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Application of geometric morphometric analyses to confirm two new species of Karatavitidae (Hymenoptera: Karatavitoidea) from northeastern China

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Two new species, *Praeratavites rasnitsyni* and *Karatavites ningchengensis* in the wasp family Karatavitidae, are described and illustrated. These specimens were collected from the uppermost Middle Jurassic Jiulongshan Formation at Daohugou Village in Inner Mongolia, China. Key venation characters, as measured by relative positions or length ratios, are summarized for all documented species of *Karatavites* and *Praeratavites* to facilitate morphological comparisons and assess whether the studied specimens are referable to new species. In addition, geometric morphometric analyses were conducted to confirm the distinction of the new species, which add to the diversity of these genera in the Middle Jurassic.

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Key words: Praeratavites, Karatavites, Jiulongshan Formation, Middle Jurassic, Daohugou, Inner Mongolia.

The extinct family Karatavitidae Rasnitsyn, 1963 belongs to the superfamily Karatavitoidea Rasnitsyn, 1963. Karatavitoidea also contains Orussidae Newman, 1834. So far, seven genera have been assigned to Karatavitidae: *Karatavites* Rasnitsyn, 1963 from the Late Jurassic of Kazakhstan and latest Middle Jurassic of China, *Grimmaratavites* Rasnitsyn *et al.* 2006 from the Early Jurassic of Germany, and *Praeratavites* Rasnitsyn *et al.* 2006, *Praporyssites* Rasnitsyn *et al.* 2006, *Postxiphidria*, Rasnitsyn & Zhang, 2010, *Postxiphidroides* Rasnitsyn & Zhang, 2010 and *Praeratavitioides* Rasnitsyn & Zhang, 2010 from the latest Middle Jurassic of China (Rasnitsyn 1963, Rasnitsyn *et al.* 2006, Rasnitsyn & Zhang 2010).

Karatavitidae genera played important roles in the early evolution of hymenopterans on the lineage leading to Apocrita. Rasnitsyn *et al.* (2006) inferred a gradual transition from *Praeratavites*, with a sub-basal loop of vein 2A in the forewing, which resembles the common ancestor of all Vespina *s.l.* to *Karatavites*, which lacks the loop of 2A and resembles the common ancestor of Apocrita.

Here we describe two new species, *Praeratavites rasnitsyni* and *Karatavites ningchengensis*, based on three specimens collected from the uppermost Middle

Jurassic beds at Daohugou Village, Shantou Township, Ningcheng County, Inner Mongolia, northeastern China (41°18.979'N, 119°14.318'E). The stratigraphic unit yielding the studied materials is the Jiulongshan Formation of late Callovian age, latest Middle Jurassic (165–164 Ma), determined by a ⁴⁰Ar/³⁹Ar isotopic dating (He *et al.* 2004) calibrated to a standard international time-scale (He *et al.* 2004, Walker *et al.* 2013).

Materials and methods

All type specimens are deposited in the Key Lab of Insect Evolution & Environmental Changes, Capital Normal University, Beijing, China (CNUB; Dong Ren, Curator). These specimens were examined and photographed using a Nikon SMZ25 microscope, with an attached Nikon DS-Ri2 digital camera system. The line drawings were composed with Adobe Illustrator CC and Adobe Photoshop CS5 software.

The nomenclature for wing venation is adapted from Rasnitsyn *et al.* (2006): Rs, radial sector; M, media; Cu, cubitus; 1r-rs, first radial crossvein; 2r-rs, second radial crossvein; cu-a, first anal crossvein; 2cu-a, second anal crossvein; 1 m-cu, first mediocubital crossvein; 2 m-cu, second mediocubital crossvein; 3r-m, second radiomedial crossvein.

Geometric morphometric analyses (GMA) have been applied widely to the study of phenetic relationships

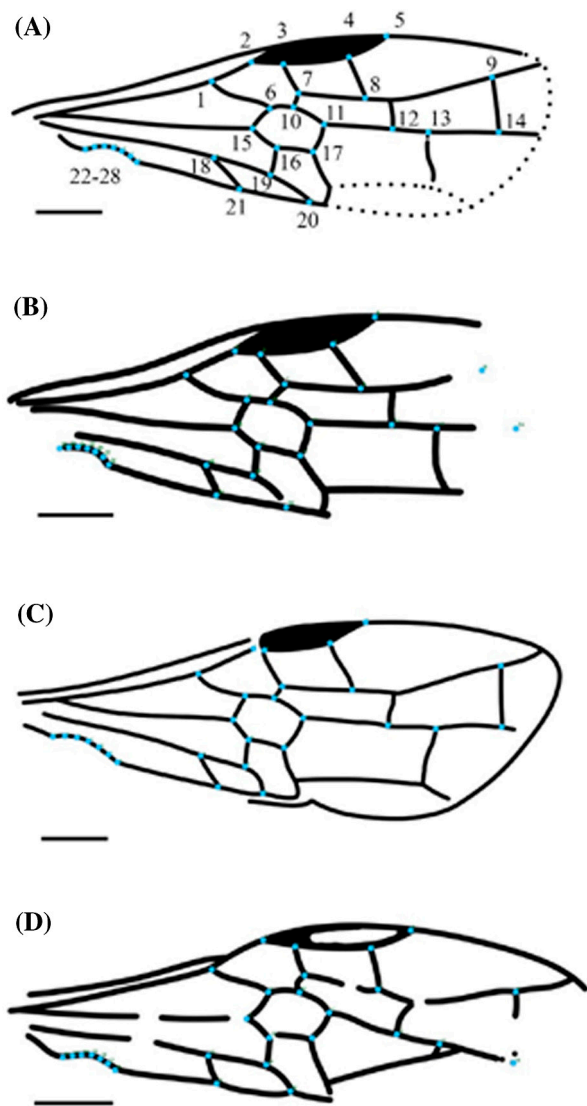


Fig. 1. Landmark position of the four forewing samples of *Praeratavites*: **A**, *P. rasnitsyni* sp. nov. holotype (original); **B**, *P. rasnitsyni* sp. nov. paratype (original) with inferred positions of landmarks 9 and 14; **C**, *P. daohugou* [from Rasnitsyn *et al.* (2006)]; **D**, *P. perspicuus* [from Rasnitsyn & Zhang (2010)] with inferred positions of landmark 14. Scale bars = 1 mm.

(without consideration of evolutionary relationships) among extant and fossil insects and/or their associations with plants (Wang *et al.* 2012, Perrard *et al.* 2012, Bai *et al.* 2013, Lin *et al.* 2016). Adobe Photoshop CS5 was used to re-draw the wing and venation of the karatavitid specimens used in the analyses based on new photos or previously published figures. The JPEG images were then exported to tps-UTILS (Rohlf 2006b) and converted into TPS files. Using tps-DIG (Rohlf 2006a), we selected 28 landmarks for *Praeratavites* (Fig. 1) and 21 for *Karatavites* (Fig. 2) representing key points on the wing veins. Because the loop of A2 is crucial to differentiate genera in Karatavitidae, seven landmarks were designated to represent the loop. For the specimen with the loop, a path was drawn on the loop, and seven landmarks were added from the

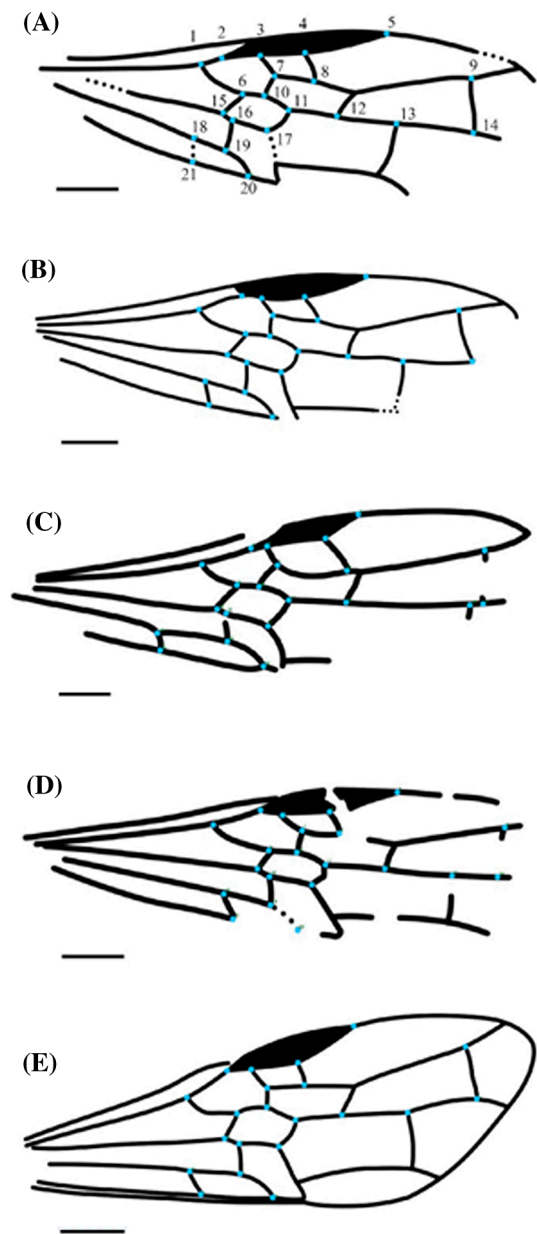


Fig. 2. Landmark position of the five forewing samples of *Karatavites*: **A**, *K. ningchengensis* sp. nov. with inferred positions of landmarks 17, 18 and 21 (original); **B**, new material of *K. medius* (original); **C**, *K. angustus* [from Rasnitsyn (1963)]; **D**, *K. junfengi* [from Rasnitsyn & Zhang (2010)] with inferred positions of landmarks 14 and 20; **E**, *K. medius* (from Rasnitsyn 1969). Scale bars = 1 mm.

beginning to the end of the loop with equal distance between two landmarks by using a tool available in tps-DIG (Fig. 1). If comparison of specimens with and without the loop was necessary, seven landmarks were drawn for the loop-less specimen where the loop was assumed to be, based on relative distances from specimens with the loop. Minor assumptions were required owing to some missing veins in the available fossils, and these assumptions of inferred positions of landmarks are documented in the figure captions (Figs 1, 2). The collection of landmarks was used as data inputs for tps-SPLIN (Rohlf 2004), and a global least-square reference was calculated by the computer. The program

generated a table containing the Procrustes distances of all specimens in relation to each other. The table was then used by the NTSYSpc program (Rohlf 2007) with the unweighted pair-group method using the arithmetic averages (UPGMA) method to create a tree showing the phenetic relationships among these studied specimens.

Systematic palaeontology

Order HYMENOPTERA Linnaeus, 1758

Suborder VESPINA Laichartring, 1781

Superfamily KARATAVITOIDEA Rasnitsyn, 1963

Family KARATAVITIDAE Rasnitsyn, 1963

Praeratavites Rasnitsyn *et al.* 2006

Type species. *Praeratavites daohugou* Rasnitsyn *et al.* 2006, latest Middle Jurassic, northeast China.

Included species. Type species, *P. wuhuaensis* Rasnitsyn & Zhang, 2010, *P. perspicuus* Rasnitsyn & Zhang, 2010 and *P. rasnitsyni* sp. nov.

Praeratavites rasnitsyni sp. nov. (Figs 3, 4)

Type materials. Holotype, female, No. CNU-HYM-NN-2016001P/C (part and counterpart; Fig. 3). Paratype, female, No. CNU-HYM-NN-2016003 (Fig. 4).

Locality unit and age. Daohugou Village, Shantou Township, Ningcheng County, Inner Mongolia, China; Jiulongshan Formation; latest Middle Jurassic (late Callovian).

Etymology. The specific epithet is in honour of Dr Alexandr Rasnitsyn for his significant contribution to palaeoentomology, especially to the early evolution and development of Hymenoptera, and for his erection of Karatavitidae in 1963.

Diagnosis. A combination of the following three characters are used to differentiate the new species from the three congeners: 1, the length ratio (2.3–2.4) of the 1st abscissa of Rs vs that of M; 2, the relative position (72–74%) of 2r-rs intersecting the top of cell 2rm; 3,

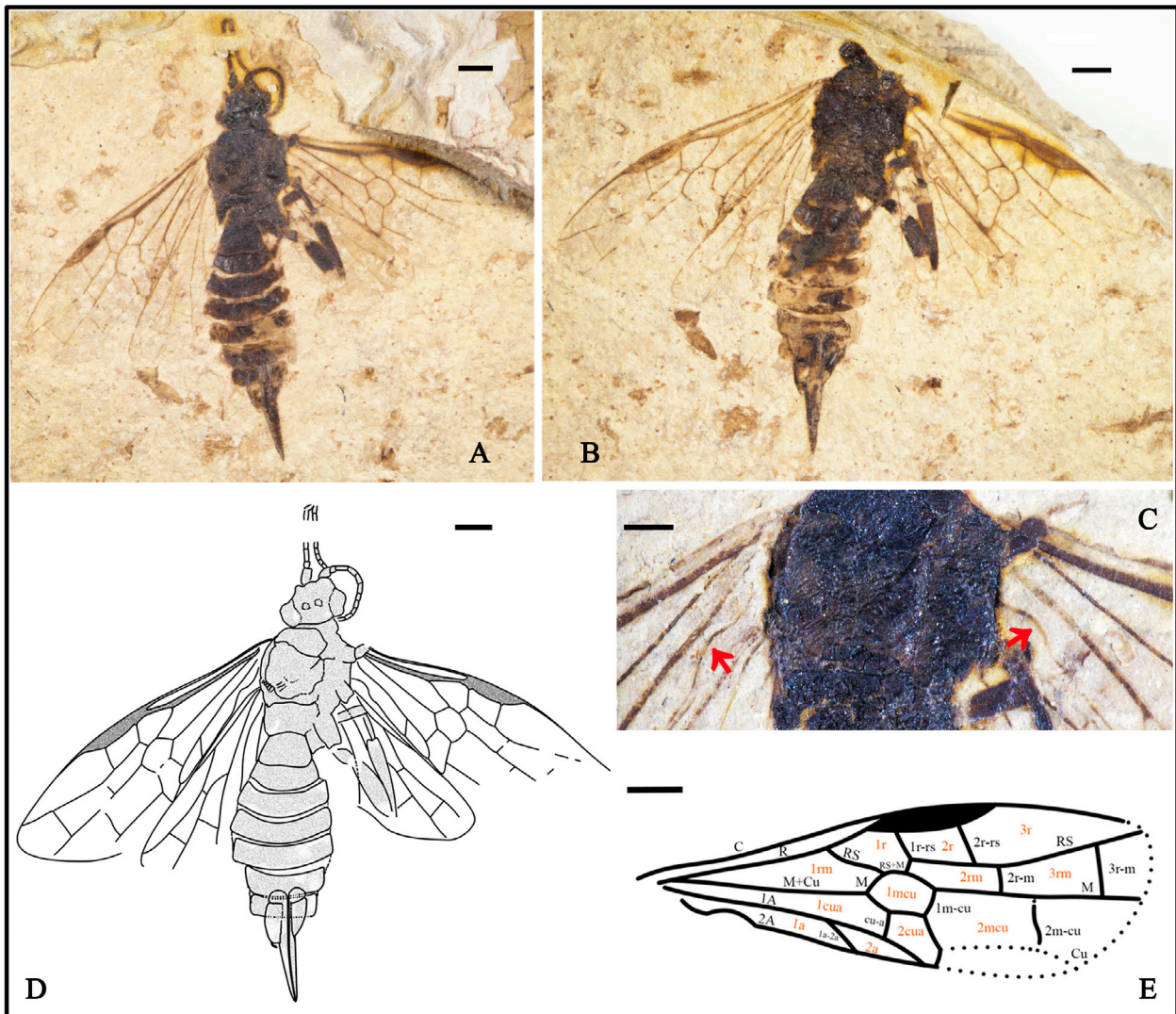


Fig. 3. *Praeratavites rasnitsyni* sp. nov. Holotype, CNU-HYM-NN-2016001P/C; A–B, Habitus; C, basal forewing indicating the sub-basal loop of 2A; D, Line drawing of the habitus; E, Line drawing of forewing. A, B, D and E with scale bars 1 mm; C, 0.5 mm.

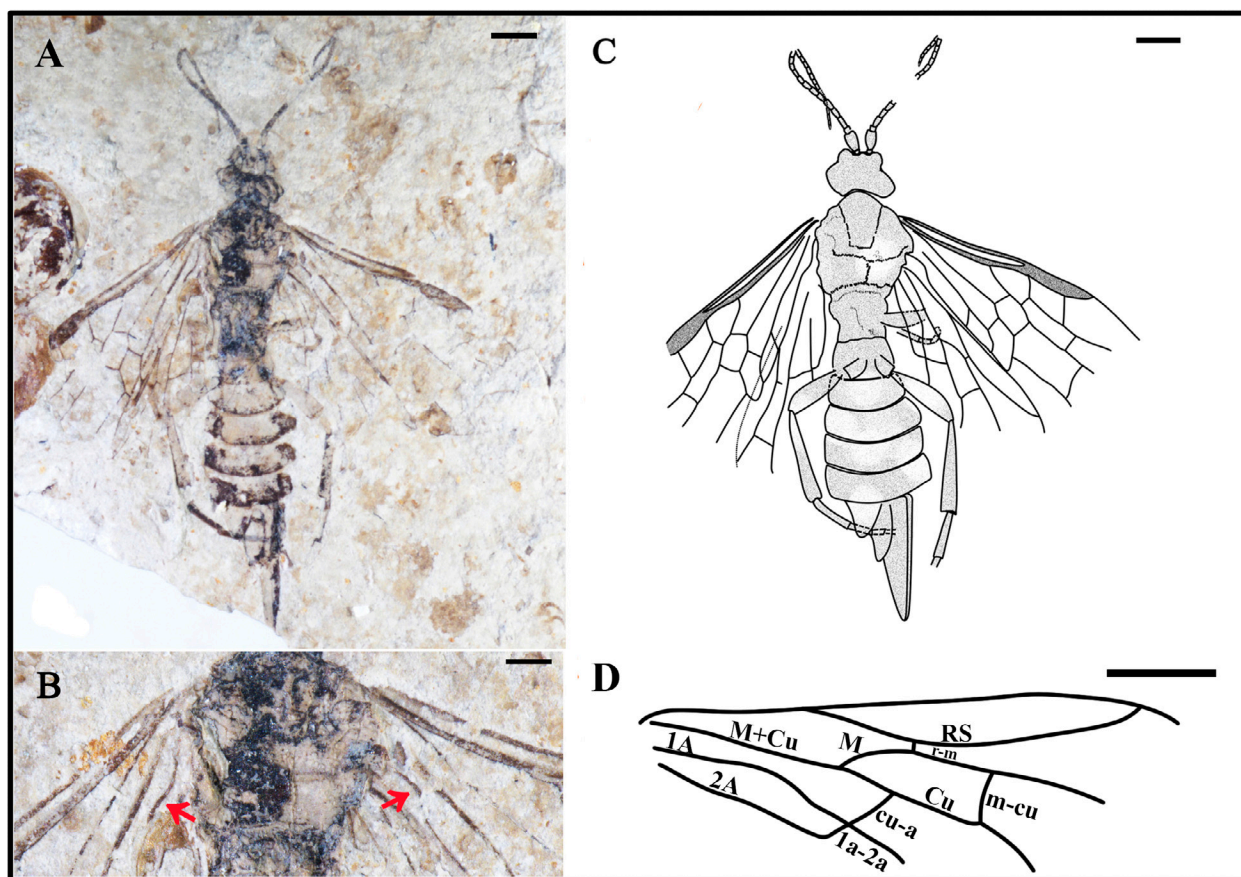


Fig. 4. *Praeratavites rasnitsyni* sp. nov. Paratype, CNU-HYM-NN-2016003; A, Habitus; B, Basal forewing indicating the sub-basal loop of 2A; C, Line drawing of the habitus; D, Line drawing of the hind wing. A, C, and D with scale bars 1 mm, B, 0.5 mm.

the relative position (33%) of 2 m-cu intersecting the bottom of cell 3m.

Remarks. This species is assigned to *Praeratavites* based on the consistency of its key characters with the generic diagnosis given by Rasnitsyn & Zhang (2010). We summarize the relative position (measured by the intersection point as a percentage from the basalmost point to the terminus) and length ratio data for key venational characters (columns 4–12 of Table 1). The holotype and paratype have similar values for the three diagnostic characters (Table 1, columns 4–6). On the other hand, the holotype and paratype of the new species differ significantly from all three congeners on the basis of these diagnostic characters. In addition, the new species differs from *P. daohugou* and *P. wuhuaensis* in that the body is smaller, and the mesosoma is broader; it differs from *P. perapicuius* in that the head is narrower, and the mesosoma is much longer.

Description. Holotype CNU-HYM-NN-2016001P/C, female, body mostly dark, of medium size (about 10.9 mm long, excluding antenna, including ovipositor; Fig. 3). Head circular, length 1.3 mm, width 1.7 mm; antennae partly preserved, with scape long and thick, pedicel distinctly shorter and narrower than scape.

Mesosoma approximately 3.8 mm long and 2.3 mm wide; mesonotum with mesoscutum broad and round; propodeum trapezoid, nearly as long and wide as first metasomal segment. Metasoma elongate with seven segments; first metasomal segment trapezoid, distinctly longer than other segments; following metasomal segments nearly equal in length, and the 4th and 5th being widest. Ovipositor short and slightly curved, sheaths tapering (Fig. 3A, B, D). Forewing (Fig. 3A, B, D, E) length 8.0 mm, width 2.4 mm as preserved, the pterostigma large, with 2r-rs issuing from near its apical quarter, 1r-rs slightly shorter than 2r-rs, issuing from near its basal quarter; R distinctly angular at Rs base, Rs gently arching basally, the first abscissa of Rs about twice as long as that of M, Rs+M not reaching the mid-length of the anterior side of cell 1m-cu; cell 1m-cu of medium width, with cu-a nearly reaching midlength of posterior side of 1m-cu; cell 3r acuminate; cell 2rm distinctly narrower but slightly shorter than 3rm; crossvein 3r-m about twice as long as 2r-m; 2 m-cu twice as long as 1 m-cu; 1a-2a positioned much more basally than M+Cu forking; the sub-basal loop of 2A present (Fig. 3C). Hind wing (Fig. 3A, B, D) length 5.4 mm, with Rs initiating far basad of M+Cu forking, both 1r-m and 2r-m present, 2r-m more distant to 1r-m than

	2. Wing length (mm)	3. Body length (mm)	4. Ratio of 1st abscissa of Rs vs. that of M	5. Position* of		7. Ratio of width of cell 3rm vs. that of cell 2rm	8. Ratio of (1r-rs to base of Rs)/(1r-rs to 2r-rs)	9. Position of Rs intersecting top of cell 1m-cu (%)		10. Position of cu-a intersecting bottom of cell 1m-cu (%)		11. Position of cu-a intersecting top of cell 2a (%)		12. Position of 2r-m intersecting top of cell 2 m-cu (%)		13. Sex
				2r-rs intersecting top of cell 2rm (%)	2 m-cu intersecting bottom of cell 3rm (%)			Rs intersecting top of cell 1m-cu (%)	cu-a intersecting bottom of cell 1m-cu (%)	cu-a intersecting top of cell 2a (%)	cu-a intersecting top of cell 2 m-cu (%)					
<i>P. daohugou</i>	8.80	10.45	1.82	63.6	41.7	0.96	1.00	44.0	41.7	60.0	63.5			Female		
<i>P. wuhuaensis</i>	7.4 as pre.	11.40	1.90	64.7	27.3	1.10	1.10	37.5	41.2	58.3	NA			Female		
<i>P. perspicus</i>	7.3 as pre.	8.80	1.80	68.8	37.5	1.07	1.09	42.1	40.0	59.3	62.5			Female		
<i>P. rasnitsyni</i>	8.00	NA	2.38	73.8	33.0	1.06	1.10	44.4	43.8	56.0	66.0			Female		
sp. nov. (holotype)																
<i>P. rasnitsyni</i>	NA	9.00	2.33	71.9	NA	NA	1.05	38.1	38.1	55.6	64.0			Female		
sp. nov. (paratype)																

Table 1. Body characters and relative position and length ratio data of key venation characters for species in *Praeratavites* Rasnitsyn *et al.* 2006. *Position is the intersection point as a percentage from the basalmost point to the terminus.

	<i>P. rasnitsyni</i> sp. nov. (holotype)	<i>P. rasnitsyni</i> sp. nov. (paratype)	<i>P. daohugou</i>	<i>P. perspicuus</i>
<i>P. rasnitsyni</i> sp. nov. (holotype)	0.0000			
<i>P. rasnitsyni</i> sp. nov. (paratype)	0.0531	0.0000		
<i>P. daohugou</i>	0.0803	0.0745	0.0000	
<i>P. perspicuus</i>	0.1039	0.1170	0.1156	0.0000

Table 2. Relative Procrustes distance for species in *Praeratavites* Rasnitsyn *et al.* 2006.

to apex of cell r, and four times as long as 1r-m; cu-a meeting cell 2rm medially, cu-a slightly longer than 2r-m; 1A and 2A partly preserved.

Paratype CNU-HYM-NN-2016003, female (Fig. 4), major characters equivalent to those of the holotype, except for slight differences in some dimensions. Some characters present in the paratype are not preserved in the holotype: body length 10.6 mm, antenna long and thin, with more than 25 flagellomeres; legs partly preserved, hind femur wider but shorter than tibia; hind wing with cu-a meeting Cu quite distal to M+Cu forking; 1a-2a aligned with 2A and reaching 1A in contact with cu-a (Fig. 4A, C, D).

Results of GMA. Based on the Procrustes distance of all *Praeratavites* species in relationship to each other (Table 2), we obtained a tree showing their phenetic relationships using the NTSYSpc program (Rohlf 2007) with the UPGMA method. The tree (Fig. 5A) confirms that *Praeratavites rasnitsyni* clearly differs from other congeners, confirming its specific status.

Karatavites Rasnitsyn, 1963

Type species. *Karatavites angustus* Rasnitsyn, 1963, Upper Jurassic, southern Kazakhstan.

Included species. Type species, *K. medius* Rasnitsyn, 1969, *K. junfengi* Rasnitsyn & Zhang, 2010 and *K. ningchengensis* sp. nov.

Karatavites ningchengensis sp. nov. (Fig. 6)

Type material. Holotype, male, No. CNU-HYM-NN-2016004 (Fig. 6).

Locality unit and age. Daohugou Village, Shantou Township, Ningcheng County, Inner Mongolia, China; Jiulongshan Formation; latest Middle Jurassic (late Callovian).

Etymology. The specific epithet refers to Ningcheng County, from which many scientifically important fossils have been documented.

Diagnosis. A combination of the following four characters differentiates the new species from the three congeners: 1, the length ratio (*ca* 1.7) of the 1st abscissa of Rs vs that of M; 2, the relative position (*ca* 49%) of 2r-rs intersecting the top of cell 2rm; 3, the relative position (*ca* 43%) of 2 m-cu intersecting the bottom of cell 3rm; 4, the ratio (*ca* 1.8) of width of cell 3rm vs that of cell 2rm.

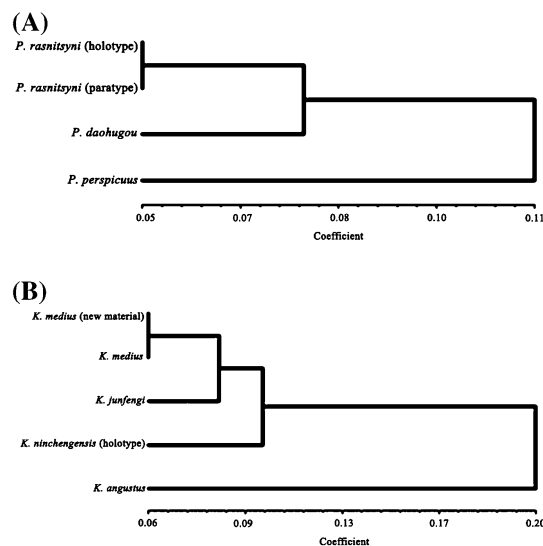


Fig. 5. Tree resulting from GMA showing the phenetic relationships. **A**, For all species of *Praeratavites* confirming that *Praeratavites rasnitsyni* sp. nov. is a new species; **B**, For all species of *Karatavites* confirming that *K. ningchengensis* sp. nov. is a new species and CNU-HYM-NN-2016002P/C represents a new material of *K. medius*.

Remarks. This species is assigned to *Karatavites* based on the consistency of its key characters with the generic diagnosis provided by Rasnitsyn & Zhang (2010). We determined the relative position (measured by the intersection point as a percentage from the basalmost point to the terminus) and length ratio data for key venation characters (columns 4–12 of Table 3). The data in columns 4–7 (Table 3) show that the new species is similar to *K. medius* in the ratio of the length of the 1st abscissa of Rs vs that of M (1.76 vs 1.73 for the new species) and the ratio of width of cell 3rm vs that of cell 2rm (1.77 vs 1.76), but different in the relative position of 2r-rs intersecting the top of cell 2rm (45% vs 49%) and the relative position of 2 m-cu intersecting the bottom of cell 3rm (48% vs 43%). Based on the data in columns 8 [Ratio of (1r-rs to base of Rs)/(1r-rs to 2r-rs)], 9 (Position of Rs intersecting the top of cell 1mcu), 11 (Position of cu-a intersecting the top of cell 2a) and 12 (Position of 2r-m intersecting the top of cell 2mcu) (Table 3), the new species differs from *K. medius*. In addition, the new species differs from *K. angustus* and *K. junfengi* in all of the four diagnostic characters (Table 3, columns 4–7). Furthermore, the new species differs from the three known congeners in having a small body size, mesosoma and metasoma short but broad, and a very broad head with thick scape.

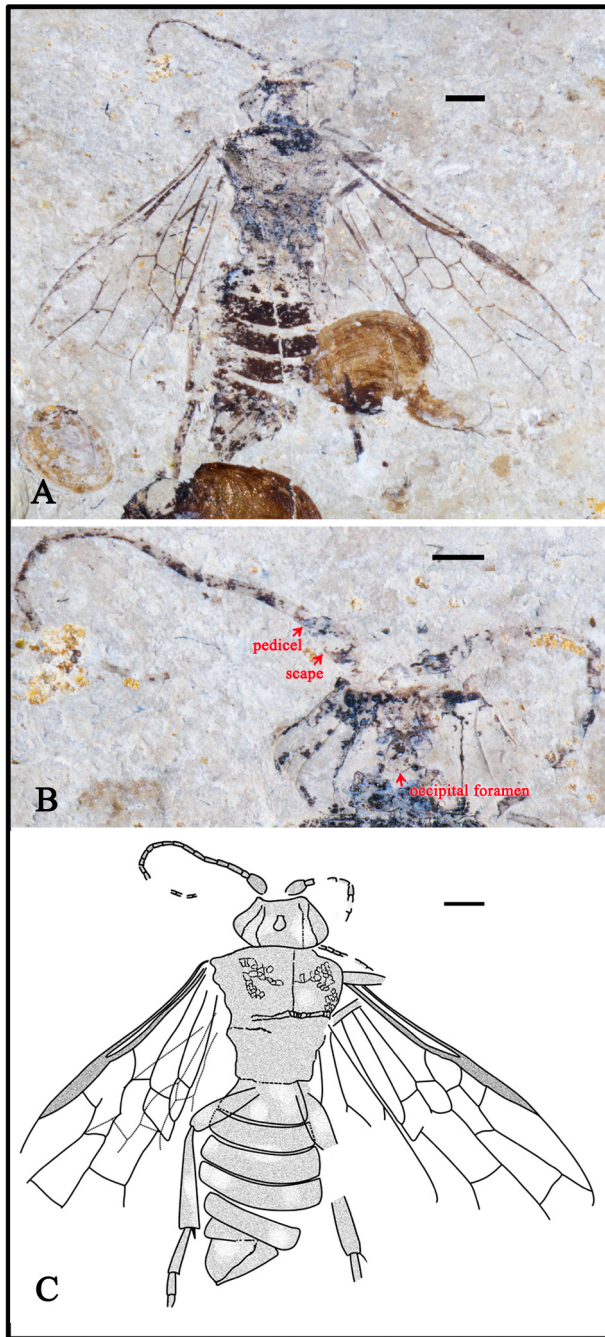


Fig. 6. *Karatavites ningchengensis* sp. nov. Holotype, CNU-HYM-NN-2016004; A, Habitus; B, Head; C, Line drawing of the habitus. Scale bars in A and C = 1 mm, B = 0.5 mm.

Description. Male, body mostly brown, medium sized (about 9.5 mm long, excluding antennae). Head transversely oval, length 1.4 mm, width 2.6 mm; antenna with 19 flagellomeres as preserved (Fig. 6B), scape long and thick (0.6 mm long, 0.3 mm wide), pedicel distinctly shorter and narrower than scape, first flagellomere longest, remaining flagellomeres gradually becoming shorter from basal to apical; occipital foramen circular. Mesosoma broad, distinctly wider than head, approximately 3.2 mm long and 2.9 mm wide (Fig. 6A, C). Metasoma with seven visible segments;

the first metasomal segment trapezoid, distinctly longer than other segments; the 2nd, 3rd and 4th metasomal segments nearly equal in length and width; remaining segments gradually becoming narrower. Forewing (Fig. 6A, C) length 8.3 mm, width 2.5 mm as preserved, the pterostigma long and narrower, with 2r-rs issuing from the middle of pterostigma, 1r-rs nearly as long as 2r-rs, issuing from nearly the base of pterostigma; R distinctly angular at Rs base, Rs gently arching basally, the first abscissa of Rs about twice as long as that of M, Rs+M nearly reaching the midlength of anterior side of 1mcu; cell 1mcu about twice as long as wide, with cu-a postfurcal, cu-a significantly more basal than 1r-m; cell 3r acuminate, cell 2rm distinctly narrower than 3rm and distinctly shorter than 3rm, 3r-m about twice as long as 2r-m; 2 m-cu twice as long as 1 m-cu, 1a-2a slightly more basal than 1 M; the sub-basal loop of 2A absent. Hind wing poorly preserved, but, crossveins 2r-m, m-cu and cu-a clearly discernible.

Results of GMA. Based on the Procrustes distance of all *Karatavites* species in relationship to each other (Table 4), we obtained a tree showing their phenetic relationships (Fig. 5B) that confirms *Karatavites ningchengensis* sp. nov. differs from other congeners.

***Karatavites medius* Rasnitsyn, 1969 (Fig. 7)**

Description of new material. No. CNU-HYM-NN-2016002P/C (part and counterpart, Fig. 7), female, collected from the same locality as the other specimens described in this paper. Assigned to *K. medius* Rasnitsyn, 1969 based mainly on the forewing lacking a sub-basal loop of 2A and cu-a being postfurcal (the distance about one-third length of 1mcu). Further, the new material provides additional characters that are not preserved in the holotype: body size about 12.2 mm long, excluding antennae; head transversely ovate (1.2 mm long, 2.1 mm wide). Mesosoma slightly wider than head, about 3.2 mm long and 2.6 mm wide. Metasoma with seven segments visible, the first metasomal segment about twice as long as any other segments, and other segments nearly equal in length; ovipositor short, sheath tapering (Fig. 7A, B, C). Forewing length 9.1 mm, width 2.8 mm as preserved, both 1r-rs and 2r-rs short, and separately issuing from nearly one-third and two-thirds basal position of pterostigma; 2r-m distinctly shorter than 3r-m, but cell 3rm distinctly longer than cell 2rm; cell 1mcu nearly twice as long as wide, cell 2mcu much larger than 1mcu; 1a-2a much more basal than cu-a and slightly shorter than it. Hind wing with Rs starting from R distal to M+Cu forking, both 1r-m and 2r-m present; cu-a meeting Cu quite distal to M+Cu forking; 1a-2a aligned with 2A and reaching 1A basad of cu-a (Fig. 7C, D).

Remarks. The relative position and length ratio data for the forewing of the new material, albeit having some similarities, do not closely resemble those of *K. medius*

	2. Wing length (mm)	3. Body length (mm)	4. Ratio of 1st abscissa of Rs vs. that of M	5. Position* of 2r-rs intersecting top of cell 2rm (%)	6. Position of 2m-cu intersecting bottom of cell 3rm (%)	7. Ratio of width of cell 3rm vs. that of cell 2rm	8. Ratio of (1r-rs to base of Rs)/(1r-rs to 2r-rs)	9. Position of Rs intersecting top of cell 1mcu (%)	10. Position		13. Sex	
									of cu-a intersecting bottom of cell 1mcu (%)	of cu-a intersecting top of cell 2a (%)		of 2r-m intersecting top of cell 2mcu (%)
<i>K. angustus</i>	11.6 as pre.	15.3	1.39	87.0	89.2	1.54	1.12	40.0	12.9	60.0	31.3	female
<i>K. medius</i>	8.3	NA	1.76	44.7	48.4	1.77	1.48	50.0	25.0	54.8	41.0	NA
<i>K. medius</i> (new material)	9.1	12.2	1.93	53.2	43.3	1.52	1.43	43.3	33.3	52.4	48.2	female
<i>K. junfengi</i>	8.0 as pre.	9.6	2.44	41.2	55.6	1.36	1.33	47.6	20.0	46.7	46.8	female
<i>K. ningchengensis</i> sp. nov. (right wing)	8.3	9.7	1.73	49.4	42.6	1.76	1.35	44.4	24.0	47.9	45.5	Male

Table 3. Body characters and relative position and length ratio data of key venation characters for species in *Karatavites* Rasnitsyn, 1963. *Position is the intersection point as a percentage from the basalmost point to the terminus.

	<i>K. medius</i> (new material)	<i>K. ningchengensis</i> sp. nov.	<i>K. augustus</i>	<i>K. junfengi</i>	<i>K. medius</i>
<i>K. medius</i> (new material)	0.0000				
<i>K. ningchengensis</i> sp. nov.	0.0926	0.0000			
<i>K. augustus</i>	0.2033	0.2194	0.0000		
<i>K. junfengi</i>	0.0784	0.1203	0.2002	0.0000	
<i>K. medius</i>	0.0564	0.0869	0.1851	0.0901	0.0000

Table 4. Relative Procrustes distance for species in *Karatavites* Rasnitsyn, 1963.

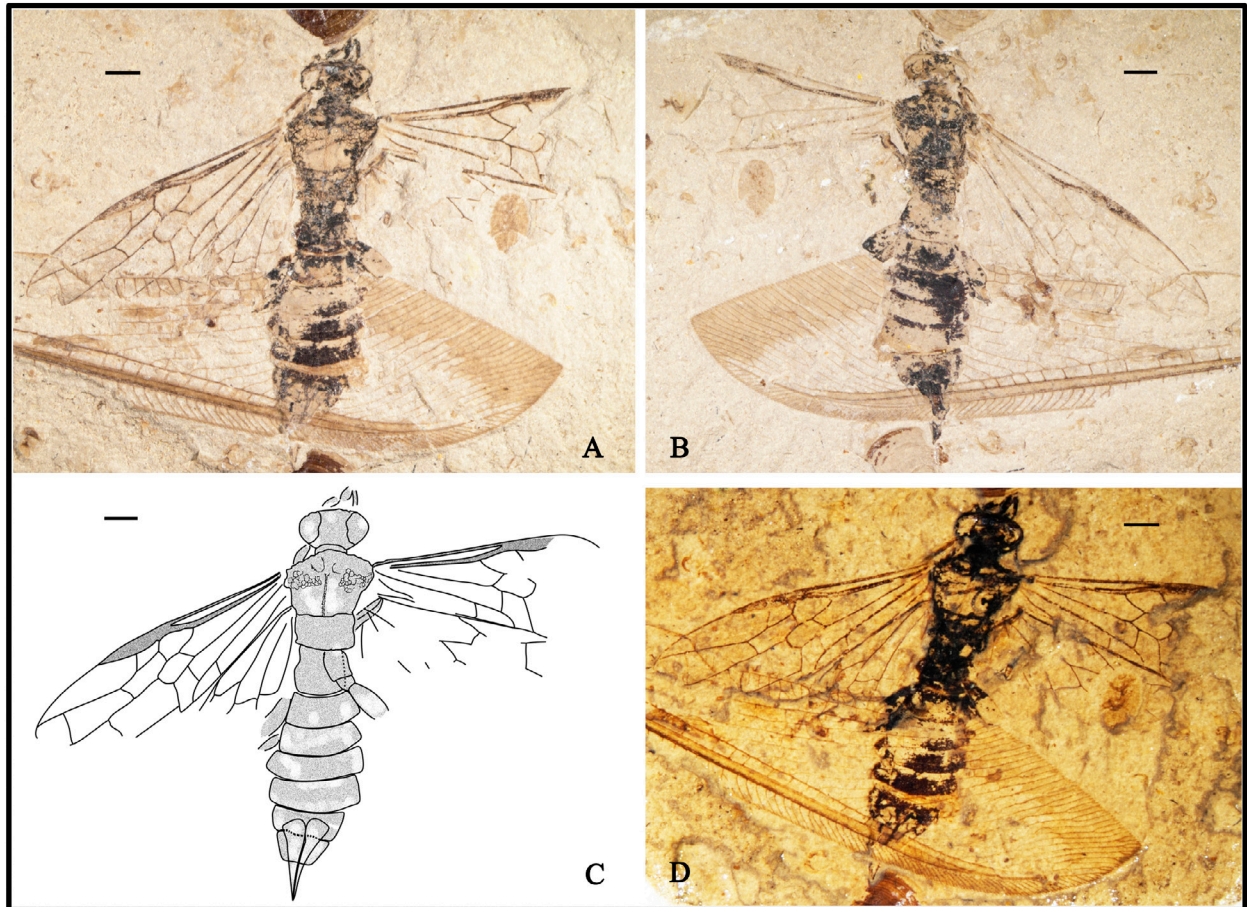


Fig. 7. *Karatavites medius* Rasnitsyn, 1969, new material, CNU-HYM-NN-2016002P/C; A–B, Habitus without alcohol; C, Line drawing of the habitus; D, Habitus with alcohol. Scale bars = 1 mm.

based on our collected data (Table 3). After including the data in the GMA (Fig. 5B), the results indicate that this new material is very similar to the described specimen of *K. medius* Rasnitsyn, 1969. We deem this new material referable to *K. medius* and any differences in character values represent intraspecific variations.

Discussion

Karatavitids played important roles in the early evolution of hymenopteran lineages leading to Apocrita. Rasnitsyn *et al.* (2006) inferred a gradual transition from *Praeratavites*, which resembles the common ancestor of all Vespina *s.l.*, to *Karatavites*, which resembles the common ancestor of Apocrita. Our findings of *Praeratavites rasnitsyni* sp. nov., *Karatavites ningchengensis*

sp. nov. and a new specimen of *K. medius* enhance our understanding of their morphological characters and broaden the known diversity of these genera in the Middle Jurassic of northeastern China.

The use of GMA in this study has revealed its effectiveness but also some drawbacks. One pitfall of this methodology is that absent landmarks for a specimen are not allowed, in contrast to using ‘unknown’ or ‘not available’ conditions for missing character states in a phylogenetic analysis. Since it is quite common for fossil specimens to lack some preserved parts essential for determining landmarks, to proceed with the GMA we may need to assume landmark positions based on inferences from other related or similar fossils. The assumptions for the analyses are clearly stated in the legends of Figs 1 and 2.

For the GMA, all landmarks chosen are considered to be of equal weight, in contrast to the option of using weighting factors for individual characters in phylogenetic analyses. To accommodate for this issue, we may select more landmarks in areas deemed to host ‘important’ characters (e.g., diagnostic characters). On the other hand, for characters judged as ‘not important’ (e.g., features that typically show intraspecific variations), we may not select any landmarks for that area.

One advantage of the GMA is that this methodology can handle landmarks on a continuum basis, in contrast to the discrete character states in the phylogenetic analyses. Furthermore, the GMA takes an overarching approach to make comparisons based on all landmarks, e.g., by calculating the ‘Procrustes distance’ (i.e., the square root of the sum of all squares of the distances between sample landmarks versus references in all axes) for each specimen. In Table 3, there are nine sets of venation data (Columns 4 to 12) calculated from relative positions or length ratios, which are more comprehensive than some other morphological comparisons with only a few key characters. These data sets, most of which are measurements along the x-axis of wing length, are treated as independent variables in diagnostic comparisons. If based on the data in Table 3, it would appear that CNU-HYM-NN-2016002P/C is a new species. However, after running the GMA, the resulting tree (Fig. 5B) shows that it is very similar (and here deemed conspecific) to *K. medius*. In the GMA, a total of 21 landmarks (Fig. 2A) are used to calculate the ‘Procrustes distance’ using both x- and y-axes. The inter-relationships of all landmarks are inherently incorporated into the ‘Procrustes distance’ analyses. Hence, it is deemed that CNU-HYM-NN-2016002P/C is a new specimen of *K. medius* rather than a new species.

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Disclosure statement

No potential conflict of interest was reported by the authors.

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