

A Second Unicorn Darwin Wasp Species *Gilen principissa* sp. nov. (Hymenoptera: Ichneumonidae, Ctenopelmatinae) from Thailand

KITTIPUM CHANSRI¹, PORNTAP KERKIG¹, ALEXEY RESHCHIKOV², DONALD L. J. QUICKE¹,
VORANAN PUENGCHANCHAIKUL³ AND BUNTIKA AREEKUL BUTCHER^{1*}

¹*Integrative Insect Ecology Research Unit, Department of Biology, Faculty of Science, Chulalongkorn University, Phayathai Road, Pathumwan, Bangkok 10330, THAILAND*

²*Biodiversity and Environmental Change Lab, School of Biological Sciences, University of Hong Kong, Kadoorie Biological Sciences Building, Pokfulam Road, Hong Kong SAR, CHINA*

³*Ruamrudee International School, Ramkhamhaeng, Minburi, Bangkok 10510, THAILAND*

*Corresponding author. Buntika A. Butcher (buntika.a@chula.ac.th)

Received: 19 March 2025; Accepted: 29 August 2025; Date of Publication: 20 October 2025

https://zoobank.org/urn:lsid:zoobank.org:pub: 65738993-1081-4CD9-A1AB-254E810243FE

ABSTRACT.— A new species of the genus *Gilen* Reshchikov & van Achterberg, 2018 (Hymenoptera, Ichneumonidae, Ctenopelmatinae), *G. principissa* Chansri, Kerkig & Reshchikov, sp. nov., from Thailand is described and illustrated based on female specimens collected with Malaise traps. A molecular phylogenetic tree is presented based on DNA barcode sequences of representative Ctenopelmatinae, including sequences from both known *Gilen* species. The new species was recovered as sister to *G. orientalis* Reshchikov & van Achterberg, 2018 with 100% bootstrap support, but on a long branch. Comparison of the sequences revealed that they differ at 88 positions out of 658 (13.4%) possibly indicating that their lineages diverged between six and 13 million years ago.

KEYWORDS: facial projection, key to species, Khao Yai National Park, new species, Perilissini

INTRODUCTION

The Darwin wasp subfamily Ctenopelmatinae consists of 114 genera (Yu et al., 2016; Broad et al., 2018; Reshchikov and van Achterberg, 2018; Kasparvan, 2020a, b; Li et al., 2022; Reshchikov et al., 2022; Ranjith et al., 2024) classified into nine tribes (Gauld et al., 1997; Broad et al., 2018; Bennett et al., 2019). However, recent molecular and combined phylogenetic analyses (Quicke et al., 2009; Bennett et al., 2019) have suggested that they are a poly- or paraphyletic group with respect to some other subfamilies and enigmatic genera (Bennett et al., 2019). The prominent feature of Ctenopelmatinae s.s. defining them from other Darwin wasps are a short, notched or needle-like ovipositor together with the presence of an acute dorsal tooth on the apex of the fore tibia (Townes, 1970) although both characters are also present in some members of other subfamilies (Broad et al., 2018). With the exception of some species of the genera *Lathrolestes* Förster, 1869 and *Megaceria* Szépligeti, 1908 (Gauld, 1984; Barron, 1994; Reshchikov et al., 2010), all ctenopelmatines whose biology is known are koinobiont endoparasitoids of sawflies (Hymenoptera, Pamphilioidea and Tenthredinoidea) (Broad et al., 2018).

The known Oriental ctenopelmatine fauna comprises 85 species belonging to 30 genera (Yu et al., 2016; Reshchikov et al., 2017a, b, 2022; Reshchikov and van Achterberg 2018; Li et al., 2022; Ranjith et al.,

2024). One of these is the genus *Gilen* Reshchikov & van Achterberg, 2018 which was recently described from Southeast Asia (Reshchikov & van Achterberg, 2018). It belongs to the tribe Perilissini as indicated by the combination of tyloids on the first flagellomeres, pectinate tarsal claws and large glymma. *Gilen* along with the genera *Lathrolestes* Förster, 1869, *Priopoda* Holmgren, 1856 and *Neurogenia* Roman, 1910, have the hypo-stomal carina separated from the occipital carina ventrally, sometimes joining the occipital carina at the base of the mandible. The genus can be distinguished from all other genera of Ctenopelmatinae, and indeed all other Darwin wasps, by its produced mid-longitudinal facial projection, and also from other Perilissini by the lower mandibular tooth being much longer than the upper, the occipital carina incomplete dorsally and joining the hypostomal carina at the base of the mandible, the occiput with distinct concavity, T1–3 with weak transverse impressions, and the last visible sternites of the male having concave hind margins.

The initially monotypic genus was based on the type species, *G. orientalis* Reshchikov & van Achterberg, 2018, which is known from Laos, Northern Thailand and Vietnam. Here we describe a second species, *Gilen principissa* Chansri, Kerkig & Reshchikov sp. nov., from central Thailand and provide a molecular phylogeny based on the barcoding region of cytochrome oxidase *c* subunit 1 (COI) including representatives of all Ctenopelmatinae tribes.

TABLE 1. *Gilen* and outgroup specimens used for molecular analyses with their provenances and GenBank accession numbers for sequence analysed.

Tribe	Species	Provenance	GenBank accession No.
Ctenopelmatini	<i>Ctenopelma nigrum</i>	Finland	JF963180
Ctenopelmatini	<i>Ctenopelma sanguineum</i>	USA	MK959405
Ctenopelmatini	<i>Xenoschesis fulvicornis</i>	Switzerland	MW056248
Ctenopelmatini	<i>Xenoschesis limata</i>	Canada	MK959495
Ctenopelmatini	<i>Xenoschesis ustulata</i>	Finland	MZ626537
Euryproctini	<i>Barytarbes honestus</i>	USA	MK959387
Euryproctini	<i>Euryproctus nemoralis</i>	Germany	MK642994
Euryproctini	<i>Euryproctus sentinis</i>	USA	MK959423
Euryproctini	<i>Gunomeria sordida</i>	Austria	JF963363
Euryproctini	<i>Hadrodactylus seldoviae</i>	USA	KU496749
Euryproctini	<i>Hadrodactylus vulneratus</i>	Finland	JF963368
Euryproctini	<i>Hypamblys albopictus</i>	Canada	KR790876
Euryproctini	<i>Hypamblys</i> sp.	Canada	KR406928
Euryproctini	<i>Mesoleptidea cingulata</i>	Canada	MG354808
Euryproctini	<i>Mesoleptidea</i> sp.	Canada	KR928907
Euryproctini	<i>Mesoleptidea stalii</i>	Denmark	JF963574
Euryproctini	<i>Occapes hinzi</i>	Denmark	KU373457
Euryproctini	<i>Pantorhaestes xanthostomus</i>	Canada	MG349317
Euryproctini	<i>Phobetes nigriceps</i>	Finland	JF963753
Euryproctini	<i>Rhytidiphora thailandica</i>	Thailand	OK623371
Euryproctini	<i>Syndipnus lateralis</i>	Canada	MG349607
Euryproctini	<i>Syndipnus</i> sp.	Canada	HQ566593
Euryproctini	<i>Synodites lineiger</i>	Finland	JF963864
Euryproctini	<i>Synomelix albipes</i>	Canada	MG503577
Euryproctini	<i>Synomelix faciator</i>	Finland	JF963865
Euryproctini	<i>Synomelix</i> sp.	Canada	KR797773
Mesoleiini	<i>Alexeter gracilentus</i>	Finland	JF962870
Mesoleiini	<i>Alexeter multicolor</i>	Finland	JF962872
Mesoleiini	<i>Alexeter nebulator</i>	China	MT252844
Mesoleiini	<i>Anoncus bipunctatus</i>	Finland	MZ622856
Mesoleiini	<i>Campodorus ultimus</i>	Canada	MN674254
Mesoleiini	<i>Himerta</i> sp.	Canada	KR933726
Mesoleiini	<i>Hyperbatus segmentator</i>	Finland	MZ628970
Mesoleiini	<i>Lagarotis debitor</i>	Finland	MZ627298
Mesoleiini	<i>Mesoleius affinis</i>	Finland	JF963569
Mesoleiini	<i>Otlophorus hypomelas</i>	Finland	MZ628273
Mesoleiini	<i>Rhinotorus</i> sp.	Canada	FJ414416
Mesoleiini	<i>Saotis longiventris</i>	Canada	MN683217
Mesoleiini	<i>Scopesis polita</i>	Canada	MG497546
Perilissini	<i>Absyrtus vicinator</i>	Germany	MK643008
Perilissini	<i>Gilen orientalis</i>	Thailand	PQ576533
Perilissini	<i>Gilen orientalis</i>	Thailand	PQ576534
Perilissini	<i>Gilen principissa</i> sp. nov.	Thailand	PQ576535
Perilissini	<i>Lathrolestes nigricollis</i>	USA	GQ325435
Perilissini	<i>Lophyproplectus oblongopunctatus</i>	Canada	KR874312
Perilissini	<i>Neurogenia</i> sp.	China	JF963655
Perilissini	<i>Oetophorus naevius</i>	Canada	MG350538
Perilissini	<i>Opheltes</i> sp.	Canada	MW056298
Perilissini	<i>Perilissus albitarsis</i>	United Kingdom	JF963715
Perilissini	<i>Perilissus concolor</i>	USA	MK959461
Perilissini	<i>Perilissus spilonotus</i>	Finland	MZ627144
Perilissini	<i>Priopoda</i> sp.	Russia	JF963793
Perilissini	<i>Zaplethocornia procurator</i>	United Kingdom	JF963963
Pionini	<i>Pion fortipes</i>	Finland	MZ625773
Pionini	<i>Pion nigripes</i>	Finland	MZ625741
Pionini	<i>Pion</i> sp.	Germany	MK642990
Pionini	<i>Rhorus longigena</i>	Canada	MN666112
Pionini	<i>Sympherta fucata</i>	USA	MK959487

TABLE 1. continued.

Tribe	Species	Provenance	GenBank accession No.
Pionini	<i>Trematopygus micrator</i>	Canada	KR791240
Pionini	<i>Trematopygus</i> sp.	Germany	JF963903
Scolobatini	<i>Scolobates auriculatus</i>	Canada	KR416726
Scolobatini	<i>Scolobates ruficeps</i>	South Korea	KU753367
Seleucini	<i>Seleucua cuneiformis</i>	Japan	MK959479
Westwoodiini	<i>Physotarsus fabioi</i>	Costa Rica	HQ548633
Outgroup	<i>Eclytus ornatus</i>	Finland	MZ625402
Outgroup	<i>Oedemopsis scabricula</i>	Finland	MZ628004
Outgroup	<i>Polyblastus varitarsus</i>	Canada	HM414321

MATERIALS AND METHODS

Specimens included in the present study were collected using Malaise traps. This research was carried out under the National Park Permission (0907.4/18722). Type specimens are deposited in the Collection of the Insect Museum, Chulalongkorn University Museum of Natural History, Bangkok, Thailand (CUMZ).

The previous records of *G. orientalis* distributions (Reshchikov and van Achterberg, 2018) and the new information on *G. orientalis* and *G. principissa* in this study were utilised to modify the distribution map of both *Gilen* species in Southeast Asia.

A sequence was generated for the COI barcoding region from a leg of the holotype of the new species by the Centre for Biodiversity Genomics, University of Guelph, based on standard protocols (Hebert et al., 2003; Park et al., 2010).

A data matrix was assembled including sequences from both *Gilen* species together with other Ctenopelmatinae species, collectively representing all tribes and almost all genera for which sequence data are available (Table 1). Alignment was trivial, as there were no indels. A maximum likelihood phylogeny was generated using raxmlGUI 2.0 with a GTRGAMMA substitution model applied to each codon position and employing rapid bootstrap (Silvestro and Michalak, 2012; Stamatakis, 2014; Edler et al., 2021). The phylogeny was rooted using representatives of three different tribes of Tryphoninae. Rapid bootstrap support was assessed using 1,000 replicates with the following command: -T 2 -f a -x 714733 -p 714733 -N 1000 -m GTRGAMMA -k -O.

Images were acquired digitally using a Leica M205 C stereomicroscope with a Leica DMC5400 digital camera and stacked using LAS X software.

Morphological terminology follows Broad et al. (2018) and is aligned with the Hymenoptera Anatomy Ontology (HAO) (Yoder et al., 2010). For cuticular sculpture terminology we follow Harris (1979).

World checklist and distribution of *Gilen* species

Gilen orientalis Reshchikov & van Achterberg, 2018
Laos (Khammouane), Thailand (Phitsanulok and Chiang Mai) [additionally recorded from Nakhon Ratchasima, see Discussion] and Vietnam (Dak Lak and Dong Nai)

Gilen principissa Chansri, Kerkig & Reshchikov sp. nov. Thailand (Nakhon Nayok) (Fig. 1)

Key to species of genus *Gilen* Reshchikov & van Achterberg

1. Height of facial projection $0.57 \times$ width of face (Fig 4B). Dorsal part of mesopleuron and mesosternum yellowish (Fig. 4A, C, D). First tarsomere of hind leg 6.6 times as long as broad and *G. orientalis*
- Height of facial projection $0.47 \times$ width of face (Fig 2C). Dorsal part of mesopleuron and mesosternum black (Figs 2A, 3B). First tarsomere of hind leg 8.0 times as long as broad *G. principissa* sp. nov.

RESULTS

Systematics

Subfamily Ctenopelmatinae Förster, 1869

Genus *Gilen* Reshchikov & van Achterberg, 2018

Type species.— *Gilen orientalis* Reshchikov & van Achterberg, 2018

Gilen principissa Chansri, Kerkig & Reshchikov, sp. nov.

<http://zoobank.org/urn:lsid:zoobank.org:act:BF0B455F-8784-4959-9CE9-B9890D37A2B0>

(Figs 2, 3)

Material examined.— Holotype ♀, THAILAND, Nakhon Nayok, Khao Yai National Park, 1–14.viii.2019,

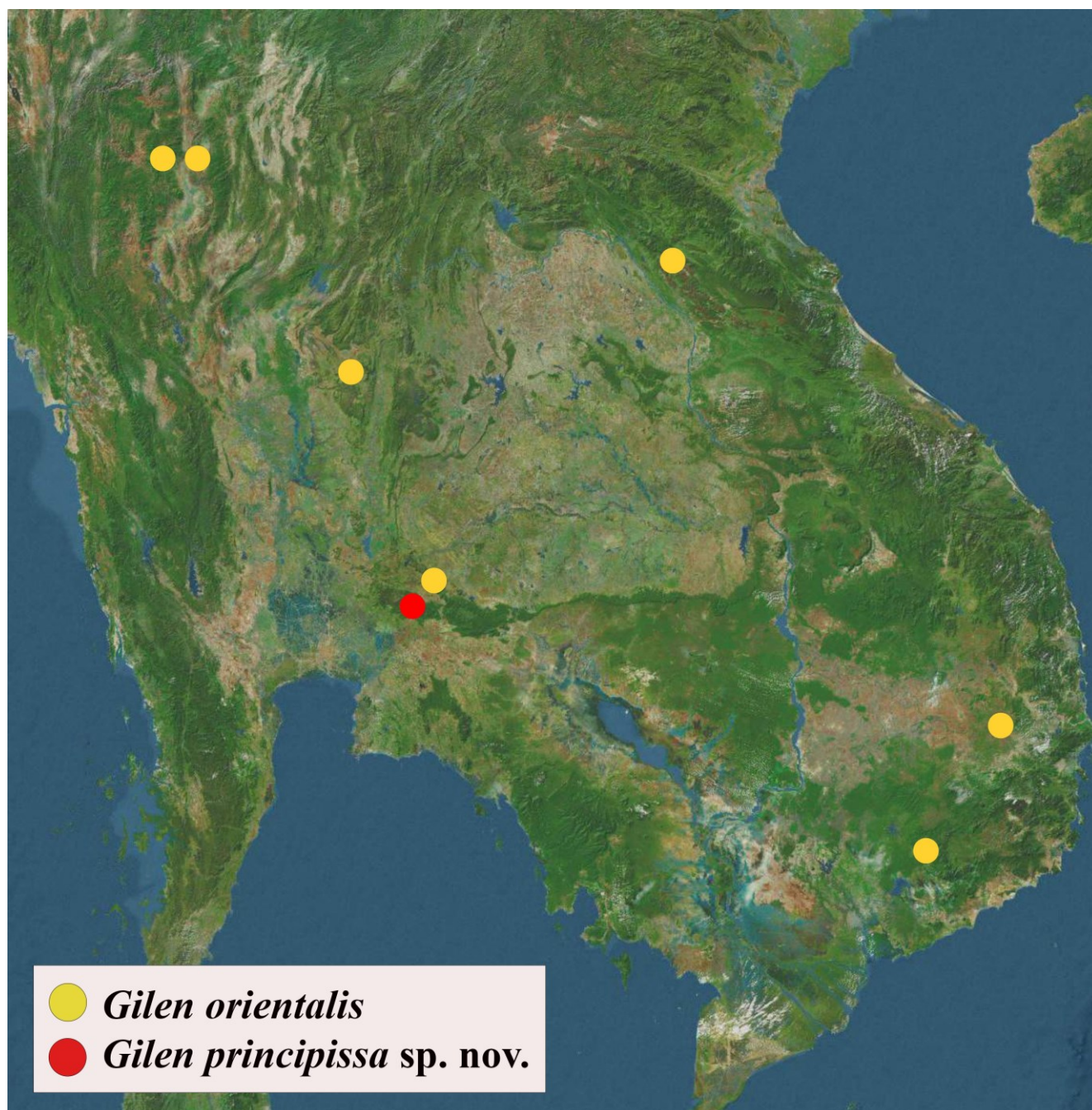


FIGURE 1. Distribution of the genus *Gilen* in Southeast Asia.

14°26.044'N, 101°22.596'E, 694m., Malaise trap, col. W. Atsawasiramanee, DNA voucher CCDB-45428-H11, BIN BOLD:AFJ0103, GenBank accession number PQ576535 (CUMZ). Paratypes 1♀, THAILAND, Nakhon Nayok, Khao Yai National Park, 1–14.viii.2019, 14°26.044'N, 101°22.596'E, 694m., Malaise trap, col. W. Atsawasiramanee (CUMZ), and 2♀, THAILAND, Nakhon Nayok, Khao Yai National Park, 15–28.viii.2020, 14°26.044'N, 101°22.596'E, 694m., Malaise trap, col. W. Atsawasiramanee (CUMZ).

Diagnosis.— *Gilen principissa* sp. nov. can be differentiated from *Gilen orientalis* as follows: height of facial projection $0.47\times$ width of face ($0.57\times$ width of face in *G. orientalis*), blackish markings on dorsal part of mesopleuron and mesosternum (pale yellow in *G. orientalis*), first tarsomere of hind leg 8.0 times as long as broad (6.6 times as long as broad in *G. orientalis*).

Description.— Holotype. ♀, length of body 7.0 mm. Fore wing 7.7 mm.

Head. Antenna slender, approximately as long as fore wing, with 37–39 flagellomeres. Scape almost as

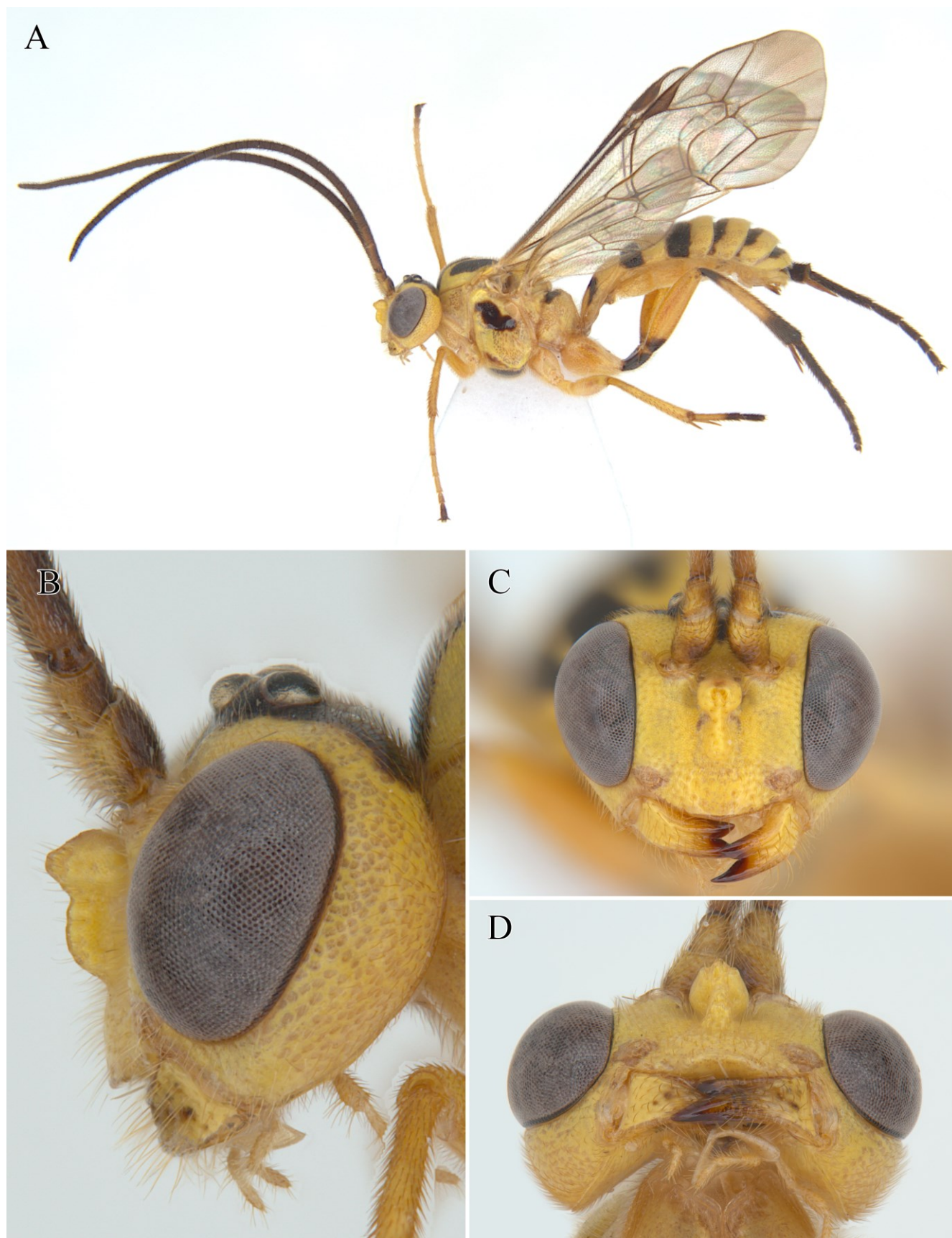


FIGURE 2. Light micrographs of *Gilen principissa* sp. nov., holotype female **A** habitus, lateral view **B** head, lateral view **C** face, anterior view **D** head, ventral view.



FIGURE 3. Light micrographs of *Gilen principissa* sp. nov., holotype female **A** mesosoma (apical part), dorsal view **B** mesosoma, lateral view **C** propodeum, dorsal view **D** mesosoma, propodeum and metasoma, dorsal view.

long as broad (Fig. 2A, B). Clypeus flat (Fig. 2C), its lower margin blunt and more or less bulging apically. Head narrowed behind eyes, matt, impunctate and shagreened. Lateral ocellus separated from eye margin by 1.5 times its widest diameter. Face with mid-longitudinal projection (goblet-shaped in anterior view) (Fig. 2C). In its dorsal part it is joined by carina to antennal socket, distal tip of this projection with a lateral impression (Fig. 2D). Clypeus 0.2 times as high as wide, not separated from face. Malar space 0.38 times basal mandible width.

Mesosoma. Mesoscutum matt, finely punctate. Mesopleuron weakly shining, setose and sparsely punctate (Fig. 3A, B). Propodeal carina complete (Fig. 3C, D). Area basalis absent (fused with area superomedia). Area superomedia heptagonal. Spiracles round, as long as broad.

Wings. Fore wing with areolet petiolate. Pterostigma receiving vein Rs+2r at its basal 0.35. Vein 2m-cu with a single bulla. Hind wing with cu-a receiving Cu1 well below middle (Fig. 2A).

Legs. Hind femur 4.0 times as long as broad. Hind tibia 7.0 times as long as apically broad (Fig. 2A). First tarsomere of hind leg 8.0 times as long as broad and 2.2 times as long as second tarsomere. Ovipositor sheath 0.2 times as long as hind tibia.

Metasoma. Distinctly and densely punctate, sparsely setose. T1 as long as broad with latero-median carina defined. Glymma deep. T1–3 with slight transverse impression (Fig. 3D). Ovipositor sheath 0.2 times as long as hind tibia.

Colour. Body yellow, except for the following, which are marked with black or piceous: antenna (dorsally), teeth of mandible, dorsal part of head (frons medio-posteriorly, vertex and occiput medially), pterostigma, fifth tarsomere of fore leg, distal part of first tarsomere and second to fifth tarsomeres of middle leg, hind trochanter, proximal edge of hind femora, proximal and distal edges of hind tibia, hind tarsus entirely, most of mesonotum, dorsal part of mesopleuron, mesosternum, anterior part of propodeum, middle transverse stripe of T1 and dorso-anteriorly parts of further tergites.

Distribution.– Khao Yai National Park, Nakhon Nayok, Thailand.

Biology.– Unknown.

Etymology.– This species name “*principissa*” refers to Her Royal Highness Princess Maha Chakri Sirindhorn, noun in apposition, gender feminine

***Gilen orientalis* Reshchikov & van Achterberg 2018**
(Fig. 4)

Material examined.– ♂, THAILAND, Nakhon Ratchasima, Sakaerat Environmental Research Station, 14°49.672'N, 101°91.615'E, 496m., 30.iv.2021–10.v.2021, Malaise trap, col. K. Chansri, DNA voucher CCDB-32186-D09 (CUMZ). 1♂, THAILAND, Nakhon Ratchasima, Sakaerat Environmental Research Station, 14°49.672'N, 101°91.615'E, 496m., 21–31.v.2021, Malaise trap, col. K. Chansri, DNA voucher CCDB-32186-D10 (CUMZ). 1♂, THAILAND, Nakhon Ratchasima, Sakaerat Environmental Research Station, 14°49.672'N, 101°91.615'E, 496m., 21–31.v.2021, Malaise trap, col. K. Chansri, DNA voucher CCDB-45428-H10, BIN BOLD:AFI9295, GenBank accession number PQ576536 (CUMZ). 1♂, THAILAND, Nakhon Ratchasima, Sakaerat Environmental Research Station, 14°49.672'N, 101°91.615'E, 496m., 21–31.v.2021, Malaise trap, col. K. Chansri, DNA voucher CCDB-45428-H11, BIN BOLD:AFI9295, GenBank accession number PQ576537 (CUMZ).

Phylogenetic analysis and sequence divergence

The molecular phylogeny is shown in Figure 5. Bootstrap support was generally weak except for clades of closely related species, and none of the traditional tribes were recovered as monophyletic; however, the tribes are difficult to separate morphologically and it is quite possible that some are actually polyphyletic or paraphyletic with respect to members of other tribes.

The majority of Perilissini were recovered in one clade except for the sequence of *Zaplethocornia procurator*. However, the Scolobatini (two representatives of the genus *Scolobates*) were recovered nested within this clade. *Gilen principissa* sp. nov. was recovered with 100% bootstrap support as sister to *Gilen orientalis*, nested within the Perilissini. However, the internal branch leading to them is one of the longest in the tree, and inspection of the sequences shows that the two species differ at 88 positions out of 658 (13.4%) a large degree of divergence for congeners. More than 50% of these differences were C ↔ T transitions.

DISCUSSION

The morphological characters of the new species, *Gilen principissa* sp. nov., readily place it within the genus *Gilen* and in the molecular phylogeny the two species formed a monophyletic group with 100% bootstrap support. However, despite the large molecular divergence, it is morphologically very similar to *G.*

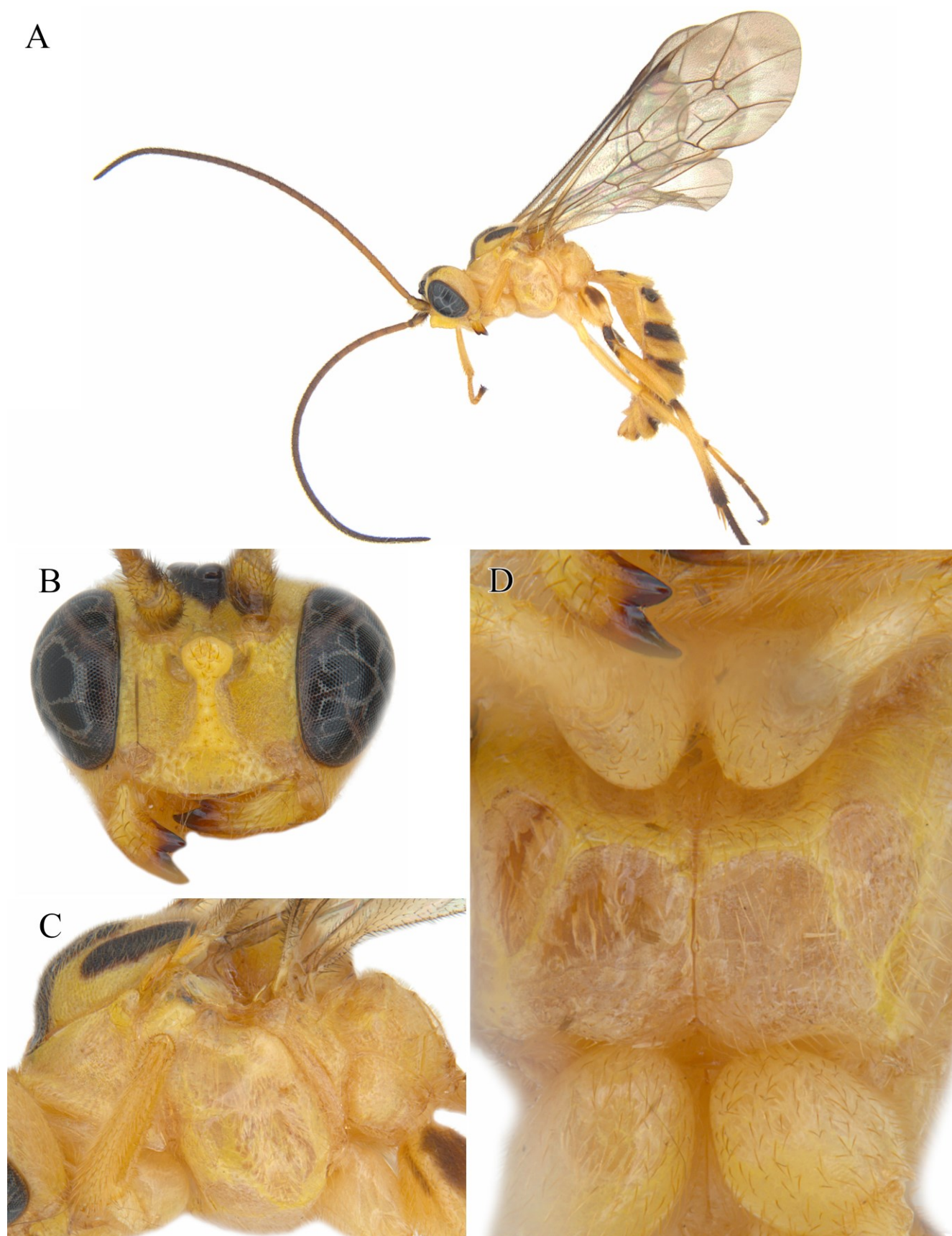


FIGURE 4. Light micrographs of *Gilen orientalis* Reshchikov & van Achterberg 2018 **A** habitus, lateral view **B** face, anterior view **C** mesosoma, lateral view **D** mesosoma, ventral view.

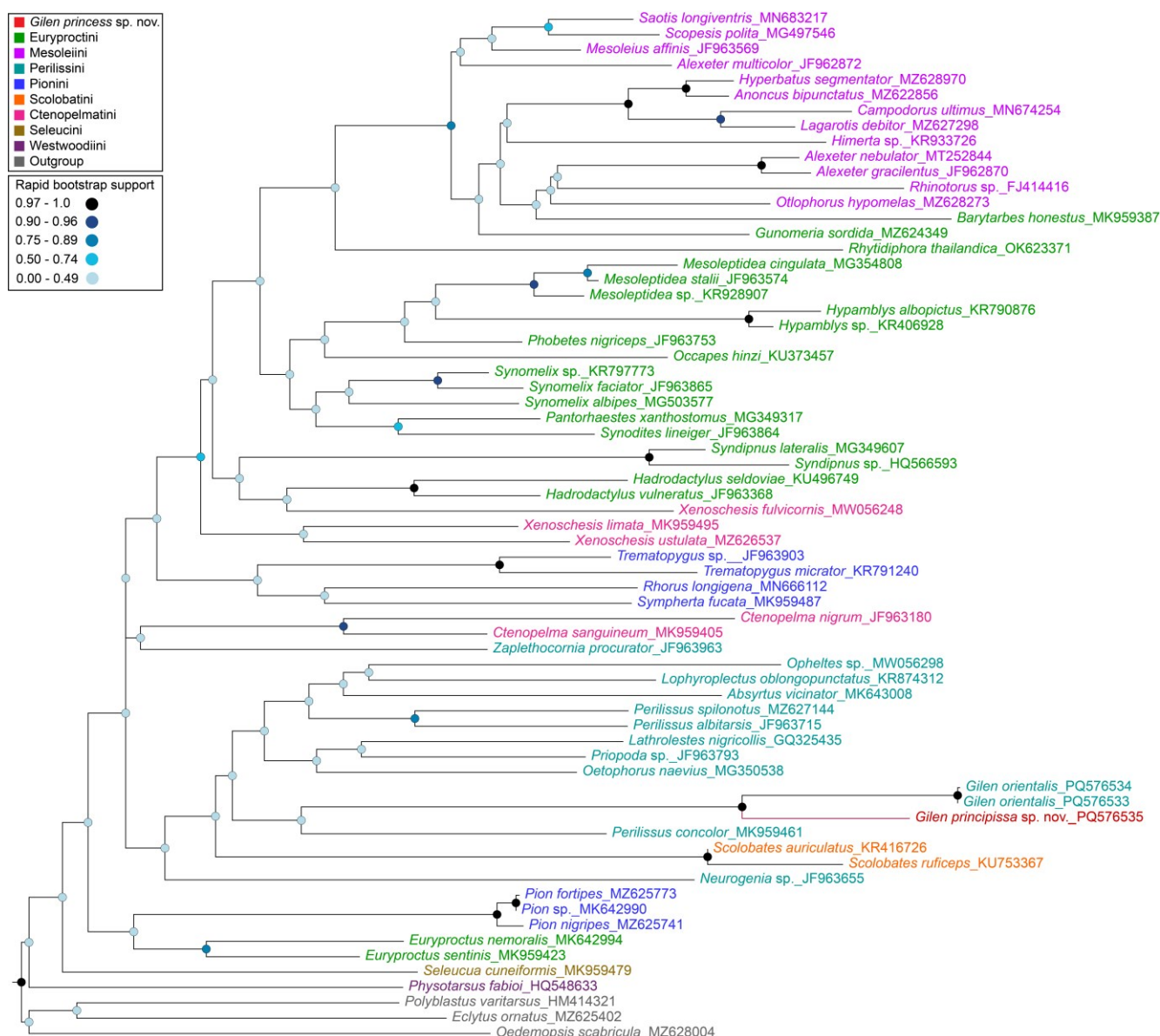


FIGURE 5. Maximum likelihood tree showing the relationship of *Gilen* with respect to other members of the Ctenopelmatinae based on the barcoding region of cytochrome oxidase subunit 1 (COI) with rapid bootstrap support values.

orientalis. *G. orientalis* was recorded for the first time in northeastern Thailand.

The very large molecular divergence between *G. principissa* sp. nov. and *G. orientalis*, suggests that they probably diverged more than six and 13 million years ago, but in the absence of a dated molecular phylogeny of ichneumonid subfamilies and reasonable estimate of the age of the crown ctenopelmatines, we cannot apply a dated molecular clock to the data.

ACKNOWLEDGEMENTS

We are grateful to the Department of National Parks, Wildlife and Plant Conservation for permission to collecting the specimens; Khao Yai National Park

Officers for help and providing facilities at Khao Yai National Park; Mr Surachit Waengsothorn for providing facilities at the Sakaerat Environmental Research Station. KC was supported by CU Graduate School Thesis Grant (GCUGR1225641025D), and The Second Century Fund (C2F), Chulalongkorn University. PK was supported by CU Graduate School Thesis Grant (GCUGR1225641029D). DLJQ was supported by a postdoctoral fellowship from the Rachadaphiseksomphot Fund, Graduate School, Chulalongkorn University. This research is funded by Thailand Science Research and Innovation Fund Chulalongkorn University (BCG_FF_68_178_2300_039), Rachadaphiseksomphot Fund (RU66_008_2300_002) and RSPG Chula to BAB.

LITERATURE CITED

- Barron, J.R. 1994. The Nearctic species of *Lathrolestes* (Hymenoptera, Ichneumonidae, Ctenopelmatinae). Contributions of the American Entomological Institute, 28: 1–135.
- Bennett, A.M.R., Cardinal, S., Gauld, I.D. and Wahl, D.B. 2019. Phylogeny of the subfamilies of Ichneumonidae (Hymenoptera). Journal of Hymenoptera Research, 71: 1–156.
- Broad, G.R., Shaw, M.R. and Fitton, M.G. 2018. Ichneumonid Wasps (Hymenoptera: Ichneumonidae): their Classification and Biology. Royal Entomological Society and the Field Studies Council, Handbooks for the Identification of British Insects, 7: 1–418.
- Edler, D., Klein, J., Antonelli, A. and Silvestro, D. 2021. raxmlGUI 2.0: A graphical interface and toolkit for phylogenetic analyses using RAxML. Methods in Ecology and Evolution, 12: 373–377.
- Gauld, I.D. 1984. An Introduction to the Ichneumonidae of Australia. British Museum (Natural History), London 413 pp.
- Gauld, I.D., Wahl, D., Bradshaw, K. and Hanson, W.S. 1997. The Ichneumonidae of Costa Rica, 2. Introduction and keys to species of the smaller subfamilies, Anomaloninae, Ctenopelmatinae, Diplazontinae, Lycorininae, Phrudinae, Tryphoninae (excluding Netelia) and Xoridinae, with an appendices on the Rhyssinae. Memoirs of the American Entomological Institute, 57: 1–485.
- Harris, R.A. 1979. A glossary of surface sculpturing. Occasional Papers in Entomology of the California Department of Food and Agriculture, 28: 1–31.
- Hebert, P.D.N., Cywinska, A., Ball, S.L. and de Waard J.R. 2003. Biological identification through DNA barcodes. Proceedings of the Royal Society of London Series A: Biological Sciences, 270: 96–99.
- Kasparyan, D.R. 2020a. A new ichneumonid genus (Hymenoptera: Ichneumonidae: Ctenopelmatinae) from the south of Russian Far East. Zoosystematica Rossica, 29: 296–300.
- Kasparyan, D.R. 2020b. Two New Palaearctic genera of the Ichneumon wasp Tribe Mesoleiini (Hymenoptera, Ichneumonidae: Ctenopelmatinae) with pectinate tarsal claws. Entomological Review, 100: 1370–1386.
- Li, T., Sun, S.P. and Sheng, M.L. 2022. A new genus and species of Ctenopelmatinae (Hymenoptera, Ichneumonidae) from China. Journal of Hymenoptera Research, 92: 199–210.
- Park, D.S., Suh, S.J., Oh, H.W. and Hebert, P.D.N. 2010. Recovery of the mitochondrial COI barcode region in diverse Hexapoda through tRNA-based primers. BMC Genomics, 11: 1–7.
- Quicke, D.L.J., Laurenne, N.M., Fitton, M.G. and Broad, G.R. 2009. A thousand and one wasps: a 28S rDNA and morphological phylogeny of the Ichneumonidae (Insecta: Hymenoptera) with an investigation into alignment parameter space and elision. Journal of Natural History, 43: 1305–1421.
- Ranjith, A.P., Quicke, D.L.J., Reshchikov, A. and Butcher, B.A. 2024. A new enigmatic genus of the ichneumonid subfamily Ctenopelmatinae (Hymenoptera, Ichneumonidae) from Thailand. Journal of Hymenoptera Research, 97: 491–504.
- Reshchikov, A. and van Achterberg, C. 2018. The Unicorn exists! A remarkable new genus and species of Perilissini (Hymenoptera: Ichneumonidae) from South East Asia. Acta Entomologica Musei Nationalis Pragae, 58: 523–529.
- Reshchikov, A., Choi, J.K. and Lee, J.W. 2017a. Four new species of the genus *Lathrolestes* Förster, 1869 from South Korea (Hymenoptera, Ichneumonidae, Ctenopelmatinae). ZooKeys, 657: 81–92.
- Reshchikov, A., Choi, J.K., Xu, Z.F. and Pang, H. 2017b. Two new species of the genus *Rhorus* Förster, 1869 from Thailand (Hymenoptera, Ichneumonidae). Journal of Hymenoptera Research, 54: 79–92.
- Reshchikov, A., Quicke, D.L.J. and Butcher, B.A. 2022. A remarkable new genus and species of Euryproctini (Hymenoptera: Ichneumonidae, Ctenopelmatinae) from Thailand. European Journal of Taxonomy, 834: 102–116.
- Reshchikov, A.V., Soper, A. and Van Driesche R.G. 2010. Review and key to Nearctic *Lathrolestes* Foerster (Hymenoptera: Ichneumonidae), with special reference to species attacking leaf mining tenthredinid sawflies in *Betula* Linnaeus (Betulaceae). Zootaxa, 2614: 1–17.
- Silvestro, D. and Michalak, I. 2012. raxmlGUI: a graphical front-end for RAxML. Organisms Diversity and Evolution, 12: 335–337.
- Stamatakis, A. 2014. Raxml version 8: a tool for phylogenetic analysis and post-analysis of large phylogenies. Bioinformatics, 30: 1312–1313.
- Townes H.K. 1970. The genera of Ichneumonidae, Part 3. Memoirs of the American Entomological Institute, 13: 307.
- Yoder, M.J., Mikó, I., Seltmann, K.C., Bertone, M.A. and Deans, A.R. 2010. A gross anatomy ontology for Hymenoptera. PLoS ONE, 5: e15991.
- Yu, D.S., van Achterberg, K. and Horstmann, K. 2016. World Ichneumonidea 2015. Taxonomy, Biology, Morphology and Distribution. [Flash drive]. Taxapad®, Vancouver, Canada.