Ancestry of the orussoid wasps, with description of three new genera and species of Karatavitidae (Hymenoptera = Vespida: Karatavitoidea stat. nov.)

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Praeratavites daohugou Rasnitsyn, Ansorge & Zhang, gen. et sp. n., *Grimmaratavites mirabilis* Rasnitsyn, Ansorge & Zhang, gen. et sp. n., and *Praeparyssites orientalis* Rasnitsyn, Ansorge & Zhang, sp. n. are described from the Lower Jurassic (Lower Toarcian) of Grimmen, NE Germany (*G. mirabilis*) and Middle Jurassic of Daohugou. Karatavitidae Rasnitsyn, 1963, is transferred from Ephialtitoidea into now paraphyletic infraorder Orussomorpha, and elevated to superfamily Karatavitoidea. The described genera, jointly with those earlier described in Karatavitidae and Paroryssidae, are found to form a smooth succession that model evolutionary transition from the basalmost Vespina toward the extant Orussidae.

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Introduction

Orussoidea comprising extant Orussidae and extinct Paroryssidae are currently considered to be the sister group of Apocrita; together, they comprise the Vespina (Rasnitsyn 1988, Rasnitsyn & Quicke 2002; Vilhelmsen 2001, 2004; Ronquist et al. 1999: fig. 9; Schulmeister 2003). In other words, these authors hypothesize that the first dichotomy within the higher (entomophagous) hymenopterans (suborder Vespina) has resulted in origin of two monophyletic sister groups. One of them is the superfamily Orussoidea that has reduced wing venation (most of the 2nd anal vein and crossveins 1r-rs, 3r-m, 2m-cu in the forewing and all crossveins but 1r-m in the hind wing are lost; for the vein nomenclature see below) but retain the wide abdominal base and the wing attachment device composed of metanotal flaps (cenchri) that fix the forewings at rest by interlocking with the rough area aspera at the posterior basal part of the wing. In contrast, the other sister group Apocrita retains more complete wing venation in its groundplan including all hymenopteran groundplan veins except SC, forewing RS_2, and in hindwing, 2A and the 2nd (intermediate) crossvein 2r-m, all of which are equally lost in Orussoidea. Instead, Apocrita have lost the above wing attachment device and gradually evolved the wasp waist, the narrow and highly flexible articulation between the first and second abdominal segments (only incipient in some of the earliest representatives).

The newly discovered Jurassic fossils from Germany and China apparently falsify this hypothesis: they indicate that the above dichotomy has proceeded in small steps recorded palaeontologically and are traceable as a morphological continuum which is not easy to split into holophyletic taxa. The aim of the present publication is to describe these fossils and to analyze their relations to other basal Vespina.

The senior author is exclusively responsible for the phylogenetic and taxonomic interpretation of

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the results when they deviate from strict cladistic principles for reasons explained in Rasnitsyn (1996).

The venational symbols used here can be specified as follows: symbols in capitals denote the longitudinal veins (C - costal, SC - subcostal, R – radial, RS – radial sector, M – medial, Cu – cubital, A – anal). Dashed lower case symbols denote crossveins between the longitudinal ones, numbered consequently from the wing base outward: 1r-rs – the basalmost crossvein between R (as forming the pterostigma) and RS, 3r-m – the distalmost crossvein between RS and M (rs is reduced here to r for shortness), and so on. Lower case not dashed symbols denote cells between respective longitudinal veins (except for the cells between R and RS which are termed interradial and symbolized just 'r'): 3r – the distalmost interradial cell (marginal in the traditional nomenclature), 1mcu – basalmost mediocubital ('1st discoidal'), etc.

Material

The present publication is based on three recently discovered fossils from the Lower Toarcian (upper Lower Jurassic) of Grimmen in Germany and from the Middle Jurassic of Daohugou in China.

Hymenopterans are extremely rare fossils in the Lower Toarcian (185 Ma) marine insect taphocoenoses of Central Europe (Ansorge 2003, Rasnitsyn et al. 2003, Nel & Petrulevicius 2004). They constitute less than 1 ‰ of all insect remains in the major Lower Toarcian insect localities of Dobbertin (Mecklenburg, NE Germany), Grimmen (Western Pomerania, NE Germay), Schandelah (Lower Saxony, Germany) and Bascharage (Luxembourg). Hymenopterans are represented by members of Sepulcidae Rasnitsyn 1968 (one species), Xyelotomidae Rasnitsyn 1968 (one species), Symphyta *inc. sedis* (one species), and Ephialtitidae Handlirsch 1906 (five species). Except *Xyelula benderi* Rasnitsyn et al. 2003, these species are known only from their holotypes (isolated forewings). Of *X. benderi* some bodies with and without wings are also known. Most of these are females, suggesting active dispersed flights over the sea. Besides an isolated forewing of *X. benderi*, the holotype of *Grimmatavites mirabilis* is only the second hymenopteran fossil from the Grimmen locality.

The systematic diversity of Early Toarcian hymenopterans clearly shows that the first initial radiation of the order Hymenoptera took place in the Late Triassic or at least in the earliest Jurassic. The further Jurassic diversification of Hymenoptera is remarkably illustrated by a wealth of Middle and Late Jurassic fossils from Daohugou (China) and Karatau (Kazakhstan).

The Chinese fossils are preserved as impressions on the surface of grey tuffaceous siltstones from the Middle Jurassic Daohugou deposits (N41º18'37·6'', E119º13'20·4'') near Daohugou Village, Ningcheng, Neimonggol (Inner Mongolia). More detailed information and discussion on the age, stratigraphy, and fauna of the locality can be found in Rasnitsyn et al. (2006) and references therein, the hymenopteran assemblage of Daohugou is discussed by Rasnitsyn & Zhang (2004). In short, the fossils under description come from deposits of a lake in a mountaneous, volcanic country with comparatively warm climate (indicated by the low proportion of Xyelidae) and with rich and diverse insect fauna. In particular, the hymenopteran assemblage of Daohugou is intermediate in its taxonomic composition between those of the Early (or earlier Middle) and Late Jurassic age.

The type depositories are specified below.

Infraorder **Orussomorpha** Newman, 1834

Superfamily **Karatavitoidea** Rasnitsyn, 1963, *stat. nov.*

Diagnosis. – Similar to Orussoidea, the only other superfamily in Orussomorpha, in having in its groundplan the forewing 2A looped to accommodate the rough area fixed over the metathoracic cenchri at rest (a hymenopteran synapomorphy lost in Apocrita, and homoplastically in Cephidae). Differs in wide, flat ovipositor (thin needle-like in Orussoidea) and, less distinctly, in more complete wing venation: 2r-rs, 3r-m, 2m-cu crossveins developed at least as rudiments on respective longitudinal veins, 2A basad of interanal crossvein present at least in the loop area, hindwing with m-cu (lost even in the putatively most plesiomorphic Paroryssidae; i.e., *Paroryssus* Martynov, 1925 and *Praeoryssus* Rasnitsyn, 1968).

Included families. – Karatavitidae Rasnitsyn, 1963 (Jurassic of Eurasia).

Remark. – For an explanation of the transfer of Karatavitidae to Orussomorpha refer to the Discussion section.

Family **Karatavitidae** Rasnitsyn, 1963

Genus ***Praeratavites*** Rasnitsyn, Ansorge & Zhang, **gen. n.**

"pre-Karatavites" (informal name): Rasnitsyn & Zhang, 2004: 1508, 1510.

Type species. – *P. daohugou* Rasnitsyn, Ansorge & Zhang, sp. n. by present designation and monotypy.

Etymology. – Generic name is from *prae-* (Greek for before) and modified generic name *Karatavites*. Gender masculine.

Diagnosis. – Similar to *Karatavites* except 2r-rs joining distal 0.3 of pterostigma (before pterostigmal midlength in *Karatavites*), cu-a joining mid 0.3 of 1mcu cell (basal 0.3 in *Karatavites*), and subbasal loop of 2A and metanotal cenchri present (lost in *Karatavites*).

Included species. – Type species only.

Praeratavites daohugou Rasnitsyn, Ansorge & Zhang, **sp. n.**

(Figs 1-4)

Type material. – Holotype NND087/NIGP139744 housed in the Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences; near complete female fossil with legs poorly preserved and part of antennal and thoracic structure difficult to decipher; Daohugou Village near Chifeng City in Inner Mongolia, China; Middle Jurassic.

Etymology. – Species name is the name of fossil site (noun in apposition).

Description. – Pterostigma distinctly infuscate, otherwise colour pattern poorly preserved: apparently antennae, head and thorax with propodeum at least predominantly, metasoma with at least hind part of most or all terga, and at least dorsum of saw sheaths dark. Antenna long, thin, gradually narrowing toward apex, with more than 20 flagellomeres, basal flagellomeres some 3 times as long as wide, medial ones 2.5 times so. Head large, roundish, with huge eyes. Pronotum not preserved. Mesonotum with notauli, midscutal and transverse sutures complete, notauli distant from transverse suture. Propodeum about as long as metanotum (unless damaged). Forewing with pterostigma medium large, acuminate, with 2r-rs at about its apical 0.3. R distinctly angular at RS base. RS gently arching basally, its 1st abscissa twice as long as that of M, RS+M near reaching midlength of fore side of 1mcu cell, 1r-rs equidistant to 2r-rs and to RS base, subparallel to and slightly shorter than 2r-rs, cell 3r acuminate. Cells 2-3rm of equal length (about four times as long as 2r-m), 2-3r-m both subvertical, 3r-m much longer than 2r-m, distant from apex of 3r cell for about 0.7 its length. Cell 1mcu 1.5 times as long as high, almost symmetrical except fore margin gently curved and hind one slightly angular at junction to cu-a which placed basal comparing apex of RS+M. 1m-cu about as long as section of Cu adjacent distally. 2a cell as long as 1mcu. Hindwing with RS starting far basad of M&Cu fork, 1r-m at about midlength of mcu cell, 2r-m more distant to 1r-m than to apex of 3r cell and four times as long as 1r-m, m-cu meeting 2rm medially, cu-a at about 0.4 of 1mcu length, 1a-2a aligned with 2A, reaching 1A distinctly before cu-a. Metasoma fusiform, 1st tergum trapezoid, 1.5 times as wide as long, following distinctly shorter, 4th and 5th the widest. Ovipositor downcurved, sheathes tapering, rounded apically. Total length of ovipositor about 0.3 times as long as forewing, its protruding part slightly shorter than pterostigma. Surface sculpture not discernible on head and metasoma beyond 1st tergum, mesonotum and 1st metasomal tergum finely rugose (1st metasomal transversely rugose toward apex), metanotum and propodeum roughly areolate rugose. Body length without ovipositor 11 mm, forewing length 8.8 mm, ovipositor length 3.1 mm.

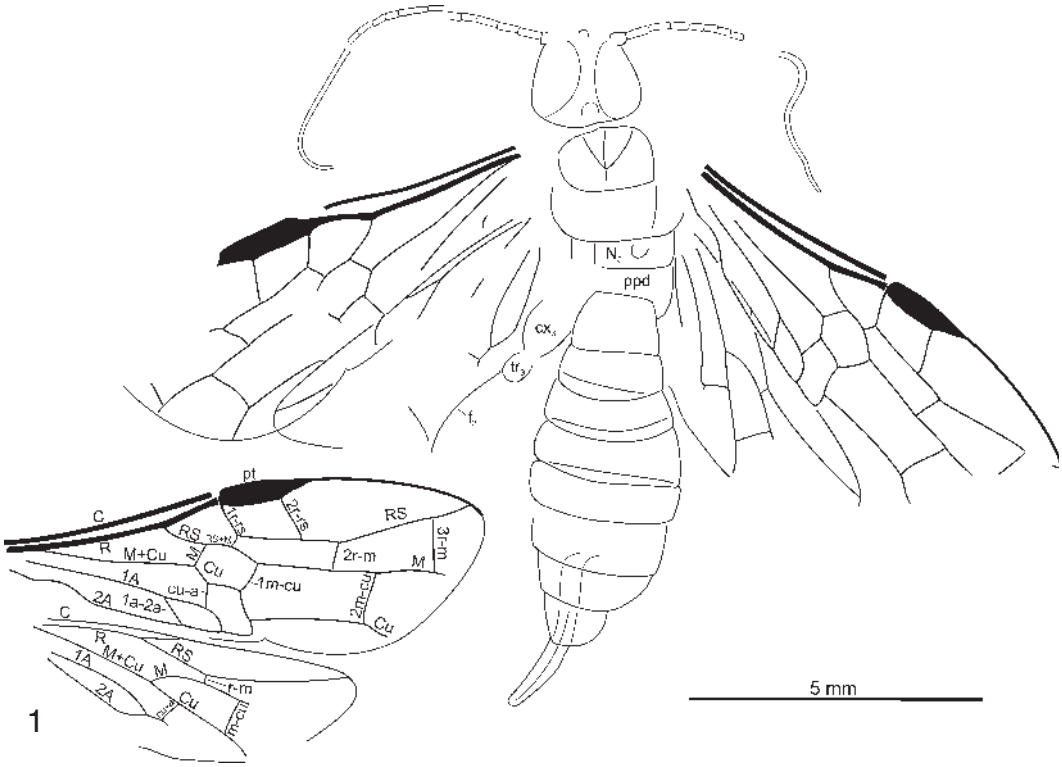
Genus ***Grimmaratavites*** Rasnitsyn, Ansorge & Zhang, **gen. n.**

Type species. – *G. mirabilis* Rasnitsyn, Ansorge & Zhang, sp. n.

Etymology. – Generic name is from the type locality Grimmen and modified generic name *Karatavites*. Gender masculine.

Diagnosis. – As known, similar to *Karatavites* and *Praeratavites* but differs in having forewing crossveins 3r-m and 2m-cu reduced (annulate and easily flexible as described by Wootton, 1981), and size almost twice less. Additionally differing from *Karatavites* in cenchri present, 2A looped subbasally, pterostigma larger and meeting 2r-rs more distally, cu-a more distal in respect to cell 1mcu.

Included species. – Type species only.



Figs 1-4. *Praeratavites daohugou* Rasnitsyn, Ansorge & Zhang, sp. n., holotype. 1, line drawing of insect and of its wings to show veinal symbols. 2, general view, 3, head and thorax, 4, ovipositor. Veinal symbols standard (for cell symbols see Fig. 5); other symbols: cx_3 – hind coxa, f_3 – hind femur, N_3 – metanotum, ppd – propodeum. →

Grimmaratavites mirabilis Rasnitsyn, Ansorge & Zhang, **sp. n.**

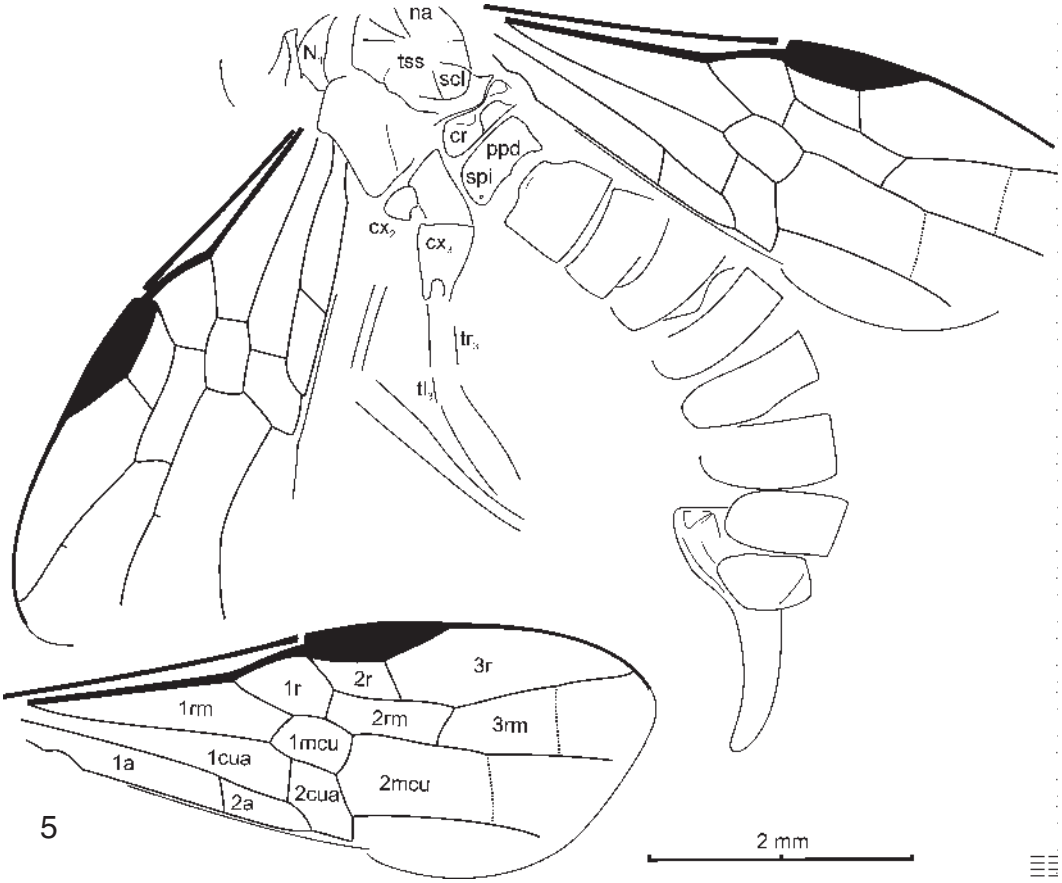
(Figs 5-10)

Type material. – Holotype LGA 2510 part and counterpart, coll. J. Ansorge, to be deposited in Museum für Naturkunde, Humboldt University, Berlin. Female generally well preserved except head, fore and mid legs, and hind wings; clay pit Klein Lehmhagen in the vicinity of Grimmen (Western Pomerania/NE-Germany); limestone concretions within the Lower Toarcian "Green Series", ammonite zone of *Harpoceras falciferum*, Lower Jurassic.

Etymology. – The species is named in homage of the younger daughter of JA, Mira, and Latin *mirabilis*, meaning wonderful .

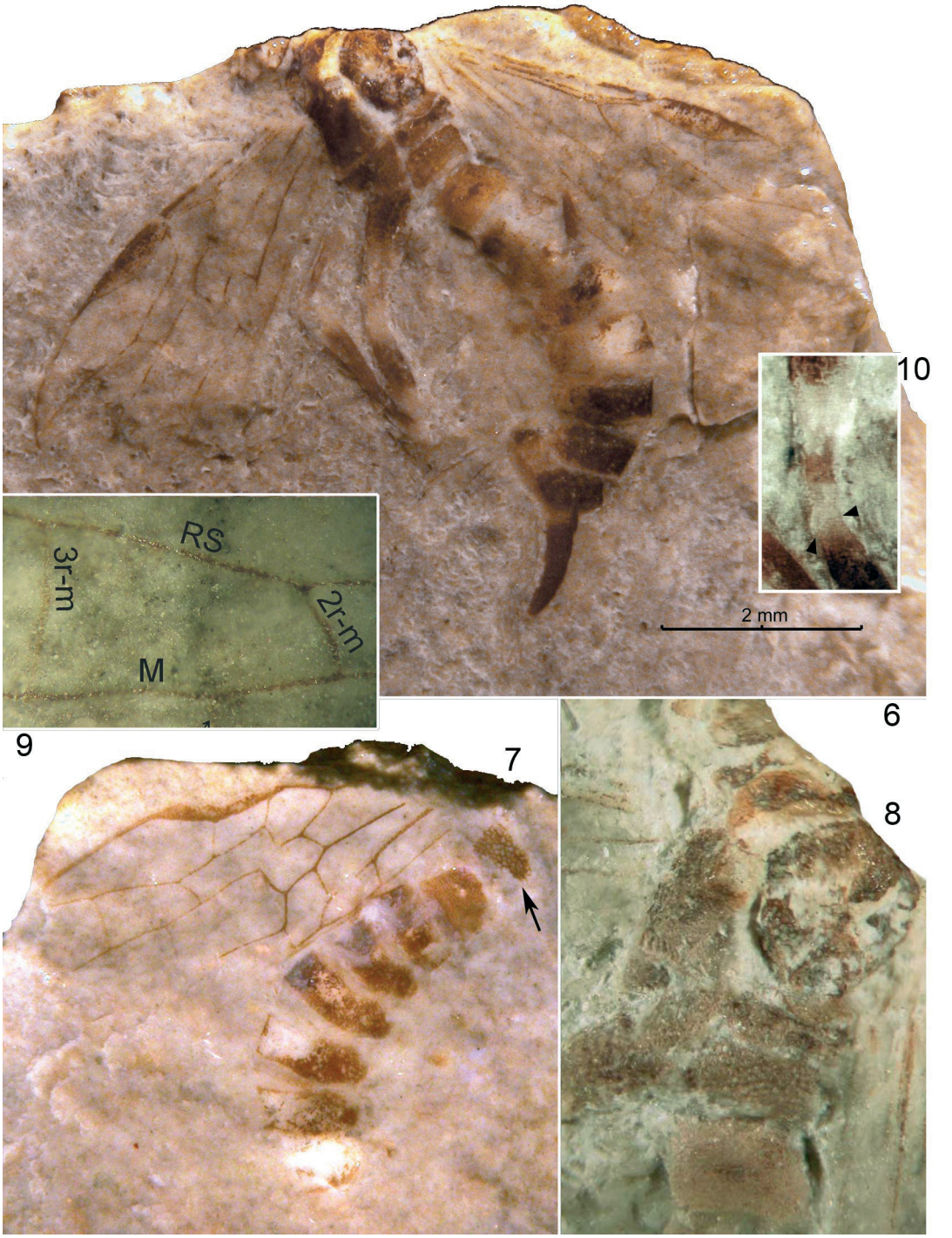
Description. – Apparently all body (unknown for head), pterostigma, hind coxa, hind femur except base and apex, hind tibia except apex, hind basitarsus, and saw sheath distinctly infuscate, hind trochanter apically slightly infuscate. Pronotum short, with straight hind margin. Relation between notauli, midscutal and transverse sutures, and scutellum unclear (mesonotum poorly preserved centrally), scutellum narrow. Metascutellum transverse, cenchri subtriangular, not wide. Propodeum about as long as the shortest (4th and 5th) metasomal terga, convex transversally but not so longitudinally, medially, apparently with small, ovate spiracle in its posterolateral corners and with weak, distant, articulatory processes apically, submedially, with very flat excisions in-between. Hind leg with coxa moderately large, subconical, femur narrow, not very long (with trochantellus, slightly longer than coxa + trochanter), tibia long, narrow in basal half, wide apically, basitarsus long, narrow. Forewing with pterostigma rather large, acuminate, with 2r-rs near its midlength. R distinctly angular at RS base. RS almost straight, its

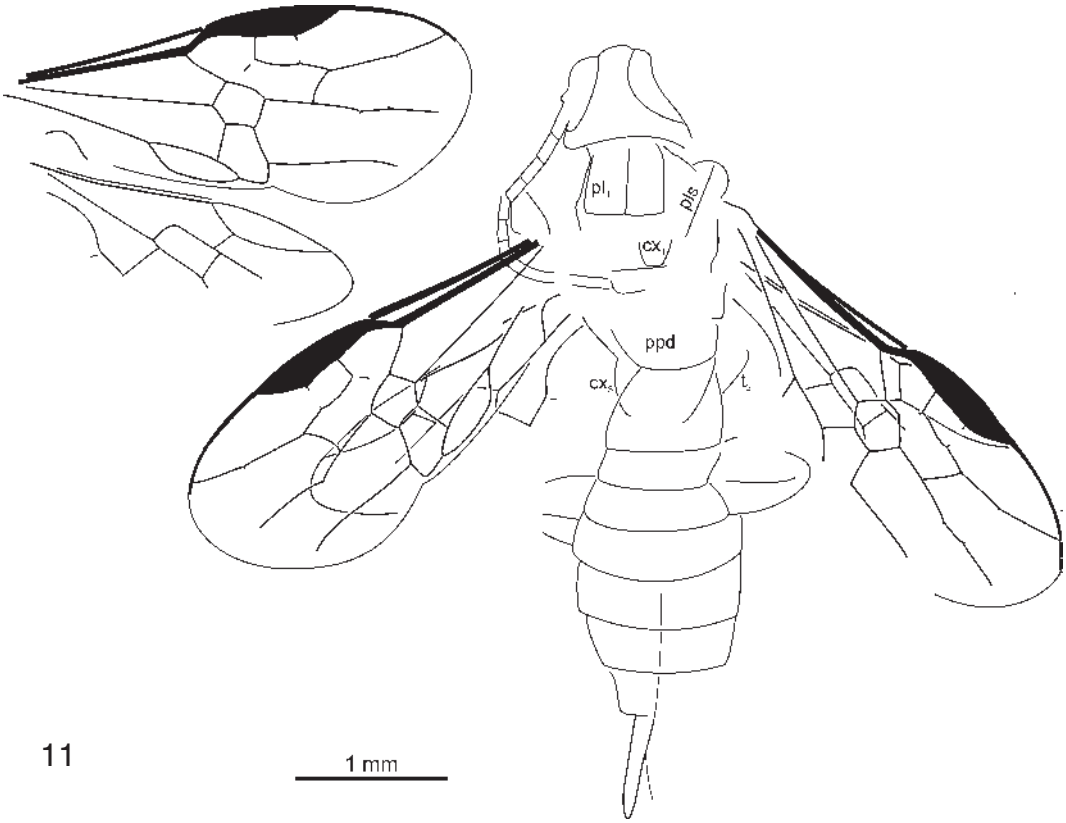
1 mm
2
3
4



Figs 5-10. *Grimmaratavites mirabilis* Rasnitsyn, Ansorge & Zhang, sp. n., holotype. 5, line drawing of insect and of its fore wing to show cell symbols. 6, general view, 7, counterpart to show venation (propodeum arrowed), 8, thorax to show sculpture, 9, wing cell 3rm to show different structure of 2r-m (right) and 3r-m, 10, part of hindleg to show boundary between trochantellus and femur (arrowheads). Cell symbols standard; other symbols: cr – cenchrus, $cx_{2,3}$ – middle and hind coxa, N_1 – pronotum, na – notaulus, ppd – propodeum, scl – mesoscutellum, spi – propodeal spiracle, tl_3 – hind trochantellus, tr_3 – hind trochanter, tss – transverse mesoscutal suture. →

1st abscissa almost twice as long as that of M, RS+M nearly reaching midlength of fore side of 1mcu cell, 1r-rs equidistant to 2r-rs and to RS base, subparallel and subequal to 2r-rs, cell 3r acuminate. Cells 2-3rm of subequal length (about three times as long as 2r-m), 2r-m oblique, 3r-m subvertical, much longer than 2r-m, distant from apex of 3r cell about for its length. Cell 1mcu 1.5 times as long as high, with cu-a distinctly before its midlength. 1m-cu about as long as section of Cu adjacent distally. 2A cell distinctly longer than 1mcu. Metasoma probably not fusiform, as preserved widest well beyond midlength. 1st metasomal tergum distinctly wider than long, with fore margin modified for enhanced articulation with propodeum (slightly extending forward and upcurved in about mid half). 2nd through 5th metasomal terga about 0.7 times as long as 1st, following distinctly longer. Ovipositor downcurved, sheaths wide, weakly tapering, rounded apically. Total length of ovipositor almost 0.4 times as long as forewing, its external part about as long as pterostigma. Meso- and metathorax including coxae and propodeum coarsely rugose-punctate; except that anterior surface of mesopleuron (behind and below pronotum) more sparsely punctuate,


10
2 mm
6
RS
3r-m
2r-m
M
9
7
8



Figs 11-14. *Praeparyssites orientalis* Rasnitsyn, Ansorge & Zhang, sp. n., holotype. 11, line drawing of insect and of its wings. 12, general view, 13, head and thorax, 14, ovipositor. Symbols as on Figs 1, 5; additionally: cx_1 – fore coxa, pl_1 – propleuron, pls – pleural suture.

→

with interspaces flat, and lower mesopleuron adjacent midcoxa with wide trans-costate belt. Pronotum finely transversally striate. 1st metasomal tergum finely, irregularly, transversally rugose (particularly fine in rear half). Surface sculpture not discernible on head, hind leg beyond coxa and metasoma beyond 1st tergum. Body length without ovipositor 6.3 mm, forewing length 5 mm, ovipositor length 1.9 mm, sheath length 1.1 mm.

Genus ***Praeparyssites*** Rasnitsyn, Ansorge & Zhang, **gen. n.**

Paroryssidae gen. nov.: Rasnitsyn & Zhang, 2004, Pl. 2, Fig. 2.

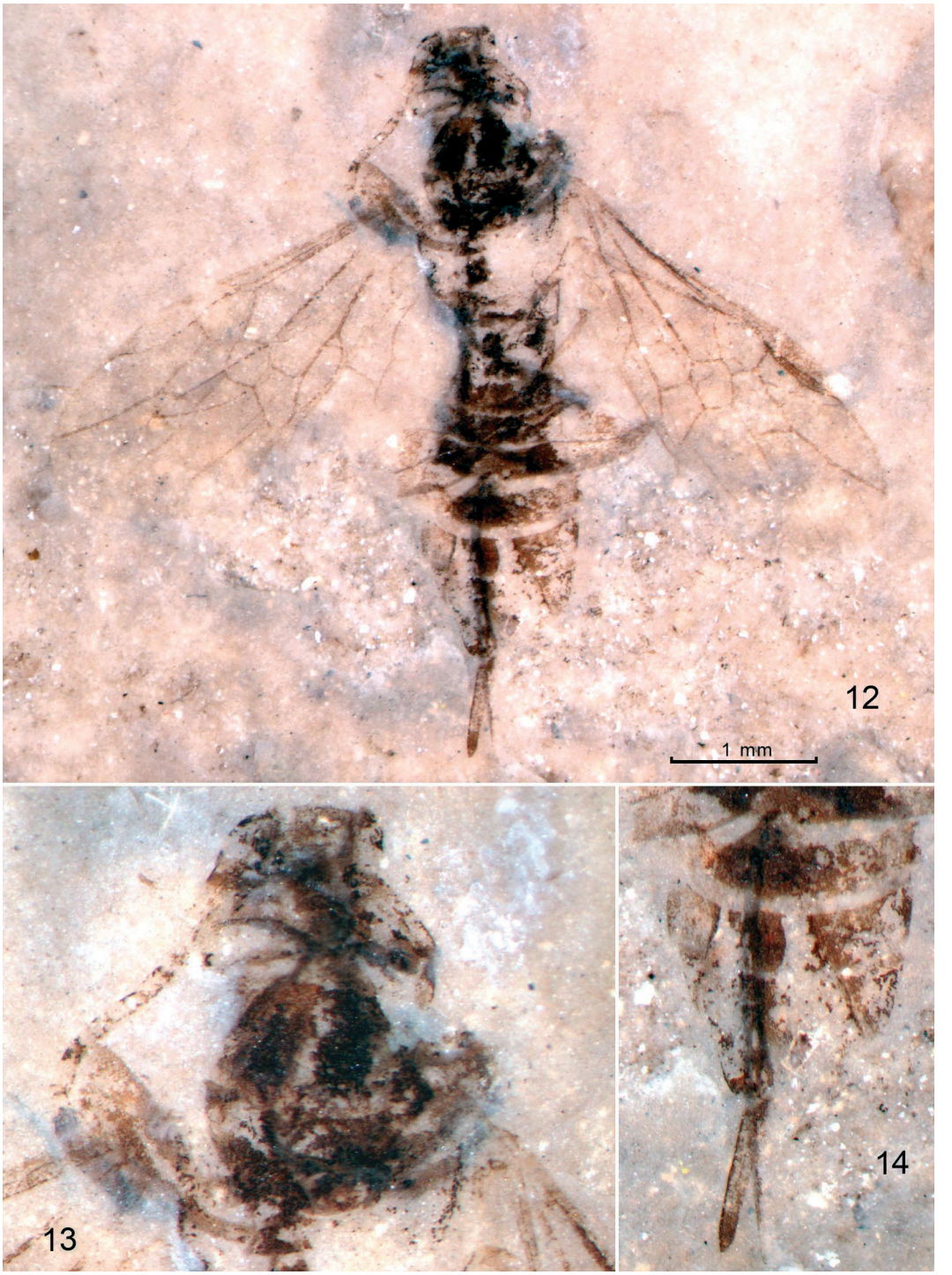
Type species. – *P. orientalis* Rasnitsyn, Ansorge & Zhang, sp. n.

Etymology. – Generic name is from the modified generic name *Paroryssus*; prae- is the Greek for *before*, *earlier*, and -ites is a usual ending of names of fossils. Gender masculine.

Diagnosis. – Differing from other Karatavitidae in being smaller and having forewing venation further reduced: 2r-rs, 3r-m, 2m-cu, and RS incomplete at best between RS+M and 1r-rs, 2A lost between basal loop and 1a-2a. Further differing from the other genera in pterostigma extending basad far beyond 1r-rs, and in particularly long cell 2a, and in hindwing, in relatively basal position of crossveins m-cu, cu-a, and 1a-2a.

Species included. – Type species only.

Remarks. – The genus is particularly similar to Paroryssidae in small size, in unusual form of pterostigma (extending far basad of 1r-rs), and in the similar type of the vein reduction: first lost are


12
1 mm
13
14

2r-rs, 3r-m, 2m-cu, and 2A basad of the anal crossveins. This was the reason to attribute the type species to Paroryssidae by Rasnitsyn & Zhang (2004). However, there are important differences in the genus possessing far less reduced venation, less incrassate R and pterostigma, and unique vein reduction (in *Praeparyssites* RS between RS+M and 1r-rs reduced while 2r-m is present, in Paroryssidae the trend is reverse). Unfortunately one more, and possibly the most important, character is unknown for the new genus, viz., whether or not the ovipositor is needle-like thin, as in Paroryssidae, or flat and high in cross-section, as in Karatavitidae. Because of the general balance of available similarities, the new genus is tentatively placed in Karatavitidae.

Praeparyssites orientalis Rasnitsyn, Ansorge & Zhang, **sp. n.**

(Figs 11-14)

Type material. – Holotype NND086/NIGP139745 housed in the Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences; almost complete female fossil with legs poorly preserved and part of antennal and thoracic structure difficult to decipher; Daohugou Village near Chifeng City in Inner Mongolia, China; Middle Jurassic.

Etymology. – Species name is from Latin *orientalis*, meaning eastern.

Description. – Apparently entire body and antenna dark, legs less dark, pterostigma still less dark. Head long in dorsal view, trapezoid, with eyes occupying most of its sides. Antenna comparatively thick, filiform as preserved (apex unknown), 6 basal flagellomeres of similar form except slightly decreasing in length apicad, more than twice as long as wide. Thoracic morphology unknown except for wide, short propleura throughout contiguous mesally. Hind femur and tibia apparently short and thick. Forewing with pterostigma large, acuminate, starting rather close to RS base, with 1-2r-rs slightly more close to each other than to pterostigmal base and apex, respectively. R distinctly angular at RS base. 1r-rs subparallel to but slightly shorter than 2r-rs, 2r-rs spectral for its middle section. RS almost straight, its 1st abscissa less than twice as long as that of M, RS+M apparently reaching 0.3 of foreside of 1mcu cell. RS rudimentary between cells 1r and 2rm. Cells 2-3rm of subequal length (about twice as long as 2r-m), 2r-m oblique, 3r-m spectral except for the very base and apex, apparently subvertical, somewhat longer than 2r-m, distant from apex of 3r cell for more than its length. Cell 1mcu slightly longer than high, with cu-a slightly before its midlength. 2A cell twice as long as 1mcu. Hindwing with RS starting far distad of M&Cu fork, 1r-m near end of m-cu cell, 2r-m lost, cu-a near base of 1mcu, 1a-2a distant from cu-a almost for length of cu-a, 2A incomplete. Metasoma possibly fusiform, widest near midlength. 1st metasomal tergum distinctly wider than long, with convex sides. Following terga roughly half as long as 1st (2nd and 3rd look shorter probably because of a kind of damage). Ovipositor seen strictly from above, its form unclear, at least half as long as forewing, its basal part distinctly longer than sheath, as long as (very long) pterostigma. Surface sculpture not discernible. Body length without ovipositor 4.4 mm, forewing length 3 mm, ovipositor length 1.5 mm, sheath length 0.7 mm.

Discussion

The family Karatavitidae has been described within the superfamily Siricoidea (Rasnitsyn, 1963) and later transferred to Apocrita and included into Stephanoidea together with Ephialtitidae (Rasnitsyn, 1980). Later Karatavitidae and Ephialtitidae have been placed in the separate infraorder Ephialtitomorpha and superfamily Ephialtitoidea, the basalmost group of Vespina except for Orussomorpha (Rasnitsyn, 1988).

Herein we expand Karatavitidae not only taxonomically but also morphologically. We infer a smooth transition that connects, at one extreme, *Praeratavites* gen. n. that resembles the common ancestor of all Vespina *s.l.* Another extreme of that continuum is formed by *Karatavites* Rasnitsyn, 1963 which resembles the common ancestor of Apocrita, and the third extreme, *Praeparyssites* gen. n., perfectly resembles the hypothesized common ancestor of the Orussoidea. This makes it impossible to retain Karatavitidae as a member of Ephialtitoidea. A fragmentation of Karatavitidae with the transfer of its genera to different clades (*Karatavites* to Apocrita, *Praeparyssites* and possibly *Grimmaratavites* gen. n. – to Orussomorpha), suggested by the anonymous reviewer to keep taxonomy correct cladistically, is rejected because it will inflate the number of higher-level categories at the base of the Vespina. Additionally, it would be impractical because, the genera in question are very close to each other both phylogenetically and phenetically. Preliminary observa-

tions of the Daohugou fossils indicate that loss of the anal loop, the only observable synapomorphy of Apocrita, may proceed gradually in the transition from *Praeratavites* to *Karatavites*. Hence attribution of these two genera to different infraorders would make the highest level taxonomy of the order built on a very shaky base. The strict cladistic approach in taxonomy has been questioned (Rasnitsyn, 1996), that is why we dare to retain the explicitly paraphyletic taxa Karatavitidae and Karatavitoidea. Because of the particularly smooth transition between Karatavitidae and Paroryssidae (via genera *Praeparyssites* and *Praeoryssus* Rasnitsyn, 1968), we include Karatavitoidea into the infraorder Orussomorpha, thus making it explicitly paraphyletic as well. The only plausible alternative, i.e. erection of a new infraorder for Karatavitidae, looks inadequate resulting in a redundant inflation of the system and creation a higher ranked paraphyletic taxon with a very weak diagnosis (ovipositor flat instead of round in cross section, and several rudimentary crossveins present).

The flat ovipositor of Karatavitidae (including the type genus: Rasnitsyn, 1969: fig.114) creates a problem that may concern mainly the phylogeny of Siricoidea (Protosiricidae + Anaxyelidae + Siricidae + Xiphydriidae); as defined here, this is a paraphyletic taxon (Vilhelmsen, 2001; Schulmeister, 2003). The flat, high, laterally compressed saw-like ovipositor is characteristic and apparently plesiomorphic for lower hymenopterans, viz. Xyelidae, Tenthredinoidea, and Cephoidea. The other extreme, the needle-like ovipositor (round or oval in cross-section) is characteristic of Siricidae, Anaxyelidae, and Apocrita, as well as of several unrelated subtaxa of *Xyela* Dalman, 1819 in Xyelidae, and of Trematothoracinae and *Onokhoius* Rasnitsyn, 1990 (Xyelulinae) within Sepulcidae. The intermediate character state, the compressed but low ovipositor, is found in Karatavitidae s.l. (not confirmed yet for *Praeparyssites*) as well as in several unrelated taxa within both Siricoidea (Xiphydriidae and possibly Protosiricidae) and Apocrita (various Ichneumonidae: Quicke et al., 1994: figs. 23, 76, 83, 126, 151). This suggests a choice between two hypotheses. One hypothesis suggests that a low, compressed ovipositor was acquired and retained in the main lineage of Siricoidea + Vespomorpha (Protosiricidae -> Xiphydriidae -> Karatavitidae -> basal Ichneumonidae), while the true needle-like ovipositor appears homoplastically in Siricidae, Anaxyelidae, Orussoidea, and in all main lineages within Apocrita. The alternative hypothesis is that the needle-like ovipositor can transform secondarily into the low, compressed one. This version leaves open a wealth of more detailed hypotheses on particular transformations pathways of the ovipositor in a particular lineage. E.g., that the low, compressed ovipositor is always secondary in respect to the needle-like. Or reverse, that it has been only derived once from the plesiomorphic, high-and-flat ovipositor, maybe in Xiphydriidae or in Protosiricidae, and then persisted continuously up to *Karatavites.* This version implies that the low-and-compressed ovipositor has homoplastically originated only in the higher apocritans (some Ichneumonidae). These hypotheses deserve to be explored, but they do not seem to impact on the above considerations on the phylogenetic and taxonomic position of the family Karatavitidae and its constituent genera.

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References

Ansorge, J. (2003) Insects from the Lower Toarcian of Middle Europe and England. *Proceedings of the Second Palaeoentomological Congress, Krakow 2001 – Acta Zoologica Cracoviensia* 46 *(suppl. – Fossil Insects)*: 291-310.

Martynov, A.V. (1925) To the knowledge of fossil insects from Jurassic beds in Turkestan. 3. Hymenoptera, Mecoptera. *Bulletin de l´Academie des sciences de l´URSS* 19: 753-762.

Nel, A., Petrulevicius, J.F. & Henrotay, M. (2004) New Early Jurassic sawflies from Luxembourg: the oldest record of Tenthredinoidea (Hymenoptera: "Symphyta"). *Acta Palaeontologica Polonica* 49: 283-288.

Quicke, D.L.J., Fitton, M.G., Tunstead, J.R., Ingram, S.N. & Gaitens, P.V. (1994) Ovipositor structure and relationships within Hymenoptera, with special reference to Ichneumonoidea. *Journal of Natural History* 28: 635-682.

Rasnitsyn, A.P. (1963) Late Jurassic Hymenoptera of Karatau. *Paleontologicheskiy Zhurnal* 1963 No 1: 86-99 (in Russian).

Rasnitsyn, A.P. (1968) New Mesozoic sawflies (Hymenoptera, Symphyta). 190-236, *in* Rohdendorf B.B. (ed.). *Jurassic insects of Karatau*. 252 pp, Nauka Press, Moscow: (in Russian).

Rasnitsyn, A.P. (1969) *Origin and evolution of lower Hymenoptera*. Trudy. Paleontologicheskogo Instituta Academii Nauk SSSR. 123 196 pp. Nauka Press, Moscow. (in Russian).

Rasnitsyn, A.P. (1980) *Origin and evolution of Hymenoptera*. Trudy Paleontologicheskogo Instituta Academii Nauk SSSR. 174. 192 pp. Nauka Press, Moscow. (in Russian).

Rasnitsyn, A.P. (1988) An outline of evolution of the hymenopterous insects (order Vespida). *Oriental Insects* 22: 115-145.

Rasnitsyn, A.P. (1996) Conceptual issues in phylogeny, taxonomy, and nomenclature. *Contributions to Zoology* 66 (1): 3-41.

Rasnitsyn, A.P., Ansorge, J. & Zessin, W. (2003) New hymenopterous insects (Insecta: Hymenoptera) from the Lower Toarcian (Lower Jurassic) of Germany. *Neues Jahrbuch für Geologie und Paläontologie* Abh. 227(3): 321-342.

Rasnitsyn, A.P. & Zhang Haichun (2004) Composition and age of the Daohugou hymenopteran (Insecta, Hymenoptera = Vespida) assemblage from Inner Mongolia, China. *Palaeontology* 47: 1507-1517.

Rasnitsyn, A.P., Zhang Haichun & Wang Bo (in press). Bizarre fossil insects: the webspinning sawflies of the genus *Ferganolyda* (Vespida, Pamphilioidea) from the Middle Jurassic of Daohugou, Inner Mongolia, China. *Palaeontology* 49(4): xx-xx.

Rasnitsyn, A.P. & Quicke, D.L.J. (eds.). (2002) *History of Insects*. xii + 517 pp. Kluwer Academic Publishers, Dordrecht.

Ronquist, F., Rasnitsyn, A. P., Roy, A., Eriksson, K. & Lindgren, M. (1999) Phylogeny of the Hymenoptera: A cladistic reanalysis of Rasnitsyn's (1988) data. *Zoologica Scripta* 28: 13-50.

Schulmeister, S. (2003) Simultaneous analysis of basal Hymenoptera (Insecta), introducing robust-choice sensitivity analysis. *Biological Journal of the Linnean Society* 79: 245-275.

Schulmeister, S., Wheeler, W. C. & Carpenter, J. M. (2002) Simultaneous analysis of the basal lineages of Hymenoptera (Insecta) using sensitivity analysis. *Cladistics* 18: 455-484.

Vilhelmsen, L. (2001) Phylogeny and classification of the extant basal lineages of the Hymenoptera. (Insecta). *Zoological Journal of the Linnean Society* 131: 393-442.

Vilhelmsen, L. (2004) The old wasp and the tree: fossils, phylogeny and biogeography in the Orussidae (Insecta, Hymenoptera). *Biological Journal of the Linnean Society* 82: 139-160.

Wootton, R.J. (1981) Support and deformability in insect wings. *Journal of Zoology* 193: 447-468.

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