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Under the Cretaceous bark: Fossil evidence for the ancient origin of subcortical lifestyle of clown beetles (Coleoptera: Histeridae)

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Abstract

We describe three new genera and four new species of the Histeridae (Coleoptera) from the mid-Cretaceous amber in Myanmar. *Platycretus muscularis* Simon Pražák & Lackner **gen. & sp. nov.** represents the first known fossil of the subfamily Histerinae from the Cretaceous. We assign the remaining three fossils, *Olexum complanatum* Simon Pražák & Lackner **gen. & sp. nov.**, *Cretanapleus seideli* Simon Pražák & Lackner **gen. & sp. nov.**, and *Yethiha pubescens* Simon Pražák & Lackner **sp. nov.** to the subfamily Dendrophilinae. *Platycretus muscularis* and *O. complanatum* have adaptations typical for the subcortical lifestyle (flattened body shape, dilated protibiae), proving this life strategy existed in independent lineages of clown beetles already in the Cretaceous. We also provide a review of all Histeridae fossil species described up to date and test the phylogenetic position of all of them including the newly described ones.

Key words

Burmese amber, Cenomanian, Histeroidea, Myanmar, phylogeny, Polyphaga

1. Introduction

Histeridae, or clown beetles (named after their flattened tibiae resembling wide clown's trousers), represent the largest group of the polyphagan beetle superfamily Histeroidea. Their more than 4500 species can be found in surprisingly diverse environments – animal faeces and carcasses, forest litter, subcortical spaces, tunnels of wood-boring beetles, rotting cacti and other succulents, decomposing plant or fungi material, mammal burrows and bird nests, colonies of ants and termites, subterranean cavities and caves, sand dunes, etc. (Kryzhanovskij and Reichardt 1976, Caterino and Dégallier 2007, Lackner 2010, Kovarik and Skelley 2019). Specialisation for a

specific habitat typically leads to morphological adaptations, sometimes even radical changes of body morphology and particularly body shape (Kovarik and Caterino 2016).

Only a limited number of relatively young (Cenozoic) fossil species of Histeridae was described in the 19th and 20th centuries (Heer 1862; Piton and Théobald 1935; Handschin 1944). In recent years, fossil Histeridae have received increased attention. Inclusions in Burmese amber (also called burmite or Kachin amber) from northern Myanmar are especially of high interest due to their ancient mid-Cretaceous origin (99 million years, My; Shi et al. 2012). As phylogenetic studies suggest, deep radiation of Histeridae took place in the Lower Cretaceous (Zhou et al. 2020). Thus, fossil species from Burmese amber provide key information for reconstructing the evolutionary history of the family.

There are twelve species of Histeridae described from the Cretaceous up to date. These represent recent subfamilies Abraeinae, Dendrophilinae, Haeteriinae and Onthophilinae, and the extinct Antigracilinae. Another 17 species from subfamilies Abraeinae, Dendrophilinae, Histerinae and Onthophilinae have been described from younger deposits (see Table 1).

Flattened body shape is found in several unrelated histerid lineages (Dendrophilinae: Paromalini; Histerinae: Platysomatini, Hololeptini, Exosternini; Haeteriinae), undoubtedly as a result of parallel evolution (Kovarik and Caterino 2016; Helava et al. 1985; Zhou et al. 2020). Flattened clown beetles' taxa typically inhabit subcortical spaces of dead trees in the early stages of decay and feed on insect larvae (Kovarik and Caterino 2016). Despite being common in modern fauna, and supposedly of ancient origin, the subcortical lineages characterized by the flat body shape were absent from the fossil record until recently. Caterino (2021) described the first species with rectangular and flattened body shape, belonging to the subfamily Dendrophilinae: *Druantia aeterna* Caterino, 2021. In this study, we describe two other species adapted to the subcortical lifestyle – *Platycretus muscularis* **gen. et sp. nov.** and *Olexum complanatum* **gen. et sp. nov.**, representing subfamilies Histerinae and Dendrophilinae, respectively. These fossils provide further evidence for the ancient origin of subcortical lifestyle in Histeridae, and indicate this strategy was already present in multiple unrelated lineages during the Cretaceous period.

2. Material and methods

2.1. Samples

Amber specimens were purchased online from authorized sellers. All specimens come from the deposits in the Hukawng Valley, with age estimated as Cenomanian ca. 99 Ma (Shi et al. 2012). All holotypes are deposited at the collections of the Museum of Eastern Bohemia, Hradec Králové, Czech Republic. Inventory numbers are provided for each holotype specimen.

2.2. Preparation, imaging, classification and LSID registration

Histeridae inclusions were cut out using Dremel Work Station 220 (cut offs are stored together with the respective type specimens) and further polished with 600 and 1200 wet sand papers. Final polishing was performed with toothpaste. Observation of morphological characters was done through Nikon 102 binocular microscope. Measurements were taken through an ocular micrometre. The selected specimens were examined under an Olympus IX81 inverted fluorescence microscope with UIS2 objective lenses and equipped with an ORCA-AG monochromatic 12-bit charge coupled device camera (Hamamatsu, Japan). The mirror images were pseudocoloured (red for Cy3, blue for DAPI and green for fluorescence) and superimposed with cell^r software (Olympus Soft Imaging Solutions, Japan). Specimens were photographed through Canon EOS 550 mounted on Olympus BX40 with Mplan and LUCPlanFLN lenses, images were stacked in Zerene Stacker (Rik Littlefield, Zerene Systems LLC). All photographs including those not shown here are available at the Zenodo archive under https://doi.org/10.5281/zenodo.7777690. SEM micrographs were taken with a JSM 6301F camera.

Classification and nomenclature follow Mazur (2011). Terminology is used according to Ôhara (1994) and Lackner (2010).

The publication and included nomenclatural acts have been registered in ZooBank (www.zoobank.org), the online registration system for the ICZN. The LSID for this publication is: urn:lsid:zoobank.org:pub:879AE99E-6987-4A83-B10F-E38BF7D545BF.

2.3. Phylogenetic analyses

We used the morphological dataset of Zhou et al. (2020) into which we added characters of the newly described taxa as well as of all other amber fossil Histeridae species described up to date (see Supplementary Material 1). We performed a maximum parsimony analysis with constrained topology: the topology of the backbone tree of modern species was fixed to that congruent with the combined morphological-molecular analysis by Zhou et al. (2020). Only the fossil taxa were allowed to move freely across the constrained tree (see Fikáček et al. 2019 for details of the method). The reference tree was created in WinClada. The phylogenetic analysis was run in TNT, using the exhaustive search ("implicit enumeration"). We ran two separate analyses: (1) with only the fossils newly described herein included together with the early-branching *Antigracilus costatus* and *Cretohister sinensis*; and (2) with all described Histeridae amber fossils included (both Mesozoic and Cenozoic).

Table 1. All described fossil Histeridae up to date. Sub – subfamily; Ant – Antigracilinae; Abr – Abraeinae; Den – Dendrophilinae; Hae – Haeterinae; His – Histerinae; Ont – Onthophilinae; FT – fossil type; A – amber inclusion; C – compression fossil; Ca – phosphatised cast.

Sub	Species	Age (Mya)	Deposit	FT	Reference
Cretaceous					
Ant	*Antigracilus costatus*	125	Yixian Form., China	C	Zhou et al. (2020)
Abr	*Pantostictus burmanicus*	99	Kachin, Myanmar	A	Poinar and Brown (2009) Zhou et al. (2020)
Den	*Yethiha peregrina*	99	Kachin, Myanmar	A	Caterino (2021)
Den	*Yethiha pubescens* **sp. n.**	99	Kachin, Myanmar	A	Present paper
Den	*Druantia aeterna*	99	Kachin, Myanmar	A	Caterino (2021)
Den	*Anapleus kachinensis*	99	Kachin, Myanmar	A	Jiang et al. (2022)
Den	*Cretanapleus seideli* **sp. n.**	99	Kachin, Myanmar	A	Present paper
Den	*Olexum complanatum* **sp. n.**	99	Kachin, Myanmar	A	Present paper
Hae	*Promyrmister kistneri*	99	Kachin, Myanmar	A	Zhou et al. (2019)
His	*Platycretus muscularis* **sp. n.**	99	Kachin, Myanmar	A	Present paper
Ont	*Cretonthophilus tuberculatus*	99	Kachin, Myanmar	A	Caterino et al. (2015)
Ont	*Carinumerus yingae*	99	Kachin, Myanmar	A	Jiang et al. (2020), Caterino (2021)
Ont	*Carinumerus maddisoni*	99	Kachin, Myanmar	A	Caterino (2021)
Ont	*Phasmister cristatus*	99	Kachin, Myanmar	A	Caterino (2021)
?	*Amplectister tenax*	99	Kachin, Myanmar	A	Caterino and Maddison (2018)
?	*Amplectister terapoides*	99	Kachin, Myanmar	A	Yamamoto and Caterino (2022)
Eocene					
Abr	*Acritus sutirca*	48–34	Kaliningrad, Russia	A	Alekseev and Bukejs (2021b)
Den	*Carcinops donelaitisi*	55.8–33.9	Kaliningrad, Russia	A	Alekseev (2016)
Den	*Xestipyge ikanti*	55.8–33.9	Kaliningrad, Russia	A	Alekseev (2016)
Den	*Bacanius kirejtshuki*	55.8–33.9	Rovno, Ukraine	A	Sokolov and Perkovsky (2020)
Den	*Bacanius goorskii*	55.8–33.9	Gdańsk, Poland	A	Alekseev and Bukejs (2021a)
Ont	*Onthophilus intermedius*	45–25	Quercy, France	Ca	Handschin (1944)
Oligocene					
His	*Hister cerestensis*	33.9–28.1	Céreste, France	C	Dégallier et al. (2019)
Miocene					
Abr	*Trypanaeus hispaniolus*	20.43–15.97	Dominican Republic	A	Chatzimanolis et al. (2006)
His	*Hister aemulus*	23–5.3	Oeningen, Germany	C	Heer (1862)
His	*Hister antiquus*	23–5.3	Oeningen, Germany	C	Heer (1862)
His	*Hister coprolithorum*	23–5.3	Oeningen, Germany	C	Heer (1862)
His	*Hister maculigerus*	23–5.3	Oeningen, Germany	C	Heer (1862)
His	*Hister marmoratus*	23–5.3	Oeningen, Germany	C	Heer (1862)
His	*Hister mastodontis*	23–5.3	Oeningen, Germany	C	Heer (1862)
His	*Hister morosus*	23–5.3	Oeningen, Germany	C	Heer (1862)
His	*Hister vetustus*	23–5.3	Oeningen, Germany	C	Heer (1862)
Pliocene					
Abr	*Plegaderus pitoni*	2.5–1.8	Lac Chambon, France	C	Piton and Théobald (1935), Dégallier et al. (2019)

3. Results

3.1. Phylogenetic analyses

We recovered identical positions of the newly described fossil species in both analyses (with and without the inclusion of other described histerid amber fossils; see Fig. 5 and Supplementary Material 2).

3.2. Systematic palaeontology

Family Histeridae Gyllenhal, 1808

Subfamily Histerinae Gyllenhal, 1808

Without tribal placement

Platycretus Simon Pražák & Lackner, gen. nov.

https://zoobank.org/38FFA746-5C40-4E2A-AB1B-F5E90257ABDD

Type species. *Platycretus muscularis* Simon Pražák & Lackner**, sp. nov.**

Diagnosis. Body rectangular, flattened, dorsally with large irregular depressions. Labrum asetose, without punctures. Mandibles massive, carinate, outer margin almost perpendicular. Pronotum with a complete marginal pronotal stria, basal fragment of outer lateral stria and incomplete inner lateral stria interrupted at anterior pronotal angles. Prosternal lobe present, massive. Antennal cavity present, partially closed by prosternal alae. Elytra with a complete, deeply impressed marginal elytral stria. Tibiae very broad, without teeth, with denticles along their outer margins. Meso- and metafemora extremely thickened, triangular in cross section.

Etymology. Name of the genus was chosen to point out its Cretaceous origin and flattened shape.

Platycretus muscularis Simon Pražák & Lackner, sp. nov.

https://zoobank.org/EC2A7606-C255-404B-B9F0-7DA856D33498

Type material. Holotype specimen (1407/E), unknown sex, Northern Myanmar, inclusion in burmite, Cenomanian (ca. 99 Ma), amber piece somewhat opaque, with significant amount of debris and bubbles, ca. 6×4×2 mm, synclusions: plant material, minute seeds, unidentified insect fragments.

Description. ***Measurements.*** Head width: 0.2 mm, width between anterior pronotal angles: 0.41 mm, width between pronotal prosternal angles: 0.93 mm, pronotal length: 0.75 mm, elytral length: 1.11 mm, elytral width (across widest point): 0.93 mm. — ***Body.*** Rectangular, flattened, dorsal cuticle wholly covered with irregular prominent tubercles and depressions. Cuticle pitch black, legs chestnut brown. — ***Head.*** Frons with deep anteromedian depression, punctate. Supraorbital stria present, carinate. Frontal stria carinate, widely interrupted medially, extending to the clypeolabral suture, convergent anteriorly. Mandibles stout, massive, outer margin almost perpendicular, carinate. Labrum long, almost square-shaped, asetose, without punctures, appears to be fused with clypeus. Left mandible with acute prominent tip, rest of the mandibles invisible. Terminal maxillary palpomere thin and long, flattened. Remaining mouthparts unobservable. Scape curved, as long as antennomeres 2–8 combined, outer margin distinctly carinate. Pedicel slightly longer than antennomere 3. Antennomeres 3–8 short, becoming wider apically. Antennal club large, round, covered with a velvet-like white layer (short setation). Two intersegmental sutures of antennal club visible, straight. Eyes flattened. — ***Thorax.*** Pronotum rectangular, very wide, flat, with large depressions and irregular large shallow punctures of various sizes mostly in the anterolateral region. Anterior pronotal angles prominent, obtuse. Basal margin of pronotum significantly curved posteriorly. Lateral edges parallel with and subsequent to the lateral edges of elytra. Marginal pronotal stria complete. Outer lateral stria present as a short thin basal fragment reaching approximately 1/3 of pronotal length apically. Inner lateral pronotal stria deeply impressed, complete laterally, absent anteriorly (interrupted at the anterolateral angles of the pronotum). Surface between marginal and lateral pronotal striae convex. Scutellar shield small, triangular. Elytra without punctuation, with extensive depressions covering its entire dorsal area. Marginal elytral stria deeply impressed, complete, wider anteriorly. Dorsal striae I and II faintly present on posterior half of elytra. Elytral epipleural stria complete, carinate. Prosternal lobe large, broad, delicately punctuate, with two thin transverse lines. Anterior prosternal margin almost straight medially. Marginal prosternal stria not distinguishable. Prosternal process obfuscated by debris. Antennal cavity present, partially closed by prosternal alae. Mesoventrite with irregular depressions, surface structures unclear. Meso-metaventral area with large depression, most likely caused by external factors (and hence likely representing an artefact), making the striation on mesoventrite and metaventrite indiscernible. Metaventrite with shallow punctures. Metepisternum depressed and irregularly sculptured. — ***Abdomen.*** First visible abdominal ventrite square-shaped, with deep punctures separated by their diameter. Rest of abdomen missing. — ***Legs.*** Profemur flat. Protibia flat and very broad, with 6 short and thick denticles on outer margin. Protarsal groove present, faintly S-shaped. Protibial spur well developed. Protarsus short. Mesofemur massively

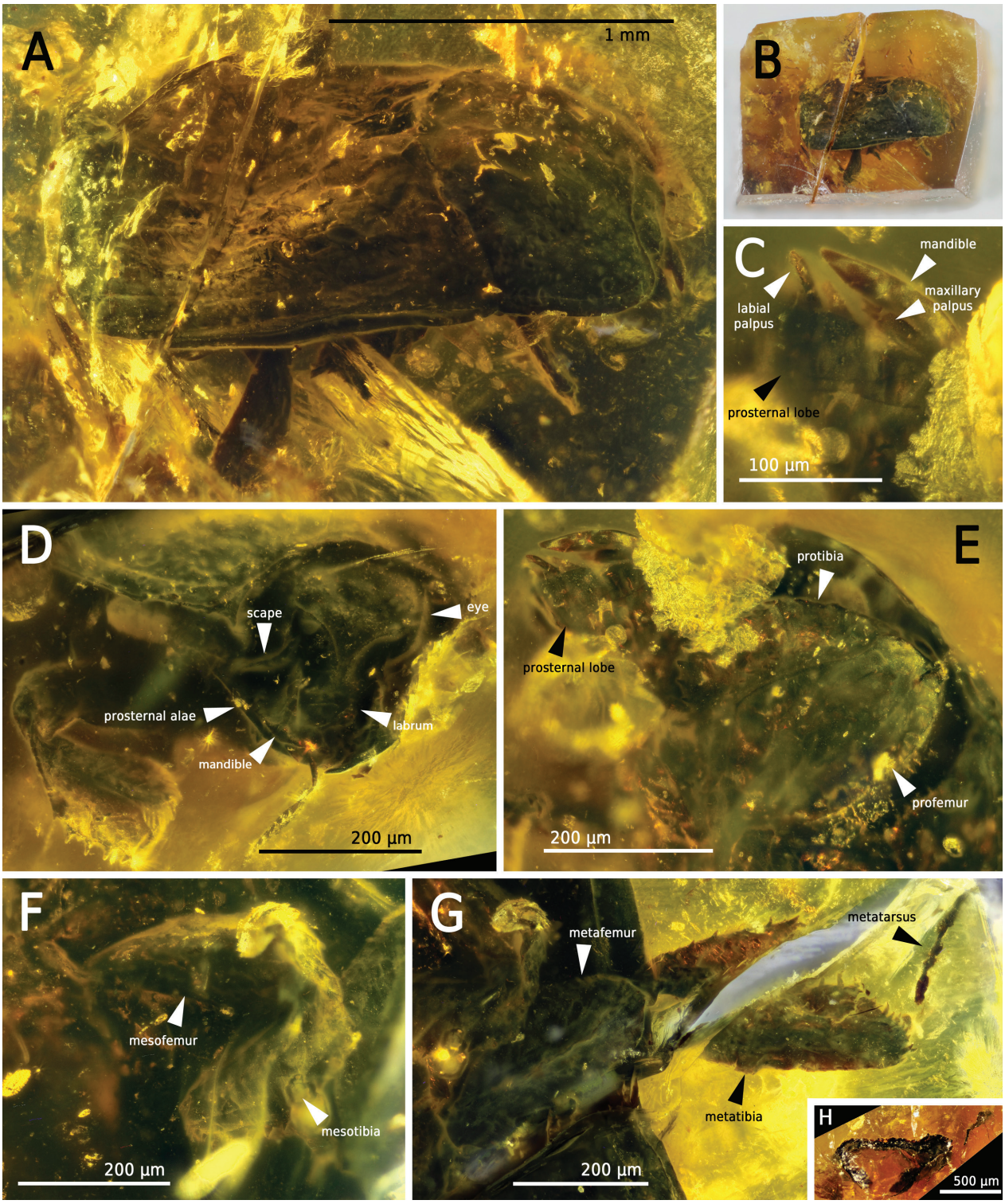

Figure 1. *Platycretus muscularis* Simon Pražák & Lackner, gen. & sp. nov. **A** dorsal view; **B** amber specimen; **C** mouthparts; **D** frontal view; **E** foreleg; **F** middle leg; **G** hind leg; **H** cross section at the breakage point – posterior part.

thickened, triangular in cross section. Mesotibia relatively short (shorter than mesofemur), flat and very broad (broader than protibia), with short thick denticles along its outer margin. Mesotarsus not visible. Metafemur very thickened, triangular in cross section. Metatibia largely similar to mesotibia but not as wide, with short thick denticles and numerous shorter setae along the outer margin. Large accumulation of short slender denticles present apically around the metatibia-metatarsal articulation. Metatarsus long (about 3/4 of the metatibial length).

Taxonomic assignment. The present species undoubtedly belongs to the subfamily Histerinae due to the combination of the following characters: asetose and impunctate labrum (Fig. 1D), well-developed prosternal lobe, antennal cavity partially closed by prosternal alae (Fig. 1D, E).

Platycretus muscularis was resolved as sister group to Haeteriinae in the phylogenetic analyses. They share several synapomorphies – very wide profemur and long, square shaped labrum which appears to be fused with clypeus (see Fig. 5C). However, the species lacks other defining characters of the Haeteriinae – namely the robust triangular scape. Some characters important for tribal assignment (e.g., meso- and metaventrite) are obfuscated.

Etymology. The Latin adjective *muscularis* (muscular) refers to the thickened meso- and metafemora most likely accommodating a large amount of muscle tissue.

Subfamily Dendrophilinae Reitter, 1909

Without tribal placement

Olexum Simon Pražák & Lackner, gen. nov.

https://zoobank.org/DB13F9F0-9C34-4CF3-9204-D8EB70A64A8B

Type species. *Olexum complanatum* Simon Pražák & Lackner, **sp. nov.**

Diagnosis. Body elongate oval, flattened, dorsally convex. Labrum multisetose. Right mandible apically bidentate. Pronotum and elytra with elongate furrows laterally. Scutellar shield invisible. Propygidium almost entirely covered by elytra. Protibia very broad, with a row of denticles on the outer margin and with a prominent apical spur. All tibiae with tarsal grooves.

Etymology. We name the genus in honour of Aldo Olexa, an excellent Czech specialist of the Histeridae.

Olexum complanatum Simon Pražák & Lackner, sp. nov.

https://zoobank.org/3967566C-8B2C-46F4-A09F-FD3D79C1C4CE

Type material. Holotype specimen (1408/E), female, Northern Myanmar, inclusion in burmite (ca. 99 Ma), amber piece clear, ca. 11×5×1 mm, with unidentified insect fragments and pieces of debris.

Description. ***Measurements.*** Head width: 0.2 mm, width between anterior pronotal angles: 0.23 mm, width between posterior pronotal angles: 0.4 mm, pronotal length: 0.2 mm, elytral length: 0.53 mm, elytral width (across widest point): 0.48 mm. — ***Body*** shape elongate oval, flattened, dorsally convex. Head separated from body, located next to the specimen. Cuticle chestnut brown to black. Pronotum with a fairly dense punctuation, punctures (diameter 5 microns) separated approximately by 2 times their diameters. Punctuation of elytra not visible due to white coating covering dorsal surface. Body venter without visible punctuation. Legs light, brown. Female genitalia exposed. — ***Head*** almost quadrate, clypeus massive, its length approximately 2/3 of frontal length. Clypeus with irregular sparse prominent setae. Setation of frons not observable. Supraorbital area with a row of regularly separated prominent setae (length 50 microns). Frontal and supraorbital striae indiscernible. Clypeolabral suture well visible. Gular sutures narrowly separated. Labrum short, rectangular, dorsally multisetose, with two pairs of long labral setae located at anterolateral corners, intermingled with shorter sparse setae. Right lateral side of labrum with clearly protruding labral fringe. Right mandible bidentate. Subapical tooth prominent and acute, subparallel with outer mandibular margin. Left mandible and rest of the mouthparts missing. Antennal scape short, thickened, apically truncate with several setae. Pedicel at least 3/4 of scape length, thickened, oval, with individual setae. Antennomeres 3–8 approximately of the same length as scape and pedicel combined. Antennomere 8 significantly wider than antennomeres 3–7. Antennal club slightly longer than antennomeres 3–8, strongly flattened with dense setation. Eyes small, almost completely flattened, almost invisible from dorsal view. — ***Thorax.*** Pronotum rectangular, ca. 1.5× wider than long across midline. Lateral stria present, cariniform. Lateral pronotal margin slightly bisinuate, anterior angles rather broadly and obliquely truncate. Pronotal disc asymmetrical (possibly a teratological specimen?). Right lateral area with a single elongate furrow like depression subparallel to the lateral pronotal margin. Left lateral area with two furrow-like depressions, both parallel to the lateral pronotal margin. Single depression at the left anterior angle. Scutellar shield invisible. Elytra longer than wide. Elytral humeri not prominent. Outer lateral margin keel-like, next to it a longitudinal furrow present, reaching approximately 2/3 of elytral length apically. Next to the furrow two faint longitudinal tubercles present medio-apically. Rest of elytral disk without sculpture, elytral suture elevated in apical third. Propygidium almost entirely covered by elytra. Elytral epipleuron with keel-like structures and depressions. Prosternum with a short and broad prosternal lobe with antennal fissures laterally. Basal half of prosternal process between procoxae parallel sided, thence strongly diverging apically. Carinal prosternal stria absent on prosternal apophysis, parallel sided between procoxae, thence strongly diverging anteriorly, concurrent with the prosternal margin. Lateral prosternal stria absent. Antennal cavity present, open anteriorly. Mesoventrite very broad, subtrapezoidal, 4× wider than long. Marginal mesoventral stria faint. Mesoventral disc glabrous. Meso-metaventral suture present. Metaventrite very large and broad, 1.5× wider than long. Marginal metaventral stria absent, postmesocoxal stria faint. Lateral metaventral disc not clearly separated from metaventral disc. Metepisternum fully covered by elytral epipleuron. Lateral disc of metaventrite glabrous. — ***Abdomen.*** First visible abdominal ventrite rectangular, glabrous, twice as long as wide, without striae. Rest of the abdomen telescopically inflexed. Propygidium almost entirely covered with elytra. Pygidium short, triangular, bistriate. Female genitalia exposed, apex of valvifers cut off during polishing process. — ***Legs.*** Profemur

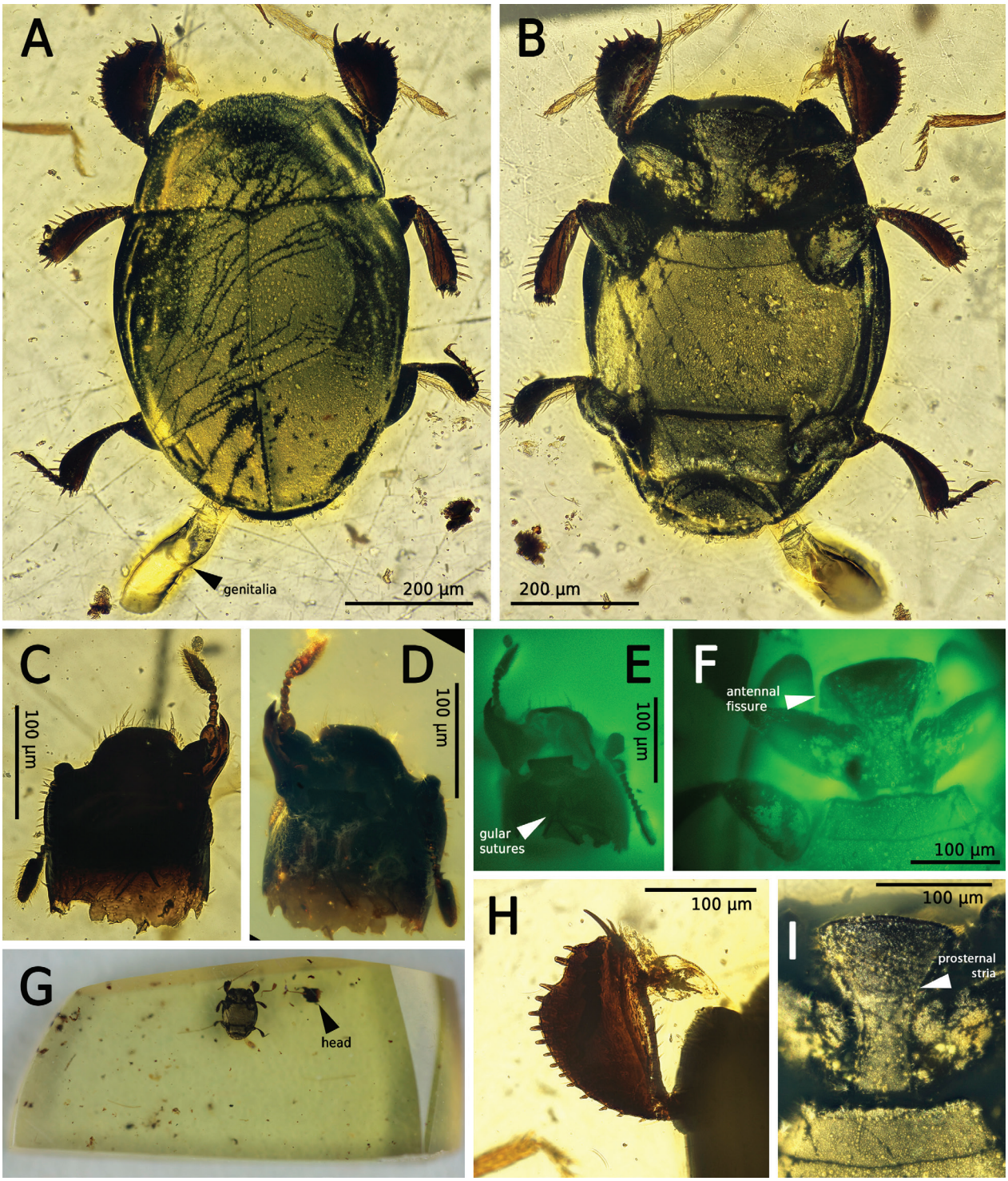

Figure 2. *Olexum complanatum* Simon Pražák & Lackner, gen. & sp. nov. **A** dorsal view; **B** ventral view; **C** head, dorsal view (underlight); **D** ditto, ventral view (overlight); **E** ditto, ventral view (fluorescence); **F** prosternum, mesoventrite (fluorescence); **G** amber specimen; **H** protibia; **I** prosternal process, mesoventrite.

flattened. Protibia strongly dilated, rounded, protibial spur massive; smaller apical spur present underneath it. Outer protibial margin slightly inwardly arcuate in the first anterior forth. Rest of the outer protibial margin round, with regularly separated short denticles, diminishing in size in basal direction, absent in the inwardly arcuate part. Inner protibial margin with a row of setae. Protarsal groove deep, well developed. Terminal protarsomere as long as protarsomeres 1–4 combined. Mesofemur flattened. Outer margin of mesotibia with a row of regularly separated denticles, diminishing in size in posterior direction. Mesotibia with tarsal groove. Mesotarsus with 5 tarsomeres. Mesotarsal claws well developed, longer than half of the terminal mesotarsomere. Metatibia slenderer than mesotibia, curved, with a row of spikes on outer margin sparser than in mesotibia. Metafemur flat. Metatibia with a tarsal groove. Metatarsus with five tarsomeres; tarsomere 5 2.5×

longer than 4; metatarsal claws well developed, longer than half of terminal metatarsomere.

Taxonomic assignment. *Olexum complanatum* can be placed within the subfamily Dendrophilinae based on the following characters: prosternal lobe short, with incision for the passage of antenna (Fig. 2F), antennal cavities widely open.

According to the phylogenetic analysis the species is related to the extant genus *Dendrophilus* Leach, 1817, as well as fossil Dendrophilinae genera *Yethiha* Caterino, 2021 and *Druantia* Caterino, 2021 (Fig. 5). Dendrophilinae subfamily is most likely polyphyletic (Zhou et al., 2020) and comprehensive phylogenetic study is desirable. Hence, we refrain from placing *O. complanatum* into a tribe.

Etymology. The specific name *complanatum* refers to the flattened body shape of this species.

Tribe Anapleini Olexa, 1982

Cretanapleus Simon Pražák & Lackner, gen. nov.

https://zoobank.org/FC48B6D2-709B-4B10-82B7-932267291A26

Type species. *Cretanapleus seideli* Simon Pražák & Lackner, **sp. nov.**

Diagnosis. Body regularly round, convex with lateral and anterior margins strongly emarginated. Head with a carinate frontal stria. Closed antennal cavity located next to procoxae. Elytra strongly truncate apically, elytral epipleuron with two prominent costae on basal half. Protarsal groove with distinctly elevated margins. Outer protibial margin simple, without teeth or denticles, with a row of simple setae.

Etymology. The name consists of the prefix *cret-* referring to the Cretaceous origin of the species, and *Anapleus*, i.e. the extant genus to which the new genus is similar.

Cretanapleus seideli Simon Pražák & Lackner, sp. nov.

https://zoobank.org/1E124B42-BF71-4DA4-9171-60B147356678

Type material. Holotype specimen (1409/E), unknown sex, Northern Myanmar, inclusion in burmite (ca. 99 Ma), amber piece clear, 15×6×2 mm, with small pieces of debris.

Description. ***Measurements.*** Head width: 0.14 mm, width between anterior pronotal angles: 0.175 mm, width between posterior pronotal angles: 0.4 mm, pronotal length: 0.21 mm, elytral length: 0.38 mm, elytral width (across widest point): 0.46 mm. — ***Body*** regularly round, convex, cuticle brown to black, covered with white debris coating. Body margins dorsally explanate. Elytra with punctures (diameter 10 microns) separated by their diameter. Pronotum with irregular weak longitudinal rugae. — ***Head.*** Frontoclypeal area laterally depressed, almost constricted. Frontal stria carinate, widely interrupted medially, slightly continuous to clypeus. Frontal surface laterad of frontal stria forming a depression fit to receive antennal scape in repose, pressed against outer margin of frontal stria. Clypeus anteriorly elevated with large punctures. Labrum dorsally with depressions, with a pair of long prominent setae. Right mandible bidentate with a prominent acute subapical tooth, inner margin of left mandible not visible. Terminal maxillary palpomere elongate, apically acute, slightly flattened. Antennal scape long and robust. Shape of the scape coincident with frontal carina. Pedicel as long as antennomeres 3–6 combined. Antennomeres 3–8 short. Antennal club round, with two apparent straight annuli. Eyes not visible. — ***Thorax.*** Pronotal margins narrowing anteriorly; anterior angles acute. Lateral and anterior margins explanate. Median part of frontal disc punctuate, convex with irregular longitudinal rugae. Posterior margin subungulate. Scutellum minute, triangular. Elytra apically truncate. Lateral and basal elytral margins distinctly explanate. Elytral suture elevated. Elytra punctuate at least medially (punctures separated by their diameter); rest of elytral surface covered with debris. Dorsal striation not discernible. Elytral epipleuron unusually wide with two protuberant costae on basal half. Epipleuron largely conceals metepisternum. Prosternal process rectangular, medially depressed. Prosternal lobe short with distinct margin and with antennal fissures laterally. Apex of prosternal lobe keel-like, elevated. Antennal cavity located near procoxa, deep, closed anteriorly. Mesoventrite transverse, 4x wider than long. Meso-metaventral suture invisible. Meso-metaventral stria carinate, anteriorly arcuate. Anterolateral corners with distinct round depressions. Metaventrite with delicate sparse punctures. Lateral metaventral stria complete, carinate. Metaventral disc convex. Metepisternum largely concealed by elytral epipleuron, with rugose punctuation. — ***Abdomen.*** First visible abdominal sternite with large punctures separated by their diameter. Pygidium with similarly patterned punctures. Other abdominal segments inflexed and covered with debris, unobservable. — ***Legs.*** Profemur with a weakly developed groove for protibial reception. Protibia moderately broad, with a costa along inner margin and slightly thickened along the outer margin, creating a tarsal groove. Outer protibial margin with a dense row of short setae diminishing in size basally, a row of short slender setae also present on the inner margin. Protibial spur tiny. Terminal protarsomere as long as tarsomeres 2–4 combined, claws 1/3 of terminal tarsomere length. Mesotibia slenderer, with a row of short slender setae both on outer and inner margin. Mesotibia with a shallow groove for mesofemoral reception. Me-

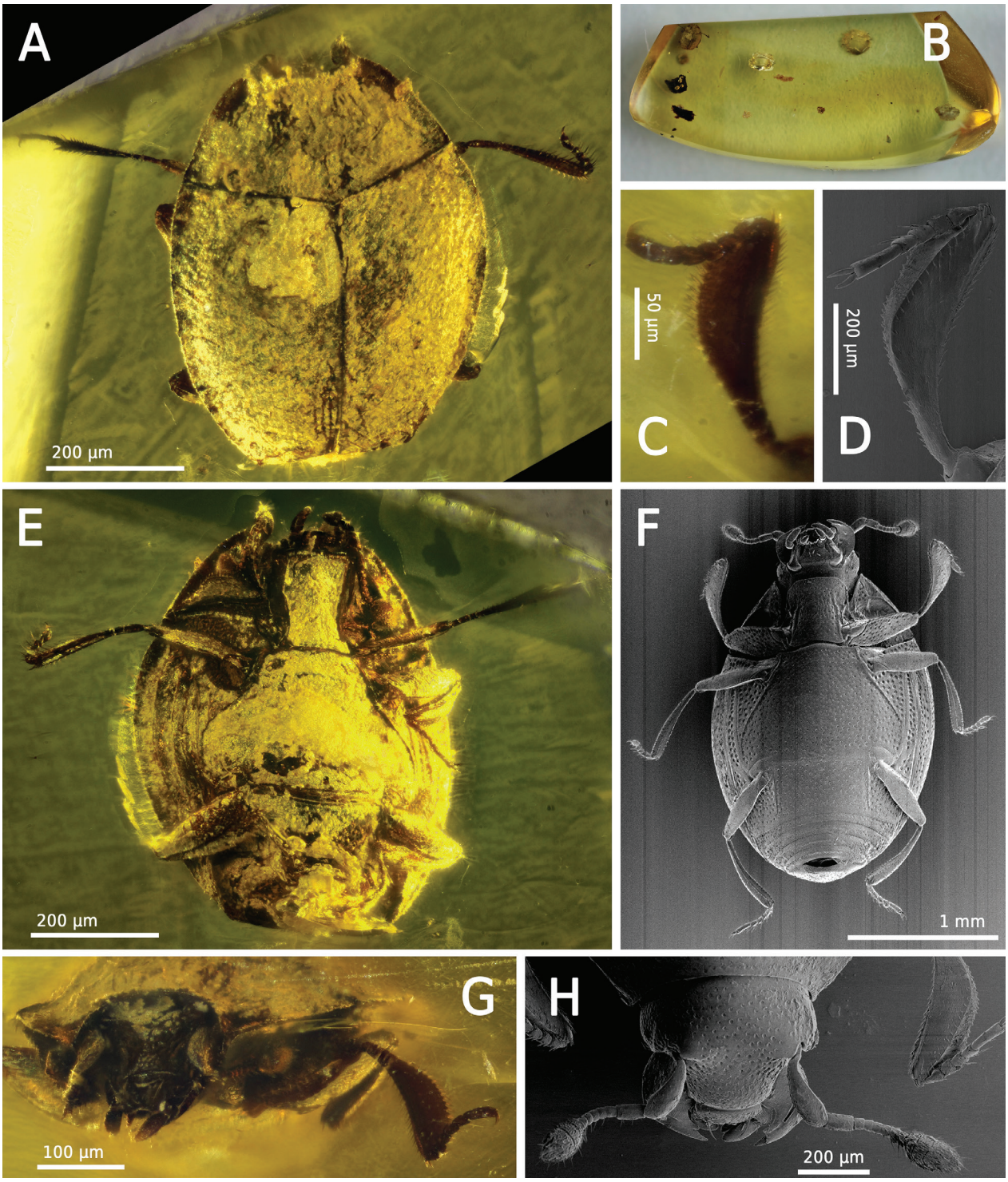

Figure 3. *Cretanapleus seideli* Simon Pražák & Lackner, gen. & sp. nov. (A, B, C, E, G) and *Anapleus* sp. (Turkey; D, F, H; SEM micrographs). **A** dorsal view; **B** amber specimen; **C**–**D** protibia; **E**–**F** ventral view; **G**–**H** frontal view.

sotarsus similar to protarsus. Metafemur with a groove for metatibial reception, otherwise hind leg identical to middle leg.

Taxonomic assignment. *Cretanapleus seideli* can be clearly placed in the Dendrophilinae based on the prosternum with a short prosternal lobe with antennal fissures laterally. We further place this species in the monophyletic tribe Anapleini (Zhou et al. 2020), as defined by Olexa (1984), based on protibial characters: protarsal groove with distinctly elevated margins, outer protibial margin simple, devoid of teeth or denticles, with a simple row of setae (Fig. 3C, D). However, *C. seideli* differs from the only extant genus of the tribe, *Anapleus* Horn, 1873, in several significant characters: presence of frontal stria (absent in *Anapleus*, Fig. 3G, H), deep and closed antennal cavity (shallow and widely open in *Anapleus*), and strongly emarginated lateral

body margins (Fig. 3G, rounded in *Anapleus*). Our phylogenetic analyses confirmed the placement of *C. seideli* in Anapleini (Fig. 5).

Etymology. We dedicate the species to Dr. Matthias Seidel (Naturhistorisches Museum, Vienna, Austria) who introduced the first author of this paper to the study of fossil beetle inclusions.

Without tribal placement

Genus *Yethiha* Caterino, 2021

Yethiha pubescens Simon Pražák & Lackner, sp. nov.

https://zoobank.org/B238C826-97E4-4BD4-893F-261D3B783036

Type material. Holotype specimen (1410/E), unknown sex, Northern Myanmar, inclusion in burmite (ca. 99 Ma), amber piece clear, ca. 14x5x1 mm, without synclusions.

Description. ***Measurements*.** Head width: 0.25 mm, width between anterior pronotal angles: 0.29 mm, width between posterior pronotal angles: 0.61 mm, pronotal length: 0.33 mm, elytral length: 0.6 mm, elytral width (across widest point): 0.7 mm. — ***Body*** round, strongly convex dorsally; dorsum with visible pubescence. Colour dark reddish brown, covered with white debris. — ***Head.*** Supraorbital area with a row of prominent setae continuous along the occipital ridge. Clypeus densely setose, setae prominent. Labrum subtrapezoidal, lateral margins rounded, labral disc multisetose, with a prominent long seta (approximately 3× as long as the remaining labral setae) on each side. Outer lateral margin of mandible setose. Mandibular apex acute, each mandible with a prominent subapical tooth; mandibular prostheca well developed. Maxillary galea round, setose, lacinia setose, with a clearly developed lacinial fringe. Lacinial hook (uncus) well developed, prominent. Terminal maxillary palpomere long and slender. Terminal labial palpomere thickened, pointed apically. Antennal scape thick. Pedicel thickened, approximately as long as antennomeres 3–5 combined. Antennomere 8 dilated. Each antennomere 3–8 with at least two prominent setae. Antennal club rounded, flattened, densely setose, sparse long setae intermingled with short denser setae, with 2 clearly visible sutures. Eyes flattened, well visible from above. — ***Thorax.*** Base of the pronotum with sparse microscopic setation (setae 20 microns long). Marginal pronotal stria present, complete. Basal margin almost rounded, slightly pointed. Scutellum invisible. Elytral base, apex and elytral disc pubescent. Setae brown, each located in a pore, separated approximately by four times of the pore diameter. Elytral flanks with shorter and denser setation. Elytral epipleuron with a single well-developed complete stria. Other striation not visible. Prosternal lobe short and broad, incised laterally for the antennal passage. Antennal cavities widely open anteriorly. Prosternal process square shaped. Prosternal striation not visible. Mesoventrite short and wide (4x wider than long). Mesoventral striation not visible. Metaventrite very large, broad, convex, with scattered irregular shallow punctures. Lateral metaventral stria absent. Post mesocoxal striae present, thin, attaining metepisternum. — ***Abdomen.*** Propygidium almost entirely covered with elytra. Pygidium covered with debris. — ***Legs.*** Profemur with a deep groove for protibial reception. Protibia very broad with short denticles along the outer margin and very short thick setae along inner margin. Protibial spur thick, prominent. Protarsal groove developed, margined by another row of prominent setae. Terminal protarsomere as long as protarsomeres 1–4 combined. Tarsal claws short, approximately one third of the terminal tarsomere length. Mesotibia slender, outer margin with relatively long sparse denticles, diminishing in size in basal direction. Inner margin with a row of short thick setae. Tarsal groove not present. Tarsal claws short, approximately one third of the terminal tarsomere length. Metatibia and metafemur largely similar to mesotibia and mesofemur. Terminal metatarsomere significantly thickened. Tarsal claws short, approximately half of the terminal metatarsomere length.

Taxonomic assignment. The present species falls within the recently described genus *Yethiha* Caterino, 2021 based on the strongly convex dorsum lacking striae and carinae, invisible scutellum (observed by Caterino (2021) as "tiny or absent") and broad protibia with a prominent apical spur.

According to the phylogenetic analyses, genus *Yethiha* proved to be a part of the Dendrophilinae as suggested by Caterino (2021). In our analyses (Fig. 5), it was revealed as closely related to the extant *Dendrophilus* Leach, 1817 and the extinct *Druantia* Caterino, 2021 (Fig. 5). Future analyses would be required in order to unequivocally place *Yethiha* into an existing dendrophiline tribe.

Differential diagnosis. *Yethiha pubescens* **sp. nov.** differs from *Y. peregrina* Caterino, 2021 by the presence of elytral and pronotal pubescence (Fig. 4F). Head pubescence is also denser and more prominent than that of *Y. peregrina.* Furthermore, the present species is characterised by prominent thick setae on the inner and more robust denticles on the outer protibial margin. Meso- and metatibiae are likewise significantly more robust (Fig. 4B; width:length ratio in *Y. peregrina*: mesotarsomeres 1–4: 2:5, mesotarsomere 5: 1:5, metatarsomeres 1–4: 1:2–3, metatarsomere 5: 3:10; width:length ration in *Y. pubescens*: mesotarsomeres 1–4: 1:1, mesotarsomere 5: 1:2, metatarsomeres 1–4: 1:1, metatarsomere 5: 1:2).

Etymology. Latin term *pubescens* refers to the hirsute cuticle of the species.

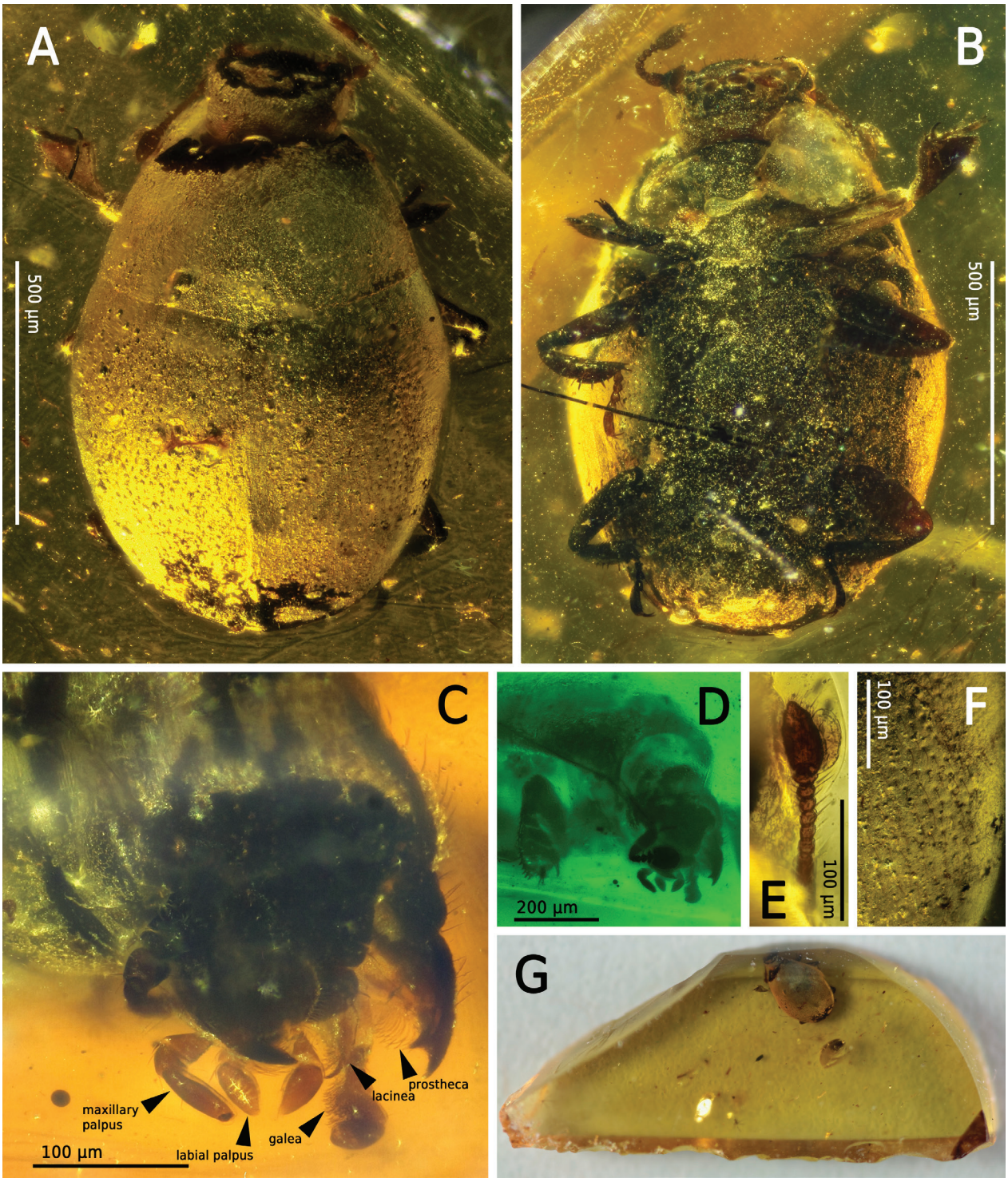

Figure 4. *Yethiha pubescens* Simon Pražák & Lackner sp. nov. **A** dorsal view; **B** ventral view; **C** head, frontal view; **D** ditto, oblique view; **E** flagellum; **F** elytral setation; **G** amber specimen.

4. Discussion

4.1. Phylogenetic analyses

Olexum, *Yethiha* and *Druantia* nested in a lineage sister to the genus *Dendrophilus*. They share several features with *Dendrophilus*, namely the invisible scutellar shield and multisetose labrum. Dendrophilinae have been proven polyphyletic and can be revised only after a robust phylogenetic study of the Histeridae (Ślipiński and Mazur 1999, Caterino and Vogler 2002, Zhou et al. 2020). Hence, the exact position of the mentioned dendrophiline fossils remains unresolved.

Onthophilinae-like fossil taxa form a lineage separate from the extant *Onthophilus* and *Epiechinus*. This finding supports the suggestion of Caterino (2021) who proposed that *Cretonthophilus*, *Carinumerus* and *Phas-*

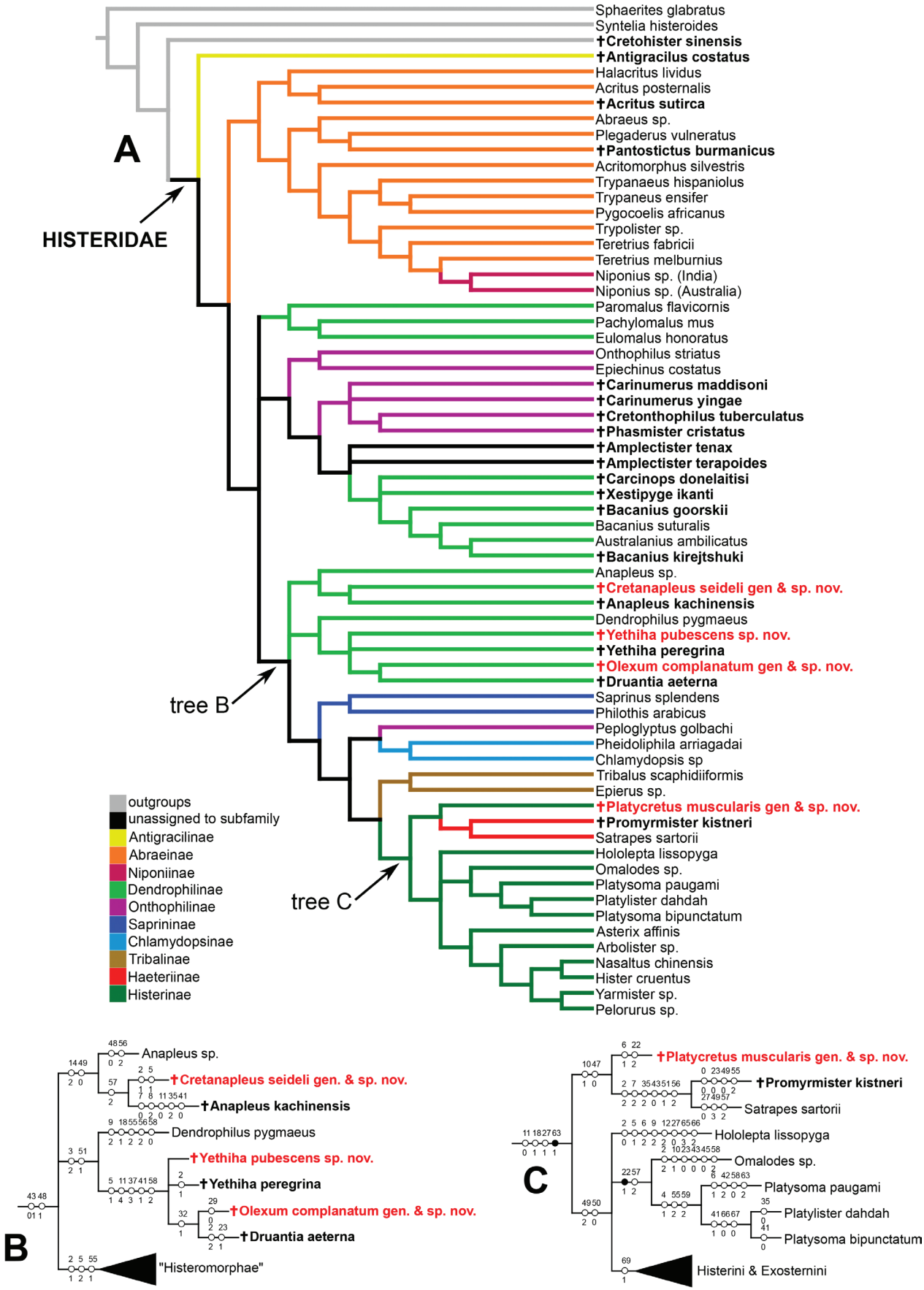

Figure 5. Maximum parsimony analysis of the position of known fossil species of the Histeridae. **A** the complete tree showing the position of the fossils and the current subfamily classification of the lineages; **B** Dendrophilinae part of the tree with mapped characters; **C** Histerinae part of the tree with mapped characters. Bold taxa = fossils, red taxa = fossils described in this paper. For characters see Zhou et al. (2020).

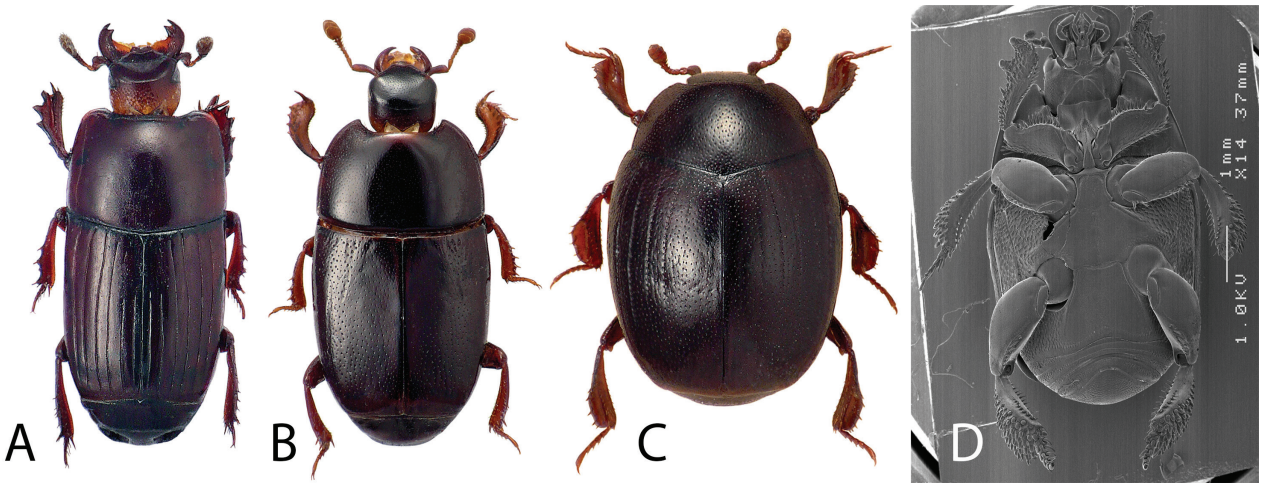

Figure 6. Morphological adaptations in today's Histeridae. **A** flattened body shape, subcortical space: *Nicotikis gratus* Cooman, 1941 (Histerinae: Platysomatini); **B** flattened body shape, subcortical space: *Platylomalus complanatus* (Panzer, 1797) (Dendrophilinae: Paromalini); **C** convex body shape, dilated tibiae, rotten wood: *Dendrophilus punctatus* (Herbst, 1791) (Dendrophilinae: Dendrophilini); **D** enlarged femora, littoral environment: *Pachylopus rossi* Kovarik & Verity, 1999 (Saprininae).

mister might form a distinct lineage based on several possible synapomorphies that separate them from all extant Onthophilinae (e.g., hypomeral antennal cavity, broad humeral expansion of the elytra). However, the sampling of Onthophilinae in the study of Zhou et al. (2020) is low. We propose that a more comprehensive study of the Onthophilinae phylogeny with sufficient sampling of both extant and extinct taxa is needed to unequivocally resolve the position of fossil Onthophilinae.

Platycretus muscularis is the first representative of the Histerinae from the mid-Cretaceous, only known from Cenozoic compressed fossils so far. Multiple clown beetle species assigned to the genus *Hister* have been described from the Oligocene and Miocene deposits of Céreste (France) and Oeningen (Germany) (Heer 1862; Dégallier et al. 2019). As recent phylogenetic studies suggest, Histerinae are paraphyletic, due to the inclusion of both Haeteriinae and Chlamydopsinae (Caterino and Tishechkin 2015; Zhou et al. 2020), but the formal reclassification of those subfamilies has not yet taken place. Thus, *Platycretus muscularis* is the second known Mesozoic fossil of the Histerinae+Haeteriinae+Chlamydopsinae lineage, after the highly modified "haeterine" *Promyrmister kistneri* (Zhou et al. 2019). According to the topology recovered in our analysis, *Platycretus muscularis* represents a sister group to the Haeteriinae subfamily.

4.2. Palaeobiology and palaeoecology implications

The flattened body shape of *Platycretus muscularis* is analogous to the body shape of Histeridae with subcortical life style (Fig. 6A, B). The beetle possesses strikingly thickened meso- and metafemora. Similar enlarged femora are found in some Saprininae (with convex body shape) inhabiting littoral environments, where the enlarged femora accommodate increased amount of muscle tissue (Lackner 2010) in order to dig and push through wet substrates, mostly sand (Fig. 6D). We expect that *P. muscularis* used the enlarged legs for pushing through tight crevices in decaying wood or subcortical spaces of (possibly freshly) dead trees (similar as Hololeptini). The triangular cross section of femurs, strongly carinate elytral epipleuron and frontal stria also present an adaptation making the beetle more resistant to external pressures. Dilated protibiae were presumably used as a tool for digging through soft materials found under bark.

Olexum complanatum is likewise strongly dorsoventrally flattened. The broad but not thick protibiae probably allowed the beetle to shovel through soft material under bark of decaying trees. Similar morphotype is typical for some extant dendrophiline taxa that inhabit subcortical spaces (Fig. 6B).

The subcortical spaces and rotten wood of substantially decayed trees may also host histerid species with more convex body shape (e.g., *Dendrophilus* spp., *Carcinops* spp.). This could also be the case of the *Yethiha*. Its overall appearance resembles that of *Dendrophilus* (Fig. 6C) but is more convex. Dilated protibiae are typical for histerid taxa inhabiting soft decaying wood material. *Yethiha pubescens* was most likely associated with decaying wood, either in fallen tree trunks or in tree cavities, as is the majority of the Dendrophilinae subfamily where it belongs.

Little is known about biology of the genus *Anapleus*. Some species have been collected via deep soil traps (Ôhara, personal communication to TL in 2010). *A. wenzeli* has been found in a cave (Vomero 1977). Mazur (2001) states that many species of the genus inhabit rodent burrows. These findings suggest a tendency of the genus to inhabit underground spaces. Unlike extant species of *Anapleus* (Olexa 1982), *Cretanapleus seideli* has a strongly developed carinate frontal stria (see Fig. 3G, H), which can provide better protection when the head is retracted and antennae pressed against it. Well developed antennal cavity also has a protectory function. It is

likely the taxon lived in more exposed habitats (not underground), which is also supported by the fact that the beetle was trapped in resin.

5. Conclusion

Our study, along with other recently published papers (Caterino and Maddison 2018, Zhou et al. 2019, Jiang et al. 2020, 2022, Caterino 2021, Yamamoto and Caterino 2022), suggests that the significant diversity of Histeridae life strategies is of ancient origin. By the mid-Cretaceous, myrmecophily or other form of inquilinism developed in at least two unrelated lineages – *Promyrmister* and *Amplectister* (Caterino and Maddison 2018, Zhou et al. 2019, Yamamoto and Caterino 2022) and at least two unrelated lineages adopted subcortical strategy – *Platycretus* and *Olexum+Druantia*.

6. Acknowledgements

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Supplementary Material 1

Character matrix

Authors: Simon Pražák J, Fikáček M, Prokop J, Lackner T (2023)
Data type: .txt
Explanation note: Matrix contains morphological dataset of Zhou et al. (2020) with added fossil taxa.

Link: https://doi.org/asp.81.e102404.suppl1

Supplementary Material 2

Newick tree

Authors: Simon Pražák J, Fikáček M, Prokop J, Lackner T (2023)
Data type: .tre
Explanation note: Phylogenetic tree containing all described fossil Histeridae.

Link: https://doi.org/asp.81.e102404.suppl2