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# New fossil species of Ephialtitidae and Baissidae (Hymenoptera, Apocrita) from the mid-Mesozoic of northeastern China

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One new species of Ephialtitidae—*Stephanogaster integra* sp. nov.—from the uppermost Middle Jurassic Jiulongshan Formation at Daohugou Village, Inner Mongolia, China, and four new species of Baissidae—*Manlaya proba* sp. nov., *Manlaya magna* sp. nov., *Manlaya ultima* sp. nov. and *Mesepipolaea parva* sp. nov.—from the Lower Cretaceous Yixian Formation at Huangbanjigou Village, Liaoning, China, are described and illustrated. In addition, all described fossils of the genera *Manlaya* Rasnitsyn, 1980b and *Stephanogaster* Rasnitsyn, 1975 are listed with their distributions, geological ages, and key forewing characters. This list allows the comparison of interspecific venational differences within the two genera, which in turn highlights high levels of species-level diversity among both the Cretaceous species of *Manlaya* and Jurassic species of *Stephanogaster*.

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Key words: Huangbanjigou, Daohugou, *Stephanogaster*, *Manlaya*, *Mesepipolaea*, taxonomy.

EPHIALTITIDAE, an extinct family of Hymenoptera, presently contains 29 genera described from the Early Jurassic to the Early Cretaceous. This family was widely distributed in Kazakhstan, China, Spain, Germany, Russia, Mongolia and Brazil, although nearly 70% of reported species are from Kazakhstan (Meunier 1903, Rasnitsyn 1975, 1977, 1990, 1999, 2008a, b, Zessin 1981, 1985, Zhang 1986, Darling & Sharkey 1990, Rasnitsyn & Ansoerge 2000, Rasnitsyn & Martínez-Delclòs 2000, Zhang *et al.* 2002, Rasnitsyn *et al.* 2003, Rasnitsyn & Zhang 2004, 2010, Ding *et al.* 2013, Li *et al.* 2013, 2016).

Baissidae was first established by Rasnitsyn (1975) for an enigmatic hymenopteran species from the Early Cretaceous (Berriasian) of Baissa, in central Siberia. Although the Baissidae were later downgraded to a subfamily of the Gasteruptionidae by Rasnitsyn (1980a, b), we maintain Baissidae as a separate family based on the analysis of Engel (2013). Baissidae presently contains six genera: *Baissa* Rasnitsyn, 1975, *Humiryssus* Lin, 1980, *Manlaya* Rasnitsyn, 1980b, *Tillywhimia* Rasnitsyn *et al.* 1998, *Mesepipolaea* Zhang

& Rasnitsyn, 2004 and *Electrobaissa* Engel, 2013 (Engel 2013).

We recently collected five well-preserved fossil hymenopterans (including one with part and counterpart) assignable to these two families: one fossil from the uppermost Middle Jurassic Jiulongshan Formation at Daohugou Village, Inner Mongolia, and four specimens from the Lower Cretaceous Yixian Formation of Huangbanjigou Village, Liaoning. The Daohugou locality is recognized as an important insect lagersätten (Rasnitsyn & Zhang 2004, Ren *et al.* 2010, Gao *et al.* 2013, Yao *et al.* 2014, Shi *et al.* 2015, Meng *et al.* 2019), and is considered late Callovian in age, dated to approximately 165 Ma based on  $^{40}\text{Ar}/^{39}\text{Ar}$  and SHRIMP  $^{206}\text{Pb}/^{238}\text{U}$  dating (He *et al.* 2004). The Yixian Formation is an important component of the Jehol entomofauna of northern China, which is considered Early Cretaceous in age (late Barremian to earliest Aptian), with an absolute age estimate of approximately 125 Ma based on  $^{40}\text{Ar}/^{39}\text{Ar}$  and SHRIMP  $^{206}\text{Pb}/^{238}\text{U}$  dating (Wang *et al.* 2005, Walker *et al.* 2013, Li *et al.* 2018).

Based on the morphological characteristics of these new fossils, five new species—*Stephanogaster integra* sp. nov. of the Ephialtitidae, and *Manlaya proba* sp.

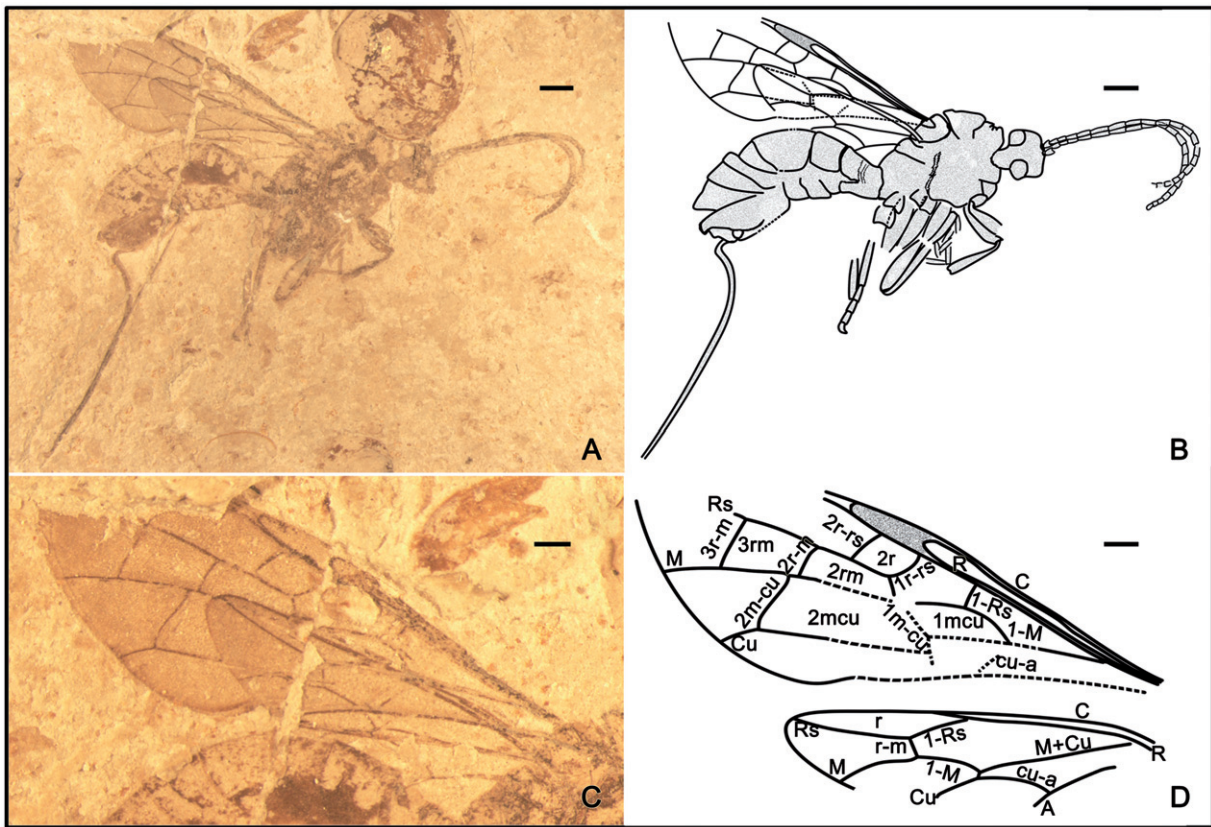


Fig. 1. *Stephanogaster integra* sp. nov. A–D, Holotype, CNU-HYM-NN-2015001: A, Photo of specimen; B, Line drawing of habitus; C, Photo of forewing; D, Line drawing of forewing. Scale bars: A, B = 1 mm; C, D = 0.5 mm.

nov., *Manlaya magna* sp. nov., *Manlaya ultima* sp. nov. and *Mesepipolaea parva* sp. nov. of the Baissidae—are described herein.

## Materials and methods

The type specimens described herein are housed in the Key Laboratory of Insect Evolution and Environmental Changes, College of Life Sciences, Capital Normal University, Beijing, China (material prefixed CNUB). Specimen part/counterpart components are given p/c suffixes, respectively. All specimens were examined and photographed using a Leica MZ16.5 dissecting microscope (Leica, Wetzlar, Germany) with an attached Leica DFC500 digital camera. The specimens were illustrated with the aid of a camera lucida microscope attachment, and figures were compiled using CorelDraw 12.0 and Adobe Photoshop CS5 software. The venation terminology used here follows that of Ding *et al.* (2013) and Engel (2013).

## Systematic palaeontology

Family EPHIALTITIDAE Handlirsch, 1906

**Stephanogaster** Rasnitsyn, 1975

*Type species.* *Stephanogaster magna* Rasnitsyn, 1975.

*Emended diagnosis.* Antenna filiform with over 20 antennomeres. Forewing venation complete, 1r-rs complete (rudimentary) or lost, 1-Rs sub-vertical to Rs, base of 2rm nearly at level of pterostigma base, 1cu-a interstitial or slightly postfurcal. Hindwing with 1-Rs longer than r-m, 1-M slightly bent. Metasoma widest distal of its middle, with first metasomal segment wide basally and either columnar or truncated conical in shape. Ovipositor long, usually longer than metasoma or whole body.

*Included species.* *S. magna* Rasnitsyn, 1975, *S. similis* Rasnitsyn, 1975, *S. longipalpa* Rasnitsyn, 1975, *S. pyri-formis* Rasnitsyn, 1975, *S. brachyura* Rasnitsyn, 1975, *S. pristinus* Rasnitsyn & Zhang, 2010, *S. ningchengensis* Ding, Zheng, Zhang & Zhang, 2013 and *S. integra* sp. nov.

***Stephanogaster integra* sp. nov.**  
(Fig. 1)

*Etymology.* The specific name is derived from the Latin word ‘integer’ meaning complete, referring to forewing with complete 1r-rs.

*Diagnosis.* Forewing with 1r-rs complete, 1-Rs short and sub-perpendicular to Rs and 1-M, 1-M about 2.4 times longer than 1-Rs. Hindwing with 1-M and cu-a

nearly parallel, cu-a slightly distad the fork of M + Cu. Metasoma longer than mesosoma, with first metasomal segment only slightly widened distally.

*Type material.* Holotype, CNU-HYM-NN-2015 001, female.

*Locality and horizon.* Daohugou Village, Shantou Township, Ningcheng County, Inner Mongolia, China; uppermost Middle Jurassic Jiulongshan Formation.

*Description.* Total body length 9.95 mm, forewing length 7.67 mm, hindwing length 5.16 mm. Head small, about 1.50 mm long and 1.37 mm wide, compound eyes small and rounded. Antenna thin, about 6.31 mm long; scape cylindrical, about 0.23 mm long and 0.18 mm wide; pedicel distinctly narrower than scape, slightly shorter in length; flagellomere I nearly as long and wide as pedicel, flagellomeres II–III gradually becoming longer; flagellomeres IV–VI nearly equal in length and width, and distinctly longer than any other flagellomeres; the remaining flagellomeres gradually shortening from VII to the apex.

Mesosoma about 3.57 mm long and 2.75 mm high; mesonotum with mesoscutellum about twice as long as pronotum; propleuron broad, contacting procoxa; metanotum 0.53 mm long; propodeum 0.62 mm long, slightly longer than metanotum. Legs poorly preserved. Metasoma longer than mesosoma, about 5.40 mm long, first metasomal segment only slightly widened distally, 1.37 mm long and 1.25 mm wide; remaining segments slightly shorter and wider than first segment. Ovipositor longer than metasoma, about 8.52 mm long.

Forewing with pterostigma elongate, 1.25 mm long and 0.34 mm wide; 1-Rs originating proximad of pterostigmal base, separated by a distance of about 0.95 mm, slightly shorter than pterostigma; 1-Rs and 1-M strongly angular at the junction of Rs + M, about 90°; 1-Rs (length 0.36 mm) sub-perpendicular to R, distinctly shorter than 1-M (length 0.86 mm); 1r-rs complete, nearly as long as 2r-rs; 2r-rs originating from pterostigma mid-length; 2r-m distal to 2r-rs; cell 2rm relatively narrow; 3r-m straight, about 1.5 times longer than 2r-m; 2m-cu with slight sigmoidal curve, longer than 3r-m. Hindwing with venation complete, closed cell r large, 2.52 mm long; 1-Rs (length 0.91 mm) connecting to R more distally than M + Cu fork; r-m straight, 0.3 times the length of 1-Rs; free Rs slightly concavely curved, almost reaching wing apex; M + Cu longer and almost extending to wing base; 1-M (length 0.95 mm) concavely curved and longer than 1-Rs; 1-Cu very short; cu-a (length 1.06 mm) longer than 1-M, slightly beyond the fork of M + Cu and nearly parallel to 1-M; A complete.

*Remarks.* The new species differs from all other species of *Stephanogaster* in having 1r-rs complete, 1-Rs short

and sub-perpendicular to Rs and 1-M and hindwing with 1-M distinct shorter than cu-a.

*Key to the species of Stephanogaster Rasnitsyn, 1975*

1. Forewing with 1-Rs much shorter than its distance from pterostigma base.....2  
Forewing with 1-Rs longer than its distance from pterostigma base.....4
2. Forewing with crossvein a1–a2 present.....  
.....*S. pristinus*  
Forewing with crossvein a1–a2 absent.....3
3. Hindwing with 1-M nearly as long as cu-a, cell 2rm longer than 3rm.....*S. integra*  
Hindwing with 1-M distinct shorter than cu-a, cell 2rm shorter than 3rm.....*S. ningchengensis*
4. Forewing with 1r-rs absent.....  
.....*S. brachyura*  
Forewing with 1r-rs present.....5
5. Forewing with cu-a slightly postfurcal.....  
.....*S. similis*  
Forewing with cu-a interstitial.....6
6. Forewing with 1r-rs nearly complete, slightly longer than 2r-rs.....*S. magna*  
Forewing with 1r-rs a short stub, distinctly shorter than 2r-rs.....7
7. Forewing with 2r-rs straight, issuing beyond the middle of pterostigma.....*S. pyriformis*  
Forewing with 2r-rs bent, issuing from the middle of pterostigma.....*S. longipalpa*

Family BAISSIDAE Rasnitsyn, 1975

**Manlaya** Rasnitsyn, 1980b

*Type species.* *Manlaya mongolica* Rasnitsyn, 1980b

*Emended diagnosis.* Forewing with marginal cell large, distalmost abscissa of Rs reaching nearly to wing apex; distalmost abscissa of Rs relatively straight beyond point where distal 3r-m originates; 1-Rs originating strongly proximad of pterostigma base, separated by a distance longer than pterostigma basal width; 1cu-a interstitial, or faintly postfurcal; Rs + M present and A extending to wing base; cell 2rm much narrower than 3r at the level of pterostigmal apex.

*Species included.* *M. mongolica* Rasnitsyn, 1980b, *M. undurgensis* (Rasnitsyn, 1975), *M. caudata* Rasnitsyn, 1986, *M. corrugata* Rasnitsyn, 1986, *M. gurvanica* Rasnitsyn, 1986, *M. laevinota* Rasnitsyn, 1986, *M. obscura* Rasnitsyn, 1986, *M. pallida* Rasnitsyn, 1986, *M. pinguis* Rasnitsyn, 1986, *M. ventricosa* Rasnitsyn, 1986, *M. ghidarina* Rasnitsyn, 1990, *M. pachyura* Rasnitsyn, 1990, *M. flexuosa* Ren et al. 1995, *M. anglica* Rasnitsyn et al. 1998, *M. ockleyensis* Rasnitsyn et al. 1998, *M. capelensis* Rasnitsyn et al. 1998, *M. lacabrua* Rasnitsyn & Ansoerge, 2000, *M. ansorgei* Rasnitsyn & Martínez-Delclòs, 2000, *M. proba* sp. nov., *M. magna* sp. nov., and *M. ultima* sp. nov.

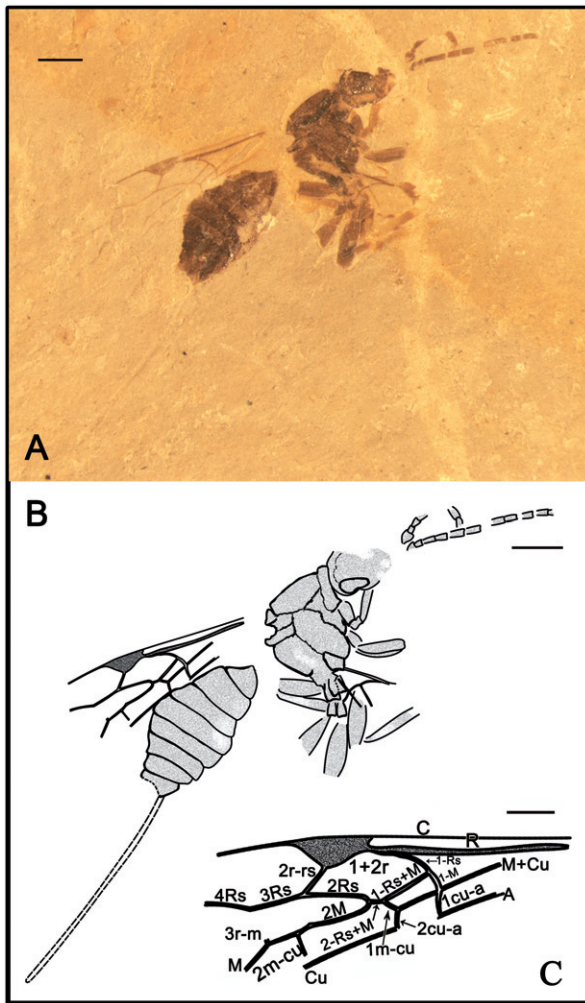


Fig. 2. *Manlaya proba* sp. nov. A–C, Holotype, CNU-HYM-LB-2015004: A, Photo of specimen; B, line drawing of habitus; C, Line drawing of forewing. Scale bars: A, B = 1 mm; C = 0.5 mm.

### *Manlaya proba* sp. nov.

(Fig. 2)

*Etymology.* The specific name is derived from the Latin word ‘proba’ meaning fine, referring to this wasp with its long ovipositor, which is longer than the metasoma.

*Diagnosis.* Forewing with broadly triangular pterostigma; 2r-rs strongly inclined, originating at pterostigma mid-length; 1-Rs slightly longer than 1-M; 1cu-a interstitial; 2m-cu present; only a short stub of 3r-m visible.

*Type material.* Holotype, CNU-HYM-LB-2015004, female.

*Locality and horizon.* Huangbanjigou Village, Beipiao City, western Liaoning Province, China; Lower Cretaceous Yixian Formation.

*Description.* Total body length 6.45 mm, forewing length 3.86 mm. Head elongate oval with kidney-

shaped eyes. Antenna with 10 antennomeres preserved, scape short, 0.25 mm long and 0.20 mm wide; pedicel cylindrical, distinctly narrower and shorter than scape.

Mesosoma stout, about 2.08 mm long and 1.80 mm high; pronotum rectangular, 4 times longer than wide; mesonotum about 5 times longer than pronotum; metasoma sharply reduced in length. Legs partly preserved. Metasoma elongate ovoid, length 3.14 mm, first metasomal segment triangular, gradually widening distally from base; second segment slightly longer and wider than first segment; remaining segments nearly equal in length, but become narrower from the middle of the metasoma onwards; ovipositor 4.42 mm long.

Forewing with pterostigma broadly triangular, 0.78 mm long and 0.34 mm wide; 1-Rs originating proximal of pterostigma base, separated by a distance of about 0.33 mm; 1-Rs and 1-M curved, 1-Rs (length 0.28 mm) longer than 1-M (length 0.22 mm); 1cu-a interstitial, slightly curved; Rs + M present, divided by 1m-cu into longer abscissa 1-Rs + M (length 0.55 mm) and shorter abscissa 2-Rs + M (length 0.15 mm); 1m-cu (length 0.19 mm) slightly longer than 2-Rs + M; cell 1m-cu about 3 times longer than wide; 2m-cu present, distinctly distal of 2r-rs, 2m-cu about 3 times longer than wide; 1cu-a reaching A, A complete, present both proximally and distally of 1cu-a; 2r-rs strongly inclined, originating at pterostigma mid-length, about 0.34 mm long, as long as pterostigma width; cell 1 + 2r nearly as wide as 3r; 2r-m absent, 3r-m present as a very short stub; 2M geniculate at the same level of 2r-rs.

*Remarks.* The new species differs from all other species of *Manlaya* in having its forewing with 2r-rs long and inclined, 3r-m present as a short stub and ovipositor much longer than metasoma.

### *Manlaya magna* sp. nov.

(Fig. 3)

*Etymology.* The specific name is derived from the Latin word ‘magnus’ meaning large, referring to the wasp’s large forewing, which is slightly longer than its body length.

*Diagnosis.* Forewing very large, slightly longer than body length, with pterostigma broadly triangular, 2r-rs straight and very short; 1-Rs nearly twice as long as 1-M; 1cu-a faintly postfurcal; 2m-cu present; M geniculate at the point where 3r-m should be present. Metasoma short and rounded.

*Type material.* Holotype, CNU-HYM-LB-2015005, male.

*Locality and horizon.* Huangbanjigou Village, Beipiao City, western Liaoning Province, China; Lower Cretaceous Yixian Formation.

*Description.* Total body length 6.18 mm, forewing length 6.23 mm. Head medium sized, nearly as wide as mesosoma; antenna with 7 antennomeres preserved.

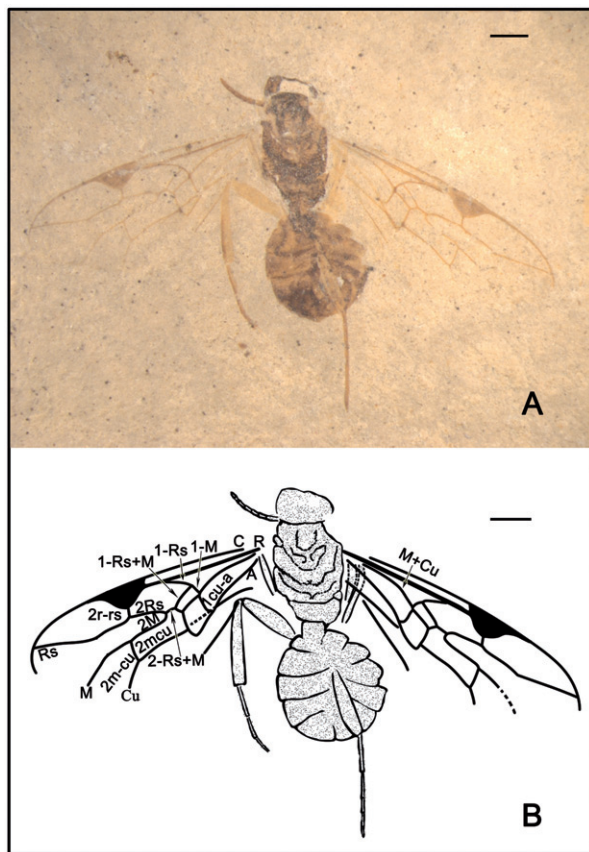


Fig. 3. *Manlaya magna* sp. nov. A, B, Holotype, CNU-HYM-LB-2015005: A, Photo of specimen; B, line drawing of habitus. Scale bars: A, B = 1 mm.

Mesosoma about 2.37 mm long and 1.65 mm wide; the shape and size of pronotum and mesonotum are difficult to distinguish owing to poor preservation. Propodeum about 0.48 mm long and 1.21 mm wide. Legs partly preserved, hind tibia slightly longer than femur, five tarsomeres. Metasoma rounded and short, about 2.90 mm long and 2.75 mm wide. Specimen is considered male as metasoma lacks any vestige of ovipositor.

Forewing with pterostigma broadly triangular, 1.33 mm long and 0.60 mm wide; 1-Rs originating proximad of pterostigmal base, separated by a distance of about 0.47 mm; 1-Rs and 1-M curved, 1-Rs (length 0.66 mm) longer than 1-M (length 0.27 mm); 1cu-a faintly postfurcal, slightly curved; Rs + M present, divided by 1m-cu into longer abscissa 1-Rs + M (length 0.68 mm) and shorter abscissa 2-Rs + M (length 0.26 mm); 1m-cu (length 0.19 mm) longer than 2-Rs + M; cell 1m-cu more than 3 times longer than wide; 2m-cu present, distinctly distal of 2r-rs, 2m-cu about 3 times longer than wide; A complete, both 1cu-a and 2cu-a reaching it, 1cu-a present both proximad and distad; 2r-rs straight and short, about 0.23 mm long, about 0.4 times the width of the pterostigma; cell 1 + 2r slightly narrower than 3r; free Rs curved concavely, reaching the apical margin anterior of the apex; 3r large, about twice as long as 1 + 2r; 2r-m absent, both

free Rs and M geniculate at the level where 3r-m should be present.

*Remarks.* The new species differs from all other species of *Manlaya* in having 1-Rs about twice as long as 1-M and cu-a slightly postfurcal, and from all species except *M. gurvanica* and *M. obscura* in having its forewing slightly longer than the whole body.

#### ***Manlaya ultima* sp. nov.**

(Fig. 4)

*Etymology.* The specific name is derived from the Latin word 'ultimus' meaning farthest, referring to the forewing with 1-Rs originating strongly proximad of pterostigmal base, separated by a length much longer than 1-Rs and 1-M combined.

*Diagnosis.* Forewing with pterostigma semi-circular; 1-Rs shorter than 1-M; 1-Rs originating strongly proximad of pterostigmal base, separated by a length much longer than 1-Rs and 1-M combined; 1cu-a interstitial; 2m-cu present; 2-Rs + M longer than 1m-cu; both Rs and M geniculate at the point where 2r-m and 3r-m should be present.

*Type material.* Holotype, CNU-HYM-LB-2015006, female.

*Locality and horizon.* Huangbanjigou Village, Beipiao City, western Liaoning Province, China; Lower Cretaceous Yixian Formation.

*Description.* Total body length 4.92 mm, forewing length 3.34 mm. Head large in size, about 1.05 mm long and 1.13 mm wide; compound eyes large and kidney-shaped. Antenna thin, with 14 antennomeres; scape slightly longer than pedicel, but nearly equal in width; flagellomeres slightly narrower from mid-antenna onwards.

Mesosoma very short, about 1.63 mm long and 1.66 mm wide. Legs poorly preserved. Metasoma longer than mesosoma, about 2.56 mm long and 1.58 mm wide; only basal part of ovipositor preserved, about 1.10 mm long.

Forewing with pterostigma semi-circular, 0.66 mm long and 0.27 mm wide; 1-Rs originating proximad of pterostigma base, separated by a distance of about 0.51 mm; 1-Rs and 1-M curved, 1-Rs (length 0.13 mm) shorter than 1-M (length 0.19 mm); 1cu-a interstitial, slightly curved; Rs + M present, divided by 1m-cu into longer abscissa 1-Rs + M (length 0.47 mm) and shorter abscissa 2-Rs + M (length 0.29 mm); 1m-cu (length 0.16 mm) shorter than 2-Rs + M; cell 1m-cu about 2.5 times longer than wide; 2m-cu present, distinctly distal of 2r-rs, 2m-cu about 4 times longer than wide; A complete, both 1cu-a and 2cu-a reaching it, 1cu-a present proximad and distad; 2r-rs originates from pterostigma at mid-length, about 0.23 mm long, slightly shorter than pterostigma width; cell 1 + 2r nearly as wide as the base of 3r; free Rs reaching the apical wing margin; 3r large, about twice as long as 1 + 2r; both free Rs and

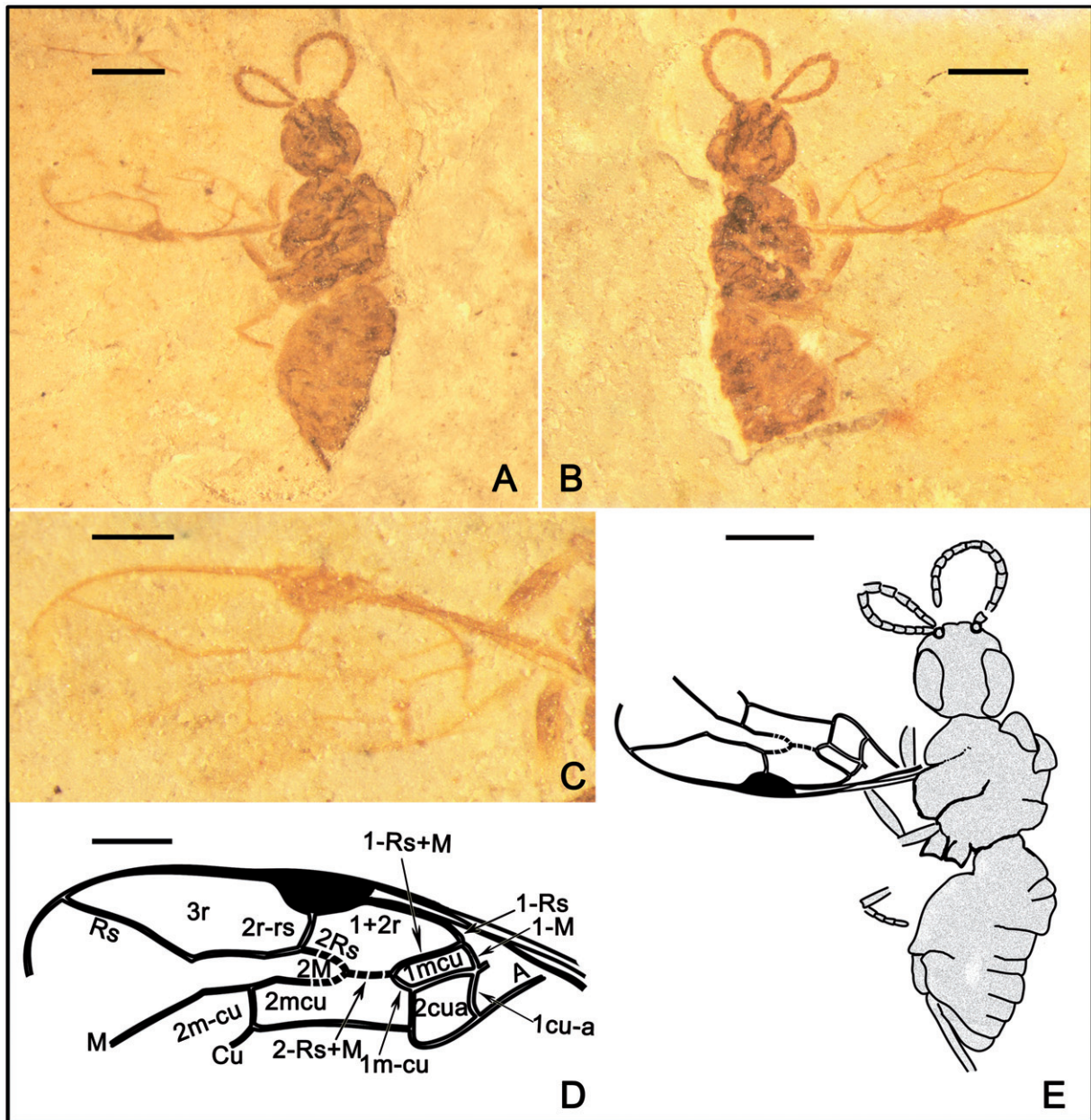


Fig. 4. *Manlaya ultima* sp. nov. A–E, Holotype, CNU-HYM-LB-2015006: A–B, Photo of specimen; C, Photo of forewing; D, Line drawing of forewing; E, Line drawing of habitus. Scale bars: A, B, E = 1 mm; C, D = 0.5 mm.

M geniculate at the levels that 2r-m and 3r-m should be present.

**Remarks.** The new species differs from all other species of *Manlaya* in having pterostigma semi-circular, and forewing with 2r-rs nearly as long as 2m-cu and 2-Rs + M nearly as long as 2-Rs.

**Mesepipolaea** Zhang & Rasnitsyn, 2004

*Type species.* *Mesepipolaea nanligezhuangica* Zhang & Rasnitsyn, 2004

**Emended diagnosis.** Forewing with pterostigma semi-circular, 1-Rs originating close to pterostigma base; 1-Rs much longer than 1-M; Rs + M present, 1-Rs + M

much longer than 2-Rs + M; 1cu-a interstitial or post-furcal; Rs slightly angular at 3r-m, reaching margin near wing apex (if preserved); A complete, not reduced basally of 1cu-a; ovipositor about 0.25 times the length of the forewing in female. Metasoma short, nearly as long as, or slightly shorter than, mesosoma.

**Species included.** *M. nanligezhuangica* Zhang & Rasnitsyn, 2004 and *M. parva* sp. nov.

**Mesepipolaea parva** sp. nov.  
(Fig. 5)

**Etymology.** The specific name is derived from the Latin word 'parvus' meaning small, referring to the short, ovate metasoma of this wasp.

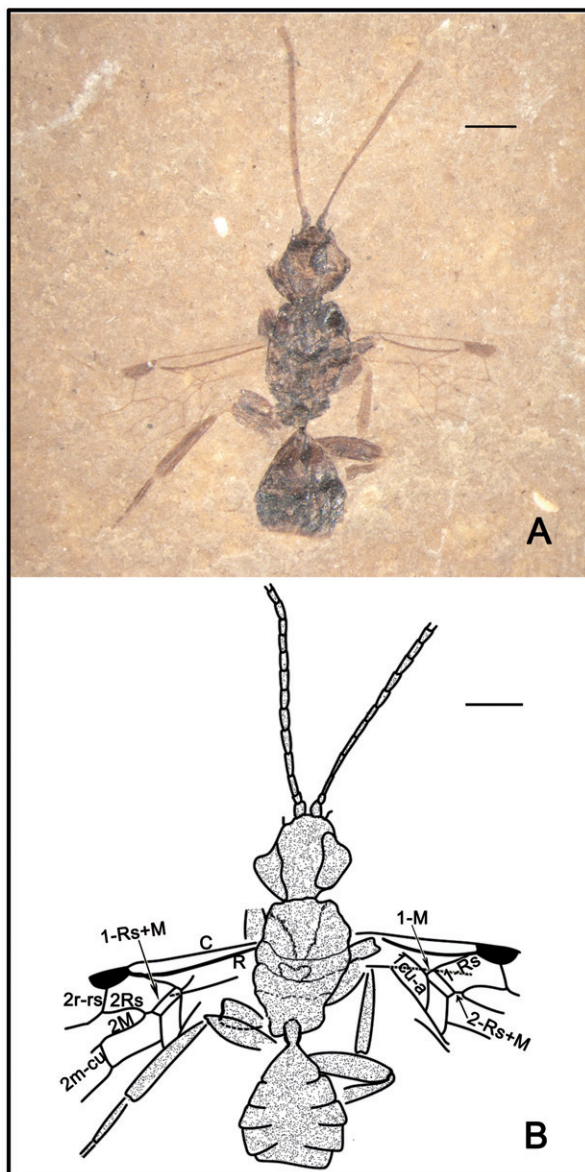


Fig. 5. *Mesepipolaea parva* sp. nov. A, B, Holotype, CNU-HYM-LB-2015007: A, Photo of specimen; B, Line drawing of habitus. Scale bars: A, B = 1 mm.

**Diagnosis.** Head slightly wider than mesosoma, with large ovate compound eyes. Forewing with 1-Rs about 4 times longer than 1-M; 1cu-a postfurcal, reaching A; 3r-m absent, 2m-cu present. Metasoma short and ovate, with first metasomal segment formed like the short petiole and nearly as wider as hind tibia.

**Type material.** Holotype, CNU-HYM-LB-2015 007, male.

**Locality and horizon.** Huangbanjigou Village, Beipiao City, western Liaoning Province, China; Lower Cretaceous Yixian Formation.

**Description.** Total body length 5.91 mm, forewing length 4.15 mm as preserved. Head large, about 1.42 mm long and 1.64 mm wide; compound eyes large and ovate. Antenna thin, with 13 antennomeres; scape

cylindrical, about 0.26 mm long and 0.19 mm wide, 1.4 times longer than wide; pedicel distinctly shorter and narrower than scape; flagellomeres I–IV nearly equal in length and width; the remaining antennal segments gradually shorter than basal segments.

Mesosoma slender, about 2.31 mm long and 1.61 mm wide; mesonotum with notauli distinct; metanotum nearly as long as mesoscutellum; propodeum longer but narrower than metanotum. Legs poorly preserved, hind legs longer than mid legs, hind femur wider but shorter than tibia, tarsomeres distinctly narrower than tibia. Metasoma shorter than mesosoma, about 2.35 mm long; petiole short and strongly developed, remaining segments nearly equal in width.

Forewing with pterostigma broad and semi-circular, 0.68 mm long and 0.32 mm wide; 1-Rs originating proximad of pterostigmal base, separated by a distance of about 0.24 mm; 1-Rs and 1-M nearly straight, 1-Rs (length 0.54 mm) about 4 times longer than 1-M (length 0.14 mm); 1cu-a postfurcal; Rs + M present, divided by 1m-cu into longer abscissa 1-Rs + M (length 0.59 mm) and shorter abscissa 2-Rs + M (length 0.12 mm); 1m-cu (length 0.16 mm) longer than 2-Rs + M; cell 1m-cu about 2.5 times longer than wide; 2m-cu present, distinctly distal of 2r-rs, 2m-cu about 4 times longer than wide; A complete, both 1cu-a and 2cu-a reaching it; 2r-rs originating distad of pterostigma's mid-length, about 0.39 mm from pterostigma base, slightly longer than pterostigma width; cell 1 + 2r nearly as wide as the base of 3r; 2r-m and 3r-m absent, free Rs and M geniculate at the level where these crossveins would be expected to originate.

**Remarks.** This new species differs from the type species of *Mesepipolaea* in having its forewing 1cu-a distinctly postfurcal, and in having an ovate metasoma with strongly narrowed petiole.

## Discussion

We conducted a literature search for all described species of *Manlaya*, summarizing their localities, horizons and forewing characters (Table 1). In total, there are 21 species reported from the Early Cretaceous in Transbaikalia, Mongolia, China, England and Spain. By comparing the venation of all species in the genus *Manlaya* (Table 1, Fig. 6), we identify the following venational characteristics:

1. Three states exist for forewing 1-Rs and 1-M: 1-Rs is shorter than 1-M (e.g., *M. mongolica*), 1-Rs is nearly as long as 1-M (e.g., *M. corrugata*), or 1-Rs is longer than 1-M (e.g., *M. pallida*).
2. Two states exist for forewing 1cu-a: either 1cu-a is interstitial (e.g., *M. gurvanica*), or 1cu-a is postfurcal (e.g., *M. corrugata*).
3. Two states exist for forewing 2Rs + M: either 2Rs + M is absent (e.g., *M. gurvanica*), or 2Rs + M is present (e.g., *M. capelensis*).



Table 1. Locality, age and morphological characteristics of forewings in all recorded fossil species of *Manlaya* Rasnitsyn, 1980b.

Species name	Locality	Age	Main characters of forewing
<i>Manlaya undurgensis</i> (Rasnitsyn, 1975)	Eastern Transbaikalia	Early Cretaceous	Pterostigma broad, 1r-rs long
<i>Manlaya mongolica</i> Rasnitsyn, 1980	Southwestern Mongolia	Early Cretaceous	Pterostigma broad, 1r-rs very short, 1-M much longer than 1-Rs, cu-a interstitial, 2m-cu present
<i>Manlaya caudata</i> Rasnitsyn, 1986	Western Mongolia	Early Cretaceous	Poorly preserved
<i>Manlaya corrugata</i> Rasnitsyn, 1986	Western Mongolia	Early Cretaceous	Pterostigma broad, 1-M nearly as long as 1-Rs, cu-a postfurcal
<i>Manlaya gurvania</i> Rasnitsyn, 1986	Western Mongolia	Early Cretaceous	Pterostigma broad, 1r-rs long, 1-M much shorter than 1-Rs, cu-a interstitial, 2m-cu present
<i>Manlaya laevinota</i> Rasnitsyn, 1986	Western Mongolia	Early Cretaceous	Pterostigma broad, 1r-rs long, 1-M slightly longer than 1-Rs, cu-a interstitial, 2m-cu present
<i>Manlaya obscura</i> Rasnitsyn, 1986	Western Mongolia	Early Cretaceous	Pterostigma broad
<i>Manlaya pallida</i> Rasnitsyn, 1986	Western Mongolia	Early Cretaceous	Pterostigma broad, 1-M slightly shorter than 1-Rs
<i>Manlaya pinguis</i> Rasnitsyn, 1986	Western Mongolia	Early Cretaceous	Pterostigma broad, 1r-rs longer
<i>Manlaya ventricosa</i> Rasnitsyn, 1986	Western Mongolia	Early Cretaceous	Pterostigma broad
<i>Manlaya ghidarina</i> Rasnitsyn, 1990	Eastern Transbaikalia	Early Cretaceous	Pterostigma broad, 1r-rs relatively short, 1-M nearly as long as 1-Rs, cu-a interstitial
<i>Manlaya pachyura</i> Rasnitsyn, 1990	Eastern Transbaikalia	Early Cretaceous	1-M slightly longer than 1-Rs, cu-a interstitial, 2m-cu present
<i>Manlaya flexuosa</i> Ren, Lu & Guo, 1995	Northeastern China	Early Cretaceous	Pterostigma broad, 1r-rs very short, 1-M longer than 1-Rs, cu-a interstitial, 2m-cu present
<i>Manlaya anglica</i> Rasnitsyn & Jarzembowski, 1998	Southern England	Early Cretaceous	Pterostigma broad, 1r-rs very short, 1-M longer than 1-Rs, cu-a interstitial
<i>Manlaya ockleyensis</i> Rasnitsyn & Jarzembowski, 1998	Southern England	Early Cretaceous	Pterostigma broad, 1r-rs relatively short, 1-M longer than 1-Rs, cu-a interstitial, 2 + 3r-m and 2m-cu present
<i>Manlaya capelensis</i> Rasnitsyn & Jarzembowski, 1998	Southern England	Early Cretaceous	Pterostigma broad, 1r-rs very short, 1-M slightly shorter than 1-Rs, cu-a interstitial
<i>Manlaya lacabrua</i> Rasnitsyn & Ansoerge, 2000	Spain	Early Cretaceous	Pterostigma broad, 1r-rs very short, 1-M longer than 1-Rs, cu-a interstitial, 2m-cu present
<i>Manlaya ansorgei</i> Rasnitsyn & Martínez-Delclòs, 2000	Spain	Early Cretaceous	Pterostigma broad, 1r-rs relatively short, 1-M nearly as long as 1-Rs, cu-a interstitial, 2m-cu present
<i>Manlaya proba</i> sp. nov.	Northeastern China	Early Cretaceous	Pterostigma broad, 1r-rs long, 1-M nearly as long as 1-Rs, cu-a interstitial, 2m-cu present
<i>Manlaya magna</i> sp. nov.	Northeastern China	Early Cretaceous	Pterostigma broad, 1r-rs very short, 1-M slightly shorter than 1-Rs, cu-a postfurcal, 2m-cu present
<i>Manlaya ultima</i> sp. nov.	Northeastern China	Early Cretaceous	Pterostigma broad, 1r-rs relatively long, 1-M longer than 1-Rs, cu-a interstitial, 2m-cu present

4. Two states exist for forewing 2 + 3r-m: 2 + 3r-m is absent (e.g., *M. flexuosa*) or presented as short stubs on Rs and M (e.g., *M. proba*), or 2 + 3r-m is spectral and reaches Rs and M (e.g., *M. ockleyensis*).

These four forewing characters are considered to be diagnostic at an interspecific level within *Manlaya*. Moreover, except for several poorly preserved species, all *Manlaya* species have broadly triangular or rounded pterostigma; five other genera of the Baissidae—

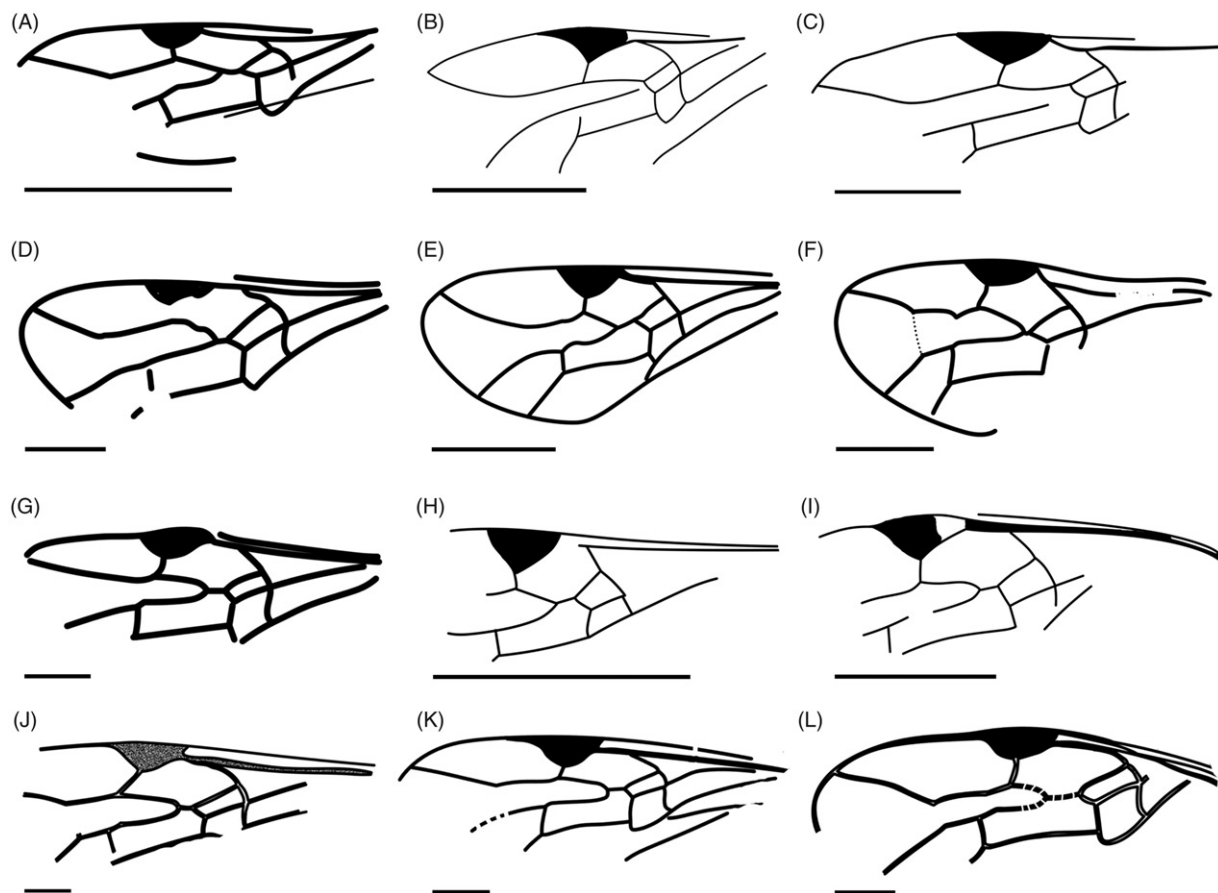


Fig. 6. Line drawings of selected forewings of *Manlaya* Rasnitsyn, 1980b. A, *M. mongolica* Rasnitsyn, 1980b; B, *M. gurbanica* Rasnitsyn, 1986; C, *M. laevinota* Rasnitsyn, 1986; D, *M. pachyura* Rasnitsyn, 1990; E, *M. flexuosa* Ren, Luo & Guo, 1995; F, *M. ockleyensis* Rasnitsyn & Jarzembowski, 1998; G, *M. capelensis* Rasnitsyn & Jarzembowski, 1998; H, *M. lacabrua* Rasnitsyn & Ansorge, 2000; I, *M. ansorgei* Rasnitsyn & Martínez-Delclòs, 2000; J, *M. proba* sp. nov.; K, *M. magna* sp. nov.; L, *M. ultima* sp. nov. Scale bars = 1 mm. All wings re-drawn in Adobe Photoshop CS5 by the first author.

*Humirysus*, *Tillywhimia*, *Mesepipolaea*, *Baissa* and *Electrobaissa*—also preserve similar pterostigma, which suggests that pterostigma shape is a stable generic character. Li *et al.* (2015) suggested that a distinct evolutionary trend of pterostigma enlargement occurred in the Praeaulacidae from the Jurassic to the Cretaceous. As previous researchers have proposed that Praeaulacidae is the precursor taxa to remaining families of Evanioidea, including Baissidae (Li *et al.* 2013, 2018), this trend in the Praeaulacidae, in combination with the Early Cretaceous radiation time and broad pterostigma of Baissidae, suggests that *Manlaya* most likely originated near the Jurassic–Cretaceous boundary.

Similarly, the localities, horizons and forewing characters of *Stephanogaster* are also summarized (Table 2). In total, there are only eight species, reported from the Jurassic of southern Kazakhstan and northeastern China. By comparing the venation in these species (Table 2, Fig. 7), we identify the following venational characteristics within fossil *Stephanogaster* species:

1. Three states exist for forewing 1r-rs: 1r-rs is absent (e.g., *S. brachyura*); 1r-rs is incomplete, developed as a short stub (e.g., *S. pyriformis*) or not reaching

the pterostigma (e.g., *S. magna*); or 1r-rs is complete and reaches the pterostigma (e.g., *S. ningchengensis*).

2. Two states exist for forewing 1cu-a: either 1cu-a is interstitial (e.g., *S. longipalpa*), or 1cu-a is postfurcal (e.g., *S. ningchengensis*).
3. Two states exist for forewing 3rm cell: either 3rm length is greater than four times width (e.g., *S. similis*), or 3rm length is less than two times width (e.g., *S. pristinus*).
4. Two states exist for forewing a1–a2: either a1–a2 is present (e.g., *S. pristinus*) or it is absent (e.g., *S. magna*).

Based on the four forewing characters above, *Stephanogaster* species from the Middle Jurassic of China have more plesiomorphic characters compared with those species from the Late Jurassic of southern Kazakhstan; examples of these plesiomorphic features include the complete 1r-rs and postfurcal cu-a in *S. ningchengensis*, well-preserved a1–a2 and 2A in *S. pristinus*, and complete 1r-rs in *S. integra*, all of which are seen extensively in the Symphyta.

Table 2. Locality, age and morphological characteristics of forewings in all recorded fossil species of *Stephanogaster* Rasnitsyn, 1975.

Species name	Locality	Age	Main characters of forewing
<i>Stephanogaster magna</i> Rasnitsyn, 1975	Southern Kazakhstan	Late Jurassic	Cu-a interstitial, 1-Rs longer than its distance from pterostigma base, 1r-rs nearly as long as 2r-rs, cell 3m very long and narrower, more than twice as long as 2m
<i>Stephanogaster similis</i> Rasnitsyn, 1975	Southern Kazakhstan	Late Jurassic	Cu-a postfurcal, 1-Rs longer than its distance from pterostigma base, 1r-rs nearly as long as 2r-rs, cell 3m very long and narrower, more than twice as long as 2m
<i>Stephanogaster longipalpa</i> Rasnitsyn, 1975	Southern Kazakhstan	Late Jurassic	Cu-a interstitial, 1-Rs longer than its distance from pterostigma base, 1r-rs presented as short stub, distinctly shorter than 2r-rs, cell 3m very long and narrower, more than twice as long as 2m
<i>Stephanogaster pyriformis</i> Rasnitsyn, 1975	Southern Kazakhstan	Late Jurassic	Cu-a interstitial, 1-Rs longer than its distance from pterostigma base, 1r-rs presented as short stub, distinctly shorter than 2r-rs, cell 3m very long and narrower, more than twice as long as 2m
<i>Stephanogaster brachyura</i> Rasnitsyn, 1975	Southern Kazakhstan	Late Jurassic	Cu-a interstitial, 1-Rs longer than its distance from pterostigma base, 1r-rs absent, cell 3m long and narrower, about 1.5 times as long as 2m
<i>Stephanogaster pristinus</i> Rasnitsyn & Zhang, 2010	Northeastern China	Middle Jurassic	Cu-a interstitial, 1-Rs much shorter than its distance from pterostigma base, 1r-rs shorter than 2r-rs, cell 3m short and broad, distinctly shorter than 2m, a1-a2 present
<i>Stephanogaster ningchengensis</i> Ding, Zheng, Zhang & Zhang, 2013	Northeastern China	Middle Jurassic	Cu-a postfurcal, 1-Rs much shorter than its distance from pterostigma base, 1r-rs complete and longer than 2r-rs, cell 3m short and broad, slightly longer than 2m
<i>Stephanogaster integra</i> sp. nov.	Northeastern China	Middle Jurassic	1-Rs much shorter than its distance from pterostigma base, 1r-rs complete and longer than 2r-rs, cell 3m short and broad, slightly shorter than 2m

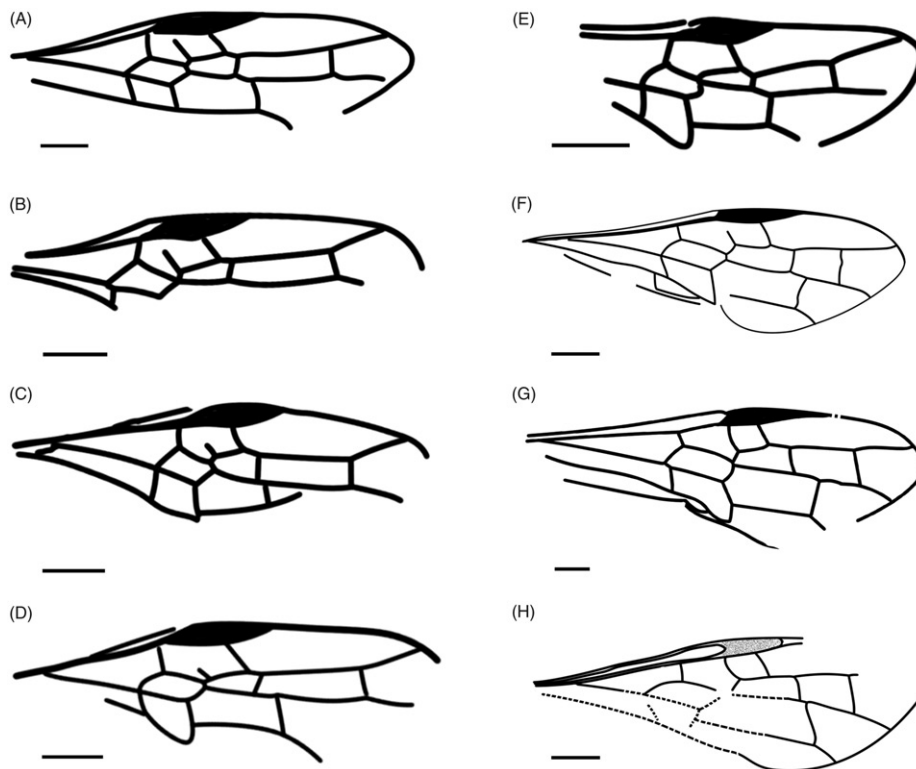


Fig. 7. Line drawings of forewings of *Stephanogaster* Rasnitsyn, 1975. A, *S. magna* Rasnitsyn, 1975; B, *S. similis* Rasnitsyn, 1975; C, *S. longipalpa* Rasnitsyn, 1975; D, *S. pyriformis* Rasnitsyn, 1975; E, *S. brachyuran* Rasnitsyn, 1975; F, *S. pristinus* Rasnitsyn & Zhang, 2010; G, *S. ningchengensis* Ding, Zheng, Zhang & Zhang, 2013; H, *S. integra* sp. nov. Scale bars = 1 mm. All wings re-drawn in Adobe Photoshop CS5 by the first author.

## Disclosure statement

No potential conflict of interest was reported by the authors.

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