

The most advanced family Curculionidae, appeared in the Early Cretaceous of Asia, but have yet to be found in the Crato Formation.

11.18 Hymenoptera: bees, wasps and ants

Till Osten

Hymenoptera is one of the most diverse Recent insect orders with at least 110,000 described species. The eusocial lifestyle and forming of complex societies with castes in some of the families (Formicidae, Vespidae and Apidae) also accounts for the fact that Hymenoptera are the most individual-rich insect group, which has conquered nearly all suitable biotopes. Consequently, the probability of fossilization should also be relatively high (Burnham, 1978). Nonetheless, the work of Darling and Sharkey (1990) and Martill (1993) documented comparatively few fossils of this group for the Crato Formation. In contrast to this, Rasnitsyn (1988; see also Grimaldi, 1990 and Grimaldi and Engel, 2005) presents a comprehensive summary of fossilized Hymenoptera from the Cretaceous from various other localities, which documents representatives from nearly all Recent families as well as several extinct families. Wasps from the group Parasitica are the most abundant elements, followed by Aculeata and comparatively few 'Symphyta'.

However, the Hymenoptera from the Crato Formation that were studied for this work show yet another grouping. The evolution, especially of the social Aculeata, had still not progressed far at this point in the Earth's history. The eusocial societies of the primitive Formicidae, Vespidae and Apidae consisted only of a few individuals; the separation into castes and therefore the increase of number of individuals had only just begun. Within the most primitive Formicidae ('Ponerinae', Myrmecinae) this condition is still visible today (Wilson, 1971; Hölldobler and Wilson, 1990).

In most cases, the preservation of the fossils only allows a rough identification to familial level, and in some cases to subfamily or genus and even the description of new species. In contrast to amber inclusions, the specimens can usually only be examined from the single preserved side, and the important characters for confident determinations are often not visible.

Of special importance is the first record of a fossilized Sapygidae of the subfamily Fedtschenkiinae. However, some characteristics are unfortunately not visible in this specimen (shape of the compound eyes, toruli and the cleft between first and second sternum). Only the comparison with Recent material, and morphologically similar but unrelated representatives of the Vespoidea (Tiphidae, Sapyginae), allowed a determination and classification by successive exclusion of all other possibilities. The primitive aculeate Hymenoptera of the Lower Cretaceous were still very similar,

and their group-defining characteristics were not as well developed or not developed at all compared with Recent representatives.

Only very vague conclusions about the habitat and the climate can be made on the basis of the fossil Hymenoptera assemblage of the Crato Formation. Overall, it seems that the habitat was very heterogeneous, with relatively humid biotopes with rather dense vegetation, as well as dry and relatively hot savannah and desert areas with sparse vegetation.

‘Symphyta’: sawflies

The Anaxyelidae–Syntexinae (Plates 15f and g) and Siricidae (Plate 15h) were the predominant groups in the Mesozoic. From the former family, the holotype (AMNH 43270) of *Prosyntexis gouleti* (Figure 11.76b) was described by Darling and Sharkey (1990), but Rasnitsyn *et al.* (1998) transferred the genus *Prosyntexis* to the family Sepulcidae in the subfamily Thrematothoracinae. Martins-Neto *et al.* (2007) described a second species, *Prosyntexis legitima*, in the family Sepulcidae. The family Siricidae (female specimen without number in coll. MURJ; Plate 15h) is reported here for the first time for the Crato Formation.

Apocrita/Parasitica: parasitic wasps

Cratephialtites kourios of the family Ephialtitidae is not rare in the Crato Formation. Darling and Sharkey (1990) had described the species as genus *Karatous* based on two specimens (AMNH 43269 and 43263; Figure 11.75d). A further specimen (AMNH 46321) was published by Grimaldi and Engel (2005: figure 11.11), and a similar, undescribed specimen has been studied by the author (SMNS 66296). However, a new specimen without number in coll. MURJ shows crucial new details of the legs and particularly the complete wing venation (Plates 15j and k). In the same collection, a possible representative of the Ichneumonoidea (Plate 15i) can be found which would be a first record of this group for the Crato Formation. Apart from these, only the families Proctotrupidae (*Protoprocto asodes*, AMNH 44101; Figure 11.76a) and Mesoserphidae (AMNH 43272; Figure 11.74) have been recorded by Darling and Sharkey (1990).

The parasitic larvae of the Apocrita prefer as hosts the adults, larvae and eggs of species of the orders Lepidoptera, Hymenoptera (‘Symphyta’), and Diptera.

Apocrita/Aculeata: stinging wasps

The Apoidea (Apidae+‘Sphecidae’) represent nearly 50% of the fossil aculeate Hymenoptera from this locality. Their abundance suggests a rich flower assemblage

as a food resource for the adult animals, thus also a moderately dry and warm climate. Furthermore, a large and suitable contingent of food (spiders and insects such as Diptera, Hymenoptera, Orthoptera, Lepidoptera or Coleoptera and their larvae) must have been available for the larval development of the 'Sphecidae'. A sufficient amount of nectar and pollen must also have been available for the Apidae and their larvae.

The Vespoidea are represented by Scoliidae–Archaeoscoliinae (Figure 11.72c), some Tiphiidae (Rasnitsyn, 1986a; Figure 11.72a, Plates 15n and o), a single specimen of Sapygidae–Fedtschenkiinae (Figure 11.72b), and one questionable Mutillidae and Pompilidae (Plate 15l), as well as some Vespidae–Eumenidae (Carpenter and Rasnitsyn, 1990) (Plate 15p) and two specimens of the Formicidae–Myrmeciinae (Figure 11.77, Plate 15m; Wilson *et al.*, 1967; Wilson, 1985; Brandao *et al.*, 1989). These representatives of the Vespoidea rather suggest a dry, very warm, subtropical climate. Some areas might have had a savannah or desert-like type of vegetation (*Salicornia*-, *Salsola*- or *Arthemisia*-steppe for Fedtschenkiinae). These Vespoidea need other insects or spiders for the development of their larvae. Except for Formicidae, the adult animals are mostly visitors to flowers.

Mesorhopalosoma ceareae (holotype AMNH 44266, and two further specimens AMNH 43276 and 44109; Figures 11.75f and g), which was described by Darling and Sharkey (1990) as a species of Rhopalosomatidae, definitely does not belong to the Rhopalosomatidae or Pompilidae, but is more likely a further representative of the Angarosphecidae ('Sphecidae').

Pompilidae: spider wasps

Currently, only a single fossil that could be a possible representative of this family is known from the collection of MURJ (Plate 15l). This is even more surprising, as the Pompilidae are surely a very old subgroup of the Aculeata. This is already shown in their very limited prey spectrum, which the adults catch as food for their larvae: all Pompilidae exclusively hunt spiders, which explains their English vernacular name, spider wasps. Fossil spiders are relatively frequently found in the Crato Formation. The Pompilidae are cosmopolitan, but around 4,200 species populate tropical areas (Ceropalinae, Pepsinae, Pompilinae). The present fossil could belong to the subfamily Pompilinae due to its coiled antenna, the shape of the compound eyes, the pronotum, the wing venation (so far as can be seen), the comparatively short hind legs and the wide metasoma.

Formicidae: ants

The fossil record of ants (Figure 11.77, Plate 15m) is quite extensive (Grimaldi and Engel, 2005; for a review see Brandao *et al.*, 1989). Ants are, for example, very

abundant in Tertiary Baltic and Dominican amber. However, the older the formation, the more sparse are the fossil records of ants. As mentioned above, this is probably due to the evolution of the eusocial societies, which consisted of very few individuals in the earlier stages, with hardly differentiated castes. Therefore, the first record of a fossilized ant (*Sphecomyrma freyi*) in the amber of the Upper Cretaceous of North America (Wilson *et al.*, 1967) was particularly interesting. Because of its primitive morphological structures, it was very difficult to classify the fossil in one of the Recent subfamilies. The authors therefore created the subfamily †Sphecomyrminae. Wilson (1985) described another species of *Sphecomyrma*, but at the same time also described some further Formicidae from the Eocene of Canada.

A real surprise was the record of a Formicidae from the Lower Cretaceous of the Crato Formation (Brandao *et al.*, 1989). However, the attribution of the specimen was at first not very confident at all, and is still disputed to this day (J. Rust, personal communication). The preservation of the holotype is relatively poor, with indistinct edges and incomplete cephalic area. Furthermore, it is not possible to see whether the specimen had wings or not. Subsequently, the animal has been mistaken for a representative of the Ampulicidae ('Sphecidae'), which often have an extremely similar general habitus (Figure 11.72e). However, the structure of the petiolus indicates that the fossil indeed belongs to the Formicidae of the subfamily Myrmeciinae (bulldog ants), whose distribution is now limited to Australia. As it was not possible to attribute the new fossil species to the single Recent genus *Myrmecia*, it was named *Cariridris bipetiolata* Brandao *et al.*, 1989.

Two further specimens of *Cariridris* may have been discovered while examining fossil material for the present volume. There is no doubt that these two fossils also belong to the same genus and species *Cariridris bipetiolata* (Figure 11.77). The specimen SMNS 66565 (Plate 15m) is much better preserved than the holotype, and supports the attribution to Formicidae–Myrmeciinae (petiolus and head structures). The absence of wings in this specimen is of course no valid evidence against such an attribution.

Tiphiidae: flower wasps

With a worldwide distribution of 1,500 species, the family Tiphiidae (Figures 11.72a and 11.75e, Plates 15n and o) is a very heterogeneous subgroup of Aculeata. According to Kimsey (1991), they can be classified in seven subfamilies: Anthoboscinae, Tiphiinae, Brachycistidinae, Myzininae, Methochinae, Thynninae and Diamminae. Extreme sexual dimorphism is an often-occurring phenomenon in this family. The recognition of the conspecific status of both sexes is in most cases only possible if the animals are found in copula (e.g. in the case of Methochinae, Myzininae and Thynninae). This makes a proper classification of fossil representatives even more difficult or even impossible. Anthoboscinae and Tiphiinae present a less-marked

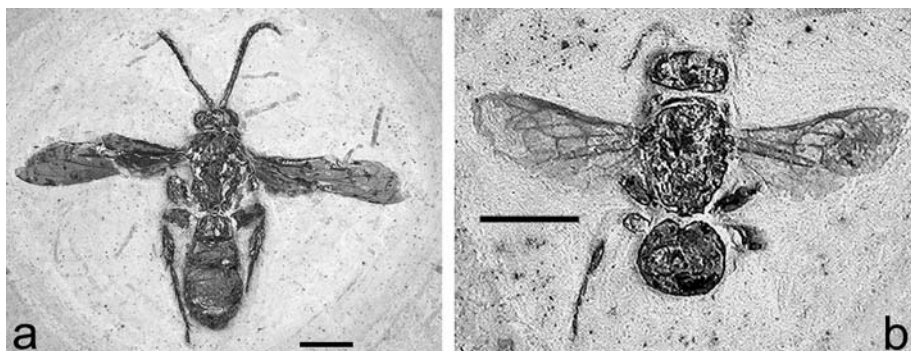


Fig. 11.71. Crato Formation Hymenoptera: (a) Angarosphecidae, *Cretohestiola* spec., SMNS 66297; scale bar, 5 mm; (b) Apidae, coll Murata; scale bar, 2 mm.

sexual dimorphism. All Tiphidae are ectoparasitoids that feed on live beetle larvae living underground, except for the Australian Diamminae that feed on Gryllotalpidae. In terms of Earth history, they seem to represent a rather old group. Anthoboscinae are particularly distinguished by a high number of plesiomorphies (Brothers, 1975). A review of fossil Tiphidae was provided by Rasnitsyn (1986a).

Architiphia rasnitsyni was described as first fossil Tiphidae (Anthoboscinae) from the Crato Formation by Darling and Sharkey (1990) based on a single holotype specimen (AMNH 43265), which was excellently preserved with clearly recognizable wing venation (Figure 11.75e). A further specimen of the same species was discovered by looking through the fossil material for the present work. The fossil is also preserved in ventral aspect and also shows legs and wing venation very clearly (Plate 15n). In addition, two undescribed specimens of putative Tiphidae were found, for which a confident determination was not yet possible (Figure 11.72a, Plate 15o).

Sapygidae: club-horned wasps

Records of fossil Sapygidae (Figures 11.72b and 11.73a) are very rare (in Spahr, 1987: Gattung *Sapyga* von Brischke, 1886; Handlirsch, 1925). Therefore, the description of a fossil male sapygid from Middle Cretaceous Burmese amber by Bennet and Engel (2005) was of great importance. The Sapygidae have been classified in two subfamilies, Sapyginae and Fedtschenkiinae, by Pate (1947). Tobias (1965) elevated the taxonomic ranks without any plausible arguments to two families Sapygidae and Fedtschenkiidae in a superfamily Sapygoidea. However, the recently discovered fossil exhibited so many morphological differences to the Recent Sapygidae (Sapyginae, Fedtschenkiinae), that Bennet and Engel (2005) decided to create a new subfamily †Cretosapyginae. The justification for the attribution of this amber fossil to the family Sapygidae is doubtful to the present

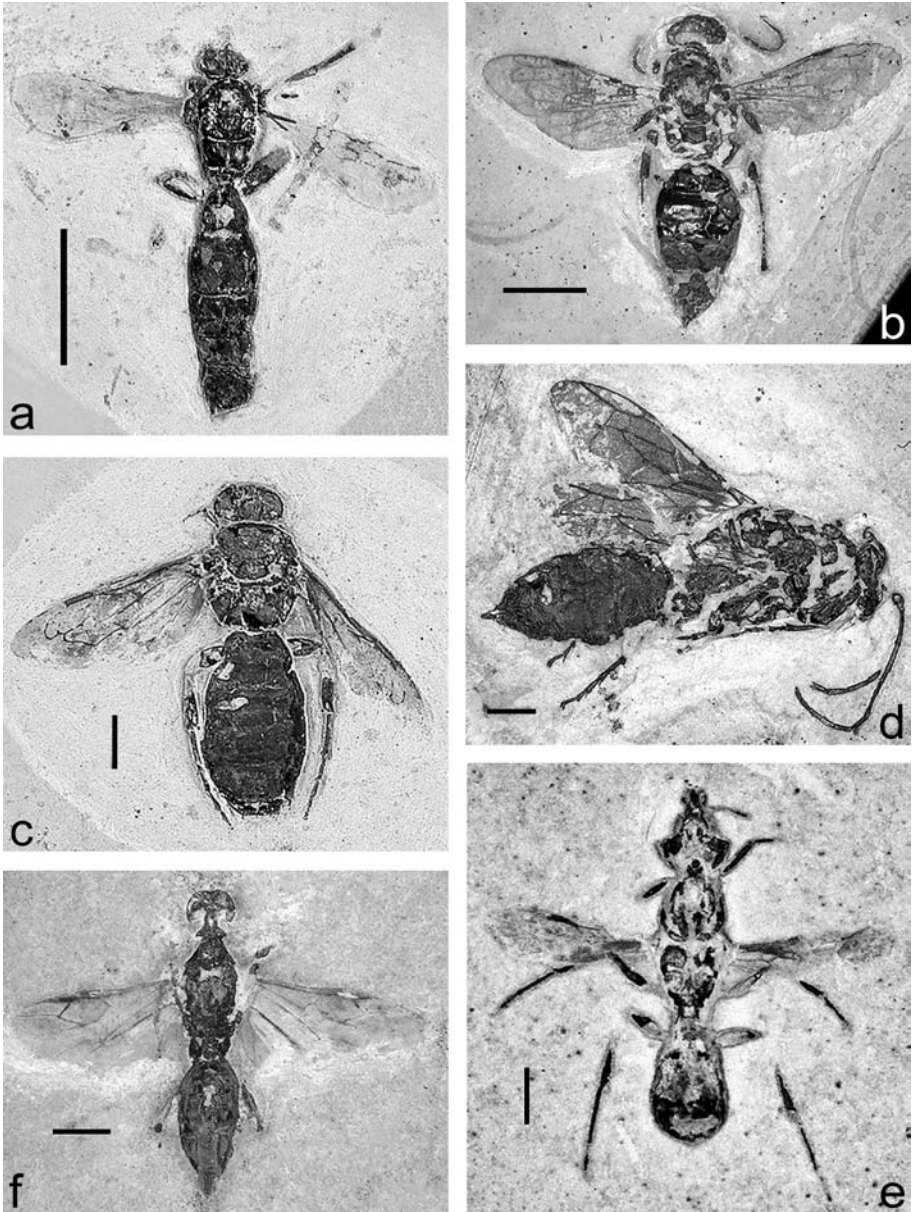


Fig. 11.72. Crato Formation Hymenoptera: (a) Tiphidae, Tiphinae?, coll Murata; (b) Sapygidae, *Cretofedtschenkia santanensis* gen. et sp. nov., holotype SMNS 66594; (c) Scoliidae, *Cretoscolia brasiliensis* sp. nov., holotype MURJ without number; (d) Angarosphecidae, *Cretosphex magnus*, F103 coll. MSF; (e) Ampulicidae, N69 coll. MSF; (f) Ampulicidae, SMNS 66291. Scale bar: a,b, 5 mm; c–f, 2 mm.

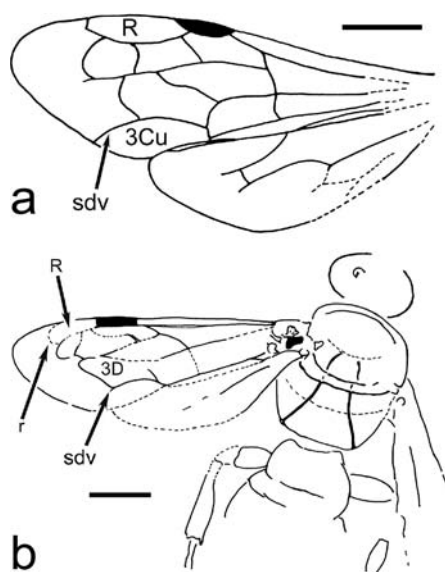


Fig. 11.73. Crato Formation Hymenoptera: (a) Sapygidae, *Cretofedschenkia santanensis* gen. et sp. nov., holotype SMNS 66594, wings; (b) Scoliidae, *Cretoscolia brasiliensis* sp. nov., wings, holotype MURJ. Scale bar, 2 mm.

author: although the specimen is an amber fossil, which is much better preserved and shows many more details than those of the Crato Formation specimens, it simply lacks certain characteristics of the Sapygidae. Additionally, a referral to the sister group of the Sapygidae, the Mutillidae, could also be considered (Brothers, 1975).

The first record of a very well-preserved fossil Sapygidae, Fedtschenkiinae from the Lower Cretaceous Crato Formation of Brazil justifies a more exhaustive treatment of this taxon in the present work. The 80 Recent species are cleptoparasites or ectoparasitoids of Megachilidae, Apidae (Anthophorinae) and Eumeninae. The Recent representatives are widely distributed, except for the Australian region. A synapomorphy of all Sapygidae is the transformation of the sixth metasomal sternum of the female. It forms a cone at the metasomal apex from which the sting (or more precisely the ovipositor) extends. The strong sting of the Sapygidae does not only function as a defence device, but also still as an ovipositor, as in Chrysididae and Dryinidae. The rear edge of the pronotum is slightly concave, and its rounded sides reach the tegulae.

Due to the relative abundance of the Recent Sapyginae, much work has been done on their distribution, determination, systematics and biology (Bischoff, 1927; Pate, 1946, 1947; Bradley, 1955; Malyshev, 1968; Königsmann, 1976; Gauld and Bolton, 1988; Goulet and Huber, 1993; Gusenleitner, 1994, 1996, 1997; Yildirim and

Gusenleitner, 2001). In contrast to this, the living Fedtschenkiinae are comparatively rare, and show an extremely disjunctive distribution: *Fedtschenkia anthracina* Ashmead in the desert areas of California and Colorado, *F. grossa* Saussure in Turkey, Turkmenistan, Uzbekistan, Tajikistan and Iran, *F. indigotea* Radoszkowsky in Turkmenistan, *F. palaestinensis* Guiglia in Israel and *F. libanoi* Guiglia in Lebanon (Guiglia, 1955, 1969, 1972; Osten, 2004). According to Tobias (1965) and Y. Popov (personal communication), the relict-like distributional pattern of the Fedtschenkiinae suggest a Tertiary or even pre-Tertiary origin. The flower-visiting habit of *F. grossa*, which feeds on *Salsola subaphylla*, suggests an old desert flora as the ancestral biotope. It is remarkable that the very primitive genus *Crioscolia* (Scoliidae) shows an almost identical distribution to the Fedtschenkiinae (Osten, 2004).

The fossil Fedtschenkiinae from the Crato Formation, a complete female specimen, unfortunately does not exhibit all constituent characteristics of the group due to preservational circumstances. Particularly in the area of the head, the most important characters cannot be seen: the compound eyes are only weakly sinuate (reniform in Sapyginae), and the toruli are close together (widely separated in Sapyginae). The shape of the pronotum is visible. In the dorsal antero-lateral area it is rounded and flat (contrary to a very acute carina in Sapyginae). The wing venation is excellently preserved. It hardly differs from that of the Recent species. This wing venation is very primitive for Aculeata, and rather similar to other basal groups, for example within the Tiphidae (Anthoboscinae or Tiphinae). This restricts the value of the wing venation as a phylogenetic character. However, some peculiarities in the venation of the forewing allow a rather confident attribution to the Fedtschenkiinae: R truncated at the apical end (acute in Sapyginae), two *s-m* bulging (sigmoidal in Sapyginae). Tibiae of the hind legs are robust and thorned (burrowing devices; slim in Sapyginae). The metasoma is depressed and egg shaped (cylindrical in Sapyginae). Not visible in the fossil is the notch between sternum 1 and 2 (Sapyginae without notch). Clearly visible is the transformed sixth metasomal sternum with the protruding sting/ovipositor.

Eumeninae have been shown to be the hosts of the ectoparasitic larvae of the Recent species *Fedtschenkia anthracina*, while the cleptoparasitic larvae of the Sapyginae use Apidae as a food resource.

If fossil representatives of Sapygidae are compared with the very diverse groups of the Tiphidae and Anthoboscidae, several similarities (symplesiomorphies and convergences) become apparent. The morphological differentiation of the basal representatives within the Vespoidea still had not progressed very far. For instance, the wing venation of certain representatives of Tiphidae (Tiphinae, Myzininae) and Anthoboscidae exhibits many symplesiomorphic similarities (Rasnitsyn, 1986), but a truncated radial cell can only be found in the Fedtschenkiinae as autapomorphy (Figure 11.73a). The shape of the pronotum is also very similar in the mentioned

groups. The front edge of the pronotum is more or less straight in these groups, whereas it has a u-shape in the Fedtschenkiinae (Figure 11.72b). The females of Anthoboscidae and of some Tiphidae have distinct pygidial plates, whereas the metasoma of the Fedtschenkiinae ends evenly conical without such a plate. In the females it ends in the characteristically protruding sting/ovipositor apparatus (Figure 11.72b). Despite many remarkable similarities, there are also sufficient characteristics that distinguish the Fedtschenkiinae from these other groups.

Fedtschenkiinae André, 1903

Cretofedtschenkia gen. nov.

Type species: *C. santanensis* sp. nov., by present designation.

Derivation of name: named after the Cretaceous age and the genus *Fedtschenkia*.

Diagnosis: as for type species, by monotypy.

C. santanensis sp. nov.

Material: holotype SMNS 66594 (Figures 11.72b and 11.73a).

Type locality: Chapada do Araripe, vicinity of Nova Olinda, southern Ceará, north-east Brazil.

Type horizon: Lower Cretaceous, Upper Aptian, Nova Olinda Member, of the Crato Formation.

Derivation of name: named after the town of Santana in the area of the type locality.

Diagnosis and description: the only specimen, a female, is characterized by the following features. The tibiae of the hind legs are robust and spinous, and suggestive of burrowing devices. The metasoma has an ovoid shape and extends in the visible sting/ovipositor apparatus. Tergites are partly finely dotted, but this is rather an artefact of preservation. The body length is 18 mm and forewing length is 10 mm. Radial cell of the forewing (R) is truncated at the apex. The subdiscoidal vein (sdv) reaches the outer forewing margin, so that there is a third closed cubital cell (3 Cu) developed.

Scoliidae: scoliid wasps

The Scoliidae (Figures 11.72c and 11.73b) form a comparatively small, monophyletic group within Vespoidea. Their sister group is the family Vespidae (Brothers, 1975; Carpenter, 1982). Approximately 570 Recent species of Scoliidae have been described to date (Osten, 2005). Their larvae develop as ectoparasitoids on beetle larvae, preferably Scarabaeidae. Based on the works of Rasnitsyn (1977), Day *et al.* (1981) and Osten (2001), they are classified in the subfamilies †Archaeoscoliinae (Rasnitsyn, 1993), Proscoliinae (Recent, one genus with two species; Osten, 1987,

1988, 1993) and the Scoliinae (tribes Campsomerini and Scoliini). The species of this family are morphologically very similar, which often makes a specific identification very difficult. The tribe Campsomerini shows in some species a very remarkable sexual dimorphism. Several species of the extinct subfamily †Archaeoscoliinae have been described by Rasnitsyn (1993), Rasnitsyn and Martínez-Delclòs (1999, 2000) and Zhang *et al.* (2002) from the Cretaceous localities in Asia (China, Siberia), Europe (Spain) and South America (Brazil).

Currently, there exists only one questionable record of a Proscoliinae: *Cretaproscolia josai* Rasnitsyn and Martínez-Delclòs (1999) from the Crato Formation. Only the wing venation is preserved in the holotype specimen. Representatives of the †Archaeoscoliinae (*Archaeoscolia*, *Cretoscolia*, and *Protoscolia*) have not yet been found at this locality. The first fossil record of †Archaeoscoliinae, *Cretoscolia brasiliensis* sp. nov., from the Lower Cretaceous of Brazil is therefore quite remarkable. The female holotype specimen is relatively well preserved (Figure 11.72c). The complete habitus already suggests a Scoliidae. Unfortunately, some important characteristics of this group are not visible, such as the separated position of the metacoxae, due to the fact that the animal is preserved in the dorsal aspect. However, the elongate and tripartite propodeum and the venation of the frontal wing clearly support the attribution to Scoliidae (Figure 11.73b). The longitudinally wrinkled structure of the apical parts of the forewings, which is a characteristic of Recent Scoliidae, is still absent in the genera of *Archaeoscolia* and *Cretoscolia* (but not in *Cretaproscolia*). The slight constriction between the first and second metasomal tergite and sternum is a further evidence for the attribution to Scoliidae, especially in combination with the previously mentioned characters. As the wing venation is not fully preserved, the drawing (Figure 11.73b) of the holotype has been supplemented with a few slight hypothetical reconstructions, but they are all clearly marked with dotted lines. Problems of preservation are apparent particularly in the area of the radial cell (R) and the cubital cell.

The genus *Archaeoscolia* Rasnitsyn (1993) is characterized by the apex of the radial cell which hardly extends over the crossvein 3 *r-m*. For *Cretoscolia* the radial cell extends clearly over the crossvein. Unfortunately, the venation of the radial cell is not preserved in the holotype specimen. On the other hand, the long and slender third pair of legs (particularly the slim femur) suggests an attribution to the genus *Cretoscolia* (Figure 11.72c).

It could be argued that (if it is a male specimen) sexual dimorphism could be involved, because even the males of Recent Scoliidae do not possess the robust burrowing legs of the females. Only the females of the Recent Scoliidae species dig into the soil to either look for their hosts or to rest overnight. In contrast, the males rest on plants in the open. However, the wide head, the round metasoma and the lack of the three apical thorns in the holotype clearly show that it is a

female specimen. The relatively slim and long hind legs of the genus *Cretoscolia* have to be considered a primitive character state (symplesiomorphy). Originally, Scoliidae attacked as hosts for their parasitoid larvae only larvae of the beetle family Scarabaeidae that live in or directly under the surface of rotten wood. Only during the course of evolution of the Scarabaeidae did these beetles also populate dry biotopes (Krell, 2000). To survive, deeper layers of soil in savannahs or deserts had to be chosen as habitat for the beetle larvae, instead of the original humid forests. The Scoliidae followed their hosts. To progress into the deeper soil, the hind legs developed into robust burrowing legs in the female sex, which also uses the mandibles for digging.

†*Archaeoscoliinae* Rasnitsyn 1993

Cretoscolia Rasnitsyn 1993

Type species: *C. promissiva* Rasnitsyn from the Late Cretaceous of north-east Siberia.

Diagnosis: see Rasnitsyn (1993).

Cretoscolia brasiliensis sp. nov.

Material: holotype specimen without number in coll. MURJ (Figures 11.72c and 11.73b).

Type locality: Chapada do Araripe, vicinity of Nova Olinda, southern Ceará, north-east Brazil.

Type horizon: Lower Cretaceous, Upper Aptian, Nova Olinda Member of the Crato Formation.

Derivation of name: the species name is feminine and named after the country of the type locality.

Diagnosis and description: a single female holotype specimen. In contrast to the types of *Cretoscolia promissiva* Rasnitsyn and *C. patiens* Rasnitsyn, the specimen of *C. brasiliensis* is significantly better and more completely preserved. Neither body length nor sex is known for *C. patiens*. This makes a direct comparison of many morphological structures problematic. The wing venation of the holotype mostly agrees with that of the other two species. However, the third discoidal cell (3D) is substantially shorter and wider in *C. brasiliensis*. There is also an indication of a subdiscoidal vein (sdv; Figure 11.73b). Body length is 13 mm and forewing length is 7.8 mm. The metasoma is wider than in *C. promissiva*.

Vespidae: wasps

Records of fossil Vespidae are extremely rare in the Lower Cretaceous (Carpenter and Rasnitsyn, 1990). Their Recent subfamilies (Euparagiinae, Masarinae, Eumeninae, Stenogastrinae, Vespinae and Polistinae; Carpenter, 1987) are distributed

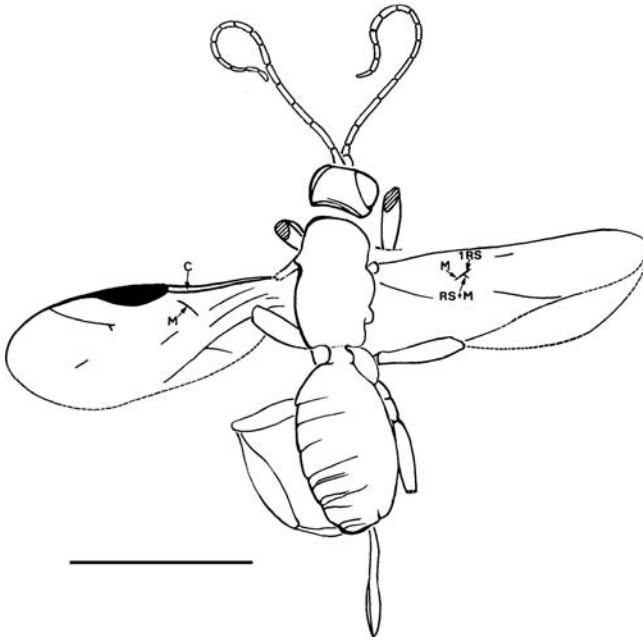


Fig. 11.74. Crato Formation Mesoserphidae: a mesoserphid hymenopteran with out-splayed wings, AMNH 43272; scale bar, 2 mm. After Darling and Sharkey, 1990: figure 5).

worldwide with approximately 4,000 species. These aculeate hymenopterans occur everywhere, not only because of the high number of species, but also based on the highly organized societies of the Vespinae and Polistinae. Their existence has substantial ecological significance (pollination, reduction of other insects as food for their larvae).

Although Carpenter and Rasnitsyn (1990) referred their described genera (*Curiosivespa* and *Priorvespa*) and species to the extinct subfamily †Priorvespinae (which is the sister group of all Recent crown group Vespidae), the newly discovered specimen SMNS 66295 could be referred to an Recent subgroup: based on its specific shape of the first metasomal segment, it could be classified as an Eumeninae (Plate 15p). Unfortunately the important shape of the compound eyes (reniform) is not visible in the fossil. The characteristic morphology of the forewing of Vespidae (longitudinal folding) is not visible in this fossil either. Therefore, better material and more work are needed before a formal taxonomic description is possible.

Apoidea: digger wasps and bees

Fossil Apoidea (Figures 11.71a and b, 11.72d–f and 11.75a–c) are of particular interest for the phylogeny of the Aculeata, but also associated with great problems of

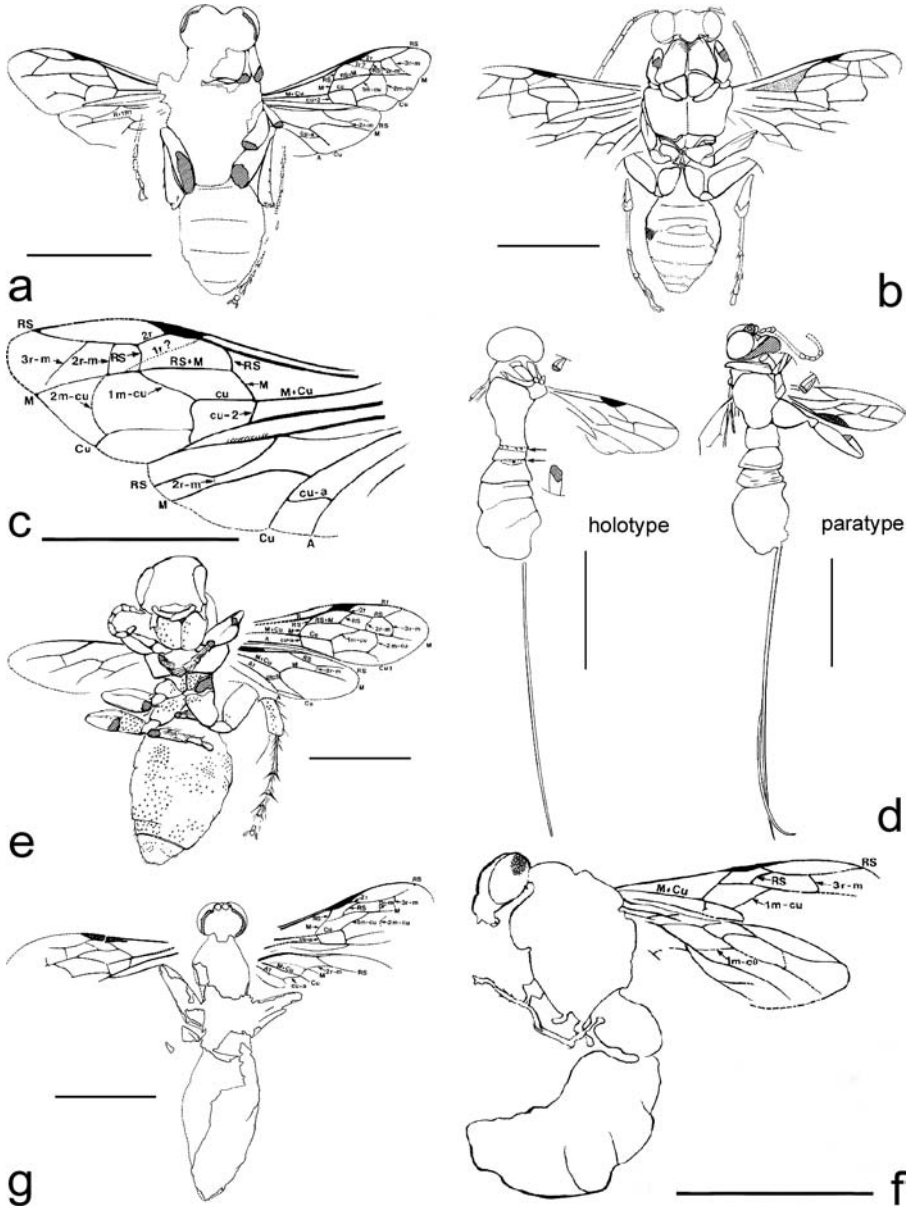


Fig. 11.75. Crato Formation Hymenoptera: (a) Sphecidae, *Cretosphex parvus* Darling, 1990, holotype, AMNH 43264; (b) *Cretosphex magnus* Darling, 1990, holotype, AMNH 44107; (c) *Cretosphex magnus* wing venation of paratype, AMNH 43267; (d) Ephialtitidae, *Cratephialtites kourios*, holotype, AMNH 43269 and paratype AMNH 43263; (e) Tiphiidae, *Architiphia rasnitsyni* Darling, and Sharkes 1990, holotype AMNH 43265; (f, g) ?Angarosphecidae, *Mesorhopalosoma ceara* Darling, 1990; (f) paratype AMNH 44103; (g) holotype AMNH 43266. Scale bars, 5 mm. All illustrations after Darling and Sharkey (1990).

classification. According to more recent results (Bohart and Menke, 1976; Lomhold, 1982; O'Tool and Raw, 1991; Alexander, 1992; Ohl, 1995, 1996, 2000; Prentice, 1998; Melo, 1999; Michener, 2000; Engel, 2001), the traditional and still common division of Apoidea into 'Sphecidae' and Apidae cannot be upheld. The family 'Sphecidae' is non-monophyletic (at least in its wide definition), whereas the Apidae are clearly monophyletic. The sister group of the Apidae are the Crabronidae, and the 'Sphecidae' *sensu stricto* are the sister group of both of these taxa. The most primitive group within the Apoidea is the family Ampulicidae, which is also represented in the fossil material from the Crato Formation (Figures 11.72e and f).

The discovery of the Recent genus *Heterogyna* (Nagy, 1969) and the controversial discussion of the position of the Heterogynidae in the system of the Apoidea has been fully discussed recently by Ohl and Bleidorn (2006): *Heterogyna* is either the sister group of the Crabronidae+Apidae (Alexander, 1992), or the sister group of all remaining Apoidea (Prentice, 1998), or only the sister group of the Ampulicidae (Prentice, 1998; Melo, 1999), or the sister group of the 'Sphecidae'+Crabronidae+Apidae (Melo, 1999). Different views concerning the phylogenetic relationships also prevail within these subgroups. These circumstances lead to particular difficulties with the classification of fossils: while fossils from the comparably young Dominican and Baltic amber (Engel, 2001) can clearly be classified in either Apidae or Sphecidae or any other hymenopteran subgroup, this attribution is much more problematic with primitive fossil representatives from Mesozoic outcrops like the Crato Formation.

Nevertheless a number of these fossils can be attributed to the extinct family †Angarosphecidae (Rasnitsyn *et al.*, 1999; Pulawski and Rasnitsyn, 2000; Grimaldi and Engel, 2005). This includes the two species *Cretosphex parvus* (Figure 11.75a) and *Cretosphex magnus* (Figures 11.72d and 11.75b and c) which, based on five specimens (*Cretosphex parvus*: AMNH 43264, 44106 and 44104; *C. magnus*: AMNH 44107 and 43267) were described by Darling and Sharkey (1990) as 'Sphecidae'. They belong to the most abundant fossil hymenopterans of the Crato Formation. It seems that the family of †Angarosphecidae had been rather common and widely distributed in the Lower Cretaceous. Specimen SMNS 66297 (Figure 11.71a) seems to represent a new species and first New World record of the angarosphecine genus *Cretobestiola* Pulawski and Rasnitsyn, 2000. Additionally, Ampulicidae (Figures 11.72e and f) are here recorded for the first time, as Darling and Sharkey (1990) only had a doubtful specimen of the Ampulicinae (AMNH 44108).

There are a number of fossil Hymenoptera from this locality that might be typologically identified as 'bees'. Only a very small number would really stand up to a more thorough and more critical examination. The difficulty or even impossibility of distinguishing primitive apids from primitive 'sphecids' has been mentioned

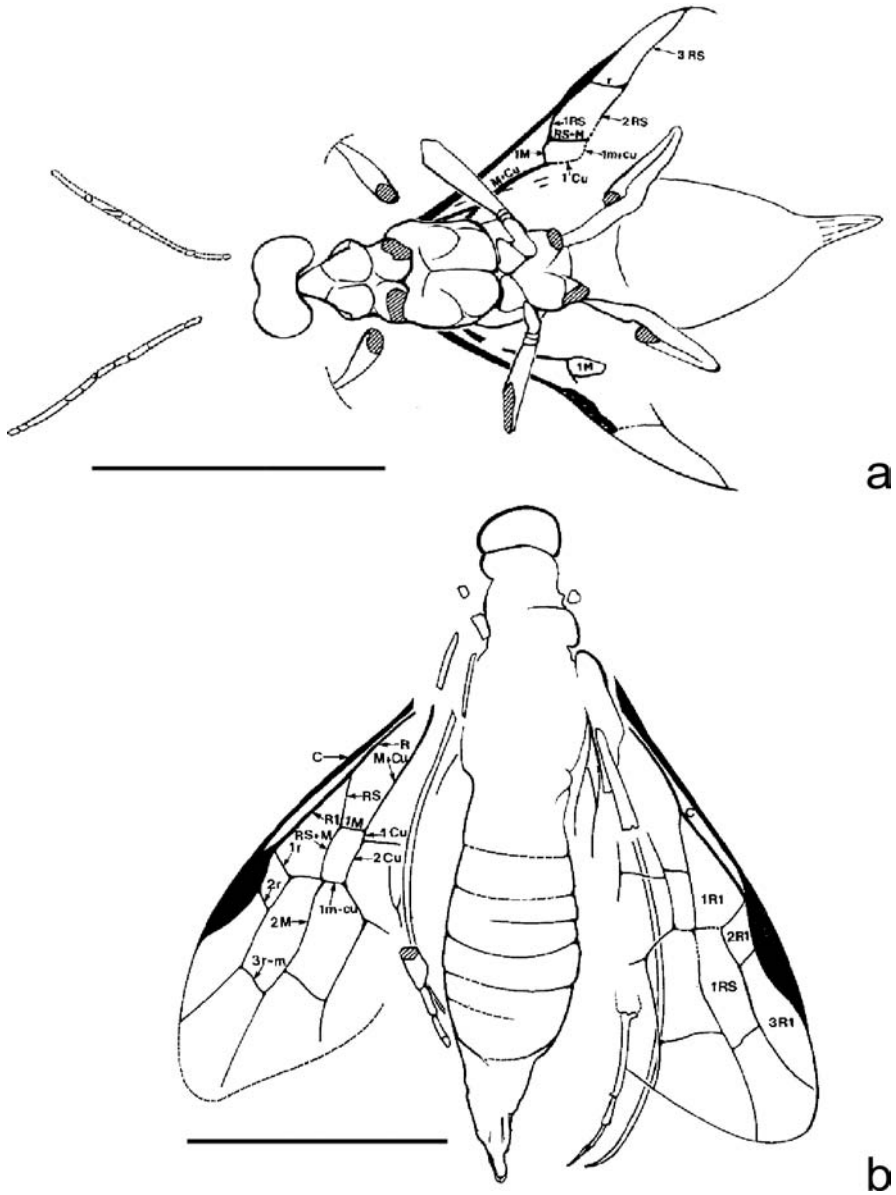


Fig. 11.76. Crato Formation Hymenoptera: (a) Proctotrupidae? *Protoprocto asodes* Sharkey, 1990, holotype, AMNH 44101; (b) Anaxyelidae, *Prosyntexis gouleti* Sharkey, 1990, holotype, AMNH 43270. Scale bars, 5 mm. After Darling and Sharkey (1990).



Fig. 11.77. A possible Crato Formation ant: *Cariridris bipetiolata* Brandao and Martins-Neto, 1989, holotype, private coll. Vulcano no. CV-293; scale bar, 2 mm. After Brandao *et al.* (1989).

above, and was already discussed in detail by Darling and Sharkey (1990). However, a very well-preserved bee-like fossil without number (Figure 11.71b) from coll. MURJ is very probably indeed a genuine apid, because it has a general habitus that is virtually unknown within the complete ‘sphecoid’ grade. This specimen could therefore represent the oldest fossil record of bees, which are otherwise first known from the Upper Cretaceous amber of North America (however, just recently Poinar and Danforth, 2006, described the new fossil bee family Melittospecidae from the Lower Cretaceous amber of Burma). Further research and more material would of course be necessary to confirm and test this important discovery.

11.19 Mecoptera: scorpionflies

Günter Bechly

Mecopterans, the scorpion flies, are small-to-medium-sized (1.7–35 mm) insects, often with a fly-like habitus. Most of them have filiform antennae and orthognathous chewing mouthparts. In most taxa, anterior and lateral portions of the head and some

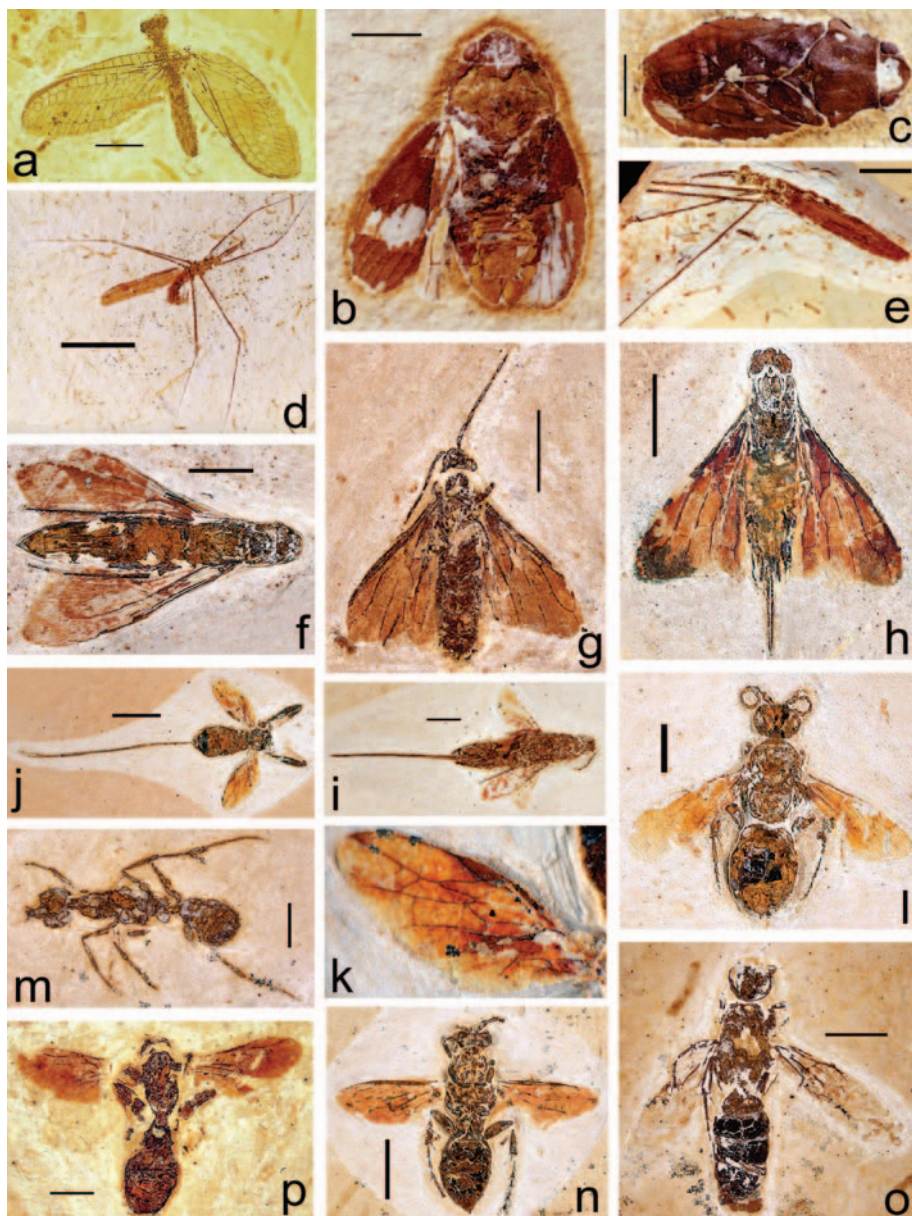


Plate 15. Crato insects: (a) Neuroptera, Hemerobiiformia, Mesochrysopidae gen. et sp. nov., priv. coll.; scale bar, 5 mm; (b) Coleorrhyncha, Progonocimidae gen. et sp. nov. SMNS 66423; scale bar, 2 mm; (c) Coleorrhyncha, Progonocimidae gen. et sp. nov. SMNS 66431; scale bar, 2 mm; (d) Chresmododea, Chresmodidae, *Chresmoda* sp. nov., SMNS prelim. no. 0134 (old no. H56), scale bar = 20 mm; (e) Chresmododea, Chresmodidae, *Chresmoda* sp. nov., ex MSF coll G88; scale bar, 10 mm; (f) Hymenoptera, Anaxyelidae, MURJ without number; scale bar, 5 mm; (g) Anaxyelidae, *Protsyntexis* sp., SMNS 66304; scale bar, 5 mm; (h) Siricidae, MURJ without number; scale bar, 5 mm; (i) ?Ichneumonoidea, MURJ without number; scale bar, 5 mm; (j) Ephialtitidae, *Cretephialtites kourios*, MURJ without number; scale bar, 5 mm; (k) Ephialtitidae, *Cretephialtites kourios*, right wings, MURJ without number, without scale; (l) ?Pompilidae, MURJ without number; scale bar, 2 mm; (m) Formicidae, Mymeciinae, *Caridris bipetiolata*, SMNS 66565; scale bar, 2 mm; (n) Tiphidae, *Architiphia rasnitsyni*, MURJ without number; scale bar, 5 mm; (o) Tiphidae, ?Myzininae, SMNS 66303; scale bar, 5 mm; (p) Vespidae, ?Eumeninae, SMNS 66295; scale bar, 2 mm.