
k
l
m
n
o
1a
11
C
b
e
d
c
h
a
g
i
f
j
2b
5
D
k
l
m
n
p
2a
13
E
b
e
d
c
h
a
g
i
f
j
12
7
F
b
e
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6
R

Fig. 10

Altogether, more specimens and particularly internal views of the European specimens of *Theriosynoecum fittoni* (and *T. alleni* as well) are required for better identification of the relevant characters, more exact measures for morphometric analyses, and to prevent wrong measurements resulting from measuring less diagnostic characters. Yet, some characters, such as the straight dorsal part of the anterior margin, are better to identify and to locate from the outer view.

6.1.2. The taxonomic status of the North American taxon assigned to *Theriosynoecum fittoni*

Apart from the results of the outline comparison, one question remains: Can the North American species from the Lower Cretaceous Lakota Formation be identified as *Theriosynoecum fittoni* (Mantell 1844), and what are the arguments to support or refute this hypothesis?

The specimens from the Lakota Formation identified as *Theriosynoecum fittoni* (Mantell) herein (including other North American species integrated as given in the synonymy list), lack strong ornamentation, especially the anterolateral node-like tubercles (A1-A3, cf. Fig. 6/E) very common to the Wealden specimens of England (pointing to different paleoenvironmental conditions, e.g. salinity realm, salinity concentration, precipitation, type and permanence of water bodies, which cannot be elucidated in detail here and are to be published elsewhere), but are in most other respects very similar if not identical to the latter. This concerns the lateral and dorsal outlines including the relatively short anterior end in front of the posterolateral inflation, the position of maximum length and height, the moderate convex overreach of the ventrolateral carapace inflation over the ventral margin, the strong posterior dorsolateral overreach, the length and inclination of the dorsal straight part of the anterior margin, the development of the cardinal angles, the broad anterior marginal zone and its marginal shape as well as its weak cover by area-wide ornamentation elements, the position of major pores around which tubercles or node-like tubercles can be developed; and the position, length and development of the sulci.

Altogether, the arguments for *Theriosynoecum fittoni* of NW Europe being conspecific with the North American species are very strong, although there are some slight differences in shape and more data about internal features of the former are needed. In addition, the age of the North American sediments is roughly the same, even when just based on the available data from the second half of the 20th century. Moreover, representatives of the Timiriaseviinae, which all have brood care, can be distributed alive over long distances (especially females carrying eggs/juveniles) by larger animals migrating between permanent water bodies, and possibly storms carrying considerable amounts of water (hurricanes/cyclones, typhoons).

With the data at hand, it makes no sense to assign the North American species to a different, potentially even new, taxon. Quite the contrary: assigning this species to *Theriosynoecum fittoni* (Mantell 1844) is the most justifiable solution at the moment. Concerning the relationship of *T. alleni* and *T. fittoni*, an inclusion of the American specimens of *T. fittoni* might be helpful towards a solution of this problem.

6.2. Stratigraphic distribution, paleobiogeography and extinction of *Theriosynoecum* in North America and other continents

The extinction of most fossil representatives of the Timiriaseviinae (*Theriosynoecum*, *Timiriasevia*, early *Metacypris*) has been discussed in some detail by Colin and Danielopol (1979). These authors favor a combination of intrinsic and extrinsic factors that led to the worldwide extinction of representatives of *Theriosynoecum* during Aptian to Albian times (note of the present author: some forms possibly survived till Cenomanian times, see also discussion in Chapter 5.2 herein, under 'stratigraphic range' of the genus), as well as those of *Timiriasevia* during the Paleocene. Their (Colin and Danielopol 1979) arguments are based on the linking of recent and fossil representatives of the Timiriaseviinae (cf. Colin and Danieleopol 1978, 1980) and the conclusion that a K-strategy [also K-selection] is conceivable for the fossil representatives, as Colin and Danielopol (1979) presume for most of the taxa of recent Timiriaseviinae.

Following Colin and Danielopol (op. cit., p. 746), recent Timiriaseviinae "… live in ecologically stable and/or biologically controlled environments …" and "… evolve toward the maintenance of their population at the equilibrium level …". Such species "develop specializations toward the lowering of fecundity [a measure of fertility, i.e. the actual number of offprings an organism can produce during its lifetime], the increasing of the parental care and of interspecific competitivity" (op. cit., p. 746). Fossil Timiriaseviinae, i.e. *Theriosynoecum* and *Metacypris*, are believed to have had a similar reproductive strategy (Colin and Danielopol 1979) due to the possession of posteriorly inflated female carapaces (brood pouches), indicating brood care and a relatively low number of offspring. The same authors (op. cit.) also argue that these fossil Timiriaseviinae had narrow ecologic tolerance limits and seem to have been restricted by the dominating Cyprid<u>e</u>idae (as used herein, fam. Cyprididae/subfam. Cyprid<u>e</u>inae therein!). Colin and Danielopol (1979) conclude that:

> 1) where great numbers (diversity) of the Timiriaseviinae occur, there are no or few Cyprideidae,
> 2) Timiriaseviinae progressively disappear while the Cyprideidae persist,
> 3) once a timiriaseviinid species had disappeared from a certain stratigraphic level, there was nearly no chance for it to reoccur in higher levels,
> 4) the fossil Timiriaseviinae as a whole occurred on the main continents [except Australia and Antarctica thus far] but the majority of the species were relatively endemic,
> 5) many species of the Timiriaseviinae are either stenotopic (i.e. able to adapt only to a narrow range of environmental conditions) or have/had low possibilities of expansion into other habitats or distribution to other geographic areas.

However, our knowledge about occurrence and the worldwide distribution of Lower Cretaceous nonmarine ostracods has increased since, as well as our understanding of dispersal and reproduction mechanisms of nonmarine Ostracoda. Thus, some arguments of Colin and Danielopol (1979) have to be taken up and discussed from new points of view (numbers in brackets in the following refer to the arguments of Colin and Danieleopol as summarized above):

A) Regarding the occurrence of Timiriaseviinae together with Cyprideidae (1), there is evidence now that representatives of both groups can co-occur in great numbers. Some of the author's own samples from the Lakota Formation—e.g. samples SBCR LAg3* with more than five hundred specimens of *Theriosynoecum pahasapensis*, several hundred specimens of *Cypridea (Pseudocypridina) piedmonti* and few darwinuloids, and HSDC3 with more than hundred specimens of *Theriosynoecum fittoni*, several hundred specimens of *Cypridea (Pseudocypridina) piedmonti* as well as few specimens of *C. (P.) piedmonti* var. *henrybelli*—show high numbers of Cyprideidae (*Cypridea*) and Timiriaseviinae (*Theriosynoecum*) together, although the particular genera are represented by low diversity assemblages—the reasons for both phenomena still having to be analyzed. After Horne (2002, p. 63) "… associations of *Theriosynoecum*, *Darwinula* and cypridoideans including *Cypridea* could represent the anion-enrichment pathway …", one possible concentration path followed by nonmarine waters during evaporation. If such a co-occurence of Cyprideidae and Timiriaseviinae is not the case, which seems to be the common situation, one important cause might be that the timiriaseviins (e.g. *Theriosynoecum* with its recent counterpart *Gomphodella*) are presumed to have been living in permanent water bodies (Horne 2002)—i.e. lakes, in particular, that were possibly saline (but athalassic, i.e. characterized by waters not deriving their salinity from the influence of marine waters) in part and that represent the relatively stable environments necessary for Timiriaseviinae—and not in ephemeral lakes and ponds or temporary pools, like many nonmarine Cypridoidea (e.g. representatives of *Cypridea*). The 'characteristic' domination (diversity) of many Purbeck/Wealden-like faunas by representatives of the Cyprideidae is therefore to a great extent related to the paleoenvironment. Furthermore, the domination (diversity) of Cyprideidae (as well as other cypridoidean taxa, respectively) in Purbeck/Wealden-like deposits is still to be questioned. Cytheroidea may have been overlooked, in part certainly due to their (small) size, ignored or misidentified (refer to Chapter 6.3 below also).

B) Colin and Danielopol argued that Timiriaseviinae were suppressed where the Cyprideidae persisted and hardly ever reappeared in higher stratigraphic levels once they had gone (2 and 3). This seems not to be the case for the Lower Cretaceous Lakota Formation in South Dakota, for example, but since stratigraphic uncertainties remain, a final conclusion cannot be drawn. Many Purbeck/Wealden-like sediments (in Europe, West Africa, eastern South America) including those of the type area of the Purbeck and Wealden (southern England), have most probably been deposited in paleoenvironments close to and with periodic connection to/influence by the sea, whereas the paleoecosystems in the gigantic Western Interior foreland basin were mostly far from the sea and show no marine influence during Early Cretaceous times until middle/late Albian. This does, of course, not exclude athalassic (waters not deriving their salinity from the influence of marine waters) saline inland waterbodies in the Western Interior. Concerning the Timiriaseviinae, the extensive nonmarine Western Interior foreland basin seems to have been a retreat area that enabled the reoccupation of local areas where these ostracods disappeared for some time due to local causes (or are just not preserved or not yet documented). This concept might also apply to large areas in Central Asia. Thus, North America and Central Asia are special cases in comparison to the "classical" Purbeck/Wealden-like areas, or these paleoenvironments are rather not directly comparable.

However, as for the detailed successive stratigraphic distribution of nonmarine Upper Jurassic/Lower Cretaceous ostracods in North America the data are not yet sufficient to draw final conclusions. Nevertheless, the results presented herein provide a good base for future research and show that the concept applied is promising.

C) Fossil representatives of the Timiriaseviinae (e.g. *Theriosynoecum*, *Metacypris*) were not as endemic as formerly believed (4 and 5). This is an essential starting point of the project from which this paper originates because it renders an intercontinental biostratigraphic application of representatives of these genera possible, a concept that can be demonstrated by the results of this project.

In the early 1970s, McKenzie (1971) summarized and discussed some ideas—although mostly speculative (op. cit., p. 228) at the time—about variable possibilities of dispersal mechanisms in nonmarine Ostracoda in the context of their reproduction modes, but also pointed out that "the interpretations offered … may seem speculative but are susceptible to the objective test provided by the fossil record" (op. cit., p 228). He (op. cit.) also considered distribution through transport of ostracod eggs (desiccation resistant eggs) and whole ostracods by wind (in a stage of torpidity) or larger animals. The wind-transportation hypothesis has also been inferred by Sohn (1969) for Lower Cretaceous ostracods (e.g. *Cypridea*). Later, Sohn (1992) even considered high-altitude winds as a possible transportation medium for ostracods. Based on widely distributed representatives of *Theriosynoecum* in the northern hemisphere, Helmdach (1979) resumed the discussion focusing on possible long-distance wind distribution (by trade winds) during Late Jurassic to Cretaceous times.

Since the publication of McKenzie's (1971) paper, the fossil record and intercontinental correlations of Late Mesozoic Timiriaseviinae have successively expanded to some extent (e.g. Grekoff 1953, 1960, Pinto and Sanguinetti 1962, Krömmelbein 1966, Quiquing and Whatley 1990, Schudack 1996, Schudack 1998). Combined with the increased knowledge and better understanding of distributional and reproduction mechanisms and ecology of ostracods (see, for example, Carbonel et al. 1988, Whatley 1990, 1992, Griffiths and Horne 1998, Horne and Martens 1998, Horne 2002, 2003) as well as cognition of the fact that carapace ornamentation has been strongly overestimated in the past (see herein), it must be concluded to date that representatives of the Timiriaseviinae had a good potential to be distributed over long distances, even intercontinentally.

Considering the high number of publications on Late Jurassic/Early Cretaceous nonmarine ostracods from China, there are few reports of representatives of *Theriosynoecum* (or alternatively *Metacypris*, *Bisulcocypris*, *Gomphocythere*) from the Early Cretaceous of China (e.g. Li 1988, Qiquing and Whatley 1990, Ye 1994, Ye and Zhang 1991, Zhang 1987, Zhang et al. 2006), some of them stratigraphic overviews just mentioning the genus name. Other Timiriaseviinae (e.g. *Timiriasevia*) are reported more often and with moderate diversity in part. The reasons are not clear yet and have to be investigated.

Concerning the U.S. part of the Western Interior foreland basin as well as the Canadian part, representatives of *Theriosynoecum* seem to have been finally become extinct during Albian times, possibly caused by climatic changes and/or the disappearance of the lacustrine basins in the foreland basin, resulting from the marine transgressions that started in middle-late Albian times and led to the Late Cretaceous "Western Interior Seaway". An occurrence of *Theriosynoecum* up to the Albian of the U.S. Western Interior has been documented by Peck (1956, 1959) or Peck and Craig (1962), for example. Based on the sparse information available from Peck's localities and sample horizons, it cannot totally be ruled out that in proximal parts of the foreland basin (e.g. upper Cedar Mountain Formation, Utah, or Bear River Formation, Wyoming and Idaho) some forms survived until early Cenomanian times because they were affected by transgressive events at a later date.

Regarding the intensity of the effect of "Mid-Cretaceous" (Aptian to Cenomanian) climatic changes on the extinction of *Theriosynoecum*, this must remain speculative to date particularly with regard to the different climate model simulations and their interpretations, in part being controversially disputed, as well as regional modifications of these. Another question remaining is: Has *Theriosynoecum* become extinct or just been replaced by/evolved to *Metacypris* (or another taxon)? However, this goes beyond the scope of this paper and has to be dealt with separately. But again, the results presented herein provide the first step on the way towards answers to such questions

6.3. What about other Timiriaseviinae in the North American nonmarine Lower Cretaceous?

For unknown reasons, other representatives of the Timiriaseviinae common to Cretaceous nonmarine deposits worldwide, particularly those of the genus *Timiriasevia*, have neither been documented nor obtained (yet?) from such sediments in the U.S. Western Interior, particularly the Lower Cretaceous formations, but are known from the Upper Jurassic Morrison Formation. Their absence might be due to unsuitable paleoenvironmental conditions during Early Cretaceous times, low tolerance limits, and low competitiveness (vs. Cypridoidea), or that representatives of *Timiriasevia* were rare and have thus far been overlooked. Another possibility is that species of *Timiriasevia* have been incorrectly identified due to the difficulties in the morphologic differentiation of younger representatives of *Metacypris* and *Timiriasevia* (Upper Cretaceous to Paleocene ones in particular, see Chapter 6.4 below for discussion)—some representatives of *Timiriasevia* may have been designated as *Metacypris* or vice versa.

However, a sample (REKO 04, taken by Reko and Jennifer Hargrave) from the upper Lakota Formation in the eastern Black Hills (Fig. 2, locality 9) revealed numerous specimens of a small sized cytheroid taxon, the genus (*Stenestroemia*?) and species of which are not known thus far from Lower Cretaceous nonmarine formations in North America and which remains to be described. This example demonstrates that our knowledge of the nonmarine ostracod fauna of Lower Cretaceous deposits in North America is still incomplete and new research is both wanting and promising.

6.4. Discussion of the taxonomic comparison of selected genera of the Limnocytheridae

Table 1 lists important carapace characters to compare and differentiate several members of the family Limnocytheridae Klie 1938. In general and as usual, there are still discrepancies between the taxonomy based on hard parts and soft parts (specifically regarding tribes within the two limnocytherid subfamilies and their assignment to either of the subfamilies). In their cladistic analysis of the phylogenetic relationships of *Gomphocythere*, Park et al. 2002 give an example for differing results when hard and soft part characters are separated, and also demonstrate that the => *inverse* lophodont *hinge* is an important synapomorphy within *Gomphocythere* with no intraspecific variation. This supports the disjunction of fossil genera now considered to belong to either *Metacypris* or *Theriosynoecum* (with 'normal' lophodont hinge; and normal pores only), and the subrecent to recent genus *Gomphocythere* with the inverse lophodont hinge, and sieve as well as normal pores. At species level, the taxonomic significance of sieve pores is poorly examined and understood to date.

Timiriasevia, *Theriosynoecum* and *Metacypris* are considered members of the subfamily Timiriaseviinae based on the presence of simple pores only, and the strong brood pouches of the females. Of these, *Metacypris* is also known to occur recently (2 extant species). Chen (1965) considered *Timiriasevia* to be invalid and a junior synonym of *Metacypris*, he included some representatives of the former in *Metacypris* and erected the new genus *Ziziphocypris* for finely striated species. Although the differentiation between the *Metacypris* and *Timiriasevia* is unclear, particularly concerning the more punctate and less striate Late Cretaceous to Paleocene representatives of both genera, Chen's (op. cit) hypothesis has not been followed by many authors and remains to be re-examined.

Following or rejecting Chen's (1965) concept, however, affects the stratigraphic distribution of *Timiriasevia*. Szczechura (1978), Van Itterbeeck and Bultynck (2004, see their discussion on p. 157 therein also) and Van Itterbeeck et al. (2007) all rejected this hypothesis, for example, thus extending the range of *Timiriasevia* to Late Paleocene.

The nonsulcate taxa *Gomphocythere* and *Timiriasevia* as well as some species of the generally monosulcate genus *Metacypris* almost always bear at least an indication of a sulcus—a shallow and broad dorsolateral indentation anteriorly of half length, not reaching further down than 2/3 of height and causing the weak anterolateral constriction in dorsal view. Representatives of *Metacypris* with a stronger sulcus sometimes also show an indication of a shorter second sulcus anterior of the main sulcus, similar to *Theriosynoecum*. Although lacking a tuberculation in general, representatives of *Metacypris* sometimes also have very weak small posterodorsal tubercles.

The genera *Cytheridella* and *Gomphocythere* were considered members of the subfamily Limnocytherinae. However, the exact phylogenetic relationships of the subfamilies have yet to be determined. Particularly the separate tribe Cytheridellini Danielopol and Martens 1990 (Danielopol et al. 1990, including *Gomphocythere* Sars, *Cytheridella* Daday and *Gomphodella* De Deckker)—having originally been placed within the subfamily Limnocytherinae by Danielopol et al. (1990) because of the fact that its representatives also possess (true) sieve pores—has been transferred to the subfamily Timiriaseviinae by Martens (1995) based on several other morphologic characters (hard and soft parts: hinge structure, mandibular palp, position of the furca on the hemipenis). Admittedly, Martens recently regards the Cytheridellini "… as a transitionary group between the Limnocytherinae and the Timiriaseviinae, although they share most characters with the latter subfamily" (Park et al. 2002, p. 16). This hypothesis is supported by the fact that, unlike as stated in Park et al. (2002, p. 18) " … the absence of open pores and the presence of sieve pores is a characteristic feature of the tribe Cytheridellini …", representatives of this tribe do have sieve pores *and* open (simple) lateral pore canals (e.g. *Gomphocythere curta* Rome; *Gomphocythere woutersi* Park and Martens in Park and Martens 2001, figs. 9H, 9K, 9L; *Cytheridella ilosvayi* Daday, Liseth Perez, TU Braunschweig, pers. comm.).

Wherever the continuing discussion may lead, it does not affect the common restriction of the genus name *Gomphocythere* to recent and subrecent taxa only, as well as its clear separation from Late Mesozoic representatives of the Timiriaseviinae, i.e., the species assigned to *Theriosynoecum* and some species of *Metacypris*. Nevertheless, attention has to be drawn to the fact that authors recently plead for

ATTRIBUTES / GENERA	*Theriosynoecum* Branson 1936 incl. junior synonyms *Bisulcocypris* *Dryelba*	*Metacypris* Brady and Robertson 1870	*Cytheridella* Daday 1905	*Gomphocythere* Sars 1924	*Timiriasevia* Mandelstam 1947
Dorsal view of females	(elongated) piriform, sometimes elongated cordiform	cordiform	cordate-piriform	oval-elongate to piriform, weak anterolateral constriction	oval-elongate to piriform, weak anterolateral constriction
Lateral view	subrhomboidal to rounded oblong	rounded oblong, ventrally convex	rhomboidal with straight to slightly concave venter	rhomboidal with straight to slightly concave venter	rounded oblong, ventrally convex
Hinge	lophodont, rarely inverse, elements smooth, strong posterior tooth/socket	lophodont, elements smooth, cardinal teeth narrow	adont	inverse lophodont	lophodont, elements smooth, cardinal teeth narrow
Anterior dorsolateral sulci	bisulcate, usually strongly developed	monosulcate, sulcus weak	monosulcate, sulcus distinct	nonsulcate	nonsulcate
Local ornamentation elements	tubercles common, males almost always tuberculate, noding common (ecophenot.)	no nodes or tubercles	no nodes or tubercles	no nodes or tubercles	no nodes or tubercles
Area-wide ornamentation elements	punctation, in part with reticulation-like pattern	punctation	punctation	punctation	concentrically striate, sometimes combined with punctation
Lateral pore canals	simple pores	simple pores	simple and sieve pores	simple and sieve pores	simple pores
Average maximum size	0.90-1.20mm	0.50-0.60mm	1.00-1.60mm	0.60-0.90mm	0.50-0.80mm
Stratigraphy	Middle Jurassic to Early Cretaceous, (up to Cenomanian?)	Early Cretaceous (Aptian) to recent	(Paleocene) Eocene to recent	subrecent to recent	Late Triassic to Late Paleocene

Table 1. Comparison of taxonomic significant carapace characters (taxonomic key) of selected genera of the Limnocytheridae and their stratigraphic distribution. See Chapter 6.4 for discussion.

a Late Mesozoic/Early Cenozoic occurrence of representatives of *Gomphocythere* in Africa and India in particular (e.g. Bhandari and Colin 1999, Whatley and Bajpai 2005, Whatley et al. 2002). As with *Cytheridella*, a much longer occurrence of the genus *Gomphocythere* is possible. The earliest report of a representative of *Cytheridella* thus far is from the Campanian to lower Maastrichtian? of Mali, West Africa (Colin et al. 1996). Martens et al. (1998, p. 45) synonymized *Gomphocythere* Sars 1924 and *Gomphodella* De Deckker 1981. However, the latter genus is considered valid now (Karanovič 2006), comprising four species: *G. maia* De Deckker 1981, *G. hirsuta* Karanovič, *G. hirsuta* Karanovič and *G. yandii* Karanovič.

In summary, the systematics and phylogeny of members of the family Limnocytheridae is not yet satisfactorily resolved, and a general review of this matter is wanting and necessary. As for *Theriosynoecum* Branson 1936, this genus can be well determined based on carapace features and be clearly distinguished from *Metacypris* Brady and Robertson 1870 and *Gomphocythere* Sars 1924 as well, yet the phylogenetic relationships of its Early Cretaceous representatives to *Metacypris* and *Timiriasevia* Mandelstam 1947 remain to be clarified. The latter is also true for the phylogenetic relationship of *Timiriasevia* and *Metacypris* (see also right below).

6.5. The nonmarine Early Cretaceous ostracod faunas of North America - some short notes and ideas

Detailed biostratigraphy and stratigraphic distribution of the faunas are not the purpose of this paper and will be dealt with elsewhere (Sames et al., paper in preparation), and a revision of the Aptian/Albian material as well as new data are necessary to complete the analysis. Yet, in the context of observations made during the project initial comments can be made:

By analyzing the morphologic development of representatives of *Theriosynoecum* in North America (but not exclusively) during Late Jurassic to Early Cretaceous times, some morphologic trends became apparent which may represent evolutionary lines from elongate and usually strongly ornamented Jurassic taxa of *Theriosynoecum*, e.g. starting from the Late Jurassic *T. wyomingensis* (Branson 1936) over *T. pahasapensis* (Roth 1933), to more compact forms with a lower L/H-coefficient and less ornamentation in the late Early Cretaceous, such as *T. angularis* (Peck), *T. persulcata* (Peck), that finally may have led to the Aptian to recent *Metacypris*-lineage with its relatives and sucessors. Alternatively, a representative of *Timiriasevia* might be ancestor to the *Metacypris*-lineage. Actually, the similarity of *Theriosynoecum kirtlingtonense* Bate 1965 from the Bathonian of the UK with *T. pahasapensis* and *T. fittoni* in lateral and dorsal outlines, the broad laterally flattened anterior marginal zone, the position and development of tubercles (mostly) as well as the sulci, the posterior dorsolateral overreach, and the inclination (around 45°) of the straight dorsal part of the anterior margin, is so striking that *T. kirtlingtonense* Bate seems much likely to be the ancestor of the latter two. However, these considerations remain speculative for the moment, and more research and data are wanting.

Altogether, combining the author's own data and that available from the literature (e.g. Harper and Sutton 1935, Hoare 1953, Loranger 1954, Peck 1941, 1959, Peck and Craig 1962, Roth 1933, Sohn 1958, 1979, 1982) the following conclusions can be drawn for North American ostracod faunas in comparison to the mainly European faunas:

The Early Cretaceous nonmarine ostracod faunas of parts of Western Interior foreland basin can be divided into at least three (perhaps more) informal successive assemblages thus far. Based on the author's own data from the Lakota Formation, South Dakota and Cedar Mountain Formation (for the latter excluding *Theriosynoecum* specimens), Utah, as well as the Bear River, Draney Limestone and Peterson formations, western Wyoming and eastern Idaho (from the literature) the following assemblages can be distinguished:

1) a "Fauna A" of the early Lower Cretaceous (upper? Berriasian to Valanginian), characterized by representatives of the *Cypridea setina*-group, i.e. *Cypridea (Pseudocypridina) setina* var. *setina* (Anderson 1939), *Cypridea (Pseudocypridina) setina* var. *rectidorsata* Sylvester-Bradley 1949; the *Cypridea alta*-group, i.e. representatives of *Cypridea (Longispinella)* Sohn; the *Cypridea tuberculata*-group, i.e. *Cypridea* ex gr. *tuberculata* cf. *C. tilleyi* Loranger 1951; and—questionably—*Theriosynoecum verrucosa* (Jones 1885) in part. Lakota Formation, lower part, southern Black Hills, Chilson? members 1 and 2.
and Cedar Mountain formations.

In the Lakota Formation this fauna also includes the North American species designated *Theriosynoecum fittoni* herein as well as *Cypridea (Pseudocypridina) piedmonti* (Roth 1933) syn. *C. (P.) henrybelli* Sohn 1979.

In comparison with the stratigraphic distribution of species of *T. fittoni* in the English Wealden (e.g. Anderson 1985, Horne 1995), some problems arise due to the taxonomic differentiation of *T. alleni* and *T. fittoni* (the former reaching through the Valanginian, but not completely, the latter reaching from Hauterivian to Barremian both being stratigraphically separated; for details refer to the discussions of the respective species in Chapter 5.4, especially *T. alleni*). However, the questions regarding the stratigraphy are not considered primary arguments to reject the taxonomy; quite the contrary, taxonomy has priority. Therefore, the North American species identified as *Theriosynoecum fittoni* is not considered applicable as index taxon at the moment.

2) a "Fauna B" of the middle Lower Cretaceous (lower? Valanginian to Hauterivian, lower/middle? Barremian)—that most probably is further differentiable—characterized by *Theriosynoecum pahasapensis* (Roth 1933) in association with *Cypridea (Pseudocypridina) piedmonti* (Roth 1933) syn. *C. (P.) henrybelli* Sohn 1979 and many representatives of the family Trapezoidellidae Sohn 1979 (*Trapezoidella*, *Limnocypridea*). Lakota Formation, upper part, eastern Black Hills (Fuson? Member).

In part, few specimens of *Theriosynoecum fittoni* occur.

3) a "Fauna C" of the upper Lower Cretaceous (middle?/upper Barremian to middle Albian, questionably Cenomanian?) including the "Aptian/Albian-faunas" of R.E. Peck (i.e. Bear River Formation, Draney Limestone Formation and Peterson Formation, western Wyoming and eastern Idaho). This fauna comprises and is characterized by *Theriosynoecum pahasapensis* (Roth 1933) in its older part, *Theriosynoecum persulcata* (Peck 1941), *Theriosynoecum angularis* (Peck 1941), *Cypridea nitidula* Peck 1941, *Cypridea? anomala* (Peck 1941), *Cypridea compta* Peck 1941.

As for the Lakota Formation of the southern Black Hills, in the youngest part of "Fauna A" (in between "Fauna A" and "Fauna B"?), right below the Minnewaste Limestone Member (Fig. 2, locality 5) a fauna comprising *Cypridea (Pseudocypridina) setina* var. *setina* (Anderson 1939) in association with *Cypridea obesa* Peck 1951, *Cypridea (Ulwellia) minuta* Peck 1951 in its youngermost part occurs (right below the Minnewaste Limestone Member; after Peck 1951, this assemblage also occurs within this member and is confined to it and the bed directly above and below it).

In contrast to the assumptions of Schudack et al. (1998) and according to the current state of knowledge after revision, the Early Cretaceous nonmarine ostracod faunas of North America have no faunal elements in common with the Late Jurassic faunas of the Morrison Formation.

6.6. Synopsis of the discussion

In the Upper Jurassic? (probably lowermost Cretaceous) upper part of the Morrison Formation and in the Lower Cretaceous Lakota Formation of the Black Hills Area, South Dakota, the following representatives of *Theriosynoecum* occur: *Theriosynoecum fittoni* (Mantell 1844) – Lakota Formation, *Theriosynoecum pahasapensis* (Roth 1933) – Lakota Formation, and *Theriosynoecum verrucosa* (Jones 1885), uppermost Morrison Formation. Of these, only *T. pahasapensis* is endemic to North America according to the current state of knowledge.

The problem of the separation of *Theriosynoecum alleni* and *T. fittoni*, or whether the former is a junior synonomy of the latter, remains to be solved. However, the presented revision of *Theriosynoecum* provides more arguments to deal with the problem, and the inclusion of the North American representatives of *T. fittoni* will help to solve this question.

Athough representatives of *Theriosynoecum* are not yet good index fossils in the nonmarine Lower Cretaceous deposits of North America (representatives of *Cypridea* give a better resolution), the taxonomic revision conducted herein is a considerable step towards a better knowledge and understanding of the North American fauna and shows the potential of this genus for a future application to biozonation. In addition, the potential for a paleoecologic applicability of *Theriosynoecum* is enhanced by identification and definition of some characters as ecophenotypic.

There are substantial faunal links between the European and North American faunas, as can be demonstrated, but also considerable differences in the faunal development, the latter being mainly connected with different paleoenvironmental conditions. Representatives of *Theriosynoecum* seem to have finally died out during Albian times (questionably not until Early Cenomanian) in North America or, alternatively, may have evolved to or been replaced by *Metacypris* or another timiriaseviinid taxon. For thus far unclear reasons, representatives of the Timiriaseviinae, other than *Theriosynoecum* and *Metacypris*, that are common to Lower Cretaceous nonmarine deposits of the world, are unknown from North America.

As for the family Limnocytheridae, its phylogeny and systematics are not yet satisfactorily resolved. However, the comprehensive integrated revision of *Theriosynoecum* and the detailed comparison of revised carapace characters of the latter with morphologically similar fossil to recent genera of the Limnocytheridae resulted in a scheme (Table 1) that allows a good distinction of these and is, thus, a good fundament for further studies.

Finally, the North American Early Cretaceous ostracod fauna provides valuable information concerning the phylogeny and distribution of the Timiriaseviinae during the late Mesozoic, potentially about the origin and early evolution of *Metacypris*. At species level, there are no faunal elements in common with the nonmarine Upper Jurassic Morrison Formation. In association with representatives of *Cypridea*, three informal successive assemblages can be distinguished in some Lower Cretaceous nonmarine formations of the Western Interior foreland basin, which are considered better definable and further differentiable with more data in the future.

7. Conclusions

It has already been conjectured that the diversity of representatives of the '*Metacypris*'-*Bisulcocypris*-*Theriosynoecum* group is lower than given in the literature. The high rate of endemicity widely assumed in the past is herein identified as being mainly a taxonomic problem, in many cases resulting from an overestimation or wrong interpretation of some => *local ornamentation elements* in *Theriosynoecum* Branson 1936 and related genera, and the too regional view of the faunas. Using the detailed morphologic analysis and descriptions herein as well as the identification and revised definition of many carapace characters as being mostly optional (particularly local ornamentation elements, in *Theriosynoecum* at least) and widely taxonomically insignificant, an extended and new perception of the taxonomy of fossil Timiriaseviinae with emphasis on *Theriosynoecum* has been established. Based thereupon, the view on the stratigraphic and paleobiogeographic distribution as well as the distribution potential and supraregional applicability of the Middle Jurassic to Early Cretaceous genus *Theriosynoecum* becomes considerably different.

Major evolutionary lineages of the Timiriaseviinae seem to have been distributed worldwide in the Mesozoic (with the exception of Australia and Antarctica thus far, lacking data); only some species are endemic, many of them are likely to be considered more widely distributed once the new taxonomic concept is applied, e.g. weighting particular local ornamentation elements (i.e. nodes, tubercles, node-like tubercles) as taxonomically much less significant, and when new occurrences of related taxa are discovered. For representatives of the Limnocytheridae/Timiriaseviinae (Cytheroidea) with brood care, transport by migratory animals as well as wet storms (e.g. hurricanes/cyclones) is very possible.

As a result, it can be demonstrated that accurate "classic", carapace-based ostracod taxonomy integrated with recent findings in ostracod biology can provide an immense advance towards an application and robust discussion of Mesozoic nonmarine ostracods, as well as new perceptions in their phylogeny and palaeobiogeography (distributional mechanisms). To identify such coherences, an approach in the global context is necessary, bearing the paleoenvironmental and palaeoecologic background in mind. Future research activities are likely to be much more successful when more faunas from other continents are analysed in order to draw taxonomic conclusions.

Now that a first step towards identification and better differentiation between taxonomically significant and insignificant (ecophenotypic, ontogenetic) characters has been achieved, additional methods, such as geometric morphometrics (e.g. outline analysis or landmarks—pore position etc.) and their statistical analysis can be better applied to support or reject taxonomic hypotheses, because it is possible to focus on significant characters as base data to measure, and appropriate methods can be chosen. Moreover, an improved paleoecologic application of the taxa is rendered possible.

As for the stratigraphic and paleoecologic application of the taxa described herein as well as their biostratigraphy, considerable progress has been achieved and will be dealt with in separate publications. *Theriosynoecum* does not have significant biostratigraphic value in North America. However, this situation is identified as resulting from an insufficient amount of data. In contrast, the application potential of these taxa can be considered very promising, biostratigraphically as well as paleoecologically, with better base data from more formations of the Western Interior foreland basin and more stratigraphically consecutive ostracod assemblages.

The carapace character based comparison of important fossil to recent Limnocytherid genera resulted in the successful feasibility of their differentiation. This is the fundamental step forward and basis for future studies of the limnocytherid phylogeny and evolution.

Altogether, the approach followed herein led to satisfactory results as to the aims given in Chapter 2. A taxonomy-based utilization of representatives of *Theriosynoecum*, particularly with emphasis on Early Cretaceous North American species has been sucessfully accomplished and provides the basis for future research.

8. Acknowledgements

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Appendix: Taxonomic Glossary

Specific taxonomically significant characters of ostracods and the genus *Theriosynoecum* Branson 1936 in particular, as used in this paper (compiled after various authors, modified and supplemented; for illustration see Figs. 3 to 8). Terms in alphabetical order:

The intention of the following comprehensive remarks is to achieve a standardized concept in terminology that is comprehensible, easily reproducible and criticizable. Since the Ostracod Treatise is now more than four decades old, as are many of the publications dealing with the general terminology of the ostracod hard parts, many terms need to be specified. Most recent works are still based on these older publications (see below).

Only selected terms that require clarification are quoted here. Other definitions of general terms of hard parts can be found in Zalányi (1929), Klie (1938), Kesling (1951), the Ostracod-Treatise (Moore 1961), van Morkhoven (1962), Hartmann (1966-1989), Sylvester-Bradley (1941), Sylvester-Bradley and Benson (1971), Hartmann and Guillaume (1996), and Yamada (2007), to specify a few selected ones, and references therein.

It should be noted that the terminology given is in part adjusted and specifically optimized for the fossil Limnocytheridae/Timiriaseviinae, particularly *Theriosynoecum* (e.g. ornamentation).

Some terms can vary in meaning if applied to other Mesozoic to recent ostracod groups, or Paleozoic ostracods.

Remarks concerning the carapace margins and outlines (cf. Figs. 3, 4, 5, 6, 7, 8):

Regarding the margins and outlines of ostracod carapaces, some confusion in the literature needs to be clarified. Especially in the context with the dorsal and, in part, the ventral carapace borders, the unambiguous differentiation of the two terms is often not recognized and pointed out. For the dorsal region in lateral view, the terms hinge margin, hinge line, dorsal margin, dorsal outline (herein, the dorsal lateral outline and dorsal outline are differentiated!) and dorsal border are used, for example. By describing ostracods with commonly occurring depressions of the hinge, overreaches of lateral carapace regions, and strong => *local ornamentation elements*, a strict differentiation became necessary. As far as possible, commonly used terms and their application in the known context have been adopted. It is also attempted to define the extent of the single outer carapace regions by comprehensible geometric or morphologic elements (see Figs. 3 and 4). In general, the terms margin and outline are defined and applied as follows:

A ***margin*** is the valve's border directly adjoining the => *free valve margin*, and the hinge respectively, often only completely visible in an internal view of the single valve.

The ***outline*** is defined here as the outer border of the lateral 2D-projection of the valve, the carapace, or parts of any of these. The outline often differs from a margin, because lateral prolongations of the carapace overreach it (e.g. ridges, lobes, brood pouches etc.). The => *local ornamentation elements* as defined herein and used for the specific ostracod groups concerned, are excluded from defining the outline in *Theriosynoecum* because of their highly variable character assumed to be mostly ecophenotypic in this taxon.

Combined, all partial lateral outlines, i.e. the terms anterior, dorsal, posterior and ventral lateral outlines proposed here, define the lateral => *carapace outline* in its "classical" meaning (e.g. Kesling 1951, Moore 1961, and others).

The specific definitions for partial sections of the carapace's outer borders can be found in context with the main carapace regions, i.e. => *anterior*, *dorsal (hinge)*, *posterior*, *ventral margin/lateral outline* (e.g. *anterior margin* etc.).

As for the structure and terminology of the carapace margin, its revision by Yamada (2007) has considerable effects on the hitherto conventional (called "classical" terminology herein) definition, utilization, applicability and interpretation of morphologic terms such as => *duplicature*, => *flange*, => *inner lamella*, => *outer lamella*, and => *selvage*. For reasons of usefulness, to avoid confusion, and because Yamada's (op. cit.) concept has not yet been tested on many taxa (especially fossil ones), the "classical", i.e. mostly paleontologic, terminology is retained here. Nevertheless, wherever applicable, to facilitate future application and to offer different views, the new terminology and its effects on particular terms and interpretations are given/integrated in the glossary and discussed or commented in the definition of the carapace terminology herein.

Irrespective of the necessary and endorsed integration and standardization of recent biologic and paleontologic taxonomy or of whether preference is given to the "classical" view or to that of Yamada (2007), some terms, such as *selvage*, should be retained owing to their usefulness, regardless of the partially different meaning/definition resulting from the concept used by the particular researcher.

GLOSSARY:

Accommodation groove: An elongated, sometimes subtriangular furrow above the median hinge element (usually a => *hinge bar*) of the larger valve which receives the dorsal edge of the opposite valve.

In the uncommon case of an => *inverse* hinge, the accommodation groove and the median hinge element are situated in the smaller valve.

Anterior cardinal angle (ACA): The anterior of the two => *cardinal angles*.

Anterior (part of) lateral outline: Equivalent to => *anterior margin* because both always coincide.

Anterior margin: Anterior part of the carapace/valves in lateral view, adjoining the anterior part of the => *free (carapace/valve) margin*. It extends between the angular peaks of the anterior => *cardinal angle* and the => *anteroventral region*. The anterior margin always coincides with the => *anterior lateral outline*.

Anterior marginal (laterally flattened) zone (AMZ): Occurring in all representatives of *Theriosynoecum*, this is a more or less broadly developed, mostly well defined zone in both valves at the anterior carapace end. It is laterally flattened and appears in dorsal or ventral view as a constriction close to the anterior apex. It is developed mainly in the lower 2/3 of the anterior margin, ending below the anterior hinge element. This zone may or may not bear => *area-wide ornamentation elements/surface characters* and => *local ornamentation elements*, or be rather smooth. Depending on the development (length and angle) of the dorsal part of the anterior margin, it more ore less extends mainly along the middle to ventral part of the anterior margin including the => *anteroventral region*. Sometimes (e.g. in *Theriosynoecum fittoni*), lateral edges bound the zone towards the margin, thereby forming a widened 'T-structure'. The width of the AMS is directly connected to the width of the anterior fused zone.

Anteroventral region (AVR): The anteroventral sector of the carapace's outline including the anterior part of the => *ventral margin* and the ventral part of the => *anterior margin*. The term 'anteroventral angle' is avoided because a recognizable angle is rarely visible, i.e. this region is strongly rounded in many ostracods, as it is the case in *Theriosynoecum*.

Area-wide ornamentation element(s)/surface characters: see => *ornamentation*

Attached margin: That part of the => *dorsal margin* along which both valves are held together by the => *ligament* attached to them (the other parts of the margin are called => *free margin*). This term corresponds neither to => *dorsal margin* nor to *hinge margin*, because the extension of the ligament does not equal either of these and the length of the attached margin is also linked to the type of hingement. The ligament can be of different length, and is mostly shorter than the dorsal margin because certain elements of the => *hinge* (e.g. the => *terminal elements*, i.e. the teeth and sockets in the lophodont hinge in *Theriosynoecum*) mostly diverge when the carapace is opened.

Base line: Geometric line for horizontal orientation of the carapace in relation to the => *ventral margin*. The base line can be either coincident with a straight ventral margin, or be the tangent of a convex ventral margin, or running through the two virtual tangential points of the intersection between the => *antero-* and => *posteroventral regions*, if the middle ventral margin is concave.

Calcified inner lamella: see => *inner lamella*

Carapace/valve margin: The carapace or valve margin is the complete outer border/outer margin comprising the => *free (valve) margin* and the => *attached margin*. In lateral view, it is not necessarily coincident with the lateral => *carapace/valve outline* as a result of the overreach of lateral carapace/valve prolongations.

Carapace/valve outline: The carapace/valve outline is defined as the lateral or dorsal 2D-projection of its complete outer border, partially excluding => *local ornamentation elements* (see there for explanation). The lateral outline often more or less strongly differs from the => *carapace/valve margin* due to the overreach of carapace/valve prolongations. The latter is particularly the case for the => *hinge margin*. The => *dorsal outline* often distinctly shows the sexual dimorphism (if apparent in the outer view of the particular species, e.g. brood pouches in females of *Theriosynoecum*) and can be heavily affected by different => *ornamentation* elements. Since the dorsal *view* is taxonomically more significant, it is the one commonly used for description, and so is the dorsal outline. Dorsal and ventral outlines (not to be confused with => *ventral lateral outline*) are congruent, and therefore the usage of the term ventral outline becomes dispensable (but not the ventral view!).

Carina (pl. *carinae*, Latin for keel; English adj. carinate): see => *ornamentation*, => *area-wide ornamentation elements/surface characters*

Cardinal angles: A dorsal feature only, defining the junction between the => *hinge margin* and the => *anterior/posterior margin*s and marking the position of the terminal => *hinge elements*. Their shape and angularity are strongly variable. In most cases the cardinal angles are obtuse- angled and more or less strongly rounded. Depending on the shape of the terminal hinge elements (terminal teeth/sockets, or processes/recesses of some authors), the cardinal angles can coincide with the dorsal margin or protrude. The frontal angle is the => *anterior cardinal angle*, the posterior one the => *posterior cardinal angle*.

Because of the fact that the development of the dorsal internal features belonging to the hinge directly influences and is connected with the => *dorsal lateral outline* and/or margin, the terms 'anteroventral cardinal angle' or 'posteroventral cardinal angle' should be avoided for the equivalents in the ventral areas, where this is not the case. Therefore, these ventral characters are herein defined as => *anteroventral region* or => *posteroventral region* instead.

Central muscle scar field: The main muscle scar field, somewhat anterior of the carapace's mid-length, composed of the adductor muscle scars, frontal scar(s) and mandibular scars.

Contact margin: Internal edge part of the valves, excluding the => *hing*e (Moore 1961). The contact margins of both valves are in contact when the valves are closed.

Cordiform (from Latin *cor* for heart): Heart-shaped.

Curvature (of => *anterior* and => *posterior margins*): The anterior and posterior margins can be curved in three ways (Terminology after Lüttig 1962, cf. Fig. 5 herein, translated from German). Lüttig's terminology is adopted and preferred here because it is precise and short:

1. **Equicurvate:** (in German "äquikurvat") describes an equally rounded margin.
2. **Infracurvate:** (in German "infrakurvat") describes a margin that is more narrowly rounded towards venter.
3. **Supracurvate:** (in German "suprakurvat") describes a margin that is more narrowly rounded towards dorsum.

Denticulate: Term for => *hinge* elements that bear a finer dentition or are separated into several smaller teeth.

Dorsal margin: The dorsal part of the carapace's/valve's margin adjoining the hinge (including the => *hinge margin*), extending between both angular peaks of the => *cardinal angles*. Either the dorsal margin coincides with the => *dorsal lateral outline* and/or it is overreached and covered by dorsolateral elevations/inflations of the carapace, and then only partially visible in lateral view and not congruent with the dorsal outline. The term dorsal margin is not completely equivalent to the => *hinge margin*, which is only a limited part of the former.

Dorsal (part of) lateral outline: The dorsal part of the carapace's outline (border) in lateral 2D-projection, either coincident or (often) not coincident with the => *dorsal margin*. This term is to be clearly distinguished from and must not be confused with => *dorsal outline*, which is the outline of the carapace in dorsal view.

Dorsal outline: The 2D-projection of the carapace's outline (border) in dorsal view. This is a taxonomically significant feature not to be confused with the => *dorsal lateral outline*, which is the dorsal part of an ostracod's outline in lateral view. The dorsal outline often distinctly shows the sexual dimorphism (if apparent in the outer view of the particular species, e.g. brood pouches in females of

Theriosynoecum) and can be heavily affected by different => *ornamentation* elements. Since the dorsal *view* is taxonomically more significant than the ventral view, it is the one commonly used for description, and so is the dorsal outline. Dorsal and ventral outlines are congruent, and usage of the latter is therefore dispensable.

Duplicature: A "classical" morphologic term for the peripheral => *free margin*, where – also in the "classical" view – the => *outer lamella* and (the calcified part of the) => *inner lamella* are in contact, i.e. fused together. This view emanates from and differs between two separate lamellae that are fused together on a plane called => *marginal zone/fused zone*. The calcified part of the inner lamella can be totally fused either to the outer one, or alternatively, the more or less proximal part (depending on the width of the => *marginal zone*) of the calcified *inner lamella* can be partially separated from the *outer lamella* by a => *vestibulum*, and is then sometimes called the 'free inner lamella').

Yamada (2007) also uses the term duplicature, though in a different meaning. He (op. cit.) distinguishes the "dual lamellae structure" (two calcified lamella cuticles, see fig. 1c in Yamada 2007, although the internal part of the outer lamella underneath the "outer lamella cuticle" is never labelled therein) of the calcified carapace and identifies the "classical" *calcified inner lamella* as a continuous extension (not separate structure) of his "outer lamella cuticle" that is bent inwards. Therefore, he (op. cit.) replaces the term *calcified inner lamella* with the term "marginal infold" adopted from other authors.

<u>Remarks:</u> The classical view possibly derives from the concept that an ostracod's carapace consists of two separate valves instead of one continuous (organic) carapace that is just specifically calcified with a complete separation of its mineralized parts. The former, in turn, most probably derives from the paleontological point of view in that the paleontologists usually work with the fossil preserved relics of an ostracod, the remains of the bivalved calcified parts of the carapace.

Equicurvate: see => *curvature*

Equivalve: A description of the carapace valves, if these are of almost equal size and shape, i.e. lateral outline in particular (see also => *inequivalve* and => *subequivalve*).

Flange: More or less prominent ridge/excrescence deriving from the outer lamella (more precisely from the outer lamella cuticle following Yamada 2007) forming the outer margin of a valve when the => *selvage* and outer margin are displaced inwards. Yamada (2007, see also fig. 7 therein) points out that terms like *flange*, => *selvage*, and (inner) *list* are not appropriate to be applied universally. However, it is used herein to describe the particular morphology of the outer antero/posteroventral margins of *Theriosynoecum*, which are turned inwards (see Fig. 7 herein).

Free (carapace/valve) margin: A term for that part of the => *carapace/valve margin* along which the valves are not held together by the => *ligament* attached to them (this would be => *attached margin*).

Fossa (pl. *fossae*, Latin for groove/pit): A single polygonal element (pit, mesh) of a specific type of => *area-wide ornamentation elements*, the => *reticulation*.

Fused zone: see => *marginal zone*

Hinge: Internal structure of the valves along the => *dorsal margin*, where the valves are articulated when the carapace is closed. In contrast to published "classical" definitions and following more recent perceptions, the hinge in ostracods is less a joint forming the axis of rotation when the valves are opened and more a structure to inhibit the dislocation of the valves against each other when the carapace is closed. As can be observed in recent ostracods, certain elements of the => *hinge* (e.g. the

=> *terminal elements*, i.e. the teeth and sockets in the lophodont hinge of *Metacypris*, for example) mostly diverge when the carapace is opened.

Merodont and of lophodont type in *Theriosynoecum* (see description of the genus), all elements being smooth.

Hinge bar: A term for the median hinge element in the larger valve (if the hingement is not => *inverse*), if it is developed as a ridge, smooth (which is the case in *Theriosynoecum*) or finely crenulate (=> *denticulate*), which rises up from the valve's margin behind it (Sylvester-Bradley 1956). Its counterpart in the smaller valve is a (hinge) groove. The hinge bar is often situated under an => *accommodation groove*. The hinge bar as well as the corresponding groove can be bipartite, then consisting of an anterior and a posterior part of different shape (as is the case in *Theriosynoecum*).

Hinge elements: The single parts that form the hinge. The hinge in *Theriosynoecum* is tripartite (lophodont hinge), consisting of an anterior and a posterior => *terminal element* (its shape defining the => *cardinal angles*) and a median hinge element. A terminal element is usually developed as *tooth* (or process of some authors) in the smaller right valve (or the other way round if the hingement is => *inverse*), and a corresponding *socket* (or recess of some authors) in the larger left valve (or the other way round if the hingement is => *inverse*). The median hinge element in *Theriosynoecum* is the => *hinge bar*.

Hinge, inverse: see => *inverse*

Hinge line: Line in dorsal view of the carapace along which the valves articulate when the valves are closed, including the area of the terminal => *hinge elements* and thus also including a small dorsal part of the anterior and posterior margins. May be straight or meandering. The hinge line must not be confused with the => *dorsal margin* or the => *hinge margin*!

Hinge margin: Part of the => *dorsal margin*, extending in between the => *cardinal angles* and being the outer equivalent to the internal extension of the median => *hinge* element, excluding the terminal elements (cf. => *hinge bar* also). The hinge margin is not coincident with the => *attached margin*.

Inequivalve: A description of the carapace valves when they differ in size and/or shape, i.e. lateral outline in particular (see also => *subequivalve*, => *equivalve*). The degree of the differences may vary considerably between the species.

Infracurvate: see => *curvature*

Inner (calcified) lamella: In "classical" terminology, this is a separate inner calcified part of the carapace/valve lamella being fused or, partially (i.e. in its proximal part), not fused to the => *outer lamella* (also called => *free inner lamella* then; also refer to => *duplicature* and => *vestibulum*). For the probable derivation of such a view of (partially) fused but morphologically separate lamellae please refer to the remarks under the definition of => *duplicature*.

Yamada (2007) identifies this structure (based on Transmission Electron Microscopy) as continuous extension (not separate structure) of his "outer lamella cuticle" that is bent inwards. Therefore, he (op. cit.) replaces the term *calcified inner lamella* with the term "marginal infold" adopted from other authors.

Inner lamella cuticle: A term used by Yamada (2007) for the chitinous noncalcified part of the "classical" => *inner lamella*; its connection to his "outer lamella cuticle" (or proximal limit as well) being the => *inner margin*.

Inner margin: This is the proximal limit of => *duplicature* and/or => *inner (calcified) lamella* in the "classical" terminology. Following Yamada (2007) this would be the proximal limit of the => *marginal infold.*

In some ostracod taxa, the inner and outer lamella are linked directly at and along the outer margin (e.g. some Podocopica: Darwinuloidea or some Platycopida), and then the inner and outer margins (outer margin is equal to => *carapace/valve margin*) are congruent.

Inverse (from Latin *inversus* for turned/reverted/vice versa—regarding valve size relation and overlap, or hinge as well, "reverse" of some authors): This term refers to either the valve size relation, or the position of the hinge elements in relation to the larger and smaller valve in ostracods, both in comparison to the most common situation within a taxon (mostly referring to a genus). However, both are features independent of each other in their occurrence, not necessarily showing a coherence. Inverse valve size relation usually affects the overlap as well as the hingement (i.e. position of the hinge elements in the left and right valves), and thus, in a taxon with inverse valve size relation, the position of the hinge elements is reversed, but still to be defined as 'normal hingement' if the median hinge element is located in the larger valve and the terminal hinge elements are located in the smaller valve.

1) An ***inverse valve size (relation)***, a comparative term, characterizes an ostracod taxon that shows the opposite ('inverse') valve size relation of the situation that is common ('normal') to a particular group of higher hierarchy to which it belongs. In most ostracods, one of the valves (the LV mostly) is distinctly larger than the other and often overlaps and/or overreaches the smaller one more or less strongly, and therefore has a different lateral outline. In *Theriosynoecum*, the valve size relation is almost always LV>RV, which is also the case for most representatives of the Ostracoda, and therefore designated as "normal" valve size relation. This far, the only known exception of a representative of *Theriosynoecum* that has an => *inverse hinge* is the species *Theriosynoecum pricei* (Pinto and Sanguinetti 1958).

However, a "normal" valve size relation is also existent if the valve size relation is RV>LV and if this situation commonly occurs within a taxon. For example, the RV>LV relation in the species *Darwinula* (sensu stricto, Rossetti and Martens 1998) is "normal" and characteristic of this genus, whereas within and in relation to the family Darwinulidae it would be called "inverse", because all other genera (*Alicenula*, *Microdarwinula*, *Penthesilenula* and *Vestalenula*) have the "normal" valve size relation of LV>RV (see Rossetti and Martens 1998).

In *Theriosynoecum*, the true valve size relation can be determined with certainty by the hinge elements (the hinge bar and the anterior and posterior sockets are on the larger valve, the anterior and posterior teeth are on the smaller valve), because there is only one species known thus far that shows an *inverse hinge* (see above and below). If no internal view is available, the tongue-like convex section of the ventral margin below the S2-sulcus, overlapping the smaller valve clearly indicates the larger valve (note: there also is a similar element in the smaller valve at the same position, but it lies internally).

It remains unclear whether an inverse valve size relation is a diagnostic character or a variation/mutation, and if either, on what taxonomic level (species and/or genus level?), because there are very similar forms within some ostracod taxa (e.g. in *Cypridea* Bosquet 1852, Cypridoidea) just differing in their valve size relations. Furthermore, it is possible that either concept is not applicable to all Ostracoda (the present author does not believe this character to be significant at generic or specific level). This is irrelevant for *Theriosynoecum* anyway, because a discussion of the taxonomic (in-)significance of valve size relation in general and in detail is not the purpose of this paper and will be the subject of further studies.

2) The ***inverse hinge*** is a comparative term to characterize the situation of the position of the hinge elements in contrast to the situation common to a particular group of higher

> hierarchy to which it belongs. The "normal" state (i.e. the most common situation within a taxon of certain hierarchy, and also the common situation in most ostracods) is that the median hinge element (a simple or bipartite hinge bar in *Theriosynoecum*) as well as the corresponding grooves (sockets in *Theriosynoecum*) of the terminal hinge elements are situated in the larger valve, whereas the terminal hinge elements (teeth in *Theriosynoecum*) and the median groove are situated in the smaller valve – independently of whether this is the LV or the RV in both cases. Thus, an *inverse hinge* is the situation where the median hinge element occurs in the *smaller* valve, whereas the terminal hinge elements occur in the *larger* valve.

Examples for Cytheroidea with an inverse hinge are *Theriosynoecum pricei* (Pinto and Sanguinetti 1958) or the late Quaternary to recent genus *Gomphocythere.*

Lateral ridge(s): A => *local ornamentation element.* The occurrence, shape and number of ridges are taxonomically diagnostic and, in most cases, genetically fixed (however, there are exceptions), and the => *area-wide ornamentation elements/surface characters* may be distorted on and around them.

In *Theriosynoecum* these are well delimited, relatively narrow and low, distinct ridge-like extensions of variable scale on the lateral (also dorsolateral or ventrolateral) surface of both valves. Their outer edge is often sharp. Because of their good delimitation and sharp outer edges they are easily distinguishable from => *lobes.*

Ligament: This is an uncalcified organic cuticular structure connecting both valves dorsally and corresponding to the cuticle of the outer lamella (e.g. Yamada 2007). It has specialized fibrous structures to strengthen it (op. cit.). In contrast to the information given in most textbooks, the (podocopid) ligament most probably has no elasticity (Yamada 2007) and does not support/cause the aperture of the valves (e.g. Meisch 2000), which is caused by the internal hydraulic pressure of the body liquids instead.

Line of concrescence: This term designates the proximal (inner) line of the plane of fusion (=> *marginal zone*) between the calcified => *inner lamella* and the => *outer lamella* in the "classical" terminology. It can either be congruent or not congruent with the => *inner margin*, depending on whether a => *vestibulum* is developed. In the latter case, the line of concrescence and the inner margin are not congruent.

Lobe(s): A => *local ornamentation element.* These are diagnostic, well-rounded major protuberances of the valve, either covered by or alternatively without other => *ornamentation* elements, and often associated with a => *sulcus.* The dimensions vary and generally, their boundaries smoothly pass into the carapace. Usually, close to and on the lobes, any potential => *area-wide ornamentation elements/surface characters* are distorted or differ in their dimensions from those covering other areas of the outer carapace's surface.

Lobes are morphologically clearly distinct from => *ridges*, which are well delimited from the surrounding carapace, and lobes are also genetically fixed diagnostic characters of the carapace.

Local ornamentation element(s): see => *ornamentation*

Lophodont: see => *hinge*

Marginal infold: A term adopted by Yamada (2007, refer to p. 204 therein) from other authors based on his new findings concerning the ultrastructure of the carapace margin of the Podocopida. Yamada (op. cit.) uses this term to replace the "classical" term => *(calcified) inner lamella.*

Marginal pore (canal): see => *pore*

Marginal zone (fused zone): This is the part of the carapace where the inner and outer lamellae are fused together. Its width greatly varies, and the => *marginal pore canals* extend through it (van Morkhoven 1962). The inappropriate term "adhesive strip" (for the very thin chitinous layer beween => *inner* and => *outer lamella*), as used by Kesling (1951) and Moore (1961) for example, should be avoided, because it gives the impression that the calcified elements of inner and outer lamellae on the fossil valve may be separated. The latter is only the case in some taxa that, in consequence, have no true marginal zone then.

Yamada (2007) does not mention this term, but following his results, a fused zone would not exist because he does not differentiate between inner and outer lamellae in a classical sense (see => *duplicature* for more information). In deduction from Yamada's (op. cit.) perception, the 'marginal zone' would therefore just be the plane through which the => *marginal pore canals* extend, rather than being a fused zone.

Median hinge element: see => *hinge elements*

Merodont: see => *hinge*

Murus (pl. *muri*, Latin for wall; English adj. mural): The wall of a => *fossa* in a => *reticulum* (Sylvester-Bradley and Benson 1971).

Node(s)/Noding: see => *ornamentation*, => *local ornamentation elements*

Node-like tuberculum (-i): see => *ornamentation*, => *local ornamentation elements*

Ornamentation (ornamentation elements): For reasons of clarification and potential (paleoenvironmental) application, the ornamentation as used in this paper and in part specified for *Theriosynoecum*, is subclassified into => *local ornamentation elements* and => *area-wide ornamentation elements* herein. However, this classification is not intended to be applied to ostracods universally, and should be applied only conditionally to other ostracod taxa, or, alternatively, tested and appropriately modified.

The meaning of ornamentation and its subdivision applied to *Theriosynoecum* herein must not be confused with "surface ornament", as used by Kesling (1951, p. 121), or in the Treatise of Invertebrate Paleontology by Moore (1961, p. Q55), or by Sylvester-Bradley and Benson (1971)—an unfavorable, ambiguous term for => *area-wide ornamentation elements/surface characters* of the valves, as proposed herein, because in the mentioned publications no distinction is made between area-wide and local (and delimited) characters and because the term is used regardless of genesis and possible reflection on the valve's inner surface.

Sylvester-Bradley and Benson (1971) used the term "ornate" to describe ostracods with => *local ornamentation elements* and => *area-wide ornamentation elements/surface characters*, and established a terminology for ornamentation types and elements. The latter authors also proposed to differentiate between "negative" (puncta, pores, sulci etc.) and "positive" (tubercles, spines etc.) features but at the same time pointed out that they did not intend to convey concepts of genesis therewith (op. cit.). This distinction appears to be superfluous, not least because of the latter objection, since many ornamentation elements that would be of "opposite" character as deriving from the definition of Sylvester-Bradley and Benson (op. cit.) are related in their genesis (e.g. certain pores, being 'negative', and tubercles, being 'positive').

The usage of *ornamentation* herein should also not be confused with "ornamentation" sensu van Morkhoven (1962, p. 37); his particular definition is also considered capable of being misunderstood and only partially applied herein (see remarks/discussion under this item below).

The term "sculpture", which is probably appropriate for some extremely ornamented Paleozoic Ostracoda or extremely velate marine taxa, for example, that look heavily adorned, is avoided for Mesozoic nonmarine ostracods herein.

Although often diffuse in their delimitation, structures such as => *lobe* and => *sulcus* are included in => *local ornamentation elements* for the reason that one element never covers the main part of the carapace's outer surface. Ridges (=> *lateral ridges*) are included as well. However, for better clarity the latter three terms are listed separately, not under this item.

Characters, such as => *pores*, are excluded from ornamentation because the apertures of the pores are only the external termination of the pore canals that in turn are a character located internally in the valve or penetrating the whole valve, respectively.

The following terms for the different ornament types in *Theriosynoecum* are used herein:

A) **Local ornamentation elements:** are defined as the total of all local(!), well delimited and more or less distinct elevations of the valves at their outer lateral surface, that are (mostly) reflected on the inner surface. In general, such ornamentation patterns are nearly symmetric in both valves and major ornamentation elements occur pairwise opposite to each other. The occurrence of local ornamentation elements in *Theriosynoecum* is mostly a facultative and an ecophenotypic character, whereas the intensity of their development seems to be mainly or even entirely controlled by environmental factors.

1. **Node(s)/Noding:** Clearly distinct from => *lobes*, nodes are medium to large hollow protuberances (also "bulges" or "outward flexions" in some publications) of the carapace, rarely elevated so strongly that they form properly bubbles (3/4 spheres). They are a facultative (eco-)phenotypical feature of the carapace, taxonomically insignificant. Noding is, generally, a phenotypical response to environmental changes (e.g. van Harten 2000, Keyser 2005). The shape of nodes is variable, but mostly hemispherical to broadly hemispherical-elliptic. If nodes occur, their location on the carapace usually follows a certain pattern (see Keyser 2005 for the reasons), but sometimes they can also be irregularly placed. In most cases, the process of noding is combined with a distortion of the => *area-wide ornamentation elements/surface characters* on, and partially around, the nodes.

   Regarding the main ornamentation of *Theriosynoecum*, => *node-like tubercles* (see below), if present, are more common within this genus than nodes.

2. **Tubercles/Tuberculation/tuberculum** (pl. *tubercula*, from Latin *tuberculum*, meaning small bump/protuberance; English adj. tuberculate): Tubercles are rounded, relatively low protuberances of intermediate size (usually smaller than => *nodes* in diameter) on the valve surface and/or along the margins. The tubercles can be either conical (sometimes even concave laterally) or cylindrical, hollow or solid with a more or less rounded or flattened point alternatively. In some cases, the tubercles can be inflated and have a hemispherical node-like shape (=> *node-like tuberculum*). Typically, a tubercle forms around a => *pore*, thus being a hollow expanded pore conulus and always having a simple normal pore canal in its center as well as a pore at its summit. An ornamentation characterized by many tubercles is called *tuberculation*. Tubercles always occur pairwise, one on each valve lying opposite each other, although their size or intensity of development may slightly differ between both valves.

   If a tubercle-like structure has a strongly tapering distal end, no matter whether rounded or sharply pointed, it is called "spine" (not occurring in *Theriosynoecum*).

3. **Node-like tuberculum (-a):** These are strongly inflated hollow tubercles (see => *tuberculum* above) having a hemispherical rather than conical shape. They differ from => *nodes* (see above) in (when smaller) often bearing no => *area-wide ornamentation elements/surface characters* and always forming from a tubercle and therefore around a (simple) normal (lateral) => *pore*. The position of these pores in the carapace is fixed. Node-like tubercles are a typical ecophenotypic feature for representatives of *Theriosynoecum* Branson 1936, possibly caused by osmoregulatory problems during ecdysis, i.e. a swelling of the osmoregulatory glands that may be caused by increasing

salinity (Do Carmo et al. 1999). In the past, these have erroneously been used by some authors as diagnostic feature on species level.

Node-like tubercles always occur pairwise, one on each valve lying opposite each other, although their size or intensity of development may slightly differ between both valves.

4. **Other *local ornamentation elements*:** => *(Lateral) ridge*, => *lobe*, => *sulcus*

B) **Area-wide ornamentation elements/surface characters:** Surface characters, as used herein for abridgement, are defined as the total of all area-wide (!) ornamentation elements covering most of the outer valve's surface, such as elevations and depressions (thickenings or thinnings) of the valves. The scale of the single elements varies, but is mostly small (< 50µm), the intensity (size, in part) of their development can be influenced by environmental factors (e.g. calcium availability and salinity sensu lato).

Anderson et al. (1967, p. 202) called the surface characters "surface sculpture", a misleading term giving the impression of large and very strongly developed single elements, and thus to be abandoned. To preclude confusion, the term "surface ornament", as proposed in the Treatise (Moore 1961, p. Q55), and the very general term "ornamentation" as used by van Morkhoven (1962, p. 37), although being the overall term, should be avoided to specify area-wide ornamentation elements.

Three different types of area-wide ornamentation elements/surface characters occur among the representatives of *Theriosynoecum* described herein:

1. **Punctate/punctation:** Puncta (plural of *punctum*, Latin for stitch, point, small spot; English adj. *punctate*) are small (between 20 and 50µm) pit-like depressions in the valve's surface (Moore 1961). In general, they are regularly distributed on the valve, their density varies, and their shape can be hemispherical or conical. In some areas of the carapace, like the ventral margin or close to and on => *local ornamentation elements*, they are distorted – elongated mostly. Almost always, the (simple) normal => *pores* occur between, or rarely in a marginal position within the puncta, respectively. As proposed herein, the difference to => *reticulation* is that the *puncta* are always roundish, whereas the => *fossae* of a => *reticulum* are polygonal.

2. **Reticulation/reticulum** (*reticulum*, pl. *reticula*, Latin for small net; English adj. reticulate): A reticulation describes a carapace surface having a netlike pattern of small intersecting crests/small bars (=> *murus*, *-i*) forming the walls of single meshes that are deep dimples/pits (=> *fossa*) of (rounded-)polygonal outline. The pattern is more or less regular, the crests are equally narrow and straight or slightly concave laterally and their junctions are small (if no ornamentation element is present). The transition to => *punctation* is smooth and not accurately definable. It is proposed that when the pits (either => *fossae* or => *puncta*) are roundish and no polygonal outline is apparent anymore, the netlike pattern is no longer realized and the term => *punctation* is more appropriate. Punctation also implies that the => *muri* then are broad, rounded as well as heavily concave laterally and the junctions are as big as, or larger than, the relatively shallow => *fossae* or => *puncta*.

   In many nonmarine ostracod taxa, a reticulation in more or less early ontogenetic stages is reduced to a punctation in adults. In *Theriosynoecum*, a true reticulation seems almost never to be realized in adults because the puncta are almost always roundish. However, there are some exceptional examples where a full reticulation (at least in some specimens, perhaps ecophenotypic) seems to be realized (e.g. *Theriosynoecum alleni* as figured by Anderson 1985, pl. 7, fig. 15). Aside from this, reticulation in *Theriosynoecum* and other Mesozoic relatives of the Timiriaseviinae is always a first-order reticulation, i.e. with no additional smaller network within the primary fossae (cf. Sylvester-Bradley and Benson 1971, p. 284). In general, Middle to Late

Jurassic representatives of *Theriosynoecum* more often show a trend towards reticulation than the Early Cretaceous ones.

3. **Carina** (pl. *carinae*, Latin for keel; English adj. carinate): A well-defined, narrow and somewhat strongly projecting ridge on the outer surface, usually with a sharp edge. Several of these usually occur ventrally in *Theriosynoecum*). Although of more or less local character, carinae are included in area-wide ornamentation elements herein because they derive from a reticulation or punctation, thus being a particular development of the => *muri*.

Remarks/Discussion: Van Morkhoven (1962), for example, used ornamentation for all features occurring on a non-smooth valve surface "... that are not reflected on the inner surface ..." (op. cit., p. 37). However, somewhat later on the same page, he also includes massive "protuberances (tubercles or knobs)", features that, at least in *Theriosynoecum* and other Limnocytheridae, are often reflected on the inner surface. In the glossary of the Ostracod Treatise (Moore 1961), the term ornamentation in general is neither used nor mentioned. Instead, the term "surface ornament" is given for "relatively subordinate elevations, depressions, and varied sorts of markings on valve surface, mostly useful in taxonomy" (op. cit., p. Q55). However, "relatively subordinate" is a most elastic term and thus inappropriate to separate ornamentation elements from each other or from other carapace features. In the view of the present author, tubercles, nodes or spines can morphologically be quite significant, prominent, and may change the morphology of a specimen to a great extent. Notwithstanding, Moore (1961, p. Q55) defines "tuberculate" as "surface ornament characterized by many tubercles" and consequently, a tuberculation would be "relatively subordinate" following his view, for example. Kesling (1951, p. 121) uses a similarly imprecise term and definition: "Surface ornamentation – small structures modifying or 'decorating' the surface", and includes as well as describes several different types, such as punctate, reticulate, striate, and tuberculate.

However, all the definitions mentioned above fail to determine size and delimitation of the included ornamentation elements more precisely; they also completely disregard their genesis and their separation from each other or from similar carapace features not implicated therein (e.g. ridges, lobes). For this reason and based on new findings of the last thirty years, a revised terminology and definition became imperative.

Thus, the conceptual subdivision of *ornamentation* into => *local ornamentation elements* and => *area-wide ornamentation elements/surface* characters is established herein to clarify and define the (almost always) optional occurrence and always local attribute of the *local ornamentation elements* on the one hand, and the fixed diagnostic attribute of the *area-wide ornamentation elements/surface characters* (though ecophenotypically influenced in their intensity or weakened/absent through diagenesis and/or processing) on the other hand – as well as paying attention to the genesis of these characters. Moreover, emphasis is placed on giving a clear and comprehensible concept for separating different characters from each other by implementation of their genesis, occurrence, position on the carapace, shape, variation, and finally, by taking the parameters influencing all these processes and characters into consideration.

Some local ornamentation elements in *Theriosynoecum* are highly variable and have been used as important taxonomic features in the past (e.g. particularly by Pinto and Sanguinetti 1962 for the designation of *Bisulcocypris*). The application of this concept by various authors resulted in the designation of an enormous quantity of subgenera (supraregionally) as well as species and subspecies (regionally) worldwide. By continuous designation of new names in different continents and regions, the supraregional biostratigraphic application of several groups (e.g. *Theriosynoecum-Bisulcocypris*-group, *Cypridea*-lineage) was extremely limited, because the authors were convinced of the high (if not total) endemicity of the faunas. A problem for current research is the enormous number of different taxa resulting from the application of this concept and, in part, the difficulty of reproducing some older concepts.

However, comparison of numerous references to the faunas in different continents shows that ornament patterns of local elements may not have such high taxonomic significance as has been presumed in the past. Quite the contrary, there are commonly ornamented taxa (e.g. representatives of *Theriosynoecum* or *Cypridea*) appearing very similar or even identical in all their characters apart from some of their => *local ornamentation elements* (as defined herein). In fact, by disregarding some elements of this type of ornamentation, relying on all other characters and bearing in mind general morphological trends (in Mesozoic to recent ostracods) for the identification of juveniles as well as the differentiation of sexual dimorphs, many subgenera, species and subspecies names become dispensable.

Such a concept does, of course, have considerable influence on taxonomy and, therewith, on paleogeographic distribution, correlation and paleoecology of the particular ostracods. However, the application of this concept makes much more sense in the attempt to solve many problems, and notable scientific advancement is achieved thereby.

This concept is by no means new. The British ostracodologist T.R. Jones (e.g. Jones 1893) already speculated about the possibly mutable character of some carapace features and their causes. Scientists working for the oil industry, such as J. Wolburg in the 1950s, successfully applied a morphogroup concept (species-groups) in *Cypridea* to the biostratigraphy of the "NW-German Wealden", trying to define related species-groups as phylogenetic lineages by their shape in conjunction with their stratigraphic distribution/evolution (Wolburg 1959). Being aware that the species definitions were often based on single (local) ornamentation elements and phylogenetic relationships on coincidentally similar characters, Wolburg (op. cit.) established species groups including subspecies and variants to remove their taxonomically strong inhomogeneous ranking (op. cit., p. 238) and to include the taxa in an inartificial (i.e. 'natural') framework. However, such concepts seem not to have received the attention they deserve. Possibly, they were not well noticed due to the fact that these articles were not published in English or fell into oblivion because the topic has been dealt with only intermittently during the second half of the 20th century. Nevertheless, some obscurities remain. Wolburg (1959, p. 228), for instance, mentions the written and personal exchange of experience with F.W. Anderson, regarding the problems of speciation and stratigraphy in the English Wealden Basin in comparison to the NW German area. Yet in spite of everything, Anderson seems to have stuck to his concept of basing taxa on (mostly local) ornamentation elements (as defined herein) and even developed a concept to locate, define, and index tubercles and spines by designing a geometric map of the valve surface for *Cypridea* (Anderson et al. 1967, p. 202-204). Notwithstanding, for unknown reasons Anderson never discussed Wolburg's (1959) approach in his publications.

Regarding the causes of node-like tubercles, for the fossil taxon *Theriosynoecum kirtlingtonense* Bate 1965, Do Carmo et al. (1999, p. 31) showed that "... the presence of nodes and the degree of their expression must be used with great caution in specific or generic diagnoses ..." because they might [!!!] be a phenotypic expression in response to changes in water chemistry. In contrast to the noding process in the recent *Cyprideis torosa* (Cytheroidea - Cytherideidae, caused by lowering salinity during ecdysis, see Keyser 2005), Do Carmo et al. (op. cit., p. 31) suggest a direct correlation between increasing strength of nodes (=> *node-like tubercles* herein) and elevated salinity for *Theriosynoecum kirtlingtonense*, "... caused by the enhanced activity of the excretory mechanism in order to maintain osmoregulation".

There are also other examples from the superfamily Cypridoidea: Yang et al. (2002) studied => *local ornamentation elements* in a large number of Quaternary and recent representatives of *Ilyocypris* (*I. echinata*, *I. gibba* and *I. salebrosa*, Cypridoidea - Ilyocyprididae) from the Qaidam Basin (Tibet) and also favored a low taxonomic but more ecophenotypic significance of the nodes and tubercles (=> *node-like tubercles* herein); they discovered that the number of specimens with node-like tubercles tends to be much higher in juveniles than in adults. They (op. cit.) tentatively relate the lower expressivity or absence of node-like tubercles to ontogenetic effects (i.e. the juveniles have stronger node-like tubercles, the adults weaker or none) as well as temperature drop or temporary dryness in combination with salinity increase.

Many local ornamentation elements as defined herein and applicable to the fossil Timiriaseviinae (Cytheroidea – Limnocytheridae) at least, seem to be ecophenotypic – either caused (e.g. nodes) or influenced in size/development (e.g. tubercles) by abiotic factors taking effect during ecdysis. Then, the morphologic changes of the carapace during its soft stage are preserved when the carapace is hardened by calcification afterwards. In contrast, area-wide ornamentation elements are genetically fixed characters, relatively stable in their size and mostly just varying in their degree of expression. The latter can be influenced by environmental factors (e.g. calcium availability, water chemistry, temperature etc.). It must be carefully assessed how local ornamentation elements can be applied to paleoenvironmental analysis and to which taxonomic groups the concept is applicable, as well as whether local ornamentation elements are applicable at all to a paleoenvironmental analysis of a particular taxon. As for the duration of the paleoenvironmental changes, it remains to be investigated whether such changes are only short-term events *during* ecdysis—more precisely, *beginning* during ecdysis (e.g. abrupt significant salinity decreases through rainfall in a temporary pond)—or whether these are longer lasting events just *taking effect* during the soft stage of ecdysis (e.g. osmoregulatory problems not lethal to the ostracod but leading to swollen osmoregulatory glands or increased pressure of the body liquids, that can change the shape of the carapace only while it is soft).

A mixed assemblage, including representatives of the same taxon with and without local ornamentation elements (pay attention to differences in this type of ornamentation caused by sexual dimorphism, e.g. in *Theriosynoecum*) can indicate (relatively) short-term environmental changes, whereas a stratigraphic succession of such assemblages with a higher (or lower) proportion of ornamented specimens can indicate a trend to an increase (or decrease) of the frequency of these events

Based on the findings described above, the concept applied to (fossil) representatives of the Timiriaseviinae in this paper is that, in contrast to the patterns of distribution (position), the presence of some *local ornamentation elements* (tubercles, nodes, node-like tubercles) as well as their degree of expression, are considered to be of low taxonomic relevance, and will not be used to distinguish species or genera, if all other carapace characters (such as outline, area-wide ornamentation elements/surface characters, internal features) are very similar or identical. If applicable, local ornamentation elements can be used for paleoenvironmental interpretation (i.e. salinity realms and changes) as well as identification of sexual dimorphism in certain cases (e.g. *Theriosynoecum*), and possibly to support the identification of juveniles in some cases (e.g. *Cypridea*). By contrast, type, occurrence and shape of *area-wide ornamentation elements* are always taxonomically relevant characters, provided that similar ontogenetic stages, i.e. adults ideally, are compared.

Outer lamella: A "classical" morphologic term for the external part of the calcified part of the carapace/valve. The outer lamella is—in its "classical" view—morphologically separate from the => *inner lamella*, although both are at least partially in contact, i.e. fused together (=> *marginal zone/fused zone*) along the => *free margin* or held together by the => *ligament* along the => *attached margin.*

This view emanates from and distinguishes two separate lamellae that are fused together on a plane called => *marginal zone/fused zone.* The calcified part of the outer lamella can be either totally fused to the inner one, or alternatively, the more or less proximal part (depending on the width of the => *marginal zone*) of the calcified *inner lamella* can be partially separated from the *outer lamella* (then sometimes called 'free inner lamella') by a => *vestibulum.*

Yamada (2007) uses the term "outer lamella cuticle" instead.

Remarks: The classical view possibly derives from the concept that an ostracod's carapace consists of two separate valves, instead of one continuous (organic) carapace that is just specifically calcified – with a complete separation of its mineralized parts. The former view, in turn, most probably derives from the paleontologic point of view in that the paleontologists usually work with the fossil preserved relics of an ostracod, the remains of the bivalved calcified parts of the carapace.

Outer margin: see => *carapace/valve margin*

Outline (lateral/dorsal): see => *carapace/valve outline*

Piriform (from Latin *pirum* for pear): Pear-shaped. Some authors spell it "pyriform".

Pore(s) (canals): Pores are the external termination of a pore canal. There are two main types of pore canals: marginal pore canals and normal pore canals. The so-called "false marginal pore canals" are something in between (see below). Most or all pores have a sensorial function (Meisch 2000); it has been suggested that some are part of the excretory system (e.g. Keyser 1982, Okada 1983, Do Carmo et al. 1999).

1. **Marginal pore/radial pore (canals):** Pore canals of variable shape extending through the => *marginal zone*. All radial pore canals originate at the => *line of concrescence* and run in the plane of fusion (=> *marginal zone*) to the outer margin (*true* marginal pore canals, in contrast to => *false marginal pore canals*). The canals can be single tubes (termed "simple pore canals"), branched (branching or bifurcated zones) and/or have a bulbous enlargement near the middle or somewhat towards the outer margin (marking the base of a hair/bristle => *seta*). The approximate number and shape of the marginal pore canals are an important taxonomic feature.

2. **False marginal pore (canals):** These are pore canals originating at the => *line of concrescence* but not penetrating the plane of fusion (=> *marginal zone*). They either run through the marginal part of the outer lamella or, partly, through the inner lamella and surface distally from the outer margin.

   However, adopting Yamada's (2007) view would lead to the conclusion that the => *marginal zone* does not exist and the false pore canals would also be marginal pore canals extending through a different virtual plane of the valve's margin.

3. **Normal (lateral) pore (canals:** These are tubuli (small tubes) that perpendicularly pierce the outer lamella, scattered over the carapace's/valve's lateral surface. There are two distinguishable types of normal pores:

   A) **Simple** (single) normal pores, very small (1-3µm) and common in most ostracods. In recent taxa they bear hair-like bristles (=> *setae*), and are sometimes widened towards the interior (for the base of the bristles).

   B) **Sieve-type** normal pores comprise a plate bearing many tiny openings around a subcentral larger pore canal and are usually much larger (10-20µm) than simple ones. Okada (1983) divided these pores into sensillum pores and exocrine pores. However, representatives of the subfamily Limnocytherinae have many tiny (~ 5µm in diameter) pores not including normal pore canals and not bearing bristles.

Posterior cardinal angle (PCA): The posterior of the two => *cardinal angles*.

Posterior margin: Posterior part of the valve or carapace in lateral view, adjoining the posterior part of the => *free carapace/valve margin*. It extends between the angular peaks of the posterior => *cardinal angle* and the => *posteroventral region* (or, in the larger valve of morphologically modified ostracods like *Cypridea* for example, the point of the => *cyathus*). The posterior margin either coincides with the => *posterior lateral outline* or is overreached and covered by posterolateral expansions of the carapace (e.g. brood pouches in females of *Theriosynoecum*).

Posterior (part of) lateral outline: Posterior part of carapace outline (border) in lateral 2D-projection, either coincident or (sometimes) not coincident with the => *posterior margin*.

Posteroventral region (PVR): The posteroventral sector of the carapace outline including the posterior part of the => *ventral margin* and the ventral part of the => *posterior margin*. The term posteroventral angle is avoided because a recognizable angle is often not visible. Instead, the posteroventral region is more or less strongly rounded, elongated and pointed, or even developed as a cyathus (i.e. in *Cypridea*, for example).

Precocious sexual dimorphism (preadult sexual dimorphism): This term (also "preadult sexual dimorphism" after Rohr 1979) has been used by Whatley and Stevens (1977) for morphologic sexual dimorphism in instars that "... does not in any way imply precocious sexual maturity ..." (op. cit., p. 89). The latter authors differ between 'protomales' and 'protofemales'. It is often possible to separate female and male lineages in *Theriosynoecum* earlier, at least from A-2 instars onwards (A-4, A-5?). Rohr (1979) noticed that the maximum size of ontogenetic stages can vary to a great extent within a species. Male and female instars (protomales and protofemales) can be distinguished by differences in lateral and dorsal outlines (higher length/width and lower length/height relation of protomales). Protomales also usually have a stronger => *tuberculation* and more strongly developed, reticulation-like => *area-wide ornamentation elements/surface characters*.

For discussion of precocious sexual dimorphism regarding *Theriosynoecum* see Chapter 5.2, paragraph "Dimorphism" in the section of the genus' description.

Proto(fe)males: see => *precocious sexual dimorphism*

Punctum (pl. *puncta*, Latin for stitch, point, small spot, English adj. punctate): Puncta are small (between 20 and 50µm) pit-like depressions in the valve's surface (Moore 1961). They are a specific element of an => *area-wide ornamentation element/surface character*, the => *punctation* (refer to => *ornamentation*).

Punctation: see => *ornamentation*, => *area-wide ornamentation elements/surface characters*

Reticulation/reticulum/reticulate: see => *ornamentation*, => *area-wide ornamentation elements/surface characters*

Relative valve size (relation): A comparative term designating the carapace's valve size relation of an ostracod. In most cases, the left valve is larger than the right valve (LV>RV), and thus, this is called "normal" valve size relation. In some ostracod taxa, however, the opposite (RV>LV) can be the "normal" state (e.g. within the family Darwinulidae, see Rossetti and Martens 1998). For detailed elucidation, see => *inverse*. The relative valve size can be diagnostic at species or genus level in particular for ostracod taxa.

Ridge: see => *lateral ridge*

Selvage: This is an uncalcified thin translucent membrane that marks the peripheral limit between the *outer lamella* and *inner lamella* (Meisch 2000, following the "classical" terminology based on identifying the carapace margin being composed of two separate lamellae=duplicature) – or the *outer margin* and the *marginal infold*, respectively (after Yamada 2007, who redefined the *inner lamella* as the extension of the calcified outer lamella cuticle and uses the term *marginal infold*. In fossil specimens, the selvage is preserved as a slight ridge which represents the slightly calcified root of the otherwise organic selvage in living taxa (see remarks below).

Originally, the selvage forms the free valve margin, but is often secondarily displaced inwards (Meisch 2000). In this case "the free valve margin is formed by a more or less prominent excrescence, designated as => *flange*, of the outer lamella" (op. cit., p. 8). Only then and as applicable to *Theriosynoecum*, the selvage forms the middle ridge of the => *contact margin* forming the principal ridge of the calcified inner lamella and serving to seal the valves when the carapace is closed, as defined by Moore (1961). After Yamada (2007), the selvage does not correspond to the => *ligament* but to the lamella cuticle instead.

Remarks: Yamada (2007, p. 205) in his very recent review of the ultrastructure and terminology of the carapace margin in recent podocopid ostracods, particularly Cytheroidea, demonstrates by Transmission Electron Microscopy that the selvage is only composed of a—noncalcified—epicuticle, and just "… around its root, lattice structures of feather-like fibres develop, and this region seems to be slightly calcified". Yamada (op. cit.) also considers this calcified part, a slight ridge, should be identified with the ["classical", author's note] selvage as defined by Sylvester-Bradley (1941). Thus, it is also appropriate to use this term in fossil specimens for the slight ridge being calcified and, thus, also fossil preserved.

Solum (pl. *sola*; Latin for floor, bottom): The floor of a => *fossa* in a => *reticulum* (Sylvester-Bradley and Benson 1971).

Subequivalve (subequal valves): Refers to a weak difference in size and shape, i.e. lateral outline in particular, of the two carapace valves (see also => *equivalve*, => *inequivalve*).

Sulcus (pl. *sulci*, from Latin: furrow, groove; English adj. sulcate): A => *local ornamentation element.* This is a groove or trench (depending on its width and outline) of variable prominence, often trending "dorsoventrally" (i.e. perpendicular) and generally best developed in the dorsal half of the carapace (Moore 1961). Any sulci can be reduced to faint depressions. Often, a sulcus is associated with a => *lobe.* Taxa with "dorsoventral" sulci can be designated as monosulcate (one sulcus), bisulcate (two sulci) etc., depending on the number of sulci (i.e. "*Bisulcocypris*" syn. *Theriosynoecum*). As well as lobes, the sulci are => *local ornamentation elements.* Although their delimitation is diffuse, a single sulcus never covers the main part of the carapace's outer surface. Sulci are a genetically fixed diagnostic character.

Remarks: The causes of the development of "dorsoventral sulci" (better: dorsolateral sulci that are nearly perpendicular) have been discussed comprehensively by Triebel (1941) and by Hartmann (1966-89). Triebel (1941, p. 296-321) considered the tension of various muscles attached to the carapace (adductor muscles, mandibular muscles etc.) to be the cause for such sulci as local crenation of the carapace, forming during ecdysis, when the carapace is in a soft phase. He (op. cit.) believed that the reason for the occurrence of these sulci in only certain taxa is connected to their outline and its resulting tensile strength as well as the statics of the carapace. Triebel (1941) stated that only taxa with a straight dorsal margin show this feature. Triebel's arguments have been reconsidered by Hartmann (1966-89). Hartmann (op. cit., p. 53-54) gives the insufficient stability of the dorsal margin in some ostracods during ecdysis as reason for dorsolateral sulci. For Hartmann, this process is logical because the calcification starts at the valve margins, and all deformations of the valve's center are fixated through calcification (op. cit., p. 54) later than the margins.

There is without doubt a correlation between the position of the dorsolateral sulci and the position of the => *central muscle scar field.* Considering the ontogenetic line of *Theriosynoecum*, it is evident that the sulci become better developed in later stages.

Admittedly, Triebel's (1941) concept still lacks calculations and proof concerning statics of the carapace (see above). For example, it does not explain why there are (two) sulci in the subgenus *Cypridea (Bisulcocypridea)* Sohn, 1969, which has straight dorsal and hinge margins, but no sulci in other representatives of *Cypridea* which also have thin carapaces, straight dorsal margins and a variety of carapace statics configurations similar to those of *Cypridea (Bisulcocypridea)*. In addition, if the sole determining factors for dorsolateral sulci are the stability of the chitinous carapace in its uncalcified phase during ecdysis and the muscle tension, i.e. just morphologically induced, one would expect distinct variations in the appearance (shape, strength of incision) more frequently. In addition, no distortions of the sulci are known in specimens having faced strong fluctuations of environmental factors that affect the calcification process and statics of the carapace (i.e. specimens having strong nodes/node-like tubercles). An observation of many specimens of *Theriosynoecum* in collections, publications, and own samples led to the result that such variation cannot be confirmed. In contrast, shape and development of the sulci seem to be very consistent and are a diagnostic character. In summary, it must be stated that the genesis of the sulci has not yet been satisfactorily resolved and has to be reviewed.

Supracurvate: see => *curvature*

Surface characters: see => *ornamentation*, => *area-wide ornamentation elements*

Terminal (hinge) element(s): see => *hinge elements*

Tubercle(s): see => *ornamentation*, => *local ornamentation elements*

Tuberculation: An ornamentation characterized by many tubercles (see => *ornamentation*, => *local ornamentation elements*).

Valve size relation: see => *relative valve size*

Ventral margin: Ventral part of valves in lateral view, adjoining the ventral part of the free valve margin. It extends between both angular peaks of the => *antero-* and => *posteroventral regions*. The ventral margin either coincides with the => *ventral lateral outline* or is overreached and covered by ventrolateral prolongations of the carapace.

Ventral (part of) lateral outline: Ventral part of carapace outline (border) in lateral 2D-projection, either coincident or (often) not coincident with the => *ventral margin*.

Ventral outline: The 2D-projection of the carapace outline in ventral view. Since this outline is congruent with the more commonly used => *dorsal outline* (deriving from the more diagnostic and more often figured dorsal view of the carapace), its usage for describing a taxon or specimen becomes more or less dispensable.

Vestibulum/vestibule (pl. *vestibula*, Latin for front court; English adj. vestibular): Term for an internal feature defining the space between the free part of the => *inner calcified lamella* (see => *duplicatur*e) and the => *outer lamella* when not completely fused. A vestibulum can occur along anterior, ventral and posterior margins.

Plate 1

Scale bar = 100µm, specimens to scale (except Fig. 14), see Fig. 9 for stratigraphic distribution of samples.

Theriosynoecum fittoni (Mantell 1844)

1. LV, lateral view, adult female carapace, sample BCB1, Lakota Formation, Buck Canyon, SD, Fig. 2, loc. 1.

2. Dorsal view, slightly damaged, anterior end to the right, adult female carapace, sample HSDC3, Lakota Formation, Horse Sactuary - Devil's Canyon, SD, Fig. 2, loc. 2.

3. Ventral view, anterior end to the right, adult female carapace, sample BCB1, Lakota Formation, Buck Canyon, SD, Fig. 2, loc. 1.

4. LV, lateral view, adult male carapace, sample BCB1, Lakota Formation, Buck Canyon, SD, Fig. 2, loc. 1.

5. Dorsal view, anterior end to the right, preadult (A-1 instar) male carapace, sample BCB1, Lakota Formation, Buck Canyon, SD, Fig. 2, loc. 1.

6. Ventral view, anterior end to the right, adult male carapace, sample BCB1, Lakota Formation, Buck Canyon, SD, Fig. 2, loc. 1.

7. Anterior view, adult female carapace, sample BCB1, Lakota Formation, Buck Canyon, SD, Fig. 2, loc. 1.

8. Posterior view, adult female carapace, sample BCB1, Lakota Formation, Buck Canyon, SD, Fig. 2, loc. 1, .

9. Anterior view, adult male carapace, sample BCB1, Lakota Formation, Buck Canyon, SD, Fig. 2, loc. 1.

10. Posterior view, preadult (A-1 instar) male carapace, sample BCB1, Lakota Formation, Buck Canyon, SD, Fig. 2, loc. 1.

Theriosynoecum pahasapensis (Peck 1941)

11. LV, internal view, preadult? (A-1 instar?) male valve, sample SBCR LAg2, Lakota Formation, Stage Barn Canyon Road, SD, Fig. 2, loc. 8.

12. LV (broken), internal view, adult female valve, sample SBCR LAg2, Lakota Formation, Stage Barn Canyon Road, SD, Fig. 2, loc. 8.

13. RV, lateral view, adult male carapace, slightly inclined to the right to show posterior dorsolateral ridge-like protrusions, sample SBCR LAg2, Lakota Formation, Stage Barn Canyon Road, SD, Fig. 2, loc. 8.

14. Tripartite hinge of *Theriosynoecum* with bipartite median hinge element internal view of LV, anterior end to the right, magnification of specimen 11 of this plate. The downwards inclined elongate anterior and the swollen roundish posterior socket are clearly visible. The hinge bar is bipartite with its upwards contorted posterior part (see also Fig. 8).

PLATE 1

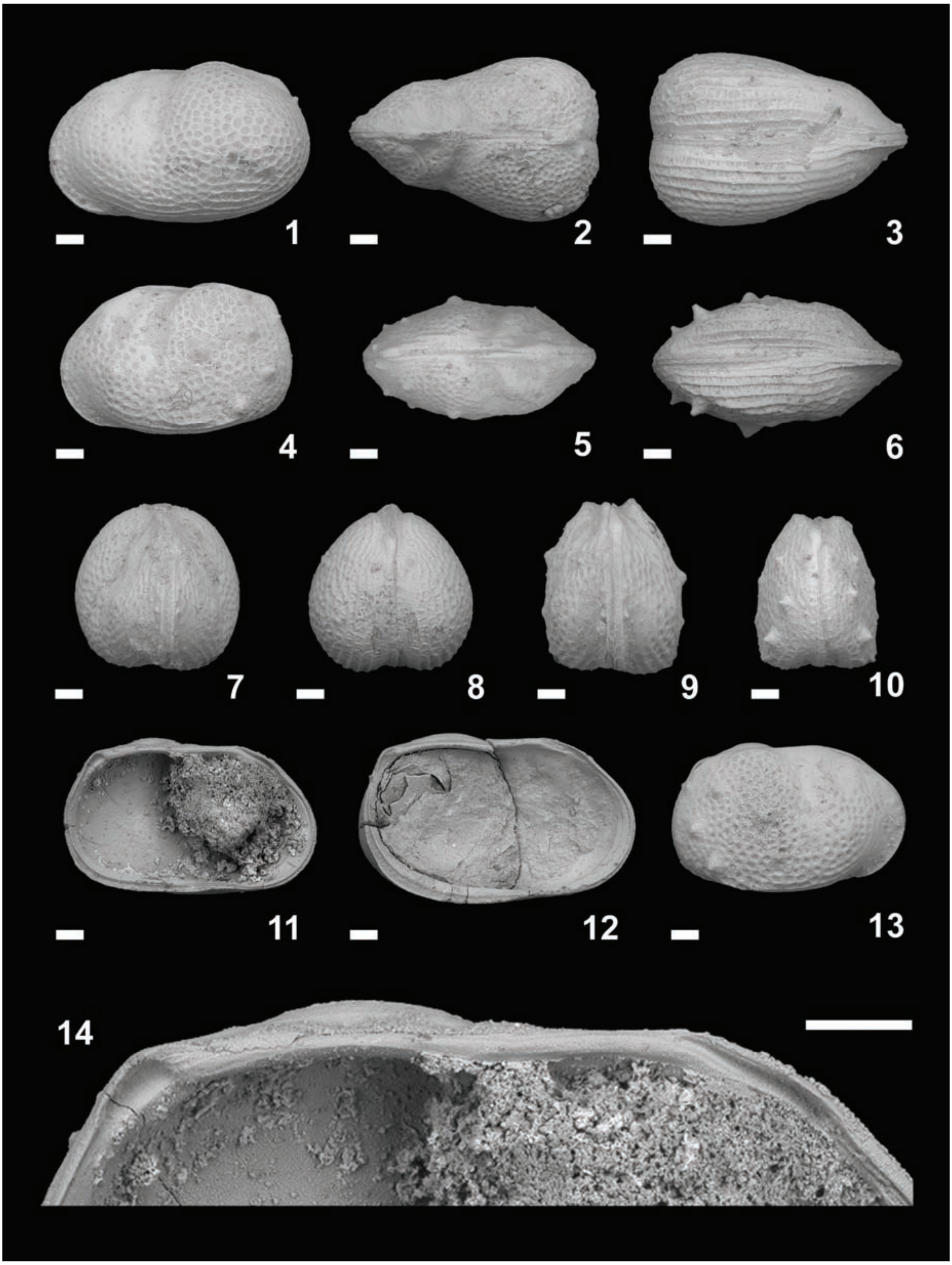


Plate 2

Scale bar = 100µm, specimens to scale (except Figs. 1 and 2), see Fig. 9 for stratigraphic distribution of samples.

Theriosynoecum fittoni (Mantell 1844)

1. Magnification of tubercle No. 4 (see Fig. 6/E) and surrounding punctation of a male specimen, LV, sample HSDC3, Lakota Formation, Horse Sanctuary - Devil's Canyon, SD. The central pore is well visible as well as the rounded puncta, the latter partially filled with sediment. All puncta adjacent to the tubercle are deformed and displaced, Fig. 2, loc. 2.

2. Lateral view of the ventral part of the anterior marginal zone with the two characteristic rows of anterolateral minor tubercles (see Fig. 6/E). Magnification of the specimen figured in Pl. 1, Fig. 1 herein.

3. LV, lateral view, preadult (A-1) female valve, posterodorsally compressed, sample HSDC3, Lakota Formation, Horse Sanctuary - Devil's Canyon, SD, Fig. 2, loc. 2.

4. RV, lateral view, adult female carapace, slightly dipping towards right, sample BCB1, Lakota Formation, Buck Canyon, SD, Fig. 2, loc. 1.

5. Dorsal view, anterior end to the right, preadult (A-1 instar) female carapace, sample BCB1, Lakota Formation, Buck Canyon, SD, Fig. 2, loc. 1.

6. Ventral view, with anterior crack, anterior end to the left, adult female carapace, overlap of LV (upper valve) over RV clearly visible, sample HSDC3, Lakota Formation, Horse Sanctuary - Devil's Canyon, SD, Fig. 2, loc. 2.

7. RV, lateral view, adult male carapace, slightly laterally compressed, A2 and A3 node-like tuberculum slightly developed, sample BCB1, Lakota Formation, Buck Canyon, SD, Fig. 2, loc. 1.

8. Ventrolateral view, anterior end to the left, adult male carapace, ventral carinae and A3 node-liker tuberculum visible, sample HSDC3, Lakota Formation, Horse Sanctuary - Devil's Canyon, SD, Fig. 2, loc. 2.

9. Ventral view, anterior end to the right - lower valve = LV , adult male carapace with weak ornamentation and indistinctly developed anterior marginal zone (copressed anteriorly, ample HSDC3, Lakota Formation, Horse Sanctuary - Devil's Canyon, SD, Fig. 2, loc. 2.

10. LV, lateral view, adult male valve, sample BC5 04, Lakota Formation, Buck Canyon, SD, Fig. 2, loc. 1.

11. RV, lateral view, adult male valve, sample BC5 04, Lakota Formation, Buck Canyon, SD, Fig. 2, loc. 1.

12. LV, lateral view, preadult? (A-1) male valve with well developed tubercle No. 3, slight A1 and A2 node-like tubercle, strongly developed surface characters and well developed anterior marginal zone, sample HSDC3, Lakota Formation, Horse Sanctuary - Devil's Canyon, SD, Fig. 2, loc. 2.

13. Dorsal view, anterior end to the right, preadult (A-2) male carapace, strongly recrystallized internal mold determinable through its outline, sample FRCA, Lakota Formation, Fall River Canyon, SD, Fig. 2, loc. 3.

14. Dorsal view, anterior end to the right, adult male carapace, badly preserved but determinable by the broadened anterior outer margin ("T-structure"), sample FRCA, Lakota Formation, Fall River Canyon, SD, Fig. 2, loc. 3.

15. Dorsal view, anterior end to the right, preadult (A-1) female carapace, weathered, sample BCB2, Lakota Formation, Buck Canyon, SD, Fig. 2, loc. 1.

PLATE 2

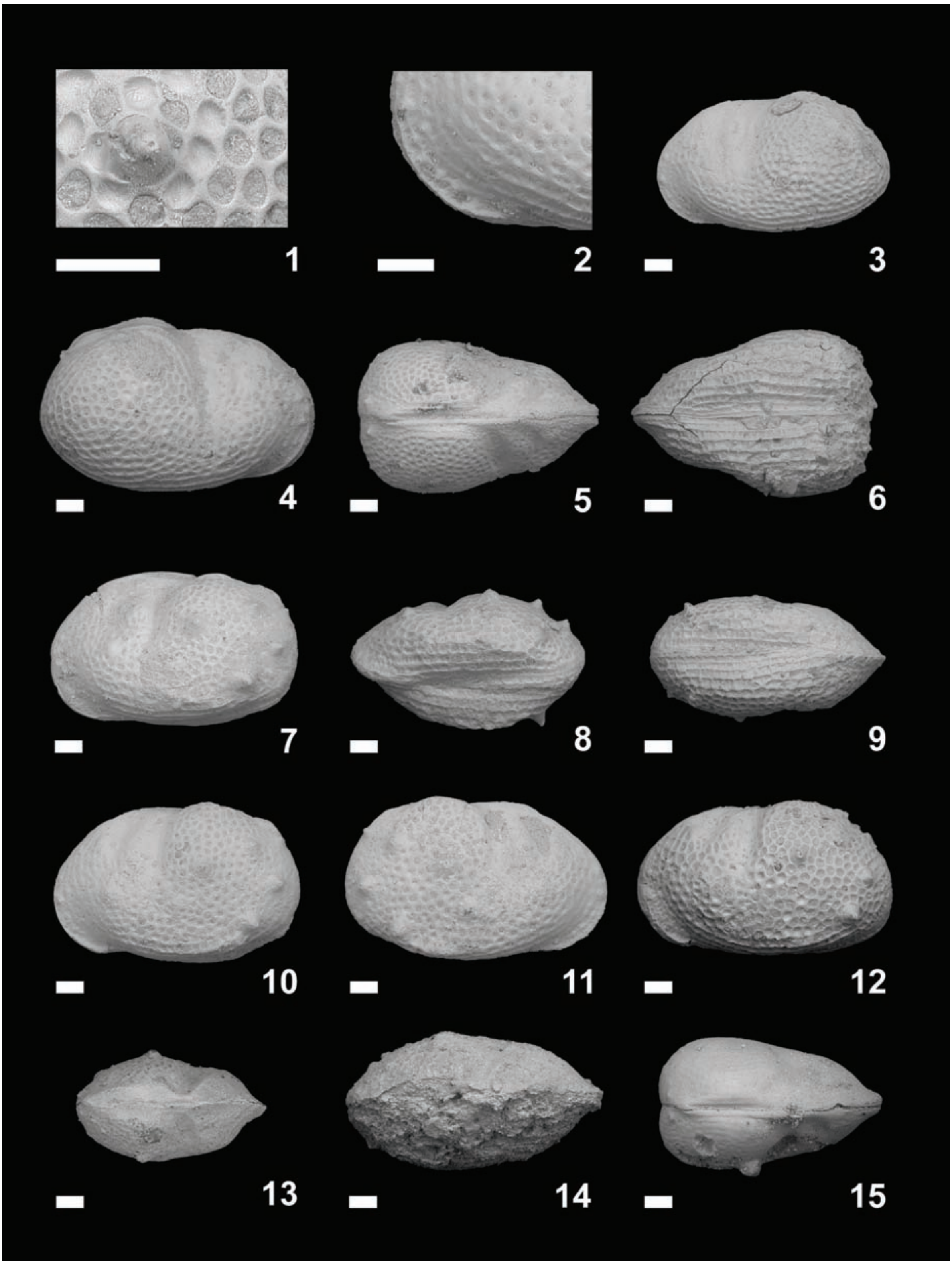


Plate 3

Scale bar = 100μm, specimens to scale (except Fig. 19), see Fig. 9 for stratigraphic distribution of samples.

Theriosynoecum verrucosa (Jones 1885)

1. LV (partially broken and laterally compressed), lateral view, preadult (A-1?) female valve, sample RCS MO3, Morrison Formation, Red Canyon, SD, Fig. 2, loc. 4.
2. LV (damaged, with sediment posterodorsally), lateral view, preadult(?) female valve, sample RCS MO3, Morrison Formation, Red Canyon, SD, Fig. 2, loc. 4.
3. LV (slighty laterally compressed), lateral view, preadult (A-2?) female? valve, sample RCS MO3, Morrison Formation, Red Canyon, SD, Fig. 2, loc. 4.
4. LV (laterally compressed), lateral view, adult male valve, sample RCS MO3, Morrison Formation, Red Canyon, SD, Fig. 2, loc. 4.
5. RV (inclined to the left), lateral view, adult male valve, sample RCS MO3, Morrison Formation, Red Canyon, SD, Fig. 2, loc. 4.
6. LV (anteriorly covered with sediment), lateral view, adult male valve, sample RCS MO3, Morrison Formation, Red Canyon, SD, Fig. 2, loc. 4.
7. RV, lateral view, juvenile (A-4?) carapace, protomale?, sample RCS MO3, Morrison Formation, Red Canyon, SD, Fig. 2, loc. 4.
8. LV, lateral view, juvenile (A-4?) carapace, protomale?, sample RCS MO3, Morrison Formation, Red Canyon, SD, Fig. 2, loc. 4.
9. RV, lateral view, juvenile (A-4?) carapace, protofemale?, sample RCS MO3, Morrison Formation, Red Canyon, SD, Fig. 2, loc. 4.
10. LV, lateral view, juvenile (A-4?) carapace, protofemale?, sample RCS MO3, Morrison Formation, Red Canyon, SD, Fig. 2, loc. 4.

Theriosynoecum pahasapensis (Peck 1941)

11. RV (broken), lateral view, juvenile (A-3?) valve, protomale?, sample REKO 04, Lakota Formation, Boxelder Creek, SD, Fig. 2, loc. 9.
12. RV, internal view, juvenile (A-3?) valve, protomale?, sample REKO 04, Lakota Formation, Boxelder Creek, SD, Fig. 2, loc. 9.
13. RV, lateral view, juvenile (A-5?) valve, protofemale??, sample REKO 04, Lakota Formation, Boxelder Creek, SD, Fig. 2, loc. 9.
14. LV, lateral view, juvenile (A-5?) valve, protomale??, sample REKO 04, Lakota Formation, Boxelder Creek, SD, Fig. 2, loc. 9.
15. Dorsal view, anterior end to the left, juvenile (A-5?) carapace, sample REKO 04, Lakota Formation, Boxelder Creek, SD, Fig. 2, loc. 9.
16. LV, internal view, juvenile (A-5?) carapace, protomale??, sample REKO 04, Lakota Formation, Boxelder Creek, SD, Fig. 2, loc. 9.
17. RV, internal view, juvenile (A-5?) carapace, protofemale??, sample REKO 04, Lakota Formation, Boxelder Creek, SD, Fig. 2, loc. 9.
18. RV, internal view, juvenile (A-5?) carapace, protomale??, sample REKO 04, Lakota Formation, Boxelder Creek, SD, Fig. 2, loc. 9.
19. Bipartite hinge in juveniles, RV, magnification of specimen 12 of this plate.

PLATE 3

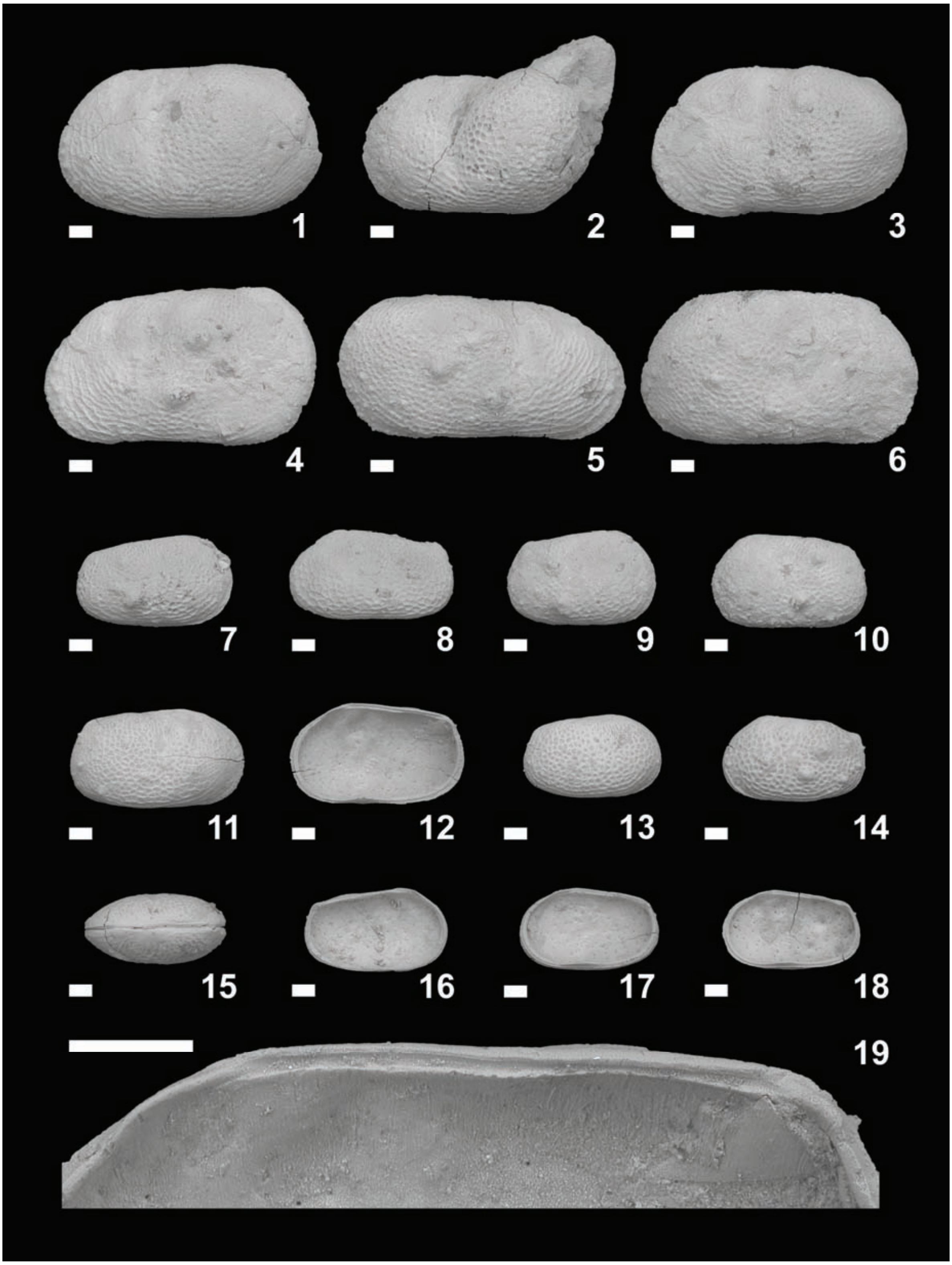


Plate 4

Scale bar = 100µm, specimens to scale (except Fig. 14), see Fig. 9 for stratigraphic distribution of samples.

***Theriosynoecum pahasapensis* (Peck 1941)**

1. LV, lateral view, adult female valve, ventrally slightly damaged, sample SBCR LAg3*, Lakota Formation, Stage Barn Canyon Road, SD, Fig. 2, loc. 8.

2. Dorsal view (with slight cracks), anterior end to the left, adult female carapace, sample SBCR LAg3*, Lakota Formation, Stage Barn Canyon Road, SD, Fig. 2, loc. 8.

3. LV, internal view, adult female carapace, with central muscle scar field, sample SBCR LAg3*, Lakota Formation, Stage Barn Canyon Road, SD, Fig. 2, loc. 8.

4. RV, lateral view, adult female valve, sample SBCR DC Strat. Column, Lakota Formation, Stage Barn Canyon Road, SD, Fig. 2, loc. 8.

5. RV, lateral view slightly inclined to the right, adult female carapace without tuberculum on posterolateral cusp, sample SBCR LAg3*, Lakota Formation, Stage Barn Canyon Road, SD, Fig. 2, loc. 8.

6. RV, lateral view, adult female valve with rounded posterolateral cusp lacking a tuberculum, sample SBCR DC Strat. Column, Lakota Formation, Stage Barn Canyon Road, SD, Fig. 2, loc. 8.

7. LV, lateral view, adult male valve, surface partly weathered (smoothing), sample SBCR LAg3*, Lakota Formation, Stage Barn Canyon Road, SD, Fig. 2, loc. 8.

8. Dorsal view, anterior end to the left, adult male carapace with slight cracks, sample SBCR LAg3*, Lakota Formation, Stage Barn Canyon Road, SD, Fig. 2, loc. 8.

9. RV, lateral view, pre(?)adult male carapace, sample SBCR LAg3*, Lakota Formation, Stage Barn Canyon Road, SD, Fig. 2, loc. 8.

10. RV, internal view, adult male valve with cracks anteriorly, slightly weathered, sample SBCR LAg3*, Lakota Formation, Stage Barn Canyon Road, SD, Fig. 2, loc. 8.

11. RV, lateral view, adult male valve, slightly damaged anteroventrally, sample SBCR DC Strat. Column, Lakota Formation, Stage Barn Canyon Road, SD, Fig. 2, loc. 8.

12. LV, lateral view, adult male carapace, weathered (smoothing), sample SBCR LAg3*, Lakota Formation, Stage Barn Canyon Road, SD, Fig. 2, loc. 8.

13. LV, lateral view, preadult (A-4?) proto-female carapace, surface partially covered with small crystals, sample SBCR LAg1, Lakota Formation, Stage Barn Canyon Road, SD, Fig. 2, loc. 8.

14. Bipartite hinge, internal view of RV, magnification of specimen 3 of this plate.

PLATE 4

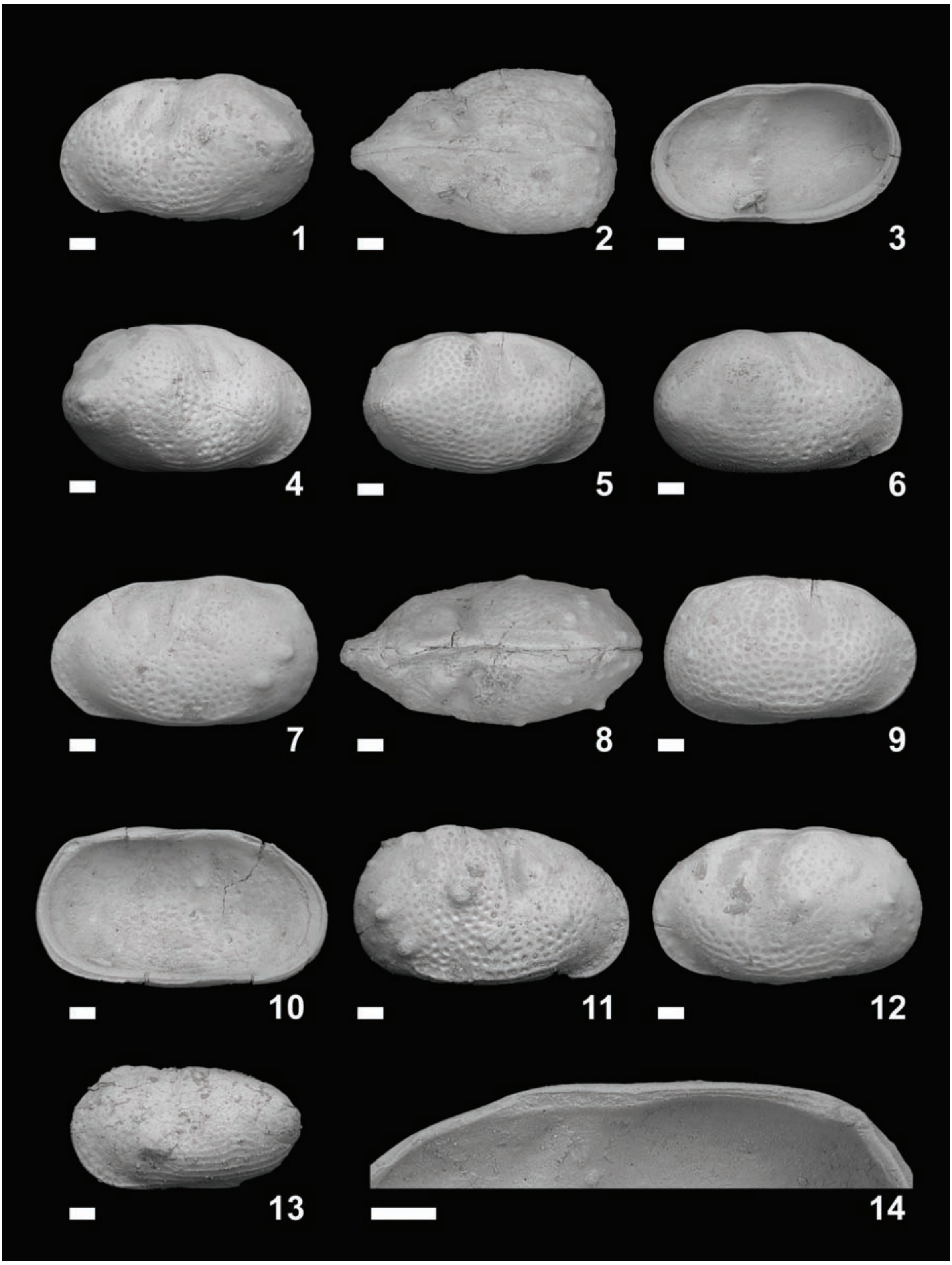


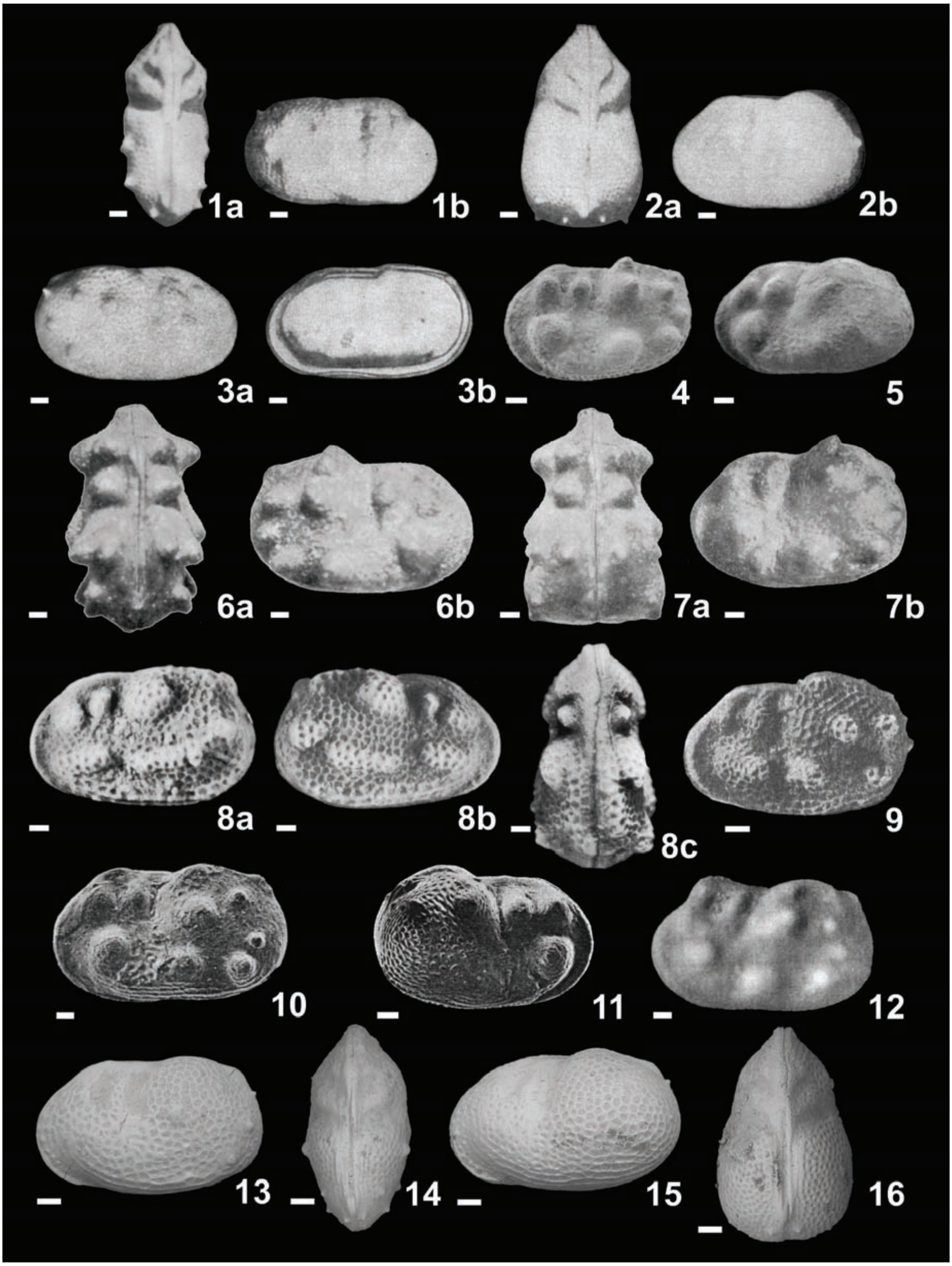
Plate 5

Refigured types and other specimens considered to be representatives of *T. fittoni* (Mantell 1844)

Scale bar = 100µm, specimens NOT to scale.

1. ***Theriosynoecum alleni* (Pinto and Sanguinetti 1962)**, holotype M.P., U.R.G.S., M.P.-0-50A. Refigured from Pinto and Sanguinetti (1962), pl. 9: 1a) pl. 9, fig. 6a, dorsal view of a male, anterior end upwards; 1b) pl. 9, fig. 6b, right lateral view of the same.
2. ***Theriosynoecum alleni* (Pinto and Sanguinetti 1962)**, paratype M.P., U.R.G.S., M.P.-0-50B. Refigured from Pinto and Sanguinetti (1962), pl. 9: 2a) pl. 9, fig. 7a, dorsal view of a female, anterior end upwards; 2b) pl. 9, fig. 7b, right lateral view of the same.
3. ***Theriosynoecum alleni* (Pinto and Sanguinetti 1962)**, paratype M.P., U.R.G.S., M.P.-0-51A. Refigured from Pinto and Sanguinetti (1962), pl. 9: 3a) right lateral view of a male, op. cit., pl. 9, fig. 8b; 3b) internal view of the same, op. cit., pl. 9, fig. 8a.
4. ***Theriosynoecum fittoni* (Mantell 1844)**, male(?) left valve with extremely strong tuberculation, probably an A-1 or A-2 instar with precocious sexual dimorphism, BGS Mik(M) 4498, refigured from Anderson (1985), pl. 9, fig. 13.
5. ***Theriosynoecum fittoni* (Mantell 1844)**, lectotype BGS Mik(M) 1905, adult female left valve with node-like tubercles, especially the anterior ones (A1 to A3), refigured from Anderson (1985), pl. 9, fig. 12.
6. ***Theriosynoecum fittoni* (Mantell 1844)**, M.P., U.R.G.S., M.P.-0-24A, adult male carapace with strong tuberculation, refigured from Pinto and Sanguinetti (1962): 6a) dorsal view, anterior end pointing upwards, pl. 11, fig. 9a; 6b) right lateral view of the same, op. cit., pl. 11, fig. 9b.
7. ***Theriosynoecum fittoni* (Mantell 1844)**, M.P., U.R.G.S., M.P.-0-24B, adult female carapace with strong tuberculation, refigured from Pinto and Sanguinetti (1962): 7a) dorsal view, anterior end pointing upwards, op. cit., pl. 11, fig. 10a; 6b) left lateral view of the same, op. cit., pl. 11, fig. 10b.
8. ***Theriosynoecum papillaris americanum* Krömmelbein and Weber 1971**, holotype, BfB No. 7821, refigured from op. cit.: 8a) left view of male carapace with nodes and node-like tubercles, op. cit., pl. 10, fig. 44a; 8b) right view of the same, op. cit., pl. 10, fig. 44b; 8c) dorsal view of the same, anterior ends upwards, op. cit., pl. 10, fig. 44c.
9. **'*Metacypris*' sp. 1 Krömmelbein 1962**, SMF Xe 4244, lateral view of female carapace with strong tubercles, op. cit., pl. 62, fig. 64a.
10. ***Theriosynoecum fittoni* (Mantell 1844)**, refigured from Kilenyi and Neale (1978), left lateral view of male left valve (designated as female specimen by Kilenyi and Neale), SJCC 68/28.5, op. cit., pl. 5, fig. 10.
11. ***Theriosynoecum fittoni* (Mantell 1844)**, refigured from Kilenyi and Neale (1978), right lateral view of female carapace, SJCC 68/28.6, op. cit., pl. 5, fig. 9.
12. **'*Gomphocythere berwickensis*' Martin 1940**, male left valve with tuberculation and distorting node at the anterior cardinal angle, SMF X/E 800, op. cit., pl. 12, fig. 176.
13. ***Theriosynoecum fittoni* (Mantell 1844)**, lateral view of male left valve with weak tuberculation, sample REKO 04, Lakota Formation, Boxelder Creek, SD.
14. ***Theriosynoecum fittoni* (Mantell 1844)**, dorsal view of male carapace, anterior end upwards, sample BCB1, Lakota Formation, Buck Canyon, SD.
15. ***Theriosynoecum fittoni* (Mantell 1844)**, lateral view of female left valve without nodes or tubercles, sample BCB1, Lakota Formation, Buck Canyon, SD.
16. ***Theriosynoecum fittoni* (Mantell 1844)**, dorsal view of female carapace, anterior end upwards, sample BCB1, Lakota Formation, Buck Canyon, SD.

PLATE 5



2.3. Publication No. 3

Revision of the genus *Cypridea* Bosquet (Ostracoda, Crustacea) and some of its species from the nonmarine Lower Cretaceous Lakota and Cedar Mountain formations of the U.S. Western Interior and the European 'Purbeck/Wealden'

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Abstract:

Cypridea Bosquet 1852 (Cypridoidea, Cyprideidae) is an important Kimmeridgian to Lower Eocene nonmarine ostracod genus, the representatives of which dominate Late Tithonian to Barremian Purbeck/Wealden-like nonmarine ostracod faunas of the world. A comprehensive revision of the genus focusing on North American representatives led to considerable progress in its taxonomy, and a breakthrough in its biostratigraphic application in the Western Interior foreland basin. Early Cretaceous representatives of *Cypridea* have great utility in improving the biostratigraphic age determination for and correlation of relevant formations of this basin. Key to their successful application is an upgraded taxonomic concept including new insights in the coherences of specific reproductive mechanisms (asexual and mixed reproduction) in the context with diversity and dispersal modes, together with the understanding and evidence that these ostracods are not as endemic as erstwhile believed. This taxonomic concept resolves crucial problems resulting from an overestimation of the taxonomic significance of several carapace characters (particularly local ornamentation elements as defined herein, and the outline), and facilitates improved stratigraphic and paleoecologic applications as well as providing the basis for further taxonomic research. The revision includes an extensive historic overview of most relevant publications and is supported by a detailed glossary of revised and clarified taxonomic terms, including the newly defined term *alveolar ridge* and complemental illustrations.

With respect to suprageneric taxonomy, the family Cyprideidae Martin 1940 is partially revised as well. *Longispinella* Sohn 1979 is now considered a subgenus of *Cypridea* while *Cypridea (Guangdongia)* Guan 1978 is allocated to *Bisulcocypridea* Sohn 1969. As for the subgeneric taxonomy, the North American species *Cypridea (Pseudocypridina) inornata* (Peck 1951) is now considered a junior synonym of *Cypridea (P.) setina* (Anderson 1939), *Cypridea (P.) laeli* Sohn 1979 considered an ecophenotype of *Cypridea (P.) piedmonti* (Roth 1933), and *Cypridea (Longispinella) asymmetrica* Sohn 1979 designated synonymous (sexual dimorph) to *C. (L.) longispina* Peck 1941. Sexual dimorphism is presumed in several species of *Cypridea* and mixed reproduction corroborated as being the most likely reproductive mechanism among taxa of this genus. *Cypridea? minuta* (Peck 1951) most probably represents an early representative of the sulcate *Bisulcocypridea* Sohn.

Ostracod correlations mainly based on representatives of *Cypridea* strongly suggest a much higher maximum age for some Lower Cretaceous formations (Lakota Formation, South Dakota and Wyoming, and Cedar Mountain Formation, Utah) of the Western Interior foreland basin, i.e., Berriasian to Early Valanginian instead of Barremian or Aptian. These results affect the correlatives of these formations as well. The upgraded taxonomic approach provides a considerable step towards an

improved general application of species of *Cypridea* as well as a good basis regarding future research in phylogeny, evolution and distribution of the representatives of the cypridoid family Cyprideidae.

Keywords: Western Interior foreland basin, nonmarine Ostracoda, taxonomy, Lower Cretaceous, biostratigraphy, Black Hills, San Rafael Swell

1. Introduction

Ostracods are among the most common fossils in late Mesozoic nonmarine deposits of the world. Because of their small size, good fossil record and preservation, as well as their ecology and dispersal strategies these ostracods have a high potential to be good index fossils with at least moderate resolution. *Cypridea* Bosquet 1852 is a fossil (Kimmeridgian to Lower Eocene) nonmarine genus of the superfamily Cypridoidea, and the extinct family Cyprideidae Martin 1940 (not to confuse with the extant family Cyprididae Baird 1845). Representatives of *Cypridea* are common faunal elements of nonmarine late Mesozoic to early Cenozoic deposits virtually worldwide (except for Australia and Antarctica). In latest Jurassic to Cretaceous nonmarine sediments, representatives of this genus and its close relatives account for a large, if not dominant, proportion of the ostracod diversity. Representatives of *Cypridea* have successfully been used for local biozonation in nonmarine deposits of uppermost Jurassic (upper Tithonian) and Lower Cretaceous age (Berriasian to Barremian, earliest Aptian) age, i.e. the so-called Purbeck/Wealden-like facies with particular good resolution in the NW European Purbeck/Wealden Basin: the Purbeck/Wealden facies of England, UK (type area) and the Netherlands (subsurface), as well as the "German Wealden" of NW Germany.

Despite such excellent regional examples, it hitherto seemed barely possible to apply species of this genus to supraregional (i.e. inter-basinal and intercontinental) biostratigraphy. In contrast to other common contemporaneous taxa (e.g. representatives of the still extant subfamily Timiriaseviinae, like the extinct genus *Theriosynoecum*), *Cypridea* and its close relatives, that is the whole family Cyprideidae Martin 1940, are extinct. With exception of a few, mostly not very comprehensive publications, there have been almost no major revisions of the taxonomy, relationships and phylogeny of the genus *Cypridea* or the family Cyprideidae during about the past 50 to 60 years, but multitudinous thematically confined publications describing new genera, subgenera, species, and subspecies thereby complicating the taxonomy and increasing the assumed factor of endemism. Furthermore, a biostratigraphic application was not the main object of these revisions, and many aspects remained controversial.

In the view of the present author, the central issue inhibiting the harmonization of taxonomy and supraregional correlations has been the different usage, interpretation and evaluation of the morphologic terminology (notably "local ornamentation elements" as defined herein) resulting in relatively restrictive or wrong taxonomic concepts of (sub-)species and (sub-)genera (i.e., based on very few or even single characters). Therefore, to render a wider and global utilization possible, a new revision that places emphasis on specifying, redefining and harmonizing the morphologic terminology of *Cypridea* and its representatives became necessary, therewith including and discussing new discoveries in ostracod biology that were published in the last two decades (e.g. new insights in the influence of ecologic parameters on some ornamentation elements, reproduction and dispersal mechanisms etc.).

Within the scope of a project carried out in cooperation with a research group from the Sam Noble Oklahoma Museum of Natural History, Norman, Oklahoma (lead by Richard L. Cifelli), dealing with early mammals, the taxonomy of an important genus (*Cypridea* Bosquet 1852) of nonmarine Lower Cretaceous ostracods of the U.S. Western Interior as well as other contemporaneous deposits of the world is revised. The main object of this project and cooperation was an examination of the ostracods retrieved from some Early Cretaceous formations of the U.S. Western Interior where vertebrate remains (particularly early mammals) had been found, and to improve the age determination of such formations, if possible. During the project, it soon became clear that a comprehensive revision of the most important nonmarine ostracod index genera/species during Latest Jurassic-Early Cretaceous times (i.e. *Cypridea*, and *Theriosynoecum* Branson 1936, the latter to be dealt with in another paper) was necessary to apply these to the biostratigraphy of North American Lower Cretaceous nonmarine formations. Many of these formations are poorly dated, often just known to lie above the Late Jurassic Morrison Formation and to be of Early Cretaceous (pre-middle Albian) age. In addition, a lowermost Cretaceous age of some top parts of the Morrison Formation seems to be probable.

Consequently, this work focuses on selected *Cypridea* species of the Lower Cretaceous U.S. Western Interior, their comparison to the most adjacent faunas in Western Europe at that time (English Purbeck/Wealden, "German Wealden", "Spanish Wealden") as well as other continents in part, and their potential usability for supraregional and regional biostratigraphy, and paleoecology. The detailed implications and consequences of the taxonomic results for paleobiogeography of the North American taxa of *Cypridea* as well as the biostratigraphy and paleoecology of selected formations (top Morrison Formation and Lakota Formation, South Dakota; and Cedar Mountain Formation, Utah) of the U.S. Western Interior foreland basin and other areas will be published elsewhere, including the authors results of the revision of the genus *Theriosynoecum*, as well as the analysis of other taxa.

Lacking own data from the Lakota and Cedar Mountain formations regarding the “Aptian-Albian fauna” of Peck (1956, 1959; deriving from partially younger formations: Bear River Formation and upper Cloverly Formation, Wyoming; upper Gannett Group – Peterson, Bechler and Draney limestones, Wyoming and Idaho; Kootenai Formation, Montana; upper Cedar Mountain Formation, Utah), this fauna is mostly excluded thus far. Some important taxa are discussed, however.

2. Previous work and aims

2.1. Previous work regarding general taxonomy, biostratigraphy and paleogeography of *Cypridea*

As already mentioned, there are relatively few publications giving either a) a comprehensive survey of the general taxonomy of the genus *Cypridea* and/or the family Cyprideidae a wider context, or b) an approach to analyze the paleogeographic distribution of representatives of *Cypridea* and its close relatives in the global context, particularly with the aim of an application to supraregional biostratigraphy. Some major taxonomic and systematic contributions include Martin (1940), Sylvester-Bradley (1949), Wolburg (1959), Szczechura (1981), Horne and Colin (2005), and finally, this work. With respect to the biostratigraphic application, the British micropaleontologist F. W. Anderson (1905-1982) is the most prominent pioneer for the successful biostratigraphic application of representatives of *Cypridea* and other ostracods of the English Purbeck/Wealden. In fact, the extensive publications of F.W. Anderson on mostly nonmarine English Purbeck/Wealden ostracods and their biostratigraphic application (Anderson 1939, 1941, 1962, 1967, 1971, 1973, 1985; Anderson and Bazley 1971, Anderson et al. 1967) are regarded as classic examples of an application of ostracods to biostratigraphy in general (Horne 1995). Anderson's (1985) zonations are still applied and, as for the Berriasian to Barremian part, have been correlated to contemporaneous Boreal deposits of NW Europe as well as the marine Tethyan standard sections in SW Europe (see Hoedemaeker and Herngreen 2003 and references therein). Anderson's (1985) zonations have been critically revised by Horne (1995). A detailed historic overview of this topic is provided below (section 5.2.2).

2.2. Previous work regarding nonmarine Late Jurassic to Early Cretaceous ostracods in North America

The scientific history of Late Jurassic - Early Cretaceous nonmarine Ostracoda of North America (U.S. Western Interior and Canada) began in 1886, when the well-known British paleontologist Thomas Rupert Jones (1819-1911) published a paper on "Some fossil Ostracoda from Colorado" (Jones 1886) he had received from the U.S. Geological Survey paleontologist C. A. White. The samples came from the "*Atlantosaurus* beds" (Upper Jurassic Morrison Formation near Cañon City, Colorado) and lack any representatives of *Cypridea*. A few years later, Jones (1893) published another paper about (Early Cretaceous) ostracods from SW Wyoming and Utah, including representatives of *Cypridea*.

It was not until the late 1920s–early 1930s that this kind of work was continued. Besides other marine invertebrate taxa V. H. Vanderpool (1928) described some nonmarine ostracods from the Glen Rose and De Queen limestones of the Aptian-Albian Trinity Group in Arkansas and Texas, among them three representatives of *Cypridea*. Robert I. Roth (1933) was the pioneer to describe ostracods from the (eastern) Black Hills area followed by Harper and Sutton (1935). At that time, the authors (Roth 1933, Harper and Sutton 1935) believed the ostracod-bearing beds in the Black Hills to be part of the Morrison Formation. Peck and Reker (1948) were committed to be able to differ Upper Jurassic Morrison deposits from Lower Cretaceous ones by means of microfossils (and/or molluscs), regarding the ostracods, mainly by the absence of typical Morrison taxa (op. cit.). However, as already stated by Sohn (1958), the deposits described by Roth (1933) and Harper and Sutton (1935) from the eastern Black Hills area (South Dakota) were part of the Lower Cretaceous Lakota Formation. Sohn (1958) based his conclusions on the presence of representatives of the Cyprideinae (recte Cyprideidae Martin 1940, see Chapters 5.2.1 to 5.2.3 below for details), that is to say representatives of *Cypridea*.

During the middle of the 20th century, R. E. Peck was one of the main U.S. authors dealing with Mesozoic nonmarine charophytes and ostracods in the Rocky Mountain area, applying them for regional biostratigraphy (e.g. Peck 1937, 1941, 1951, 1956, 1959; Peck and Craig 1962). At the University of Missouri, Columbia, he also had some Master's students working about ostracods (Looney 1948, Hoare 1953, Craig 1961) but, unfortunately, all the theses remained unpublished—although Peck and Craig (1962) published a general paper about ostracods and charophytes in Wyoming and adjacent areas. The new taxa erected in these theses therefore remain *nomina nuda*.

As for Canada, few papers have been published about Lower Cretaceous ostracods so far the one from Diane M. Loranger (1951; 1954, reprint of the 1951 paper with revisions) who described ostracods from the Ostracod/Calcareous Member of the Blairmore Formation of Alberta and southern British Columbia, this paper being the most important as to *Cypridea*. Later publications from Finger (1983) as well as Tatman and Whatley (1996, 2001) again dealt with ostracods of this unit but more focus on the whole fauna and the biostratigraphy and paleoecology (Finger 1983, Whatley and Tatman 1996) or on the taxonomy of ostracods other than *Cypridea* (Tatman and Whatley 2001).

Swain and Brown (1964, 1972) described Mesozoic nonmarine ostracods that include representatives of *Cypridea*, along with marine ostracods, from the southeastern United States and its Atlantic coastal region. These areas, however, are not part of the Western Interior foreland basin.

With respect to the Lower Cretaceous Lakota Formation, Black Hills area (South Dakota and Wyoming), I. G. Sohn was the main author in the second half of the 20th century. Sohn described the ostracods recovered by field parties mapping the southern and eastern Black Hills area between 1954 and 1958 (Sohn 1958, 1979). These field campaigns were carried out in collaboration of the U.S. Geological Survey and the U.S Atomic Energy Commission due to the discovery of detritic Uranium within the Mesozoic deposits of the Black Hills in 1951, and Sohn joined the field parties in 1957 to obtain additional collections (Gott et al. 1974, Sohn 1979). Sohn (1969) also described nonmarine Lower Cretaceous ostracods from NE Nevada.

The ostracods of the Cedar Mountain Formation (Utah) have never been described. Stokes (1952) only mentions ostracods (and charophytes) from the "Burro Canyon Formation", now considered to be part Cedar Mountain Formation (see Kirkland et al. 1997), of eastern Utah (Salt Valley Anticline, Grand County) which were determined by R. E. Peck (Stokes 1952).

For over 25 years, the nonmarine Early Cretaceous ostracods in the North American Western interior foreland basin, including the representatives of *Cypridea* Bosquet, have not been subject to detailed research, and barely have been dealt with in a global context in the time before. One reason may be that these ostracod faunas were considered to be endemic traditionally and not well applicable to biostratigraphy. As Michael E. Schudack (1995, 1996, 1999, Schudack et al. 1998) has shown for the ostracods (and charophytes) of the nonmarine Upper Jurassic Morrison Formation that underlies many of the nonmarine Lower Cretaceous formations, the ostracod endemicity is not as strong as believed in the past. Quite the contrary, there are many close relations to the Iberian faunas (Spain) usable for biostratigraphy, biogeography and paleoecology/paleoclimate applications. Accordingly, there was a high probability that this is also true for the Lower Cretaceous faunas—which was the starting point of the new research presented herein.

Sohn (1958) had already suggested and later confirmed (Sohn 1979) a Valanginian to Barremian age for the Lakota Formation of the Black Hills area (as can be confirmed here) based on comparison of the ostracod fauna to contemporaneous European and Asian faunas. Sohn (1979), though, only discussed similarities of representatives of these faunas, but retained established local taxon names and erected new ones. Sohn (1958, 1979) however, never went one step further and reevaluated his analyses of the taxa to make closer correlations

As for *Cypridea* and its representatives, relevant publications including the North American works are listed and commented in Chapter 5.2.2.

2.3. Aims

Altogether, the reasons given might explain why no or only tentative attempts for supraregional comparison and correlation of Early Cretaceous nonmarine ostracods of the U.S. Western Interior was made in the second half of the 20th century. Hitherto, the supraregional nonmarine ostracod biostratigraphy of Lower Cretaceous rocks of North America is still poorly developed, a gap to be partially filled with the results of this paper. A comprehensive review of the taxonomy shall provide the basis for a utilization of the nonmarine ostracods for applications like biostratigraphy, paleobiogeography and paleoecology.

The comprehensive nature of this paper, necessarily including long synonymy lists, descriptions and discussions, derives—in the view of the author—from the need for:

A) compiling an enourmous amount of information scattered throughout hundreds of publications in many different languages, some difficult to obtain,

B) a detailed review, definition, and illustration of specific taxonomic terms in conjunction with progress in research of ostracod phylogeny, biology and ecology (this led to the detailed glossary at the end of this paper),

C) and describing and figuring as many carapace features as possible as well as discussing their taxonomic value,

D) a better global approach to the comparison of the taxa, a matter having often been neglected in the past due to language barriers and partial unavailability of references in pre-Internet times.

One aim of this paper is to provide a synopsis within one publication that is hoped to be a good basis for future research regarding *Cypridea*—its taxonomy, phylogeny, and its stratigraphic and paleobiogeographic distribution worldwide. For the purpose of a better global approach, it is attempted to implicate as many references as possible in non-English languages and from continents other than

North America and Europe, specifically South America (Spanish, Portugese, German) and Asia (Russian, Chinese), as well as Africa in part (French, German; altogether, the state knowlegde about Upper Jurassic to Cretaceous nonmarine ostracods in Africa is not that good yet, except for central West Africa). As for the Central Asian ostracods, luckily there are some comprehensive newer publications, practically taxonomic atlases, summarizing and refiguring the so far published species: Hou et al. (2002), Nikolaeva and Neustrueva (1999) and Neustrueva et al. (2005).

For a revsion of the genus *Theriosynoecum* Branson, the second most important genus for biostratigraphy in nonmarine Lower Cretaceous deposits of Europe, and some North American representatives refer to Sames (submitted).

3. Geologic overview, stratigraphy and localities

The North American Cordilleran foreland basin (U.S. Western Interior Basin) is the largest of its type known, reaching from northeast Canada to central Mexico and occupying an area of more than five million square kilometers (e.g. Kauffman and Caldwell 1993; see Fig. 1 herein). During Late Jurassic times, the basin began to develop between the North American Cordilleran orogenic belt to the west and the North American craton to the east in response to the subduction of oceanic plates of the pacific domain (Kauffman and Caldwell 1993, DeCelles 2004). Contemporaneously, and in various types of process-response and feedback relationships, the orogenic belt and the foreland basin evolved together until Eocene times. Altogether, this evolution lasted for about 100myr, including two main orogenic phases: the Sevier orogeny ("Middle" to Late Cretaceous) and the Laramide orogeny (Late Cretaceous to Eocene). Basin subsidence was caused by flexural thrust-loading – a combination of the flexure of the lower crust due to overthrust, sediment load and longer wavelength (>400km) dynamic subsidence (e.g. DeCelles and Giles 1996, DeCelles 2004, Miall et al. 2008). Deposition during Late Jurassic to Early Createaceous times was strongly connected with the tectonic coevolution of both the proto-Cordillera and its associated foreland basin, which affects source, supply rate and depozone of the nonmarine sediments (Kauffman and Caldwell 1993). DeCelles and Giles (1996, p. 117) point out that in their expanded definition for foreland basin systems "… a depozone is defined in terms of its position during deposition, rather than its eventual position with respect to the thrust belt", which is important to understand the interaction of tectonics and syndepositional stratigraphic architecture, and its regional differences.

Stratigraphic correlation and refined dating of Late Jurassic to Early Cretaceous Western Interior nonmarine strata, having been problematic throughout the 20th century, improved since integrated stratigraphy was applied (e.g. Currie 1997, 1998, Way et al. 1998, Zaleha 2006). However, dating such formations is still a problem and especially the maximum age of the Lower Cretaceous formations or rather the hiatus between their base and the underlying Morrison Formation is controversially under discussion, a problem hoped to be solved by improving age estimations due to combined ostracod/charophyte biostratigraphy.

The Lakota Formation (Black Hills, South Dakota and Wyoming) was deposited in the distal part of the foreland basin, whereas the Cedar Mountain Formation (San Rafael Swell, Utah) represents its very proximal deposits (Fig. 1). The Laramide event led to fracturing of the craton and partitioned a part of the foreland basin ito a mosaic of smaller foreland basins and uplifts (e.g. DeCelles 2004, Dickinson 2004), like the Black Hills uplift for example, the easternmost of the Laramide foreland uplifts.

The Inyan Kara Group, consisting of the Lakota Formation in its lower part and the overlying Fall River Formation, crops out along the flanks of the Black Hills uplift, South Dakota and Wyoming (Fig. 2). In most areas, the Morrison Formation unconformably underlies the Inyan Kara Group except for the southeastern area, where it is substituted by the locally occurring Unkpapa Sandstone, a white eolean siltstone. In his revision of the Lakota Formation, Waagé (1959) subdivided the Lakota

Formation into "the Lakota formation below [the] Minnewaste limestone member" (op. cit., p. 86), the Minnewaste limestone member and the Fuson member. Furthermore, Waagé (1959) restricted the term Inyan Kara Group and its formations to the Black Hills area, differentiated several sequences of the Lakota Formation in the Black Hills (the northwestern, the coal-bearing, the eastern, and the southern sequence, whereas the southern is the stratigraphic most complex and probably most complete) to illustrate some of its principal variations, and also defined a new reference section for it in the Fall River Canyon (Fig. 2, No. 3). Post and Bell (1961) designated the lower part of the Lakota Formation as Chilson Member, particularly in the southern Black Hills.

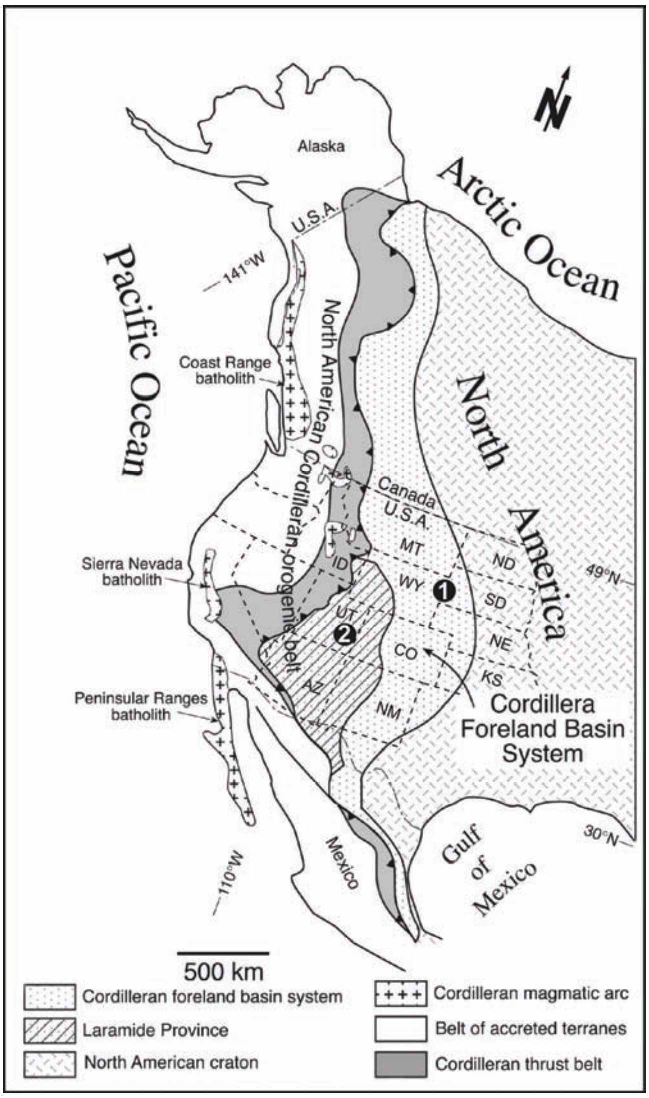

Fig. 1. Generalized tectonic map of western North America (modified after DeCelles 2004), showing the Cordilleran foreland basin system and the geographic position of the Black Hills uplift, South Dakota (1), as well as the distal position of the Lakota Formation within the foreland basin, and the position of the San Rafael Swell, Utah (2), with the more proximal position of the Cedar Mountain Formation within the foreland basin and in relation to the Cordilleran orogenic belt. Abbreviations for indicated states within the U.S.A.: ID–Idaho, ND–North Dakota, SD–South Dakota, MT–Montana, WY–Wyoming, UT–Utah, CO–Colorado, NE–Nebraska, KS–Kansas, AZ–Arizona, NM–New Mexico.

Way et al. (1998) subdivided the Lakota Formation in the northern Black Hills into three informal intervals (L1, L2 and L3), L1 corresponding to the Chilson Member including the Minewaste Limestone Member restricted to the southern Black Hills (Zaleha 2006, see Fig. 2 herein also), L2 correlating with the lower part of the Fuson Member as defined for the western Black Hills by Post and Bell (1961), and L3 with the upper part of the Fuson Member of workers like Post and Bell (1961) or Dahlstrom and Fox (1995). Zaleha (2006) correlates these informal intervals with Lower Cretaceous rocks of central and western Wyoming, thereby giving an Barremian to Aptian (112.2 Ma), age for the Lakota Formation, possibly Hauterivian and even Valanginian for some deposits of the L1 interval.

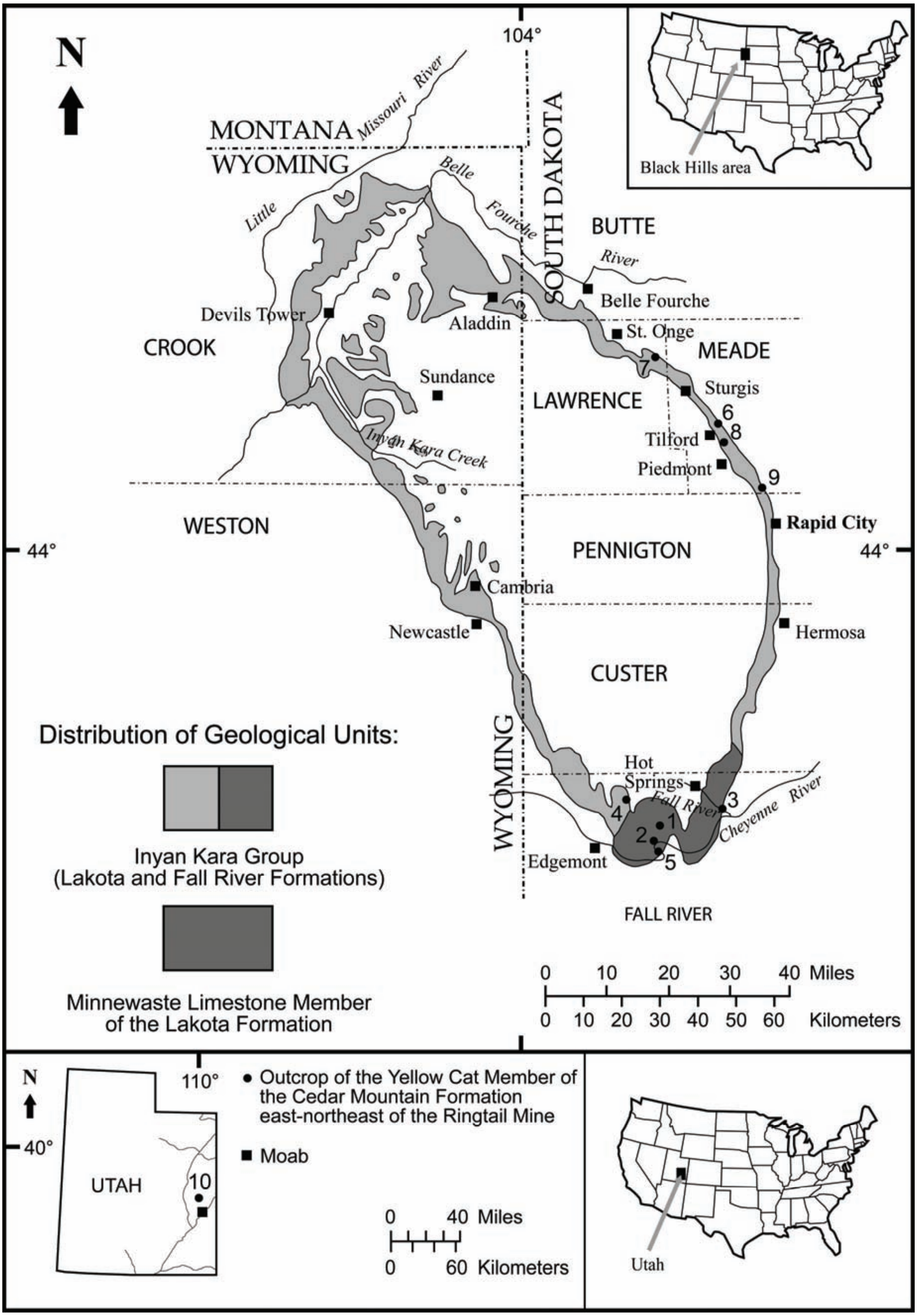
N
104°
MONTANA
WYOMING
Missouri River
Belle Fourche
Little
SOUTH DAKOTA
BUTTE
River
Black Hills area
Belle Fourche
Devils Tower
Aladdin
St. Onge
CROOK
MEADE
7
Sundance
LAWRENCE
Sturgis
6
8
Tilford
Inyan Kara Creek
Piedmont
9
WESTON
Rapid City
44°
PENNINGTON
44°
Cambria
Newcastle
Hermosa
CUSTER
WYOMING
Hot Springs
Fall River
3
Cheyenne River
4
1
2
5
Edgemont
FALL RIVER
Distribution of Geological Units:
Inyan Kara Group (Lakota and Fall River Formations)
Minnewaste Limestone Member of the Lakota Formation
0 10 20 30 40 Miles
0 10 20 30 40 50 60 Kilometers
N
110°
40°
UTAH
10
● Outcrop of the Yellow Cat Member of the Cedar Mountain Formation east-northeast of the Ringtail Mine
■ Moab
0 40 Miles
0 60 Kilometers
Utah

Fig. 2

The Cedar Mountain Formation has been defined by Stokes (1952) based on a type section at the northern San Rafael Swell, Emery County, Utah. He (op. cit.) included the Buckhorn Conglomerate as its basal member and the shale below the Dakota Formation. Kirkland et al. (1997, 1999) defined four additional members based on the distribution of four distinct dinosaur faunas (in ascending order): the Yellow Cat Member, the Poison Strip Sandstone (cf. Fig. 11 herein), the Ruby Ranch Member, and the Mussentuchit Member.

The ostracod samples dealt with in this paper derive from the Lakota Formation in its eastern and southern sequence of South Dakota (Fig. 1, No. 1; Fig. 2, localities), and the Yellow Cat Member of the Cedar Mountain Formation in the San Rafael Swell area of Utah (Fig. 1, No. 2; Fig. 2, No. 10).

As mentioned before, detailed implications and consequences of the taxonomic results for biogeography, biostratigraphy, and paleoecology will be analyzed and discussed elsewhere. An overview with reference to the stratigraphy of the Western Interior foreland basin and some implications of new biostratigraphic results from ostracod correlations (with emphasis on higher maximum ages of Lower Cretaceous formations) on the basin's geology and paleontology is given in Sames et al. (submitted).

Fig. 2. (see previous page): Locality Maps. Upper part: Black Hills area of South Dakota and Wyoming showing the distribution of the Inyan Kara Group (Lakota and Fall River formations) deposits (modified after Waagé 1959, and Sohn 1979), and the sample localities discussed herein (Nos. 1-9). Lower part: San Rafael Swell area of Utah with the sample locality in the Cedar Mountain Formation (No. 10). GPS coordinates in UTM projection (NAD 27). **1.** Buck Canyon, section label BC (BCB, BCE; loc. 17 of Sohn, 1979), section of Post and Bell (1971, p. 530-531), northeastern Flint Hill Quadrangle, UTM: 13 T 611329E 4800660N. **2.** Horse Sanctuary/Devil's Canyon, section label HSDC, section of Post and Bell (1971, p. 538-539), eastern Flint Hill Quadrangle. **3.** Fall River Canyon, section label FRCA (close to loc. 12 of Sohn, 1979), SE of Hot Springs, southeastern Hot Springs Quadrangle. UTM: 13 T 625855E 4807594N. **4.** Red Canyon, section label RCS (loc. 9? of Sohn, 1979), southeastern Edgemont NE Quadrangle, Fall River County, UTM: 13 T 598799E 4804793N. **5.** Angell Ranch/Cheyenne River, section label ARCR, southeastern Flint Hill Quadrangle, Fall River County, UTM: 13 T 611226E 4792665N. **6.** Little Elk Creek, section label LEC NE of Tilford, Meade County, UTM: 13 T 629259E 4901379N. **7.** East of road to Belle Fourche, north of Whitewood, section label EBF (close to loc. 2 of Sohn, 1979), Hot Springs Quadrangle, Lawrence County, UTM: 13 T 608929E 4928509N. **8.** Stage Barn Canyon Road, section label SBCR, SE of Tilford, Rapid City Quadrangle, Meade County, Roth's (1933) type locality (?), UTM: 13 T 633461E 4894622N. **9.** Boxelder Creek east of Blackhawk, section label REKO04, southeastern Black Hawk Quadrangle, Meade County, UTM: 13 T 638901E 4887800N. **10.**Yellow Cat Member of the Cedar Mountain Formation, section label PS, north of Moab, east-northeast of the Ringtail Mine, UT, U.S.A.

4. Material and methods

Surface bulk samples from promising lithologies (calcareous claystones, marls and calcareous silt- and sandstones) were taken from several sections of the Lakota Formation in the southern and eastern Black Hills (South Dakota, Figs. 1 and 2) and a locality from the Cedar Mountain Formation (Utah, Figs. 1 and 2). Processing was done using standard methods, treating the samples with warm water, and 2-8% hydrogen peroxide (0.5-3 hours), if necessary (i.e. if samples did not disperse in warm water only). The samples were then washed through sieves (500, 250, and 125m), picked and scanned uncoated with a LEO 1450 VP Scanning Electron Microscope at the Sam Noble Oklahoma Museum of Natural History (Norman, Oklahoma) in variable pressure mode using the four-quadrant backscatter detector. Some type and reference material from the collection of The National Museum of Natural History, Smithsonian Institution, Washington was scanned there, also using backscatter mode. The backscatter mode proved to be ideal for displaying and analyzing ornamentation and surface characters.

The specimens were mounted using needle and wax, which, without coating, may appear as small black grains on the specimens, because without coating the contrast between organic (dark, very low conductivity) and anorganic (bright, stronger conductivity) matter is very strong.

For purposes of clarity, the taxonomic descriptions follow a consistant scheme as far as possible, maintaining the same succession of terms within paragraphs. To enable the reader of a better evaluation of the hypotheses and results presented herein, the discussion section of each species reviewed herein is detailed and sucessively deals with nearly all species as listed in the synonymy that required further comments.

Occasionally, specific terms that the author thinks need to be clarified in context of their usage, are highlighted by an arrow (=>) in combination with *italic type*, especially when they occur for the first time. This refers to the glossary at the end of this paper where these terms are elucidated and partially discussed.

The size parameters used are as follows: Very small: 0.20-0.60mm; Small: 0.60-1.00mm; Medium: 1.00-1.50mm; Large: 1.5-5mm (in relation to maximum length parallel to basic line). For purpose of better readability and intelligibility, abbreviations are avoided mostly. The few common abbreviations used are: LV for left valve, RV for right valve, L/H for length/height-coefficient, L/W for length/width-coefficient, L for length, H for height and W for width. For better accuracy, measurements were obtained digitally from the SEM pictures by using the CANVAS (ACD Systems) program.

The measured parameters in order to describe the carapace are illustrated in Fig. 4. In lateral view, the carapace is oriented in relation to the => *base line*. Maximum length, height, and width include all protrusions that overreach the outline but not the very variable and environmentally influenced => *local ornamentation elements* such as tubercles and spines. Thus, the carapace outline is significant prior to the outer margins where applicable (e.g. ventral overreach due to ventral ridge which is a genetically fixed character).

The abbreviations for "plate(s)" and "figure(s)" are given in upper case (Pl. and Fig.) when referring to those in this publication whereas lower case (pl. and fig.) indicates those of cited references.

For the reason to give a comprehensive revision that shall provide a fundamental basis for future taxonomic and stratigraphic research, the synonymy lists are as complete as possible, depending on the references available and accessible. As for the discussion of synonymy, this has been done as comprehensively as necessary in the view of the present author. However, to avoid an exorbitant dimension of the already comprehensive manuscript, only ambiguous taxa (with question mark in synonymy), taxa with different names and/or rank, taxa that needed discussion for particular reasons (terminologically, taxonomically etc.) as well as those of actual or potential stratigraphic significance were particularly addressed. Others, like those having repeatedly used by the same author(s) in the same context or taxonomic name and rank as well as those conform with the present author's view not having to be auxiliary commented, are just listed and cited.

Owing to the impossibility to fully accomplish the comprehensiveness of a global approach, the data given under the item "stratigraphic and geographic distribution" of the respective taxa must inevitably remain a selection, which was conducted appropriate to facilitate biostratigraphic application. Therefore, most data derive from Europe, from where the best data with good resolution is available, particularly the English Purbeck/Wealden (Anderson 1939 et seq.). Information from other continents and areas have been implemented to the best extend possible (i.e., available data and publications). For more information, the reader be kindly referred to the references in respecrtive publications, stratigraphic atlases or databases, such as that of Kempf (1980 et. seq.).

With respect to salinity (sensu lato) tolerances and paleoecology, the classification of brackish waters is based on the Venice System according to Oertli (1964).

The item "faunal association" in the taxonomic description refers to North American assemblages only. Regarding species belonging to other genera than *Cypridea*, these will be dealt with in other papers, concerning *Theriosynoecum* refer to Sames (submitted).

The correlation and age determination of NW European Purbeck/Wealden deposits follows the local zonation schemes, particularly the revised ostracod biozonation scheme for the English Purbeck/Wealden after Horne (1995), and the extensive integrated and supraregional correlation-chart of Hoedemaeker and Herngreen (2003). Although there are still a few details to be discussed, the latter is the most recent and comprehensible dataset available, which is also very useful dataset in a practical format because of the detailed information given therein. Accordingly, if there will be future additions to or changes in this chart, any data in the publication at hand adopted therefrom that might be affected by such changes, can be easily retraced and corrected as well.

Abbreviations and symbols used in the synonymy list follows the established biologic nomenclature (cf. Granzow 2000, for example).

As for those species reported from material of the collection of R. E. Peck at the University of Missouri, Columbia (Missouri, U.S.A.), no data of faunal associations is available at all, neither from the records in the collection (visit of BS in 2005) nor from his publications (Peck 1941, 1951, 1956, 1959; Peck and Craig 1962; Peck and Reker 1948). The tables in the publications only list species of the same sample localities, but there is no information if they derive from the same samples/sample horizons. Since the whereabouts of Peck's type material at his collection at the University of Missouri (see item 5.1 below) are unknown, some Master's theses of students of Peck (Looney 1948, Craig 1961) are cited here, because these—particularly Craig (1961)—provide much valuable additional information that are not available from Peck's (1941, 1951, 1956, 1959; Peck and Craig 1962; Peck and Reker 1948) publications and his location catalog. Unfortunately, the whereabouts of "type" material of the theses (Looney 1948, Craig 1961) are unknown as well.

For practical purposes, the "International Code of Zoological Nomenclature" (International Commision on Zoological Nomenclature 1999, online) is abbreviated and cited under ICZN (1999) in the text.

Remarks: Concerning the carapace margin, a recent publication by Yamada (2007) revises some widely used terms based on new findings in its ultrastructure. This has more or less stronger effects regarding the definition, usage, usability and interpretation of morphologic terms such as flange, selvage, duplicature, (calcified) inner lamella, outer lamella, (inner) list, contact margin etc. For reasons of usefulness, to avoid confusion, and because Yamada's (op. cit.) concept has not been tested on many taxa (especially fossil ones) yet, the "classic" terminology is used herein. Nevertheless, wherever applicable, the new terminology and its effects on particular terms and interpretations are integrated and discussed in the definition of the carapace terminology of the taxonomic glossary herein (see there).

5. Systematic section

5.1. Repositories and their abbreviations

The specimens figured herein will be deposited at the National Museum of Natural History, Smithsonian Institution, Washington, DC, U.S.A. (USNM) under the numbers given.

- BMNH – The Natural History Museum (formerly the British Museum, Natural History), London, UK.
- BGS – British Geological Survey Palaeontological Collections, BGS Headquarters Keyworth, Nottingham: Mik (M) xxxx.001 (.001 suffix of earlier citations)
- U.M. – University of Missouri Collection, Columbia, Missouri, U.S.A. Unfortunately, the disposition of the ostracod type material and many of the figured specimens is unknown, although it is listed in the catalog (visit of the author May, 2005; pers. comm., R.L. Ethington, University of Missouri).
- USNM – The National Museum of Natural History, Smithsonian Institution, Washington, DC, U.S.A.

5.2. Taxonomy

5.2.1. Suprageneric taxonomy

Class **Ostracoda** Latreille 1802
Order **Podocopida** Müller 1894
Suborder **Cypridocopina** Jones 1901

Superfamily **Cypridoidea** Baird 1845

Remarks: According to the International Code for Zoological Nomenclature and as suggested by Martens et al. (1998a, p. 41) the ending "-oidea" is used for superfamily level (i.e. Cypridoidea instead of Cypridacea), thereby avoiding confusion with plant taxa.

Family **Cyprideidae** Martin 1940 **emend.**

Diagnosis: (Author's translation of Martin's diagnosis 1958, p. 313): "Ostracods of the suborder Podocopa [order Podocopida, suborder Cypridocopina, superfamily Cypridoidea after Horne et al. 2002] with the following particularities: Both valves bear a more or less well pronounced rostrum (hook, beak) at the anterior half of the ventral margin that is a integrating, non-decorative element of the valve. Situated directly behind is a sligthly to deeper incised recess (rostral groove [i.e. => *alveolus*]). Beak or groove may be only allusively present in some cases but are never missing. The central muscle scar field consists of 6 adductor muscle scars approximately in the center of the valve, as well as anterior of and transversely below it two small scars of the mandibles, and transversely above it two small scars of the antennae, respectively. Four large scars lie in the central field, three of which lie transversely above each other in a semi-circle whereas the fourth is situated behind them; one very small roundish scar each lies so close to the two lowermost main scars that they are often hardly ever or not at all to distinguish from the latter. – The marginal pore canals are bulbous inflated close to their [outer] aperture. – Simple notched hinge without teeth. – Strong ventral overlap of either the left or the right valve."

Addition to diagnosis: Internal view showing => *local widening of inner lamella* (where rostrum/beak-like extension and alveolus/incision occur), and marginal pore canals are missing in this => *attached area* above alveolar notch (Fig. 8). Selvage interrupted (=> *interrupted selvage*) along the posterior part of the rostrum, or a similar anteroventral structure. Valve size relation generally => *inequivalve* (besides the ventral overlap), normal or => *inverse*. Inner lamella usually well developed—broad anteriorly, moderate posteriorly, and widest anteroventrally and posteroventrally. With dorsal furrow or => *hinge incisure* of variable intensity, but usually well developed.

Remark: Sexual dimorphism may not be apparent in (fossil) valves of representatives of the Cypridoidea (e.g. Horne and Martens 1998). However, some taxa of the Cyprideidae Martin 1940 including representatives of *Cypridea* show clear sexual dimorphism (see paragraph 'sexual dimorphism' under genus *Cypridea* below for details).

Discussion: Regarding the systematics above family level, this article follows Horne et al. (2002) who place the extant nonmarine Cypridoidea under the infraorder Cypridocopina. As for the assignment to a family/subfamily, this has been under discussion for a long time and different authors subsequently placed *Cypridea* and closely related genera in different Cypridoidean families (see Szczechura 1981, p. 262 *et seqq.*).

Recapitulatory, Martin (1940) established the Cyprideinae as subfamily of the 'Cypridae' (recte Cyprididae Baird 1845) because the subfamily Rostrocyprinae erected by Anderson (1939) was not consistent with the International Code of Zoological Nomenclature since it did not comprise the nominate genus (*Cypridea*) and had, thus, to be considered invalid. This systematic position of *Cypridea* (Cyprididae–Cyprideinae) was maintained by many authors. However, Sylvester-Bradley and Harding (1953), when reviewing the nomenclature of the genus *Cytherideis*, proposed the family Cyprideidae Martin while also keeping the subfamily Cyprideinae Martin with *Cypridea* as type genus.

Not mentioning Sylvester-Bradley and Harding (1953), Martin (1958) emended his subfamily (Cyprideinae) to family status, the Cyprideidae Martin 1940, thereby making the subfamily superfluous. He (op. cit., p. 313 et *seqq.*) argued and discussed at length that there would be no reason anymore to assign the forms deriving from or related to *Cypridea* to the 'Cypridae' (recte Cyprididae) due to diagnostic carapace features differing from any other fossil and recent ostracod family. Many subsequent authors cited Hartmann and Puri (1974, p. 57) as reference for the emendation of the Cyprideinae to family level, but this is neither correct nor do Hartmann and Puri explain or comment their decision at all. Therefore, the correct author and date of the family name Cyprideidae is Martin (1940).

The closer relations of the Cyprideidae to extant families are controversial and not satisfactory resolved to date. Depending on the view how the extinct genus *Cypridea* is related to extant representatives of the Cypridoidea there are several possibilities:

1) We can keep *Cypridea* in the separate family of the Cypridoidea, the Cyprideidae Martin 1940 (based on a separate *Cypridea-Bisulcocypridea* lineage, then to be considered extinct), the view adopted here.

2) We regard the group as more closely related and belonging to the extant Cyprididae Baird 1845, which would result in its designation as subfamily Cyprideinae Martin 1940 (extinct) under the latter family. Horne and Colin (2005) show that the modern cypridoidean with closest affinities to *Cypridea* is *Bennelongia* De Deckker and McKenzie 1981, a genus, however, being restricted to New Zealand and Australia, a continent which has failed to reveal any *Cypridea* representatives to date as well as other pre-Pliocene nonmarine ostracods. Based on soft parts, *Bennelongia* belongs to the extant family Cyprididae

Baird 1845, subfamily Cypridi̲nae, but since the soft-parts of *Cypridea* are unknown, no further arguments supporting a closer relation of both genera are available so far.

3) We retain the "classic" view of putting *Cypridea* under the subfamily Cyprideinae into the family Ilyocyprididae Kaufmann 1900(a). Based on Swain's (1949) account on "early Tertiary" Ostracoda from the U.S. Western Interior, particularly his *Cypridea bisulcata* (recte *Bisulcocypridea bisulcata*). Sylvester-Bradley (1976; title of Swain 1949 wrongly cited therein) already discussed a possible lineage from *Cypridea* to the modern *Ilyocypris* (*Cypridea-Bisulcocypridea-Ilyocypris* lineage), i.e., from the Cypride̲idae Martin 1940 to the Ilyocyprididae Kaufmann 1900(a). The latter is, in turn, based on the similarities of *Bisulcocypridea* Sohn 1969 to *Cypridea* by, amongst other characters, possessing a rostrum; and to *Ilyocypris* by possessing two dorsolateral sulci.

Although the view given in number one right above is followed herein, either concept cannot be ruled out thus far.

Horne and Colin (2005) had analyzed and discussed possible relations of *Cypridea* s.l. (see Chapter 5.2.2 "Historic overview" below also)—that is the Cypride̲idae—to fossil to recent representatives of the cypridoidean families Ilyocyprididae, Cypridi̲dae and Notodromadidae by emphasizing the adductor muscle scar patterns and the => *marginal zone* structures. While not ruling out a *Cypridea-Bisulcocypridea-Ilyocypris* lineage, these authors (op. cit.) point out that the fossil record can as well be interpreted as "… indicating two parallel lineages: the [extant] Ilyocyprididae (*Rhinocypris-Ilyocypris*) and the [extinct] Cyprideidae (*Cypridea-Bisulcopridea*)" (op. cit., p. 27).

When phylogeny is interpreted, chronologic or stratigraphic aspects must also be taken into account alongside morphology. For example, if the view of a *Cypridea-Bisulcocypridea* lineage that belongs to the Ilyocyprididae (see No. 3 above) would be accepted, this would pose several questions as to the phylogeny of *Bisulcocypridea* Sohn 1969 in context with the Ilyocyprididae. Undoubted representatives of the Ilyocyprididae (i.e., Late Jurassic – Kimmeridgian, Schudack and Schudack 2002, representatives of the genus *Rhinocypris* Anderson 1941) occur much earlier than any representatives of *Bisulcocypridea* Sohn (Late Cretaceous?-Paleogene). It is much unlikely that the *Cypridea*-lineage (Kimmeridgian-Eocene) totally lost the (one or two) pair(s) of median dorsolateral sulci (as always present in the Ilyocyprididae) before these reappeared in *Bisulcocypridea* tens of million years later. The herein described species *Cypridea? minuta* (Peck 1951) shows a weak pair of dorsolateral sulci and could come into consideration as ancestor of an *Cypridea-Bisulcocypridea(-Ilyocypris?)*-lineage, thus supporting Swain's (1949) arguments that *Bisulcocypridea* was a *Cypridea* that had become bisulcate and Sylvester-Bradley's (1976) tentative suggestion of *Bisulcocypridea* as being the intermediate (in time and morphology) form between *Cypridea* and *Ilyocypris*. Based on this and the fact that the oldest known representatives of both, *Rhinocypris* and *Cypridea*, are of Kimmeridgian age (e.g. Schudack and Schudack 2002), it is not clear how *Rhinocypris* would fit into such hypothesis.

Whichever argumentation is followed, the last example clearly shows that the fundamental problem remains: there is still not enough data available yet. Many concepts are based on sparse information (stratigraphic record) and few arguments (number of carapace characters). As stated by Horne and Colin (2005), the adductor muscle scar patterns are no sufficient indicators to clarify the affinities of the Cypride̲idae to other cypridoidean families. Whereas the presence or absence of the *Cypridea*-type rostrum and alveolus, for example, seems to be a strong argument in consequence of these character's complexity (see glossary), ornamentation elements occurring in the taxa involved are, in contrast, often not diagnostic. Moreover, there are many transitions in the development of several characters in the Cyprideidae, e.g. the => *cyathus-like protrusion* and the => *cyathus* (see Fig. 5C) or the develoment of the => *alveolar notch* (Fig. 5B), in part having been a terminologic problem to find solutions of which considerable efforts have been made herein (elaboration of the glossary with specifications where necessary).

In summary, this article follows the most convincing data and line of argument available which is the carapace-based taxonomy in Martin (1958, see diagnosis above), Szczechura (1981) as well as

Horne and Colin (2005), thus placing *Cypridea* in the family Cyprideidae Martin 1940, along with *Paracypridea* Swain 1946, *Bisulcocypridea* Sohn 1969, and *Mongolocypris* Szczechura 1978. Unlike given in Horne and Colin (2005, table 1), the genus *Longispinella* Sohn 1979 is regarded and justified as being a representative (subgenus) of *Cypridea* herein, instead of considering it a discrete genus within the Cyprideidae (see Table 1). In addition, the new genus *Praecypridea* Sames, Whatley and Schudack is integrated (Sames et al. in review).

Additional remarks concerning usage of the family/subfamily: Several authors (e.g. Mandelstam and Schneider 1963) also used the family/subfamily Cyprideidae/Cyprideinae in a wider sense by including genera without a beak, that is: *Latonia* Mandelstam, *Limnocypridea* Ljubimova, *Zejaina* Mandelstam, *Cyprideamorphella* Mandelstam, *Mongolianella* Mandelstam, *Hourcqia* Krömmelbein (pars, Do Carmo et al. 2008, see under description of the genus *Cypridea* below for comments), and *Ilyocyprimorpha* Mandelstam—a view not followed herein.

Other taxa bearing homeomorphic beak-like structures (also called rostrum-like processes) on the valves have been included in the Cyprididae Baird 1845 (see for example Khand 2000: *Bogdocypris*, *Talicypridea*; or Szczechura 1978: *Altanicypris*, *Khandia*) for the reason of their different internal valve structure (i.e. their beak-like structure is formed by the outer lamella only, not by the fused outer lamella and selvage as in *Cypridea*, cf. fig. 4 in Horne and Colin 2005 and Fig. 8 herein). We owe it to Szczechura (1981), who demonstrated that it is essential to analyze internal and external valve morphology to distinguish between *Cypridea* and these superficially similar genera with beak/rostrum-like processes. This provided the basis and data to exclude such taxa from the Cyprideidae Martin and to relate them to other families, e.g. the Cyprididae Baird.

Some authors, e.g. Peck 1951, also used the subfamily name Cyprideinae Martin 1940 in the meaning of *Cypridea sensu lato* as resulting from the view to integrate *Cypridea* and its relatives in either the cypridoid families Cyprididae Baird 1845 or Ilyocyprididae Kaufmann 1900(a).

Horne and Colin (2005) point out that earlier concepts of the Cyprididae—i.e. those of Triebel (1960) and Sczcechura (1981)—"… were approximately equivalent to our [i.e. Horne et al. 2002] concept of the Suborder Cypridocopina and Superfamily Cypridoidea, respectively …" (Horne and Colin 2005, p. 27).

A particular case is the Pliocene nonmarine genus *Karshicypridea* Gramm and Burkharina 1967 possessing a rostrum very similar to that of *Cypridea*, separated from the ventral margin by a broad incision but lacking an alveolar furrow-like structure. Also, the anteroventral part of the zone of concrescence in *Karshicypridea* is homogeneous in internal view, without an => *attached zone* being devoid of marginal pore canals as occurring in *Cypridea*. Since the anteroventral characters in *Karshicypridea* are only outwardly similar to *Cypridea* and the adductor muscle scar pattern of the former does more resemble that one of the Candonidae Kaufmann 1900(b) rather than that of the Cyprideidae Martin 1940, a closer relation of the two seems improbable. However, a modern revision of *Karshicypridea* based on more material is wanting and no substantiated hypothesis can be given at the moment.

Genera of the family Cyprideidae Martin 1940: This includes representatives of the genus *Cypridea* sensus stricto—i.e., *Cypridea (Cypridea)*—and *Cypridea* sensu lato (see Chapter 5.2.2: Historic overview below as well as the synonymy list regarding the genus *Cypridea*, and Table 1), as well as: *Bisulcocypridea* Sohn 1969, *Mongolocypris* Szczechura 1978, and *Paracypridea* Swain 1946. In addition, the genus *Longispinella* Sohn 1979 is herein considered and defined as subgenus of *Cypridea*, and the genus *Praecypridea* Sames, Whatley and Schudack (Sames et al. in review) is newly included.

Cypridea (Sebastianites) Krömmelbein 1962 will probably have to be separated from *Cypridea* and raised to genus rank (see Table 1 and discussion of synonymy of the genus *Cypridea* below) but remain in the Cyprideidae Martin 1940.

The genus *Cultella* Lyubimova 1959, as wrongly included into the Cyprideidae Martin 1940 in the Ostracod Treatise (Moore and Pitrat 1961), questionably belongs to the family Trapezoidellidae Sohn 1979 following Nikolaeva and Neustrueva (1999, p. 34).

Cypridea (*Yumenia)* Hou 1958 is excluded from being a representative of *Cypridea* Bosquet 1852 as well as the Cyprideidae Martin 1940 here for the reasons of lacking many diagnostic characters: rostrum, alveolus and cyathus as well as the incised hinge margin and the dorsal furrow. *Yumenia* has been placed into the Trapezoidellidae Sohn 1979 by Nikolaeva and Neustrueva (1999, p. 34).

Family **Cyprideidae** Martin 1940	
Valid representatives:	Questionable and invalid representatives:
Genus ***Bisulcocypridea*** Sohn 1969 Genus ***Cypridea*** Bosquet 1852 *Cypridea (Cyamocypris)* (Anderson 1939) *Cypridea (Cypridea)* Bosquet 1852 *Cypridea (Longispinella*) (Sohn 1979) **stat. nov.** *Cypridea (Morinina)* (Anderson 1939) *Cypridea (Morininoides)* Krömmelbein 1962 *Cypridea (Pseudocypridina)* (Roth 1933) syn. *Langtonia* Anderson 1939 Genus ***Mongolocypris*** Szczechura 1978 Genus ***Paracypridea*** Swain 1946 Genus ***Praecypridea*** Sames, Whatley and Schudack	Genus ***Cultella*** Lyubimova 1959[a] Genus ***Cypridea*** Bosquet 1852 *Cypridea (Guangdongia)* Guan 1978[b] *Cypridea (Ulwellia)* Anderson 1939[c] *Cypridea (Sebastianites)* Krömmelbein 1962[d] *Cypridea (Yumenia)* Hou 1958[e]
a) wrongly included into the Cyprideidae Martin 1940 in the Ostracod Treatise (Moore and Pitrat 1960, p. Q243-Q245, fig. 179A); questionably belonging to the family Trapezoidellidae Sohn 1979 following Nikolaeva and Neustrueva (1999, p. 34) **b)** allocated to *Bisculcocypridea* herein **c)** rejected (see text for explanation) **d)** to be revised, questionably belonging to the Cyprideidae Martin, will probably have to be raised to genus rank; tentatively placed in the subfamily Ilyocyprimorphinae Sinitsa 1999 of the Trapezoidellidae Sohn 1979 by Nikolaeva and Neustrueva (1999, p. 35) **e)** different genus most probably not belonging to the Cyprideidae Martin due to the lack of many diagnostic characters (rostrum, alveolus, cyathus, incised hinge margin/dorsal furrow); placed into the Trapezoidellidae Sohn 1979 by Nikolaeva and Neustrueva (1999, p. 34)	

Table 1. Overview of genera included in (or excluded from) the family Cyprideidae Martin 1940, Late Jurassic to Paleogene (Kimmeridgian to early Eocene) as discussed herein (Chapter 5.2.1; compare to Table 1 of Horne and Colin 2005 also).

5.2.2. Historic overview – Chronology of the genus *Cypridea* Bosquet 1852

The literature about the overwhelming amount of representatives of *Cypridea* (refer to Kempf 1980-2002, for example) is vast and nearly impractical to capture, to compile, and to summarize. Hence, this it seemed appropriate and essential to include a (partially commented) synopsis of relevant publications and facts at this point. In the following historic overview, however, only a confined selection can be given. On the one hand, that concerns the taxonomic and application-oriented relevant publications in the view of the author, on the other hand that concerns taxa from the areas this research mainly focuses on: the European Purbeck/Wealden and and the North American Western Interior foreland basin as well as relevant Purbeck/Wealden like deposits in other parts of the world.

In 1852, Bosquet proposed the new genus *Cypridea* from the Wealden of England and Germany for some species not mentioned by name and referred them to have been described by Sowerby, Roemer and Dunker as *Cypris* Müller 1776, but did not give a reference (he most certainly referred to Sowerby 1836, Roemer 1839, and Dunker 1846). Bosquet (1852) noticed the difference of these species from the living *Cypris* in possessing "... a small hook or prolongation in the form of a beak. That difference to me appears being of sufficient importance to establish a new genus, and I propose to name this genus *Cypridea*" (translated from Bosquet 1852, p. 47: "... un petit crochet ou prolongement en forme de bec. Cette différence me semble être d'une importance suffisante pour l'etablissement d'un nouveau genre, et je propose de donner à ce genre le nom de *Cypridea* ..."). Sylvester-Bradley (1949, p. 125) noted: "In a footnote he [Bosquet] mentions that a considerable number of new species were soon to be described by 'M. le professeur E. Forbes, de Londres.' Actually Forbes never lived to describe these species, though in 1855 Sir Charles Lyell published woodcuts of some of them in the fifth edition of his Manual of Elementary Geology, with Forbes' name attached (Forbes 1855). One, designated '*Cypris punctata* E. Forbes', was quoted from the Lower Purbeck." However, the designation of this species as genotype by Anderson (1939) is invalid, because "*Cypris punctata* Forbes was not published until three years after Bosquet's proposal for *Cypridea*" (Sylvester-Bradley 1949, p. 126). Therefore and for additional reasons, Sylvester-Bradley (1949) designated *Cypris granulosa* Sowerby 1836 as lectotype ("genolectotype" in Sylvester-Bradley 1949) of *Cypridea* (Sylvester-Bradley 1949, see p. 125-126, firstly [uncommented] having been designated by Sylvester-Bradley 1947 in a short note).

As for the genus *Cypridea* Bosquet 1852, name and author are valid because they meet the requirements of the International Code of Zoological Nomenclature (ICZN, 4th Edition 1999) for a genus erected in at that time, as given in article 11 and 12 therein.

Important to note is the fact, that *Cypris granulosa* (Sowerby 1936) as given by Dunker (1846) is not identic to the type species of *Cypridea* Bosquet 1852 as designated by Sylvester-Bradley (1949). In his invaluable "Index and Bibliography of Nonmarine Ostracoda" Kempf (1980a) gave this case as example for man-made complex taxonomic problems occurring casually: "The story of this case reveals that Dunker, 1946, described a species under the name of *Cypris granulosa* Sowerby. This was regarded by Jones, 1978, as a wrong identification and for that reason newly combined in the form of *Cypridea granulosa* (Dunker), not *Cythere* ? *granulosa* (Sowerby). In 1885, however, Jones introduced the new combination *Cypridea granulosa* (Sowerby, 1836), which even became the type species of the genus *Cypridea* [as designated by Sylvester-Bradley 1949]. Instead of the earlier combination *Cypridea granulosa* (Dunker, 1846) the new name *Cypridea dunkeri* was introduced by Jones in the same paper" (Kempf 1980a, p. 17).

More than thirty years later, T.R. Jones (1885, p. 336) described the genus *Cypridea* Bosquet 1852 in greater detail as follows: "Carapace-valves subtriangular, obovate, or ovate-oblong; convex in the middle; broad (high) at the anterior third; narrower behind, one or both ends obliquely rounded; somewhat compressed anteriorly; notched at the antero-ventral angle, behind a small beak-like process; sometimes having only a slight indentation below and behind a thickening of the antero-ventral angle; sometimes this is traceable only by a curvature of the edge inside. Edge-view more or less narrow-ovate. End-view subovate. Surface punctate; sometimes almost smooth; often tuberculate; tubercles small or large, variously disposed. The hinge-margin is definitely straight along the middle third or more of the dorsal edge, with the hinge-angles more or less defined, and is oblique to the main axis of the valve. The left valve is the largest, and receives the dorsal edge and a straight ridge of the other valve in grooves on its dorsal and ventral contact-margins, the outer edge of the ventral margin of the left valve overlapping that of the right valve. The ridges and furrows or ledges of contact vary in intensity in different individuals." Remarkably, although partially described with other terms, Jones (1885) already gave most of the valid diagnostic characters: rostrum ("beak-like process"), alveolar notch, => *interrupted selvage* ("curvature of the edge inside"), carapace surface mostly punctate, rarely smooth, often tuberculate, LV>RV, hinge margin straight and so forth.

A year later, Jones (1886) published a short article about some ostracods from Colorado (U.S.A.) that derived from a sample he had received from U.S. Geological Survey Geologist C. A. White. However, this sample from the Morrison Formation does not contain representatives of *Cypridea*.

In 1893, Jones again described ostracods from the U.S.A. from samples he had received from C. A. White, this time from Wyoming and Utah. A sample from the Bear River Formation near Cokeville (WY) revealed a species of *Cypridea*, Jones designated as *Cypridea tuberculata* var. *wyomingensis* nov.

Vanderpool (1928) described and figured three species of *Cypridea* from the southern U.S.A. (Trinity Group of Arkansas, Oklahoma, Texas and Louisiana).

Roth (1933) erected the genus *Pseudocypridina* based on (smaller) size and position of the beak (rostrum) and absent alveolar notch, one of the taxa now considered being a subgenus of *Cypridea* from North American nonmarine deposits (actually from the Lakota Formation, not the Morrison Formation as Roth believed).

Harper and Sutton (1935) pointed out that Roth (1933) had failed to demonstrate the absence of a notch in the description of his new genus *Pseudocypridina* as well as in the illustrations and suggested to better refer it to *Cypridea*.

Anderson (1939), had established the new subfamily 'Rostrocyprinae' (a name not according to the International Code of Zoological Nomenclature and thus changed to Cyprid<u>e</u>inae by Martin 1940; see discussion of the family Cyprideidae Martin 1940 above) and had subdivided the genus *Cypridea* Bosquet 1852 into five genera (*Cypridea*, *Cyamocypris*, *Langtonia*, *Morinina*, *Ulwellia*), only to be lumped together soon (Martin 1940) and later defined as *Cypridea* s.l. (Sylvester-Bradley 1949, see below).

In his extensive monograph of the North-German "Purbeck/Wealden" ostracods, Martin (1940, p. 281-284) described the genus *Cypridea* in detail, particularly treating the characters of the valve margin and the pore canals (=> *marginal* and => *normal pores*). He (Martin 1940) already noted the strong => *ventral overlap* of the larger valve. Martin (op. cit.) also revised the genus *Cypridea* and lumped Anderson's (1939) new genera with rostrum (beak) and alveolar notch (*Cypridea*, *Cyamocypris*, *Langtonia*, *Morinina*, *Ulwellia*) plus *Pseudocypridina* Roth 1933 together under *Cypridea*, as well as shortly discusses the stratigraphic distribution and the potential of the taxa for biostratigraphic application.

One of the classic substantial works about Lower Cretaceous nonmarine microfossils of the U.S.A. (ostracods and charophytes) is that of Peck (1941). Peck (op. cit.) described many new species from Lower Cretaceous deposits of Colorado, Utah, Idaho, Wyoming and Montana, among them eight species of *Cypridea*, six of these which were new. Peck (op. cit.) denoted the similarities of his faunas and floras to the Purbeck and Wealden of England and the potential stratigraphic value of these.

Swain (1946), in his work about nonmarine ostracods of Brazil and New Mexico, did establish a new subgenus of *Cypridea*: *Paracypridea*, which few years later was challenged and raised to generic rank by Sylvester-Bradley (1949; see right below). Swain (op. cit., p. 548) also proposed the redefinition of *Pseudocypridina* Roth 1933 as subgenus of *Cypridea*.

In a short note, Sylvester-Bradley (1947) did uncommented designate *Cypris granulosa* Sowerby 1836 as new type species of *Cypridea* Bosquet 1852, which he later (Sylvester-Bradley 1949, p. 125-126) constituted and elaborated.

In the year 1948, Hugh Marvin Looney—a student of Raymond E. Peck at the University of Missouri—presented his Master's thesis (Looney 1948) about ostracods from the Lower Cretaceous Bear River Formation of Wyoming (U.S.A.) which, unfortunately, remained unpublished (as well as the thesis of Craig 1961, see below). The thesis is cited here because it contains valuable information about the concerning ostracod fauna (thesis available upon request from the Library of the University of Missouri). Since Looney's (1948) thesis remained unpublished, however, several new species therein were/are *nomina nuda*, and concerninc representatives of *Cypridea*, these are: *Cypridea laevicula*, *Cypridea nodulata*, *Cypridea pyriformis*, as well as *Cypridea sulcata*. However, *Cypridea laevicula* has been published as *Pseudocypridina laevicula* sp. nov. [recte *Cypridea (Pseudocypridina) laevicula*] by Peck (1951), and *Cypridea sulcata* has been used by Mandelstam (1955) to newly describe a species from Mongolia (Kempf 1980d). Unfortunately, the specimens are indeed registered in the catalog of the University of Missouri Collection, Columbia (Missouri, U.S.A.), but are not in the collection anymore (their whereabouts are unknown, R. L. Ethington, pers. comm., BS visit 2005).

Taxonomically most important is the work of Sylvester-Bradley (1949), who, in this publication about the genus *Cypridea* of the English Purbeck, emended and clarified the taxonomy of *Cypridea* and designated a valid lectotype for the type species (*Cypris granulosa* Sowerby 1836, see above for details). He (Sylvester-Bradley 1949, p. 130) was the the first to point out the beak/=> *rostrum* and => *alveolar notch* as most important diagnostic characters as well as the typical central muscle scar field, and comprehensively described the genus including many internal features, e.g. the => *marginal pore canals* plus cross-sections of the margin, the => *duplicature*, a detailed description of the hinge as well as that he discussed related (North) American species. Sylvester-Bradley (1949) changed the rank of Anderson's (1939) new genera with rostrum (beak) and alveolar notch (*Cypridea*, *Cyamocypris*, *Langtonia*, *Morinina*, *Ulwellia*) to subgenera of *Cypridea*, also including *Pseudocypridina* Roth 1933 (as proposed by Swain 1946), which he (Sylvester-Bradley 1949) synonymized with *Langtonia* Anderson 1939 (Sylvester-Bradley 1949, p. 126-127), the latter thus being a junior synonym of the former. As for *Cypridea (Paracypridea)* Swain 1946, Sylvester-Bradley (1949) raised this subgenus to generic rank, for the reasons of its different shape and muscle scar field. Sylvester-Bradley (op. cit.) as well defined *Cypridea (Cypridea*) Bosquet 1852 as (subgenus) *Cypridea sensu stricto* (*Cypridea* s.s.), and therefore, the other included subgenera were later subsequently combined under *Cypridea sensu lato* (*Cypridea* s.l.) by many authors (see this paragraph below, particularly Horne and Colin 2005; and Table 1).

Peck (1951, p. 318-319) supported Roth's (1933) view in keeping *Pseudocypridina* Roth 1933 a from *Cypridea* separate genus with weak beaks and notches, and weak ornamentation (punctation, a category of => *surface ornamentation* herein), a view that was refused by authors of subsequent publications.

Hanai (1951) described some ostracods from the "Sungari Group" in Manchuria (today NE China and SE Russia comprising the Quantou [spelled Chuantou in Hanai 1951], Qingshankou, Yaojia, and Nenjiang [spelled Nengkiang in Hanai 1951] formations, Albian to Campanian, see table 1 in Sha 2007, for example), including four new species of *Cypridea*. He (Hanai 1951) also was the first author to concretely consider, describe and figure sexual dimorphism in a species of *Cypridea* that is *Cypridea subvaldensis* Hanai 1951.

One of the early pioneer works in attempting relatively precise nonmarine ostracod-based biostratigraphy at the Jurassic-Cretaceous transition and possible correlations over long distances is that of Grekoff (1953). He (op. cit.) analyzed and compared representatives of Late Jurassic to Early Cretaceous (Purbeck/Wealden-like) nonmarine ostracod faunas known at the time (southern England, France, Switzerland, NW Germany, North Cameroon [then northern "French Cameroun"], Gabon [then "French Equatorial Africa"], Canada [Alberta], U.S.A., and Brazil) as well as that he gave some perspectives for possible circum-atlantic correlations of the Purbeck/Wealden-like deposits, and an alphabetic list of index taxa.

One of the few reports about Early Cretaceous nonmarine ostracods from Canada (including a few charophytes) is by Loranger (1951, 1954), whereas the 1954 publication is merely a reprint of that of 1951 with revisions. Loranger analyzed subsurface samples of the Blairmore Group from drillings in

Alberta (geochronologic age of the Blairmore Group is 115-103 Ma following Ross et al. 2005). Amongst others, Loranger (op. cit.) described two species of *Cypridea*: *Cypridea tilleyi* sp. nov. and *Cypridea wyomingensis*.

Oertli (in Bernard et al. 1956) described *Cypridea postelongata* from the upper Bajocian (believed to be lower Bathonian at the time of publication, op. cit.) of the Paris Basin. This species is now integrated into the new genus *Praecypridea* (Sames et al. in review).

Martin (1958) confirmed his opinion (Martin 1940) to include many thus far established separate genera into *Cypridea* (*Cyamocypris*, *Langtonia*, *Morinina*, *Ulwellia*) for the reason that differences in valve size [and differences in => *valve size relation* and => *inverse* forms], ornamentation, development of the rostrum and the alveolus are not sufficient for a generic separation. He (Martin 1958) as well confirmed his perception of the inclusion of *Pseudocypridina* Roth 1933 as subtaxon of *Cypridea* (also followed by Sylvester-Bradley 1949 (but challenged by Peck 1951, see right above) and established the new family Cyprid<u>e</u>idae (for details refer to the discussion of the family above).

Sohn (1958) published his first (short) account about the ostracods of the Upper Jurassic Morrison Formation and Lower Cretaceous Lakota Formation in the Black Hills. He (op. cit.) developed some ideas to differentiate between the ostracods of these formations and pointed out that the ostracods described by Roth (1933) as well as Harper and Sutton (1935) from the Black Hills area derived from the Lakota Formation rather than the Morrison Formation. In addition, Sohn (1958) made first estimations as to the age of the Lakota Formation and suggested: "… that the basal part of the Lakota formation will probably prove to be older than is indicated on the chart [Aptian] …" (op. cit., p. 122).

One of the notable early Chinese works about nonmarine Jurassic-Cretaceous nonmarine Cyprideidae is that of Hou (1958). Most helpful for many readers is the fact that Hou (op. cit.)—unlike most other Chinese authors up to date, unfortunately—published his complete article bilingually (Chinese/English). Hou (op. cit.) also established the subgenus *Cypridea (Yumenia)* which is, however, excluded from being a representative of *Cypridea* as well as the Cyprideidae Martin 1940 herein for the reasons of lacking many diagnostic characters (see discussion of synonymy under genus *Cypridea*, Chapter 5.2.3 below).

With regards to the biostratigraphic application of *Cypridea*, one most eminent early work and outstanding methodology in the view of the present author is that of Wolburg (1959, in German), who taxonomically dealt with the representatives of *Cypridea* from the "NW-German Wealden" in greater detail, with emphasis on their application. The highly remarkable advantage in Wolburg's (op. cit.) approach is that it renders an (successful!) application of long-lasting taxa possible, and he furthermore attributed the same stratigraphic value to these taxa as to the "… so-called index taxa that are confined to a particular horizon" (present author's translation, op. cit., p. 228). Based on the ample amount of data from the British Purbeck and Wealden as well as contemporaneous deposits in NW Germany already available at the time, Wolburg (op. cit.) established species groups which he considered as phylogenetic lineages, and successfully applied these to improve the biostratigraphic subdivision of the "NW German Wealden". The fundamental point of Wolburg's (1959) successful approach was and is his methodology: his taxonomy is based on carapace shape (outline, L/H-coefficients, position of maximum height, shape differences between the valves) rather than ornamentation, thereby diminishing the taxonomic significance of => *ornamentation* (particularly => *local ornamentation elements*). This is conform with the concept on the ecophenotypic or ontogenetic character of many of these ornamentation elements (nodes, tubercles and spines) as revised and elaborated herein, based on new insights in the coherences of reproductive modes and genetic and morphologic diversity in cypridoid ostracods (see glossary for terminologic details and Chapters 5.4.1 and Chapter 6.1 and 6.3 for elucidation). Wolburg's results, as published in several articles (Wolburg 1949, 1950, 1959, 1962b), later flew into the comprehensive book "Leitfossilien der Mikropaläontologie" (Micropaleontologic Index Fossils) for Central Europe with emphasis on Germany (Wolburg 1962a).

As to the early publications in Russian, the late 1950s and 1960s saw many comprehensive fundamental publications about, or including, Early Cretaceous ostracods from the former Soviet Union and The People's Republic of Mongolia mainly, just to give a few: Lyubimova (1956, 1965), Lyubimova et al. (1960; that is the chapter about Cypridoidea in the "Russian Ostracod Treatise"), Mandelstam (1955), and Mandelstam and Schneider (1963).

Major contributions to our knowledge about Late Jurassic to Cretaceous nonmarine ostracods of West Africa were provided by Nicolas Grekoff (1957, 1960a), who published several monographies about Late Jurassic to Neogene (only Jurassic to Cretaceous cited here) nonmarine ostracods of the Congo Basin, today Democratic Republic of the Congo and Republic of the Congo, from surface samples and drillings. The ostracods described by Grekoff (1957, 1960a) include several representatives of *Cypridea* of different subgenera. Based on this research, Grekoff (1960b) again discussed the possibility of correlations of circumatlantic nonmarine deposits of Early Cretaceous age (from Europe, and North and South America) with the ostracods from in Equatorial (West) Africa, mainly representatives of *Cypridea (Cypridea)*. He (op. cit.) furthermore considered their possible distribution by migrating dinosaurs and came to the conclusion that long-distance correlations are possible with nonmarine late Mesozoic ostracods!

William W. Craig, another student of Raymond E. Peck at the University of Missouri, presented a Master's thesis about "Aptian nonmarine ostracods of the subfamily Cyprideinae from the Northern Rocky Mountain area" (Craig 1961) which, like the thesis of Looney (1948, see above), remained unpublished (thesis available upon request from the Library of the University of Missouri). The thesis is likewise cited here because it contains valuable information about the concerning ostracod fauna. Craig (op. cit.) as well erected, amongst others, some new species of *Cypridea* from the Cloverly Formation, Wyoming, which are *nomina nuda*, since the thesis remained unpublished: *Cypridea grandis*, *Cypridea hudsoni*, *Cypridea ovata* [having been erected as *Cypridea (Yumenia) ovata* sp. nov. Qi 1988 (according to Kempf 1997b, 1997d); *Yumenia*, however, is considered neither to belong to *Cypridea* nor to the Cypride̲idae at all (see synonymy and discussion of genus *Cypridea* below)], *Cypridea trispinosa* [used by Zhang (1985), who erected *Cypridea (Cypridea) trispinosa* sp. nov. Zhang], and *Ulwellia crescenti* [recte *Cypridea crescenti*]. As for most of Peck's type material, the specimens are indeed registered in the catalog of the University of Missouri Collection, Columbia (Missouri, U.S.A.), but, unfortunately, are not in the collection anymore (its whereabouts are unknown, R.L. Ethington, pers. comm., BS visit 2005).

One year later, however, Peck and Craig (1962) published a stratigraphic synopsis of their results regarding "Lower Cretaceous nonmarine ostracods and charophytes of Wyoming and adjacent area", giving an overview of the stratigraphically important taxa and their distribution. Unfortunately, this was the last of Peck's as well as Craig's publications on the topic, and the taxonomy remained unpublished. Like in all of Peck's publications (as well as Peck's locality catalog, present author's visit 2005), the exact position or coordinates of the collecting localities, and particularly the stratigraphic position of the samples, are imprecise and hardly traceable, and if at all to relocate, this must be done in the field.

Within the scope of ostracod studies in Lebanon, Bischoff (1963) described seven new taxa of *Cypridea* he partially related to those heving been described from Brazil by Krömmelbein (1962).

Major early contributions to the Early Cretaceous nonmarine ostracods of Brazil (and West Africa to a minor part) were published by Karl Krömmelbein during the 1960s and early 1970s, regarding *Cypridea* and close relatives these are: Krömmelbein 1961, 1962, 1964, 1966, and Krömmelbein and Weber 1971. Krömmelbein established two new subgenera of *Cypridea*, *Cypridea (Morininoides)* Krömmelbein 1962 and *Cypridea (Sebastianites)*, the latter questioned to be a representative of *Cypridea* here (see discussion of synonymy of the genus *Cypridea* below, and Table 1).

In his frequently cited compendium about post-Paleozoic Ostracoda, van Morkhoven (1963, p. 93, fig. 128) incorrectly refigured a drawing (having-been as well frequently reproduced and cited) of the internal view of the LV of *Cypridea propunctata* from Sylvester-Bradley (1949, p. 131, fig. 17a). The former figure shows marginal pore canals in the => *attached area*, where they do not occur *per definitionem*.

Bielecka and Sztejn (1966) described the Jurassic-Cretaceous transition beds of northern Poland from 16 boreholes, and distinguished six local ostracod horizons with slightly different assemblages, including many typical representatives of *Cypridea*.

In the late 1960s, Grekoff and Krömmelbein (1967) published a comprehensive comparison of the Early Cretaceous nonmarine ostracods assemblages from South America (Brazil) and West Africa (Gabon), comprising taxa of *Cypridea* and listing the deposits where these occur.

Based on Wolburg's (1959) and his own data, Anderson (1962) published a first attempt to correlate the English Purbeck with the "German Wealden" using the *Cypridea setina*-group and the *C. propunctata*-group.

With reference to the documentation of the ostracod stratigraphy and subdivision of the NW-German Upper Jurassic and the "German Wealden", two important publications are included in the reference book "Leitfossilien der Mikropaläontologie" (Micropaleontologic Index Fossils): Klingler et al. (1962) and Wolburg (1962a), in which the stratigraphically important ostracods are described and figured, and their stratigraphic distribution is given and documented in detailed stratigraphic charts.

Wolburg (1962b) published an outstanding paper in which he documented the morphologic transition from *Cypridea fasciculata* (Forbes 1855) and *Cypridea altissima* Martin 1940, two taxa formerly believed to be entirely separate. Although Wolburg (1962b) mainly put emphasis on the L/H-coefficient and minor tubercles/node-like tubercles and his interpretation regarding the taxonomic significance of the latter is outdated (see here), his conclusions were groundbreaking because he deduced a phylogenetic relationship from a continuous development from one form to the other over time, documented by many specimens from different localities and supported by morphometric analysis (L/H-coefficient), and he tried to utilize these for biostratigraphic application.

Oertli (1963) gave an account of the "Purbeck" ostracods of the Paris Basin comprising several species of *Cypridea*.

As for the Iberian Peninsula, an importat work is that of Kneuper-Haack (1966), who described nonmarine ostracods from the "Spanish Wealden" (NW Iberian Chains), including many new species of *Cypridea*. The author (op. cit.) noted that the research had already been done and finished between 1954 and 1957, and that due to the work of Wolburg (1959) some of the newly described species and subspecies of *Cypridea* in Kneuper-Haack (1966) are to be assigned to the groups described and already published by Wolburg (1959). This needs to be revised. The research on nonmarine Early Cretaceous ostracods of North Spain is recently continued by U. Schudack and M. E. Schudack (Schudack in review; Schudack and Schudack 2009a). Owing to its paleogeographic position between Europe, North America and Africa during Late Jurassic to Cretaceous times, the Iberian Peninsula certainly played an important role as a bridge for the longitudinal distribution of nonmarine ostracods on the one hand, and for the latitudinal distribution and faunal exchange between Boreal and Tethyan faunas.

Viana (1966) published a detailed account on the stratigraphic distribution of ostracods in the Upper Jurassic? to Lower Cretaceous Bahia supergroup of Brazil. This includes several species of *Cypridea*, six of which were new.

Gramm and Burkharina (1967) described the new Pliocene genus *Karshicypridea* (extinct) from Uzbekistan, showing a rostrum similar to that of *Cypridea*. *Karshicypridea*, however, is not closer related to *Cypridea* and is only outwardly similar to the latter (name!; see also end of discussion of the family Cyprideidae under Chapter 5.2.1 herein for details).

Other taxonomically and stratigraphically important works are that of Anderson et al. (1967) about the Wadhurst Clay (regarded Wadhurst Formation of the Hastings Group in modern terminology) ostracods, and that about the Weald Clay (regarded Weald Clay Group of the Wealden Series Supergroup in modern terminology) ostracods (Anderson 1967) of southern England, UK, both including numerous new species and subspecies (most of these considered variants here) of *Cypridea* and their stratigraphic distribution. In the former (Anderson et al. 1967), Anderson introduced his famous "faunicycles" (critically reviewed by Horne 1995), and defined some new terms for characters mostly diagnostic to *Cypridea*: => *alveolus*, => *cyathus*, and => *rostrum* (see glossary for discussion).

Anderson (in Anderson et al. 1967, p. 202-204) as well classified the carapace ornamentation elements into "surface sculpture" (redefined => *area wide ornamentation elements/surface characters* herein) and "surface ornament" (redefined => *local ornamentation elements* herein). He (Anderson in Anderson et al. 1967) also developed a labeled grid for the identification of individual tubercles or spines in *Cypridea* (op. cit., p. 203, figs. 1 and 2), which was applied for several taxa in the latter publication (Anderson 1967, p. 239, Fig. 1). However, since local ornamentation elements are considered of low taxonomic relevance (see remarks/discussion of => *ornamentation* in the glossary), Anderson's complex model is taxonomically relatively useless. This does, notwithstanding, exclude that a revised version might provide a useful basis for future research regarding the evolution and development of tuberculation and spines in *Cypridea* and related taxa in context of their ecophenotypy and ontogenesis.

Andreev and Mandelstam (1968) described and figured another example of sexual dimorphism in *Cypridea* (see discussion of sexual dimorphism in Chapter 5.2.3 below for details).

The U.S. American ostracodologist Israel Gregory Sohn (1969) erected a new subgenus of *Cypridea*: *Cypridea (Bisulcocypridea)* from Aptian[?] deposits of Nevada. This taxon is now regarded a separate genus closely related to *Cypridea* and integrated into the extinct family Cyprideidae Martin 1940 (see Horne and Colin 2005, and Table 1 herein).

From several boreholes penetrating the Purbeck Beds (Purbeck Group in modern terminology) of southern England, Anderson and Bazley (1971) described and reviewed many ostracod taxa with emphasis on their stratigraphic distribution and application for these beds, many of these being representatives of *Cypridea*, including some new species and subspecies. They (op. cit.) also defined and described the faunicycles for these deposits. As for the Warlingham Borehole in Surrey (England, UK), which documents a virtually complete ostracod sequence of the English Purbeck/Wealden, this was published in Anderson (1971).

Musacchio (1971) described, among others, several representatives of Early Cretaceous *Cypridea* from the Argentinian province of Neuquen. Among these were four new species and one new subspecies, all of which show an => *inverse valve size relation* [considered of low or none taxonomic significance herein] but are otherwise very similar to well known contemporaneous taxa of Europe.

In a recapitulatory paper, Anderson (1973) gave a survey and review about the Late Jurassic to Early Cretaceous non-marine ostracod faunas (Purbeck/Wealden type) of the northern hemisphere, focusing on the dominating assemblages of representatives of *Cypridea* ("Cypridean assemblages"). Some subsequent authors mistook his assemblage scheme (op. cit., fig. 1) as zonation scheme (see Horne 1995, p. 648-651 for elucidation). Anderson (1973) also shortly outlined the until then known assemblages of England, Germany, The Netherlands, Denmark, Sweden, France, Spain, Switzerland, Poland, The Soviet Union, and North America, and listed important relevant publications.

From Gabon (West Africa), De Klasz and Uliczny (1975) described some new nonmarine Early Cretaceous ostracod species, among them a species of *Cypridea (Sebastianites)* Krömmelbein (here considered questionably belonging to the Cyprideidae Martin, see Chapter 5.2.1 and Table 1), and another representative of the Cyprideidae Martin 1940.

With respect to the South American faunas of the Province Neuquen (Argentina), Musacchio and Chebli (1975) described several new species from the Chubut Group, among them three belonging to *Cypridea*.

In a more general but ground-breaking publication about speciation patterns in Ostracoda, Sylvester-Bradley (1976) puts up polymorphism in *Cypridea* for discussion and some other ideas concerning intraspecific variation and reproduction mechanisms (parthenogenesis), as well as favoring the term "morphotypes" for several of Anderson's (1971) subspecies that occur in the same sample (a concept also followed herein). Sylvester-Bradley (1976) also was the first to consider polyploidy through interspecific hybridization as reason for polymorphism among representatives of *Cypridea*.

Brenner (1976) published his comprehensive work about ostracods and charophytes of the "Spanish Wealden" of NE Spain including, amongst others, 14 species of *Cypridea*, 5 of them he designated as new.

Guan (1978) erected the new subgenus *Cypridea (Guangdongia)* which is, however, considered being representative of *Bisulcocypridea* Sohn 1969 here (See Chapter 5.2.1 and Table 1).

Within "The Stratigraphical Index of British Ostracoda", Kilenyi and Neale (1978) summarized the Purbeck/Wealden of England with the index ostracods figured, most of them belonging to *Cypridea*. With respect to the zonation scheme, however, Kilenyi and Neale (1978) mistook Anderson's (1973) assemblages as (bio-)zones (see Horne 1995, p. 648-651, and Horne 2009 for elucidation).

An important publication (and one of the few more recent ones) concerning North American representatives of *Cypridea* is that of Sohn (1979), who comprehensively described the ostracod fauna from the Lakota Formation, Black Hills area (South Dakota; also the main working area of the present author) wherein he erected the new genus *Longispinella* Sohn that is considered a subgenus of *Cypridea* here (see Table 1 and Chapter 5.4.3). Among other groups (e.g. his new family Trapezoidellidae), Sohn (1979) also discussed the family Cyprideidae Martin 1940 and presented a key to its genera, as well as that he emended the subgenera *Cypridea (Cypridea)* and *Cypridea (Pseudocypridina)*.

One of the major contributions to the taxonomy of *Cypridea* Bosquet is that of Szczechura (1981). Szczechura (1978) had had described many nonmarine ostracod taxa from the Upper Cretaceous of Mongolia and introduced the terms => *limen* and guttur. Based on many new data from the "Polish-Mongolian Palaeontological Expeditions" (op. cit.), Szczechura (1981) expatiated upon *Cypridea* and morphologically similar forms which she merged into the Family Cyprididae Baird 1845, placing *Cypridea* under the subfamily Cyprideinae Martin 1940 (a view modified herein, see Chapter 5.2.1 above). This work (Szczechura 1981) is outstanding, because the author described and figured(!) many characters of the carapace margin (also internally and specifically the anteroventral area) in detail, and discussed their value for taxonomy, particularly for the position of *Cypridea* among morphologically similar contemporaneous ostracods and their suprageneric taxonomy. It is Szczechura's (1981) merit to have demonstrated that the internal features are essential to distinguish between *Cypridea* and superficially similar genera with beak/rostrum-like processes.

A major contribution concerning the Purbeck/Wealden ostracods of south-east England (UK) is the posthumously published synopsis (Anderson 1985) on their stratigraphic distribution based on Anderson's compilations, as he had nearly completed this work at the time of his death in 1982. For the first time (Anderson 1985), the ostracods were illustrated with SEM photographs, and the publication includes detailed schemes on their stratigraphic distribution.

In 1985, the "Atlas des Ostracodes de France" was published, containing the stratigraphically important taxa. Colin and Oertli (1985) therein gave an overview of the stratigraphy of the Berriasian to Valanginian taxa (Purbeck *sensu gallico*) of France, including several species of *Cypridea*.

Qi (1988) newly described the subgenus *Cypridea (Ordosia)* and four new species of it (as given in the Kempf Database Ostracoda, Kempf 1997a): *C. (O.) elongata*, *C. (O.) linguida*, *C. (O.) subdepressa* and *C. (O.) subelliptica*, the latter being the type species. Unfortunately, however, Kempf never received a copy of this publication. He took information in from a third source because Qi (op. cit) described the high number of about 120 new taxa but this was long ago and Kempf cannot retrace the source anymore (E. K. Kempf, written communication, November 2008). The present author also was unable to get a copy of Qi's (1988) article. Curiously, none of the mentioned species as well as the subgenus are mentioned in the voluminous Chinese "Atlas" of fossil Ostracoda, volume one (Hou et al. 2002) and, thus, the taxonomic position of these taxa has to be reappraised on the basis of the original publication.

A concise overview of the Mesozoic sequence of nonmarine ostracods of northern China as well as its faunas and assemblages has been given in Quiquing and Whatley (1990), who also extensively dealt with the *Cypridea* fauna of the uppermost Jurassic and the Cretaceous

Sztejn (1991) reviewed the taxonomy and biostratigraphy of the ostracods of the 'Purbeckian' of central Poland, confirmed the validity of the existing six ostracod zones, and described several new species, among which are eleven new species and subspecies of *Cypridea*.

Ye (1994, in English) gave a long anticipated synoptic account of the nonmarine Cretaceous stratigraphy in China (including the Jurassic-Cretaceous and Cretaceous-Paleogene transition) as subdivided into eight (northern China) and nine (southern China) ostracod assemblage zones by representatives of the Cypridoidea (mainly representatives of *Cypridea* and closely related taxa). However, since there are many taxonomic problems remaining to be reappraised (difficult up to today often due to the strongly limited readability of the many papers and books in Chinese, as well as a too regional view on the faunas) which may have considerable implications on the age determination of nonmarine Cretaceous deposits of China.

Newer works about the NW German Late Jurassic to Early Cretaceous nonmarine ostracods are from Ulla Schudack, who dealt with the revision, documentation and biostratigraphy of these in her doctoral thesis (Schudack 1994; including several species of *Cypridea*), the results of which later flew into Elstner and Mutterlose (1996), Gramann et al. (1997), and Schudack (2004).

In a stratigraphically most significant contribution with respect to a modern ostracod zonation of the English Purbeck/Wealden, Horne (1995) critically reviewed and revised the ostracod biostratigraphy for the Purbeck/Wealden of England, as based on Anderson's (1939 *et seqq.*) work and proposed a new rigorously defined ostracod zonation scheme for these deposits. Anderson's (1967 *et seqq.*) schemes had proved to be largely unrepeatable due to inadequate definition.

With respect to the Lower Cretaceous of NW Germany (Berriasian-Valanginian, including the "German Wealden"), Elstner and Mutterlose (1996) revised its ostracod biozonation as developed by Wolburg (1949, 1959, 1962a) and proposed a new zonation scheme mainly based on representatives of *Cypridea*, that is, however, only applicable to the central part of the NW German Basin (op. cit., p. 122).

An important publication as to the stratigraphic range of *Cypridea* is that of Guan et al. (1997), who described *Cypridea (Cypridea) pingyiensis* sp. nov. from the Lower Eocene Middle Member of the Bianqiao Formation, Shandong (China), extending the stratigraphic range of *Cypridea* into the Early Eocene.

In a compendium of Devonian to Pleistocene fossil nonmarine ostracods of the U.S.A., Swain (1999) gave an overview of the known taxa, listed their stratigraphic distribution and occurrences chronologically, and refigured type specimens. The book is, however, just a review of literature and does neither contain new or up-to-date information nor discussions, evaluations or refinement of data that exceed the original publications.

Nikolaeva and Neustrueva (1999) published a most valuable taxonomic atlas of the Mesozoic ostracods of Russia and adjacent areas, refigured and reillustrated types of older workers so far only available as drawings, gave and reported revised taxonomic views, and added biostratigraphic schemes and recommendations.

From Mongolian evidence and perspective, Khand (2000) outlined the Late Cretaceous to Early Paleogene development and evolution of nonmarine ostracod faunas and morphologically separated the representatives of the Cypridеidae Martin 1940 from representatives of the early Cyprididae Baird 1985, particularly the Talicyprideinae Hou 1982. In the same year, Khand et al. (2000) also published a revised overview on the (nonmarine) Cretaceous of Mongolia and the regional correlation, including its biozonation based on different fossil groups among which are ostracods including representatives of *Cypridea.*

Luger and Schudack (2001) described charophytes and ostracods from the "Wealden" of northern Somalia for the first time. The ostracod fauna is dominated by representatives of *Cypridea*, five species of which are described, two of them new. The maximum age of the fauna was given as earliest Aptian (op. cit.) may be older in part.

As for the late Mesozoic to Paleogene nonmarine ostracods of China, Hou et al. (2002) published the huge atlas of Mesozoic to recent ostracods of China (part one with Cypridoidea and Darwinuloidea) with over 300 plates, describing, reviewing and (re-)figuring the local taxa that had been described at the time.

Mojon (2002), in his PhD thesis about sedimentology, micropaleontology, and biostratigraphy of Middle Jurassic to Lower Cretaceous deposits of the Jura platform (southeastern France and Western Switzerland) dealing with charophytes mostly, also figured and discussed Berriasian to Valanginian Purbeck/Wealden-facies ostracods as well as the biozonation and Tethyan-Boreal correlation in western Europe based on them.

The so far earliest representatives of (true) *Cypridea* Bosquet (Late Jurassic, Kimmeridgian) were documented by Schudack and Schudack (2002) from the Middle Saurian Member of the Tendaguru Formation, SE Tanzania, East Africa.

Schudack (2004) revised the Late Jurassic to basal Early Cretaceous (Berriasian) ostracods of northeastern Germany—until then insufficiently analyzed (e.g. Wienholz 1968)—and newly documented their biostratigraphy in detailed range charts, including several lower Berriasian species of *Cypridea*.

In an important taxonomic paper, Horne and Colin (2005) analyzed the morphologic affinities of *Cypridea* s.l. (i.e., *Cypridea* including all its subgenera as given herein) to other cypridoideans, particularly focusing on the evaluation of some key features: the adductor muscle scar patterns and the complex structures of the anterior marginal zone (rostrum and alveolus and beak-like or lip-like anteroventral structures). The authors (op. cit.) concluded that the modern genus having the closest affinities to *Cypridea* Bosquet is the cypridid genus *Bennelongia* De Deckker and McKenzie 1981. According to Horne and Colin (2005), the adductor muscle scar pattern is not a sufficient character to indicate affinities of the family Cyprideidae Martin 1940 to other Cypridoidean families. The authors (Horne and Colin 2005, table 1) gave a table of the taxa included in the Cyprideidae Martin 1940, where they listed *Guangdongia* Guan 1978 as subgenus of *Cypridea* and *Longispinella* Sohn 1979 as separate genus within the Cyprideidae. This view is challenged herein (Table 1). *Guangdongia* Guan 1978 most probably belongs to *Bisulcocypridea* Sohn 1969 (Chapter 5.2.1), whereas *Longispinella* Sohn 1979 is here considered a representative (subgenus rank) of *Cypridea* Bosquet 1852 (Chapter 5.4.3).

As for the Mongolian Lower Cretaceous, Neustrueva et al. (2005) published a taxonomic atlas of late Mesozoic to Paleogene nonmarine ostracods of Mongolia including many species of *Cypridea*, therein refiguring and reillustrating types of older workers so far only available as drawings, reporting revised taxonomic views, and giving biostratigraphic charts.

In his comprehensive PhD thesis, Stoica (2007, in Romanian) analyzed and described the Purbeck-type ostracods from the southern Dobrudja (Romania), their research history, geologic background and stratigraphy as well as correlation and faunal association, including several species of *Cypridea*.

Do Carmo et al. (2008) emended *Cypridea* by adding the high degree of variability in outline and size of the beak and alveolar notch and the variable ornamentation (smooth, punctate or tuberculate) as well as integrating the species *Cypridea africana* (Krömmelbein 1965), formerly *Hourcqia africana* Krömmelbein (1965b). This view (Do Carmo et al. 2008) is partially challenged herein, and *Cypridea* is emended anew (see discussion of the genus in Chapter 5.2.3 below).

In a very recent applied publication, Arp and Mennerich (2008) described ostracod assemblages, including several species of *Cypridea*, from the Purbeck-type sediments of the upper part of the Münder Formation of NW-Germany, wherein they reconstructed paleoenvironments and cyclicity of these.

Sames (2008) confirmed the occurrence of Kimmeridgian representatives of true *Cypridea* from new samples of the Tendaguru Formation (Tanzania, East Africa) and discovered three species different from the one having been reported by Schudack and Schudack (2002) from the same member of the Tendaguru Formation.

In the new "stratigraphic atlas" of British ostracods, Horne (2009) gave an updated account on the British Purbeck/Wealden (Berriasian–earliest Aptian) ostracods. This includes a definition of revised stratigraphic charts (adapted from Horne 1995) and the major ostracod zones as defined by species of *Theriosynoecum* and its subzones (Horne 1995, defined by species of *Cypridea*) as well as reproductions of Anderson's (1985) SEM photographs of relevant taxa and some new ones. Horne (2009) also gave a short synopsis of the current research status concerning stratigraphy, paleoecology and taxonomy, and perspectives for future research.

Sames et al. (in review) erected the Middle to Late Jurassic new genus *Praecypridea* from Europe, North America and Africa, which they consider to be the ancestor of *Cypridea* Bosquet 1852. *Praecypridea* does not have a true rostrum and alveolus yet, but a right-angled intersection of the anteroventral area instead or a slightly developed beak-like anteroventral protrusion lacking an alveolus (no alveolar notch and furrow are developed). Neither does it show a true => *cyathus*, but a => *cyathus-like protrusion* (as defined herein).

Schudack and Schudack (2009a) revised the Lower Cretaceous ostracod biostratigraphy of the Iberian Chains (eastern Spain), and evaluated its local usability. The authors (op. cit.) differentiate 11 associations based on 87 species, 40 of these belonging to *Cypridea*. The Berriasian to Barremian ("Spanish Wealden") nonmarine associations are dominated by representatives of this genus.

Sames (this work) emends and confirms the validity of the family Cyprideidae Martin 1940, emends the genus *Cypridea* Bosquet 1852 again based on a detailed revision of carapace terminology, integrates the genus *Longispinella* Sohn 1979 into *Cypridea*, challenges the validity of the subgenus *Ulwellia* Anderson 1939, and redescribes and emends some North American species of *Cypridea* (refer to the appropriate chapters for details).

With respect to the distribution mechanisms in context of reproductive modes, the reader is referred to Chapter 6.1 herein. As for the sexual dimorphism in *Cypridea*, the details are presented in the discussion under the genus' taxonomy in Chapter 5.2.3 right below. Table 1 summarizes the taxonomic notes and interpretation given above and below concerning the representatives of the family Cyprideidae Martin 1940 and the subgenera of *Cypridea*.

5.2.3. Generic taxonomy

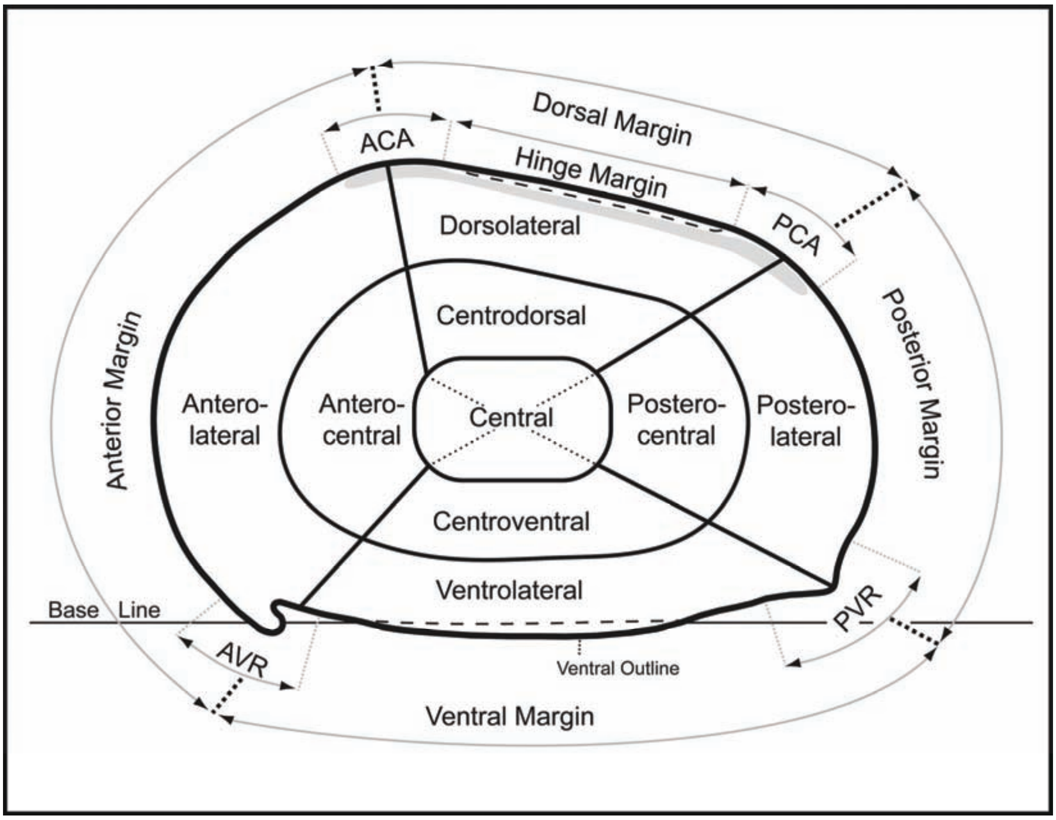

Fig. 3. Terminology for outline, outline regions, margins and carapace regions of the genus *Cypridea* (exemplified on as representative of the *C. alta*-group) as proposed and defined in this paper. Caparace regions modified based on Kesling (1951). ACA: Anterior Cardinal Angle. AVR: Anteroventral region. PCA: Posterior Cardinal Angle. PVR: Posteroventral region.

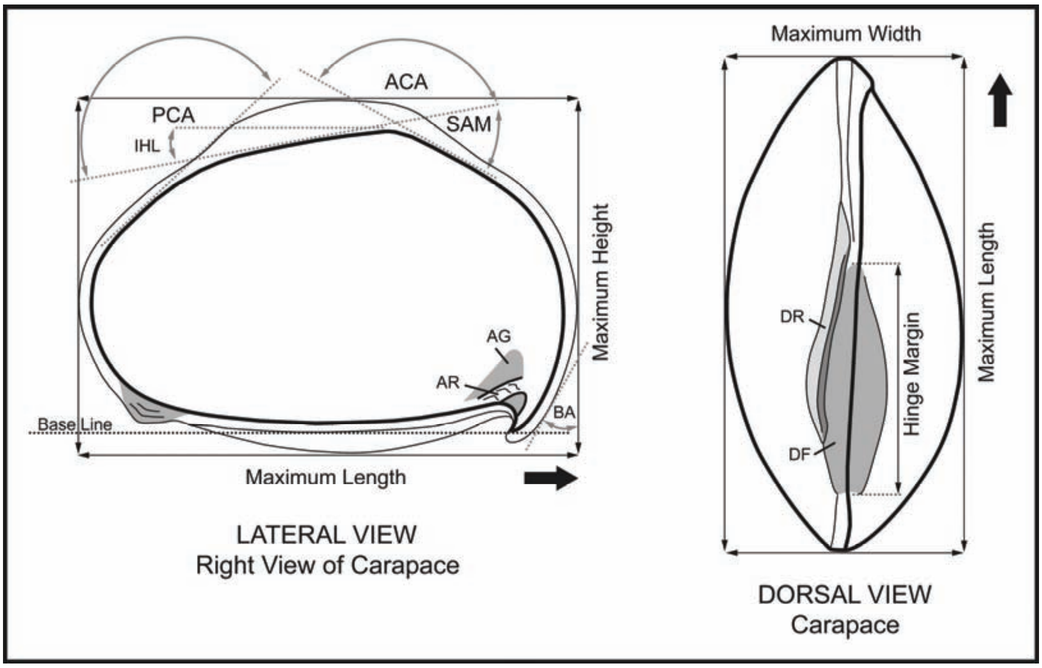

Fig. 4. Illustration of methods of measurement in *Cypridea* in relation to the carapace orientation. Note that parameters of length/height/width exclude ornamentation elements but do include carapace protrusions, i.e. where not congruent, the outline defines the outer delimitation prior to the margins (e.g. ventral ridge). This example demonstrates that in the strongly inequivalve case the protrusions of the LV overreach its own margin as well as the smaller RV, that is the LV has a much different shape bases on the outline than based on the margins. Thus, the better measurements for the cardinal angles and inclination of the hinge margin have to be obtained from the RV. The ventral margin is oriented along the base line. ACA: Anterior cardinal angle, AG: Alveolar groove, AR: Alveolar ridge, BA: Bending angle (of rostrum), DF: Dorsal furrow, DR: Dorsal ridge, PCA: Posterior cardinal angle, SAM: Inclination of the straight dorsal part of the anterior margin, IHM: inclination of hinge margin in relation to base line.

Fig. 5. (see following page):

A) Terminology of curvature of anterior and posterior ostracod carapace margins after Lüttig (1962). Arrows indicate the area of maximum curvature. These very useful terms are adopted here and translated into English: **1.** Equicurvate (in German "äquikurvat") means equally rounded, **2.** Infracurvate (in German "infrakurvat") stands for narrower rounded towards venter, **3.** Supracurvate (in German "suprakurvat") defines a dorsally narrower rounded margin.

B) Illustration of different degrees of the development of the => *alveolar notch*. Arrows indicate the position of the absent alveolar notch (then it is the angular point of the angle between posterior part of rostrum and ventral outline) or present alveolar notch (apex of the curve). **4./5.** Sketch of a left lateral view of a taxon with very weak (4, RV) to absent (5, LV) alveolar notch, like in many representatives of *Cypridea (Pseudocypridina)*, for example. Note that in the illustrated example (4 and 5), the alveolar notch is termed *absent* in the LV (4) because the ventral outline is not noticeable curved upwards and meets the posterior part of the rostrum in a purpendicular angle (see glossary for details) whereas in the smaller RV (5) the ventral outline right behind the rostrum is curved upwards causing a small alveolar furrow (upper arrow). **6.** Sketch of a right lateral view of a representative of *Cypridea* with a strongly developed alveolar notch in both valves (lower arrow; usually combined with a well-developed alveolar furrow/groove not as shown), e.g. *Cypridea alta* Wolburg 1959. Note that in forms with well-developed/deeply incised alveolar notch, the notch itself can here be stronger developed in the *smaller* valve instead of the larger one. The => *alveolar furrow*, however, is mostly stronger developed in the larger valve (see glossary for details).

C) Illustration of the development of the => *cyathus* and the => *cyathus-like protrusion*. Arrows indicate the apex of either the former or the latter in the larger valve only (7) or in both valves (8 and 9). **7.** 'True' cyathus: triangular extension of the posteroventral margin only developed in the larger valve, no indication of such extension in the smaller valve. Example

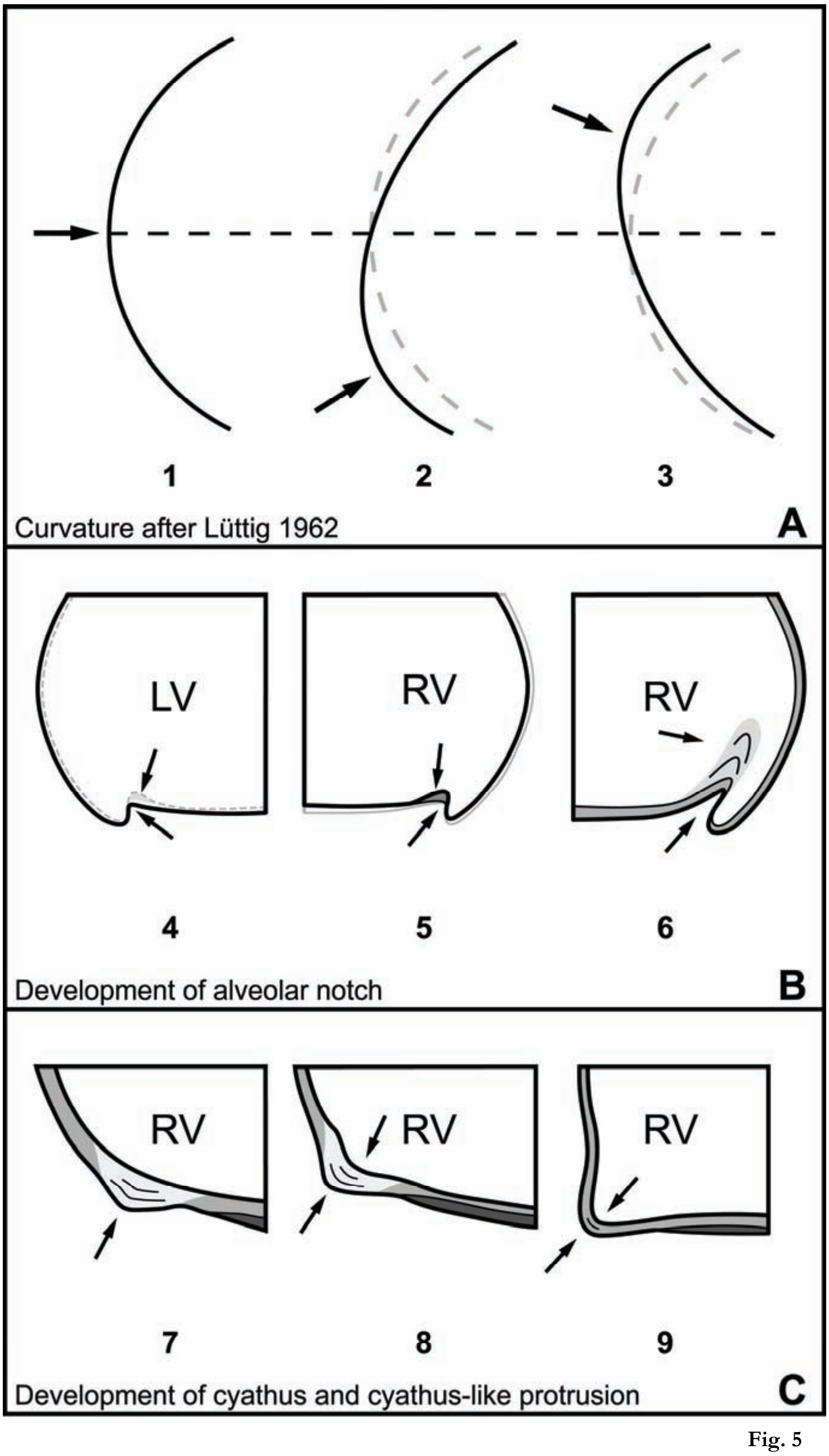

Fig. 5

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shows right lateral view of this particular region of *Cypridea (Pseudocypridina) piedmonti* (Roth 1933). **8.** Weakly developed cyathus-like protrusion: triangular extension of the posteroventral margin visible in both valves, distinct in the larger valve whereas only weakly indicated in the smaller valve. Example shows right lateral view of this particular region of *Cypridea (Longispinella) longispina* (Peck 1941). **9.** Strongly developed cyathus-like protrusion: triangular extension of the posteroventral margin distinctly developed in both valves, even weakly acute in this example showing the right lateral view of this particular area of *Cypridea nitidula* Peck 1941.

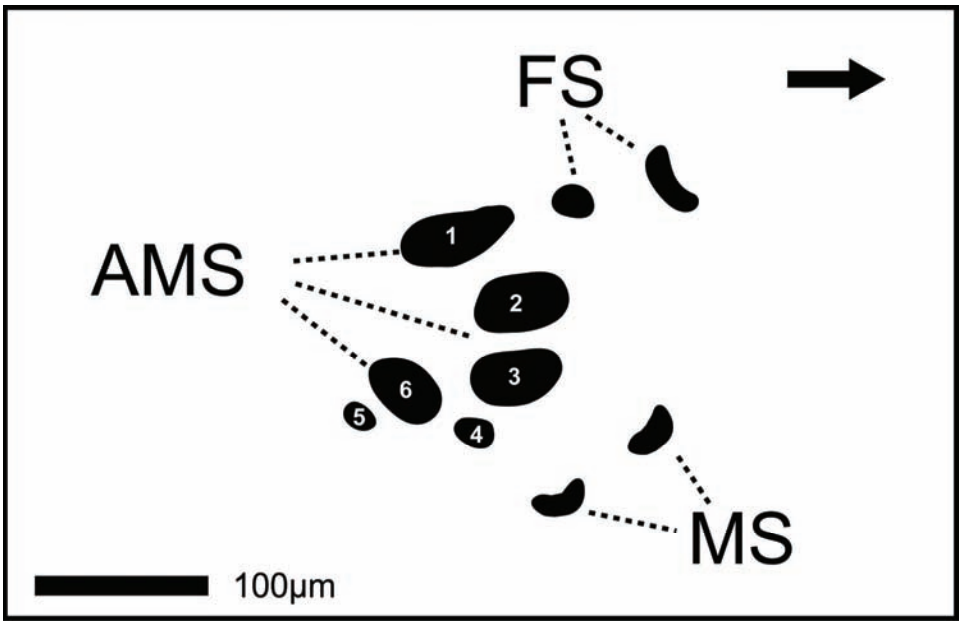

Fig. 6. Muscle scar pattern in *Cypridea.* The sketch shows an *averaged* general pattern of the central muscle scar field of the LV as occurring in *Cypridea.* Main variations occur in size and shape of the scars of the adductor muscle scar field (AMS, Nos. 1-6), and their relative distances to a lesser degree, particularly the position of the posterior scars (5 and 6). Labeling of single scars adopted from Horne and Colin (2005). The general pattern of scars is constant. FS: Frontal scars, MS: Mandibular scars.

Genus ***Cypridea*** Bosquet 1852 **emend.**

* 1836 *Cypris granulosa* sp. nov. – Sowerby, p. 345, pl. 21, fig. 4

pars 1852 *Cypridea* nom. nov. pro *Cypris* Müller 1776 – Bosquet, p. 47

1933 *Pseudocypridina* gen. nov. – Roth, p. 404 [syn. *Langtonia* Anderson 1939]

pars 1939 *Cypridea* – Anderson, p. 294 [diagnosis therein not including all forms, e.g. "*Ulwellia*"]

1939 *Cyamocypris* gen. nov. – Anderson, p. 305

1939 *Langtonia* gen. nov. – Anderson, p. 304 [syn. *Pseudocypridina* Roth 1933]

1939 *Morinina* gen. nov. – Anderson, p. 302

1939 *Ulwellia* gen. nov. – Anderson, p. 300

1949 *Cypridea* – Sylvester-Bradley, p. 130 [*Cypridea* s.l.]

1949 *Cypridea (Cypridea)* – Sylvester-Bradley, p. 135 [*Cypridea* s.s.]

non 1958 *Cypridea (Yumenia)* subgen. nov. – Hou, p. 93

1962 *Cypridea (Morininoides)* subgen. nov. – Krömmelbein, p. 471

? 1962 *Cypridea (Sebastianites)* subgen. nov. – Krömmelbein, p. 460

?pars 1965b *Hourcqia* gen. nov. – Krömmelbein, p. 68-69 [including *H. africana* Krömmelbein 1965b, *H. africana africana* Krömmelbein and Weber 1971, *H. africana confluens* Krömmelbein and Weber 1971]

non 1978 *Cypridea (Guangdongia)* – Guan 1978 [this is most probably *Bisulcocypridea*]

• 1979 *Longispinella* gen. nov. – Sohn, p. 18

? 2008 *Cypridea africana* (Krömmelbein) comb. nov. – Do Carmo et al., p. 793 [non *Hourcqia angulata angulata*, *H. angulata salitrensis*, *H. angulata sinuata*, *H. angulata symmetrica* Krömmelbein und Weber 1971]

Type species (subsequent designation), lectotype: *Cypris granulosa* Sowerby 1836, p. 345, pl. 21, fig. 4, designated by Sylvester-Bradley (1947), p.VIII.

Remark: *Cypris granulosa* (Sowerby 1936) as given by Dunker (1846) is not identic to the type species of *Cypridea* Bosquet 1852 as designated by Sylvester-Bradley (1949), see Kempf (1980a, p. 17 for details).

Neotype: *Cypridea granulosa* (Sowerby 1836), designated by Sylvester-Bradley (1949), BMNH No. In 39024 (Jones' No. 229.13), The Natural History Museum, London.

Diagnosis (emend): Small- to medium-sized, rarely large, with ovate, rectangular, triangular or oblique-trapezoidal lateral outline. With anteroventral rostrum (beak) and adjoining alveolus posterior to it extending upwards, with => *alveolar notch*. Development of => *alveolar furrow* highly variable, sometimes nearly absent and often delimited by an => *alveolar ridge*. LV>RV mostly, rarely with => *inverse* (RV>LV) overlap but hinge always normal, inequivalve. Strong tongue-like => *ventral overlap*. Posteroventrally with a curved or triangular => *cyathus* usually in larger valve only, sometimes hardly apparent; some forms with => *cyathus like protrusion* (cyathus like structure in smaller valves also). Hinge margin distinctly incised (=> *hinge incisure*), causing the => *dorsal furrow*. With or without => *local ornamentation* elements (nodes and/or spines and tubercles). Surface finely to moderately punctate, rarely totally smooth, in the latter case also lacking any => *ornamentation* elements.

Remarks: The adductor muscle scar (AMS) pattern is not considered very diagnostic at genus level (also refer to Horne and Colin 2005, p. 27 for details). *Cypridea* is once more emended (last emendation by Do Carmo et al. 2008) for several reasons (see discussion below for explanation).

Description: Carapace shape: Small to medium sized (usually 0.70-1.1mm), rarely large (e.g. *Cypridea gigantissima* Mojon 1990, 1.7-2.0mm, in Mojon and Médus 1990); and *Cypridea* cf. *clavata* of Jordan and Bless 1971, up to 2.1mm). Later outline variable, generally ovate modified in various ways: elongated ovate, rectangular, triangular or oblique-trapezoidal with many transitions. LV>RV, rarely => *inverse* (never combined with => *inverse hinge*), valve shape and valve size relation variable, either => *equivalve*, => *subequivalve* to strongly => *inequivalve*, usually subequivalve to moderately inequivalve. Maximum height usually in front of or otherwise close to mid-length. Maximum width at around mid-length or between mid-length and 4/5 of length.

Anterior margin anteroventrally passing into a tapering => *rostrum* (beak) of variable shape, width and length; bending backwards (=> *bending angle*) between nearly 0° to nearly 90°, usually around 30-60°. Point of rostrum mostly overreaching the ventral margin (more infrequent simultaneously protruding over the ventral outline), in some lineages barely or not at all reaching the ventral margin. Usually with, sometimes (almost) without an => *alveolar notch* breaking the lateral outline in the => *anteroventral region* immediately behind the rostrum which continues upwards as => *alveolar furrow/groove*. Alveolar furrow extremely variable depending on the species and concerning degree of incision, shape, width and length (in some species taxa reaching up to 5/6 of height, causing a => *rostral bulge*), sometimes almost not present. Alveolar furrow frequently delimited ventrally by an => *alveolar ridge*. Posteroventrally with a => *cyathus* in the larger valve only, some forms with weaker cyathus in smaller valves also (=> *cyathus-like protrusion*). Cyathus outline either rounded perpendicular to obtuse-angled, mostly not overreaching ventral and posterior valve margins, or (infrequently) tapering and then protruding over the posterior margin to a different degree.

Dorsal margin straight, rarely concave; dorsal outline slightly to strongly convex, sometimes feigned through a => *dorsal ridge*. Hinge margin incised (=> *hinge incisure*), forming a dorsal furrow with its flank being less inclined and wider in the larger valve (=> *lateral offset*). The hinge margin (not visible in lateral outer view) almost always (at least slightly) more or less inclined towards posterior end in relation to base line (Fig. 4, abbr.: IHL), rarely almost parallel to ventral margin. Ventral margin straight to convex, in many taxa with a => *ventral ridge* in the larger valve.

Dorsal view compressed to elongated ovate or rather narrow elliptic, tapering towards both ends, stronger to the anterior end. In taxa with broadly developed and long alveolar furrow, the anterior end shows lateral constrictions. In case of the occurrence of a larger cyathus or a protruding cyathus-like extension also slightly lateral constricted. Maximum width usually between around mid-length (in some taxa slightly anterior of it) and 3/5 of length.

Ventral overlap strong and convex (Fig. 7/C). If present, even the weak alveolar ridge is well visible in ventral view and connects the rostrum and the ventral margin.

Ornamentation:

1. Area-wide ornamentation elements/surface characters: Carapace surface finely to moderately punctate, smooth in some taxa. Diameter of puncta variable, generally larger (about 15-20µm) in centrolateral areas of the valves, and smaller (6-10µm) towards marginal areas, close to the margins being partially arranged in rows running parallel to these. Punctation intensity (depth of puncta) variable: all transitions from very faint and shallow to => *reticulation*-like with deep puncta. Puncta mostly relatively evenly distributed and the punctation pattern being relatively consistent. Several relatively evenly dispersed normal pores of 1-2µm diameter. Rostrum area often with a higher density of scattered normal pores.

Local ornamentation elements: With or without => *local ornamentation* elements (nodes and/or spines/tubercles or node like tubercles), but occurrence/non-occurrence as well as size and position these highly variable (see discussion for => *ornamentation* in glossary also), as well as their distribution. Most common are tubercles and node-like tuberculi, spines often larger but few in number, some forms with one pair of large spines only.

Fig. 7. (see following page): Terms for carapace description in *Cypridea* (without ornamentation and surface characters, refer to glossary for explanation). ACA: Anterior cardinal angle, AG: Alveolar groove, AMS: Adductor muscle scars, AN: Alveolar notch, AR: Alveolar ridge, DF: Dorsal furrow, DR: Dorsal ridge, FS: Frontal scar, IL: Inner lamella; ILT: Inner list, IM: Inner margin, IS: Interrupted Selvage, MS: Mandibular scars, MZ: Marginal zone, LO: Flexure/Lateral offset, LV: Left valve, NP: Normal (lateral) pores, PCA: Posterior cardinal angle, RV: Right valve, SV: Selvage, VO: Ventral (tongue–like overlap), VR: Ventral ridge.

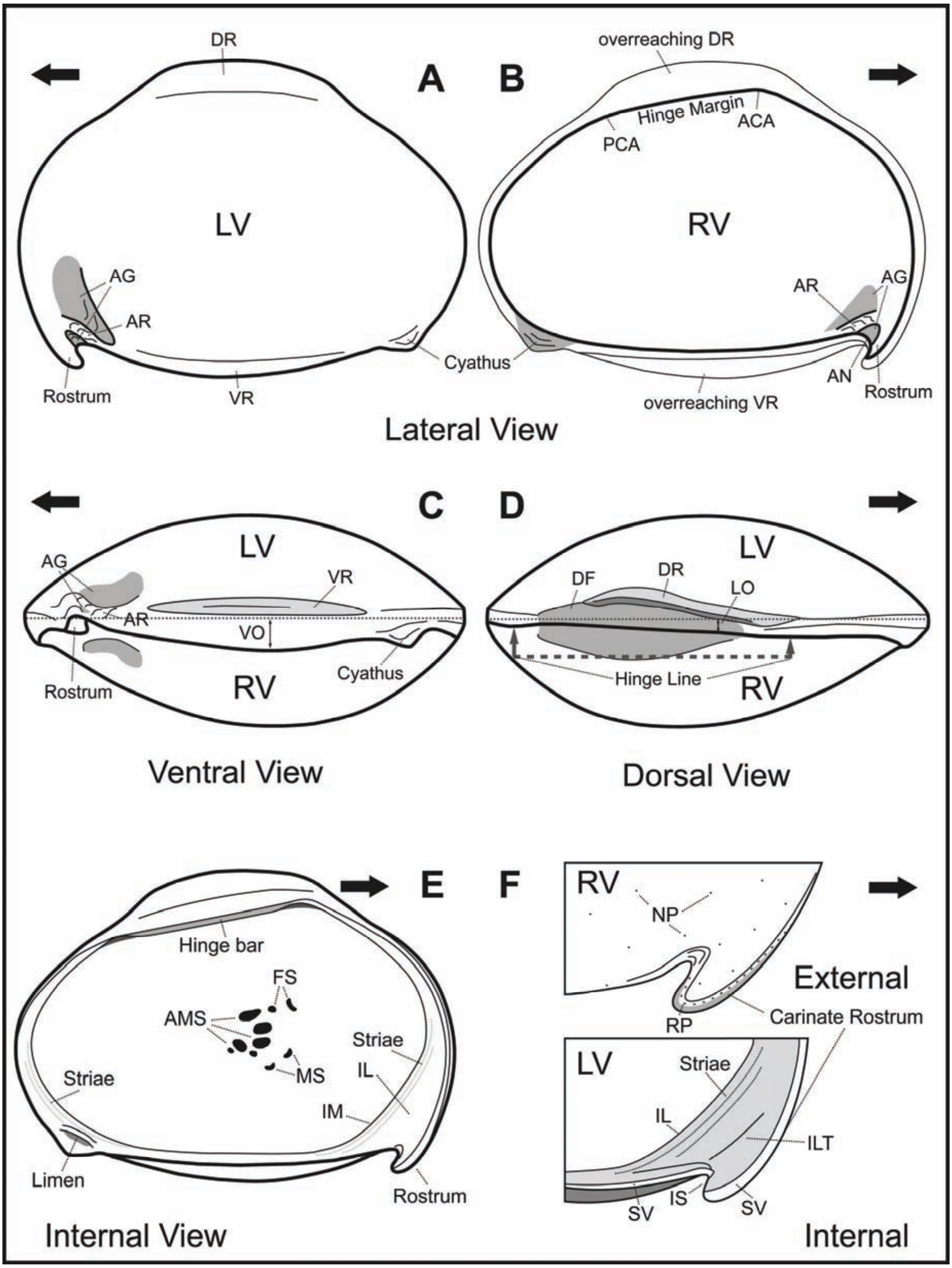
A
B
DR
overreaching DR
Hinge Margin
ACA
PCA
LV
RV
AG
AR
AR
AG
Cyathus
Rostrum
VR
overreaching VR
AN
Rostrum
Lateral View
C
D
LV
AG
VR
AR
VO
Rostrum
Cyathus
RV
LV
DF
DR
LO
Hinge Line
RV
Ventral View
Dorsal View
E
F
Hinge bar
FS
AMS
Striae
MS
IL
Striae
IM
Limen
Rostrum
Internal View
RV
NP
External
RP
Carinate Rostrum
LV
Striae
IL
ILT
SV
IS
SV
Internal

Fig. 7

Internal characters: Inner lamella usually well developed, being broad anteriorly and moderate posteriorly with highest width antero- and posteroventrally (Figs. 7/E, 8 and 9). Narrow to moderately broad => *free inner lamella* with maximum width at anteroventral and posteroventral areas of valves. With => *local widening of the inner lamella* (where rostrum/beak-like extension and alveolus/alveolar notch occur). Marginal pore canals absent in the => *attached area* above alveolar notch (Fig. 8). Selvage interrupted (=> *interrupted selvage*, Figs. 7/F, 8) along the posterior part of the rostrum. Larger valve often with posterior => *limen* in cyathus area (Figs. 7/E and 9).

The => *hinge* is tripartite, merodont (i.e. it has two terminal teeth in one valve with corresponding sockets in the other) and of lophodont type (i.e. tripartite with all elements not subdivides and being smooth; cf. Fig. 9), always "normal" (i.e. *terminal hinge elements* in the *smaller valve*, *median hinge element* in the *larger valve*), no => *inverse hinge* known in *Cypridea*. Hinge line straight. Anterior terminal hinge element represented by a relatively long narrow tooth-like ridge being about 35-45° flexed towards venter in relation to the median element and fitting in a matching socket in the larger valve. Median hinge element represented by a simple narrow bar in the larger valve. No real median groove developed in the smaller valve, the hinge bar of the larger valve is only attached to the smaller with its ventral part, thus merely resting on the dorsal margin of the smaller valve. Posterior terminal hinge element about in line with the median hinge element, being represented by an elongated, slightly swollen tooth in the smaller valve fitting into a matching socket of the larger valve. All elements smooth (Remark: Sylvester- Bradley 1949, p. 132, claimed to have detected a faint crenulation of the posterior tooth in some well preserved specimens. However, a crenulation of these elements could not be confirmed thus far).

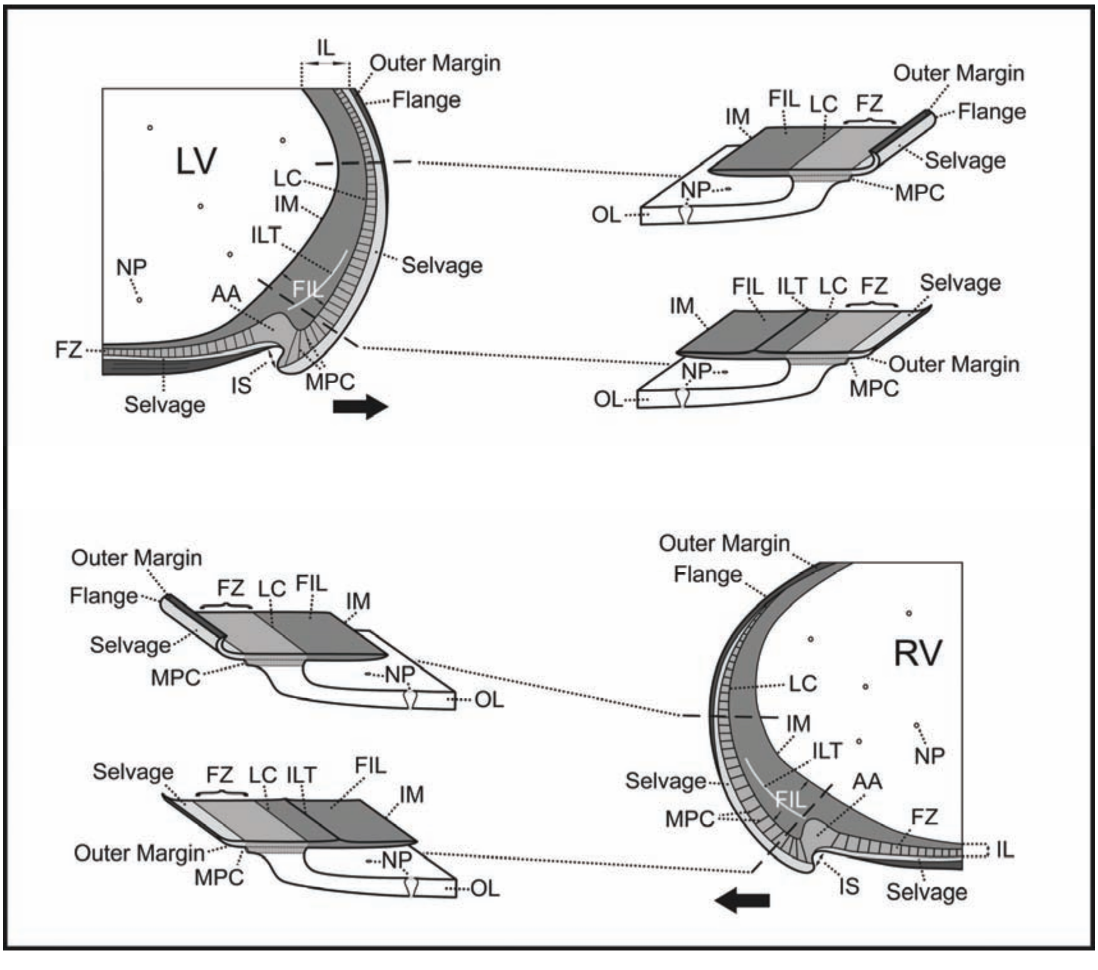

Fig. 8

Muscle scar pattern: Adductor muscle scar (AMS) field (Fig. 6, labeling of individual scars adopted from Horne and Colin, 2005) consisting of 6 scars. Number 1 to 4 are arranged in a row, convex towards anterior end, while 4 is often considerably smaller than 1-3. Scars 5 and 6 posterior of the row in while 6 is somewhat higher than 5, but not above scar 2. Scar 6 mostly larger than scar 5, at about the same size of 1-3. Size of scar 5 is small, like 4. One round frontal scar, relatively small and close to adductor muscle scars 1 and 2. Two crescentic mandibular scars.

Remark: For detailed discussion and comparison of the AMS to taxa with similar patterns refer to Horne and Colin (2005, p. 27 and fig. 3 therein).

Christensen (1968, p. 23, fig. 6) gives one of the best photographs of the muscle scar pattern of *Cypridea* available from the literature, which is from an internal view of a fragment of *Cypridea* ex gr. *setina* (Anderson), nicely showing all central, frontal and mandibular scars as well as some dorsal ones.

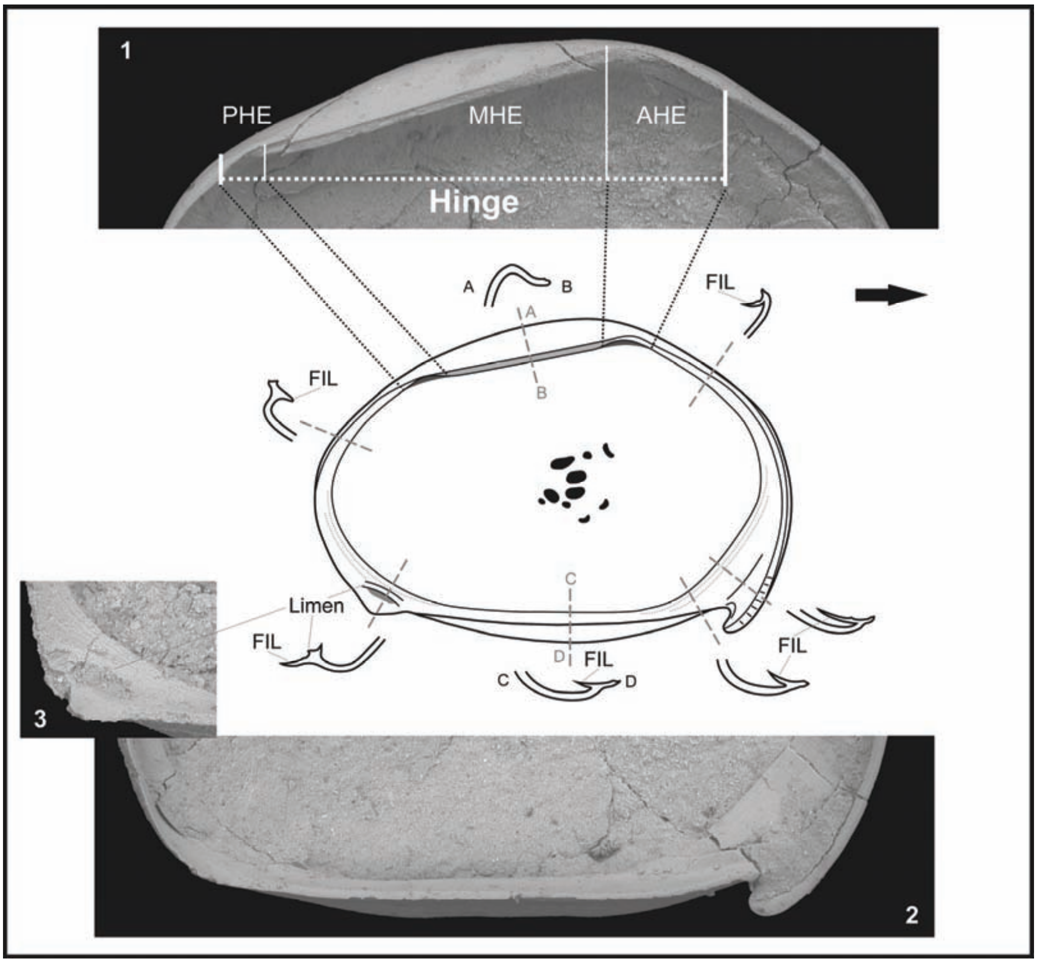

Fig. 9. Hinge area and sketches of cross-sections through the marginal zones of a LV of *Cypridea* (internal view), newly drawn as inspired by a figure by Sylvester-Bradley (1949, fig. 18) and complemented with photographs of the left valves upper (1) and lower part (2) of a *Cypridea (Pseudocypridina) laeli* Sohn 1979, and the cyathus (3) with limen of *Cypridea* ex. gr. *tuberculata* cf. *C. tilleyi* Loranger 1951. AHE: Anterior hinge element, FIL: Free inner lamella (absent in hinge area), MHE: Median hinge element, PHE: Posterior hinge element.

Fig. 8. (see preceding page): Detailed sketches of the internal views and sections of the anterior marginal zone of the LV and RV in *Cypridea*. Note that the extract of the RV captures a somewhat larger area (i.e. in height) than that of the LV. AA: Attached area, FIL: Free inner lamella, FZ: Fused zone (marginal zone), IL: Inner lamella, ILT: Inner list, IM: Inner margin, IS: Interrupted selvage, LC: Line of concrescence, MPC: Marginal pore channel, NP: Normal Pore. OL: Outer lamella.

Sexual Dimorphism: Present in some representatives (listed right below**,** for illustration refer to Fig. 10). Presumed females generally more rectangular in lateral view, having a lower inclination of the hinge margin towards posterior end than the males and a higher maximum height (lower L/H-ratio) as well as being wider in dorsal view, thus appearing more inflated. Male dimorphs are by trend more elongate in lateral view than their female counterparts, having a higher inclination of the hinge margin towards posterior end (because of the narrower posterior margin), a lesser maximum height (higher L/H-ration) and narrower and stretched in dorsal view. The position of maximum width can be the same in both dimorphs, e.g. *Cypridea (Pseudocypridina) piedmonti* (Roth 1933) herein, or not, e.g. *Cypridea gissarensis* Andreev 1968 (in Andreev and Mandelstam 1968), where the maximum width in the male is somewhat more posterior. Dorsal overreach of the left valve may be somewhat stronger in females.

Generally, the sexual dimorphism in Cypridoidea does not have to be pronounced and the morphologic variability among parthenogenetic females of one population can be higher than between males and females of sexual populations (e.g. Horne and Martens 1998).

List of some selected representatives of *Cypridea* with sexual dimorphism (as presumed by the author herein and given in the literature; in alphabetic order):

- *Cypridea dunkeri carinata* Martin 1940 – Stoica (2007, p. 108, pl. 3-8)
- *Cypridea gissarensis* Andreev 1968 – Andreev and Mandelstam (1968, p. 80)
- *Cypridea (Longispinella) longispina* (Peck 1941) syn. *Cypridea (Longispinella) asymmetrica* (Sohn 1979) – herein
- *Cypridea (Pseudocypridina) piedmonti* (Roth 1933) syn. *Cypridea (Pseudocypridina) henrybelli* Sohn 1979 – herein
- *Cypridea (Pseudocypridina) setina* (Anderson 1939) – herein
- *Cypridea subvaldensis* Hanai 1951 – Hanai (1951, p. 411, figs. 2-7)

Questionable sexual dimorphism:

- *Cypridea clavata* (Anderson 1939) – in Nye et al. (figs. 10 D, G, presumed female; E, H and F, I, presumed male)
- *Cypridea obesa* Peck 1951 (herein)

Sexual dimorphism – discussion: The debate whether the reproductive mode of the Cyprideidae Martin 1940, particularly the *Cypridea*-lineage, is exclusively parthenogenetic or not reaches back to the early 1950's. Hanai (1951) already discussed females and males of *Cypridea subvaldensis* Hanai 1951. Although there have been some reports of presumed sexual dimorphism in *Cypridea* s.l. (sensu Sylvester-Bradley 1949) ever since, some authors persisted in the viewpoint that representatives of *Cypridea* reproduced entirely parthenogenetic, which, in conjunction with the desiccation and freezing-resistant resting egg, was presumed to have had facilitated the adaptive radiation and global dispersion of the group in latest Jurassic to Early Cretaceous times (e.g. Whatley 1990, 1992). Whatley's ideas about the coherence of sex/parthenogenesis and dispersal in context with the differential success of the Cyprideidae Martin have been challenged by Horne and Martens (1998, see Chapter 6.1 also). Sylvester-Bradley (1947, 1976) dealt with the subject of reproductive modes in *Cypridea* and suggested parthenogenetic reproduction in some (not all!) of its representatives. He (Sylvester-Bradley 1976) already pointed out that the high degree of polymorphism (the morphs either regarded as species, subspecies or variants by different authors) "… might be due to polyploidy after [interspecific] hybridization …" (Sylvester-Bradley 1976, p. 32, see Chapter 6.1. for more details regarding this topic).

Krömmelbein (1961) was the first to discuss and to provide evidence for sexual dimorphism of other representatives of the family Cyprideidae Martin 1940 (designated as subfamily Cyprideinae by Krömmelbein 1961), i.e. some species of *Paracypridea* Swain 1946: *Paracypridea langdoni* Krömmelbein 1961, *Paracypridea obovata obovata* (Swain 1946), *Paracypridea quadrirugosa weberi* Krömmelbein 1961 and

Paracypridea similis Krömmelbein 1961. Krömmelbein (op. cit.) differentiated "a-forms" and "b-forms" of the mentioned taxa, interpreted the morphologic differences as sexual dimorphism while pointing out that he was not sure, which form would have to be designated as either of the sexual dimorphs. However, in the absence of direct indications, such as imprints of ovaries or tubes of the testes, as well as close recent relatives (the family Cyprideidae is extinct), Krömmelbein (op. cit.) already considered indirect carapace characters to distinguish the sexes: size relations, proportion of the quantity of the forms within a sample and specific morphologic characters (lateral widening of the posterior carapace half and ornamentation elements). Sohn (1969, p. B2), while mentioning the paper of Krömmelbein (1961), states that (sexual) dimorphism is unknown in *Cypridea*, but corrects this statement in a later publication (Sohn 1979, p. 13).

In 1968, Andreev and Mandelstam (1968) describe and figure sexual dimorphs of *Cypridea gissarensis* Andreev (op. cit., p. 80-81, pl. 1, figs. 13a, b, male; and 14a, b, female) that differ in lateral and dorsal outlines, that is to say the male has a much less higher posterior margin and the hinge margin shows considerable inclination towards posterior end while the female is more oblong in lateral view whereas in dorsal view the male is less wide with its maximum width at 4/5 of length while the female is considerably wider and has its maximum width at or anterior of 3/5 of length.

Sohn (1979) takes sexual dimorphism in *Cypridea (Pseudocypridina) piedmonti* and '*Longispinella*' *longispina*, recte *Cypridea (Longispinella) longispina*, into account, based on differences in the maximum carapace width in dorsal view. Regarding the latter, this case is interpreted somewhat more different and complex (refer to chapter 5.4.3 herein under this species).

Sames (2002) tentatively assumed sexual dimorphism in some of his *Cypridea* specimens (*Cypridea* sp. B, presumed female, and *Cypridea* sp. C, presumed male, p. 21-22, pl. 2, figs. 6 and 7, and within *Cypridea* sp. D, p. 23, pl. 2, figs. 9 and 10).

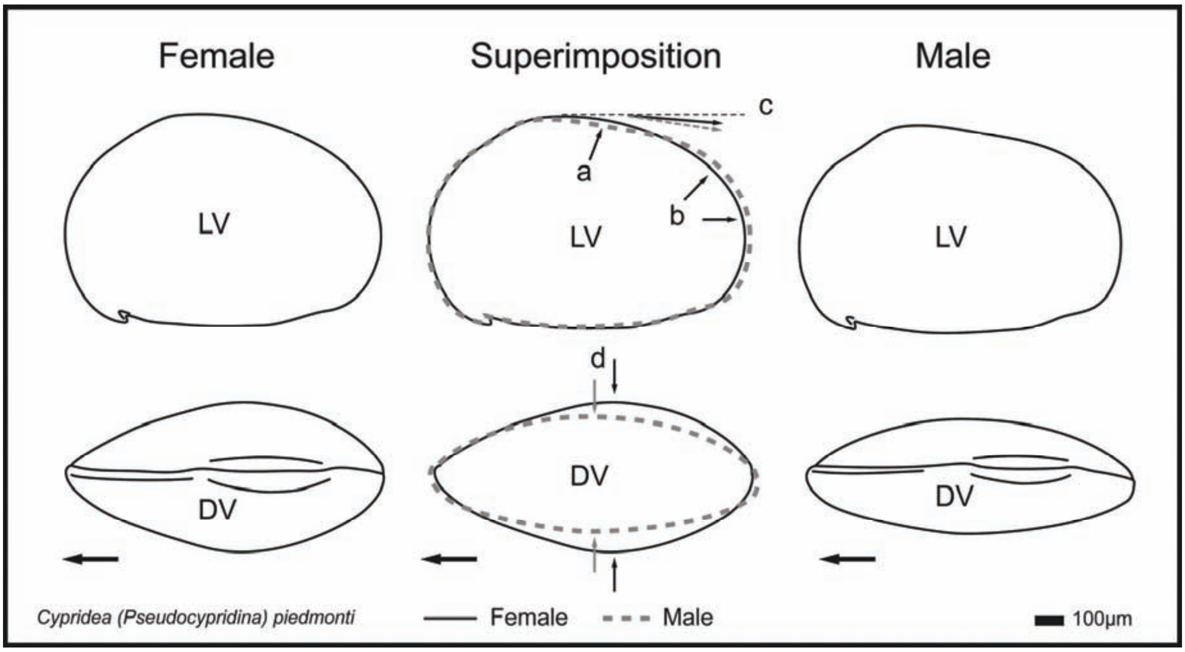

Fig. 10. Identification of sexual dimorphism in representatives of *Cypridea* Bosquet 1852 as exemplified by means of *Cypridea (Pseudocypridina) piedmonti* (Roth 1933) var. *henrybelli* (without nodes). Specimens to scale. Superimposition of both sexual dimorphs: female with black line, male with dashed grey line. LV: Lateral left view, DV: Dorsal view. a) difference in overreach of left valve over hinge line (stronger in female, not very pronounced here), b) difference in shape and maximum length (only slightly in this case), c) different inclination of the hinge margin (slightly in this case), d) considerable difference in degree (important character) and position (variable, not diagnostic) of maximum width.

Stoica (2007) described and figured sexual dimorphism in *Cypridea dunkeri carinata* and his dimorphs satisfy the criteria of sexual dimorphism in *Cypridea* as given on top of this paragraph very well. Stoica's (op. cit.) evidence is well supported by numerous specimens that are very well preserved (Stoica, pers. comm., September 2007).

Altogether, the sum of facts given in the literature is evaluated, elaborated (refer to beginning of this paragraph above), and applied herein, see *Cypridea (Longispinella) longispina*, *Cypridea (Pseudocypridina) piedmonti* or *Cypridea (P.) setina* for example, and Fig. 10. Many a morphs of *Cypridea* as known to date that occur in the same samples and/or stratigraphic level—regardless whether having been determined species, subspecies or variants—probably represent unrecognized sexual dimorphs. Unfortunately, the dorsal view, which could make recognitions of sexual dimorphs much easier in many cases (somewhat wider carapaces in females), is often missing in publications.

A survey at background and coherences (genetics, reproductive modes, evolutionary ecology etc.) is given in Chapter 6.1. In the past, sexual dimorphism in many fossil cypridoidean ostracods including *Cypridea* may have been overlooked due to a "cytheroid-centric" view on sexual dimorphism in the carapace shape, i.e., based on representatives of the Cytheroidea (deriving from the fact that these were studied more intensively). Carapaces of males of typical cytheroid species without broodcare are usually more elongate than females in lateral outline because of the large copulatory appendages to accommodate within the posterior part of the carapace. In those with broodcare, however (e.g. *Metacypris*, *Theriosynoecum*), males do not always appear more elongate since the females are larger with an posteriorly inflated carapace.

An identification of sexual dimorphism in many cypridoideans solely from the carapace shape may is difficult in many cases, particularly since the Cypridoidea neither have brood care (Martens et al. 1998a) that can lead to a much broader posterior carapace in the females (brood pouches) nor do they distincly show the more elongate carapaces in the male dimorphs in comparison to the females.

General trends in ontogeny: Instars of *Cypridea* can, conditionally and not overall applicable (see discussion and remarks below), be identified through several characteristic features and trends. Younger instars tend to have a stronger inclined hinge margin (considerably more than 25°), thus being more triangular in lateral outline. In some forms the hinge margin is less incised and sometimes the dorsal outline between the cardinal angles is concave. Also, the surface characters seem to be coarser and more towards a reticulation rather than punctation (sensu Sames herein). However, this considered an optic illusion caused by the fact that the diameter of the single elements of the surface characters (puncta) is the same as in adults, but they are less in number and closer to each other since the carapace surface is much smaller. The cyathus in the larger valve tends to be weaker developed and less prominent the younger the instar is. Concerning size, most adult specimens of representatives of *Cypridea* fall within a range of 0.7-1.1mm length (Nye et al. 2008), and thus, specimens with a maximum length considerably below 0.7mm are most probably juveniles.

<u>Discussion and remarks concerning ontogeny:</u> In the case of the plethora of taxa (many hundred) in *Cypridea*, many a species and/or subspecies are suspected to conceal either ecophenotypes, sexual dimorphs, and ontogenetic stages respectively (see Chapter 6.1 also). Wolburg (1959, p. 233) was the first one to take juveniles of *Cypridea* into account for taxonomy and discuss ontogenetic lineages and their value for application but did not yet provide details on how to generally identify juveniles. Anderson himself (Anderson 1939, 1967, 1985, Anderson and Bazley 1971, Anderson et al. 1967) as well as Sylvester-Bradley (1949) seem never to have considered ontogenetic stages in their analyses and discussion of morphologic variations in *Cypridea*.

Jordan and Bless (1971) separated and described adult and juvenile(?) inverse specimens belonging to one species of *Cypridea (Ulwellia)* (Anderson 1939) in their perception and took one step further by morphologically characterizing the juveniles and highlighting ontogenetic trends, particularly regarding => *ornamentation*, i.e. that the surface characters are coarser in the instars (reticulation like punctation) and finer (punctation) to absent in adults, and that the "sculpture", such as nodes, tubercles or spines (=> *local ornamentation elements*) tend to be more numerous and stronger developed in juveniles. Although ornamentation, particularly concerning the => *local ornamentation elements* as defined herein, is considered taxonomically insignificant as to designation and differentiation of species or genera of the Cyprideidae Martin 1940—leaving ecophenotypic effects out of consideration—it cannot totally be ruled out either that in some forms there may be certain ontogenetic trends in *Cypridea* (see below). However, the problem regarding the line of argument of Jordan and Bless (1971) in conjunction with the discussion of ontogenetic trends is that, on the one hand, these authors convincingly discuss the enormous morphologic variability in the genus *Cypridea* and the possible occurrence of certain characters (normal and inverse valve size relation, maximum size, occurrence and degree of development of local ornamentation elements and surface characters) even within one species, but on the other hand, the maximum length of their presumed juveniles (0.78-0.98mm) easily falls within the length range of most representatives of *Cypridea* (0.7-1.1mm, Nye et al. 2008), while the largest specimens are 1.25 to 2.1mm(!) long. Although all the specimens come from one sample, the authors admit (Jordan and Bless 1971, p. 686) that they are not sure if the material is autochthonous.

More evidence for the possible ontogenetic character of ornamentation, local ornamentation elements particularly, is given by Horne and Smith (2004) who describe prominent tubercles in combination with pitted/reticulate ornament (=> *area-wide ornamentation elements/surface characters herein*) in juveniles and preadults (up to A-1) of the extant *Potamocypris humilis* (Sars 1924), while the adults are completely devoid of tubercles, being punctate (to reticulation-like punctate) and just show faint indications of a distortions of the punctation where the major tubercles were situated in the younger instars. Since this particular type of ornamentation has been described for the first time in the Cypridoidea therein (Horne and Smith 2004, p. 304) and *P. humilis* belongs to the family Cyprididae Baird 1845 and is thus not closely related to representatives of the extinct family Cyprideidae Martin 1940, no general conclusions can and should be drawn so far regarding the possible meaning of this character for other cypridoidean groups. However, the pattern of the tubercles is strikingly similar to that of many *Cypridea*, and the data provided by Horne and Smith (2004) implies that tuberculation/and or spines (=> *local ornamentation elements*) and its degree of development have at least to be considered to occur as ontogenetic character in other taxa also, particularly *Cypridea* with its many highly spinose and/or tuberculate forms.

Very recently, Nye et al. 2008 considered differently tuberculate subspecies of *Cypridea clavata* (Anderson 1939), including *Cypridea bogdenensis* Anderson 1967 and questionably *Cypridea insulae* Anderson 1967 to be intrapopulational variants of a single species: *Cypridea clavata*. Their (Nye et al. 2008) adult forms show different degrees of variation ranging from nearly devoid of tubercles to strongly tuberculate as partially visible in the juveniles as well. The fact that all of these derive from the same very small interval at one locality makes a stronger argument for them all belonging to one species.

Altogether, the conclusion is that the identification of juveniles in *Cypridea* still remains problematic. Ornamentation, i.e. => *local ornamentation elements*, is not significant for the designation of juveniles and due to considerable variation in lateral outline within the genus *Cypridea*, the narrow posterior margin (in comparison to the anterior one) in combination with the strong inclination of the hinge margin towards posterior end are not always reliable characters as well. The same is true for the less well developed and protruding cyathus. What can be stated with some certainty is that a maximum carapace length being considerably less than the typical range of maximum length of most *Cypridea* species (0.7-1.1mm after Nye et al. 2008) points to juveniles.

Discussion: Synonymy: Most subgenera of *Cypridea* have been extensively discussed in the literature (see Chapter 5.2.2, Historic remarks, herein for synopsis and references as well as Horne and Colin (2005) and the list of valid subgenera of *Cypridea* below).

Yumenia Hou 1958 is excluded from being a representative of *Cypridea* Bosquet 1852 as well as the Cyprideidae Martin 1940 here for the reasons of lacking many diagnostic characters: rostrum, alveolus and cyathus as well as the incised hinge margin and the dorsal furrow. *Yumenia* has been placed into the Trapezoidellidae Sohn 1979 by Nikolaeva and Neustrueva (1999, p. 34).

As for *Cypridea (Ulwellia)* (Anderson 1939), the validity of this subgenus is strongly connected with the interpretation of the taxonomic significance of an => *inverse valve size relation*, which is considered taxonomically insignificant here (see glossary and 5.4.3 herein; this subgenus has RV>LV). Although Anderson's (1939) diagnosis includes several other morphologic characters, many authors formerly focused on the inverse (RV>LV) valve size relation and simply assigned inverse representatives of *Cypridea* to this subgenus regardless of the overall carapace shape and potential relationships. Therefore, the validity and the prevalent usage of the subgenus *Ulwellia* is challenged and rejected here (see discussion under the description of the subgenus in Chapter 5.4.3 for details).

Cypridea (Sebastianites) Krömmelbein 1962 is indicated with a question mark because of the strong trend towards a reduced rostrum and the dorsolateral sulcus at about mid-length. In his remarks to his diagnosis, Krömmelbein (1962, p. 460) notes that he includes those forms into the subgenus which lack a rostrum, this group from which he also chose the type species ("subgenerotype"). Taxa with a rostrum he (op. cit.) indicated with a question mark. From this point of view, *Sebastianites* would have to be excluded from being a representative of *Cypridea* and the taxa with (weak) rostrum—i.e., those of *Cypridea (Sebastianites?)* Krömmelbein 1962—to be otherwise assigned to *Cypridea*. In his later publications including true or questionable representatives of *Cypridea (Sebastianites)*, Krömmelbein (1965b, Krömmelbein und Weber 1971) never again commented on the subject. Consequently, it also will have to be reviewed, whether *Sebastianites* will be furthermore considered as representative of the family Cyprideidae Martin 1940. This matter goes beyond the scope of this paper.

Guan (1978) erected the new subgenus *Cypridea (Guangdongia)* which is, however, considered being representative of *Bisulcocypridea* Sohn 1969 here for the reason of, aside being similar to *Cypridea* and having a rostrum and alveolus, showing two dorsolateral sulci.

Longispinella Sohn 1979 is considered being a representative of *Cypridea* herein and designated as subgenus of the latter. Sohn's (1979, p. 18) diagnosis is insufficient in giving few significant specific characters and most characters correspond to *Cypridea*. *Longispinella* has a well developed rostrum, alveolar notch and alveolar furrow, even the alveolar ridge newly described herein is present, as well as a cyathus and the incised hinge margin forming the dorsal furrow (for details refer to description and discussion of *Cypridea (Longispinella)* in Chapter 5.4 herein and the thereof described species).

Very recently, Do Carmo et al. (2008, p. 791) emended the diagnosis of *Cypridea*, and included some representatives of the genus *Hourcqia* Krömmelbein 1965(b) into *Cypridea* [*sensu lato*]. Based on advanced revision and information herein, however, it again became necessary to emend the genus for several reasons, as discussed right below.

Comments regarding the emendation: An anew emendation of *Cypridea* as well as its diagnosis became necessary for the following reasons:

1) The changed status of *Longispinella* Sohn 1979, herein integrated into *Cypridea*,
2) the revised terminology of some important characters (e.g. alveolus with its elements, ornamentation etc.)
3) the different perception of the taxonomic significance of some characters (e.g. particularly *local ornamentation elements* as defined herein),
4) the inclusion of the => *hinge incisure* and the thereby caused => *dorsal furrow* as well as the => *cyathus* into the diagnosis, and
5) the inclusion of a newly described character, the => *alveolar ridge*, into the taxonomic analysis,
6) the emended diagnosis of Do Carmo et al. 2008 is considered partially insufficient for the reasons given below.

The emendation of the diagnosis of *Cypridea* by Do Carmo et al. (2008) focuses on the rostrum (beak therein) mainly, while being very short and general regarding other characters and lacking many of the new facts as given here. Undoubtedly, the rostrum is one of the most diagnostic characters in *Cypridea*, the cases of the contemporaneous genus *Bisulcocypridea* Sohn 1969 or the much younger genus *Karshicypridea* Gramm and Burkharina 1967 show that a rostrum (or beak) alone, particularly in outer view only, is herein considered insufficient to diagnose *Cypridea*. Based on the typical appearance of most representatives of *Cypridea* including its type species, only the rostrum/beak in combination(!) with a present => *alveolar notch* (see glossary for discussion) and => *alveolar furrow* as well as the hinge incisure/dorsal furrow and the cyathus are, altogether, diagnostic to *Cypridea*.

In the view of the present author, the diagnosis of the genus *Cypridea* should be kept as accurate and appropriate as possible to differentiate *Cypridea* from other taxa (e.g. *Bisulcocypridea* or *Karshicypridea*), or to reduce problems in this context, at least. The weak development or absence of single characters in some subtaxa newly integrated is not considered a good reason to change or even adopt the diagnosis of a genus of which the type species as well as the majority of representatives do show all of these characters more or less well developed. If a diagnosis is changed or generalized, a detailed justification and discussion is necessary in the view of the present author. Do Carmo et al. (2008, p. 791), however, only note that " … the diagnosis proposed is [therein] emended in order to present a concept with the up-to-date synonym[y] list [therein]". Since synonymy and many morphologic characters of *Cypridea* are thoroughly described, revised and discussed herein, and led new results, an anew emendation is proposed.

The inclusion of *Hourcqia africana* Krömmelbein 1965(b) into *Cypridea* as given and figured by Do Carmo et al. (2008) seems convincing thus far. However, the overall morphology of the former is here considered relatively different from most representatives of *Cypridea* by belonging to a lineage with weak rostrum, very weak to absent alveolar notch (i.e. the => *ventral outline* and => *ventral margin*, if coincident, right behind the => *rostrum* are not curved upwards but meeting the posterior part of the rostrum in a more or less perpendicular angle, as defined herein) and absent alveolar furrow. Unfortunately, Do Carmo et al. (2008) provide no figure or photograph of the central muscle scar field of *Cypridea africana* (also not given by Krömmelbein 1965b), which is described as only consisting of 5 scars (anterior row only having 3 scars), and thus atypical. Therefore, the synonymy of *Hourcqia africana* Krömmelbein 1965(b) to *Cypridea* is considered to be in need of further investigation and for the present indicated with a question mark here.

Evolutionary trends: Aside from the fact that some early forms of *Cypridea* already may possess a weakly developed rostrum, alveolar notch plus alveolar furrow, and cyathus, there seems to be a general evolutionary trend from an acute => *cyathus-like protrusion* combined with strongly developed rostrum, alveolar notch and furrow in early forms towards a weak and rounded or even reduced cyathus and weak or absent => *alveolar notch* (see glossary for definition) and furrow (see Chapter 6.3 for details).

List of valid subgenera of *Cypridea* (see discussion above for comments):

- *Cypridea (Cyamocypris)* (Anderson 1939),
- *Cypridea (Cypridea)* Bosquet 1852
- *Cypridea (Longispinella*) (Sohn 1979) stat. nov.
- *Cypridea (Morinina)* (Anderson 1939)
- *Cypridea (Morininoides)* Krömmelbein 1962
- *Cypridea (Pseudocypridina)* (Roth 1933) syn. *Langtonia* Anderson 1939

List of invalid or questionable subgenera of *Cypridea* (see discussion above, Table 1, and Chapters 5.2.1 and 5.4.3 for details)

- *Cypridea (Guangdongia)* Guan 1978 – moved to *Bisulcocypridea* Sphn 1969
- *Cypridea (Sebastianites)* Krömmelbein 1962 - questionable subgenus (remaining to be investigated in the future)
- *Cypridea (Ulwellia)* (Anderson 1939) - rejected (herein, see Chapter 5.4.3 below):
- *Cypridea (Yumenia)* Hou 1958 – placed in the Trapezoidellidae Sohn 1979 by Nikolaeva and Neustrueva (1999, p. 34)

List of invalid species names (unpublished) for North America (unpublished theses of Looney 1948, Craig 1961, see Chapter 5.2.2 above):

- *Cypridea grandis* sp. nov. Craig, 1961
- *Cypridea hudsoni* sp. nov. Craig, 1961
- *Cypridea ovata* sp. nov. Craig, 1961
- *Cypridea trispinosa* sp. nov. Craig, 1961
- *Ulwellia crescenti* sp. nov. Craig, 1961
- *Cypridea laevicula* sp. nov. Looney, 1948
- *Cypridea sulcata* sp. nov. Looney, 1948 – preoccupied, used by Mandelstam 1955
- *Cypridea nodulata* sp. nov. Looney, 1948
- *Cypridea pyriformis* sp. nov. Looney, 1948

Stratigraphic range: Late Jurassic to Paleogene (Kimmeridgian to Lower Eocene).

Remarks: Recent publications revealed a longer stratigraphic distribution of true (taxa with true, fully developed rostrum and otherwise diagnostic characters), i.e. *Cypridea* s.l. (sensu Sylvester-Bradley 1949). For example, Schudack and Schudack (2002) and Sames (2008) demonstrated a Kimmeridgian occurrence of true *Cypridea* from the Tendaguru formation of Tanzania, East Africa while Guan et al. (1997) described *Cypridea (Cypridea) pingyiensis* Guan from the Lower Eocene Middle Member of the Bianqiao Formation, Pingyi, China.

Geographic distribution: Worldwide, except Australia and Antarctica (the following list was considerably complemented by Jean-Paul Colin, Cestas, France, which is gratefully acknowledged):

Europe: Denmark, Former USSR, France, Germany, United Kingdom (England), Ireland (offshore), Italy (Sardinia), The Netherlands, Poland, Portugal, Romania, Spain, Sweden, Switzerland.

Asia: China, Former USSR, Japan, Korea, Mongolia.

Middle East: Israel, Lebanon.

Africa: Angola, Cameroon, Chad, Democratic Republic of the Congo, Republic of the Congo, Ghana, Ethiopia (unpublished), Gabon, Liberia (unpublished), Morocco, Niger, South Africa, Sudan, Tanzania, Tunisia.

North America: Canada, U.S.A.

South America: Argentina, Bolivia, Brazil.

Paleoecology: Salinity: (Classification of brackish waters according to the Venice System as published by Oertli 1964): Presumed salinity tolerance: freshwater (0-0,5‰ TDS) after Neale (1988); freshwater to (β-)oligohaline (0-3.0‰ TDS) after Schudack, 1993. Indicative for lower alkalinity (<5-15mEq/L) by tentative analogue comparison with modern representatives of *Stenocypris* and *Mecynocypris* (Colin and Dépêche 1997). Dominantly freshwater, not to rule out that some taxa possible inhabited saline lakes (Horne 2002).

Habitat/life mode: Nonmarine temporal (ephemeral) waterbodies (pools, ponds), and in part nonmarine permanent water bodies (lakes) (Horne 2002). Benthic, crawling; possibly with swimming capability (Whatley 1990, 1992, Horne and Martens 1998).

5.3. Index of described taxa

Genus *Cypridea* Bosquet 1852

Cypridea nitidula Peck 1941

Cypridea obesa Peck 1951

Cypridea? minuta (Peck 1951) emend.

Subgenus *Longispinella* Sohn 1979 stat. nov. emend.

Cypridea (Longispinella) longispina Peck 1941 syn. *C. (L.) asymmetrica* (Sohn 1979) emend.

Subgenus *Pseudocypridina* Roth 1933 emend.

Cypridea (Pseudocypridina) laeli Sohn 1979 cf. *Cypridea (P.) moneta* Kneuper-Haack 1966
Cypridea (Pseudocypridina) piedmonti (Roth 1933) syn. *C. (P.) henrybelli* Sohn 1979 emend.

Cypridea setina-group
Cypridea (Pseudocypridina) setina (Anderson 1939)
  Cypridea (Pseudocypridina) setina var. *rectidorsata* Sylvester-Bradley 1949
  Cypridea (Pseudocypridina) setina var. *setina* (Anderson 1939)

Cypridea alta-group
Cypridea ex gr. *alta* Wolburg 1959

Cypridea tuberculata-group
Cypridea ex gr. *tuberculata* (Sowerby 1836) cf. *C. tilleyi* Loranger 1951

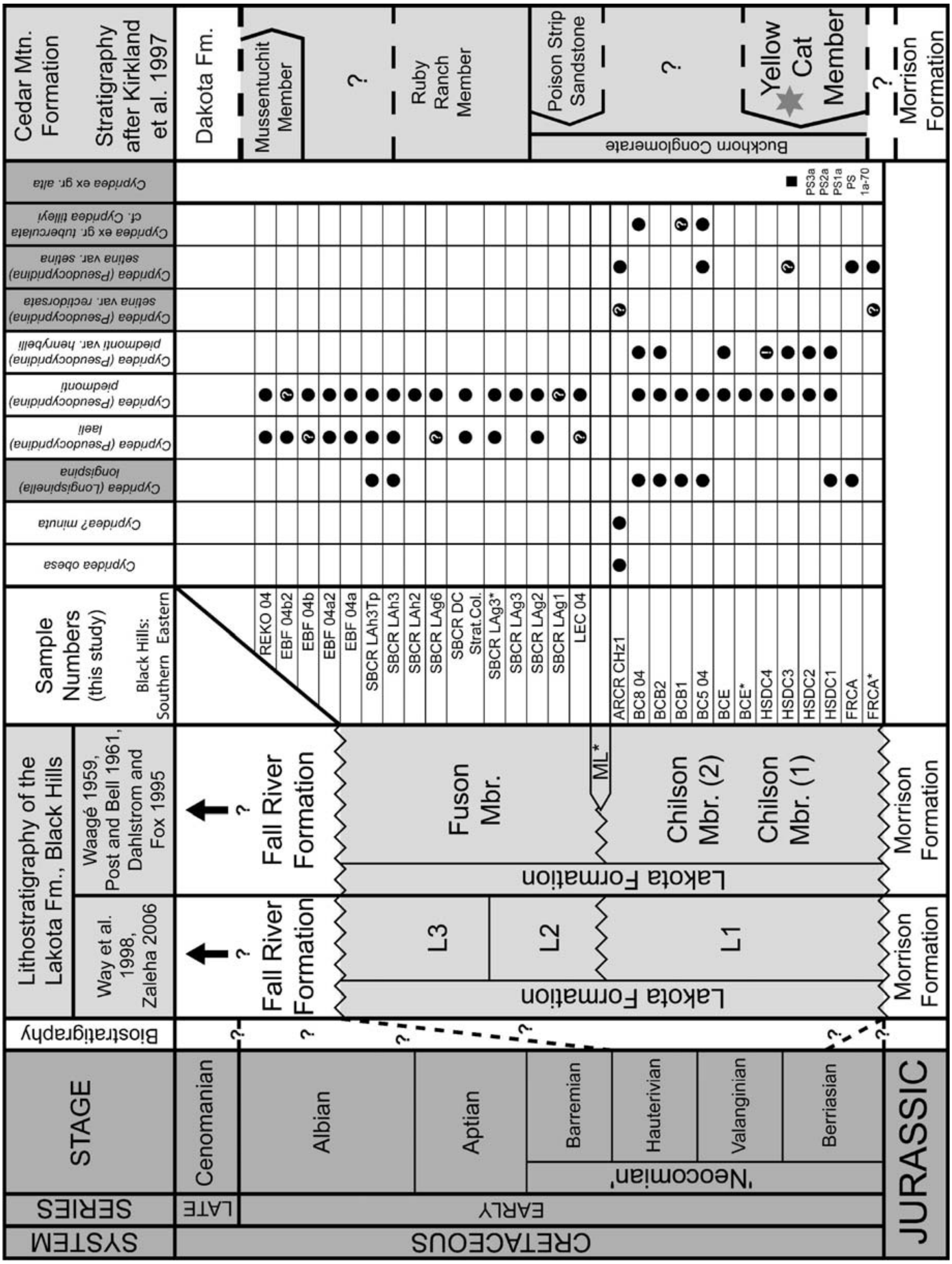
SYSTEM
SERIES
STAGE
Biostratigraphy
Lithostratigraphy of the Lakota Fm., Black Hills
Way et al. 1998, Zaleha 2006
Waagé 1959, Post and Bell 1961, Dahlstrom and Fox 1995
Sample Numbers (this study)
Black Hills: Southern Eastern
Cypridea obesa
Cypridea? minuta
Cypridea (Longispinella) longispina
Cypridea (Pseudocypridina) laeli
Cypridea (Pseudocypridina) piedmonti
Cypridea (Pseudocypridina) piedmonti var. henrybelli
Cypridea (Pseudocypridina) setina var. rectidorsata
Cypridea (Pseudocypridina) setina var. setina
Cypridea ex gr. tuberculata cf. Cypridea tilleyi
Cypridea ex gr. alta
Cedar Mtn. Formation
Stratigraphy after Kirkland et al. 1997
CRETACEOUS
JURASSIC
LATE
EARLY
Cenomanian
Albian
Aptian
Barremian
Hauterivian
Valanginian
Berriasian
'Neocomian'
Fall River Formation
Lakota Formation
L3
L2
L1
Fuson Mbr.
ML*
Chilson Mbr. (2)
Chilson Mbr. (1)
Morrison Formation
REKO 04
EBF 04b2
EBF 04b
EBF 04a2
EBF 04a
SBCR LAh3Tp
SBCR LAh3
SBCR LAh2
SBCR LAg6
SBCR DC Strat.Col.
SBCR LAg3*
SBCR LAg3
SBCR LAg2
SBCR LAg1
LEC 04
ARCR CHz1
BC8 04
BCB2
BCB1
BC5 04
BCE
BCE*
HSDC4
HSDC3
HSDC2
HSDC1
FRCA
FRCA*
PS3a
PS2a
PS1a
PS
1a-70
Dakota Fm.
Mussentuchit Member
Ruby Ranch Member
Poison Strip Sandstone
Buckhorn Conglomerate
Yellow Cat Member
Morrison Formation
?

Fig. 11

5.4. Description and taxonomy

5.4.1. Preceding general remarks regarding the usage of subgeneric groups: Subgenera and species-groups

Establishing and using subgenera as classificatory category in paleontologic systematics is debatable but has proved to be quite useful. The past century revealed that experienced taxonomists can establish a good taxonomic system (i.e., an artificial but useful one) applying subgenera and subspecies. However, particularly the last few decades also revealed increasing discrepancies between taxonomy and nomenclature: By applying some articles of the International Code of Zoological Nomenclature (1999; e.g. article 43.- Principle of coordination, regarding the genus-group) workers have mixed up genera and subgenera, for example, and dealt with them at the same level or treated them as separate genera, thereby destroying a well justified taxonomy. Certainly, this is not generally wrong as long as the reasons to do so are given—which is often not the case—otherwise the differentiation of these taxa and included problems are nothing but elevated to a higher level (genus or tribus; I thank E. K. Kempf, Cologne, pers. comm. 2006, for pointing this out). The best way to avoid such problems is to avoid the erection of subspecies and especially new subgenera.

Be that as it may, we should not forget that taxonomy is a tool, and we do not need to—and should not—always stick to established taxonomic dogmata. There are cases in which subgenera and/or species groups prove to be an excellent tool, and such a case is the biostratigraphic application of Mesozoic nonmarine ostracods, particularly as to representatives of *Cypridea* Bosquet (see right below and refer to Chapters 6.1 to 6.3 for substantiation).

Subgenera are, by definition, taxa below genus and above species rank. In paleontology these are morphogroups comprising of taxa considered to belong to different(!) species but sharing several characters that distinguish them from other groups within the same genus. They are believed to be related and having a common ancestor. Using subgenera is practical for the following reasons: Their usage allows a better handling of a high number of representatives of the particular genus they belong to and their potential application, as is the case for *Cypridea*, and can accelerate the process of identification by narrowing down the number of species coming into consideration. Furthermore, the

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Fig. 11. (see preceding page): Stratigraphic distribution of representatives of *Cypridea* in the Lakota Formation, Black Hills area, South Dakota. Taxa highlighted in grey also, or solely (black square), occurring in the Yellow Cat Member of the Cedar Mountain Formation (sample position indicated with grey star), San Rafael Swell, Utah.

Overview—no true lithostratigraphic or chronostratigraphic correlation intended here! The stratigraphic succession of samples from different localities is only an approximation and may be subject to change when all faunal elements have been analyzed. A detailed correlation and stratigraphy is beyond the scope of this paper and will be dealt with elsewhere. For elucidation of the newer and older lithostratigraphic terminology (see references in table head) refer to Zaleha (2006). There are still conflicting discussions regarding parts of the lithostratigraphy, particularly the position of the Minnewaste Limestone Member (ML*), whether it be the top of L1 informal interval of the base of L2. The dated term "Neocomian", still widely-used but not well defined in the North American literature, is considered avoidable and confusing.

Signs and symbols: Black circle: taxon present; black circle with question mark: taxon questionable in this sample (mostly resulting from bad preservation); black circle with exclamation point: ample occurrence (>1000 specimens) of the particular taxon; black square: taxon solely occurring in the Cedar Mountain Formation. Grey star: position of ostracod samples in the Cedar Mountain Formation (sample labels: PS)

Section labels: FRCA: Fall River Canyon Road (Fig. 2, loc. 3; HSDC: Horse Sanctuary/Devil's Canyon (Fig. 2, loc. 2); BC (BCE, BCB): Buck Canyon (Fig. 2, loc. 1); ARCR: Angell Ranch/Cheyenne River (Fig. 2, loc. 5); LEC: Little Elk Creek (Fig. 2, loc. 6; SBCR: Stage Barn Canyon Road (Fig. 2, loc. 8); EBF: East of road to Belle Fourche (Fig. 2, loc. 7), REKO: Boxelder Creek east of Blackhawk (Fig. 2, loc. 9, sample taken by Reko Hargrave 2004). PS: Cedar Mountain Formation east-northeast of the Ringtail Mine, Utah (Fig. 2, loc. 10).

application of subgenus names also allows a conservation and better traceability of the historical development of the taxonomy of a certain genus. Finally, subgenera (should) depict phylogenetic lineages.

Whether definition and application of subgenus names in paleontology makes sense, has been under controversial discussion for a long time. Nevertheless, the view held up here is that it is possible and makes sense (for the reasons given above). Furthermore, the abandonment of the usage of subgenera in representatives of *Cypridea* Bosquet, for example, would lead to the consequence having to give *Cypridea* a higher hierarchic rank. This would just but raise the problems to a higher level and destroy a well justifiable (and established) and applicable taxonomy and, therefore, such approach is dispensable and should be rejected.

In contrast, species groups are no nominal taxa but morphogroups believed to belong to one genus (and subgenus if applicable)—quasi "superspecies"—that represent a developing fossil "population" in more or less limited time and space or, alternatively, a phylogenetic lineage. Species groups should be possible to ascribe to a common principal form (ancestor) or include at least such species that appear to be closely related (Wolburg 1959, p. 238).
When a species group is defined and applied, this usually is an interpretation of representatives of a taxon that are:

1) assumed to belong to one genus (and subgenus, if applicable) by sharing its diagnostic characters,
2) differentiated based on characters considered not taxonomically significant at genus or subgenus level while at the same time interpreted as being too variable for a population of one species at a certain time and locality, and
3) considered closely related by depicting a species in development over time and space (ideally a phylogenetic lineage), thus representing a developing fossil population in more or less limited time and geographic area, and including a relatively high degree of morphologic variation that can be transitional over time and space.

Since the taxonomic significance of specific(!) morphologic characters may be highly debatable, the definition of species groups provides a practical tool for application without having to clarify the taxonomic significance of all characters, allowing considerable variation of certain characters (e.g. outline, single ornamentation elements) and including (even not clearly identified) ontogenetic stages and dimorphs. As pointed out by Wolburg (1959, p. 238) and as based on and supported by the interpretation of certain carapace characters herein (mainly => *local ornamentation* and lateral outline), an application of species-groups also has the advantage of giving a better image of the natural hierarchy of the to date existing, quite non-equivalent *Cypridea*-species (i.e. based on characters and/or combinations of characters of different taxonomic significance and value). This is practical for two reasons: a) an application is possible now, and b) the "real" biologic hierarchy of the taxa as well as their phylogenetic relationships can be better examined and assessed without the distracting taxonomic details of a "wrong" taxonomy.

Therefore, working with species groups can be advantageous—especially when applying representatives of the Cypridoidea (i.e., such forms with mixed reproduction, see also Chapter 6.1 for details) to biostratigraphy—if taxonomy at species level is difficult due to high variability and particularly if no better option is available, that is, the application of species groups produces better results than any other method. This is the case in the application of *Cypridea* to many Upper Jurassic to Lower Cretaceous nonmarine deposits in the world. By exclusion of carapace characters of high variability, doubtful taxonomic significance (at the particular taxonomic level but particularly at species level) or arguable stratigraphic range, the effects of uncertainties in taxonomy are reduced and supraregional correlations become more easily possible. That particularly applies to cases where areas with different paleoenvironment (e.g., different types of water bodies, salinities, supraregional and regional climates) are compared. It has to be admitted though that *Cypridea* Bosquet 1852, as it is defined at present, is a genus to which morphogroups can be easily applied, because some of its diagnostic characters or their development are unique amongst podocopid ostracods, and the significance of these characters at genus level is widely accepted. Thus, the genus is easy to identify and characters at (and below) genus level are more or less easy to distinguish.

Well defined morphogroups also have the advantage that they are easy to identify and applicable (e.g. in biostratigraphy) by non-specialists after short training. Particular attention, however, should be paid to their accurate definition (as accurate and conscientious as possible) as well as their clear indication and discussion! This has to be done by specialists.

Consequently, no "new" subgenera are erected herein, except for the lowering of *Longispinella* Sohn 1979 to a subgenus of *Cypridea* Bosquet 1852. This is done herein and considered practical for the following reasons: Thereby, the consideration of all its representatives as representative of *Cypridea* is indicated, while retaining the name has the effect to make it easier for other workers to follow descriptions and mentionings of such representatives through the literature. Indicating *Longispinella* as a subgenus of *Cypridea* Bosquet also defines it as a morphogroup with specific characters that improves its (actual and potential) biostratigraphic usability. In contrast, the subgenus *Cypridea (Ulwellia)* (Anderson 1939) is rejected here (see below), since an => *inverse valve size (relation)* is not considered taxonomically significant anymore—it can occur in many different and not closely related representatives of *Cypridea*.

In summary, the taxonomic approach followed herein is geared to the targeted biostratigraphic application without loosing track of achieving an as realistic and comprehensible taxonomy and systematics as possible. The approach of pooling many (sub-)taxa of *Cypridea*, including geographically separated forms, is also consitent with new insights in the (partially enourmous) morphologic and genetic variability within recent cypridoidean species or populations in the context with specific dispersal and reproductive mechanisms (refer to Chapter 6.1 for details).

5.4.2. Key to the described species in *Cypridea*

1a	Carapace surface with area-wide ornamentation (punctation)	2
1b	Carapace surface smooth	*Cypridea (P.) setina*
2a	Carapace devoid of dorsolateral sulcus (nonsulcate)	3
2b	Carapace with dorsolateral sulcus	*Cypridea*? *minuta*
3a	Moderately to strongly inequivalve	4
3b	Slightly inequivalve to subequivalve	5
4a	Dorsal ridge and small alveolar furrow	*Cypridea* ex gr. *alta*
4b	Without dorsal ridge, large and wide alveolar furrow	*Cypridea (L.) longispina*
5a	Rostrum indistinct, alveolar notch and furrow almost absent	*Cypridea obesa*
5b	Rostrum small but distinct, alveolar notch clear	6
6a	Strongly developed rectangular cyathus-like protrusion	*Cypridea nitidula*
6b	"True" cyathus	7
7a	Carapace surface moderately puctate	8
7b	Carapace surface strongly tuberculate and punctate	*Cypridea* ex gr. *tuberculata*
8a	Distinct alveolar notch, rostrum clearly overreaching ventral margins	*Cypridea (P.) laeli*
8b	Alveolar notch weak, rostrum almost	*Cypridea (P.) piedmonti*

5.4.3. Descriptions of subgenera, species groups and species

Cypridea nitidula **Peck 1941 emend.**

(Pl. 1, Figs. 1-8)

*	1941	*Cypridea nitidula* sp. nov. – Peck, p. 301, pl. 43, figs. 1-5
	1951	*Cypridea nitidula* Peck – Peck, p. 312, pl. 49, fig. 5
?	1959	*Cypridea nitidula* Peck – Wicher, p. 45, pl. 9, fig. 4a, b
	1961	*Cypridea nitidula* Peck – Craig, p. 65, pl. 3, figs. 11-12 [unpubl.]
	1962	*Cypridea nitidula* Peck – Peck and Craig, pl. 2, fig. 2
	1999	*Cypridea nitidula* Peck – Swain, p. 121, pl. 13, figs. 9-11 [refigured from Peck 1941]

Material: Six specimens from the collection of R. E. Peck, University of Missouri, Columbia, Missouri, U.S.A., in part badly preserved.

Dimensions (in mm): Overall length: 0.90-1.10
Specimens from the Peck collection:
L: 0.99-1.10 H: 0.58-0.67 W: n/a

As given in the literature (various references):
L: 0.90-1.00 H: 0.57-0.72 W: 0.38-0.51

Type locality and horizon: Not exactly given by Peck (1941). Draney Limestone(Sub-?)Formation at Tincup Creek Canyon, Freemont quadrangle, Idaho-Wyoming.

Holotype: U.M. 0-975-3, possibly lost. As stated before, the whereabouts of Peck's ostracod type material is unknown.

Diagnosis (emended): Medium sized (up to >1mm), punctate and slender *Cypridea* with equicurvate anterior margin, distinct but short and pointed rostrum, strong rectangular cyathus-like protrusion in both valves, dorsal and hinge margins considerably (15-20°) inclined to baseline towards posterior end. Alveolar furrow narrow, reaching up to 1/3 of height. Prominent anterior cardinal angle, posterior cardinal angle strongly rounded and inconspicuous. Weak ventral ridge, ventral margin and outline nearly congruent.

Remarks: Peck (1941, p. 301) does not indicate and separate the diagnosis and the (short) description. However, Craig (1961, p. 65) gives a diagnosis in his Master's thesis but it unfortunately remained unpublished. Therefore, an emended diagnosis is proposed herein.

Description: Carapace Shape: Medium sized. Lateral outline suboblong with trend to a more triangular shape. Maximum length below mid-height, either at base line for the case that the cyathus is well developed and not broken, or at 1/3 of height by excluding the cyathus. Maximum height at anterior cardinal angle according to 1/3 of length, maximum width at about 3/5 of length. LV>RV, slightly overreaching and overlapping the latter along entire margin in lateral view, except for the hinge margin. Overreach somewhat stronger at ventral margin due to weak ventral ridge in LV. Overlap moderate at anterior and posterior margins, somewhat stronger at ventral margin due to convex tongue-like run of LV's selvage, weaker along hinge margin.

Anterior margin broad and equicurvate with moderately long straight dorsal part. Rostrum small and narrow, distinctly pointed towards apex and bent backwards with 60-70°, close- fitting, somewhat overreaching ventral margin and outline. Alveolus weakly developed, alveolar notch very weak to almost absent, alveolar furrow oblong, narrow and shallow, reaching up to about 1/3 of carapace height. Posterior margin of both valves narrow and about equicurvate to slightly infracurvate meeting the ventral margin almost at right angle due to bearing a strongly developed => *cyathus-like protrusion* with rectangular to pointed outline, its apex sometimes overreaching the posterior margins and its sides being slightly concave. Cyathus-like protrusion somewhat smaller in RV and being overlapped by its counterpart in the LV. Dorsal margin straight to slightly convex, considerably (between 15° to 20°) inclined to baseline of carapace towards posterior end, hinge margin straight. Anterior cardinal angle distinct, obtuse-angled with about 135-140°, somewhat protruding in LV. Posterior cardinal angle strongly rounded and indistinct, about 125°. Ventral margin straight to slightly concave, parallel to base line and meeting the posterior margin almost at right angle (cyathus). Ventral outline straight.

Weakly developed local lateral flattening/very weak depression of carapace at centrodorsal to anterocentral area, corresponding to the assumed position of the central muscle scar field.

Dorsal view elongated-ovoid. Hinge margin moderately indented, i.e. moderate dorsal furrow with left flank broader and less inclined than right one. Along hinge margin, the smaller RV slightly overlaps the LV. At both cardinal angles, the overlap of the LV is somewhat stronger than elsewhere and convex. Ventral view showing flattening and very weak ventral ridge in LV. Overlap along venter gently convex.

Ornamentation:

1. Area-wide ornamentation elements: Whole carapace regularly and distinctly punctated, including rostrum, alveolus and dorsal furrow. Diameter of puncta variable, larger (about 15μm) in centrolateral areas of the valves, and smaller (6-10μm) towards marginal areas, close to the margins being partially arranged in rows running parallel to them. Several, more or less irregularly distributed, normal pores of 1-2μm diameter, usually in between the puncta. Some normal pores swollen with up to 3μm diameter, having small tuberculi (15-20μm diameter) developed around them, usually occurring close and in rows parallel to anterior and posterior margins.

2. Local ornamentation elements: Usually weak or almost not present, characterized by few small tuberculi (15-20μm diameter) located close to anterior and posterior margins and arranged in rows parallel to them. Rarely with paired massive posterocentral spine of around 70-100μm diameter (Pl. 1, Fig. 5.).

Internal characters: Described as apparent from Peck 1941, pl. 43, fig. 3 (drawing, specimen not in collection, probably lost): Hinge merodont and of lophodont type. A straight ridge with widened grooves anteriorly and posteriorly in the LV fits. Inner lamella moderately broad with highest width anteroventral (widening of inner lamella) and posteroventrally (cyathus area), thereabouts the inner margin being much less curved. Inner lamella anteriorly and posteriorly reaching up to and tapering off right below the terminal hinge elements.

Muscle scar pattern: Neither observed nor documented in the literature.

Morphologic variation: Minor. Lateral outline relatively stable, sometimes the cyathus-like protrusion not very prominent (bent inwards—diagenetically, or broken). Moderate variation in ornamentation (all probably ecophenotypic or ontogentic): presence, number and intensity in development of antero- and posterolateral small tuberculi, as well as absence or presence of the paired posterocentral major tuberculum/node like tuberculum.

Ontogenetic variation: Unknown thus far.

Dimorphism: Not observed.

Discussion: Remarks: Although none of the authors samples includes this species, it has been included based on the material found in the collection of R. E. Peck at the University of Missouri because it is a representative of considerable potential concerning the biostratigraphic application (se below), particularly due to the fact that it is easy to identify by means of its characteristic cyathus-like protrusion.

Discussion of synonymy and relations: Wicher (1959) listed *Cypridea nitidula* from the Recôncavo Bahiano of Brazil. He, however, gave no description and only two photographs of poor quality (op. cit., pl. 9, figs. 4a, b) and from these, no accurate statement is possible. The original material is needed. The statement of Wicher (op. cit.) that the Brazilian specimens are rather small (0.97mm) in comparison with the North American ones (0.99-1.11mm) is not true.

Cypridea nitidula Peck shows striking similarities to the following species in lateral outline, presence and development of the *cyathus-like protrusion*, the development of the alveolar furrow, the surface characters, the common presence of a central to posterocentral pair of large spines, as well as shape and alignment of the rostrum:

a) *Cypridea aemulans* Anderson 1985 nom. nov. pro *C. acuta* Anderson 1971 (preoccupied by *C. acuta* Wicher 1959), inverse species (RV>LV), Corfe (No. 26) to Nutfield (No. 44) faunicycles of Anderson 1985
b) *Cypridea asseri* Anderson 1967, inverse (RV>LV), Fairlight (No. 53) to Hawkhurst (No. 57) faunicycles of Anderson 1985
c) *Cypridea bispinosa* Jones 1878 (including *C. b. bispinosa* Anderson 1967, *C. b. birini* Jones 1878, *C. b. suthrigensis* Anderson 1967), inverse (RV>LV), Kingsclere (No. 51) to Cuckfield (No. 67) faunicycles of Anderson 1985
d) *Cypridea helenae* Anderson 1967, inverse (RV>LV), St. Leonards (No. 52) to Hawkhurst (No. 57) faunicycles of Anderson 1985
e) *Cypridea primaeva* Anderson 1941, Warren (No. 2) to Corfe (No. 26) faunicycles of Anderson 1985
f) *Cypridea paulsgrovensis* (Anderson 1939), inverse (RV>LV), Hastings (No. 41) to Fletching (No. 58) faunicycles of Anderson 1985
g) *Cypridea simplissima* Anderson 1985 nom. nov. pro *C. simplex* Anderson 1971 (preoccupied by *C. simplex* Galeeva 1955), Upper Soft Cockle (No. 10) to Hythe (No. 46) faunicycles of Anderson 1985
h) *Cypridea varians* Anderson 1971, Mountfield (No. 15) to Hastings (No. 41) faunicycles of Anderson 1985
i) *Cypridea wicheri* Wolburg 1959 (including all subspecies as listed by Anderson 1985, p. 33), Bacon (No. 31) to Bexhill (No. 42) faunicycles of Anderson 1985

It is noteworthy that all the European species of this morphotype are distributed in the Purbeck to Hastings groups of the English Purbeck/Wealden (up to the Cuckfield faunicycle No. 67 of Anderson 1985), an thus are of pre-Hauterivian age according to Hoedemaeker and Herngreen (2003). Even more intriguing is the fact that many of the English species have an inverse valve size, but those with 'normal' valve size relation (LV>RV), i.e., *Cypridea primaeva*, *C. simplissima*, *C. varians*, *C. wicheri*—as is also the case in *Cypridea nitidula* Peck 1941—are in trend even older, that is up to Hythe faunicycle No. 46 of Anderson (1985) being (lower) Valanginian following Hoedemaeker and Herngreen (2003). *Cypridea sagena* Anderson 1971, a species with 'normal' valve size relation (LV>RV) as well that occurs in the English Purbeck from the Burwash (No. 14) to Nothe (No. 23) faunicycles of Anderson 1985 (Berriasian after Hoedemaeker and Herngreen 2003), is also considered to belong to this morphogroup but slightly differs in that its rostrum is not as strong bent backwards as in the other representatives.

To narrow the stratigraphic distribution of *Cypridea nitidula* down, it seems helpful to consider the 'normal' and inverse valve size relation (see stratigraphic range below). The 'normal' forms in England seem by trend to be older than the inverse ones, though with a big temporal overlap. However, aside from being considered taxonomically insignificant, the inversion of the valve size is as well considered to occur repeatedly in geologic times and to be possible to evolve in both directions!

There is little doubt that the forms of the *Cypridea nitidula*-like species group are all very similar. The descriptions and figures in Anderson's (1941, 1967, 1971, 1985) publications are partially insufficient and well demonstrate—particularly concerning representatives of *Cypridea*—the necessity of good SEM pictures of all views of the carapace if possible. Many of Anderson's figures only show the partially disadvantageous view on the larger valve only, which makes it impossible to see the character of the cyathus ('true' cyathus of cyathus-like protrusion), and the degree of size differences between the valves, for example, especially when comprehensive descriptions are lacking.

Differential diagnosis: *Cypridea nitidula* differs from the other species described here in its strong and distinct cyathus-like protrusion in combination with a short but distinct rostrum that is strongly bent backwards. *C. nitidula* is easily distinguishable from the somewhat similar *C. obesa* by the distinct rostrum and alveolar furrow.

Paleoecology: As for the genus.

Faunal association: No information avilable from the literature (Peck 1941, 1951, 1959; Peck and Craig 1962; Craig 1961) at all, only tables of occurrences at the same localities are available.

Stratigraphic and geographic distribution (Stratigraphic terms follow the most recent terminology available):

North America:
+ Draney Limestone (Sub-?)Formation at Tincup Creek canyon about 1/2 mile east of the mouth of South Fork of Tincup Creek, Lower Cretaceous, Freemont quadrangle, Idaho-Wyoming (Peck 1941, loc. 5, equivalent to loc. 51P of Peck and Craig 1962).
+ Draney Limestone (Sub-?)Formation and shales, Lower Cretaceous, on the divide east of Draney Ranch in T. 8 S., R. 46 E., Crow Creek Quadrangle, Montana-Wyoming, U.S.A. (Peck 1941, 1951, loc. 9; equivalent to loc. 147P of Peck and Craig 1962)
+ Limestone and shale series, probably Draney Limestone (Sub-?)Formation. Early Cretaceous, along the road in Tincup Creek canyon at the extreme western edge of R. 45 E., T. 5 S., Freedom quadrangle, Idaho-Wyoming, U.S.A. (Peck 1941, 1951, loc. 7)
+ Draney Limestone (Sub-)Formation, Lower Cretaceous, along the Montpelier-Afton Highway in SE 1/4 NE 1/4 sec, 24, T. 29 N., R. 119 W., Lincoln County, Wyoming, U.S.A. (Peck 1941, 1951, loc. 14)
+ Draney Limestone (Sub-?)Formation and lower Bear River Formation, Early Cretaceous, on the north side of Thomas Fork Creek in the N 1/2 sec. 26, T. 28 N., R. 119 W., Cokeville quadrangle, Lincoln County, Wyoming, U.S.A. (Peck 1941, loc. 3a)
+ Draney Limestone (Sub-?)Formation, 0.7 of a mile east of the mouth of South Fork of Tincup Creek canyon, Freedom quadrangle, Idaho-Wyoming (Craig 1961, equivalent to loc. 164-P)

+ Gannett Group, shales in and near the Peterson Formation, Lower Cretaceous, on the south side of the road in Tincup Creek canyon 1.7 miles west of Freedom School, T. 5 S., R. 46 E., Freedom quadrangle, Idaho-Wyoming, U.S.A. (Peck 1941, loc. 4 as referred to in Peck 1951)

Questionable occurrence:

South America:
+ Recôncavo Bahiano, Ilhas Formation and Itaparica Formation, Early Cretaceous, Brazil (Wicher 1959)

Stratigraphic range in North America: As inferred from the English Purbeck/Wealden by comparison to a morphogroup of very similar species (see discussion of synonymy and relations above, and stratigraphic range outside North America right below) the most probable stratigraphic range is uppermost Tithonian to (uppermost) Valanginian.

Stratigraphic range outside North America: Not applicable for this species. As for the morphogroup including the inverse species (maximum range; see discussion of synonymy and relations above): uppermost Tithonian to uppermost Valanginian; excluding the inverse species (minimum range) uppermost Tithonian to (lower) Valanginian.

Cypridea obesa Peck 1951 emend.

(Pl. 1, Figs. 9-15)

* 1951 *Cypridea obesa* sp. nov. – Peck, p. 318, pl. 50, figs. 19-21

1961 *Cypridea obesa* Peck – Craig (unpubl.), p. 55, pl. 3, figs. 8-10

1962 *Cypridea obesa* Peck – Peck and Craig, pl. 2, fig. 5

non 1974 *Cypridea obesa* sp. nov. – Hao et al., p. 42, pl. 14, figs. 3a-c

Material: About 50 carapaces, moderately preserved, sample ARCR CHz1 (Angell Ranch Cheyenne River), Chilson Member of the Lakota Formation right below Minnewaste Limestone Member, Fall River County, South Dakota, U.S.A. (Fig. 2, locality 5).

Dimensions (in mm): Overall length: 0.76-1.10
Own specimens:
L: 0.94-1.08 H: 0.60-0.64 W: 0.48-0.56

As given in the literature (Craig 1961):
L: 0.76-1.10 H: 0.55-0.84 W: 0.60-0.83(?)

Type locality and horizon: Not clearly given by Peck. Samples came from the Cloverly Formation west and southwest of Lander, Wyoming (localities 32 and 33 of Peck 1951), from "shales associated with dense limestone beds above lowest variecolored beds and about fifteen feet below the prominent conglomerate" (Peck 1951, p. 310). Peck (op. cit) also refers to the number 4 of measured section in Peck and Reker (1948, pp. 127, 132).

Holotype: U.M. 0-1205-3, possibly lost, the whereabouts of Peck's ostracod type material is unknown (present author's visit, summer 2005).

Diagnosis (emend.): Highly angular in lateral outline with strongly inclined Dorsal/hinge margin. Weakly developed incospicuous rostrum and alveolar notch, alveolar furrow almost absent. Whole carapace surface covered with reticulation-like punctation. Strongly obese, i.e., width about half or more than half the carapace's length.

Remarks: Peck (1951, p. 318) did not indicate and separate the diagnosis and the (short) description. However, Craig (1961, p. 56) gave a diagnosis in his Master's thesis but it unfortunately remained unpublished. Therefore, an emended diagnosis is proposed herein.

Description: Carapace Shape: Small to medium sized. Carapace subtriangular in lateral view with clear angularities. Maximum length below mid-height, maximum height at anterior cardinal angle at 1/3 of length, maximum width at or slightly anterior of 3/5 of length. LV>RV, slightly overreaching the latter along entire margin, LV with weak ventral ridge. Overlap weak at anterior and posterior margins, very weak at hinge margin, and moderate at ventral margin.

Anterior margin broad and slightly infracurvate with a moderate, nearly straight dorsal part. Rostrum and alveolus weakly developed and inconspicuous but cognizable in both valves. Alveolar notch narrow and weakly incising, alveolar furrow almost not developed (only faint depressions visible in ventral view). Rostrum blunt, bent backwards (circa 55°), and barely overreaching ventral margin, but not reaching ventral outline as defined by LV's ventral ridge. Alveolus barely cognizable in both valves, alveolar notch very weak and alveolar furrow very short and shallow to about undeveloped in both valves.

Posterior margin distinctly narrower than anterior one, infracurvate in general trend but with long nearly straight dorsal part steeply dipping (around 70°) towards posterior end. Ventral part of posterior margin strongly curved. Cyathus narrowly crescent with well rounded outer margin, cyathus angle about 105°, with slight trend to => *cyathus-like protrusion*. Dorsal margin considerably sloping (around 20°) towards posterior end and very weakly convex in posterior part. Hinge margin straight with total length about half carapace length. Anterior cardinal angle rounded but well defined, obtuse angled with about 130° angular dimensions; posterior cardinal angle well rounded, poorly defined with around 130°. Ventral margin straight to slightly concave, ventral outline weakly convex defined by weak ventral ridge of the LV.

Dorsal view very characteristic of the species: obese (=corpulent—name!), i.e. compressed-ovoid with high width in adults (L/W-coefficient less than 2, i.e. width about or more than half the carapace's length) and slightly pointed towards anterior and posterior end but the latter are well rounded. Hinge margin moderately incising forming a ralatively narrow dorsal furrow. LV with weak ventral ridge as well as moderately and slightly convex overlapping the RV in ventral view.

Ornamentation:

1. Area-wide ornamentation elements/surface characters: Punctation with strong trend to reticulation; with pentangular to slightly elongated-elliptic, shallow fossae of about 20µm diameter and muri of about 5µm width as well as diffuse delimitation. Some variation and stronger gradation towards reticulation in less well preserved specimens. Towards all margins, the fossae become smaller, less well developed, and are somewhat more elongated parallel to the particular margin.

2. Local ornamentation elements: None (sensu Sames herein) do occur.

Internal characters: Unknown.

Muscle scar pattern: Unknown.

Morphologic variation: Minor variation regarding the definition/rounding of the posterior cardinal angle connected with a somewhat narrower posterior margin (?sexual dimorphism?, see below).

There seems to be some variation in the magnitude of the carapace's obesity (as already stated by Craig 1961), as well as some variation in the position of the maximum width. The former is most probably an ontogenetic feature, the latter doubtful for the following reasons: Drawings of dorsal and ventral views of the holotype (Peck 1951, pl. 50, figs. 19, 21) show a width of more than half the length but, as stated before, unfortunately the holotype is not in the collection. The photographs of other specimens shown in Craig (1961, pl. 88, figs. 8, 10, U.M. 0-1226-2) show the same while own specimens (Pl. 1, figs. 13, 14) have the maximum width always behind mid-length, at 3/5 or slightly anterior of total length. Since Peck's (1951) holotype as well as much figured material is not in the collection, it cannot be verified how correct the drawings are and if just the holotype shows this feature. As for Craig's (1961) specimens, one ventral view (pl. 3, fig. 8) seems to have the maximum width behind mid-length but this is not clearly apparent, and the other ventral view (pl. 3, fig. 10) is strongly dipped leftwards and appears to be as long as wide.

Therefore, based on numerous specimens in the author's own material the characteristic position of the maximum width is distinctly posterior of mid-length, at or slightly anterior of 3/5 of carapace length.

Ontogenetic variation: Own material (very few specimens, presumably not younger than A-2) specimens shows lesser obesity (Pl. 1, Fig. 14), with L/W-coefficient of or greater than 2, i.e. the width is half or less than half the carapace's length. Also, the surface characters are stronger trending towards reticulation.

Dimorphism: Not clearly identified yet (too few specimens). Some specimens (Pl. 1, Fig. 14) appear a bit more elongate and acute posteriorly due to a somewhat better defined posterior cardinal angle connected with a slightly narrower/less higher posterior margin. These might be male dimorphs or juveniles (A-1 or A-2?). The more obese specimen figured in Pl. 1, Fig. 13 might be a female.

Craig (1961, p. 56) already noted a variation in the obesity but was not able to determine "… if this was due to posthumous compression or if this is a valid variation of the species". However, for a better support of this hypothesis more and better preserved material is necessary and should be subject to a thorough morphometric analysis.

Discussion: *Cypridea obesa* Peck is a relatively atypical representative of its genus, a form with a very weakly developed rostrum and alveolus, and a high width that makes up more than half of the total carapace length. Also, it has a slight cyathus-like extension in the smaller right valve also, thus trending towards a => *cyathus-like protrusion*.

The obesity seems not to be as unique as Peck (1951) believed. For example, *Cypridea recta inflata* Wolburg 1959 or the in much different species '*Pseudocypridina*' *sambaensis* Grekoff 1957 (fig. 20, pl. 3, figs. 47-49) also show the same feature. However, affilations of the latter species with *Cypridea (Pseudocypridina)* are doubtful and have to be verified by restudying the original material. To the best of the present author's knowledge, there no other species known or published thus far, that show considerable similarity to *Cypridea obesa* Peck 1959. Many species that seem to similar to it at first glance are not as angular in lateral view, or either have a much stronger developed rostrum and alveolus or these are totally absent.

As for the obesity, the diagnostic nature of this character debatable. Considered female dimorphs of other species of *Cypridea* have about similar length-width ratios, e.g. *Cypridea (Longispinella) longispina* Peck 1941 or *Cypridea (Pseudocypridina) piedmonti* (Roth 1933). Apart from sexual dimorphism—the occurrence of which cannot yet be confirmed for *C. obesa* (see above)—possible vertical compression has to be taken into account Craig (1961, p. 56-57). Diagenetic compression of the carapaces is quite common in nonmarine Early Cretaceous ostracods of the Western Interior and the figures.

The species *Cypridea obesa* of Hao et al. (1974) is no *Cypridea*, but a *Talicypridea* Khand 1977 instead.

Differential diagnosis: *Cypridea obesa* generally differs from other species described herein in its highly angular outline combined with a strongly inclined dorsal/hinge margin, its inconspicuous rostrum and almost absent alveolar notch and furrow as well as the strong obesity. *Cypridea nitidula* is clearly distinguishable from *C. obesa* by its strong rectangular cyathus-like protrusion and the distinct rostrum and alveolar furrow. Representatives of *Cypridea (Pseudocypridina) piedmonti* syn. *C. (P.) laeli* have a distinct rostrum and alveolar notch, the rostrum clearly overreaching the ventral margin. The same applies to *Cypridea (Pseudocypridina) laeli.*

Paleoecology: As for the genus.

Faunal association (see Fig. 11 also): In the present author's sample ARCR CHz1 associated with *Cypridea setina* (Anderson 1939), *Cypridea? minuta* (Peck 1951), some representatives of the Darwinulidae: *Alicenula?* sp. and some Ostracoda indet. Candonidae?

Stratigraphic and geographic distribution (Stratigraphic terms follow the most recent terminology available):

North America:
+ Chilson Member of the Lakota Formation right below Minnewaste Limestone Member, Early Cretaceous, Fall River County, South Dakota, U.S.A. (this work Fig. 2, locality 5)

+ Lakota Formation, Lower Cretaceous, cut on old road on north side of Fall River 3.2 miles east of 1940 city limits of Hot Springs, Fall River County, South Dakota, U.S.A. (Peck and Craig 1962, loc. D286)
+ Cloverly Formation, Lower Cretaceous, approximately 4 miles west of Lander, on the north side of Baldwin Creek, in S1/2 SE 1/2, Sec. 5, T. 33 N., R. 100 W., Fremont County, Wyoming, U.S.A. (loc. 32 of Peck 1951, same as Craig's 1961 loc. 21)
+ Cloverly Formation, Lower Cretaceous, approximately 3 miles southwest of Lander, about halfway between the roads in Squaw Creek and Middle Fork of the Popo Agie River, in sec. 15, T. 33. N., R. 100 W., Mt. Arter SE quadrangle, Wyoming, U.S.A. (Peck 1951, lo. 33 equivalent to Craig 1961, loc. 95P)
+ Cloverly Formation, Lower Cretaceous, north side of Baldwin Creek 4 miles northwest of Lander, Fremont County, in sec. 9, T. 33 N., R. 100 W., Mt. Arter SE quadrangle, Wyoming, U.S.A. (Peck and Craig 1962, loc. 658P; see specimen on Pl. 1, Fig. 10 herein).

Questionable occurrence: Not applicable.

Stratigraphic range in North America: As deduced from the association with *Cypridea (Pseudocypridina) setina* var. *setina* and its stratigraphic distribution in Europe: Early Cretaceous, upper Berriasian to lower Valanginian.

Stratigraphic range outside North America: Not applicable.

Subgenus *Ulwellia* Anderson 1939 emend. and rejected

*	1939	*Ulwellia clavata* sp. nov. – Anderson, p. 300, pl. 13, figs. 1, 9a-b
	1940	*Cypridea (Ulwellia)* stat. nov. – Martin, p. 281

Type species: *Ulwellia clavata* Anderson 1939

Original diagnosis: "Valves obovate or ovate-oblong. Anterodorsal margin slightly concave. Posteroventral angle of right valve reflexed. Carapace of medium thickness, evenly convex, widest in middle of in posterior half of shell. Surface smooth, punctate or reticulate, may be ornamented with spines or ridges. Right valve larger than left, overlapping it on all margins especially ventrally. Hinge-line knurled anteriorly and posteriorly. Beak and notch often very strongly marked" (Anderson 1939, p. 300).

Anderson also did remark: "This genus has been created for those species of the Rostrocypridae [literal error, recte Rostrocyprinae, i.e., with subfamily suffix, as newly erected by Anderson in this paper; declared invalid by Martin 1940, see Chapter 5.2.1 herein] in which the right valve is the larger. It is considered that this feature, like shape and hingement, is a character of generic importance, whereas sculpture and ornament are specific characters" (Anderson 1939, p. 300).

Discussion: Any of Anderson's (1939) given characters is here considered of no or rather negligible taxonomic significance, whether on generic or specific level. This applies to the slightly concave dorsal margin, the carapace thickness and mode convexity as well as the position of maximum width as well. The reflexed posteroventral angle of the RV (here the larger one), i.e., the => *cyathus*, is not significant at species level (several representatives of *Cypridea* have this character) or genus level (possession of a cyathus is a diagnostic character of *Cypridea*). Surface characters, such as smoothness, reticulation (defined => *reticulation-like punctation* for representatives of *Cypridea* herein) and => *tuberculation*, and the pattern of the latter two, are of no generic and minor specific significance. The => *inverse* valve size (RV>LV) is not considered taxonomically significant here at all (see glossary). Larger, clearly marked rostra and alveolar notches do as well commonly occur in different representatives of *Cypridea* Bosquet and can be of subgeneric importance. The overall shape and development of the valve overlap is similar in most representatives of *Cypridea*, the variation of which mostly pertains the degree of intensity of overlap in different carapace regions. With respect to the shape of the hinge as given in Anderson's (op. cit.) diagnosis above—as more comprehensible explained by Sylvester-Bradley (1949, p. 132): "At the anterior end the *selvage* is swollen and overhangs the recess (the 'knurling' of Anderson 1939), partly hiding it in lateral view"—is also not significant at species level, and occurs in many representatives of *Cypridea*.

What remains is that the validity of *Cypridea (Ulwellia)* (Anderson 1939) is strongly connected with the interpretation of the taxonomic significance of an => *inverse valve size relation*, which is considered taxonomically insignificant here (see glossary). Although Anderson's (1939) diagnosis included several other morphologic characters as given above, many author's just focused on the inverse (RV>LV) valve size relation and simply assigned inverse representatives of *Cypridea* to this subgenus regardless of the overall morphology and potential relationships to "normal" forms of the same morphology (e.g. Anderson 1967, Christensen 1963, Hou 1958, Li 1984, 1988, Musacchio 1990, 1995 based on his inverse species erected in the 1971 paper; Peck 1951, Sohn 1967, Sylvester-Bradley 1949, Zhang 1985). In addition, the subgenus *Cypridea (Ulwellia)* has also been inconsistently used and applied by many authors (e.g. not used in Musacchio 1971 for several new inverse species, but applied in Musacchio 1990, 1995 for the same species).

Therefore, the validity and the prevalent usage of the subgenus *Ulwellia* is challenged and rejected here. Most of the included species should, therefore, have a morphologic equal counterpart except for the opposite ("normal") valve size relation (LV>RV) and the inverse forms should be considered a variety (mutant?) of the particular species. The remaining species are representatives of *Cypridea* with inverse valve size relation (RV>LV) and should be reassigned accordingly, i.e., without applying this subgenus name (but possibly another valid one) and for most of them the "normal" counterparts can be looked for.

Consequently, the subgenus *Cypridea (Ulwellia)* (Anderson 1939) is rejected here. An application of the name *Ulwellia* should be avoided because it causes confusion in that it implies relationships between its "representatives" that do not exit. The genetic processes controlling the inverse valve size relation in ostracods (inversity of whole body symmetry?) remain to be investigated and discussed.

Cypridea? minuta **(Peck 1951) emend.**

(Pl. 2, Figs. 1-15)

* 1951 *Ulwellia minuta* sp. nov. – Peck, p. 320, pl. 49, figs. 9-11

1961 *Ulwellia minuta* Peck – Craig, p. 77, pl. 3, figs. 1-2 [unpublished]

1962 *Ulwellia minuta* – Peck and Craig, pl. 1, fig. 7

1999 *Cypridea (Ulwellia) minuta* – Swain, p. 121, pl. 34, figs. 31-33

Material: Few carapaces, badly preserved, sample ARCR CHz1 (Angell Ranch Cheyenne River), Chilson Member of the Lakota formation right below Minnewaste Limestone Member Fall River County, South Dakota, U.S.A. (Fig. 2, locality 5); few specimens from the Peck collection, badly preserved.

Dimensions (in mm): Overall length: 0.71-0.88
Own specimens:
L: 0.71-0.84 H: 0.43-0.50 W: 0.35-0.40

As given in the literature (Craig 1961; Peck 1951 only gives length around 0.8mm):
L: 0.71-0.88 H: 0.50-0.51 W: 0.40-0.50

Type locality and horizon: Not clearly given by Peck (1951). Samples came from the Cloverly Formation west and southwest of Lander, Wyoming (localities 32 and 33 of Peck 1951), from "shales associated with dense limestone beds above lowest varicolored beds and about fifteen feet below the prominent conglomerate" (Peck 1951, p. 310). Peck (op. cit) also refers to the number 4 of measured section in Peck and Reker (1948, pp. 127, 132).

Holotype: U.M. 0-1202-2, possibly lost, the whereabouts of Peck's ostracod type material is unknown (present author's visit, summer 2005).

Diagnosis (emend.): Inverse (RV>LV) form, suboblong in lateral outline, with concave indention of the dorsal outline at position of mid-length and dorsolateral sulcus at the same position. Anterior cardinal angle well defined, weak inclination (max. 10°) of the hinge and dorsal margins. Cyathus absent or very inconspicuous. Rostrum and alveolus well developed, alveolar furrow ventrally delimited by an alveolar ridge.

Remarks: Peck (1951, p. 320) did not indicate and separate the diagnosis and the (short) description and assigned the species to *Ulwellia* Anderson 1939. However, Craig (1961, p. 65) gave a diagnosis in his Master's thesis which unfortunately remained unpublished. Therefore, an emended diagnosis is proposed herein.

Diagnosis as given by Craig (1961, p. 77): "Small, subquadrate form with distinct notch and beak, well defined anterocardinal angle, and with the dorsal margin indented at about mid-length."

Description: Carapace Shape: Small sized (below 1mm). Suboblong in lateral outline. Maximum length at about slightly below mid-height, maximum height at about 1/5 of length (at anterior cardinal angle), maximum width considerably behind mid-length, between 3/5 and 4/5 of length. RV>LV, slightly inequivalve, RV slightly overreaching LV along entire margin except for the ventral margin, where the overreach is moderate, intensified by a ventral ridge. Valve overlap moderate along anterior and posterior margins, somewhat stronger ventrally (=> *ventral overlap*), weak along hinge line.

Anterior margin broad and slightly infracurvate with short straight dorsal part. Anteroventrally prolongating into a well-developed rostrum strongly bending backwards with 55-60°, that is not attached to the ventral margin and overreaches the ventral margin and can slightly overreach the ventral outline. Rostrum moderately broad with rounded point. Rostrum of smaller LV somewhat weaker developed. Alveolus well developed, alveolar notch distinct and moderately broad. Alveolar furrow elongate and slightly crescent and moderately incising, somewhat stronger developed in smaller left valve, and reaching almost up to mid-height. Alveolar furrow ventrally delimited by a weak alveolar ridge.

Posterior margin equicurvate and well-rounded, slightly narrower than anterior margin and having a short straight dorsal part. Occurrence and development of cyathus somewhat unclear due to bad preservation (posteroventral region mostly damaged) and insufficient figures and descriptions in the literature (see discussion below). However, three specimens from Peck's collection (Pl. 2, Figs. 10, 13, 14, 15; see discussion below also) clearly point to an absent cyathus.

Dorsal margin straight, dorsal outline slightly but distinctly concave (indention) at about mid-length. Hinge margin weakly inclined towards posterior end with circa 10°. Anterior cardinal angle well defined and only weakly rounded, circa 140°, posterior cardinal angle less distinct and strongly rounded, its angular dimension circa 140-150°.

Ventral margin straight to slightly concave, being coincident with the ventral outline in the smaller LV. Ventral outline in the larger RV considerably divergent from the ventral margin due to the RV's overreaching moderate ventral ridge.

Dorsal view elongate-ovate, laterally flattened towards both ends, the anterior end being somewhat more acute. With lateral constriction of variable degree at mid-length or slightly in front of it (caused by the dorsolateral sulci), more distinct in the assumed females (refer to item dimorphism below).

Ventral view showing slight anterolateral constriction caused by the alveolar furrow, as well as the ventral (tongue-like) overlap and the ventral ridge. Punctation less well developed ventrally.

Both valves with broad dorsolateral depression/sulcus at about or slightly anterior of mid-length, reaching down to almost 3/4 of height; the sulcus mostly being clearly delimited anteriorly and posteriorly by an edge.

Ornamentation:

1. Area-wide ornamentation elements/surface characters: Whole carapace surface, including the dorsolateral sulci, covered by moderate to deep roundish to elongate-ovate puncta which are separated

by broad muri, except ventral region where the punctation is weak or almost reduced. Puncta in the area where the central muscle scar field is located internally seem to be considerably deformed (elongated)

Several lateral pore canals (simple pores) of about 2-3µm diameter, more or less evenly distributed over the valve, some of these slightly widened up to 5µm.

2. Local ornamentation elements: No larger spines, tubercles or nodes reported in the literature or visible in the available material. Rows of few minor tubercles (around 10µm in diameter) in the anterolateral region along and close to the anterior margin and including the rostrum.

Internal characters: Unknown.

Muscle scar pattern: Unknown.

Morphologic variation: Minor. Some variation in the distinctness of the indention of the dorsal outline, some specimens almost lacking this character. Degree of development of punctation varying to some extend as well as the slight anterolateral tuberculation (absent or present). Some variation in maximum width and its position. Note: These statements are in part not considered fully reliable because the preservation of the material is bad.

Ontogenetic variation: No data.

Dimorphism: Sexual dimorphism tentatively(!) assigned on the basis of few badly preserved specimens. Supposed female (Pl. 2, Figs. 2, 5, 6, 11, 12) ovate in dorsal view with distinct lateral constriction at about mid-length and position of maximum width at 3/5 of length. Supposed males (Pl. X, Figs. 1, 4, 13, and 14) elongated-ovate with weak lateral constriction at mid-length and position of maximum width behind 3/5 of length.

Discussion: *Cypridea? minuta* (Peck 1951) is thus far only known from the Lower Cretaceous of North America. Its assignment to the Cyprideidae Martin 1940 is unquestionable based on the well-developed rostrum and alveolus. Its assignment to *Cypridea* Bosquet 1852, however, is debatable. *Cypridea? minuta* could either belong to *Cypridea* based on the rostrum, alveolus with well developed alveolar furrow and alveolar ridge—or be probably assigned to *Bisulcocypridea* Sohn 1969 based on the dorsal incision, the dorsolateral sulcus and the potentially absent cyathus, in combination with rostrum and alveolus. As far as apparent from the few badly preserved specimens, the dorsolateral sulcus is not subdivided. Peck and Craig (1962, pl. 1, fig. 7 therein), however, picture (drawing) a specimen with two distinct sulci being separated by a lobe, a specimen without number. Two specimens have been found in Peck's collection at the University of Missouri (SEM figures of these given on Pl. 2, Figs. 13, 14), being labeled as *Ulwellia minuta* and the indication of having been figured in this publication (op. cit.), one of them (Pl. 2, Fig. 13 here). Yet, both of them are badly preserved and none of them shows two sulci as well as all other specimens. Whoever did the drawings for the Peck and Craig (1962) publication, probably mistook the margins of the single sulcus for 2 separate sulci.

A single sulcus could be an ancestral state in the evolution towards *Bisulcocypridea*. *Cypridea? minuta* thereby potentially holds a key position (ancestor?) in the early evolution of *Bisulcocypridea* Sohn 1969 and a *Cypridea-Bisulcocypridea(-Ilyocypris?)*-lineage (refer to discussion of the family Cyprideidae Martin, Chapter 5.2.1 herein) and should be further investigated. Better material is essential to get more details of the carapace morphology.

An interesting thing to note and to investigate further is that *Cypridea? minuta* also possesses a well-developed alveolar ridge, which would also occur amongst representatives of *Bisulcocypridea* following the line of argument given above, and confirm a closer relation between certain *Cypridea*-lineages and *Bisulcocypridea*.

Cypridea? minuta shows some similarities to *Cypridea skeeteri* Peck 1951. Because of the two distinct sulci and absent cyathus, however, the latter is certainly a true representative of *Bisulcocypridea* Sohn 1969.

Differential diagnosis: *Cypridea*? *minuta* differs from the other *Cypridea*-species described here in its slight indention in the dorsal outline, and the dorsolateral sulcus. It is also the only form with inverse valve size relation (RV>LV) described among these.

Paleoecology: As for the genus.

Faunal association (see Fig. 11 also): In the present author's sample ARCR CHz1 associated with *Cypridea setina* (Anderson 1939), *Cypridea obesa* Peck 1951, some representatives of the Darwinulidae: *Alicenula?* sp.

No information about faunal association available from the literature (Peck 1951, Peck and Craig 1962, Craig 1961).

Stratigraphic and geographic distribution (Stratigraphic terms follow the most recent terminology available):

North America:

+ Chilson Member of the Lakota Formation right below Minnewaste Limestone Member, Lower Cretaceous, Fall River County, South Dakota, U.S.A. (this work Fig. 2, locality 5)

+ Minnewaste Limestone Member of the Lakota Formation, Lower Cretaceous, Calico Canyon south of Buffalo Gap [but NE of the town of Buffalo Gap!] in the SE1/4 sec. 24, T. 6 S., R. 6 E., Custer County, South Dakota, U.S.A. (Peck 1951 loc. 28, as equivalent to Peck and Craig 1962 and Craig 1961, loc. 184P [not Fall River County!])
+ Minnewaste Limestone Member of the Lakota Formation, Lower Cretaceous, partings in exposure of Skyline Drive, east of Hot Springs, Fall River County, South Dakota, U.S.A. (Peck 1951, loc. 29 as equivalent to Craig's 1961 loc. 439P as also listed in Peck's locality catalog)

Questionable occurrence:

West Africa:

+ Cocobeach Series, Lower Cretaceous, Gabon [then "Afrique Équatoriale Française – AEF", that is, "French Equatorial Africa"] after Grekoff (1953 and 1960); questionably because the species is only listed, neither figured nor described (correct taxonomy has to be verified on the original material)

Stratigraphic range in North America: As deduced from the co-occurrence with *Cypridea (Pseudocypridina) setina* [var. *setina*] and its stratigraphic distribution in Europe: Early Cretaceous, [upper] Berriasian to [lower] Valanginian.

Stratigraphic range outside North America: Not applicable (yet). A potential occurrence of *Cypridea? minuta* in West Africa as noted by Grekoff (1953, 1960b) remains to be verified.

Subgenus *Longispinella* Sohn 1979 stat. nov., emend.

v* 1979 *Longispinella asymmetrica* gen. nov. sp. nov. – Sohn, p. 18-19, pl. 4, figs. 7-20; pl. 5, figs. 1-7, 13-16

1941 *Cypridea longispina* sp. nov. – Peck, p. 300, pl. 43, figs. 6-9

non 1962 *Cypridea armata* sp. nov. – Krömmelbein, p. 455, pl. 56, fig. 27a, b

non 1965a *Cypridea tucanoensis* sp. nov. – Krömmelbein, p. 180, fig. 1a-c

• 2003 *Cypridea daoudensis* sp. nov. – Andreu et al., p. 206, pl. 3, figs. 5-9

Remarks: Sohn (1979) established *Longispinella* as separate genus and placed it within the Cyprideidae Martin 1940, a view still shared by authors in recent publications (e.g. Horne and Colin 2005). However, in the view of the present author this is not plausible anymore for the reasons given in the discussion below, and accordingly the status of *Longispinella* is changed to subgenus and placed within *Cypridea* s.l. (sensu Sylvester-Bradley 1949) herein.

Type species: *Longispinella asymmetrica* Sohn 1979

Diagnosis (emended): A small-sized (< 1mm) *Cypridea* with subtriangular outline. LV>RV, moderately inequivalve with distinct dorsal overreach of the larger LV. Rostrum pronounced, alveolus well-developed and broad, deep and broad alveolar furrow reaching up to mid-height (in some representatives?) being ventrally delimited by an alveolar ridge. With => *cyathus-like protrusion* ('cyathus' in both valves). Dorsal outline, as defined by larger LV, slightly concave in hinge area. Carapace weakly to strongly punctate except for the anterolateral and posterolateral areas. Local ornamentation elements (tubercles, paired spines) may occur.

Sexual dimorphism presumed to occur, then being distinct: males much more elongate in lateral view and slender in dorsal view; females more compact in lateral view and piriform in dorsal view.

Other representatives: *Cypridea daoudensis* Andreu et al. 2003 (see discussion of synonymy below).

Discussion: This taxon was established by I.G. Sohn for "… those species previously referred to *Cypridea* Bosquet, 1852, that have a robust lateral spine on each valve an that do not have accessory smaller spines" (op. cit., p. 18). Since => *ornamentation*, and particularly => *local ornamentation elements* are considered taxonomically insignificant, and taking into account Sohn's diagnosis of the genus *Longispinella* [Original diagnosis: "Relatively small, to 1 mm in greatest length, subtriangular in lateral outline; surface punctate, with one subcentral large spine, without nodes, small spines or ridges; rostrum and alveolus well-developed, cyathus usually subtriangular. Dimorphic in width of posterior" (Sohn, 1979, p. 18)], which includes occurrence of rostrum, alveolus and cyathus(!), this diagnosis appears insufficient, and it remains strongly curious in the view of the present author that Sohn defined this new genus. Except for the single robust spine on each valve, *Longispinella* Sohn 1979 shows external features (internal features are unknown) all consistent with the genus *Cypridea* Bosquet: a rostrum, a well-developed alveolus with a distinct => *alveolar ridge*, a => *cyathus-like protrusion*, a (weak) ventral ridge and the hinge incisure forming the dorsal furrow. Thus, there is no reason for establishing a new genus but rather many arguments to include this taxon into *Cypridea*, as, based on the available characters, correctly done by Peck (1941) already.

The question, if the definition and retention of a subgenus is justifiable in general is survey-like discussed in Chapter 5.4.1, but approved here. The subgenus *Longispinella* is here considered a well recognizable representative and "ancient" morphotype of *Cypridea*, therefore useful for application, and the retention of this name also facilitates and simplifies a tracing of representatives within the literature.

Presumed sexual dimorphism: Sohn (1979, p. 18) already included the statement " … dimorphic in width of posterior" in his diagnosis of *Longispinella* and presumed sexual dimorphism in his *Longispinella longispina* (Peck 1941). The view of the present author is that *Longispinella longispina* (Peck) of Sohn 1979 represents the female dimorph and *Longispinella asymmetrica* Sohn 1979 the male, as discussed in item "Dimorphism" of the species description of *Cypridea (Longispinella) longispina* below.

Phylogenetic considerations: Representatives of *Cypridea (Longispinella)* belong to a more primordial lineage of *Cypridea*. Its characteristics are: the strong (dorsal) overreach of the larger valve (i.e., considerably => *inequivalve*)—like present in several of such earlier groups of the older Early Cretaceous, e.g., the *Cypridea alta-*, *Cypridea angulata-*, *Cypridea lata-*groups of Wolburg (1959)—in the case of the *C. (Longispinella)*-lineage combined with a broad and deep alveolar furrow and a => *cyathus-like protrusion*. The latter is assumed to be the plesiomorphic state within the evolution of the *Praecypridea-Cypridea-*lineage (see Sames et al. in review). *Cypridea*-lineages showing a considerable inequivalve carapace seem to be restricted to the Late Jurassic to older Early Cretaceous (Berriasian to Valanginian; up to Barremian?) interval (see Chapter 6.3 for discussion).

Discussion of synonymy: I.G. Sohn (1979) also assigned *Cypridea armata* Krömmelbein 1962 and *Cypridea tucanoensis* Krömmelbein 1965(a) from the Lower Cretaceous of Brazil to his *Longispinella*, along with *Cypridea longispina* Peck 1941. However, both taxa are strongly different from *Cypridea (Longispinella)* and considered not to belong in this group for the following reasons: As for *Cypridea armata* Krömmelbein 1962, its lateral outline is very different form representative of *Cypridea (Longispinella)*, it only has a weakly developed rostrum and alveolus, and the paired "thorn" is no robust spine, but a tubercle instead. *Cypridea tucanoensis* Krömmelbein 1965(a) does not even have the "diagnostic" spine but only shows a "weak/flat, node-like protrusion, in an approximately postero/dorso-median position" (see diagnosis given in Krömmelbein 1965a, p. 180). This structure is hollow and neither well-defined nor distinctly pointed, and can thus not be designated as a (robust) spine but is an inflated tubercle instead. Altogether, *C. tucanoensis* rather fits into *Cypridea (Cyamocypris)* Anderson 1939 than into *Cypridea (Longispinella)* because its alveolar furrow is narrower that in the latter, the overreach of the LV is much stronger along the entire margin and the cyathus is much more rounded and wider.

Cypridea daoudensis Andreu et al. 2003 has all diagnostic characters of *Cypridea (Longispinella)* and is, therefore, included into the subgenus. It as well shows strong similarities to the type species of this subgenus—particularly to the slender morphotype formerly designated *Longispinella longispina*, herein considered the male dimorph of *Cypridea (Longispinella) longispina* Peck 1941 (see discussion there for more details). Apart from that *Cypridea daoudensis* has a distinct punctation and shows several smaller tubercles—both characters not considered taxonomically significant—its cyathus-like protrusion in the smaller RV is much stronger developed than that in *C. (L.) longispina* and no perpendicular ridge and sulcus occur in the larger LV as well as no large spines. However, the latter characters are considered significant at species level (the spines might not even be significant at species level).

It is also not totally clear, whether *Cypridea daoudensis* has an alveolar ridge, because Andreu et al. (2003) neither describe such a character nor do the figured specimens explicitly show it. It seems, however, not to be present; if there is an alveolar ridge in *C. daoudensis*, it is very weak. This raises the (open) question about the taxonomic significance of the alveolar ridge—and if it is taxonomic relevant, at what taxonomic level—as well as its function (see glossary for discussion).

Stratigraphic range: Early Cretaceous (Berriasian to Barremian?).

Geographic distribution: North America (U.S.A.); questionably Morocco, North Africa (*Cypridea daoudensis* Andreu et al. 2003).

Paleoecology: Presumed salinity range as for the genus.

Cypridea (Longispinella) longispina Peck 1941 syn. *C. (L.) asymmetrica* (Sohn 1979), emend.

(Pl. 3, Figs. 1-15)

* 1941 *Cypridea longispina* sp. nov. – Peck, p. 300, pl. 43, figs. 6-9

1948 *Cypridea longispina* Peck – Peck and Reker, pl. 3, fig. 22

1951 *Cypridea longispina* Peck – Peck, p. 312, pl. 48, figs. 12-15

1958 *Cypridea longispina?* Peck – Sohn, pl. 1, figs. 1-4

1961 *Cypridea longispina* Peck – Craig, p. 63, figs. 13-15

1962 *Cypridea longispina* Peck – Peck and Craig, pl. 1, figs. 4, 21

v• 1979 *Longispinella asymmetrica* gen. nov. sp. nov. – Sohn, p. 18-19, pl. 4, figs. 7-20; pl. 5, figs. 1-7, 13-16

v 1979 *Longispinella longispina* (Peck, 1941) – Sohn, p. 19-29, pl. 4, figs. 1-6, pl. 5, figs. 8-12 and 17-23, pl. 7, figs. 5-7 [comb. nov.]

? 1986 *Cypridea (Cypridea)* cf. *longispina* Peck – Cao, p. 241, p. 1, figs. 13, 14, 21, 22

? 1994 *Cypridea (Cypridea) longispina* Peck – Ye, p. 292, fig. 9

Material: About seventy carapaces, mostly moderately to well-preserved. Samples: PS1a-70 and PS2a (Yellow Cat Member of the Cedar Mountain Formation, Fig. 2, loc. 10). FRCA, HSDC1, BC5 04, BCB1, BCB2, BC8 04 (Chilson Member or L1 Interval of the Lakota Formation); SBCR LAh3 and LAh3Tp (Fuson? Member or L2/L3? Interval of the Lakota Formation, Fig. 2, locs. 1, 2, 3, 8).

Dimensions (in mm): Overall length: 0.85-0.93
Own specimens:
Presumed females L: 0.85-0.93 H: 0.60-0.64 W: 0.45-0.47
Presumed males L: 0.85-0.91 H: 0.54-0.55 W: no data

As given in the literature (Peck 1941):
species *longispina* L: ~0.90 H: ~0.55 W: ~0.45

Type locality and horizon: Kootenai Formation, Montana. "Shales around a nodular limestone underlain by red clay along the road 1 mile southwest of Griffin, about 14 miles southeast of Great Falls, Montana, in T. 18 N., R. 4 E …" (Peck 1941, p. 288, locality 23).

Holotype: U.M. 0-974-1, whereabouts unknown (lost?).

Diagnosis (emended): LV>RV, strongly inequivalve, lateral outline more or less strongly rounded subtriangular. LV strongly overreaching the RV along dorsal margin. Rostrum well-developed, its point not overreaching the ventral outline, separated from the ventral margin by a broad alveolar notch. Broad and elongate alveolar furrow in LV, reaching up to slightly above mid-height, subtriangular in RV and not reaching mid-height. Alveolar furrow deeply incised and ventrally delimited by a strong alveolar ridge. LV anterocentrally, just behind upper end of alveolar furrow, with short perpendicular shallow sulcus bounded anteriorly by a rounded ridge. With => *cyathus-like protrusion*, triangular and moderately strong developed. Coarsely punctate and mostly with paired and robust posterocentral spine being bent backwards. Strong sexual dimorphism.

Remarks: Peck (1941, p. 300) gave no particular indication of a diagnosis but only a short description of the species: "Carapace of medium size, subovate to subtriangular in lateral outline, highest just anterior to the middle; dorsal and ventral margins rounded, overlap strong. Anterior and posterior margins unequally rounded with a strong beak and notch, the posterior margin greatly contracted, almost pointed; cardinal angles prominent. Hinge deeply indented, with strong posterior slope, forming an angle of 35° or more with the long axis of the carapace. Ventral margin curved, almost parallel to longitudinal axis. Surface of the valves smooth [not true] except for a long blunt spine in the posterior ventral portion."

Description: Carapace Shape: Small sized. General shape of carapace in lateral view rounded subtriangular, tapering to posterior end. Maximum length at about 2/5 of height, maximum height at about 2/5 of length (at anterior cardinal angle), sometimes more backwards depending on the development of the LV's dorsolateral overreach (in the presumed females), but always anterior of mid-length. Maximum width (excluding spines) at about 3/5 of length or slightly anterior in females. LV>RV, distinctly inequivalve, LV moderately overreaching the smaller right valve along entire margin except for the dorsal margin, where the overreach is increased by a dorsal ridge in the LV, usually stronger developed in presumed females. Valve overlap strong, along entire margin, except hinge margin where the overlap is very slight or not existent.

Anterior margin broadly infracurvate, anteroventrally prolongating into a moderately pointed rostrum bending backwards with about 25-30°. Rostrum at the LV barely extending to the ventral margin line and never overreaching the ventral outline. Rostrum of smaller RV less developed, somewhat shorter and less pointed. Alveolus strongly developed with broad alveolar notch. Broad and elongate alveolar furrow in LV, reaching up to slightly above mid-height, subtriangular in RV and not reaching mid-height. Alveolar furrow deeply incised and ventrally delimited by a strong alveolar ridge, its outline in the LV more rectangular-crescent, in RV triangular.

LV (only) with anterocentral short perpendicular shallow sulcus bounded anteriorly by a rounded ridge, the latter being located just behind upper end of alveolar furrow,.

Posterior margin infracurvate, always narrower than anterior margin, well-rounded and relatively broad in females, narrow (half the width of the anterior one) and with long nearly straight dorsal part in male dimorphs. With => *cyathus-like protrusion*, i.e. 'cyathus' developed in both valves but larger in the LV and more or less overreaching its counterpart in the RV, moderately strong and triangular with an outer angle of about 130°; somewhat less conspicuous in males. Position of cyathus-like protrusion clearly in front of posterior margin's maximum extension, at about position of posterior cardinal angle.

Dorsal margin straight to slightly convex, not coincident with dorsal outline in both valves. Dorsal outline convex, particularly strong in the LV of the females due to strong dorsolateral overreach. Hinge margin straight to slightly concave, considerably inclined towards posterior end with about 30-35°, somewhat more in the LV, particularly in females, due to dorsolateral overreach. Cardinal angles more or less prominent, less distinct in LV. Anterior cardinal angle strongly rounded, circa 120°, posterior cardinal angle usually more distinct and less rounded, circa 140-145°.

Ventral margin straight to slightly convex, being coincident with the ventral outline in the smaller RV, but strongly divergent from the latter in the larger LV due to ventral overreach.

Dorsal view of males elongated-ovate tapering towards anterior end, females ovate to piriform tapering towards anterior end. Both dimorphs with a slight lateral constriction anteriorly at position of alveolus. Hinge incision/dorsal furrow moderate, hinge line straight, lateral offset weak, slightly towards RV. Strong convex tongue-like overlap of LV in ventral view, also along the ventral ridge (Pl. 3, Fig. 6).

LV of both dimorphs with short perpendicular shallow sulcus bounded anteriorly by a rounded ridge, located anterocentrally just behind upper end of the alveolar furrow and considerably variable in its degree of expression.

Ornamentation:

1. Area-wide ornamentation elements/surface characters: Surface covered more or less regularly distributed roundish puncta of about 20µm diameter, often with very diffuse limitation, mainly occurring in and around the central region, attenuating towards anterior and posterior regions. No puncta in alveolus region and by trend in anterolateral region absent in general.

Valves with relatively regularly scattered normal pores of 1-2µm diameter and 40-50µm relative distance.

2. Local ornamentation elements: None, except one larger, posterocentral to posterior centroventral robust spine that is bending backwards. It seems as if there is a fine pore canal running through its center. Spines always pairwise occurring but not necessarily in exact opposite relative position. Quite the contrary, the relative position of the two spines can be quite divergent, vertically as well as horizontally. Size, shape and absolute position of these spines can vary considerably (see, for example, Sohn 1979, pl. 4, figs. 11, 13, 17; pl. 5, figs. 2, 4, 5). They can be straight or arcuate (always backwards), long (up to about 100µm) or very small and short, very acute or blunt, slender or sturdy, and even broad-conic, the diameter of their base varying between 20µm and 100µm, usually being about 40-60µm.

Although sometimes being small and hardly recognizable, there seem to be hardly any specimens totally devoid of spines (cf. pl. 5, fig. 19 in Sohn 1979). In most cases, specimens seeming to have no spines at first glance turned out to have either very small spines or these were broken off directly at the valve surface. However, due to their extreme morphologic variability these spines are not considered being of strong significant taxonomic value (see discussion below for mote details)

Internal characters: Not observed and unknown.

Muscle scar pattern: Unknown.

Morphologic variation: Aside from the strong sexual dimorphism (see below), mostly concerning the lateral outline: slightly variation in position of maximum height (between 2/5 of length and slightly before mid-length) and curvature of dorsal outline, being usually convex to straight, but sometimes slightly convex (mainly in those specimens having the position of maximum height/anterior cardinal angle somewhat more posterior). To a lesser extend, the size and degree of development of the anterocentral perpendicular ridge and sulcus in the LV varies. Concerning the pair of posterocentral spines, these may be present—and then vary in their relative position to each other as well as their position on the valve, and in shape and size—or absent.

There is some variation in the development of the surface characters, the reasons for which are not clear but may be ecophenotypic (salinity s.l.?, calcium concentration?). The puncta are more or less distinct, depending on the width and intensity of the muri. This seems to be partially linked to the thickness of the valves (degree of calcification) rather than the preservation. Most of the present author's specimens show, either well- or moderately preserved, show a diffuse limitation and elongation of the puncta in both morphotypes (considered sexual dimorphs here) whereas in the material of Sohn (1979, see pls. 4, 5 therein; and his collection at the USNM) well-delimited and diffuse puncta occur, but in both morphotypes as well.

Ontogenetic variation: No data available.

Dimorphism: Strong sexual dimorphism inferred and described herein: Females more compact in lateral view, somewhat higher maximum height (lower L/H-ratio), mostly with less well-defined (i.e. stronger rounded) posterior cardinal angle and well-rounded, relatively high posterior margin. In addition, the angular dimension of the females' anterior cardinal angle is somewhat lesser (117°-122°) than in males due to the stronger hinge margin inclination (~30°) of the former. Females piriform in dorsal view.

Males more elongate in lateral view, with lesser absolute maximum height (higher L/H-ratio), well-defined (i.e. weakly rounded) posterior cardinal angle, and low, weakly rounded posterior margin. Angular dimension of the anterior cardinal angle somewhat higher (125-130) than in females due to lesser hinge margin inclination (~27°) of the males. Dorsal outline of males elongated elliptic with distinct anterior and somewhat weaker posterior lateral constriction.

Sohn (1979) presumed a sexual dimorphism within his *Longispinella longispina* only, indicated by the different width of the posterior end with his 'males' being narrower and females wider. However, the differences are minor and barely recognizable, and consequently considered to represent normal morphologic variation within females (or, hypothetically, may represent => *precocious sexual dimorphism*). These specimens—having also been inspected personally by the present author—given in Sohn's (1979, p. 19) discussion as male dimorphs of his *Longispinella longispina* are diagenetically deformed (laterally compressed) to a different degree: pl. 4, figs. 3, 5; pl. 5, fig. 9, 19. It is, thus, no surprise that these specimens are more slender in dorsal view than the uncompressed ones considered females by Sohn (1979; pl. 5, figs. 12, 22).

Both, *Longispinella longispina* and *L. asymmetrica* of Sohn (1979) are herein inferred to belong to one species, *Cypridea (Longispinella) longispina* Peck 1941) and to represent sexual dimorphs, with *L. longispinella* (Peck 1941) of Sohn being the female dimorph and *L. asymmetrica* Sohn 1979 being the male dimorph, for the following reasons:

In contrast to Sohn's (1979, p. 19) diagnosis that his *Longispinella longispina*, inter alia, differs from his *L. asymmetrica* in "… having a smaller perpendicular shallow sulcus bounded anteriorly by a rounded ridge behind the alveolus of the left valve, or not having that structure", the combined perpendicular sulcus and ridge in the LV are always present—in the specimens of Sohn in the USNM collection (new SEM pictures taken, Pl. 3, Figs. 10, 11, 12 herein) as well as in the author's own samples. Even badly preserved and strongly diagenetically altered specimens show this character [It remains unknown why Sohn (1979) chose this character as one main reason to distinguish his two taxa]. The other morphologic differences as described above, well match typical characters of sexual dimorphism in cypridoid ostracods (if realized and visible in the carapace) and are strongly connected with the different shape and size of the sexual organs. In addition, both of Sohn's (1979) taxa (almost) always co-occur, in Sohn's samples as well as in the author's own ones, which also is a strong argument against a separation of the two morphotypes into different species. Finally, both morphotypes are of the same overall size and show the same variation, distribution and pattern of puncta..

Altogether, under todays perspective of consideration (even under those of the late 1970's), Sohn's (1979) arguments for establishing two species are very weak and a strong sexual dimorphism is much more probable.

Discussion: Both, *Cypridea (Longispinella) longispina* Peck 1941 and *C. (L.) assymetrica* (Sohn 1979) are combined under the former species because they are considered sexual dimorphs (see above) and considered be representatives of *Cypridea*, subgenus *Longispinella*. Another reason is that they almost always co-occur in Sohn's (1979) as well as in the present author's samples (presumed males are missing sometimes).

Although most likely, from the material available it is not possible to determine with certainty whether the occurrence of the large spines in *Cypridea (Longispinella) longispina* is always bound to a normal pore, because the spines are strongly mineralized (and diagenetically recrystallized?) and the fine central pore is often not observable. In addition, the causation as well as the processes controlling shape, size and position of this single pair of spines are unknown. Especially the spine in the smaller (right) valve seems to be highly variable in its position in the posterocentral to posterolateral area (Fig. 3)

The spines might or might not be characteristic at species level. Resulting from material and data from Sohn (1979), Peck (1941), and the present author's own observations, these spines are definitely no ontogenetic features since they are always present in adults, which would support the hypothesis that they are truly characteristic but not diagnostic at species level (see below). Degree of expression (and occurrence?) in the spines of the described species seems to be influenced, if not totally controlled, by extrinsic (abiotic environmental?) factors, speculatively also stronger developed when required as reaction to selection pressure caused by predators.

With regards to the => *area-wide ornamentation* elements in *C. (L.) longispina*, its diffuse pattern and shape seems to be unique, but is, basically, a punctation (see Pl. 3, Figs. 1, 10, 14 herein, and Sohn 1979, pl. 4, figs. 9, 12, 13, pl. 5, figs. 18, 21, 23, for example). The reason for distortion or the superimposing (Pl. 3, Figs. 9, 13) of the puncta is not clear, though it might derive from strong calcification and thickening of the carapace that leads to swollen "muri" between the puncta.

The closer phylogenetic relationships of *Cypridea (Longispinella) longispina* are not yet well understood and require more research. Particularly the question of the taxonomic significance of the pair of robust lateral => *spines* and the LV's anterolateral perpendicular ridge and sulcus are of interest. Although many representatives of *Cypridea* show a single pair of major lateral spines (in combination with total absence of other spines or tubercles) in their central, centrodorsal or posterocentral areas (cf. Fig. 3; e.g. *Cypridea bispinosa bispinosa* Jones 1878, *Cypridea spinigera* Sowerby 1836, *Cypridea alta wicki* Wolburg 1959, as well as many others), these belong to morphologically strongly different groups. Therefore, the pair of spines is neither a good diagnostic character for *C. (L.) longispina* nor suitable to justify closer affinities between species with this character. The LV's (larger valves?) anterocentral perpendicular ridge and sulcus in *C. (L.) longispina* Peck 1941 syn. *C. (L.) asymmetrica* (Sohn) is unique among representatives of *Cypridea* and the representatives of the Cyprideidae Martin 1940. Its function is unknown and its taxonomic significance cannot yet be assessed.

However, even when disregarding the pair of spines and the LV's perpendicular ridge and sulcus in *C. (P.) longispina* syn. *C. (P.) asymmetrica*, the combination of the strong alveolar ridge, moderately incising alveolar notch, broad and long alveolar furrow, cyathus-like protrusion, punctation and the carapace being moderately inequivalve makes it difficult to find closer relations to other taxa of *Cypridea*. More research is necessary. There are, however, some similarities to *Cypridea dolabrata* (Anderson 1939) and its subspecies (variants) as well as *Cypridea inaequalis* Wolburg 1959 in general shape, lateral outline and the mode and degree of valve size relation, for example.

<u>Discussion of synonymy:</u> *Cypridea (Cypridea)* cf. *longispina* Peck of Cao (1986) is (very) questionably included here, because the specimens of Cao (op. cit.) are badly preserved and strongly deformed, his photographs of bad quality and the details not distinguishable. The case remains to be reappraised on the original material.

Cypridea (Cypridea) cf. *longispina* Peck as figured (drawing) in Ye (1994, fig. 9B; from Cao's 1986 material and publication?) and given to be of Albian age is most probably no representative of *Cypridea (Longispinella) longispina* Peck 1941, because it is of different outline, it is not distinctly inequivalve, lacks the broad alveolar furrow as well as the cyathus-like protrusion, and the position of the spine is central (posterocentral to posterolateral in the latter). The specimen figured by Ye (1994) is much more similar to *Cypridea brevicornis* Peck 1941.

As for Ye's (1994) synopsis and stated before (Chapter 5.2.2), there are problems remaining to be reappraised regarding the taxonomy of nonmarine Cretaceous ostracods of China. Such problems become apparent using the example of Ye (op. cit.), who, on the one hand cites *Cypridea (Cypridea)* cf. *longispina*, while at the same time (op. cit., fig. 1., drawing) refigures *Longispinella longispina* (Peck 1941) (correctly identified as far as evident from the drawing) without comments.

Differential diagnosis: Leaving aside the single robust pair of spines, *Cypridea (Longispinella) longispina* Peck 1941 syn. *C. (L.) asymmetrica* (Sohn 1979) differs from most taxa described here in its broad alveolar furrow and strongly developed alveolar ridge, in being strongly inequivalve with distinct dorsal overreach of the larger LV, and the larger valve's anterocentral to anterolateral perpendicular ridge and sulcus. *Cypridea* ex gr. *alta* is also strongly inequivale but clearly differs in being rather rectangular than subtriangular in lateral outline, in having a weaker rostrum and alveolus, a very distinct and strong dorsal ridge and a small and short alveolar furrow.

Paleoecology: As for the genus.

Faunal association (see Fig. 11 also): In the Lakota Formation: with *Theriosynoecum fittoni* (Mantell 1944) [see Sames in review, this volume], *Cypridea (Pseudocypridina) piedmonti* (Roth 1933), *Cypridea (Pseudocypridina) laeli* Sohn 1979, *Cypridea* ex gr. *tuberculata* cf. *C. tilleyi* Loranger 1951, *Cypridea (Pseudocypridina) setina* (Anderson 1939), representatives of the family Darwinulidae Brady and Norman 1889, and representatives of the Trapezoidellidae Sohn 1979: *Trapezoidella trapezoidalis* (Roth), *Limnocypridea? morrisonensis* (Roth 1933).

In the Cedar Mountain Formation: with *Cypridea* ex. gr. *alta* Wolburg 1959, *Cypridea (Pseudocypridina) setina* (Anderson 1939), *Cypridea* ex. gr. *tuberculata* cf. *C. tilleyi* Loranger 1951, representatives of the family Darwinulidae Brady and Norman 1889 (*Alicenula?* sp.).

Stratigraphic and geographic distribution (Stratigraphic terms follow the most recent terminology available; as for this study, see Fig. 11):

North America:
+ Chilson Member of the Lakota Formation (corresponding to L1 informal interval after Way et al. 1998), Early Cretaceous, southern Black Hills, South Dakota, U.S.A. (Sohn 1979; and this study, Fig. 2, locs. 1, 3)
+ Fuson(?) Member of the Lakota Formation (corresponding to L2 and L3 informal interval after Way et al. 1998)
+ upper part of the Yellow Cat Member of the Cedar Mountain Formation north of Moab east-northeast of the Ringtail Mine, Utah, U.S.A. (this study, Fig. 2, loc. 10)

+ [lower] Lakota Formation on old road on north side of Fall River 3.2 miles east of 1940 city limit of Hot Springs, southern Black Hills, South Dakota, U.S.A. (Peck and Craig 1962, loc. D286 therein)
+ [lower] Lakota Formation, SW1/4 sec. 15, T 8 S., R. 4 E., Flint Hill quadrangle, Fall River County, South Dakota, U.S.A. (Peck 1951, loc. 30; Peck and Craig 1962, loc. D432 therein)

+ Cloverly Formation, north side of Baldwin Creek, approximately 4 miles NW of Lander, sec. 9, T. 33 N., R. 100 W. Mt. Arter SE quadrangle, Wyoming, U.S.A. (Craig 1961, loc. 21 therein)
+ Cloverly Formation, northwest end of Lander anticline, about 2 miles north of Lander, NW 1/4, sec. 12, T. 2 S., R. 2 E., Lander NW quadrangle, Wyoming, U.S.A. (Craig 1961, loc. 22 therein)

+ Cloverly Formation, Lower Cretaceous, approximately 3 miles southwest of Lander, about halfway between the roads in Squaw Creek and Middle Fork of the Popo Agie River, in sec. 15, T. 33. N., R. 100 W., Mt. Arter SE quadrangle, Wyoming, U.S.A. (Peck 1951, loc. 33 as equivalent to Craig's 1961, loc. 95P)
+ Cloverly Formation, north side of Baldwin Creek 4 miles northwest of Lander, Fremont County, in sec. 9, T. 33 N., R. 100 W., Mt. Arter SE quadrangle, Wyoming, U.S.A. (Peck and Craig 1962, loc. 658P therein)
+ Cloverly Formation, southeast flank of Rawlins uplift northeast of Rawlins, MW1/4 sec. 6, T. 21 N., R. 86 W., Rawlins quadrangle, Carbon County, Wyoming, U.S.A. (Peck and Craig 1962, loc. 954P therein)

+ Kootenai Formation, along road 1 mile southwest of Griffin and about 14 miles southeast of Great Falls, in T. 18 N., R. 4 E., Montana, U.S.A. (type locality of the species, Peck 1941, loc. 23 therein and equivalent to Craig 1961, loc. 62aP therein)

Questionable occurrence:

Asia:
+ Lower Cretaceous deposits of China (Ye 1994).

Stratigraphic range in North America: As inferred from the faunal assemblage with *Cypridea (Pseudocypridina) setina*, *C. (P.) piedmonti* and *C. (P.) laeli* (Late?) Berriasian to Hauterivian(?).

Stratigraphic range outside North America: Lower Cretaceous (China).

Subgenus *Pseudocypridina* Roth 1933 emend. Sylvester-Bradley 1949, emend.

v* 1933 *Pseudocypridina piedmonti* gen. et sp. nov. – Roth, pp. 404-405, pl. 48, figs. 7a-h

1935 *Cypridea piedmonti* (Roth) comb. nov. – Harper and Sutton, p. 625, pl. 76, figs. 12-15

1939 *Langtonia setina* sp. nov. – Anderson, p. 305, pl. 12, figs. 7a, b; pl. 13, figs. 12a,b

1949 *Cypridea (Pseudocypridina) setina rectidorsata* subsp. nov. – Sylvester-Bradley, p. 147, fig. 24

1949 *Cypridea (Pseudocypridina) setina setina* (Anderson) – Sylvester-Bradley, p. 146

1961 *Cypridea (Pseudocypridina)* Roth – Swain *in* Moore 1961, p. Q242

1966 *Cypridea (Pseudocypridina)* – Kneuper-Haack, p. 187

? 1971 *Cypridea granulosa* (Sowerby) syn. *Cypridea fasciculata* – Anderson, p. 63

? 1979 *Cypridea (Pseudocypridina) laeli* sp. nov. – Sohn, p. 16, pl. 3, figs. 1-13, 24-25, 32; pl. 7, fig. 1; pl. 8, figs. 26-30

Type-species (monotypy): *Pseudocypridina piedmonti* Roth 1933, Lakota Formation (Lower Cretaceous), South Dakota, U.S.A..

Diagnosis (emended): Relatively large *Cypridea* (up to 2 mm maximum length) with LV>RV overlap. Outline subovoid or suboblong to rounded pentagonal. Rostrum poorly to moderately developed, short and with its apex well-rounded. Alveolus consisting of a weak to almost absent alveolar notch and a short, weakly defined or even absent alveolar furrow. Cyathus crescent and indistinct. Surface finely and weakly punctate, rarely smooth. With or without nodes, with or without small scattered tubercles—the latter being always smaller than the combined diameters of two puncta and usually occurring in antero- or posterodorsal areas, and/or ventral ridges. Never with large spines or tubercles, sometimes with nodes. Anterior cardinal angle at larger LV usually indistinct. Several scattered normal pores of 1-2 μm diameter.

Note: The diagnosis is compiled after Swain 1946, Sylvester-Bradley 1949, and Sohn 1979 as well as emended and supplemented.

Remarks: A comprehensive list of many species that have been included within *Cypridea (Pseudocypridina)* can be found in Sohn (1979, p. 14-15). However, it is not the purpose of this paper to deal with a detailed revision of the subgenus and therefore, only taxa described and/or discussed herein are listed in the synonymy of this subspecies.

Harper and Sutton (1935, see synonymy on p. 625 therein), without any comment however, already considered this subgenus to be congeneric with *Cypridea*. Martin (1940) reduced all this far existing *Cypridea*-genera and subgenera (*Ulwellia* Anderson 1939, *Langtonia* Anderson 1939, *Morinina* Anderson 1939, *Cyamocypris* Anderson 1939) to the synonymy of *Cypridea*, comprising *Pseudocypridina* Roth 1933. In his revision of *Cypridea*, Sylvester-Bradley (1949) differs between the genus *Cypridea* sensu lato, comprising all the mentioned taxa as subgenera, and *Cypridea* sensu stricto=*Cypridea (Cypridea)*, thus being another subgenus of *Cypridea* Bosquet 1852. He (Sylvester-Bradley 1949, p. 127 and 146) quotes *Langtonia* to be a junior synonym of *Pseudocypridina*, considering the absence of punctation as insufficient to distinguish the two and states that Anderson's genotype of *Langtonia* (i.e. *Langtonia setina*) is also referable to *Pseudocypridina*. This view has been adopted by most authors (e.g. Wolburg 1959, Moore 1961, Sohn 1969, 1979, Horne and Colin 2005), including Anderson himself (e.g. Anderson 1962, 1971, 1985, Anderson and Bazley 1971), although not by all (e.g. Neustrueva 1989).

To review whether all the subgenera of *Cypridea* s.l. are considered valid and useful is not the purpose of this paper and will have to be analyzed and discussed in the future. In its current status, the subgenus *Pseudocypridina* Roth represents a morphotype that is relatively easy to identify most probably represents a group of phylogenetically closer related taxa in its current status.

The assignment of *Cypridea (P.) laeli* Sohn 1959 to this subgenus is slightly questionable. While matching most diagnostic characters of *Pseudocypridina*, *Cypridea (P.) laeli* differs in having a relatively broad and deeply incising alveolar notch and a broad rostrum.

Leaving nodes or tubercles aside, *Cypridea granulosa* (Sowerby 1836) syn. *Cypridea fasciculata* (Forbes 1855) according to Anderson (1971) well fits into this subgenus with respect to overall shape, development of rostrum, alveolus, and cyathus as well as the degree of valve inequality, a fact to be considered in future research.

Stratigraphic range: Lower Cretaceous (Berriasian) to Upper Cretaceous.

Geographic distribution: All continents, except Australia and Antarctica.

Paleoecology: Presumend salinity tolerance as for the genus *Cypridea*.

Cypridea (Pseudocypridina) laeli **Sohn 1979 cf.** ***C. (P.) moneta*** **Kneuper-Haack 1966, emend.**

(Plate 6, Figs. 1-15)

v* 1979 *Cypridea (Pseudocypridina) laeli* sp. nov. – Sohn, p. 16, pl. 3, figs. 1-13, 24-25, 32; pl. 7, fig. 1; pl. 8, figs. 26-30

v? 1966 *Cypridea (Pseudocypridina) moneta* sp. nov. – Kneuper-Haack, p. 189, pl. 46, Fig. 21a-c

? 1984 *Cypridea (Pseudocypridina) piedmonti* (Roth) – Li and Zhao, p. 191, pl. 2, figs. 4-6

? 1984 *Cypridea (Pseudocypridina)* cf. *piedmonti* (Roth) – Li and Zhao, p. 191, pl. 2, figs. 1-3

1999 *Cypridea (Pseudocypridina) laeli* Sohn – Swain 1999, p. 120, pl. 12, figs. 41-44 [refigured from Sohn 1979]

? 2009 *Cypridea piedmonti* (Roth) – Schudack and Schudack (2009a) , fig. 9 No. 18 [figured]

? 200X *Cypridea piedmonti* (Roth) – Schudack, in review, pl. 2, figs. 2, 3 [figured]

Material: Few hundred carapaces and many valves, more ore less well preserve, mostly compressed. Samples: LEC 04?, SBCR LAg2, SBCR LAg3*, SBCR DC Strat. Col.?, SBCR LAg6?, SBCR LAh3, SBCR LAh3Tp, EBF 04a, EBF 04a2, EBF 04b?, REKO 04; all believed to be Fuson Member (L2/L3 informal interval after Way et al. 1998) of the Lakota Formation (see Fig. 11 also). Fig. 2, locs. 6, 7, 8, 9.

Dimensions (in mm): Overall length: 1.12-1.23

Own Specimens:
L: 1.12-1.23 H: 0.71-0.75 W: ~0.5

No information in the literature (Sohn 1979).

Type locality and horizon: Lakota Formation at Inyan Kara Creek, Western Black Hills, Crook County, Wyoming NE1/4 sec. 20, and NW1/4 sec. 21, T. 51 N., R. 65 W. (Sohn 1979, p. 16); shale near top of Lakota Formation (Sohn 1979).

Holotype: USNM No. 129 644, figured in Sohn (1979, pl. 3, figs. 10-13) and Sohn (1958, *Pseudocypridina?* n. sp., pl. 1, figs. 9-12).

Diagnosis (emend): Medium sized (>1mm) representative of *Cypridea (Pseudocypridina)* emend. (herein). LV>RV, inequivalve, rounded-subovate outline with convex dorsal margin and strong ventral ridge in the LV. Hinge deeply incised, dorsal furrow very narrow, distinctly slender in dorsal view. Rostrum well-developed and distinctly overreaching the ventral margin in both valves and reaching the ventral outline of the LV as defined by the ventral ridge. Alveolar notch and groove short but distinct. Carapace surface finely punctate, may bear scattered minor tubercles.

Remarks: The emendation became necessary because Sohn (1979) partially integrated optional, taxonomically insignificant characters (=> *local ornamentation elements*, considered ecophenotypic here) in his diagnosis (given below), that is the anterodorsal node and the small tubercles, called spinelets by Sohn (op. cit.).

The original diagnosis of Sohn (1979. p. 16) is as follows: "Subovate, with arched dorsal margin, ventral lateral ridge and dorsoanterior node on larger left valve; right valve with curved irregular ridge subparallel and slightly removed from dorsal margin. Surface finely punctate, with scattered minute spinelets more common on anterior and posterior quarters than on center."

Description: Carapace Shape: Medium sized (>1mm). Carapace strongly rounded-subovate in lateral view, outline defined by the larger LV. Maximum length slightly above mid-height, maximum height at mid-length or slightly in front of it (not defined by anterior cardinal angle), maximum width at 3/5 of length. LV>RV, inequivalve, LV slightly overreaching and overlapping the RV along entire margin. Overreach of LV stronger (moderate to strong) along ventral margin due to ventral ridge.

Anterior margin, almost equicurvate to slightly infracurvate in LV, infracurvate in smaller RV. LV with moderately long straight dorsal part of anterior margin, even longer in the RV, both inclined towards anterior end with about 25-30° in relation to base line. Well-developed => *carinate rostrum* (in both valves Pl. 6, Fig. 4 and 5) with bending angle of 50-55°, its apex being well rounded in the LV, somewhat acute in the RV. Rostrum clearly separated from ventral margin by moderately broad and incising alveolar notch and distinctly overreaching the ventral margin of both valves and reaching (or sometimes slightly overreaching) the ventral outline of the larger LV. Alveolar furrow absent.

Posterior margin almost equicurvate in the LV, slightly infracurvate in the RV, in the LV ventrally passing into a weakly developed, well-rounded, narrow and crescent (true) cyathus, being very obtuse-angled (circa 150°).

Dorsal outline distinctly convex in LV, slightly convex in RV. Dorsal margin straight, dorsal margin and outline strongly divergent due to strong incision of hinge margin, moderately inclined towards posterior end with 10-15° (dorsal outline feigns stronger inclination). Anterior cardinal angle very inconspicuous in LV (often almost invisible owing to deeply incised hinge margin), better defined in RV, about 140-145°. Posterior cardinal angle well-rounded and inconspicuous in both valves, about 140°.

Ventral margin straight, almost coincident with ventral outline in smaller RV. Ventral outline of larger LV being strongly divergent from ventral margin and more or less distinctly convex depending on the development of the ventral ridge. Straight ventral ridge well-developed to strongly developed, often swollen (see discussion for details).

Carapace elongated-elliptic and slender in dorsal view (Pl. 6, Fig. 3), acute towards both ends, slightly more towards anterior end. Narrow but deep dorsal furrow with distinctly bulged flanks. Hinge line straight, at mid-width position with almost no lateral offset.

Ventral view showing strong ventral ridge (e.g. Sohn 1979, pl. 3, figs. 7) with distinct lateral offset towards LV and a moderate ventral tongue-like overlap of the LV.

Ornamentation:

1. Are-wide ornamentation elements: Whole carapace surface—except rostrum and ventral ridge—finely punctate with trend to reticulation-like pattern. Puncta often elongated about parallel to the margins outside the central area, ventrally sometimes forming weak striate rows.

2. Local ornamentation elements: Small, shallow and broad tubercles (minute spinelets of Sohn 1979) around the pores common, merely swollen normal pores and being of about 15-20µm diameter. Somewhat stronger and more acute tubercles in most of Sohn's (1979) specimens. All these tubercles seem to occur preferentially in posterolateral and anterolateral areas of the carapace, but also in the dorsolateral to central areas. No specific general pattern distinguishable.

Specimens of Sohn (1979, see discussion below for details)—including the holotype—having a large (up to about 80µm) anterodorsal node in the LV at position of the anterior cardinal angle (a character considered diagnostic by Sohn, op. cit., see original diagnosis given above). In addition, Sohn's specimens as figure by him (op. cit.; material also personally studied by the present author in Sohn's collection) have swollen, ridge-like protrusions of the margin of the dorsal furrow (running between the dorsal angles) in either both valves or the LV only, often slightly meandering. Ventral ridge also swollen and distorted ("inflated") and sometimes slightly meandering. All latter elements mostly lack any sign of surface characters.

Internal characters: Lophodont hinge with narrow (edged) hinge bar in the larger LV and narrow anterior and posterior teeth in the smaller RV, corresponding groove and sockets developed accordingly. Anterior tooth and socket considerably inclined (~40°) in relation to median hinge element, posterior tooth and weakly to not inclined.

Inner lamella narrow posteriorly with maximum width in cyathus area, and moderately broad anteriorly with typical widening and straight inner margin above rostrum and alveolus. Interrupted selvage conspicuous.

Muscle scar pattern: Pattern as typical in *Cypridea* (see Fig. 6) with the following specifications (Fig. 12): dorsal adductor scar 1 largest and elongate; scar 2 parallel to the former but shorter and oblong; scar 3 smaller again, inclined in relation to the dorsal ones and rounded oblong; scar 4 the smallest of the anterior scars and ovate. Posterior scar 6 in partially or fully covered in the material and, possibly not very exact, posterior scar 5 the smallest and ovate. Tiny roundish scar (dotted) above the anterior frontal scar.

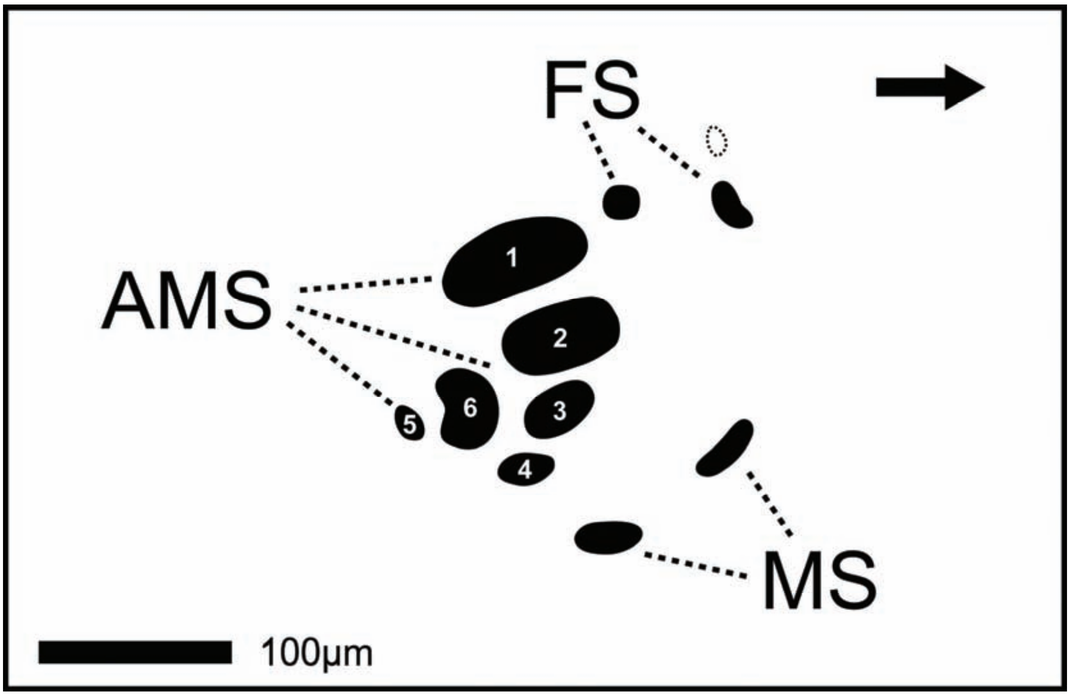

Fig. 12. Muscle scar pattern in *Cypridea (Pseudocypridina) laeli?* Sohn 1979. AMS: Adductor muscle scars, labeling of single scars adopted from Horne and Colin (2005), FS: Frontal scars, MS: Mandibular scars.

Morphologic variation: Variations considered "diagnostic" (i.e., not ecophenotypically induced) mostly concerning slight variations in the lateral outline.

Variations assumed to be of ecophenotypic origin concern the => *local ornamentation elements*: Occurrence or absence of 1) the anterodorsal node in the LV, 2) the tubercles, 3) the ridge-like protrusions of the carapace along the flanks of the dorsal furrow, and 4) the "inflation" or deformation of the ventral ridge (see first paragraph of discussion below for details).

Ontogenetic variation: Few data. The specimen figured on Plate 1, Fig. 10 (A-2?) shows the typical lower posterior margin associated with the somewhat stronger inclined posterior and hinge margins.

Dimorphism: Not identified with high confidence, but presumed to occur. Presumed females (Pl. 6, Figs. 1-3, 6, 13) stronger rounded and higher in lateral view and somewhat wider in dorsal view; presumed males (Pl. 6, Figs. 7, 9) more elongate-elliptic in lateral view and more slender in dorsal view. See also Sohn (1979, presumed females: pl. 3, figs. 1-9, 24-25 – same as in pl. 7, fig.1, pl. 8, figs. 26-30; presumed males: pl. 3, figs. 10-13).

Discussion: Taxonomic remarks: The taxonomy of *Cypridea (Pseudocypridina) laeli* Sohn is problematic, because Sohn (op. cit.) has chosen an ecophenotype with strong morphologic particularities as holotype, i.e., the anterodorsal node, the ridge-like dorsal protrusions ("curved irregular ridge" of Sohn), and the small tubercles, all of phenotypic origin (see glossary under the respective terms for explanation). Leaving the said characters out of consideration, the morphology of Sohn's specimens is that of the specimens described here. This statement is also supported by the fact that Sohn's specimens derive from one locality and horizon only (Sohn 1979). The strong ventrolateral ridge should not be considered diagnostic because there are also specimens of *C. (P.) piedmonti* with stronger developed ventral ridge (Sohn 1978, pl. 6, figs. 5, 10, 12, 21 for example) but otherwise clearly different from *C. (P.) laeli* (see differential diagnosis below). The present author's own samples derive from three localities in the eastern Black Hills area (Lawrence and Meade counties of South Dakota) from many horizons (see Fig. 11 also), all of which, however, seem to derive from the same up to 10 m thick unit mainly comprising of claystones that may represent a large paleolake.

Possible closer phylogenetic relations of *C. (P.) laeli* to the associated and anteceding North American taxa—if there are some, this species might have been newly immigrated—have to be investigated further (continuous stratigraphic data necessary). This species resembles *C. (P.) piedmonti* at first glance only, but differs in detail, particularly in development of rostrum and alveolus (see differential diagnosis below). For that reason, its integration into the subgenus *Pseudocypridina* might also have to be discussed, because representatives of this subgenus typically have a more inconspicuous alveolar notch and a weaker developed rostrum.

As already noted by Sohn (1979), *C. (P.) laeli* resembles the *Cypridea fasciculata*-group, which is herein renamed as *Cypridea granulosa*-group (see below), and the *Cypridea alta*-group of Wolburg (1959). *C. (P.) laeli* Sohn 1979, however, much more resembles the *Cypridea alta*-group with regard to its broad alveolar notch and the well-developed rostrum that is not almost attached to the ventral margin as is the case in the *Cypridea granulosa*-group. The occurrence and distribution pattern of small => *nodes*, => *node-like tubercles* or small => *tubercles* (spinelets of Sohn 1979) as used by previous authors (e.g. Wolburg 1959, Sohn 1979, Schudack 1994) to distinguish between taxa are not considered taxonomically significant herein at all.

Cypridea (Pseudocypridina) laeli Sohn 1979 is definitely not a younger variation of *C. (P.) piedmonti* (Roth 1933) syn. *C. (P.) henrybelli* Sohn 1979, but a separate lineage not very closely related to the latter. Although *C. (P.) laeli* starts to set in later stratigraphically and only occurs in the upper (Fuson Member?), but not necessarily considerable younger part, of the Lakota Formation (see remarks to stratigraphic distribution right below), it does not replace *C. (P.) piedmonti* and distinctly differs in some characters (see above and differential diagnosis below).

Discussion of synonymy: *Cypridea (Pseudocypridina) laeli* Sohn shows strong similarities to *Cypridea (Pseudocypridina) moneta* Kneuper-Haack 1966 including *C. (P.) moneta logronana* Kneuper-Haack 1966. Although Kneuper-Haack (op. cit.) discussed similarities of her taxa to *C. (P.) piedmonti* (Roth)—(*Cypridea (P.) laeli* Sohn 1979 had, of course, not yet been described at that time—all characters described by her, i.e., particularly the broadely-ovate lateral outline with the rounded cardinal angles and very inconspicuous posterior cardinal angle, the well-marked rostrum with the small but distinct alveolar notch. The figures of Kneuper-Haack (1966, drawings, pl. 46, figs. 21a-c, 23) are misleading with respect to the surface ornamentation insofar that smooth specimens are shown. Kneuper-Haack (1966, p. 189) states that the surface of her specimens of *C. (P.) moneta* and *C. (P.) moneta longronana* is "smooth or with weak to stronger dimples [i.e., puncta]". As apparent from Kneuper-Haack's material (now in possession of Ulla Schudack, Freie Universität Berlin, Institut für Geologische Wissenschaften, Fachrichtung Paläontologie), the representatives of this *C. (P.) moneta* are punctated and the feigned smoothness of some specimens is due to preservation/diagenesis.

If *Cypridea (P.) moneta* Kneuper-Haack 1966 prooves to be a junior synonym of *C. (P.) laeli* Sohn 1979, priority would have been given to former, i.e., the oldest available name.

In a footnote to her foreword, Kneuper-Haack (1966, p. 167) has stated that after completion of her work (manuscript completed December 1960, that is long before the actual printing), among others, the comprehensive article of Wolburg (1959) was published, including many new taxonomic data. Kneuper-Haack (1966), therefore, concluded that many of her taxa could be assigned to one of Woulburg's (1959) taxa or groups and that many of her (Kneuper-Haack 1966) new species and subspecies would be mere "subspecies or mutants" (op. cit.; better: varieties) of Wolburg's (1959) taxa. After start of the printing, it was just possible to include some of the new data as footnotes (Kneuper-Haack 1966). *Cypridea (Pseudocypridina) laeli* Sohn 1979 and *C. (P.) moneta* Kneuper-Haack 1966 show strong affinities to the *Cypridea fasciculata*-group (synonym to *C. granulosa* according to Anderson 1971) of Wolburg (1959).

A complete revision of Kneuper-Haack's material is not yet accomplished but Schudack (in review) is dealing with this in her ongoing research.

Cypridea (Pseudocypridina) cf. *piedmonti* of Li and Zhao (1984, pl. 2, figs. 1-3) has a distinct alveolar notch and furrow and more overall similarities to *Cypridea (Pseudocypridina) laeli* Sohn 1979 than to *C. (.P) piedmonti*. The attribution is, however, uncertain since the available figures alone are not significant enough to confirm it. The identification of *Cypridea (Pseudocypridina) piedmonti* of Li and Zhao (1984, pl. 2, figs. 4-6) cannot be confirmed as well due to the more insufficient quality of figures and the few characters visible. From the few characters apparent from the figures, the specimens would have more similarities to *C. P.) laeli* Sohn than *C. (P.) piedmonti* (Roth), if they belong one of these species at all.

Schudack (in review) synonymizes *Cypridea (P.) moneta* Kneuper-Haack 1966 with *Cypridea piedmonti* (Roth) and gives its stratigraphic range as Valanginian to Barremian. As elucidated above, these specimens should better be assigned to *Cypridea (P.) laeli* Sohn 1979 (see above). The same applies to *Cypridea piedmonti* (Roth) of Schudack and Schudack (2009a).

Remarks as for stratigraphic distribution: As for the stratigraphy, *Cypridea (P.) laeli* seems to be restricted to the upper part of the Lakota Formation (Fuson? Member), and therefore is a potential index fossil for the Fuson Member (L2/L3 informal interval after Way et al. 1998). It can be used to correlate the eastern Black Hills sections (Fig. 2, locs. 6 to 9) as well as the Lakota Formation of the Western Black Hills (Sohn 1979, loc. 5).

The exact stratigraphic distribution in the eastern Black Hills (see Fig. 11, samples with question mark) is difficult to determine, because many of the samples (claystone) contain well-preserved but mostly compressed and broken specimens. Thus, it is sometimes difficult to distinguish *C. (P.) laeli* from *C.(P.) piedmonti* under the Light-Microscope, and numerous SEM-photographs from every sample are necessary.

Differential diagnosis: *Cypridea (Pseudocypridina) laeli* Sohn differs from *C. (P.) piedmonti* (Roth) syn. *C. (P.) henrybelli* Sohn in being more ovate in lateral outline and a bit larger in trend. More important is the better developed rostrum in the former, which is broader and longer than in the latter and distinctly overreaches the ventral margins. In addition, the alveolar notch is considerably deeper and broader in *C. (P.) laeli* and the rostrum is not (almost) attached to the ventral margin.

Apart from that, *C. (P.) laeli* is clearly distinguishable from other taxa dealt with here: *Cypridea (Pseudocypridina) setina* as remaining representative of this subgenus shows no ornamentation at all, the other taxa are different in several characters: *Cypridea obesa* has a very weakly developed rostrum and an almost absent alveolar notch and furrow, and is strongly obese. *Cypridea nitidula* has a subtriangular lateral outline and a distinct cyathus-like protrusion. Representatives of *Cypridea (Pseudocypridina) setina* are entirely devoid of ornamentation elements with a smooth carapace surface.

The remaining taxa are strongly different (se there) and cannot be confused with *C. (P.) laeli.*

Paleoecology: As for the genus; freshwater if the synonymization with *Cypridea piedmonti* of Schudack and Schudack (2009a) from the Spanish Hauterivian-Barremian freshwater associations is correct.

Faunal association (see Fig. 11 also): In the Lakota Formation with *Theriosynoecum pahasapensis* (Roth 1933) [see Sames in review: Theriosynoecum, this volume], *Cypridea (Pseudocypridina) piedmonti* (Roth 1933), *Cypridea (Longispinella) longispina* Peck 1941 syn. *C. (L.) asymmetrica* Sohn 1979, representatives of the family Darwinulidae Brady and Norman 1889, and representatives of the Trapezoidellidae Sohn 1979: *Trapezoidella trapezoidalis* (Roth), *Limnocypridea? morrisonensis* (Roth 1933).

Stratigraphic and geographic distribution: (Stratigraphic terms follow the most recent terminology available):

North America:
+ Fuson Member? of the Lakota Formation, Lower Cretaceous, eastern Black hills, Lawrence and Meade Counties, South Dakota, U.S.A. (this study, fig. 2, locs. 7, 8, 9)

+ Lakota Formation near top [Fuson Member?], Inyan Kara Creek – near Corral Creek, western Black Hills area, NE1/2 sec. 20 and NW1/4 sec. 21, T. 51 N., R. 65 W., Crook County, Wyoming, U.S.A. (fig. 2, loc. 5 in Sohn 1979)

Questionable occurrence:

North America:
+ Fuson Member? of the Lakota Formation (L2? informal interval after Way et al. 1998), Lower Cretaceous, eastern Black Hills, Meade County, South Dakota, U.S.A. (this study, Fig. 2, loc. 6)

Europe:
+ Middle Enciso Group, Lower Cretaceous, northeastern Spain, Iberian Chains, Sierra de los Cameros, "Upper Purbeck" according to Kneuper-Haack (1966); Valanginian, Early Hauterivian to Barremian (after Schudack in review, and Schudack and Schudack 2009a)

+ Iberian Chain, eastern Spain Early Cretaceous (Schudack and Schudack 2009a) designated *Cypridea piedmonti* therein):
- middle and upper Enciso Group of the eastern Cameros sub-basin, eastern Spain, Hauterivian to Barremian
- Torrelapaja Formation, Central Iberian Ranges, eastern Spain, Hauterivian to Barremian

- Polacos Formation, Maestrazgo sub-basin, eastern Spain, Early Hauterivian
- Artoles Formation, Maestrazgo sub-basin, eastern Spain, Barremian

Asia:
+ Tungulu Group, Lower Cretaceous, Xinjiang Autonomous Region, northeastern China

Stratigraphic range in North America: Lower Cretaceous, as deduced from similarity to *C. (P.) moneta* Kneuper-Haack 1966 (after Schudack in review, and Schudack and Schudack 2009a): (Valanginian) Early Hauterivian to Barremian.

Stratigraphic range outside North America: If synonymous with *Cypridea moneta* Kneuper-Haack 1966, Valanginian to Barremian according to Schudack (in review, designated *Cypridea piedmonti* Sohn therein), typically for Early Hauterivian to Barremian assemblages of the Iberian Chain, eastern Spain (Schudack and Schudack 2009a, designated *Cypridea piedmonti* Sohn therein).

Cypridea (Pseudocypridina) piedmonti **(Roth 1933) syn.** ***C. (P.) henrybelli*** **Sohn 1979, emend.**

(Pl. 4, Figs. 1-15; Pl. 5, Figs. 1-15)

v*	1933	*Pseudocypridina piedmonti* gen. et sp. nov. – Roth, p. 404, pl. 48, figs. 7a-h
	1935	*Cypridea piedmonti* (Roth) comb. nov. – Harper and Sutton, p. 625, pl. 76, figs. 12-15
non	1946	*Cypridea (Pseudocypridina) piedmonti* (Roth) – Swain, p. 550, pl. 83, figs. 10-12 [see Swain 1999, p. 123]
	1951	*Pseudocypridina piedmonti* Roth – Peck, p. 319, pl. 48, fig. 16-20
	1956	*Pseudocypridina piedmonti* Roth – Peck, fig. 23
v	1958	*Pseudocypridina piedmonti* Roth – Sohn, p. 123, pl. 1, figs. 5-8
v•	1958	*Cypridea*? sp. – Sohn, pl. 1, figs. 13-15, 16
?	1959	*Cypridea (Pseudocypridina) piedmonti* (Roth) – Wicher, p. 47, pl. 9, fig. 6
	1961	*Cypridea piedmonti* (Roth) - Craig (unpubl.), p. 45-47, pl. 1, figs. 4, 6, 10
	1962	*Cypridea piedmonti* (Roth) – Peck and Craig, pl. 2, fig. 3
	1979	*Cypridea (Pseudocypridina) piedmonti* (Roth) – Sohn, p. 15, pl. 6, figs. 1-47
•	1979	*Cypridea (Pseudocypridina) henrybelli* sp. nov. – Sohn, pl. 3, figs. 14-17; pl. 8, figs. 1-25
non?	1984	*Cypridea (Pseudocypridina) piedmonti* (Roth) – Li and Zhao, p. 191, pl. 2, figs. 4-6
non	1984	*Cypridea (Pseudocypridina)* cf. *piedmonti* (Roth) – Li and Zhao, p. 191, pl. 2, figs. 1-3

1999 *Cypridea (Pseudocypridina) piedmonti* (Roth) – Swain, p. 122, pl. 7, figs. 29, 30; pl. 8, fig. 19; pl. 13, figs. 5, 19-22 [refigured after Roth 1933, Peck 1951, Sohn 1958, 1979]

1999 *Cypridea (Pseudocypridina) henrybelli* Sohn – Swain, p. 119, pl. 12, figs. 38-40 [refigured after Sohn 1979]

non 2009 *Cypridea piedmonti* (Roth) – Schudack and Schudack (2009a), fig. 9 No. 18 [figured]

non 200X *Cypridea piedmonti* (Roth) – Schudack, in review, pl. 2, figs. 2, 3 [figured]

Material: Several thousand carapaces and valves, moderately to well-preserved. (#) indicates samples including *C. (P.) piedmonti* var. *henrybelli*, which only seems to occur in the lower Lakota Formation (Chilson Member). Chilson and Fuson Members of the Lakota Formation.

Samples: Lakota Formation: FRCA*?, HSDC1(#), HSDC2(#), HSDC3(#), HSDC4(#), BCE*, BCE(#), BC5 04, BCB1, BCB2(#), BC8 04(#), LEC 04, SBCR LAg1?, SBCR LAg2, SBCR LAg3, SBCR LAg3*(#), SBCR DC Strat. Col., SBCR LAg6, SBCR LAh2, SBCR LAh3, SBCR LAh3Tp, EBF 04a, EBF 04a2, EBF 04b, EBF 04b2? (see Fig. 11). Localities: Fig. 2, locs. 1, 2, 6, 7, 8 and 9.

Dimensions (in mm): Overall length: 1.03-1.14

Own specimens:

C. (P.) piedmonti var. *henrybelli*

Presumed males	L: 1.03-1.13	H: 0.61-0.69	W: 0.40-0.480
Presumed females	L: 1.07-1.21	H: 0.71-0.76	W: 0.49-0.57

C. (P.) piedmonti

Presumed males:	L: 1.06-1.17	H: 0.67-0.71	W: ~0.45
Presumed females:	L: 1.14-1.22	H: 0.74-0.75	W: ~0.58

As given in the literature (various references):

C. (P.) henrybelli	not given by Sohn (1979)		
C. (P.) piedmonti	L: ~1.08	H: ~0.72	W: ~0.52

Type locality and horizon: Chilson Member of the Lakota Formation, T. 4 N. R. 6 E., Meade County, 3 miles north of Piedmont, South Dakota, U.S.A. (Roth's 1933 locality, corresponding to Sohn's 1979 fig. 2, locality 8/USGS Mesozoic collection locality: USGS 30998; about corresponding to Fig. 2, locality 8 herein).

Holotype: USNM No. 70 473.

Diagnosis (emend): Rounded-suboblong species of *Cypridea (Pseudocypridina)*, with moderate reticulation-like punctation covering the whole surface. Alveolar notch very weak to almost absent, alveolar furrow almost absent. Weak ventrolateral ridge. LV barely or not overreaching RV along posterior margin in lateral right view. Generally without local ornamentation elements, noding common, sometimes with small antero- and posterolateral tubercles.

Remarks: Sohn's (1979, p. 15) original diagnosis: "A species of *Pseudocypridina* with a ventrolateral in left valve, with few, small (less than twice the diameter of puncta), subdued, scattered tubercles near end margins" is considered insufficient for several reasons (see discussion below.)

Description: Carapace shape: Medium sized (>1mm). Carapace rounded-suboblong in lateral view. Maximum length at about mid-height, maximum height slightly below middle and at anterior cardinal angle (2/5 of length), maximum width between half and 3/5 of length in both sexes. Subequivalve, LV>RV, slightly overreaching and overlapping the latter along the entire margin except alveolar area. Overreach of larger LV weaker at posterior margin, sometimes even not apparent (Pl. 4, Fig. 2).

Anterior margin broad and almost equicurvate with a moderately long straight dorsal part being inclined about 30-35° in relation to base line of carapace (Fig. 4). Small tapering anteroventral rostrum, strongly bending backwards with 50-60°, moderately overreaching the ventral margin, weaker developed in smaller RV, there being narrower and less prominent. The LV's rostrum also slightly overreaches the ventral outline. Alveolus small and weakly developed, alveolar notch narrow and weak. Alveolar furrow barely cognizable in both valves being very shallow and broadly triangular ad somewhat stronger developed in RV, ventrally delimited by a very faint alveolar ridge (e.g. Pl. 4, Fig. 1; Pl. 5, Fig. 1).

Posterior margin narrower than anterior one, equicurvate to weakly infracurvate in larger LV, there passing into an obtuse and well-rounded true cyathus. Cyathus narrowly crescent, indistinct, with its angle circa 140-145°. Posterior margin of smaller RV very slightly infracurvate to nearly equicurvate.

Dorsal outline straight to weakly convex, in both valves slightly overreaching the straight hinge margin and gently (8-14°) dipping towards posterior end. Anterior cardinal angle rounded but well cognizable, 135-140°, posterior cardinal angle strongly rounded and relatively indistinct, even less distinct in smaller RV, circa 130°.

Ventral margin straight to gently convex, ventral outline convex in larger left valve through moderately overreaching ventrolateral ridge.

Dorsal view elongated-ellipsoid in males, more ovoid in females, tapering towards both ends, somewhat more tapering to anterior end. Hinge line straight and indented in dorsal view forming a moderate dorsal furrow with its left flank broader and less steep resulting in a slight lateral offset towards right valve. Overlap of LV somewhat stronger and arched at both cardinal angles.

Ventral view shows arched, tongue-like overlap of the larger LV over the right one, with short, slightly concave part in front of the cyathus. The ventral ridge weak to moderately developed and displaced towards left side, thus better to define as ventrolateral ridge.

Ornamentation:

1. Area-wide ornamentation elements/surface characters: Surface moderately punctate—partially tending towards reticulation—except for the marginal regions, the ventral ridge as well as the lateral nodes, if applicable (see local ornamentation elements below). Puncta rounded polygonal (pentangular) to roundish with a diameter of 20-30μm, becoming more elongated towards the margins forming rows parallel to the latter. Several irregularly scattered normal pores of 1-2μm diameter, almost always between the puncta, rarely having a marginal position inside of the puncta.

Surface characters often distorted in the centrodorsal to dorsolateral regions of both valves, especially in these regions below anterior cardinal angle and anterior part of hinge margin (Pl. 5, Fig. 4). This involves lateral flattening or even a weak recess of the carapace in this area. The cause of this character remains unknown thus far. Speculatively, these distortions are caused by tractive force of the organs that connected to the carapace by the dorsal muscle scar group during the soft stage of the molting process. Surface characters strongly distorted or missing (i.e. extremely stretched until not visible anymore) at the nodes.

2. Local ornamentation: With or without scattered, usually improminent and very shallow, conic tuberculi (always with pore in center) developed around the somewhat bigger normal pores in between

the puncta, located generally outside the central and centrolateral areas. Diameter of tubercles observed and documented in the literature (Sohn 1979) always smaller than two times the diameter of a punctum.

Occurrence of circular to perpendicular elliptic true nodes common (these specimens have formerly been designated as a discrete species, *C. (P.) henrybelli* Sohn 1979). The position of the nodes is consistent, being antero- and posterocentrally. Nodation greatly varies in number and intensity (height) of the development of the nodes (Pl. 5, Figs. 1-5, 7-14), but much less in length and width. One, two, three or four nodes can occur, their occurrence not usually being pairwise. Nodes generally stronger developed in the LV and anterocentrally stronger than posterocentrally, if not all four nodes occur. Consistent succession of intensity of node development realized (Pl. 5, Figs. 7-12), always starting with the a weak anterocentral node in the LV (Pl. 5, Fig. 7) only, followed by a somewhat stronger anterocentral node and a weaker posterocentral one in the LV only (Pl. 5, Fig. 8) or with a weak anterocentral node in the RV also (Pl. 5, Fig. 9), the latter then being weaker than the posterocentral one of the LV. The following stage shows strong anterocentral nodes in both valves, a strong posterocentral node in the LV (about as strong as the anterior one in the RV, both less strong than anterocentral of the LV), and a weak posterocentral node in the RV (Pl. 5, Fig. 10). Last stage is with all four nodes more or less strongly developed, the anterocentral one in the LV being the largest and the other three of about the same size (Pl. 5, Figs. 11, 12), not ruling out some minor variations.

Remarks: The noding pattern in *Cypridea (Pseudocypridina) piedmonti* var. *henrybelli* is nearly the same as that of the recent cytheroid ostracod species *Cyprideis torosa* (Jones). Interestingly, although the former belongs to the superfamily Cypridoidea whereas *Cyprideis torosa* belongs to the Cytheroidea (genus name of the latter might be misleading), the pattern of the primary nodes is nearly the same (four nodes, antero- and posterocentrally), thus raising the question, if the causes of the noding process in both cases might be more or less or exactly the same, which seems to be the case. More research is wanting. There are many more Mesozoic and Cenozoic ostracods showing this pattern of noding. Additionally, like in *Cyprideis torosa*, "erratic" additional nodes can occur in representatives of *Cypridea* (not to confuse with obvious => *node-like tuberculi* like in *Cypridea verrucosa* Jones or *Cypridea morula* Anderson, for example), that might point to higher environmental stress, like assumed for *Cyprideis torosa*.

Internal characters: Hinge lophodont (sensu Sylvester-Bradley, 1956). Hinge line straight, about half the length of carapace. Narrow (edged) hinge bar in the larger LV resting on the margin on the margin of the smaller RV (no real corresponding groove developed) combined with narrow anterior and posterior teeth of the RV with corresponding grooves in the LV. Anterior tooth and socket considerably inclined (~40°), posterior tooth and socket weakly inclined (~15-20°).

Inner lamella anteriorly moderately broad with typical => *local widening of inner lamella* and straight inner margin in alveolus area, narrow posteriorly with maximum width and straight inner margin in cyathus area. With anterodorsal and posterodorsal flange, stronger developed anteriorly, and overall trend stronger in the LV.

Harper and Sutton (1935, pl. 76, fig. 15, upside down, anterodorsal part broken away, valve filled with sediment) already figured some internal features.

Muscle scar pattern: Details unknown, having not yet been observed or documented.

Dimorphism: Sexual dimorphism assumed herein, as already tentatively mentioned by Sohn (1979, p. 15) for *Cypridea (Pseudocypridina) piedmonti*. Presumed females (e.g. Plate 5, Figs. 1, 2, 10) somewhat higher and ovate in lateral view with a convex dorsal margin and wider (piriform) in dorsal view, presumed males (e.g. Plate 5, Figs. 3, 12, 13) less high and more slender in lateral view with a more straight dorsal margin and elongate-elliptic in dorsal view.

Morphologic variation: Minor, except presumed sexual dimorphism (see above) and noding (see local ornamentation above.

Ontogenetic variation: Few data available. Presumed late ontogenetic stages (A-1 to A-2, Plate 4, Figs. 3, 6?, 7) show somewhat lower posterior margin, a somewhat stronger inclination of the hinge margin and generally follow the morphology of the male(?) dimorph.

Discussion: Sohn's (1979) diagnosis of *Cypridea (Pseudocypridina) piedmonti* is considered insufficient, because the ventrolateral ridge or the small "scattered tubercles" (op. cit., p. 15) are not diagnostic in general (refer to the description of the genus *Cypridea*, Chapter 5.2.3, and to the glossary under => *ornamentation*). Additionally, this diagnosis is unsuitable to differ *C. (P.) piedmonti* from *C. (P.) henrybelli* Sohn (see right below) and from *C. (P.) laeli*, respectively (the latter also having a ventrolateral ridge and can show minor tubercles). The ventrolateral ridge is mostly well visible in Sohn's material (USNM collection).

Cypridea (P.) henrybelli Sohn 1979 is considered a junior synonym of *C. (P.) piedmonti* (Roth 1933) here for several reasons. Sohn's (1979, p. 17) original diagnosis for *C. (P.) henrybelli* is as follows: "Straight backed, with anterodorsal angulation, finely punctate; commonly with distinct nodes at mid-height on anterior and posterior quarters of each valve; sometimes one or both nodes may be smaller, more subdued, or entirely missing on the right valve." However, either the "straight back" (i.e., the straight dorsal margin) or the anterodorsal angulation (i.e., a weakly rounded anterior cardinal angle) and least of all, the punctation, are diagnostic. Sohn (1979) did not include a differential diagnosis of his species, but from his plates the inconsistency between his diagnosis and the assigned specimens becomes apparent: Specimens assigned to *C. (P.) piedmonti* by him have the straight dorsal margin and weakly rounded anterior cardinal angle (op. cit., pl. 6, figs. 25, 29/31, 35/36, 42/45), while specimens of Sohn's *C. (P.) henrybelli* have a convex dorsal margin and a strongly rounded anterior cardinal angle (op. cit., pl. 8, figs. 1/3, 10, 21), for example. The => *nodes* are not taxonomically but rather ecophenotypically significant. Altogether, both of Sohn's species do share the same characters except for the nodes, and show similar morphological variations, which are interpreted as intraspecific variations (particularly the presumed sexual dimorphism) herein. In addition, in the authors own samples, *Cypridea (P.) piedmonti* var. *henrybelli* also does always co-occur with *C. (P.) piedmonti*. For unknown reasons, a faunal association of these is not mentioned by Sohn (1979) under his item "geographic distribution" of both taxa.

With reference to noding in *C. (P.) piedmonti* var. *henrybelli*, Sohn (1979, p. 17) already discussed the problem but did not draw the correct consequences (that is, its taxonomic insignificance) and did not yet take ecophenotypy into consideration.

However, Craig (1961, p. 46) already discussed the nodes as variation of the same species (although he did—and could not yet—explain its origins) for the reasons that all other characters are the same as in the unnoded forms! He also figured a noded specimen and assigned it to *Cypridea piedmonti* (op. cit., pl. 1, fig. 4).

Roth (1933) as well as Harper and Sutton (1935) still considered *C (P.) piedmonti* to occur in the Morrison Formation of the Black Hills area by mistake, later taken over by Peck (1951, 1956). Sohn (1958) demonstrated these to having derived from the Lakota Formation.

Cypridea (Pseudocypridina) piedmonti as has been described and figured by Swain (1946, p. 550, pl. 83, figs. 10-12) is rather *Cypridea? salvadoriensis* Krömmelbein 1962 as indicated by Swain (1999, p. 123). A personal examination of the specimen (USNM 103 845, BS visit 2006) showed that this specimen is not well preserved and probably a juvenile of a thus far unidentified species of *Cypridea (Pseudocypridina)*.

The specimens designated as *Cypridea?* sp. and figured by Sohn (1958) have been personally examined by the present author and, although not specifically indicated by Sohn (1979), are representatives of *C. (P.) piedmonti* var. *henrybelli*. The one specimen of *Cypridea?* sp. as figured by Sohn (1958, pl. 1, figs. 13-15) became the holotype of the latter (Sohn 1979).

Pseudocypridina piedmonti Roth as figured in Peck (1951, 1956) is still by mistake considered to be of Late Jurassic age (taken over from Roth 1933 and Harper and Sutton 135) and to derive from the Morrison Formation, an interpretation having been challenged and disproven by Sohn (1958). Being not considered a later stratigraphic overview of Peck (1959) anymore, this species, now designated *Cypridea piedmonti* (Roth), is mentioned to occur in the Lakota Formation in Peck and Craig (1962), but for unknown reasons not listed in the overview of the distribution of species (op. cit., fig. 1).

The specimens assigned to *C. (P.) piedmonti* (Roth) by Wicher (1959) do not belong to this species. Wicher (1959, p. 47) himself states that his identification are tentative, because the single adult specimen is crumpled and the others are juveniles. The latter, however, Wicher (op. cit.) indicates not to correspond to the specimens of Swain (see above), but to resemble the figures of the North American specimens (i.e., Roth 1933, Harper and Sutton 1935). However, lacking any description, this is highly doubtful here because the specimen figured by Wicher (1959, pl, 9, fig. 6) does not show any similarities to *C. (P.) piedmonti* at all, not even a rostrum is visible.

The identification of *Cypridea (Pseudocypridina) piedmonti* of Li and Zhao (1984, pl. 2, figs. 4-6) cannot be confirmed due to the insufficient quality of figures and the few characters visible.

Cypridea (Pseudocypridina) cf. *piedmonti* of Li and Zhao (1984, pl. 2, figs. 1-3) has a distinct alveolar notch and furrow and more overall similarities to *Cypridea (Pseudocypridina) laeli* Sohn 1979 than to *C. (.P) piedmonti*.

The two specimens of *Cypridea piedmonti* (Roth) as figured by Schudack (in review) do potentially not belong to this species, because both are roundish-elongate in lateral view and the alveolar furrow is distinct and reaches up to above 1/3 of height (see *Cypridea (P.) laeli* above).

Schudack and Schudack's (2009a) *Cypridea piedmonti* (Roth) as figured is similar to the North American species, but the identification cannot be fully confirmed from this moderately preserved specimen. It is more likely to be related to *Cypridea (Pseudicypridina) laeli* sohn 1979 (see there).

Discussion of phylognetic relations: Sohn (1979) related his *Cypridea (Pseudocypridina) henrybelli* to the *parallela*-line *Cypridea valdensis-parallela*-group of Wolburg (1959) on the basis of lateral outline and rostrum. All representatives of the latter group, however, have a much stronger (broader) developed rostrum, the alveolar furrow is much more distinct (deeper and longer, reaching up from 1/5 to 3/4 of height), and the hinge margin relatively long and slightly inclined and, therefore, this view cannot be followed here.

Cypridea (Pseudocypridina) piedmonti syn. *C. (P.) henrybelli* has much more similarities to the *Cyridea granulosa*-group. This group has been first defined as "*fasciculata*-group" by Wolburg (1959), who already pointed out the close relation of *Cypridea fasciculata* (Forbes 1855) to *C. granulosa* (Sowerby 1836) and *C. buxtorfi* Martin 1958. Consequently, Anderson (in Anderson and Bazley 1971, p. 63-68) synonymizes *Cypridea fasciculata* with *C. granulosa*, the former being the junior synonym, but retains the two morphologic variants as subspecies of *Cypridea granulosa* for the reason that they do not completely overlap stratigraphically. Kilenyi and Neale (1978. p. 304) also point out that all transitions between these two morphotypes exist but follow Anderson (in Anderson and Bazley 1971) in retaining his subspecies *Cypridea granulosa granulosa* (Sowerby) and *C. granulosa fasciculata* (Forbes 1855) for their biostratigraphic value in the English Purbeck. Schudack (1994, p. 20-21) as well followed this view for the reason that a partial stratigraphic separation is also observable in contemporaneous deposits of NW-Germany and could detect the transition of one form (subspecies) to the other in her material.

Representatives of the *Cypridea granulosa*-group should considered to be included into *Cypridea (Pseudocypridina)* because of the fact that they show many diagnostic characters of the latter (see above). Except for the taxonomically insignificant nodes and tubercles, *Cypridea (Pseudocypridina) piedmonti* syn. *C. (P.) henrybelli* shows strong similarities to *Cypridea granulosa* (Sowerby 1836), in general shape, development of rostrum and alveolus, the narrow cyathus, the ventrolateral ridge and slight valve inequality. More research is necessary for clarification. For the moment it can be stated that *Cypridea granulosa* and representatives of this group could be probable ancestors of a somewhat younger lineage to which *Cypridea (Pseudocypridina) piedmonti* syn. *C. (P.) henrybelli* belongs to.

Differential Diagnosis: *Cypridea (Pseudocypridina) piedmonti* (Roth 1933) syn. *C. (P.) henrybelli* Sohn 1979 differs from *C. (P.) laeli* Sohn 1979 in being less ovate in lateral outline and a bit smaller in trend. More important is the weaker developed rostrum in the former, which is narrower and shorter than in *C. (P.) laeli* and brelay overreaching the ventral margins. In addition, the alveolar notch is inconspicuous to absent (sensu Sames herein) in *C. (P.) piedmonti* and the rostrum is almost attached to the ventral margin, while in *C. (P.) laeli* the alveolar notch is clearly defined and the rostrum separated from the ventral margin.

Cypridea (Pseudocypridina) piedmonti (Roth 1933) syn. *C. (P.) henrybelli* Sohn 1979 is clearly distinguishable from other taxa dealt with here. *Cypridea (Pseudocypridina) setina* as remaining representative of this subgenus shows no ornamentation at all, the other taxa are different in several characters: *Cypridea obesa* has a very weakly developed rostrum and an almost absent alveolar notch and furrow, and is strongly obese while *Cypridea nitidula* has a subtriangular lateral outline and a distinct cyathus-like protrusion.

The other remainig taxa are totally different in their characters and cannot be confused with *C. (P.) piedmonti* (Roth 1933) syn. *C. (P.) henrybelli* Sohn 1979.

Paleoecology: Generally, as for the genus. *Cypridea (P.) piedmonti* var. *henrybelli* is considered to point to low salinity (rapid desalination during moult, e.g. through rainfall in ponds) and/or low calcium content as derived from the recent *Cyprideis torosa* (see Keyser 2005, and discussion of => *ornamentation* elements in the glossary).

Faunal association (see Fig. 11, and Sohn 1979): In the Lakota Formation associated with *Cypridea (Longispinella) longispina* (Sohn 1979), *Cypridea (Pseudocypridina) setina* var. *setina* (Anderson 1939), *Cypridea* ex gr. *tuberculata* cf. *C. tilleyi* Loranger 1951. Taxa other than *Cypridea* (with respect to *Theriosynoecum*, see Sames in review): associated with *Theriosynoecum fittoni* (Mantell 1844) and with *Theriosynoecum pahasapensis* (Roth 1933). Also, with representatives of the Darwinulidae Brady and Robertson 1889 (*Alicenula?* sp.) and of the Trapezoidellidae Sohn 1979 (see therein also).

Stratigraphic and geographic distribution (Stratigraphic terms follow the most recent terminology available):

North America:

+ Chilson Member (both varieties) of the Lakota Formation, Lower Cretaceous, southern Black Hills, South Dakota, U.S.A. (Sohn 1979; and this work, Fig. 2, locs. 1-4, 6-9), and Fuson(?) Member of the Lakota Formation (*C. (P.) piedmonti* only), eastern Black Hill area, South Dakota, U.S.A.

+ Lakota Formation North of Sturgis, eastern Black Hills area (Craig 1961)

Stratigraphic range in North America: Valanginian to Barremian (Sohn 1979, this work).

Stratigraphic range outside North America: Not applicable.

Cypridea (Pseudocypridina) setina-group

Diagnosis (emend.): Representatives of *Cypridea (Pseudocypridina)* lacking any ornamentation elements (=> *area-wide* as well as => *local* ones), i.e. having a completely smooth carapace surface.

Remarks: This group was established by Wolburg (1959; *Cypridea setina*-group therein) for those species of the "German Wealden" that are completely smooth and, according to Wolburg (op. cit.), correspond to the diagnosis of the genus *Langtonia* Anderson 1939. In his first attempt to correlate the Upper Purbeck of England to the "German Wealden", Anderson (1962) revised the group and included several of his new subspecies (regarded variants herein) into the group, most of them subspecies names for morphologic variants having been described by Wolburg (1959).

In a recent work Schudack and Schudack (2009b) synonymize the species *Cypridea setina* (Anderson 1939) and *Cypridea laevigata* (Dunker 1846) under the oldest valid name: *Cypridea laevigata* (Dunker 1836), because of their identical diagnostic characters (see discussion of preference of the species below). Schudack and Schudack's (2009b) line of argument is comprehensible, her view is (yet) not followed herein for the reasons given (see item "Preference of *Cypridea setina* to *C. laevigata*" under discussion of *C. setina* below).

Schudack and Schudack (2009b) also account all subspecies of *Cypridea setina* and *C. laevigata* (Sylvester-Bradley 1949, Anderson 1962, 1971, 1985, Anderson et al. 1967, Kneuper-Haack 1966) as varieties, a view also hold by the present author for the reasons that a), these are often not well defined or figured and, therefore, irreproducible, and b), rarely have limited stratigraphic or paleogeographic distribution. A circumstantial revision of *Cypridea setina* s.l., i.e., the *Cypridea (Pseudocypridina) setina*-group emphasizing a close analysis of the varieties including sexual dimorphism, genetics of mixed reproduction in the context of morphologic variation within a population, and ontogeny, remains to be conducted.

The *Cypridea (P.) setina*-group is a very useful index group for biostratigraphic correlation since its stratigraphic range is relatively restricted (upper Berriasian to [lower, if not synonymized with *C. laevigata*] Valanginian) and since it is easily identifiable by its absence of all ornamentation elements, which is unique among all representatives of *Cypridea*. It is assigned to *Cypridea (Pseudocypridina)* herein.

With respect to the uniqueness of a totally smooth carapace surface in *Cypridea (Pseudocypridina) setina*/*Cypridea laevigata*-group in Early Cretaceous Purbeck/Wealden-like deposits it has to be mentioned that there are some data of older representatives of *Cypridea* also showing this character. In his Master's thesis, Sames (2002, p. 22, pl. 2, figs. 6-8) described two taxa of *Cypridea*, *Cypridea* sp. B and *Cypridea* sp. C from the Middle Saurian Member (Kimmeridgian, see Sames 2008) of the Tendaguru Formation (Upper Jurassic to Lower Cretaceous of southeastern Tanzania, East Africa), most probably belonging to one species. These forms, considered to represent an early lineage of *Cypridea*, are smooth and devoid of any ornamentation elements, and show a distinct cyathus-like protrusion in combination with a weak dorsal furrow, a well-developed and broad rostrum, as well as inconspicuous to almost absent alveolar notch and furrow. No statements concerning possible phylogenetic relationships of the Tanzanian species and *Cypridea (P.) setina* can be made so far, the absence of ornamentation elements in representatives of *Cypridea* may or not be a plesiomorph character in the *Praecypridea*/*Cypridea* lineage (Sames et al. in review). More data and research is necessary.

Note: The specimen (topotype) of *Cypridea (Pseudocypridina) setina* var. *florida* Anderson 1971 figured in Anderson (1985, pl. 18, fig. 17, right view of carapace) was photographed in unfavorable orientation and does not show the rostrum this way. Illustrations (drawings) in Anderson 1962 (pl. 1, fig. 8, holotype as designated by Anderson 1971) and Anderson (1971, pl. 17, fig. 8) are preferable in this case. The same applies to *Cypridea (Pseudocypridina) setina* var. *deburghi* Anderson 1971, also unfavorably figured in Anderson (1985, pl. 6, fig. 7) and not showing the rostrum. The holotype as pictured in Anderson (1971, pl. 18, fig. 1 in right lateral view) does show the rostrum.

Cypridea (Pseudocypridina) setina (Anderson 1939) emend.

? 1846 *Cypris laevigata* sp. nov. – Dunker, p. 59, pl. 13, fig. 25

* 1939 *Langtonia setina* sp. nov. – Anderson, p. 305, pl. 12, figs. 7a, b; pl. 13, figs. 12a,b

• 1940 *Cypridea laevigata* (Dunker) – Martin, p. 286 [comb. nov.]

1940 *Cypridea setina* (Anderson) – Martin, p. 287 [comb. nov.]

• 1941 *Cypridea inornata* sp. nov. – Peck, p. 301, pl. 44, figs. 33-36

1949 *Cypridea (Pseudocypridina) setina rectidorsata* subsp. nov. – Sylvester-Bradley, p. 147, fig. 24

1949 *Cypridea (Pseudocypridina) setina setina* (Anderson) – Sylvester-Bradley, p. 146

1962 *Cypridea (Pseudocypridina) setina acerata* subsp. nov. – Anderson, p. 25, pl. 1, figs. 7, 8

1962 *Cypridea (Pseudocypridina) setina camelodes* subsp. nov. – Anderson, p. 25, pl. 1, fig.6

1962 *Cypridea (Pseudocypridina) setina dotica* subsp. nov. – Anderson, p. 25, pl. 1, figs. 3, 4

1962 *Cypridea (Pseudocypridina) setina erumna* subsp. nov. – Anderson, p. 24, pl. 1, fig. 5

1966 *Cypridea (Pseudocypridina) setina fiteriensis* subsp. nov. – Kneuper-Haack, p. 187, pl. 45, fig. 19

1967 *Cypridea laevigata fairlightensis* subsp. nov. – Anderson et al., p. 216, pl. 13, fig. 59

1967 *Cypridea laevigata hawkhurstensis* subsp. nov. – Anderson et al., p. 217, pl. 13, fig. 62

1967 *Cypridea laevigata laevigata* (Dunker) – Anderson et al., p. 215, pl 13, fig. 57

1967 *Cypridea laevigata leonardi* subsp. nov. – Anderson et al., p. 216, pl. 13, fig. 58

1967 *Cypridea laevigata philpottsi* subsp. nov. – Anderson et al., p. 217, pl. 12, fig. 55

1967 *Cypridea laevigata subquadrata* subsp. nov. – Anderson et al., p. 216, pl. 13, fig. 60

1967 *Cypridea laevigata wadhurstensis* subsp. nov. – Anderson et al., p. 216, pl. 13, fig. 61

1971 *Cypridea setina bellatula* subsp. nov. – Anderson, p. 82, pl. 17, figs. 2-3

1971 *Cypridea setina deburghi* subsp. nov. – Anderson, p. 83, pl. 18, fig. 1

1971 *Cypridea setina florida* subsp. nov. – Anderson, p. 84, pl. 17, fig. 8

1985 *Cypridea setina pelota* subsp. nov. – Anderson, p. 31, pl. 11, fig. 10

? 1988 *Cypridea setina acerata* Anderson – Li, p. 1249, textfig. 3, fig. 23

? 1988 *Cypridea setina bellatula* Anderson – Li, p. 1249, textfig. 3, fig. 24

? 1988 *Cypridea setina florida* Anderson – Li, p. 1249, textfig. 3, fig. 22

Preceding remarks: In a recent publication, Schudack and Schudack (2009b) consider *Cypridea setina* (Anderson 1939) to be a junior synonym of *Cypridea laevigata* (Dunker 1846)—based on diagnostic characters all being identic to *Cypridea laevigata*, particularly the complete absence of ornamentation elements—and thus considers all its subspecies described by Sylvester-Bradley (1949, Anderson (1962, 1971, 1985), Anderson et al. (1967) and Kneuper-Haack (1966) as subspecies (considered varieties by Schudack and Schudack 2009b) of *Cypridea laevigata* (Dunker 1846).

Preference of *Cypridea setina* to *C. laevigata* herein: Synonymizing *Cypridea (Pseudocypridina) setina* Anderson (1939) and *C. (P.) laevigata* (Dunker 1846) poses the question of the priority of the older name *C. laevigata* versus a long-accepted name, i.e., *Cypridea setina* (see discussion of synonymy below and "Preference of *Cypridea setina* to *C. laevigata*").

Lectotype: GSM Mik(M) 535001, formerly GSM 60682, as selected by Sylvester-Bradley (1949), syntypy with *Cypridea setina* var. *setina* (Anderson 1939).

Diagnosis (emend.): Small to medium sized (circa 0.90-1.40mm), considerably variable in lateral outline: rounded oblong or trapezoidal to elongate ovate. Carapace surface smooth, completely devoid of any ornamentation elements, local elements as well as area-wide. LV>RV, rarely inverse (RV>LV), slightly overreaching the latter along entire margin. Rostrum weakly defined, never overreaching the ventral outline of the larger valve. Alveolar notch distinct but weakly developed, alveolar furrow barely developed, triangular and very shallow. Slight indication of alveolar ridge. Cyathus weakly developed, narrow and strongly rounded.

Remarks: The diagnosis has been emended here to point out the highly variable lateral outline and the complete absence of ornamentation elements (which is unique in this species—when *Cypridea lavigata* is synonymized with it) and to include inverse and larger forms as well as representatives of *Cypridea (Pseudocypridina) laevigata* (Dunker 1846).

Description - Remarks: The representatives of this species have relatively few and consistent characters, except for their high variation in lateral outline. Since this is interpreted to be related to sexual dimorphism and different reproductive modes (see below and discussion Chapter 6.2, the *Cypridea (P.) setina* case) as well as that the variants have different stratigraphic and, in particular, different (paleo-)geographic distributions, the variants of particular interest in this study are described separately (refer to the particular variants of this species as described below). As for the application aspect, that is biostratigraphic utilization in North America, dealing with the variants and their stratigraphic and (paleo-)geographic separately is hoped to potentially allow a higher biostratigraphic resolution in future studies once more data regarding their stratigraphic distribution is available from areas outside Central to Western Europe.

Muscle scars: As figured by Wolburg (1959, pl. 5, fig. 16 – refigured in Fig. 13 herein) for *Cypridea setina* (Anderson 1939).

Christensen (1968, p. 23, fig. 6) gives a very good photograph of an internal view of a fragment of "*Cypridea* ex gr. *setina* (Anderson)", nicely showing all central, frontal and mandibular scars as well as some dorsal ones. The correct taxonomic designation, however, cannot be verified from this fragment, and in the description Christensen (1968, p. 22) only states that the "… fragments [are] of more ore less smooth thin valves of a large *Cypridea* with diminutive rostra …".

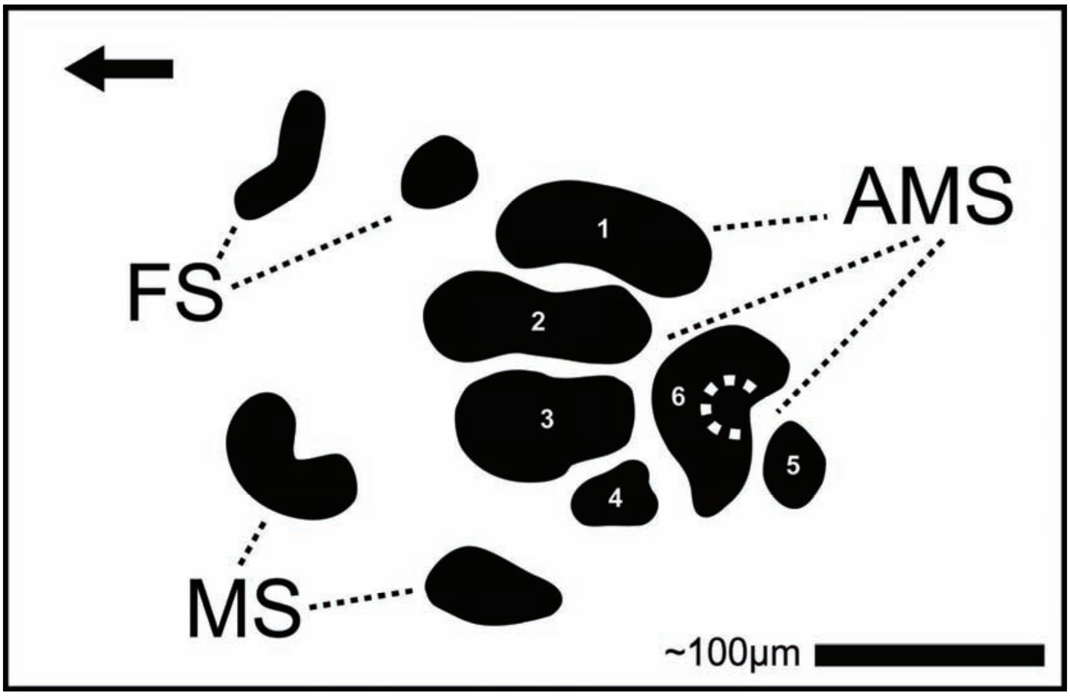

Fig. 13. Muscle scar pattern in *Cypridea (Pseudocypridina) setina* (Anderson 1939) redrawn after Wolburg (1959, pl. 5, fig. 16. The sketch shows the pattern of the central muscle scar field of the RV. AMS: Adductor muscle scars, labeling of single scars adopted from Horne and Colin (2005), the spot in scar No. 6 as indicated here by the white dotted line was outlined by Wolburg (1959) and not specifically explained. FS: Frontal scars, MS: Mandibular scars.

Dimorphism: Sexual dimorphism (see below for reasons) conjectured herein. *Cypridea (Pseudocypridina) setina* var. *rectidorsata* is conditionally believed to be the female dimorph capable of parthenogenetic reproduction, whereas *C. (P.) setina* var. *setina* is tentatively assumed to represent a male dimorph (see remarks right below and of the particular variants for details, and also Chapter 6.2). This conclusion is made by analogy to morphologic trends in the carapace shape of modern cypridoid ostracods—although sexual dimorphism does not have to be apparent in the valve shape of Cypridoideans according to Horne and Martens (1998).

Remarks: Lacking distinct differences in the width of the posterior end of the carapace, one "classic" general trend presented in many older textbooks for Mesozoic to recent ostracods is that female carapaces often are more compact in lateral view, i.e., shorter in relation to the height due to the smaller female reproduction organ. Male carapaces often tend to be more elongate, i.e., having a longer posterior end because of the space needed for the large hemipenises. This, however, might not be the case as in the Cypridoidea males also have Zenker's organs (sperm pumps) anterodorsally of the hemipenises, which may lead to higher posterior ends in the males as well.

Taking a mixed reproduction into consideration for (at least some) representatives of *Cypridea* and for *Cypridea (P.) setina* in particular, a parthenogenetic population can only emanate from a sexual population (see Martens et al. 1998b, for example). As given by Anderson (1985), however, *Cypridea (P.) setina* var. *rectidorsata*, tentatively presumed to be the female dimorph herein, starts to occur considerably earlier stratigraphically than all other variants of this species or the probably synonymous *Cypridea laevigata*, particularly those variants believed to be potential male dimorphs of either of these (see below). This should not be possible but may be a problem of inaccuracy in the definition of this variant and could probably be solved by revision of Anderson's material from the Studland to Greenwood faunicycles (cycles Nos. 30-33, Anderson 1985). *C. (P.) setina* var. *setina*, tentatively presumed be the male dimorph herein, is the most dominant variant in deposits from North America, as far as known. If the American populations should mainly represent populations of parthenogenetic females deriving from passively transported eggs, *C. (P.) setina* var. *rectidorsata* and similar morphotypes (see discussion under this variant below) should be the dominant form, and not *C.(P.) setina* var. *rectidorsata*. This problem is not yet satisfactory solved and has to be further investigated.

Discussion: The morphologic variation within *Cypridea setina*-group is almost exclusively expressed in the lateral outline as far as known, because only sparse data of the internal features are available.

<u>Discussion of synonymy:</u> Then North American species *Cypridea inornata* Peck 1941, also given as *Pseudocypridina inornata* (Peck) or *Cypridea (Pseudocypridina) inornata* Peck, is considered synonymous with *Cypridea (Pseudocypridina) setina* (Anderson 1939) here, particularly with *C. (P.) setina* var. *setina* (Anderson). Peck's (1941) description and figures as well as the specimens in his collection (excluding the type material the whereabouts of which are unknown) match the latter species. The specimen figured by Peck (1941, pl. 44, fig. 35) looks different and had been excluded from being synonym with *C. inornata* by Craig (1961) and assigned to a new species *Ulwellia crescenti* Craig 1961, which is a *nomen nudum* since Craig's work remained unpublished. Its assignment to *Cypridea (P.) setina* is probable but could not verified because the material is not in the collection (University of Missouri, Columbia, visit of BS visit, summer 2005). However, in his description of the latter, Craig (op. cit.) designates its surface as "unornamented" (i.e., smooth and lacking local ornamentation elements), and since *C. (P.) setina* is the sole representative of its genus lacking any ornamentation, Peck's (1941, pl. 44, fig. 35) specimen as well as those of "*Ulwellia*" *crescenti* Craig 1961 are likely to belong to *C. (P.) setina*.

Synonymizing *Cypridea (Pseudocypridina) setina* (Anderson 1939) with *Cypridea lavigata* (Dunker 1846) would—aside from making it a representative of the subgenus *Pseudocypridina*—extend the maximum stratigraphic distribution and range of this species (no matter whether it will be under the name "*setina*" or "*laevigata*") considerably: *C. (P.) setina* (Anderson 1939) occurs from the Studland to Rye faunicycles (cycles Nos. 30 to 47) of Anderson (1985), which is upper Berriasian to lower Valanginian according to Hoedemaeker and Herngreen (2003). *Cypridea laevigata* (Dunker 1846) occurs from the Mupes to Cuckfield faunicycles (cycles Nos. 35 to 67) of Anderson (1985), being upper Berriasian to uppermost Valanginian according to Hoedemaeker and Herngreen (2003). However, as indicated in fig. 5 of Anderson (1985, p. 12), the maximum abundance of the latter species is Mupes to Lydd faunicycles (cycles Nos. 35 to 49), that is upper Berriasian to lower/middle Valanginian (Hoedemaeker and Herngreen 2003), which is approximately the same as the distribution of *Cypridea (P.) setina*.

Cypridea setina acerata Anderson, *C. setina bellatula* Anderson and *C. setina florida* Anderson as given by Li (1988) as figures in the stratigraphic chart cannot be taxonomically verified from drawings and are therefore given with questions mark. Actually, all three forms given in Li (op. cit.) look quite different from *Cypridea (Pseudocypridina) setina* in general and its variants in each case: in outline and development of rostrum and alveolus, as well as valve size relation (*C. s. florida*).

The question, if *Cypridea setina* (Anderson 1939) and *Cypridea laevigata* (Dunker 1846) belong to the subgenus *Pseudocypridina* or may represent a separate lineage, remains to be discussed.

<u>Preference of *Cypridea setina* to *C. laevigata*:</u> According to the ICZN (1999), the determination of the principle of priority (ICZN 1999, Art. 23) of valid taxon names is based on their availability (op. cit., Art. 10). *Cypridea (P.) laevigata* (Dunker 1846) is an available (and valid) name because it meets the requirements of Article 11 and 12 (ICZN 1999) in that it has been published with a (short) description and figured (application of rules for a name published before 1931 as given in Article 12).

Cypridea (P.) laevigata (Dunker 1846) indeed meets the "Statement of the Principle of Priority" (ICZN 1999, Art. 23.1) but—in the view of the present author—*not* necessarily the "purpose" (op. cit., Art. 23.2) of the Principle of Priority in that its preference to *C. (P.) setina* (Anderson 1939) would upset a long-accepted name (i.e., *Cypridea setina*) in its accustomed meaning. For such a case, Article 23.9. "Reversal of Precedence" (op. cit.) would apply. In the case described here, however, one of the prerequisites (op. cit., Art. 23.9.1.1) for such reversal is not met, because the species name *laevigata* has been used as valid name after 1899, and therefore, the Principle of Priority would have to be applied in synonymizing the two taxa under the oldest valid name *Cypridea (P.) laevigata* (Dunker 1846). Owing to the fact that *Cypridea (P.) setina* is the by far more widely used name (regarding the frequency of usage in general, in biostratigraphy and by most authors from different countries), the present author disagrees with Schudack and Schudack (2009) for the moment with respect to that preference should be given to *Cypridea laevigata*. This case may have to be referred to the International Commission on Zoological Nomenclature, but, until it is solved, the more frequently used name is applied here, particularly to avoid confusion when dealing with the stratigraphic literature.

Differential diagnosis: *Cypridea (Pseudocypridina) setina*, including *Cypridea laevigata* (Dunker), is different from all other species of *Cypridea (Pseudocypridina)* and all species of *Cypridea* discussed here in having a totally smooth carapace always being devoid of any ornamentation elements.

Stratigraphic and geographic distribution (Stratigraphic terms follow the most recent terminology available):

North America:

+ Chilson Member of the Lakota Formation, Lower Cretaceous, southern Black Hills Area (Fig. 2, locs. 1, 3 and 5), South Dakota, U.S.A. (this work)
+ Yellow Cat Member of the Cedar Mountain Formation, Lower Cretaceous, Fig. 2, loc. 10, Utah, U.S.A. (this work)

As for older reports of occurrences in North America, the forms were formerly designated and published under *Cypridea inornata* Peck 1941, *Pseudocypridina inornata* (Peck 1941) or *Cypridea (Pseudocypridina) inornata* Peck 1941:

+ Minnewaste Limestone Member of the Lakota Formation, Lower Cretaceous, southeastern Black Hills area, South Dakota, U.S.A. (Peck 1951, Peck and Craig 1962)
+ Chilson Member of the Lakota Formation, Lower Cretaceous, Black Hills area, (Peck 1951, Peck and Craig 1962)
+ Lakota Formation [Chilson Member], Lower Cretaceous, southern Black Hills area, South Dakota, U.S.A. (Sohn 1979)
+ Cloverly Formation, Early Cretaceous, southeastern flank of Rawlins uplift, Wyoming, U.S.A. (Peck and Craig 1962)
+ Kootenai Formation, Lower Cretaceous, Montana, U.S.A (Peck 1941)

Europe:

+ Studland to Rye faunicycles (cycles Nos. 30 to 47) of Anderson (1985) as equivalent to upper Purbeck Group (Durlston Formation) to Lower Wealden Supergroup (Ashdown and lowermost Wadhurst formations of the Hastings Group), that is *Cypridea propunctata* to *Cypridea menevensis*-subzones of Horne (1995); upper Berriasian to lower Valanginian according to Hoedemaeker and Herngreen (2003)

+ *Cypridea setina*-zone of Clements (1993) "Upper" Purbeck; Broken – Shell Limestone Member, *Unio*-Member and Upper '*Cypris*' Clays and Shales Member of the Durlston Formation, type-section of the

Purbeck-Limestone Group, Durlston Bay, Swanage, England, UK; upper Berriasian according to Hoedemaeker and Herngreen (2003)

+ Middle to upper "German Wealden 3 to 5 (W3 to W5)" after Wolburg (1962), NW Germany; upper Berriasian to lower Valanginian according to Hoedemaeker and Herngreen (2003)

+ North Celtic Sea and Fastnet Basin, offshore southern Ireland, occurrence of *C. (P.) setina dotica*, Early Valanginian, Ainsworth et al. (1987)

+ lower 'Purbeck' of the southern Dobrudja, Romania, Zavoiana Member of the Amara Formation *Cypridea dunkeri* to *Cypridea granulosa* zone, Berriasian (Stoica 2007)

+ Cabretón Beds of the Urbión Group Northern Spain, Iberian Chains, Sierra de los Cameros, "Middle Purbeck" according to Kneuper-Haack (1966)

Stratigraphic range in North America: Upper Berriasian to lower Valanginian as inferred from the distribution in Europe, maximum distribution up to upper Valanginian (if synonymized with *Cypridea laevigata*).

Stratigraphic range outside North America: Europe (best data): Upper Berriasian to lower Valanginian, up to uppermost Valanginian if synonymized with *Cypridea laevigata* (Dunker 1846).

Cypridea (Pseudocypridina) setina **var.** ***rectidorsata*** **Sylvester-Bradley 1949**

(Pl. 7, Figs. 9-11, 13-15)

pars	1939	*Langtonia setina* sp. nov. – Anderson, p. 305, pl. 12, figs. 7a [not 7b]
•	1941	*Cypridea inornata* sp. nov. – Peck, p. 301, pl. 44, figs. 33-34, 36, [35 questionable]
*	1949	*Cypridea (Pseudocypridina) setina rectidorsata* subsp. nov. – Sylvester-Bradley, p. 147, fig. 24
	1951	*Pseudocypridina inornata* (Peck) – Peck, p. 319, pl. 48, figs. 10, 11 [non pl. 48, figs. 8, 9]
	1958	*Cypridea inornata*? Peck – Sohn, pl. 1, figs. 17, 18
	1959	*Cypridea rectidorsata* Sylvester-Bradley – Wolburg, p. 293, pl. 5, fig. 1
	1962	*Cypridea (Pseudocypridina) setina rectidorsata* Sylvester-Bradley – Anderson, p. 23, pl. 1, fig. 1
	1962a	*Cypridea rectidorsata* Sylvester-Bradley – Wolburg, p. 211, pl. 31b, fig. 8
•	1962a	*Cypridea setina* (Anderson) – Wolburg, p. 211, pl. 31b, fig. 12
non	1962a	*Cypridea setina* (Anderson) – Wolburg, p. 211, pl. 31b, figs. 9-11 [*C. setina setina*]
	1971	*Cypridea setina rectidorsata* – Anderson and Bazley, p. 84, pl. 16, fig. 9

- 1979 *Cypridea (Pseudocypridina) inornata* (Peck) – Sohn, p. 15-16, pl. 3, figs. 18-23 [non pl. 7, figs. 2-4]
- 2007 *Cypridea setina* ssp. 1 – Stoica, p. 11, pl. 11, figs. 1-3; pl. 12, figs. 1-3; textfig. 72a, b

Material: Few carapaces, questionably in samples of the Lakota Formation BCE, FRCA, and ARCR CHz1. Fig. 2, loc. 1, 3 and 5, Chilson Member of the Lakota Formation. Some carapaces from the Cedar Mountain Formation (upper part of the Yellow Cat Member), sample PS 1a-70, Fig. 2, loc. 10. See Fig. 11 also.

Dimensions (in mm): Overall length: 1.05-1.24
Own Specimens:

(Presumed females)	L: 1.05-1.24	H: 0.63-0.73	W: ~0.48

As given in the literature (various references):

(Presumed females)	L: ~1.05	H: ~0.68	W: ~0.50

Type locality and horizon: Chilcomb Down No. 1 Borehole, Hampshire, at 1710 ft., Hastings Group of the Wealden Supergroup

Holotype: Actual number is In. 39180 (BMNH, London) as selected by Sylvester-Bradley (1949).

Diagnosis: A variety of *C. (P.) setina* with rounded-oblong carapace, dorsal outline and margins straight in both valves. Anterior and posterior margins of about equal height, inclination of dorsal margin and outline weak to barely cognizable.

Description: Carapace Shape: Small to medium sized. Carapace shape in lateral view oblong, well-rounded and slightly to barely tapering towards posterior end. Maximum length slightly below middle height, maximum height at 2/5 of length (at anterior cardinal angle), maximum width at or hardly behind middle length. LV>RV, weakly inequivalve, slightly overreaching along entire margin except for the point as well as posterior part of rostrum and alveolus. Overreach (excluding cyathus) most distinctive at anterodorsal margin, posterodorsal margin including posterior hinge margin; at ventral margin stronger overreach due to ventral ridge of LV. Overlap moderate at anterior and posterior margins, strong at ventral margin. No overlap at hinge margin area.

Anterior margin broad and slightly infracurvate, ventrally prolongating into a well-developed rostrum, with a moderately long, slightly convex dorsal part. Rostrum moderately bending backwards with about 45°, its point slightly overreaching the ventral margin of the smaller RV, but hardly ever reaching the ventral outline of the LV. Alveolus weakly developed, with slightly incising and narrow alveolar notch in LV, somewhat stronger developed in RV. Alveolar furrow hardly present in both valves, triangular, very shallow and rather developed as a weak anteroventral lateral flattening, being ventrally delimited by a very weak alveolar ridge.

Posterior margin equicurvate to slightly infracurvate, only slightly narrower than anterior margin. LV's posterior margin ventrally passing into a narrow crescent cyathus being obtuse and rounded.

Dorsal margin partly incised (hinge), dorsal outline about straight in both valves, weakly inclined towards posterior end with an angle of about 45°. Anterior cardinal angle rounded, obtuse but relatively well-marked, about 140-145°. Posterior cardinal angle well-rounded, gently passing into posterior margin and thus its apex is difficult to position, about 145-150°. Hinge margin straight to slightly concave, about 1/4 of total carapace length, overreached by both cardinal angles.

Ventral margin straight to slightly concave; convex venter in larger LV feigned through weakly developed overreaching ventral ridge.

Carapace elongated-ovate (drop-shaped) in dorsal view, tapering towards anterior end. Hinge margin weakly incised, forming a shallow furrow of moderate width and with nearly no lateral offset of the dorsal furrow.

Ventral overlap strong and moderately convex. Ventral view showing diffusely delimited ventral ridge of overlapping LV. A vague outline of alveolar furrows and alveolar ridges visible in ventral view.

Ornamentation:
1. Area-wide ornamentation elements/surface characters: None. Surface smooth with very few simple pores of 1-2µm diameter, barely to detect; evenly scattered with a mean distance of about 70µm to each other.

2. Local ornamentation elements: None, totally absent.

Internal characters: Not well known. Free inner lamella of moderate width anteroventrally, posteroventrally being narrow (cf. sketches of Sylvester-Bradley 1949, fig. 25).

Muscle scar pattern: As figured by Wolburg (1959, pl. 5, fig. 16 – refigured in Fig. 13 herein) for *Cypridea setina* (Anderson 1939).

Morphologic variation: Some variation in dorsal outline, which can be straight to slightly convex.

Ontogenetic variation: No data.

Dimorphism: Sexual dimorphism present as tentatively assumed herein in analogy to morphologic trends in modern ostracods. *C. (P.) setina* var. *rectidorsata* is considered to be the female dimorph of *C. (P.) setina* var. *setina* herein (see also under dimorphism of the latter taxon below), because it is somewhat shorter and higher, thus appearing more compact (see Chapter 6.2. also).

Discussion: This variant is rare in North America, based on the few published (formerly under the name *Cypridea inornata*) and own data available. From the two samples of the Lakota Formation the occurrence of this variant is questionable, because of the bad preservation. Unquestionable is its the presence in the Yellow Cat Member of the Cedar Mountain Formation, Utah (see Pl. 7, Figs. 13, 14).

If *Cypridea (Pseudocypridina) setina* (Anderson 1939) and *Cypridea (Pseudocypridina) laevigata* (Dunker 1846) are synonymized (refer to discussion of *Cypridea (P.) setina* above), this has consequences on the stratigraphic distribution of the species. In addition, the following variants of *C. (P.) laevigata* (being regarded subspecies by F. W. Anderson in Anderson et al. 1967) are believed to be synonymous to *C. (P.) setina* var. *rectidorsata* by the present author:

a) *Cypridea (Pseudocypridina) laevigata* var. *hawkhurstensis* Anderson 1967
b) *Cypridea (Pseudocypridina) laevigata* var. *philpottsi* Anderson 1967
c) *Cypridea (Pseudocypridina) laevigata* var. *subquadrata* Anderson 1967

Differential diagnosis: In contrast to *Cypridea (Pseudocypridina) setina* var. *rectidorsata*, *C. (P.) s.* var. *setina* is more elongate (higher L/H-coefficient), has a distinct inclination of the dorsal margin and outline with its posterior margin is distinctly narrower than the anterior one, and thus tapering towards posterior end in lateral view. In dorsal view, it appears very elongate, only slightly tapering towards anterior end.

As for the species *Cypridea (P.) setina* in general (see above), this variant is different from other species in lacking any ornamentation elements.

Paleoecology: As for the genus.

Faunal association (See Fig. 11 also): In the present author's sample ARCR CHz1 (Lakota Formation) associated with *Cypridea (Pseudocypridina) setina* var. *setina* (Anderson 1939), *Cypridea? minuta* (Peck 1951), *Cypridea obesa* Peck 1951 some representatives of the Darwinulidae: *Alicenula?* sp., and some Ostracoda indet. (Candonidae?). In sample PS2a (Cedar Mountain Formation) associated with *Cypridea (Pseudocypridina) setina* var. *setina* (Anderson 1939), *Cypridea (Longispinella) longispina* Peck 1941 and *Cypridea* ex gr. *tuberculata* cf. *C. tilleyi* Loranger 1951.

Stratigraphic and geographic distribution (Stratigraphic terms follow the most recent terminology available):

North America:
+ Yellow Cat Member of the Cedar Mountain Formation, Lower Cretaceous, north of Moab, east-northeast of the Ringtail Mine, UT, U.S.A. (Fig. 2, loc. 10, this study)

+ Minnewaste Limestone Member of the Lakota Formation, Lower Cretaceous, Calico Canyon south of Buffalo Gap [but NE of the town of Buffalo Gap!] in the SE1/4 sec. 24, T. 6 S., R. 6 E., Custer County, South Dakota, U.S.A. (Peck 1951 loc. 28, as equivalent to Peck and Craig 1962 and Craig 1961, loc. 184P [not Fall River County!])

Europe:
+ Studland to Battle faunicycles (cycles Nos. 30 to 40) of Anderson (1985) as equivalent to upper Purbeck Group (Durlston Formation) to Lower Wealden Supergroup (Ashdown and lowermost Wadhurst formations of the Hastings Group), that is *Cypridea propunctata* subzone of Horne (1995); upper Berriasian to lowermost Valanginian according to Hoedemaeker and Herngreen (2003)

+ lower 'Purbeck' of the southern Dobrudja, Romania, Zavoiana Member of the Amara Formation *Cypridea dunkeri* to *Cypridea granulosa* zone, Berriasian (Stoica 2007)

Questionable occurrence:

North America:
+ Chilson Member of the Lakota Formation, Lower Cretaceous, Buck and Devil's canyons, southern Black Hills Area (Fig. 2, locs. 1 and 2), South Dakota, U.S.A. (this work)

Stratigraphic range in North America: As inferred from the English Purbeck/Wealden: upper Berriasian to lower Valanginian; maximum distribution up to upper Valanginian (if synonymized with *Cypridea laevigata*).

Stratigraphic range outside North America: Upper Berriasian to lower Valanginian. Up to upper Valanginian if *Cypridea (Pseudocypridina) setina* is synonymized with *Cypridea (Pseudocypridina) laevigata* (Dunker 1846), some variants of which are also very oblong and similar to *C. (P.) setina* var. *rectidorsata* (refer to discussion right above).

***Cypridea (Pseudocypridina) setina* var. *setina* (Anderson 1939)**

(Pl. 7, Figs. 1-8, 12)

pars*	1939	*Langtonia setina* sp. nov. – Anderson, p. 305, pl. 12, fig. 7b [not 7a]
•	1941	*Cypridea inornata* sp. nov. – Peck, p. 301, pl. 44, figs. 33, 34, 36 [35 questionable]
	1949	*Cypridea (Pseudocypridina) setina* setina (Anderson 1939) comb. nov. – Sylvester-Bradley, p. 146
	1951	*Pseudocypridina inornata* (Peck) – Peck, p. 319, pl. 48, figs. 8, 9 [non pl. 48, figs. 10, 11]
	1958	*Cypridea inornata*? Peck – Sohn, pl. 1, figs. 17, 18
	1959	*Cypridea setina* (Anderson) – Wolburg, p. 294, pl. 5, figs. 2, 15-17
	1962	*Cypridea (Pseudocypridina) setina setina* (Anderson) – Anderson, p. 24, pl. 1, fig. 2
•	1962a	*Cypridea setina* (Anderson) – Wolburg, p. 211, pl. 31b, figs. 9-11
non	1962a	*Cypridea setina* (Anderson) – Wolburg, p. 211, pl. 31b, fig. 12 [*C. setina rectidorsata*]
	1971	*Cypridea setina setina* (Anderson) – Anderson and Bazley, p. 85, pl. 17, fig. 10
•	1979	*Cypridea (Pseudocypridina) inornata* (Peck) – Sohn, p. 15-16, pl. 7, figs. 2-4 [non pl. 3, figs. 18-23]
v	1985	*Cypridea setina setina* (Anderson) – Anderson, p. 31, pl. 5, fig. 9 [lectotype]
•	2007	*Cypridea setina* ssp. 2 – Stoica, p. 113, pl. 11, figs. 4-7; pl. 12, figs. 4-6

Material: About 200 carapaces and few valves, moderately to well-preserved. Samples: PS 1a-70, PS 2a, SKM 060705 (=PS 2c), Yellow Cat Member of the Cedar Mountain Formation, Fig. 2, loc. 10. FRCA*, FRCA, BC5 04, ARCR CHz1, Chilson Member of the Lakota Formation. Few specimens from the Peck Collection, University of Missouri, Columbia (MO), U.S.A.

Dimensions (in mm): Overall length: 0.95-1.41
Own specimens:
Presumed males L: 1.05-1.24 H: 0.63-0.73 W: ~0.31

As given in the literature (various references):
Presumed males L: 0.95-1.41 H: 0.60-0.91 W: ~0.50

Type locality and horizon: Chilcomb Down No. 1 Borehole, Hampshire, at 1710 ft., Hastings Group of the Wealden Supergroup, UK.

Lectotype: GSM Mik(M) 535001, formerly GSM 60682, as selected by Sylvester-Bradley (1949), Anderson collection, BGS Headquarters, Keyworth, UK.

Diagnosis: A variety of *C. (P.) setina* with elongated-rectangular carapace tapering towards posterior end, dorsal outline and margins moderately inclined. Anterior margin higher than posterior one. Elongated-ellipsoid in dorsal view, weakly tapering towards anterior end.

Description: Carapace Shape: Small to medium sized. Carapace shape in lateral view elongated-rectangular, well-rounded and slightly tapering to posterior end. Maximum length slightly below middle height, maximum height at 2/5 of length (at anterior cardinal angle), maximum width at or hardly behind middle length (anterior of 3/5 of length). LV>RV, LV slightly overreaching RV along entire margin except for the point and posterior part of rostrum, and alveolus. Overreach (excluding cyathus) most distinctive at anterodorsal margin, posterodorsal margin including posterior hinge margin, and ventral margin, additionally overreached by ventral ridge of LV. Overlap moderate at anterior and posterior margins, strong at ventral margin, weak at hinge margin area Pl. 7, Fig. 4).

Anterior margin broadly infracurvate with long straight dorsal part. Rostrum short, broad and strongly tapering, with bending (backwards) angle of 45°, its point slightly overreaching the ventral margin of the smaller RV, but hardly ever reaching the ventral outline of the LV. Alveolus weakly developed, alveolar notch narrow and slightly incising in LV, somewhat stronger developed in RV. Alveolar furrow hardly present in both valves, triangular, very shallow and rather developed as a weak anteroventral lateral flattening, being ventrally delimited by a very weak alveolar ridge.

Posterior margin weakly infracurvate, slightly stronger in smaller RV, both distinctly narrower than anterior margin. LV's posterior margin ventrally passing into a narrow crescent cyathus, strongly obtuse and rounded, sometimes hardly visible in left lateral view.

Dorsal margin partly incised (hinge), dorsal outline of LV gently convex, nearly straight. RV usually less convex, straight in most cases. Dorsal margin and outline inclined in relation to the base line, with an angle of about 15°. Anterior cardinal angle rounded, obtuse but relatively well-marked, about 140-145°. Posterior cardinal angle well-rounded, gently passing into posterior margin and thus its apex difficult to position, about 150-155°. Hinge margin straight to slightly concave, about 1/4 of total carapace length, overreached by both cardinal angles.

Ventral margin straight to slightly concave; convex venter in larger LV feigned through weakly developed overreaching ventral ridge.

Carapace elongated-ellipsoid in dorsal view, gently tapering towards anterior end. Hinge margin weakly incised, forming a shallow furrow of moderate width. Sinuous appearing overlap in dorsal view due to convex overlap of LV over RV at the cardinal angles and flange of RV overlapping the LV along hinge margin. Strong ventral overlap, moderately convex.

Ventral view showing diffusely delimited weak ventral ridge in overlapping LV. In ventral view, a vague outline of the alveolar grooves and ridges is visible.

Ornamentation:
1. Area-wide ornamentation elements/surface characters: Surface smooth with very few simple pores of 1-2µm diameter, barely to detect; about evenly scattered with a mean distance of about 70µm to each other.

2. Local ornamentation elements: None, absent.

Internal characters: Not observed or described. Sylvester-Bradley (1949, fig. 25) figures two sketches of internal views of *C. (P.) setina rectidorsata* (dealt with under this variety herein, see above).

Muscle scar pattern: As figured by Wolburg (1959, pl. 5, fig. 16 – refigured in Fig. 13 herein) for *Cypridea setina* (Anderson 1939).

Morphologic variation:
straight dorsal margin feigned through dipping to the left (RV margin visible only)

Ontogenetic variation: Few data available (see Pl. 7, Fig. 10). In comparison with the adults, the juveniles have a less higher posterior margin (hinge margin inclination more than 10°) which also seems to be less well-rounded in earlier instars, i.e. more distinctly infracurvate, and also show a smooth carapace surface (no ornamentation elements at all). In addition, the juvenile specimens tend have a less relative height (higher L/H-coefficient), being combined with higher values of the anterior (around 150°) and posterior cardinal angles as well as a lower angle of inclination of the straight dorsal part of the anterior margin (around or below 20°).

Dimorphism: Sexual dimorphism tentatively assumed herein. *Cypridea (Pseudocypridina) setina* var. *setina* is believed to be the male dimorph (see Chapter 6.2. also).

Discussion: *Cypridea (P.) setina* var. *setina* is the more common variant known thus far in North America (as given in the stratigraphic and geographic distribution below).

Cypridea inornata Peck 1941 in Peck (op. cit.) and Sohn (1979) are assigned to this variant because they perfectly match Anderson's (1939, pars; 1985, pl. 5, fig. 9, lectotype) specimens. One well preserved specimen from Peck's collection is figured here (Pl. 7, Fig. 2). Both specimens have been personally studied by the present author.

Cypridea setina ssp. 2 of Stoica (2007) is assigned to this variant because of its striking similarity in outline.

If *Cypridea (Pseudocypridina) setina* (Anderson 1939) and *Cypridea (Pseudocypridina) laevigata* (Dunker 1846) are synonymized (refer to discussion of *Cypridea (P.) setina* above), this has consequences on the stratigraphic distribution of the species. In addition, the following variants (being regarded subspecies by F. W. Anderson in Anderson et al. 1967) of *C. (P.) laevigata* are believed to be synonymous to *C. (P.) setina* var. *setina* by the present author:

a) *Cypridea (Pseudocypridina) laevigata* var. *fairlightensis* Anderson 1967
b) *Cypridea (Pseudocypridina) laevigata* var. *laevigata* (Dunker 1846)
c) *Cypridea (Pseudocypridina) laevigata* var. *leonardi* Anderson 1967
d) *Cypridea (Pseudocypridina) laevigata* var. *wadhurstensis* Anderson 1967

Differential diagnosis: In contrast to *Cypridea (Pseudocypridina) setina* var. *setina*, *C. (P.) s.* var. *rectidorsata* is less elongate and more oblong (lower L/H-coefficient), barely shows an inclination of the dorsal margin and outline, the anterior and posterior margins are of about equal height, and thus not tapering towards posterior end. In dorsal view, it appears elongated-ovate, distinctly tapering towards anterior end.

As for the species *Cypridea (P.) setina* in general (see above), this variant is different from other species in lacking any ornamentation elements.

Paleoecology: As for the genus.

Faunal association (see Fig. 11 also): In the Lakota Formation: with *Theriosynoecum fittoni* (Mantell 1944) [see Sames in review], *Cypridea (Pseudocypridina) piedmonti* (Roth 1933), *Cypridea* ex gr. *tuberculata* cf. *C. tilleyi* Loranger 1951, *Cypridea (Longispinella) longispina* Peck 1941 syn. *C. (L.) asymmetrica* (Sohn 1979), representatives of the family Darwinulidae Brady and Norman 1889 (*Alicenula?* sp.), and representatives of the Trapezoidellidae Sohn 1979: *Trapezoidella trapezoidalis* (Roth), *Limnocypridea? morrisonensis* (Roth 1933), *Cypridea? minuta* (Peck 1951).

In the Cedar Mountain Formation: with *Cypridea* ex. gr. *alta* Wolburg 1959, *Cypridea (Longispinella) longispina* Peck 1941, *Cypridea* ex. gr. *tuberculata* cf. *C. tilleyi* Loranger 1951, representatives of the family Darwinulidae Brady and Norman 1889 (*Alicenula?* sp.).

As given in the literature (Sohn 1979, Lakota Formation), additionally associated with *Trapezoidella rothi* Sohn 1979.

Stratigraphic and geographic distribution (Stratigraphic terms follow the most recent terminology available):

North America:

+ Chilson Member of the Lakota Formation, Lower Cretaceous, southern Black Hills Area (Fig. 2, locs. 1, 3 and 5), South Dakota, U.S.A. (this work)

+ Yellow Cat Member of the Cedar Mountain Formation, Lower Cretaceous, Fig. 2, loc. 10, Utah, U.S.A. (this work)

As for the occurrence in North America, the forms were formerly designated and published under *Cypridea inornata* Peck 1941, *Pseudocypridina inornata* (Peck 1941) or *Cypridea (Pseudocypridina) inornata* Peck 1941:

+ Minnewaste Limestone Member of the Lakota Formation, Lower Cretaceous, Calico Canyon south of Buffalo Gap [but NE of the town of Buffalo Gap!] in the SE1/4 sec. 24, T. 6 S., R. 6 E., Custer County, South Dakota, U.S.A. (Peck 1951 loc. 28, as equivalent to Peck and Craig 1962 and Craig 1961, loc. 184P [not Fall River County!])
+ Minnewaste Limestone Member of the Lakota Formation, Lower Cretaceous, partings in exposure of Skyline Drive, east of Hot Springs, Fall River County, South Dakota, U.S.A. (Peck 1951, loc. 29)
+ [Chilson Member of the] Lakota Formation, Lower Cretaceous, north side of Fall river Road 3.2. miles southeast of 1940 city limits Hot Springs, Fall River County, South Dakota, U.S.A. (Peck 1951, loc. 30 as equivalent to Peck and Craig's 1962 loc. D286 and Craig's 1961 loc. 435P; about loc. 3, Fig. 2 herein)
+ Lakota Formation [Chilson Member], Lower Cretaceous, Black Hills area, Sohn's (1979, fig. 2 therein) loc. 2, Lawrence County (about equivalent to loc. 7, Fig. 2 herein), and localities Sohn's (1979, fig. 2 therein) localities 13 to 18, Fall River County, South Dakota, U.S.A

+ Cloverly Formation, Early Cretaceous, southeastern flank of Rawlins uplift, about 1/4 mile north of unimproved road bypassing Rawlins on the northeast, in the NW1/4 sec. 6, T. 21 N., R. 86 W., Rawlins quadrangle, Carbon County, Wyoming, U.S.A. (Peck and Craig 1962, loc. 954P)

+ Kootenai Formation, Lower Cretaceous, along the road 1 mile southwest of Griffin, about 14 miles southeast of Great Falls, T. 18 N., R. 4 E., Montana, U.S.A (Peck 1941, loc. 23)

Europe:

+ Lulworth to Battle faunicycles (cycles Nos. 34 to 40) of Anderson (1985) as equivalent to upper Purbeck Group (Durlston Formation) to Lower Wealden Supergroup (Ashdown and lowermost Wadhurst formations of the Hastings Group), that is *Cypridea propunctata* subzone of Horne (1995); upper Berriasian to lowermost Valanginian according to Hoedemaeker and Herngreen (2003)

+ lower 'Purbeck' of the southern Dobrudja, Romania, Zavoiana Member of the Amara Formation *Cypridea dunkeri* to *Cypridea granulosa* zone, Berriasian (Stoica 2007)

Questionable occurrence:

North America:

+ Lakota Formation [Chilson Member?], Lower Cretaceous, cut on railroad through a Lakota hodgeback just north of Sturgis, South Dakota, U.S.A. (Craig 1961, loc. 416P as also given in the locality catalog of Peck at the University of Missouri, Columbia)

Note: The sample comes from "a shale below a thick and massive sandstone" being questionably equivalent to the mudstones sampled by the present author at localities 6, 8 and 9 (Fig. 2 herein) and believed to be equivalent to the Fuson Member of the Lakota. Since Craig's material is not in Peck's collection, the species identification cannot be verified, and all the present author's samples from the same area and (tentatively) assumed same stratigraphic level do not contain any specimens of *Cypridea (P.) setina*.

Stratigraphic range in North America: Upper Berriasian to lower Valanginian as inferred from the English Purbeck/Wealden) distribution in Europe; maximum distribution up to upper Valanginian (if synonymized with *Cypridea laevigata*).

Stratigraphic range outside North America: Europe (best data): Upper Berriasian to lower Valanginian. Up to upper Valanginian if *Cypridea (Pseudocypridina) setina* is synonymized with *Cypridea (Pseudocypridina) laevigata* (Dunker 1846), some variants of which are also very oblong and similar to *C. (P.) setina* var. *setina* (refer to discussion right above).

***Cypridea alta*-group**

Remarks: This species group has been first defined by Wolburg (1959), who erected the new species *Cypridea alta* Wolburg 1959 and included the taxa *Cypridea alta alta* Wolburg 1959, *Cypridea alta formosa* Wolburg 1959 and *Cypridea alta wicki* Wolburg 1959. According to Wolburg (op. cit., p. 262), this group is characterized by a relatively high carapace [i.e., low L/H-coefficient], a distinct punctation and a short but well-developed rostrum.

Additionally, representatives of this group all are strongly inequivalve, have a distinct but small cyathus with a narrow basis and being weakly obtuse, bear a strong ventral ridge. Most conspicuous character is strong ridge- or bulge-like overreach (=> *dorsal ridge*) of the larger valve (LV mostly) along the dorsal margin (e.g. Fig. 7/B), often covering the cardinal angles and being highest in the anterior part of the dorsal margin. For this reason, the name *Cypridea alta*-group (from Latin *altus* – high), although other species included (see below) might be considered more characteristic.

Based on the diagnostic characters, this group includes the following species in the present author's view (species in alphabetical order):

- *Cypridea alta alta* Wolburg 1959 (dorsal ridge weak)
- *Cypridea alta formosa* Wolburg 1959
- *Cypridea alta wicki* Wolburg 1959
- *Cypridea dolabrata angulata* (Martin 1940) syn. *Cypridea angulata* Martin 1940

- *Cypridea dolabrata dolabrata* (Anderson 1939)
- *Cypridea dolabrata kingsclerensis* Anderson 1971
- *Cypridea inaequalis* Wolburg 1959

Questionable (as found in the literature, to be further investigated):
- *Cypridea amisia* Wolburg 1959
- *Cypridea cymerata* Musacchio 1971 (inverse!)
- *Cypridea dromedarius* Krömmelbein 1962
- *Cypridea latiovata* Hou 1958 [*Cypridea (Cyamocypris) latiovata* therein]
- *Cypridea ludica* Musacchio 1971
- *Cypridea mundula* Lyubimova 1956
- *Cypridea triangula* Liu 1959 (with distinct => *alveolar ridge*!)
- *Cypridea verrucosa* Jones 1878
- *Cypridea valdensis valdensis* (Sowerby 1836) as figured by Anderson (1985, pl. 8, fig. 18)
- *Cypridea zhijiangensis* Zhao 1978

Cypridea ex gr. *alta* described here (see below) has the strongest similarities to *Cypridea alta formosa* Wolburg 1959 syn. *Cypridea alta wicki* Wolburg 1959 (spines of the latter considered taxonomically insignificant here).

Stratigraphic range:
- *Cypridea alta* Wolburg 1959, "German Wealden", 'Wealden 3' and 'Wealden 4' (Wolburg 1959), upper Berriasian to lowermost Valanginian after Hoedemaeker and Herngreen (2003)
- *Cypridea dolabrata* (Anderson 1939), Scallop to Hythe faunicycles (cycle No. 29 to No. 46) of Anderson (1985), being middle/upper to lower Valanginian according to Hoedemaeker and Herngreen (2003)
- *Cypridea inaequalis* Wolburg 1959, "German Wealden", upper 'Wealden 2' to 'Wealden 3' (Wolburg 1959), middle Berriasian to upper Berriasian according to Hoedemaeker and Herngreen (2003).

Note: To the best knowledge and investigation of the present author, ostracods of the *Cypridea alta*-group as defined here, particularly showing the strong dorsal ridge and small cyathus in combination with being strongly inequivalve, generally occur in the lower part of the Lower Cretaceous (Berriasian to Valanginian; or older), mainly. Some exceptions, however, do occur: *Cypridea cymerata* Musacchio 1971, [upper?] Hauterivian-Barremian, and *Cypridea valdensis valdensis* (Sowerby 1836), (Valanginian) Hauterivian-Barremian, for example. Owing to the common uncertainties in the age determination of Lower Cretaceous nonmarine deposits, however, this matter has to be further investigated.

Cypridea ex gr. *alta* Wolburg 1959

(Pl. 8, Figs. 1-6)

? *Cypridea alta formosa* subsp. nov. – Wolburg, p. 264, pl. 3, figs. 2, 11, 12

? *Cypridea alta wicki* subsp. nov. – Wolburg, p. 266, pl. 3, figs. 2, 11, 12

Material: Eight carapaces, badly preserved, on part close to "steinkern" preservation.

Dimensions (in mm): Overall length: 0.86-0.97
Own specimens (RV distinctly smaller):
L: 0.86-0.97 H: 0.64-0.69 L: ~0.41

Type locality and horizon: Not applicable (yet). Only known from the upper Yellow Cat Member of the Cedar Mountain Formation at one locality (Fig. 2, loc. 10), north of Moab, east-northeast of the Ringtail Mine, UT, U.S.A.

Holotype: Not applicable (yet).

Diagnosis: LV>RV, strongly inequivalve. Lateral outline as given by the LV inflated ovate, with strong dorsal ridge in the LV

Remarks: The taxonomic status of this species is kept open for the reason that only few badly preserved specimens do exist this far. Better material is necessary. The similarity to known taxa is strong, nevertheless, this could be a true new species, but with such bad preservation a description of a new species cannot be justified in the view of the present author.

Description: Carapace Shape: Small sized (<1mm). General outline, as defined by LV, inflated ovoid in lateral view, dorsal outline somewhat more prominent due to dorsal ridge. LV>RV, strongly inequivalve, outline of LV and RV strongly different. LV: Maximum length at mid-height, maximum height at mid-length. RV: Maximum length slightly below mid-height, maximum height at 2/5 length. Maximum width at about or slightly behind mid-length. Overlap of LV moderate to strong at all margins except hinge margin area. Very strong overreach of LV along hinge margin through dorsal ridge, strong overreach at ventral margin through ventral ridge.

Anterior margin of both valves weakly infracurvate, with a long straight dorsal part, inclined with about 30°. Anterior margin ventrally passing into a well-defined rostrum, moderately (about 50°) bending backwards. Alveolar notch well-defined and moderately broad, somewhat less at RV, upwards continuing into a very narrow triangular groove behind the rostrum, separated from the main alveolar furrow by a strong, slightly undulated alveolar ridge. Alveolar furrow triangular and broad, but very short, reaching not higher than 1/4 of maximum height, and relatively shallow. Rostrum, alveolar furrow and alveolar ridge less developed at RV, but still recognizable.

Posterior margin nearly equicurvate, ventrally protruding into a well-developed, weakly obtuse-angled cyathus (circa 110°) in LV, being relatively narrow in its width along the outline.

Dorsal margin of LV strongly convex along hinge margin because of protruding dorsal ridge, anteriorly and posteriorly passing into the respective margins with a slightly concave, nearly straight curvature. LV's cardinal angles masked due to dorsal ridge, position of the anterior one between 1/5 and 2/5 of maximum length, anterior one not truly definable, but definitely posterior to dorsal ridge. Dorsal margin of RV straight to slightly convex, weakly inclined (circa 12°) towards posterior end. RV's anterior cardinal angle distinct, circa 140°, its angular point rounded, located between 1/5 and 2/5 of maximum length. Posterior cardinal angle of RV strongly rounded and thus, barely recognizable, circa 150°. Length of hinge margin about 2/5 of total carapace length.

Ventral margin of both valves straight to very little convex. Moderately convex ventral margin feigned through presence of a well-developed and strongly overreaching ventral ridge at LV.

Carapace outline ellipsoidal in dorsal view, moderately tapering to both ends. Hinge incisure present, forming a moderately deep dorsal furrow with broad flanks; partially covered on the LV by a strong narrow, undulated ridge beginning at the anterior cardinal angles position and ending anteriorly of the posterior cardinal angle and dorsal furrow end. Position of dorsal furrow slightly oblique towards RV.

LV strongly convex overlapping the RV in ventral view. LV with moderately protruding, narrow ventral ridge, reaching from posterior alveolar region to anterior cyathus region.

Ornamentation:

1. Area-wide ornamentation elements: Because of weathering, the carapace surface is strongly degenerated. It is, however, covered with many pustulae that are considered to represent remains of internal (normal) pore fillings. In some specimens, a linear pattern in the ventrolateral and posterolateral regions can be recognized, running subparallel to the outer margins.

2. Local ornamentation elements: Not observed, perhaps due to preservation. No indication for strong elements (nodes, spines, tubercles), thus very improbable. Most probably punctated, better preserved material necessary.

Internal characters: Not observed.

Muscle scar pattern: Not observed.

Morphologic variation: Minor. Most of the slight differences in outline and shape recognizable so far result from preservation and diagenesis (deformation of carapace).

Ontogenetic variation: Not observed.

Dimorphism: No dimorphism recognized.

Discussion: Although the specimens from the Cedar Mountain Formation are more or less badly preserved, most important characters are well-visible, i.e., lateral outline, rostrum, alveolus, cyathus, dorsal and ventral ridges, and the different valves. Owing to the striking similarity of the species described here to *Cypridea alta formosa* Wolburg 1959 syn. *Cypridea alta wicki* Wolburg 1959 (spines/tubercles or node like-tubercles of the latter considered taxonomically insignificant herein) in overall shape and characters, it is assigned to the *Cypridea alta*-group. However, since its surface characters are not visible anymore and, in particular, it bears a strong alveolar ridge, the presence of which has to be verified in the types of Wolburg's (1959) specimens—it is not visible in Wolburg's (1959) figures, but in some figures of specimens assigned to *Cypridea alta* in other publications—the species described her is not definitely assigned to *Cypridea alta* (yet).

Differential Diagnosis: *Cypridea* ex gr. *alta* Wolburg distinctly differs from all other taxa described here in its outline, the presence of the strong dorsal ridge and that it is strongly inequivalve.

The sole other species described here being moderately to strongly inequivalve (lesser than the former) is *Cypridea (Longispinella) longispina* Peck syn. *C. (L.) asymmetrica* (Sohn). The latter, however, differs from *Cypridea* ex gr. *alta* Wolburg in having a much larger alveolar furrow and no true dorsal ridge, but an overreach of the LV instead, which is a (hollow) protrusion of the dorsal part of the valve.

Paleoecology: As for the genus.

Faunal association (see Fig. 11 also): In the Yellow Cat Member of the Cedar Mountain Formation with *Cypridea (Pseudocypridina) setina* var. *setina* (Anderson 1939), *Cypridea (Pseudocypridina) setina* var. *rectidorsata* Sylvester-Bradley 1949, *Cypridea (Longispinella) longispina* Peck 1941 and *Cypridea* ex gr. *tuberculata* cf. *Cypridea tilleyi* Loranger 1951.

Stratigraphic and geographic distribution (Stratigraphic terms follow the most recent terminology available):

+ Yellow Cat Member of the Cedar Mountain Formation, north of Moab, east-northeast of the Ringtail Mine, UT, U.S.A. (Fig. 2, loc. 10)

Questionable occurrence: Not applicable (identic forms unknown thus far).

Stratigraphic range in North America: As deduced from the faunal association with *Cypridea (Pseudocypridina) setina* var. *setina* (Anderson 1939): upper Berriasian to lower Valanginian, up to upper Valanginian if *Cypridea (P.) setina* (Anderson 1939) and *Cypridea laevigata* (Dunker 1846) are synonymized. As deduced from the striking similarity to *Cypridea alta formosa* Wolburg 1959 as occurring in the English Purbeck/Wealden: upper Berriasian to lowermost Valanginian.

Stratigraphic range outside North America: Not applicable.

Cypridea tuberculata-group

Remarks: Eponymous species is *Cypridea tuberculata* (Sowerby 1836). As defined herein, this morphogroup comprises of an inhomogenous combination of representatives of *Cypridea* (not necessarily closely related) with distinct and more or less strongly developed => *tuberculation* (not to be confused with => *nodes*!!!, the smaller of which are sometimes called "granules", e.g. *Cypridea granulosa*, however, these are in fact swollen => *node-like tubercles*), mainly characterized by numerous paired tubercles (i.e. these are arranged oppositely to each other) that are of about equal size and more ore less evenly distributed on the valve's surface. Alternatively, there are more or less regular patterns of two horseshoe-shaped rows of tubercles covering the anterocentral, centroventral and posterocentral areas (cf. Fig. 3), thereby omitting the (central) area where the central muscle scar field is located, and opening towards dorsal margin (centrodorsal). The latter are complemented by anterolateral, ventrolateral and posterolateral tubercles that are irregularly distributed to a greater or lesser extend. In any case and even if the central- and centrodorsal to dorsolateral regions (see Fig. 3) are omitted, the remaining areas show a regular pattern. Single "erratic" tubercles of the same or smaller size can occur as well as single, central to subcentral larger spines.

Species with such typical tuberculate pattern (cf. also Anderson 1967, p. 239, fig. I/l) are pooled and defined as *Cypridea tuberculata*-group herein and considered to represent a phylogenetic lineage of *Cypridea tuberculata*, including its varieties. Other carapace characters are as for *Cypridea tuberculata*: Lateral outline suboblong, anterior cardinal angle somewhat prominent, rostrum relatively broad and short, alveolar furrow narrow and shallow but distinct and reaching up to 1/3 of height, with alveolar ridge(?), cyathus moderately developed and slightly obtuse—thereby possibly including forms such as *Cypridea jonesi* Martin 1940 and *Cypridea aculeata aculeata* (Jones 1885), *Cypridea comptonensis* Anderson 1967.

However, there are other representatives of *Cypridea* with strongly asymmetrically distributed tubercles and/or spines that herein are excluded from the *Cypridea tuberculata*-group as defined herein. This is an almost purely descriptive group (except for potentially unrecognized taxa related to *Cypridea tuberculata*) that includes phylogenetically (most probably) not closely related taxa as well as potential ecophenotypes and/or juveniles of other groups. This includes varieties (subspecies) of *Cypridea aculeata* Jones 1885 as designated by Anderson (1967; except *Cypridea aculeata aculeata* Jones) as well as *Cypridea brendae* Anderson 1985, *Cypridea compta* Peck 1951, *Cypridea dequeenensis* Swain and Brown 1964, *Cypridea dunkeri carinata* Martin 1940, *Cypridea hispida* Anderson 1985, *Cypridea lasius* Anderson 1967, *Cypridea marina* Anderson 1967, *Cypridea melvillei* Anderson 1967, *Cypridea warlinghamensis* Anderson 1967, *Cypridea wyomingensis* (Jones 1893), for example. These species also differ in shape, development of rostrum and alveolus, and other characters from the *Cypridea tuberculata* lineage.

Concerning these tuberculate taxa, there is still a lot of taxonomic confusion needing detailed revision that is beyond the scope of this paper. Many more forms have to be included in such a review because many local ornamentation elements designated as "granules" and spines are in fact swollen tubercles (=> *node like tuberculi*).

Cypridea **ex gr.** ***tuberculata*** **(Sowerby 1836) cf.** ***Cypridea tilleyi*** **Loranger 1951**

(Pl. 8, Figs. 7-14)

non	1893	*Cypridea tuberculata* (Sow.) var. *wyomingensis* nov. var. – Jones, p. 386, pl. 15, figs. 5a-b, 6a-b
non,v	1928	*Cypridea tuberculata* var. *gypsumensis* var. nov. – Vanderpool, p. 103, pl. 13, figs. 9-12
non	1941	*Cypridea wyomingensis* Jones – Peck, p. 297, pl. 42, figs. 10-17
non	1946	*Cypridea* cf. *C. wyomingensis* Jones – Swartz and Swain, p. 372, pl. 52, figs. 19-22
?	1951	*Cypridea tilleyi* sp. nov. – Loranger, p. 2363, pl. 3, fig. 1
non	1951	*Cypridea wyomingensis* Jones – Loranger, p. 2363, pl. 2, fig. 22
?	1954	*Cypridea tilleyi* sp. nov. – Loranger, p. 292, pl. 3, fig. 1
non	1954	*Cypridea wyomingensis* Jones – Loranger, p. 293, pl. 2, fig. 22
non	1964	*Cypridea wyomingensis* Jones – Swain and Brown, p. 16, pl. 4, fig. 10; pl. 5, figs. 1a-c, textfig. 4b
non	1971	*Cypridea tuberculata langtonensis* Anderson – Anderson, p. 88, pl. 13, fig. 4
?	1971	*Cypridea australis* sp. nov. – Musacchio, p. 112, pl. 1, figs. 5, 6; pl. 2, figs. 6, 7; pl. 3, figs. 9, 10
non	1972	*Cypridea (Cypridea) wyomingensis* Jones – Swain and Brown, p. 14, pl. 1, figs. 19-20; pl. 3, fig. 1
v	1979	New genus undescribed "*Cypridea*" sp. 1 – Sohn, p. 18, pl. 7, figs. 8-12

Material: Over 100 carapaces an few valves. Samples: BC5 04, BCB1?, BC8 04, Chilson Member of the Lakota Formation, Fig. 2, loc. 1. PS 2a, Yellow Cat Member of the Cedar Mountain Formation, Fig. 2, loc. 10.

Dimensions (in mm): Overall length: 0.83-0.92
Own specimens:
L: 0.83-0.92 H: 0.57-0.63 W: ~0.39

As given in the literature (various references):
L: ~0.90

Type locality and horizon: Not applicable yet.

Holotype: Not applicable. If this proves to be a new species, then to be designated from Sohn's (1979) or material of the present author (to be deposited at the USNM).

Diagnosis: Small sized tuberculate representative of *Cypridea* with suboblong outline, well-developed rostrum only slightly bending backwards, short but deeply incising alveolar furrow being ventrally delimited by a strong alveolar ridge. Well-developed, about right-angled true cyathus with distinct limen and prominent anterior cardinal angles. Surface strongly punctate with deep puncta. Typically bearing a pronounced subcentral robust spine on each valve, and two rows of tubercles in a horseshoe-shaped pattern opening towards dorsal margin.

Description: Carapace Shape: Small sized. General shape of carapace truncated pentangular, nearly oblong. Maximum length between 1/3 and mid-height, maximum height at anterior cardinal angle, between 1/5 and 2/5 of length, maximum width at 3/5 of length. LV>RV, moderately inequivalve. LV slightly overreaching the RV along entire margin; except for venter, where LV bears a ventral ridge that moderately overreaches the ventral margin. Overlap moderate at anterior, posterior and ventral margins, weak at dorsal margin.

Anterior margin broad and slightly infracurvate to nearly equicurvate with short straight dorsal part, the latter being inclined with circa 35-40°. Rostrum broad and short, weakly tapering and with rounded point, slightly bending backwards with circa 20-25° and moderately overreaching the ventral margin while hardly reaching the LV's ventral outline. Alveolus well-developed. Rostrum separated from the ventral margin by a well incising but narrow alveolar notch. Alveolar furrow distinct and well-developed, somewhat less expressed in RV, triangular and short, deeply incised and reaching up to 1/3 of height, with small puncta. Alveolar furrow ventrally delimited by a strong alveolar ridge, which in the smaller RV separates the furrow into two parts, a very small part being below the ridge.

Posterior margin narrower than anterior one and slightly infracurvate, ventrally passing into a well-developed true cyathus that reaches or even slightly overreaches the posterior margin as well as the ventral margin (not outline) of the LV. Cyathus broad, right—angled to weakly obtuse (90-110°), its apex slightly rounded.

Dorsal margin nearly straight, the cardinal angles slightly overreaching it, not coincident with dorsal outline, the latter being slightly convex. Both, dorsal outline and dorsal margin moderately inclined towards posterior end, with about 10-17°.

Anterior cardinal angle well-marked, distinctly protruding at LV and (somewhat less) at RV, 125-135°, weakly rounded. Posterior cardinal angle strongly rounded, 135-140°. Hinge margin length about half total carapace length.

Ventral margin gently convex to straight, ventral outline moderately convex through the well-developed overreaching ventral ridge of in the LV.

Dorsal view elongated-ovoid, slightly tapering towards anterior end. Hinge margin area strongly incised, forming a well-developed dorsal furrow of 80-100µm width, slight lateral offset towards RV, and even flanks. Hinge line about straight with slight lateral offset towards right valve.

Ventral view showing distinct ridge on the overlapping LV running parallel to its margin. Ventral part of LV weekly striated, 3-4 striae with a width of one mesh diameter, meshes in between them lined up. Overlap along venter gently convex.

Ornamentation:

1. Area-wide ornamentation elements/surface characters: Whole carapace distinctly punctate tending towards reticulation, with round to ovate deep puncta of about 10-15µm diameter in a relatively fine network, except for point of rostrum, cyathus, as well as anterior and posterior area of valve overlap. Dorsal furrow and ventral overlap area also punctate, but with more indistinct (shallower) puncta. Puncta in alveolus area much smaller (< 5µm), distorted (elongated) towards rostrum.

Many irregularly scattered normal pores of 1-3µm diameter and with a mean relative distance of about 30-35µm, always in between the puncta (i.e. surrounded by a group of 3 or 4 puncta).

<u>2. Local ornamentation elements:</u> One large, robust central to centroventral or centrodorsal spine of up to circa 80µm length on each valve, always slightly posterior to mid-length, basal diameter 30-40µm. Spines in more or less opposite position to each other, weakly tapering and slightly bending backwards, point strongly rounded.

Several smaller (20-40µm), conic tubercles of about the same basal diameter (15-20µm) each, with a normal pore going through in center; mainly distributed in two rows around central area (with about 10 tubercles each), forming a horseshoe-shaped pattern opening towards centrodorsal/dorsolateral (central muscle scar) area, with some "erratic" tubercles in between or around it. All of about the same overall size. Some smaller additional tubercles anterolaterally and posterolaterally. The horseshoe-like pattern is often somewhat less recognizable on the RV. Normal pores in center of the tubercles of 1-3µm diameter, somewhat widened at emersion point (apex of tubercle) to 4-5µm.

A few smaller (5-10µm diameter) tubercles at the rostrum and in a row along most frontal part of anterior margin of the larger LV, but not on the overlapping part of this valve. Tubercles rarely overreach dorsal and posterior margins, but very often the anterior margin. Alveolus, cyathus, as well as ventral, dorsal (dorsal furrow) and posterior margin areas without tubercles.

<u>Internal characters:</u> Hinge lophodont (Pl. 8, Fig. 14). A straight and smooth ridge with widened sockets anteriorly and posteriorly on the LV fits into appropriate groove and teeth of the RV. Fused zone of inner lamella moderately broad, except for the lower third of height antero- and posteroventrally, where a crescent free part of is developed. Free inner margin only slightly concave, nearly straight, dipping about 30° towards middle of carapace, causing small semicircle-shaped vestibuli (Pl. 8, Fig. 12). Horizontal extension of free inner lamella at ventral margin: 2/5 of length anteriorly, 1/5 of length posteriorly. Striate crenulation occurring on introversive surface of inner lamella. Distinct and broad limen in cyathus area, being of about 10µm width and 40µm length.

<u>Muscle scar pattern:</u> Unknown.

<u>Morphologic variation</u>: As well as the position in relation to the valves, the relative position of the two central spines in relation to each other is subject to slight variation. In general, the LV spine is in a higher position, i.e. located hardly above mid-height, than the one of the RV, which is located scarcely below mid-height. Regarding horizontal position, either spine may lie slightly more anteriorly than the other.

As for the smaller tubercles, the general pattern (horseshoe-shaped) seems to be relatively stable with minor variations in presence or absence of single tubercles in different locations, particularly dorsolateral. Only size and degree of expression of the tubercles vary.

<u>Ontogenetic variation:</u> Not observed.

<u>Dimorphism:</u> Not observed.

Discussion: Sohn (1979, p. 18) considered *Cypridea tuberculata* (Sowerby) var. *wyomingensis* Jones 1893 (i.e., *Cypridea (Cypridea) wyomingensis* Jones therein) as given in Swain and Brown (1972) to belong to his 'New genus undescribed "*Cypridea*" sp. 1' but referable to another (probably new) species. Considering the diagnostic characters of the latter species—rostrum and alveolus with alveolar ridge, true cyathus, dorsal furrow, ventral ridge—it well fits into *Cypridea* and there is no justifiable reason to establish a new genus, and Sohn's (1979) decision to do this is hardly comprehensible.

Peck (1941) already had synonymized *Cypridea tuberculata* var. *wyomingensis* Jones with *Cypridea tuberculata* var. *gypsumensis* Vanderpool 1928 under *Cypridea wyomingensis* Jones 1893. Loranger (1951, 1954, the latter being a reprint of the former with some revisions) also reported and figured *Cypridea wyomingensis* Jones, as well as Swain and Brown (1964, 1972, see synonymies therein), and Swartz and

Swain (1946, *Cypridea* cf. *C. wyomingensis*). However, apart from the taxonomically less significant => *local ornamentation elements* and the similar => *area-wide ornamentation elements*, all of these specimens considerably differ from *Cypridea* ex gr. *tuberculata* cf. *C. tilleyi* Loranger herein (some types were inspected by the author), in being much more elongate (having a higher L/H-ratio) and having a relatively narrow posterior margin, showing a shallow dorsolateral sulcus at 2/5 of length (above the central muscle scar field), having a less well-developed cyathus and alveolar furrow as well as a weakly developed ventral ridge and no prominent anterior cardinal angle. In addition, it is even questionably if all of these specimens belong to one species; a detailed investigation is necessary. Altogether, the specimens included in *Cypridea (Cypridea) wyomingensis* Jones definitely belong to the *Cypridea tuberculata*-group, but have no closer relations to the species described here!

Since Sohn (1979) potentially included *Cypridea (Cypridea) wyomingensis* Jones1893 in his 'New genus undescribed "*Cypridea*" sp. 1', the taxa included in the former are clearly excluded from *Cypridea* ex. gr. *tuberculata* cf. *C. tilleyi* in the synonymy list above.

Considering the shape, particularly the relatively narrow posterior margin, as well as the strong tuberculation, the representatives of *Cypridea (Cypridea) wyomingensis* Jones might be regarded as juveniles. Notwithstanding, the possibility that all or some of these species represent juvenile stages of *Cypridea* ex gr. *tuberculata* (or the other way round) seems rather impossible due to the fact that most of them have the same size or are even bigger than the latter.

Cypridea tilleyi Loranger 1951 resembles *Cypridea* ex gr. *tuberculata* in general shape and outline, valve overlap, tubercle pattern, punctation and the prominent anterior cardinal angle. However, the available description of *C. tilleyi* is short, Loranger (1951) only gives one scarcely moderate photograph of the holotype, and the taxon lacks the subcentral robust spine. Since the type material was not restudied and internal characters were not given by Loranger (op. cit.), a reliable attribution of the species described here to *Cypridea tilleyi* Loranger is impossible and remains arguable. Although this is highly speculative, it might also be considered and cannot be totally ruled out that *Cypridea tilleyi*, being a bit larger on average than the specimens from the Lakota Formation, represents adults of the latter, whereas these might be A-1 to A-2 instars then, showing stronger tuberculation as well as the main central spine (cf. chapter 5.2, genus *Cypridea* under 'sexual dimorphism' for details and Remarks/discussion under => *ornamentation* in the glossary).

At first sight—except for the subcentral spine—the species described herein shows similarities to *Cypridea tuberculata langtonensis* Anderson 1971 (also as figured in Anderson 1985, pl. 5, fig. 5) in lateral outline, the development of the anterior cardinal angle and the cyathus. However, the alveolar furrow of the latter is longer and narrower and lacks an alveolar ridge and therefore these are considered different species.

The species described here also shows strong similarities to *Cypridea australis* Musacchio 1971 in outline, development of the rostrum, alveolus and cyathus, surface characters and tuberculation pattern, except that the latter is an => *inverse* (not considered taxonomically significant here) form.

Differential diagnosis: *Cypridea* ex gr. *tuberculata* (Sowerby 1836) cf. *Cypridea tilleyi* Loranger 1951 differs from the other species described here in its strong tuberculation with the characteristic horseshoe pattern, and its well-developed reticulation-like punctation with deep puncta.

Paleoecology: As for the genus.

Faunal association (see Fig. 11 also): In the Lakota Formation associated with *Theriosynoecum fittoni* (Mantell 1844) [potentially synonym to *Theriosynoecum alleni* (Pinto and Sanguinetti 1962) refer to Sames in review], *Cypridea (Longispinella) longispina* Peck 1941, *Cypridea (Pseudocypridina) piedmonti* (Roth 1933), *Cypridea (Pseudocypridina) piedmonti* var. *henrybelli* Sohn 1979, *Cypridea (Pseudocypridina) setina* var. *setina* Anderson (1939) and representatives of the Darwinuloidea, family Darwinulidae (*Alicenula?* sp.).

In the Cedar Mountain associated with *Cypridea (Longispinella) longispina* Peck 1941, *Cypridea (Pseudocypridina) setina* var. *rectidorsata* Sylvester-Bradley 1949, *Cypridea (Pseudocypridina) setina* var. *setina* Anderson (1939).

Stratigraphic and geographic distribution (Stratigraphic terms follow the most recent terminology available):

North America:
+ Chilson Member of the Lakota Formation, Lower Cretaceous, Buck Canyon, southern Black Hills area (Fig. 2, loc. 1), South Dakota, U.S.A. (this study)

+ Chilson Member of the Lakota Formation, Lower Cretaceous, Buck Canyon, unit 10 of Bell and Post (1971, p. 531) after Sohn (1979, loc. 17 as equivalent to loc. 1, Buck Canyon herein), South Dakota, U.S.A.

+ Blairmore Group, Lower Cretaceous (late Aptian to Albian after Ross et al. 2005), Alberta, Canada, North America, as reported by Loranger (1951, 1954)

Questionable occurrence:
+ La Amarga Formation, Lower Cretaceous (Barremian?), Neuquén Province, Argentina (if closely related to *Cypridea australis* Musacchio 1971)

Stratigraphic range in North America: As documented this far and deduced from the faunal association with *Cypridea (Pseudocypridina) setina* mainly: upper Berriasian to (uppermost) Valanginian.

Theoretical maximum range as resulting from the range of *Cypridea tuberculata* (Sowerby 1863) in the English Purbeck/Wealden given by Anderson's (1985) Worth to Pluckley faunicycles (cycles Nos. 27 to 91), middle/upper Berriasian to middle Barremian according to Hoedemaeker and Herngreen (2003).

Stratigraphic range outside North America: Not directly applicable (taxonomic status). Range of *Cypridea tuberculata* (Sowerby 1863) in the English Purbeck/Wealden given by Anderson's (1985) Worth to Pluckley faunicycles (cycles Nos. 27 to 91), middle/upper Berriasian to middle Barremian according to Hoedemaeker and Herngreen (2003).

6. Discussion/Synopsis

The high rate of endemicity in North American representatives of *Cypridea* (*sensu lato*) assumed in the past and hampering further application, has mainly been a taxonomic problem as well as the general perception of these and other contemporaneous North American nonmarine ostracods as being entirely endemic. Many of the reasons of this perceptions identified and discussed here (in the taxonomic part and in the glossary) led to a strongly modified view on the taxonomy of *Cypridea* that has considerably implications, for representatives of *Cypridea* and their application possibilities in general, and the North American representatives in specific. Some additional topics emanating from this study and considered to be of interest or basis for further research are addressed in the following.

6.1. Reproductive modes and sexual dimorphism—their significance for the taxonomy, evolution, distribution and ecology of *Cypridea*

The knowledge of dispersal and reproductive modes in nonmarine ostracods (representatives of the Cypridoidea, Cytheroidea and Darwinuloidea), as well as the worldwide distribution of Lower Cretaceous nonmarine ostracods has expanded considerably during the last 30 years. The Superfamily Cypridoidea, of which *Cypridea* is a representative, is of particular interest because its representatives are the most diverse in today's nonmarine waters and dominate the nonmarine faunas since Early Cretaceous times (e.g. Horne 2003 and references therein).

Most representatives of *Cypridea* have long been considered to reproduce entirely asexual. This assumption mostly derived from the fact that sexual dimorphism in *Cypridea* has rarely been reported or considered. Although there have been some reports of presumed sexual dimorphism in *Cypridea* ever since the first one of Hanai (1951; see Chapter 5.2.3 for overview and the discussion of sexual dimorphism in the genus *Cypridea*), the established and prevalent view of an entirely asexual (parthenogenetic) *Cypridea* lineage persisted till the 1990's (e.g. Whatley 1992). According to newer evidence, however, this view cannot be sustained anymore. Firstly, more recent findings in cypridoidean ostracods have lead to the conclusion that a "… lack of obvious sexual dimorphism of the fossilized shell does not necessarily mean lack of sexual reproduction" (Horne and Martens 1998, p. 557). Strong sexual dimorphism might be overlooked and misinterpreted in fossil ostracod material, like it has been the case of *Cypridea (Longispinella) longispina* Peck 1941 (herein), but weak sexual dimorphism (see Fig. 10 also) as apparent in the carapace morphology, like in many cypridoideans and darwinuloideans, may be easily overlooked as well. Secondly, according to the present state of knowledge there is no nonmarine ostracod superfamily or family that can be considered fully asexual; most show sexual or mixed reproduction, and none of the Cypridoidea are brooders, i.e., none of these features brood care (Martens et al. 1998a). Recent discovery of living males of the darwinulid genus *Vestalenula* even calls into question that the family Darwinulidae is an ancient asexual group having reproduced asexually for over 200 million years (Smith et al. 2006). Thirdly, the high diversity and speciation rates of *Cypridea* and its allies are very much unlikely to have been achieved by an exclusively parthenogenetic lineage (Horne and Martens 1998, Martens 1998).

Therefore, according to Horne and Martens (1998), Martens (1998), Martens et al. (1998a) and results and conclusions concerning sexual dimorphism in *Cypridea* presented herein, mixed reproduction is the most likely reproductive mode in the extinct genus *Cypridea* of the cypridoid family Cypride̲idae Martin 1940!

This hypothesis has considerable effects on the interpretation of morphologic variation (mainly shape), taxonomy and diversity, distribution potential and distribution mechanisms, and evolution of representatives of the genus *Cypridea* Bosquet.

Modern research in ostracod genetic diversity and mixed reproduction (not only but particularly in cypridoideans) lead to the awareness that the morphologic variation (shape, i.e., lateral outline mainly, and size in part) within one population may be considerable. Modern cypridoideans often show minor sexual dimorphism in their carapace shape but can show less morphologic variation between males and females of sexual populations than among parthenogenetic females (e.g. Horne and Martens 1998, Martens et al. 1998b). Species with mixed reproduction can comprise separated parthenogenetically and sexually (syngamically) reproducing populations, or bisexual populations (i.e., populations with mixed reproduction). With respect to polymorphism in representatives of *Cypridea*, Sylvester-Bradley (1976) was the first to discuss this subject, and he suggested an attribution to polyploidy after *inter*specific hybridization. According to recent findings, similar (strong) morphologic variability can be obtained by *intra*specific hybridization (gene flow between sexual and asexual lineages and populations of one species). This leads to an "inclusive species concept" (Martens et al. 1998b) with large intraspecific genetic and morphologic variability (see Rossi et al. 2008, Schön et al. 2000, for recent studies on genetic diversity and mixed reproduction in the cypridoidean species *Eucypris virens*; for a detailed discussion of taxonomic problems in the context of reproductive modes, the reader is referred to Martens et al. 1998b; for an overview of the coherences of sexuality, asexuality, genetic diversity and possible routes to parthenogenesis in animals including ostracods see Simon et al. 2003, for example). Some implications of this modified perception for fossil cypridoidean ostracods are elucidated herein by example of *Cypridea (Pseudocypridina) setina* (Anderson 1939) (see Chapter 6.2 below).

Thus, based on the fact of an assumed—and now well justifiable—mixed reproduction in *Cypridea* as presented here as well as new interpretations on the taxonomic significance of certain carapace characters, the taxonomy of the genus *Cypridea* is strongly modified in part (this paper) and will undergo considerable changes in the future, including all consequences for its diversity, biostratigraphy, paleobiogeography, and dispersal mechanisms.

Coming from the assumption that many taxa of *Cypridea*—whether having been regarded species, subspecies or variants by different authors—conceal sexual dimorphs, ontogenetic stages, ecophenotypes or morphologic variants deriving from intraspecific hybridization, it can be deduced that the diversity of *Cypridea* has been, and still is, in general highly overestimated. According to the discussed concepts and by a speculative rough estimation, it seems possible that up to half or even two third of the taxa of *Cypridea* may well conceal the given intraspecific variations. This hypothesis of a much lower specific diversity, in turn, would affect the hypothesis of the (Middle) Jurassic-Cretaceous expansion of the Cypridoidea (e.g. Whatley 1992, Horne and Martens 1998) that is mainly represented by a global diversification of one lineage: the Cyprideidae Martin 1940 typified by its most important genus *Cypridea* (see Whatley 1990, fig. 1, simplified reproduced in Horne and Martens 1998, fig. 3). In his Table 1, Whatley (1992) summarized the numerical distribution of nonmarine ostracod genera and species recorded from the Late Jurassic and Cretaceous and gave 698 cypridoidean (Cypridacea therein) species, 38 cytheroidean (Cytheracea therein) species and 14 darwinuloidean (Darwinulacea therein) species for the pre-Aptian Early Cretaceous ("Neocomian" therein). From these numbers, he (Whatley 1992) stated that the "… rise in the fortunes of the cyprids from the Kimmeridgian to the Neocomian [pre-Aptian Early Cretaceous] is nothing short of dramatic" (op. cit., p. 181) and interpreted that the nonmarine species of the pre-Aptian Early Cretaceous (overwhelmingly comprising of representatives of the Cyprideidae Martin, that is species of *Cypridea*, at that time) represented more than 70% of the total number of ostracod species (including marine ones) recorded for that interval. A much lower species diversity in *Cypridea*, however, would challenge Whatley's (1992) hypothesis of a dramatic rise in the fortunes of the Cypridoidea as well as require a strongly modified view on the Late Jurassic-Cretaceous evolution of the Cyprideidae in specific as well as the Cypridoidea in general. If the example given by Nye et al. (2008), who convincingly consider all five subspecies of *Cypridea clavata* Anderson 1939 plus *Cypridea bogdenensis* Anderson 1967 (in Anderson et al 1967), is typical, then Anderson's (1939 *et seqq.*) *Cypridea* diversity would be exaggerated by a factor of five. This demonstrates that the diversity of *Cypridea* has most likely been, and still is, grossly overestimated!

A revised interpretation of the specific taxonomy in *Cypridea* also requires and facilitates different interpretations concerning the interrelations of reproductive modes, dispersal mechanisms and paleobiogeography. The (passive) dispersal of parthenogenetic females, or rather their eggs, is much easier (and faster) and allows a long-distance dispersion even across migration barriers while the supraregional dispersal of sexual populations and lineages is much more difficult. This leads to typical distribution patterns (e.g. Baltanás 1998), i.e., the asexuals are widespread while the sexuals have a restricted distribution. For an application and interpretation of such concepts to *Cypridea*, however, the temporal framework (many million years) has to be taken into consideration. Identification and analysis of fossil sexual, asexual or bisexual populations in *Cypridea* can, therefore, give new insights into dispersal mechanisms and patterns, faunal exchange, and evolutionary ecology of its representatives that, in turn, might lead to new options of application of these ostracods (e.g. paleoecology, paleoclimate, paleogeography).

With respect to the importance of resting eggs and parthenogenetic reproduction for the differential Late Mesozoic success of the Cyprideidae Martin 1940 (i.e., species of *Cypridea* mostly) and the global distribution and high diversity in it representatives, Horne and Martens (1998) challenged Whatley's (1990, 1992) hypothesis of these being the most important factors. Since representatives of other nonmarine ostracod lineages also possess resting eggs, this character "… cannot be held responsible for the differential success of the Cyprideidae, as compared to other cypridoidean lineages" (Horne and Martens 1998, p. 558). Also, as discussed above mixed reproduction is the most likely reproductive mode in *Cypridea*, not the entirely asexual (parthenogenetic) reproduction. Therefore, resting eggs and parthenogenesis are unlikely to have been the key factors. Horne and Martens (1998) favor the idea that the differential success of *Cypridea* and its allies is associated with their most characteristic carapace features: the rostrum and alveolus. However, since the functional significance of these features is not known, the specific reasons for the Late Mesozoic differential success of the Cyprideidae still remain to be identified.

6.2. Variability within one species, and its possible causal connection regarding reproductive modes, distribution and paleoenvironment: The *Cypridea (Pseudocypridina) setina*-case

Representatives of the *Cypridea (Pseudocypridina) setina*-group (including *Cypridea laevigata* Dunker 1846; refer to Schudack and Schudack 2009b also) are common within Purbeck/Wealden like deposits of Europe and North America and a good index group for the Late Berriasian-Valanginian nonmarine Early Cretaceous of the northern hemisphere. Among other representatives of *Cypridea*, these are easily to identify because this is the only group with a smooth carapace surface and completely lacking any ornamentation elements. The morphologic variation within this group is, therefore, almost exclusively expressed in the lateral and dorsal outlines (so far, only sparse data of internal characters are available). For the synonymy and detailed information, the reader is referred to the taxonomic section (Chapter 5.2.3). Many subspecies (18, considered varieties herein) have been described from Europe, the majority of these by Anderson (1939, 1962, 1971, 1985, Anderson et al. 1967) from the English Purbeck/Wealden. However, many of these are stratigraphically co-occurring, some even belonging to the same fossil population (i.e., deriving from the same layer).

The English case, as based on Anderson's (1985) data, is particularly interesting because of the outstanding documentation and biostratigraphic resolution. With respect to the most likely reproductive mode in *Cypridea* (mixed reproduction) and based on assumed sexual dimorphism in *Cypridea (P.) setina* as presented here, new interpretations of the causes of morphologic variability, dispersal and distribution of this species' variants can be made.

Whether the hypothesis presented herein, i.e., that *Cypridea (P.) setina* var. *rectidorsata* is the (sexual?) female and *C. (P.) s.* var. *setina* the male dimorph, is correct or if it is the other way round, the fact is that few variants of this species have been described from Europe outside England, and only two variants are known from North America thus far.

This matter is in need of further investigation and different hypothesis can and should be tested by geometric morphometrics (outline analysis) and by inclusion of internal features into the analysis wherever possible. Several matters are in need of clarification:

1) Which variants can be assigned to the different morphs: sexual males and females and parthenogenetic females.

2) Did bisexual populations firstly evolve in England and were the asexually (parthenogenetically) reproducing females, potentially deriving from these, the first to invade the North American continent (and were they followed by males?)?

3) With respect to the impression of a very high diversity of *Cypridea (P.) setina* in England, this might be a problem of Anderson's (1939, 1962, 1971, 1985, Anderson et al. 1967) taxonomy in combination with

the excellent documentation (more data) in England. According to modern insights in genetics and reproductive mechanisms (see e.g. Simon et al. 2003 for overview), Anderson's (1939, 1962, 1971, 1985, Anderson et al. 1967) subtaxa of *Cypridea setina* could well fit into possible morphologic variations ranges of single populations of recent nonmarine ostracods (Cypridoidea) with mixed reproduction (pers. comm. Valeria Rossi, Parma, 2008). Taking this into account, it has to be reassessed whether the much lower diversity documented in other areas of Europe and other continents is due to a really existent lesser diversity (fewer morphotypes) in these areas or due to lesser data available (insufficient documentation and taxonomic treatment) or incomplete stratigraphic record outside England? As for North America, the documentation of Early Cretaceous nonmarine ostracods to date can at best be designated moderate, irrespective of the work that has been done.

4) Parthenogenetic lineages can only evolve from sexual ones (e.g. Simon et al. 2003), that is to say, the earliest populations should have had lesser morphologic variability (which is the case in England, e.g. Anderson 1985) and sexual dimorphism should be observable (if apparent in the carapace).

6.3. Some notes and ideas on trends in the evolution of some lineages of *Cypridea*

As elucidated in Chapter 5.4.1, Wolburg developed and applied the morphogroup concept to the biostratigraphy of the "NW German Wealden". Herein, morphogroups are successfully applied for taxonomic and biostratigraphic purposes. Application of the morphogroup concept also requires the consideration of morphologic trends in the evolution of the concerning taxa through time. Although a comprehensive analysis of these trends in *Cypridea* is hitherto lacking and cannot be given here, some observations and ideas resulting from the author's recent works in North America are elucidated in the following to provide a basis and some perspectives for future works.

Analyzing the morphologic development in *Cypridea* Bosquet during Late Jurassic to Early Cretaceous times, several trends become apparent that are, or may become, stratigraphically useful. Conclusions must remain tentative at the moment since the detailed stratigraphy of most Purbeck/Wealden-like deposits of the world, including North America, is still inaccurate and under discussion and much more taxonomic research on a world scale is necessary. However, though possibly not universally valid and whether taking *Praecypridea* Sames et al. (in review) into consideration as ancestor of *Cypridea* or not, the following morphologic trends have been recognized, for example:

1) Many more ancient (circa Kimmeridgian to Valanginian-Hauterivian) forms of *Cypridea* often possess a prominent, rounded-rectangular to pointed => *cyathus-like protrusion* that may or may not distinctly overreach the posterior margin, while most younger forms have a true => *cyathus*. The cyathus is in most cases not as strongly developed as the cyathus-like protrusion, i.e., not as distinct as the latter, more strongly rounded and not overreaching the posterior margin. *Cypridea nitidula* Peck 1951 and *Cypridea (Longispinella) longispina* (Sohn 1979) described herein show a distinct cyathus-like protrusion, in *Cypridea obesa* Peck 1951 it is developed to a lesser degree. Representatives of the *Cypridea setina*-group and of *Cypridea (Pseudocypridina)* in general, have a true cyathus, which is crescent and narrow.

2) Many Late Jurassic-lowermost Cretaceous show a strong degree of inequality of the valves. This feature, however, seems to be limited to certain lineages of *Cypridea*. Among the species described here, *Cypridea (Longispinella) longispina* (Sohn 1979) and *Cypridea* ex gr. *alta* Wolburg 1959 are strongly inequivalve. Most of the younger (post-Valanginian-Hauterivian) forms are less than moderately inequivalve or subequivalve.

3) The development of dorsolateral sulci in some (one or several?) lineages of *Cypridea* (see discussion of a *Cypridea-Bisulcocypridea* lineage in Chapter 5.2.1 also) seems to be a relatively late acquisition (the

known stratigraphic distribution of *Bisulcocypridea* Sohn is Late Cretaceous-Early Paleogene) in the evolution of *Cypridea* Bosquet 1852 to *Bisulcocypridea* Sohn 1969. New data from North America presented herein point to a pre-Barremian first appearance of sulcate taxa, that is *Cypridea? minuta* (Peck 1951).

However, these are only trends that cannot be applicated to all groups or lineages of *Cypridea*. Much more data and research is necessary! The early pre-uppermost Tithonian evolution of *Cypridea* is not yet well known. Sames et al. (in review) introduce a new genus, *Praecypridea*, they consider to represent the ancestor of *Cypridea* Bosquet, with North American, European and West African representative. A successive evolutionary lineage from the former to the latter has not been documented so far. The oldest representatives of 'true' *Cypridea* have been reported from the Kimmeridgian of the Tendaguru Formation (Tanzania, East Africa) by Schudack and Schudack (2002) and Sames (2008). With respect to Europe, the oldest known species of *Cypridea* derive from the Lower Tithonian of the Île d'Oléron (Island of Oleron, Bay of Biscay, France, J.-P. Colin, Cestas, France, pers. comm. 2006).

It seems likely that the oldest true representatives of *Cypridea* are older than Kimmeridgian-Early Tithonian. These early representatives are already strongly different, some are smooth (Sames 2002) others punctated (Schudack and Schudack 2002), and they distinctly differ in outline, development of rostrum and alveolus as well as the cyathus-like protrusion. Several lineages seem to have been established in the Early Tithonian already and further differentiated in the latest Tithonian to Berriasian. As the example of *Cypridea (Pseudocypridina)* shows, which can be exemplified on *Cypridea (P.) setina* and *C. (P.) piedmonti* here, "younger morphotypes", being subequivalve and having a true (and weakly developed), cyathus already existed during the Berriasian.

Based on the most recent data, the evolution of *Cypridea* Bosquet 1852 (Kimmeridgian to Early Eocene) spanned some 100 Ma (cf. Gradstein et al. 2004) and its representatives are known from all continents except Antarctica and Australia. Taking such a long period of time into consideration in the context with mixed reproduction and different dispersal modes and the development of the earth during that time, it is not surprising that cypridean evolution took different directions in different areas of the world.

Neither climatic changes nor the flooding of the Western Interior foreland basin caused by major area-wide marine transgressions starting in Middle Albian times and leading to the Cretaceous "Western Interior Seaway" (e.g. Kauffman and Caldwell 1993, Miall et al. 2008) has wiped-out representatives of *Cypridea* (or *Bisulcocypridea*) in North America (see Swain 1999 and references therein).

Lower Cretaceous nonmarine deposits of the North American Western Interior foreland basin play an important role in the documentation of the evolution and dispersion of *Cypridea* and *Bisulcocypridea*, particularly on the northern hemisphere and in relation to European and Asian faunas, and in relation to South America. In turn, new findings in this regard allow, amongst other things, the biostratigraphic application of taxa of *Cypridea* in North America and are capable of improving the Early Cretaceous chronostratigraphy of the Western Interior foreland basin.

6.4. General stratigraphic considerations for the nonmarine Lower Cretaceous of the Western Interior foreland basin

The specific stratigraphic implications of this taxonomic review and that of representatives of *Theriosynoecum* (Sames in review, this volume) for the North American Western Interior foreland basin are published elsewhere (Sames et al. submitted) or are in preparation. Sames et al. (submitted) give a comprehensive overview of the stratigraphy and age determination (chronostratigraphy and geochronology) of the basin, associated problems and perspectives, and a synopsis of the most important implications of a higher maximum age (Late Berriasian to Valanginian) of some of the basin's

Lower Cretaceous formations as based on ostracod correlations. These derive from ongoing taxonomic revisions, of which Sames (in review, this volume) and the paper at hand are parts of.

At this point, a short overview and synopsis of some important aspects related to the North American representatives of *Cypridea* is given.

Peck (1956, 1959) combined the Late Jurassic to Paleocene nonmarine ostracod fauna (representatives of *Theriosynoecum*, all the latter allocated to the genus *Metacypris* by Peck, and *Cypridea* mainly) and charophyte flora of the U.S.A. (Rocky Mountain area, Western Interior foreland basin, mainly Wyoming, South Dakota, Montana, Idaho and Utah) into four assemblages:

a) the (Late) Jurassic "Morrison assemblage",

b) the Early Cretaceous "Gannett-Cloverly assemblage" (Gannett Group: Ephraim Formation, Peterson Limestone, Bechler Formation and Draney limestone; and the Cloverly Formation of Wyoming; pre-Albian Lower Cretaceous according to Peck 1956, Aptian according to Peck 1959),

c) the Early Cretaceous (Albian according to Peck 1956, 1959) "Bear River assemblage" (Bear River Formation of Wyoming),

d) and the Paleocene "Hoback-Flagstaff assemblage" (after the Hoback Formation of Wyoming and the Flagstaff Formation of Utah, including other correlatables, see Peck 1959).

In his first publication (Peck 1956, fig. 23) still had included a representative of *Cypridea*, i.e., *Cypridea (Pseudocypridina) piedmonti*, in his "Morrison assemblage". Sohn (1958), however, had demonstrated that the rocks from which Roth (1933) or Harper and Sutton (1935) had described ostracods from the Black Hills area (South Dakota), were actually from the Lakota Formation and not the Morrison Formation as given by these authors. Consequently, Peck (1959) removed representatives of *Cypridea* from his "Morrison assemblage"; he also changed the name of his "Gannett-Cloverly assemblage" (Peck 1956) to "Gannett-Cedar Mountain assemblage" (Peck 1959) and supplemented all of his four assemblages with additional ostracod and charophyte taxa. To the current state of knowledge, the Morrison Formation is entirely devoid of true representatives of *Cypridea* Bosquet. Schudack (1995, 1996, Schudack in Schudack et al. 1998) was the first to systematically deal with and describe ostracods and charophytes from the Morrison Formation. *Cypridea acuticyatha* Schudack 1998 (in Schudack et al. 1998) and as given in Schudack (1995, 1996) is considered not to be a true *Cypridea* but rather an ancestral form belonging to a different genus and has currently been chosen by Sames et al. (in review) as the type species for a new genus: *Praecypridea* Sames, Whatley and Schudack.

Peck's (1956, 1959) assemblages require extensive revision, and his age determinations are outdated (see Sames et al. submitted). In addition, a complete taxonomic revision of all of Peck's taxa and material is still pending (but will be partially difficult since the whereabouts of most of the material is unknown).

Based on the literature (Harper and Sutton 1935, Peck 1941 *et seqq.*, Peck and Craig 1962, Roth 1933, Sohn 1958, 1979, Schudack 1995, 1996, Schudack et al. 1998) as well as results from the Lakota and Cedar Mountain formations presented here and in Sames (in review, this volume), the Early Cretaceous nonmarine ostracod faunas of North America can be divided into at least three informal successive assemblages, perhaps even more but this remains subject to upcoming publications and studies. These exclude the assemblages of the Upper Jurassic (to Berriasian?, see Sames et al. submitted) Morrison Formation, which are characterized by distinct species of *Theriosynoecum* Branson 1936, representatives of *Cetacella* and *Timiriasevia*, and the absence of representatives of *Cypridea* Bosquet (cf. Sohn 1958). In contrast to the assumptions of Schudack (in Schudack et al. 1998) and according to the results of the author's ongoing research, the Early Cretaceous nonmarine ostracod faunas have no taxa in common with the Morrison Formation at species level.

The Early Cretaceous informal ostracod faunas of the Western Interior foreland basin comprise:

1) a "Fauna A" of the early Lower Cretaceous (upper? Berriasian-Valanginian), besides the common occurrence of *Cypridea (Pseudocypridina) piedmonti* (Roth 1933) syn. *C. (P.) laeli* Sohn 1979 characterized by

representatives of the *Cypridea setina*-group, the *Cypridea alta*-group and representatives of *Cypridea nitidula* Peck 1941,

2) a "Fauna B" of the middle Lower Cretaceous (middle/upper? Valanginian, Hauterivian to lower/middle? Barremian) that is most probably further differentiable and which, besides comprising *Cypridea (Pseudocypridina) piedmonti* (Roth 1933) syn. *C. (P.) laeli* Sohn 1979, is mainly characterized by *Cypridea (Pseudocypridina) laeli* Sohn 1979 and *Theriosynoecum pahasapensis* (Roth 1933).

3) a "Fauna C" of the upper (middle?/upper Barremian to middle Albian, questionably Cenomanian) that is only partially according to Peck's (1956, 1959) "Bear River assemblage" (revision required), and comprises *Cypridea? anomala* (Peck 1941), *Cypridea compta* Peck 1941, *Theriosynoecum persulcata* (Peck 1941), and *Theriosynoecum angularis* (Peck 1941) (see Sames (in review, this volume also).

With regard to the ostracods of the Lakota Formation of the Black Hills area, to the present state of knowledge the Lakota, even its upper parts (Fuson Member or informal L2 and L3 interval of Way et al. 1998) in the eastern Black Hills, only comprises of faunal elements that belong to the informal "faunas A and B", and has no faunal elements in common with Peck's (1956, 1959) "Bear River assemblage". Therefore, the entire Lakota Formation is considered distinctly older than Middle?/Late Barremian–Aptian. Ostracod-bearing samples from the Yellow Cat Member of the Cedar Mountain Formation (Utah) mostly comprise elements of "Fauna A".

7. Conclusions

The detailed taxonomic revision of the genus *Cypridea* Bosquet with emphasis on some North American Early Cretaceous species resulted in considerable progress concerning the taxonomy, paleoecology, paleogeography and evolution of the genus and some subgenera as well as selected representatives, and a breakthrough in their biostratigraphic application in North America.

The high rate of (even total) endemicity widely assumed for the Early Cretaceous North American representatives of *Cypridea* in the past has been highly overestimated, as well as the species diversity within this genus. The main reason for these views is here identified as having been basically a taxonomic problem. In most cases, overestimation or wrong interpretation of => *local ornamentation elements*, outline, or the too regional view on the faunas led to the erection and retention of numerous new species names, some subgenera or even few different genera in North America (as well as other continents). In addition, the taxonomic confusion also derives from the factually existing strong variability within *Cypridea* that is difficult to deal with and could not be explained for a lineage having been believed to reproduce exclusively parthenogenetic. Now that more and more sexual dimorphs are presumed, the hypothesis of a mixed reproduction can be well supported. Based thereupon, the high morphologic variability and different paleogeographic distribution patterns become much better explainable (geographic parthenogenesis).

The conducted comprehensive "classic" morphologic analyses and descriptions including a revised definition of the (in-)significance of certain carapace characters, detailed and "standardized" descriptions as well as new insights in ostracod biology and reproduction, facilitate a modified and new perception of the taxonomy of the representatives of the fossil genus *Cypridea*. First steps towards identification and better differentiation between taxonomically significant and insignificant (ecophenotypic, ontogenetic, intraspecific variation) carapace characters have been achieved. That facilitates a more effective choice and application of additional methods, such as geometric morphometrics, for example, in that it is possible to focus on significant characters as base data to measure depending on the hypothesis to test.

As can be demonstrated, a biostratigraphic application of representatives of *Cypridea* and an improvement of the age determination of nonmarine Lower Cretaceous formations of the North American Western Interior foreland basin is possible. With respect to the maximum age of these formations that has been under discussion for the entire 20th century and remains controversial to date, first biostratigraphic applications are pathbreaking (Sames et al., submitted). New results strongly suggest that the maximum age of some of these formations (Lakota Formation, South Dakota, and Cedar Mountain Formation, Utah) is Late Berriasian to Valanginian, and therefore much higher than most published lines of evidence have given in the past (Barremian or Aptian-Albian, respectively). These results have considerable implications for the geology and paleontology (chronostratigraphic framework) of the basin (Sames et al., submitted).

Within the framework of a revision of *Cypridea*, a different and updated systematics of the family Cyprideidae Martin 1940 has been elaborated and is proposed (see Table 1). Within the scope of further research in the evolution and distribution of the *Cypridea-Bisulcocypridea* lineage in time and space as well as the diverse application of its representatives, the Lower Cretaceous formations of the North American Western Interior foreland basin provide an important resource of information

Altogether, the approach followed herein led to satisfactory results as to the aims given in Chapter 2.3. A taxonomy-based progress and improvement of the utilization of representatives of *Cypridea*, particularly its Early Cretaceous North American species has been successfully accomplished and provides the basis for results presented here as well as future research.

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Appendix: Taxonomic Glossary

Specific taxonomically significant characters of the genus *Cypridea* Bosquet 1852, as used in this paper (compiled after various authors, modified and supplemented; for illustration see Figs. 3 to 9). Terms in alphabetic order:

The intention of the following comprehensive remarks is the attempt of a standardized concept in terminology that is comprehensible, easily reproducible and criticizable. Since the Ostracod-Treatise is dated, as are many of the publications dealing with the general terminology of the ostracod hard and soft parts, many terms need to be specified. Most recent works are still based on these older publications (see below).

Only selected terms, which have to be clarified, are quoted here. Other definitions of general terms of hard parts can be found in Zalányi (1929), Klie (1938), Kesling (1951), the Ostracod-Treatise (Moore 1961), van Morkhoven (1962), Hartmann (1966-1989), Sylvester-Bradley and Benson (1971), Hartmann and Guillaume (1996), and Yamada (2007), to specify a few selected ones, and references therein.

It must be noted that the terminology given is in part adjusted and specifically optimized for the Cyprideidae, particularly *Cypridea*.

Some terms can vary in their meaning if applied to other Mesozoic to recent ostracod groups, or Paleozoic ostracods (e.g. => *rostrum*).

Remarks concerning the carapace margins and outlines (cf. Figs. 3, 7, 8):

Regarding the margins and outline of ostracod carapaces, there is some confusion in the literature having to be clarified. Especially in context with the dorsal and, in part, the ventral carapace borders, the unambiguous differentiation of the two terms is often not recognized and pointed out. For the dorsal region in lateral view the terms hinge margin, hinge line, dorsal margin, dorsal outline (herein, the dorsal lateral outline and dorsal outline are differentiated!) and dorsal border are used, for example. By describing ostracods with commonly occurring depressions of the hinge, overreaches of lateral carapace regions and strong => *local ornamentation elements*, a strict differentiation became necessary. As far as possible, commonly used terms and their application in the known context have been adopted. It is also attempted to define the extend of the single outer carapace regions by comprehensible geometric or morphologic elements (see Fig. 3). In general, the terms margin and outline are defined and applicated as follows:

A ***margin*** is the valves border directly adjoining the => *free valve margin*, and the hinge respectively, often only completely visible in an internal view of the single valve.

The ***outline*** is defined here as the outer border of the lateral 2D-projection of the valve, carapace or parts of any of these. The outline often differs from a margin, because lateral prolongations of the carapace overreach it (e.g. ridges, lobes, brood pouches etc.). Most => *local ornamentation elements* as defined herein and used for the specific ostracod groups concerned, are excluded from defining and having influence on the outline of *Cypridea* (e.g. *spines* and *nodes*, but not *ridges*) because of their highly variable character assumed of being ecophenotypic or ontogenetic in this taxon.

Combined, all partial outlines, i.e. the terms anterior, dorsal, posterior and ventral outlines proposed here, define the => *carapace outline* in its "classic" meaning (e.g. Kesling 1951, Moore 1961, and others).

The specific definitions for partial sections of the carapace's outer borders can be found in context with the main carapace regions, i.e. => *anterior*, *dorsal (hinge)*, *posterior*, *ventral margin/lateral outline* (e.g. *anterior margin* etc.).

As for the structure and terminology of the carapace margin, its revision by Yamada (2007) has considerable effects on the hitherto conventional (called "classical" terminology herein) definition, utilization, applicability and interpretation of morphologic terms such as => *duplicature*, => *flange*, => *inner lamella*, => *outer lamella*, and => *selvage*. For reasons of usefulness, to avoid confusion, and because Yamada's (op. cit.) concept has not yet been tested on many taxa (especially fossil ones) and is in part specified for cytheroid ostracods, the "classical", i.e. mostly paleontologic, terminology is retained here. Nevertheless, wherever applicable, to facilitate future application and to offer different views, the new terminology and its effects on particular terms and interpretations are given/integrated in the glossary and discussed or commented in the definition of the carapace terminology herein.

Irrespective of the necessary and endorsed integration and standardization of recent biologic and paleontologic taxonomy or of whether preference is given to the "classical" view or to that of Yamada (2007), some terms, such as *selvage*, should be retained owing to their usefulness, regardless of the partially different meaning/definition resulting from the concept used by the particular researcher.

GLOSSARY:

Accomodation groove: An elongated, sometimes subtriangular furrow above the median hinge element (usually a => *hinge bar*) of the larger valve which receives the dorsal edge of the opposite valve.

In the uncommon case of an => *inverse* hinge, the accomodation groove as well as the median hinge element are situated in the smaller valve.

Alveolus (pl. *alveoli*, Latin for small trough; diagnostic to the Cyprideidae Martin 1940; English adj. alveolar): This term determines an indentation starting behind the => *rostrum*, comprising of two or three parts:

1) an incision (=> ***alveolar notch***, Figs. 5B, 7/B) of the outer anteroventral outline/margin (can be present or absent) which continues upwards as
2) an => ***alveolar furrow*** (Figs. 7/A, B; here narrow and elongate) or *alveolar groove* ("rostral sulcus" of some authors) in both valves; present or absent and in the former case of highly variable size, shape and depth, and
3) an => ***alveolar ridge*** (Figs. 7/A, B; only present in some representatives of the Cyprideidae Martin 1940).

Remarks: The strength of development of the alveolus as well as depth, width and length of the furrow/groove are considerably variable in the different species. Together with the => *rostrum* and => *cyathus* it is the most important diagnostic character of *Cypridea*.

In some cases, the alveolar furrow or groove is divided into two parts by an => *alveolar ridge*. Internally, the position of the alveolus is indicated by a local widening of the => *inner lamella*, a diagnostic character of the Cyprideidae Martin 1940, and the => *attached area*, where the marginal => *pore canals* are missing (Fig. 8).

In the case of an => *inverse valve size relation*, the relative size and shape relations regarding the alveolus remain (i.e. alveolar notch in trend stronger in the *smaller* valve while the alveolar furrow is often somewhat larger and less triangular in the *larger* valve).

Alveolar furrow: Also alveolar groove or "rostral sulcus" of some authors (see also => *alveolus*). The alveolar furrow can be present or absent, and its size, depth and shape are highly variable. Its length may vary between a short narrow indentation behind the rostrum with barely recognizable or even absent furrow/groove and alveolar notch—cf. *Cypridea (Pseudocypridina) piedmonti* herein, for example—and a deep, wide and long furrow/groove extending almost up to 4/5 of carapace height (e.g. *Cypridea parallela*-group, see Wolburg 1959, for example), or even up to the lower internal limit of the anterior hinge element. In the latter cases, the rostrum forms a => *rostral bulge*.

Usually, the alveolar furrow is more or less larger and often more distinct in the *larger* valve (i.e. the LV mostly). In case of strongly developed alveolar furrows, that one in the *larger* valve is in trend more elongate while that in the *smaller* valve more (sub-)triangular (broad at the base and pointed in dorsal direction).

Alveolar groove: synonym to => *alveolar furrow*

Alveolar notch: This is an incision of the anteroventral outline or margin, if both are coincident (see Figs. 5B, 7/B) which may be present with different degrees of development, or absent, and usually continues upwards as => *alveolar furrow* (see => *alveolus* also). Since the majority of species diagnoses is based on characters visible in external view only (owing to the frequent unavailability of internal views), the definitions herein are adjusted to the external view. Thus, absence as well as presence of the alveolar notch and degree of its development are defined in relation to the anteroventral *outline* of the valves mainly, rather than the margins, because the latter are often not visible on the whole carapace (that is particularly the outer margin of the smaller valve being concealed by the overlapping larger valve).

Since no exact definition is given in the literature when exactly it is appropriate to term the alveolar notch as absent or present, the following definition is proposed herein (refer to Fig. 5/B, Nos. 4-6 for illustration):

The ***alveolar notch*** is termed ***absent*** herein, if the => *ventral outline* (and => *ventral margin*, if coincident) right behind the => *rostrum* is not curved upwards but meeting the posterior part of the rostrum in a more or less perpendicular angle. This also depends on how strong the rostrum is bent backwards see => *bending angle*) and if its apex well-rounded or not (Fig. 5/B, Nos. 4 and 5).

A weakly developed or absent alveolar notch is mostly combined with weakly developed (i.e. shallow and short, or even absent) alveolar furrows/grooves in both valves. In many (if not most) cases, the alveolar notch is (or in external view merely *appears*) somewhat stronger and distinct in the *smaller* valve, e.g. if the larger valve has no alveolar notch, then it is often weakly developed but present in the smaller valve, like in many representatives of *Cypridea (Pseudocypridina)*, for example.

The ***alveolar notch*** is termed ***present*** herein, if the => *ventral outline* (and => *ventral margin*, if coincident) right behind the => *rostrum* is more or less distinctly curved upwards and meets the posterior part of the rostrum in an acute angle that has a well and broadly rounded apex (Fig. 5/B, 6), like in *Cypridea alta* Wolburg 1959, for example.

A strongly developed alveolar notch is mostly combined with well-developed alveolar furrow/groove. Also in taxa with well-developed/deeply incising alveolar notch, the notch itself is (or in external view merely *appears*) mostly stronger developed in the *smaller* valve. However, it is important to note that this is not true for the alveolar furrows. Quite the contrary, the alveolar furrow is mostly stronger developed in the *larger* valve, like in most representatives of *Cypridea (Cypridea)*, for example.

Alveolar ridge: This is a new term introduced and defined herein for representatives of *Cypridea*. An alveolar ridge is a straight, arched, or rarely slightly undulated, ventrolateral ridge directly behind the rostrum, and occurs in both valves (Figs. 7/A, B). It either is the ventral boundary of the alveolar furrow/groove without a cavity behind the rostrum or divides the alveolar furrow/groove into two parts – a small cavity in anteroventral (above alveolar notch) direction, and the main alveolar furrow or groove above it. Such division of the alveolar furrow is often more distinct in the *smaller* valve, or rather occurring in this valve only, particularly in taxa with large and deep alveolar furrow.

The alveolar ridge begins at the posterior part of the rostrum above or at the alveolar notch, then running towards and meeting the => *ventral margin*, thus connecting the rostrum to the valve surface. Depending on the depth of the alveolar furrow/groove, the flanks of the alveolar ridge are more or less steep. Its width ranges from about 15 to 30µm and its function remains unknown.

Remarks: Sohn (1979) already mentioned this character in his description of *Cypridea (Longispinella) asymmetrica* [recte *C. (L.) longispina* var. *asymmetrica*]: "The alveolus extends upwards about halfway to the curve of the anterior margin; it has a horizontal ridge at its base. The rounded ridge connects the rostrum to the valve surface" (op. cit., p. 18), but never defined this character. It remains a mystery why this partially very obvious, frequently figured, and potentially important taxonomic character has neither been described nor defined by so many authors, not to mention that its functional morphology and taxonomic significance is of interest.

The alveolar ridge does not only occur among different taxa of *Cypridea* but also in representatives of all continents where this genus is known from: Africa, Asia, Europe, North America, and South America (see examples given below). Thus far, it cannot be stated if the alveolar ridge is a homologous character within *Cypridea*. Furthermore, the alveolar ridge potentially occurs among representatives of *Bisulcocypridea* Sohn 1969 also (refer to *Cypridea? minuta* herein), a matter remaining to be investigated like taxonomic significance of the alveolar ridge and its function as well.

Examples for representatives of *Cypridea* with an alveolar ridge:

This paper:

- *Cypridea* ex. gr. *alta* Wolburg 1959
- *Cypridea (Longispinella) longispina* Peck 1941 syn. *C. (L.) asymmetrica* (Sohn 1979)
- *Cypridea? minuta* (Peck 1951) comb. nov.
- *Cypridea (Pseudocypridina) setina* (Anderson 1939)
- *Cypridea* ex. gr. *tuberculata* cf. *C. tilleyi* Loranger 1951

In the literature (only figures showing the alveolar ridge are indicated):

- *Cypridea almahdoensis* Luger and Schudack 2001, Fig. 5, 1-5
- *Cypridea (Cypridea) alta formosa* Wolburg 1959 – as figured in Christensen 1963, pl. 1, figs. 1a, 1d
- *Cypridea cavernosa* Galeeva 1955 – as figured in Hao et al. 1974, pl. 12, figs. 1a, b, e, d
- *Cypridea cymerata* Musacchio 1971, pl. 1, figs. 14, 15
- *Cypridea dromedarius* Krömmelbein 1962, pl. 56, figs. 22 a, b
- *Cypridea fasciculata* Forbes – as figured in Nikolaeva and Neustrueva 1999, pl. 6, fig. 3
- *Cypridea (Ulwellia)* aff. *inversa inversa* Martin 1940 – as figured in Chistensen 1963, pl. 2, figs. 1a and 1c
- *Cypridea laevigata hawkhurstensis* Anderson 1967 – as figured in Anderson 1985, pl. 7, fig. 12
- *Cypridea laevigata laevigata* (Dunker 1846) – as figured in Anderson 1985, pl. 7, fig. 3
- *Cypridea lavigata leonardi* Anderson 1967 – as figured in Anderson 1985, pl. 7, fig. 8
- *Cypridea lucida* Musacchio 1971, pl. 1, figs. 12, 13
- *Cypridea maior* Krömmelbein 1965a, pl. 11, figs. 3a, b
- *Cypridea opifera* Krömmelbein 1965a, pl. 56, fig. 23a, b

- *Cypridea* aff. *opifera* Krömmelbein 1962 – Krömmelbein 1965a, pl. 11, fig. 1a, b
- *Cypridea subtilis* Krömmelbein 1965a, pl. 11, figs. 4a, b
- *Cypridea triangula* Liu 1959 – figured in Hao et al. 1974, pl. 7, fig. 5a; figured in Hou et al. 2002, pl. 182, fig. 12
- *Cypridea tucanoensis* Krömmelbein 1965a, pl. 11, figs. 2a, b
- *Cypridea rhahelensis* Andreu et al. 2003, pl. 3, figs. 1-4
- *Cypridea recta recta* Wolburg 1959 – as figured in Anderson 1985, pl. 8, fig. 4
- *Cypridea recta* Wolburg 1959 – as figured in Hao et al. 1974, pl. 12, figs. 2a, b

Anterior cardinal angle (ACA): The anterior of the two => *cardinal angles* (Figs. 3, 4).

Anterior margin: Anterior part of the carapace/valves in lateral view, adjoining the anterior part of the => *free carapace/valve margin*. It extends between the angular peaks of the anterior => *cardinal angle* and the => *anteroventral region* (or, in the larger valve of *Cypridea*, the point of the => *rostrum*). The anterior margin always coincides with the => *anterior lateral outline* (Fig. 3).

Anterior (part of) lateral outline: Equivalent to => *anterior margin* because both always coincide.

Anteroventral region (AVR): The anteroventral sector of the carapace's outline including the anterior part of the => *ventral margin* and the ventral part of the => *anterior margin*. The term 'anteroventral angle' is avoided because a recognizable angle is rarely realized but strongly rounded in many ostracods. In *Cypridea*, the AVR is morphologically modified and characterized by a => *rostrum* and an => *alveolus* (see Figs. 3, 5/B, 7/F, 8).

Area-wide ornamentation element(s)/surface characters: see => *ornamentation*

Attached area: A diagnostic morphologic term for representatives of 'true' *Cypridea* only (*Cypridea* sensu stricto excluding closely related genera such as *Bisulcocypridea*, *Mongolocypris* or *Paracypridea*; see diagnosis of the genus also), used by some authors (e.g. Szczechura 1981) to describe a small loop shaped area above the => *alveolus* that is visible in the light-optic microscope in internal view, where => *inner lamella* and => *outer lamella* are fused together (quasi a local widening of the => *marginal zone/fused zone*), as illustrated in Fig. 8 (cf. => *local widening of inner lamella* also). No => *marginal pore canals* pierce through this area.

The figure of *Cypridea punctata* Sylvester-Bradley 1949 as redrawn and given in van Morkhoven (1963, p. 93, fig.128) does mistakenly show marginal pore canals in the attached area, none of which are shown in the original figures (Sylvester-Bradley 1949, p. 131, fig. 17a; p. 134, fig. 19b).

Attached margin: This is that part of the => *dorsal margin* along which both valves are held together by the => *ligament* attached to them (the other parts of the margin are called => *free margin*). This term does neither correspond to => *dorsal margin* nor to => *hinge margin*, because the extension of the ligament does not equal either of these and the length of the attached margin is also linked to the type of hingement. The ligament can be of different length, and is mostly shorter than the dorsal margin because certain elements of the => *hinge* (e.g. the => *terminal elements*, i.e. the teeth and sockets in the lophodont hinge on *Cypridea*) mostly diverge when the carapace is opened.

Base line: Geometric line for horizontal orientation of the carapace in relation to the => *ventral margin*. The base line can be either coincident with a straight ventral margin, or be the tangent of a convex ventral margin, or running through the two virtual tangential points of the intersection between the => *antero-* and => *posteroventral regions*, if the middle ventral margin is convex (see Fig. 4).

Beak: see => *rostrum*

Bending (backwards) angle (of => *rostrum*): This is defined herein as a measurement for the angle between the outer tangent of the rostrum and the anterior tangent perpendicular in relation to the => *base line*. The bending angle defines how strongly the rostrum is bending backwards, i.e. how close its center line lies in relation to the => *ventral margin* (Fig. 4). In theory, this character can vary between an angle somewhat more than 0° (i.e. the rostrum would be about perpendicular, e.g. *Cypridea marina* Anderson) and about 60-65° (i.e. the rostrum is nearly fully attached to the ventral margin, e.g. *Cypridea laevigata hawkhurstensis* Anderson). However, the magnitude of the angular dimension is not necessarily connected with the ventral width of the alveolar furrow/groove and alveolar notch, i.e., a low value of the angle does not need to be combined with a broad alveolar furrow/groove and notch, and a high value does not imply a narrow alveolar furrow/groove and notch, respectively. The higher the value of the angle, the stronger the rostrum is bending backwards.

Calcified inner lamella: see => *inner lamella*

Carapace/valve margin: The carapace or valve margin is the complete outer border/outer margin comprising the => *free (valve) margin* and the => *attached margin*. In lateral view, it is not necessarily coincident with the lateral => *carapace/valve outline* as a result of the overreach of lateral carapace/valve prolongations.

Carapace/valve outline: The carapace/valve outline is defined as the lateral or dorsal 2D-projection of its complete outer border, partially excluding => *local ornamentation elements* (see there for explanation). The lateral outline often more or less strongly differs from the => *carapace/valve margin* due to the overreach of carapace/valve prolongations. The latter is particularly the case for the => *hinge margin*. The => *dorsal outline* often distinctly shows the sexual dimorphism (if apparent in the outer view of the particular species, e.g. brood pouches in females of *Theriosynoecum*, or, as for *Cypridea*, the at mid-length more rotund females in *Cypridea (Pseudocypridina) piedmonti* (here) and can be heavily affected by different => *ornamentation* elements. Since the dorsal *view* is taxonomically more significant, it is the one commonly used for description, and so is the dorsal outline. Dorsal and ventral outlines (not to confuse with => *ventral lateral outline*) are congruent, and therefore the usage of the term ventral outline becomes dispensable (but not the ventral view!).

Carina (pl. *carinae*, Latin for keel; English adj. carinate): see => *area-wide ornamentation elements/surface characters*

Carinate rostrum (adj. from Latin *carina* = keel; rostrum with keel): This is a new term introduced herein which refers to a => *rostrum* with a keel-like, laterally flattened margin (Fig. 7/F).

In some species of *Cypridea*, the => *selvage* of the larger valve at the rostrum does not envelop the rostrum of the smaller valve. Instead of this, the selvage of the anterior margin is bent outward in both(!) valves, thereby adjoining, and forming a narrow keel. The keel proceeds around the point of the rostrum and ends before reaching the alveolar notch. Combined therewith is a row of => *marginal pores* in both valves (=> *rostral keel pores*), following the inner boundary of the keel along the rostrum. So far, a carinate rostrum is only known from a few species lacking a distinct => *alveolar furrow* (see below for examples). Its function remains unknown.

Thus far, however, the carinate rostrum has been observed in single valves only and it is not totally clear yet, if such structure is real or just a result of post-mortem or post-ecdysis compression and outward bending of the selvage along the rostrum—particularly if occurring in the smaller valve where the smaller valve's selvage is usually bent inwards and overlapped by that one of the larger valve. More research is necessary.

Examples for Taxa in which a carinate rostrum occurs:

1. *Cypridea (Pseudocypridina) laeli* Sohn 1979 (Pl. 6, Figs. 4 and 5, herein)
2. *Cypridea (Pseudocypridina) setina* (Anderson 1939) (herein, Pl. 14, Fig. 14)
3. *Cypridea valdensis* (J. de C. Sowerby 1836), slide BGS Mik(M) 647, field 27, 28, Anderson collection
4. questionably in *Cypridea swanagensis swanagensis* Anderson, 1971, slide BGS Mik(M) 3161, holotype, Anderson collection (SEM pictures necessary)

Cardinal angles: A dorsal feature only, defining the junction between => *hinge margin* and => *anterior/posterior margin*s position of the terminal => *hinge elements*. Their shape and angularity are strongly variable, mostly, the cardinal angles are obtuse angled and more or less strongly rounded. Depending on the shape of the terminal hinge elements (terminal teeth/sockets, or processes/recesses of some authors), the cardinal angles can coincide with the dorsal margin or protrude. The frontal angle is the => *anterior cardinal angle*, the posterior one the => *posterior cardinal angle* (Fig. 3).

Because of the fact that the development of the dorsal internal features belonging to the hinge has direct influence on, and is connected with, the => *dorsal lateral outline* and/or margin, the terms 'anteroventral cardinal angle' or 'posteroventral cardinal angle' should be avoided for the equivalents in the ventral areas, where this is not the case. Therefore, these ventral characters are designated as => *anteroventral region* or => *posteroventral region* instead (see Fig. 4).

Central muscle scar field: The main muscle scar field, somewhat anterior of mid-length in *Cypridea*, composed of the adductor muscle scars, frontal scar(s) and mandibular scars (Fig. 6, 7/E).

Contact margin: Edge part of valve, excluding the => *hing*e (Moore 1961). The contact margins of both valves are in contact when the valves are closed.

Curvature (of => *anterior* and => *posterior margins*): The anterior and posterior margins can be curved in three ways (Terminology after Lüttig 1962, cf. Fig. 5/A, translated from German). Lüttig's terminology is adopted and preferred here because it is precise and short:

1) **Equicurvate:** (in German "äquikurvat") describes an equally rounded margin.
2) **Infracurvate:** (in German "infrakurvat") describes a margin that is more narrowly rounded towards venter.
3) **Supracurvate:** (in German "suprakurvat") describes a margin being more narrowly rounded towards dorsum.

Cyathus (pl. *cyathi*, Ancient Greek/Latin, meaning "scoop cup", ladle): The 'true' cyathus is a crescent, semicircular or triangular extension of the posteroventral margin (at or close to the posteroventral angle) of the larger valve only. It is concave internally and strengthened by fine ribs - sometimes associated with an arcuate central ridge, the => *limen*, and the direction of its angularity or cusp may be towards venter as well as posteroventral or posterior directions (see Fig. 7/B, E; 9). The size, shape, orientation, and angle of the cyathus are considerably valuable for taxonomy, while its function remains unclear (see also => *lunate*).

More rarely, this extension may also be present in the smaller valve, e.g. *Cypridea nitidula* Peck 1941 (Fig. 5C/9), *Cypridea (Longispinella) longispina* (Peck 1941) (Fig. 5C/8); and then the "scoop cup", i.e. the 'true' cyathus, is not realized anymore. For practical reasons and the close phylogenetic relations of the taxa, no new term is introduced here for such a case, and a "cyathus" appearing in both valves is called a ***cyathus-like protrusion***, assumed to be the plesiomorphic state within the evolution of the *Praecypridea*/*Cypridea*-lineage (see Sames et al. in review). However, more data is necessary for a justification of such a statement. The cyathus-like protrusion can be strongly developed with about equal triangular extensions in both valves (Fig. 5C/9); or weakly developed, i.e. the triangular is well-developed in the larger valve but only weakly in the smaller valve (Fig. 5C/8). All transitions are possible, the cyathus-like protrusion can even be strongly developed, elongated and acute, e.g. in *Praecypridea* Sames et al. (in review).

Cyathus-like protrusion: see => *cyathus*

Dorsal furrow: see => *hinge incisure*

Dorsal margin: The dorsal part of the carapace's/valve's margin adjoining the hinge (including the => *hinge margin*), extending between both angular peaks of the => *cardinal angles* (Fig. 3). The dorsal margin either coincides with the => *dorsal lateral outline* and/or it is overreached and covered by dorsolateral elevations/inflations of the carapace, and then only partially visible in lateral view and not congruent with the dorsal outline. The term dorsal margin is as well not completely equivalent to the => *hinge margin* which is only a limited part of the former!

Dorsal (part of) lateral outline: The dorsal part of the carapace's outline (border) in lateral 2D-projection, either coincident or (often) not coincident with the => *dorsal margin* (Fig. 3). This term is to be clearly distinguished from and must not be confused with => *dorsal outline*, which is the outline of the carapace in dorsal view!

Dorsal outline: The 2D-projection of the carapace's outline (border) in dorsal view (Fig. 7/D). This is a taxonomically significant feature not to be confused with the => *dorsal lateral outline*, which is the dorsal part of an ostracod's outline in lateral view. The dorsal outline can distinctly show the sexual dimorphism—if apparent in the outer view of the particular species, e.g. the at mid-length more rotund females in *Cypridea (Pseudocypridina) piedmonti*—and can be heavily affected by different => *ornamentation* elements. Since the dorsal *view* is taxonomically more significant than the ventral view, it is the one commonly used for description, and so is the dorsal outline. Dorsal and ventral outlines are congruent and the usage of the latter is therefore dispensable.

Dorsal ridge: This character is a dorsal extension of the larger valve only (Fig. 7/A, B). It is either straight or arcuate and is situated somewhat lateral to hinge margin, at about the margin of the dorsal furrow. It approximately extends between the cardinal angles but mostly masks them beginning in front of the anterior cardinal angle and ending at about or behind the posterior cardinal angle. In lateral view the dorsal ridge forms a false dorsal margin/outline. Its function is unknown. An example is *Cypridea* ex gr. *alta* Wolburg 1959 (best visible in right lateral view, Pl. 8, Fig. 2).

Duplicature: A "classic" morphologic term for the peripheral => *free margin*, where—also in the "classic" view —the => *outer lamella* and (the calcified part of the) free => *inner lamella* are in contact, i.e. fused together (Fig. 8). This view emanates from and differs between two separate lamellae that are fused together on a plane called => *marginal zone/fused zone*. The calcified part of the inner lamella can be either totally fused to the outer one, or alternatively, the more or less proximal part (depending on the width of the => *marginal zone*) of the calcified *inner lamella* can be partially separated from the *outer lamella* by a => *vestibulum*, and is then sometimes called 'free inner lamella').

Yamada (2007) also uses the term duplicature, though in a different meaning. He (op. cit.) distinguishes the "dual lamellae structure" (two calcified lamella cuticles, see fig. 1c in Yamada 2007, although the internal part of the outer lamella underneath the "outer lamella cuticle" is never labelled therein) of the calcified carapace and identifies the "classic" *calcified inner lamella* as continuous extension (not separate structure) of his "outer lamella cuticle" being bent inwards as well as therefore replaces the term *calcified inner lamella* with the term "marginal infold" adopted from other authors.

Remarks: The classic view possibly derives from the concept that an ostracod's carapace consists of two separate valves instead of one continuous (organic) carapace that is just specifically calcified with a complete separation of its mineralized parts. The former, in turn, most probably derives from the paleontologic point of view in that the paleontologists usually work with the fossil preserved relics of an ostracod, the remains of the bivalved calcified parts of the carapace.

Equicurvate: see => *curvature*

Equivalve: A denomination of the carapace valves, if these are of almost equal size and shape, i.e. lateral outline in particular (see also => *inequivalve* and => *subequivalve*).

Flange: More or less prominent ridge/excrescence deriving from the => *outer lamella* (more precisely from the outer lamella cuticle following Yamada 2007) forming the outer margin of a valve when the => *selvage* and outer margin are displaced inwards. Yamada (2007, see also fig. 7 therein) points out, that terms like *flange*, => *selvage*, and (inner) *list* are not appropriate to be applied universally. However, it is used herein to describe the particular morphology of the outer antero/posteroventral margins of *Cypridea* being turned inwards (see Fig. 8 herein).

Free inner lamella: see => *inner lamella* and => *duplicature*

Free (carapace/valve) margin: A term for that part of the => *carapace/valve margin* along which the valves are not held together by the => *ligament* attached to them (this would be => *attached margin*).

Fossa (pl. *fossae*, Latin for groove, pit; English adj. *fossal*): This is the single mesh in a => *reticulum*, composed of the surrounding => *murus* and a => *solum*.

Fused Zone: see => *marginal zone*

Hinge: Internal structure of the valves along the => *dorsal margin*, where the valves are articulated when the carapace is closed. In contrast to published "classic" definitions and following more recent perceptions, the hinge in ostracods is to a lesser extent a joint forming the axis of rotation when the valves are opened, but instead much more a structure to inhibit the dislocation of the valves against each other when the carapace is closed. As can be observed in recent ostracods, certain elements of the => *hinge* (e.g. the => *terminal elements*, i.e. the teeth and sockets in the lophodont hinge of *Metacypris*, for example) mostly diverge when the carapace is opened.

The hinge in *Cypridea* (Fig. 9) is divided into three elements and has been described in detail by Sylvester-Bradley (1949). The hinge line is straight and occupies about half the carapace's length. The larger valve bears a groove along the median part "... which at each end is dilated and makes a scalloped recess. At the anterior end the [=>] *selvage* is swollen and overhangs the recess (the 'knurling' of Anderson 1939), partly hiding it in lateral view. The posterior end is even more obscured by the swollen [=>] *selvage* which overhangs it ('flexure', Anderson 1939) ..." (Sylvester-Bradley 1949, p. 132). At the smaller valve the median hinge part is a slightly swollen bar fitting into the groove of the larger valve. Its posterior end "...projects in the form of a swollen cusp which fits into the posterior recess of the larger valve" (Sylvester-Bradley 1949, p. 132). Sylvester-Bradley (op. cit., p. 132) also notes a faint crenulation on the posterior process of some species "... suggesting that it may become denticulate ... The anterior part of the hinge also projects, and fits into the anterior recess of the larger valve, but is not swollen, and has a slightly concave ventral surface." However, a crenulation of single elements could not be confirmed thus far.

Thus, following this characterization and codifying it into the classic hinge taxonomy (Gründel 1974, Sylvester-Bradley 1956, and the Treatise of Invertebrate Palaeontology, i.e. Moore 1961), the hinge of *Cypridea* is to be designated ***merodont*** (i.e. it has two terminal teeth in one valve with corresponding sockets in the other) and of ***lophodont*** type (i.e. tripartite with all elements not subdivided and all being smooth), cf. => *inverse hinge* also.

Hinge bar: A term for the median hinge element in the larger valve (if the hingement is not => *inverse*), if it is developed as a ridge, smooth (which is the case in *Cypridea*) or finely crenulate (=> *denticulate*), which rises up from the valves margin behind it (Sylvester-Bradley 1956), see Fig. 7/E. Its counterpart in the smaller valve is a (hinge) groove. The hinge bar is often situated under an => *accommodation groove*. The hinge bar as well as the corresponding groove can be bipartite, then consisting of an anterior and posterior part of strongly different shape (being not the case in *Cypridea*).

Cypridea has no real median groove developed in the smaller valve; the hinge bar of the larger valve is only attached to the smaller with its ventral part, thus merely resting on the dorsal margin of the smaller valve.

Hinge elements: The single parts that form the hinge. A terminal element is usually developed as *tooth* (or process of some authors) in the smaller right valve (or the other way round if the hingement is => *inverse*), and a corresponding *socket* (or recess of some authors) in the larger left valve (or the other way round if the hingement is => *inverse*).

The hinge in *Cypridea* is tripartite (lophodont hinge), consisting of an anterior and a posterior => *terminal element* (its shape defining the => *cardinal angles*) and a median hinge element (Fig. 9). The median hinge element in *Cypridea* is the simple => *hinge bar*.

Hinge incisure/dorsal furrow: A feature characteristic to *Cypridea* (and the Cyprideidae Martin 1940 sensu Sames herein, but not exclusively; see Fig. 7/D for illustration). The => *hinge margin* is indented causing an elongated ovate dorsal furrow with its maximum width at about mid-length of the hinge margin, usually overreached by the higher dorsolateral region of both valves. Depending on the position of the maximum width (i.e. the distance from the hinge margin at mid-length) the outline of the hinge incisure varies from symmetric-elliptic to ovate. In most cases the larger valve's dorsal overreach is stronger than that of the smaller valve – in some taxa the latter is increased by a => *dorsal ridge* – whereas the smaller valves overreach may only be barely recognizable in some species. The dorsal furrow's maximum length/extension is in lateral view approximately defined by the angular points of the => *cardinal angles*. Strong variations in the grade of incisure occur, ranging from a deep furrow to a very shallow or flat area, being of taxonomic significance at species level (more seldom for subgenera of some authors). In relation to the longitudinal axis of the carapace in dorsal view, the dorsal furrow is either centered or oblique towards the smaller valve (called => *lateral offset*) which is mostly the case when a => *dorsal ridge* at the larger valve is present. The lateral offset results from the fact that the flank of the larger valve's part of the dorsal furrow is usually wider than the flank of the smaller valve, which, in turn, is a result of the overlap of the larger valve's outer margin (the hinge bar resting on the smaller valve) along the => *hinge margin*.

Hinge, inverse: see => *inverse*

Hinge line: Line in dorsal view of the carapace along which the valves articulate when the valves are closed, including the area of the terminal => *hinge elements* and thus also including a small dorsal part of the anterior and posterior margins (Fig. 7/D). May be straight or meandering. The hinge line must not be confused with the => *dorsal margin* or the => *hinge margin*!

Hinge margin: Part of the => *dorsal margin*, extending in between the => *cardinal angles* and being the outer equivalent to the internal extension of the median => *hinge* element, excluding the terminal elements (cf. => *hinge bar* also; see Fig. 3). The hinge margin is not coincident with the => *attached margin*.

Inequivalve: A denomination of the carapace valves when they differ in size and/or shape, i.e. lateral outline in particular (see also => *subequivalve*, => *equivalve*). The degree of the differences may vary considerably between the species.

Infracurvate: see => *curvature*

Inner (calcified) lamella: In the "classic" terminology, this is a separate inner calcified part of the carapace/valve lamella being fused or, partially (i.e. in its proximal part), not fused to the => *outer lamella* (also called => *free inner lamella* then; also refer to => *duplicature* and => *vestibulum*), as illustrated in Figs. 7/E, Fig. 8, 9). For the probable derivation of such a view of (partially) fused but morphologically separate lamellae please refer to the remarks under the definition of => *duplicature*. Concerning *Cypridea* and its close relatives, also refer to => *local widening of inner lamella*, a diagnostic feature of the Cyprideidae Martin 1940.

Yamada (2007) identifies this structure (based on Transmission Electron Microscopy) as continuous extension (not separate structure) of his "outer lamella cuticle" being bent inwards as well as therefore replaces the term *calcified inner lamella* with the term "marginal infold" adopted from other authors.

Inner lamella cuticle: A term used by Yamada (2007) for the chitinous noncalcified part of the "classic" => *inner lamella*; its connection to his "outer lamella cuticle" (or proximal limit as well) being the => *inner margin*.

Inner list: According to Kesling (1951, p. 123), the (inner) list is "a proximal ridge on the [=>] *contact margin*, absent in some ostracods". However, it occurs in *Cypridea* and related genera (e.g. *Talicypridea*, *Bennelongia*, *Chlamydotheca*, *Cypris*), see Horne & Colin (2005), for example (Figs. 7/F and 8). It is neither coinciding with the inner margin nor with the => *selvage* or the => *line of concrescence*. For *Cypridea*, see => *limen* also.

Inner margin: This is the proximal limit of => *duplicature* and/or => *inner (calcified) lamella* in the "classic" terminology (Fig 7/E and 8). Following Yamada (2007) this would be the proximal limit of the => *marginal infold*.

In some ostracod taxa, the inner and outer lamella are linked directly at and along the outer margin (e.g. some Podocopida: Darwinuloidea or some Platycopida), and then the inner and outer margins (outer margin is equal to => *carapace/valve margin*) are congruent.

Interrupted selvage: A feature diagnostic to the extinct family Cyprideidae Martin 1940, in contrast to its extant relatives of the family Cyprididae Baird 1845 (e.g. *Bennelongia*, *Chlamydotheca*, *Cypris*; refer to Horne and Colin 2005, and see Figs. 7/F, and 8 herein), which is connected with the => *rostrum* in this respect that the posterior part of the latter is characterized by the absence of the selvage in this area. The selvage is interrupted in the anteroventral region of the valves. In *Cypridea*, the selvage runs along the anterior part of the rostrum to its point, is interrupted along its posterior part and continues at the angular point of the => *alveolar notch*, there being about 90° rotated compared to the selvage of the rostrum.

Inverse (from Latin *inversus* for turned/reverted/vice versa—regarding valve size relation and overlap, or hinge as well; "reverse" of some authors): This term refers to either the valve size relation (see item 1 below), or the position of the hinge elements in relation to the larger and smaller valve in ostracods (see item 2 below), both in comparison to the most common situation within a taxon (mostly referring to a genus). However, both are features independent of each other in their occurrence, not necessarily showing a coherence.

Inversion of the valve size relation affects the overlap as well as the hingement (i.e. position of the hinge elements in the left and right valves), and thus, in a taxon with inverse valve size relation, the position of the hinge elements is reversed, but still to be defined "normal hingement" if the position of the particular hinge elements remain in the *larger* or *smaller* valve, respectively (e.g. assuming that the terminal hinge elements are located in the smaller valve being the RV in the 'normal' state, they still remain in the *smaller* valve in the 'inverse' form, the latter valve just being the LV then).

> 1) An ***inverse valve size (relation)***, a comparative term, characterizes an ostracod taxon that shows the opposite ("inverse") valve size relation of the situation common ("normal") to the group of higher hierarchy to which it belongs to. In most ostracods, one of the valves (the LV mostly) is distinctly larger than the other and often overlaps and/or overreaches the smaller more or less strongly and has therefore a different lateral outline. In *Cypridea*, for example, the normal valve size relation is LV>RV, which is also the case for most representatives of the Ostracoda, and therefore designated as "normal" valve size relation. Thus, species like *C. clavata clavata* (Anderson 1939) with RV>LV, are determined "inverse" representatives of *Cypridea*. Many inverse *Cypridea*-like taxa have had been designated as a separate genus, *Ulwellia* Anderson 1939, but later then, following Sylvester-Bradley (1949) or Sohn (1969, p. B4), most inverse representatives were regarded as subgenus of *Cypridea*: *C. (Ulwellia)* by many authors. The subgenus *Ulwellia* however, is rejected herein (see Chapter 5.4.3 herein for details). The inverse valve size relation does not necessarily implicate an => *inverse hinge* (see there).
>
> In *Cypridea*, the inverse valve size relation does *not* involve the inversion of the hinge, i.e. the *median hinge element* remains being located in the *larger* valve and the *terminal hinge elements* remain being located in the *smaller* valve. Likewise, the size and shape relations of the => *alveolar notch* and => *alveolar furrow* also remain in the valve of particular size, that is the alveolar notch still remains by trend more distinct in the *smaller* valve, while moderately to strongly developed alveolar furrows by trend still remain more elongate and longer in the *larger* valve and more triangular in the *smaller* valve.

Remarks: It is important to note that a "normal" valve size relation is also existent if the relation is RV>LV, for the case that this situation does commonly occur within a taxon. For example, the RV>LV relation in the recent *Darwinula* (sensu stricto, Rossetti and Martens 1998) is normal and characteristic to this genus whereas within and in relation to the family Darwinulidae it would be called 'inverse', because all other genera (*Alicenula*, *Microdarwinula*, *Penthesilenula* and *Vestalenula*) have the 'normal' valve size relation of LV>RV (cf. Rossetti and Martens 1998).

The inverse valve size relation in *Cypridea* is not considered to be taxonomically significant by the recent author, neither at genus nor species level. As for *Cypridea*, there are some species that look exactly the same except that they differ in their valve size relation by appearing to be mirror-inverted. The taxonomic significance or insignificance has to be reviewed in the genetic and phylogenetic context and could be tested by statistic analyses of morphometric data. Taking the reproductive mode in *Cypridea* (exclusively or mainly parthenogenetic? – most probably sexual with intermittent parthenogenesis) into consideration, an inverse valve size may be likely to occur in some populations descending from parthenogenetic reproduction of a single specimen with inverse valve size relation, possibly through mutation or other genetically induced mechanisms. It also can be discussed, if geographically and/or chronologically separated(!) populations that have different valve size relations and are assumed to belong to one species, should be differentiated by applying varieties or subspecies names.

Most of the species of *Cypridea* with inverse valve size relation should, therefore, have a morphologic equal counterpart except for the opposite ("normal") valve size relation (LV>RV) and should be considered a variety of the particular species. Musacchio (1971) described several new inverse species of *Cypridea*, e.g. *Cypridea cymerata*, *Cypridea ludica*, *Cypridea modesta* (preoccupied by the inverse

Cypridea (Cypridea) modesta Kneuper-Haack 1966, both, however, strongly differing morphologically), the morphotype of all of which is very similar to well-known European taxa, for example.

Yet, to discuss the taxonomic (in-)significance of valve size relation in *Cypridea* in general and in detail is not the purpose of this paper and must remain subject to further studies.

> 2) The ***inverse hinge*** is a comparative term to characterize the situation of the position of the hinge elements in contrast to the situation common to the group of higher hierarchy it belongs to. The "normal" state (i.e. most common situation within a taxon of certain hierarchy and also the common situation in most ostracods) is that the median hinge element (a simple hinge bar in *Cypridea*) as well as the corresponding grooves (sockets in *Cypridea*) of the terminal hinge elements are situated in the larger valve, whereas the terminal hinge elements (teeth in *Cypridea*) and the median groove are situated in the smaller valve, independently of whether this be the LV or the RV in both cases. Thus, a 'true' *inverse hinge* is the situation where the *median hinge element occurs* in the *smaller* valve, while the *terminal hinge elements* occur in the *larger valve*.

Remarks: As for *Cypridea*, there is no case of an inverse hinge known thus far. In contrast to statements of other authors (e.g. Horne and Colin 2005, p. 27, who term it "reverse"), no 'true' *inverse hinge* is known to occur in representatives of *Cypridea*, based on the revised definition given here. The taxa of *Cypridea* with an *inverse valve size relation* have thus a "normal" hingement.

Examples for taxa with a 'true' *inverse hinge* are *Theriosynoecum pricei* (Pinto and Sanguinetti 1958) or the late 'Quaternary' to recent genus *Gomphocythere* (both Cytheroidea).

Lateral offset (of hinge incisure/dorsal furrow): This character defines an obliquity of the => *hinge incisure* (dorsal furrow) in relation to the longitudinal center line (equals half width) of the carapace in dorsal view (see Fig. 7/D). Such an offset is common in taxa with a => *dorsal ridge* present in the larger valve (e.g. *Cypridea alta*-group).

In representatives of *Cypridea* without a dorsal ridge, the lateral offset is weaker and resulting from the fact that the flank of the larger valve's part of the hinge incisure is usually somewhat wider than the flank of the smaller valve, which, in turn, is a result of the overlap of the larger valve's outer margin (flange) along the => *hinge margin*.

Limen (from Latin, meaning treshold/swell; see => *inner list* also): This term was introduced by Szczechura (1978, p. 77) as "… a thickening (or bent) of the proximal part of the inner lamella in the posteroventral part of the valve, displayed by the representatives of the genera *Cypridea*, *?Paracypridea* und *Mongolocypris* gen. nov. … This structure is developed on one (the left, i.e. the larger) valve ..." (for illustration see Fig. 7/E, *Cypridea* ex gr. *tuberculata*, Pl. 8, Fig. 12, and Fig. 9/3-magnification).

Taking an => *inverse* valve size relation into account, the limen is defined here as an arcuate ridge-like structure parallel to the striae/septa in the distal calcified part of the posteroventral inner lamella of the larger valve, sometimes associated with a groove towards the outer margin (if strongly developed). It is interpreted to be a local thickening of the => *inner list* (as generally used for Ostracoda, e.g. Kesling 1951; and as specifically used by Horne and Colin 2005, for representatives of the Cypridoidea), presumably acting as stopping ridge for the opposite valve when carapace is closed and/or as strengthening of the relevant valve area.

Ligament: This is an uncalcified organic cuticular structure connecting both valves dorsally and corresponding to the cuticle of the outer lamella (e.g. Yamada 2007). It has specialized fibrous structures to provide its strength (op. cit.). Unlike still given in most textbooks, the (podocopid) ligament most probably has no elasticity (Yamada 2007) and does not support/cause the aperture of the valves (e.g. Meisch 2000), that is caused by the internal hydraulic pressure of the body liquids instead.

Line of concrescence: This term designates the proximal (inner) line of the plane of fusion (=> *marginal zone*) between the calcified => *inner lamella* and the => *outer lamella* in the "classic" terminology (Fig. 8). It can either be congruent or not congruent with the => *inner margin*, depending on whether a => *vestibulum* is developed. In the latter case, the line of concrescence and the inner margin are not congruent.

Lobe(s): A => *local ornamentation element.* These are diagnostic, well-rounded major protuberances of the valve, either covered by or without other => *ornamentation* elements, and often associated with a => *sulcus*. The dimensions vary and generally, their boundaries smoothly pass into the carapace. Usually, close to and on the lobes, any potential => *area-wide ornamentation elements/surface characters* are distorted or differ in their dimensions from other areas of the carapace.

Lobes are morphologically clearly distinct from => *ridges*, which are well-delimited from the surrounding carapace and are genetically fixed diagnostic characters in the carapace.

Local ornamentation element(s): see => *ornamentation*

Local widening of the inner lamella: This term characterizes a widening of the anteroventral part of the => *inner lamella* along and where => *rostrum* and => *alveolus* are situated (see Fig. 8). In 'true' *Cypridea*, it is combined with the => *attached area.* However, a widened inner lamella occurs in true representatives of *Cypridea* (*Cypridea* s.l.) as well as in closely related taxa such as *Bisulcocypridea* Sohn 1969, *Mongolocypris* Szczechura 1978, *Paracypridea* Swain 1946, and *Praecypridea* Sames, Whatley and Schudack (Sames et al in review).

Lophodont: see => *hinge*

Lunate (=> *cyathus*): A term typically used by some authors to describe and designate the falcate/falciform (crescent or sickle-shaped) shape of the rostrum in *Cypridea setina* (Anderson 1939), e.g. F.W. Anderson (in Anderson, Bazley and Shepard-Thorn 1967, and in Anderson and Bazley 1971). However, Wolburg (1959) used it to describe the shape of the rostrum in some representatives of *Cypridea* (in German: *sichelförmig*, meaning sickle-shaped).

Marginal infold: A term adopted by Yamada (2007, refer to p. 204 therein) from other authors based on his new findings concerning the ultrastructure of the carapace margin of the Podocopida. Yamada (op. cit.) uses this term to replace the "classic" term => *(calcified) inner lamella.*

Marginal pore (canal): see => *pore*

Marginal zone (fused zone): This is the part of the carapace where the inner and outer lamella are fused together (Fig. 8). Its width greatly varies and the => *marginal pore canals* extend through it (van Morkhoven 1962). The inappropriate term "adhesive strip" (for the very thin chitinous layer between => *inner* and => *outer lamella*), as used by Kesling (1951) and Moore (1961) for example, should be avoided and restricted, because it gives the impression that the calcified elements of inner and outer lamella on the fossil valve may be separated. The latter is only the case in some taxa that, consequentially, have no true marginal zone then.

Yamada (2007) does not mention and discuss this term, but following his results, a fused zone would not exist because he does not differentiate between inner and outer lamellae in a classic sense (see => *duplicature* for more information). Deducing from Yamada's (op. cit.) perception, the 'marginal zone' would therefore just be the plane where the => *marginal pore canals* extend through, and not be a fused zone.

Median hinge element: see => *hinge elements*

Merodont: see => *hinge*

Murus (pl. *muri*, Latin for wall; English adj. mural): The wall of a => *fossa* in a => *reticulum* (Sylvester-Bradley and Benson 1971).

Node(s)/Noding: see => *ornamentation*, => *local ornamentation elements*

Node-like tuberculum (-i)/tubercle: see => *ornamentation*, => *local ornamentation elements*

Ornamentation (ornamentation elements): For reasons of clarification and potential (paleoenvironmental) application, the ornamentation as used in this paper and in part specified for *Cypridea*, is subclassified into => *local ornamentation elements* and => *area-wide ornamentation elements* herein.

The meaning of ornamentation and its subdivision applied to *Cypridea* herein must not be confused with "surface ornament", as used by Kesling (1951, p. 121), in the Treatise of Invertebrate Paleontology by Moore (1961, p. Q55), or by Sylvester-Bradley and Benson (1971) – an unfavorable, mistakable term for => *area-wide ornamentation elements/surface characters* of the valves, as proposed herein, for the reason that in the mentioned publications no distinction between area-wide and local (and delimited) characters is made as well as that the term is used regardless of genesis of these characters and their possible reflection on the valve's inner surface.

Sylvester-Bradley and Benson (1971) used the term "ornate" to describe ostracods with => *local ornamentation elements* and => *area-wide ornamentation elements/surface characters*, and established a terminology for ornamentation types and elements. The latter authors also proposed to differentiate between "negative" (puncta, pores, sulci etc.) and "positive" (tubercles, spines etc.) features but at the same time pointed out that they did not intend to convey concepts of genesis therewith. This distinction appears to be superfluous, not least because of the latter objection, since many ornamentation elements that would be of "opposite" character following Sylvester-Bradley and Benson (1971) are related in their genesis (e.g. certain pores, 'negative', and tubercles, 'positive').

The usage of *ornamentation* herein must also not be confused with "ornamentation" sensu van Morkhoven (1962, p. 37), in his particular definition also considered capable of being misunderstood and only partially applied herein (see remarks/discussion below).

The term "sculpture", which is probably appropriate for some extremely ornamented Paleozoic Ostracoda that look closely to being heavily adorned, is avoided for Mesozoic nonmarine ostracods herein.

Although often being diffuse in their delimitation, structures like => *lobe* and => *sulcus* are included in => *local ornamentation elements* for the reason that one element does never cover most of the carapace's outer surface. Ridges (=> *lateral ridges*) are included as well.

Characters, such as => *pores* are excluded from ornamentation because these are only the external termination of the pore canals that are a character being located internally in the valve.

The following terms for the different ornament types in *Cypridea* are used herein:

A) **Local ornamentation elements:** are defined as the total of all local(!), well-delimited and distinct elevations of the valves at their outer lateral surface that are (mostly) reflected on the inner surface. In general, such ornamentation patterns are nearly symmetric in both valves and major ornamentation elements are occurring pairwise opposite to each other. However, exceptions frequently occur in *Cypridea* and the following types of irregularities can also be combined:

a) there can be a displacement of one or more elements so that they are not exactly in opposition to each other anymore,
b) the elements of one valve (the smaller valve mostly) are less well-developed or completely lacking,
c) single "erratic" elements, without a counterpart on the other valve, occur.

The occurrence of some local ornamentation elements in *Cypridea* is considered taxonomically more or less significant (see the particular elements and the remarks/discussion below.

1) **Node(s)/Noding:** Clearly distinct from => *lobes*, nodes are medium to large sized hollow protuberances (also "bulges, outward flexions" in some publications) of the carapace, rarely elevated so strongly that they form properly bubbles (3/4 spheres). They are a facultative (eco-)phenotypical feature of the carapace, taxonomically insignificant. Noding is, generally, a phenotypical response to environmental changes (e.g. van Harten 2000, Keyser 2005). The shape of nodes is variable, but mostly about hemispheric to broadly hemispheric-elliptic. If nodes occur, their location on the carapace usually follows a certain pattern (see Keyser 2005 for the reasons), but they can also be irregularly placed sometimes. In most cases, the process of noding is combined with a distortion of the => *area-wide ornamentation elements/surface characters* on, and partially around, the nodes. The term 'verrucose' (warty) is sometimes used to describe specimens with many nodes or even to name species or subspecies.
Regarding representatives of *Cypridea*, nodes are quite common characters and have been highly overestimated and used as taxonomic feature, e.g. *Cypridea (Pseudocypridina) piedmonti* herein, or *Cypridea verrucosa* Jones.

2) **Tubercles/Tuberculation/tuberculum** (pl. *tuberculi*, from Latin *tuberculum*, meaning small bump/protuberance; English adj. tuberculate): Tubercles are rounded, relatively low prominences of intermediate size (usually smaller than => *nodes* in diameter) on the valve surface and/or along the margins. The tubercles can be either conic (sometimes even concave laterally) or cylindric, hollow or solid with a more or less rounded, or flattened point. In some cases, the tuberculi can be inflated and have a hemispheric node-like shape (see => *node-like tuberculum* below). Typically, a tubercle forms around a pore, thus being an expanded pore conulus and always having a (simple) normal => *pore* canal in its center as well as a pore at its summit. An ornamentation characterized by many tubercles is called => *tuberculation*. If a tubercle-like structure has a tapering distal end, no matter if rounded or sharply pointed, it is called a => *spine*. Tuberculi always occur pairwise, one on each valve lying oppositely to each other, although their size, intensity of development, and position may slightly differ between both valves.

3) **Node-like tuberculum(-i)/tubercle(-s):** These are more or less strongly inflated hollow tuberculi (see above), thereby having a more hemispheric than conic shape. They differ from => *nodes* (see above) in (mostly) bearing no => *surface characters* and always forming from a normal (lateral) => *pore*. The position of these pores on the carapace is fixed.
Node–like tuberculi are a typical ecophenotypic feature for representatives of *Theriosynoecum* Branson 1936 due to increasing salinity (Do Carmo et al. 1999) while the carapace is soft during molt, as well as they occur in some representatives of *Cypridea*, e.g. *Cypridea clavata* (Anderson 1939), *Cypridea dunkeri* Jones 1885, *Cypridea granulosa* (Sowerby 1836) and *Cypridea pumila* Anderson. However, because the mentioned two genera belong to different superfamilies, it remains unclear thus far, if the presumed responsible process in *Theriosynoecum* can be assigned to *Cypridea* as well. Quite the contrary, deriving from new findings in the extant *Potamocypris humilis* (Horne and Smith 2004, see remarks and discussion herein right below), strong tuberculation in many *Cypridea* might be an ontogenetic character instead, thereby not excluding the possible control of its degree of development by environmental factors. In the past, node-

like tuberculi have erroneously been used by some authors as diagnostic feature at species or genus level.

Node-like tuberculi almost always occur pairwise, one on each valve lying oppositly to each other, although their size or intensity of development may slightly differ between both valves.

4) **Spine(s):** Spines are solid or hollow, more or less elongated projections from the valves surface (cf. Moore 1961), with a sharply pointed or rounded, tapering distal end. Shape and size of the spines vary greatly, they may be conic-compact or very prolate, straight or bent (backwards mostly). In *Cypridea*, like => *tubercles*, spines often (not always) also have (simple) pore canals in (or close to) their center and summit. The main difference of spines in comparison to => *tubercles*, both being just descritive terms, is the pointed distal end and that tubercles are always bound to pores whereas spines do not always seem to be. Some major spines seem to be genetically fixed in their occurrence (but not always in their position, e.g. *Cypridea (Longispinella) longispina* Peck 1941 herein), but most of them—especially when occurring in higher numbers and being lesser in size—may be an ontogenetic character mainly, at least in *Cypridea* (cf. discussion below).

Spines mostly occur pairwise, one on each valve lying oppositly to each other, although their size or intensity of development may slightly to moderately differ between both valves. However, major single-paired spines that seeming to be genetically fixed(?) in their occurrence, are not lying opposite to each other. Quite the contrary, the position of the spines in relation to the valve can and does vary considerably in both valves at a time (usually within central to posterocentral/posteroventral regions), as can their position in relation to each other, e.g. *Cypridea (Longispinella) longispina*, *Cypridea* ex gr. *tuberculata* cf. *C. tilleyi*. Accordingly, such spines rarely lie oppositely to each other but show a more or less considerable offset instead.

5) **Other *local ornamentation elements*:** => *dorsal ridge*, => *ventral ridge*, => *lobe*, => *sulcus*

B) **Area-wide ornamentation elements/surface characters:** Surface characters, used herein sometimes for abridgement, are defined as the total of area-wide(!) ornamentation elements covering most of the outer valve's surface, such as elevations and depressions (thickenings or thinnings) of the valves. The scale of the single elements varies, but mostly is small (< 50µm), the intensity (size, in part) of their development can be influenced by ecological factors (e.g. Calcium availability and salinity sensu lato).

Anderson et al. (1967, p. 202) called the surface characters "surface sculpture", a misleading term giving the impression of very strong single elements, and thus to be abandoned. To preclude confusion, the term "surface ornament", as proposed in the Treatise (Moore 1961, p. Q55), and "ornamentation" as used by van Morkhoven (1962, p. 37, see remarks to => *ornamentation*, herein), should be avoided to specify area-wide ornamentation elements.

Four different types of area-wide ornamentation elements/surface characters occur among the representatives of *Cypridea*:

1) **Smooth:** Taxa without any area-wide ornamentation elements. Only the pores are visible. Sometimes, generally smooth ostracods (e.g. representatives of *Cypridea (Pseudocypridina) setina*), if well-preserved, show a very faint rhombic to honeycombed pattern, which is slightly distorted (stretched) where a => *lobe* and/or => *sulcus* occurs. It looks somewhat like an inverse (micro-) => *reticulation*. The size of about 15-20µm, as well as shape and distortion suggest that these are imprints of cuticular cells.

2) **Punctate/punctation:** Puncta (plural of *punctum*, Latin for point, small spot, English adj. punctate) are small (between 20 and 50µm) pit-like depressions in the valve's surface (Moore 1961). In general, they are regularly distributed on the valve, their density varies, and their shape can be hemispheric or conic. In some areas of the carapace, like the ventral margin or close to and on => *local ornamentation elements*, they are distorted – elongated mostly. Almost always, the (simple) normal => *pores* occurring are in between, rarely in a marginal position within the puncta. As proposed herein, the difference to => *reticulation* is that the *puncta* are always roundish whereas the => *fossae* of a => *reticulum* are polygonal.

3) **Reticulation, reticulum** (pl. *reticula*, Latin for small net; English adj. reticulate): A reticulation describes a carapace surface having a netlike pattern of small intersecting crests/small bars (=> *murus)* forming the walls of single meshes that are deep dimples/pits (=> *fossa*, -ae) of rounded or polygonal outline. The pattern is more or less regularly, the crests are equally narrow and straight or slightly concave laterally and their junctions are small (if no ornamentation element is present). The transition to => *punctation* is smooth and not accurately definable. It is proposed that when the => *muri* are broad, rounded as well as heavily concave laterally and the junctions are as big as or larger than the relatively shallow => *fossae*, the netlike pattern is not realized anymore and the term => *punctation* (***reticulation-like punctation***) is more appropriate.

In many ostracod taxa, a reticulation in more or less early ontogenetic stages is 'reduced' to a punctation in adults.

4) **Carina** (pl. *carinae*, Latin for keel; English adj. carinate): A well-defined, narrow and somewhat strongly projecting ridge on the outer surface, usually with a sharp edge, e.g. ventrally in *Cypridea* ex gr. *tuberculata* cf. *C. tilleyi* herein. Although of more or less local character, carinae are included in area-wide ornamentation elements herein bacause they derive from a reticulation, thus being a particular development of the => *muri*.

Remarks/Discussion: Van Morkhoven (1962) used ornamentation for all features occurring on a non-smooth valve surface "... that are not reflected on the inner surface ..." (op. cit., p. 37). However, somewhat later on the same page, he also includes massive "protuberances (tubercles or knobs)", features that, at least in *Theriosynoecum*, are often reflected on the inner surface. The conceptual division of ornamentation and => *surface characters* is chosen here to clarify the optional occurrence and local attribute of the ornamentation elements on the one hand, and the fixed (though ecophenotypically influenced in their intensity or weakened/absent through diagenesis and/or processing) diagnostic attribute of the surface characters.

Ornamentation in *Cypridea* is highly variable and has been used as important taxonomic feature in the past (particularly by F.W. Anderson). Anderson (1967, p. 239, fig. 1) developed a geometric scheme for the ornament pattern in *Cypridea* to locate and label the position of single => *tuberculi* and => *spines* on the carapace for taxonomic purposes. He (op. cit.) even listed three categories of these: Primaries, secondaries and tertiaries, with different percentages of chances to occur in all individuals of one taxon. Since local ornamentation elements are considered of low taxonomic relevance here, Anderson's (op. cit.) complex model is taxonomically relatively useless. This does, however, not exclude that a revised version and new interpretation of the model might provide a useful basis for future research regarding the evolution and development of tuberculation and spines in representatives of *Cypridea* and related taxa in conjunction with their ecophenotypy, ontogenesis and the distribution of lateral pores. Testing hypotheses in this context with morphometric methods is considered promising.

It remains unknown why Anderson (1967) again started to develop and refine this model for taxonomic (not ecologic or ontogenetic) purposes—the first ideas of which he already had outlined much earlier (Anderson 1941, p. 296, figs. B1-B4)—although he knew Wolburg's (1959) publication and was in written and personal contact with Wolburg (1959, p. 228) for exchange of experiences.

The overestimation of the taxonomic value of tubercles and spines in *Cypridea* and its application by various authors resulted in the designation of an enormous quantity of subgenera (supraregionally), species and subspecies (regionally) worldwide. By continuous designation of new names in different continents, the supraregional biostratigaphic application of the *Cypridea*-lineage has been extremely limited, because the authors were convinced of the high (if not total) endemicity of the faunas. A problem for the current researcher is the enormous number of different taxa resulting from the application of this concept and, in part, the difficulty to reproduce some of these older concepts.

However, by comparison of numerous references of the faunas in different continents it becomes apparent that ornament patterns may not have such high taxonomic significance as thought in the past (cf. Anderson et al. 1967, p. 202, for example). In fact, there are commonly ornamented taxa (like representatives of *Cypridea* or the cytheroid *Theriosynoecum*) appearing very similar or even identical in all their characters simply apart from the ornamentation.

There seems to be a certain main overall pattern of ornament in *Cypridea*, approximately a horseshoe-shaped single or double row of tubercles and/or spines (about 10) opening dorsally and placed around the location of the adductor muscle scars. This pattern (connected with the location of pores) is most likely genetically fixed, as seems the occurrence(?) but not position of some major spines (cf. *Cypridea (Longispinella) longispina* and *Cypridea* ex gr. *tuberculata* cf. *C. tilleyi* herein). Problematical is the variable occurrence, development and size of the single ornamentation elements as well as the fact that several or many "erratic" elements are frequently present. Sometimes it seems that a few smaller elements fuse to form a large one. If ornamentation is a response to environmental factors (e.g. salinity s.l. changes during ecdysis) and/or an ontogenetic feature is much likely but cannot be definitely stated to date concerning extinct ostracod taxa. Nonetheless, there are applicable recent cognitions:

New results in the biology of living Ostracoda point to the high possibility of ontogenetic and/or ecophenotypic coherences regarding the ornamentation in the extinct genus *Cypridea*. Yang et al. (2002) studied => *local ornamentation elements* in a large number of Quaternary and recent representatives of *Ilyocypris* (*I. echinata*, *I. gibba* and *I. salebrosa*, Cypridoidea - Ilyocyprididae) from the Qaidam Basin (Tibet) and also favor a low taxonomic but more ecophenotypic significance of the nodes and tubercles (=> *node-like tuberculi* herein) and discovered that the number of specimen with node-like tuberculi tends to be much higher in juveniles than in adults. They (op. cit.) tentatively relate the lower expressivity or absence of node-like tuberculi to ontogenetic effects (i.e. the juveniles have stronger node-like tuberculi, the adults weaker or none) as well as temperature drop or temporary dryness in combination with salinity increase.

Horne and Smith (2004) figured juveniles and adults of the recent ostracod *Potamocypris humilis* Sars 1924 (Cypridoidea - Cyprididae). Although not closely related to *Cypridea* (the latter belonging to another family, the Cyprid<u>e</u>idae Martin) and its modern relatives, the juveniles of *P. humilis* show strong => *tuberculation* (and => *reticulation*-like punctation) in a pattern very similar to that of *Cypridea*. Even more intriguing is the fact that the adults show no ornamentation at all (anymore) whereas the A-1 instars do. Only the dense => *punctation* (deriving from the juvenile's reticulation) covering the surface is in part slightly distorted where the => *tubercles* were located in the A-1 instars. A similar concept may apply to *Cypridea* as well (pers. comm. Dave Horne, September 2005) implying that strong tuberculation in *Cypridea* may be considered being an (facultative?) ontogenetic character in some, but not all, cases. Actually, there are some representatives of *Cypridea* with such ornamentation that from their size and the very short posterior margin in relation to the anterior one are certainly juveniles (e.g. *Cypridea melvillei* Anderson). However, others in turn are probably adults but it has to be taken into account that these might also be A-1 instars, e.g. in the case of *Cypridea tuberculata* (J. de C. Sowerby).

Very recently, Nye et al. (2008)—on the basis of otherwise consistent characters (valve size relation, lateral and dorsal outline, development of rostrum and alveolus, development of the cyathus)—comprehensibly demonstrated a case of taxonomic insignificance of tuberculation, as exemplified by adults of *Cypridea clavata* (Anderson 1939). In the latter example, tubercles and node-like tubercles are also shown not to be characteristic, in the juveniles of this species at least. Thus, tuberculation should definitely not be retained as taxonomically significant character in *Cypridea*.

Causes and influence factors of variable noding have been dealt with over a long time analyzing the brackish water species *Cyprideis torosa* (Jones 1850) (Limnocytheridae, Cytheroidea), recently by van Harten (1996, 2000). A breakthrough is the study of Keyser (2005) who resolved the histologic peculiarities and causes of => *node* development in *Cyprideis torosa* and demonstrated that the occurrence, but not position, of nodes is environmentally induced and that "... the use of noding as an environmental marker for low salinity and/or low calcium content is correct" (op. cit., p. 106), at least regarding the problems of noding in this particular species. Nodes are mainly caused by problems in osmoregulation during ecdysis due to low salinity (op. cit.). Keyser (2005) also proposes explanations for the problems of having specimens with and without nodes in one sample, why nodes mostly develop in certain places in the carapace (anatomic) and why they are differently strong developed on the left and right valves of some individuals. An assignment of Keyser's concepts to fossil nonmarine taxa, though slightly conditionally because the taxa might not be physiologically comparable (different superfamilies, see below), led the present author to designate *Cypridea (Pseudocypridina) henrybelli* Sohn 1979 as an ecophenotype of *Cypridea (Pseudocypridina) piedmonti* Sohn 1979, for example.

The question, why the nodes are mostly (always?) stronger developed in the larger valve cannot be satisfactory answered thus far. Dietmar Keyser (Hamburg) made a mechanistic point: the specimens would often lie on the smaller valve during and after ecdysis, thereby limiting the size of the nodes in this valve through the body load (D. Keyser, personal communication 2007).

Interestingly, although the latter belong to the superfamily Cypridoidea whereas *Cyprideis torosa* belongs to the Cytheroidea (genus name might be misleading), the pattern of the primary nodes is nearly the same (four nodes, antero- and posterocentrally), thus raising the question, if the causes of the noding process in both cases might be more or less the same. More research is wanting. There are many more Mesozoic and Cainozoic ostracods showing this pattern of noding. Additionally, like in *Cyprideis torosa*, "erratic" additional nodes can occur in representatives of *Cypridea* (not to confuse with obvious => *node-like tuberculi* like in *Cypridea verrucosa* Jones or *Cypridea morula* Anderson, for example), that might point to higher environmental stress, like assumed for *Cyprideis torosa*.

For the fossil taxon *Theriosynoecum kirtlingtonense* Bate 1965 (Limnocytheridae), Do Carmo et al. (1999, p. 31) showed that "... the presence of nodes and the degree of their expression must be used with great caution in specific or generic diagnoses ..." because they might be a phenotypic expression in response to changes water chemistry. In contrast to *Cyprideis torosa* (see above), Do Carmo et al. (op. cit., p. 31) suggest a direct correlation between increasing strength of nodes and elevated salinity for *Theriosynoecum kirtlingtonense*, "... caused by the enhanced activity of the excretory mechanism in order to maintain osmoregulation", an argument having to be tested and discussed further.

The conceptual subdivision of ornamentation into => *local ornamentation elements* and => *area-wide ornamentation elements/surface characters* is established here to clarify and define the (mostly) optional occurrence and local attribute of common major local ornamentation elements (e.g. *tuberculi*) on the one hand, and the fixed diagnostic attribute of the area-wide element/surface characters (though ecophenotypically influenced in their intensity; or weakened/absent through diagenesis and/or processing).

Many local ornamentation elements as defined herein and applicable to the fossil Cyprideidae at least, seem to be ontogenetic or ecophenotypic, either caused (e.g. nodes) or influenced in size/development (e.g. tubercles) by abiotic factors taking effect during ecdysis. Then, the morphologic changes of the carapace during its soft stage are preserved when the carapace is hardened by calcification afterwards. In contrast, area-wide ornamentation elements are genetically fixed characters, relatively stable in their size and mostly just varying in their degree of expression. The latter can be influenced by environmental factors (e.g. calcium availability, water chemistry, temperature etc.)

Based on the findings elucidated beforehand, the concept applied in this paper (for the Cyprideidae) is that, in contrast to the patterns of distribution (position), the presence of the presence of *local ornamentation elements* as well as their degree of expression, are considered to be of low taxonomic relevance, and will not be used to separate species or genera, if all other carapace characters (like lateral and dorsal outlines, area-wide ornamentation elements/surface characters, development of rostrum and alveolus, internal features) are very similar or identical. If applicable, local ornamentation elements can be used for paleoenvironmental interpretation (i.e. salinity realms and changes) as well as to possibly support the identification of juveniles in some cases. By contrast, type, occurrence and shape of *area-wide ornamentation elements* are always taxonomically (more or less) relevant characters, provided that similar ontogenetic stages, i.e. adults ideally, are compared.

Outer lamella: A "classic" morphologic term for the external part of the calcified part of the carapace/valve. The outer lamella is—in its "classic" view—morphologically separated from the => *inner lamella*, although both are at least partially in contact, i.e. fused together (=> *marginal zone/fused zone*) along the => *free margin* or held together by the => *ligament* along the => *attached margin* (see. Fig. 8).

This view emanates from and differs between two separate lamellae that are fused together on a plane called => *marginal zone/fused zone*. The calcified part of the outer lamella can be either totally fused to the inner one, or alternatively, the more or less proximal part (depending on the width of the => *marginal zone*) of the calcified *inner lamella* can be partially separated from the *outer lamella* (then sometimes called 'free inner lamella') by a => *vestibulum*.

Yamada (2007) uses the term "outer lamella cuticle" instead.

Remarks: The classic view results from the concept that an ostracod's carapace consists of two separate valves, instead of one continuous (organic) carapace that is just specifically calcified – with a complete separation of its mineralized parts. The former derives from the paleontologic point of view in that paleontologists usually work with the fossil preserved relics of an ostracod, the remains of the bivalved calcified parts of the carapace.

Outer margin: see => *carapace/valve margin*

Outline (lateral/dorsal): see => *carapace/valve outline*

Pore(s) (canals): Pores are the external termination of a pore canal. There are two main types of pore canals: marginal pore canals and normal pore canals. The so-called "false marginal pore canals" are something in between (see below). Most or all pores have a sensorial function (Meisch 2000), some have been suggested to be part of the excretory system (e.g. Keyser 1982, Okada 1983, Do Carmo et al. 1999).

1) **Marginal pore/radial pore (canals):** Pore canals of variable shape extending through the => *marginal zone* (also fused zone), e.g. Fig. 8. All radial pore canals originate at the => *line of concrescence* and run in the plane of fusion (=> *marginal zone*) of inner and outer lamella to the outer margin (*true* marginal pore canals, in contrast to => *false marginal pore canals*). The canals can be single tubes (termed "simple pore canals"), branched (branching or bifurcated zones) and/or having a bulbous enlargement near the middle or somewhat towards the outer margin (marking the base of a hair/bristle => *seta*). The approximate number and shape of the marginal pore canals are an important taxonomic feature.

2) **False marginal pore (canals):** This are pore canals originating at the => *line of concrescence* but not penetrating the plane of fusion (=> *marginal zone*). They either run through the marginal part of the outer lamella or, partly, through the inner lamella and surface distally from the outer margin.

However, adopting Yamada's (2007) view would lead to the conclusion that the => *marginal zone* does not exist and the false pore canals would also be marginal pore canals extending through a different virtual plane of the valve's margin.

3) **Normal (lateral) pore (canals):** These are tubuli (small tubes) that perpendicularly pierce the outer lamella, scattered over the lateral surface. There are two types of normal pores distinguishable:
A) Simple (single) normal pores, very small (1-3µm) and common in most ostracods. In recent taxa they bear hair-like bristles (=> *setae*), and are sometimes widened towards the interior (for the base of the bristles).
B) Sieve-type normal pores (in some Cytheroidea) comprise of a plate bearing many tiny openings around a subcentral larger pore canal and are much larger (10-20µm) than simple ones. Okada (1983) divided these pores into sensillum pores and exocrine pores.

Posterior cardinal angle (PCA): The posterior of the two => *cardinal angles* (Fig. 3).

Posterior margin: Posterior part of the valve or carapace in lateral view, adjoining the posterior part of the => *free carapace/valve margin* (Fig. 3). It extends between the angular peaks of the posterior => *cardinal angle* and the => *posteroventral region* (or, in the larger valve of morphologically modified ostracods like *Cypridea* for example, the point of the => *cyathus*). The posterior margin either coincides with the => *posterior lateral outline* or it is overreached and covered by posterolateral expansions of the carapace (e.g. brood pouches in females of *Theriosynoecum*), the latter not being applicable to representatives of *Cypridea*.

Posterior (part of) lateral outline: Posterior part of carapace outline (border) in lateral 2D-projection, either coincident or (sometimes) not coincident with the => *posterior margin*.

Posteroventral region (PVR): The posteroventral sector of the carapace outline including the posterior part of the => *ventral margin* and the ventral part of the => *posterior margin* (Fig. 3). The term anteroventral angle is avoided because a recognizable angle is often not realized. Instead, the posteroventral region is more or less strongly rounded, elongated and pointed or developed as a cyathus (i.e. in *Cypridea*, for example).

Precocious sexual dimorphism (preadult => *sexual dimorphism*): This term (also "preadult sexual dimorphism" after Rohr 1979) has been used by Whatley and Stevens (1977) for morphologic => *sexual dimorphism* in instars that "... does not in any way imply precocious sexual maturity ..." (op. cit., p. 89), who differ between 'protomales' and 'protofemales' of fossil podocopid (Cytheroidea) ostracods.

Since sexual dimorphism is inferred to occur in representatives of *Cypridea* as well (refer chapter 5.2, description of the genus under sexual dimorphism for more detail), the possibility of the occurrence of precocious sexual dimorphism has to be considered too, see discussion of *Cypridea (Longispinella) longispina* (Peck 1941) herein, for example. However, this is strongly hypothetical since a detailed investigation of this topic is still wanting. Precocious sexual dimorphism has been demonstrated on fossil Cytheroidea and might be difficult to identify in fossil Cypridoidea for the reason that the cypridoids commonly show lesser or no expression of their sexual dimorphism in the shape of their carapace.

Punctum (pl. *puncta*, Latin for stitch, point, small spot; English adj. *punctate*): Puncta are small (between 20 and 50µm) pit-like depressions in the valve's surface (Moore 1961). They are a specific element of an => *area-wide ornamentation element/surface character*, the => *punctation* (refer to => *ornamentation*).

Punctation: see => *ornamentation*, => *area-wide ornamentation elements/surface characters*

Reticulation/reticulum/reticulate: see => *ornamentation*, => *area-wide ornamentation elements/surface characters*

Relative valve size: A comparative term designating the ostracods carapace's valve size relation. In most cases, the left valve is larger than the right valve (LV>RV), and thus this is called "normal" valve size relation. In some ostracod taxa, however, the opposite (RV>LV) can be the "normal" state (e.g. within the family Darwinulidae, see Rossetti and Martens 1998). For detailed elucidation, see => *inverse.*

Ridge: see => *dorsal ridge* or => *ventral ridge*

Rostral bending angle: see => *bending angle*

Rostral bulge: This term defines a strongly upwards elongated => *rostrum* as result of a very long => *alveolar furrow* reaching up to above half carapace height to more than 4/5 of height (*Cypridea parallela*-group, see Wolburg 1959, for example). If this is the case, the alveolar furrow is usually narrow and runs parallel to the anterior margin. The alveolar furrow can even reach up to the lower internal limit of the anterior hinge element (about 7/8 of height).

This term has frequently been used by German authors (German "Rostralwulst"), for example.

Rostral (keel) pores: A regular row of simple pores following the outer margin of the => *rostrum*, or the inner boundary of the keel along a => *carinate rostrum*, if the latter is well-developed. These pores are the continuance of the marginal emersion points (external termination) of the marginal => *pore canals* at the rostrum, or—in a carinate rostrum—possibly a special type of => *marginal pores* of currently unknown function, alternatively (see Pl. 6, Figs. 4 and 5 for example).

Rostrum (pl. *rostra*, Latin for beak and used this way by some authors; English adj. *rostral*): This is a more or less pointed and curved triangular prolongation of the anteroventral angle, bounded by the anterior margin in front and by an => *alveolar notch* and => *alveolar furrow* (see => *alveolus*) behind it (Figs. 5, 7/A-B and F, Fig. 8). Its dimension varies from "large and strong or so ill defined as to be barely recognizable" (Anderson et al. 1967, p. 202). Usually, it is bending backwards; rarely the point is sharp and curved forwards. Its extension is strongly variable depending on the species; in most cases it more or less strongly overreaches the ventral margin, sometimes it only almost reaches the ventral margin or ends above it (For clarification it must be noticed that an overreaching ventral ridge may feign a more extensive false ventral margin!). The rostrum may be attached to the ventral margin behind it (strongly bending backwards and then with very narrow => *alveolus*; see => *bending angle* also) or it is considerably separated from the latter by an => *alveolar notch* and *furrow* of variable width (weakly bending backwards, low => *bending angle*). Rarely, the rostrum bears a keel (=> *carinate rostrum*). Internally, the posterior (directed towards alveolus) side of the rostrum is characterized by an interrupted selvage.

If the alveolar furrow is very long and reaches very high upwards, a => *rostral bulge* is formed.

Remarks: The term *rostrum* (Latin for beak, mouth, trunk) is purely descriptive, and used for beak-like or other structures in a variety of organisms (e.g. insects, fishes, belemnites). Within Ostracoda, it is an analog character occurring in the Cypridinoidea (=Cypridinacea) (Myodocopida) in several families and genera, as well as in Cyprideinae (Podocopida, Cypridoidea=Cypridacea), e.g. the genera *Cypridea, Praecypridea* (Sames et al. in review), and others. Regarding *Cypridea*, for many authors in the past "rostrum" has proved to be an appropriate (descriptive, not functional) term for the beak-like anteroventral projection of the carapace. There is no reason for proposing a new term just because it occurs twice within the Ostracoda. The Cypridinoidea and Cypridoidea are not closely related and the function as well as shape and position of the rostrum are different in these two groups: the rostrum of the Cypridinoidea is located anteriorly at mid-height of the valves or above and is associated with an aperture for the antennae which are modified as swimming organs.

The rostrum within the Cyprideidae lies anteroventrally and its function is unknown. Both, the rostrum as well as => *alveolus* in Cypridea " … may have been connected with feeding and/or swimming activity …" (Horne and Martens 1998, p. 558), or possibly sensory perception.

Selvage: This is a thin translucent membrane that marks the peripheral limit between the outer and inner lamella (Meisch 2000). Originally, the selvage forms the free valve margin, but is often secondarily displaced inwards (op. cit.). In this case "the free valve margin is formed by a more or less prominent excrescence, designated as => *flange*, of the outer lamella" (op. cit., p. 8). Only then, the selvage forms the middle ridge of the => *contact margin* comprising the principal ridge of the duplicature (=calcified inner lamella) and serving to seal the valves when the carapace is closed, as defined by Moore (1961).

In representatives of the extinct family Cyprid<u>e</u>idae Martin 1940 (in contrast to its extant relatives of the family Cyprid<u>i</u>dae Baird 1845), the selvage is discontinuous and interrupted (=> *interrupted selvage*) in the anteroventral region of both valves (see also Horne and Colin 2005). In *Cypridea*, the selvage runs along the anterior part of the => *rostrum* to its point, is interrupted along the rostrum's posterior part and continues at the angular point of the => *alveolar notch* (see Figs. 7/F and 8).

Seta (pl. *setae*, also *saeta*, *-ae*; Latin for strong hair or bristle; English adj. *setal*, *setose*): A bristle protruding from a => *pore* canal having a sensorial function mostly.

Solum (pl. *sola*; Latin for floor, bottom): The floor of a => *fossa* in a => *reticulum* (Sylvester-Bradley and Benson 1971).

Spine(s): see => *ornamentation*, => *local ornamentation elements*

Subequivalve (subequal valves): Refers to a weak difference in size and shape, i.e. lateral outline in particular, of the two carapace valves (see also => *equivalve*, => *inequivalve*), see Fig. 7/B, for example.

Sulcus (pl. *sulci*, Latin for furrow, groove; English adj. *sulcate*): A groove or trench (depending on its width and outline) of variable prominence, often trending "dorsoventrally" (i.e. perpendicular) and generally best developed in the dorsal half of the carapace (Moore 1961). Any sulci can be reduced to faint depressions. Often, a sulcus is associated with a => *lobe*. Taxa with "dorsoventral" sulci can be designated as monosulcate (one sulcus), bisulcate (two sulci) etc., depending on the number of sulci (e.g. *Bisulcocypridea* Sohn 1969, *Bisulcocypris/Theriosynoecum*). As well as lobes, the sulci are => *local ornamentation elements*. Although their delimitation is diffuse, a single sulcus never covers the main part of the carapace's outer surface. Sulci are a genetically fixed diagnostic character.

<u>Remarks:</u> Regarding the causes for the development of "dorsoventral sulci" (better: dorsolateral sulci that are nearly perpendicular), this has been discussed by Triebel (1941) comprehensively, and Hartmann (1966-89). Triebel (1941, p. 296-321) considered the tension of various muscles attached to the carapace (adductor muscles, mandibular muscles etc.) during ecdysis, when the carapace is in a soft phase, to be the cause for such sulci as local crenation of the carapace. He (op. cit.) believed that the reason for occurrence of these sulci in certain taxa only is connected to their outline and resulting tensile strength and statics of the carapace, and that only taxa with a straight dorsal margin show this feature. Triebel's arguments have been reconsidered by Hartmann (1966-89). Hartmann (op. cit., p. 53-54) gives the insufficient stability of the dorsal margin in some ostracods during ecdysis as reason for dorsolateral sulci. For him, this process is logic because the calcification starts at the valve margins and deformations of the valves center is later fixated through calcification (op. cit., p. 54).

There is without doubt a correlation between the position of the dorsolateral sulci and the position of the => *central muscle scar field*. Considering the ontogenetic line of *Bisulcocypris/Theriosynoecum*, it is evident that the sulci become better developed in later stages.

Admittedly, Triebel's (1941) concept still lacks calculations and proof concerning statics of the carapace (see above). It does, for example, not explain why there are (two) sulci in the subgenus *Cypridea (Bisulcocypridea)* Sohn 1969, which has a straight dorsal and hinge margin, but not in other representatives of *Cypridea* also having thin carapaces, straight dorsal margins and a variety of carapace statics configurations similar to *C. (Bisulcocypridea)*. In addition, if the determining factors for dorsolateral sulci are the stability of the chintinous carapace in its uncalcified phase during ecdysis and the muscle tension only, i.e. just morphologically induced, one would expect distinct variations in their appearance more frequently. An observation of many specimens of *Theriosynoecum* in own samples such variation cannot be confirmed. In contrast, shape and development of the sulci seem to be very consistent. Recapitulating, it must be stated that this problem is not yet satisfactory resolved to date.

Supracurvate: see => *curvature*

Surface characters (=area-wide ornamentation elements): see => *ornamentation*, => *area-wide ornamentation elements*

'True' cyathus: see => *cyathus*

Tuberculum/Tubercle(s)/Tuberculi: see => *ornamentation*, => *local ornamentation elements*

Tuberculation: An ornamentation characterized by many tubercles (see => *ornamentation*, => *local ornamentation elements*).

Valve size (relative, relation), inverse: see => *inverse*

Ventral margin: Ventral part of valves in lateral view, adjoining the ventral part of the free valve margin. It extends between both angular peaks of the ventral anterior and posterior angles. The ventral margin either coincides with the => *ventral outline* or it is overreached and covered by ventrolateral prolongations of the carapace (Fig. 3).

Ventral outline: Ventral part of carapace outline (border) in lateral 2D-projection, either coincident or (often) not coincident with the => *ventral margin* (Fig. 3).

Ventral (tongue-like) **overlap:** The ventral overlap of the larger valve over the smaller one is often considerably stronger than along the other margins of the carapace. In *Cypridea*, this is the case, and the ventral part of the overlapping LV is distinctly convex, tongue-like, with its maximum overlap at about the same position of the maximum width (Fig. /C).

Ventral ridge: The ventral ridge is a straight or slightly arcuate extension of the larger valve only, situated somewhat laterally to the central axis of length but clearly within the ventral area (Figs. 7/A, B, C). The delimitation of the ventral ridge is only clearly visible in ventral – not in lateral – view of the larger valve, and thus the term ventro*lateral* ridge as used by some authors (e.g. Sohn 1979) is rejected. The ventral ridge occurs in most representatives of *Cypridea*, extending between the alveolus and cyathus, or with some offset from the midline towards the ventrolateral region of the larger valve (=> *ventrolateral ridge*).

The intensity of the development of the ventral ridge is variable. It may internally form a groove for the ventral margin of the smaller valve to fit in. Its function remains unclear. Speculatively, this may be a structure of stabilization, or did possibly allow the animal to stick and "ice-skate" upside down on the lower water surface (using the water surface tension), similar to some recent Notodromadidae although the latter have different carapace structures to facilitate this type of movement.

Ventrolateral ridge: Almost equivalent to => *ventral ridge* except that the ridge is somewhat more displaced towards ventrolateral region of the larger valve (out of midline, i.e. half width in ventral view, e.g. in *Cypridea (Pseudocypridina) piedmonti*.

Vestibulum/vestibule (pl. *vestibula*, Latin, meaning front court; English adj. *vestibular*): The space between the free part of the calcified inner lamella (=duplicature) and the outer lamella when not completely fused.

Widened inner lamella: See => *local widening of the inner lamella*

Plate 1

Scale bar: 100µm; specimens to scale (except Figs. 3, 7, 8, 11, 12). SD: South Dakota.

Cypridea nitidula Peck 1941

Note: Greyish stains are caused by glue covering of material from Peck's collection; small needles are splints from the cardboard microcells. The latter were not dealt with for the reason not to damage the fragile original material.

1. Right lateral view of adult carapace, weathered anteriorly but weak alveolar notch in larger LV well visible, punctation well-defined, cyathus-like protrusion broken off. Specimen from Peck's collection, Peck's locality 82P (Draney Limestone(Sub-?)Formation?), specimen figured in Peck 1959, pl. 2, fig. 18, and Peck and Craig 1962, pl. 2, fig. 2).

2. Right lateral view of adult carapace, ventrolaterally partially covered with glue and sediment, punctation well-developed, antero- and posterolateral small tubercles visible as well as cyathus-like protrusion in the LV (see Fig. 3 of this plate for magnification). Specimen from Peck's collection, Peck's locality 82P (Draney Limestone(Sub-?)Formation?).

3. Magnification of figure 2 of this plate, right lateral view posteroventral area with the true (undeformed) shape (attached sediment retouched) of the cyathus-like protrusion; partially covered with sediment and glue.

4. Left lateral view of weathered (corroded through processing?) carapace, slightly compressed and deformed, with sediment particles in centroventral area, cyathus-like protrusion clearly visible, punctation only faintly. Specimen from Peck's Collection, Peck's locality 280P, Bear River Formation at Thomas Fork Creek, Lincoln County, Wyoming, U.S.A.

5. Left lateral view of weathered (corroded through processing?) carapace, slightly deformed, with stub (basis) of massive posterocentral spine that is broken away, cyathus-like protrusion clearly visible, punctation only faintly. Specimen from Peck's Collection, Peck's locality 280P, Bear River Formation at Thomas Fork Creek, Lincoln County, Wyoming, U.S.A.

6. Right ventrolateral view of weathered (corroded through processing?) carapace, cyathus-like protrusion of RV well visible, anteroventral region damaged. Specimen from Peck's Collection, Peck's locality 280P, Bear River Formation at Thomas Fork Creek, Lincoln County, Wyoming, U.S.A.

7. Left lateral view of posteroventral area with LV's cyathus-like protrusion. Magnification of Fig. 4 of this plate.

8. Right lateral view of posteroventral area with cyathus-like protrusion in the RV and LV (slightly shifted in relation to each other). Magnification of Fig. 6 of this plate.

Cypridea obesa Peck 1941

9. Left lateral view of adult carapace, punctation and faint alveolar notch well visible. Sample ARCR CHz1, uppermost Chilson Member of the Lakota Formation right below Minnewaste Limestone Member, Angell Ranch - Cheyenne River, SD, U.S.A. (Fig. 2, loc. 5).

10. Right lateral view of adult carapace, dipped to the left, posteroventral part of LV with cyathus broken apart, ventral overreach and ventral ridge of LV visible as well as faint rostrum and alveolar notch of RV. Sample ARCR CHz1, uppermost Chilson Member of the Lakota Formation right below Minnewaste Limestone Member Angell Ranch - Cheyenne River, SD, U.S.A. (Fig. 2, loc. 5).

11. Left lateral view of anteroventral region with faintly visible rostrum and alveolar notch. Magnification Fig. 9 of this plate.

12. Right lateral view of anteroventral region with faintly visible rostrum, alveolar notch and furrow. Magnification of Fig. 15 of this plate.

Plate 1 (continued)

***Cypridea obesa* Peck 1941**

13. Ventral view of adult carapace, anterior end to the right, potentially a female dimorph, anterior end to the right, adult carapace, with weak rostrum visible at right end. Sample ARCR CHz1, uppermost Chilson Member of the Lakota Formation right below Minnewaste Limestone Member, Angell Ranch - Cheyenne River, SD, U.S.A. (Fig. 2, loc. 5).

14. Dorsal view of carapace, anterior end to the right, male dimorph? or A-1? preadult, narrow dorsal furrow and anterior and posterior overlap of larger LV well visible. Sample ARCR CHz1, uppermost Chilson Member of the Lakota Formation right below Minnewaste Limestone Member, Angell Ranch - Cheyenne River, SD, U.S.A. (Fig. 2, loc. 5).

15. Right lateral view of well preserved adult carapace, partially covered with glue and organic crystals of some sort, elongate puncta forming ventral rows well visible. Specimen from the Peck collection, labeled to have been figured in Peck and Craig (1962, pl. 2, fig. 5, locality 658P therein), Cloverly Formation northwest of Lander, Fremont County, Wyoming, U.S.A.

Plate 2

Scale bar: 100µm; specimens to scale (except Figs. 3, 15). SD: South Dakota.

***Cypridea? minuta* (Peck 1951)**

1. Left lateral view of well preserved (male?) carapace, slightly compressed at mid-length in vertical direction, alveolar furrow, dorsolateral sulcus and reticulation-like punctation well visible, cyathus in larger RV broken off, outline retouched (large sediment particles overreaching dorsally removed). Specimen from the Peck collection, Minnewaste Limestone Member of the Lakota Formation, locality 439P, Skyline Drive east of Hot Springs, Fall River County, SD, U.S.A.

2. Left lateral view of well preserved (female?) carapace, with some sediment remains and edged cavities of sediment grains, overreach of larger LV, dorsolateral sulcus and punctation pattern well visible; posteroventral area of RV broken off. Specimen from the Peck collection, Minnewaste Limestone Member of the Lakota Formation, locality 439P, Skyline Drive east of Hot Springs, Fall River County, SD, U.S.A.

3. Left lateral view of anteroventral region with rostrum, alveolus, normal pores and small tubercles at the anterior margin. Magnification of Fig. 2 of this plate.

4. Dorsal view of moderately preserved carapace, anterior end to the left, presumed male (slender), dorsolateral region of right valve compressed. Specimen from the Peck collection, Minnewaste Limestone Member of the Lakota Formation, locality 439P, Skyline Drive east of Hot Springs, Fall River County, SD, U.S.A.

5. Ventral view of carapace, anterior end to the left, moderately to well-preserved, alveolar furrow well visible, inflated posterior end. Specimen from the Peck collection, Minnewaste Limestone Member of the Lakota Formation, locality 439P, Skyline Drive east of Hot Springs, Fall River County, SD, U.S.A.

6. Dorsal view of moderately to badly preserved adult carapace, anterior end to the right, typical lateral constriction at mid-length, strongly inflated dorsally. Sample ARCR Chz1, uppermost Chilson Member of the Lakota Formation right below Minnewaste Limestone Member, Fall River County, SD, U.S.A. (Fig. 2, loc. 5).

PLATE 1

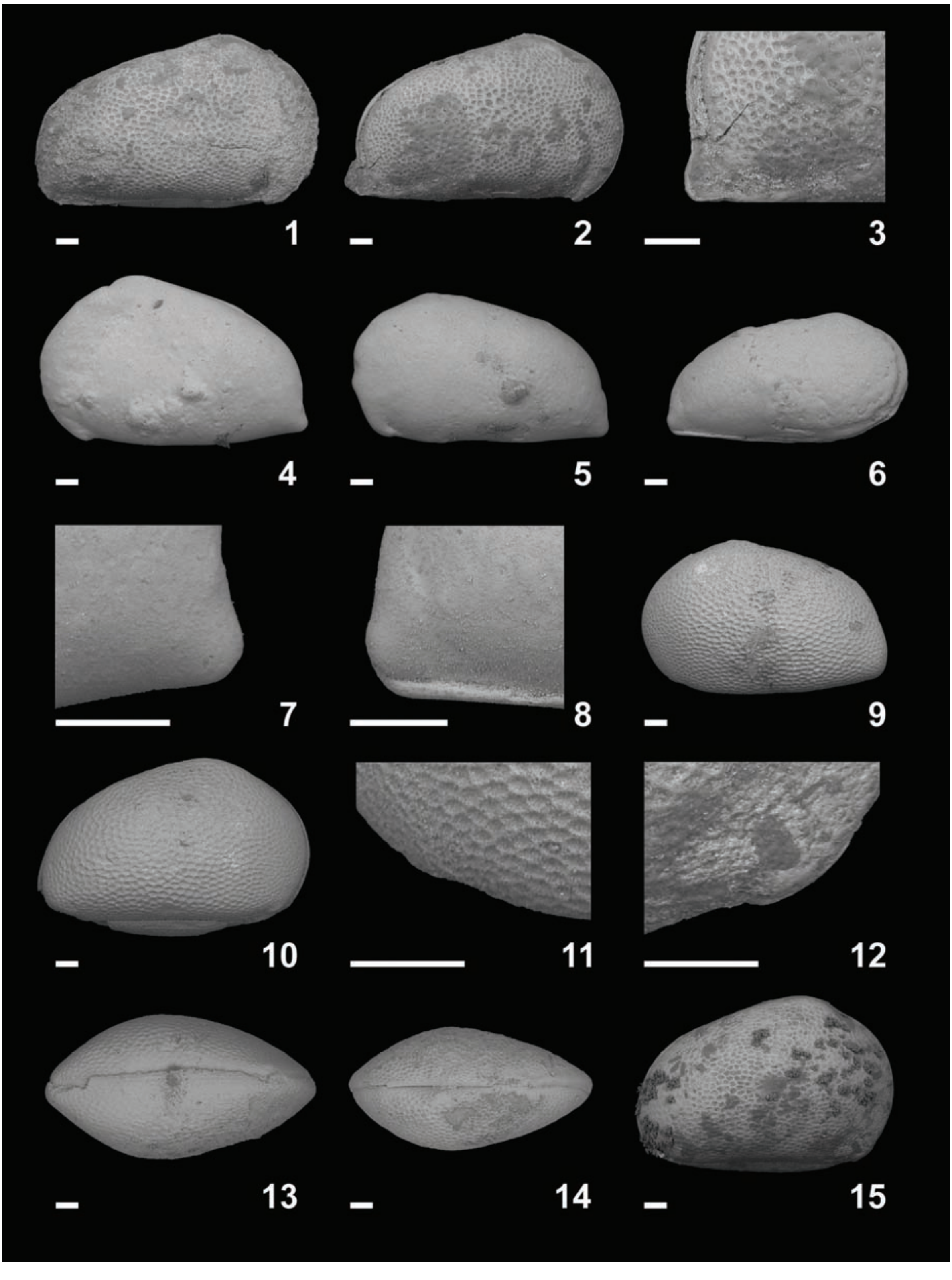


Plate 2 (continued)

***Cypridea? minuta* (Peck 1951)**

7. Left lateral view of strongly altered, badly preserved ("steinkern") carapace with slight imprints of the central muscle scar field, anterior mandibular scar well visible (arrow), alveolar notch and alveolar furrow. Sample ARCR Chz1, uppermost Chilson Member of the Lakota Formation right below Minnewaste Limestone Member, Fall River County, SD, U.S.A. (Fig. 2, loc. 5).

8. Left lateral view of badly preserved carapace, sediment attached posteroventrally and posterodorsally, RV>LV overlap apparent. Sample ARCR Chz1, uppermost Chilson Member of the Lakota Formation right below Minnewaste Limestone Member, Fall River County, SD, U.S.A. (Fig. 2, loc. 5).

9. Left lateral view of badly preserved carapace, preadult (A-2?) specimen, dorsolateral sulcus slightly visible as well as alveolar notch. Specimen from the Peck collection, Minnewaste Limestone Member of the Lakota Formation, locality 439P, Skyline Drive east of Hot Springs, Fall River County, SD, U.S.A.

10. Left ventrolateral view of badly preserved adult (or preadult A-1?) carapace, RV attached to another ostracod valve, female? specimen (posterolaterally inflated), RV>LV overlap distinctly visible, with dorsolateral sulcus. Posteroventral area showing no sign of a cyathus. Specimen from the Peck collection, Minnewaste Limestone Member of the Lakota Formation, locality 439P, Skyline Drive east of Hot Springs, Fall River County, SD, U.S.A.

11. Right lateral view of badly preserved adult carapace, with edged cavities of sediment grains, female? specimen (posterolaterally inflated), rostrum and alveolar furrow visible. Specimen from the Peck collection, Minnewaste Limestone Member of the Lakota Formation, locality 439P, Skyline Drive east of Hot Springs, Fall River County, SD, U.S.A.

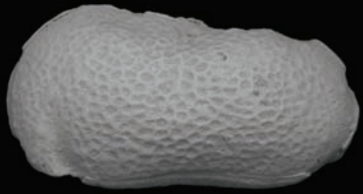
12. Left lateral view of a badly preserved carapace with much sediment attached to it, female? specimen. Specimen from the Peck collection, Minnewaste Limestone Member of the Lakota Formation, locality 439P, Skyline Drive east of Hot Springs, Fall River County, SD, U.S.A.

13. Left lateral view of adult male? (slender) carapace, covered with recrystallized glue, RV>LV overlap apparent, punctation still visible. Specimen figured in Peck and Craig (1962, pl. 1, fig. 7 therein), Peck collection, Minnewaste Limestone Member of the Lakota Formation, locality 439P, Skyline Drive east of Hot Springs, Fall River County, SD, U.S.A.

14. Left lateral view of adult male? (slender) carapace, covered with recrystallized glue, RV>LV overlap apparent. Specimen (like specimen in Fig. 13 of this plate) labeled as having been figured in Peck and Craig (1962), but looking different from the drawing therein. Peck collection, Minnewaste Limestone Member of the Lakota Formation, locality 439P, Skyline Drive east of Hot Springs, Fall River County, SD, U.S.A.

15. Left lateral view of posteroventral region, no cyathus cognizable. Magnification of Fig. 13 of this plate.

PLATE 2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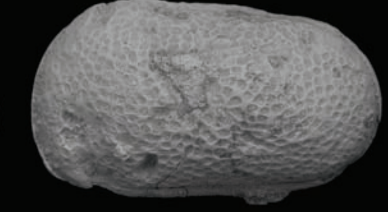
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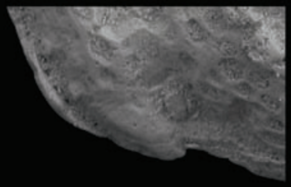
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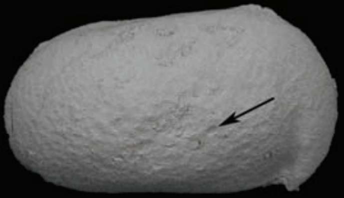
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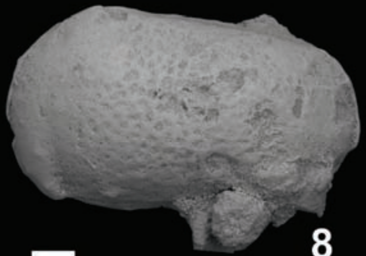
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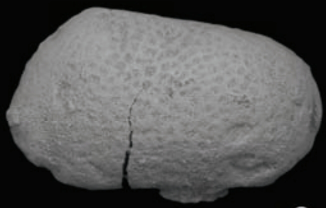
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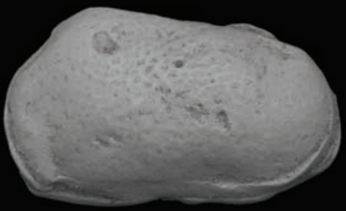
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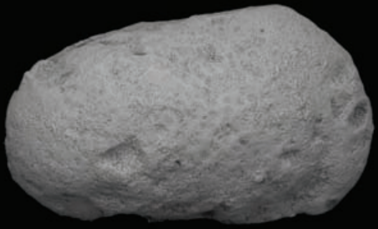
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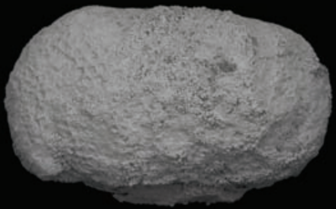
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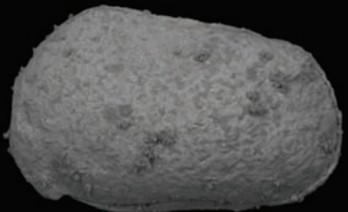
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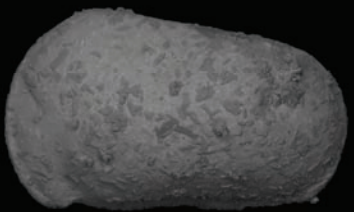
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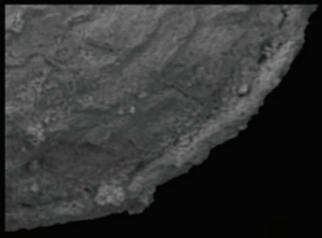
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Plate 3

Scale bar: 100µm; specimens to scale (except Figs. 13-15). SD: South Dakota, UT: Utah.

Cypridea (Longispinella) longispina Peck 1941

1. Left lateral view, adult carapace of presumed female, rostrum point and spine broken off, Anterocentral perpendicular ridge and sulcus of LV well visible (see also Fig. 14 of this plate for magnification). Sample BCB2, Chilson Member of the Lakota Formation, Buck Canyon, SD, U.S.A. (Fig. 2, loc. 1).

2. Right lateral view, adult carapace of presumed female, point of rostrum and spine broken off, specimen partially covered with dirt. Strong overreach of LV and lateral pores visible. Sample BCB2, Chilson Member of the Lakota Formation, Buck Canyon, SD, U.S.A. (Fig. 2, loc. 1).

3. RV, lateral view of moderately presumed female valve, point of rostrum and spine broken away. Different shape of RV clearly visible, as well as the alveolar ridge and the small cyathus-like protrusion in the RV. Sample BC5 04, Chilson Member of the Lakota Formation, Buck Canyon, SD, U.S.A. (Fig. 2, loc. 1).

4. Left lateral view of presumed female carapace, point of rostrum and spine broken off, moderately preserved and in part diagenetically altered. Surface characters not visible anymore, alveolar ridge, alveolar furrow and cyathus distinct. Sample PS1a-70, Yellow Cat Member of the Cedar Mountain Formation, north of Moab, east-northeast of the Ringtail Mine, UT, U.S.A. (Fig. 2, loc. 10).

5. Dorsal view, anterior end to the left, adult carapace of presumed female, posterior part somewhat covered with sediment. Spine well visible as well as anterocentral ridge and sulcus on the LV only. Sample BC5 04, Chilson Member of the Lakota Formation, Buck Canyon, SD, U.S.A. (Fig. 2, loc. 1).

6. Ventral view, anterior end to the left, adult carapace of presumed female, posterior end somewhat covered with sediment. Spines and anterocentral ridge and sulcus on the LV only well visible as well as strong ventral overlap of LV, the deeply incising alveolar furrow (even along the alveolar ridge) and the strong alveolar ridge on both valves. Sample BC5 04, Chilson Member of the Lakota Formation, Buck Canyon, SD, U.S.A. (Fig. 2, loc. 1).

7. RV, lateral view of presumed female valve, point of rostrum broken off, spine partially covered with sediment. Valve moderately preserved. Different shape of RV clearly visible, as well as the alveolar ridge and the small cyathus-like protrusion in the RV. Sample BC5 04, Chilson Member of the Lakota Formation, Buck Canyon, SD, U.S.A. (Fig. 2, loc. 1).

8. Right lateral view of adult carapace of presumed female dimorph, diagenetically altered, posterior region partially damaged, dark stains are impressions of sediment grains. Cyathus-like protrusion in both valves. Sample SBCR Lah3Tp, Lakota Formation, Stage Barn Canyon Road, SD, U.S.A., (Fig. 2, loc. 8).

9. Right dorsolateral view (specimen inclined to the left), adult carapace of presumed female. Strong perpendicular anterocentral ridge, well-developed spine and strongly developed surface characters. Sample BC5 04, Chilson Member of the Lakota Formation, Buck Canyon, SD, U.S.A. (Fig. 2, loc. 1).

10. Right lateral view, adult carapace of presumed male. Areas appearing dark are covered with glue. Spine and cyathus of left valve broken off. Specimen from the collection of I. G. Sohn, assemblage slide USNM 242984, Chilson Member of the Lakota Formation, Fall River Canyon (locality 12 in Sohn 1979), SD, U.S.A. (about Fig. 2, loc. 3 here).

11. Left lateral view, strongly diagenetically altered and partly deformed adult carapace of presumed male. Dorsally und laterally compressed, anterodorsal part of outline anterolateral area atypical through deformation of carapace. Anterocentral ridge visible, spine small and mostly broken off. Dark areas covered with glue. Specimen from the collection of I. G. Sohn, assemblage slide USNM 242984, Chilson Member of the Lakota Formation, Fall River Canyon (locality 12 in Sohn 1979), SD, U.S.A. (about Fig. 2, loc. 3 here).

PLATE 3


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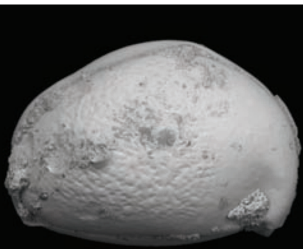
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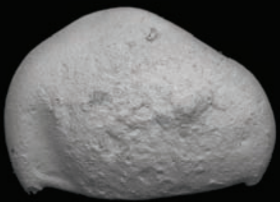
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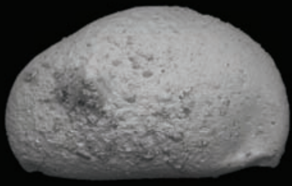
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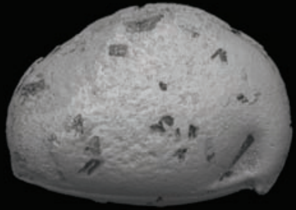
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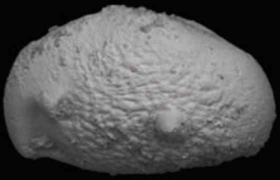
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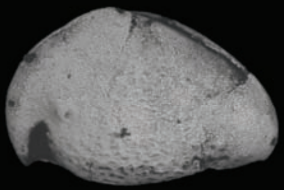
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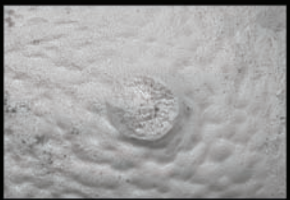
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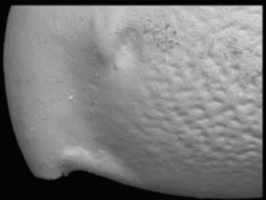
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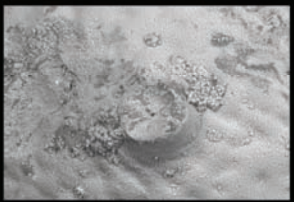
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Plate 3 (continued)

***Cypridea (Longispinella) longispina* Peck 1941**

12. Left lateral view, adult carapace of presumed male, partially vertically compressed and slightly deformed. Areas appearing dark covered with glue. Surface characters and anterocentral ridge and sulcus developed, no spine. Specimen from the collection of I. G. Sohn, assemblage slide USNM 242984, Chilson Member of the Lakota Formation, Fall River Canyon (locality 12 in Sohn 1979), SD, U.S.A. (about Fig. 2, loc. 3 here).

13. Magnification of a section of specimen 1 of this plate. Basal part of broken off spine, surface characters and lateral pores.

14. Magnification of a section of specimen 1 of this plate. Alveolar furrow, alveolar ridge and perpendicular anterocentral ridge and sulcus of the LV (only).

15. Magnification of specimen 2 of this plate. Basal part of broken off spine with clearly visible normal pore in its center.

Plate 4

Scale bar: 100μm; specimens to scale (except Figs. 13-15). SD: South Dakota, UT: Utah.

***Cypridea (Pseudocypridina) piedmonti* Sohn 1979**

1. LV, lateral view of adult, slightly compressed laterally and partially covered with sediment. Sample BCB1, Chilson Member of the Lakota Formation, Buck Canyon, SD, U.S.A. (Fig. 2, loc. 1).

2. Right lateral view of adult carapace, dorsolaterally slightly weathered. Sample PS1a-70, Yellow Cat Member of the Cedar Mountain Formation, north of Moab, east-northeast of the Ringtail Mine, UT, U.S.A. (Fig. 2, loc. 10).

3. LV, internal view, preadult? (A-2?) valve, partially filled with sediment. Sample BCB1, Chilson Member of the Lakota Formation, Buck Canyon, SD, U.S.A. (Fig. 2, loc. 1).

4. Dorsal view, anterior end to the left, adult carapace showing incised hinge margin, posteriorly slightly covered with sediment. Sample BCB1, Chilson Member of the Lakota Formation, Buck Canyon, SD, U.S.A. (Fig. 2, loc. 1).

5. Ventral view, anterior end to the right, adult carapace (with wax stain) showing convex overlap of the LV. Sample BCB1, Chilson Member of the Lakota Formation, Buck Canyon, SD, U.S.A. (Fig. 2, loc. 1).

6. Right lateral view of carapace (view from slightly ventrolateral), adult, specimen from Sohn's collection, specimen No. USNM 242939, loc. 8 of Sohn (1979, fig. 2 therein), Chilson[?] Member of the Lakota Formation, eastern Black Hills, SD, U.S.A. (close to Fig. 2, loc. 8 herein).

7. Right lateral view of preadult (A-1) carapace, with faint striation anteroventrally and posterodorsally due to slightly sheared sediment. Sample BCB1, Chilson Member of the Lakota Formation, Buck Canyon, SD, U.S.A. (Fig. 2, loc. 1).

8.-12. Right lateral views, series of photos showing deformation by lateral compression of adult carapaces and resulting changes in carapace outline. Sample HSDC3, Chilson Member of the Lakota Formation, Horse Sanctuary - Devil's Canyon, SD, U.S.A. (Fig. 2, loc. 2).

13. LV, internal view of rostrum, magnification of specimen 1 of this plate.

14. Rostrum, lateral view, anteroventral region of carapace with rostrum, rostral part of right valve partially missing and thus showing part of the internal view of the left valve's rostral region. Sample HSDC3, Chilson Member of the Lakota Formation, Horse Sanctuary - Devil's Canyon, SD, U.S.A. (Fig. 2, loc. 2).

15. Cyathus, internal view of LV, partially covered with sediment. Sample HSDC3, Chilson Member of the Lakota Formation, Horse Sanctuary - Devil's Canyon, SD, U.S.A. (Fig. 2, loc. 2).

PLATE 4

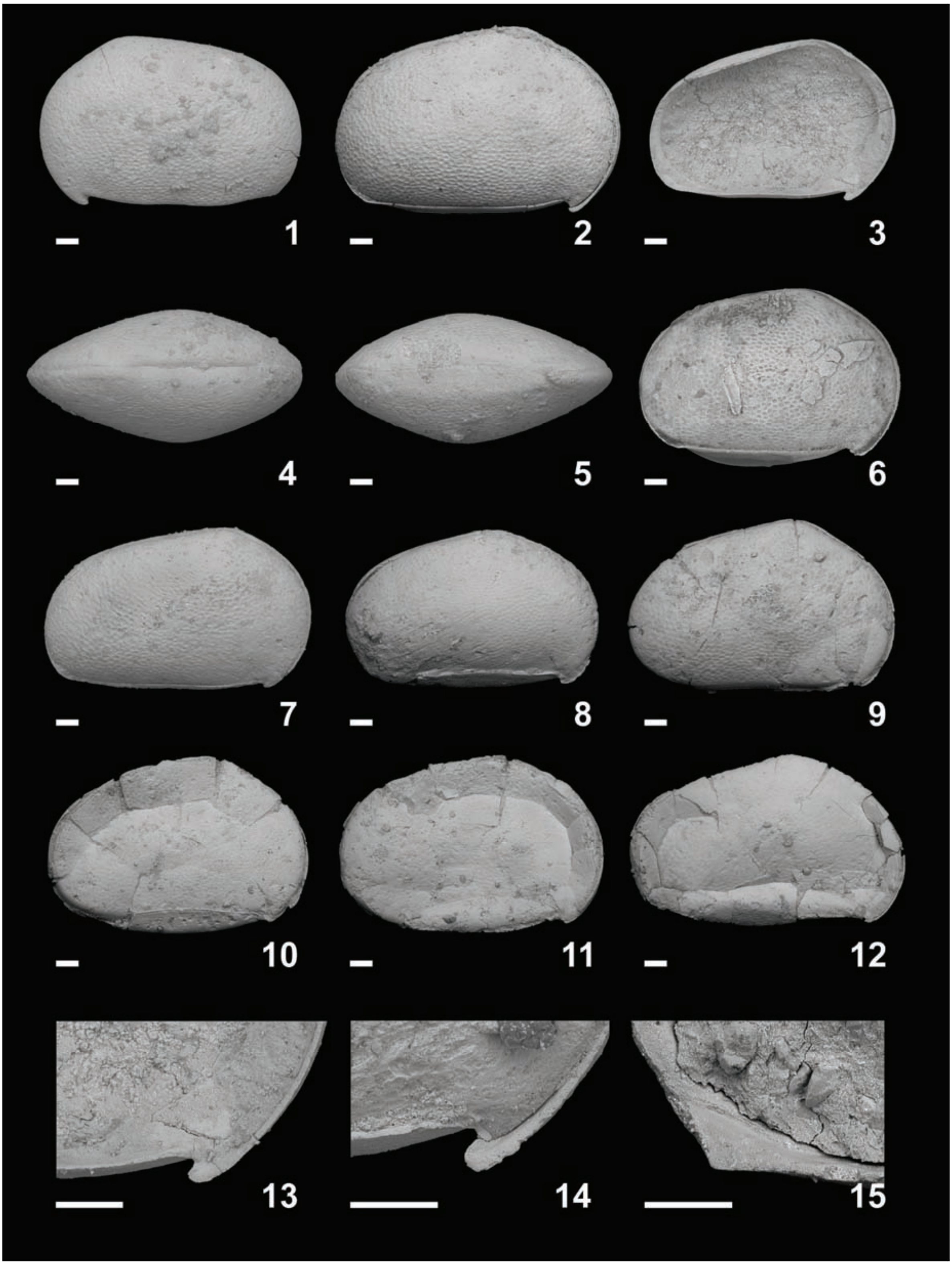


Plate 5

Scale bar: 100µm; specimens to scale. SD: South Dakota

Cypridea (Pseudocypridina) piedmonti var. *henrybelli* Sohn 1979

1. LV, lateral view, adult presumed female valve with slight cracks and moderate anterolateral node. Sample HSDC1, Chilson Member of the Lakota Formation, Horse Sanctuary - Devil's Canyon, SD, U.S.A. (Fig. 2, loc. 2).

2. LV, lateral view, adult presumed female valve, damages anterodorsally, with strong anterolateral and moderate posterolateral node. Sample HSDC4, Chilson Member of the Lakota Formation, Horse Sanctuary - Devil's Canyon, SD, U.S.A. (Fig. 2, loc. 2).

3. LV, lateral view, adult presumed male valve, with strong anterolateral and moderate posterolateral nodes. Sample HSDC4, Chilson Member of the Lakota Formation, Horse Sanctuary - Devil's Canyon, SD, U.S.A. (Fig. 2, loc. 2).

4. Right lateral view, adult carapace, without nodes, ventral overreach of LV distinct. Sample BCB2, Chilson Member of the Lakota Formation, Buck Canyon, SD, U.S.A. (Fig. 2, loc. 1).

5. Right lateral view, adult carapace, with small but strongly developed anterolateral and posterolateral nodes. Sample BCB2, Chilson Member of the Lakota Formation, Buck Canyon, SD, U.S.A. (Fig. 2, loc. 1).

6. RV, internal view, adult carapace, partially filled with sediment. Sample HSDC4, Chilson Member of the Lakota Formation, Horse Sanctuary - Devil's Canyon, SD, U.S.A. (Fig. 2, loc. 2).

7.-12. Dorsal views, series of photos showing prograding development of noding: 7. starting with a very weakly developed anterior node in the LV only (anterior end to the right, presumed male, sample HSDC3); 8. then followed by a stronger anterior left node and a weak posterior left node (anterior end to the right, presumed female, sample HSDC3); 9. next stage with relatively strong anterior and posterior nodes in the LV and a barely noticeable anterior node in the RV (anterior end to the left, sample BCE*); 10. stage with four nodes, those in the LV larger than in the RV (anterior end to the left, sample BCE*); 11. specimen with four strong nodes, those of the LV much stronger developed (anterior end to the left, presumed male, sample HSDC4); 12. specimen with four very strong nodes of about the same size, except the anterior left one still being the largest (anterior end to the left, presumed female, sample HSDC4). Sample BCE*: Chilson Member of the Lakota Formation, Buck Canyon, SD, U.S.A. (Fig. 2, loc. 1). Samples HSDC3 and HSDC4: Chilson Member of the Lakota Formation, Horse Sanctuary - Devil's Canyon, SD, U.S.A. (Fig. 2, loc. 2).

13. LV, lateral view, adult valve, presumed male, rostrum broken apart, antero- and posterolateral nodes broken/deformed, sample BCB2, Lakota Formation, Buck Canyon, SD U.S.A. (Fig. 2, loc. 1).

14. LV, lateral view, adult valve, strongly damaged and partially weathered, anterolateral node broken on top showing its hollow interior. Sample BCB2, Chilson Member of the Lakota Formation, Buck Canyon, SD, U.S.A. (Fig. 2, loc. 1).

15. LV, internal view, adult valve, partially filled with sediment, rostrum missing, sample HSDC4, Chilson Member of the Lakota Formation, Horse Sanctuary - Devil's Canyon, SD, U.S.A. (Fig. 2, loc. 2).

PLATE 5

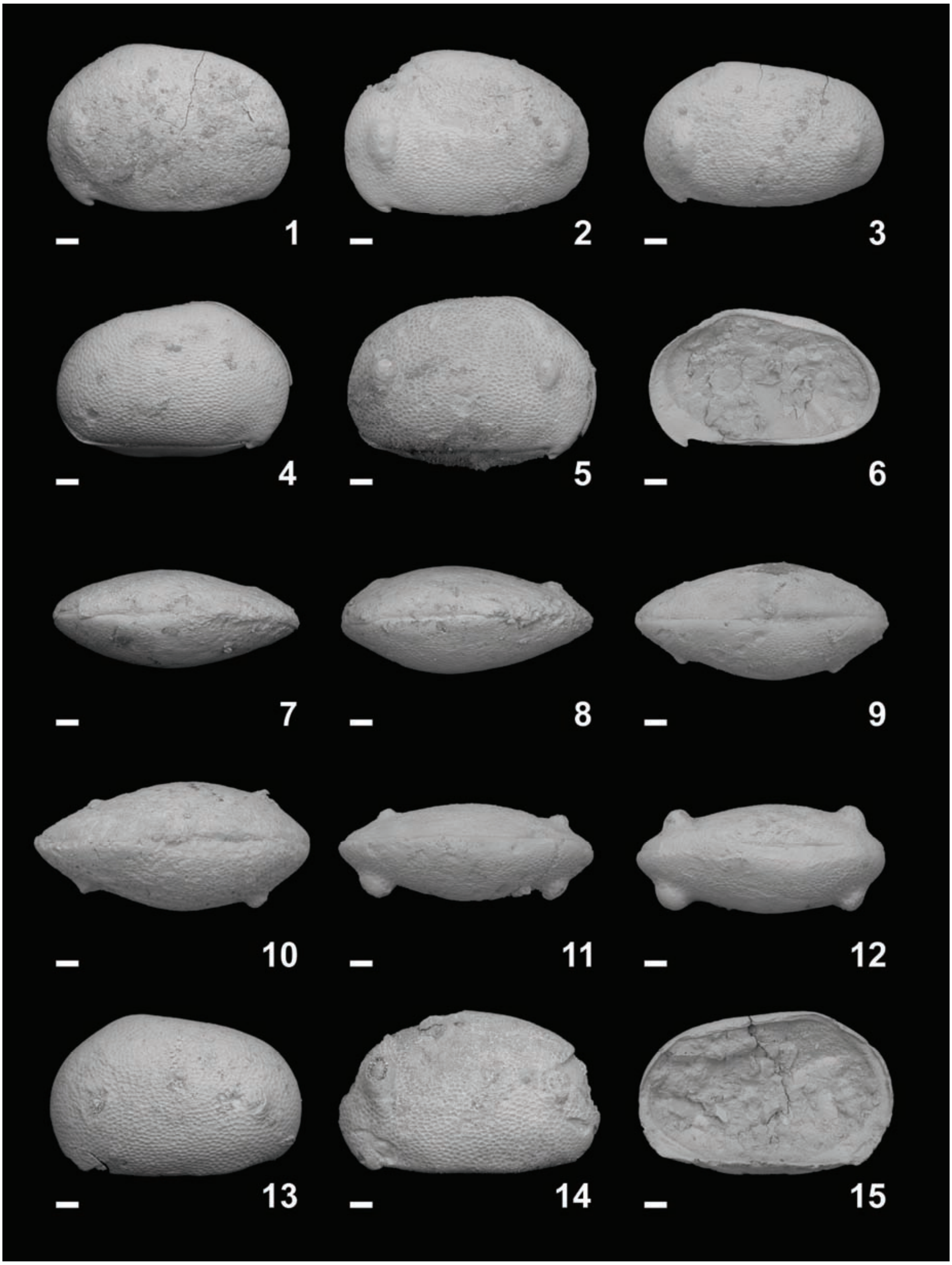


Plate 6

Scale bar: 100µm; specimens to scale (except Figs. 4, 5, 15). SD: South Dakota.

***Cypridea (Pseudocypridina) laeli* Sohn 1979 cf. *C. (P.) moneta* Kneuper-Haack 1966**

1. LV, lateral view, adult (female?) valve, with cracks but nearly true outline, lateral normal pores visible, carinate rostrum. Sample REKO 04, Fuson Member of the Lakota Formation, Boxelder Creek, SD, U.S.A. (Fig. 2, loc. 9).

2. RV, lateral view, adult (female?) valve, broken. Sample SBCR LAg2, Fuson Member of the Lakota Formation, Stage Barn Canyon Road, SD, U.S.A. (Fig. 2, loc. 8).

3. Dorsal view, anterior end to the left, adult (female?) carapace, with strong crack in center. Sample SBCR LAg2, Fuson Member of the Lakota Formation, Stage Barn Canyon Road, SD, U.S.A. (Fig. 2, loc. 8).

4. LV, lateral view, anteroventral region with carinate rostrum in LV. Sample EBF 04b2, Fuson Member of the Lakota Formation, East of Belle Fourche Road, SD, U.S.A. (Fig. 2, loc. 7).

5. RV, lateral view, magnification of specimen 2 of this plate, anteroventral region with carinate rostrum in RV. Sample SBCR LAg2, Fuson Member of the Lakota Formation, Stage Barn Canyon Road, SD, U.S.A. (Fig. 2, loc. 8).

6. RV, internal view, preadult (A-1?, female?) valve, mostly filled with broken parts of LV. Sample SBCR LAg2, Fuson Member of the Lakota Formation, Stage Barn Canyon Road, SD, U.S.A. (Fig. 2, loc. 8).

7. LV, lateral view, adult (male?) valve, lateral pores visible, with very weak tubercles posterolaterally, alveolus masked by sediment behind it, carinate rostrum, ventral ridge. Sample SBCR Lag3*, Fuson Member of the Lakota Formation, Stage Barn Canyon Road, SD, U.S.A. (Fig. 2, loc. 8).

8. RV, lateral view, adult valve, broken/laterally compressed, rostral keel not visible. Sample SBCR Lag3*, Fuson Member of the Lakota Formation, Stage Barn Canyon Road, SD, U.S.A. (Fig. 2, loc. 8).

9. RV, lateral view, adult (male?) valve, rostral keel not visible, sample SBCRClay v1254 (=SBCR LAg3* here), Fuson Member of the Lakota Formation, Stage Barn Canyon Road, SD, U.S.A. (Fig. 2, loc. 8).

10. RV, lateral view, preadult (A-2?) valve, with moderate punctation being somewhat stronger than in adults of the same sample, sample SBCRClay v1254 (=SBCR LAg3* here), Fuson Member of the Lakota Formation, Stage Barn Canyon Road, SD, U.S.A. (Fig. 2, loc. 8).

11. Right ventrolateral view, internal mold of adult carapace with typical outline following that of the RV. Sample SBCR LAg2, Fuson Member of the Lakota Formation, Stage Barn Canyon Road, SD, U.S.A. (Fig. 2, loc. 8).

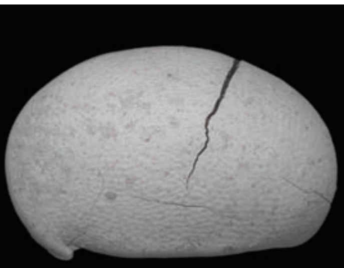
12. Left lateral view, internal mould of preadult (A-2?) carapace, laterally compressed. Sample SBCRClay v1254 (=SBCR LAg3* here), Fuson Member of the Lakota Formation, Stage Barn Canyon Road, SD, U.S.A. (Fig. 2, loc. 8).

13. LV, internal view, adult (female?) carapace, partially filled with sediment, with carinate rostrum. Deep incision of the hinge margin visible. Sample REKO 04, Fuson Member of the Lakota Formation, Boxelder Creek, SD, U.S.A. (Fig. 2, loc. 9).

14. RV, internal view, adult valve, posterior end broken apart, muscle scars visible in part. Sample REKO 04, Fuson Member of the Lakota Formation, Boxelder Creek, SD, U.S.A. (Fig. 2, loc. 9).

15. RV, internal view, magnification of specimen 14 of this plate, rostrum in RV. Sample REKO 04, Fuson Member of the Lakota Formation, Boxelder Creek, SD, U.S.A. (Fig. 2, loc. 9).

PLATE 6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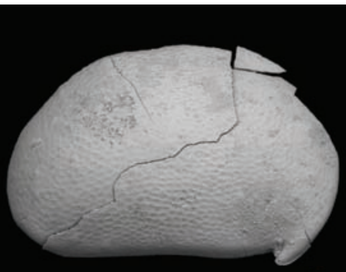
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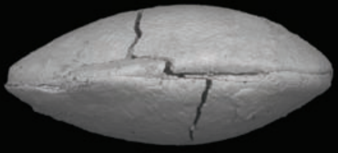
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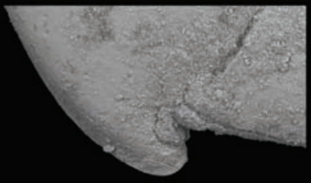
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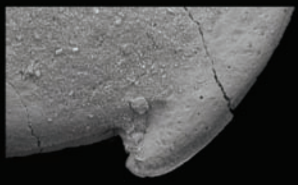
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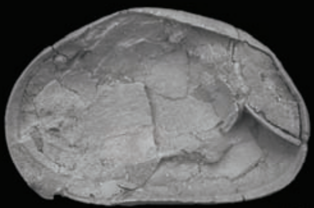
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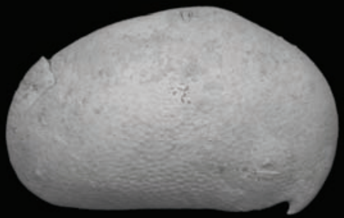
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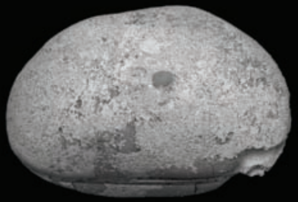
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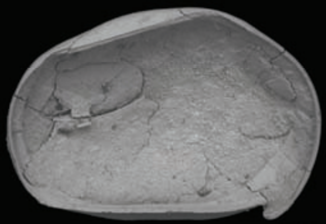
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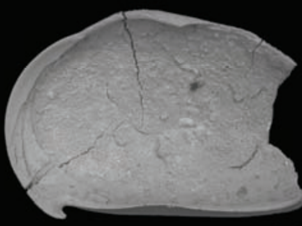
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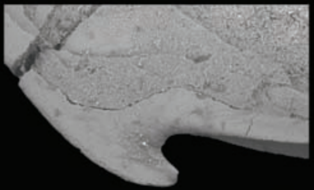
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Plate 7

Scale bar: 100µm; specimens to scale. SD: South Dakota, UT: Utah.

Cypridea (Pseudocypridina) setina **var.** ***setina*** **(Anderson 1939)**

1. Left lateral view, point of rostrum not complete, adult carapace. Sample BCE, Chilson Member of the Lakota Formation, Buck Canyon, SD, U.S.A. (Fig. 2, loc. 1).

2. Right lateral view, complete adult(?) carapace, cyathus and parts of rostrum of LV missing, specimen from the collection of R. E. Peck at the University of Missouri, Columbia (MO). Lower Lakota Formation (Chilson Member), USGS locality D 432 (cf. Peck and Craig 1962, p. 41), SW section of Flint Hill quadrangle, Fall River County, Black Hills, SD (collected by Henry Bell III. and E. V. Post).

3. Right lateral view, complete adult carapace, weathered, cyathus and rostrum of LV broken away. Sample BC5 04, Chilson Member of the Lakota Formation, Buck Canyon, SD, U.S.A. (Fig. 2, loc. 1).

4. Ventral view, anterior end to the left, upper valve = LV, point of rostrum and posteroventral part of LV broken away. Sample PS 1a-70, Yellow Cat Member of the Cedar Mountain Formation, north of Moab, east-northeast of the Ringtail Mine, UT, U.S.A. (Fig. 2, loc. 10).

5. Dorsal view, anterior end to the right, upper valve = LV, preadult (A-1?) carapace. Sample PS 1a-70, Yellow Cat Member of the Cedar Mountain Formation, north of Moab, east-northeast of the Ringtail Mine, UT, U.S.A. (Fig. 2, loc. 10).

6. Dorsal view, anterior end to the right, adult (female?) carapace. Sample PS 1a-70, Yellow Cat Member of the Cedar Mountain Formation, north of Moab, east-northeast of the Ringtail Mine, UT, U.S.A. (Fig. 2, loc. 10).

7. Left lateral view of adult carapace, strongly weathered, point of rostrum broken away. Sample PS 1a-70, Yellow Cat Member of the Cedar Mountain Formation, north of Moab, east-northeast of the Ringtail Mine, UT, U.S.A. (Fig. 2, loc. 10).

8. Right lateral view of adult carapace, weathered, cyathus present, point of LV's rostrum broken away. Sample PS 1a-70, Yellow Cat Member of the Cedar Mountain Formation, north of Moab, east-northeast of the Ringtail Mine, UT, U.S.A. (Fig. 2, loc. 10).

Cypridea (Pseudocypridina) setina **var.** ***rectidorsata*** **Sylvester-Bradley 1949**

9. Right lateral view of adult carapace, point of rostrum and cyathus broken away, specimen from the collection of R.E. Peck at the University of Missouri, Columbia (MO). Peck's locality 184-P, Minnewaste Limestone Member of the Lakota Formation, Calico Canyon north of the town of Buffalo Gap, Custer County, SD, U.S.A.

10. Right lateral view of juvenile (A-2/A-3?) carapace, strongly weathered, ventral part of LV missing Sample ARCR CHz1, uppermost Chilson Member of the Lakota Formation right below Minnewaste Limestone Member, Fall River County, SD, U.S.A. (Fig. 2, loc. 5).

Cypridea (Pseudocypridina) setina **var.** ***setina*** **(Anderson 1939)**

11. RV, lateral view of preadult (A-1?) carapace, posterior marginal part of LV missing, sample PS 1a-70, Yellow Cat Member of the Cedar Mountain Formation, north of Moab, east-northeast of the Ringtail Mine, UT, U.S.A. (Fig. 2, loc. 10).

12. Left lateral view of strongly weathered adult carapace. Sample FRCA, basal Chilson Member of the Lakota Formation, Fall River Canyon, SD, U.S.A. (Fig. 2, loc. 3).

PLATE 7

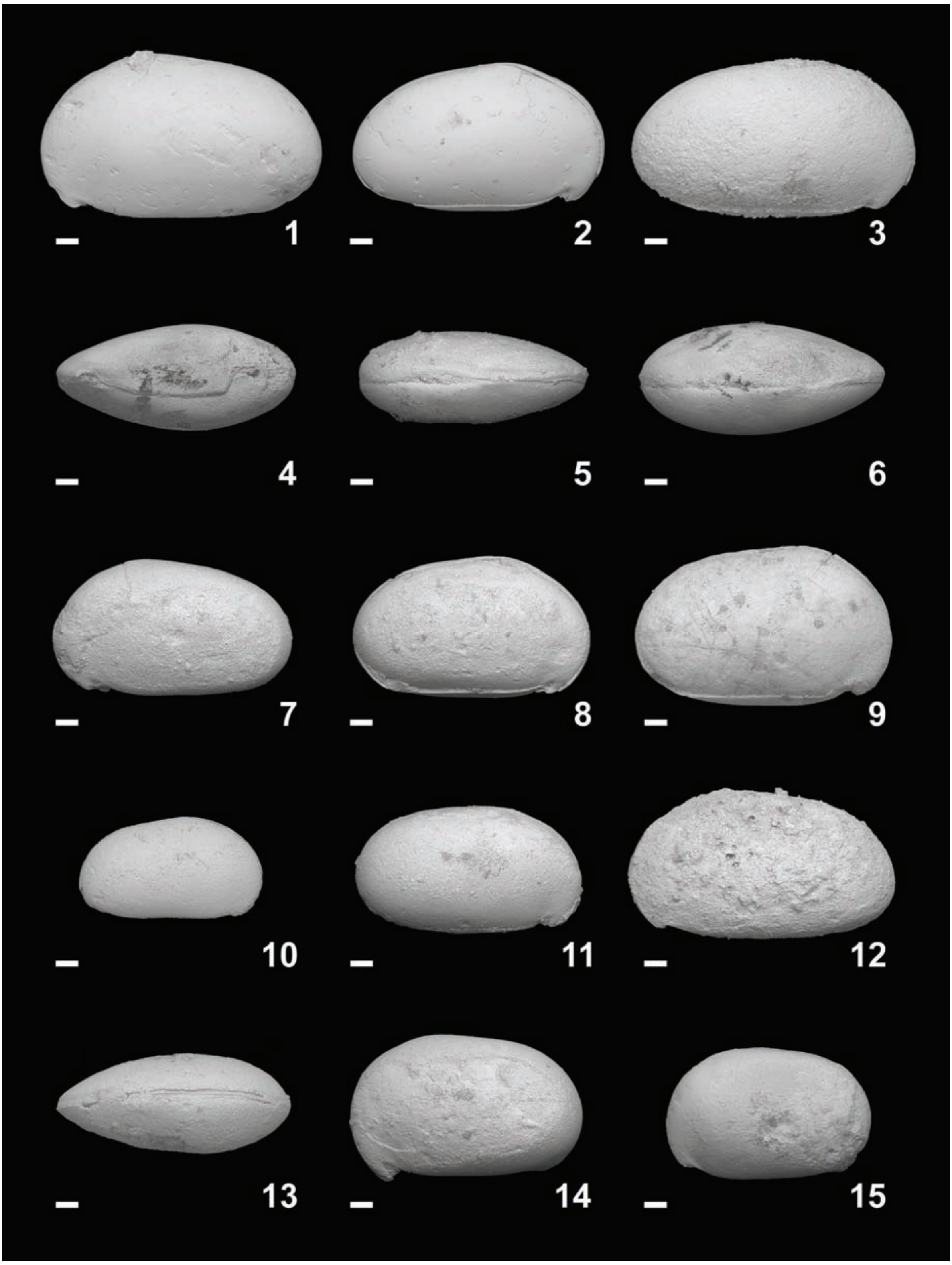


Plate 7 (continued)

Cypridea (Pseudocypridina) setina **var.** ***rectidorsata*** **Sylvester-Bradley 1949**

13. Dorsal view, badly weathered adult specimen and steinkern in part, anterior end to the left, internal imprint of hinge area visible, slightly inclined to the right. Sample ARCR CHz1, uppermost Chilson Member of the Lakota Formation right below Minnewaste Limestone Member, Fall River County, SD, U.S.A. (Fig. 2, loc. 5).

14. Left lateral view, weathered adult species with central parts of its valve missing, partial steinkern. Sample PS 1a-70, Yellow Cat Member of the Cedar Mountain Formation, north of Moab, east-northeast of the Ringtail Mine, UT, U.S.A. (Fig. 2, loc. 10).

15. Left lateral view, weathered and slightly (horizontally) compressed specimen, rostrum broken off but alveolar ridge well visible. Sample PS 1a-70, Yellow Cat Member of the Cedar Mountain Formation, north of Moab, east-northeast of the Ringtail Mine, UT, U.S.A. (Fig. 2, loc. 10).

Plate 8

Scale bar: 100μm; specimens to scale (except Figs. 4, 13, 14). SD: South Dakota, UT: Utah.

Cypridea **ex gr.** ***alta*** **Wolburg 1959**

1. Left lateral view, adult carapace, weathered, point of rostrum broken, alveolar ridge well visible. Sample PS1a-70, Yellow Cat Member of the Cedar Mountain Formation, north of Moab, east-northeast of the Ringtail Mine, UT, U.S.A. (Fig. 2, loc. 10).

2. Right lateral view, adult carapace, weathered, rostrum broken apart, strong dorsal overreach (dorsal ridge) of larger LV clearly visible, faint indication of alveolar ridge in RV. Sample PS1a-70, Yellow Cat Member of the Cedar Mountain Formation, north of Moab, east-northeast of the Ringtail Mine, UT, U.S.A. (Fig. 2, loc. 10).

3. Dorsal view, adult carapace, anterior end to the right, weathered, with some wax stains, showing sinuous dorsal ridge in the LV and strong anterior overlap. Sample PS1a-70, Yellow Cat Member of the Cedar Mountain Formation, north of Moab, east-northeast of the Ringtail Mine, UT, U.S.A. (Fig. 2, loc. 10).

4. Left lateral view, anteroventral region with rostrum and alveolus with alveolar ridge. Magnification of specimen 1 of this plate.

5. Left lateral view, deformed and strongly weathered carapace. Sample PS1a-70, Yellow Cat Member of the Cedar Mountain Formation, north of Moab, east-northeast of the Ringtail Mine, UT, U.S.A. (Fig. 2, loc. 10)

6. Right lateral view, adult carapace, strongly weathered, rostrum, and cyathus broken apart. Sample PS1a-70, Yellow Cat Member of the Cedar Mountain Formation, north of Moab, east-northeast of the Ringtail Mine, UT, U.S.A. (Fig. 2, loc. 10).

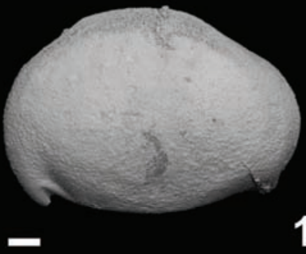
Cypridea **ex gr.** ***tuberculata*** **cf.** ***C. tilleyi*** **Loranger 1951**

7. Left lateral view, adult? carapace, slightly dipped to the left, spined with dominant central spine and alveolar ridge. Sample BC504, Chilson Member of the Lakota Formation, Buck Canyon, SD, U.S.A. (Fig. 2, loc. 1).

8. Right lateral view, adult? carapace, partially covered with sediment, showing overlap and overreach of LV over RV. Sample BC504, Chilson Member of the Lakota Formation, Buck Canyon, SD, U.S.A. (Fig. 2, loc. 1).

(continued)

PLATE 8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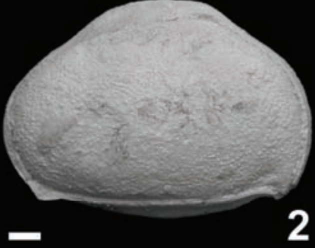
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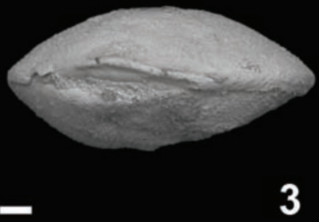
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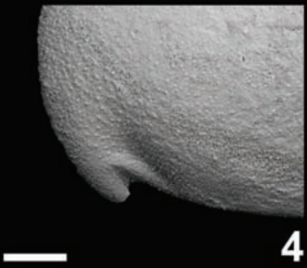
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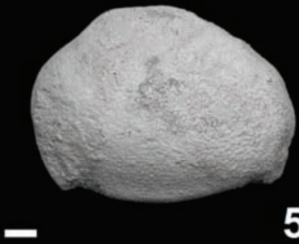
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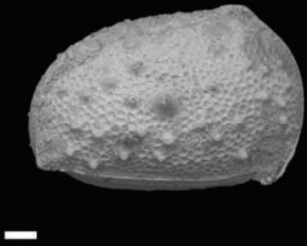
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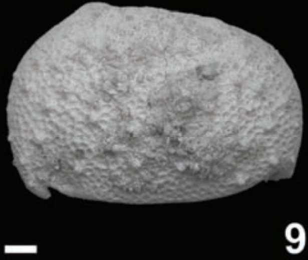
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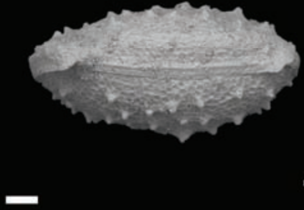
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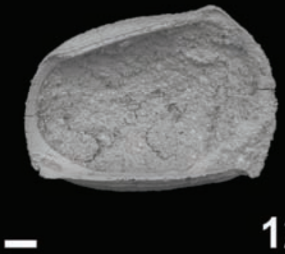
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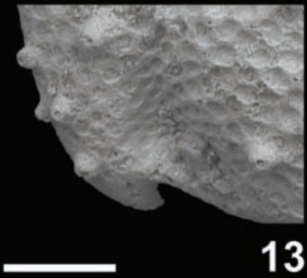
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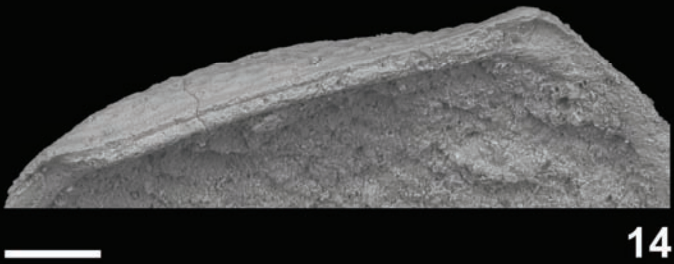
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Plate 8 (continued)

***Cypridea* ex gr. *tuberculata* cf. *C. tilleyi* Loranger 1951**

9. Left lateral view, adult? valve, prominent anterior cardinal angle visible, partially covered with sediment. Sample BC504, Chilson Member of the Lakota Formation, Buck Canyon, SD, U.S.A. (Fig. 2, loc. 1).

10. Dorsal view, anterior end to the left, adult? carapace, slightly dipped to the right, showing broad dorsal furrow. Sample BC504, Chilson Member of the Lakota Formation, Buck Canyon, SD, U.S.A. (Fig. 2, loc. 1).

11. Ventral view, anterior end to the left, adult? carapace, strong overlap of LV visible. Sample BC5 04, Chilson Member of the Lakota Formation, Buck Canyon, SD, U.S.A. (Fig. 2, loc. 1).

12. LV, internal view, adult? carapace, partially filled with sediment, posterior limen visible. Sample BC5 04, Chilson Member of the Lakota Formation, Buck Canyon, SD, U.S.A. (Fig. 2, loc. 1).

13. Left lateral view of anteroventral region. Magnification of Fig. 7 of this plate. Rostrum with minor tubercles, alveolar ridge and alveolar furrow (with puncta!), and several normal pores well visible.

14. LV, internal view of hinge. Magnification of Fig. 12 of this plate. Elongate sockets and broad median ridge, all elements smooth.

2.4. Publication No. 4

SAMES, B., CIFELLI, R.L. and SCHUDACK, M.E., 2010. The nonmarine Lower Cretaceous of the North American Western Interior foreland basin: New biostratigraphic results from ostracod correlations and early mammals, and their implications for paleontology and geology of the basin—An overview. *Earth-Science Reviews*, 101: 207-224.

The original article is available online at http://dx.doi.org/10.1016/j.earscirev.2010.05.001

303 - 328

2.5. Publication No. 5

KHAND, Y., **SAMES, B.** and Schudack, M.E., 2007. New ostracod species from the non-marine Cretaceous of Mongolia. *Revista Española de Micropaleontología*, 39(1-2): 71-80.

This article is not available online. Please refer to the printed journal or contact the second author (B. Sames) for reprint or pdf request.

329 - 338

2.6. Publication No. 6

SAMES, B., 2010. To correlate or not to correlate—That is not the question anymore! Continental Late Jurassic to Early Cretaceous supraregional correlation based on freshwater to brackish-water ostracodes. *Palaios*, 25(1-2): 3-5.

This article is available online at http://palaios.sepmonline.org/cgi/reprint/25/1/3

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3. Discussion and Synopsis

"*We have told each other so often and with such force and such eloquence of the uses to which the study of ostracodes has been applied that we have overlooked one startling fact: almost no one uses ostracodes for anything.*"

Roger L. Kaesler (1937-2007)

3.1. Starting Point and Philosophical Approach

What Kaesler (1983, p. 9, see quotation above) mainly wanted to emphasize is the fact that—with exception of the few specialists—ostracods are not used by nonspecialists to find solutions to biostratigraphic, paleoenvironmental, biogeographic, ecologic or other practical problems. There are many reasons for that, the main reason for which R.L. Kaesler can be quoted again: " … ostracode specialists have devoted most of their efforts to taxonomic revisions rather than applications" (Kaesler 1983, p. 8). That is to say, we are dealing with an old problem: Taxonomy is most important to provide a basis for application but is often still an insular "playground for specialists". However, we have to remember the fact that taxonomy is a scientific method and tool, and we are not forced to stick to established taxonomic dogmata. Quite the contrary, it is up to the taxonomist to provide applicable categories, i.e., groups usable by nonspecialists, as long as these are well defined and indicated as such.

Consequently, the taxonomic approach followed in this thesis has been designed and conducted from the perspective of application, which had been designated as one of the primary objectives from the start. Therefore, once it had become clear that an *a priori* application (mainly biostratigraphic but also paleoecologic and others) of the North American Early Cretaceous nonmarine ostracods was impossible, and the reasons had become apparent (compare Chapter 1.6), the consequences led to a modified approach and an additional intention for the thesis: to demonstrate that integrated "classic" taxonomy (i.e., qualitative-descriptive with consideration of newer biologic insights) is still able to provide, and is *essential* as, a basis for any application—including "modern" (quantitative-mathematical etc.) taxonomy. Particularly since we are approaching a new electronic age of "modern" taxonomy—dealing with large databases, morphometrics, automated taxon identification and the like—the role of the taxonomist becomes more important to control and evaluate the base data for quantitative analyses and the results of these. Most important for application is an evaluation of the (in-)significance of a character in relation to the organism, i.e., is this character taxonomically, ecologically, or otherwise significant. Such information can only be given by the specialist (taxonomist).

Thus, the subtitle of the thesis could be: "A modern hymn to classic taxonomy: providing a basis for application". By means of some Early Cretaceous nonmarine ostracods from the U.S. Western Interior foreland basin, it is demonstrated that nonmarine, late Mesozoic ostracods are of great utility for a variety of applications (even supraregional, intercontinental correlation) and that the immense effort for taxonomic and systematic revision has proven worthwhile.

3.2. Discussion of Results in Relation to Aims and Working Hypotheses

The initial aims of the project are given in the introduction in Chapter 1.5, while the working hypotheses are listed in Chapter 1.7. Numbers (referring to the aims: 1–4) and letters (referring to the working hypotheses: A–H) used in the following passages refer to those given in the respective chapters. Taking the development of the project and consequential modifications into account (see Chapter 1.6; e.g. exclusion of Charophyta from the thesis), the results are discussed in relation to the working hypotheses but are thematically differentiated based on the aims here (Chapter 3.2).

3.2.1. Biostratigraphy

The biostratigraphic application of ostracods to Lower Cretaceous nonmarine formations of the North American Western Interior (W.I.) foreland basin, and particularly the improvement of the age determination of these formations, has been the primary objective of the project this thesis derives from. Taxonomy, the subject in which most of the effort went into, is *just* the basis for it, a basis, however, that previously was not available in applicable form. By means of the taxonomic revision, a biostratigraphic application, amongst others, has been rendered possible, and one of the main aims (No. 1) could be achieved and some working hypotheses (A, B, C, and H) confirmed.

Ongoing research in taxonomic revision led to significant progress in the biostratigraphic application of the respective North American ostracods in that supraregional correlations are demonstrated to be possible and in that these led to the first results with considerable implications. Though previous authors (e.g. Peck 1956, 1959, Peck and Craig 1962, Sohn 1958, 1979) had conducted faunal comparisons to other continents and made biostratigraphic considerations to some extent, a breakthrough was hampered in the past by the lack of a (taxonomic) step to synonymize North American taxa with those from other continents.

A major part of the geologic and chronostratigraphic background referred to in the following is presented in Publication No. 4, Chapter 2.4.

1) The ostracods are suitable for supraregional correlation and are of biostratigraphic utility (hypothesis A).

Just as presumed (see Chapter 1.4), the Early Cretaceous nonmarine ostracods of North America have proven not to be entirely endemic. Quite the contrary, many North American representatives of *Theriosynoecum* and *Cypridea* (and other genera not yet anew revised) either belong to species also known from other continents or, particularly concerning *Cypridea* taxa, have at least strong similarities to species known outside of North America. In certain cases, such as the nonmarine Lower Cretaceous of North America with its very low biostratigraphic resolution, even these similarities can be used to improve the chronostratigraphy of respective geologic units.

Consequently, the biostratigraphic utility of North American Early Cretaceous nonmarine ostracods is obvious and cannot be questioned in principle any longer. Supraregional correlation based on these ostracods is possible (hypothesis A) as is demonstrated through taxonomic revision and by means of correlation to Europe (England, UK; Spain and NW Germany mainly) herein (see Publications Nos. 2, 3, 4 and 6, Chapters 2.2, 2.3, 2.4 and 2.6). Based on the results of taxonomic revisions, the biostratigraphic utility of these ostracods can be considered good at the present state of ongoing research, and the statement that the ostracods have excellent further potential as a biostratigraphic tool can be well justified.

2) Ostracod correlations do improve the age determination of some Lower Cretaceous formations of the W.I. foreland basin (hypothesis A; The details of the results discussed in the following are presented in Publication No. 4, Chapter 2.4 unless otherwise indicated).

Correlations based on representatives of *Cypridea* Bosquet 1852 strongly suggest a maximum age of Late Berriasian to Valanginian (~ 142–13 Ma) for the lower part of the Lakota Formation (Black Hills area, South Dakota) and the Yellow Cat Member of the Cedar Mountain Formation (San Rafael Swell, Utah) as well as a pre-Albian (or even pre-Middle?–Late Barremian) age for the entire succession of the Lakota Formation of the southern and eastern Black Hills margin (see Fig. 1.4 for lithostratigraphy of these formations). This is considerably older than most other published lines of evidence have indicated, which widely have given a Barremian or Aptian (~ 130–125 Ma) maximum age for these two formations, or even younger ages. This affects the correlatives of the Lakota and Cedar Mountain formations in the W.I. foreland basin as well.

It has to be admitted that the higher maximum ages so far heavily rely on representatives of *Cypridea (Pseudocypridina) setina* (Anderson 1939), that is *C. (P.) setina* var. *setina* (see Publication No. 3, Chapter 2.3 also). These had been identified as *Cypridea inornata* Peck 1941 in North America ever since, but are here considered a junior synonym of *C. (P.) setina* Anderson. Representatives of the *Cypridea setina*-group are easily distinguishable, have a relatively limited stratigraphic range in the Purbeck/Wealden and Purbeck/Wealden-like deposits of Europe (e.g. Anderson 1985, Horne 2009, Schudack and Schudack 2009a, b), and are restricted to the lower part of the Lakota Formation (Black Hills area), that is the Chilson Member and Minnewaste Limestone members or L1 interval, respectively (see Fig. 1.4 in Chapter 1 of the thesis). Although the taxonomy of *Cypridea (P.) setina* is complex and in flux (Publications Nos. 3 and 4, Chapters 2.3 and 2.4), the age determinations based on its representatives are reliable due to their easy identification and the extensive, high-resolution biostratigraphic reference data from Europe (e.g. Anderson 1985, Horne 1995, 2009, Hoedemaeker and Herngreen 2003). Moreover, with regard to the Yellow Cat Member of the Cedar Mountain Formation, these results are supported by the occurrence of representatives of the *Cypridea alta*-group and palynologic evidence (refer to Publication No. 4, Chapter 2.4).

As to the Lakota Formation, a higher maximum age based on ostracod correlation is supported by, and consistent with, mammal evidence. The Chilson Member of the Lakota Formation yielded a diverse microvertebrate fauna that, amongst others, comprises eight mammal taxa (R.L. Cifelli research in progress, Publication No. 4, Chapter 2.4). These are of special interest in that they represent an undocumented interval in the history of North American mammals. The entire mammalian assemblage from the Lakota appears to be new. Based on the known record of North American Cretaceous mammals, the fauna, on the one hand little resembles Aptian–Albian faunas, and on the other hand shows clear ties to the mammalian fauna of the Late Jurassic Morrison Formation, the elements of which are otherwise unknown later than Kimmeridgian–Tithonian (Early Berriasian?) in North America.

These mammal data from the Lakota Formation are of utmost importance: 1) with regard to the higher maximum ages given based on ostracod evidence, which they support; and 2) with regard to the starting point of the project (Chapter 1.4) i.e., the assumption that many (all?) Lower Cretaceous formations of the W.I. foreland basin have higher maximum ages, and the timespan represented by the hiatus between them and the underlying Upper Jurassic (to Early Berriasian?) Morrison/Kootenay formations is considerably shorter than has been indicated in the past. The point is that both the ostracods and mammals support each other independently. Although the more precise presumed age-constraint of this mammal fauna derives from ostracod data, the mammal fauna itself is clearly distinct from those known from the documented intervals in the history of North American mammals (Tithonian and older, Aptian and younger) and, therefore, comes from this previously undocumented interval (Berriasian to Barremian).

Recapitulatory, the data presented convincingly confirm that the ostracods can improve the age determination of respective Early Cretaceous formations of the W.I. foreland basin, particularly with respect to maximum ages and age constraints, but also regarding the chronostratigraphy of these (see sections 3 and 4 below).

3) Ostracods are suitable for inter- and intraformational correlations in the W.I. foreland basin (hypothesis B)

Stratigraphic correlation is *the* prerequisite to establish a chronostratigraphy of geologic units of every dimension, whether this be a single member of a formation or a large geologic structural unit such as the entire W.I. foreland basin (see sections 4 and 5 below also). Resulting from lateral facies changes and numerous stratigraphic unconformities of different nature, correlation of the Lower Cretaceous formations in the basin is difficult (see Publication No. 4, Chapter 2.4 for details). However, organisms, that is to say ostracods in our case, are not limited to certain depositional areas. Representatives of the superfamily Cypridoidea in particular (*Cypridea* and related genera, for example) have developed dispersal mechanisms that facilitate their long-distance passive dispersal, even intercontinentally (see Publication No. 3, Chapter 2.3). In combination with their abundance in nonmarine environments and their good fossilization potential, not to mention the absence of better suitable groups of organisms, the ostracods should be the "perfect" tool for biostratigraphic correlation. They are, indeed, but application has been hampered by taxonomic problems and moderate data in the past. Now that the first step toward a better application has been achieved by the taxonomic revision of some important ostracod taxa of *Theriosynoecum* and *Cypridea*, first results confirm the presumed biostratigraphic utility of the ostracods (see below) and, as well, confirm the assumption of their great further potential with regard to the W.I. foreland basin.

Using the example of the Lakota and Cedar Mountain formations, inter- and intraformational correlation based on ostracods can be shown. At least parts of the Yellow Cat Member of the Cedar Mountain formation correlate to the Chilson Member (L1 interval) of the Lakota Formation as based on representatives of *Cypridea* (see Fig. 11, Publication No. 3, Chapter 2.3). Though ostracod data from the Cedar Mountain Formation is sparse (though in that samples derive from a very limited stratigraphic interval at one locality only), these are the first ostracods having been described from this formation (previously to this project, ostracods had only been mentioned). This is a successful test for a long-distance ostracod correlation within North America also demonstrating the further potential of these ostracods and the need for more data (ostracod samples) from the respective formations. The as yet moderate data with respect to ostracods (and charophytes) is considered to be one of the main limiting factors for their application.

With regard to interformational correlation, the example of the Lakota Formation clearly shows the potential of ostracods as a suitable tool. The herein revised taxonomic data from earlier publications (Roth 1933, Harper and Sutton 1935, Sohn 1958, 1979) and the authors own data (see Fig. 11 in each case in Publications Nos. 2 and 3, Chapters 2.2 and 2.3) show a clear difference in the Lakota ostracod assemblages of the southern and eastern Black Hills margin. This indicates a difference in age between the respective units and points to the fact that the Chilson Member or L1 interval of the Lakota Formation is missing in much of the eastern Black Hills margin area (South Dakota), as it is the case for the Minnewaste Limestone Member (cf. Fig. 1.3 in Chapter 1 of the thesis). The lithostratigraphy of the Lakota Formation remains to be discussed. Many recent works (e.g. Way et al. 1998, Zaleha 2006) focus on the western and northwestern part (Wyoming) of the Black Hills margin and remain to be integrated with those dealing with the succession of the Lakota Formation along the southern and eastern Black Hills margin.

As can be shown with the example of the Lakota Formation, and as presumed to apply to other nonmarine Lower Cretaceous formations of the basin, ostracods are well suited to support intraformational correlations and also to potentially biostratigraphically constrain the identification and stratigraphy of single members. Ostracods are furthermore expected to support the identification and justification of stratigraphic unconformities in the future, once the ongoing taxonomic revisions of more taxa have been completed and more ostracod data are available from measured sections of these formations.

4) Ostracods are suitable, or have the potential, for establishing a chronostratigraphy of respective formations (hypothesis C).

Since it has been shown in sections 2 and 3 above that ostracods can be used to improve the age determination of the basin's nonmarine Lower Cretaceous formations, as well as their inter- and intraformational correlations, the prerequisites for establishing a chronostratigraphy are met. Though results presented here *just* provide the basis for further research within this scope, these results are essential to demonstrate the utility of ostracods and their great potential as to future research.

Deriving from ostracod correlations with northwestern Europe, the chronostratigraphy of the Lakota Formation can be constrained as follows: the maximum age of the Lakota Formation at its base (the base of the Chilson Member) in the southern Black Hills area (see Fig. 1.3 in Chapter 1 of this thesis) is Late Berriasian to Early Valanginian (~ 142–138 Ma) and the whole formation, as documented at the southern and eastern Black Hills margin (South Dakota), is older than (Middle?) Late Barremian. The Chilson member only yielded elements of the informal "Faunas A and B" (refer to stratigraphic notes in the discussion section, Chapters 6 in each case, of Publications Nos. 2 and 3, Chapters 2.2 and 2.3 herein). In addition, the Chilson and Fuson Members of the Lakota Formation in that area strongly differ in the composition of their ostracod assemblages and the Chilson Member is, more or less, distinctly older (Late Berriasian–Valanginian) than the Fuson Member (Middle/Late? Valanginian, Hauterivian–Middle? Barremian).

These results are preliminary and remain to be confirmed and specified in upcoming future research. They, nevertheless, demonstrate the further potential of ostracods as a tool for the improvement of the chronostratigraphy of the W.I. foreland basin at smaller (formation) and larger (entire basin, see section 5 below) scales, as well as the potential for the future establishment of an ostracod biozonation.

Admittedly, such chronostratigraphic considerations are not new and have already been made by Peck (1956, 1959). Peck's (1956, 1959) ostracod and charophyte assemblages, however, require extensive revision regarding their reliability, including the taxonomic revision of many of the ostracods and charophytes, (re-)correlation of sample horizons and age determinations (cf. Publication No. 4, Chapter 2.4 also). Moreover, Peck's ostracod type material is missing from his collection (University of Missouri, Columbia, MO, U.S.A.) and its whereabouts are unknown. That is to say, much of Peck's (1941, 1951, 1956, 1959, Peck and Craig 1962) data are inapplicable in their available form. Considerable effort will be necessary to retrace and utilize his information, but such efforts are expected to be rewarding.

5) The chronostratigraphic results derived from ostracod correlations have considerable implications on the geology and paleontology of the W.I. foreland basin (hypothesis H).

This topic is the central issue of Publication No. 4 (Chapter 2.4) and extensively discussed, therein emphasizing the implications of higher maximum ages for respective Lower Cretaceous formations. It is also partially outlined in Publication No. 6 (Chapter 2.6).

There is not much left to add, with exception of the implications of an improved chronostratigraphy with a better subdivision of the nonmarine Lower Cretaceous of the basin, i.e., a higher resolution than exists so far. Preliminary results deriving from partial revision of previous works and data of the current author suggest 3–4 (so far informal) distinct ostracod assemblages (refer to stratigraphic notes in the discussion section, Chapters 6 in each case, of Publications Nos. 2 and 3, Chapters 2.2 and 2.3 herein), which remain to be tested, confirmed and clearly defined. These results strongly suggest that an ostracod biozonation of Lower Cretaceous deposits of parts, as well as the entire, W.I. foreland basin can be established in the near future. As noted in section 3 above, ostracods are also expected to support the identification and justification of stratigraphic unconformities, another tool to improve the chronostratigraphic framework of the basin at smaller and larger scale.

3.2.2. Paleoecology and Paleoenvironment

One of the original aims (No. 2) was to provide ostracod-based contributions to improve the paleoecologic/paleoenvironmental interpretation of respective Lower Cretaceous formations in North America. The presented results obtained from ostracods demonstrate the potential to improve the paleoecologic and paleoenvironmental interpretation of the respective geological units (hypothesis E).

As noted and justified in Chapters 1.6 and 4.1, the detailed analyses and results have been excluded from the thesis and will be published separately since they require assemblage analyses that can only be conducted after taxonomic and systematic revision of the other elements within the respective assemblages. Paleoecologic and paleoenvironmental aspects have not played a significant role in ostracod research from the nonmarine Lower Cretaceous of the W.I. foreland basin (e.g. Finger 1983, Harper and Sutton 1935, Jones 1893, Loranger 1951, 1954, Peck 1941, 1951, 1956, 1959, Peck and Craig 1962, Peck and Reker 1948, Roth 1933, Sohn 1958, 1979, Vanderpool 1928). There are different reasons for that, historical as well as to systematics. The paleoecology of nonmarine Mesozoic ostracods was not an important issue in most taxonomic papers until the 1980s. It was both not considered of higher significance and could often not be considered because of the lack of data. Taxonomy and systematics also played (and continue to do so) an important role in the paleoecologic and paleoenvironmental reconstruction because the actualistic approach for fossil taxa depends on their correct identification (taxonomy) and linkage to recent relatives (systematics).

The fact that paleoecology was not considered important combined with lacking knowledge and data, in turn, manifested itself in the taxonomy in that ecophenotypic morphologic characters were not identified as such (e.g. noding, see taxonomic glossaries of Publications Nos. 2 and 3, Chapters 2.2 and 2.3 herein) and rather treated as taxonomically significant. This lead to the designation of numerous new taxa, thereby lowering, or hampering, their application in various ways. A good example is that of *Cypridea (Pseudocypridina) piedmonti* (Roth 1933) and *Cypridea (P.) henrybelli* Sohn 1979, the latter now considered to be a junior synonym and simply a noded variant of the former (Publication No. 2, Chapter 2.2). Therefore, if the interpretation that noding is caused by an abrupt and considerable decrease in salinity during moulting is correct with respect to extinct representatives of *Cypridea*, the occurrence of noded forms points to intermittent variable salinities in the waterbodies where these lived, regardless of the variety of potential causes (e.g. strong freshwater influx into smaller, slightly saline waterbodies through heavy rainfall). The frequent occurrence of *Cypridea (Pseudocypridina) piedmonti* var. *henrybelli* in samples of the Fuson Member of the Lakota Formation along the eastern Black Hills margin, and their complete absence in the Chilson Member of the southern Black Hills (see Fig. 11 in Publication No. 2, Chapter 2.2), indicate different paleoenvironmental conditions, or, their stronger variation with respect to the Fuson Member in comparison to the Chilson Member. The specific context of this remains to be investigated (e.g. controlling factors, and whether this is a function of time, which is probable since the Fuson Member is of younger age, or a function of depositional setting and area; or the context is more complex).

The example given has been chosen to demonstrate the application potential of the Early Cretaceous ostracods in North America. Prerequisite is a good taxonomy (herein and in progress) and terminology, that is, the identification of the mode of significance of a carapace character (ecophenotypic in our case) and its cause (also herein and in progress). To identify the links to recent relatives for better actualistic approaches, a review of the systematics of many of these ostracods is necessary as well. In addition, there has been (and there is ongoing) progress in the paleoecology of the respective taxa and their close relatives in other areas of the world (e.g. Neale 1988, Horne 2002, Schudack and Schudack 2009a).

In summary, the way for future research and paleoecologic and paleoenvironmental application of the respective ostracods has been paved through this thesis: it 1), presents considerable progress in the taxonomy of important groups and their Early Cretaceous North American representatives, including paleoecologic data as far as available; and 2), it presents considerable progress in the revision of the terminology of carapace characters and, where applicable, identifies and discusses the paleoecologic significance or context of these (Publications Nos. 2 and 3, Chapters 2.2 and 2.3).

3.2.3. Paleobiogeography

In the context of the biostratigraphic utilization of the North American Early Cretaceous nonmarine ostracods, the analysis of the supraregional paleobiogeographic distribution of relevant taxa (aim 3, in part) is one of the most important prerequisites, all depending on taxonomy as the fundamental basis. By the taxonomic revisions conducted within the frame of this project and thesis (Publications Nos. 2, 3 and 5, Chapters 2.2, 2.3 and 2.5), the endemism of the respective ostracods has been widely disproved, thereby confirming the initial assumption that the Early Cretaceous nonmarine ostracods of the W.I. foreland basin are not entirely endemic. Quite the contrary to being endemic, it is now apparent that the degree of their endemism is still highly overestimated, and expected to significantly decrease once further taxonomic revisions have been conducted and with more data becoming available in the future. The integration of new insights into the reproductive and dispersal mechanisms (hypothesis D, in part) supports the taxonomy in that a wide spatial distribution of the taxa and their distribution patterns can be explained.

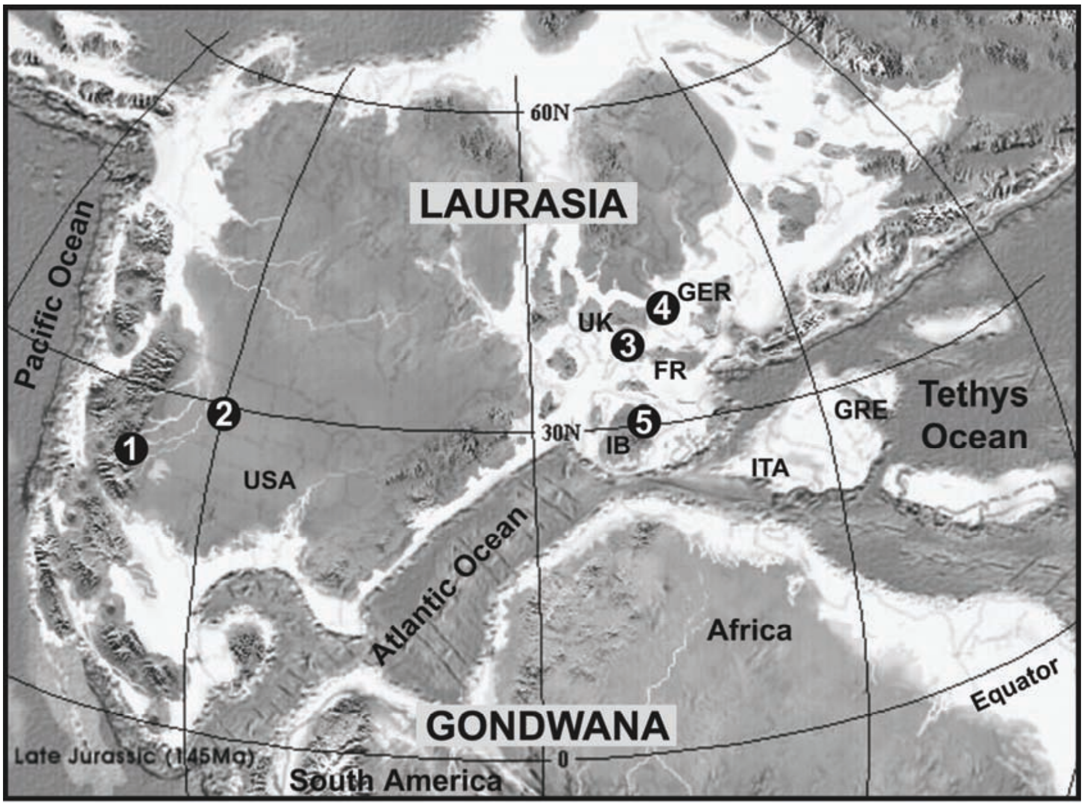

Fig. 3.1. Paleogeographic map of parts the northern hemisphere at the Jurassic-Cretaceous boundary (~145 Ma, modified after Ron C. Blakey http://jan.ucc.nau.edu/~rcb7/150NAt.jpg) showing the (paleo-)position of the depositional areas of the Cedar Mountain Formation (1), the Lakota Formation (2), the Purbeck/Wealden of England (3), the "German Wealden" of NW-Germany (4), and the "Spanish Wealden" (5) (refer to Chapter 2.3, Publication No. 4 also). Scale: ~5000km at Equator. Abbreviations: USA: United States of America; UK: United Kingdom; GER: Germany; IB: Spain (Iberian Peninsula); FR: France; ITA: Italy (Adriatic plate); GRE: Greece.

The detailed paleobiogeographic analyses (in progress) have been excluded from the thesis due to the modified approach (Chapters 1.6. and 4.1.) and will be published separately including representatives of genera other than *Theriosynoecum* and *Cypridea*. This also includes the analysis of the evolution of major groups (Cypridoidea: Cyprideidae, Cytheroidea: Timiriaseviinae) in context to plate tectonic and paleoclimatic developments with the respective reproduction and dispersal mechanisms (aim 4). What can be said, based on the available data and the author's own results, is that the North American Berriasian to Aptian nonmarine ostracod faunas are strongly related to their Western European contemporaries (southern England, NW Germany and Spain in particular; see Fig. 3.1). There are also presumed faunal links to Asia, South America and West Africa that have yet to be investigated, as even more are thought to be concealed by different taxonomic views and their resulting varying taxon names. For yet unknown reasons, representatives of the subfamily Timiriaseviinae (Limnocytheridae, Cytheroidea) other than *Theriosynoecum*—that are common to Cretaceous nonmarine deposits worldwide (e.g. representatives of *Timiriasevia*)—have not been documented from the Lower Cretaceous of the W.I. foreland basin. However, as the example of the new discovery of a small sized cytheroid taxon (*Stenestroemia?*) from the eastern Black Hills margin (Fuson Member of the Lakota Formation) shows, these small forms might have been overlooked in the past and more are presumably waiting to be discovered. As to *Cypridea*, the dispersal of its representatives strongly depends on the reproductive mode (refer to chapters 6.1 and 6.2 in Publication No. 3, Chapter 2.3 of the thesis), which has to be considered in the paleobiogeographic analysis but can, in turn, be applied to reconstruct the control factors (wind directions, migration routes of animals helping in the ostracods passive dispersal etc.). Particularly with respect to *Cypridea*, but also other contemporaneous cypridoidean taxa, a consistent integrated taxonomy—i.e., the identification of, and differentiation between, variants, sexual dimorphs, and asexual females—is essential for the biogeographic analysis.

The current state of research does not yet allow a well justifiable assignment of the North American Early Cretaceous ostracods to Boreal and Tethyan bioprovinces. More research and (qualitative and quantitative) data analyses are necessary with respect to their taxonomy, biogeographic distribution, and paleoenvironment, particularly for North America. In addition, the strong continental setting of large parts of the Western Interior foreland basin has to be considered, as well as the presumably different effect of the "Mid-Cretaceous" (Aptian to Cenomanian) climatic changes in North America in comparison to other areas of the world (see Chapter 3.2.5. below). This thesis provides a portion of the fundamental taxonomic basis toward application and integrated analyses (such as paleobiogeography) of the nonmarine North American Early Cretaceous ostracods.

3.2.4. Progress in Taxonomy of Important Higher Taxonomic Groups (Cypridoidea–Cyprideidae, Cytheroidea–Timiriaseviinae) and its Implications

The comprehensive taxonomic revision of the genera *Theriosynoecum* and *Cypridea*, with emphasis on North American Early Cretaceous representatives, coupled with the revision of carapace terminology (Publications Nos.1, 2 and 3, Chapters 2.1, 2.2 and 2.3), led to important progress in the taxonomy of some major groups: the Timiriaseviinae Mandelstam 1960 and the Cyprideidae Martin 1940 (hypothesis D in part, hypothesis F). By integration of newer insights into ostracod biology, physiology, reproductive and dispersal mechanisms, genetics, ecology, and evolution into the analyses, the taxonomy of these fossil ostracods has been improved (hypothesis D).

This is by example of the taxonomic comparison of selected genera of the subfamily Timiriaseviinae (chapter 6.4 and table 1 of Publication No. 2) and the partial revision of the family Cyprideidae (chapter 5.2.1 and table 1 of Publication No. 3). As frequently stated herein, the identification of the taxonomic (in-)significance of carapace characters (at certain taxonomic levels) and their potential variability is the key toward better taxonomy, a fact that cannot be stressed often enough. The modifications in the taxonomy of the examples given are based on the methodic acquisition of as many carapace characters as possible in combination with the designation of their taxonomic (or otherwise) significance, which then were weighed against each other based on their number and/or siginificance. With that, the disjunction of fossil representatives of the genera *Theriosynoecum* (extinct) and *Metacypris* (extant) is now possible, as is the differentiation of important genera of the Timiriaseviinae, based on carapace characters alone (chapter 6.4 and table 1 of Publication No. 2). With respect to the Cyprideidae (extinct), modifications in the assignment of some of its representatives are as well based on the above methodology. For example, the rejection of the subgenus *Ulwellia* of the genus *Cypridea* results from the identification of the inverse valve size relation (right valve larger than left valve) as taxonomically insignificant at and above species level based on a), the insight that many morphologically significantly distinct species of *Cypridea* share this character that cannot belong to a closer related group by weighing many different carapace characters against the common inverse valve size relation, and b), newer insights into ostracod biology, genetics and reproduction, particularly the relatively high possibility that asexual populations can derive from one egg or one parthenogenetic female only. If this one is a mutant with the inverse valve size relation and transported over a long distance, the result would be a geographically separated asexual population with inverse valve size. From the actualistic perspective, such events are likely to have happened relatively often, especially when the long time span for the uppermost Jurassic to Early Cretaceous, some 45 Ma, is taken into consideration.

As to "explosive" radiation and faunal domination of representatives of the family Cyprideidae Martin 1940 during the Late Jurassic/Early Cretaceous (hypothesis F), this is discussed at length in Publication No. 3 (chapter 6.1 therein) and will not be repeated here. Three important facts just have to be highlighted at this point:

1) The most likely reproductive mode in *Cypridea* was mixed reproduction, which has consequences as to dispersal modes and potential, distribution patterns, and morphologic variability and taxonomy. Many presumed sexual dimorphs have been identified.

2) By consideration of mixed reproduction in *Cypridea* and its considerable consequences for genetic and morphologic variability, the hypothesis of an Upper Jurassic/Early Cretaceous faunal dominance (diversity at species level, not abundance) of representatives of the Cypridoidea (overwhelmingly comprising representatives of the Cyprideidae, i.e., taxa of *Cypridea* mainly) in comparison to those of the Cytheroidea and Darwinuloidea is strongly challenged. So far, there is no reliable quantitative statement possible except for the insight that diversity in *Cypridea* has been grossly overestimated, potentially exaggerated by a factor of five (Nye et al. 2008), if the example given therein is indicative for most of its representatives. What must also be taken into consideration is that knowledge on diversity in other cypridoid families (e.g. Trapezoidellidae, Cyprididae) is still sparse (many smooth and roundish forms are often just designated "candonids", for example).

3) Whether the differential success of the representatives of the Cyprideidae during the Late Jurassic/Early Cretaceous is a function of their particular anatomy (i.e., the rostrum, alveolus and cyathus etc.) or rather a function of the combination of intrinsic and extrinsic factors (i.e., the possible reproduction mode, the distribution mechanisms, and the habitat characteristics) still remains to be clarified. Results deriving from this thesis just contribute to this topic insofar as that they support the hypothesis that the differential success of the Cyprideidae has to be partially qualified, at least regarding species diversity.

The taxonomic glossaries are a major component of Publications Nos. 2 and 3 and required considerable work. As such, these have in part been specified to the ostracod groups dealt with herein. They are an essential prerequisite for a "standardized" taxonomic concept based on a terminologically consistent taxonomy, and are planned to be further developed, supplemented and generalized in the future. The update of older glossaries has long been wanting. Once published, it is hoped they will be considered for use by many ostracodologists, and criticized and developed over time.

3.2.5. The North American Early Cretaceous Ostracods in the Context of the World's Purbeck/Wealden-like Deposits

The results presented herein do not significantly contribute to the improvement of our understanding of the latest Jurassic/Early Cretaceous nonmarine Purbeck/Wealden-like deposits of the world (hypothesis G). Too many related questions remain to be clarified or put into context in North America. The basis toward solutions of some of these, however, is provided herein (taxonomic revision and supraregional correlations, thereby making long-distance comparisons accessible).

Taking the gigantic, fully continental (in the climatic context) setting of large parts of the North American Western Interior foreland basin into consideration, the question might be asked whether this depositional environment can be designated a "Purbeck/Wealden-like" deposit. With exception of some contemporaneous Asian depositional areas, most other Purbeck/Wealden-like depositional areas of the world were of much smaller spatial extent, located closer to the sea (with resulting climatic effects), and, in part, occasionally underwent influence from marine waters. This is important in context of the degree of the stability of these paleoenvironments and included habitats at smaller and larger scale, which would strongly affect the spatial and temporal ostracod distribution as well as their morphology and evolution. As to the latter two, unstable environmental conditions are thought to favor—or, from the view of the ostracods, rather require—asexual reproduction, for example. A synthesis of this topic in a global context remains a required challenge.

3.3. Synopsis

The results presented by this thesis constitute considerable progress in Early Cretaceous nonmarine ostracodology in North America. Though it just marks the beginning of a revival of ostracod applications, there is not only the theoretic assumption but ample evidence for the utility of the respective ostracods.

The main intention of this project and thesis was to demonstrate that an application of nonmarine ostracods from the Lower Cretaceous of the North American Western Interior foreland basin is possible. A central issue was the use of their biostratigraphic information to improve the chronostratigraphy of selected Lower Cretaceous formations of North America. This was not possible *a priori*. The main limiting factors for such application have been identified: taxonomic problems and base data unusable in their present form, i.e., prior to revision.

The principal tasks of this thesis have been achieved by a modified approach that is strongly different from the initial plans for the project: the taxonomy of selected (biostratigraphically relevant) groups has been comprehensively dealt with, thereby rendering an application of the studied ostracods possible. These comprise some North American taxa of the genera *Theriosynoecum* Branson 1936 and *Cypridea* Bosquet 1852, representatives of which are used for biozonation of the Purbeck/Wealden of southern England or the "German Wealden" of NW Germany. The taxonomic revisions confirm the assumption that the degree of endemism of respective ostracods in North America is, by far, not as high as hitherto believed, and demonstrate the ostracod's good actual utility and great further application potential (requiring more taxonomic revisions, research and data). By disproving their endemism, an application of the ostracods has been rendered possible and carried out by means of biostratigraphy mainly, within the scope of this thesis and one of its principal tasks.

To provide a consistent and traceable taxonomy, which is fundamental for all further research and application, comprehensive updated, commented and discussed taxonomic glossaries of relevant terms has been elaborated and supplemented by newly developed illustrations.

Three representatives of *Theriosynoecum*, *T. verrucosa* (Jones 1885), *T. fittoni* (Mantell 1844) and *T. pahasapensis* (Roth 1933), have been described from North America (top Morrison and Lakota formations along the southern and eastern Black Hills margin, South Dakota). After extensive revision, only *T. pahasapensis* is endemic to this continent. Though these are not yet well-applicable index fossils, there are substantial faunal links to Europe. The genus *Bisulcocypris* Pinto and Sanguinetti 1958 has been confirmed and justified to be a junior synonym of *Theriosynoecum*. Fossil representatives of the extant genus *Metacypris* Brady and Robertson 1870 can be clearly distinguished from those of *Theriosynoecum* (extinct). A representative of the latter is thought to have been the ancestor of the former. North American Early Cretaceous representatives of genera other than *Theriosynoecum* and *Metacypris* are yet unknown. The North American early Cretaceous ostracod fauna provides valuable information concerning the phylogeny and distribution of the Timiriaseviinae during the late Mesozoic, and potentially about the origin and early evolution of *Metacypris* Brady and Robertson 1870.

Ten species of *Cypridea* have been described and extensively revised. Though some taxonomic problems remain, the degree of endemism of this part of the North American *Cypridea* fauna is, by far, not as high as previously believed. Because of the complexity of the taxonomy in species of *Cypridea*, presumed largely the consequence of mixed reproduction and its implications, few direct supraregional correlations can be made at species level at the present state of knowledge. However, since the taxonomic revision was conducted from the perspective of applications (mainly biostratigraphic), the method of applying species-groups (quasi “superspecies”) allowed a considerable improvement to the chronostratigraphy of the respective Lower Cretaceous formations of the W.I. foreland basin (see below). Representatives of *Cypridea* are of great utility concerning biostratigraphic applications in the basin and are considered to have even greater further potential. The comprehensive revision of the genus *Cypridea*, as well as the partial revision of the family Cyprideidae, also led, amongst others, to the following results: The taxonomy of the Cyprideidae Martin 1940 has been modified in that *Praecypridea* Sames, Whatley and Schudack (in review) has been integrated and *Longispinella* Sohn 1979 is now assigned a subgenus of *Cypridea*. Much more evidence for sexual dimorphism in *Cypridea* is presented and the faunal dominance of its relatives in Late Jurassic/Early Cretaceous nonmarine deposits of the world becomes arguable.

With regard to biostratigraphy, results presented in this thesis provide the basis for the revival—or, in the view of the author, rather the real advent—of a biostratigraphic application of nonmarine Early Cretaceous ostracods of the Western Interior foreland basin. By correlation of these ostracods to well dated western European strata (Purbeck/Wealden of England and “German Wealden” of NW-Germany), significant progress in their biostratigraphic application has been achieved. New results strongly suggest that the maximum age of the lower part of both the Lakota Formation (Black Hills, South Dakota and Wyoming) and the Cedar Mountain Formation (San Rafael Swell, Utah), is upper Berriasian to lowermost Valanginian (~142–138 Ma, refer to Figs. 1.3 and 1.4). These results are partially supported by palynologic and mammal evidence. This is considerably older than most other published lines of evidence have indicated in the past (Barremian to Albian) and has considerable implications as to the correlatives of the mentioned formations (e.g. the Cloverly and Kootenai formations) and, therefore, as to the geology (chronostratigraphic framework) and paleontology (temporal development of the paleoenvironment and huge paleoecosystem) of the basin. Formations correlatable to the Lakota and Cedar Mountain formations by means of other chronostratigraphic and geochronologic methods can now be tested for these correlations and the given ages based on ostracods. There is strong evidence that Berriasian to Barremian strata do exist in (at least parts of) the Western Interior foreland basin.

Although the progress achieved with this thesis is just the beginning of an improved chronostratigraphy of single formations and the entire W.I. foreland basin, the fundaments for a potential basal chronostratigraphy (at least 3–4 distinct faunal assemblages), to be better defined and confirmed in the near future, can be constrained. Therewith, the possibility for a future ostracod biozonation in North America (possibly to be coupled with charophytes and/or vertebrates, i.e., mammals and dinosaurs) can be confidently proposed.

Higher maximum ages (upper Berriasian–lower Valanginian) have a wide array of considerable implications on the geology and paleontology of the Lower Cretaceous North American Western Interior foreland basin. Lower Cretaceous strata of pre-Aptian and even pre-Barremian age are definitely present in the basin. Resulting from the new maximum ages, the time interval represented by the hiatus separating nonmarine Upper Jurassic (Lower Berriasian?) and Lower Cretaceous rocks in the basin is reduced to about 5–10 million years for at least some formations (instead of 15–20 to about 35 million years). This affects the whole chronostratigraphic framework of the basin within the scope of its geologic development over time and in the context of the paleoecosystem it provided, and the age and evolution of the organisms that lived in these habitats.

The data presented in this thesis provide the basis for future research, constrain many remaining problems and thereby help to define future approaches and projects.

4. Conclusions and Perspectives

It is almost impossible to carry the torch of truth through a throng of people without singeing someone's beard.

Georg Christoph Lichtenberg (1742-1799)

4.1. Conclusions

Dated and inconsistent taxonomy was the main problem hampering the application of nonmarine Early Cretaceous ostracods of the North American Western Interior foreland basin. Any application can, however, only be as good as the taxonomy on which it is built. As a major result, it has been demonstrated that accurate, carapace-based ostracod taxonomy that is integrated with recent findings in ostracod biology and reproduction, provides an immense advance toward application and robust taxonomic and systematic discussion of these nonmarine ostracods in North America. Such taxonomy is only possible when based on accurate and consistent morphologic terminology and with consideration of the respective ostracod's paleobiology, paleoecology, and paleoenvironment. Prerequisite for this is the identification of the mode of significance of the morphologic characters under consideration, i.e., is the particular character taxonomically significant or not—and if not, is it of other significance, e.g. ecophenotypic or ontogenetic. A revision and clarification of the respective significances of many carapace characters facilitated fundamental progress in the taxonomy of the extinct genera *Theriosynoecum* and *Cypridea*, and some of their Early Cretaceous North American representatives. As far as can be overviewed at present, the Early Cretaceous ostracod fauna has, at species level, nothing in common with the Late Jurassic (to Early Berriasian?) fauna of the Morrison Formation.

This upgraded taxonomic concept is the key to 1), the understanding and evidence that the degree of endemism in these ostracods is not as high as erstwhile believed; 2), their successful application; and 3), the demonstration that the immense effort for taxonomic and systematic revision has proven worthwhile. The latter as well applies to the from the initial plans strongly modified approach that was developed during the progress of this thesis.

From the perspective of application, the consideration of the fact that taxonomy is also a tool that can be adjusted to specific purposes is of utmost importance. The adoption, reassessment, and application of the morphogroup-concept, developed for German representatives of *Cypridea* in the 1950s and successfully applied for biostratigraphic purposes, proved to be a powerful tool with great potential in North America in consideration of species-groups of *Cypridea*. As a side effect, such groups also have the potential to be easily identified and effectively applied by non-specialists in the future, after short training, and with low error rates.

Since much of the ostracod data are not usable for biostratigraphy in the available form, strong need exists for for better data documentation and knowledge management. With a view toward the future (quantitative analyses, databases and the electronic age of taxonomy) and to avoid repetitive (and costly) research programs, we need well-documented, traceable data from measured section and cores, the significance and reliability of which has, furthermore, to be critically evaluated. After a long time that was characterized by an increasing amount of specific publications, a comprehensive interdisciplinary overview and synthesis (as conducted herein, Publications Nos. 2, 3 and 4) becomes essential to stimulate the discussions and accelerate the scientific progress.

The studies presented here demonstrate and confirm that nonmarine Early Cretaceous ostracods are well applicable to improve the biostratigraphic age determination and chronostratigraphy of relevant formations of the North American Western Interior foreland basin. These ostracods have great potential to confirm or improve both intra- and interformational correlations throughout the basin. Being among the most common fossils in the deposits under consideration, due to their small size as well as their good distribution and preservation potential, the ostracods provide reliable data and are well suited and promising for a wider application.

New ostracod correlations strongly suggest a maximum age of Late Berriasian to Early Valanginian (~142–138 Ma) for the lower Lakota Formation (Chilson Member, southern Black Hills margin, South Dakota) and the lower part of the Cedar Mountain Formation (Yellow Cat Member, San Rafael Swell, Utah), if not older as for the Cedar Mountain Formation. Thereby, the time interval represented by the hiatus separating nonmarine Upper Jurassic (Lower Berriasian?) and Lower Cretaceous rocks in the North American W.I. foreland basin is reduced to well below 10 million years as to these formations. This as well implies higher maximum ages for their correlatives. A central issue in the controversial discussion about the chronostratigraphy of the basin is that throughout much of the literature, this regional unconformity seems to be widely assumed as being firmly established, and is, or was, rarely questioned within any geologic field of study. Stratigraphy and age determination of the nonmarine Western Interior foreland basin of North America remain controversial, but are now partly challenged based on ostracod evidence.

Implications of a higher maximum age of some Lower Cretaceous formations affect a wide scope of geologic and paleontologic topics in the context of the basin's structural and chronostratigraphic framework at smaller and larger scale. The evidence of the presence of deposits of Berriasian to Barremian age in the W.I. foreland basin consequently implies a longer depositional history in (at least parts of) the basin. That poses many questions as to the progressional development of the basin and a necessary re-calculation of temporal relationships between geologic processes and their sedimentary products, as well as their controlling factors (e.g. tectonics, climate). All these modifications have, in turn, consequences for the progressional development of the basin's paleoenvironments, and the paleogeographic and stratigraphic distribution and evolution of the organisms that occupied the paleoecosystems the basin provided. Everything stands and falls with the chronostratigraphic framework of the basin, and refinement of the chronostratigraphy is essential in order to progress the reconstruction of the basin and related processes and events.

Several distinct successive nonmarine ostracod faunas have been preliminarily identified in the Lower Cretaceous of North America that remain to be constrained and defined by means of upcoming research. Particularly concerning chronostratigraphic issues in the nonmarine North American Lower Cretaceous, ostracods are considered to be an excellent tool and to be regularly applied in the near future!

4.2. Perspectives

4.2.1. Taxonomy

Since this thesis has been composed with regard to the aspect of biostratigraphic utilization and application of the nonmarine North American Early Cretaceous ostracods, the taxonomic revision has, at present, been limited to the stratigraphically most important representatives of *Theriosynoecum* and *Cypridea*. Many other North American taxa remain to be revised or newly described, some of them are also considered to be of biostratigraphic or other use in the future. These comprise:

1) Representatives of the Trapezoidellidae (Cypridoidea): e.g. taxa of the genera *Trapezoidella*, *Limnocypridea*
2) Representatives of *Mantelliana* (Cypridoidea, Notodromadidae and/or Cyprididae)
3) Other representatives of the Cyprideidae (Cypridoidea): e.g. *Paracypridea*, *Bisulcocypridea*
4) Smooth and roundish ostracods that are not uncommon in the respective deposits and that have been largely ignored in the past and often (wrongly) designated species of *Candona*, or just mentioned under "candonids"

5) Representatives of the Darwinuloidea
6) Representatives of the Limnocytheridae (Cytheroidea): e.g. *Metacypris* (Timiriaseviinae), and (partially also newly discovered) representatives of the Limnocytherinae

The North American Lower Cretaceous (and Upper Jurassic) provides valuable information concerning the phylogeny of major ostracod groups, e.g. the Limnocytheridae, Cyprideidae, and Trapezoidellidae. Taking the upgraded taxonomic concept presented in parts of this thesis into account, its application to more North American taxa and similar considerable work input is considered worthwhile and expected to lead to similar progress in the taxonomy and the utilization of these ostracods. Since the upgraded taxonomic concept and the glossaries have now been elaborated and successfully tested, future research based on these will be more efficient (better defined approaches and partially lesser necessary work input).

Upcoming taxonomic revisions of North American Early Cretaceous nonmarine ostracods (and those of other continents) have to be conducted within the scope of a supraregional and/or global view. This is expected to reveal or confirm many faunal links to other continents and allow further applications based thereon (biostratigraphy, biogeography). Well-founded taxonomic revisions (like those conducted herein) allow the application of quantitative analyses, whether to test the taxonomy itself, or to conduct such analyses (e.g. assemblage analysis) for the purpose of further applications (paleoecology and others).

Starting from the new data regarding the taxonomic (in-)significance of carapace characters provided herein, the application of different methods of geometric morphometrics is hoped to become more efficient (selection of data to measure and analyze). The other way round, many of the hypothesis given (e.g. different modes of significance, different degrees of variation of characters, sexual dimorphism or synonymy of taxa), might be tested by morphometrics and statistics.

Based on the increased evidence of sexual dimorphism in *Cypridea* presented here, and the confirmed assumption that mixed reproduction was the most likely reproductive mode in its representatives, the taxonomy of most of these has to be reassessed and revised. This also implies significant consequences for the diversity, abundance, stratigraphic distribution and range, as well as the paleogeographic distribution patterns of these taxa. The hypothesis that representatives of *Cypridea* overwhelmingly dominated (with respect to diversity, not abundance) the world's latest Jurassic to Early Cretaceous nonmarine ostracod faunas remains to be reevaluated.

On the North American continent, taxonomic progress, which also includes taxa other than representatives of *Theriosynoecum* and *Cypridea*, is expected to allow a better constraint of the assumed successive Early Cretaceous faunal assemblages. It is also hoped to lead to the discovery of several more of these assemblages, particularly for Hauterivian–Barremian times. Another fundamental question to be posed is: what happened during the timespan represented by the hiatus separating Upper Jurassic (Early Berriasian?) and unconformably overlying Lower Cretaceous deposits throughout the basin? Since the Upper Jurassic Morrison Formation and the Lower Cretaceous formations have no ostracod taxa in common at or below species level (at present state of research) and no representative of *Cypridea* is known from the Morrison, the reasons for this faunal development have to be clarified and, in turn, it is hoped doing so will provide further information with regard to the duration of the timespan represented by the hiatus and its causes.

4.2.2. Methodology and Application

Analyses of the author's samples and material from collections led to the conclusion that our knowledge about the Early Cretaceous ostracod fauna of the North American Western Interior foreland basin is skewed and not complete by far. Owing to the fact that many of the Early Cretaceous nonmarine ostracods (e.g. most Cypridoidea) are of more than 1mm in length, some even up about

2.7mm, the smaller fraction of ostracods might have been partly, or even largely, overlooked in the past, either primarily due to the method of processing and analysis, or by exclusion of small or fragile taxa from the analyses and publications. More attention will have to be paid to cautious sample processing (in a chemical and mechanical sense) and the analysis of finer fractions (e.g. 250µm) to also obtain small as well as fragile ostracods, such as representatives of the Limnocytheridae, and, potentially, to also obtain specimens from limestones.

More material from measured and well-documented sections and cores is necessary to provide comprehensible data on the stratigraphic distribution of the ostracods in the Lower Cretaceous formations of the W.I. foreland basin. Particularly the numerous and comprehensive works of R.E. Peck have to be revised, reassessed and re-evaluated, an effort that would be highly rewarding.

The first major step towards the multifaceted, particularly biostratigraphic, application of Early Cretaceous nonmarine ostracods in North America has been made. Results of taxonomic revisions facilitate further research in the ostracod-based improvement of the W.I. foreland basin's Early Cretaceous chronostratigraphy. An application of ostracod biostratigraphy to other Lower Cretaceous formations of the basin in conjunction with other stratigraphic methods is expected to considerably improve the Lower Cretaceous nonmarine stratigraphy in the Western Interior by also providing a better chronologic framework and additional correlating ties, potentially for nonmarine-marine correlation in the northern and southern parts of the basin. Based on a refined biostratigraphy, ostracods are also expected to support the identification and justification of stratigraphic unconformities in the future. Combining the present state of research and presuming soon further progress regarding the ostracod taxonomy and stratigraphic distribution in North America, an ostracod biozonation of the nonmarine Lower Cretaceous is almost within reach, potentially in combination with charophytes and mammals or dinosaurs.

4.2.3. Summary

As has been satisfactorily demonstrated herein, the ostracods of the North American Western Interior foreland basin are of significant utility and have even greater potential with regard to a wide array of applications in the near future. We are just approaching the advent of ostracod application in the nonmarine Lower Cretaceous of North America. An upgraded taxonomy is the key to providing such base data, and the immense effort for taxonomic revision has proven, and is expected to remain, worthwhile. The revival and further development of Early Cretaceous ostracod biostratigraphy reinvigorates and stimulates the discussion of establishment of a refined chronostratigraphic framework of the W.I. foreland basin, with all associated consequences for the interpretation of its geology and paleontology. Concerning this issue, instead of taking long available data and interpretations as established, critical questions need to be asked and many hypotheses to be reassessed and tested for their probability and reliability. Ostracods are expected to become an important tool in this context. This is definitely not the last word on the subject but rather it is hoped to be the basis for fruitful future research!

5. References

"It seems that those who run the scholary publishing industry are unable to accept that someone can have an idea that does not originate from quotation."

Mihai Nadin, 1997. *The Civilization of Illiteracy.* Dresden University Press, p. 12.

Remarks: All references appearing in the thesis, including all of its chapters, manuscripts, and publications, as well as the figures, are given. For good scientific practice and as recommended to avoid confusion and additional effort for the reader, citations regarding the authors of taxa of higher taxonomic hierarchy levels are cited as well (in many publications this is just provided to the family level). The necessity for this can be demonstrated by one example:

In 1900, Alfred Kaufmann published four taxonomic articles on (freshwater) ostracods from Switzerland, only two of which are cited herein. The one cited here as Kaufmann (1900b) is the major work with over 200 pages, but there are some overlaps with the others which were published earlier. It seems probable that Kaufmann knew of the upcoming publication of G. W. Müller about freshwater ostracods of Germany, and he himself wanted to secure the rights to the taxonomic priorities with the three minor advanced publications (I thank E. K. Kempf, Universität Köln, pers. comm., July 2008, for pointing the details and history of this problem out to me). Anyway, with respect to the families Ilyocyprididae Kaufmann 1900(a) and Candonidae Kaufmann 1900(b), for example, the consequence is that Kaufmann's 1900 works are often confused in the literature and then difficult to comprehend.

Several systems are in use for the transliteration of Cyrillic letters into Roman characters, particularly leading to different quotations of many authors from countries of the former Soviet Union, the former Socialist Federal Republic Yugoslavia, the Republic of Bulgaria and Mongolia in the western literature. For practical reasons, the transliteration of authors and publication titles as used in Kempf's (1980 *et seqq.*) substantial database of Ostracoda and as commented in Kempf (1980d, p. 11), have been adopted.

Additionally, abbreviations are avoided in the reference list and references are given in as much detail as possible. Unpublished works (many U.S. American PhD and Master's theses) with relevant data are cited as well.

Since this is a cumulative thesis, some publications of the same author and year have been used in different combinations in the respective manuscripts or publications. For example: Manuscript 2.2 (Sames, B., Revision of the genus *Theriosynoecum* …) of this thesis cites Whatley (1990) only, which is listed as Whatley (1990b) in the cumulative reference list given below because two different publications of Whatley (1990a, 1990b) had to be cited altogether. In case of doubt, this is indicated with a note in brackets "[ ]" in the reference list below, i.e., the citation of Whatley (1990b) is followed by the note "[given as Whatley 1990 in Publication No. 2, Chapter 2.2 herein]".

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Appendix

Abstracts Related to the Project

(in chronologic order)

1) SAMES, B., 2004. Ostracoda der nichtmarinen Unterkreide des U. S. Western Interior: Biostratigraphie, Paläoökologie, Biogeographie und Phylogenie. In: Reitner, J., Reich, M. and Schmidt, G., Eds. *Geobiologie 2*. 74. Jahrestagung der Paläontologischen Gesellschaft, Göttingen 02.-08. Oktober 2004 – Exkursionen und Workshops. Göttingen, Universitätsverlag Göttingen: 249-250. (Poster)

In Zusammenarbeit mit Forschungsprojekten am Sam Noble Oklahoma Museum of Natural History (Leitung: Richard L. Cifelli), hauptsächlich über die Evolution früher Säugetiere, werden nichtmarine Ostracoda (und Charophyta) der unterkretazischen Lakota Formation (Black Hills, South Dakota und Wyoming), Cloverly Formation (Bighorn Basin, Wyoming und Montana) sowie Cedar Mountain Formation (Utah) untersucht. Bisher gibt es zur genauen Alterstellung dieser Formationen nur wenige, sehr unterschiedliche Aussagen. Auch wenn sie traditionell als stratigraphisch äquivalent angesehen werden, sind, wegen ihrer lithologischen Komplexität (starker lateraler und vertikaler Fazieswechsel), lithostratigraphische Korrelationen innerhalb und zwischen den Formationen nur beschränkt möglich oder erfolgreich. Bisherige radiometrische Altersdaten sind zu ungenau, um zur Diskussion der Altersstellung beizutragen. Biostratigraphie ist als chronologisches Werkzeug bis heute ebenfalls nur begrenzt nutzbar, denn Fossilien sind relativ selten und werden als endemisch angesehen. Dazu kommt, dass Altersangaben aufgrund verschiedenen Fossilmaterials widersprüchlich sind. Zusätzlich sind viele Publikationen, gerade auch über Ostracoda und Charophyta, zumeist weit älter als 25 Jahre und fallen damit in einen Zeitraum, in dem die Stufendefinitionen der Unterkreide in Europa und Nord Amerika ständigen Veränderungen unterlagen. Eine Stufenzuordnung der genannten Formationen ist immer noch sehr unsicher. Das maximale und minimale Alter („Neokom" bis Mittel-Albium) ist gegeben durch die oberjurassische Morrison Formation, auf der die Lakota-, Cloverly- und Cedar Mountain Formationen diskordant auflagern und marinen Sedimenten der Mittel-Albium-Transgression.

Zielstellungen dieses Projektes sind deshalb: a) eine Verbesserung der biostratigraphischen Einstufungen einiger wichtiger Formationen der nichtmarinen Unterkreide im U.S. Western Interior, b) Beiträge zu deren genaueren paläoökologischen Interpretationen, c) die hierzu notwendigen Verbesserungen in der systematischen Erfassung der relevanten Ostracodenfaunen, d) eine biogeographische Analyse und Interpretation dieser Faunen im überregionalen Kontext, e) die hierzu notwendigen Vergleiche der nordamerikanischen Taxa mit gleichalten Faunen in Europa (England, Spanien, NW-Deutschland) und f), als Fernziel, Beiträge zur Interpretation der Evolution spezieller Gruppen, wie der Cyprideidae und Timiriaseviinae, im Zusammenhang mit plattentektonischen und paläoklimatischen Entwicklungen und den jeweiligen Fortpflanzungs- und Ausbreitungsmechanismen. Zentrale Rolle bei stratigraphischen Auswertungen nehmen dabei die *Cypridea*-Gemeinschaften ein, denn speziell für diese Gruppe (wie auch für andere Cypridacea) ist zweifelhaft, ob in den USA nur endemische Formen existieren, wie von früheren Bearbeitern angenommen wurde. Für Oberjura-Formen (Cypridacea) der Morrison Formation zum Beispiel wurde in den 90-er Jahren nachgewiesen, dass zahlreiche Arten auch auf der Iberischen Halbinsel sowie in Mitteleuropa vorkommen. Schließlich hat (und hatte) ein Großteil der Cypridacea-Arten die Möglichkeit, sich sehr schnell und über weite Entfernungen (mit Jet Streams auch über Ozeane hinweg) auszubreiten.

2) SAMES, B., 2005. Ostracoda of the nonmarine Early Cretaceous of the U.S. Western Interior (Lakota, Cloverly and Cedar Mountain formations). Biostratigraphy and palaeogeography - A preliminary report. In: Godet, A., Mort, H. and Bodin, S., Eds. 7th International Symposium on the Cretaceous, Neuchatêl, Switzerland, 5-9 September 2005 - Scientific Program and Abstracts: 188. (Poster)

In cooperation with research projects at the Sam Noble Oklahoma Museum of Natural History, mostly about vertebrate (early mammal) evolution, Ostracoda (and Charophyta) from the Lakota Formation (Black Hills, South Dakota/Wyoming – main focus), Cloverly Formation (Wyoming/Montana) and Cedar Mountain Formation (San Rafael Swell, Utah) are examined. The primary objectives are: an improvement of the systematic record and a taxonomic revision of some North American nonmarine ostracode faunae for the purpose of improving the biostratigraphic age determination of the mentioned formations. Age determination of the nonmarine Early Cretaceous formations in the U.S. Western Interior is still a problem. Lithologic heterogenity (strong lateral and vertical facies change) limits lithostratigraphic correlation, formation contacts are problematic and their continuous redefinition by various authors has created a lot of nomenclatural problems. The situation is further complicated by intra- and inter-formational unconformities associated with localized structural deformation. In addition there is the problem of a poor absolute age control. Several attempts using surface and subsurface lithostratigraphic correlation techniques integrated with magnetostratigraphy, fission track and Ar^{40}/Ar^{39} dating had limited success. Finally, biostratigraphy as chronologic tool is limited up to now because fossils are more or less scarce and considered to be endemic, most biostratigraphic publications are dated and the ostracode groups involved are taxonomically complex and/or problematic.

That is the starting point of the project. Ostracodes (and charophytes) are partially very common within the North American formations mentioned and there is a good ostracode zonation existing in the European nonmarine Early Cretaceous of England, NW Germany and Spain. Through new perceptions in ostracode biology (reproduction and dispersal mechanisms) and palaeontology (biostratigraphic record), a faunal connection between North America and Europe seems to be most probable. This assumption is supported eminently, because such connections have been proven for the nonmarine Late Jurassic Morrison Formation which underlies many Early Cretaceous formations in the U.S. Western Interior. Thus, based on new data (including own material) a detailed taxonomic revision and faunal comparision with other continents (mainly Europe) shall result in utilising the nonmarine Early Cretaceous ostracodes of North America for biostratigraphy, and the application of the results on some formations as initial step. An integration of and calibration with charophytes is part of the project, too.

Fieldwork, sample processing and SEM-work results are promising so far: nearly the whole succession of the Lakota Formation (all members, including the very base) could be sampled. Commonly, the specimens are well preserved. A faunal development is recogniseable and seems to represent an evolutionary progression, as far as one can say by now.

3) SAMES, B., 2005. Revision of nonmarine Early Cretaceous Ostracoda of the U.S. Western Interior - Is there a chance of biostratigraphic utilisation? - A preliminary report. In: Kohring, R. and **Sames, B.**, Eds. 15th International Symposium on Ostracoda, Berlin, September 12-15, 2005 - Program and Abstracts. *Berliner Paläobiologische Abhandlungen*, 6: 102-103. (Poster)

For a long time, ostracodes of the nonmarine Early Cretaceous in North America have been considered as endemic. But within the last 20 to 30 years it became clear, that faunal connections between North America and other continents seem to be probable. New perceptions in ostracode biology (reproduction and dispersal mechanisms) and palaeontology (biostratigraphic record) result in the hypothesis that a faunal connection between North America and Europe (besides other continents) is very likely. This assumption is reinforced eminently, because in the 1990's such connections have been proven for the nonmarine Late Jurassic Morrison Formation which underlies many Early Cretaceous formations in the U.S. Western Interior (see Schudack et al. 1998). Taxonomic problems, complexity of contemplated ostracode groups, less infomation and misinterpretation seem to have been the escrow issues in the past.

Among others, the main groups concerned are the *Cypridea*-lineage and the *Bisulcocypris*/*Theriosynoecum*-Group (both Cypridoidea), which enclose many species usable for biozonation in the British Purbeck and Wealden, for instance (see the publications of F.W. Anderson and Horne, 1995 and 2002). Based on the fact that species of the *Cypridea*-lineage are deemed to have had mixed reproductive strategies with a high asexual (parthenogenetic) rate and their desiccation resistant eggs are assumed to have been distributed by wind (and/or animals) easily, it seems to be very implausible that this should not have happend several times within a timespan of about 40 Ma. Thus, based on new data (including own material) a detailed taxonomic revision and faunal comparision with other continents (mainly Europe) shall result in utilising the nonmarine Early Cretaceous ostracodes of North America for biostratigraphy. The application of the results on certain formations (Lakota Formation, Black Hills, South Dakota/Wyoming – main focus; Cloverly Formation, Wyoming/Montana and Cedar Mountain Formation, San Rafael Swell, Utah) shall be an initial step. Where applicable, an integration of and calibration with charophytes is part of the project, too. The project is carried out in cooperation with research projects at the Sam Noble Oklahoma Museum of Natural History, mostly about vertebrate (early mammal) evolution and funded by the DFG (German Science Foundation - Schu 694/14-1 and 14-2).

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4) SAMES, B. and MADSEN, S. K., 2007. Ostracod evidence of a Berriasian Age for the lower Yellow Cat Member of the Cedar Mountain Formation, Utah. *Geological Society of America Abstracts with Programs*, 39(5): 10. (Poster)

As part of a research project (German Science Foundation, M.E. Schudack, Freie Universität Berlin, in cooperation with Richard L. Cifelli, Sam Noble Oklahoma Museum of Natural History), Lower Cretaceous ostracods of the U.S. Western Interior were taxonomically revised and applied to biostratigraphy of the Cedar Mountain Formation (CMF). A sample from within the Yellow Cat Member of the CMF near the type locality of the Poison Strip Member northeast of Arches National Park, revealed a moderately diverse ostracod fauna consisting of at least four taxa of *Cypridea* Bosquet, an important index taxon in sediments of Purbeck/Wealden-like facies worldwide. All of these taxa occur in the Berriasian (145.5±4.0 to 140.2±3.0 Ma) of the English upper Purbeck Group (Durlston Formation) and lower Wealden Series (lower Ashdown Formation), and three of them in the Berriasian of NW Germany. Three of the four taxa are restricted to the Berriasian, the remainder occurs from the Berriasian to the Valanginian. Therefore, a Berriasian age of part of the Yellow Cat is most probable. A second sample from a site in central Yellow Cat exposures that produced Tithonian-Berriasian age palynomorphs, contained poorly preserved ostracods; one species could be identified that also occurs in the first sample and is restricted to the Berriasian in English Purbeck/Wealden deposits. New evidence inferred from ostracods strongly suggests that the lower part of the Cedar Mountain Formation is of Berriasian age, and considerably older than other published lines of evidence have indicated.

5) SAMES, B. and MADSEN, S. K., 2007. Ostracod evidence of a Berriasian Age for the lower Yellow Cat Member of the Cedar Mountain Formation, Utah – An example for biostratigraphy in Lower Cretaceous nonmarine deposits of the U.S. Western Interior. In: Elicki, O. & Schneider, J.W. (Hrsg.): Fossile Ökosysteme 77. Jahrestagung der Paläontologischen Gesellschaft, Freiberg, 17.-19.9.2007 – Kurzfassungen der Vorträge und Poster. *Wissenschaftliche Mitteilungen des Institutes für Geologie der TU Bergakademie Freiberg*, 36: 119. (Poster)

As part of a research project (German Science Foundation, M.E. Schudack, Freie Universität Berlin, in cooperation with Richard L. Cifelli, Sam Noble Oklahoma Museum of Natural History), Lower Cretaceous ostracods of the U.S. Western Interior were taxonomically revised and applied to biostratigraphy of the Cedar Mountain Formation (CMF). A sample from within the Yellow Cat Member of the CMF near the type locality of the Poison Strip Member northeast of Arches National Park, Utah, revealed a moderately diverse ostracod fauna consisting of at least four taxa of *Cypridea* Bosquet, an important index taxon in sediments of Purbeck/Wealden-like facies worldwide. All of these taxa occur in the Berriasian (145.5 ± 4.0 to 140.2 ± 3.0 Ma) of the English upper Purbeck Group (Durlston Formation) and lower Wealden Series (lower Ashdown Formation), and three of them in the Berriasian of NW Germany. Two of the four taxa are restricted to the upper Berriasian/lowermost Valanginian, the remainder occur from the Berriasian to the Valanginian. Therefore, a Berriasian age of part of the Yellow Cat is most probable. A second sample from a site in central Yellow Cat exposures that produced Tithonian-Berriasian age palynomorphs contained poorly preserved ostracods; one species could be identified that also occurs in the first sample and is restricted to the Berriasian/lowermost Valanginian in English Purbeck/Wealden deposits. New evidence inferred from ostracods strongly suggests that the lower part of the Cedar Mountain Formation is of Berriasian age, and considerably older than other published lines of evidence have indicated. This example clearly demonstrates that in contrast to erstwhile assumptions, a biostratigraphy with nonmarine ostracods based on supraregional correlations is applicable to Lower Cretaceous formations of the U.S. Western Interior.

6) SCHUDACK, M., WHATLEY, R. and **SAMES, B.**, 2007. Ursprung und frühe Evolution (Trias bis Kreide) der nichtmarinen Cypridoidea (Süßwasserostracoden). In: Elicki, O. and Schneider, J. W., Eds. Fossile Ökosysteme. 77. Jahrestagung der Paläontologischen Gesellschaft, Freiberg, 17.-19.9.2007 – Kurzfassungen der Vorträge und Poster. *Wissenschaftliche Mitteilungen des Institutes für Geologie der TU Bergakademie Freiberg*, 36: 119. (Talk by BS)

Die Cypridoidea stellen heute die arten- und individuenreichste Gruppe (Überfamilie) von Süßwasserostracoden dar. Ihre Entstehungsgeschichte, vor allem die Frühphase, ist allerdings noch sehr umstritten, was zumeist daran liegt, dass die genaue systematische Stellung anhand der Kalkschalen wohl definierter Gattungen im durch „Weichteile" definierten taxonomischen System der Ostracoden oft schwer nachzuweisen ist. Hinzu kommen große Überlieferungslücken bzw. eine noch zu geringe Funddichte in vielen Zeitscheiben und auf vielen Kontinenten. Hier wird ein Überblick über den noch sehr lückenhaften, in den letzten Jahren allerdings etwas verbesserten Kenntnisstand zu Ursprung und Frühevolution der zu den nichtmarinen Cypridoidea gehörenden, heute ausgestorbenen Familie der Cyprideidae gegeben. Vielen mit der Kreidezeit vertrauten Paläontologen ist die Familie durch die besonders in den nichtmarinen Ablagerungen der Unterkreide häufige und artenreiche Gattung *Cypridea* bekannt, die in diesen Gesteinen auch stratigraphisch sehr wichtig ist. Diese an ihrem Rostrum (anteroventraler „Schnabel“) leicht kenntlichen Formen haben zur Zeit der Jura/Kreide-Wende eine geradezu explosive Radiation durchgemacht, vermutlich bedingt durch eine Kombination intrinsischer (Erwerb von Schwimmfähigkeit, austrocknungsresistenten Eiern und parthenogenetischer Fortpflanzung, sicherlich aber auch noch weiterer, bis dato unbekannter Weichteilmerkmale) und extrinsischer (Zerfall Pangäas in kleinere Einzelkontinente, Umstellung der Windsysteme von meridional auf zonal und Etablierung planktonreicherer Binnenseen) Faktoren. Die Cyprideidae, zu denen neben *Cypridea* noch wenige weitere Gattungen gehören, sind mit dem Paläogen ausgestorben und nach herkömmlicher Vorstellung erst im späten Oberjura (Tithonium) entstanden.

Hier stellen wir nun nicht nur stratigraphisch etwas ältere *Cypridea*-Funde, sondern auch eine direkte Vorläufergattung mit noch nicht so stark ausgeprägtem Rostrum (Cyprideidae gen. nov.) aus dem Oberjura von Nordamerika, Afrika und Europa sowie aus dem Mitteljura von Südfrankreich vor. Diese erweitern die Frühgeschichte der Cyprideidae auf jeden Fall bis in das Bajocium. Weitere, den Cypridoidea zumindest nahe stehende Faunen, deren Zugehörigkeit zu dieser Gruppe noch diskutiert wird, sind aus dem Unterjura von Südamerika und – weiter verbreitet – der Trias von Südamerika und Asien bekannt geworden. Derzeit wird aber angenommen, dass dies nicht die Vorläufer der späteren Cyprideidae sind, sondern dass diese sich unabhängig von den Trias- und Unterjura-Vertretern nach einer weiteren, eigenständigen „Invasion“ des Süßwassers im Bajocium bis Bathonium (Mitteljura) entwickelt haben. Grundproblem ist hierbei aber der immer noch sehr lückenhafte Kenntnisstand. Spekulativ ist folgendes Szenario: Trotz wiederholter Entstehung solcher Süßwasserfaunen in Trias, Unterjura und Mitteljura kam es wegen der damals noch bevorzugten meridionalen Windsysteme (Pangäa-Megamonsun) zu keiner nennenswerten Radiation, da diese durch Wind verbreiteten Formen die großen Wüstengebiete nur schlecht „überqueren“ konnten. Erst mit der Etablierung der heute noch existierenden, bevorzugt zonalen Windsysteme im späteren Oberjura (Jet Streams) konnten sich die Cypridoidea auf Nord- und Südhalbkugel (hier aber noch mit extrem schlechtem Kenntnisstand) durchsetzen, wobei es seitdem nur noch geringe Beziehungen zwischen beiden Hemisphären gibt.

7) **SAMES, B.**, SCHUDACK, M. and CIFELLI R., 2008. Western Interior Early Cretaceous hiatus likely to be much shorter than previously reported—new biostratigraphic results derived from nonmarine ostracod correlations. *Geological Society of America Abstracts with Programs*, 40(6): 540. (Talk by BS)

The timespan represented by the unconformity separating nonmarine Upper Jurassic and Lower Cretaceous rocks in the North American Western Interior foreland basin is controversial and has been under discussion for decades. Despite an integration of different geological, geophysical, and paleontological methods, there has been no major breakthrough regarding the age determination during the last fifteen years—particularly the maximum age—of Lower Cretaceous nonmarine formations in the U.S. Western Interior. Time intervals ranging from at least 15–20 up to 35 Ma have been given, according to assumed ages of middle Albian to Barremian for these. In particular, the usage of the term Neocomian and the difficulty in determining exactly the age of the unconformity surface of the Morrison Formation may have intensified inconsistencies.

As part of a joint research project, Lower Cretaceous ostracods (microcrustaceans with a calcified shell) of the Lakota (Black Hills, SD) and Cedar Mountain formations (San Rafael Swell, UT) were taxonomically revised and tested for their potential for biostratigraphical application. Despite some remaining taxonomical problems, a supraregional correlation with well dated contemporary European strata strongly suggests that the most probable maximum age of the lower part of both these formations is upper Berriasian to lowermost Valanginian, and therefore considerably older than other published lines of evidence have indicated. Thereby, the Upper Jurassic-Lower Cretaceous hiatus would be reduced to a time interval less than 10 Ma, if not less than 5 Ma. However, that is not the end of the matter. Ostracods are considered to have the potential to improve both intra- and interformational correlations, and along with an integration with other stratigraphical methods and an application of ostracod biostratigraphy to other formations, it is possible to further improve the Lower Cretaceous stratigraphy in the Western Interior.

8) SAMES, B., SCHUDACK, M. and CIFELLI R., 2008. Ostracod evidence for an Berriasian to Valanginian maximum age of some nonmarine Formations in the U.S. Western Interior Foreland Basin—Early Cretaceous hiatus likely to be shorter than previously reported. *Geological Society of America Abstracts with Programs*, 40(6): 374. (Poster)

The taxonomic revision of nonmarine Lower Cretaceous ostracods (microcrustaceans with a calcified shell) of the Cedar Mountain (San Rafael Swell, Utah) and Lakota (Black Hills, South Dakota) formations led to their successful application to biostratigraphy and an improvement of the age determination of these units. It can be demonstrated that these ostracods are not as endemic as formerly presumed. Therefore, based on intercontinental correlations of representatives of the genera *Theriosynoecum* and *Cypridea*, two important ostracod index taxa in Lower Cretaceous nonmarine sediments worldwide, many North American taxa can be tied to well dated contemporary European strata ('Purbeck/Wealden' of England, UK, NW Germany, and Spain). Therefore, a Berriasian to lowermost Valanginian maximum age of the lower part of both the Cedar Mountain and Lakota formations is most probable. Regarding the Cedar Mountain Formation, the results are also supported by palynomorphs. This new evidence leads to the conclusion that the Upper Jurassic-Early Cretaceous hiatus in the Western Interior foreland basin is much likely to be considerably shorter than most published results (15-35 Ma, upper Tithonian to Barremian-middle Albian) have indicated, i.e., not longer than 10 Ma and perhaps below 5 Ma. Many other Lower Cretaceous formations in the Western Interior basin are likely to have a much higher maximum age as well. Furthermore, the ostracods also have the potential to improve intra- and interformational correlations and a further biostratigraphical subdivision of the particular units. An integration with other chronostratigraphic methods and an application of ostracod biostratigraphy to other Lower Cretaceous formations are hoped to further contribute to the controversial discussion about the age of these formations and to improve the nonmarine Lower Cretaceous stratigraphy in the Western Interior.

9) SAMES, B., CIFELLI, R. L. and SCHUDACK, M. E., 2009. A breakthrough in ostracod biostratigraphy and the "twilight zone" of early mammals in North America: News from the nonmarine Lower Cretaceous of the Western Interior foreland basin. *79. Jahrestagung der Paläontologischen Gesellschaft*, Bonn, 5.-7. Oktober 2009. (Talk by BS)

The timespan represented by the unconformity separating nonmarine Upper Jurassic (Morrison Formation in the U.S.A., may extend into the Berriasian; Kootenay Formation in Canada) and Lower Cretaceous rocks in the North American Western Interior foreland basin has been under discussion for the entire 20th century, and remains controversial to date. Time intervals ranging from at least 15–20 up to 35–40 million years have been given, according to assumed maximum ages of Middle Albian (~108 Ma) to Barremian (Hauterivian?) for Lower Cretaceous formations and Early Tithonian (~148 Ma) minimum age of the Morrison Formation. At the same time there has been continual, major scientific interest in the Lower Cretaceous formations insofar as they document the early development of both the world's largest foreland basin and the coevolving eastern Cordillera, as well as the enormous continental ecosystem it comprised. In this context, the maximum age of Lower Cretaceous formations and the coinciding duration of the hiatus' time period are of particular concern.

Ongoing studies demonstrate and confirm that nonmarine Early Cretaceous ostracods—as well as those from the Late Jurassic—have great utility in improving the biostratigraphic age determination for relevant formations of the North American Western Interior foreland basin. Key to their successful application is an upgraded taxonomic concept, together with the understanding and evidence that these ostracods are not endemic as erstwhile believed. New ostracod correlations strongly suggest a maximum age of Late Berriasian to Early Valanginian (~142–138 Ma) for the lower Lakota Formation (South Dakota and Wyoming) and the lower Cedar Mountain Formation (Utah), if not greater for the Cedar Mountain Formation, and these results are partially supported by mammal and palynologic evidence. Hence, the time interval represented by the hiatus separating nonmarine Upper Jurassic (Early Berriasian?) and Lower Cretaceous rocks in the Western Interior foreland basin of North America is reduced to about 10 million years (or less) for the relevant formations. Implications of these results affect the correlatives of these formations and therewith a wide scope of geologic and paleontologic topics (e.g. early mammal, dinosaur and angiosperm fossil record and evolution) in the context of the basin's structural and chronostratigraphic framework.

Microvertebrates including mammals, not hitherto reported for any North American rocks older than Aptian-Albian and younger than Tithonian, are now represented by a small assemblage from the lower part of the Lakota Formation. Results corroborate the revised biostratigraphic interpretation based on nonmarine ostracods. While new at the genus and species levels, the mammalian taxa show close affinity with those from the underlying Morrison Formation (and with the Purbeck/Wealden of Britain) rather than later Cretaceous North American forms, including, for example, last appearances of Amphilestidae, Dryolestidae, and plagiaulacoid-grade multituberculates.

Curriculum Vitae

The curriculum has been omitted from the online-version for the reason of data privacy protection.