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New species of Tridactyloidea (Orthoptera, Caelifera) from mid-Cretaceous Burmese amber show an intermediate evolutionary state between extant lineages

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https://zoobank.org/A2AB47B6-4F23-4FA8-A8C5-0E12327540D7

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Abstract

Two new genera and species of Tridactyloidea Brullé, 1835 from mid-Cretaceous Burmese amber are described. *Abaddonella nwarrngaal* **gen. et sp. nov**. is based on a well-preserved male specimen. It is assigned to Ripipterygidae Ander, 1939 due to its one-segemented cercus and the mesotibia not being significantly wider than mesofemur. The new genus is similar to *Burmaripipteryx* Zhao, Xu, Jarzembowski, Fang & Xiao, 2023 in regard to its abdominal and external genitalia morphology, but it differs from the latter genus (as well as other Ripipterygidae) by two small bumps on the vertex in front of the eyes. The second new taxon described is named *Naginipteryx pinna* **gen. et sp. nov.** Despite exhibiting a distinct ripipterygid-like morphology of the external genitalia, it shows a very inflated mesotibia with a marked triangular shape. This feature is usually considered to be diagnostic of Tridactylidae Brullé, 1835. The taxonomic position of *N. pinna*, therefore, is difficult. For now, the species is placed outside both families (Ripipterygidae and Tridactylidae) and is suggested to be an ancestor of both lineages, prior to the evolutionary separation being completed. An identification key to the genera of Ripipterygidae from Burmese amber is provided.

Key Words

Fossil, identification key, Kachin, mud crickets, pygmy mole crickets, taxonomy

Introduction

Tridactyloidea Brullé, 1835 is a superfamily inside the Caelifera Ander, 1936 suborder of the Orthoptera Olivier, 1789. It includes three families which are the Cylindrachetidae Giglio-Tos, 1914, Ripipterygidae Ander, 1939 and Tridactylidae Brullé, 1835. Cylindrachetidae are heavily adapted to a fossorial lifestyle with an almost worm-like habitus and can be found in 16 species throughout Australia and New Guinea as well as parts of South America (Heads 2009). For now, they are not known from the fossil record. Ripipterygidae and Tridactylidae are similar in appearance. However, they can be told apart by several morphological characters: 1) The cercus of Ripipterygidae is one-segmented, in Tridactylidae two-segmented. 2) The mesotibia of Ripipterygidae is roughly of the same width as the mesofemur, in Tridactylidae the mesotibia is distinctly inflated and of greater width than the mesofemur. 3) The ovipositor is still visible in female Ripipterygidae, whereas in Tridactylidae it is too reduced to be

seen. 4) Paraproctal lobes of Ripipterygidae apically with distinct array of setae, which is not present in Tridactylidae (characters after Gorochov 2010; Heads 2010; Gu et al. 2022). Some authors also mention 5) modified paraproctal lobes in Ripipterygidae of a more elaborate shape while the paraproctal lobes of Tridactylidae look like a second pair of cerci (Gu et al. 2022).

The fossil record of Tridactylidae and Ripipterygidae is not rich, but especially during the last 15 years, many remarkable findings have been made in Burmese amber from the mid-Cretaceous of what is now Myanmar (Zhao et al. 2024). In fact, both families appear to have been incredibly diverse in the Burmese amber fauna with seven genera of Tridactylidae (compared to ten extant genera) and also seven (!) genera of Ripipterygidae (compared to only two extant genera) having been reported from this origin (Zhao et al. 2024; Cigliano et al. 2025).

In this study, we report two new genera and species of Tridactyloidea from Burmese amber. One of them is assigned to Ripipterygidae based on the diagnostic characters mentioned above. The second new addition could possibly hold a taxonomic position closer to the base of Tridactyloidea, as an ancestor of both lineages Ripipterygidae and Tridactylidae.

Materials and methods

Amber pieces in this study are in the collection of the Leibniz Institute for the Analysis of Biodiversity Change (Hamburg) (collection numbers GPIH07231 and GPIH07232). They were excavated in Myanmar in 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 ± 0.62 My old (Shi et al. 2012), amber from Hkamti is ca. 110 My old (Xing and Qiu 2020). We think, it is important not to let the severe humanitarian situation currently in place in Myanmar go unmentioned. Regarding the use of amber specimens from Tanai, Kachin State for scientific purpose we take the position of Haug et al. (2020). We wish to recognize the fossils' origin described herein by giving them names to connect them with their home country.

Imaging of the specimens was conducted using a DUN. Inc. stacking system with a Canon EOS 5Dsr Camera having 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 the PHOTOSHOP CS6 Extended application by Adobe Inc. (USA; https://www.adobe.com). Further modifications (e. g. scale-bars) and creation of image collections was done in INKSCAPE (v. 1.4.2) (Inkscape-Team, 2025). Drawings were created in GIMP (v. 3.0.2-1) (GIMP Team, 2025) by direct layer copying.

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 *Abaddonella* gen. nov.

https://zoobank.org/2961DF57-95B1-41A1-9CF0-803E1B9808F2

Type species. *Abaddonella nwarrngaal* sp. nov.

Etymology. Named after Abaddon, angel of the abyss from the Book of Revelation in connection with -ella meant as a suffix functioning as diminutive. A translation would be "little abaddon" or "little demon", referring to the small bumps on the type species' vertex which remind a little of demon horns.

Diagnosis. Antenna 10-segmented. Compound eyes laterally placed on head. Two small bumps on vertex in front of the compound eyes. Pronotum more or less quadrangular in shape. Forewings and hindwings present. Hindwings slightly longer than abdomen. Protibia with hairs on entire surface. Apically with three strong dactyls. Mesotibia not distinctly wider than mesofemur. Metafemur inflated along entire length. Metatibial fin with distinct serration. Subapical and apical spurs approximately of equal length, much shorter than metatarsus. Metatarsus with rather long fine hairs on ventral margin. Abdomen with cercus one-segmented and heavily setulose. Paraproctal lobes much shorter than cercus, inconspicuous and not setulose. Subgenital plate elongated, much longer than paraproctal lobes and with long hairs. Coloration on head with distinct light/dark contrast over the eye. Pronotum with light coloration and several dark colored spots.

Abaddonella nwarrngaal sp. nov.

https://zoobank.org/BA107602-EA55-4D8D-A787-C1BEE259D095

Figs 1, 2

Etymology. Nwarr ngaal is Burmese and means "little cow". It refers to the conspicuous color markings on the species' head and pronotum.

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. Male. Specimen part of the LIB-Hamburg collection; collection number GPIH07231 (ex coll. Martin Husemann, coll. no. MH0086).

Diagnosis of species. As for genus (monotypic).

Description. A fully preserved specimen, except for left metathoracic leg.

Measurements: Values given with a "ca." indicate measurements based partly on estimation. Body-length ca. 1.83 mm. Head height 0.68 mm. Compound eye height 0.31 mm, width 0.21 mm. Antenna length

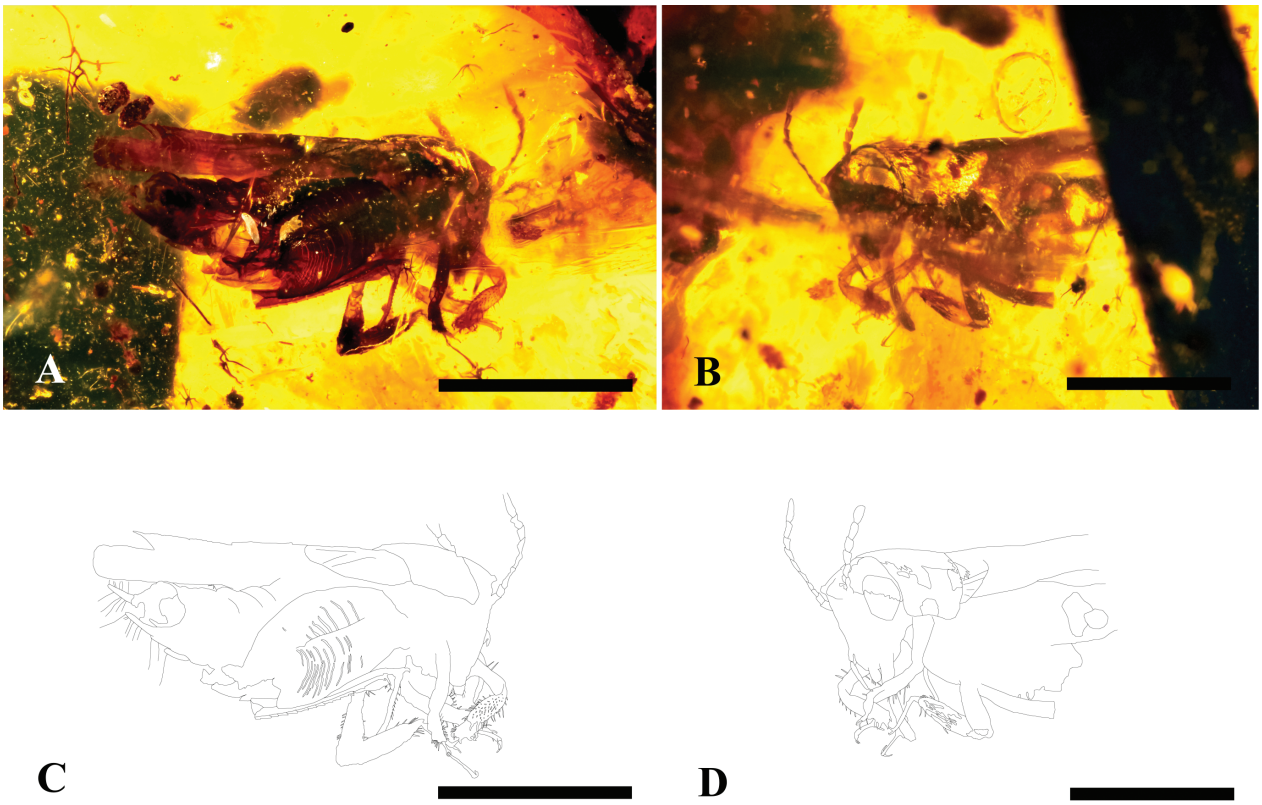

Figure 1. *Abaddonella nwarrngaal* gen. et sp. nov. holotype male GPIH07231 (ex collection Martin Husemann MH0086). **A, C.** Specimen in postero-lateral view; **B, D.** Specimen in antero-lateral view. Scale bars: 1 mm.

0.85 mm. Pronotum length 0.54 mm, height 0.4 mm. Forewing length 0.55 mm, hindwing length 1.64 mm. Prothoracic leg: femur 0.38 mm long. Tibia 0.36 mm long. Mesothoracic leg: tibia 0.5 mm long. Femur/Tibia width = 1.07 (at mid of both). Metathoracic leg: femur ca. 0.86 mm long, 0.51 mm wide. Tibia ca. 0.79 mm long, ca. 0.09 mm wide (around mid-length). Tarsus > 0.31 mm long. Cercus 0.15 mm long. Paraproctal lobe ca. 0.05 mm long. Subgenital plate 0.18 mm long.

Head: Antennae 10-segmented, moniliform. Pedicel and scape wider than antennomeres. Head with two small bumps on the vertex in front of the compound eyes. Compound eyes placed laterally on the head. Head with distinct coloration; a lighter area crosses the eye dividing it into two equal parts and continuing on the dorso-lateral portion of the head. Ocelli not seen.

Thorax: Pronotum with similar light/dark contrasting colors as head, but here the base color is light and several dark spots are scattered across the surface. Pronotum without elevation. Both fore- and hindwings present. Forewings with same color pattern as pronotum, hindwings uniformly dark. Hindwing slightly longer than abdomen.

Legs: Prothoracic leg: femur bearing some long hairs. Tibia slightly inflated, completely covered with shorter to longer hairs. Apically with three dactyls, the longest of which is 0.05 mm long. Tarsus slender, only distal segment can be seen, bearing two curved claws.

Mesothoracic leg: femur with some short hairs on both margins. Femur rather slender towards coxa, becoming wider towards tibia. Tibia slightly inflated, but not as wide as distal part of femur. Tibia apically with dense long hair. Tarsus slender with two claws.

Metathoracic leg: femur inflated along its entire length. Tiger stripe coloration, which can be seen on the metafemur of the specimen is probably due to fissures in the amber and not actual coloration. Connection to tibia damaged. Tibia with lateral carina that runs until apex. Fin with distinct serration. Subapical and apical spurs present, approximately the same length. Tarsus proportionally long and rather thin. Ventrally with eight to nine hairs. Apex of tarsus hidden behind mesotibia.

Abdomen: Epiproct short, not covering cercus. Cercus one-segmented, cylindrical in shape and with many long hairs. Paraproct distinct with paraproctal lobe in ventral position. Paraproctal lobe significantly smaller than cercus (both length and width), cylindrical without hairs. Subgenital plate elongated, approximately the length of the cercus and with long hairs; one especially long hair on the apex. Subgenital plate mostly dark in coloration becoming slightly lighter towards apex. Cercus completely of lighter color.

Remarks. The new genus is assigned to Ripipterygidae based on the following characters: 1) cercus one-segmented. 2) Mesotibia not inflated. It is most similar to *Burmaripipteryx* Zhao, Xu, Jarzembowski, Fang & Xiao, 2023 but differs from the latter by the two bumps on its forehead and the coloration pattern of the head, pronotum as well as external genitalia (*B. oblongus* Zhao, Xu, Jarzembowski, Fang & Xiao, 2023, only species of the genus,

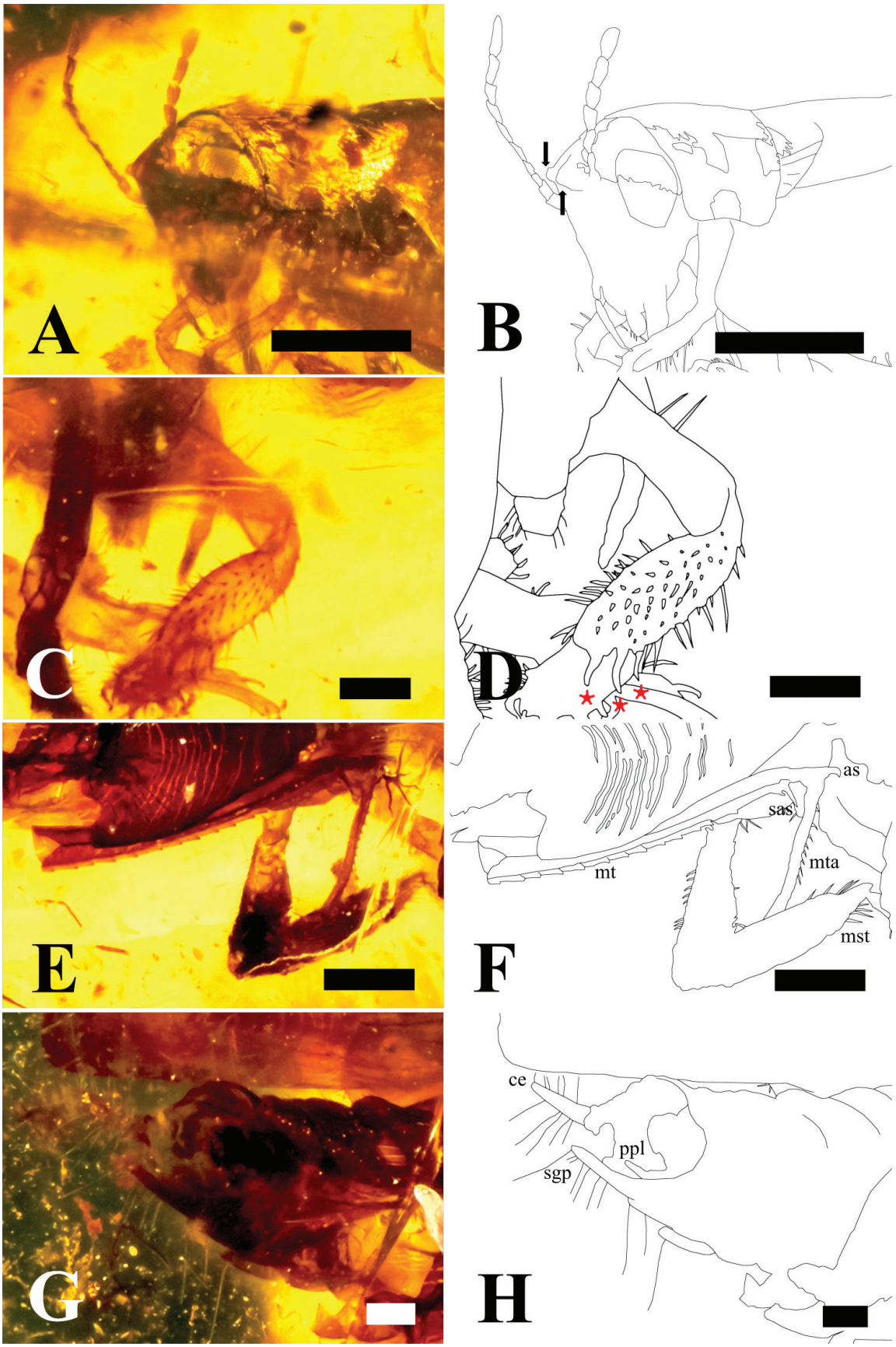

Figure 2. *Abaddonella nwarrngaal* gen. et sp. nov. holotype male GPIH07231. **A, B.** Detail of head and pronotum. Black arrows mark little bumps on the vertex; **C, D.** Detail of prothoracic leg. Red stars mark dactyls; **E, F.** Detail of metatibia and mesothoracic leg. Abbreviations: as = apical spur; mst = mesotibia; mt = metatibia; mta = metatarsus; sas = subapical spur; **G, H.** Detail of abdominal apex. Abbreviations: ce = cercus; ppl = paraproctal lobe; sgp = subgenital plate. Scale bars: 0.5 mm (**A, B**); 0.1 mm (**C, D, G, H**); 0.2 mm (**E, F**).

has cerci with the basal half light in color and the distal half dark, while the subgenital plate is completely light. Head and pronotum show no noteworthy color pattern). These characters also differentiate *Abaddonella* from any other ripipterygid-genus. The underdeveloped paraproctal lobes of this genus and also *Burmaripipteryx* (much smaller than cerci, of no distinct shape and without apical setae) are rather unusual for Ripipterygidae. According to Song et al. (2015), the estimated split between the lineages of Ripipterygidae and Tridactylidae occurred 153.45 Mya, ca. 50 My prior to the formation of the Kachin amber from Tanai. Maybe, at this point in time the separation of the two families had not yet been fully completed and a third lineage, ancestral to both, still existed. This is a question that will be answered with more findings of Tridactyloidea from Kachin amber in the future. For now, we follow Zhao et al. (2023) and place *Abaddonella* in Ripipterygidae.

Superfamily: Tridactyloidea Brullé, 1835

Genus *Naginipteryx* gen. nov.

https://zoobank.org/91DB496C-97FC-4723-8872-9D67C3217368

Type species. *Naginipteryx pinna* sp. nov.

Etymology. Named after the naga (female nagini), a mythological creature from Asian religions such as Hinduism and Buddhism. It is also found in the mythology of Myanmar. Nagas are usually portrayed as half-human, half serpent beings, but can also be found as dragons. This is why the name has been chosen, for the triangularly shaped mesotibia of the genus, reminding of a classical dragons' tail.

Diagnosis. Protibia with four dactyls. Fore- and hindwings present, hindwings just as long as abdomen. Apical metatibial spurs slightly longer than subapical. Ventral margin of apical spurs with four distinct long hairs. External genitalia very similar to *Yakkhapipteryx* Schall, Cao & Husemann, 2025 more specifically *Y. gracilis* (Gu, Zheng, Cao & Yue, 2022) (this includes morphology of the cerci, paraproctal lobes and ovipositor valves): cercus one-segmented, cylindrical and setulose with long hairs. Paraproctal lobes two-segmented and longer than cerci, apically swollen and clavate with distinct long hair. Ovipositor visible, approximately as long as cerci, valve rather thick (more similar to *Y. gracilis* than *Y. mira* (Gu, Zheng, Cao & Yue, 2022)). Differs from *Yakkhapipteryx* by 1) the mesotibia being distinctly inflated and triangular in shape. 2) Ventral appendages with an inserted hair on the abdomen. 3) A blunt (rather than pointed) metatarsus with one row of serration and one row with hairs (rather than no row).

Naginipteryx pinna sp. nov.

https://zoobank.org/9A6AD0E2-F314-40D2-BC0A-858307362D97

Figs 3–5

Etymology. Named after the latin word "pinna" (fin) because of the ventral appendages on the abdomen, reminding of the dorsal fin of some fish, for example male sea goldies or the threadfin butterflyfish.

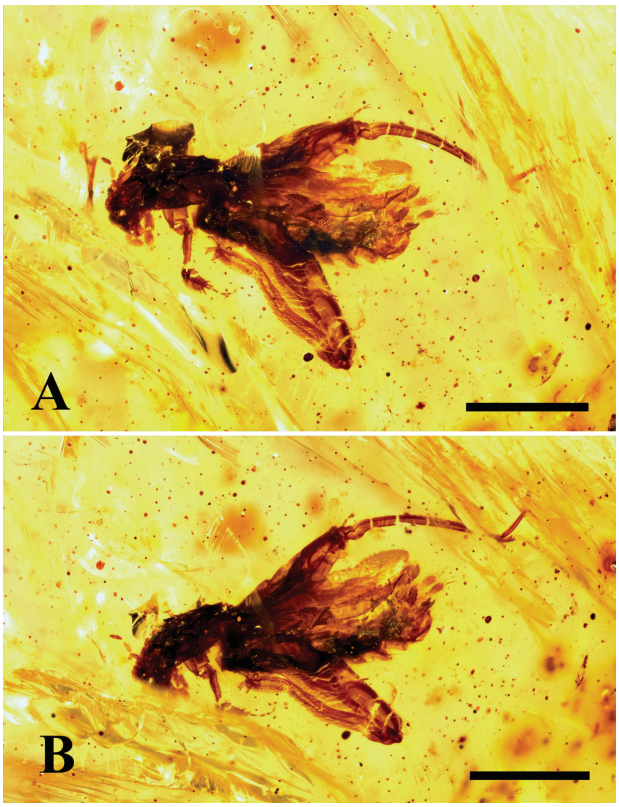

Figure 3. *Naginipteryx pinna* gen. et sp. nov. holotype female GPIH07232 (ex collection Martin Husemann MH0011). **A, B.** Specimen, left side. **B.** is taken from a slightly different angle. Scale bars: 1 mm.

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 GPIH07232 (ex coll. Martin Husemann, coll. no. MH0011).

Diagnosis of species. As for genus (monotypic).

Description. The specimen is well preserved, but most of the head and thorax are somewhat contorted due to internal damage of the amber structure.

Measurements: Body-length 2.52 mm (head to abdominal apex). Pronotum length 0.62 mm, height 0.38 mm. Prothoracic leg: femur ca. 0.35 mm long. Tibia ca. 0.27 mm long. Tarsus ca. 0.25 mm long (including claws). Forewing ca. 0.79 mm long. Hindwing ca. 1.53 mm long. Mesothoracic leg: tibia 0.39 mm long, 0.25 mm wide (max width). Tarsus 0.35 mm long. Metathoracic leg: femur 1.36 mm long. Tibia 1.41 mm long, 0.09 mm wide. Tarsus 0.32 mm long. Subapical spurs ca. 0.05 mm long. Apical spurs 0.08 mm long. Cercus 0.19 mm long. Paraproctal lobes 0.3 mm long (not including hairs). Ovipositor (longest valve) 0.17 mm long.

Head: Morphology uncertain due to internal damage in the amber.

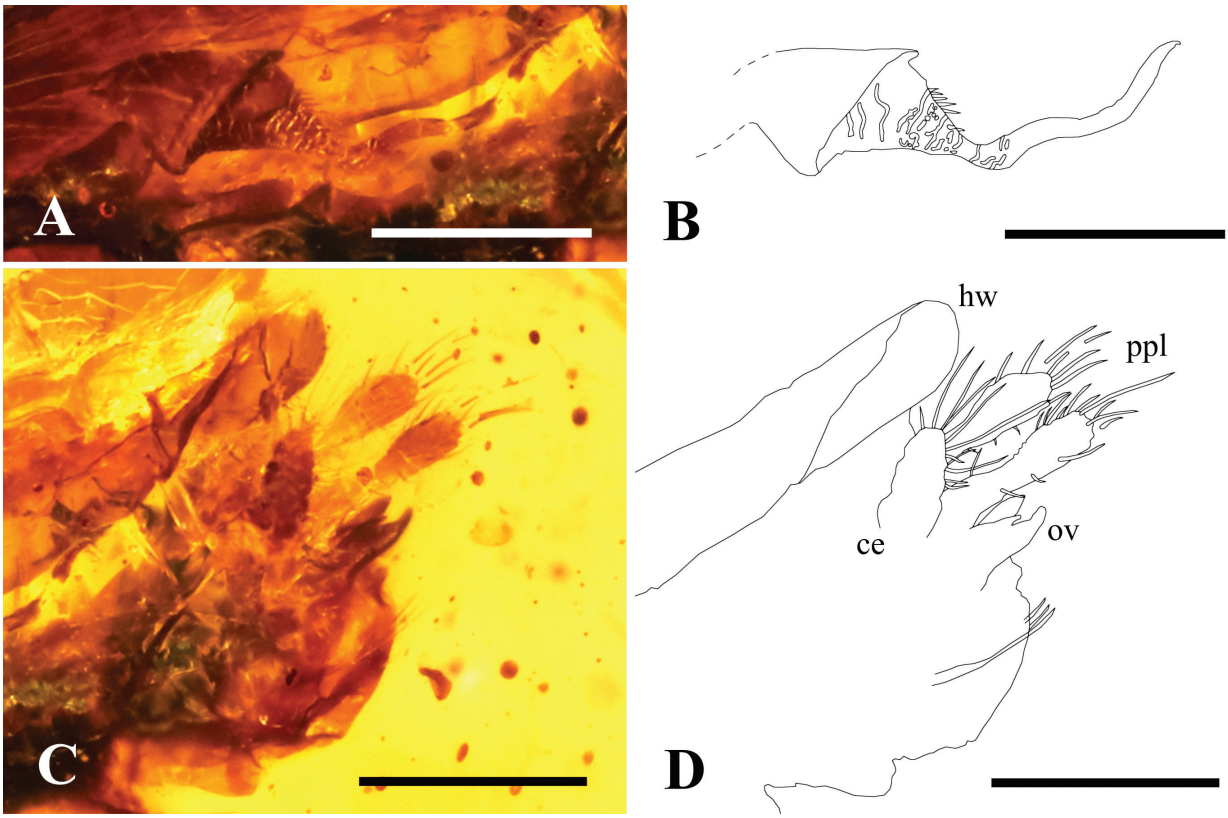

Figure 4. *Naginipteryx pinna* gen. et sp. nov. holotype female GPIH07232. **A**, **B.** Detail of mesothoracic leg with triangularly shaped tibia; **C, D.** Detail of abdominal apex (including tip of hindwing). Abbreviations: ce = cercus; hw = hindwing; ov = ovipositor; ppl = paraproctal lobe. Scale bars: 0.1 mm.

Thorax: Pronotum without elevation. Very deep laterally, covering the entire height of the thorax. Fore- and hindwings present. Venation undiscernible (lines seen on the wings are fissures in the amber, not actual veins). Hindwings just as long as abdomen.

Legs: Prothoracic leg: Coxa big, about 2.5× the width of femur with sparse hair. Trochanter halfway in width between coxa and femur. Femur with numerous hairs. Tibia with numerous hairs, too. Apically with four dactyls, the longest of which is 0.05 mm long. Tarsus damaged. Slender without hair and ending in two claws.

Mesothoracic leg: only tibia and tarsus can be seen. Tibia with very distinct shape, looking like it is made up of two triangles, where the distal half is inserted into the bigger (both wider and thicker) proximal half. Greatly inflated. Apically with some hairs. Tarsus two-segmented, slender, no hair and with two claws.

Metathoracic leg: femur apically with sparse hair. Tapering toward apex, only somewhat inflated. Tibial fin with serration. A pair of subapical and apical spurs. Apical spurs with four conspicuous hairs on ventral margin. Tarsus blunt with two rows ventrally, one metatibial fin serrated, the other with hair.

Abdomen: Proximal to abdominal apex are three finlike appendages of which the anterior two have singe hair inserted. Posterior fin probably lost the hair during preservation. More fins may be present but are covered by the metafemur. Cercus one-segmented, cylindrical in shape and setulose. Paraproctal lobes two-segmented, longer than cercus. Distal segment swollen, clavate in shape with distinct long hairs, especially on the apex of distal segment. Ovipositor visible, with narrower pointed end.

Remarks. Based on the structure of the external genitalia (cercus one-segmented; paraproctal lobes longer than cercus, modified in shape and with distinct apical hair; ovipositor visible), the new species should be assigned to Ripipterygidae. However, this family is usually recognized by an uninflated mesotibia, too (Heads 2010). Some species from Burmese amber that were previously assigned to Ripipterygidae were noted to have an untypical mesotibia, for example Zhao, Xu, Cao, Jarzembowski, Fang and Xiao (2024) remarked in their description of *Kallosripipteryx zhangi* "mesotibia slightly fusiform, not slender as typical of ripipterygids". In *Naginipteryx pinna*, this character is extremely pronounced, with an inflation of the mesotibia surpassing what is common for Tridactylidae (who are characterized by an inflation of the mesotibia) (compare for example *Latedactylus longapedi* Zheng, Cao & Gu, 2023 or *Burmadactylus tenuicerci* Fan, Gu & Cao, 2023). As suggested for *Abaddonella nwarrngaal* gen. et sp. nov. (see above), this strange combination of characters may indicate the presence of an ancestral lineage (or perhaps several ancestral lineages?) of Tridactyloidea in the Burmese amber forest that had not yet completed the evolutionary separation between Tridactylidae and Ripipterygidae.

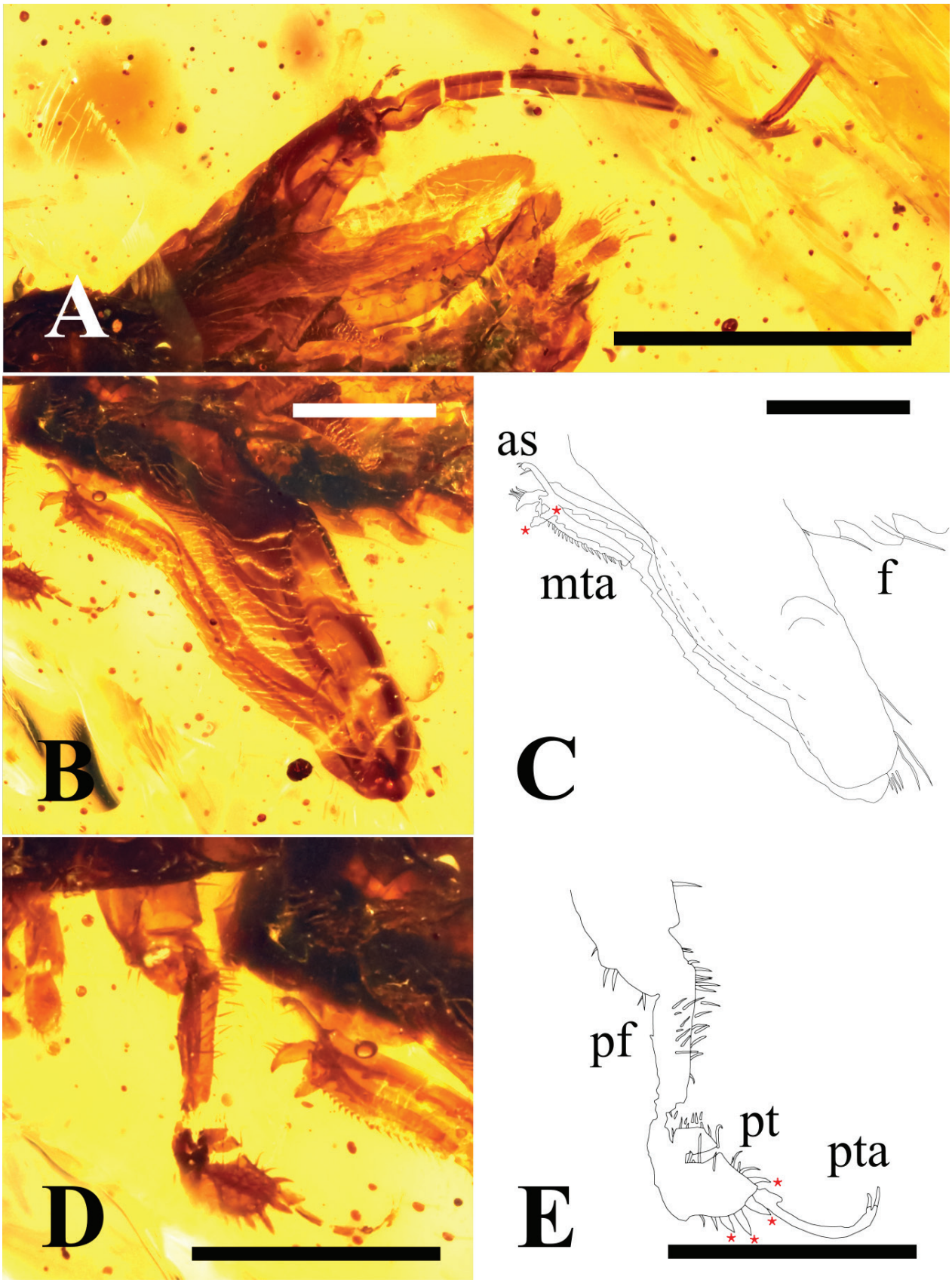

Figure 5. *Naginipteryx pinna* gen. et sp. nov. holotype female GPIH07232. **A.** Detail of right metathoracic leg; **B, C.** Detail of left metathoracic leg (including abdominal fins). Red stars mark subapical spurs. Abbreviations: as = apical spurs; f = fins; mta = metatarsus; **D, E.** Detail of prothoracic leg. Red stars mark dactyls. Abbreviations: pf = profemur; pt = protibia; pta = protarsus. Scale bars: 1 mm (**A**); 0.5 mm (**B–E**).

Key to the genera of Ripipterygidae found in Burmese amber

The increasing number of Ripipterygidae genera described from Burmese amber makes it appropriate to provide an up-to-date identification key to the diversity of the family known from this locality. As most of the genera are currently monotypic, this key is restricted to the genus-level.

Included genera (n species): *Abaddonella* gen. nov., herein (1); *Archaicaripipteryx* Xu, Zhang, Jarzembowski & Fang, 2020 (2); *Burmaripipteryx* Zhao, Xu, Jarzembowski, Fang & Xiao, 2023 (1); *Ciconipteryx* Schall, Cao & Husemann, 2025 (1); *Kallosripipteryx* Zhao, Xu, Cao, Jarzembowski, Fang & Xiao, 2024 (1); *Magnidactylus* Xu, Fang & Jarzembowski, 2020 (1); *Naginipteryx* gen. nov., herein (1); *Ozymandipterx* Schall, Cao & Husemann, 2025 (1); *Yakkhapipteryx* Schall, Cao & Husemann, 2025 (2).

1 Metatarsus absent/fully reduced (not visible in the fossil) 2
– Metatarsus visible 3
2 Body-length ca. 6 mm; protibia with dactyls ..... *Magnidactylus*
– Body-length < 2 mm; protibia without dactyls ..... *Ozymandipteryx*
3 Cercus longer than paraproctal lobe 4
– Cercus shorter than paraproctal lobe or equally long 5
4 Two small bumps on the vertex in front of the compound eyes; distinct light and dark coloration on head and pronotum ..... *Abaddonella*
– No such bumps; coloration different ..... *Burmaripipteryx*
5 Mesotibia very inflated and with distinct triangular shape; abdomen with fin-like appendages ..... *Naginipteryx*
– Mesotibia without triangular shape; abdomen without fin-like appendages 6
6 Mesothoracic leg longer than body; metafemur as long as body ..... *Ciconipteryx*
– Mesothoracic leg and metafemur both shorter than body 7
7 Cercus as long as paraproctal lobe ..... *Archaicaripipteryx*
– Cercus shorter than paraproctal lobe 8
8 Presence of one prosternal process ..... *Kallosripipteryx*
– Presence of no such prosternal process ..... *Yakkhapipteryx*

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