## 11.8 'Blattaria': cockroaches and roachoids

Günter Bechly

Cockroaches and their relatives are often found in abundance and are familiar insects, especially in the tropics. Fossil cockroaches and roachoids are also often abundant, and are especially common in the Crato Formation. About 4,000 Recent species of cockroaches plus about 1,000 fossil roachoid species have been described (Vršanský, 2005). Living cockroaches are usually small to large insects with long filiform antennae. They possess hypognathous chewing mouthparts with well-developed mandibles. The compound eyes are large with two lateral ocelli present. Usually they have two pairs of wings, but some are secondarily wingless. The forewings are heavily sclerotized as tegmina and are much more slender than the broad hind wings, which have a large anal fan. In the forewings vein CuP is strongly curved and delimits a rounded anal field. The abdominal cerci are relatively long with numerous segments and the female ovipositor is reduced in modern cockroaches, but is still present in fossil roachoids that seem to belong to stem group Dictyoptera rather than the crown group Blattaria. The discovery of an undescribed living cockroach with ovipositor is mentioned by Vršanský (2003a: 30). All living cockroaches lay large pods of eggs called oothecae. Development is paurometabolous with a gradual development from larva to imago. Cockroaches are omnivores with cosmopolitan distribution in arid as well as humid environments, and a few species are considered pests.

### Systematics and phylogeny

Within modern pterygote insects (Pterygota: Neoptera) the cockroaches belong to the clade Dictyoptera, which also includes Isoptera (termites) and Mantodea (praying mantids).

Almost certainly the Recent roaches do not constitute a monophyletic clade, but have to be considered as paraphyletic with regard to termites, because polyphagid roaches in general, and the genus *Cryptocercus* in particular, are more closely related to termites than to other roach taxa (see Section 11.9). Furthermore, many of the 'fossil roachoids', especially from the Palaeozoic, possess a long ovipositor and therefore cannot be Blattaria but have to be attributed to the stem group of all Dictyoptera. These forms look like roaches because a roach-like habitus is the typical 'groundplan' of Dictyoptera. Such stem group roachoids with long ovipositors also occur in the Lower Cretaceous of Mongolia (Vršanský, 2003b), but have yet to be discovered in the Crato Formation. The Jurassic and Cretaceous Umenocoleidae also retain an ovipositor, albeit a short one, and therefore also probably belong to the stem group Dictyoptera rather than to Blattaria (+Isoptera) (see below).

The true cockroaches are usually classified in nine Recent families with the following relationships (Klass, 2001; Bohn, 2003a; Grimaldi and Engel, 2005): (Blattidae+(Tryonicidae+((Polyphagidae+Lamproblattidae)+(Cryptocercidae+ termites)) + (Nocticolidae? + Anaplectidae + ("Blattellidae" + Blaberidae)))). Of these Recent families only the family Blattellidae, which has to be regarded as highly paraphyletic with the subfamilies Anaplectinae and 'Plectopterinae' being most basal, is known from the Crato Formation.

## Fossil record

Unlike many other groups of fossil insects there is no up-to-date revision of fossil roaches. Most works recording the presence of fossil roaches note the urgent need of such a revision and refrain from describing new species (e.g. Maisey, 1991; Grimaldi and Engel, 2005) because of the taxonomic mess in 'palaeocockroachology'. Consequently, despite the abundance of material and quality of preservation of Crato Formation roaches, they have hardly been studied. The current state of knowledge of the fossil record of Blattaria in general, and of Cretaceous roaches in particular, has been summarized by Carpenter (1992), Vršanský (1999a, 2004), Vršanský *et al*. (2002a) and Grimaldi and Engel (2005).

## Palaeobiology and palaeoecology

Cockroaches are sometimes highly habitat-specific and their presence and general abundance can provide useful clues for the reconstruction of palaeoenvironments and palaeoclimate (Vršanský *et al*., 2002b). The large percentage of roaches in the Crato taphocoenosis is typical for a warm climate, probably more arid than humid or with strong seasonality. A similar composition of Recent terrestrial arthropods dominated by roaches, orthopterans and spiders is, for example, found in the seasonal forests of Hong Kong (Kwok and Corlett, 2002). According to Vršanský (personal communication) most cockroach species from Crato are characteristic of shrub vegetation.

## Crato fossils

Fossil cockroaches were first described from the Crato Formation by Pinto and Purper (1986) and Pinto (1989). Even though many hundreds of specimens have been discovered already, such that cockroaches are one of the most abundant fossils in the Nova Olinda Member, only a few species have been formally described. Photographs and brief discussions of Crato cockroaches have appeared in Grimaldi and Maisey (1990: 10, figure 3), Maisey (1991: 381 and 386), Martill (1993: plate 6,

figure 5), Mendes (1991a, 1991b, 1993, 1995, 1997b, 1998b, 2000), Bechly (1998: 151, Abb. 5), Bechly *et al*. (2001a: 26, Abb. 17), Vršanský (1999a, 2002, 2004), Martins-Neto (2005b) and Grimaldi and Engel (2005: 235, figure 7.72).

About 26% (960 from a sample of 3,651 fossil insects) of the many thousands of Crato insects discovered are cockroaches and roachoids. According to Vršanský (2004), among the hundreds specimens only seven different species are present, dominated by Blattellidae (60%), with subdominant †Blattulidae (25%), as well as †Umenocoleidae (15%) and a single species of †Mesoblattinidae. Even though there may be a few more species, this is a relatively small diversity of species compared to the thousands of specimens collected.

Some of the Crato cockroaches have an exceptional quality of preservation, with preserved colour pattern of the wings (Bechly *et al*., 2001a: Abb. 17; Martill and Frey, 1995: incorrectly identified as a bug) and sometimes even preserved soft parts including nerves, eye lenses (Vršanský, 2003a), guts and oothecae (Grimaldi and Engel, 2005).

### †Mesoblattinidae

Although Mendes (1995) mentions three undescribed species of *Mesoblattina*, according to Vršanský (2004) only a single species of this extinct family is present among the Crato roaches and represents a new undescribed genus and species. †Mesoblattinidae belong to the stem group of all Dictyoptera (Vršanský *et al*., 2002a; Grimaldi and Engel, 2005) because their females have retained a relatively distinct external ovipositor. Unfortunately, I did not find any material with mesoblattinid affinities among the numerous fossil roaches from this locality that I have studied.

### †Raphidiomimidae

An undescribed member of this erratic and predatory Mesozoic roach family, which seems to be the sister group of Mesoblattinidae (Grimaldi and Engel, 2005: 229), is recorded from the Crato Formation by Mendes (1991b). A possible fossil of this family is also featured on Figure 11.90c.

### †Umenocoleoidea

*Diagnosis*: small roachoid habitus but with beetle-like appearance; large compound eyes; antennae filiform but shorter than body; forewing sclerotized; hind wings membranous and with prominent pterostigma; hind wing venation similar to Blattulidae; roach-like cerci.

*Comment*: here re-defined to include the three fossil families †Vitismidae, †Cratovitismidae fam. nov. and †Umenocoleidae, but excluding the Recent taxa Anaplectidae and Oulopterygidae that are here considered as unrelated to †Umenocoleidae (*contra* Vršanský, 2003a).

†Cratovitismidae fam. nov.

*Type genus*: *Cratovitisma* gen. nov., by present designation.

*Diagnosis*: like †Vitismidae, intermediate between Blattulidae and †Umenocoleidae; with strongly sclerotized forewings, pterostigmata in the hind wings, transverse head (different to Vitismidae) with relatively short antennae and a short ovipositor, but with curved CuP in the broader forewings, a more dense venation in the hind wings, and a disc-like pronotum (different to most Umenocoleidae).

*Comment*: Peter Vršanský (personal communication) thinks that this new taxon could rather represent a transition between †Liberiblattinidae and †Umenocoleidae. He doubts that it is related to †Vitisminae, which belong to †Holocompsidae and have a reduced ovipositor and a very different forewing venation. A very similar animal, belonging to a closely related new genus, was recently discovered in deposits 50 myr older from Asia, and is the oldest representative of the Umenocoleoidea.

*Cratovitisma* gen. nov.

*Type species*: *Cratovitisma oldreadi* sp. nov., by present designation.

*Derivation of name*: named after the Crato Formation and the similar fossil roach genus *Vitisma*.

*Diagnosis*: as for type species, since monotypic.

*Cratovitisma oldreadi* sp. nov.

*Material*: holotype SMNS 66000-127 (Figure 11.23a); paratype without number at SMF; and a third specimen with no. N63 in coll. MSF.

*Type locality*: 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 Mr Chuck Oldread from Summerville, South Carolina, USA, for his invaluable help preparing Crato fossils.

*Diagnosis and description*: cockroach with adult body length of 6.9 mm and forewing length of 5.3 mm. As in *Vitisma*, the forewings are broader than in *Ponopterix* (maximum 2 mm wide), strongly sclerotized, but with vestiges of the wing veins still clearly visible. Vein CuP is strongly curved and delimits a typical roachoid anal field in the forewings. The hind wing venation is very similar to *Vitisma*, and thus more dense than in *Ponopterix*, but of similar pattern and with

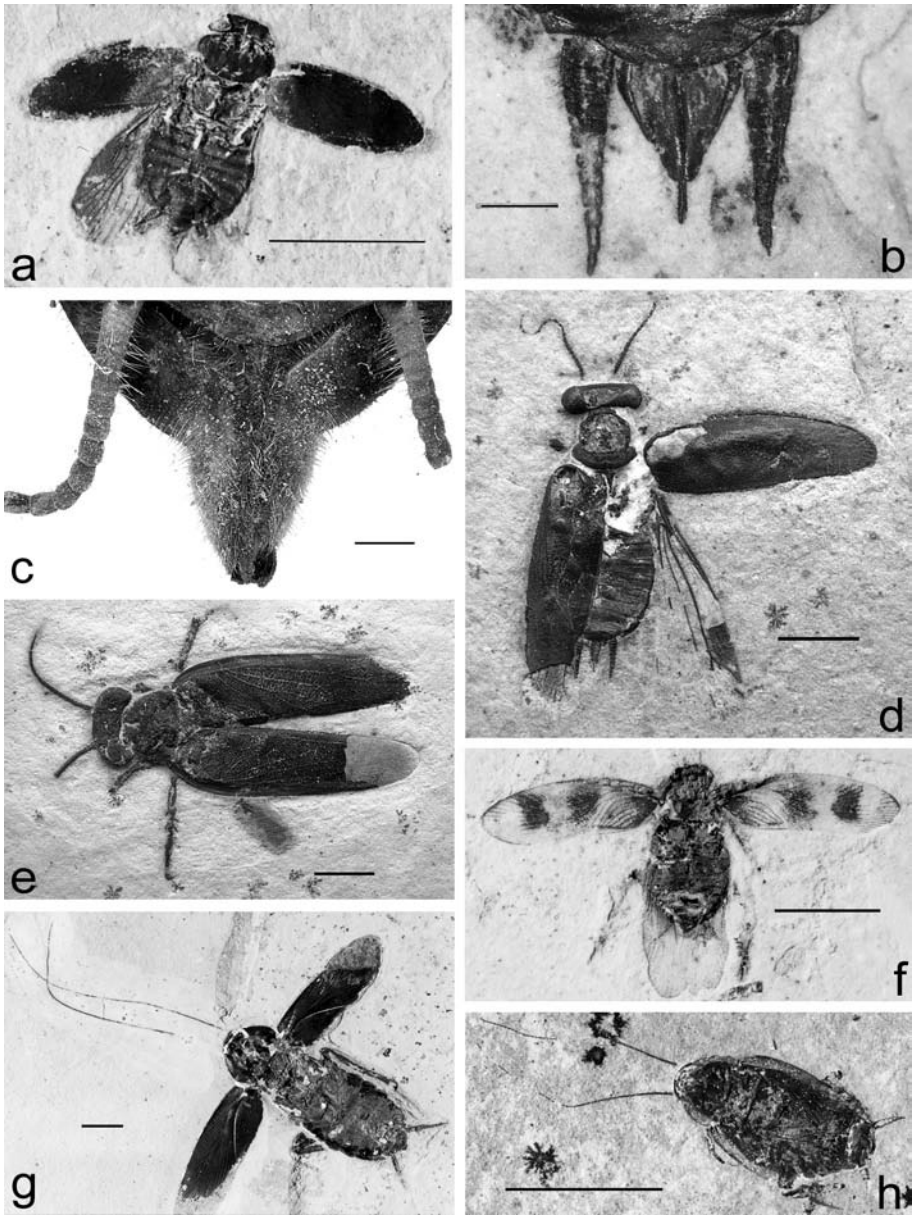


Fig. 11.23. Crato Formation cockroaches: (a) Umenocoleoidea, Cratovitismidae fam. nov., *Cratovitisma oldreadi* gen. et sp. nov, holotype SMNS 66000-127; scale bar, 5 mm; (b) Umenocoleoidea, Umencoleidae, *Ponopterix maxima* sp. nov., SMNS 66328, ovipositor; scale bar, 5 mm; (c) Mantodea, Mantidae, *Sphodromantis viridis*, ovipositor, Recent; scale bar, 1 mm; (d) Umenocoleoidea, Umencoleidae, *Ponopterix axelrodi*, SMNS 66338; scale bar, 2 mm; (e) Umenocoleoidea, Umencoleidae, *Ponopterix maxima* sp. nov., holotype SMNS 66332; scale bar, 2 mm; (f) Blattulidae, *Elisama americana*, SMNS 66558, with original colour pattern preservation; scale bar, 5 mm; (g) Blattellidae, undescribed new genus and species, SMNS 66318; scale bar, 5 mm; (h) Blattaria, Familia *incerae sedis*, undescribed new genus and species, SMNS 66308; scale bar, 5 mm.

pterostigma. The head is transverse as in Umenocoleidae (different from *Vitisma*) and the antennae are also similar to Umenocoleidae, and thus shorter than the body. The pronotum is flat and disc-like as in *Vitisma* and true cockroaches, but very different from *Ponopterix* and *Umenocoleus*. A protruding ovipositor seems to be present, but is somewhat less conspicuous than in *Ponopterix* (similar to Blattulidae).

*Comment*: the transverse head seems to place this new genus and species closer to †Umenocoleidae than *Vitisma*, so that a new family would be justified.

### †Umenocoleidae

*Diagnosis*: head transverse; pronotum saddle-like and much narrower than head (except in the most basal *Jantaropterix lebani*); sclerotized forewing only with vestiges of the reduced wing venation still visible (CuP curved in basal genera, but not curved in the more derived ones); derived cup-like ultrastructures on forewings (Vršanský, 2003a); legs spiny and tarsi very long (nearly as long as tibia) and apparently five-segmented (first segment the longest, second segment the second longest) as in cockroaches; cerci with about 13 segments; females with a short but distinctly prominent ovipositor (Figure 11.23b).

*Comments*: according to Vršanský (2004) about 15% of the fossil roaches from the Crato Formation belong to †Umenocoleidae. Currently †Umenocoleidae contains six genera with 11 species from the Lower Cretaceous of Gansu, China (*Blattapterix* Vršanský, 2003b; *Umenocoleus* Chen and Tian, 1973; *Petropterix* Vršanský, 2003b), Baissa, Transbaikalia, Siberia (*Petropterix* Vršanský, 2003b), Bon Tsagaan Mongolia (*Elytropterix* Vršanský, 2003b; *Petropterix* Vršanský, 2003b), Lebanon amber (*Jantaropterix* Vršanský, 2003b) and the Crato Formation of Brazil (*Ponopterix* Vršanský and Grimaldi in Vršanský, 1999a). *Jantaropterix* is also known from Upper Cretaceous New Jersey amber.

Originally described as a family of fossil Coleoptera by Chen and Tian (1973), it was incorrectly transferred by Carpenter (1992: 149–150) to †Protelytroptera (= Protocoleoptera), but considered as Blattaria by Vršanský *et al*. (2002a) and Andrew Ross (personal communication). More recently it was considered a stem group dictyopteran by Grimaldi and Engel (2005). This latter view seems reasonable, because the distinct external ovipositor (Figure 11.23b) excludes it from a position within crown group Dictyoptera. On the other hand, a polyphagoid relationship, as proposed by Vršanský (1999b, 2003a), would not necessarily imply an unlikely convergent evolution of the dictyopteran genital chamber and oviposition with oothecae (Vršanský, 2003a: 30; *contra* Vršanský, 1999a), because Recent Mantodea also have a small external ovipositor that is not much less developed than that seen in †Umenocoleidae (see Figure 11.23c). Consequently, the only implied

assumption would be the multiple parallel invagination of the ovipositor into the genital chamber within the various lineages of Recent cockroaches.

An alleged relationship of †Umenocoleidae with Mantodea, proposed by Gorochov (2001: 357), was convincingly ruled out by Grimaldi (2003).

Similarities of †Umenocoleidae with the fossil roach genus *Vitisma*, described by Vršanský (1999b) as the most basal Polyphagidae (Vitisminae), include a strongly sclerotized forewing, a distinct pterostigma in the hind wing, and a near-identical hind wing venation. However, the forewing venation, which lacks the typical roachoid CuP curvature, is very different between some †Umenocoleidae (*Ponopterix* and *Blattapterix*) and the remaining †Umenocoleoidea (e.g. *Vitisma*, *Elytropterix* and *Petropterix*) and is strikingly different between these umenocoleidids and any other Blattaria (including roachoid stem group Dictyoptera from the Carboniferous). The presence of a saddle-shaped pronotum instead of a shield-like pronotal disc is a further difference between roaches and roachoids. Both characters have to be considered as autapomorphic reversals.

*Jantaropterix lebani* described by Vršanský and Grimaldi (in Vršanský, 2003a) had previously been figured by Grimaldi (1996: 37) and is noteworthy because of two striking symplesiomorphies with *Vitisma*: a strongly curved CuP in the forewings and a shield-like pronotum; furthermore it has a fore- and hind wing venation that is nearly identical to *Vitisma*. This heterobathmic (*sensu* Hennig) distribution of character states suggests that †Umenocoleidae evolved from more roach-like ancestors like *Vitisma* (which should be transferred from Polyphagidae to †Umenocoleoidea as its most basal member) with *Cratovitisma* gen. nov. and *Jantaropterix lebani* as intermediate links between Vitismidae and 'higher' †Umenocoleidae. The similarities in hind wing venation of †Umenocoleidae, †Vitismidae stat. nov., Blattulidae and modern Polyphagidae could well be symplesiomorphic and are not reliable evidence for a polyphagoid relationship.

According to Grimaldi and Engel (2005: 235), Vršanský has described a putative living species of †Umenocoleidae. If the phylogenetic analysis of this Recent species supports a position outside crown group Dictyoptera, a new Recent insect order should be erected for this species!

For such a new order the name †Protocoleoptera should not be used (*contra* Bechly *et al*., 2001b: 49) because it was recently re-defined as a coleopteroid clade including †Tshekardocoleidae (Grimaldi and Engel, 2005: 361–362). *Contra* Carpenter (1992), †Protocoleoptera is also not a synonym of the dermapteroid stem group †Protelytroptera, because †*Protocoleus* Tillyard, 1924 is not sharing the typical patches in the hind wing venation that are very well defined in †Protelytridae and Recent Dermaptera.

With regard to alleged living Umenocoleoidea it should be noted that the statement by Vršanský (2003a: 6, 30), that living genera of beetle-mimicking

cockroaches like *Anaplecta* (Anaplectidae) and Melyroidea, *Prosoplecta* and *Oulopteryx* are probably Umenocoleoidea, has to be considered erroneous, as these insects are typical cockroaches with reduced ovipositor, broad shield-like pronotum, broad head and very different wing venation with blattoid curved CuP in the forewings and without the umenocoleoid pterostigmata in the hind wings. Furthermore, the latter three genera are placed in subordinate position within Blattellidae-Pseudophyllodromiinae by the leading specialist on Recent cockroaches (Roth, 1994), who also considers the former family Oulopterygidae as a synonym of Blatellidae-Pseudophyllodromiinae. Until the existence of an unambiguous surviving Umenocoleoidea is demonstrated this group has to be considered extinct.

*Ponopterix axelrodi* Vršanský and Grimaldi in Vršanský, 1999a

*Material*: holotype AMNH 43800 and six additional specimens (SMNS 66326, 66329, 66334, 66335, 66336 and 66338) at SMNS (the very well-preserved specimen SMNS 66338 is featured in Figure 11.23d). Two further specimens (SMNS 66325 and SMNS 66331) are just in between the size range of *P. axelrodi* and the new species described below.

*Diagnosis*: body length 4.9–7.5 mm; forewing length 4.3–6.5 mm; head capsule distinctly narrowed between the large and globular compound eyes; pronotum very small and bell-shaped; vestigial wing venation on elytra usually less distinct than in the following new species.

*Ponopterix maxima* spec. nov.

*Material*: specimen no. SMNS 66332 (holotype) (Figure 11.23e) and eight further specimens (SMNS 66323, 66324, 66327, 66328 (Figure 11.23b), 66330, 66333, 66337 and 66562) at SMNS.

*Type locality*: 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 because of its larger body size than *Ponopterix axelrodi*.

*Diagnosis*: body length 7.5–12.5 mm; forewing length 6.5–10.5 mm; head broader than in previous species, especially between the compound eyes; pronotum comparatively larger and broader and saddle-shaped; otherwise very similar to *P. axelrodi*, therefore very probably belonging to the same genus.

*Comment*: this new species was figured by Bechly *et al*. (2001: 49, Abb. 38) as Protocoleoptera.

*Cercopisblatta* Martins-Neto, 2005a

*Comment*: this genus was mentioned without specific designation by Martins-Neto (2005b) and is here regarded as a *nomen nudum* until a proper designation, diagnosis and figure are published.

## †Blattulidae

*Comment*: †Blattulidae are represented in the Crato Formation by two genera and species; *Elisama americana* and an undescribed genus and species. This family could either belong to the stem group of Dictyoptera (Grimaldi and Engel, 2005) or might be related to Polyphagidae (Vršanský, 1999b). Vršanský (2003b) described structural similarities of the external ovipositor in †Blattulidae and †Umenocoleidae.

*Elisama americana* Vršanský, 2002

*Material*: holotype AMNH XX (stated this way by Vršanský, 2002, probably due to a lapse) at the American Museum of Natural History in New York, USA; and three additional specimens, SMNS 66558 with colour preservation (Figure 11.23f), SMNS 66000-125, and SMNS 66316.

*Diagnosis*: body length 6.5–8.5 mm; antennae about as long as body; head with very large and globular compound eyes; width of pronotum is 146% of head width; pronotum is broadest in the middle, thus with about equal anterior and posterior halves; forewing length 7.5–10.2 mm; forewing venation with an extremely curved CuP and anal veins that reach the hind margin; Sc very short; M with three or four branches; R/RS with nine to 10 branches; forewings sometimes preserved with a distinctly banded color pattern (Bechly *et al.*, 2001a: Abb. 17), for example in specimen SMNS 66558 (Figure 11.23f).

*Comment*: because of the long and free fore coxae and the structure of styli and cerci Vršanský (2002) considers this species and some other polyphagoid cockroaches to be more closely related to Mantodea. I strongly disagree with this view, because it is contradicted by molecular data and by several unique plesiomorphies of Mantodea (three ocelli, long vein Sc) that are synapomorphically absent in all Recent cockroaches and termites.

## Blattellidae

Two species of Blattelidae occur in the Crato Formation, each in its own genus. One of these species was described by Pinto and Purper (1986), but incorrectly placed in the mesoblattinid genus *Mesoblattina* (see below), and the other is currently still undescribed. A preliminary analysis suggests that blatellids represent the most

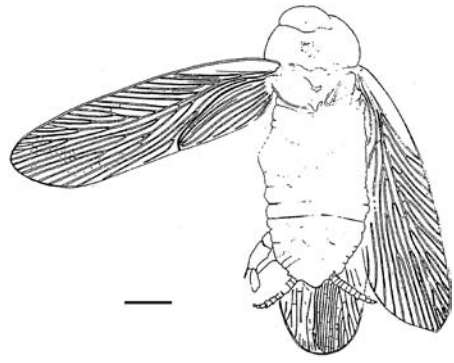

Fig. 11.24. Crato Formation cockroach: Blattellidae, *Mesoblattina limai* Pinto and Purper, 1986, holotype, MP-1–6400; scale bar, 2 mm. Based on Pinto and Purper (1986).

abundant cockroaches in the Crato Formation, comprising 60% of all fossil roaches (Vršanský, 2004). An appraisal of Crato Blattellidae and a formal description of the undescribed taxon seem to be in progress (F. Menon, personal communication).

*'Mesoblattina' limai* Pinto and Purper, 1986

*Material*: holotype no. MP-I-6400 (Figure 11.24) at the coll. Prof. Lima at the University of São Paulo and four specimens (SMNS 66314, 66315, 66319 and maybe 66311) at SMNS.

*Diagnosis*: body length 11–14 mm; antenna about as long as body; pronotum subcircular, very broad (about 200–233% of head width) with very broad lateral lobes; forewing venation typically blattellid with Sc bifurcated, R with eight to 11 branches (some of them bifurcated), MA and CuA free and branched, several anal veins simple and ending on CuP, intercalary veins and crossveins present (not as few as mentioned in the original description).

*Comment*: this species was incorrectly placed in *Mesoblattina*, belonging instead to a distinct, but undescribed new blattellid genus according to Vršanský (2004).

**Unnamed new genus and species A**

*Material*: three specimens with nos SMNS 66313, SMNS 66317 and SMNS 66318 (Figure 11.23g), as well as a putative further specimen with preliminary no. SMNS 0116 (K9).

*Diagnosis*: body length 18.3–27.0 mm; antennae distinctly longer than body (31 mm in a specimen with 25 mm body length); pronotum very large, with 215–233% of head width and with very broad lateral lobes; pronotum broadest in the middle of the posterior half; forewing venation typically blattellid.

*Comment*: very similar to '*M.*' *limai*, except for the distinctly larger size, and thus probably belonging to the same new genus. It has not been possible to determine whether this new taxon is conspecific with the undescribed new genus and species mentioned by Vršanský (2004) or instead represents a third blattellid taxon from Crato.

### Blattidae

The presence of the Blattidae in the Crato Formation was first noted by Mendes (1993), who recognized that *Mesoblattinopsis schneideri* Pinto, 1989 was a blattid.

*Mesoblattinopsis schneideri* Pinto, 1989

*Comment*: two further new species of *Mesoblattinopsis* are reported by Mendes (1997b).

### Family *incertae sedis*

### Unnamed new genus and species B

*Material*: three specimens with nos SMNS 66321, SMNS 66308 (Figure 11.23h) and SMNS 66309.

*Diagnosis*: body length about 8.7–9.5 mm; shape of body longish oval; antennae about as long as body; pronotum much broader than head (width 3.0–3.7 mm, thus 180–195% of head width), posteriorly broader than anteriorly, but with narrower lateral lobes than the new blattellid species mentioned above; forewing venation unknown, but with a broad costal margin; cerci with about 10 segments.

## 11.9 Isoptera: termites

Günter Bechly

There are about 2,800 Recent and about 130 fossil termite species, usually classified in seven families (see below). Termites are relatively small insects with a body length that is usually much less than 3 cm. They are soft-bodied and often called white ants because they are small colonial insects of more or less whitish color. They are, however, completely unrelated to ants, but closely related to cockroaches and mantids. Their antennae are filiform or moniliform, usually relatively short, with 10–32 segments. They possess prognathous chewing mouthparts with well-developed mandibles, and their compound eyes and ocelli are often reduced, except in alate stages. Wings are only present in the reproductive stages and are shed after the mating flight. Both pairs of wings are membranous and much longer than the