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# A new stem bythinine in Cretaceous Burmese amber and early evolution of specialized predatory behaviour in pselaphine rove beetles (Coleoptera: Staphylinidae)

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Comprising more than 10,000 valid species, the staphylinid subfamily Pselaphinae is a major element of epigean habitats, and among the most diverse groups of rove beetles. Pselaphinae is split basally into two principal clades: the small supertribe Faronitae, and its sister group, the hyper-diverse ‘higher Pselaphinae’ containing the remaining five supertribes. Deducing the origins and divergence times of major higher Pselaphinae clades requires direct fossil evidence. Here we describe a new pselaphine rove beetle, *Cretobythus excavatus* Yin, Parker & Cai gen. et sp. nov., based on a well-preserved individual embedded in mid-Cretaceous amber from Myanmar (Cenomanian, *c*. 99 Ma). *Cretobythus* does not obviously belong to any Recent tribe, but Bayesian phylogenetic placement using morphological characters supports a position within the stem-group of the tribe Bythinini, sister to *Boreotethys* Parker, a genus also recently described from Burmese amber. Together, *Cretobythus* + *Boreotethys* comprise the sister group of modern Bythinini. Despite some external similarities to Recent Bythinini, *Cretobythus* exhibits several plesiomorphic traits, including a generally flattened body plan, and metacoxae that are positioned close to the ventral midline. The resemblance in form of the enlarged maxillary palpi of *Cretobythus* to extant bythinines implies a similar function in prey capture, indicating that the unusual employment of the maxillary palps to trap moving prey in Bythinini had probably evolved by the mid-Cretaceous, at the latest.

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**Keywords**: Pselaphinae; Bythinini; new taxon; feeding behaviour; Mesozoic

## Introduction

With over 62,800 species classified in 32 extant subfamilies, the mega-diverse rove beetles (Staphylinidae) are the largest family within the animal kingdom. The subfamily Pselaphinae, or ant-loving beetles, comprises the second largest group of staphylinids (after Aleocharinae), containing 9964 extant and 42 extinct species classified into 1270 genera (of which 21 are extinct) and 40 tribes (of which one is extinct) (A. F. Newton pers. comm.). Pselaphines were maintained as a separate family for nearly 200 years, and only recently, based on a broad morphology-based phylogenetic analysis, were they placed in the ‘omaliine group’ of subfamilies in the Staphylinidae, as a sister taxon to Protopselaphinae (Lawrence & Newton 1982; Newton & Thayer 1992, 1995). The history of the internal classification of Pselaphinae was reviewed by Newton & Chandler (1989), and the current supertribal classification within the subfamily was largely based on the work by Newton & Thayer (1995) and Chandler (2001a). The monophyly of Pselaphinae as a whole is strongly supported by many synapomorphies, most notably the presence of well-developed foveae on all major body segments and a relatively inflexible abdomen.

Six supertribes are currently recognized within the Pselaphinae: Faronitae, Euplectitae, Goniaceritae, Batrisitae, Pselaphitae and Clavigeritae (Chandler 2001a). The Faronitae, exhibiting the maximum number of foveae among all pselaphines and an elongate and flattened, staphylinid-like body form, is generally recognized as the sister group to the remaining Pselaphinae, a scenario supported by both morphological and molecular phylogenies (Newton & Thayer 1995; Parker 2016). The remaining five supertribes, termed the ‘higher Pselaphinae’ (Parker 2016), exhibit a complex and mosaic pattern of morphological evolution, and their systematic relationships are

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incompletely worked out. A group comprising Pselaphitae + Clavigeritae (the so-called ‘Macroscelia’ on account of their shared possession of elongate metacoxae) was established as monophyletic by Newton & Thayer (1995). Whereas Pselaphitae has a cosmopolitan distribution, and comprises mostly leaf litter inhabitants plus many specialized myrmecophiles or termitophiles scattered in a variety of tribes, Clavigeritae is composed exclusively of obligate myrmecophiles and occurs in all zoogeographical regions except New Zealand and southern South America. However, the relationship between Pselaphitae and Clavigeritae remains unclear, and was further obscured when Besuchet (1991) established his new tribe Colilodionini and placed it within the Clavigeritae. Eight species of Colilodionini are known from tropical areas of Asia, all possessing a few characters typical of Pselaphitae, e.g. third tarsomeres longer than second and free seventh abdominal sternite (morphologically sternite IX) in males (Löbl 1994; Yin & Cuccodoro 2016). Additionally, Parker (2016) demonstrated using molecular evidence that Pselaphitae may be polyphyletic, with the tribes Pselaphini and Arhytodini widely separated from the remainder of the supertribe in the phylogeny. Euplectitae and Goniaceritae are problematic in terms of their phylogenetic placements, since both groups lack unambiguous autapomorphies and are either paraphyletic or (more likely) polyphyletic. Recent cladistic analysis showed that Euplectitae is paraphyletic with regard to Batrisitae and, independently, paraphyletic also to two groups of Goniaceritae (Parker 2016), although taxon and gene sampling were limited. The Batrisitae is probably a monophyletic group based on their antennal and aedeagal features (Chandler 2001a). A recent study discovered a probable autapomorphy of the group (Kurbatov 2007), but the relationship of Batrisitae to Euplectitae (or to Goniaceritae) remains elusive.

Fossil evidence is crucial for understanding the evolutionary histories and divergence times of the major pselaphine clades. However, unsurprisingly for a poorly studied taxon, the fossil record of Pselaphinae is poorly documented in the literature. The most extensive work is that of Schaufuss (1890a) who described a handful of species from Eocene Baltic amber, but like the other fossil taxa he described (e.g. Scydmaeninae; Schaufuss 1890b), all species lack a detailed description including diagnostic characters that permit their accurate generic or even tribal placement. Since all type specimens of Schaufuss’s fossil species are impossible to locate at present (presumed lost or destroyed), the taxonomic placements of these taxa within Pselaphinae should be treated as tentative. An undescribed specimen from the early Cretaceous Koonwarra fossil bed (Aptian), Australia, was interpreted by Jell & Duncan (1986) and Jell (2006) as the oldest known Pselaphinae, but the placement of this fossil in Pselaphinae was recently challenged by Parker (2016) who reinterpreted the fossil as a compression of an unknown beetle family with several characters that are inconsistent with the Pselaphinae diagnosis.

Fossil Pselaphinae with adequate descriptions have been provided only by recent authors. Parker & Grimaldi (2014) reported a stem-group member of Clavigeritae, *Protoclaviger trichodens* Parker & Grimaldi, in early Eocene (Ypresian) Cambay amber from India. *Protoclaviger* is not only the earliest known obligate myrmecophile, but also provides a key window into the evolutionary development of Clavigeritae. The beetle exhibits transitional morphology, with several ancestral characters not known in modern clavigerines, i.e. relatively large maxillary palpi, each antenna with eight antennomeres, and visible abdominal tergites 1–3 (morphologically IV–VI) not fused. The fossil nevertheless possesses several clavigerite autapomorphies, raising doubts about Besuchet’s aforementioned interpretation of *Colilodion* as representing a transitional condition between Pselaphitae and other Clavigeritae. Peris *et al.* (2014), in their study of the staphylinid fauna from Early Cretaceous Spanish amber, described two new genera: *Cretasonoma* Peris, Chatzimanolis & Delclòs and *Penarhytus* Peris, Chatzimanolis & Delclòs. The former genus was placed in the supertribe Faronitae, and the latter in Pselaphitae: Arhytodini. Parker (2016) reviewed Cretaceous Pselaphinae, arguing that *Cretasonoma* may not necessarily belong to the crown-group Faronitae, and excluding *Penarhytus* from the higher Pselaphinae. In the same paper, Parker also described two new genera in mid-Cretaceous Burmese amber, *Protrichonyx* Parker and *Boreotethys* Parker. *Protrichonyx* shows affinities to Euplectitae: Trichonychini, but was placed as *incertae sedis* within the higher Pselaphinae because neither Euplectitae nor Trichonychini are demonstrably monophyletic. *Boreotethys* generally fits well in the tribe Bythinini, but possesses a few primitive character states not found in modern bythinines, especially in the length ratio of tarsomeres 2 and 3. In *Boreotethys*, tarsomere 2 is much shorter than tarsomere 3, whereas modern Bythinini exhibit the converse condition of this character state.

Our overall impression is that the pselaphine fauna embedded in Cretaceous Burmese amber is very diverse, and future studies of this material will likely yield key insights into the early evolution of this hyper-diverse group of beetles. Here, we report a new genus of the supertribe Goniaceritae: Bythinini based on an exquisitely preserved individual in Burmese amber, and evaluate its systematic position in a phylogenetic framework. The new discovery sheds light on the palaeodiversity and palaeobiology of the higher Pselaphinae, especially of the Bythinini, during the Cretaceous.

## Material and methods

### Repository, horizon, and specimen handling and imaging

The amber specimen described in this paper is housed in the Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, Nanjing, Jiangsu Province, China. The single specimen was 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 currently considered earliest Cenomanian in age based on U-Pb dating of zircons from the volcaniclastic matrix of the amber (Grimaldi *et al.* 2002; Cruickshank & Ko 2003; Shi *et al.* 2012). The amber piece was prepared, first being cut by a handheld engraving tool with a diamond blade, and polished using sandpapers of different grain sizes and rare earth polishing powder. The beetle specimen is embedded within a polished block of amber measuring approximately 3.5 × 3.5 mm. Habitus images were taken using a Canon 5D Mark III camera attached to an Olympus Plan C 10 × Objective Lens and a Canon MT-24EX Macro Twin Lite Flash. Images of morphological details were made using a Canon G9 camera mounted on an Olympus CX31 microscope. Photomicrographs with a green background were taken using widefield fluorescence microscopy with an Olympus BX51 light microscope. Use of a fluorescent light source was successful in imaging particularly dark regions and fine details of specimens that standard lighting failed to illuminate adequately. Zerene Stacker (version 1.04) was used for image stacking. All images were modified and arranged in Adobe Photoshop CS5 Extended.

### Measurements of the beetle and morphological description

The following abbreviations are employed in the description of the new species: **AL**, length of the dorsally visible part of the abdomen (posterior to elytra) along the midline; **AnL**, length of the antenna; **AW**, maximum width of the abdomen; **EL**, length of the elytra along the suture; **EW**, maximum width of the elytra; **HL**, length of the head from the anterior clypeal margin to the occipital constriction; **HW**, width of the head across eyes; **PL**, length of the pronotum along the midline; **PW**, maximum width of the pronotum. Length of the body is a sum of HL + PL + EL + AL. The terminology of the morphological terms follows Chandler (2001a), except that we use ‘ventrite’ instead of ‘sternite’ when describing meso- and metathoracic structures (Beutel & Lawrence 2005).

### Phylogenetic analysis

To resolve the phylogenetic position of the new Cretaceous genus within Pselaphinae, we performed a phylogenetic analysis, scoring character states for the new genus that were used previously by Parker (2016) for placement of Cretaceous pselaphines. This data set contains 41 ingroup Pselaphinae representing all six supertribes (including the new fossil) and a broad range of tribes. Fifteen outgroup taxa are also included from the four ‘subfamily groups’ of Staphylinidae (Lawrence & Newton 1982), as well as the early diverging polyphagan *Scirtes hemisphericus* (Scirtidae) as a more distant outgroup. A total of 58 non-additive and unordered adult morphological characters were included. These comprised the 57 characters used by Parker (2016) and an additional character (58: the relative lengths of tarsomeres 2 and 3). We augmented Parker’s matrix with the new data. Inapplicable character states are indicated by dashes (–) and missing data indicated by question marks (?). The morphological data matrix, and the characters and character states, are listed in Supplemental File S1. Additionally, a molecular matrix from Parker (2016) containing a short but informative region of 28s ribosomal RNA (28s rRNA) was used. We performed partitioned Bayesian analysis on the combined morphology + 28s rRNA matrix with MrBayes 3.2.6 (Ronquist *et al.* 2012), employing the same sequence alignment and substitution model settings as Parker (2016): the GTR + I + G model was specified for the molecular data, and the Mkv + G model (Lewis 2001) for the morphological data. Two Markov chain Monte Carlo (MCMC) searches of four chains each were run for 10 million generations, at which point convergence was reached, as assessed by the standard deviation of split frequencies dropping below 0.01, and estimated sample sizes > 200 in Tracer (Rambaut *et al.* 2013). The first 25% of trees were treated as burn-in. The consensus tree of the two MCMC runs was rooted with *Scirtes.* The MrBayes Nexus file used for this analysis is presented in Supplemental File S2. In addition, a separate analysis was performed on the morphological data alone. Both analyses were run on the Cipres Science Gateway (Miller *et al.* 2010).

## Systematic palaeontology

Order **Coleoptera** Linnaeus, 1758
Family **Staphylinidae** Latreille, 1802
Subfamily **Pselaphinae** Latreille, 1802
Supertribe **Goniaceritae** Reitter, 1882
Tribe **Bythinini** Raffray, 1890
***Cretobythus*** Yin, Parker & Cai gen. nov.

**Type species.** *Cretobythus excavatus* Yin, Parker & Cai sp. nov.

**Diagnosis.** Antennomere 1 (scape) as long as antennomeres 3–5 combined; maxillary palpus longer than head, greater than half antennal length, with basally pedunculate palpomere 2, transversely triangular palpomere 2, and enlarged, oval palpomere 4 which bears a distinct apical palpal cone; mesotrochanter short; metacoxae close to each other; tarsomeres 2 as long as to slightly longer than tarsomeres 3; each leg with a large and a secondary strongly reduced tarsal claw.

**Derivation of name.** A combination of *creto*-, in reference to the Cretaceous, and '*bythus*', a common stem used in many modern bythinine genera. Gender masculine.

**Occurrence.** Upper Cretaceous, lowermost Cenomanian, Myanmar.

**Description.** Body relatively flattened dorsoventrally and slightly broadened posteriorly, with elytra and abdomen distinctly wider than head and pronotum. Head nearly triangular (Figs 1B, 2C), slightly transverse; vertexal foveae obscured or absent, with short mediobasal carina; postocular margins as long as length of eyes, roundly narrowing to occipital constriction (Fig 2B). Head anterior to eyes narrowing, with frontolateral margins gently sloping to clypeus; lacking frontal rostrum; antennal bases widely separated by flat to weakly impressed interantennal region. Head venter difficult to observe. Each antenna with 11 antennomeres (Fig. 2D); antennomere 1 elongate, equal in length to antennomeres 3–5 combined, antennomere 2 (pedicel) relatively enlarged, about half length of antennomere 1, antennomeres 3–8 each transverse, roughly of same width, antennal club (Fig. 1D) loosely formed by enlarged antennomeres 9–11, with 11 more than 2.5 times as long as 10. Posteroantennal notch present (Fig. 2C). Maxillary palpus enlarged (Fig. 1E), longer than head length, also longer than half antennal length, with small palpomere 1, elongate, basally pedunculate palpomere 2, small, rounded-triangular palpomere 3, and large, roughly ovoidal palpomere 4 which bears one distinct palpal cone at apex. Pronotum (Fig. 3C) narrower than head, slightly wider than long, widest at anterior third, anterolateral margins rounded, short mediobasal carina present, foveae obscured. Elytra slightly transverse, narrower and shorter than abdomen, with narrow base and rounded lateral margins; discal stria (Fig. 2A) extending from base to at least one-third elytral length. Elytra foveae not clearly observable, but possibly with two basal foveae; sutural stria present. Hind wing fully developed (Figs 1B, 2E). Prosternum with lateral procoxal foveae putatively present. Meso- and metaventrite laterally margined (Fig. 1A), other ventral thoracic structures not decipherable. Abdomen (Figs 1A, B, 2A, B) slightly transverse, widest at lateral margins of first visible tergite; five tergites visible, tergites 1–3 subequal in length, margins of tergites 1 and 2 narrowing to their bases, margins of tergites 3–5 narrowing to their apices; broad paratergites present on tergites 1–3, smaller paratergites present on tergite 4. Abdomen ventrally with six sternites (morphologically III–VIII) visible; posterior margin of sternite 1 entire (Fig 2B), uninterrupted by metacoxae; sternites 2–5 subequal in length; visible (apical) region of sternite 6 much shorter, with rounded apex. Procoxae and mesocoxae contiguous, metacoxae (Fig. 1F) narrowly separated; short mesotrochanters with apex of mesocoxa nearly touching base of mesofemur; metatrochanters weakly projecting posteriorly; tarsi (Fig. 1G, H) three-segmented; tarsomere 1 short, tarsomere 2 five times as long as tarsomere 1; tarsomere 3 slightly shorter than tarsomere 2; two asymmetric tarsal claws present.

### *Cretobythus excavatus* Yin, Parker & Cai sp. nov.
(Figs 1, 2)

**Diagnosis.** As for the genus.

**Derivation of name.** The specific epithet refers to the presence of a vertexal cavity in this species.

**Material.** Holotype, NIGP164515, a completely preserved adult (Fig. 1C), presumably a male, housed in the Nanjing Institute of Geology and Palaeontology, CAS, Nanjing, Jiangsu Province, China.

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

**Description.** Body (Fig. 1A, B) length 1.29 mm, slightly shiny, light reddish brown, appendages lighter in colour; most body regions covered with moderate density of short, thin, translucent setae. Head (Fig. 2C) slightly transverse, HL 0.26 mm, HW 0.30 mm; vertex with one large cavity (this cavity is presumably to be genuine rather than compression of the fossil due to its symmetrical shape), posterolateral margin of cavity with row of long setae pointed towards middle; postocular margins with moderate density of long, thin, sub-erect setae; eyes prominent, each composed of about 30 facets. Antenna (Figs 1D, 2D) 0.56 mm in length, densely setose; antennomere 1 elongate-cylindrical, slightly curved mesally at apical half, equal in length to antennomeres 3–5 combined, antennomere 2 roundly cylindrical, slightly elongate, 1.1 times longer than wide, equal in width to antennomere 1 but half the length, antennomeres 3 and 4 smaller than 2, of similar width, 4 slightly larger than 3, antennomere 5 larger than 4 and 6, antennomere 7 similar to 5 in size, antennomeres 8–10 strongly transverse, 8 small, dome shaped, 9–10 successively wider and larger, 11 largest, robust, 1.3 times longer than wide, with rounded apex. Entire length of maxillary palpus (Fig. 1E) 0.32 mm, length of palpomeres 1–4: 1 = 0.02 mm, 2 = 0.10 mm, 3 = 0.03 mm, 4 = 0.17 mm. Pronotum (Fig. 2C) about as long as wide, PL 0.24 mm, PW 0.26 mm, with distal and lateral cavities separated by lateral ridges, with sparse,

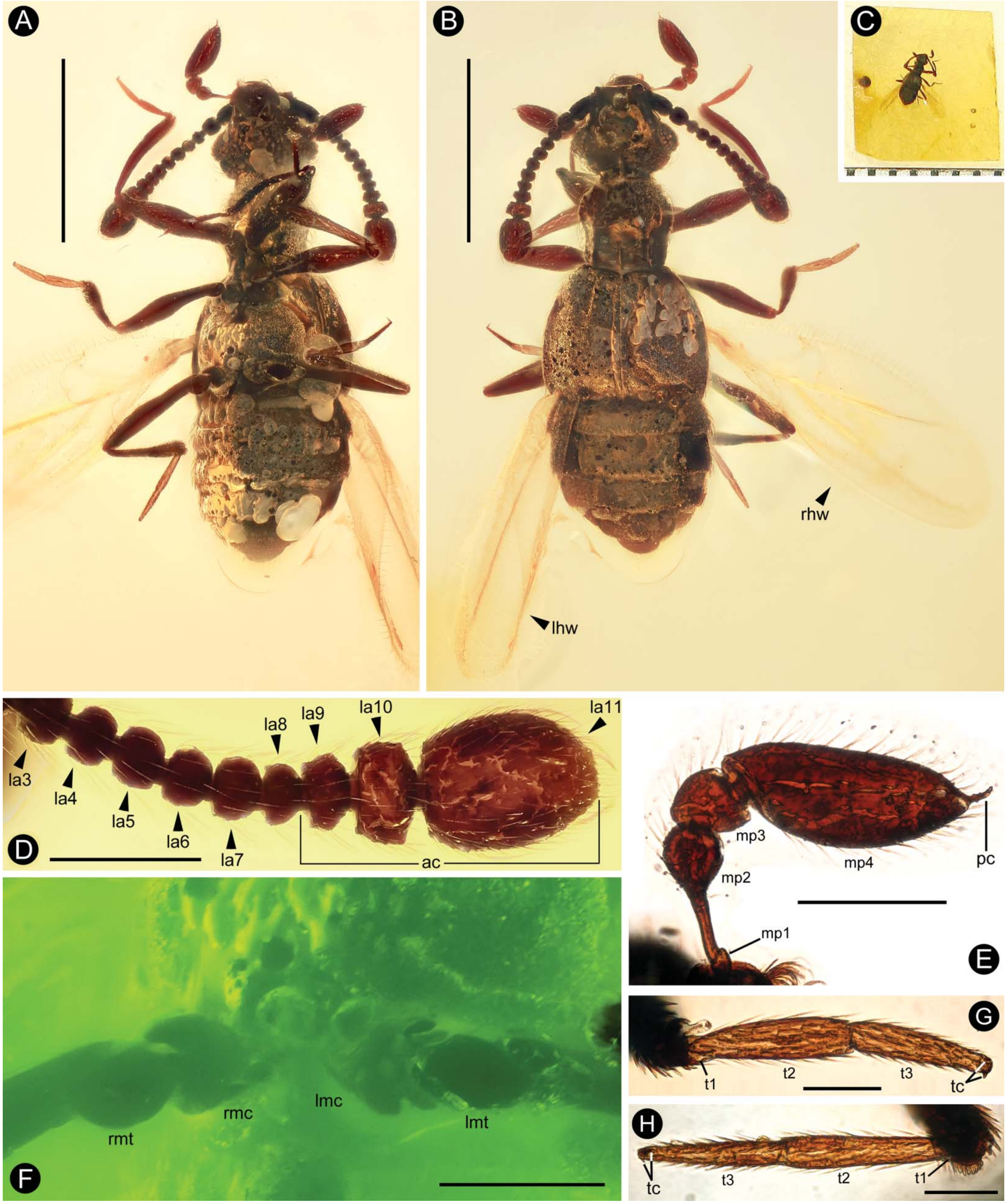

**Figure 1.** *Cretobythus excavatus* Yin, Parker & Cai gen. et sp. nov., holotype, NIGP164515. **A,** ventral habitus; **B,** dorsal habitus; **C,** complete view of the amber piece with scale (each grid represents 0.5 mm); **D,** left antennomeres 3–11, showing antennal club; **E,** right maxillary palpus, in ventral view; **F,** metacoxae and metatrochanters; **G,** right mesotarsomeres and tarsal claws; **H,** right metatarsomeres and tarsal claws. Abbreviations: ac, antennal club; la3–11, left antennomeres 3–11; lhw, left hind wing; lmc, left metacoxa; lmt, left metatrochanter; mp1–4, maxillary palpomeres 1–4; pc, palpal cone; rhw, right hind wing; rmc, right metacoxa; rmt, right metatrochanter; t1–3, tarsomeres 1–3; tc, tarsal claw. Scale bars: A, B = 0.5 mm; D, E, F = 0.3 mm, G, H = 0.05 mm.

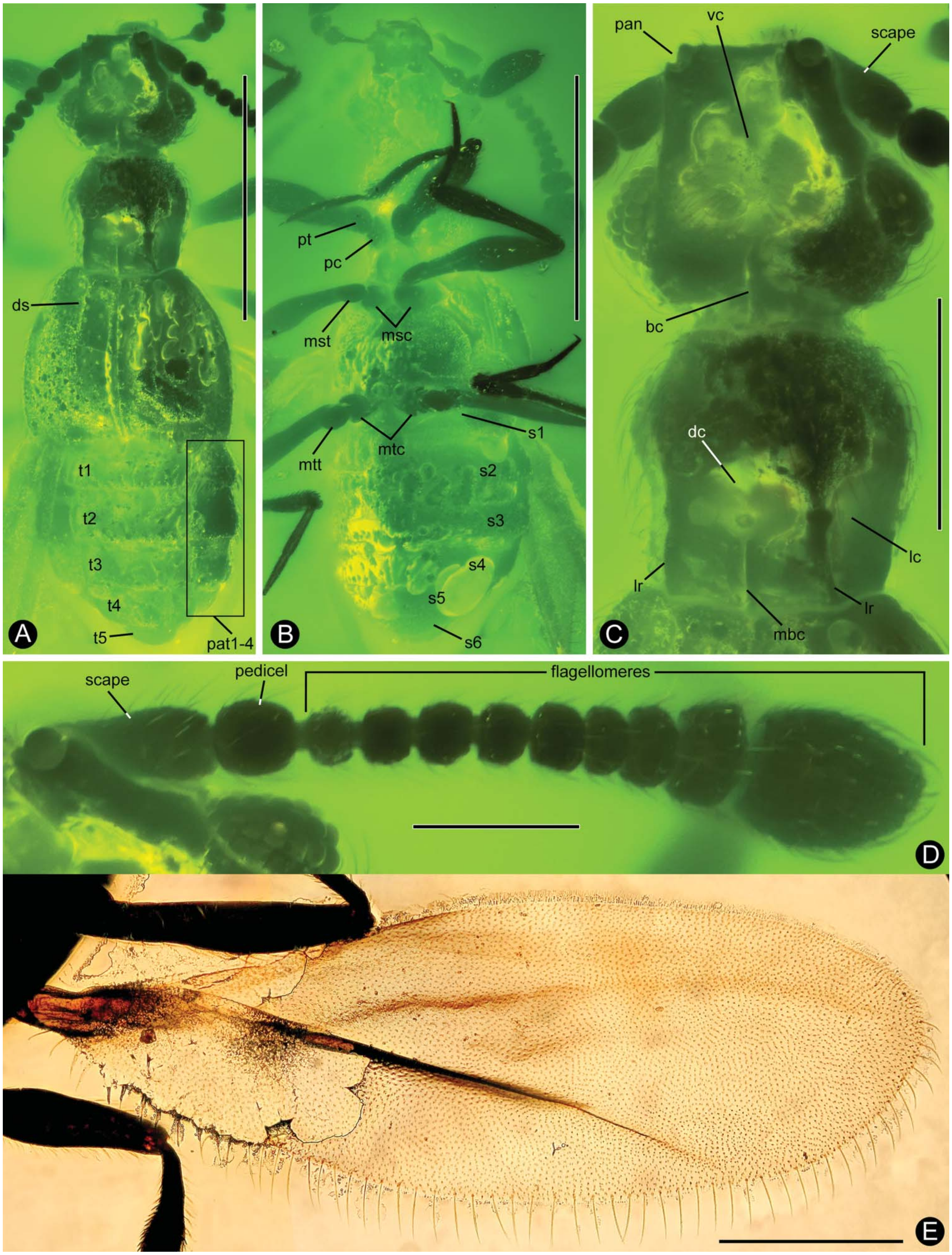

**Figure 2.** Morphological details of *Cretobythus excavatus* Yin, Parker & Cai gen. et sp. nov. (A–D, under green fluorescence; E, under transmitted white light). **A,** dorsal view of the body; **B,** ventral view of the body; **C,** head and pronotum, enlarged; **D,** right antenna; **E,** right hind wing. Abbreviations: bc, basal carina; dc, discal cavity; ds, discal stria; lc, lateral cavity; lr, lateral ridge; mbc, mediobasal carina; msc, mesocoxa; mst, mesotrochanter; mtc, metacoxa; mtt, metatrochanter; t1–5, first to fifth visible tergites; pan, posteroantennal notch; pat1–4, first to fourth paratergites; pc, procoxa; pt, protrochanter; s1–6, first to sixth visible sternites; vc, vertexal cavity. Scale bars: A, B = 0.5 mm; C, E = 0.2 mm; D = 0.1 mm.

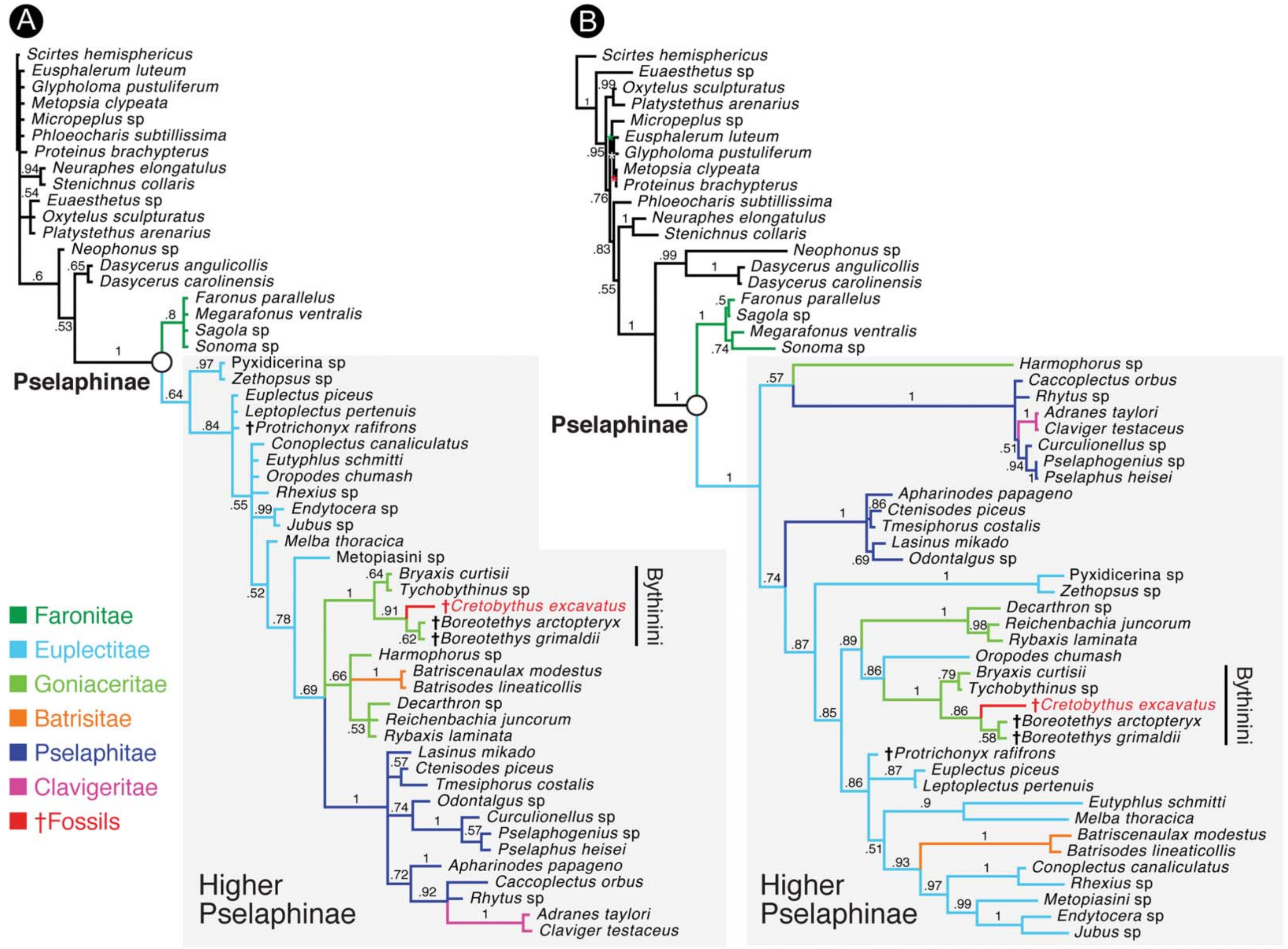

**Figure 3.** Phylogenetic placement of *Cretobythus excavatus* Yin, Parker & Cai gen. et sp. nov. Bayesian consensus trees produced by analysis of morphology alone (**A**) and morphology and molecular data combined (**B**). Values above branches are posterior probabilities (PP). Within Pselaphinae, branches are coloured according to supertribe, with *Cretobythus* in red. In both analyses, *Cretobythus* emerges as sister to *Boreotethys*, these two genera forming a sister group to Recent Bythinini with maximum clade support. PP values for asterisked nodes in B are 0.61 (green asterisk), 0.78 (white asterisk) and 0.86 (red asterisk).

long, suberect setae. Elytra (Figs 1B, 2A) slightly wider than long, EL 0.36 mm, EW 0.38 mm, surface covered with thin, moderately long setae, posterior margin with row of thick setae. Metathoracic wings (Fig. 2E) fully developed, with simple venation, narrowed at base and rounded at apex, fringe setose, setae of posterior margin distinctly longer. Abdomen (Fig. 2A, B) slightly wider than long, AL 0.43 mm, AW 0.46 mm; posterior and lateral margins of at least paratergites 4 covered with dense, thick setae. All legs (Fig. 2B) lacking modification; tarsomeres 2 thick and slightly longer than tarsomeres 3; tarsal claws (Fig. 1G, H) unequal, each tarsus with one large, distinct claw and one much smaller secondary claw.

## Systematic position of *Cretobythus*

Among the 32 extant and one extinct subfamilies of the Staphylinidae (Bouchard *et al.* 2011), *Cretobythus* can be readily placed in the Pselaphinae based on its small body size; a general habitus that is more compact than that of most other staphylinids; head and pronotum narrower than the elytra; clubbed antennae; maxillary palpi with four palpomeres and with an apical palpal cone; tarsi 3-3-3 segmented; abdomen with first four visible segments each possessing a pair of paratergites; and six visible abdominal sternites (Chandler 2001b). Among the six pselaphine supertribes (Chandler 2001a), *Cretobythus* can be easily ruled out of the earliest diverging supertribe Faronitae due to the presence of several derived character states, which are lacking in that group: a compact body form with a short, broad abdomen; a three-segmented antennal club; lack of fovea on the elytral disc; metacoxae not strongly projecting posteriorly; tarsomere 2 distinctly longer than tarsomere 1, and each tarsus with a large claw and a much smaller accessory claw. Within the remaining 'higher pselaphine' supertribes, an affinity of *Cretobythus* with the supertribe Goniaceritae is well supported by the antennal scape lacking the apicoventral and apicodorsal emarginations that are seen in Batrisitae, as well as distinct, dorsoventrally unfused tergites and sternites; short mesotrochanters with the dorsal extension of the femur close to the coxal articulation (i.e. not the derived 'macrosceline'-type mesotrochanters of Pselaphitae and Clavigeritae); unequal tarsal claws; and short tarsomere 1 and elongate tarsomeres 2 and 3, with tarsomere 2 slightly longer than tarsomere 3. Although the metacoxae are relatively contiguous at the ventral midline (a primitive state), they do not project strongly posteriorly, separating *Cretobythus* from Euplectitae.

Fourteen tribes and 260 genera are recognized in Goniaceritae (Chandler 2001a; Bouchard *et al*. 2011). Among them, placement of *Cretobythus* in the largely Holarctic tribe Bythinini is supported by the presence of several putative synapomorphies of this group (discussed in Park 1953 and Parker 2016): enlarged maxillary palpus (Fig. 1E) longer than half of the antennal length, with elongate palpomere 2, small, sub-triangular palpomere 3, and large, elliptical palpomere 4 which bears a distinct apical palpal cone; antenna with large scape and pedicel (Fig. 2D), with scape as long as antennomeres 3–5 combined; short trochanters (Fig. 2B); and presence of two unequal-sized tarsal claws (Fig. 1G, H). Although *Cretobythus* embodies the majority of bythinine characters, it also shows some primitive character states not found in extant Bythinini. These include a more flattened body form, the metacoxae close to the ventral midline, and tarsomere 2 being slightly longer than tarsomere 3. In contrast, modern bythinines have a dorso-ventrally convex body, the metacoxae are distant from each other, and tarsomere 2 is much longer than tarsomere 3.

*Cretobythus* appears to be most similar to the recently described genus *Boreotethys* also known from Cretaceous Burmese amber (Parker 2016), and both genera are placed phylogenetically into the stem group of the tribe Bythinini. *Boreotethys* shares most of the primitive character states of *Cretobythus*, but can be readily separated by tarsomeres 2, which in *Boreotethys* are distinctly shorter than tarsomeres 3 (an ancestral condition). Additionally, there is only a single tarsal claw on each leg in the latter genus (a derived condition). These discrepancies imply the reciprocal monophyly of the two genera. We evaluated our *a priori* placement of *Cretobythus* phylogenetically, and the results indeed support a close relationship between *Cretobythus* and *Boreotethys*. Bayesian inference based on both morphological data alone (Fig. 3A, PP = 0.91) and combined morphology and molecular data (Fig. 3B, PP = 0.86) consistently placed *Cretobythus* as a sister taxon to *Boreotethys*, with these genera emerging together as sister to Recent Bythinini (Fig. 3A, B; PP = 1.0 in both analyses). We conclude that *Cretobythus* is indeed most likely a bythinine stem-group member as our *a priori* judgment indicated, and an inferred sister taxon of *Boreotethys*.

## Discussion

The discovery of *Cretobythus*, a second stem-group genus of Bythinini in mid-Cretaceous Burmese amber, further strengthens the hypothesis that Bythinini are a Laurasian radiation of pselaphines (Parker 2016). Current knowledge of the palaeodistribution of the tribe during the Mesozoic agrees well with the present-day Holarctic range of bythinines, which are largely a northern temperate group absent in the tropics. Together with the recent discovery of *Boreotethys* in Burmese amber, a potentially rich palaeofauna of Bythinini may have existed by the mid-Cretaceous, suggesting that the origin of the tribe probably predates the Cenomanian. Although it remains unclear when crown-group members of the tribe evolved, the morphology of *Cretobythus* nevertheless indicates that a characteristic feature of modern bythinines was already established in the Mesozoic: their specialized feeding behaviour.

All pselaphines are presumed to be predatory as larvae and adults (Chandler 2001a, b), with potential prey including mites, springtails, worms, symphylans, insect larvae and small flies (Park 1932, 1933, 1942, 1947a, b; Jeannel 1950; Engelmann 1956; Pearce 1957; Reichle 1969). The predatory behaviour of only a limited number of species has been documented, with Engelmann (1956) being the first to provide detailed descriptions of the prey-capture behaviour in adult beetles. Five species were included in his observations: *Cedius spinosus obsoletus* Park (now a junior synonym of *C. spinosus* LeConte; see Chandler 1997) of the tribe Tyrini; *Tmesiphorus costalis* LeConte of the tribe Tmesiphorini; *Batrisodes globosus* (LeConte) of the tribe Batrisini; and *Bibloplectus* sp. and *Euplectus* sp. of the tribe Euplectini. Three of these species, *B. globosus*, *Bibloplectus* sp. and *Euplectus* sp., show a relatively simple behaviour: after detecting the prey, the beetles briefly hesitate before lunging forward and directly grasping the prey with their mandibles (an eastern Asian batrisine species, *Physomerinus pedator* (Sharp), also shows this simple strike behaviour; Z. Yin pers. obs.). *Cedius spinosus* and *Tmesiphorus costalis* seem to have a more derived and efficient pattern: when striking, the beetles simultaneously grasp the prey in their mouthparts and between the protibia and profemur, securing the prey with the spines or dense setae on their forelegs. Consistent with Engelmann's work, subsequent descriptions of predatory behaviour in several European pselaphines were provided by Schomann *et al*. (2008) for seven species: *Brachygluta fossulata* (Reichenbach) and *Rybaxis longicornis* (Leach) of the tribe Brachyglutini; *Bryaxis puncticollis* (Denny), *Bryaxis bulbifer*

**Figure 4.** Ecological reconstruction of *Cretobythus excavatus* Yin, Parker & Cai gen. et sp. nov. The beetle restrained its prey using the elongate maxillary palpi.

(Reichenbach) and *Bythinus burrelli* (Denny) of the tribe Bythinini; and *Pselaphus heisei* (Herbst) and *Tyrus mucronatus* (Panzer) of the tribe Tyrini. *Rybaxis longicornis* shows a similar behaviour to those of Batrisini and Euplectini, capturing its prey simply using the mandibles. The behaviour of *T. mucronatus* resembles that of *Cedius spinosus* and *Tmesiphorus costalis*, with the predatory process enhanced by raptorial forelegs.

Strikingly, however, the two *Bryaxis* species observed by Schomann *et al*. (2008) show a quite different pattern: they stretched out their maxillary palpi and placed them upon the dorsal surface of the prey item, restraining it by what was presumed to be the palpomeres' sticky surface. The beetles then grasped the prey with their mandibles. Based on the presently available information, the predatory behaviours of Pselaphinae are probably similar in closely related groups with similar mouthpart morphology, and potentially somewhat tribe specific, as suggested by Schomann *et al*. (2008). Given the exaggerated maxillary palpi of all Recent Bythinini, as well as the stem-group *Cretobythus*, it follows that this sophisticated mode of predatory behaviour was also exhibited by the fossil genus (Fig. 4). Notably, scanning electron microscope (SEM) observations of the fourth maxillary palpomere of Recent species of *Bryaxis* revealed putatively adhesive setae, and transmission electron microscopy (TEM) observations indicated the sensory function of the palpal cone (Schomann *et al.* 2008). The exquisite preservation of *Cretobythus* allows for a closer observation of its maxillary palpomeres. *Cretobythus* likewise possesses long, enlarged maxillary palpi that are similar to those of Recent members of Bythinini, such as *Bryaxis* and *Bythinus* Leach, and is the earliest known bythinine taxon that provides clear evidence of smaller, putatively predatory-related structures: the apex of palpomere 2 and the entirety of palpomeres 3–4 are densely covered with thick setae, and there is a distinct palpal cone at the apex of palpomere 4 (Fig. 1E). Similar maxillary palp morphology may also be present in *Boreotethys*, although the preservation of these specimens precludes clear assessment (Parker 2016). Such resemblance in form and structure of the maxillary palpi between *Cretobythus* and modern bythinines suggests a similar function. We therefore posit that this specialized mode of predation in Bythinini had already evolved by the mid-Cretaceous, in the Bythinini stem group.

## Conclusions

The discovery of a new pselaphine genus from mid-Cretaceous (Cenomanian, *c*. 99 Ma) Burmese amber highlights the early palaeodiversity of the supertribe Goniaceritae: tribe Bythinini, indicating that the origin of Bythinini probably extends further back in the Early Cretaceous. The similarity in form and structure of the maxillary palpomeres between *Cretobythus* and modern bythinines suggests a similar function in predation, implying that the derived mode of predatory behaviour in Recent Bythinini is ancient, and originated at least 99 million years ago, providing a potential insight into the palaeobiology of bythinines.

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## Supplemental data

Supplementary material for this article can be accessed at: https://dx.doi.org/10.1080/14772019.2017.1313790

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