# CONTRIBUTIONS TO ENTOMOLOGY

## **SENCKENBERG**

Research Article

# New genera and species of Ripipterygidae (Orthoptera, Tridactyloidea) from mid-Cretaceous Kachin amber

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https://zoobank.org/510CDD4C-55BA-496A-9457-C0275FC7EBDF

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### **Abstract**

Two new genera and species of Ripipterygidae Ander, 1939 are described from mid-Cretaceous Kachin amber of Northern Myanmar. Ozymandipteryx campana gen. et sp. nov. is remarkable for its absent or very reduced metatarsus. In modern species of Tridactyloidea, a reduced metatarsus can only be found in the Tridactylidae Brullé, 1835 genera Ellipes Scudder, 1902 and Xya Latreille, 1809, but not in Ripipterygidae. Magnidactylus robustus Xu et al., 2020, type species of the genus, is found to share the character of a fully reduced metatarsus (apical spurs were previously misinterpreted as metatarsus), but M. robustus differs from O. campana in several important characters and hence remains a separate genus. However, a new genus Yakkhapipteryx is erected to include the other two former Magnidactylus species M. mirus Gu et al., 2022 (Yakkhapipteryx mirus comb. nov.) and M. gracilis Gu et al., 2022 (Yakkhapipteryx gracilis comb. nov.), which both have a metatarsus in normal condition. Another newly described taxon is Ciconipteryx bidactylus gen. et sp. nov. This species is the first fossil Ripipterygidae with only two dactyls on its protibia, a feature it shares with the modern species Mirhipipteryx pulicaria (Saussure, 1896). Ciconipteryx bidactylus stands out due to its long mid- and hindlegs in relation to its body size. This character may have enabled it to perform very efficient jumps. The new species add to the diversity of Ripipterygidae from Kachin amber, expanding our knowledge of this little studied family and raising new possibilities for interpreting their evolutionary history.

# Key Words

Caelifera, fossil, jumping behavior, mud crickets, pygmy mole crickets, taxonomy

### Introduction

Alongside the more diverse and well-known Acrididea Targioni-Tozzetti, 1882, Tridactylidea Brullé, 1835 is one of the two infraorders of the Caelifera Ander, 1936, the short-horned grasshoppers, which include more than 40% of modern-day orthopteran diversity (Cigliano et al. 2025). However, next to their grasshopper relatives, which are larger, more conspicuous, and generally gain more attention both from science and laypersons alike, the Tridactylidea are a group with

many aspects of their behavior and ecology still poorly understood (Ugolini 2021).

Systematically, Tridactylidea consist of two superfamilies, the Dzhajloutshelloidea Gorochov, 1994 (entirely fossil, 9 species) and the Tridactyloidea Brullé, 1835 (257 species, both extant and fossil). A third taxon, the enigmatic Burmecaelidae Uchida et al., 2024, is currently considered Tridactylidea *incerta sedis* (Schall et al. 2025). Within Tridactyloidea are three families. The Cylindrachetidae Giglio-Tos, 1914 are exclusively found in Argentina, Australia and Papua New Guinea,

and are heavily adapted to an underground lifestyle. Their habitus has become almost worm-like with completely reduced or absent wings and ovipositor and very shortened legs. There is no fossil record of this family as of yet. The other two families are the Tridactylidae Brullé, 1835 and the Ripipterygidae Ander, 1939. In modern representatives, Ripipterygidae can be differentiated from Tridactylidae by 1) their cerci being one-segmented (two-segmented in Tridactylidae), 2) their mesotibiae being of roughly the same width as their mesofemora (in Tridactylidae the mesotibiae are distinctly inflated and wider than the mesofemora), 3) visible valves of the ovipositor (the ovipositor is reduced to the point where it is invisible in Tridactylidae), and 4) paraproctal lobes apically with a distinct array of setae (distinct apical setae not present in Tridactylidae) (Gorochov 2010; Heads 2010; Gu et al. 2022). Tridactylidae have a cosmopolitan distribution (except for Antarctica), whereas Ripipterygidae are only known from South and Central America (Cigliano et al. 2025).

The fossil record of Tridactylidae and Ripipterygidae is not very extensive, but several findings have been made during recent years in Kachin amber from the mid-Cretaceous of Myanmar which has revealed a stunning diversity of these groups (Zhao et al. 2024). Other localities with reported occurrences of fossil Tridactylidae and Ripipterygidae are the Crato Formation of Brazil (Lower Cretaceous) (Martins-Neto 1990), amber from the Dominican Republic (Miocene) (Heads 2010; Poinar 2018), France (Eocene) (Azar and Nel 2008), Great Britain (Lower Cretaceous) (Gorochov et al. 2006), Russia (Lower Cretaceous) (Gorochov in Kopylov et al. 2020; Sharov 1968) and Mongolia (Lower Cretaceous) (Gorochov 1992) (for a comprehensive table of the known fossil record of Tridactyloidea see Zhao et al. 2024). The Tridactyloidea found in amber from Myanmar are especially important for understanding the evolution of the superfamily, because they are very diverse (ca. 50% of fossil Tridactyloidea have been found in Kachin amber) and are often preserved with almost life-like detail.

In this study, we describe three new genera and two new species of Ripipterygidae from mid-Cretaceous Kachin amber. Both exhibit an intriguing combination of characters which provide important insights into the evolutionary history that led to the distinct modern clades Ripipterygidae and Tridactylidae.

### Materials and methods

The amber pieces presented in this study are housed in the collection of the Leibniz Institute for the Analysis of Biodiversity Change (Hamburg) (collection numbers GPIH07209 and GPIH07210). They originate from Myanmar and were discovered at a mining site either near Tanai village or Hkamti village. The age of the two amber sites differs by ca. 10 my.; amber from Tanai is estimated

to be  $98.79 \pm 0.62$  My old (Shi et al. 2012), whereas amber from Hkamti is ca. 110 My old (Xing and Qiu 2020). Tragically, political instability and enforcement of human rights continue to be problematic in Myanmar. Unfortunately, we do not know the year the amber pieces in this study were originally obtained, i. e. pre- or post-2017. However, after considering the local situation in Myanmar as described in Peretti (2020) and Peretti (2021), we think that stopping scientific amber research (as demanded by Engel (2020)) is unjustified.

Imaging of the specimens was conducted using a DUN. Inc. stacking system with a Canon EOS 5Dsr Camera. We used a 65 mm lens and a magnification of 2.5×. Individual pictures were taken with VD Passport and Capture One program (Capture One A/S, Denmark) and stacked with Zerene Stacker (Zerene Systems LLC, Washington, USA). They were edited with Photoshop CS6 Extended application by Adobe Inc. (USA; https://www.adobe.com). Further modifications (e. g. scale-bars) and creation of image collections were done in Inkscape (v. 1.3.2) (the INKSCAPE Team 2025). Drawings were created in GIMP (v. 2.10.30) (the GIMP Team 2025).

The jitter plot featured in the comparison of leg lengths of Tridactyloidea Brullé, 1835 species in the discussion was created with PAST5 (Hammer et al. 2001) and Inkscape.

The taxonomy in this study follows the Orthoptera Species File (OSF) (https://orthoptera.speciesfile.org/, Cigliano et al. 2025).

# Systematic paleontology

Order Orthoptera Olivier, 1789 Suborder Caelifera Ander, 1936 Infraorder Tridactylidea Brullé, 1835 Superfamily Tridactyloidea Brullé, 1835 Family Ripipterygidae Ander, 1939

Genus Ozymandipteryx gen. nov.

https://zoobank.org/A66BF25D-834A-4457-97B9-6419485A66E8

Type species. Ozymandipteryx campana sp. nov.

**Etymology.** Named after Ozymandias, a poem by Percy Bysshe Shelley (1818) about the loss of greatness and forgetting of glory by the passing of time. It refers to the state of absent/very reduced metatarsi in the genus, which can be found in the modern-day Tridactylidae genera *Ellipes* Scudder, 1902 and *Xya* Latreille, 1809, but is not present in any extant Ripipterygidae.

**Diagnosis.** Absence or almost complete reduction of the metatarsus. Protibiae without dactyls. Mesotibiae not inflated. Cerci one-segmented, cylindrical, with long hairs. Forewing and hindwing present. Metafemur with two small apical protrusions. Dorsal metatibial ridge distally with slight serration. Apical spurs of metatibia much longer (4×) than subapical spurs.

#### Ozymandipteryx campana sp. nov.

https://zoobank.org/49DE4348-1B1C-4B44-B2FC-9087CACB8272 Figs 1, 2

**Etymology.** The species' name is Latin for "bell". It is meant to refer to the "Great Bell of Dhammazedi", a treasure lost in time.

**Locality and horizon.** The specimen was included in amber found in Hkamti, Sagaing Division, Myanmar or Tanai, Kachin State Burma, Myanmar, two nearby amber mining locations. The amber from Hkamti is ca. 110 My and the amber from Tanai is ca. 99 My old.

**Holotype.** Sex unknown. Specimen part of the LIB-Hamburg collection; collection number GPIH07209 (ex collection Martin Husemann MH0082).

Diagnosis of species. As for genus (monotypic).

**Description.** Preservation of complete specimen, unfortunately with some parts obscured by structural damage inside the amber.

*Measurements*: Some measurements could not be precisely made, because the corresponding feature was somewhat obscured. Such measurements are indicated with a "ca.". Body length ca. 1.72–1.76 mm (head to abdominal apex). Forewing length ca. 0.72 mm. Hindwing length ca. 1.26 mm. Head height ca. 0.5 mm. Mesofemur length 0.89 mm. Mesotibia length 0.72 mm.

Mesofemur width/mesotibia width 1.18 (both at max. width). Pronotum length (dorsal) 0.42 mm. Metafemur length 1.18 mm, width 0.54 mm. Metatibia length 1.17 mm, width 0.09 mm. Length of subapical spurs 0.08 mm and of apical spurs 0.32 mm. Cercus length ca. 0.24 mm.

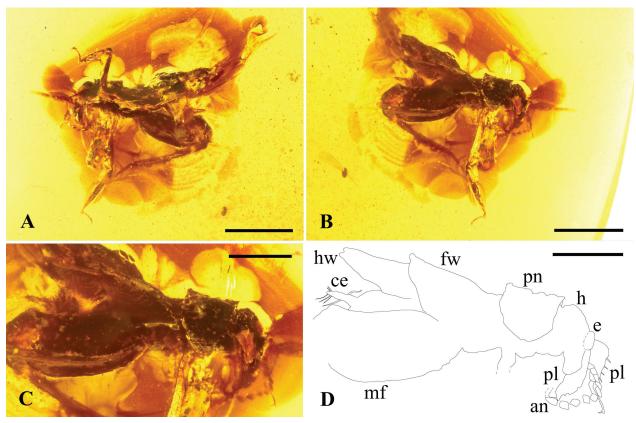
*Head*: Antennae 10-segmented (including scape and pedicel). 10<sup>th</sup> antennomere larger than previous and bean shaped. Compound eyes protruding from head. Ocelli not visible.

**Thorax:** Pronotum not prolonged over abdomen, with elevation from thorax. Both forewings and hindwings present. Hindwings not prolonged over abdomen.

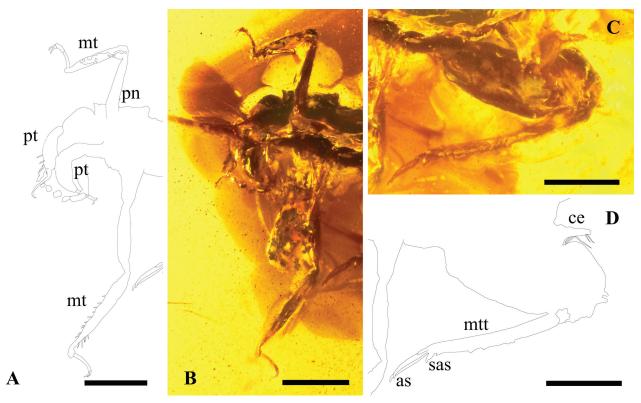
**Legs:** Prothoracic leg: Tibia inflated. Dorsal margin with four evenly spaced hairs. No dactyls present. Tarsus very slender, with two claws.

Mesothoracic leg: Femur without hair or appendages. Tibia not inflated, with hairs on ventral margin along the entire length and also on dorsal margin towards apex. Tarsus two-segmented, bearing two claws.

Metathoracic leg: Femur greatly inflated along its entire length. Two small protrusions apically. Dorsal tibial ridge distally with slight serration proximal to subapical spurs. Two subapical and two apical spurs present. Apical spurs much longer than subapical spurs. Metatarsus not visible, either absent or too vestigial to be seen.



**Figure 1.** Ozymandipteryx campana gen. et sp. nov. holotype (sex unknown), collection number GPIH07209. **A.** Specimen, left; **B.** Specimen, right; **C, D.** Detail of body excluding legs as image and schematic drawing. **Abbreviations:** hw = hindwing; ce = cercus; fw = forewing; pn = pronotum; h = head; e = compound eye; pl = prothoracic leg; an = antenna; mf = metafemur. Scale bars:  $1 \text{ mm } (\mathbf{A}, \mathbf{B})$ ;  $0.5 \text{ mm } (\mathbf{C}, \mathbf{D})$ .



**Figure 2.** *Ozymandipteryx campana* gen. et sp. nov. holotype (sex unknown), collection number GPIH07209. **A, B.** Detail of head, prothoracic- and mesothoracic legs as image and schematic drawing. **Abbreviations:** pt = protibia; mt = mesotibia; pn = pronotum; **C, D.** Detail of metathoracic leg and cercus as image and schematic drawing. **Abbreviations:** as = apical spurs; sas = subapical spurs; mtt = metatibia; ce = cercus. Scale bars: 0.5 mm.

**Abdomen:** Only one cercus visible, one-segmented and cylindrical in shape. Setulose with long hair.

Remarks. The new species can be assigned to the Ripipterygidae based on the following characters: 1) Cercus one-segmented and 2) mesotibiae not inflated. In this family, it differs from the other members found in Kachin amber by an absent or very vestigial metatarsus, a protibia without dactyls and two small protrusions on the apex of its metafemur. The protibia without dactyls is a character the new species shares with some members of fossil Tridactylidae: *Burmadactylus grimaldii* Heads, 2009, *Paraxya hui* Cao et al., 2019 and *Ellipes dominicana* Poinar, 2020. Likewise, a vestigial metatarsus is also present in some extant Tridactylidae, namely the genera *Ellipes* Scudder, 1902 and *Xya* Latreille, 1809 (Günther 1977; Heads 2010).

Based on our current understanding of Tridactyloidea morphology, the presence of characters only known from Tridactylidae among the extant fauna in a fossil specimen that should be placed in Ripipterygidae, suggests four possible conclusions: 1) Our understanding of Tridactyloidea morphology is not complete. 2) A fully reduced metatarsus and protibia without dactyls were present for some time in the ancestors of modern Ripipterygidae, but this lineage was subsequently lost. 3) *Ozymandipteryx* does not actually belong to the Ripipterygidae but is instead a member of a stem-group Tridactyloidea occurring prior to the split of Tridactylidae and Ripipterygidae. 4) *Ozymandipteryx* is part of a separate lineage of

Tridactyloidea not yet described. If one of the last two hypotheses is true, attribution of fossil Tridactyloidea from the Cretaceous may have to be reconsidered; however, this can only be validated by future findings.

Interestingly, O. campana is not the first fossil species with a fully reduced metatarsus. In the description of Magnidactylus robustus Xu et al., 2020, the apical spurs of the specimen were interpreted as the metatarsus. But in fact, the metatarsus appears to be absent in M. robustus just like in O. campana. This finding may suggest a closer phylogenetic relationship between the two species. However, M. robustus differs from O. campana by the presence of four dactyls on its protibia, no hairs on the cerci and no apical protrusions on the metafemur. Further, M. robustus is more than three times the size of O. campana (Xu et al., 2020). With this re-interpretation of the morphology of M. robustus, the species does not belong to the same genus as Magnidactylus mirus Gu et al., 2022 and M. gracilis Gu et al., 2022, which both possess a normal (for Tridactyloidea) metatarsus. We propose Yakkhapipteryx gen nov. as a new genus to house M. mirus and M. gracilis.

### Genus Yakkhapipteryx gen. nov.

https://zoobank.org/CB55611A-D029-4FB1-A374-7154C54C006B

**Type species.** *Yakkhapipteryx mirus* comb. nov. (Gu et al., 2022)

**Included species.** *Yakkhapipteryx mirus* comb. nov., *Y. gracilis* comb. nov. (Gu et al., 2022)

**Etymology.** Named after the Yakkha (Sanskrit: Yaksha), guardians of buried treasures (in reference to amber) from Burmese mythology.

**Diagnosis.** As provided by Gu et al. (2022) for *Magnidactylus*, which the authors based on the specimens now assigned to *Yakkhapipteryx*.

#### Genus Ciconipteryx gen. nov.

https://zoobank.org/984DDC59-027C-466D-8AF0-7C2A8758B3C4

**Type species.** Ciconipteryx bidactylus sp. nov.

**Etymology.** The new genus is named after its long legs. Ciconi- is derived from the bird family Ciconiidae, the storks.

**Diagnosis.** Very small body. Interocular distance larger than width of compound eye. Protibia with two dactyls. Mesothoracic leg longer than body (head to abdominal apex) and very slender along entire length (femur and tibia not much wider than tarsus). Metafemur as long as body. Forewings present, four to five veins visible. Cercus somewhat longer than paraproctal lobes. Both structures setulose; setae more prominent on paraproctal lobes. Valves of ovipositor visible, much shorter than paraproctal lobes.

#### Ciconipteryx bidactylus sp. nov.

 $https://zoobank.org/209312AD-9098-4290-A0F6-ED5A0D9D2814\\ Figs~3-6$ 

**Etymology.** The species' name refers to the protibia with (only) two dactyls.

**Locality and horizon.** The specimen was included in amber found in Hkamti, Sagaing Division, Myanmar or Tanai, Kachin State Burma, Myanmar, two nearby amber mining locations. The amber from Hkamti is ca. 110 My and the amber from Tanai ca. 99 My old.

**Holotype.** Female. Specimen part of the LIB-Hamburg collection, collection number GPIH07210 (ex collection Martin Husemann MH0093).

Diagnosis of species. As for genus (monotypic).

**Description.** The specimen is relatively well preserved, but unfortunately the apical region of the metatibia and the metatarsus are missing.

*Measurements*: Body length (head to abdominal apex) 1.4 mm. Head height 0.6 mm. Eye height 0.21 mm, width 0.11 mm. Interocular distance (mid-eye level) ca. 0.2 mm. Protibia 0.24 mm long. Longest dactyl 0.05 mm long. Mesofemur 0.67 mm long. Mesotibia 0.59 mm long. Mesotarsus 0.27 mm long. Metafemur 1.4 mm. Cercus 0.12 mm long. Paraproctal lobes 0.1 mm long.

*Head*: Antennae not preserved. Interocular distance wider than compound eye width. Eyes somewhat tearshaped, laterally protruding from head. Ocelli not visible.

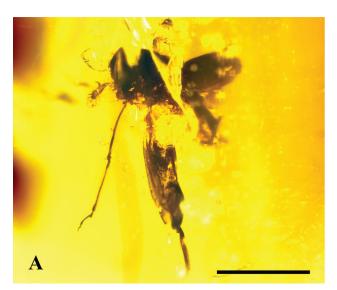
**Thorax:** Pronotum with posterior margin straight (not rounded or pointed), covering base of forewings. Pronotum without elevation. Forewings present with four or five simple veins visible. Hindwings present, shorter than abdomen.

**Legs:** Prothoracic leg: Femur and tibia setulose with long hairs. Tibia only slightly inflated with two relatively long dactyls. Tarsus with two claws.

Mesothoracic leg: Very long and slender along entire length. Femur inconspicuous. Tibia not inflated. With 8–11 fine spines on the ventral margin of the distal half and five hairs subapically on the dorsal side. Tarsus two-segmented with first segment much shorter than second. Bulbous apical lobe on first tarsal segment. Second tarsal segment with two claws.

Metathoracic leg: Femur long and inflated along its entire length. Only ca. proximal third of metatibia preserved.

**Abdomen:** Cercus one-segmented, cylindrical in shape with some hairs. Paraproctal lobes one-segmented, sligthly clavate and slightly shorter than cercus; setulose with long hair, especially apically. From a dorsal view apices of ovipositor valves just visible between paraproctal lobes.



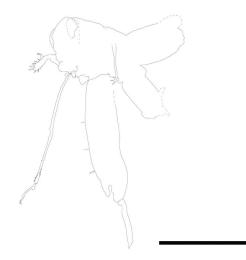
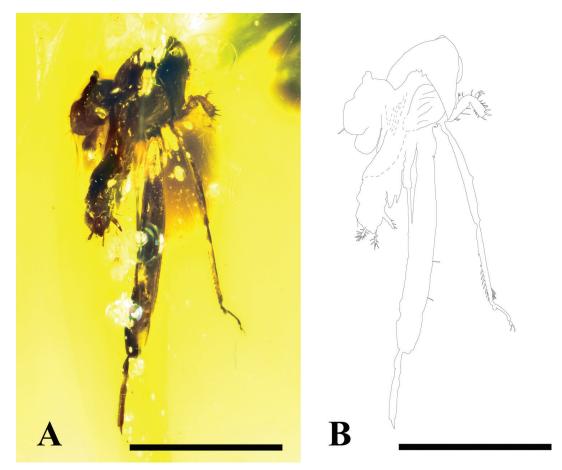
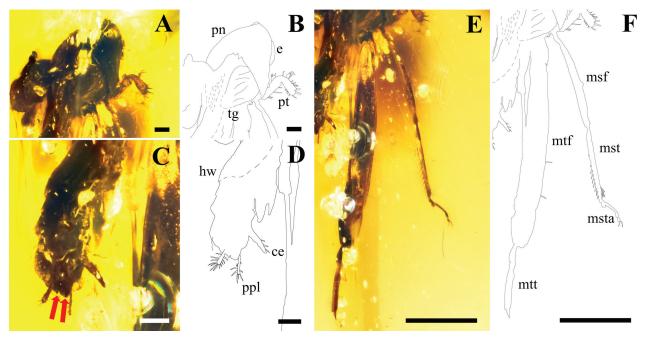


Figure 3. Ciconipteryx bidactylus gen. et sp. nov. holotype female, collection number GPIH07210. A, B. Specimen in frontal view. Scale bars: 1 mm.

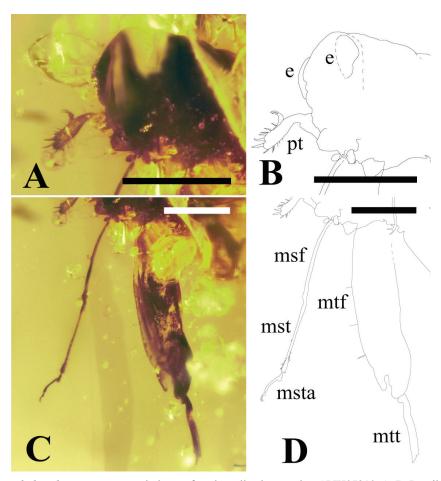
B



**Figure 4.** *Ciconipteryx bidactylus* gen. et sp. nov. holotype female, collection number GPIH07210. **A, B.** Specimen in dorsal view. Scale bars: 1 mm.



**Figure 5.** *Ciconipteryx bidactylus* gen. et sp. nov. holotype female, collection number GPIH07210. **A, B.** Detail of head region in dorsal view as image and schematic drawing. **Abbreviations:** pn = pronotum; tg = tegmen; e = eye; pt = prothoracic leg; **C, D.** Detail of abdominal region in dorsal view as image and schematic drawing. Red arrows in C mark valves of ovipositor just visible between paraproctal lobes. **Abbreviations:** hw = hindwing; ppl = paraproctal lobe; ce = cercus; **E, F.** Detail of meso- and metathoracic leg in dorsal view as image and schematic drawing. **Abbreviations:** mtt = metatibia; mtf = metafemur; msf = mesofemur; mst = mesotibia; msta = mesotarsus. Scale bars: 0.1 mm (**A–D**); 0.5 mm (**E, F**).



**Figure 6.** *Ciconipteryx bidactylus* gen. et sp. nov. holotype female, collection number GPIH07210. **A, B.** Detail of head and prothoracic leg in frontal view as image and schematic drawing. **Abbreviations:** e = compound eye; pt = prothoracic leg; **C, D.** Detail of meso- and metathoracic leg in frontal view as image and schematic drawing. **Abbreviations:** msf = mesofemur; mst = mesotibia; msta = mesotarsus; mtf = metafemur; mtt = metatibia. Scale bars: 0.5 mm.

Remarks. Ciconipteryx bidactylus gen. et sp. nov. is assigned to Ripipterygidae based on the following characters: 1) Cercus one-segmented. 2) Mesotibiae not inflated. 3) Ovipositor visible. 4) Paraproctal lobes with distinct array of setae. It differs from previously described genera of Kachin amber Ripipterygidae by its two dactyls on the protibia (in other species from this locality and horizon there are either four dactyls or 0, as in Ozymandipteryx campana gen. et sp. nov.) and the markedly longer mesothoracic leg and metafemur which are longer or just as long as the body, respectively. The two dactyls on the protibia represent a character shared between Ciconipteryx and some species of the fossil as well as extant genus Mirhipipteryx Günther, 1969. While certain species of this genus, such as M. antillarum Heads, 2010, are reported to have three protibial dactyls (Heads 2010), some modern species such as M. pulicaria (Saussure, 1896) are said to have only two (Baena-Bejarano et al. 2018), as in C. bidactylus. However, Ciconipteryx can be differentiated from Mirhipipteryx by its proportionally longer legs (in M. pulicaria the mesothoracic leg length is only ca. 60% of the total body length) and its interocular distance between the compound eyes, which is wider than the compound eye width in Ciconipteryx,

but significantly shorter in *Mirhipipteryx* (Heads 2010; Baena-Bejarano 2018). Species of the other extant Ripipterygidae genus, *Ripipteryx* Newman, 1834, are much larger than *Ciconipteryx* and *Mirhipipteryx* (Heads 2010).

### Discussion

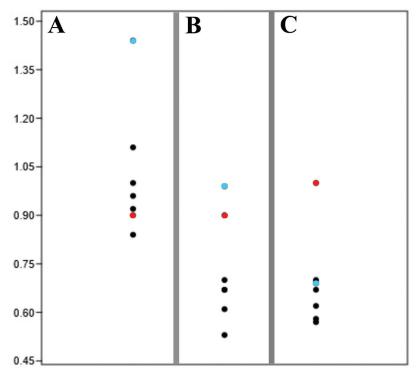
In this study, we described two new members of Ripipterygidae Ander, 1939 from mid-Cretaceous Kachin amber from Myanmar, Ozymandipteryx campana gen. et sp. nov. and Ciconipteryx bidactylus gen. et sp. nov. Both taxa stand out from previously described fossil ripipterygids as well as extant representatives due to their unique combination of morphological characters. These findings have intriguing implications for the diversity and evolution of Ripipterygidae and also Tridactyloidea Brullé, 1835. Numerous findings during recent years (Xu et al. 2020a, 2020b; Gu et al. 2022; Zhu et al. 2023; Zhao et al. 2023, 2024) strongly suggest that the diversity of ripipterygids was high in the Myanmar amber forest. Not only were numerous species present, these taxa also show a surprising variation of characters, many of which cannot be found in modern members of the family, but

are present in members of the sister family Tridactylidae Brullé, 1835. These include the presence of a vestigial metatarsus (fossil: *O. campana, Magnidactylus robustus* Xu et al., 2020 – Ripipterygidae; extant: *Xya* Latreille, 1809, *Ellipes* Scudder, 1902 – Tridactylidae), the inflation of the mesotibia (fossil *Kallosripipteryx zhangi* Zhao et al., 2024 – Ripipterygidae; extant: Tridactylidae (an inflated mesotibia is diagnostic of all modern tridactylids) and the presence of a subapical denticular process of the metatarsus, which can be found in fossil members of Ripipterygidae (e. g. Gu et al. 2022; Zhao et al. 2023) and Tridactylidae (Heads 2009; Fan et al. 2023), but is exclusively present in the latter family in the extant fauna.

The presence of several characters in fossil Ripipterygidae that were previously considered to be diagnostic of certain groups within Tridactylidae (or in the case of an inflated mesotibia for Tridactylidae as a whole) presents both a problem and an opportunity for resolving

phylogenetic relationships within both families. Ideally, attempts towards this endeavor should either be based on molecular data (which cannot be fooled by the conflicting presence/absence of certain morphological characters in fossil vs. extant forms) or, better still, should incorporate as much of the fossil diversity of pygmy mole crickets and mud crickets as possible.

An aspect of morphology that is not known from any extant or fossil form and, therefore, currently completely unique, is the disproportionate relationship of mid- and hindleg length compared to body length of *Ciconipteryx bidactylus* gen. et sp. nov. Noticeably, it is not the legs itself that are unusually long in the new species, but rather the body seems to be strangely short in relation to them (Table 1, Fig. 7). The extant species *Ripipteryx guacharoensis* Baena-Bejarano & Heads, 2015 shares the character of extensively long mesothoracic legs in relation to body length, but the species has normal-sized metafem-



**Figure 7.** Data from Table 1 as jitter plot. **A.** Mesothoracic leg/metafemur length; **B.** Mesothoracic leg/body length; **C.** Metafemur/body length. *Ciconipteryx bidactylus* gen. et sp. nov. marked by red dots. *Ripipteryx guacharoensis* Baena-Bejarano & Heads, 2015 marked by blue dots.

**Table 1.** Some length ratios of Tridactyloidea Brullé, 1835. For the mesothoracic leg only the length of the mesofemur and mesotibia was combined for each species, as other parts were sometimes difficult to observe.

Family	Species	Mesothoracic leg/ metafemur length	Mesothoracic leg/body length	Metafemur/ body length	Reference
Ripipterygidae Ander, 1939	Kallosripipteryx zhangi Zhao et al., 2024	0.96	0.67	0.7	Zhao et al. 2024
	Ripipteryx gorgonaensis Baena-Bejarano & Heads, 2015	1.11	0.7	0.62	Baena-Bejarano and Heads 2015
	<i>Ripipteryx guacharoensis</i> Baena-Bejarano & Heads, 2015	1.44	0.99	0.69	Baena-Bejarano and Heads 2015
	Mirhipipteryx pulicaria (Saussure, 1896)	0.92	0.53	0.58	Baena-Bejarano et al. 2018
	Ciconipteryx bidactylus gen. et sp. nov.	0.9	0.9	1	herein
Tridactylidae Brullé, 1835	Xya sichuanensis Cao et al., 2018	0.84	0.61	0.57	Zhang et al. 2022
	Burmadactylus tenuicerci Fan et al., 2023	1	0.67	0.67	Fan et al. 2023

ora in comparison to the over proportionate metafemora of *C. bidactylus*. Tridactyloidea are generally thought to exhibit a four-legged walking behaviour, whereby they use only their fore- and mid-legs and the hind legs are kept completely off the ground (Zhang et al. 2022). To compensate for the posteriorly shifted center of gravity due to their heavy hindlegs, tridactylids use the abdomen as a fifth fulcrum for support during walking (Zhang et al. 2022). Perhaps the proportionally long mid-legs and shorter abdomen allowed *C. bidactylus* to walk without dragging the abdomen, as the center of gravity was shifted anteriorly. This may have led to an increase in mobility.

The hindlegs and strong femora of tridactylids enable them to be among the most efficient jumpers within Orthoptera and the insect world (Burrows and Picker 2010). Because they serve no function in walking, it is likely that they evolved to be specialized for jumping (Zhang et al. 2022). As the metafemora of *C. bidactylus* are the largest currently known for any tridactyloid, it is possible that this species may have been the best jumper of the taxon.

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# References

- Ander K (1936) Orthoptera Saltatorias fylogeni pa grundval av amforande anatomiska studier. In: Kemner NA (Ed.) Det femte Nordiska Entomologmetet i Lund 3–6 augusti 1936. Opuscula Entomologica. Edidit Societas Entomologica Lundensis 1: 93–94.
- Ander K (1939) Vergleichend-anatomische und phylogenetische Studien über die Ensifera (Saltatoria). Opuscula Entomologica. Edidit Societas Entomologica Lundensis, 2(Suppl.), 306 pp. [172 figs]
- Azar D, Nel A (2008) First Tridactylidae from the Eocene French amber (Insecta: Orthoptera). Alavesia 2: 169–175.
- Baena-Bejarano N, Heads SW (2015) Three new species of the genus *Ripipteryx* from Colombia (Orthoptera, Ripipterygidae). ZooKeys 502: 129–143. https://doi.org/10.3897/zookeys.502.8871
- Baena-Bejarano N, Heads SW, Taylor SJ (2018) Comments on the neglected nymphs of mud crickets in the genus *Mirhipipteryx* (Caelifera: Tridactyloidea: Ripipterygidae). Zootaxa 4486(2): 180–188. https://doi.org/10.11646/zootaxa.4486.2.7
- Brullé GA (1835) Cinquième Ordre. Orthoptères. In: Histoire naturelle des insectes: Vol. 9 [1] (5). Société bibliophile, Paris, 1–225. [225–416 in 1836]

- Burrows M, Picker MD (2010) Jumping mechanisms and performance of pygmy mole crickets (Orthoptera, Tridactylidae). Journal of Experimental Biology 213(14): 2386–2398. https://doi.org/10.1242/jeb.042192
- Cao CQ, Shi JP, Yin Z (2018) A new species of the genus *Xya* Latreille, 1809 from China (Orthoptra, Tridctyloidea, Tridactylidae). Zootaxa, 4413(2): 397–400. https://doi.org/10.11646/zootaxa.4413.2.13
- Cao CQ, Chen SZ, Yin Z (2019) A new genus and a new species of pygmy mole cricket in Cretaceous amber from Burma (Orthoptera: Tridactylidae). Zootaxa 4559(1): 193–195. https://doi.org/10.11646/ zootaxa.4559.1.12
- Cigliano MM, Braun H, Eades DC, Otte D (2025) Orthoptera Species File [12.05.2025] http://orthoptera.speciesfile.org/
- de Saussure H (1896) Orthoptera. Fam. Gryllidae. Biologia Centrali-Americana, 1, 201–216.
- Deyrup MA (2005) A new species of flightless pygmy mole cricket from a Florida sand ridge (Orthoptera: Tridactylidae). The Florida Entomologist 88(2): 141–145. https://doi.org/10.1653/0015-4040(2005) 088[0141:ANSOFP]2.0.CO;2
- Engel MS (2020) Myanmar: palaeontologists must stop buying conflict amber. Nature 584(7822): 525–526. https://doi.org/10.1038/d41586-020-02432-z
- Fan SL, Gu JJ, Cao CQ (2023) A new species of the genus *Burmadactylus* Heads, 2009 from mid-Cretaceous amber in north Myanmar (Orthoptera: Caelifera: Tridactyloidea). Zootaxa 5306(5): 595–598. https://doi.org/10.11646/zootaxa.5306.5.7
- Giglio-Tos E (1914) Sulla posizione sistematica del gen. *Cylindracheta*Kirby. Annali del Museo Civico di Storia Naturale di Genova 46:
  81–101. https://doi.org/10.5962/bhl.part.14781
- The GIMP Team (2025) GIMP v. 2.10.30. https://www.gimp.org/
- Gorochov AV (1992) New fossil Orthoptera and Phasmoptera from the Mesozoic and Cainozoic of Mongolia [in: New taxa of fossil invertebrates from Mongolia]. Trudy - Sovmestnaya Sovetsko-Mongol'skaya Paleontologicheskaya Ekspeditsiya [Transaction - Joint Russian-Mongolian Paleontological Expedition] 41: 117–121.
- Gorochov AV (1994) New data on Triassic Orthoptera from Middle Asia. Zoosystematica Rossica 3(1): 53–54. [illustr]
- Gorochov AV, Jarzembowski EA, Coram RA (2006) Grasshoppers and crickets (Insecta: Orthoptera) from the Lower Cretaceous of southern England. Cretaceous Research 27(5): 641–662. https://doi. org/10.1016/j.cretres.2006.03.007
- Gorochov AV (2010) New and little-known orthopteroid insects (Polyneoptera) from fossil resins: Communication 4. Paleontological Journal 44: 657–671. https://doi.org/10.1134/S0031030110060080
- Gu JJ, Zheng CJ, Ren D, Cao CQ, Yue YL (2022) Two new species of Ripipterygidae (Orthoptera, Tridactyloidea) from Mid-Cretaceous of Myanmar with a key to the genera of Tridactyloidea in amber. Insects 13(11): 979. https://doi.org/10.3390/insects13110979
- Günther KK (1969) Revision der Familie Rhipipterygidae Chopard, 1949 (Saltatoria, Insecta). Mitteilungen aus dem Zoologischen Museum in Berlin 45(2): 259–425. https://doi.org/10.1002/mmnz.19690450209
- Günther KK (1977) Revision der Gattung *Ellipes* Scudder, 1902. Deutsche Entomologische Zeitschrift 24(1–3): 47–122. https://doi.org/10.1002/mmnd.4800240104
- Hammer Ø, Harper DAT, Ryan PD (2001) PAST: Paleontological statistics software package for education and data analysis. Palaeontologia electronica 4(1): 1. http://palaeo-electronica.org/2001\_1/past/issue1 01.htm

- Heads SW (2009) A new pygmy mole cricket in cretaceous amber from Burma (Orthoptera: Tridactylidae). Denisia 26: 75–82.
- Heads SW (2010) New Tridactyloidea in Miocene amber from the Dominican Republic (Orthoptera: Caelifera). Annales de la Société Entomologique de France 46(1–2): 204–210. https://doi.org/10.1080/00379271.2010.10697659
- The INKSCAPE-Team (2025) Inkscape v. 1.3.2. https://inkscape.org/de/Kopylov DS, Rasnitsyn AP, Aristov DS, Bashkuev AS, Bazhenova NV, Dmitriev VY, Gorochov AV, Ignatov MS, Ivanov VD, Khramov AV, Legalov AA, Lukashevich ED, Mamontov YS, Melnitsky SI, Ogłaza B, Ponomarenko AG, Prokin AA, Ryzhkova OV, Shmakov AS, Sinitshenkova ND, Solodovnikov AY, Strelnikova OD, Sukacheva ID, Uliakhin AV, Vasilenko DV, Wegierek P, Yan EV, Zmarzły M (2020) The Khasurty fossil insect lagerstätte. Paleontological Journal 54: 1221–1394. https://doi.org/10.1134/S0031030120110027
- Latreille PA (1809) Histoire Naturelle, genérale et particuliere, des Crustacés et des Insectes, 4.
- Martins-Neto RG (1990) Um novo genero e duas novas especies de Tridactylidae (Insecta, Orthopteridea) na Formacao Santana (Cretaceo Interior do nordeste do Brasil). Anais da Academia Brasileira de Ciências 62(1): 51–59.
- Newman E (1834) Entomological Notes. Entomological Magazine, 2, 200–205. [pl. 7, fig. 1]
- Olivier AG (1789) Encyclopedie methodique, dictionnaire des insectes, Vol. 4. Paris: Pankouke, 373, 331.
- Peretti A (2020) Ethical guidelines for Burmese amber acquisitions. Journal of Applied Ethical Mining of Natural Resources and Paleontology 1(2020): 4–78. www.pmf.org/journal
- Peretti A (2021) An alternative perspective for acquisitions of amber from Myanmar including recommendations of the United Nations Human Rights Council. Journal of International Humanitarian Action 6(1): 12. https://doi.org/10.1186/s41018-021-00101-y
- Poinar Jr GO (2018) Pygmy mole crickets (Orthoptera: Tridactylidae) in Dominican and Burmese amber. Historical Biology 32(2): 238–243. https://doi.org/10.1080/08912963.2018.1483362
- Schall OKO, Cumming R, Lian Z, Husemann M (2025) A new species of Burmecaelidae (Orthoptera: Caelifera) sheds light on the family's possible taxonomic placement. Zootaxa 5636(1): 174–182. https:// doi.org/10.11646/zootaxa.5636.1.8
- Scudder SH (1902) On the United States Orthoptera which have been referred to the genus *Tridactylus*. Psyche, a Journal of Entomology, 9(310): 308–310. https://doi.org/10.1155/1902/519583
- Sharov AG (1968) Filogniya orthopteroidnykh nasekomykh [1971 English translation: Phylogeny of the Orthopteroidea]. Trudy Paleontologicheskogo Instituta, Akademiia Nauk SSSR [= Transactions of the Institute of Paleontology, USSR Academy of Sciences] 118: 1–216.
- Shi G, Grimaldi DA, Harlow GE, Wang J, Wang J, Yang MC, Lei W, Li Q, Li XH (2012) Age constraint on Burmese amber based on U–Pb

- dating of zircons. Cretaceous Research 37: 155–163. https://doi.org/10.1016/j.cretres.2012.03.014
- Targioni-Tozzetti A (1882) In Ortotteri agrari cioè dei diversi insetti dell'ordine degli ortotteri nocivi o vantaggiosi all'agricoltura o all'economia domestica e principalmente delle cavallette. Annali di Agricoltura, Firenze, Bencini, 238 pp. [68 figs]
- Uchida K, Husemann M, Kotthoff U (2024) A new Cretaceous orthopteran family of the Caelifera (order: Orthoptera) from Burmese amber of northern Myanmar. Paläontologische Zeitschrift 98(1): 117–125. https://doi.org/10.1007/s12542-023-00670-w
- Ugolini A (2021) Notes on feeding, locomotor activity rhythms and orientation in the pygmy mole cricket Afrotridactylus cf. usambaricus in Kenya (Orthoptera: Tridactyloidea). European Journal of Entomology 118: 210–213. https://doi.org/10.14411/eje.2021.022
- Woo B (2021) A new species of pygmy mole cricket (Orthoptera: Tridactylidae) from the Lake Wales ridge of Florida and new records of *Ellipes eisneri* from the northern Brooksville ridge. Journal of Orthoptera Research 30(2): 131–143. https://doi.org/10.3897/ior.30.65603
- Xing L, Qiu L (2020) Zircon UPb age constraints on the mid-Cretaceous Hkamti amber biota in northern Myanmar. Palaeogeography, Palaeoclimatology, Palaeoecology 558: 109960. https://doi.org/10.1016/j.palaeo.2020.109960
- Xu CP, Zhang H, Jarzembowski EA, Fang Y (2020a) The first Ripipterygidae (Orthoptera: Caelifera: Tridactyloidea) from mid-Cretaceous Burmese amber. Cretaceous Research 112: 104356. https://doi.org/10.1016/j.cretres.2019.104356
- Xu CP, Fang Y, Jarzembowski EA (2020b) A new pygmy mole cricket (Orthoptera: Tridactyloidea: Tridactylidae) from mid-Cretaceous Burmese amber. Cretaceous Research 111: 104371. https://doi.org/10.1016/j.cretres.2020.104371
- Zhang Y, Wang SY, Feng ZJ, Liu TX, Cao CQ (2022) The physiological, structural, and behavioral adaptations of the "fore-mid" four-legged walking of the pygmy mole cricket *Xya sichuanensis* (Orthoptera: Tridactylidae). Applied Entomology and Zoology 57(2): 161–170. https://doi.org/10.1007/s13355-022-00775-9
- Zhao JY, Xu CP, Jarzembowski EA, Fang Y, XIao CT (2023) A new genus and species of Ripipterygidae (Orthoptera: Tridactyloidea) from mid-Cretaceous Kachin amber, northern Myanmar. Cretaceous Research 144: 1–6. https://doi.org/10.1016/j.cretres.2022.105429
- Zhao JY, Xu CP, Cao CQ, Jarzembowski EA, Fang Y, Xiao CT (2024) A new genus and species of mud cricket (Orthoptera: Ripipterygidae) from mid-Cretaceous Kachin amber of northern Myanmar. Cretaceous Research 160: 105880. https://doi.org/10.1016/j.cretres.2024.105880
- Zhu XP, Li Q, Xu CP, Jarzembowski EA, Fang Y, Zhang L (2023) A new mud cricket species (Insecta: Orthoptera: Tridactyloidea: Ripipterygidae) from mid Cretaceous Kachin amber in north Myanmar. Palaeontographica. Beitraege zur Naturgeschichte der Vorzeit 327(1–3): 45–54. https://doi.org/10.1127/pala/2023/0141