scientific reports

OPEN

Click beetle larvae from Cretaceous Burmese amber represent an ancient Gondwanan lineage

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The click beetles (Elateridae) represent the major and well-known group of the polyphagan superfamily Elateroidea. Despite a relatively rich fossil record of Mesozoic Elateridae, only a few species are described from the Upper Cretaceous Burmese amber. Although Elateridae spend most of their lives as larvae, our knowledge on immature stages of this family is limited, which is especially valid for the fossils. So far, only a single larval click beetle has been reported from Burmese amber. Here, we describe two larval specimens from the same deposit which based on their morphology unambiguously belong to the predominantly Southern Hemisphere subfamily Pityobiinae, being the most similar to the representatives of tribe Tibionemini. However, since the larvae of the closely related bioluminescent Campyloxenini have not yet been described, we place our specimens to Tibionemini only tentatively. One species of Pityobiinae was recently described from Burmese amber based on adults, and we discuss if it can be congeneric with the here-reported larvae. Recent representatives of the Tibionemini + Campyloxenini clade are known from South America and New Zealand, and this group is hypothesized to have a Gondwanan origin. Hence, the newly discovered Burmese amber larvae may further contribute to a recently highly debated hypothesis that biota of the resin-producing forest on the Burma Terrane, which was probably an island drifting northward at the time of amber deposition, had at least partly Gondwanan affinities. The discovery of enigmatic click beetle larvae in the Upper Cretaceous Burmese amber sheds further light on the palaeodiversity and distribution of the relatively species-poor Gondwanan clade of click beetles, which contain a recent bioluminescent lineage, as well as on the taxonomic composition of the extinct Mesozoic ecosystem.

Keywords Australia, Elateridae, Distribution, Fossil, Morphology, Pityobiinae

The Upper Cretaceous amber of northern Myanmar, also known as Burmese amber, Burmite, or Kachin amber, is recently one of the best explored fossilized resins in the World. After its re-discovery in the beginning of the 21st century[1], it has become to be one of the most important sources of our knowledge on the Cretaceous biota. The known palaeodiversity of organisms trapped in Burmese amber has increased dramatically over the past few years. In 2019, Ross[2] published the complete list of taxa preserved in Burmese amber, which has been updated annually since then[3–7]. Since 2019, the total known number of species has more than doubled. Up to the end of 2023, about 2,800 species have been described or recorded from Cretaceous amber of Myanmar[8].

The Burmese amber is sourced from the Hukawng Valley in the Myitkyina District of Kachin State in northern Myanmar. The U–Pb dating of zircon crystals of volcanic clasts within the amber bearing horizons has given a maximum age of 98.79 ± 0.62 Ma, making the deposit Upper Cretaceous (lower Cenomanian) in age[9]. It is distinct and differs in age from the Tilin amber (~ 72.1 Ma)[10] found in central Myanmar. Relatively recently, also the Hkamti site (109.7 ± 0.4 Ma)[11] located southwest of the Hukawng Basin started producing amber. Burmese amber is thought to have been produced by trees belonging to either the Araucariaceae or Cupressaceae/Sciadopityaceae[1,12,13]. The organisms trapped in Burmese amber suggest a warm, tropical ecosystem[14]. The inclusions of not only terrestrial but also of aquatic species suggest that the resin-producing forests were located near estuarine or freshwater habitats[15–17].

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The amber deposit lies on the Burma Terrane, or West Burma Block, a former Gondwanan landmass presently situated in Myanmar which has a debated tectonic history[18–20]. The Burma Terrane broke off from northeastern Australia and drifted northward; however, the timings of when it broke off and when it accreted to the southern margin of Asia and became to be a part of Southeast Asia are unclear as various studies produce contradictory results[20–24]. Westerweel et al.[22] proposed that the Burma Terrane was part of a Trans-Tethyan island arc and stood at a near-equatorial southern latitude at ~95 Ma which suggests an island endemism for the organisms trapped in Burmese amber[25]. Nevertheless, there is an ongoing debate if the Upper Cretaceous biota trapped in Burmese amber has more affinities to Gondwana or Laurasia[21,23,26–29].

The click beetles (Elateridae) represent the major group in the polyphagan superfamily Elateroidea. More than 11,000 described extant and extinct species from all zoogeographic realms are currently classified in 18 subfamilies[30,31]. This group is famous for both scientists and non-scientists due to the presence of a clicking mechanism in vast majority of its species[32,33] and because it contains important economic pests[34], bioluminescent groups[35,36], and several morphologically modified paedomorphic lineages[37,38]. It is, therefore, rather surprising, that the monophyly, classification and phylogenetic relationships of Elateridae are still a matter of debates[30,31,39–42]. The immature stages are insufficiently researched in Elateridae; however, the known information suggests that the larval morphology may provide an important source of data for phylogenetic reconstructions as well as for defining higher taxa[35,43–46]. For example, the differences in larval morphology are the most reliable characters to separate two large and well-known subfamilies Elaterinae and Dendrometrinae[35,47].

Fossil Elateridae are represented by more than 250 described species, of which more than half are Mesozoic[48]. Although several click beetle species were described from Triassic, their systematic placement is largely unclear[48,49]. However, the Triassic origin of the group cannot be ruled out since the Jurassic click beetle fauna already consisted of more than 100 described species[48,50]. Although the click beetle fauna is well represented in Burmese amber, only several species have been formally described to date, all from adult males[51]. So far, only one click beetle larva has been reported from Burmese amber[52].

In this study, we report two larval specimens from the Upper Cretaceous amber of northern Myanmar which based on their morphology belong to the mostly Southern Hemisphere click beetle subfamily Pityobiinae[31,39,53].

Systematic palaeontology

Order Coleoptera Linnaeus, 1758.
Suborder Polyphaga Emery, 1886.
Superfamily Elateroidea Leach, 1815.
Family Elateridae Leach, 1815.
Subfamily Pityobiinae Hyslop, 1917.
Tribe Tibionemini Motyka et al., 2023.

Remarks. The here-examined larvae are placed in Pityobiinae based on the following combination of characters: dorsoventrally flattened body, more depressed on head and prothorax, the cuticle of head and prothorax more sclerotized than that of abdomen, the ventral surface of abdomen less sclerotized than the dorsal surface, the head subparallel-sided, the mandible with retinaculum, the labium with postmentum triangular, the apices of maxillary stipites approximate, antennal sensorium dome-shaped, the segment IX with a notch at apex and a pair of urogomphi, and anal hooks absent[53,54]. Within Pityobiinae, we place the larvae tentatively in Tibionemini based on the following combination of characters: adnasalia approximate and longer than nasale, the absence of a transverse carina as well as a median longitudinal suture on sternum IX, and the lateral region of tergum IX as sclerotized and heavily pigmented as a dorsal region (Fig. 2F)[53,55]. The only genus of Pityobiinae known from Burmese amber is *Cretopityobius* Otto. However, *Cretopityobius* is more similar to *Pityobius* LeConte (Pityobiini) than to *Tibionema* Solier (Tibionemini). Hence, the generic placement of the here-reported fossil larvae remains unclear. For more details see Discussion.

Unidentified genus (larval stage)

Figures 1, 2, 3, 4 and 5.

Material examined

Two larval specimens deposited in NMPC: NM-T3536 (BUR0112) and NM-T3537 (BUR0113). The specimen NM-T3536 is included in a transparent, pale yellow amber piece with dimensions of about 20.5 × 14.5 × 4.0 mm, with several syninclusions (debris and remains of an unidentified insect). The specimen NM-T3537 is included in a transparent, dark yellow amber piece with dimensions of about 20.0 × 15.2 × 4.0 mm, with numerous syninclusions (debris and an unidentified small arachnid).

Type horizon and locality

Upper Cretaceous, lower Cenomanian (98.79 ± 0.62 Ma), based on U–Pb dating of zircons by Shi et al.[9]; from amber mine in Hukawng Valley, Tanai Township, Myitkyina District, Kachin State, northern Myanmar.

Diagnosis

The here-examined fossil larvae can be easily recognized based on the following combination of characters. Body dorsoventrally flattened, head and prothorax apparently more sclerotized than metathorax and abdomen, intersegmental membranes visible, vestiture consisting of fine long setae, without asperite-like setae. Head flat, nasale produced, wider than long, tridentate, adnasalia approximate, frons lyre-shaped with posterior part abruptly narrowed and tapered at apical 2/3, dorsal epicranial ridges absent, epicranial stem short, coronal

Fig. 1. Habitus of click beetle larvae from Burmese amber. (**A**–**B**) Larval specimen NM-T3536; dorsal and ventral view, respectively. (**C**–**D**) Larval specimen NM-T3537; dorsal and ventral view, respectively. Scale bars: 2 mm.

suture absent, postmentum triangular, stipites contiguous at base, mandible unidentate, with small retinaculum mesally. Mesonotum, metanotum and abdominal mediotergites I–VIII with L-shaped pigmented impressions near anterior corners; legs with spine-like setae. Abdominal segment IX with long bifurcated urogomphi and spine-like setose tubercles; transverse carina of sternum IX and anal hooks absent. For comparison with related groups see Table 1 and Discussion.

Description

Body about 9.5 mm long and about 1.6 mm wide at the widest place in specimen NM-T3536 (Fig. 1A,B), about 9.0 mm long and about 1.1 mm wide at the widest place in specimen NM-T3537 (Fig. 1C,D), dorsoventrally flattened. Tegument of head and prothorax evenly darkly sclerotized, brown, dorsal surface of mesothorax, metathorax and abdominal segments I–VIII partly or entirely lighter than prothorax; articulating area between segments and median exuvial line membranous; ventral surface of abdominal segments I–VIII and segment X lighter than dorsal surface; anterolateral region of mesonotum, metanotum and abdominal mediotergites I–VIII with prominent pigmented L-shaped impression extending from lateral part mesally in about 90-degree angle (Fig. 5F,H,J); claws and spine-like setae on legs darker. Vestiture consisting of sparse long and short brownish setae; asperities absent.

Head (Figs. 2A,B and 4A,B and 5A,B,I) excluding mouthparts 1.2–1.3 times wider than long, sides parallel, prognathous, sclerotized, flattened, shortly retractable into prothorax; dorsal surface flat, moderately densely punctate, punctures large, each side with one lateral long seta at antennifer base, one dorsolateral long seta posterior to antennifer (at anterior third), one long seta dorsally and one long seta laterally between mid and posterior third, one large puncture dorsally near posterior margin; dorsal epicranial ridges and stemmata absent; epicranial stem very short, coronal suture and endocarina absent.

Frontal arms lyre-shaped, frons with anterior corners rounded, one long seta at base of adnasalia and sparse punctures mainly distributed on margins; posterior part of frons abruptly narrowed and tapered at apical 2/3. Nasale (Figs. 2A, 4A,B, and 5A,I) produced, about 3 times wider than long, tridentate, median tooth longer than lateral teeth, few fine setae at base between lateral and median teeth; adnasalia twice longer than nasale,

Fig. 2. Body parts of click beetle larva from Burmese amber (specimen NM-T3536). (**A**) Head; dorsal view. (**B**) Head; ventral view. (**C**) Left antenna; dorsal view. (**D**) Abdominal apex; dorsal view. (**E**) Abdominal apex; ventral view. (**F**) Abdominal apex; lateral view. Scale bars: (**A**, **B**, **D**–**F**) 0.50 mm, (**C**) 0.25 mm.

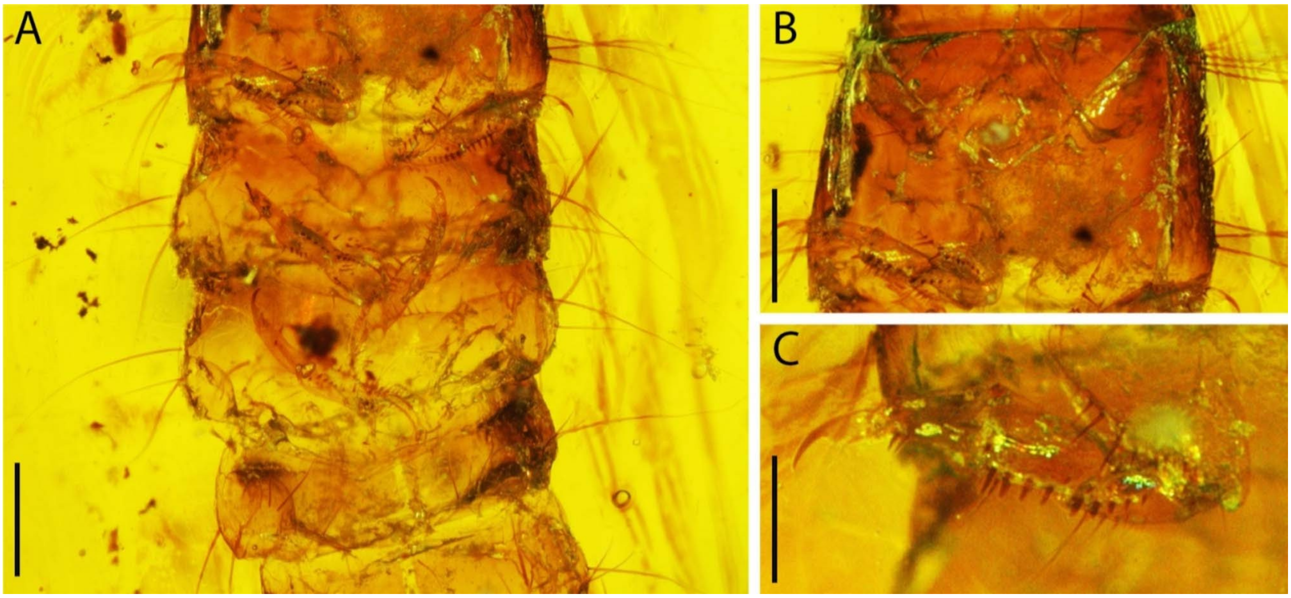

Fig. 3. Body parts of clickbeetle larva from Burmese amber (specimen NM-T3536). (**A**) Thorax with legs; ventral view. (**B**) Prothorax; ventral view. (C) Right proleg; ventral view. Scale bars: (**A**, **B**) 0.50 mm, (**C**) 0.25 mm.

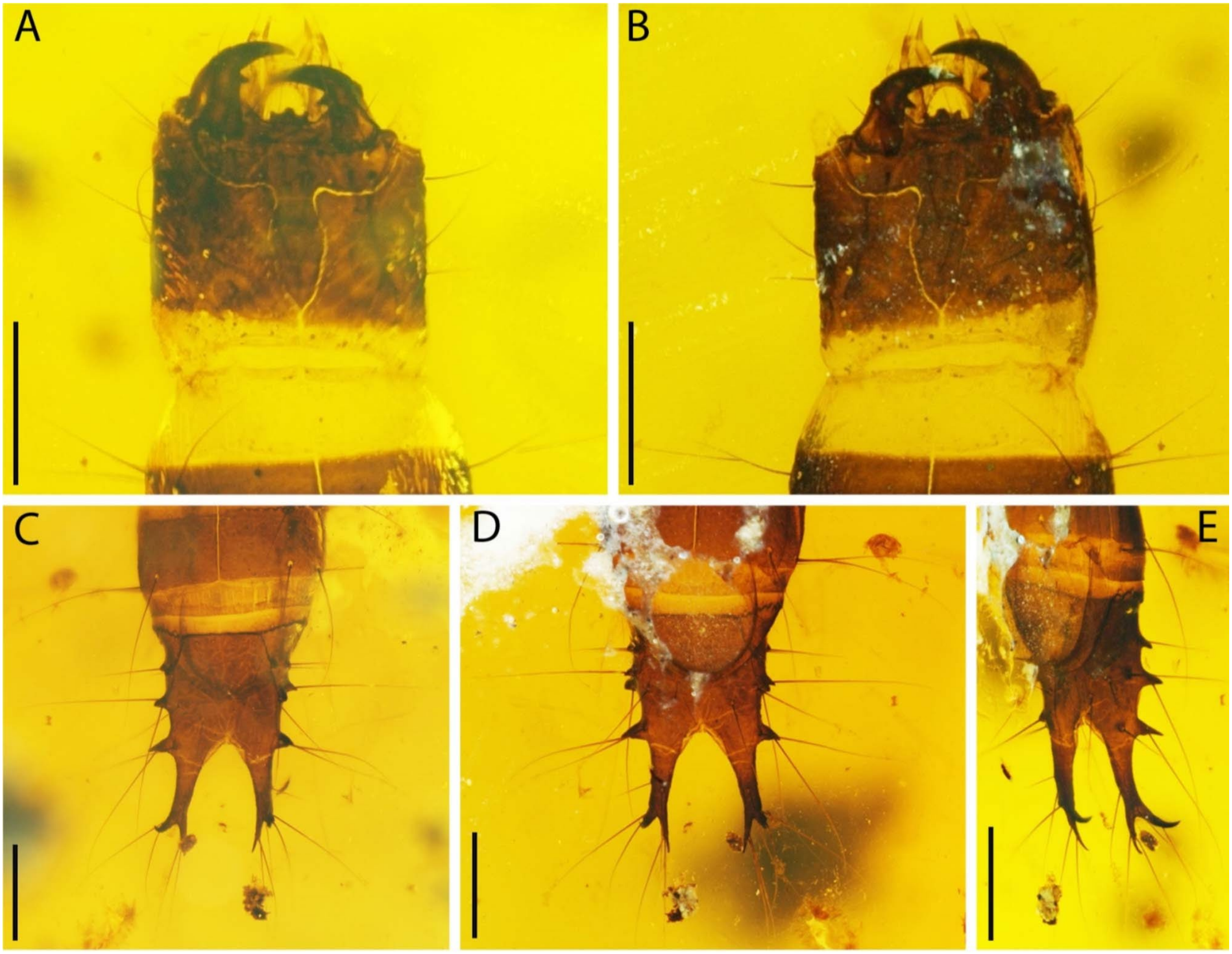

Fig. 4. Body parts of click beetle larva from Burmese amber (specimen NM-T3537). (**A**) Head; dorsal view. (**B**) Head; ventral view. (**C**) Abdominal apex; dorsal view. (**D**) Abdominal apex; ventral view. (**E**) Abdominal apex; lateral view. Scale bars: 0.5 mm.

approximate, separated by distance 0.6–0.7 times as wide as width of one adnasal lobe (measured at base), fringed by setae. Ventral surface (Fig. 5B) smooth except long setae on lateral margins and few shorter setae along outer edge of ventral ridges; ventral ridges almost reaching anterior margin; gular region probably with two sutures (sulci).

Antenna (Figs. 2C and 5C) with three antennomeres, sparsely setose; basal antennomere about 1.2 times as long as median one; median antennomere 1.8 times as long as apical one; apex of median antennomere with minute dome-shaped sensorium lateroventrally; apical antennomere with one long seta and a few short stiff setae. Mandible (Figs. 2A,B, 4A,B, and 5A,B,I) about twice as long as wide, narrow, unidentate, incisor edge with small retinaculum, lateral surface of basal half concave, penicillus not visible; one seta dorsolaterally and few setae near apex.

Maxilla (Figs. 2B and 5B) with stipites 3.3 times as long as wide, gradually narrowed posteriorly, almost contiguous at base, anterior margin narrowed and membranous; lateral margin with sparse punctures, few long setae on anterior corner; maxillary palp four-segmented, elongate, sparsely setose, palpomere I as long as palpomere II, palpomere III 1.3 times as long as palpomere II, palpomere IV 0.7 times as long as palpomere III; galea palpiform, two-segmented; lacinia possibly reduced to densely setose area; cardines hidden.

Labium (Figs. 2B and 5B) with prementum trapezoidal, 1.3 times as wide as long, weakly sclerotized, with a pair of long setae near anterior margin; postmentum elongate, triangular, membranous anteriorly; two pairs of punctures anteriorly and medially (setae missing), apex with two long setae; palp 2-segmented, elongate, apical palpomere strongly tapered, basal palpomere 2.3 times longer than apical palpomere.

Prothorax (Figs. 1A–D and 3B) 1.3–1.4 times as wide as long, about twice as long as mesothorax; mesothorax 2.7–2.9 times as wide as long; mesothorax and metathorax (Fig. 3A) subequal in size; pronotum with 2–3 long setae at anterior and posterior corners and a pair of shorter setae dorsolaterally near posterior margin, prosternum (Figs. 3B and 5D) twice wider than long, triangular; meso- and metathorax with 2–3 long setae laterally and one pair of setae dorsolaterally at posterior third. Leg (Figs. 3C and 5E) with sparse short to long

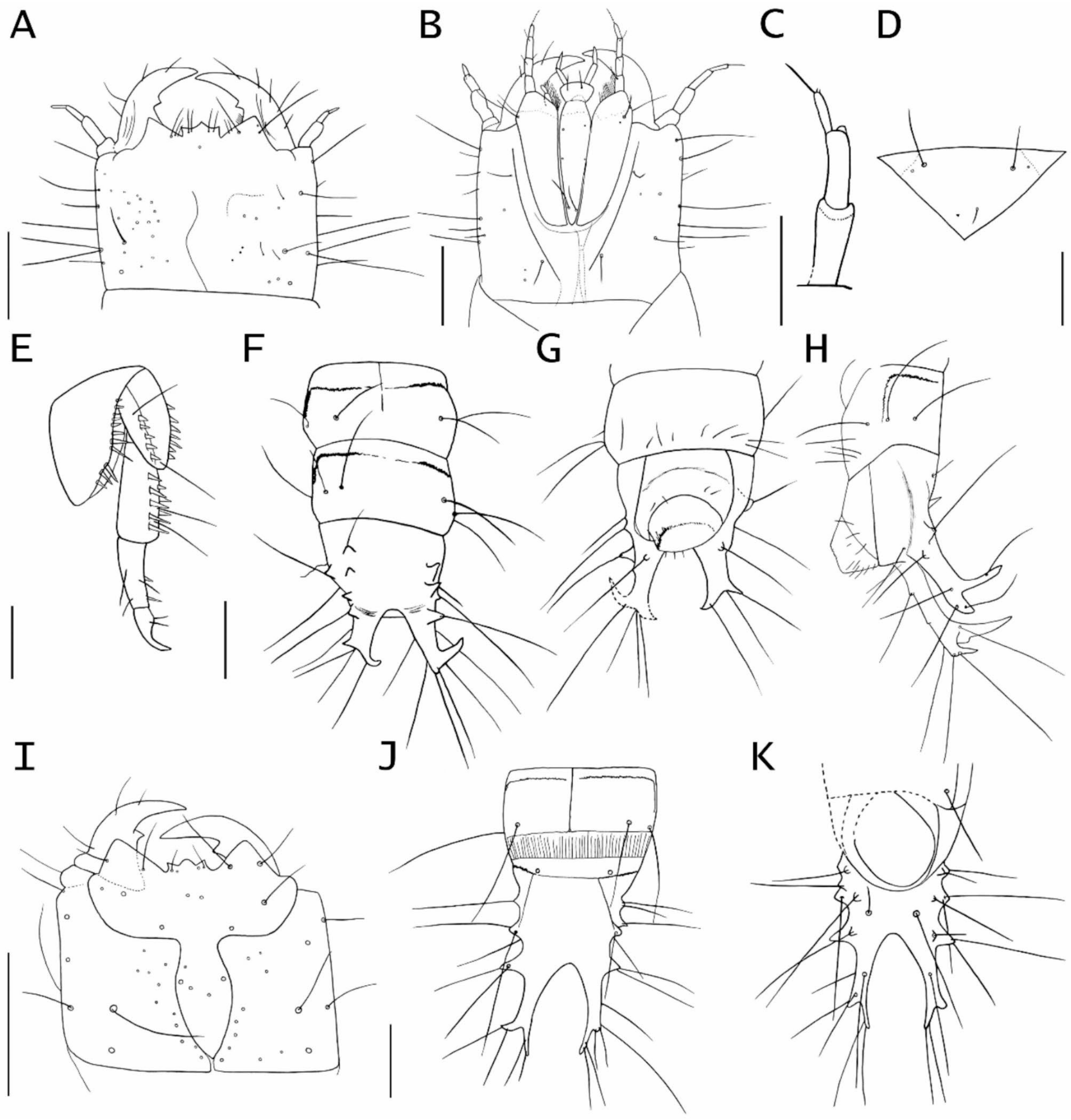

Fig. 5. Drawings of body parts of click beetle larvae from Burmese amber. (**A**–**H**) Specimen NM-T3536. (**A**) Head; dorsal view. (**B**) Head; ventral view. (**C**) Left antenna; dorsal view. (**D**) Prosternum; ventral view. (**E**) Right proleg; ventral view. (**F**) Abdominal segments VII–IX; dorsal view. (**G**) Abdominal segments VIII–X; ventral view (**H**) Abdominal segments VIII–X; lateral view. (**I**–**K**) Specimen NM-T3537. (**I**) Head; dorsal view. (**J**) Abdominal segments VIII–IX; dorsal view. (**K**) Abdominal segments IX–X; ventral view. Scale bars: (**A**–**B**, **D**–**K)** 1.0 mm, (**C**) 0.5 mm.

fine setae, strongly sclerotized short spine-like setae along two lateroventral rows; pretarsus slender with two setae at inner base.

Abdomen (Fig. 1A–D) subparallel up to segment VII, slightly narrowed apically; terga I–VIII divided into medio- and laterotergites, all mediotergites (dorsal sclerotized regions) with each side near posterior margin with two long setae laterally and one long seta dorsolaterally, ventral surface of segments I–VIII with row of setae on posterior margin. Segment IX (Figs. 2D–F, 4C–E and 5F–H,J,K) with tergum undivided, extending ventrally around posterior and lateral parts of segment X, dorsal region flat, without elevated borders, sparsely punctate, lateral margin posteriorly with row of three spine-like tubercles (teeth) increasing in length posterad, each

Tribe	Parablacini			Pityobiini	Tibionemini		
Genus/species	*Metablax acutipennis*	African unknown genus	Australian unknown genus	*Pityobius anguinus*	*Tibionema abdominalis*	New Zealand unknown genus	Burmese amber unknown genus
Sides of head	Subparallel	Subparallel	Subparallel	Subparallel	Subparallel	Subparallel	Subparallel
Antennal sensorium, shape	Dome-shaped	Dome-shaped	Dome-shaped	Dome-shaped	Dome-shaped	Dome-shaped	Dome-shaped
Postmentum, shape	Triangular	Triangular	Triangular	triangular	Triangular	Triangular	Triangular
Retinaculum	Present	Present	Present	Present	Present	Present	Present
Mandible, number of teeth	1	1	1	2	1	1	1
Adnasalia length/nasale length	Equal	Equal	Equal	Shorter	Longer	Longer	Longer
Adnasalia distance/adnasalium lobe width	< 1 (approximate)	< 1 (approximate)	< 1 (approximate)	> 1 (widely separated)	< 1 (approximate)	< 1 (approximate)	< 1 (approximate)
Nasal teeth	3	3	3	4	3	3	3
Gular region	One longitudinal sulcus	One longitudinal sulcus	One longitudinal sulcus	One longitudinal sulcus	Pair of longitudinal sulci	Pair of longitudinal sulci	Pair of longitudinal sulci (probably)
Mediotergites with pigmented impressions	Present	Present	Present	Absent	Present	Present	Present
Segment IX, teeth on lateral margin	Present	Present	Present	Present	Present	Present	Present
Urogomphus, inner prong	Directed upward and slightly inward	Directed upward and slightly forward	Directed upward and slightly inward	Directed upward	Directed slightly inward and posteriad	Directed upward and slightly inward	Directed upward or posteriad
Lateral area of tergum IX as sclerotized and pigmented as dorsal part	No	No	No	No	Yes	Yes	Yes
Transverse carina on sternum IX	Present	Present	Present	Present	Absent	Absent	Absent
Median longitudinal suture on anterior portion of sternum IX	Present	Present	Present	Present	Absent	Absent	Absent
Anal hooks	Absent	Absent	Absent	Absent	Absent	Absent	Absent

Table 1. Overview of the principal diagnostic morphological characters of larval Pityobiinae.

bearing one long seta; laterodorsal and lateroventral regions with small tubercles with long setae; urogomphi long, about 0.8 times as long as basal part of segment IX, bifurcate in two sharp prongs, each bearing 1–3 long setae, outer prongs either slightly longer than inner prongs (NM-T3537) or distinctly longer than inner prongs (NM-T3536), outer prongs either bent upward at slightly more than 45 degrees (NM-T3537) or at almost 90 degrees (NM-T3536), inner prongs either bent upward at about 45 degrees (NM-T3536) or oriented posteriad (NM-T3537); ventral surface of each urogomphus with one seta arising from minute tubercle; sternum IX with anterior part membranous, without transverse carina. Segment X (Figs. 2E,F, 4D,E and 5G,H,K) conical, ventral, membranous, with few fine setae, without anal hooks.

Remarks. Two here examined larvae are very similar to each other so that the most characters given in the description are present in both of them; however, the details of the ventral head, mouthparts, and sterna are based on the specimen NM-T3536 only, because those parts are either not present (ventral head, including mouthparts) or not well visible on the specimen NM-T3537. Those features, however, usually do not vary among species of the same genus. We unambiguously consider both larvae belonging to a single genus. However, there is a question if they also represent two younger instars (possibly first and second) of the same species or if they belong to two different species. Specimen NM-T3537 is about 9 mm long and 1.1 mm wide, while specimen NM-T3536 is about 9.5 mm long and 1.6 mm wide when measured at the widest place. If these are the only differences, we would consider both larvae being different younger instars of the same species. However, they substantially differ in the relative lengths of inner and outer prongs of urogomphi and their orientation, which could be a difference between two species. Therefore, we keep open the question whether the here-examined larvae represent a single species or not.

Discussion

The first possible larva of Elateridae from the Upper Cretaceous Burmese amber was recently reported by Zippel et al.[52]; however, no subfamily-level characters are well visible on that specimen, making its systematic placement unclear. Despite this fact, Zippel et al.[52] interpreted it as a possible member of Elaterinae, stating that “the overall arrangement of the antennae and mouthparts, although only seen in antero-lateral view, is strongly resembling that in modern larvae of Elaterinae”. The here-examined two larval specimens, however, have different morphology (Figs. 1, 2, 3, 4 and 5) and represent another subgroup of click beetles, Pityobiinae (sensu Motyka et al.[31]). Based on the general shape and sclerotization of the body, they also remind larvae of Agrypninae and share some characters with Dendrometrinae.

The newly reported larvae from Burmese amber share with Agrypninae and Pityobiinae a dorsoventrally flattened body, more flattened on head and prothorax, the cuticle of head and prothorax more sclerotized than abdomen, the ventral surface of abdomen less sclerotized than the dorsal surface, the labium with postmentum triangular, the apices of maxillary stipites approximate, the prosternum undivided, the segment IX with a notch at apex, and a pair of urogomphi[46,53]. However, the fossil larvae differ from Agrypninae in having the mandibles with retinaculum, the antennal sensorium dome-shaped, the mesonotum, metanotum and abdominal mediotergites

I–VIII with prominent pigmented impressions, and anal hooks absent. Agrypninae usually lack retinaculum (with the exception of *Meristhus (Sulcimerus) niponensis* Lewis) as well as the mediotergite impressions, and have the antennal sensorium conical and, with some exceptions in Hemirhipini, have anal hooks[44–46,56,57].

The Burmese amber larvae share with Dendrometrinae (and also with all known Pityobiinae with an exception of genus *Pityobius*) the mandibles with retinaculum, the adnasalia approximate and longer than nasale, the paired pigmented impressions extending mesally in about 90 degrees angle on mesonotum, metanotum and abdominal mediotergites, the ventral surface of segment IX with setae arising from minute to prominent tubercles, the caudal notch separating two urogomphi, and segment X without anal hooks[44,45,58–61]. Dendrometrinae and Pityobiinae have also mediotergite IX with a dorsal plate delimited anteriorly and laterally by an elevated and carinate border marginated by a row of prominent tubercles; however, the dorsal plate is indistinct in the fossil specimens, nevertheless a carina on anterior and lateral borders seems to be present in the specimen NM-T3537 (Fig. 4C). On the other hand, Dendrometrinae larvae clearly differ from here-examined fossil larvae as well as from recent Pityobiinae[53] in having the body evenly sclerotized (versus progressively less sclerotized segments from mesonotum to abdominal segment VIII), the antennal sensorium long, 1/3 or more of the apical antennomere length (versus very small and short), the apical setae on antennomere 3 short and subequal (versus one very long seta), the postmentum subparallel-sided (versus triangular), and the caudal notch usually almost circular (sometimes lozenge-shaped) due to inner prongs of urogomphi being strongly directed inward (versus U- or V-shaped notch and urogomphal inner prongs bent upward, posteriad or only slightly inward).

Based on the available morphological evidence we place two newly reported larvae unequivocally in the small subfamily Pityobiinae. Hyslop[43] originally erected tribe Pityobiini for a single North American genus *Pityobius* primarily based on larval characters. Hyslop classified it in his "Pyrophorinae" based mainly on the presence of the paired urogomphi, separating it from other groups currently classified in Agrypninae, Dendrometrinae and Oestodinae by the additional combination of anal hooks lacking, postmentum triangular, and mandibles with three teeth (i.e., two apical teeth and a retinaculum). Later authors added several genera from New Zealand, South America and Australia, including unassociated larvae from South Africa[30,31,47,53,62–64]. Dolin[63] defined the Pityobiinae larvae as having retinaculum, postmentum triangular, stipites joined by their bases, cardo with one sclerite, galea two-segmented, head and prothorax heavily sclerotized and remaining segments leathery, and segment IX notched. Ulrich[53] examined the larval morphology of Pityobiinae in detail, improved their diagnosis, and divided the group into Pityobiini (*Pityobius*, *Metablax* Candèze pars and unassociated species from Australia and South Africa) and Tibionemini (*Tibionema*, and an unassociated New Zealand species). Ulrich's larval diagnosis of Pityobiinae includes the abdominal segment IX with paired urogomphi, the postmentum triangular, the anal hooks absent, the anterior margin of sternum IX sclerotized and pigmented, forming a divided transverse carina (absent in Tibionemini), the cardines divided into four sclerites, and the antennal sensorium dome-shaped, arising from a circular, sclerotized base[53]. Except for the division of the cardines into four sclerites, which cannot be observed in fossil specimens, the Burmese amber larvae share all of these features but the presence of a transverse carina on sternum IX.

The recent phylogenetic analyses placed Pityobiinae in a clade with Hapatesinae from Australasia[30,31,41] (Fig. 6). Larva of *Hapatesus* Candèze shares some features with Pityobiinae, including the presence of retinaculum and absence of anal hooks, and especially with the Southern Hemisphere groups, including the fossils, with which they share approximate adnasalia, tridentate nasale, and prominent pigmented impressions on thoracic and abdominal mediotergites[53,65]. Nevertheless, the *Hapatesus* larva bears unique features such as the rounded sides of the head, the parallel-sided postmentum, the absence of laterodorsal prominent teeth (tubercles) or any tuberculate setae on lateral and ventral parts of segment IX, the dorsal plate on segment IX without elevated and carinate borders, and the inner prongs of urogomphi strongly directed inward[65,66].

Pityobiinae as currently defined[31] are classified into four tribes, i.e., Pityobiini (*Pityobius* from North America, *Cretopityobius* from Burmese amber), Tibionemini (*Tibionema* from South America, unassociated larva from New Zealand), Parablacini (several genera from Australia, New Zealand, South America, and unassociated larvae from South Africa), and Campyloxenini (bioluminescent *Campyloxenus* Fairmaire & Germain and *Malalcahuello* Arias-Bohart from South America) (Fig. 6; Table 2). It should be noted that two latter tribes were separate subfamilies until recently and that there is no information on immature stages for Campyloxenini[31,39]. Larval Pityobiini strikingly differ from the here-examined Burmese amber larvae in having bidentate mandibles, nasale with four teeth, adnasalia widely separate and shorter than nasale, disticardines absent, labial sclerite fused, gular sulcus short, postgular sclerite long, pigmented impressions on mediotergites and dorsal plate on tergum IX less distinct, without elevated and carinate borders[43,53,67]. Parablacini larvae differ from fossil larvae in having the adnasalia as long as nasale, the transverse carina on sternum IX, and the lateral region of tergum IX not as sclerotized and heavily pigmented as a dorsal region[53,54].

Our Burmese-amber larvae are most similar to Tibionemini (Table 1), with which they share unidentate mandibles, tridentate nasale, approximate adnasalia which are longer than nasale, the lateral region of tergum IX as sclerotized and heavily pigmented as a dorsal region, the absence of a transverse carina on sternum IX, and the anterior portion of sternum IX entire, not divided by longitudinal suture[53,55]. According to Ulrich[53], Tibionemini contain two species, i.e., the only formally described *Tibionema abdominale* (Guérin-Méneville) from Chile and an unassociated larva from New Zealand, previously erroneously associated to *Metablax*, a genus in Parablacini. The fossil larvae from Burmese amber are morphologically more similar to the New Zealand larva by the posterior set of long setae on abdominal mediotergites, with each mediotergite bearing two lateral setae and one dorsolateral seta (several setae along anterior margin in *Tibionema*). Tibionemini were found to be a sister-group of Campyloxenini in a recent phylogenetic analysis[31]. Since the larvae of Campyloxenini have not yet been described, we cannot exclude the possibility that our fossil larvae are in fact members of Campyloxenini or the stem group of Campyloxenini + Tibionemini. According to Motyka et al.[31], these two tribes originated at

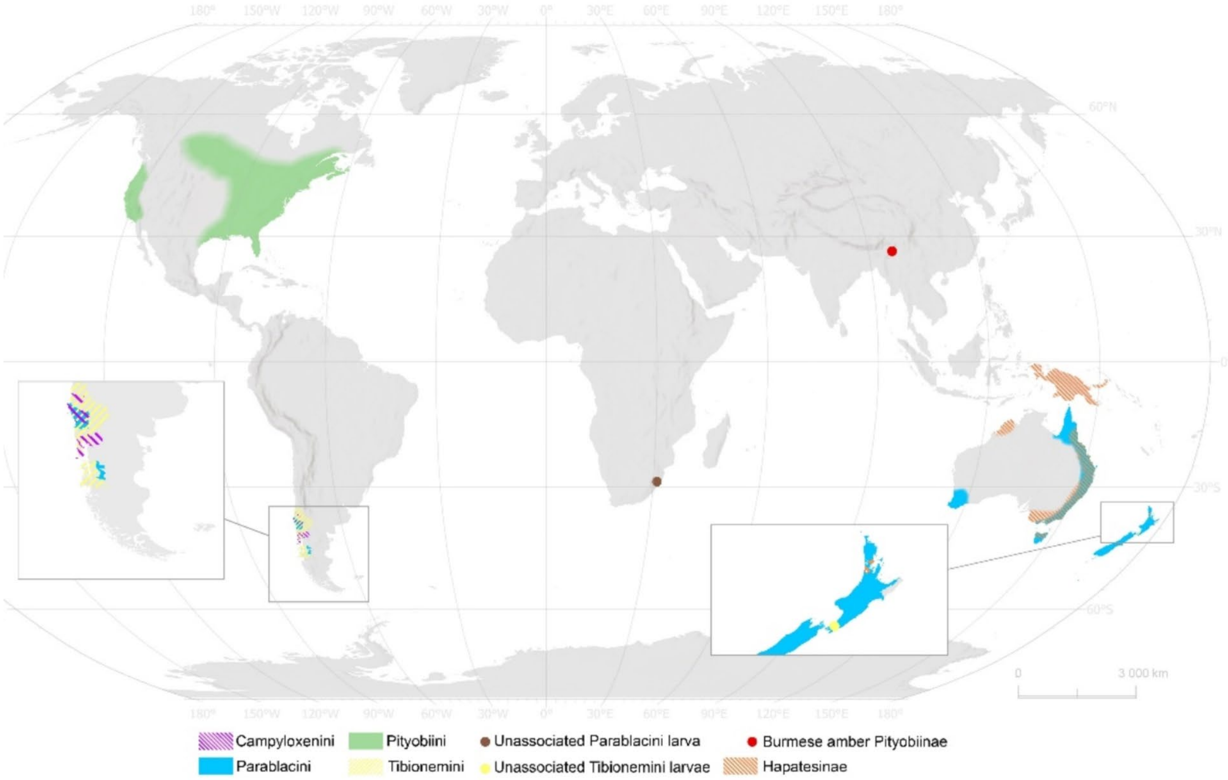

Fig. 6. Distribution map of Pityobiinae and Hapatesinae, including the fossil records.

Tribe	Genus	spp.	Distribution
Pityobiini Hyslop, 1917	*Pityobius* LeConte, 1853	2	Canada, USA
	†*Cretopityobius* Otto, 2019	1	Cretaceous Burmese amber
Parablacini Kundrata et al., 2016	*Elatichrosis* Hyslop, 1921	13+	Australia (incl. Tasmania)
	Metablax Candèze, 1869	5	New Zealand
	Ophidius Candèze, 1863	4	Australia
	Parablax Schwarz, 1906	9+	Australia (incl. Tasmania)
	Parasaphes Candèze, 1882	1+	Australia
	Rousia Calder, 1996	1+	Australia
	Sharon Arias-Bohart & Elgueta, 2015	2	Chile
	Tasmanelater Calder, 1996	1	Australia (Tasmania)
	Wynarka Calder, 1996	1	Australia
	Xuthelater Calder, 1996	1	Australia
	unknown genus	2?	South Africa
Campyloxenini Costa, 1975	*Campyloxenus* Fairmaire & Germain, 1860	1	Argentina, Chile
	Malalcahuello Arias-Bohart, 2015	1	Chile
Tibionemini Motyka et al., 2023	*Tibionema* Solier, 1851	1	Argentina, Chile
	unknown genus	1	New Zealand
	†unknown genus	1 or 2	Cretaceous Burmese amber

Table 2. Overview of the Pityobiinae diversity and distribution. Extinct taxa are marked with "†". Number of species under described genera means only described species, "+" denotes additional known undescribed species.

~ 96 Mya, while Burmese amber is dated to 99 Mya[9]. The morphological descriptions of larvae of Campyloxenini are crucial for further conclusions.

The Burmese larvae differ from all other Pityobiinae in their longer body vestiture, the antennae, maxillary palpi, labial palpi and urogomphi being relatively slender and longer, and the segment IX having its dorsal surface rather flat and without elevated edges. However, at least some of these characters may be related to differences between younger and older larval instars, as the fossil larvae certainly represent younger larvae (at least specimen NM-T3537 is possibly the first instar). First-instar larvae of Elateridae usually have sparser and longer body vestiture and the abdominal apical notch can be longer and narrower, forming longer and slenderer urogomphi[58,68,69]).

The fossil record of Pityobiinae includes so far only a single recently described monotypic genus, i.e., *Cretopityobius* Otto from Burmese amber[70]. This taxon shared the general appearance and some characters, e.g., the biflabellate antennae, with the North American *Pityobius* and was included in the tribe Pityobiini by Motyka et al.[31]. This would mean our fossil larvae from the same deposit, being tentatively classified in Tibionemini, are not congeneric with *Cretopityobius*; however, the placement of the latter needs thorough examination when more material is available. Therefore, we keep open the question whether the fossil larvae reported in our study can be congeneric with *Cretopityobius* or not. It should be noted, that except for the pityobiine *Cretopityobius*, only representatives of Agrypninae (one species), Dendrometrinae (one species) and Elaterinae (four species) have been formally described to date from Burmese amber, with two additional species being classified as *incertae sedis* but morphologically very different from Pityobiinae[51]. Considering a high number of still undescribed elaterid taxa from Burmese amber (RK, pers. observ.), it is likely that the larvae belong to a yet undiscovered taxon (although the *Cretopityobius* hypothesis is still on the table).

There is an ongoing debate about the origin of Burmese amber and its biota, and the principal questions are where exactly was the Burma Terrane at the time of the amber formation and deposition, and if the bioinclusions trapped in Burmese amber were of a Gondwanan or a South East Asian origin[21,23,26–28,71]. There is a more or less accepted hypothesis that at the time of the amber deposition, the Burma Terrane was an isolated island drifting northward[22]. Recently, dramatically increased number of studies documenting biota of Burmese amber[8] brought some interesting insights about its affinities to either Laurasia or Gondwana. Increasing number of discoveries suggest that the Burmese amber insects often have Gondwanan affinities, especially with Australian and Neotropical regions[26–28,72–82]. Most recent study by Wood & Wunderlich[83] not only provided further evidence that the Burmese amber fauna has ties to Gondwana but they also suggested that the Burma Terrane served as a biotic ferry transporting specimens from Gondwana to the Northern Hemisphere, similar to what has been suggested for the Indian Plate. On the other hand, some other authors report Burmese amber taxa had their close relatives in Laurasia[29,84,85], and, more importantly, Peris & Jelínek[86] argued that there are many examples of taxa found in various Cretaceous ambers (e.g., from France, Spain, or Canada) whose current relatives are found exclusively in Australasian and Neotropical realms, and which do not have a Gondwanan origin (see also Peris et al.[87]). They attributed the differences between modern and past distributions of many taxa to changes in the vegetation and the wider distribution of the forests found in the Southern hemisphere during the Cretaceous[86]. It is becoming more and more evident that Burmese amber contains lineages from both landmasses, and there are various hypotheses why either Gondwanan or Laurasian fauna was present in the tropical amber forest of Burma Terrane (some taxa were previously widely distributed but recently have a relict southern distribution, some taxa could have flown from Asia to the Burma Terrane when it was still an island but relatively close to the Laurasian coast, etc[22,83,88,89]). Since the Burma Terrane was likely an isolated island for large periods of time, numerous taxa were probably also island endemics. This hypothesis is confirmed by numerous taxa being known exclusively from Burmese amber, including the insect families from various orders[90–95].

The pityobiine tribes Campyloxenini, Parablacini and Tibionemini, all with Southern Hemisphere distributions (Table 2; Fig. 6), were suggested to have a Gondwanan origin by previous study[31]. On the other hand, Pityobiini, with the recent species occurring in North America and *Cretopityobius* known from Burmese amber, may have been more widely distributed in the past. Further research should be focused on *Cretopityobius*, as its proper systematic placement is crucial for understanding the diversity, distribution and evolution of the interesting click beetle lineage which supposedly might have originated in Gondwana and contain a recent bioluminescent lineage[31].

Materials and methods

This study is based on two larval specimens entombed in amber. They were bought from a commercial fossil dealer by the first author. To our knowledge, both examined amber pieces were mined and sourced before June 2017. They are deposited in the collection of the Department of Palaeontology of the National Museum, Prague, Czech Republic (NMPC). The amber pieces were already polished before we examined them, and later (post-acquisition) they were only very slightly polished by hand, which allowed improved views of the included specimens. The amber pieces were not subjected to any supplemental fixation. Observations of the specimens were made using an Olympus SZX12 stereomicroscope, and the photographs (Figs. 1, 2, 3 and 4) were taken using a Canon EOS M6 Mark II camera mounted on a stereomicroscope. The amber piece was submerged in glycerine during imaging to improve light dispersion and reduce reflections. Stacks of photographs were combined with the software Helicon Focus Pro (version 7.6.4, Kharkiv, Ukraine), applying the rendering method 'depth map' or 'weighted average'. Adobe Photoshop CC (version 2019-20.0.5) was used for the contrast enhancing. Line drawings (Fig. 5) were made based on photographs and revised upon detailed specimen examination under stereomicroscope. The measurements were taken with a scale bar in an eyepiece. Body length of both examined specimens was measured from the nasale to the apex of urogomphi, and the body width was measured at the widest part. Morphological terminology follows partly Costa et al.[35], Ulrich[53], and Glen[58], and the classification of Pityobiinae follows Motyka et al.[31]. The distributional map of Pityobiinae and Hapatesinae (Fig. 6) was created using ArcGIS Pro 3.0 and GIMP 2.10.36 (GNU Image Manipulation Program), with data coming from Natural Earth (https://www.naturalearthdata.com) and Esri Living Atlas of the World (https://livingatlas.arcgis.com). Distribution estimation is based on data published in literature[47,53,54,96–101] and/or available from publicly available internet sources (GBIF; www.gbif.org; iNaturalist, www.inaturalist.org). The spatial distribution is portrayed by blurring to visualize a certain degree of uncertainty[102]. The ZooBank LSID number for this publication is: urn:lsid:zoobank.org:pub:54CF94C4-7442-400B-88C9-C2AAF7CB3B5D.

Data availability

All data needed to evaluate the conclusions in the paper are present in the paper. The high resolution photographs of the examined specimens are available from the corresponding author upon reasonable request.

Received: 2 August 2024; Accepted: 22 November 2024

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Acknowledgements

We thank Jiří Kvaček and Jiřina Dašková (both NMPC) for their help during our research, Paul J. Johnson (South Dakota State University, SD, USA) for information on the distribution of *Pityobius*, and David Peris (Botanical Institute of Barcelona, Spain) and one anonymous reviewer for their invaluable comments leading to the improvement of our manuscript.

Author Statement

This is to declare that we would support repatriation efforts and the future return of the examined specimens to Myanmar for deposition and curation in an appropriate public institutional collection.

Author contributions

R.K. conceived and designed the study. K.T. and R.K. prepared amber pieces, made photographs, and created figure plates. S.P.R. (lead) and R.K. carried out the morphological investigation. S.P.R. prepared line drawings. J.B. (lead), R.K. and J.H. prepared the distributional map. R.K. (lead) and S.P.R. wrote the initial manuscript with help of G.P. All authors performed the literature search, discussed the results, and edited, reviewed and approved the manuscript.

Funding

This study was funded by the internal grant of the Faculty of Science, UP Olomouc (IGA_PrF_2024_029; to RK, KT, GP) and the National Natural Science Foundation of China (No. 32270483; to RK).

Declarations

Competing interests

The authors declare no competing interests.

Additional information

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