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## MESOZOIC VESPIDAE

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### INTRODUCTION

Mesozoic Vespidae were first described from the wasps themselves by Rasnitsyn (1975), who assigned the new genus *Curiosivespa* to the Euparagiinae. The two species in the genus were collected in lower Upper Cretaceous deposits in Kazakhstan. Earlier, Brown (1941) had described *Celliforma favosites*, from the Upper Cretaceous in Utah, as the nest of a social wasp, but this assignment was disputed by Bequaert and Carpenter (1941). Wenzel (1990) argues that *Celliforma* is indeed a social wasp nest, but the subfamily cannot be specified. Rasnitsyn (1980) mentioned additional adult material from the Lower Cretaceous, but this remained undescribed until now. During a recent visit to the Museum of Comparative Zoology, APR was able to bring all of the known Mesozoic Vespidae for joint study with JMC. The present paper describes this material.

Mesozoic Vespidae have been collected at four localities, referred to in this paper under the following names. For more details concerning the insect assemblages found at these sites see Zherichin (1978) and Rasnitsyn (1988); for a review of the hymenopteran fauna see Rasnitsyn (1980).

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*Baissa*: lower Lower Cretaceous deposits of the Zaza Formation, on the left bank of the upper Vitim River, 3 km downstream from the former winter lodge Baysa and 45 air km upstream from Romanovka Village, in the Buryatskaya Republic of the U.S.S.R.

*Turga*: deposits of approximately the same age as the Turga Formation, on the right bank of the Turga River, 1.5 km from the mouth of the Byrka River, Borzya District of the Chita Region of the U.S.S.R.

*Bon-Tsagan*: upper Lower Cretaceous deposits probably of Barremian or Aptian age, 5–8 km north of Boon Tsagaan Nuur Lake, Bayanhongor Aymag [Region] in Central Mongolia.

*Kzyl-Zhar*: lower Upper Cretaceous deposits of Turonian age, Kzyl-Zhar Hill at Kzyl-Zhar well in the northern part of the Karatau Range, Chiili District of the Kzyl-Orda Region, Kazakh Republic of the U.S.S.R.

Morphological terminology largely follows Carpenter (1981, 1989), except that the recommendations of Day (1988) on wing venation are adopted here. Thus, CuA is used instead of Cu<sub>1</sub> and its branches are denoted CuA<sub>1</sub> and CuA<sub>2</sub>, A instead of 1A, rs-m for the crossveins previously termed r-m, the marginal cell is R instead of 3R<sub>1</sub>, first discal cell (RS+M) is used instead of discal and (M<sub>1</sub>), first subdiscal cell (1CuA) is used instead of second discoidal and (Cu<sub>1b</sub>), and subbasal cell is substituted for submedian.

#### KEY TO MESOZOIC VESPIDAE

1. Forewing with first subdiscal cell (1CuA) strongly produced dorsoapically, abscissa of CuA beyond 1m-cu strongly recurrent, almost aligned with 1m-cu; first discal cell (RS+M) much longer than subbasal cell (M+CUA); first abscissa of M longer than RS+M (Figs. 1– 5)
  - Curiosivespa* Rasnitsyn, (Euparagiinae) 2
- Forewing with first subdiscal cell not produced, CuA beyond 1m-cu at most weakly recurrent, angled with 1m-cu; first discal cell ≤ subbasal cell; first abscissa of M with length subequal to that of RS+M (Figs. 6–11)
  - Priorvespa*, n. gen., (Priorvespinae, new subfamily) 5

2. Forewing with CuA<sub>2</sub> smoothly aligned with A (Figs. 1-3);  
Upper Cretaceous species 3
- Forewing with CuA<sub>2</sub> angled with A (Figs. 4-5); Lower Cretaceous species 4
3. Forewing length about 10 mm; first subdiscal cell longer than length of all submarginal cells combined (Figs. 1-2)  
*Curiosivespa curiosa* Rasnitsyn
- Forewing length about 20 mm; first subdiscal cell shorter (Fig. 3)  
*Curiosivespa magna* Rasnitsyn
4. Forewing with 2m-cu received in second submarginal cell (1RS); pterostigma probably very short (Fig. 4)  
*Curiosivespa derivata*, n.sp.
- Forewing with 2m-cu received in third submarginal cell (2RS); pterostigma much longer than pterostigma (Fig. 5)  
*Curiosivespa antiqua*, n. sp.
5. Forewing with second abscissa of M and RS+M aligned in a straight line; second abscissa of M more than half the length of the first abscissa of RS (Fig. 10)  
*Priorvespa directa*, n.sp.
- Forewing with second abscissa of M and RS+M angled; M shorter than half the length of RS (Figs. 6-9, 11) 6
6. Hindwing with first abscissa of CuA about half as long as cu-a; forewing with second discal cell (1M) produced into a narrow pocket posterobasally; head very short, wide (Fig. 11)  
*Priorvespa bullata*, n.sp.
- Hindwing with first abscissa of CuA shorter (Figs. 6-8); forewing with second discal cell not so produced posterobasally (Figs. 6-9); head normal (Figs. 6-7) 7
7. Forewing with cu-a situated slightly basad of the fork of M and CuA; forewing length 11-12 mm (Figs. 7-8)  
*Priorvespa quadrata*, n.sp.
- Forewing with cu-a situated distad of the fork of M and CuA; forewing length about 6-8 mm (Figs. 6, 9) 8

8. Forewing with second submarginal cell higher than long; abscissa of CuA beyond 1m-cu recurrent (Fig. 6)  
*Priorvespa recidiva*, n.sp.
- Forewing with second submarginal cell longer than high; CuA beyond 1m-cu almost vertical (Fig. 9)  
*Priorvespa minuta*, n.sp.

An additional new species, *Priorvespa longiceps*, cannot be keyed because the forewings are absent. It belongs in Vespidae, because of the presence of subocular furrows (“lateral sulcus of the postgena” of Duncan, 1939; actually the occipital suture, see Tikhomirova and Rasnitsyn, 1981), and can be placed in Priorvespinae because of the apically wide hindwing subbasal cell.

#### TAXONOMY

Family Vespidae Latreille, 1802

Subfamily Euparagiinae Ashmead, 1902

*Curiosivespa* Rasnitsyn, 1975

*Curiosivespa* Rasnitsyn, 1975:113 [Eumenidae in text, Masaridae Euparagiinae in footnote].

Type species *Curiosivespa curiosa* Rasnitsyn, 1975, by original designation.

Head with eyes long, emarginate; tempora moderately wide in lateral view; gena narrow. Antenna (in specimen of unknown sex) with all articles elongate, flagellomeres very thin. Mesopleuron with dorsal groove and lower part of scrobal furrow aligned, precoxal sulcus subparallel to this; metapleuron not constricted at endophragmal pit, lower part (katepisternum) well differentiated from upper part (anepisternum) and propodeum, with episternal line running anteroventrally from pit. Forewing as in *Euparagia* Cresson (first subdiscal cell strongly produced dorsoapically, second abscissa of CuA almost aligned with 1m-cu, first discal cell much longer than subbasal cell, first abscissa of M longer than RS+M, cu-a long and curved) except third submarginal cell at most subequal to second in length, not extending as far as the apex of the marginal cell, and 3rs-m smoothly curved instead of strongly sinuous. Body moderately slender. Metasoma moderately elongate; first segment probably longer than wide but not petiolate; no evident constriction between segments.

*Curiosivespa curiosa* Rasnitsyn, 1975 (Figs. 1, 2)

*Curiosivespa curiosa* Rasnitsyn, 1975:114, fig. 127a.

*Curiosivespa magna* Rasnitsyn, 1980: fig. 197b (misidentification)

The skeletal characters from the generic description above are based on a representative of this species originally (Rasnitsyn, 1980) erroneously identified as *magna*, but its small size and long second abscissa of CuA indicate that it is *curiosa*.

Scape longer than half eye height; pedicel twice as long as wide; length of first flagellomere about half eye height and about 10× width; second flagellomere about two thirds the length and width of the first; third flagellomere of similar length but still narrower. Forewing with pterostigma of moderate size; R<sub>1</sub> beyond this along wing margin; second submarginal cell about as long as high, longer than third submarginal (subequal in paratype evidently due to wing deformation), with basal angle acute and not clearly situated above mid-height of cell; third submarginal cell much shorter than high; 2m-cu inserting on M scarcely beyond 2rs-m; second abscissa of CuA longer than 1m-cu; CuA<sub>2</sub> aligned with A in a smooth curve; cu-a beyond fork of M and CuA. First metasomal segment probably longer than wide, of subtriangular form; second segment much shorter; each succeeding segment a little shorter than preceding except sixth which is subequal to the third. Size small: forewing length 10 mm, body length 13 mm. Thoracic sides and venter of lighter color than head and metasoma. Integument without coarse sculpture.

Material examined: holotype No. 2383/143 and specimen No. 2783/261, both from Kzyl-Zhar.

*Curiosivespa magna* Rasnitsyn, 1975 (Fig. 3)

*Curiosivespa magna* Rasnitsyn, 1975:114, fig. 127b.

Forewing with pterostigma moderately long; R<sub>1</sub> clearly separated from wing margin for most of its length; second submarginal cell longer than high, longer than third submarginal, with basal angle acute and clearly situated above mid-height of cell; second abscissa of CuA shorter than 1m-cu; CuA<sub>2</sub> aligned with A in a very obtuse angle; cu-a beyond fork of M and CuA. Size large: forewing length 22 mm.

Material examined: holotype no. 2783/190; Kzyl-Zhar.



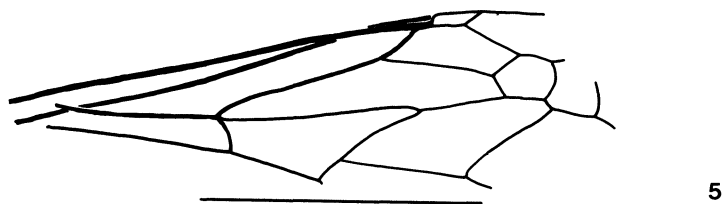
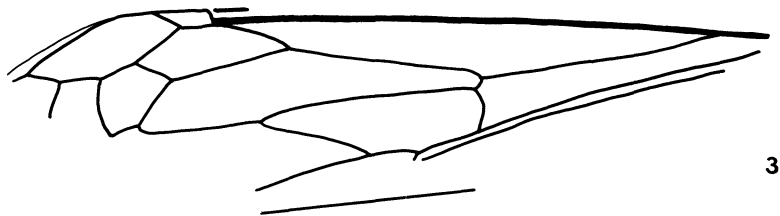


Fig. 3. *Curiosivespa magna* Rasnitsyn, holotype.

Fig. 4. *Curiosivespa derivata* n. sp., holotype.

Fig. 5. *Curiosivespa antiqua* n. sp., holotype.

of cell; 2m-cu received in second submarginal cell; second abscissa of CuA shorter than 1m-cu; CuA<sub>2</sub> aligned with second abscissa of CuA and strongly angled with A; cu-a at fork of M and CuA. Size moderate: forewing length 15 mm.

Material examined: holotype No. 3559/4527; Bon-Tsagan, site 87-8.

Etymology: the name refers to the inferred apomorphic condition of the pterostigma and 2m-cu.

***Curiosivespa antiqua* Carpenter *et* Rasnitsyn, n.sp (Fig. 5)**

Forewing covered with setae as in preceding species, or slightly sparser; pterostigma moderately long; R<sub>1</sub> beyond this probably

along wing margin; second submarginal cell longer than high, a little longer than third submarginal, with basal angle more than  $90^\circ$ , not above cell mid-height; 2m-cu received in third submarginal cell; second abscissa of CuA subequal to 1m-cu; CuA<sub>2</sub> more or less aligned with second abscissa of CuA and strongly angled with A; cu-a scarcely beyond fork of M and CuA. Size small: forewing length 12 mm.

Material examined: holotype No. 3064/2063; Baissa, bed 15.

Etymology: the name refers to the great age of this species.

Subfamily **Priorvespinae** Carpenter et Rasnitsyn, new subfamily

Type genus **Priorvespa** Carpenter et Rasnitsyn, n.gen.

Head with clypeus very short and wide, reaching antenna bases and produced slightly between them; preoccipital carina and subocular furrow both present. Mouth parts short; prementum subquadrate; stipes narrow. Forewing not longitudinally plaited; with first discal cell shorter than subbasal, unlike other Vespidae except Gayellini; first abscissa of M shorter than RS+M; 2m-cu received in third submarginal cell; 3rs-m sinuous; first subdiscal cell not elongated dorsoapically, with 1m-cu aligned with first and not second abscissa of CuA, unlike Euparagiinae; cu-a long and curved, unlike other Vespidae except Euparagiinae. Hindwing with cu-a inserting on CuA after its divergence from M+CuA, strongly angled with A; subbasal cell wider at divergence of A than other Vespidae. Metasoma with first segment somewhat narrowed.

Etymology: the name denotes the relatively basal relationship of this group to other Vespidae.

**Priorvespa** Carpenter et Rasnitsyn, n.gen.

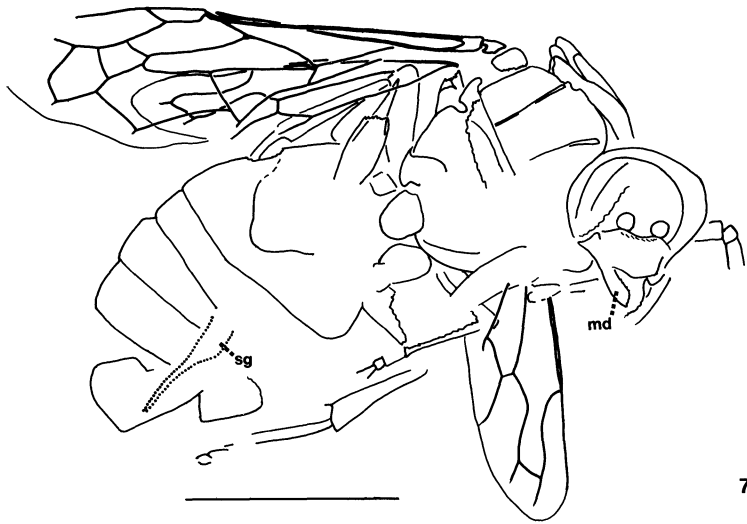
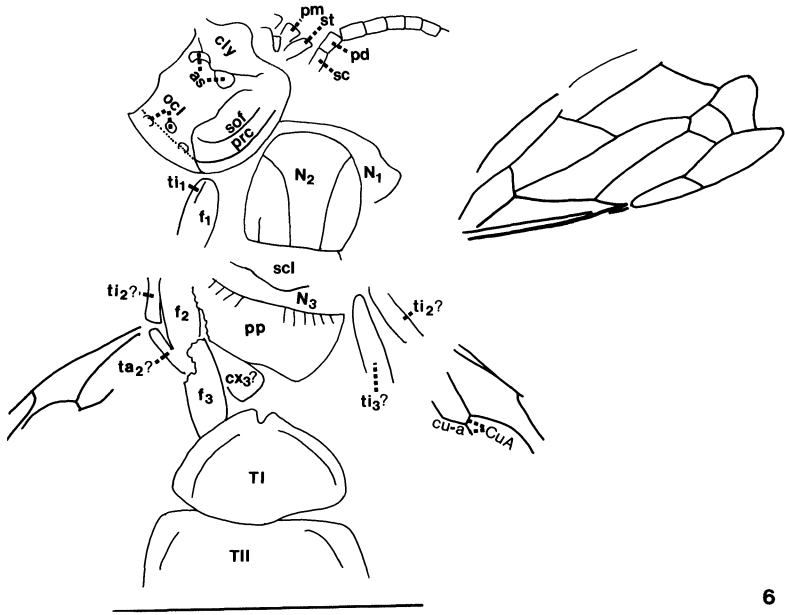
Type species *Priorvespa recidiva* Carpenter et Rasnitsyn, n.sp.

Head transverse; ocellar triangle low; eyes large, weakly emarginate; antennae with flagellomeres not elongated; clypeal apex rounded, projecting; subocular furrows subparallel to preoccipital carina laterally. Propodeum short, longitudinally ridged basally

Fig. 6. *Priorvespa recidiva* n. sp., holotype. as-antennal socket; cly-clypeus; f<sub>2</sub>-midfemur; ocl-ocellus; pm-prementum; prc-preoccipital carina; sof-subocular furrow; st-stipes; ta<sub>2</sub>-midtarsus; ti<sub>2</sub>-midtibia; TII-second metasomal tergum; other abbreviations as in Figs. 1 and 2.

Fig. 7 *Priorvespa quadrata* n.sp., holotype. md-mandible; sg-sting.





except medially. Wings as described above. First metasomal segment with anterolateral line, interrupted medially (unless it reflects some internal structure), with length about half width. Second metasomal tergum with similar lateral line at least basally.

**Priorvespa recidiva** Carpenter *et* Rasnitsyn, n. sp. (Fig. 6)

Lateral ocelli separated from eye by less than their diameter, separated from median ocellus by about their diameter. Interantennal distance about half the diameter of the antenna sockets. Scape short as seen, but probably incomplete; pedicel cylindrical, length subequal to third flagellomere; flagellomeres (five basal ones seen) with length about 1.2–1.3× width, reduced in size apically. Clypeal length about 0.7× width. Forewing with prestigma very short; marginal cell not appendiculate; second submarginal cell short and high; third submarginal cell much longer; 2rs-m arched; M angled at 1 m-cu; second abscissa of CuA recurrent; CuA<sub>1</sub> not strongly curving to form posterobasal pocket in second discal cell; cu-a distal to fork of M and CuA. Hindwing with first abscissa of CuA short; A hardly visible beyond cu-a. Size small: forewing length probably 7–7.5 mm; body length scarcely more than twice this. Color of body more or less dark; flagellum, tibiae and tarsi lighter. Metasomal sculpturing not coarse; mesosomal sculpturing possibly the same.

Material examined: holotype No. 3559/4532; Bon-Tsagan, site 87–8.

Etymology: the name refers to the recurrent second abscissa of CuA.

**Priorvespa quadrata** Carpenter *et* Rasnitsyn, n.sp. (Figs 7, 8)

Head little transverse. Scape not very long; pedicel subquadrate. Clypeus wide, moderately long, apically wide and subtruncate, dorsally weakly bisinuate, reaching antennal sockets. Preoccipital carina and subocular furrow converging towards mandibular base. Mandible moderately long. Transscutal and scuto-scutellars sutures well defined, separated. Tegula large. Forewing with prestigma moderately long; marginal cell appendiculate; second submarginal cell slightly longer than high, a little shorter than third; 2rs-m arched; M angled at 1m-cu; second abscissa of CuA somewhat recurrent; CuA<sub>1</sub> not strongly curving to form posterobasal pocket in second discal cell; cu-a slightly basal to fork of M and CuA. Hind-

wing with first abscissa of CuA *ca.* 0.35–0.4× length of cu-a. Coxae short; femora not wide; tibiae slightly longer than femora; basitarsi long, remaining tarsomeres short. Size moderate: forewing length 11 mm, body length *ca.* 15 mm. Color dark, hind tibiae lighter except apically.

Material examined: holotype No. 3559/4537; Bon-Tsagan, site 87–8; paratype No. 3554/698; Bon-Tsagan, site 45–19.

Etymology: the name refers to the quadrate second submarginal cell.

**Priorvespa minuta** Carpenter *et* Rasnitsyn, n.sp. (Fig. 9)

Forewing with prestigma short; marginal cell weakly appendiculate; second submarginal cell longer than high, scarcely shorter than third submarginal; 2rs-m arched; M angled at 1m-cu; second abscissa of CuA not recurrent; CuA<sub>1</sub> not strongly curving basally; cu-a distal to fork of M and CuA. Size small; forewing length 6.5 mm.

Material examined: holotype No. 3559/716; Bon-Tsagan, site 45–19.

Etymology: the name is from the small size of this species.

**Priorvespa directa** Carpenter *et* Rasnitsyn, n.sp. (Fig. 10)

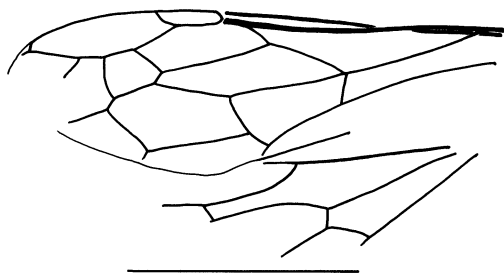
Mesosomal structure difficult to interpret because of deformation. Forewing with prestigma very short; second submarginal cell much longer than high; 2rs-m and M before 2rs-m straight; cu-a distal to fork of M and CuA. Hindfemur short and wide, almost half the length of the tibia. First metasomal tergum with length and width subequal, constricted anteriorly, laterally rounded, with two sublateral lines converging basally. Second metasomal tergum almost circular except basally, with thin sublateral line, longer and wider than first tergum. Size moderate: forewing length about 10–11 mm. Mesosomal integument coarsely punctate in part; metasomal integument without coarse sculpturing.

Material examined: holotype No. 3559/685; Bon-Tsagan, site 35.

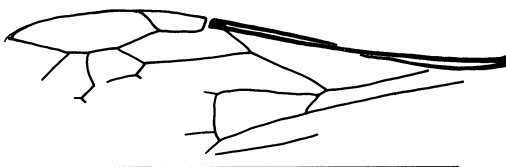
Etymology: the name is for the straight M and 2rs-m veins.

**Priorvespa bullata** Carpenter *et* Rasnitsyn, n.sp. (Fig. 11)

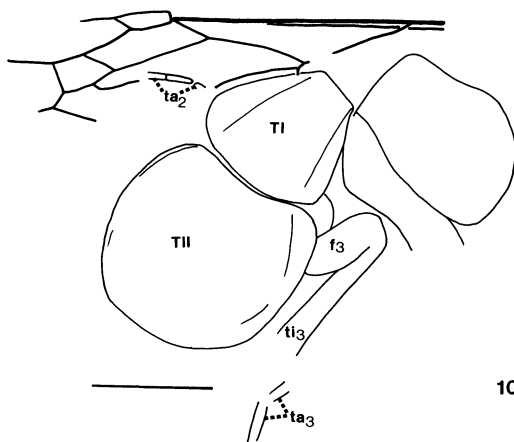
This species is quite distinctive in the form of the head and of the second discal cell, but has the apically wide hindwing subbasal cell found in other members of this group.



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Fig. 8. *Priorvespa quadrata* n.sp., specimen No. 3559/698.

Fig. 9. *Priorvespa minuta* n.sp., holotype.

Fig. 10. *Priorvespa directa* n.sp., holotype. ta<sub>2</sub>—hindtarsus; ti<sub>3</sub>—hindtibia; other abbreviations as in Figs. 2 and 6.

Head short, morphology difficult to interpret. Clypeus apically rounded, unless this is the labrum, in which case the clypeus is truncate. Vertex possibly with rounded, raised area that includes ocelli (only lateral ocelli seen), with impression anterior to ocelli. Head posteriorly with preoccipital carina and a pair of long oval impressions, possibly modified subocular furrows—otherwise these could be the eyes, but then of highly unusual size and form. Mandibles long, straight, tapering, and combined with the clypeus possibly not produced, they recall some ant mandibles rather than those of vespids. Mesosoma stout, propodeum short. Forewing with prestigma moderately short; second abscissa of CuA not recurrent; CuA<sub>1</sub> strongly curving to form posterobasal pocket in second discal cell; cu-a basal to fork of M and CuA; wing apex not seen. Hindwing with first abscissa of CuA longer than half the length of cu-a; A clearly visible beyond cu-a. Legs not long, femora a little narrowed apically. First three metasomal segments transverse; second sternum with basal furrow crenate, anterior rim thick and arching downward. Size moderate: forewing length to the apex of the pterostigma 7.5 mm, probably with a full length of about 12 mm, body length 15 mm. Color dark. Integument probably without coarse sculpture, at least on metasoma.

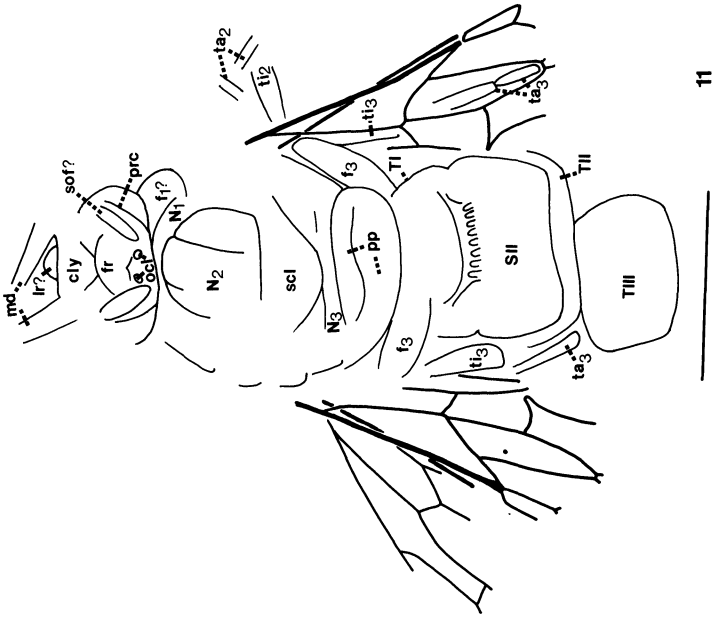
Material examined: holotype No. 4210/1201; Baissa, bed 22.

Etymology: the name refers to the posterobasal pocket in the second discal cell.

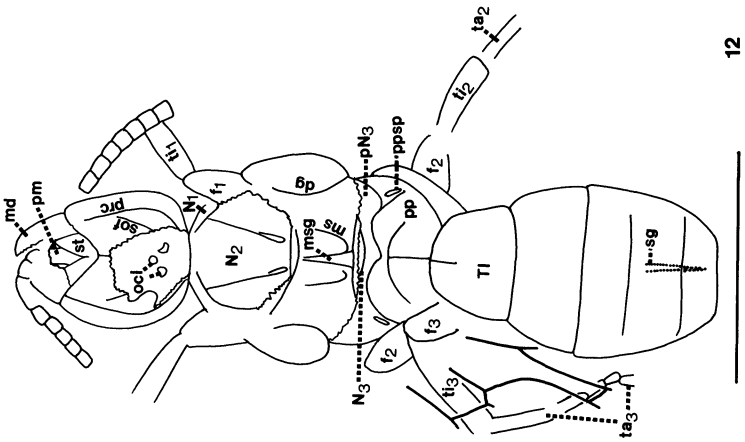
***Priorvespa longiceps* Carpenter *et* Rasnitsyn, n.sp. (Fig. 12)**

Although the forewings are absent, this fossil belongs to the Vespidae as shown by the subocular furrows, which are not contradicted by other characters. The specimen can be assigned to the *Priorvespinae* because of its apically wide hindwing subbasal cell.

Head long, slightly tapered; eyes probably strongly emarginate with upper lobe small; ocellar triangle moderately low; subocular furrows not reaching preoccipital carina; preoccipital carina extending to hypostoma near mandibular bases. Mandibles moderately long, broad, with external margin weakly curved, possibly aligned along clypeus margin and not decussate, although the clypeus itself is not preserved. Flagellum short, becoming thicker toward apex, flagellomeres subquadrate except basal two, which have a length about 1.3–1.5× width; flagellomeres covered with numerous small,



11



12

subcircular sensilla. Mesosoma above dorsal groove evidently bulging; precoxal sulci visible near median sternal groove, diverging anteriorly; metapostnotum narrow, posteromedially produced; propodeum short, with curved transverse line and longitudinal line beyond this; propodeal spiracle near and subparallel to unidentified suture, not long. Hindwing with cu-a inserting on CuA after its divergence from M+CuA, strongly angled with A; subbasal cell wide at divergence of A; A clearly visible beyond cu-a. Femora and tibiae short, stout; femora narrowing apically. Metasoma small; first segment narrowed anteriorly, little wider than long, with median longitudinal line in anterior third; succeeding segments short and wide; second tergum distinctly constricted at intersegmental boundary with first. Size moderate: body length 15 mm. Color of head, mesosoma, metasomal tergum IV and III laterally, dark, possibly legs and antennae also, rest of metasoma lighter. Integument without coarse sculpture.

Material examined: holotype No. 1742/141; Turga.

Etymology: the name refers to the elongate head.

#### RELATIONSHIPS

##### *Curiosivespa*

This genus is clearly correctly placed in Euparagiinae, as shown by its possession of dorsoapically produced first subdiscal cell. This is the outstanding apomorphy of the subfamily (Carpenter, 1981). Other features of the wing venation accord with those of extant members of the subfamily, with the exception of the radial region. Unlike *Euparagia*, *Curiosivespa* has the second and third submarginal cells approximately equal in length, the third not extending as far as the apex of the marginal cell, and the 3rs-m vein slightly curved instead of strongly sinuous. The condition of 3rs-m is certainly derived within Vespidae, as extant species have this vein strongly sinuous, including *Euparagia* and Masarinae (except

Fig. 11. *Priorvespa bullata* n.sp., holotype. fr—frons; lr—labrum; SII—second metasomal sternum; TIII—third metasomal tergum; other abbreviations as in Figs. 2, 6, 7, and 10.

Fig. 12. *Priorvespa longiceps* n.sp., holotype. msg—median sternal groove; pN<sub>3</sub>—metapostnotum; ppsp—propodeal spiracle; other abbreviations as in Figs. 2, 6, 7, and 10.

*Paramasaris*, where it is straight). This is also the state in *Priorvespa*, which is here inferred to be the most basal Vespidae. By contrast, the subequal submarginal cells and third not extending as far as the apex of the marginal cell are perhaps plesiomorphic. The former is a general condition in those subfamilies with three submarginal cells (not Gayellini nor Stenogastrinae, but the latter have the second longer than the third, which is certainly derived), while the latter is general except for Masarini (which have only two submarginal cells, with the composite second extending as far as the marginal cell). In any event, the elongated shape of the third submarginal cell in *Euparagia* is at least an exaggeration of that found in other Vespidae. The recognition of two genera in Euparagiinae thus appears justified on the grounds of separate apomorphies, coupled with the great difference in age and distribution.

Extant Euparagiinae comprise the genus *Euparagia*, which is known from nine species endemic to southwestern North America (Bohart, 1989). The Lower Cretaceous–lower Upper Cretaceous Central Asian *Curiosivespa* indicates that the subfamily is of Laurasian origin, contrary to Carpenter (1981), who suggested that it might possibly be southern.

### *Priorvespa*

This genus cannot be placed in any extant subfamily of Vespidae based on the characters of the forewing venation. Plesiomorphic states of the forewing are the first discal cell shorter than the subbasal (other Vespidae except Gayellini have it at least as long; Gayellini are inferred to have a secondary shortening of the cell, Carpenter, 1981, 1989), the first abscissa of M shorter than RS+M (the condition varies only within Masarinae), 2m-cu received in the third submarginal cell (found in Euparagiinae, Gayellini and a few Eumeninae; see Carpenter, 1981), 3rs-m sinuous, the first subdiscal cell not elongated dorsoapically with 1m-cu aligned with the first and not the second abscissa of CuA (the alternative comprises the diagnostic apomorphy of Euparagiinae; see above), and cu-a long and curved (found in Euparagiinae). This combination of characters is uniquely primitive in Vespidae, and based just on this, *Priorvespa* could be the ancestral or stem-group of the entire family.

By contrast, the hindwing has what are perhaps derived features: cu-a inserting on CuA after its divergence from M+CuA (found in Eumeninae + Stenogastrinae + Polistinae + Vespinae) and the



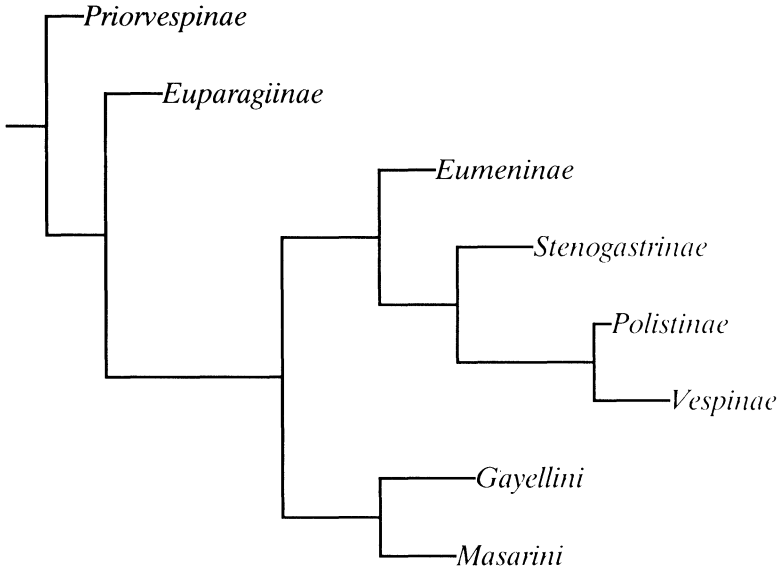


Fig. 13. Cladogram resulting from analysis of the data of Table 1, including an ancestor, with the exact algorithm of Hennig86 (Farris, 1988). The length is 45, the consistency index is 0.75, and the retention index is 0.76.

subbasal cell wider at the divergence of A than other Vespidae. The insertion of cu-a before the divergence of M+CuA was inferred by Brothers (1975) to be plesiomorphic in Aculeata as a whole; in Vespidae this state is found only in Gayellini, which is apparently secondary (Carpenter, 1981). Euparagiinae has cu-a inserting at the divergence of M+CuA, and Masarini has it inserting after, but aligned rather than angled with A (secondarily angled in species of the *Quartinia* group). The diverse conditions in Euparagiinae and Masarinae, the relatively basal taxa, led to the inference of an apomorphy in the Eumeninae + Stenogastrinae + Polistinae + Vespinae clade (Carpenter, 1981), despite the vespidae groundplan being unclear. The state in *Priorvespa* may thus represent a convergent development with this clade, but the conditions in Euparagiinae and Masarinae could have been derived from this state. That is, it might be the vespidae groundplan, an interpretation that would accord with the view of *Priorvespa* as ancestral. By contrast, the subbasal cell wide at the divergence of A is unique in Vespidae, but occurs com-

monly in various other aculeates. In view of the current uncertainty regarding the sister-group of Vespidae (*cf.* Brothers, 1975; Rasnitsyn, 1988; Carpenter, 1990) the polarity is unclear. In the absence of other information (i.e., specific reasons for not doing so) we are treating the state diagnostic of *Priorvespa* as a tentative apomorphy.

The effect of these considerations is that *Priorvespa* is best treated as monophyletic, and must be assigned to a new subfamily. This subfamily is then the sister-group of other Vespidae. This is shown by cladistic analysis of the data of Table 1. These are the informative characters of the vespidae subfamilies and tribes recognized by Carpenter (1981); autapomorphies are not included except as parts of a multistate transformation series. *Priorvespa* has been scored for these features, and despite the large proportion of missing data, there is only one parsimonious cladogram for these data (Fig. 13), placing Priorvespinae as the sister-group of the remainder of the family.

#### SUMMARY

The Mesozoic Vespidae are reviewed. Two subfamilies are known from Cretaceous deposits in Mongolia, Kazakhstan and Siberia. *Curiosivespa* Rasnitsyn is a representative of the Euparagiinae; two new species, *derivata* and *antiqua*, are added to the known fauna. *Priorvespa* is newly described, and represents a new subfamily, which is evidently the most basal group of Vespidae. Six species are described: *recidiva* (the type species), *quadrata*, *minuta*, *directa*, *bulbata*, and *longiceps*.

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Table 1. Informative data for vespid subfamilies and tribes coded from Carpenter (1981). The Mesozoic *Priorvespa* has been scored for these characters.

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Characters

1. Forewing longitudinal plaiting. None 0, present 1.
2. Forewing first discal cell length. Shorter than subbasal cell 0, as long or longer 1.
3. Forewing cu-a curve. Present 0, none 1.
4. Forewing cu-a length. Long 0, short 1.
5. Forewing recurrent veins. Received in two cells 0, in one 1.
6. Forewing marginal cell. Rounded away from margin 0, rounded toward apex 1, pointed 2.
7. Hindwing jugal lobe. Large 0, small 1, absent 2. Not ordered additively.
8. Hindwing cu-a. Transverse 0, angled with A 1, aligned with A 2. Not ordered additively.
9. Hindwing CuA. Diverging at cu-a 0, distal to cu-a 1, basal to cu-a 2. Not ordered additively.
10. Acroglossal buttons. None 0, present 1.
11. Posterior lingual plate. Narrow 0, broad 1.
12. Preoccipital and postocular carinae. Present 0, fused 1, evanescent 2.
13. Hypostomal apodemes. None 0, present 1.
14. Scutal lamella. Present 0, none 1.
15. Scutellum. Rounded 0, pointed 1.
16. Trochantellus. Present 0, none 1.
17. Coxa. Smooth 0, carinate 1.
18. Claws. Simple 0, toothed 1.
19. Metasomal tergum and sternum I. Unfused 0, fused 1.
20. Metasomal retraction. None 0, present 1.
21. Parameral spines. Present 0, reduced 1.
22. Volsella. No apodeme present 0, present 1.
23. Van der Vecht's gland. None 0, present 1.
24. Larval clypeus. Broad 0, narrow 1.
25. Provisions. Insects 0, pollen 1.
26. Sociality. None 0, progressive provisioning 1, permanent eusociality present 2, long-term monogyny 3.

Taxa

Priorvespinae	?00000?12????0???????????
Euparagiinae	01000000100000100000000000
Gayellini	00110010010011010111000010
Masarini	01111012210011110100000010
Eumeninae	11111111210100001211000000
Stenogastrinae	01111211200200000111000101
Polistinae	11111211211100000011111102
Vespinae	11111221211100001011111103

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