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Proapocritus lini sp. nov., a new ephialtitid wasp (Hymenoptera: Apocrita) from the Middle-Upper Jurassic of Daohugou, NE China

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The Ephialtitidae is an extinct family of wasps, with 29 genera reported from the Lower Jurassic-Lower Cretaceous in Kyrgyzstan, Kazakhstan, China, Mongolia, Russia, Spain, Germany and Brazil, and flourished in the Middle–Late Jurassic (Meunier, 1903; Rasnitsyn, 1975, 1977, 1990, 1999, 2008a, b; Zessin, 1981, 1985; Zhang, 1986; Darling & Sharkey, 1990; Rasnitsyn & Ansorge, 2000; Rasnitsyn & Martínez-Delclòs, 2000; Zhang *et al*., 2002; Rasnitsyn *et al*., 2003; Rasnitsyn & Zhang, 2004, 2010; Zhang *et al*., 2010; Ding *et al*., 2013, 2016; Li *et al*., 2013, 2014, 2015; Zhang *et al*., 2014). It is considered to be the most basal group of the Apocrita, one of two suborders of the order Hymenoptera (Rasnitsyn & Zhang, 2010).

The family is divided into two subfamilies: Ephialtitinae Handlirsch, 1906 and Symphytopterinae Rasnitsyn, 1980 (Handlirsch, 1906–1908; Rasnitsyn, 1980; Zhang *et al*., 2002; Rasnitsyn *et al*., 2003; Rasnitsyn & Zhang, 2010). The Ephialtitinae differs from the Symphytopterinae in having a long ovipositor and an interstitial (or nearly interstitial) cu-a crossvein in the forewing, and includes 21 genera: *Acephialtitia* Li *et al*., 2015, *Altephialtites* Rasnitsyn, 2008, *Asiephialtites* Rasnitsyn, 1975, *Cratephialtites* Rasnitsyn, 1999, *Crephanogaster* Rasnitsyn, 1990, *Cretephialtites* Rasnitsyn & Ansorge, 2000, *Ephialtites* Meunier, 1903, *Leptephialtites* Rasnitsyn 1975, *Liadobracona* Zessin, 1981, *Mesephialtites* Rasnitsyn, 1975, *Montsecephialtites* Rasnitsyn & Martínez-Delclòs, 2000, *Parephialtites* Rasnitsyn, 1975, *Praeproapocritus* Rasnitsyn & Zhang, 2010, *Proapocritus* Rasnitsyn, 1975, *Proephialtitia* Li *et al*., 2015, *Sessiliventer* Rasnitsyn, 1975, *Sinephialtites* Zhang 1986, *Sinocephus* Hong, 1983, *Stephanogaster* Rasnitsyn, 1975, *Thilopterus* Rasnitsyn, Ansorge & Zessin, 2003, and *Tuphephialtites* Zhang, Rasnitsyn & Zhang, 2002 (Rasnitsyn, 1975; Rasnitsyn & Zhang, 2010; Li *et al*., 2015).

Owing to lack of a reliable phylogenetic analysis, the genus *Proapocritus* is putatively considered to be a basal group of Ephialtitinae and includes nine species from the Jurassic of Asia: *P. atropus* Rasnitsyn & Zhang, 2010, *P. bialatus* Li, Shih & Ren, 2014, *P. densipediculus* Rasnitsyn & Zhang, 2010, *P. elegans* Rasnitsyn & Zhang, 2010, *P. formosus* Rasnitsyn & Zhang, 2010, *P. longantennatus* Rasnitsyn & Zhang, 2010, *P. parallelus* Li, Shih & Ren, 2013, *P. praecursor* Rasnitsyn, 1975 and *P. sculptus* Rasnitsyn & Zhang, 2010 (Rasnitsyn, 1975; Rasnitsyn & Zhang, 2010; Li *et al*., 2013, 2014). Here a new species attributed to *Proapocritus* is described based on a female wasp from the Middle-Upper Jurassic Daohugou Beds of NE China, adding to the diversity of *Proapocritus* and of Ephialtitidae.

Material and methods

The new species established herein is based on a specimen from the Daohugou Beds at Daohugou Village, Ningcheng County, Chifeng City, Inner Mongolia, China. The Daohugou Beds were previously considered to be Bathonian to Callovian (Middle Jurassic) in age and to belong to the Jiulongshan Formation (*e.g*., Li *et al*., 2013). However, recent biostratigraphic and radiometric dating results suggest that they are of Callovian–Oxfordian age (latest Middle–earliest Late Jurassic) (*e.g*., Liu *et al*., 2006; Liu *et al*., 2012; Cohen *et al*., 2013; Wang *et al*., 2013; Huang, 2016; Wang *et al*., 2018).

The specimen described herein was prepared with PaleoTools Micro-Jack 3, observed dry and under ethanol using a light microscope (NIKON SMZ1000) and photographed with a digital camera (DXM1200) connected to the microscope at the State Key Laboratory of Palaeobiology and Stratigraphy, Nanjing. Line drawings were made using CorelDRAW X8 software. Wing-venation terminology of Rasnitsyn (1969) and Rasnitsyn & Zhang (2010) is adopted herein.

The specimen described herein is housed at the Nanjing Institute of Geology and Palaeontology (NIGP), Chinese Academy of Sciences.

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Systematic palaeontology

Order Hymenoptera Linnaeus, 1758
Suborder Apocrita Gerstaecker, 1867
Family Ephialtitidae Handlirsch, 1906
Subfamily Ephialtitinae Handlirsch, 1906
Genus *Proapocritus* Rasnitsyn, 1975

Type species. *Proapocritus praecursor* Rasnitsyn, 1975.

Included species. Ten species: *P. praecursor* Rasnitsyn, 1975 from the Lower Jurassic Sagul Formation of Fergana, Kyrgyzstan, and *P. atropus* Rasnitsyn & Zhang, 2010, *P. bialatus* Li, Shih & Ren, 2014, *P. densipediculus* Rasnitsyn & Zhang, 2010, *P. elegans* Rasnitsyn & Zhang, 2010, *P. formosus* Rasnitsyn & Zhang, 2010, *P. longantennatus* Rasnitsyn & Zhang, 2010, *P. parallelus* Li, Shih & Ren, 2013, *P. sculptus* Rasnitsyn & Zhang, 2010, and *P. lini* **sp. nov.** from the Middle-Upper Jurassic Daohugou Beds of NE China.

Diagnosis. Wing venation complete. Forewing with first abscissa of Rs directed slightly posterodistally; 1r-rs at least indicated by geniculated second section of Rs; 3r-m, 2m-cu tubular; cu-a interstitial; 2A at least rudimentary, 2a closed. Hindwing with C present; Rs originating not basad of M+Cu fork.

***Proapocritus lini* sp. nov.**
(Figs 1 and 2)

Holotype. NIGP172172, a female wasp in ventral view; with both antennae, forewings distally, and hindwings posteriorly missing, and legs partly damaged.

Etymology. The specific name is dedicated to Prof. Qi-Bin Lin, a well-known Chinese palaeoentomologist.

Diagnosis. Forewing with first abscissa of Rs distinctly shorter than that of M; 1r-rs rudimentary; cu-a slightly postfurcal, and as long as first abscissa of M; 2A lost basad of 1a-2a. First metasomal segment frustum-like. Ovipositor greatly long with sheaths longer than body and forewing.

Locality and horizon. Daohugou Beds, Middle-Upper Jurassic; Daohugou Village, Wuhua Town, Ningcheng County, Chifeng City, Inner Mongolia, China.

Description. Head comparatively large with eyes large and occupying almost all sides of head. Mesosoma slightly broader than head and about 1.7 times as long as wide. Fore and mid legs small. Hind leg much longer than mid one, with coxa stout and about 1.5 times as long as mid one; trochanter small; femur clavate, about 1.3 times as long as mid one; tibia 1.2 times as long as femur; tarsus thin, slightly longer than tibia, with basitarsomere nearly half of tibial length,

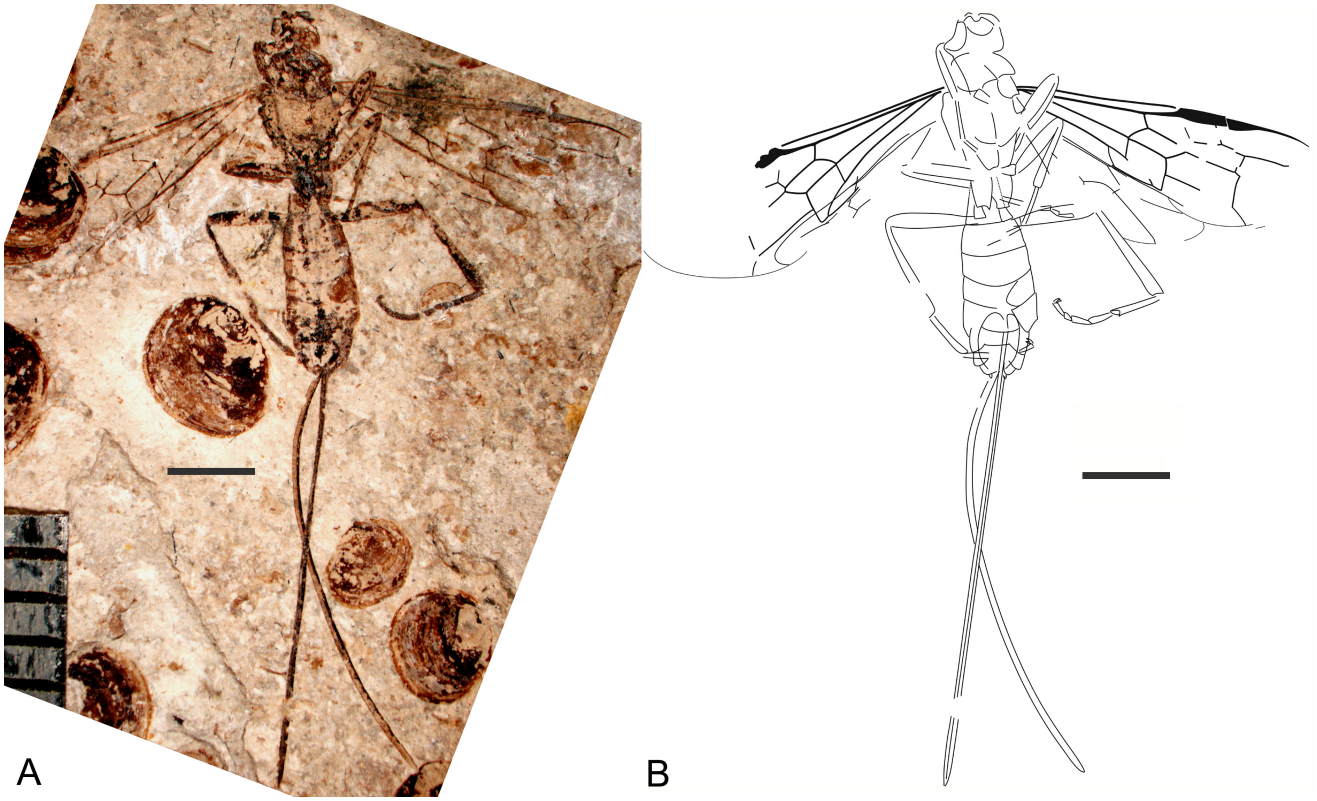

FIGURE 1. *Proapocritus lini* **sp. nov.**, holotype NIGP172172, a wasp in ventral view. **A**, Photograph. **B**, Line drawing. Scale bars = 2 mm.

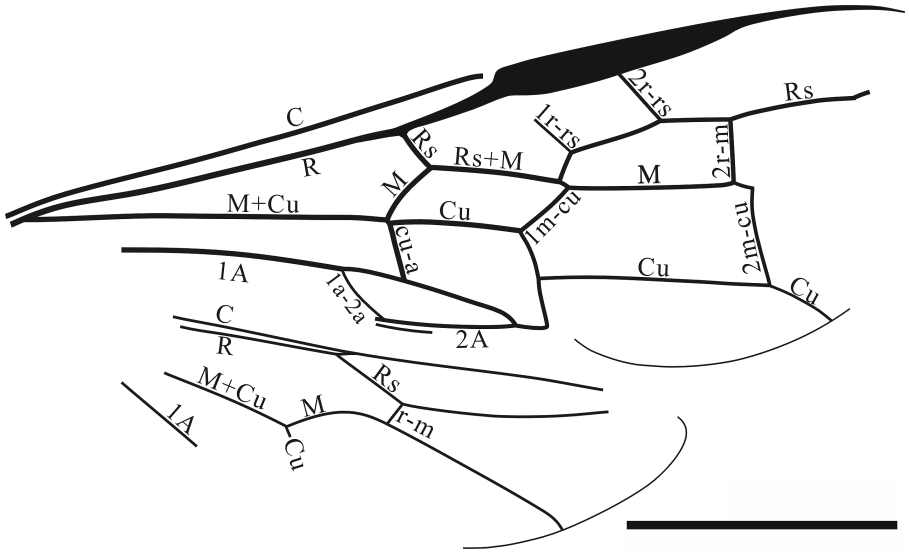

FIGURE 2. *Proapocritus lini* **sp. nov.**, holotype NIGP172172, reconstruction of forewing and hindwing. Scale bar = 2 mm.

and segmental length ratio = 1.00 : 0.50 : 0.40 : 0.17 : 0.33. Forewing with first abscissa of Rs 2/3 length of that of M, and about 2/5 of its distance to pterostigma; pterostigma narrow, elongate and acuminate, with 2r-rs issuing at its mid-length and slightly shorter than maximal width of 2rm; 1r-rs incomplete, subparallel to 2r-rs; 2r-rm subvertical, as long as 2r-rs; 3r-m not preserved but its position indicated by a curve on Rs quite beyond 2r-m, and therefore 2rm very possibly longer than 3rm; 1m-cu subparallel to first abscissa of M, and meeting M slightly beyond fork of Rs+M; 2m-cu meeting M slightly beyond 2r-m, slightly curved basally, and generally subvertical; 1mcu parallelogrammical, 2.5 times as long as wide; 2mcu slightly widening distally, and about 2.5 times as long as wide; cu-a just postfurcal, and as long as first abscissa of M; 2cua as long as 1mcu, and distally twice as wide as basally; 2A rudimentary subdistally; 1a-2a complete, and quite basad of cu-a. Hindwing with Rs originating slightly distad of M+Cu fork; first abscissa of Rs 3.5 times as long as r-m, and slightly shorter than that of M; first abscissa of M greatly curved. Metasoma spindle-like with fifth segment broadest; first segment frustum-like, about as long as broad distally; second segment trapezoid, about 2/3 length of first, remaining slightly shorter. Ovipositor straight with sheaths slightly longer than body and forewing.

Measurements in mm: head length 0.9, width 1.3; mesosomal length 2.9, width 1.7; forewing length 7.9 (as estimated), width 2.5; hindwing length 5.0, width (as preserved) 1.3; metasomal length 4.6; ovipositor length 10.8, sheath length 9.5.

Discussion

The genus *Proapocritus* was established based on an insect forewing from the Lower Jurassic of Kyrgyzstan and temporarily assigned to the family Karatavitidae (Rasnitsyn, 1975). It was considered to almost completely fill the gap in forewing venation between Karatavitidae in Symphyta and Ephialtitidae in Apocrita (Rasnitsyn, 1975, 1980). Abundant and well-preserved specimens from Daohugou indicate that this genus should be assigned to the subfamily Ephialtitinae of Ephialtitidae and is very homogenous in wing venation and propodeum, but diverse morphologically in the first metasomal segment (Rasnitsyn & Zhang, 2010).

Nine species assigned to this genus were previously reported from the Jurassic in Asia. This new species differs from *P. praecursor*, the type species of *Proapocritus* known from a forewing, in having a much smaller forewing with pterostigma much narrower and longer, 1r-rs incomplete, 2r-m subvertical, and 2m-cu curved basally; from *P. densipediculus* (known from an incomplete wasp with hindwings and metasoma beyond the second segment missing) in the first metasomal segment frustum-like (*vs*. thick and subcylindrical in the latter); from *P. sculptus* (known from a specimen with left forewing and hindwing damaged distally and right forewing folded, and metasoma beyond the second segment missing) in the first metasomal segment much thicker, especially for its basal part (*vs*. thin basally and elongate conical); from *P. bialatus* (known from a female with wings incomplete and ovipositor missing distally) in the first metasomal segment frustum-like (vs. thick and subcylindrical), and the forewing with 2A lost basad of 1a-2a (*vs*. complete); from *P. elegans* (known from a female with wings slightly damaged and distal part of ovipositor missing) in having a much smaller body (8.3 mm *vs*. 13.5 mm in length) but their forewings are of equal length (7.5 mm); and from *P. parallelus* (known from a female with antennae and ovipositor incomplete) in the first metasomal

segment much slender (*vs*. transversely broad), the forewing with 1r-rs rudimentary (*vs*. complete), 2r-rs issuing from pterostigma at its mid-length (*vs*. beyond its mid-length) and 2m-cu slightly curved and subvertical generally (*vs*. distinctly curved and directed posterodistally), and the hindwing with the first sections of both Rs and M greatly long relative to r-m and the first abscissa of M distinctly arched. It is also distinguishable from *P. atropus*, *P. formosus* and *P. longantennatus* by its greatly long ovipositor (with sheaths longer than the body), and further from *P. longantennatus* by the first metasomal segment frustum-like and not swollen medially (*vs*. thin basally, subconical, and distinctly swollen submedially), the forewing with 1r-rs rudimentary (*vs*. completely lost), and the hindwing with the first abscissae of Rs and M greatly long relative to r-m and the first abscissa of M distinctly arched.

Ephialtitids have a thin and long ovipositor and an often trans-striate mesonotum, indicating that they are most likely parasitoids of xylophagous insect larvae (beetle and/or horntail), but details of their biology are unknown (Rasnitsyn, 1980; Li *et al*., 2015). In the subfamily Ephialtitinae, the ovipositors distinctly vary in length, e.g. with sheaths 50.6 mm long and 1.8 times as long as the body in *Acephialtitia colossa* Li *et al*., 2015, but only 2.8–3.1 mm long and 0.6 times in *Asiephialtites niger* Rasnitsyn, 1975 (Rasnitsyn, 1975; Li *et al*., 2015), indicating that their hosts are highly diverse. The same holds true for the genus *Proapocritus*, with the ovipositor sheaths, for example, 9.5 mm long and 1.1 times as long as the body in the new species, 8.0 mm and 0.6 times in *P. atropus*, 5.6 mm and 0.5 times in *P. formosus,* and 3.1 mm and about 0.4 times in *P. longantennatus*.

Conclusion

The genus *Proapocritus* Rasnitsyn, 1975 is putatively a basal group of the subfamily Ephialtitinae, with nine species previously reported from the Jurassic of Asia. The new species, *Proapocritus lini* **sp. nov.**, is established based on a female wasp from the Middle-Upper Jurassic Daohugou Beds with the typical wing venation of *Proapocritus*, the frustum-like first metasomal segment, and a quite long ovipositor, adding to the diversity of *Proapocritus* and of Ephialtitidae. The ovipositors distinctly vary in length in *Proapocritus*, suggesting that the hosts of this genus were diverse.

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