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A new species of Protopsyllidioidea from Cretaceous amber

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Abstract

With new fossils of Protopsyllidioidea discovered from amber, our knowledge of the biodiversity in the superfamily increases, and so does our understanding of the evolution of suborder Sternorrhyncha and its 'basal' groups. The new species *Burmapsyllidium grimaldii* Hakim, Azar & Huang **sp. nov.**, assigned to the family Paraprotopsyllidiidae, is reported from the mid-Cretaceous Burmese amber, and described and illustrated.

Keywords: Insecta, Hemiptera, Myanmar, mid-Cretaceous

Introduction

Over the years, numerous fossil taxa belonging to the superfamily Protopsyllidioidea have been collected and described from various localities worldwide. Preserved in amber or as rock impressions, the geological age of these records widely ranges from Early Permian (Artinskian) to Late Cretaceous (Turonian) (*e.g.*, Becker-Migdisova, 1985; Grimaldi, 2003; Yang *et al.*, 2012, 2013; Drohojowska *et al.*, 2013, 2022; Lara & Wang, 2016; Hakim *et al.*, 2019a, b, 2021; Huang *et al.*, 2022).

Extinct family Paraprotopsyllidiidae is comprised of four monospecific genera (*Angustipsyllidium minutum* Hakim, Azar, & Huang, 2021; *Burmapsyllidium setosum* Hakim, Azar, & Huang, 2021; *Maliawa akrawna* Drohojowska & Szwedo, 2021; *Paraprotopsyllidium spinosum* Hakim, Azar, & Huang, 2021), all discovered from mid-Cretaceous Burmese amber. Paraprotopsyllidiids are characterised by their narrowed wings with long marginal setae, a typical feature observed in many very minute flying insects. This design of the wings is hypothesised to play an aerodynamic role during wing movement and posture while decreasing the weight of the insect and providing the minimum required wing surface for effective flight, as commonly observed in some Diptera (Nymphomyiidae), Coleoptera (Ptiliidae), parasitic Hymenoptera (Mymaridae, Trichogrammatidae), Lepidoptera (Epermeniidae, Nepticulidae, Pterophoridae) and Thysanoptera (Horridge, 1956; Ellington, 1980, 1984; Wootton, 1992; Sunada *et al.*, 2002; Huber & Noyes, 2013; Sato *et al.*, 2013; Santhanakrishnan *et al.*, 2014; Jones *et al.*, 2015, 2016; Cheng & Sun, 2018; Kasoju *et al.*, 2018; Ford *et al.*, 2019; Lyu *et al.*, 2019; Yavorskaya *et al.*, 2019; Zhao *et al.*, 2019; Lee *et al.*, 2020; Kolomenskiy *et al.*, 2020; Jiang *et al.*, 2022). Some additional functions of bristles have been suggested, *i.e.* mechanosensory purposes (Ai, 2013; Valmalette *et al.*, 2015).

Herein, we describe a new species, *Burmapsyllidium grimaldii* **sp. nov.**, from Burmese amber. This discovery provides more insight into this family's biodiversity and additional data for future studies on the group's functional morphology.

Material and methods

The material consists of a single inclusion contained in a piece of amber, collected from a mining site located near Noije Bum Village, Tanai Township, in the Myitkyina and Upper Chindwin districts, Hukawng Valley, northern state of Kachin, Myanmar (Yin *et al.*, 2018). This specimen was studied in compliance with the recommendations of the International Palaeoentomological Society (see IPS statement on Kachin amber *in* Szwedo *et al.*, 2020). The amber piece was cut manually using denticulate shaving blades, and polished with increasing grade emery papers and diatomite, until the surface has become clear for observation.

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The specimen was examined and photographed with a Zeiss AXIO Imager.Z2 compound microscope and a Zeiss AXIO Zoom.V16 stereomicroscope, both equipped with Zeiss AxioCam HRc digital cameras. Photographs under green light were obtained using a fluorescent light source attached to the compound microscope. Immersion oil was used to enhance the green fluorescent microscopy while photographing. The figures and illustrations were processed with Helicon Focus 6 and Adobe Photoshop CS6 software.

The type material is deposited in the Nanjing Institute of Geology and Palaeontology (NIGPAS), Chinese Academy of Sciences (CAS), Nanjing, China.

We mainly adopt the wing venation nomenclature and the terminology of body structures of Nel *et al*. (2012) and Drohojowska (2015). Abbreviations: A, anal vein; AP, areola postica; CuA, cubitus anterior; CuP, cubitus posterior; MP, media posterior; RA, radius anterior; RP, radius posterior.

Systematic palaeontology

Order Hemiptera Linnaeus, 1758
Suborder Sternorrhyncha Amyot & Audinet-Serville, 1843
Superfamily Protopsyllidioidea Carpenter, 1931
Family Paraprotopsyllidiidae Hakim, Azar, Szwedo, Drohojowska & Huang, 2021

Genus *Burmapsyllidium* Hakim, Azar & Huang, 2021 *in* Hakim *et al*., 2021

Type species. *Burmapsyllidium setosum* Hakim, Azar & Huang, 2021 *in* Hakim *et al*., 2021; by original designation and monotypy.

***Burmapsyllidium grimaldii* Hakim, Azar & Huang sp. nov.**
(Figs 1–5)

Material. Holotype: specimen number NIGP201137, well-preserved (Fig. 1A), female; syninclusion: one Acari.

Etymology. The specific epithet is given in honour of Dr David Grimaldi, a world authority on fossil insects and their evolution.

Diagnosis. Apical tarsomere bearing a single small lobe and two fully visible claws, the latter without preapical teeth and not covered by membrane; forewings with common stem MP + CuA 1/5 the length of vein CuA, fork of MP 2/3 the length of common stem MP and 1/3 the length of forewing, and AP shorter than common stem CuA (about 78.5% the length); female ovipositor 1/3 shorter than that of *B. setosum*; gonapophysis VIII about 2/3 the length of gonapophysis IX.

Locality and horizon. Hukawng Valley, Kachin State, northern Myanmar; mid-Cretaceous (Shi *et al*., 2012; Mao *et al*., 2018).

Description. Head (Fig. 1B) about 1.55 mm wide; 12 bristles, long and sharp, placed in a symmetrical pattern along vertex (row of 6 setae on each side); several thin setae on frons and clypeus. Three bulbous ocelli visible, arranged in a triangle on vertex. Compound eyes bulbous, ellipsoid, posterior margin slightly concave, about 1.30 mm long and 0.73 mm wide; ommatidia devoid of setae. Antennae emerging between compound eyes, near upper anterior margin of eyes; at least six flagellomeres (both antennae not preserved completely) with sharp bristles, slender and rod-shaped, with no secondary annulations. Rostrum elongated; labium three-segmented, emerging between fore coxae, about 4.80 mm long; presence of long, thin setae, mainly on mid- and apical segments, no secondary annulations on any segment; stylets not visible.

Thorax: with multiple sharp, long bristles; pronotum *ca*. 1.25 mm long, with 16 visible bristles (2 near middle of anterior margin, 14 in a row along posterior margin); mesonotum + metanotum around 6.60 mm long; mesonotum with 20 visible bristles, spread across mesoscutum; metanotum obscured by forewings and air bubble.

Legs: setose; coxae large; trochanters well-developed; femora slender, with multiple setae, particularly on dorsal margin; fore and mid tibiae with sharp and short setae, hind tibiae with numerous, slightly longer, setae and 2–3 spines at apex (Fig. 1C); tarsi two-segmented, apical tarsomere bearing single small lobe and two claws; claws long, slender and curved with no preapical teeth and not covered by membrane (Fig. 1B, C); tarsomeres about equal in length in fore and mid legs, basal tarsomere longer than apical segment (1.5–2.0 times the length) in hind legs. Forewing (Figs 2–3, basal section of wing in curved position due to preservation) 1.73 mm long, 0.49 mm wide, membranous, with long marginal setae; wing membrane light brown in colour, covered with numerous dark microsetae; fringe composed of two rows of setae, ending shortly before CuP reaches wing margin; veins thickened, bearing sharp bristles except for CuP; R branched into RA and RP at 0.70 mm from wing base (before wing's mid-length); RA almost straight, reaching margin at 0.95 mm; RP simple, curved and reaching margin at 1.51 mm; common stem MP + CuA about 11% the length of forewing and 20% the length of vein CuA (including AP); MP and CuA separated at 0.36 mm; very long common vein MP1 + MP2; MP branched at 1.21 mm; fork of MP about 65% the length of common stem MP and 32% the length of forewing; MP1 curved and MP2 sigmoidal, reaching margin respectively at 1.73 mm and 1.49 mm; CuA branched at 0.92 mm, near wing margin; AP shorter than common stem CuA, about 78.5% the length; CuA1 strongly curved apically, reaching margin at 1.33 mm; CuA2 very short, almost none existent; CuP almost straight, much thinner than other veins, reaching margin at 0.60 mm; A1 thin, joining CuP at wing margin; A2 probably present but evanescent, with strong setae, very close to wing margin. Hind wing membranous, with fringe of long setae; wing membrane with numerous dark microsetae, colour the same shade as forewings; fringe with one row of setae; RP and MP very long, simple, reaching wing margin; other veins, if present, not visible due to air bubble and wing position.

Abdomen: dorsally obscured by large air bubble; bearing a few thin setae ventrally; anal tube elongated and segmented, apical segment setose. Female ovipositor with well-developed gonapophyses, emerging distally from abdomen (Fig. 4); gonapophyses very short (compared to other paraprotopsyllidiid species); gonapophysis VIII distinctly shorter than gonapophysis IX (about 66% the

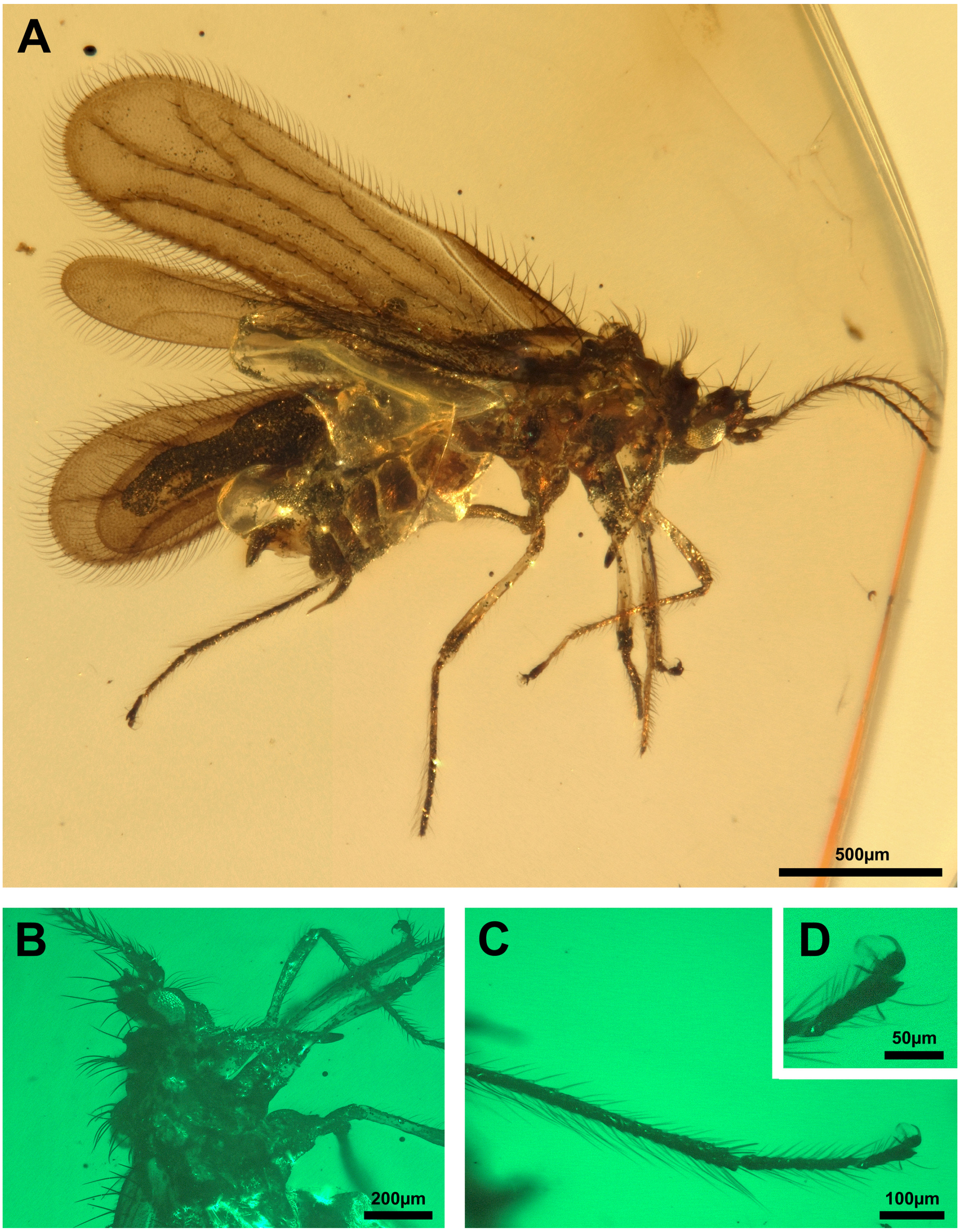

FIGURE 1. *Burmapsyllidium grimaldii* **sp. nov.**, holotype. **A**, Habitus. **B**, Details of head and thorax. **C**, Details of hind leg. **D,** Details of claws.

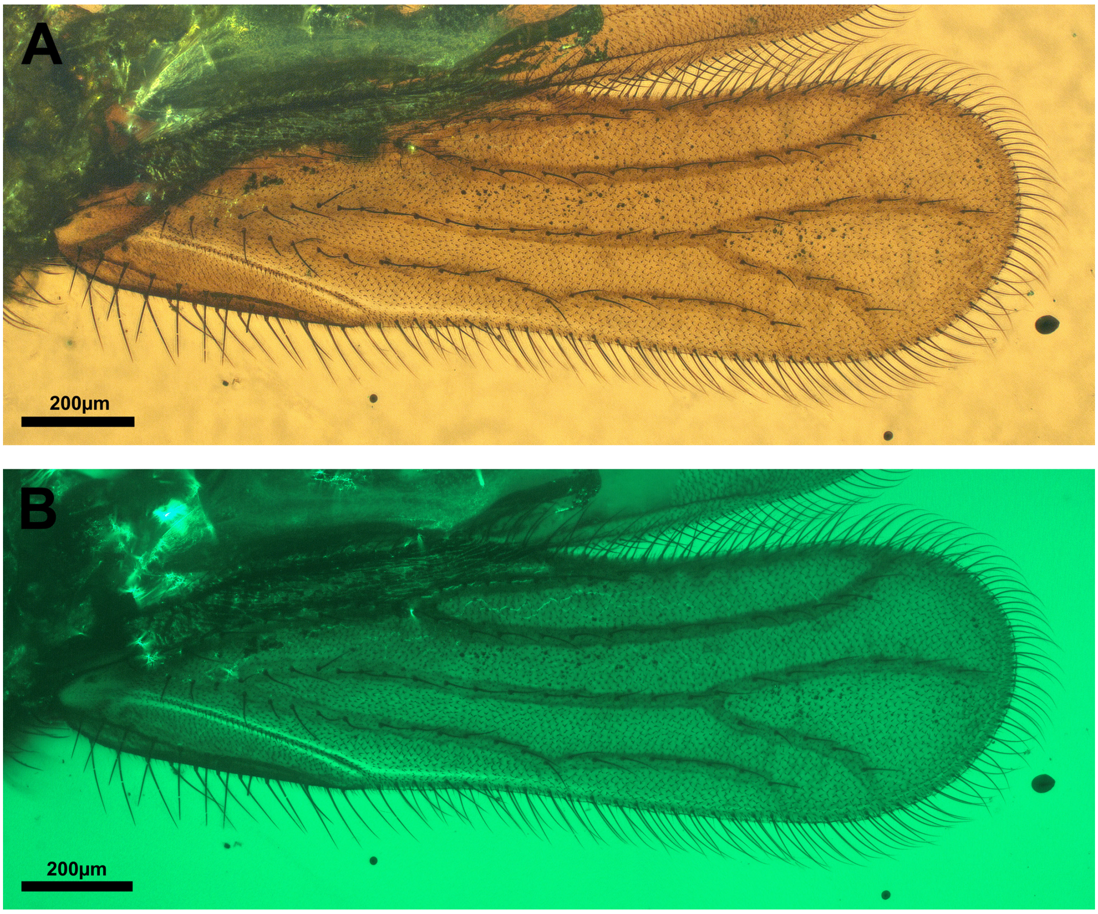

FIGURE 2. *Burmapsyllidium grimaldii* **sp. nov.**, holotype. **A**, Forewing. **B**, Forewing, in green light.

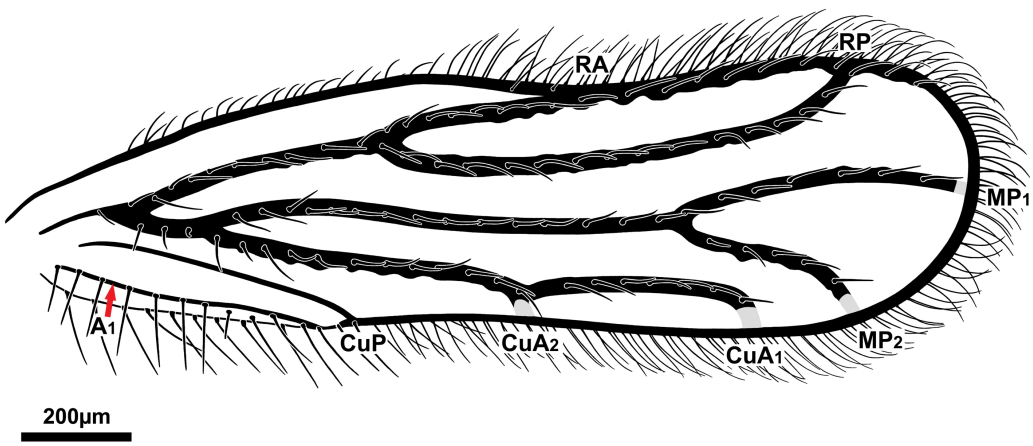

FIGURE 3. *Burmapsyllidium grimaldii* **sp. nov.**, holotype. Illustration of forewing.

length), covered with setae; gonapophysis IX acute, needle-like. Male genitalia unknown (likely as in family diagnosis).

Remarks. After observing and comparing the structures of the antennae in both species of *Burmapsyllidium*, it is most probable that *B. setosum* has 10 antennomeres (like *Maliawa* Drohojowska & Szwedo, 2021) and not 11 as previously assumed.

Discussion

Burmapsyllidium grimaldii **sp. nov.** appears to closely resemble *Burmapsyllidium setosum*. They share similarities in features such as the shape of the wings and several body structures, the venation pattern, and the presence of sharp setae symmetrically distributed on the head and thorax. Unlike *B. setosum*, the new species

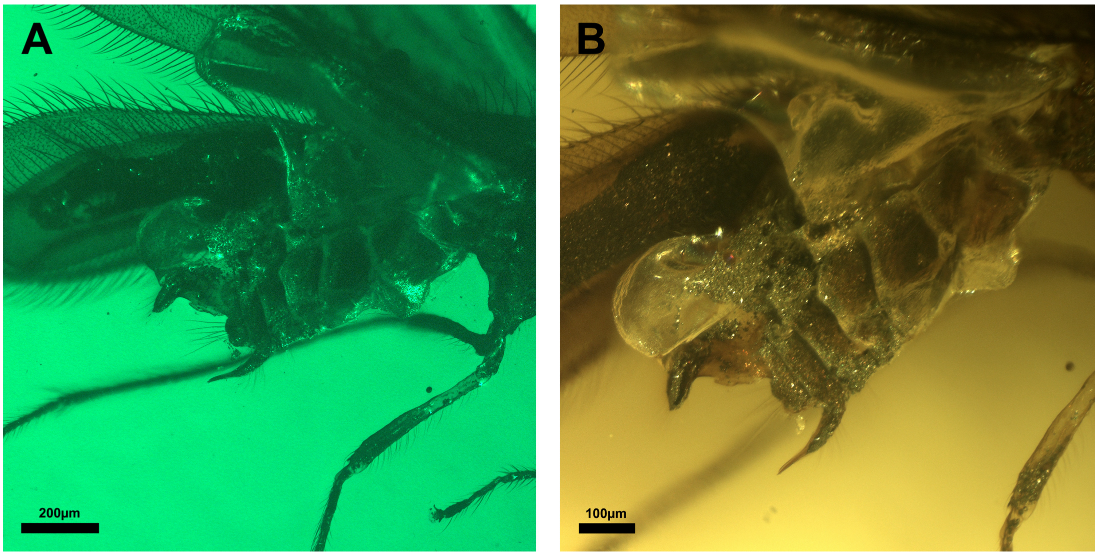

FIGURE 4. *Burmapsyllidium grimaldii* **sp. nov.**, holotype. **A**, Abdomen and genitalia, in green light. **B**, Details of abdomen and genitalia.

presents fully visible claws (which seem to be covered in *B. setosum*), some differences in the forewing venation pattern, mainly a shorter common stem MP + CuA (20% the length of vein CuA *vs*. 35% in *B. setosum*), a longer fork of vein MP (65% the length of common stem MP *vs*. 40% in *B. setosum* and 32% the length of forewing *vs*. 20% in *B. setosum*), and cell AP shorter than common stem CuA (about 78.5% the length of common stem CuA *vs*. AP longer in *B. setosum*), and a shorter ovipositor. Although it is not conclusive evidence, vein RP being simple in *Burmapsyllidium grimaldii* **sp. nov.** strongly supports the hypothesis that the fork of RP in *B. setosum* might be a malformation, as all other species in Paraprotopsyllididae also have RP simple.

Burmapsyllidium grimaldii **sp. nov.** differs from the species of genera *Paraprotopsyllidium* Hakim, Azar, & Huang, 2021, *Angustipsyllidium* Hakim, Azar, & Huang, 2021, and *Maliawa* in the shape and venation pattern of the wings (vein MP branched *vs*. simple, and different shape and length of AP in *Paraprotopsyllidium* and *Maliawa*) (Fig. 5). The fringe on the wings in *Burmapsyllidium grimaldii* **sp. nov.** is shorter than those of *Paraprotopsyllidium* and *Angustipsyllidium*, the latter genus having a less complex venation pattern compared to all other species. Additionally, unlike *Angustipsyllidium*, *Burmapsyllidium grimaldii* **sp. nov.** has no membrane on the claws and is much larger; unlike *Paraprotopsyllidium*, the head and thorax have shorter and thinner setae in *Burmapsyllidium grimaldii* **sp. nov.**, no secondary annulations on mouthparts, no thick spines on hind legs, and much shorter structures of the female genitalia (emerging distally from the abdomen).

Burmapsyllidium grimaldii **sp. nov.** differs from Postopsyllidiidae in the setae and venation of the wings: forewing with a fringe composed of two rows of setae *vs*. one row, MP with two branches *vs*. MP with three branches, and a differently shaped AP; hind wing with a fringe *vs*. no fringe, and a less complex venation pattern. They also differ in the shape and/or length of several body structures, *e.g*. the head, thorax and female genitalia. Additional differences observed in Postopsyllidiidae include large fore femora with sharp spines (not present in *Burmapsyllidium grimaldii* **sp. nov.**), and tarsi one-segmented in forelegs then three-segmented in mid and hind legs (*vs*. two-segmented in all legs in *Burmapsyllidium grimaldii* **sp. nov.**) (Grimaldi, 2003; Hakim *et al*., 2019b; Drohojowska *et al*., 2022).

All these differences justify the establishment of a new species, *Burmapsyllidium grimaldii* **sp. nov.**

Conclusion

Burmese amber is rich in biological inclusions, such as plants and invertebrates (Ross, 2019, 2020, 2021, 2022), and thus provides valuable knowledge on Cretaceous life forms and their ecosystems. As of now, Paraprotopsyllidiidae is recognised with five species from Burmese amber. This family is yet to be recorded from a different deposit. New discoveries will shed more light on its biogeographic distribution and functional morphology, which in turn will help to clarify the behaviour and evolutionary history of suborder Sternorrhyncha and its 'basal' groups.

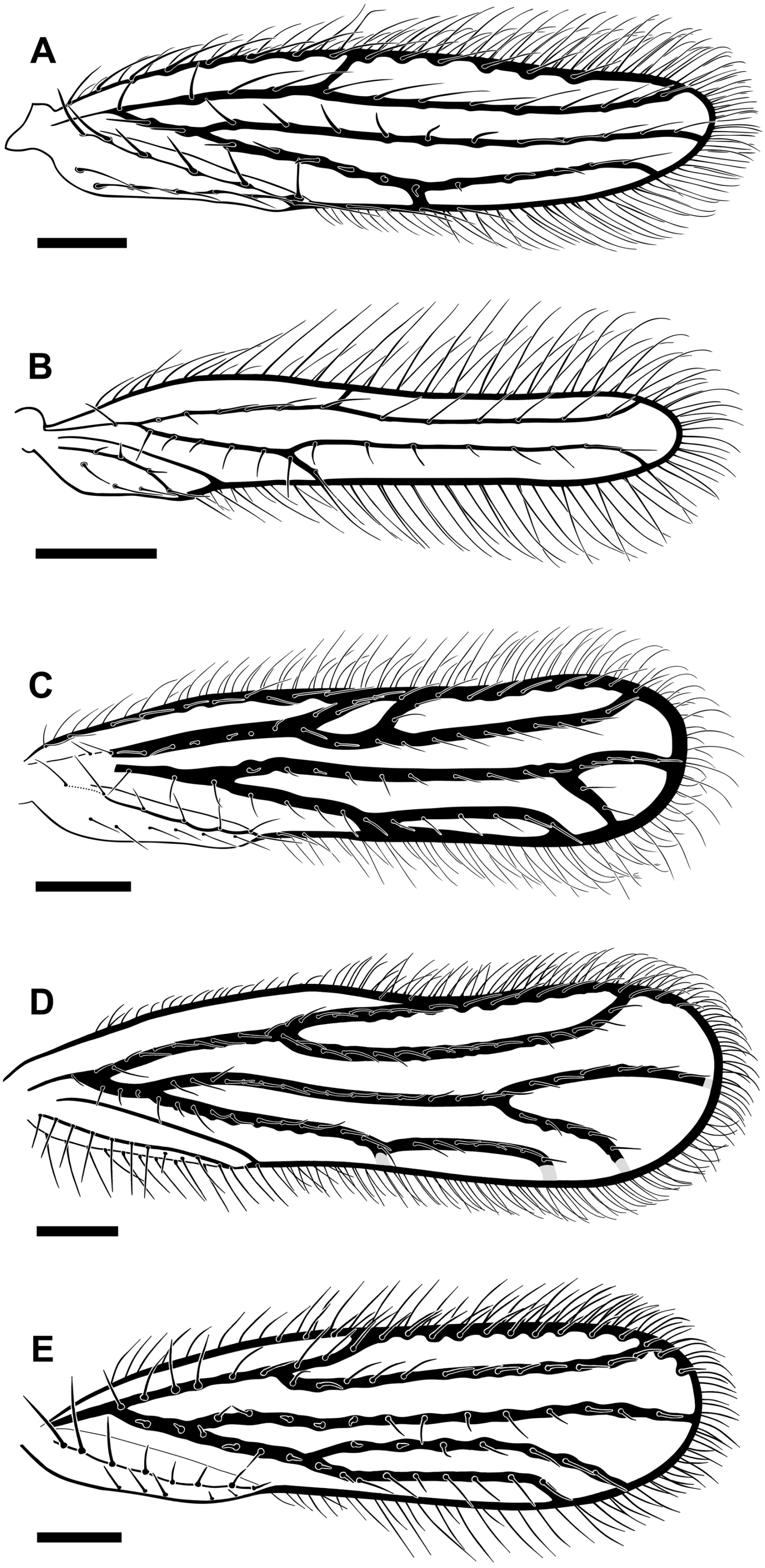

FIGURE 5. Wing venation patterns of paraprotopsyllidiid species. **A**, *Paraprotopsyllidium spinosum*. **B**, *Angustipsyllidium minutum*. **C**, *Burmapsyllidium setosum*. **D**, *Burmapsyllidium grimaldii* **sp. nov. E**, *Maliawa akrawna*. Scale bars = 200µm.

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References

Ai, H. (2013) Sensors and sensory processing for airborne vibrations in silk moths and honeybees. *Sensors*, 13 (7), 9344–9363. https://doi.org/10.3390/s130709344

Amyot, C.J.B. & Audinet-Serville, A. (1843) *Histoire naturelle des insectes: Hémiptères*. Librairie Encyclopédique de Roret, Paris, 675 pp. https://doi.org/10.5962/bhl.title.8471

Becker-Migdisova, E.E. (1985) Iskopaemye nasekomye psillomorfy [Fossil Psyllomorpha insects]. *Trudy Paleontologicheskogo Instituta Akademii Nauk SSSR*, 206, 1–92. [In Russian]

Carpenter, F.M. (1931) The Lower Permian insects of Kansas. Part 4. The order Hemiptera, and additions to the Paleodictyoptera and Protohymenoptera. *American Journal of Science*, 22, 113–130. https://doi.org/10.2475/ajs.s5-22.128.113

Cheng, X. & Sun, M. (2018) Very small insects use novel wing flapping and drag principle to generate the weight-supporting vertical force. *Journal of Fluid Mechanics*, 855, 646–670. https://doi.org/10.1017/jfm.2018.668

Drohojowska, J. (2015) *Thorax morphology and its importance in establishing relationships within Psylloidea (Hemiptera: Sternorrhyncha)*. Wydawnictwo Uniwersytetu Śląskiego, Katowice, 171 pp.

Drohojowska, J., Szwedo, J. & Azar, D. (2013) *Talaya batraba* gen. et sp. nov.—the first nymph of a protopsyllidiid (Hemiptera: Sternorrhyncha: Psyllomorpha) from the Lower Cretaceous amber of Lebanon. *Acta Geologica Sinica*, 87 (l), 21–31. https://doi.org/10.1111/1755-6724.12027

Drohojowska, J., Zmarzły, M. & Szwedo, J. (2022) Evolutionary implications of new Postopsyllidiidae from mid-Cretaceous amber from Myanmar and sternorrhynchan nymphal conservatism. *Scientific Reports*, 12, 16446. https://doi.org/10.1038/s41598-022-20897-y

Ellington, C.P. (1980) Wing mechanics and take-off preparation of thrips (Thysanoptera). *Journal of Experimental Biology*, 85, 129–136. https://doi.org/10.1242/jeb.85.1.129

Ellington, C.P. (1984) The aerodynamics of hovering insect flight. I. The quasi-steady analysis. *Philosophical Transactions of the Royal Society of London, Series B: Biological Sciences*, 305 (1122), 1–15. https://www.jstor.org/stable/2396072

Ford, M.P., Kasoju, V.T., Gaddam, M.G. & Santhanakrishnan, A. (2019) Aerodynamic effects of varying solid surface area of bristled wings performing clap and fling. *Bioinspiration & Biomimetics*, 14 (4), 046003. https://doi.org/10.1088/1748-3190/ab1a00

Grimaldi, D.A. (2003) First amber fossils of the extinct family Protopsyllidiidae, and their phylogenetic significance among Hemiptera. *Insect Systematics & Evolution*, 34 (3), 329–344. https://doi.org/10.1163/187631203788964746

Hakim, M., Azar, D. & Huang, D.Y. (2019a) Protopsyllidioids and their behaviour "frozen" in mid-Cretaceous Burmese amber. *Palaeoentomology*, 2 (3), 271–278. https://doi.org/10.11646/palaeoentomology.2.3.12

Hakim, M., Azar, D., Szwedo, J., Brysz, A.M. & Huang, D.Y. (2019b) New paraneopterans (Protopsyllidioidea, Hemiptera) from the mid-Cretaceous amber of northern Myanmar. *Cretaceous Research*, 98, 136–152. https://doi.org/10.1016/j.cretres.2018.12.012

Hakim, M., Azar, D., Szwedo, J., Drohojowska, J. & Huang, D.Y. (2021) Paraprotopsyllidiidae fam. nov., a new thrips-like protopsyllidioid family from mid-Cretaceous Burmese amber (Hemiptera; Sternorrhyncha). *Cretaceous Research*, 120, 104726. https://doi.org/10.1016/j.cretres.2020.104726

Horridge, G.A. (1956) The flight of very small insects. *Nature*, 178 (4546), 1334–1335. https://doi.org/10.1038/1781334a0

Huang, D.Y., Hakim, M., Fu, Y.Z. & Nel, A. (2022) A new sternorrhynchan genus and species from the Triassic period of China that is likely related to Protopsyllidioid (Insecta, Hemiptera). *Insects*, 13 (7), 592. https://doi.org/10.3390/insects13070592

Huber, J.T. & Noyes, J.S. (2013) A new genus and species of fairyfly, *Tinkerbella nana* (Hymenoptera, Mymaridae), with comments on its sister genus *Kikiki*, and discussion on small size limits in arthropods. *Journal of Hymenoptera*, 32, 17–44.

Jiang, Y.G., Zhao, P., Cai, X.F., Rong, J.X., Dong, Z.H., Chen, H.W., Wu, P., Hu, H.Y., Jin, X.X., Zhang, D.Y. & Liu, H. (2022). Bristled-wing design of materials, microstructures, and aerodynamics enables flapping flight in tiny wasps. *iScience*, 25 (1), 103692. https://doi.org/10.1016/j.isci.2021.103692

Jones, S.K., Laurenza, R., Hedrick, T.L., Griffith, B.E & Miller, L.A. (2015) Lift *vs*. drag based mechanisms for vertical force production in the smallest flying insects. *Journal of Theoretical Biology*, 384, 105–120. https://doi.org/10.1016/j.jtbi.2015.07.035

Jones, S.K., Yun, Y.J.J., Hedrick, T.L., Griffith, B.E. & Miller, L.A. (2016) Bristles reduce the force required to 'fling' wings apart in the smallest insects. *Journal of Experimental Biology*, 219

(23), 3759–3772.
https://doi.org/10.1242/jeb.143362
Kasoju, V.T., Terrill, C.L., Ford, M.P. & Santhanakrishnan, A. (2018) Leaky flow through simplified physical models of bristled wings of tiny insects during clap and fling. *Fluids*, 3 (2), 44.
https://doi.org/10.3390/fluids3020044
Kolomenskiy, D., Farisenkov, S., Engels, T., Lapina, N., Petrov, P., Lehmann, F.-O., Onishi, R., Liu, H. & Polilov, A. (2020) Aerodynamic performance of a bristled wing of a very small insect. *Experiments in Fluids*, 61 (9), 194.
https://doi.org/10.1007/s00348-020-03027-0
Lara, M.B. & Wang, B. (2016) New hemipteran insects (Eoscarterellidae, Scytinopteridae, and Protopsyllidiidae) from the Upper Triassic Potrerillos Formation of Mendoza, Argentina. *Paläontologische Zeitschrift*, 90, 49–61.
https://doi.org/10.1007/s12542-016-0286-8
Lee, S.H., Lee, M. & Kim, D. (2020) Optimal configuration of a two-dimensional bristled wing. *Journal of Fluid Mechanics*, 888, A23.
https://doi.org/10.1017/jfm.2020.64
Linnaeus, C. (1758) *Systema naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis*. Tomus I. Editio decima, reformata. Laurentii Salvii, Holmiae [= Stockholm], 824 pp.
https://doi.org/10.5962/bhl.title.542
Lyu, Y.Z., Zhu, H.J. & Sun, M. (2019) Flapping-mode changes and aerodynamic mechanisms in miniature insects. *Physical Review E*, 99, 012419.
https://doi.org/10.1103/PhysRevE.99.012419
Mao, Y.Y., Liang, K., Su, Y.T., Li, J.G., Rao, X., Zhang, H., Xia, F.Y., Fu, Y.Z., Cai, C.Y. & Huang, D.Y. (2018) Various amberground marine animals on Burmese amber with discussions on its age. *Palaeoentomology*, 1 (1), 91–103.
https://doi.org/10.11646/palaeoentomology.1.1.11
Nel, A., Prokop, J., Nel, P., Grandcolas, P., Huang, D.Y., Roques, P., Guilbert, E., Dostál, O. & Szwedo, J. (2012) Traits and evolution of wing venation pattern in paraneopteran insects. *Journal of Morphology*, 273 (5), 480–506.
https://doi.org/10.1002/jmor.11036
Ross, A.J. (2019) Burmese (Myanmar) amber checklist and bibliography 2018. *Palaeoentomology*, 2 (1), 22–84.
https://doi.org/10.11646/palaeoentomology.2.1.5
Ross, A.J. (2020) Supplement to the Burmese (Myanmar) amber checklist and bibliography, 2019. *Palaeoentomology*, 3 (1), 103–118.
https://doi.org/10.11646/palaeoentomology.3.1.14
Ross, A.J. (2021) Supplement to the Burmese (Myanmar) amber checklist and bibliography, 2020. *Palaeoentomology*, 4 (1), 57–76.
https://doi.org/10.11646/palaeoentomology.4.1.11
Ross, A.J. (2022) Supplement to the Burmese (Myanmar) amber checklist and bibliography, 2021. *Palaeoentomology*, 5 (1), 27–45.
https://doi.org/10.11646/palaeoentomology.5.1.4
Santhanakrishnan, A., Robinson, A.K., Jones, S., Low, A.A., Gadi, S., Hedrick, T.L. & Miller, L.A. (2014) Clap and fling mechanism with interacting porous wings in tiny insect flight. *Journal of Experimental Biology*, 217 (21), 3898–3909.
https://doi.org/10.1242/jeb.084897
Sato, K., Takahashi, H., Nguyen, M.D., Matsumoto, K. & Shimoyama, I. (2013) Effectiveness of bristled wing of thrips. *In*: 2013 IEEE 26th International Conference on Micro Electro Mechanical Systems (MEMS), pp 21–24.
https://doi.org/10.1109/MEMSYS.2013.6474166
Shi, G.L., Grimaldi, D.A., Harlow, G.E., Wang, J., Wang, J., Yang, M.C., Lei, W.Y., Li, Q.L. & Li, X.H. (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
Sunada, S., Takashima, H., Hattori, T., Yasuda, K. & Kawachi, K. (2002) Fluid-dynamic characteristics of a bristled wing. *Journal of Experimental Biology*, 205, 2737–2744.
https://doi.org/10.1242/jeb.205.17.2737
Szwedo, J., Wang, B., Soszyńska-Maj, A., Azar, D. & Ross, A. (2020) International Palaeoentomological Society Statement. *Palaeoentomology*, 3 (3), 221–222.
https://doi.org/10.11646/palaeoentomology.3.3.1
Valmalette, J.C., Raad, H., Qiu, N., Ohara, S., Capovilla, M. & Robichon, A. (2015) Nanoarchitecture of gustatory chemosensory bristles and trachea in *Drosophila* wings. *Scientific Reports*, 5, 14198.
https://doi.org/10.1038/srep14198
Wootton, R.J. (1992) Functional morphology of insect wings. *Annual Review of Entomology*, 37, 113–140.
https://doi.org/10.1146/annurev.en.37.010192.000553
Yang, G., Yao, Y.Z. & Ren, D. (2012) A new species of Protopsyllidiidae (Hemiptera, Sternorrhyncha) from the Middle Jurassic of China. *Zootaxa*, 3274, 36–42.
https://doi.org/10.11646/zootaxa.3274.1.4
Yang, G., Yao, Y.Z. & Ren, D. (2013) *Poljanka strigosa*, a new species of Protopsyllidiidae (Hemiptera, Sternorrhyncha) from the Middle Jurassic of China. *Alcheringa*, 37 (1), 125–130.
https://doi.org/10.1080/03115518.2012.715325
Yavorskaya, M.I., Beutel, R.G., Farisenkov, S.E. & Polilov, A.A. (2019) The locomotor apparatus of one of the smallest beetles—The thoracic skeletomuscular system of *Nephanes titan* (Coleoptera, Ptiliidae). *Arthropod Structure & Development*, 48, 71–82.
https://doi.org/10.1016/j.asd.2019.01.002
Yin, Z.W., Cai, C.Y. & Huang, D.Y. (2018) New zorapterans (Zoraptera) from Burmese amber suggest higher paleodiversity of the order in tropical forests. *Cretaceous Research*, 84, 168–172.
https://doi.org/10.1016/j.cretres.2017.11.028
Zhao, P., Dong, Z.H., Jiang, Y.G., Liu, H., Hu, H.Y., Zhu, Y.F. & Zhang, D.Y. (2019) Evaluation of drag force of a thrip wing by using a microcantilever. *Journal of Applied Physics*, 126 (22), 224701.
https://doi.org/10.1063/1.5126617