

**The internal structure of growth interruptions and the dorsal  
shell wall of Mesozoic ammonoids and its phylogenetic and  
taxonomic implications**

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*“Pleasure to me is wonder —  
the unexplored, the unexpected,  
the thing that is hidden and the changeless thing  
that lurks behind superficial mutability.”*

H. P. Lovecraft, American author



**Abstract**

The structure of pristine preserved shells of Mesozoic (Triassic-Cretaceous) ammonoids was examined in order to identify whether there are homologous or homoplastic traits in the internal structure and morphogenesis of the shell wall that can be used for phylogeny and taxonomy, particularly in regard to episodic growth interruptions and the dorsal shell wall.

Different sculptural elements that are usually associated with an interruption in shell growth were analysed to determine whether these have a general ground plan and/or have sculpture- or taxa-specific variations in internal structure. These sculptural elements are varices, constrictions, megastriae such as flares and parabolae, and radial lirae. The internal structure of the varices and constrictions shows no interruptions in shell growth, which implies that varices and constrictions were formed by continuous secretion. The absence of an interruption in shell secretion differs from the well-examined nepionic constriction of the ammonitella. The internal thickenings of varices and constrictions are formed by the nacreous layer and probably subsequent to the formation of a distinct aperture, e.g. furrows or ridges, i.e. not at the same time the aperture is formed. Morphological transition from smooth-shelled varices to ridged or constricted appearance proves to be a homology. Owing to the general structural conformity of varices and constrictions in the shells of Jurassic and Cretaceous taxa, this study supports the theory that they are homologous traits. Flares, parabolae and radial lirae are characterized by an interruption in growth, they mark the succession of two different shell generations, which is similar to the nepionic constriction. New shell is attached from within after withdrawal of the shell-secreting mantle. It is likely that parabolae and flares represent different expressions of a homologous structure. Both mark an interruption of shell growth caused by the formation of a frill-like, outwardly bent temporary aperture, but differ in their general shape. The frill of the parabolae is folded and forms ventrolateral parabolic notches and nodes. A frilled aperture is built by the outer prismatic layer, the nacreous layer and an apertural prismatic coating. The apertural prismatic coating indicates a permanent mantle cover during a resting stage after formation of the frill. Probably parabolae and radial lirae are homologous, but differ in internal structure. Radial lirae are formed by imbrication of two successive sigmoid shell lamellae, formed either by the organic periostracum, as in *Phylloceratinae*, or the outer prismatic layer, as in *Aspidoceratinae*. Each lira has a characteristic adorally-projecting, scythe-like appendage arising from its crest, i.e. an enlargement of a temporary aperture as well.

Mesozoic Ammonoidea had different construction and formation types of the dorsal shell wall. The vast majority of planispirally coiled Ammonoidea forms a prismatic reduced dorsal shell

wall, i.e. the dorsal shell wall consists of a primary built outer organic component (e.g. wrinkle layer, spiral ornament) and the subsequent formed dorsal inner prismatic layer. The dorsal inner prismatic layer is only secreted in the rear of the living chamber, probably in association with the formation of the septa. The outer organic component has a diverse appearance (e.g. wrinkle layer, coating layer, spiral ornament, spherulithic-prismatic layer) but derives from a simple wrinkle layer in ontogeny. Reduced dorsal shell wall construction of Ammonoidea is generally homologous and exists in the early ontogenetic stages of all taxa. Rather few ammonoid taxa reinforce the dorsal shell wall. At least Stephanoceratoidea, Perisphinctoidea, Desmoceratoidea and Deshayesitoidea had the ability to form a nacreous reduced dorsal shell wall in the rear part of the living chamber, which is reinforced by secondary pair of nacreous and inner prismatic layers. It is morphogenetically identical with a shell doubling of ventral and lateral shell portions. Heteromorph taxa, i.e. secondarily decoiled, and some planispirally coiled taxa of Lytoceratoidea, Eoderoceratoidea, Stephanoceratoidea, Perisphinctoidea, Haploceratoidea, Desmoceratoidea, Hoplitoidea and Douvilleiceratoidea, secrete a complete dorsal shell wall at the aperture, i.e. the ventral, lateral and dorsal shell wall form a continuum aperturally and adapically. The dorsal shell layers are identical with the ventral shell wall. The broad phylogenetic distribution of dorsally secreted nacre indicates a plesiomorphic relic trait of the orthocone ammonoid ancestors. Every ammonoid probably had the ability to form nacre dorsally or even a complete dorsal shell wall.

### **Zusammenfassung**

In dieser Studie wurde die Struktur von hervorragend erhaltenen Schalen mesozoischer (Trias-Kreide) Ammonoideen untersucht, um zu ermitteln, ob der interne Aufbau und die Morphogenese der Schalenwand homologe oder homoplasische Eigenschaften aufweist, die für die Phylogenie und Taxonomie angewendet werden können; im Speziellen bei episodischen Wachstumsunterbrechungen und bei der dorsalen Schalenwand.

Verschiedene Skulpturelemente, die für gewöhnlich mit einer Unterbrechung des Schalenwachstums assoziiert werden, wurden daraufhin untersucht, ob diese einem generellen Grundbauplan folgen und/oder skulptur- oder taxonspezifische Variationen der internen Struktur aufweisen. Dies sind Varizen, Einschnürungen, Megastriae, wie Krägen und Parabelrippen, und radiale Lirae. Die interne Struktur von Varizen und Einschnürungen zeigt keine Unterbrechungen im Schalenwachstum, was darauf hinweist, dass diese durch eine kontinuierliche Sekretion gebildet wurden. Das Fehlen einer Sekretionsunterbrechung unterscheidet sich vom internen Aufbau der gut untersuchten nepionischen Einschnürung der Ammonitella. Die internen Verdickungen von Varizen und Einschnürungen werden von der Perlmuttertschicht gebildet und wahrscheinlich erst nach der Ausbildung einer Mündung, z.B. als Furchen oder Wülste, angelegt; also nicht zeitgleich mit der Mündung. Morphologische Übergänge von Varizen mit glatter Schalenoberfläche zu Varizen mit äußeren Wülsten oder Einschnürungen mit einer äußeren Furche belegen die Homologie der drei Erscheinungsformen. Aufgrund der generellen strukturellen Übereinstimmung von Varizen und Einschnürungen in den Schalen jurassischer und kretazischer Taxa, kann angenommen werden, dass es sich um homologe Strukturen handelt. Für Krägen, Parabelrippen und radiale Lirae ist eine Unterbrechung des Schalenwachstums charakteristisch. Diese Skulpturelemente markieren die Abfolge zweier verschiedener Schalengenerationen, ähnlich der Konstruktion der nepionischen Einschnürung. Nach einem Zurückziehen des schalenbildenden Mantels wird neues Schalenmaterial von innen angesetzt. Es ist anzunehmen, dass Parabelrippen und Krägen verschiedene Ausprägungen einer homologen Struktur sind. Beide bilden eine kragenartige, nach außen gestülpte Erweiterung einer interimistischen Mündung, die mit einer Unterbrechung des Wachstums einherging. Sie unterscheiden sich aber in ihrer äußeren Gestalt; die kragenartige Erweiterung der Parabelrippen war gefaltet und bildet ventrolaterale Parabelsinuse mit Parabelknoten. Parabelrippen und Krägen werden aus der äußeren Prismenschicht, der Perlmuttertschicht und einer aperturalen Prismenschicht gebildet. Die aperturale Prismenschicht weist auf eine andauernde Anheftung des Mantels während der Ruhephase nach der Bildung der Mündung hin. Wahrscheinlich sind Parabelrippen und radiale Lirae ebenfalls homologe

Strukturen, unterscheiden sich aber in ihrer internen Struktur. Radiale Lirae entstehen durch die Imbrikation zweier sigmoider Schalenlamellen. Diese werden entweder vom organischen Periostrakum geformt, wie bei den Phylloceratinae, oder nur durch die äußere Prismenschicht, wie bei den Aspidoceratinae. Jede Lira besitzt einen charakteristischen adoralen, sensenartigen Fortsatz, der dem Scheitel der Lirae entspringt; d.h. auch hier findet eine Vergrößerung der Mündung statt.

Mesozoische Ammonoideen besaßen unterschiedliche Typen des Aufbaus und der Bildung der dorsalen Schalenwand. Der Großteil der planspiral aufgerollten Ammonoideen bildete eine prismatische reduzierte dorsale Schalenwand, d.h. die dorsale Schale besteht aus einer äußeren, organischen Komponente (z.B. Runzelschicht, Spiralornament), die zuerst angelegt wird, und der später gebildeten dorsalen inneren Prismenschicht. Die dorsale innere Prismenschicht wird nur im hinteren Teil der Wohnkammer angelegt, wahrscheinlich im Zusammenhang mit den Kammerscheidewänden. Die äußere, organische Komponente kann sehr verschieden ausgebildet sein (z.B. Runzelschicht, 'Coating layer', Spiralornament, sphärolitsch-prismatische Schicht), lässt sich aber innerhalb der Ontogenie auf eine einfache Runzelschicht zurückführen. Der Aufbau der reduzierten Dorsalschale der Ammonoideen ist generell als homolog zu betrachten. Nur wenige Ammonoideentaxa verstärken die dorsale Schalenwand. Zumindest Stephanoceratoidea, Perisphinctoidea, Desmoceratoidea und Deshayesitoidea hatten die Möglichkeit, eine perlmuttige reduzierte dorsale Schalenwand in den hinteren Bereichen der Wohnkammer auszuscheiden, die verstärkt wird durch eine zusätzliche sekundäre Permuttschicht und innere Prismenschicht. Diese ist morphogenetisch identisch mit einer Schalenverdopplung der ventralen und lateralen Schalenbereiche. Heteromorphe Taxa, d.h. sekundär entrollte, und auch einige planspirale Taxa der Lytoceratoidea, Eoderoceratoidea, Stephanoceratoidea, Perisphinctoidea, Haploceratoidea, Desmoceratoidea, Hoplitoidea und Douvilleiceratoidea bilden eine komplette dorsale Schalenwand an der Apertur, d.h. die ventrale, laterale und dorsale Schalenwand bilden ein Kontinuum, sowohl apertural als auch apikal. Die dorsalen Schalenlagen sind identisch mit denen der ventralen Schalenwand. Die weite phylogenetische Verteilung von dorsal gebildetem Perlmutter weist auf eine plesiomorphe Eigenschaft hin, die ihren Ursprung in den orthoconen Vorfahren der Ammonoideen hat. Möglicherweise hatte jeder Ammonoid die Fähigkeit Perlmutter in den dorsalen Schalenpartien zu bilden oder sogar eine komplette dorsale Schalenwand.





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**List of abbreviations**

<b>apc</b>	—	<i>apertural prismatic coating</i>
<b>c</b>	—	<i>complete dorsal shell wall</i>
<b>C, con</b>	—	<i>constriction</i>
<b>cl</b>	—	<i>coating layer</i>
<b>D</b>	—	<i>diameter</i>
<b>dipl</b>	—	<i>dorsal inner prismatic layer</i>
<b>dipl 1/2</b>	—	<i>primary/secondary dorsal inner prismatic layer</i>
<b>dncl</b>	—	<i>dorsal nacreous layer</i>
<b>dncl 1/2</b>	—	<i>primary/secondary dorsal nacreous layer</i>
<b>dopl</b>	—	<i>dorsal outer prismatic layer</i>
<b>dspl</b>	—	<i>dorsal septal prismatic layer</i>
<b>dsw</b>	—	<i>dorsal shell wall</i>
<b>DV</b>	—	<i>discontinuous varix</i>
<b>enc</b>	—	<i>encruster</i>
<b>FV</b>	—	<i>flared varix</i>
<b>hbl</b>	—	<i>herringbone layer</i>
<b>if</b>	—	<i>infilling</i>
<b>ipl</b>	—	<i>inner prismatic layer</i>
<b>ipl 1/2</b>	—	<i>primary/secondary inner prismatic layer</i>
<b>n.p.</b>	—	<i>not preserved shell portion</i>
<b>NC</b>	—	<i>nepionic constriction</i>
<b>ncl</b>	—	<i>nacreous layer</i>
<b>ncl 1/2</b>	—	<i>primary/secondary nacreous layer</i>
<b>nr</b>	—	<i>nacreous reduced dorsal shell wall</i>
<b>ol</b>	—	<i>organic layer</i>
<b>oL</b>	—	<i>organic lirae</i>
<b>opl</b>	—	<i>outer prismatic layer</i>
<b>opl 1/2</b>	—	<i>primary/secondary outer prismatic layer</i>
<b>pc</b>	—	<i>prismatic cement</i>

## List of abbreviations

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<b>pe</b>	—	<i>periostracal extension</i>
<b>pel</b>	—	<i>pelicula</i>
<b>per</b>	—	<i>periostracum</i>
<b>per 1/2</b>	—	<i>primary/secondary periostracum</i>
<b>pi</b>	—	<i>prismatic inclusion</i>
<b>pL</b>	—	<i>prismatic lirae</i>
<b>pt</b>	—	<i>prismatic (angle) thickening</i>
<b>pvar</b>	—	<i>primary varix</i>
<b>r</b>	—	<i>prismatic reduced dorsal shell wall</i>
<b>rc</b>	—	<i>recrystallized shell wall</i>
<b>REM</b>	—	<i>Rasterelektronenmikroskop(ie)</i>
<b>ric</b>	—	<i>reinforced complete dorsal shell wall</i>
<b>rk</b>	—	<i>'Ritzknoten'</i>
<b>rs</b>	—	<i>'Ritzstreifen'</i>
<b>RV</b>	—	<i>ridged varix</i>
<b>S, s</b>	—	<i>septum</i>
<b>sb</b>	—	<i>shell bulge</i>
<b>sc</b>	—	<i>seemingly complete dorsal shell wall</i>
<b>SEM</b>	—	<i>scanning electron microscopy</i>
<b>siph</b>	—	<i>siphon</i>
<b>so</b>	—	<i>spiral ornamentation</i>
<b>SOM</b>	—	<i>Supplementary Online Material</i>
<b>sphpr</b>	—	<i>spherulitic-prismatic layer</i>
<b>spl</b>	—	<i>septal prismatic layer</i>
<b>TEM</b>	—	<i>transmission electron microscopy</i>
<b>V, var</b>	—	<i>varix</i>
<b>vsw</b>	—	<i>ventral shell wall</i>
<b>wl</b>	—	<i>wrinkle layer</i>

## Table of content

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### Table of content

Abstract.....	vii
Zusammenfassung.....	ix
Danksagung.....	xii
List of abbreviations.....	xiv
Table of content .....	xvi
Introduction.....	1
Phylogenetic background of the Ammonoidea .....	2
The ammonoid animal: Its conch and soft body.....	4
The ammonoid shell wall .....	6
Problem definition.....	8
Complex 1 (Manuscript I-III).....	8
Complex 2 (Manuscript IV) .....	9
Aims .....	10
Material and Methods .....	12
Material .....	12
Methods.....	12
Publications.....	13
Manuscript I — The internal structure of varices and constrictions in Jurassic and Cretaceous ammonoid shells.....	15
Manuscript II — Form and formation of flares and parabolae based on new observations of the internal shell structure of two lycoceratids and one perisphinctid (Ammonoidea).....	31
Manuscript III — Imbricate radial sculpture: a convergent feature within externally shelled cephalopods ....	47
Manuscript IV — The dorsal shell wall structure of Mesozoic ammonoids .....	61
Conclusions.....	161

## Table of content

---

References.....	165
Appendix.....	173
Eidesstattliche Erklärung.....	173
Erklärung zum Eigenanteil.....	173
Lebenslauf.....	175
Publikationen.....	176
Autoren.....	177
Konferenzbeiträge.....	178



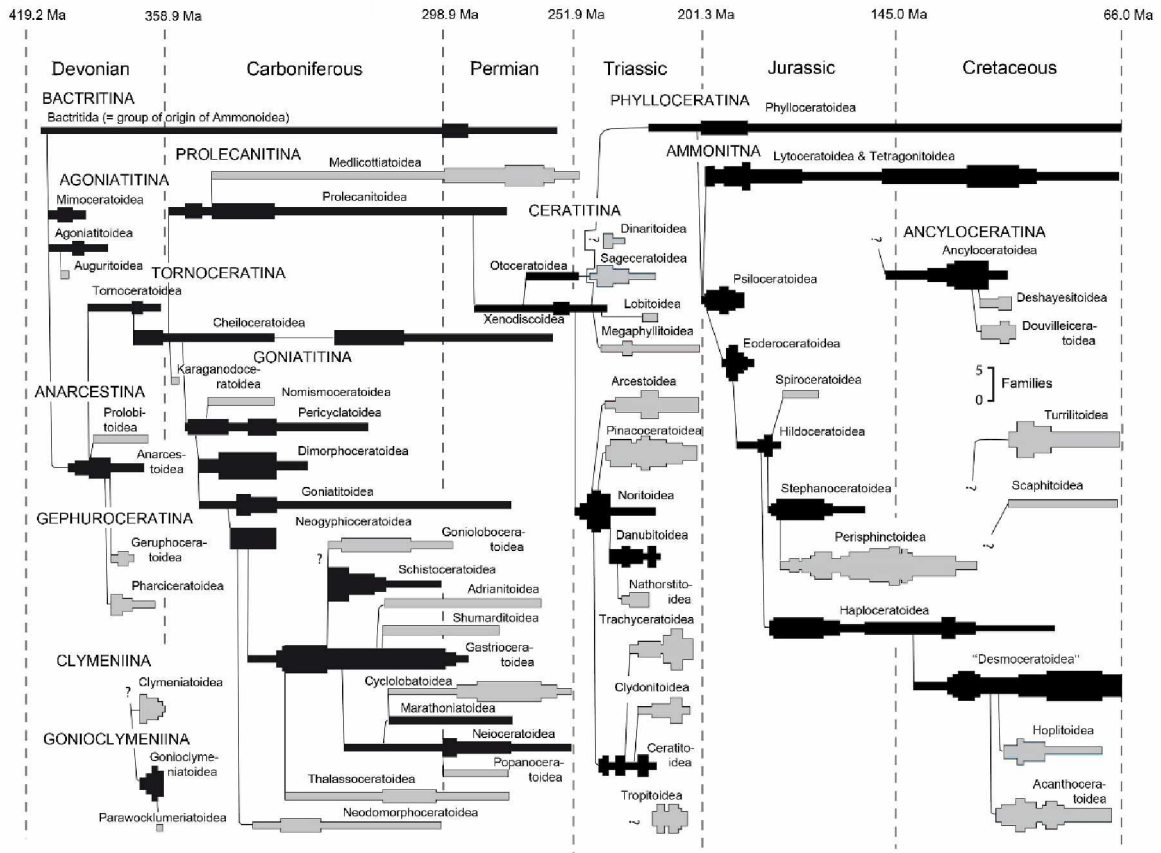


### **Introduction**

Since ancient times ammonoids, or rather their shells, have fascinated humanity. Already humans from the Upper Paleolithic processed ammonoid remains, probably for cultic use (Riek 1934). Also later cultures (e.g. Ancient Egypt, Hinduism) believed that these ‘rock moldings’ (Hagn 1977, Rätsch 1992a, b, Thenius & Vara 1996, Keupp 2000) had mystical powers. For the early humans, ammonoids were an ideograph of a cosmic energy and a basic natural order. In particular, the readily apparent, regular, mathematically exact spiral shape made people wonder, and still does.

Much later in human history, it was recognized that ammonoids are no spontaneous or divine accretions of the earth soils, but represent the fossil remains of formerly living animals. The first scientific descriptions and studies started around 300 years ago and have been continued up to our modern times with great diligence. In the last centuries, the external and internal morphology, the ontogeny, the phylogeny, and the ecology of ammonoids have been studied (but are still under debate). Basically, ammonoids are a group of marine beings that inhabited the Paleozoic and Mesozoic seas and developed a nearly unmanageable diversity during this time interval but died out at the end of Cretaceous without any descendants. The ammonoids pass through various phases, each of them characterized by its own forms and shapes: e.g. Goniatitina in the Paleozoic, Ceratitina in the late Paleozoic and Triassic, Ammonitina in the Jurassic and Cretaceous (Fig. 1). Due to their general abundance and vast diversity of shape, ammonoids have become very important marker fossils of marine sediments for the period between their appearance in the early Devonian and their disappearance at the Cretaceous-Paleogene boundary. The ammonoid biostratigraphy is made possible by a complex taxonomy and phylogeny (Fig. 1) generally based only on morphological features of the shell (e.g. sculpture, size, septal suture) and the buccal apparatus (e.g. apertures, anapertures). With the exception of some organic coatings, preservations of the animal’s soft body are not known, or are rather dubious. Interpretation of the relations of ammonoid groups proves difficult because of the low variety of combinations of features and because these features are mainly controlled by functional constraints, i.e. susceptible to convergence. It is therefore expedient to introduce further distinguishing features. This study suggests the internal structure of the ammonoid shell wall as a promising candidate. Since the function and formation of several of the sculptural

features under study are rarely understood or even speculated about, ultrastructural investigation suggests a way of interpreting their function and formation.



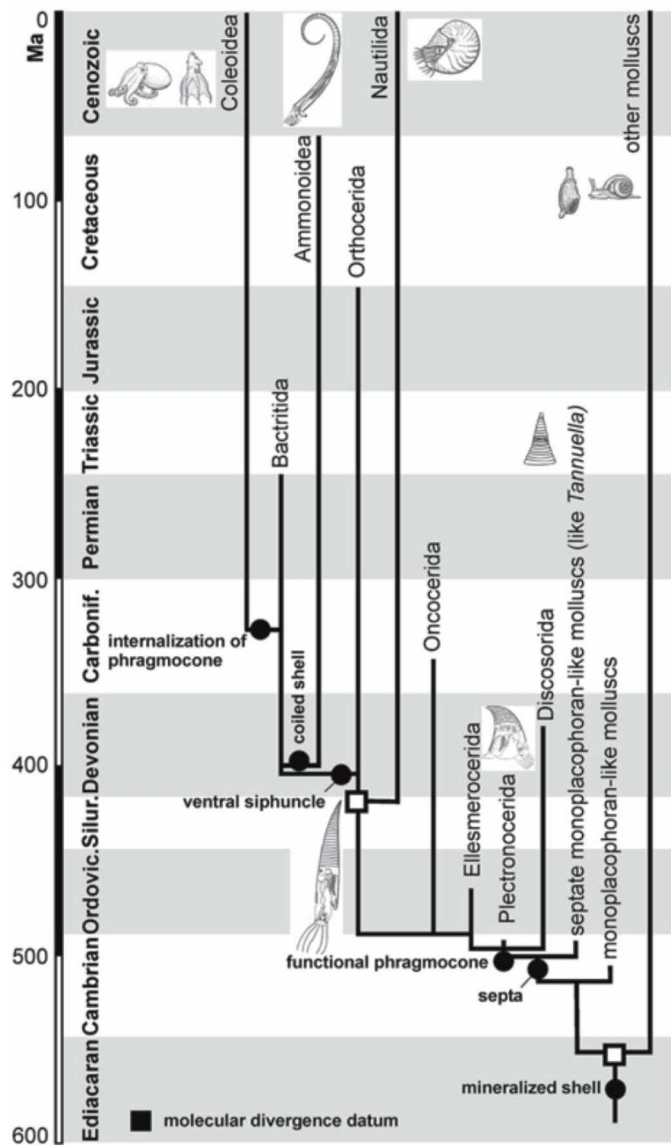
**Fig. 1:** Phylogenetic relations between ammonoid suborders and superfamilies (after Rouget et al. 2004). Grey - monophyletic superfamilies, black - paraphyletic (or polyphyletic) superfamilies.

*Phylogenetic background of the Ammonoidea*

What are Ammonoidea? Within the phylum Mollusca, ammonoids are assigned to the class of Cephalopoda, the sister taxon of Gastropoda. As members of the Mollusca, Ammonoidea should have had a shell-secreting mantle that provides the calcareous, external, planispiral shell typical of ammonoids. This external shell gives the Ammonoidea an outer appearance resembling the recent *Nautilus* and *Allonautilus* (Nautiloidea), relic remnants (i.e. living fossils) of a formerly very diverse cephalopod group named Palcephalopoda. Palcephalopods (e.g. Nautiloidea) are a paraphylum generally reserved for externally shelled cephalopods. However, the Ammonoidea belong to the Neocephalopoda, recent members of which still populate the modern seas. The neocephalopods of recent times, the nearest relatives of ammonoidea, are the Coleoidea including inter alia Decabrachia (e.g. Spirulida, Sepiida, Teuthida) and Octopodiformis (e.g. Vampyromorphida, Octopoda). Coleoidea shifted the conch into the soft

body (e.g. Decabrachia, Vampyromorphida), i.e. form an internal shell, or reduced it completely (e.g. Octopoda). However, similarities in early ontogeny and the buccal apparatus indicate a close relation between Ammonoidea and Coleoidea: 1) (relative) r-strategy for reproduction accompanied by a small hatching size (mm-scale), 2) a spherical protoconch (first chamber) with homogenous mineralization and 3) a slim radula (9 elements per row). Palcephalopods differ by establishing 1) a K-strategy for reproduction accompanied by a bigger hatching size (cm-scale), 2) hat-like successively mineralized protoconchs and 3) a broad radula (13 elements per row). Recently, ammonoids and coleoids have both been treated as offspring of the Bactritoidea (Fig. 2, e.g. Jacobs & Landmann 1993, Engeser 1996, Keupp 2000, Doguzhaeva 2002, Kröger et al. 2011, Klug et al. 2015), an externally shelled cephalopod group with straight (orthocone) conches that shares their characteristics. The external shell of Ammonoidea is a plesimorphic feature inherited by their ancestors, but more or less reduced in

**Fig. 2:** Phylogeny of Cephalopoda (after Klug et al. 2015).



Coloidea. The planispiral coiling of the ammonoid conch is an apomorphic feature but repeatedly reoccurs within cephalopod phylogeny, e.g. within Nautiloidea and Spirulida.

Originating in the Bactritoidea in the early Devonian, Ammonoidea began a diverse but discontinuous evolution characterized by several bursts of ‘explosive’ radiations determined by minor and major extinction events (Fig. 1) which each gave rise to individual faunal shapings with high numbers of new species, genera, families and superfamilies (e.g. Arkell et al. 1957, House 1985, Keupp 2000, Rouget et al. 2004). However, most of these high order taxa are paraphyletic (or polyphyletic). The first Devonian radiations were dominated by members of the Agoniatitina, Anarcestina, Clymeniina, Gonioclymeniina, Gephuroceratitina and Tornoceratitina. These clades persisted up to the end of the Devonian (the Kellwasser and the Hangenberg events) when the last members went extinct. During the post-Devonian radiation, two new orders conquered the Carboniferous and Permian seas, the Prolecanitina and Gonititina. The goniatids in particular created a high number of new superfamilies that dominate the cephalopod fauna worldwide. These new orders originate in the cheiloceratids, which is the only group to cross the Devonian-Carboniferous boundary. The prime of the goniatids lasted until the end of the Permian. However, with the end of the Permian and the beginning of the Triassic, prolecanitids and gonititids vanish from the earth. Only the prolecanitid Xenodiscoidea and their offspring the Otoceratoidea successfully cross the boundary and provide the diverse radiation of the Ceratitina that rule the Triassic seas. With the end of Triassic, the prime of ceratids declines and ends. As the sole survivors the phylloceratids persisted to the Jurassic and, together with their offspring the psiloceratids, lay the foundation for the Ammonitina (including Ancyloceratina) radiation, the diverse groups of which persisted up to the final extinction event at the Cretaceous-Paleogene boundary.

### *The ammonoid animal: Its conch and soft body*

To understand the shell wall of the ammonoid conch, it is important to develop an understanding of the ammonoid animal and its relation to the conch. Since the shell is the primary preserved remains of Ammonoidea (with exception of chitinous and calcareous beaks and radulae), ammonoid reconstruction is mainly based on the fossil conch (Fig. 3) and comparison with recent cephalopods (e.g. Lehman 1990, Engeser 1996, Keupp 2000). Because of its external shell, most assumptions about the living ammonoid are derived from the recent *Nautilus* and *Allonautilus*. The ammonoids’ calcareous shell not only protected and supported the fragile soft body of the animal but served as hydrostatic apparatus in order to achieve buoyancy and allow

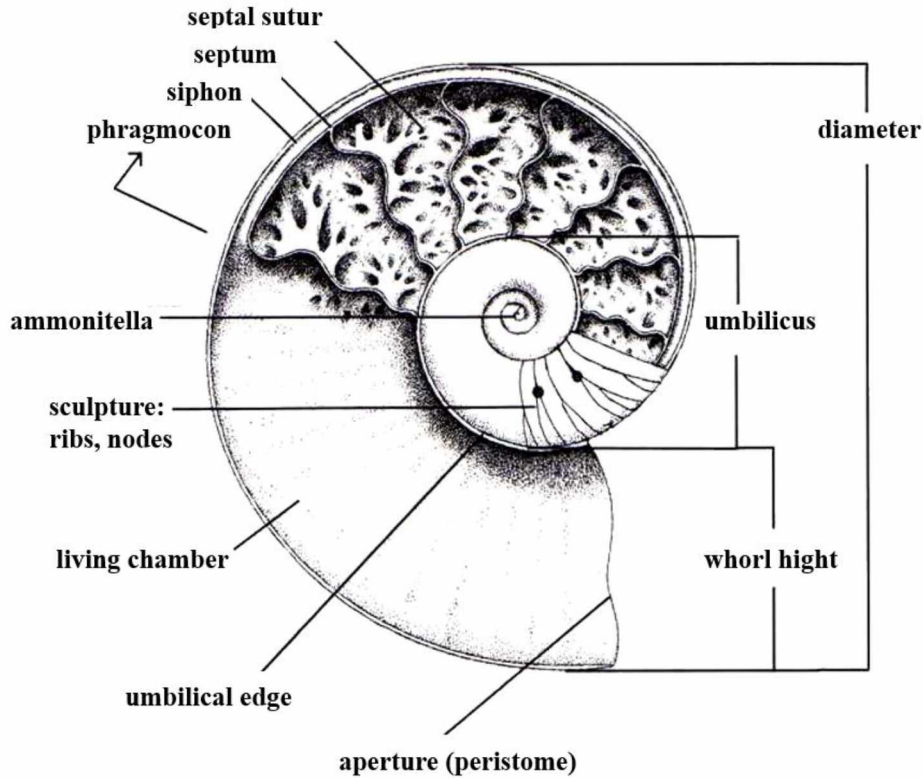


Fig. 3: Construction of the ammonoid conch (after Keupp 2000).

an upwards and downwards movement within the water column using the chambered portions of the ammonoid conch, similar to a human-made submarine. In somewhat simplified terms, the ammonoid shell is a planispirally coiled shell tube. The chambered part of the conch, the so-called phragmocone, is formed by a sequence of calcareous walls, the septa, which are repeatedly inserted into the whorls of the conch. A sophisticated system of osmotic processes, controlled by an absorptive pellicula (an organic chamber-coating) and the organic siphon (a cord-like continuation of the soft body), allowed the filling and emptying of chambers whereby the relative weight of the animal was changed, enabling movement upwards and downwards in the water column (e.g. Jacobs & Chamberlain 1996). The last chamber housed the soft body. This living chamber was not sealed orally, allowing the exposure of the ammonoid soft body through the oral aperture. The ontogenetically youngest (or innermost) portions of the conch are called ammonitella, which represents the shell formed in the egg prior to hatching. It consists of a protoconch, the first spherical chamber, and a first whorl containing some septa. The transition to the posthatching shell, i.e. teleoconch, is usually marked by a prominent narrowing of the tube accompanied by an internal ridge-like thickening, the so-called nepionic constriction. In contrast to the *Nautilus*, the conchs were mostly less than 1 mm in size after

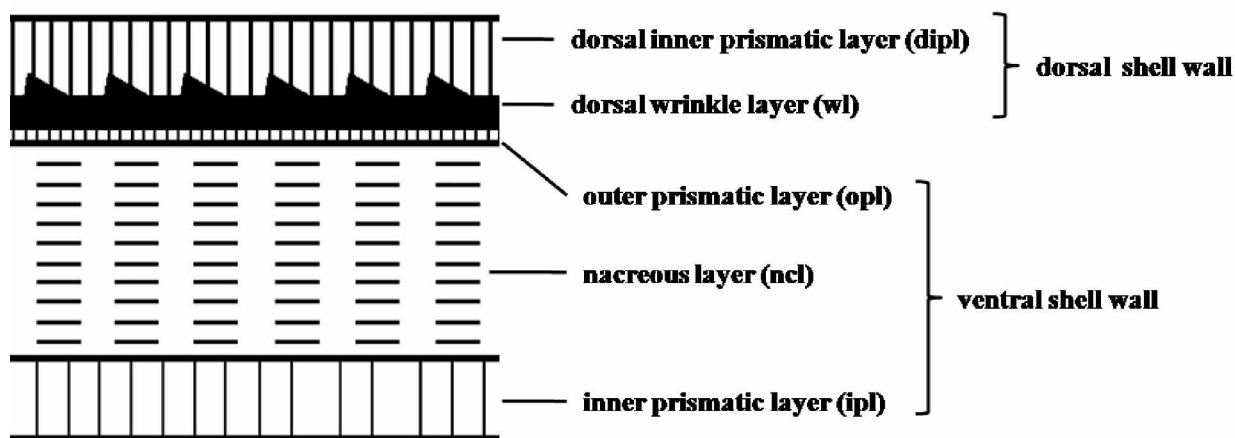
hatching, similar to modern coleoids (e.g. Erben et al. 1968, 1969, Drushits & Khiami 1970, Drushits & Doguzhaeva 1974).

The soft body of an ammonoid consisted presumably of two portions: the head with the brain, eyes, beak, arms and funnel, and the visceral sack. It is assumed that ammonoids primarily had ten arms, like modern coleoids. This is also different from the externally shelled modern *Nautilus* and *Allonautilus*, which secondarily form a whole bunch of arms. However, these also originate in ten arm buds, i.e. the ground plan (e.g. Shigeno et al. 2008, 2010). The ventral funnel allowed movement by jet propulsion through muscular contraction. Arms and funnel are equivalent with the molluscan foot, anterior and posterior, respectively. The second part of the soft body is the visceral sack, enclosing all vital organs such as the heart, digestive system and two gills. The outer boundary of the visceral sack is formed by the mantle. The mantle is the tissue that gave the Ammonoidea (and all other molluscs) the ability to secrete a calcareous shell. In contrast to the modern nautilids, whose soft bodies are fixed to the shell wall by a complex system of muscular bands, i.e. annular area (Mutvei 1957, Doguzhaeva & Mutvei 1991, 1996, Mutvei et al. 1993), ammonoids only ensured attachment with three muscle pairs (ventral, ventrolateral and dorsolateral) and a limited dorsal adherence zone of the mantle (e.g. Doguzhaeva & Mutvei 1991, 1996, Dagens & Keupp 1998, Keupp 2000).

### *The ammonoid shell wall*

Indeed, it was known that ammonoids build a calcareous shell but its ultrastructure remained enigmatic for a long time. Initial investigations of the ultrastructure of the ammonoid shell wall, prior to the introduction of transmission and scanning electron microscopy (TEM and SEM), were based on macroscopic and light microscopic observations. However, researchers in the late 19<sup>th</sup> and early 20<sup>th</sup> century were able to grasp the fundamentals of the ammonoid shell (see Birkelund 1980). The shell wall consists of at least three aragonite shell layers, with prismatic or nacreous appearance. The aragonite primary structure of the shell in particular complicates the ultrastructural analyses of the shell wall. The metastable aragonite is susceptible for diagenesis. Often the material is dissolved or replaced by stable calcite or other minerals; as a result the primary structure is lost. Therefore, the ultrastructure of Paleozoic (and Triassic) taxa is mostly unknown. Our present knowledge is mainly based on observations of Mesozoic taxa. The first clear descriptions of the ammonoid shell ultrastructure based on electron microscopy followed in the 1960ies (e.g. Birkelund 1967, Erben et al. 1968, 1969) but focused on the embryonic shell portions (ammonitella), the wall of which generally consists of (sub-)prismatic layers.

Since then further studies have established a more or less regular picture of the ammonoid shell wall; it consists of four layers, an organic periostracum and three aragonitic layers, the outer prismatic, the median nacreous and the inner prismatic layer (Fig. 4, e.g. Birkelund 1967, 1980, Birkelund & Hansen 1968, 1974, 1975, Erben et al. 1968, 1969, Drushits & Khiami 1970, Walliser 1970, Bayer 1974, Howarth 1975, Lehman 1976, 1990, Kulicki 1979, 1996, Doguzhaeva 1980, 1981, 2002, 2012, Doguzhaeva & Mikhailova 1982, Zakharov & Grabovskaya 1984, Doguzhaeva & Mutvei 1986, 1989, 1991, 1993a, b, Landman 1987, Dauphine 1989, Checa 1994, Zakharov 1996, Kulicki & Tanabe 1999, Keupp 2000, Kulicki et al. 2001, Sprey 2002, Doguzhaeva et al. 2010). The outermost periostracum is mostly not preserved (Checa 1994), probably it was shed after shell mineralization (Keupp 2000). Both prismatic layers consist of elongated crystals arranged parallel to each other (palisade pattern), usually the inner layer is much thicker than the outer. The nacreous layer consists of columns of stacked polygonal crystal plates (stacked coin pattern). Also the septa are mainly formed by nacre. The four layers are secreted successively one after another by different portions of the ammonoid mantle.



**Fig. 4:** Construction of the ammonoid shell wall (*growth direction to the left*). The ventral shell wall consists of three aragonitic shell layers (opl, ncl, ipl); the outer organic periostracum is generally lacking. Due to the planspiral construction, the dorsal shell wall of the succeeding whorl overgrowth the ventral shell wall of the preceding whorl. The dorsal shell wall is usually reduced and consists of an outer organic component, e.g. wrinkle layer (wl), and an aragonitic inner prismatic layer (dipl).

The periostracum, the outermost layer, is formed by a fold of the mantle at its (ad)oral edge. It serves as a stencil for the outer prismatic layer, which is also formed at the adoral mantle edge. The nacreous layer is secreted by or near the mantle edge. Probably the whole mantle or broad portions of it were able to form nacre. So the nacreous septa are a product of the apical mantle tissue. The innermost of the shell layers, the inner prismatic layer, is only aborally formed in

the rear living chamber by the apical mantle, usually it wedges out in front of the last septum. The septa are inserted right after or parallel with the inner prismatic layer. The inner prismatic layer is the attachment site for the soft body; it can thicken where muscles adhere to the shell interior (muscle adhesive layer). However, there are reasons to think that the whole mantle tissue itself attaches to the shell interior, resulting in an additional thin prismatic sublayer in the inner prismatic layer (Doguzhaeva 1981, Doguzhaeva & Mutvei 1986, 1993a). This mantle adhesive layer could already be formed adorally in the front living chamber prior to the formation of the thicker muscle adhesive (sub-)layer.

### *Problem definition*

The above-mentioned studies suggest a primary, universal ground plan of the shell wall based on general observation. However, several studies of the ammonoid shell wall show that these animals repeatedly modify the primary three-layered shell wall (aragonite layers). Ammonoids form hollow floors of spines or keels by a secondary generation of the inner prismatic layer (Hölder 1952, Erben 1972, Birkelund 1980, Checa & Martin-Ramos 1989) or form shell doublings like the Dactiloceratidae (Howarth 1975), *Ptychoceras* (Doguzhaeva & Mutvei 1989) or *Aconeceras* (Doguzhaeva & Mutvei 1991) by secreting additional shell layers. Phylloceratids seem to form extraordinarily thick inner prismatic layers (e.g. Birkelund & Hansen 1974, 1975, Drushits & Khiami 1970). Other taxa reduce single layers completely (e.g. Doguzhaeva & Mutvei 1989). The shell wall of ammonoids is by no means constant, which makes taxa-based variation a possibility. Usually the modification of the shell wall can be interpreted in terms of functional morphology, e.g. the attachment of muscles or the smoothing of the shell interior. An essential aspect of shell ultrastructure is therefore the function. Both aspects are the basis of my considerations:

**Complex 1 (Manuscript I-III)** — Several sculptural elements are assumed to represent pauses in the growth of the ammonoid shell, during which time the animal interrupted the shell secretion (e.g. Arkell et al. 1957, Bucher et al. 1996, Bucher 1997). Typical sculptures associated with this are constrictions and varices (internal thickenings of the shell wall in part associated with local shell undulations) and megastriae, like flares (local frill-like enlargements of the whorl) and parabolae (sinuous linear elements cutting the adoral sculpture). Bucher et al. (2003) assume that radial lirae, a form of fine radial striation, are also formed during an interruption in shell growth. Furthermore, it is possible that similar structures also occur in other sculptural elements as well: for example, in the nautiloid *Cymatoceras*, each rib of the shell marks a halt in growth (Chirat & Bucher 2006). All of these special sculptures occur in a broad



variety of taxa that are only directly related in a few cases. Usually these are restricted to individual taxonomic groups (nevertheless sculptural elements of the same designation can occur in different taxa). However, their broad distribution and recurrent occurrence in ammonoid phylogeny probably hints at a plesimorphy, i.e. a common bauplan can be assumed. The nepionic constriction is probably the best proven growth interruption and the only one associated with all ammonoids, it separates the embryonic ammonitella from the juvenile teleoconch (e.g. Birkelund 1967, 1980, Birkelund & Hansen 1968, 1974, Erben et al. 1968, 1969, Drushits & Khiami 1970, Howarth 1975, Lehman 1976, 1990, Kulicki 1979, 1996, Doguzhaeva & Mikhailova 1982, Bandel 1986, Landman 1987, Doguzhaeva & Mutvei 1989, Kulicki & Doguzhaeva 1994, Kulicki & Tanabe 1999, Keupp 2000, Kulicki et al. 2001, Sprey 2002, Tanabe et al. 2008, Doguzhaeva et al. 2010). In fact, the nepionic constriction develops a prominent discordance in the shell wall: The ammonitella wall gradually disappears towards the end of the ammonitella (nepionic constriction) and a new shell generation continues the shell growth beginning from within. The new shell shows all the characteristics of the aragonitic three-layered shell wall. Scholars of this phenomenon assume that this discontinuity is the result of a withdrawal of the shell-secreting mantle that continues growth from within. It is likely that sculptures associated with a growth interruption, like varices, constrictions, megastriae and radial lirae, show a similar internal structure.

**Complex 2 (Manuscript IV)** — It is assumed that typically all planispirally coiled ammonoid taxa reduce the number of participating dorsal shell layers, i.e. form a reduced dorsal shell wall (Fig. 4). Because the subsequent whorl attaches to the previous whorl, dorsally, the whorl is supported by the ventral shell of the preceding whorl. Ammonoids used this circumstance to build their shell much more economically, i.e. with lower material consumption and secretion effort. Usually at the whorls' point of contact, the outer prismatic layer and the median nacreous layer of the lateral wall wedge out. Only in the rear portions of the living chamber did the inner prismatic layer coat the overgrown shell portions (e.g. Palfram 1967, Birkelund & Hansen 1968, 1974, 1975, Erben et al. 1968, 1969, Drushits & Khiami 1970, Walliser 1970, Westermann 1971, Bayer 1974, Howarth 1975, Lehmann 1976, 1990, Kulick 1979, 1996, Doguzhaeva 1980, 1981, 2002, Birkelund 1980, Zakharov & Garbovskaya 1984, Doguzhaeva & Mutvei 1986, 1991, 1993a, b, Zakharov 1996, Kulicki & Tanabe 1999, Kulicki et al. 1999, 2001, 2002, Keupp 2000, Doguzhaeva et al. 2010). However, it is known that heteromorph taxa, ammonoids whose shell decoils to form open spirals or shafts, have a complete, aragonitic, three-layered dorsal shell wall which forms a continuum with the lateral and ventral shell walls, i.e. outer prismatic layer, nacreous layer and inner prismatic layer (Erben et al. 1969, Doguzhaeva &

Mikhailova 1982, Landman 1987, Doguzhaeva & Mutvei 1989). This occurs due to the missing support of the preceding whorl. Shells of Scaphitids are secondarily heteromorph, the phragmocone is planispiral and only the adult living chamber is formed like a hook. Indeed, both portions differ in the construction of the dorsal shell wall. Actually the reduced dorsal shell wall of the phragmocon is replaced by a complete dorsal shell wall as the hook decoils (Erben et al. 1969, Landman 1987). This observation may indicate that ammonoids were generally able to develop a complete dorsal shell wall in ontogeny. This is plausible because the ancestors of planispiral Ammonoidea were orthocones (Bactritoidea) and because heteromorph taxa have to evolve from planispiral ones. My observations from former studies (e.g. Radtke 2012) prove that planispirally coiled taxa (e.g. *Puzosia*, *Desmoceras*) were able to at least form nacre dorsally as well. The occurrence of dorsal nacre and a secondary complete dorsal shell probably indicate a plesiomorphy, inherited by orthocone ancestors, or a new unique feature. Secondary formation of a complete dorsal shell wall is essential for whorl detachment, i.e. formation of heteromorphs. The question is which taxonomic groups are the best match as ancestors of heteromorphs.

Indeed, several taxa reduce the number of involved dorsal shell layers, but studies of the ultrastructure show that ammonoid taxa often develop an additional unique dorsal shell component which directly attaches to and coats the overgrown ventral shell portions. For example, wrinkle layers (a layer of fingerprint-like relief) have been described, as well as coating layers (a thick organic layer of lamellar internal structure) and spiral ornaments (a layer with several spiral striae) (e.g. Hölder 1973, Drushits et al. 1978, Kulick 1979, 1996, Doguzhaeva 1980, 1981, Birkelund 1980, Zakharov & Garbovskaya 1984, Zakharov 1996, Kulicki et al. 2001, Doguzhaeva et al. 2010). It is assumed that these are homologous structures of different deviation, or rather appearance, and are expressions of a general feature. Often it is assumed that the wrinkle layer covers the whole interior of the living chamber, dorsally to ventrally (e.g. Walliser 1970, House 1971, Senior 1971, Doguzhaeva 1980, 1981, Korn 1985). Other authors (e.g. Tozer 1972, Keupp 2008, Mironenko 2015) distinguish the ‘ventral wrinkle layer’ as separate component of the shell wall, i.e. ‘Ritzstreifen’.

### *Aims*

This study was held to investigate the applicability of the ammonoid shell structure for taxonomic, phylogenetic and functional-morphologic use, in particular the structure of sculptures associated with growth interruptions and the construction of the ammonoid dorsal shell wall. Different sculptural elements, e.g. varices, constrictions, flares, parabolae or radial

lirae, are interpreted as representing a stop in shell growth. This study shows which sculptures of the ammonoid shell are indeed associated with an interruption in shell growth and which are not (Manuscript I-III). Their structures are discussed in view of the following questions: Is there a general bauplan for all of these or individual sculptures that support a general plesiomorphic trait, even when direct connections in phylogeny are missing and outer morphology differs? Is the nepionic constriction common to all ammonoids the prototype of deviated structures? Is it possible to separate individual ammonoid taxa (e.g. species, genera, families, superfamilies) based on the detailed internal structure and formation of the sculptures under study? Are there transitional formations in ultrastructure connected to different morphologies or are there structural differences separating morphologically similar structures? How are these sculptures formed? What does the internal structure and formation reveal about the function? Do the differences in construction and formation influence the function or vice versa? Does the scale of such structures influence the internal construction?

The dorsal shell portions of various planispirally coiled ammonoid shells are formed by a reduced dorsal shell wall composed of one inner prismatic and an outer organic (wrinkle) layer, while several heteromorph taxa form a complete dorsal shell wall consisting of three aragonitic layers (i.e. outer prismatic layer, nacreous layer and inner prismatic layer). Some ammonoids seem to have been able to secondarily build a complete dorsal shell wall, either locally (e.g. *Puzosia*, *Desmoceras*) or during ontogeny (e.g. Scaphitoidea). The knowledge to date of the dorsal shell wall comes from the studies of comparatively few genera, so it is therefore likely that diverse expressions of dorsal shell wall exist that can be used for taxonomic and phylogenetic purposes. To date it is not clear if the formation of a reduced dorsal shell wall represents a general pattern, or if some ammonoids had the ability to form more shell layers. This study solves the following accompanying questions (Manuscript IV): Are there differences in the internal structure, compartments, formation, and ontogeny of the dorsal shell wall that can be used to distinguish individual ammonoid groups (e.g. species, genera, families, superfamilies)? Which taxa form a reduced dorsal shell wall and which taxa form a complete one? Do taxa that form a reduced dorsal shell wall have the general ability to form an optional complete dorsal shell wall during ontogeny or in reaction to triggers (e.g. injuries, overgrowth of encrusters)? Is the ability to build a complete dorsal shell wall a precondition for developing heteromorphic decoiled taxa? Is the wrinkle layer a general feature of every ammonoid order (e.g. Doguzhaeva & Mutvei 1986)? Are the coating layers of *Gaudryceras tenuiliratum*, the spiral ornament of Amaltheidae or the 'Ritzstreifen' homologous or analogous structures of the wrinkle layer?

## **Material and Methods**

### *Material*

This study is based on more than 290 well-preserved ammonoid shells from different Triassic, Jurassic and Cretaceous localities in France, Germany, Greenland, Japan, Madagascar, Russia and the USA (Manuscript IV SOM: table A). Most specimens are housed in the Bavarian State Collection for Palaeontology and Geology, Munich, as part of H. Keupp's collection (number indices: MAm, MAn, MAo, PA). Other specimens were a loan of the American Museum of Natural History New York (number indices: AMNH-FI). According to the SEM preservation index (PI) by Cochran et al. (2010), the examined shell material has a predominantly aragonitic preservation of a good (PI = 3) to poor (PI = 1) state. The shells of several taxa were completely recrystallised without preserved ultrastructure of the shell wall.

### *Methods*

Freshly broken material and etched median and transversal sections were analysed. Etched sections were polished with aluminium oxide and afterward treated with 10% formic acid for 5 to 10 seconds. All samples were fixed on aluminium stubs with conductive carbon glue and sputtered with gold. Observations were made and pictures were taken with the scanning electron microscope (Type: Zeiss SUPRA 40VP) of the palaeontological section of the FU Berlin.

**Publications**

- Manuscript I (*accepted version from 08 July 2015*) — The internal structure of varices and constrictions in Jurassic and Cretaceous ammonoid shells. [*Swiss Journal of Palaeontology* 2016, 135 (1): 109-124. doi: [10.1007/s13358-015-0095-9](https://doi.org/10.1007/s13358-015-0095-9).] ..... 15
- Manuscript II (*accepted version from 04 April 2016*) — Form and formation of flares and parabolae based on new observations of the internal shell structure of two lycoceratids and one perisphinctid (Ammonoidea). [*Acta Palaeontologica Polonica* 2016, 61 (3): 503-517. doi: [10.4202/app.00154.2015](https://doi.org/10.4202/app.00154.2015).] ..... 31
- Manuscript III (*accepted version from 12 January 2016*) — Imbricate radial sculpture: a convergent feature within externally shelled cephalopods. [*Paleontology* 2016, 59 (3): 409-421. doi: [10.1111/pala.12233](https://doi.org/10.1111/pala.12233).] ..... 47
- Manuscript IV (*accepted version from 05 January 2017*) — The dorsal shell wall structure of Mesozoic ammonoids. [*Acta Palaeontologica Polonica* 2017, 62 (1): 59-96. doi: [10.4202/app.00263.2016](https://doi.org/10.4202/app.00263.2016).] ..... 61



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Aus Urheberrechtsgründen wurde das folgende Kapitel der Dissertation entfernt.

For copyright reasons, the following chapter of the doctoral thesis was removed.

Radtke, G. and Keupp, H. 2016. The internal structure of varices and constrictions in Jurassic and Cretaceous ammonoid shells. *Swiss Journal of Palaeontology*, 135 (1): 109-124. doi: [10.1007/s13358-015-0095-9](https://doi.org/10.1007/s13358-015-0095-9).

*Manuscript II* (accepted version from 04 April 2016) *Acta Palaeontologica Polonica* 2016, 61 (3): 503-517. doi: [10.4202/app.00154.2015](https://doi.org/10.4202/app.00154.2015).

Editors' choice

## Form and formation of flares and parabolae based on new observations of the internal shell structure in lytoceratid and perisphinctid ammonoids

GREGOR RADTKE, RENÉ HOFFMANN, and HELMUT KEUPP



Radtke, G., Hoffmann, R., and Keupp, H. 2016. Form and formation of flares and parabolae based on new observations of the internal shell structure in lytoceratid and perisphinctid ammonoids. *Acta Palaeontologica Polonica* 61 (3): 503–517.

The ultrastructure of pristine shells of Jurassic and Cretaceous lytoceratid and perisphinctid ammonoids indicates that flares and parabolae represent homologous structures. Both mark an interruption of shell growth. We dismiss earlier interpretations of parabolae as actual aperture, relics of resorbed apophyses or superstructure of the musculature associated to a semi-internal shell. Instead we propose an episodic growth model including several growth stops at the aperture during the formation of a frill-like aperture for parabolae and flares. Such an aperture is composed of the outer prismatic layer, the nacreous layer and an apertural prismatic coating. Here, we observed the apertural prismatic coating for the first time as an integral part of flares and parabolae. The apertural prismatic coating covers only the inner surface of the frill and was secreted by a permanent mantle cover indicating a prolonged period without the production of new shell material. Parabolae differ from flares by their general shape and the presence of ventro-lateral parabolic notches and nodes. The notches were formed by folding of the frill and had the potential to form semi-open spines. The corresponding parabolic nodes are caused by an outward swelling of the shell-secreting mantle tissue producing new shell material at the position of the folding. New shell material that belongs to the conch tube is attached to the base of flares and parabolae after withdrawal of the mantle edge representing the continuation of shell growth. Usually, the frilled aperture associated with flares and parabolae were removed during lifetime. This study reports on flares in *Argonauticeras* for the first time. In this genus they are typically associated with varices.

**Key words:** Ammonoidea, ultrastructure, megastriata, temporary aperture, episodic growth, Jurassic, Cretaceous.

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### Introduction

The accretion of ammonoid shells is assumed to be more or less continuous, comparable to the modern *Nautilus* and other shell bearing molluscs (e.g., Martin et al. 1978; Saunders 1983, Cochran and Landman 1984; Ward 1987; Westermann et al. 2004). However, some shell elements, e.g., flares, parabolae, have been suggested to represent temporary apertures indicating growth stops during ontogeny (e.g., Neumayr 1884; Arkell et al. 1957; Bucher et al. 1996). Flares typically occur in Lytoceratoidea while parabolae are reported for Clymeniida, Phylloceratoidea, Lytoceratoidea, and Perisphinctoidea (Wähner 1894; Michalski 1908; Arkell et al. 1957; Keupp 2000; Hoffmann 2010; Hoffmann and Keupp 2010). Both, flares and parabolae are radial linear

elements, which encircle the whorl except for the dorsal part (Fig. 1). Flares are prominent, smooth to crenulated rib-, frill-like or sometimes funnel-shaped shell extensions (Fig. 1A) paralleling the growth lines. Flares are underpinned by new shell material, which continues the growth of the conch tube. However, Drushits et al. (1978) describe the flares of *Tetragonites* and *Gaudryceras* only as nacreous thickenings and do not mention an interruption in shell growth. Drushits and Doguzhaeva (1981: fig. 31) demonstrate that the outer prismatic layer is involved in the formation of flares of *Eurystomiceras* (junior subjective synonym of *Nannolytoceras*; see Hoffmann 2010). Hence the outer prismatic layer shows an episodic growth interruption. Recently, it has been shown that the flares of *Anagaudryceras* (Bucher et al. 1996: fig. 11) and *Eogaudryceras* (Doguzhaeva et al.



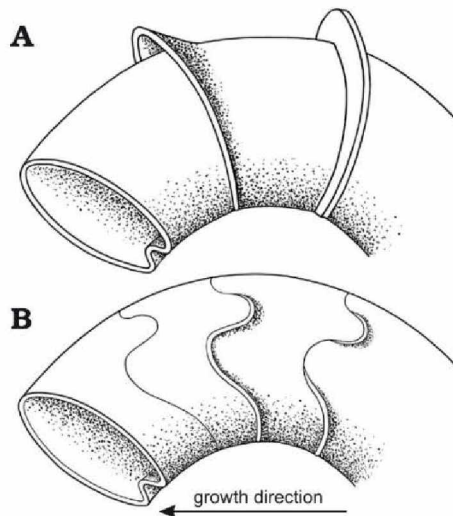


Fig. 1. Different expressions of flares (A) and parabolaes (B).

2010: fig. 3) are composed of the outer prismatic and nacreous layer. However, none of the above descriptions show complete flares.

Parabolaes represent thin raised lines or ribs, which form prominent symmetrical sinuses, the paired parabolic notches (Fig. 1B), at the ventro-lateral edge. Ventrally and laterally parabolaes form adorally projecting saddles. Parabolaes are oblique to, and hence cut growth lines or other sculptures (e.g., Bucher et al. 1996). Additional structures often associated with parabolaes are the parabolic nodes, smooth elevations formed in the parabolic notches. While it is generally accepted that parabolaes represent an interruption in shell growth, their primary shape is still under debate. Some authors assumed that parabolaes represent the actual moulding of the temporary aperture (e.g., Pompeckj 1894; Keupp 1973), probably formed due to lower growth rates at the position of the parabolic notches (Keupp 1973: fig. 4). In contrast, a secondary state, e.g., resorption of apophyses (Teisseyre 1883, 1889; Siemiradzki 1898–1899; Brinkmann 1929; Hiltermann 1939), or the resorption of semi-closed to closed ventro-lateral, hollow spines with parabolic notches as their former bases (Stieler 1922; Wendt 1968; Guex 1989; Bucher and Guex 1990), or removal of a frill through breakage (Michalski 1908) were assumed by others. Bucher and Guex (1990) supposed that parabolaes and flares share a similar ultrastructure (also Bucher et al. 1996; Bucher 1997). Accordingly, flares and parabolaes represent different expressions of their concept of megastriae. Both flares and parabolaes are assumed to be the result of withdrawal of the shell-secreting mantle. A similar genesis and internal structure (outer prismatic and nacreous layer) suggest that flares and parabolaes were homologous structures. A third interpretation was provided by Doguzhaeva (2012). Based on observations of *Indosphinctes*, parabolaes were interpreted as a superstructure of the muscular system serving predominantly for the secure attachment

of muscles to the inner and outer shell surface. That interpretation points to a semi-internal shell without episodic growth stops during the formation of parabolaes.

By comparing concurring hypotheses about the internal structure, formation and shape of flares and parabolaes the following questions arise: (i) What was the original shape and potential function of flares and parabolaes? (ii) Which processes took part in their formation and/or removal? (iii) Do flares and parabolaes represent homologous structures? (iv) Do parabolaes indicate a semi-internal shell?

*Institutional abbreviations.*—BSPG, Bavarian State Collection for Palaeontology and Geology, Munich, Germany.

*Other abbreviations.*—apc, apertural prismatic coating; ipl, inner prismatic layer; ncl 1/2, nacreous layer of primary/secondary shell; opl 1/2, outer prismatic layer of primary/secondary shell; PI, SEM preservation index; pt, prismatic thickening; sb, shell bulge; var, varix.

## Material and methods

The present study is based on pristine shells of *Choffatia* sp. (Perisphinctoidea) from SW Russia, *Argonauticeras besairiei* Collignon, 1949 from NW Madagascar, and *Protetragonites fraasi* (Daqué, 1910) from SW Madagascar (both Lytoceratoidea). All specimens are housed in BSPG (Coll. H. Keupp) (Table 1). According to the SEM preservation index (PI) by Cochran et al. (2010), the examined shell material has a predominantly aragonitic preservation of a good (PI = 3) to fair (PI = 2) state. In all specimens only the phragmocone is preserved. Russian samples show a partial pyritic overprint; the chamber walls are coated with diagenetic pyrite crystals. The remaining hollow spaces are filled with fine loose sediment, which was removed for observation. Madagascan ammonoids are filled with coarse, marly, glauconitic sediment or are completely filled with drusy calcite.

Freshly broken pieces and etched sections of shell material were analysed. Etched sections were prepared by polishing with aluminium oxide and were afterwards treated with 10% formic acid for 5–10 s. All samples were fixed with conductive carbon glue on aluminium stubs and then sputtered with gold. Observations were made and pictures were taken with the scanning electron microscope (Type: Zeiss SUPRA 40VP) of the palaeontological section of the Freie Universität Berlin.

## Results and discussion

**Flares.**—*Protetragonites fraasi* and *Argonauticeras besairiei* developed regularly spaced flares. *Protetragonites* has 5–6 and *Argonauticeras* 7–10 flares per whorl. Each flare marks the junction of two shell generations. The older



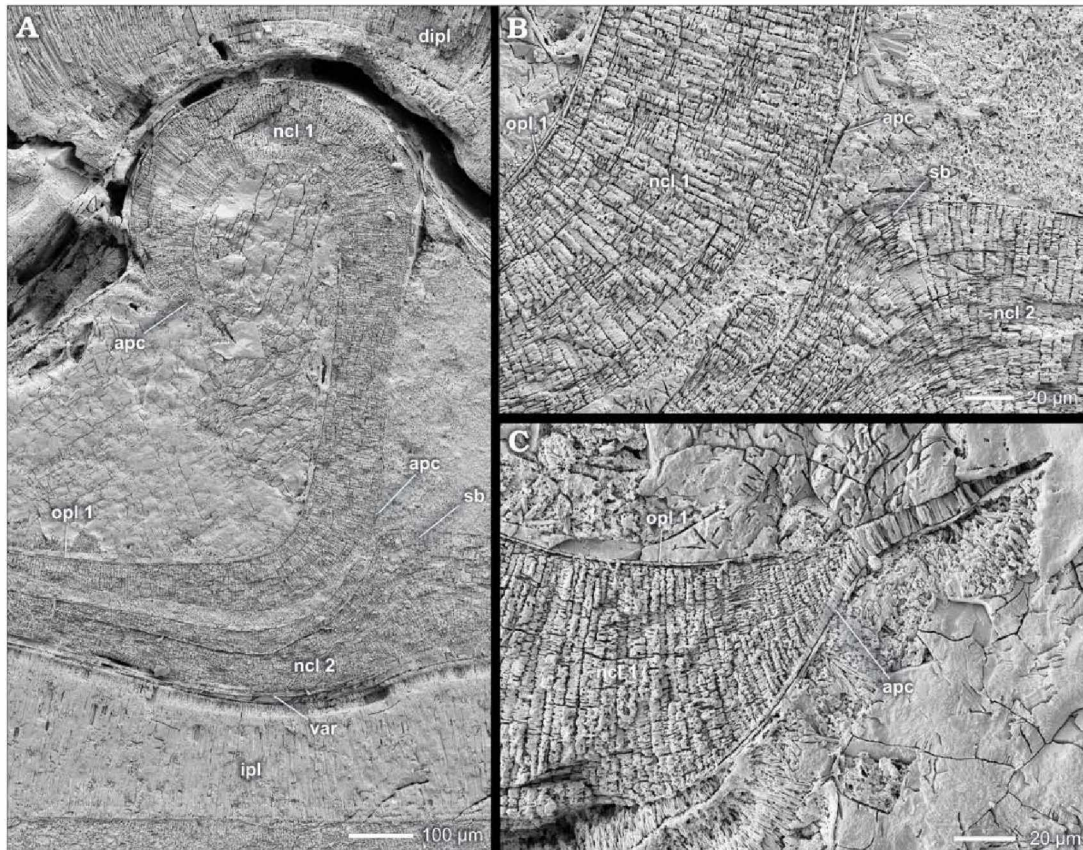


Fig. 2. Internal structure of flares (median section, growth direction right) in *Argonauticeras besairiei* Collignon, 1949 (BSPG MAo-1801) from Ambatolafia, Mahajanga Basin, NW Madagascar; Lower Albian, Cretaceous. **A.** Complete flare, the primary shell bends outwards and forms a frill. The flare ends in a backward reflection of the shell, i.e., apertural margin. Secondary shell material is attached from beneath and forms a prominent bulge in front of the flare. **B.** Close-up of A, contact of the primary shell and the secondary shell. The interior of the flares is covered by an apertural prismatic coating. **C.** Apertural margin of the flare, the primary shell wedges out. The primary outer prismatic layer and the apertural prismatic coating form a vanishing prismatic wedge. Abbreviations: apc, apertural prismatic coating; dipl, dorsal inner prismatic layer; ipl, inner prismatic layer; ncl 1/2, nacreous layer of the primary/secondary shell; opl 1/2, outer prismatic layer of the primary/secondary shell; sb, shell bulge; var, varix.

shell generation is called the primary shell and the new one is called the secondary shell. The formation of the flares indicates the end of one formation cycle. Two flares of *Argonauticeras* are preserved completely intact, forming a frill (Fig. 2A). They reach a height of up to 800 µm and a thickness of up to 100 µm. The proximal part is straight but slightly adorally inclined, while the most distal part forms a backward inflection that results in a hook-like appearance in cross section. The flare consists of a thin outer prismatic and an underlying thick nacreous layer (opl 1 and ncl 1 in Figs. 2, 3A<sub>1</sub>, B<sub>1</sub>, 4A), which is in accordance with the observations of Bucher et al. (1996: fig. 11) and Doguzhaeva et al. (2010: figs. 3, 5). The inner surface of the frilled aperture is covered by a prismatic layer (apc in Figs. 2B, C, 3, 4C, 5A). This layer is called the apertural prismatic coating (apc) here. The flare thins out distally and vanishes forming a delicate prismatic wedge, a product of the opl 1 and the apc (Fig. 2C). In distal parts of flares as well as in non-flared apertural edges the

ncl 1 thins out (e.g., Mutvei 2014). Flares at the umbilical edge are less conspicuous and made of a small wedge of the opl 1 (and apc?), which rises slightly (ca. 20 µm) above the shell surface (opl 1/apc in Fig. 4D). The majority of flares have been morphologically altered, i.e., they do not show their original shape. Ventrally, the flares are often preserved as short, rounded stumps projecting above the shell surface (Figs. 3A<sub>1</sub>, 4A, B), up to 400 µm high, or are completely cut off sub-parallel ending at the level of the shell surface (Fig. 3B), i.e., horizontally cut flare-bases (compare Bucher et al. 1996; Doguzhaeva et al. 2010).

Beneath the actual flare a new shell generation (secondary shell), comprised of a secondary outer prismatic and nacreous layer (opl 2 and ncl 2 in Figs. 2A, B, 3, 4A, C, D), is formed. Thus, the shell seems to be doubled in that area. The new opl 2 begins immediately at the base of the flare and is in direct contact with the apc (Fig. 3A<sub>2</sub>, B<sub>2</sub>). The ncl 1 and the ncl 2 can only be separated in proximity to the flare,

Table 1. Ammonoid taxa studied, their locality and age, and occurrence of flares and parabolae. All specimens housed in the BSPG (Coll. H. Keupp). ×, present; –, absent.

Taxon	Specimen number	Locality	Age	Flares	Parabolae
Lytoceraoidea					
<i>Protetragonites fraasi</i> (Daqué, 1910)	BSPG MAn-4530 BSPG MAn-4734	Sakaraha area, Morondava Basin, SW Madagascar	Upper Oxfordian, Jurassic	×	–
<i>Argonauticeras besairiei</i> Collignon, 1949	BSPG MAo-1705a BSPG MAo-1772 BSPG MAo-1801 BSPG MAo-1802	Ambatolafia area, Mahajanga Basin, NW Madagascar	Lower Albian, Cretaceous	×	–
Perisphinctoidea					
<i>Choffatia</i> sp.	BSPG MAn-4519 BSPG MAn-4520	Dubki near Saratov, SW Russia	Upper Callovian, Jurassic	–	×

because they merge in the aboral direction (Figs. 3A<sub>1</sub>, B<sub>1</sub>, 4A, D). Directly in front of each flare, the secondary shell forms a bulge at the base of each flare that vanishes in the adoral direction (sb in Figs. 2A, B, 3A<sub>1</sub>, B<sub>1</sub>, 4A, D, 5E). In *Argonauticeras* the bulge and the horizontally cut base of the flare have the same height and form rib-like ridges ventrally (Fig. 3B<sub>1</sub>). Furthermore, in *Argonauticeras*, the ncl 2 forms an internal thickening beneath the flare, i.e., an internal varix (var in Fig. 3B<sub>1</sub>). The innermost contributing layer is the inner prismatic layer (ipl), which is uninterrupted, and covers and smoothes the inner shell surface.

**Formation of the flares.**—During periodic flare formation shell growth ceased and the frilled aperture was presumably covered with mantle tissue, as indicated by the apc (Fig. 5A). In modern *Nautilus*, a probably homologous prismatic coating (mantle adhesive layer secreted by the adoral mantle) appears at the terminal aperture (Erben et al. 1969; Doguzhaeva and Mutvei 1986; Mutvei and Doguzhaeva 1997; Mutvei 2014). The apc occurs also in *Anagaudryceras* (Bucher et al. 1996: fig. 11) and *Eogaudryceras* (Doguzhaeva et al. 2010: pr in figs. 3, 5), hence we assume a similar genesis for all lytoceratids. Shell growth proceeds with the formation of a new segment of the conch tube at the base of the flare (shell duplication) (Fig. 5D, E). Therefore, the mantle was retracted into the living chamber. It is likely that the mantle edge attaches in front of the flare, since the opl 2 begins in direct contact with the apc. The bulge was probably a reaction to the retraction of the mantle whereby the mantle tissue was compressed and thus was pressed outwards. Similar structures occur in flares of *Anagaudryceras* (Bucher et al. 1996: fig. 11) and *Eogaudryceras* (Doguzhaeva et al. 2010: figs. 3, 5) and can also be seen during shell repair after injuries (e.g., Keupp 1998, 2012). Finally, in the rear parts of the living chamber, the ipl was laid down by the apical mantle as the growth continued (e.g., Kulicki 1979, 1996; Birkelund 1980).

**Modification of the flares.**—The majority of examined flares was removed or modified (Figs. 3A<sub>1</sub>, B<sub>1</sub>, 4A). The

question is which processes took place during their alteration. In rare cases, removed flares show irregularly broken surfaces (Fig. 4E). For those we assume a breakage due to mechanical stress. It seems likely that those structures represent accidents (e.g., collision, attacks). However, the majority of flares was presumably removed due to the resorption activity of mantle tissue on two occasions, namely during the formation of the actual whorl and again during overgrowth by the following whorl 360° later. Our interpretation is based on the following observations.

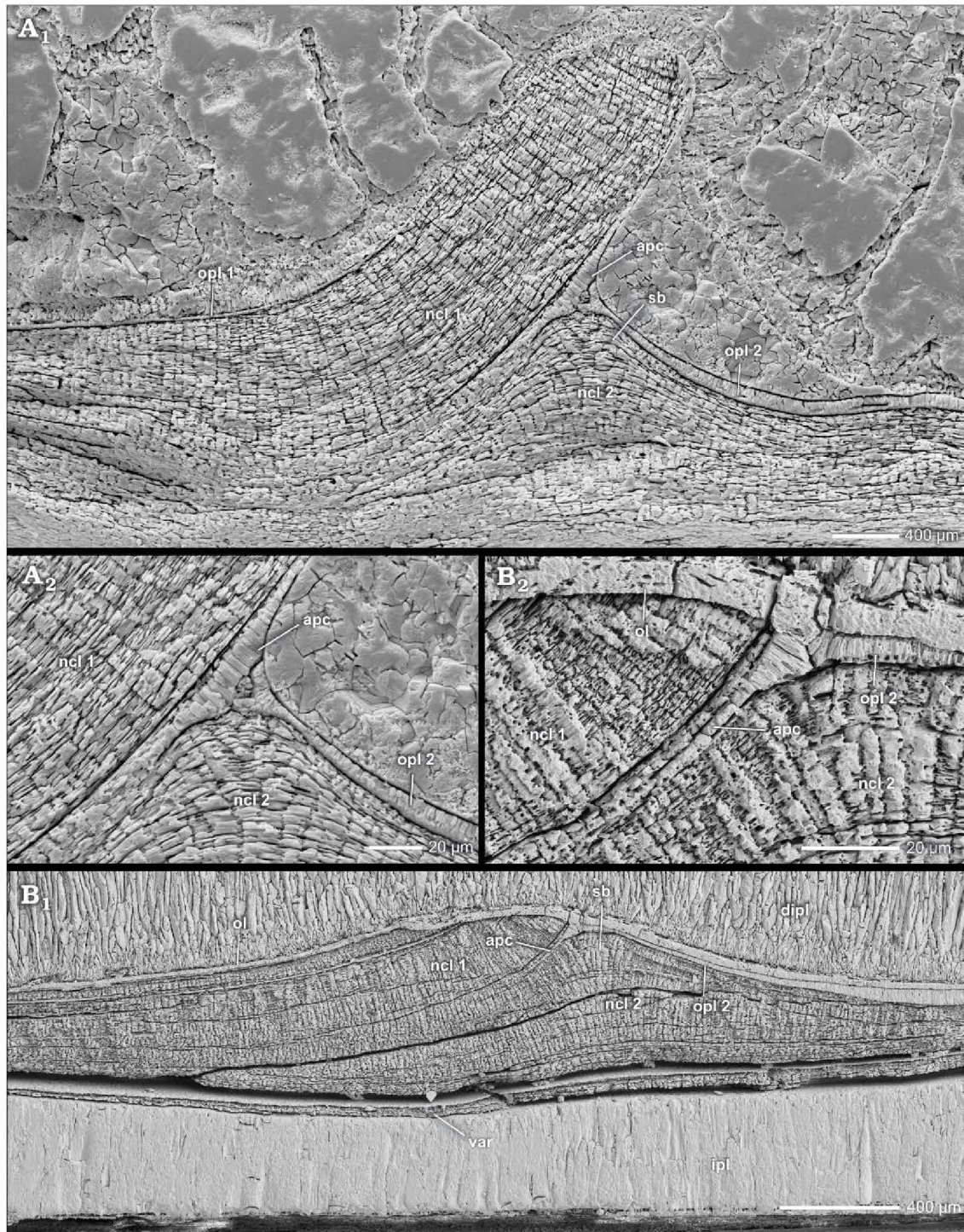
(i) Most of the flares show a more or less regular and recurring pattern of modification (rounded stumps of and/or horizontally cut flares) indicating a controlled process (e.g., resorption; Figs. 3A<sub>1</sub>, B<sub>1</sub>, 4A). Accordingly, we reject diagenesis or erosion that would produce irregular patterns. Broken flares as mentioned above are probably unaffected (irregular edge) because these are (already) short enough, making subsequent biologically controlled removal unnecessary.

(ii) All flares reduced in height show that all constituting shell layers (opl 1, ncl 1, apc) are affected (Figs. 3A<sub>1</sub>, B, 4A, B). In particular, thereby, the remaining cut base of *Argonauticeras*' flares and the associated bulge together form a rib-like ridge ventrally. The relief of the shell is significantly reduced at these positions. Similar phenomena were reported for Recent gastropods during resorption activities of their mantle tissue on the inner shell surface (e.g., Kohn et al. 1979).

(iii) One specimen of *Argonauticeras* preserved a rounded stump of a flare (Fig. 3A<sub>1</sub>) at the lower shell flank (whereas it is ventrally covered by the following whorl and is horizontally cut, i.e. rib-like ridges; Fig. 3B<sub>1</sub>). We assume that this lateral portion was out of reach of the mantle of the following whorl. Therefore, the mantle of the actual whorl resorbed the major part of the flare prior to the beginning of a new shell formation cycle, probably during withdrawal (Fig. 5A–C). The distal part of the flare was probably shed through destabilization (resorption) of its base and the resulting breaking surface was smoothed directly afterwards

Fig. 3. Internal structure of flares (median section, growth direction right) in *Argonauticeras besairiei* Collignon, 1949 from Ambatolafia, Mahajanga Basin, NW Madagascar; Lower Albian, Cretaceous. A. BSPG MAo-1705a. A<sub>1</sub>. Partially resorbed flare, the primary shell bends outwards and ends in a round stump; secondary shell material is attached from beneath and forms a prominent bulge in front of the flare. A<sub>2</sub>. Close-up of A<sub>1</sub>, contact of the primary shell and secondary shell, the apertural prismatic coating of the primary shell and the outer prismatic layer of the secondary shell are in direct





contact. **B.** BSPG MAo-1772. B<sub>1</sub>. Resorbed flare, the primary shell bends outwards and is cut off horizontally to the shell surface; secondary shell material is attached from beneath and forms a prominent bulge in front of the flare and a varix beneath. B<sub>2</sub>. Close up of B<sub>1</sub>, the flare is cut independently of the shell layers; condition of apertural prismatic coating and new outer prismatic layer as in A<sub>2</sub>. Abbreviations: apc, apertural prismatic coating; dipl, dorsal inner prismatic layer; ipl, inner prismatic layer; ncl 1/2, nacreous layer of the primary/secondary shell; opl 1/2, outer prismatic layer of the primary/secondary shell; ol, organic layer; sb, shell bulge; var, varix.



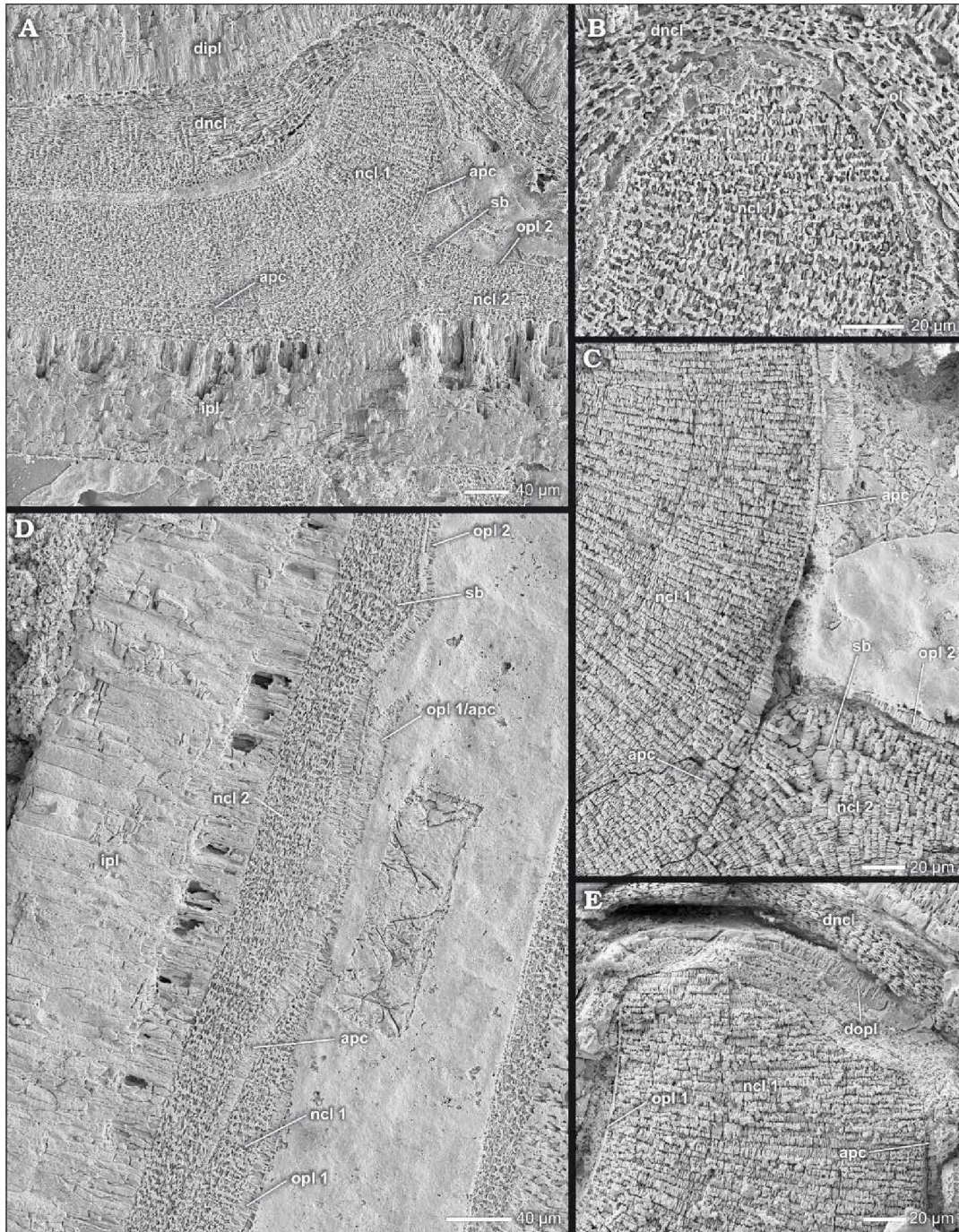


Fig. 4. Internal structure of flares (median section, growth direction right) in *Protetragonites fraasi* (Daqué, 1910) (BSPG MAN-4734) from Sakaraha, Morondava Basin, SW Madagascar; Upper Oxfordian, Jurassic. **A.** Partially resorbed flare, the primary shell bends outwards and ends in a round stump; secondary shell material is attached from beneath and forms a prominent bulge in front of the flare. **B.** Close-up of A, the flare's end is rounded through resorption. **C.** Contact of the primary shell with the secondary shell; the apertural prismatic coating is in contact with the outer prismatic layer of the secondary shell. **D.** Dorso-lateral equivalent of a flare, only a short shell extension is formed by the outer prismatic layer. **E.** Overgrown and broken flare, the →

by the mantle; Seilacher and Gunji (1993: 255) show corresponding, isolated “apertural rings” in the *Posidonia* Shale basin of Germany. We expect that this applies generally for removed flares with rounded stumps.

(iv) In several lytoceratid taxa, the resorption of flares is restricted to the contact area of the subsequent whorl; the frills are preserved at the whorl flanks. At the position of the subsequent whorl the flare has a cutting hole that matches with the perimeter of the subsequent whorl (e.g., Drushits et al. 1978; Doguzhaeva et al. 2010), indicating activity of the mantle of the following whorl. This is similar to the observations in *Argonauticeras* mentioned above; horizontally cut flare-bases are restricted to the ventral shell portions (Fig. 3B<sub>1</sub>) whereas lateral, rounded stumps of the flares prevail (Fig. 3A<sub>1</sub>). In *Argonauticeras*, each ventral, cut flare represents a cutting hole caused by the mantle of the following whorl. The horizontal cutting edge ends at the same height as the adoral bulge of the second shell generation. The bulge acts as a template for height (Fig. 5F, H, I). It is rather unlikely that the actual mantle could anticipate the needed height of the rib-like ridges or cut off the flare frill horizontally.

However, observations of an organic-rich dorsal coating layer covering the complete conch of *Gaudryceras* (Drushits et al. 1978; Birkelund 1980) may indicate a significantly larger potential extension of the mantle. It provides an explanation how flares of older, preceding whorls could be resorbed ventrally and laterally by the mantle of the following whorl (Fig. 5A, G–I). If this is true, the amount of resorption of the flare seems to be dependent on the position in the whorl, ventral (cut flare-bases) or lateral (rounded flare stumps), at least in *Argonauticeras*.

We prefer the possibility that the mantle removed and smoothed portions of the flares on two occasions, namely during formation of the actual aperture and during overgrowth by the following whorl (after 360°). Still, we cannot exclude the possibility that ventral and lateral portions of the flares were removed and smoothed by the mantle tissue on only one occasion—overgrowth by the following whorl.

According to our interpretation, ammonoid mantle tissue removes flares that are about 100 µm thick. Thus, the resorption ability in ammonoids resembles that of recent *Nautilus*, which is able to resorb outer shell portions of up to 150–200 µm thickness during overgrowth (Signor 1985; Ward 1987). It has to be noted that the removal of flares has a potential for misinterpretation. The varices associated with the rib-like ridges of *Argonauticeras* indicate the presence of flares but were handled as common ribs or varices in other works (e.g., Arkell et al. 1957; Hoffmann 2010). In this study we report on flares in *Argonauticeras* for the first time.

**Secondary flares.**—Secondary flares occur on the outer whorls as a sequence of 4–12 regularly spaced, weak rib-like

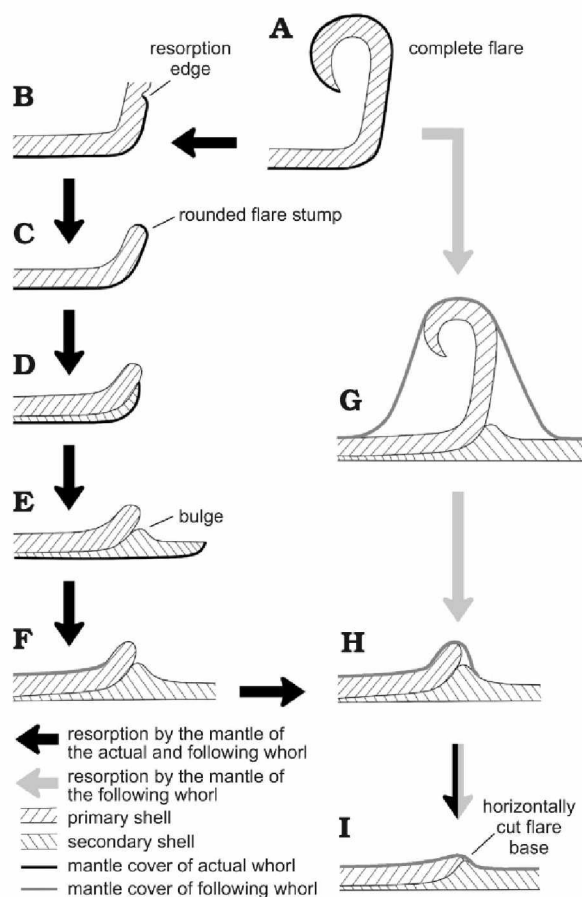


Fig. 5. Resorption process in flares of Lytoceratoidea. A. A complete flare with mantle cover. B. The retracting mantle begins resorption of shell material at the base of the flare. C. The mantle tissue rounds the flare stump after resorption. D. The retracted mantle begins secretion of secondary shell material. E. The mantle continues secreting the secondary shell. F. The mantle of the subsequent whorl begins to overgrow the flare stump of the preceding whorl. G. The mantle of the subsequent whorl overgrows the complete flare of the preceding whorl and begins its resorption. H. The mantle of the subsequent whorl resorbs the flare stump of the preceding whorl. I. The mantle of the subsequent whorl has smoothed the shell surface of the preceding whorl.

ridges preceding the formation of a fully developed flare in *Argonauticeras* (Fig. 6) but they had smaller dimensions. Similar to the primary flares, secondary flares mark the junction of two shell generations; ventrally, they appear like primary flares with a horizontally cut base (opl 1 and ncl 1 in Fig. 6). In contrast to the primary flare the participating nacreous layer is significantly thinner (ncl 1 in Fig. 6). In front of the cut secondary flare a bulge is present contributing to its rib-like appearance (sb in Fig. 6). The relief of the

primary shell ends in an irregular breaking edge. Abbreviations: apc, apertural prismatic coating; dipl, dorsal inner prismatic layer; dncl, dorsal nacreous layer; dopl, dorsal outer prismatic layer; ipl, inner prismatic layer; ncl 1/2, nacreous layer of the primary/secondary shell; opl 1/2, outer prismatic layer of the primary/secondary shell; ol, organic layer; sb, shell bulge.



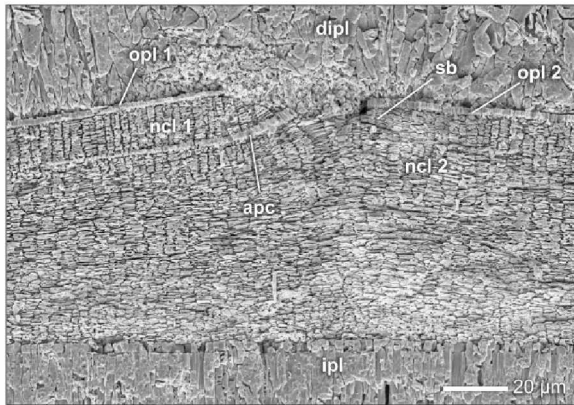


Fig. 6. Internal structure of a secondary flare (median section, growth direction right) in *Argonauticeras besairiei* Collignon, 1949 (BSPG MAO-1802) from Ambatolafia, Mahajanga Basin, NW Madagascar; Lower Albian, Cretaceous. Abbreviations: apc, apertural prismatic coating; dipl, dorsal inner prismatic layer; ipl, inner prismatic layer; ncl 1/2, nacreous layer of the primary/secondary shell; opl 1/2, outer prismatic layer of the primary/secondary shell; sb, shell bulge.

bulges can form a corresponding internal furrow, i.e., an undulation of the shell wall that the ipl smoothes out. It is likely that secondary flares developed like primary flares but were probably smaller marking a shorter interruption of growth.

**Parabola.**—*Choffatia* developed a regularly spaced number of parabola, up to nine per whorl. None of the observed parabola is completely preserved. Structurally, parabola resemble flares in several aspects in particular showing the junction of two shell generations, the primary and secondary shell. In median cross section, the primary shell appears to be cut perpendicular or sub-perpendicular to the shell surface (ncl 1 in Fig. 7A, B), at the position of parabola. It changes the relative orientation to the shell surface depending on its position in the shell whorl. At the ventral saddle, the primary shell has a horizontal orientation, parallel to the shell surface. At shell portions adjoined to the notches, the shell bends slightly outwards (Fig. 7D) and at the notches, the cutting edge remains clearly elevated (80 μm) above the shell surface (Fig. 7C). In transversal cross section, the primary shell forms characteristic slots at the parabolic notches (Fig. 8); the primary shell ends abruptly (ncl 1 in Fig. 8B–E), being similar to the observation in median section. The primary shell seems to be simply constructed; only the involvement of a thin ncl 1 (16–20 μm) was usually observed. Although the opl 1 is not preserved, we assume its presence. This is because Sprey (2002: pl. 4: 7) shows that parabola of juvenile *Binatisphinctes* are exclusively composed of the opl 1. Similar to the flares, parabola form an apc but only at the position of the notches as part of the outward bending shell edge (apc in Fig. 7C). The apc thickens distally but vanishes nearly completely towards the parabola-base.

As in flares the shell wall is locally doubled at the position of parabola through the formation of the secondary

shell from beneath (ncl 2 in Figs. 7, 8). It is this new generation that forms the parabolic nodes by undulation within the parabolic notches (Fig. 7D). The secondary shell seems to consist only of an ncl 2. A thin prismatic layer, or in most cases a void, separates the two shell generations (Fig. 7A, B). The ncl 1 and ncl 2 merge at varying distances aboral of the cutting edge (up to a half length of a septal chamber); therefore the beginning of the ncl 2 cannot be determined. Only at the notches, the secondary shell forms a prominent prismatic thickening (pt in Fig. 7C). In cross section, the pt has a symmetric triangular outline and has the same height as the outward bending cutting edge in front of which it is formed. The outer prisms habitus is much fainter than at the broad pt-base. The aboral margin of the pt wedges out underneath the free cutting edge and in the adoral direction. The pt and the apc of the free edge are separated by a discontinuity. Interestingly, Doguzhaeva (2012) describes prismatic “lens-like inclusions” at the same position (parabolic notches) in *Indosphinctes* (Perisphinctoidea). Each parabola is underpinned by a continuous inner prismatic layer (Fig. 8B–D).

**Formation of parabola.**—As in flares, the junction of two shell generations in parabola indicates the end of a secretion cycle, which is accompanied by the formation of a (not preserved) temporary aperture (halt in growth), and the subsequent withdrawal of the mantle for secretion of a new shell segment of the conch tube (continuing growth). The temporary aperture of parabola was probably covered with mantle tissue as in flares (apc): it is likely that the apc of both is equivalent, but was perhaps diagenetically altered here (change in thickness). However, the temporary aperture was modified afterwards (cutting-edge, see below).

After formation of the aperture, the mantle retracted into the living chamber to begin secretion of the new shell segment in front of it (shell duplication). The withdrawal of the mantle edge was probably very extensive, as is indicated by the wide aboral extension of the prismatic separation layer of the shell generations. This layer could be the opl 2 (usually secreted by the adoral mantle edge). However, we prefer the possibility that the separation is accomplished by the apc and that the opl 2 begins near the cutting-edge, which is more in accordance with the observations in flares (beginning at the base). Also in shell injuries, the opl 2 of the replacement shell begins immediately beneath the breaking-edge (e.g., Keupp 1998, 2012; GR personal observations). Similar to flares, there is evidence suggesting compression of the mantle tissue during formation of the parabolic nodes of the secondary shell (undulation). The soft tissue is probably compressed during withdrawal of the mantle and thus pressed outwards in reaction (compare Teisseyre 1883, 1889).

It is very likely that the prismatic “lens-like inclusions” described by Doguzhaeva (2012) and our pt are equivalent structures indicating a general feature for parabola, probably of biological origin. This pt could originate in the opl 2. However, we cannot exclude a diagenetic formation. The gradual fainting of its prisms from the inside to the out-

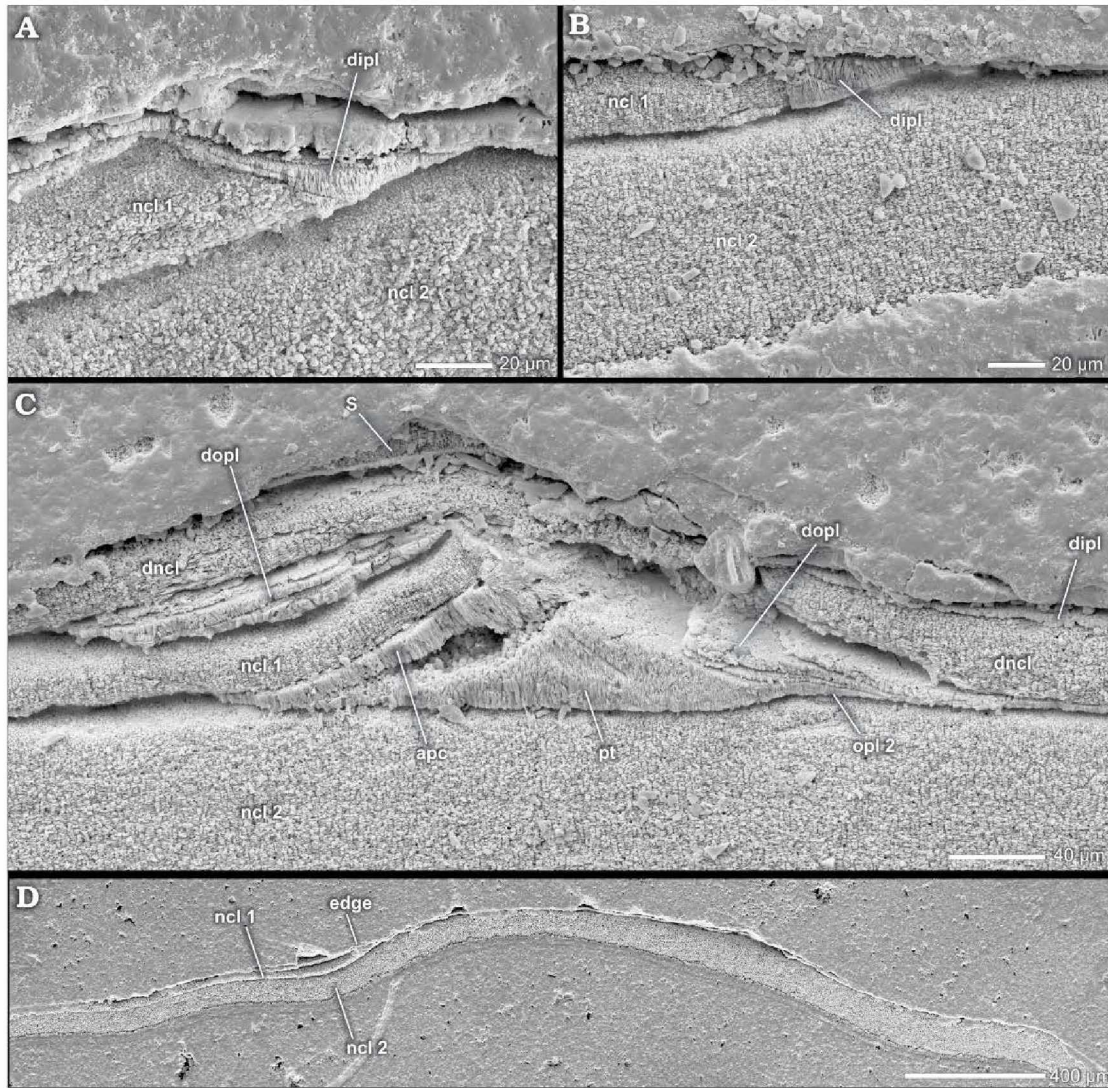


Fig. 7. Internal structure of parabolae (median section, growth direction right) in *Choffatia* sp. (BSPG MAN-4520) from Dubki near Saratov, SW Russia; Upper Callovian, Jurassic. **A, B.** Discontinuity of the parabola, the primary nacreous layer ends abruptly. A secondary nacreous layer is attached from beneath. The relief is compensated by the dorsal inner prismatic layer. **C.** Discontinuity of parabolae at the position of the notches. The primary shell bends outwards and has an apertural prismatic coating. The secondary shell is attached from beneath. In front of the free edge of the primary shell a symmetric, prismatic thickening is formed. The dorsal shell compensates the relief. **D.** Lateral parts of the notches show the typical outward undulation of the new shell of the parabolic node. Abbreviations: apc, apertural prismatic coating; dipl, dorsal inner prismatic layer; dncl, dorsal nacreous layer; dopl, dorsal outer prismatic layer; ncl 1/2, nacreous layer of the primary/secondary shell; opl 1/2, outer prismatic layer of the primary/secondary shell; pt, prismatic thickening; S, septum.

side indicates an outward-tending growth independent of the mantle tissue. This could be the product of diagenetic epitaxy or remote shell biomineralization, e.g., it mineralized out of a plug of extrapalial fluid with the opl 2 as the nucleolus for mineralization without direct control by the mantle tissue (Chinzei and Seilacher 1993; Seilacher and Chinzei 1993).

Finally, with continuing shell growth, the apical mantle portions secrete the inner prismatic layer (e.g., Kulicki 1979,

1996; Birkelund 1980), covering (and smoothing) the inner surface of the whorl.

**Modification of parabolae.**—A complete temporary aperture is not preserved; the primary shell is cut off. It is rather unlikely that the changing orientation of the primary shell and its cutting edges at the ventral saddle and the parabolic notches was caused by resorption (actual or subsequent whorl). Furthermore, the expected smoothing



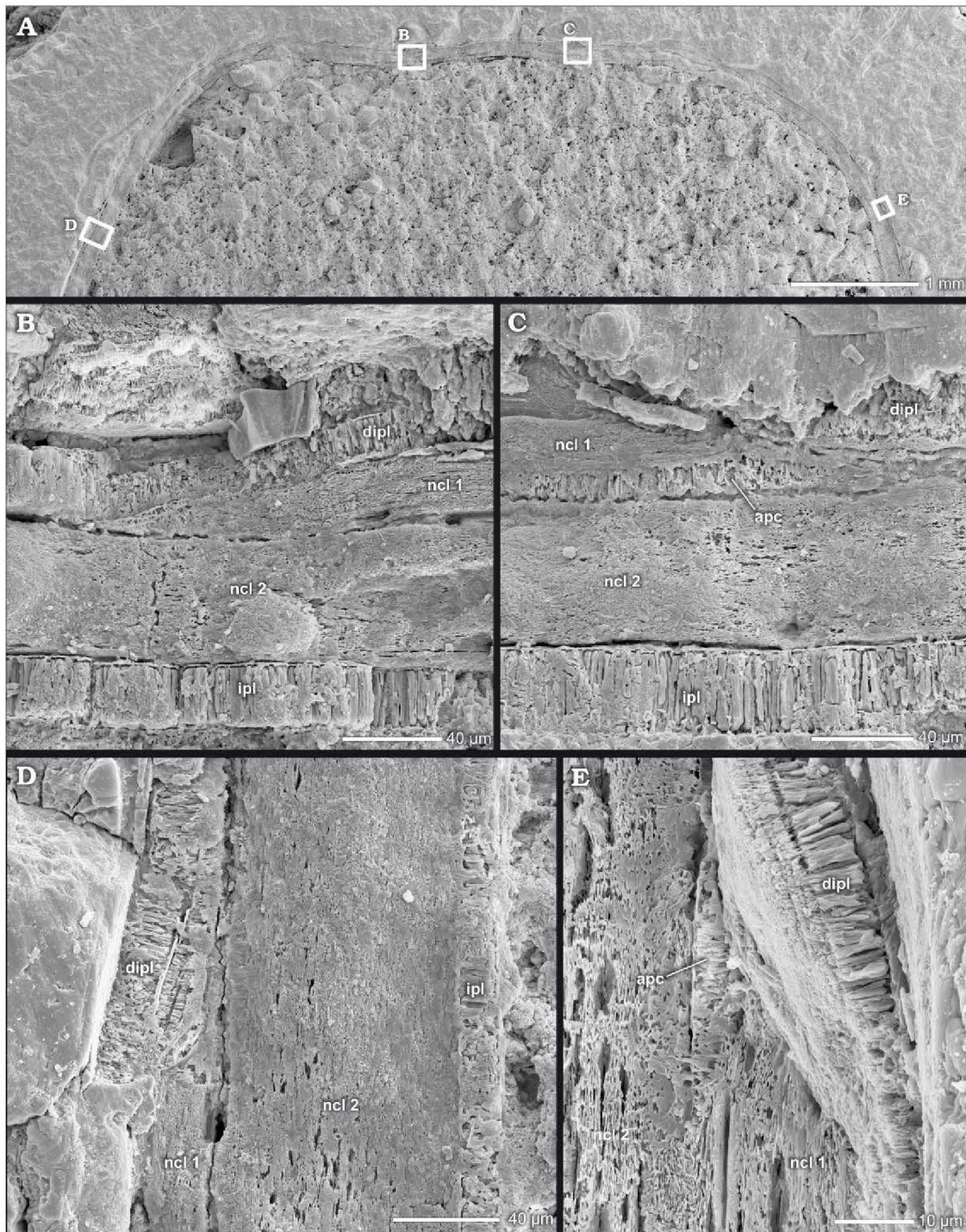


Fig. 8. Internal structure of paraboliae (transversal section) in *Choffatia* sp. (BSPG MAn-4519) from Dubki near Saratov, SW Russia; Upper Callovian, Jurassic. **A.** Parabola with notches. **B–E.** Discontinuity of the paraboliae, the primary shell forms slots at the position of the notches. A secondary shell is attached from beneath. The relief is compensated by the dorsal inner prismatic layer. Abbreviations: apc, apertural prismatic coating; dipl, dorsal inner prismatic layer; ipl, inner prismatic layer; ncl 1/2, nacreous layer of the primary/secondary shell.

or rounding of the shell is absent (e.g., Kohn et al. 1979). However, observed cutting edges are similar to reported breaking-edges of injuries (e.g., Keupp 1998, 2012; GR personal observations). Hence, we propose that the removal of the former aperture results from breakage, probably caused by the overgrowth of the subsequent whorl. Due to the more or less fragile character of the primary shell, shell portions would easily break off.

**Primary shape of parabolae.**—The ultrastructural data allow some substantiated assumptions about the original morphology of parabolae. Our observations contradict the model of resorbed, temporary apophyses (Teisseyre 1883, 1889; Siemiradzki 1898–1899; Brinkmann 1929; Hiltermann 1939). According to this model the ventro-lateral sinus of the parabolic notch is equivalent to the sinus of the apophyse. Both are supposed to be formed by the same processes, which for the apophyse are a local decrease in shell growth rates, i.e., it is not affected by resorption (or other kind of shell removal). In the apophyse model, resorption takes place only laterally (shortening of the apophyse) and ventrally at the aperture. Contrary to that, the removal (breakage or resorption) takes place along the complete length of parabolae. Furthermore, the original aperture of parabolae was enlarged at the position of the notches, an observation more or less unknown from the sinus of the apophyse, and the shell relief is rather smooth. The notch results from a folding of the aperture (see below). Several macroscopic aspects give further support, i.e., parabolae are affected by sculptural compensation in reaction to injuries; their position in the shell is not determined in contrast to that of apophyses which are always unaffected, even by previous injuries (Keupp 1973, 2000, 2012; Keupp and Dietze 1987), indicating a different formation process. The difference is also reflected in dimorphism, whereas parabolae occur in micro- and macroconchs of the same species. Namely, only adult microconchs develop apophyses, and smooth apertures are typical for adult macroconchs. The formation of the terminal aperture seems to be decoupled from the development of parabolae. It is rather unlikely that juvenile parabolae are ontogenetically connected to adult apophyses.

The enlargement of the parabolic aperture at the notches points to at least two possible primary shapes prior to removal.

(i) It was presumed that a parabolic notch could be a relic of a spine (Stieler 1922; Wendt 1968; Bucher and Guex 1990). In fact, Checa and Martin-Ramos (1989) highlighted the similarity of spines of *Aspidoceras* to those of parabolae in other Aspidoceratinae and assumed a morphogenetic connection. The outward bending cutting-edge of each notch would represent the aboral base of a former spine and parts of its flank. These spines have to be adorally open, as indicated by the apc (Fig. 1B: right expression), which corresponds to the assumptions of Stieler (1922) and Wendt (1968). Similar spines are known from some Recent gastropods, e.g., *Murex*.

(ii) Why, however, is the breaking edge not restricted to parabolic notches but continues at the flank? The ob-

Table 2. Shell wall components of shell generations of flares and parabolae.

Shell	Primary	Secondary
Outer prismatic layer	opl 1	opl 2
Nacreous layer	ncl 1	ncl 2
Apertural prismatic coating	apc	
Inner prismatic layer		ipl

servations match with Michalski's (1908) assumption that parabolic lines are the remains of a flare-like extended aperture, i.e., a frill. A parabolic notch represents a local folding of the frill. Michalski (1908) based his interpretation on the morphological transition of parabolae into flares in the Early Jurassic lycoceratid Pleuroacanthitinae (compare Wähner 1894). Recently Hoffmann and Keupp (2010) examined the phylogenetic relationship between parabolae and flares in well-preserved specimens of early Liassic *Analytoceras* from Timor and confirmed that flares represent morphological derivatives of parabolae (Fig. 9). Hence, parabolae and flares are not only similar in internal structure (Table 2) but are alike in appearance (Fig. 1B: middle expression).

In large specimens of *Analytoceras* the folds of parabolae are morphologically similar to adorally open, semi-closed spines (e.g., Bucher 1997; Hoffmann and Keupp 2010). This observation is in line with the assumed formation process of aspidoceratid spines (Checa and Martin-Ramos 1989). Therefore, we regard parabolae as frilled, temporary apertures with local folding at the future notches that can form spine-like extensions. The parabolae and their parabolic spines probably formed a rather small enlargement of the aperture. In our parabolae, the thin shell lamellae of the ncl 1, in comparison to the thick ncl 2 (Figs. 7B, 8B–D), indicate an early mineralization state near the former apertural edge, or rather secretion area. Therefore, the frills (and spines) were probably not much larger than the preserved outward bending cutting edges at the notches, probably slightly higher than the observed 80  $\mu\text{m}$ .

A frill-like enlargement probably does not prevail for the whole parabola. For example, the ventral saddle of parabolae in *Analytoceras* forms a ridge-like undulation and end parallel to the shell surface (Fig. 9A). This could also explain the horizontal orientation of the primary shell at the ventral saddle in our parabolae; ventrally the apertural edge could be horizontally orientated (Fig. 1B: middle and right expression) as in other ammonoids (e.g., Mutvei 2014). Alternatively, the frill could break off at its base. In some Perisphinctoidea, like *Orthosphinctes*, the lateral parabolae form a rib-like undulation of the aperture; the shell bends outwards and then returns to the height of the normal shell surface, no frill is formed.

**Secondary effects of frilled parabolae.**—The frill-like aperture assumption for parabolae results in several implications: analogously to flares we assumed that some parabolic ribs represent shortened or stumps of frills which are reinforced by the secondary shell.



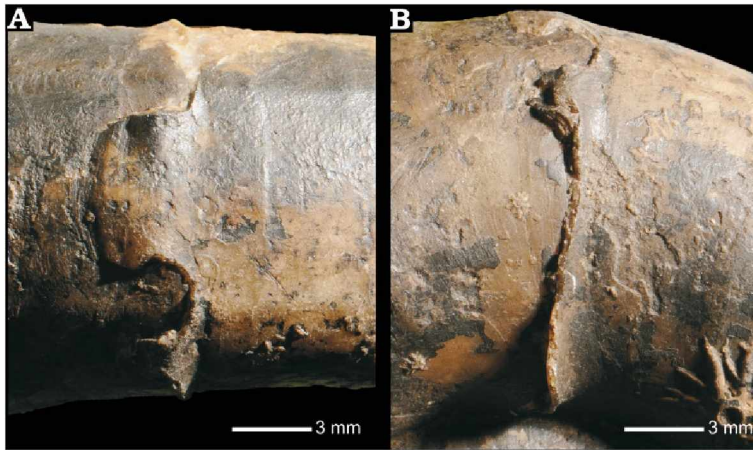


Fig. 9. Transition of parabolae and flares in *Analytoceras hermanni* (Gümbel, 1868) (BSPG Man-x) from Bihati river valley south of Baun, SW Timor, Hettangian, Jurassic (compare Hoffmann and Keupp 2010); in ventral (A) and lateral (B) views.

The sculptural discontinuity is a morphogenetic effect of frill formation, its subsequent removal and the reattachment of the shell-secreting mantle tissue. After withdrawal, the mantle edge attaches to the curved base of the parabolae (note that in flares the base is usually straight and therefore paralleling the growth lines) and bridges the slots of the notches. The sculpture of the secondary shell was formed parallel to the attachment line of the mantle edge and is therefore independent of the aboral sculpture of the primary shell that is to be cut off. Furthermore, it is likely that the aboral sculpture continues at the frill, probably influenced by the folding. The parabolic notches represent a lack of shell material (frill-folds/spines), instead of a cut through the adoral sculpture, increasing the impression of different sculptural orientation of the primary and secondary shell. Formation of the frill-folds/spines was presumably the reason for the often-observed local deceleration in growing near the parabolic notches and the accompanied compression of growth lines (Keupp 1973).

As previously indicated, the parabolic nodes are secondary infillings of the parabolic notches resulting from the reattachment of the mantle and secretion of new shell material while the mantle is pressed outwards. The mineralized shell copies the resulting outer relief of the mantle. Hence, the parabolic nodes are equivalent to the hollow floors in hollow spines of other ammonoids (e.g., *Pleuroceras*, *Kosmoceras*), which are subsequently added as shell growth continues (e.g., Erben 1972; Keupp 1973; Birkelund 1980).

**Derivation of frill-model from superstructure-model for parabolae.**—Doguzhaeva (2012) proposed the interesting hypothesis that parabolae represent a band-like superstructure of the musculature. According to her, the parabolic line represents the trace of a simultaneous internal and outer attachment of the musculature indicating a (semi-) internal shell. The interpretations of parabolae as temporary apertures were therefore dismissed by her. The hypothesis of Doguzhaeva (2012) is based on the following observations and interpretations: (i) Impressions of parabolic notches pre-

served as nodes (knobs) at the internal mould represent pits of the shell wall which reflect sites of muscle attachment at the position of the notches. (ii) The dorsal shell portions bear parabolic nodes as well, which represent dorsal muscle attachment. (iii) The ventral saddle and lateral areas adjoining the parabolic notches have a characteristic striation representing a part of the band superstructure. (iv) Instead of an interruption in shell growth, the parabolic notches are represented by prismatic lens-like embeddings in the nacreous layer. These are accompanied by small nacreous chips denoting compression pressure from muscular activity.

The interpretation of Doguzhaeva (2012) is in contradiction to observations reported in the sections above. However, her observations can be reinterpreted in favour of the frill-model. In this study the whole parabolic line as well as the notches are associated with a discontinuity in shell growth (junction of two shell generations, withdrawal of the mantle). (i) Instead of representing muscular attachment pits, the parabolic nodes are formed as secondary infillings of an undulated secondary shell within the parabolic notches (Fig. 7D), caused by reattachment accompanied by compression of the mantle. The internal relief of the node is preserved as a knob-like mark on the internal mould (Fig. 7D) as Doguzhaeva (2012) observed. (ii) A dorsal equivalent of parabolae could not be recognized in median or transversal cross section but the dorsal shell of the succeeding whorl compensates the relief. Accordingly, dorsal parabolic nodes merely represent the cast of the former whorl in the dorsal shell (Fig. 7C). (iii) The striations of the ventral saddle and of the adjoined areas of the notches are probably equal to common growth increments, which were interrupted due to the loss of the parabolic folds/spines (notches). (iv) The pt associated with the frill-fold/spines (Fig. 7C) is probably equivalent to the prismatic embeddings found by Doguzhaeva (2012). Doguzhaeva (2012) cut this pt in transversal cross sections, simulating an embedding in the nacreous layer, but representing the ncl 1 and the ncl 2 separated by the pt. Only the embedded nacreous chips were

not recognized by us but they could be a product of diagenetic disruption of the shell.

**Homology.**—Based on the identical internal structure (opl 1, ncl 2, apc; Table 2) and formation process, the similar primary shape and transitional structures in Pleuroacanthitinae, we propose a general homology for flares and parabolae. Occurrences of parabolae in Phylloceratoidea—the stem group of Jurassic and Cretaceous Ammonitina—suggest that these were passed on to the Lytoceratoidea and Perisphinctoidea, probably as a facultative feature. Accordingly, their internal construction is identical. Parabolae seem to be the primary state whereas the simpler flares of Lytoceratoidea are the derived state (Michalski 1908; Hoffmann 2010; Hoffmann and Keupp 2010). It can be assumed that in the perisphinctids a second evolutionary trend can be recognized in addition to the flares in lytoceratids: the closed hollow spines of aspidoceratids are probably derived from the parabolae, i.e., the parabolic folding forms the spines (Checa and Martin-Ramos 1989). For the Late Devonian parabolae-bearing Clymeniida the relation to Jurassic and Cretaceous taxa is difficult to estimate but a similar structure and formation process of their parabolae is likely.

**Megastriae.**—Parabolae, flares and secondary flares are in accordance with the definition of megastriae proposed by Bucher and Guex (1990), i.e., radial linear elements associated with a discontinuity in shell growth comprising the outer prismatic (opl 1 × opl 2) and the nacreous (ncl 1 × ncl 2) layer (compare Bucher et al. 1996; Bucher 1997). It is questionable whether this strict definition can be always used for radial linear elements associated with an interruption in shell growth that are normally assigned to megastriae. For example, Drushits and Doguzhaeva (1981) and Sprey (2002) show flares and (juvenile) parabolae that are only formed by the opl 1. Strictly speaking, these sculptural elements cannot be taken as megastriae according to Bucher and Guex (1990). However, the observations of Sprey (2002) may indicate a structural change of parabolae during ontogeny. Parabolae of juveniles are composed of the opl 1 while parabolae of adults are composed of the opl 1 and the ncl 1. This is likely since Sprey's (2002) and our observations were made in closely related genera: *Binatisphinctes* and *Choffatia*. In our opinion, the differences in structure do not necessarily imply a different morphogenesis, i.e., the withdrawal of the mantle edge. Instead, they indicate earlier activity of additional shell-secreting mantle tissue prior to retraction, i.e., formation of the ncl 1. Variations in structure may just indicate a different timing of formation (prolonged or short periods of shell precipitation). Although structurally very similar, the primary and secondary flares represent a difference in time of formation, too, as indicated by their different scale. However, both would be handled equally as megastriae according to Bucher and Guex (1990). In our opinion the strict definition of megastriae excludes a number of related, radial linear sculptures or does not consider morphological or temporal differences. We recom-

mend a broader definition of megastriae, i.e., radial linear elements associated with an observable interruption of shell growth in a single or multiple shell layers. For the distinction of megastriae subtypes, different time frames have to be taken into account. It is noteworthy that the identification of a megastriae (sensu Bucher and Guex 1990; Bucher et al. 1996 and as defined here) does not automatically imply the presence of an originally enlarged aperture, comparable to flares or parabolae.

**Possible function of a frilled aperture.**—Since the frill formation constituted a certain effort for the animal, it is likely that the frill was used for a special purpose and was not instantly replaced as proven by the apc of flares and parabolae which indicates a resting stage (permanent mantle attachment).

Flares and parabolae extend the effective radius of the aperture. Similar apertural modifications are observed in some modern gastropods, such as Cassidae, Ranellidae, Personidae, and Muricidae (Wendt 1968; Linsley and Javidpour 1980; Seilacher and Gunji 1993; Vermeij 1993) and have a primary function of protection against predators. This kind of interpretation for flares and parabolae is supported by the fact that parabolae are predominantly restricted to juvenile ammonoid shells. Their small diameter made them vulnerable to attack. Development of some protective shell elements or strategies likely helped them to survive this critical period of their ontogeny. The ammonoid frill could impede attacks on the aperture. The larger radius probably complicates the grabbing of the whole aperture. We assume that flares and parabolae are very fragile structures that easily break off during an attack, allowing the ammonoid to escape or to withdraw the soft body into its living chamber, i.e., an easy-to-tear strategy (Checa 1994; see also Keupp 2012: 79). Additionally, it could serve as a certain deterrent of potential attackers, especially when armoured with spines. The permanent mantle cover (apc) possibly renders deterring colour patterns, as seen in modern molluscs (e.g., Vermeij 1993). Deterrence would be useful since flares and parabolae hinder fast movement in an escape. On the other hand, the extended surface of the aperture and its mantle cover could fulfil a sensory function. The frill could improve the perception of movements in the immediate vicinity and the chemical perception of predators, prey or mating partners.

In present day gastropods, e.g., *Murex*, similar temporary apertural frills are associated with an episodic growth mode (Wendt 1968; Vermeij 1993; Checa 1994; Bucher et al. 1996). The shell portion between frills represents a stage of fast growing periostracum whereas a frill represents a long lasting mineralization stage and pause in growth. The shell structure of ammonoid flares and parabolae reflects this situation, i.e., junction of two shell generations and pause in secretion. Hence, the apc indicates an episodic rhythm of growth in flares and parabolae. However, in *Argonauticeras*, two episodic patterns overlap each other: the pattern of the

primary flares and that of secondary flares. The explicit formation of primary flares in contrast to secondary flares underlines its needed function.

Several authors have assumed that the repeated interruptions of growth represent a controlled reorientation of the shell aperture to compensate fabrication conflicts that disturb spiral growth (Seilacher and Gunji 1993; Bucher et al. 1996; Bucher 1997). Furthermore, these authors argue that the sculptural discontinuity seen in parabolae is directly related to the controlled reorientation of the aperture. Whereas a reorientation is within the realm of possibility, the sculptural discontinuity in parabolae is a morpho-fabricational secondary effect of frill formation and its removal, as mentioned above.

## Conclusions

The internal structure of lycoceratid flares and perispinctid parabolae indicate that both represent homologous constructions associated with episodic growth. Both structures represent the junction of two different shell generations, comprising the outer prismatic (opl 1 × opl 2) and nacreous (ncl 1 × ncl 2) layer. The second shell generation is formed after withdrawal and reattachment of the mantle tissue that causes the discontinuity of shell layers. Therefore, the term megastriae proposed by Bucher and Guex (1990) is applicable to both, flares and parabolae. During the final step of shell formation, the mantle tissue secretes the inner prismatic layer (ipl). Due to the internal structure of parabolae, an affiliation to a superstructure of the musculature system, hypothesized by Doguzhaeva (2012), can be dismissed.

Flares and parabolae are formed as episodic, temporary frill-like extensions of the aperture during pauses in growth. Their inner surface was covered by the mantle as indicated by an apertural prismatic coating (apc), which we report for the first time. The coating is probably homologous with the mantle adhesive layer of *Nautilus* (Erben et al. 1969; Doguzhaeva and Mutvei 1986; Mutvei and Doguzhaeva 1997; Mutvei 2014). The complete preserved flares of *Argonauticeras* show that these end in a backward reflection of the shell. A complete parabola was not observed. Their prominent parabolic notches represent traces of local foldings that can form open spines. The sculptural discontinuity usually associated with parabolae is not caused by resorption but is a morphogenetic effect that results from the withdrawal and reattachment of the mantle edge at the curved base of parabolae.

However, flares show evidence of resorption of the shell. Resorbed flares take the form of rounded stumps or were cut horizontally at their bases. Cut bases and the bulge (an undulation of the secondary shell in front of the flares) form weak rib-like ridges. These (false) ribs can be easily distinguished from common ribs (undulation) by the structural discontinuity but have the potential for macroscopic misinterpretation: for example, this study is a first report

of flares for *Argonauticeras*, which have previously been described as ribs (Hoffmann 2010). We propose a removal of flares by the mantle tissue of the actual whorl and of the following whorl. The actual mantle tissue resorbed the distal parts of the flare prior to secretion of the secondary shell, forming rounded stumps as a result. The horizontally cut flares are the result of resorption of the ventral flare-stumps by the mantle of the following whorl during overgrowth. In contrast to resorption, breakage is assumed for the fragile parabolic frills of *Choffatia*.

The enlargement of the aperture of flares and parabolae probably had a certain defensive purpose against predatory attacks (e.g., expandable shell, deterrence). This effect could have been enhanced through coloured mantle tissue (warning or camouflage pattern) that might also have had a sensitive function.

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Aus Urheberrechtsgründen wurde das folgende Kapitel der Dissertation entfernt.

For copyright reasons, the following chapter of the doctoral thesis was removed.

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## The dorsal shell wall structure of Mesozoic ammonoids

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The study of pristine preserved shells of Mesozoic Ammonoidea shows different types of construction and formation of the dorsal shell wall. We observe three major types: (i) The vast majority of Ammonoidea, usually planispirally coiled, has a prismatic reduced dorsal shell wall which consists of an outer organic component (e.g., wrinkle layer), which is the first layer to be formed, and the subsequently formed dorsal inner prismatic layer. The dorsal mantle tissue suppresses the formation of the outer prismatic layer and nacreous layer. With the exception of the outer organic component, secretion of a shell wall is omitted at the aperture. A prismatic reduced dorsal shell wall is always secreted immediately after the hatching during early teleoconch formation. Due to its broad distribution in (planispiral) Ammonoidea, the prismatic reduced dorsal shell wall is probably the general state. (ii) Some planispirally coiled Ammonoidea have a nacreous reduced dorsal shell wall which consists of three mineralized layers: two prismatic layers (primary and secondary dorsal inner prismatic layer) and an enclosed nacreous layer (secondary dorsal nacreous layer). The dorsal shell wall is omitted at the aperture and was secreted in the rear living chamber. Its layers are a continuation of an umbilical shell doubling (reinforcement by additional shell layers) that extends towards the ventral crest of the preceding whorl. The nacreous reduced dorsal shell wall is formed in the process of ontogeny following a prismatic reduced dorsal shell wall. (iii) Heteromorph and some planispirally coiled taxa secrete a complete dorsal shell wall which forms a continuation of the ventral and lateral shell layers. It is formed during ontogeny following a prismatic reduced dorsal shell wall *a priori*. The construction is identical with the ventral and lateral shell wall, including a dorsal nacreous layer. The wide distribution of the ability to form dorsal nacre indicates that it is a plesiomorphic trait which either was passed on from gyrocone ammonoid ancestors or (re-)developed in post-Triassic ammonoids.

**Key words:** Ammonoidea, internal structure, dorsal shell wall, wrinkle layer, spiral ornament, Ritzstreifen, Mesozoic.

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### Introduction

Ammonoid conchs are built of a conservatively constructed aragonitic shell wall. In simplified terms their shell wall consists of four layers: an outer organic periostracum, an outer prismatic layer, a middle nacreous layer, and an inner prismatic layer (Fig. 1A; e.g., Birkelund 1967, 1980; Erben et al. 1968, 1969; Kulicki 1979, 1996; Keupp 2000; Doguzhaeva et al. 2010; Kulicki et al. 2016; Radtke and Keupp 2016; Radtke et al. 2016). In most cases, the periostracum is not preserved; it was probably shed during lifetime (Checa 1994; Keupp 2000). This general configuration can be modified, for example with omitted or additional shell layers (Howarth 1975; Birkelund 1980; Doguzhaeva and Mutvei 1989, 1991). Different portions of the shell-secreting mantle form the individual shell layers. It is assumed that the outer organic periostracum and the outer prismatic layer were secreted at the aperture by the oral

edge of the mantle. Also the middle nacreous layer was formed near the aperture but more adapically. The adapical parts of the mantle secreted the inner prismatic layer in the rear of the living chamber, maybe in connection with the formation of the nacreous layer of the septa (e.g., Blind 1975; Howarth 1975).

Most ammonoids form a planispirally coiled conch by flanging the outer whorl on the preceding whorl. In general, during that process, ammonoids omit a dorsal shell wall in the contact area of the whorls (Fig. 2A) and the dorsal shell wall is reduced in this way. Mineralized shell material is formed only in the rear parts of the living chamber (Fig. 2A<sub>2</sub>) and consists often only of the inner prismatic layer (Fig. 1D). The outer prismatic and the nacreous shell layer wedge out at the umbilical contact (Fig. 1F; Palframan 1967; Birkelund and Hansen 1968, 1974, 1975; Erben et al. 1968, 1969; Drushits and Khiami 1970; Walliser 1970; Erben and Reid 1971; Bayer 1974; Howarth 1975; Lehmann 1976, 1990;

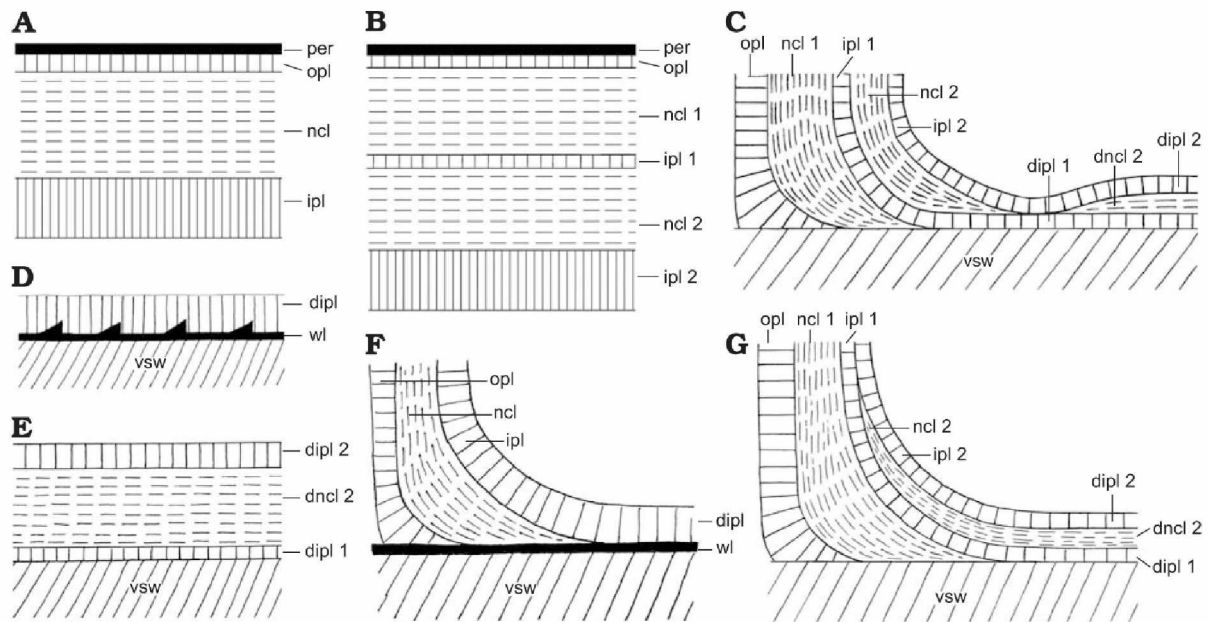


Fig. 1. Schematic construction of the ventral and dorsal shell wall (A, B, D, E, median section, growth direction right, centrifugal; C, F, G, transversal section, centrifugal). A. Simple ventral shell wall. B. Ventral shell wall with a doubling. C, E, G. Nacreous reduced dorsal shell wall. D, F. Prismatic reduced dorsal shell wall. Abbreviations: dipl, dorsal inner prismatic layer; dipl 1/2, primary/secondary dorsal inner prismatic layer; dncl, dorsal nacreous layer; dncl 1/2, primary/secondary dorsal nacreous layer; ipl, inner prismatic layer; ipl 1/2, primary/secondary inner prismatic layer; ncl, nacreous layer; ncl 1/2, primary/secondary nacreous layer; opl, outer prismatic layer; per, periostracum; vsw, ventral shell wall of the preceding whorl; wl, wrinkle layer.

Drushits et al. 1977; Kulicki 1979, 1996; Doguzhaeva 1980, 1981, 2002; Birkelund 1980; Zakharov and Graboskaya 1984; Doguzhaeva and Mutvei 1986, 1991, 1993a, b; Bucher et al. 1996; Zakharov 1996; Kulicki and Tanabe 1999; Keupp 2000; Kulicki et al. 1999, 2001, 2002, 2016; Doguzhaeva et al. 2010; Doguzhaeva 2012).

Several ammonoid taxa have a wrinkle layer as an additional element of the dorsal shell wall, namely an outer component (Fig. 1D, F; Kulicki 1979; Doguzhaeva 1980, 1981; Zakharov and Graboskaya 1984; Zakharov 1996; Kulicki and Tanabe 1999; Kulicki et al. 2001) which is probably an equivalent formation to the black layer of *Nautilus*. Similar to the black layer this layer forms a highly variable, fingerprint-like relief of small ridges and knobs (wrinkles) at the surface of the preceding whorl (e.g., Walliser 1970; House 1971; Senior 1971; Tozer 1972; Hölder 1973; Korn 1985; Keupp 2000).

Given that the ancestors of planispirally coiled ammonoids had gyrocone conchs with whorls that are detached from each other and therefore do not support each other, it is likely that these ancestors formed a complete dorsal shell wall, which mean that the ventral, lateral, and dorsal shell wall form a continuum aperturally and adapically (Fig. 2B). Indeed, heteromorph ammonoids, taxa with a secondarily decoiled shell, reveal a uniformly three-layered shell tube ventrally, laterally and dorsally (Figs. 1A, 3A, B; Erben et al. 1969; Doguzhaeva and Mikhailova 1982; Landman 1987; Doguzhaeva and Mutvei 1989). A complete dorsal shell wall

could be already formed right after the end of the embryonic ammonitella (first whorl and protoconch), as observed in the heteromorph *Luppiovia* (Doguzhaeva and Mikhailova 1982) and *Ptychoceras* (Doguzhaeva and Mutvei 1989). Planispirally coiled taxa probably merely suppressed the secretion of the outer shell layers (i.e., dorsal outer prismatic layer and dorsal nacreous layer).

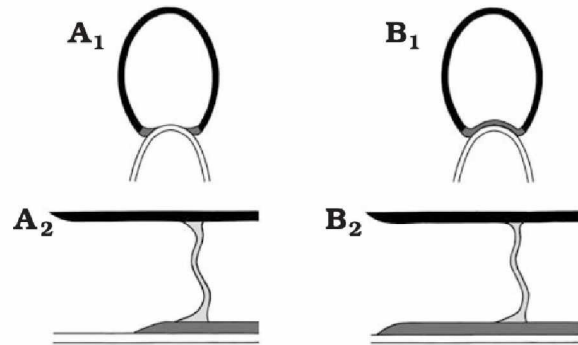


Fig. 2. Schematic drawing of general dorsal shell wall types (A<sub>1</sub>, B<sub>1</sub>, transversal section, centrifugal; A<sub>2</sub>, B<sub>2</sub>, median section, growth direction left, centrifugal). A. Reduced dorsal shell wall. The lateral shell wall wedges out at the contact with the preceding whorl. The dorsal wall is omitted at the aperture. B. Complete dorsal shell wall. The ventral, lateral, and dorsal shell walls form a continuum. The dorsal wall is present at the aperture. Colouring: black, ventral/lateral wall of the succeeding whorl; dark grey, dorsal wall of the succeeding whorl; light grey, septum of the succeeding whorl; white, ventral wall of the preceding whorl.



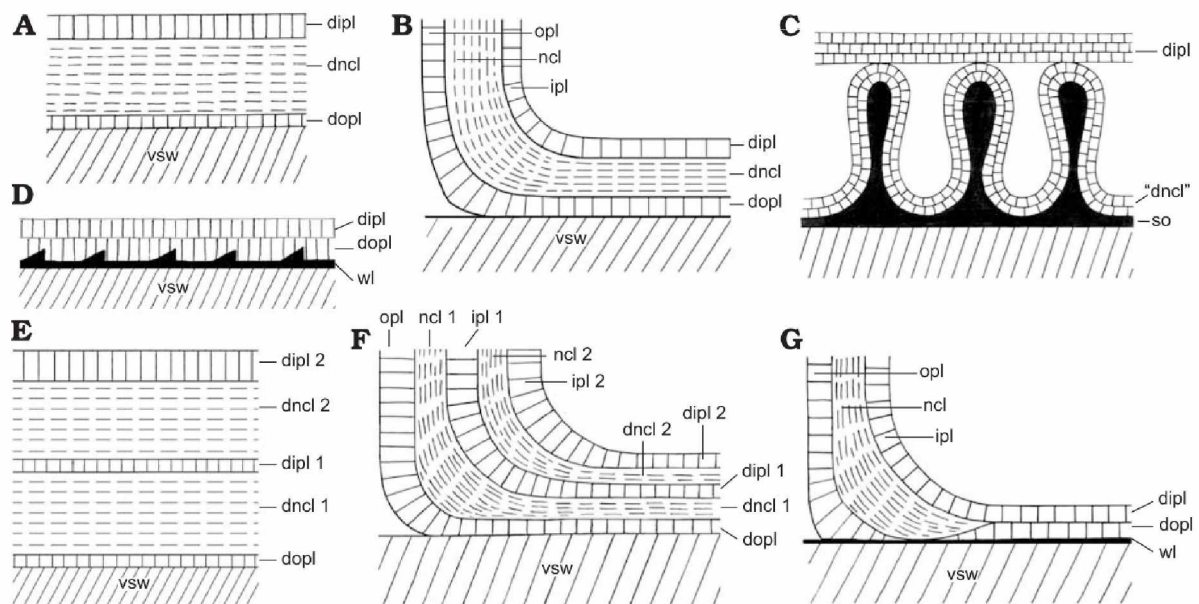


Fig. 3. Schematic construction of the dorsal shell wall (A, D, E, median section, growth direction right, centrifugal; B, C, F, G, transversal section, centrifugal). A, B. Complete dorsal shell wall. D, G. Seemingly complete dorsal shell wall. C. Complete dorsal shell wall of *Amaltheidae*. E, F. Reinforced complete dorsal shell wall. Abbreviations: dipl, dorsal inner prismatic layer; dipl 1/2, primary/secondary dorsal inner prismatic layer; dncl, dorsal nacreous layer; dncl 1/2, primary/secondary dorsal nacreous layer; dopl, dorsal outer prismatic layer; ipl, inner prismatic layer; ipl 1/2, primary/secondary inner prismatic layer; ncl, nacreous layer; ncl 1/2, primary/secondary nacreous layer; opl, outer prismatic layer; so, spiral ornament; vsw, ventral shell wall of the preceding whorl; wl, wrinkle layer.

In this study, we aimed to determine whether the dorsal shell wall of ammonoids has any potential for phylogenetical and/or taxonomical purposes. Of particular interest is the question whether there are any systematically important similarities or differences in the internal structure, formation, or ontogeny (e.g., the morphological expression of the inner prismatic layer or the wrinkle layer). Primarily, this work is intended to clarify which ammonoid taxa form a complete dorsal shell wall. Do taxa, that form a reduced dorsal shell wall, have the general ability to form an optional complete dorsal shell wall during ontogeny or in reaction to some triggers (e.g., injuries, overgrowth of encrusters)? We also check whether the ability to form a complete dorsal shell wall is a requirement for the development of heteromorph taxa.

*Institutional abbreviations.*—AMNH, American Museum of Natural History, New York City, USA; FU, Freie Universität, Berlin, Germany; BSPG, Bavarian State Collection for Palaeontology and Geology, Munich, Germany.

*Other abbreviations.*—cl, coating layer; D, diameter; dipl, dorsal inner prismatic layer; dipl 1/2, primary/secondary dorsal inner prismatic layer; dncl, dorsal nacreous layer; dncl 1/2, primary/secondary nacreous layer; dopl, dorsal outer prismatic layer; dspl, dorsal septal prismatic layer; dsw, dorsal shell wall; if, infilling; ipl, inner prismatic layer; ipl 1/2, primary/secondary inner prismatic layer; ncl, nacreous layer; ncl 1/2, primary/secondary nacreous layer; ol, organic layer;

ooc, outer organic component; opl, outer prismatic layer; opl 1/2, primary/secondary outer prismatic layer; per, periostracum; PI, preservation index; s, septum; so, spiral ornament; sphpr, spherulitic-prismatic layer; spl, septal prismatic layer; vsw, ventral shell wall; wl, wrinkle layer.

## Material and methods

This study is based on more than 290 well preserved shells of more than 200 different ammonoid taxa from different Triassic, Jurassic, and Cretaceous localities in England, France, Germany, Greenland, Japan, Madagascar, Russia, and the USA (see SOM: table A, Supplementary Online Material [http://app.pan.pl/SOM/app62-Radtke\\_Keupp\\_SOM.pdf](http://app.pan.pl/SOM/app62-Radtke_Keupp_SOM.pdf)). The specimens are housed at BSPG (as part of H. Keupp's collection) and AMNH. According to the SEM preservation index by Cochran et al. (2010), the examined shell material has a predominantly aragonitic preservation of a good (PI = 3) to poor (PI = 1) state. The shells of several taxa, mainly from the Triassic, were completely recrystallized without a preserved ultrastructure of the shell wall.

Freshly broken material and etched median and transversal sections were analyzed. Etched sections were polished with aluminum oxide and afterwards treated with 10% formic acid for 5–10 seconds. All samples were fixed on aluminum stubs with conductive carbon glue and sputtered with gold. Observations were made and pictures were taken

with the scanning electron microscope Zeiss SUPRA 40VP at the palaeontological section of the FU.

## Results and discussion

**The ventral and lateral shell wall.**—In all studied taxa with preserved shell, the ventral and lateral shell wall of the postembryonic conch consists of the typical three aragonitic shell layers: an outer prismatic layer, a middle nacreous layer and an inner prismatic layer (Figs. 1A, 4A<sub>1</sub>, B<sub>1</sub>, C, F<sub>1</sub>, 5A<sub>1</sub>, A<sub>2</sub>). An organic periostracum was only observed with certainty in some Phylloceratoidea (e.g., *Phylloceras* [*Euphylloceras*] cf. *velledae*) and Desmoceratoidea (e.g., *Desmophyllites diphylloides*) forming conspicuous extensions (see below). The outer and inner prismatic layers consist of parallel, elongated prisms that are perpendicular to the shell surface, i.e., regular simple prismatic microstructure. The median naere layer is formed by stacks of polygonal aragonite plates, i.e., columnar naere (Carter and Clark 1985; Carter et al. 1989).

The thickness of these mineralized layers can vary greatly within individual taxa. In particular, the members of the Perisphinctoidea seem to reduce the prismatic layers in late ontogenetic stages. Other taxa modify the shell wall by adding a secondary nacreous layer and secondary inner prismatic layer to the internal surface of the trilayered shell wall, e.g., *Aconeceras* sp. 1 (Haploceratoidea), *Rondiceras* sp. (Stephanoceratoidea), *Speetoniceris* sp., *Aspidoceras* sp. (both Perisphinctoidea), *Beudanticeras* sp. (Desmoceratoidea). These additional layers are called a shell doubling, i.e., the resulting shell wall has five mineralized layers (Fig. 1B; cf. Howarth 1975; Birkelund 1980; Doguzhaeva and Mutvei 1989, 1991).

The septa of all taxa attach to the inner surface of the inner prismatic layer. They are made of a layer of columnar naere. Also prismatic structures can occur, particularly at the contact of the septum with the shell wall, e.g., local thickenings of the inner prismatic layer or a proximal prismatic coating of the adoral septal surface (spl in Figs. 4C<sub>2</sub>, 5A<sub>3</sub>).

**The prismatic reduced dorsal shell wall.**—The dorsal shell walls of this type consist basically of two components, an outer organic component, in most cases a wrinkle layer, which attaches to the previous whorl, and a dorsal inner pris-

matic layer which seals the inner surface of the outer organic component (Figs. 1D, 4A<sub>1</sub>, B<sub>1</sub>, C<sub>2</sub>, 6A, 7A<sub>1</sub>, 8A). With the exception of the outer component, dorsal shell material is omitted at the aperture, i.e., the inner prismatic layer wedges out towards the aperture in the rear living chamber (Figs. 2A<sub>2</sub>, 6).

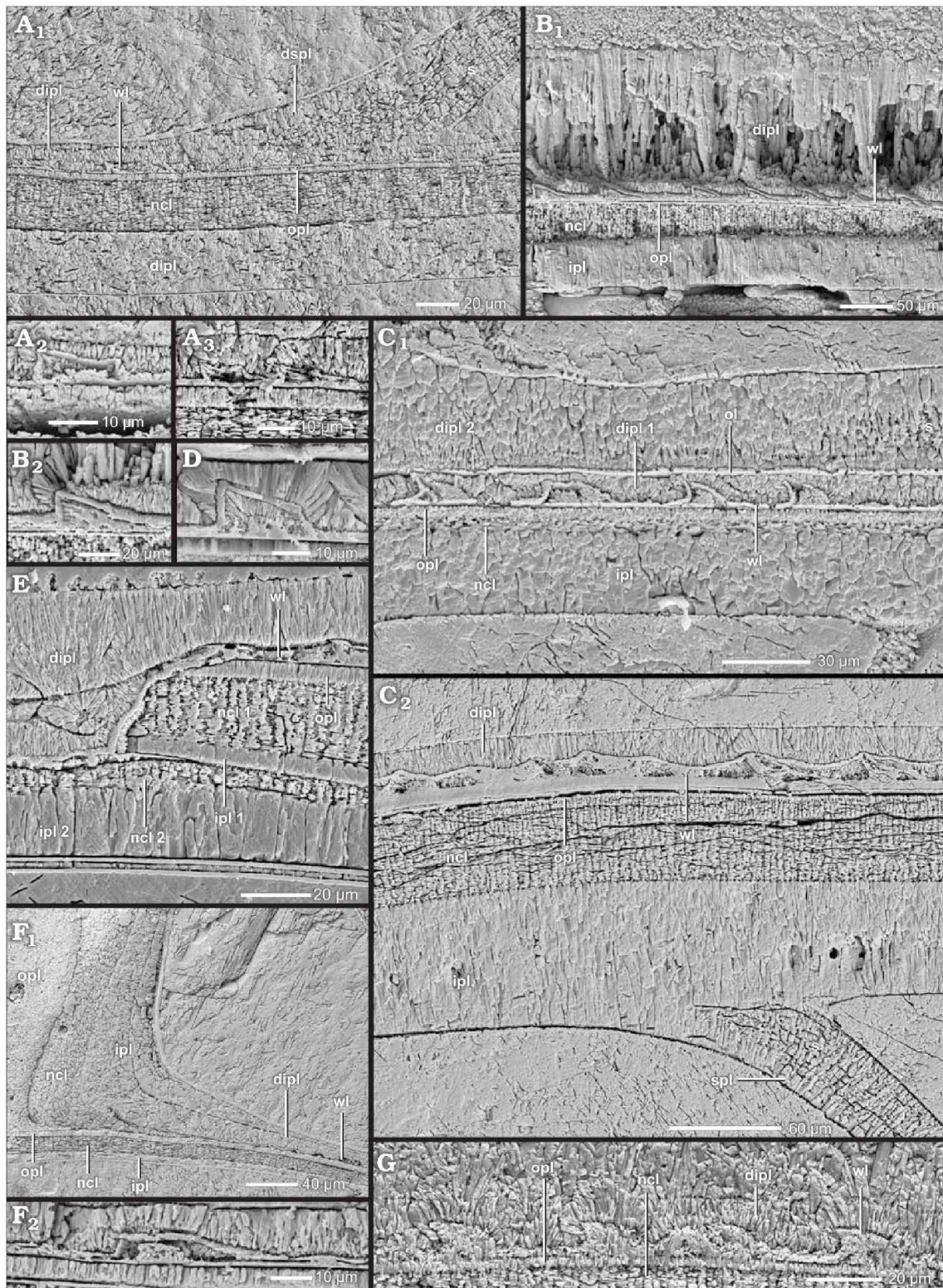
A prismatic reduced dorsal shell wall is typical for the vast majority of planispirally coiled taxa and occurs throughout the whole Mesozoic in nearly all groups (Fig. 9; SOM: table A). Generally, even taxa which develop another dorsal shell wall type during ontogeny (see below) pass through an early ontogenetic stage of a prismatic reduced dorsal shell wall after hatching, e.g., heteromorphs like the Scaphitoidea.

**The wrinkle layer.**—The outer organic component is one of the integral parts of the prismatic reduced dorsal shell wall. The most common and distributed formation is the wrinkle layer (see SOM: table A). A genuine wrinkle layer can be observed in smooth or only weakly sculptured taxa of the Phylloceratoidea (e.g., *Phylloceras* [*Euphylloceras*] cf. *velledae*), Lytoceratoidea (e.g., *Argonauticeras besairiei*), Tetragonitoidea (e.g., *Eogaudryceras* [*Eotetragonites*] *umbilicostriatus*), Stephanoceratoidea (e.g., *Quenstedtoceras lamberti*) and Desmoceratoidea (e.g., *Desmoceras* [*Desmoceras*] *latidorsatum*), but occurs also in Eoderoceratoidea (e.g., *Pleuroceras salebrosum*), Hildoceratoidea (e.g., *Leioceras opalinum*), Haploceratoidea (e.g., *Aconeceras* sp. 1), Perisphinctoidea (e.g., *Proplanulites* sp., *Divisosphinctes* sp. 2), Hoplitoidea (e.g., *Metaplacenticeris subtilistriatum*), Douvilleiceratoidea (e.g., *Douvilleiceris mammillatum*), and Scaphitoidea (e.g., *Scaphites whitfieldi*).

The wrinkle layer has a fingerprint-like relief which is formed as a sequence of more or less regularly spaced faint ridges and/or knobs (Fig. 8B, C) which are usually triangular or trapezoidal in cross section (Figs. 4A<sub>2</sub>, A<sub>3</sub>, B<sub>2</sub>, D, F<sub>2</sub>, 7A<sub>3</sub>), i.e., the individual wrinkles. The ridges are restricted in radial length; up to 200 µm (Fig. 8B). The wrinkle layer attaches directly to the ventral shell wall of the preceding whorl, even covering its injuries (Figs. 4E, 7A<sub>5</sub>, 8A). The wrinkle layer extends throughout the whole living chamber (Fig. 6) but is restricted to the attachment area of the succeeding to the preceding whorl. The wrinkle layer either wedges out towards (Fig. 4F<sub>1</sub>), or often ends abruptly at (Fig. 10A), the umbilical seam. The wrinkle layer has no equivalent in the ventral/lateral (mineralized) shell layers (i.e., opl,

Fig. 4. Construction of the prismatic reduced dorsal shell wall (A–E, G, median section, growth direction to the left, centrifugal; F, transversal section, centrifugal). A. *Phylloceras* (*Euphylloceras*) sp., BSPG MAO-1769, early Albian, Cretaceous, Ambatolafia, Mahajanga Basin, NW Madagascar; A<sub>1</sub>, the dorsal shell wall consists of an outer wrinkle layer and a dorsal inner prismatic layer; A<sub>2</sub>, A<sub>3</sub>, organic wrinkles. B. *Ptychophylloceras* sp., BSPG MAO-4516, late Oxfordian, Jurassic, Sakaraha, Morondava Basin, SW Madagascar; B<sub>1</sub>, the dorsal shell wall consists of an outer wrinkle layer and a dorsal inner prismatic layer; B<sub>2</sub>, organic wrinkle. C–E, G. *Desmoceras* (*Desmoceras*) *latidorsatum* (Michelin, 1838), early Albian, Cretaceous, Ambatolafia, Mahajanga Basin, NW Madagascar. C. BSPG MAO-1783; C<sub>1</sub>, the dorsal shell wall forms a wrinkle layer-complex; C<sub>2</sub>, the wrinkle layer is enriched with organic material. D. BSPG MAO-1839, organic wrinkle. E. BSPG MAO-1788, the relief of an injury of the preceding whorl (i.e., forma aegra substructa of Hölder (1973) is overgrown by the outer wrinkle layer and compensated by the dorsal inner prismatic layer. G. BSPG MAO-1782, the wrinkle layer of the dorsal shell wall becomes prismatic. F. *Neosilesites ambatolafrensis* Collignon, 1963, BSPG MAO-1780, early Albian, Cretaceous, Ambatolafia, Mahajanga Basin, NW Madagascar; F<sub>1</sub>, at the umbilical seam, the outer prismatic layer and the nacreous layer of the attaching whorl wedge out; only the inner prismatic layer continues towards the spiral plane; the wrinkle layer wedges out towards the umbilical seam; F<sub>2</sub>, organic wrinkle. Abbreviations: dipl, dorsal inner prismatic layer; dipl 1/2, primary/secondary dorsal inner prismatic layer; dspl, dorsal septal prismatic layer; ipl, inner prismatic layer; ipl 1/2, primary/secondary inner prismatic layer; ncl, nacreous layer; ncl 1/2, primary/secondary nacreous layer; opl, outer prismatic layer; s, septum; spl, septal prismatic layer; wl, wrinkle layer.







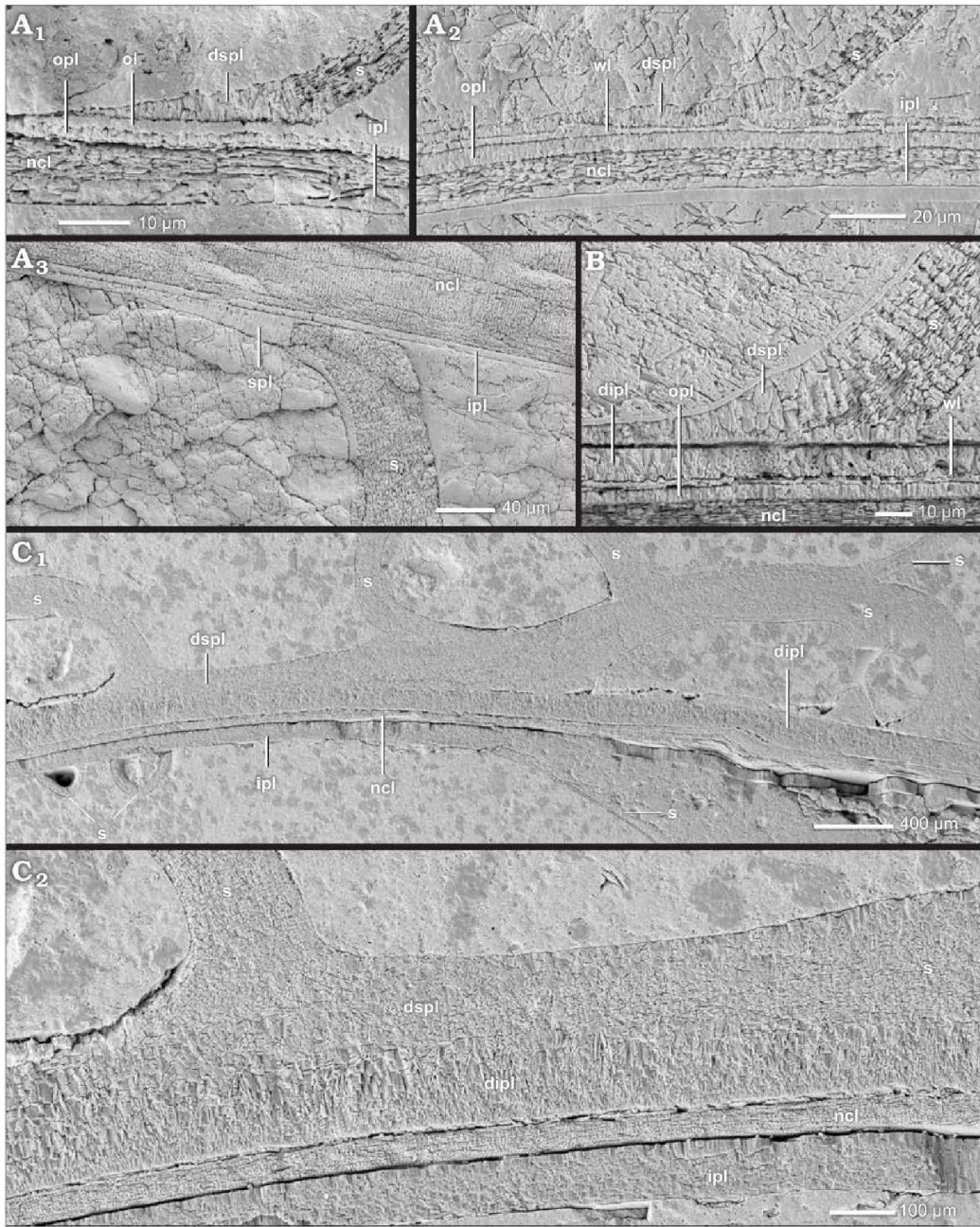


Fig. 5. Construction of the prismatic reduced dorsal shell wall (median section, growth direction to the left, centrifugal). **A.** *Desmoceras (Desmoceras) latidorsatum* (Michelin, 1838), BSPG MAo-1786, early Albian, Cretaceous, Ambatolafia, Mahajanga Basin, NW Madagascar; A<sub>1</sub>, the early dorsal shell wall consists of a smooth organic layer and (prismatic) septal mural parts; A<sub>2</sub>, later in ontogeny, the septal mural parts extend and seem to form the first dorsal inner prismatic layer; A<sub>3</sub>, the prismatic mural part of a nacreous septum can form an own layer which is separated from the ventral inner prismatic layer; the nacreous and prismatic materials of a septum merge. **B.** *Neosilesites ambatolafiensis* Collignon, 1963, BSPG MAo-1779, early Albian, Cretaceous, Ambatolafia, Mahajanga Basin, NW Madagascar; the prismatic mural part of a nacreous septum can form an own layer which is separated from the dorsal inner prismatic layer; the nacreous and prismatic materials of a septum merge. **C.** *Argonauticeras besairiei* Collignon, 1949, BSPG MAo-1705, early Albian, Cretaceous, Ambatolafia, Mahajanga Basin, NW Madagascar; C<sub>1</sub>, the septal mural part seems to be the origin of the inner sub-layer of the dorsal inner prismatic layer; C<sub>2</sub>, close up of C<sub>1</sub>. Abbreviations: dipl, dorsal inner prismatic layer; dspl, dorsal septal prismatic layer; ipl, inner prismatic layer; ncl, nacreous layer; ol, organic layer; opl, outer prismatic layer; s, septum; spl, septal prismatic layer; wl, wrinkle layer.

ncl, and ipl) but these layers attach to the wrinkle layer at the umbilical seam (Figs. 1F, 4F<sub>1</sub>, 10A).

Well preserved wrinkles are “hollow” organic structures; they consist of a small organic core with a prismatic coating which is covered by an organic surrounding (Figs. 4A<sub>2</sub>, A<sub>3</sub>, D, F<sub>2</sub>, 7A<sub>3</sub>). Often the ultrastructure of the wrinkles is altered: the wrinkle layer or parts of it can be preserved as a granular layer (Fig. 8D), prismatic layer (Fig. 4G) or hollow space. Sometimes the wrinkle layer forms a thick homogeneous organic layer with an undulating relief (the wrinkles can be still differentiated; Fig. 4C<sub>2</sub>).

Our observations show that the wrinkle layer relief develops during ontogeny. The early appearance of the wrinkle layer is a relief-less, smooth organic layer that covers the previous whorl (Fig. 5A<sub>1</sub>). The first wrinkles occur suddenly between diameters of 2 to 10 mm (Fig. 5A<sub>2</sub>). These diameters probably correspond with the third to fourth whorl as derived from a few taxa with preserved ammonitella (first whorl and protoconch). On occasion, wrinkles cover the ammonitella, e.g., *Eogaudryceras* (*Eotetragonites*) *umbilicostriatum* (Tetragonitoidea). Ontogenetic young wrinkles in particular often seem to be entirely hollow (i.e., lacking prismatic portions) or consist only of organic material.

*Derivates of the wrinkle layer.*—During ontogeny, some taxa develop individual or special morphological expressions of the wrinkle layer or the outer organic component, respectively. For example, in the outer whorls of *Douvilleicerias mammillatum* (Douvilleiceratoidea) individual wrinkles (Fig. 7A<sub>2</sub>, A<sub>3</sub>) cannot be recognized any more and the prismatic portions of the wrinkles merge (Fig. 7A<sub>4</sub>). However, the organic cores of the wrinkles can be still distinguished. The results are elongated, large wrinkles or even a (discontinuous) prismatic-spherulitic layer.

In the Madagascan and Russian specimens of *Aconeceras* sp. 1 and 2 (Haploceratoidea), the wrinkle layer of the outer whorls forms a strong thickening at the ventral crest of the preceding whorl (sphpr in Fig. 8E<sub>1</sub>, E<sub>2</sub>). The overgrown flanks of the preceding whorl are covered by normal wrinkles (Fig. 8E<sub>3</sub>, F). At the ventral edges of the preceding whorl, both appearances merge (Fig. 8E<sub>3</sub>). The thickening is dominated by an organic composition but shows several disordered spherulitic-prismatic inclusions (Fig. 8E<sub>2</sub>); it is called the spherulitic-prismatic layer (cf. Doguzhaeva and Mutvei 1991, 1993b). Two other haploceratids, *Taramelliceras externodosum* and *Sanmartinoceras* sp., develop similar structures. However, thick prismatic portions dominate the layer in *Sanmartinoceras* sp. (Fig. 10B). Interestingly, *Puzosia saintoursi* (Desmoceratoidea) develops a similar organic-prismatic package of the wrinkle layer at local ridge-like thickenings (Fig. 11A<sub>1</sub>, A<sub>2</sub>).

The outer organic component of the dorsal shell wall of Scythian *Hedenstroemia hedenstroemi* (Sageceratoidea) thickens towards the ventral crest of the preceding whorl (ol in Fig. 10C). On top of the venter of the preceding whorl, it is up to twelve times thicker than at the shell flanks.

*Gaudryceras tenuiliratum* (Tetragonitoidea) develops a

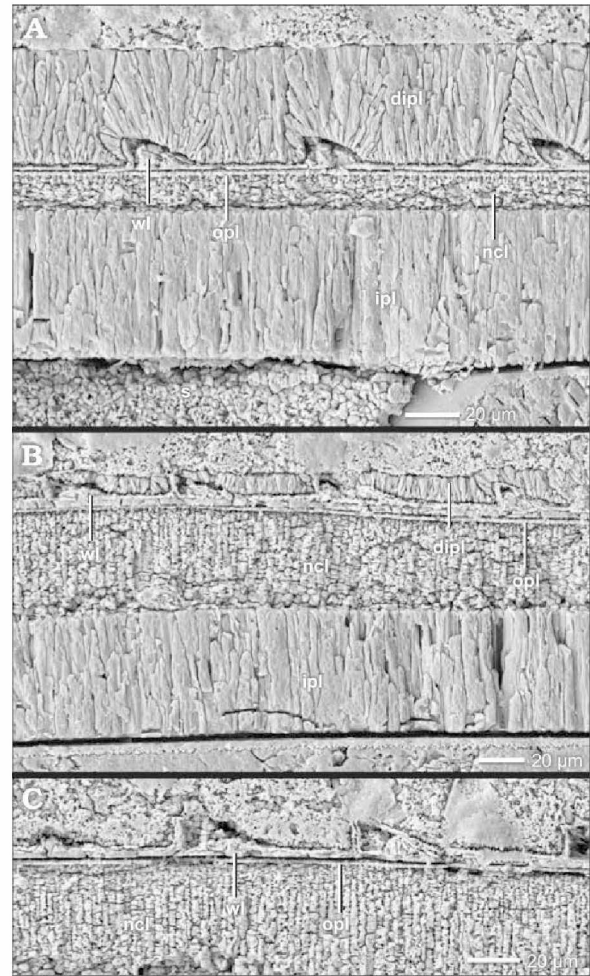


Fig. 6. Construction of the prismatic reduced dorsal shell wall (median section, growth direction to the left, centrifugal). *Ptychophylloceras* cf. *daequiei* Joly, 1976, BSPG MAN-4516, late Oxfordian, Jurassic, Sakaraha, Morondava Basin, SW Madagascar. The dorsal shell wall consists of an outer wrinkle layer and dorsal inner prismatic layer. The dorsal inner prismatic layer becomes thinner towards the aperture (A, B) and vanishes completely (C). Abbreviations: dipl, dorsal inner prismatic layer; ipl, inner prismatic layer; ncl, nacreous layer; opl, outer prismatic layer; s, septum; wl, wrinkle layer.

thick, homogeneous organic layer (Fig. 10D) which is called the coating layer here (cf. Drushits et al. 1978; Birkelund 1980; Doguzhaeva and Mutvei 1993b; Kulicki 1996; Kulicki et al. 2001). It traces the relief of the preceding whorl. Furthermore, several taxa form only a smooth organic layer instead of a wrinkle layer, e.g., *Rudolphtruempiceras planorbis* (Dinaritoidea).

*The formation and function of the outer organic component.*—The ammonoid preceding whorl was covered by an organic outer component of the ammonoid dorsal shell wall, e.g., a wrinkle layer, a spherulitic-prismatic layer, a thick coating layer or a smooth organic layer.



The wrinkle layer with its relief is the most peculiar and common character in our specimens. In contrast to some other opinions (e.g., Walliser 1970; House 1971; Senior 1971; Doguzhaeva 1980, 1981; Korn 1985) we conclude that the wrinkle layer is a distinct element of the dorsal shell wall (Tozer 1972; Kulicki et al. 2001; Klug et al. 2004; Keupp 2008; Mironenko 2015) which is not related to any other (mineralized) shell layer of the ventral/lateral shell wall (i.e., opl, ncl, and ipl).

We assign this layer to the dorsal shell wall due to the following characteristics: (i) The wrinkle layer occurs only dorsally covering the venter of the preceding whorl. Internal ventral and lateral wrinkle-like reliefs, e.g. "Ritzstreifen", are formed by the inner prismatic layer (see below). (ii) It acts like a subsequent coating of the ventral shell wall (e.g., covering of injuries). (iii) The wrinkle layer has no connection to other shell layers (at least none was observed) and seems to be an individual element of the shell wall. However, we cannot exclude the possible assignment of the wrinkle layer to the dorsal periostracum.

Since the wrinkle layer attaches directly to the previous whorl and further layers attach to its internal surface, the wrinkle layer was the first of all dorsal shell layers to be secreted. Its wide extension within the living chamber, probably up to the aperture, indicates a formation at or at least near the aperture. Indeed, several authors have shown that the wrinkle layer extends beyond the aperture (e.g., Walliser 1970; House 1971; Tozer 1972; Korn 1985; Keupp 2000; Mironenko 2015). Current interpretations of the wrinkle layer assume a secretion of it in front of the aperture by a supracerphalic mantle fold (e.g., Kulicki et al. 2001; Klug et al. 2004; Mironenko 2015). This explanation matches best with our observation and those of other authors, i.e., extension beyond the aperture.

The wrinkle layer or rather its relief is usually attributed to a roughness effect (e.g., Walliser 1970; Ristedt 1971; Doguzhaeva and Mutvei 1986; Lehman 1990; Keupp 2000) analogous to the black layer of *Nautilus* (Kulicki et al. 2001; Klug et al. 2004). The individual wrinkles had probably the function of a ratchet (e.g., asymmetric triangles in cross-section), so that the soft body had a better grip in the living chamber and beyond. This function is most probable because wrinkles are most prominent in weakly sculptured

taxa. The delayed occurrence of the wrinkle layer relief indicates that it is not needed from the beginning of ontogeny. Its formation probably represents a more active life style that requires a movement of the soft body within the living chamber, i.e., the transition from planktonic to nectonic? In some ammonoids like *Eogaudryceras* (*Eotetragonites*) *umbilicostriatus* (Tetragonitoidea), this stage starts earlier than in other taxa, maybe corresponding to a temporal shift in ontogeny, i.e., heterochrony.

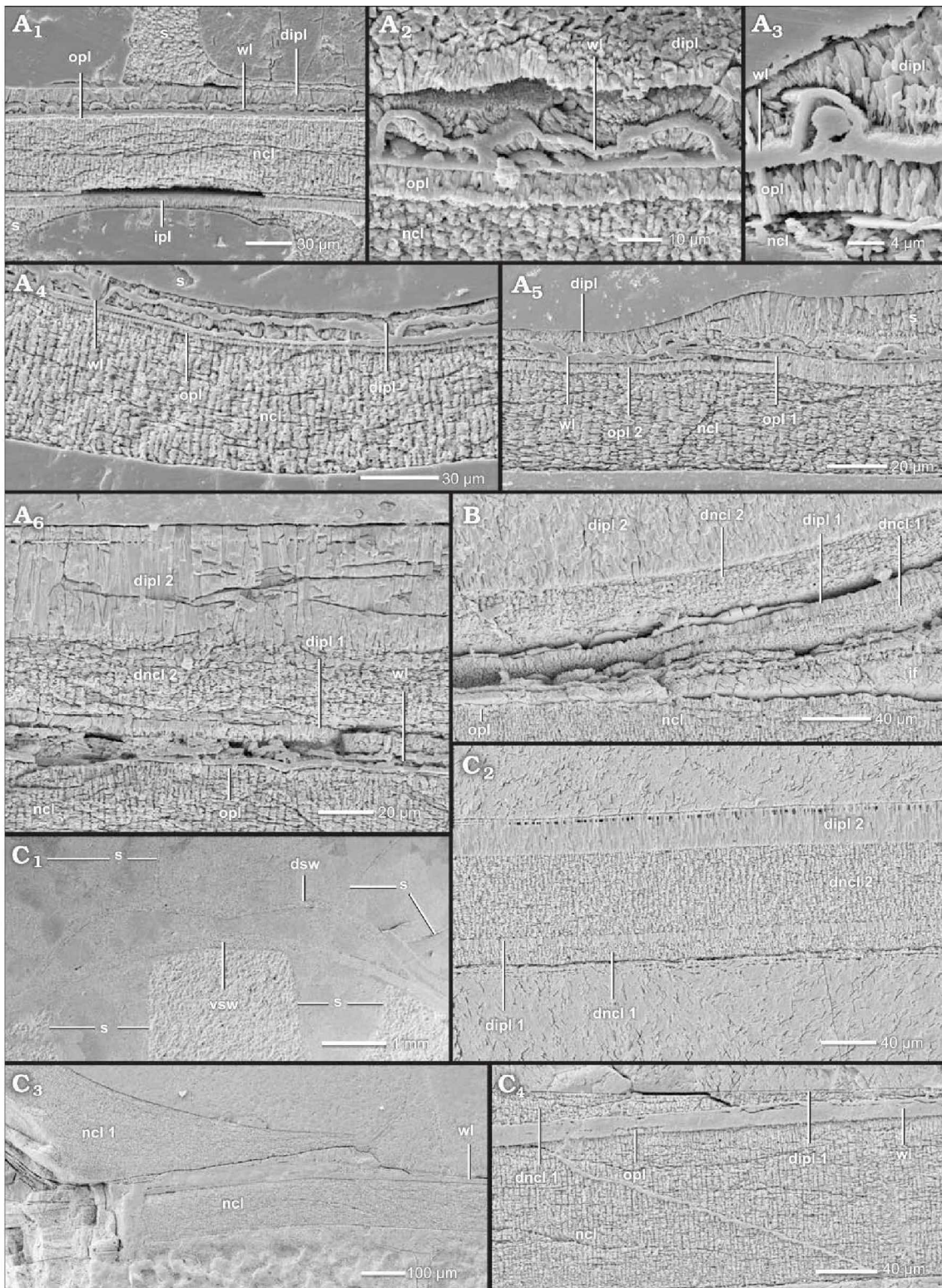
In particular, the wrinkle layer is liable to modification of its usual ridge- and knob-like appearance (cf. Korn et al. 2014; Mironenko 2015): The wrinkles of *Douvilleiceras mammillatum* merge in late ontogeny. The spherulitic-prismatic layer of several haploceratids (e.g., *Aconecer* sp. 1 and 2, *Taramelliceras externodosum*, *Sanmartinoceras* sp.) replaces the normal wrinkle layer. It is equivalent to Doguzhaeva and Mutvei's (1991, 1993b) spherulitic-prismatic layer of *Aconecer* *trautscholdi*. They assigned this layer to the ventral shell wall secreted by an outer mantle epithelium, i.e., (semi-)internal shell. However, we show it is a derivative of the wrinkle layer, e.g., spatial (ventral vs. lateral cover) and ontogenetic transition of both morphological expressions. The thickening of the outer component at the venter of the preceding whorl in *Hedenstroemia hedenstroemi* could be an analogous formation as all these taxa are oxycones.

*Gaudryceras tenuiliratum* develops a prominent, thick, homogeneous layer. It probably represents the thick, smooth coating layer described by Drushits et al. (1978). However, a nacreous-like appearance, as observed by Drushits et al. (1978) and Birkelund (1980), is not preserved, nor are there indications of a lateral shell cover of the whole shell as typical for that layer. These are probably effects of diagenetic alterations in our specimens. Kulicki et al. (2001) identifies the coating layer as a late ontogenetic derivation of the wrinkle layer. Although we cannot observe wrinkles in *G. tenuiliratum* or in other members of the genus, a wrinkle layer can be at least identified in related genera, e.g., *Eogaudryceras* (*Eotetragonites*) *umbilicostriatus* or *Tetragonites popetensis*, proving a common feature in Tetragonitoidea which is therefore a likely precursory structure.

Several specimens lack a distinct wrinkle layer but have preserved a discrete, smooth organic layer instead. It is likely that it is an equivalent structure, or rather represents

Fig. 7. Construction of the dorsal shell wall of Douvilleiceratoidea (A, median section, growth direction to the left, centrifugal; B, C, transversal section, → centrifugal). *Douvilleicer* *mammillatum* (Schlotheim, 1813), early Albian, Cretaceous, Ambatolafia, Mahajanga Basin, NW Madagascar. A. BSPG MAO-1808; A<sub>1</sub>, the juvenile dorsal shell wall consists of an outer wrinkle layer and a dorsal inner prismatic layer; A<sub>2</sub>, A<sub>3</sub>, organic wrinkles; A<sub>4</sub>, merged wrinkles; A<sub>5</sub>, the relief of an injury of the preceding whorl (forma aegra substructa of Hölder [1973]) is overgrown by the outer wrinkle layer and the dorsal inner prismatic layer; A<sub>6</sub>, dorsal shell wall close to the detachment (overgrowth of spines) from the ventral shell wall of the preceding whorl; the dorsal shell wall consists of an outer wrinkle layer, a primary dorsal inner prismatic layer, a secondary dorsal nacreous layer and a secondary dorsal inner prismatic layer; the primary dorsal nacreous layer is not formed yet but at complete detachment. B. BSPG MAO-1809, a reinforced complete dorsal shell is formed during detachment from the preceding whorl; the shell wall consists of a primary dorsal nacreous layer, a primary dorsal inner prismatic layer, a secondary dorsal nacreous layer and a secondary dorsal inner prismatic layer. C. BSPG MAO-1810; C<sub>1</sub>, the dorsal shell wall (dsw) detaches from the ventral shell wall (vsw) during overgrowth of the ventral relief; C<sub>2</sub>, Same as in B; C<sub>3</sub>, at the umbilical seam, the attaching shell wall vanishes towards the spiral plane; C<sub>4</sub>, close up of C<sub>3</sub>. Abbreviations: dipl, dorsal inner prismatic layer; dipl 1/2, primary/secondary dorsal inner prismatic layer; dnc1 1/2, primary/secondary dorsal nacreous layer; dsw, dorsal shell wall; if, infilling; ipl, inner prismatic layer; ncl, nacreous layer; ncl 1, primary nacreous layer; opl, outer prismatic layer; opl 1/2, primary/secondary outer prismatic layer; vsw, ventral shell wall; wl, wrinkle layer; s, septum.







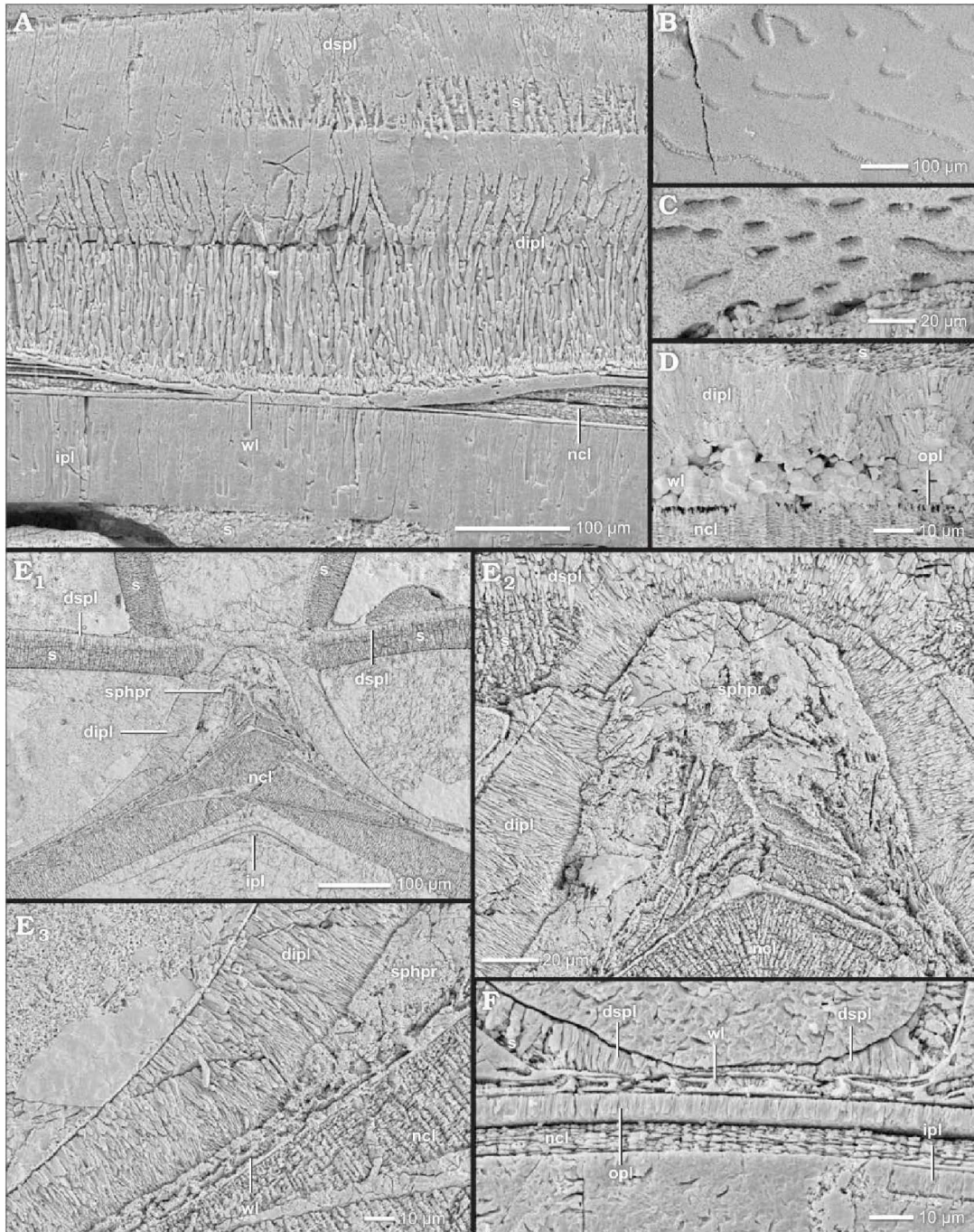


Fig. 8. Construction of the prismatic reduced dorsal shell wall (A–C, F, median, section, growth direction to the left, centrifugal; D, E, transversal section, centrifugal). **A.** *Argonauticeras besairiei* Collignon, 1949, BSPG MAo-1772, early Albian, Cretaceous, Ambatolafia, Mahajanga Basin, NW Madagascar; the dorsal shell wall consists of an outer wrinkle layer and a dorsal inner prismatic layer which has two sub-layers; the relief of an injury of the preceding whorl is overgrown by both layers. **B.** *Calliphylloceras* sp., BSPG MAN-4512, late Oxfordian, Jurassic, Sakaraha, Morondava Basin, SW Madagascar; the wrinkle layer left imprints in the dorsal inner prismatic layer. **C.** *Desmoceras (Desmoceras) latidorsatum* (Michelin, 1838), BSPG MAo-1839, early Albian, Cretaceous, Ambatolafia, Mahajanga Basin, NW Madagascar; the same as in B. **D.** *Cadoceras stupachenkoi* Mitta, 1998, BSPG MAN-4790, early Callovian, Jurassic, Makaryev on Unzha River, Russia; the dorsal wrinkle layer is completely replaced by pyrite, i.e., diagenesis. **E, F.** *Aconeceras* sp. 1, →

an initial state of the wrinkle layer since the early wrinkle layer is smooth as well. However, these layers also could be the ventral periostracum of the preceding whorl.

Since all of these structures are (more or less) derivatives of the wrinkle layer, a similar formation can be assumed.

Appearances of the wrinkle layer characterized by higher organic content, like the spherulitic-prismatic layer, the coating layer or simple thick “homogeneous” wrinkle layers (Fig. 4C<sub>2</sub>), may indicate a (temporary) higher production of organic compounds.

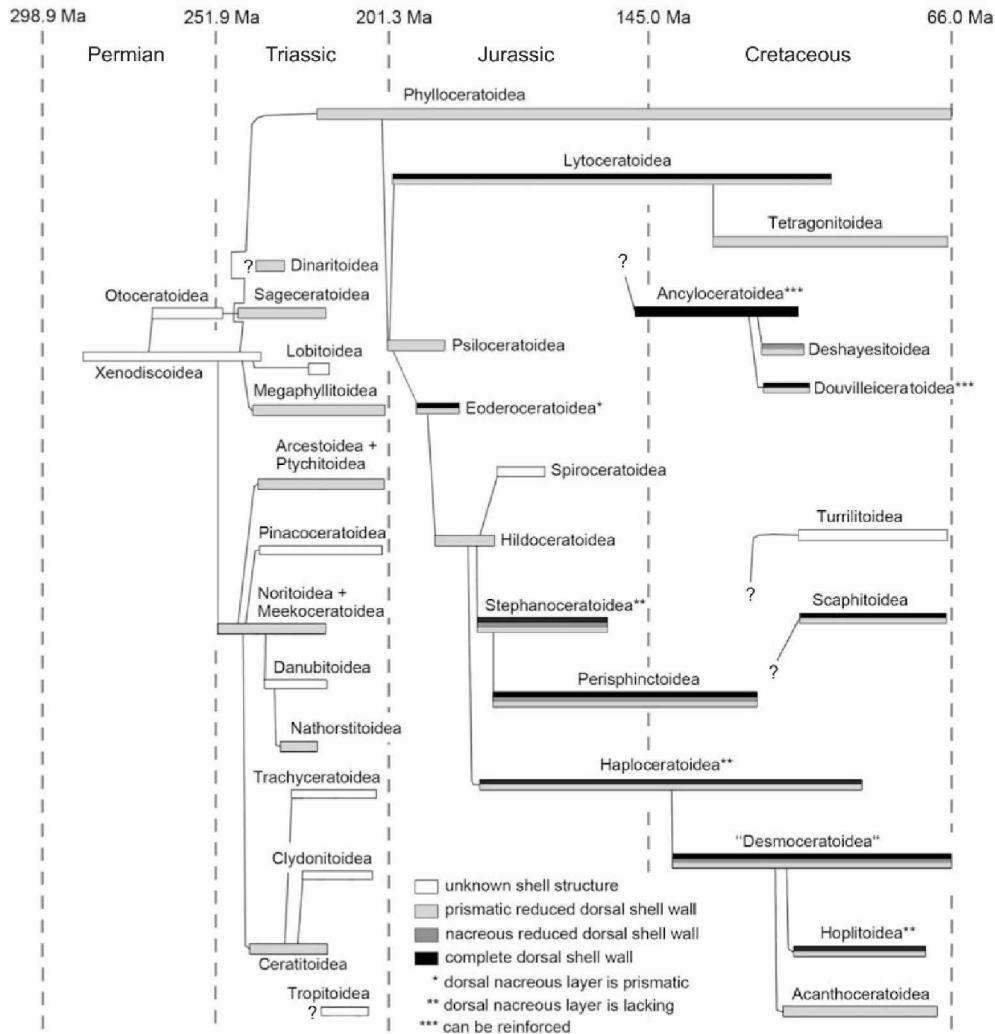


Fig. 9. Occurrences of dorsal shell wall types in Mesozoic ammonoid superfamilies (after Rouget et al. 2004; cf. Tables 1, 2, SOM: table A). The wide distribution of reduced dorsal shell walls in Mesozoic taxa suggests a plesiomorphy. In general, nacreous reduced dorsal shell walls or complete dorsal shell walls follow a stage of a prismatic reduced dorsal shell wall. The wide distribution of nacreous reduced dorsal shell walls and complete dorsal shell walls in Mesozoic ammonoid taxa suggests that the ability to form dorsal nacre is also a plesiomorph feature. Note: The dorsal nacreous layer of Eoderoceratoidea (Amaltheidae) has a prismatic appearance (\*). The complete dorsal shell walls in Stephanoceratoidea, Haploceratoidea, and Hoplitoidea lack a dorsal nacreous layer, i.e., seemingly complete dorsal shell wall (\*\*). The complete dorsal shell walls of Ancyloceratoidea and Douvilleiceratoidea can be reinforced by additional pair of nacreous and prismatic layers, i.e., reinforced complete dorsal shell wall (\*\*\*).

early Albian, Cretaceous, Ambatolafia, Mahajanga Basin, NW Madagascar. E. BSPG MAo-1851; E<sub>1</sub>, at the ventral crest of the preceding whorl, the wrinkle layer forms a thickening, i.e., spherulitic-prismatic layer; the dorsal inner prismatic layer is only present at the ventral crest of the preceding whorl and vanishes towards the flanks; E<sub>2</sub>, close-up of E<sub>1</sub>; the spherulitic-prismatic layer contains prismatic portions; E<sub>3</sub>, close-up of E<sub>1</sub>; the wrinkle layer transforms into the spherulitic-prismatic layer. F. BSPG MAo-1852; the juvenile dorsal shell wall consists of a wrinkle layer and septal mural parts. Abbreviations: dipl, dorsal inner prismatic layer; dspl, dorsal septal prismatic layer; ipl, inner prismatic layer; ncl, nacreous layer; opl, outer prismatic layer; s, septum; sphpr, spherulitic-prismatic layer; wl, wrinkle layer.

*Phylogenetic and taxonomic implications of the outer organic component.*—The wrinkle layer (and its derivatives) is a frequent element of nearly all Jurassic and Cretaceous ammonoid superfamilies (SOM: table A). Its position in the shell wall and its extension as well as the ultrastructure of the wrinkles of the different taxa is more or less uniform. Therefore, we assume that it is a homologous shell feature and a plesiomorphy at least for Jurassic and Cretaceous taxa. The repeated development of similar structures is possible but since all these taxa are phylogenetically connected, it is most likely (by law of parsimony) that this feature appeared only once in the evolution of the Mesozoic ammonoids. Macroscopic and microscopic observations prove that wrinkle layers are common in Palaeozoic and Triassic taxa as well (e.g., Walliser 1970; House 1971; Tozer 1972; Doguzhaeva 1980, 1981; Korn 1985; Keupp 2000). These are probably homologous to the Jurassic and Cretaceous counterparts but their state must be evaluated in detail.

Our observations of the wrinkle ultrastructure match with the basal findings and descriptions of Doguzhaeva (1980: fig. 2A, B, 1981: fig. 2) and Kulicki et al. (2001) that include Carboniferous and Triassic taxa as well. However, these authors also report on prismatic and granular cores or completely prismatic wrinkles. Some wrinkles described show also a homogeneous (Doguzhaeva 1980, 1981: fig. 3B), lamellar (Zakharov and Grabovskaya 1984; Zakharov 1996), or predominantly prismatic (Doguzhaeva and Mutvei 1993b) ultrastructure. We suppose a secondary alteration of the wrinkle layer in all these cases of deviating appearance. Our findings suggest that the primary organic character of the wrinkle layer is prone to diagenetic alteration: e.g., hollow spaces (dissolution), granular layers (pyritization?), or prismatic layers (crystallization). In particular, the transition or parallel occurrence of pristine wrinkles and prismatic wrinkles is proved in some specimens (Fig. 4G).

The ultrastructure of wrinkles is unsuited for taxonomy. The various macroscopic patterns associated with the wrinkle layer are probably better suited for defining taxa (House 1971; Senior 1971; Tozer 1972). Korn (1985) assumed that differentiation of patterns is subjective too.

However, special deviations of the normal wrinkle layer (i.e., ridges and knobs) are unusual and are potentially characteristic for several taxa: e.g., (i) the merging wrinkles of *Douvilleiceras mammillatum* (Douvilleiceratoidea), (ii) the thick coating layer of *Gaudryceras tenuiliratum* (Tetragonitoidea), and (iii) the spherulitic prismatic layer of several genera of Haploceratoidea/Oppeliidea (e.g., *Aconeceras* sp. 1 and 2, *Sanmartinoceras* sp., and *Taramelliceras externodosum*).

All these structures are reoccurring features. Merging

wrinkles are typical in all of our four specimens of *D. mammillatum*. The coating layer was identified several times (e.g., Drushits et al. 1978; Birkelund 1980; Doguzhaeva and Mutvei 1993b; Kulicki et al. 2001). The spherulitic prismatic layer was observed in several specimens by us and other authors (e.g., Doguzhaeva and Mutvei 1991, 1993b) but seems to be lacking in the related genus *Hecticoceras*. However, our specimens of this genus and those of other studies (e.g., Sprey 2002) are poorly preserved.

*The dorsal inner prismatic layer.*—The dorsal inner prismatic layer is the second and dominant component of the prismatic reduced dorsal shell wall (Figs. 1D, 4A<sub>1</sub>, B<sub>1</sub>, C<sub>2</sub>, 6A, 7A<sub>1</sub>). It attaches directly to the outer organic component (e.g., wrinkle layer). Nearly all observed ammonoid groups develop at least a short ontogenetic stage after the hatching that forms only this single aragonite layer dorsally (Fig. 9; SOM: table A).

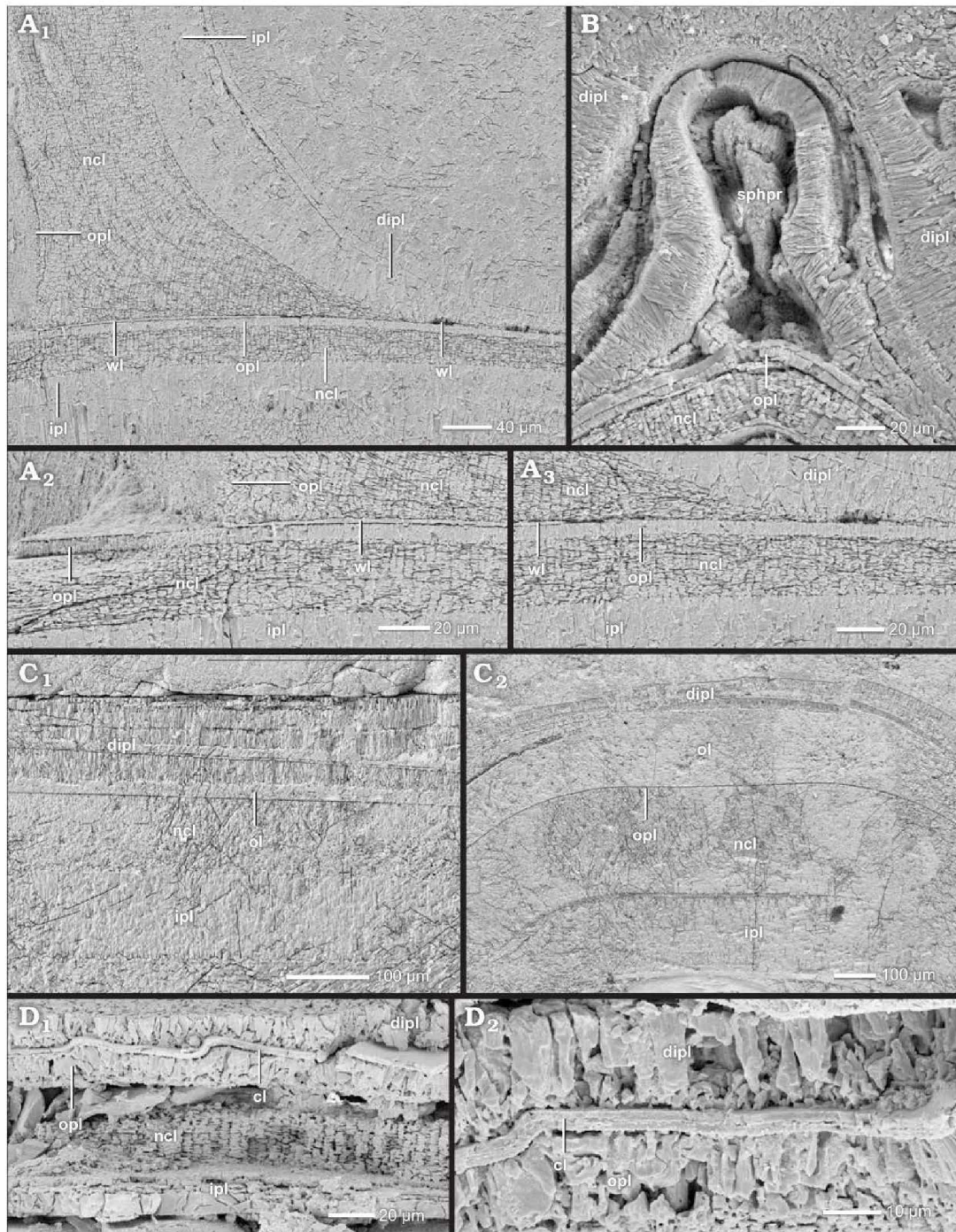
In general, the innermost whorls lack a distinct dorsal inner prismatic layer. The early dorsal shell wall consists of (prismatic) septal mural parts and a thin, smooth outer organic component (dspl and ol in Fig. 5A<sub>1</sub>). Several of our specimens have not exceeded this ontogenetic stage due to their small diameter, e.g., *Rudolphtruempiceras planorbis* (Dinaritoidea), *Pleuroceras solare* (Eoderoceratoidea). In our specimens a continuous dorsal inner prismatic layer occurs between diameters of 2 to 8 mm. This is similar to the occurrence of the wrinkle layer (third to fourth whorl). However, its relief occurs mostly prior to the dorsal inner prismatic layer.

The dorsal inner prismatic layer is equivalent to its ventral/lateral counterpart, i.e., its continuation. The outer prismatic layer and middle nacreous layer of the ventral/lateral shell wall wedge out towards the spiral plane as they attach to the preceding whorl (Figs. 1F, 4F<sub>1</sub>, 10A). Only the inner prismatic layer coats the surface of the preceding whorl. Generally, the dorsal inner prismatic layer thickens towards the venter of the preceding whorl where it reaches maximal thickness: a circumstance best observed in phylloceratids and desmoceratids. In contrast to the wrinkle layer, the dorsal inner prismatic layer is restricted to the rear parts of the living chamber. It wedges out towards the aperture, leaving the wrinkle layer uncovered in the living chamber (Fig. 6). However, the ventral/lateral inner prismatic layer extends much further into the living chamber.

The dorsal inner prismatic layer can be thin, thick, single-layered or constructed of several sub-layers. Organic layers can separate the individual sub-layers. The morphological expression of the dorsal inner prismatic layer changes during ontogeny, e.g., changes in the thickness (normally an

Fig. 10. Construction of the prismatic reduced dorsal shell wall (A–C, transversal section, centrifugal; D, median section, growth direction to the left, centrifugal). A. *Umsinenoceras linguatuberculatum* Kennedy, Wright, and Klinger, 1979, BSPG MAo-1844, early Albian, Cretaceous, Ambatolafia, Mahajanga Basin, NW Madagascar; A<sub>1</sub>, at the umbilical seam, the outer prismatic layer and the nacreous layer of the attaching whorl wedge out; the inner prismatic layer continues towards the ventral crest of the preceding whorl; all three layers attach to the wrinkle layer which ends abruptly at the umbilical seam; the resulting dorsal shell wall consists of an outer wrinkle layer and a dorsal inner prismatic layer; A<sub>2</sub>, A<sub>3</sub>, close up of A<sub>1</sub>. B. *Sanmartinoceras* sp., BSPG MAo-1854, early Albian, Cretaceous, Ambatolafia, Mahajanga Basin, NW Madagascar; the spherulitic-prismatic layer is dominated by prismatic portions. →





**C.** *Hedenstroemia hedenstroemi* Keyserling, 1845, BSPG MAm-1651, early Olenekian, Triassic, Buur River, Olenek River Basin, Siberia, Russia; C<sub>1</sub>, the dorsal shell wall cover of the shell flanks of the preceding whorl consists of a thin outer organic layer and several sub-layers of the dorsal inner prismatic layer; C<sub>2</sub>, at the ventral crest of the preceding whorl, the dorsal outer organic layer forms a thickening. **D.** *Gaudryceras tenuilivatum* Yabe, 1903, BSPG MAo-1875, Campanian, Cretaceous, Teshio-Nakagawa area, Hokkaido, Japan; the dorsal shell wall consists of an outer organic coating layer and a dorsal inner prismatic layer (D<sub>2</sub>, close-up of the coating layer in the same specimen). Abbreviations: cl, coating layer; dipl, dorsal inner prismatic layer; ipl, inner prismatic layer; ncl, nacreous layer; ol, organic layer; opl, outer prismatic layer; s, septum; sphpr, spherulitic-prismatic layer; wl, wrinkle layer.

increase; Fig. 4A<sub>1</sub>, B<sub>1</sub>) or local appearance or disappearance of sub-layers (Fig. 4C). Sub-layering often occurs locally in several taxa but disappears afterwards, e.g., *Phylloceras* (*Phylloceras*) *plicatum* (Phylloceratoidea), *Chamoussetia stuckenbergi* (Stephanoceratoidea). With some exceptions, we cannot separate specific taxonomic groups by the internal structure or morphological expression of the dorsal inner prismatic layer (see below).

The dorsal inner prismatic layer acts as a sculptural compensator. It evens out the wrinkle layer relief (Figs. 1D, 4A<sub>1</sub>, B<sub>1</sub>, C<sub>2</sub>, 6A, B) and the sculpture of the preceding whorl (Fig. 10D<sub>1</sub>). In particular, the relief of rib concavities, constriction furrows or injuries (Figs. 4E, 8A) is compensated through local thickening. Often the dorsal inner prismatic layer becomes spherulitic or reveals a sub-layering. In the umbilical angle it usually forms a local thickening (Figs. 4F<sub>1</sub>, 10A<sub>1</sub>). Higher elevations of the sculpture can be bridged, leaving cavities (Fig. 11B). Sometimes the inner prismatic layer only adopts the relief of the preceding whorl.

*The wrinkle layer complex.*—A special kind of sub-layering of the dorsal inner prismatic layer can (sometimes) be observed during smoothing of the relief of the wrinkle layer (cf. Kulicki 1979; Zakharov 1996): e.g., in Phylloceratoidea, Amaltheidae, and Desmoceratoidea. A wrinkle layer complex consists of a sequence of four sub-layers: (i) the wrinkle layer, (ii) a primary dorsal inner prismatic sub-layer, (iii) an organic separation layer, and (iv) a secondary dorsal inner prismatic sub-layer (wl, dipl 1, ol, and dipl 2 in Fig. 4C<sub>1</sub>). The interspaces between individual wrinkles are filled by the first generation of the dorsal inner prismatic layer. This sub-layer and the tops of the wrinkles are coated with the thin organic layer on the inner surface. The secondary dorsal inner prismatic layer covers the arising undulating surface. Often, the organic separation layer is not present.

*Unusual aspects of the dorsal inner prismatic layer.*—Usually we cannot define specific taxonomic groups by the internal structure or morphological expressions of the dorsal inner prismatic layer. However, there are some exceptions:

In *Lobolytoceras costellatum*, *Protetragonites fraasi*, and *Argonauticeras besairiei* (all Lytoceratoidea), the dorsal inner prismatic layer is usually subdivided into two very thick sub-layers (Fig. 8A). The thickness of the dorsal inner prismatic layer exceeds that of the entire ventral shell wall of the overgrown, preceding whorl by a factor of 1.5 to 2. A comparable thickness is not observed in any other of our taxa. Solely some Phylloceratoidea, e.g., *Phylloceras* (*Euphylloceras*) cf. *velledae*, *Holcophylloceras polyolcum*, *Ptychophylloceras* cf. *dacquei*, develop similar ratios (1:1) in outer whorls of large diameter (Fig. 4B<sub>1</sub>).

In *Aconeceras* sp. 1 and 2, the dorsal inner prismatic layer only covers the venter of the preceding whorl, where it reaches an enormous thickness (Fig. 8E<sub>1</sub>). At the ventral edge of the preceding whorl, the layer wedges out. The lateral whorl cover is usually absent. In the related

*Sanmartinoceras* sp. the dorsal inner prismatic layer is similarly developed but transforms into a thin layer that covers the flanks of the preceding whorl.

*Hedenstroemia hedenstroemi* forms a prominent sub-layered dorsal inner prismatic layer of up to three different sub-layers (Fig. 10C<sub>1</sub>).

*The dorsal septal prismatic layer.*—It appears that the septal mural parts affect the dorsal shell wall. The inner prismatic layer has a tendency to merge with the inserted septa on contact (spl and dspl in Figs. 4C<sub>2</sub>, 8E<sub>1</sub>, E<sub>2</sub>). Several times, the septa and the inner prismatic layer show gradual transitions between the naere of the septal wall and prisms of the inner prismatic layer (cf. septal prismatic layer in Howarth 1975). These structural transitions affect only the adoral saddles of the septa. In cross-section, the inner prismatic layer forms wedges at the septal contact which vanish towards the mouth (spl and dspl in Figs. 4A<sub>1</sub>, C<sub>2</sub>, 5A<sub>3</sub>, B, C). Locally, this often increases the thickness of the (dorsal) inner prismatic layer. Furthermore, the proximal, adoral septal surface is often covered by a prismatic layer (spl and dspl in Figs. 4C<sub>2</sub>, 5A<sub>3</sub>, B, 8E<sub>1</sub>, E<sub>2</sub>).

It is likely that all these septal-prismatic formations are connected to the septal mural parts. In particular, in specimens of Phylloceratoidea, Tetragonitoidea, and Desmoceratoidea, several times a distinct prismatic layer can be distinguished that originates in the septa (Fig. 5A<sub>3</sub>, B). This septal prismatic layer coats the inner surface of the inner prismatic layer. It can be separated by a thin organic layer from the actual inner prismatic layer. In general, at the umbilical edge the separation is most obvious. However, the separation of the dorsal inner prismatic layer and the dorsal septal prismatic layer becomes vague and both layers merge towards the crest of the former whorl.

In *Argonauticeras besairiei* the inner sub-layer of the dorsal inner prismatic layer seems to originate in the septa and fuses with them (dspl in Fig. 5C; inner part of dipl in Fig. 8A). Sometimes it even seems that the inner sub-layer wedges out adorally like a septal mural part (Fig. 5C). Also *Hedenstroemia hedenstroemi* forms a septal prismatic layer; hence some of the prismatic sub-layers of the dorsal shell wall (Fig. 10C<sub>1</sub>) may represent septal mural parts. Since the entire unusually distributed dorsal inner prismatic layer of *Aconeceras* sp. 1 and 2 (and *Sanmartinoceras* sp.) is usually associated with the septal contact zone, and otherwise is absent, it is possible that their dorsal inner prismatic layer is only of septal origin (Fig. 8E<sub>1</sub>, E<sub>2</sub>).

In several phylloceratid, perisphinctid, and desmoceratid specimens (where the dorsal inner prismatic layer is still absent), the adoral septal mural parts of the juvenile whorls (dspl in Fig. 5A<sub>1</sub>) gradually elongate, bridge the distance between the single septa (dspl in Fig. 5A<sub>2</sub>) and ultimately fuse to the continuous dorsal inner prismatic layer in the course of shell growth. In one specimen of *Eogaudryceras* (*Eotetragonites*) *umbilicostratus* (BSPG MAo-1775), the dorsal inner prismatic layer seems to originate at its 20th septum, i.e., its mural part.



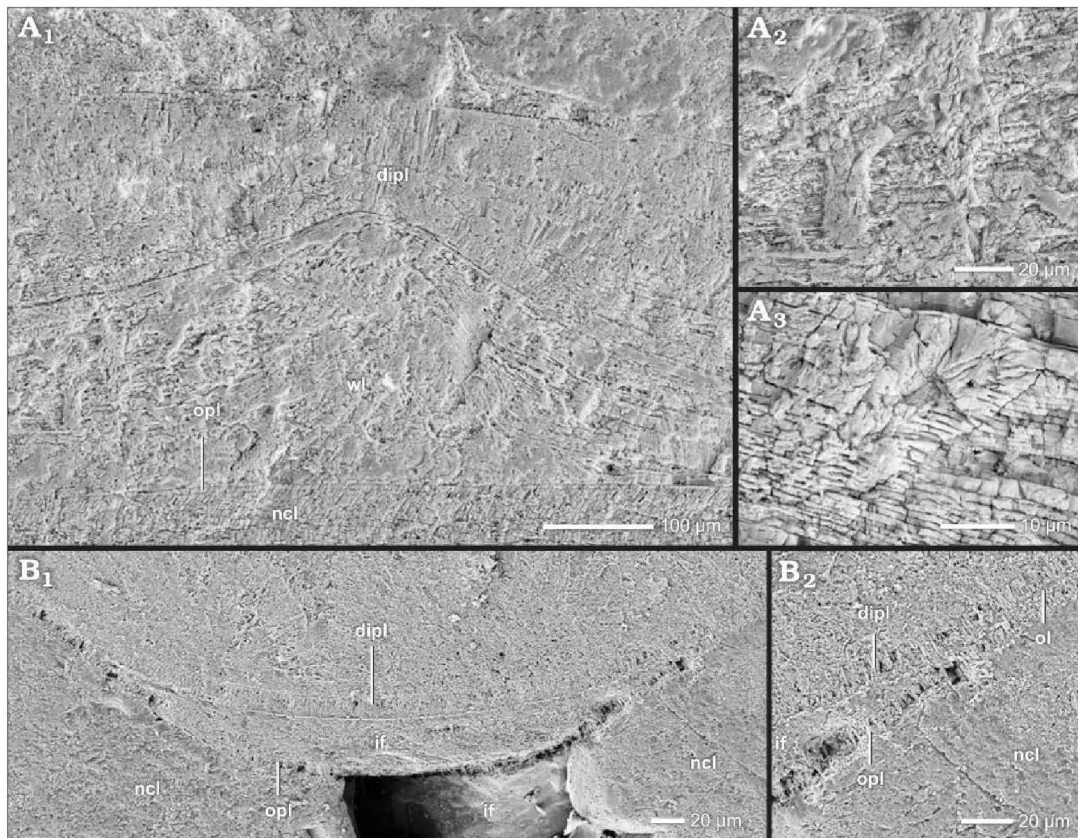


Fig. 11. Construction of the dorsal shell wall (median section, growth direction to the left, centrifugal). **A.** *Puzosia saintoursi* Collignon, 1963, BSPG MAO-1797, early Albian, Cretaceous, Ambatolafia, Mahajanga Basin, NW Madagascar; A<sub>1</sub>, the wrinkle layer forms an unusual cone-like thickening; the compensating thick dorsal inner prismatic layer forms nacreous inclusions; A<sub>2</sub>, close-up of A<sub>1</sub>; the organo-prismatic structure of the wrinkle layer thickening; A<sub>3</sub>, close-up of A<sub>1</sub>; the thickening of the dorsal inner prismatic layer shows nacreous inclusions. **B.** *Perisphinctes (Kranaosphinctes)* sp., BSPG MAN-4756, late Oxfordian, Jurassic, Sakaraha, Morondava Basin, SW Madagascar; B<sub>1</sub>, the dorsal inner prismatic layer bridges the relief of two ribs forming a crescent hollow space; the ventral nacre layer of this shell portion is diagenetic altered; B<sub>2</sub>, close-up of B<sub>1</sub>. Abbreviations: dipl, dorsal inner prismatic layer; if, infilling; ncl, nacreous layer; opl, outer prismatic layer; wl, wrinkle layer.

*The formation and function of the dorsal inner prismatic layer.*—Apparently, the dorsal inner prismatic layer was the second layer to be formed in the prismatic reduced dorsal shell wall, i.e., it directly attaches to the outer organic component, e.g., wrinkle layer. Its restricted extension within the living chamber (it wedges out towards the aperture in the rear) indicates a secretion in the rear part of the living chamber. However, the ventral/lateral inner prismatic layer extends much further into the living chamber, implying a disparity between the ventral, lateral, and dorsal secretion zones for the inner prismatic layer. Reoccurring sub-layers (e.g., wrinkle layer complex) probably indicate an intermittent secretion process or at least (brief) interruption during mineralization.

The primary task of this layer seems to be to smooth out the internal relief of the living chamber. Apparently, smoothing of the shell interior was crucial for an ammonoid, probably to facilitate the attachment of the nacreous septa that are subsequently inserted adapically. The dorsal inner

prismatic layer and the nacreous layer of the septa argue for two distinct secretion regimes of the adapical mantle epithelium, i.e., prismatic and nacreous.

However, at the septal contact, wedge-like thickenings of the dorsal inner prismatic layer or even a separate septal prismatic layer often merge with the nacre layer of the septa, therefore suggesting that adapical mantle portions are able to form both materials. These structures and transitions could represent diagenetic alteration (e.g., recrystallization, epitaxial crystal growth) but widespread and recurrent observations of these in different ammonoid taxa and fossil localities by us and in other studies (e.g., Hölder 1952; Birkelund and Hansen 1968, 1974; Blind 1975, 1976; Howarth 1975; Kulicki 1979, 1996; Birkelund 1980; Doguzhaeva and Mutvei 1986; Kulicki et al. 2016) argue for a distinct element of the shell wall, which Howarth (1975) first described as a discrete septal prismatic layer of the dorsal (and ventral/lateral) shell wall of Dactylioceratidae. We consider the septal prismatic

layer as proven. The septal prismatic layer probably represents an additional secretion stage which begins with the formation of the septa, either as a discrete generation of the inner prismatic layer or as prismatic mural parts which can fuse with formerly secreted prismatic material.

In general, a strict chemical (i.e., specific matrix proteins) and spatial separated formation of prismatic and nacreous material by the molluscan mantle (i.e., distinct mantle portions with probably appropriate differentiated cells form distinct materials) is assumed and partly proven (e.g., in the pearl oyster *Pinctada*; Joubert et al. 2010; Marie et al. 2012; Funabara et al. 2014). Our observations of transition structures in ammonoid aragonitic shell wall indicate that at least the adapical mantle portions, that form the septa, were able to form both materials. A strict chemical and spatial separation is not necessarily given. This either means that two different cell types (i.e., prismatic vs. nacre secreting) existed simultaneously, that the concurrent cells were able to do multiple tasks (i.e., formation of different matrix proteins) or that both chemical secretion processes are closely linked (i.e., related or identical matrix proteins) in ammonoids. Blind (1975, 1976) already assumed that the mantle epithelium that secretes the septa could change its secretion mode depending on function. Cell secretion plasticity is at least known in Gastropoda (Fleury et al. 2008) and Bivalvia (Cuif et al. 2011). Carter and Clark (1985) even assume that the nacreous layer is derived from the aragonitic prismatic layer (cf. Bandel 1977; Fleury et al. 2008).

*Phylogenetic and taxonomic implications of the prismatic reduced dorsal shell wall.*—The vast majority of our Mesozoic ammonoids forms a prismatic reduced dorsal shell wall which is in accordance with former studies of the dorsal shell wall of planispirally coiled ammonoids (see Introduction, Fig. 9; SOM: table A). Because of the wide distribution of this dorsal shell wall type within the phylogenetic tree in combination with its usual early ontogenetic formation (subsequent, diverging ontogenetic changes are possible, see below), we assume that the prismatic reduced dorsal shell wall represents the primary state of dorsal shell wall construction at least in Mesozoic ammonoid taxa. Observations in members of the Goniatitina (Erben et al. 1968, 1969; Walliser 1970; Kulicki et al. 1999, 2001, 2002; Doguzhaeva 2002) imply similar conditions already in Devonian, Carboniferous, and Permian ammonoids (SOM:

table A). Therefore, we presume that the prismatic reduced dorsal shell wall is a synapomorphic character of all coiled ammonoids. It is likely that in order to reduce weight, material consumption and formation effort, the dorsal shell was usually suppressed in planispiral ammonoids analogous to the planispiral Nautilidae.

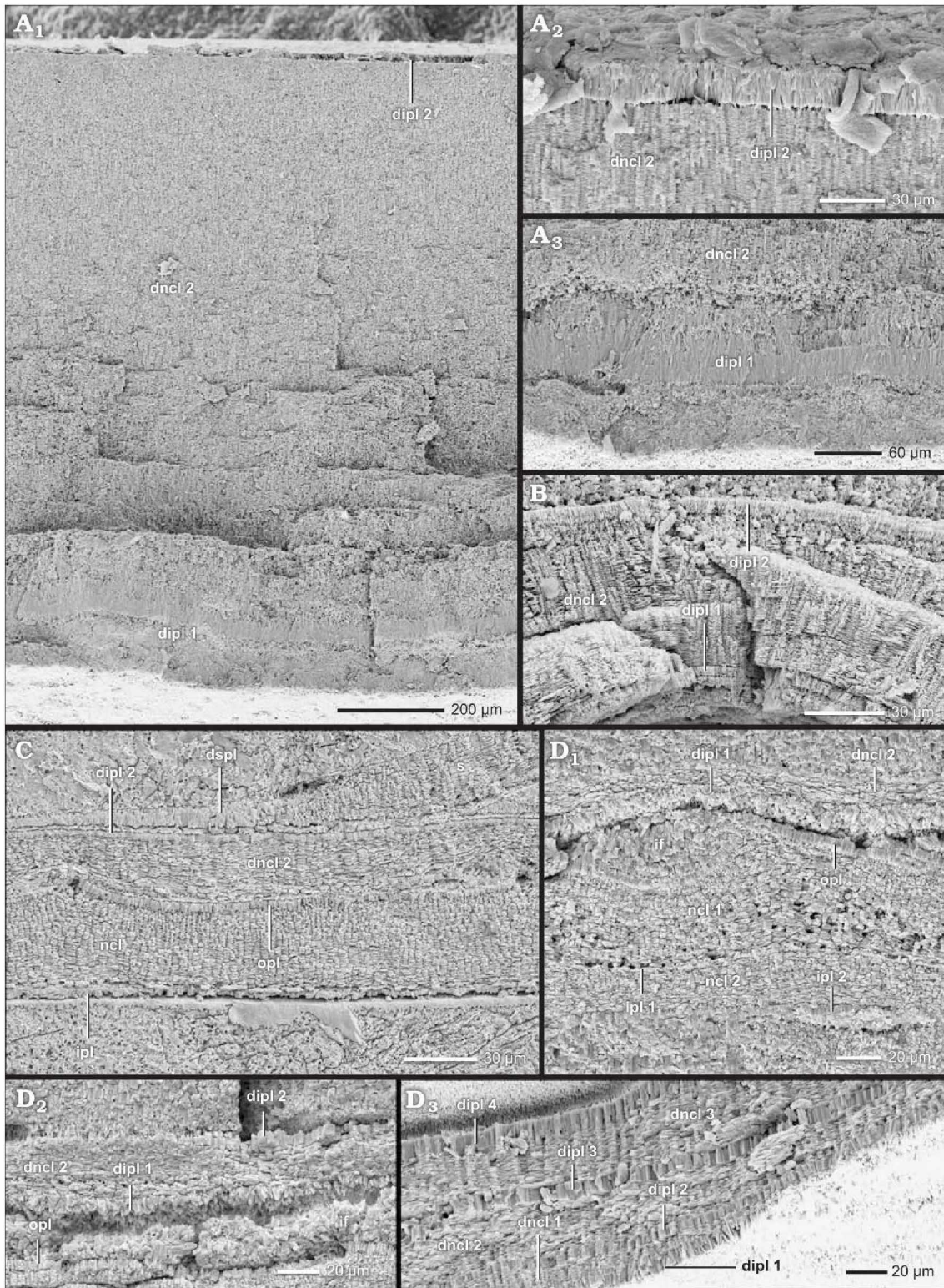
However, variations in the outer organic component are probably taxon-specific (see above). In particular, the occurrence and morphological expression of the inner prismatic layer vary widely and may allow the distinction of individual taxa at the genus or species level or higher order taxa. Some phylloceratids have an extraordinarily thick dorsal inner prismatic layer, however, it cannot be observed in all of our specimens. With the exception of *Argonauticeras besairiei*, *Lobolytoceras costellatum*, and *Protetragonites fraasi* (all Lytoceratoidea), no other ammonoid in our study forms a comparably thick dorsal inner prismatic layer. The dorsal inner prismatic layer of the genus *Aconeceras* attracts attention through its unusual restriction to the ventral crest of the preceding whorl. Since our knowledge of the individual shell structures is still limited, these characteristics and findings have to be used with caution.

**The nacreous reduced dorsal shell wall.**—The dorsal shell wall of this type is three-layered consisting of two prismatic layers that enclose a nacreous layer (Figs. 1E, 12A–C, D<sub>1</sub>, D<sub>2</sub>, 13B, C<sub>1</sub>, 14A<sub>1</sub>). These layers do not form a continuum with the three layers of the ventral/lateral shell wall but rather correspond to an umbilical shell doubling that extends towards the ventral crest of the preceding whorl (Figs. 1G, 12D<sub>3</sub>). At the aperture, the dorsal shell wall is absent (Fig. 2A<sub>2</sub>). A nacreous reduced dorsal shell wall can be observed in some planispirally coiled genera of Stephanoceratoidea (e.g., *Keplerites galilaei*), Perisphinctoidea (e.g., *Perisphinctes* [*Kranaosphinctes*] *mahabokensis*), Desmoceratoidea (e.g., *Eupachydiscus* sp.) and Deshayesitoidea (e.g., *Colombiceras* sp.) (Fig. 9, Table 1; SOM: table A).

The morphological expression of the three layers of the nacreous reduced dorsal shell wall looks very similar to the proportions observed in the ventral/lateral shell wall simulating a connection (Figs. 12C, D<sub>1</sub>, 14A<sub>1</sub>), but the dorsal and ventral/lateral shell layers are not equivalent. The outer prismatic and nacreous layer of the ventral/lateral shell wall wedge out towards the spiral plane at the umbilical seam (Fig. 1G). The actual nacreous reduced dorsal shell wall

Fig. 12. Construction of the nacreous reduced dorsal shell wall (A, D<sub>3</sub>, transversal section, centrifugal, B, C, D<sub>1</sub>, D<sub>2</sub>, median section, growth direction → to the left, centrifugal). **A.** *Perisphinctes* (*Kranaosphinctes*) *mahabokensis* (Collignon, 1959), BSPG MAn-4835, late Oxfordian, Jurassic, Sakaraha, Morondava Basin, SW Madagascar; A<sub>1</sub>, the dorsal shell wall consists of a primary dorsal inner prismatic layer, a secondary dorsal nacreous layer and a secondary dorsal inner prismatic layer; A<sub>2</sub>, the secondary dorsal inner prismatic layer; A<sub>3</sub>, the primary dorsal inner prismatic layer. **B.** *Keplerites galilaei* (Oppel, 1862), BSPG MAn-4783, early Callovian, Jurassic, Znamenka on Unzha River, Russia; same as in A<sub>1</sub>. **C.** *Mirosphinctes* sp. 1, BSPG MAn-1769, late Oxfordian, Jurassic, Sakaraha, Morondava Basin, SW Madagascar; the dorsal shell wall consists of a secondary dorsal nacreous layer and a secondary dorsal inner prismatic layer. **D.** *Aspidoceras* sp., BSPG MAn-4507, late Oxfordian, Jurassic, Sakaraha, Morondava Basin, SW Madagascar; D<sub>1</sub>, D<sub>2</sub>, the same as in A<sub>1</sub>; D<sub>3</sub>, at the umbilical seam multiple new shell layers are formed; the inner layers of the (dorsal) nacreous layer (dncl 1–3) and of the (dorsal) inner prismatic layer (dipl 1–4) wedge out towards the spiral plane; the inner layers form the nacreous reduced dorsal shell wall. Abbreviations: dipl 1/2/3/4, primary/secondary/tertiary/quaternary dorsal inner prismatic layer; dncl 1/2/3/4, primary/secondary/tertiary/quaternary dorsal nacreous layer; dsp1, dorsal septal prismatic layer; if, infilling; ipl, inner prismatic layer; ipl 1/2, primary/secondary inner prismatic layer; ncl, nacreous layer; ncl 1/2, primary/secondary nacreous layer; opl, outer prismatic layer; s, septum.





begins as a (strong) umbilical shell doubling that reinforces the three-layered ventral/lateral shell wall with a secondary nacreous layer and secondary inner prismatic layer. The shell doubling continues as the dorsal shell wall towards the ventral crest of the preceding whorl (Fig. 1G). The three layers of the dorsal shell wall are equivalent to the (primary) inner prismatic layer, the secondary nacreous layer and the secondary inner prismatic layer of the ventral/lateral wall and the umbilical shell doubling, and therefore are called the primary dorsal inner prismatic layer, the secondary dorsal nacreous layer and the secondary dorsal inner prismatic layer of the dorsal shell wall. In the outer whorls of some taxa (e.g., *Aspidoceras* sp.), at the umbilical edge further additional inner prismatic and nacreous layers can develop but only the three innermost layers continue towards the ventral crest of the preceding whorl. The remaining outermost layers wedge out towards the spiral plane at the umbilical seam (dnc1 1–3 and dipl 1–4 in Fig. 12D<sub>3</sub>).

Typically, the whole nacreous reduced dorsal shell wedges out towards the aperture in the rear living chamber adorally of the last septum (Figs. 2A<sub>2</sub>, 14A). The primary dorsal inner prismatic layer usually attaches directly to the preceding whorl. The nacreous reduced dorsal shell wall smooths the sculpture of the preceding whorl (Fig. 12C, D<sub>1</sub>). Often the whole package bridges the relief (Fig. 15A). In other cases, it thickens during compensation. In particular, the secondary dorsal nacreous layer thickens in the rib cavities, but thins at the rib crests (Figs. 12B, C, 15A).

The ontogenetic development shows that a nacreous reduced dorsal shell wall replaces a prismatic reduced dorsal shell wall (i.e., wl and ipl). With the exception of the Aspidoceratinae (see below), additional shell layers appear at diameters of 25 to 79 mm (Table 1). However, in part the values represent the first possible observations due to inadequate preservation of inner whorls, i.e., earlier occurrences are possible. Because of this preservation gap, data on the whorl number cannot be given.

The first nacreous structures are part of the outer portions of the (secondary) dorsal inner prismatic layer. The outer portion of the layer develops nacreous inclusions which originate in the prisms, i.e., “partitioning of the prisms” (Fig. 14B, C). With further growth a separate shell layer is clearly defined. The juvenile secondary dorsal nacreous layer is rather thin, consisting of few nacre lamellae, but thickens gradually during progressive growth and usually becomes the main component of the dorsal

shell. Thus the dorsal shell wall of large *Perisphinctes* (*Kranaosphinctes*) *mahabokensis* (D = 210 mm, BSPG MAN-4835) is dominated by a very thick secondary dorsal nacreous layer (Fig. 12A<sub>1</sub>). The primary dorsal inner prismatic layer (Fig. 12A<sub>3</sub>) and secondary dorsal inner prismatic layer (Fig. 12A<sub>2</sub>) are subordinate components. Also in large specimens of *Eupachydiscus* sp. (D ≥ 300–450 mm, BSPG MAO-1832–1834) the secondary dorsal nacreous layer becomes an essential and dominant dorsal shell element (Fig. 13C<sub>1</sub>). However, the primary and secondary dorsal inner prismatic layers are of comparable thickness. In both taxa the primary dorsal inner prismatic layer develops two sub-layers and a more or less spherulitic-prismatic appearance (Figs. 12A<sub>3</sub>, 13B, C<sub>1</sub>). In *Eupachydiscus*, the inner sub-layer has a more palisade-like structure. The outer spherulitic sub-layer often appears granular. Also the secondary dorsal inner prismatic layer consists of two sub-layers in *Eupachydiscus* (Fig. 13C<sub>1</sub>).

Interestingly in *Eupachydiscus* sp., the secondary dorsal nacreous layer wedges out near the umbilical seam (Fig. 1C). It reappears as a thin cover of the preceding whorl at its mid-flank. Towards the ventral crest of the preceding whorl the layer thickens. There, it is up to 10 times thicker than at the mid-flank.

A particularity of the outer whorls in *Colombiceras* sp. is that the outer prismatic layer of the ventral/lateral shell wall does not wedge out at the umbilical seam but extends up to the ventral edges of the preceding whorl. Therefore, the dorsal shell wall consists of four shell layers at the flanks of the preceding whorl (Fig. 14D) but three layers at its crest.

*The nacreous reduced dorsal shell wall of Aspidoceratinae.*—Members of the Aspidoceratinae (Perisphinctoidea) form a nacreous reduced dorsal shell wall most frequently and significantly earlier in ontogeny than other taxa (Figs. 12C, D<sub>1</sub>, D<sub>2</sub>, 14A<sub>1</sub>, C, Table 1; SOM: table A). In most members of Aspidoceratinae (e.g., *Aspidoceras* sp., *Euaspidoceras* sp. 2, *Mirosphinctes* sp. 1 and 2, *Pseudowaagenia* sp.), the first nacreous structures occur at diameters between 6 and 9 mm. Nacre onset usually coincides with the beginning of the sculpture of the preceding whorl (Fig. 12C, D<sub>1</sub>), i.e., prismatic radial lirae (cf. Radtke and Keupp 2016). The nacreous reduced dorsal shell wall compensates the relief.

*Epaspidoceras jeanetti* seems to be an exception to this common observation. Three (of four) specimens maintain

Fig. 13. Construction of a secondary complete dorsal shell wall and the nacreous reduced dorsal shell wall (A, median section, growth direction to the left, centrifugal; B, C, transversal section, centrifugal). A. *Cleoniceras* (*Grycia*) *besairiei* Collignon, 1949, BSPG PA-33582, early Albian, Cretaceous, Ambatolafia, Mahajanga Basin, NW Madagascar; in reaction to a forma aegra aptycha of Keupp (1977), the dorsal shell wall is secondarily complete; it consists of an outer wrinkle layer, a dorsal nacreous layer and a dorsal inner prismatic layer. B, C. *Eupachydiscus* sp., Campanian, Cretaceous, Teshio-Nakagawa area, Hokkaido, Japan. B. BSPG MAO-1832, the primary dorsal inner prismatic layer consists of two sub-layers. C. BSPG MAO-1834; C<sub>1</sub>, the dorsal shell wall consists of a primary dorsal inner prismatic layer, a secondary dorsal nacreous layer and a secondary dorsal inner prismatic layer; the primary and the secondary dorsal inner prismatic layer develop sub-layers; the primary dorsal inner prismatic layer shows a relief (i.e., “Ritzknoten”); C<sub>2</sub>, C<sub>3</sub>, umbilical-lateral, the primary inner prismatic layer forms cone-like elevations, i.e., “Ritzknoten”; C<sub>4</sub>, C<sub>5</sub>, the “Ritzknoten” reach up to the umbilical seam and the dorsum. Abbreviations: dipl, dorsal inner prismatic layer; dipl 1/2, primary/secondary dorsal inner prismatic layer; dnc1, dorsal nacreous layer; dnc1 2, secondary dorsal nacreous layer; if, infilling; ncl, nacreous layer; wl, wrinkle layer. →



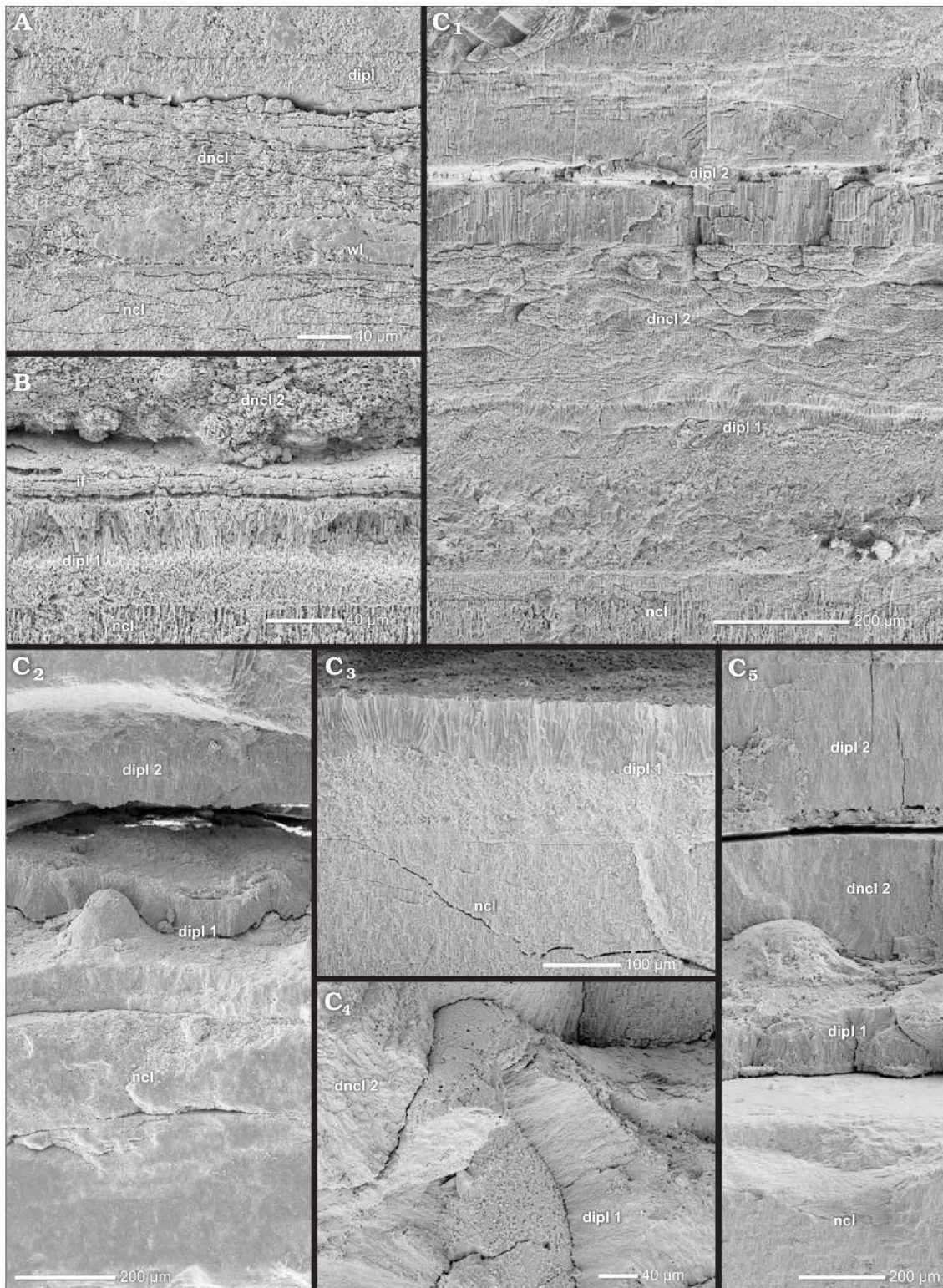


Table 1. Ammonoid specimens which develop the nacreous reduced dorsal shell wall. &lt;, &gt; indicate that the proper onset of the nacreous reduced dorsal shell wall cannot be accurately determined due to hiatus in shell preservation or preparation (e.g., transversal section).

Taxon	Collection number	Preservation index	Age, period	Location	Diameter at which nacreous reduced dorsal shell wall begins to form (mm)
<b>Stephanocerozoidea</b>					
<i>Kepplerites galilaeii</i> (Oppel, 1862)	BSPG MAn-4783	1–2	early Callovian, Jurassic	Znamenka on Unzha River, Russia	> 44 < 79
<i>Kosmoceras</i> ( <i>Kosmoceras</i> ) cf. <i>duncani</i> (Sowerby, 1816)	BSPG MAn-4788	1–2	late Callovian, Jurassic	Dubki near Saratov, Russia	< 90 (estimated)
<b>Perisphinctoidea</b>					
<i>Perisphinctes</i> ( <i>Kranaosphinctes</i> ) <i>mahabokensis</i> (Collignon, 1959)	BSPG MAn-4834	2–3	late Oxfordian, Jurassic	Sakaraha, Morondava Basin, SW Madagascar	54
<i>Perisphinctes</i> ( <i>Kranaosphinctes</i> ) <i>mahabokensis</i> (Collignon, 1959)	BSPG MAn-4835	2–3	late Oxfordian, Jurassic	Sakaraha, Morondava Basin, SW Madagascar	< 210
<i>Speetonicerias versicolor</i> (Trautschold, 1865)	BSPG MAo-1861	1–2	Aptian, Cretaceous	Simbirsk, Uljanowsk, Volga Basin, Russia	< 200
<b>Aspidoceratidae: Aspidoceratinae</b>					
<i>Aspidoceras</i> sp.	BSPG MAn-4506	2–3	late Oxfordian, Jurassic	Sakaraha, Morondava Basin, SW Madagascar	< 11
<i>Aspidoceras</i> sp.	BSPG MAn-4507	2–3	late Oxfordian, Jurassic	Sakaraha, Morondava Basin, SW Madagascar	8
<i>Aspidoceras</i> sp.	BSPG MAn-4046b	2–3	late Oxfordian, Jurassic	Sakaraha, Morondava Basin, SW Madagascar	7
<i>Aspidoceras</i> sp.	BSPG MAn-3193	2–3	late Oxfordian, Jurassic	Sakaraha, Morondava Basin, SW Madagascar	7
<i>Epaspidoceras jeannetti</i> (Collignon, 1959)	BSPG MAn-4505	2–3	late Oxfordian, Jurassic	Sakaraha, Morondava Basin, SW Madagascar	31
<i>Euaspidoceras</i> sp. 1	BSPG MAn-4750	2–3	late Callovian, Jurassic	Dubki near Saratov, Russia	< 110 (estimated)
<i>Euaspidoceras</i> sp. 2	BSPG MAn-4751	2–3	late Oxfordian, Jurassic	Sakaraha, Morondava Basin, SW Madagascar	9
<i>Mirosphinctes</i> sp. 1	BSPG MAn-1769	2–3	late Oxfordian, Jurassic	Sakaraha, Morondava Basin, SW Madagascar	7
<i>Mirosphinctes</i> sp. 2	BSPG MAn-4747	2–3	late Oxfordian, Jurassic	Sakaraha, Morondava Basin, SW Madagascar	> 7 < 25
<i>Pseudowaagenia</i> sp.	BSPG MAn-4502	2–3	late Oxfordian, Jurassic	Sakaraha, Morondava Basin, SW Madagascar	< 6
<b>Desmocerozoidea</b>					
<i>Desmoceras</i> ( <i>D.</i> ) <i>latidorsatum</i> (Michelin, 1838)	BSPG MAo-1787	2–3	early Albian, Cretaceous	Ambatolafia, Mahajanga Basin, NW Madagascar	9 (secondary, local)
<i>Eupachydiscus</i> sp.	BSPG MAo-1831	2	Campanian, Cretaceous	Teshio-Nakagawa area, Hokkaido, Japan	54
<i>Eupachydiscus</i> sp.	BSPG MAo-1832	2	Campanian, Cretaceous	Teshio-Nakagawa area, Hokkaido, Japan	< 430 (estimated)
<i>Eupachydiscus</i> sp.	BSPG MAo-1833	2	Campanian, Cretaceous	Teshio-Nakagawa area, Hokkaido, Japan	< 340 (estimated)
<i>Eupachydiscus</i> sp.	BSPG MAo-1834	2	Campanian, Cretaceous	Teshio-Nakagawa area, Hokkaido, Japan	< 470 (estimated)
<i>Puzosia saintoursi</i> (Collignon, 1963)	BSPG MAo-1797	2–3	early Albian, Cretaceous	Ambatolafia, Mahajanga Basin, NW Madagascar	17–19 (secondary, local) 35–39 (secondary, local)
<b>Deshayesitoidea</b>					
<i>Colombiceras</i> sp.	BSPG MAo-1884	1–2	Aptian, Cretaceous	Caucasus region, Russia	< 25

the state of a prismatic reduced dorsal shell wall, even up to a diameter of 72 mm (BSPG MAn-4503). Nevertheless, this species was probably also able to form a nacreous reduced dorsal shell during ontogeny. At least one specimen (BSPG

MAn-4505) develops this dorsal shell type at a diameter of 31 mm. Conch fragments of a large *Euaspidoceras* sp. 1 (BSPG MAn-4750) seem to prove at least an ontogenetic late existence at a diameter of 110 mm.

In contrast to other taxa, where the nacreous reduced dorsal shell wall corresponds only to an umbilical shell doubling, the shell doubling can coat the whole interior of the conch in Aspidoceratinae (Fig. 12D<sub>1</sub>).

*The formation and function of the nacreous reduced dorsal shell wall.*—The nacreous reduced dorsal shell has to be secreted in the rear living chamber since it does not extend up to the aperture, i.e., it wedges out. Ventral and lateral shell doublings were probably similarly formed but could adorally extend much further into the living chamber as associated muscle scars imply (Doguzhaeva and Mutvei 1991).

The adapical mantle portions, that formed this dorsal shell wall type, had the ability to form prismatic and nacreous material. Our observations imply that the secondary dorsal nacreous layer appears to be derived from the (secondary) dorsal inner prismatic layer (i.e., partitioning) of a prismatic reduced dorsal shell wall. We assume that this early stage shows a rearrangement of the adapical mantle. Its cells seem to develop new secretion abilities. The clear separation of all three layers in later ontogeny implies the emergence of distinct apical mantle sections for each layer.

The nacreous reduced dorsal shell wall is a product of ongoing ontogeny replacing a prismatic reduced dorsal shell wall. Apparently, the taxa have to reach a certain size ( $D = 6\text{--}79$  mm) or age. However, size alone seems not to be the determining trigger; there is no general ontogenetic pattern of occurrence in size. Even large specimens of e.g., *Argonauticeras besairiei* (BSPG MAO-1802,  $D = 102$  mm), *Phylloceras (Euphyllloceras) cf. velledae* (BSPG MAO-1880,  $D = 106$  mm), or *Diviosphinctes* sp. 1 (BSPG MAn-4499,  $D = 74$  mm) can lack a nacreous reduced dorsal shell wall.

An important trigger seems to be the relief of the preceding whorl. The nacreous reduced dorsal shell wall of aspidoceratids commences with the formation of prismatic radial lirae (cf. Radtke and Keupp 2016). It also smooths out the sculpture of *Kepplerites galilaeii*, *Perisphinctes (Kraanosphinctes) mahabokensis*, and *Colombiceras* sp. which develop prominent ribs. It can be assumed that relief smoothing facilitates the attachment of the septa. However, the prismatic reduced dorsal shell wall adopts the same function but the nacreous reduced dorsal shell wall was probably much more robust due to its nacreous character. Nacre exhibits an extremely high resistance to fracture (Jackson et al. 1988).

*Likely occurrences of the nacreous reduced dorsal shell wall.*—Some rather inconspicuous formations of dorsal nacre are probably expressions of the nacreous reduced dorsal shell wall. All these formations are associated with, or are rather a part of, the dorsal inner prismatic layer. Often both materials merge with each other. An assignment to the septa can be excluded. At least we assume a similar place of secretion as the nacreous reduced dorsal shell wall.

At two points, at a distance of  $360^\circ$ , the dorsal inner prismatic layer of one specimen of *Puzosia saintoursi* (Desmoceratoidea, BSPG MAO-1797) develops nacre-like

structures (Fig. 11A<sub>1</sub>, A<sub>3</sub>) which in the following shell portions repeatedly disappear and reappear. Similar to *Eupachydiscus* sp., *P. saintoursi* can form an umbilical shell doubling which probably is responsible for the formation of dorsal nacre. Also one specimen of *Desmoceras (Desmoceras) latidorsatum* (Desmoceratoidea, BSPG MAO-1787) develops similar nacreous portions (Fig. 14E).

One large specimen of *Kosmoceras cf. duncani* (Stephanoceratoidea, BSPG MAn-4788,  $D = 90$  mm) forms inclusions of nacreous material within thickenings of the dorsal inner prismatic layer (Fig. 15B) which weaken the relief of ventro-lateral spines of the preceding whorls. Fragments of the dorsal shell wall of a large *Speetoniceras versicolor* (Perisphinctoidea, BSPG MAO-1861,  $D = 200$  mm) show prismatic material which is interbedded with patches of nacre (Fig. 15C).

**The complete dorsal shell wall.**—Several heteromorph and planispirally coiled taxa develop a complete dorsal shell wall (Fig. 9, Table 2; SOM: table A) that corresponds to its ventral and lateral equivalents (Figs. 2B, 3A, B). A complete dorsal shell wall can be observed in heteromorph taxa of Scaphitoidea (e.g., *Hoploscaphites nicoletti*) and Ancyloceratoidea (e.g., Ancyloceratoidea indet.) as well as in some planispirally coiled taxa of Lytoceratoidea (e.g., *Lobolytocras costellatum*), Eoderoceratoidea (e.g., *Amaltheus margaritatus*), Stephanoceratoidea (e.g., *Quenstedtoceras henrici*), Perisphinctoidea (e.g., *Coffatia [Grossouvria]* sp. 2), Haploceratoidea (e.g., *Hecticoceras (Sublunuloceras)* sp.), Desmoceratoidea (e.g., *Cleoniceris (Grycia) besairiei*), Hoplitoidea (e.g., *Metaplacenticeras subtilistriatum*), and Douvilleiceratoidea (e.g., *Douvilleiceris mammilliatum*).

In this dorsal shell wall type, the three shell layers of the ventral, lateral, and dorsal shell wall form a more or less continuous conch tube around the aperture (Figs. 2B, 3A, B). The wall consists of the same outer prismatic layer, median nacre layer, and inner prismatic layer all around (Figs. 16, 17A, 18). Our heteromorphs show that at least the dorsal nacreous layer extends up to the aperture (Fig. 18D). There, it ends simultaneously with its ventral and lateral counterparts. The dorsal inner prismatic layer is only formed in the rear parts of the living chamber. However, several taxa developed structural variations differing from the common case (see below).

*The complete dorsal shell wall of Scaphitoidea.*—Complete dorsal shell walls are favoured in heteromorph conchs like those of Scaphitpidea (Fig. 18). Our observations show that the dorsal shell wall of scaphitoids undergo an ontogenetic development. The planispiral, juvenile conch (phragomocone) is characterized by a prismatic reduced dorsal shell wall and can even form a wrinkle layer (Fig. 18B, C). A complete dorsal shell wall is accompanied by the detachment of their hook-like living chamber. Usually, already prior to the detachment, a first very thin dorsal nacreous layer and sometimes a first thin dorsal outer prismatic layer appear attaching to the preceding whorl, and internally sealed by



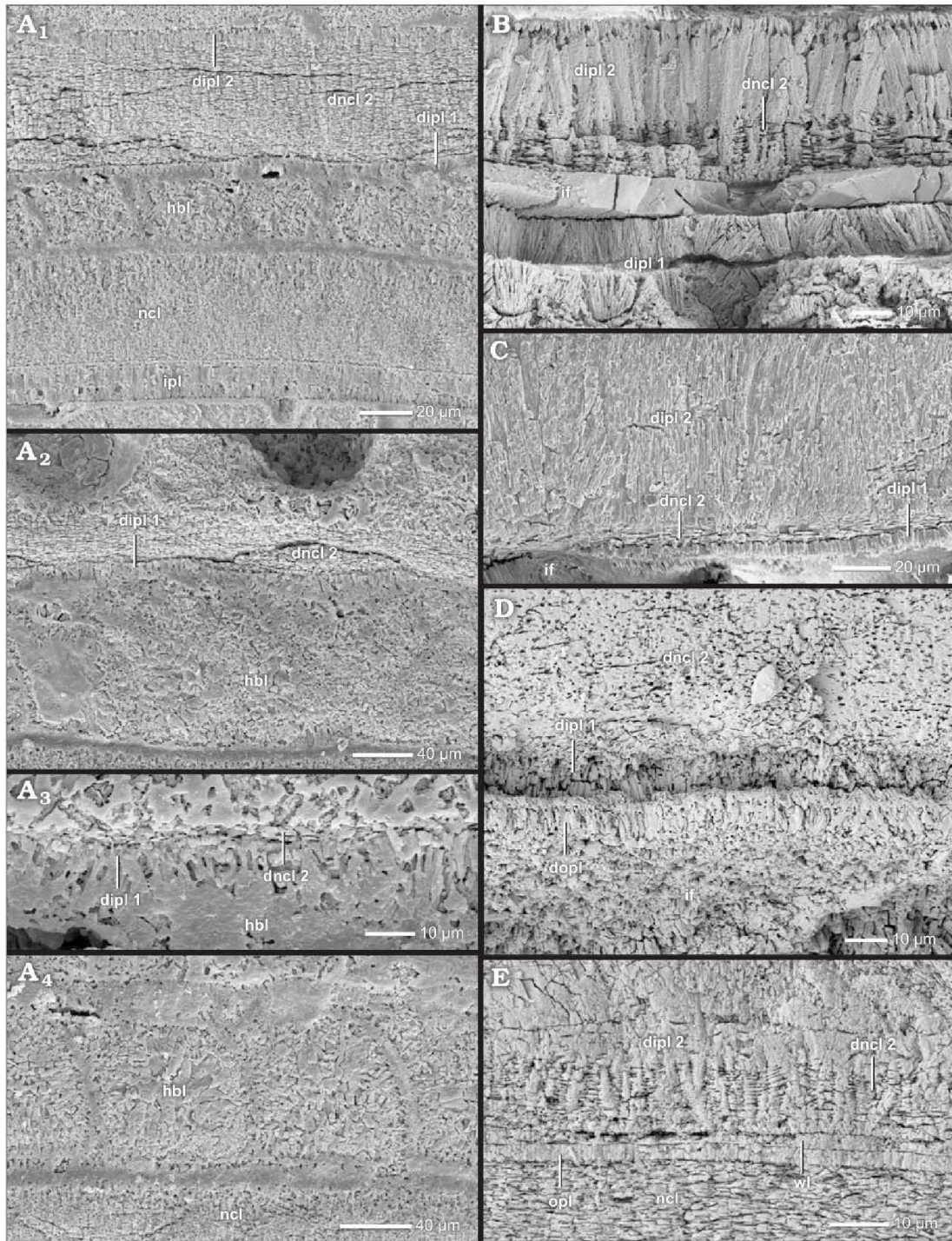


Fig. 14. Construction of the nacreous reduced dorsal shell wall (A–C, E, median section, growth direction to the right, centrifugal; D, transversal section, centrifugal). **A.** *Aspidoceras* sp., BSPG MA-3193, late Oxfordian, Jurassic, Sakaraha, Morondava Basin, SW Madagascar; the dorsal shell wall consists of a primary dorsal inner prismatic layer, a secondary dorsal nacreous layer and a secondary dorsal inner prismatic layer; the dorsal shell wall becomes thinner towards the aperture (A<sub>1</sub>–A<sub>3</sub>) and vanishes completely (A<sub>4</sub>). **B.** *Eupachydiscus* sp., BSPG MAo-1831, Campanian, Cretaceous, Teshio-Nakagawa →

the dorsal inner prismatic layer (Fig. 18A–C). We find diameter values of ca. 16 to 56 mm (Table 2). Observations in *Hoploscaphites nicolletti* show that the primary formation of the dorsal nacreous layer is not coeval in the whole conch tube. The dorsal nacre layer thus becomes thinner from the ventral crest of the preceding whorl towards its ventral edge and completely disappears at its flanks. The dorsal shell wall that covers the lateral shell portions consists of a dorsal inner prismatic layer only.

However, there are individual differences occurring in the ontogeny of particular taxa. For example, in *Scaphites whitfieldi* the first thin nacreous portions occur in the “phragmocone” (D = 22 mm). Then,  $\frac{1}{4}$  whorl later, shortly before the detachment of the hooked living chamber, the dorsal nacreous layer thickens episodically (D = 27 mm): A new nacre package is attached repeatedly from within, i.e., imbrications (dnc1 A–C in Fig. 19A). However, the older nacre packages persist and the overall shell thickness increases. The thickening starts at a distance of ca. 4 septal spaces (adult septa compression) in front of the living chamber and ends with the last septum (or rather the development of the adult aperture).

In *H. nicolletti*, the dorsal nacreous layer begins in the adult living chamber. The diameter of the initiation of the dorsal nacreous layer changes depending on the beginning of whorl detachment. It varies between 16 and 56 mm (sexual dimorphism). In the rear living chamber, as well as in the phragmocone, only a prismatic reduced dorsal shell wall is formed. A short distance before the detachment of the hook (distance equivalent of 1–3 septal spaces) the first nacreous lamellae appear (Fig. 18A–C). The layer becomes successively thicker towards the aperture (Fig. 18D).

*The complete dorsal shell wall of planispirally coiled ammonoids.*—A complete dorsal shell wall can also be observed in planispirally coiled ammonoid taxa (Fig. 9, Table 2; SOM: table A) like *Lobolytoceras costellatum* (Lytocerozoidea; Fig. 16) and *Choffatia (Grossouvria)* sp. 2 (Perisphinctoidea; Fig. 17A). In both taxa we observe a continuum of the ventral, lateral, and dorsal shell layers (Fig. 3B). At least the nacreous layer and the inner prismatic layer extend up to the ventral crest of the preceding whorl. On occasion, a dorsal outer prismatic layer can be observed (Figs. 16C, 17A<sub>2</sub>).

Similar to the scaphitids, a complete dorsal shell wall develops after a prismatic reduced dorsal shell wall. The first thin nacreous structures occur as an outer cover of the dorsal inner prismatic layer around a diameter of 66 mm in *L. costellatum* and 22 mm in *Choffatia (Grossouvria)* sp.

2. Unfortunately, the inner whorls of these specimens are lacking, therefore a connection with whorl number cannot be determined. In this early stage, the dorsal nacreous layer is thin but becomes thicker with progressing ontogeny. Thus in large specimens of *L. costellatum* (BSPG MAn-3059, D = 620 mm), the dorsal nacreous layer is of similar dimensions to the thick dorsal inner prismatic layer (Fig. 16A, B).

The specimen of *Choffatia (Grossouvria)* sp. 2 is probably an isolated case. At least two larger specimens of *Choffatia (Grossouvria)* sp. 1 maintain a prismatic reduced dorsal shell wall up to a diameter of 60 mm.

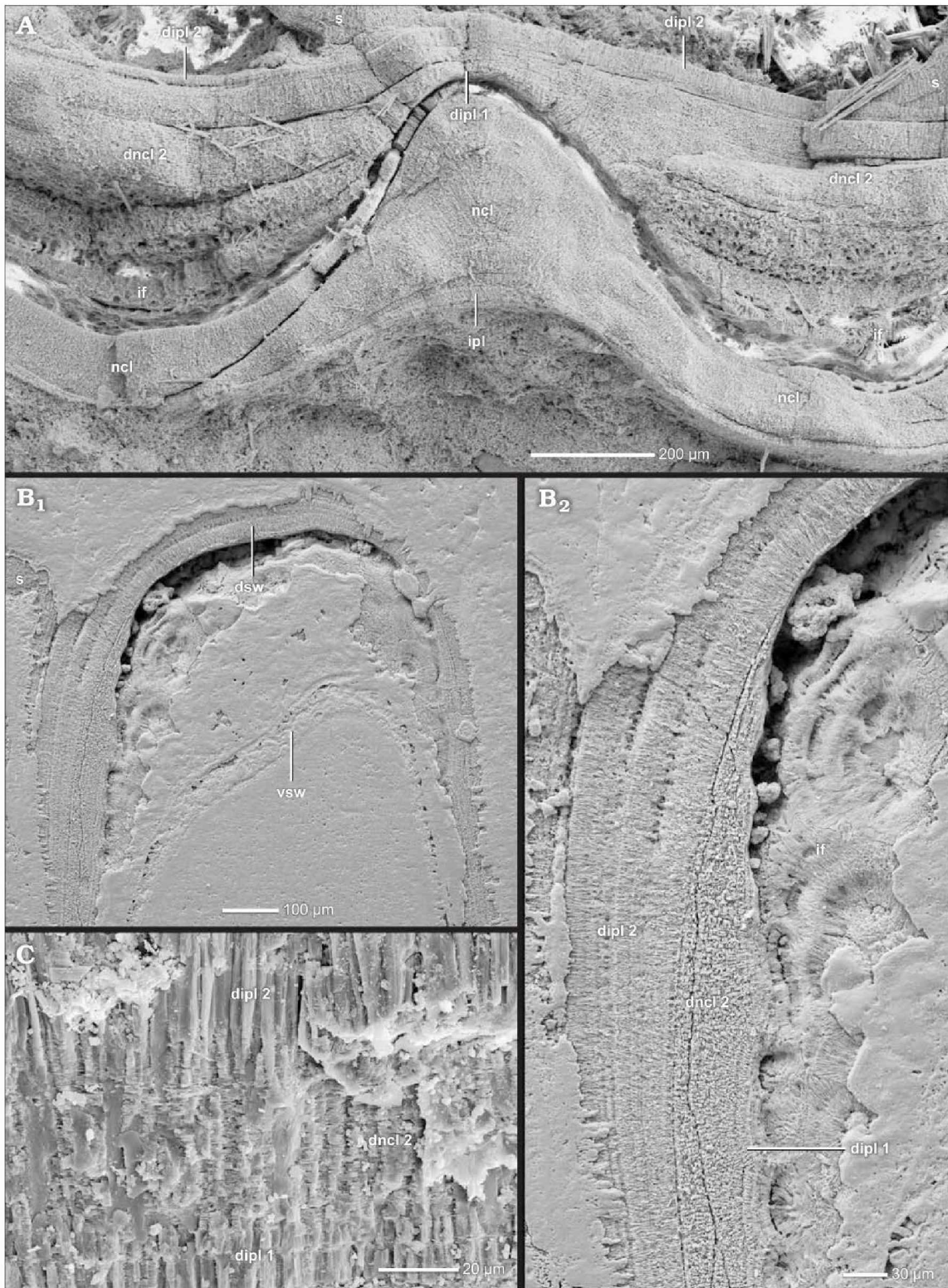
*Secondarily formed complete dorsal shell walls.*—On two occasions we observed the formation of a (secondary) complete dorsal shell wall as a result of an external trigger (e.g., encrusting, injury) in planispirally coiled taxa (Table 2). It is preceded by a prismatic reduced dorsal shell wall.

One specimen of *Divisosphinctes besairiei* (Persphinctoidea, BSPG PA-10151b) develops a complete dorsal shell wall during overgrowth of a ventrally attached oyster (Fig. 17B<sub>1</sub>; cf. Keupp 2012; fig. 238 left). The dorsal shell wall detaches from the preceding whorl to overgrow the oyster, forming cavities adorally and abapically. The dorsal shell wall forms a continuum with the ventral/lateral shell portions and their internal structures are identical (Fig. 17B<sub>2</sub>, B<sub>4</sub>). The complete dorsal wall begins adapically to the oyster while the dorsal shell wall still attaches to the preceding whorl. At a length of approximately 9 septal spaces adapically to, or rather before, the encruster (D = 39 mm), the first nacreous lamellae (1–3) occur. The early dorsal outer prismatic layer is absent or later not well defined (Fig. 17B<sub>2</sub>) but becomes rather clearer with progressing growth (Fig. 17B<sub>3</sub>–B<sub>5</sub>). The complete dorsal shell can be observed for a length of at least 9 septal spaces behind (or adorally of) the oyster (as far as the preserved end of the specimens' shell). However, the dorsal nacre of this late stage is only formed in rib interspaces of the preceding whorl. There the dorsal shell wall thickens to smooth the relief of the ribs.

In one specimen of *Cleoniceras (Grycia) besairiei* (Desmocerozoidea, BSPG PA-33582) a secondarily formed dorsal nacreous layer, set between the wrinkle layer and the dorsal inner prismatic layer, reinforces a prismatic reduced dorsal shell wall (Fig. 13A). The dorsal nacreous layer is formed simultaneously, or rather in reaction, to a forma aegra aptycha (Keupp 1977, 2012; Drobniewski 2014), an internal shell lamella which underpins a broken shell portion and is formed after a withdrawal of the mantle edge (Drobniewski 2014; personal observations GR and HK). We assume the contemporaneous formation of both features.

area, Hokkaido, Japan; the early secondary nacreous layer is part of the secondary inner prismatic layer. C. *Euaspidoceras* sp. 2, BSPG MAn-4751, late Oxfordian, Jurassic, Sakaraha, Morondava Basin, SW Madagascar; same as in B. D. *Colombiceras* sp., BSPG MAo-1884, Aptian, Cretaceous, Caucasus region, Russia; the dorsal shell wall cover of the flanks of the preceding whorl consists of a dorsal outer prismatic layer, a primary dorsal inner prismatic layer, a secondary dorsal nacreous layer (and a secondary dorsal inner prismatic layer). E. *Desmoceras (Desmoceras) latidorsatum* (Michelin, 1838), BSPG MAo-1787, early Albian, Cretaceous, Ambatolafia, Mahajanga Basin, NW Madagascar; the dorsal shell wall can develop nacreous material within the dorsal inner prismatic layer. Abbreviations: dipl 1/2, primary/secondary dorsal inner prismatic layer; dnc1 2, secondary dorsal nacreous layer; hbl, herringbone layer; if, infilling; ipl, inner prismatic layer; ncl, nacreous layer; opl, outer prismatic layer; wl, wrinkle layer.





*The formation and function of the complete dorsal shell wall.*—We assume that the above mentioned complete dorsal shell walls were formed in a similar way. Our observations imply that the ventral, lateral, and dorsal shell walls were secreted more or less contemporaneously by the same mantle portions: All shell layers, at least the nacreous layer and inner prismatic layer, were observed to form a continuum ventrally, laterally and dorsally. At least the dorsal, lateral and ventral nacreous layers form the aperture in heteromorphs, indicating a secretion near the mantle edge. It results from the secretion sequence (opl → ncl → ipl) that the dorsal outer prismatic layer has to be formed at the aperture as well. However, the dorsal inner prismatic layer was secreted by adapical mantle portions as inferred from evidence in the rear living chamber only. For planispirally ammonoids the same processes are likely.

Complete dorsal shell walls of heteromorph and planispiral taxa follow a prismatic reduced dorsal shell wall in ontogeny. Actually, size or age seems to be a determining factor. However, there is no general ontogenetic pattern of occurrence. Even closely related taxa of similar or larger size do not have a complete dorsal shell wall: e.g., *Argonauticeras besairiei* (Lytocerozoidea, BSPG MAn-1802, D = 102 mm) or *Divisosphinctes* sp. 1 (Perisphinctoidea, BSPG MAn-4499, D = 74 mm). It is likely that beside the age and size another factor has to be considered.

In heteromorph Scaphitoidea, the detachment of the dorsal shell wall from the preceding whorl induces the formation of a complete dorsal shell. Only apertural secreted portions of the dorsal shell wall can ensure integrity of the whole shell tube during detachment because the preceding whorl does not support the succeeding one. This is a general observation in heteromorphs (Erben et al. 1969; Doguzhaeva



← Fig. 15. Construction of the nacreous reduced dorsal shell wall (A, median section, growth direction to the left, centrifugal; B, C, transversal section, centrifugal). A. *Keplerites galilaei* (Oppel, 1862), BSPG MAn-4783, early Callovian, Jurassic, Znamenka on Unzha River, Russia; a thickening of the secondary dorsal nacreous layer compensates the rib relief; the layer thickens in the rib concavities, but thins at the rib crest (compare Fig. 12B). B. *Kosmoceras* (*Kosmoceras*) cf. *duncani* (Sowerby, 1816), BSPG MAn-4788, late Callovian, Jurassic, Dubki near Saratov, Russia; B<sub>1</sub>, the spines (vsw) are overgrown by a thick dorsal shell wall (dsw) which forms nacreous portions; B<sub>2</sub>, close-up of B<sub>1</sub>; at the left flank of the spine a nacreous portion occurs in the dorsal shell wall. C. *Speetonoceras versicolor* (Trautschold, 1865), BSPG MAo-1861, early Aptian, Cretaceous, Simbirsk, Ulyanovsk, Volga Basin region, Russia; the dorsal inner prismatic layer develops inclusions of nacre. Abbreviations: dipl 1/2, primary/secondary dorsal inner prismatic layer; dncl 2, secondary dorsal nacreous layer; dsw, dorsal shell wall; if, infilling; s, septum; vsw, ventral shell wall.

Fig. 16. Construction of the complete dorsal shell wall (transversal section, centrifugal). *Lobolytoceras costellatum* (Pavia, 2002), BSPG MAn-3059, late Oxfordian, Sakaraha, Morondava Basin, SW Madagascar. A. The dorsal shell wall consists of a dorsal outer prismatic layer, a dorsal nacreous layer and a dorsal inner prismatic layer. B. Close-up of A; the thick dorsal inner prismatic layer consists of two sub-layers. C. Close-up of A; the dorsal outer prismatic layer. Abbreviations: dipl, dorsal inner prismatic layer; dncl, dorsal nacreous layer; dopl, dorsal outer prismatic layer.



Table 2. Ammonoid specimens which develop the complete dorsal shell wall. <, > indicate that the proper onset of the complete dorsal shell wall cannot be accurately determined due to hiatus in shell preservation or preparation (e.g., transversal section). \*, the dorsal nacreous layer has a prismatic appearance; \*\*, seemingly complete dorsal shell wall. (The complete dorsal shell wall lacks the dorsal nacreous layer). \*\*\*, reinforced complete dorsal shell wall. (The complete dorsal shell wall is reinforced by additional pair of nacreous and prismatic layers).

Taxon	Collection number	Preservation index	Age, period	Location	Diameter at which complete dorsal shell wall begins to form (mm)
<b>Lytoceroidea</b>					
<i>Lobolytoceras costellatum</i> (Pavia, 2002)	BSPG MAn-2061	2	late Oxfordian, Jurassic	Sakaraha, Morondava Basin, SW Madagascar	> 37 < 66
<i>Lobolytoceras costellatum</i> (Pavia, 2002)	BSPG MAn-3059	2	late Oxfordian, Jurassic	Sakaraha, Morondava Basin, SW Madagascar	< 620
<b>Eoderoceroidea</b>					
<i>Amaltheus margaritatus</i> de Monfort, 1808*	BSPG MAn-4798	2	late Pliensbachian, Jurassic	Buttenheim, Bavaria, SE Germany	< 72
<i>Amaltheus margaritatus</i> de Monfort, 1808*	BSPG MAn-4799	2	late Pliensbachian, Jurassic	Buttenheim, Bavaria, SE Germany	< 140
<b>Stephanoceroidea</b>					
<i>Quenstedtoceras henrici</i> Douville, 1912**	BSPG MAn-4768	1–2	early Callovian, Jurassic	Dubki near Saratov, Russia	< 15
<i>Sigaloceras (Sigaloceras) calloviense</i> (Sowerby, 1815)**	BSPG MAn-4785	1–2	late Callovian, Jurassic	Znamenka on Unzha River, Russia	< 85 (estimated)
<b>Perisphinctoidea</b>					
<i>Choffatia (Grossouvreia) sp. 2</i>	BSPG MAn-4520	1–2	late Callovian, Jurassic	Dubki near Saratov, Russia	~ 22
<i>Divisosphinctes besairiei</i> Collignon, 1960	BSPG PA-10151	2–3	late Oxfordian, Jurassic	Sakaraha, Morondava Basin, SW Madagascar	39 (secondary formation)
<b>Haploceroidea</b>					
<i>Hectioceras (Sublumloceras) sp. **</i>	BSPG MAn-4739	1–2	late Callovian, Jurassic	Dubki near Saratov, Russia	< 47 (estimated)
<b>Desmoceroidea</b>					
<i>Cleoniceras (Grycia) besairiei</i> Collignon, 1949	BSPG PA-33582	2–3	early Albian, Cretaceous	Ambatolafia, Mahajanga Basin, NW Madagascar	65 (secondary formation)
<b>Hoplitoidea</b>					
<i>Metaplacentoceras subtilistriatum</i> (Jimbo, 1894)**	BSPG MAo-1824	2–3	Campanian, Cretaceous	Teshio-Nakagawa area, Hokkaido, Japan	> 10 < 18
<b>Ancyloceroidea</b>					
Ancyloceroidea indet.***	BSPG MAo-1813	2–3	Aptian, Cretaceous	Shilovka near Volga River, Russia	< 2nd shaft
<b>Douvilleiceroidea</b>					
<i>Douvilleiceras mammilliatum</i> (Schlotheim, 1813)***	BSPG MAo-1808	2–3	early Albian, Cretaceous	Ambatolafia, Mahajanga Basin, NW Madagascar	29
<i>Douvilleiceras mammilliatum</i> (Schlotheim, 1813)***	BSPG MAo-1809	2–3	early Albian, Cretaceous	Ambatolafia, Mahajanga Basin, NW Madagascar	> 16 < 21
<i>Douvilleiceras mammilliatum</i> (Schlotheim, 1813)***	BSPG MAo-1810	2–3	early Albian, Cretaceous	Ambatolafia, Mahajanga Basin, NW Madagascar	< 23
<i>Douvilleiceras mammilliatum</i> (Schlotheim, 1813)***	BSPG MAo-1811	2–3	early Albian, Cretaceous	Ambatolafia, Mahajanga Basin, NW Madagascar	24
<i>Douvilleiceras sp.***</i>	BSPG MAo-1812	2	Early Cretaceous	Bally, Normandy, France	< 23
<b>Scaphitoidea</b>					
<i>Hoploscaphites nicoletii</i> (Morton, 1842)	AMNH-FI-99141	2	Maastrichtian, Cretaceous	Fox Hills Formation (Loc. #3272), S Dakota, USA	< 56
<i>Hoploscaphites nicoletii</i> (Morton, 1842)	AMNH-FI-99143	2	Maastrichtian, Cretaceous	Fox Hills Formation (Loc. #3272), S Dakota, USA	< 16
<i>Scaphites whitfieldi</i> Cobban, 1951	AMNH-FI-99144	2	Turonian, Cretaceous	Turner Sandy Member (Loc. #3190), Wyoming, USA	< 22

and Mikhailova 1982; Landman 1987; Doguzhaeva and Mutvei 1989). In our specimens of *Hoploscaphites nicoletii* and *Scaphites whitfieldi* the formation already begins

prior to detachment. Considering the length of the living chamber, it is likely that these initial, thin stages of the dorsal nacre layer were formed in aboral portions while at

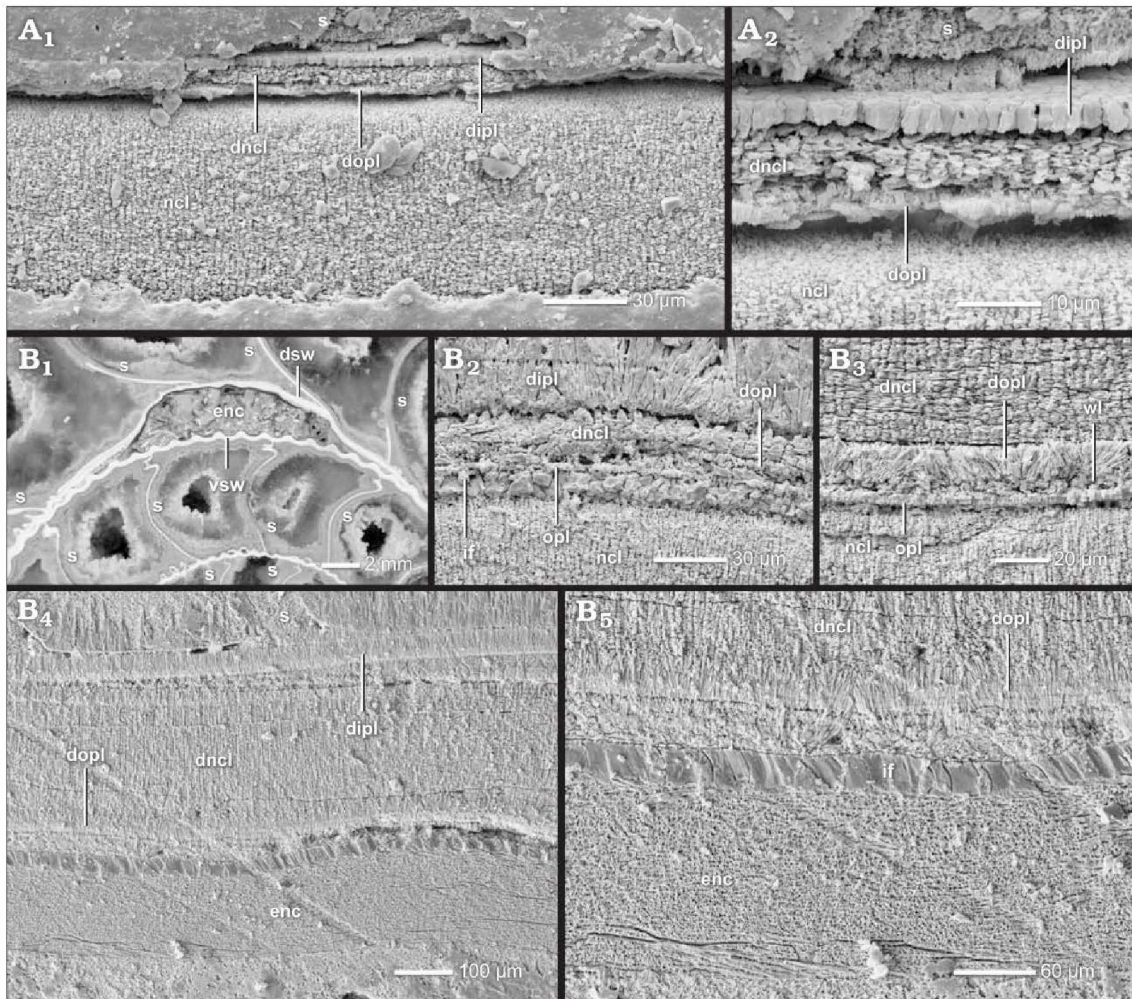


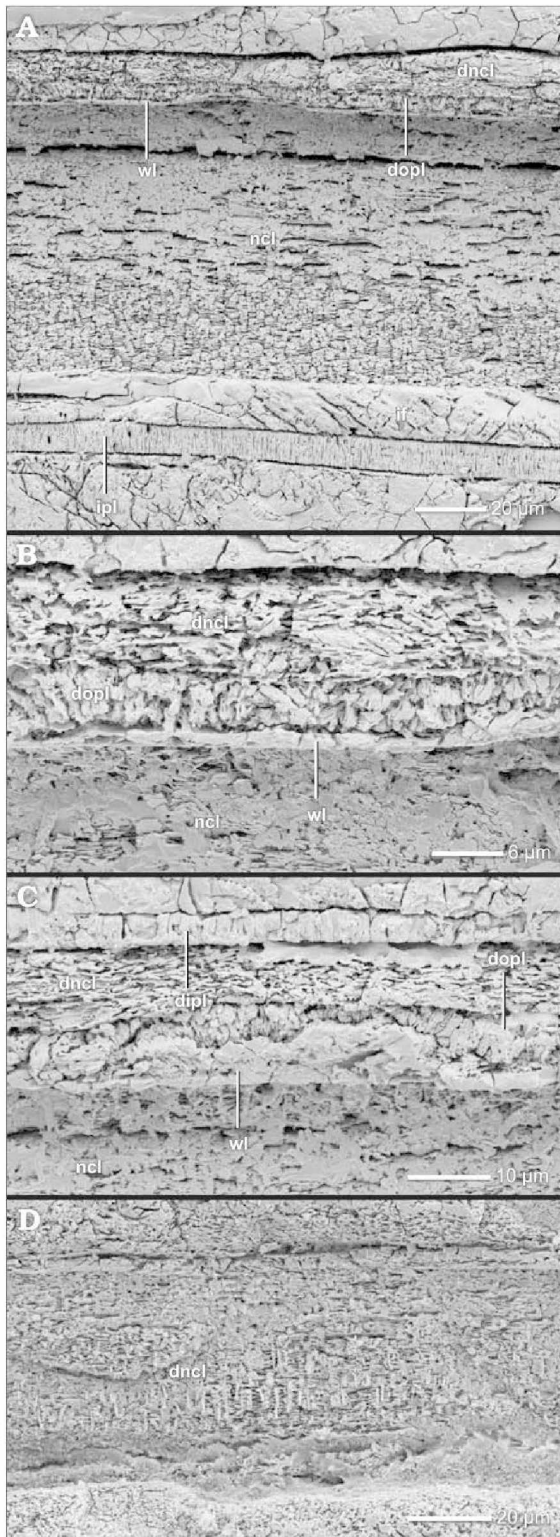
Fig. 17. Construction of the complete dorsal shell wall (median section, growth direction to the left, centrifugal). **A.** *Choffatia (Grossouvreia)* sp. 1, BSPG MAh-4520, late Callovian, Jurassic, Dubki near Saratov, Russia; A<sub>1</sub>, the dorsal shell wall consists of a dorsal outer prismatic layer, a dorsal nacreous layer and a dorsal inner prismatic layer; A<sub>2</sub>, close-up of A<sub>1</sub>. **B.** *Divisosphinctes besairiei* Collignon, 1960, BSPG PA-10151b, late Oxfordian, Jurassic, Sakaraha, Morondava Basin, SW Madagascar; B<sub>1</sub>, the ventral shell wall (vsw) is overgrown by an encruster (enc) which is in turn overgrown by the succeeding whorl (dsw); B<sub>2</sub>, the thin early complete dorsal shell is formed in contact with the ventral shell wall; it consists of (a wrinkle layer), a dorsal outer prismatic layer, a dorsal nacreous layer and a dorsal inner prismatic layer; B<sub>3</sub>, the dorsal outer prismatic layer; B<sub>4</sub>, the older, thick, detached dorsal shell wall consists of the same three layers as in B<sub>2</sub>; B<sub>5</sub>, close-up of B<sub>4</sub>. Abbreviations: dipl, dorsal inner prismatic layer; dncl, dorsal nacreous layer; dopl, dorsal outer prismatic layer; dsw, dorsal shell wall; enc, encruster; if, infilling; ncl, nacreous layer; opl, outer prismatic layer; s, septum; vsw, ventral shell wall; wl, wrinkle layer.

the aperture the detachment of the whorl had already begun. This presumes large secretion zones at least in some taxa, i.e., *Scaphites whitfieldi*. Similar to heteromorphs, the secondary complete dorsal shell wall can be formed during detachment from the preceding whorl during overgrowth of encrusters in *Divisosphinctes*. Probably early occurrences of a thin complete dorsal shell wall (ca. 9 septal chambers prior to the detachment) reflect a broad extension of the secretion zone of the mantle as well. Whorl detachment probably also accounts for the complete dorsal shell wall of *Lobolytoceras costellatum*. The whorls of its serpenticone, planispirally shell have only a small contact area. However,

*Protetragonites fraasi* does not form a complete dorsal shell wall although its contact area is smaller.

*The reinforced complete dorsal shell wall of Ancyloceratoidea and Douvilleiceratoidea.*—Several members of the heteromorph Ancyloceratoidea (e.g., *Ancyloceratoidea* indet.) and planispiral Douvilleiceratoidea (e.g., *Douvilleiceratid*) combine the characteristics of the complete dorsal shell wall and a nacreous reduced dorsal shell wall (Table 2; SOM: table A). The dorsal shell wall of studied adult specimens consists of up to five shell layers: a dorsal outer prismatic layer, a primary dorsal nacreous layer and a





primary dorsal inner prismatic layer, i.e., the complete dorsal shell wall; which are reinforced by a second generation of the dorsal nacreous and the dorsal inner prismatic layer, i.e., the nacreous reduced dorsal shell wall (Figs. 3E, F, 7C<sub>2</sub>, 19B). In other words the complete dorsal shell wall displays shell doubling.

In our specimen of *Ancyloceratoidea* indet., the reinforced complete dorsal shell wall is present in both preserved, juvenile shafts (Fig. 19B). However, in specimens of *D. mammilliatum* the transition of a prismatic reduced dorsal shell wall (i.e., wl and dipl) (Fig. 7A<sub>1</sub>, A<sub>4</sub>) into a reinforced complete dorsal shell wall can be observed (Fig. 7C<sub>2</sub>). A thin primary dorsal nacreous layer is established at diameters of 21 to 29 mm (Table 2). With further growth the primary dorsal nacreous layer becomes thicker, the primary dorsal inner prismatic layer becomes thinner and the both inner layers (i.e., dncl 2 and dipl 2) are added.

In *Ancyloceratoidea* indet., all shell layers form a continuum encircling the whole conch tube dorsally, laterally and ventrally (Fig. 3E, F). However, the dorsal shell wall of the genus *Douvilleicerias* (e.g., *D. mammilliatum*, *Douvilleicerias* sp.) shows some special characteristics. For example, the dorsal outer prismatic layer is absent. A further peculiarity, in *Douvilleicerias*, a direct connection of the ventral/lateral and the dorsal shell portions cannot be observed; instead the lateral shell wall wedges out at the umbilical seam (Fig. 7C<sub>3</sub>, C<sub>4</sub>). With the exception of the wrinkle layer, the dorsal shell wall does not cover the whole overgrown portions of the preceding whorl but only the ventral and adjacent portions.

The internal structure can change from the ventral crest of the preceding whorl towards the umbilicus: The dorsal shell wall of *Douvilleicerias* overgrows a row of ventral spines (a row of ventro-lateral spines is uncovered). Usually the dorsal shell wall detaches from the preceding whorl during overgrowth whereby cavities are formed (Fig. 7C<sub>1</sub>). Only at these detached portions does the dorsal shell form the described complete dorsal shell wall with shell doubling (Fig. 7B, C<sub>2</sub>). When the dorsal shell wall attaches to the preceding whorl, the two outer layers (i.e., dncl 1 and dipl 1) wedge out towards the umbilicus and the two inner layers (i.e., dncl 2 and dipl 2) continue and cover the ventro-lateral flanks (Fig. 7A<sub>6</sub>, B). Occasionally, the dorsal shell wall can appear as trilayered through the local disappearance of only the primary dorsal nacreous layer. The primary dorsal

Fig. 18. Construction of the complete dorsal shell wall (transversal section, centrifugal). *Hoploscaphites nicoletii* (Morton, 1842), AMNH-FI-99143, Maastrichtian, Cretaceous, Fox Hills Formation (Loc. 3272), S Dakota, USA. A–C. Prior to the detachment of the living chamber, the dorsal shell wall is already complete and consists of a wrinkle layer, a dorsal outer prismatic layer, a dorsal nacreous layer and a dorsal inner prismatic layer. B. Close-up of A. D. In the detached living chamber, at least a dorsal nacreous layer is formed. The dorsal outer prismatic layer and the dorsal inner prismatic layer are not preserved. Abbreviations: dipl, dorsal inner prismatic layer; dncl, dorsal nacreous layer; dopl, dorsal outer prismatic layer; if, infilling; ipl, inner prismatic layer; ncl, nacreous layer; wl, wrinkle layer.

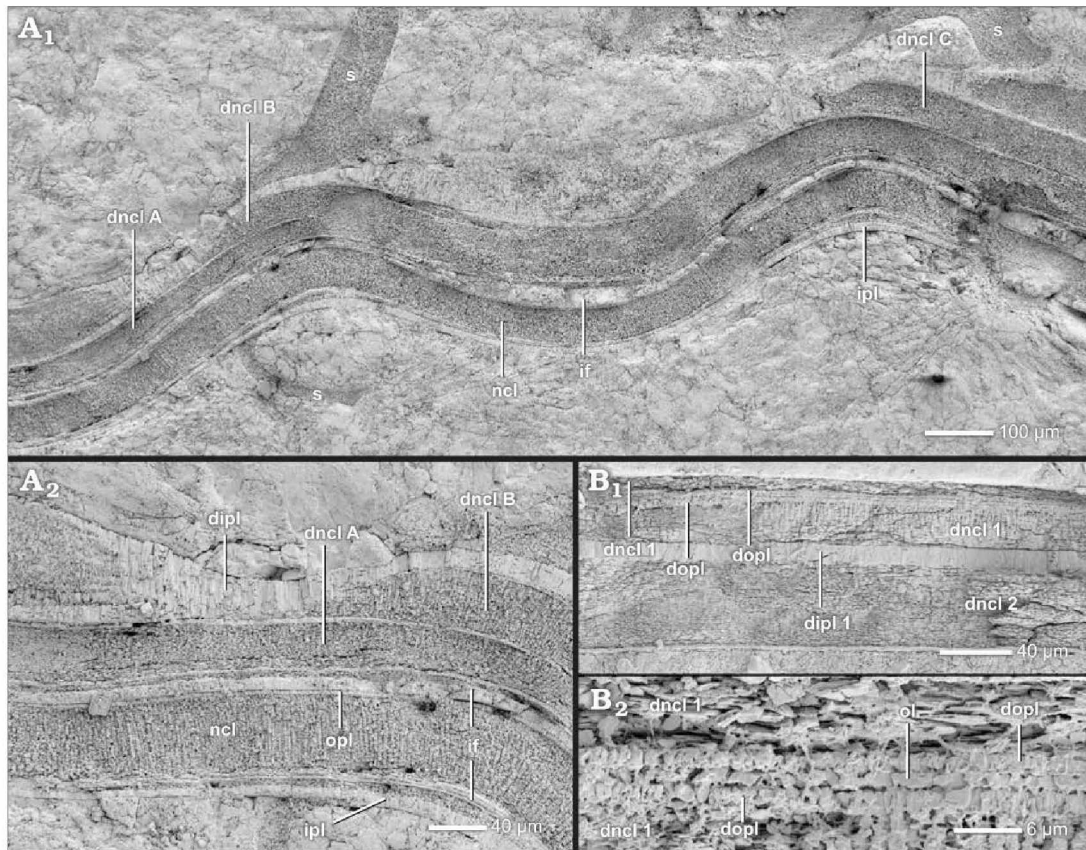


Fig. 19. Construction of the complete dorsal shell wall (A, median section, growth direction to the right, centrifugal; B, transversal section, centrifugal). A. *Scaphites whitfieldi* Cobban, 1951, AMNH-FI-99144, Tournian, Cretaceous, Turner Sandy Member (Loc. 3190), Wyoming, USA; A<sub>1</sub>, shortly before complete detachment of the living chamber, the dorsal nacreous layer is repeatedly reinforced by new generations of the dorsal nacreous layer (dncl A–C); A<sub>2</sub>, close-up of A<sub>1</sub>. B. *Ancyloceratoidea* indet., BSPG MAo-1813, Aptian, Cretaceous, Shilovka near Volga River, Russia; B<sub>1</sub>, contact of both dorsal shell portion of two succeeding shafts; the dorsal shell wall consists of a dorsal outer prismatic layer, a primary dorsal nacreous layer, a primary dorsal inner prismatic layer and a secondary dorsal nacreous layer; the secondary dorsal inner prismatic layer is not preserved; B<sub>2</sub>, close-up of B<sub>1</sub>. Abbreviations: dipl, dorsal inner prismatic layer; dipl 1/2, primary/secondary dorsal inner prismatic layer; dncl, dorsal nacreous layer; dncl 1/2, primary/secondary dorsal nacreous layer; dncl A–C, generations of the dorsal nacreous layer; if, infilling; ipl, inner prismatic layer; ncl, nacreous layer; ol, organic layer; s, septum.

inner prismatic layer forms a “dorsal outer prismatic layer” in these cases (Fig. 7A<sub>6</sub>).

*The formation and function of the reinforced complete dorsal shell wall.*—The reinforced complete dorsal shell walls combine characteristics of a normal complete dorsal shell wall (i.e., dopl and dncl 1) and a nacreous reduced dorsal shell wall (i.e., dipl 1, dncl 2, and dipl 2). Accordingly, we assume that during their formation adoral and adapical mantle portions were involved. The outer layers of the dorsal shell wall (i.e., dopl and dncl 1) were formed at the aperture. The inner layers (i.e., dipl 1, dncl 2, and dipl 2) were secreted in the rear living chamber, i.e., equivalent to the formation of a nacreous reduced dorsal shell wall. *Douvilleiceras* suppress the formation of an outer prismatic layer dorsally.

As in a normal complete dorsal shell wall, detachment from the preceding whorl/shell section seems to induce the formation of a reinforced complete dorsal shell wall.

This is more or less obvious in our shafted specimen of *Ancyloceratoidea* indet. Also other shafted ancyloceratids like *Ptychoceras* (Doguzhaeva and Mutvei 1991, 1993a, b) have a similar construction of the dorsal and ventral shell wall. It is possible that the strong sculpture of *Douvilleiceras*, e.g., spines, and the accompanying detachments of the whorl cause the formation of the reinforced complete dorsal shell wall. It smooths out the relief, probably to facilitate the attachment of the septa. Furthermore, the spines may injure the animal’s soft body during overgrowth. The formation of a dorsal shell wall at the aperture could prevent it.

*The complete dorsal shell wall of Amaltheidae.*—The juvenile whorls of the Amaltheidae (Eoderoceratoidea) form a prismatic reduced dorsal shell wall (i.e., wl and dipl) including a prominent wrinkle layer. In the outer whorls of large *Amaltheus margaritatus* (BSPG MAn-4798, 4799, D > 72 mm), the dorsal shell wall consists of an outer spi-



ral ornament (Fig. 20A; cf. Hölder 1973; Walliser 1970; Birkelund 1980), replacing the wrinkle layer, and an inner bunch of prismatic sub-layers corresponding to the dorsal nacreous layer and dorsal inner prismatic layer (Figs. 3C, 20B<sub>1</sub>, B<sub>2</sub>). The whole dorsal shell wall is almost 2.5 times thicker than the overgrown shell wall of the preceding whorl.

The spiral ornament is a conspicuous coating layer of the preceding whorl which forms raised spiral lines (Fig. 20A). It can be only observed in the overgrown area of the preceding whorl. Each raised line appears as a long pin-like structure in cross section (Figs. 3C, 20B<sub>1</sub>, B<sub>2</sub>). A pin has a broad base, forms a thinner shaft and ends in a pinhead. Nearly identical pin-like structures can be observed in the outer whorls ( $D > 46$  mm) of a *Pleuroceras salebrosum* specimen (BSPG MAn-4804) too: In its living chamber we observe isolated structures at the venter of the preceding whorl and near the umbilical edge (Fig. 20C).

In *Amaltheus margaritatus* the pins (or spiral lines) of the spiral ornament are enclosed by multiple prismatic to spherulitic sub-layers which bend around the pins (dncl in Figs. 3C, 20B<sub>2</sub>). A further inner bunch of prismatic sub-layers, each a few micrometer thick, bridges the relief of the pins leaving cavities between the pins (dipl in Figs. 3C, 20B<sub>1</sub>, B<sub>2</sub>). These outer and inner sub-layers are the dorsal continuation of the ventral/lateral nacreous layer and inner prismatic layer, respectively. Only the inner sub-layers, which bridge the spiral ornament (pins), are the continuation of the inner prismatic layer of the ventral/lateral shell wall (dipl in Fig. 20B<sub>1</sub>, B<sub>2</sub>). The outer prismatic bands, which encrust the pins, originate in the nacreous layer of the ventral/lateral shell wall (dncl in Fig. 20B<sub>2</sub>, B<sub>3</sub>). The ventral/lateral nacreous layer thins at the whorl contact and extends towards the spiral plane along the surface of the preceding whorl up to its mid-flank, where the layer gradually transforms into several prismatic sub-layers (Fig. 20B<sub>2</sub>, B<sub>3</sub>) which continue towards the ventral crest of the preceding whorl, i.e., dorsal nacreous layer.

*The formation and function of the complete dorsal shell wall of Amaltheidae.*—Extension and position of the dorsal spiral ornament are similar to those of the wrinkle layer. Furthermore, the amaltheid juvenile wrinkle layer and adult spiral ornament seem to replace each other (e.g., *Pleuroceras salebrosum*) and both structures are not simultaneously present at the same whorl section (e.g., *Amaltheus margaritatus*), i.e., spatial and ontogenetic separation. Therefore, it is likely that the spiral ornament represents an ontogenetic derivation of the wrinkle layer (e.g., Walliser 1970; Hölder 1973). According to Birkelund (1980), a wrinkle layer can cover the spiral ornament, an observation we can reject (see

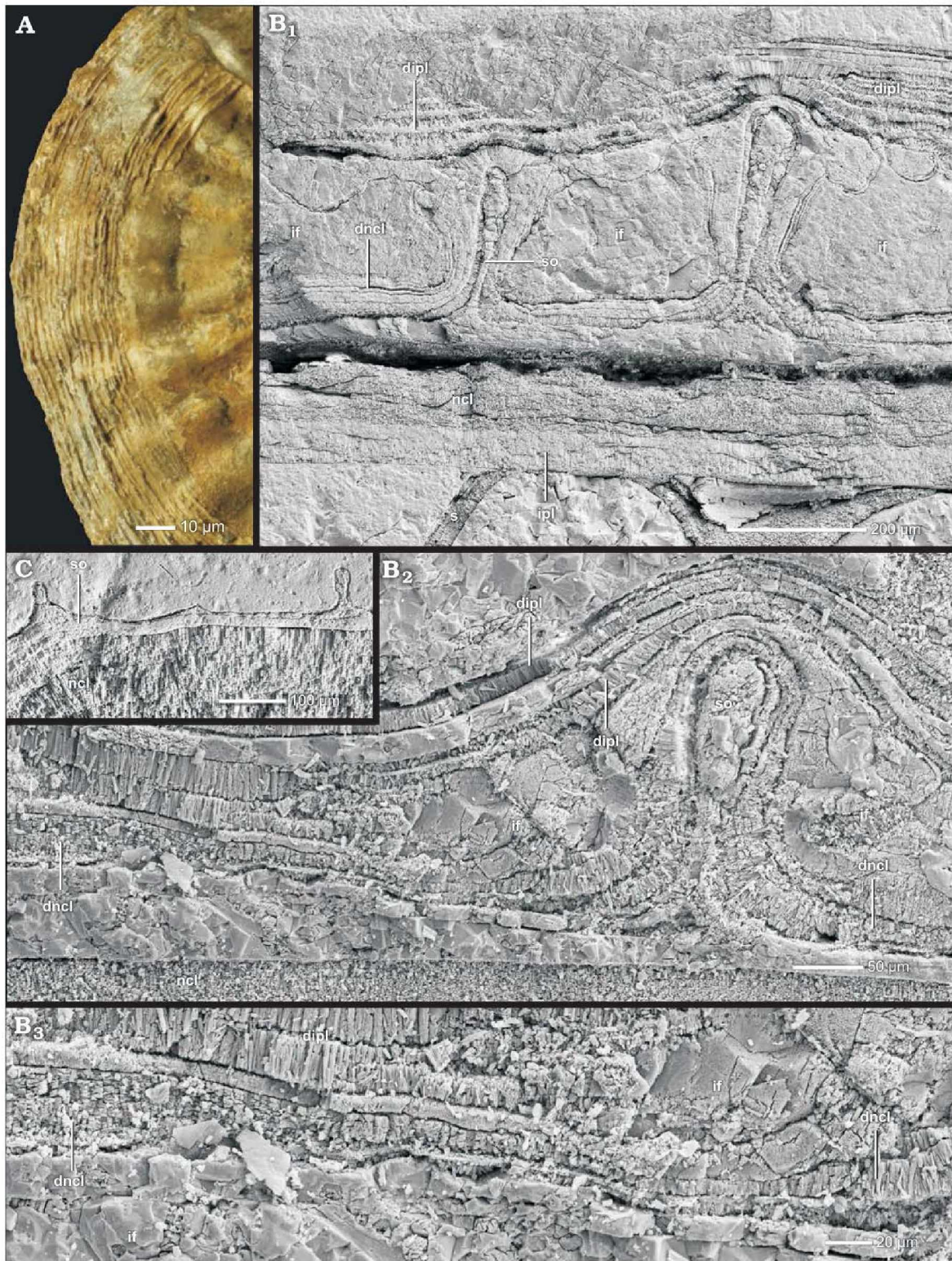
immediately above). Additionally, Birkelund (1980) mentions an *Amaltheus* whose living chamber is covered by the spiral ornament, and assigns it therefore to the ventral/lateral shell wall. We doubt this assertion, since to our knowledge and according to our observations the spiral ornament is only preserved in formerly overgrown portions. Birkelund (1980) probably misinterpreted the often observed prominent spiral sculpture (an undulation of the shell wall) and/or spiral colour pattern of the ventral/lateral shell wall as equivalent expressions of the spiral ornament. Hölder (1973) assumed an internal folding of the spiral ornament layer (= "Leistenschicht"), indicated by undulating shell lamellae. He probably observed the undulated prismatic sub-layers of the dorsal nacreous layer (and inner prismatic layer).

We assume that the spiral ornament, like the wrinkle layer, was secreted by a supracephalic mantle fold at or beyond the aperture. It probably had a similar function as a common wrinkle layer. The spiral lines (and corresponding furrows) may serve in the attachment of the dorsal mantle. The dorsal nacreous and inner prismatic layers weaken the relief of the spiral ornament, probably to facilitate the attachment of the septa.

Apparently, the ventral, lateral, and dorsal nacreous layer and the ventral, lateral, and dorsal inner prismatic layer form a continuum. A secretion similar to a normal complete dorsal shell wall can be assumed: the dorsal inner prismatic layer in the rear living chamber and the dorsal nacreous layer near the aperture. The dorsal shell wall is probably not completely omitted at the aperture. The multi-layering of the dorsal inner prismatic layers is already known from the prismatic reduced dorsal shell wall and probably indicates an intermittent secretion process or at least (brief) interruption during mineralization. However, the dorsal nacreous layer shows a structural alteration from the umbilicus (nacre) towards the crest of the preceding whorl (prismatic). We exclude diagenetic alteration because two specimens develop these structures, each at a different whorl size, and their nacre is usually preserved. The prismatic multi-layering probably reflects the original nacreous lamellae. We assume that the mantle portion that forms the nacre ventrally, laterally and dorsally has changed its secretion ability from nacreous to prismatic dorsally. Apparently, the mantle tissue was able to locally change its secretion ability, i.e., cell secretion plasticity (Fleury et al. 2008; Cuif et al. 2011).

*The seemingly complete dorsal shell wall.*—Some specimens of Stephanoceratoidea (e.g., *Quenstedtoceras henrici*, *Sigaloceras (Sigaloceras) calloviense*), Haploceratoidea (e.g., *Hecticoceras [Sublunuloceras] sp.*), and Hoplitioidea

Fig. 20. Construction of the complete dorsal shell wall of Amaltheidae (A, lateral view, growth direction to the bottom; B, C, transversal section, centrifugal). A. *Amaltheus cf. margaritatus* de Monfort, 1808, BSPG MAn-100, late Pliensbachian, Jurassic, Eype Mouth, Dorset, England; a spiral ornament covers the overlap area of two whorls; the succeeding whorl was removed. The coated venter of the preceding whorl shows the typical pattern of several spiral lines. B. *Amaltheus margaritatus* de Monfort, 1808, BSPG MAn-4798, late Pliensbachian, Jurassic, Buttenheim, Bavaria, SE Germany; B<sub>1</sub>, the dorsal shell wall consists of an outer spiral ornament and inner bunches of prismatic sub-layers that correspond to the dorsal nacreous layer and the dorsal inner prismatic layer; B<sub>2</sub>, the dorsal nacreous layer transforms into prismatic layers; B<sub>3</sub>, close-up of B<sub>2</sub>. C. *Pleuroceras salebrosum* Hyatt, 1867, BSPG MAn-4804, late Pliensbachian, Jurassic, Buttenheim, Bavaria, SE Germany; the dorsal shell wall forms a spiral ornament. Abbreviations: dipl, dorsal inner prismatic layer; dncl, dorsal nacreous layer; if, infilling; ipl, inner prismatic layer; ncl, nacreous layer; s, septum; so, spiral ornament.





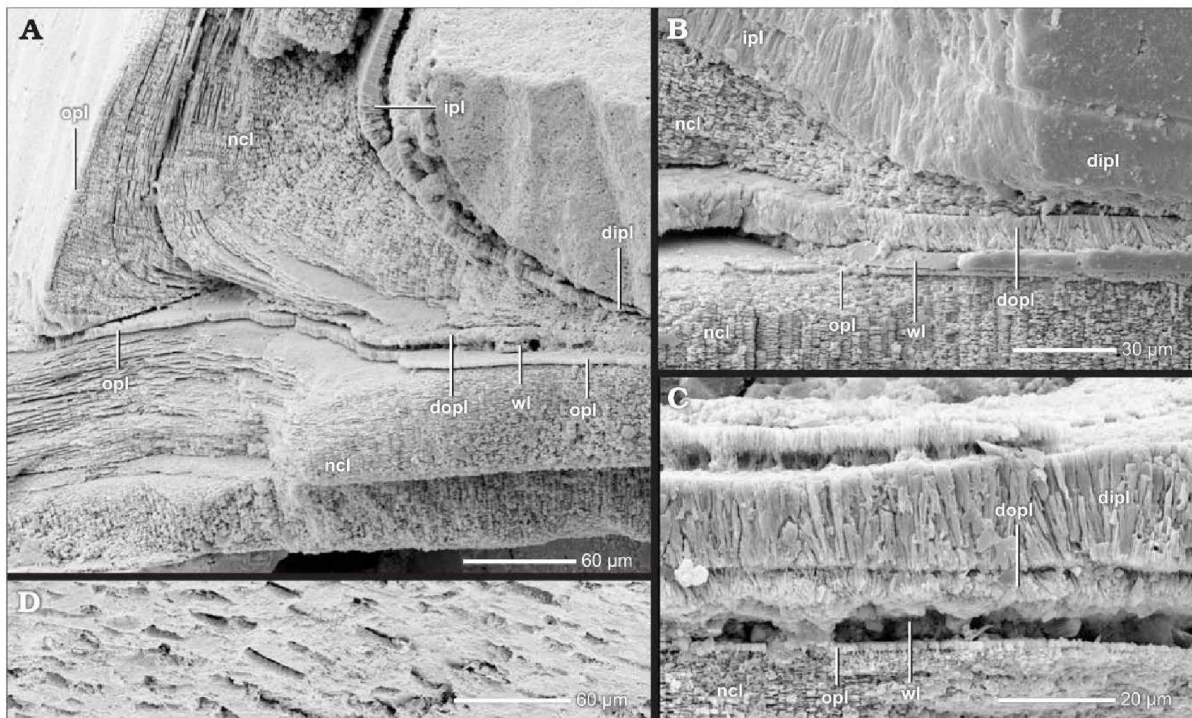


Fig. 21. Construction of the seemingly complete dorsal shell wall (transversal section, centrifugal). *Quenstedtoceras henrici* Douville, 1912, BSPG MAN-4768, early Callovian, Jurassic, Dubki near Saratov, Russia. **A.** At the contact of two whorls the outer prismatic layer and the nacreous layer of the attaching whorl wedge out but a “new” dorsal outer prismatic layer is formed towards the spiral plane which covers the wrinkle layer; the inner prismatic layer is continuous. **B.** The (dorsal) nacreous layer and the (dorsal) inner prismatic layer attach to the “new” dorsal outer prismatic layer which compensates the relief of the wrinkle layer. **C.** The dorsal shell wall consists of a wrinkle layer, a dorsal outer prismatic layer and a dorsal inner prismatic layer. **D.** The wrinkle layer left imprints in the dorsal outer prismatic layer. Abbreviations: dipl, dorsal inner prismatic layer; dopl, dorsal outer prismatic layer; ipl, inner prismatic layer, ncl, nacreous layer, opl, outer prismatic layer; wl, wrinkle layer.

(e.g., *Metaplaticeras subtilistriatum*) form a dorsal outer prismatic layer as a further dorsal shell wall component that basically displays all characteristics of a prismatic reduced dorsal shell wall (i.e., wl and dipl) (Fig. 9, Table 2; SOM: table A). The dorsal shell wall is therefore three-layered (i.e., wl, dopl, and dipl).

The dorsal outer prismatic layer is set between the wrinkle layer and the dorsal inner prismatic layer (Figs. 3D, G, 21A–C). It evens out the wrinkle layer’s relief (Fig. 21D). The dorsal outer prismatic layer only extends from the left to the right umbilical margin. It neither represents a direct continuation of the ventral/lateral outer prismatic layer nor is it a sub-layer of the dorsal inner prismatic layer: After the ventral/lateral outer prismatic layer wedges out at the umbilical seam (Figs. 3G, 21A), the dorsal outer prismatic layer immediately appears as a new thin lamella, which thickens towards the spiral plane (Figs. 3G, 21A). Both the ventral/lateral nacreous layer and inner prismatic layer attach to the dorsal outer prismatic layer at the umbilical seam (Figs. 3G, 21A, B). However, the nacreous layer vanishes completely and only the inner prismatic layer continues as an inner cover of the dorsal outer prismatic layer towards the ventral crest.

*The formation and function of the seemingly complete dorsal shell wall.*—The wrinkle layer and the dorsal inner prismatic layer of this dorsal shell type were probably formed as described in the sections above. The function of the dorsal outer prismatic layer is similar to that of the dorsal inner prismatic layer, i.e., evening out the internal relief and sealing the soft tissue from possible encrusters. Kulicki (1979) highlights a similar layer in one specimen of *Quenstedtoceras* sp., but he interprets it as an alternative appearance of the wrinkle layer. We think this is a misinterpretation; both the dorsal outer prismatic and the wrinkle layer can be clearly separated in our specimens. This layer has to be secreted after the wrinkle layer but before the nacreous layer and inner prismatic layer. The latter two can be excluded as equivalents as well, i.e., no connection but attachment to the dorsal outer prismatic layer. There are no signs of a shell doubling at the umbilicus. An assignment to a primary (dorsal) inner prismatic layer can be therefore excluded as well. It is most likely that the dorsal outer prismatic layer of these specimens is equivalent to the actual (ventral/lateral) outer prismatic layer. Therefore, the layer was probably secreted at the aperture and the dorsal shell should be regarded as

some kind of complete dorsal shell wall in which, however the dorsal nacreous layer was not formed. It is nevertheless unclear why the dorsal outer prismatic layer is interrupted at the umbilical seam.

*Phylogenetic and taxonomic implications of nacreous reduced and complete dorsal shell walls.*—The patchy occurrence of nacreous reduced and complete dorsal shell walls within the ammonoid phylogenetic tree (Fig. 9; SOM: table A) makes a clear assignment to a proper high-order group of Ammonoidea difficult. The prismatic reduced dorsal shell wall is still the most often and dominant type of dorsal shell. The other dorsal shell wall types are indeed a typical characteristic of individual genera or species but a generalization of a diagnostic feature for an entire high-order group (e.g., superfamily) is not advisable as long as only sporadic evidence exists. It is not certain if these examples are outliers or are representative of an entire group of ammonoids.

In spite of this, the scattered occurrence of nacreous reduced and complete dorsal shell walls gives rise to several possible interpretations:

(i) Since all these observations were made in individual genera or species, all of them could represent independent apomorphies of these low-order taxa. The entire subfamily of Aspidoceratinae (e.g., *Aspidoceras* sp. and *Mirosphinctes* sp. 1) seems to be unusual in this respect as all its members seem to have the ability to form a nacreous reduced dorsal shell wall.

However, this interpretation ignores secondary formations of nacreous reduced (e.g., *Puzosia saintoursi*, *Desmoceras* [*Desmoceras*] *latidorsatum*) as well as of complete dorsal shell walls (e.g., *Divisosphinctes besairiei*, *Cleoniceras* [*Grycia*] *besairiei*). We assume that the secondary formation ability is a general ammonoid feature and that primary nacreous reduced and complete dorsal shell walls (i.e., formed during ontogeny) are an expression of that feature. The ammonoid dorsal mantle tissue does not lose the ability to form additional shell layers, especially nacre, but suppresses it in general. The dorsal mantle had the same secretion abilities as the ventral and lateral portions. Coinciding occurrences of both dorsal shell wall types in Perisphinctoidea and Desmoceratoidea may even indicate that both types are connected. Since ventral and lateral shell doublings are commonly observed in ammonoids, e.g., Eoderoceratoidea, Haploceratoidea, Stephanoceratoidea, Perisphinctoidea, Desmoceratoidea (cf. Howarth 1975; Birkelund 1980; Doguzahava and Mutvei 1989, 1991; this study), the nacreous reduced dorsal shell wall probably constitutes its homologous expression. Ventral, lateral as well as dorsal reinforcement of the shell wall (i.e., shell doubling) may represent a general ability. The reinforced complete dorsal shell wall of Ancyloceratoidea and Douvilleiceratoidea may reflect the ground plan of the entire ventral, lateral, and dorsal shell wall. Therefore, we assume that both dorsal shell wall expressions can be regarded as one feature representing the original dorsal shell wall.

The broad distribution of complete and nacreous reduced

dorsal shell walls in the phylogenetic tree (Fig. 9; SOM: table A) indicates a plesiomorph ability to form these dorsal shell wall types, or rather dorsal nacre.

(ii) Based on our data collection (Fig. 9; SOM: table A), this ability seems to have evolved only in post-Triassic ammonoids after the separation from the Phylloceratoidea. As all occurrences are observed in taxa that are descendants of Psiloceratoidea, an origin within this group is likely although not proved yet. In Lytoceratoidea and Eoderoceratoidea (as well as in their descendants) it seems to be a symplesiomorphy. Due to its patchy occurrence we suppose a facultative feature that can be activated when needed.

(iii) Jurassic and Cretaceous samples are over-represented in our collection. Furthermore, the observed occurrences of dorsal nacre are less frequent compared to those of a prismatic reduced dorsal shell wall. There are probably pre-Jurassic and further Jurassic and Cretaceous samples not observed yet. We assume that the ability to form dorsal nacre is a relic feature of the gyrocone ancestors and therefore a plesiomorphy. A facultative feature is likely too.

In both variants, the plesiomorphy of dorsal nacre complicates the usage for phylogeny and taxonomy at lower levels, e.g., superfamilies or families. We even anticipate that an ammonoid could generally pass through a stage of complete or nacreous reduced dorsal shell wall in a theoretical ontogenetic late stage when it reached a certain size or age (although not observed yet). Our observations of these dorsal shell wall types probably represent heterochrony. Nonetheless, we suggest using these features only as an additional taxonomic trait for genera and species (facultative feature) at the current state of knowledge.

Some groups seem to be exceptions and always form at least one expression:

(i) A complete dorsal shell wall is characteristic for the probably polyphyletic Jurassic and Cretaceous heteromorphs (Engeser and Keupp 2002), e.g., Ancyloceratoidea, Scaphitoidea. However, this is a secondary effect of whorl decoiling/detachment, i.e., lacking whorl support, and cannot be used as diagnostic feature.

Considering the dorsal wall structure only, the origin of heteromorphs could be in every ammonoid superfamily, i.e., facultative, plesiomorphic complete dorsal shell wall. However, proven occurrences of a complete dorsal shell wall and time-overlap in the geological record are only given in Lytoceratoidea (e.g., *Lobolytoceras costellatum*), Perisphinctoidea (e.g., *Choffatia* [*Grossouvria*] sp. 2, *Divisosphinctes besairiei*) and Desmoceratoidea (e.g., *Cleoniceras* [*Grycia*] *besairiei*). Despite the assumed general ability to form a complete dorsal shell wall among all ammonoids, these three superfamilies seem to be the most likely candidates as ancestors at the current state of knowledge (Fig. 9).

(ii) In Aspidoceratinae, a nacreous reduced dorsal shell wall is repeatedly formed and usually occurs very early in ontogeny (under 10 mm in diameter). We assume that the ontogenetically early occurrence indicates a characteristic heterochrony of this group.



(iii) The heteromorph superfamily Ancyloceratoidea and their planispiral descendants, Douvilleiceratoidea and Deshayesitoidea (Fig. 9; e.g., House 1993; Rouget et al. 2004; Yacobucci 2016), seemingly share the same characteristics of their dorsal shell wall, i.e., reinforced complete dorsal shell wall. This dorsal shell wall type may underline their close relation. The dorsal shell walls of *Douvilleiceras* (Douvilleiceratoidea) and *Colombiceras* (Deshayesitoidea) can be interpreted as derived from Ancyloceratoidea. The dorsal shell wall of *Douvilleiceras* and *Colombiceras* are nearly identical to those of our Ancyloceratoidea indet. and *Ptychoceras* (Doguzhaeva and Mutvei 1991, 1993a, b) with the exception of a missing dorsal outer prismatic layer in *Douvilleiceras* and a missing primary dorsal nacreous layer in *Colombiceras*. Also *Ptychoceras* omits the outer prismatic layer in older shafts. However, the shell doubling does not encircle the whole shell tube in both derived taxa. Further, the dorsal outer prismatic layer of *Colombiceras* does not cover the ventral crest, i.e., nacreous reduced dorsal shell wall. Other taxa of Deshayesitoidea (e.g., *Deshayesites* sp.) develop only a prismatic reduced dorsal shell wall (SOM; table A). Indeed, in *Lupprovia* (Ancyloceratoidea), a complete dorsal shell wall is described but it is not reinforced (Doguzhaeva and Mikhailova 1982). On the other hand, *Ptychoceras* as well as *Douvilleiceras* form primarily a similar, simple complete dorsal shell wall.

(iv) Nacreous reduced dorsal shell walls occur often in taxa that derived from Hildoceratoidea (Rouget et al. 2004) or Stephanoceratoidea (Yacobucci 2016), respectively. This could mean that the ability originates in these taxa (instead of Psiloceratoidea).

**Replacement structures of the dorsal wrinkle layer.—**

Several elements of the ammonoid shell wall can develop structures that are similar in appearance to the wrinkle layer or rather have analogous functions. There are extensions of the periostracum and modifications of the (dorsal) inner prismatic layer. These shell elements replace the wrinkle layer during ontogeny, and the formation of the latter stops.

*Periostracal extensions of the ventral shell wall.*—The periostracum forms the outermost layer of the ventral and lateral shell wall. The layer usually has an organic composition, i.e., homogeneous appearance, and is followed by the outer prismatic layer at its internal surface. With some exceptions, the periostracum is not preserved. However, in several phylloceratids and desmoceratids, the periostracum forms conspicuous extensions that stick out from the ventral/lateral shell wall (Fig. 22). These extensions occur during late ontogeny and are not present in the innermost whorls. The wrinkle layer is contemporaneously abandoned and disappears. Both structures never appear simultaneously in the same shell portion. In *Phylloceras* (*Phylloceras*) *plicatum*, *Phylloceras* (*Euphylloceras*) cf. *velledae*, and *Phylloceras* (*Euphylloceras*) sp., the periostracum forms conspicuous projecting, scythe-like extensions in cross-section (Fig. 22A,

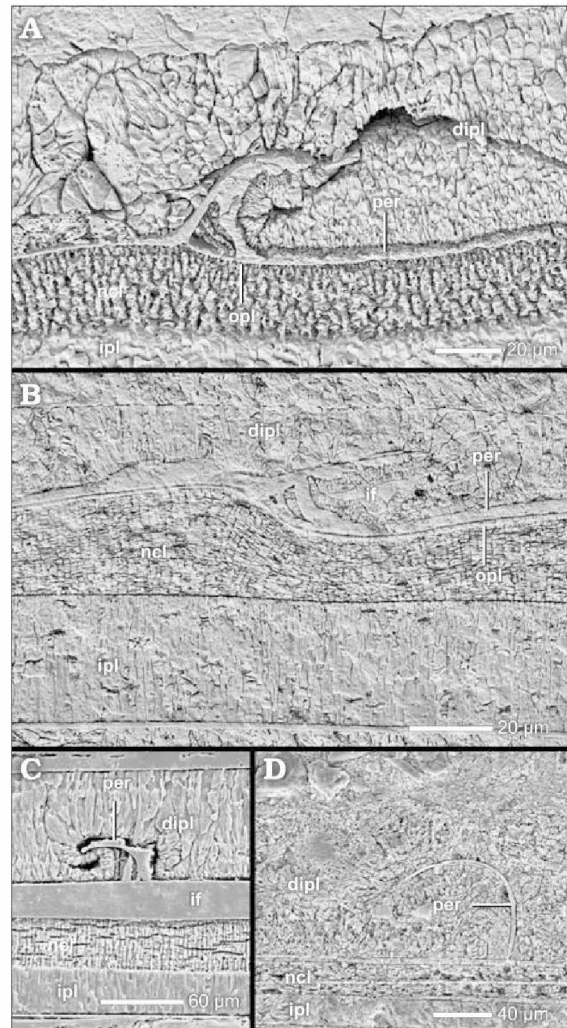


Fig. 22. Periostracal extension of the ventral shell wall (median section, growth direction to the right, centrifugal). **A.** *Phylloceras* (*Euphylloceras*) cf. *velledae* (Michelin, 1934), BSPG MAo-1770, early Albian, Cretaceous, Ambatolafia, Mahajanga Basin, NW Madagascar; a scythe-like extension of the ventral organic periostracum forms an organic radial lirae (Radtke and Keupp 2016); the dorsal inner prismatic layer of the succeeding whorl smoothes out the periostracum relief. **B.** *Phylloceras* (*Euphylloceras*) sp., BSPG MAo-1769, early Albian, Cretaceous, Ambatolafia, Mahajanga Basin, NW Madagascar; the same as in A. **C.** *Phylloceras* (*Phylloceras*) *plicatum* Neumayr, 1871, BSPG MAn-4509, late Oxfordian, Jurassic, Sakaraha, Morondava Basin, SW Madagascar; the ventral organic periostracum forms convex periostracal extensions; the dorsal inner prismatic layer of the succeeding whorl smoothes out the periostracum relief. **D.** *Desmophyllites diphylloides* (Forbes, 1846), BSPG MAo-1838, Campanian, Cretaceous, Teshio-Nakagawa area, Hokkaido, Japan; the same as in C. Abbreviations: dipl, dorsal inner prismatic layer; if, infilling; ipl, inner prismatic layer, ncl, nacreous layer, opl, outer prismatic layer, per, periostracum.

**B)** causing the formation of organic radial lirae (Radtke and Keupp 2016). The newly formed lirae relief is much more pronounced than that of the dorsal wrinkles. The relief is

smoothed out by the dorsal inner prismatic layer during overgrowth. It bridges the lira-concavity forming characteristic oval cavities (Fig. 22B). The lirae occur at diameters of 5 to 10 mm in those taxa. The dorsal wrinkle layer disappears accordingly at diameters of 12 to 24 mm of the succeeding whorl. Similar lirae, albeit made from (segments of) the outer prismatic layer, i.e., prismatic radial lirae (Radtke and Keupp 2016), are formed in several Aspidoceratinae, e.g., *Aspidoceras* sp., *Pseudowaagenia* sp. (Fig. 12D<sub>1</sub>).

*Phyllopacchyceras* sp. (Phylloceratoidea) and *Desmophyllites diphyllides* (Desmoceratoidea) form thin, convex periostracal extensions in cross-section (Fig. 22C, D) instead of a wrinkle layer of the succeeding whorl in late ontogeny. They are present at diameters of at least 20 and 5 mm, respectively. Periostracal extensions that appear similar are formed by some Aspidoceratinae (Perisphinctoidea), i.e., a herringbone layer (Fig. 14A<sub>1</sub>, A<sub>4</sub>; Radtke and Keupp 2016).

*Formation and function of periostracal extensions.*—Periostracal extensions as mentioned above are identical with older findings in other phylloceratids (cf. Birkelund and Hansen 1974, 1975; Kulicki et al. 2001; Bucher et al. 2003; Radtke and Keupp 2016), e.g., *Hypophylloceras* and *Calliphylloceras* with organic radial lirae and *Phyllopacchyceras* with convex arcs.

The assignment of these shell elements to the ventral shell wall is based on their internal structure. The scythe-appendage of the organic radial lirae implies a moderate withdrawal of the ventral/lateral mantle edge accompanied by an interruption in growth (Radtke and Keupp 2016). The scythe-appendage represents a first shell generation and the new periostracum generation is formed from within at the lira-crest. The formation of the scythe-appendage by the dorsal mantle seems to be rather difficult. For the convex arcs we assume a similar episodic growth. However, we cannot entirely exclude an assignment to the dorsal shell wall for this type.

The wrinkle layer is associated with a roughness effect (see above). In the special case of the periostracal extensions of the ventral shell wall, these form a new and usually much more pronounced relief than that of the wrinkles. With the formation of periostracal extensions, the relief of the wrinkle layer becomes obsolete and was probably therefore reduced.

*Phylogenetic and taxonomic implications of periostracal extensions.*—Our observations prove that ammonoids had the ability to form a periostracum but it is seldom preserved. Since the periostracum is a compartment of all molluscan shells, i.e., its template, it is likely that all ammonoids formed one to build their shells but usually shed it later on.

Due to the rarity of periostracal preservation and the conspicuous appearance, the periostracal extensions of Phylloceratoidea (e.g., scythe extensions, convex arcs) are likely taxon-specific but the record is incomplete. Radial lirae are a widely distributed shell element in Ammonoidea, at least in Phylloceratoidea, however. A uniform or at least similar formation can be generally assumed for radial li-

rae (cf. Bucher et al. 2003) but has to be proved yet. The relationship of radial lirae within Ammonoidea is likely but needs additional evidence, e.g., structural conformity. Radtke and Keupp (2016) assume at last a relation of organic radial lirae of Phylloceratoidea to prismatic radial lirae of Aspidoceratinae due to similarities in construction, e.g., episodic growth interruption, scythe appendages.

For the time being, the convex arc-like extensions are unique observations for the genera *Phyllopacchyceras* and *Desmophyllites*, and they could be a result of convergent development. On the other hand, several authors assume a polyphyly of desmoceratids. Several families are believed to be direct descendants of Phylloceratoidea (Engeser and Keupp 2002). The structural consistence may indicate the relationship of at least *Desmophyllites* with Phylloceratoidea. So far, the herringbone layer of Aspidoceratinae is restricted to that group but although similar in appearance probably an analogous formation to the periostracal extensions of *Phyllopacchyceras* and *Desmophyllites* (Radtke and Keupp 2016).

*The "Ritzknoten".*—One large specimen of *Eupachydiscus* sp. (Desmoceratoidea, BSPG MAO-1834) does not form the dorsal wrinkle layer but instead secretes structures we named here "Ritzknoten" (German: scratch knobles). These are small, cone-like internal elevations (Fig. 13C<sub>2</sub>–C<sub>5</sub>) affecting at least the dorsal and umbilical-lateral portions of the ammonoid shell wall. Ventrally they seem not to be formed. The "Ritzknoten" originate in the dorsal and umbilical inner prismatic layer, respectively, i.e., the layers form a continuum.

*Eupachydiscus* sp. develops a nacreous reduced dorsal shell wall that originates in an umbilical shell doubling. The "Ritzknoten" are formed by the primary (dorsal) inner prismatic layer, in an umbilical-lateral as well as dorsal position (Fig. 13C<sub>2</sub>–C<sub>5</sub>). The actual relief is formed by a thickening of an outer sub-layer while an inner sub-layer adopts it (Fig. 13C<sub>3</sub>, C<sub>4</sub>). Its internal relief is evened out by the secondary (dorsal) inner prismatic layer (Fig. 13C<sub>2</sub>) or the secondary (dorsal) nacreous layer (Fig. 13C<sub>4</sub>, C<sub>5</sub>), respectively.

*The formation and function of "Ritzknoten".*—The "Ritzknoten" are relief formations of the inner prismatic layer and therefore were probably formed in the rear living chamber. A direct relation to the wrinkle layer can be ruled out. It is likely that the "Ritzknoten" relief had a similar function (roughness effect) and the wrinkle layer therefore became obsolete and was reduced. However, the wrinkle layer extends up to the aperture but the "Ritzknoten" do not.

Keupp (2008) described another internal relief structure formed by the inner prismatic layer: "Ritzstreifen" (German: scratch lines, stripes), known also as "ventral wrinkle layer". "Ritzstreifen" are common features in Palaeozoic ammonoids and usually form a ventral and lateral pattern of striae and/or pits at internal moulds which is probably caused by an internal relief (e.g., fine ridges and knobs) of the conch wall (e.g., Walliser 1970; House 1971; Senior 1971; Doguzhaeva 1980, 1981; Korn 1985). According to Keupp (2008), "Ritzstreifen"



of Cretaceous *Desmoceras* (*Pseudouhligella*) *intrapunctatum* represent indeed ridges and knobs of the initial, still incomplete mineralized inner prismatic layer, i.e., whiskers, that are integrated into the complete layer afterwards.

Since “Ritzknoten” form a relief of the fully mineralized inner prismatic layer and “Ritzstreifen” form it by an incomplete inner prismatic layer (i.e., whiskers), “Ritzknoten” and “Ritzstreifen” are apparently analogous formations. Following the formation model of “Ritzstreifen” of Keupp (2008), we propose the new term “Ritzknoten”.

The findings of “Ritzstreifen” and “Ritzknoten” are important to avoid misunderstandings as for the wrinkle layer. Several studies imply that the wrinkle layer covers the whole interior of the living chamber or conch wall, respectively (e.g., Walliser 1970; House 1971; Senior 1971; Doguzhaeva 1980, 1981; Korn 1985). This assumption is mainly based on taxa that form dorsal and ventral finger-print pattern. Sometimes, even a dorsal and lateral transition of both reliefs can be observed at the internal mold (e.g., Walliser 1970; House 1971; Korn 1985). However, our observations of “Ritzknoten” and Keupp’s (2008) observations of “Ritzstreifen” prove that the previous interpretations of an enclosing wrinkle layer are better explainable by a ventral, lateral, and dorsal internal relief of the inner prismatic layer formed in the rear of the living chamber. The wrinkle layer, as we understand it, is formed at the aperture, coats only the preceding ventral whorl and does not form ventral and/or lateral internal reliefs (see above). We assume that ventral/lateral internal reliefs of the shell wall, like fine ridges and knobs, were formed by the inner prismatic layer in general and not by a wrinkle layer. Dorsally, one of the two layers (either wl or dipl) may cause an internal relief but they differ in their position of formation. In such cases where indeed ventral/lateral “Ritzstreifen”/“Ritzknoten” and dorsal wrinkle layers occur simultaneously, internal molds may display transitions between these structures even though they are not related.

*Phylogenetic and taxonomic implications of “Ritzknoten” and “Ritzstreifen”.*—Apparently, the inner prismatic layer can form internal reliefs in different ways that indicate a tendency for convergence of comparable structures. Palaeozoic taxa may form their “Ritzstreifen” similarly, but how they relate to the structures observed in their Mesozoic counterparts remains an open question.

## Conclusions

The Ammonoidea had several modifications of ultrastructure of the shell wall what is reflected not only in the ventral and lateral shell portions but also in the dorsal shell wall. The dorsal shell wall can display great variability. The dorsal mantle tissue of Ammonoidea was able to secrete organic, prismatic, and nacreous material. The ability to form nacreous portions is a new observation in the dorsal shell

wall (of planispirally coiled taxa). Adoral as well as adapical mantle tissues were involved. Furthermore, we assume that the mantle tissue maintains secretion plasticity, i.e., the mantle tissue was able to change its secretion abilities.

The majority of ammonoids, usually planispiral taxa, forms a prismatic reduced dorsal shell wall which is omitted at the aperture. It consists of an outer organic component, e.g., wrinkle layer, which is secreted by a suprachealic mantle fold in front of the aperture, and a dominant dorsal inner prismatic layer which is secreted in the rear living chamber. The wrinkle layer has no equivalent in the ventral/lateral wall but could be a derivate of the dorsal periostracum. The dorsal inner prismatic layer is a continuation of its ventral/lateral equivalent. Other layers of the ventral/lateral wall, i.e., outer prismatic layer and the nacreous layer, are suppressed. Usually all ammonoids go through such a stage, at least after hatching. However, some taxa form other dorsal shell wall types during ontogeny.

Several planispiral ammonoids form a nacreous reduced dorsal shell wall which is omitted at the aperture. It consists of a so-called primary dorsal inner prismatic layer, a secondary dorsal nacreous layer and a secondary dorsal inner prismatic layer. All three layers are continuations of an umbilical shell doubling (i.e., reinforcement of the shell wall) which is secreted in the rear living chamber where they wedge out towards the aperture. Prismatic and nacreous reduced dorsal shell walls are mainly used for smoothing the sculpture in planispirally coiled taxa, probably to facilitate the attachment of the septa.

Heteromorph as well as some planispirally coiled taxa form a complete dorsal shell wall at the aperture in continuation of the ventral and lateral shell wall’s outer prismatic layer, nacreous layer and inner prismatic layer. The (dorsal) outer prismatic layer and the (dorsal) nacreous layer are secreted at/near the aperture. The (dorsal) inner prismatic layer is restricted to the rear living chamber. Some taxa seem to form only the dorsal outer and inner prismatic layer but lack the dorsal nacreous layer, e.g., *Quenstedtoceras henrici*. Other taxa reinforced the trilayered shell wall by additional layers, i.e., a secondary nacreous and a secondary inner prismatic layer (shell doubling), e.g., *Douvilleiceras mammilliatum*.

The prismatic reduced dorsal shell wall probably represents the primary or plesiomorph state, respectively, in all Ammonoidea or at least in Mesozoic taxa. The ability to form dorsal nacre, hence to form nacreous reduced or complete dorsal shell walls, either represents a plesiomorphy retained from the gyrocone ammonoid ancestors, or (re-)developed in post-Triassic forms. Although a general ability to form complete dorsal shell walls is likely in all (Jurassic and Cretaceous) ammonoids, the Lytoceratoidea, Perisphinctoidea or Desmoceratoidea are probable ancestors for Jurassic and Cretaceous heteromorphs due to the proven occurrence of complete dorsal shell walls in combination with stratigraphic overlaps of these superfamilies with heteromorphs in earth’s history.

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SUPPLEMENTARY ONLINE MATERIAL FOR

The dorsal shell wall structure of Mesozoic ammonoids  
*Gregor Radtke and Helmut Keupp*

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**Supplementary Online Material**

Table A. Data collection of ultrastructurally analysed ammonoids and their bearing on the dorsal shell wall. The specimens with the number indices MAM, MAN, MAo and PA are housed at the Bavarian State Collection for Palaeontology and Geology (Munich, Germany) as part of H. Keupp's collection. Those specimens with the number indices AMNH-FI are housed at the American Museum of Natural History (New York City, USA). Abbreviations: c, complete dorsal shell wall; cl, coating layer; dipl, dorsal inner prismatic layer; dipl 1/2, primary/secondary dorsal inner prismatic layer; dncl, dorsal nacreous layer; dncl 1/2, primary/secondary dorsal nacreous layer; dopl, dorsal outer prismatic layer; hbl, heringbone layer of the preceding whorl; n.p., not preserved; nr, nacreous reduced dorsal shell wall; ol, organic layer; pe, periostracal extensions of the preceding whorl; r, prismatic reduced dorsal shell wall; rc, recrystallized shell wall; ric, reinforced complete dorsal shell wall; rk, "Ritzknoten"; rs, "Ritzstreifen"; sc, seemingly complete dorsal shell wall; so, spiral ornamentation; sphpr, spherulitic-prismatic layer; wl, wrinkle layer.

Taxon	References / collection number	Preservation index	Age, period	Location	Type of dorsal shell wall	Outer components	Inner components	Special features
Goniatitina indet	Kulicki et al. 1999, 2001, 2002	1	Pensylvanian, Carboniferous	Buckhorn Asphalt, Oklahoma, USA	r	wl	dipl	The wrinkle layer disappears in the post-nepionic shell.
Goniatitina indet	Doguzhaeva 2002	1-2	Pensylvanian, Carboniferous	Creek Aidaralash, S Urals, Russia	r	-	dipl	
Goniatitina indet	Doguzhaeva 2002	1-2	Artinskian, Permian	Sim River Basin, S Urals, Russia	r	-	dipl	
<b>Anarcestoidea</b>								
<i>Cabrieroceras crispiforme</i> (Kayser, 1879)	Walliser 1970	rc-1	Middle Devonian	Eifel, W Germany	r	wl?, (rs)	dipl	The inner prismatic layer forms ' <b>Ritzstreifen</b> ' ventrally, laterally and probably dorsally (dorsal wrinkle layer?).
<i>Sellanarcestes wenkenbachi</i> (Kayser, 1884)	Walliser 1970	rc-1	Middle Devonian	Eifel, W Germany	r	wl?, (rs)	dipl	The inner prismatic layer forms ' <b>Ritzstreifen</b> ' ventrally, laterally and probably dorsally (wrinkle layer?).



Taxon	References / collection number	Preservation index	Age, period	Location	Type of dorsal shell wall	Outer components	Inner components	Special features
<b>Gastrioceratoidea</b>								
<i>Gastrioceras occidentale</i> (Miller & Faber, 1892)	Erben et al. 1968, 1969	1-2	Pensylvanian, Carboniferous	Cow-Creek near Prestonburg, Floyd Country, SE Kentucky, USA	r	-	dipl	
<b>Agathiceratoidea</b>								
<i>Agathiceras uralicum</i> Karpinsky, 1874	Doguzhaeva & Mutvei 1986	1-2	early Permian	N Urals, Russia	r	-	dipl	
<i>Agathiceras</i> sp.	Doguzhaeva 2002	1-2	Artinskian, Permian	Sim River Basin, S Urals, Russia	r	-	dipl	
<b>Xenodiscoidea</b>								
<i>Preflorianites toulai</i> (Smith, 1932)	MAM-1636	rc	Olenekian, Triassic	Crittenden Springs, Elko Country, Nevada, USA	r?	wl?	n. p.	The ultrastructure is not preserved. At the whorl contact, the umbilical / dorsal shell wall becomes very thin (reduced?). There is a homogeneous layer separating the recrystallized shell package; it seems to develop a relief (wrinkle layer?).

Taxon	References / collection number	Preservation index	Age, period	Location	Type of dorsal shell wall	Outer components	Inner components	Special features
<i>Xenoceltites subevolutus</i> Spath, 1930	MAM-1643	rc	Olenekian, Triassic	Wallenberg- fjellet, Spitzbergen	n. p.	n. p.	n. p.	The ultrastructure is not preserved.
<b>Dinaritoidea</b>								
<i>Columbites</i> sp.	Erben et al. 1968, 1969	rc-2	Olenekian, Triassic	Hot Springs, Idaho, USA	r	-	dipl	
<i>Rudolfruempyiceras planorbis</i> (Dagys & Ermakova, 1988)	MAM-1634	2-3	late Olenekian, Triassic	Cheznokh- zebetnaya River, E Taimyr, Siberia, Russia	r	ol	-	
<b>Sageceratoidea</b>								
<i>Hedenstroemia hedenstroemi</i> (Keyserling, 1845)	MAM-1651	2-3	early Olenekian, Triassic	Buur River, Olenek River Basin, Siberia, Russia	r	ol	dipl	In the outer whorls, the dorsal inner prismatic layer can develop up to three sub-layers (multi-layering). At the ventral crest, the outer component of the dorsal shell wall forms a thickening.
<i>Pseudosageceras multilobatum</i> Noetling, 1905	MAM-1632	rc	Olenekian, Triassic	Crittenden Springs, Elko Country, Nevada, USA	n. p.	n. p.	n. p.	The ultrastructure is not preserved.

Taxon	References / collection number	Preservation index	Age, period	Location	Type of dorsal shell wall	Outer components	Inner components	Special features
<i>Pseudosageceras</i> sp.	Kulicki et al. 2001	1-2	Olenekian, Triassic	Mengilyakh on Olenek River, Siberia, Russia	r	wl	dipl	
<b>Meekoceratoidea</b>								
<i>Arctoceras tuberculatum</i> Smith, 1932	MAm-1630	rc	Olenekian, Triassic	Crittenden Springs, Elko Country, Nevada, USA	r?	n. p.	n. p.	The ultrastructure is not preserved. At the whorl contact, the umbilical / dorsal shell wall becomes very thin (reduced?).
<i>Arctoprionites nodosus</i> (Frebold, 1930)	MAm-1584 MAm-1585	rc	Olenekian, Triassic	Stensiöfjellet, Spitzbergen	n. p.	n. p.	n. p.	The ultrastructure is not preserved.
<i>Dieneroceras dieneri</i> (Hyatt & Smith, 1905)	MAm-1578	rc	Olenekian, Triassic	Crittenden Springs, Elko Country, Nevada, USA	r?	n. p.	n. p.	The ultrastructure is not preserved. At the whorl contact, the umbilical / dorsal shell wall becomes very thin (reduced?).
<i>Dieneroceras</i> sp.	MAm-1649	rc	Olenekian, Triassic	Crittenden Springs, Elko Country, Nevada, USA	n. p.	n. p.	n. p.	The ultrastructure is not preserved.
' <i>Dieneroceras</i> ' <i>subquadratum</i> (Smith, 1932)	MAm-1573	rc	Olenekian, Triassic	Crittenden Springs, Elko Country, Nevada, USA	r?	n. p.	n. p.	The ultrastructure is not preserved. At the whorl contact, the umbilical / dorsal shell wall becomes very thin (reduced?).



Taxon	References / collection number	Preservation index	Age, period	Location	Type of dorsal shell wall	Outer components	Inner components	Special features
<i>Hemiprionites</i> sp.	MAM-1647	rc	Olenekian, Triassic	Crittenden Springs, Elko Country, Nevada, USA	r?	n. p.	n. p.	The ultrastructure is not preserved. At the whorl contact, the umbilical / dorsal shell wall becomes very thin (reduced?).
<i>Juvenites septentrionalis</i> Smith, 1932	MAM-1608 MAM-1609	rc	Olenekian, Triassic	Crittenden Springs, Elko Country, Nevada, USA	n. p.	n. p.	n. p.	The ultrastructure is not preserved.
<i>Meekoceras gracilitatis</i> (White, 1879)	MAM-1589	rc	Olenekian, Triassic	Crittenden Springs, Elko Country, Nevada, USA	n. p.	n. p.	n. p.	The ultrastructure is not preserved. The dorsal shell wall is thick.
<i>Owenites koeneni</i> Hyatt & Smith, 1905	MAM-1596 MAM-1599 MAM-1600	rc	Olenekian, Triassic	Crittenden Springs, Elko Country, Nevada, USA	r?	n. p.	n. p.	The ultrastructure is not preserved. At the whorl contact, the umbilical / dorsal shell wall becomes very thin (reduced?).
<i>Parannites aspenensis</i> Hyatt & Smith, 1905	MAM-1623 MAM-1624	rc	Olenekian, Triassic	Crittenden Springs, Elko Country, Nevada, USA	r?	n. p.	n. p.	The ultrastructure is not preserved. At the whorl contact, the umbilical / dorsal shell wall becomes very thin (reduced?).
<i>Parannites slossi</i> Kummel & Steele, 1962	MAM-1617	rc	Olenekian, Triassic	Crittenden Springs, Elko Country, Nevada, USA	r?	n. p.	n. p.	The ultrastructure is not preserved. At the whorl contact, the umbilical / dorsal shell wall becomes very thin (reduced?).

Taxon	References / collection number	Preservation index	Age, period	Location	Type of dorsal shell wall	Outer components	Inner components	Special features
<i>Popovites occidentalis</i> Tozer, 1965	MAM-1594	rc	Olenekian, Triassic	Stensiöfjellet, Spitzbergen	n. p.	n. p.	n. p.	The ultrastructure is not preserved.
Prionitidae indet	MAM-1592 MAM-1633	rc	Olenekian, Triassic	Crittenden Springs, Elko Country, Nevada, USA	r?	n. p.	n. p.	The ultrastructure is not preserved. At the whorl contact, the umbilical / dorsal shell wall becomes very thin (reduced?).
<i>Prospiringites slossi</i> (Kummel & Steele, 1962)	MAM-1604 MAM-1605	rc	Olenekian, Triassic	Crittenden Springs, Elko Country, Nevada, USA	r?	n. p.	n. p.	The ultrastructure is not preserved. At the whorl contact, the umbilical / dorsal shell wall becomes very thin (reduced?).
<i>Wasatchites tridentinus</i> Spath, 1934	MAM-1587	rc	Olenekian, Triassic	Stensiöfjellet, Spitzbergen	n. p.	n. p.	n. p.	The ultrastructure is not preserved.
<i>Wyomingites whiteanus</i> (Waagen, 1895)	MAM-1572	rc	Olenekian, Triassic	Crittenden Springs, Elko Country, Nevada, USA	n. p.	n. p.	n. p.	The ultrastructure is not preserved.
<b>Ptychitoidea</b>								
<i>Aristoptychites kolymensis</i> (Kiprisova, 1937)	MAM-1551 MAM-1552 MAM-1553	rc	late Ladinian, Triassic	Botneheia, Spitzbergen	r?	n. p.	n. p.	The ultrastructure is not preserved. At the whorl contact, the umbilical / dorsal shell wall becomes very thin (reduced?).
<i>Aristoptychites trochleaeformis</i> (Lindstrom, 1865)	MAM-1554	rc	late Anisian, Triassic	Kongressfjellet, Spitzbergen	n. p.	n. p.	n. p.	The ultrastructure is not preserved.

Taxon	References / collection number	Preservation index	Age, period	Location	Type of dorsal shell wall	Outer components	Inner components	Special features
<i>Ptychites</i> sp.	Erben et al. 1969	rc-1	Ladinian, Triassic	Kongressfjelett, Spitzbergen	r	-	dipl	
<b>Arcestoidea</b>								
<i>Arcestes</i> sp. 1	MAm-1566 MAm-1567	rc	Norian, Triassic	Bihati River, Timor	n. p.	ol?	n. p.	The ultrastructure is not preserved. There is a homogeneous layer separating the recrystallized shell package (organic layer?).
<i>Arcestes</i> sp. 2	MAm-1569	rc	Middle to Upper Triassic	Tepeköi, Turkey	n. p.	n. p.	n. p.	The ultrastructure is not preserved.
<i>Phyllocladiscites acheshbokensis</i> Shevyrev, 1968	Doguzhayeva & Mutvei 1986	1-2	middle Anisian, Triassic	River Tach, NW Caucasus, Russia	r	wl	dipl	In outer whorls, the dorsal inner prismatic layer develops two sub-layers (multi-layering). The inner sub-layer of the dorsal inner prismatic layer thickens at the contact of the septa and wedges out episodically adoral of the septum (septal prismatic layer?).
<i>Proarcestes</i> sp.	Doguzhayeva & Mutvei 1986	1-2	middle Anisian, Triassic	River Tach, NW Caucasus, Russia	r	wl	dipl	



Taxon	References / collection number	Preservation index	Age, period	Location	Type of dorsal shell wall	Outer components	Inner components	Special features
<b>Nathorstitoidea</b>								
<i>Indigirites boehmi</i> Tozer, 1994	MAM-1559	rc	early Ladinian, Triassic	Fulmardalen, Spitzbergen	n. p.	n. p.	n. p.	The ultrastructure is not preserved.
<i>Indigirites tozeri</i> Weitschat & Landman, 1983	MAM-1556	rc	early Ladinian, Triassic	Botneheia, Spitzbergen	n. p.	n. p.	n. p.	The ultrastructure is not preserved.
<i>Stolleyites tenuis</i> (Stolley, 1911)	Kulicki et al. 2001	1-2	early Carnian, Triassic	Kongressfjelett, Spitzbergen	r	wl	-	
<i>Stolleyites tenuis</i> (Stolley, 1911)	MAM-1560 MAM-1563	1	late Carnian, Triassic	Druschedalen, Dicksonland, Spitzbergen	r	wl?	-	The outer component of the dorsal shell wall seems to develop a relief. On occasion, isolated wrinkles can be discerned.
<b>Ceratitoidea</b>								
<i>Sibirites eichwaldi</i> (Keyserling, 1845)	Kulicki et al. 2001	1-2	Olenekian, Triassic	Mengilyakh on Olenek River, Siberia, Russia	r	wl	dipl	The inner prismatic layer of the dorsal shell wall can develop two sub-layers (multi-layering).
<i>Subolenekites altus</i> (Mojsisovic, 1886)	Kulicki et al. 2001	1	Olenekian, Triassic	Mengilyakh on Olenek River, Siberia, Russia	r	wl	dipl	

Taxon	References / collection number	Preservation index	Age, period	Location	Type of dorsal shell wall	Outer components	Inner components	Special features
<b>Tropitoidea</b>								
<i>Anatomites</i> sp.	MAM-1570	rc	Upper Triassic	SW Timor	n. p.	n. p.	n. p.	The ultrastructure is not preserved.
<i>Dydimites</i> sp.	MAM-1571	rc	Ladinian, Triassic	SW Timor	r?	n. p.	n. p.	The ultrastructure is not preserved. At the whorl contact, the umbilical / dorsal shell wall becomes very thin (reduced?).
<b>Megaphyllitoidea</b>								
<i>Megaphyllites prometheus</i> Shevyrev, 1861	Doguzhayeva 1980, 1981, Doguzhayeva & Mutvei 1986	1-2	middle Anisian, Triassic	Mount/River Tach, NW Caucasus, Russia	r	wl	dipl	
<i>Parapopanoceras malmgreni</i> (Lindstrom, 1865)	MAM-1549	rc	late Anisian, Triassic	Vikingshögda, Spitzbergen	n. p.	n. p.	n. p.	The ultrastructure is not preserved.
<b>Phylloceratoidea</b>								
<i>Calliphylloceras</i> sp.	MAn-4511 MAn-4512 MAn-4513	2-3	late Oxfordian, Jurassic	Sakaraha, Morondava Basin, SW Madagascar	r	wl	dipl	In the outer whorls, the dorsal shell wall develops a thick dorsal inner prismatic layer.

Taxon	References / collection number	Preservation index	Age, period	Location	Type of dorsal shell wall	Outer components	Inner components	Special features
<i>Holcophylloceras polyolcum</i> (Benecke, 1865)	MAN-4833	2-3	late Oxfordian, Jurassic	Sakaraha, Morondava Basin, SW Madagascar	r	wl	dipl	In the outer whorls, the dorsal shell wall develops a thick dorsal inner prismatic layer which can develop several sub-layers (multi-layering).
<i>Holcophylloceras</i> sp.	Drushits & Doguzhayeva 1974, Doguzhaeva 1981	1-2	Bajocian, Jurassic	N Caucasus, Russia	r	wl?	dipl	
<i>Holcophylloceras</i> sp.	Keupp 2000	2-3	late Oxfordian, Jurassic	Sakaraha, Morondava Basin, SW Madagascar	r	wl	dipl	
<i>Holcophyllocera</i> sp.	MAN-4510	2-3	late Oxfordian, Jurassic	Sakaraha, Morondava Basin, SW Madagascar	r	wl	dipl	



Taxon	References / collection number	Preservation index	Age, period	Location	Type of dorsal shell wall	Outer components	Inner components	Special features
<i>Hypophylloceras</i> ( <i>Neophylloceras</i> ) <i>groenlandicum</i> Birkelund, 1965	Birkelund & Hansen 1968, 1974, 1975, Birkelund 1980	1-2	Maastrichtian, Cretaceous	Agatalen, Nûgssuaq, W Greenland	r	(pe)	dipl	In the outer whorls, the dorsal shell wall develops a thick dorsal inner prismatic layer which can develop several sub-layers (multi-layering). The wrinkle layer is probably replaced by scythe-like <b>periostracal extensions</b> of the preceding whorl (organic radial lirae).
<i>Hypophylloceras</i> ( <i>Neophylloceras</i> ) <i>ramosum</i> Meek, 1857	MAo-1879	1-2	Campanian, Cretaceous	Teshio-Nakagawa area, Hokkaido, Japan	r	(pe)	dipl	In the outer whorls, the dorsal shell wall develops a thick dorsal inner prismatic layer. The wrinkle layer is probably replaced by scythe-like <b>periostracal extensions</b> of the preceding whorl (organic radial lirae).
<i>Hypophylloceras</i> ( <i>Neophylloceras</i> ) <i>subramosum</i> (Shimizu, 1934)	Kulicki & Tanabe 1999, Kulicki et al. 2001	1-2	middle Campanian, Cretaceous	Teshio-Nakagawa area, Hokkaido, Japan	r	(pe)	dipl	In the outer whorls, the dorsal shell wall develops a thick dorsal inner prismatic layer. The wrinkle layer is probably replaced by scythe-like <b>periostracal extensions</b> of the preceding whorl (organic radial lirae).

Taxon	References / collection number	Preservation index	Age, period	Location	Type of dorsal shell wall	Outer components	Inner components	Special features
<i>Phylloceras</i> ( <i>Euphylloceras</i> ) cf. <i>velledae</i> (Michelin, 1934)	MAo-1770 MAo-1880	2-3	early Albian, Cretaceous	Ambatolafia, Mahajanga Basin, NW Madagascar	r	wl (→ pe)	dipl	In the outer whorls, the dorsal shell wall develops a thick dorsal inner prismatic layer. The wrinkle layer is replaced by scythe-like <b>periostracal extensions</b> of the preceding whorl (organic radial lirae).
<i>Phylloceras</i> ( <i>Euphylloceras</i> ) sp.	MAo-1769	2-3	early Albian, Cretaceous	Ambatolafia, Mahajanga Basin, NW Madagascar	r	wl (→ pe)	dipl	In the outer whorls, the dorsal shell wall develops a thick dorsal inner prismatic layer. The wrinkle layer is replaced by scythe-like <b>periostracal extensions</b> of the preceding whorl (organic radial lirae).
<i>Phylloceras</i> ( <i>Phylloceras</i> ) <i>plicatum</i> Neumayr, 1871	MAo-4509	2-3	late Oxfordian, Jurassic	Sakaraha, Morondava Basin, SW Madagascar	r	wl (→ pe)	dipl	In the outer whorls, the dorsal shell wall develops a thick dorsal inner prismatic layer. The wrinkle layer is replaced by scythe-like <b>periostracal extensions</b> of the preceding whorl (organic radial lirae).
<i>Phylloceras</i> ( <i>Salfeldiella</i> ) <i>guettardi</i> (Raspail, 1831)	Drushits & Khiami 1970	1-2	late Aptian, Cretaceous	Laba River, N Caucasus, Russia	r	-	dipl?	

Taxon	References / collection number	Preservation index	Age, period	Location	Type of dorsal shell wall	Outer components	Inner components	Special features
<i>Phyllopachyceras ezoense</i> Yokoyama, 1890	Kulicki & Tanabe 1999, Kulicki et al. 2001, 2016	1-2	middle Campanian, Cretaceous	Teshio-Nakagawa area, Hokkaido, Japan	r	(pe)	dipl	In the outer whorls, the dorsal shell wall develops a thick dorsal inner prismatic layer. It has a sperulithic appearance. The wrinkle layer is replaced by convex <b>periostracal extensions</b> of the preceding whorl.
<i>Phyllopachyceras</i> sp.	MAo-1771	2-3	early Albian, Cretaceous	Ambatolafia, Mahajanga Basin, NW Madagascar	r	wl (→ pe)	dipl	In the outer whorls, the dorsal shell wall develops a thick dorsal inner prismatic layer. The wrinkle layer is replaced by convex <b>periostracal extensions</b> of the preceding whorl.
<i>Ptychophylloceras</i> cf. <i>dacquei</i> Joly, 1976	MAN-4514 MAN-4515 MAN-4516 MAN-4748	2-3	late Oxfordian, Jurassic	Sakaraha, Morondava Basin, SW Madagascar	r	wl	dipl	In the outer whorls, the dorsal shell wall develops a thick dorsal inner prismatic layer.
<i>Ptychophylloceras</i> sp.	MAN-4749	2-3	late Oxfordian, Jurassic	Sakaraha, Morondava Basin, SW Madagascar	r	wl	dipl	In the outer whorls, the dorsal shell wall develops a thick dorsal inner prismatic layer.



Taxon	References / collection number	Preservation index	Age, period	Location	Type of dorsal shell wall	Outer components	Inner components	Special features
<b>Lytoceroidea</b>								
<i>Argonauticeras besairiei</i> Collignon, 1949	MAo-1705 MAo-1772 MAo-1801 MAo-1802	2-3	early Albian, Cretaceous	Ambatolafia, Mahajanga Basin, NW Madagascar	r	wl	dipl	In the outer whorls, the dorsal shell wall develops a thick dorsal inner prismatic layer which consists of two sub-layers (multi-layering).
<i>Lobolytoceras costellatum</i> (Pavia, 2002)	MAN-1743 MAN-2061 MAN-3059	2	late Oxfordian, Jurassic	Sakaraha, Morondava Basin, SW Madagascar	r? → c	ol?	dipl → dopl, dncl, dipl	In the outer whorls, the shell develops a <b>complete dorsal shell wall</b> . The inner whorls probably form a prismatic reduced dorsal shell wall (i.e. the juvenile dorsal nacreous layer is very thin). The early complete dorsal shell wall is dominated by a thick dorsal inner prismatic layer which has two sub-layers (multi-layering). In later whorls, the dorsal nacreous layer grows in thickness and is of similar dimension to the thick dipl.
<i>Lytoceras batesi</i> (Trask, 1855)	Westermann 1971	1	Lower Cretaceous	Cottenwood Creek, Californian, USA	r	-	dipl	

Taxon	References / collection number	Preservation index	Age, period	Location	Type of dorsal shell wall	Outer components	Inner components	Special features
<i>Lytoceras</i> cf. <i>cornucopiae</i> (Young & Bird, 1822)	Westermann 1971	1	early Toarcian, Jurassic	Ilminster, England	r	-	dipl	
<i>Pachylytoceras torulosum</i> (Schübler, 1831)	Erben et al. 1968, 1969	1-3	Aalenian, Jurassic	Heiningen, Baden-Württemberg, Germany	r	-	dipl	
<i>Pachylytoceras</i> sp.	MAn-4832	2	early Aalenian, Jurassic	Heinigen, Baden-Württemberg, Germany	r	wl?	dipl	The outer component of the dorsal shell wall develops a relief (wrinkle layer?).
<i>Protetragonites fraasi</i> (Daqué, 1910)	MAn-4530 MAn-4734 MAn-4831	2-3	late Oxfordian, Jurassic	Sakaraha, Morondava Basin, SW Madagascar	r	ol	dipl	In the outer whorls, the dorsal shell wall develops a thick dorsal inner prismatic layer.
<i>Protetragonites tauricus</i> Kuljinskaia-Voronetz, 1933	Drushits & Khiami 1970	1-2	Berriasian, Cretaceous	Sarysu River, Crimea	r	n. p.	dipl	
<b>Tetragonitoidea</b>								
<i>Anagaudryceras limatum</i> (Yabe, 1903)	Bucher et al. 1996	1-2	Upper Cretaceous	Hokkaido, Japan	r	-	dipl?	

Taxon	References / collection number	Preservation index	Age, period	Location	Type of dorsal shell wall	Outer components	Inner components	Special features
<i>Anagaudryceras limatum</i> (Yabe, 1903)	MAo-1865	1-2	Coniacian, Cretaceous	Haboro, Hokkaido, Japan	r	ol	dipl	
<i>Anagaudryceras yokoyamai</i> (Yabe, 1903)	MAo-1866	2-3	Campanian, Cretaceous	Teshio-Nakagawa area, Hokkaido, Japan	r	n. p.	n. p.	At least in the living chamber, the dorsal shell wall is completely absent.
<i>Eogaudryceras</i> ( <i>Eotetragonites</i> ) <i>umbilicostriatus</i> (Collignon, 1963)	MAo-1773 MAo-1774 MAo-1775 MAo-1776	2-3	early Albian, Cretaceous	Ambatolafia, Mahajanga Basin, NW Madagascar	r	wl	dipl	
<i>Eogaudryceras</i> sp.	Doguzhaeva et al. 2010	2-3	late Aptian, Cretaceous	Hokodz River region, Belaya River Valley, Adygeya, NW Caucasus, Russia	r	wl	dipl	The dorsal shell wall develops a thick dorsal inner prismatic layer.
<i>Gaudryceras intermedium</i> Yabe, 1903	MAo-1869 MAo-1870	2	Campanian, Cretaceous	Teshio-Nakagawa area, Hokkaido, Japan	r	ol / wl?	dipl	



Taxon	References / collection number	Preservation index	Age, period	Location	Type of dorsal shell wall	Outer components	Inner components	Special features
<i>Gaudryceras striatum</i> (Jimbo, 1894)	MAo-1868	2	Campanian, Cretaceous	Teshio-Nakagawa area, Hokkaido, Japan	r	ol	dipl	
<i>Gaudryceras tenuiliratum</i> Yabe, 1903	Drushits et al. 1978, Birkelund 1980, Doguzhaeva & Mutvei 1993a, Kulicki et al. 2001, 2016	1-2	Turonian-Campanian, Cretaceous	Hokkaido, Japan and Sakhalin, Russia	r	wl → cl	dipl	In the outer whorls, the wrinkle layer transforms into an organic, lamellar <b>coating layer</b> which covers the ventral and lateral portions of the preceding whorl and the flanks of all preceding whorls.
<i>Gaudryceras tenuiliratum</i> Yabe, 1903	MAo-1871 MAo-1872 MAo-1873 MAo-1874 MAo-1875	2	Campanian, Cretaceous	Teshio-Nakagawa area, Hokkaido, Japan	r	cl	dipl	A thick homogeneous, organic <b>coating layer</b> covers the preceding whorl.
<i>Gaudryceras</i> sp.	Kulicki 1996	-	Cretaceous	Russia	r	cl	dipl	
<i>Gaudryceras</i> sp.	MAo-1867	1-2	Campanian, Cretaceous	Teshio-Nakagawa area, Hokkaido, Japan	r	ol?	dipl	

Taxon	References / collection number	Preservation index	Age, period	Location	Type of dorsal shell wall	Outer components	Inner components	Special features
<i>Pseudophyllites</i> sp.	Westermann 1971	1	Upper Cretaceous	Fossil Beach, Vancouver Island	r	-	dipl	
<i>Saghalinites wrighti</i> Birkelund, 1965	Birkelund 1967, 1980, Birkelund & Hansen 1968, 1974	1-2	Maastrichtian, Cretaceous	Agatalen, Nûgssuaq, W Greenland	r	-	dipl	
<i>Saghalinites wrighti</i> Birkelund, 1965	MAo-1876	1-3	Maastrichtian, Cretaceous	Nûgssuaq, W Greenland	r	wl.	dipl	
<i>Tetragonites popetensis</i> Yabe, 1903	MAo-1798 MAo-1878	2	Campanian, Cretaceous	Teshio-Nakagawa area, Hokkaido, Japan	r	wl	dipl	
<i>Tetragonites duvalianus</i> d'Orbigny, 1840	Drushits & Doguzhayeva 1974	1-2	Aptian, Cretaceous	N Caucasus, Russia	r	-	dipl	
<i>Tetragonites glabrus</i> (Jimbo, 1910)	Kulicki & Tanabe 1999, Kulicki et al. 2001	2-3	early Campanian, Cretaceous	Teshio-Nakagawa area, Hokkaido, Japan	r	wl	dipl	

Taxon	References / collection number	Preservation index	Age, period	Location	Type of dorsal shell wall	Outer components	Inner components	Special features
<i>Zelandites japonicus</i> Matsumoto, 1938	Zakharov & Grabovskaya 1984, Zakharov 1996	1-2	early Maastrichtian, Cretaceous	Nayba River, Sakhalin, Russia	r	wl	dipl	
<b>Psiloceratoidea</b>								
<i>Agassiceras</i> cf. <i>scipionianum</i> (d'Orbigny, 1844)	Erben et al. 1968, 1969	1-3	Sinemurian, Jurassic	Lyme Regis, Dorset, England	r	-	dipl	
<i>Alsatites</i> <i>quedlinburgensis</i> Lange, 1924	MAn-4827	rc	Hettangian- Sinemurian, Jurassic	Angersbach, Germany	n. p.	n. p.	n. p.	The ultrastructure is not preserved.
<i>Asteroceras obtusum</i> Sowerby, 1817	Erben et al. 1968, 1969	1-2	Sinemurian, Jurassic	Lyme Regis, Dorset, England	r	-	dipl	
<i>Coroniceras westfalicum</i> Lange, 1925	MAn-4828	1-2	Hettangian- Sinemurian, Jurassic	Oldentrup near Bielefeld, Germany	r	ol?	dipl	
<i>Psiloceras</i> ( <i>Caloceras</i> ) cf. <i>torus</i> (d'Orbigny, 1844)	MAn-4826	rc	Hettangian- Sinemurian, Jurassic	Aaberg near Bünde, Germany	n. p.	n. p.	n. p.	The ultrastructure is not preserved.

Taxon	References / collection number	Preservation index	Age, period	Location	Type of dorsal shell wall	Outer components	Inner components	Special features
<i>Schlotheimia</i> ( <i>Scamnoceras</i> ) <i>angulata</i> (Schlotheim, 1820)	MAN-4851 MAN-4852	rc	Hettangian-Sinemurian, Jurassic	Bichfeld clay pit at Spiltar, Germany	n. p.	n. p.	n. p.	The ultrastructure is not preserved.
<b>Eoderoceratoidea</b>								
<i>Aegoceras</i> ( <i>Beaniceras</i> ) <i>centaurus</i> (d'Orbigny, 1844)	MAN-4820 MAN-4853	1-2	Pliensbachian, Jurassic	Lühnde canal, Sehnde near Hannover, Germany	r	wl	dipl	
<i>Aegoceras</i> ( <i>Beaniceras</i> ) cf. <i>luridum</i> (Simpson, 1855)	Erben et al. 1968, 1969	rc-2	early Pliensbachian, Jurassic	Blockley near Mareton-in-March, England	r	-	dipl	
<i>Androgynoceras</i> <i>capricornu</i> (Schlotheim, 1820)	MAN-4821	rc	early Pliensbachian, Jurassic	Robin Hoods Bay, Yorkshire, England	n. p.	n. p.	n. p.	The ultrastructure is not preserved.
<i>Androgynoceras</i> cf. <i>planicosta</i> (Sowerby, 1814)	Erben et al. 1968, 1969	1-3	early Pliensbachian, Jurassic	Lyme Regis, Dorset, England	r	-	dipl	
<i>Dactylioceras</i> cf. <i>anguinum</i> (Reinecke, 1818)	MAN-4823	rc	Pliensbachian-Toarcian, Jurassic	Stich canal, Sehnde near Hannover, Germany	n. p.	n. p.	n. p.	The ultrastructure is not preserved.



Taxon	References / collection number	Preservation index	Age, period	Location	Type of dorsal shell wall	Outer components	Inner components	Special features
<i>Dactylioceras tenuicostatum</i> (Young & Bird, 1822)	MAN-4824	rc	early Toracian, Jurassic	Kettleless, Yorkshire, England	n. p.	n. p.	n. p.	The ultrastructure is not preserved.
<i>Peronoceras fibulatum</i> (Sowerby, 1823)	Howarth 1975, Birkelund 1980	1-3	Toarcian, Jurassic	Eydon, W Northamptonshire, England	r	wl?	dipl	
<i>Promicroceras marstonense</i> Spath, 1925	Palframan 1967, Erben et al. 1968, 1969	1-2	Sinemurian, Jurassic	near Marston, Somerset, England	r	-	dipl	
<i>Promicroceras planicosta</i> (Sowerby, 1914)	Mutvei 1967, 1970, Erben et al. 1969	1	Sinemurian, Jurassic	Yeovil, Sommerset, England	r	-	dipl	
<i>Xipheroceras ziphus</i> (Zieten, 1830)	Erben et al. 1968, 1969	1-3	Sinemurian, Jurassic	Lyme Regis, Dorset, England	r	-	dipl	
<i>Zugodactylites braunianus</i> (d'Orbigny, 1844)	Howarth 1975, Birkelund 1980	2-3	Toarcian, Jurassic	Eydon, W Northamptonshire, England	r	wl?	dipl	

Taxon	References / collection number	Preservation index	Age, period	Location	Type of dorsal shell wall	Outer components	Inner components	Special features
<b>Amaltheidae</b>								
<i>Amaltheus gibbosus</i> (Schlotheim, 1820)	MAn-4800 MAn-4801 MAn-4802	2	late Pliensbachian, Jurassic	Buttenheim, Bavaria, SE Germany	r	wl	dipl	
<i>Amaltheus margaritatus</i> de Monfort 1808	MAn-4797	rc	Pliensbachian, Jurassic	Lühnde canal, Sehnde near Hannover, Germany	n. p.	n. p.	n. p.	The ultrastructure is not preserved.
<i>Amaltheus margaritatus</i> de Monfort 1808	MAn-4798 MAn-4799	2	late Pliensbachian, Jurassic	Buttenheim, Bavaria, SE Germany	r → 'c'	so	'dncl', dipl	In outer whorls, the outer component of the dorsal shell wall forms a <b>spiral ornament</b> . A bunch of prismatic bands forms the inner components of the dorsal shell wall. The inner prismatic bands are equal to the dorsal inner prismatic layer (multi-layering). The outer prismatic bands represent the continuation of the ventral / lateral nacreous layer, i.e. <b>complete dorsal shell wall</b> .
<i>Amaltheus</i> sp.	MAn-4803	2	late Pliensbachian, Jurassic	ICE tunnel at Kulch near Lichtenfels, Germany	r?	n. p.	n. p.	

Taxon	References / collection number	Preservation index	Age, period	Location	Type of dorsal shell wall	Outer components	Inner components	Special features
<i>Amauroceras ferrugineum</i> (Simpson, 1855)	Lehman 1990, Weitschat 1999, Keupp 2000	2-3	late Pliensbachian, Jurassic	Ahrensburg near Hamburg, Germany	r	wl	-	
<i>Amauroceras</i> sp.	Bayer 1974	1-2	Pliensbachian, Jurassic	Lühnde near Hannover, Germany	r	wl	dipl	The inner prismatic layer of the dorsal shell wall forms several knob-like undulations (imprints of wrinkles), which was misinterpreted by Bayer (1974) as a prismatic wrinkle layer.
<i>Pleuroceras salebrosum</i> (Hyatt, 1867)	MAn-4804 MAn-4805 MAn-4806 MAn-4807 MAn-4808 MAn-4809 MAn-4810 MAn-4811 MAn-4812 MAn-4813 MAn-4837 MAn-4838	2	late Pliensbachian, Jurassic	Buttenheim, Bavaria, SE Germany	r	wl → so	dipl	In the outer whorls, one specimen (MAn-4804) develops isolated elements of a <b>spiral ornament</b> instead of wrinkles.

Taxon	References / collection number	Preservation index	Age, period	Location	Type of dorsal shell wall	Outer components	Inner components	Special features
<i>Pleuroceras solare</i> (Phillips, 1829)	MAn-4814	2	late Pliensbachian, Jurassic	Buttenheim, Bavaria, SE Germany	r	ol	-	
<i>Pleuroceras spinatum</i> (Bruguière, 1789)	Erben et al. 1968, 1969	rc-2	late Pliensbachian, Jurassic	Ockerhütte, Harz and Banz, Franconia, Germany	r	-	dipl	
<i>Pleuroceras spinatum</i> (Bruguière, 1789)	MAn-4815 MAn-4816 MAn-4817 MAn-4818 MAn-4839	2	late Pliensbachian, Jurassic	Buttenheim, Bavaria, SE Germany	r	wl	dipl	
<i>Pleuroceras</i> sp.	Bayer 1974	1-2	Pliensbachian, Jurassic	Lühnde near Hannover, Germany	r	wl	dipl	The inner prismatic layer of the dorsal shell wall forms several knob-like undulations (imprints of wrinkles), which was misinterpreted by Bayer (1974) as a prismatic wrinkle layer.



Taxon	References / collection number	Preservation index	Age, period	Location	Type of dorsal shell wall	Outer components	Inner components	Special features
<b>Hildoceratoidea</b>								
<i>Dorsetensia complanata</i> Buckman, 1892	Erben et al. 1968, 1969	rc-2	Bajocian, Jurassic	Gerzen near Alfeld, Hannover, Germany	r	-	dipl	
<i>Dorsetensia edouardiana</i> (d'Orbigny, 1845)	Erben et al. 1968, 1969	1-2	Bajocian, Jurassic	Gerzen near Alfeld, Hannover, Germany	r	-	dipl	
<i>Dorsetensia pinguis</i> (Roemer, 1836)	Erben et al. 1968, 1969	1-3	Bajocian, Jurassic	Gerzen near Alfeld, Hannover, Germany	r	-	dipl	
<i>Eleganticerias elegantulum</i> (Young & Bird, 1828)	Erben et al. 1968, 1969	1-3	Toarcian, Jurassic	Gravel pit near Ahrensburg, NE of Hamburg, Germany	r	-	dipl	
<i>Haugia illustris</i> (Denckmann, 1887)	Erben et al. 1968, 1969	1-2	Toarcian, Jurassic	Doernten near Goslar, Germany	r	-	dipl	
<i>Harpoceras</i> sp.	MAN-4796	rc	Toarcian, Jurassic	Stich canal, Sehnde near Hannover, Germany	n. p.	n. p.	n. p.	The ultrastructure is not preserved.

Taxon	References / collection number	Preservation index	Age, period	Location	Type of dorsal shell wall	Outer components	Inner components	Special features
<i>Leioceras opalinum</i> (Reinecke, 1818)	Erben et al. 1968, 1969	1-2	Aalenian, Jurassic	Otterbach, Gandershofen and Aalen, Germany	r	-	dipl	
<i>Leioceras opalinum</i> (Reinecke, 1818)	MAn-4518 MAn-4792 MAn-4793 MAn-4794 MAn-4795	2	early Aalenian, Jurassic	Heinigen, Baden-Württemberg, Germany	r	wl	dipl	
<i>Pleydellia</i> sp.	Erben et al. 1968, 1969	1-2	late Toarcian, Jurassic	'Gisement des Grottes', N of Millau, Aveyron, France	r	-	dipl	
<b>Stephanoceratoidea</b>								
<i>Cadoceras stupachenkoi</i> Mita, 1998	MAn-4790	1-2	early Callovian, Jurassic	Makaryev on Unzha River, Russia	r	wl	dipl	On occasion, the dorsal inner prismatic layer has two sub-layers (multi-layering).
<i>Cadoceras</i> sp.	Drushits et al. 1977	1-2	Callovian, Jurassic	Yelat'ma village on Oka River, Ryazan Province, Russia	r	-	dipl	

Taxon	References / collection number	Preservation index	Age, period	Location	Type of dorsal shell wall	Outer components	Inner components	Special features
<i>Chamoussetia stuckenbergi</i> (Lahusen, 1875)	MAAn-4777 MAAn-4778	1-2	early Callovian, Jurassic	Makaryev on Unzha River, Russia	r	wl?	dipl	On occasion, the dorsal inner prismatic layer has several sub-layers (multi-layering).
<i>Keplerites galilaeii</i> (Oppel, 1862)	MAAn-4783	1-2	early Callovian, Jurassic	Znamenka on Unzha River, Russia	r → nr	wl	dipl → dipl 1, dnc1 2, dipl 2	In the inner whorls, the shell forms a prismatic reduced dorsal shell wall. Its dorsal inner prismatic layer is thick and can consist of several sub-layers (multi-layering). In the outer whorls, the shell develops a <b>nacreous reduced dorsal shell wall</b> .
<i>Kosmoceras</i> ( <i>Kosmoceras</i> ) <i>duncani</i> (Sowerby, 1816)	Kulicki 1979	1-2	Callovian, Jurassic	Luckow, Poland	r	wl	dipl	
<i>Kosmoceras</i> ( <i>Kosmoceras</i> ) cf. <i>duncani</i> (Sowerby, 1816)	MAAn-4788	1-2	late Callovian, Jurassic	Dubki near Saratov, Russia	r (nr local)	wl	dipl (dipl 1, dnc1 2, dipl 2)	During overgrowth of the ventro-lateral spines, the dorsal inner prismatic layer develops inclusions of nacre, i.e. <b>nacreous reduced dorsal shell wall</b> .
<i>Kosmoceras</i> ( <i>Kosmoceras</i> ) <i>spinosum</i> (Sowerby, 1826)	Erben et al. 1968, 1969	1-2	Callovian, Jurassic	Popilany, Lithuania	r	-	dipl	

Taxon	References / collection number	Preservation index	Age, period	Location	Type of dorsal shell wall	Outer components	Inner components	Special features
<i>Kosmoceras</i> ( <i>Spinikosmoceras</i> ) <i>ornatum</i> (Schlotheim, 1820)	Sprey 2002	1-2	middle-late Callovian, Jurassic	Ryazan, Russia	r?	n. p.	n. p.	At least a dorsal shell wall does not cover the ammnointella.
<i>Kosmoceras</i> ( <i>Spinikosmoceras</i> ) <i>pollux</i> (Reinecke, 1818)	Sprey 2002	1-2	middle-late Callovian, Jurassic	Ryazan, Russia	r?	n. p.	n. p.	At least a dorsal shell wall does not cover the ammnointella.
<i>Kosmoceras</i> ( <i>Spinikosmoceras</i> ) cf. <i>pollux</i> (Reinecke, 1818)	MAn-4786 MAn-4787	1-2	late Callovian, Jurassic	Ryazan, Russia	r	-	-	
<i>Kosmoceras</i> ( <i>Spinikosmoceras</i> ) sp.	Erben et al. 1968, 1969	1-3	Callovian, Jurassic	Niegranden, Latvia	r	-	dipl	
<i>Kosmoceras</i> ( <i>Spinikosmoceras</i> ) sp.	Sprey 2002	1-2	middle-late Callovian, Jurassic	Ryazan, Russia	r?	n. p.	n. p.	At least a dorsal shell wall does not cover the ammnointella.
<i>Kosmoceras</i> sp.	Kulicki 1979	1-2	Callovian, Jurassic	Luckow, Poland	r	wl	dipl	
<i>Kosmoceras</i> sp.	Drushits et al. 1977	1-2	Callovian, Jurassic	Yelat'ma village on Oka River, Ryazan Province, Russia	r	ol	dipl	



Taxon	References / collection number	Preservation index	Age, period	Location	Type of dorsal shell wall	Outer components	Inner components	Special features
<i>Kosmoceras</i> sp.	MAAn-4789	1-2	early Callovian, Jurassic	Dubki near Saratov, Russia	r	-	dipl?	
<i>Pseudocadoceras mundum</i> (Sasonov, 1957)	MAAn-4791	1-2	early Callovian, Jurassic	Poretskoe on Sura River, Russia	r	wl	dipl	
<i>Pseudocadoceras</i> sp.	Drushits et al. 1977	1-2	Callovian, Jurassic	Yelat'ma village on Oka River, Ryazan Province, Russia	r	-	-	
<i>Quenstedtoceras henrici</i> Douville, 1912	Erben et al. 1968, 1969, Kulicki 1974, 1979	1-3	Callovian, Jurassic	Luckow near Lapiguz, S of Siedlce, Poland	r	wl	dipl	
<i>Quenstedtoceras henrici</i> Douville, 1912	MAAn-4768	1-2	early Callovian, Jurassic	Dubki near Saratov, Russia	sc	wl	dopl, dipl	The dorsal shell wall forms a dorsal outer prismatic layer as an additional inner component, i.e. <b>seemingly complete dorsal shell wall</b> .
<i>Quenstedtoceras lamberti</i> (Sowerby, 1819)	MAAn-4769 MAAn-4770 MAAn-4771	1-2	early Callovian, Jurassic	Dubki near Saratov, Russia	r	wl	dipl	The thickness of the dorsal inner prismatic layer varies from specimen to specimen. On occasion, the dorsal inner prismatic layer has several sub-layers (multi-layering).

Taxon	References / collection number	Preservation index	Age, period	Location	Type of dorsal shell wall	Outer components	Inner components	Special features
<i>Quenstedtoceras</i> sp.	Bandel 1989	1-2	Callovian, Jurassic	Luckow near Lapiguz, S of Siedlce, Poland	r?	n. p.	n. p.	
<i>Quenstedtoceras</i> sp.	Kulicki 1979, 1996, Kulicki & Tanabe 1999, Kulicki et al. 2001, Keupp 2000	1-2	Callovian, Jurassic	Luckow near Lapiguz, S of Siedlce, Poland	r	wl	dipl	
<i>Quenstedtoceras</i> sp.	Mutvei 1967	1	Callovian, Jurassic	Luckow near Lapiguz, S of Siedlce, Poland	r	-	-	
<i>Quenstedtoceras</i> sp. 1	MAn-4772 MAn-4773 MAn-4774 MAn-4775	1-2	late Callovian, Jurassic	Dubki near Saratov, Russia	r	wl	dipl	On occasion, the dorsal inner prismatic layer has several sub-layers (multi-layering).
<i>Quenstedtoceras</i> sp. 2	MAn-4776	1-2	early Callovian, Jurassic	Dubki near Saratov, Russia	r	wl	dipl	
<i>Rondiceras</i> sp.	MAn-4779 MAn-4780 MAn-4781 MAn-4782	1-2	early Callovian, Jurassic	Znamenka on Unzha River, Russia	r	wl	dipl	Sometimes the dorsal inner prismatic layer is locally absent.

Taxon	References / collection number	Preservation index	Age, period	Location	Type of dorsal shell wall	Outer components	Inner components	Special features
<i>Sigaloceras</i> ( <i>Sigaloceras</i> ) <i>calloviense</i> (Sowerby, 1815)	MAn-4784 MAn-4785	1-2	late Callovian, Jurassic	Znamenka on Unzha River, Russia	sc?	wl?	dopl?, dipl	The outer component of the dorsal shell wall develops a relief (wrinkle layer?). The dorsal shell wall probably forms a dorsal outer prismatic layer as an additional inner component, i.e. <b>seemingly complete dorsal shell wall</b> . The dorsal inner prismatic layer is only formed sporadically for relief smoothing.
<i>Sigaloceras</i> ( <i>Sigaloceras</i> ) <i>enodatum</i> (Nikitin, 1881)	Drushits et al. 1977	1-2	Callovian, Jurassic	Yelat'ma village on Oka River, Ryazan Province, Russia	r	ol	dipl	
<b>Perisphinctoidea</b>								
<i>Binatisphinctes</i> <i>mosquensis</i> (Fischer, 1843)	Sprey 2002	1-2	middle Callovian, Jurassic	Ryazan, Russia	r?	n. p.	n. p.	At least a dorsal shell wall does not cover the amnointella.

Taxon	References / collection number	Preservation index	Age, period	Location	Type of dorsal shell wall	Outer components	Inner components	Special features
<i>Binatisphinctes</i> sp.	MAN-4760 MAN-4761 MAN-4762 MAN-4763 MAN-4764 MAN-4765 MAN-4766	rc-2	middle Callovian, Jurassic	Ryazan, Russia	r (c local)	ol	dipl (dipl → dncl, dipl)	In general, the species forms a prismatic reduced dorsal shell wall. One specimen (MAN-4760) seems to develop a local dorsal nacreous layer when compensating the sculpture of the preceding whorl.
<i>Choffatia (Grossouvria)</i> sp. 1	MAN-4519 MAN-4759	1-2	late Callovian, Jurassic	Dubki near Saratov, Russia	r	wl?	dipl	The outer component of the dorsal shell wall develops a relief (wrinkle layer?). There is only one isolated occurrence of wrinkles. On occasion, the dorsal inner prismatic layer has several sub-layers (multi-layering).
<i>Choffatia (Grossouvria)</i> sp. 2	MAN-4520	rc-2	late Callovian, Jurassic	Dubki near Saratov, Russia	r → c	ol	dipl → dopl, dncl, dipl	The inner whorls form a prismatic reduced dorsal shell wall. In outer whorls, the shell develops a <b>complete dorsal shell wall</b> .
<i>Craspedites subditus</i> (Trautschold, 1887)	MAN-4745	1-2	Jurassic	Khoroshovo, NW part of Moscow, Russia	r	n. p.	n. p.	At least in the living chamber, the dorsal shell wall is completely absent.



Taxon	References / collection number	Preservation index	Age, period	Location	Type of dorsal shell wall	Outer components	Inner components	Special features
<i>Craspedites okensis</i> (d'Orbigny, 1845)	MAAn-4746 MAAn-4830	rc-2	Tithonian, Jurassic	Uljanowsk on Volga River, Russia	r	wl?	dipl	The outer component of the dorsal shell wall develops a relief (wrinkle layer?).
<i>Craspedites</i> sp.	MAAn-4744 MAAn-4829	rc-2	Callovian, Jurassic	Saratov, on Volga Riva, Russia	r	wl?	-	The outer component of the dorsal shell wall develops a relief (wrinkle layer?).
<i>Divisosphinctes besairiei</i> Collignon, 1960	PA-10151b MAAn-4758	2-3	late Oxfordian, Jurassic	Sakaraha, Morondava Basin, SW Madagascar	r (c local)	wl	dipl (dopl, dncl, dipl)	The outer component of the dorsal shell wall develops a relief; on occasion isolated wrinkles can be discerned. During overgrowth of an encruster, the shell of one specimen (PA-10151) develops a <b>complete dorsal shell wall</b> .
<i>Divisosphinctes</i> sp. 1	MAAn-4499	2-3	late Oxfordian, Jurassic	Sakaraha, Morondava Basin, SW Madagascar	r	wl?	dipl	The outer component of the dorsal shell wall develops a relief (wrinkle layer?).
<i>Divisosphinctes</i> sp. 2	MAAn-4498	2-3	late Oxfordian, Jurassic	Sakaraha, Morondava Basin, SW Madagascar	r	wl	dipl	The outer component of the dorsal shell wall develops a relief; on occasion isolated wrinkles can be discerned.
<i>Garniericeras catenulatum</i> (Fischer, 1830)	MAAn-4743	1-2	Jurassic	Khoroshovo, NW part of Moscow, Russia	r	-	dipl	

Taxon	References / collection number	Preservation index	Age, period	Location	Type of dorsal shell wall	Outer components	Inner components	Special features
<i>Indosphinctes (Elatmites) submutatus</i> (Nikitin, 1881)	Doguzhaeva 2012	1-2	Calloviaian, Jurassic	Ryazan, Russia	r	ol	dipl	The outer component of the dorsal shell wall has a micro-granular structure.
<i>Kachpurites cf. fulgens</i> (Trautschold, 1861)	Erben et al. 1968, 1969	1-2	Tithonian, Jurassic	Kaschpur, Volga River Basin, Russia	r	-	dipl	
<i>Pavlovia</i> sp.	Erben et al. 1968, 1969, Erben & Reid 1971	2-3	Kimmeridgian, Jurassic	Hartwell, Buckinghamshire, England	r	-	dipl	
<i>Perisphinctes (Kraoaosphinctes) mahabokensis</i> (Collignon, 1959)	MAn-4834 MAn-4835	2-3	late Oxfordian, Jurassic	Sakaraha, Morondava Basin, SW Madagascar	r → nr	wl?	dipl → dipl 1, dncl 2, dipl 2	The inner whorls form a prismatic reduced dorsal shell wall. The outer component of the dorsal shell wall probably develops a relief (wrinkle layer?). In the outer whorls, the shell develops a <b>nacreous reduced dorsal shell wall</b> . The appearance of the primary dorsal inner prismatic layer is sperulithic. The secondary dorsal inner prismatic layer is very thin.
<i>Perisphinctes (Kraoaosphinctes)</i> sp.	MAn-4500 MAn-4755 MAn-4756	2-3	late Oxfordian, Jurassic	Sakaraha, Morondava Basin, SW Madagascar	r	ol?	dipl?	The dorsal inner prismatic layer appears only in contact of the septa (small whorls).

Taxon	References / collection number	Preservation index	Age, period	Location	Type of dorsal shell wall	Outer components	Inner components	Special features
Perisphinctidae indet	Dauphin 1989	1-2	Jurassic	Madagascar	r?	n. p.	n. p.	
Perisphinctidae indet	MAo-4501	2	late Oxfordian, Jurassic	Sakaraha, Morondava Basin, SW Madagascar	r	ol	-	
<i>Proplanulites</i> sp.	MAo-4767	2	early Callovian, Jurassic	Znamenka on Unzha River, Russia	r	wl	dipl	
<i>Riasanites</i> sp. 1	MAo-1855	1-2	Berriasian, Cretaceous	Moscow region, Russia	r → c?	wl?	dipl → dncl?, dipl	In the outer whorl, it seems that the nacreous layer of the lateral shell wall does not wedge out at the whorl contact. The dorsal nacreous layer seems to cover wide portions of the preceding whorl (complete dorsal shell wall?).
<i>Riasanites</i> sp. 2	MAo-1856	1-2	Berriasian, Cretaceous	Ryazan, Russia	r?	-	dipl?	
<i>Simbirskites</i> sp. 1	MAo-1857 MAo-1858 MAo-1859	rc-1	late Hauterivian, Cretaceous	Mourberg at Hildesheim, Germany	n. p.	n. p.	n. p.	The ultrastructure is not preserved.

Taxon	References / collection number	Preservation index	Age, period	Location	Type of dorsal shell wall	Outer components	Inner components	Special features
<i>Simbirskites</i> sp. 2	MAo-1860	rc-1	Hauterivian, Cretaceous	Speeta, Yorkshire, England	r	ol?	dipl	The inner prismatic layer of the dorsal shell wall can develop two sub-layers (multi-layering).
<i>Speetonicerias versicolor</i> (Trautschold, 1865)	MAo-1861	1-2	Aptian, Cretaceous	Simbirsk, Uljanowsk, Volga Basin region, Russia	nr	n. p.	dncl 2, dipl 2	In the outer whorls, the dorsal inner prismatic layer develops inclusions of nacre, i.e. <b>nacreous reduced dorsal shell wall</b> .
<i>Speetonicerias</i> sp.	MAAn-4741 MAAn-4742	rc-2	Callovian, Jurassic	Saratov on Volga River, Russia	r	wl	dipl	The outer component of the dorsal shell wall develops a relief of tiny triangular structures (wrinkle layer).
<i>Virgatites pallasianus</i> (d'Orbigny, 1845)	MAAn-4754 MAAn-4836	1-2	Tithonian, Jurassic	Voskresensk near Moscow, Russia	r	ol	dipl?	
<b>Aspidoceratidae: Peltoceratinae</b>								
<i>Peltoceratoides</i> sp.	MAAn-4752 MAAn-4753	1-2	late Callovian, Jurassic	Dubki near Saratov, Russia	r	wl?	dipl	On occasion, the outer component of the dorsal shell wall develops a relief (wrinkle layer?).



Taxon	References / collection number	Preservation index	Age, period	Location	Type of dorsal shell wall	Outer components	Inner components	Special features
<b>Aspidoceratidae: Aspidoceratinae</b>								
<i>Aspidoceras</i> sp.	MAN-3193 MAN-4046b MAN-4506 MAN-4507	2-3	late Oxfordian, Jurassic	Sakaraha, Morondava Basin, SW Madagascar	r → nr	ol (→ hbl)	dipl → dipl 1, dnc1 2, dipl 2	The inner whorls form a prismatic reduced dorsal shell wall. In the outer whorls, the shell develops a <b>nacreous reduced dorsal shell wall</b> .
<i>Epaspidoceras jeannetti</i> (Collignon, 1959)	MAN-3195 MAN-4503 MAN-4504 MAN-4505	2-3	late Oxfordian, Jurassic	Sakaraha, Morondava Basin, SW Madagascar	r (r → nr)	ol	dipl (dipl → dipl 1, dnc1 2, dipl 2)	In general, the species forms a prismatic reduced dorsal shell wall. One specimen (MAN-4505) develops a <b>nacreous reduced dorsal shell wall</b> in the outer whorls.
<i>Euaspidoceras</i> sp. 1	MAN-4750	2-3	late Callovian, Jurassic	Dubki near Saratov, Russia	nr	n. p.	dnc1 2, dipl 2	In the outer whorls, the shell develops a <b>nacreous reduced dorsal shell wall</b> .
<i>Euaspidoceras</i> sp. 2	MAN-4751	2-3	late Oxfordian, Jurassic	Sakaraha, Morondava Basin, SW Madagascar	r → nr	ol	dipl → dipl 1, dnc1 2, dipl 2	The inner whorls form a prismatic reduced dorsal shell wall. In the outer whorls, the shell develops a <b>nacreous reduced dorsal shell wall</b> .

Taxon	References / collection number	Preservation index	Age, period	Location	Type of dorsal shell wall	Outer components	Inner components	Special features
<i>Mirosphinctes</i> sp. 1	MAN-1769	2-3	late Oxfordian, Jurassic	Sakaraha, Morondava Basin, SW Madagascar	r → nr	ol	dipl → dipl 1, dncl 2, dipl 2	The inner whorls form a prismatic reduced dorsal shell wall. In the outer whorls, the shell develops a <b>nacreous reduced dorsal shell wall</b> .
<i>Mirosphinctes</i> sp. 2	MAN-4747	2-3	late Oxfordian, Jurassic	Sakaraha, Morondava Basin, SW Madagascar	r → nr	wl	dipl → dipl 1, dncl 2, dipl 2	The inner whorls form a prismatic reduced dorsal shell wall. In the outer whorls, the shell develops a <b>nacreous reduced dorsal shell wall</b> . Some isolated wrinkles occur.
<i>Pseudowaagenia</i> sp.	MAN-4502	2-3	late Oxfordian, Jurassic	Sakaraha, Morondava Basin, SW Madagascar	nr	ol (→ hbl)	dipl 1, dncl 2, dipl 2	In the outer whorls, the shell develops a <b>nacreous reduced dorsal shell wall</b> .
<b>Haploceratoidea</b>								
<i>Aconeceras trautscholdi</i> (Sinzow, 1870)	Erben et al. 1968, 1969, Drushits & Khiami 1970, Doguzhaeva & Mutvei 1991, 1993a, Kulicki & Tanabe 1999, Kulicki et al. 2001, 2016	2-3	early Aptian, Cretaceous	Simbirsk, Uljanowsk, Volga River Basin, Russia	r	wl, sphpr	dipl	In the outer whorls, a <b>spherulitic-prismatic layer</b> covers the ventral keel of the preceding whorl; it forms a strong thickening.

Taxon	References / collection number	Preservation index	Age, period	Location	Type of dorsal shell wall	Outer components	Inner components	Special features
<i>Aconeceras</i> sp. 1	MAo-1851 MAo-1852 MAo-1853	2-3	early Albian, Cretaceous	Ambatolafia, Mahajanga Basin, NW Madagascar	r	wl → sphpr	dipl	In the outer whorls, the wrinkle layer transforms into a <b>spherulitic-prismatic layer</b> . At the ventral keel of the preceding whorl, the layer forms a strong thickening with several prismatic inclusions. At the flanks of the preceding whorl, a regular wrinkle layer persists. The extension of the dorsal inner prismatic layer is restricted to the ventral keel of the preceding whorl and vanishes ventro-laterally.
<i>Aconeceras</i> sp. 2	MAo-1849 MAo-1850	1-2	Aptian, Cretaceous	Shilovka near Volga, Russia	r	sphpr?	dipl	In the outer whorls, a <b>spherulitic-prismatic layer</b> covers the ventral keel of the preceding whorl; it forms a strong thickening. The extension of the dorsal inner prismatic layer is restricted to the ventral keel of the preceding whorl and vanishes ventro-laterally.

Taxon	References / collection number	Preservation index	Age, period	Location	Type of dorsal shell wall	Outer components	Inner components	Special features
<i>Hecticoceras</i> ( <i>Hecticoceras</i> ) sp.	MAn-1528 MAn-4735 MAn-4736 MAn-4737 MAn-4738 MAn-4849 MAn-4850	rc-1	early Callovian, Jurassic	Ryazan, Russia	r	ol?	dipl?	
<i>Hecticoceras</i> ( <i>Lunuloceras</i> ) <i>brightii</i> (Pratt, 1841)	Sprey 2002	1-2	middle-late Callovian, Jurassic	Ryazan, Russia	r?	n. p.	n.d	At least a dorsal shell wall does not cover the ammnointella.
<i>Hecticoceras</i> ( <i>Lunuloceras</i> ) <i>lunula</i> (Reinecke, 1818)	Sprey 2002	1-2	middle-late Callovian, Jurassic	Ryazan, Russia	r?	n. p.	n. p.	At least a dorsal shell wall does not cover the ammnointella.
<i>Hecticoceras</i> ( <i>Sublunuloceras</i> ) <i>nodosulcatum</i> (Lahusen, 1883)	Sprey 2002	1-2	middle-late Callovian, Jurassic	Ryazan, Russia	r?	n. p.	n. p.	At least a dorsal shell wall does not cover the ammnointella.



Taxon	References / collection number	Preservation index	Age, period	Location	Type of dorsal shell wall	Outer components	Inner components	Special features
<i>Hecticoceras</i> ( <i>Sublunuloceras</i> ) sp.	MAAn-4739	1-2	late Callovian, Jurassic	Dubki near Saratov, Russia	sc?	wl?	dopl?, dipl	The outer component of the dorsal shell wall develops a relief (wrinkle layer?). The dorsal shell wall probably forms a dorsal outer prismatic layer as an additional inner component, i.e. <b>seemingly complete dorsal shell wall</b> .
<i>Lissoceras erato</i> (d'Orbigny, 1850)	MAAn-4740	2-3	late Oxfordian, Jurassic	Sakaraha, Morondava Basin, SW Madagascar	r	wl	dipl	
<i>Oecoptychius</i> cf. <i>refractus</i> (Reinecke, 1818)	Erben et al. 1968, 1969	1-2	Callovian, Jurassic	Niegranden, Latvia	r	-	dipl	
<i>Sanmartinoceras</i> sp.	MAo-1854	2-3	early Albian, Cretaceous	Ambatolafia, Mahajanga Basin, NW Madagascar	r	sphpr	dipl	In the outer whorls, a <b>spherulitic-prismatic layer</b> covers the ventral keel of the preceding whorl; it is dominated by spherulitic-prismatic inclusions. The dorsal inner prismatic layer is thickest at position of the ventral keel of the preceding whorl and becomes very thin ventro-laterally.

Taxon	References / collection number	Preservation index	Age, period	Location	Type of dorsal shell wall	Outer components	Inner components	Special features
<i>Taramelliceras externnodosum</i> Dorn, 1930	MAAn-1528	2-3	late Oxfordian, Jurassic	Sakaraha, Morondava Basin, SW Madagascar	r	sphpr	dipl	In the outer whorls, a <b>spherulitic-prismatic layer</b> covers the venter of the preceding whorl; it forms a strong thickening with several prismatic inclusions (only median section).
<b>"Desmoceratoidea"</b>								
<i>Beudanticeras</i> sp.	MAo-1845	2-3	early Albian, Cretaceous	Ambatolafia, Mahajanga Basin, NW Madagascar	r	wl	dipl	
<i>Canadoceras kossmati</i> Matsumoto, 1954	MAo-1799	rc-2	Campanian, Cretaceous	Teshio-Nakagawa area, Hokkaido, Japan	r	wl	dipl	
<i>Cleoniceras (Grycia) besairiei</i> (Collignon, 1949)	PA-21489b PA-29534a PA-33582	2-3	early Albian, Cretaceous	Ambatolafia, Mahajanga Basin, NW Madagascar	r (c local)	wl	dipl (dncl, dipl)	One specimen (PA-33582) forms a <b>local complete dorsal shell wall</b> in reaction to a forma aegra aptycha (shell anomaly).
<i>Cleoniceras (Grycia)</i> sp.	MAo-1829 MAo-1830 MAo-1882	2-3	early Albian, Cretaceous	Ambatolafia, Mahajanga Basin, NW Madagascar	r	wl	dipl	

Taxon	References / collection number	Preservation index	Age, period	Location	Type of dorsal shell wall	Outer components	Inner components	Special features
<i>Damesites semicostatus</i> Matsumoto, 1942	MAo-1848	2-3	Campanian, Cretaceous	Teshio- Nakagawa area, Hokkaido, Japan	r	wl	dipl	
<i>Damesites sugata</i> (Forbes, 1846)	Kulicki & Tanabe 1999, Kulicki et al. 2001, 2016	1-3	Coniacian, Cretaceous	Haboro area, NW Hokkaido, Japan	r	wl	dipl	
<i>Damesites</i> sp.	MAo-1846	2	Campanian, Cretaceous	Teshio- Nakagawa area, Hokkaido, Japan	r	wl	dipl	
<i>Desmoceras</i> ( <i>Desmoceras</i> ) <i>latidorsatum</i> (Michelin, 1838)	MAo-1781 MAo-1782 MAo-1783 MAo-1784 MAo-1785 MAo-1786 MAo-1787 MAo-1788 MAo-1789 MAo-1839	2-3	early Albian, Cretaceous	Ambatolafia, Mahajanga Basin, NW Madagascar	r (local nr)	wl	dipl (dnc1 2, dipl 2)	One specimen (MAo-1787) develops local patches of nacre in the dorsal inner prismatic layer, i.e. <b>nacreous reduced dorsal shell wall</b> .

Taxon	References / collection number	Preservation index	Age, period	Location	Type of dorsal shell wall	Outer components	Inner components	Special features
<i>Desmoceras</i> ( <i>Pseudouhligella</i> ) <i>intrapunctatum</i> Keupp, 2008	Keupp 2008	2-3	early Albian, Cretaceous	Ambatolafia, Mahajanga Basin, NW Madagascar	r?	(rs)	n. p.	In the rear living chamber, the inner prismatic layer forms ' <b>Ritzstreifen</b> ' ventrally and laterally.
<i>Desmoceras</i> ( <i>Pseudouhligella</i> ) <i>intrapunctatum</i> Keupp, 2008	MAo-1883	2-3	early Albian, Cretaceous	Ambatolafia, Mahajanga Basin, NW Madagascar	r	wl	dipl	
<i>Desmophyllites diphylloides</i> (Forbes, 1846)	MAo-1838	1-2	Campanian, Cretaceous	Teshio-Nakagawa area, Hokkaido, Japan	-	(pe)	dipl	Instead of a relief of a wrinkle layer, a relief is formed by convex <b>periostracal extensions</b> of the preceding whorl.
<i>Eupachydiscus</i> sp.	MAo-1830 MAo-1831 MAo-1832 MAo-1833 MAo-1834 MAo-1835	rc-3	Campanian, Cretaceous	Teshio-Nakagawa area, Hokkaido, Japan	r → nr	wl (→ rk)	dipl → dipl 1, dnc1 2, dipl 2	The inner whorls form a prismatic reduced dorsal shell wall. In the outer whorls, the shell develops a <b>nacreous reduced dorsal shell wall</b> . The dorsal outer and the inner prismatic layer are each formed of two sub-layers. The outer sub-layer of the dorsal outer prismatic layer forms the relief of ' <b>Ritzknoten</b> ' that extends at least to the umbilical-lateral flanks and replaces the wrinkle layer in the outer whorls.

Taxon	References / collection number	Preservation index	Age, period	Location	Type of dorsal shell wall	Outer components	Inner components	Special features
<i>Hauericeras angustum</i> Yabe, 1904	MAo-1836 MAo-1837	2	Campanian, Cretaceous	Teshio- Nakagawa area, Hokkaido, Japan	r	wl	n. p.	
<i>Kitchinites</i> sp.	MAo-1842 MAo-1843	1-3	Campanian, Cretaceous	Teshio- Nakagawa area, Hokkaido, Japan	r	wl	dipl	
<i>Menuites</i> sp.	MAo-1800 MAo-1894	rc-2	Campanian, Cretaceous	Teshio- Nakagawa area, Hokkaido, Japan	r	wl	dipl	
<i>Neosilesites ambatolafiensis</i> Collignon, 1963	MAo-1779 MAo-1780	2-3	early Albian, Cretaceous	Ambatolafia, Mahajanga Basin, NW Madagascar	r	wl	dipl	
<i>Neosilesites</i> sp.	MAo-1777 MAo-1778	2-3	early Albian, Cretaceous	Ambatolafia, Mahajanga Basin, NW Madagascar	r	wl	dipl	
<i>Puzosia</i> cf. <i>mozambica</i> Collignon, 1963	MAo-485	2-3	early Albian, Cretaceous	Ambatolafia, Mahajanga Basin, NW Madagascar	r	wl	dipl	



Taxon	References / collection number	Preservation index	Age, period	Location	Type of dorsal shell wall	Outer components	Inner components	Special features
<i>Puzosia saintoursi</i> (Collignon, 1963)	MAo-1792 MAo-1793 MAo-1794 MAo-1795 MAo-1796 MAo-1797	2-3	early Albian, Cretaceous	Ambatolafia, Mahajanga Basin, NW Madagascar	r (nr local)	wl	dipl (dncl 2, dipl 2)	One specimen (MAo-1797) develops local patches of nacre in the dorsal inner prismatic layer, i.e. <b>nacreous reduced dorsal shell wall</b> . On occasion, the dorsal nacre has a lamellar ultrastructure.
<i>Umsinenoceras linguatuberculatum</i> Kennedy et al., 1979	MAo-1791 MAo-1844	2-3	early Albian, Cretaceous	Ambatolafia, Mahajanga Basin, NW Madagascar	r	wl	dipl	
<i>Yokoyamaoceras jimboi</i> Matsumoto, 1955	Kulicki & Tanabe 1999, Kulicki et al. 2001, 2016	2-3	early Santonian- middle Campanian, Cretaceous	Obira Area and Teshio- Nakagawa area, Hokaido, Japan	r	wl	dipl	
<b>Acanthoceratoidea</b>								
<i>Proleymeriella schrammeni</i> Jacob, 1907	MAo-1828	2	early Albian, Cretaceous	Vöhrum, near Hannover, Lower Saxony, Germany	r	wl?	dipl	The outer component of the dorsal shell wall develops a relief (wrinkle layer?).

Taxon	References / collection number	Preservation index	Age, period	Location	Type of dorsal shell wall	Outer components	Inner components	Special features
<b>Hoplitoidea</b>								
<i>Anahoplites</i> cf. <i>planus</i> (Mantell, 1822)	MAo-1815	1-2	middle Albian, Cretaceous	Wissant, Nord-Pas-de-Calais, France	r	-	dipl?	
<i>Anahoplites</i> sp.	MAo-1814	1-2	middle Albian, Cretaceous	Wissant, Nord-Pas-de-Calais, France	r	-	dipl	
<i>Euhoplites</i> cf. <i>nitidus</i> Spath, 1925	MAo-1817	rc	middle-late Albian, Cretaceous	Wissant, Nord-Pas-de-Calais, France	r?	wl?	n. p.	The ultrastructure is not preserved. There are probably relics of a wrinkle layer.
<i>Euhoplites trapezoidalis</i> Spath, 1928	MAo-1816	rc-1	late Albian, Cretaceous	Wissant, Nord-Pas-de-Calais, France	r	-	dipl	
<i>Euhoplites</i> gr. <i>tuberculatus</i> Sowerby, 1821	Erben et al. 1968, 1969	1-2	Albian, Cretaceous	Folkestone, Kent, England	r	-	dipl	
Hoplitidae indet	MAo-1818 MAo-1819 MAo-1820 MAo-1821	rc-1	middle Albian, Cretaceous	Wissant, Nord-Pas-de-Calais, France	r	-	dipl?	The ultrastructure is generally not preserved. However, in one specimen (MAo-1819) there are relics of a dorsal inner prismatic layer.

Taxon	References / collection number	Preservation index	Age, period	Location	Type of dorsal shell wall	Outer components	Inner components	Special features
<i>Placenticer</i> cf. <i>placenta</i> (DeKay, 1828)	Erben et al. 1968, 1969	1-2	Upper Cretaceous	Cheyenne River, Badlands, S Dakota, USA	r	-	dipl	
<i>Placenticer</i> <i>whitfieldi</i> Hyatt, 1903	Westermann 1971	1	Campanian, Cretaceous	Lethbridge, Alberta, Canada	r	-	dipl	
<i>Metaplacenticer</i> <i>subtilistriatum</i> (Jimbo, 1894)	MAo-1822 MAo-1823 MAo-1824 MAo-1825 MAo-1862 MAo-1863	2-3	Campanian, Cretaceous	Teshio-Nakagawa area, Hokkaido, Japan	r, (sc)	wl	dipl (dopl, dipl)	In one specimen (MAo-1824), the dorsal shell wall forms a dorsal outer prismatic layer as an additional inner component, i.e. <b>seemingly complete dorsal shell wall</b> .
<b>Ancyloceratoidea</b>								
Ancyloceratoidea indet	MAo-1813	2-3	Aptian, Cretaceous	Shilovka near Volga River, Russia	ric	ol	dopl, dncl 1, dipl 1, dncl 2, dipl 2	In the outer shafts, the conch develops a <b>reinforced complete dorsal shell wall</b> .
<i>Luppovia</i> sp.	Doguzhaeva & Mikhailova 1982	1-2	Aptian, Cretaceous	Bolshoj Balkhan, W Turkmenia	c	-	dopl, dncl, dipl	Right after the nepionic constriction (end of larval phase, begin of decoiling), the conch develops a <b>complete dorsal shell wall</b> .

Taxon	References / collection number	Preservation index	Age, period	Location	Type of dorsal shell wall	Outer components	Inner components	Special features
<i>Ptychoceras laevigatum</i> Egoian, 1969	Doguzhaeva & Mutvei 1989, 1993a, b	1-2	late Aptian, Cretaceous	Hokodz River and Kurdzhips River, NW Caucasus, Russia	c → ric	cl	dopl, dncl, dipl → dncl 1, dipl 1, dncl 2, dipl 2 → dncl	The young shafts form a simple <b>complete dorsal shell wall</b> . In the outer shafts, the conch develops a <b>reinforced complete dorsal shell wall</b> . During ontogeny, the outer prismatic layer is reduced dorsally (and ventrally). The last shaft consists only of the nacreous layer (dorsally and ventrally). The whole adult aperture is coated by a 'nacreous' <b>coating layer</b> .
<i>Ptychoceras minimum</i> Rouchadze, 1933	Doguzhaeva & Mutvei 1989, 1993a, b	1-2	late Aptian, Cretaceous	Hokodz River and Kurdzhips River, NW Caucasus, Russia	c → ric	cl	dopl, dncl, dipl → dncl 1, dipl 1, dncl 2, dipl 2 → dncl	The young shafts form a simple <b>complete dorsal shell wall</b> . In the outer shafts, the conch develops a <b>reinforced complete dorsal shell wall</b> . During ontogeny, the outer prismatic layer is reduced dorsally (and ventrally). The last shaft consists only of the nacreous layer (dorsally and ventrally). The whole adult aperture is coated by a 'nacreous' <b>coating layer</b> .

Taxon	References / collection number	Preservation index	Age, period	Location	Type of dorsal shell wall	Outer components	Inner components	Special features
<i>Ptychoceras parvum</i> Egoian, 1969	Doguzhaeva & Mutvei 1989, 1993a, b	1-2	late Aptian, Cretaceous	Hokodz River and Kurdzhips River, NW Caucasus, Russia	c → ric	cl	dopl, dncl, dipl → dncl 1, dipl 1, dncl 2, dipl 2 → dncl	The young shafts form a simple <b>complete dorsal shell wall</b> . In the outer shafts, the conch develops a <b>reinforced complete dorsal shell wall</b> . During ontogeny, the outer prismatic layer is reduced dorsally (and ventrally). The last shaft consists only of the nacreous layer (dorsally and ventrally). The whole adult aperture is coated by a 'nacreous' <b>coating layer</b> .
<i>Ptychoceras renngarteni</i> Egoian, 1969	Doguzhaeva & Mutvei 1989, 1993a, b	1-2	late Aptian, Cretaceous	Hokodz River and Kurdzhips River, NW Caucasus, Russia	c → ric	cl	dopl, dncl, dipl → dncl 1, dipl 1, dncl 2, dipl 2 → dncl	The young shafts form a simple <b>complete dorsal shell wall</b> . In the outer shafts, the conch develops a <b>reinforced complete dorsal shell wall</b> . During ontogeny, the outer prismatic layer is reduced dorsally (and ventrally). The last shaft consists only of the nacreous layer (dorsally and ventrally). The whole adult aperture is coated by a 'nacreous' <b>coating layer</b> .



Taxon	References / collection number	Preservation index	Age, period	Location	Type of dorsal shell wall	Outer components	Inner components	Special features
<b>Douvilleiceratoidea</b>								
<i>Douvilleiceras mammillatum</i> (Schlotheim, 1813)	MAo-1808 MAo-1809 MAo-1810 MAo-1811	2-3	early Albian, Cretaceous	Ambatolafia, Mahajanga Basin, NW Madagascar	r → ric	wl	dipl → dncl 1, dipl 1, dncl 2, dipl 2	The inner whorls form a prismatic reduced dorsal shell wall. In the outer whorls, the shell develops a <b>reinforced complete dorsal shell wall</b> . Only, at the ventral crest of the preceding whorl, the complete dorsal shell wall develops a local shell doubling (dncl 1, dipl 1, dncl 2, dipl 2). The cover of the flanks consists only of the inner portions (dncl 2, dipl 2). The wrinkles of the outer whorls fuse.
<i>Douvilleiceras</i> sp.	MAo-1812	2	Lower Cretaceous	Bully, Rhône, France	r → ric	wl?	dipl → dncl 1, dipl 1, dncl 2, dipl 2	The inner whorls form a prismatic reduced dorsal shell wall. In the outer whorls, the shell develops a <b>reinforced complete dorsal shell wall</b> . Only, at the ventral crest of the preceding whorl, the complete dorsal shell wall develops a local shell doubling (dncl 1, dipl 1, dncl 2, dipl 2). The cover of the flanks consists only of the inner portions (dncl 2, dipl 2). The wrinkles of the outer whorls fuse.

Taxon	References / collection number	Preservation index	Age, period	Location	Type of dorsal shell wall	Outer components	Inner components	Special features
<i>Douvilleiceras</i> sp.	Dauphin 1989	2-3	Albian, Cretaceous	Bully, Rhône, France	r?	n. p.	n. p.	
<b>Deshayesitoidea</b>								
<i>Acanthohoplites bergeroni</i> (Seunes, 1887)	Erben et al. 1968, 1969	rc-2	middle-late Aptian, Cretaceous	Algermissen near Hildesheim, Germany	r	-	dipl	
<i>Colombiceras</i> sp.	MAo-1884	1-2	Aptian, Cretaceous	Kaukasus region, Russia	nr	-	dipl 1, dnc1 2, dipl 2	The shell develops a <b>nacreous reduced dorsal shell wall</b> . In the outer whorls, the dorsal shell wall can be reinforced by a dorsal outer prismatic layer. However, it covers only the flanks of the preceding whorl and vanishes completely towards the venter.
<i>Deshayesites</i> sp.	MAo-1806 MAo-1807	1-2	Aptian, Cretaceous	Shilovka near Volga, Russia	r	wl	dipl	On occasion, the dorsal inner prismatic layer appears only in contact of the septa.
<i>Dufrenoyia</i> sp.	MAo-1808	1-2	Lower Cretaceous	Bully, Rhône, France	r	n. p.	n. p.	At least in the living chamber, the dorsal shell wall is completely absent.

Taxon	References / collection number	Preservation index	Age, period	Location	Type of dorsal shell wall	Outer components	Inner components	Special features
<i>Parahoplites</i> sp.	MAo-1804	rc-1	Aptian, Cretaceous	Daghestan	nr?	-	dncl?	The diagenetically altered dorsal shell wall preserves relics of nacreous appearance.
<b>Scaphitoidea</b>								
<i>Clioscaphtes vermiformis</i> (Meek & Hayden, 1862)	Landman 1987	1-2	Turonian-Santonian, Cretaceous	Big Horn Country and Tool Country, Montana	r→c	-	dipl → dopl, dncl, dipl	The planispirally coiled phragomocone has a prismatic reduced dorsal shell wall. The detached, hook-like living chamber develops a <b>complete dorsal shell wall</b> .
<i>Discoscaphites</i> cf. <i>conradi</i> (Morton, 1834)	Erben et al. 1968, 1969	1-2	Upper Cretaceous	Rock Creek, S Dakota, USA	r→c	-	dipl → dopl, dncl, dipl	The planispirally coiled phragomocone has a prismatic reduced dorsal shell wall. The detached, hook-like living chamber develops (probably) a <b>complete dorsal shell wall</b> .
<i>Discoscaphites</i> sp.	Birkelund 1967, 1980, Birkelund & Hansen 1968, 1974	1-2	Maastrichtian, Cretaceous	Agatalen, Nūgssuaq, W Greenland	r	-	dipl	The planispirally coiled phragomocone has a prismatic reduced dorsal shell wall.

Taxon	References / collection number	Preservation index	Age, period	Location	Type of dorsal shell wall	Outer components	Inner components	Special features
<i>Discoscaphites</i> sp.	MAo-1803	2	Maastrichtian, Cretaceous	Fox Hills Formation, North Central, S Dakota, USA	r	ol	n. p.	The planispirally coiled phragmocone has a prismatic reduced dorsal shell wall.
<i>Hoploscaphites nicoletii</i> (Morton, 1842)	AMNH-FI-99141 AMNH-FI-99142 AMNH-FI-99143	2	Maastrichtian, Cretaceous	Fox Hills Formation (Loc. #3272), S Dakota, USA	r → c	wl?	dipl → dopl, dncl, dipl	The planispirally coiled phragmocone has a prismatic reduced dorsal shell wall. The detached, hook-like living chamber develops a <b>complete dorsal shell wall</b> . The outer component of the dorsal shell wall develops a relief of small wrinkle-like structures.
<i>Hoploscaphites</i> sp.	MAo-1802	2	Maastrichtian, Cretaceous	Fox Hills Formation, North Central, S Dakota, USA	r	wl?	n. p.	The planispirally coiled phragmocone has a prismatic reduced dorsal shell wall. The outer component of the dorsal shell wall develops some isolated wrinkle-like ridges.
<i>Jeletzkytes nodosus</i> (Owen, 1852)	Erben et al. 1968, 1969	1-2	Pierre Shale, Cretaceous	Cheyenne River and Wasta, S Dakota, USA	r → c	-	dipl → dopl, dncl, dipl	The planispirally coiled phragmocone has a prismatic reduced dorsal shell wall. The detached, hook-like living chamber develops (probably) a <b>complete dorsal shell wall</b> .

Taxon	References / collection number	Preservation index	Age, period	Location	Type of dorsal shell wall	Outer components	Inner components	Special features
<i>Scaphites</i> ( <i>Pteroscaphites</i> ) <i>auriculatus</i> (Cobban, 1952)	Landman 1987	1-2	Turonian-Santonian, Cretaceous	Tool Country, Montana	r → c	-	dopl, dncl, dipl	The planispirally coiled phragmocone has a prismatic reduced dorsal shell wall. The detached, hook-like living chamber develops a <b>complete dorsal shell wall</b> .
<i>Scaphites</i> cf. <i>hippocrepis</i> (DeKay, 1828)	Westermann 1971	1	Upper Cretaceous	Black Hills, S Dakota, USA	r	-	dipl	The planispirally coiled phragmocone has a prismatic reduced dorsal shell wall.
<i>Scaphites preventricosus</i> Cobban, 1951	Landman 1987	1-2	Turonian-Santonian, Cretaceous	Cascade Country and Tool Country, Montana	r → c	-	dopl, dncl, dipl	The planispirally coiled phragmocone has a prismatic reduced dorsal shell wall. The detached, hook-like living chamber develops a <b>complete dorsal shell wall</b> .
<i>Scaphites whitfieldi</i> Cobban, 1951	Landman 1987	1-2	Turonian-Santonian, Cretaceous	Niobrara Country and Albany Country, Wyoming; Butte Country and Fall River Country, S Dakota; Emery Country, Utah	r → c	-	dopl, dncl, dipl	The planispirally coiled phragmocone has a prismatic reduced dorsal shell wall. The detached, hook-like living chamber develops a <b>complete dorsal shell wall</b> .



Taxon	References / collection number	Preservation index	Age, period	Location	Type of dorsal shell wall	Outer components	Inner components	Special features
<i>Scaphites whitfieldi</i> Cobban, 1951	AMNH- FI-99144	2	Turonian, Cretaceous	Turner Sandy Member, Wyoming, USA	r → c	wl	dipl → dopl, dncl, dipl	The planispirally coiled phragmocone has a prismatic reduced dorsal shell wall. The detached, hook-like living chamber develops a <b>complete dorsal shell wall</b> . The outer component of the dorsal shell wall develops a relief; on occasion, isolated wrinkles can be discerned.
<i>Scaphites</i> sp.	Erben et al. 1968, 1969	1-3	Upper Cretaceous	Rock Creek, S Dakota, USA	r → c	-	dipl → dopl, dncl, dipl	The planispirally coiled phragmocone has a prismatic reduced dorsal shell wall. The detached, hook-like living chamber develops (probably) a <b>complete dorsal shell wall</b> .

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## Conclusions

The ultrastructure of the ammonoid shell wall not only has potential for phylogenetic, morphogenetic and paleobiological questions but is crucial for understanding the shell wall. For example, ultrastructural observations allow for description of sculptural elements normally only studied and interpreted on a macroscopic scale, which enable detailed proof or disproof of ideas and models only assumed so far. Parabolae do indeed mark interruptions in shell growth (**Manuscript II**) but constrictions and varices do not (**Manuscript I**). Similarities in ultrastructural construction indicate relation: the aragonitic, three-layered ventral and lateral shell wall, the prismatic reduced dorsal shell wall (**Manuscript IV**), the varices (**Manuscript I**) or the withdrawal of the shell-secreting mantle (**Manuscript I-III**) are plesiomorphic features characterizing (Mesozoic) ammonoids. Structural differences allow the differentiation of distinct groups: e.g. organic radial lirae of Phylloceratinae and prismatic radial lirae of Aspidoceratinae (**Manuscript III**).

The following observations were made with a view to the phylogentic and taxonomic implications:

- 1) All (Mesozoic) Ammonoidea form primarily a three-layered shell wall (outer prismatic layer, middle nacreous layer, inner prismatic layer), which is interpreted as a plesiomorphic, hence homologous, trait of all Ammonoidea (**Manuscript I-IV**).
- 2) The three-layered shell wall can be modified by complete reduction or addition (e.g. shell doubling) of individual layers. Since this occurs ventrally and dorsally in a broad range of high order taxa (e.g. superfamilies), it seems to be a general ability of the ammonoid mantle as well. The individual occurrence can characterize distinct taxa, for example *Aconeceras* or Aspidoceratinae (**Manuscript IV**).
- 3) Ammonoids built the shell in a manner similar to recent molluscs by secreting an organic periostracum as stencil, as the rare preserved occurrences prove (**Manuscript II, IV**).
  - a. The periostracum can form extensions (e.g. scythe-like or convex) that are in part characteristic of some groups, e.g. Phylloceratoidea and Aspidoceratinae.
- 4) Ammonoids had the general ability to withdraw the mantle, as widespread withdrawal structures like injuries, the nepionic constriction, radial lirae, flares and parabolae prove (**Manuscript I-III**).
  - a. The nepionic constriction marks the end of the embryonic shell (ammonitella).

- b. Radial lirae, flares and parabolae are associated with some kind of episodic growth but differ in time and duration of formation.
- 5) Radial lirae are formed by the imbrication of sigmoid, organic lamellae of the periostracum or by corresponding prismatic lamellae of the outer prismatic layer, indicating their formation by withdrawal of the shell-secreting mantle. A comarginal formation or formation through undulation of the shell wall is not involved. Organic radial lirae seem to be diagnostic for Phylloceratoidea and prismatic radial lirae for Aspidoceratinae. It is possible that the prismatic radial lirae are derived from the organic radial lirae. However, a phylogenetic connection does not exist, maybe indicating a homoplasy (**Manuscript II**).
- 6) Lytoceratid flares and perisphinctid parabolae are the relics of a formerly frill-like, enlarged, temporary aperture that was formed at the end of a growth episode. Each of them marks an interruption in shell growth. Structurally they are very similar and are connected through transitional forms in Lytoceratoidea indicating near relation. It is probably a homologous trait. The frill was formed by the outer prismatic layer, the nacreous layer and an apertural prismatic coating (which indicates a cover by the mantle tissue). New shell (outer prismatic layer, middle nacreous layer and inner prismatic layer) is attached from within at the interior of shell wall. Particularly in flares, resorption by the mantle tissue was responsible for the removal of the frill-like enlargement of the shell. Parabolae might only be altered by breakage (**Manuscript III**).
- a. Morphological transitions of (prismatic) radial lirae to parabolae in Aspidoceratinae may indicate a direct relation, independent of the structural composition.
- 7) Varices and constrictions of the teleoconch do not mark an interruption in shell growth but merely represent continuous growth with local higher secretion of nacreous material that forms the local thickening. The uniform construction in combination with the widespread occurrence probably indicates a plesiomorphic feature (**Manuscript I**).
- a. Constrictions and ridged varices are derived from simple varices, by forming a surface undulation of the outer prismatic layer.
- b. The nacreous thickening is probably formed subsequent to the former aperture.
- c. The overall nepionic constriction is not the ground plan for varices and constrictions because the nepionic constriction marks a discontinuity in the shell

growth. At the nepionic constriction the nacreous thickening is formed as part of a temporary aperture.

- 8) In general, the dorsal shell wall of planspirally coiled Ammonoidea is reduced, consisting of an outer organic component and a dorsal inner prismatic layer, i.e. prismatic reduced dorsal shell wall. The mineralized shell layers are not secreted at the aperture. Probably it is an apomorphy accompanied by the coiling of the shell (**Manuscript IV**).
- a. The dorsal inner prismatic layer is a continuation of the inner prismatic layer of the ventral and lateral walls, formed in the rear of the living chamber.
  - b. The outer component is diverse in its morphological expression. In contrast to the inner prismatic layer it has no equivalent layer in the ventral and lateral shell wall and is formed in front of the aperture.
- 9) All Ammonoidea have an outer organic component of the dorsal shell wall, be it a smooth organic layer, relief wrinkle layer, spiral ornament, spherulithic-prismatic layer or coating layer (**Manuscript IV**).
- a. The outer organic component is primarily smooth, i.e. a simple organic layer.
  - b. The wrinkle layer is the most common morphological expression in (Mesozoic) ammonoids. Its structure (hollow organic ridges and knobs with prismatic infilling) is identical and probably therefore homologous at least throughout the Jurassic and Cretaceous taxa.
  - c. Other modifications of the outer organic component (e.g. spiral ornament, spherulithic-prismatic layer, coating layer) are derived from the wrinkle layer.
- 10) Modifications of the inner prismatic layer, e.g. 'Ritzstreifen' or 'Ritzknoten', can create a similar relief (small ridges and knobs) as the wrinkle layer in ventral, lateral and dorsal parts of the conch. In part this circumstance was interpreted by several authors as the organic wrinkle layer continuing to the ventral shell portions rather than being restricted to the contact area of the former whorl (**Manuscript IV**).
- 11) All ammonoids probably had the ability to form nacreous material dorsally. It is likely that the whole mantle was able to form nacre. This is a plesiomorphic trait of the orthocone ancestors of Ammonoidea (**Manuscript IV**).
- 12) The prismatic reduced dorsal shell wall can be modified by additional nacreous and prismatic layers, i.e. nacreous reduced dorsal shell wall. A nacreous reduced dorsal shell wall is equivalent to a shell doubling in the ventral and/or lateral shell wall and is formed in the rear part of the living chamber. Mineralized shell material is not formed at the

aperture. Its widespread or scattered occurrence in Mesozoic taxa indicates a plesiomorphic or homologous trait proper to all (Mesozoic) Ammonoidea (**Manuscript IV**).

- a. A nacreous reduced dorsal shell wall occurs mainly where the relief of the preceding whorl has to be smoothed.
- b. Heterochronic occurrences are probably diagnostic for some taxa, e.g. Aspidoceratinae.

13) The relation to orthocone ancestors allowed heteromorph (secondary decoiled) and some coiled taxa to develop a complete dorsal shell wall, consisting of the same three aragonitic layers as ventrally and laterally. This ability is probably only suppressed in coiled taxa, a plesiomorphy, and can be reactivated when needed or when growth exceeds a certain size (**Manuscript IV**).

- a. A complete dorsal shell wall is formed when the shell whorls detach from each other: e.g. heteromorphy, small area of whorl contact.
- b. A complete dorsal shell wall can be secondarily formed during overgrowth of encrusters or in reaction to a shell disturbance (e.g. injuries).
- c. It is likely that a complete dorsal shell wall could be developed during late ontogeny in most taxa.

14) Despite the assumed general ability to form a complete dorsal shell wall among all ammonoids, the Lytoceratoidea, Perisphinctoidea and Desmoceratoidea seem to be the most likely candidates as ancestors for Jurassic and Cretaceous heteromorphs, due to the occurrence of complete dorsal shell walls in these taxa in combination with time-overlap in the geological record of these taxa (**Manuscript IV**).

15) The dorsal shell wall of Ancyloceratoidea and Douvilleiceratoidea combine characteristics of simple complete dorsal shell walls and nacreous reduced dorsal shell walls; dorsally the shell wall is doubled, i.e. reinforced complete dorsal shell wall (**Manuscript IV**).

- a. Similarities in the construction of the dorsal shell wall of ancyloceratid taxa with that of douvilleiceratids (and deshayesitoids) may support their phylogenetic connection, i.e. ancestors and offspring.
- b. The ability to form a doubled shell package ventrally and dorsally represents probably the ground plan of shell construction.



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## **Appendix**

### *Eidesstattliche Erklärung*

Hiermit erkläre ich, dass diese Arbeit selbständig verfasst, alle verwendeten Hilfsmittel und Hilfen angegeben und sämtliche inhaltlichen und wörtlichen Zitate hervorgehoben sind. Diese Arbeit ist nicht schon einmal in einem früheren Promotionsverfahren eingereicht worden.

Berlin, 20.03.2016

### *Erklärung zum Eigenanteil*

Hiermit versichere ich, dass mein eigener Anteil an den Bestandteilen dieser Arbeit 90% einnimmt. Sämtliche Proben zur rasterelektronenmikroskopischen Untersuchung wurden von mir selbständig vorbereitet und analysiert. Die Dünnschliffe triassischer Ammonoideen wurden von Marc Barlage zur Analyse vorbereitet (Manuskript IV). Die Artikelmanuskripte wurden von mir grundlegend konzeptualisiert und abgefasst. Der Anteil meiner Co-Autoren beschränkte sich im Wesentlichen auf die Diskussion der individuellen Probleme und in Teilen zur Konzeption der Artikel. Lediglich Manuskript II wurde in Zusammenarbeit mit René Hoffmann eingehend gekürzt. Die Zeichnungen der Manuskripte wurden von Frau Monika Bulang-Lörcher in ihre Reinform gebracht. Bildtafeln und Abbildungen wurden von mir sämtlich erstellt.

Berlin, 20.03.2016

**Tabelle:** Auflistung des Eigenanteils an den einzelnen Bestandteilen der vorliegenden Arbeit.

<b>Arbeitsschritt</b>	<b>Eigenanteil in %</b>
<b>Manuskript I</b>	
Konzeption	90%
Durchführung	95%
Berichtsabfassung	100%
<b>Manuskript II</b>	
Konzeption	90%
Durchführung	95%
Berichtsabfassung	85%
<b>Manuskript III</b>	
Konzeption	90%
Durchführung	95%
Berichtsabfassung	100%
<b>Manuskript IV</b>	
Konzeption	90%
Durchführung	85%
Berichtsabfassung	100%



*Lebenslauf*

Der Lebenslauf ist in der Online-Version aus Gründen des Datenschutzes nicht enthalten.

*Publikationen*

- Radtke, G. 2013. The ultrastructural construction of Mesozoic ammonoid shell wall. In: J.R. Reitner, Y. Qun, W. Yongdong and M. Reich (eds.), *Palaeobiology and Geobiology of Fossil Lagerstätten through Earth History, Conference Abstract Volume*, S. 125. Universitätsverlag, Göttingen. (Konferenzbeitrag)
- Radtke, G. 2014. Complete dorsal ammonoid shell - A facultative character of phylogenetic importance? In: C. Klug and D. Fuchs (eds.), *Cephalopods – Present and Past 9 & Coleoid Cephalopods through Time 5, Conference Abstract Volume*, S. 75. Paläontologisches Institut und Museum, Universität Zürich. (Konferenzbeitrag)
- Radtke, G. 2014. Continuous or discontinuous? - The ultrastructure of flares, parabolae, constrictions and varices within ammonoid shell. In: C. Klug and D. Fuchs (eds.), *Cephalopods – Present and Past 9 & Coleoid Cephalopods through Time 5, Conference*

*Abstract Volume*, S. 135. Paläontologisches Institut und Museum, Universität Zürich.  
(Konferenzbeitrag)

Radtke, G. and Keupp, H. 2016. The internal structure of varices and constrictions in Jurassic and Cretaceous ammonoid shells. *Swiss Journal of Palaeontology*, 135 (1): 109-124. doi: [10.1007/s13358-015-0095-9](https://doi.org/10.1007/s13358-015-0095-9). (Manuskript I)

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Radtke, G., Hoffmann, R. and Keupp, H. 2016. Form and formation of flares and parabolae based on new observations of the internal shell structure in lycoceratid and perisphinctid ammonoids. *Acta Palaeontologica Polonica*, 61 (3): 503-517. doi: [10.4202/app.00154.2015](https://doi.org/10.4202/app.00154.2015). (Manuskript II)

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cally higher sites yielded further new taxa based on associated skulls and shells. The excellent preservation of these specimens provides us with great insights into the plesiomorphic anatomy of crown-cryptodires, the most diverse group of living turtles, and, together with other Mesozoic taxa from the Junggar Basin, they are particularly relevant for understanding the origin and early divergence of the primary clades of extant turtles.

### The ultrastructural construction of Mesozoic ammonoid shell wall

[oral presentation]

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In the last decades, the ammonoid ventral and dorsal shell wall was part of multiple studies, but its ultrastructural construction still keeps some secrets and opportunities for future investigations. The examination of different taxa of Ceratitina (*Rudolfsruempiceras*), Lytoceratina (*Eotetragonites*, *Lobolytoceras*), Phylloceratina (*Calliphylloceras*, *Holcophylloceras*, *Euphylloceras*) and Ammonitina (*Desmoceras*, *Puzosia*, *Umsinenoceras*, *Neosilesites*, *Kranaosphinctes*, *Aspidoceras*, *Euaspidoceras*, *Pseudowaagenia*) proves this. The simple three-layered main shell of most ammonoids is modified in some taxa, e.g.: *Puzosia* develops a shell doubling at the umbilical corner and a high organic bearing outer prismatic layer. *Umsinenoceras* forms a weak relief out of the outer prismatic layer prior to the development of a wrinkle layer. The varices and constrictions of the Lytoceratina, Phylloceratina and Desmoceratids are formed by a thickening of the middle nacreous layer. Generally, no obvious discontinuity exists, but it seems that some nacreous lamellae wedge out. *Eotetragonites* is an exception with the formation of the constriction, a new generation of the outer prismatic layer is formed, which is shown in form of a discontinuity of the outer prismatic layer. It is well known that plan spiral ammonoids have a reduced dorsal shell, consisting only of the inner prismatic layer and sometimes an additional outer textured wrinkle layer. For the studied taxa, this opinion can be confirmed. But there are reasons that some other ammonoids develop a complete dorsal shell: so as local secondary formation in *Puzosia*'s shell or during late ontogeny of *Lobolytoceras* or *Kranaosphinctes*. This modality seems to be a general feature in the family Aspidoceratidae. These different shell structures may have the potential for phylogenetic interpretations.



## Complete dorsal ammonoid shell - A facultative character of phylogenetic importance?

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In the last decades, multiple studies focused on the structure of the ammonoid shell and established the image of a reduced dorsal shell within planispirally coiled ammonoids. Whereas ventral and lateral shell portions are generally constructed of three distinct shell layers (outer prismatic layer, median nacre layer, inner prismatic layer), the dorsal shell portions are constructed only by the inner prismatic layer, sometimes accompanied by a previously secreted organic wrinkle layer, which forms an outer component (see Birkelund 1980; Kulicki 1996; Kulicki et al. 2001).

This common conception must be aligned. It is already known that several heteromorphic taxa form a complete dorsal shell within their loosely coiled portions (e.g., *Lupprovia*, *Ptychoceras*, *Scaphites*; Doguzhaeva & Mikhailova 1982; Landman 1987; Doguzhaeva & Mutvei 1989). But studies on several planspiral lycoceratids (*Lobolytoceras*) and ammonites (*Amaltheus*, *Kosmoceras*, *Kranaosphinctes*, *Simbirskites*, *Euaspidoceras*, *Mirosphinctes*, *Aspidoceras*, *Pseudowaagenia*, *Puzosia*, *Douvilleicerias*) revealed nacreous structures of the dorsal shell, too. Within some taxa, dorsal nacreous shell material is restricted to local compensating structures like the relief of spines, which supports a secondary, optional formation of these structures. By contrast, a complete dorsal shell appears to be an aspect of (ongoing) ontogeny within several taxa: So *Lobolytoceras* and *Kranaosphinctes* developed a distinct nacreous layer only during late ontogeny ( $\emptyset > 20$  cm). A complete dorsal shell seems to be a general feature in the family Aspidoceratinae. Its development begins early in ontogeny ( $\emptyset < 3$  cm), where it is characteristically three-layered. Taxa of the sister taxon Peltoceratinae (*Peltoceratoides*) miss this feature. Therefore, the complete dorsal shell may have the potential for phylogenetic interpretations.

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## Continuous or discontinuous? - The ultrastructure of flares, parabolae, constrictions and varices within ammonoid shell

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The sculpture of ammonoid shells encloses a high variety of structures like ribs, nodes, keels, etc., which were formed during a more or less constant growth of the shell tube. But it also includes several shell morphologies, which are thought to represent certain growth halts, e.g. flares, parabolae, constrictions or varices (see Arkell et al. 1957; Bucher et al. 1996). The question is whether the internal structure actually reflects this assumption: Does a general functional morphologic construction exist or do different constructional concepts evolve, which need an individual interpretation? Ultrastructural observations show differences between these structures. A better understanding could be the key for palaeobiological or phylogenetic considerations. Indeed, flares of *Argonauticeras* (Lytoceratoidea) and parabolae of *Binatisphinctes* (Persphinctoidea) represent temporary growth halts. The outer shell portions (outer prismatic layer, nacreous layer) form a distinct interruption, which forms a distinct "breaking edge". At flares, it is bent outward. The edge of the primary shell generation is underlain by a new shell package, which proceeded to grow. The inner prismatic layer is unaffected, which denotes its subsequent formation. The overall appearance resembles a healed injury. During the formation of the new shell generation, a certain withdrawal of the mantle edge can be assumed. Sectioned shell material of the edge may show a certain shell resorption (Kohn et al. 1979) or controlled breakage. The general construction of constrictions misses a distinct interruption of shell layers within phylloceratids, perisphinctids and desmoceratids. The typical furrow of the shell surface is formed by an undulation of the outer prismatic layer. The often accompanied inner thickening is formed by the nacre layer, which forms the internal ridges of varices, too. Within these thickening, some outer nacreous lamellae may wedge out. The inner prismatic layer thins to compensate the inner relief. The absence of a distinct interruption of the shell argues against a long lasting growth halt but the formation of the nacre thickening probably denotes a slowing of shell formation with probable pauses in the deposition of nacre as indicated by its "internal interruption". *Eotetragonites*, a member of the Lytoceratoidea, forms a weak discontinuity in the outer prismatic layer at its constrictions. At the adoral edge of constrictions, a new generation of the outer prismatic layer is added from within. The remaining features, nacre thickening, thinning of inner prismatic layer, are similarly developed as in other constrictions (and varices) and seem to be formed subsequently. This interruption is probably related to the construction of the lytoceratid flares, which raises the question of a general "episodic" growth pattern accompanied in flared and constricted Lytoceratids.

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