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 abdomen. Fore- and hind wings are similar in size (hence their scientific name Isoptera) and are similar in shape and venation, except in the most basal family Mastotermitidae that have retained a broader hind wing. The abdominal cerci are relatively short with one to eight segments (usually two to four segments) and the female ovipositor is reduced, as are all other genital appendages. Termites lay single eggs, except Mastotermitidae, which lay pods of up to 24 eggs. The development is paurometabolous with a gradual development from larva to imago. Termites mainly feed on cellulose but also feed on fungi and organic detritus. Consequently, they are often considered a pest. They are polymorphic eusocial insects with different castes, either nesting in small colonies in their feeding wood (“one-piece nesting”) or in large colonies in the soil from which they forage in search for wood. Termites have a worldwide distribution in all subtropical and tropical regions where woody plants are available. In tropical areas termites and ants form the largest fraction of the animal biomass.

Systematics and phylogeny

The monophyly of Isoptera has never been disputed and is very well supported by numerous synapomorphies. Together with mantids and cockroaches the termites belong to the monophyletic Dictyoptera within modern pterygote insects (Pterygota: Neoptera). Termites are closely related to polyphagid cockroaches, and the sister group of Isoptera is the North American wood-feeding cockroach genus *Cryptocercus*. In addition to the general dictyopteran characters, *Cryptocercus* and primitive termites share a social behaviour, wood-feeding, the possession of intracellular endosymbiontic bacteria and protists (Lo *et al*., 2003), the specific structure of the proventriculus (Klass, 1997b), the mandibular dentition and the moniliform antennae (Grimaldi and Engel, 2005).

All fossil and Recent termites are classified within the seven Recent families Mastotermitidae, Hodotermitidae (including the extinct subfamily Carinatermitinae), Termopsidae (including the extinct subfamily Cretatermitinae), Kalotermitidae, Serritermitidae, Rhinotermitidae (including the extinct subfamily Archaeorhinotermitinae) and Termitidae. It is often assumed that these families are successively more closely related to the most modern and most derived family Termitidae. However, because of several very primitive characters of Termopsidae (long cerci with four to eight segments, vestige of fifth tarsal segment and one-piece nesting without a worker caste) and Kalotermitidae, I concur with Bohn (2003b: 248), who suggested the sequence Mastotermitidae, Termopsidae (?paraphyletic), Kalotermitidae and Hodotermitidae to be successively closely related to the clade of ‘higher’ termites formed by Termitidae and ‘Rhinotermitidae’+Serritermitidae (the latter should instead be included as a subfamily within Rhinotermitidae because Rhinotermitidae is paraphyletic to Serritermitidae). Despite this, Mastotermitidae, Termopsidae, Hodotermitidae and Kalotermitidae all represent very basal and ancient lineages, and are the only taxa already present by the Lower Cretaceous.

The Australian relic species *Mastotermes darwinianus* (Mastotermitidae) is the most basal living termite and the only one to have retained certain blattarian characters like a larger size, a broader pronotum, an anal fan in the hind wings, tarsi with five distinct segments, vestige of ovipositor still present, deposition of eggs in pods (oothecae) and endosymbiontic bacteria.

The primitive families Hodotermitidae and Termopsidae have often been considered as closest relatives, but recent phylogenetic studies contradict this hypothesis (Grimaldi and Engel, 2005). The common presence of four or five cercal segments is only a symplesiomorphy of Hodotermitidae and Termopsidae that is actually absent in the most primitive Mastotermitidae. Furthermore, the reduction of the ocelli in Hodotermitidae and Termopsidae can hardly be considered as a convincing synapomorphy, as the ocelli are also reduced in other subordinate taxa within Isoptera, which in any case have a trend towards reduction of the eyes and ocelli.

Evolution

According to some early authors, Mantodea and Isoptera should have diverged during the Permian, a view supported by Krishna (1990). However, this hypothesis is now considered unlikely as it is neither supported by the fossil record nor by any modern phylogenetic analyses (Grimaldi and Engel, 2005). Living members of the most basal taxa Mastotermitidae and Hodotermitidae, even though they have retained a relatively primitive morphology, show a mixture of both primitive and derived traits in their social organization. The common presence of true workers and foraging behavior in the basal Mastotermitidae and Hodotermitidae as well as in the derived clade formed by Serritermitidae+Rhinotermitidae+Termitidae seems to support the so-called ancestral worker hypothesis, but from the viewpoint of evolutionary biology it is more probable that this is due to a triple parallel development, and that the one-piece nesting of Termopsidae and Kalotermitidae represents the ancestral condition for termite social organization (Thorne and Traniello, 2002). Nevertheless, currently it cannot be definitely decided if one-piece nesting (groups that consume only the wood in which they live and in which helpers have developmental flexibility) or organized foraging away from the nest (correlated with a true worker caste and soil nesting) represents the primitive state within termites.

Fossil record

The most recent systematic revision of all fossil termites was provided by Nel and Paicheler (1993), while Thorne *et al.* (2000), Belayeva (2002), Thorne and Traniello (2002) and Grimaldi and Engel (2005) summarized the current state of knowledge of their fossil record. Unfortunately, there is no fossil record of primitive proto-termites that could illustrate the evolutionary transition from blattarian ancestors to modern termites, which is suggested by a comparison of the Recent wood roach *Cryptocercus* and primitive Recent termites like *Mastotermes darwiniensis*. Except for *Meiatermes bertrani* from the lowermost Cretaceous of Spain, the fossil termites from the Crato limestones belong to the oldest known fossil termites of all. All alleged termites from the Upper Jurassic Solnhofen limestones of Bavaria in Germany are based on incorrect determinations (e.g. *Gigantotermes excelsus* is a lacewing) or on dubious specimens that have to be considered as indeterminable fossil problematica.

Several alleged fossil termite nests have been described from the Upper Triassic of North America (Hasiotis and Dubiel, 1995; Hasiotis *et al.*, 1997), the Lower Jurassic of South Africa (Bordy *et al.*, 2004) and the Upper Cretaceous of Texas (Rohr *et al.*, 1986).

The taxonomy and phylogenetic systematics of fossil termites requires urgent revision to better understand termite evolution. An example is *Valditermes* from the Cretaceous Weald Clay of England, which is still attributed to Hodotermitidae by Engel and Grimaldi (2005), as it was by Jarzembowski (1991), even though the well-developed anal area clearly excludes any position within the clade formed by all non-mastotermitid termite families. Jarzembowski (1991) even discussed this character and correctly stated that it is only a symplesiomorphy with Mastotermitidae, but ignored its phylogenetic implications. Likewise, the several fossil termite genera attributed to Hodotermitidae have five-segmented tarsi, which prohibits such a referral, and were mostly ignored or not considered in phylogenetic terms. The referral of *Carinatermes nascimbeni* from Upper Cretaceous New Jersey amber to Hodotermitidae must also be questioned, as it appears to have five-segmented tarsi, a broad pronotum and keeled fore coxae as in Mastotermitidae (Engel and Grimaldi, 2005: 246).

Palaeobiology and palaeoecology

About 1% of the several ten thousands of Crato insects so far discovered are termites. This small number actually represents several hundred specimens, indicating a high abundance in the hinterland, and indirect evidence for abundant woody plants and trees in the region, which is otherwise not well documented. Fossils of shrubby plants and herbs are common in the Crato Formation, but large logs of wood are very rare indeed. The biggest piece found was less than 1 m long. In fact, termites are more common than bits of wood over 10 cm in length. Maybe Crato termites foraged on smaller, stick-like plant material, which was provided by the abundant gnetaleans.

All fossil termites from this locality represent alate stages, except for one of the 21 specimens studied by Fontes and Vulcano (1998) that appears not to be a worker or soldier, but simply an alate stage with shed wings. This lack of workers and soldiers is odd considering that they occur frequently in Tertiary amber. Furthermore, the frequent occurrence of other flightless terrestrial arthropods (e.g. spiders or nymphs of bugs and cicadas) in the Crato Formation suggests that the absence of worker and soldier termites can hardly be attributed to biostratinomic processes. It may possibly hint at one-piece nesting behavior in the Crato termites, because the absence of foraging behavior would explain why only alate stages were likely to end up in the Crato lagoon. It is also quite obvious that Crato termites did not nest underground in the river valleys, because if they did, then whole nests would have been washed into the Crato lagoon during floods. So they must have nested in drier ground, above the floor of the river valleys.

Crato termites

Six termite species have been described from the Crato Formation (Krishna, 1990; Fontes and Vulcano, 1998; Martins-Neto *et al.*, 2006). Furthermore, images of Crato termites have been published (Maisey, 1991: 384; a specimen of *Mariconitermes talicei*; Bechly *et al.*, 2001a: figure 47, a specimen of *Nordestinatermes araripena*; and Fontes and Vulcano, 2004: figures 1 and 2, *Nordestinatermes araripena*; figure 3, *Mariconitermes talicei*).

Mastotermitidae

Diagnosis: short cerci with only two segments is the single autapomorphy for the group (at least in the Recent genus *Mastotermes*, convergent to all modern termites except Hodotermitidae and Termopsidae). The remaining characters are plesiomorphic: relatively large size; antennae long with more than 29–32 segments in alates; large compound eyes; ocelli present; fontanelle absent; pronotum distinctly broader than head capsule in alates; wings with complete venation with distinct and branched RS, M, and Cu; RS with anterior branches; anal fan of hind wing well developed; basal transverse suture absent in hind wings; five distinct tarsomeres; eggs produced in pods (homologous to the oothecae of Blattaria and Mantodea); eusocial with true worker caste and foraging behavior (probably convergent to Hodotermitidae and more modern termites).

Cratomastotermes gen. nov.

Type species: *Cratomastotermes wolfschwenningeri* sp. nov., by present designation.

Derivation of name: named after the Crato Formation and the Recent relic genus *Mastotermes*.

Diagnosis: same as type species, since it is monotypic.

Cratomastotermes wolfschwenningeri sp. nov.

Material: holotype SMNS 66186 (Figure 11.25a) and paratypes SMNS 66187 and SMNS 66188 (Figure 11.25b). A further but somewhat smaller specimen (SMNS 66189) with a body length of 11 mm and a wing length of 14 mm might also belong to this species.

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 Dr Karin Wolf-Schwenninger for her invaluable help with my studies on fossil insects.

Diagnosis and description of alates (Figures 11.25a and b): body length 12–15 mm; compound eyes large; area of ocelli not preserved; pronotum broader than head (4–5 mm wide) and cockroach-like (plesiomorphy); legs and tarsi not preserved, thus number of tarsomeres unknown; forewings 17 mm, hind wings 16 mm long; SC long; veins RS, M and Cu in both pairs of wings well developed and richly branched; scales of wings not preserved; hind wing much broader than forewing with a well-developed anal fan; cerci not preserved, thus number of cercal segments unknown. The paratype specimen no. SMNS 66188 (Figure 11.25b) even shows soft-tissue preservation of abdominal internal organs including parts of the gut.

Comments: the comparably large size, the well-developed pronotal lobes, the complete wing venation, and the broad hind wings with anal fan strongly suggest referral to Mastotermitidae, even though this is based on symplesiomorphies. Although Mastotermitidae represents the most basal and most primitive family of termites (Grimaldi and Engel, 2005), which should be expected to be abundant among Mesozoic termites, this family is exceptionally rare in the Mesozoic. However, the occurrence of Mastotermitidae in the New World and in South America has previously been documented by four Tertiary species (Fontes and Vulcano, 1998: 280–281).

Termopsidae

Diagnosis: the following are apomorphies: ocelli absent (convergent to or synapomorphic with Hodotermitidae); antennae shorter with only 11–21 segments; pronotum flat (not saddle-shaped as in Hodotermitidae), usually less wide than head.

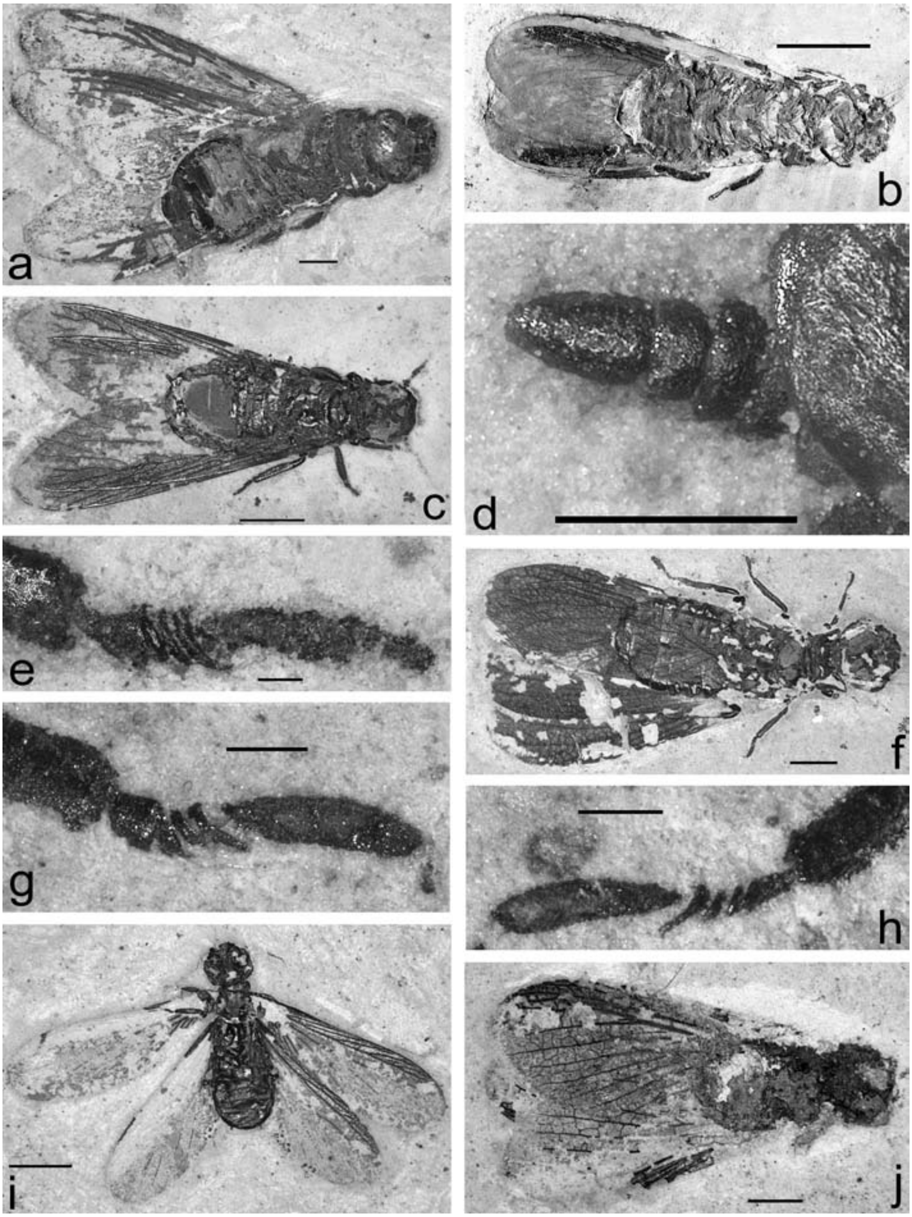

Fig. 11.25. Crato Formation Isoptera: (a) Mastotermitidae, *Cratomastotermes wolfschwenningeri* gen. et sp. nov., holotype, SMNS 66186; scale bar, 2 mm; (b) Mastotermitidae, *Cratomastotermes wolfschwenningeri* gen. et sp. nov., paratype, SMNS 66188; scale bar, 5 mm; (c) Termopsidae, *Nordestinatermes araripena*, SMNS 66190; scale bar, 2 mm; (d) Termopsidae, *Nordestinatermes araripena*, SMNS 66190, left cercus; scale bar, 1.4 mm; (e) Termopsidae, *Nordestinatermes araripena*, SMNS 66190, right hindtarsus; scale bar, 0.1 mm; (f) Termopsidae, *Mariconitermes talicei*, SMNS 66193; scale bar, 2 mm; (g) Termopsidae, *Mariconitermes talicei*, SMNS 66193, right midtarsus; scale bar, 0.25 mm; (h) Termopsidae, *Mariconitermes talicei*, SMNS 66193, left midtarsus; scale bar, 0.25 mm; (i) Kalotermitidae, *Cratokalotermes santanensis* gen. et sp. nov., holotype SMNS 66195 scale bar, 2 mm; (j) Rhinotermitidae, *Cretarhinotermes novaolindense* gen. et sp. nov., holotype SMNS 66196; scale bar, 2 mm.

The remaining characters are plesiomorphic: fontanelle absent; pronotum and width increasing from posterior to anterior side; wings with complete venation; Rs with anterior branches; anal fan of hind wing reduced (synapomorphy of all non-mastotermitid termites); scales of forewings shorter than those of hind wings; four or five tarsomeres (plesiomorphy of fossil members, in Recent members only a vestigial fifth segment); cerci with four to eight segments, usually with four or five segments (all Hodotermitidae have four cercal segments, all other termites only one or two segments); eusocial with pseudergates instead of a true worker caste and with one-piece nesting (otherwise only retained in Kalotermitidae).

Comments: the wing venational characters previously used to diagnose Termopsidae and Hodotermitidae are homoplastic and the arguments and attributions of different authors are consequently confusing and often conflicting. I therefore doubt the value of the wing-venation criteria employed by Krishna (1990) and Fontes and Vulcano (1998, 2004) to attribute Cretatermitinae to Hodotermitidae rather than Termopsidae.

Cretatermitinae

Nordestinatermes araripena (Krishna, 1990)

Material: three specimens: AMNH 43902 (holotype; Figure 11.26c), AMNH 43901 (paratype) and AMNH 43903 (paratype); in addition, 16 specimens with nos 580, 581, 582, 856, 1533, 1718, 2071, 2072, 2074, 2075, 2453, 5001, 5002, 5003, 5004 and 5008 in the Vulcano collection, Brazil, and three SMNS specimens (SMNS 66190 (Figures 11.25c–e), 66191 and 66192).

Diagnosis of alates: body length 7.0–8.5 mm; ocelli absent; pronotum about as broad as head or even slightly broader; tarsi five-segmented (Figure 11.25e); antennae with 18–22 segments; cerci definitely four-segmented (Figure 11.25d), not five-segmented as stated by Krishna (1990) and Fontes and Vulcano (1998); anal fan of hind wing reduced.

Comments: this species was transferred by Fontes and Vulcano (1998) from *Meiatermes* and the subfamily Hodotermitinae to *Cretatermes* and the subfamily †Cretatermitinae within Hodotermitidae. Martins-Neto *et al.* (2006) established a new genus *Nordestinatermes* which seems to be poorly defined, but is here accepted until a revision is available. However, referral to Hodotermitidae by Krishna (1990), Fontes and Vulcano (1998, 2004) and Martins-Neto *et al.* (2006) cannot be upheld: firstly, †Cretatermitinae was considered by all other authors to belong within Termopsidae rather than Hodotermitidae *sensu stricto*, and secondly, because five-segmented tarsi are absent in all termites (including all Recent Hodotermitidae) except Mastotermitidae and some Termopsidae. However, referral to

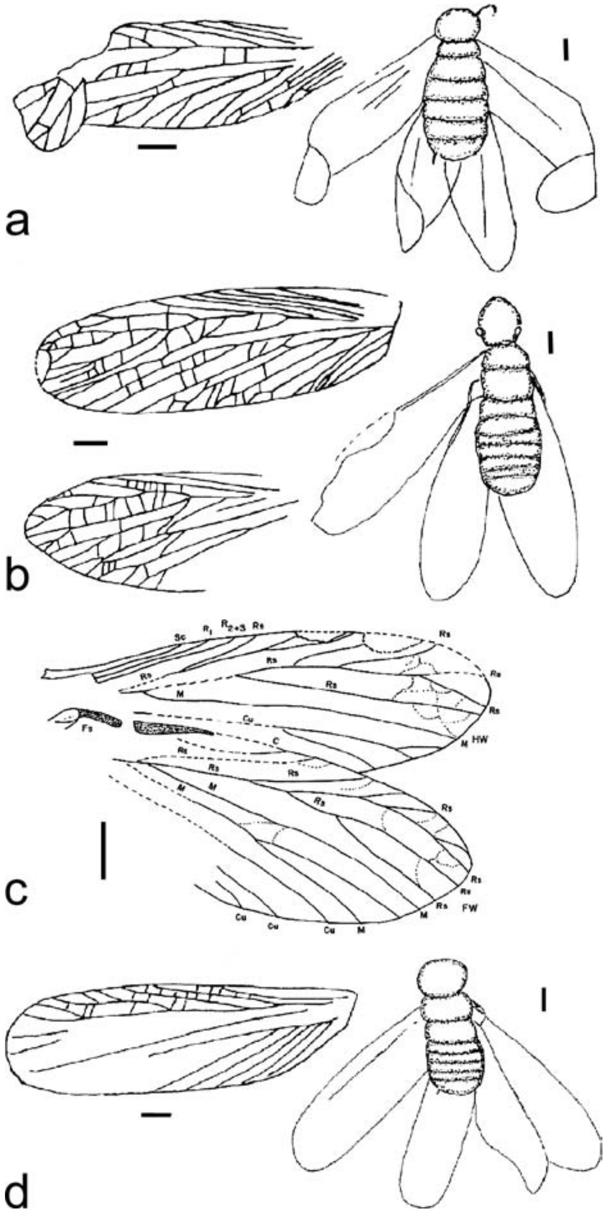

Fig. 11.26. Crato Formation Isoptera: (a) *Araripetermes nativa* Martins-Neto *et al.* 2006, habitus and wing venation; scale bars, 1 mm; **b**, *Caatingatermes megacephalus* Martins-Neto *et al.* 2006, habitus and fore- (below) and hind wing venation; (c) *Nordestinatermes araripena* (Krishna, 1990), holotype AMNH 43902, fore- and hind wings; (d) *Nordestinatermes obesa* Martins-Neto *et al.* 2006, habitus and forewing. Scale bars, 1 mm. (a,b,d) After Martins-Neto *et al.* 2006); (c) after Krishna (1990).

Mastotermitidae would be ill-founded on such a symplesiomorphy because all other characters show more modern states. *Termopsis heeri* from Baltic amber, the type species of *Termopsis* which is the type genus of Termopsinae, still has five-segmented tarsi (at least on the hind legs), while Recent Termopsinae rarely retain a vestigial fifth segment, which could suggest a more basal position within Isoptera than Hodotermitidae, that would correspond to their primitive social behavior (one-piece nesting). Either way, referral to Termopsidae-Cretatermitinae currently is best supported by the available characters. Also, the absence of a true worker caste and foraging behavior (suggested by the absence of non-alate stages among Crato termites) would be a symplesiomorphic similarity between *Nordestinatermes araripena* and Recent Termopsidae, while a fossil termite worker from the Lower Cretaceous of Spain (attributed to *Meiatermes bertrani*) seems to indicate that Hodotermitidae was already eusocial with a true worker caste in this early period of termite evolution.

It must also be noted that the figures of the wing venation of the original description (Krishna, 1990: figure 3) and the re-description (Fontes and Vulcano, 1998: figure 1) have little in common, so that it must be questioned if they indeed illustrate the same species. Furthermore, both figures are clearly incorrect, because they either show an impossible venation for Isoptera (Krishna, 1990), which always have separate stems for RS, M, and Cu, or the drawings differ from the venation seen in the photograph of the same specimen (Fontes and Vulcano, 1998: figures 1 and 11). All three specimens in the collection of SMNS, which can be clearly attributed to the present species, have a wing-venation pattern (especially of RS) that agrees with the original drawing of Krishna (1990) more than the confusing re-description of Fontes and Vulcano (1998). Obviously, all Cretatermitinae from the Crato Formation are in need of revision.

Nordestinatermes obesa Martins-Neto *et al.,* 2006

Material: holotype RGMN-T149 (Figure 11.26d), Martins-Neto collection, belonging to the Sociedade Brasileira de Paleoartropodologia.

Diagnosis: body length 6.3 mm and tegmen length 10.5 mm; body very robust. Otherwise the characters of the genus *Nordestinatermes*: head circular, pronotum about as long and wide as head, forewing with reduced number of R branches, origin of M close to wing base, M unbranched.

Cretatermes pereirai Fontes and Vulcano, 1998

Material: 2452 (holotype), 849 and 5005 (paratypes) in Vulcano collection, Brazil; specimen SMNS 66517, with a body length of 9 mm, may belong to this species.

Diagnosis of alates: body length 9.0–10.5 mm; otherwise more or less identical to *Cretatermes araripena.*

Comments: it appears very doubtful if *Cretatermes pereirai* is a good species at all, because there is only a very small size difference and other insignificant differences to *C. araripena* and the original description is flawed (see above). Nevertheless, the question of synonymy should be left open until a better and more detailed revision of Crato termites is available. This species was not discussed at all by Martins-Neto *et al.* (2006) and therefore might also belong to their new genus *Nordestinatermes*.

Termopsidae

Subfamilia *incertae sedis*

Mariconitermes Fontes and Vulcano, 1989

Mariconitermes talicei Fontes and Vulcano, 1998

Material: no. 5006 (holotype) and no. 5007 (paratype) in coll. Vulcano, Brazil; specimens SMNS 66193 (body length 12 mm, wing length 13 mm; Figures 11.25f–h) and SMNS 66194 (body length 8 mm, wing length 12 mm) are referred to this species.

Revised diagnosis of alates: body length 8–15 mm; ocelli apparently absent; pronotum of characteristic shape (typical for Termopsidae and Hodotermitidae), less wide than head, but with well-developed lateral lobes with concave margin; width of pronotum increasing from posterior to anterior side; tarsi five-segmented (Figures 11.25g and h); wings reticulated; cerci with five segments.

Comment: this taxon was placed in Hodotermitinae by Fontes and Vulcano (1998), but can now be referred to Termopsidae, because a new and very well-preserved specimen of this species in the in Stuttgart distinctly displays five tarsal segments on both mesotarsi. All Hodotermitidae possess only four tarsomeres like all other termites, except the most primitive Mastotermitidae and Termopsidae. The absence of a well-defined anal lobe on the hind wings and the five-segmented cerci excludes referral to Mastotermitidae. Likewise, all other so-called fossil Hodotermitidae with five-segmented tarsi (e.g. *Ulmeriella* spp.) must probably be transferred to Termopsidae.

Hodotermitidae?

Caatingatermitinae

Comment: this new subfamily was established within Hodotermitidae by Martins-Neto *et al.* (2006) and is distinguished from all other subfamilies of Termopsidae and Hodotermitidae by the origin of M very far from the wing base and distally fused to Cu. Unfortunately, Martins-*Neto et al.* (2006) did not describe the tarsus, so that no definite attribution to either Hodotermitidae or Termopsidae is presently possible. Martins-Neto (2005a, 2005b) erected two new taxa of Hodotermitidae as *nomina nuda* from the Crato Formation, which were formally described by Martins-Neto *et al.* (2006).

Caatingatermes megacephalus Martins-Neto *et al.*, 2006

Material: holotype RGMN-T147 (Figure 11.26b), Martins-Neto collection.

Diagnosis: body length 9 mm and tegmen length 11 mm, head pentagonal, longer than wide, eyes small and not prominent but displaced under the mid-length of head, pronotum trapezoidal and as wide as head base, size of pronotum about two-thirds of head size, forewing with the humeral suture well-defined, straight and perpendicular to costal margin, vein R secondarily branched with five long, pectinate anterior radial branches and five relatively short posterior radial branches that sometimes have secondary branches.

Araripetermes nativa Martins-Neto *et al.*, 2006

Material: holotype RGMN-T148 (Figure 11.26a), part and counterpart, Martins-Neto collection.

Diagnosis: body length 8 mm and tegmen length 10 mm, head ellipsoid, 20% wider than long, with rounded margins, forewing with sigmoidal M that is distally fused to Cu, origin of M distally of midwing position.

Kalotermitidae

Diagnosis: apomorphies include RS closely parallel to costal margin; antennae shorter with only 10–21 segments. The following features are plesiomorphic: small ocelli present in alates; fontanelle absent; pronotum flat and as broad or broader than head capsule; wings with less complete venation (synapomorphy with modern termites); RS with anterior branches, but the latter only short, oblique, and unforked or only weakly forked branches (apomorphy in the groundplan of modern termites, while the RS branches are completely reduced in Serritermitidae+Rhinotermitidae+Termitidae); anal fan of hind wing reduced (synapomorphy of all non-mastotermitid termites); scales of forewings much larger than those of hind wings; only four tarsomeres; cerci very short with only two (rarely three) segments (apomorphy of modern termites); eusocial with pseudergates instead of a true worker caste and with one-piece nesting (plesiomorphy, otherwise only retained in Termopsidae).

Cratokalotermes gen. nov.

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

Derivation of name: named after the Crato Formation and the Recent genus *Kalotermes*.

Diagnosis: as for type species, by monotypy.

Cratokalotermes santanensis sp. nov.

Material: only known by the holotype SMNS 66195 (Figure 11.25i).

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: after the town of Santana do Cariri in the type area.

Diagnosis and description of alates: body length 6.1 mm; head very large and distinctly broader than pronotum (apomorphy); compound eyes small; area of ocelli not preserved; forewings 7.5 mm long and a maximum of 2.2 mm wide, hind wings 7.0 mm long and a maximum of 2.3 mm wide, thus wings not very elongate but rather broad; Sc very short; RS in both pairs of wings closely parallel to costal margin and with short, oblique, and five unforked or only weakly forked branches; M more closely parallel to Cu; area of M wider than that of RS or Cu; M and Cu branched and less strongly sclerotized than RS; scale of forewing much larger than in hind wing (the scales are well-preserved in the right pair of wings); cerci inconspicuous, extremely short and two-segmented.

Comments: this new taxon represents the first Mesozoic record and the first New World record of the Kalotermitidae. However, an undescribed kalotermitid has apparently been discovered in Lower Cretaceous Lebanese amber by André Nel (cited in Grimaldi and Engel, 2005: 247).

Rhinotermitidae

Diagnosis: apomorphies include antennae shorter with 14–22 segments; M weakly branched and area of M narrow; Cu terminating at wing apex, richly branched, occupying more than half of the wing; eusocial with a true worker caste. The following are plesimorphic: small ocelli present in alates; fontanelle present; pronotum more or less flat; wings with less complete venation (synapomorphy with modern termites); RS without distinct branches and closely parallel to costal margin (synapomorphy of Serritermitidae+Rhinotermitidae+Termitidae); anal fan of hind wing reduced (synapomorphy of all non-mastotermitid termites); wing venation distinctly reticulate (absent in Termitidae); scales of forewings much larger than those of hind wings; only three or four tarsomeres; cerci very short with only two segments (apomorphy of modern termites);

Cretarhinotermes gen. nov.

Type species: *Cretarhinotermes novaolindense* sp. nov., by present designation.

Derivation of name: after the Cretaceous age and the Recent genus *Rhinotermes*.

Diagnosis: as for type species, by monotypy.

Cretarhinotermes novaolindense sp. nov.

Material: holotype SMNS 66196 (Figure 11.25j); paratype SMNS 66197.

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: after the type locality.

Diagnosis and description of alates: body length 7.2–9.4 mm; head and thorax poorly preserved without details; legs and tarsi not preserved; wings about 12–13 mm long and rather broad (maximum width 4.2 mm) with a strongly reticulated venation; RS closely parallel to costal margin and apparently without long branches; M closely parallel to RS and apparently unbranched; Cu richly branched and apparently reaching the apex of the wing so that more than half of the wing is occupied by the Cu branches; cerci not preserved.

Comments: the wings are so different in shape and venation from other described species that there is no doubt that these two fossils represent an additional Crato taxon. Unfortunately, the bodies are very poorly preserved and the wings superimposed, so that it is difficult to recognize the precise venation. However, the visible parts of RS, M and Cu suggest that these two fossils constitute the oldest record of the modern family Rhinotermitidae and consequently also represent a *terminus post quem non* for the origin of the most derived clade within Isoptera that includes the Termitidae.

11.10 Chresmododea: fossil 'water striders'

Günter Bechly

Chresmodids are large insects with a water-strider-like habitus that are only known as fossils. They have short, thick antennae and prognathous chewing mouthparts with strong mandibles. Their compound eyes are large and their legs are extremely prolonged with very long femora, shorter tibiae, and long, multi-segmented, flagellate tarsi with more than 40 tarsomeres, which is unique within Insecta (Nel *et al.*, 2004). The forelegs are usually directed anteriorly, while the middle and hind legs are directed latero-caudally. Female chresmodids have two pairs of membranous wings with a slender forewing with long and parallel longitudinal veins and a broad