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Unveiled: *Prototrichalus* from the mid-Cretaceous Burmese amber represents a yet oldest record of Ischaliidae Blair, 1920 (Coleoptera: Tenebrionoidea)

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ABSTRACT

The genus *Prototrichalus* Molino-Olmedo, Ferreira, Branham and Ivie, 2020 known from Burmese amber was initially attributed to the family of net-winged beetles (Coleoptera: Lycidae) in the superfamily Elateroidea, and soon after transferred to Tenebrionoidea *incertae sedis* and compared with *Ischalia* Pascoe, 1860. Here, we examined additional material of *Prototrichalus* and confirmed it is the first known Mesozoic subgroup of the family of false fire-coloured beetles (Coleoptera: Ischaliidae) in superfamily Tenebrionoidea. This oldest yet available record of the Ischaliidae suggests their at least Cretaceous origin. A re-defined set of the diagnostic features is provided for the family Ischaliidae to incorporate the unique combination of morphological features of *Prototrichalus*. One new species, *P. jingpo* Telnov and Kundrata, sp. nov., is described and compared with its congeners. A key to supraspecific taxa of Ischaliidae and an annotated checklist of extinct species of the family are provided.

1. Introduction

Ischaliidae (false fire-coloured beetles) represent a small group in the beetle superfamily Tenebrionoidea restricted in its extant distribution to East and Southeast Asia, the Himalayas, and boreal North America (Lawrence et al., 2010; Young, 2011; Telnov and Barclay, 2019). It includes 57 extant species classified in a single genus *Ischalia* Pascoe, 1860, with three subgenera (Gusakov and Telnov, 2007; Young, 2008, 2011, 2014; Kazantsev and Young, 2011; Kazantsev and Telnov, 2019; Telnov and Barclay, 2019; Telnov, 2020). Until this study, only three ischaliid fossils were known, each representing different subgenus including one additional (fourth) extinct and all from the Eocene Baltic amber (Telnov and Bukejs, 2019). Although recent phylogenomic studies suggested the Cretaceous origin of Ischaliidae (e.g., Zhang et al., 2018; Cai et al., 2022), no direct evidence has been reported to date.

Here, we studied the mid-Cretaceous Myanmar amber fossils of the charismatic genus *Prototrichalus* Molino-Olmedo et al., 2020 which was originally erroneously attributed to the net-winged beetles (Coleoptera: Elateroidea: Lycidae) (Molino-Olmedo et al., 2020) and soon after transferred to superfamily Tenebrionoidea *incertae sedis* and compared with *Ischalia* by Bocak et al. (2022). *Prototrichalus* is unmistakably a new representative of false fire-coloured beetles (Coleoptera: Tenebrionoidea: Ischaliidae) and represents the first Mesozoic member of this small family. A set of the diagnostic features of adult Ischaliidae is herein re-defined and supplemented with the features appearing in *Prototrichalus*. Additionally, we supplemented and updated the key to include all supraspecific taxa on the family Ischaliidae, including its unique new member.

2. Material and methods

The studied materials of *Prototrichalus* spp. (Figs. 1–7) are the inclusions each embedded in a piece of amber from the Hukawng Valley in Kachin State, northern Myanmar. The age of this amber-bearing locality is earliest Cenomanian, 98.79 ± 0.62 Ma

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Fig. 1. Studied amber pieces containing *Prototrichalus* inclusions: (A) *Prototrichalus* sp. A (NM-T3533, BUR0025 - NMPC); (B) *Prototrichalus* sp. B (NM-T3534, BUR0026 - NMPC); (C) *Prototrichalus jingpo* Telnov and Kundrata, sp. nov. (NM-T3535. BUR0007 - NMPC). Scale bars: A–C = 10 mm.

(Cruickshank and Ko, 2003; Shi et al., 2012). The amber pieces were mined before 2017, and they are deposited in the collection of the Department of Palaeontology of the National Museum, Prague, Czech Republic (NMPC) (see "Museum Catalogue Entry" in Supplementary Material). In total, three amber pieces, each with a single beetle specimen included, were available for the present study (Fig. 1). The first piece (Fig. 1A) was of irregular form of maximum dimensions 36 × 19 × 12 mm and contained the specimen tentatively identified as *Prototrichalus* sp. A (NM-T3533, BUR0025) The second piece (Fig. 1B) was flattened box-shaped of maximum dimensions 21 × 16 × 6 mm and contained the specimen tentatively identified as *Prototrichalus* sp. B (NM-T3534, BUR0026). The third amber piece (Fig. 1C) was flattened-ovoid of maximum dimensions 24 × 20 × 7 mm and contained the specimen identified as a new species of *Prototrichalus* described here (NM-T3535, BUR0007) (see Discussion for comments on the identifications). Morphological terminology describing elytral costae follows Young (1975, 1976) with a new term, subhumeral costa, introduced here for the first time to describe an additional elytral costa present in *Prototrichalus* and situated between humeral and lateral costae.

The amber pieces were polished by hand, allowing improved views of the included specimens, and were not subjected to any supplementary fixation. For morphological studies, a Leica S6D stereomicroscope was used. Digital images were made using a Canon EOS 77D SLR camera mounted on a stand with a Canon EFS

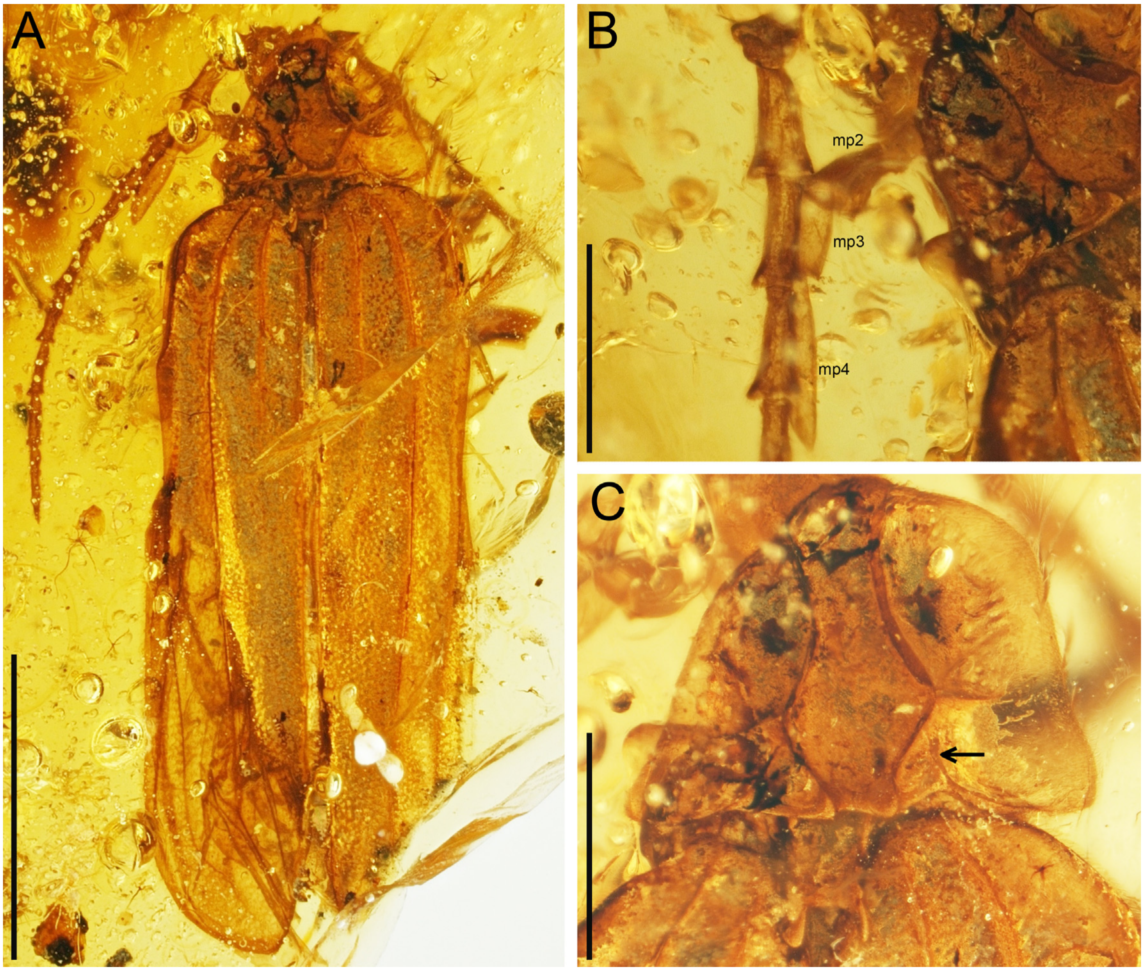

Fig. 2. *Prototrichalus* sp. A, (NM-T3533, BUR0025 - NMPC), likely a female: (A) habitus, dorsal view; (B) basal portion of left antenna and last three palpomeres of left maxillary palpus, dorsal view; (C) pronotum, dorsal view. mp2–4 = maxillary palpomeres 2–4; arrow points to the posterior carina *sensu* Bocak et al. (2022). Scale bars = A = 3 mm; B–C = 1 mm.

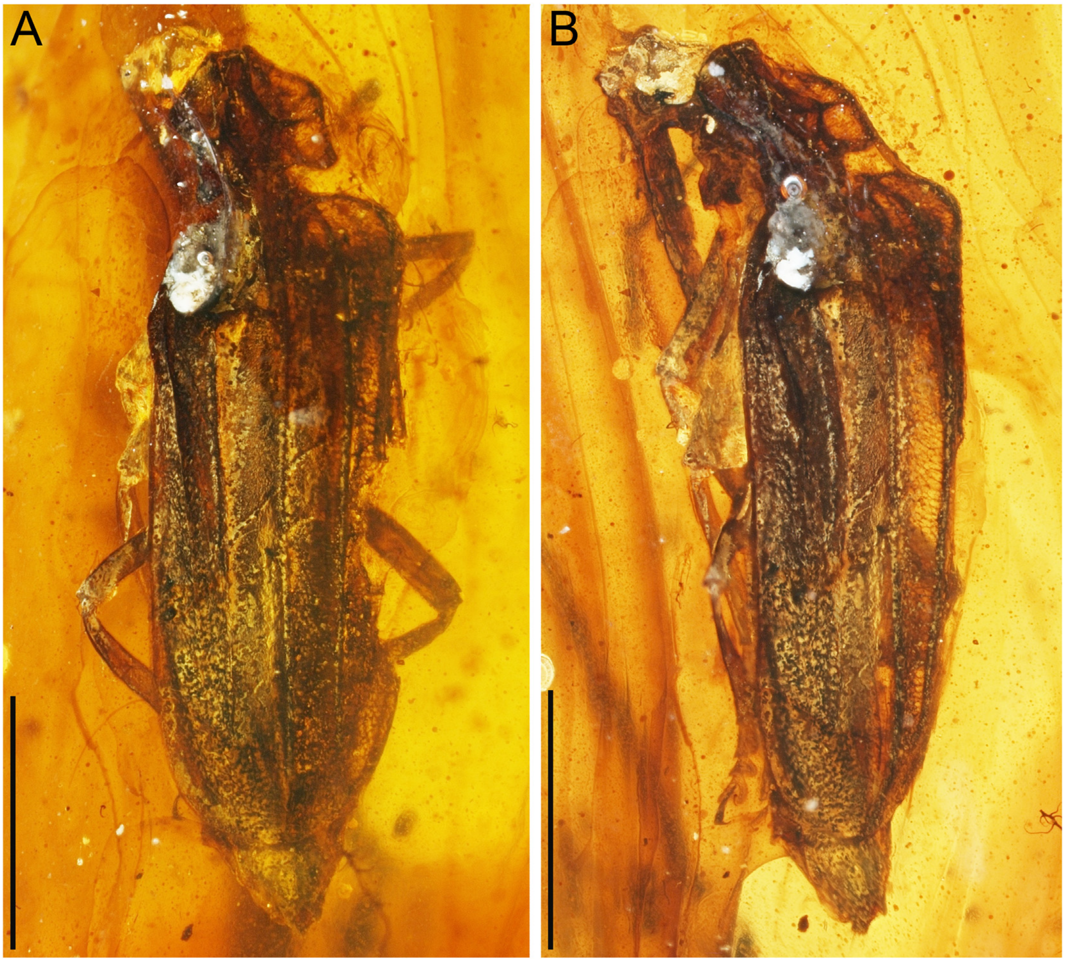

Fig. 3. *Prototrichalus* sp. B, (NM-T3534, BUR0026 - NMPC), female: (A) habitus, dorsal view; (B) habitus, left dorsolateral view. Scale bars: A–B = 2 mm.

60 mm lens. Helicon Focus 7 software (Helicon Soft, Kharkiv, Ukraine) was used for image stacking.

The X-ray micro-CT observations were conducted at the Daugavpils University, Daugavpils, Latvia using Zeiss Xradia 510 Versa system. Scans were performed with a polychromatic X-ray beam at an energy of 30 kV and power of 2 W. Sample to detector distance was set to 25.9 mm and source to sample distance 29 mm. Tomographic slices were generated from 1601 rotation steps through a 360-degree rotation, using a 4× objective and exposure time during each projection was set to 15 s. Acquired images were binned (2 × 2 × 2) giving a voxel size of 3.56 μm. Since specimen length was bigger than the field of view for selected parameters, we carried out image acquisition using automated vertical stitch function for three consecutive scans with identical scanning parameters. Between those scans field of view was set to overlap at least 35% of data between adjacent fields of view. Prior to the full scan, the 15-min warmup scan was conducted with identical stitch parameters but with reduced rotational steps 201 and exposure time was set to 1 s. Acquired images were imported into Dragonfly PRO (ver. 2021.3) software platform for interactive segmentation and 3D visualization. For the segmentation of the images artificial intelligence model was trained using U-net architecture with input dimension being 2.5D, initial filter count 64 and depth level 5. In total 92 epochs were trained for 2 h and 26 min of training time. For the training dataset 7 frames were segmented manually and used for training of the model. Further image manipulations were performed using the GNU Image Manipulation Program (GIMP – gimp.org). Volume renderings of X-ray microtomography of habitus of *Prototrichalus* sp. C are available upon reasonable request from the first author. Measurements of specimens were taken either with a scale bar in an eyepiece or using 3D reconstructions. Body length was measured from frons to apex of elytra, body width at the humeral portion of elytra; length of pronotum medially, and width of pronotum at the posterior angles.

This published work and the nomenclatural acts it contains have been registered in ZooBank, the online registration system for the ICZN (International Code of Zoological Nomenclature). The ZooBank LSID number for this publication is: urn:lsid:zoobank.org:pub:54898729-F601-447A-B921-0EDFD2B905C8.

3. Systematic palaeontology

Order Coleoptera Linnaeus, 1758.
Superfamily Tenebrionoidea Latreille, 1802.
Family Ischaliidae Blair, 1920.

Remark. Detailed morphology of adults and immature Ischaliidae was provided by Lawrence et al. (2010).

3.1. Morphological support for placement of *Prototrichalus* in Ischaliidae

After study of the available fossil materials as well as the information and figures published by Molino-Olmedo et al. (2020) and Bocak et al. (2022), we here assign *Prototrichalus* to

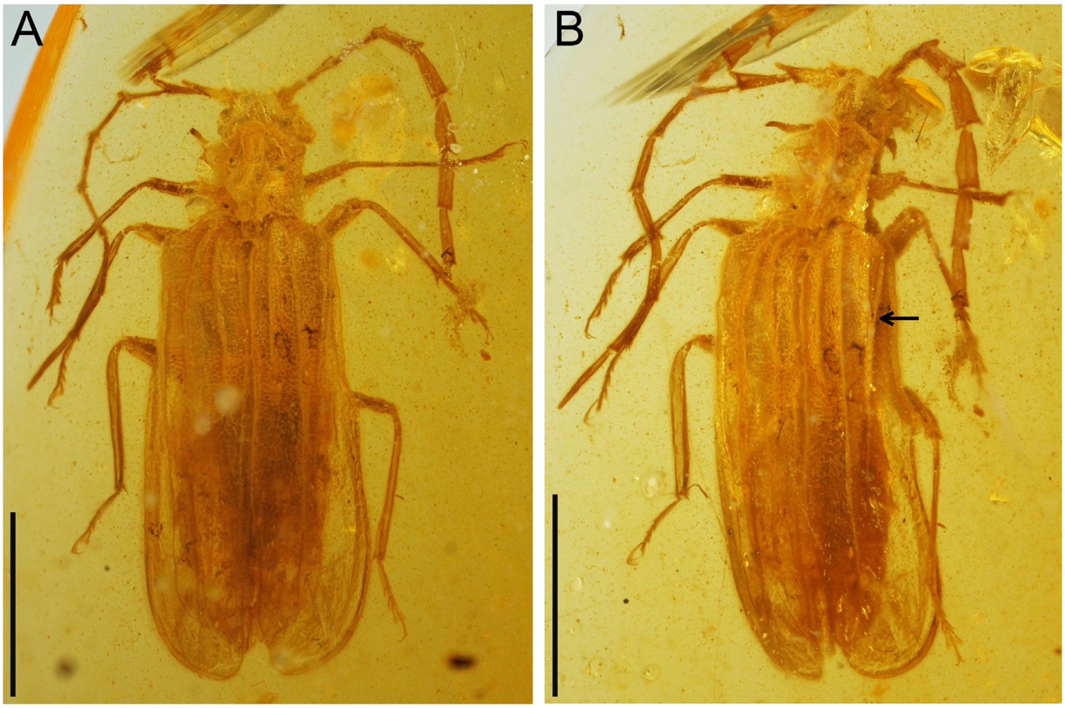

Fig. 4. *Prototrichalus jingpo* Telnov and Kundrata, sp. nov., male holotype, (NM-T3535. BUR0007 - NMPC): (A) habitus, dorsal view; (B) habitus, right dorsolateral view. Arrow points to the connection of humeral and subhumeral costae. Scale bars: A–B = 2 mm.

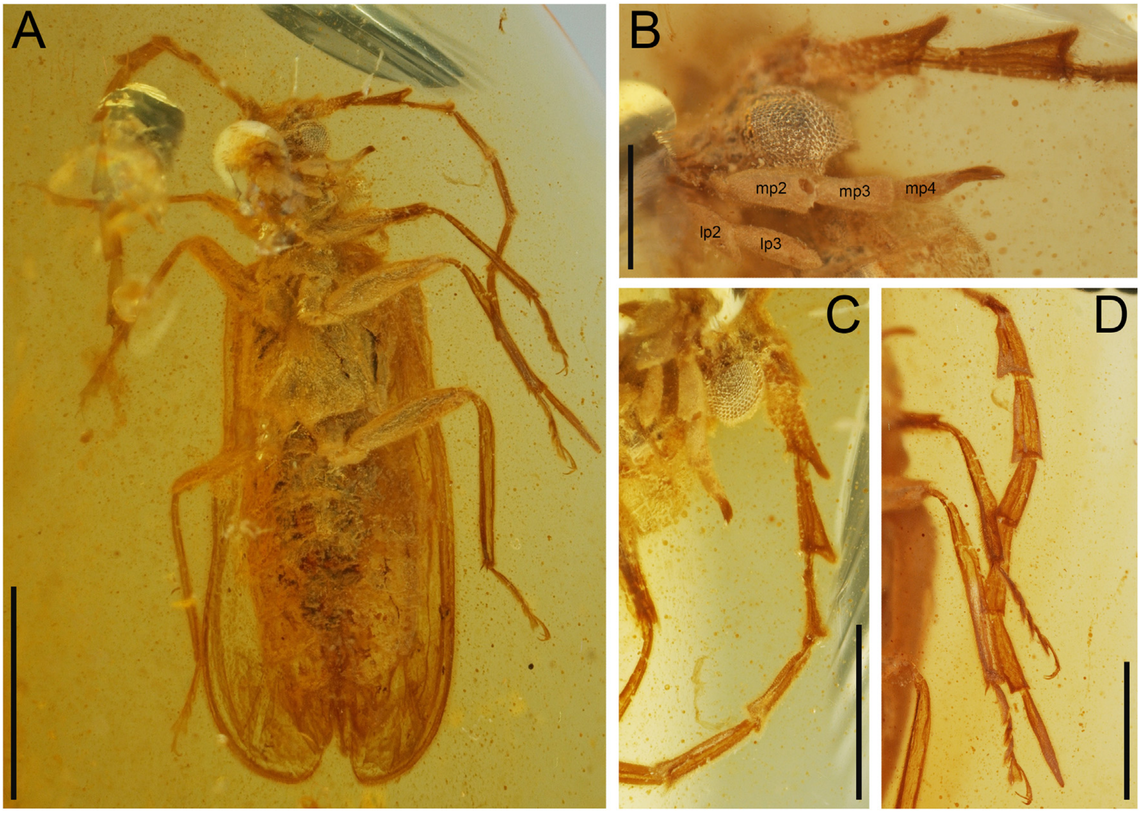

Fig. 5. *Prototrichalus jingpo* Telnov and Kundrata, sp. nov., male holotype: (A) habitus, ventral view; (B) detail of head showing maxillary palpus, ventrolateral view; (C) basal half of antenna, ventral view; (D) apical half of antenna, ventral view. lp2–3 = labial palpomeres 2–3; mp2–4 = maxillary palpomeres 2–4. Scale bars: A = 2 mm; B = 0.5 mm; C–D = 1 mm.

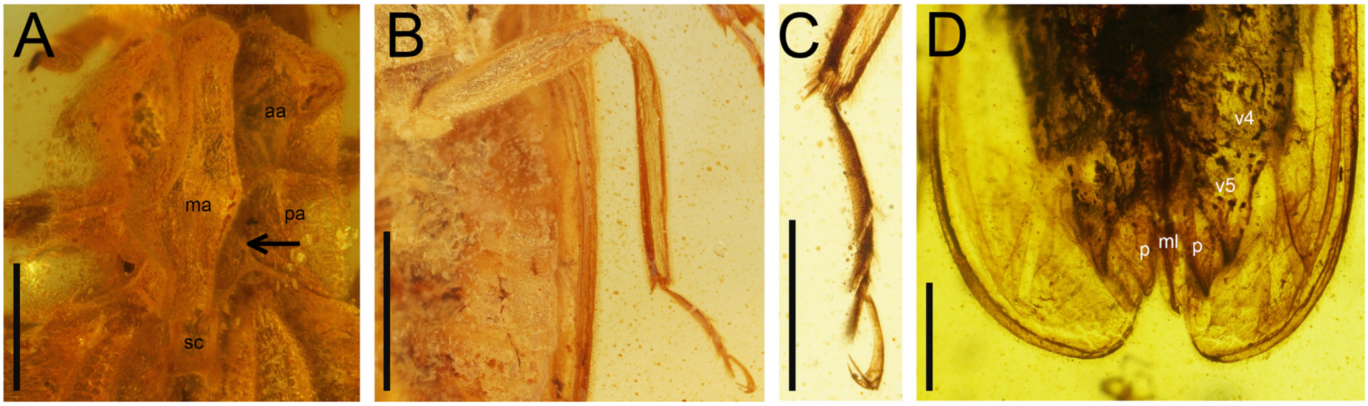

Fig. 6. *Prototrichalus jingpo* Telnov and Kundrata, sp. nov., male holotype: (A) pronotum, dorsal view; (B) left metaleg, ventral view; (C) left metatarsus, lateral view; (D) last abdominal ventrites and aedeagus, ventral view. aa = anterior areola; ma = median areola; pa = posterior areola; arrow points to the posterior carina *sensu* Bocak et al. (2022); sc = scutellar shield; ml = median lobe; p = paramere; v4–5 = abdominal ventrites 4–5. Scale bars: A, C–D = 0.5 mm; B = 1 mm.

Ischaliidae based on a combination of the following morphological characters (though some of these features are present also in other families or subfamilies of Tenebrionoidea): (1) tarsal formula 5-5-4; (2) head moderately strongly declined to hypognathous, somewhat prolonged anterior to compound eyes; (3) compound eye prominent, strongly emarginate at anterior margin, apparently glabrous; (4) antennal insertion exposed in dorsal view, anterolateral margin of frons slightly raised at antennal insertion; (5) frons longitudinally declivous between antennal insertions; (6) strong transverse impression at place of frontoclypeal suture; (7) antenna long, inserted at side of frons in emargination of compound eye, filiform, serrate to pectinate; (8) maxillary palpus quadrimerous, apical palpomere securiform to cultriform; (9) pronotum narrower than basal width of elytra; (10) cranial "neck" concealed by anterior margin of pronotum; (11) pronotum with prominent carinae; (12) pronotum without antebasal sulcus; (13) prothoracic trochantins slightly exposed; (14) prothoracic coxa conical and projecting; (15) mesoventrite globose; (16) elytron with prominent longitudinal costae; (17) elytral epipleuron well-developed, broad at least in basal half of elytron; (18) abdomen with six ventrites, first two connate (erroneously identified as "with seven visible ventrites" (female) or "presumably with eight visible ventrites (not visible)" (male) by Molino-Olmedo et al. (2020)); (19) penultimate tarsomere of all legs lobed; (20) pretarsal claws non-appendiculate; (21) tegmen of aedeagus without accessory lobes; (22) parameres partly fused and apparently fused to phallobase, partly enclosing tegmen.

3.2. Differences between Prototrichalus and Ischalia

Only one genus, *Ischalia* Pascoe, 1860, was hitherto included in Ischaliidae, a beetle family considered morphologically homogenous and well-defined within Tenebrionoidea. *Prototrichalus* differs from *Ischalia* (including all its subgenera) in the combination of the following characters (which also serves as an emended diagnosis of *Prototrichalus*): (1) antenna filiform, serrate or pectinate; (2) maxillary palpomeres 2–3 elongate, large; (3) terminal maxillary palpomere cultriform to securiform; (4) penultimate labial palpomere subtriangular, widened distally; (5) terminal labial palpomere distinctly elongate; (6) lateral pronotal margin flattened, carinate, more or less strongly expanded; (7) scutellar shield emarginate at posterior margin, dorsally depressed or flattened (not convex), its lateral margins costate, in some species projected well beyond posterior margin of scutellar shield ("posteriorly bifurcated" as of Molino-Olmedo et al. (2020)); (8) tibial terminal spurs present on all tibiae, paired; (9) pro- and mesocoxae large, conical and contiguous, the prosternal intercoxal process is low but more strongly raised than that in *Ischalia* (cf. Bocak et al., 2022, Fig. 1H, p. 3), therefore the procoxae are contiguous at most of their length except at base; the mesoventrite with the short, triangular intercoxal process, which does not separate the contiguous mesocoxae. Molino-Olmedo et al. (2020) mentioned 'the presence of a carina on the mesoventrite' but this is considered a taphonomic deformation and appears to be a longitudinal median sulcus instead); (10) male terminal sterna deeply emarginate at the posterior margin.

3.3. An updated set of diagnostic features of adult Ischaliidae

Prototrichalus appears to be well-defined within ischaliids due to its unique combination of morphological features. Considering the fact that some of these features appear randomly also in other subgroups of Tenebrionoidea, we here refrain from erecting a new subfamily for *Prototrichalus*. However, the peculiarities of the adult morphology of *Prototrichalus* contributed significantly to our present knowledge of the ischaliids as a uniform group. Therefore, herein we highlight changes in a set of diagnostic features defining the family. These features are discussed below.

The supplemented set of diagnostic features of adult Ischaliidae therefore appears as follows (cf. Nikitsky, 1992; Young, 1985; Lawrence et al., 2010; Telnov & Barclay, 2019, and others):

(1) body moderately flattened dorsally, slightly to moderately convex ventrally; (2) dorsal vestiture of short, sparse, decumbent to suberect setae or dorsum nearly glabrous; (3) head moderately strongly declined to hypognathous, prolonged anterior to compound eyes; (4) head without distinct tempora; (5) compound eye emarginate at anterior, sometimes also vaguely emarginate at posterior margin; (6) interfacetal setae not present; (7) frons declivous between antennal insertions; (8) antennal insertion exposed from above, borne on slightly elevated tubercles; (9) anterolateral margin of frons slightly raised, not concealing antennal insertion; (10) subantennal groove not present; (11) shallow or strong transverse impression at place of frontoclypeal suture; (12) anterior margin of clypeus truncate; (13) anterior margin of labrum subtruncate to emarginate; (14) labrum transverse; (15) antenna 11-segmented, filiform, serrate or pectinate; (16) maxillary palpomeres 2–3 variably strongly developed, short to large; (17) terminal maxillary palpomere cultriform to strongly

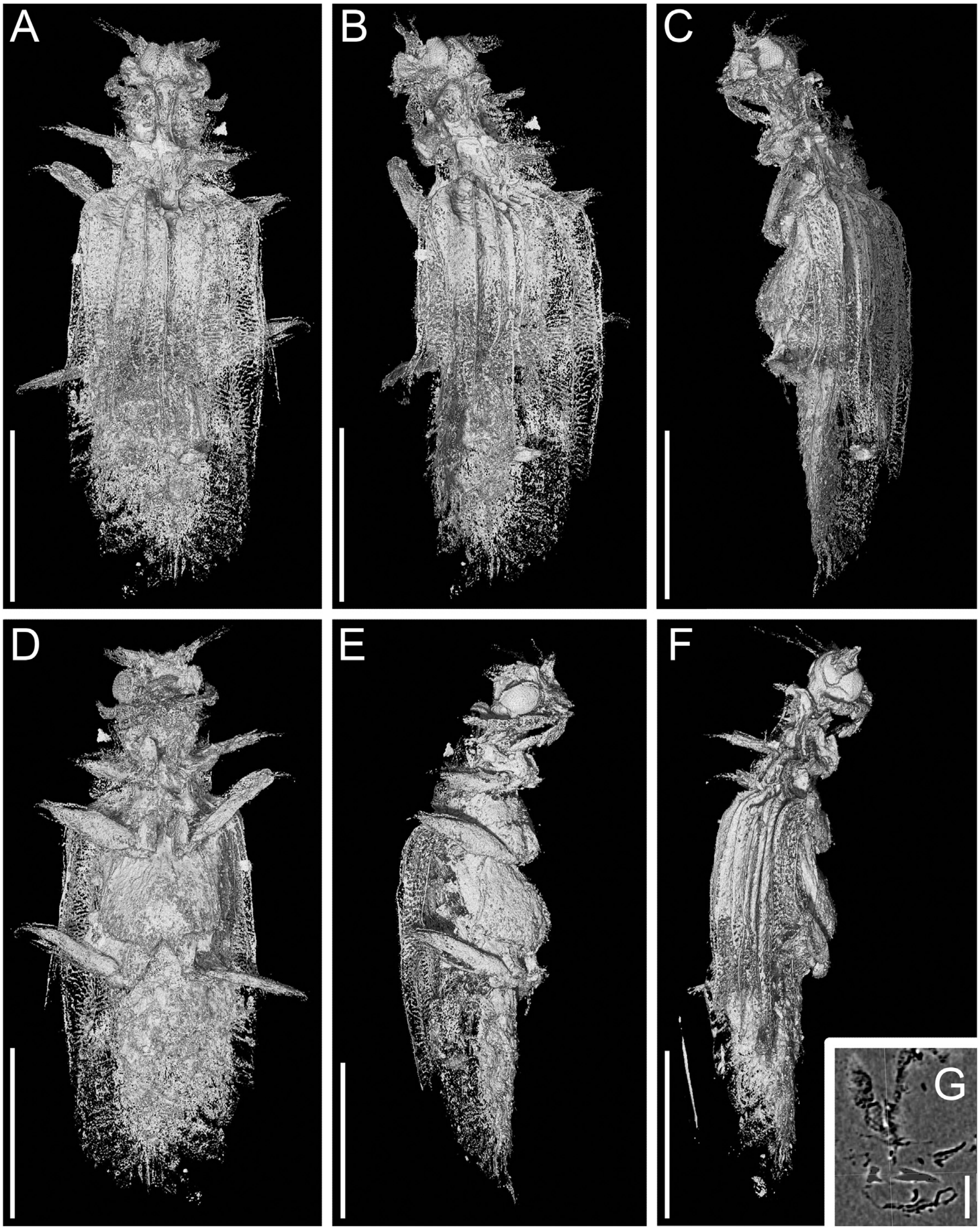

Fig. 7. *Prototrichalus jingpo* Telnov and Kundrata, sp. nov., male holotype, CT micrographs: (A) habitus, dorsal view; (B) habitus, left dorsolateral view; (C) habitus, left lateral view; (D) habitus, ventral view; (E) habitus, right ventrolateral view; (F) habitus, right lateral view; (G) mandibles (shaded dark green). Scale bars: A–F = 2 mm; G = 0.1 mm.

axeform (securiform); (18) penultimate labial palpomere small, subcylindrical, or subtriangular, widened distally; (19) terminal labial palpomere elongate to strongly axeform (securiform); (20) mandible apex bidentate (including that in *Prototrichalus*, Fig. 7G); (21) maxilla with distinct galea and lacinia; (22) lacinia without uncus; (23) ligula not divided; (24) cervical sclerites well developed; (25) cranial “neck” moderately broad; (26) cranial “neck” with paired lateral pit or without it; (27) pronotum narrowest across anterior one third; (28) pronotum narrower than basal width of elytra; (29) cranial “neck” concealed by anterior margin of pronotum; (30) pronotum with prominent carinae, areolate or not; (31) pronotum without antebasal sulcus; (32) pronotum without anterior rim; (33) lateral pronotal carinae complete or nearly so; (34) anterolateral pronotal angles not produced; (35) posterolateral pronotal angles slightly to distinctly produced posteriad or posterolaterad; (36) lateral margin of pronotum expanded or not; (37) lateral margin of pronotum carinate or flattened; (38) posterior margin of pronotum sinuate or bi-emarginate; (39) pronotal median costa, if present, usually extending beyond posterior margin of pronotum; (40) prosternum anteriad to procoxae narrower than shortest diameter of procoxal cavity; (41) prosternal intercoxal process incomplete, narrowed and angulate apically, or complete, low to moderately raised between procoxal bases; (42) notosternal suture not present; (43) procoxa projecting below prosternum, without concealed lateral extension; (44) prothoracic trochantins at least slightly exposed; (45) prothoracic coxa conical and projecting; (46) procoxal cavity slightly transverse, contiguous, externally broadly open, without narrow lateral extensions (this feature unknown for fossil taxa); (47) procoxal cavity internally open (this feature unknown for fossil taxa); (48) scutellar shield rounded or emarginate at posterior margin; (49) scutellar shield laterally costate (raised) or not); (50) elytron distinctly, densely, irregularly punctate; (51) elytra costate, with sutural, humeral, lateral discal, and lateral costae variably present; (52) epipleuron complete, often rather broad all along; (53) mesoventrite separated from mesanepisterna by complete sutures (this feature unknown for several fossil taxa); (54) mesanepisterna widely or narrowly separated by mesoventrite, or contiguous; (55) mesoventrite globose (this feature unknown for several fossil taxa); (56) procoxal rests not present (this feature unknown for several fossil taxa); (57) mesoventral cavity not present; (58) mesocoxa conical, projecting, with exposed mesothoracic trochantins; (59) mesocoxal cavities contiguous, open laterally (this feature unknown for fossil taxa); (60) metathoracic discrimen present or absent; (61) postcoxal lines absent (this feature unknown for fossil taxa); metacoxae narrowly to moderately widely separated, not extending laterally to meet elytra (this feature unknown for several fossil taxa); (62) metacoxal plates not present; (63) metendosternite with short to long stalk and moderately to very long lateral arms (this feature unknown for fossil taxa); (64) macro- brachy- or apterous; (65) metathoracic wing, if present, with long apical field bearing four sclerites, a short, slender one beyond the radial cell and three larger, weakly indicated ones, radial cell without basal edge, cross-veins r3 and r4 absent, basal portion of RP very short; medial spur long, straight and extending to margin, medial field with three free veins and no medial fleck, MP_{3+4} incomplete at base, wedge cell not present, AA_4 not present, anal embayment not present (wing morphology unknown for fossil taxa); (66) abdomen of five to six ventrites, two basal usually connate (this feature unknown for several fossil taxa); (67) intercoxal process of ventrite acute to broadly rounded apically; (68) male terminal sterna shallowly to deeply emarginate at posterior margin; (69) aedeagus inverted, without struts (this feature unknown for several fossil taxa); (70) tegmen without struts (this feature unknown for several fossil taxa); (71) parameres partly or entirely fused together and to phallobase forming single piece, which partly encloses penis (this feature unknown for several fossil taxa); (72) ovipositor about 3× as long as wide (this feature unknown for several fossil taxa); (73) gonostyli subapical, moderately developed (this feature remains unknown for fossil taxa); (74) tibiae slender, not expanding apically; (75) tibial terminal spurs not present, present on every tibia, or present on metathoracic tibia only; (76) tarsal formula 5-5-4; (77) penultimate tarsomere of every leg lobed; (78) pretarsal claws simple.

It is worth mentioning Ischaliidae are specifically different from related and similar tenebrionoid families in larval morphology (Young, 1985; Nikitsky, 1992; Lawrence et al., 2010). On the other hand, adult morphology, as it is re-defined herein, may be misleading since tenebrionoid families are widely known for their morphological plasticity and often closely resemble even unrelated beetles (Smith et al., 2015) like, in our case, the ones from different superfamilies. This makes the simplified approach for separating some tenebrionoid families based on adult features only nearly impossible.

3.4. *An updated key to supraspecific taxa of Ischaliidae*

The present key to genera and subgenera of Ischaliidae is partially based on Young (2011).

1. Tibial terminal spurs present on all legs; terminal maxillary palpomere elongate securiform; terminal labial palpomere elongate; lateral margins of scutellar shield costate (raised); lateral margin of pronotum expanded, flattened, carinate in laterodorsal view; pronotal disc areolate ....*Prototrichalus* Molino-Olmedo et al., 2020
   – Tibial terminal spurs not present or present only on metathoracic tibia; terminal maxillary palpomere shortly and broadly securiform; terminal labial palpomere subtriangular to securiform; lateral margins of scutellar shield not raised; lateral margin of pronotum not expanded and flattened, not carinate in laterodorsal view; pronotal disc usually with one median longitudinal costa and sometimes with additional, shorter, longitudinal or transverse costae, but lacking distinct areolae...2
2. Tibial terminal spurs present on metathoracic tibia, paired; elytron with rather short, longitudinal discal costa in basal one fourth............*Ischalia* subg. *Telnovia* Alekseev and Bukejs, 2017
   – Tibial terminal spurs not present; elytron without discal costa..3
3. Mesanepisterna narrowly separated by mesoventrite or contiguous; elytral humeral costa not present; apterous taxa ....*Ischalia* subg. *Eupleurida* LeConte, 1862
   – Mesanepisterna widely separated by mesoventrite; elytral humeral costa well-developed or reduced but present; macro- or brachypterous taxa.......................................4
4. Elytral humeral costa strongly reduced; dorsal pronotal vestiture strongly reduced (pronotum appears subglabrous); dorsal pronotal pits and depressions greatly reduced ....*Ischalia* subg. *Nitidischalia* Young, 2011
   – Elytral humeral costa well-developed; pronotal vestiture short but distinct; pronotal dorsal pronotal pits and depressions usually well-developed with some exceptions ....*Ischalia* s. str. Pascoe, 1860

3.5. *Description of a new species of Prototrichalus*

Prototrichalus jingpo Telnov and Kundrata, sp. nov (Figs. 4–7).
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Type material. Holotype, adult male, Burmese amber, NM-T3535, BUR0007 (NMPC).
Type locality. Hukawng Valley, Tanai Township, Myitkyina District, Kachin State, northern Myanmar.
Etymology. This species is named in honour of Jingpo people, an ethnic group from Kachin State in northern Myanmar, where all known amber stones with *Prototrichalus* spp. were mined. Noun in apposition.
Diagnosis. Male. This species is about 6.5 mm long (i.e., the smallest yet reported specimen of *Prototrichalus*) and has filiform antennae extending at least towards midlength of elytra when directed posteriad, with antennomeres 3–5 subserrate (this can be a taphonomic deformation), terminal maxillary palpomere elongate, narrow (this can be a taphonomic deformation), and subhumeral costa very short, fused with lateral humeral costa shortly beyond humerus (the character not yet reported for any other *Prototrichalus* species).

Description. Adult male. Body (Figs. 4A–B, 5A, 7A–F) elongate, rather flattened, about 6.5 mm long and 2 mm wide. Dorsal vestiture of short, subdecumbent setae, all ridges on pronotum and costae on elytra with dense suberect setae all along; vestiture of ventral pterothorax short and dense, plush-like; femora and tibiae with short, dense, suberect setae.

Head including eyes slightly narrower than anterior pronotal width. Frons slightly longitudinally declivous between antennal insertions. Compound eye large, emarginate at anterior margin to accommodate antennal insertion. Antenna (Fig. 5C–D) long, slender, filiform, with antennomeres 3–5 subserrate (this can be a taphonomic deformation), extending at least towards midlength of elytra when directed posteriad; terminal antennomere elongate cylindrical, slightly longer than preceding antennomere. Maxillary palpus (Fig. 5B) long; maxillary palpomeres 2–3 subequal in length, second palpomere somewhat stronger thickened, terminal maxillary palpomere elongate, narrow (this can be a taphonomic deformation), apically rounded, slightly longer than penultimate maxillary palpomere. Labial palpus (Fig. 5B) about half-length of maxillary palpus; penultimate labial palpomere elongate subtriangular, terminal labial palpomere fusiform to narrowly cylindrical, rounded apically.

Pronotum (Fig. 6A) slightly wider than long, about 0.65 times as wide as elytra across humeri, widest across posterior angles; posterior margin tri-emarginate, medially slightly produced posteriad; pronotal disc divided into five large deep areolae by distinct ridges, with posterior areolae each divided by short posterior carina (sensu Bocak et al., 2022) into two parts, forming additional, small posteromedian areolae; median areola longitudinal, formed by two ridges running from frontal to posterior margin of pronotum. Procoxae contiguous at least mesally. Scutellar shield subrectangular, dorsally depressed, lateral margins raised (costate), produced beyond subtruncate posterior margin. Elytra (Fig. 4A) together 2.45 as long as wide and 3.9 times as long as pronotum, widest across 3/4, subparallel-sided, gradually, slightly widened towards apex; elytron apex separately rounded; surface with distinctly raised costae; discal elytral costa extending towards about 2/5 of elytral length; subhumeral costa shortened, fused with humeral costa shortly beyond humerus (Fig. 4B); humeral costa rather obsolete in apical third of elytral length; epipleuron complete, basally rather narrow and even stronger narrowed at metacoxae, shortly setose all along. Mesocoxa conical, very narrowly separated; mesoventral intercoxal process short, narrowly triangular. Metaventrite slightly wider than long. Leg (Figs. 4A–B, 5A, 6B) relatively long and slender; trochanter short; femur robust; every tibia longer than corresponding femur, about twice as long as corresponding tarsus, and with pair of distinct, straight terminal spurs; tarsus (Fig. 6C) rather short; tarsomeres II–III with short ventral lobes; terminal tarsomere elongate; basal metatarsomere shorter than combined length of remaining metatarsomeres; pretarsal claws simple, slender, long, moderately curved.

Abdomen (Figs. 5A, 6D) with five ventrites; ventrites 1–4 wide; ventrite 4 moderately deeply emarginate posteromedially; ventrite 5 slightly narrower than preceding ventrites, deeply emarginate posteromedially. Aedeagus trilobate, symmetrical; parameres elongate, partly enclosing median lobe, with inner sides slightly sinuate, setose along apical margin; median lobe slightly exceeding apices of parameres, elongate, narrow, laterally flattened and apically rounded (this can be a taphonomic deformation).

Immature stages and female unknown.

3.6. Checklist of extinct Ischaliidae species

Ischalia (s. str.) *youngi* Alekseev and Telnov, 2016.
Alekseev and Telnov (2016: 595) – original description (Baltic amber, Prussian Formation (Priabonian)); Alekseev and Bukejs (2017: 229, 237) – note, key; Telnov and Bukejs (2019: 17) – checklist.
Strata: Baltic amber, Late Eocene 37.8–33.9 Ma.

Ischalia (*Eupleurida*) *dohnaturris* Alekseev and Bukejs, 2017.
Alekseev and Bukejs (2017: 230–232, 237) – original description, key; Telnov and Bukejs (2019: 17) – checklist.
Strata: Baltic amber, Late Eocene 37.8–33.9 Ma.

Ischalia (*Telnovia*) *danieli* Alekseev and Bukejs, 2017.
Alekseev and Bukejs (2017: 233–237) – original description (Baltic amber, Prussian Formation (Priabonian)); Telnov and Bukejs (2019: 17) – checklist.
Strata: Baltic amber, Late Eocene 37.8–33.9 Ma.

Prototrichalus jingpo Telnov and Kundrata, sp. nov.
Described herein.
Strata: Burmese amber, mid-Cretaceous 98.79 ± 0.62 Ma.

Prototrichalus meiyingae Molino-Olmedo et al., 2020.
Molino-Olmedo et al. (2020: 6) – original description (Burmese amber, Hukawng Valley); Bocak et al. (2022: 2, 4–6) – morphology, taxonomy.
Strata: Burmese amber, mid-Cretaceous 98.79 ± 0.62 Ma.

Prototrichalus milleri Molino-Olmedo et al., 2020.
Molino-Olmedo et al. (2020: 6) – original description (Burmese amber, Hukawng Valley); Bocak et al. (2022: 2, 4–6) – morphology, taxonomy.
Strata: Burmese amber, mid-Cretaceous 98.79 ± 0.62 Ma.

Prototrichalus sepronai Molino-Olmedo et al., 2020.
Molino-Olmedo et al. (2020: 6) – original description (Burmese amber, Hukawng Valley), assigned the type species of *Prototrichalus*.
Strata: Burmese amber, mid-Cretaceous 98.79 ± 0.62 Ma.

4. Discussion

4.1. Systematic placement of Prototrichalus and evolution of Ischaliidae

The extinct genus *Prototrichalus* Molino-Olmedo et al., 2020 was recently erected to accommodate three species from mid-Cretaceous Burmese amber, all described in the same paper (Molino-Olmedo et al., 2020). The authors believed this genus represents the family Lycidae in Elateroidea, and placed it in relationships with extant trichaline genera and formally classified *Prototrichalus* in Metriorrhynchini *incertae sedis*. Such placement was based on several misinterpreted morphological features (see above and below) and soon after the description, *Prototrichalus* had been transferred to the superfamily Tenebrionoidea (Bocak et al., 2022). The transfer was justified mainly by the following characters in *Prototrichalus*: the presence of the tetramerous metathoracic tarsomere, the short trochanters, the kidney-like shape of the compound eye, and the number of the visible abdominal ventrites, which are considered characteristic to Tenebrionoidea rather than to soft-bodied Elateroidea (e.g., Lawrence et al., 2011). Bocak et al. (2022) suggested possible relationships of *Prototrichalus* with the Ischaliidae due to the structure of elytral costae and costal interspaces, vestigial pronotal carinae, and 'characteristically shaped head'. However, they did not formally assign *Prototrichalus* to any of the tenebrionoid families due to the absence of well-preserved specimens which would unable to clearly observe the critical characters.

Here, we strongly support the proposed placement of *Prototrichalus* in superfamily Tenebrionoidea. This charismatic genus comprises a set of features of several family-rank tenebrionoid taxa (Molino-Olmedo et al., 2020; Bocak et al., 2022; and data herein) worth discussing in detail to justify the proposed family placement of the genus in Ischaliidae. Moreover, as it is typical for Tenebrionoidea, a single diagnosis for adult of a family at the global level is difficult since several tenebrionoid families or their subgroups exhibit disparate morphological features.

Noteworthy, besides the characters which place *Prototrichalus* into the Ischaliidae (see Systematic Palaeontology section above), this genus also displays external similarity to Pyrochroidae. However, it differs from all six yet known pyrochroid subfamilies in the following combination of characters: (1) head moderately strongly deflexed to hypognathous; (2) frons longitudinally declivous between the antennal insertions; (3) cranial “neck” concealed by the anterior margin of the pronotum; (4) pronotal disc distinctly areolate, the areolas separated by high, thin carinae; (5) lateral pronotal margin flattened, expanded, laterally carinate; (6) scutellar shield not costate at lateral margins; (7) elytral epipleuron wide, well-developed at least in the basal half of the elytron; (8) simple (non-appendiculate) pretarsal claws of all legs. Indeed, Ischaliidae and Pyrochroidae are best treated based on larval morphology (Lawrence et al., 2010; Young and Pollock, 2010) and it seems unlikely to obtain immature material of *Prototrichalus* in near future. Therefore, the proposed placement of *Prototrichalus* in Ischaliidae may be re-evaluated another time.

It appears untimely to hypothesise possible ecological preferences and bionomy of mid-Cretaceous genus *Prototrichalus*, but the presence of the elongate palpomeres in this ischaliid subgroup may suggest its possible connection with flowering angiosperms (Peris, 2017; Bao et al., 2019). Obviously, additional material is required to test this hypothesis. Contrary to this hypothesis, extant species of *Ischalia* are not known to be visitors of flowering plants. Similarly, *Prototrichalus* had vestigial pronotal carinae and distinct elytral costae which have been apparently reduced or lost in extant ischaliids (Bocak et al., 2022).

4.2. *Past diversity and morphology of Prototrichalus*

Although many Mesozoic fossil taxa are known from a single specimen only or at most a few specimens, *Prototrichalus* appears to be rather abundant in Burmese amber. Molino-Olmedo et al. (2020) based their descriptions on four specimens; two males of *P. sepronai*, one female of *P. meiyingae*, and one female of *P. milleri*. Later, Bocak et al. (2022) reported additional two specimens, one female of *P. meiyingae*, and one specimen of an undetermined sex of *P. milleri*. Here, we studied three specimens and we know about several more which probably belong to *Prototrichalus* but are not well preserved (R. Kundrata, personal observations). Although the taxonomic revision of the group is well beyond the scope of this study, we report here an interesting morphological diversity of *Prototrichalus*. Noteworthy, one of our specimens represent a new species, and neither of two remaining *Prototrichalus* inclusions examined in the present study can be assigned with certainty to one of the three yet known species using the identification key or the original descriptions by Molino-Olmedo et al. (2020). Unknown intraspecific variability and sexual dimorphism in this group are among the factors that preclude the correct assignment of available specimens to known species. Based on the previous studies, one would think that males have pectinate antennae and somewhat securiform terminal maxillary palpomeres, while females have filiform to serrate antennae and elongate-acuminate terminal maxillary palpomeres (Molino-Olmedo et al., 2020; Bocak et al., 2022). However, the situation is not so straightforward when we look at the specimens studied herein.

The specimen tentatively identified as *Prototrichalus* sp. A (Fig. 2) is likely a female. It shares with *P. milleri* the body length of slightly more than 9 mm and the pronotal disc with seven areolae but its antenna is filiform (antenna slightly serrate in the female holotype of *P. milleri*), and maxillary palpus is less than half antennal length (half antennal length in *P. milleri* according to the original description).

The specimen tentatively identified as *Prototrichalus* sp. B (Fig. 3) is a female. It resembles *P. meiyingae* by its body size (almost 7 mm long, slightly more than 8 mm in *P. meiyingae*) and lateral discal and humeral costae (‘costae II and III’ as of Molino-Olmedo et al. (2020), in fact being the third and fourth costae counting from a sutural one; note that they identified them correctly only in their Fig. 3B) fused in the preapical area of elytron. However, it differs in having at least antennomeres 3–6 subpectinate with anterodistal angles moderately produced (antenna filiform to subserrate in the female holotype of *P. meiyingae*), and maxillary palpus less than half antennal length (half antennal length in *P. meiyingae* according to the original description).

The third specimen available for the present study is a male with partly exposed aedeagus, which we described as a new species, *P. jingpo* Telnov and Kundrata, sp. nov. (Figs. 4–7). It has filiform antennae, with antennomeres 3–5 subserrate, and terminal maxillary palpomere elongate and rather narrow.

The unique combinations of features in *Prototrichalus* sp. A and sp. B suggest that these specimens either show intraspecific variability of already described species or, less likely, they represent new taxa. Here, we refrain from describing new species until more materials of *Prototrichalus* are available and their morphological variability is better understood.

5. Conclusion

The mid-Cretaceous record of Ischaliidae as discussed in the present paper reveals the possibly of at least the Cretaceous origin of the family. However, additional material is required to test this hypothesis. *Prototrichalus*, with its unique set of morphological features partly different from the extant Ischaliidae, highlights the well-known phenomenon that although in Cretaceous most of extant beetle families were already present (Zhang et al., 2018; Cai et al., 2022), they contained representatives with various unique characters not known in extant taxa. These apomorphies should always be assessed carefully.

Data availability

Data will be made available on request.

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References

Alekseev, V.I., Bukejs, A., 2017. New fossil taxa of *Ischalia* Pascoe (Coleoptera: Ischaliidae) from Eocene Baltic amber. Zootaxa 4323, 229–238. https://doi.org/10.11646/zootaxa.4323.2.6.

Alekseev, V., Telnov, D., 2016. First fossil record of Ischaliidae Blair, 1920 (Coleoptera) from Eocene Baltic amber. Zootaxa 4109 (5), 595–599. https://doi.org/10.11646/zootaxa.4109.5.8.

Bao, T., Wang, B., Li, J., Dilcher, D., 2019. Pollination of Cretaceous flowers. Proceedings of the National Academy of Sciences 116 (49), 24707–24711. https://doi.org/10.1073/pnas.1916186116.

Bocak, L., Müller, P., Motyka, M., Kusy, D., 2022. *Prototrichalus* is transferred to the Tenebrionoidea: A comment on Molino-Olmedo et al., 2020, 'The description of *Prototrichalus* gen. nov. and three new species from Burmese amber supports a mid-Cretaceous origin of the Metriorrhynchini (Coleoptera, Lycidae)'. Cretaceous Research 133, 104837. https://doi.org/10.1016/j.cretres.2021.104837.

Cai, C., Tihelka, E., Giacomelli, M., Lawrence, J.F., Ślipiński, A., Kundrata, R., Yamamoto, S., Thayer, M.K., Newton, A.F., Leschen, R.A.B., Gimmel, M.L., Lü, L., Engel, M.S., Bouchard, P., Huang, D., Pisani, D., Donoghue, P.C.J., 2022. Integrated phylogenomics and fossil data illuminate the evolution of beetles. Royal Society Open Science 9 (3), 211771. https://doi.org/10.1098/rsos.211771.

Cruickshank, R.D., Ko, K., 2003. Geology of an amber locality in the Hukawng Valley, Northern Myanmar. Journal of Asian Earth Sciences 21, 441–455. https://doi.org/10.1016/S1367-9120(02)00044-5.

Gusakov, A., Telnov, D., 2007. Systematic changes and new species of Ischaliidae (Coleoptera). Folia Heyrovskyana, Series A 15 (1), 39–46.

Kazantsev, S.V., Telnov, D., 2019. New species of *Ischalia* Pascoe, 1860 (Coleoptera: Ischaliidae), with a key to aposematically coloured species from continental Asia, and new notes on their mimicry. Zootaxa 4555 (3), 441–450. https://doi.org/10.11646/zootaxa.4555.3.13.

Kazantsev, S.V., Young, D.K., 2011. Two new species of *Ischalia* Pascoe, 1860 from China, with observations on previously described Chinese species and notes on mimicry in the Palaearctic and Nearctic members of the genus (Coleoptera: Ischaliidae). Russian Entomological Journal 19 (4), 307–312.

Lawrence, J.F., Escalona, H., Leschen, R.A.B., 2010. 11.29. Tenebrionoidea incertae sedis. In: Beutel, R.G., Leschen, R.A.B. (Eds.), Handbook of Zoology. Insecta: Coleoptera, Beetles, vol. 2. W. de Gruyter Inc., Berlin, pp. 750–760. https://doi.org/10.1515/9783110911213.750.

Lawrence, J.F., Ślipiński, A., Seago, A.E., Thayer, M.K., Newton, A.F., Marvaldi, A.E., 2011. Phylogeny of the Coleoptera based on morphological characters of adults and larvae. Annales Zoologici 61 (1), 1–217.

Molino-Olmedo, F., Ferreira, V.S., Branham, M.A., Ivie, M.A., 2020. The description of *Prototrichalus* gen. nov. and three new species from Burmese amber supports a mid-Cretaceous origin of the Metriorrhynchini (Coleoptera, Lycidae). Cretaceous Research 111, 104452. https://doi.org/10.1016/j.cretres.2020.104452.

Nikitsky, N.B., 1992. Fam. Ischaliidae, stat. n. – False fire-red beetles: 497–498. In: Ler, P.A. (Ed.), Keys to insects of the Far East of the USSR in six volumes. Volume 3, Coleoptera or Beetles, Part 2. Nauka Press, Moscow [in Russian].

Peris, D., 2017. Early Cretaceous origin of pollen-feeding beetles (Insecta: Coleoptera: Oedemeridae). Cladistics 33 (3), 268–278. https://doi.org/10.1111/cla.12168.

Shi, G., Grimaldi, D.A., Harlow, G.E., Wang, J., Wang, J., Yang, M., Lei, W., Li, Q., Li, X., 2012. Age constraint on Burmese amber based on UePb dating of zircons. Cretaceous Research 37, 155e163. https://doi.org/10.1016/j.cretres.2012.03.014.

Smith, A.D., Wilson, J.S., Cognato, A.I., 2015. The evolution of Batesian mimicry within the North American Asidini (Coleoptera: Tenebrionidae). Cladistics 31, 441e454. https://doi.org/10.1111/cla.12101.

Telnov, D., 2020. New East Asian species of Ischaliidae (Insecta: Coleoptera), with a key to Palaearctic Eupleurida Le Conte, 1862. Annales Zoologici 70 (2), 181–203. https://doi.org/10.3161/00034541ANZ2020.70.2.002.

Telnov, D., Barclay, M.V.L., 2019. Ischaliidae (Insecta: Coleoptera) in the collection of the Natural History Museum, London. Annales Zoologici 69 (4), 785–804. https://doi.org/10.3161/00034541ANZ2019.69.4.011.

Telnov, D., Bukejs, A., 2019. Catalogue and composition of fossil Anthicidae and Ischaliidae (Insecta: Coleoptera). Palaeontologia Electronica 22 (1), 1–27. https://doi.org/10.26879/885.

Young, D.K., 1975. A revision of the family Pyrochroidae (Coleoptera: Heteromera) for North America based on the larvae, pupae, and adults. Contributions of the American Entomological Institute 11 (3), 1–39.

Young, D.K., 1976. A new species of *Ischalia* from Southeastern China. Pan-Pacific Entomologist 52 (3), 213–215.

Young, D.K., 1985. Description of the larva of *Ischalia vancouverensis* Harrington (Coleoptera: Anthicidae: Ischaliinae), with observations on the systematic position of the genus. The Coleopterists Bulletin 39, 201–206.

Young, D.K., 2008. Three new Asian species of *Ischalia* Pascoe, 1860 (Coleoptera: Ischaliidae), with a world checklist of subgenera and species. Pan-Pacific Entomologist 83 (4), 321–331.

Young, D.K., 2011. A new Asian subgenus and species of *Ischalia* (Coleoptera: Ischaliidae) with an assessment of subgeneric concepts, revised world checklist, and keys to the subgenera and "blue elytra" species. Zootaxa 2811, 53–58.

Young, D.K., 2014. A new Philippine species of *Ischalia* (Coleoptera: Ischaliidae), with a checklist and a key to the Philippine species. Insecta Mundi 375, 1–7.

Young, D.K., Pollock, D.A., 2010. 11.24. Pyrochroidae Latreille, 1807. In: Beutel, R.G., Leschen, R.A.B. (Eds.), Handbook of Zoology. Insecta: Coleoptera, Beetles, vol. 2. W. de Gruyter Inc., Berlin, pp. 715–721. https://doi.org/10.1515/9783110911213.715.

Zhang, S.-Q., Che, L.-H., Li, Y., Liang, D., Pang, H., Ślipiński, A., Zhang, P., 2018. Evolutionary history of Coleoptera revealed by extensive sampling of genes and species. Nature Communications 9 (1), 205. https://doi.org/10.1038/s41467-017-02644-4.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.cretres.2023.105634.