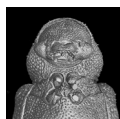


Earliest fossil record of Eucradinae in mid-Cretaceous amber from northern Myanmar (Coleoptera: Ptinidae)

YAN-DA LI, T. KEITH PHILIPS, DI-YING HUANG & CHEN-YANG CAI



Ptinidae is currently a diverse family of beetles with a sparse Mesozoic fossil record. Here a new ptinid fossil, *Granulobium whitei* Li, Philips & Cai gen. et sp. nov., is reported from mid-Cretaceous Burmese amber, which represents the earliest record of the extant subfamily Eucradinae. *Granulobium* can be recognized within Eucradinae by its coarsely granulated pronotum with no carinae or ridges, narrowly separated procoxae, irregularly punctate elytra, and relatively short abdominal ventrite 4. Our discovery indicates that Mesozoic Ptinidae were more biodiverse than previously appreciated. • Key words: Burmese amber, Cretaceous, anobiid, fossil.

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Ptinidae is a diverse family with more 230 genera distributed worldwide (Philips & Bell 2010). This group had long been considered as two separate families: Ptinidae *sensu stricto* (now Ptininae *sensu* Bouchard *et al.* 2011) and Anobiidae (*e.g.* Crowson 1955), but in more recent works they are united as a single family (*e.g.* Lawrence & Newton 1995, Arango & Young 2012, Zahradník & Háva 2014a). Ivie (1985) proposed the ptinids *s.s.* as a derived clade within the anobiids. However, later phylogenetic studies based on both morphological and molecular data suggested that the anobiid group and Ptininae may be two closely related but likely separated lineages (Philips 2000, Bell & Philips 2012, McKenna *et al.* 2019). The large-scale phylogenomic studies, although with limited taxon sampling density, indicated a sister relationship between the anobiid group and Ptininae, and the united Ptinidae as sister to Bostrichidae (McKenna *et al.* 2019, Cai *et al.* 2022).

Numerous fossils of Ptinidae have been reported from Cenozoic deposits (as listed by Zahradník & Háva 2014b, Bukejs & Alekseev 2015). The majority of them are described from Eocene Baltic amber, covering seven of the ten currently recognized subfamilies (*e.g.* Bukejs *et al.* 2017, Alekseev *et al.* 2019, Háva & Zahradník 2020). In contrast, few fossils are known from Mesozoic

(all Cretaceous). The only four described species are *Stegobium raritanensis* Peris, Philips & Delclòs, 2015 from Raritan amber, *Actenobius magneoculus* Peris, Philips & Delclòs, 2015 from San Just amber, and *Molinerobius fuentesi* Molino-Olmedo, 2017 and *Cretasernus spinosus* Peris & Philips, 2019 in Peris *et al.* (2020) from Burmese amber.

In this study, we report a new fossil from mid-Cretaceous Burmese amber, which represents the only Mesozoic record of the extant subfamily Eucradinae.

Materials and Methods

The Burmese amber specimen studied herein (Figs 1–4) originated from amber mines near Noiye Bum (26° 20' N, 96° 36' E), Hukawng Valley, Kachin State, northern Myanmar. The specimen is deposited in the Nanjing Institute of Geology and Palaeontology (NIGP), Chinese Academy of Sciences, Nanjing, China. The amber piece was trimmed with a small table saw, ground with emery papers of different grit sizes, and finally polished with polishing powder.

Brightfield images were taken with a Zeiss Discovery V20 stereo microscope. Widefield fluorescence images



Figure 1. General habitus of *Granulobium whitei* Li, Philips & Cai gen. et sp. nov., holotype, NIGP201648, under incident light. A – dorsal view. B – ventral view. Scale bars: 500 μ m.

were captured with a Zeiss Axio Imager 2 light microscope combined with a fluorescence imaging system. Confocal images were obtained with a Zeiss LSM710 confocal laser scanning microscope, using the 488 nm Argon laser excitation line (Fu *et al.* 2021, Li *et al.* 2023). Brightfield images were stacked with Helicon Focus 7.0.2. Confocal images were semi-manually stacked with Helicon Focus 7.0.2 and Adobe Photoshop CC. Microtomographic data were obtained with a Zeiss Xradia 520 Versa 3D X-ray microscope at the micro-CT laboratory of NIGP and analyzed in VGStudio MAX 3.0. Scanning parameters were as follows: isotropic voxel size, 2.6255 μ m; power, 4 W; acceleration voltage, 50 kV; exposure time, 1.5 s; projections, 3001. Images were further processed in Adobe Photoshop CC to adjust brightness and contrast.

To evaluate the systematic placement of the new species, a constrained morphological phylogenetic analysis was performed under Bayesian inference. The data matrix (Electronic supplement) was derived from a previously published dataset (Philips 2000). The char-

acter list remained the same with Philips (2000). The character 86 in Philips (2000) was described as “protibia: (0) one spur; (1) spurs absent”. When evaluating the placement of the fossil *Cretasernus spinosus*, Peris *et al.* (2020) added a state for this character: “(2) two spurs”. Only their new fossil was coded as this new state. However, the double articulated tibial spurs (*sensu* Lawrence & Ślipiński 2013) occur frequently in Ptinidae (*e.g.* White 1969, 1971a; Mosneagu 2012). The character 86 in Philips (2000) actually refers to the stout and curved spur present in *Endecatomois* Mellié, 1847 and some bostrichids (Fisher 1950). The tip labeled as *Hedobia* Dejean, 1821 in Philips (2000) was coded based on *H. granosa* LeConte, 1874, which is now usually classified in genus *Ptinomorphus* Mulsant & Rey, 1868 as *P. granosus* (LeConte, 1874) (*e.g.* Español 1970, Zahradník 2018). The constraints were set up based on the molecular phylogeny by McKenna *et al.* (2015, 2019). *Endecatomois* was selected as the outgroup based on McKenna *et al.* (2015).

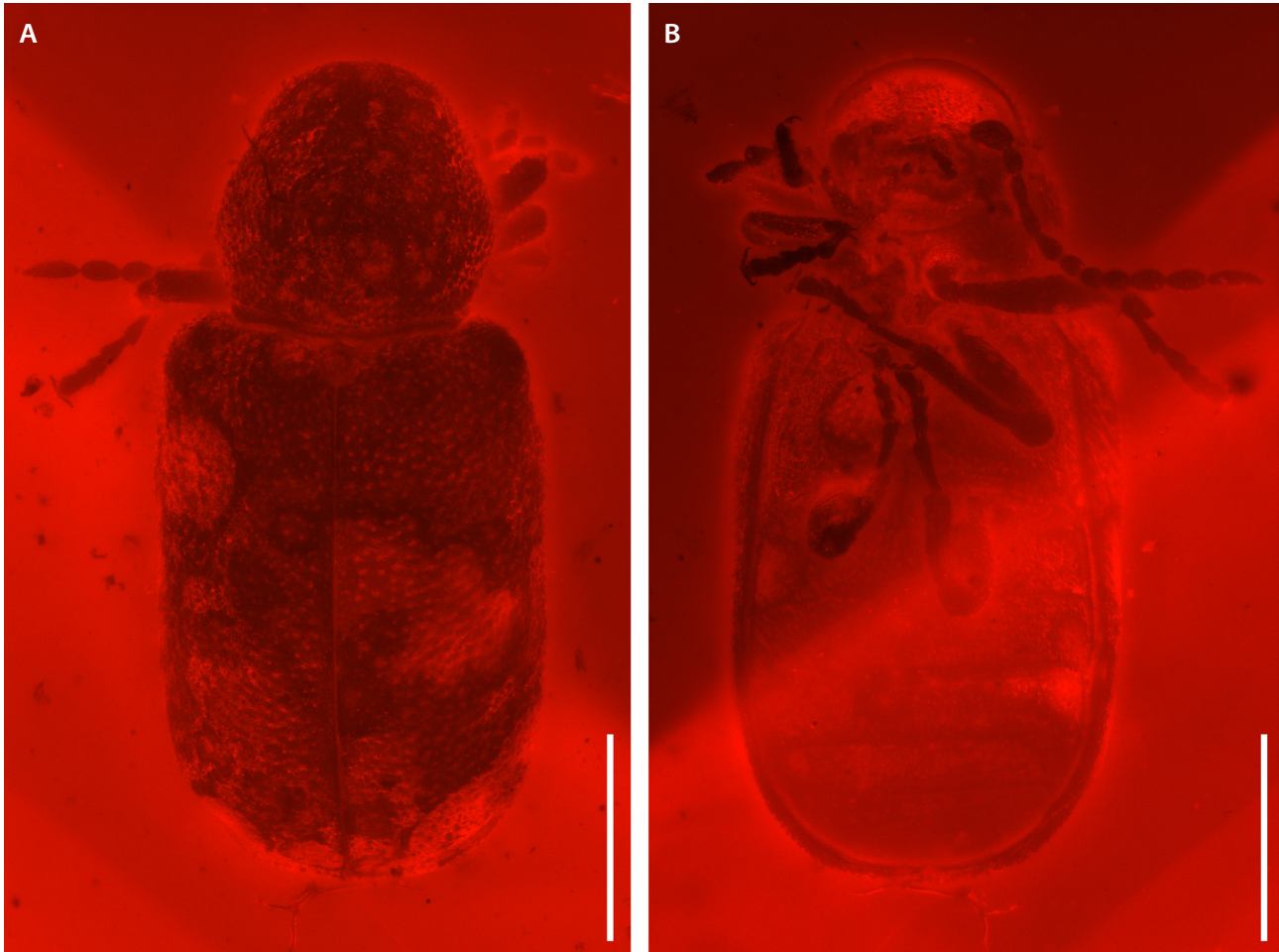


Figure 2. General habitus of *Granulobium whitei* Li, Philips & Cai gen. et sp. nov., holotype, NIGP201648, under widefield fluorescence. A – dorsal view. B – ventral view. Scale bars: 500 μ m.

The Bayesian analysis was performed using MrBayes 3.2.6 (Ronquist *et al.* 2012). Two MCMC analyses were run simultaneously, each with one cold chain and three heated chains. Trees were sampled every 2,000 generations. Analyses were stopped when the average standard deviation of split frequencies remained below 0.01. The first 25% of sampled trees were discarded as burn-in, and the remains were used to build a majority-rule consensus tree.

The trees were drawn with the online tool iTOL 6.5.2 (Letunic & Bork 2021) and graphically edited with Adobe Illustrator CC 2017.

Systematic paleontology

Order Coleoptera Linnaeus, 1758
 Family Ptinidae Latreille, 1802
 Subfamily Eucradinae LeConte, 1861
 Tribe Hedobiini Mulsant & Rey, 1868

Genus *Granulobium* Li, Philips & Cai gen. nov.

Type species. – *Granulobium whitei* sp. nov.

Etymology. – The generic name is derived from a combination of “granules”, referring to the distinct head and pronotal morphology of this unique taxon, together with an abbreviation of the well-known anobiid generic name *Anobium* Fabricius, 1775. The name is neuter in gender.

Diagnosis. – Body with scattered fine short suberect setae. Antennae serrate, without club (Figs 3A, 4D); antennomeres 3 and 4 longer than width (Figs 3C, 4B). Pronotum without lateral pronotal carinae or median ridge; surface densely and coarsely granulated (Figs 3A, B; 4E). Prothorax unmodified ventrally (Figs 3C; 4C, E). Procoxae narrowly separated by procoxal process (Figs 3C, 4C). Elytra with irregularly distributed fine punctures, without longitudinal carinae (Figs 1A; 4A, E). Metacoxae with vestigial coxal plates (Figs 3C, 4C). Abdominal



Figure 3. *Granulobium whitei* Li, Philips & Cai gen. et sp. nov., holotype, NIGP201648, under confocal microscopy. A – anterior view. B – dorsal view. C – ventral view. Scale bars: 400 μ m.

ventrite 1 with intercoxal process smoothly rounded; ventrite 4 relatively short (Figs 3C, 4C) (compared to other Eucradinae).

***Granulobium whitei* Li, Philips & Cai sp. nov.**

Figures 1–4

LSID. – urn:lsid:zoobank.org:act:779BB6A8-7856-48F3-91B9-AE978B19E178

Type. – Holotype, NIGP201648.

Type horizon and locality. – Unnamed horizon, mid-Cretaceous, Upper Albian to Lower Cenomanian. Amber mine located near Noije Bum Village, Tanai Township, Myitkyina District, Kachin State, Myanmar.

Material. – Type only.

Etymology. – The species is named after Richard E. White, in recognition of his contribution to the systematics of anobiids.

Diagnosis. – As for the genus.

Description. – Body moderately elongate, somewhat cylindrical, about 2.0 mm long, 0.9 mm wide; surface with fine, short, suberect setae.

Head well inserted into prothorax, inclined downwards, dorsally concealed by pronotum; dorsal surface densely granulated; granulation finer than that on pronotum. Compound eyes round, moderately large, strongly protruding. Antennal insertions widely separated, located

near inner margin of eyes. Antennae 11-segmented, elongate; antennomere 1 stout, antennomere 2 slightly shorter than 3; antennomere 3 subrectangular, more than 1.5× as long as width; antennomeres 4–10 moderately elongate, weakly serrate, subequal in length; antennomere

11 slightly longer than 10, apically acute. Anterior edge of clypeus shallowly emarginate. Mandible short and broad; left mandible with a subapical tooth on incisor edge near apical tooth, and a tooth on dorsal side. Apical maxillary palpomere with subparallel sides, flattened apically.

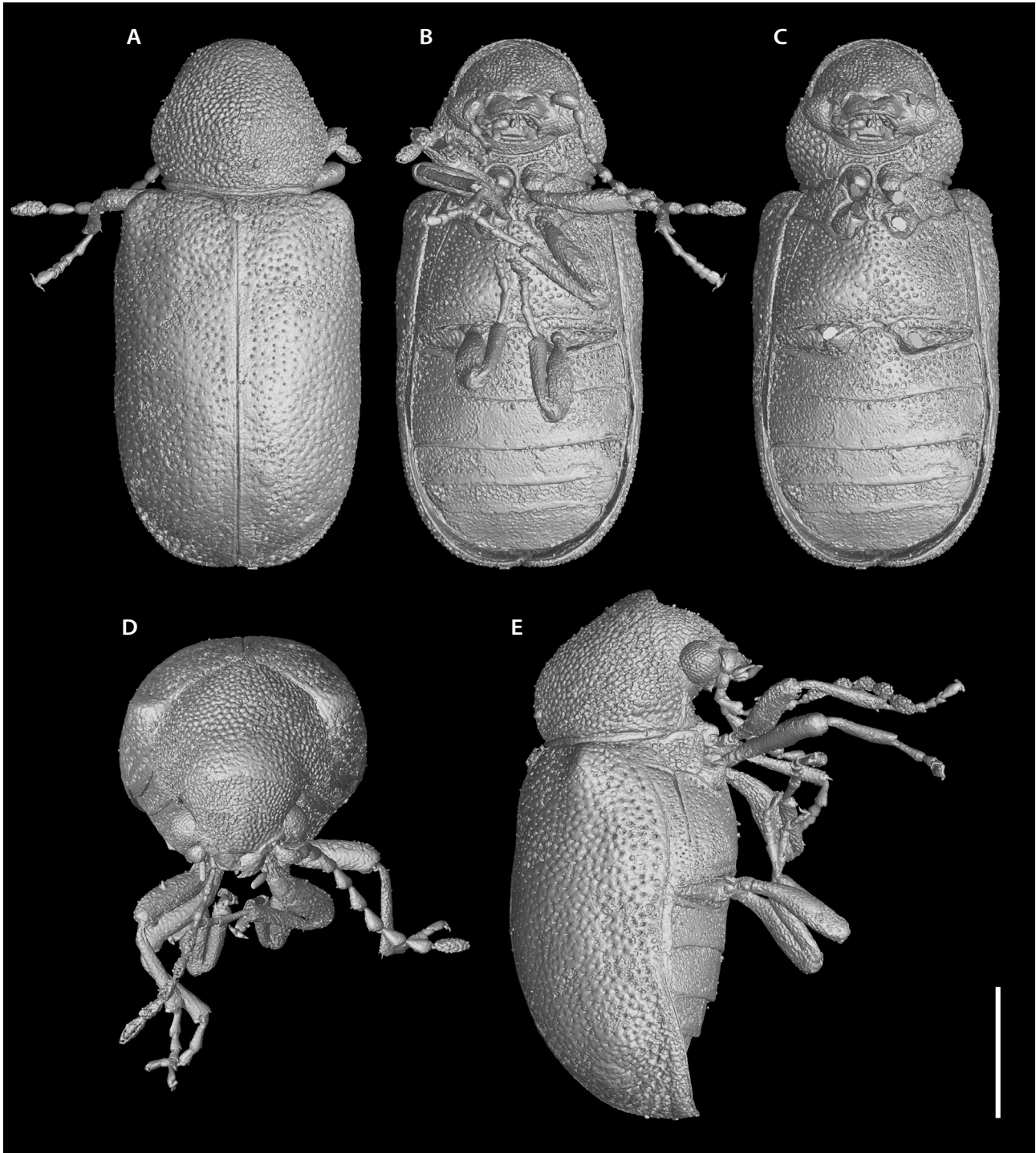


Figure 4. X-ray microtomographic reconstruction of *Granulobium whitei* Li, Philips & Cai gen. et sp. nov., holotype, NIGP201648. A – dorsal view. B – ventral view. C – ventral view, with legs removed. D – anterior view. E – lateral view. Scale bar: 500 μ m.

Pronotum about as long as width, about $0.7\times$ as wide as combined width of elytra, widest at basal $\frac{2}{5}$; surface with dense and relatively coarse granulation; lateral pronotal carinae completely absent; median longitudinal ridge absent. Prothorax ventrally unmodified; surface not excavated. Prosternum in front of coxae shorter than half length of procoxae; prosternal process very narrow, extending about $\frac{2}{3}$ length of procoxae and reaching mesoventrite. Notosternal sutures present. Procoxal cavities circular, narrowly separated, broadly open externally.

Scutellar shield posteriorly broadly rounded. Elytra about $1.5\times$ as long as combined width, parallel-sided, conjointly rounded at apex; humeral angles pronounced; surface somewhat irregularly punctate, without longitudinal ridges. Mesoventrite with median discrimen, anteriorly with well-developed procoxal rests; mesoventral process reaching middle of mesocoxae, apically truncate. Mesocoxal cavities circular, moderately narrowly separated, laterally closed. Metaventricle broad. Exposed portion of metanepisternum elongate and parallel-sided (in lateral view). Metacoxae with vestigial coxal plates.

Femora stout, subparallel-sided in distal half and thinner in proximal half. Tibiae slender, weakly and gradually expanded distally; each with two apical spurs (as least as seen on fore and mid legs). Tarsi 5-5-5; tarsomeres simple; tarsomere 1 longest, about twice as long as 2; tarsomeres 2–4 slightly decreasing in length; tarsomere 5 slightly longer than 3 or 4. Pretarsal claws distinctly swelling (dentate) at base.

Abdomen with five ventrites; first two ventrites coplanar (possibly indicating connation). Ratio of ventrite lengths along middle: $\sim 4.7:3.3:2.5:2.0:2.9$. Ventrite 1 with intercoxal process broadly rounded; postcoxal lines absent.

Discussion

Granulobium clearly belongs to the anobiid group of Ptinidae, which generally differs from Ptininae in having well separated antennal insertions. Other characters differentiating anobiids from ptinines as listed by Philips (2000), including the connation of abdominal ventrites, are difficult to determine in the fossil. Among the anobiids, *Granulobium* shares with Eucradinae and Dryophilinae the ventrally unmodified prothorax, *i.e.* not inflated, flat, concave, or reduced and concealed when the head is withdrawn (White 1971b, 1974a). Additionally, the pronotum of *Granulobium* is laterally rounded and lacks any margin or ridge as is true for most but not all taxa in these two subfamilies.

The differentiation between Eucradinae and Dryophilinae largely relies on the male genitalia (Español 1970), and determining the subfamilial attribution could

be contentious even for extant genera (*e.g.* Zahradník 2021). For example, the circumscriptions of the two subfamilies defined by Español (1970) and White (1974b) are quite different. It might be better to consider these two subfamilies as synonymous, but this issue has not been seriously studied in a phylogenetic framework. Nevertheless, most members of Dryophilinae have distinctly elongated antennomeres 9–11, and the pronotum is often less strongly curved (Español 1968, Español & Viñolas 1995). Certainly, the antennal character of *Granulobium*, *i.e.* the last three antennomeres equal or barely larger than the more proximal antennomeres, fits with the characters currently used to define the eucradines. Thus, we suggest that *Granulobium* most likely belongs to the subfamily Eucradinae. Our phylogenetic analysis also supports the eucradine placement of *Granulobium*, although Dryophilinae is not sampled in the analysis (Fig. 5).

There are some major differences between *Granulobium* and extant Eucradinae. In the latter, the third and fourth abdominal ventrites are usually about the same length, while in *Granulobium* the fourth is distinctly shorter than the third. In extant Eucradinae, the procoxae are contiguous or nearly so, with prosternal process reduced or absent (Español 1970). By contrast, the procoxae in *Granulobium* are narrowly but completely separated by a prosternal process. The pronotum may be somewhat more coarsely granulated in *Granulobium* compared to other taxa within the subfamily as well.

Granulobium can be separated from the following eucradine genera based on some additional characters. *Anhedobia* Nakane, 1963 has a lateral pronotal carina (absent in all other eucradines) and a median pronotal ridge (Español 1970, Zahradník 2013), which are both absent in *Granulobium*. *Granulobium* shares with *Ptinomorphus* the non-striate elytra. However, *Ptinomorphus*, and *Eucrada* LeConte, 1861 as well can be easily separated from *Granulobium* by the presence of a median longitudinal ridge on the basal half of the pronotum, which often appears strongly pinched in the basal part (Español 1970, Toskina 2001, Levey 2021). *Eucrada* additionally differs from *Granulobium* in the striate elytra and the more strongly serrate to pectinate antennae (Español 1970).

Neohedobia Fisher, 1919 morphologically appears similar to *Granulobium* as both have very similar pronotal widths compared to that of the elytra and head and pronotal morphologies in lateral view. In anterior view, the pronotum in *Neohedobia* appears a little more angulate with relatively flat surfaces expanding dorsally to a more narrowly rounded median peak. The granulations on the head and pronotum are somewhat similar as well. But in contrast, *Neohedobia* has deep elytral punctures that are approximately aligned in rows while *Granulobium*

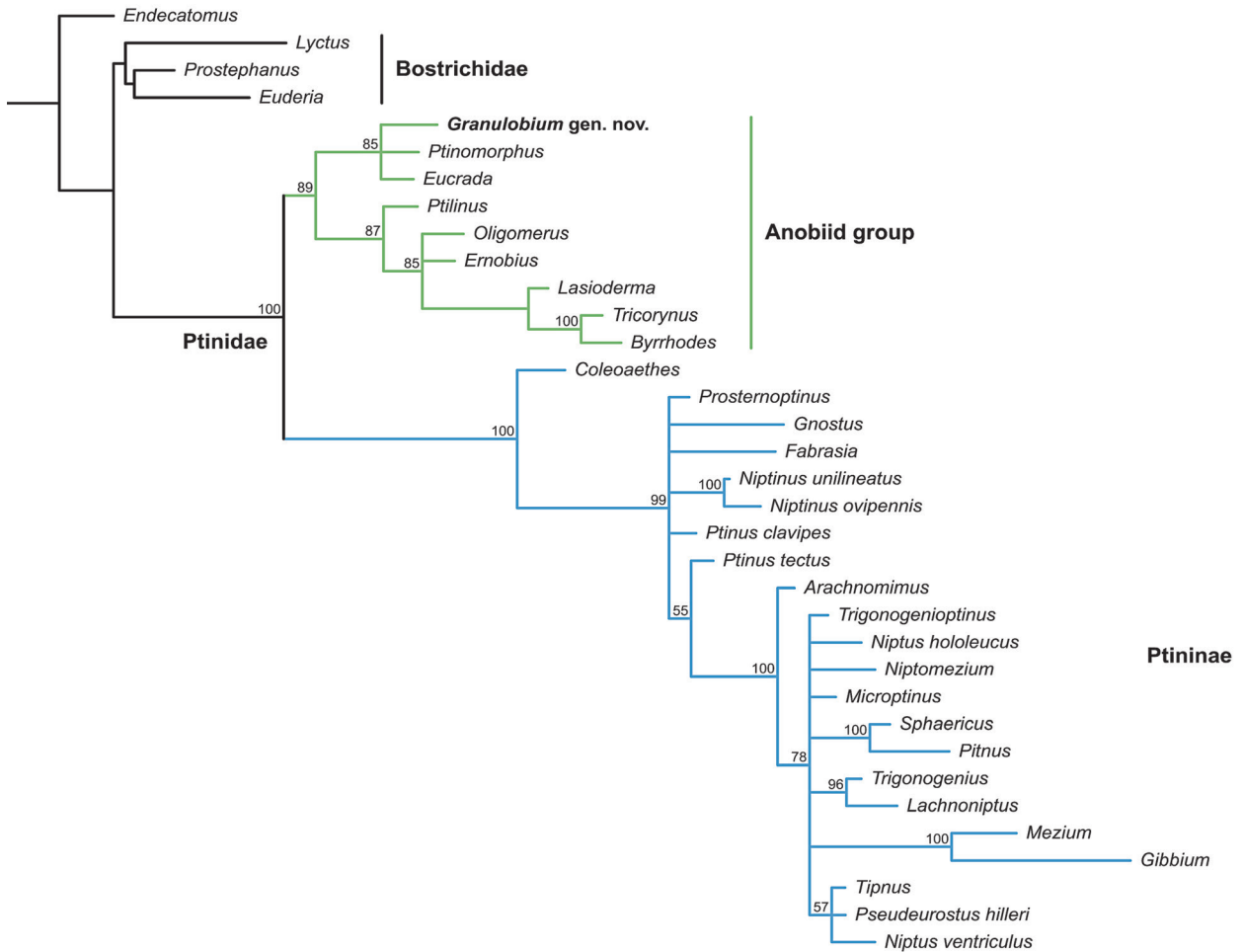


Figure 5. Suggested placement of *Granulobium* Li, Philips & Cai gen. nov. within Ptinidae. Tree resulting from the Bayesian analysis constrained by a molecular backbone tree.

has elytra with fine scattered punctures. Further, the antennomeres 3 and 4 in *Neohedobia* are short and moniliform (Fisher 1919, White 1971b), while those in *Granulobium* are distinctly longer than the width.

The taxon most closely related to *Granulobium* is possibly *Clada* Pascoe, 1887. Notably the latter may need to include the Old World *Hedobia* (the latter name with priority); these two genera are certainly closely related and based on available morphological evidence they may need to be eventually synonymized (Zahradník pers. comm.). Like *Granulobium*, some species of *Clada* have a rounded pronotal dorsal protuberance (Zahradník 2013). *Clada* also has short erect or suberect pubescence covering the body as in *Granulobium*. While most species of *Clada* have elytra with some degree of longitudinal costae, not all have this feature like *Granulobium* (Zahradník 2013). Similarly, in *Clada* the elytral punctures are usually somewhat irregularly scattered like *Granulobium* (Zahradník 2013). *Clada* differs from *Granulobium* in often having more strongly serrate to pectinate antennae

especially in the males, and having coarser elytral punctures (Español 1970, Zahradník & Trýzna 2018, Kono & Yoshitomi 2021), although these features may not be very stable in Ptinidae, which can vary even within a genus.

Eucradinae is possibly the basal-most lineage of the anobiid group. The only fossil of Eucradinae described previously came from Eocene Baltic amber (Abdullah & Abdullah 1967), which was placed in the extant genus *Eucrada* by White (1969). Our discovery of the Cretaceous *Granulobium* is accordant with the presumed antiquity of this subfamily and adds valuable information about the morphological diversity, origin and evolution of the group.

Data availability. The data matrix for the phylogenetic analysis is available in the Electronic supplement. The original confocal and micro-CT data are available in Zenodo repository (<https://doi.org/10.5281/zenodo.7888505>).

Electronic supplement. Morphological dataset used for the phylogenetic analysis, derived from Philips (2000).

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