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A new species of *Manlaya* (Hymenoptera: Baissidae) from the Lower Cretaceous Shouchang Formation, Eastern China

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Abstract

Baissid wasps (Hymenoptera: Baissidae) represent a family within the superfamily Evanioidea composed of 36 species in seven genera restricted to a period spanning from the Berriasian (earliest Cretaceous) to the Turonian (early Late Cretaceous). The status and rank of the family have been changing over time, and recent phylogenetic analyses indicate that Baissidae may be paraphyletic to Aulacidae + Gasteruptiidae. The genus *Manlaya* Rasnitsyn, 1980 is the most diverse and widespread in the family, including representatives from western and eastern Laurasia. Here, we describe *Manlaya minima* **sp. nov.** from the Lower Cretaceous Shouchang Formation (Zhejiang Province, China). The new species has elbowed second medial cell, similar to *Electrobaissa* Engel, 2013, although the rest of the characters match with *Manlaya*, indicating that this character might be related to interspecific variability rather than differences between genera. The co-occurrence of *Manlaya* in the contemporaneous Shouchang Formation and the Jehol biota may point to a connection between the two entomofaunas. A key to the species of the family Baissidae from China is provided.

Key words: Evanioidea, Aulaciformes, taxonomy, Early Cretaceous, wasps

Introduction

The family Baissidae is a group of apocritan wasps within the superfamily Evanioidea characterised by having a compact body, not elbowed antenna, mesonotum slightly humped above the pronotum, developed forewing venation with crossvein 2m-cu present, extended propodeal dorsal surface, metasoma articulating high on the propodeum (typical evanioid feature), ovoid and not compressed metasoma, first metasomal segment rounded basally, and not fused tergites I and II (Zhang & Rasnitsyn 2004; Engel 2013; Li *et al*. 2018). This family includes 36 species within seven genera: *Baissa* Rasnitsyn, 1975 (three species), *Electrobaissa* Engel, 2013 (one species), *Heterobaissa* Li, Rasnitsyn & Ren, 2018 (one species), *Humiryssus* Lin, 1980 (six species), *Manlaya* Rasnitsyn, 1980 (twenty-one species), *Mesepipolaea* Zhang & Rasnitsyn, 2004 (two species), and *Tillywhimia* Rasnitsyn & Jarzembowski, 1998 (two species). The representatives of the family are restricted to a period spanning from the Berriasian (Early Cretaceous) to the Turonian (Late Cretaceous), being a key group for understanding the Late Jurassic–Early Cretaceous transition of entomofaunal assemblages (Zhang & Rasnitsyn 2004). During the Early Cretaceous, most of the baissid species were distributed across eastern Laurasia, while only a few species were present in western Laurasia (Rasnitsyn 1986; Rasnitsyn *et al*. 1998; Rasnitsyn & Martínez-Delclòs 2000; Zhang & Rasnitsyn 2004; Li *et al*. 2018, 2019). However, this difference on diversity across Laurasia might be related to a bias in the fossil record, due to the availability of fossil localities. A single species, *Electrobaissa omega* Engel, 2013, was described from Turonian amber of New Jersey, in North America. The species *Hyptiogastrites electrinus* Cockerell, 1917 from Burmese amber was moved to Baissidae (Li *et al*. 2018) and then transferred to Aulacidae (Jouault *et al*. 2022). Additional possible baissid specimens from compression outcrops of Russia and Mongolia and from Lebanese amber are yet to be studied (Rasnitsyn *et al*. 1998; Álvarez-Parra & Azar 2024).

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Baissidae was first erected for *Baissa anomala* Rasnitsyn, 1975, an enigmatic evanioid species from the Lower Cretaceous of Siberia, while *Manlaya undurgensis* (Rasnitsyn, 1975) (originally *Cretocleistogaster undurgensis* Rasnitsyn, 1975) was placed in the family Megalyridae (Rasnitsyn 1975). Rasnitsyn (1980) synonymised Baissidae under Aulacidae, adding *Manlaya mongolica* Rasnitsyn, 1980 also to this family. Rasnitsyn (1986) established the subfamily Manlayinae, including only the genus *Manlaya*, within Aulacidae. Later, the genera *Baissa*, *Manlaya*, *Humiryssus*, *Aulocopsis* Hong & Wang, 1990 (eventually synonymised under *Humiryssus*), *Tillywhimia*, and *Mesepipolaea* were considered members of the subfamily Baissinae within the expanded concept of the family Gasteruptiidae (Rasnitsyn 1990; Rasnitsyn *et al*. 1998; Zhang & Rasnitsyn 2004). Subsequently, the family rank for Baissidae was reinstated and considered sister to the clade Aulacidae + Gasteruptiidae within Aulaciformes (Grimaldi & Engel 2005; Engel 2013). Thereafter, the status of Baissidae was stable, and new species were added to the family (Li *et al*. 2018, 2019). However, recent phylogenetic analyses indicate that Baissidae may represent a paraphyletic grouping (Li *et al*. 2018; Jouault *et al*. 2022).

The genus *Manlaya* is the most diverse and widely distributed within the Baissidae. Species of *Manlaya* have been found in compression outcrops from England, Spain, Russia, Mongolia, and China, spanning from the Berriasian to the Aptian (Li *et al*. 2019). Here, we describe a new species of the genus *Manlaya* based on a female specimen from the Lower Cretaceous Shouchang Formation in Zhejiang Province (China), expanding the known distribution of this genus to southeastern Laurasia.

Material and methods

The holotype is preserved in a green-greyish shale collected from the Shanghujia Village, Shouchang Township, Jiande City, Zhejiang Province, East China. An introduction to the locality is presented by Huang *et al*. (2022). The age of the corresponding section within the Shouchang Formation ranges from the late Barremian to the early Aptian (Huang *et al*. 2022; Hakim *et al*. 2023). The new fossil co-occurred with abundant and diverse fossil insects, conchostracans, and shrimps (Huang *et al*. 2022; Hakim *et al*. 2023).

The specimen was examined and photographed dry with a digital camera attached to a Zeiss Discovery V16 stereomicroscope. The line drawings and the figures were prepared using Adobe Photoshop CS6 software. The venation terminology used in the work refers to the forewing and follows Zhang & Rasnitsyn (2004), Engel (2013), and Li *et al*. (2019). The holotype is housed in the Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, Nanjing, China.

Systematic palaeontology

Superfamily Evanioidea Latreille, 1802

Family Baissidae Rasnitsyn, 1975

Genus *Manlaya* Rasnitsyn, 1980

Type species. *Manlaya mongolica* Rasnitsyn, 1980

Other species. *Manlaya anglica* Rasnitsyn & Jarzembowski, 1998*; M. ansorgei* Rasnitsyn & Martínez-Delclòs, 2000; *M. capelensis* Rasnitsyn & Jarzembowski, 1998; *M. caudata* Rasnitsyn, 1986; *M. corrugata* Rasnitsyn, 1986; *M. flexuosa* Ren, Lu & Guo, 1995; *M. ghidarina* Rasnitsyn, 1990; *M. gurvanica* Rasnitsyn, 1986; *M. lacabrua* Rasnitsyn & Ansorge, 2000; *M. laevinota* Rasnitsyn, 1986; *M. magna* Li, Shih, Li & Ren, 2019; *M. minima* **sp. nov.**; *M. obscura* Rasnitsyn, 1986; *M. ockleyensis* Rasnitsyn & Jarzembowski, 1998; *M. pachyura* Rasnitsyn, 1990; *M. pallida* Rasnitsyn, 1986; *M. pinguis* Rasnitsyn, 1986; *M. proba* Li, Shih, Li & Ren, 2019; *M. undurgensis* (Rasnitsyn, 1975); *M. ultima* Li, Shih, Li & Ren, 2019, *M. ventricosa* Rasnitsyn, 1986.

***Manlaya minima* sp. nov.**
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(Figs 1–3)

Type material. Holotype NIGP206130, a female specimen from lateral view, distalmost parts of wings and ovipositor not preserved.

Type locality and horizon. Lower Cretaceous Shouchang Formation (upper Barremian to lower Aptian); Shanghujia Village (Dongcun section), Shouchang Township, Jiande City, Zhejiang Province, China.

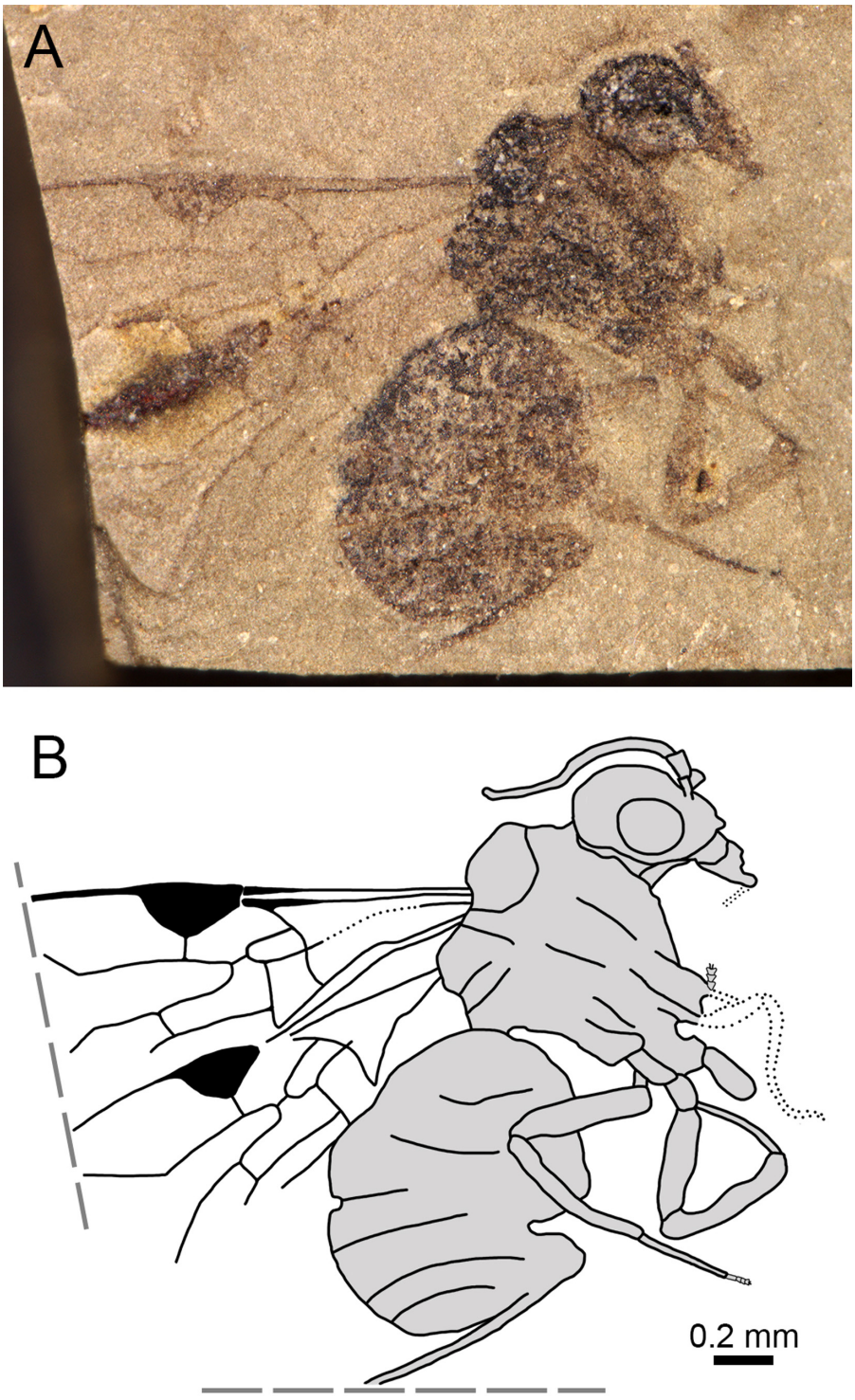

FIGURE 1. *Manlaya minima* **sp. nov.**, holotype NIGP206130, female, from Lower Cretaceous Shouchang Formation (China). **A**, Photograph of the habitus. **B**, Interpretative drawing of the habitus. Both at the same scale.

Etymology. From the Latin word *minimus*, meaning very small, referring to the small body size in comparison to other species of the genus.

Diagnosis. Body size small (about 2 mm long); pedicel thicker than scape; pterostigma broad, with anterior margin straight and posterior margin curved; r-rs slightly inclivous, half longer than pterostigma width; 1Rs separated from pterostigma base by length 2× pterostigma basal width, slightly longer than 1M; cell 1mcu strongly transverse, with 1Rs+M and 1Cu parallel; 2Rs+M as long as 1m-cu; 1cu-a slightly postfurcal; cell 2mcu elbowed; vein A sigmoidal basally.

Description. Female. Body stout, 2.07 mm long (Fig. 1). Colour dark brown, head and mesonotum darker than rest of body. No setation.

Head: 0.34 mm long and 0.43 mm high (Fig. 2A); eyes large, rounded, occupying most of side of head, 0.22 mm in diameter; preserved part of antenna about 0.68 mm long, pedicel 0.08 mm long and 0.06 mm wide, thicker than scape (number of flagellomeres uncertain); mouthparts apparently protruded.

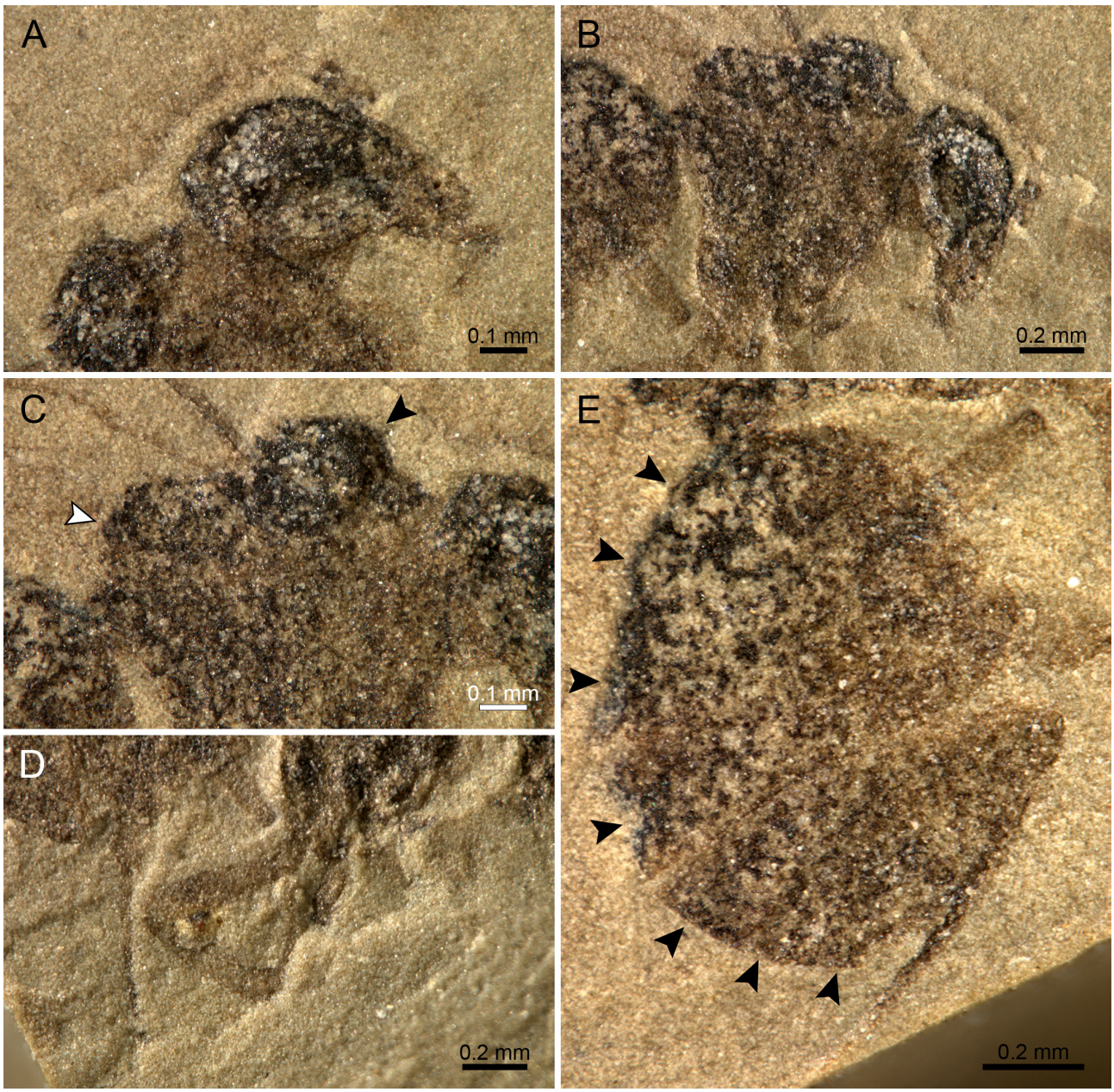

FIGURE 2. *Manlaya minima* **sp. nov.**, holotype NIGP206130, female, from Lower Cretaceous Shouchang Formation (China). **A**, Head. **B**, Mesosoma and head. **C**, Dorsal part of the mesosoma with indication of the mesonotum humped antero-dorsally (black arrowhead) and the propodeum with extended surface and slightly protruding posteriorly (white arrowhead). **D**, Legs. **E**, Metasoma with indication of metasomal segments.

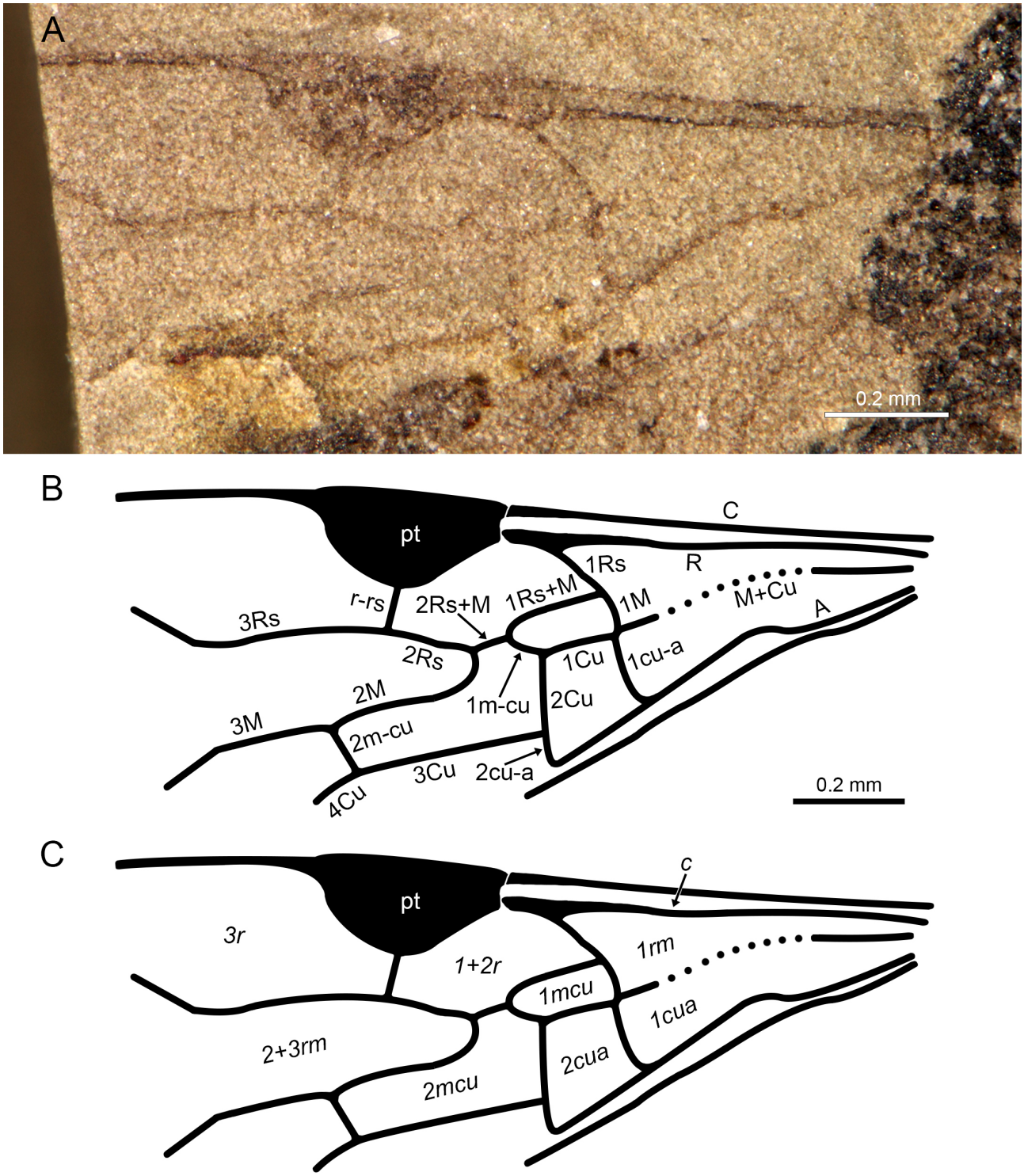

FIGURE 3. Forewing of *Manlaya minima* **sp. nov.**, holotype NIGP206130. **A**, Photograph of the forewing. **B**, Name of veins. **C**, Name of cells. **B** and **C** at the same scale.

Mesosoma: stout (Fig. 2B), 0.70 mm long, as long as high (height measured from just above the procoxa); pronotum about 0.15 mm long; mesonotum humped antero-dorsally (Fig. 2C), 0.35 mm long and 0.22 mm high; metanotum narrow, 0.10 mm long; propodeum with extended surface, slightly protruding posteriorly.

Forewing: incomplete, at least 1.55 mm long (Fig. 3); costal cell narrower than pterostigma; pterostigma broad, 1.8× longer than wide; crossvein r-rs arising medially from pterostigma, slightly inclivous, half longer than

pterostigma width; vein 1Rs originating proximad pterostigma base, separated from pterostigma base by length 2× pterostigma basal width; veins 1Rs and 1M aligned, curved; 1Rs 1.3× longer than 1M; 1Rs+M 2.3× longer than 2Rs+M; cell 1mcu strongly transverse, parallel-sided, 3× longer than wide; 2Rs+M about as long as crossvein 1m-cu; crossveins 2r-m and 3r-m completely absent (no stubs); distal abscissa of Rs strongly bent anteriorly at point where distal r-m should be present, virtually extending straight towards nearly wing apex; cell 2+3rm narrower than cell 3r at level of pterostigma apex; distal abscissa of M strongly bent posteriorly at point where distal r-m should be present, straight; vein M+Cu mostly spectral; crossvein 1cu-a slightly postfurcal; cell 2mcu elbowed; crossvein 2m-cu distinctly distad r-rs, as long as r-rs level; vein A sigmoidal basally.

Hind wing: not visible.

Legs: partly preserved, thin (Fig. 2D); hind femur nearly as long as hind tibia; hind femur about 5× longer than wide; hind tibia about 6× longer than wide; tarsi pentamerous; hind basitarsus much longer than remainder tarsomeres combined.

Metasoma: ovoid from lateral view (Fig. 2E), 1.03 mm long and 0.76 mm wide; metasoma 1.5× longer than mesosoma; seven metasomal segments distinguished, first segment the longest; ovipositor incomplete, thin, slightly bent upwards, length as preserved: 0.64 mm.

Key to the species of the family Baissidae from China

The record of Baissidae from China is represented by one species of *Heterobaissa*, five species of *Humiryssus*, five species of *Manlaya*, and two species of *Mesepipolaea*, collected from Yixian Formation (Hebei and Liaoning provinces), Laiyang Formation (Shandong Province), Laocun Formation, and Shouchang Formation (both in Zhejiang Province), spanning from the Barremian to the Aptian in the Early Cretaceous (Lin 1980; Hong & Wang 1990; Ren *et al*. 1995; Zhang & Rasnitsyn 2004; Li *et al*. 2018, 2019; Zhang 2021). A key to the species of Baissidae found in China is presented below. Couplets 2 and 3 are modified from those of Zhang & Rasnitsyn (2004). The venation terminology refers to the forewing.

1. Distalmost abscissa of Rs slightly curved and not directed towards wing apex 2
- Distalmost abscissa of Rs mostly straight and directed nearly towards wing apex 6
2. Crossvein r-rs nearly as long as pterostigma width 3
- Crossvein r-rs shorter than pterostigma width 4
3. Pterostigma triangular; cell 3r 1.7× as long as wide; first abscissae of Rs and M meeting at angle; metasoma paler before midlength . . . . . *Humiryssus specialis* Zhang & Rasnitsyn, 2004
- Pterostigma not triangular; cell 3r about twice as long as wide; first abscissae of Rs and M forming smooth line; metasoma uniformly dark . . . . . *Humiryssus laiyangensis* (Hong & Wang 1990)
4. Crossvein r-rs sub-vertical; 2Rs+M present; crossveins 2r-m and 3r-m present as stubs on Rs and M . . . . . *Humiryssus leucus* Lin, 1980 (Zhang 2021)
- Crossvein r-rs sub-vertical; 2Rs+M absent; crossvein 3r-m present as a stub only on Rs. 5
5. Metanotum and propodeum irregularly and coarsely reticulate; 1Rs and 1M streamlined; vein 1M about as long as 1m-cu . . . . . *Humiryssus cancellatus* Zhang & Rasnitsyn, 2004
- Metanotum and propodeum not reticulate; 1Rs and 1M forming a line; 1M longer than 1m-cu . . . . . *Humiryssus vulgatus* Zhang & Rasnitsyn, 2004
6. Propleura forming a neck; metasoma conical; ovipositor not exerted . . . . . .*Heterobaissa apetiola* Li, Rasnitsyn & Ren, 2018
- Propleura not forming a neck; metasoma ovoid; ovipositor exerted 7
7. Costal cell broad; vein 1Rs originating near pterostigma base; metasoma as long as or shorter than mesosoma. 8
- Costal cell much narrower than pterostigma; vein 1Rs originating far from pterostigma base; metasoma longer than mesosoma 9
8. Crossvein 1cu-a interstitial to 1M; metasoma not petiolate . . . . . *Mesepipolaea nanligezhuangica* Zhang & Rasnitsyn, 2004
- Crossvein 1cu-a distinctly postfurcal to 1M; metasoma petiolate . . . . . *Mesepipolaea parva* Li, Shih, Li & Ren, 2019
9. Cell 2mcu not elbowed; crossvein 1cu-a interstitial to 1M 10
- Cell 2mcu elbowed; crossvein 1cu-a slightly postfurcal to 1M 12
10. Cell 1mcu not parallel-sided; distal section of 2M sigmoidal . . . . . *Manlaya flexuosa* Ren, Lu & Guo, 1995
- Cell 1mcu strongly transverse and parallel-sided; distal section of 2M slightly geniculate at level that 2r-m should be present 11
11. Pterostigma triangular; crossvein r-rs strongly inclivous; 1Rs longer than 1M; 3r-m present as a short stub on M . . . . . *Manlaya proba* Li, Shih, Li & Ren, 2019
- Pterostigma semi-circular; crossvein r-rs slightly inclivous; 1Rs shorter than 1M; 3r-m absent. . . . . *Manlaya ultima* Li, Shih, Li & Ren, 2019

12. Pterostigma triangular; crossvein r-rs less than half length pterostigma width; 1Rs about twice longer than 1M . . . . . .*Manlaya magna* Li, Shih, Li & Ren, 2019

- Pterostigma not triangular; crossvein r-rs half longer than pterostigma width; 1Rs slightly longer than 1M . . . . . .*Manlaya minima* **sp. nov.**

Discussion

The studied specimen belongs to Evanioidea based on the metasomal articulation high on the propodeum and the conspicuous and long ovipositor (Mason 1993). It is assigned to the family Baissidae based on: stout body; not elbowed antenna; slightly humped mesonotum; developed forewing venation matching that of the members of the family including broad pterostigma, two sections of Rs+M and crossvein 2m-cu; extended propodeum surface with metasoma articulating far from metanotum; ovoid and not compressed metasoma; and tergites I and II not fused (Zhang & Rasnitsyn 2004; Engel 2013; Li *et al*. 2018).

Following the key to Baissidae genera by Engel (2013), the specimen would fall into the genus *Electrobaissa* based on: forewing marginal cell (3r) large with distalmost abscissa of Rs straight directed towards near wing apex; origin of 1Rs separated by a distance greater than pterostigma basal width; Rs+M present and crossvein 1cu-a confluent with 1M or slightly postfurcal; vein A present proximad and apicad 1cu-a; and vein 2M strongly curved basally resulting in an elbowed second medial cell (2mcu). In addition to the above, the studied specimen shares several diagnostic characters with *Electrobaissa*, such as the small body size, the strongly transverse and parallel-sided first medial cell (1mcu), and the vein 2Rs+M about as long as 1m-cu (Engel 2013). However, these features are also widely present in the genus *Manlaya* or at least in some species. For example, the body length of the studied specimen is similar to that of *M. lacabrua*, about 2 mm (Rasnitsyn & Ansorge 2000), the strongly transverse and parallel-sided first medial cell is found also in *M. laevinota*, *M. gurvanica*, *M. capelensis*, *M. proba*, *M. magna*, and *M. ultima* (Rasnitsyn 1986; Rasnitsyn *et al*. 1998; Li *et al*. 2019), and the vein 2Rs+M about as long as 1m-cu is present in *M. capelensis*, *M. lacabrua*, and *M. proba* (Rasnitsyn *et al*. 1998; Rasnitsyn & Ansorge 2000; Li *et al*. 2019). Furthermore, a putative key characteristic of *Electrobaissa*, the elbowed second medial cell (Engel 2013), is also present in *M. lacabrua* and *M. magna* (Rasnitsyn & Ansorge 2000; Li *et al*. 2019). Nonetheless, the genus *Electrobaissa* differs from the studied specimen and with the species of *Manlaya* in its costal cell (c) nearly as broad as the pterostigma (*vs*. costal cell narrower in *Manlaya*), its relatively narrow pterostigma (*vs*. broad), its crossvein r-rs originating distad pterostigma midlength (*vs*. arising medially from pterostigma), its marginal cell narrower than the cell 2+3rm (*vs*. much wider), and its vein 1Rs twice as long as 1M (*vs*. less than twice). The genera *Baissa*, *Humiryssus*, and *Tillywhimia* are discarded based on the complete vein A, the distalmost abscissa of Rs straight and directed towards wing apex, and the vein Rs+M present, respectively (Rasnitsyn 1975; Rasnitsyn *et al*. 1998; Zhang & Rasnitsyn 2004). The genus *Mesepipolaea* is excluded not only because of the vein 1Rs originating far from pterostigma base, but also for its costal cell narrower than pterostigma (*vs*. as broad in *Mesepipolaea*), its not semi-circular pterostigma (*vs*. semi-circular), its vein 1Rs slightly longer than 1M (*vs*. much longer), and its metasoma longer than its mesosoma (*vs*. nearly as long as or shorter) (Zhang & Rasnitsyn 2004; Li *et al*. 2019). Finally, the studied specimen is separated from *Heterobaissa* based on its thin antennomeres (*vs*. stout in *Heterobaissa*), its lack of neck (*vs*. propleura forming a neck), and its metasoma ovoid with a long ovipositor (*vs*. metasoma conical with short ovipositor). Therefore, despite the superficial similarities with *Electrobaissa*, and considering the significant differences between the latter and the other baissid genera, the new specimen is assigned to *Manlaya*, as it matches the diagnostic characters of this genus and shares the forewing venational features (Li *et al*. 2019).

Regarding interspecific differences, *Manlaya minima* **sp. nov.** differs from all the rest of *Manlaya* species, except *M. lacabrua* and *M. magna*, in having an elbowed second medial cell. Despite the similar body size, *M. minima* **sp. nov.** shows eyes circular and larger than *M. lacabrua*, a vein 1Rs originating farther from pterostigma base, and the first medial cell parallel-sided contrasting with the trapezoidal first medial cell of *M. lacabrua* (Rasnitsyn & Ansorge 2000). The new species differs from *M. magna* based on the shape of its pterostigma (broad and with anterior margin straight and posterior margin curved *vs*. triangular in *M. magna*), the length of the crossvein r-rs in relation to the pterostigma width (half longer than pterostigma width *vs*. shorter), and the relative lengths of the veins 1Rs and 1M (1Rs slightly longer than 1M *vs*. about twice longer) (Li *et al*. 2019).

Zhang & Rasnitsyn (2004) pointed out that *M. lacabrua* might be an aberrant species of *Mesepipolaea* based on the vein 1Rs originating close to the pterostigma base (Rasnitsyn & Ansorge (2000). However, the shape of

the pterostigma (not semi-circular), the veins 1Rs and 1M of similar lengths, and the metasoma longer than the mesosoma discard its assignment to *Mesepipolaea*. In fact, it is possible that the characters "1Rs originating close to pterostigma base" of *Mesepipolaea* and "second medial cell distinctly elbowed" of *Electrobaissa* are not appropriate diagnostic characters for these genera, as they might be related to interspecific variability rather than differences between genera. Furthermore, the genus *Mesepipolaea* has turned out to be a polyphyletic grouping after several phylogenetic analyses (Jouault *et al*. 2022).

The finding of *M*. *minima* **sp. nov.** allows us to expand the known palaeodistribution of the genus to southeastern Laurasia. The co-occurrence of the genus *Manlaya* in the Shouchang Formation and in the contemporaneous Jehol biota from northern China helps to establish a link between the two insect communities (Li *et al*. 2019). However, additional information is required to assess possible palaeobiogeographic or palaeoecological factors explaining a connection between the two entomofaunas.

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