

# A new extinct genus of Glandulariini with two species from Upper Cretaceous Burmese amber (Coleoptera: Staphylinidae: Scydmaeninae)



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## ABSTRACT

The Glandulariini (=Cyrtoscydmini) is today the largest, most species-rich and most diverse tribe of Scydmaeninae comprising over 70% of the extant species of this subfamily. Named genera and species of Glandulariini are known mostly from Miocene to Eocene ambers, with only one, recently described Mesozoic taxon. Here we report the second genus of Glandulariini from Upper Cretaceous Burmese amber, *Cenomaniola* Jałoszyński and Yamamoto, gen. nov., with two species, *C. carinata* Jałoszyński and Yamamoto, sp. nov. and *C. macrophthalma* Jałoszyński and Yamamoto, sp. nov. *Cenomaniola* shows the general body plan typical of the 'Euconnus complex' within Glandulariini, with thick bristles on the sides of head and pronotum, a character conserved for nearly a hundred million years. With the previous discovery of *Scydmbisetia* Jałoszyński and Yamamoto, two major body forms typical of the extant Glandulariini are already proved to have differentiated in or before the Late Cretaceous. This demonstrates early origins and a long conservation of 'Euconnus-like' and 'Sciacharis/Horaemorphus-like' body plan in the currently largest group among Scydmaeninae.

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## 1. Introduction

Glandulariini Schaufuss, 1889 (=Cyrtoscydmini Schaufuss, 1889; synonymized by Newton, 2015) is the most successful of all tribes of ant-like stone beetles, or Scydmaeninae, in terms of abundance, species richness and morphological diversity (Jałoszyński, 2016a). All remaining nine tribes include 43 extant genera, whereas Glandulariini comprises 64 extant genera and accounts for over 70% of the known species richness of scydmaenines. This tribe also includes one of the largest genera of any organisms on Earth, *Euconnus* Thomson, 1859, currently comprising an astounding number of about 2500 nominal species (Newton and Franz, 1998). Members of Glandulariini can be found in forests of all continents; they are especially common and abundant in the tropics, and their

true species richness is estimated to be several times higher than the number of nominal species (e.g., Jałoszyński, 2016a).

Glandulariini shows a high diversity of body forms and structures, but an ant-like form predominates, with a deep constriction between the head and pronotum and between the pronotum and elytra. These are small beetles; adults rarely exceed 3 mm in length, and body smaller than 1 mm is not uncommon. All species currently classified in this tribe share a unique apomorphy that readily identifies glandulariines: the maxillary palpomere 4 subconical, elongate, usually pointed, broadest at or near base, much narrower than apex of enlarged, elongate palpomere 3 (e.g., Jałoszyński, 2012a). As for such a large and cosmopolitan group, our knowledge of immature stages and biology of glandulariines is extremely fragmentary. Larvae of merely four species were adequately described and illustrated with their chaetotaxic structures coded (Wheeler and Pakaluk, 1983; Jałoszyński, 2013, 2015a, 2016b), and only one species was a subject of a detailed behavioral study focused on the feeding process (Jałoszyński and Olszanowski, 2013).

Similarly, also fossils of Glandulariini are poorly studied, despite their relative commonness in large amber collections (amber being

Abbreviations: AMNH, American Museum of Natural History, New York, USA.

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so far the only source of the Scydmaeninae fossil record). An annotated catalog of nominal species of Scydmaeninae known in the fossil record was recently given by Jałoszyński and Perkovsky (2016); among 43 species names listed, 17 are those of Glandulariini. However, generic placement of ten of them is uncertain, and only six were described and illustrated in detail, providing morphological details that can be used in reconstructing the evolutionary history of the tribe (Jałoszyński and Perkovsky, 2016). All hitherto described and named glandulariine fossils come from Eocene, Oligocene and Miocene, except one genus and species known from Upper Cretaceous Burmese amber (Jałoszyński et al., 2016). *Scydmbisetia vetustissima* Jałoszyński & Yamamoto, 2016, was to date the only Mesozoic taxon unambiguously placed in Glandulariini.

In the present study we report another definite extinct Glandulariini genus from Upper Cretaceous amber of Myanmar, represented by two species, linked by several shared synapomorphies with their extant Oriental and Nearctic relatives.

## 2. Geographic and geological context

Although several localities yield Burmese amber, commercial extraction and scientific studies are focused only on a single site in the Hukawng Valley, Kachin State of northern Myanmar (Fig. 1). The specimens used in this study also come from this locality. The valley is a flat alluvial plain surrounded by hills and the amber mine is located on the northern part of the Noije Bum Hill (26°15'N; 96°34'E), which consists of folded Cretaceous and Paleogene deposits (Cruickshank and Ko, 2003). A variety of clastic sedimentary deposits with thin limestone beds, and abundant coaly and carbonaceous materials are recognized at the mine (Cruickshank and Ko, 2003). Amber is associated with a narrow horizon in fine-grained facies and the earliest Cenomanian age ( $98.79 \pm 0.62$  Ma) is indicated by the radioisotopic dating of zircon crystals obtained from the amber matrix (Cruickshank and 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 suggest that depositional environment must have been nearshore (Cruickshank and Ko, 2003).

## 3. Material and methods

### 3.1. Specimen handling and imaging

The fossil specimens here described are deposited in AMNH and were assigned collection numbers AMNH Bu-SY7–9. The inclusions were observed (as dry specimens and submerged in cedar oil) under a 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. Measurement convention and the terminology of morphological structures follow those of Jałoszyński (2015b). The work is registered in ZooBank under urn:lsid:zoobank.org:pub:47D1AC8D-92A6-41B7-9C77-C33CF696FE5D.

## 4. Systematic palaeontology

Suborder: Polyphaga Emery, 1886

Superfamily: Staphylinoidea Latreille, 1802

Family: Staphylinidae Latreille, 1802

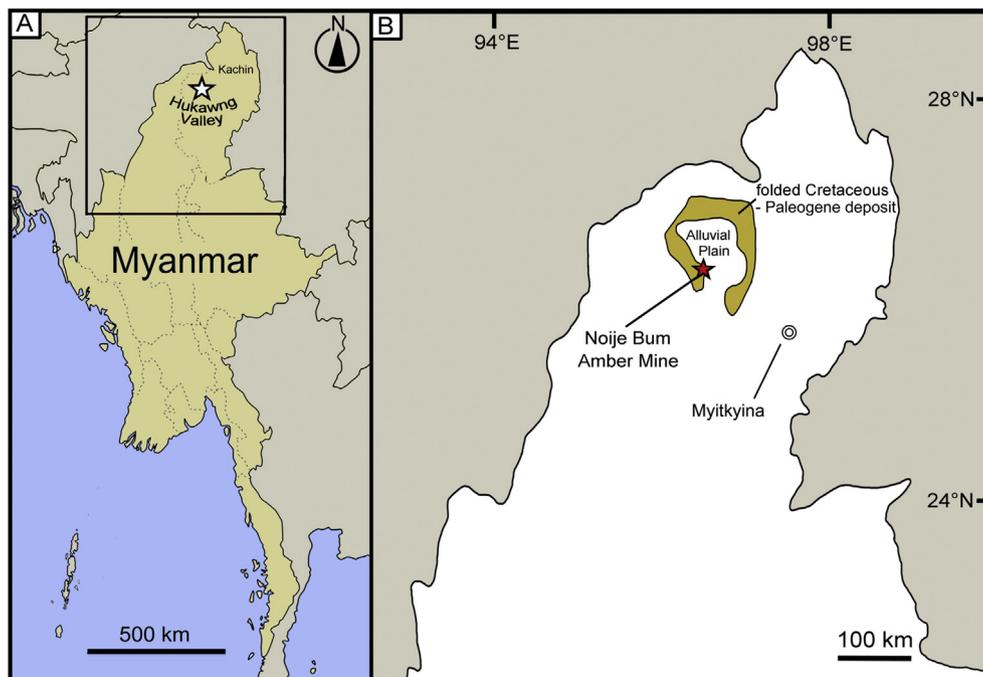
Subfamily: Scydmaeninae Leach, 1815

Tribe: Glandulariini Schaufuss, 1889

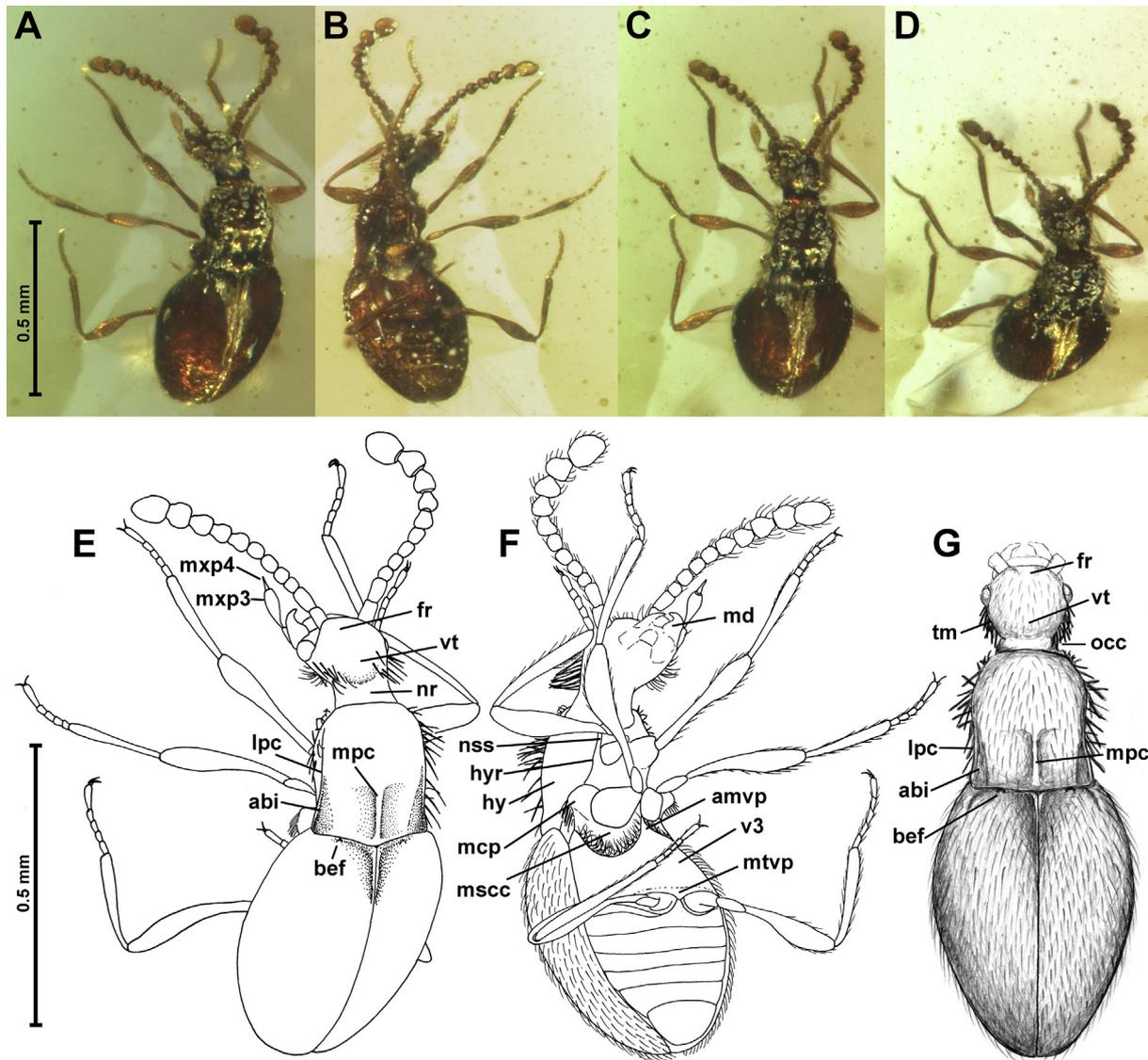
Genus *Cenomaniola* Jałoszyński and Yamamoto gen. nov.

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Figs. 2–4



**Fig. 1.** The location of amber deposits (after Cruickshank and Ko, 2003). **A.** Map of Burma. The star represents the location of the Hukawng Valley situated in the Kachin State. **B.** The locality of the amber mine in the Hukawng Valley. The star represents Noije Bum Amber Mine.

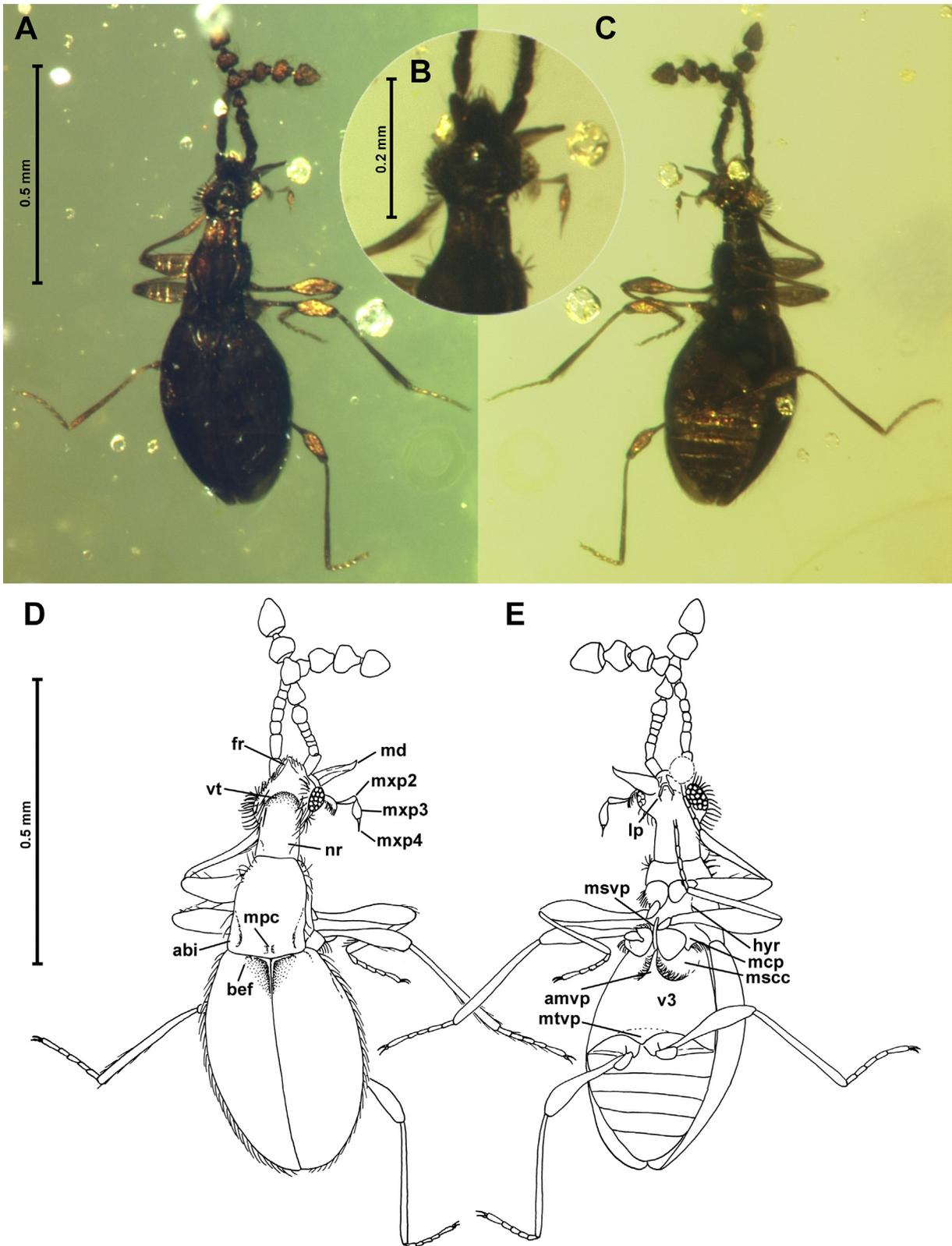


**Fig. 2.** Holotype (AMNH Bu-SY7) of *Cenomaniola carinata* gen. and sp. nov. **A, E.** Laterodorsal habitus. **B, F.** Letarovenral habitus. **C, D.** Anterodorsal habitus. **G.** Reconstruction of dorsal habitus. Abbreviations: abi, antebasal impression; amvp, anterior metaventral process; bef, basal elytral fovea; fr, frons; hy, hypomeron; hyr, hypomeral ridge; lpc, lateral pronotal carina; mcp, mesocoxal projection; md, mandible; mpc, median pronotal carina; msc, mesocoxal cavity; mtvp, metaventral intermetacoxal process; mxp3–4, maxillary palpomere 3–4; nr, 'neck' region; nss, notosternal suture; occ, occipital constriction; tm, temple; v3, metaventrite; vt, vertex.

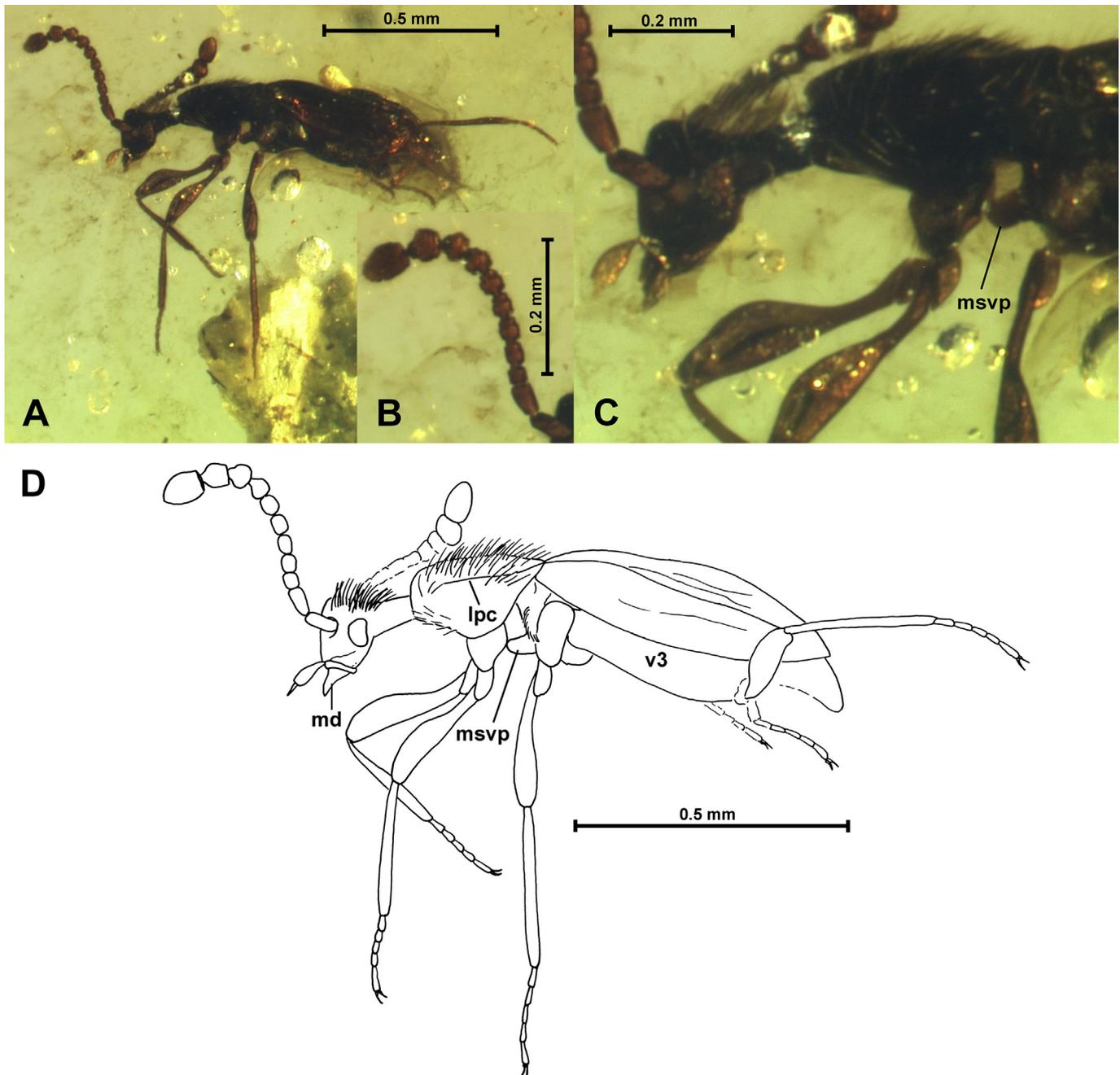
**Derivation of name.** After the Cenomanian; gender feminine.  
**Type species:** *Cenomaniola carinata* Jałoszyński and Yamamoto.

**Diagnosis.** *Cenomaniola* is a glandulariine genus showing a unique apomorphy, mesoventral intercoxal process strongly expanded anteroventrally and forming elongate projection in front of mesocoxal cavities; additionally a set of synapomorphies known in other genera, but in different combinations or incomplete, characterizes the new genus: head in lateral view highest in front of eyes and strongly declined anteriorly and posteriorly, with occipital constriction only slightly narrower than vertex; sides of head and prothorax with thick bristles; antennae gradually thickened; pronotum broadest at base, with nearly complete lateral edges, a pair of elongate lateral antebasal impressions and median longitudinal antebasal carina; each elytron with one small basal fovea; mesoscutellum not exposed between elytral bases; metaventrite with strongly elongate, narrow and slender anterior intermesocoxal process; and metaventral intermetacoxal process broadly subtriangular, lacking median notch, not separating metacoxae.

**Description.** Body (Figs. 2A–G, 3A, C–E, 4A–D) small, 0.75–0.88 mm, elongate and moderately convex, strongly constricted between head and pronotum and between pronotum and elytra. Head capsule (Figs. 2E–G, 3B, D–E, 4C–D) divided into large and exposed anterior part and smaller posterior 'neck' region (Figs. 2E, 3D; nr) largely retracted into prothorax, relatively long and demarcated by indistinct occipital constriction (Fig. 2G; occ), which is nearly as wide as vertex; anterior part of head in dorsal view rounded (distorted in Figs. 3A–E); vertex (Figs. 2E, G, 3D; vt) transverse, with posterior margin not demarcated by edge (posteriorly collapsed in two out of three studied specimens); tempora (Fig. 2G; tm) distinct, shorter or longer than eyes; frons (Figs. 2E, G, 3D; fr) subtrapezoidal or subtriangular (in Fig. 3A–E presumably distorted); clypeus in studied specimens poorly visible, presumably not demarcated from frons; antennal insertions moderately broadly separated and not visible in dorsal view; compound eyes moderately to very large and located anteriorly or submedially. Head with bristles on tempora, but not



**Fig. 3.** Holotype (AMNH Bu-SY8) of *Cenomaniola macrophthalma* gen. and sp. nov. **A, D.** Laterodorsal habitus. **B.** Head in dorsal view. **C, E.** Lateroventral habitus. Abbreviations: abi, antebasal impression; amvp, anterior metaventral process; bef, basal elytral fovea; fr, frons; hy, hypomeron; hyr, hypomeronal ridge; lp, labial palp; mcp, mesocoxal projection; md, mandible; mpc, median pronotal carina; msc, mesocoxal suture; mtvp, metaventral intermetacoxal process; mxp2–4, maxillary palpomere 2–4; nr, 'neck' region; nss, notosternal suture; tm, temple; v3, metaventrite; vt, vertex.



**Fig. 4.** Specimen (AMNH Bu-SY9) of *Cenomaniola* sp. **A, D.** Lateral habitus. **B.** Left antennae in lateral view. **C.** Head and prothorax in lateral view. Abbreviations: lpc, lateral pronotal carina; md, mandible; msvp, mesoventral intercoxal process; v3, metaventrite.

on posterior margin of vertex. Antennae (Figs. 2A–F, 3A, C–E, 4A, B, D) gradually and distinctly thickened distally, distal flagellomeres except 11 with subcylindrical proximal and subconical distal portions. Mouthparts only partly visible; mandibles (Figs. 2F, 3D, 4D; *md*) subtriangular, in two studied specimens moderately long and with curved distal portion (Figs. 2E–G, 4D), in one specimen strikingly long and with feebly curved apices (Figs. 3B, D, E); maxillary palp composed of barely noticeable, minute palpomere 1, strongly elongate and broadened distally palpomere 2 (Fig. 3D; *mxp2*), large, elongate and broadest near distal third palpomere 3 (Figs. 2E, 3D; *mxp3*) and strongly elongate, subcylindrical, slender and pointed palpomere 4 (Figs. 2E, 3D; *mxp4*). Labial palps (Fig. 3E; *lp*) slender and strongly elongate, longer than prementum.

Prothorax (Figs. 2A–G, 3A, C–E, 4A, C, D) strongly elongate and flattened; pronotum broadest at base, with anterior margin weakly rounded or nearly straight; sides rounded in anterior third and slightly sinuate in posterior half; posterior margin slightly arcuate; anterior pronotal corners obtuse-angled, posterior corners nearly straight. Pronotum with nearly complete lateral edges or carinae (Figs. 2A, 4D; *lpc*), lateral pair of strongly elongate, subtriangular antebasal impressions (Figs. 2E, G, 3D; *abi*), and median longitudinal carina (Figs. 2E, G, 3D; *mpc*). Pronotal disc covered with thin suberect to erect setae, with thick bristles on sides; prothoracic hypomera (Fig. 2 F; *hy*) largely aetose, with only a few bristles visible in one specimen (Fig. 4D); hypomeral ridges (Fig. 2F; *hyr*) seem complete; notosternal sutures (Fig. 2F; *nss*) only partly visible, presumably complete; basisternal and intercoxal regions poorly

visible; position of procoxae in relation to hypomerid ridges indicates that procoxal cavities are closed.

Elytra (Figs. 2A C, E, G, 3A, D, 4A, D) oval, elongate and strongly or moderately convex, broadest in front of middle; humeral calli distinct and developed as elongate protuberances; base of each elytron with one well-visible but small and asetose basal elytral fovea (Figs. 2E, G, 3D; *bef*) located in broad subtriangular impression (which may be a distortion caused by collapsing of this region); surface of elytra covered with unremarkable and unordered fine punctures and suberect setae. Mesoscutellum not visible between elytral bases.

Details of mesoventrite poorly visible except for prominent mesocoxal projections (Figs. 2F, 3E; *mcp*) and narrow, strongly elongate, strongly elevated and projecting anteriorly mesoventral intercoxal process (Figs. 3E, 4D; *msvp*), posteriorly adjacent to anterior tip of anterior metaventral process.

Metaventrite (Figs. 2F, 3E, 4D; *v3*) with prominent anterior metaventral process (Figs. 2F, 3E; *amvp*), subtriangular in shape and with its tip located between mesocoxae; sides of process extend as curved and densely setose lateral ridges bordering posteriorly mesocoxal cavities (Figs. 2F, 3E; *mssc*). Metaventral intermetacoxal process (Figs. 2F, 3E; *mtvp*) short and broad, subtriangular, lacking median notch and not separating metacoxae.

Abdomen with six visible and unmodified sternites (Figs. 2F); terminal abdominal tergite not exposed.

Legs (Figs. 2A–F, 3 A, C–E, 4A, C, D) long and slender; pro- and mesocoxae (Fig. 4E) elongate, ovoid or subconical, metacoxae strongly transverse. All trochanters subtriangular and weakly elongate, trochantero-femoral articulation oblique in relation to long axis of femur; all femora strongly elongate and slender, distinctly but relatively weakly clavate; all tibiae long and slender, protibiae slightly recurved in one specimen (Figs. 3D, E); tarsi long and slender, all tarsomeres elongate, claws long.

**Remarks.** *Cenomaniola* is unambiguously placed in Glandulariini on the basis of the autapomorphy of this tribe, the maxillary palpomere 4 subconical, elongate and pointed, much smaller than broadened and elongate palpomere 3 (Figs. 2E, F, 3B, D, E, 4C, D). Additional characters typical of Glandulariini and clearly observable in *Cenomaniola* are: the ant-like body form, i.e., the body deeply constricted between the head and pronotum and between pronotum and elytra (shared with Mastigitae, Scydmaenini, Chevrolatiini and Leptoscydmini, all of which have broadly separated metacoxae); and the antennal scape lacking apical notch (shared with Cephenniitae, which are suboval or nearly parallel-sided beetles with very shallow or absent occipital constriction and feebly marked constriction between the pronotum and elytra).

Among extant Glandulariini, only two genera, Oriental *Elacatophora* Schaufuss, 1884 and Nearctic *Lophioderus* Casey, 1897 have a similar shape of the head capsule as *Cenomaniola*. In all these genera, the head in lateral view is highest in front of eyes and strongly declined anteriorly and posteriorly; among extant taxa this character alone can be used to distinguish *Elacatophora* and *Lophioderus* from all remaining glandulariines (Jałoszyński, 2004, 2005, 2008, 2015c, 2016c). *Cenomaniola*, *Elacatophora* and *Lophioderus* share several more characters: antennae gradually thickened distally (although in *Elacatophora* antennomere 11 is typically strongly enlarged, much more so than antennomere 10, and in *Lophioderus* antennomeres 7–9 are broadening distally vs. strongly narrowing in distal half in *Cenomaniola*); pronotum in dorsal view broadest near base and with its anterior margin shorter than posterior margin, with distinct anterior and posterior corners; presence of elongate lateral antebasal pronotal impressions (variously developed in *Elacatophora*, but typically long, subtriangular and

adjacent to sides of pronotum, as in *Cenomaniola*); each elytron with single basal fovea; mesoscutellum not visible between elytral bases; similar distribution of erect bristles on head and prothorax; lateral pronotal edges (typically incomplete in *Elacatophora*, restricted to the posterior half of pronotum); carinate and elevated mesoventral intercoxal process (in *Lophioderus* short and visible only in front of mesocoxae, and not between them, as in *Cenomaniola*); broadly subtriangular metaventral intercoxal process, not separating metacoxae; and relatively slender and long legs, with weakly clavate femora. Additionally, in some species of *Elacatophora* a short median longitudinal antebasal carina can be seen (e.g., in *E. malaysiae* (Franz, 1984)), the carina in *Lophioderus* is barely discernible or absent. *Cenomaniola* clearly differs from *Elacatophora* in the maxillary palpomere 3 weakly narrowing distally (strongly narrowing in *Elacatophora*), narrow but subconical palpomere 4 (in *Elacatophora* narrow and nearly rod-like); labial palps longer than prementum (strongly reduced, shorter than prementum in *Elacatophora*); slender and laterally setose anterior metaventral process (absent in *Elacatophora*), and its autapomorphy, the anterior portion of mesoventral intercoxal process forming an elongate lobe or projection (anterior portion of mesoventral process not projected anteriorly in *Elacatophora*). A larger number of character states is shared by *Cenomaniola* and *Lophioderus*; but the mesoventral process in the latter genus is not anteriorly projected, and in *Lophioderus* there is a transverse antebasal pronotal groove, absent in *Cenomaniola*. *Cenomaniola*, *Elacatophora* and *Lophioderus* are similar to a degree that suggests a possible common ancestor.

The shape and structures of pronotum, especially the nearly complete lateral carinae or edges, lateral impressions and median antebasal carina of *Cenomaniola* strongly resemble those of the extant Palaearctic *Neuraphes* Thomson, 1859. However, the latter genus differs from *Cenomaniola* in several important characters, as the subtriangular and weakly convex head with eyes adjacent or nearly adjacent to the occipital constriction; mesoventral intercoxal process weakly elevated and not projecting anteriorly; the anterior metaventral process of different shape and with its tip separated from posterior margin of mesoventral process by a distinct gap; the metaventral intermetacoxal process with a deep median notch; and distinctly setose basal elytral foveae (illustrated or discussed in Jałoszyński (2015b, d)). Differences between *Cenomaniola* and *Neuraphes* are more numerous than between the newly described taxon and *Elacatophora* and *Lophioderus*.

Species ***Cenomaniola carinata*** Jałoszyński and Yamamoto sp. nov. urn:lsid:zoobank.org:act:4866B0E2-E4B1-4984-A391-31B1675D8CF5

Fig. 2

**Material studied.** Holotype (AMNH Bu-SY7), from Burmese amber, sex unknown.

**Derivation of name.** The name *carinata* refers to the long median pronotal carina.

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

**Diagnosis.** Tempora much longer than eyes; median antebasal pronotal carina longer than 1/3 of pronotum.

**Description.** Body (Fig. 2) moderately slender, length 0.85 mm, pigmentation reddish-brown. Anterior part of head weakly elongate, length 0.15 mm, width 0.13 mm; tempora much longer than compound eyes; frons and vertex weakly convex (posterior portion of vertex collapsed in the studied specimen), covered with inconspicuous punctures and short, sparse, suberect and erect setae; tempora with sparse, strongly erect bristles directed posterodorsally. Antennae slender, length 0.40 mm, all antennomeres

except for 3, 4 and 10 at least slightly elongate (best observable in left antenna, Fig. 2E), antennomeres 3, 4 and 10 about as long as broad, 11 oval, much shorter than 9 and 10 combined, with blunt apex.

Pronotum distinctly elongate and broadest at base, but only weakly narrowing anteriorly, length 0.25 mm, width 0.20 mm. Anterior margin weakly arcuate, sides rounded in anterior third, broadly and shallowly constricted in posterior third, posterior margin nearly straight; base with long median longitudinal carina exceeding basal third of pronotal length and one pair of strongly elongate, subtriangular impressions adjacent to lateral pronotal margins. Disc covered with moderately dense, suberect to erect short setae; sides with thick bristles.

Elytra oval, length 0.45 mm, width 0.28 mm; broadest near anterior third and strongly narrowing posteriorly, covered with fine, inconspicuous punctures and moderately dense, short and suberect setae.

Legs long and slender; covered with short suberect setae.

**Remarks.** In addition to the characters listed in the diagnosis, *Cenomaniola carinata* differs from *C. macrophthalma* described below in its larger body (0.85 mm vs. 0.75 mm) and clearly different ratios of elytral length/width (1.64 vs. 1.55) and pronotal length/width (1.25 vs. 1.40). A possibility of dealing with a larger female and smaller male of the same species can be ruled out on the basis of the remarkable difference in the length of the median pronotal carina; it seems unlikely that males and females would differ in this character, based on the extent of variability known in extant Glandulariini.

Species ***Cenomaniola macrophthalma*** Jałoszyński and Yamamoto sp. nov.

urn:lsid:zoobank.org:act:06E6A180-C29C-4D40-9413-E3DBC117577C

Fig. 3

**Material studied.** Holotype (AMNH Bu-SY8), from Burmese amber, sex unknown.

**Derivation of name.** The name *macrophthalma* refers to the remarkably large compound eyes.

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

**Diagnosis.** Tempora shorter than eyes; median antebasal pronotal carina barely longer than broad.

**Description.** Body (Fig. 3) moderately slender, length 0.75 mm, pigmentation reddish-brown. Anterior part of head weakly elongate, length 0.15 mm, width 0.13 mm; tempora nearly as short as 1/3 length of eyes; frons and anterior portion of vertex weakly convex (posterior portion of vertex collapsed in the studied specimen), covered with inconspicuous punctures and short, sparse, suberect and erect setae; tempora with sparse, strongly erect bristles directed more dorsally than posteriorly. Antennae slender, length 0.40 mm, scape and pedicel strongly elongate, shapes of proximal flagellomeres difficult to assess, antennomeres 7–10 seem to be about as long as broad, antennomere 11 much shorter than 9 and 10 combined, subtriangular in lateral outline, with blunt apex.

Pronotum distinctly elongate and broadest at base, distinctly narrowing anteriorly in anterior third, length 0.18 mm, width 0.13 mm. Anterior margin nearly straight, sides rounded in anterior third, shallowly sinuate in posterior third, posterior margin weakly arcuate; base with very short median longitudinal carina and a pair of strongly elongate, subtriangular impressions adjacent to lateral pronotal margins. Disc covered with moderately dense, suberect to erect short setae; sides with sparse thick bristles.

Elytra oval, length 0.43 mm, width 0.28 mm; broadest between middle and anterior third and moderately strongly narrowing posteriorly, covered with fine, inconspicuous punctures and moderately dense, short and suberect setae.

Legs long and slender; covered with short suberect setae.

**Remarks.** The abdomen of this species appears composed of five visible sternites (Fig. 3E). However, in Glandulariini it is common that the suture between the sternites 5 and 6 is poorly visible, even in relatively large adults of extant genera, and SEM studies or macerated transparent specimens observed under a compound microscope are needed to reveal that the abdomen is always composed of six externally visible sternites. All genera of Scydmaeninae have six visible sternites, and there is no reason to believe that *C. macrophthalma* has only five sternites; most likely the suture between 5 and 6 is as indistinct as in many extant Glandulariini.

Species *Cenomaniola* sp.

Fig. 4

**Material studied.** Specimen AMNH Bu-SY9, from Burmese amber, sex unknown.

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

This specimen is visible only in lateral view and has the elytra dorsally strongly distorted, partly collapsed. Body length 0.88 mm; length of head 0.15 mm; length of antenna 0.48 mm; length of pronotum 0.25 mm; length of elytra 0.48 mm. Shapes of head, pronotum and elytra in dorsal view not possible to assess, although structures visible in lateral view seem to be similar to those of the two named species.

## 5. Discussion

The three specimens described in the present paper differ slightly in the body length and proportions of body parts, they are also visible in different positions in amber pieces. However, they all can be assigned to one genus, basing on shared structures of the antennae, head, pronotum and elytra, and unusually slender legs, even though important ventral characters are only partly visible, and not all of them are observable in all specimens. *Cenomaniola* represents a different morphological type of glandulariine ant-like stone beetles than the previously described *Scydmbisetia* Jałoszyński & Yamamoto, 2016. Consequently, discovery of this genus broadens our knowledge of morphological structures present in Mesozoic Glandulariini, a group today highly successful, but exceptionally poorly studied in the fossil record.

While *Scydmbisetia*, also known from Burmese amber, is most similar to chiefly Southern Hemisphere extant taxa as *Sciacharis* Broun, 1893 and its relatives, *Cenomaniola* has the general body form strongly resembling the cosmopolitan 'Euconmus complex' or the Northern Hemisphere *Neuraphes*. The flat, strongly elongate body of *Scydmbisetia*, its subpentagonal, 'anthiciform' head, and slender, only weakly thickened antennae (illustrated in Jałoszyński et al., 2016) are similar to the body plan characteristic of South American, Australian or New Zealand *Sciacharis*, Chilean *Anthicimimus* Franz, 1993 and Australian *Spinosciacharis* Jałoszyński, 2014, but also that of Australo-Oriental *Horaemorphus* Schaufuss, 1889. This body form is relatively uncommon among extant Glandulariini. The newly discovered *Cenomaniola*, however, has a *Euconmus*-like body form, with strongly convex elytra much broader than pronotum, subprognathous head and thick bristles on the sides of head and pronotum. This is today a predominating body form among Glandulariini, known also in Eocene fossils (e.g., Jałoszyński and Perkovsky, 2016), and here for the first time recorded from

deposits as old as about 99 Ma. The presence of the bristles is especially interesting; among extant and extinct Scydmaeninae they occur on the tempora (and often on genae, postgenae and vertex) and sides of pronotum (often also on hypomera) only in Glandulariini. Their function remains unknown, but they seem important, as in large extant genera or complexes of genera typically characterized by a dense and evenly distributed vestiture of setae on all body parts, one or several species are known with setae nearly entirely reduced, with a notable exception of bristles on tempora and anterolateral margins of prothorax (e.g., in subgenera of *Euconnus* Thomson, 1859: *Filonapochus* Franz, 1986a; *Rhombocunnus* Franz, 1986b; *Glabricunnus* Jałoszyński, 2016d). The bristles are conserved even if the remaining dorsal and lateral surface of head, prothorax and elytra becomes glabrous; and in the present paper we provide evidence that the bristles were present in Glandulariini for nearly a hundred million years. These two facts support a hypothesis that the bristles may play a vital function, which is yet to be discovered. Presumable glandular structures were recently discovered within the dense bristles on tempora (Jałoszyński, in preparation), and a hypothesis of the system of bristles functioning as an evaporation apparatus for defensive secretions might, therefore, offer an explanation for this highly conserved structure found only in one, presumably monophyletic, group of Scydmaeninae.

Among the extant members of the 'Euconnus complex' (see Jałoszyński, 2012b, 2013, 2015e–g, 2016d–f), *Cenomaniola* most resembles *Elacatophora* (= *Borneosabahia* Franz, 1992), represented by ten extant species distributed in the Malay Peninsula, Borneo and Java (Jałoszyński, 2004, 2005, 2008, 2015c, 2016c), and *Lophiderus*, occurring in North America and comprising 36 spp. (O'Keefe, 1996). There are, however, important morphological differences between these three genera, most notably in the shape of mesoventral intercoxal process. Two structures of *Cenomaniola* and *Lophiderus*, the maxillary and labial palps, are plesiomorphic, in contrast to certainly derived character states known in *Elacatophora*. In the latter genus, maxillary palpomeres 3 and 4 are uniquely modified and labial palps are strongly shortened (both illustrated in Jałoszyński, 2004), whereas these structures in *Cenomaniola* do not differ from those present in *Lophiderus* and most extant and all known extinct Glandulariini. However, the anteriorly projecting mesoventral intercoxal process is not known in any hitherto described or revised extant or extinct Glandulariini; this apomorphy makes *Cenomaniola* unique within the tribe. Although true relationships of *Cenomaniola* within the tribe remain unclear, it may belong to the stem group of the present-day 'Euconnus complex', to which *Elacatophora* is related.

## 6. Conclusions

The second known Mesozoic genus of the tribe Glandulariini is described and characterized. *Cenomaniola* provides firm evidence that the unique bristles present on tempora and pronotum in majority of extant genera of Glandulariini is a highly conservative character, supporting a hypothesis that these bristles play a vital, but yet unclear function. With the previously discovered *Scydmo-bisetia*, two main types of the body form known in extant Glandulariini are now documented from the Late Cretaceous, demonstrating early origins and a long conservation of 'Euconnus-like' and '*Sciacharis/Horaemorphus*-like' body plans in the currently largest group among Scydmaeninae.

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