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## New praeaulacid and ephialtitid hymenopterans (Apocrita) from the Middle Jurassic of northeastern China

Longfeng Li, Peter J. M. Shih, Jingtao Yang, Chungkun Shih, and Dong Ren 

### ABSTRACT

Fossil hymenopterans incorporating two new species, *Nevania deviata* sp. nov. and *Praeaulacus grossus* sp. nov., and one new specimen of *Praeaulacus scabratus* referred to Praeaulacidae, together with another new species, *Proapocritus habitus* sp. nov., assigned to Ephialtitidae are described. These taxa were collected from outcrops of the Middle Jurassic Haifanggou Formation at Yujiagou village near Beipiao in Liaoning Province, China. We also summarize the distribution, stratigraphical range and diagnostic forewing character states of the genus *Nevania* to assess inter-specific venational differences. Our study thus recognizes substantial diversity amongst the Middle Jurassic species of this lineage.

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PRAEAULACIDAE is an extinct family within Evanioidea that consists of 21 genera incorporating 75 species stratigraphically ranging from the Jurassic to Cretaceous (Li *et al.* 2018, Ren *et al.* 2019). The group is characterized by complete forewing venation (except for some species within the subfamily Cretocleistogastrinae), hind wings with at least the basal cell enclosed, retention of the medial mesonotal suture, and elongate external ovipositors; these character states suggest that the clade is ancestral to other families of Evanioidea (Li *et al.* 2018, Rasnitsyn 1988, Zhang & Rasnitsyn 2008). Amongst extant evanioids, aulacids are endoparasitoids on wood-boring larvae of xiphydriid hymenopterans and buprestid or cerambycid coleopterans (Turrisi 2011), while gasteruptiids are predator-inquilines that lay their eggs inside the cells of solitary bees and wasps nesting in plant stems, tunnels of wood, or underground nests with the larvae subsequently consuming the stored food or nest inhabitants (Zhao *et al.* 2012). Both aulacids and gasteruptiids have elongate ovipositors, implying that praeaulacids (except for nevaniines) were likewise probably parasitoids on xylophagous insect larvae.

The extinct family Ephialtitidae is considered to be the most basal group within Apocrita, and includes two subfamilies: Ephialtitinae Handlirsch, 1906, and Symphyopterinae Rasnitsyn, 1980. To date, 29 genera and 77 species have been described from Jurassic and Cretaceous strata (Li *et al.* 2015, Ren *et al.* 2019). Although ephialtitids are most likely parasitoids of xylophagous insect larvae (e.g., beetles and/or horntails) as suggested by their elongate

ovipositors and often trans-striate mesonotum, other details of their biology are at present uncertain (Li *et al.* 2015).

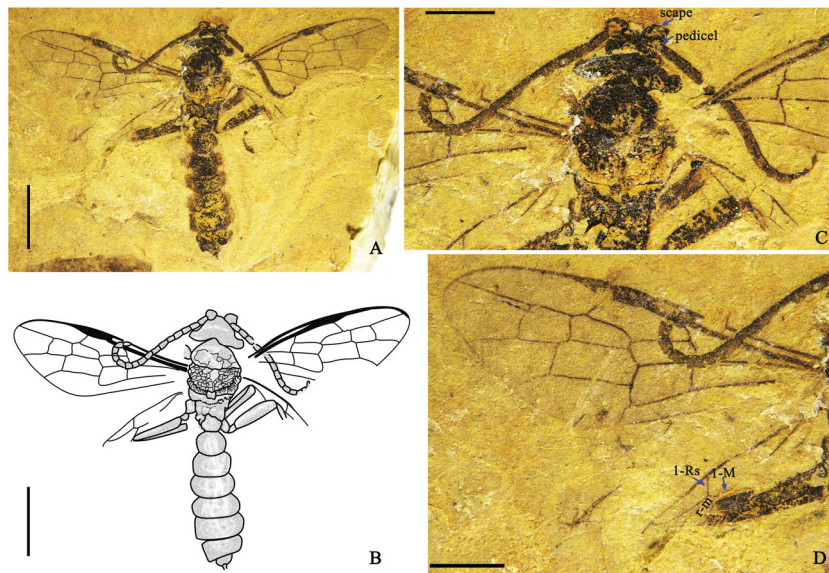
We recovered four well-preserved fossil hymenopteran fossils (including two specimens with parts and counterparts) assignable to Praeaulacidae and Ephialtitidae. These remains were derived from the uppermost Middle Jurassic (upper Callovian) Haifanggou Formation at Yujiagou village near Beipiao in the Liaoning Province of China. The Haifanggou Formation has been  $^{40}\text{Ar}/^{39}\text{Ar}$  and SHRIMP  $^{206}\text{Pb}/^{238}\text{U}$  dated to 165–161 million years ago (Ma) (Li *et al.* 2021, Ren *et al.* 2019, Xu *et al.* 2016). These new fossils are described in this paper, along with a summary of the praeaulacid genus *Nevania* Zhang & Rasnitsyn, 2007, which is a species-rich Mesozoic taxon with wide distribution, stratigraphical age range, and diagnostic forewing character states.

### Material and methods

Our fossils are housed in the Key Laboratory of Insect Evolution and Environmental Changes, College of Life Sciences and Academy for Multidisciplinary Studies, Capital Normal University, Beijing, China (CNUB). Part/counterpart samples are given p/c suffixes, respectively. All specimens were examined and photographed using a Leica MZ 16.5 dissecting microscope (Leica, Wetzlar, Germany) with a Leica DFC500 digital camera system. Illustrations were made with a camera lucida microscope attachment, and the figures compiled using CorelDraw 12.0 and Adobe Photoshop CS5 software. Venation terminology used herein follows Li *et al.* (2018).







**Figure 2.** *Praeaulacus scabratus* (CNU-HYM-LB-2022002). A, Photo of specimen; B, line drawing of habitus; C, head with antennae; D, wings. Scale bars: A, B = 2 mm; C, D = 1 mm.

**Remarks.** *Nevania deviata* differs from *Nevania aspectabilis*, *Nevania perbella*, *Nevania malleata*, *Nevania robusta* and *Nevania exquisita* by possessing an interstitial versus post-furcal 1cu-a. It can also be distinguished from *Nevania ferocula*, *Nevania retenta* and *Nevania karatau* in 1-Rs being shorter, rather than sub-equal in length to 1-M. Finally, *N. deviata* differs from all other *Nevania* spp. in having a very short (transverse) cell 3rm.

Subfamily PRAEAULACINAE Rasnitsyn, 1972

*Praeaulacus* Rasnitsyn, 1972

*Praeaulacus scabratus* Zhang & Rasnitsyn, 2008 (Fig. 2)

**Referred material.** CNU-HYM-LB-2022002 (Yp101/607), complete male individual.

**Locality, unit and age.** Yujiagou village near Beipiao in Liaoning Province, China; Haifanggou Formation, uppermost Middle Jurassic (upper Callovian), ~165–161 Ma (Xu *et al.* 2016, Ren *et al.* 2019, Li *et al.* 2021).

**Description.** The body length is 7.68 mm, with forewing length being 5.28 mm. The head is nearly as wide as the mesosoma. The antenna has 16 segments with a swollen scape that is distinctly wider than the pedicel. The mesosoma is stout and wider than the metasoma; the mesonotum is long and broad; both the metanotum and propodeum are short. The metasoma has a small first metasomal segment; the remaining segments are nearly equal in length. The forewing has 1-Rs that are shorter than 1-M; a postfurcal 1cu-a. The 2r-rs is straight and issues from the distal part of the pterostigma. Cell 1mcu is in contact with 2rm via a short section of M; 2r-m is straight and shorter than 2r-rs; 2m-cu is straight and ends at 3rm; the 3r-m is bent. Cell 2rm is longer and narrower than 3rm. The hind wing has a closed cell r; r-m is straight and shorter than 1-Rs and 1-M; M + Cu is present.

**Remarks.** CNU-HYM-LB-2022002 is referred to *Praeaulacus scabratus* based on the following character states (see Zhang & Rasnitsyn 2008): forewing with 1cu-a postfurcal; 2r-rs meeting Rs basal to 2r-m; 2m-cu meeting 3rm at about the basal 1/4 length of its posterior margin; and a short propodeum. Unfortunately, the diagnostic arched 1-M on the hind wing (see Zhang & Rasnitsyn 2008) is incomplete in CNU-HYM-LB-2022002, and thus may prove to be morphologically distinct.

*Praeaulacon* Rasnitsyn, 1972

*Praeaulacon grossus* sp. nov. Li, Shih & Ren (Fig. 3)

**Diagnosis.** First metasomal segments wide triangle-shaped. Hind legs thick. Forewing with 1cu-a interstitial, 1-Rs shorter than 1-M, cell 2rm longer than 3rm, 2r-rs longer than the width of 2rm.

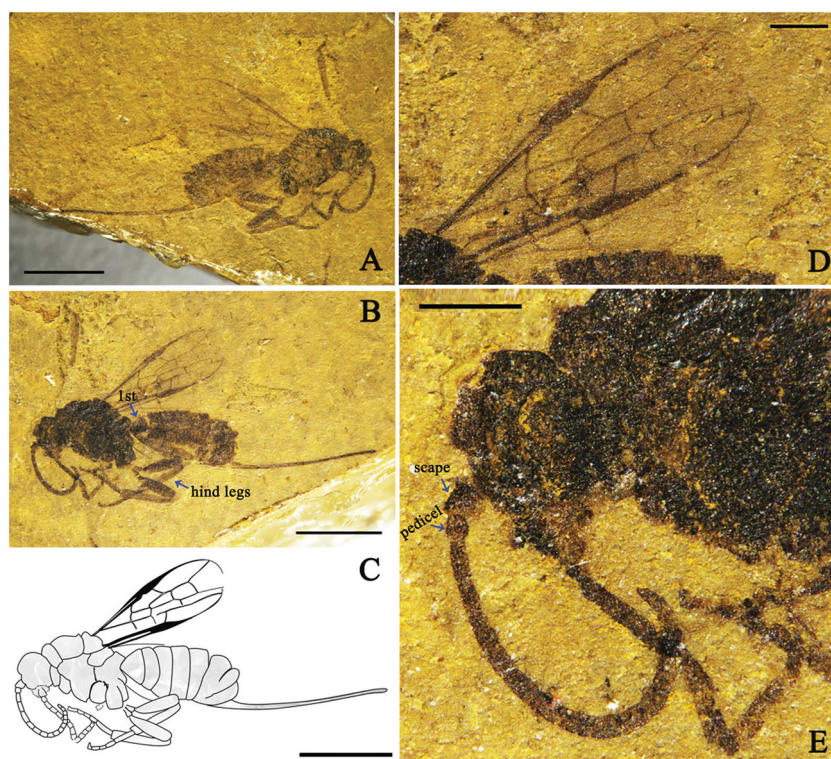
**Etymology.** From the Latin *grossus*, meaning thick; referring to both the first metasomal segment and hind legs.

**Holotype.** CNU-HYM-LB-2022003 (Yp101/627), complete female individual.

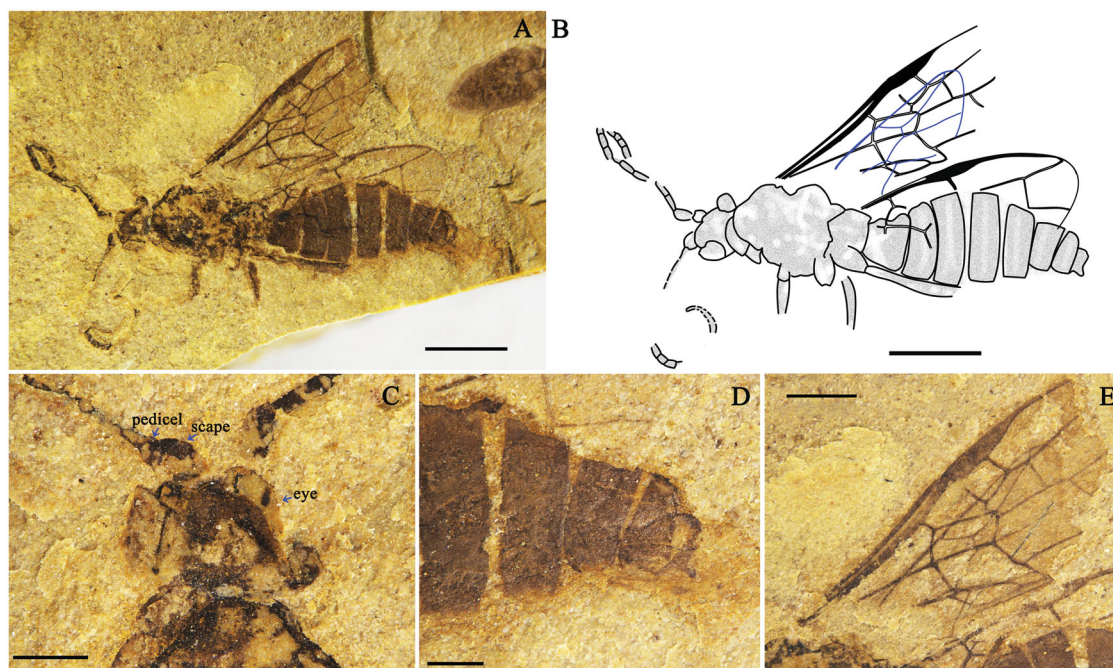
**Type locality, unit and age.** Yujiagou village near Beipiao in Liaoning Province, China; Haifanggou Formation, uppermost Middle Jurassic (upper Callovian), ~165–161 Ma (Xu *et al.* 2016, Ren *et al.* 2019, Li *et al.* 2021).

**Description.** The body length is 4.67 mm (excluding the ovipositor); the forewing length is 3.17 mm. The head is medium sized with long antennae that have 17 segments and a swollen scape that is distinctly wider than the pedicel; the flagellomeres are sub-equal in width. The mesosoma are slightly longer than high with the mesonotum being transversely ridged; the mesoscutellum is shorter than the





**Figure 3.** *Praeaulacon grossus* sp. nov. (CNU-HYM-LB-2022003). A, B, Photo of specimen; C, line drawing of forewing; D, photo of forewing; E, head with antennae. Scale bars: A, B, C = 2 mm; D, E = 0.5 mm. Abbreviation: 1-st, first metasomal segment.



**Figure 4.** *Proapocritus habitus* sp. nov. (CNU-HYM-LB-2022004). A, Photo of specimen; B, line drawing of habitus; C, photo of head; D, photo of terminal parts of metasoma; E, photo of wings. Scale bars: A, B = 2 mm; C, D = 0.5 mm; E = 1 mm.

mesoscutum. The metanotum is short and the mesopleuron broad, being coarse in its upper part and areolate in its lower part. The propodeum is nearly as long as the metanotum. The metasoma is elongate with eight segments; the first metasomal segment is conical, with the following segments being distinctly wider than the first segment. The ovipositor

is 3.42 mm long, and distinctly longer than the forewing. The forewing has 1-Rs shorter than 1-M; 2r-rs issuing from near the middle of the pterostigma; cell 1mcu in contact with 2rm by a short section of M; 2r-rs longer than 2r-m; 2m-cu partly preserved; cell 3rm much broader than 2rm; both 2r-m and 3r-m slightly bent; and 1cu-a interstitial.

Table 1. Summary of all described species of *Nevania* Zhang & Rasnitsyn, 2007 (emended from Li *et al.* 2014).

Species name/specimen ID	Body length (mm)	Wing venation	First metasomal segment L. (mm)	Second metasomal segment L. (mm)	Sex	Wing length and width (mm)	Wing L./ Body L. ratio
<i>N. feracula</i> Zhang & Rasnitsyn, 2007 Holotype NND2124/NIGP143698	11.4	cu-a interstitial; first abscissa of Rs subequal to that of M in length; 2A complete.	1.8	1.6	F	L.5.8 as pres.; W.1.7 as pres.	?
<i>N. exquisita</i> Zhang & Rasnitsyn, 2007 Holotype NND0613-0614/ NIGP143694-143695	15.8	cu-a postfurcal; first abscissa of Rs shorter than that of M. 1r-rs spectral; 2A complete.	2.4	2.4	F	L.9.5; W.2.9 as pres.	0.601
<i>N. robusta</i> Zhang & Rasnitsyn, 2007 Holotype NND0816/NIGP143693	18.1	cu-a postfurcal; first abscissa of Rs shorter than that of M. 2rm in contact with 1m-cu by a short, second section of M; 2A complete.	2.7	2.6	F	L.9.6; W.3.6	0.530
Additional specimen: CNU-HYM- NN-2012002	15.5		2.3	2.3	F	L.8.1; W.2.9	0.523
Additional specimen: CNU-HYM- NN-2012015	12.5	cu-a postfurcal; first abscissa of Rs shorter than that of M. 2rm in contact with 1m-cu by a point; 2A complete.	1.8	1.9	F	L.6.4; W.0.9 as pres.	0.512
<i>N. malleata</i> Zhang & Rasnitsyn, 2007 Holotype NND2099-2100/ NIGP 143696-143697	13.5 as pres.	cu-a postfurcal, first abscissa of Rs shorter than that of M. 2rm not in contact with 1m-cu; 2A complete.	2.5	2.4	F	L.8.3 as pres.; W.2.3 as pres.	?
<i>N. retenta</i> Zhang & Rasnitsyn, 2007 Holotype NND0815/NIGP143699 Other specimen: CNU-HYM-NN- 2012001 (P/C)	9.6 12.4 as pres.		1.6 2.0	1.6 1.8	F F	L.4.5 as pres.; W.2.2 as pres. L.5.1; W.2.3	? ?
<i>N. karatau</i> Zhang & Rasnitsyn, 2007 Holotype PIN2997-4157, forewing only.	?	cu-a interstitial; the first abscissa of Rs nearly as long as that of M; 2rm in contact with 1m-cu by a short, second section of M; 2A complete.	?	?	?	L.4.2; W.1.7	?
<i>N. perbella</i> Li <i>et al.</i> , 2014 Holotype CNU-HYM-NN-2012003	15.8	cu-a postfurcal the first abscissa of Rs shorter M. 2rm and 1m-cu in contact by a point; 2A complete.	2.6	2.7	F	L.8.6; W.2.7	0.544
Paratype CNU-HYM-NN-2012018 (P/C)	9.7		1.5	1.5	F	L.3.9 as pres.; W.?	?
Paratype CNU-HYM-NN-2012010	11.2		1.9	1.9	?	L.5.9; W.2.0	0.527
Paratype CNU-HYM-NN-2012014	12.8		1.9	1.9	F	L.7.0; W.2.1	0.547
<i>N. aspectabilis</i> Li <i>et al.</i> , 2014		cu-a postfurcal; the first abscissa of Rs nearly as long as that of M; 2rm in contact with 1m-cu by a point; 2A complete.					
Holotype CNU-HYM-NN-2012005	15.1		2.8	2.7	F	L.8.5; W.3.3	0.563
Paratype CNU-HYM-NN-2012012	14.2		2.2	2.1	F	L.5.9 as pres.; W.?	?
Paratype CNU-HYM-NN-2012013	11.9	cu-a interstitial; first abscissa of Rs shorter than that of M in length; 2A complete.	1.9	2.0	?	L.3.6 as pres.; W.?	?
<i>Nevania deviata</i> Li, Shih & Ren sp. nov.							
CNU-HYM-LB-2022001P/C	8.13		1.2	1.2	F	L.3.8; W.1.4	0.467

Abbreviations: L., length; W., width; F, female; ?, unknown; as pres., as preserved; ID = identification.

**Remarks.** *Praeaulacon grossus* differs from others *Praeaulacon* spp. in its first metasomal segments forming a wide triangular shape, and in having thick hind legs. The wing venation is similar to *Praeaulacon ningchengensis* Zhang & Rasnitsyn, 2008 in the following character states: forewing with 1cu-a interstitial; 1-Rs shorter than 1-M; cell 2rm longer than 3rm; 2r-rs longer than the width of 2rm; and the first metasomal segment being conical.

Family EPHIALTITIDAE Handlirsch, 1906

**Proapocritus** Rasnitsyn, 1975

***Proapocritus habitus*** sp. nov. Li, Shih & Ren (Fig. 4)

**Diagnosis.** First metasomal segments wide trapezoid, wider than long. Forewing with 1cu-a interstitial, 1-Rs shorter than 1-M, 1r-rs incomplete, 2r-rs nearly parallel to 1r-rs, a1-a2 present, cell 1mcu contact with 2rm by a short section of 2-M.

**Etymology.** From the Latin *habitus*, meaning plump; referring to the first metasomal segment broad, wider than long.

**Holotype.** CNU-HYM-LB-2022004 (Yp101/1304), complete male individual.

**Type locality, unit and age.** Yujiagou village near Beipiao in Liaoning Province, China; Haifanggou Formation, uppermost Middle Jurassic (upper Callovian), ~165–161 Ma (Xu *et al.* 2016, Ren *et al.* 2019, Li *et al.* 2021).

**Description.** The body length is 8.60 mm, with the forewing length being 5.70 mm. The head is medium sized with large eyes on either side. The antenna is partly preserved with a swollen scape that is distinctly longer and wider than the pedicel. The mesosoma is slightly longer than high with the propodeum being distinctly smaller than the first metasomal segment. The metasoma is fusiform with eight segments; the first metasomal segment is trapezoidal and wider (1.14 mm) than long (0.88 mm); the following segments are distinctly shorter than the first segment. The forewing has 1-Rs vertical to Rs and 1-Rs shorter than 1-M; 1r-rs is incomplete and does not reach the pterostigma. 2r-rs is straight and parallel to 1r-rs; it issues from near the middle of the pterostigma. Cell 1mcu is connected with 2rm by a short section of 2-M; 2r-m is slightly longer than 2r-rs; 2m-cu is only partly preserved; a1-a2 is present. The hind wing has a closed cell r; r-m is straight and shorter than 1-Rs and 1-M; the M + Cu fork is more basal than the cu-a fork.

**Remarks.** *Proapocritus habitus* differs all other *Proapocritus* spp. in its first metasomal segments being trapezoidal in shape and wider than long.

## Discussion

To date, the fossils of *Nevania* have only been collected from the Middle Jurassic of northeastern China and Late Jurassic of Kazakhstan (see Table 1 for references). Using

this material we distinguish two defining character states for the genus.

1. First and second metasomal segments being tube-like and much longer than the other remaining metasomal segments. Shih *et al.* (2009, 2010) suggested that a larger body with longer metasoma provided female pelecynids with more flexibility to reach, probe and deposit eggs into larval hosts hidden underground. We propose that lengthening of the first two long metasomal segments in our *Nevania* specimens might have had a comparable function.
2. Forewing with vein 2A and 11 closed cells. These features are widely seen in Symphyta and Ephialtidae (Rasnitsyn 1969, 1975). By contrast, *Nevania* spp. display variable venation, including postfurcal versus interstitial 1cu-a, absent versus spectral 1r-rs, 1-M longer than versus sub-equal to 1-Rs, and 1mcu in contact with 2rm by a point versus a short section of M. M + Cu can also be short, sub-equal or shorter than 1-Rs and 1-M (basal vein) resulting in 1-Rs and 1-M being strongly oblique.

We document the first examples of *Nevania* from the new fossil insect locality at Yujiagou village (Li *et al.* 2021, Xu *et al.* 2016). *Nevania deviata* is distinguished as the smallest (8.1 mm) species within the genus, whereas *Nevania robusta* is the largest (18.1 mm). Four other species described from the Haifanggou Formation (= Jiulongshan Formation) exhibit body lengths between 15 mm and 16 mm (Li *et al.* 2021, Xu *et al.* 2016), indicating a relatively broad size range. More fossil data and further studies are needed to elucidate this patterns of body size across different species and localities.

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No potential conflict of interest was reported by the author(s).

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