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 'sphecid' 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

of the mouthparts are more or less prolonged as a rostrum. The compound eyes are large and ocelli are either present or reduced. The legs have elongate coxae, long femora and tibiae, and five-segmented tarsi (except in Boreidae) with paired claws (except in Bittacidae). Two pairs of membranous wings of subequal size, similar shape and complete venation are usually present, except in a few apterous taxa and in the extinct Pseudopolycentropidae with much-reduced hind wings. The first abdominal tergum is fused to the metanotum. Males usually have a prominent genital apparatus which gave rise to their vernacular name. The abdominal cerci are relatively short with only one to three segments in the females and one segment in the males, but they are completely reduced in the males of the apterous Boreidae and Apteropanorpidae (but not in *Apterobittacus* and other wingless species). The development is holometabolous with a distinct eruciform or campodeiform larval stage with compound eyes, and an adult-like pupal stage. Mecoptera are either carnivorous, phytophagous, or saprophagous, and generally prefer moist habitats while only a few species are adapted to arid environments. Recent Mecoptera have a cosmopolitan distribution.

Systematics, phylogeny and evolution

There are about 600 extant species of Mecoptera and about 400 fossil species of 'mecopteroid taxa', but not all of the latter are necessarily members of the Mecoptera (see below). The extant species are classified in nine families, but the monophyly of extant Mecoptera is still under discussion, mainly because of a possibly more basal position of Nannochoristidae and a putative in-group position of Siphonaptera (Grimaldi and Engel, 2005). Together with the orders Siphonaptera, Diptera and possibly Strepsiptera (the relationship of Strepsiptera with Antliophora is still very disputed, but is apparently not only supported by molecular evidence, but as well by unpublished new morphological data (according to Mickoleit, personal communication), the order Mecoptera belongs to the clade Antliophora within Holometabola. Most probably Siphonaptera (fleas) represents either the sister group of Mecoptera or (more likely) the sister group of Boreidae within Mecoptera (see Willmann (1987, 1989) for a discussion of the internal phylogeny of Mecoptera). Nannochoristidae could be the sister group of only Boreidae+Siphonaptera or rather the sister group of all other Mecoptera (including Siphonaptera). The still three-segmented female cerci and the primary absence of a rostrum are plesiomorphies within Mecoptera (otherwise only present in the boreid genus *Caurinus*) that support the latter hypothesis, which also agrees with the oldest fossil occurrence. All other extant Mecoptera (except Nannochoristidae and Boreidae) belong to a clade Pistillifera that is diagnosed by the synapomorphic possession of a sperm pump in the male genital apparatus.

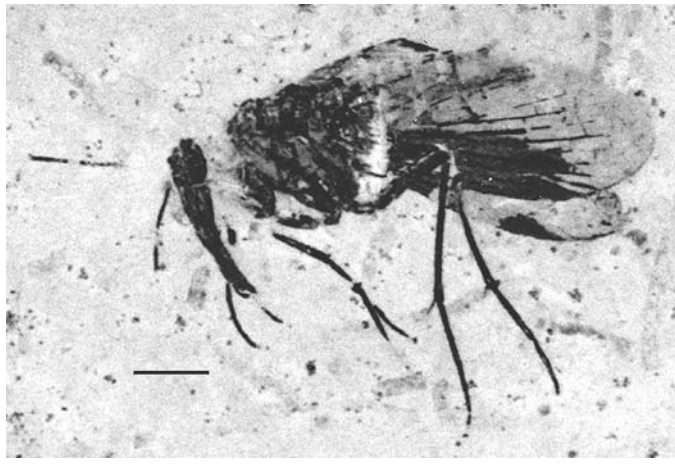

Fig. 11.78. Crato Formation Mecoptera: Familia indet., undescribed gen. et sp. nov., no. N72 at KMNH. Scale bar, 2 mm.

Fossil record

The fossil history of Mecoptera was discussed by Handlirsch (1906–1908), Willmann (1978), Carpenter (1992), Novokschonov (1997, 2002) and Grimaldi and Engel (2005). The oldest representatives of the crown group clade Mecoptera are fossil Nannochoristidae from the Upper Permian. Older fossil records are problematic because most fossils are isolated wings, and the wing venation of basal Mecoptera is hardly differentiated from the ancestral condition of Antliophora and Amphiesmenoptera (caddisflies and butterflies). Consequently, such Palaeozoic mecopteroid fossils could not only belong to the stem group of Mecoptera but could also belong to a mecopteroid grade of the stem group of Mecopteroidea (Antliophora+Amphiesmenoptera), Amphiesmenoptera, Antliophora or could represent still mecopteroid-like stem group representatives of Siphonaptera and/or Diptera.

Mecopterans are extremely rare in the Crato Formation, but are quite diverse and abundant in other Lower Cretaceous outcrops such as Liaoning (China), so that their rarity in the Crato Formation is somewhat unexpected and in need of explanation. Most likely, the arid conditions of the Crato habitat were unsuitable for Mecoptera. Therefore, their near absence or extreme rarity can be considered as a further corroboration of an arid environment of the Crato lagoon.

Crato fossils

Among the several tens of thousands of Crato insects there were no fleas at all (fossil fleas are extremely rare anyway) and only two specimens of Mecoptera (Figures 11.78 and 11.79).

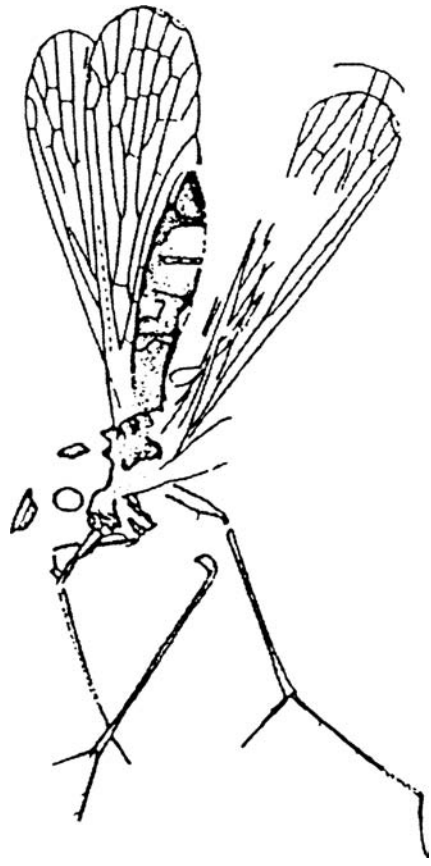

Fig. 11.79. Crato Formation Mecoptera: Bittacidae, gen. et sp. nov., coll Vulcano. Redrawn after Petrulevicius and Martins-Neto (2001: figure 1). Scale unknown.

Martins-Neto (2005b: 481) lists an undescribed mecopteran from the Crato Formation as 'Bittacidae Gen. et sp. n. Martins Neto, 1999'. However, this fossil from the private collection of Mrs Maria Aparecida Vulcano (São Paulo, Brazil) was briefly described and figured (Figure 11.79) as a putative new genus of Bittacidae, but not named, by Petrulevičius and Martins-Neto (2001). This fossil hangingfly was first mentioned by Petrulevičius (1998), and according to Willmann (personal communication) it is indeed a Bittacidae *sensu stricto*.

The second specimen (Figure 11.78) is still undescribed and figured here for the first time. It is deposited with no. 443 (old no. N72) at KMNH. It has a very long rostrum, short antennae and the wings are relatively broad with a dark colour pattern. According to Willmann (personal communication) it could be a stem group representative of Panorpini or Panorpoidea (first New World record) but, unfortunately, some important characters of the wing venation, like the structure of the

Media, are not clearly preserved. Most probably it is a new genus and species, but I here refrain from its formal description because it should be undertaken by a Mecoptera specialist.

11.20 Diptera: true flies, gnats, and crane flies

Jana Willkommen and David A. Grimaldi

Besides the Coleoptera (beetles) and Lepidoptera (butterflies) the order Diptera (true flies) is, with about 134,000 species, one of the most diverse insect groups (Gullan and Cranston, 2005). Their success is partly reflected by the diverse life histories and body forms. For example the largest fly has a body length of about 60 mm and wing span of 100 mm, which is the Neotropical *Mydas heros* Cole, 1969 (Mydidae–Brachycera). Among the smallest Diptera are certain gall midges (Cecidomyiidae) and biting midges (Ceratopogonidae): with about 0.5 mm body length and 1 mm wing span.

The Diptera inhabit nearly all aquatic and terrestrial habitats. Their larvae live in semi-aquatic or aquatic environments. The adults are predators, ectoparasites, saprophages, bloodsuckers or feed on nectar and pollen. The order has a worldwide distribution and can be found in all zoogeographic regions. They occur in humid and hot tropical regions, mountains and dry deserts, and in boreal regions flies are the dominant insect group (Hennig, 1973).

The Diptera are placed in the group Antliophora as sister group to the scorpionflies (Mecoptera, which are paraphyletic)+fleas (Siphonaptera). Diptera appear to have originated in the latest Permian or earliest Triassic and suddenly diversified into major living lineages (i.e. infraorders) some 20 myr later in the Late Triassic (Grimaldi and Engel, 2005; Blagoderov and Grimaldi, 2007). It was not until the Early to Mid Jurassic, approximately 200–175 mya, that the abundance of Diptera in palaeoecosystems approached the abundance and biomass we see today (Blagoderov and Grimaldi, 2007). This has been attributed to the diversification within the infraorders, especially of brachyceran flies (Krzeminski and Evenhuis, 2000; Blagoderov and Grimaldi, 2007), which took place in the Jurassic and later.

The Diptera have only one pair of fully developed wings in the body plan, with the hind wings reduced to club-like organs, the halteres, which maintain stability in flight as balance organs (McAlpine, 1981). The forewings are the functional flight organs, in which the narrow wing base allows the increased mobility of the wing. With halteres and other wing specializations Diptera are excellent flyers.

In compressed fossils the wing venation is very often the most important and consistent source of taxonomic characters.