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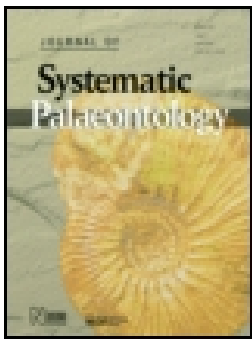
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## ***Pangusyndicus* gen. nov.: a new mid-Cretaceous scydmaenine with reduced antennae and prothoracic gland (Coleoptera, Staphylinidae: Scydmaeninae)**

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The ant-like stone beetle tribe Glandulariini harbours approximately 3700 species, representing more than 70% of the extant diversity of the subfamily Scydmaeninae. Fossil records of this large tribe are rare, and are mostly confined to Eocene to Miocene amber, whereas only four genera were known from Mesozoic deposits. Here we report a new Mesozoic taxon, *Pangusyndicus excavatus* Yin, Zhou & Cai gen. et sp. nov., from Cenomanian Burmese amber. For the first time the ventral cephalic structures of an extinct Glandulariini are observable, a character system usually difficult to discern, especially in fossil scydmaenines. *Pangusyndicus* clearly lacks lateral sulci on the submentum, a critical character state that justifies the placement of *Pangusyndicus* in one of the two assumedly ‘natural groups’ of Glandulariini. *Pangusyndicus* displays strongly reduced antennomeres XI, similar to those found only in the extant Australo-Oriental genus *Syndicus* Motschulsky. To test the phylogenetic position of *Pangusyndicus*, cladistic analyses were performed based on morphological data. Both parsimonious and maximum likelihood cladograms recovered a close relationship between *Pangusyndicus*, *Syndicus* and *Loeblites* Franz, indicating the unique reduction of apical antennomeres in this group may have originated once, and by the mid-Cretaceous at the latest. More strikingly, *Pangusyndicus* possesses a large cavity on the mediobasal surface of the pronotal disc, a feature previously unknown among all scydmaenines. We interpret this as a specialized glandular structure, although its function remains uncertain. The presence of such a cavity in *Pangusyndicus* represents the earliest known presumably glandular structure in Staphylinidae. Moreover, *Pangusyndicus* and several recently described mid-Cretaceous scydmaenines belonging to various tribes exhibit notably longer legs than their extant relatives, indicating shifts in habitat and prey preferences may have occurred during the evolution of these groups.

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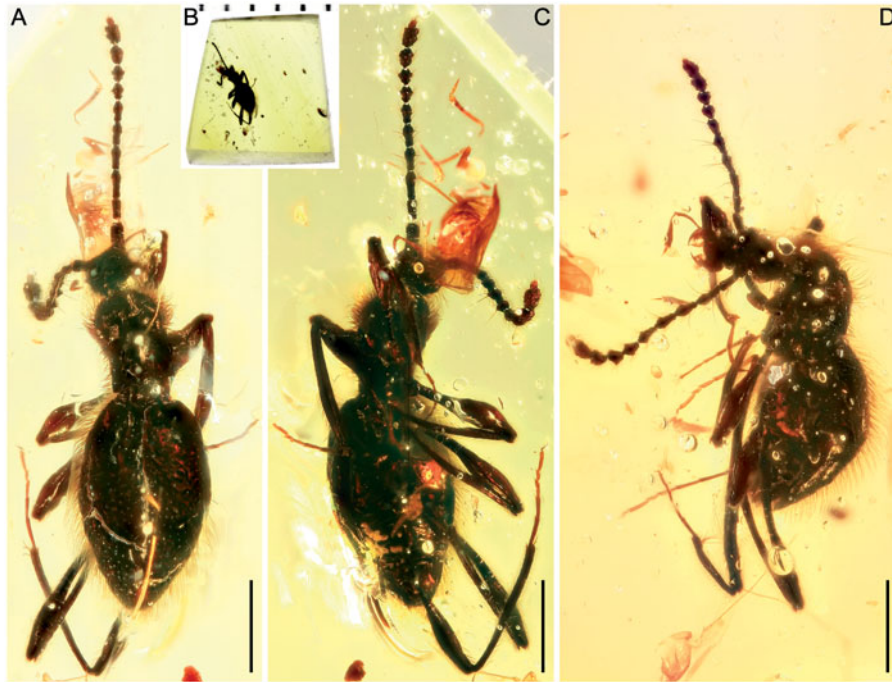
**Keywords:** Fossil; ant-like stone beetles; Glandulariini; Burmese amber; Mesozoic

### **Introduction**

The subfamily Scydmaeninae, also known as ant-like stone beetles, is a diverse lineage of the rove beetle family Staphylinidae, containing more than 5200 extant and 46 extinct species grouped in four supertribes (Jałoszyński & Perkovsky 2016a; Jałoszyński *et al.* 2016, 2017a, b). The small and entirely extinct Hapsomelitae is a poorly defined and probably heterogeneous group formed by three genera in Cretaceous amber from Myanmar (Poinar & Brown 2004; Chatzimanolis *et al.* 2010). Cephenniitae is a well-studied monophyletic lineage with 26 extant genera placed in three tribes, i.e. Cephenniini, Eutheini and

Marcepaniini (Jałoszyński 2014). Extinct taxa of Cephenniitae were reported from Rovno, Baltic, Siberian, Spanish and Burmese ambers, showing an early diversification and wide dispersal of the group (Peris *et al.* 2014; Jałoszyński & Kubisz 2016; Jałoszyński & Peris 2016; Jałoszyński & Perkovsky 2016b). Mastigitae is a small lineage of nine extant genera holding no more than 100 species. The monophyly of this supertribe and relationships among its constituent genera were recently tested, and its fossil taxa are among the best studied of extinct scydmaenines (O’Keefe *et al.* 1997; Jałoszyński 2012, 2016a, 2017; Cai & Huang 2016; Yin *et al.* 2017a). Scydmaenitae, comprising nearly 90% of all ant-like stone beetle species and over half of

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**Figure 1.** *Pangusyndicus excavatus* gen. et sp. nov., male holotype (SNUC-Paleo-0013). **A**, dorsal habitus; **B**, complete view of the amber piece; **C**, ventral habitus; **D**, dorso-lateral habitus. Scale bars: A, C, D = 0.5 mm; scale bar unit in B = 1 mm.

all known genera, is the largest but also the least-studied supertribe (Jałoszyński *et al.* 2016).

The worldwide Glandulariini is a diverse tribe of the Scydmaenitae, holding more than 3700 species grouped in 64 extant genera. In contrast to this great species richness, until now only nine genera and 20 extinct species of the tribe have been known from fossil deposits; most of these taxa were from Eocene and Miocene ambers, and only four Mesozoic genera, *Scydmbisetia* Jałoszyński & Yamamoto, *Cenomaniola* Jałoszyński & Yamamoto, *Hyperstenichnus* Jałoszyński & Perrichot and *Nuegua* Yin, Cai & Newton, have been confidently placed in Glandulariini (Jałoszyński & Perkovsky 2016a; Jałoszyński *et al.* 2016, 2017a, b; Yin *et al.* 2018a). In the present study, we report a new extinct glandulariine genus *Pangusyndicus* Yin, Zhou & Cai gen. nov. from mid-Cretaceous Burmese amber. The new genus exhibits unique morphological traits unknown among all other living and extinct scydmaenines, which broadens our knowledge of the early divergence and morphological disparity of the presently hyperdiverse tribe Glandulariini.

## Material and methods

### Material

The male holotype (Fig. 1B; accession number: SNUC-Paleo-0013) and eight unsexed paratypes (accession number: SNUC-Paleo-0014–15, 22, 28–32) are deposited in the

Insect Collection of Shanghai Normal University, Shanghai, China; one female paratype (Fig. 4C, accession number: NIGP165286) is deposited in the Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, Nanjing, China. The specimens described in this paper were obtained from amber deposits in the Hukawng Valley of Kachin, northern Myanmar (26°21'33.41"N, 96°43'11.88"E), once thought to be of Eocene origin, but now recognized as earliest Cenomanian based on U–Pb dating of zircons from the volcanoclastic matrix of the amber (Shi *et al.* 2012), which corresponds with a general age predicted by Grimaldi *et al.* (2002) based on key bioinclusions. Other workers have argued for slightly older ages, albeit at times on less than solid reasoning, either within the late Albian (Cruickshank & Ko 2003; Ross *et al.* 2010), or right at the Albian–Cenomanian boundary (Rasnitsyn *et al.* 2016). Maps showing amber-yielding localities were provided in Cruickshank & Ko (2003), Kania *et al.* (2015) and Yin *et al.* (2018b).

Six extant glandulariine taxa were examined for comparative morphological studies. A list of these taxa and two additional figure plates can be found in Supplemental material, File 1 and Supplemental Figures 1 and 2.

### Methods

The holotype (SNUC-Paleo-0013) and female paratype (NIGP165286) were cut using a handheld engraving



**Figure 2.** *Pangusyndicus excavatus* Yin, Zhou & Cai gen. et sp. nov., male holotype (SNUC-Paleo-0013). **A**, dorsal habitus; **B**, ventral habitus; **C**, right antenna. Abbreviations: a1–11, antennomeres I–XI; an, apical nodule; ant, antenna; bef, basal elytral fovea; hd, head; hy, hypomeron; mst, mesotrochanter; mtc, metacoxa; mtr, metatrochanter; pn, pronotum; prc, procoxa; st3–8, sternites III–VIII. Scale bars: A, B = 0.5 mm; C = 0.2 mm.

tool, and polished using sandpapers of different grits and rare earth polishing powder. Habitus pictures were made either using a Canon EOS 5D Mark III digital camera, equipped with a Canon MP-E 65 mm macro lens (F2.8, 1–5X), and an attached Canon MT-24EX twin flash as light source (Fig. 1), or using a Zeiss Axio Imager 2 light microscope with an attached digital camera (Fig. 4A, B). The beetles were well preserved but difficult to observe under standard lighting due to their dark pigmentation; thus, we employed fluorescence microscopy to produce images with fine details and high-resolution, using a Zeiss Axio Imager 2 light microscope (Figs 2, 3, 4D–F, 5). Habitus and morphological details of the extant taxa were made using a Canon EOS 5D Mark III digital camera (Supplemental Fig. 1), or a Canon G9 camera mounted on an Olympus CX31 microscope (Supplemental Fig. 2). Montage images were produced in Zerene Stacker (version 1.04), and all images were modified and grouped in Adobe Photoshop CS5 Extended.

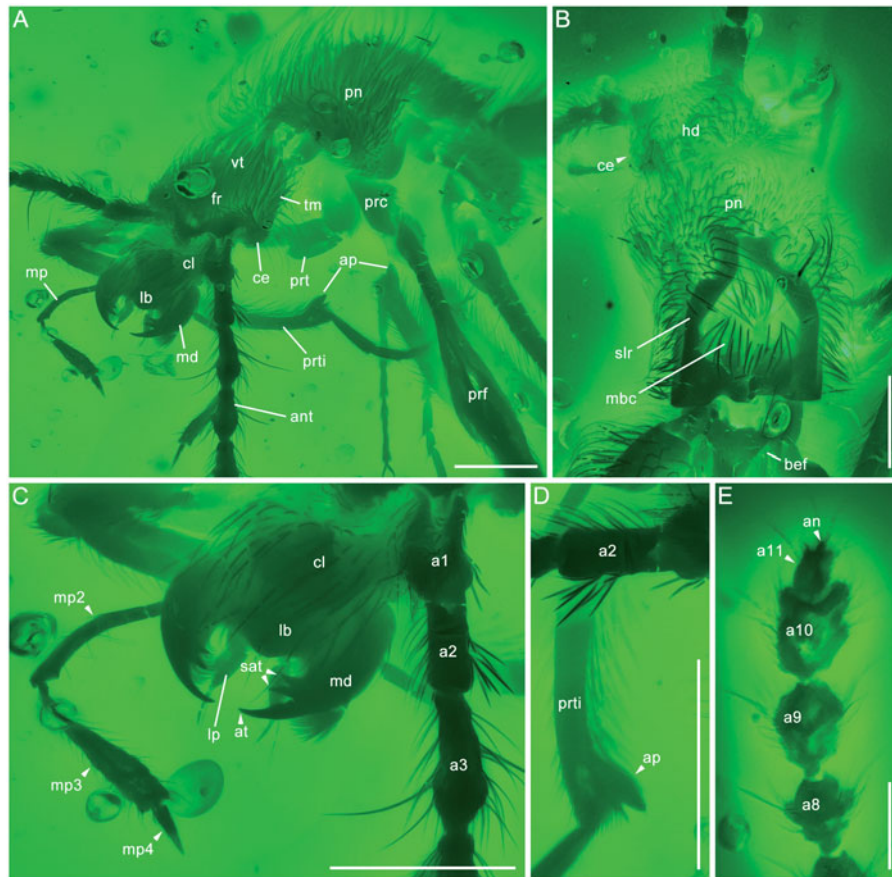
### Phylogenetic analysis

To test the phylogenetic position of the new genus within Glandulariini, we performed morphology-based cladistic analyses, scoring character states for the new genus that were used previously by Jałoszyński (2014).

Since the original data set was designed for ascertaining relationships within the supertribe Cephenniitae, we reduced the number of taxa of that group and added two glandulariine genera and one subgenus, *Horaeomorphus* Schaufuss, *Loeblites* Franz, and *Syndicus* (*Semisyndicus*) Jałoszyński. A total of 135 non-additive and unordered adult morphological characters were included. These include the 133 characters used by Jałoszyński (2014) and two additional characters (133: pronotal cavity, and 134: antennomere XI). Inapplicable character states are indicated by en dashes (–) and missing data are indicated by question marks (?). The data matrix was assembled in WinClada v. 1.00.08 (Nixon 2002); characters are numbered starting from 0 (as required by TNT).

Parsimony analyses were conducted in TNT v. 1.5-beta (Goloboff & Catalano 2016) under implied weighting (default weighting function  $K=3$ ) using the ‘traditional search’ strategy, with 1000 replicates of tree bisection reconnection (TBR) branch swapping and saving 1000 trees per replicate. The symmetric resampling ( $P=33$ ) and calculation of absolute Bremer support values were also conducted in TNT. Character mapping on the strict consensus tree was made in WinClada.

Maximum likelihood analyses were conducted using IQ-TREE v. 1.6.1 (Nguyen *et al.* 2015) under the MK + G model. Branch support was estimated using the Ultrafast option for bootstrap analysis, with 1000



**Figure 3.** *Pangusyndicus excavatus* Yin, Zhou & Cai gen. et sp. nov., male holotype (SNUC-Paleo-0013). **A**, anterolateral view of forebody; **B**, dorsal view of forebody; **C**, mouthparts; **D**, apical portion of protibia; **E**, right antennomeres VIII–XI. Abbreviations: a1–3 and 8–11, antennomeres I–III and VIII–XI; an, apical nodule; ant, antenna; ap, apical projection; at, apical tooth; bef, basal elytral fovea; ce, compound eye; cl, clypeus; fr, frons; hd, head; lb, labrum; lp, labial palpus; mbc, mediobasal cavity; md, mandible; mp, maxillary palpus; mp2–4, maxillary palpomeres II–IV; pn, pronotum; prc, procoxa; prf, profemur; prt, protrochanter; prti, protibial; sat, subapical tooth; slr, sublateral ridge; tm, temple; vt, vertex. Scale bars: A–D = 0.2 mm; E = 0.1 mm.

replicates. The detailed commands are as follows: iqtree -s iqtree\_Morphology.phy -st MORPH -m MK + G -bb 1000 -minsup 0.5.

Bayesian analyses were performed using MrBayes 3.2.6 under the Mk model. The search consisted of two Markov chain Monte Carlo (MCMC) runs of two chains and was terminated at 1,000,000 generations. Convergence was determined by the standard deviation of split frequencies having dropped below 0.0075, and further verified by estimated sample sizes higher than 200 in Tracer v. 1.6 (Rambaut *et al.* 2013), indicating sufficient estimation of the posterior. The first 10% of trees were discarded as burn-in. The consensus tree of both MCMC runs was rooted using *Euaesthetus ruficapillus* (Lacordaire). The Nexus file used for this analysis is available in Supplemental material, File 4.

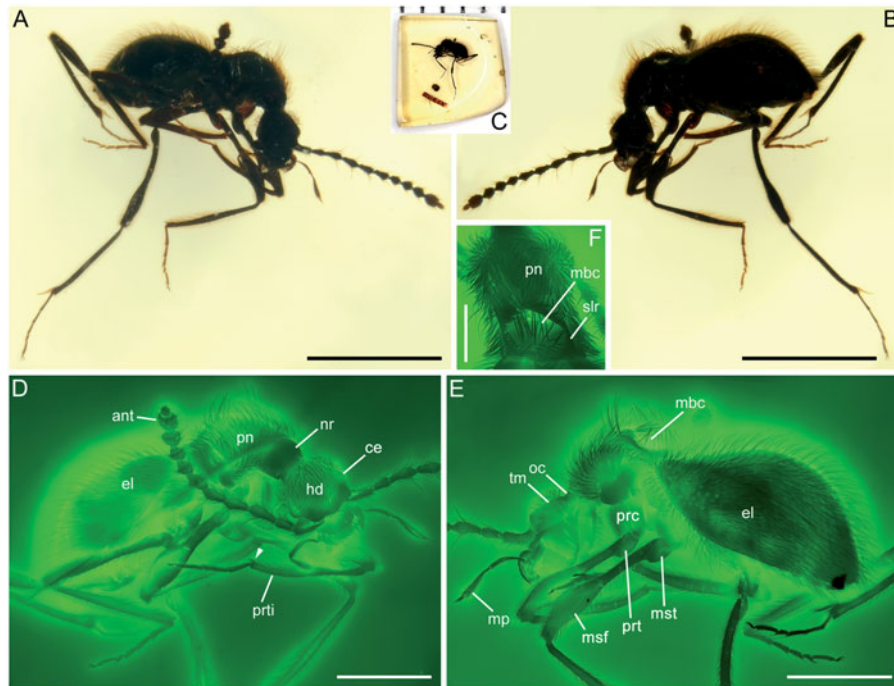
All trees were annotated in FigTree v. 1.4.3, Adobe Illustrator CS5 and Adobe Photoshop CS5 Extended. The morphological data matrix and the character list and states are presented in Supplemental material, Files 2 and 3.

## Systematic palaeontology

Order **Coleoptera** Linnaeus, 1758  
 Family **Staphylinidae** Latreille, 1802  
 Subfamily **Scydmaeninae** Leach, 1815  
 Tribe **Glandulariini** Schauffuss, 1889  
*Pangusyndicus* Yin, Zhou & Cai gen. nov.  
 (Figs 1–5)

**Type species.** *Pangusyndicus excavatus* sp. nov.

**Diagnosis.** Body elongate and slender, ant-like, with elongate appendages; vertex, temples and sides of pronotum with dense bristles. Head subhexagonal, occipital constriction as wide as about half of head width; clypeus clearly demarcated from frons (i.e. frontoclypeal sulcus present); antennal insertions broadly separated; temples longer than compound eyes; submentum lacking lateral sulci. Antennae slender, antennomeres gradually shortened and thickened distally, loosely assembled;



**Figure 4.** *Pangusyndicus excavatus* Yin, Zhou & Cai gen. et sp. nov., female paratype (NIGP165286). **A, D**, right side of lateral habitus; **B, E**, left side of lateral habitus; **C**, complete view of the amber piece; **F**, pronotum, in dorsal view. Abbreviations: ant, antenna; ce, compound eye; el, elytra; hd, head; mbc, mediobasal cavity; mp, maxillary palpus; msf, mesofemur; mst, mesotrochanter; nr, neck region; oc, ocular constriction; pn, pronotum; pnc, procoxa; prt, protrochanter; prti, protibia (arrow indicates lack of apical projection); slr, sublateral ridge; tm, temple. Scale bars: A, B, D, E = 0.5 mm; F = 0.2 mm; scale bar unit in C = 1 mm.

antennomere XI strongly reduced, its base about half as wide as apex of antennomere X, with small apical nodule. Pronotum strongly elongate and broadest anterior of the midpoint, with thick lateral ridges demarcating broad, deep mediobasal cavity, with roundly angulate posterolateral corners; basisternal part of prosternum about as long as coxal part. All coxae contiguous; femora lacking a dorsal groove. Suture between abdominal sternites 7 and 8 distinct. Male protibia modified, elongate, arched and bearing large apical projection; female protibia not so modified.

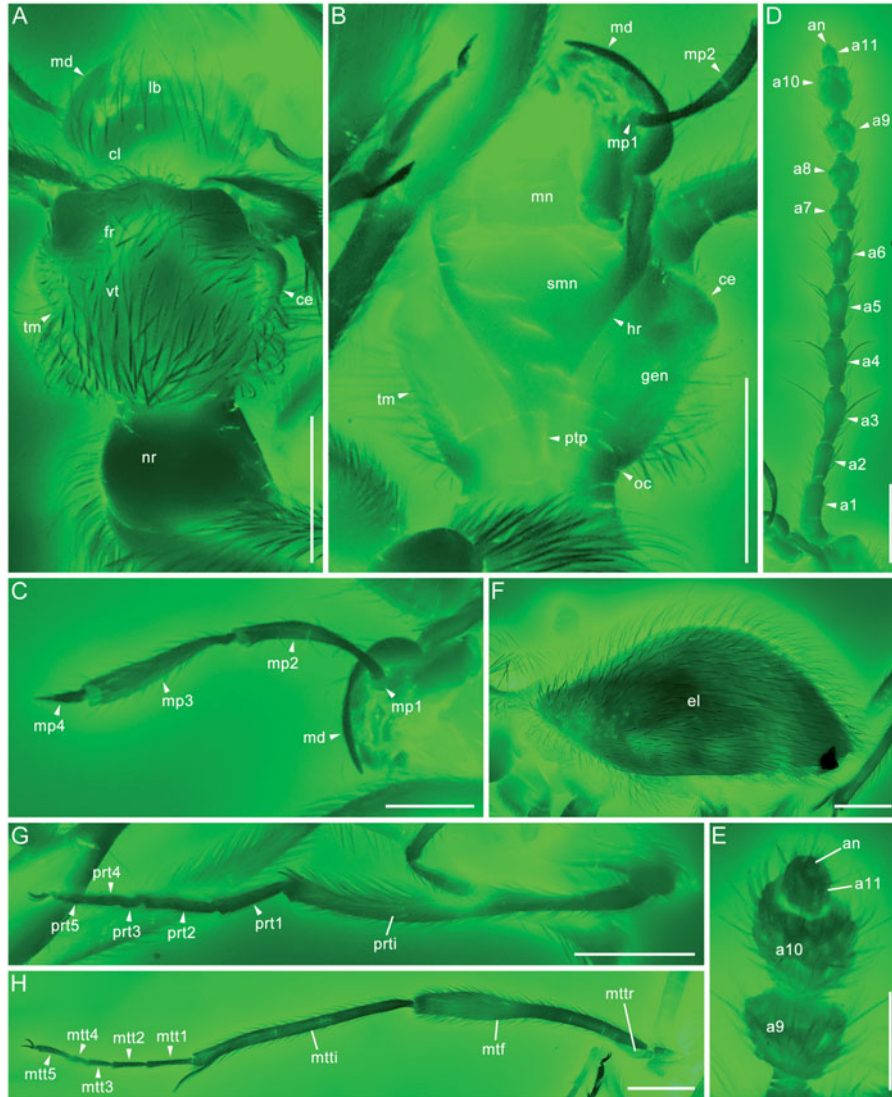
**Etymology.** The new generic name is a combination of ‘Pangu’ (in Chinese mythology the first living being and the creator of all) and ‘Syndicus’ (an extant related genus). The gender of the name is masculine.

**Occurrence.** Lowermost Cenomanian, Late Cretaceous of northern Myanmar.

**Description.** Body elongate and slender (Figs 1A, C, D, 4A, B), ant-like, strongly constricted between head and pronotum and between pronotum and elytra (Figs 2A, B, 4D, E).

Head capsule (Figs 2A, 3B, 4D) divided into large and exposed anterior part and smaller posterior ‘neck’ region (Figs 4D, 5A), largely retracted into prothorax and demarcated by occipital constriction (Figs 4E, 5B),

which is as wide as about half of head width; anterior part of head in dorsal view subhexagonal; vertex (Figs 3A, 5A) strongly transverse; temples (Figs 3A, 4E, 5A, B) much longer than compound eyes in dorsal view, convergent posteromesally; frons (Figs 3A, 5A) subtrapezoidal; clypeus (Figs 3A, C, 5A) well demarcated from frons by distinct inter-frontoclypeal impression; antennal sockets broadly separated and located in large anterolateral antennal cavities (Figs 3A, 4D); compound eyes (Figs 3A, B, 5A, B) large and located near middle of anterior part of head capsule. Head with thick bristles on vertex and temples (Figs 3A, 5A), bristles lacking on genae (Fig. 5B). Antennae (Figs 2A–C, 4D, 5D) gradually thickened distally; antennomeres I–VI strongly elongate, VII–IX short and broad, X much larger than IX, XI strongly reduced and with small, dome-like apical nodule (Figs 2C, 3C, E, 5D, E). Mouthparts (clearly visible in both specimens): labrum (Figs 3A, C, 5A) transverse and with triangularly rounded anterior margin; mandibles (Figs 3A, C, 5B, C) falciform, symmetrical, each subtriangular with broad base and robust apical tooth (Fig. 3C), mesal margin with two smaller and acute subapical teeth (Fig. 3C); maxillary palpi (Figs 3A, C, 4E, 5C) composed of barely noticeable, minute palpomere 1 (Fig. 5B, C), strongly elongate, curved, and distally broadened palpomere 2, large,



**Figure 5.** *Pangusyndicus excavatus* Yin, Zhou & Cai gen. et sp. nov., female paratype (NIGP165286). **A**, head, in dorsal view; **B**, same, in ventral view; **C**, left maxillary palpus; **D**, left antenna, **E**, right antennomeres IX–XI; **F**, elytra; **G**, left protibia and protarsomeres; **H**, left hind leg. Abbreviations: a1–11, antennomeres I–XI; an, apical nodule; ce, compound eye; cl, clypeus; el, elytra; fr, frons; gen, gena; hr, hypostomal ridge; lb, labrum; md, mandible; mn, mentum; mp1–4, maxillary palpomeres I–IV; mtf, metafemur; mtt1–5, metatarsomeres I–V; mtti, metatibia; mtr, metatrochanter; nr, neck region; oc, ocular constriction; prti, protibia; prt1–5, protarsomeres I–V; ptp, post tentorial pit; smn, submentum; tm, temple; vt, vertex. Scale bars: A, B, D, F, G = 0.2 mm; C, E = 0.1 mm.

elongate and distally broadening palpomere 3, and strongly elongate and subconical palpomere 4 (Figs 3C, 5B, C). Submentum (Fig. 5B) triangularly transverse, with long and nearly straight hypostomal ridges (Fig. 5B) extending posteromesally to exceed elongate posterior tentorial pit (Fig. 5B), not connected; mentum sub-rectangular (Fig. 5B); prementum not visible due to taphonomic artefacts; with three labial palpomeres (Fig. 3C).

Prothorax strongly elongate and dorsoventrally flattened, lateral margins with thick bristles (Figs 2A,

3B, 4D–F). Pronotum (Figs 2A, 3B, 4F) broadest in front of middle, lacking lateral ante-basal pits, with thick sublateral ridges demarcating broad and deep mediobasal cavity (Figs 2A, 3B, 4E, F), posterolateral corners roundly angulate. Prothorax lacking marginal carinae or edges, with hypomera (Fig. 2B) strongly elongate; basisternal part of prosternum about as long as coxal part; intercoxal area concealed by contiguous procoxae (Figs 2B, 3A), indicative of lacking or narrowly carinate and very weakly elevated prosternal process.



Elytra (Figs 2A, 4D, E, 5F) oval, elongate and flattened, slightly concave at base; lacking striae; humeral calli present; base of each elytron putatively with one basal fovea (Fig. 2A) located in broad but shallow basal impression.

Details of mesoventrite (Fig. 2B) not visible except for generally subtrapezoidal shape with narrow anterior portion; intermesocoxal area poorly visible, mesoventral intercoxal process putatively lacking or narrow and weakly elevated. Metaventrite (Fig. 2B) strongly elongate, with rounded sides, anteriorly fused with mesoventrite and with moderately marked posterior margins of mesocoxal cavities, intermetacoxal process not visible but assumedly very short and not separating metacoxae.

Abdomen with six visible sternites (Fig. 2B), sternites III–V subequal in length, VI slightly longer than V, sternites VII and VIII distinctly longer, suture between sternites VII and VIII distinct.

Legs long and slender; pro- (Figs 2B, 3A) and mesocoxae strongly elongate, subconical, metacoxae (Fig. 2B) strongly transverse; all trochanters (Figs 2B, 3A, 4E, 5H) elongate, trochanterofemoral articulation oblique in relation to long axis of femur; all femora (Figs 3A, 4E, 5H) strongly elongate and slender, broadening at distal half; all tibiae (Fig. 5G, H) long and slender, protibiae (Figs 3A, D, 4D) slightly curved, with large apical projection (Fig. 3A, D) in males, projection lacking in females (Fig. 4D, indicated by arrow); tarsi (Fig. 1D) long and slender, all tarsomeres (Fig. 5G, H) elongate, with long tarsomeres I, II, V and short tarsomeres III–IV; two pretarsal claws subequal in size.

**Remarks.** With respect to the two previously described genera from Burmese amber, *Pangusyndicus* resembles *Scydmbisetia* in general body form; both genera have a distinctly elongate body, with a pronotum widest at the anterolateral portion, and modified male protibiae. However, *Pangusyndicus* lacks the presumable apomorphy of *Scydmbisetia* in which the head capsule has a pair of long vertexal sensilla chaetica at the posterolateral margins (Jałoszyński *et al.* 2016). Furthermore, the temples and sides of the prothorax of *Pangusyndicus* are covered with numerous thick bristles which are lacking in *Scydmbisetia*. The other genus known from Burmese amber, *Cenomaniola*, possess thick bristles at the sides of the head and prothorax, but the unique presence of an anteroventrally expanded mesoventral intercoxal process, combined with the strongly compact ‘*Euconnus*-like’ body form, distinctly raised head in front of the compound eyes that is strongly declined anteriorly and posteriorly, and pronotum broadest at the base indicate that *Cenomaniola* are more closely related to the extant Oriental *Elacatophora* Schaufuss and Nearctic *Lophoderus* Casey (Jałoszyński *et al.* 2017b), and a

close relationship between *Cenomaniola* and *Pangusyndicus* seems improbable. A third Mesozoic genus, *Hyperstenichnus*, was recently described (Jałoszyński *et al.* 2017a) based on a partially preserved specimen from Late Cretaceous Vendean amber. *Hyperstenichnus* are morphologically similar to the extant genus *Stenichnus* Thomson, and exhibit highly modified adhesive labial suckers, a structure likely to have functioned in chasing heavily sclerotized armoured mites. The affinities between *Hyperstenichnus* and *Stenichnus* indicate the former genus can be only remotely related to the ‘*Syndicus* group of genera’ to which *Pangusyndicus* belongs (see below).

*Pangusyndicus excavatus* Yin, Zhou & Cai sp. nov.  
(Figs 1–5)

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

**Etymology.** The specific epithet refers to the strongly excavated pronotum in the new species.

**Type material.** Holotype: ♂ (SNUC-Paleo-0013), lowermost Cenomanian, from an amber mine located near Noije Bum Village, Tanaing Town, Hukawng Valley, northern Myanmar; deposited in SNUC. Paratypes: one ♀ (NIGP165286) deposited in NIGP; eight unsexed individuals (SNUC-Paleo-0014–0015, 0022, 0028–0032) deposited in SNUC; same locality and horizon as the holotype.

**Type locality and horizon.** Hukawng Valley (26°21′33.41″N, 96°43′11.88″E), Kachin State, northern Myanmar; lowermost Cenomanian (98.79 ± 0.62 Ma), Late Cretaceous.

**Description.** Body (Figs 1A, C, D, 4A, B) slender, length 2.12 (female)–2.15 (male) mm (measurements were only taken from SNUC-Paleo-0013 and NIGP165286 which are preserved in an excellent condition), pigmentation dark reddish-brown as preserved.

Head elongate (Figs 3A, 5A), length from anterior clypeal margin to occipital constriction 0.43 (male)–0.45 (female) mm, width across compound eyes 0.33 (male)–0.35 (female) mm; temples slightly rounded and strongly convergent behind compound eyes; vertex wider than long, anteriorly confluent with strongly transverse frons (Figs 3A, 5A); clypeus strongly transverse and broadly rounded anteriorly; supra-antennal tubercles moderately raised (Figs 3A, 5A); compound eyes (Figs 3B, 4D, 5A) nearly circular, protruding from silhouette of head. Posterior portion of vertex and temples with dense, thick bristles (Figs 3A, 5A). Antennae (Figs 1D, 2C, 5D) long and slender, length 1.27 (male)–1.28 (female) mm, flagellum loosely assembled, antennomeres I–VI each elongate, VII–IX distinctly shorter, X

large, about 1.3 times as long as broad, XI (Figs 3E, 5E) strongly reduced, its base about half as broad as apex of X, with small dome-like nodule at apex; most flagellomeres with distinctly demarcated basal stalk and narrowing distally; all antennomeres covered with sparse, long, suberect and erect setae; lengths of antennomeres I–XI of holotype: 0.18 mm (I), 0.10 mm (II), 0.15 mm (III), 0.13 mm (IV), 0.13 mm (V), 0.11 mm (VI), 0.09 mm (VII), 0.10 mm (VIII), 0.11 mm (IX), 0.11 mm (X), 0.06 mm (XI); lengths of antennomeres I–XI of paratype: 0.16 mm (I), 0.10 mm (II), 0.14 mm (III), 0.13 mm (IV), 0.13 mm (V), 0.12 mm (VI), 0.10 mm (VII), 0.11 mm (VIII), 0.11 mm (IX), 0.11 mm (X), 0.07 mm (XI).

Pronotum (Figs 3B, 4F) about 1.5 times as long as broad, length along midline 0.52 (female)–0.55 (male) mm, maximum width 0.38 (male)–0.40 (female) mm, width at base 0.32 mm in male; broadest near anterior third; anterior margin lightly truncate, laterally confluent with lateral margins, sides rounded in anterior half and distinctly narrowing posteriorly, posterolateral margins nearly parallel; posterolateral corners slightly obtuse angled and blunt; posterior margin nearly straight; sublateral ridges distinct, and thick, demarcating large, deep mediobasal cavity (Figs 3B, 4F), with many thick bristles pointed medially; disc, sides and part of prothoracic hypomera with thick, dense bristles.

Elytra (Figs 2A, 4E, 5F) elongate oval, length along suture 1.14 (female)–1.17 (male) mm, maximum width 0.71 mm in male, elytral length/elytral width = 1.65 (elytral index) in male; base slightly concave; each elytron putatively with one basal fovea (Fig. 2A); entire elytral surface covered with fine punctures not arranged in rows and dense, long, suberect to erect setae and pubescence, also not arranged in rows.

Legs (Figs 1A, 1C, D, 2A, B) slender, covered with short suberect setae, subapical area of protibiae with short bristles (Fig. 3A); male protibia with large, blade-like apical projection (Fig. 3D).

**Remarks.** One impressive feature of *Pangusyndicus* is the distinct apical projection on the protibia, present in the holotype, while this structure is lacking in the female paratype (NIGP165286). Modified protibiae are not common among modern glandulariine taxa, where they are present only in some species of the genus *Euconnus* Thomson as a male sexual character, e.g. the European *Euconnus* (*Tetramelus*) *oblongus* Sturm, African *E.* (*Paratetramelus*) *kenyae* Franz, and Madagascan *E.* (*Glabriconnus*) *banari* Jałoszyński (Jałoszyński 2015b, 2016c). Thus, we treat the fossil specimen with modified tibiae as a male. Based on the similar size and proportions of the body parts, and the shared similar structure and size of the antennomeres,

we treat SNUC-Paleo-0013 and NIGP165286 as conspecific specimens of the opposite sex. As for the other eight unsexed paratypes, the protibiae cannot be clearly seen, but they share a similar size and proportions of the body and antennomeres, and the presence of a cavity on the posterior half of the pronotum. Thus, we treat these individuals as conspecific with SNUC-Paleo-0013 and NIGP165286.

### Systematic position of *Pangusyndicus*

*Pangusyndicus* is the fifth Mesozoic genus of the Scydmaeninae that can be definitely placed in the tribe Glandulariini. This placement is evidenced by the subconical, elongate and pointed maxillary palpomere 4 being much smaller than the broadened and elongate palpomere 3 (Figs 3C, 5C), a probable autapomorphy of the tribe. Other typical characters indicative of a glandulariine, discussed in Jałoszyński *et al.* (2016, 2017b), are also found in *Pangusyndicus*: (1) the ant-like body form (Figs 1, 4), i.e. the body deeply constricted between head and pronotum and between pronotum and elytra (shared with Mastigitae, Scydmaenini, Chevrolatiini and Leptoscydmini, all of which have broadly separated metacoxae), and (2) the antennal scape lacking an apical notch (Figs 2C, 5D) (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).

The extant genera of Glandulariini are divided into two presumably ‘natural’ groups based on the presence or absence of lateral sulci on the submentum (Jałoszyński 2015a, as ‘lateral sutures’). This character was not observable in the previously described Mesozoic taxa of the tribe, i.e. *Scydmobisetia*, *Cenomaniola* and *Hyperstenichnus* (Jałoszyński *et al.* 2016, 2017a), making further assessments of the relationships of these extinct taxa within Glandulariini difficult. *Pangusyndicus* represents the first extinct glandulariine genus that allows for a clear observation of the ventral cephalic structures. Under fluorescence microscopy, it is clear that the pair of lateral sulci on the submentum are lacking in *Pangusyndicus* (Fig. 5B). Among the group where species lack these sulci (examples of the extant glandulariine taxa without or with the lateral submental sulci are illustrated in Supplemental Fig. 2B, D, F, I), *Pangusyndicus* shows affinities to the extant Australo-Oriental genus *Syndicus* in possessing the strongly reduced antennomere XI. The latter genus is the only member of the Glandulariini (also among all scydmaenines) that possesses a reduced antennomere



XI. *Syndicus* includes 48 extant species classified in two subgenera (Yin & Zhou 2016). The nominotypical subgenus is characterized by the base of antennomere XI being nearly as broad as the apex of antennomere X, whereas the subgenus *Semisyndicus* Jąłoszyński has the base of antennomere XI being much narrower than the apex of antennomere X (Jąłoszyński 2004) (habitus and apical antennal structures of *Syndicus* and two morphologically similar genera, *Loeblites* Franz and *Horaemorphus* Schaufuss, are shown in Supplemental Fig. 1). *Pangusyndicus* further shares with *Syndicus* the strongly convex prothorax and elytra; frons well demarcated from the clypeus by a frontoclypeal groove (examples of extant glandulariine taxa with or without this groove are illustrated in Supplemental Fig. 2A, C, E, G, H); similar shape of the antennomeres; presence of sparse, long, erect setae on the antennae; thick bristles on the temples, genae and sides of the pronotum; and two subapical teeth on each mandible. The form of antennomeres XI in *Pangusyndicus* seems to be intermediary between those of *Syndicus sensu stricto* and *Semisyndicus*, as they are longer (in relation to antennomere X) than in most species of *Syndicus sensu stricto*, but distinctly smaller than those found among *Semisyndicus*, while the length of antennomere XI in *Pangusyndicus* is greater than that in many species of *Syndicus sensu stricto*. The presence of a dome-like apical nodule at the apex of antennomere XI in *Pangusyndicus* is shared with many species of *Syndicus sensu stricto*, among which it is a common structure but normally difficult to observe because of the dense setae. *Pangusyndicus* distinctly differs from *Syndicus* in the slightly elongate head (i.e. long temples and extended clypeus), more extended maxillary palpi and tarsomeres, much less distinctly clavate femora, modified male protibiae and, most importantly, lack of dorsal grooves on the femora. In contrast, all *Syndicus* species have a transverse head, the maxillary palpi are similarly elongate but much less so than in *Pangusyndicus*, the tarsomeres are more compact and relatively shorter, the femora are strongly and abruptly clavate at the distal half, the protibiae are simple in the male, and all femora have a variously developed groove on the dorsal surface.

To test the position of *Pangusyndicus* within the Glandulariini, we evaluated the placement of *Pangusyndicus* in a phylogenetic context. Our results support a close relationship among *Pangusyndicus*, *Syndicus* and *Loeblites*. A polytomy of *Pangusyndicus*, *Syndicus* and *Loeblites*, together sister to *Horaemorphus*, is recovered by parsimonious and maximum likelihood analyses (Fig. 6), or *Pangusyndicus* as a sister group to *Syndicus* + *Loeblites* is recovered by

Bayesian inference (Supplemental Fig. 3). *Syndicus* and *Loeblites* form a small group within the modern Glandulariini, linked by the unique presence of a dorsal femoral groove in all species, but they are distinctly differed in the well-separated antennomeres XI and presence of a single subapical tooth in *Loeblites*. The majority-rule consensus tree of Bayesian analysis (Supplemental Fig. 3) indicates that the lack of femoral grooves and the reduced apical antennomeres in *Pangusyndicus* may represent ancestral states of this group, with the femoral grooves subsequently occurring in *Syndicus* and *Loeblites*, while *Syndicus* retained the reduced antennomeres XI, and this character may later have been reversed in *Loeblites*. Although a more precise relationship of *Pangusyndicus* within the tribe requires further phylogenetic analysis based on a more extensive sampling of taxa, we argue that *Pangusyndicus* is likely a stem-group member of the present-day ‘*Syndicus* group of genera’ (comprising *Syndicus* and *Loeblites*) as our *a priori* judgment indicated.

## Discussion

The discovery of *Pangusyndicus* in Cenomanian Burmese amber provides further evidence that the tribe had already diversified by this time. *Pangusyndicus* shows several strikingly enigmatic morphological traits previously unknown among all living and extinct glandulariines. The most remarkable structure of *Pangusyndicus* is the presence of a large cavity on the mediobasal surface of the pronotal disc, which is demarcated by a pair of thick sublateral ridges. Interpretation of such a character in small fossil beetles requires particular caution, but it seems clear that this is not the result of deformation during preservation and is instead an actual structural feature of the beetle. In particular, the areas around the pronotum show no sign of obvious distortion and the cavities in all 10 specimens are identical and clearly observable.

Such a large pronotal cavity is an unusual structure unknown in any other scydmaenines. It seems improbable that this cavity would not serve a function, especially given that it is surrounded by many thick setae directed towards its middle. The most plausible function of this cavity, if any, seems to be glandular. Pronotal glandular structures are rare among living scydmaenines. Similar but much smaller pronotal glands with cuticular openings are known only in a few extant genera, e.g. in *Trurlia* Jąłoszyński and *Trichokrater* Jąłoszyński of the Cephennini, and *Heteroconnus* Franz (subgenus of *Euconnus* Thomson) of the Glandulariini (Jąłoszyński

2011, 2015b). The pronota of *Trurlia* and *Trichokrater* bear a pair of mediolateral foveae, with their openings surrounded by a semicircular fringe of setae leading to long subcuticular pockets (Jałoszyński 2011, fig. 9D). Although histological examinations were not possible for dry-mounted specimens, a glandular function was suggested based on the general structure of these foveae. Many species of *Heteroconnus* similarly have anteromedian impressions on the pronotal disc which are covered by a group of fine setae (Jałoszyński 2015b, figs 46, 47); however, these pronotal structures are probably restricted only to males. The presence of large cavities on the head were reported in two groups of the tribe Scydmaenini. *Scydmaenus (Cholerus) hellwigii* (Herbst) exhibits a large vertexal cavity on the head dorsum; both scanning electron microscope and transmission electron microscopy observations of this structure revealed voluminous glands near the occipital constriction and their secretion accumulates in the cavity (Jałoszyński *et al.* 2012). The cryptic, wingless and blind genus *Liliputella* Jałoszyński, comprising a single species from Papua New Guinea, bears a large transverse and deep cavity between the gular plate and mouthparts on the ventral surface of the head. Although the function of this structure remains uncertain, the cavity is again surrounded by a fringe of dense setae (Jałoszyński 2016b, fig. 3), indicating a probable glandular structure. Within Staphylinidae, glandular structures are commonly found on the abdomen and thorax of various free-living groups. These glands often serve a chemical defensive purpose against offending agents (various staphylinid subfamilies), or sometimes increase locomotion for escaping potential predators (Steninae) (Huth & Dettner 1990; Dettner & Reissenweber 1991; Dettner 1993; Caron *et al.* 2008; Schierling & Dettner 2013). In the case of *Philonthus varians* (Paykull) (Staphylininae: Staphylinini), the beetle has a pair of prototergal glands behind the first spiracle, the longitudinal openings of the glands are covered with a grille of long setae, and these glands may help to lower the risk of pathogenic infection (Quenedey *et al.* 2002). The pronotal cavity surrounded by many thick setae in *Pangusyndicus* strongly suggests a glandular structure, which is largely analogous to the functional glands among many of the aforementioned scydmaenine and staphylinid groups. Our discovery thus sets an earliest date for a probable highly modified pronotal glandular structure in fossil rove beetles in the mid-Cretaceous.

It is noteworthy that several recently discovered Cretaceous scydmaenines have much more slender legs than their extant relatives. These include *Clidicostigus* Jałoszyński, Brunke & Bai and *Cascomastigus* Yin & Cai of the Mastigini, *Cretoleptochromus* Cai & Huang

(probably related to the Clidicini), and the presently described *Pangusyndicus* of the tribe Glandulariini (Cai & Huang 2016; Jałoszyński *et al.* 2017c; Yin *et al.* 2017b). Recent scydmaenines with distinctly elongate legs belong to the tribe Mastigini; in contrast to most known scydmaenines with a more compact body plan and much shorter legs that are adaptive for living in cryptic environments (i.e. leaf litter, moss, decomposing log, under bark, *etc.*), many mastigines are diurnal predators actively patrolling in open environments (Jałoszyński *et al.* 2015). The long legs are apparently more suitable for fast locomotion, and additional morphological adaptations for this mode of life include anteriorly placed and large compound eyes, long antennae and palpi for prey detection, and specialized mandibles for prey capture (Jałoszyński *et al.* 2012). Thus, it is possible that there were shifts in feeding habits and habitat preferences during the evolutionary history of these groups, especially for glandulariines and clidicines, from open to more cryptic environments. Consequently, the strongly extended legs and mouthparts so characteristic among Mesozoic scydmaenines might have become reduced in length over time, giving rise to those forms (those with much shorter mouthparts and legs that inhabit cryptic environments) so familiar among the modern fauna.

## Conclusions

*Pangusyndicus* gen. nov. is the first extinct scydmaenine of the tribe Glandulariini with critical ventral cephalic structures observable, allowing us to establish its placement in one of the two presumably natural groups of the tribe where members lack submental lateral sulci. The new genus shows affinities to the extant glandulariine genus *Syndicus* by sharing a strongly reduced antennomere XI, and this relationship is preliminarily supported by phylogenetic analyses based on 135 morphological characters. *Pangusyndicus excavatus* strikingly possesses a large dorsal cavity on the pronotal disc, unknown among all extant and extinct scydmaenines, and we interpret this as the earliest evidence of a glandular structure among the family Staphylinidae. Some recently described mid-Cretaceous scydmaenines, including *Pangusyndicus*, have notably much longer legs than their extant relatives, indicating shifts of feeding habitat preferences may have occurred during the evolutionary history of these lineages.

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## Supplemental material

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