

A new species of Burmecaelidae (Orthoptera: Caelifera) sheds light on the family's possible taxonomic placement

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
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Abstract

A new species of the family Burmecaelidae Uchida *et al.*, 2024 is described as *Burmecaelinus yungyenwangae* **sp. nov.** based on a well-preserved adult female specimen from mid-Cretaceous Burmese amber. Due to similarities in morphology of the paraproctal lobes and ovipositor to Ripipterygidae Ander, 1939 (Caelifera: Tridactylidea: Tridactylidea), as well as in forewing venation to Mongoloxysiinae Gorochov, 1992 (Tridactylidea: Tridactylidae), a taxonomic position of Burmecaelidae within Tridactylidea Brullé, 1835 is suggested. The specimen ECNU-AM-0079, formerly interpreted as *Burmecaelinus armis* Uchida *et al.*, 2024 by Hu & He (2024) probably does not belong to that genus, but rather to *Moban* Hu & He, 2024.

Key words: Burmese amber, *Burmecaelinus yungyenwangae*, Tridactylidea, *Moban*

Introduction

Burmecaelidae Uchida *et al.*, 2024 is a family within the suborder Caelifera Ander, 1936 of Orthoptera Olivier, 1789. Caelifera are subdivided into two infraorders, the Tridactylidea Brullé, 1835 and Acrididea Targioni-Tozzetti, 1882. Until now, only two monotypic genera of Burmecaelidae have been described based on three specimens found in mid-Cretaceous amber from Myanmar (known as Burmese or Kachin amber): the type species *Burmecaelinus armis* Uchida *et al.* 2024, described from a single nymphal specimen, and *Moban zhengzhemini* Hu & He 2024, described from a single adult specimen. The later authors also reported a second adult specimen which they attributed to *B. armis*. The taxonomic position of Burmecaelidae within the Caelifera is enigmatic due to the family's intriguing morphology. While many characters (such as the legs and abdomen) are similar to the families Tridactylidae Brullé, 1835 and Ripipterygidae Ander, 1939 from the Tridactylidea, other features (especially the head morphology) suggest a placement closer to Acrididea. Uchida *et al.* (2024) proposed two hypotheses for the placement of the group: 1) at the base of Caelifera, prior to the split of Acrididea and Tridactylidea, or 2) within Tridactylidea, prior to the split of Tridactylidae and Ripipterygidae. Hu & He (2024) pointed out that the absence of fully sclerotized abdominal sternites, which are present in Tridactylidea (Heads, 2009), exclude Burmecaelidae from Tridactylidea, and suggested instead a sister group relationship between these two taxa.

In order to shed light on the taxonomy of Burmecaelidae, additional specimens are needed. In this study, we present a new species of Burmecaelidae based on a well-preserved adult female specimen. The new taxon provides additional insights into the position of the family within the Caelifera.

Materials and methods

The holotype specimen herein described was purchased by the third author (ZL) from Myanmar as raw ore in accordance with national customs declaration procedures. The amber piece was discovered in a mining facility in Tanai, Kachin State Burma, Northern Myanmar, circa 2015. Amber from this site is estimated to be 98.79 ± 0.62 My old (Shi *et al.* 2012). The specimen is currently housed in the private collection of the third author (ZL) (Tainan, Taiwan) and is available to researchers upon reasonable request. The holotype specimen is catalogued as specimen number OA-2025-03-WYY P.S. The specimen will eventually be transferred to the new gallery of the private museum (Asian Amber Biological Museum: Tainan, Taiwan) which is currently being developed (anticipated opening in 2027); upon opening of the museum, the holotype will be publicly available for visiting researchers. The specimen was cut from a piece of raw amber ore, initially shaped with a polishing wheel and roughly ground with a water-fed flat mill; the finer work was done by hand with a wet grinding stone (grits 800, 1200, 3000, 5000). Incident and transmitted light photographs were taken with a Nikon SMZ1270 stereo microscope (Tokyo, Japan) with attached Nikon 1xWF WD:70 200x and 800x lens and 4k resolution, Spotlight O13A DC 12v (Luzon, Philippines) and yellow-white reflector under the microscope for illumination. Measurements were taken with xyz-axis level attached to the stereo microscope. The images were stacked with the Nikon application Capture V2.2 (New York City, USA). The images were edited in Adobe Photoshop CC 13.0.1 (San Jose, USA) to enhance contrast.

Drawings were created in GIMP v. 2.10.36 (the GIMP Team, 2025). Further modifications (scale-bars, labelling) and creation of image plates were done in Inkscape v. 1.3 (the Inkscape Team, 2025).

The taxonomy in this study follows the Orthoptera Species File (Cigliano *et al.*, 2025). Wing venation nomenclature follows Gorochoff *et al.* (2006). Abbreviations of wing venation are: ScA/ScP = anterior/posterior subcosta; R = radius; MA1/2 = first/second branch of anterior media; CuP = posterior cubitus; 1A = anterior anal vein.

Systematic paleontology

Order: Orthoptera Olivier, 1789

Suborder: Caelifera Ander, 1936

Infraorder: Tridactylidea Brullé, 1835

Family: Burmecalidae Uchida *et al.*, 2024

Genus: *Burmecaelinus* Uchida *et al.*, 2024

Type species: *B. armis* Uchida *et al.*, 2024

Species: *Burmecaelinus yungyenwangae* sp. nov.

Figs. 1–3

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Etymology: Patronym. The species is named after Yungyen-Wang, mother of the third author (ZL), to thank her for her years of support and encouragement.

Locality and horizon: Tanai, Kachin State Burma, Myanmar, an amber mining location. The amber from Tanai is estimated to be ca. 99 My old.

Holotype: The holotype, an adult female, is currently in the collection of the third author (ZL), catalogued as collection number OA-2025-03-WYY P.S. The holotype will eventually be transferred to the Asian Amber Biological Museum, Tainan, Taiwan upon the museum's completion.

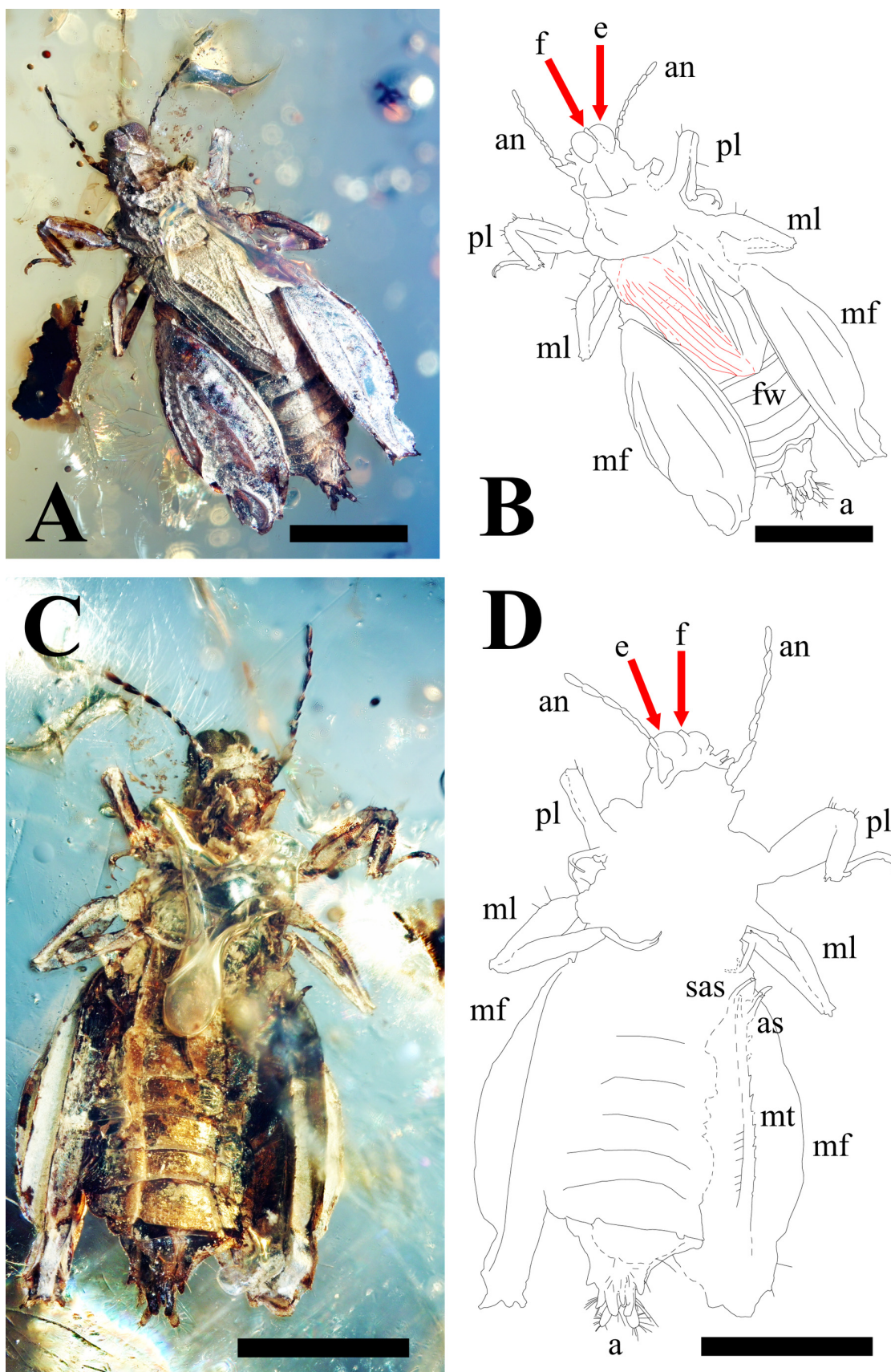


FIGURE 1. *Burmecaelinus yungyenwangae* sp. nov. holotype female, coll. no. OA-2025-03-WYY P.S. **A.** and **B.** Dorsal view of the specimen. **C.** and **D.** Ventral view. **Abbreviations:** a = abdomen; an = antenna; as = apical spur; e = compound eye; f = fastigium; fw = forewing; mf = metafemur; ml = mesothoracic leg; mt = metatibia; pl = prothoracic leg; sas = subapical spur. **Scale bars** = 2 mm.

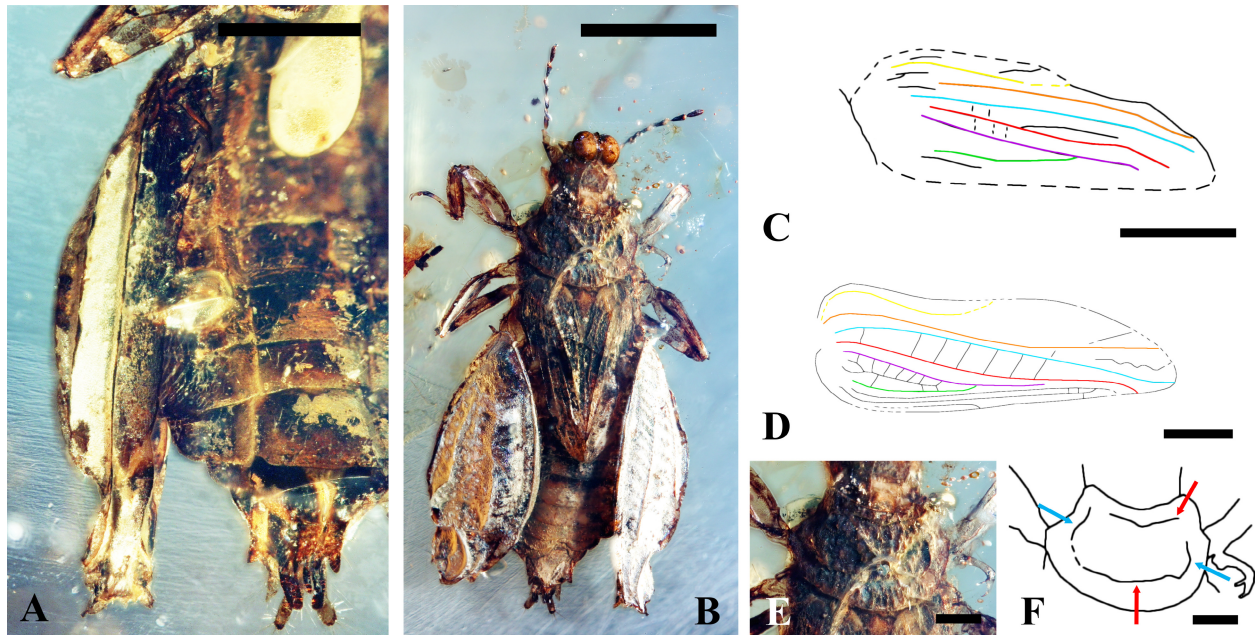


FIGURE 2. *Burmecaelinus yungyenwangae* sp. nov. holotype female, coll. no. OA-2025-03-WYY P.S. **A.** Ventral view of right metatibia. **B.** Specimen in dorsal view with different lighting. **C.** and **D.** Comparison of the forewings of *B. yungyenwangae* (C) and *Cretoxya rasnitsyni* Gorochov *et al.*, 2006 (Tridacytlidae: Mongoloxynaie) (D). Note the apparent similarities in venation. (Anteriormost area of the wing of *B. yungyenwangae* not discernible). Yellow = ScA; orange = ScP; blue = R + MA1; red = MA2; purple = CuP; green = 1A. Forewing of *C. rasnitsyni* redrawn and modified after Gorochov *et al.*, 2006. **E.** and **F.** Detail of pronotum in dorsal view. Red arrows mark anterior and posterior longitudinal carina. Blue arrows mark left and right latitudinal carina. **Scale bars** = 1 mm (A, C, D); 2 mm (B); 0.5 mm (E, F).

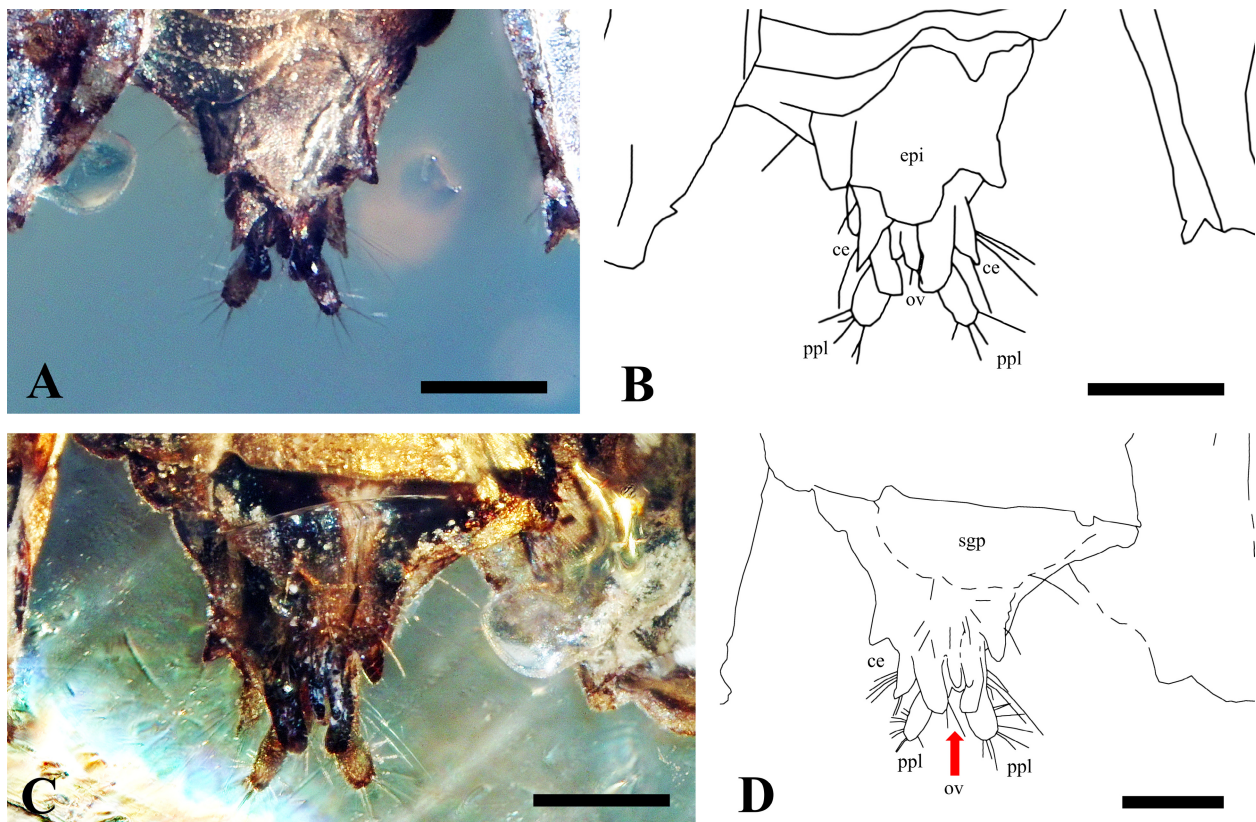


FIGURE 3. *Burmecaelinus yungyenwangae* sp. nov. holotype female, coll. no. OA-2025-03-WYY P.S. **A.** and **B.** Abdominal appendages in dorsal view. **C.** and **D.** Abdominal appendages in ventral view. **Abbreviations:** ce = cercus; epi = epiproct; ov = ovipositor; ppl = paraproctal lobe; sgp = subgenital plate. **Scale bars** = 0.5 mm.

Diagnosis: Pronotum with dorso-anterior and dorso-posterior carinae, as well as dorso-lateral carina on each side. Protibia apically with two spines. Forewing venation rather dense, with at least five well-developed longitudinal veins. Abdominal apex with epiproct with two lateral pointed extensions and one medial rounded extension. Subgenital plate short. Cerci half the length of paraproctal lobes; one-segmented and pointed with long setae. Paraproctal lobes cylindrical in shape, with long apical setae. Valves of ovipositor visible, slightly longer than cerci.

Description

Measurements (mm): Body length (tip of fastigium to tip of paraproctal lobe) 7.1. Dorsal length of pronotum (midline) 1.15. Dorsal width of pronotum along anterior margin 1.3; along posterior margin 1.75. Prothoracic leg: femur length 1.0; tibia length 0.85; tarsus length (including tarsal claws) 0.76. Mesothoracic leg: femur 1.16 ; tibia 1.3. Metathoracic leg: femur 4.0; tibia ca. 3.3. Forewing 2.8.

Head: Hypognathous. Antennae moniliform with eight segments (including scape and pedicel). Antennomeres longer than wide. Antennal scapes enlarged. Compound eyes egg-shaped, protruding from head dorsally. Fastigium between compound eyes very narrow.

Thorax: Pronotum trapezoid in dorsal view. Anterior margin concave, posterior margin convex, distinctly wider than anterior margin. An anterior and posterior dorsal carina, as well as two lateral carinae (one on each side) present. Entire surface of pronotum very rugged. Forewings present, ca. half the length of abdomen. Dense in venation with ScA, ScP, R + MA1, MA2 and CuP visible as distinct single longitudinal veins.

Legs: Prothoracic leg with femur greatly inflated and bearing long setae. Tibia normal (not inflated), showing similar setae; apically bearing two small spines. Tarsus two-segmented with two tarsal pads; apically bearing two curved claws. Mesothoracic leg unspecialized i.e. neither femur nor tibia inflated. Femur proximally with two long setae. Tarsus two-segmented with two claws. Metathoracic leg heavily inflated along the entire length. Several longitudinal carinae and semilunar process present. Tibia with serration that becomes prominent towards apex (i.e. the spines become larger). Apex of tibia with two subapical and two apical spurs of similar length. Tarsus not visible.

Abdomen: Epiproct with three extensions, two laterally rather pointed, one in the middle that is broader and more rounded. Cerci rather short and triangular with long setae. Paraproctal lobes prominent, cylindrical in shape and about twice the length of cerci, with long setae towards apex. Ovipositor valves visible. Subgenital plate rather short, being distinctly surpassed by the other abdominal structures.

Remarks: *Burmecaelinus yungyenwangae* **sp. nov.** is assigned to Burmecaelidae based on the following combination of characters: head with compound eyes protruding dorsally and fastigium between compound eyes very narrow; antennae moniliform with eight segments; tarsi of pro- and mesothoracic leg two-segmented; metafemur greatly inflated along its entire length; metatibia with serration and two subapical as well as apical spurs.

It is further assigned to the genus *Burmecaelinus* due to the presence of two protarsal pads and the subgenital plate being short, only reaching to the base of the paraproctal lobes. Table 1 shows characters of taxonomic importance for Burmecaelidae for all four specimens of the family reported so far (Uchida *et al.*, 2024; Hu *et al.*, 2024; this study). The pronotum of all four specimens shows a similar pattern of lateral carinae as well as posterior and anterior carinae. The four additional latitudinal carinae on the pronotal disc of ECNU-AM-0079 (cf. *Burmecaelinus armis*) reported in Hu *et al.*, (2024) are likely not a reliable character in an amber fossil; this was acknowledged by the authors as well. ECNU-AM-0079 exhibits a different general shape of the pronotum in that it appears to be wider than long compared to the other three specimens. However, we think this may be the result of dorso-ventral compression of the specimen, effectively squashing the pronotum, as damage to the fossil can be seen in the ruptured head and abdomen. The two tarsal pads described by Uchida *et al.* (2024) for the holotype of *B. armis* are also present in *B. yungyenwangae*. However, they are not mentioned in the description of the ECNU specimens. The metatibia is serrated in all specimens. The abdominal apex is where the specimens differ most: the holotype of *B. armis*, as well as the second specimen reported by Hu *et al.* (2024), have an epiproct with a lateral extension on each side that is short and blunt and a medial extension that is round with a narrow inward fold. In *Moban zhengzhemini* Hu & He, 2024 the inward fold of the medial extension is missing. The same is true for *B. yungyenwangae*, and this species has the two lateral extensions which are pointed. The cerci of *B. armis* are of

the same length as the paraproctal lobes (the structure interpreted as the ovipositor in the original description of *B. armis* is more likely to represent the paraproctal lobes). In ECNU-AM-0079 only one cercus is preserved. This cercus appears to be longer than in the holotype of *B. armis*, but the paraproctal lobes are not seen in this specimen. In *M. zhengzhemini*, two very short structures on either side of the abdomen were interpreted as probable cerci and paraproctal lobes. However, these structures also resemble ovipositor valves, as are found in Ripterygidae Ander, 1939 and our specimen of *B. yungyenwangae*. The identity of these structures, therefore, is questionable. The cerci of *B. yungyenwangae* are only about half the length of the paraproctal lobes. Lastly, the subgenital plates of *B. armis* and *B. yungyenwangae* are similar. Both are short, reaching only to the base of the paraproctal lobes. In contrast, the subgenital plates of the ECNU specimens are elongated and possess numerous long setae. They have a distinct medial appendix that extends up to the length of the cercus in ECNU-AM-0079.

TABLE 1. Morphological comparison of the four known specimens of Burmecaelidae Uchida *et al.*, 2024.

	Specimen	UNIT MA33905 (holotype <i>Burmecaelinus armis</i> Uchida <i>et al.</i> , 2024)	ECNU-AM-0079 (cf. <i>Burmecaelinus armis</i> in Hu <i>et al.</i> , 2024)	ECNU-AM-0080 (holotype <i>Moban zhengzhemini</i> Hu & He, 2024)	OA-2025-03-WYY P.S (holotype <i>Burmecaelinus yungyenwangae</i> sp. nov. , herein)
Character					
Sex		Unknown (nymph)	Male	Female (?)	Female
Pronotum		Two longitudinal carinae (anterior/posterior) + latitudinal carinae (left/right)	Two longitudinal carinae (anterior/posterior) + latitudinal carinae (left/right); four additional latitudinal carinae dorsally	Two longitudinal carinae (anterior/posterior) + latitudinal carinae (left/right)	Two longitudinal carinae (anterior/posterior) + latitudinal carinae (left/right)
Tarsal pads		Present	Absent	Absent	Present
Metatibia serrated		Yes (only proximal part preserved)	Yes	Yes	Yes
Epiproct		Lateral extensions short and blunt, medial extension round with inward fold	Lateral extensions short and blunt, medial extension round with inward fold	Lateral extensions short and blunt, medial extension round (?)	Lateral extensions short and pointed, medial extension round
Cerci		As long as paraproctal lobes	Rather long (paraproctal lobes absent or not preserved)	? (see remarks section)	Half the length of paraproctal lobes
Paraproctal lobes		Cylindrically stunted; as long as cerci	Absent	? (see remarks section)	Cylindrical; twice the length of cerci
Subgenital plate		Short, reaching just base of paraproctal lobes	Elongated and distinctly covered with long setae; medial extension narrow-cylindrical, reaching ca. length of cerci	Elongated and distinctly covered with long setae; medial extension broad-cylindrical	Short, reaching just base of paraproctal lobes

In conclusion, we argue that the morphology of the pronotum and serration of the metatibia is relatively similar in all four specimens. The epiproct only shows small variation, which may not be sufficient for taxonomic separation (the inward fold could perhaps be due to sexual dimorphism). The ECNU specimens differ from the holotypes of *B. armis* and *B. yungyenwangae* by the morphology of their subgenital plates and the absence of protarsal pads. The structure of the cerci and paraproctal lobes cannot be determined for either ECNU specimen. *Burmecaelinus armis* differs from *B. yungyenwangae* mainly in the morphology of the paraproctal lobes. Thus, we suggest that ECNU-AM-0079 is perhaps more likely to belong to the genus *Moban* rather than *Burmecaelinus*.

Hu *et al.* (2024) described a structure on the dorsal side of the ECNU specimens as a “scutellum” or posterior process of the pronotum (in relation to the posteriorly extremely elongated pronotum of Tetrigidae Rambur, 1838). However, judging by the same, well visible area in *B. yungyenwangae*, it seems more likely that this structure is part of the forewing instead.

Discussion

In this study, we describe a new species of Burmecaelidae Uchida *et al.*, 2024. The new specimen possesses some characters that are very similar to Tridactyloidea Brullé, 1835 and more specifically Ripterygidae Ander, 1939. These characters include: pro- and mesotarsus two-segmented; metafemur greatly inflated across the entire length; metatibia serrated; metatibia apically with a pair of subapical and apical spurs; paraproctal lobes longer than cerci and with array of apical setae; valvulae of ovipositor barely visible. The only features that separate Burmecaelidae from a placement within Tridactyloidea are the general head morphology and the incompletely sclerotized sternites of the abdomen (fully sclerotized in Tridactyloidea (Heads, 2009)). Here, we explore the implications for the possible taxonomy of Burmecaelidae based on the new findings.

Phylogenetic placement of Burmecaelidae

Despite showing some similarities to Tetrigidae and other taxa found in Acrididea Targioni-Tozzetti, 1882, most characters of Burmecaelidae are shared with the other major group within Caelifera, the Tridactylidea. Tridactylidea includes two superfamilies: Tridactyloidea and the entirely fossil Dzhajloutshelloidea Gorochov, 1994 which houses the Dzhajloutshellidae Gorochov, 1994 from the Triassic of Madygen (Kyrgyzstan) and the Regiatidae Gorochov, 1995 from the Jurassic of Germany and the UK. Dzhajloutshelloidea differs from Tridactyloidea by a more elaborate forewing venation (Gorochov *et al.*, 2006). The density of forewing venation decreased during Tridactylidea evolution. In modern species of Tridactylidae and Ripterygidae only two to four relatively weak longitudinal veins are present (Gorochov *et al.*, 2006). However, there is an entirely fossil subfamily of Tridactylidae—the Mongoloxyna Gorochov, 1992—with an intermediate state regarding wing venation between Dzhajloutshelloidea and Tridactyloidea. Interestingly, the forewing morphology of Mongoloxyna shows striking similarity to that of Burmecaelidae (Fig. 2C–D). Mongoloxyna, unfortunately, are poorly understood due to being mostly known from isolated forewings. Azar & Nel (2008) considered the group to be paraphyletic which, given the similarly dense venation of Burmecaelidae and *Cratodactylus* Martins-Neto, 1990 (Tridactylidae: Tridactylinae), could well be true. Nonetheless, the similarities of Burmecaelidae and Mongoloxyna venation suggests a close relationship of these groups. Hu *et al.* (2024) proposed a position of Burmecaelidae as sister taxon to Tridactyloidea, because the unsclerotized abdominal sternites exclude them from the latter group. If this was true, Tridactylidea could either consist of Burmecaelidae + Dzhajloutshelloidea as a sister clade to Tridactyloidea (Fig. 4, Hypothesis A1) or Burmecaelidae + Tridactyloidea as a sister clade to Dzhajloutshelloidea (Fig. 4, Hypothesis A2). Additionally, we think it is also possible for Burmecaelidae to be included in Tridactyloidea, but at a basal position prior to the split of Cylindrachetidae Giglio-Tos, 1914 (the third lineage of the superfamily with a morphology quite unlike Tridactylidae and Ripterygidae) and Tridactylidae + Ripterygidae (Fig. 4, Hypothesis B1). Under this scenario, the complete sclerotization of the abdominal sternites would have occurred after the last common ancestor of Burmecaelidae and the remainder of Tridactyloidea. Support for this hypothesis is given by the strong resemblance of the paraproctal lobe and ovipositor morphology of *Burmecaelinus yungyenwangae* to early Ripterygidae such as *Magnidactylus gracilis* Gu *et al.*, 2022 and *M. mirus* Gu *et al.*, 2022. Furthermore, it is possible that Burmecaelidae evolved as a sister

group only to Tridactylidae + Ripterygidae, if the abdominal sternites in Burmecaelidae returned to the ancestral state (i.e. not being fully sclerotized) (Fig. 4, Hypothesis B2). At our current state of knowledge, estimates of which of the hypotheses presented is most plausible are difficult. All groups assumed to be closely related to Burmecaelidae (i.e. Dzhajloutshelloidea and Tridactyloidea) are little known taxa themselves. Systematics of Ripterygidae are unresolved (Baena-Bejarano *et al.*, 2015) and Tridactylidae have never been examined in a phylogenetic analysis. No fossils of Cylindrachetidae are known, and hence we are unaware of what the earliest representatives of their lineage might have looked like. Dzhajloutshelloidea are based entirely on isolated forewings, meaning aspects of their body morphology, which are crucial for taxonomic relationships in Tridactylidea are missing.

The question of the taxonomic placement of Burmecaelidae within Caelifera Ander, 1936 will require additional fossils from early members of Burmecaelidae and Tridactylidea. For now, we suggest placement of the family as Tridactylidea *incertae sedis*.

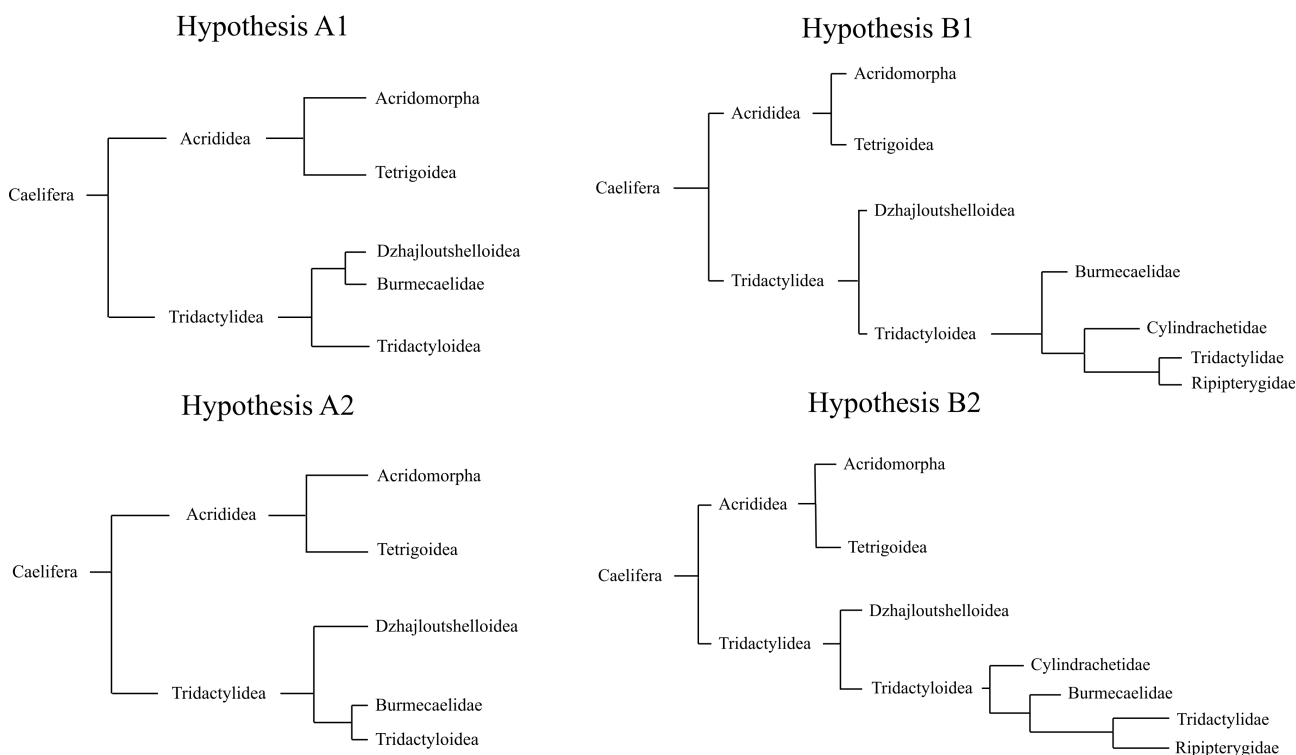


FIGURE 4. Hypotheses for the taxonomic placement of Burmecaelidae Uchida *et al.* (2024). **Hypothesis A1 and A2:** Burmecaelidae are placed in Tridactylidea Brullé, 1835, but outside Tridactyloidea Brullé, 1835 due to their incompletely sclerotized abdominal sternites. Here, they could either be placed as a sister taxon to Dzhajloutshelloidea Gorochoy, 1994 or Tridactyloidea. Given the close likeness of forewing venation between Burmecaelidae and the Tridactylidae Brullé, 1835 subfamily Mongoloxyna Gorochoy, 1992 as well as the older age of Dzhajloutshelloidea (Triassic-Early Jurassic) Hypothesis A2 seems more likely. **Hypothesis B1:** Burmecaelidae are placed inside Tridactyloidea, as a sister taxon to the other three families. In this case, full sclerotization of the abdominal sternites would not have been present in the last common ancestor of Tridactyloidea but occurred after the last common ancestor of Burmecaelidae and Cylindrachetidae + (Ripterygidae + Tridactylidae). **Hypothesis B2:** Burmecaelidae are placed within Tridactyloidea as a sister group only to Tridactylidae and Ripterygidae. This scenario assumes reversal of the evolution of fully sclerotized abdominal sternites to the ancestral state (i. e. not fully sclerotized) in Burmecaelidae. **Note:** Diagrams are made for visualization purposes only. They do not represent dendrograms created by means of a cladistic method. Branch length not to scale (does not represent evolutionary distance).

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