Nevaniinae subfam. n., a new fossil taxon (Insecta: Hymenoptera: Evanioidea: Praeaulacidae) from the Middle Jurassic of Daohugou in Inner Mongolia, China

HAICHUN ZHANG and ALEXANDR P. RASNITSYN

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A new subfamily, Nevaniinae Zhang & Rasnitsyn, subfam. n., is established and assigned to Praeaulacidae (Hymenoptera: Evanioidea). It only comprises one genus, the type *Nevania* Zhang & Rasnitsyn, gen. n., consisting of six species: *N. robusta* Zhang & Rasnitsyn, sp. n., *N. exquisita* Zhang & Rasnitsyn, sp. n., *N. malleata* Zhang & Rasnitsyn, sp. n., *N. ferocula* Zhang & Rasnitsyn, sp. n., *N. retenta* Zhang & Rasnitsyn, sp. n., and *N. delicata* Zhang & Rasnitsyn, sp. n., from the Middle Jurassic of Daohugou in Inner Mongolia, China. Analyses show that Nevaniinae has a combination of ancestral and derived characters and additionally a few autapomorphies, and probably represents an early clade of the Praeaulacidae, and that the Evanioidea has an ancestor at least as venationally plesiomorphic as basal Ephialtitidae. *N. delicata*, possessing many more putatively plesiomorphic characters than its congeners, probably occupies the most basal position of the *Nevania* clade. Characteristics shown by *Nevania* suggest that these wasps were parasitoids of wood-boring insects.

H. Zhang, State Key Laboratory of Palaeobiology and Stratigraphy (Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences), Nanjing 210008, China (hczhang@nigpas.ac.cn).
A.P. Rasnitsyn, Palaeontological Institute, Russian Academy of Sciences, 117868 Moscow, Russia, and The Natural History Museum, Cromwell Road, London SW7 5BD, UK (rasnaa@mail.ru).

Introduction

The Evanioidea comprises two extant families, Gasteruptiidae and Evaniidae (Townes 1950; Rasnitsyn 1988, 2002); many authors (e.g., Hanson & Gauld 1995; Gauld & Bolton 1996; Grimaldi & Engel, 2005) assign family rank to Aulacidae as well, but we consider it a subfamily of Gasteruptiidae. Additionally, two extinct families, Praeaulacidae and Andreneliidae, have been placed in Evanioidea (Rasnitsyn 1972, 2002; Rasnitsyn & Martínez-Delclòs 2000). Andreneliidae have recently been synonymized with Evaniidae, and Baissinae, a stem subfamily of Gasteruptiidae s.l., was given family rank (Grimaldi & Engel, 2005; Engel, 2006). The proposal is questionable because of the characters cited as putative synapomorphies for Andreneliidae and Evaniidae, only the petiolate 1st metasomal segment is truly shared by all the included taxa. This is a character state well known to appear homoplastically in related taxa (e.g., various Praeaulacidae including those described below, *Baissa* Rasnitsyn 1975, and extant Gasteruptiidae s.l.). Furthermore, *Andrenelia* Rasnitsyn et Martínez-Delclòs, 2000 lacks important synapomorphies of Evaniidae, viz., large head and massive, short and high mesosoma. At the same time, it possesses some synapomorphies in common with either Gasteruptiidae s.l. (somewhat incrassate pterostigma) or with its subclade Kotujellitinae + Aulacinae + Gasteruptiinae (distinctly elongate propleurae; cf. Rasnitsyn & Martínez-Delclòs 2000 and Basibuyuk et al. 2002). Also, the phylogenetic analysis by Basibuyuk et al. (2002) gave inconclusive results concerning

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Andrenelia assigning it to various nodes within the resultant tree including a position far from Evaniidae (fig. 11). Consequently, the phylogenetic position of the Andreneliidae could not be decided with certainty in the analyses performed by Basibuyuk et al. (2002). It cannot be ruled out that Andreneliidae should be included in Evaniidae, but the evidence is inconclusive yet. Following a conservative approach we prefer to recognise Andreneliidae as a family until more information accumulates. Regarding Baissinae, neither the present authors nor Grimaldi & Engel (2005) or Engel (2006) were able to identify any autapomorphy of Baissinae separating them from Gasteruptiinae or Aulacinae. We therefore retain the Baissinae as a subfamily within Gasteruptiidae s. lat.

The Cretevaniidae from the Cretaceous of Eurasia has previously been considered a separate family in Evanioidea (Rasnitsyn 1975, 1991; Jarzembowski 1984; Rasnitsyn et al. 1998; Zhang & Zhang 2000), but its constituent genera are now included in the Evaniidae (Basibuyuk et al. 2002; Zhang et al. 2007).

The Praeaulacidae consists of three subfamilies, Cretocleistogastrinae, from the Lower Cretaceous of East Asia and Australia (Rasnitsyn 1990a,b), Praeaulacinae and Anomopterellinae, from the Upper Jurassic of South Kazakhstan (Rasnitsyn 1972, 1975, 1990b), and has been proposed as representing the ancestral group of the whole Evanioidea (Rasnitsyn 1988).

Here a new subfamily is established and assigned to Praeaulacidae based on specimens from the Daohugou beds in Inner Mongolia, China.

Materials and methods

The present publication is based on six recently discovered specimens from the Middle Jurassic of Daohugou near Chifeng City in Inner Mongolia, China. The Daohugou beds yield diverse and abundant insects as well as other fossils, and are generally considered to be Middle Jurassic in age (for details, see Wang et al. 2006). These specimens described below are housed in the Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences.

Observations of these specimens were made under a light microscope (NIKON SMZ1000) and photographs were prepared with a digital camera (DXM1200) connected to this microscope at the State Key Laboratory of Palaeobiology and Stratigraphy, Nanjing. Line drawings were made by Zhang using the software CorelDRAW 9.

Systematic palaeontology

Superfamily Evanioidea Latreille, 1802

Family Praeaulacidae Rasnitsyn, 1972

Subfamily Nevaniinae Zhang & Rasnitsyn, subfam. n.

Type genus. – *Nevania* gen. n. (from the Middle Jurassic of Daohugou, Inner Mongolia, China).

Diagnosis. – Head small to medium-sized with occipital foramen closed ventrally. Antenna filiform and polymerous with scape short. Pronotum comparatively long, not short medially. Pronotum and mesonotum transversely ridged. Mesonotum with median and transscutal sutures, and notauli present. Metapostnotum present. Forewing venation complete with 2-3rm and 2m-cu tubular; basal vein (Rs&M) meeting M+Cu far basad of pterostigma; cu-a postfurcal (meeting Cu beyond M+Cu fork) or interstitial (meeting M+Cu just at its fork into M and Cu); 2A present. Hindwing venation complete with C, r-m and cu-a present; r closed. Metasoma attached to propodeum about halfway between metapostnotum and hind coxa, with two basal metasomal segments tube-like. Ovipositor short and slightly exserted.

Remarks. – The high attachment of mesosoma to the metasoma undoubtedly places this group of wasps in the Evanioidea. Furthermore some important characters, e.g. antennae with usually above 28 segments, complete wing venation, and the presence of notauli, median and transscutal sutures on the mesonotum, indicate their similarity to (symplesiomorphy with) Praeaulacidae and separate them from the rest Evanioidea. Nevertheless, any known subfamily within Praeaulacidae is not in a position to accommodate them, and therefore it is necessary to establish a new subfamily for them.

The new subfamily differs from other Praeaulacidae in having a forewing with 2A present, and M+Cu fork far basad of pterostigma, a metasoma with two basal segments tubular, and a very short ovipositor (slightly exserted). It further differs from Praeaulacinae in having a hindwing with C present; from Anomopterellinae in having a

forewing with two r-m crossveins present and two mcu cells normal in width; and from Cretocleistogastrinae in having complete wing venation.

Composition. – The type genus only.

Genus *Nevania* Zhang & Rasnitsyn, gen. n.

Type species. – *N. robusta* Zhang & Rasnitsyn, sp. n. by present designation.

Etymology. – Generic name is from *ne-* (Greek for no) and generic name *Evania*. Gender feminine.

Diagnosis. – Known from female and specimens where the sex could not be determined. Medium-sized (body about 10 to 18 mm in length). Antenna inserted far above mandibles, usually consisting of over 28 segments, distinctly longer than head and mesosoma combined; flagellum slightly and gradually increasing in thickness submedially, with first flagellomere longer than any other antennal segment. Occipital carina present but not circular. Mesosoma short and slightly high; pronotum and mesoscutum transversely, and mesopleura archedly ridged; metapostnotum very short; propodeum dorsally and laterally reticulate. Legs slender; midcoxa much closer to hind coxa than to fore coxa, and touching hind coxa when projecting posteriorly; trochantellus present; hind tibia possessing an apical spur. Forewing venation complete with 11 closed cells; costal area narrow; pterostigma narrow basally, gradually widened distally until its meeting 2r-rs before pterostigmal midlength, and then gradually narrowed apically; Rs&M more or less straight, not strongly angled at the junction of Rs and M, as long as or longer than M+Cu, meeting R well before pterostigma, first abscissa of Rs at most as long as that of M; Rs nearly straight beyond 2r-rs; 1r-rs spectral or completely absent; 2r-rs slightly shorter than maximal width of 2rm; 2m-cu slightly distad of 2r-m; cu-a interstitial or slightly postfurcal; 2cua large, distinctly longer than wide, and broadened apically; 2A complete; cell 1+2a much wider than 2cua basally but slightly narrower than that distally. Hindwing venation complete with C tubular; Rs reaching wing apex; r closed; M reaching wing margin; r-m strongly inclined towards wing base; first section of Cu smoothly connected with cu-a, free Cu vestigial or completely absent; A distinctly angulate quite basad of cu-a (indicating a position of disappeared crossvein a_1-a_2), free A distinct. Metasoma with first and second segments long tube-like, swollen apically, and subequal in length; remaining part generally not longer than first and second segments combined. Ovipositor short, slightly protruding out of metasomal apex.

Included species. – Six species including the type.

Remarks. – Comparison of the included species is presented in the key below.

Key to species assigned to *Nevania* Zhang & Rasnitsyn, gen. n.

1. Forewing with cu-a interstitial; first abscissa of Rs subequal to that of M in length ..... *N. ferocula* Zhang & Rasnitsyn, sp. n.
– Forewing with cu-a postfurcal; first abscissa of Rs shorter than that of M 2
2. Forewing with 1r-rs spectral or rudimentary..... 3
– Forewing with 1r-rs absent..... 4
3. Hindwing with r-m shorter than first abscissa of Rs; first and second metasomal segments stout..... *N. exquisita* Zhang & Rasnitsyn, sp. n.
– Hindwing with r-m longer than first abscissa of Rs; first and second metasomal segments slender ..... *N. delicata* Zhang & Rasnitsyn, sp. n.
4. Forewing with 2rm in contact with 1mcu by a short, second section of M..... *N. robusta* Zhang & Rasnitsyn, sp. n.
– Forewing with 2rm in contact with 1mcu by a point or not in contact with 1mcu 5
5. 2rm in contact with 1m-cu by a point; first and second metasomal segments stout ..... *N. malleata* Zhang & Rasnitsyn, sp. n.
– 2rm not in contact with 1m-cu; first and second metasomal segments slender..... *N. retenta* Zhang & Rasnitsyn, sp. n.

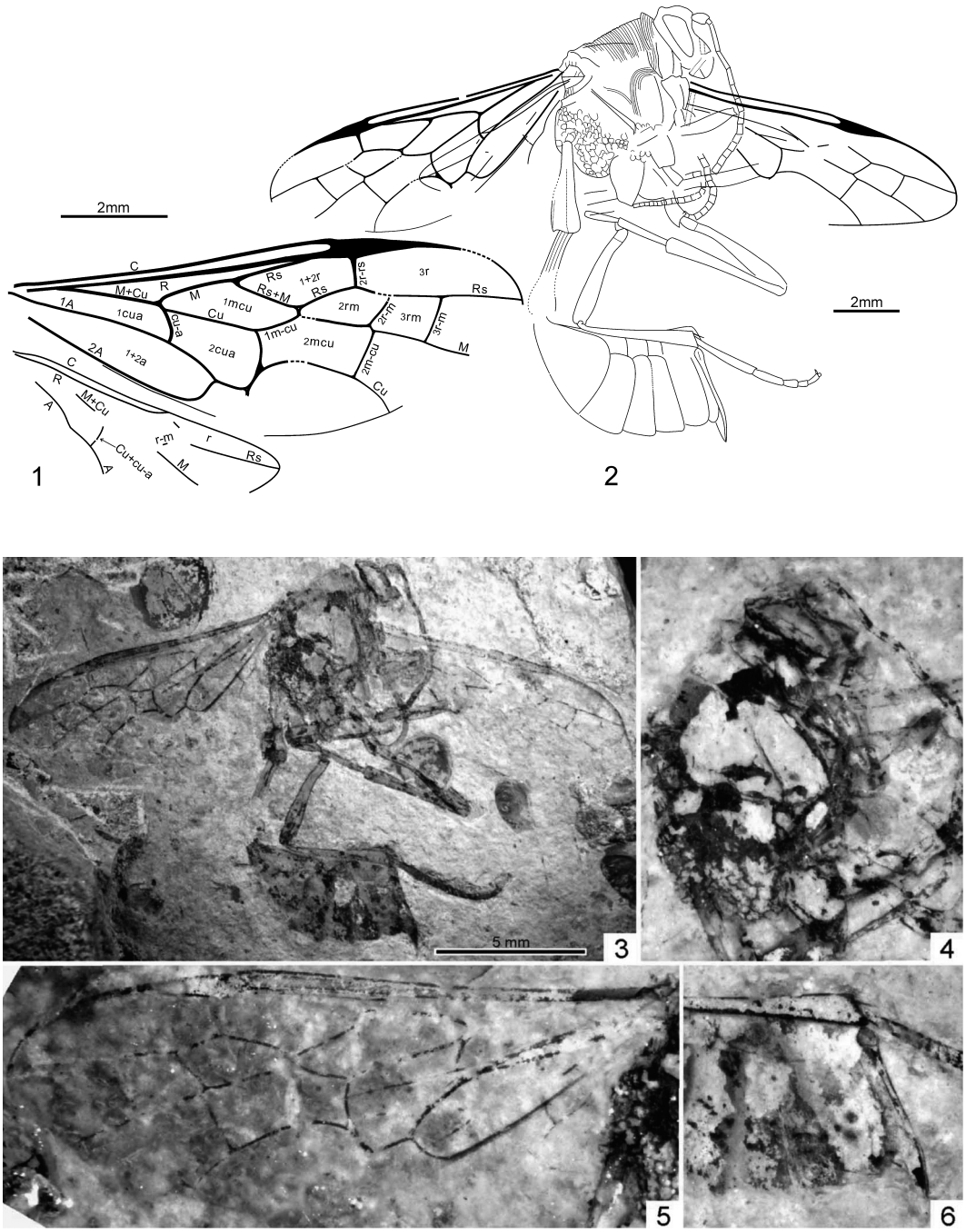
Nevania robusta Zhang & Rasnitsyn, sp. n.

(Figs 1-6)

Type material. – Holotype NND0816/NIGP143693, in lateral aspect, nearly complete female with antennae, wings, legs and second metasomal segment slightly damaged.

Etymology. – Latin *robustus*, strong.

Description. – Brown in colour. Head short, and about twice as high as long. Eyes large, and elongate ovoid. Antenna with 28 segments preserved; scape 1.5 times as long as broad; pedicel distinctly narrower than scape distally, and about as long as wide; first flagellomere cylindrical, as wide as pedicel, and about twice as long as scape; second 0.7 times as long as first, and correspondingly, third 0.6, fourth 0.53, fifth 0.45, sixth 0.4, seventh 0.35; remaining flagellomeres with each one slightly longer than or as long as broad. Pronotum comparatively long, and transversely ridged.



Figs 1-6. *Nevania robusta* Zhang & Rasnitsyn, sp. n., holotype. 1, line drawing of wings, 2, line drawing of entire specimen, 3, general view, 4, head and mesosoma (in alcohol), 5, forewing and hindwing (in alcohol), 6, metasomal apex and ovipositor (in alcohol).

Mesonotum with mesoscutum finely transversely ridged, and three times as long as scutellum; notauli distinct. Mesopleuron partly archedly ridged. Metanotum about as long as mesoscutellum, metapostnotum short. Propodeum rounded dorsally and apically, with fine and dense reticula. Foreleg thin and short. Midleg larger than foreleg. Hindleg with coxa distinctly larger than midcoxa, thick basally, greatly swollen subbasally, and becoming thin distally; trochanter nearly half as long as coxa; femur elongate, slightly swollen subdistally, and 1.4 times as long as first metasomal segment; tibia thin, as long as femur (including trochantellus), with apical spur comparatively long; tarsus slightly longer than tibia with a short claw preserved, basitarsomere half as long as tibia, segmental length ratio from basitarsomere to terminal tarsomere = 1.00 : 0.48 : 0.22: 0.15 : 0.19. Forewing with M+Cu fork slightly closer to wing base than to pterostigma; pterostigmal base slightly closer to 2r-rs than to Rs origin; first abscissa of Rs 0.7 times as long as that of M; 2r-rs subvertical, meeting pterostigma at its basal one-fourth length, and 1.5 times as long as pterostigmal width; 3r 1.4 times as long as 1+2r; 2rm and 1mcu in contact by a very short, second section of M (2M); 2rm two-thirds as long as 1+2r and 1.3 times as long as 3rm; cu-a slightly postfurcal and curved outwards. Hingwing poorly preserved with free Rs and M distinguishable; Cu+cu-a distinct; free A long. Metasoma with first segment thin for basal one-third, and gradually thickened distally for remaining part; second as long as first, slightly thicker than first basally for basal half, and damaged for distal half; third tergum slightly longer than second segment, and round triangular in lateral aspect; fourth half as long as third, fifth to seventh subequal in length and distinctly shorter than fourth; terminal very short. Ovipositor slightly exserted.

Measurements in mm: head length 1.2; antennal length (as preserved) 8.4; mesosomal length 4.6; forewing length 9.6, width 3.6; hindwing length 5.5, width (as preserved) 1.6; first metasomal segment length 2.7, second 2.6, remaining segments (combined) 6.3; ovipositor length 2.9, exerted for 0.7.

Nevania exquisita Zhang & Rasnitsyn, sp. n.

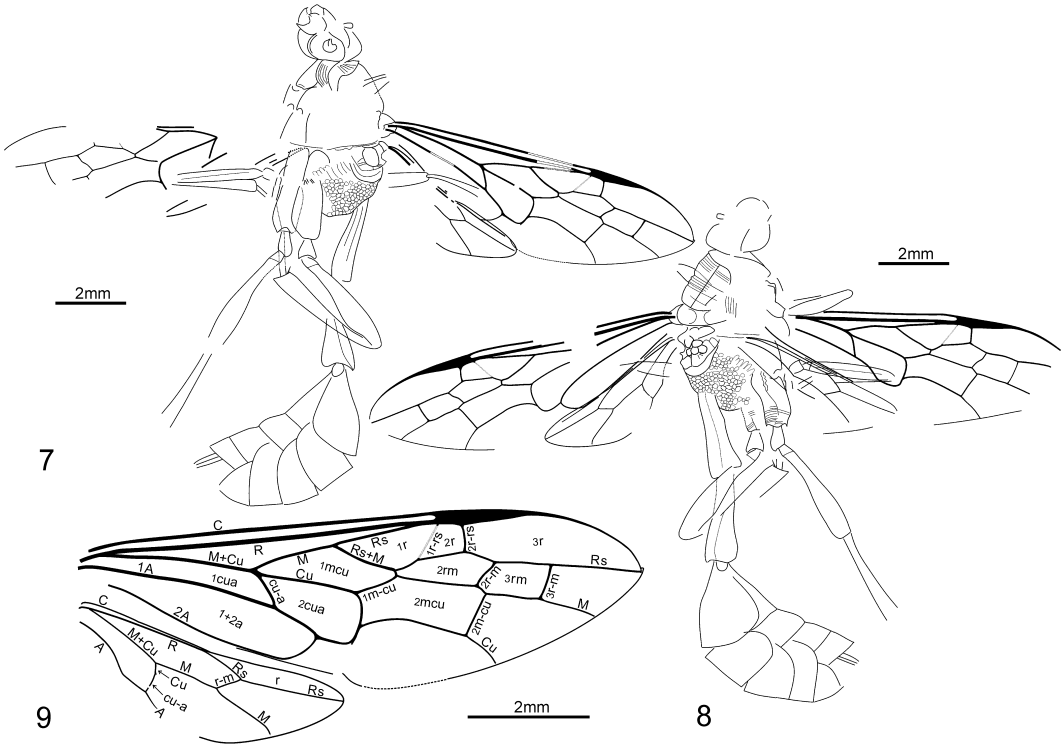
(Figs 7-15)

Type material. – Holotype NND0613-0614/NIGP 143694-143695 part and counterpart, in slightly ventrolateral and dorsolateral aspect, respectively; female with antennae missing, legs incomplete and wings slightly damaged.

Etymology. – Latin *exquisitus*, exquisite.

Description. – Brown in colour. Head medium-sized, and slightly broader than high (excluding mandibles) with occipital carina meeting hypostomal sutures; occipital foramen small. Pronotum comparatively long and ridged. Mesonotum with mesoscutum transversely ridged, and 3 times as long as scutellum; median mesocutal sulcus distinct. Metanotum about twice as long as mesoscutellum; metapostnotum distinctly shorter than metanotum. Propodeum rounded dorsally and apically, with fine and dense reticula. Fore- and midleg thin and short. Hindleg distinctly larger than midleg with coxa thick; trochanter short and swollen subapically; femur (including trochantellus) 1.3 times as long as first metasomal segment; tibia as long as femur with apical spur short; tarsus incomplete, thin. Forewing with M+Cu fork about midway between wing base and pterostigma; pterostigmal base slightly closer to 2r-rs than to Rs origin; first abscissa of Rs slightly shorter than that of M; 1r-rs spectral, straight, meeting 2Rs (section Rs between Rs+M and 2r-rs) where Rs is geniculate; 2r-rs meeting pterostigma at its basal one-fourth length, and nearly twice as long as pterostigmal width; 3r 1.4 times as long as 1+2r; 1mcu in contact with 2rm by very short 2M; 2rm 0.7 times as long as 1+2r, and 1.5 times as long as 3rm; 2m-cu slightly oblique towards wing base and parallel to 3r-m; cu-a slightly postfurcal, and slightly curved outwards; 1mcu nearly parallelogrammic, about as long as but third-fourths as wide as 2cua distally; 2mcu slightly longer and broader than 1mcu. Hindwing with first abscissa of Rs 1.5 times as long as r-m; r-m 0.4 times as long as section M before r-m; first section of Cu very short and 0.4 times as long as r-m, free Cu extremely short like a stub; cu-a twice as long as first section of Cu. Metasoma with first segment comparatively thin basally, gradually thickened distally, and twice as wide distally as basally; second very similar to first; remaining part about twice as long as second segment, with third tergum as long as second segment and semicircular in lateral aspect. Ovipositor slightly exserted, and damaged apically.

Measurements in mm: head width 1.8; mesosomal length 4.0; forewing length 9.5, width (as preserved) 2.9; hindwing length 4.8, width (as pre-



served) 1.4; first metasomal segment length 2.4, second 2.4, remaining segments (combined) 5.1; ovipositor (as preserved) length 0.6.

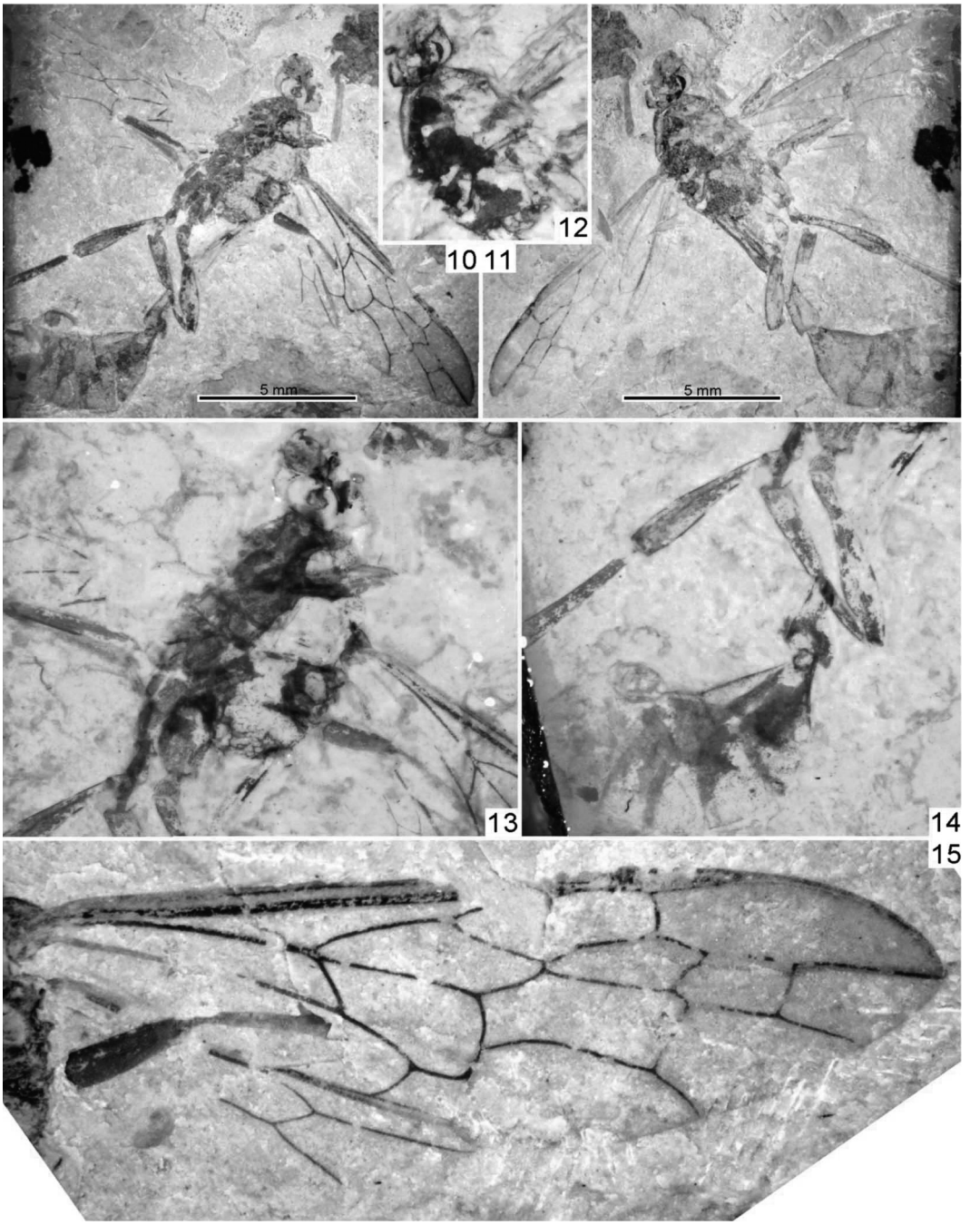
Nevania malleata Zhang & Rasnitsyn, sp. n.

(Figs 16-24)

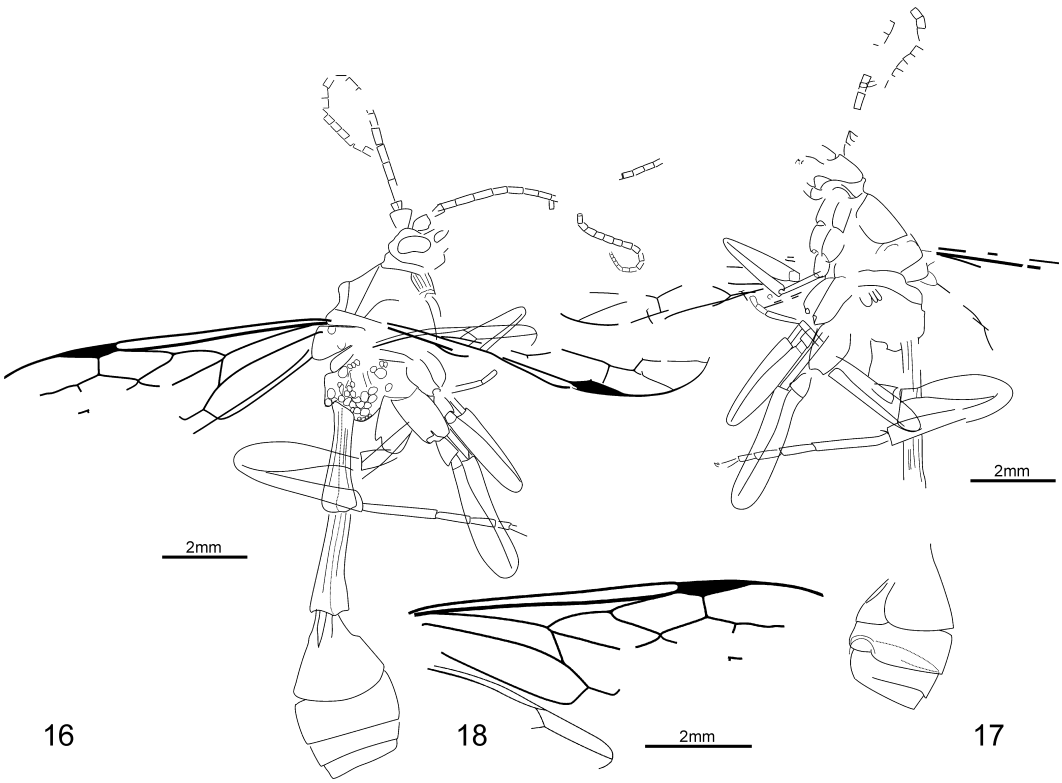
Type material. – Holotype NND2099-2100/NIGP 143696-143697 part and counterpart, in respectively slightly ventrolateral and dorsolateral aspect, sex unknown; comparatively complete wasp with antennae, wings and legs more or less damaged, and metasomal apex missing.

Etymology. – Latin *malleatus*, hammer-like.

Description. – Brown in colour. Head small. Eyes small and kidney-like. Antenna with 28 segments preserved; scape inversely trapezoid and as long as wide; pedicel distinctly narrower than scape, inversely trapzoid and slightly longer than wide; first flagellomere cylindrical, distinctly narrower than pedicel distally, and slightly longer than scape; second through seventh gradually becoming shortened in turn; middle and subdistal flagellomeres as wide as basal ones with each slightly longer than wide; apical ones gradually increasing in thickness with each slightly longer than wide. Pronotum comparatively long. Propleuron longitudinally ridged. Mesonotum with median mesoscutal sulcus distinct; notauli curved laterally. Propodeum protruding backwards, coarsely reticulate dorsally and laterally. Foreleg small. Midleg distinctly longer than foreleg. Hindleg long with coxa large and subcylindrical; trochanter small; femur 1.2 times as long as first metasomal segment; tibia thin and as long as femur (including trochantellus) with apical spur short; tarsus 1.3 times as long as tibia with basitarsomere 0.6 as long as tibia, segmental length ratio from basitarsomere to terminal tarsomere = 1.00 : 0.44 : 0.33: 0.22 : 0.25; only one distal claw preserved, short. Forewing incomplete with M+Cu fork midway between wing base and pterostigma; pterostigmal base 1.6 times as distant to Rs origin as to 2r-rs; first abscissa of Rs about half as long as that of M; 2r-rs meeting pterostigma at its basal one-third length, and 1.2 times as long as pterostigmal width; 2rm in contact



Figs 7-15. *Nevania exquisita* Zhang & Rasnitsyn, sp. n., holotype. 7, line drawing of part, 8, line drawing counterpart, 9, line drawing of wings, 10, general view (part), 11, general view (counterpart), 12, head and mesosoma (counterpart, in alcohol), 13, head and mesosoma (part, in alcohol), 14, metasoma (part, in alcohol), 15, forewing and hindwing (part).



with 1mcu by a point; cu-a oblique, and slightly postfurcal. Hindwing incomplete with C and R distinct, Rs straight beyond r-m. Metasoma with first segment thin basally, slightly becoming thinner distally for basal one-third, gradually increasing in thickness apically for remaining part, and about 1.5 times as broad distally as basally; second similar to first but cylindrical for basal half; third tergum slightly shorter than second segment; fourth distinctly shorter than third, fifth and sixth very short.

Measurements in mm: head width 1.3; antennal length (as preserved) 6.8; mesosomal length 3.9; forewing (as preserved) length 8.3, width 2.3; hindwing length 3.8, width (as preserved) 0.5; first metasomal segment length 2.5, second 2.4, remaining segments (combined) (as preserved) 3.8.

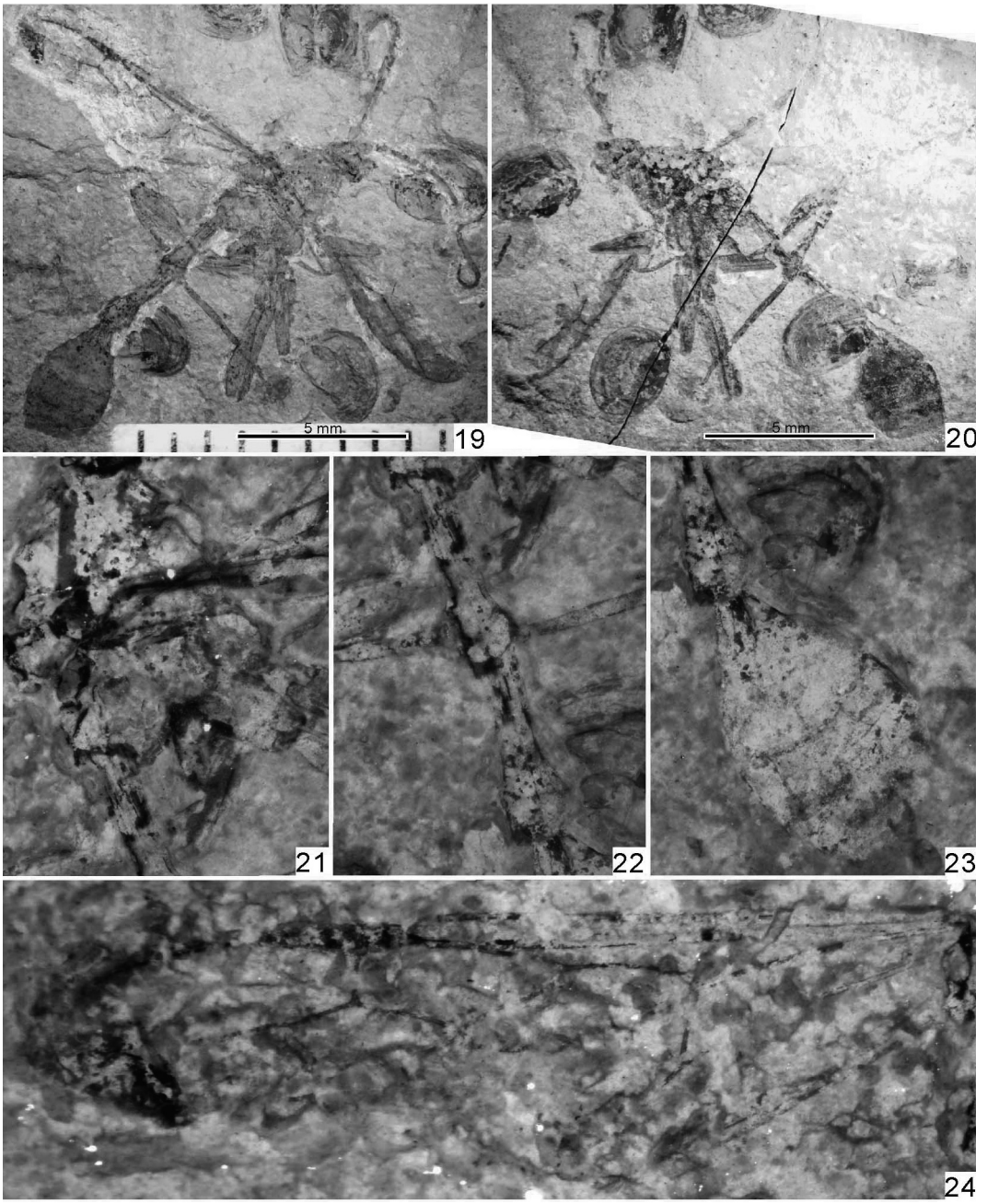
Nevania ferocula Zhang & Rasnitsyn, sp. n.

(Figs 25-30)

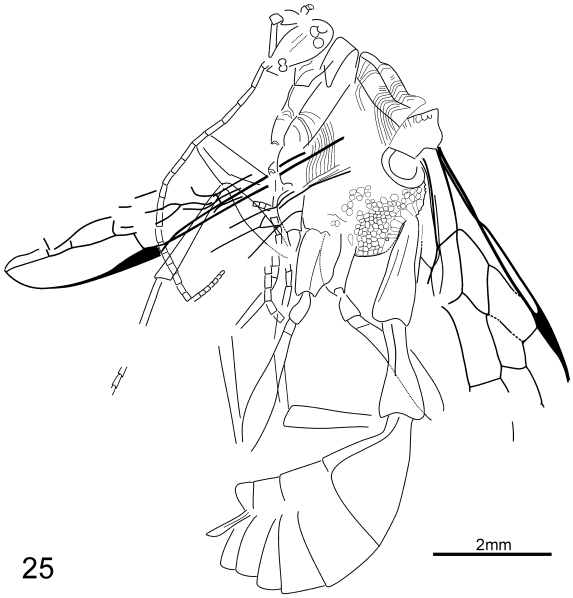
Type material. – Holotype NND2124/NIGP143698, in lateral aspect, female with antennae, wings and legs slightly damaged, and wings incomplete or deformed.

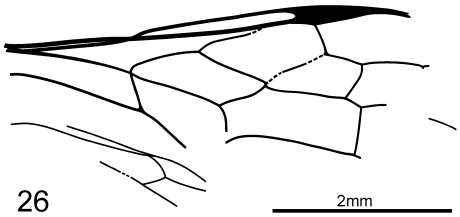
Etymology. – Latin *feroculus*, ferocious.

Description. – Brown in colour. Head small, and about twice as high as long. Eyes indistinguishable; ocelli large with hind two distant to each other but very close to fore one. Antenna at least 29-segmented; scape damaged basally, and longer than wide; pedicel distinctly narrower than scape distally, and slightly longer than wide; first flagellomere subcylindrical, distinctly thinner than pedicel apically, and four times as long as wide; second (?) only distinguishable apically; third to sixth subequal in length, and 0.6 as long as first; remaining flagellomeres gradually becoming short in turn, but each at least longer than wide. Pronotum comparatively long. Mesoscutum transversely and curvedly ridged, and twice as long as scutellum. Mesopleuron with curved ridges. Metanotum about as long as mesoscutellum; metapostnotum very short. Propodeum rounded dorsally and apically, with fine and dense reticula dorsally and lat-



Figs 16-24. *Nevania malleata* Zhang & Rasnitsyn, sp. n., holotype. 16, line drawing of part, 17, line drawing of counterpart, 18, line drawing of wings, 19, general view (part), 20, general view (counterpart), 21, mesosoma (part, in alcohol), 22, two basal metasomal segments (part, in alcohol), 23, metasoma beyond first segment (part, in alcohol), 24, forewing and hindwing (part, in alcohol).





erally. Fore- and midleg small. Hindleg distinctly longer than midleg with coxa thick basally and gradually becoming thin distally, and 1.7 times as long as mid coxa; trochanter small; femur 1.3 times as long as first metasomal segment, gradually thickened subapically; tibia as long as femur; tarsus incomplete. Forewing with M+Cu fork slightly closer to wing base than to pterostigma; pterostigmal base 1.5 (?) times as distant to Rs origin as to 2r-rs; first abscissa of Rs about as long as that of M; 2r-rs meeting pterostigma at its basal one-fourth length, and nearly twice as long as pterostigmal width; 3r 1.7 times as long as 1+2r; 2rm in contact with 1mcu by extremely short 2M; 2rm two-thirds as long as 1+2r; 1mcu parallelogrammic, and two-thirds as long as 2mcu; cu-a oblique and interstitial. Hindwing incomplete with C and R distinct, r-m about as long as first abscissa of Rs. Metasoma with first segment thin basally, gradually increasing in thickness distally, and about 3 times as thick distally as basally; second slightly shorter than first, distinctly thinner basally than first distally, and cylindrical for basal one-third, gradually becoming thickened distally for remaining part, and twice as thick distally as basally; third tergum slightly longer than second segment; fourth half as long as third, fifth 0.7 times as long as fourth, remaining terga distinctly short. Ovipositor slightly exserted.

Measurements in mm: head length 0.6; antenna length (as preserved) 6.7; mesosomal length 3.3; forewing (as preserved) length (up to apex of cell 3r) 5.8, width 1.7; hindwing (as preserved) length 2.7, width 0.6; first metasomal segment length 1.8, second 1.6, remaining segments (combined) 4.1; ovipositor length 0.8.

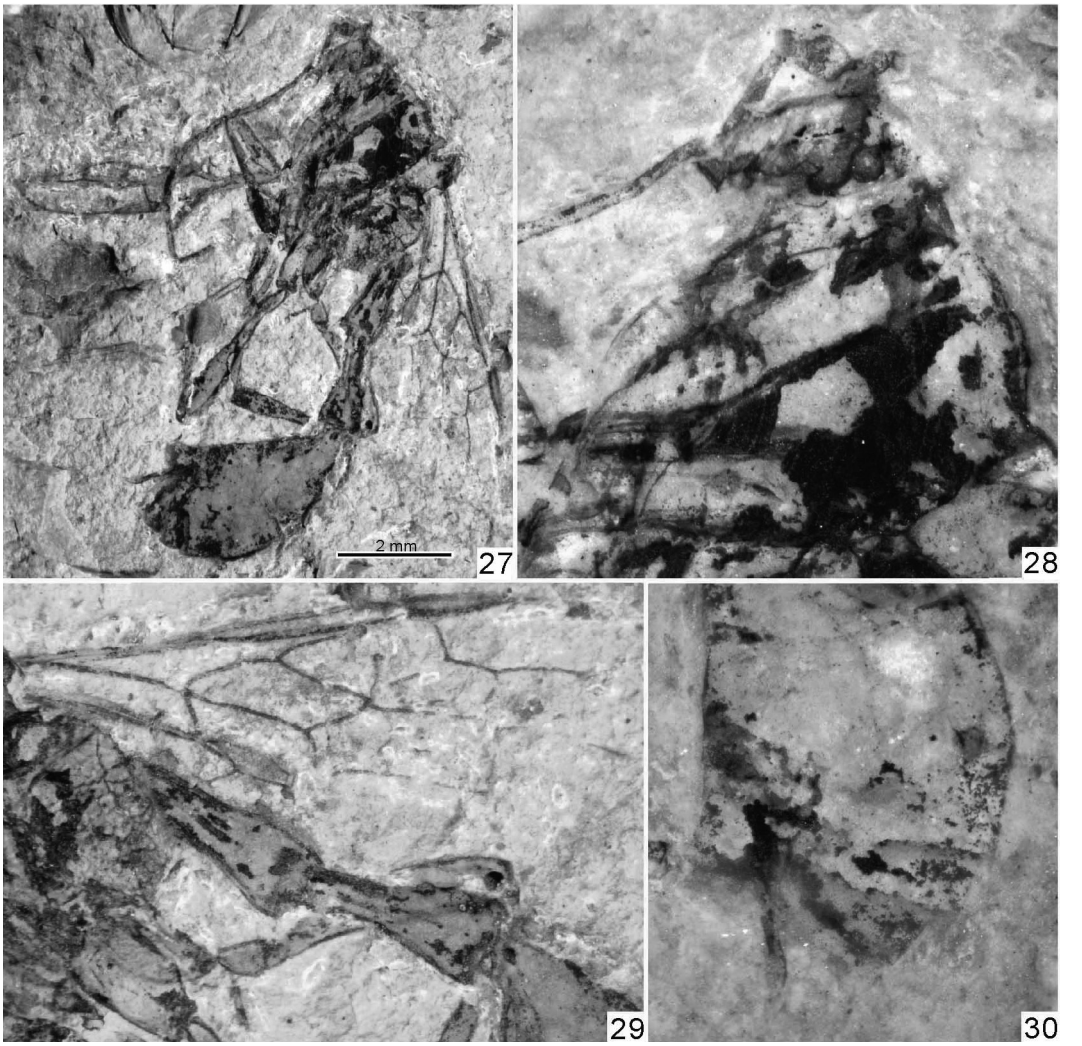
Nevania retenta Zhang & Rasnitsyn, sp. n.

(Figs 31-36)

Type material. – Holotype NND0815/NIGP143699, in dorsoventral aspect, poorly preserved female with head, antennae, mesosoma, legs and wings damaged.

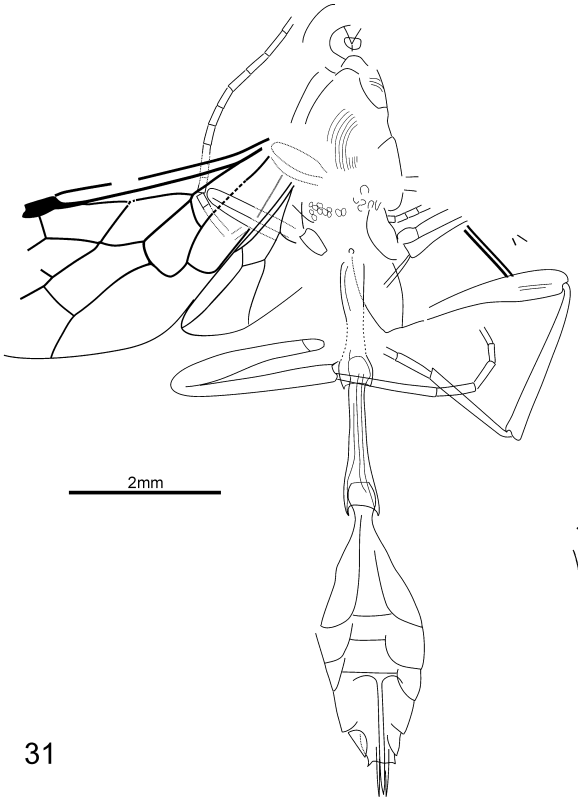
Etymology. – Latin- *retentus*, retentive.

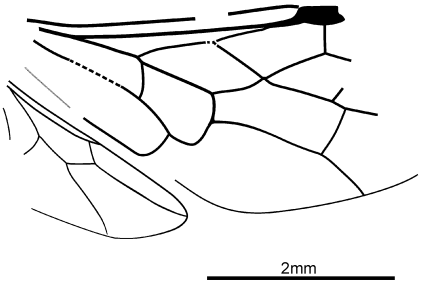
Description. – Brown in colour. Head with occipital foramen small; occipital carina meeting hypostomal suture. Antenna with only 14 basal flagellomeres preserved, each being subcylindrical; first preserved segment distinguishable distally; second four times as long as wide, remaining segments gradually becoming shortened in turn but each at least longer than wide. Mesopleuron with arched ridges. Fore femur short. Midleg longer than foreleg. Hind leg with coxa thick basally and gradually decreasing in thickness apically for distal half; femur 1.3 times as long as first metasomal segment; tibia thin, and as long as femur (including



Figs 25-30. *Nevania ferocula* Zhang & Rasnitsyn, sp. n., holotype. 25, line drawing entire specimen, 26, line drawing of wings. 27, general view, 28, head and mesosoma partly (in alcohol), 29, wings, distal mesosoma and two basal metasomal segments (in alcohol), 30, metasomal apex and ovipositor (in alcohol).

trochantellus), apical spur short; tarsus damaged apically, and at least 1.3 times as long as tibia with basitarsomere 0.6 times as long as tibia, second tarsomere 0.4 times as long as basitarsomere, third 0.77 as long as second, fourth 0.6 as long as third, terminal incomplete. Forewing incomplete with M+Cu fork much closer to wing base than to pterostigma; pterostigmal base slightly closer to 2r-rs than to Rs origin; first abscissa of Rs 0.7 times as long as that of M; 2r-rs vertical and 1.5 times as long as pterostigmal width; 2rm not in contact with 1mcu; 2rm two-thirds as long as 1+2r; 2m-cu slightly curved outwards; cu-a slightly postfurcal, and slightly curved outwards; 1mcu quadrate, about as long as but slightly narrower than cua distally; 2mcu 1.5 times as long as, and slightly broader than 1mcu. Hindwing with r-m slightly longer than first abscissa of Rs, and 0.6 times as long as section M before r-m; Cu+cu-a unpreserved distally. Metasoma with first segment





Figs 31-36. *Nevania retenta* Zhang & Rasnitsyn, sp. n., holotype. 31, line drawing of entire specimen, 32, line drawing of wings. 33, general view, 34, metasoma beyond first metasomal segment (in alcohol), 35, head and mesosoma (in alcohol), 36, forewing and hindwing (in alcohol).

thin basally, subcylindrical for basal one-third, probably becoming thinner submedially, and swollen distally; second slightly thinner basally than first basally, cylindrical for basal half, and gradually becoming thickened apically for distal half; remaining segments (combined) spindle-like with third tergum about as long as second segment. Ovipositor slightly exserted.

Measurements in mm: head width (as preserved) 0.8; antenna length (as preserved) 3.5; mesosomal length 2.5; forewing length (as preserved) 4.5, width 2.2; hindwing (as preserved) length 2.5, width 1.0; first metasomal segment length 1.6, second 1.6, remaining segments (combined) 3.4; ovipositor length 1.6, exerted for 0.4.

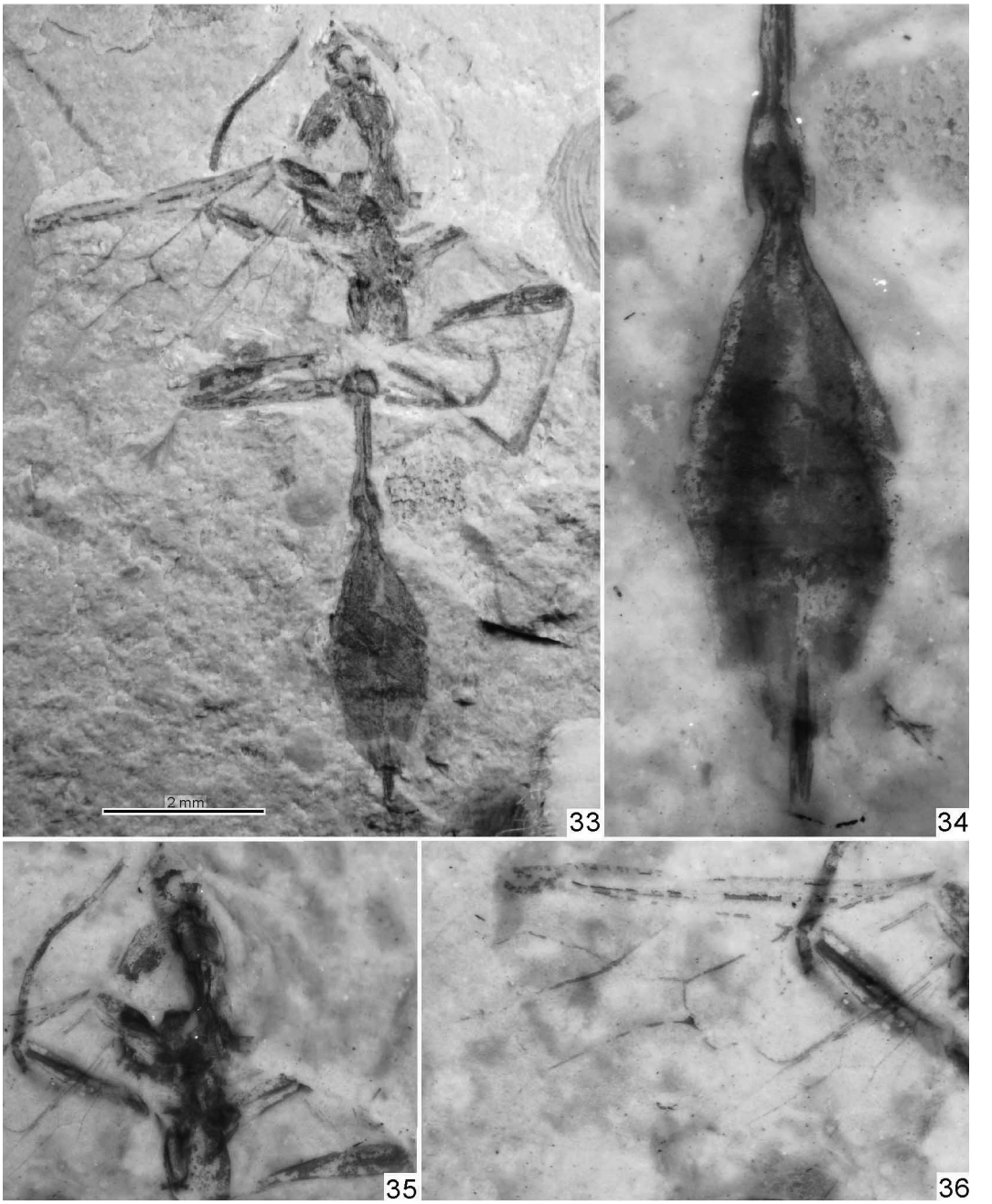
Nevania delicata Zhang & Rasnitsyn, sp. n.

(Figs 37-43)

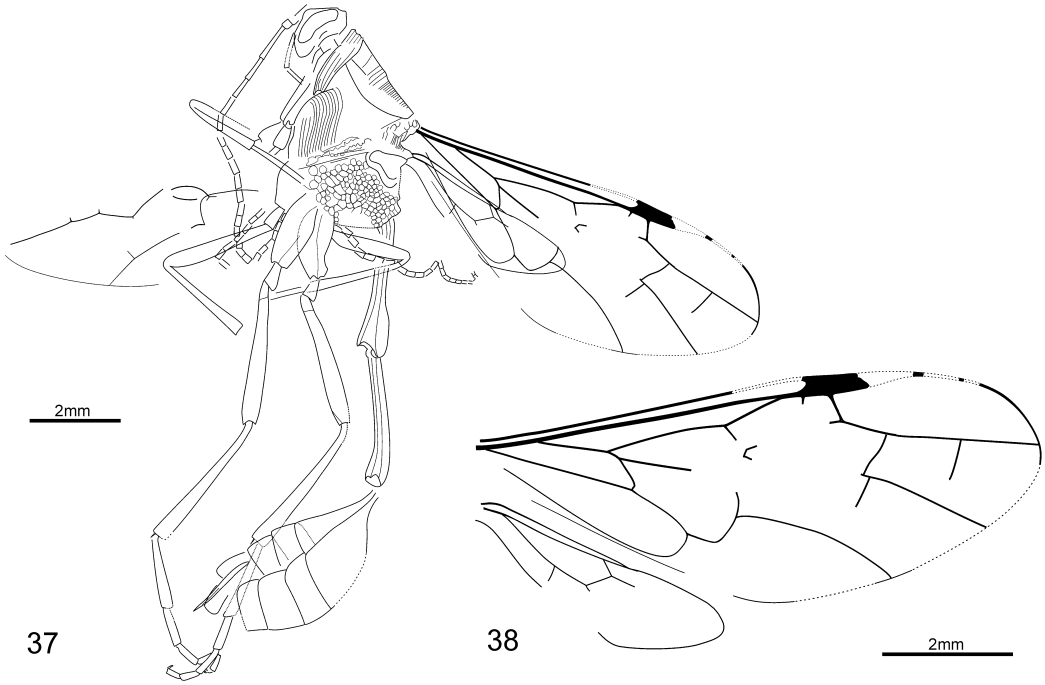
Type material. – Holotype NND0856/NIGP143700, in lateral aspect, nearly complete female with antennae, wings and legs slightly damaged.

Etymology. – Latin *delicatus*, delicate, tender.

Description. – Brown in colour. Body slender. Head small, and nearly twice as high as long. Eyes large, long kidney-shaped. Antenna with 31 segments preserved; scape poorly preserved; pedicel broad, as long as wide; first flagellomere distinctly thinner basally than pedicel, slightly gradually thickened apically, 4.5 times as long as pedicel; second and third similar to first in form with second, 0.7 times as long as first, third 0.55; fourth cylindrical, and as long as third; remaining flagel-



lomeres similar to fourth in form with each twice as long as wide or slightly longer than wide. Pronotum comparatively long, and transversely ridged. Mesonotum with mesoscutum transversely ridged, and greatly longer than scutellum; mesopleuron with densely curved ridges. Propodeum protruding backwards, and coarsely reticulate laterally. Fore leg thin. Midleg distinctly larger than



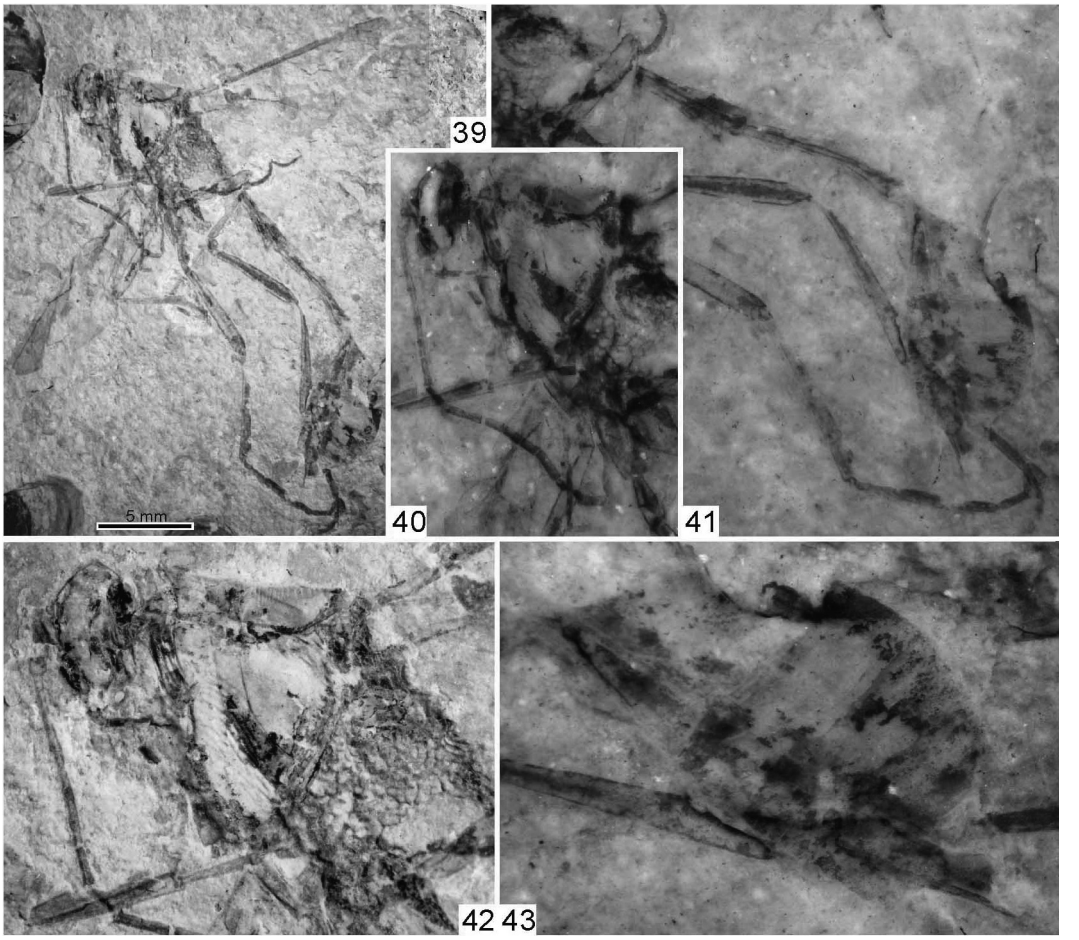
foreleg. Hindleg distinctly longer than midleg with coxa comparatively narrow basally and apically, gradually broadened medially, and 1.8 times as long as mid coxa; trochanter small; femur as long as first metasomal segment; tibia thin, and as long as femur (including trochantellus) with apical spur very short; tarsus 1.2 times as long as tibia with basitarsomere half as long as tibia, segmental length ratio from basitarsomere to terminal tarsomere = 1.00 : 0.43 : 0.37: 0.22 : 0.17; only a distal claw preserved, short. Forewing incomplete with M+Cu fork much closer to wing base than to pterostigma; pterostigmal base about equidistant both to 2r-rs and to Rs origin; first abscissa half as long as that of M; 1r-rs at least like a stub on R; 2r-rs 1.5 times as long as pterostigmal width; 3r nearly twice as long as 1+2r; 1mcu in contact with 2rm by a very short 2M; 2rm slightly longer than 1+2r and 1.5 times as long as 3rm; cu-a quite postfurcal. Hindwing poorly preserved; C and R distinct; r-m 1.5 times as long as first abscissa of Rs, and 0.7 times as long as section M basad of r-m. Metasoma with first segment thin and cylindrical for basal two-thirds, and gradually thickened distally for remaining part; second similar to first, but slightly thickened and curved ventrally for distal one-third; third tergum slightly shorter than second segment, others much shorter. Ovipositor slightly exserted.

Measurements in mm: head length 0.7, antennal length (as preserved) 9.3, mesosomal length 3.9, forewing length 8.6, width 3.3, hindwing length 4.1, width 1.2, first metasomal segment length 3.0, second one length 3.0, remaining segments (combined) length 4.5, ovipositor length 1.6, exserted for 0.3.

Discussion

Two other praeaulacid subfamilies, Praeaulacinae and Anomopterellinae, known mostly from the Upper Jurassic of South Kazakhstan (Rasnitsyn 1972, 1975, 1990b), also occurred in the Daohugou biota but were less diverse (Rasnitsyn & Zhang 2004; Zhang & Rasnitsyn in preparation).

Nevaniinae has a multisegmented (>28) antenna with a short scape as in other Praeaulacidae, being a ground plan character of Evanioidea (Basibuyuk et al., 2002). Similarly, the medially long pronotum and the presence of notauli, median and transscutal sutures on the mesonotum, which are



Figs 37-43. *Nevania delicata* Zhang & Rasnitsyn, sp. n., holotype. 37, line drawing of entire specimen, 38, line drawing of wings. 39, general view, 40, head and mesosoma (in alcohol), 41, metasoma (in alcohol), 42, head and mesosoma to show sculpture, 43, metasoma, beyond second metasomal segment, and ovipositor (in alcohol).

visible in this subfamily and other Praeaulacidae, are also ground plan traits of Evanioidea (Basibuyuk et al., 2002).

The subfamily possesses the following venational characters that are considered plesiomorphic for Evanioidea: (1) the presence of forewing 2A, which is widely seen in Symphyta and Ephialtitidae (Rasnitsyn 1969, 1975), the basalmost Apocrita, but not observed in any known Evanioidea and most Apocrita (except for the most basal extinct taxa and for rudiments in few extant Ichneumonoidea); (2) 11 closed cells in the forewing, which, relative to 10 in Praeaulacinae (Rasnitsyn 1972) and much fewer in rest Praeaulacidae (Rasnitsyn 1975, 1990a,b) and other evanioids, can be treated as a ground plan character; (3) the presence of hindwing C vein, which is widely visible in Symphyta but infrequently in Apocrita (Rasnitsyn 1969, 1975; Ronquist et al. 1999) and represents the ground plan condition within Evanioidea; (4) four closed cells in the hindwing (c, r, rm, mcu), which appears in some Ephialtitidae (Rasnitsyn 1975) but rarely in other Apocrita, and can be treated as a ground plan character. By contrast, the far basal location of M+Cu fork in the forewing is only present in extant and some

Mesozoic evaniids (Rasnitsyn 1975; Zhang & Zhang, 2000; Deans & Huben, 2003; Deans et al. 2004; Zhang et al. 2007), and therefore is derived for Evanioidea. Forewing cell 1+2a, which is absent from any known evanioids owing to the disappearance of vein 2A, is quite high in *Nevania*; this character is barely observed in other Hymenoptera, and is treated autapomorphic for Nevaniinae or probably only for *Nevania*.

Interestingly, this subfamily has a metasoma with the two basal metasomal segments tubular and the rest less modified. A tubular first metasomal segment is widely visible in Apocrita, and even, within the Evanioidea, in Evaniidae (Deans & Huben 2003) and some Praeaulacinae (*Evanigaster* and *Evaniops*; Rasnitsyn 1972). On the contrary, that both the first and second segments are all tubular is very rare in Hymenoptera, being observed only in the extant Mymarommatidae (Rasnitsyn 1988) and extinct Serphitidae (Kozlov & Rasnitsyn 1979; Rasnitsyn 1988). However, these small wasps are not closely related to Evanioidea. Hence, the presence of two tubular basal metasomal segments is exceptional and is considered autapomorphic for Nevaniinae /*Nevania*.

Nevaniinae has a short and slightly exserted ovipositor as in extant Evaniidae. A long and obviously exserted ovipositor is widely present in Evanioidea, including Praeaulacidae Praeaulacinae and Cretocleistogastrinae (Rasnitsyn 1972, 1990a,b), Gasteruptiidae *s.l.* Aulacinae, partly Gasteruptiinae, Bassinae and Kotujellitinae (Rasnitsyn 1975, 1991; Gauld & Bolton 1996; Rasnitsyn et al. 1998), Andreneliidae (Rasnitsyn & Martínez-Delclòs 2000) and some Mesozoic evaniids (Basibuyuk et al. 2000; Deans et al. 2004; Zhang et al. 2007). In Anomopterellinae, the ovipositor is short but exserted well beyond the apex of metasoma (Rasnitsyn 1975). Therefore the short and slightly exserted ovipositor can be considered derived for both Evanioidea and Praeaulacidae.

The discussion above shows that Nevaniinae has a combination of plesiomorphic and apomorphic characters and additionally a few autapomorphies. However, the rich venation indicates that this subfamily probably represents an early clade of the Praeaulacidae and the Evanioidea has an ancestor at least as venationally plesiomorphic as basal Ephialtitidae.

For the genus *Nevaniia*, some characters are considered plesiomorphic including: (1) the appearance of forewing crossvein 1r-rs, which, shown by *N. exquisita* (Figs 7-15) and *N. delicata* (Figs 37-43) although vestigial, is extensively visible in Symphyta and rudimentarily in some Apocrita, e.g. some Ephialtitidae (Rasnitsyn 1975), and can be considered a ground plan trait; (2) forewing cell 1mcu in contact with 2rm (Basibuyuk et al. 2002), which is visible in *Nevania* except *N. retenta* (Figs 31-36); (3) postfurcal forewing crossvein cu-a, which is observed in *Nevania* except *N. ferocula* (Figs 25-30), widely seen in Symphyta, and can be treated as a plesiomorphic character; (4) slightly conical dorsoposterior face of the propodeum (Deans et al., 2004), which is exhibited in *N. malleata* (Figs 16-24) and *N. delicata* (Figs 37-43). These conditions show that *N. delicata* possesses less derived characters than its congeners, and probably occupies the most basal position of the clade *Nevania.* On the other hand, this genus also shows several derived characters: the straight forewing Rs, which, unlike most Evanioidea, is bent neither at 3r-m nor beyond it, and straight hindwing M between M+Cu and r-m (on the contrary, M is bent in less modified Praeaulacinae *Praeaulacus* like in Symphyta, Ephialtitidae and many Aculeata.

Like extant aulacines, wasps parasitizing endoxylous hosts usually have strong transverse sculpture on the mesoscutum, which perhaps aids the wasp in egressing from the pupation site (Quicke 1997). Nevaniines possess transverse ridges not only on the mesoscutum but also on the pronotum, and even have arched ridges on mesopleura at least visible in *Nevania*, which strongly suggests that they pupated in wood and, by inference, were parasitoids of wood-boring insects. Aulacines possess a quite long ovipositor used for locating eggs of their hosts in bark crevices and laying eggs in (Jennings & Deans 2006). The Nevaninae, however, appears to have a very short ovipositor, implying that eggs of its hosts were much easier to reach, and probably very close to the surface of the bark. Therefore, the host was probably not a horntail (Hymenoptera: Siricidae), whose modern relatives usually place their eggs deep into wood, but a beetle who normally oviposited less deep leaving eggs available for parasites with the ovipositor as long as in *Nevania*. It was the eclosed larva which burrowed deep into wood bringing its parasite there.

For each species of *Nevania*, respectively between the first and second metasomal segments and between the second and third, there apparent-

ly exists an articulation suggested by the swollen ends of the first and second metasomal segments, which probably made the corresponding metasomal segments nimbly movable, at least forwards and backwards, deduced from their preservation state. However, such a long two-segmented petiole with a highly movable articulation in the middle and at both of its ends has yet to be observed in other insects and, at present, it is difficult to decide its function, especially in oviposition.

Metasomal morphology of *Nevania* shows apomorphies similar to those known in Evaniidae, viz., the tubular first metasomal segment, short ovipositor and ball-and-socket articulation between the first and second metasomal segments, with the former forming the socket, and the latter the ball (cf. Figs 31, 33). Additionally, *Nevania* is similar to the most advanced (Cainozoic) Evaniidae in having forewing with M+Cu fork shifted far basad in respect to pterostigma. We do not consider these similarities as undoubted synapomorphies for the following reasons. Some older Evaniidae (*Mesevania* Basibuyuk et al., 2000 from the mid-Cretaceous Burmese amber and *Eovernevania* Deans in Deans et al., 2004 from the Lower Cretaceous Lebanese amber) have a long ovipositor indicating that this character state was present in the ground plan of the family. Furthermore, the ball-and-socket articulation between the first and second metasomal segments is apparently not unique for *Nevania* and Evaniidae: Mymarommatidae (Gibson, 1986: Fig. 36), Serphitidae, Roproniidae, Heloridae, Monomachidae and Chalcididae (APR, personal observation) resemble *Nevania* and Evaniidae in that aspect. The most important, however, is that, to hypothesize synapomorphy of *Nevania* and Evaniidae in the above character states, we should hypothesize homoplastic nature of all apomorphic character states that Evaniidae have in common with Gasteruptiidae s.l., viz., pronotum short along midline, medial mesoscutal sulcus lost, and hindwing with no cell enclosed. Additionally this hypothesis infers either independent shortening of the ovipositor in *Nevania* and in Evaniidae other than *Mesevania* and *Eovernevania,* or its independent elongation of these two distantly related genera. Treating the basal position of the M+Cu fork as the synapomorphy of *Nevania* and Cainozoic Evaniidae means inferring still wider array of homoplasies gained independently by the Mesozoic and Cainozoic Evaniidae.

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Andrenelia assigning it to various nodes within the resultant tree including a position far from Evaniidae (fig. 11). Consequently, the phylogenetic position of the Andreneliidae could not be decided with certainty in the analyses performed by Basibuyuk et al. (2002). It cannot be ruled out that Andreneliidae should be included in Evaniidae, but the evidence is inconclusive yet. Following a conservative approach we prefer to recognise Andreneliidae as a family until more information accumulates. Regarding Baissinae, neither the present authors nor Grimaldi & Engel (2005) or Engel (2006) were able to identify any autapomorphy of Baissinae separating them from Gasteruptiinae or Aulacinae. We therefore retain the Baissinae as a subfamily within Gasteruptiidae s. lat.

The Cretevaniidae from the Cretaceous of Eurasia has previously been considered a separate family in Evanioidea (Rasnitsyn 1975, 1991; Jarzembowski 1984; Rasnitsyn et al. 1998; Zhang & Zhang 2000), but its constituent genera are now included in the Evaniidae (Basibuyuk et al. 2002; Zhang et al. 2007).

The Praeaulacidae consists of three subfamilies, Cretocleistogastrinae, from the Lower Cretaceous of East Asia and Australia (Rasnitsyn 1990a,b), Praeaulacinae and Anomopterellinae, from the Upper Jurassic of South Kazakhstan (Rasnitsyn 1972, 1975, 1990b), and has been proposed as representing the ancestral group of the whole Evanioidea (Rasnitsyn 1988).

Here a new subfamily is established and assigned to Praeaulacidae based on specimens from the Daohugou beds in Inner Mongolia, China.

Materials and methods

The present publication is based on six recently discovered specimens from the Middle Jurassic of Daohugou near Chifeng City in Inner Mongolia, China. The Daohugou beds yield diverse and abundant insects as well as other fossils, and are generally considered to be Middle Jurassic in age (for details, see Wang et al. 2006). These specimens described below are housed in the Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences.

Observations of these specimens were made under a light microscope (NIKON SMZ1000) and photographs were prepared with a digital camera (DXM1200) connected to this microscope at the State Key Laboratory of Palaeobiology and Stratigraphy, Nanjing. Line drawings were made by Zhang using the software CorelDRAW 9.

Systematic palaeontology

Superfamily Evanioidea Latreille, 1802

Family Praeaulacidae Rasnitsyn, 1972

Subfamily Nevaniinae Zhang & Rasnitsyn, subfam. n.

Type genus. – *Nevania* gen. n. (from the Middle Jurassic of Daohugou, Inner Mongolia, China).

Diagnosis. – Head small to medium-sized with occipital foramen closed ventrally. Antenna filiform and polymerous with scape short. Pronotum comparatively long, not short medially. Pronotum and mesonotum transversely ridged. Mesonotum with median and transscutal sutures, and notauli present. Metapostnotum present. Forewing venation complete with 2-3rm and 2m-cu tubular; basal vein (Rs&M) meeting M+Cu far basad of pterostigma; cu-a postfurcal (meeting Cu beyond M+Cu fork) or interstitial (meeting M+Cu just at its fork into M and Cu); 2A present. Hindwing venation complete with C, r-m and cu-a present; r closed. Metasoma attached to propodeum about halfway between metapostnotum and hind coxa, with two basal metasomal segments tube-like. Ovipositor short and slightly exserted.

Remarks. – The high attachment of mesosoma to the metasoma undoubtedly places this group of wasps in the Evanioidea. Furthermore some important characters, e.g. antennae with usually above 28 segments, complete wing venation, and the presence of notauli, median and transscutal sutures on the mesonotum, indicate their similarity to (symplesiomorphy with) Praeaulacidae and separate them from the rest Evanioidea. Nevertheless, any known subfamily within Praeaulacidae is not in a position to accommodate them, and therefore it is necessary to establish a new subfamily for them.

The new subfamily differs from other Praeaulacidae in having a forewing with 2A present, and M+Cu fork far basad of pterostigma, a metasoma with two basal segments tubular, and a very short ovipositor (slightly exserted). It further differs from Praeaulacinae in having a hindwing with C present; from Anomopterellinae in having a

forewing with two r-m crossveins present and two mcu cells normal in width; and from Cretocleistogastrinae in having complete wing venation.

Composition. – The type genus only.

Genus *Nevania* Zhang & Rasnitsyn, gen. n.

Type species. – *N. robusta* Zhang & Rasnitsyn, sp. n. by present designation.

Etymology. – Generic name is from *ne-* (Greek for no) and generic name *Evania*. Gender feminine.

Diagnosis. – Known from female and specimens where the sex could not be determined. Medium-sized (body about 10 to 18 mm in length). Antenna inserted far above mandibles, usually consisting of over 28 segments, distinctly longer than head and mesosoma combined; flagellum slightly and gradually increasing in thickness submedially, with first flagellomere longer than any other antennal segment. Occipital carina present but not circular. Mesosoma short and slightly high; pronotum and mesoscutum transversely, and mesopleura archedly ridged; metapostnotum very short; propodeum dorsally and laterally reticulate. Legs slender; midcoxa much closer to hind coxa than to fore coxa, and touching hind coxa when projecting posteriorly; trochantellus present; hind tibia possessing an apical spur. Forewing venation complete with 11 closed cells; costal area narrow; pterostigma narrow basally, gradually widened distally until its meeting 2r-rs before pterostigmal midlength, and then gradually narrowed apically; Rs&M more or less straight, not strongly angled at the junction of Rs and M, as long as or longer than M+Cu, meeting R well before pterostigma, first abscissa of Rs at most as long as that of M; Rs nearly straight beyond 2r-rs; 1r-rs spectral or completely absent; 2r-rs slightly shorter than maximal width of 2rm; 2m-cu slightly distad of 2r-m; cu-a interstitial or slightly postfurcal; 2cua large, distinctly longer than wide, and broadened apically; 2A complete; cell 1+2a much wider than 2cua basally but slightly narrower than that distally. Hindwing venation complete with C tubular; Rs reaching wing apex; r closed; M reaching wing margin; r-m strongly inclined towards wing base; first section of Cu smoothly connected with cu-a, free Cu vestigial or completely absent; A distinctly angulate quite basad of cu-a (indicating a position of disappeared crossvein a_1-a_2), free A distinct. Metasoma with first and second segments long tube-like, swollen apically, and subequal in length; remaining part generally not longer than first and second segments combined. Ovipositor short, slightly protruding out of metasomal apex.

Included species. – Six species including the type.

Remarks. – Comparison of the included species is presented in the key below.

Key to species assigned to *Nevania* Zhang & Rasnitsyn, gen. n.

1. Forewing with cu-a interstitial; first abscissa of Rs subequal to that of M in length ..... *N. ferocula* Zhang & Rasnitsyn, sp. n.
– Forewing with cu-a postfurcal; first abscissa of Rs shorter than that of M 2
2. Forewing with 1r-rs spectral or rudimentary..... 3
– Forewing with 1r-rs absent..... 4
3. Hindwing with r-m shorter than first abscissa of Rs; first and second metasomal segments stout..... *N. exquisita* Zhang & Rasnitsyn, sp. n.
– Hindwing with r-m longer than first abscissa of Rs; first and second metasomal segments slender ..... *N. delicata* Zhang & Rasnitsyn, sp. n.
4. Forewing with 2rm in contact with 1mcu by a short, second section of M..... *N. robusta* Zhang & Rasnitsyn, sp. n.
– Forewing with 2rm in contact with 1mcu by a point or not in contact with 1mcu 5
5. 2rm in contact with 1m-cu by a point; first and second metasomal segments stout ..... *N. malleata* Zhang & Rasnitsyn, sp. n.
– 2rm not in contact with 1m-cu; first and second metasomal segments slender..... *N. retenta* Zhang & Rasnitsyn, sp. n.

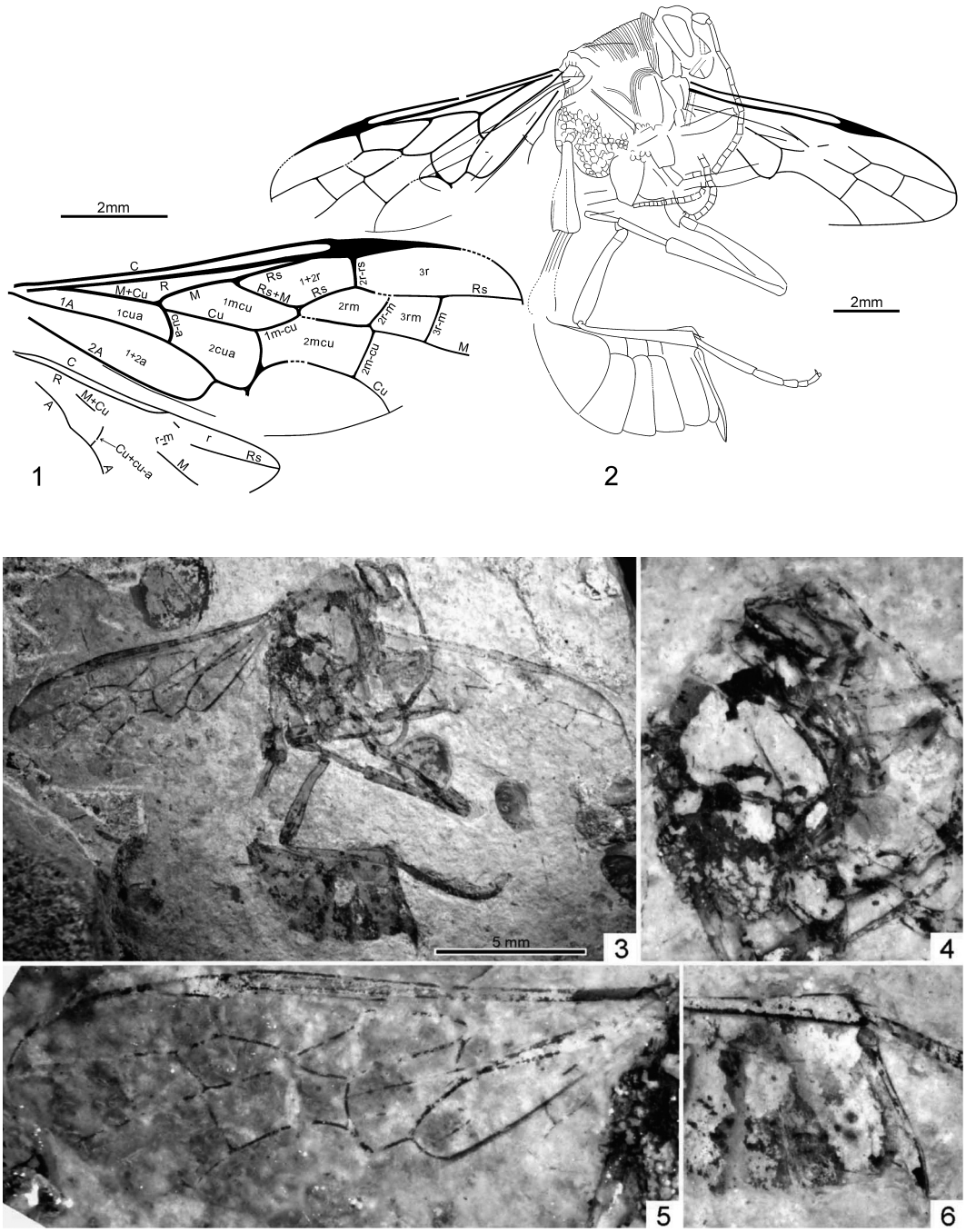
Nevania robusta Zhang & Rasnitsyn, sp. n.

(Figs 1-6)

Type material. – Holotype NND0816/NIGP143693, in lateral aspect, nearly complete female with antennae, wings, legs and second metasomal segment slightly damaged.

Etymology. – Latin *robustus*, strong.

Description. – Brown in colour. Head short, and about twice as high as long. Eyes large, and elongate ovoid. Antenna with 28 segments preserved; scape 1.5 times as long as broad; pedicel distinctly narrower than scape distally, and about as long as wide; first flagellomere cylindrical, as wide as pedicel, and about twice as long as scape; second 0.7 times as long as first, and correspondingly, third 0.6, fourth 0.53, fifth 0.45, sixth 0.4, seventh 0.35; remaining flagellomeres with each one slightly longer than or as long as broad. Pronotum comparatively long, and transversely ridged.



Figs 1-6. *Nevania robusta* Zhang & Rasnitsyn, sp. n., holotype. 1, line drawing of wings, 2, line drawing of entire specimen, 3, general view, 4, head and mesosoma (in alcohol), 5, forewing and hindwing (in alcohol), 6, metasomal apex and ovipositor (in alcohol).

Mesonotum with mesoscutum finely transversely ridged, and three times as long as scutellum; notauli distinct. Mesopleuron partly archedly ridged. Metanotum about as long as mesoscutellum, metapostnotum short. Propodeum rounded dorsally and apically, with fine and dense reticula. Foreleg thin and short. Midleg larger than foreleg. Hindleg with coxa distinctly larger than midcoxa, thick basally, greatly swollen subbasally, and becoming thin distally; trochanter nearly half as long as coxa; femur elongate, slightly swollen subdistally, and 1.4 times as long as first metasomal segment; tibia thin, as long as femur (including trochantellus), with apical spur comparatively long; tarsus slightly longer than tibia with a short claw preserved, basitarsomere half as long as tibia, segmental length ratio from basitarsomere to terminal tarsomere = 1.00 : 0.48 : 0.22: 0.15 : 0.19. Forewing with M+Cu fork slightly closer to wing base than to pterostigma; pterostigmal base slightly closer to 2r-rs than to Rs origin; first abscissa of Rs 0.7 times as long as that of M; 2r-rs subvertical, meeting pterostigma at its basal one-fourth length, and 1.5 times as long as pterostigmal width; 3r 1.4 times as long as 1+2r; 2rm and 1mcu in contact by a very short, second section of M (2M); 2rm two-thirds as long as 1+2r and 1.3 times as long as 3rm; cu-a slightly postfurcal and curved outwards. Hingwing poorly preserved with free Rs and M distinguishable; Cu+cu-a distinct; free A long. Metasoma with first segment thin for basal one-third, and gradually thickened distally for remaining part; second as long as first, slightly thicker than first basally for basal half, and damaged for distal half; third tergum slightly longer than second segment, and round triangular in lateral aspect; fourth half as long as third, fifth to seventh subequal in length and distinctly shorter than fourth; terminal very short. Ovipositor slightly exserted.

Measurements in mm: head length 1.2; antennal length (as preserved) 8.4; mesosomal length 4.6; forewing length 9.6, width 3.6; hindwing length 5.5, width (as preserved) 1.6; first metasomal segment length 2.7, second 2.6, remaining segments (combined) 6.3; ovipositor length 2.9, exerted for 0.7.

Nevania exquisita Zhang & Rasnitsyn, sp. n.

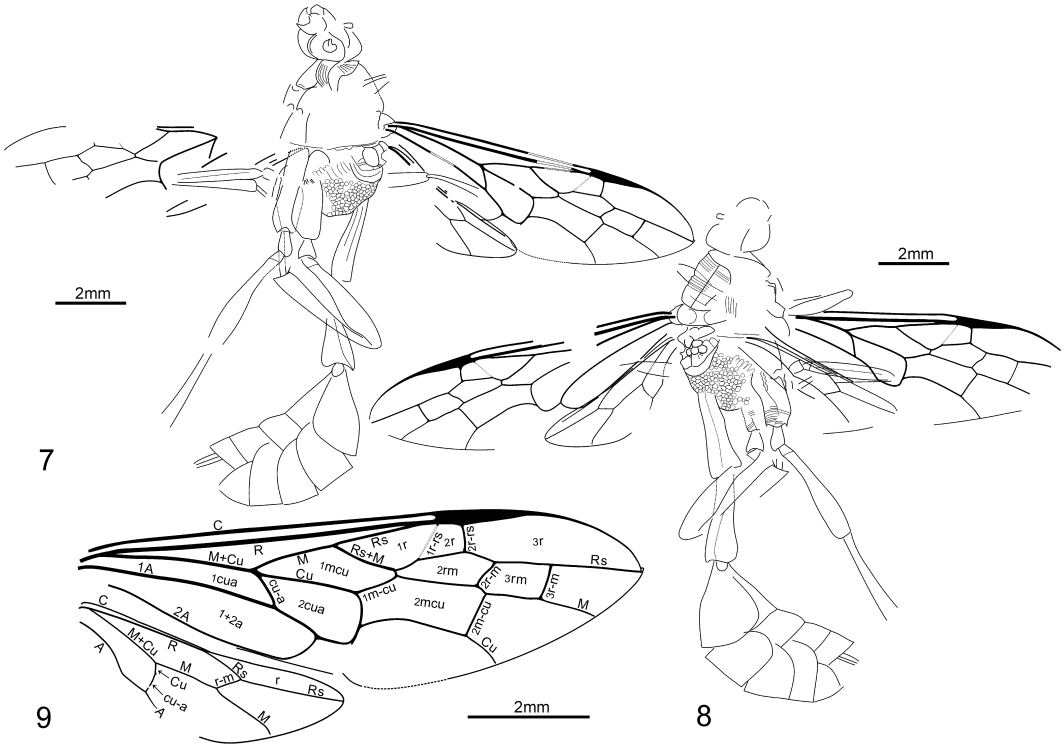
(Figs 7-15)

Type material. – Holotype NND0613-0614/NIGP 143694-143695 part and counterpart, in slightly ventrolateral and dorsolateral aspect, respectively; female with antennae missing, legs incomplete and wings slightly damaged.

Etymology. – Latin *exquisitus*, exquisite.

Description. – Brown in colour. Head medium-sized, and slightly broader than high (excluding mandibles) with occipital carina meeting hypostomal sutures; occipital foramen small. Pronotum comparatively long and ridged. Mesonotum with mesoscutum transversely ridged, and 3 times as long as scutellum; median mesocutal sulcus distinct. Metanotum about twice as long as mesoscutellum; metapostnotum distinctly shorter than metanotum. Propodeum rounded dorsally and apically, with fine and dense reticula. Fore- and midleg thin and short. Hindleg distinctly larger than midleg with coxa thick; trochanter short and swollen subapically; femur (including trochantellus) 1.3 times as long as first metasomal segment; tibia as long as femur with apical spur short; tarsus incomplete, thin. Forewing with M+Cu fork about midway between wing base and pterostigma; pterostigmal base slightly closer to 2r-rs than to Rs origin; first abscissa of Rs slightly shorter than that of M; 1r-rs spectral, straight, meeting 2Rs (section Rs between Rs+M and 2r-rs) where Rs is geniculate; 2r-rs meeting pterostigma at its basal one-fourth length, and nearly twice as long as pterostigmal width; 3r 1.4 times as long as 1+2r; 1mcu in contact with 2rm by very short 2M; 2rm 0.7 times as long as 1+2r, and 1.5 times as long as 3rm; 2m-cu slightly oblique towards wing base and parallel to 3r-m; cu-a slightly postfurcal, and slightly curved outwards; 1mcu nearly parallelogrammic, about as long as but third-fourths as wide as 2cua distally; 2mcu slightly longer and broader than 1mcu. Hindwing with first abscissa of Rs 1.5 times as long as r-m; r-m 0.4 times as long as section M before r-m; first section of Cu very short and 0.4 times as long as r-m, free Cu extremely short like a stub; cu-a twice as long as first section of Cu. Metasoma with first segment comparatively thin basally, gradually thickened distally, and twice as wide distally as basally; second very similar to first; remaining part about twice as long as second segment, with third tergum as long as second segment and semicircular in lateral aspect. Ovipositor slightly exserted, and damaged apically.

Measurements in mm: head width 1.8; mesosomal length 4.0; forewing length 9.5, width (as preserved) 2.9; hindwing length 4.8, width (as pre-



served) 1.4; first metasomal segment length 2.4, second 2.4, remaining segments (combined) 5.1; ovipositor (as preserved) length 0.6.

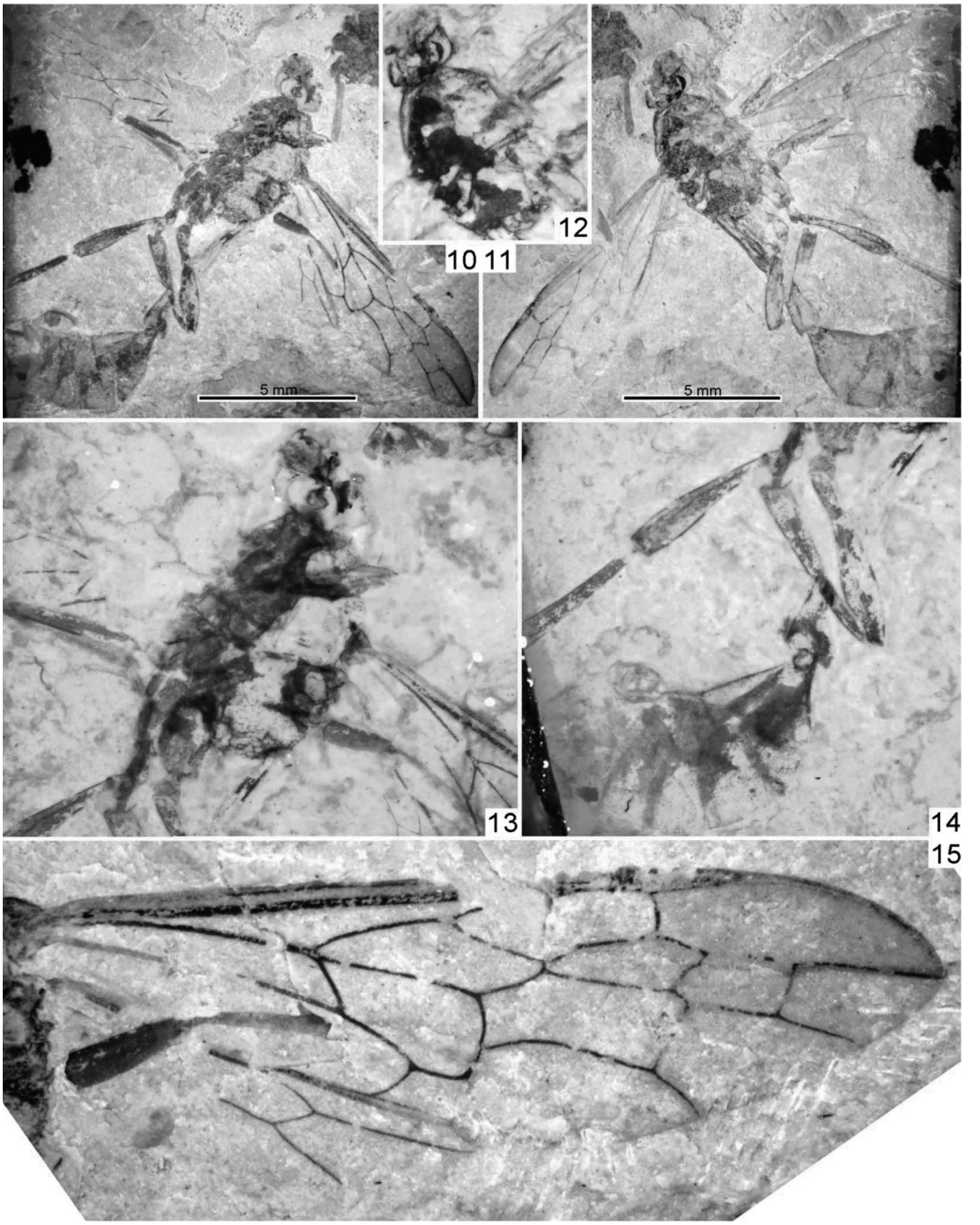
Nevania malleata Zhang & Rasnitsyn, sp. n.

(Figs 16-24)

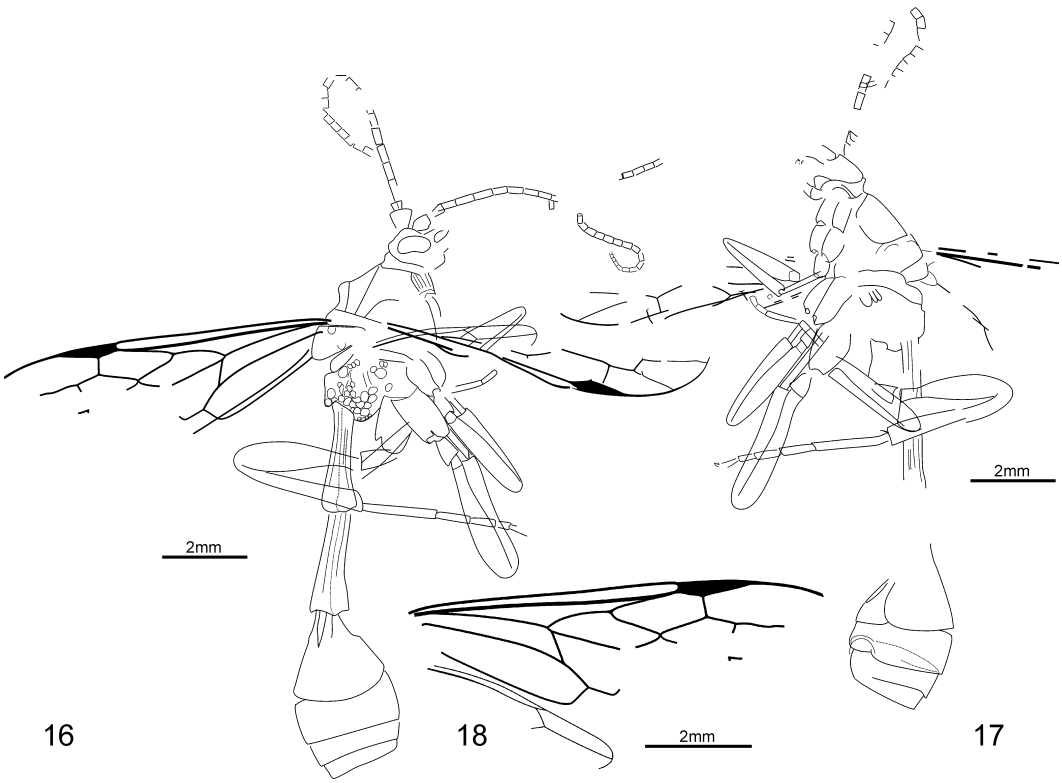
Type material. – Holotype NND2099-2100/NIGP 143696-143697 part and counterpart, in respectively slightly ventrolateral and dorsolateral aspect, sex unknown; comparatively complete wasp with antennae, wings and legs more or less damaged, and metasomal apex missing.

Etymology. – Latin *malleatus*, hammer-like.

Description. – Brown in colour. Head small. Eyes small and kidney-like. Antenna with 28 segments preserved; scape inversely trapezoid and as long as wide; pedicel distinctly narrower than scape, inversely trapzoid and slightly longer than wide; first flagellomere cylindrical, distinctly narrower than pedicel distally, and slightly longer than scape; second through seventh gradually becoming shortened in turn; middle and subdistal flagellomeres as wide as basal ones with each slightly longer than wide; apical ones gradually increasing in thickness with each slightly longer than wide. Pronotum comparatively long. Propleuron longitudinally ridged. Mesonotum with median mesoscutal sulcus distinct; notauli curved laterally. Propodeum protruding backwards, coarsely reticulate dorsally and laterally. Foreleg small. Midleg distinctly longer than foreleg. Hindleg long with coxa large and subcylindrical; trochanter small; femur 1.2 times as long as first metasomal segment; tibia thin and as long as femur (including trochantellus) with apical spur short; tarsus 1.3 times as long as tibia with basitarsomere 0.6 as long as tibia, segmental length ratio from basitarsomere to terminal tarsomere = 1.00 : 0.44 : 0.33: 0.22 : 0.25; only one distal claw preserved, short. Forewing incomplete with M+Cu fork midway between wing base and pterostigma; pterostigmal base 1.6 times as distant to Rs origin as to 2r-rs; first abscissa of Rs about half as long as that of M; 2r-rs meeting pterostigma at its basal one-third length, and 1.2 times as long as pterostigmal width; 2rm in contact



Figs 7-15. *Nevania exquisita* Zhang & Rasnitsyn, sp. n., holotype. 7, line drawing of part, 8, line drawing counterpart, 9, line drawing of wings, 10, general view (part), 11, general view (counterpart), 12, head and mesosoma (counterpart, in alcohol), 13, head and mesosoma (part, in alcohol), 14, metasoma (part, in alcohol), 15, forewing and hindwing (part).



with 1mcu by a point; cu-a oblique, and slightly postfurcal. Hindwing incomplete with C and R distinct, Rs straight beyond r-m. Metasoma with first segment thin basally, slightly becoming thinner distally for basal one-third, gradually increasing in thickness apically for remaining part, and about 1.5 times as broad distally as basally; second similar to first but cylindrical for basal half; third tergum slightly shorter than second segment; fourth distinctly shorter than third, fifth and sixth very short.

Measurements in mm: head width 1.3; antennal length (as preserved) 6.8; mesosomal length 3.9; forewing (as preserved) length 8.3, width 2.3; hindwing length 3.8, width (as preserved) 0.5; first metasomal segment length 2.5, second 2.4, remaining segments (combined) (as preserved) 3.8.

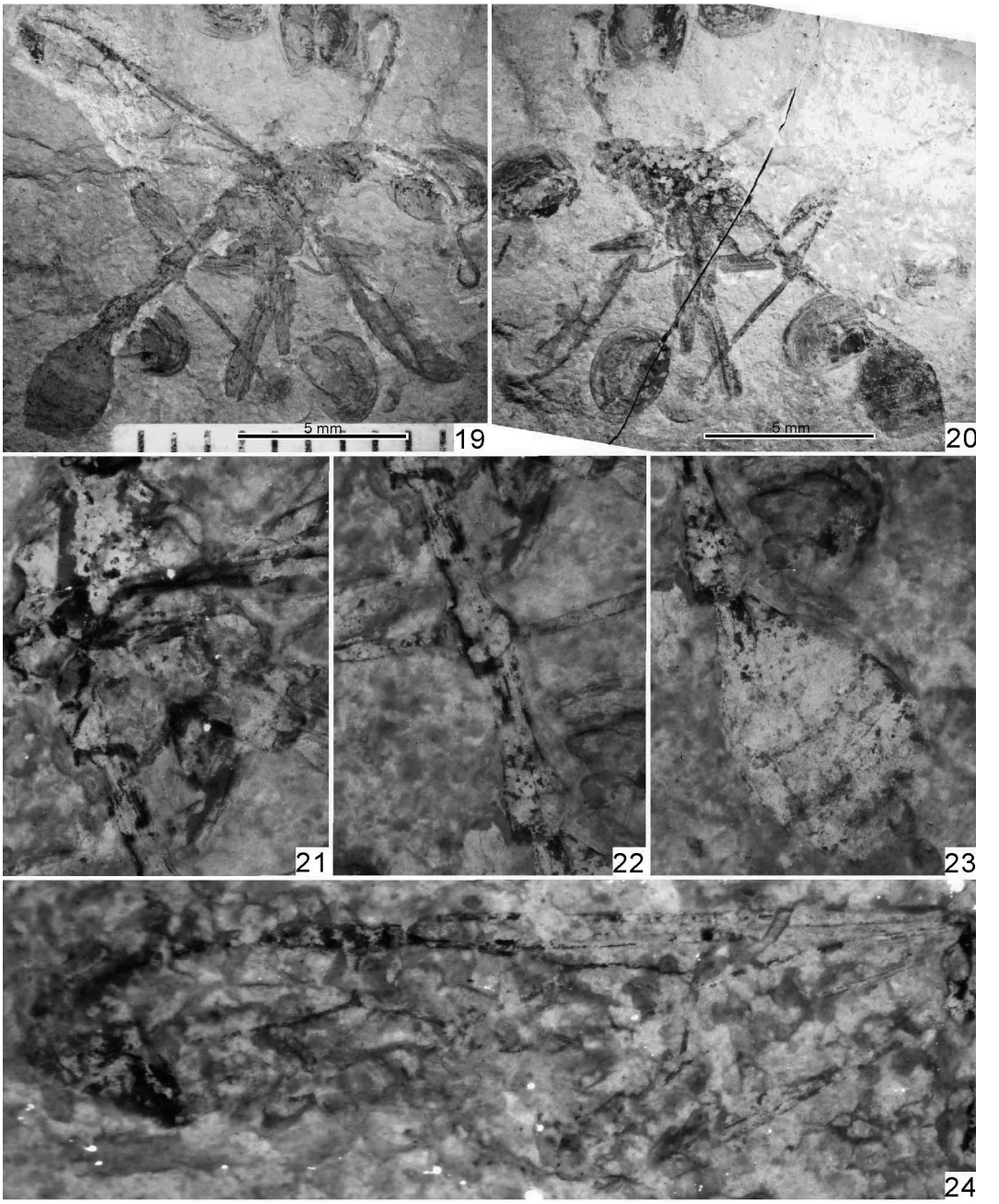
Nevania ferocula Zhang & Rasnitsyn, sp. n.

(Figs 25-30)

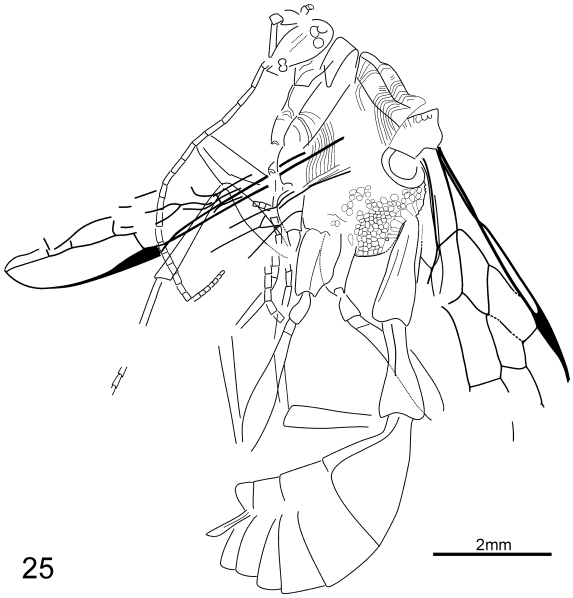
Type material. – Holotype NND2124/NIGP143698, in lateral aspect, female with antennae, wings and legs slightly damaged, and wings incomplete or deformed.

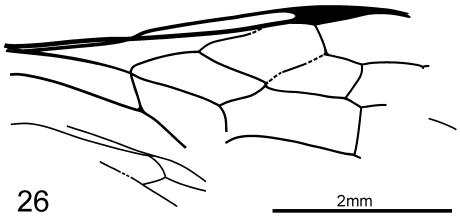
Etymology. – Latin *feroculus*, ferocious.

Description. – Brown in colour. Head small, and about twice as high as long. Eyes indistinguishable; ocelli large with hind two distant to each other but very close to fore one. Antenna at least 29-segmented; scape damaged basally, and longer than wide; pedicel distinctly narrower than scape distally, and slightly longer than wide; first flagellomere subcylindrical, distinctly thinner than pedicel apically, and four times as long as wide; second (?) only distinguishable apically; third to sixth subequal in length, and 0.6 as long as first; remaining flagellomeres gradually becoming short in turn, but each at least longer than wide. Pronotum comparatively long. Mesoscutum transversely and curvedly ridged, and twice as long as scutellum. Mesopleuron with curved ridges. Metanotum about as long as mesoscutellum; metapostnotum very short. Propodeum rounded dorsally and apically, with fine and dense reticula dorsally and lat-



Figs 16-24. *Nevania malleata* Zhang & Rasnitsyn, sp. n., holotype. 16, line drawing of part, 17, line drawing of counterpart, 18, line drawing of wings, 19, general view (part), 20, general view (counterpart), 21, mesosoma (part, in alcohol), 22, two basal metasomal segments (part, in alcohol), 23, metasoma beyond first segment (part, in alcohol), 24, forewing and hindwing (part, in alcohol).





erally. Fore- and midleg small. Hindleg distinctly longer than midleg with coxa thick basally and gradually becoming thin distally, and 1.7 times as long as mid coxa; trochanter small; femur 1.3 times as long as first metasomal segment, gradually thickened subapically; tibia as long as femur; tarsus incomplete. Forewing with M+Cu fork slightly closer to wing base than to pterostigma; pterostigmal base 1.5 (?) times as distant to Rs origin as to 2r-rs; first abscissa of Rs about as long as that of M; 2r-rs meeting pterostigma at its basal one-fourth length, and nearly twice as long as pterostigmal width; 3r 1.7 times as long as 1+2r; 2rm in contact with 1mcu by extremely short 2M; 2rm two-thirds as long as 1+2r; 1mcu parallelogrammic, and two-thirds as long as 2mcu; cu-a oblique and interstitial. Hindwing incomplete with C and R distinct, r-m about as long as first abscissa of Rs. Metasoma with first segment thin basally, gradually increasing in thickness distally, and about 3 times as thick distally as basally; second slightly shorter than first, distinctly thinner basally than first distally, and cylindrical for basal one-third, gradually becoming thickened distally for remaining part, and twice as thick distally as basally; third tergum slightly longer than second segment; fourth half as long as third, fifth 0.7 times as long as fourth, remaining terga distinctly short. Ovipositor slightly exserted.

Measurements in mm: head length 0.6; antenna length (as preserved) 6.7; mesosomal length 3.3; forewing (as preserved) length (up to apex of cell 3r) 5.8, width 1.7; hindwing (as preserved) length 2.7, width 0.6; first metasomal segment length 1.8, second 1.6, remaining segments (combined) 4.1; ovipositor length 0.8.

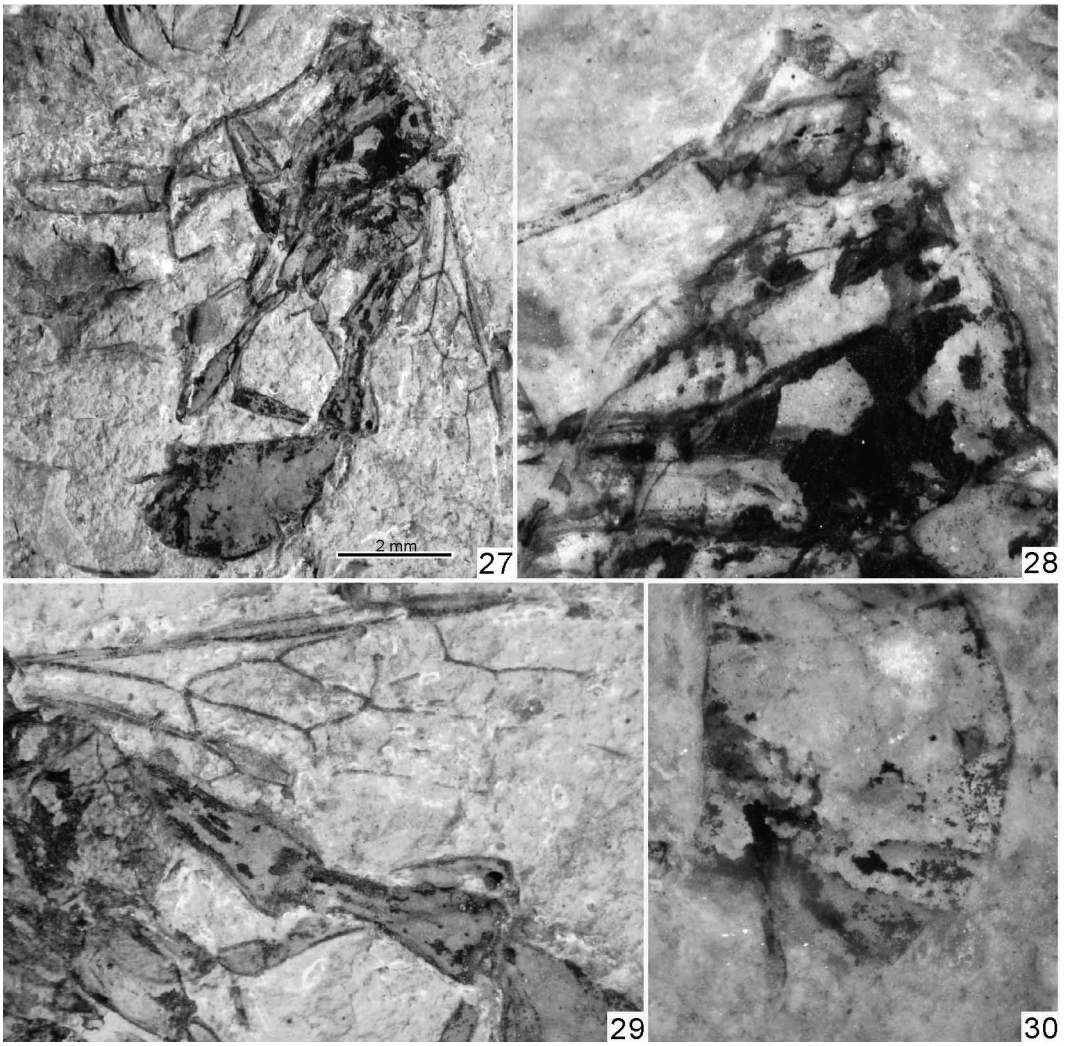
Nevania retenta Zhang & Rasnitsyn, sp. n.

(Figs 31-36)

Type material. – Holotype NND0815/NIGP143699, in dorsoventral aspect, poorly preserved female with head, antennae, mesosoma, legs and wings damaged.

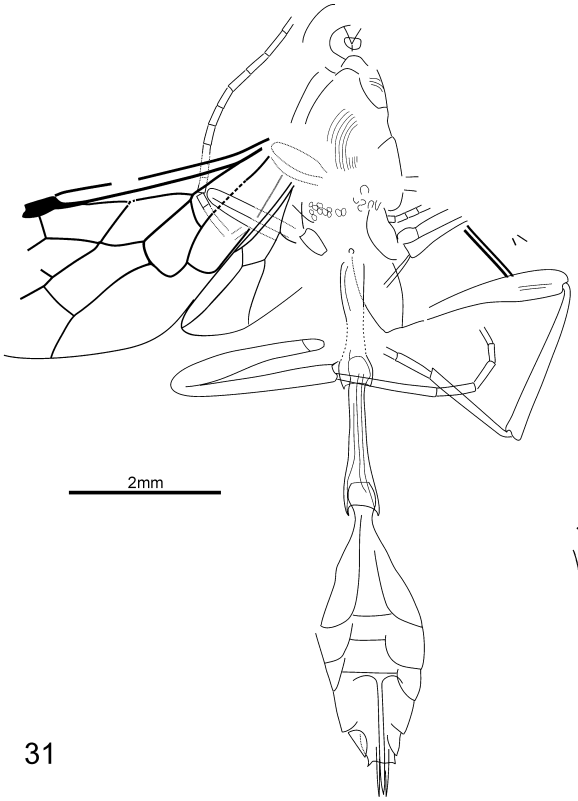
Etymology. – Latin- *retentus*, retentive.

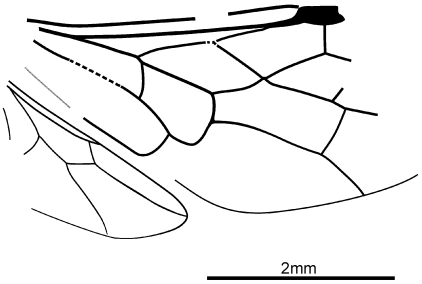
Description. – Brown in colour. Head with occipital foramen small; occipital carina meeting hypostomal suture. Antenna with only 14 basal flagellomeres preserved, each being subcylindrical; first preserved segment distinguishable distally; second four times as long as wide, remaining segments gradually becoming shortened in turn but each at least longer than wide. Mesopleuron with arched ridges. Fore femur short. Midleg longer than foreleg. Hind leg with coxa thick basally and gradually decreasing in thickness apically for distal half; femur 1.3 times as long as first metasomal segment; tibia thin, and as long as femur (including



Figs 25-30. *Nevania ferocula* Zhang & Rasnitsyn, sp. n., holotype. 25, line drawing entire specimen, 26, line drawing of wings. 27, general view, 28, head and mesosoma partly (in alcohol), 29, wings, distal mesosoma and two basal metasomal segments (in alcohol), 30, metasomal apex and ovipositor (in alcohol).

trochantellus), apical spur short; tarsus damaged apically, and at least 1.3 times as long as tibia with basitarsomere 0.6 times as long as tibia, second tarsomere 0.4 times as long as basitarsomere, third 0.77 as long as second, fourth 0.6 as long as third, terminal incomplete. Forewing incomplete with M+Cu fork much closer to wing base than to pterostigma; pterostigmal base slightly closer to 2r-rs than to Rs origin; first abscissa of Rs 0.7 times as long as that of M; 2r-rs vertical and 1.5 times as long as pterostigmal width; 2rm not in contact with 1mcu; 2rm two-thirds as long as 1+2r; 2m-cu slightly curved outwards; cu-a slightly postfurcal, and slightly curved outwards; 1mcu quadrate, about as long as but slightly narrower than cua distally; 2mcu 1.5 times as long as, and slightly broader than 1mcu. Hindwing with r-m slightly longer than first abscissa of Rs, and 0.6 times as long as section M before r-m; Cu+cu-a unpreserved distally. Metasoma with first segment





Figs 31-36. *Nevania retenta* Zhang & Rasnitsyn, sp. n., holotype. 31, line drawing of entire specimen, 32, line drawing of wings. 33, general view, 34, metasoma beyond first metasomal segment (in alcohol), 35, head and mesosoma (in alcohol), 36, forewing and hindwing (in alcohol).

thin basally, subcylindrical for basal one-third, probably becoming thinner submedially, and swollen distally; second slightly thinner basally than first basally, cylindrical for basal half, and gradually becoming thickened apically for distal half; remaining segments (combined) spindle-like with third tergum about as long as second segment. Ovipositor slightly exserted.

Measurements in mm: head width (as preserved) 0.8; antenna length (as preserved) 3.5; mesosomal length 2.5; forewing length (as preserved) 4.5, width 2.2; hindwing (as preserved) length 2.5, width 1.0; first metasomal segment length 1.6, second 1.6, remaining segments (combined) 3.4; ovipositor length 1.6, exerted for 0.4.

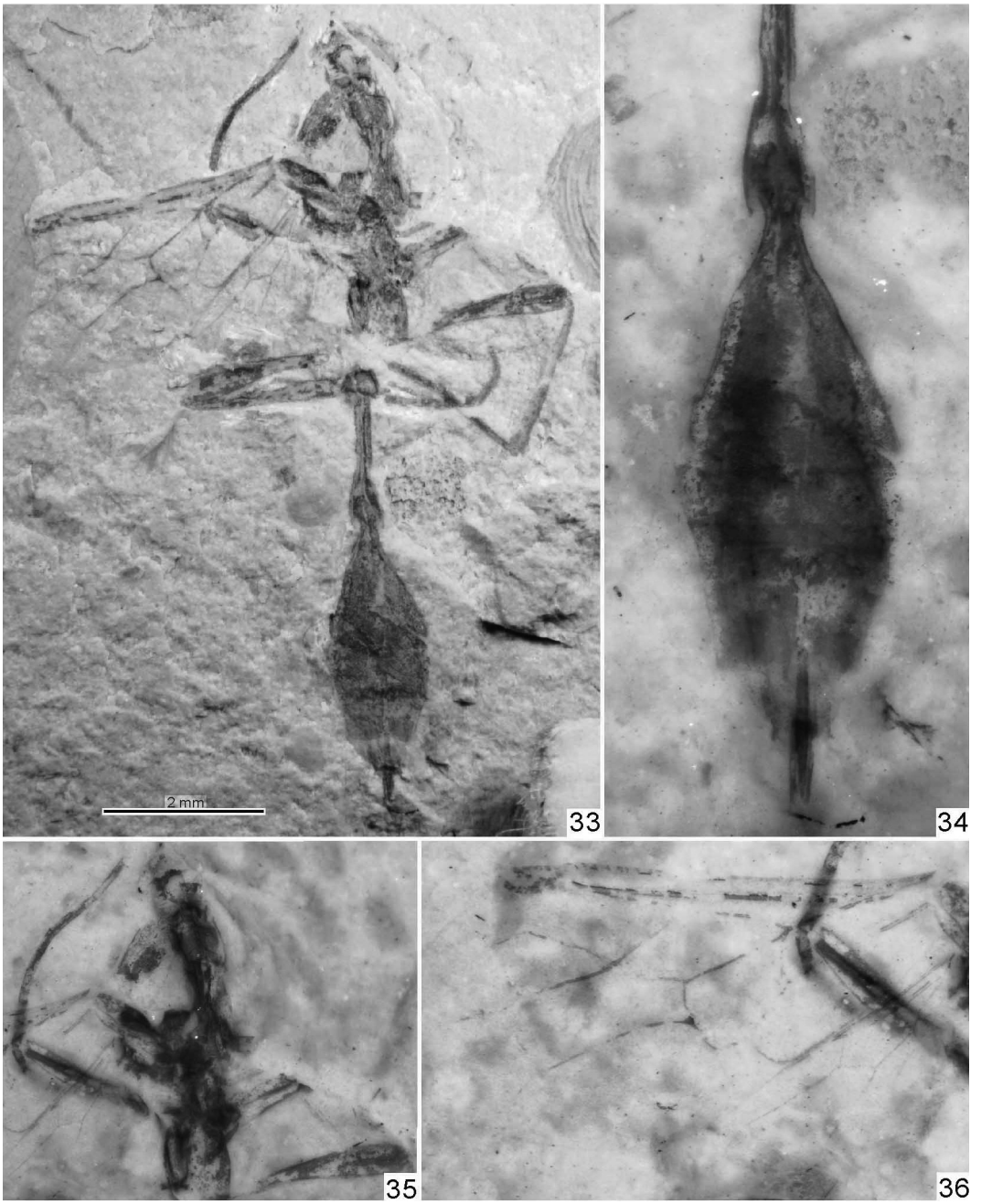
Nevania delicata Zhang & Rasnitsyn, sp. n.

(Figs 37-43)

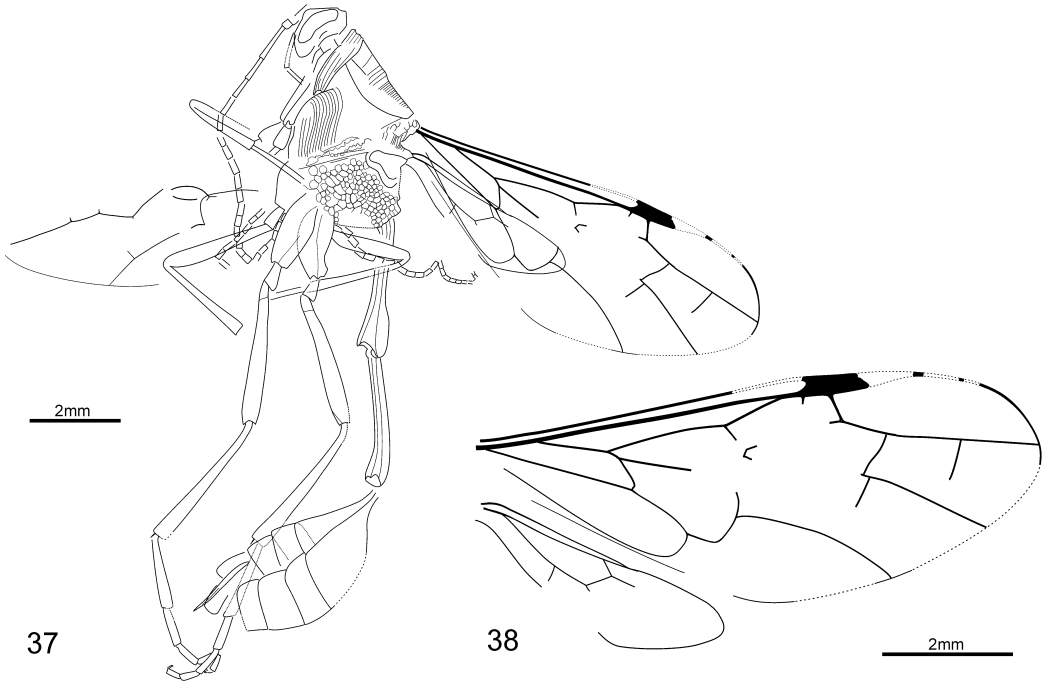
Type material. – Holotype NND0856/NIGP143700, in lateral aspect, nearly complete female with antennae, wings and legs slightly damaged.

Etymology. – Latin *delicatus*, delicate, tender.

Description. – Brown in colour. Body slender. Head small, and nearly twice as high as long. Eyes large, long kidney-shaped. Antenna with 31 segments preserved; scape poorly preserved; pedicel broad, as long as wide; first flagellomere distinctly thinner basally than pedicel, slightly gradually thickened apically, 4.5 times as long as pedicel; second and third similar to first in form with second, 0.7 times as long as first, third 0.55; fourth cylindrical, and as long as third; remaining flagel-



lomeres similar to fourth in form with each twice as long as wide or slightly longer than wide. Pronotum comparatively long, and transversely ridged. Mesonotum with mesoscutum transversely ridged, and greatly longer than scutellum; mesopleuron with densely curved ridges. Propodeum protruding backwards, and coarsely reticulate laterally. Fore leg thin. Midleg distinctly larger than



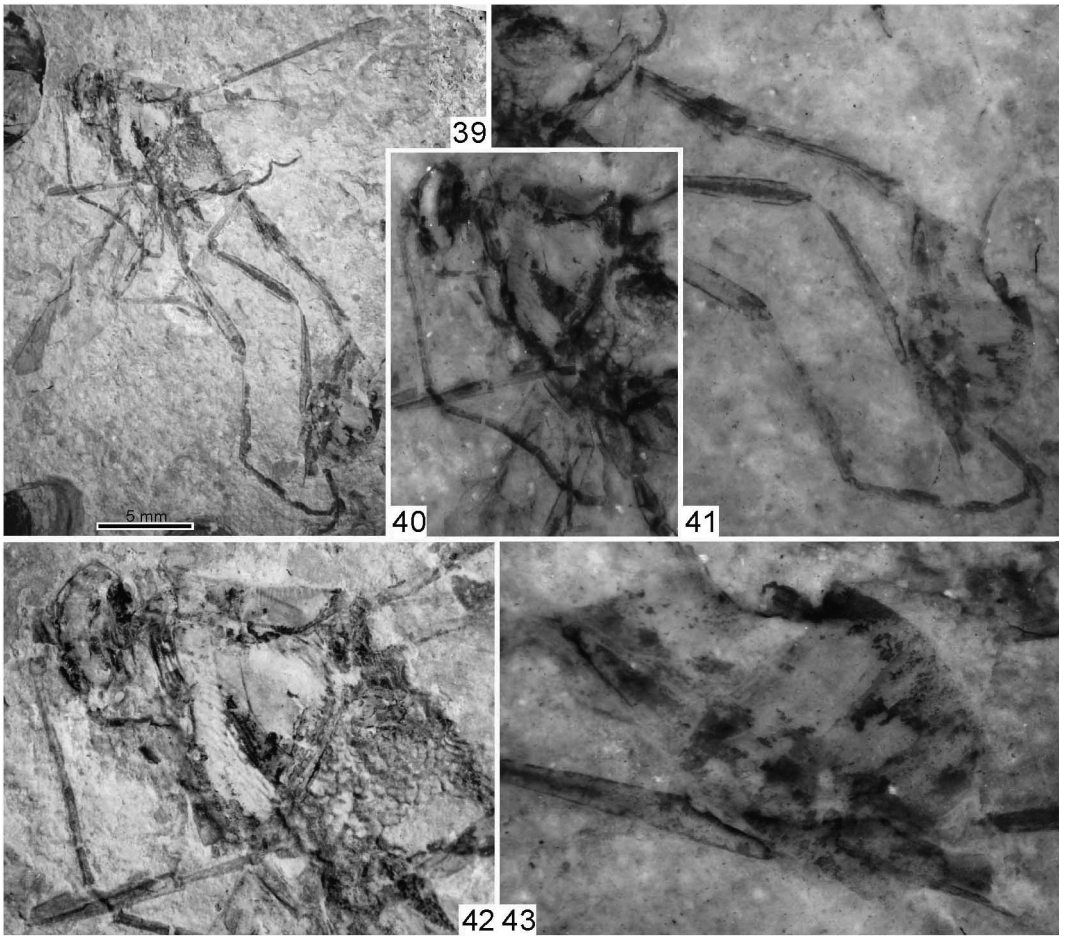
foreleg. Hindleg distinctly longer than midleg with coxa comparatively narrow basally and apically, gradually broadened medially, and 1.8 times as long as mid coxa; trochanter small; femur as long as first metasomal segment; tibia thin, and as long as femur (including trochantellus) with apical spur very short; tarsus 1.2 times as long as tibia with basitarsomere half as long as tibia, segmental length ratio from basitarsomere to terminal tarsomere = 1.00 : 0.43 : 0.37: 0.22 : 0.17; only a distal claw preserved, short. Forewing incomplete with M+Cu fork much closer to wing base than to pterostigma; pterostigmal base about equidistant both to 2r-rs and to Rs origin; first abscissa half as long as that of M; 1r-rs at least like a stub on R; 2r-rs 1.5 times as long as pterostigmal width; 3r nearly twice as long as 1+2r; 1mcu in contact with 2rm by a very short 2M; 2rm slightly longer than 1+2r and 1.5 times as long as 3rm; cu-a quite postfurcal. Hindwing poorly preserved; C and R distinct; r-m 1.5 times as long as first abscissa of Rs, and 0.7 times as long as section M basad of r-m. Metasoma with first segment thin and cylindrical for basal two-thirds, and gradually thickened distally for remaining part; second similar to first, but slightly thickened and curved ventrally for distal one-third; third tergum slightly shorter than second segment, others much shorter. Ovipositor slightly exserted.

Measurements in mm: head length 0.7, antennal length (as preserved) 9.3, mesosomal length 3.9, forewing length 8.6, width 3.3, hindwing length 4.1, width 1.2, first metasomal segment length 3.0, second one length 3.0, remaining segments (combined) length 4.5, ovipositor length 1.6, exserted for 0.3.

Discussion

Two other praeaulacid subfamilies, Praeaulacinae and Anomopterellinae, known mostly from the Upper Jurassic of South Kazakhstan (Rasnitsyn 1972, 1975, 1990b), also occurred in the Daohugou biota but were less diverse (Rasnitsyn & Zhang 2004; Zhang & Rasnitsyn in preparation).

Nevaniinae has a multisegmented (>28) antenna with a short scape as in other Praeaulacidae, being a ground plan character of Evanioidea (Basibuyuk et al., 2002). Similarly, the medially long pronotum and the presence of notauli, median and transscutal sutures on the mesonotum, which are



Figs 37-43. *Nevania delicata* Zhang & Rasnitsyn, sp. n., holotype. 37, line drawing of entire specimen, 38, line drawing of wings. 39, general view, 40, head and mesosoma (in alcohol), 41, metasoma (in alcohol), 42, head and mesosoma to show sculpture, 43, metasoma, beyond second metasomal segment, and ovipositor (in alcohol).

visible in this subfamily and other Praeaulacidae, are also ground plan traits of Evanioidea (Basibuyuk et al., 2002).

The subfamily possesses the following venational characters that are considered plesiomorphic for Evanioidea: (1) the presence of forewing 2A, which is widely seen in Symphyta and Ephialtitidae (Rasnitsyn 1969, 1975), the basalmost Apocrita, but not observed in any known Evanioidea and most Apocrita (except for the most basal extinct taxa and for rudiments in few extant Ichneumonoidea); (2) 11 closed cells in the forewing, which, relative to 10 in Praeaulacinae (Rasnitsyn 1972) and much fewer in rest Praeaulacidae (Rasnitsyn 1975, 1990a,b) and other evanioids, can be treated as a ground plan character; (3) the presence of hindwing C vein, which is widely visible in Symphyta but infrequently in Apocrita (Rasnitsyn 1969, 1975; Ronquist et al. 1999) and represents the ground plan condition within Evanioidea; (4) four closed cells in the hindwing (c, r, rm, mcu), which appears in some Ephialtitidae (Rasnitsyn 1975) but rarely in other Apocrita, and can be treated as a ground plan character. By contrast, the far basal location of M+Cu fork in the forewing is only present in extant and some

Mesozoic evaniids (Rasnitsyn 1975; Zhang & Zhang, 2000; Deans & Huben, 2003; Deans et al. 2004; Zhang et al. 2007), and therefore is derived for Evanioidea. Forewing cell 1+2a, which is absent from any known evanioids owing to the disappearance of vein 2A, is quite high in *Nevania*; this character is barely observed in other Hymenoptera, and is treated autapomorphic for Nevaniinae or probably only for *Nevania*.

Interestingly, this subfamily has a metasoma with the two basal metasomal segments tubular and the rest less modified. A tubular first metasomal segment is widely visible in Apocrita, and even, within the Evanioidea, in Evaniidae (Deans & Huben 2003) and some Praeaulacinae (*Evanigaster* and *Evaniops*; Rasnitsyn 1972). On the contrary, that both the first and second segments are all tubular is very rare in Hymenoptera, being observed only in the extant Mymarommatidae (Rasnitsyn 1988) and extinct Serphitidae (Kozlov & Rasnitsyn 1979; Rasnitsyn 1988). However, these small wasps are not closely related to Evanioidea. Hence, the presence of two tubular basal metasomal segments is exceptional and is considered autapomorphic for Nevaniinae /*Nevania*.

Nevaniinae has a short and slightly exserted ovipositor as in extant Evaniidae. A long and obviously exserted ovipositor is widely present in Evanioidea, including Praeaulacidae Praeaulacinae and Cretocleistogastrinae (Rasnitsyn 1972, 1990a,b), Gasteruptiidae *s.l.* Aulacinae, partly Gasteruptiinae, Bassinae and Kotujellitinae (Rasnitsyn 1975, 1991; Gauld & Bolton 1996; Rasnitsyn et al. 1998), Andreneliidae (Rasnitsyn & Martínez-Delclòs 2000) and some Mesozoic evaniids (Basibuyuk et al. 2000; Deans et al. 2004; Zhang et al. 2007). In Anomopterellinae, the ovipositor is short but exserted well beyond the apex of metasoma (Rasnitsyn 1975). Therefore the short and slightly exserted ovipositor can be considered derived for both Evanioidea and Praeaulacidae.

The discussion above shows that Nevaniinae has a combination of plesiomorphic and apomorphic characters and additionally a few autapomorphies. However, the rich venation indicates that this subfamily probably represents an early clade of the Praeaulacidae and the Evanioidea has an ancestor at least as venationally plesiomorphic as basal Ephialtitidae.

For the genus *Nevaniia*, some characters are considered plesiomorphic including: (1) the appearance of forewing crossvein 1r-rs, which, shown by *N. exquisita* (Figs 7-15) and *N. delicata* (Figs 37-43) although vestigial, is extensively visible in Symphyta and rudimentarily in some Apocrita, e.g. some Ephialtitidae (Rasnitsyn 1975), and can be considered a ground plan trait; (2) forewing cell 1mcu in contact with 2rm (Basibuyuk et al. 2002), which is visible in *Nevania* except *N. retenta* (Figs 31-36); (3) postfurcal forewing crossvein cu-a, which is observed in *Nevania* except *N. ferocula* (Figs 25-30), widely seen in Symphyta, and can be treated as a plesiomorphic character; (4) slightly conical dorsoposterior face of the propodeum (Deans et al., 2004), which is exhibited in *N. malleata* (Figs 16-24) and *N. delicata* (Figs 37-43). These conditions show that *N. delicata* possesses less derived characters than its congeners, and probably occupies the most basal position of the clade *Nevania.* On the other hand, this genus also shows several derived characters: the straight forewing Rs, which, unlike most Evanioidea, is bent neither at 3r-m nor beyond it, and straight hindwing M between M+Cu and r-m (on the contrary, M is bent in less modified Praeaulacinae *Praeaulacus* like in Symphyta, Ephialtitidae and many Aculeata.

Like extant aulacines, wasps parasitizing endoxylous hosts usually have strong transverse sculpture on the mesoscutum, which perhaps aids the wasp in egressing from the pupation site (Quicke 1997). Nevaniines possess transverse ridges not only on the mesoscutum but also on the pronotum, and even have arched ridges on mesopleura at least visible in *Nevania*, which strongly suggests that they pupated in wood and, by inference, were parasitoids of wood-boring insects. Aulacines possess a quite long ovipositor used for locating eggs of their hosts in bark crevices and laying eggs in (Jennings & Deans 2006). The Nevaninae, however, appears to have a very short ovipositor, implying that eggs of its hosts were much easier to reach, and probably very close to the surface of the bark. Therefore, the host was probably not a horntail (Hymenoptera: Siricidae), whose modern relatives usually place their eggs deep into wood, but a beetle who normally oviposited less deep leaving eggs available for parasites with the ovipositor as long as in *Nevania*. It was the eclosed larva which burrowed deep into wood bringing its parasite there.

For each species of *Nevania*, respectively between the first and second metasomal segments and between the second and third, there apparent-

ly exists an articulation suggested by the swollen ends of the first and second metasomal segments, which probably made the corresponding metasomal segments nimbly movable, at least forwards and backwards, deduced from their preservation state. However, such a long two-segmented petiole with a highly movable articulation in the middle and at both of its ends has yet to be observed in other insects and, at present, it is difficult to decide its function, especially in oviposition.

Metasomal morphology of *Nevania* shows apomorphies similar to those known in Evaniidae, viz., the tubular first metasomal segment, short ovipositor and ball-and-socket articulation between the first and second metasomal segments, with the former forming the socket, and the latter the ball (cf. Figs 31, 33). Additionally, *Nevania* is similar to the most advanced (Cainozoic) Evaniidae in having forewing with M+Cu fork shifted far basad in respect to pterostigma. We do not consider these similarities as undoubted synapomorphies for the following reasons. Some older Evaniidae (*Mesevania* Basibuyuk et al., 2000 from the mid-Cretaceous Burmese amber and *Eovernevania* Deans in Deans et al., 2004 from the Lower Cretaceous Lebanese amber) have a long ovipositor indicating that this character state was present in the ground plan of the family. Furthermore, the ball-and-socket articulation between the first and second metasomal segments is apparently not unique for *Nevania* and Evaniidae: Mymarommatidae (Gibson, 1986: Fig. 36), Serphitidae, Roproniidae, Heloridae, Monomachidae and Chalcididae (APR, personal observation) resemble *Nevania* and Evaniidae in that aspect. The most important, however, is that, to hypothesize synapomorphy of *Nevania* and Evaniidae in the above character states, we should hypothesize homoplastic nature of all apomorphic character states that Evaniidae have in common with Gasteruptiidae s.l., viz., pronotum short along midline, medial mesoscutal sulcus lost, and hindwing with no cell enclosed. Additionally this hypothesis infers either independent shortening of the ovipositor in *Nevania* and in Evaniidae other than *Mesevania* and *Eovernevania,* or its independent elongation of these two distantly related genera. Treating the basal position of the M+Cu fork as the synapomorphy of *Nevania* and Cainozoic Evaniidae means inferring still wider array of homoplasies gained independently by the Mesozoic and Cainozoic Evaniidae.

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