

# †*Praphennium* gen. nov.: Extant mite killers meet their Cenomanian relatives (Coleoptera: Staphylinidae: Scydmaeninae: Cephenniini)

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## ABSTRACT

†*Praphennium* gen. nov. is described to include †*Praphennium carinatum* sp. nov. from the Cenomanian Myanmar amber. Two other species are placed in the same genus, but they remain unnamed. This is the first known extinct genus of the large tribe Cephenniini that includes cosmopolitan extant ant-like stone beetles with uniquely modified mouthparts adapted to feed on armored mites. †*Praphennium* shares most exoskeletal characters with its extant relatives, and the structure and position of its hypognathous head suggest that the adults were also specialized predators that fed on heavily sclerotized oribatid or uropodine mites. One of the studied specimens seems to be teratological, with a reduced number of antennomeres, representing the first such a case in the fossil record of Scydmaeninae. Together with a previously known Turonian †*Hyperstenichnus* of Glandulariini, the discovery of †*Praphennium* supports early origins of acarophagy among Scydmaeninae, the only group of beetles that have adapted to feeding on this well-protected group of soil arthropods. A preliminary phylogenetic analysis suggests a close relationship between †*Praphennium* and the extant genera *Cephennodes* and *Hlavaciellus*, and this clade might have likely evolved within the Eurasian part of Laurasia.

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## 1. Introduction

The tribe Cephenniini of ant-like stone beetles (Scydmaeninae) comprises 19 genera with ~560 extant species and subspecies distributed worldwide (Jałoszyński, 2014, and numerous later additions). These beetles can be readily identified on the basis of their body form, which is not 'ant-like', as that in most scydmaenines, but stout and suboval, with weakly marked or absent constriction between the pronotum and elytra. The hallmark of Cephenniini is a strikingly short head capsule lacking the occipital constriction; the head in natural position is tilted ventrad, so that the frons is nearly perpendicular to the long axis of the body and the mouthparts are directed ventrad; and the labium is modified, bearing two or six pairs of lateral discs. Modifications of the head and mouthparts have evolved as adaptations to feed on heavily armored mites (Oribatida and Mesostigmata: Uropodina). Beetles attack their prey from above to access the large dorsal or laterodorsal surface of thorax, and attach the mite to the labial discs, which function as suckers that tightly adhere to the smooth cuticle. The complex

internal structure of the labium and the suckers was studied by Jałoszyński & Beutel (2012), and the feeding mechanism, behavior and preferences toward only certain families and genera of Oribatida were described for some species by Jałoszyński & Olszanowski (2016). The labial suckers require a subglobose, rigid and smooth surface to function, and the mandibles are modified to slowly scrape through the mite's cuticle. As all Cephenniini have similarly modified labium, presumably all species can use only armored mites as the source of food. Although morphological structures of all extant cephenniine genera have been studied in detail (e.g., Jałoszyński, 2011a, 2012a, 2014), the question when and how such narrow feeding adaptations originated remains unanswered. Only recently two extant genera of Cephenniini (*Cephennodes* Reitter and *Cephennomicrus* Reitter) have been reported from Eocene Baltic amber (Jałoszyński & Kubisz, 2016; Jałoszyński & Perkovsky, 2016), and an undetermined species from a Cenomanian Myanmar amber has been illustrated, but not assigned to any genus (Jałoszyński & Peris, 2016). It was not possible to study the ventral surface of this single recorded Cretaceous cephenniine beetle, and even though it highly resembled extant Cephenniini in dorsal view, its relationships within the tribe remained unknown. Its head was detached from the body, so that its natural position (prognathous or hypognathous) was unclear. Extremely uniform dorsal

Abbreviations: CNC, Canadian National Collection of Insects, Arachnids and Nematodes, Ottawa, Canada.

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morphology of adults makes it difficult to identify even extant genera without studying their fine ventral structures, especially those of the thorax. Furthermore, the body length, typically around or often below 1 mm, is another obstacle in finding diagnostic characters in only partly observable fossils.

In the present paper the first extinct, Upper Cretaceous, genus of Cephenniini is described, and its possible relationships with all other members of this large tribe are analyzed to propose a preliminary phylogenetic hypothesis that can facilitate further study of cephenniine fossils.

## 2. Geographic and geological context

Several localities in Myanmar are known to yield a Cretaceous amber, but commercial extraction and scientific studies are focused only on a mine in the Hukawng Valley, Kachin State of northern Myanmar (Fig. 1). The amber mine is located in the northern part of the Noije Bum Hill (26°15'N; 96°34'E), which consists of folded Cretaceous and Paleogene deposits (Cruickshank & Ko, 2003). A variety of clastic sedimentary deposits with thin limestone beds, and abundant coaly and carbonaceous materials are recognized at the mine (Cruickshank & Ko, 2003). Amber is associated with a narrow horizon in fine-grained facies and it was dated as of the earliest Cenomanian age ( $98.79 \pm 0.62$  Ma) by the radioisotopic dating of zircon crystals obtained from the amber matrix (Cruickshank & Ko, 2003; Shi et al., 2012). Marine fossils such as ammonites and foraminifers, abundance of amber, coalified plant materials and common coal laminations in the fine clastic facies



Fig. 1. Location of amber deposits studied in this work, the Noije Bum hill mines (Tanai, Kachin State, Myanmar) (marked with a circle).

suggest that depositional environment must have been nearshore (Cruickshank & Ko, 2003).

## 3. Material and methods

### 3.1. Specimen handling and imaging

The fossil specimens here described are deposited at CNC, with collection numbers OSAC0002900145, OSAC0002900226, and OSAC0002900227. The inclusions were observed (as dry specimens and submerged in cedar oil for better visibility) under Nikon SMS1500 (Nikon, Tokyo, Japan) and Leica M205C (Leica Microsystems, Wetzlar, Germany) stereomicroscopes. Photographs were taken on white background using a KYF75U digital camera (JVC, Yokohama, Japan) mounted to the Leica microscope. Image stacks were processed using COMBINE ZP (Hadley, 2010) and edited with Corel PhotoPaint 9.397. Morphological structures were figured by freehand drawing, with exact proportions and general shapes sketched from photographs, using specimens observed at various angles. Measurement convention and the terminology of morphological structures follow those of Jałoszyński (2014). The work is registered in ZooBank under urn:lsid:zoobank.org:pub:E6DDCC88-8B64-44E7-8B59-775BCBF8A1F9.

### 3.2. Phylogenetic analysis

In order to place the studied fossil taxa in a systematic context and provide bases for future studies, morphological structures of all nominal and two undescribed genera of extant Cephenniini were analyzed. The list of species, their countries of origin, study methods and depositories are listed in Appendix A. The character states of Cenomanian specimens were incorporated into a section of an existing dataset used to test the monophyly of Cephenniitae by Jałoszyński (2014). The dataset was slightly modified in relation to that used previously; mainly characters related to the meso- and metaventrite were revisited to exclude those that proved variable within genera, as the knowledge of Cephenniini has significantly grown during the past few years. The dataset was restricted to members of Cephenniini only, with *Marcepania* Jałoszyński, the sole genus of Marcepaniini, as the outgroup. Marcepaniini were established as a sister group of Cephenniini by Jałoszyński (2014).

Phylogenetic analysis of 24 ingroup taxa was based on 63 non-additive and unordered adult morphological characters; inapplicable entries were assigned a gap value (“–”) and treated equivalent to missing data (“?”). Character states coded as 0 do not indicate plesiomorphies. The data matrix was assembled in Nexus Data Editor for Windows v. 0.5.0 (Page, 2001); characters were numbered starting from zero (as required by TNT); parsimony analyses were conducted in TNT (Goloboff et al., 2008) in two variants: under equal weights and with implied weighting (at the weighting function K values ranging from 3 to 12), using the ‘traditional search’ strategy, with 1000 replicates of tree bisection-reconnection (TBR) branch swapping and saving 1000 trees per replicate. Standard bootstrap analysis (1000 replicates) was also conducted in TNT, and character mapping was made in WinClada v. 1.00.08 (Nixon, 1999). Trees were annotated in Corel Photo Paint. The characters and character states are given in Appendix B; the data matrix is presented in Appendix C.

## 4. Systematic palaeontology

Suborder: Polyphaga Emery, 1886  
 Superfamily: Staphylinoidea Latreille, 1802  
 Family: Staphylinidae Latreille, 1802

Subfamily: Scydmaeninae Leach, 1815

Supertribe: Cephenniitae Reitter, 1882

Tribe: Cephenniini Reitter, 1882

Genus †*Praphennium* Jąłoszyński gen. nov.

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Figs. 2A–F, 3A–G, 4A–H

*Type species.* †*Praphennium carinatum* Jąłoszyński; here designated.

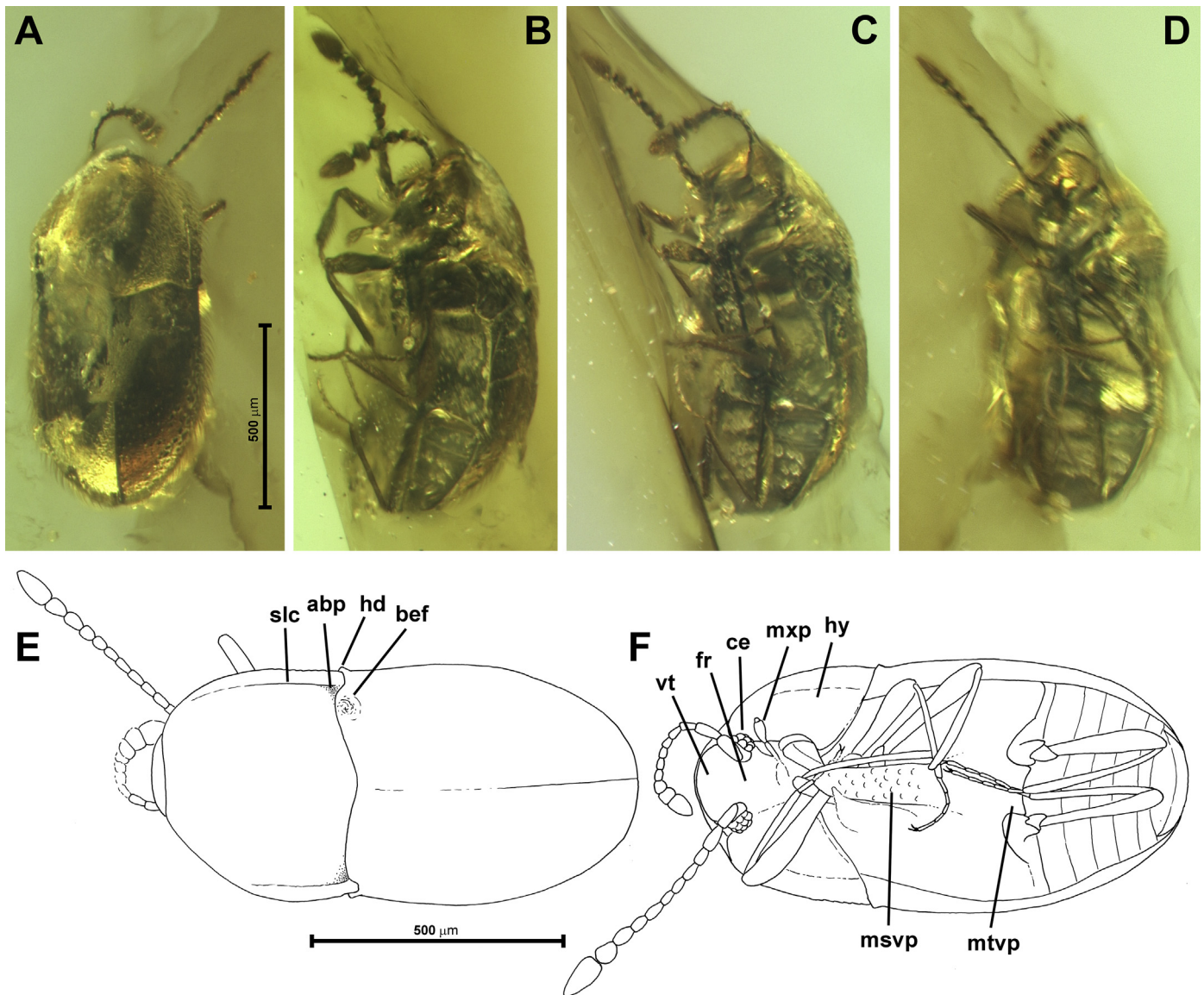
*Derivation of name.* The name is a combination of the prefix *pra-* indicating an old age, and a part of the extant genus name *Cephennium*. Gender neutrum.

*Diagnosis.* †*Praphennium* is a cephenniine genus showing two unique apomorphies: i) the prosternal intercoxal region lacking any traces of prosternal process, but deeply emarginate posteriorly to receive the mesoventral intercoxal process; ii) the mesoventral intercoxal process nearly parallel-sided, extending from anterior ridge of mesoventrite to posterior margins of mesocoxae, with its

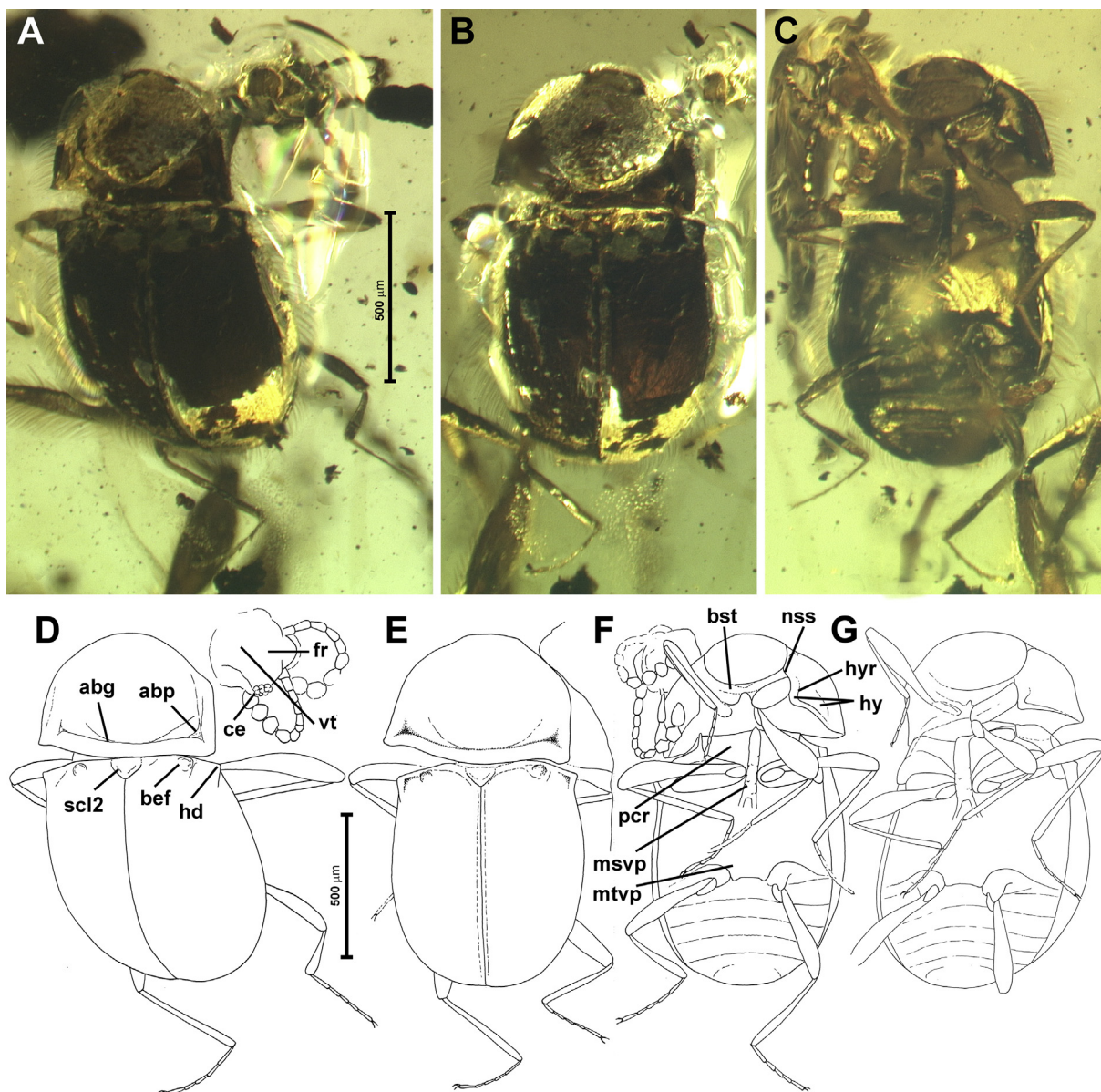
ventral surface forming a flat plate with its lateral margins overhanging its base, so that the process is indistinctly inversely T-shaped in cross-section and in strictly ventral view mesal portions of mesocoxae are not visible.

†*Praphennium* has also the following set of characters that, in a different combination or only some, occur in other genera of Cephenniini: frontal glands missing; antennae gradually thickened distad; maxillary palpomere 4 subconical with truncate apex, about as long as broad at base; pronotum with one pair of antebasal pits developed as diffuse and shallow impressions; prosternum with basisternal part shorter than coxal part; each elytron with one large and setose basal fovea; anterolateral impressions of mesoventrite functioning as procoxal rests subtriangular, with posterior margins strongly oblique in relation to the long axis of body; metacoxae very broadly separated; posterior margin of metaventral intercoxal process weakly concave.

*Description* (based on characters visible in all studied specimens). Body shape (Figs. 2A, E, 3A, B, D, E, 4A, E) as in most Cephenniini,



**Fig. 2.** †*Praphennium carinatum* gen. et sp. nov. Dorsal (A, E), lateroventral (B, C) and ventral habitus (D, F) of the holotype (OSAC0002900227). Abbreviations: abp, antebasal pit; bef, basal elytral fovea; ce, composite eye; fr, frons; hd, humeral denticle; hy, hypomeron; msvp, mesoventral intercoxal process; mtvp, metaventral intercoxal process; mxp, maxillary palp; slc, sublateral carina; vt, vertex.

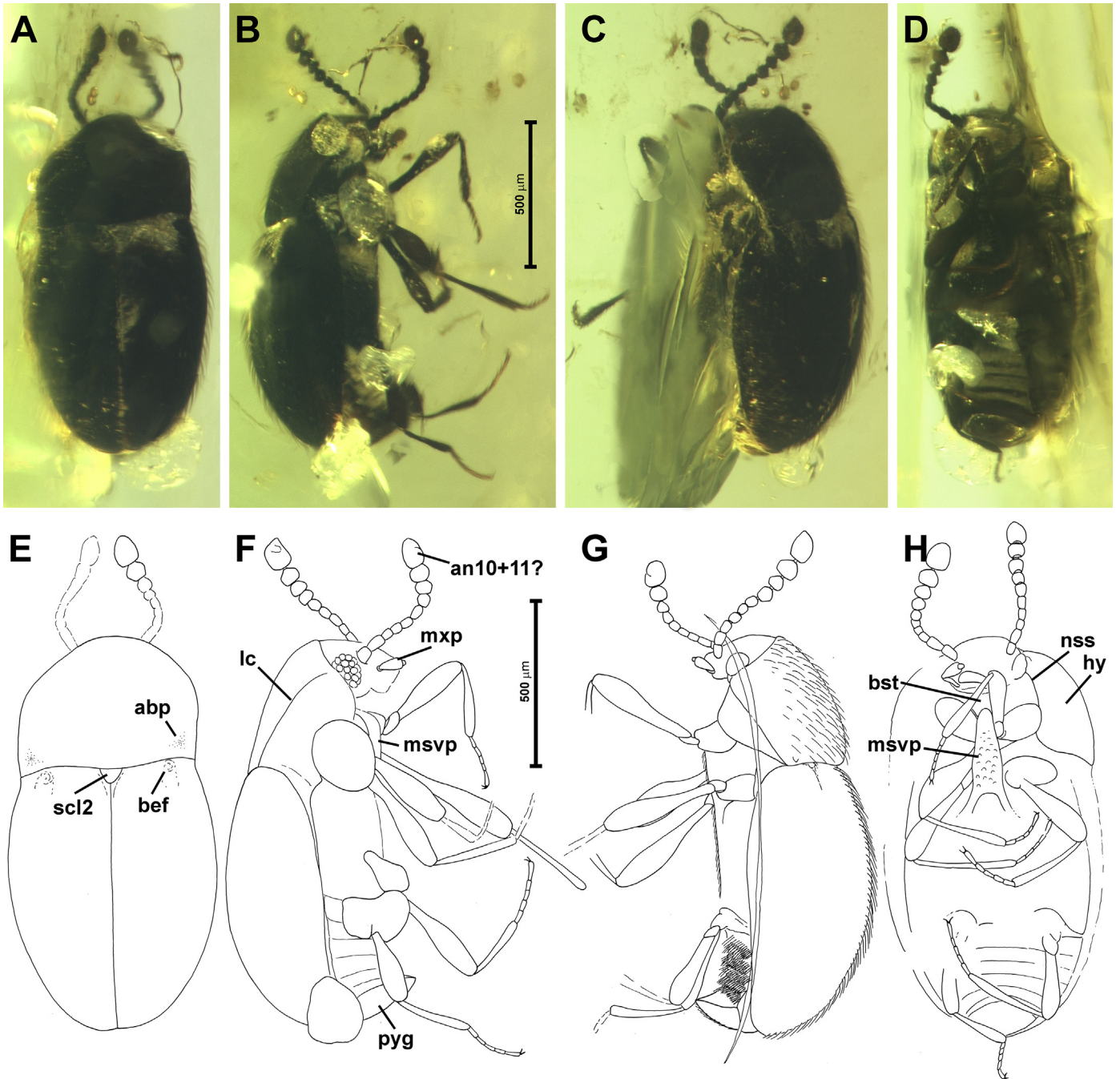


**Fig. 3.** †*Praphennium* sp. 1. Laterodorsal (A, D), dorsal (B, E), ventral (C, F), and lateroventral (G) view of specimen OSAC0002900145. Abbreviations: abg, antebasal groove; abp, antebasal pit; bef, basal elytral fovea; bst, basisternal part of prosternum; ce, composite eye; fr, frons; hd, humeral denticle; hy, hypomeron; hyr, hypomeral ridge; msvp, mesoventral intercoxal process; mtvp, metaventral intercoxal process; nss, notosternal suture; pcr, procoxal rest; scl2, mesoscutellum; vt, vertex.

suboval, compact, with indistinct constriction between pronotum and elytra, covered with short suberect setae. Head (Figs. 2F, 3D, 4F–H) strongly tilted ventrad, with mouthparts directed ventrad or even posteroventrad; head capsule short, lacking any trace of occipital constriction and retracted into prothorax up to posterior margins of composite eyes, so that tempora are absent. Vertex and frons confluent and weakly convex; supraantennal tubercles weakly elevated; antennal insertions broadly separated; eyes large, strongly projecting from the silhouette of the head and relatively coarsely faceted. Mouthparts largely concealed in all studied specimens, only details of maxillary palp visible (Fig. 2F): palpomere 2 strongly elongate, palpomere 3 broadened, palpomere 4 minute, much narrower than palpomere 3, subconical, truncated at apex and about as long as broad at base. Antennae (Figs. 2E, F, 3D, F, 4E–H) short and slender, gradually thickened; in one specimen (OSAC0002900226) possibly teratological.

Pronotum (Figs. 2E, 3D, E, 4E–G) nearly semicircular with sides rounded in anterior half and weakly rounded or nearly straight posteriorly, posterior margin deeply bisinuate; sides with complete or nearly complete lateral carinae, in one specimen (OSAC0002900227) with distinct sublateral carinae; pronotal base with one (lateral) pair of very shallow and diffuse impressions, in one specimen (OSAC0002900145) also with a shallow arcuate transverse antebasal groove. Prosternum (Figs. 2F, 3F, G, 4H) with complete notosternal sutures and very short basisternal part, between procoxae flat and with its posterior margin deeply and relatively narrowly emarginate to receive mesoventral intercoxal process. Hypomeral ridges poorly visible, present at least in posterior half of prothoracic hypomeron, presumably complete or nearly complete.

Mesoventrite (Figs. 2F, 3F, G, 4F–H) with transverse, sub-triangular anterolateral asetose impressions functioning as



**Fig. 4.** †*Praphennium* sp. 1. Dorsal (A, E), right lateral (B, F), left lateral (C, G), and ventral (D, H) view of specimen OSAC0002900226. Abbreviations: abp, antebasal pit; an10 + 11?, presumably fused antennomeres 10 and 11; bef, basal elytral fovea; bst, basisternal part of prosternum; hy, hypomeron; lc, lateral carina; msvp, mesoventral intercoxal process; mxp, maxillary palp; nss, notosternal suture; scl2, mesoscutellum; pyg, pygidium.

procoxal rests, their posterior margins oblique in relation to the long body axis; mesoventral intercoxal process massive, moderately broad, very long, extending from anterior ridge of mesoventrite to beyond posterior margins of mesocoxae, strongly elevated and with flat ventral surface that laterally slightly overhangs its base, so that in cross-section the process is slightly inversely T-shaped and in strictly ventral view mesal portions of mesocoxae are hidden under sides of the process; posterior margin of process with distinct posterolateral arms. Mesocoxal cavities lacking posterior carinae.

Metaventrite (Figs. 2F, 3F, G, 4F–H) subquadrate, anteriorly fused with mesoventrite, posteriorly concave in front of metacoxae, with very broad and short metaventral intercoxal process, its posteromedian margin slightly concave.

Elytra (Figs. 2E, 3D, E, 4E–G) oval, each with small but distinct humeral denticle and large, setose basal elytral fovea, which is closer to humeral denticle than to mesoscutellum.

Abdomen (Figs. 2E, 3F, G, 4F–H) with six visible sternites covered with rows of suberect setae (Fig. 4G), pygidium subventral, subtriangular.

Legs (Figs. 2F, 3D–G, 4F–H) unmodified; pro- and mesocoxae subconical, metacoxae strongly transverse; all trochanters small, subtriangular; 'trochantelli' absent; all femora gradually clavate; all tibiae slender and straight or nearly straight, slightly broadened distad; tarsi slender and long, tarsomeres in all studied specimens elongate.

**Remarks.** The most striking autapomorphy of Cephenniini is the modified labium with paired suckers. In cases when it is not possible to examine the microscopic labial structures (which happens also when extant species with extremely tiny adults are studied), specimens can be unambiguously assigned to Cephenniini on the basis of the following set of characters, in all known taxa occurring together: the body suboval and compact; the head strongly tilted ventrad, short, lacking the occipital constriction and with antennal insertions broadly separated; maxillary palpomere 4 either very broad and extremely short (button-like) or subconical but clearly truncate at apex, never pointed; the pronotum semicircular or subquadrate, with complete or nearly complete lateral carinae, typically with bisinuate posterior margin; the mesoscutellum exposed between elytral bases; the humeral denticles present; the notosternal sutures complete (in rare cases partly obscured by a mesal expansion of hypomerion, but still traceable in transparent mounts); the hypomerion ridges present; the mesocoxae and metacoxae distinctly separated, the latter usually broadly so; the tarsal claws simple, unmodified; and the pygidium subvertical. †*Praphennium* gen. nov. shows all of these characters, and for this reason it is placed within Cephenniini. Only *Marcepania* of Marcepaniini, the sister group of Cephenniini, shares with Cephenniini most of the characters listed above (but it lacks the labial suckers; has a sclerotized spermatheca, the latter not known in any Cephenniini; and has a strikingly different structure of the metendosternite; all these characters not possible to study in intact specimens). †*Praphennium* does not have the following features unique for Marcepaniini: the head capsule with an indistinct occipital constriction; the metaventricle with a long median longitudinal carina and lateral longitudinal carinae convergent posterad; the very short, robust tarsi with transverse tarsomeres 1–4 bearing conspicuously dense, modified setae; and the modified tarsal claws, which in *Marcepania* have a broad basal part with a subtriangular tooth, distinctly delimited by a constriction from a slender distal part. Consequently, †*Praphennium* cannot be placed within Marcepaniini.

Within Cephenniini, the most valuable (the least variable within genera) diagnostic generic characters are associated with the ventral structures of the pro- and pterothorax. Most genera are primarily defined on the basis of the absence/presence (and then the shape) of the prosternal intercoxal process, and the shapes of meso- and metaventral intercoxal processes. Prosternal and ventral prothoracic structures of all known genera of Cephenniini, including †*Praphennium*, are compiled in Figs. 5, 6 to facilitate comparisons and identifications. Additionally, the number of pronotal antebasal pits, the number of basal elytral foveae, presence or absence of dense setae inside the elytral foveae, the width of metacoxae, and presence or absence of the enigmatic and recently discovered 'additional' sections of legs, the 'trochantelli', are used to classify the extant genera. All these characters can be observed in the three studied specimens of †*Praphennium*, although not all of them are easily visible in each specimen. The structure of prosternum in †*Praphennium* is most similar to that of the extant Neotropical genus *Furcodes* (Fig. 5), in which the prosternum has a similarly narrow and deep emargination to receive the anterior tip of the mesoventral intercoxal process. However, in *Furcodes* the emargination of the posterior prosternal margin is additionally accompanied by a large, also

emarginated prosternal process (absent in †*Praphennium*), the mesoventral intercoxal process (Fig. 6) is strongly broadened in its posterior half, with its lateral margins clearly divergent caudad, and the legs have the 'trochantelli' (illustrated in Jatoszyński (2012a)). All genera that lack any traces of the prosternal intercoxal process or carina (*Cephennium* Müller & Kunze, *Nanophthalmus* Motschulsky, and *Pseudocephennium* Reitter) clearly differ from †*Praphennium* either in the presence of the 'trochantelli' (*Pseudocephennium*), or in lacking the antebasal pronotal pits, having the metacoxae indistinctly broader than long, and the mesoventral intercoxal process subrectangular in cross-section (*Cephennium* and *Nanophthalmus*). Consequently, †*Praphennium* is a distinct genus, clearly differentiated from all previously known Cephenniini.

Of the three specimens studied, only one (OSAC0002900227) shows characters that can be used to define a new species; the two remaining specimens clearly belong to two different species (judging from the measurements, structure of the antennae and pronotum). However, they are unremarkable and if described as new species, may in future pose serious identification problems, as they differ from OSAC0002900227 in lacking the sublateral pronotal carinae, but not in having any distinct apomorphies.

Species †*Praphennium carinatum* sp. nov.

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Fig. 2

**Material studied.** Holotype (OSAC0002900227), from Myanmar amber, sex unknown (CNC).

**Derivation of name.** The name refers to the distinct sublateral pronotal carinae.

**Type locality and horizon.** Hukawng Valley, Kachin State, northern Myanmar (Fig. 1); lowermost Cenomanian, Upper Cretaceous.

**Diagnosis.** Body length 1.10 mm, elytral index 1.33; pronotum with complete sublateral carinae; punctures on pronotum distinct, sharply marked but fine, those slightly mesad sublateral carinae (surface of this area is best visible) separated by spaces distinctly shorter than diameters of punctures, those between sublateral and lateral carinae denser, nearly adjacent one to another.

**Description.** Body (Fig. 2) brown and moderately densely setose, length 1.10 mm, constriction between pronotum and elytra virtually absent. Head (Fig. 2F) with vertex and frons confluent and weakly convex, punctures not discernible, length of head 0.15 mm, width 0.20 mm; composite eyes moderately large, strongly convex. Antennae in the studied specimen laterally compressed, and consequently shapes of antennomeres difficult to assess, except that scape and pedicel are distinctly elongate and antennomeres 8–10 about as long as broad or slightly transverse (the latter best visible in Fig. 2B), length of antenna 0.53 mm.

Pronotum nearly semicircular, broadest slightly in front of base, length 0.35 mm, width 0.44 mm. Anterior margin nearly straight, sides rounded in anterior half, nearly parallel in posterior half, posterior margin deeply bisinuate; antebasal pits developed as shallow and diffuse impressions adjacent to posterior mesal portion of sublateral carinae, which are distinct and nearly complete. Disc covered with distinct but small punctures, which are sharply marked, those slightly mesad sublateral carinae (surface of this area is best visible) separated by spaces shorter than diameters of punctures, those between sublateral and lateral carinae distinctly denser, nearly adjacent one to another.

Elytra oval, broadest near middle but very weakly narrowing anterad; length 0.60 mm, width 0.45 mm, elytral index (length/width) 1.33; elytral apices rounded together; basal elytral fovea on

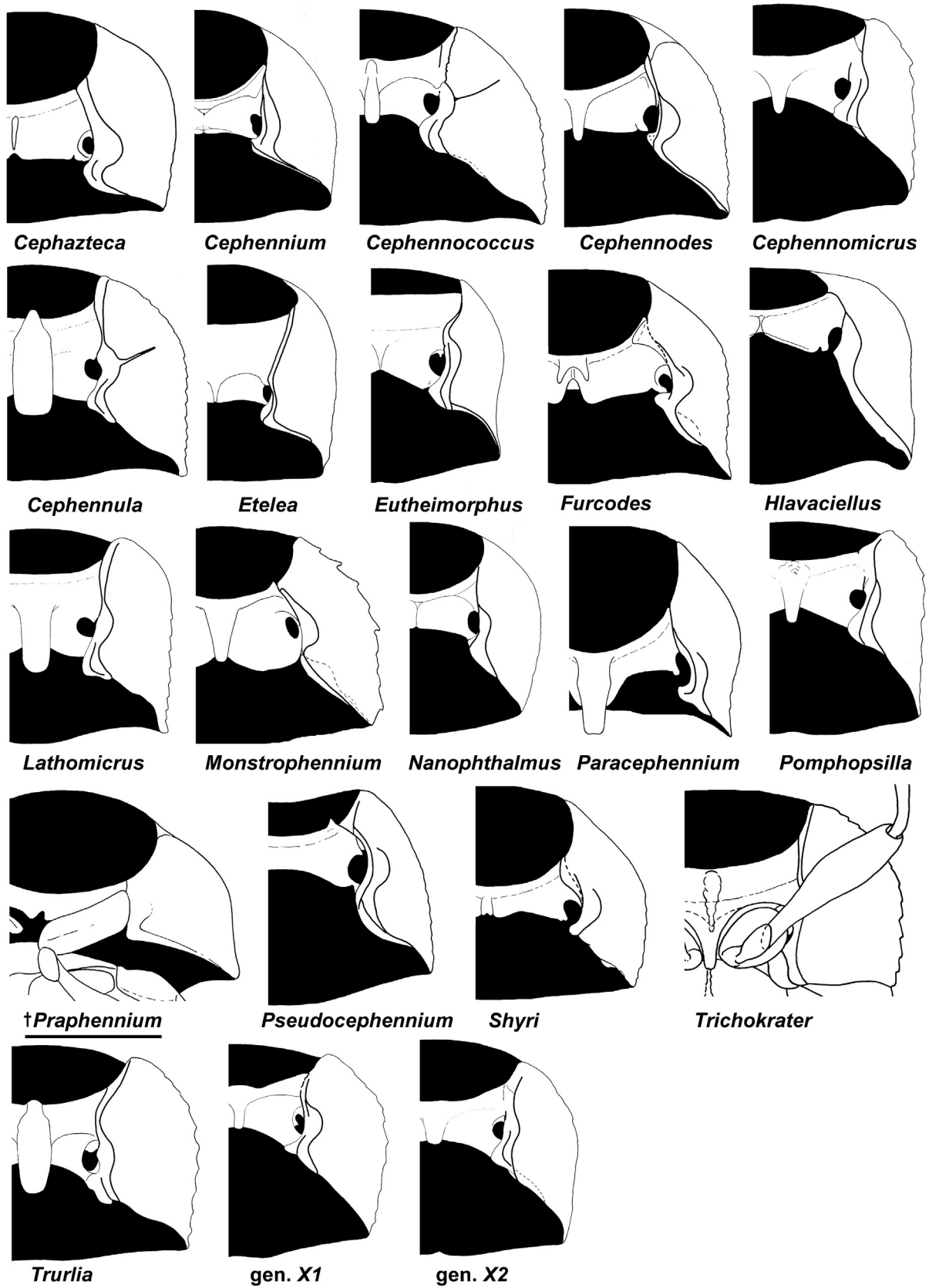


Fig. 5. Comparison of ventral prothoracic structures of all extant and extinct genera of Cephenniini.

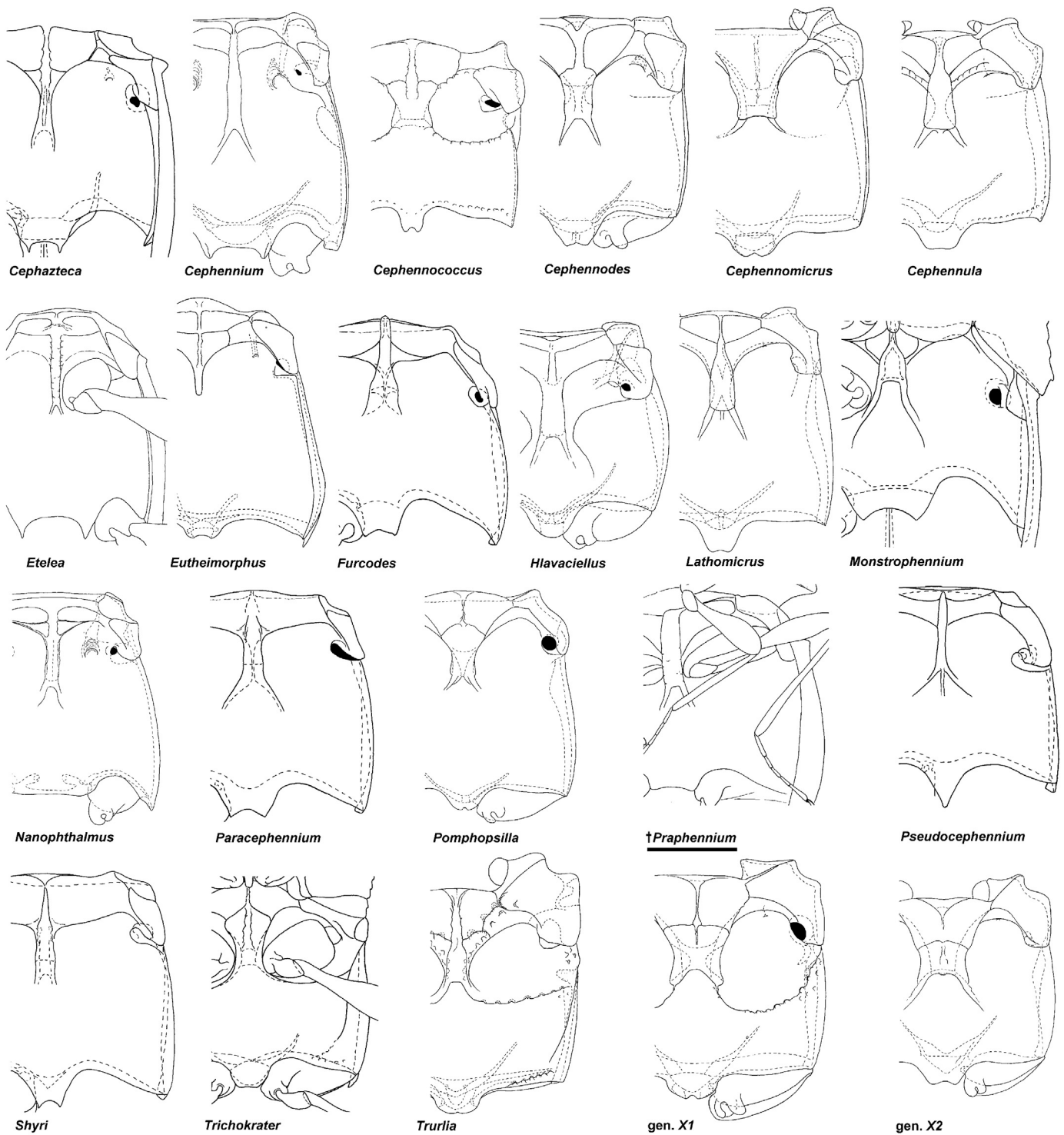


Fig. 6. Comparison of ventral pterothoracic structures of all extant and extinct genera of Cephenniini.

each elytron close to humerus; lateral margin behind humeral denticle flattened and forming a humeral carina as long as about 1/5 of elytra; scutellum obscured by milky cloud. Punctures fine but distinct, much sparser than those on pronotum, separated by spaces subequal to diameters of punctures.

Legs moderately long and slender.

Species †*Prapheennium* sp. 1

Fig. 3.

*Material studied.* Specimen OSAC0002900145, from Myanmar amber, sex unknown (CNC).

*Locality and horizon.* Hukawng Valley, Kachin State, northern Myanmar (Fig. 1); lowermost Cenomanian, Upper Cretaceous.



Body length 1.31 mm; length of head 0.18 mm, width 0.20 mm, length of antenna ~0.50 mm; length of pronotum 0.39 mm, width 0.55 mm; length of elytra 0.75 mm, width 0.55 mm, elytral index 1.36.

This specimen clearly differs from †*Praphennium carinatum* sp. nov. in lacking the pronotal sublateral carinae, distinctly larger body size, shape of pronotum and proportions of body parts. It has clearly visible mesoscutellum (Fig. 3D, E), which is large and subtriangular; an arcuate transverse antebasal pronotal groove (Fig. 3D, E); the head separated from body (Fig. 3D, F), which shows typical for Cephenniini shape and structure; deeply emarginate prosternum (Fig. 3F, G), and parallel-sided, long mesoventral intercoxal process strongly elevated on its entire length (Fig. 3F, G).

The sublateral carinae of pronotum are known to be highly variable within the extant genus *Cephennodes* Reitter (known also from Eocene Baltic amber; Jałoszyński & Kubisz (2016)), in which within groups of species that are otherwise very similar one to another (including genital structures) the carinae can be absent or present, and when present, they may be entire or developed only posteriorly. The antebasal pronotal groove, in turn, is variable within *Cephennomicrus* Reitter; in this large genus species with and without the groove are known. These characters, useful in defining species, cannot be used to define a genus, and they are treated here as variable within †*Praphennium*. Moreover, it cannot be excluded that the transverse groove visible on the pronotum of †*Praphennium* sp. 1 is a distortion, as it is accompanied by another arcuate and not entirely symmetrical impression, which may indicate a slightly collapsed surface.

#### Species †*Praphennium* sp. 2

##### Fig. 3

**Material studied.** Specimen OSAC0002900226, from Myanmar amber, sex unknown (CNC).

**Locality and horizon.** Hukawng Valley, Kachin State, northern Myanmar (Fig. 1); lowermost Cenomanian, Upper Cretaceous.

Body length 1.40 mm; length of head 0.25 mm, width not possible to measure, length of antenna ~0.50 mm; length of pronotum 0.38 mm, width 0.53 mm; length of elytra 0.78 mm, width 0.63 mm, elytral index 1.24.

This specimen also represents a species clearly different from †*Praphennium carinatum* sp. nov. in lacking the pronotal sublateral carinae, a larger body (it is the largest of the three studied specimens), the shape of pronotum and proportions of body parts. It is also different from †*Praphennium* sp. 1 in proportions of body parts and shape of the pronotum, which lacks the transverse antebasal groove.

This specimen is highly interesting, because it has clearly only ten, and not eleven, antennomeres (Fig. 3F–H). This feature is here interpreted as teratological; see the Discussion.

## 5. Relationships of †*Praphennium* within Cephenniini

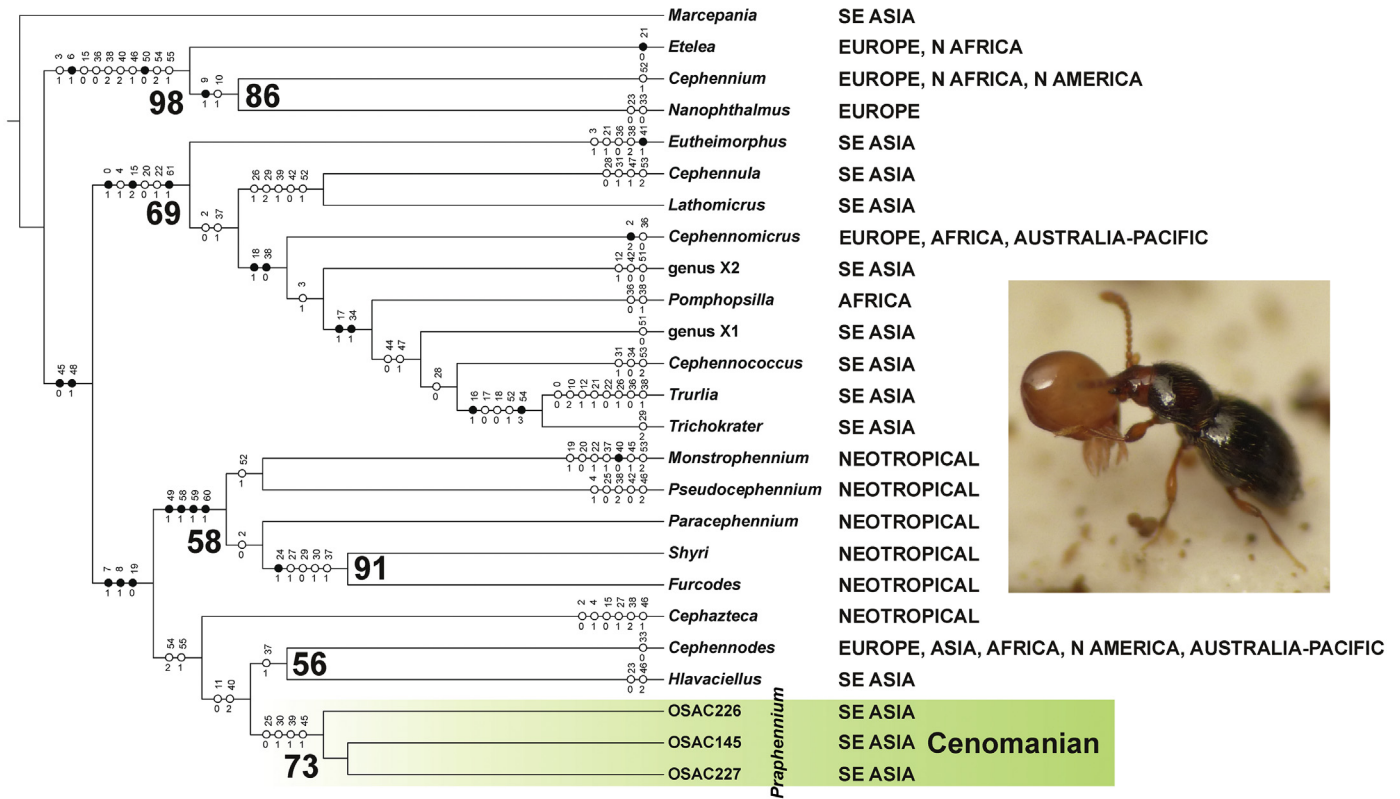
In order to place †*Praphennium* gen. nov. in a taxonomic context and to establish its relationships to the extant members of this tribe, a phylogenetic analysis was carried out. The analysis under equal weights resulted in 29 equally most parsimonious trees (MPTs) (tree length,  $L = 161$ ; consistency index,  $CI = 0.45$ ; retention index,  $RI = 0.68$ ). The strict consensus tree (not shown) was largely unresolved, and the following terminal taxa were placed in a polytomy: i) *Cephazteca* Jałoszyński; ii) *Hlavaciellus* Jałoszyński + *Cephennodes*; iii) *Etelea* Csiki + (*Cephennium* + *Nanophthalmus*); iv) a clade composed of all Neotropical Cephenniini except for *Cephazteca*; v) the '*Cephennomicrus* group' (i.e., *Eutheimorphus*

Franz & Löbl, *Cephennula* Jałoszyński, *Lathomicrus* Jałoszyński, *Cephennomicrus*, *Pomphopsilla* Jałoszyński, *Cephennococcus* Jałoszyński, *Trurlia* Jałoszyński, *Trichokrater* Jałoszyński, and two undescribed genera X1 and X2); and vi) all species placed here in †*Praphennium*. A re-analysis under implied weights resulted in a reducing the number of MPTs, and at the weighting function  $K = 4$  only one MPT was obtained (Fig. 7),  $L = 163$ ,  $CI = 0.45$ ;  $RI = 0.67$ . Results of the latter analysis are chosen as a phylogenetic hypothesis discussed in this study. All three specimens of Cenomanian amber inclusions assigned here to the genus †*Praphennium* were resolved as a clade supported by a bootstrap value 73, and sharing the prosternal process absent [25(0)], the posterior margin of prosternum strongly emarginate [30(1)], the mesoventral process in cross-section slightly inversely T-shaped [39(1)], and the meta-ventral intercoxal process as broad as  $1/4$ – $1/3$  of the posterior margin of ventrite [45(1)]. †*Praphennium* was placed as a sister group of *Cephennodes* + *Hlavaciellus*, but this relationship is supported by only two synapomorphies (maxillary palpomere 4 about as long as broad or slightly elongate [11(0)]; and posterior margin of mesoventral intercoxal process reaching behind posterior margins of mesocoxal cavities [40(2)]). The clade *Cephazteca* + ((*Cephennodes* + *Hlavaciellus*) + †*Praphennium*) was placed as a sister group to a clade composed of all Neotropical genera with the 'trochantellus' (i.e., *Monstrophennium* Jałoszyński, *Pseudocephennium*, *Paracephennium* O'Keefe, *Shyri* Jałoszyński and *Furcodes*). This relationship was supported by three unique apomorphies (labrum weakly transverse [7(1)]; mandible strongly curved ventrad [8(1)]; and notch in the posterior margin of prosternum demarcating postcoxal process absent [19(1)]), but with a bootstrap below 50. This clade was sister to the '*Cephennomicrus* group' of genera (a clade supported by a low bootstrap = 69, but also by three unique apomorphies (frontal glands present [0(1)]; pronotum with two pairs of antebasal pits [15(2)]; and base of parameres with lateral lobes [61(1)]), a relationship again not supported by a bootstrap, but all its genera sharing two unique apomorphies (metaventral intercoxal process narrower than  $1/4$  of posterior margin of metaventrite [45(0)]; and metacoxae strongly transverse, at least twice as broad as long [48(1)]). The '*Cephennium* group' (i.e., *Cephennium*, *Nanophthalmus* and *Etelea*) was recovered as monophyletic and strongly supported by the bootstrap = 98, and two unique apomorphies: the prementum with an anteroventral fringe of setae [6(1)]; and elytra fused along suture [50(0)], and placed as sister to all remaining extant and extinct Cephenniini.

As a result, †*Praphennium* is hypothesized to be a member of a clade of Cephenniini that has differentiated later than the currently Holarctic '*Cephennium* group' and currently predominantly Oriental '*Cephennomicrus* group'. It was recovered as sister to the extant genera *Cephennodes* and *Hlavaciellus*, which are currently distributed in Europe, Asia, North America, Australia and Pacific (*Cephennodes*; with a clear diversity hotspot in Southeast and East Asia), and in Southeast Asia (*Hlavaciellus*). However, these relationships were weakly supported.

## 6. Discussion

A single specimen found in the Cenomanian Myanmar amber and attributed to Cephenniini has been recently recorded in the literature. Jałoszyński and Peris (2016) provided an illustration of an undetermined genus, on the basis of a specimen whose ventral surface was not possible to examine, and having the head detached from the body. The discovery of specimens described in the present study extends our knowledge on the origins of Cephenniini and makes it possible to discuss the origins of their unusual feeding habits that require peculiar modifications not only in the



**Fig. 7.** Results of the parsimony analysis of the phylogenetic relationships of Cephenniini focused on clarifying the placement of †*Praphennium* gen. nov. Single most parsimonious tree rooted on *Marcepania* and obtained under implied weighting, at the weighting function value  $K = 4$ . Standard bootstrap support values are shown below branches (values <50 are omitted). Unambiguously optimized character changes are plotted along the internodes. Black circles indicate unique character changes; white circles indicate parallelisms or reversals; character numbers are above circles; character states below circles. Geographic distribution of extant and extinct species is listed at each taxon; photo shows a typical member of Cephenniini, *Cephennium ruthenum* Machulka (Poland) feeding on a ptyctimous oribatid mite.

mouthparts (difficult or not possible to examine in such tiny fossils), but also in the entire head capsule.

Among Scydmaeninae, the modified labium specialized to capture and immobilize armored mites can be found only in Cephenniini and two genera of Glandulariini. However, the labial suckers of Cephenniini and Glandulariini seem to differ not only in number (four or six in Cephenniini, two in Glandulariini), but also in structure. Moreover, the extant mite-eating Glandulariini (*Stenichnus* Thomson) are less specialized predators that use the modified labium only for the attack, but once the mite is captured, slender and long falciform mandibles take over and the prey is killed by inserting one mandible into the mite's mouth opening on the gnathosoma; the labial suckers are not used during feeding on a killed mite (Jałoszyński, 2016). In Cephenniini, the tribe that includes only species with modified labium (Jałoszyński, 2011a, 2012a; 2014; Jałoszyński & Beutel, 2012), the specialization is more pronounced. In species studied so far, the mite remains attached to the suckers from the moment of attack till the end of feeding, until an empty mite 'shell' is abandoned (Jałoszyński & Olszanowski, 2016). The prey is killed by a more time-consuming method; the mandibles slowly scrape through the cuticle and the feeding takes place through the resulting tiny hole, by injecting digestive juices and ingesting liquefied soft tissues (Jałoszyński & Olszanowski, 2016). This narrowly specialized method restricts the choice of prey to heavily armored, subglobose, asetose or sparsely setose and smooth oribatid mites and requires not only morphological, but also behavioral adaptations (Jałoszyński & Olszanowski, 2016). The origins and evolution of such a unique feeding strategy remain poorly understood, but already existing

evidence demonstrates the antiquity of at least morphological adaptations to use armored mites as a source of food. A recently discovered Turonian fossil (in Vendean French amber), *Hyperstenichnus vendeanus* Jałoszyński & Perrichot, 2017 (Glandulariini), shows a strong modification of the labium, with a pair of suckers that are distinctly larger than even those in extant, presumably closely related genus *Stenichnus* (Jałoszyński et al., 2017). *Stenichnus* can feed not only on smooth, but also on relatively coarsely sculptured mites (including Uropodina and Oribatida), because the labial suckers do not play a major role in feeding; it is the large mandibles that kill the prey, and the feeding takes place through the damaged, broadly open gnathosomal opening (Jałoszyński, 2016). The origins of the unusual feeding of more strictly specialized 'hole scrapers' cephenniine scydmaenines, for which the suckers play the central role, and whose choice of prey is relatively narrow (Jałoszyński & Olszanowski, 2016), remained unknown.

*Stenichnus* attacks its prey from any position, by lifting the mite attached to the labial suckers, repositioning it so that the mite is held vertically (gnathosoma up) touching the ground, and then the mandibles attack the mouth opening (Jałoszyński, 2016; Jałoszyński et al., 2017). The evolution of this strategy of attack has not required any changes in the head capsule itself in relation to other genera of Glandulariini, which are also known to feed on armored mites, but have unmodified labia. An example of such a genus is *Euconnus* Thomson, which does not have labial suckers, but can lift a mite by means of a droplet of a sticky liquid produced on its mouthparts, and the next steps of killing and feeding are similar as those in *Stenichnus* (Jałoszyński & Olszanowski, 2013). Also in *Scydmaenus* Latreille (Scydmaenini), of which at least one

species is known to feed on armored mites (other species hunt soft-bodied arthropods (Jałoszyński & Kilian, 2012; Jałoszyński, 2012b)), the labium does not have suckers, and the mite prey is captured and lifted by mandibles assisted by adhesive spatulate setae on the protibial apices, and again, the killing and feeding steps are similar to those in *Stenichnus* (Jałoszyński & Olszanowski, 2015). All these genera have adults showing a very similar head structure: the head is prognathous or nearly prognathous, so that the attack is performed by the beetle moving forward. Moreover, the head is divided into exposed anterior part and a subcylindrical 'neck' region delimited by a distinct occipital constriction, which presumably increases the range of head movements. The same head structure can be found in Scydmaeninae that do not feed on mites, but on springtails and similar soft-bodied prey. Cephenniini, in contrast, typically attack their prey from above (Jałoszyński & Olszanowski, 2016), and the head capsule is uniquely adapted to this strategy. The head capsule is not divided, there is no occipital constriction, and the head in natural position is always strongly tilted ventrad, so that it is hypognathous, with the mouthparts directed ventrad, the eyes (when present) adjacent to the anterior pronotal margin, and the plane of frons perpendicular in relation to the long body axis. The head can be tilted even further posterovertrud to adopt the position seen in †*Praphennium carinatum* sp. nov. (Fig. 2F). In no other tribe of Scydmaeninae the head is modified in such a way (although in dry-mounted specimens the head may be artificially tilted ventrad).

Even though the mouthparts, and especially the tiny labium with its even smaller prementum, cannot be examined in such tiny fossils as those described in the present study, the unique position of the head strongly supports the hypothesis that †*Praphennium* was a specialized mite predator. It seems that the development of suckers in beetles like *Stenichnus* (and possibly its Turonian cousin †*Hyperstenichnus*) facilitated catching armored mites (and consequently gaining access to a very rich source of food, rarely used by other soil predators). However, the suckers only slightly modified the less advanced method of feeding on armored mites, which is almost the same as still used by *Euconnus* and *Scydmaenus*. They rely on a brutal force in breaching the prey's defense, and *Stenichnus* does not use suckers during killing and feeding. The method used by Cephenniini seems more advanced, with the mandibles adapted to 'drill' a hole, with the mouthparts modified to seal the connection between the punctured prey's cuticle and the mouth opening in order to ingest the liquefied mite's tissues; all these actions taken while the mite is still attached to the suckers, often for several hours (Jałoszyński & Beutel, 2012; Jałoszyński & Olszanowski, 2016). The head might have been modified to adopt a hypognathous position late in the evolution of this feeding mechanism, to enable the attack from above, which made it possible to conveniently find an attachment site on the large dorsal or laterodorsal surface of an oribatid, instead of trying to go past the laterally stretched and often setose legs of the mite. This hypothesis is supported by the fact that Marcepaniini and Eutheiniini (the latter being a sister group of Marcepaniini + Cephenniini), have adults with prognathous or nearly prognathous heads, likely representing an ancestral state. Therefore, †*Praphennium* might have been an already narrowly specialized, efficient mite predator during the Cenomanian.

This hypothesis is also supported by the placement of †*Praphennium* on the obtained cladogram (Fig. 7). It was recovered as a member of the clade that includes the extant genera *Hlavaciellus* and *Cephennodes*. Although poorly supported by a bootstrap and synapomorphies, this relationship seems possible. More importantly, it points at the possibly Eurasian origins of this entire clade (i.e., †*Praphennium* + (*Cephennodes* + *Hlavaciellus*)). Although *Cephennodes* is currently broadly distributed (Fig. 7), it shows a

clear diversity hotspot (both in terms of species richness and body structures) in Southeast and East Asia. Even if †*Praphennium* is not a sister group of *Cephennodes* + *Hlavaciellus*, it is morphologically distant from the 'Cephennomicrus group' (which has four antebasal pronotal pits, frontal glands and extremely short and broad, button-like maxillary palpomere 4). A close relationship between †*Praphennium* and the Neotropical genera *Monstrophennium*, *Pseudocephennium*, *Paracephennium*, *Shyri*, and *Furcodes* can also be excluded on the basis of a unique (and highly unusual) apomorphy of the latter group, a 'trochantellus' (illustrated in Jałoszyński (2012a)). This leaves the 'Cephennium group' as an alternative sister group for †*Praphennium* (assuming that the phylogenetic hypothesis obtained during the present study is false). This group is currently Holarctic, with the genus *Cephennium* especially species rich in western Europe, reaching to the east as far as to Kyrgyzstan, and present also in North America (Jałoszyński & Stevanović, 2015). This alternative hypothesis again leads to a conclusion of a presumably Eurasian origins of †*Praphennium* + 'Cephennium group'.

Another interesting discovery is the presumably teratological condition of the antennae in †*Praphennium* sp. 2 (Fig. 4). This specimen does not differ from †*Praphennium carinatum* and †*Praphennium* sp. 1 in any important structures, but its antennae are composed of 10, not 11 antennomeres. Interestingly, the terminal antennomere has a diffuse groove on its surface (Fig. 4F), marking a possible site of fusion of antennomeres 10 and 11. Antennal teratologies among Scydmaeninae are infrequent (Jałoszyński, unpublished obs.), but a subgenus of *Euconnus* has been described based on specimens with a reduced number of antennomeres by Ganglbauer (1900), and therefore this problem was discussed in the literature (Jałoszyński, 2017). Interestingly, among Scydmaeninae, only Cephenniini include a genus that has antennae truly composed of ten antennomeres. It was demonstrated that the extant Oriental *Trurlia* (member of the 'Cephennomicrus group') has the antennomeres 10 and 11 fused together, and the fusion site can be recognized, at least in some specimens, as a circumferential impression and a ring of setae (Jałoszyński, 2009; 2011a; b). This condition can be found in all nominal species of *Trurlia*, but Jałoszyński (2011a) recorded and illustrated female specimens that do not differ from the type species of this genus in any important characters, except for having the antennomeres 10 and 11 fully separated. †*Praphennium* sp. 2 is the only teratological specimen of Scydmaeninae found as a fossil.

A serious drawback of phylogenetic reconstructions is the inevitably fragmentary character of any taxon sampling. Not only the diversity of recent Cephenniini remains partly studied (9 out of 19 known genera have been discovered during the past 10 years), but the fossil record is hardly existing. So far, only four specimens of Mesozoic Cephenniini have been described: an undetermined genus with unknown relationships within the tribe by Jałoszyński & Peris (2016), and three specimens of †*Praphennium*. Moreover, it was not possible to examine all important fine structures in the fossils. A possibly important source of phylogenetic data, the male and female terminalia and genital structures, can be only rarely examined in fossil beetles (e.g., Jałoszyński et al., 2018). If the extinct diversity of Cephenniini was comparable or greater than today, the analyzed dataset is highly fragmentary, and taxa crucial for reconstructing relationships and origins of each known genus may be absent from the matrix. The missing data strongly reduce the informative value of obtained cladograms, and make the resultant hypotheses poorly supported. The present study should be treated as a documentation of morphological structures of a new extinct genus of Cretaceous Cephenniini, whereas the attempt to include it into a phylogenetic reconstruction is preliminary and intended to facilitate future studies. Fossils of Cephenniini have been only very recently recorded even from relatively well-studied

Eocene Baltic amber (Jałoszyński & Kubisz, 2016; Jałoszyński & Perkovsky, 2016), and it should be expected that any new specimens found in older deposits will contribute to solving the mystery of the origins of acarophagy by Cephenniini.

## 7. Conclusions

The first diagnosable new genus of Cephenniini, †*Praphennium* from the Cenomanian Myanmar amber, provides a new insight into the evolution of this large group of Scydmaeninae. †*Praphennium* has characters known in extant genera, and the structure and position of its hypognathous head support the hypothesis that already during Cenomanian Cephenniini fed on armored mites using the same morphological and presumably behavioral adaptations that can be observed in extant taxa. Together with a younger Turonian †*Hyperstenichnus vendeanus*, †*Praphennium* supports early origins of acarophagy among Scydmaeninae, the only group of beetles that have adapted to feeding on one of the best protected arthropods of the soil and leaf litter.

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## Appendix A. Supplementary data

Supplementary data related to this article can be found at <https://doi.org/10.1016/j.cretres.2018.04.017>.