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On the value of Burmese amber for understanding insect evolution: Insights from †*Heterobathmilla* – an exceptional stem group genus of Strepsiptera (Insecta)

Hans Pohl*[a], Benjamin Wipfler[b], Brendon Boudinot[c] and Rolf Georg Beutel*[a]

[a]*Entomology Group, Institut für Zoologie und Evolutionsforschung, Friedrich-Schiller-Universität Jena, Erbertstrasse 1, Jena, D-07743, Germany;* [b]*Zoologisches Forschungsmuseum Alexander Koenig, Bonn, Germany;* [c]*Department of Entomology/Nematology, University of California, One Shields Ave., Davis,Davis, CA, 95616, USA*

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Abstract

Burmese amber and amber from other periods and regions became a rich source of new extinct insect species and yielded important insights in insect evolution in the dimension of time. Amber fossils have contributed to the understanding of the phylogeny, biology, and biogeography of insects and other groups, and have also gained great importance for dating molecular trees. Another major potential is the documentation of faunal, floral and climatic shifts. Evolutionary transitions can be well-documented in amber fossils and can reveal anatomical transformations and the age of appearance of structural features. Here, using a new stem group species of Strepsiptera from Burmite, we evaluate this potential of amber insect fossils to assess the current phylogeny of Strepsiptera, with the main emphasis on the early splitting events in the stem group. Amber fossils have greatly contributed to the understanding of the evolution of Strepsiptera in the late Mesozoic and the Cenozoic. †*Heterobathmilla kakopoios* Pohl and Beutel **gen. et sp. n.** described here is placed in the stem group of the order, in a clade with †*Kinzelbachilla* (†Kinzelbachillidae) and †*Phthanoxenos* (†Phthanoxenidae). †Phthanoxenidae has priority over †Kinzelbachillidae, and the latter is synonymised. The superb details available from this new fossil allowed us to explore unique features of the antennae, mouthparts, and male copulatory apparatus, and to provide a phylogenetic hypothesis for the order. The younger †*Protoxenos* from Eocene Baltic amber was confirmed as sister to all remaining extinct and extant groups of Strepsiptera, whereas the position of the Cretaceous †*Cretostylops* in the stem group remains ambivalent. While the value of Burmite and amber from other periods has a recognized impact on our knowledge of the evolution in various lineages, this new fossil does not fundamentally change our picture of the phylogeny and evolution of early Strepsiptera. However, it offers new insights into the morphological diversity in the early evolution of the group.

Introduction

Burmese Cretaceous amber of the Albian/Cenomanian boundary (e.g. Zherikin and Ross, 2000; Grimaldi et al., 2002; Cruickshank and Ko, 2003; Shi et al., 2012), has turned out to be a very rich source of extinct species of insects and other groups, and the pace of studying amber fossils has distinctly accelerated since this fossil site was rediscovered (e.g. Grimaldi et al., 2002; Ross, 2019a, b, 2020). Numerous new extinct species from 569 families of organisms (Ross, 2019a, b, 2020) have yielded important insights in insect evolution in the dimension of time (e.g. Grimaldi and Engel, 2005; Ross et al., 2010; Poinar, 2018; Ross, 2019a). Interesting newly discovered insect taxa include the plecopteran †Petroperlidae (Sroka et al., 2018), the dictyopteran †Alienoptera (e.g., Bai et al., 2016, 2018; Kočárek, 2019), the hemipteran †Progonocimicidae (Jiang et al., 2019), the psocopteran †Cormopsocidae (Yoshizawa and Lienhard, 2020), the neuropteran †Babinskaiidae (Lu et al., 2017), the stem

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*Corresponding authors: *E-mail address*: hans.pohl@uni-jena.de, rolf.beutel@uni-jena.de group amphiesmenopteran †Tarachocelidae (Mey et al., 2018), and among numerous ant species, the specialized predatory "iron maiden ants" of †*Zigrasimeciini* (Barden and Grimaldi, 2013; Perrichot, 2014; Cao et al. 2020) and the trap-jawed "hell ants" of †Haidomyrmecinae (Barden and Grimaldi, 2012; Perrichot et al., 2008, 2016, 2020; Barden et al., 2017a, 2017b). The number of species of the small, cryptic and phylogenetically challenging polyneopteran order Zoraptera is constantly increasing (e.g. Engel and Grimaldi, 2002; Liu et al., 2018; Mashimo et al., 2018, 2019; Yin et al., 2018), indicating a distinctly larger diversity in the past (Yin et al., 2018). New important beetle fossils were also described, for instance from the suborder Myxophaga, which was previously largely (†Catiniidae?; Crowson, 1975; Beutel et al., 2008) or completely missing from the fossil record (e.g., Jałoszyński et al., 2017; see also Fikáček et al., 2020).

Occasionally amber fossils provide insights in features linked to life habits, for instance feeding, prey capture, or reproduction. Cretaceous amber fossils of †Archipsyllidae (†Permopsocida) with well-preserved skeletal features helped to bridge the gap between chewing and sucking feeding habits in Paraneoptera (Huang et al., 2016; Yoshizawa and Lienhard, 2016).

Long-proboscid scorpionflies from Cretaceous amber give an indirect evidence of uptake of liquid from gymno- and angiosperm reproductive organs, and the detection of pollen grains adjacent to the fossils support pollinator activity of these species (Lin et al., 2019). Direct evidence of angiosperm pollinivory in Coleoptera has been recently recorded for two families, Mordellidae (Bao et al., 2019) and Kateretidae (Peris et al., 2020), while two records of stem *Anthophila* (Poinar and Danforth, 2006; Danforth and Poinar, 2011; Poinar, 2020) and an unplaced aculeate, †*Prosphex* (Grimaldi et al., 2019), provide evidence for increasing angiosperm-dependence in Mesozoic Hymenoptera. Locomotion and climbing on broad leaves, as of angiosperms, or wet branches is indicated by the specialized and enlarged tarsal pads of Timematodea (Phasmatodea) from Cretaceous Burmese amber (Chen et al., 2019). Social behaviours are also observed, as in brood care by a 100-million-year-old scale insect documented by Wang et al. (2015), and possible inter-colonial combat in the stem ant genus †*Gerontoformica* by Barden and Grimaldi (2016). Specialized predatory habits are amply evinced by stem Formicidae (e.g. Perrichot, 2014; Perrichot et al., 2020), and even by the dictyopteroid †Alienoptera, for which a unique type of cephalo-prothoracic prey-catching mechanism was recently described (Bai et al., 2018; Kočárek, 2019). Debris-carrying camouflage among predaceous larvae is reported from Cretaceous Burmese, French, and Lebanese ambers, including Chrysopoidea, Myrmeleontoidea, and Reduviidae (Wang et al., 2016a; see also Pérez de la Fuente et al., 2012). Moreover, ectoparasitism has been confirmed via preservation of a rhopalosomatid larva in its host gryllid (Lohrmann and Engel, 2017), and feather-feeding has been suggested by preservation of partially damaged dinosaur feathers with fossil nymphs of †Mesophthiridae (Gao et al., 2019). Endoparasitism is indicated by the presence of a minute strepsipteran primary larva in Burmite, which is extremely similar to extant first-instar larvae (Pohl et al., 2018).

Amber inclusions (and impression fossils) of different periods and regions have gained great importance for dating molecular trees (e.g. Ronquist et al., 2012; Wahlberg et al., 2013; Misof et al., 2014; Espeland et al., 2018; McKenna et al., 2019; Matsumura et al., 2019). The importance of a reliable identification of extinct species has been recently underlined in a study on a Triassic impression fossil, †*Leehermania prorova* Chatzimanolis, Grimaldi and Engel, which was originally placed in the polyphagan beetle family Staphylinidae (Chatzimanolis et al., 2012). It was transferred to the suborder Myxophaga based on in-depth phylogenetic analyses with cladistic and Bayesian methods (Fikáček et al., 2020). This transfer has a strong impact on future dating of the megadiverse beetle suborder Polyphaga and the series Staphyliniformia (see e.g. Misof et al., 2014). The "peril of dating beetles" was also emphasized by Toussaint et al. (2017).

Amber fossils can provide crucial insights on the emergence of biogeographic patterns (e.g. Rust et al., 2010; Abellan et al., 2011; Jałoszyński, 2012; Barden and Ware, 2017; Cai et al., 2017; Poinar, 2018; Gimmel et al., 2019; Mashimo et al., 2019). For example, re-evaluation of taxonomic assumptions for fossils attributed to or near the ant genus *Leptomyrmex* resolved decades of speculation about the biogeographic origin of the Australasian radiation of the genus, clearly demonstrating a Neotropical origin for the clade with probable Oligocene trans-Antarctic dispersal (Boudinot et al., 2016; Barden et al., 2017). More recently, a *Baeomorpha* (Hymenoptera, Rotoitidae) from mid-Cretaceous Burmese amber, extends the distribution of fossil Rotoitidae from northern Laurasia to the southern Hemisphere, where the two extant genera are restricted to Chile and New Zealand (Huber et al., 2019). A Gondwanan origin of Zoraptera was suggested based on fossil material embedded in Burmese amber (Mashimo et al., 2019). Whereas Myanmar was traditionally considered as part of Laurasia (Mitchell, 1993; Boucot et al., 2013), it is now assumed that the West Burma Block, which includes the early Cretaceous fossil site of Burmese amber, was originally attached to Gondwana (e.g. Metcalfe, 2017; Poinar, 2018).

A major potential of Mesozoic and Tertiary amber fossils is the documentation of faunal, floral and climatic shifts. A brief comparison of the late Cretaceous flora and fauna preserved in Tilin amber (central Myanmar) with early Cretaceous and Eocene biota was presented by Zheng at al. (2018), describing for instance a pre-Cenozoic transition from stem group to crown group Formicidae. A snapshot of the Middle Eocene northern European staphylinine rove beetle diversity was recently presented in Brunke et al. (2019) and compared to the extant fauna of this area. However, comprehensive comparisons between biota documented by amber fossils of different world regions and geological periods are still missing, although taxonomically comprehensive work has been published (e.g. Rasnitsyn and Quicke, 2002). Systematic reviews are accumulating for different groups, such as for the ants (e.g. LaPolla et al., 2013; Barden, 2017) and various beetle taxa (e.g. Krell, 2006; Abellán et al., 2011; Legalov, 2012, 2020; Peris, 2020), and also studies on the palaeobiology of predators, parasitoids and parasites, plant-arthropod associations, and the diversification of insects based on disparity of mouthparts (e.g. Labandeira, 2002, 2006a, b; Labandeira and Currano, 2013; Ponomarenko and Prokin, 2015; Nel et al., 2018). Because of the rapid accumulation of new fossil taxa in recent years (e.g. Ross, 2019a, b, 2020), the need for comprehensive reviews is acute.

Anatomical insights can be gained from amber fossils on principle. However, preservation of internal soft parts of fossil insects is very rare, and Cretaceous amber fossils with well-preserved internal organs have not been described yet. An exception are mummified tissues in amber documented by Grimaldi et al. (1994), and indirect flight and leg muscles observed in some aculeate fossils in Burmite (B. Boudinot pers. obs.). Specimens of insect Tertiary fossils with preserved internal organs are known but also extremely rare. Soft parts of cantharid and nitidulid beetles embedded in Miocene Dominican amber were reported by Henwood (1992a), and the same author found exceptionally well-preserved flight muscles in fossil dipterans extending even to cell ultrastructure (Henwood, 1992b). The almost complete anatomical reconstruction of the Eocene stem group strepsipteran †*Mengea tertiara* (Menge) (Pohl et al., 2010; Hünefeld et al., 2011) remains a unique exception. It was shown that the internal structures of this species, as documented with μ-computed tomography (μ-CT), do not differ distinctly from those of extant strepsipteran males of Mengenillidae. If turbidity is present in the amber, e.g. in the case of the larva of †*Mengea* (Pohl et al., 2019), or if important syninclusions prohibit grinding of the amber for better examination of the fossils, μ-CT provides an opportunity to examine amber fossils. This was emphasized in Soriano et al. (2010), although the potentially destructive effects of the procedure were also noted in that study. Very good results were repeatedly obtained at DESY (Deutsches Elektronen-Synchrotron, Hamburg, Germany) (e.g. Pohl et al., 2010, 2019) and other facilities (e.g. Bai et al., 2016, 2018), usually without recognizable negative effects on the specimens. However, a discoloration such as a darker stripe in the amber can sometimes be caused by X-radiation during scanning (Pohl et al., 2019). Methods for preparing small-sized 3D amber samples were discussed in detail by Sidorchuk and Vorontsov (2018). These techniques distinctly facilitate and improve the study of very small insects or other minute organisms. In the case of the species described here, the use of μ-CT was not necessary because the amber was very clear, and all morphological details of the new fossil were visible without μ-CT scanning.

Burmese amber has provided new insights into a number of different areas, and our ability to describe morphological details of the fossils is constantly improving. This raises the question whether accumulating information necessarily improves our phylogenetic understanding of the investigated group, such as Strepsiptera, which is increasingly well represented in Cretaceous amber (e.g. Grimaldi et al., 2005; Pohl and Beutel, 2016). The phylogenetic placement of this small and highly specialized holometabolous order (c. 600 spp.) (e.g. Pohl and Beutel, 2008, 2013) has been strongly disputed over a long time (e.g. Kinzelbach, 1971; Pohl and Beutel, 2013), but was reliably settled recently. A systematic position in a clade Coleopterida, together with the megadiverse Coleoptera, is supported by large morphological (Beutel et al., 2011, 2018) and molecular data sets, including transcriptomes and genomes (Wiegmann et al., 2009; Niehuis et al., 2012; Boussau et al., 2014; Misof et al., 2014; Peters et al., 2014). Strepsiptera is mainly characterized by the endoparasitic ecology of the larvae and usually also of females (Stylopidia, ca. 97% of all species). Linked with this specialized lifestyle are the extremely miniaturized 1st instar larvae and extreme sexual dimorphism (e.g. Pohl and Beutel, 2008).

Strepsiptera have been poorly represented in the fossil record and was missing from Mesozoic deposits before Cretaceous Burmese amber was explored (e.g. Kinzelbach and Pohl, 1994). This situation has changed distinctly. Whereas impression fossils are still rare, a considerable number of well-preserved fossils from Miocene Dominican amber, Eocene Baltic and Cretaceous Burmese amber have been described recently (Kathirithamby and Grimaldi, 1993; Kinzelbach and Pohl, 1994; Pohl and Kinzelbach, 1995, 2001; Grimaldi et al., 2005; Pohl et al., 2005; Kathirithamby and Henderickx, 2008; Pohl, 2009; Henderickx et al., 2013; Engel et al., 2016; Pohl and Beutel, 2016; Kogan and Poinar, 2019) (see also Pohl and Beutel, 2013).

†*Mengea tertiara* (Menge) from the Middle Eocene (Lutetian) was the first discovered fossil strepsipteran, initially designated as a "Rhipidopteron" (Rhipiptera [=Strepsiptera] sensu Latreille, 1817) by Menge (1866). †*Protoxenos janzeni* Pohl, Beutel et Kinzelbach, also embedded in Baltic amber, was identified as the sister group of all the remaining Strepsiptera (Pohl et al., 2005; Pohl and Beutel, 2016), even though it is much younger than †*Cretostylops engeli* Grimaldi and Kathirithamby from Burmese amber (Grimaldi et al., 2005).

The new fossil strepsipteran is described and its morphology documented. The phylogenetic placement is evaluated by adding the observed structural features to previously published data matrices (Pohl and Beutel, 2005, 2016; Bravo et al., 2009). The character evolution linked with early splitting events in the order is discussed, with special emphasis on the unique condition of the copulatory apparatus.

Materials and methods

Material

The single specimen (holotype) of †*Heterobathmilla kakopoios* Pohl and Beutel, gen. et sp. n. in Burmese amber is from the well-known deposit of the southwest corner of the Hukawng Valley (26°20′N, 96°36′E) in Myanmar, dated as 98.79 ± 0.62 Ma (e.g. Shi et al., 2012; Poinar, 2018). It is part of the collection of the Zoologisches Forschungsmuseum Alexander Koenig in Bonn, Germany (accession number ZFMK-STR-00000104). In order to document the head of the fossil in frontal view, the amber was trimmed with a razor blade and then polished with emery papers and mud chalk.

Specimen imaging

The piece of amber was temporarily mounted on a glass microscope slide using glycerine and covered with a glass coverslip. A Leica MZ 12.5 stereomicroscope with magnifications up to 100× was used for observations (Leica Microsystems GmbH). The images of the entire specimen were taken with a Canon EOS 7D equipped with a Canon MP-E 65 mm macro lens fitted with a StackShot macro rail (Cognisys). Images of the head and the terminal segments were taken with a Canon EOS 7D equipped with a Nikon M Plan 20 ELWD microscopic lens, plus an adjustable extensions bellow and illuminated with two flashlights. An Axio Zoom.V16 with a Plan NeoFluar Z 1.0× (Carl Zeiss Microscopy GmbH) was used for the tarsi and the images were saved as CZI files. An Axiovert S100 inverted fluorescence microscope, equipped with a Spot CCD camera (Visitron Systems GmbH), was used for autofluorescence images of the terminal segments of the fossil.

Stacks of several partially focused images were recorded for overcoming limited depth of field. Single images of the Axio Zoom.V16 were exported with ZEN 2.3 lite. All images were stacked with Zerene Stacker (Zerene Systems LLC). They were processed using Adobe Photoshop CS6 (Adobe System Incorporated) and arranged as plates. Adobe Illustrator CS6 (Adobe Systems Incorporated) was used for lettering. Drawings are based on the micrographs and observations made with the Leica MZ 12.5 stereomicroscope.

Phylogenetic analyses

The characters of †*Heterobathmilla* were added to the data matrix published by Pohl and Beutel (2005) with Mesquite (Maddison and Maddison, 2018). In addition, the characters of later described extant and fossil taxa such as *Bahiaxenos*, †*Kinzelbachilla*, †*Phthanoxenos*, the larvae of †*Mengea* and †*Eocenoxenos* were added to the matrix (Bravo et al., 2009; Henderickx et al., 2013; Engel et al., 2016; Pohl and Beutel, 2016; Pohl et al., 2019). Parsimony analyses were carried out with NONA version 2.0 (ratchet, 1000 replicates) (Goloboff, 1999) and TNT (Goloboff et al., 2008) (default parameters and 100 random addition traditional searches).

Results

†*Phthanoxenidae Engel and Huang, 2016*

†Phthanoxenidae Engel and Huang, 2016: 161. Type species: †*Phthanoxenos nervosus* Engel and Huang, 2016. Designation by monotypy.

†Kinzelbachillidae Pohl and Beutel, 2016: 288 **syn. nov.**

Diagnosis. *Male*. Distinguished from all other strepsipteran families on the basis of the following features: Size less than 6 mm; antennal foramen distinctly widened, about twice as wide as diameter of scapus; labrum free, with paired anterolateral processes; galea present.

Nomenclature. In their original descriptions, †*Kinzelbachilla* and †*Phthanoxenos* were placed in separate families, †Kinzelbachillidae and †Phthanoxenidae by Pohl and Beutel (2016) and Engel et al. (2016), respectively. Considering the combination of a unique apomorphy (dorsal antennal processes) with a unique plesiomorphy (presence of parameres), it appears tempting to erect a new family for †*Heterobathmilla*. The monophyly of other groups would not be affected by this taxonomic rank. However, as the results of the analysis (see below) suggest a very close relationship of †*Heterobathmilla* with †*Kinzelbachilla* and †*Phthanoxenos*, we prefer to place the three described species in a single family.

The question of priority for †Kinzelbachillidae and †Phthanoxenidae was complicated by an online-early article distribution that was compounded by a misleading publication date. Specifically, the name †Phthanoxenidae was provided in the online advance copy of Engel et al., with the date given as "Available online 13 November 2015". However, this version cannot be considered as published because the work does not contain evidence of registration in ZooBank (Articles 8.5.3 and 9.9, International Commission on Zoological Nomenclature, 2012). Consequently, as specified by Article 21.9 of the code, the nomenclatural acts of Engel et al. are to be considered valid and available based on the publication date of the print version, which is recorded as March 2016 in the text of Volume 58 of *Cretaceous Research*. Although this implies priority for †Kinzelbachillidae, validly published on 4 January 2016 in an online-early version registered in ZooBank, the managing editor of *Cretaceous Research* confirmed that Volume 58 was mailed on 1 December 2015, conferring availability of †*Phthanoxenos* at that time by article 21.4 addressing incorrect dates. For these reasons, we recognize †Phthanoxenidae as the senior synonym of †Kinzelbachillidae syn. n.

Key to adult males with main focus on fossil families

1.	Tarsi 5-segmented, with large claws; scuto-prescutal region of metathorax strongly arched and prominent	2
–	Tarsi either with 2–5 segments without claws, or with 5 segments either with a pair of small claws or only a small single claw; scuto-prescutal region of metathorax weakly arched, almost flat	Stylopidia
2.	Antenna 8-segmented	3
–	Antenna with 6–7 segments	6
3.	Labrum with paired anterolateral processes, galea present	4
–	Labrum without anterolateral processes, galea absent	5
4.	Size between 7–8 mm; antennal foramen slightly wider than diameter of scapus; entire mandible robust, with broad base and very evenly narrowing and curved inward distally	†Protoxenidae
–	Size less than 6 mm; antennal foramen distinctly widened, about twice as wide as diameter of scapus; mandibles strongly narrowing and curved inward distad of moderately broad basal region	†Phthanoxenidae
5.	Labrum distinctly narrower than distance between mandibular bases	†Cretostylopidae
–	Labrum at least reaching inner margin of mandibular bases	Bahiaxenidae
6.	Antenna 7-segmented, with flabella on antennomeres 3 and 4; hind wing with one cell	†Mengeidae
–	Antenna 6-segmented, with flabella on antennomeres 3 and 4 or 3–5; hind wing without cell	Mengenillidae

† means that the taxa in question are extinct.

†Heterobathmilla Pohl and Beutel, gen. n.. http://zoobank.org/urn:lsid:zoobank.org:act:EE3D6E65-B9A4-47ED-B47D-DFCED07BC1AE

Etymology. The name is derived from “Heterobathmie”, used by W. Hennig (1974) to characterize a mosaic pattern of plesiomorphic and apomorphic features (“Heterobathmie der Merkmale”). The ending -*illa* is used in several generic names in the order, for instance in *Mengenilla* or *Bohartilla*.

Diagnosis. Differs from all other known extant or extinct Strepsiptera by the bipectinate antenna and the presence of parameres, the latter subdivided into a proximal and a distal portion.

Description. Head capsule entirely sclerotized, lacking membranized regions. Coronal suture and oblique frontal sutures present. Ocelli missing. Compound eyes with small ommatidia not separated by chitinous bars, without microtrichia between them. Labrum well-developed and free, with distinct paired distolateral processes. Mouthfield sclerite not developed. Anterolateral antennal foramina large, almost one third as wide as head anterior to compound eyes. Eight-segmented antenna bipectinate; antennomeres 3–8 with lateral flabellae, and 4–8 with additional dorsal processes; Mandibles strongly developed, with distinct primary and secondary articulation; with apically pointed distal part almost forming right angle with robust base. Maxilla not divided into cardo and stipes; lacinia absent; galea distinct, maxillary palp one-segmented, with oviform sensillum. No individual labial elements recognizable; labial palp absent.

Prothorax small, with vestigial pronotum. Mesothorax much smaller than metathorax, with flattened halteres. Mesonotum undivided, transverse. Metathorax strongly enlarged, more than four times as long as pro- and mesothorax combined. Scuto-prescutal part of metanotum strongly arched and prominent. Metaventrite with indistinct median suture (discrimen). Legs elongate and slender; pro- and mesocoxae large, conical and prominent; metacoxa more transverse; pro- and mesothoracic trochanters fused with femoral base; metatrochanter large; femora relatively wide; tibiae narrower, without recognizable terminal spurs; tarsi 5-segmented, cylindrical; sensorial spots missing; vestiture of adhesive hairs present on tarsomeres 1 and 2 (Fig. 7); accessory claws absent; terminal claws distinct. Halteres flattened, with widened distal region. Hind wings fan-shaped, broader than long, without closed cells and transverse veins; venation with c and sc closely connected, partly overlapped by r_1; r_2, r_3 and r_4 detached; r_5 extending from base; ma_1 and ma_2 almost reaching wing base, ma_3 and cua_1 extending from base.

Abdomen 10-segmented. Tergites slightly smaller than sternites. Segment IX not elongated, with tergum short and transverse; ventral part of segment IX strongly developed, enclosing copulatory organ, apically bent upwards. Segment X prominent and elongated. Spiracles not recognizable. Penis with broad base, almost straight; paired “parameres present”.

Type species: †*Heterobathmilla kakopoios* Pohl and Beutel, sp. n.

†Heterobathmilla kakopoios Pohl and Beutel, sp. n. (Figs 1–9)

http://zoobank.org/urn:lsid:zoobank.org:act:33D2E45C-1E4B-4EE8-B902-C514F41F2254

Fossil Material. The piece of amber containing the holotype is approximately semicircular (9×8×3 mm). There are no syninclusions apart from small particles of debris. It is deposited in the collection of the Zoologisches Forschungsmuseum Alexander Koenig (ZFMK) (accession number: ZFMK-STR-00000104).

Etymology. From Greek, meaning an evil doer. The name alludes to the similarity of the species to the face of the hitman Anton Chigurh in the movie "No country for old men" (Ethan and Noel Coen, based on the novel of Cormack McCarthy).

Description. Total length ca. 3.7 mm; maximum width of head (between outer margins of compound eyes) ca. 0.72 mm; approximate length of antenna ca. 0.66 mm; length of fore wing ca. 0.62 mm; radial length of hind wing ca. 2.53 mm; length of metathorax ca. 1.18 mm; length of abdomen ca. 1.64 mm. Colour of head and body mostly brown; membranous areas as between abdominal segments whitish; legs of very light brownish coloration. Body surface except for eyes, antennae and mandibles almost completely covered with microtrichia.

Head anteriorly with shallow median emargination (Figs 1, 2, 5A,C, 6A). Posterodorsal margin moderately concave. Coronal suture very distinct, slightly less than half as along as dorsal side of head (Figs 2, 6A); nearly straight, oblique frontal sutures less distinct, reaching enclosure of large antennal foramina anterolaterally (Figs 2, 6A). Frontoclypeal strengthening ridge separating clypeus from frons absent. Longitudinal parallel furrows extend anterad from subapical region of frontal sutures, obliterating shortly before reaching anterior frontoclypeal edge (Fig. 2, 5C). Compound eyes strongly convex, with small cornea lenses, with more than 80 ommatidia visible in dorsal view (Figs 5, 6). Antenna about as long as maximum width of head; scapus and pedicellus approximately cylindrical (Fig. 6A); antennomere three triangular, slightly extended basally, with shovel-shaped flabellum; flabella of antennomeres 3–5 slightly increasing in length from proximal to distal; flabella of antennomeres 6–8 slightly shorter than proximal ones;

Fig. 1. †*Heterobathmilla kakopoios* Pohl and Beutel, gen. et sp. n. in Burmese amber, dorsal view; photomicrograph. Scale bar 500 µm. [Colour figure can be viewed at wileyonlinelibrary.com]

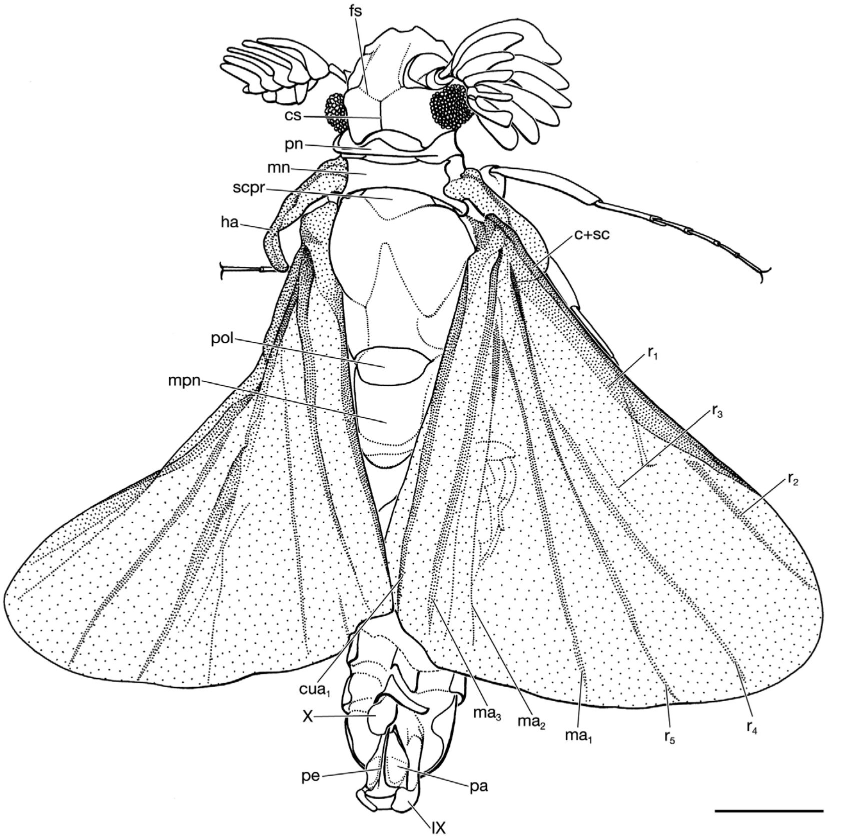

Fig. 2. †*Heterobathmilla kakopoios* Pohl and Beutel, gen. et sp. n., dorsal view. Abbreviations: c, costa; cs, coronal suture; cua_1, cubitus anterior; fs, frontal suture; ha, halter; IX, ninth abdominal segment; ma_{1-3}, media anterior; mn, mesonotum; mpn, metapostnotum; pa, paramere; pe, penis; pn, pronotum; po, postlumbium; r_1–r_5, radius; sc, subcosta; scpr, scuto-prescutal region; X, abdominal segment X; drawing. Scale bar 500 µm.

dorsal processes of antennomeres 4–8 slightly decreasing in length. Galea about twice as long as broad, very slightly curved inwards, with rounded apical margin (Fig. 6A). Curved filament-like structure visible posterior to mouth opening (homology unclear) (Figs 5C, 6B).

Anterior pronotal border strongly convex (Fig. 2). Mesonotum with distinct posterolateral process; anterior and posterior border concave (Fig. 2). Discrimen of metaventrite reaching about half length of sclerite (Fig. 4); distinct anteriorly converging furrows reach beyond anterior end of discrimen; additional oblique lines originate from furrow and extend anterolateral towards lateral edge of ventrite. Metatrochanter with oblique distal edge and apical excavation for insertion of metafemoral base (Fig 4); femora with slightly convex edges; tibiae slightly curved; tarsi very slender, with diameter very slightly decreasing distally; basitarsomere of pro- and middle legs about twice as long as following segment; tarsomeres 2 and 3 about equally long; tarsomere 4 shortest; tarsomere 5 about twice as long as 4 (Fig. 4). R_1 reaches distal $3/4^{th}$ of wing and then merges with anterior margin (Fig. 2); r_2 short, restricted to distal region, nearly reaching tip of wing; r_3 short; r_4 longer; r_5 reaching posterior margin, strongly pigmented basally; ma_1 and ma_2 long, almost reaching wing margin; ma_3 extending from base to hind margin or at least ending very close to it; cua_1 extending from base to hind margin.

Abdomen slightly less than half as long as entire body, subparallel (Figs 3, 4). Sternites I–VII between 3 and 3.5 times as wide as long. Sternum VIII rounded posteriorly. Penis with very slender distal part, apically pointed (Figs 8A,B, 9); parameres appear divided into proximal and distal portion by transverse membranous zone; apically strongly sclerotized and pointed (Fig. 9).

Results of the phylogenetic analyses

The analysis of the matrix with 218 characters (83 character of adult males coded for †*Heterobathmilla*) yielded 39 minimum length trees with NONA with 355 steps and a consistency index of 0.77 and a retention index of 0.9. Forty-eight equally parsimonious trees

Fig. 3. †*Heterobathmilla kakopoios* Pohl and Beutel, gen. et sp. n. in Burmese amber, ventral view; photomicrograph. Scale bar 500 µm. [Colour figure can be viewed at wileyonlinelibrary.com]

with the same number of steps were obtained with TNT (traditional search). The strict consensus tree in both analyses was identical (Fig. 10).

Strepsiptera including the stem group is strongly supported (Bs [=Bremer support] 12), and also Strepsiptera *s. str.* (crown group) + †*Mengea* (Bs 6), Stylopidia (Bs 8) and Stylopiformia (1). Strepsiptera excl. †*Protoxenos*, a clade †*Phthanoxenos* + (†*Heterobathmilla* + †*Kinzelbachilla*), and Strepsiptera *s. str.* excl. *Bahiaxenos* (Bahiaxenidae) have support values of 1. †*Cretostylops* is placed in a trichotomy with the †*Phthanoxenos* + (†*Heterobathmilla* + †*Kinzelbachilla*) clade, †*Mengea* and extant Strepsiptera (Strepsiptera *s. str.*).

Discussion

As in several other groups, the knowledge of the past diversity of Strepsiptera has been distinctly improved by amber fossils. A total of 41 fossil strepsipteran species are presently described (see Kogan and Poinar, [2019] for a current checklist). Of these, 20 species are from Miocene Dominican amber, 13 species from Eocene Baltic amber, two compression fossils from the Eocene Green River formation (USA), one species from Eocene Fushun Amber (China), one from Eocene Brown coal Geisel Valley (Germany), and one from Colombian copal (Holocene – Pleistocene). It is noteworthy that all known strepsipterans from the Cretaceous belong to the stem group. Members of extant groups, like representatives of Stylopidia, are completely absent in late Mesozoic deposits. In contrast, various representatives of this large strepsipteran subunit that have endoparasitic adult females are recorded from the Eocene, including Corioxenidae, Elenchidae, Myrmecolacidae and Stylopidae (see below). This suggests that the transition of the females to permanent endoparasitism did not occur before the Paleogene.

Usually, adult males are discovered as amber inclusions, for instance †*Mengea tertiara* (Menge, 1866; see also Kinzelbach and Pohl, 1994) and †*Protoxenos* (Pohl et al., 2005) from Baltic amber, †*Cretostylops* Grimaldi et Kathirithamby, †*Kinzelbachilla* and †*Phthanoxenos* Engel and Huang from Burmese amber (Grimaldi et al., 2005; Kathirithamby and Engel, 2014; Pohl and Beutel, 2016; Engel et al., 2016),

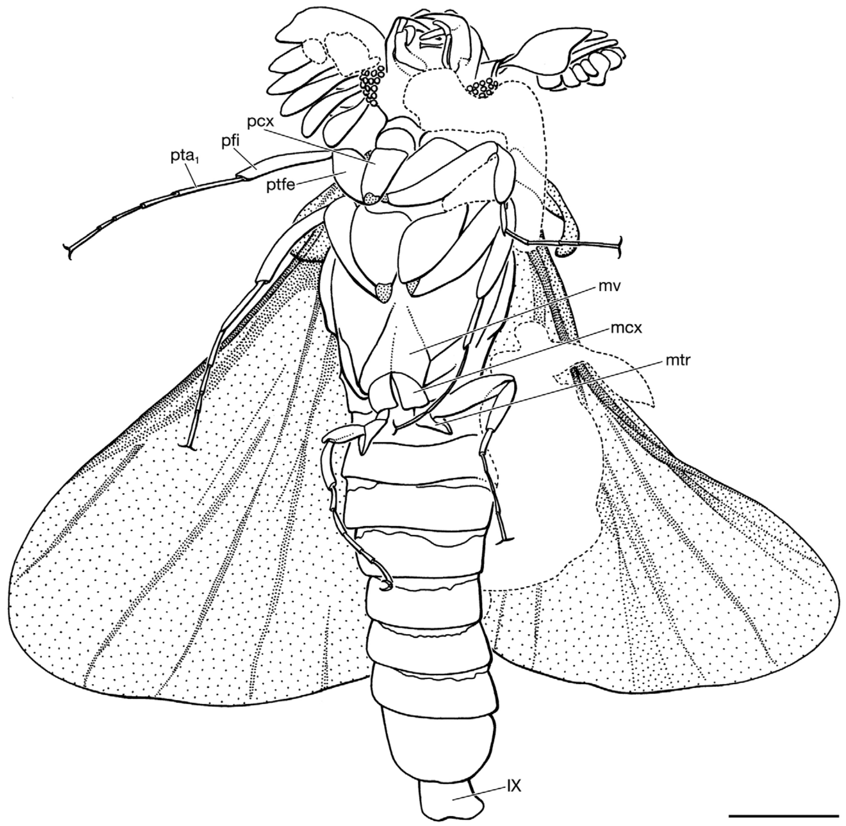

Fig. 4. †*Heterobathmilla kakopoios* Pohl and Beutel, gen. et sp. n., ventral view. Abbreviations: IX, abdominal segment IX; mcx, metacoxa; mtr, metatrochanter; mv, metaventrite; pcx, procoxa; pta$_1$, protarsomere 1; pti, protibia; ptfe, protrochanterofemur; drawing. Scale bar 500 µm.

†*Protelencholax* Kinzelbach from Dominican amber (Kinzelbach and Pohl, 1994), or a species of the extant family Myrmecolacidae from Eocene amber from north-eastern China (Wang et al., 2016b). Amber fossils of adult females of the basal groups of Strepsiptera remain unknown (in contrast to Kathirithamby, [2018]). A tiny primary larva from Burmese amber was discovered recently (Pohl et al., 2018), and also a free-living late instar, very likely an immature stage of †*Mengea tertiara* from Baltic amber (Pohl et al., 2019).

Amber fossils have greatly contributed to the understanding of the evolution of Strepsiptera in the late Mesozoic and the Cenozoic. In our analyses, the relatively young †*Protoxenos* (†Protoxenidae) from Eocene Baltic amber was clearly confirmed as sister to all remaining extinct and extant groups. A slender distal mandibular part (char. 42.1) and broad fan-shaped hind wing (char. 62.1) are unambiguous apomorphies of Strepsiptera excl. †Protoxenidae. An additional potential apomorphy of this clade is the distinctly reduced size and less robust body (Pohl and Beutel, 2016). A large, free and bi-lobed labrum (chars. 38.0, 39.1), very robust mandibles (char. 42.0), eight-segmented antennae (char. 21.1) with lateral flabellae on antennomeres 3–7, maxillae with a galea (char. 47.0), and hind wings longer than wide (char. 62.0) are strepsipteran groundplan features preserved in †*Protoxenos*. It is conceivable that males of †*Protoxenos* were still taking up food, in contrast to extant strepsipterans. However, gut contents could not be reliably identified in the Eocene species (Pohl et al., 2005). Despite the clarified first split in Strepsiptera, the fossil evidence concerning the area of origin remains ambiguous. †*Protoxenos* (Pohl et al., 2005) was discovered in Baltic amber, whereas the oldest known species are preserved in Cretaceous Burmese amber.

The new Cretaceous genus †*Heterobathmilla* displays a conspicuous mixture of plesiomorphies and unusual derived features (Hennig, 1974: “Heterobathmie der Merkmale”): notably a unique type of bipectinate antenna on one hand, and a male copulatory apparatus with distinctly developed “parameres” on the other. The latter condition is common in Coleoptera, the sister group of Strepsiptera (e.g. Lawrence et al., 2011), but was hitherto unknown in extant or extinct

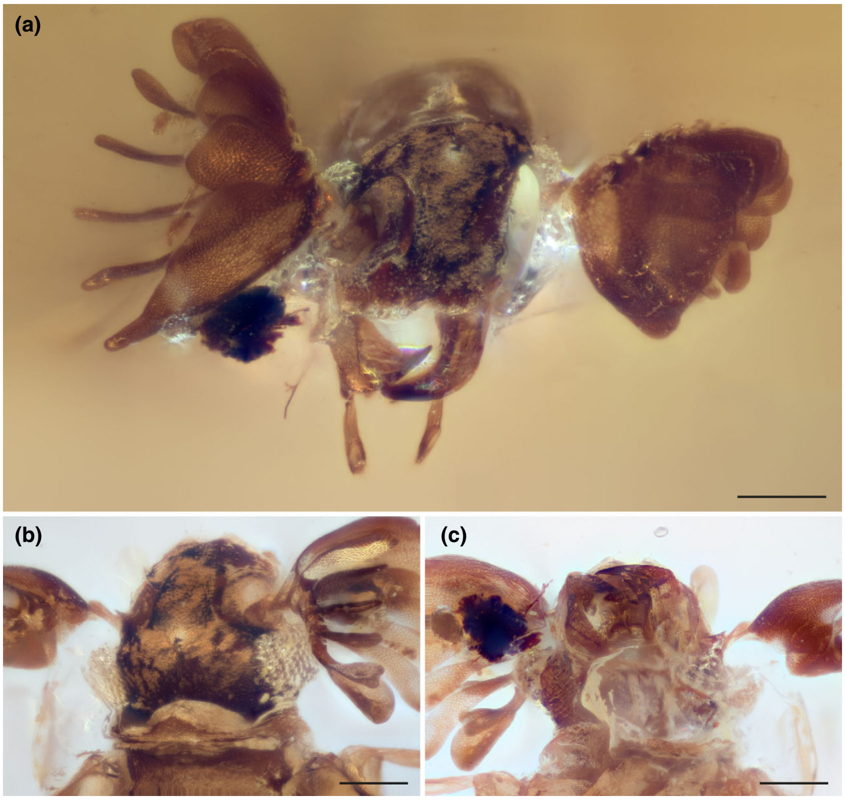

Fig. 5. †*Heterobathmilla kakopoios* Pohl and Beutel, gen. et sp. n. in Burmese amber. a. Head, frontal view; b. Head, dorsal view; c. Head ventral view. Photomicrographs. Scale bars 200 µm. [Colour figure can be viewed at wileyonlinelibrary.com]

representatives of Strepsiptera. †*Heterobathmilla* is unambiguously placed in a clade with †*Kinzelbachilla* and †*Phthanoxenos*, supported by a distinctly widened antennal foramen (19.0). Another potential synapomorphy is the position of the oviform sensillum near the tip of the maxillary palp (56.1). However, this feature, like many others, is not recognizable in †*Phthanoxenos* (Engel et al., 2016) and is thus ambiguous at this node. Another shared feature is the presence of an anterolateral labral process (39.1). However, this structure is also present in †*Protoxenos*, and thus likely a groundplan feature of the order. The monophyly of †Phthanoxenidae and the absence of "parameres" in all hitherto known fossil or extant members of the order (including †*Protoxenos*), raises the question of the evolutionary background of these lateral lobes of the penis ("aedeagus").

The term "paramere" has been contentious for generations (e.g. Snodgrass, 1935, 1957; Crampton, 1938), and its evolutionary identity as a distinct structure without homologs in hemimetabolous groups is further called into question by †*Heterobathmilla*. Two anatomical observations support the interpretation that these paired structures are gonopods, or genital appendages of other Hexapoda (Boudinot, 2018). First, the "parameres" of †*Heterobathmilla* correspond positionally to the gonopods of other Holometabola – including Hymenoptera, Raphidioptera, and Mecopterida. Second, the apparent transverse line of the structure matches the coxa-stylus pattern of abdominal appendages IX across the winged insects (Boudinot, 2018), a pattern also consistent among Paleozoic Pterygota (Pecharová et al., 2020; Prokop et al., 2020). The primary point of uncertainty is that the penis hinges on abdominal sternum IX, similar to other Strepsiptera, rather than within the gonopods as observed in those Holometabola that retain these appendages (Boudinot, 2018). Despite this, it remains plausible that the apparent "parameres" of †*Heterobathmilla* and "lateral lobes" of Coleoptera are at least partially homologous with gonopods, albeit integrated developmentally. Although re-expression of genital appendages in the case of †*Heterobathmilla* would be more parsimonious, multiple independent losses cannot be ruled out considering the presently known stem group taxa. Moreover, parallel losses of structures across the phylogeny, such as wing vein abscissae and muscles, are known to occur based on rigorous

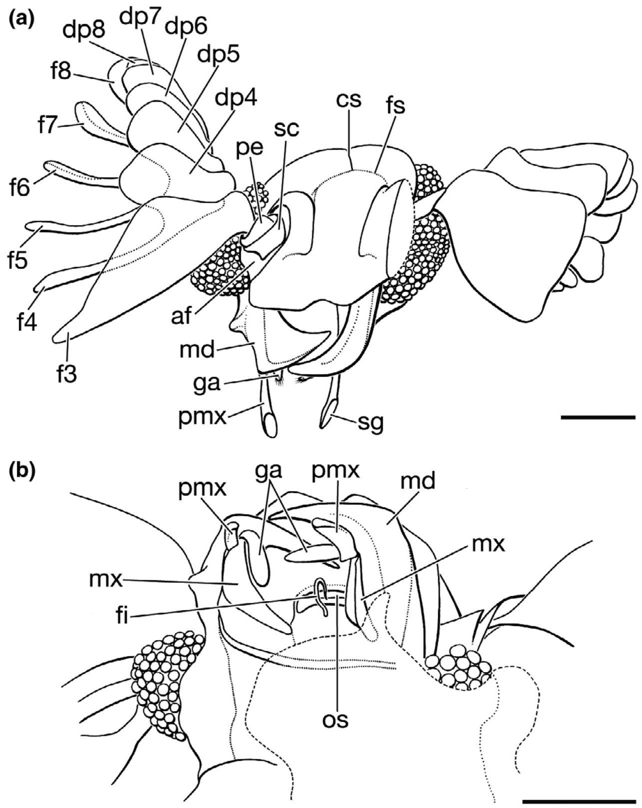

Fig. 6. †*Heterobathmilla kakopoios* Pohl and Beutel, gen. et sp. n. a. Head, frontal view; b. Head, ventral view. Abbreviations: af, antennal foramen; cs, coronal suture; dp4–8, dorsal processes of antennomeres 4–8; f3–8, lateral flabellae of antennomeres 3–8; fi, filament-like structure; fs, frontal suture; ga, galea; md, mandible; mx, maxilla; os, mouth opening; pe, pedicellus; pmx, maxillary palp; sc, scapus; sg, sensory pit; drawings. Scale bars 200 μm.

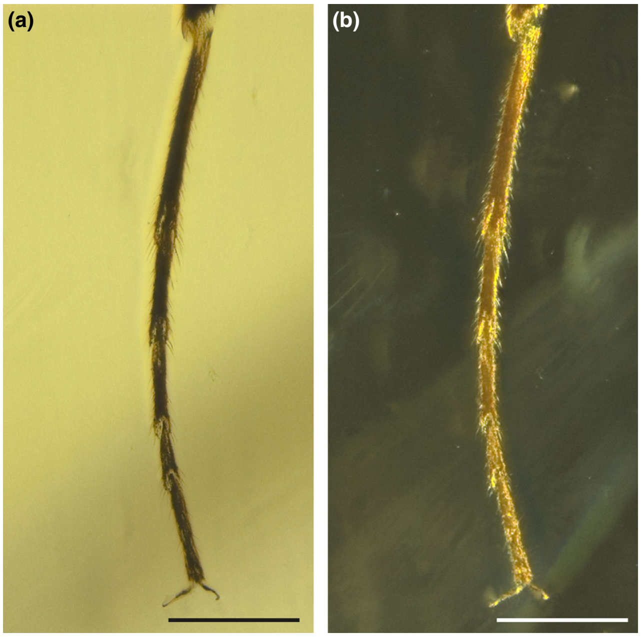

Fig. 7. †*Heterobathmilla kakopoios* Pohl and Beutel, gen. et sp. n. in Burmese amber. Protarsomeres, ventral view. a. Brightfield. b. Darkfield. Photomicrographs with an Axio Zoom.V16. Scale bars 200 μm. [Colour figure can be viewed at wileyonlinelibrary.com]

statistical modeling (e.g. Klopfstein et al., 2015). Further resolution on this issue of genital homologies and functional morphology may be provided by μ-CT scanning, as in Pohl et al. (2010), if the specimen is fine enough to have preserved muscular tissue.

The position of †*Cretostylops* in the stem group remains uncertain. The genus is placed in a trichotomy with the †*Phthanoxenos* – †*Heterobathmilla* – †*Kinzelbachilla* – clade and the monophylum comprising †*Mengea* and extant Strepsiptera. Presently no features are available to solve this phylogenetic ambiguity. The placement of the extant *Bahiaxenos* from Brazil (known only from the male holotype) in an unresolved trichotomy with †*Mengea* and crown group Strepsiptera, is likely due to the lack of any characters of immature stages or females. As a whole, fossils have not fundamentally changed our picture of the phylogeny and evolution of Strepsiptera but have provided tantalizing clues to ancient morphological transformations. Relationships in crown group Strepsiptera are not affected at all by extinct taxa (e.g. Henderickx et al., 2013; see also Fig. 10 and Pohl and Beutel, 2005: Fig. 28).

The age of origin of Strepsiptera, the late Carboniferous (or earliest Permian), can be assessed based on the well-established sister group relationship with Coleoptera and the fossil record of beetles (e.g. Ponomarenko, 1969; Niehuis et al., 2012; Boussau et al., 2014; Beutel et al., 2018; see also Kinzelbach, 1971). The splitting event was dated as ca. 300 Mya in Misof et al. (2014) and as ca. 350 Mya in McKenna et al. (2019). Unambiguous beetle fossils from the Lower Permian are usually comparatively large and well-sclerotized species (e.g. Ponomarenko, 1969; Kirejtshuk et al., 2014). In contrast to this, strepsipterans, except for the minute primary larvae (Pohl, 2000, 2002; Pohl et al., 2018) or the cephalothorax of endoparasitic females (e.g. Richter et al., 2017) and male puparia (e.g. Kinzelbach, 1971), are weakly sclerotized and fragile. Consequently, the chances to be preserved as impression fossils are low. The vast majority of the fossils are amber inclusions, even though specimens in Eocene oil shale or Eocene limestone are also known (Kinzelbach and Pohl, 1994; Antell and Kathirithamby, 2016), although a single primary larva was found in Eocene brown coal from the Geisel valley in Germany (Kinzelbach and Lutz, 1985; Pohl, 2009). As already pointed out in Pohl and Beutel (2016), the

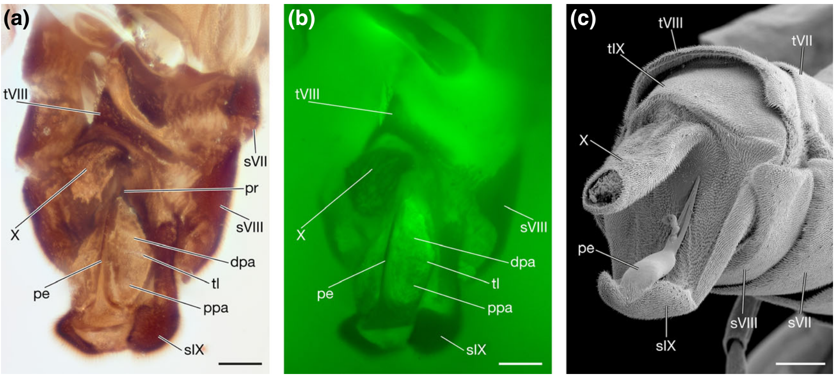

Fig. 8. a, b. †*Heterobathmilla kakopoios* Pohl and Beutel, gen. et sp. n. Terminal segments with external genitalia in Burmese amber, dorsal view in comparison with a basal extant representative, oblique caudal view. a. Brightfield photomicrograph. b. Autofluorescence photomicrograph. c. *Mengenilla moldrzyki* (Mengenillidae) SEM (modified from Hünefeld et al., 2011). Abbreviations: dpa, distal portion of paramere; ppa, proximal portion of paramere; pe, penis; sVII–sIX, sternites VII–IX; tVII–tIX, tergites VII–IX; tl, transverse line; X, abdominal segment X. Scale bars 100 µm. [Colour figure can be viewed at wileyonlinelibrary.com]

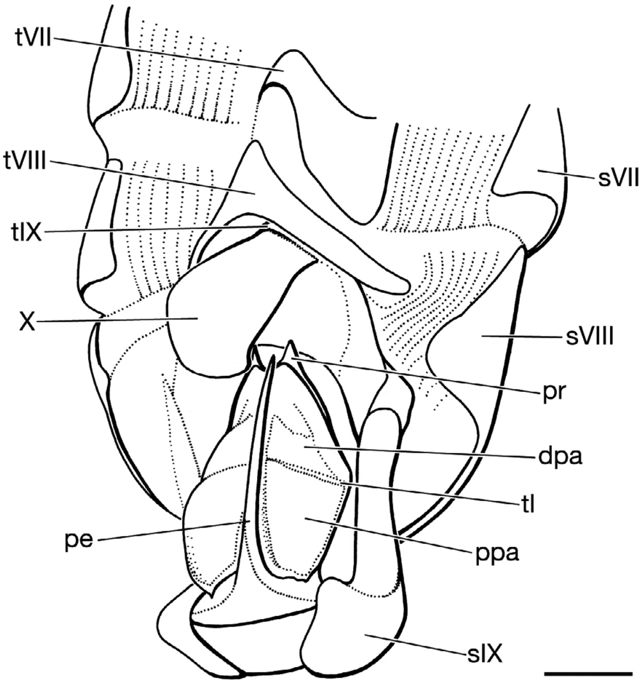

Fig. 9. †*Heterobathmilla kakopoios* Pohl and Beutel, gen. et sp. n. Terminal segments with external genitalia, dorsal view. Abbreviations: dpa, distal portion of paramere; ppa, proximal portion of paramere; pe, penis; pr, process; sVII–sIX, sternites VII–IX; tVII–tIX, tergites VII–IX; tl, transverse line; X, abdominal segment X. Scale bar 100 µm.

early evolutionary history of the order in the late Palaeozoic and earlier Mesozoic remains completely in the dark. The Carboniferous genus †*Stephanastus*, represented by the incompletely preserved holotype, was assigned to a new extinct order †Skleroptera by Kirejtshuk and Nel (2013). This taxon was interpreted as a subgroup of Coleopterida, supposedly the sister group of Strepsiptera + Coleoptera (Kirejtshuk and Nel, 2013). However, this hypothesized placement of the fossil was rejected as unfounded and very unlikely by Beutel et al. (2019).

A recently discovered Cretaceous primary larva (Pohl et al., 2018) is nearly identical with recent first instars. It underlines a remarkable evolutionary stasis in the order over ca. 100 million years, and it discards earlier alleged findings of strepsipteran immatures (e.g. Grimaldi et al., 2005), which very likely belong to the beetle family Ripiphoridae (Beutel et al., 2016; Batelka et al., 2018). As far as adults are concerned, the oldest known fossils differ only in details from the extant forms (e.g., Grimaldi et al., 2005; Pohl and Beutel, 2016). Unless well-preserved impression fossils from the early Mesozoic or Permian are discovered, the morphological gap between Strepsiptera and Coleoptera will remain large (Beutel et al., 2018).

Burmese Cretaceous amber has turned out to be a rich source of new extinct species of Strepsiptera and other insects. Since the description of the first fossil strepsipteran from Burmese amber in 2005, three new species have been discovered. However, except for one primary larva, only males have been found. The minute 1st instar larva has revealed a Mesozoic origin of endoparasitism. Moreover, the amber fossils have contributed greatly to the understanding of the evolution and morphological diversity of the group in the late Mesozoic and Cenozoic. With the clarified position of †*Protoxenos* from Eocene Baltic amber as sister to all remaining strepsipteran groups, the area of origin of Strepsiptera remains still ambiguous.

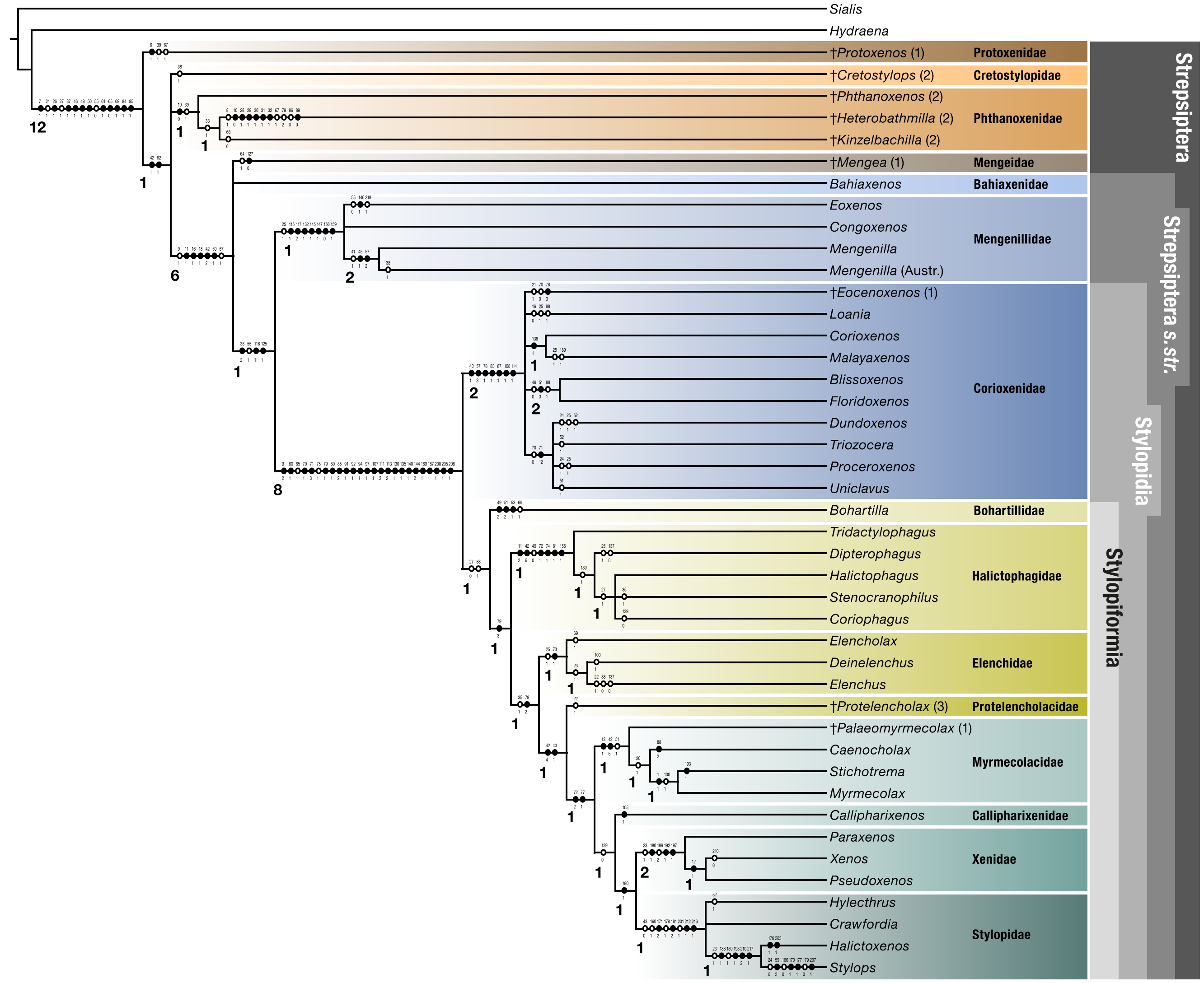

Fig. 10. Strepsipteran phylogeny, strict consensus tree of 39 minimum length trees obtained with NONA; Bremer indices are given as bold numbers beneath branches; (1) Baltic amber (minimum age approx. 42–49 Ma, probable maximum age 54 Ma [Odin and Luterbacher, 1992; Ritzkowski, 1997]), (2) Burmese amber (98.79 ± 0.62 Ma [Shi et al., 2012; Poinar, 2018]), (3) Dominican amber (15–20 Ma [Iturralde-Vinent and MacPhee, 1996; Iturralde-Vinent, 2001]). [Colour figure can be viewed at wileyonlinelibrary.com]

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References

Abellan, P., Bennetti, C.J., Angus, R.B. and Ribera, I., 2011. A review of Quaternary range shifts in European aquatic Coleoptera. Global Ecol. Biogeogr., 20, 87–100.

Antell, G.S. and Kathirithamby, J., 2016) The first twisted-wing parasitoids (Insecta: Strepsiptera) from the Early Eocene Green River Formation of Colorado. Bull., Peabody Mus. Nat., 57, 165–174.

Bai, M., Beutel, R.G., Klass, K.D., Zhang, W.W., Yang, X.K. and Wipfler, B., 2016. †Alienoptera - A new insect order in the roach-mantodean twilight zone. Gondwana Res., 39, 317–326.

Bai, M., Beutel, R.G., Zhang, W., Wang, S., Hörnig, M., Gröhn, C., Yan, E., Yang, X.K. and Wipfler, B., 2018. A new Cretaceous insect with a unique cephalo-thoracic scissor device. Curr. Biol., 28(3), 438–443.

Bao, T., Wang, B., Li, J. and Dilcher, D., 2019) Pollination of Cretaceous flowers. Proc. Nat. Acad. Sci., 116, 24707–24711.

Barden, P., 2017. Fossil ants (Hymenoptera: Formicidae): ancient diversity and the rise of modern lineages. Myrmecol. News, 24, 1–30.

Barden, P. and Grimaldi, D., 2012. Rediscovery of the bizarre Cretaceous ant *Haidomyrmex* Dlussky (Hymenoptera: Formicidae), with two new species. Amer. Mus. Novitates, 3755, 1–17.

Barden, P. and Grimaldi, D., 2013. A new genus of highly specialized ants in Cretaceous Burmese amber (Hymenoptera: Formicidae). Zootaxa, 3681, 405–412.

Barden, P. and Grimaldi, D., 2016. Adaptive radiation in socially advanced stem-group ants from the Cretaceous. Curr. Biol., 26, 1–7.

Barden, P. and Ware, J.L., 2017. Relevant relicts: the impact of fossil distributions on biogeographic reconstruction. Insect Syst. Div., 1(1), 73–80.

Barden, P., Boudinot, B. and Lucky, A., 2017a. Where fossils dare and males matter: combined morphological and molecular analysis untangles the evolutionary history of the spider ant genus *Leptomyrmex* Mayr (Hymenoptera: Dolichoderinae). Invert. Syst., 31, 765–780.

Barden, P., Herhold, H.W. and Grimaldi, D.A., 2017b. A new genus of hell ants from the Cretaceous (Hymenoptera: Formicidae: Haidomyrmecini) with a novel head structure. Syst. Entomol., 42 (4), 837–846.

Batelka, J., Prokop, J., Pohl, H., Bai, M., Zhang, W.W. and Beutel, R.G., 2018. Highly specialized Cretaceous beetle parasitoids (Ripiphoridae) identified with optimized visualization of microstructures. Syst. Entomol., 44(2), 396–407.

Beutel, R.G. and Pohl, H., 2006. Head structures of males of Strepsiptera (Hexapoda) with emphasis on basal splitting events within the order. J. Morph., 267, 536–554.

Beutel, R.G., Ge, S.-Q. and Hörnschemeyer, T. (2008) On the head morphology *Tetraphalerus*, the phylogeny of Archostemata and the basal branching events in Coleoptera. Cladistics, 23, 1–29.

Beutel, R.G., Friedrich, F., Hörnschemeyer, T., Pohl, H., Hünefeld, F., Beckmann, F., Meier, R., Misof, B., Whiting, M.F. and Vilhemsen, L., 2011. Morphological and molecular evidence converging upon a robust phylogeny of the megadiverse Holometabola. Cladistics, 26, 1–15.

Beutel, R.G., Zhang, W.W., Pohl, H., Wappler, T. and Bai, M., 2016. A miniaturized beetle larva in Cretaceous Burmese amber: reinterpretation of a fossil “strepsipteran triungulin”. Ins. Syst. Evol., 47(1), 83–91.

Beutel, R.G., Pohl, H., Yan, E.V., Anton, E., Liu, S.-P., Ślipiński, S.A., McKenna, D. and Friedrich, F., 2018. The phylogeny of Coleopterida (Hexapoda) – morphological characters and molecular phylogenies. Syst. Entomol., 74(1), 75–102.

Beutel, R.G., Yan, E.V. and Kukalová-Peck, J., 2019. Is †Skleroptera (†*Stephanastus*) an order in the stemgroup of Coleopterida (Insecta)? Ins. Syst. Evol., 50(5), 670–678.

Boucot, A.J., Xu, C., Scotese, C. and Morley, R.J., 2013. Phanerozoic paleoclimate: an atlas of lithologic indications of climate. SEPM Conc. Sedimentol. Paleontol., 1, 1–478.

Boudinot, B.E., 2018. A general theory of genital homologies for the Hexapoda (*Pancrustacea*) derived from skeletomuscular correspondences, with emphasis on the Endopterygota. Arthropod Struct. Dev., 47, 563–613.

Boudinot, B.E., Probst, R.S., Brandão, C.R.F., Feitosa, R.M. and Ward, P.S., 2016. Out of the Neotropics: newly discovered relictual species sheds light on the biogeographical history of spider ants (*Leptomyrmex*, Dolichoderinae, Formicidae). Syst. Entomol., 41, 658–671.

Boussau, B., Walton, Z., Delgado, J.A., Collantes, F., Beani, L., Stewart, I.J., Cameron, S.A., Whitfield, J.B., Johnston, J.S., Holland, P.W.H., Bachtrog, D., Kathirthamby, J. and Huelsenbeck, J.P., 2014. Strepsiptera, phylogenomics and the long branch attraction problem. PLoS One, 9, e107709.

Bravo, F., Pohl, H., Neto, A. and Beutel, R.G., 2009. Bahiaxenidae, a “living fossil” and a new family of Strepsiptera (Hexapoda) discovered in Brazil. Cladistics, 25, 614–623.

Brunke, A.J., Żyła, D., Yamamoto, S. and Solodovnikov, A., 2019. Baltic amber Staphylinini (Coleoptera: Staphylinidae: Staphylininae): a rove beetle fauna on the eve of our modern climate. Zool. J. Linn. Soc., 187, 166–197.

Cai, C., Slipinski, A., Leschen, R.A.B., Yin, Z., Zhuo, D. and Huang, D., 2017. The first Mesozoic Jacobson’s beetle (Coleoptera: Jacobsoniidae) in Cretaceous Burmese amber and biogeographical stasis. J. Syst. Palaeont., https://doi.org/10.1080/14772019.2017.1314388.

Cao, H., Boudinot, B.E., Wang, Z., Miao, X., Shih, C., Ren, D. and Gao, T. (2020) Two new iron maiden ants from Burmese amber (Hymenoptera: Formicidae: †Zigrasimeciini). Myrmecol. News, 30, 161–173.

Chatzimanolis, S., Grimaldi, D.A., Engel, M.S. and Fraser, N.C., 2012. *Leehermania prorova*, the earliest staphyliniform beetle, from the Late Triassic of Virginia (Coleoptera: Staphylinidae). Amer. Mus. Novitates, 3761, 1–28.

Chen, S., Deng, S.W., Shih, C., Zhang, W.W., Zhang, P., Ren, D., Zhu, Y.N. and Gao, T.P., 2019. The earliest Timematids in Burmese amber reveal diverse tarsal pads of stick insects in the mid-Cretaceous. Insect Sci., 26, 945–957.

Crampton, G.G., 1938. The structure called parameres in male insects. Bull. Brooklyn Entomol Soc., 33, 16–24.

Crowson, R.A., 1975. Evolutionary history of Coleoptera, as documented by fossil and comparative evidence. Atti del X Congresso Nazionale Italiano di Entomologia. Firenze. Accademia Nazionale Italiana di Entomología. Palermo, Italy: pp. 47–90.

Cruickshank, R.D. and Ko, K., 2003. Geology of an amber locality in the Hukawng Valley, Northern Myanmar. J. Asian Earth Sci., 21, 441–455.

Danforth, B.N. and Poinar, G.O. Jr., 2011. Morphology, classification, and antiquity of *Melittosphex burmensis* (Apoidea: Melittosphecidae) and implications for early bee evolution. J. Paleont., 85, 882–891.

Engel, M.S. and Grimaldi, D.A., 2002. The first Mesozoic Zoraptera (Insecta). Amer. Mus. Novitates, 3362, 1–20.

Engel, M.S., Huang, D., Breitkreuz, L.C., Azar, D., Cai, C. and Alvarado, M., 2016. A new twisted-wing parasitoid from mid-Cretaceous amber of Myanmar (Strepsiptera). Cret. Res., 58, 160–167.

Espeland, M., Breinholt, J., Willmott, K.R., Warren, A.D., Vila, R., Toussaint, E.F., Maunsell, S.C., Aduse-Poku, K., Talavera, G., Eastwood, R., Jarzyna, M.A., Guralnick, R., Lohmann, D.J., Pierce, N.E. and Kawahara, A., 2018. A comprehensive and dated phylogenomic analysis of butterflies. Curr. Biol., 28(5), 770–778.

Fikáček, M., Beutel, R.G., Cai, Ch, Lawrence, J.F., Newton, A.F., Solodovnikov, A., Ślipiński, M.A., Thayer, M.K. and Yamamoto, S.H., 2020. Reliable placement of beetle fossils via phylogenetic analyses – Triassic *Leehermania* as a case study (Staphylinidae or Myxophaga?). Syst. Entomol., 45, 175–187.

Gao, T., Yin, X., Shih, C., Rasnitsyn, A.P., Xu, X., Chen, S., Wang, C. and Ren, D., 2019. New insects feeding on dinosaur feathers in mid-Cretaceous amber. Nat. Commun., 10, 5424.

Gimmel, M.L., Szawaryn, K., Cai, C. and Leschen, R.A., 2019. Mesozoic sooty mould beetles as living relicts in New Zealand. Proc. Roy. Soc. B, 286(1917), 20192176.

Goloboff, P.A., 1999. NONA, Version 2.0. Distributed by the American Museum of Natural History. New York, NY.

Goloboff, P.A., Farris, J. and Nixon, K., 2008. TNT, a free program for phylogenetic analysis. Cladistics, 24, 774–786.

Grimaldi, D.A. and Engel, M.S., 2005. Evolution of the Insects. New York, USA: Cambridge University Press.

Grimaldi, D.A., Bonwich, E., Delannoy, M. and Doberstein, S., 1994. Electron microscopic studies of mummified tissues in amber fossils. Am. Mus. Nov., 3097, 1–31.

Grimaldi, D.A., Engel, M.S. and Nascimbene, P.C., 2002. Fossiliferous Cretaceous amber from Myanmar (Burma): its rediscovery, biotic diversity, and paleontological significance. Amer. Mus. Novitates, 3361, 1–71.

Grimaldi, D., Kathirithamby, J. and Schawaroch, V., 2005. Strepsiptera and triungula in Cretaceous amber. Ins. Syst. Evol., 36, 1–20.

Grimaldi, D.A., Peñalver, E., Barrón, E., Herhold, H.W. and Engel, M.S. (2019) Direct evidence for eudicot pollen-feeding in a Cretaceous stinging wasp (Angiospermae; Hymenoptera, Aculeata) preserved in Burmese amber. Commun. Biol., 2, 408.

Henderickx, H., Bosselaers, J., Pauwels, E., van Hoorebeke, L. and Boone, M., 2013. X-ray micro-CT reconstruction reveals eight antennomeres in a new fossil taxon that constitutes a sister clade to *Dundoxenos* and *Triozocera* (Strepsiptera: Corioxenidae). Palaeont. Electr., 16(3), 16–31.

Hennig, W., 1974. Kritische Bemerkungen zur Frage, Cladistic analysis or cladistic classification? J. Zool. Syst. Evol. Res., 12(1), 279–294.

Henwood, A., 1992a) Soft-part preservation of beetles in Tertiary amber from the Dominican Republic. Palaeontol., 35(4), 901–12.

Henwood, A., 1992b) Exceptional preservation of dipteran flight muscle and the taphonomy of insects in amber. Palaios, 7, 203–212.

Huang, D.Y., Bechly, G., Nel, P., Engel, M.S., Prokop, J., Azar, D., Cai, C.Y., Van De Kamp, T., Staniczek, A.H., Garrouste, R. and Krogmann, L., 2016. New fossil insect order Permopsocida elucidates major radiation and evolution of suction feeding in hemimetabolous insects (Hexapoda: Acercaria). Sci. Rep., 6, 23004.

Huber, J.T., Shih, C. and Ren, D., 2019. A new species of *Baeomorpha* (Hymenoptera, Rotoitidae) from mid-Cretaceous Burmese amber. J. Hymenoptera Res., 72, 1–10.

Hünefeld, F., Pohl, H., Wipfler, B., Beckmann, F. and Beutel, R.G., 2011. The male postabdomen and genital apparatus of †*Mengea tertiaria*, a strepsipteran amber fossil (Insecta). J. Zool. Syst. Evolut. Res., 49(4), 298–308.

International Commission on Zoological Nomenclature, 2012. Amendment of Articles 8, 9, 10, 21 and 78 of the *International Code of Zoological Nomenclature* to expand and refine methods of publication. ZooKeys, 219, 1–10.

Iturralde-Vinent, M.A., 2001. Geology of the amber-bearing deposits of the greater Antilles. Carribean J. Sci., 37, 141–166.

Iturralde-Vinent, M.A. and MacPhee, R.D.E., 1996. Age and paleogeographical origin of Dominican amber. Science, 273, 1850–1852.

Jałoszyński, P., 2012. Description of *Euroleptochromus* gen.n. (Coleoptera, Staphylinidae, Scydmaeninae) from Baltic amber, with discussion of biogeography and mouthpart evolution within Clidicini. Syst. Entomol., 37(2), 346–359.

Jałoszyński, P., Yamamoto, S. and Takahashi, Y., 2017. Discovery of a new Mesozoic species of the ancient genus *Lepicerus* (Coleoptera: Myxophagfa: Lepiceridae), with implications for the systematic placement of all previously described extinct ‘lepiceroids’. Cret. Res., 78, 95–102.

Jiang, T., Wang, B. and Szwedo, J., 2019. The first representative of Progonocimicidae (Hemiptera: Coleorrhyncha) from mid-Cretaceous Burmese amber. Cret. Res., 93, 346–359.

Kathirithamby, J., 2018. Biodiversity of Strepsiptera. In: Foottit, R.G. and Adler, P.H. (Eds.) Insect Biodiversity Science and Society. Blackwell, Hoboken, N.J.: Wiley, pp. 673–704.

Kathirithamby, J. and Engel, M.S., 2014. A revised key to the living and fossil families of Strepsiptera, with the description of a new family, Cretostylopidae. J. Kansas Entomol. Soc., 87(4), 385–388.

Kathirithamby, J. and Grimaldi, D., 1993. Remarkable stasis in some Lower Tertiary parasitoids: descriptions, new records, and review of Strepsiptera in the Oligo-Miocene amber of the Dominican Republic. Entomol. Scand., 24, 31–41.

Kathirithamby, J. and Henderickx, H., 2008. First record of the Strepsiptera genus *Caenocholax* in Baltic amber with the description of a new species. Phegea, 36, 149–152.

Kinzelbach, R.K., 1971. Morphologische Befunde an Fächerflüglern und ihre phylogenetische Bedeutung (Insecta: Strepsiptera). Stuttgart: Schweizerbart'sche Verlagsbuchhandlung.

Kinzelbach, R.K., 1978. Fächerflügler (Strepsiptera). Die Tierwelt Deutschlands. Jena: VEB Gustav Fischer Verlag, Jena.

Kinzelbach, R. and Lutz, H., 1985. Stylopid larva from the Eocene – a spotlight on the phylogeny of the stylopids (Strepsiptera). Ann. Entomol. Soc. Am., 78, 600–602.

Kinzelbach, R. and Pohl, H., 1994. The fossil Strepsiptera (Insecta: Strepsiptera). Ann. Entomol. Soc. Am., 87, 59–70.

Kirejtshuk, A.G. and Nel, A., 2013. Skleroptera, a new order of holometabolous insects (Insecta) from the Carboniferous. Zoosyst. Ros., 22(2), 247–257.

Kirejtshuk, A.G., Poschmann, M., Prokop, J., Garrouste, R. and Nel, A., 2014. Evolution of the elytral venation and structural adaptations in the oldest Palaeozoic beetles (Insecta: Coleoptera: Tshekardocoleidae). J. Syst. Palaeont., 12(5), 575–600.

Klopfstein, S., Vilhelmsen, L. and Ronquist, F., 2015. A nonstationary Markov model detects directional evolution in hymenopteran morphology. Syst. Biol., 64, 1089–1103.

Kočárek, P., 2019. *Alienopterella stigmatica* gen. et sp. nov.: the second known species and specimen of †Alienoptera extends knowledge about this Cretaceous order (Insecta: Polyneoptera). J. Syst. Palaeontol., 17, 491–499.

Kogan, M. and Poinar, G.O., 2019. Fossil Strepsiptera (Insecta) of the Poinar Amber Collection with description of one new genus and 12 new neotropical species in the families Protelencholacidae, Elenchidae, and Myrmecolacidae. Hist. Biol., 57, 1–62.

Krell, F.-T., 2006. Fossil record and evolution of Scarabaeoidea (Coleoptera: Polyphaga). Coleopt. Soc. Monograph, 5, 120–143.

Labandeira, C.C., 2002. Paleobiology of predators, parasitoids, and parasites: death and accommodation in the fossil record of continental invertebrates. Paleont. Soc. Papers, 8, 211–249.

Labandeira, C.C., 2006a) The four phases of plant-arthropod associations in deep time. Geol. Act., 4, 409–438.

Labandeira, C.C., 2006b) Silurian to Triassic plant and hexapod clades and their associations: new data, a review, and interpretations. Arthropod Syst. Phylog., 64, 53–94.

Labandeira, C.C. and Currano, E.D., 2013. The fossil record of plant-insect dynamics. Annu. Rev. Earth Planet. Sci., 41, 287–311.

LaPolla, J.S., Dlussky, G.M. and Perrichot, V., 2013. Ants and the fossil record. Annu. Rev. Entomol., 58, 609–630.

Latreille, P.A., 1817. Rhipiptera, Cuvier's Regne Animal. Insects. Rev. Germar's Mag. Entomol., 3, 356–359.

Lawrence, J.F., Ślipiński, A., Seago, A.E., Thayer, M.K., Newton, A.F. and Marvaldi, A.E., 2011. Phylogeny of the Coleoptera based on morphological characters of adults and larvae. Ann. Zoologici, 61, 1–217.

Legalov, A.A., 2012. Fossil history of Mesozoic weevils (Coleoptera: Curculionoidea). Insect Sci., 19, 683–698.

Legalov, A.A., 2020. Two new weevil tribes (Coleoptera: Curculionoidea) from Burmese amber. Hist. Biol., 32(1), 128–136.

Lin, X., Labandeira, C.C., Shih, C., Hotton, C.L. and Ren, D., 2019. Life habits and evolutionary biology of new two-winged long-proboscid scorpionflies from mid-Cretaceous Myanmar amber. Nat. Commun., 10, 1–14.

Liu, J., Zhang, W., Cai, W. and Li, H., 2018. Two new species of angel insects in mid-Cretaceous Burmese amber (Zoraptera: Zorotypidae). Cret. Res., 90, 259–264.

Lohrmann, V. and Engel, M.S., 2017. The wasp larva's last supper: 100 million years of evolutionary stasis in the larval development of rhopalosomatid wasps (Hymenoptera: Rhopalosomatidae. Foss. Rec., 20, 239–244.

Lu, X., Zhang, W. and Liu, X., 2017. Discovery of the family Babinskaiidae (Insecta: Neuroptera) in mid-Cretaceous amber from Myanmar. Cret. Res., 71, 14–23.

Maddison, W.P. and Maddison, D.R., 2018. Mesquite: A modular system for evolutionary analysis. Version 3.51. http://mesquite project.org

Mashimo, Y., Müller, P., Pohl, H. and Beutel, R.G., 2018. The “hairy beast” - *Zorotypus hirsutus* sp.n., an unusual new species of Zoraptera (Insecta) from Burmese amber. Zootaxa, 4508(4), 562–568.

Mashimo, Y., Müller, P. and Beutel, R.G., 2019. *Zorotypus pecten*, a new species of Zoraptera (Insecta) from mid-Cretaceous Burmese amber. Zootaxa, 4651(3), 565–577.

Matsumura, Y., Beutel, R.G., Rafael, J.A., Yao, I., Câmara, J.T., Lima, ShP and Yoshizawa, K., 2019. The evolution of Zoraptera. Syst. Entomol., 45(2), 349–364.

McKenna, D.D., Shin, S., Ahrens, D., Balke, M., Beza-Beza, C., Clarke, D.J., Donath, A., Escalona, H.E., Friedrich, F., Letsch, H., Liu, Sh, Maddison, D., Mayer, Ch, Misof, B., Murin, P.J., Niehuis, O., Peters, R.S., Podsiadlowski, L., Pohl, H., Scully, E.D., Yan, E.V., Zhou, X., Ślipiński, A. and Beutel, R.G., 2019. The evolution and genomic basis of beetle diversity. Proc. Natl Acad. Sci., 116(49), 24729–24737.

Menge, A., 1866. Über ein Rhipidopteron und einige Helminthen im Bernstein. Schr. Naturforsch. Ges. Danzig, 2, 1–8.

Metcalfe, I., 2017. Tectonic evolution of Sundaland. Bull. Geol. Soc. Malay., 63, 27–60.

Mey, W., Wichard, W., Ross, E. and Ross, A., 2018. On the systematic position of a highly derived amphiesmenopteran insect from Burmese amber (Insecta, Amphiesmenoptera). Earth Environm. Sci. Trans. R. Soc. Edinburgh, 107(2–3), 249–254.

Misof, B., Liu, S., Meusemann, K., Peters, R.S., Donath, A., Mayer, C., Frandsen, P.B., Ware, J., Flouri, T., Beutel, R.G., Niehuis, O., Petersen, M., Izquierdo-Carrasco, F., Wappler, T., Rust, J., Aberer, A.J., Aspock, U., Aspock, H., Bartel, D., Blanke, A., Berger, S., Bohm, A., Buckley, T.R., Calcott, B., Chen, J., Friedrich, F., Fukui, M., Fujita, M., Greve, C., Grobe, P., Gu, S., Huang, Y., Jermiin, L.S., Kawahara, A.Y., Krogmann, L., Kubiak, M., Lanfear, R., Letsch, H., Li, Y., Li, Z., Li, J., Lu, H., Machida, R., Mashimo, Y., Kapli, P., McKenna, D.D., Meng, G., Nakagaki, Y., Navarrete-Heredia, J.L., Ott, M., Ou, Y., Pass, G., Podsiadlowski, L., Pohl, H., von Reumont, B.M., Schutte, K., Sekiya, K., Shimizu, S., Slipinski, A., Stamatakis, A., Song, W., Su, X., Szucsich, N.U., Tan, M., Tan, X., Tang, M., Tang, J., Timelthaler, G., Tomizuka, S., Trautwein, M., Tong, X., Uchifune, T., Walzl, M.G., Wiegmann, B.M., Wilbrandt, J., Wipfler, B., Wong, T.K.F., Wu, Q., Wu, G., Xie, Y., Yang, S., Yang, Q., Yeates, D.K., Yoshizawa, K., Zhang, Q., Zhang, R., Zhang, W., Zhang, Y., Zhao, J., Zhou, C., Zhou, L., Ziesmann, T., Zou, S., Li, Y., Xu, X., Zhang, Y., Yang, H., Wang, J., Wang, J., Kjer, K.M. and Zhou, X., 2014. Phylogenomics resolves the timing and pattern of insect evolution. Science, 346, 763–767.

Mitchell, A.H.G., 1993. Cretaceous-Cenozoic tectonic events in the western Myanmar (Burma)-Assam region. J. Geol. Soc. London, 150, 1089–1102.

Nel, P., Bertrand, S. and Nel, A., 2018. Diversification of insects since the Devonian: A new approach based on morphological disparity of mouthparts. Sci. Rep., 8, 3516.

Niehuis, O., Hartig, G., Grath, S., Pohl, H., Lehmann, J., Tafer, H., Donath, A., Krauss, V., Eisenhardt, C., Hertel, J., Petersen, M., Mayer, C., Meusemann, K., Peters, R.S., Stadler, P.F., Beutel, R.G., Bornberg-Bauer, E., McKenna, D.D. and Misof, B., 2012. Genomic and morphological evidence converge to resolve the enigma of Strepsiptera. Curr. Biol., 22(14), 1309–1313.

Odin, G.S. and Luterbacher, H.P., 1992. The age of the Paleogene stage boundaries. Neues Jahrb. Geol. Paläont., 186, 21–48.

Pecharová, M., Sinetshenkova, N.D. and Prokop, J., 2020. On the morphology of the Late Paleozoic insect families Bardohymenidae and Aspidothoracidae (Palaeodictyoptera: Megasecoptera). Arthropod Struct. Dev., 55, 1–16.

Pérez-de la Fuente, R., Delclòs, X., Peñalver, E., Speranza, M., Wierzchos, J., Ascaso, C. and Engel, M.S., 2012. Early evolution and ecology of camouflage in insects. Proc. Nat. Acad. Sci., 109 (52), 21414–21419.

Peris, D., 2020. Coleoptera in amber from Cretaceous resiniferous forests. Cretac. Res., 113, 104484.

Peris, D., Labandeira, C.C., Barrón, E., Delclòs, X., Rust, J. and Wang, B., 2020. Generalist pollen-feeding beetles during the Mid-Cretaceous. iSci, 100913, 1–14.

Perrichot, V., 2014. A new species of the Cretaceous ant *Zigrasimecia* based on the worker caste reveals placement of the genus in Sphecomyrminae (Hymenoptera: Formicidae). Myrmecol. News, 19, 165–169.

Perrichot, V., Nel, A., Néraudeau, D., Lacau, S. and Guyot, T., 2008. New fossil ants in French cretaceous amber (Hymenoptera: Formicidae). Naturwiss., 95(2), 91–97.

Perrichot, V., Wang, B. and Engel, M.S., 2016. Extreme morphogenesis and ecological specialization among Cretaceous basal ants. Curr. Biol., 26, 1468–1472.

Perrichot, V., Wang, B. and Barden, P., 2020. New remarkable hell ants (Formicidae: Haidomyrmecinae stat. nov.) from mid-Cretaceous amber of northern Myanmar. Cretac. Res., 109, 104381.

Peters, R.S., Meusemann, K., Petersen, M., Wilbrandt, J., Ziesmann, J., Donath, A., Mayer, C., Kjer, K.M., Aspöck, U., Aspöck, H., Aberer, A., Stamatakis, A., Friedrich, F., Hünefeld, F., Niehuis, O., Beutel, R.G. and Misof, B., 2014. The evolutionary history of holometabolous insects inferred from transcriptome-based phylogeny and comprehensive morphological data. BMC Evolut. Biol., 14(1), 52.

Pohl, H., 2000. Die Primärlarven der Fächerflügler – evolutionäre Trends (Insecta, Strepsiptera). Kaupia, 10, 1–144.

Pohl, H., 2002. Phylogeny of the Strepsiptera based on morphological data of the first instar larvae. Zool. Scr., 31, 123–134.

Pohl, H., 2009. The oldest fossil strepsipteran larva (Insecta: Strepsiptera) from the Geisel Valley, Germany (Eocene). Ins. Syst. Evol., 40, 333–347.

Pohl, H. and Beutel, R.G., 2004. Fine structure of adhesive devices of Strepsiptera (Insecta). Arthr. Str. Dev., 33, 31–43.

Pohl, H. and Beutel, R.G., 2005. The phylogeny of Strepsiptera (Hexapoda). Cladistics, 21, 328–374.

Pohl, H. and Beutel, R.G., 2008. The evolution of Strepsiptera (Hexapoda). Zool., 111, 318–338.

Pohl, H. and Beutel, R.G., 2013. The Strepsiptera-Odyssey - the history of the systematic placement of an enigmatic parasitic insect order. Entomologia, 1(1), e4.

Pohl, H. and Beutel, R.G., 2016. †*Kinzelbachilla ellenbergeri* – a new ancestral species, genus and family of Strepsiptera (Insecta). Syst. Entomol., 41(1), 287–297.

Pohl, H. and Kinzelbach, R., 1995. Neufunde von Fächerflüglern aus dem Baltischen und Dominikanischen Bernstein (Strepsiptera: Bohartillidae and Myrmecolacidae). Mitt. Geol. - Paläont. Inst. Univ. Hamburg, 78, 197–209.

Pohl, H. and Kinzelbach, R., 2001. First record of a female stylopid (Strepsiptera: ?Myrmecolacidae) parasite of a prionomyrmecine ant (Hymenoptera: Formicidae) in Baltic amber. Ins. Syst. Evol., 32, 143–146.

Pohl, H., Beutel, R.G. and Kinzelbach, R., 2005. Protoxenidae fam. nov. (Insecta, Strepsiptera) from Baltic amber – a 'missing link' in strepsipteran phylogeny. Zool. Scr., 34, 57–69.

Pohl, H., Wipfler, B., Grimaldi, D., Beckmann, F. and Beutel, R.G., 2010. Reconstructing the anatomy of the 42 million-year-old fossil †*Mengea tertiara* (Insecta, Strepsiptera). Naturwiss., 97, 855–859.

Pohl, H., Batelka, J., Prokop, J., Müller, P., Yavorskaya, M. and Beutel, R.G., 2018. A needle in a haystack: Mesozoic origin of parasitism in Strepsiptera revealed by first definite Cretaceous primary larva (Insecta). PeerJ, 6, e5943.

Pohl, H., Hammel, J.U., Richter, A. and Beutel, R.G., 2019. The first fossil free-living late instar larva of Strepsiptera (Insecta). Arthr. Syst. Phyl., 77(1), 125–140.

Poinar, G.O. Jr., 2018. Burmese amber: evidence of Gondwanan origin and Cretaceous dispersion. Hist. Biol., 31(10), 1304–1309.

Poinar, G.O. Jr., 2020. Discoscapidae fam. nov. (Hymenoptera: Apoidea), a new family of stem lineage bees with associated beetle triungulins in Mid-Cretaceous Burmese amber. Palaeodiv., 13, 1–9.

Poinar, G.O. Jr and Danforth, B.N., 2006. A fossil bee from Early Cretaceous Burmese amber. Sci., 314, 614.

Ponomarenko, A.G., 1969. The historical development of archostematan beetles. Tr. Paleontol. Inst. Akad. Nauk SSSR, 125, 1–238 [in Russian.].

Ponomarenko, A.G. and Prokin, A.A., 2015. Review of paleontological data on the evolution of aquatic beetles (Coleoptera). Paleont. J., 13, 1383–1412.

Prokop, J., Pecharová, M., Sinitshenkova, N.D. and Klass, K.-D., 2020. Male postabdomen reveals ancestral traits of Megasecoptera among winged insects. Arthropod Struct. Dev., 57, 1–4.

Rasnitsyn, A.P. and Quicke, D.L., 2002. History of Insects. Dordrecht: Kluwer Academic Publishers.

Richter, A., Beutel, R.G. and Pohl, H., 2017. The female cephalothorax of *Xenos vesparum* Rossi, 1793 (Strepsiptera: Xenidae) Arthr. Syst. Phyl., 75(2), 327–347.

Ritzkowski, S., 1997. K-Ar Altersbestimmung der bernsteinführenden Sedimente des Samlandes (Paläogen, Bezirk Kaliningrad). Metalla, 66, 19–23.

Ronquist, F., Klopfstein, S., Vilhelmsen, L., Schulmeister, S., Murray, D.L. and Rasnitsyn, A.P., 2012. A total-evidence approach to dating with fossils, applied to the early radiation of the Hymenoptera. Syst. Biol., 61, 973–999.

Ross, A.J., 2019a) Burmese (Myanmar) amber checklist and bibliography 2018. Palaeoentomol., 2(1), 22–84.

Ross, A.J., 2019b). Burmese (Myanmar) amber taxa, on-line supplement vol 2019.2. 33pp. http://www.nms.ac.uk/explore/stories/natural-world/Burmese-amber (accessed 1.1.2020).

Ross, A.J., 2020. Supplement to the Burmese (Myanmar) amber checklist and bibliography. Palaeoentomol., 3(1), 103–118.

Ross, A.J., Mellish, C., York, P. and Crighton, B., 2010. Burmese Amber. In: Penney, D. (Ed.) Biodiversity of Fossils in Amber from the Major World Deposits. Manchester: Siri Scientific Press, pp. 208–235.

Rust, J., Singh, H., Rana, R.S., McCann, T., Singh, L., Anderson, K., Sarkar, N., Nascimbene, P.C., Stebner, F., Thomas, J.C., Kraemer, M.S., Williams, C.J., Engel, M.S., Sahni, A. and Grimaldi, D., 2010. Biogeographic and evolutionary implications of a diverse paleobiota in amber from the early Eocene of India. Proc. Nat. Acad. Sci., 107(43), 18360–18365.

Shi, G.H., Grimaldi, D.A., Harlow, G.E., Wang, J., Wang, J., Yang, M.C., Lei, W.Y., Li, Q.L. and Li, X.H., 2012. Age constraint on Burmese amber based on UePb dating of zircons. Cret. Res., 37, 155–163.

Sidorchuk, E.A. and Vorontsov, D.D., 2018. Preparation of small-sized 3D amber samples: state of the technique. Palaeoentomol., 1(1), 80–90.

Snodgrass, R.E., 1935. Principles of Insect Morphology. New York: McGraw-Hill Book Company Inc.

Snodgrass, R.E., 1957. A revised interpretation of the external reproductive organs of male insects. Smithson. Misc. Coll., 135, 1–135.

Soriano, C., Archer, M., Azar, D., Creaser, P., Delclòs, X., Godthelp, H., Hand, S., Jones, A., Nel, A., Néroudaux, D., Ortega-Blanco, J., Pérez-de la Fuente, R., Perrichot, V., Saupe, E. Kraemer, M. S. and Tafforeau, P., 2010. Synchrotron X-ray imaging of inclusions in amber. C.R. Palevol, 9(6–7), 361–368.

Sroka, P., Staniczek, A.H. and Kondratieff, B.C., 2018. 'Rolling'stoneflies (Insecta: Plecoptera) from mid-Cretaceous Burmese amber. PeerJ, 6, e5354.

Toussaint, E.F., Seidel, M., Arriaga-Varela, E., Hájek, J., Kral, D., Sekerka, L., Short, A.E.Z. and Fikáček, M., 2017. The peril of dating beetles. Syst. Entomol., 42(1), 1–10.

Wahlberg, N., Wheat, C.W. and Peña, C., 2013. Timing and patterns in the taxonomic diversification of Lepidoptera (butterflies and moths). PLoS One, 8(11), e80875.

Wang, B., Xia, F., Wappler, T., Simon, E., Zhang, H., Jarzembowski, E.A. and Szwedo, J., 2015. Brood care in a 100-million-year-old scale insect. Elife, 4, e5447.

Wang, B., Xia, F., Engel, M.S., Perrichot, V., Shi, G., Zhang, H., Chen, J., Jarzembowski, E.A., Wappler, T. and Rust, J., 2016a) Debris-carrying camouflage among diverse lineages of Cretaceous insects. Science Advances, 2, e1501918.

Wang, B., Kathirithamby, J. and Engel, M.S., 2016b) The first twisted-wing parasitoid in Eocene amber from north-eastern China (Strepsiptera: Myrmecolacidae). J. Nat. Hist., 50(21–22), 1305–1313.

Wiegmann, B.M., Trautwein, M.D., Kim, J.W., Cassel, B.K., Bertone, M.A., Winterton, S.L. and Yeates, D.K., 2009. Single-copy nuclear genes resolve the phylogeny of the holometabolous insects. BMC Biol., 7(1), 34.

Yin, Z., Cai, C. and Huang, D., 2018. New zorapterans (Zoraptera) from Burmese amber suggest higher paleodiversity of the order in tropical forests. Cret. Res., 84, 168–172.

Yoshizawa, K. and Lienhard, C., 2016. Bridging the gap between chewing and sucking in the hemipteroid insects: new insights from Cretaceous amber. Zootaxa, 4079(2), 229–245.

Yoshizawa, K. and Lienhard, C., 2020. †Cormopsocidae: A new family of the suborder Trogiomorpha (Insecta: Psocodea) from Burmese amber. Entomol. Sci., 18, 1–8.

Zheng, D., Chang, S.C., Perrichot, V., Dutta, S., Rudra, A., Mu, L., Kelly, R.S., Li, Sh, Zhang, Q., Zhang, Q.-Q., Wong, J., Wang, J., Wang, H. and Wang, B., 2018. A Late Cretaceous amber biota from central Myanmar. Nat. comm., 9(1), 3170.

Zherikin, V.V. and Ross, A.J., 2000. A review of the history, geology and age of Burmese amber (Burmite). Bull. Nat. Hist. Mus. London (Geol.), 56, 3–10.

Appendix 1

List of characters

General features

From Pohl and Beutel (2005) and Bravo et al. (2009). Characters with modified coding marked by an asterisk. Information on †*Cretostylops* and †*Phthanoxenos* was obtained from Grimaldi et al. (2005) and Engel et al. (2016), respectively. For characters 89–217 (characters of females and immature stages, not known for †*Heterobathmilla*) see Pohl and Beutel (2005). Characters of free-living larvae of †*Mengea* (chars. 106–146) were taken from Pohl et al. (2019). Character numbers in brackets correspond to character numbers in Pohl and Beutel (2005), if they differ.

1. Size relationship between males and females: (0) equally sized or females slightly larger; (1) females distinctly larger. This and the following four characters are unknown in extinct taxa including †*Heterobathmilla* (coded as ?).

2. Reproduction: (0) oviparous; (1) viviparous.

3. Host dimorphism: (0) absent; (1) present.

4. Life span of adult males: (0) distinctly more than 5 hours; (1) 5 hours or less.

5. (7) Trophic behavior of adult males: (0) feeding; (1) non-feeding.

Characters of adult males

6. (5) Size: (0) more than 10 mm; (1) 7–8 mm; (2) less than 6 mm. Distinctly less than 6 mm in †*Heterobathmilla* (2), like all other strepsipterans with the exception of †*Protoxenos*.

7. (6) Surface of cuticle: (0) not densely covered with microtrichia; (1) large parts very densely covered with microtrichia. Densely covered with microtrichia like in all other strepsipterans.

8. Epistomal suture (=frontoclypeal suture): (0) present; (1) absent. Reduced in †*Heterobathmilla* (1) like in extant strepsipteran groups.

9. Coronal suture (=epicranial suture): (0) present as ecdysial suture, about as long as distance between compound eyes; (1) distinctly shorter than distance between compound eyes or absent; (2) membranized. Present in †*Heterobathmilla* (0) like in other members of the stem group.

10. Frontal suture: (0) present as ecdysial suture; (1) absent. Distinctly recognizable in †*Heterobathmilla* (0). Absent in all other groups.

11. (10) Dorsomedian frontal impression: (0) absent; (1) present, v- or u-shaped; (2) very wide, trapezoid. Absent in †*Heterobathmilla* (0) like in other stem group members except for †*Mengea.*

12. (11) Dorsal part of head capsule (vertex) subdivided in several plates ("Vertexplatten"; Kinzelbach, 1971, 1978): (0) absent; (1) present. Absent in †*Heterobathmilla* (0).

13. (12) Postoccipital region completely membranized: (0) absent; (1) present. Not membranized in †*Heterobathmilla* (0).

14. (13) Gula: (0) present; (1) absent. Not visible in †*Heterobathmilla*, very likely absent (?) like in all other strepsipterans.

15. (14) Tentorium: (0) present; (1) absent. Unknown in †*Heterobathmilla* (?).

16. (15) Ommatidia: (0) not separated by chitinous bridges; (1) distinctly separated by chitinous bridges. Not separated by chitinous bridges in †*Heterobathmilla*, †*Kinzelbachilla*, †*Phthanoxenos,* †*Protoxenos* and †*Cretostylops*. Chitinous bridges more or less densely covered with microtrichia in extant Strepsiptera (e.g., Pohl and Beutel, 2005).

17. (16) Ocelli: (0) present; (1) absent. Absent in †*Heterobathmilla* (1) as in all other strepsipterans.

18. (17) Insertion of antenna: (0) laterally, anterior to compound eyes; (1) dorsally. Laterally inserted in †*Heterobathmilla* (1) like in other stem group members except for †*Mengea.*

19. Antennal foramen: (0) about twice as wide as diameter of scapus (1) slightly wider than diameter of scapus. Distinctly widened in †*Heterobathmilla,* †*Kinzelbachilla* and †*Phthanoxenos* (0).

20. (18) Length of antennae: (0) less than 50% of hind wing; (1) at least 75% of hind wing. Short in †*Heterobathmilla* (0) like in all other strepsipteran groups except *Stichotrema*, *Myrmecolax* and *Caenocholax.*

21. (19) Number of antennomeres: (0) more than 8; (1) 8; (2) 7 or less. Eight in †*Heterobathmilla* (1) like in extant *Bahiaxenos* and in other stem group members except for †*Mengea.*

22. (20) Fusion of antennomeres 3 and 4: (0) absent; (1) present. Absent in †*Heterobathmilla* (0).

23. (21) Fusion of antennomeres 4 and 5: (0) absent; (1) present. Absent in †*Heterobathmilla* (0).

24. (22) Fusion of antennomeres 5 and 6: (0) absent; (1) present. Absent in †*Heterobathmilla* (0).

25. (23) Fusion of antennomeres 6 and 7: (0) absent; (1) present. Absent in †*Heterobathmilla* (0).

26. (24) Lateral process (flabellum) of antennomere 3: (0) absent; (1) present. Present in †*Heterobathmilla* (1)

27. (25) Lateral process of antennomere 4: (0) absent; (1) present. Present in †*Heterobathmilla* (1).

28. Dorsal process of antennomere 4: (0) absent; (1) present. Only present in †*Heterobathmilla* (1), like the dorsal process of segments 5–8.

29. Dorsal process of antennomere 5: (0) absent; (1) present. Present in †*Heterobathmilla* (1)

30. Dorsal process of antennomere 6: (0) absent; (1) present. Present in †*Heterobathmilla* (1)

31. Dorsal process of antennomere 7: (0) absent; (1) present. Present in †*Heterobathmilla* (1)

32. Dorsal process of antennomere 8: (0) absent; (1) present. Present in †*Heterobathmilla* (1)

33. (26) Shape of flabellum of antennomere 3: (0) narrow; (1) wide and flattened. Wide and flattened in †*Heterobathmilla* (1), like in †*Kinzelbachilla*, †*Palaeomyrmecolax* (Myrmecolacidae), Xenidae and Stylopidae.

34. (27) Shape of antennomere 5: (0) round in cross section; (1) wide and flattened. Round in cross section in †*Heterobathmilla* (0) like in other basal groups. Wide and flattened in †*Palaeomyrmecolax* (Myrmecolacidae), Xenidae and Stylopidae.

35. (28) Length of antennomere 5: (0) as long as antennomere 3; (1) at least twice as long. As long as antennomere 3 in †*Heterobathmilla* (0).

36. (29) Sensorial groove of antennomere 4 (Hofenedersches organ; Kinzelbach, 1971): (0) absent, (1) present. Present in †*Cretostylops* (verified with new material). Not recognizable in †*Heterobathmilla* (?).

37. (30) Dome-shaped chemoreceptors on flagellomeres: (0) absent; (1) present. Always present (1).

*38. (31 Labrum: (0) free, at least reaching inner margin of mandibles; (1) present, distinctly narrower than distance between mandibular bases; (2) absent; (3) narrow, completely fused with clypeus. Free and broad in †*Heterobathmilla* (0), like in extant *Bahiaxenos* and other stem group members except for †*Cretostylops.*

39. (32) Anterolateral labral process: (0) absent; (1) present. Present in †*Heterobathmilla* (1) like in †*Kinzelbachilla*, †*Phthanoxenos* and †*Protoxenos.*

40. (33) Mandibles: (0) well-developed; (1) absent or vestigial. Well-developed in †*Heterobathmilla* (0) like in other groups except for Corioxenidae.

41. (34) Articulation of mandibles: (0) well-developed primary and secondary mandibular joint, broad mandibular base in close contact with head capsule; (1) primary and secondary mandibular joint reduced, separated from clypeal margin and lower margin of genae by membrane (Beutel and Pohl, 2006). Well-developed primary and secondary mandibular joint present in †*Heterobathmilla* (0), like in other members of the stem groups and in *Eoxenos* and *Bahiaxenos.*

*42. (35) Shape of mandibles: (0) entire mandible robust, with broad base and very evenly narrowing and curved inward distally; (1) well-developed, distinctly narrowing and curved inward distad of moderately broad basal region; (2) well-developed, base straight, only apices curved inwards; (3) robust, slightly curved outwards, apices do not meet at median line; (4) slender, apices crossing medially; (5) extremely slender, curved outwards, apices crossing medially; (6) short, conical, not meeting at median line. Mandible moderately broad proximally in †*Heterobathmilla*, distinctly narrowing and evenly curved inwards distally, with pointed apex (1).

43. (36) Shape of distal parts of mandible: (0) not blade-like and flattened; (1) blade-like and flattened, with sharp external and internal edge. Not blade-like and flattened in †*Heterobathmilla* (0), like in most other groups.

44. (37) Position of mandibles: (0) not posterior to mouthfield sclerite or hypopharynx; (1) posterior to mouthfield sclerite. Not posterior to mouthfield sclerite or hypopharynx in †*Heterobathmilla* (0), like in other stem group members and in Bahiaxenidae and Mengenillidae.

45. (38) Movability of maxilla: (0) not restricted; (1) immobilized. Not restricted in †*Heterobathmilla* (0) like in all other groups except for *Mengenilla.*

46. (39) Cardo: (0) separate sclerite; (1) not present as separate sclerite. Never present as separate sclerite (1).

47. (40) Galea: (0) present; (1) absent. Distinctly developed in †*Heterobathmilla* (0) like in †*Kinzelbachilla,* †*Phthanoxenos* and †*Protoxenos.*

48. (41) Lacinia: (0) present; (1) absent. Generally absent (1).

49. (42) Size and shape of maxilla (without palp): (0) smaller than half of head width, globular, as long as wide; (1) smaller than half of head width, elongate; (2) longer than half of head width. Less than half of head width in †*Heterobathmilla* (1).

50. (43) Palpus maxillaris: (0) several palpomeres; (1) 1-segmented. Always one-segmented in Strepsiptera (1).

51. (44) Length of palpus maxillaris: (0) not longer than twice the length of the corpus maxillaris (=stipes or stipes incl. fused cardo); (1) more than 3 × as long as the corpus maxillaris; (2) strongly shortened; (3) absent or vestigial. Less than twice the length of the corpus maxillaris in †*Heterobathmilla* (0).

52. (45) Insertion of palpus maxillaris: (0) on apical margin of stipes; (1) proximad of apical stipital margin. On apical margin of stipes in †*Heterobathmilla* (0) like in most other groups.

53. (46) Microtrichia of palpus maxillaris: (0) unmodified (1); mushroom-shaped. Unmodified in †*Heterobathmilla* (0).

*54. (47) Sensilla of distal part of palpus maxillaris: (0) absent or few scattered chemoreceptors; (1) numerous cupuliform chemoreceptors. Absent in †*Heterobathmilla* (0)

55. (48) Oviform sensillum of palpus maxillaris: (0) present; (1) absent. Present in †*Heterobathmilla* (0) like in other stem group members and *Eoxenos*.

56. Position of oviform sensillum: (0) approximately in middle region of palpus maxillaris; (1) apical region of palpus maxillaris. Near the tip of the palp in †*Heterobathmilla* (1) like in †*Kinzelbachilla*.

57. (49) Subdivision of labium: (0) submentum, mentum, prementum; (1) ventral part of mouthfield sclerite and posterior transverse part of head capsule; (2) completely undivided; (3) posterior part completely reduced, mouthfield sclerite reaches hind margin of head capsule. Not clearly recognizable in †*Heterobathmilla* (?).

58. (50) Labial palps: (0) present; (1) absent; (2) modified as labellae. Always absent (1).

59. (51) Mouthfield sclerite: (0) absent; (1) present, without separate dorsal part; (2) present, with separate dorsal part. Absent in †*Heterobathmilla* (0) like in other stem group members.

60. (52) Size of mouthfield sclerite: (0) width less than 30% of the distance between the outer edge of the mandibular bases; (1) width at least 70% of the distance between the outer edge of the mandibular bases. Not applicable in †*Heterobathmilla* (-).

61. (53) Mesothoracic halteres: (0) absent; (1) present. Generally present (1).

*62. (54) Shape of hind wings: (0) longer than maximum width; (1) broader than long. Broader than long and fan-shaped in †*Heterobathmilla* (1), like in all other groups except for †*Protoxenos*.

63. (55) Transverse veins of hind wings: (0) present; (1) absent. Absent in †*Heterobathmilla* (1) like in all other groups.

64. (56) Cells of hind wings; (0) more than one; (1) one cell; (2) absent. Absent in †*Heterobathmilla* (2) like in all other groups except for †*Mengea*.

65. (57) Scuto-prescutal region of metathorax: (0) strongly arched and prominent; (1) weakly arched and almost flat. Strongly arched and prominent in †*Heterobathmilla* (0).

66. (58) Metapostnotum: (0) external part transverse; (1) external part plate-like, approximately as long as broad; (2) external part shield-like, distinctly longer than wide, covering the median part of several abdominal tergites. External part shield-like, distinctly longer than wide in †*Heterobathmilla* (2).

67. (59) Trochanter and femur of fore legs: (0) separated; (1) fused. Fused in †*Heterobathmilla* (1).

68. (60) Trochanter and femur of middle legs: (0) separated; (1) fused. Fused in †*Heterobathmilla* (1).

69. (61) Distal margin of tibiae: (0) straight; (1) acuminate (with "accessory claw"). Always straight (0).

70. (62) Number of tarsomeres: (0) 5; (1) 4; (2) 3; (3) 2. Five in †*Heterobathmilla* (0).

71. (63) Claws: (0) paired, normally developed; (1) paired, strongly reduced in size; (2) single small claw; (3) claws absent. Paired and well-developed in †*Heterobathmilla* (0) like in other stem group members and Bahiaxenidae and Mengenillidae.

72. (64) Shape of basitarsus of fore legs: (0) cylindrical; (1) disc-shaped; (2) triangular. Cylindrical in †*Heterobathmilla* (0).

73. (65) Accessory claws of basitarsus of fore legs (Kinzelbach, 1971): (0) absent; (1) present. Absent in †*Heterobathmilla* (0) like in most other groups except for Elenchidae.

74. (66) Accessory claws of basitarsus of middle- and hind legs (apex of tarsomere acuminate; Kinzelbach, 1971): (0) absent; (1) present. Absent in †*Heterobathmilla* (0) like in most other groups.

75. (67) Shape of tarsomere 4: (0) cylindrical, at least twice as long as wide; (1) shortened, approximately as long as wide or wider than long; (2) shortened, triangular. Cylindrical and at least twice as long as wide in †*Heterobathmilla* (0).

76. (68) Diameter of tarsomere 5: (0) approximately like tarsomere 4; (1) at most 50% of tarsomere 4. Similar to tarsomere 4 in †*Heterobathmilla* (0).

77. (69) Ventral surface of tarsomeres: (0) normally developed; (1) elongated. Normally developed in †*Heterobathmilla* (0).

*78. (70) Sensorial spot on surface of tarsi: (0) absent; (1) present on tarsomeres 1–3; (2) present on tarsomere 1; (3) present on tarsomere 2 and 3. Absent in †*Heterobathmilla* (0) like in other stem group members and some other groups (Pohl and Beutel, 2004).

*79. (71) Hairy adhesive ventral tarsal surfaces: (0) absent; (1) present on tarsomere 4; (2) present on tarsomere 1 and 2; (3) present on all tarsomeres. Present on tarsomere 1 and 2 in †*Heterobathmilla* (2).

Abdomen of adult males

*80. (81) Relative size of abdominal tergites: (0) slightly smaller than sternites; (1) tergites strongly reduced in size. Tergites slightly smaller than sternites in †*Heterobathmilla* (0) and other basal groups. Distinctly reduced in size in Stylopidia.

81. (74) Sternite VIII: (0) caudal margin straight; (1) acuminate. Straight in †*Heterobathmilla* (0).

82. (75) Sclerotization of abdominal segment IX: (0) weakly sclerotized; (1) strongly sclerotized. Strongly sclerotized in †*Heterobathmilla* (1) like in all other groups.

83. (76) Shape of abdominal segment IX: (0) not elongated; (1) ventrally elongated. Not elongated in †*Heterobathmilla* (0).

84. (77) Abdominal segment X: (0) strongly reduced or absent; (1) prominent and elongated. Prominent and elongated in †*Heterobathmilla* (1) like in all other groups.

85. (82) Abdominal spiracles: (0) on segments I–VIII; (1) on segments I–VII; (2) on segment I. Not recognizable in †*Heterobathmilla* (?).

86. (78) Parameres: (0) present; (1) absent. Only present in †*Heterobathmilla* (0).

87. (79) Length of penis: (0) short; (1) elongated. Apparently short in †*Heterobathmilla* like in other stemgroup strepsipterans (0).

88. (80) Shape of penis: (0) almost straight; (1) hook- or anchor-shaped apex, without spinae laterales; (2) anchor-shaped, apex with spinae laterales; (3) with two pairs of rounded lobes and slender apex. Almost straight in †*Heterobathmilla* (0).

89. Base of penis: (0) broad; (1) narrow. Broad in †*Heterobathmilla*. Narrow in all other strepsipteran groups. Homology in outgroups uncertain.