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## Eucnemidae from Burmese Amber

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## The late Cretaceous amber Eucnemidae fossils from Myanmar

JYRKI MUONA

### Abstract

Eight new genera and twenty new species of Eucnemidae are described from Cretaceous Myanmar amber: *Cupressicharis* n. gen. (type-species *Cupressicharis elongatus* n. sp.), *Cylus* n. gen. (type species *Cylus carinifer* n. sp.), *Falsethambus* n. gen. (type species *Falsethambus burmensis* n. sp.), *Fiegelia* n. gen. (type species *Fiegelia antennata* n. sp.), *Paleoeucnemis* n. gen. (type species *Paleoeucnemis minutus* n. sp.), *Protomicrorhagus* n. gen. (type species *Protomicrorhagus antennatus* n. sp.), *Protovitellius* n. gen. (type species *Protovitellius deceptus* n. sp.) and *Pseudomyall* n. gen. (type species *Pseudomyall elongatulus* n. sp.). Eleven further species are described: *Coenomana brevicornis* n. sp., *Euryptychus acutangulus* n. sp., *Euryptychus burmensis* n. sp., *Euryptychus elegantulus* n. sp., *Euryptychus mysticus* n. sp., *Epiphania burmensis* n. sp., *Falsethambus gracilicornis* n. sp., *Fiegelia tarsalis* n. sp., *Jenibuntor pusillus* n. sp., *Myall burmensis* n. sp., *Protomicrorhagus brevis* n. sp., *Sieglindea antiqua* n. sp.

*Coenomana clavata* Otto is transferred from tribe Jenibuntorini to tribe Dirhagini. *Muonabuntor grandinotalis* Li, Tihelka & Cai is transferred from tribe Jenibuntorini to tribe Euryptychini.

### Introduction

MUONA et al. (2020b) discussed the evidence needed for placing a fossil clicking Elateroidea species in a correct family. The main thing to consider was that Eucnemidae (MUONA, 1993a; LAWRENCE ET AL., 2007; MUONA & TERÄVÄINEN, 2020a), Cerophytidae (YU ET AL., 2019) and Throscidae (MUONA, 2019) have external synapomorphies supporting the monophyly of these clades. Elateridae on the other hand cannot be defined with external synapomorphies, but their monophyly is supported by Maximum Average Likelihood analyses of molecular data (e.g. KUNDRATA ET AL., 2014). Thus, a fossil can be classified as being an Elateridae only if the synapomorphies of the three other families are not present. As long as this situation obtains, the identification of Elateridae fossils remains difficult.

This paper deals with Mesozoic amber Eucnemidae fossils from deposits in Myanmar, often known also as Burmese amber (CRUICKSHANK & KO, 2007). These have become available in considerable numbers during the last decade and clicking Elateroidea are frequent in the material. As the offerings rarely separate the Elateroidea families from each other, it is possible to get a rough idea of their frequencies in the material. Specimens belonging to Eucnemidae and Elateridae are frequent, Cerophytidae less so and the rarest ones are the Throscidae. The author has obtained about 60

Burmese amber samples with Eucnemidae inclusions this far. A study of this material provides a first extensive view of the composition of the false click-beetle fauna 99 million years ago. This first installment of the material is limited to twenty species category taxa as more than half of the samples require further technical work.

Two Eucnemidae species have been described from Myanmar material earlier (OTTO, 2019; LI et al., 2020). Their status is discussed here as well.

### Material and methods

All the samples originated from the Hukawng Valley, northern Myanmar and belong to the author's collection (JMC), currently located in the Finnish Museum of Natural History, Helsinki University, Finland (MZH).

Specimens were screened with a binocular microscope under variable magnifications and lightning regimes. Samples were secured in different position with a small piece of modelling clay before inspection. Once the required features had been observed, the samples were taken to a microscope facility providing video equipment for obtaining images. Image stacking was not used as the required angles usually were hampered by problematic areas of unequal amber

densities and single shots seemed to work better. The features searched for were in approximate order: excretory punctures on elytral apices placed in J-formed deeper grooves (OTTO & GRUBER, 2016; MUONA & TERÄVÄINEN, 2010a); number of protibial spines (MUONA, 1993a); basal and apical structure of antennae (MUONA, 1993a); type and visibility of labrum (MUONA, 1993a); presence and type of antennal grooves (MUONA, 1993a; MUONA, 2019); structure of tibiae and tibial spine combs (MUONA, 1993a); presence and type of sex-combs on protarsomere one (MUONA, 1993a) as well as presence of dorsal carinae on pronotum. If structures placing the sample in a presently accepted Eucnemidae subfamily were found, tribal synapomorphies presented in MUONA (1993a) were searched for next.

The descriptions focus in evolutionary essential features, i.e. synapomorphies of categorical rank in question, and no attempt were made to describe all possible details of the species. After all, most of the species are known from singletons in less than perfect condition. Special attention is drawn to characters conflicting with the structures found in extant putative relatives. Such new character combinations necessitate a new global analysis of all the taxa in order to assess their evolutionary importance, i.e. whether they are synapomorphies or not. No such analyses were attempted at this time as new Burmese fossil taxa keep turning up all the time. Recovery of new specimens of already known species is very rare, however, indicating that our knowledge of the whole fauna is still inadequate.

In order to keep the descriptions short and clear, the following terms have been abbreviated: scape, pedicel and nine flagellomeres are referred to as antennomeres a1-a11.

## Systematic paleontology

### Order Coleoptera Linnaeus, 1758

#### Superfamily Elateroidea LEACH, 1815

#### Family Eucnemidae ESCHSCHOLTZ, 1829

#### Subfamily Palaeoxeninae MUONA, 1993a

#### Genus *Cupressicharis* new genus

##### Type species: *Cupressicharis elongatus* new species

Derivation of name: assumed to be connected with ancient Cupressaceae trees, indicating “to love cypresses”, gender masculine.

#### Diagnosis

Elateroidea synapomorphy: promesothoracic clicking mechanism present.

Eucnemidae synapomorphies: a2 attached sub-

apically to a1, labrum attached underneath the frontoclypeal region, hidden.

Palaeoxeninae synapomorphies: a9 – a11 forming flattened club with apically concave antennomeres.

Diagnostic other Palaeoxeninae characters: protibiae with two apical spines, antennal insertions in pits, widely separated, mandibles long and slender, meso- and metatibiae with numerous irregular spine-combs on lateral surfaces.

## Description

Body slender (figs. 1, 2). Dorsum obfuscated, ventrum partly as well, pro-mesocoxal region slightly visible and head, mouthparts, antennae and all legs well exposed (fig. 3). Labrum hidden under frontoclypeal region, mandibles long and slender. Antennae attached widely apart, loosely composed, with three-segmented flattened club, a9 – a11 apically excavated, a2 attached subapically to a1 (fig. 3). Protibiae with two apical spines (fig. 5), meso- and metatibiae with strong irregular spine-combs, tarsomeres stout, tubular, ventrally densely covered with stout hairs, apically with several short spines, claws elongate, simple (fig. 4).

### *Cupressicharis elongatus* new species

Derivation of name: body form elongate, narrower than other Palaeoxeninae species.

#### Holotype

Sex unknown, embedded in oval, flat amber piece, 32 mm x 23 mm. Much of the amber is clouded by debris.

## Description

Form slender, legs and antennae long. Characterized by the generic features. Length 6.5 mm.

#### Note

Although much of the sample remains obscure, Palaeoxeninae apomorphy as well as other typical external characters for this subfamily can be observed. From the only previously known genus, *Palaeoxenus* Horn, *Cupressicharis* differs sharply by narrower form, elongated legs and loosely organized antennae.

#### Superfamily Elateroidea LEACH, 1815

#### Family Eucnemidae ESCHSCHOLTZ, 1829

#### Subfamily Eucneminae ESCHSCHOLTZ, 1829

#### Tribe Dyscharacthini MUONA, 1993a (tentatively)

#### *Cylus* new genus

Type species: *Cylus carinifer* new species

Derivation of name: formed by rearranging the letters of the generic name *Lycus* (family Lycidae), having similar kind of surface structure, gender masculine.

### Diagnosis

Elateroidea synapomorphy: promesothoracic clicking mechanism present (figs. 7, 8).

Eucnemidae synapomorphies: a2 attached subapically to a1, labrum attached ventrally to clypeus, partly visible (fig. 8), abdominal ventrites connate, elytral interstices with excretory pores at apex (fig. 6).

Features suggesting Eucneminae: antennal grooves basally closed, metaventrite with medial tarsal grooves, meso- and metatibiae without spine-combs.

Features suggesting Dyscharachthini: frontoclypeal region with strong lateral ridges, hypomera without sensory pits or hair-fringes, antennae with nearly uniform, slightly dentate, slender a3 – a11.

Generic characters: hypomera with sublateral antennal grooves (figs. 7, 8), pronotum and elytra with unique carinae (fig. 6).

### Description

Head evenly curved, strongly declined, a2 small, attached subapically to long a1, 3rd longer than subsequent antennomeres, a2 – a10 slender, close to equal but becoming slightly longer towards apex, a11 longer than a10, all nearly moniliform, a4 – a9 slightly dentate. Frontoclypeal region strongly widening apically, with powerful lateral ridges extending from apex to past antennal insertions, labrum partly exposed, mandibles stout, bifid.

Hypomera without hair-fringes or excretory pockets, with medially located antennal grooves narrowing caudad and closing there. Prosternal peg is very high, excavated in lateral view with equally long dorsal and ventral apices, arrowhead-shaped in ventral view. Metaventrite on both sides with pronounced pockets and long median groove. Legs delicate, without spine-combs, tarsi moderately long, tarsomere 4 excavated, claws simple.

Dorsum characteristic. Pronotum with four partially united crests similar to those found in many Lycidae, elytra with strongly punctate striae and ridge-like sharp interstices, apically with specialized excretory punctures in first and lateral outermost interstices.

### *Cylus carinifer* n. sp.

Derivation of name: carrying many ridges on its back.

#### Holotype

Embedded in triangular, cone-shaped amber piece, 25 mm x 15 mm, 12 mm, sex unknown.

### Diagnosis

Highly characteristic due to the dorsal surface structure in combination with the clicking mechanism and antennal structure described for the genus.

### Description

Both dorsum and ventrum densely and fairly strongly punctate, eyes large, occiput narrow, conspicuously widening toward mouth, metacoxal plates sharply angled close mid-line, about three times as wide there as at sides.

Length 3.9 mm.

Note

This genus differs from all previously known Eucnemidae by its peculiar dorsal structure. The presence of strong striae with large punctures and the strong dorsal carinae are aberrant features for all Eucneminae clades. The position of antennal grooves is very unusual as well, resembling those of the Dirrhagini genus *Porraulacus* Fleutaux. However, in that genus the grooves are notosternal, not separate from the notosternal suture as in *Cylus*. The partly exposed labrum, attached underneath clypeus, is known from Baltic and Burmese Amber Euryptychini and extant Anischiinae and Melasinae.

This genus is placed in Eucneminae and is tentatively considered to belong to Dyscharachthini on the basis of the structure of the antennae and the frontoclypeal region.

### Superfamily Elateroidea LEACH, 1815 Family Eucnemidae ESCHSCHOLTZ, 1829 Subfamily Melasinae FLEMING, 1821

### Tribe Epiphanini MUONA, 1993a

### *Epiphanis burmensis* new species

Derivation of name: Found in Myanmar, aka Burma.

#### Holotype

Embedded in rectangular Burmese Amber piece, 13 mm x 8.2 mm, sex male.

### Diagnosis

Elateroidea synapomorphy: promesothoracic clicking mechanism present (fig. 11)

Eucnemidae synapomorphies: a2 attached subapically to a2 (fig. 10), labrum attached underneath the frontoclypeal region, hidden, elytral striae with apical excretory punctures.

Melasinae, Epiphanini other diagnostic characters: a8 – a11 greatly elongated, hypomera simple,

frontoclypeal region expanded, with small knob-like keel, male protarsomere 1 without sex-comb.

### Description

Length 4.0 mm.

Form elongated, narrowing conspicuously both cranially and caudally (fig. 9). Head elongated, densely hairy, frontoclypeal region expanded towards apex, slightly keeled in front, labrum hidden, mandibles bifid. Pronotum with long, acute hind angles, evenly and strongly narrowing cranially, very densely punctate (fig. 9). Elytra with sharp striae, these strongly deepening at caudal end, the first with apical excretory punctures, intervals flat on disk, strongly convex at apex, densely punctate, vestiture inconspicuous. Antennae inserted in pits, long, a1 very long, elongated, a2 long as well, subapically attached to a1, a3 – a7 relatively short, a8 – a11 elongated, of about equal length, individually about half the length of scape (fig. 10). Hypomera unmodified, prosternal peg acute in ventral view, slightly deflexed in lateral view. Mesosternal sclerites fused, last abdominal ventrite connate. Metacoxal plates strongly oblique. Legs elongated, meso- and metatarsi longer than corresponding tibiae, these with sparsely set strong spines intermixed with hairs. Meso- and metatrochanters elongated (fig. 11).

#### Note

With respect to antennae, metacoxal plates and frontoclypeal expansion similar to the extant *Epiphania cornutus* ESCHSCHOLTZ, but with exceptionally long a1 and elongated meso- and metatrochanters, slender and flat body, rounded frons with minimally developed keel and very long legs. The greatly elongated a8 – a11 are a male characteristic of *Epiphania cornutus* ESCHSCHOLTZ and the holotype of *E. burmensis* n. sp. is no doubt a male as well.

There is no phylogenetic reason to erect a new genus for this species, as it obviously is a close relative of the extant *Epiphania cornutus*.

### Superfamily Elateroidea LEACH, 1815 Family Eucnemidae ESCHSCHOLTZ, 1829 Subfamily Macraulacinae FLEUTIAUX, 1922

### Tribe Euryptychini MAMAEV, 1976 (probably)

#### *Euryptychus acutangulus* new species

Derivation of name: pronotal hind angles are especially acute.

#### Holotype

Embedded in oval amber piece, 13 mm x 21 mm, sex probably female.

### Diagnosis

Elateroidea synapomorphy: promesothoracic clicking mechanism present (fig. 12).

Eucnemidae synapomorphies: labrum attached underneath the frontoclypeal region, hidden, a2 attached subapically to a1 (fig. 12), mesoventrites fused, abdominal ventrites connate, elytral striae apically with excretory punctures (fig. 14).

Euryptychini diagnostic other characters: a9–a11 elongated, hypomera simple, tibiae with numerous spine-combs, protibiae with one spur. There is only one recognized genus in the tribe, *Euryptychus* LeConte.

Differs from all other Burmese *Euryptychus* species by the acutely produced pronotal hind angles (fig. 13).

### Description

Length 6.0 mm.

Pronotum longer than wide, very densely and minutely punctate, hind angles acute, caudad extended, apices slightly ventrally curved (fig. 13). Elytra feebly striate, striae with distinct punctures, interstices densely punctate, slightly coarser than pronotum (fig. 13). Elytral apices with large excretory punctures on 1st and outermost striae (fig. 14).

Mandibles long and slender, labrum hidden. Antennae moderately long, a2 short, attached subapically to a1, a3 and a4 about equal, elongate, a5 – a8 slightly longer than wide and becoming shorter towards apex, a9 – a11 elongated, a10 about three times as long as wide, a11 apically acute, longest of all (fig. 12, 13). Hypomera simple, prosternal process wide, abruptly narrowing to form short, acute peg. Mesoventrites fused, metaventrite without tarsal grooves, abdominal ventrites connate. Labrum hidden, mandibles long, ventrally expanded. Legs slender, tibiae with numerous spine-combs, protibiae with one apical spine, tarsi moderately slender, metatarsomere 1 distinctly shorter than 2 – 5 combined, claws simple, protarsomere one without sex-comb.

The holotype is partly deformed.

#### Note

As defined by MUONA (1993a), the tribe Euryptychini differs from the tribe Oroditini by having a male sex-comb on protarsomere one. The general form and structure of *E. acutangulus* n. sp. suggest it belongs to Euryptychini and is then a female. Species belonging to these two tribes are the commonest Burmese Amber eucnemids and a future analysis including this material as well as the extant forms and the many Baltic Amber specimens hopefully clarifies further the relationship of these two tribes and the generic placement of all the species.

**Superfamily Elateroidea LEACH, 1815**  
**Family Eucnemidae ESCHSCHOLTZ, 1829**  
**Subfamily Macraulacinae FLEUTIAUX, 1922**

**Tribe Euryptychini MAMAEV, 1976 (probably)**

***Euryptychus burmensis* new species**

Derivation of name: Found in Myanmar, aka Burma.

**Holotype**

Embedded in rectangular amber piece, corners widely rounded, 14 mm x 17 mm, sex most likely female.

**Diagnosis**

Elateroidea synapomorphy: promesothoracic clicking mechanism present (fig. 15, 16)

Eucnemidae synapomorphies: a2 attached subapically to a1, labrum attached underneath the frontoclypeal region, hidden (fig. 16), abdominal ventrites connate (fig. 15).

Euryptychini diagnostic other characters: a9-a11 elongated, hypomera simple, tibiae with numerous spine-combs, protibiae with one spur.

There is only one recognized genus in the tribe, *Euryptychus* LeConte.

Differs from *E. acutangulus* n. sp. by the short hind angles of pronotum, from *E. elegantulus* n. sp. by the wide, rounded form and shorter and wider pronotum and from *E. mysticus* n. sp. by the hidden labrum.

**Description**

Dorsum visible only for a short distance from side (fig. 15). Elytra with distinctly punctate striae, interstices finely and densely punctate. Pronotal hind angles acute, short. Mandibles long, ventrally expanded, punctate, labrum hidden (fig. 16). Antennae moderately long, a2 short, attached subapically to a1, a4-a8 slightly longer than wide, a9-a11 elongated, a10 less than three times as long as wide a11 slightly longer (fig. 16). Hypomera simple, prosternal peg abruptly narrowing caudally, short, lancet-shaped in ventral view (fig. 16). Abdominal ventrites connate (fig. 15).

All femora and tibiae strongly built, prolegs short, meso- and metalegs long, meso- and metatibia with spine-combs, meso- and metatarsi very long, mesotarsomere 1 distinctly longer than 2-5 combined (fig. 17), protarsomere one without sex comb. Length 5.5 mm.

**Note**

As MUONA (1993a) pointed out, the tribe Euryptychini can be separated from the tribe Oroditini only by the presence of male sex-comb on protarsomere 1. The general form and structure of *E. burmensis* n. sp.

suggest it belongs to Euryptychini and is then a female. The head is evenly rounded, but the mandibles have expanded margin, suggesting also tribe Jenibuntorini.

**Superfamily Elateroidea LEACH, 1815**  
**Family Eucnemidae ESCHSCHOLTZ, 1829**  
**Subfamily Macraulacinae FLEUTIAUX, 1922**

**Tribe Euryptychini MAMAEV, 1976**

***Euryptychus elegantulus* new species**

Derivation of name: elegant, slender shape.

**Holotype**

Embedded in an amber piece resembling a halved egg, 10.5 mm x 16.5 mm, height 8.0 mm, sex male.

**Diagnosis**

Elateroidea synapomorphy: promesothoracic clicking mechanism present

Eucnemidae synapomorphies: a2 attached subapically to a1 (fig. 19), labrum attached underneath the frontoclypeal region, hidden.

Euryptychini diagnostic other characters: a9 – a11 elongated (fig. 19), hypomera simple, tibiae with numerous spine-combs, protibiae with one spur, male protarsomere one with sex-comb. There is only one recognized genus in the tribe, *Euryptychus* LeConte.

Differs from all other Burmese amber *Euryptychus* by the slender elytra, about three times as long as pronotum.

**Description**

Body elongated, parallel-sided, moderately flat (fig. 18). Pronotum longer than wide, elytra about three times as long as pronotal length, distinctly striate (fig. 18). Head strongly deflexed, labrum hidden, mandibles not visible, antennal insertions widely separate, a2 attached subapically to a1, about as long as wide, a3 slightly longer than wide, a4 – a8 increasingly wider than long, a9 – a11 very long, combined 1.3 times longer than rest of antennae (fig. 19). Meso- and metatibiae elongated, with delicate spines and small spine-combs, meso- and metatarsi long and delicate. Protibiae shorter, apically expanded, protarsi slender, protarsomere one with long sex-comb.

Length 2.8 mm.

**Note**

The male sex-comb places this species in Euryptychini. As pointed out earlier, this character state is a plesiomorphy, however (MUONA, 1993a).

**Superfamily Elateroidea LEACH, 1815**  
**Family Eucnemidae ESCHSCHOLTZ, 1829**  
**Subfamily Macraulacinae FLEUTIAUX, 1922**

**Tribe Euryptychini MAMAEV, 1976 (probably)**

***Euryptychus mysticus* new species**

Derivation of name: refers to the unexpectedly visible labrum.

**Description**

**Holotype**

Embedded in rectangular, flat amber piece, 12 mm x 10 mm, sex probably female.

**Diagnosis**

Elateroidea synapomorphy: promesothoracic clicking mechanism present (fig. 22)

Eucnemidae synapomorphies: a2 attached subapically to a1, labrum attached ventrally to clypeus, visible (fig. 23), all ventrites connate (fig. 20), elytral striae apically with excretory punctures (fig. 21).

Euryptychini diagnostic other characters: a9 – a11 elongated, hypomera simple, tibiae with numerous spine-combs, protibiae with one spur. There is only one recognized genus in the tribe, *Euryptychus* LeConte.

Differs from all Burmese amber *Euryptychus* species by the prominent labrum.

**Description**

Form wide, pronotum close to parallel-sided in middle, wider than long, hind angles short (Fig 21). Elytra slightly more than two times as long as pronotum, with fine striae, very densely and minutely punctate, apically with strong excretory pores on first and outer interstices (fig. 21). Antennae elongated, a2 unusually long, a3 only slightly longer than a2, a4 – a8 gradually less elongated, a9-a11 greatly elongated (fig. 22). Frontoclypeal region with rounded apex, labrum attached under it, well-sclerotized and visible, partly bilobed, mandibles long, with expanded ventral surfaces (fig. 23). Hypomera simple, prosternal peg abruptly acute, short (fig. 22). Metasternum simple, epipleura wide in basal third, abdominal ventrites connate (fig. 20). Meso- and metatibiae with spine-combs, meso- and metatarsi very long, tarsomeres delicate, claws simple. Protarsomere one without sex-comb.

Length 5.2 mm.

**Note**

As MUONA (1993a) defined it, the tribe Euryptychini could be separated from the tribe Oroditini only by the presence of male sex-comb on protar-

somere 1. The form and structure of *E. mysticus* n. sp. suggest it belongs to Euryptychini and is then a female. The expanded mandibular lateral margin suggest Jenibuntorini as well, however.

**Superfamily Elateroidea LEACH, 1815**  
**Family Eucnemidae ESCHSCHOLTZ, 1829**

**Genus: *Fiegelia* new genus**

**Type species: *Fiegelia antennata* new species**

Derivation of name: because of the massive front tibiae resembles the well-known cartoon character Popeye. The genus name is an arbitrary combination of letters, inspired by Frank “Rocky” Fiegel, the inspiration behind the Popeye character, gender feminine.

**Diagnosis**

Elateroidea synapomorphy: promesothoracic clicking apparatus present (fig. 26, 29-32)

Eucnemidae synapomorphies: labrum attached underneath the frontoclypeal region, hidden, a2 attached subapically to a1, ventrites connate, elytral striae apically with excretory punctures (figs. 25, 27, 30, 32).

Diagnostic other characters: protibiae with one apical spur (figs. 27, 31).

**Description**

This genus is easily identified by the swollen profemora, huge protibiae, very slender tarsi and comparatively small antennae.

***Fiegelia antennata* new species**

Derivation of name: refers to the slender, loosely organized antennae.

**Holotype**

Embedded in rounded amber piece, 17 mm x 15 mm, sex unknown.

**Diagnosis**

Separated from the only other similar species, *F. tarsalis* n. sp., by the delicate antennae

**Description**

Body large, wide and flat (fig. 24). Dorsum with semi-erect vestiture. Elytra apically with small projecting medial tooth, without striae except for a sharp and complete sutural one, this apically with excretory punctures (fig. 24, 25). Most ventrites destroyed, last present, attached solidly (fig. 26). Metathorax poorly

visible, sclerites appear fused. Pronotal hind angles expanded, slightly inwards turned, elytra with fitting soft invagination (fig. 24). Left antenna complete, loosely organized, delicate, with three-segmented loose club, a2 subapically attached to a1, a3 elongated, a2-a8 very slender, antennomeres drop-like, covered with sparse and evenly spaced semi-erect vestiture (fig. 28). Front tibiae huge, towards apex gradually swollen, medially grooved, with one large apical spine, slightly bent at tip (fig. 27), profemora swollen, excavated to fit tibiae tightly, all tarsi very long and very slender, meso- and metatarsomeres with stout hairs and apically with dense group of stout setae. Mouth compressed, slightly damaged, mandibles long and slender, labrum hidden. Length 7.5 mm.

#### Note

The single protibial spine place *Fiegelia* n. gen. among the derived Eucnemidae subfamilies (MUONA, 1993a; MUONA & TERÄVÄINEN, 2020). It does not fit in any of the existing subfamilies or tribes and should be placed only after a comprehensive analysis of all extant and extinct genera becomes available. Besides the legs and antennae, the triangular mesocoxae are highly characteristic (see *F. tarsalis* n. sp.).

### Superfamily Elateroidea LEACH, 1815 Family Eucnemidae ESCHSCHOLTZ, 1829

#### *Fiegelia tarsalis* new species

Derivation of name: refers to the extremely elongated tarsi.

#### Holotype

Embedded in triangular amber piece, 15 mm x 16 mm, sex unknown.

#### Diagnosis

Separated from the only similar species, *F. antennata* n. sp., by the stouter antennae and even longer tarsi.

#### Description

Form similar to that of *F. antennata* n. sp. (fig. 29). Dorsum largely obfuscated, extreme apex of elytra showing apical elytral excretory punctures, sutural striae ending in small tooth as in *F. antennata* n.sp. Labrum hidden, mandibles long and slender (fig. 32). Antennae stouter than those of *F. antennata*, a1-a5 present, a2 attached subapically to a1 (fig. 30, 32). Hypomera simple, prosternal peg with rounded tip (fig. 31), mesocoxal cavities triangular, mesocoxal line complete from one side of metathorax to other, in middle deeply plunging between the triangular coxal cavities (fig. 29). Metacoxal plates huge, strongly

narrowing laterad, sharply pointed caudad (fig. 29). Meso- and metatibiae with strong spine-combs, apically with group of stout spines (fig. 29, 31). All tarsi very slender, longer than corresponding tibiae (fig. 29). Protibiae swollen, apically excavated, with large apical spine with slightly bent tip (fig. 30), profemora enlarged as well, excavated to fit the tibiae. Length 6.0 mm.

#### Note

See *F. antennata* n. sp.

### Superfamily Elateroidea LEACH, 1815 Family Eucnemidae ESCHSCHOLTZ, 1829 Subfamily Eucneminae ESCHSCHOLTZ, 1829

#### Genus: *Falsothambus* new genus

#### Type species: *Falsothambus burmensis* new species

Derivation of name: resembles the Macraulaciinae genus *Thambus* Bonvouloir, gender masculine.

#### Diagnosis

Elateroidea synapomorphy: promesothoracic clicking mechanism present (fig. 33, 35, 37)

Eucnemidae synapomorphies: a2 attached subapically to a1, labrum attached underneath the frontoclypeal region, hidden, ventrites connate, sutural elytral striae with excretory punctures apically.

Eucneminae synapomorphies: lateral antennal grooves closed basally, meso- and metatibiae flattened with sharp angle between lateral and caudal surfaces, tarsomere 4 simple. Diagnostic other characters: a9-a11 enlarged, hypomera simple, without excretory organs, metaventrite with complete mesocoxal line, without pockets or grooves for tibiae and/or tarsi, mandibles short and broad.

Basally closed antennal grooves in combination with three enlarged apical antennomeres suggest relationship with the tribe Proutianini, but the modified mandibles do not support this. This genus cannot be placed in the present hypothesis of Eucnemidae phylogeny beyond the subfamily Eucneminae, where it can be securely included on the basis of several synapomorphies (MUONA, 1993a). The exact placement requires a new analysis of all related genera.

#### *Falsothambus burmensis* new species

Derivation of name: found in Myanmar, aka Burma.

#### Holotype

Embedded in semicircular, thin piece of amber, 23 mm x 11 mm, sex unknown. Two other specimens embedded in two slightly smaller dark pieces of Burmese amber are regarded as paratypes.

## Diagnosis

The flattened, elongated triangular body separates this species from *F. gracilicornis* n. sp. The generic characters are diagnostic for the two taxa.

## Description

Body relatively flat, widest at pronotum, strongly narrowing cranially, more elongated caudad (figs. 33 – 35). Dorsum poorly visible, pronotum partly broken, elytra with strong striae, interstices punctate, sutural striae apically with excretory punctures. Head strongly deflexed, antennal insertions widely separated, labrum hidden, mandibles short with expanded lateral surface, antennae nearly reaching pronotal hind angles, a1 as long as a2 – a4 combined, a5 – a6 longer than wide, a7 – a8 short, about as long as wide (fig. 37), a9 – a11 flattened, enlarged, rounded, serrate (figs. 37, 38). Hypomera with basally closed lateral antennal grooves, without excretory organs (figs. 35 – 37). Prosternal peg deflexed, pointed, mesocoxal lines complete, tarsal grooves not present, tarsomere 4 simple, mesothrochanters elongated, mesotibiae without spine combs (fig. 36). Length 2.9 mm (holotype), 3.4–3.5 mm (paratypes).

### Superfamily Elateroidea LEACH, 1815 Family Eucnemidae ESCHSCHOLTZ, 1829 Subfamily Eucneminae ESCHSCHOLTZ, 1829

#### *Falothambus gracilicornis* new species

Derivation of name: refers to the long, graceful antennae.

#### Holotype

Embedded in round amber piece, 11 mm x 10 mm, sex unknown.

**Paratype** embedded in flat, egg-shaped amber piece, 11 mm x 15 mm, sex unknown.

#### Diagnosis

Separated from *F. burmensis* n. sp. by plump body, short elytra being less than 2.5 times as long as pronotum and by slender antennae, especially a4–a11 (figs. 38).

#### Description

Body plump, rounded both dorsally and ventrally, widest in middle, about equally narrowing cranially and caudad (fig. 39). Elytra with strong striae, interstices punctate, sutural striae apically with excretory punctures. Head deflexed, antennal insertions widely separated, labrum hidden, mandibles short with ex-

panded lateral surfaces, antennae reaching past pronotal hind angles, a1 shorter than a2–a4 combined, a5–a8 all considerably longer than wide (fig. 39), a9–a11 flattened, enlarged, elongated, slightly dentate (figs. 39). Hypomera without excretory organs, with lateral antennal grooves, these basally closed (figs. 35–37). Prosternal peg pointed, mesocoxal tarsal grooves not present, tarsomere 4 simple, mesothrochanters elongated, meso- and metatibiae flattened with sharp angle between lateral and caudal surfaces, meso- and metatibiae without spine combs (fig. 39). Length 1.8 mm (holotype) – 2.1 mm (paratype).

#### Note

The antennal structure, especially the elongated a9–a11, may well be a sexual character, but the body form and proportions are not known to vary in this fashion within Eucnemidae and both *Falothambus* examples are considered to belong to separate species.

### Superfamily Elateroidea LEACH, 1815 Family Eucnemidae ESCHSCHOLTZ, 1829 Subfamily Eucneminae ESCHSCHOLTZ, 1829

#### Tribe Proutianini MUONA, 1993a

#### *Myall burmensis* new species

Derivation of name: found in Myanmar, aka Burma.

#### Holotype

Embedded in rounded amber piece, 26 mm x 19 mm, sex unknown.

#### Diagnosis

Elateroidea synapomorphy: promesothoracic clicking mechanism present (fig. 40, 43)

Eucnemidae synapomorphies: a2 attached subapically to a1, labrum attached underneath the frontoclypeal region, hidden, ventrites connate, sutural elytral striae with excretory punctures.

Eucneminae synapomorphies: lateral antennal grooves closed basally (fig. 43), meso- and metatibiae flattened with sharp angle between lateral and caudal surfaces, tarsomere 4 simple.

Diagnostic other characters: a9–a11 enlarged, hypomera simple, without excretory organs, metathorax with complete mesocoxal line, without pockets or grooves for tibiae and/or tarsi, mandibles slender, laterally expanded.

The combination of simply rounded head, basally closed antennal grooves and mandibles with expanded lateral surfaces places this species in tribe Proutianini and the simple antennae, well-developed lateral antennal grooves place it in the genus *Myall* MUONA. There are no known synapomorphies for Proutianini.

## Description

Body elongated, fairly parallel, about equally narrowing craniad and caudad (fig. 40). Dorsum poorly visible, elytra with striae. Head deflexed, antennal insertions widely separated, labrum hidden, mandibles slender, with expanded lateral surfaces (fig. 43), antennae nearly reaching pronotal hind angles, a1 about long as a2 – a3 combined (fig. 43, lower antenna), a4–a10 about slightly wider than long dentate, round in cross-section, a11 apically pointed, longer than a10 (fig. 43, upper antenna). Hypomera without excretory organs, with basally closed lateral antennal grooves (fig. 40, 43). Prosternal peg pointed (figs. 40, 43), metaventrite with vestigial mesocoxal tarsal grooves (figs. 41), mesothrochanters elongated, meso- and metatibiae flattened with sharp angle between lateral and caudal surfaces, tibiae without spine combs (fig. 41, 44), protibiae short, apically swollen, with densely set spines close to apex (fig. 42) metafemura with group of long hairs close to apex (fig. 42), tarsomere 4 simple, protarsomere one without sex-comb.

Length 3.5 mm.

Note

The group of setae-like hairs on protibiae and metafemura could be sexual characters of a male. In that case the absence of male sex-comb on protarsomere one would be another character placing this species in *Myall*. The vestigial metathoracic grooves are present in *Myall clavicornis* (LEA) as well.

### Superfamily Elateroidea LEACH, 1815 Family Eucnemidae ESCHSCHOLTZ, 1829 Subfamily Eucneminae ESCHSCHOLTZ, 1829

#### Trib Proutianini MUONA, 1993a (tentatively)

#### Genus: *Pseudomyall* new genus

#### Type species: *Pseudomyall elongatulus* new species

Derivation of name: resembles the genus *Myall* MUONA, gender masculine.

#### Diagnosis

Elateroidea synapomorphy: promesothoracic clicking mechanism present (fig. 45)

Eucnemidae synapomorphies: a2 attached subapically to a1, labrum attached underneath the frontoclypeal region, hidden, ventrites connate.

Eucneminae synapomorphies: lateral antennal grooves closed basally, meso- and metatibiae flattened with sharp angle between lateral and caudal surfaces, tarsomere 4 simple.

Diagnostic other characters: a9 – a11 greatly enlarged, hypomera simple, without excretory organs, metaventrite without pockets or grooves for tibiae

and/or tarsi, meso- and metatibiae with strong spine combs, mandibles short and wide.

Basally closed antennal grooves in combination with three enlarged apical antennomeres and meso- and metatibial spines suggest relationship with the tribe Proutianini, but the modified mandibles do not support this. This genus cannot be placed certainly in the present hypothesis of Eucnemidae phylogeny beyond the subfamily Eucneminae, where it can be securely included on the basis of several synapomorphies (MUONA, 1993a). The exact placement requires a new analysis of all related genera; it is placed in the tribe Proutianini for the time being. In this tribe the short mandibles would be a derived feature separating it from its sister-group, *Myall*.

## Description

Body elongated. Dorsum poorly visible, elytra with striae. Antennal insertions widely separated, labrum attached underneath the frontoclypeal region, hidden, mandibles short, wide, with expanded lateral surfaces (fig. 45), antennae reaching past pronotal hind angles, a9–a11 about as long as a1 – a8 combined (fig. 46). Hypomera simple, with basally closed shallow lateral antennal grooves.

#### *Pseudomyall elongatulus* new species

Derivation of name: body shape is unusually elongate.

#### Holotype

Embedded in rounded amber piece, 26 mm x 19 mm, sex unknown.

#### Diagnosis

Easily recognized by the basally closed lateral antennal grooves, the extremely elongated a9 – a11 and the very long and slender meso- and metalegs in combination with the short mandibles.

#### Description

Small, slender body. Relatively short pronotum strongly narrowing craniad and long elytra smoothly narrowing caudad (fig. 46). Head deflexed, antennal insertions widely separated, antennae reaching past pronotal hind angles, a1–a3 about as long as a4 – a8, these five individually shorter than wide, a9–a11 about as long as a1 – a8 combined (fig. 45). Hypomera without excretory organs, with shallow lateral antennal grooves, these basally closed. Prosternal peg narrow, pointed (fig. 45), metaventrite without mesocoxal tarsal grooves (fig. 46), mesothrochanters elongated, meso- and metatibiae flattened with sharp angle between lateral and caudal surfaces, tibiae with spine

combs (fig. 46), meso- and metalegs very long, tibiae much shorter than tarsi, tarsomere 4 simple (fig. 46).

Length 3.5 mm.

**Superfamily Elateroidea LEACH, 1815**  
**Family Eucnemidae ESCHSCHOLTZ, 1829**  
**Subfamily Eucneminae ESCHSCHOLTZ, 1829**

**Tribe Mesogenini MUONA, 1993a (tentatively)**

**Genus: *Paleoeucnemis* new genus**

**Type species: *Paleoeucnemis minutus* new species**

Derivation of name: old form superficially resembling the extant genus *Eucnemis* Ahrens, gender masculine.

**Generic diagnosis**

Elateroidea synapomorphy: promesothoracic clicking mechanism present

Eucnemidae synapomorphies: a2 attached subapically to a1, labrum attached underneath the frontoclypeal region, hidden.

Eucneminae synapomorphies: hypomera with basally closed lateral antennal grooves (fig. 47, 50), meso- and metatibiae flattened with sharp angle between lateral and caudal surfaces tarsomere 4 simple (fig. 48, 50).

Diagnostic other characters: a9 – a11 slightly enlarged (fig. 49), hypomera without excretory organs, metaventrite without pockets or grooves for tibiae and/or tarsi (fig. 50), meso- and metatibiae without spines, mandibles short and wide. Basally closed antennal grooves in combination with three enlarged apical antennomeres with the tribe Proutianini, but the absence of meso- and metatibial lateral spines do not support this. With the exception of the apical club, the antennal structure is clearly of Eucnemini-Mesogenini-Galbitini type, i.e. a3 is elongated and from a4 on single antennomeres become shorter and more serrate towards apex. This in combination of elytra being apically bent slightly upwards in lateral view as in some Mesogenini (e.g. *Submesogenus* FLEUTIAUX) and most Galbitini (e.g. *Galbites* FLEUTIAUX) exclude Proutianini. This genus cannot be placed certainly in the present hypothesis of Eucnemidae phylogeny beyond the subfamily Eucneminae, where it can be securely on the basis of several synapomorphies (MUONA, 1993a). The exact placement of this genus requires a new analysis of all related genera; it is placed in the tribe Mesogenini for the time being. Mesogenini are defined by spermathecal structure but as this species lacks hypomeral excretory organs (an Eucnemini apomorphy) and has simple, not lobed tarsomere 4 (a Galbitini apomorphy) it is placed in Mesogenini. The antennal structure is unique, however.

***Paleoeucnemis minutus* new species**

Derivation of name: very small size.

**Holotype**

Embedded in rectangular amber piece, 10.5 mm x 10.5 mm, sex unknown.

**Diagnosis**

The antennal structure in combination with the Eucneminae features separate this species from all other Eucnemidae.

**Description**

Body relatively short and wide, compact, strongly narrowing caudad, pronotum globular, short, dorsally convex, elytra slightly curved dorsally in lateral view, apically bent upwards, ventral surface in even plane except for last ventrite (fig. 48, 50). Dorsum minutely and densely punctate, elytra with faint striae. Antennae short, unique in shape, with definite club in combination with a3-a8 becoming shorter and wider towards apex (fig. 49). Labrum hidden, mandibles short and strong (fig. 47). Hypomera without excretory pits, lateral antennal grooves closed apically, sharply defined medially (fig. 47, 50). Metaventrite without tibiotarsal grooves, metanepisterna fairly wide, rectangular (fig. 50). Metacoxal plates only slightly narrowing laterad, legs short, tibiae shorter than femora, flattened, without rows of spines, meso- and metatarsi slender, delicate, tarsomere 1 longer than others combined, claws minute.

Length 2.8 mm.

**Superfamily Elateroidea LEACH, 1815**  
**Family Eucnemidae ESCHSCHOLTZ, 1829**

**Tribe: Melasinae, Dirhagini REITTER, 1911 (tentatively)**

**Genus: *Protomicrorhagus* new genus**

**Type species: *Protomicrorhagus antennatus* new species**

Derivation of name: species fits the idea of an “early” *Microrhagus*-like eucnemid, gender masculine.

**Diagnosis**

Elateroidea synapomorphy: promesothoracic clicking mechanism present.

Eucnemidae synapomorphies: a2 attached subapically to a1, labrum attached underneath the frontoclypeal region, hidden (fig. 54).

Eucnemidae other characters: all ventrites connate.

Tribe Dirhagini synapomorphies: pronotal lateral ridge serrate along dorsal front margin (fig. 52, 59), hypomera with deep pits close to front coxae (fig. 56). Dirhagini other characters: pronotal hind angles with carinae (fig. 53, 56), lateral pronotal carinae complete, pronotum with an extra carina at front corner (fig. 51, 52, 53, 56), tibiae without spine-combs, not flattened (fig. 51, 55).

## Description

Body narrow, small, elytra twice or more as long as pronotum, legs long, slender, tibiae without spine-combs, tarsi about as long as tibiae (fig. 51, 55), eyes very large, labrum hidden, mandibles short, bifid, antennomeres conspicuously elongated, especially a2, a9 to a11 wider than previous ones (fig. 51, 53, 59), hypomera simple with deep pits close to procoxae, notosternal suture complete (fig. 53, 65), pronotal hind angles acute, with sharp keels (fig. 51, 58), pronotum with complete lateral carinae, these united over the front dorsal ridge of pronotum, here serrate, front edge of pronotum with double carinae (fig. 53, 56), elytra with well-developed punctured striae (fig. 51, 58), epipleura densely punctate and abruptly wider from metacoxae to front (fig. 51, 57).

### *Protomicrorhagus antennatus* new species

Derivation of name: prominent antennae.

#### Holotype

Embedded in large cone-shaped amber piece, 20 mm x 16 mm, height 20 mm, sex unknown.

#### Diagnosis

Characterized by enlarged a9-a11, slender body and faintly striate elytra. Differs from *Protomicrorhagus brevis* n. sp. and *Coenomana brevicornis* n. sp. by being considerably slenderer than either of them (fig. 57).

#### Description

Body densely punctate, mostly rugose, head with short carinae over antennal insertions, antennae slender extending to metaventricle, all antennomeres except 10 distinctly elongate, a2 more than twice as long as wide, a1 more than twice as long as a2, a3 slightly less than twice as long as a2, a9-a11 form a club, a10 being widest of the three (fig. 51, 53, 54). Legs slender, all tarsi longer than corresponding tibiae, metacoxal plates strongly narrowing laterad, at midline about 4 times as wide as at sides.

Length 3.2 mm.

Note.

With one exception the characters of this genus shows strong affinities with the tribe Dirhagini. The enlarged a9-a11 is entirely aberrant, however. It fits with the idea that all derived Eucnemidae (sensu Muona & Teräväinen, 2020a) showed this feature, the origins of which dates back to the Schizophilineae (Muona et al., 2020b), but this hypothesis can be evaluated properly only with a new global analysis. For the time being it is placed in Dirhagini.

## Superfamily Elateroidea LEACH, 1815 Family Eucnemidae ESCHSCHOLTZ, 1829

### Tribe Melasinae, Dirhagini REITTER, 1911 (tentatively)

#### *Protomicrorhagus brevis* new species

Derivation of name: relatively short and wide body.

#### Holotype.

Embedded in round amber piece, 17 mm x 13 mm, sex unknown.

#### Diagnosis

Much stouter in form than *Protomicrorhagus antennatus* n. sp. (fig. 55, 57), in this respect similar to *Coenomana brevicornis* n.sp., but with considerably shorter antennae and stronger striae on elytra compared to that species (fig. 58, 59).

#### Description

Body densely punctate, mostly rugose, antennae slender, extending to metaventricle, all antennomeres except 9 and 10 distinctly elongate, a2 more than twice as long as wide, a1 more than twice as long as a2, a3 less than twice as long as a2, a9-a11 form a club, both a9 and a10 being stouter than those of *P. antennatus* n. sp. (fig. 57). Legs slender, all tarsi longer than corresponding tibiae, metacoxal plates strongly narrowing laterad, at midline about 4 times as wide as at sides.

Length 3.0 mm.

## Superfamily Elateroidea LEACH, 1815 Family Eucnemidae ESCHSCHOLTZ, 1829

### Tribe Melasinae, Dirhagini REITTER, 1911 (tentatively)

#### *Coenomana brevicornis* new species

Derivation of name: short antennae.

**Holotype**

Embedded in round amber piece, 17 mm x 13 mm, sex unknown.

**Diagnosis**

Differs from both *Protomicrorhagus antennatus* n.sp. and *Protomicrorhagus brevis* n. sp. by the strongly developed elytral striae, almost keeled interstices (fig. 58) and the conspicuous upwards turned carina on the front edge of pronotum. Differs from *Coenomana clavata* Otto by the shorter and slender antennae and less elongate body. In form similar to *Protomicrorhagus brevis* n. sp., but elytra with stronger striae with large punctures and convex interstices.

**Description**

Body densely punctate, antennae slender and short, extending to hind angles of pronotum, all antennomeres increasingly elongate towards apex, a2 small, a1 more than six times as long as a2, a9-a11 similar to those of *P. brevis* n. sp., forming a club (fig. 59). Elytral punctation conspicuous, interstices strongly convex, rugose, striae with large densely set punctures (fig. 59). Legs slender, all tarsi about as long as corresponding tibiae, metacoxal plates poorly visible, but distinctly widening laterad.

Length 3.0 mm.

Note

Otto (2019) placed *Coenomana* Otto in subfamily Macraulacinae, tribe Jenibuntorini. The main reasons were the simple hypomera and the three enlarged apical antennomeres. The external key features to identify *Jenibuntor* MUONA (MUONA, 1993a: 21) are the long, slender mandibles with expanded lateral margins and the expanded frontoclypeal region of the head. The hind angles of pronotum of *Coenomana clavata* appear to be carinate and there is a strongly upwards bent carina along the front margin of pronotum (Otto, 2017: figure 1). In addition, *C. clavata* has long and slender legs, short bifid mandibles and what appear to be smooth areas along notosternal sutures (Otto, 2017: figure 2). All these features remind of Dirrhagini. *Coenomana brevicornis* n. sp. shares many features with *C. clavata*, i.e. the peculiar elytral structure, the strong anterior edge carina on pronotum and the sharply carinate pronotal hind angles. It appears that both these species belong to the same genus.

Enlarged apical antennomeres is a common feature in many basal Eucnemidae. *Protomicrorhagus* n. gen. and *Coenomana* Otto are the first Dirrhagini genera with seem to show this feature. Only a global analysis of all relevant Eucnemidae taxa can indicate, whether it is a plesiomorphy or a synapomorphy in this group and will help to settle the tribal placement definitely. See also note under *Protomicrorhagus*.

**Superfamily Elateroidea LEACH, 1815**  
**Family Eucnemidae ESCHSCHOLTZ, 1829**  
**Subfamily Eucneminae ESCHSCHOLTZ, 1829**

**Tribe Mesogenini MUONA, 1993a*****Sieglindea antiqua* new species**

Derivation of name: oldest known *Sieglindea*-species.

**Holotype**

Embedded in rectangular Burmese Amber piece, 22.5 mm x 12 mm, sex unknown (fig. 63, 64).

**Paratype.** Embedded in drop-shaped Burmese amber piece, 13.5 mm x 9.5 mm, sex unknown (fig. 60-62).

**Diagnosis**

Elateroidea synapomorphy: promesothoracic clicking mechanism present (fig. 60, 63)

Eucnemidae synapomorphies: a2 attached subapically to a1 (fig. 61), labrum attached underneath the frontoclypeal region, hidden (fig. 60, 61), ventrites connate (fig. 60).

Eucneminae synapomorphies: lateral antennal grooves closed basally (fig. 62, 63), meso- and metatibiae flattened with sharp angle between lateral and caudal surfaces, tarsomere 4 simple.

**Tribe Mesogenini**

Mesogenini are defined by spermathecal structure but as this species lacks hypomeral excretory organs (an Eucnemini apomorphy) and has simple, not lobed tarsomere 4 (a Galbitini apomorphy) it is placed in Mesogenini. Diagnostic other characters: hypomera simple, without excretory organs, metaventricle with grooves for tibiae and tarsi, mandibles short and broad. Because of the sharp and well defined metathoracic tarsal grooves it belongs to the extinct genus *Sieglindea* MUONA, 1993a, formerly known from Baltic amber only.

**Diagnosis**

Differs from the Baltic amber fossil species *S. siegfriedi* MUONA and *S. hundingi* MUONA by the laterad narrowing metacoxal plates.

**Description**

Body stocky, abruptly narrowing on both ends. Dorsum shiny, densely and orderly punctate, intervals smooth, elytra without striae (fig. 64). Venter densely punctate, punctures smaller on abdomen and metathorax, stronger on hypomera and prosternum

(fig. 61), A1 bulbous, carinate, a2 small, carinate, a3 to a8 not visible, a9 to a11 protruding but covered with milk-colored water (fig. 62, 65), apparently serrate as in extant genus *Eucnemis* Ahrens. Front margin of prosternum deeply grooved (fig. 61), prosternal peg acute, on both sides with carina. Metasternal tarsal grooves providing a tight fit, curved, metanepisterna very slender, about parallel (fig. 62). Metacoxal plates at their widest about two times as wide as at sides.

Length 4.7 mm (paratype) - 5.7 mm (holotype).

**Superfamily Elateroidea LEACH, 1815**  
**Family Eucnemidae ESCHSCHOLTZ, 1829**  
**Subfamily Eucneminae ESCHSCHOLTZ, 1829**

**Tribe Mesogenini MUONA, 1993a**

***Protovitellius* new genus**

**Type species: *Protovitellius deceptus* new species**

Derivation of name: structure of exposed male genitalia shows that this genus belongs to tribe Mesogenini, although the antennae and body form are deceptively different; gender masculine.

**Diagnosis**

Elateroidea synapomorphy: promesothoracic clicking mechanism present.

Eucnemidae synapomorphies: a2 attached subapically to a1, labrum attached underneath the frontoclypeal region, hidden, elytra with sutural and lateral striae with excretory punctures apically (fig. 66).

Eucneminae synapomorphies: lateral antennal grooves closed basally, a2 attached subapically to a1, meso- and metatibiae flattened with sharp angle between lateral and caudal surfaces, tarsomere 4 simple. Aedeagus highly characteristic, with plate-like median sclerite, long basal struts and short lateral lobes, subgenital plate with characteristic median part (fig. 67).

Diagnostic other characters: hypomera simple, without excretory organs, meso- and metatibiae without spine-combs, meso- and metatarsi with tarsomere 1 longer than others combined, tarsomere 2 longer than 3-5 combined and these three apical ones small and simple, claws minute. Mandibles are short and wide.

The basally closed antennal grooves and apically slightly widening slender antennae with elongate antennomeres form a character combination not known in any other Eucnemidae (fig. 65). The protruding aedeagus is highly characteristic and places this genus in Mesogenini or Eucnemini and the simple hypomera support the former. The subgenital plate is very similar to that of the extant genus *Vitellius* BONVOULOIR.

***Protovitellius deceptus* new species**

**Holotype**

Embedded in a slightly oval, flat amber piece, 15 mm x 13 mm, male (fig. 65).

Derivation of name: from the deceptive combination of characters.

**Diagnosis**

The generic characters separate this species from all other known eucnemids. The simple antenna in combination with closed lateral antennal grooves are a diagnostic feature (fig. 65)

**Description**

Body small, more strongly narrowing caudad than cranial, top-heavy in appearance. Dorsum faintly punctate, intervals smooth, elytra without striae. Venter poorly visible (fig. 65). Antennomeres longer than wide, antennae slender and delicate, slightly longer than the length of pronotum (fig. 65). All femora short, tibiae long, smooth, sparsely hirsute, apically with ring of stiff setae along margin. Mesotibia with one large lancet-shaped apical spur, metatibia with one unusually long and strong apical spine (fig. 65), protibiae poorly visible, short, meso- and metatarsi with very short and delicate apical three tarsomeres and minute claws.

Length 2.2 mm.

**Superfamily Elateroidea LEACH, 1815**  
**Family Eucnemidae ESCHSCHOLTZ, 1829**  
**Subfamily Macraulacinae FLEUTIAUX, 1922**

**Tribe Euryptychini MAMAEV, 1976 (probably)**

***Muonabuntor grandinotalis* LI, TIHELKA & CAI**

Li et al (2020) placed this taxon in the Macraulacinae, tribe Jenibuntorini MUONA. The rationale for this decision was not explained, however. The subapically attached a2, strongly developed excretory punctures on elytral apices and hidden labrum clearly show *Muonabuntor* belongs to Eucnemidae. The elongated a9-a11, simple hypomera and single protibial spurs place it among basal Macraulacinae (MUONA, 1993a; MUONA & TERÄVÄINEN, 2020). The frontoclypeal region is not expanded however (fig. 68), and the mandibles seem to lack expanded lateral margins (fig. 69), both these features characterizing Jenibuntorini and being lost in more derived Macraulacinae. Unfortunately, Li et al. (2020) did not describe the structure of the head or the mandibles. They compared *Muonabuntor* to *Jenibuntor* and *Euryptychus* LeConte and noted

that *Muonabuntor* had a proportionately larger pronotum than either of these. This holds for *Jenibuntor* but many *Euryptychus* species have even shorter elytra than *Muonabuntor*. One should also note that Li & al. (2020: figure 3 A-C) did not show the type species of the genus, *Jenibuntor tabang* MUONA as they claimed, but another undescribed species (fig. 68-70).

The relationships of basal Macraulacinae are poorly known (for a lengthy discussion of this, see MUONA, 1993a: 32-33). The structures of mandibles and head separate Jenibuntorini from Oisocerini, Euryptychini and Orodotini, all of which share the derived states, i.e. simple curved head and mandibles without laterally expanded margins. Both these features seem to be lacking in *Muonabuntor* as well, thus it is placed in Euryptychini for the time being.

**Superfamily Elateroidea LEACH, 1815**  
**Family Eucnemidae ESCHSCHOLTZ, 1829**  
**Subfamily Macraulacinae MUONA, 1993a**

**Tribe Jenibuntorini MUONA, 1993a**

***Jenibuntor pusillus* new species**

Elateroidea synapomorphy: promesothoracic clicking mechanism present.

Eucnemidae synapomorphies: a2 attached subapically to a1, labrum attached underneath the frontoclypeal region, hidden, elytral apices with excretory punctures along innermost and outermost striae.

Macraulacinae diagnostic characters: a9 – a11 forming club, hypomera simple, protibiae with one spur.

Jenibuntorini synapomorphy: head expanded (fig. 70). Jenibuntorini other diagnostic features: mandibles with expanded lateral margin (fig. 72).

**Description**

Body robust (Fig, 70, 71). Dorsum and ventrum clearly visible, head, mouthparts, antennae and all legs well exposed (fig. 70-73). Labrum hidden under frontoclypeal region, mandibles long and slender with laterally expanded margin. Antennae attached fairly widely apart, stout, a4-a8 wider than long, a9-a11 tubular, slightly flattened, forming a club (fig. 70). Protibiae with one apical spine (fig. 73), meso- and metatibiae with strong spine-combs, tarsomeres apically with several short spines, elongate, claws long, simple (fig. 73). *Jenibuntor pusillus* new species

Derivation of name: by far the smallest known Jenibuntorini species.

**Holotype**

Embedded in nearly round amber piece, 11 mm x 10 mm, flat on one side, concave on the other one, sex unknown.

**Description**

Body, legs and antennae robust. Characterized by the generic features, especially the expanded frontoclypeal region and the small size. Length 2.5 mm.

**Note**

This tiny creatures looks like a miniature version of the type species of the tribe, *Jenibuntor tabang* MUONA, but its form is less parallel.

**Discussion**

The twenty-two described Burmese amber fossil Eucnemidae species and their tentative taxonomic placement is presented in table 1. As pointed out earlier in this article, the placement of several Burmese Eucnemidae fossils within the family is provisory and requires a new global analysis of all fossil and extant forms. Nevertheless, it is of interest to shortly describe the situation.

The present world fauna is dominated by what MUONA & TERÄVÄINEN (2020a) called the “Derived Eucnemidae” (=DE), i.e. the clade (Eucneminae, Melasinae, Macraulacinae). These three subfamilies include more than 95% of the extant species. The Macraulacinae tribe Macraulacini is by far the largest tribe, it contains today about as many species as all the other tribes combined.

The mostly Eocene Baltic amber Eucnemidae fauna has been shown to resemble the extant Indo-australian one both in proportions of species in tribes and in generic composition (MUONA, 1993b). The early Cretaceous fauna, much more limited in extent, is radically different (MUONA et al., 2020b). The more recent Burmese material here discussed shows affinities with the Baltic and extant faunas. It differs from both of those by the lack of two major components present in them: modern type Dirhagini and the today dominant Macraulacini. Basal Macraulacinae tribes Jenibuntorini and Euryptychini are present, however. The fossil material suggests that the early diversification of clicking elateroids will most likely be clarified once the Jurassic and early Cretaceous fossils are properly studied and analyzed (MUONA et al., 2020). The origins of the later radiations within Eucnemidae have clearly taken place after this. In order to clarify their evolution, the inclusion of the late Cretaceous fossils will be crucial.

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**Table 1. Eucnemidae species from Myanmar Cretaceous amber.**

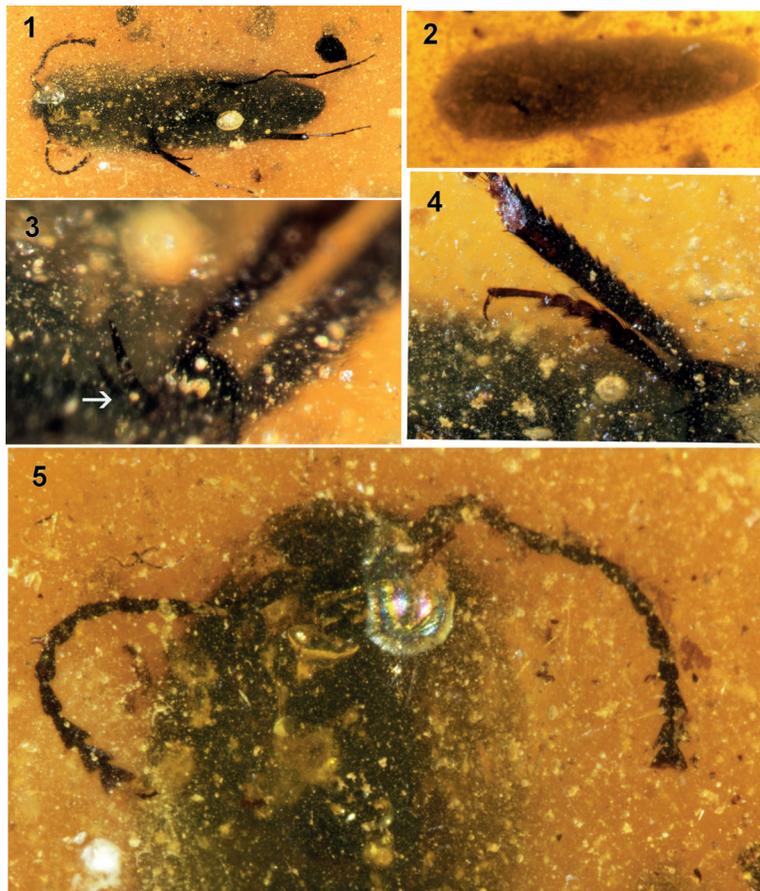
Palaeoxeninae Muona, 1993
Palaeoxenini Muona, 1993
<i>Cupressicharis</i> new genus
<i>elongatus</i> new species
Melasinae Fleming, 1821
Epiphanini Muona, 1993
<i>Epiphanis</i> Eschscholtz, 1829
<i>burmensis</i> new species
Dirhagini Reitter, 1911
<i>Protomicrorhagus</i> new genus
<i>antennatus</i> new species
<i>brevis</i> new species
<i>Coenomana</i> Otto, 2019
<i>clavata</i> Otto, 2019
<i>brevicornis</i> new species
Macraulacinae Fleutiaux, 1922
Jenibuntorini Muona, 1993
<i>Jenibuntor</i> Muona, 1993
<i>pusillus</i> new species
Euryptychini Mamaev, 1976
<i>Euryptychus</i> LeConte, 1852
<i>acutangulus</i> new species
<i>burmensis</i> new species
<i>elegantulus</i> new species
<i>mysticus</i> new species
<i>Muonabuntor</i> Li, Thielka & Cai, 2020
<i>grandinotalis</i> Li, Thielka & Cai, 2020
Eucneminae Eschscholtz, 1829
Dyscharachthini Muona, 1993
<i>Cylus</i> new genus
<i>carinifer</i> new species
Proutianini Muona, 1993
<i>Myall</i> Muona
<i>burmensis</i> new species
<i>Pseudomyall</i> new genus
<i>elongatulus</i> new species

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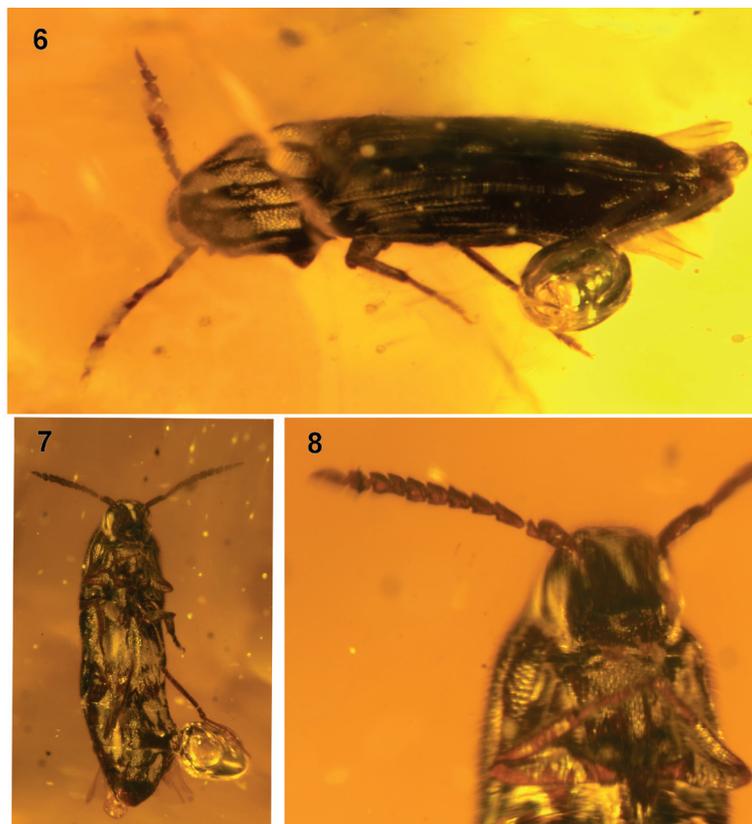
Mesogenini Muona, 1993  
  *Paleoeucnemis* new genus  
    *minutus* new species  
  *Sieglindea* Muona, 1993  
    *antiqua* new species  
  *Protovitellius* new genus  
    *deceptus* new species  
Unknown tribe  
  *Falsothambus* new genus  
    *burmensis* new species  
    *gracilicornis* new species  
Unknown subfamily  
  unknown tribe  
    *Fiegelia* new genus  
    *antennata* new species  
    *tarsalis* new species

### **Authors' address**

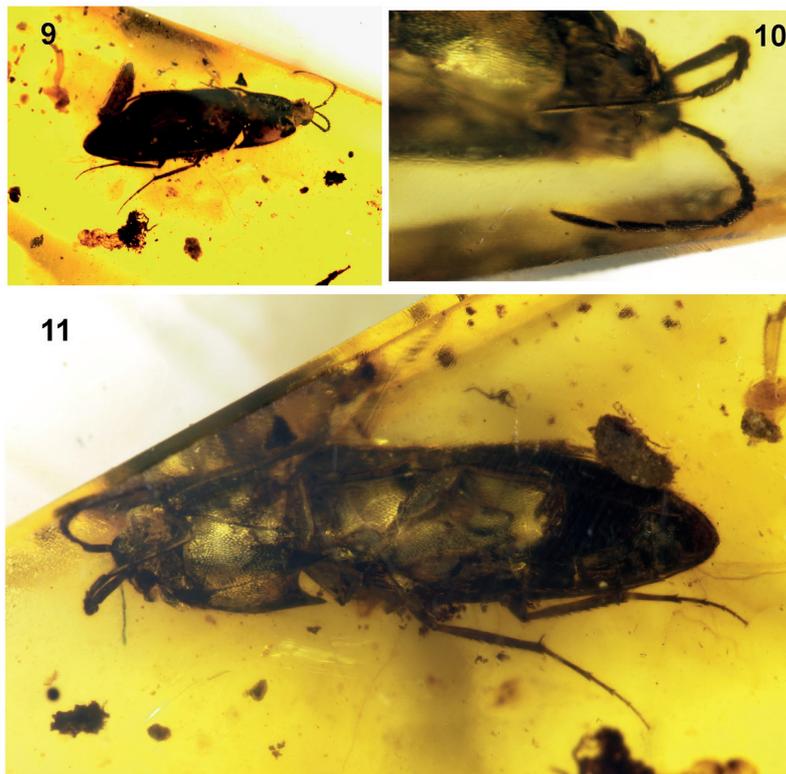
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FIN-00014-University of Helsinki, Finland  
E-mail: [jyrki.muona@helsinki.fi](mailto:jyrki.muona@helsinki.fi)  
<https://orcid.org/0000-0003-2771-1171>



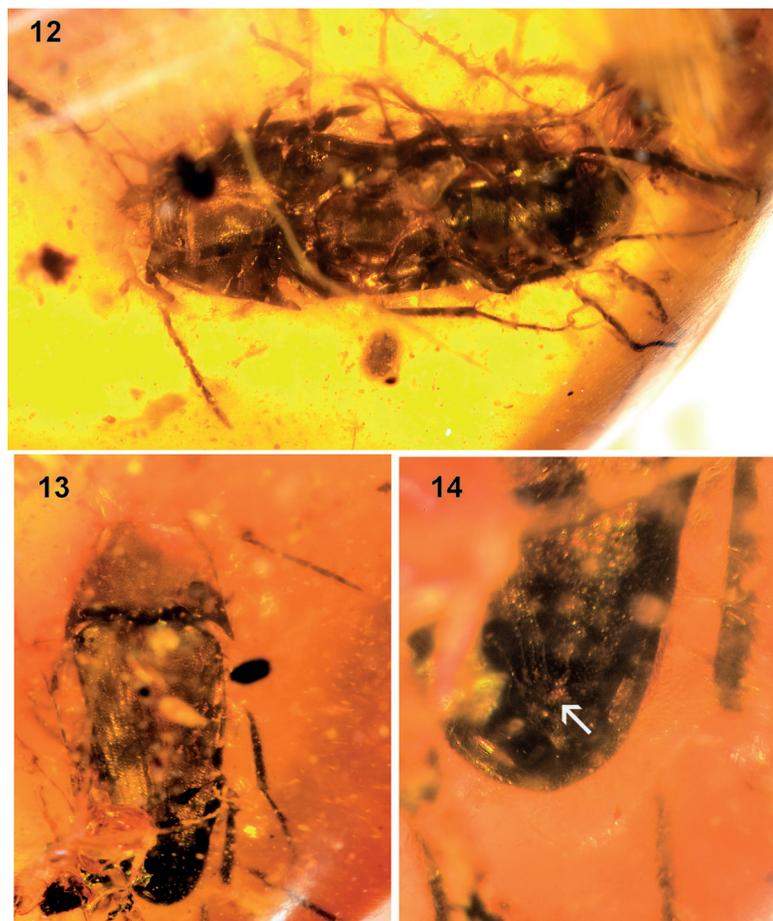
Figures 1-5. *Cupressicharis elongatus* n. gen., n. sp. Holotype, length 6.5 mm. Ventral view (1), dorsal view (2), protibial apex, arrow indicates two apical spines (3), protarsus and metatibia (4), face and antennae (5).



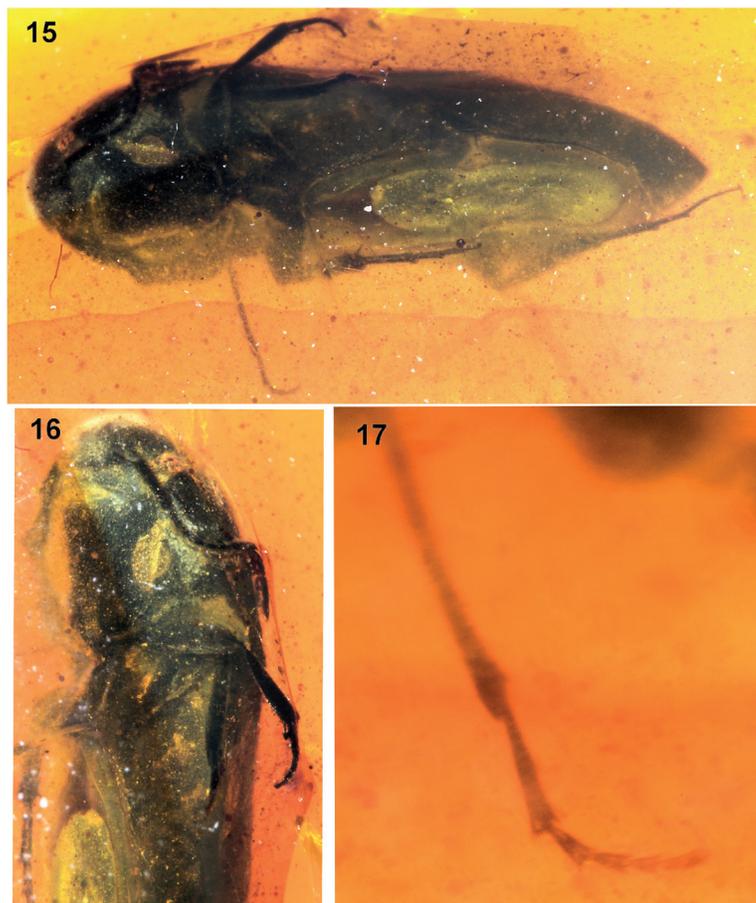
Figures 6-8. *Cylus carinifer* n. gen., n. sp. Holotype, length 3.9 mm. Dorsal view (6), ventral view (7), head and prothorax, ventral view (8).



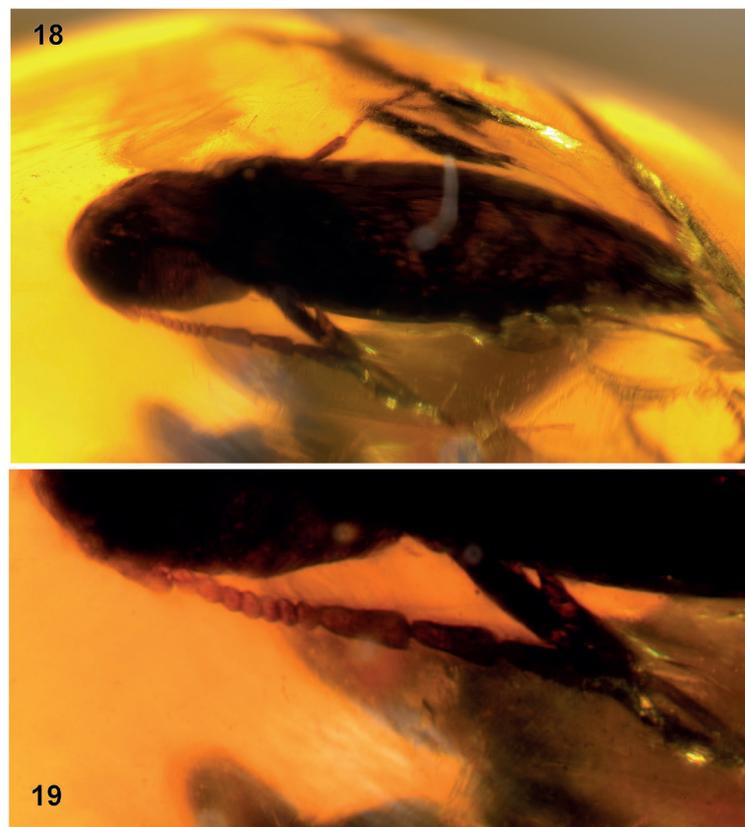
Figures 9-11. *Epiphanis burmensis* n. sp. Holotype, length 4.0 mm. Dorsal view (9), antennae (10), ventral view (11).



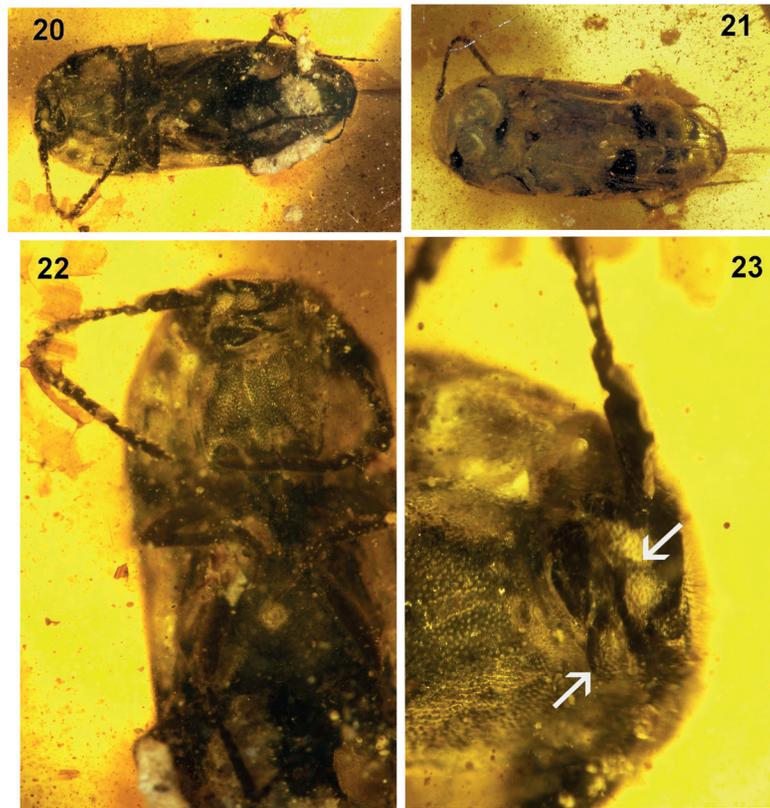
Figures 12-14. *Euryptychus acutangulus* n. sp. Holotype, length 6.0 mm. Ventral view (12), dorsal view (13), elytral apices, arrow indicates enlarged excretory punctures (14).



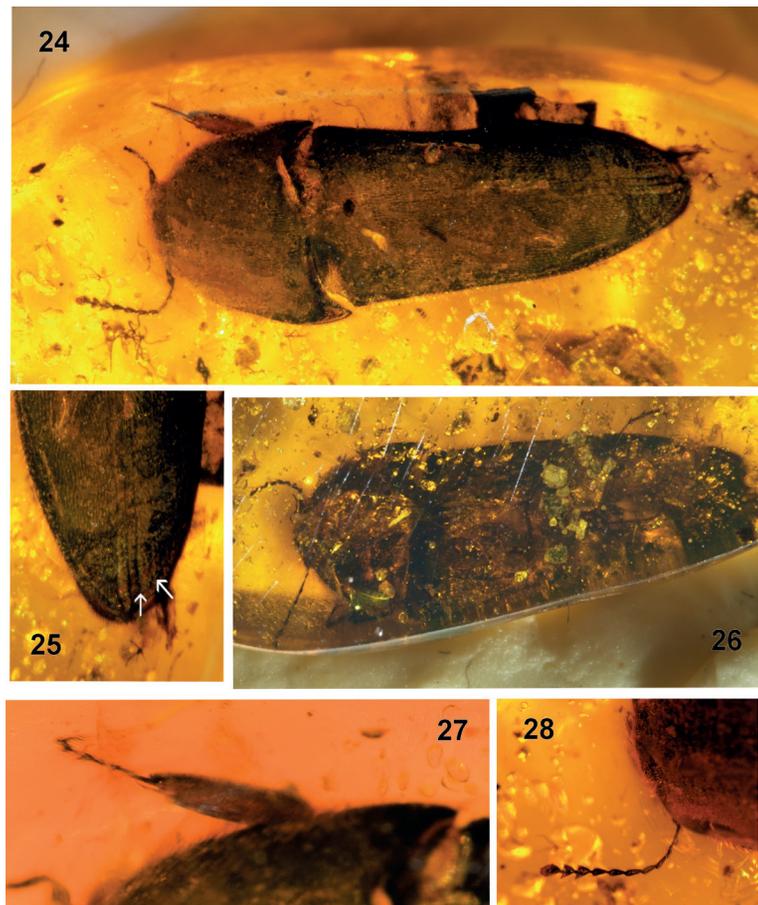
Figures 15-17. *Euryptychus burmensis* n.sp. Holotype, length 5.5 mm. Dorsal view (15), dorsal view showing hypomera and antenna (16), mesotarsus (17).



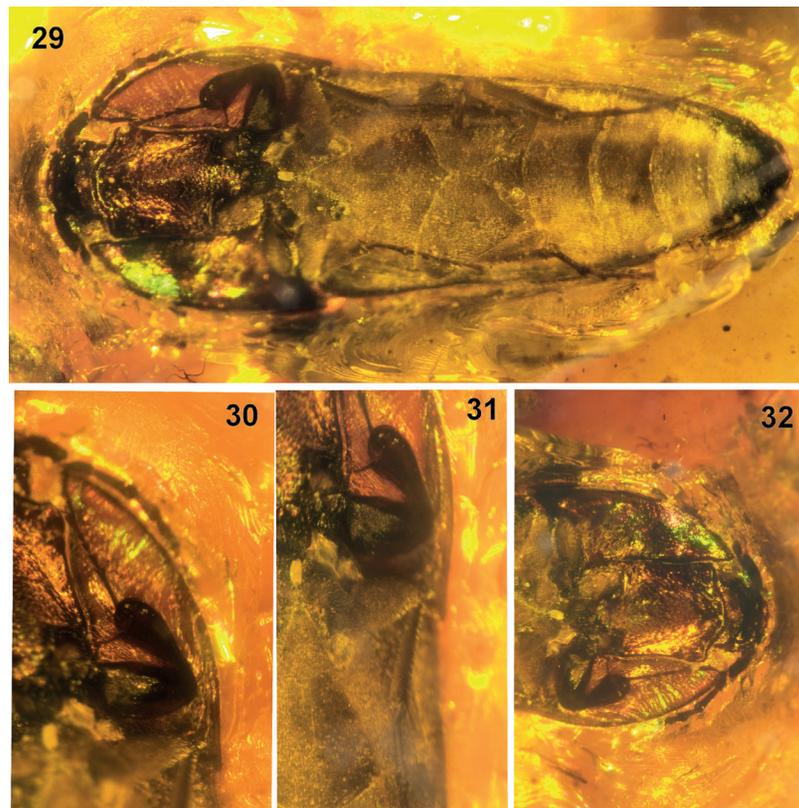
Figures 18-19. *Euryptychus elegantulus* n. sp. Holotype, length 2.8 mm. Ventrolateral view (18), detail showing right antenna (19).



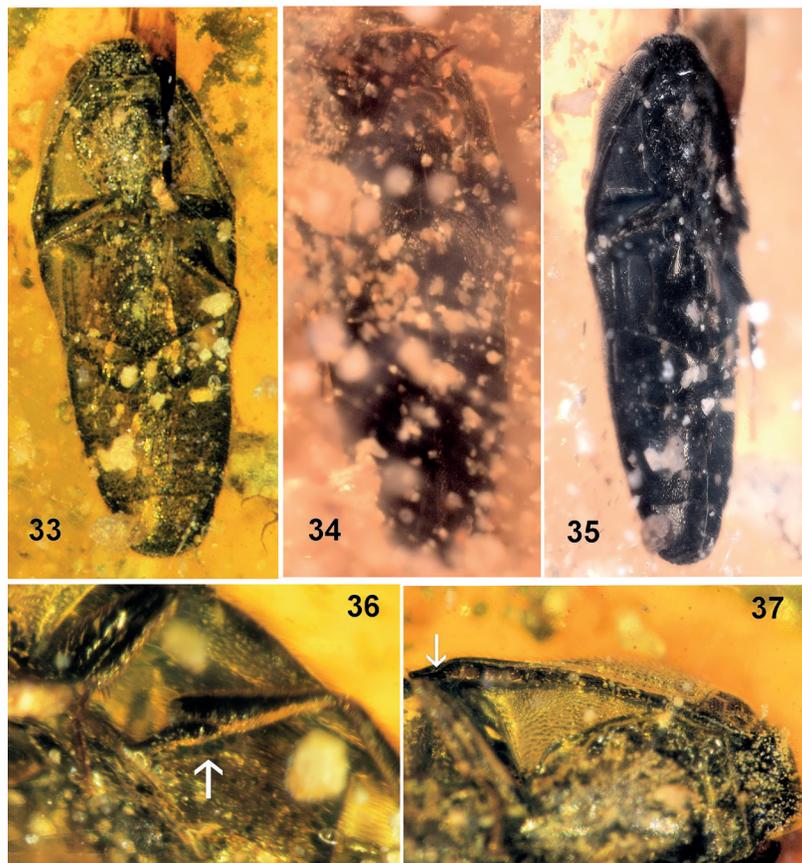
Figures 20-23. *Euryptychus mysticus* n. sp. Holotype, length 5.2 mm. Ventral view (20), dorsal view (21), head, pro- and mesothorax, ventral view (22), head, ventral view, showing sclerotized labrum (upper arrow) and shape of mandibles (lower arrow) (23).



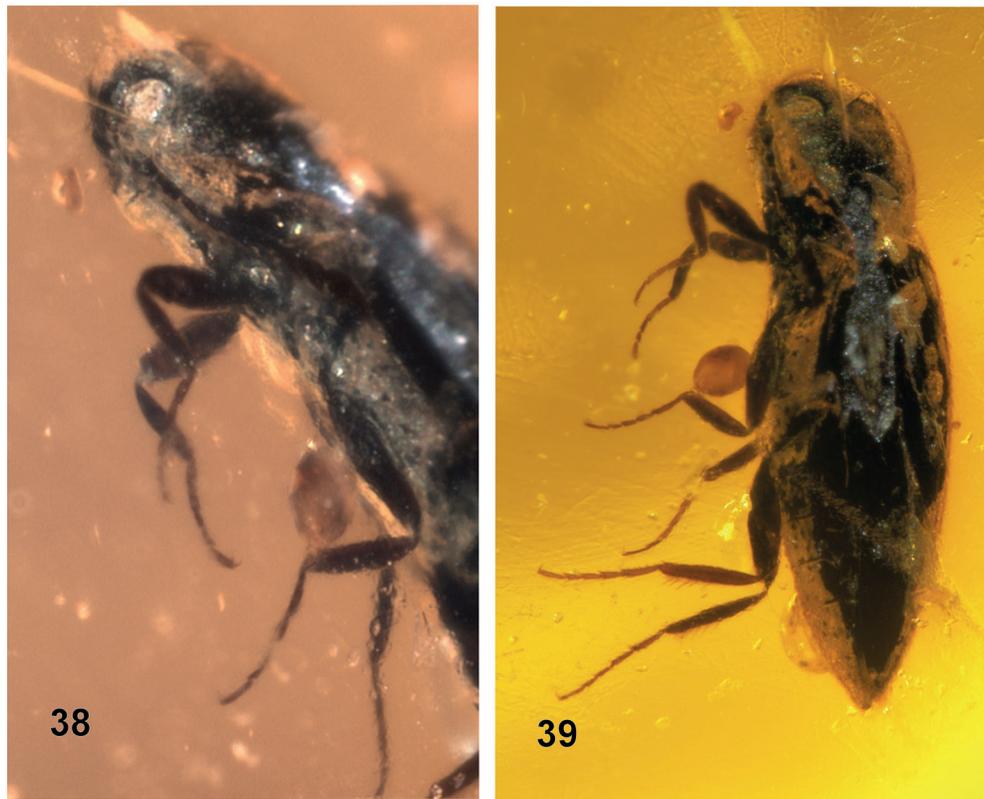
Figures 24-28. *Fiegelia antennata* n. gen., n. sp. Holotype, length 7.5 mm. Dorsal view (24), elytral apices with enlarged excretory punctures (25), ventral view (26), detail of the apically excavated expanded protibia with long, curved spur (27), left antenna (28)



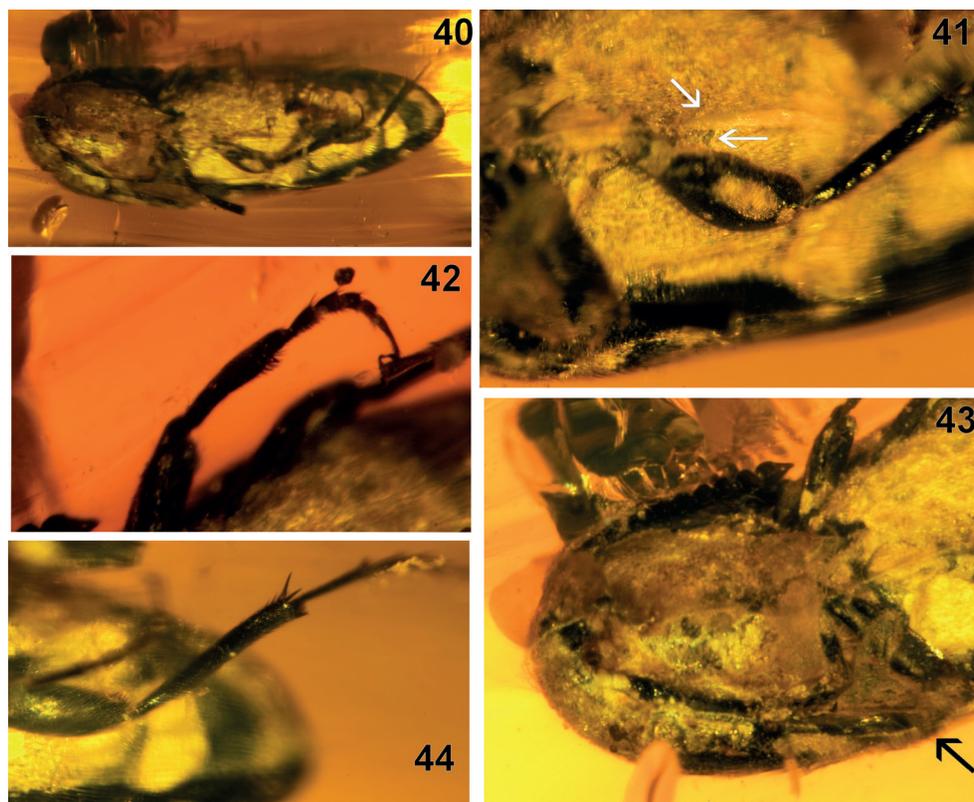
Figures 29-32. *Fiegelia tarsalis* n. gen., n. sp. Holotype, length 6.0 mm. Ventral view (29), hypomera and proleg (30), proleg, meso- and metathorax in ventral view (31), head and prothorax in ventral view (32).



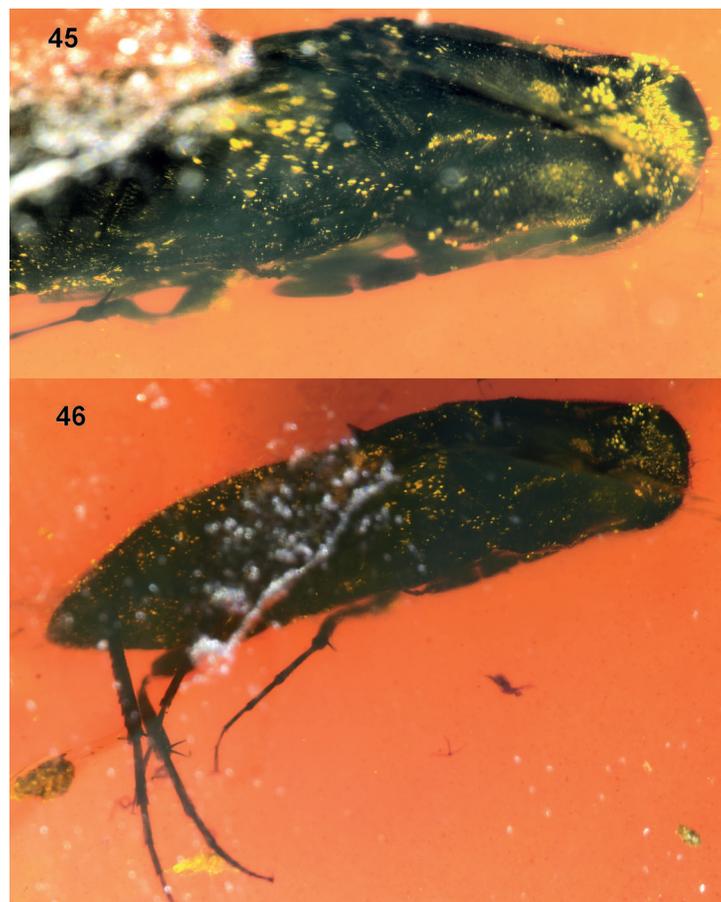
Figures 33-37. *Falsothambus burmensis* n. gen., n. sp. Holotype, length 2.9 mm. Ventral view (33), dorsal view (34), ventral view, slightly tilted (35), pro-mesothoracic region, front to left, showing mesotibia without spine-combs, complete mesocoxal line (arrow) and absence of tarsal grooves on metasternite (36), head and prothorax in ventral view showing short, bifid mandibles, hypomera without excretory organs and basally closed (arrow) and medially defined lateral antennal groove (37).



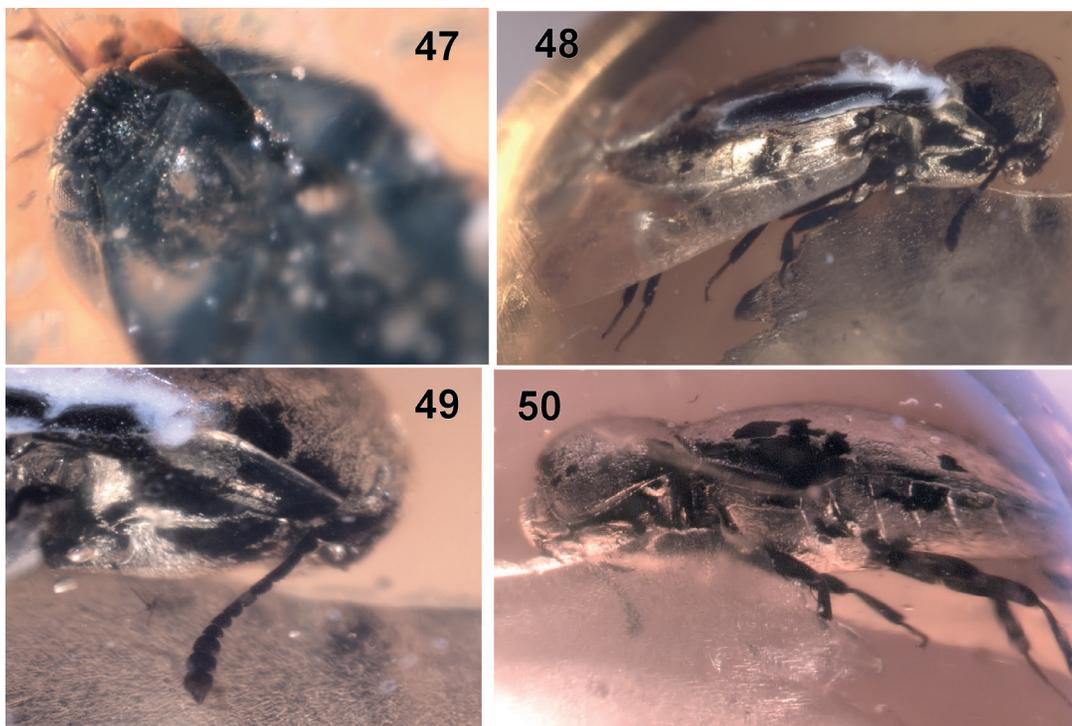
Figures 38-39. *Falsothambus gracilicornis* n. gen., n. sp. Holotype. length 1.8 mm. Lateral view, showing structure of antenna (38), lateral view, showing proportions of body and flattened tibiae (3).



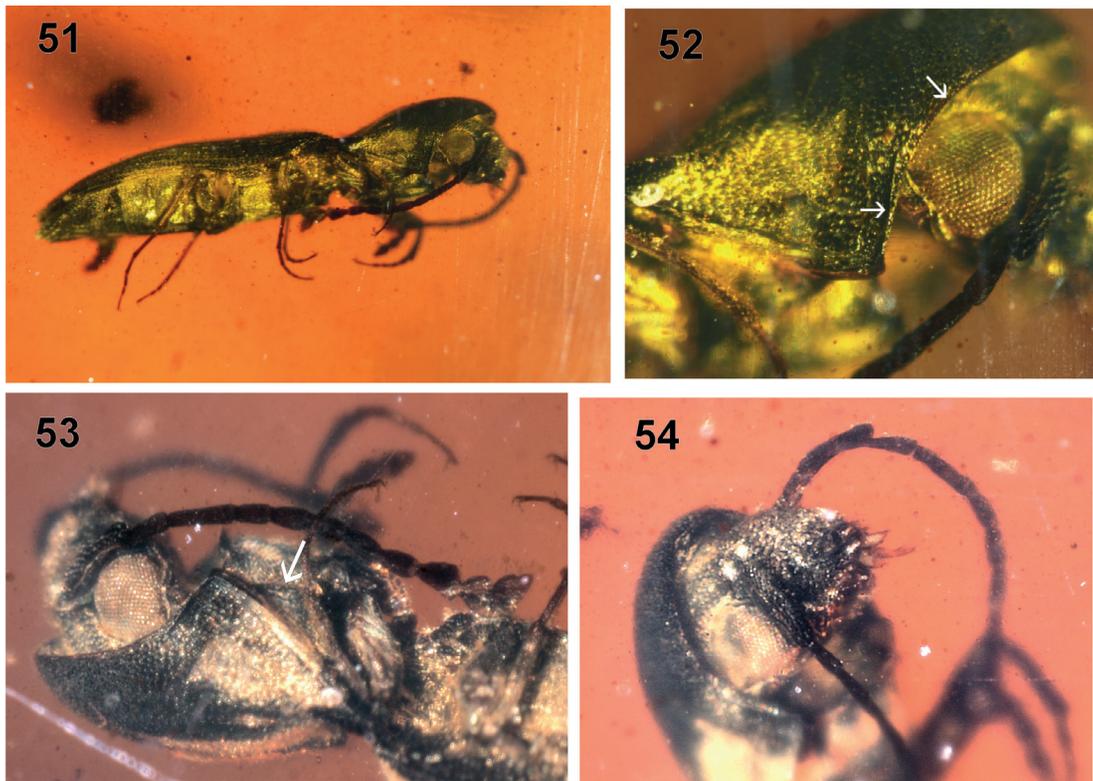
Figures 40-44. *Myall burmensis* n. sp. Holotype. Holotype, length 3.5 mm. Ventral view, slightly tilted (40), mesocoxal region and metasternite, showing short tarsal groove on metasternite caudad to mesotibia, limited by ridge on both sides (arrows) (41), proleg (42), head and prothorax, ventral view, showing basally closed (arrow) and medially defined lateral antennal grooves, unmodified hypomera and mandibles with expanded lateral margins (43), metalegs, without tibial spine-combs (44).



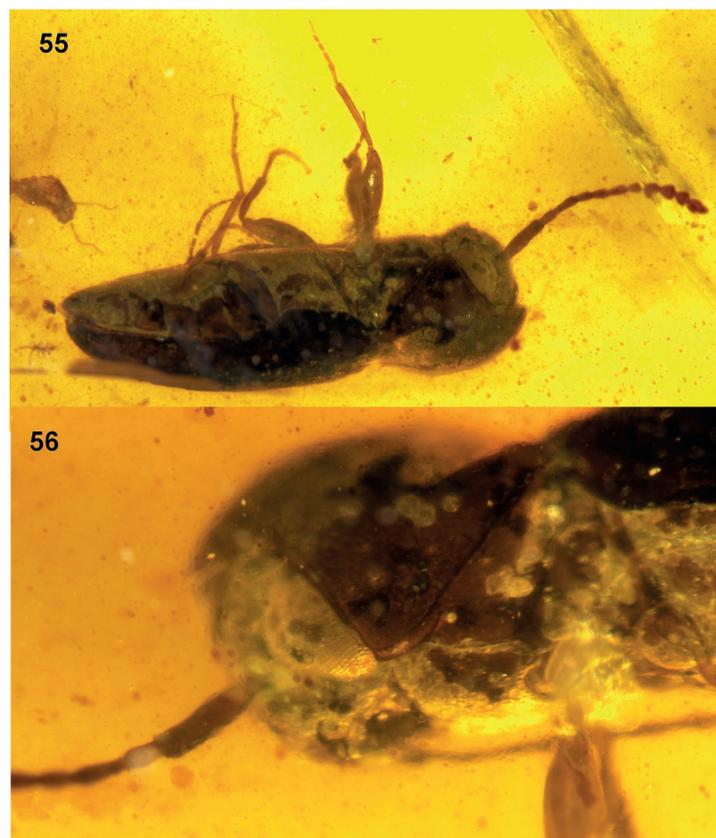
Figures 45-46. *Pseudomyall elongatulus* n. gen., n. sp. Holotype. length 3.5 mm. Ventrolateral view of front body showing antennae with elongated apical antennomeres, basally closed antennal grooves and short mandibles with expanded lateral margins (45), ventrolateral view showing elongated legs and long antennae (46).



Figures 47-50. *Paleoeucnemis minutus* n. gen., n. sp. Holotype, length 2.8 mm. Face and prothoracic venter, showing strong, short mandibles and lateral antennal grooves (47), lateral view showing boat-shaped venter and flat dorsum, these turning slightly upwards apically (48), antennae with three apical enlarged flagellomeres (49), ventral view showing smooth metaventrite (50).



Figures 51-54. *Protomicrorhagus antennatus* n. gen., n. sp. Holotype, length 3.2 mm. Lateral view (51), view of face from side, showing doubled lateral and frontal ridge (lower arrow) on pronotum and serrate pronotal front margin (upper arrow) (52), lateral view showing complete notosternal suture (arrow) and antennal proportions (53), head, showing short mandibles and hidden labrum (54).



Figures 55-56. *Protomicrorhagus brevis* n. gen., n. sp. Holotype, length 3.0 mm. Lateral view (55), lateral view of front body showing doubled pronotal ridges, complete notosternal suture and keeled pronotal hind angle (56).

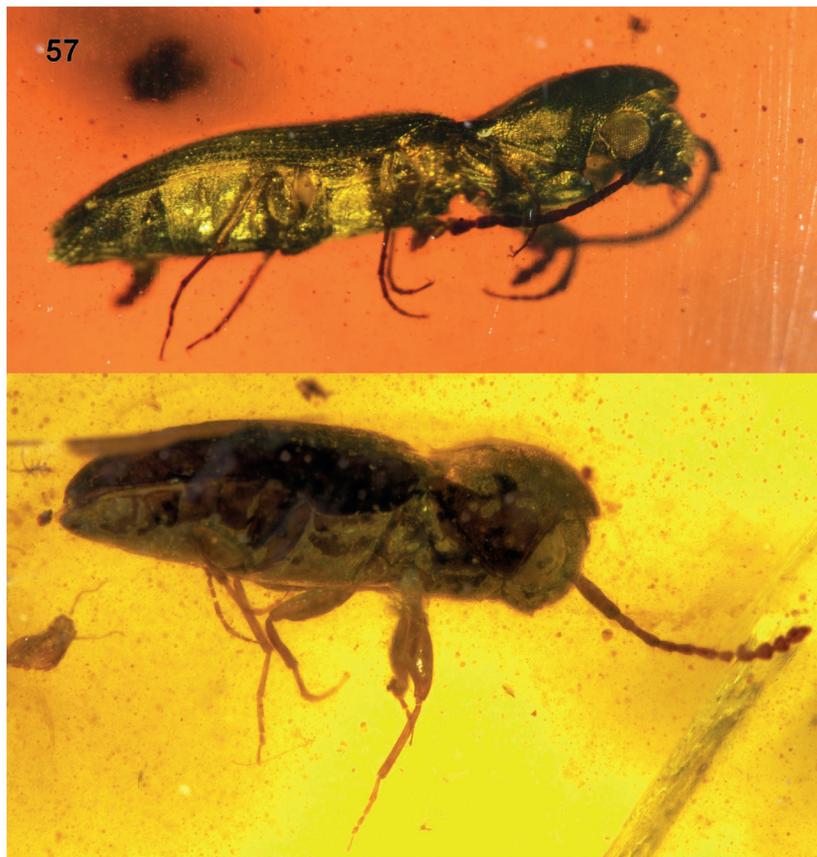
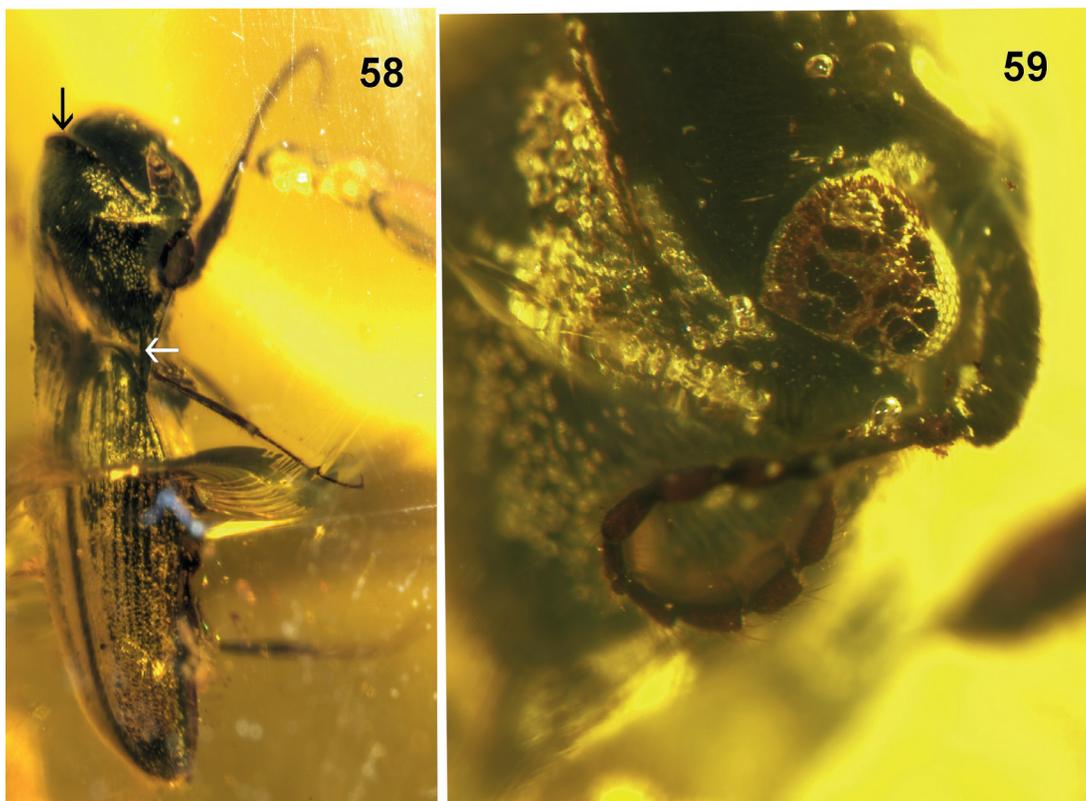
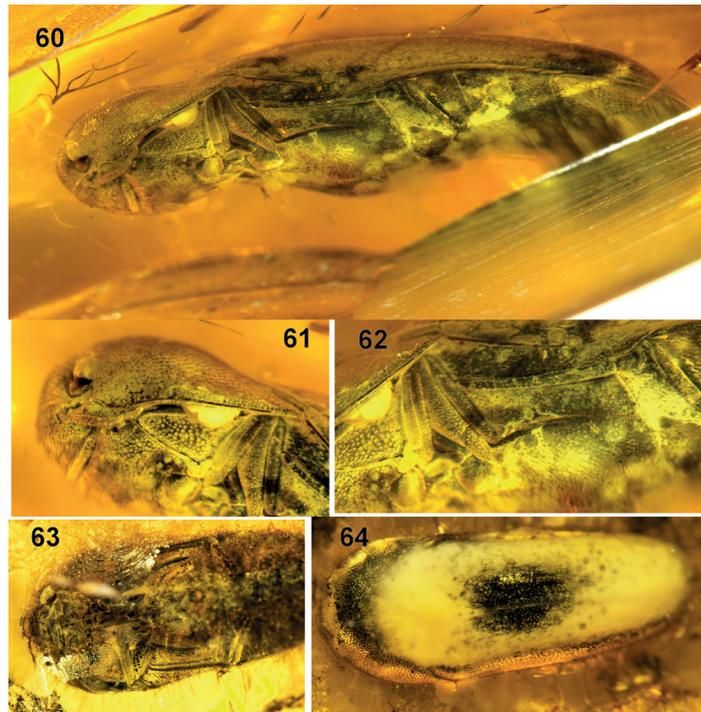


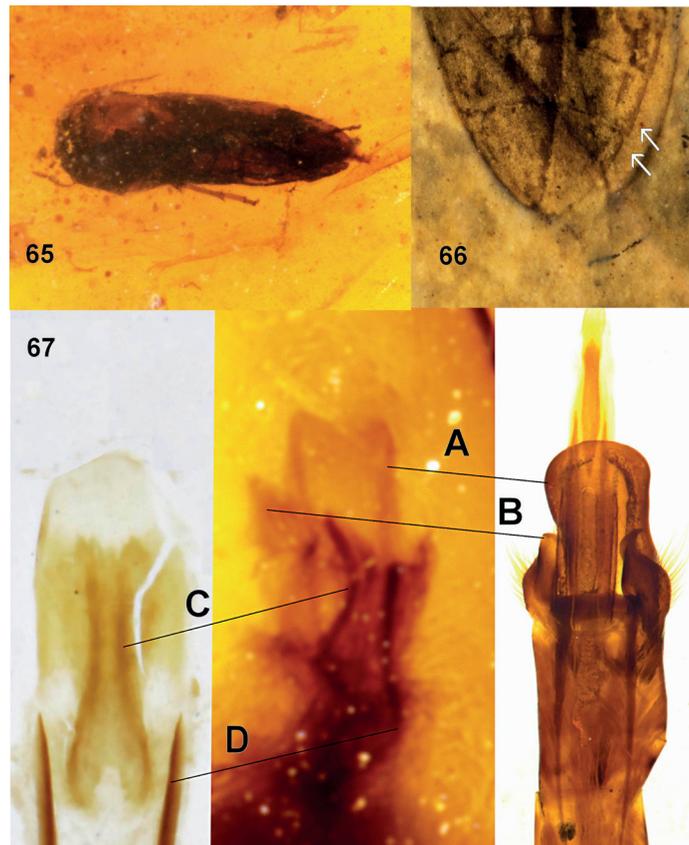
Figure 57. *Protomicrorhagus antennatus* n. sp. Holotype (upper image), *Protomicrorhagus brevis* n. sp. Holotype, (lower image), showing different body proportions.



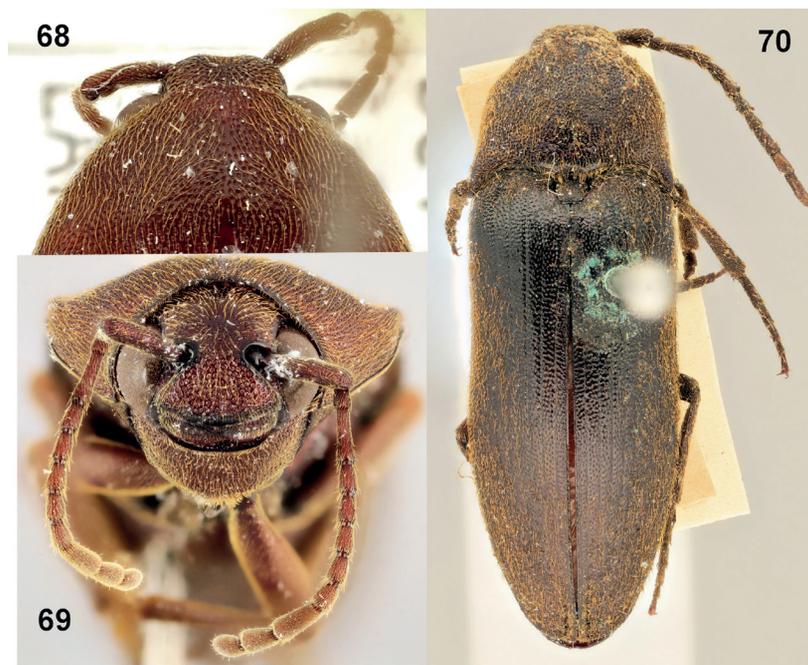
Figures 58-59. *Coenomana brevicornis* n. sp. Holotype, length 3.0 mm. Frontolateral view, showing the strongly keeled elytra, keeled pronotal hind angle (white arrow) and the strongly upwards turned front ridge on pronotum (black arrow) (58), antenna with three flattened and enlarged apical antennomeres and pronotum with strong doubled ridge along front margin (59).



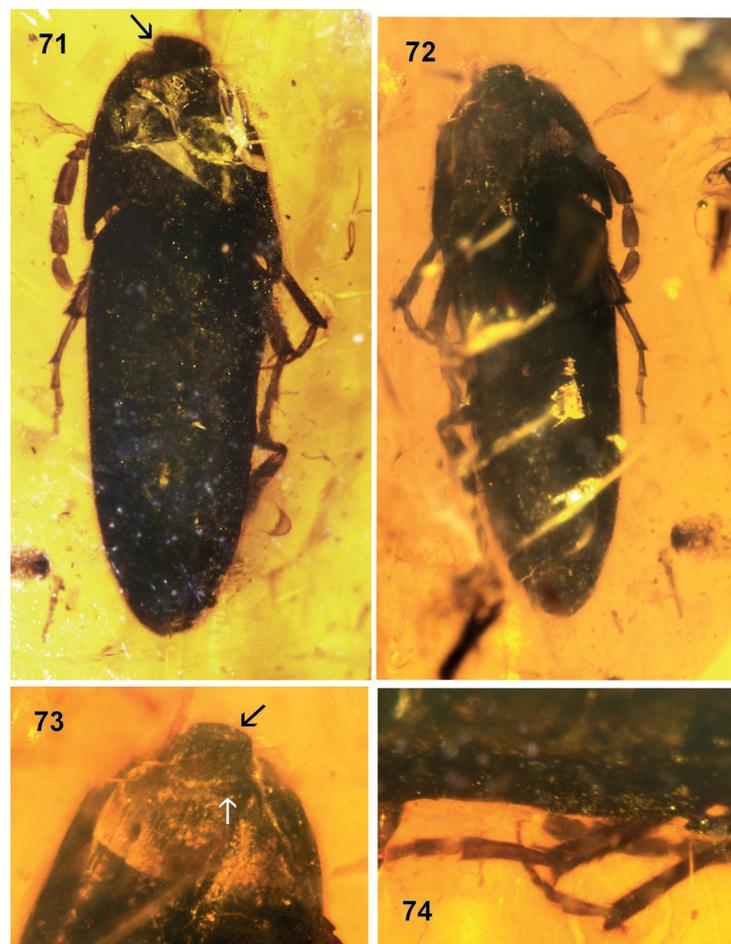
Figures 60-64. *Sieglindea antiqua* n. sp. Paratype (figs 60-62), length 4.7 mm; holotype (fig. 63-64), length 5.7 mm. Lateroventral view (60), head and prothorax, lateroventral view, showing basally closed medially defined antennal grooves, short mandibles and hypomera without excretory organs (61), metaventrite with sharply defined tarsal grooves (62), antennal grooves (63), dorsal view (64).



Figures 65-67. *Protovitellius deceptus* n. gen. n. sp. Holotype, length 2.2 mm. Ventral view (65), tip of abdomen, arrows showing apical excretory punctures on elytra (66), *Vitellius* sp., part of subgenital plate, ventral view (left); *Protovitellius deceptus* n.sp, ventral view of partly exposed aedeagus and subgenital plate (center); *Mesogenus siamensis* Fleutiaux, apical part of aedeagus in ventral view (right). A = median sclerite of median lobe, B = tips of lateral lobes, C = ventral supporting part of subgenital plate, D = lateral parts of subgenital plate (67).



Figures 68-70. *Jenibuntor* species. *Jenibuntor* sp., Australia, Queensland, head and part of pronotum showing the medially expanded frontoclypeal region (68), ditto, frontal view showing expanded lateral margin of mandibles (69), *Jenibuntor tabang* Muona, paratype, dorsal view (70).



Figures 71-74. *Jenibuntor pusillus* n. sp. Holotype, length 2.5 mm. Dorsal view, arrow indicates enlarged frontoclypeal region (71), ventral view (72), face and part of prothorax in ventral view, showing expanded frontoclypeal region (black arrow) and expanded lateral margin of mandible (white arrow) (73), pro- and mesolegs (74).