

The oldest representatives of the family Throscidae (Coleoptera: Elateriformia) from the Lower Cretaceous Lebanese amber



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ABSTRACT

Two new genera and two new species of fossil Throscidae: *Potergosoma gratiosa* gen. et sp. nov. and *Rhombospis laticollis* gen. et sp. nov. are described from the Lower Cretaceous Lebanese amber and are compared with extant and extinct genera. The described amber inclusions are the oldest known representatives of the family Throscidae. Some hypotheses on the phylogeny of the family Throscidae and the position of it in the superfamily Elateroidea are discussed.

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1. Introduction

The Throscidae Laporte, 1840 is a relatively small family within Elateroidea (with nearly 200 described species) with a worldwide distributed. Currently, the fossils belonging to this family are known from the Dominican, Baltic, Oise, Bitterfeld and Fushun ambers (Caeonozoic: first Miocene, remainder Eocene); from the Sakhalin and Burmese ambers (Upper and Lower Cretaceous respectively); and also as compression fossils from the Khetana River (Lower Cretaceous), London Clay (Lower Eocene), Messel (Middle Eocene), Florissant (uppermost Eocene–lowermost Oligocene), and Amagu River (Miocene) (Kovalev et al., 2012; Kirejtshuk and Ponomarenko, 2013). However, they are mostly undescribed and some published descriptions are not sufficiently detailed or precise to draw conclusions on the systematic position of the described forms. These uncertain taxa are *Palaeothroscus sosnovskiyi* Iablokoff-Khinzorian, 1962 and *Troscites tschitscherini* Iablokoff-Khinzorian, 1962 from Baltic amber (the first was transferred by Cobos (1963) to the genus *Trixagus* Kugelann, 1794 and second to *Aulonothroscus* Horn, 1890); also, *Megocephalites eocenicus* Hong, 2001 from the Fushun amber; *Pactopus americanus*

Wickham, 1914 from Florissant, and *P. avitus* Britton, 1960 from the London Clay. Also, an unnamed species was described from the Middle Eocene of Messel (Wedmann, 1994). Other fossil representatives from Baltic amber, *Pactopus fasolti* Muona, 1993, *P. fajneri* Muona, 1993, *Jaira bella* Muona, 1993, *Potergus frochi* Muona, 1993, *P. logei* Muona, 1993 and from the lowermost Eocene amber of Oise, *Trixagus majusculus* Kovalev, Kirejtshuk & Nel, 2012, are better known for comparison. The specimens from Lebanese amber described herein are the oldest representatives of the family Throscidae. A more detailed overview of this family in the fossil record can be obtained from the catalogue by Kirejtshuk and Ponomarenko (2013).

2. Material and methods

The Lebanese amber specimens examined are temporarily deposited in the Muséum National d'Histoire Naturelle, Paris (MNHN) until the establishment of a national natural history museum in Lebanon. For this study, basic optical equipment was used, in particular a stereomicroscope (Leica MZ 16.0) in the St. Petersburg Institute and a stereomicroscope (Olympus SCX9) in the Paris Museum. The method of preparation of the specimens for study was described in Azar et al. (2003).

Strata. Lower Cretaceous; Barremian–lowermost Aptian (circa 125–135 My), but could be earlier (Azar, 2012).

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Localities. Hammana – Mdeyrij; Bouarij; Falougha (all in Central Lebanon) (Fig. 1). The last outcrop is newly discovered in 2012 by Dany Azar and Sibelle Maksoud (Kirejtshuk and Azar, 2013 (in press)), and the beetle described herein is the first specimen studied in detail from this locality.

3. Systematic paleontology. Descriptions of new taxa

Order Coleoptera Linnaeus, 1758

Infraorder Elateriformia Crowson, 1960

Superfamily Elateroidea Leach, 1815

Family Throscidae Laporte de Castelnau, 1840

Notes. The specimens examined demonstrate clear diagnostic characters of the family, some of which could be regarded as family apomorphies, namely: developed metacoxal plates; exposed and heavily sclerotized labrum; antennae with distinctly enlarged apical antennomeres forming elongate antennal club; peculiar grooves on underside for receiving antennae and legs similar to those characteristic of recent representatives; wide prosternal process and rather widely separated mesocoxae.

(?) Tribe Potergini Cobos, 1961

Genus *Potergosoma* Kovalev et Kirejtshuk, gen. nov.

Type species. *Potergosoma gratiosa* sp. nov.

Derivation of name. The name of this new genus is derived from the recent generic name “*Potergus*” and from the Greek “σῶμα” meaning “body” and refers to the similarity in the shape of the body.

Diagnosis. Body medium-size, elongate, convex both dorsally and ventrally. Frons with long median carina. Eyes small. Labrum short and rounded at sides. Antennae with antennomeres 9–11 forming elongate oval club. Posterior angles of pronotum with a long additional carina along lateral carina reaching the middle of pronotal length. Lateral prothoracic carina reaching anterior edge of prothorax. Scutellum small, scarcely longer than broad, with rounded sides and oval at apex. Prosternum without chin piece. Prosternal plate large, slightly constricted in the middle, strongly impressed in posterior half and with narrow lateral borders. Prohypomera with deep sinuous antennal grooves, their visible part large and subtriangular. Metepisterna narrow, subparallel-sided. Metaventrite with shallow depressions for receipt of mesotarsi. Abdomen only with shallow depressions on ventrites 1–3 (without distinct tarsal grooves). Pro- and mesocoxae oval, metacoxal femoral plates moderately narrow, distinctly shortened laterally. Legs rather short; tibial apices simple; tarsi slender, moderately long and with simple tarsomeres.

Comparison. The structure of the frons with a median carina and the elongate shape of the body suggest a close relationship with the genera *Potergus* Bonvouloir, 1871 and *Jaira* Muona, 1993. The new genus is similar to the extant *Potergus* in the small and very narrow eyes, but differs from it in the structure of the prothorax without a chin piece, wider visible parts of the prohypomera, metacoxal plates shortening laterally, lack of tarsal grooves on both metaventrite and abdominal ventrites, and enlarged apical antennomeres forming a distinct antennal club; also, in the much smaller body. *Jaira* is similar to the new genus in the lack of tarsal grooves on the metaventrite and abdominal ventrites, as well as in the wider subtriangular part, and the prohypomera exposed beyond the antennal grooves; but it is distinguished from the new genus by

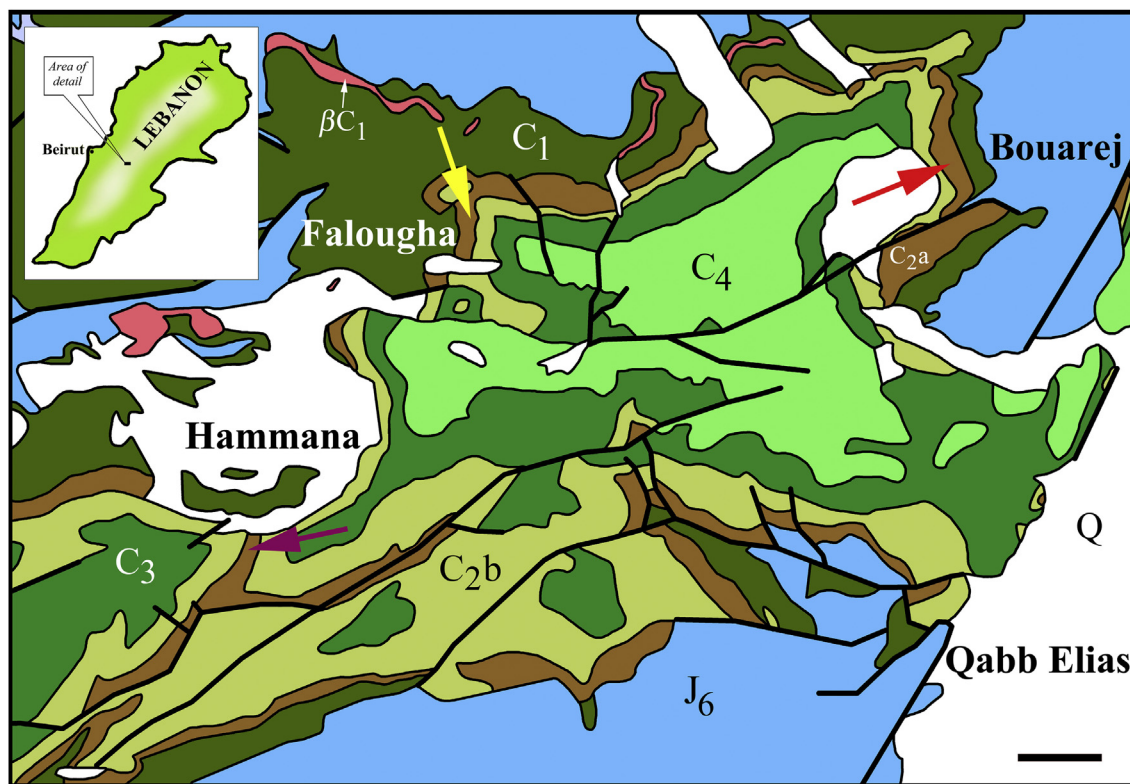


Fig. 1. Geological map of Hammana, Falougha and Bouarej amber outcrops. Abbreviations: J6 = Kimmeridgian; βJ6 = volcanic Kimmeridgian; C1 = Neocomian; βC1 = volcanic Neocomian; C2a = Lower Aptian; C2b = Late Aptian; C3 = Albian; C4 = Cenomanian; Q = Quaternary; thickened lines represent faults; scale bar = 1 km. Purple arrow indicates the Hammana outcrop; yellow arrow indicates the Falougha outcrop; red arrow indicates the Bouarej outcrop. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

the antennae with four enlarged subapical antennomeres, subparallel anterior and posterior edges of the femoral plates of the metacoxae being somewhat longer externally, very widened apices of the tibiae and tarsomeres 2–4 lobed underneath, as well as in the large oval eyes and the distinctly larger body.

Potergosoma gratiosa Kovalev et Kirejtshuk, sp. nov.

Figs. 2, 3

Derivation of name. Epithet of this new species is formed from the Latin “*gratia*” (grace or graceful) and “*-osus*” (having the quality of).

Holotype. “750” [outcrop Hammana – Mdeirij, Caza Baabda, Mouhafzet (Governorate) Jabal Loubnan (Mount Lebanon)], probable male; complete specimen with exposed apex of right posterior hindwing and missing right pro- and mesotarsi, right posterior leg, part of left profemur and part of left protibia; inclusion in a thin quadrangular piece of homogeneous amber (2.4 mm long and 2.4 mm wide) with one oblique and other small cracks at the middle of the dorsum of the specimen. The piece of amber was prepared and embedded between two round microscope cover slips in a Canada Balsam medium.

Description. Body length 1.9 mm, width 0.6 mm, elongate, about three times as long as broad, convex both dorsally and ventrally,



Fig. 2. *Potergosoma gratiosa* gen. et sp. nov. (Throscidae), photographs of holotype. A, body of holotype, dorsal. B, ditto, ventral. Length 1.85 mm.

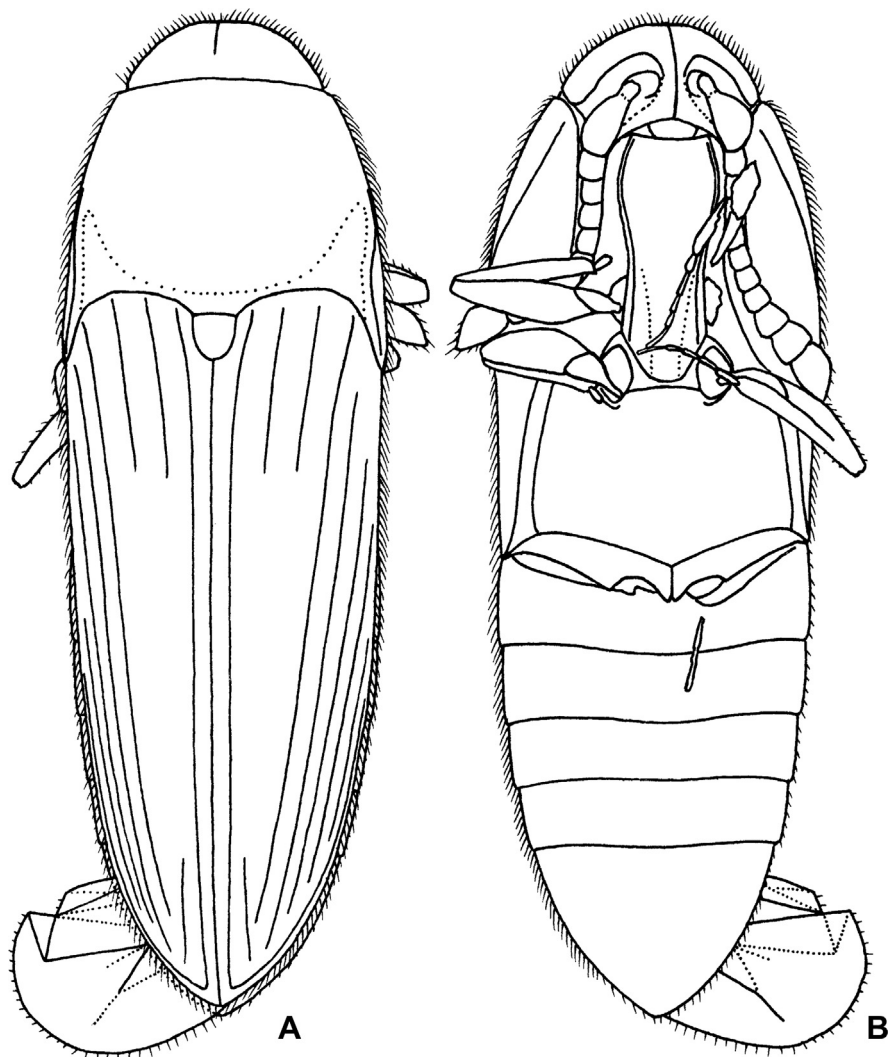


Fig. 3. *Potergosoma gratiosa* gen. et sp. nov. (Throscidae), line drawings of holotype. A, body of holotype, dorsal. B, ditto, ventral. Length 1.85 mm.

dark brown to blackish, with uniform, rather short and very dense suberect yellowish hairs; dorsal surface with a slight shine.

Head large; frons convex with a feeble median carina from anterior edge of the frons to occiput. Eyes scarcely visible, apparently very small and lineiform. Labrum free, small and semi-elliptical. Antennae long and relatively stout: antennomere 1 (scape) large, longer than wide; antennomere 2 slightly narrower than scape and about as long as wide; antennomeres 3–8 comparatively small (antennomeres 3–5 somewhat elongate, antennomeres 6–8 subquadrate); 9–11 distinctly enlarged, forming moderately large and elongate oval club, antennomere 9 slightly transverse and widening to apex; antennomere 10 transversely subtrapezoidal, slightly larger than previous one; antennomere 11 large, slightly shorter than antennomeres 9 and 10 combined, oblong subtrapezoidal with subacute apex. Pronotum about 1.4 times as wide as long along the middle, evenly arcuate at sides, with posterior angles projecting far and much longer than median part of posterior edge; strongly impressed at sides along lateral carina; median part of posterior edge briefly projecting and slightly convex at apex. Elytra elongate, widest at base, about 2.15 times as long as wide combined and about three times as long as pronotum, gradually narrowing to apices, with well-developed fine striae and intervals between them subflattened. Mesoventrite short, of usual structure. Metaventrite relatively convex and with

shallow depressions only. Epipleura at anterior third of length rather wide and gradually narrowing to their middle. Hindwings with rather long marginal fringe. Anal ventrite of abdomen narrowly rounded at apex.

Head and pronotum with subuniform fine and dense punctures. Elytra with striae punctated with punctures larger than those on intervals. Intervals subflattened, with subuniform irregular and very dense punctures, interspaces slightly rugose. Underside with subuniform fine and dense punctation.

Genus *Romboaspis* Kovalev et Kirejtshuk, gen. nov.

Type species. *Romboaspis laticollis* sp. nov.

Derivation of name. The name of the new genus is derived from the Greek “ρόμβος” (rhombus) and “ασπίς” (shield) and refers to the peculiar dilated body form.

Diagnosis. Body small, wide, subpentagonal, moderately convex both dorsally and ventrally. Frons convex with a feeble median carina. Eyes rather small, oval. Labrum small, transverse. Antennae with subapical antennomeres forming weak elongate club. Pronotum subtrapezoidal, widest before posterior angles, its base clearly bisinuate with distinct basal impressions; posterior angles somewhat dilated,

long, and covering elytral shoulders. Lateral prothoracic carina almost reaching anterior edge of prothorax. Scutellum small, sub-pentagonal, nearly as long as wide. Prosternum without chin piece. Prosternal plate subflattened, moderately large, scarcely constricted in its anterior part and bordered laterally. Prohypomera with deep sinuous antennal grooves restricting large and subtriangular visible part of prohypomera. Metepisterna narrow, subparallel sided. Metaventricle relatively convex, with rather long, oblique and slightly bent outward grooves for receipt of mesotarsi. Abdomen with well-developed, long, narrow grooves for receipt of metatarsi on ventrites 1–3. Legs rather short; tibial apices slightly enlarged; tarsi long and rather slender, simple.

Comparison. The new genus is similar to extant species of *Potergus* Bonvouloir, 1871 in the frons with a median carina and well-developed tarsal grooves on the metaventricle and abdominal ventrites, but differs from it in the lack of a chin piece, wide and subtriangular visible part of the prohypomera, metacoxal femoral plates somewhat shortened laterally, longer metatarsal grooves on

the abdomen, and apparently larger eyes, as well as in the wider and larger body. However, the extinct species from Baltic Amber described as *Potergus* have a rather wide body (*P. frohi* Muona, 1993 and *P. logei* Muona, 1993), rather small oval eyes, and metacoxal plates distinctly shortened laterally; but they differ from the type species of the new genus in the rather narrow subparallel-sided visible part of the prohypomera. Also, the new genus can be compared with *Pactopus* LeConte, 1868 in the presence of the well-outlined tarsal grooves on the metaventricle and abdominal ventrites, oval eyes, metacoxal femoral plates shortened laterally and subtriangular visible part of the prohypomera; but differs from the latter in the median carina on the frons and wider body, although the enlarged base of the pronotum in the new genus appears to be a sexual character of the male, which is rather common among members of this family.

Rhombospis laticollis Kovalev et Kirejtshuk, sp. nov.

Figs. 4, 5

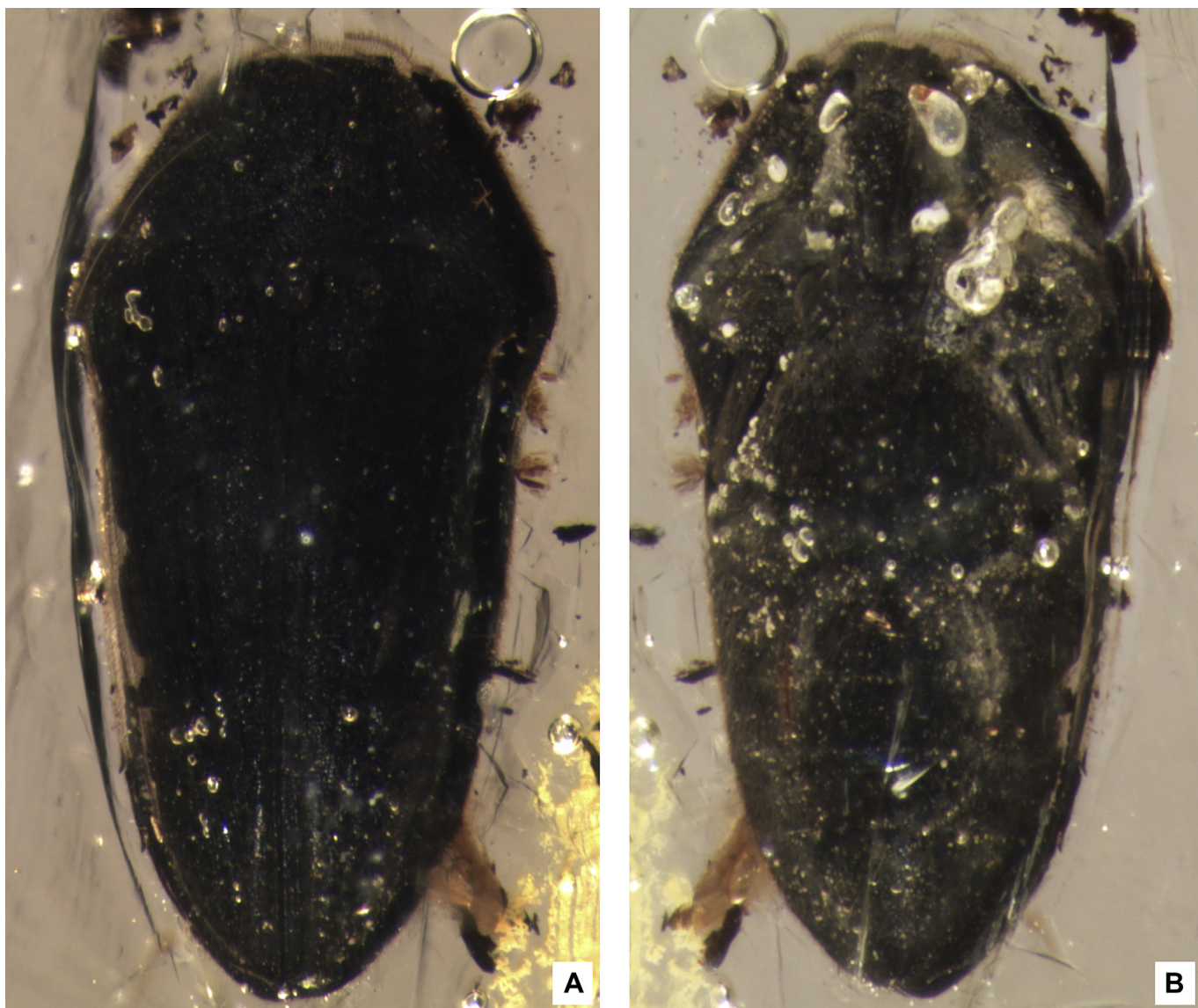


Fig. 4. *Rhombospis laticollis* gen. et sp. nov. (Throscidae), photographs of holotype. A, body of holotype, dorsal. B, ditto, ventral. Length 2.4 mm.

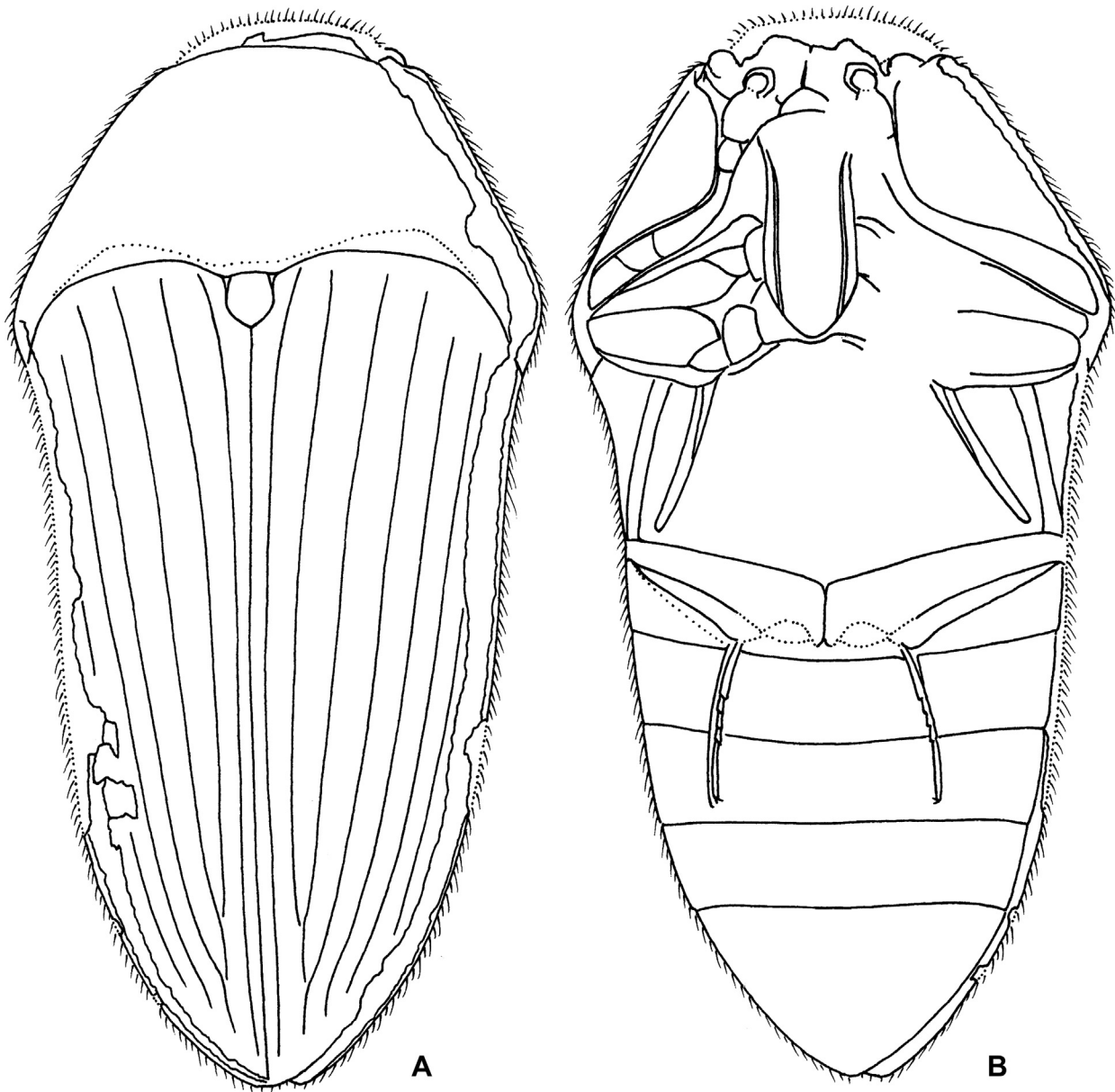


Fig. 5. *Rhomboaspis laticollis* gen. et sp. nov. (Throscidae), line drawings of holotype. A, body of holotype, dorsal. B, ditto, ventral. Length 2.4 mm.

Derivation of name. The epithet of the new species refers to the rather wide pronotum of the new species.

Holotype. “TAR-165C” [Bouarij outcrop, Caza Baabda, Mouhafazet (Governorate), Jabal Loubnan (Mount Lebanon)], probable male; a complete specimen broken along its lateral sides in the dorsal and ventral planes, with the anterior part of the head and part of left elytron destroyed; inclusion in a thin quadrangular piece of homogeneous amber (5.8 mm long and 4.8 mm wide) with one gas spherical vesicle at the right anterior angle of the pronotum, many small gas vesicles along the underside of the anterior half of the body; also, many small pieces of organic matter of black and brownish colour spread along both sides of the body, one small crack located along the whole left lateral edge of the body underneath and another smaller crack along the middle of the posterior half of the body also underneath; the integument of the underside is covered with a clear “milky cover” of dark colour and the dorsal integument is covered with a much thinner and less conspicuous

dark “milky cover”. The piece of amber was embedded between two round microscope cover slips in a Canada Balsam medium.

Description. Body length 2.4 mm, width 1.2 mm, elongate sub-pentagonal, about two times as long as wide, pitch brown, with short and dense subrecumbent hairs intermixed with rather long and suberect hairs, dorsal surface rather shiny.

Antennae moderately long: antennomere 1 large and longer than wide; antennomere 2 slightly narrower than previous one and about as long as wide; following antennomeres not clearly visible because of insertion in antennal grooves of prothorax and “milky” cover, but apparently the apical antennomeres form a large elongate club. Pronotum about 2.4 times as wide as long along the middle. Scutellum with rounded sides and subacute apex. Elytra elongate, widest behind the base, about 1.6 times as long as wide combined, narrowing to apices, with distinct fine striae and intervals between them subflattened. Apices of elytra narrow and rounded. Epipleura rather wide in anterior third and narrow posteriorly. Mesoventrite

short, of usual structure. Pro- and mesocoxae oval, metacoxal femoral plates moderately narrow, distinctly shortened laterally.

Pronotum with double punctuation formed by coarse and rather dense punctures interspaced with finer and very dense punctures. Elytra with fine striae punctated by rather large and moderately dense punctures; intervals between them almost flat, with irregular, very dense and almost rugose punctuation. Punctuation of underside formed by coarse and moderately dense punctures interspaced with fine and dense to very dense punctures, much smoother on prosternal plate and metaventrite.

Gen. et sp. 1

Fig. 6A

Material. Specimen “FAL-3B” [Falougha outcrop, Caza Baabda, Mouhafazet (Governorate) Jabal Loubnan (Mount Lebanon)], sex unknown; complete specimen covered with many small reddish pieces of organic matter making it very difficult to observe the integument; inclusion in a thin quadrangular piece of amber (4.1 mm long and 1.8 mm wide), the beetle is situated along the border between two amber layers. The piece of amber was embedded between two round microscope cover slips in a Canada Balsam medium.

Body length 1.77 mm, width 0.7 mm. In the general shape of the body structure, metaventrite (with oblique grooves for reception of mesotarsi), antennal grooves, and metacoxal femoral plates, it is possible to assign this specimen to the Throscidae and probably near to *Potergosoma* gen. nov.

Gen. et sp. 2

Fig. 6B, C

Material. Specimen “JG 79/71” [Jouar Es-Souss (Bkassine) outcrop, District of Jezzine Mouhafazet Loubnan El-Janoubi (Southern Lebanon)], sex unknown; complete specimen densely surrounded with many small dark pieces of organic matter intermixed with many small gas bubbles and some semi-transparent particles making it difficult to observe the integument; inclusion in a thin, subtriangular piece of amber (two sides of it about 4.1 mm long and third side 2.1 mm); the beetle is situated along the border of two amber layers. The piece of amber was embedded between two round microscope cover slips in a Canada Balsam medium.

Body length 1.8 mm, width 0.6 mm. As in the previous specimen, this one could also be related to *Potergosoma* gen. nov., although its antennal grooves, in contrast to other Lebanese specimens described here, are more gently arcuate and very enlarged posteriorly. Also, it seems that if the median carina is raised on the frons, it is rather reduced, and its last antennomere is somewhat acuminate at apex.

4. Discussion

The composition and placement of the Throscidae within the Elateroidea still remain rather disputable. The attribution of the subfamily Lissominae Laporte, 1849 after Bonvouloir (1859) and Thylacosterninae Fleutiaux, 1920 after Crowson (1955) to Throscidae

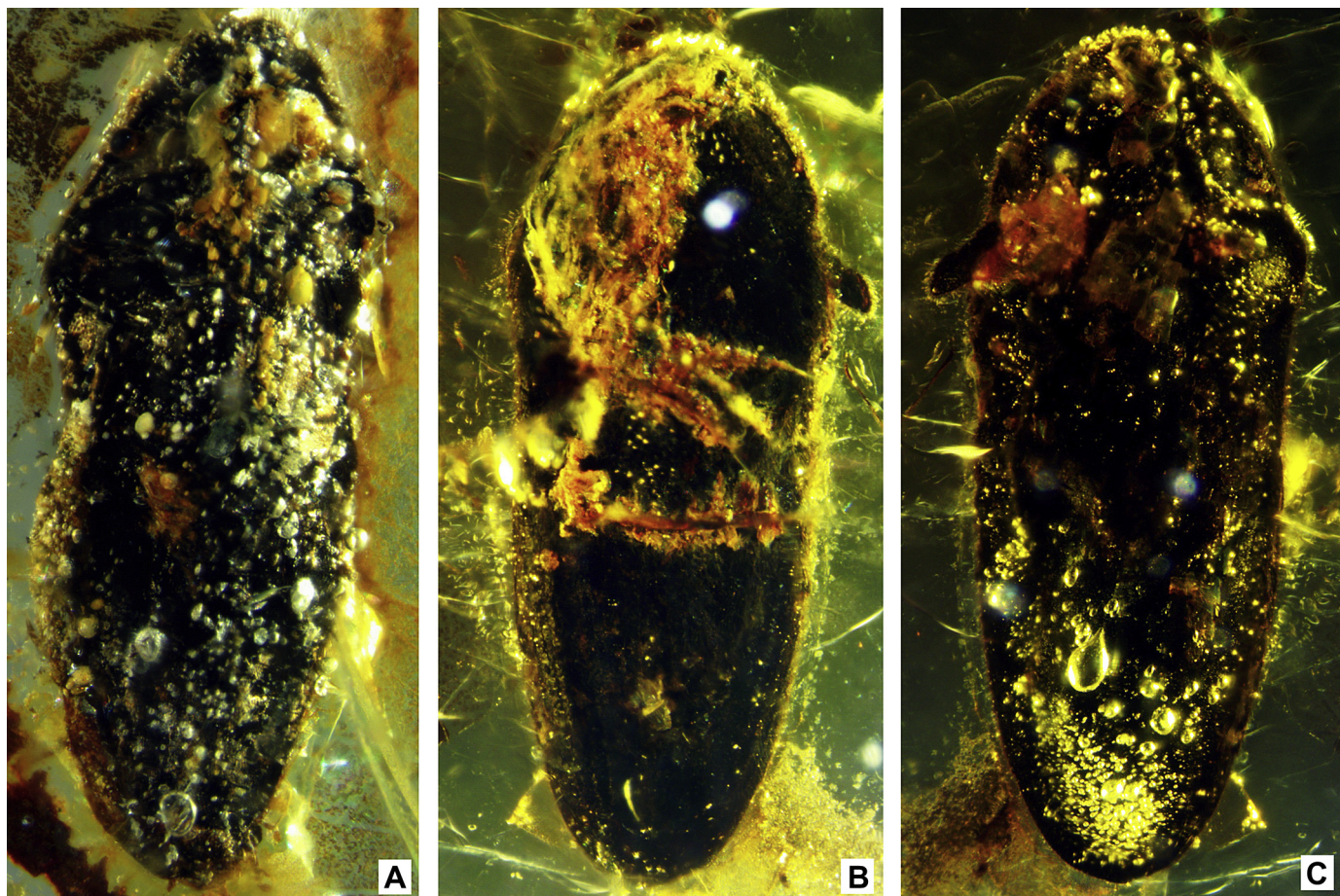


Fig. 6. Gen. et spp. (Throscidae), photographs. A, Gen. et sp. 1 (“FAL-3B”), ventral. Length 1.77 mm. B, Gen. et sp. 2 (“JG 79/71”), dorsal; C, ditto, ventral. Length 1.8 mm.

is repeatedly revised (Burakowski, 1975; Lawrence, 1988; Muona, 1995; Vahtera et al., 2009). Here is accepted that the Throscidae in current interpretation (Throscitae sensu Cobos, 1961) represents an isolated group which, together with Eucnemidae Eschscholtz, 1829, Cerophytidae Latreille, 1834 and Brachypsectridae LeConte et Horn, 1883, forms a separate lineage in Elateroidea with unclear relations. Lawrence (1988), after comparison of structural imaginal characters, placed Throscidae sensu str. together with Cerophytidae as a clade forming a sister group to Eucnemidae [Eucnemidae (Throscidae + Cerophytidae)], while Brachypsectridae is considered as a sister group to both clades, one including three families mentioned above, and second consisting of Elateridae Leach, 1815 and Cebriionidae Latreille, 1802. Beutel (1995) published similar results after comparative analysis of larval structures, but the family Brachypsectridae was placed in his cladogram together with Cantharoidea. Lawrence et al. (2007) joined Throscidae with Cerophytidae forming a sister clade to Brachypsectridae [Eucnemidae (Brachypsectridae (Throscidae + Cerophytidae))]. However, later Lawrence et al. (2011) based on comparison of both imaginal and larval characters, united Cerophytidae with Eucnemidae in one clade which is regarded as a sister one to Throscidae [Brachypsectridae (Throscidae (Cerophytidae + Eucnemidae))].

Having extrapolated the bionomic and ecological features of the recent species to similar fossil ones, some close association of the latter with decaying wood and also their larval xylomycetophagy could be admitted, which were hardly initial for the elaterid-lineage of Elateroidea and, perhaps, for the superfamily in general (Zherikhin, 1980; Chang et al., 2011). Gurjeva (1969) regarded wood habitats and predaceous diet as initial for Elateroidea sensu lato. Later Muona (1995) mentioned three living strategies in the infraorder: wood-borers (Cerophytidae–Eucnemidae), soil-dwellers (Elateridae–Cebriionidae) and free-living predators (Cantharoidea), and also Throscidae were frequently characterized by inhabiting soil and larvae feeding on ectomycorrhizalfungi on the roots of trees (Burakowski, 1975), i.e. by the modified larval xylomycetophagy.

The discovery of the oldest representatives of Throscidae in Lebanese amber rather similar to the recent members of the family show that in the Lower Cretaceous this family presented a well separated and rather diverse group. The structural features of these oldest representatives do not allow the authors to include them in a tribe using the diagnostic characters proposed for the recent species by Cobos (1961). Nevertheless, the additional characters suggest a closer relationship of the new genera and some Potergini Cobos, 1861 rather than Throscini (see above). Moreover, one specimen of this family was found in material from Baissa of comparable age. After studying the latter as well as examining unstudied specimens recorded from the Lower Cretaceous Burmese amber (Rasnitsyn and Ross, 2000) and Khetana (Gromov et al., 1993), development of a preliminary hypothesis of Mesozoic throscid diversification and its correspondence with Eocene data on this family (summarized by Muona, 1993) will be possible. No throscid specimen has been found earlier, while the elaterids appear in the fossil record in the Lower Jurassic and, therefore, it is thought that the family Throscidae is markedly younger than the Elateridae. The mode of life of recent members of the family, peculiarities of larval development and type of life circle, are certainly more modified from the ancestral ones in comparison with those in the many elaterid groups. The relationship between different groups of the Mesozoic elateriformians remains very unclear. Because of the representation of this infraorder in the Mesozoic faunas (Dolin, 1980; Kirejtshuk et al., 2010a, 2010b; Chang et al., 2010, 2011) seems to be comparatively greater than in the recent one, the study of fossils can provide a very important contribution to our knowledge of the evolution and phylogeny of the infraorder Elateriformia, which should bring many corrections to the

reconstruction proposed by Crowson (Crowson, 1975, 1981), combining both neontological and palaeontological information, and also re-defining monophyletic groups in Elateroidea.

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