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

Jan Simon Pražák1,2, Martin Fikáček3,4, Jakub Prokop1, Tomáš Lackner5

1 Charles University, Faculty of Science, Department of Zoology, Viničná 7, 12800 Prague 2, Czech Republic
2 Museum of Eastern Bohemia in Hradec Králové, Eliščino nábřeží 465, 500 03 Hradec Králové 3, Czech Republic
3 Department of Biological Sciences, National Sun Yat-sen University, No. 70, Lienhai Rd., Kaohsiung 80424, Taiwan
4 Department of Entomology, National Museum, Cirkvová 1740, Praha–Horní Počernice, Czech Republic
5 Bavarian State Collection of Zoology, Münchhausenstraße 21, 81247 Munich, Germany

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Corresponding author: Jan Simon Pražák (j.prazak@muzeumhk.cz)

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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., Cretanaplesus 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 fungal 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 Theobald 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, Haeterininae 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).


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.777690. 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.

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<td>Lac Chambon, France</td>
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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.


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, inclusions: plant material, minute seeds, unidentified insect fragments.
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. Metatibia 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).

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**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.
**Platycretus muscularis** was resolved as sister group to Haeteriniinae in the phylogenetic analyses. They share several synapomorphies – very wide profemur and long, square shaped labrum which appears to be fused with elytrum (see Fig. 5C). However, the species lacks other defining characters of the Haeteriniinae – 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 near 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 quadrato, elytrum 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. Clypealabral 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 truncated 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. Mesoscutum 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 valves cut off during polishing process. — **Legs.** Profemur
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.** *Oleum 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 *Yethiba* 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 lateral 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 epipleurum 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 indexed 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-
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

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**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.
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 multisette, 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 clear-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 microscopical setation (setae 20 microns long). Marginal pronotal stria present, complete. Basal margin almost rounded, slightly pointed. Scutellum invisible. Elytral apex, base 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 striaion not visible. Mesonotum very large, broad, convex, with scattered irregular shallow punctures. Lateral metaventral stria present. Post mesocoxal striae present, thin, attaining metapoststernum. — 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 dorsal 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 ratio 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.
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 dendrophilines 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).
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 (Vomer 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 Amplictister (Caterino and Maddison 2018, Zhou et al. 2019, Yamamoto and Caterino 2022) and at least two unrelated lineages adopted subcortical strategy – Platyceretus and Olexum+Druianta.

6. Acknowledgements

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7. References


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.

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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.

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