

Minute members of Baissinae (Insecta: Hymenoptera: Gasteruptiidae) from the upper Mesozoic of China and limits of the genus *Manlaya* Rasnitsyn, 1980

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Abstract

A brief review and discussion of baissine wasps of Gasteruptiidae, Hymenoptera is given. Eight fossil specimens of wasps from the Laiyang Formation in Laiyang, Shandong, China are described. One new genus, *Mesepipolaea*, and four new species, *M. nanligezhuangica*, *Humiryssus specialis*, *H. cancellatus* and *H. vulgatus* are established, and two new combinations are proposed: *Humiryssus laiyangensis* (Hong and Wang, 1990) (originally *Aulocopsis laiyangensis* Hong and Wang, 1990), *H. oculatissimus* (Rasnitsyn and Jarzembowski, 1998) (originally *Manlaya oculatissima* Rasnitsyn and Jarzembowski, 1998). *Sinowestratia communicata* Zhang and Zhang, 2000 is a junior synonym of *Manlaya flexuosa* (Ren et al., 1995) (originally *Manlaya flexuosus* Ren et al., 1995). Stratigraphic inferences from these finds are briefly discussed.

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1. Introduction

The subfamily Baissinae represents a basal group in the family Gasteruptiidae (s.l.) within Evanioidea, Hymenoptera, and is possibly ancestral to both of the subfamilies Aulacinae and Gasteruptiinae (Rasnitsyn, 1980, 2002). Baissine fossils are widespread in possible latest Jurassic and undoubted Early Cretaceous insect-bearing deposits of Eurasia from China to Spain but are unknown from deposits that are unquestionably Late Jurassic and Late Cretaceous in age. They represent a key group in latest Jurassic–Early Cretaceous or Early Cretaceous insect assemblages. As a result, the

hymenopteran assemblages typical of that epoch have been named the baissine type (Rasnitsyn et al., 1998; Rasnitsyn and Martínez-Delclòs, 2000). Currently the Baissinae includes four genera: *Baissa* Rasnitsyn, 1975, with three described species (Rasnitsyn, 1991); *Manlaya* Rasnitsyn, 1980, with 21 species (Rasnitsyn, 1980; Ren et al., 1995; Rasnitsyn et al., 1998; Rasnitsyn and Martínez-Delclòs, 2000); and monotypic *Humiryssus* Lin, 1980 and *Aulocopsis* Hong and Wang, 1990. Rasnitsyn et al. (1998) suggested that the last two genera deserve to be placed in synonymy under *Manlaya* but did not provide formal synonymization.

The fact that the Baissinae represents a stratigraphically and, possibly, biogeographically important element of the latest Jurassic–Early Cretaceous insect assemblages means that it deserves detailed analysis, especially since the internal structure of *Manlaya* is rather obscure

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and reliable identification of its species is sometimes problematic (Rasnitsyn et al., 1998). Chinese non-marine sedimentary deposits of latest Jurassic/Early Cretaceous age have yielded many fossils belonging or related to *Manlaya*. These have been considered in four publications to date (Lin, 1980; Hong and Wang, 1990; Ren et al., 1995; Zhang and Zhang, 2000). As a first step towards a better understanding of the group we have selected a rather clear-cut collection of the smallest fossils. Their study has unexpectedly indicated some apparent subdivisions within what one of us (APR) has regarded as *Manlaya*. This permits the definition of additional genera in the subfamily Baissinae, so making it easier handle the group.

The fossils described here were collected by JZ from two well-known localities in the villages of Nanligeshuang and Tuanwang, Laiyang, Shandong, in the uppermost Jurassic–lowermost Cretaceous deposits of the Laiyang Formation (originally recorded as Upper Jurassic; Zhang, 1992). These eight specimens are separated into four new species, one of which represents a new genus. Three other new species are referred to the genus *Humiryssus* Lin, 1980 (originally *Aulocopsis* Hong and Wang, 1990), which is not considered to be a synonym of *Manlaya*. Besides the type species, *Humiryssus leucus* Lin, 1980 from the Laocun Formation at Laocun in Jiande, Zhejiang, and the three species described here, there are two species originally referred to other genera, viz. *Humiryssus laiyangensis* (Hong and Wang, 1990), the type of *Aulocopsis*, from the Laiyang Formation in the village of Tuanwang and *H. oculatissimus* (Rasnitsyn et al., 1998), originally *Manlaya oculatissima*, from the Durlston Formation (Middle Purbeck) of Durlston Bay in southern England. Another taxon, *Sinowestratia communicata* Zhang and Zhang, 2000, which was based on a single female wasp from the Yixian Formation at Huangbanjiogou, Beipiao, Liaoning, is regarded as a junior synonym of *Manlaya flexuosa* (Ren et al., 1995) (originally *Manlaya flexuosus* Ren et al., 1995) based on a male wasp from the same locality and horizon (new synonymy).

As a result, 18 described species are now left in *Manlaya*, viz. *M. mongolica* Rasnitsyn, 1980 (type species) from the Mogotuin Formation of south-west Mongolia; *M. caudata*, *M. corrugata*, *M. gurvania*, *M. laevinota*, *M. obscura*, *M. pallida*, *M. pinguis*, and *M. ventricosa*, all described by Rasnitsyn (1986) from the Gurvan-Eren Formation of west Mongolia, *M. ghidarina* Rasnitsyn, 1990 from the Ghidara Formation, and *M. pachyura* Rasnitsyn, 1990 from the Turga Formation, both in East Transbaikalia; *Manlaya undurgensis* (Rasnitsyn, 1975) (originally *Cretocleistogaster undurgensis* Rasnitsyn, 1975) from deposits in West Transbaikalia that possibly correlate with the Turga Formation; *M. flexuosa* (Ren et al., 1995) from the Yixian Formation of north-east China; *M. anglica* Rasnitsyn and Jarzembowski, 1998 from the Lulworth

Formation of southern England, *M. ockleyensis* Rasnitsyn and Jarzembowski, 1998 and *M. capelensis* Rasnitsyn and Jarzembowski, 1998, from the Upper Weald Clay of southern England, and *M. lacabrua* Rasnitsyn and Ansoerge, 2000 and *M. ansorgei* Rasnitsyn and Martínez-Delclòs, 2000, from the locality of La Cabrua in Spain. This rather diverse assemblage badly deserves closer study, which will probably result in further splitting into more natural genera. The position of *M. lacabrua* is particularly questionable (see below).

2. Systematic palaeontology

All of the specimens described below were collected by JZ and are housed in the Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences.

Order: Hymenoptera Linnaeus, 1758
Suborder: Apocrita Gerstaecker, 1867
Superfamily: Evanioidea Latreille, 1802
Family: Gasteruptiidae Kirby, 1837
Subfamily: Baissinae Rasnitsyn, 1975

Genus *Mesepipolaea* Zhang and Rasnitsyn, gen. nov.

Type species. *M. nanligeshuangica* sp. nov.

Derivation of name. From Mesozoic and *epipolaea*, Greek for noticeable.

Species included. Type species only.

Diagnosis. Body size small (forewing length under 2.5 mm). Eyes small, scarcely elongate. Forewing with RS starting close to pterostigma; RS + M below midlength of basal vein (viz. first abscissa of RS much longer than that of M); RS slightly angular at 3r-m, reaching margin near wing apex; A complete (not reduced basad of cu-a). Ovipositor about one-quarter as long as fore wing.

Comparison. The new genus is included in the subfamily Baissinae, a paraphyletic assemblage within Gasteruptiidae, based on the absence of synapomorphies with other subfamilies, viz. notauli reaching transverse mesoscutal suture independently and not joining each other before the suture (as in Gasteruptiidae), forewing with 2m-cu present (lost in Gasteruptiidae), and the first metasomal segment rounded basally and not conical (as in both Gasteruptiidae and Aulacidae). It differs from the rest of the genera in the Baissinae in having a short ovipositor and on RS starting near the pterostigma. Additionally, it differs from *Baissa* Rasnitsyn, 1975 and *Manlaya* in its smaller size (except for *M. undurgensis* whose wing is 2.5 mm long).

Remarks. Problematic is the position of *Manlaya lacabrua*, which is similar to the new genus in its small size and the distal position of RS base but differs in having a wide pterostigma, a long first abscissa of M, and a longer ovipositor. It might be an aberrant species of *Mesepipolaea* or it may deserve full generic status. The incomplete preservation of this unique fossil makes it preferable to leave the species in *Manlaya* until more information is available or a full revision of this genus is possible.

Mesepipolaea nanligezhuangica sp. nov.

Figs. 1A–C, 2–5, 6A

Derivation of name. After the locality of Nanligezhuang, which yielded the specimens.

Material. Holotype L91466, L91447 (female in dorsal aspect), part and counterpart, with antennae, legs and

left hindwing incomplete, right fore- and hindwing lacking; and two female paratypes, also in dorsal aspect: L91470, with antennae, legs and right forewing incomplete, hindwings lacking; and L91468, with fore- and midlegs incomplete, hindwings lacking.

Description. Female; male unknown. Body dark brown. Head moderately large, transverse, widest at eyes, tapering to mouthparts, with short temples and rounded occipital contour. Eyes medium-sized, short oval, almost reaching hind margin of head and distant from mandibles. Antennae filiform, 13-segmented, shorter than head and mesosoma combined, with basal three or four flagellomere pale in colour; scape nearly as long as wide, distinctly thicker than, and about as long as, first flagellomere; pedicel relatively small and thin, subquadrate, and less than one-half of length of first flagellomere; each flagellomere oblong, and the same

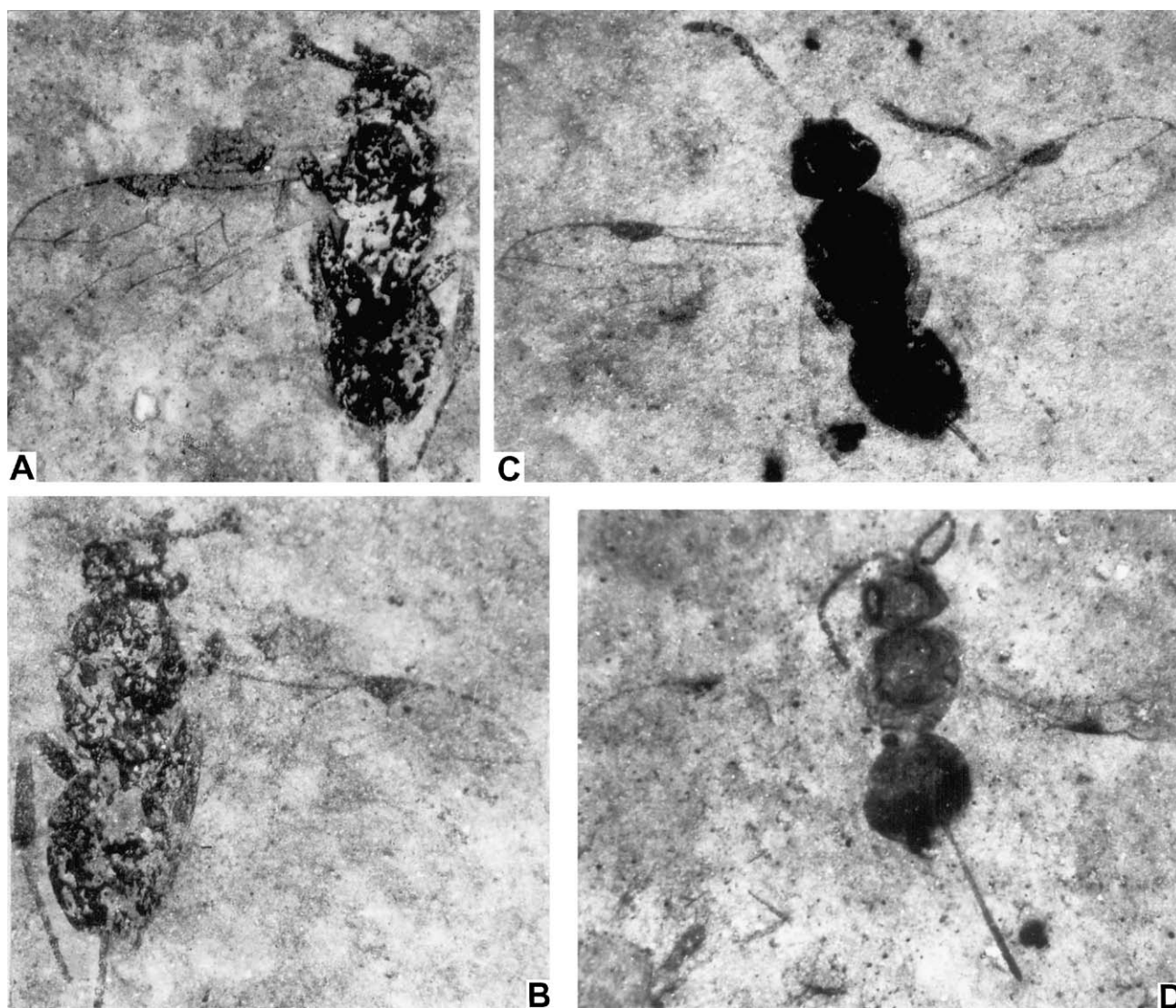


Fig. 1. A, B, *Mesepipopaea nanligezhuangica* sp. nov., holotype. A, part, L91466; $\times 19.2$. B, counterpart, L91447; $\times 21.6$. C, *Mesepipopaea nanligezhuangica* sp. nov., paratype, L91468; $\times 18.3$. D, *Humiryssus specialis* sp. nov., holotype, L91457; $\times 19.1$.

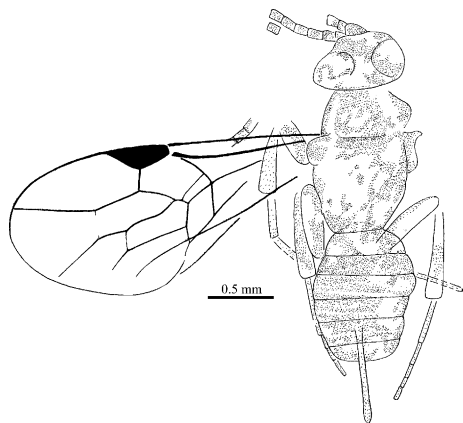


Fig. 2. *Mesepipopaea nanligezhuangica* sp. nov., female adult, dorso-ventral aspect, camera lucida drawing of specimen L91466.

length or nearly so, with the exception of first flagellomere, which is thinner basally than apically. Mesosoma elongate-oval, without transverse sculpture; metanotum and propodeum not reticulate. Legs moderately long and thick; femora clavate, thicker (slightly hindleg) and shorter than respective tibiae; hindtarsus clearly thinner and barely longer than tibia, with basitarsus shorter than remainder of tarsomeres combined, less than twice as long as second tarsomere, fourth tarsomere nearly as long as fifth. Forewing with costal area broad; pterostigma not large (about as wide as 2r-rs long), issuing 2r-rs near its midlength; first abscissa of Rs streamlined with that of M, about 2.5 times as long as the latter which is as long as, or slightly longer than, 1m-cu; cell 3r 2.3–2.6 times as long as wide; 2r-m lost, 3r-m desclerotized except for short rudiments on RS and M, cell 2 + 3rm petiolate basally (viz. Rs + M surpassing 1m-cu apically); 2m-cu complete but thin. Hindwing with C and Rs present. Metasoma suboval, shorter or longer than mesosoma depending on preservation (post-mortem desiccation vs. distention), widest at third or fourth segment. Ovipositor sheath about 0.25 times as long as forewing.

Length of head 0.4–0.6 mm, antenna 1.4 mm, mesosoma 1.0–1.1 mm, metasoma 1.0–1.7 mm; hindleg 1.8–2.1 mm, forewing 2.4–2.5 mm; width of forewing

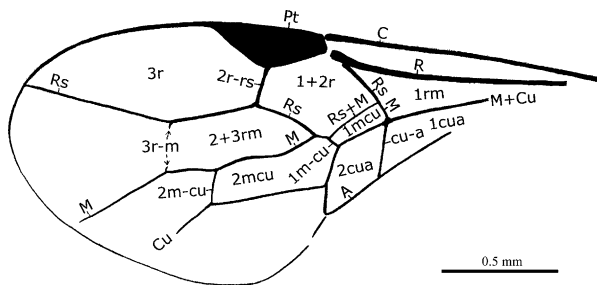


Fig. 3. *Mesepipopaea nanligezhuangica* sp. nov., left forewing, camera lucida drawing of specimen L91466.

1.0–1.1 mm; ovipositor ca. 0.5–0.7 mm long (ovipositor surpassing metasomal apex for 0.4–0.5 mm).

Genus *Humiryssus* Lin, 1980

1980 *Humiryssus* Lin, pp. 231–232.

1990 *Aulocopsis* Hong and Wang, p. 157.

Type species. Humiryssus leucus Lin, 1980

Species included. Six species keyed out below.

Diagnosis. Body size small (forewing 1.6–2.3 mm long). Eyes usually large, elongate. Forewing with RS beginning well before pterostigma; RS + M near or above midlength of basal vein (viz. first abscissa of RS as long as, or shorter than, that of M); RS strongly angular at 3r-m towards wing fore-margin, reaching margin nearly half-way between 3r-m and wing apex; A complete (not reduced basad of cu-a). Ovipositor straight or nearly so, 0.5–0.8 times as long as forewing.

Comparison. This genus is included in the subfamily Baissinae for the same reasons as *Mesepipolaea*. It differs from the rest of the genera in the Baissinae in having a short 3r cell (ending far from wing apex). Additionally, it differs from *Baissa* Rasnitsyn, 1975 and *Manlaya* in its small size (except *M. lacabrua*, for which see above; and *M. undurgensis*, which approaches *Humiryssus* in wing length), and from *Manlaya* also in having a shorter ovipositor (about one-third as long as forewing) in the majority of species but a longer one (ca. 0.9–1.0 as long as forewing) in *M. caudata* and *M. undurgensis* (ovipositor of *Baissa* is unknown).

Remarks. Originally, *Humiryssus* was placed in the family Paroryssidae (Lin, 1980). However, the features

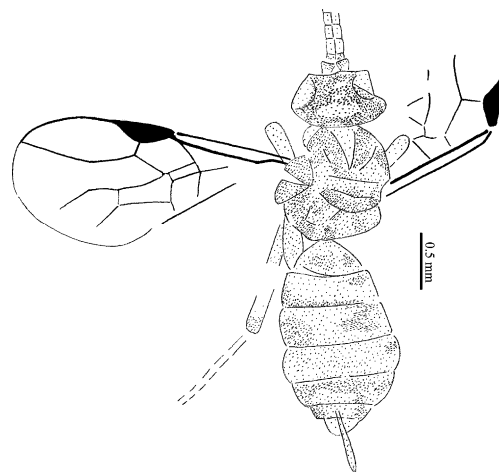


Fig. 4. *Mesepipopaea nanligezhuangica* sp. nov., female adult, dorso-ventral aspect, camera lucida drawing of specimen L91470.

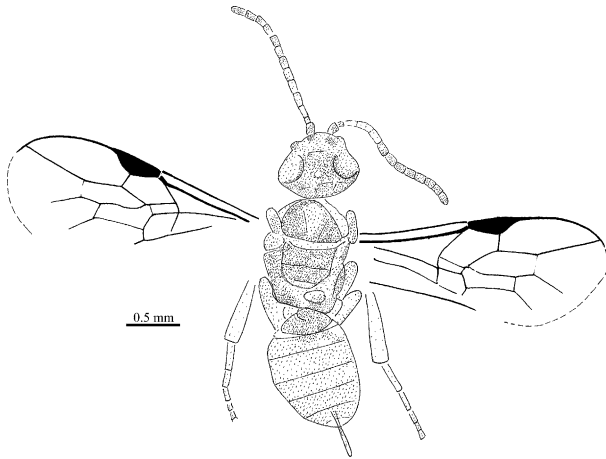


Fig. 5. *Mesepipopaea nanlizezhuangica* sp. nov., female adult, dorso-ventral aspect, camera lucida drawing of specimen L91468.

illustrated by Lin (1980, pl. 8, fig. 3) clearly indicate its position in the Baissinae (Rasnitsyn et al., 1998); the photograph shows that, unlike the description and line drawing (Lin, 1980, p. 232, fig. 21), the pterostigma is large and nearly semicircular rather than triangular; 2r-rs is shorter than the width of the pterostigma, and runs almost vertical to Rs; the third section of Rs (before 3r-m) is longer than the fourth section (beyond 3r-m); and Rs is strongly bent at 3r-m and not smoothly curved. As a result, the type species appears similar to other species of *Humiryssus* in its present interpretation, and not to any Paroryssidae, which differs considerably in its very thick R and totally different type of vein reduction (cf. Rasnitsyn, 1969, figs. 124–131).

Aulocopsis Hong and Wang, 1990 was originally described as a new genus belonging to the family Aulacidae (Hong and Wang, 1990). Like *Humiryssus*, it was later treated jointly with *Manlaya* as a possible

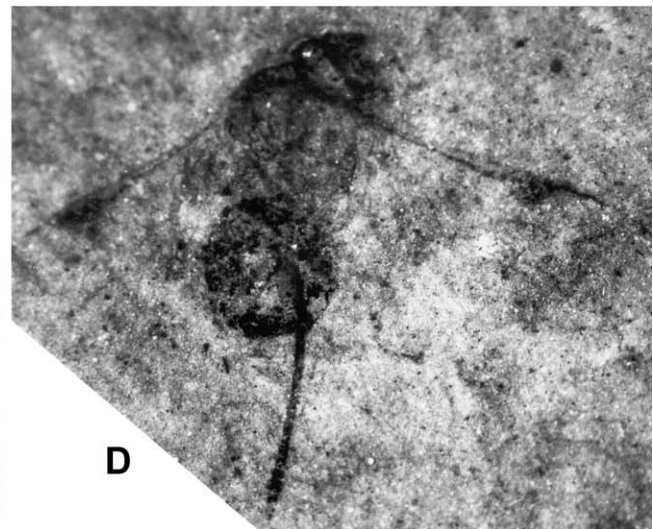
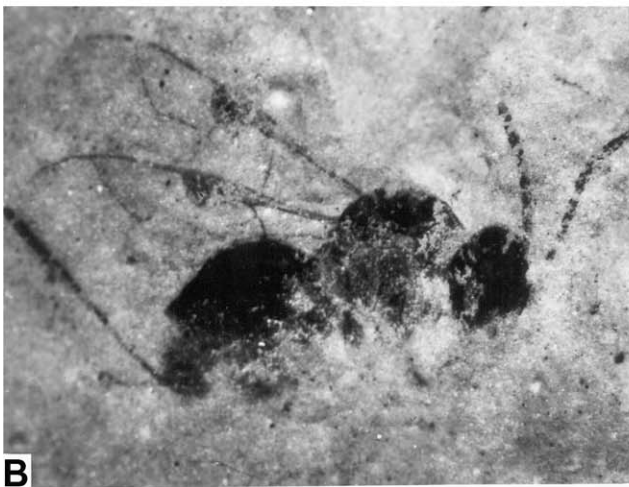
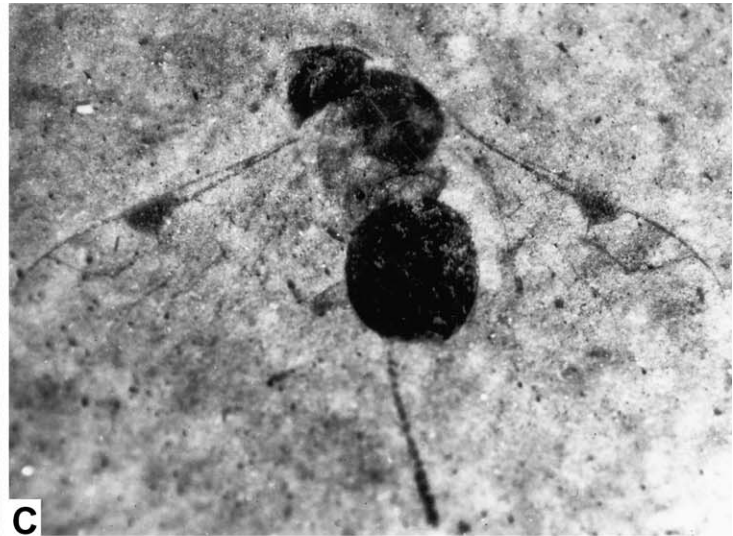
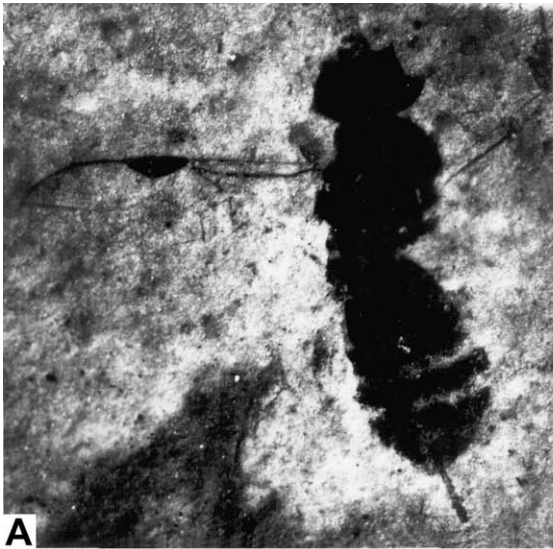


Fig. 6. A, *Mesepipopaea nanlizezhuangica* sp. nov., paratype, L91470; $\times 17.0$. B, *Humiryssus vulgata* sp. nov., holotype, L91555; $\times 27.5$. C, D, *Humiryssus cancellata* sp. nov., holotype. C, part, L91454; $\times 20.4$. D, counterpart, L91455; $\times 20.9$.

component (Rasnitsyn et al., 1998). Indeed, the subfamily Aulacinae was the first home of *Manlaya* (Rasnitsyn, 1980), and the original illustrations strongly suggest a close relationship of *Aulocopsis* to that genus. As to the extra cell 'd' in the left forewing of *H. laiyangensis* (Hong and Wang, 1990, figs. 163, 164), this is most probably an error, although Ren et al. (1995, p.115) considered 2-rm to be present. This is because (1) nothing similar has been ever described in the order Hymenoptera; and (2) this cell is not seen in the original photograph (Hong and Wang, 1990, pl. 24, fig. 4) nor in the right forewing (ibid, fig. 163).

H. oculatissimus (Rasnitsyn and Jarzembowski, 1998) from the Durlston Formation (Middle Purbeck) of Durlston Bay in southern England was originally described as *Manlaya oculatissima* Rasnitsyn and Jarzembowski, 1998 but all its characters fit the diagnosis of *Humiryssus*.

Key to species

- | | | | |
|------|---|---|--|
| 1 | Forewing 2.3 mm long, with 2r-rs nearly as long as width of pterostigma | 2 | |
| | Forewing with 2r-rs shorter than width of pterostigma | 3 | |
| 2 | Pterostigma triangular, cell 3r 1.7 times as long as wide, first abscissae of Rs and M meeting at angle, metasoma paler before middle | | <i>H. specialis</i> sp. nov. |
| | Pterostigma not triangular, cell 3r about twice as long as wide, first abscissae of Rs and M forming smooth line. Metasome uniformly dark | | <i>H. laiyangensis</i> (Hong and Wang, 1990) |
| 3(1) | Forewing 1.6 mm long | 4 | |
| | Forewing 2.0–2.3 mm long | 5 | |
| 4 | Eye long oval, propodeum coarsely sculptured | | <i>H. oculatissimus</i> (Rasnitsyn and Jarzembowski, 1998) |
| | Eye short oval, propodeum finely sculptured | | <i>H. vulgaris</i> sp. nov. |
| 5(3) | Antenna filiform, propodeum irregularly and coarsely reticulate, head and mesosoma dark, metasoma less dark, with fifth segment darker | | <i>H. cancellatus</i> sp. nov. |
| | Antenna widened apically, propodeum not reticulate, body pale except for darkened head and dorsal surface of mesosoma | | <i>H. leucus</i> Lin, 1980 |

Humiryssus specialis sp. nov.

Figs. 1D, 7

Derivation of name. Latin, *specialis*, special, alluding to the structure of the basal vein, which is unusual for Baissinae.

Material. Holotype L91457 (female in dorsoventral aspect). Right antenna and right forewing incomplete, legs and hindwings lacking.

Description. Female; male unknown. Body dark brown. Head moderately large, transversely broad and subtrapezoid, tapering toward mouthparts, widest at lower end of eyes, occipital contour rounded. Eyes large, elongate-oval, occupying entire sides of head; ocelli comparatively large, with hind ones suboval, distant from each other for more than their diameter; from fore ocellus, for about their diameter; from eye, for about twice their diameter. Antennae moderately thin, filiform, 13-segmented, shorter than head and mesosoma combined, with scape relatively large, distinctly thicker and shorter than first flagellomere; pedicel relatively small, longer than wide, and markedly shorter than first flagellomere; each flagellomere oblong, gradually reduced in length apically. Mesosoma oval, scutellum with transverse sculpture; metanotum and propodeum not reticulate. Forewing with costal area narrow but widened near pterostigma; pterostigma relatively large, triangular, and issuing 2r-rs medially, the latter oblique and nearly as long as the width of pterostigma; first abscissa of Rs half as long as that of M, meeting it at angle, cell 3r very short and wide, about 1.7 times as long as wide; first abscissa of M apparently longer than 1m-cu; 3r-m only marked by RS and M bent at its former attachment places; cell 2 + 3rm comparatively

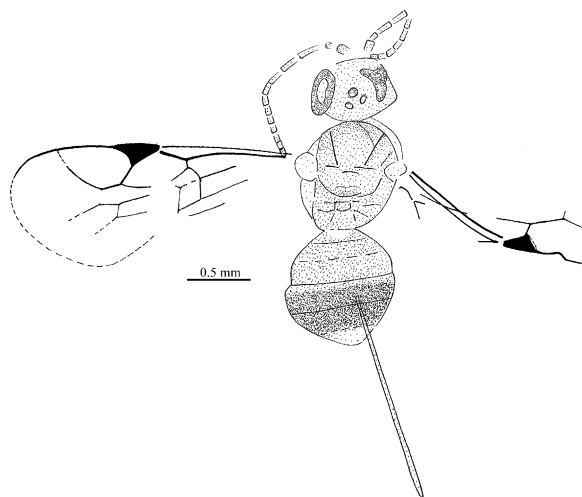


Fig. 7. *Humiryssus specialis* sp. nov., female adult, dorsoventral aspect, camera lucida drawing of specimen L91457.

narrow; 2m-cu complete but thin. Metasoma broad-oval, nearly as long as mesosoma, with six metasomal segments visible, fourth and fifth metasomal segments darker in colour than other segments, fourth metasomal segment widest. Ovipositor straight, nearly 0.8 times as long as forewing.

Length of head 0.5 mm, antenna ca. 1.5 mm, mesosoma 0.9 mm, metasoma 0.9 mm, forewing 2.3 mm; width of forewing 1.0 mm; ovipositor 1.7 mm long.

Humiryssus cancellatus sp. nov.

Figs. 6C, D, 8

Derivation of name. Latin, *cancellatus*, cancellate, alluding to the net-like structure of the metanotum and propodeum.

Material. Holotype L91454, L91455 (female in dorsolateral aspect), part and counterpart; antenna incomplete, legs and hindwings lacking.

Description. Female; male unknown. Body dark brown. Head form difficult to determine because of half-profile position. Eyes large, elongate-oval, probably occupying much or all of sides of head. Antenna with thick scape; flagellomeres thin, distinctly longer than wide. Mesosoma broad-oval; metanotum and propodeum irregularly and coarsely reticulate. Forewing with costal area narrow but widened near pterostigma; pterostigma fairly large, not triangular, issuing 2r-rs medially, 2r-rs slightly oblique, shorter than width of pterostigma; cell 3r about twice as long as wide; first abscissae of Rs and M streamlined, that of RS shorter than that of M; first abscissa of M about as long as 1m-cu; 3r-m only marked by RS and M bent at its former attachment places; cell 2 + 3rm comparatively wide; 2m-cu complete but thin. Metasoma subcircular (only slightly longer than wide), nearly as long as mesosoma, with fifth segment darker in colour than the other

segments. Ovipositor almost 0.8 times as long as metasoma.

Length of head 0.2 mm, mesosoma 0.9 mm, metasoma 0.9 mm; forewing 2.2 mm; width of forewing 1.0 mm; ovipositor 1.6 mm long.

Humiryssus vulgatus sp. nov.

Figs. 6B, 9

Derivation of name. Latin, *vulgatus*, ordinary, alluding to the non-specialized morphological characteristics of this insect.

Material. Holotype L91555 (female in lateral aspect). Legs incomplete, hindwings lacking.

Description. Female; male unknown. Body dark brown. Head large, oval. Eyes large, suboval, and not reaching hind margin of head. Antenna with scape and pedicel not preserved; flagellum 11-segmented, filiform and thin, each flagellomere slightly longer than wide. Mesosoma broad-oval, with metanotum and propodeum not reticulate. Forewing with costal area narrow but widened near pterostigma; pterostigma relatively large, semicircular, issuing 2r-rs medially; 2r-rs slightly oblique, shorter than width of pterostigma; first abscissae of Rs and M forming a line, that of RS shorter than that of M; first abscissa of M longer than 1m-cu; cell 3r short and wide, 3r-m only marked by RS and M bent at its former attachment places; cell 2 + 3rm comparatively wide; 2m-cu complete but thin. Metasoma subcircular (only slightly longer than thick), slightly longer than mesosoma, evenly coloured. Ovipositor nearly 0.8 times as long as forewing.

Length of head 0.4 mm, mesosoma 0.8 mm, metasoma 0.9 mm, forewing 1.6 mm; width of forewing 0.8 mm; ovipositor 1.2 mm long.

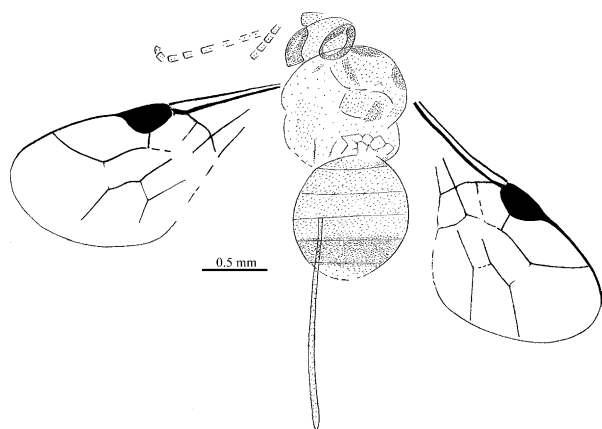


Fig. 8. *Humiryssus cancellata* sp. nov., female adult, dorso-ventral aspect, camera lucida drawing of specimen L91454.

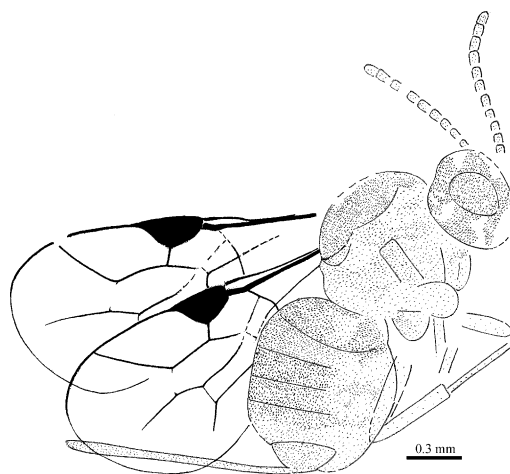


Fig. 9. *Humiryssus vulgata* sp. nov., female adult, lateral aspect, camera lucida drawing of specimen L91555.

3. Discussion

The Jehol insect fauna, forming part of the Jehol biota, is an extinct, largely endemic fauna which includes thousands of species that only lived during latest Jurassic–earliest Cretaceous in Central and East Asia. Comparison of the insect assemblage of the Laiyang Formation and its correlatives with insect fossils collected to the north and west of China is an important task. Their similarity with latest Jurassic or Early Cretaceous assemblages from Mongolia and Siberia has commonly been recorded, including the presence of species that appear to have been common and widespread in both regions (e.g., the giant mayfly *Ephemeropsis trisetalis* Eichwald and the beetle *Coptoclava longipoda* Ping) (Zhang, 1992). At the same time, some important differences have been noted, presumably reflecting differences in climate (e.g., Sinitshenkova, 2002). The study of parasitic wasps might be useful in this respect. However, the striking difference revealed by the present study that almost all representatives of Baissinae described so far from China (the exception being *Manlaya flexuosa*), belong to genera that are either rare (*Humiryssus*) or recorded nowhere else (*Mesepipolaea*). The reasons for this are unclear at present: they may reflect differences in age, palaeogeography, palaeoclimate and/or palaeoecology. The Baissinae described from Mongolia, Siberia, and Europe are mostly larger (wing length rarely less than 2.5 mm), although several larger representatives of baissine wasps closely related to *Manlaya* have been recovered from Laiyang; these are so far undescribed. The closely related species of *Humiryssus* come from the Laiyang, Laocun and Durlston formations, of which the last is well dated as earliest Cretaceous (Berriasian), the Laiyang Formation is usually considered to be latest Jurassic or earliest Cretaceous, i.e., late Tithonian–Berriasian (Zhang, 1999; Zhang and Zhang, 2001) and the Laocun Formation has been regarded as Late Jurassic (Lin, 1980), although Rasnitsyn and Zherikhin (2002, p. 441) claimed that “the insect assemblage is of the same type as in the East Siberian and Mongolian earlier Early Cretaceous”. We now believe that these baissine wasp-bearing beds are likely to be contemporaneous or nearly so.

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