geodiversitas

2025 • 47 • 6

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art. 47 (6) — Published on 20 March 2025
www.geodiversitas.com

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Geodiversitas *is a fast track journal published by the Museum Science Press, Paris*

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Diffusion – Publications scientifiques Muséum national d'Histoire naturelle
CP 41 – 57 rue Cuvier F-75231 Paris cedex 05 (France)
Tél. : 33 (0)1 40 79 48 05 / Fax : 33 (0)1 40 79 38 40
diff.pub@mnhn.fr / http://sciencepress.mnhn.fr

ISSN (imprimé / *print*) : 1280-9659/ ISSN (électronique / *electronic*) : 1638-9395

Spider wasps (Hymenoptera: Pompilidae) from Xiede (Eocene, central Tibetan Plateau): systematics and paleoecological implications

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Submitted on 6 March 2024 | accepted on 27 July 2024 | published on 20 March 2025

urn:lsid:zoobank.org:pub:95F23A1E-018C-42CA-806A-0CCD8D4FCC80

Xu X.-T., Waichert C., Deng W.-Y.-D., Su T.& Béthoux O. 2025. — Spider wasps (Hymenoptera: Pompilidae) from Xiede (Eocene, central Tibetan Plateau): systematics and paleoecological implications. *Geodiversitas* 47 (6): 313-325. https://doi.org/10.5252/geodiversitas2025v47a6. http://geodiversitas.com/47/6

ABSTRACT

Spider wasps (Pompilidae), best known for capturing and paralysing a spider to serve as food resource for the larva, commonly placed together in an underground nest, is represented by about 5000 extant species. The fossil record of this diverse family spans from the Eocene to the Miocene, with 26 occurrences to date, but only four of them are well-ascertained members of the Pompilinae, one of the most diverse Pompilidae subfamilies. Herein, we report two new records of fossil Pompilinae, namely *Gubuzhu orientalis* n. gen., n. sp. and *Paleoferreolina xiedensis* n. gen., n. sp., from the Xiede

KEY WORDS
Fossil insect,
Pompilini,
nesting behaviour,
Tibetan Plateau,
new genus,
new species.

locality (Niubao Formation, Nima Basin, central Tibetan Plateau, China). The former species can be confidently assigned to the tribe Pompilini, while the latter shares morphological similarities with members of Aporini, as well as members of other tribes within Pompilidae. The two new species represent the earliest occurrences of Pompilinae, and the first ones at Asian deposits, suggesting that the subfamily was already widespread in the Northern Hemisphere during the late Eocene. Moreover, *Gubuzhu orientalis* n. gen., n. sp. lacked a tarsal comb, indicating that it may have had a limited excavation activity in its nesting behaviour.

MOTS CLÉS
Insecte fossile,
Pompilini,
comportement de nidification,
plateau tibétain,
genre nouveau,
espèce nouvelle.

RÉSUMÉ

Les pompiles (Hymenoptera: Pompilidae) de Xiede (Éocène, plateau tibétain central): systématique et implications paléoécologiques.

Les pompiles (Pompilidae), bien connues pour capturer et paralyser une araignée pour servir de ressource alimentaire à la larve, communément placées ensemble dans un nid souterrain, sont représentées par 5000 espèces actuelles. Le registre fossile de cette famille diversifiée s'étend de l'Éocène au Miocène, avec 26 occurrences à ce jour, mais seulement quatre d'entre elles sont assignées avec certitude aux Pompilinae, une des sous-familles les plus diverses de Pompilidae. Nous signalons ici deux nouvelles occcurrences de Pompilinae fossiles, *Gubuzhu orientalis* n. gen., n. sp. et *Paleoferreolina xiedensis* n. gen., n. sp., de la localité de Xiede (Formation Niubao, Bassin de Nima, Plateau Tibétain central, Chine). La première espèce peut être attribuée avec certitude à la tribu des Pompilini, tandis que la seconde partage des similitudes morphologiques avec les membres des Aporini, ainsi qu'avec les membres d'autres tribus au sein des Pompilidae. Les deux nouvelles espèces représentent donc la plus ancienne occurrence du groupe des Pompilinae, et la première occurrence en Asie, ce qui suggère que la sous-famille était déjà répandue dans l'hémisphère nord à la fin de l'Éocène. De plus, *Gubuzhu orientalis* n. gen., n. sp. n'avait pas de peigne tarsal, ce qui indique qu'elle pourrait avoir eu une activité d'excavation limitée dans son comportement de nidification.

INTRODUCTION

Wasps of the family Pompilidae Latreille, 1804 are commonly known as 'spider wasps' for the female exclusively hunts and paralyzes a spider as provision for each larva. The majority of Pompilidae nest in underground burrows and glue a single egg on the abdomen of a paralyzed spider (Wasbauer & Kimsey 1985; Day 1988). The sequence and composition of actions undertaken by spider wasps in the oviposition process vary, allowing ethological types to be outlined. For example, the vast majority of Pompilidae belong to the ethological type VPTIOC, entailing the following sequence: Hunting → Paralysis → Transportation → Excavation of cell → Oviposition → Closing the cell (Evans 1953).

Pompilidae comprises about 217 extant genera and about 5000 species (Aguiar *et al.* 2013; Loktionov 2023). The family has traditionally been regarded as a taxonomically difficult group for their morphological homogeneity on one hand, and convergences due to similar ethological traits on the other (Waichert *et al.* 2015). Pompilidae is currently divided into five subfamilies, namely Pepsinae Lepeletier, 1845, Pompilinae Latreille, 1804, Ctenocerinae Shimizu, 1994, Ceropalinae Radoszkowski, 1888, and Notocyphinae Haupt, 1929 (Waichert *et al.* 2015). Pepsinae, Pompilinae and Ceropalinae bear cosmopolitan distribution; among them, the subfamily Pompilinae is one of the most diverse of all Pompilidae, along with Pepsinae, including approximately 2000 species (Pitts *et al.* 2006; Rodriguez *et al.* 2016a). Most of the Pompilinae inhabit relatively open habitats such as sand dunes, dry washes, margins of water bodies and forest openings (Wasbauer & Kimsey 1985). The fossil record of this diverse family spans from the Eocene to the Miocene, with 26 occurrences to date (Rodriguez *et al.* 2017 and references therein; Waichert *et al.* 2021; Loktionov *et al.* 2023; Colombo *et al.* 2024). Only six fossil species are assigned to Pompilinae, and the formal generic placement of two of them cannot be assessed (Rodriguez *et al.* 2017).

Herein, we report new material from the Xiede locality (Niubao Formation; Bartonian; central Tibetan Plateau, China) which can be assigned to two distinct species of Pompilinae, and propose a discussion regarding the age of the subfamily, as well as the ecological implications of their nesting behaviour.

MATERIAL AND METHODS

FOSSIL MATERIAL

Three fossil spider wasp adpressions investigated in this study were collected from the Xiede locality (31°58'23"N, 88°25'42"E, 4662 m a.m.s.l.; northern Kanggale Hill, central Tibetan Plateau, China; Xu *et al.* 2022: fig. 1). This locality belongs to the Xiede section of the Niubao Formation in Nima Basin. Fossil-bearing strata from this formation span across the Nima and Lunpola basins, which were considered age-equivalent. The age of the fossil site has been considered as ca. 39 Ma (Bartonian, Eocene; Fang *et al.* 2020; Xiong *et al.* 2022). It yielded a wide range of plants, vertebrates, and insects (e.g. Wu *et al.* 2017; Cai *et al.* 2019; Su *et al.* 2019; Deng *et al.* 2019; Zhang *et al.* 2022), the latter being represented by nearly four thousand specimens in the collection of the Xishuangbanna Tropical Botanical Garden (XTBG), assembled in the past few years (Xu 2024). The insect fauna has been only partly described, including a water strider (Lin 1981; Cai *et al.* 2019), a planthopper (Xu *et al.* 2021), a spittlebug (Xu *et al.* 2022), a damselfly (Xia *et al.* 2021), and a dragonfly (Huang *et al.* 2022).

The specimens described herein were excavated from two layers, XDA1 and XDB3 (see Zhang *et al.* 2022 for detailed information) and were fully exposed by the first author using preparation needles. They are housed in the Paleoecology Collections, XTBG (Mengla, China).

Data acquisition and preparation

Photographs were taken using a digital camera Canon EOS 5DS coupled to a Canon MP-E 65 mm macro lens (all Canon, Tokyo, Japan) equipped with a polarizing filter. Photographs were taken under polarized, and in some cases, ultraviolet light. The embedding rock was used as reference for white balance. The resulting photographs were optimized (and, if applicable, combined) using Adobe Photoshop CS6 (Adobe Systems, San Jose, CA, United States) and combined in various ways. The process is indicated in figure caption: for example, 'eth/b' indicates that the side B was photographed under ethanol; 'eth/ab' indicates that both sides of a specimen were photographed under ethanol and that the two resulting images were merged; and 'eth/ab-dry/ab-UV/ab' indicates that each side was photographed under ethanol, dry conditions, and UV light, and that the six resulting images were merged. Line drawings were produced using Adobe Illustrator CS6 (Adobe Systems, San Jose, CA, United States). Working document included several photographs (originals, or a combination of several) composing distinct layers of the working document. In line drawings, full lines indicate visible sclerite boundaries while translucent lines indicate supposed boundaries; the preserved colour pattern is represented in grey. Measurements were made on finalised drawings and on the best-exposed material. Both left and right sides of the specimens (e.g. both forewings) were measured if possible, and therefore a range of measurements are given.

Wing reconstruction

Insect wings are commonly crossed by flexion and folding lines (Wootton 1979), and this statement applies to Pompilidae (Danforth & Michener 1988). In resting position, folding lines allow the wing surface to fold as a fan, or an origami. In fossil specimens which experienced limited decay, folding lines may have remained active, forcing the wing in its resting configuration (i.e. folded). Conversely, more advanced decay may cause wings not only to be preserved unfolded but also possibly disrupted along flexion and folding lines, and/or damaged in their vicinity. This has been the case for some of the wings of the specimen XDA1-1419 (specifically, forewing 2 -FW2- and hindwing 2 -HW2), described herein. In order to ease comparison with extant taxa, these wings were tentatively reconstructed unfolded using the following procedure inspired by Béthoux *et al.* (2016): drawings of the unfolded wings (FW1 and HW1) were printed on tracing paper and folding lines were created and applied to these models. Successive attempts were made until the outcome would best match the venation pattern observed in the folded FW2 and HW2; concurrently, the venation pattern and the shape of the wing outline were modified. Ultimately, we resorted to the 'reflect tool' of Adobe Illustrator CS6 to ensure that the resulting, single vector drawing could be used to generate both folded (as observed on the fossil) and unfolded configurations.

Morphological terminology and homologies

Wing venation terminology follows that of Huber & Sharkey (1993: figs 19, 20). Other morphological terminology used in the descriptions is after Wasbauer & Kimsey (1985).

Abbreviations

1R1	first radial 1;
1Rs	first radial sector;
2M	second medial;
2m-cu	crossvein of second medial and cubitus;
2R1	first radial 2;
2Rs	second radial sector;
Cu	cubitus;
cu-a	crossvein of cubitus and anal vein;
de	Cu1 vein deflected downward at base;
e	compound eye;
FD	facial distance;
ft	foretarsomere;
FW	forewing;
HW	hindwing;
jl	jugal lobe;
LID	lower interocular distance;
M	media;
MID	middle interocular distance;
mst	mesotarsomere;
mtt	metatarsomere;
o	ocellus;
S	sternum;
spi	spines-like setae;
spu	spur;
T	tergite;
TFD	transfacial distance;
ti	tibia;
UID	upper interocular distance.

SYSTEMATIC PALAEONTOLOGY

Family Pompilidae Latreille, 1804
Subfamily Pompilinae Latreille, 1804
Tribe *Pompilini* Latreille, 1804

Genus *Gubuzhu* X.-T. Xu & C. Waichert, n. gen.

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Type species. — *Gubuzhu orientalis* X.-T. Xu & C. Waichert, n. sp.; monotypic genus.

Etymology. — From Chinese 'gu' (古), meaning 'ancient', and 'buzhu' (捕蛛), meaning 'catching spider'. Gender feminine.

Diagnosis. — As for the type species.

Gubuzhu orientalis X.-T. Xu & C. Waichert, n. gen., n. sp. (Figs 1-3; 5A)

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Type material. — **Holotype**. **China** • 1♀; West China, Xizang Autonomous Region, Naqu City, Shuanghu County, Xiede Village, Xiede locality; 31°58'23"N, 88°25'42"E; Xiede section, Nima Basin, Niubao Formation; Bartonian (Eocene); 4662 m a.m.s.l.; VI.2019; XTBG exped.; XTBG; XDA1-1419A, B.
Paratype. **China** • 1♀; same data as for the holotype; XDB3-0935A, B.

Etymology. — From Latin *oriēns* ('rising sun'), referring to the known area of occurrence of the species.

Type locality and stratigraphy. — Both holotype and paratype were collected at the Xiede locality (northern Kanggale Hill, Tibet, China); Xiede section, Nima Basin, Niubao Formation (see Zhang *et al.* 2022 for detailed information); Bartonian (Eocene; Fang *et al.* 2020; Xiong *et al.* 2022).

Diagnosis. — In female, the third antennal segment is about 3× as long as wide; the clypeus is trapezoidal; the pronotum is rather short; the metatibia bears apical spines-like setae, which are long, distinctly splayed, of irregular lengths and spacing; the forewing has three submarginal cells (1R1, 1Rs and 2Rs), and the vein Cu is distinctly deflected downward at base; the hindwing jugal lobe is large (about 0.70-0.75× the length of Cu cell); and the tergite 6 has dense, stiff, backward-directed bristles.

General description

Measurements (in mm)

Body length (excluding antenna) 11.8-14.8 (holotype 14.8; paratype 11.8).

Head. Compound eyes about 2.0-2.2× as long as wide (1.6-2.0 long and 0.7-1.0 wide in maximum); MID = 1.0-1.2; UID = 1.0-1.1; LID = 0.6-0.7; TFD = 3.0 (measured in holotype); FD = 2.6 (measured in holotype); third antennal segment about 2.8-2.9× as long as wide (0.7-0.8 long and 0.2-0.3 wide).

Mesosoma. 1.5× as long as wide (5.2 long and 3.5 wide in maximum; measured in holotype); propodeum 1.6 long and 3.5 wide in maximum (measured in holotype); metafemur about 3.3× as long as wide (2.0-2.7 long and 0.6-0.8 wide in maximum, measured in holotype); the longer metatibial spur 1.7-2.0× as long as third antennal segment (1.3-1.4 long); metabasitarsus 2.3-2.4 long.

Wings. Forewing 3.5-4.1× as long as wide (9.4 long and 2.7 wide in holotype; 8.2-8.3 long and 2.0-2.2 wide in paratype); hind wing 3.6× as long as wide (6.3 long and 1.7 wide in maximum; measured in holotype).

Metasoma. 6.2-7.6 long.

Head (Figs 1A, B; 2)

Almost as wide as long; TFD about 1.2× FD; TFD about 2.5× MID; compound eyes large, with inner margin slightly emarginate, 2.0-2.2× as long as wide, UID about 1.4× LID; ocelli in a compact triangle, nearer to each other than to compound eyes; vertex almost straight; clypeus short, trapezoidal, anterior margin straight; antenna elongate, thin, third antennal segment 2.8-2.9× as long as wide.

Mesosoma

Pronotum rather short, while delimitation of pronotum and scutum inconspicuous. Legs slender, metafemur 3.3-3.4× as long as wide (measured in holotype); protibia with one posterior spur (calcar), meso- and metatibia with two spurs; the longer metatibial spur 0.6× metabasitarsus length; metatibia with apical spines-like setae long, distinctly splayed, of irregular lengths and spacing (Fig. 1I, H); foretarsus lacking conspicuous spines on the outer side (Fig. 5A).

Forewing (Figs 1C, D; 3A, B)

Maximum width 0.2-0.3× its length, with 3 submarginal cells; 2R1 cell almost as long as its distance from wing tip; 2Rs cell longer than 1Rs cell; 2m-cu vein slightly bowed toward wing apex, meeting 2Rs cell 0.6× distance from base to apex of cell [i.e., length of the section of the basal posterior edge of 2Rs cell to the insertion of 2m-cu cross-vein (orange arrow on Fig. 3A) about 0.6× that of the entire posterior edge of 2Rs cell]; 2m-cu vein arising on Cu longer than or about half the distance from the base of 2M cell to the outer wing margin [i.e., section of Cu located between its insertion of 2cu-a and 2m-cu cross-veins (blue arrow on Fig. 3A), longer than or almost as long as the section of Cu located between its insertion of 2m-cu cross-vein to its projected termination on the wing margin (blue fame arrow on Fig. 3A)]; Cu vein distinctly deflected downward at base ('de' on Fig. 3A).

Hindwing (Fig. 1E, F)

With cu-a cross-vein reaching the M+Cu vein basal to the M/Cu split; jugal lobe very large, about 0.70-0.75× length of Cu cell (Fig. 1E, F; pink arrows on Fig. 3A, B).

Metasoma

First segment of metasoma inconspicuous for both specimens. Tergite 6 with dense, stiff, backward-directed bristles (Fig. 1J, K).

Coloration

Integument dark on head and mesosoma, lighter on metasoma; punctuation inconspicuous; forewing (Fig. 1C, D) hyaline, darkened in about ¼ of the apical portion, and a dark spot at ⅔ of wing length, partially covering cells 2R1, 1R1 1Rs, 2Rs, and 1M (Figs 1C; 2A).

Remarks on the type series

Holotype specimen, *XDA1-1419A,B* (Figs 1A, C, E, G, H, J; 2A; 5A), adpressions in both positive and negative aspects (but indistinguishable as a consequence of rock compression) of a nearly complete body in dorso-ventral orientation. Apex of FW2 partially folded (Figs 1A; 3A); FW1 well exposed, partly overlapping HW1 (Figs 1C; 2A). Tibia pale, almost invisible except for apical part; legs lack thick spines along length, with spurs, few apical spines on tibia and tarsi (Fig. 1G, H). Forewing coloration is well preserved (Figs 1C; 2A).

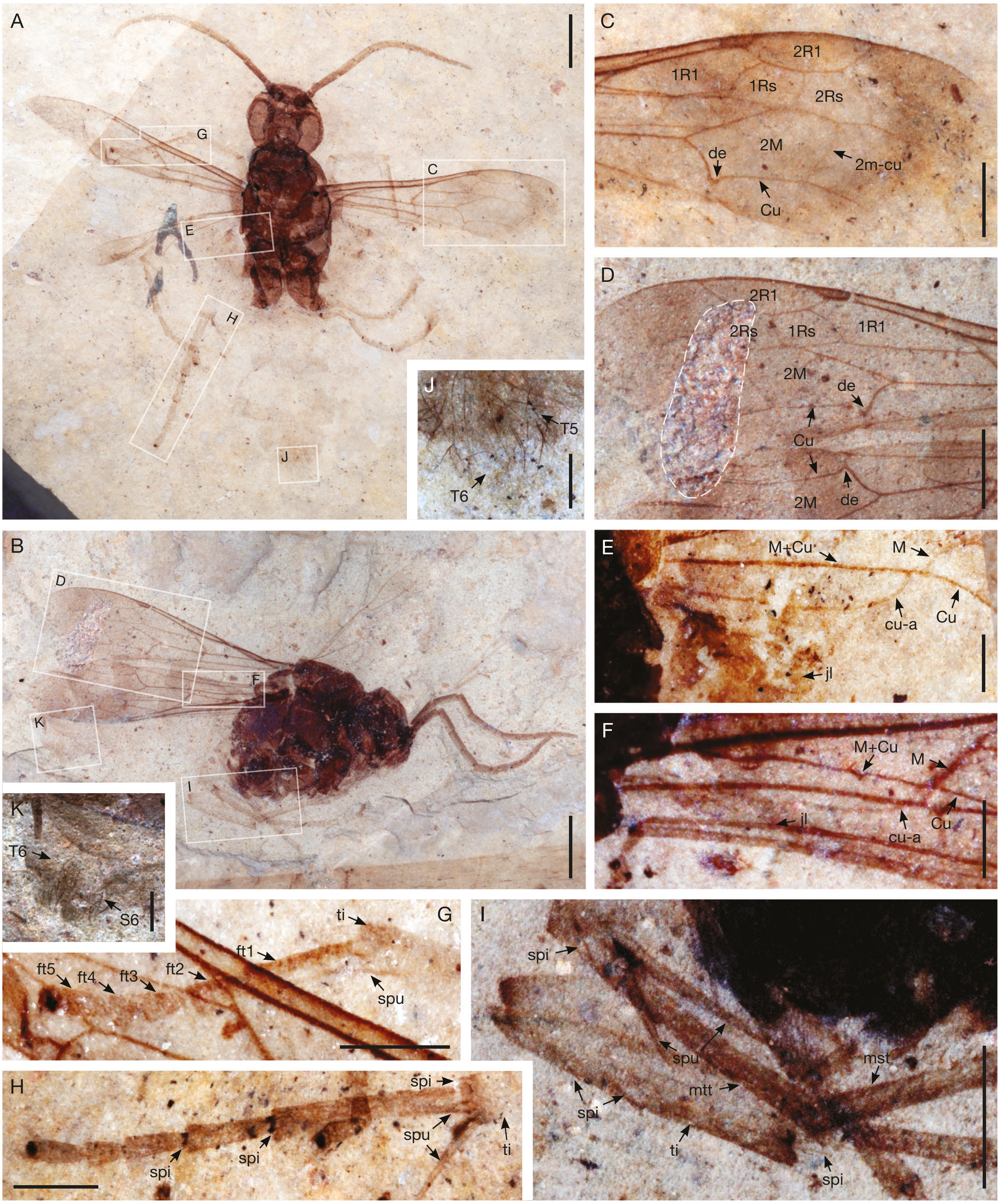

FIG. 1. — *Gubuzhu orientalis* n. gen., n. sp., photographs of type material (females): **A**, **C**, **E**, **G**, **H**, **J**, holotype specimen XDA1-1419; **B**, **D**, **F**, **I**, **K**, paratype specimen XDB3-0935; **A**, **B**, general habitus (eth/ab, following orientation of side 'A'; in A, upper left corner, side 'A' only); **C**, **D**, apical part of forewings, as shown on A and B, respectively (both eth/ab; in D, area delimited by dashed line, side 'A' only); **E**, **F**, details of hindwings, as shown in **A** and **B**, respectively (**E**, eth/b; **F**, eth/ab-UV/ab, rotated); **G**-**I**, detail of tarsus and tibia, as shown on A and B (all eth/ab-dry/ab-UV/ab); **G**, foretarsus, showing the lack of tarsal comb; **H**, metatarsus, showing two posterior spurs ('spu') on metatibia and apical spines ('spi') on metatibia and metatarsus; **I**, mesoleg and metaleg, showing the metatibia with apical spines-like setae long, of irregular lengths and spacing; **J**, **K**, (eth/ab-UV/ab), termination of abdomen, as shown on A and B, respectively, showing dense, stiff, backward-directed bristles on tergite 6 ('T6'). Scale bars: A, B, 2 mm; C, D, G-I, 1 mm; E, F, J, K, 0.5 mm. All photographs were taken by the first author.

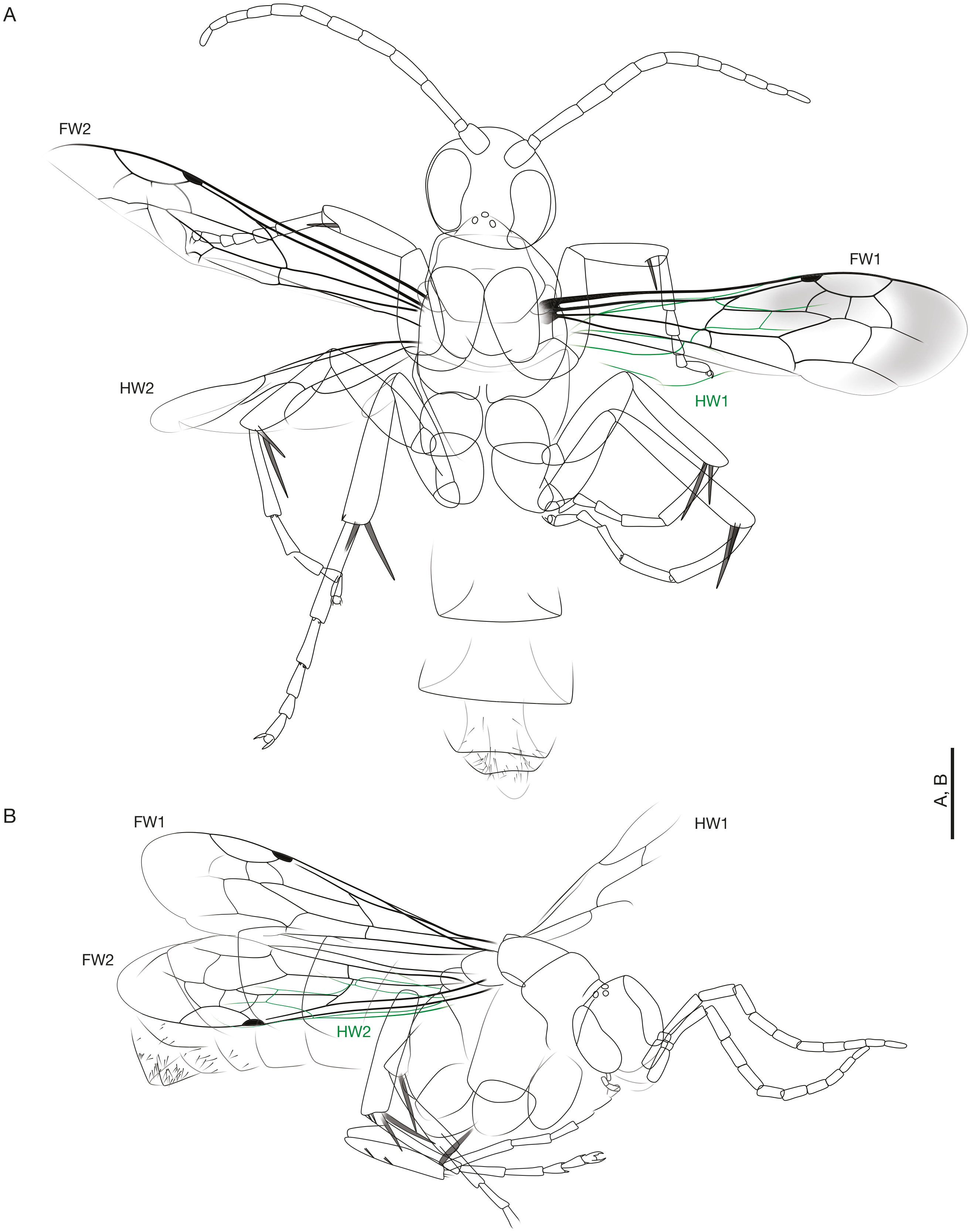

FIG. 2. — *Gubuzhu orientalis* n. gen., n. sp., line drawings of type material (females): **A**, holotype specimen XDA1-1419; **B**, paratype specimen XDB3-0935. Scale bars: 2 mm.

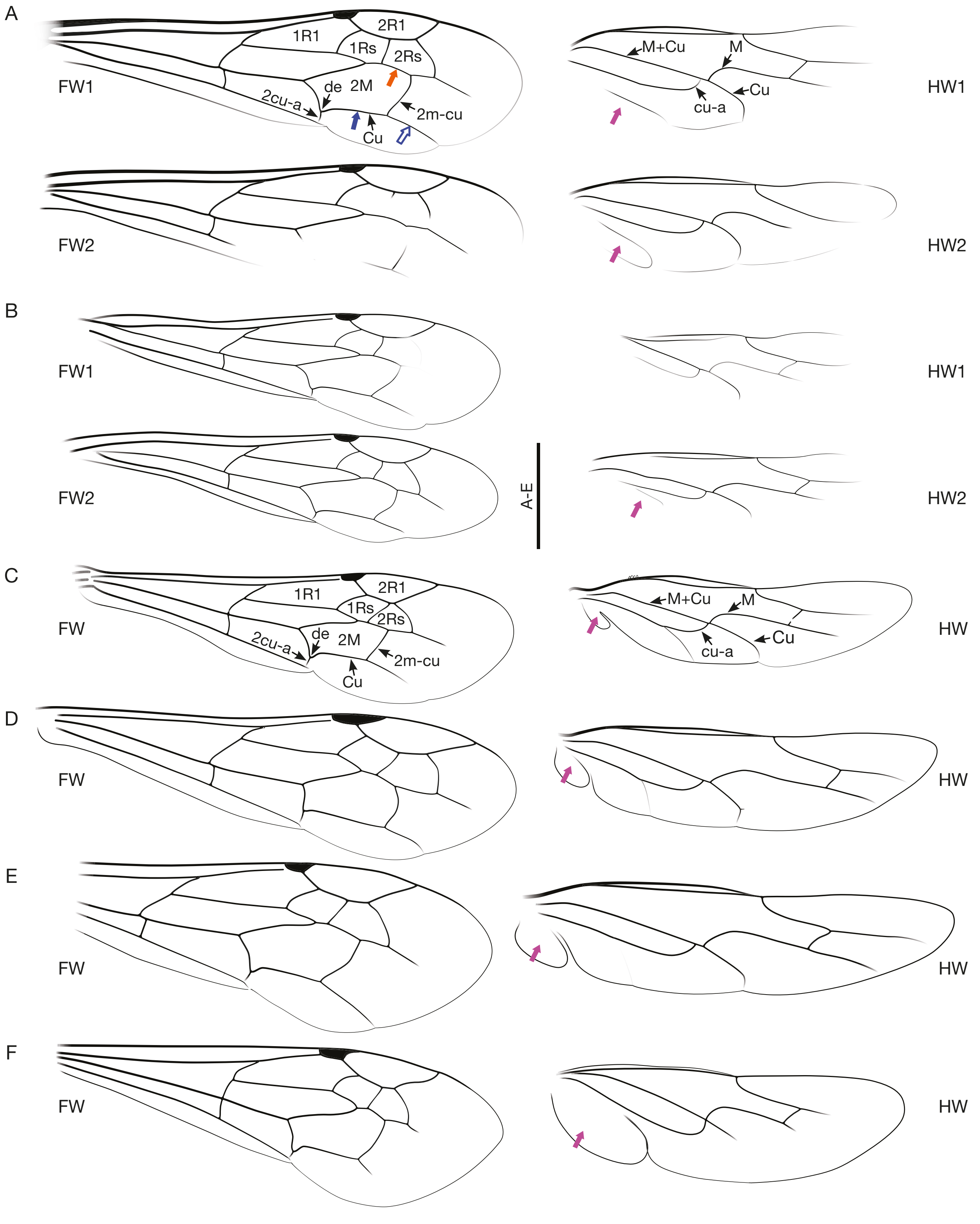

Fig. 3. — Wing venation of *Gubuzhu orientalis* n. gen., n. sp. and of selected extant Pompilidae, for comparison (pink arrows indicating the hindwing jugal lobe; see description as for orange and blue arrows): **A**, **B**, *Gubuzhu orientalis* n. gen., n. sp.; **A**, holotype specimen XDA1-1419 (FW2 and HW2 reconstructed unfolded); **B**, paratype specimen XDB3-0935; **C**-**F**, selected extant Pompilidae; **C**, *Anoplius viaticus* Linnaeus,1758 (redrawn from Day 1988: fig. 22); **D**, *Priochilus chrysopygus* Wasbauer, Cambra & Añino, 2017 (drawing based on Wasbauer *et al.* 2017: fig 2); **E**, *Anospilus carbonicolor* Gussakovskij, 1932 (drawing based on Loktionov & Lelej 2014: fig. 68.15,16); **F**, *Chalcochares hirsutifemur* (Banks, 1914) (redrawn from Wasbauer & Kimsey 1985: fig. 26; size information not available). Scale bars: 2 mm.

Paratype specimen, XDB3-0935A, B (Figs 1 B, D, F, I, K; 2B), adpression in both positive and negative aspects (but indistinguishable as a consequence of rock compression) of a nearly complete body in lateral orientation. Mouthpart poorly-exposed; antennae apparently detached from torulus; forelegs and one of the mesolegs lacking. Forewings well exposed, overlapping with one of the hindwings (HW2; Figs 1B, F; 2B). Tibia with at least two spines on the outer surface and unevenly-spaced spines, of unequal length, at the apex (Fig. 1I).

REMARKS

The specimens treated here can confidently be assigned to the family Pompilidae based on a distinctive combination of wing venation characters (see Day 1988; Rodriguez *et al.* 2017), relatively uniform for the family. The specimens can be further assigned to the Pompilinae owing to the occurrence of: 1) forewing having cell 2M deflected downward at the base ('de' on Fig. 1C, D); 2) vein M not reaching wing margin; 3) metatibia with apical spines-like setae long, distinctly splayed, of irregular lengths and spacing (Fig. 1I); and 4) eyes not close together beneath antennal socket (Day 1988). Within the subfamily, an assignment to the Pompilini is indicated by the: 1) forewing with three submarginal cells; 2) pronotum shorter than mesonotum; 3) postero-lateral angles of propodeum not produced backward (Evans 1949). At the genus level, the Pompilidae as a whole have traditionally been regarded as a taxonomically difficult group, with a systematic framework often based on slight differences or a particular combination of character states, which are often homoplasies (Wasbauer & Kimsey 1985; Waichert *et al.* 2015). Within Pompilinae, dense bristles on the tergite 6 of female are present in *Anoplius* Dufour, 1834, *Anospilus* Haupt, 1929, *Lophopompilus* Radoszkowski, 1887 (Pompilini) and some species of *Priochilus* Banks, 1944b (Priochilini; Pitts *et al.* 2006; Wasbauer *et al.* 2017; note that such bristles occur also in most Pepsinae, the sister-group of Pompilinae). We justify not placing the new specimens in *Anospilus* by the later having fine bristles, whereas they are thick in the former. (Fig. 1J, K); moreover, species of *Lophopompilus* present protarsus with comb (Loktionov & Lelej 2015), which is lacking in the new specimens (Fig. 5A). Finally, the most distinctive character state to distinguish the specimens XDA1-1419 and XDB3-0935 from these genera is a much larger hindwing jugal lobe, about 0.70-0.75× the length of Cu cell (pink arrow on Fig. 3A, B; in the other genera it is small, at most half the length of the Cu cell, see pink arrow on Fig. 3C-E for *Anoplius*, *Anospilus* and *Priochilus*, and see Regan (1923) for *Lophopompilus*). Note that, among tribe Pompilini, a large jugal lobe is also present in the genus *Chalcochares* Banks, 1917 (Fig. 3F). However, in addition to the occurrence (or lack thereof) of dense bristles, the new specimens differ from this genus by, in the hind wing, the cu-a cross-vein reaches the M+Cu vein basal to the M/Cu split (Figs 1E, F; 3A, B), whereas in *Chalcochares* the cu-a cross-vein meets M+Cu at the M/Cu split (Fig. 3F).

We also carried out a comparison with other, known fossil Pompilinae, mostly based on forewing venation. According to the revision by Rodriguez *et al.* (2017), six species can be confidently assigned to the subfamily, including *Agenioideus saxigenus* (Cockerell, 1908), *Anoplius planeta* Rodriguez & Pitts, 2016 in Rodriguez *et al.* (2016b), *Tainopompilus argentum* Rodriguez & Pitts, 2016 in Rodriguez *et al.* (2016b), *Tenthredinites bifasciata* Meunier, 1915, *Pompilinites coquandi* (Theobald, 1937) and *Pompilinites depressus* (Statz, 1936) (with the taxonomic concept '*Pompilinites*' to be understood as a 'collective group' including fossil species belonging to Pompilinae but which formal generic placement cannot be assessed; Rodriguez *et al.* 2017). The proposed new species can be easily distinguished from *Agenioideus saxigenus* by its 2m-cu vein meeting the 2Rs cell 0.6× distance from base to apex of the 2Rs cell (Fig. 3A, B), while in the latter the 2m-cu vein meets the 2Rs cell 0.95× distance from base to apex of the 2Rs cell (Rodriguez *et al.* 2017: fig. 4A). The proposed new species differs from *Anoplius planeta* by its 2m-cu vein arises on Cu cell longer than or about half the distance from the base of the 2M cell to the outer margin (see blue arrows on Fig. 3A, B), while in the latter the 2m-cu vein arises on the Cu cell less than half the distance from the base of the 2M cell to the outer wing margin (Rodriguez *et al.* 2016b). In *Tainopompilus argentum* and *Pompilinites depressus*, the pterostigma is larger than, or about half the length of the 2R1 cell, respectively (Rodriguez *et al.* 2016b: fig. 2; Statz 1936), while it is less than the third of the length of the 2R1 cell in the new specimens. The case of *Tenthredinites bifasciata* is difficult, as the location of the holotype is undetermined (Rodriguez *et al.* 2017), and the available data is limited, with, besides the original description (Meunier 1915), a revision by Theobald (1937). Moreover, according to this author, it may represent the female of *Pompilites fasciatus* (Theobald, 1937), which may not be a Pompilinae (Rodriguez *et al.* 2017). However, forewing coloration pattern, at least, indicate that the new specimens differ from this species (in which the forewing has two dark stripes, with one covering the base of the 1R1, 1M and 2Cu cells, and the other partially covering the 2R1, 1Rs, 2Rs and 2M cells). Lastly, the 2m-cu vein is straight in *Pompilinites coquandi* (Theobald, 1937), while it is slightly bowed towards the wing apex in the new specimens.

In summary, based on the unique combination of character states mentioned above, the erection of a new genus and species is supported.

Tribe *incertae sedis*

Genus *Paleoferreolina* X.-T. Xu & C. Waichert, n. gen.

urn:lsid:zoobank.org:act:0866BA28-6F31-4D12-9ABC-3A0354876AAC

TYPE SPECIES. — *Paleoferreolina xiedensis* X.-T. Xu & C. Waichert, n. sp.; monotypic genus.

ETYMOLOGY. — From grec 'palaiós' (παλαιός), meaning ancient, and 'ferreolina', a subtribe proposed by Priesner (1969), which the new species is morphologically related to. Gender feminine.

DIAGNOSIS. — As for the type species.

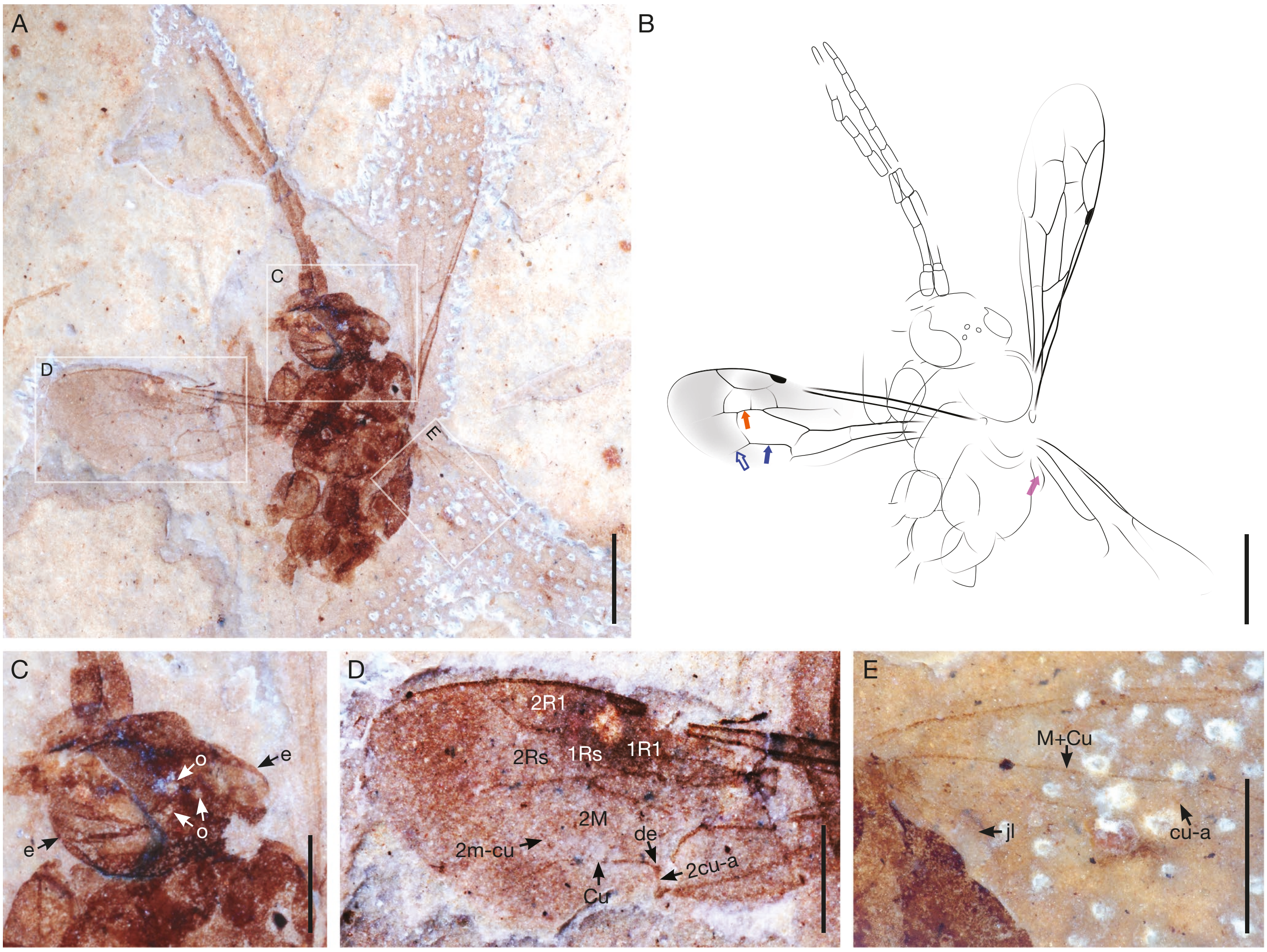

Fig. 4. — *Paleoferreolina xiedensis* n. gen., n. sp., photographs and line drawing of holotype specimen XDA1-1911: **A**, general habitus (eth); **B**, line drawing (pink arrow indicating the hindwing jugal lobe; see description as for orange and blue arrows); **C**, head; **D**, forewing; **E**, hindwing. Scale bars: A, B, 2 mm; C-E, 1 mm. All photographs were taken by the first author.

Paleoferreolina xiedensis
X.-T. Xu & C. Waichert, n. gen, n. sp.
(Fig. 4)

urn:lsid:zoobank.org:act:13C9D73F-98E9-48A9-8E7D-0F46B66C9B73

Type material. — **Holotype** (by monotypy). **China** • 1♀; West China, Xizang Autonomous Region, Naqu City, Shuanghu County, Xiede Village, Xiede locality; 31°58'23"N, 88°25'42"E; Xiede section, Niubao Formation, Nima Basin; Bartonian (Eocene); 4662 m a.m.s.l.; VI.2019; XTBG exped.; XTBG.; XDA1-1911 (one side preserved).

Etymology. — Referring to type locality of the species.

Type locality and stratigraphy. — Specimen was collected at the Xiede locality (northern Kanggale Hill, central Tibetan Plateau, China); Xiede section, Niubao Formation, Nima Basin (see Zhang *et al.* 2022 for detailed information); Bartonian (Eocene; Fang *et al.* 2020; Xiong *et al.* 2022).

Diagnosis. —In female, the third antennal segment is about 2.5× as long as wide; the head is flat and prolonged; the pronotum is prolonged with lateral margins rounded; the forewing has three submarginal cells (1R1, 1Rs and 2Rs), and the vein Cu is distinctly deflected downward at base.

Description

Mesurements (in mm)

Body length as preserved (from head to apex of metatrochanter) about 6.3.

Head. Compound eyes about 1.7× as long as wide (1.4 long and 0.8 wide in maximum); MID = 1.4; TFD = 2.0; FD = 1.7; third antennal segment 3.1-3.6× as long as wide (0.62-0.65 long and 0.18-0.20 wide).

Mesosoma. About 3.9 long.

Wings. Forewing 3.2-4.1× as long as wide (7.0-7.5 long and 1.8-2.2 wide in maximum).

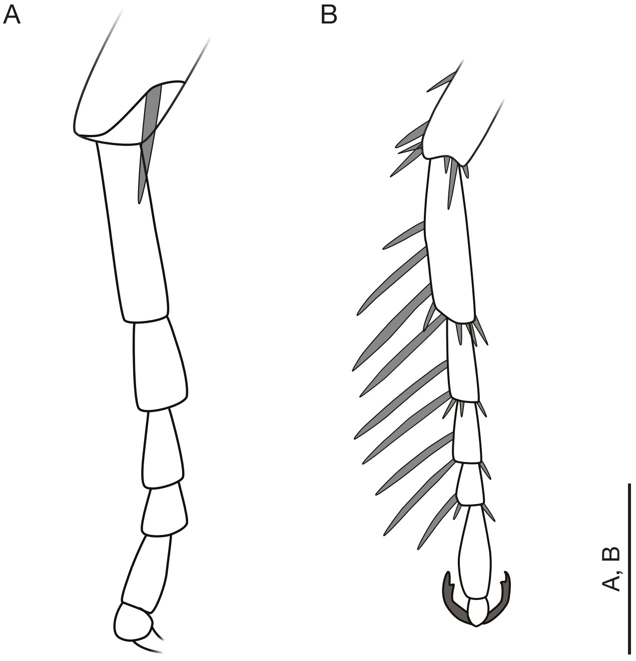

Fig. 5. — Foretarsus morphology in selected Pompilidae: **A**, *Gubuzhu orientalis* n. gen., n. sp. (drawing based on specimen XDA1-1419); **B**, *Evagetes pectinipes* Linnaeus, 1758 (redrawn from Day 1988: fig. 18). Scale bar: 1 mm.

General description

Individual preserved in lateral to dorso-ventral orientation; head and mesosoma preserved; legs with mainly coxa preserved; only one of the hindwings preserved; metasoma not preserved.

Head (Fig. 4C)

Compound eyes large, with inner margin emarginate, 1.7× as long as wide; ocelli farther to each other than to compound eyes; vertex almost straight; antenna elongate, thin; third antennal segment 3.1-3.6× as long as wide.

Mesosoma

Pronotum prolonged with lateral margins rounded, division of pronotum and scutum almost inconspicuous (Fig. 4A); legs with coxae wide; propodeum separate laterally from metapleuron by carina, posterior margin rounded.

Forewing (Fig. 4D)

With 2R1 longer than its distance from wing tip; 2Rs cell almost as long as 1Rs; 2m-cu vein slightly bowed toward wing apex, meeting 2Rs cell 0.5-0.6× distance from base to apex of cell [i.e., length of the section from the basal posterior edge of 2Rs cell to the insertion of 2m-cu cross-vein (orange arrow on Fig. 4B) about 0.5-0.6× that of the entire posterior edge of 2Rs cell]; 2m-cu vein arising on the Cu longer than half the distance from the base of the 2M cell to the outer wing margin [i.e., section of Cu located between its insertion of 2cu-a and 2m-cu cross-veins (blue arrow on Fig. 4B), longer than the section of Cu located between its insertion of 2m-cu cross-vein to its projected termination on the wing margin (blue fame arrow on Fig. 4B)]; vein Cu distinctly deflected downward at base.

Hindwing

With jugal lobe slightly shorter than half the length of Cu cell (pink arrow on Fig. 4B, E).

Coloration

integument dark on head and mesosoma. Punctuation inconspicuous. Forewings hyaline, darkened in about ¼ of the apical portion, and a dark spot at ⅔ of wing length, partially covering cell 2R1, 1R1 and 1Rs (Fig. 4B, D).

Remarks

The specimen XDA1-1911 is assigned to the Pompilinae based on the forewing having cell 2M deflected downward at the base, forming a posterior ‘pocket’ (‘de’ on Fig. 4D). Even though the colour pattern of its forewing is similar to that of *G. orientalis* n. gen, n. sp., it can be distinguished from this species by many character states, as follows: 1) the pronotum is prolonged (rather short in *G. orientalis* n. gen, n. sp.); 2) the third antennal segment is longer, about 3.1-3.6× as long as wide (2.8-2.9× as long as wide in *G. orientalis* n. gen, n. sp.); 3) the forewing is shorter, about 7.0-7.5 mm long (8.2-9.4 mm long in *G. orientalis* n. gen, n. sp.); 4) the forewing has the cell 2R1 longer than its distance from wing tip (almost equal in *G. orientalis* n. gen, n. sp.); 5) the 2Rs cell is almost as long as 1Rs (it is longer than the 1Rs cell in *G. orientalis* n. gen, n. sp.); and 6) the hindwing has the jugal lobe slightly shorter than half the length of Cu cell (it is about 0.70-0.75× the length of Cu cell in *G. orientalis* n. gen, n. sp.). The specimen XDA1-1911 therefore indicates the occurrence of a second species of Pompilinae at Xiede locality.

The specimen resembles extant species of *Ferreola* Lepeletier de Saint-Fargeau, 1845 (tribe Aporini, subtribe Eoferrolina), which has a long head, somehow compressed dorsal-ventrally, a robust body with long pronotum, and three cubital cells in the forewing (Loktionov & Lelej 2017). However, other lineages of Pompilidae, such as *Paraferreola* Šustera, 1912 (tribe Psammoderini), *Lepidocnemis* Haupt, 1930 and *Abernessia* Arlé, 1947 (Pepsinae), and Ctenocerinae genera are known to morphologically, and probably ecologically, converge to species of Aporini (Waichert *et al.* 2015). For the reason mentioned above, and the fact that the specimen lacks most of the legs and metasoma, a placement of the specimen to the tribe Aporini could be considered, but is poorly substantiated. Nonetheless, the specimen differs from all these genera for lacking vertical ridges or conical processes in the posterolateral portion of propodeum. Based on the unique combination of character states mentioned above, the erection of a new genus and species is supported.

DISCUSSION

The discovery of *Gubuzhu orientalis* n. gen, n. sp. and of *Paleoferreolina xiedensis* n. gen, n. sp. at the Xiede locality is relevant regarding the age of the Pompilinae. Considering that the subfamily is potentially the sister group of Pepsinae, although with a poorly supported phylogenetic relationship (Waichert *et al.* 2015), and the earliest fossil record of the latter, namely *Cryptocheilus leleji* Waichert, Rapoza & Rodriguez, 2021 in Waichert *et al.* (2021) (crown-Pepsinae), dating from the early Eocene Fur Formation (Denmark; Waichert *et al.* 2021), the discovery of a crown-Pompilinae of similar age is anticipated. However, the previously reported six species of fossil Pompilinae were found in deposits ranging from the latest Eocene to Miocene (Rodriguez *et al.* 2017: table 1), located in Europe and North America. Among these species, the earliest ascertained crown-group member is *Agenioideus saxigenus* (Cockerell 1908), from the Florissant Fossil Beds (Colorado, United States), of ca. 33-34 Ma in age (Prothero 2008). The material from Xiede, slightly more ancient and belonging to the crown-Pompilinae, is expected to refine the temporal calibration of the Pompilidae phylogenetic tree. Currently, estimates on the age of crown-Pompilinae suggest an origin in the early Oligocene or near the Eocene-Oligocene boundary (i.e. about 31-34 Ma), but with large uncertainties (95% HPD about 20-50 Ma) (Waichert *et al.* 2015; Rodriguez *et al.* 2017). The addition of two new species of Pompilinae from the Bartonian (ca. 39 Ma) is therefore likely to shift the estimated origin of the clade. The Xiede material is also relevant regarding ancient biogeographic distribution of the Pompilinae, a subfamily nowadays cosmopolitan. The new fossils represent its most oriental fossil occurrence to date. This new record suggests that Pompilinae was already widespread in the Northern Hemisphere during the late Eocene.

The material of *Gubuzhu orientalis* n. gen, n. sp. has also relevance regarding the evolution of the sequence and composition of actions undertaken by spider wasps in the oviposition process. The type and distribution of spines on the legs of Pompilidae bear various ecological functions. When the second foreleg tarsal segment bears a spine mid-laterally and equal in length to the spine at the apex of that segment, the series of tarsal spines is said to form a comb (Fig. 5B; Wasbauer & Kimsey 1985). Unlike Pepsini and Ageniellini that have modifications on hind tibial or mouthpart and metasomal structural for excavating (Townes 1957; Kurczewski & Kiernan 2015), many species of Pompilini (e.g. 85% species of Pompilini in North American) are equipped with a comb on foretarsus to remove soil to excavate a burrow as nest (Evans 1949, 1950, 1951; Kurczewski & Edwards 2012; Kurczewski & Kiernan 2015). To the contrary, species of Pompilini engaging in minimum or no excavation may not be equipped with such a comb (Evans 1949). For example, *Agenioideus cinctellus* Spinola, 1807 has legs weakly spinose and without a tarsal comb, thus it strictly nests in natural cavities and crevices in various substrates (Kurczewski & Kiernan 2015). This is also the case for species of subgenus *Anoplius* (*Anoplius*) Dufour, 1834, which absent tarsal comb, e.g. *Anoplius virginiensis* Cresson, 1867 nests in galleries of dead wood; *Anoplius illinoensis* Robertson, 1901 uses openings in the ground as their burrows; and *Anoplius imbellis* Banks, 1944a nests in a pile of pebbles (Evans & Yoshimoto 1962; Kurczewski & Kiernan 2015; Kurczewski *et al.* 2017). These behaviours correspond to the VPTOC type (Hunting → Paralysis → Transportation → Oviposition → Closing the cell) according to Evans (1953), which do not involve digging processes. The occurrence, or lack thereof, of a tarsal comb is a homoplastic character (with multiple acquisition and/or losses) based on recent phylogenetic analyses (Pitts *et al.* 2006; Rodriguez *et al.* 2016a). In *Anoplius* it is a plastic characteristic, being present in species of the subgenera *Anopliodes* Banks and *Arachnophroctonus* Howard, but lack in species of the subgenus *Anoplius* (Pitts *et al.* 2017). The exceptional preservation of the material of *Gubuzhu orientalis* n. gen., n. sp. allows assessing that it lacked a tarsal comb or any other lateral spines in the foreleg (Figs 1G-I; 5A), indicating that the species engaged in limited excavating activity (VPOC or VPTOC type), perhaps even using the spider's burrow as nest. More fossil material is needed to investigate the complex evolution of nesting behaviour in the tribe, as revealed by morphological characters. The spider targeted by Xiede Pompilinae remains to be found.

CONCLUSION

Gubuzhu orientalis n. gen., n. sp. and *Paleoferreolina xiedensis* n. gen, n. sp. are the earliest representative of the Pompilinae, which are expected to shift the estimated origin of the subfamily. The Pompilinae fossil record is limited yet, in particular in the oriental area. The current discovery suggests that it was already widely distributed across the Northern Hemisphere during the late Eocene. Additionally, morphological features of *Gubuzhu orientalis* n. gen., n. sp. imply that its nesting behavior may have involved minimal excavation activity only. Lastly, these fossils complement our knowledge of the diverse flora and fauna composing the complex ecosystem which existed, during the Eocene, in central Tibetan Plateau, and which were eventually extirpated as a consequence of the dramatic climate change resulting from the growth of the plateau.

Acknowledgements

We are grateful to Valery Loktionov, Fernando Fernández and an anonymous reviewer for their valuable input, and to the editorial board of *Geodiversitas* for handling peer reviewing and publication process. We are further grateful to Cédric Del Rio, Nozomu Oyama (Muséum national d'Histoire naturelle, MNHN) and Juanita Rodriguez (Australian National Insect Collection, ANIC-CSIRO) for their useful comments, and to Séverin Morel, Christophe Lair, Sandra Daillie and Vincent Pernègre (MNHN) for the valuable assistance during the former author's stay at the CR2P, MNHN. CW thanks to UnB-DPG. This work was funded by National Key R&D Program of China (2022YFF0800800), the Second Tibetan Plateau Scientific Expedition program (No. 2019QZKK0705) and China Scholarship Council (202204910191).

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Submitted on 6 March 2024;
accepted on 27 July 2024;
published on 20 March 2025.