Harvestmen (Arachnida: Opiliones) from Palaeogene European and mid-Cretaceous Burmese ambers as a model for evolution, palaeobiogeography and palaeoecology

Dissertation

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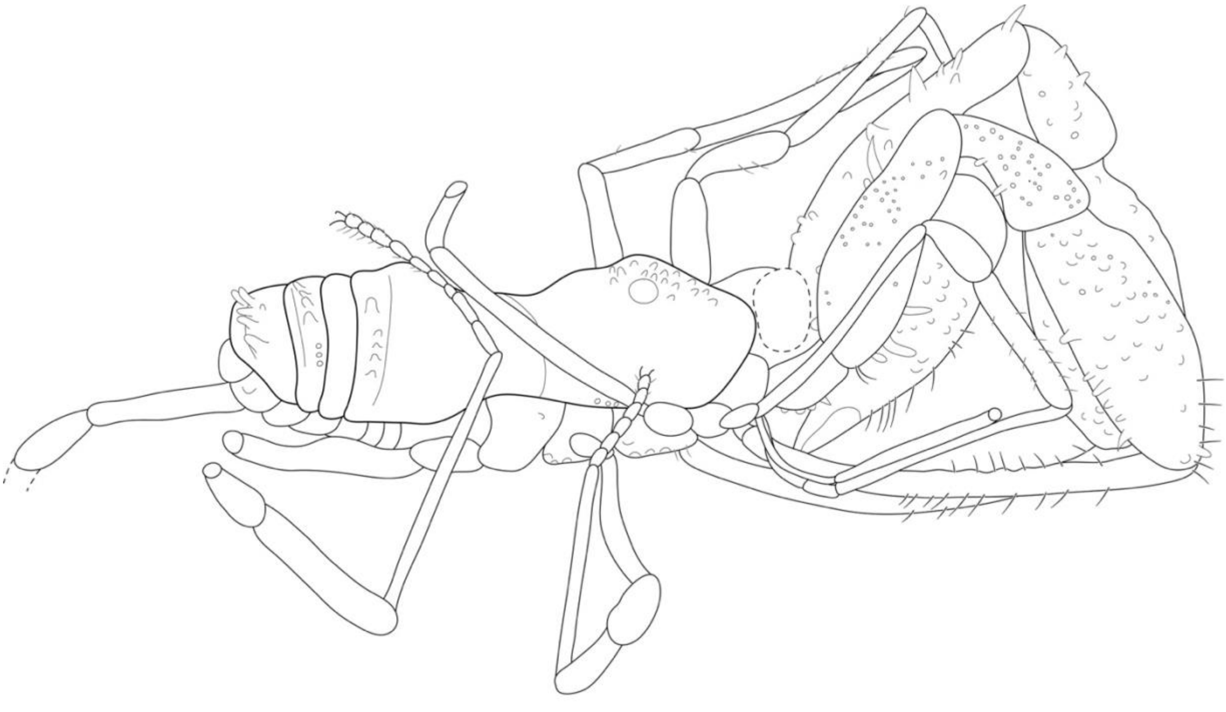

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Abstract

Harvestmen (Arachnida: Opiliones) represent the third most diverse order of arachnids following spiders (Araneae) and mites (Acari). Despite their modern species richness and importance for various ecosystems, fossils of this group are largely understudied. This also includes their evolutionary history, palaeobiogeography and palaeoecology. 156 harvestmen fossils were available for this thesis, which are mostly preserved as inclusions in Baltic (Late Eocene, Priabonian) and Burmese amber (mid-Cretaceous, Cenomanian-Albian).

Besides the description of new species, the main focus was to answer two palaeobiogeographical hypotheses: Is the Burmese fauna of Laurasian or Gondwanan origin? Does the European amber complex sample a Holarctic fauna?

The fossils were mainly examined with classical light microscopy but also with the help of micro-CT scans and then compared with their living relatives available in the literature and the collection of the Museum für Naturkunde, Berlin. 11 new fossil harvestmen species and 12 additional specimens from all four suborders (Laniatores, Eupnoi, Dyspnoi, Cyphophthalmi) are described in this thesis.

Of particular interest is the discovery and description of *Sirocellus iunctus* (Cyphophthalmi) from Burmese amber, the first dwarf harvestmen which combines characters from the families Sironidae and Stylocellidae, and thus represents a “missing link” between these two families. Based on this fossil, previous hypotheses regarding a Gondwanan origin of the Burmese amber fauna could be reconstructed and confirmed. *Tyrannobunus aculeus* (Eupnoi) is the first fossil of its suborder from Burmese amber and stands out because of its unusual body characters. Large eyes, a small but strongly armed body, spined legs and pedipalps and an undifferentiated penis indicate an early origin in the Eupnoi tree of life. Its very thin cuticle shows additionally an adaptation to humid and warm tropical climates. *Balticolasma wunderlichi* represents the first fossil from the subfamily Ortholasmatinae (Dyspnoi) and was described as a male from the Baltic and as a female from the Ukrainian Rovno amber. These ortholasmatine harvestmen only occur in North-Central America and in parts of Asia these days. This record shows once again that some groups of harvestmen were once widespread throughout the Holarctic during the Eocene and subsequently became extinct due to decreasing temperatures, at least in Europe.

The harvestmen fossils could be placed in the appropriate palaeoenvironmental context based on known reconstructions of the palaeoenvironment for the Burmese and European amber forests and on analogues to their extant relatives. The described fossil harvestmen species fit well in the proposed warm-temperate Baltic amber forests with a number of swamp and open habitats, and in the very humid and warm tropical Burmese amber forests.

All newly described fossils represent an important foundation for future phylogenetic studies, especially in the form of calibration points, which allows to calculate the origin of the individual groups more precisely. This in combination with the description of new fossils from other unexplored amber sources (e.g. Lebanese amber, African amber, Spanish amber) will further increase our knowledge of the evolution and palaeobiogeography of these animals.

Keywords: Arachnida, Opiliones, Cretaceous, Palaeogene

Kurzfassung

Weberknechte (Arachnida: Opiliones) repräsentieren nach den Webspinnen (Araneae) und Milben (Acari) die drittgrößte Ordnung der Spinnentiere. Trotz ihrer heutigen Artenvielfalt und Relevanz für die verschiedensten Ökosysteme sind Fossilien dieser Gruppe noch weitestgehend unerforscht. Dazu zählen auch ihre evolutionäre Geschichte, Paläobiogeographie und Paläoökologie. Für diese Dissertation standen 156 Weberknechtfossilien zur Verfügung, welche überwiegend als Inklusen in Baltischem (spätes Eozän, Priabonium) und Burmesischem Bernstein (mittlere Kreide, Cenomanium-Albium) erhalten sind.

Neben der Beschreibung neuer Arten stand die Beantwortung zweier Palaeobiogeographischer Hypothesen im Fokus: Ist die burmesische Fauna laurasischen oder gondwanischen Ursprungs? Enthält der europäische Bernsteinkomplex eine holarktische Fauna?

Die Fossilien wurden überwiegend mithilfe von klassischer Lichtmikroskopie aber auch anhand von Mikro-CT Scans untersucht und mit ihren lebenden Verwandten aus Literatur und der Sammlung des Museums für Naturkunde, Berlin verglichen. Diese Dissertation beschreibt u.a. 11 neue fossile Weberknechtarten und 12 zusätzliche fossile Weberknechte aus allen 4 Unterordnungen (Laniatores, Eupnoi, Dyspnoi, Cyphophthalmi).

Besonders hierbei ist die Entdeckung und Beschreibung von z.B. *Sirocellus iunctus* (Cyphophthalmi) aus Burmesischem Bernstein, dem ersten Zwergweberknecht, der Merkmale der Familien Sironidae und Stylocellidae vereint und somit einen „Missing Link“ zwischen diesen beiden Familien repräsentiert. Anhand dieses Fossils konnten vorherige Hypothesen bezüglich eines gondwanischen Ursprungs der burmesischen Fauna rekonstruiert und bestätigt werden. *Tyrannobunus aculeus* (Eupnoi) ist das erste Fossil seiner Unterordnung aus dem burmesischen Bernstein und sticht besonders aufgrund seiner ungewöhnlichen Körpermerkmale heraus. Große Augen, ein kleiner jedoch stark bewehrter Körper, stachelige Beine und Pedipalpen sowie ein undifferenzierter Penis weisen auf einen frühen Ursprung im Stammbaum der Eupnoi hin. Seine sehr dünne Cuticula zeigt außerdem eine Anpassung an feucht warme tropische Bedingungen. *Balticolasma wunderlichi* repräsentiert das erste Fossil aus der Unterfamilie Ortholasmatinae (Dyspnoi) und wurde als Männchen aus dem baltischen und als Weibchen aus dem ukrainischen Rovno Bernstein beschrieben. Diese Weberknechte leben heutzutage nur noch in Nord-Mittelamerika und in Teilen Asiens. Dieser Fund zeigt somit einmal mehr, dass einige Weberknechtgruppen während des Eozäns in der gesamten Holarktis verbreitet waren und nachfolgend aufgrund der sinkenden Temperaturen zumindest in Europa ausgestorben sind.

Die Fossilien konnten anhand von bekannten Rekonstruktionen der Paläoumwelt für die burmesischen und die europäischen Bernsteinwälder in den entsprechenden Paläoökologischen Kontext gesetzt werden basierend auf Analogien zu ihren heutigen Verwandten. Die beschriebenen fossilen Weberknechtarten passen gut in den warmgemäßigten Baltischen Bernsteinwald mit sumpfigen und offenen Habitaten, sowie in den sehr feuchtwarmen und tropischen Burmesischen Bernsteinwald.

Alle neu beschriebenen Fossilen bilden außerdem eine wichtige Grundlage für zukünftige phylogenetische Untersuchungen, insbesondere in Form von Kalibrierungspunkten, wodurch sich der Ursprung der einzelnen Gruppen genauer berechnen lässt. Dies in Kombination mit der Beschreibung von neuen Fossilien aus anderen unerforschten Bernsteinquellen (z.B. Libanesischer Bernstein, Afrikanischer Bernstein, Spanischer Bernstein) wird unser Wissen über die Evolution und Paläobiogeographie dieser Tiere zusätzlich erweitern.

Schlüsselwörter: Spinnentiere, Weberknechte, Kreide, Paläogen

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List of abbreviations used in the text and figures

ad = adenostyle
ap = anal plate/apophysis
bo = body
ca = corona analis
ch = chelicerae
cl = claw
cp = carapace process
cx = coxa
ey = eye lens
fe = femur
gl = glans
go = gonostome/genital opening
L = length
mt = metatarsus
oc = ocularium
op = opisthosoma
oz = ozophore
pa = patella
pe = penis
pp = pedipalp
sp = spiracle
st = stylus
ta = tarsus
tc = truncus
ti = tibia
tr = trochanter
W = width

1 Introduction

1.1 Preface

156 unstudied fossil harvestmen (Arachnida: Opiliones) in the mid-Cretaceous (98.79 ± 0.62 Ma) Burmese amber from Northern Myanmar (Kachin state) and in the Palaeogene (possibly Priabonian, 37.7–33.9 Ma) Baltic, Bitterfeld and Rovno ambers from Europe were available for this doctoral thesis. These derive mostly from the private collections of Patrick Müller (Zweibrücken, Germany), Jörg Wunderlich (Hirschberg, Germany) and Jonas Damzen (Vilnius, Lithuania), and also from the collections of the Senckenberg Museum Frankfurt am Main (Germany), the Natural History Museum of Geneva (Switzerland) and the Key Laboratory of Insect Evolution and Environmental Changes, at the College of Life Sciences and Academy for Multidisciplinary Studies, Capital Normal University (CNU) in Beijing (China). The newly described type material is now deposited in the Museum für Naturkunde, Berlin and in the Museum of Nature, Hamburg (Germany).

This doctoral thesis is mainly based on four peer-reviewed articles (Bartel & Dunlop, 2023; Bartel et al., 2022, 2023a, 2023c), which have all been published in different international scientific journals, as well as on two additional unpublished manuscripts. Most of these papers are dedicated to the description of new species across all four suborders from Burmese and Baltic amber. In addition to the taxonomy, the new fossils were put in the palaeobiogeographical and palaeoecological context.

In the first published manuscript “A new species of Laniatores (Arachnida: Opiliones) from Eocene Baltic amber with notes on the evolution of Insidiatores” only the second new Laniatores species from this deposit is described. Its extant relatives are in most cases blind and can usually be found in caves throughout Southern Europe. The fossil however, features a well-developed ocularium, which indicates that decreasing temperatures after the Eocene’s Thermal Maximum led to the use of caves as a refugial habitat where temperatures remained relatively stable. A second specimen, with potential characters similar to extant North American species, is described but not formally named due to its preservation. Nevertheless, it shows again that Baltic amber might contain a Holarctic fauna.

The second published manuscript “Four new Laniatorean harvestmen (Arachnida: Opiliones) from mid-Cretaceous Burmese amber” describes three new Laniatores species and one juvenile from the aforementioned deposit. The families Podoctidae and Petrobunidae were described for the first time in the fossil record. One more species could be added to the previously recorded family Epedanidae. Of particular interest is the juvenile, which shows typical claws for the infraorder Insidiatores. The latter is not known from Southeast Asia today and in combination with potential affinities to the superfamily Triaenonychoidea, this fossil might indicate a Gondwanan origin of the Burmese amber fauna.

The third published manuscript “An unexpected diversity of Cyphophthalmi (Arachnida: Opiliones) in Upper Cretaceous Burmese amber” describes ten fossils, five are recognised as new species. This more than doubles the fossil record of this group, as previously only three fossil species were known. One of the new fossils combines characters of the families Sironidae and Stylocellidae, and thus provides important insights into the biogeographical history of this group and the Burmese amber fauna in general. Two other fossils, with unknown familial affinities, show novel morphologies, which never have been observed within Cyphophthalmi before. Their ”pitted” bodies might represent a highly specialised adaptation to a semi aquatic lifestyle. This form of adaptation supports the tropical climate of the Burmese amber forests, as the habitat of these ground-dwelling specimens got potentially flooded quite frequently.

In the fourth published manuscript “The first eupnoid harvestmen (Arachnida: Opiliones: Eupnoi) from mid-Cretaceous Kachin amber, with notes on sexual dimorphism in *Halitherses grimaldii* (Arachnida: Opiliones: Dyspnoi)” a rather basal appearing Eupnoi fossil is described, which might be the common ancestor to the families Cadiddae, Sclerosomatidae and Phalangiidae based on its combination of characters. In addition, two possible phalangiids are recorded as the oldest fossils of this family together with a new specimen of *Halitherses grimaldii* with previously unknown apophyses on the second cheliceral segment, interpreted as sexual dimorphism typical for extant Dyspnoi.

The fifth manuscript “3D analyses of the first ortholasmatine harvestmen (Arachnida: Opiliones: Dyspnoi) from European Eocene ambers” has not been published yet but describes the first records for the subfamily Ortholasmatinae from Baltic and Rovno amber. The Baltic ortholasmatine was studied with the help of synchrotron micro-CT to reveal most of its characters despite the rather poor preservation. These European finds are significant as modern representatives of this subfamily are restricted to North America and parts of Asia.

The sixth and last manuscript included in this work “Palaeobiogeography and palaeoecology of harvestmen (Arachnida: Opiliones) in mid-Cretaceous Burmese and Palaeogene European ambers: A review” summarizes the latest knowledge on harvestmen preserved in amber based largely on the manuscripts above to reconstruct past origins, preferred habitats and possible extinction events.

1.2 Objectives

The main objectives of this work was to describe a significant number of new fossil harvestmen (species) from the available material, to gather new data on the diversity of extinct harvestmen and to build a foundation for evolutionary and palaeobiogeographical analyses and discussions presented in the current thesis and for the future research. The reason for this is that harvestmen are clearly underrepresented in the fossil record compared to other arachnids, in particular spiders. Before this work, there were only 51 fossil harvestmen species described compared to over 1400 fossil species of spiders (Dunlop et al., 2023). That means there are 27 times more spider than harvestman fossils described. This ratio is in strong contrast to the living animals, with ca. 51000 extant species of spiders and ca. 6600 extant species of harvestmen (8 times more spiders than harvestmen) (Kury et al., 2021b; World spider catalog, 2023).

The newly described fossil harvestmen species are used to further complete the harvestmen tree of life and to answer key biogeographical questions regarding the Burmese and European amber deposits: 1. Does the Burmese amber fauna originate from Laurasia or Gondwana? 2. Does European amber complex include a Holarctic fauna? Harvestmen are particularly suitable for reconstructing past distribution patterns, based on their old age of more than 400 million years and their low dispersal ability, which means that their evolution and distribution is largely based on vicariance (see e.g. Dunlop et al., 2003b; Giribet et al., 2012b).

1.3 Manuscripts

Since this work is a cumulative thesis, its content is largely based on four published and peer reviewed manuscripts, which can be found in chapters 3–6. Furthermore, two unpublished manuscripts, prepared for submission, are presented in chapters 7–8 to complete this work. The authors contribution to each of these manuscripts is given in percentage in table 1.1. Due to the shared framework of all manuscripts, recurring parts and repetitions are necessary.

Table 1.1. List of included manuscripts with the authors contribution in percentage.

Chapter	**Title & Authors**		**Journal & Status**
3	A new species of Laniatores (Arachnida: Opiliones) from Eocene Baltic amber with notes on the evolution of Insidiatores		Published in *Arachnologische Mitteilungen* (2022, open access) https://doi.org/10.30963/aramit6406
	Christian Bartel, Shahan Derkarabetian, Jason A. Dunlop		
	Contribution of C. Bartel:		
	Conception: 80%	Accomplishment: 85%	Publication: 70%
4	Four new Laniatorean harvestmen (Arachnida: Opiliones) from mid-Cretaceous Burmese amber		Published in *Palaeoworld* (online 08.07.2022) https://doi.org/10.1016/j.palwor.2022.06.006
	Christian Bartel, Jason A. Dunlop, Prashant P. Sharma, Paul A. Selden, Pavel E. Tarasov, Dong Ren, Chungkun Shih		
	Contribution of C. Bartel:		
	Conception: 80%	Accomplishment: 80%	Publication: 70%
5	An unexpected diversity of Cyphophthalmi (Arachnida: Opiliones) in Upper Cretaceous Burmese amber		Published in *Zootaxa* (2023) https://doi.org/10.11646/zootaxa.5296.3.6

	Christian Bartel, Jason A. Dunlop, Gonzalo Giribet		
	Contribution of C. Bartel:		
	Conception: 75%	Accomplishment: 80%	Publication: 60%
6	The first eupnoid harvestmen (Arachnida: Opiliones: Eupnoi) from mid-Cretaceous Kachin amber, with notes on sexual dimorphism in *Halitherses grimaldii* (Arachnida: Opiliones: Dyspnoi)		Published in *Palaeoentomology* (2023) https://doi.org/10.11646/palaeoentomology.6.3.11
	Christian Bartel & Jason A. Dunlop		
	Contribution of C. Bartel:		
	Conception: 80%	Accomplishment: 80%	Publication: 80%
7	3D analyses of the first ortholasmatine harvestmen (Arachnida: Opiliones: Dyspnoi) from European Eocene ambers		Prepared for submission in Acta Palaeontologica Polonica
	Christian Bartel, Plamen Mitov, Jason A. Dunlop, Jörg U. Hammel		
	Contribution of C. Bartel:		
	Conception: 60%	Accomplishment: 70%	Publication: 60%
8	Palaeobiogeography and palaeoecology of harvestmen (Arachnida: Opiliones) in mid-Cretaceous Burmese and Palaeogene European ambers: A review		Prepared for submission in Palaeo3
	Christian Bartel, Jason A. Dunlop, Eva-Maria Sadowski, Pavel E. Tarasov		
	Contribution of C. Bartel:		
	Conception: 80%	Accomplishment: 75%	Publication: 70%

1.4 Scientific background

1.4.1 Harvestman (Arachnida: Opiliones)

From the 11 extant orders of Arachnida, Opiliones represents the third most diverse following Acari (mites and ticks) and Araneae (spiders) with over 6600 described species (Kury et al., 2021b). The order Opiliones was proposed and named by Karl J. Sundevall in 1833 after the Latin word opilio, which can be translated as shepherd. This refers to ancient European shepherds who wandered on stilts, thus imitating the elevated body position of common harvestmen species (Machado et al., 2007).

Most harvestmen can easily be differentiated from other arachnids by the presence of a small circular body in combination with sometimes extremely long legs. Leg II often represents the longest of the four legs, as it is frequently used as an additional sensory organ. Furthermore all harvestmen are limited to two medial eye lenses often located on the so-called ocularium or ocular tubercle, compared to a higher number of eye lenses in e.g. spiders. Nevertheless, a significant number of harvestmen species can be found in caves and are thus blind (Curtis & Machado, 2007). Another unique character among arachnids, which can be observed in most harvestmen is the presence of a penis, sometimes also called spermatopositor (Shultz & Pinto-da-Rocha, 2007). The latter is one of the most important taxonomic characters and is often used to distinguish extant harvestmen on genus or even species level (e.g. Martens, 1978).

Another important aspect of harvestmen is their social behaviour. Large aggregations of multiple individuals occur frequently and provide several advantages in terms of reproduction, reducing water loss and protection from predators (Machado & Macías-Ordóñez, 2007). Additionally, all harvestmen can emit chemical secretions from their scent glands, which is also more effective in greater numbers (Gnaspini & Hara, 2007).

Despite their known limited dispersal ability harvestmen can be found today on all continents except Antarctica. Most of the extant fauna is concentrated in tropical areas of e.g. Southeast Asia and South America (Giribet & Kury, 2007). Due to their usually high preference for dark and humid places, individuals can often be found under rocks, in soil, moss and leaf litter or on trees. However, harvestmen in xeric environments or mountain and alpine habitats (in heights of up to 4000m) are also quite common (Curtis & Machado, 2007).

Harvestmen represent also one of the oldest arachnids. The oldest fossil *Eophalangium sheari* Dunlop et al., 2003b dates back to the Early Devonian and has already a quite modern appearance. The first fossils that can be associated with a living family (Sclerosomatidae) come from the Middle Jurassic of China (see Chapter 1.4.3). Extensive studies on fossil harvestmen began in the 19th century with a number of descriptions of fossils from Baltic amber by Koch & Berendt (1854) and Menge (1854). Further additions to the Baltic amber fauna were made by Roewer (1939). After that, it took over 60 years until the interest in fossil harvestmen reignited with studies from e.g. Starega (2002) and Dunlop (2006). In the following years 51 harvestmen fossils have been described in total, which represents a relatively small number compared to their modern diversity (Dunlop et al., 2023). The four extant suborders of Opiliones called Laniatores, Eupnoi, Dyspnoi, Cyphophthalmi and the known fossil record before this work are explained and summarized in more detail below.

1.4.2 Suborder Laniatores Thorell, 1876

This suborder is by far the most diverse with over 4100 living species in 1308 genera and 39 families (Kury et al., 2021b). Thus, it contains almost two-third of all harvestmen species. The presence of large and often heavily spined pedipalps in combination with well-developed body and leg armature leads to their common name armoured harvestmen. Additionally, the *scutum magnum* (dorsal tergites 1–5 fused, last three are free) condition is expressed in most families. All laniatoreans are further separated from the other suborders by two claws on legs III and IV, hence their German name „Krallenweberknecht". Two infraorders can be recognised based on the claw morphology. Insidiatores usually bear two claws with a single insertion (or a single claw with multiple prongs) and Grassatores bear two claws with two separate insertions (Shultz & Pinto-da-Rocha, 2007).

Figure 1.1. Examples of extant Laniatores. A) *Gnomulus* sp. (Sandokanidae); B*) Hoplodino continentalis* (Podoctidae); C) Cranaidae indet.; D) Epedanidae indet. Body length of each specimen ca. 2–5mm. All images were photographed by Nicky Bay (www.nickybay.com).

Sexual dimorphism in laniatoreans is also often strongly developed with potential differences in body size, form and length of the appendages and armature (Pinto-da-Rocha & Giribet, 2007). The largest diversity of this group can be found today in tropical or subtropical regions of the world, like South America or South East Asia. A noticeably smaller number of species inhabits the Holarctic and other parts of the world (except Antarctica) (Giribet & Kury, 2007). Most laniatoreans can frequently be observed on trees, under rocks, in leaf litter or in caves with specific adaptations for each habitat (such as longer legs or loss of eyes) (Curtis & Machado, 2007).

Despite the Devonian age of the first harvestmen, the evolutionary history of the suborder Laniatores can only be traced back to the mid-Cretaceous (Selden et al., 2016). *Petrobunoides sharmai* Selden et al., 2016 was the first Laniatores described from mid-Cretaceous Burmese amber. Six additional extinct species from the same amber source were later described by Bartel et al. (2021). These consist of: *Ellenbergellus tuberculatus* (Tithaeidae), *Mesokanus oehmkuehnlei* (Mesokanidae), *Biungulus xiai* (Epedanidae), *Gigantocheles nilsi* (Epedanidae), *Protopyramidops nalae* (Pyramidopidae) and *Palaeobeloniscus thilolebi* (Beloniscidae) (Bartel et al., 2021). All remaining Laniatores fossils are also amber inclusions. *Proholoscotolemon nemastomoides* Koch & Berendt, 1854 (redescribed by Ubick & Dunlop, 2005) is the only species described from Eocene Baltic amber. The youngest fossils were all found in Miocene Dominican amber and include:

Philacarus hispaniolensis Cokendolpher & Poinar, 1992, *Kimula* sp. Cokendolpher & Poinar, 1992, *Hummelinckiolus silhavyi* Cokendolpher & Poinar, 1998 and *Pellobunus proavus* Cokendolpher, 1987.

Phylogenetic studies of e.g. Sharma & Giribet (2011; 2014) and Fernández et al. (2017) with different approaches revealed a large time span between the Late Jurassic and the Early Devonian for the potential origin of Laniatores. The general lack of Palaeozoic fossils and the lack of Mesozoic fossils in phylogenetic studies so far presumably leads to this inaccuracy. Despite their presumably old age and their modern diversity, the fossil record remains very sparse with 12 described species prior to this work.

1.4.3 Suborder Eupnoi Hansen & Sørensen, 1904

The second largest suborder of harvestmen is called Eupnoi and contains 1806 living species in 244 genera and 7 families (Kury et al., 2021b). Furthermore, two superfamilies can be recognised, namely Caddoidea and Phalangioidea (Shear, 1982). Caddoidea includes a single family Caddidae and Phalangioidea another six families called Neopilionidae, Sclerosomatidae, Protolophidae, Monoscutidae and Phalangiidae. The family Phalangiidae contains most of the typical harvestmen species with a small rounded body and extremely long legs and Sclerosomatidae is the most diverse family of Opiliones with ca. 1270 species (Kury et al., 2021a). Another typical character of all Eupnoi is the presence of a rather small claw on the last pedipalp segment. This in combination with the already mentioned long legs, small body, lack of heavy body armature and a single claw on each leg, clearly differentiates them from the suborder Laniatores (Pinto-da-Rocha & Giribet, 2007).

Figure 1.2. Examples of extant Eupnoi. A) *Systenocentrus luteobiseriatus* (Sclerosomatidae, photo by Adriano B. Kury); B) *Megabunus diadema* (Phalangiidae, photo by Ludivine Lamare); C) *Caddo agilis* (Caddidae, photo by

Ryosuke Kuwahara); D) *Pantopsalis coronata* (Neopilionidae, photo by Steve Kerr). Body length of each specimen ca. 2–5mm. Images were taken from www.inaturalist.org.

Harvestmen from the suborder Eupnoi occur all over the world (except Antarctica) with large peaks in the Neotropics, Australasia and the Palearctic. Thus, their diversity in the Northern Hemisphere, especially in Europe, is much higher compared to laniatoreans (Giribet & Kury, 2007). The suborder Eupnoi also features the most extensive fossil record of Opiliones so far with 20 fossils from all three Eras. The oldest are *Brigantibunum listoni* Dunlop & Anderson, 2005, *Kustarachne tenuipes* Scudder, 1890 and *Macrogyion cronus* Garwood et al., 2011 from the Carboniferous of East Kirkton, Mazon Creek and the Montceau-les-Mines Lagerstätte, respectively. These are followed by *Mesobunus dunlopi* Giribet et al., 2012a, *Mesobunus martensi* Huang et al., 2009 and *Daohugopilio sheari* Huang et al., 2009 which were all found in the Jurassic of Daohugou, China. The Florissant fossil beds of the Late Eocene in Colorado revealed three further species: *Petrunkevitchiana oculata* Mello-Leitão, 1937, *Amauropilio atavus* (Cockerell, 1907) and *Amauropilio lacoei* (Petrunkevitch, 1922). Most of the remaining fossils are amber inclusions in Baltic, Bitterfeld and/or Rovno amber. *Amilenus deltshevi* Dunlop & Mitov, 2009, *Caddo dentipalpus* Koch & Berendt, 1854, *Dicranopalpus ramiger* Koch & Berendt, 1854, *Lacinius bizleyi* Mitov et al., 2015, *Stephanobunus mitovi* Dunlop & Mammitzsch, 2010, *Opilio ovalis* Koch & Berendt, 1854, *Leiobunum longipes* Menge, 1854, *Protolophus hoffeinsi* Elsaka et al., 2019 and *Eumesosoma abdelmawlai* Elsaka et al., 2019 were all found in Late Eocene Baltic amber. *Metaphalangium martensi* MItov et al., 2021 is currently restricted to Rovno amber. The youngest fossil *Cosmobunus sagani* Palencia et al., 2019 comes from Early Miocene lacustrine oil-shales of the Rubielos de Mora Basin in Spain. Sharma & Giribet (2014) estimated a divergence time for the Palpatores (Eupnoi + Dyspnoi) node of ca. 456.8 Ma via total evidence dating (using an independent gamma rates model), which creates a gap of more than 100 Ma until the first fossils.

1.4.4 Suborder Dyspnoi Hansen & Sørensen, 1904

Dyspnoi represents the third smallest suborder with only 409 species in 49 genera and 11 families (Kury et al., 2021b). All species lack a claw on the last pedipalp segment and are further known for typical apophyses on the male chelicerae or for complex structures on the ocular tubercle and/or body, best observed e.g. in the subfamily Ortholasmatinae (Shear, 2010; Pinto-da-Rocha & Giribet, 2007).

The suborder Dyspnoi is the only one which is predominantly restricted to the Northern Hemisphere with the subfamily Acropsopilionoidea being the only exception. Most of the species can be found in the western Palearctic with smaller peaks of diversity in East Asia and North America (Giribet & Kury, 2007).

Figure 1.3. Examples of extant Dyspnoi. A) *Nipponopsalis abei* (Nipponopsalididae, photo by Ryosuke Kuwahara); B) *Trogulus martensi* (Trogulidae, photo by Jörg Pageler); C) *Acropsopilio neozelandiae* (Acropsopilionidae, photo by Gonzalo Giribet); D) *Ceratolasma tricantha* (Ischyropsalididae, photo by Marshal Hedin). Body length of each specimen ca. 0.2–1cm. Images were taken from www.inaturalist.org.

The fossil record of Dyspnoi contains a relatively wide range of species from all three Eras compared to their rather low number of extant species. *Eotrogulus fayoli* Thevenin, 1901, *Nemastomoides elaveris* Thevenin, 1901, *Nemastomoides longipes* (Petrunkevitch, 1913), *Ameticos scolos* Garwood et al., 2011 and *Echinopustulatus samuelnelsoni* Dunlop, 2004b date back to the Carboniferous and are thus the oldest Dyspnoi fossils. The sole Mesozoic species is represented by *Halitherses grimaldii* Giribet & Dunlop, 2005 from mid-Cretaceous Burmese amber. Most of the Cenozoic species can again be found in Eocene Baltic amber, which includes *Piankhi steineri* Dunlop et al., 2012, *Sabacon claviger* (Menge, 1854), *Parahistricostoma tuberculatum* (Koch & Berendt, 1854), *Mitostoma denticulatum* (Koch & Berendt, 1854), *Mitostoma gruberi* Dunlop & Mitov, 2009, *?Nemastoma incertum* Koch & Berendt, 1854 and *Paragiljarovia hochae* Elsaka et al., 2019. One additional fossil from the Palaeogene was found in the Geiseltal, namely *Trogulus longipes* Haupt, 1956.

1.4.5 Suborder Cyphophthalmi Simon, 1879

Cyphophthalmi is the smallest living suborder with just 229 species in 40 genera and 6 families (Kury et al., 2021b). They are often called „dwarf harvestmen” or „mite harvestmen” due to their small size and resemblance to mites. These harvestmen have a unique appearance, as all members bear so-called ozophores, cone shaped structures on the anterior body. The latter mostly functions as a defensive mechanism in form of the opening for defensive glands or as an attachment point for the eyes (Shultz & Pinto-da-Rocha, 2007). The presence of a *scutum completum* (dorsal tergites 1–8 are fused) and short legs with a single claw further differentiates them from the other suborders (Pinto-da-Rocha & Giribet, 2007; Shultz & Pinto-da-Rocha, 2007).

Figure 1.4. Examples of living Cyphophthalmi. A) *Miopsalis* sp. (Stylocellidae, photo by Nicky Bay); B) *Siro rubens* (Sironidae, photo by Ludivine Lamare); C) *Rakaia* sp. (Pettalidae, photo by Gonzalo Giribet); D) *Troglosiro dogny* (Troglosironidae, photo by Gonzalo Giribet). Body length of each specimen ca. 1–3mm. Images were taken from www.nickybay.com and www.inaturalist.org.

The way of life is also different compared to most of the other harvestmen groups, as all Cyphophthalmi are predominantly soil- or cave-dwelling. Therefore, many species have reduced eyes or are completely blind (Pinto-da-Rocha & Giribet, 2007; Schwendinger et al., 2004).

Cyphophthalmi are distributed on all major landmasses (except Antarctica) and on most islands of continental origin. Interestingly, each of the six families is restricted to a specific biogeographic region. The family Sironidae inhabits former Laurasia, Pettalidae can only be found in former temperate Gondwana, Neogoveidae in tropical Gondwana, Troglosironidae in New Caledonia, Stylocellidae in Southeast Asia and Ogoveidae is restricted to the Gulf of Guinea in West Africa (Boyer et al., 2007; Giribet & Kury, 2007). This specific distribution combined with their low dispersal ability led to a number of studies explaining ancient biogeographic patterns (e.g. Clouse & Giribet, 2010; Stelbrink et al., 2012; Nattier et al., 2017). Their low modern diversity is reflected in a very sparse fossil record with only three fossils described from ambers. The oldest fossil *Palaeosiro burmanicum* Poinar, 2008 can just be traced back to the mid-Cretaceous Burmese amber. *Siro balticus* Dunlop & Mitov, 2011 from

Eocene Baltic amber and *Siro platypedibus* Dunlop & Giribet, 2003 from potentially Eocene or Oligocene Bitterfeld amber complete the list. Despite the small number of fossils, Oberski et al. (2018) was able to infer a potential Early Carboniferous (345 Ma) origin for Cyphophthalmi using the birth-death model with incomplete sampling.

1.4.6 Suborder Tetrophthalmi Garwood et al., 2014

Tetrophthalmi is an extinct suborder of Opiliones which accommodates two fossil species: the Devonian *Eophalangium sheari* Dunlop et al., 2003b and the Carboniferous *Hastocularis argus* Garwood et al., 2014. These crown-group harvestmen bore four eyes instead of two eyes found in all extant harvestmen. The additional lateral eyes supposedly sat on structures similar to the ozophores of Cyphophthalmi. Especially, *H. argus* shows a combination of Cyphophthalmi and Phalangida (Eupnoi+Dyspnoi+Laniatores) characters. The already mentioned ozophores, an open gonostome and a scutum completum are typical for Cyphophthalmi, while intromittent male genitalia, elongate legs with tarsomeres and an ocularium clearly indicate Phalangida (Laniatores+Eupnoi+Dyspnoi) affinities (Garwood et al., 2014).

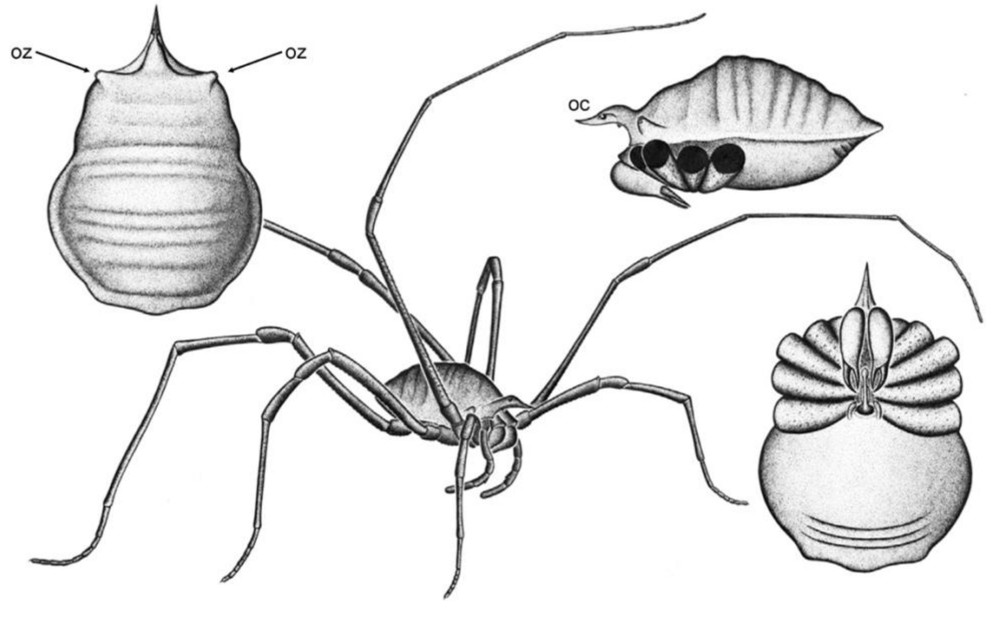

Figure 1.5. Reconstruction of *Hastocularis argus* Garwood et al., 2014. Ozophore-like structures with an eye lens are indicated by arrows. Abbreviations: oc, ocularium, oz, ozophore. Modified after Garwood et al., 2014.

1.4.7 Burmese amber

During the last two decades Burmese amber became the most important Lagerstätte for mid-Cretaceous terrestrial invertebrates. As of February 2023, 2524 species in 1622 genera and 702 families have been described from this source of fossilized tree resin (Ross, 2023). Most of the inclusions are arthropods, but dinosaur feathers (e.g. Xing et al., 2020), reptiles (e.g. Wang & Xing, 2020 and references therein) or marine animals like ammonites (Yu et al., 2019) were also found. One of the most important arachnid finds was the discovery of the tailed spider *Chimerarachne yingi* Wang et al., 2018.

The largest part of the amber-bearing material derives from the Hukawng Valley in the Kachin state of northern Myanmar. However, smaller amber-bearing outcrops from e.g. Hti Lin in the Magway Region and from Khamti in the Sagaing Region are also known (Sun et al., 2015; Nyunt et al., 2020). Most of the detailed geological analyses were done by Cruickshank & Ko (2003) and they often found the amber as discoid clasts or as runnels within clastic sedimentary rocks. These were dated by Shi et al. (2012) to an upper Albian–lower Cenomanian age (98.79 ± 0.62 Ma) based on U–Pb dating of zircons. During that time the Burma terrane was part of a Trans-Tethyan island arc with a near-equatorial southern latitude, suggested by Westerweel et al. (2019) based on palaeomagnetic studies.

Knowledge about the palaeohabitat is still relatively sparse, Grimaldi et al. (2002) proposed a tropical climate with temperatures between 32°C and 55°C. Schmidt et al. (2022) also inferred a tropical climate with high humidity, based on a number of *Selaginella* specimens. This is again supported by palaeoclimate reconstructions from Burgener et al. (2023).

The amber itself was probably produced by araucarian pines, which are related to the modern genus *Agathis* (Poinar et al., 2007). Angiosperms from the family Dipterocarpacae are also possible resin producers (Ross et al., 2010).

1.4.8 Baltic amber

Baltic amber represents one of the largest and most extensively studied amber deposits. Its variety of inclusions is already expressed in over 3000 described arthropod species in 1535 genera and 539 families (Weitschat & Wichard, 2010). Pieces of Baltic amber can be found from the southern coast of Great Britain up to the west coast of Russia. The largest mine, were amber is extracted since the end of the 19th Century, is located in the area of the Samland Peninsula in the Kaliningrad Oblast of Russia. Most of the amber-bearing material is obtained from the so-called „Blue Earth” layer, which consists of clayish, micaceous fine sands with a high concentration of glauconite (Weitschat & Wichard, 2010). These sediments were usually dated to a middle Eocene age of 41.3–47.8 Ma (Lutetian Stage) (Wolfe et al., 2016). However, in recent years many authors started to question this age because the material has potentially been reworked and proposed a younger Late Eocene age (i.e. Priabonian, 37.7–33.9 Ma) based on new palaeontological data from e.g. dinoflagellates and conifers (Iakovleva, 2017; Iakovleva et al., 2021; Sadowski et al., 2017a).

During the Eocene Europe was an archipelago and consisted of several landmasses. The probably more northerly located Baltic amber forest (Dunlop et al., 2018: fig. 1) has often been associated with a tropical or subtropical forest ecosystem (e.g. Weitschat & Wichard, 2010). Sadowski et al. (2017a) on the other hand, inferred a warm-temperate and humid climate, based on similarities of newly described conifer inclusions to extant North American and East Asian warm-temperate floras. Further habitat types present in the Baltic amber forests included lowland nearshore swamps influenced by brackish water, back swamps in floodplains and mixed mesophytic forests and meadows not affected by periodic flooding. (Sadowski et al., 2017a).

The resin producing tree(s) was also part of many debates over the last 150 years. After cedars and araucarians, Wolfe et al. (2009) suggested the umbrella pine (*Sciadopitys*) as a possible source tree. Sadowski et al. (2016) supported this after reporting the first unequivocal amber inclusion of this genus.

1.4.9 Rovno amber

After Baltic amber Rovno amber represents the second largest amber deposit of Europe. It is named after the homonymous province in North Western Ukraine (also known as Rivne). Over 292 families have been described from this amber source (Perkovsky et al., 2010). All amber-bearing deposits are located in the north-western margin of the Ukrainian Crystalline Shield. Most of the amber material derives from the so-called Obukhov and Mezhigorje Formations. Greenish grey and bluish grey sandy aleurites and glauconite-quarts dominate the Obukhov Formation, while the Mezhigorje Formation mostly consists of fine and medium-grained sands with somewhat clayey interlayers (Perkovsky et al., 2003).

For now, it is widely accepted that Rovno amber and Baltic amber are contemporary in age. However, both ambers have a different geochemical and faunal composition, suggesting a more southern origin of the Rovno amber (Mänd et al., 2018; Perkovsky, 2018).

1.4.10 Bitterfeld amber

Bitterfeld amber is the third largest amber deposit after Baltic and Rovno amber. Most of the amber material was mined between 1975–1995 in an open cast brown coal mine at Goitzsche, near Bitterfeld in Saxony-Anhalt (Germany). After that, the quarry was filled with water and transformed into a lake, which makes the appearance of new material very rare (Dunlop, 2010).

The amber-bearing material consists of silts and sands (also called „Bernsteinschluff") which are part of the Cottbus Formation (Fuhrmann, 2005). These sediments were dated to the Late Oligocene (Chattian 23–28.1 Ma) by Knuth et al. (2002), but the age is still being discussed as the amber material also become potentially reworked into younger layers (Dunlop et al., 2018).

It is still widely suggested that Bitterfeld amber represents a more southerly located outcrop of Baltic amber. Wolfe et al. (2016) showed that both ambers are geochemically different, but suggested at the same time a contemporary Eocene age. Bitterfeld amber shares many species with Baltic amber and also hosts a lot of endemic species, which might support the same age combined with a more southern distribution. However, more data needs to be collected to properly test this hypothesis (Dunlop et al., 2018).

2 Material and Methods

2.1 Analysed amber fossils

156 pieces of amber, which all include at least one harvestmen fossil, were available for this study. The largest part consists of Priabonian Baltic and mid-Cretaceous Burmese amber, followed by a single piece of Bitterfeld and Rovno amber each. These inclusions originate from the private collections of Patrick Müller (Zweibrücken, Germany, BUB), Jörg Wunderlich (Hirschberg, Germany, CJW) and Jonas Damzen (Vilnius, Lithuania, JDC), and also from the Senckenberg Museum, Frankfurt am Main (Germany), the Natural History Museum of Geneva (Switzerland) and the Key Laboratory of Insect Evolution and Environmental Changes, at the College of Life Sciences and Academy for Multidisciplinary Studies, Capital Normal University in Beijing (China). All of the Holotypes are now deposited in the Museum für Naturkunde, Berlin under the acronym MB.A (Museum Berlin Arthropoda), in the Geological-Palaeontological Institute and Museum of the University of Hamburg (GPIH) or in the Key Laboratory of Insect Evolution and Environmental Changes, at the College of Life Sciences and Academy for Multidisciplinary Studies, Capital Normal University (CNU).

All fossils were compared with extant harvestmen in the collection of the Museum für Naturkunde, Berlin and also with extinct and extant species available in the literature.

Measurements are given in mm.

2.2 Photographs and drawings

Fossils from Bartel et al., 2023a and 2023c were photographed using a Leica Z16 APO A Stereomicroscope running the software package Leica Application Suite. The remaining fossils were photographed with a Zeiss Discovery V8 and a Zeiss Axioscope 5 for small details. Stacks of 10–60 images were created at different focal planes during immersion of the amber pieces in water (to reduce reflections) and subsequently combined using Helicon Focus 7. Brightness and contrast corrections were made with Adobe Photoshop CS5/2022.

Photographs of the fossils MB.A.4453 (Figure 3.1A; 8.2B) and MB.A.4455 (Figure 7.4A, B; 7.5A; 8.2D) derive from Jonas Damzen and are used with his permission.

Drawings were first made with a pencil on a Leica M205C stereomicroscope with a camera lucida attachment (Fig. 2.1) and then digitally redrawn in Adobe Illustrator CS2/2022 using a Wacom Intuos graphic tablet. The latter step followed the methods of Coleman (2003, 2018). Comparative photographs of living harvestmen were reproduced from nickybay.com and inaturalist.org (both accessed on 15.08.23).

Figure 2.1. Leica M205C stereomicroscope with a camera lucida attachment (photo by Christian Bartel).

2.3 CT-Scans

Micro-CT scans of five Cyphophthalmi fossils from Bartel et al., 2023c were performed at the Museum für Naturkunde, Berlin by Kristin Mahlow using a Phoenix nanotom s X-ray tube (Fig. 2.2). 1440 images have been taken in total for each scan with 1000–1250 ms. Scans were created between 105–125 kV and 90–100 µA, depending on the size and preservation of the fossil. A range between 0.0017 and 0.003 mm was used for the effective voxel size.

The male ortholasmatine (MB.A.4454) from Bartel et al., 2023b was scanned by Jörg U. Hammel at the Imaging Beamline P05 operated by the Helmholtz-Zentrum Hereon at the storage ring PETRA III (Deutsches Elektronen Synchrotron DESY, Hamburg, Germany) using synchrotron radiation based computer microtomography (SRµCT). All datasets were rendered and segmented with VGSTUDIO MAX 3.4.3 at the Museum für Naturkunde, Berlin.

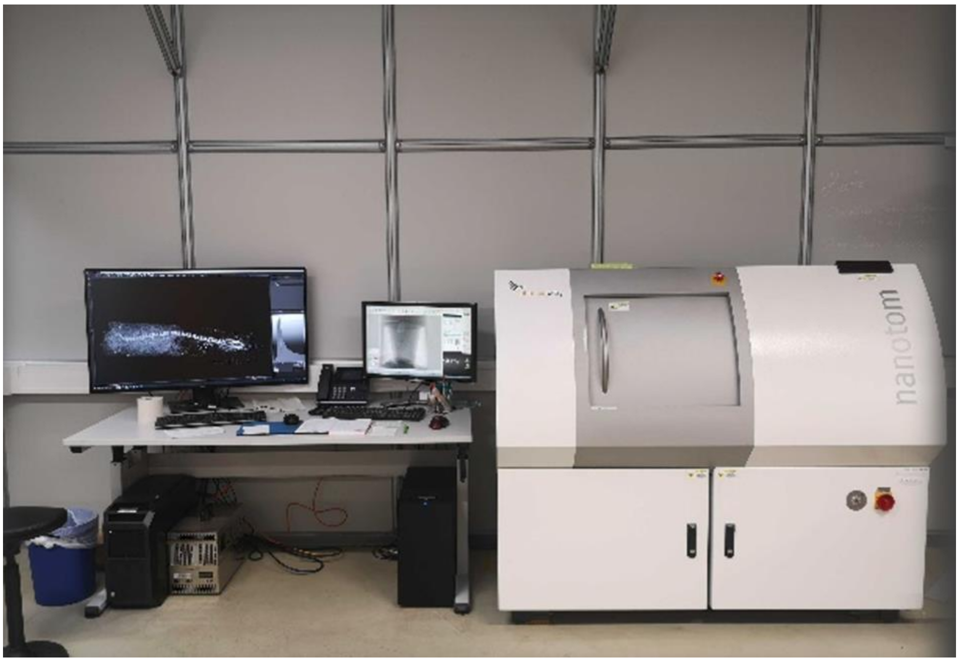

Figure 2.2. Micro-CT laboratory in the Museum für Naturkunde, Berlin (Photo by Kristin Mahlow, used with her permission).

3 A new species of Laniatores (Arachnida: Opiliones) from Eocene Baltic amber with notes on the evolution of Insidiatores

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3.1 Abstract

Two new laniatoreans from Eocene Baltic amber are described. *Baltonychia obscura* gen. et sp. nov. represents the first fossil Laniatores with a peltonychium on tarsus III–IV, implying that its closest living relatives are likely members of the extant families Cladonychiidae or Travuniidae. A second fossil is described as Insidiatores indet. as its preservation does not allow further assignment. Both fossils are substantially different to the so far only known Baltic amber laniatorean species *Proholoscotolemon nemastomoides* (Koch & Berendt, 1854), and suggest a more diverse Laniatores fauna in the Eocene of north-central Europe. The evolutionary history of the infraorder Insidiatores and their development into troglomorphic species is discussed.

3.2 Introduction

Of the four living suborders within the harvestmen (Arachnida: Opiliones), Laniatores is by far the most diverse today with over 4200 described species. In this sense, they represent almost two thirds of the total harvestman diversity (Kury, 2017; Kury et al., 2021b). The presence of large, raptorial pedipalps often combined with strongly developed body and/or leg armature, as well as two terminal (or single and branched) claws on legs III and IV, clearly distinguishes laniatoreans from the other three living harvestman suborders. Because of this ornamentation, they are also sometimes referred to as armoured harvestmen. Based on their claw morphology Laniatores can be further subdivided into two Infraorders: Insidiatores with a single claw on legs III and IV bearing smaller distal branches, and Grassatores with two claws on legs III and IV which have separate insertions (Shultz & Pinto-da-Rocha, 2007).

The largest part of the extant Laniatores fauna can be found today in tropical regions such as South and Central America or Southeast Asia. Holarctic laniatoreans are noticeably less species-rich and can usually be found under rocks and logs, leaf litter or in caves (Pinto-da-Rocha et al., 2007). Europe, in particular, is sparsely inhabited, with only a few species belonging to the relatively widespread families Cladonychiidae and Phalangodidae, and the rarer, more geographically restricted families Buemarinoidae and Travuniidae. European laniatoreans tend to be restricted today to more southern/Mediterranean regions across an area from northern Spain to Croatia (Derkarabetian et al., 2018); often from karst habitats, as reviewed by Ubick & Ozimec (2019 and references therein).

The modern diversity of Laniatores is not reflected in their current fossil record, presumably in part because of a lack of suitable fossil localities in regions where these animals are abundant today. Both molecular phylogenies (e.g. Sharma & Giribet, 2011) and the fossil records of the harvestman suborders Eupnoi and Dyspnoi, both of which are known from the Carboniferous (Garwood et al., 2011), predict that Laniatores should have been present in the Palaeozoic. However, the youngest records so far are mid-Cretaceous (Selden et al., 2016).

Fifteen fossil laniatorean species have been described in total and all of these are amber inclusions. Four are known from Miocene Dominican amber, one from Eocene Baltic amber and ten from mid-Cretaceous Burmese amber (Dunlop et al., 2020; Bartel et al., 2021, Bartel et al., 2023c and references therein). Here, we describe two new laniatorean fossils from European Baltic amber. Of the four families found in Europe today, Cladonychiidae has already been recorded (Ubick & Dunlop, 2005; Bartel & Dunlop, 2019), and we can now report the first Baltic amber Laniatores with a peltonychium. Thus, indicating potential affinities to the families Travuniidae or Cladonychiidae.

3.3 Material and methods

Two specimens from Eocene Baltic amber were available for study. One originates from the private collection of Jonas Damzen (Vilnius, Lithuania), the other from the private collection of Jörg Wunderlich (CJW; Hirschberg, Germany). The specimen from Jonas Damzen is now deposited in the Museum für Naturkunde, Berlin (repository number 4453) under the acronym MB.A. for Museum Berlin, Arthropoda.

Both inclusions were photographed using a Zeiss Axioscope 5 and a Zeiss Discovery V8. Stacks of 20–60 images were made at different focal planes and subsequently combined using Helicon Focus 7. Final corrections regarding brightness and contrast were made in Adobe Photoshop 2022. Interpretative pencil drawings were created using a Leica M205C stereomicroscope with a camera lucida attachment. Last, but not least, these were digitally redrawn following Coleman (2003, 2018) in Adobe Illustrator 2022 using a Wacom Intuos graphic tablet. The dorsal body of specimen MB.A.4453 (Fig. 3.1A) was photographed by Jonas Damzen and his original image is used with his permission. Since the drawings are not based on the photographs, there are some differences in orientation.

All measurements are given in mm and may be slight approximations due to the three-dimensional position of the amber specimens within the amber matrix. Both fossils were compared with extant laniatoreans available in the collection of the Museum für Naturkunde, Berlin, as well as with previously described fossil species (see Introduction).

3.4 Systematic Palaeontology

Order Opiliones Sundevall, 1833

Suborder Laniatores Thorell, 1876

Remarks. The fossils described herein can reliably be identified as members of the suborder Laniatores, mainly based on the presence of relatively large, raptorial pedipalps and their unique claw morphology (where visible). Potential familial affinities are separately discussed below.

Superfamily Travunioidea Absolon & Kratochvíl, 1932
Family Incertae sedis

Remarks. MB.A.4453 (Fig. 3.1A–D) probably represents a juvenile due to its rather small size and low tarsomere count. Nevertheless, the habitus and claw morphology of this specimen are of particular interest, as these are clearly different to the previously known Baltic amber species *Proholoscotolemon nemastomoides* (Koch & Berendt, 1854). Originally placed in a gonyleptid genus, this species was later transferred to an extant phalangodid genus, *Scotolemon* Lucas, 1861 by Staręga (1976, 2002), which makes more biogeographical sense for a Holarctic fossil (Lucas, 1861). It was formally redescribed, transferred to Cladonychiidae and assigned to an extinct genus by Ubick & Dunlop (2005). A juvenile assignable to this species was later documented by Bartel & Dunlop (2019), allowing some comparisons to be made across different developmental stages.

The body habitus of our new fossil is more subtrapezoidal compared to the more hourglass-shaped outline of *P. nemastomoides* (Fig. 3.1A–B). Additionally, the claws on legs III and IV of the new fossil are very different. In *P. nemastomoides* the claw bears two side branches on a single prong. By contrast, the new specimen bears a peltonychium with at least 3–4 side branches on each side (Fig. 3.1C–D). This arrangement is typical for some living members of the superfamily Travunioidea, especially in taxa that are highly troglomorphic cave obligates (see discussion in Derkarabetian et al., 2018). However, it should be noted that some Triaenonychoidea can express similar structures, for example *Picunchenops spelaeus* Maury, 1988 (Triaenonychidae) from Argentina, some *Lomanella* Pocock, 1903 (Lomanellidae) from Australia, and *Synthetonychia* Forster, 1954 (Synthetonychiidae) from New Zealand, although in the latter genus the structure was called a “synthetonychium” (Forster, 1954; Maury, 1988; Pocock, 1903; Hunt & Hickman, 1993). This convergence on the peltonychial form has been suggested to be a result of neotenic processes (Hunt & Hickman, 1993), although formal developmental studies have not been conducted.

An additional complication is the fact that the hind claws of most Insidiatores can be highly homoplastic at all taxonomic levels, even showing variation within the same species (Derkarabetian et al., 2018). Especially in the early stages of development, claws of different Insidiatores families can appear similar. For example, Briggs (1969: figs. 39–40) figured some claws of cladonychiid juveniles and among these the claws of *Erebomaster acanthina* Crosby & Bishop, 1924 which also somewhat resemble those of our fossil (Crosby & Bishop, 1924). However, the latter bears an additional arolium, typical for juveniles, which is absent in the amber specimen. Claws of juveniles without an arolium were figured by, e.g. Suzuki (1975: fig. 1A–D) for the Japanese genus *Yuria* Suzuki, 1964 (incertae sedis in Travunioidea; Derkarabetian et al., 2018), while adults have a peltonychium.

Given that the Opiliones fauna present in the Baltic (and Bitterfeld) amber deposits is unequivocally northern temperate in its affinities, the new amber specimen can be confidently assigned to either the superfamily Travunioidea or potentially Buemarinoidae (Insidiatores, Triaenonychoidea). The recently described relictual family Buemarinoidae Karaman, 2019 (Insidiatores, Triaenonychoidea) includes two species from caves in central Europe (Karaman, 2019). Adult buemarinoids do not possess a peltonychium, but juveniles of one European species for which juveniles were available, *Turonychus fadriquei* Derkarabetian, Prieto & Giribet, 2021, do possess a peltonychium (Derkarabetian et al., 2021). While Buemarinoidae is a possibility based on morphology, multiple reasons suggest why Travunioidea is more likely. First, in Europe travunioids occur at much higher latitudes than buemarinoids in the present day, which are restricted to caves in more arid regions of the Mediterranean (Spain and Sardinia). This difference in geographic distribution likely held through geologic time. Relatedly, and second, buemarinoids as a family are an ancient relictual lineage, composed of four geographically restricted monotypic genera found in the eastern United States (*Fumontana* Shear, 1977), Mediterranean (*Buemarinoa* Roewer, 1956 and *Turonychus* Derkarabetian, Prieto & Giribet, 2021) and Madagascar (*Flavonuncia* Lawrence, 1959) (Lawrence, 1959; Roewer, 1956; Shear, 1977; Derkarabetian et al., 2021).

Within Travunioidea, confidence at the family level decreases because it is possibly an immature specimen for which the most distinctive feature is a tarsal claw character. However, two families are clearly possible: Cladonychiidae, which today are widespread across the mountainous regions of central and southern Europe and Travuniidae, which are rare cave-obligate taxa currently found in the Balkan Peninsula of south-eastern Europe. Within the European Cladonychiidae, the fossil is more similar to the genus *Peltonychia* Roewer, 1935 (Roewer, 1935). *Peltonychia* possesses tarsal claws in the form of a peltonychium in adults, while *Holoscotolemon* Roewer, 1915 does not (Roewer, 1915). Important to note here is Roewer's drawing of a tarsal claw for a juvenile of *Peltonychia clavigera* Roewer, 1935 which clearly shows an arolium and is not in the form of a peltonychium (Roewer, 1935: fig. 3). Additionally, this fossil has small tubercles on the dorsal surface of the pedipalpal femur, similar to *Peltonychia*, while *Holoscotolemon* species tend to have more developed spines (Roewer, 1915). Multiple species of *Travunia* Absolon, 1920 (Travuniidae) were described as juveniles and possess a peltonychium (Absolon, 1920; Kratochvíl, 1937).

The new amber fossil could thus represent a lineage related, or ancestral to, the modern genus *Peltonychia*, or an ancestral surface-living Travuniidae, from a time prior to the family becoming restricted to cave habitats. Considering the homoplastic nature of the tarsal claw as a taxonomic character, the associated reluctance for modern opilionologists to rely on tarsal claw morphology, difficulty in assigning even some extant juveniles to genera, and the relative rarity of descriptions of juveniles in some taxa, assignment of this specimen to a family with confidence is difficult. As such, we leave this specimen at Travunioidea. Nevertheless, based on its unique appearance compared to *P. nemastomoides* and given its possibly ancestral status, we place this fossil in a new genus and species.

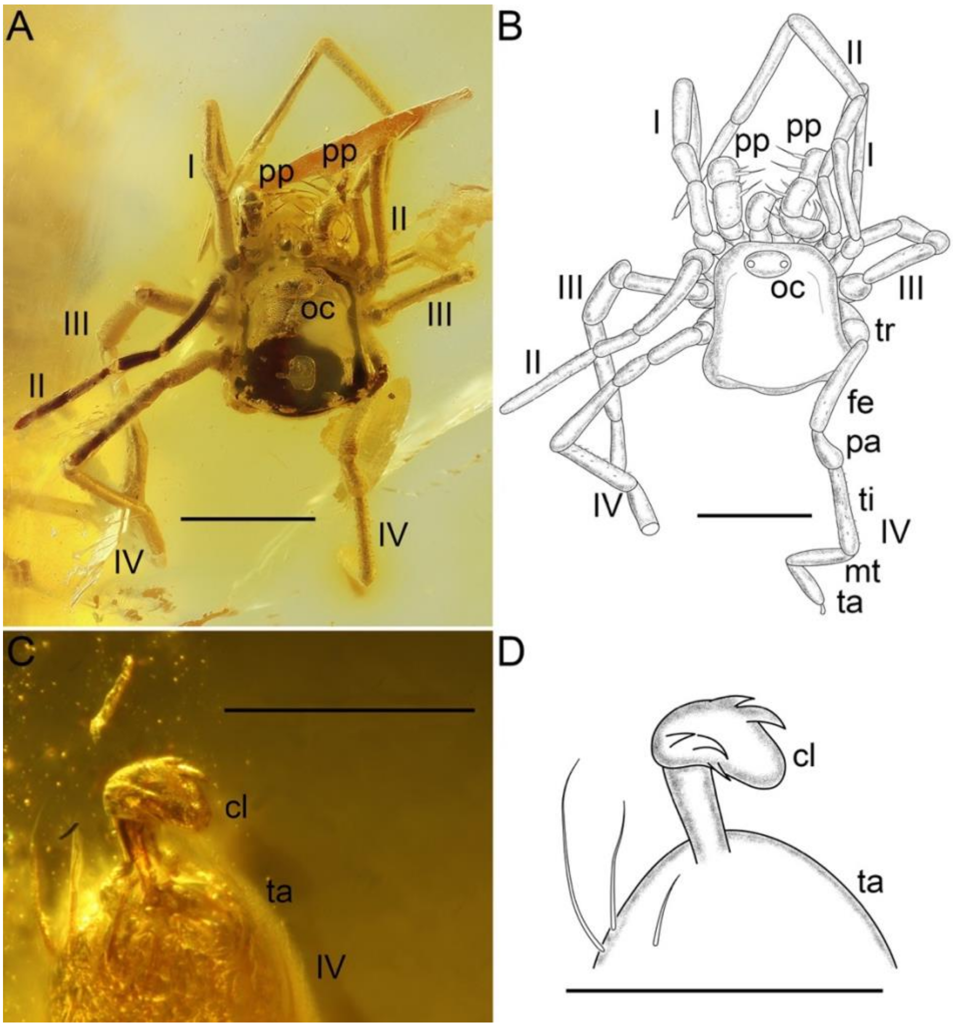

Figure 3.1. *Baltonychia obscura* gen. et sp. nov., holotype: MB.A.4453. A. Dorsal overview. B. Camera lucida drawing of A. C. Close-up of claw IV. D. Camera lucida drawing of C. Abbreviations: cl, claw; fe, femur; mt, metatarsus; oc, ocular tubercle; pa, patella; pp, pedipalp; ta, tarsus; ti, tibia; tr, trochanter. Legs numbered from I–IV. Scale bars equal 1mm (A, B) and 0.1mm (C, D).

***Baltonychia* gen. nov.**

urn:lsid:zoobank.org:act:46A5D55A-7E9C-4986-B30C- 5729596B9D9B

Type species. *Baltonychia obscura* gen. et sp. nov.

Etymology. Named after a combination from Baltic amber and the peltonychium.

Diagnosis. Can be distinguished from *Proholoscotolemon nemastomoides* Koch & Berendt, 1854 by a small subtrapezoidal body, a very large and wide ocular tubercle and by the presence of a peltonychium with at least 3–4 side branches on tarsus III–IV.

***Baltonychia obscura* gen. et sp. nov. (Fig. 3.1A–D)**

urn:lsid:zoobank.org:act:3BDBFE65-78FA-415F-934D- 76238E3518E9

Holotype. MB.A.4453 (ex coll. Jonas Damzen, JDC11158). Type-locality. Baltic amber. Palaeogene, Eocene (Late Lutetian–Early Priabonian).
Etymology. Named from the Latin adjective obscurus (obscure), which has probable Greek origin. It refers to its uncertain familial affinities. Gender feminine.
Diagnosis. As for the genus.

Description. Body subtrapezoidal and completely covered with fine granules dorsally, L 1.37, anterior W 1.09, maximum posterior W 1.35. Dorsal segments equivocal. Ocular tubercle very large and wide, oval and granulated, with lateral eye lenses, L 0.06, W 0.07. Ocular tubercle located near the anterior border. Chelicerae rather large and robust. Chelicerae proximal segment covered with at least three thicker setae. Chelicerae proximal segment L 0.35, chelicerae hand and fingers equivocal. Pedipalps longer than body, robust and raptorial. Pedipalp femur with two large ventral setiferous tubercles proximally, two mesal setiferous tubercles distally (a small one in front of a larger one) and one small ectal spine. Femur additionally cov- ered with a few tubercles. Pedipalp patella with two mesal setiferous tubercles (one of medium size and a large one) and one larger ventral spine. Patella also covered with tubercles, granules and two very small spines dorsally. Pedipalp tibia with two very large mesal setiferous tubercles and 1–2 ectal setiferous tubercles. Pedipalp tarsus with two smaller setiferous tubercles distally and 1–2 larger setiferous tubercles proximally on each side. Tarsus ends in a somewhat curved claw, L 0.14. Pedipalp length: tr 0.12, fe 0.46, pa 0.37, ti 0.30, ta 0.23, total (tr–ta) 1.48. Legs moderately long (leg II longest) and granulated. Leg tibiae I–IV with larger sometimes setiferous granules. Leg tarsi I–IV potentially subdivided, all ending in a single claw. Claw III and IV modified in form of a peltonychium with at least 3–4 side branches on each side of the median prong. Tarsal formula: 2+;2+;1–2;1–2. Leg length: Leg I cx ?, tr 0.21, fe 0.51, pa 0.37, ti 0.58, mt 0.74, ta 0.66, total (tr–ta) 3.07; Leg II cx ?, tr 0.26, fe 0.93, pa 0.42, ti 0.93, mt 1.00, ta 1.05, total (tr–ta) 4.59; Leg III cx ?, tr 0.23, fe 0.72, pa 0.28, ti 0.67, mt 0.98, ta 0.91, total (tr–ta) 3.79; Leg IV cx ?, tr 0.21, fe 0.93, pa 0.35, ti 0.81, mt 0.70, ta 0.58, total (tr–ta) 3.58.
Ventral characters obscured.

Family Insidiatores indet.

Remarks. CJW BBF2290 (Fig. 3.2A–D) could be an adult or the penultimate instar of a laniatorean, as the body is relatively large and the pedipalps seem to be well developed. The habitus of this fossil, with its strongly-armed pedipalps, is similar to modern members of the superfamily Travunioidea and to the previously known Baltic amber species

Proholoscotolemon nemastomoides. The latter bears a comparable number of spines on the pedipalp, femur and patella, but its body appears to be more hourglass-shaped than the body of this new fossil (Bartel & Dunlop, 2019). Unfortunately, most of the important characters, like the number of leg tarsomeres or the claw morphology, are not preserved in this new amber specimen and thus it is not possible to properly ascertain its affinities. Nevertheless, we suggest the possibility that this fossil could represent a new species of Baltic amber laniatorean, due to the fact that its body appears to be more compact and more granulated. This in turn might indicate a closer relationship to modern members of the family Paranonychidae, the European cladonychiid genus *Peltonychia* or even to American genera within Cladonychiidae and Cryptomastridae. For now, we refer the fossil to Insidiatores indet. and offer a short description which can be used for comparison in future studies.

Material. CJW BBF2290 from Baltic amber. Palaeogene, Eocene (Late Lutetian–Early Priabonian).

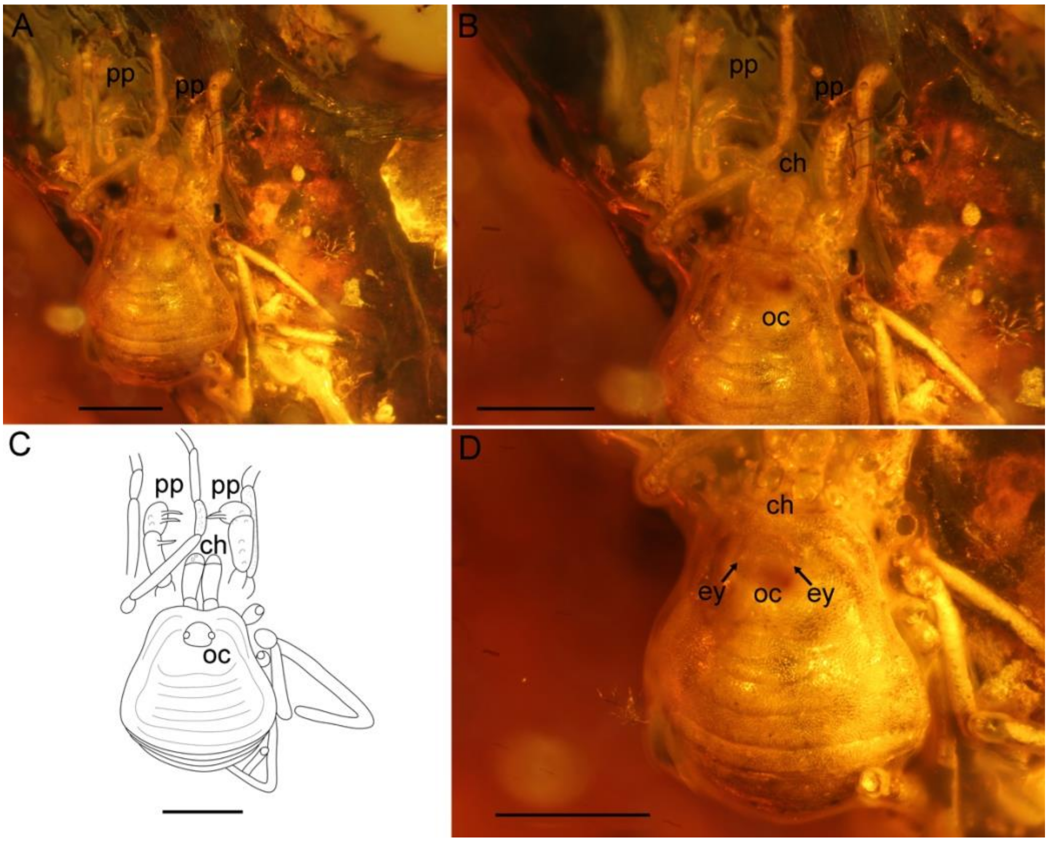

Figure 3.2. Insidiatores indet., CJW BBF2290. A. Dorsal overview. B. Close up of the chelicerae and pedipalps in dorsal view. C. Camera lucida drawing of A. D. Close-up of the dorsal body, eye lenses arrowed. Abbreviations: ch, chelicerae; ey, eye lens; oc, ocular tubercle; pp, pedipalp. Scale bars equal 1mm.

Description. Body pear-shaped and completely granulated dorsally, L 2.07, anterior W 1.36, maximum posterior W 1.96. Dorsal segments fused into scutum magnum. Rounded and relatively low ocular tubercle removed from the anterior border with lateral eye lenses, L 0.33, W 0.36, eye lens diameter 0.06. Chelicerae moderately large and sparsely covered with tubercles on the proximal segment. Chelicerae proximal segment L 0.43. Pedipalps robust and raptorial. Pedipalp femur bearing larger tubercles and 1–2 large mesal spines distally. Pedipalp patella also bearing a large tubercle and two mesal spines. Pedipalp length: fe 0.73, pa 0.40, ti ?, ta ?. Legs incomplete, relatively long, rather slender and sparsely granulated. Claws not visible. Ventral characters equivocal.

3.5 Discussion

Fossil laniatoreans in Baltic amber are extremely rare and only a few specimens have been formally described (Koch & Berendt, 1854; Ubick & Dunlop, 2005; Bartel & Dunlop, 2019; this study). At the same time, they have considerable potential to reveal new insights into the evolution and biogeographical history of this otherwise predominantly tropical harvestman suborder. The infraorder Insidiatores is of particular interest as its two superfamilies, Travunioidea and Triaenonychoidea (minus the relictual Buemarinoidae), have a disjunct distribution today being found in the temperate regions of the northern and southern hemispheres respectively (Derkarabetian et al., 2018, 2021). As noted above, all Baltic amber laniatoreans appear to be travunioids which would be expected from a biogeographical perspective and indicates that the superfamily was present in Europe by at least the Eocene. The sparse modern Laniatores fauna of Europe adds further impetus to the importance of analysing fossil specimens. Even allowing for some tectonic shifts since the Eocene, Baltic amber was deposited further north than the distribution ranges of any modern European Laniatores. A similar situation has been observed in mite harvestmen (the suborder Cyphophthalmi) which are found in more southern parts of Europe today, but at one stage occurred further north as indicated by their presence in both Bitterfeld (Dunlop & Giribet, 2003) and Baltic amber (Dunlop & Mitov, 2011). Among other arachnids, Baltic amber camel spiders (Solifugae) also occurred further north than the European distribution ranges of their living relatives (Dunlop et al., 2003a; Dunlop & Klann, 2009) and some genera of pseudoscorpions (Pseudoscorpiones) found in European ambers are restricted today to the Mediterranean basin (Harms & Dunlop, 2017).

The Eocene climate of northern Europe is also presumed to have been somewhat warmer than today, albeit not tropical, which may have allowed many groups to be more widespread in Europe at this time (Sadowski et al., 2017a). Repopulation of the more northern regions of Europe can be observed in many extant arachnid taxa like e.g. the European wasp spider, *Argiope bruennichi* (Scopoli, 1772) and the venomous yellow sac spider *Cheiracanthium punctorium* Villers, 1789 (Krehen- winkel & Tautz, 2013; Krehenwinkel et al., 2016). This phenomenon can also be observed in *Trichonephila sexpunctata* (Giebel, 1867), which is restricted to south-western South America (Bartoleti et al., 2017; Giebel, 1867). The reasons for these range expansions are manifold. The ongoing global warming and adaptive genetic changes contribute only partially to this very complex system, as discussed in more detail by Krehenwinkel et al. (2016).

Both newly described fossils demonstrate that the Laniatores fauna of Europe during the Eocene was more diverse than the single species described by Koch & Berendt (1854). Especially, *Baltonychia obscura* gen. et sp. nov., might reveal new information about the evolutionary history of European Insidiatores, despite its enigmatic familial affinities. If the fossil represents an ancestral form of the family Travuniidae, it could indicate that early members of this family lived outside of caves and retained a well-developed ocularium. Decreasing global temperatures after the Eocene may have led to a range shift towards today's more southern distribution, while some lineages might have adapted to caves as a new, possibly refugial, habitat. In fact, Travunioidea are well represented in caves, with seven genera being entirely cave-obligate, and multiple genera including both surface and cave-adapted species or populations where cave invasion and subsequent adaptation can be a common phenomenon (e.g. Derkarabetian et al., 2010).

The assignment of fossil F2290 is less clear. However, its affinities could lie with one of the extant North American laniatorean genera based on its overall habitus; a distribution pattern which already has precedent among the harvestmen. In a wider sense, Baltic amber seems to preserve an essentially Holarctic harvestman fauna, potentially supported by the presence of putative land bridges allowing migration between North America and Eurasia after the Cretaceous, evidence for which has been published for vertebrates and plants (see e.g. Bai et al., 2018; Graham, 2018). Already known examples of harvestmen found in Baltic amber that are restricted today to East Asia and/or North America include the genera *Caddo* Banks, 1892, *Eumesosoma* Cokendolpher, 1980 and *Protolophus* Banks, 1893 (see e.g. Elsaka et al., 2019). Further fossil laniatorean specimens preserving more somatic characters would undoubtedly help to test these hypotheses and perhaps contribute towards a reconstruction of the evolutionary history of Laniatores in Europe.

3.6 Acknowledgements

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4 Four new Laniatorean harvestmen (Arachnida: Opiliones) from mid-Cretaceous Burmese amber

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5 An unexpected diversity of Cyphophthalmi (Arachnida: Opiliones) in Upper Cretaceous Burmese amber

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5.1 Abstract

Ten new Cyphophthalmi specimens (Arachnida: Opiliones) from the Upper Cretaceous (Lower Cenomanian) Burmese amber of northern Myanmar are described. Seven of these are placed in Stylocellidae, the predominant extant family found today in Southeast Asia. *Sirocellus iunctus* gen. et sp. nov. represents the first fossil with a combination of sironid and stylocellid characters, suggesting a still ongoing transition in some lineages during the Upper Cretaceous. *Mesopsalis oblongus* gen. et sp. nov. represents a second fossil with elongated ozophores, a character not known from modern species. *Leptopsalis breyeri* sp. nov. is the first Cretaceous cyphophthalmid assignable to an extant genus. The species *Foveacorpus cretaceus* gen. et sp. nov. and *F. parvus* gen. et sp. nov., which cannot be placed in an extant family, show morphological novelties for Cyphophthalmi such as numerous pits covering the whole body. The possible function of these pits is discussed. Three more adult males with unique adenostyles and two juveniles are not formally named but further indicate an already highly diverse cyphophthalmid fauna during the Cretaceous. The total number of named Burmese amber Cyphophthalmi species is raised from one to six, and the total fossil record for this suborder now stands at eight.

5.2 Introduction

Cyphophthalmi represents one of the oldest (e.g., Fernández et al., 2017), and at the same time the least diverse extant suborder of Opiliones with 243 living species in 6 families (Giribet, 2020; Kury et al., 2021a). They are often described as small to medium-sized arachnids with a scutum completum (i.e. the carapace and most opisthosomal tergites are fused) and short legs. In this sense Cyphophthalmi superficially resemble certain mites, hence the common name “mite-harvestmen”. Additionally, many species are blind, as they typically inhabit soil, leaf-litter or caves (e.g. Pinto-da-Rocha et al., 2007). During the last two decades Cyphophthalmi were used as model taxa for biogeographical analyses, due to their worldwide distribution on all major continental landmasses except Antarctica, and on most islands of continental origin. This, combined with their low dispersal ability and the fact that each of the six families is restricted to a well-defined biogeographical region (see e.g. Boyer et al., 2007; Giribet et al., 2012b and references therein), have made Cyphophthalmi a paradigm group to explain ancient biogeographic patterns (e.g. Stelbrink et al., 2012; Nattier et al., 2017).

Oberski et al., (2018) inferred an early Carboniferous (345 Ma, 95% HPD [highest posterior density]: 312–373 Ma) origin for Cyphophthalmi using the birth-death model with incomplete sampling. Nevertheless, the fossil record of Cyphophthalmi is sparse, with so far only three described species and no fossils older than the Cretaceous. *Siro platypedibus* Dunlop & Giribet, 2003 is the first described cyphophthalmid fossil and it comes from the German Bitterfeld amber which goes back to the Eocene or Oligocene. It was placed in the family Sironidae, which is distributed today across the northern hemisphere. The second discovery was *Palaeosiro burmanicum* Poinar, 2008 from Upper Cretaceous (ca. 99 Ma) Burmese amber. It was originally also placed in the Sironidae, however Giribet et al. (2012) reinterpreted this fossil as a stylocellid, which better matches the modern Southeast Asian distribution of this family. *Siro balticus* Dunlop & Mitov, 2011 from Eocene (ca. 45–49 Ma) Baltic amber was the latest addition to the cyphophthalmid fossil record and was again assigned to the Sironidae.

Additional Cyphophthalmi (especially putative stylocellids) in Burmese amber are known and were reported in, for example, the unpublished master thesis of Friedrich (2015) as well as by Balashov (2021: fig. 2). These are available for future studies. Here we describe ten new cyphophthalmid fossils from Upper Cretaceous Burmese amber from which we name five new species.

5.3 Material and Methods

Ten specimens from Upper Cretaceous Burmese amber were available for study. Seven originate from the private collection of Patrick Müller (BUB, Burmesischer Bernstein) and three from the private collection of Jörg Wunderlich. All types are now deposited in the Geological-Palaeontological Institute and Museum of the University of Hamburg (GPIH) and in the Museum für Naturkunde, Berlin (MB) under repository numbers GPIH05128–GPIH05130 and MB.A.4456–MB.A.4457. The remaining unnamed fossils will be deposited in the private collections of the respective collector for the time being. Some specimens are very well preserved, others are partly desiccated, covered by bubbles, detritus, fractures or crystalline growth. Additionally, some specimens are missing body parts such as leg articles. Multiple syninclusions like insects or other arachnids are also included in the amber matrix.

A Leica Z16 APO A stereomicroscope running the software package Leica Application Suite was used to photograph the specimens, generating stacks of 15–20 images, while the amber was immersed in water to reduce reflections. These images were combined using Helicon Focus 6 and corrected for brightness and contrast using Adobe Photoshop CS5. Computer-aided illustrations were created from camera lucida drawings following the methods of Coleman (2003) with Adobe Illustrator CS2 and Adobe Photoshop 6.0 using a Wacom Intuos graphic tablet. All measurements are in mm and are slight approximations due to the three-dimensional position of the specimens in the amber matrix. Average values are marked with asterisks.

Micro-CT scans of five specimens were performed at the Museum für Naturkunde, Berlin using a Phoenix nanotom X-ray tube. A total of 1440 images were taken for each scan with 1000–1250 ms. Scans were made between 105–125 kV and 90–100 µA, depending on the specimen. Effective voxel size ranged between 0.0017 and 0.003 mm. VGSTUDIO MAX 3.4.3 was used to render and segment datasets.

Interpretation of the ozophores (types 1, 2 or 3) and body surface microstructure follow Juberthie (1970) and Murphree (1988), respectively. The new inclusions were compared with extant Cyphophthalmi available in the collections of the Museum für Naturkunde, Berlin, and in the Museum of Comparative Zoology, Cambridge, as well as with previously described fossil taxa (Dunlop & Giribet, 2003; Poinar, 2008; Dunlop & Mitov, 2011). The material described herein was collected before 2017 and thus before the current conflict in Myanmar started. Abbreviations: fe femur, L length, mt metatarsus, pa patella, pp pedipalp, ta tarsus, ti tibia, tr trochanter, W width.

5.3.1 Burmese amber

Burmese amber represents one of the most important deposits of Upper Cretaceous terrestrial invertebrates. So far, 2524 species in 1622 genera and 702 families have been described (as of April 2023). Most of the inclusions are arthropods, representing 2349 described species. Vertebrates such as reptiles, birds or dinosaurs and occasional marine animals like bivalves or ammonites have also been discovered as inclusions (Ross, 2023 and references therein). The arachnid fauna of Burmese amber has been summarized by Selden & Ren (2017). A large part of the amber-bearing material derives from the Hukawng Valley in the Kachin State of northern Myanmar were “Burmite” has been mined for over two millennia. The amber itself is often found as discoid clasts or as runnels within clastic sedimentary rocks (see Cruickshank & Ko 2003 for a detailed geological overview). Palaeomagnetic studies by Westerweel et al. (2019) suggest that during the Upper Cretaceous the Burma terrane was part of a Trans-Tethyan island arc with a near-equatorial southern latitude. Many authors assume an Upper Albian–Lower Cenomanian age based on e.g. U-Pb dating of zircons, bivalve borings and an ammonite trapped in amber (Shi et al., 2012; Smith & Ross, 2018; Yu et al., 2019). The resin from which the amber is derived was possibly produced by trees of the family Araucariaceae (Poinar et al., 2007).

5.4 Systematic Palaeontology

Order Opiliones Sundevall, 1833

Suborder Cyphophthalmi Simon, 1879

Remarks. All specimens described here can be unequivocally identified as members of the opilionid suborder Cyphophthalmi due to the presence of (1) a scutum completum, (2) raised ozophores and (3) a single claw on each tarsus of all legs. The modern families Neogoveidae and Troglosironidae can be excluded from the outset as none of the amber specimens feature a row of ventral teeth on the claw of leg II. Due to their restrictive modern day distribution we assume the affinities of the amber specimens to lie with Stylocellidae, which is the main extant cyphophthalmid family in Southeast Asia today. However, extant Pettalidae are found in Sri Lanka (and on the southern continents) and may have been previously distributed across the Indian subcontinent. Ogoveidae is today restricted to West Africa (Giribet & Prieto, 2003). We want to point out that Burmese amber has been shown to contain some groups that are typically Gondwanan, as well as taxa found today in the Neo- or Afrotropics but not in Southeast Asia. Examples belonging to arachnids include some Laniatorean harvestmen (Bartel et al., 2021) and the rare arachnid order Ricinulei (Wunderlich, 2017). The cyphophthalmid family Sironidae is distributed across former Laurasian terranes (North America, Europe, the near East and Japan) and could potentially have inhabited other Asian regions which were in contact with the Sibumasu terrane during the Cretaceous (Clouse et al., 2010; Metcalfe, 2017). Therefore the remaining cyphophthalmid families Pettalidae, Ogoveidae and Sironidae should not a priori be excluded. Furthermore, all amber specimens examined herein appear to differ from the first described Burmese amber species *Palaeosiro burmanicum*. The fossil described by Poinar (2008) features relatively long ozophores in comparison with its small body size, circular spiracles and a large sternal gland on the first sternite: a unique combination of characters not seen in our new material.

Family Stylocellidae Hansen & Sørensen, 1904

Genus *Sirocellus* gen. nov.

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Type species. *Sirocellus iunctus* sp. nov.

Etymology. A combination of the names of the modern genera *Siro* and *Stylocellus*. Masculine in gender.

Diagnosis. Body oval, completely granular dorsally as well as ventrally. Almost conical ozophores in the type 2 position. Chelicerae long and mostly smooth, with just a few granules or tubercles. Pedipalps long and rather thin. Legs robust and with a granular surface. Leg tarsi not subdivided, bearing a single smooth claw. Tarsus IV in males proximally with a large lamelliform adenostyle.

Remarks. Specimen GPIH05128 (Fig. 5.1) is recognized as an adult male due to the presence of an adenostyle on tarsus IV (Fig. 5.1C) and due to the high degree of body sclerotization. The families Ogoveidae and Pettalidae can be excluded, in this case due to the absence of a large opisthosomal apophysis on the second sternite and of a modified anal region. The subtriangular anterior part of the body in combination with type 2 ozophores (Fig.

5.1C, D) is also found in modern members of the family Stylocellidae. However, a large lamelliform adenostyle situated proximally is not known from modern stylocellid genera. There it is often described as fringed or plumose and it is situated near the middle of the tarsus. The form and position of the adenostyle is in fact more alike those of most modern sironids or neogoveids, but this could be a plesiomorphic character for Cyphophthalmi not found in extant stylocellids. We choose to place this fossil in the family Stylocellidae, which better fits the biogeographic distribution of the family and corresponds with the overall habitus of the specimen. This fossil is, however, placed in a new genus due to its unique adenostyle in combination with other characters which are otherwise stylocellid-like.

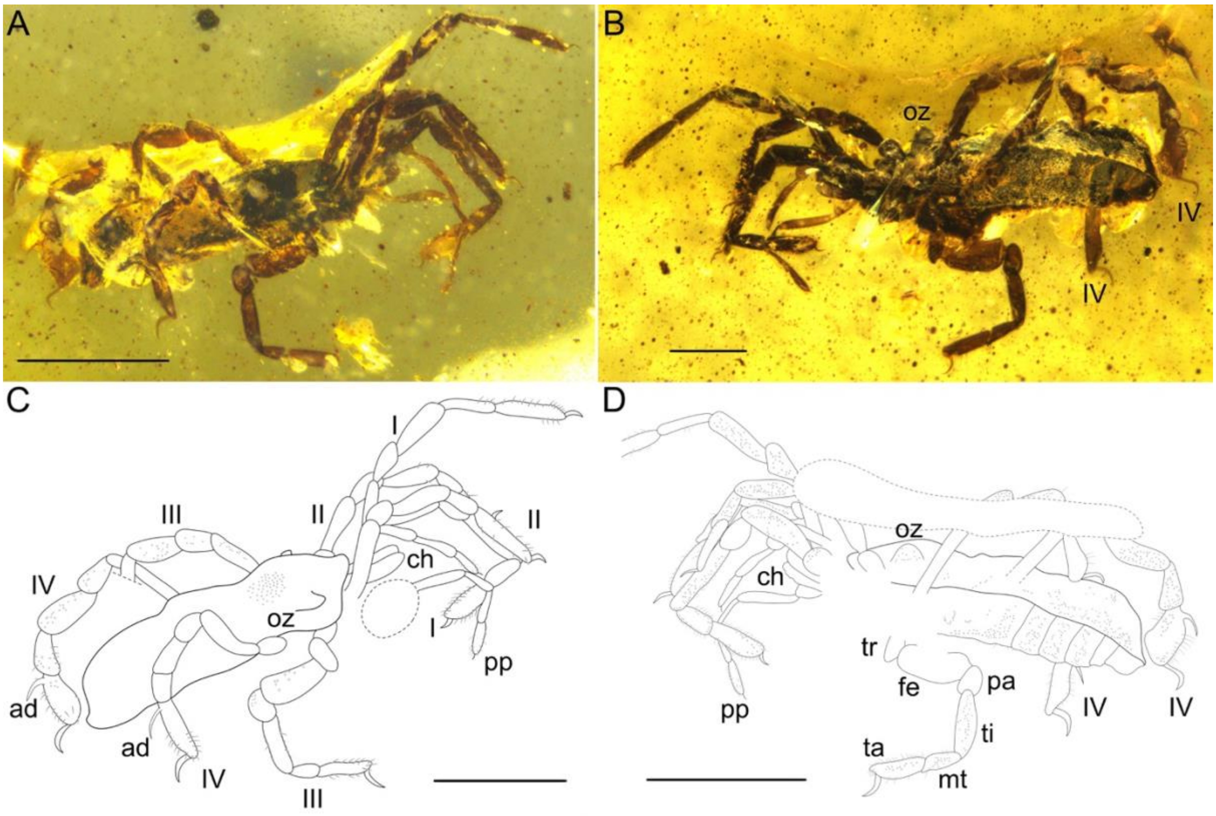

Figure 5.1. *Sirocellus iunctus* gen. et sp. nov., male holotype (GPIH05128). A. Whole specimen, dorsolateral view. B. Same, ventrolateral view. C. Camera lucida drawing of A. D. Same of B. Abbreviations: ad, adenostyle; ch, chelicerae; fe, femur; mt, metatarsus; oz, ozophore; pa, patella; pp, pedipalp; ta, tarsus; ti, tibia; tr, trochanter; legs numbered from I–IV. Scale bars equal 1 mm (A, C, D) and 0.5 mm (B).

Species *Sirocellus iunctus* sp. nov.

Fig. 5.1A–D

urn:lsid:zoobank.org:act:EF263CC3-F2A9-45E8-A237-9830DDB5B49B

Holotype. GPIH05128, ex coll. Patrick Müller, BUB3113.

Type-locality. Myanmar, Hukawng Valley; Burmese amber. Upper Cretaceous (Lower Cenomanian).

Etymology. Latin “iunctus” (= combined), referring to the unique combination of characters of this species.

Diagnosis. As for the genus.

Description. Body oval, with an almost conical rear; almost all of cuticle with a tuberculate-microgranular microstructure (Fig. 5.1A, C), total L 1.96, maximum prosomal W behind ozophores 0.48, maximum opisthosomal W 0.55. Ozophores almost conical, in type 2 position. L of ozophores 0.17, W at base 0.14, distance between base of ozophores 0.29. Chelicerae long and mostly smooth, with a few small granules and three larger tubercles on chela (Fig. 5.1B–D); dentition equivocal; basal segment L 0.43, chela 0.39. Pedipalps moderately long and thin, with few sensory setae on tarsus; pedipalp tarsus with a small claw on its tip; pedipalp length: tr ?, fe ?, pa 0.21, ti 0.24, ta 0.22. Legs robust and covered with numerous setae on tarsus and metatarsus; additionally, all legs granular, with small, partly setiferous tubercles; tarsus IV bearing a large lamelliform adenostyle proximally; leg tarsi not subdivided, bearing a single smooth claw; leg lengths: I tr 0.21, fe 0.37, pa 0.26, ti 0.38, mt 0.27, ta 0.45, total 1.94; II tr 0.20, fe 0.41, pa 0.21, ti 0.38, mt 0.22, ta 0.46, total 1.88; III tr 0.21, fe 0.41, pa 0.21, ti 0.36, mt 0.19, ta 0.36, total 1.74; IV tr 0.21, fe 0.43, pa 0.24*, ti 0.40, mt 0.28, ta 0.37*, total 1.93. Opisthosomal sternites granular, with relatively straight and parallel sulci (Fig. 5.1B, D). Spiracles equivocal. Anal plate not observed.

Genus *Mesopsalis* gen. nov.

urn:lsid:zoobank.org:act:83F375D4-A0DA-48B9-8F9F-335695979A5E

Type species. *Mesopsalis oblongus* sp. nov.

Etymology. Named after its presence in the Mesozoic and its similarities to the modern genus *Leptopsalis*. Masculine in gender.

Diagnosis. Relatively large and oval body with a markedly subtriangular anterior margin. Elongated ozophores in the type 2 position. Eyes present. Chelicerae rather small and sparsely granular. Legs relatively short and granular. Leg tarsi undivided, bearing a single smooth claw. Coxa I free, coxae II–III fused. Opisthosomal sternal sulci mostly straight and parallel. Anal plate unmodified.

Remarks. The holotype of *Mesopsalis oblongus* sp. nov. (MB.A.4456; Fig. 5.2) is very likely an adult female due to the absence of an adenostyle on tarsus IV, its relatively large size and the open gonostome. The habitus of this specimen with its elongated ozophores (Fig. 5.2A–B) appears to be similar to that of the holotype of *Palaeosiro burmanicum*. However, the new fossil is nearly three times larger and has an eye lens in front of each ozophore, which is lacking in *P. burmanicum*. The families Ogoveidae and Pettalidae can be excluded as this fossil does not show any of the typical characters like a longitudinal median furrow in the scutum completum, a large opisthosomal ventral apophysis, upwards facing ozophores and a strongly modified anal region. The free coxa I, fused coxae II–III (Fig. 5.2D) and the conical anterior end of the carapace, in combination with an unmodified anal plate, indicate affinities to the family Stylocellidae. The conical anterior margin of the body (Fig. 5.2B) of the fossil resembles that of the modern species *Leptopsalis ramblae* Giribet, 2002. The presence of eyes, slightly curved ventral opisthosomal sulci and the reduced cheliceral ornamentation is also shared between the fossil and specimens of the modern genus *Leptopsalis* Thorell, 1882. However, long and relatively thin conical ozophores cannot be observed in any of the extant *Leptopsalis* species. Based on this unique combination of characters, the fossil is placed in a new genus.

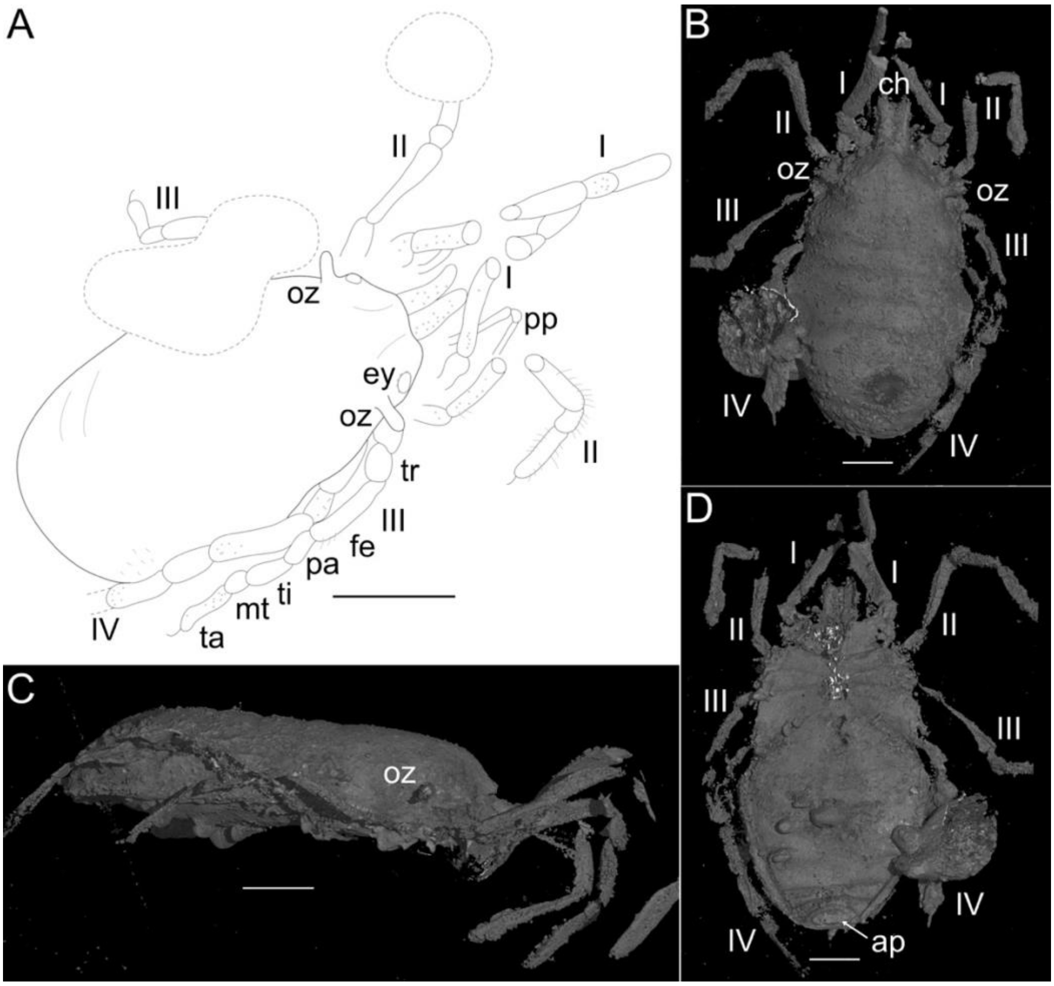

Figure 5.2. *Mesopsalis oblongus* gen. et sp. nov., female holotype (MB.A.4456). A. Camera lucida drawing of whole specimen, dorsal view. B. Micro-CT scan of whole specimen, dorsal view. C. Same, lateral view. D. Same, ventral view. Abbreviations: ap, anal plate; ch, chelicerae; ey, eye lens; fe, femur; mt, metatarsus; oz, ozophore; pa, patella; pp, pedipalp; ta, tarsus; ti, tibia; tr, trochanter; legs numbered from I–IV. Scale bars equal 1 mm (A) and 0.5 mm (B–D).

Species *Mesopsalis oblongus* sp. nov.

Fig. 5.2A–D

urn:lsid:zoobank.org:act:A0B0F3B3-97F6-47AB-B452-AA4F3E05D6E9

Holotype. Specimen MB.A.4456, ex coll. Jörg Wunderlich, K84.

Type locality. Myanmar, Hukawng Valley; Burmese amber. Upper Cretaceous (Lower Cenomanian).

Etymology. Latin adjective “oblongus” (= elongated), referring to the elongated ozophores of the holotype.

Diagnosis. As for the genus.

Description. Body oval and markedly subtriangular in profile at the anterior end; total L 3.50, maximum prosomal W behind ozophores 1.53, maximum opisthosomal W 1.90. Prosoma with a tuberculate-microgranular surface. Relatively thin and long conical ozophores in type 2 position (Fig. 5.2C). L of ozophores 0.31, W at base 0.14, distance between base of ozophores 1.11. Eyes present anterior to ozophores. Eye lenses surrounded by small tubercles (Fig. 5.2A). Chelicerae relatively small and at least granular on basal segment; basal segment L 0.55, median segment L 0.45, distal segment L 0.25. Pedipalps very small and thin; pedipalp length: fe 0.61, pa 0.23, ti 0.32, ta 0.37. Legs relatively short and somewhat granular; leg tarsi not subdivided, bearing a single smooth claw and numerous setae; tarsus IV without adenostyle; coxa I free, coxae II–III medially fused; leg lengths: I tr 0.28, fe 0.81, pa ?, ti 0.58, mt 0.25, ta 0.44; II tr 0.36, fe 0.83*, pa 0.20, ti 0.47, mt 0.20, ta 0.50, total 2.56; III tr 0.31, fe 0.69, pa 0.30, ti 0.36, mt 0.22, ta 0.47, total 2.35; IV tr 0.25, fe 0.83, pa 0.39, ti 0.53, mt 0.20, ta 0.64, total 2.84. Opisthosomal sternal sulci mostly straight and parallel. Gonostome subcircular, W 0.27, L 0.24. Spiracles difficult to determine, presumably C-shaped. Anal plate elliptical and unmodified, W 0.37, L 0.14 (Fig. 5.2D).

Genus *Leptopsalis* Thorell, 1882

Type species. *Leptopsalis beccarii* Thorell, 1882.

Diagnosis. See Clouse 2012.

Remarks. The holotype of *Leptopsalis breyeri* sp. nov. (MB.A.4457; Figs. 5.3–5.4) is an adult male, because of its large size and the presence of an adenostyle on tarsus IV. This specimen can be reliably identified as a member of the family Stylocellidae. The ornamented second cheliceral segment, type 2 ozophores, free sternites, C-shaped spiracles and the position of the fringed adenostyle are typical characters for representatives of this family.

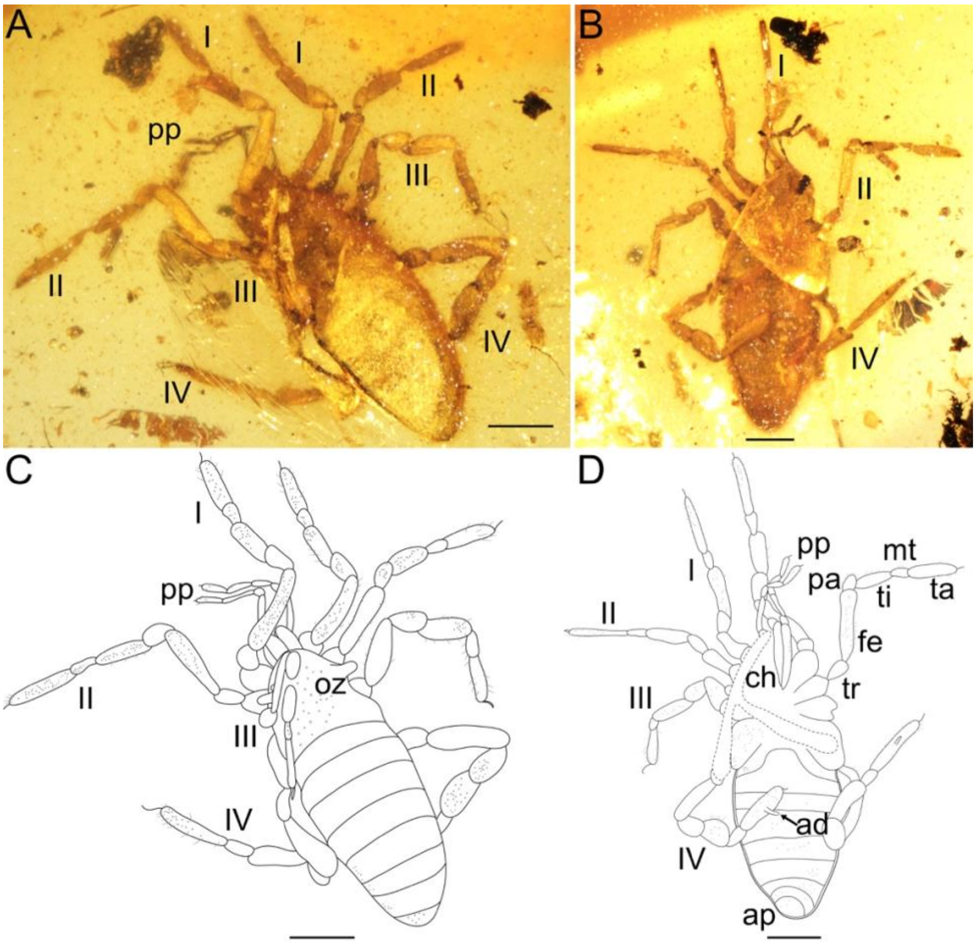

Figure 5.3. *Leptopsalis breyeri* sp. nov., male holotype (MB.A.4457). A. Whole specimen, dorsolateral view. B. Same, ventral view. C. Camera lucida drawing of A. D. Same of B. Abbreviations: ad, adenostyle; ap, anal plate; ch, chelicerae; fe, femur; mt, metatarsus; oz, ozophore; pa, patella; pp, pedipalp; ta, tarsus; ti, tibia; tr, trochanter; legs numbered from I–IV. Scale bars equal 1 mm.

The possible presence of eyes and indistinctly curved opisthosomal sternal sulci combined with the absence of anal gland pores and extensive cheliceral sculpturing suggest affinities to the extant genus *Leptopsalis*. Furthermore, the habitus of this fossil is somewhat similar to that of the holotype of *Sirocellus iunctus* sp. nov. (GPIH05128) described above. However, specimen MB.A.4457 is much larger and features a completely different adenostyle on tarsus IV. The latter cannot be observed in any of the extant species of *Leptopsalis*, which often have a rather small adenostyle. Based on these characters, this fossil is provisionally placed as an extinct species of *Leptopsalis*. However, we should keep in mind that some of the characters are possibly plesiomorphic, like the mostly straight opisthosomal sternal sulci, which is the predominant form observed in all our fossils.

Species *Leptopsalis breyeri* sp. nov.

Figs. 5.3A–D; 5.4A, B

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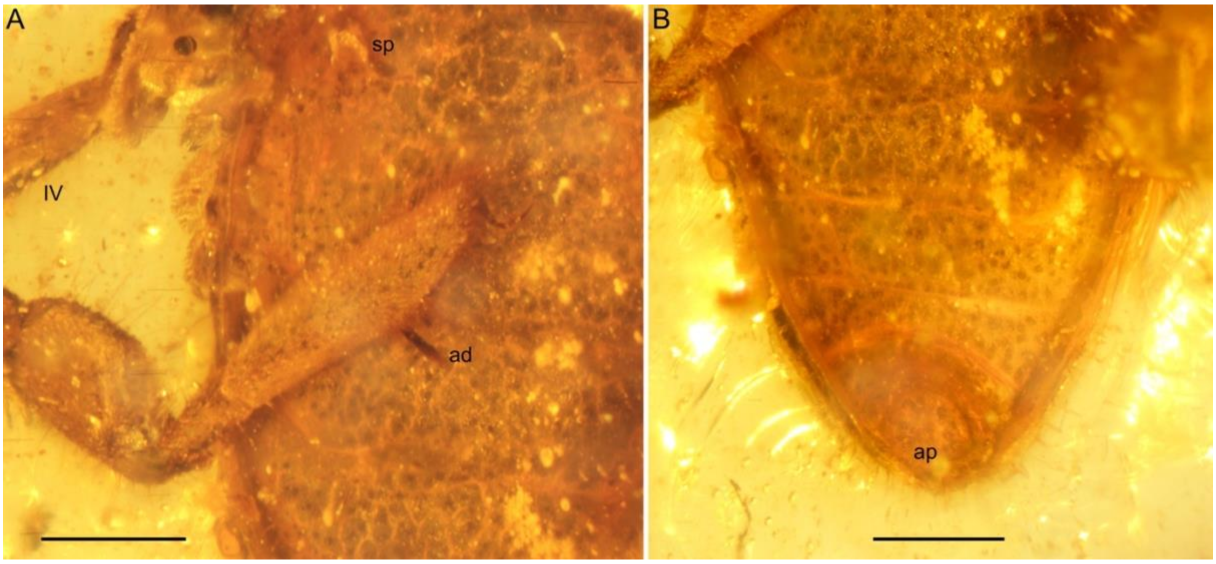

Figure 5.4. Details of *Leptopsalis breyeri* sp. nov., male holotype (MB.A.4457). A. Close-up of tarsus IV. B. Close-up of ventral side of opisthosoma. Abbreviations: ad, adenostyle; ap, anal plate; sp, spiracle; leg IV numbered. Scale bars equal 0.5 mm.

Holotype. MB.A.4457, ex coll. Jörg Wunderlich, F2636.

Type locality. Myanmar, Hukawng Valley; Burmese amber. Upper Cretaceous (Lower Cenomanian).

Etymology. Named after Horst Breyer (the grandfather of Christian Bartel), who celebrated his 100th birthday in January 2023. This is a masculine patronym in the genitive.

Diagnosis. Large and oval body, subtriangular in profile at the anterior end. Conical ozophores in type 2 position. Eyes possibly present. Chelicerae rather small and ornamented on median segment. Pedipalps thin and unmodified. Legs robust and granular. Tarsus IV with a long and fringed adenostyle near the middle. Opisthosomal sternal sulci mostly straight and parallel. Spiracles C-shaped.

Description. Body, total L 4.68, maximum prosomal W behind ozophores 1.64, maximum opisthosomal W 1.80. Conical ozophores in type 2 position (Fig. 5.3A, C). L of ozophores 0.28, W at base 0.24, distance between base of ozophores 1.16. Possible eye lens present anterior to ozophores. Chelicerae relatively small and ornamented on median segment (Fig. 5.3B, D); basal segment L 0.51, median segment L 1.16; cheliceral fingers equivocal. Pedipalps thin, its tarsus sparsely covered with sensory setae; tarsus with a small claw on its tip; pedipalp length: fe 0.68, pa 0.32*, ti 0.40, ta 0.48. Legs robust, granular and with numerous setae on tarsus; tarsus IV bearing a relatively long and fringed adenostyle near the middle (Fig. 5.4A); leg tarsi not subdivided, bearing a single smooth claw; leg lengths: I tr 0.40, fe 1.28*, pa 0.44, ti 0.70, mt 0.32, ta 0.88*, total 4.02; II tr 0.48, fe 1.28, pa 0.44, ti 0.80, mt 0.36, ta 1.02, total 4.38; III tr 0.32, fe 1.00, pa 0.48, ti 0.80, mt 0.38, ta 0.72, total 3.70; IV tr 0.48, fe 1.20, pa 0.58, ti 0.82, mt 0.36, ta 1.12, total 4.56. Opisthosomal sternites completely granular.

Sternites 2–3 fused to a subtriangular plate; sternites 4–8 free, their widths: 4, 2.06; 5, 1.87; 6, 1.69; 7, 1.44; 8, 1.13; 9, 0.81. Opisthosomal sternal sulci mostly straight and parallel. Gonostome equivocal. Spiracles C-shaped, maximum W 0.16. Anal plate rounded and unmodified, W 0.53, L 0.38 (Fig. 5.4B). Cuticle without conspicuous pits or depressions.

Stylocellidae gen. sp. 1

Figs. 5.5A–D; 5.6A, B

Material. Specimen BUB601, ex coll. Patrick Müller; Myanmar, Hukawng Valley; Burmese amber, Upper Cretaceous (Lower Cenomanian).

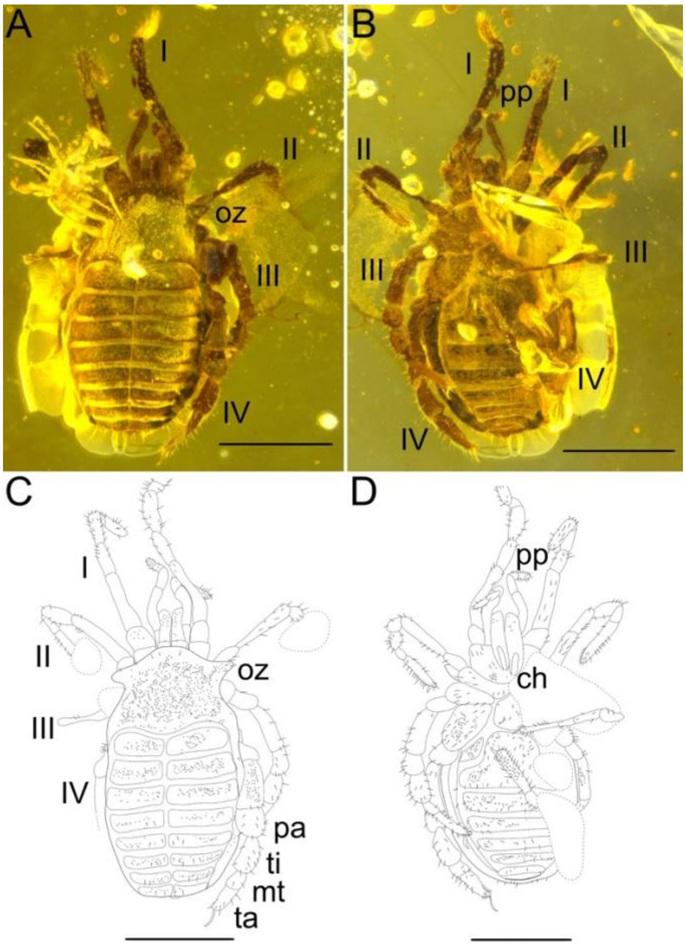

Figure 5.5. Stylocellidae gen. sp. 1 (juvenile specimen BUB601). A. Whole body, dorsal view. B. Same, ventral view. C. Camera lucida drawing of A. D. Same of B. Abbreviations: ch, chelicerae; mt, metatarsus; oz, ozophore; pa, patella; pp, pedipalp; ta, tarsus; ti, tibia; legs numbered from I–IV. Scale bars equal 1 mm.

Description. Body oval and tuberculate-microgranular across most of its surface; total L 2.33, maximum prosomal W behind ozophores 1.24, maximum opisthosomal W 1.32. Prosoma completely granular due to small and rounded tubercles, with conical ozophores of types 1 or 2 (no lateral view available) (Fig. 5.5A, C). Anterior part of prosoma and ozophores additionally furnished with small setae. L of ozophores 0.22, W at base 0.25, distance between base of ozophores 0.82. Eight opisthosomal tergites clearly delimited dorsally and uniquely separated by a smooth median groove. Tergites increasingly covered with setae posteriorly. Chelicerae relatively small, covered with small tubercles; cheliceral fingers relatively long; dentition equivocal; basal segment L 0.35, median segment L 0.51, distal segment L 0.23*. Pedipalps sparsely covered sensory setae on tibia and tarsus; tarsus with small claw on its tip; length: tr 0.21, fe 0.40, pa 0.19, ti 0.16, ta 0.17, total 1.13. Legs short and robust, bearing numerous setae on most segments; some leg segments like coxae, femur IV and tarsus IV additionally granular; coxae partly visible in dorsal view; all tarsi entire, not subdivided, with a single smooth and sickle-shaped claw; tarsus IV without adenostyle; leg lengths: I tr 0.21*, fe 0.57*, pa 0.29*, ti 0.36*, mt 0.12*, ta 0.32*, total 1.87; II tr 0.23, fe 0.52, pa 0.29, ti 0.30, mt 0.16, ta 0.46*, total 1.96; III tr 0.26, fe 0.45, pa 0.20, ti 0.28, mt 0.15, ta 0.38, total 1.72; IV tr 0.18, fe 0.46, pa 0.27, ti 0.36*, mt 0.14*, ta 0.28*, total 1.69. Opisthosomal sternites granular and furnished with setae; sternites 2–3 fused to a subtriangular plate. Sternites 4–8 free, their widths: 4, 1.03; 5, 0.96; 6, 0.78; 7, 0.63; 8, 0.45. Gonostome closed, subhexagonal and covered with tubercles of different sizes, W 0.30, L 0.35. Spiracles in the form of an open circle consisting of small denticles and surrounded by similar-sized tubercles, situated on an isolated sclerite behind coxae IV, maximum W 0.05. Anal plate with a longitudinal median carina (Fig. 5.6B).

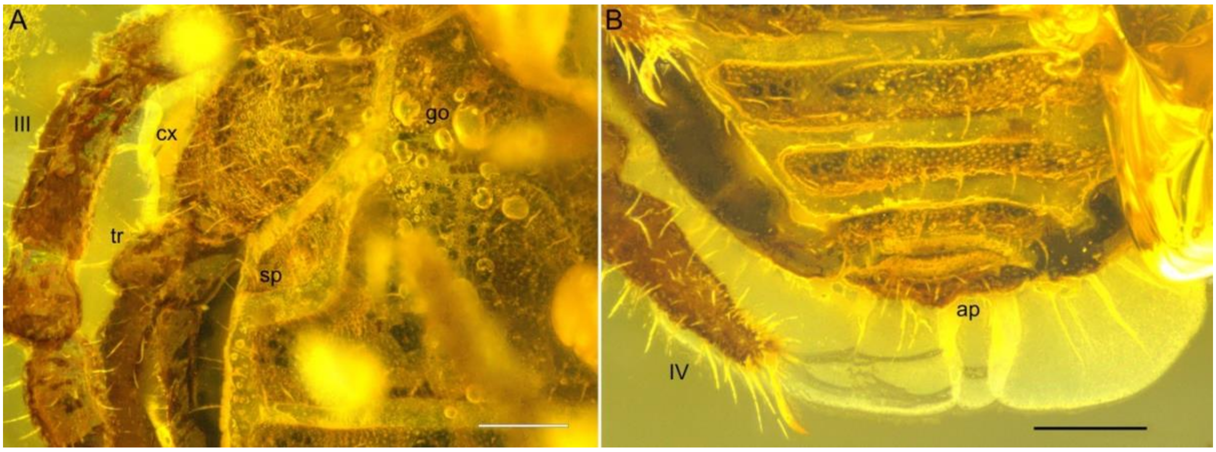

Figure 5.6. Details of Stylocellidae gen. sp. 1 (juvenile specimen BUB601). A. Close-up of left spiracle, ventral view. B. Close- up of posterior end of opisthosoma, ventral view. Abbreviations: ap, anal plate; cx, coxa IV; go, closed gonostome; sp, spiracle; tr, trochanter; legs III and IV numbered. Scale bars equal 0.2 mm.

Remarks. Specimen BUB601 (Figs. 5.5–5.6) is a juvenile. The closed gonostome and spiracles located on separate sclerites (Fig. 5.6A) clearly indicate this status. The gender of this specimen is unclear as the typical male adenostyle on tarsus IV first appears after the final moult in most species and no other somatic features allow the sex of juvenile cyphophthalmids to be identified. Due to the shape of the spiracles, which could be either interpreted as an open circle or as C-shaped, we assume that the affinities of this fossil lie with the Stylocellidae or Pettalidae. However, pettalids have much smaller, rounder and more upwards facing ozophores in comparison with the enlarged lateral ozophores observed in the fossil (Fig. 5.5A, C). The ornamented second cheliceral segment (Fig. 5.5B, D) further supports stylocellid affinities. Therefore, we place this specimen in the Stylocellidae, as it would be inappropriate to formally describe a new species based on a juvenile.

Stylocellidae gen. sp. 2

Figs. 5.7A–D; 5.8A, B

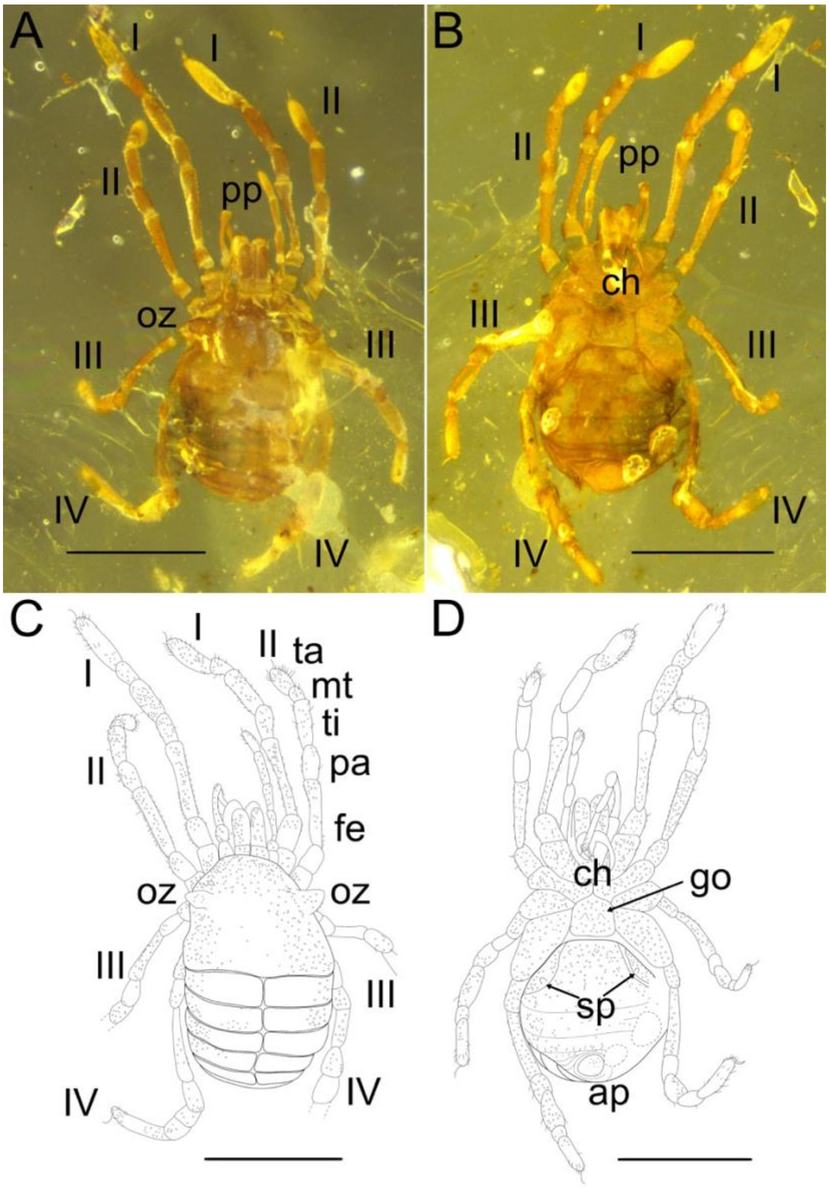

Figure 5.7. Stylocellidae gen. sp. 2 (immature specimen BUB1517). A. Whole body, dorsal view. B. Same, ventral view. C. Camera lucida drawing of A. D. Camera lucida drawing of B (closed gonostome and spiracles indicated by arrows). Abbreviations: ap, anal plate; ch, chelicerae; fe, femur; go, closed gonostome; mt, metatarsus; oz, ozophore; pa, patella; pp, pedipalp; ta, tarsus; ti, tibia; legs numbered from I–IV. Scale bars equal 1 mm.

Material. Specimen BUB1517, ex coll. Patrick Müller; Myanmar, Hukawng Valley; Burmese amber, Upper Cretaceous (Lower Cenomanian).

Description. Body oval and somewhat very widely subtriangular in profile at anterior end; total L 1.76, maximum prosomal W behind ozophores 1.11, maximum opisthosomal W 1.09. Prosoma almost completely tuberculate-microgranular, especially near outer edges (Fig. 5.7A, C). Conical ozophores with tubercles and in type 2 position. L of ozophores 0.21, W at base 0.17*, distance between base of ozophores 0.65. Eye lens present anterior to left ozophore. Six opisthosomal tergites visible, each delimited and sparsely granular near left and right edges. Borders delimiting tergites smooth. Chelicerae moderately long, somewhat protruding and completely granular; each cheliceral finger with nine small uniform teeth; basal segment L 0.32, median segment L 0.26, distal segment L 0.22. Pedipalps relatively small and granular, except for tarsus furnished with sensory setae; tarsus with small claw at its tip; pedipalp length: tr 0.14, fe 0.27*, pa 0.21, ti 0.25, ta 0.17, total 1.04. Legs relatively short, robust and strongly granular, especially leg I and II featuring additional setiferous tubercles; coxae not fused; leg tarsi entire, not subdivided, bearing a single smooth claw and numerous setae; tarsus IV without adenostyle; leg lengths: I tr 0.24, fe 0.57, pa 0.24, ti 0.33, mt 0.14, ta 0.44*, total 1.96; II tr 0.21, fe 0.51, pa 0.25, ti 0.33, mt 0.13, ta 0.39, total 1.82; III tr 0.19, fe 0.40, pa 0.21, ti 0.33, mt 0.14, ta 0.32, total 1.59; IV tr 0.22, fe 0.55, pa 0.21, ti 0.21, mt 0.14, ta 0.43, total 1.76.

Ventral side of opisthosoma covered with small tubercles and setae. Opisthosomal sulci parallel to each other. Sternites 2–3 fused to a subtrapezoidal plate; sternites 4–9 getting increasingly concentrated towards anal plate. Gonostome closed, subhexagonal, covered with numerous small and two larger tubercles proximally, W 0.33, L 0.32. Spiracles C-shaped (consisting of small denticles) and surrounded by smaller tubercles, located on isolated sclerites behind coxae IV, maximum W 0.08. Anal plate rounded, with few small tubercles, W 0.20, L 0.15 (Fig. 5.7B, D).

Remarks. Specimen BUB1517 (Figs. 5.7–5.8) is again a juvenile of uncertain gender judging from the closed gonostome and spiracles situated on separate sclerites (Figs. 5.7B, D, 5.8B). Therefore most diagnostic characters are not fully developed. Nevertheless, granular tegument, C-shaped spiracles, type 2 ozophores, uniform teeth on cheliceral fingers and an ornamented second cheliceral segment (Fig. 5.8A) suggest placement in the Stylocellidae. Within Stylocellidae two extant genera feature extensive sculpturing on the second cheliceral segment, similar to that in the fossil: *Miopsalis* Thorell, 1890 and *Stylocellus* Westwood, 1874. These can be easily distinguished by the form of the ventral opisthosomal sulci. *Stylocellus* features sinoidal ventral opisthosomal sulci and *Miopsalis* features straight ventral opisthosomal sulci (Clouse, 2012). The latter can also be observed in specimen BUB 1517. However, the fossil also shows a strong concentration of opisthosomal sternites (Fig. 5.7B, D) around the anal plate, a character not known from modern genera. This could either be a juvenile character not present in modern species, or it could be related to a deformation of the opisthosoma as a result of its preservation in amber. For that reason we prefer a cautious approach and leave this specimen unnamed.

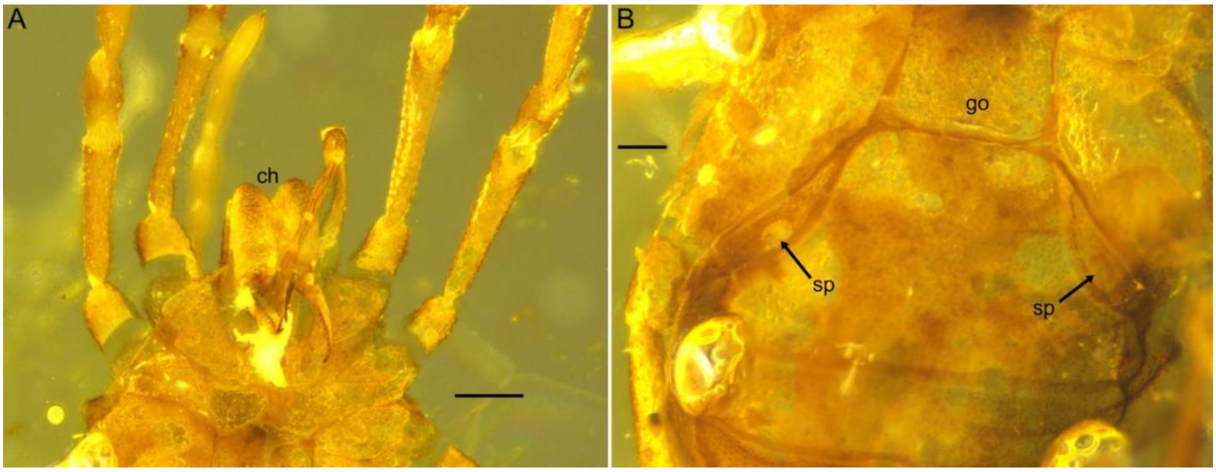

Figure 5.8. Details of Stylocellidae gen. sp. 2 (immature specimen BUB1517). A. Pedipalps and chelicerae in ventral view. B. Close-up of closed gonostome and spiracles (indicated by arrows). Abbreviations: ch, chelicerae; go, closed gonostome; sp, spiracle. Scale bars equal 0.2 mm (A) and 0.1 mm (B).

Stylocellidae gen. sp. 3

Fig. 5.9A–C

Material. Specimen BUB3653, ex coll. Patrick Müller; Myanmar, Hukawng Valley; Burmese amber, Upper Cretaceous (Lower Cenomanian).

Description. Body oval, total L 2.32, maximum opisthosomal W 1.23. Ozophores equivocal. Chelicerae rather short, its distal segment ornamented with small tubercles (Fig. 5.9A–B); basal segment L ?, median segment L 0.36, distal segment L 0.18. Pedipalps moderately long; tarsus bearing a small claw on its tip and furnished with a few sensory setae; pedipalp length: tr ?, fe ?, pa ?, ti 0.34, ta 0.27. Legs long, robust and finely granular; tarsi with a single smooth claw and additional setae; tarsus IV not subdivided, bearing a lamelliform proximal adenostyle; leg lengths: I tr 0.21, fe 0.43*, pa 0.23, ti 0.49*, mt 0.30, ta 0.41, total 2.07; II tr 0.20, fe 0.46, pa 0.14, ti 0.37, mt 0.30, ta 0.43, total 1.90; III tr 0.16, fe 0.41, pa 0.18, ti 0.42*, mt 0.28, ta 0.37, total 1.82; IV tr 0.23, fe 0.52, pa 0.18, ti 0.34, mt 0.36, ta 0.34, total 1.97. Gonostome equivocal. Opisthosomal sternites completely granular. Sternites 2–3 fused into a plate; sternites 4–8 free, their widths: 4, 0.98; 5, 0.93; 6, 0.82; 7, 0.64; 8, 0.52. Opisthosomal sternal sulci straight and parallel to each other. Anal plate rounded and unmodified (Fig. 5.9B).

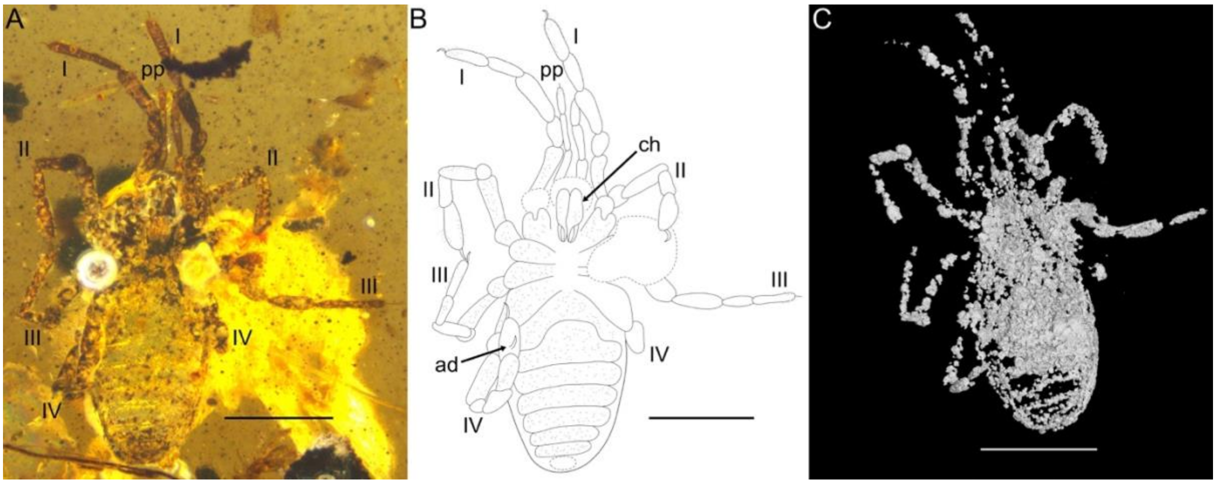

Figure 5.9. Stylocellidae gen. sp. 3 (male specimen BUB3653). A. Whole body, ventral view. B. Camera lucida drawing of A. C. 3D reconstruction of whole body, ventral view. Abbreviations: ad, adenostyle; ch, chelicerae; pp, pedipalp; legs numbered from I–IV. Scale bars equal 1 mm.

Remarks. Specimen BUB3653 (Fig. 5.9) is interpreted as an adult male as it bears an adenostyle on tarsus IV and seems heavily sclerotized. The habitus, in combination with an ornamented second cheliceral segment and free sternites, indicates stylocellid affinities. Additionally, typical pettalid or ogoveid characters, like a modified anal region or opisthosomal apophyses, are missing. The proximal position of the adenostyle (Fig. 5.9A–B) is somewhat similar to that observed in specimen GPIH05128 and is thus more typical for modern sironids or neogoveids. However, specimen GPIH05128 features a much larger and lamelliform adenostyle and a longer tarsus IV. Due to the lack of important dorsal and ventral characteristics which could not be reconstructed with the help of micro-CT (Fig. 5.9C), this fossil cannot be placed any further in the family Stylocellidae. Nevertheless, this is another interesting specimen showing a possible combination of sironid and stylocellid affinities and it is available for further studies.

Stylocellidae gen. sp. 4

Fig. 5.10A–D

Material. Specimen BUB1542, ex coll. Patrick Müller; Myanmar, Hukawng Valley; Burmese amber, Upper Cretaceous (Lower Cenomanian).

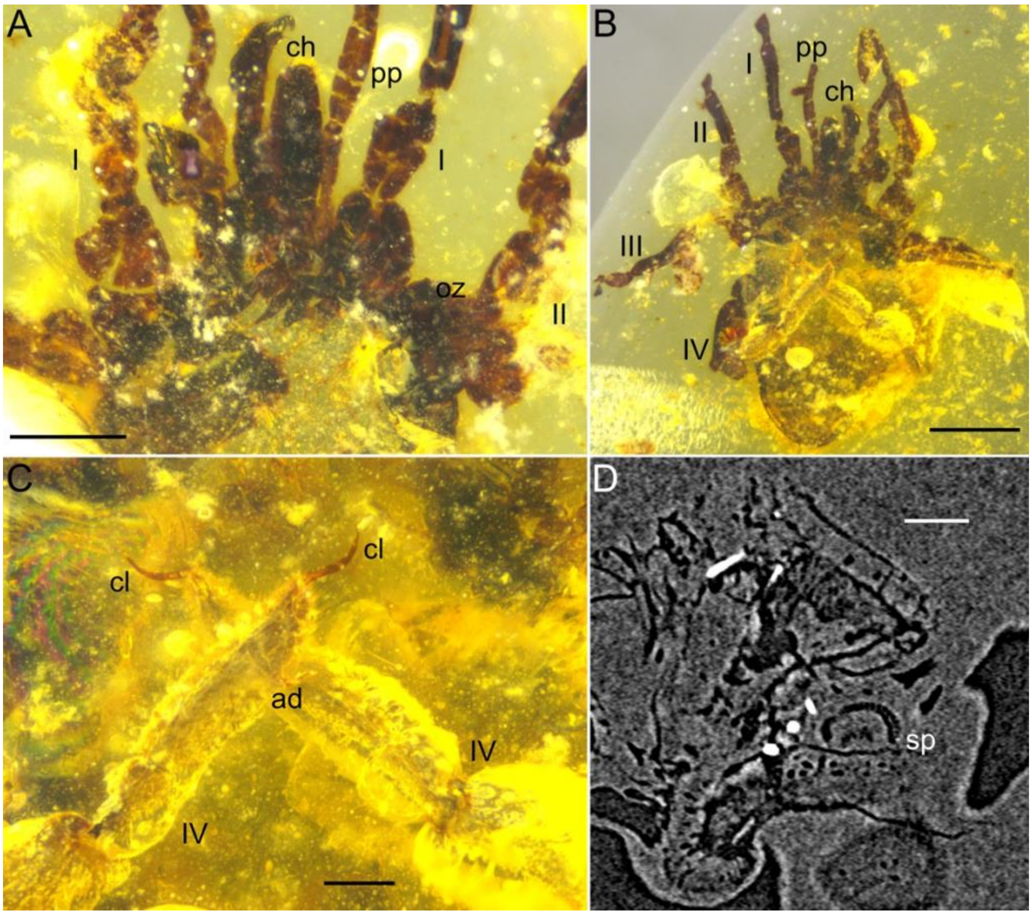

Figure 5.10. Stylocellidae gen. sp. 4 (male specimen BUB1542). A. Close up of anterior part of body, dorsal view. B. Whole body, ventral view. C. Close up of tarsus IV with adenostyle, ventral view. D. Micro-CT image of right spiracle in ventral view. Abbreviations: ad, adenostyle; ch, chelicerae; cl, claw of tarsus IV; pp, pedipalp; sp, spiracle; legs numbered from I–IV. Scale bars equal 0.5 mm (A), 1 mm (B), 0.2 mm (C) and 0.1 mm (D).

Description. Body oval, with a narrowly rounded anterior margin; total L 2.98, maximum prosomal W behind ozophores 1.49, maximum opisthosomal W 1.53. Conical ozophores in type 2 position. L of ozophores 0.23, W at base 0.28, distance between base of ozophores 1.16. Chelicerae long (Fig. 5.10A–B) and granular on basal and median segments; small additional setae on basal segment and setiferous tubercles on median segment; cheliceral fingers each with eleven uniform teeth; basal segment L 0.93*, median segment L 0.71, finger L 0.29. Pedipalps long, tarsus with few sensory setae and with a small claw on its tip; pedipalp length: tr 0.32*, fe 0.70, pa 0.23, ti 0.32, ta 0.34, total 1.91. Legs long and robust, furnished with numerous setae on tarsi and metatarsi; trochanter of leg I and II somewhat granular; tarsus IV bearing a somewhat fringed adenostyle in distal third (Fig. 5.10C); leg tarsi not subdivided, bearing a single smooth claw; leg lengths: I tr 0.44*, fe 1.04*, pa 0.32, ti ?, mt ?, ta ?; II tr 0.36, fe 0.97, pa 0.42, ti 0.56, mt 0.19, ta 0.61, total 3.11; III tr 0.46, fe 1.12, pa 0.35, ti ?, mt ?, ta ?; IV tr 0.36, fe 0.85, pa 0.34, ti 0.51, mt 0.29*, ta 0.68*, total 3.03. Gonostome circular, surrounded with small tubercles, W 0.32, L 0.24. Spiracles C-shaped (consisting of small denticles), maximum W 0.11 (Fig. 5.10D). Anal plate rounded and with a potential longitudinal carina, W 0.39, L 0.22.

Remarks. Specimen BUB1542 (Fig. 5.10) is interpreted as a mature male due to the presence of an adenostyle at the base of tarsus IV and due to its heavy sclerotization. The family Pettalidae can be excluded as the fossil lacks upwards-facing ozophores and a dual dentition on the chelicerae. A large apophysis on the second opisthosomal sternite and a thorn-like adenostyle situated near the middle of the tarsus are also absent in the fossil. Both are typical characters of the family Ogoveidae. This leaves the modern Holarctic Sironidae and the Southeast-Asian Stylocellidae as the only possible placements. The somewhat fringed adenostyle in the distal third of tarsus IV (Fig. 5.10C) indicates stylocellid affinities, especially in combination with the longitudinal carina on the anal plate, a granular second cheliceral segment and C-shaped spiracles (Fig. 5.10D). However, as the reconstruction of many characters was not possible even with the help of micro-CT, we prefer to describe this specimen without naming it as a new species. Nevertheless, this fossil can be easily distinguished from all other cyphophthalmid fossils on the basis of its unique adenostyle on tarsus IV. New material may allow the naming of a new species in the future.

Cyphophthalmi incertae sedis

Genus *Foveacorpus* gen. nov.

urn:lsid:zoobank.org:act:695BD267-DC04-4076-932D-5D0A81E2CDB5

Type species. *Foveacorpus cretaceus* gen. et sp. nov.

Etymology. From the Latin words “fovea” (= pit) and “corpus” (= body). Masculine in gender.

Diagnosis. Body oval, small and completely covered with numerous small pits. Rounded ozophores in type 1 position. Chelicerae moderately long and thin. Pedipalps rather small and unmodified. Legs relatively short and robust, with legs I and II directed forwards. Typical spiracles absent. Anal region with a corona analis (sternites 8, 9 and tergite IX fused and forming an unbroken ring around the anal plate).

Remarks. The holotype of *Foveacorpus cretaceus* sp. nov. (GPIH05129; Figs. 5.11–5.12) is interpreted as an adult female due to the open gonostome (Fig. 5.11B, D) and the absence of an adenostyle on tarsus IV. This very small specimen shows an unusual and potentially unique combination of characters. First, the whole body is completely covered with small pits (Fig. 5.11A–D), a feature which has not been observed in any modern species, and the dorsum shows no sign of segmentation or of a longitudinal opisthosomal sulcus. There are extant stylocellid species, such as *Leptopsalis foveolata* Clouse & Schwendinger, 2012, which feature a few much larger and deeper pits on the opisthosoma. It is possible that these small pits in the cuticle of this fossil are an artefact resulting from the fossilization process where, e.g., a substance coats different parts of the specimen, as seen in many Burmese amber fossils. However, the ventral region around the gonostome (Fig. 5.12A) shows no signs of a coating as many small setae are clearly visible and the pits appear to be open. We conclude that most parts of the fossil are originally preserved, and that the pits on the prosoma and opisthosoma were presumably covered by some substance.

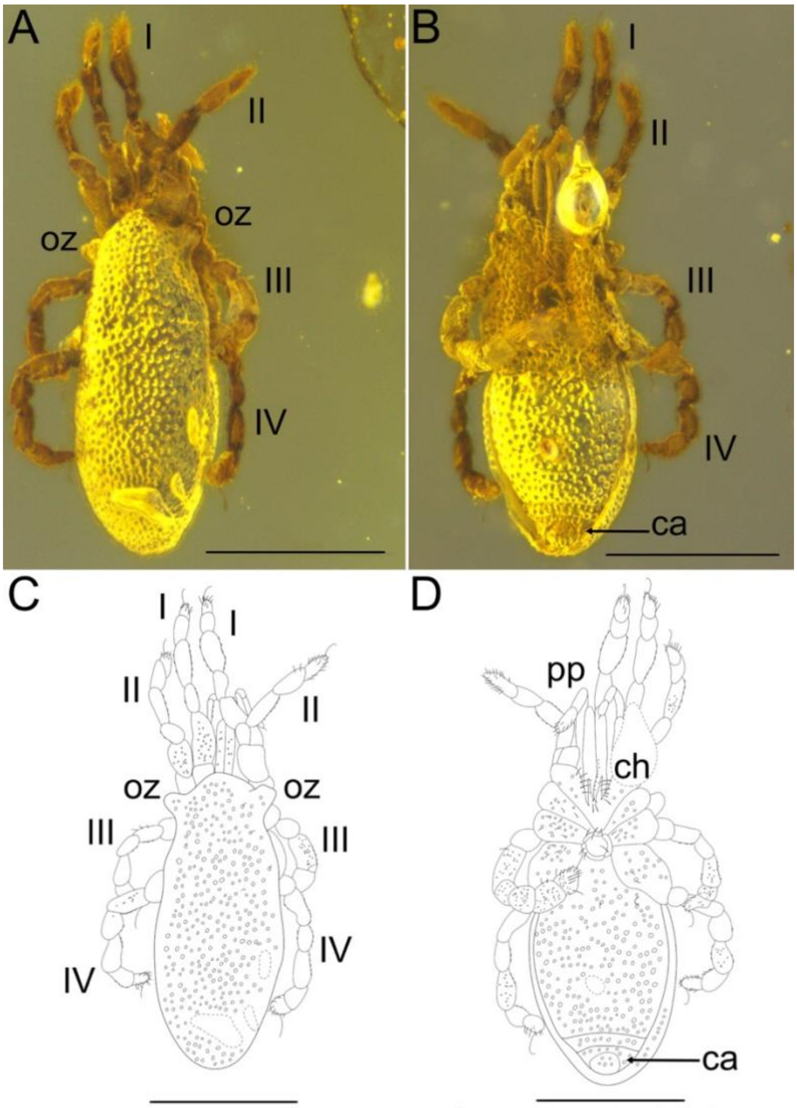

Figure 5.11. *Foveacorpus cretaceus* gen. et sp. nov., female holotype (GPIH05129). A. Whole body, dorsal view. B. Same, ventral view. C. Camera lucida drawing of A. D. Same of B. Abbreviations: ca, corona analis; ch, chelicerae; oz, ozophore; pp, pedipalp; legs numbered from I–IV. Scale bars equal 0.5 mm.

Placement of this fossil in the family Stylocellidae can be excluded with confidence due to the presence of a corona analis in the fossil where sternites 8, 9 and tergite IX are fused (Fig. 5.12B). In stylocellids, all sternites are fused except sternites 8, 9 and tergite IX that surround the anal plate. Margins between the fused tergites and sternites are completely absent in the amber specimen, whereas most modern Cyphophthalmi show at least a slight change in cuticle texture marking these borders. Besides this, there is an unusual setose region between the anterior coxae (Fig. 5.12A). The legs of the fossil are also untypical when compared to most extant Cyphophthalmi. Legs I and II seem to be directed forwards and the right leg III appears to be modified, as it looks more robust than the other legs. The latter is also covered by numerous thick setae, while the left leg III looks thinner, with normally sized setae (Fig. 5.11B, D). This limb condition (except for the modified leg III) is similar to a peculiar modern species from Kenya, *Marwe coarctata* Shear, 1985, whose family assignment (like that of the fossil) is still unclear. Additionally, both species possess a corona analis, type 1 ozophores and dorsal areas without any visible sutures between them. On the other hand, *Marwe coarctata* has a different habitus with an expanded, disc-like posterior portion of the prosoma, it is larger and has stouter chelicerae. In summary, the new fossil has a unique set of characters and cannot be easily placed within any of the extant families.

Species *Foveacorpus cretaceus* sp. nov.

Figs. 5.11A–D; 5.12A, B
urn:lsid:zoobank.org:act:D76311F9-33F8-4734-8C4F-30F02D17D35D

Holotype. Specimen GPIH05129, ex coll. Patrick Müller, BUB3645.

Type-locality. Myanmar, Hukawng Valley; Burmese amber, Upper Cretaceous (Lower Cenomanian).

Etymology. The specific epithet “cretaceus” (a Latin adjective) refers to the Cretaceous Period.

Diagnosis. Distinct from *Foveacorpus parvus* sp. nov. in more oval body, larger body size (more than 1 mm), larger pits in the tegument and less bulbous ozophores.

Description. Body oval, somewhat subtriangular in profile at anterior end and completely covered with small pits (their diameter 0.016*); total L 1.03, maximum prosomal W behind ozophores 0.39, maximum opisthosomal W 0.45. Dorsal tergites without visible sutures (Fig. 5.11A, C). Rounded ozophores covered with small pits and probably in type 1 position. L of ozophores 0.07, W at base 0.09, distance between bases of ozophores 0.24. Eyes equivocal. Chelicerae moderately long, protruding and finely granular; fingers thin and relatively long, somewhat overlapped by thicker setae originating from coxae I (Fig. 5.12A); dentition equivocal; basal segment L 0.19, median segment L 0.25, distal segment L 0.09. Pedipalps small and granular on femur; tarsus covered with sensory setae and bearing a small claw on its tip; pedipalp length: tr ?, fe ?, pa 0.07, ti 0.09, ta 0.08*. Legs relatively short, robust and granular; legs I and II are notably forward-directed and leg IV relatively far away from leg III; left leg III (in ventral view) appearing modified, more robust and with scopula on tarsus as compared to right leg III; leg tarsi not subdivided, each bearing a single smooth claw and numerous setae (sensory setae and thick setae); tarsus IV without adenostyle; leg lengths: I, tr 0.07, fe 0.18, pa 0.10, ti 0.15, mt 0.08, ta 0.08, total 0.66; II tr 0.07, fe 0.12, pa 0.09, ti 0.13, mt 0.13, ta 0.13, total 0.67; III tr 0.08, fe 0.12, pa 0.05, ti 0.09, mt 0.10, ta 0.08, total 0.52; IV tr 0.07, fe 0.13*, pa 0.09, ti 0.13, mt 0.07, ta 0.07, total 0.56. Ventral side of opisthosoma also covered with numerous small pits. Gonostome open and somewhat circular, surrounded with few thick setae, W 0.07, L 0.07. Possible spiracles indicated by a few circularly arranged denticles situated posterior to coxae IV. Anal plate rounded, with few small pits and surrounded by a corona analis, W 0.10, L 0.08 (Fig. 5.12B).

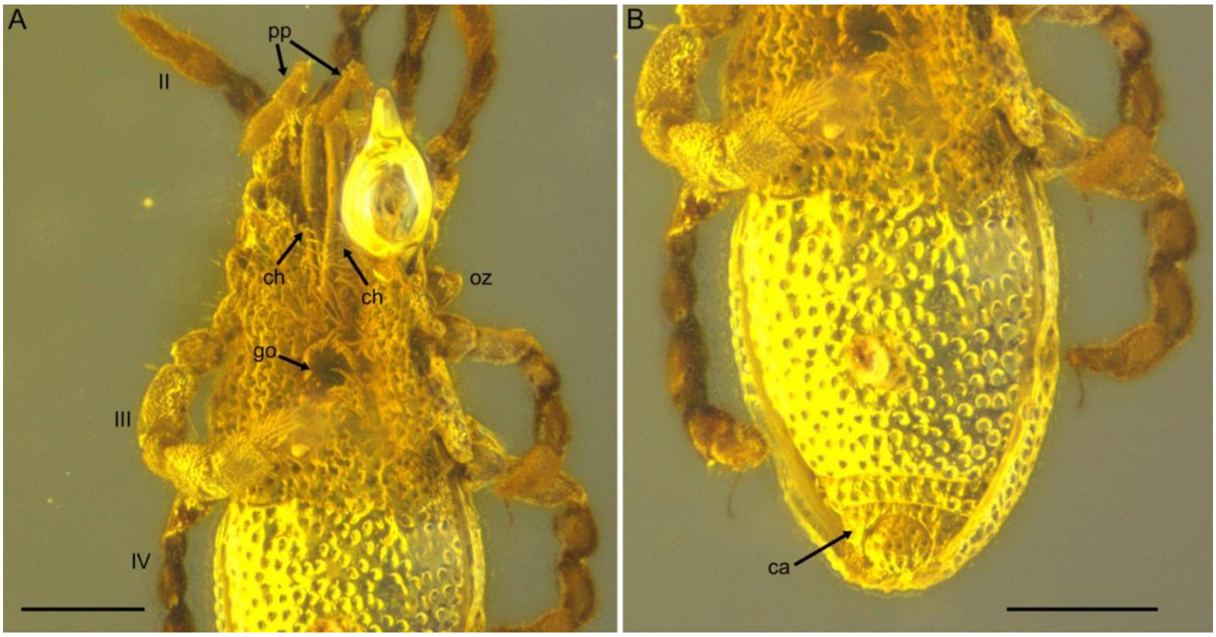

Figure 5.12. Details of *Foveacorpus cretaceus* gen. et sp. nov., female holotype (GPIH05129). A. Close-up of chelicerae, pedipalps and gonostome (indicated by arrows), ventral view. B. Close-up of opisthosoma, ventral view. Abbreviations: ca, corona analis; ch, chelicerae; go, gonostome; pp, pedipalp; oz, ozophore; legs II, III and IV numbered. Scale bars equal 0.2 mm.

Species *Foveacorpus parvus* sp. nov.

Fig. 5.13A–D

urn:lsid:zoobank.org:act:BC6852F1-9D85-46BF-9B15-EFF0F7230F9A

Holotype. Specimen GPIH05130, ex coll. Patrick Müller, BUB3634.

Type-locality. Myanmar, Hukawng Valley; Burmese amber, Upper Cretaceous (Lower Cenomanian)

Etymology. The Latin adjective “parvus, -a, -um” (= small) refers to the small size of this species.

Diagnosis. Distinct from *Foveacorpus cretaceus* sp. nov. by its more pear-shaped body, smaller body size (less than 1mm), smaller tegumental pits and more bulbous ozophores.

Description. Body pear-shaped, subtriangular at anterior end and completely covered with small pits (diameter 0.011*); total L 0.82, maximum prosomal W behind ozophores 0.39, maximum opisthosomal W 0.48. Rounded ozophores probably in type 1 position. Distal part of left ozophore appearing bulbous (Fig. 5.13A, C). L of ozophores 0.09, W at base 0.10, distance between base of ozophores 0.26. Eyes equivocal. Chelicerae moderately long, finely granular on proximal segment; dentition equivocal; basal segment L 0.20, median segment L ?, distal segment L ?. Pedipalps small and thin; pedipalp length: tr ?, fe 0.11, pa 0.03, ti 0.05, ta ?. Legs relatively short, robust and granular; tarsus I not subdivided, bearing a single smooth claw and numerous setae; leg length: I tr 0.10, fe 0.19, pa 0.07*, ti 0.09, mt 0.10, ta 0.12, total 0.67; II tr ?, fe 0.18, pa 0.06, ti ?, mt ?, ta ?; III tr ?, fe ?, pa 0.10, ti 0.10, mt ?, ta ?; IV tr ?, fe 0.16, pa 0.10, ti 0.10, mt 0.07, ta ?. Ventral side of opisthosoma also covered with numerous small pits. Possible spiracles indicated by a few small denticles situated posterior to coxa IV. Anal plate rounded, with few small pits and with a corona analis, W 0.12, L 0.07 (Fig. 5.13B, D).

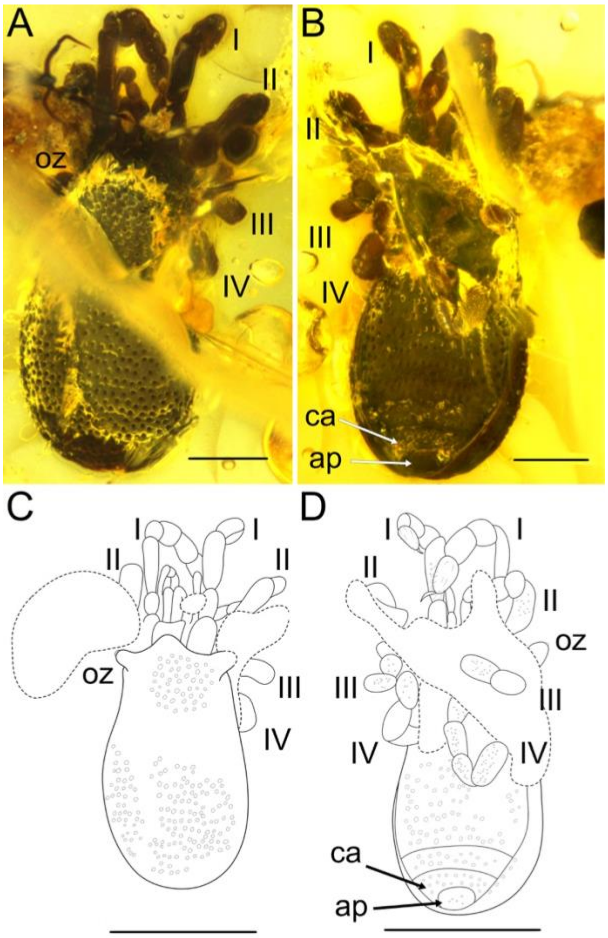

Figure 5.13. *Foveacorpus parvus* gen. et sp. nov., holotype of unclear sex (GPIH05130). A. Whole specimen, dorsal view. B. Same, ventral view. C. Camera lucida drawing of A. D. Same of B. Abbreviations: ap, anal plate; ca, corona analis; oz, ozophore; legs numbered from I–IV. Scale bars equal 0.2 mm (A–B) and 0.5 mm (C–D).

Remarks. The developmental stage of the holotype of *Foveacorpus parvus* sp. nov. (GPIH05130; Fig. 5.13A–D) is difficult to assess because important characters like the gonostome or tarsus IV are obscured. Due to its strong sclerotization and dark colouration the fossil presumably is an adult. Nevertheless, this is another interesting specimen whose body is completely covered with small pits similar to those observed in the holotype of *Foveacorpus cretaceus* sp. nov. (GPIH05129; see above). Many of these pits seem to be open and originally preserved on the ventral side of the body (Fig. 5.13B). Therefore we again exclude the possibility of an artefact. Additionally, both congeneric specimens possess a corona analis and granular legs (Fig. 5.13B, D cf. Fig. 5.11D). A modified right leg III as in specimen GPIH05129 cannot be observed in this fossil. Furthermore, GPIH05130 is smaller, features more bulbous ozophores and a more subtriangular anterior margin of the dorsal scutum. Based on these differences GPIH05130 is associated with a different new species.

Cyphophthalmi gen. sp.

Fig. 5.14A, B

Material. Specimen F2493, ex coll. Jörg Wunderlich; Myanmar, Hukawng Valley; Burmese amber, Upper Cretaceous (Lower Cenomanian).

Remarks. Specimen F2493 (Fig. 5.14A–B) is another male as it bears a prominent adenostyle on tarsus IV. Due to its poor preservation it is not possible to describe this specimen. Nevertheless, one of its tarsi IV is complete and bears a lamelliform adenostyle (Fig. 5.14B) which is not typical for modern members of the family Stylocellidae but is present in some of the species described here. This type of adenostyle also excludes Ogoveidae. It can be found in the families Sironidae, Pettalidae, Troglosironidae and in a few neogoveids. However, the families Troglosironidae and Neogoveidae can be excluded for this fossil as the claw on its leg II is smooth. Therefore we assume that the affinities of this specimen lie with the families Sironidae, Pettalidae or with an extinct lineage of Stylocellidae, seen e.g. in *Sirocellus iunctus* gen. et sp. nov. The specimen is illustrated here for the sake of completeness.

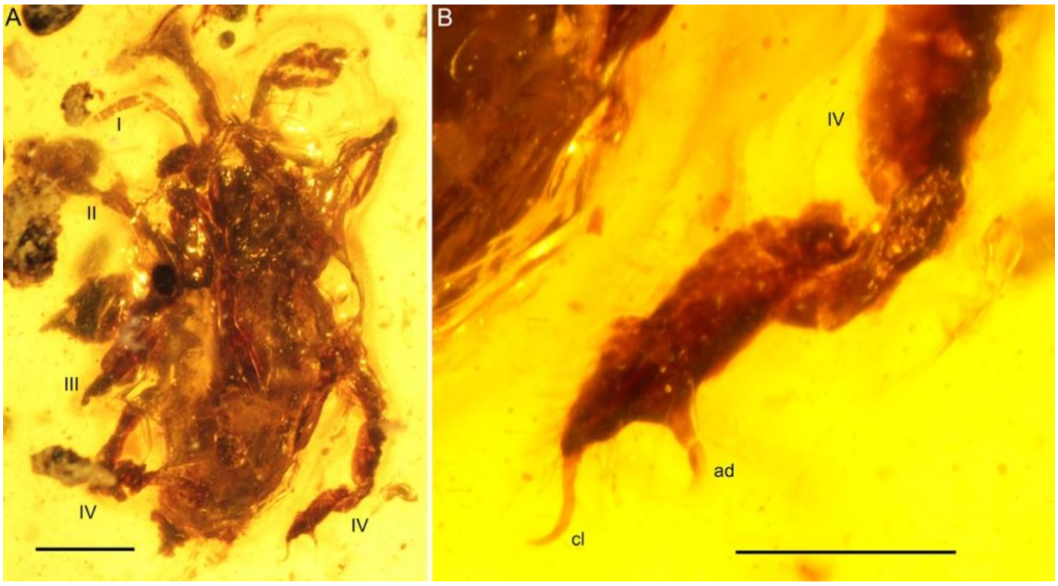

Figure 5.14. Cyphophthalmi gen. sp., male specimen F2493. A. Whole body, ventral view. B. Close-up of tarsus IV. Abbreviations: ad, adenostyle; cl, claw of tarsus IV; legs numbered from I–IV. Scale bars equal 1mm (A) and 0.5 mm (B).

5.5 Discussion

5.5.1 Biogeography

Continental Southeast Asia is today inhabited by members of a single family of Cyphophthalmi, namely the Stylocellidae. Therefore, it is not surprising that many fossil mite-harvestmen from Burmese amber show stylocellid affinities. Seven of the ten fossils described here are probably stylocellids, which suggests that this family was already predominant and abundant in the Upper Cretaceous (Cenomanian) Burmese amber forests. If the Burma terrane originated from Gondwana (see Metcalfe, 2017), the implication could be that stylocellids were originally Gondwanan too. Clouse & Giribet (2010) resolved Stylocellidae as the sister group to the now Holarctic family Sironidae. They also estimated that the split between Stylocellidae and Sironidae happened 295 Mya, with the diversification of stylocellids at 258 Mya (based on a fixed origin of Opiliones at 425 Mya) and thus long before the Upper Cretaceous. Based on their data, Clouse & Giribet (2010) already suggested a Gondwanan origin for the family Stylocellidae, which could have reached Southeast Asia via the Cimmerian palaeocontinent. By contrast, Oberski et al. (2018) estimated the diversification of stylocellids at about 164 Mya (134–192 Mya), thus nearly 100 Million years later than Clouse & Giribet (2010) did. During that time the breakup of Pangea was already underway and the Cimmerian palaeocontinent was about to reach Eurasia. An even younger diversification age for stylocellids might be possible because *Sirocellus iunctus* gen. et sp. nov. shows a combination of stylocellid and sironid characters. This potentially indicates a still ongoing transition during the Upper Cretaceous, although early Gondwanan stylocellids or sironids already inhabited the Southeast Asian area for ca. 50 million years.

Foveacorpus parvus gen. et sp. nov. and *F. cretaceus* gen. et sp. nov. are also of biogeographic interest. Both lack a clear connection to any of the living Cyphophthalmi families. The only hint of a modern relative is the peculiar Kenyan cave-adapted species *Marwe coarctata*. The latter can be considered a living fossil, as its familial affinities are still unclear, and it constitutes a relict since no other Cyphophthalmi lives in East Africa (Pettalidae are found in South Africa and Neogoveidae and Ogoveidae in the Bight of Boni and West Africa). Should *Foveacorpus parvus* gen. et sp. nov. and *F. cretaceus* gen. et sp. nov. represent a lineage related to *Marwe coarctata*, a Gondwanan origin for this group would also be possible. Another example of a modern Afrotropical group found in Burmese amber but missing from Southeast Asia today is the arachnid order Ricinulei. A similar biogeographical history for these two groups is conceivable (see e.g. Wunderlich, 2015, 2017). This shows how important it is to further study the modern fauna of Southeast Asia, as we cannot exclude the possibility of finding extant species related to *F. parvus* gen. et sp. nov. and *F. cretaceus* gen. et sp. nov. in the Southeast Asian rainforests. Due to their small size and specialized adaptations, they are possibly restricted to highly specific habitats.

5.5.2 Evolutionary history of Foveacorpus gen. nov.

The discovery of a new genus, probably belonging to an extinct family in Burmese amber, in the otherwise rather conservative Cyphophthalmi is surprising and allows a deeper look into the evolutionary history of this extraordinary suborder, which had an estimated origin ca. 345 million years ago (Oberski et al., 2018). Most of the described Cyphophthalmi fossils are from Burmese amber and are thus the oldest known representatives with an age of ca. 99 million years. The genus *Foveacorpus* gen. nov. might reveal a body plan much older than that and more typical for early diverging Cyphophthalmi. Overall, the body plan of *Foveacorpus* gen. nov. appears relatively simple. It lacks any breaks in the cuticle texture, especially dorsally, which mark the borders between the fused tergites and which are usually at least slightly expressed in extant taxa. Additionally, the spiracles of modern specimens are always clearly developed, whereas this extinct genus bears just a few very small denticles, somewhat circularly arranged and located in the expected position of a spiracle. Furthermore, an adenostyle which is typical for Cyphophthalmi males, has not been observed in *Foveacorpus* gen. nov. specimens. It remains to be seen if this character had not yet developed in this group, or if both specimens are simply females. On the other hand, the appearance of numerous tegumental pits suggests a high degree of specialization, which will be further discussed below.

5.5.3 Ecology of Foveacorpus gen. nov. and putative function of their pits

Foveacorpus parvus sp. nov. and *F. cretaceus* sp. nov. are remarkable specimens with a unique combination of characters. These Cyphophthalmi, with a body length of ca. 1 mm, are completely covered with small pits in the cuticle of the prosoma and opisthosoma (dorsal and ventral side). As mentioned before, there is one described modern stylocellid, *Leptopsalis foveolata* from Thailand, which bears a few relatively large pits at the posterior end of the opisthosoma (dorsal and ventral side). Clouse and Schwendinger (2012) suggested that these pits may represent an adaptation to the special conditions of the type locality. *Leptopsalis foveolata* was found near a waterfall and potentially experiences flooding from time to time. Therefore the authors assumed that the pits form a plastron to trap air bubbles, or that they are used for channelling water. It is possible that the pits of *Foveacorpus parvus* sp. nov. and *F. cretaceus* sp. nov. had a similar function, as these specimens probably lived in a somewhat comparable habitat. During the Upper Cretaceous the Burma terrane was potentially part of a trans-Tethyan island arc with a predominantly tropical climate where heavy rainfall and strong tropical storms occurred frequently (Grimaldi et al., 2002; Westerweel et al., 2019). For that reason it is conceivable that small ground-dwelling species often had to deal with large amounts of water and the pits could have created something like an air cushion. Using air bubbles is widely distributed across different groups of animals today. The best-known arachnid using air bubbles is probably the “diving bell spider” *Argyroneta aquatica* Clerck,

1757. The ricinuleid *Cryptocellus adisi* Platnick, 1988 has also shown facultative plastron respiration (Adis et al., 1999). Other adaptations to a very wet environment often include specialized hairs and a waxy surface coating observed in many bugs to prevent their spiracles from flooding (see e.g. Mahadik et al., 2020). Some kind of body coating is also visible in both fossils. However, it remains unclear if this coating represents an artefact of preservation or if this is a morphological character. Additionally, *Foveacorpus cretaceus* sp. nov. bears an unusually high number of relatively large setae around the gonostome and chelicerae. These could also have a similar function as the pits. It is further possible that the spiracles are reduced or not developed at all, because the pits are used for transporting oxygen.

Another interesting character of *Foveacorpus cretaceus* sp. nov. is the robustly developed left leg III (seen in ventral view) which bears additional thick setae on its tarsus and metatarsus. Similar adaptations are relatively common in arachnids, like e.g. camel spiders, and are usually used for digging holes. Nevertheless, these are always developed on both sides of the body and are more typical for legs I or IV.

5.6 Conclusion

The five new species, plus the two juveniles and three additional (but incomplete) specimens described here, suggest the existence of a diverse fauna of mite-harvestmen in Burmese amber forests. Most of them are stylocellids and they support the hypothesis that this family has a Gondwanan origin. However, dating that origin may require further data from molecular biology and historical biogeography which would allow to determine how and when this family became dominant in Southeast Asia. The Burmese amber fauna includes several Cretaceous Cyphophthalmi with unique adenostyle (see Fig. 5.15A–E) and ozophore forms.

It is also of interest for preserving at least one extant genus, *Leptopsalis*, still found in Southeast Asia today. This modern-looking fossil lived alongside several extinct genera with character combinations different from any extant taxa. Among these, *Sirocellus* gen. nov. has features intermediate between stylocellids and sironids, suggestive of a lineage which could have given rise to both families. *Foveacorpus* gen. nov. comprises unusual animals with possible affinities to an East African genus. It would be interesting to investigate the modern Asian Cyphophthalmi fauna further to see if comparable taxa are still found in this region today.

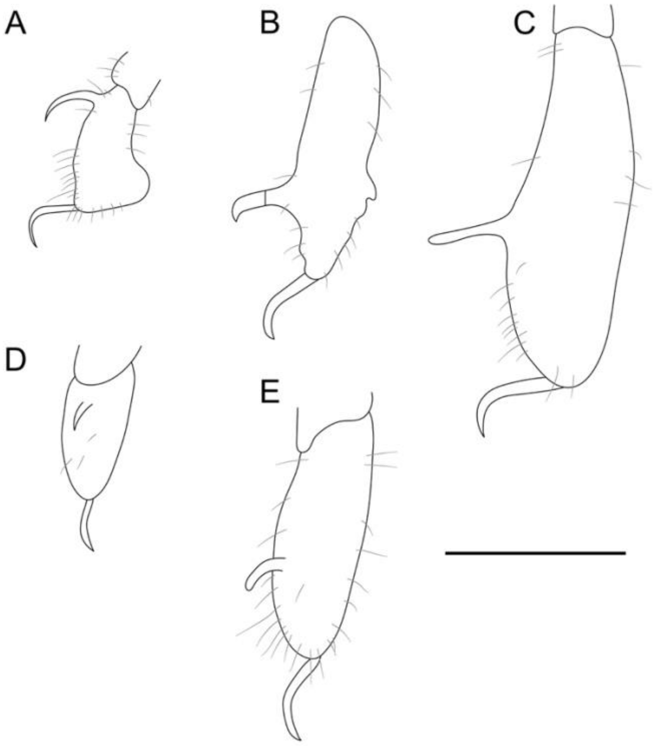

Figure 5.15. Comparison of shapes and positions of adenostyles on tarsus IV in five male specimens presented here. A. *Sirocellus iunctus* gen. et sp. nov. B. Specimen F2493. C. *Leptopsalis breyeri* sp. nov. D. Specimen BUB3653. E. Specimen BUB1542. Scale bar equals 0.5 mm.

5.7 Acknowledgements

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6 The first eupnoid harvestmen (Arachnida: Opiliones: Eupnoi) from mid-Cretaceous Kachin amber, with notes on sexual dimorphism in *Halitherses grimaldii* (Arachnida: Opiliones: Dyspnoi)

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7 3D analyses of the first ortholasmatine harvestmen (Arachnida: Opiliones: Dyspnoi) from European Eocene ambers

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7.1 Abstract

The first fossil representatives of the harvestman subfamily Ortholasmatinae (Opiliones: Dyspnoi: Nemastomatidae) are described as *Balticolasma wunderlichi* gen. et sp. nov. One male is preserved in Eocene Baltic amber and a presumably conspecific female in Eocene Rovno amber (Northwest Ukraine). Ortholasmatines are typically highly ornate arachnids, and for the first time with an amber harvestman we applied computed tomography using synchrotron radiation to investigate its three-dimensional morphology and surface structure in considerable detail. Its morphological characters, especially the dorsal ornament, appear to be closer to the extant Asian genera. In a wider biogeographic context our amber record is a significant find for the Palaeogene of Europe given that (1) it is another species apparently found in both Baltic and Rovno amber and (2) all modern ortholasmatines are restricted to East Asia and North and Central America.

7.2 Introduction

Of the four living suborders of harvestmen (Arachnida: Opiliones), the Dyspnoi group represents the second smallest with just over 385 described species. Despite this relatively restricted number, as compared to the remaining about 6250 living harvestmen species, the group is morphologically diverse (Kury, 2017). While several dyspnoids are small, dark and rather inconspicuous, others have developed structures such as a highly modified eye tubercle, or ‘hood’ such as is seen in the families Ischyropsalididae, Dicranolasmatidae, Trogulidae and the subfamily Ortholasmatinae of the Nemastomatidae (Gruber, 2007); see also below. All dyspnoids are characterized by a reduced or absent pedipalp claw and diaphanous teeth on the cheliceral fingers. Their modern biogeographic distribution is clearly focussed on the northern hemisphere (e.g. Schönhofer, 2013).

The comparably low modern diversity of Dyspnoi is reflected in their fossil record. Thirteen fossils have been formally described, with four from the Late Carboniferous belonging either to extinct families or unplaced at family level (e.g. Garwood et al., 2011; Kury et al., 2021a). Another extinct family, Halithersidae, is known from mid-Cretaceous Burmese amber (Dunlop et al., 2016). There is a questionable shale-preserved record of the living genus *Trogulus* Latreille, 1802 from Geiselthal in Germany (Haupt, 1956), while the remaining seven fossil dyspnoids all come from European ambers, i.e. Baltic, Bitterfeld and Rovno. These include an extinct genus placed in the superfamily Ischyropsalidoidea (Dunlop et al. 2012), a member of the family Sabaconidae, and five species from the subfamily Nemastomatinae of the family Nemastomatidae (e.g. Dunlop & Mitov, 2009; Elsaka et al., 2019; Mitov et al., 2021; and references therein).

Nemastomatidae also contains a second subfamily: Ortholasmatinae. These include some of the most striking-looking modern harvestmen, as they often bear a very complex and branched ocular tubercle in combination with a unique dorsal micro-sculpture consisting of so-called keel cells (e.g. Shear & Gruber, 1983; Shear, 2010; Martens, 2019). Seven extant genera with 27 species are currently recognised with a disjunct distribution. *Asiolasma* Martens, 2019 (with 6 species) and *Cladolasma* Suzuki, 1963 (with 1 species) come from mainland Southeast Asia and Japan. *Cryptolasma* Cruz-López, Cruz-Bonilla & Francke, 2018 (with 2 species), *Dendrolasma* Banks, 1894 (with 2 species), *Martensolasma* Shear, 2006 (with 2 species), *Ortholasma* Banks, 1894 (with 5 species) and *Trilasma* Goodnight & Goodnight, 1942 (with 9 species) all come from Northern and/or Central America. There are no modern representatives of this subfamily either in Europe or Central Asia. A Burmese amber dyspnoid fossil was initially placed in Ortholasmatinae, but (as noted above) this placement was questioned (Shear, 2010) and it was subsequently transferred to a new family (Dunlop et al., 2016). Here, we describe the first two unequivocal fossils of ortholasmatine harvestmen, which come from Eocene Baltic and Rovno amber dated to a still controversial age of ca. 33–37 Ma (Iakovleva, 2017; Dunlop et al., 2019; Mitov et al., 2021; and references therein). Given the often well-developed ocular process and dorsal ornamentation alluded to above, we applied for the first time high-resolution synchrotron-based computer tomography to a harvestman in amber, with the aim of facilitating better comparisons with the living genera and answering the question whether this European fossil has Asian or American affinities.

7.3 Material and methods

The specimens studied here originate from the private collection of Jörg Wunderlich, Hirschberg–Leutershausen, Germany (the Baltic specimen) and Jonas Damzen, Vilnius, Lithuania (the Rovno specimen). Both fossils are now deposited in the Museum für Naturkunde Berlin (repository numbers 4454 and 4455, under the acronym MB.A. for Museum Berlin, Arthropoda). The Baltic specimen was photographed using a Zeiss Discovery V8. A stack of images (20-50) at different focal planes were combined into a single picture using Helicon Focus 7. Afterwards the picture was corrected for brightness and contrast using Photoshop CS5. The Rovno specimen was photographed by Jonas Damzen and we use these images with his permission. Interpretative drawings were made using a Leica M205C stereomicroscope with a *camera lucida* attachment. These were digitally redrawn following the methods of Coleman (2003) with Adobe Illustrator CS2 using a Wacom Intuos graphic tablet.
The synchrotron radiation based computer microtomography (SRµCT) scan of the male (Baltic) specimen was performed at the Imaging Beamline P05 (IBL) (Greving et al., 2014; Haibel et al., 2010; Wilde et al., 2016) operated by the Helmholtz-Zentrum Hereon at the storage ring PETRA III (Deutsches Elektronen Synchrotron DESY, Hamburg, Germany) using a photon energy of 18 keV and a sample to detector distance of 80 mm. Projections were recorded using a custom developed 20 MP CMOS camera system (Lytaev et al., 2014) with

an effective pixel size of 1.27 µm. For each tomographic scan 2401 projections at equal intervals between 0 and π have been recorded. Tomographic reconstruction has been done by applying a transport of intensity phase retrieval and using the filtered back projection algorithm (FBP) implemented in a custom reconstruction pipeline (Moosmann et al., 2014) using Matlab (Math-Works) and the Astra Toolbox (van Aarle et al., 2015; van Aarle et al., 2016; Palenstijn et al., 2011). For processing raw projections were binned two times for further processing resulting in an effective pixel size of the reconstructed volume of 2.55 µm. VGSTUDIO MAX 3.4.3 was used to render and segment datasets at the Museum für Naturkunde, Berlin. Most of the important characters could be reconstructed using this method, except internal structures, which are apparently not preserved. The second (Rovno) specimen was not scanned due to its almost perfect preservation and because it was received for study at a later point.

The new fossils were compared with published descriptions of extant Ortholasmatinae harvestmen from the literature (see Introduction for references). All measurements are in mm and can represent slight approximations due to the three-dimensional position of the amber specimens in the amber matrix. Average values are marked with asterisks.

7.4 Systematic palaeontology

Order Opiliones Sundevall, 1833

Suborder Dyspnoi Hansen and Sørensen, 1904

Family Nemastomatidae Simon, 1872

Subfamily Ortholasmatinae Shear & Gruber, 1983

Remarks. MB.A.4454 (Figs. 7.1–7.3) is interpreted as a male, due to the presence of cheliceral apophyses. The missing pedipalp claw and a large ocularium extending anteriorly in the form of a hood strongly supports affinities to the Dyspnoi families Ischyropsalididae, Dicranolasmatidae, Trogulidae and Nemastomatidae (Ortholasmatinae). Of these, Trogulidae can be ruled out as the fossil bears cheliceral and pedipalpal apophyses (Figs. 7.2D; 7.3B) and more than two tarsomeres on leg II. Dicranolasmatidae can also be excluded as their eyes are usually located on a bifurcating hood. The dorsal tuberculation (Figs. 7.1A–C; 7.2A, C) of the fossil shows superficial similarities to certain genera of Ischyropsalididae, particularly *Ceratolasma* Goodnight & Goodnight, 1942 redescribed and figured by Gruber (1978). However, the overall form and structure of the pedipalp and presence of pedipalp apophyses (Figs. 7.2D; 7.3B) argues against placement in this family. Furthermore, the ‘hood’ in *Ceratolasma* is usually simple, nearly horizontal and extending in form of a blunt club. The most similar condition of the fossil’s ocular process can probably be found in the living ortholasmatine genus *Cryptolasma* Cruz-López et al., 2018 from Mexico. However, the ocular process of the latter is much thinner, less curved and "branched" – ornate dorso-laterally with many, markedly elevated, anvil-shaped tubercles. A branched ocular process seems to be absent in the amber fossil as neither the CT scan nor light microscopy reveal such a feature (Figs. 7.1A–C; 7.2A, C).

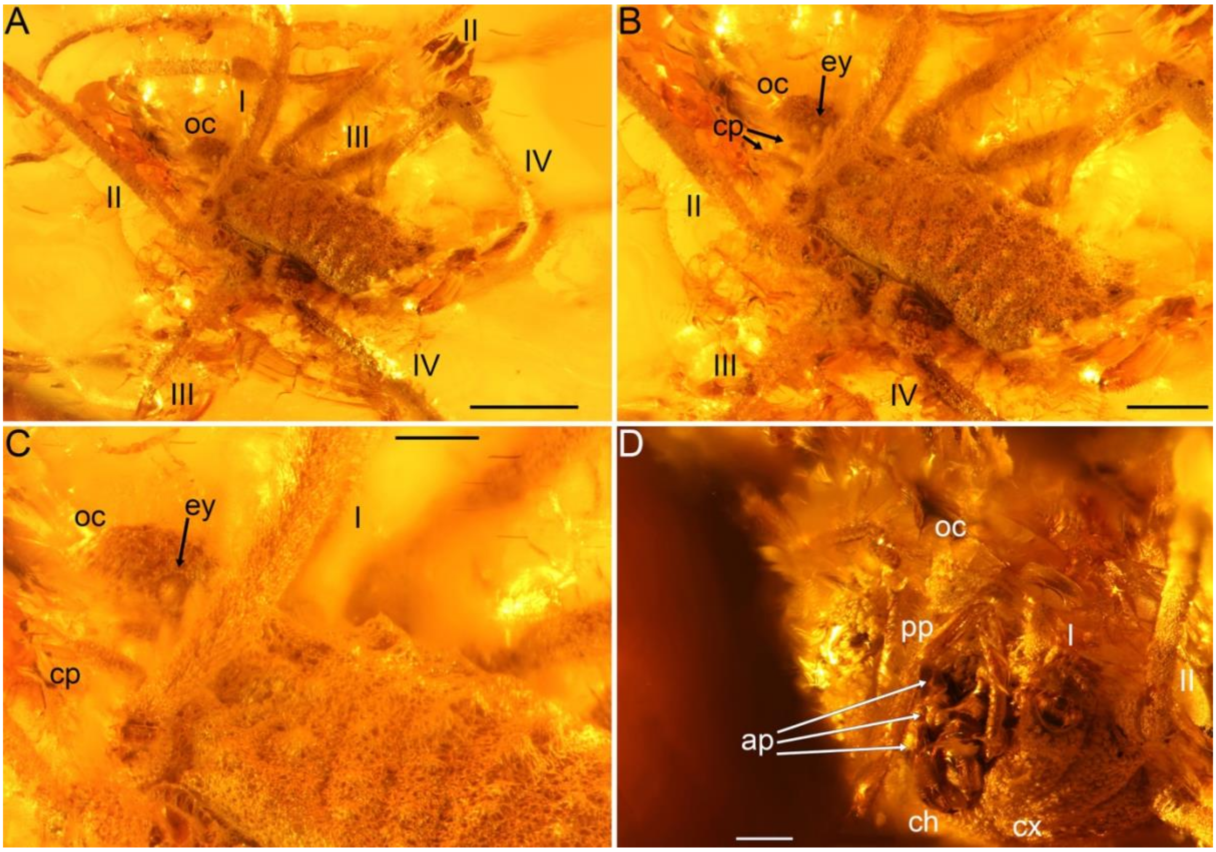

Figure 7.1. *Balticolasma wunderlichi* gen. et sp. nov., holotype: MB.A.4454. A. Dorsolateral overview. B. Close-up of the body. C. Close-up of the anterior body and ocular process. D. Close-up of the chelicerae and pedipalps. Abbreviations: ap, apophysis; ch, chelicerae; cp, carapace process; cx, coxa; ey, eye lens; oc, ocular tubercle; pp, pedipalp; legs numbered from I–IV. Scale bars equal 1mm (A), 0.5mm (B) and 0.25mm (C, D).

Most of the characters observed in the fossil are thus more consistent with members of the subfamily Ortholasmatinae, such as the presence of cheliceral and pedipalp apophyses, large lateral carapace processes, a flattened body and the hood; even though the appearance of the latter is quite unique. Another important character for most modern Ortholasmatinae is the presence of dorsal keel-cells. These are also not clearly developed in the fossil, but Martens (2019) described a new Asian species *Asiolasma billsheari* Martens, 2019 with a very indistinct network of keel-cells. This condition is again comparable to that observed in our new fossil and this character is discussed in more detail below. Martens (2019) further stated that Asian Ortholasmatinae are likely to represent a relict group indicated by plesiomorphic character states such as a poorly developed keel-cell network. We suggest that this new fossil may represent the ancestral lineage for modern ortholasmatines and based on its unique character combinations the new fossil is placed in a new genus and species.

Genus *Balticolasma* gen. nov.

Type species. *Balticolasma wunderlichi* gen. et sp. nov.

Etymology. From the Baltic region where the amber hosting one of the specimens originates from and the suffix 'lasma' applied to a few possibly closely related modern ortholasmatine genera.

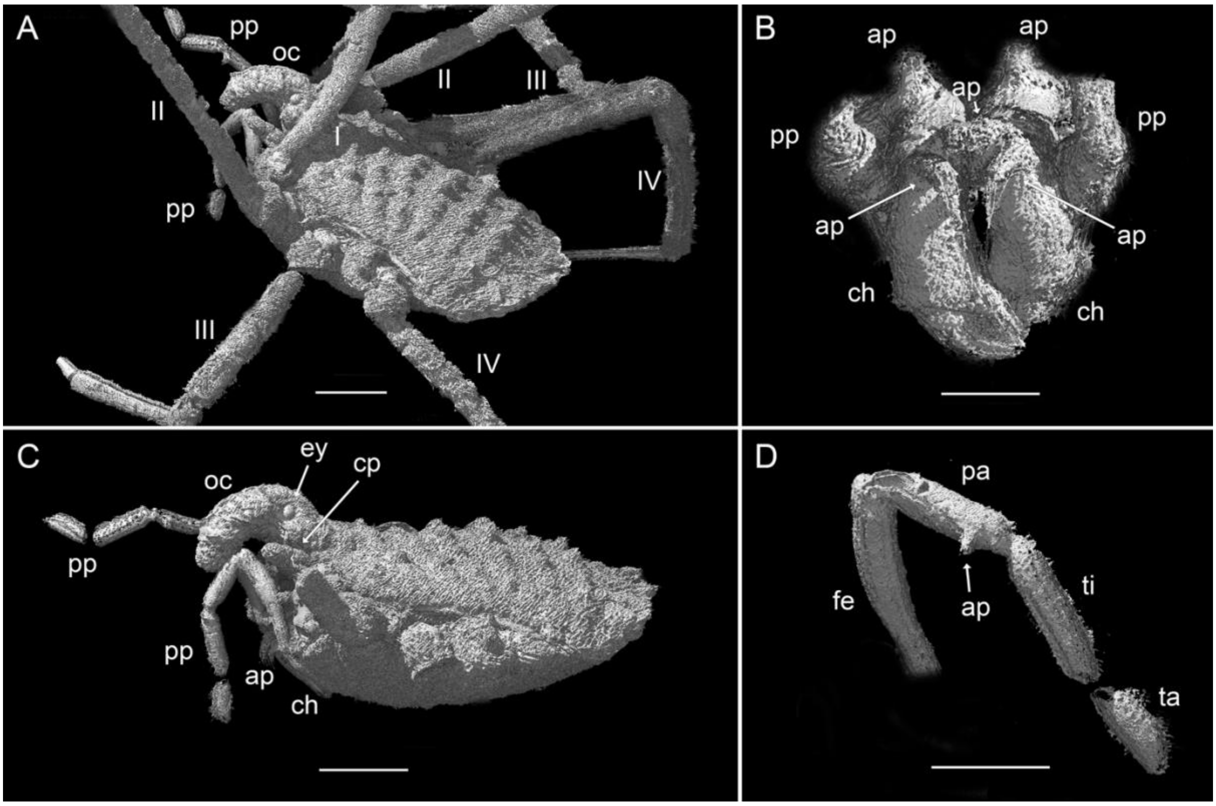

Figure 7.2. *Balticolasma wunderlichi* gen. et sp. nov., holotype: MB.A.4454. A. Dorsolateral overview of the 3D model. B. Details of the chelicerae, apophyses arrowed. C. Lateral view of the specimen without legs, eye lens and carapace process arrowed. D. Details of a pedipalp, patella apophysis arrowed. Abbreviations: ap, apophysis; ch, chelicerae; cp, carapace process; ey, eye lens; fe, femur; oc, ocular tubercle; pa, patella; pp, pedipalp; ta, tarsus; ti, tibia; legs numbered from I–IV. Scale bars equal 0.5mm (A, C); 0.2mm (B) and 0.3mm (D).

Diagnosis. Relatively small (body length less than 3.00 mm) ortholasmatine harvestman with a flattened body, covered with seven rows of prominent, distally increasing tubercles. Dorsal ornamentation in form of a complex, irregular fine weave composed of filamentous elements. Ocular process tuberculated in form of a large, arched, downwards-bending and unbranched hood extending anteriorly. Each side of the hood bears two differently sized digitiform processes projecting from the anterior margin of the prosoma. Chelicerae with three apophyses in males. First cheliceral segment with one dorsal conical apophysis proximally and an additional club like apophysis distally. Second cheliceral segment with a long, downward curved sickle-shaped apophysis proximally. Pedipalps relatively short and slender. Pedipalp patella in males with rather small medio-distal spine-like apophysis. Legs long and somewhat granulated. Ventral body completely covered with rounded tubercles. Left and right margins of the ventral abdomen with a bridge-like extension reaching the outer margin of the anal operculum.

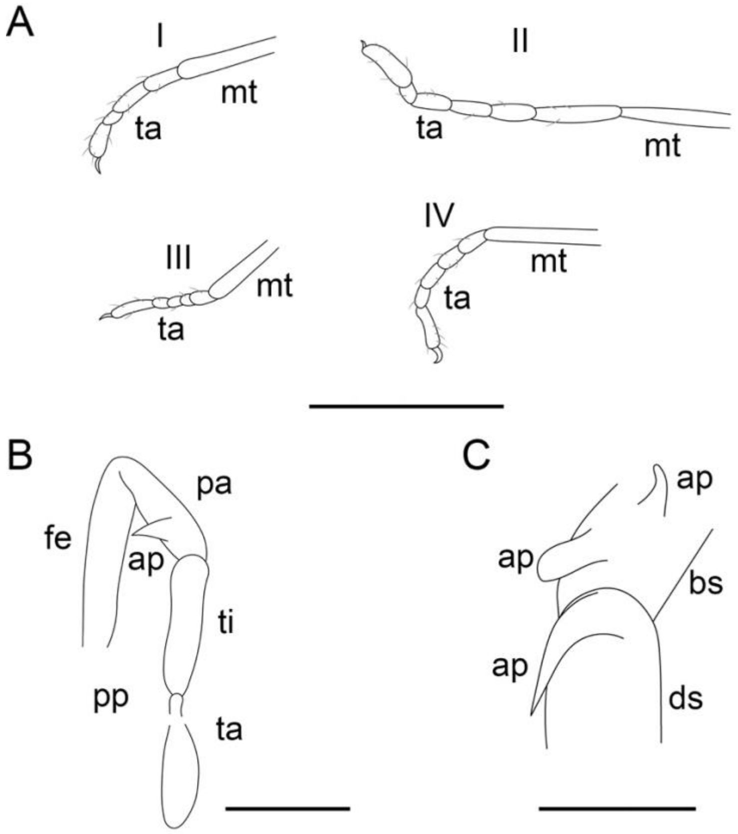

Figure 7.3. Details of *Balticolasma wunderlichi* gen. et sp. nov., holotype: MB.A.4454. A. Camera lucida drawing of the leg tarsi.. B. Camera lucida drawing of a pedipalp. C. Camera lucida drawing of a chelicerae. Abbreviations: ap, apophysis; bs, basal segment; ds, distal segment; fe, femur; mt, metatarsus, pa, patella; pp, pedipalp; ta, tarsus; ti, tibia. Scale bars 1mm (A); 0.25mm (B) and 0.2mm (C).

Species *Balticolasma wunderlichi* gen. et sp. nov.

Type material. Holotype. MB.A.4454, male, ex coll. Jörg Wunderlich. Baltic amber. Palaeogene, Eocene (Priabonian). Paratype. MB.A.4455, female, ex coll. Jonas Damzen. Ukraine: Rovno region; Rovno amber. Palaeogene, Eocene (Priabonian).

Etymology. In honour of Jörg Wunderlich (Hirschberg–Leutershausen, Germany) who has worked extensively on amber spiders and who has continued to provide the authors with many interesting harvestman fossils. Name masculine and in genitive case.

Diagnosis. As for the genus.

Description of the male holotype. Body oval, flattened and covered with seven rows of tubercles increasing in size distally, L 2.16 (excluding the hood), prosoma W 0.92, opisthosoma W 1.10 (Figs. 7.1A–C; 7.2A, C). Scutum magnum present. Ocular process tuberculated and robust, extending anteriorly and forming a large, downwards-bending hood, bearing lateral eye lenses somewhat removed from the base, L 0.55, W 0.32, eye lens diameter 0.08 (Fig. 7.2C). Carapace with two lateral digitiform processes projecting anteriorly on each side, the outer one is larger (0.50) than the inner one (0.18) (Fig. 7.2A, C). A third very small process is located below the largest process near coxa I. Chelicerae relatively small and mostly smooth. Basal segment with a conical apophysis proximally and a club like apophysis distally. Distal segment with a sickle-shaped and downwards bent apophysis proximally, L 0.17 (Figs. 7.1D; 7.2B; 7.3C). Chelicerae basal segment L 0.20, distal segment L 0.38, finger L 0.22. Pedipalps short, slender and covered with clavate setae. Pedipalp tarsus in particular setose. Pedipalp patella with a small thorn-like apophysis medio-distally (Figs. 7.2D; 7.3B). Pedipalp claw absent. Pedipalp length: fe 0.59, pa 0.35*, ti 0.46, ta 0.25, total (fe–ta) 1.65. Legs long and sometimes granulated. Leg II longest. Margins of leg coxae with anvil-shaped tubercles. Leg tarsi subdivided, ending in a single claw. Tarsal formula: 4–5; 6+; 5; 5–6. Leg length: Leg I cx 0.51, tr 0.27*, fe 1.37, pa 0.45, ti 0.92, mt 0.94, ta 0.64, total (cx–ta) 5.10; Leg II cx 0.70, tr 0.20, fe 2.10, pa 0.63, ti 2.26, mt 2.21, ta 1.31, total (cx–ta) 9.41; Leg III cx 0.68, tr 0.27, fe 1.34, pa 0.34, ti 0.68, mt 0.53, ta 0.63, total (cx–ta) 4.47; Leg IV cx 0.63, tr 0.26, fe 1.84, pa 0.33*, ti 1.63, mt 1.32, ta 0.74, total (cx–ta) 6.75. Ventral characters equivocal.

Description of the female paratype. Body somewhat pear-shaped, flattened and again covered with seven rows tubercles increasing in size distally, L 2.40 (excluding the hood), prosoma W 1.26, opisthosoma W 1.69 (Fig. 7.4A). Scutum magnum present. Last row of tubercles somewhat protruding the body posteriorly. Tuberculated ocular process robust, extending anteriorly and forming a large hood bending downwards, bearing lateral eye lenses near the middle, L 0.71, W 0.49, eye lens diameter 0.11 (Fig. 7.4B). Carapace with additional lateral processes in form of digitiform spines, one larger (L 0.48) and one smaller (at least 0.14) closer to the hood on each side (Fig. 7.4A, B). Chelicerae relatively small and sparsely covered with small setae on the distal segment (Fig. 7.5A, B). Cheliceral apophyses absent. Chelicerae basal segment L ?, distal segment L 0.25, finger L 0.22. Pedipalps short, slender and setose (often in form of clavate setae), especially on the tarsus (Fig. 7.5A, B). Pedipalp patella apophysis absent. Pedipalp length: tr 0.10, fe 0.44, pa ?, ti 0.20, ta 0.19, total (tr–ta, without pa) 0.93. Legs long and granulated. Leg II longest. Leg coxae completely tuberculated. Leg tarsi subdivided, ending in a single claw. Tarsal formula: 5; 8; 6; 6. Leg length: Leg I cx 0.59, tr 0.19, fe 1.12, pa 0.48, ti 0.84, mt 0.64, ta 0.60, total (cx–ta) 4.46; Leg II cx 0.63, tr 0.23, fe 2.80, pa 0.56, ti 2.48, mt 2.20, ta 1.16, total (cx–ta) 10.06; Leg III cx 0.61, tr 0.21, fe 1.20, pa 0.37, ti 0.60, mt 0.88, ta 0.84, total (cx–ta) 4.71; Leg IV cx 0.73, tr 0.22, fe 1.88, pa 0.40, ti 1.16, mt 1.28, ta 0.88, total (cx–ta) 6.55.

Ventral body completely covered with tubercles (Fig. 7.5A, B). Genital operculum sub-trapezoidal and rounded anteriorly, L 0.86, anterior W 0.40, maximum posterior W 1.70, with a subtle suture near the anterior margin. Anal operculum rounded L 0.43, W 0.70. Left and right margins of the ventral abdomen with well-developed pleural/intertergal membranes reaching the outer margin of the anal operculum.

Remarks. MB.A.4455 (Figs. 7.4–7.5) is an adult female, as it lacks the apophysis on the cheliceral segments and on the pedipalp patella, and due to its relatively large size. Based on the similar habitus and ornament, it is fairly certain that this remarkably well-preserved specimen represents the same species as the Baltic amber male fossil described above. The massive, unbranched and downward-bending ocular process and the dorsal ornamentation are almost identical in the two specimens (Figs. 7.2A, C; 7.4A, B). Sexually dimorphic characters such as the already mentioned absence of cheliceral and pedipalpal apophyses and the larger size of the female can also often be observed in living nemastomatids and especially ortholasmatines (e.g. Shear & Gruber, 1983; Shear, 2010).

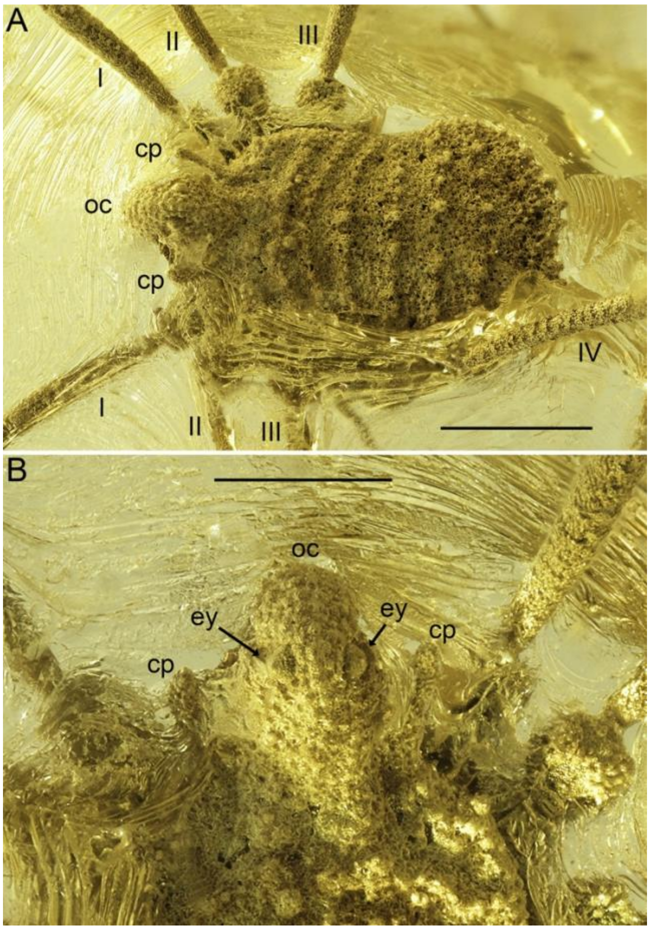

Figure 7.4. *Balticolasma wunderlichi* gen. et sp. nov., paratype: MB.A.4455. A. Dorsal view of the body. B. Close-up of the ocular process in dorsal view, eye lenses arrowed. Abbreviations: cp, carapace process; ey, eye lens; oc, ocular process; leg numbered from I–IV. Scale bars equal 1mm (A) and 0.5mm (B). Photos by Jonas Damzen.

The number of tarsomeres on the leg tarsi also differs somewhat in both fossils. Shear & Gruber (1983) already mentioned differences in the tarsal segment count, which is usually higher in living males on legs I and II. In our case, the female bears one more tarsomere on leg III. The number of tarsomeres on leg I, II and IV could be identical, however the exact number of tarsomeres remains difficult to resolve.

The almost perfect preservation of this Rovno fossil facilitates a closer look at the unusual dorsal ornamentation and it reveals further ventral details which could not be reconstructed in the Baltic specimen. As mentioned previously living ortholasmatines are typically characterized by the presence of a distinct interconnected network of so-called keel cells dorsally, which consist of numerous anvil shaped tubercles. By contrast, this fossil shows a complex and irregular filamentous ornament with additional rows of tubercles implying early ortholasmatine affinities (Fig. 7.4A). Some of the tubercles seem to be covered with a kind of secretion on their tips. Nevertheless, it remains uncertain whether these originate from the specimen or from the preservation.

The tuberculated ventral body can also often be observed in modern ortholasmatines (e.g. Zhang & Zhang, 2013). However, the region around the anal operculum seems to differ slightly from modern specimens as the left and right pleural/intertergal membranes of this fossil are more pronounced.

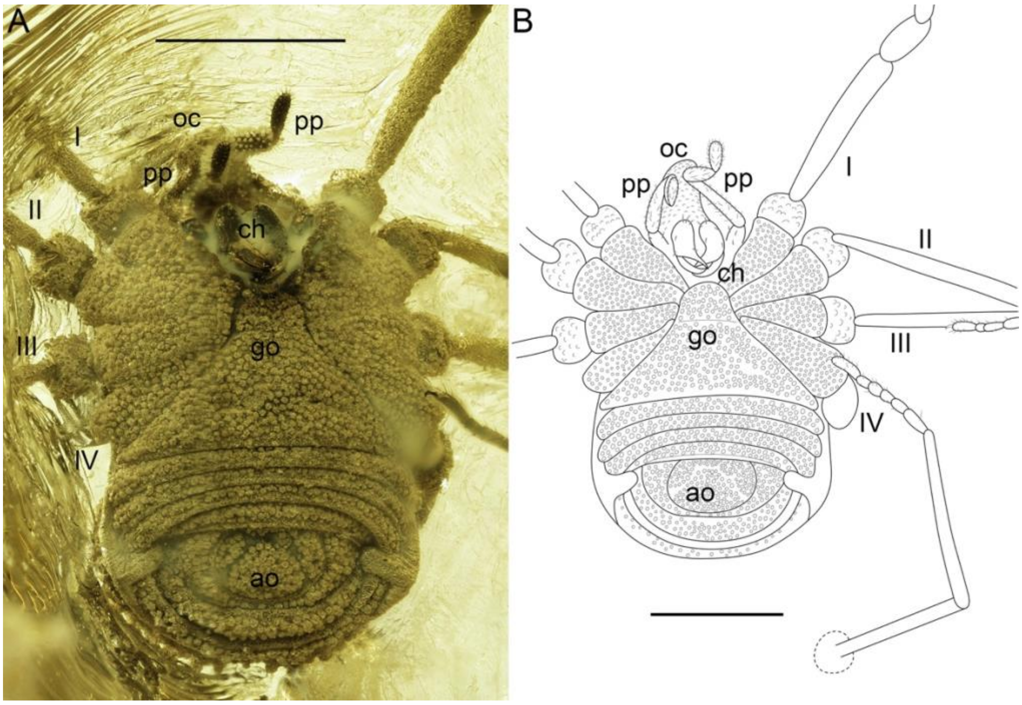

Figure 7.5. *Balticolasma wunderlichi* gen. et sp. nov., paratype: MB.A.4455. A. Close-up of the ventral body (Photo by Jonas Damzen). B. Camera lucida drawing of A. Abbreviations: ao, anal operculum; ch, chelicerae; go, genital operculum; oc, ocular process; pp, pedipalp; leg numbered from I–IV. Scale bars equal 1mm.

7.5 Discussion

Our new fossil indicates for the first time that harvestmen belonging to the subfamily Ortholasmatinae were also present in Northern Europe during the Eocene, but became extinct here at a later stage. It fits a broader geographical pattern in which Baltic amber sometimes preserves lineages which are now restricted to Asia and/or North America. Examples specifically relating to the harvestmen here would include the genera *Caddo* Banks, 1892 found today in Japan and North America and *Protolophus* Banks, 1893, and *Eumesosoma* Cokendolpher, 1980 both found in North America from the suborder Eupnoi (see Elsaka et al., 2019); see also Dunlop & Mitov, 2011 and discussions therein for *Siro* Latreille, 1797.

The morphology and ornament of the new fossil cannot be matched exactly to any of the living ortholasmatines which we believe merits the creation of a new genus. The next interesting question is whether its affinities lie with the modern East Asian or American faunas? This also relates to the wider, and still not satisfactorily resolved, question of where the subfamily originated. Shear (2010) entertained origins in the New World, but Martens (2019) suggested several lines of evidence for an Asian origin with the American species being more derived. The genital characters and ecological arguments, i.e. American species have more complex male genitalia and occupy a more diverse range of habitats, cannot be tested in the fossil. However, Martens (2019) also noted that Asian taxa tend to have a more irregular dorsal ornamentation, less clearly organised into discrete cells. Furthermore, the hood in Asian species has lateral tubercles which are free along their length while the hood of many American species is more complex with interlinking elements between the lateral tubercles to produce a net- or lattice-like morphology. The morphology of *Balticolasma wunderlichi* gen. et sp. nov. thus appears to be closer to the Asian species as in adaptations – most of its characters are even more simplified. Its ocular process is more robust, but only covered with smaller tubercles and the dorsal ornamentation lacks any particular pattern of keel cells. Martens (2019) also stated that Asian ortholasmatines preferably "live in humid litter or under pieces of dead wood in primeval forests, montane broadleaf forests, coniferous forests and (sub)tropical evergreen forests, with a closed canopy”. Most of these were not present in the humid warm-temperate climate of the ‘Baltic amber forests’, according to Sadowski et al. (2017). However, extant floras (based on conifers) which come closest in representing the ‘Baltic amber forests’ can be found today in East Asia (especially south-eastern China) and North America including Mexico (Sadowski et al., 2017a, table 12). Both areas are today still inhabited by a few of the Asian and most of the American ortholasmatines respectively. In summary, we think the new fossil lends support to Martens (2019) proposal that ortholasmatines first evolved in the Old World. We might even speculate that the group originated in the western Palaearctic, although it eventually became extinct there. In support of this scenario we could point to the relatively undifferentiated body and ornament of the new amber fossil as might be predicted from an ancestral ortholasmatine lineage, and a western Palaearctic origin would also be consistent with the concentrated high diversity of the second nemastomatid subfamily (and putative sister-group), Nemastomatinae, in this area.

7.6 Conclusion

The first fossil ortholasmatines have been described from Eocene Baltic and Rovno amber. These new finds improve our understanding of the evolutionary history and support the hypothesis of an Old World origin for this unique group of harvestmen. Baltic amber inclusions are already known for their great diversity and continue to reveal species which are not present in Europe today. The additional specimen from Rovno amber shows once more that both amber sources share a common harvestmen fauna and are thus likely contemporary. Furthermore, our new fossil represents the first calibration point for this subfamily which can be used in future studies to date the harvestman tree of life more precisely. However, many questions remain to be answered in forthcoming studies and additional finds from other sources are needed to fully reconstruct the history of Ortholasmatinae. The Southeast Asian Burmese amber from the Late Cretaceous has probably the largest potential as it is significantly older and the majority of the modern Asian ortholasmatine fauna is still living in this area.

7.7 Acknowledgements

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8 Palaeobiogeography and palaeoecology of harvestmen (Arachnida: Opiliones) from mid-Cretaceous Burmese and Palaeogene European ambers: A review

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prepared for submission in Palaeo3

8.1 Abstract

The mid-Cretaceous Burmese amber from the Kachin state in northern Myanmar and the Palaeogene European amber complex (i.e. Baltic, Bitterfeld and Rovno amber) represent the most species-rich and extensively studied amber deposits. We summarize data on fossil harvestmen (Arachnida: Opiliones) from these localities with the aim of reconstructing their palaeobiogeography and palaeoecology. For the first time arachnid data is explicitly combined with fossil plant data and the latest reconstructions of the respective palaeoenvironments to try and place the amber harvestmen in an appropriate palaeoecological context based also on their morphology and analogues to living species. For Burmese amber our results support previous hypotheses of Gondwanan affinities for the fauna. Suggested very hot and humid environments of the amber-producing forest are reflected in harvestman groups typical for modern tropical rainforests and species with possible anatomical adaptations to very wet climate. For the European amber complex our results support the idea that it sampled a Holarctic fauna, including taxa now restricted to East Asia or/and North America. The European amber forests have a flora more consistent with warm-temperate forests such as those found e.g. in south-eastern China and along the West coast of North America today, albeit with evidence for a mosaic of wetter and drier habitats which may have contributed to a more diverse harvestmen fauna with individual genera preferring different niches. Taphonomic biases of resin preservation are also discussed, such as the predominance in European ambers of harvestman groups associated with trees today.

8.2 Introduction

Harvestmen (Arachnida: Opiliones) are a diverse group of arachnids with more than 6600 living species distributed among four extant suborders (Fig. 8.1). Laniatores is by far the largest suborder with almost 4200 extant species, followed by Eupnoi with ca. 1800, Dyspnoi with 409 and Cyphophthalmi with 229 species (Kury et al., 2021b). Harvestmen are typically characterized as having a small body and extremely long legs, hence the common name “daddy long-legs”. However, as a group they are morphologically diverse and especially within Laniatores many robust and sometimes spiny individuals can be found (e.g. Pinto-da-Rocha & Giribet, 2007). Cyphophthalmi also differ from the typical picture of a harvestman, having short legs and unique cone-like structures called ozophores on the prosoma (e.g. Clouse, 2012). Harvestmen can be found across a wide range of habitats on all continents, except Antarctica (Curtis and Machado, 2007). This includes Greenland and even some remote Pacific islands (Goodnight & Goodnight, 1957; Meinertz, 1973). The highest diversity is found in the tropics, but they can also occur, albeit more rarely, in high latitudes/altitudes and/or xeric environments. Some sclerosomatids, like *Trachyrhinus marmoratus* Banks, 1894, are known to be highly abundant in arid or semiarid environments of, e.g., the Chihuahuan Desert in the southern USA and in south-western New Mexico (Cokendolpher et al., 1993; MacKay et al., 1992).

Figure 8.1. Examples of living harvestmen from each suborder. A) Laniatores (Podoctidae, photo by Nicky Bay); B) Dyspnoi (Ortholasmatinae, photo by Gonzalo Giribet); C) Cyphophthalmi (Stylocellidae, photo from Gonzalo Giribet); D) Eupnoi (Sclerosomatidae, photo by Nicky Bay). Photos are used with permission from Nicky Bay and Gonzalo Giribet).

A few harvestmen species have also adapted to a number of different habitats. The best example is probably the phalangiid *Mitopus morio* Fabricius, 1779, which can be found in woodland and tundra regions and from sea-level to high-altitude sites (Slagsvold, 1976; Tchemeris, 2000; Bliss & Arnold, 1983). In general, short-legged species tend to favour soil or leaf litter habitats, while leg length seems to increase for taxa living higher up in the vegetation. Cave-dwelling harvestmen can also be found, often revealing adaptations like the reduction or loss of eye lenses (e.g. Curtis & Machado, 2007 and references therein).

The present fossil record of harvestmen does not reflect the species richness of the living taxa. Sixty-one valid species of fossil harvestman are currently recognised in the literature (Dunlop et al., 2023). This is evidently only a fraction of their potential diversity. Fossils comprise 19 Eupnoi, 16 Laniatores, 15 Dyspnoi, 8 Cyphophthalmi, 2 species in an extinct suborder Tetrophthalmi, and a single species of uncertain affinities (Bartel et al., 2021; Bartel et al., 2022; Bartel & Dunlop, 2023; Bartel et al., 2023a, 2023b, 2023c; Dunlop et al., 2023; Elsaka et al., 2019). The oldest records date back over 400 million years (Ma) to the early Devonian (Dunlop et al., 2003b). These are followed by a few Carboniferous harvestmen, at least two of which are explicitly assignable to Eupnoi and Dyspnoi respectively (Dunlop, 2004a; Garwood et al., 2011). Most fossils derive from younger amber deposits (Fig. 8.2). Of particular interest is the mid-Cretaceous (upper Albian–lower Cenomanian) Burmese amber of Myanmar, which hosts the oldest Cyphophthalmi and Laniatores, such as *Palaeosiro burmanicum* Poinar, 2008 or *Petrobunoides sharmai* Selden et al., 2016.

Figure 8.2. Examples of fossil harvestmen in amber from each suborder. A) *Tyrannobunus aculeus* Bartel & Dunlop, 2023 (Eupnoi) from Burmese amber (reproduced with permission from the copyright holder); B) *Baltonychia obscura* Bartel et al., 2022 (Laniatores) from Baltic amber (photographed by Jonas Damzen); C) *Foveacorpus cretaceus* Bartel et al., 2023a (Cyphophthalmi) from Burmese amber; D) *Balticolasma wunderlichi* Bartel et al., 2023b in prep. (Dyspnoi) from Rovno amber (photographed by Jonas Damzen). Scale bars equal 1mm (B, D) and 0.5mm (A, C).

Also important are the Baltic, Bitterfeld (eastern Germany) and Rovno (Ukraine) ambers, sampling the Palaeogene of north-central Europe (e.g. Dunlop, 2006; Dunlop & Mitov, 2009; Mitov et al., 2021). These contain an interesting mix of genera, including some that are still found in Europe today, like *Lacinius* Thorell, 1876, *Mitostoma* Roewer, 1951 or *Siro* Latreille, 1796, but also genera restricted to East Asia and/or the Americas (e.g. *Caddo* Banks, 1893 and *Eumesosoma* Cokendolpher, 1980), and a few genera that appear to be extinct (e.g. *Baltonychia* Bartel et al., 2022, *Piankhi* Dunlop et al., 2012 and *Stephanobunus* Dunlop & Mammitzsch, 2010). Here, we focus on the two main sources of fossil harvestman data: namely Burmese amber from the Kachin state in northern Myanmar and the European Baltic/Bitterfeld/Rovno complex in order to assess their potential for understanding the palaeoecology and biogeographical distribution of harvestmen. These animals are interpreted as having a fairly low dispersal ability which, coupled with their long fossil record, makes them ideal for palaeoreconstructions (Dunlop et al., 2003b; Sharma & Giribet, 2011). Cyphophthalmi may be particularly suitable here as most families are restricted to specific geographical regions today (Boyer and Giribet, 2009; Clouse & Giribet, 2010; Giribet et al., 2012b).

Two hypotheses regarding the amber deposits under consideration are of particular interest for palaeobiogeography. One suggests that Burmese amber was deposited on a Cretaceous island which potentially rifted off from Australia and thus hosts a largely Gondwanan fauna (e.g. Hall, 2012; Metcalfe, 2009; Westerweel et al., 2019). A second hypothesis suggests that the Baltic/Bitterfeld/Rovno amber deposits were sampling a previously Holarctic arthropod assemblage, elements of which were subsequently lost in Europe, possibly due to colder climate conditions after the Eocene's Thermal Maximum (e.g. Zachos et al., 2001). In the current study, we address these hypotheses using the latest harvestmen records from the two selected regions and corresponding time intervals. Furthermore, the harvestman fossils from the respective amber deposits are discussed in terms of the appropriate palaeoecological context based on available palaeobotanical data and climate/environmental reconstructions for the respective amber deposits, as well as the ecology of modern examples of the harvestman families and genera found there as inclusions.

8.3 Regional setting / geological background

8.3.1 Burmese amber

During the past two decades the Burmese amber deposits from Myanmar have become perhaps the most important source of information about Cretaceous terrestrial invertebrates. Until now, 2524 fossil species in 1622 genera and 702 families have been described, including 2349 species of arthropods (Ross, 2023 and references therein). The largest part of the amber material derives from the Hukawng valley in the Kachin state of northern Myanmar. This area includes a number of mines like, e.g., the Khanjamaw site, the Angbamo site, the often cited Noije Bum site and the Hkamti site, which has been active since 2013 (Cruickshank & Ko, 2003; Xing & Qiu, 2020; Xing et al., 2016). A detailed study of the geology of the Noije Bum hill (Cruickshank & Ko, 2003) reported that most of the amber-bearing material consists of clastic sediments with thin limestone beds and carbonaceous rocks. The amber-bearing material from the Noije Bum site was dated to 98.79 ± 0.62 Ma based on U–Pb dating of zircons (Shi et al., 2012). This age has been widely accepted, although some authors have raised concerns about this method as it might reveal younger ages (Mao et al., 2018 and references therein). Amber pieces from the Hkamti site however, appear to be somewhat older (i.e. 109.7 ± 0.4 Ma) as suggested by Xing & Qiu (2020) based on U–Pb dating of zircons.

Another smaller amber deposit can be found near Tilin in central Myanmar. Tilin amber was dated to 72.1±0.3 Ma based on the same dating method. Mostly insects in at least 12 families have been described from this deposit so far (Zheng et al., 2018). The modern location of each deposit is shown in Fig. 8.3.

Figure 8.3. Main deposits of Myanmar amber marked with red circles. Map modified from mapchart.net.

Poinar et al. (2007) suggested members of the family Araucariaceae (in particular the genus *Agathis*) as possible resin source trees. More recent studies (Seyfullah et al., 2020) suggested a wider range of potential source trees, at least for the Early Cretaceous Crato Formation in Brazil. In addition to conifers of the families Araucariaceae and Cheirolepidiaceae, an extinct group of gymnosperms called Erdtmanithecales has been proposed as potential resin producers (Seyfullah et al., 2020 and references therein). The latter could also play an important role in the production of Burmese amber resin, as possible pollen from Erdtmanithecales trees have been found on various insect inclusions (Grimaldi et al., 2019; Tihelka et al., 2022).

8.3.2 European ambers

The three largest and most studied amber deposits within Europe consist of the Baltic, Bitterfeld and Rovno regions. Most of the Baltic amber material derives from deposits of the Samland Peninsula in the Kaliningrad Oblast of Russia, where it can be found within the so-called "Blue Earth" layer consisting of clayish, micaceous fine sand and high amounts of glauconite. Furthermore, it is also possible to find smaller amounts of Baltic amber in coastal areas of the North and Baltic seas (Weitschat & Wichard, 2010). The Bitterfeld amber deposit is restricted to the state of Saxony-Anhalt in Germany and usually occurs within layers of amber silt known as „Bernsteinschluff" (Dunlop, 2010; Dunlop et al., 2018 and references therein).

Rovno amber deposits can predominantly be found in the homonymous Rovno region in north-western Ukraine (see Fig. 8.4; Perkovsky et al., 2010). The autonomy and age of these three deposits have long been debated and still cannot be satisfactorily resolved, mainly due to potentially reworked material and the fact that amber itself cannot be dated (e.g. Grimaldi, 2019).

Figure 8.4. Main deposits of the European amber complex marked with red circles. Map modified from mapchart.net.

However, it is now widely accepted that all three should be treated as independent deposits based on geochemical differences and a partially shared fauna (Dunlop et al., 2019; Mänd et al., 2018; Mitov et al., 2021; Perkovsky, 2018; Wolfe et al., 2016). The early Eocene, i.e. Lutetian (47.8–41.2 Ma) age, especially for Baltic amber, is most frequently cited in scientific publications (Ritzkowski, 1997). However, in recent years an increasing number of authors have argued for a late Eocene, i.e. Priabonian (37.7–33.9 Ma) age, based on more reliable palaeontological data (see e.g. Dunlop et al., 2019; Kuzmina & Iakovleva, 2023; Iakovleva, 2017; Iakovleva et al., 2022; Sadowski et al., 2017a, 2022 and references therein). All three amber deposits are likely broadly contemporaneous in age, with Bitterfeld amber being potentially somewhat younger (Dunlop et al., 2018; Mänd et al., 2018).

There is still debate about where the Baltic amber source area, also called the “Baltic amber forest”, was located. Some authors concluded that the Baltic amber forest grew in Fennoscandia, thus assuming transport of the amber over a long distance into the Blue Earth layer (e.g. Weitschat, 1997, 2008); however, other studies raised doubts about this hypothesis

(Grimaldi & Ross, 2017), suggesting a close proximity between amber formation and its subsequent deposition (Sadowski et al. 2017; Standke, 2008).

Members of the family Pinaceae were initially thought to be potential amber resin source trees (e.g. Dolezych et al., 2011; Schubert, 1961), until Wolfe et al. (2009, 2016) added the conifer family Sciadopityaceae based on FTIR Analyses. Sadowski et al. (2016) supported the occurrence of this potential amber source tree with the first confirmed inclusion of *Sciadopitys* cf. *tertiaria* from Baltic amber. According to Mänd et al. (2018) similar source tree assemblages can be assumed for all three European deposits.

8.4 Material and methods

Fossil harvestman data used in this study derives from the detailed microscopic examination of a range of available amber inclusions (Table 8.1, 8.2), mostly carried out by the authors of this study. Among the analysed specimens are those hosted by the Museum für Naturkunde Berlin (MfN), the Senckenberg Museum Frankfurt am Main, the Museum of Nature Hamburg (Germany), the Natural History Museum of Geneva (Switzerland) and the Key Laboratory of Insect Evolution and Environmental Changes, at the College of Life Sciences and Academy for Multidisciplinary Studies, Capital Normal University (CNU) in Beijing (China). Other comparative material originated from the private collections of Patrick Müller (Zweibrücken, Germany), Jörg Wunderlich (Hirschberg, Germany), Carsten Gröhn (Glinde, Germany) and Jonas Damzen (Vilnius, Lithuania). All type specimens could subsequently be purchased and deposited in one or more of the museum collections noted above. Additional harvestman inclusions were reviewed from the available literature, in particular Giribet & Dunlop (2005) and Poinar (2008) for Burmese amber, Staręga (2002) for Baltic amber, Dunlop & Giribet (2003) and Dunlop & Mitov (2009) for Bitterfeld amber and Mitov et al. (2021) for the Rovno fauna.

Table 8.1. List of fossil harvestmen species in mid-Cretaceous Burmese amber.

Suborder	**Family**	**Genus**	**Species**	**Reference**	**Amber deposits**
LANIATORES	Beloniscidae	*Palaeobeloniscus*	*thilolebi*	Bartel et al. 2021	Burmese (Kachin)
	Epedanidae	*Biungulus*	*xiai*	Bartel et al. 2021	Burmese (Kachin)
		Gigantocheles	*nilsi*	Bartel et al. 2021	Burmese (Kachin)
		Mesodibunus	*tourinhoae*	Bartel et al. 2023c	Burmese (Kachin)
		Petrobunoides	*sharmai*	Selden et al. 2016	Burmese (Kachin)
	Mesokanidae	*Mesokanus*	*oehmkuehnlei*	Bartel et al. 2021	Burmese (Kachin)
	Petrobunidae	*Petroburma*	*tarsomeria*	Bartel et al. 2023c	Burmese (Kachin)
	Podoctidae	*Burmalomanius*	*circularis*	Bartel et al. 2023c	Burmese (Kachin)
	Pyramidopidae	*Protopyramidops*	*nalae*	Bartel et al. 2021	Burmese (Kachin)
	Tithaeidae	*Ellenbergellus*	*tuberculatus*	Bartel et al. 2021	Burmese (Kachin)

EUPNOI	Incertae sedis	*Tyrannobunus*	*aculeus*	Bartel & Dunlop 2023	Burmese (Kachin)
DYSPNOI	Halithersidae	*Halitherses*	*grimaldii*	Giribet & Dunlop 2005	Burmese (Kachin)
CYPHOPHTHALMI	Incertae sedis	*Foveacorpus*	*cretaceus*	Bartel et al. 2023a	Burmese (Kachin)
		Foveacorpus	*parvus*	Bartel et al. 2023a	Burmese (Kachin)
	Stylocellidae	*Leptopsalis*	*breyeri*	Bartel et al. 2023a	Burmese (Kachin)
		Mesopsalis	*oblongus*	Bartel et al. 2023a	Burmese (Kachin)
		Palaeosiro	*burmanicum*	Poinar 2008	Burmese (Kachin)
		Sirocellus	*iunctus*	Bartel et al. 2023a	Burmese (Kachin)

Fossil harvestmen species were placed in an appropriate palaeoecological context based on their preserved morphological characters and/or the preferred habitats of extant relatives, where applicable. Ecological data for living harvestmen is largely based on Martens (1978, 2006, 2015, 2019). Interpretations of the palaeoenvironment of the Baltic amber source area/Baltic amber forest mainly follow Sadowski et al., (2017, 2020, 2022 and references therein), while the studies of Burgener et al. (2023), Grimaldi et al. (2002), Schmidt et al. (2022), Westerweel et al. (2019) and Yu et al. (2019) were mainly consulted for the Burmese amber from Kachin.

Table 8.2. List of fossil harvestmen species in the European amber complex.

Suborder	**Family**	**Genus**	**Species**	**Reference**	**Amber deposits**
LANIATORES	Cladonychiidae	*Proholoscotolemon*	*nemastomoides*	Ubick & Dunlop 2005	Baltic
	Incertae sedis	*Baltonychia*	*obscura*	Bartel et al. 2022	Baltic
EUPNOI	Caddidae	*Caddo*	*dentipalpus*	Koch & Berendt 1854	Baltic/Bitterfeld/Rovno
	Phalangiidae	*Amilenus*	*deltshevi*	Dunlop & Mitov 2009	Baltic/Bitterfeld/Rovno
		Lacinius	*bizleyi*	Mitov et al. 2015	Baltic/Bitterfeld
		Opilio	*ovalis*	Koch & Berendt 1854	Baltic
		Stephanobunus	*mitovi*	Dunlop & Mammitzsch 2010	Baltic
		Metaphalangium	*martensi*	Mitov et al. 2021	Rovno
	Protolophidae	*Protolophus*	*hoffeinsi*	Elsaka et al. 2019	Baltic
	Incertae sedis	*Dicranopalpus*	*ramiger*	Koch & Berendt 1854	Baltic/Bitterfeld/Rovno
	Sclerosomatidae	*Eumesosoma*	*abdelmawlai*	Elsaka et al. 2019	Baltic
		Leiobunum	*longipes*	Menge 1854	Baltic/Bitterfeld
DYSPNOI	Incertae sedis	*Piankhi*	*steineri*	Dunlop et al. 2012	Baltic
	Sabaconidae	*Sabacon*	*claviger*	Menge 1854	Baltic/Rovno
	Nemastomatidae	*Balticolasma*	*wunderlichi*	Bartel et al. 2023b	Baltic/Rovno
		Mitostoma	*denticulatum*	Koch & Berendt 1854	Baltic
		Mitostoma	*gruberi*	Dunlop & Mitov 2009	Baltic/Bitterfeld
		?Nemastoma	*incertum*	Koch & Berendt 1854	Baltic
		Paragiljarovia	*hochae*	Elsaka et al. 2019	Baltic

CYPHOPHTHALMI	Sironidae	*Siro*	*balticus*	Dunlop & Mitov 2011	Baltic
		Siro	*platypedibus*	Dunlop & Giribet 2003	Bitterfeld

8.5 Results and discussion

8.5.1 Geographic affinities of the Burmese amber fauna

Over the last century there has been some debate in the literature about whether the Burmese amber fauna originated from the palaeocontinent of Laurasia or from Gondwanaland (e.g. De Francesco Magnussen et al., 2022; Poinar, 2018; Rasnitsyn and Öhm-Kühnle, 2018). In recent years, an increasing number of Burmese amber taxa with affinities to Gondwana have been discovered, adding weight to the hypothesis of a southern origin. Examples from among the arachnids include the hard tick fossils *Bothriocroton muelleri* Chitimia-Dobler et al., 2023 and *Archaeocroton kaufmanni* Chitimia-Dobler et al., 2023 placed in Australasian genera, the pseudoscorpions *Prionochthonius burmiticus* Wriedt et al., 2021, *Proalbiorix gracilis* Geißler et al., 2022 and *Proalbiorix compactus* Geißler et al., 2022 and the assassin spider *Afrarchaea grimaldii* Penney, 2003. A number of Ricinulei from Burmese amber described by Wunderlich (2015, 2017) could be added to the list as this group is predominantly found today in West Africa and South-Central America.

Support for this hypothesis can also be found among the harvestmen. The laniatorean *Protopyramidops nalae* Bartel et al., 2021 (Pyramidopidae) has extant Gondwanan relatives, restricted today to Africa and the neighbouring Canary Islands (Sharma et al., 2011). This family is supposed to be the sister group of Assamiidae (see e.g. Sharma et al., 2011) and assamiids are also typically Gondwanan taxa, being found from the African tropics to India and Australasia (Palmieri et al., 2023). Two further juvenile fossil laniatoreans belonging to the infraorder Insidiatores are also of palaeobiogeographical interest (Bartel et al., 2021; Bartel et al., 2023c) as they may have affinities with the modern superfamily Triaenonychoidea. Curiously, extant Insidiatores are not known from Southeast Asia. The two superfamilies making up this infraorder, Travunioidea and Triaenonychoidea, show a clear and disjunct distribution pattern in the northern (i.e. North America, Southern Europe, Korea and Japan) and southern (i.e. South America, South Africa, Madagascar, Australia and New Zealand) hemispheres respectively (see Derkarabetian et al., 2021, *fig. 2*). If the Burmese amber fossils are triaenonychoids, they would also be consistent with Gondwanan origins for the fauna.

The only known Dyspnoi from Burmese amber, *Halitherses grimaldii* Giribet and Dunlop, 2005, has extremely large eyes. Its affinities have been subject to debate, but it was placed in an extinct family Halithersidae by Dunlop et al. (2016). Subsequently, Shear and Warfel (2016) suggested that Halithersidae could belong to the superfamily Acropsopilionoidea which contains a single living family, Acropsopilionidae. If this assignment is correct, it again supports Gondwanan affinities for the Burmese amber fauna, given that Acropsopilionidae is the only extant group of dyspnoids found on all continents of the Southern Hemisphere except

Antarctica. It may be worth adding that acropsopilionids also bear very large eyes (Groh & Giribet, 2015), similar to *H. grimaldii*.

Another Burmese amber find of interest is the cyphophthalmid *Sirocellus iunctus* Bartel et al., 2023a. It is the first example of Cyphophthalmi preserving a combination of characteristics from the families Sironidae and Stylocellidae. A close relationship between these two taxa was previously proposed by Clouse & Giribet (2010) based on phylogenetic data. They also inferred a Gondwanan origin for Stylocellidae, the cyphopthamid family that predominates in Southeast Asia today. At first glance, the evolution of stylocellids from sironids might appear contradictory, as Sironidae finds clearly show a Laurasian distribution, including records in European amber (Table 8.2). However, the group's history likely dates back to the early Permian (299–284 Ma), when Laurasia and Southeast Asia were connected by a shoreline across North Africa and Arabia (see e.g. Metcalfe, 1998, 2001, 2002). During the late Permian, a large part of Southeast Asia was separated from Gondwana in the form of the Cimmerian palaeocontinent, which might even represent the starting point for the Burmese amber fauna (Metcalfe, 2002). Later on, Cimmeria collided with Laurasia between the late Middle Triassic and the Late Jurassic (Sengör, 1984). Nevertheless, Westerweel et al. (2019) showed that the Burma terrane, where the amber deposits are located today, was an island with a near-equatorial latitude at about 95 Ma ago. This means that at some point it potentially became separated from Cimmeria or, in alternative scenario, split from Gondwana (Australia?) independently in the Late Jurassic, as proposed by Metcalfe (2002).

In general, Burmese amber appears to preserve a rather unique fauna, which may have remained stable across millions of years of island endemism. Support for this scenario includes a relatively high number of rather basal-looking arachnid lineages. Among harvestmen, this includes the laniatorean *Mesokanus oehmkuehnlei* Bartel et al., 2021, bearing Insidiatores claws and a *scutum completum*, the already mentioned cyphophthalmid *Sirocellus iunctus*, the large-eyed dyspnoid *Halitherses grimaldii* Giribet & Dunlop, 2005 and the large-eyed eupnoid *Tyrannobunus aculeus* Bartel & Dunlop, 2023 (Fig. 8.2A). Other Burmese amber arachnids, which appear to represent the sister-group of major extant lineages include the tick *Khimaira fossus* Chitimia-Dobler et al., 2022, that uniquely combines characters from soft and hard ticks, and the tailed-spider *Chimerarachne yingi* Wang et al., 2018, that retains a plesiomorphic character (the tail) not seen in any living spider.

8.5.2 Palaeoenvironment of the Kachin amber forests

The Cretaceous is generally recognised as one of the warmest periods in Earth history (e.g., Huber et al., 2018; Burgener et al., 2023). The review of Burmese amber by Grimaldi et al. (2002), which largely initiated the rediscovery of this deposit and stimulated subsequent intensive investigations, also proposed a tropical climate with extremely high temperatures (ranging between 32°C–55°C) for the Burmese amber forests, based mainly on insect inclusions and palaeobotanical data from Spicer et al. (1996).

The recently discovered extraordinary diversity of ground-dwelling spike mosses *Selaginella* (20 fossil-species) from Burmese amber indicates a high level of persistent humidity in the understorey of the amber source forests (Schmidt et al., 2022). The *Selaginella* species recorded lacked morphological adaptations to dry conditions, including clustered leaves or tightly curled branches or thick small microphylls. By contrast, the *Selaginella* inclusions showed features typical for mosses thriving in humid conditions, such as thin leaves without protective elements against water loss. Many of the *Selaginella* inclusions were additionally covered with fungi, similar to fly-speck fungi of the order Capnodiales. These fungi are usually associated with free water on the plant surface and thus also imply high levels of humidity (Schmidt et al., 2022 and references therein).

Besides spike mosses, the Burmese amber forest was also species rich in other free-sporing vascular plant species, such as ferns (e.g. Schneider et al., 2016, Regalado et al., 2017a, b, 2018), which also supports similarities to tropical forest ecosystems where ferns and *Selaginella* can be highly diverse (Schmidt et al., 2022). This is in contrast to other amber source areas, like the warm-temperate Baltic amber forest, where ferns are only rarely found, probably due to the drier and cooler climate (Sadowski et al., 2019). Besides Selaginellaceae and ferns, liverworts and mosses (e.g. Hedenäs et al., 2014, Heinrichs et al., 2014, Feldberg et al., 2022) are also abundant and diverse in Kachin amber.

In summary, the high cryptogam diversity indicates a constantly humid and shaded herbaceous layer, which was rich in free-sporing plant species with Selaginellaceae being the most dominant component (Schmidt et al., 2022). These plants probably provided a wide range of microhabitats suitable for a large number of arthropods, including ground-dwelling harvestmen like, e.g., Cyphophthalmi. A permanently damp and rather dark forest floor is also implied by the presence of velvet worms (Onychophorans) in Burmese amber (Oliveira et al., 2016), as these animals are usually restricted to this kind of microhabitat. Further plant fossils found in Burmese amber and in contemporary Alaskan amber (Heinrichs et al., 2011) include specimens of the family Frullaniaceae, described by Li et al. (2021 and references therein). Members of this family commonly grow today in humid tropical, subtropical and temperate forests.

High levels of humidity could be expected as the amber forest is currently believed to have been located on an equatorial or near-equatorial Cretaceous island (Westerweel et al., 2019), where it likely occupied coastal areas. This suggestion is supported by several marine inclusions, e.g. an ammonite, marine gastropods and isopods trapped in Burmese amber, indicating that resinous trees must have been located close to the coast (Yu et al., 2019; Xing et al., 2018).

8.5.3 Palaeoecology of the Burmese amber harvestmen

A humid tropical climate in the Burmese amber forest can also be inferred from some of the harvestman fossils. In particular, the cyphophthalmids *Foveacorpus cretaceus* Bartel et al., 2023a (Fig. 8.2C) and *Foveacorpus parvus* Bartel et al., 2023a were interpreted as having possible adaptations for semi-aquatic habitats. The bodies of these unusual species are completely covered with small holes (possibly used to channel air or water), which might represent highly specialized adaptations to prevent drowning during heavy rain and/or the following flooding (Bartel et al., 2023a). Cyphophthalmi are theoretically more vulnerable to such conditions since in modern ecosystems they are usually ground-dwelling animals. For that reason, it is also surprising to find a high number of Cyphophthalmi in Burmese amber, as we are already aware of at least 10 more fossils that will be described in the future studies. None of them shows specific adaptations for an arboricolous way of life, such as longer legs or a higher number of leg tarsomeres, which would significantly increase the probability of getting trapped in resin (Shultz & Pinto-da-Rocha, 2007). Therefore, the high number of cyphophthalmid specimens could be related to extremely high species richness and/or to a very dense and compact forest with a multitude of resin producers. In this scenario, plants which produce large amounts of resin on their roots (superficially and underground) might have played an important role in trapping ground-dwelling arthropods, particularly in the Burmese amber forests. Another possibility could be the aggregation of larger resin drops, which fell to the forest floor (see e.g. Àlvarez-Parra et al., 2021; Seyfullah et al., 2018). For comparison, Bitterfeld and Baltic amber have each yielded only a single published cyphophthalmid specimen (Dunlop & Giribet, 2003; Dunlop & Mitov, 2011), even though Baltic amber has been extensively sampled for more than 200 years. A third possibility might be that many cyphophthalmids of the Burmese amber forests used tree trunks as a temporary refugial habitat during long-lasting rains, perhaps when large parts of their original habitat become inundated during flooding events, which subsequently led to their entrapment in tree resin.

The large-eyed harvestmen in Burmese amber, *Tyrannobunus aculeus* (Fig. 8.2A) from the suborder Eupnoi, also provides evidence for a very humid environment given that it appears to have an extremely thin chitinous integument. For the first time in an amber harvestman, it was possible to observe the morphology of the retracted penis through the thin body wall. This characteristic of a thin cuticle is usually associated with a humid climate, since it only offers weak protection against evaporation (Mitov et al. 2021). A similar observation was made by Mitov et al. (2021) in *Sabacon claviger* Menge, 1854 known from Baltic and Rovno amber.

The Burmese amber laniatoreans also add support for a hot tropical climate in their home forests during the mid-Cretaceous. For example, living relatives of *Protopyramidops nalae* Bartel et al., 2021 are restricted today to tropical evergreen forests in Africa (Sharma et al., 2011). Most of the remaining Burmese amber laniatoreans belong to families (i.e. Beloniscidae, Epedanidae, Petrobunidae, Podoctidae and Tithaeidae), which are still distributed in the tropics of Myanmar, Thailand and the Indo-Malay Archipelago (Bartel et al., 2021, 2023c; Selden et al., 2016). Detailed information about the ecology of living representatives are sparse, but most of these harvestmen are associated with tropical rain forests. Here, they frequently occur under bark, stumps, stones and in leaf litter in dark moist places under dense canopies (Zhang & Zhang, 2012; Zhang & Martens, 2020; Zhang et al., 2013). Some species of e.g. Tithaeidae can also be found in areas of somewhat higher altitude (between 1000 m and 1500 m) (Schmidt et al., 2019). In general, it appears that the Laniatores fauna composition remained relatively stable over the last 100 million years and that their preference for warm and humid areas has also not changed. The relatively constant humid and wet climatic conditions have been reconstructed in the Southeast Asian region during the same period of time (Burgener et al., 2023; Morley, 2012).

8.5.4 Geographic affinities of the European amber fauna

The harvestmen fauna of the Baltic, Bitterfeld and Rovno ambers is also of particular interest. In addition to many typical modern European genera, a number of fossils can be observed, whose living counterparts are today restricted to North America and/or Asia. These include *Caddo dentipalpus* Koch & Berendt, 1854, *Eumesosoma abdelmawlai* Elsaka et al., 2019, *Protolophus hoffeinsi* Elsaka et al., 2019 and *Balticolasma wunderlichi* Bartel et al., 2023b (Fig. 8.2D). As previously suggested by several authors (e.g. Elsaka et al., 2019; Perkovsky, 2016; Podènas, 2001), these observations are consistent with the hypothesis that during the Palaeogene a fairly homogeneous fauna existed across the Holarctic which is represented by the European amber deposits. Support for this from the North American record can potentially be found in the extinct genus *Amauropilio* Mello-Leitão, 1937 recovered from the fossil beds of Florissant, Colorado, USA, which shows some similarities to the extant genus *Eumesosoma* Cokendolpher, 1980 according to Cokendolpher and Cokendolpher (1982). The fossil beds of Florissant were dated by Evanoff et al. (2001) to the Priabonian (34.07 Ma) and are thus contemporary in age with Baltic amber, where *Eumesosoma abdelmawlai* has been described from (Elsaka et al., 2019). Fossils of Asian harvestmen belonging to the groups present in the European ambers have not yet been recorded, but there is high potential for future comparative finds at localities such as the Early Eocene Fushun amber site in China.

At some stage, perhaps as late as the late Pleistocene last glacial period, several lineages of harvestmen (and other arthropods) became extinct in Europe and are retained only in Asia and/or North America. Sadowski et al. (2022) also suggested that loss of the flora may have been associated with the onset of the Pleistocene glaciation given that some taxa from Baltic amber can still be found in the late Pliocene of Frankfurt am Main in Germany. Some harvestmen groups that are more tolerant to large temperature ranges might have survived until this point as well. However, the exact timing of the extinction event(s) is difficult to resolve, as there is no continuous terrestrial arthropod fossil record in Europe after the Eocene. If Bitterfeld amber could be conclusively shown to be Oligocene in age (and this is debatable), then extinction dates could at least be narrowed down to after the Oligocene since harvestmen such as *Caddo dentipalpus* are also known from this deposit (Dunlop & Mitov, 2009). This idea receives additional support from the amber species *Sabacon claviger* Menge, 1854, whose living relatives are still distributed across the entire Holarctic today. Based on their presence in Baltic amber and modern distribution, it can be assumed that the history of these taxa dates back at least to the mid-late Jurassic (probably even earlier), thus before the opening of the North Atlantic (Irving, 1977). On the other hand, we should not exclude possible exchange via one of the land bridges between North America and Eurasia which were present (but not continuous) from the Late Kimmeridgian (154 Ma) to the Early Eocene (56 Ma) (Brikiatis, 2014, 2016).

Interestingly, none of the European amber harvestmen found so far belong to groups having a typically Gondwanan distribution today. By comparison, there are records of Gondwanan arachnids in Baltic amber, such as the assassin spider *Archaea paradoxa* Koch & Berendt, 1854 and the faellid pseudoscorpion *Fealla groehni* Henderickx & Boone, 2014.

8.5.5 Palaeoenvironment of the European amber forests

For many years it was widely assumed that Baltic amber was deposited in an extremely warm and humid climate, and that the original palaeolandscape consisted mostly of tropical lowland rainforests and subtropical mountain forests (see e.g. Weitschat & Wichard, 1998, 2010). However, recent analyses of lichen and seed plant inclusions (e.g. conifers, Fagaceae; Sadowski et al., 2017a, 2018, 2020, 2022 and references therein; Sadowski & Hofmann, 2023; Kaasaleinen et al., 2017; Rikkinen & Schmidt, 2018) suggest a more heterogeneous picture for the Baltic amber source area. There is evidence of coastal lowland swamps and back swamps, bogs, riparian forests and zonal mixed conifer-angiosperm forests with open, dry areas. Comparable modern analogues are found in the subtropical to warm-temperate evergreen broadleaved and mixed mesophytic forests of East and South East Asia, as well as the warm-temperate forests of North America (i.e. Southwest and Southeast USA, Mexico; Sadowski et al., 2017a, Sadowski et al., 2022). This is important, as such pattern of vegetation would be consistent with the broader Holarctic distribution pattern of some of the harvestmen preserved in the European ambers (see 8.5.4).

Inclusions of the extinct conifer species *Cupressospermum saxonicum*, also known from the late Oligocene and Miocene of Germany, are an indicator for tidal or brackish water influenced areas. Together with members of the genera *Sciadopitys, Cryptomeria* and *Pinus*, it formed coastal swamp forests. The presence of *Sequioa abietina*, *Taxodium*, *Rhynchospora*, *Eotrigonobalanus* and *Castanopsis* a.o. in Baltic amber indicates back swamps–riparian forests (Sadowski et al., 2017a, 2022). *Castanopsis* is a genus of evergreen trees belonging to the beech family, Fagaceae. The genus comprises 110-134 species (Li et al., 2015), which are restricted to tropical and subtropical eastern Asia, with some of them very common in subtropical forests and in a wide range of habitat and soil types including peat bog, swamp and other acidic or wet soils, or even poor dry soils (Strijk, 2023). Today, about half of the species are found in China (Li et al., 2015); while the rest occurs further south, through Indochina to Indonesia and the Philippines, mountainous areas of Taiwan, and also in Japan. Mainly conifers of the genera *Cathaya*, *Nothotsuga Calocedrus*, *Pseudolarix* and *Abies,* as well as angiosperms from the family Fagaceae form zonal mixed conifer angiosperm forests. *Abies* (firs) are evergreen coniferous trees belonging to the family Pinaceae. There are approximately 48–56 extant species, found in boreal and temperate forest biomes throughout much of North and Central America, Europe, Asia, and North Africa (Prentice et al., 1992). Open areas such as meadows are represented by e.g. graminids from the families Poaceae and Cyperaceae, and shrubs from the family Roridulaceae (Sadowski et al., 2017a, 2022).

Additional plant fossils from the Eocene can be found e.g. in the well-studied Messel Formation near the city of Darmstadt (Hessen, Germany). The abundant plant fossils of Messel were summarized and used to reconstruct the palaeoclimate by Grein et al. (2011 and references therein). However, they inferred a mostly tropical climate based on more than 50 plant families with higher average temperatures and precipitation compared to the climate of the Baltic amber deposits. These differences are likely related to the more southern location of the Messel formation and the probably older age of 47 Ma.

The Geiseltal in Saxony-Anhalt, Germany is also famous for preserving middle Eocene (ca. 45 Ma) plant fossils. Simoneit et al. (2021) studied the molecular composition of resinites (fossil resins which are not consolidated to amber) from this location, which is close to the Bitterfeld amber deposits. Their results show that conifers of the family Cupressaceae (in particular the genus *Taxodium*) were the main contributors to these resinites. They also found evidence for the families Burseraceae and Dipterocarpaceae (here in particular the genera *Shorea* and *Hopea*). Based on these families they suggested a semitropical swamp as a possible palaeobiome for this deposit (Simoneit et al., 2021).

Further plant fossils from the upper Eocene (middle Priabonian), which are thus more comparable in time to the amber deposits, can be found in Schleenhain (Saxony, Germany). The Schleenhain flora is part of the Zeitz megafloral complex within the Weißelster Basin. A number of leaves, conifer branches, fruits and seeds from this locality were analysed by Hennig & Kuntzmann (2013), who reconstructed two dominant plant communities: *Steinhauera subglobosa-Rhodomyrthophyllum* riparian forest and Myricaceae-Ericaceae swamp forest.

Nevertheless, Sadowski et al. (2017a) already stated that the subtropical lignite swamps of the Zeitz complex differ from the swampy vegetation found in the Baltic amber forests, due to an only partially shared conifer flora.

Unfortunately, detailed palaeoenvironmental studies of the Bitterfeld and Rovno amber deposits are lacking. Nevertheless, it can be assumed that these areas might have been somewhat warmer compared to the Baltic amber forests based on the data from other localities in Germany mentioned above and from Herold et al. (2014). Mitov et al. (2021) summarized the available data on the palaeoenvironment of the Rovno amber deposit, where they inferred more xeric conditions and a higher number of open habitats (see also Dietrich & Perkovsky, 2020; Perkovsky et al., 2007).

8.5.6 Palaeoecology of the harvestmen from European ambers

The possibility that Baltic amber may actually have sampled a mosaic of different habitat types is reflected in the taxonomic composition of the harvestmen fauna, although it should be noted that in fossilised tree resin there is always potential bias towards taxa found more commonly on tree trunks. This was also shown in studies of e.g. Solórzano-Kraemer et al. (2018) and Penney (2002), where arthropods from other zones of the tree, except the tree trunk, have a much lower probability of getting trapped in the resin. By far, the most common harvestmen inclusions (with up to 20 and more known individuals per species; pers. obs.) are the species *Dicranopalpus ramiger* Koch & Berendt, 1854, *Caddo dentipalpus* Koch & Berendt, 1854, *Sabacon claviger* Menge, 1854 and a variety of members of the subfamily Nemastomatinae.

Of the nemastomatines, in particular the extinct species *Parahistricostoma tuberculatum* (Koch & Berendt, 1854) and representatives of the extant genus *Mitostoma* Roewer, 1951 are quite abundant. Living relatives of these taxa are often highly hygrophilous and can usually be found in dense forests and near a water source (Martens, 1978, 2006, 2015). Some species of *Mitostoma* for example are also known from swampy areas (Martens, 1978). Interestingly, species like *D. ramiger* and many of the nemastomatines often inhabit somewhat mountainous areas of e.g. the Caucasus, where especially nemastomatines are extremely species rich (Martens, 2006). Mitov et al. (2021) stated that genera like e.g. *Dicranopalpus* possibly started to adapt to the climate conditions found in mountain areas after the Eocene, as these are more tolerant to lower temperatures. The abundance of nemastomatines in Baltic amber might be also related to the fact that these were somewhat better adapted to an arboricolous way life during the late Eocene, as many specimens feature longer legs than their living relatives (Mitov et al., 2021; pers. obs.).

Suzuki (1958) collected members of the genus *Caddo* Banks, 1892 in Japan on a variety of large trees, although in altitudes of ca. 1000 m and in relatively cold temperatures.

Its preference for tree trunks has apparently not changed since the Eocene, as it is one of the most common harvestmen inclusions from European ambers of this age.

Much rarer harvestmen inclusions (between 1–5 individuals per genus in total; pers. obs.) consist of the genera *Amilenus* Martens, 1969, *Eumesosoma* Cokendolpher, 1980, *Lacinius* Thorell, 1876, *Protolophus* Banks, 1893, *Stephanobunus* Dunlop & Mammitzsch, 2010 (potentially related to the living *Megabunus* Meade, 1855), the extinct European ortholasmatine *Balticolasma* Bartel et al., 2023b, *Siro* Latreille, 1796 from the suborder Cyphophthalmi and the laniatorean genera *Proholoscotolemon* Koch & Berendt, 1854 and *Baltonychia* Bartel et al., 2022. *Eumesosoma* specimens are usually more common in open areas like meadows and grasslands today (sometimes near oak trees), where they occupy humid places under debris (Cokendolpher, 1980). Living *Lacinius* are often thermophilous and prefer open areas, which might explain their rare occurrence in amber. On the other hand, some species are hygrophilous and can be found for example on the trunk of beech trees (Martens, 1978). Some of the extant *Megabunus* species seem to be restricted to areas with limestone and high humidity according to Martens (1978), while others also occur on trees (Curtis & Machado, 2007; Phillipson, 1959). How much this is relevant to its potentially affiliated extinct genus *Stephanobunus* remains unclear, but it might be again an explanation for the rarity of the fossil genus.

Living ortholasmatines are soil- and litter-dwellers (Shear & Gruber, 1983; Zhang et al., 2018), while most Asian species prefer humid areas in e.g. conifer forests according to Martens (2019). Both habitats were sufficiently present in the Baltic amber forest, but if their lifestyle was similar to that of their modern relatives their chance of coming into contact with resin may have been rarer. European species of the cyphophthalmid genus *Siro* are also typical inhabitants of leaf-litter in dense and moist forests (Martens, 1978). Therefore, a small number of individuals trapped in resin is not surprising. A large part of the modern European laniatoreans are cave dwellers. For this reason, it would be unwise to rely too much on them to reconstruct palaeoenvironments, since their preferred habitat may have changed significantly in the wake of decreasing temperatures after the Eocene (Bartel et al., 2022 and references therein). However, a few species of the laniatorean genera *Peltonychia* and *Holoscotolemon* can be found in open areas or in beech forests respectively (Martens, 1978). All in all, many of the living harvestmen species are usually distributed in more than a single habitat, which makes reconstructions based on this group difficult. Nevertheless, the harvestmen fauna preserved in Baltic amber fits the proposed habitats, based on plant data from e.g. Sadowski et al. (2017a), relatively well.

8.6 Conclusions

Our investigation of multiple harvestmen inclusions from the mid-Cretaceous Burmese amber and the Palaeogene European amber complex contributes to the body of evidence supporting previous palaeobiogeographical hypotheses, namely that (1) the Burmese amber fauna has (at least in part) strong Gondwanan affinities and that (2) the European ambers sampled the Holarctic fauna including genera now restricted to East Asia and/or North America.

The harvestmen composition found so far is consistent with current data on habitat reconstruction based primarily on palaeobotanical data. The Burmese amber forest should have been hot and very humid. It includes harvestman families typical for modern rainforests, as well as some fossils with possible adaptations for highly humid environments such as thin cuticle or possible modifications of the cuticle for resisting flooding.

The European amber forest(s) were not rainforest analogues, but were probably closer to modern warm-temperate forests in either Asia or North America, possibly with a mosaic of habitats including both wetter and more xeric environments. This habitat diversity can be reflected in the diversity of harvestmen, which includes taxa whose modern relatives occupy a variety of ecological niches.

At the same time, our study reveals difficulties in reconstructing past environments using only one group of animals (harvestman) due to the inherent sampling bias of fossiliferous resin. It is notable that at least in the European ambers genera often associated today with trees (i.e. *Caddo*, *Dicranopalpus*) are encountered quite commonly, which is probably a taphonomic bias towards animals more likely to become entrapped in resin. Finally, we would encourage further studies combining fossil plant and animal data for more comprehensive reconstructions of past environments. At least among the arachnids, spiders would be an excellent candidate taxon for which many more inclusions are available.

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9 Conclusions and perspectives

9.1 Concluding remarks

This work consists of five taxonomical studies describing 23 new fossil harvestmen in all four suborders from mid-Cretaceous Burmese and Late Eocene European ambers, including 11 new extinct species and the first and thus oldest formal records for the families Petrobunidae, Phalangiidae, Podoctidae and the subfamily Ortholasmatinae (Nemastomatidae). In particular the Burmese harvestmen fauna of the suborders Laniatores and Cyphophthalmi was much more diverse during the Cretaceous than previously expected and the fossil record for this deposit could be doubled. Additionally, a number of extinct key fossils with unique adaptations and morphologies have been discovered. Among these are the Cyphophthalmi fossils *Sirocellus iunctus*, which confirms the phylogenetically proposed close relationship between the families Sironidae and Stylocellidae, and *Foveacorpus cretaceus* and *Foveacorpus parvus,* that bear potential semi-aquatic adaptations in form of multiple pits on the body never observed before in extant species. *Tyrannobunus aculeus* combines characters usually found in the eupnoid families Caddidae, Sclerosomatidae and Phalangiidae, and thus represents a lineage close to the common ancestor of these three.

The new fossil harvestmen records clearly support a Gondwanan origin of the Burmese amber fauna whose history potentially dates back to the Early Permian and a Holarctic fauna preserved in the European amber complex, where living relatives are restricted to North America and/or Asia today. The partial extinction of European harvestmen species took likely place between the Oligocene and the last glacial period, due to declining temperatures and the accompanying loss of microhabitats.

The sixth and final study in this work summarizes all available data on fossil harvestmen from the aforementioned localities and discusses that dataset for the first time with fossil plant data and the latest reconstructions for the Baltic and Burmese amber forests. All harvestmen inclusions strengthen the hypothesis of the proposed warm-temperate Baltic amber forests and the very humid and warm tropical rainforests of the Burmese source area.

9.2 Perspectives

The description of new fossil harvestmen species during the past three years laid an important foundation for future analyses, in particular phylogenetic ones. All newly discovered fossils represent additional calibration points, which can be used to date the harvestmen tree of life more precisely. Furthermore, the combination of DNA data from living specimens and morphological characters (from extinct and extant specimens) will allow us to reconstruct the evolutionary history.

New harvestmen fossils in Baltic, Bitterfeld and Burmese amber are already located in the MfN, Berlin and await description. There is also enormous potential in the discovery and description of harvestmen fossils from other amber deposits all around the globe. Of particular interest are e.g. the Chinese Fushun (Eocene) and Zhangpu (Miocene) amber, Dominican amber (Miocene) New Zealand amber (Oligocene-Miocene), Lebanese amber (Lower Cretaceous), Spanish amber (mid-Cretaceous), Alaskan amber (mid-Cretaceous), African amber (Mesozoic-Cenozoic) and the recently rediscovered Lausitzer amber in Eastern Germany (Miocene?). Most of these are rich of inclusions and already revealed a number of arachnids, but mostly spiders and mites. Future harvestmen fossils from these deposits will contribute further data about palaeobiogeography, palaeoecology and their evolution. Additional new fossils as compressions are rather rare, but are already known from the Messel Formation (Early Eocene), Germany. These will also be analysed in a future study.

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11 Appendix

11.1 List of publications

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Bartel, C., Konikiewicz, M., Mąkol, J., Wohltmann, A., Dunlop, J.A. 2015. Smaridid mites in Baltic and Bitterfeld amber, with notes on the fossil record of terrestrial Parasitengona (Trombidiformes: Prostigmata). Annales Zoologici, 65(4): 641–659. https://doi.org/10.3161/00034541anz2015.65.4.009

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Dunlop, J.A., Erdek, M., **Bartel, C.** 2023. A new species of camel spider (Arachnida: Solifugae) in Baltic amber. Arachnology, 19(4): 772–776. https://doi.org/10.13156/arac.2023.19.4.772

11.2 Curriculum Vitae

The CV is not included in the online version for data protection reasons.

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11.3 Declaration

Berlin, December 2023

Hereby I declare that I wrote this doctoral thesis on my own and that all used sources in the text and figures are properly acknowledged. This thesis has not been previously submitted to the Freie Universität Berlin or any other institution.

Christian Bartel