

Short communication

Beetle with long ‘nose’—A bizarre stem scydmaenine in amber from Myanmar (Coleoptera: Staphylinidae: Scydmaeninae)

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ABSTRACT

The staphylinid subfamily Scydmaeninae is a diverse assemblage of small predaceous beetles, represented by some 5360 extant and 51 extinct species. Recent explorations of Mesozoic scydmaenine fauna in Burmese, Canadian, French, and Spanish ambers have shed intriguing light on the early evolution, systematics, and particular aspects of predator-prey relationship among this group. However, in contrast to extant diversity, well-preserved fossils allowing for sufficient morphological studies and ecological reconstructions are extremely rare. Here we report a highly advanced glandularine scydmaenine, *Nuegua elongata* Yin, Cai & Newton, gen. et sp. nov., based on a large series of fifteen exquisitely preserved specimens entombed in mid-Cretaceous Burmese amber. The new genus strikingly displays an extremely prolonged preocular region that accounts for over half of the head length—a structure unknown among all known living and extinct scydmaenines, but analogous to that of certain groups of the modern Laemophloeidae, Curculionidae, Salpingidae, and Staphylinidae. We provide a formal description of the new genus, compare it with the most probably related taxa, and discuss possible functions of this bizarre head elongation. The discovery highlights the morphological disparity and palaeodiversity of the subfamily Scydmaeninae in late Mesozoic.

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1. Introduction

The ant-like stone beetles, or subfamily Scydmaeninae, represent a diverse lineage of small, predaceous beetles, comprising some 5360 extant and 51 extinct species (Newton, unpublished database) and accounting for about 8% of total staphylinid diversity (over 62820 species of the family Staphylinidae are currently known; Newton, 2017). Due to the presence of long elytra covering most or the entire abdomen, scydmaenines had been retained as a separate family for nearly 200 years (Leach, 1815). Based on a comprehensive phylogenetic analysis of adult and larval morphology, the subfamily was placed in the monophyletic “Staphylinine group” of subfamilies, sister to a clade composed of

Steninae + Euaesthetinae; that result also implied the long elytra in scydmaenines are probably secondary derived, rather than a plesiomorphic trait of non-staphylinid beetles (Grebennikov and Newton, 2009). Recent explorations of fossil scydmaenines in Burmese, Canadian, French and Spanish ambers proved that typical scydmaenine body plan (long elytra) had been well-established during early to late Cretaceous (O’Keefe et al., 1997; Kirejtshuk et al., 2015; Cai and Huang, 2016; Jałoszyński and Perkovsky, 2016; Jałoszyński and Peris, 2016; Jałoszyński et al., 2017a; Yin et al., 2018). Noting the oldest known representative of the “Staphylinine group”, *Libanoeuaesthetus pentatarsus* Lefebvre, Vincent, Azar & Nel from Lebanese amber (120–135 Ma), is a member of Euaesthetinae (Lefebvre et al., 2005), the Scydmaeninae as a whole may have originated no later than Middle Jurassic, at least comparable to the subfamilies Glypholomatinae, Omaliinae, Oxytelinae, Piestinae, Scaphidiinae, Tachyporinae and Olisthaerinae already reported from Jurassic deposits (Cai et al., 2012a, b, 2013, 2015; Cai and Huang, 2013).

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While divergence time of Scydmaeninae and evolutionary routes of major scydmaenine clades can be estimated by phylogenetic approaches from modern exemplars, the history of particular aspects of ecological adaptations, including habitus choice, feeding habitat, and mating behavior, of extinct taxa can be traced only by fossils. For example, extant species of the tribe Mastigini are active diurnal predators feeding on caterpillars or scavenging on dead arthropods (Jałoszyński, 2016a). By contrast, their Eocene and Cretaceous ancestors were speculated to apply a highly modified ‘antennal setose trap’ during predation, probably specific on springtails, indicating shifts of feeding habits (prey choice) might have occurred during the evolutionary history of this group (Jałoszyński, 2016a; Yin et al., 2017). In another case, the unique pair of ‘labial suckers’ of the mouthparts in modern *Stenichnus godarti* (Latreille) of the tribe Glandulariini plays a critical role during predation on heavily sclerotized oribatid and uropodine mites (Jałoszyński, 2016b), and this structure was even more derived (suckers were much larger) in its Mesozoic relative *Hyperstenichnus vendeanus* Jałoszyński & Perrichot, suggesting an ancient origin of a specialized predation mode in the *Stenichnus*-like scydmaenines (Jałoszyński et al., 2017b). A general impression is that aside from recent discoveries of most major scydmaenine lineages from mid to late Cretaceous deposits, our knowledge of the early evolution and paleobiology of this group is still insufficient because of limited accession to material preserved in a good condition. And probably due to their minute body size, all extinct scydmaenines have been known from ambers only, and not yet been recorded from compression fossils, which may of critical importance in deciphering ancestral character states of the subfamily. Here, we describe a new genus and species of Scydmaeninae based on fifteen well-preserved specimens in Cretaceous Burmese amber, and illustrate a new structure unknown in other extant and extinct members of the subfamily.

2. Material and methods

All amber materials were obtained from the Hukawng Valley in northern Myanmar (26°21′33.41″N, 96°43′11.88″E). Maps showing amber-yielding locality were provided in Cruickshank and Ko (2003), Kania et al. (2015), and Yin et al. (2018). The minimum age of Burmese amber is widely accepted as earliest Cenomanian (98.79 ± 0.62 Ma) based on recent U–Pb dating of zircons (Shi et al., 2012). However, other workers have argued a late Albian–Cenomanian boundary (Rasnitsyn et al., 2016) in age. A total of fifteen specimens were examined, all of which belong to a single species. The holotype (SNUC-Paleo-0016) and ten paratypes (SNUC-Paleo-0017–0021, SNUC-Paleo-0023–0027) are housed in the Insect Collection of the Shanghai Normal University, Shanghai, China (SNUC), four paratypes (NIGP166325–166327, 167527) are deposited in the Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, Nanjing, China (NIGP). Amber pieces used for photomicrography were cut using a handheld engraving tool with a diamond blade, and polished using sandpapers of different grain sizes and rare earth polishing powder.

Observations were made using a Zeiss Axio Imager 2 light microscope with a digital camera attached. The Zeiss Axio Imager 2 microscope was equipped with a mercury lamp and specific filters for DAPI, eGFP and rhodamine. Photomicrographs with a green background were taken under the eGFP mode. Other images were made using a Canon 5D Mark III camera with a Canon MP-E 65 mm macro lens (F2.8, 1–5X) or an Olympus Plan C 10× Objective Lens; and a Canon MT-24EX twin flash was used as light source. Zerene Stacker Version 1.04 was used for image stacking.

All images were modified and grouped into plates in Adobe Photoshop CS5 Extended.

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3. Systematic paleontology

Order Coleoptera Linnaeus, 1758
 Family Staphylinidae Latreille, 1802
 Subfamily Scydmaeninae Leach, 1815
 Supertribe Scydmaenitae Leach, 1815
 Tribe Glandulariini Schaufuss, 1889

Nuegua Yin, Cai & Newton, gen. nov.

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 Figs 1–4

Type species: Nuegua elongata Yin, Cai & Newton sp. nov. (by monotypy)

Etymology. Nügua is a goddess in Chinese mythology who created mankind and repaired the pillar of heaven. The gender of the name is feminine.

Diagnosis. *Nuegua* is a member of the tribe Glandulariini, showing the unique preocular elongation which is presumably an autapomorphy of the genus. Additionally *Nuegua* displays a triangular lateral profile of the head; the vertex bears two rows of dense setae; the occipital constriction is distinctly narrower than the vertex; the sides of the head and pronotum lack thick bristles; the submentum lacks lateral sulci; all antennomeres are elongate; the bell-shaped pronotum has an elongate median carina; each elytron has one small basal fovea; the mesoscutellum is not exposed between the elytral bases; the mesoventral process is distinctly prominent; and the broadly subtriangular metaventral process does not separate the metacoxae.

Description. Body (Figs 1A–B, 4A–C, E–F) moderately sized, below 2.0 mm, elongate and moderately convex, strongly constricted between head and pronotum and between pronotum and elytra. Highest place of head (Fig. 2B; *hd*) in lateral view located near antennal insertion, and frons steeply declining anteriorly and posteriorly (Figs 1C, 4D); head capsule (Figs 2B–D, 4D) divided into large and exposed anterior part and smaller posterior ‘neck’ region (Fig. 2C; *nr*) which is largely retracted into prothorax, relatively long and demarcated by indistinct occipital constriction, which is distinctly narrower than vertex; area anterior to eyes in dorsal view extremely elongate; vertex (Fig. 2C; *vt*) transverse, with posterior margin not demarcated by edge; tempora distinct, slightly shorter than eyes, evenly narrowed posteriorly; frons (Fig. 2C; *fr*) subtriangular, with two rows of dense setae posteriorly extending to vertex (Figs 2C, 4D); clypeus (Figs 2C, 4D; *cl*) greatly prolonged anteriorly (Figs 1C, 2D, 4C–F), base not demarcated from frons, broadened at apical portion; labrum (Fig. 2C; *lb*) short, transverse, slightly curved at anterior margin; antennal insertions moderately broadly separated; compound eyes (Figs 2B–D, 3A; *ce*) markedly prominent and located submedially. Head finely setose along tempora, lacking thick bristles on tempora and genae (Fig. 2D; *gen*). Antennae (Fig. 2A) longer than head and pronotum together, antennomeres (Fig. 2A; *a1–11*) each longer than wide, with subcylindrical proximal portion. Mouthparts well-exposed. Prementum (Figs 2D, 3A; *pmm*) small, subtriangular; mentum (Figs 2D, 3A; *mn*) slightly transverse, subrectangular; submentum (Figs 2D, 3A; *smn*) demarcated by pair of posteriorly convergent hypostomal ridges (Figs 2D, 3A; *hr*), lacking lateral sulci; hypostoma (Fig. 3A; *h*) elongate, posteriorly fused with submentum and gula. Mandibles (Figs 2D, 3A, 4D; *md*) small, with strongly curved apical portion, and acute apical tooth



Fig. 1. Holotype (SNUC-Paleo-0016) of *Nuegua elongata* gen. et sp. nov. A. Dorsal habitus. B. Ventral habitus. C. Head, in lateral view. D. Complete view of the amber (each grid of the bar represents 0.5 mm). Abbreviations: at = apical tooth; sat = subapical tooth. Scale bars: 0.5 mm in A–B; 0.2 mm in C.

(Figs 1C, 2D; *at*), mesal margin with one small subapical tooth (Fig. 1C; *sat*); maxillary palpi (Figs 2B, 3A, 4D; *mp*) composed of short, subrectangular, palpomere I (Figs 2D, 3A; *mp1*), strongly elongate and apically broadened palpomere II (Figs 2D–E, 3A; *mp2*), large, elongate palpomere III broadest near middle (Figs 2D–E, 3A; *mp3*), and strongly elongate, subcylindrical, slender and pointed palpomere IV (Figs 2D–E, 3A; *mp4*); palpifer (Fig. 2D; *ppf*) narrow and elongate; galea and lacinia (Fig. 2D; *gal*, *lac*) each elongate; mediostipes (Fig. 2D; *mst*) broad at base, basistipes (Fig. 2D; *bst*) triangular; cardo (Fig. 2D; *cd*) slightly transverse, rounded at posterior margin. Labial palpi (Figs 2D, 3A; *lp*) slender and strongly elongate, longer than prementum.

Prothorax (Figs. 1A–B, 2B–C, 4A–C) strongly elongate and flattened. Pronotum (Figs 2C, 3B; *pn*) bell-shaped, broadest at base, with anterior margin weakly rounded; sides rounded in anterior third, distinctly narrowed at middle, and then broad again at base; posterior margin nearly straight; anterior pronotal corners obtusely angled, posterior corners nearly straight; lacking lateral edges or carinae, disc with long median longitudinal carina (Figs 2C, 3B, 4C; *mlc*). Pronotal disc covered with thin suberect to erect setae, lacking thick bristles on sides; prothoracic hypomera (Figs 2B, 3A; *hy*) largely asetose; hypomeral ridges (Figs 2B, 3A; *hyr*) and notosternal sutures (Figs 2B, 3A; *nss*) complete. Prosternum with basisternal part (Fig. 2B; *bst*) much shorter than coxal part; procoxal cavities closed.

Elytra (Figs. 1A, 4A–C, 4F) oval, elongate, and moderately convex, broadest in front of middle; humeral calli indistinct; each elytron with one well-visible but small and asetose basal fovea (Fig. 4C; *bef*); surface of elytra covered with unremarkable and

unordered fine punctation and fine, suberect setae. Mesoscutellum not visible between elytral bases. Metathoracic wings fully-developed.

Mesoventrite (Fig. 2B, 2F) with prominent mesocoxal projections (Fig. 2B; *mcp*), and narrow, strongly elongate and elevated mesoventral intercoxal process (Figs 2F, 3C; *msvp*).

Metaventrite (Fig. 2F) subtriangular in shape, anteriorly fused with mesoventrite, and with its tip located between mesocoxae; anterior process (Fig. 3C; *amtv*) short and thin, only slightly prominent; intermetacoxal process (Figs 2F, 3C; *mtvp*) short and broad, subtriangular, lacking median notch and not separating metacoxae.

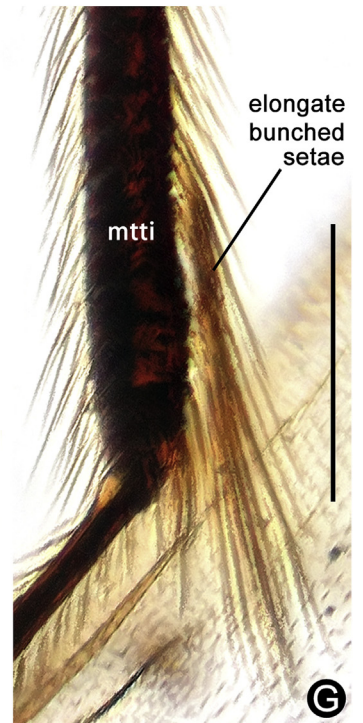
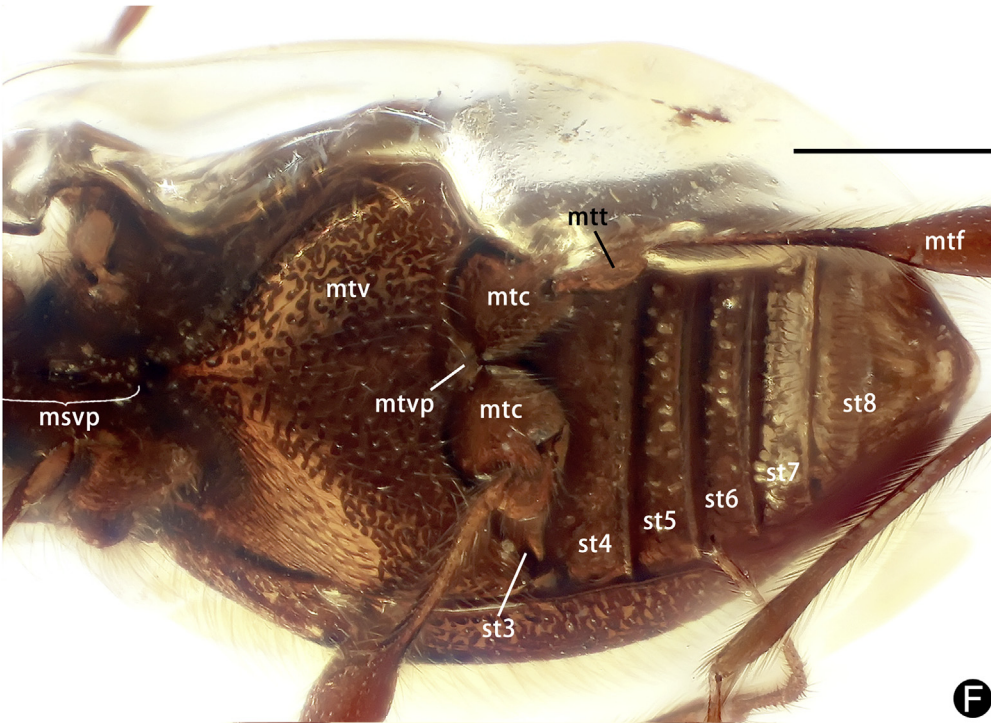
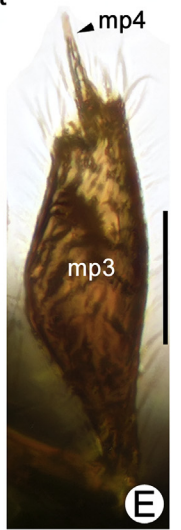
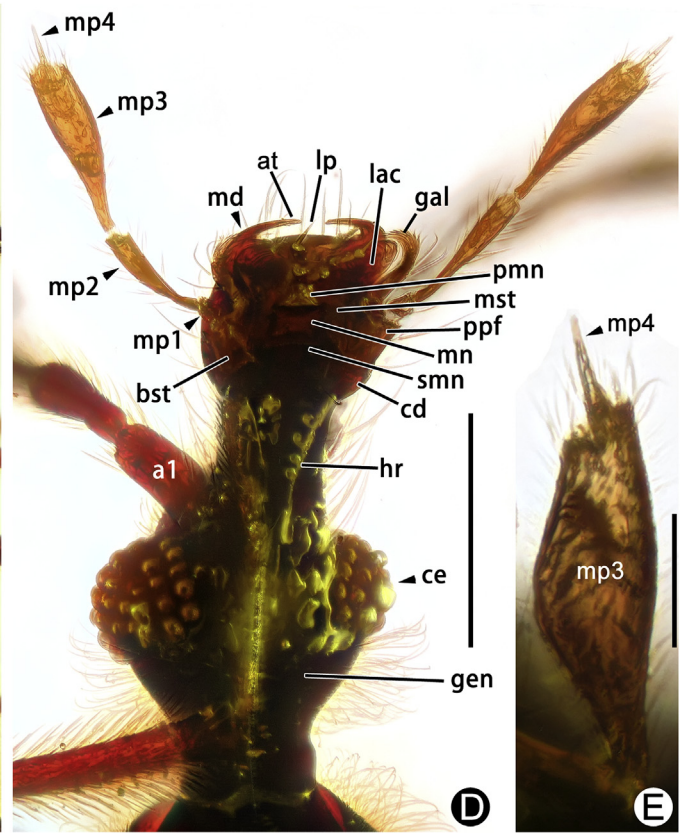
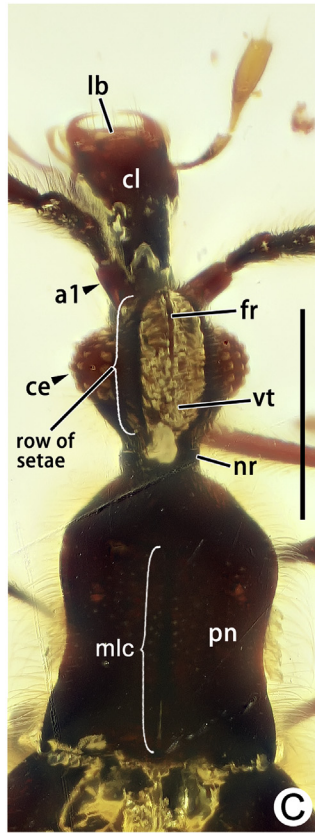
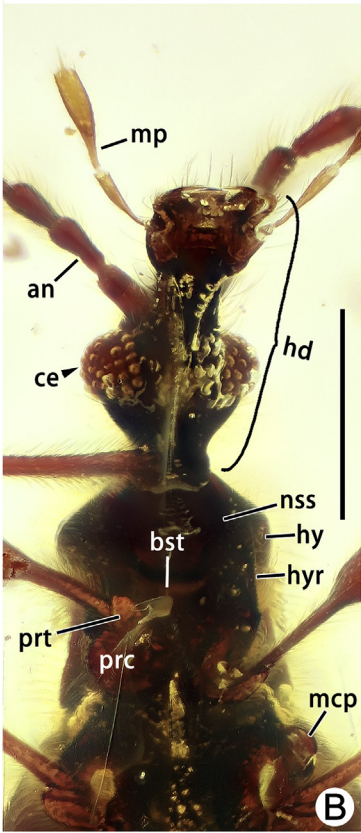
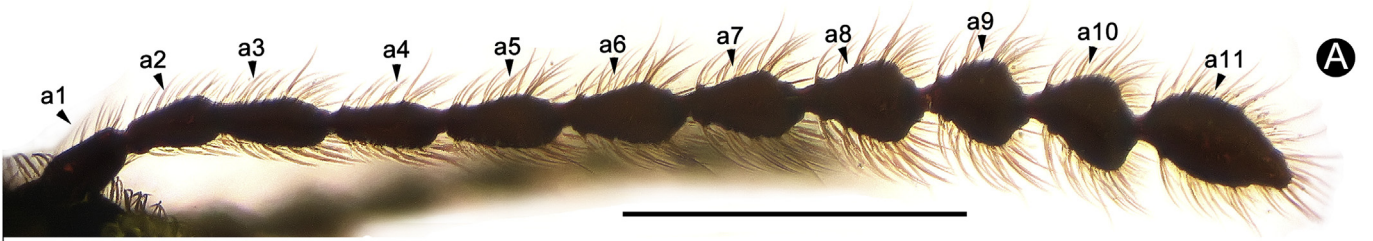
Abdomen with six visible and unmodified sternites (Figs 2F, 3D; *st3*–*8*); terminal abdominal tergite not exposed.

Legs long and slender; pro- (Fig. 2B; *prc*) and mesocoxae elongate, ovoid or subconical, metacoxae (Fig. 2F; *mtc*) strongly transverse. All trochanters (Fig. 2B, 2F; *prt*, *mtt*) subtriangular and elongate, trochantero-femoral articulation oblique in relation to long axis of femur; all femora strongly elongate and slender, distinctly clavate at apical half; all tibiae long and slender, metatibiae (Fig. 2G; *mtti*) with group of long setae at mesal margin near apex; tarsi long and slender, all tarsomeres (Fig. 1A–B) elongate, pretarsal claws long, lacking empodial setae.

Nuegua elongata Yin, Cai & Newton, sp. nov.

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Etymology. The specific epithet refers to the extremely prolonged head in the new species.



Type material (15 exs). Holotype (SNUC-Paleo-0016), a well-preserved individual contained in an approximately 5.5×9 mm amber piece (Fig. 1D), sex undetermined, lowermost Cenomanian, from an amber mine located near Noije Bum Village, Tanaing Town, Hukawng Valley, northern Myanmar; deposited in SNUC. Paratypes (SNUC-Paleo-0017–0021, SNUC-Paleo-0023–0027, NIGP166325–166327, NIGP167527), 14 unsexed specimens, same locality and horizon as the holotype, deposited in SNUC and NIGP, respectively.

Diagnosis. As for the genus (*vide supra*).

Description. Measurements of holotype: length of head from clypeal anterior margin to head base 0.45 mm; head width across compound eyes 0.26 mm; length of pronotum along mid-line 0.44 mm; maximum width of pronotum (at base) 0.35 mm; length of elytra along suture 0.93 mm; maximum width of elytra 0.66 mm. Length of body 1.82 mm.

Body slender, pigmentation reddish-brown. Anterior part of head extremely elongate; tempora about as long as large, prominent compound eyes; frons steeply declining anterior to eyes; vertex weakly convex, covered with two rows of dense, suberect setae; tempora finely setose, lacking bristles. Antennae slender and elongate, reaching past elytral midlength when retracted posteriorly; all antennomeres elongate, successively broadened distally, densely setose.

Pronotum distinctly elongate and broadest at base, narrowing anteriorly. Anterior margin weakly arcuate, sides rounded in anterior third, broadly and shallowly constricted at middle, and then broadened again toward base, posterior margin nearly straight; base with long median longitudinal carina extending from base toward apical 3/4 pronotal length. Disc covered with moderately dense, suberect to erect short setae; sides lacking bristles.

Elytra oval; broadest near anterior third and strongly narrowing posteriorly, covered with fine, inconspicuous punctation and moderately dense, short and suberect setae.

Legs long and slender; covered with short suberect setae.

Comments. All fifteen studied specimens share a similar body size, proportions of the body segments, length of the antennae, and bear a group of long setae near the apex of the metatibia. We thus assign them to a same species. Due to the distortion of various body parts and different viewing angles, measurements were taken only for the holotype preserved in an excellent condition.

3.1. Systematic placement of *Nuegua*

Nuegua is unambiguously referred to the modern ant-like stone beetle tribe Glandulariini, a diverse group including approximately 3700 modern species. This placement is evidenced by the presence of a putative autapomorphy of the tribe in *Nuegua*: the subconical, elongate, and pointed maxillary palpomere IV being much smaller than the broadened and elongate palpomere III (Fig. 2D–E). Moreover, of the two presumably ‘natural lineages’ of Glandulariini (Jałoszyński, 2015), the new genus can be further assigned to the one which lacks a pair of lateral sulci on the submentum (sulci are present in the other group). Although bearing critical importance in deciphering the systematic position of a glandulariine taxon at

generic level, the head venter is usually not possible to be observed in fossil scydmaenines unless when the specimen, particularly the head, is preserved in an excellent condition and in a proper angle. *Nuegua* is merely the second extinct scydmaenine genus that allows for a clear observation on the ventral structures of the head, the first being an undescribed new genus from Burmese amber, related to the extant “*Syndicus* group of genera” (Yin et al., submitted manuscript).

The general body form (except for the head elongation) of *Nuegua* resembles those of the previously described *Cenomaniola* Jałoszyński & Yamamoto, also known from Burmese amber (Jałoszyński et al., 2017a), and two extant genera, i.e., the Oriental *Elacatophora* Schaufuss and Nearctic *Lophioderus* Casey, to which the new genus may be related. All these taxa share a unique form of the head, which in lateral view is highest in front of the eyes and steeply declined anteriorly and also descending posteriorly. Among modern taxa, the form of the head separates *Elacatophora* and *Lophioderus* from all remaining glandulariines (O’Keefe, 1996; Jałoszyński, 2004, 2008).

The most remarkable feature of *Nuegua* is the extremely prolonged preocular region that occupies over half of the total head length (Figs 1C, 2C–D, 3C–F), which is considered an autapomorphy of the new genus. Such a bizarre modification is unknown among living and fossil scydmaenines, but is most familiar in members of the Curculionoidea (weevils), and occasionally occurs in other beetle groups such as Omaliinae (Staphylinidae), Silphidae, Salpingidae, and Laemophloeidae (see ‘Discussion’ section below). *Nuegua* shares with *Cenomaniola* the narrow and subconical maxillary palpomere IV (Fig. 2E), labial palps being longer than prementum (Fig. 2D), and presence of an anterior metaventral process; these two genera can be readily separated by the much larger body size (>1.8 mm in *Nuegua* vs. < 1.0 mm in *Cenomaniola*), long antennae with elongate antennomeres (Figs 1A–B, 2A, A–C, E–F), lack of thick bristles on sides of the head and pronotum (Fig. 2B–C), maxillary palpomere III (Fig. 2E) strongly expanded at middle of the mesal margin, long pronotal median longitudinal ridge extending from near base toward anterior 3/4 of pronotal length (Figs 2C, 3C), and mesoventral intercoxal process long and not projecting anteriorly in the new genus. By contrast, *Cenomaniola* displays gradually thickened antennae with moniliform antennomeres, presence of thick bristles on sides of the head and prothorax, the maxillary palpomere III is broadest near apical third, the pronotum bears a short median ridge accounting for 1/10 to less than half of pronotal length, and the mesoventral intercoxal process is present only in front of the mesocoxae, and distinctly projecting anteriorly (Jałoszyński et al., 2017a). The strongly expanded mesal margin of the third maxillary palps in *Nuegua* is shared with *Elacatophora*, but these two genera can be differed by numerous characters states typical in *Nuegua* but not found in *Elacatophora*: extremely extended preocular region (normal in *Elacatophora*), labial palpi much longer than prementum (palpi are much shorter than prementum in *Elacatophora*), small and conical maxillary palpus IV (thin and rod-like palpus IV in *Elacatophora*), lack of bristles on sides of the head and pronotum (bristles are present in *Elacatophora*), etc. *Lophioderus* have a transverse antebasal pronotal groove which is absent in *Cenomaniola*, neither as in the new genus.

Fig. 2. Morphological details of *Nuegua elongata* gen. et sp. nov., light microscopy (A, E, F based on NIGP166326. B–D based on SNUC-Paleo-0016. G based on NIGP166325). A. Antenna. B. Head venter and prosternum. C. Head dorsum and pronotum. D. Head venter, enlarged. E. Maxillary palpomeres III–IV. F. Meso- and metaventrite, and sternites III–VIII. G. Apical portion of metatibia. Abbreviations: a1–11 = antennomeres I–XI; an = antenna; at = apical tooth; bst = basisternal part of prosternum; cd = cardo; ce = compound eye; cl = clypeus; fr = frons; gal = galea; gen = genae; hr = hypostomal ridge; hy = hypomeron; hyr = hypomeral ridge; lac = lacinia; lb = labrum; lp = labial palpus; md = mandible; mlc = median longitudinal carina; mp = maxillary palpus; mp1–4 = maxillary palpomeres I–IV; mn = mentum; mst = mediostipes; msvp = mesoventral process; mtc = metacoxa; mtf = metafemur; mtt = metatrochanter; mti = metatibia; mtv = metaventrite; mtvp = metaventral process; nr = ‘neck’ region; nss = notosternal suture; pmn = prementum; pn = pronotum; ppf = palpifer; prc = procoxa; prt = protrochanter; smn = submentum; st3–8 = sternites III–VIII; vt = vertex. Scale bars: 0.3 mm in A–C; 0.2 mm in D, F; 0.1 mm in E, G.

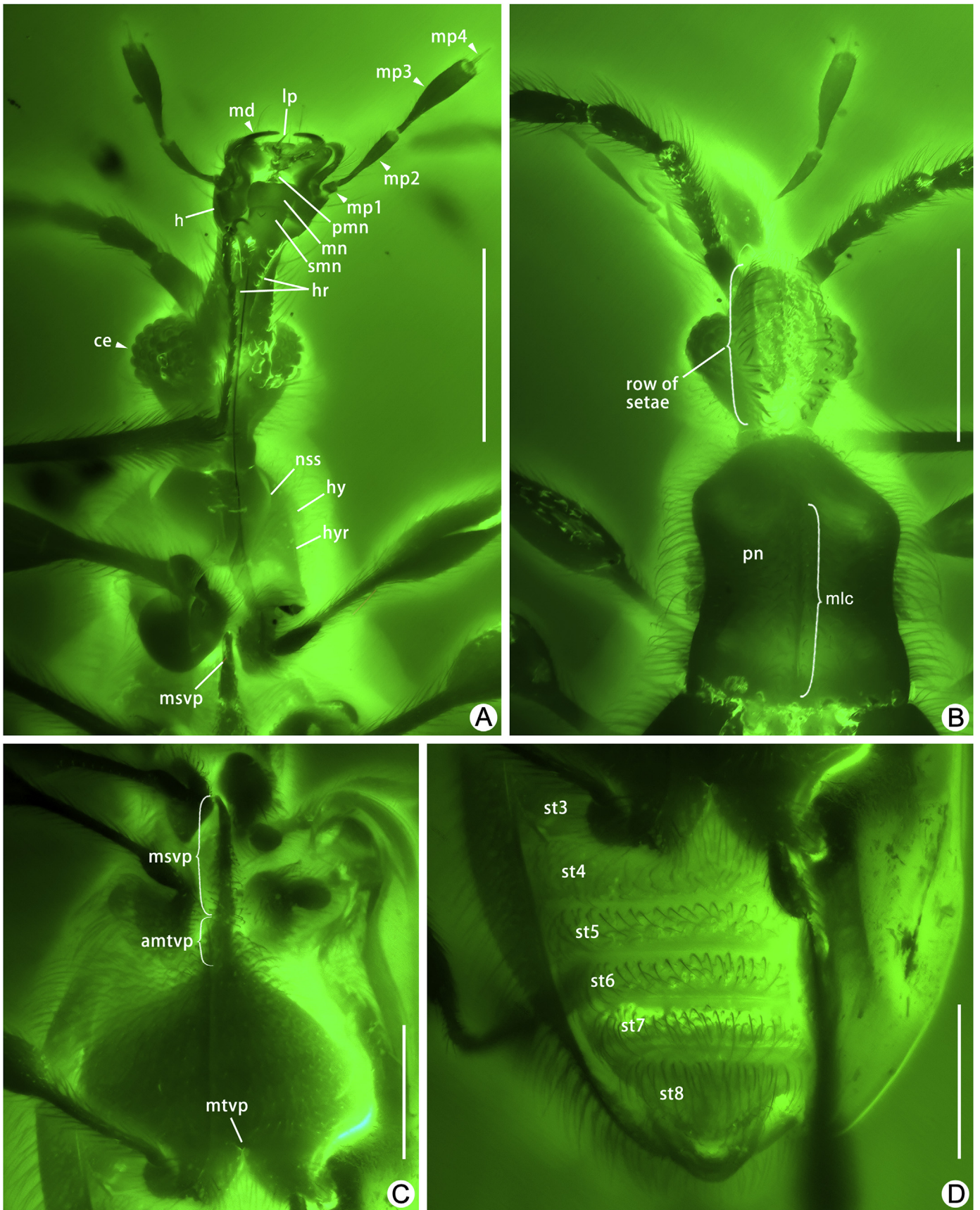


Fig. 3. Morphological details of *Nuegua elongata* gen. et sp. nov., fluorescent microscopy (A–B based on SNUC-Paleo-0016. C–D based on NIGP166326). A. Head venter and prosternum. B. Head dorsum and pronotum. C. Meso- and metaventrite. D. Sternites III–VIII. Abbreviations: amtvp = anterior metaventral process; ce = compound eye;

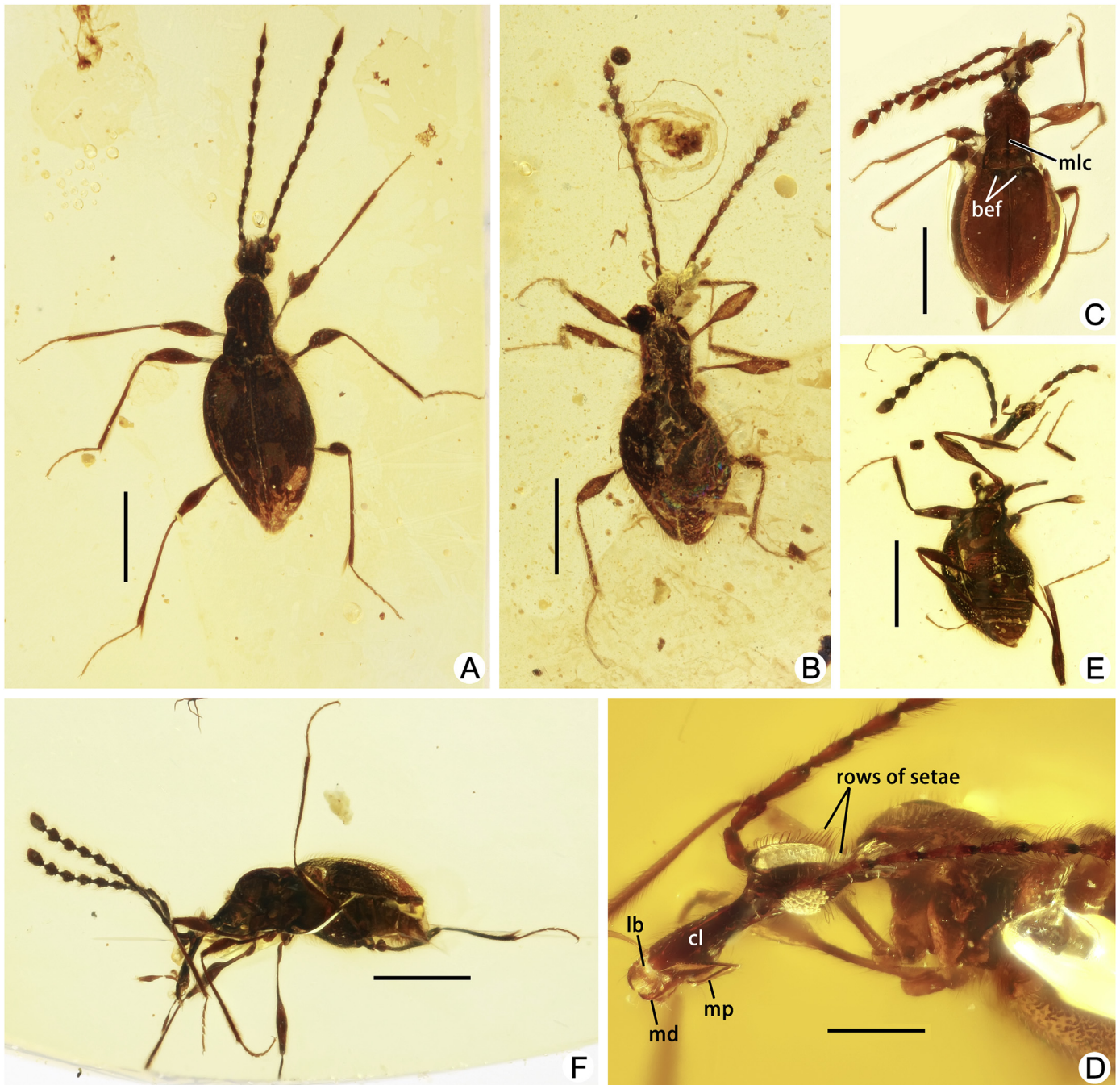


Fig. 4. Paratypes of *Nuegua elongata* gen. et sp. nov. A. NIGP166325. B. SNUC-Paleo-0017. C–D. NIGP166326. E. SNUC-Paleo-0018. F. SNUC-Paleo-0019. Abbreviations: bef = basal elytral fovea; cl = clypeus; lb = labrum; md = mandible; mp = maxillary palpus; mlc = median longitudinal carina. Scale bars: 0.5 mm in A–C, E–F; 0.2 mm in D.

The males of *Lophiderus* also have modified antennomeres IV–VI, and transverse antennomeres VII–XI (O’Keefe, 1996, 2000), while *Nuegua* have unmodified and elongate antennomeres.

Based on the aforementioned morphological evidence, we suggest a probable affinity between *Nuegua*, *Cenomaniola*, *Elacatophora*, and *Lophiderus*, which may share a common ancestor. These taxa form a small monophyletic group within Glandulariini,

as evidenced by the distinct lateral profile of the head, and other shared features on the head and the pronotum. Apparently, the glandulariines as a whole survived the K/Pg extinction event (Renne et al., 2013), and remained diverse up to the present, whereas *Nuegua*, displaying an autapomorphic elongate preocular region indicative of a narrow feeding adaptation, did not seem to persist into Paleogene.

4. Discussion

The head of *Nuegua* with its prolonged preocular region of the head that includes the clypeal region and the submentum forming a 'rostrum' is apparently without parallel in the huge group of "higher" staphylinids known as the "Staphylinine group" (Lawrence and Newton, 1982; Grebennikov and Newton, 2009). This group of 10 subfamilies and more than 25,000 species is, with the exception of the basal-most fungivorous subfamily Oxyporinae (Leschen and Allen, 1988), predatory on a wide variety of invertebrates ranging from minute Acarina (Scydmaeninae) to large flies and beetles (Staphylininae). All members (including Oxyporinae) rely, as far as known, on preoral digestion of the fungus or prey and ingestion of the resultant liquid. Thus, as a preliminary hypothesis, it can be expected that the mouthparts of *Nuegua* might be an adaptation for some type of specialized predation that requires the mouthparts to be inserted in some suitably-shaped preys, e.g., gastropods. There is precedent for this among some less closely related staphylinoid beetles, such as the silphid genera (or subgenera of *Silpha* Linnaeus) *Phosphuga* Leach and *Ablattaria* Reitter, which are snail-feeders; adults have an elongated clypeus that allows the mouthparts to be inserted into the opening of terrestrial snail shells (Heymons et al., 1927; Heymons and Lengerken, 1932, respectively). The omaliine staphylinid genus *Tanyrhinus* Mannerheim also has a remarkably similar elongation of the clypeus with mouthparts at apex, but the function in this case is unknown (adults are found on decaying mushrooms, but feeding has not been observed). Another group of 'rostrate' staphylinids, in the tribe Metopiasini of Pselaphinae, are superficially similar (e.g., Comellini, 1998; Asenjo, 2016) and are most probably predators, but in this case the 'rostrum' consists of an elongate frons, with the antennal insertions at apex, while the clypeus is short and the actual mouthparts are not at apex of the 'rostrum'.

The best-known beetles with a similar elongate clypeus, of course, are the weevils and their allies (superfamily Curculionioidea). In this primarily phytophagous group, the most widespread and presumably ancestral function of the move of the mouthparts to the apex of an elongate rostrum is to allow females to chew a narrow hole into the target plant to deposit eggs (e.g., Davis, 2014; Moon, 2015). The oldest record of beetles with a well-developed rostrum also occurs in this group, represented by the family Obrieniidae Zherikhin & Gratshev from the Triassic of Kyrgyzstan and Jurassic of Karatau (Zherikhin and Gratshev, 1994; Legalov, 2012). Using their prolonged mouthparts, female Obrieniidae were suspected to oviposit into holes on cycadophytes (Zherikhin and Gratshev, 1994). Similar mouthparts have evolved independently in at least three other groups of polyphagan beetles: Laemophloeidae (Cucujoidea), Salpingidae (Tenebrionoidea), and Lycidae (Elateroidea). In Salpingidae, adults of the genus *Rhinosimus* Latreille (Salpinginae) insert the rostrate mouthparts into the cambial layer of decaying trees to feed on the cambium (Howden and Howden, 1981). The ant-associated *Tretothorax* Lea (Dacoderinae) from Australia also exhibits a rostrate head with an elongate frontal region (Aalbu et al., 2005), but the possible functions in this and those laemophloeids with similar mouthparts (e.g., *Metaxyphloeus* Thomas) are unknown (Thomas, 1984). A few flower-visiting lycid groups (e.g., *Lygistopterus* Mulsant, *Macrolygistopterus* Pic, *Lucaina* Dugès, and *Porrostoma* Castelnau) have a long preocular region (Bocak and Bocakova, 2008), possibly related to their nectar-consuming habits. Superficially similar instances of elongation of the clypeo-frontal area of the head can be used to produce 'piercing-sucking' mouthparts, as found in the aleocharine staphylinid genus *Stylogymnusa* Hammond (Hammond, 1975), the camiarine leiodid genus *Myrmicholeva* Lea (Lea, 1910) and some genera of the families Eucinetidae (e.g., Vit,

1981) and Cerylonidae (Ślipiński and Lawrence, 2010). In the latter three cases, adults of related genera with chewing mouthparts may feed on slime mold (Myxomycete) fruiting bodies including spores, and it is presumed that the piercing mouthparts may be used to penetrate rotten wood or other substrates to extract plasmodia of Myxomycetes. Still other mechanisms have been used to remove chewing mouthparts from the main mass of the body, such as an extremely elongate neck in the mycophagous scaphidiine genus *Diatelium* Pascoe (Pascoe, 1863; Leschen and Löbl, 1995), or elongated neck plus pronotum of the predatory carabid genus *Colliuris* Degeer (Adis et al., 1997). In *Diatelium* the males usually exhibit a longer neck region than females, indicating possible sexual selection.

Clearly, rostrum-like modifications of the head capsule as found in *Nuegua* have arisen multiple times independently in beetles, and for diverse purposes including at least predation, saprophagy, mycophagy, preparation of oviposition sites, and sexual selection in particular circumstances. Given that modern scydmaenines, as far as known, feed exclusively on smaller invertebrates or scavenge on dead soil organisms (Jałoszyński, 2016c), it is very likely that members of *Nuegua* are also predacious. At present, it is challenging to provide a plausible scenario concerning the exact function of the preocular extension of *Nuegua*. The significance of the discovery of *Nuegua* is that, as in Curculionioidea, a specialized configuration of the mouthparts arose in a stem group during the early evolution of the subfamily (Glandulariini), but (unlike in weevils) it was not ultimately successful and became extinct. The paleobiology and diversity of Mesozoic scydmaenines remains an open field of investigation, and is worth continuous attention given its implications for the early evolutionary history of the entire subfamily.

5. Concluding remarks

The discovery of *Nuegua elongata* gen. et sp. nov. in mid-Cretaceous Burmese amber reveals a fascinating new structure in the subfamily Scydmaeninae. Detailed morphological investigation of *Nuegua* suggests a narrow adaptation for some type of specialized predation, corresponding to its strikingly elongate preocular region. Extension of the mouthparts also analogously occurs in some other beetle groups, most familiar in weevils and their allies which represent one of the most successive modern coleopteran lineages, while for some unknown reason, *Nuegua* seems fail to persist into Paleogene. In this regard, we hope further efforts in searching and studying Scydmaeninae in Burmese amber will unveil the enigmatic biology of *Nuegua*, and continuously broaden our knowledge of the early evolution and diversification of this group.

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