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

anal fan in the hind wings, but the males seem to be wingless. There are long, but only single-segmented, lanceolate cerci at the end of the abdomen (similar to Phasmatodea), and females have a prominent orthopteroid-like ovipositor. The nymphs are similar to the adults but are much smaller, with a distinctly shorter abdomen, and the absence of wings. Consequently their development was hemimetabolous as in orthopterans. Chresmodids probably lived on the water surface of lakes and lagoons (*contra* Baudoin, 1980, who did not know the true structure of the chresmodid legs), and fed on insects and other small animals at the water surface, just like the unrelated but morphologically similar modern Gerridae. The group is exclusively Mesozoic and may have suffered extinction during the catastrophic impact at the Cretaceous–Tertiary boundary.

Systematics, phylogeny and evolution

Contrary to Martynova (1962, 1991) here the Chresmododea are restricted to include only the family Chresmodidae, thus excluding the extinct families Aerophasmatidae, Necrophasmatidae and Aeroplanidae. However, this does not mean to say that these taxa (especially Aerophasmatidae) might not be more closely related to Chresmododea than to Orthoptera (see section 11.11), but currently there are no convincing arguments for such a relationship.

The phylogenetic relationship of chresmodids was long disputed and they have been attributed to Heteroptera-Gerromorpha, Grylloblattodea-Paraplecoptera, Mantodea, Orthoptera, Polyneoptera of uncertain affinity and most often to Phasmatodea. A sister-group relationship of Chresmododea and Phasmatodea is supported by the recent discovery of new fossil material with preserved fore- and hind wings (Martínez-Delclòs *et al.*, 2007).

Carpenter (1992) correctly recognized that fossil arthropods from the Lower Jurassic Solnhofen lithographic limestones, known under the name *Sternarthron zitteli*, are not Chelicerata-Pantopoda as previously believed, but clearly represent the nymphal stage of *Chresmoda obscura* from the same locality. A re-examination of the type specimens from the collection of the Bayerische Staatssammlung in Munich (BSPGM nos 1870 VII 45 and AS I 822) confirmed that the description and drawings of Haase (1890) are totally wrong (his drawings Figures 5 and 6 even appear to be manipulated to support his attribution) and the fossils clearly are hexapods with only three pairs of legs and structures that are very similar to adult *Chresmoda* (*contra* Bechly, 1999b: 9).

Carpenter (1992) retained the younger, and therefore junior, synonym *Propypolampis* Weyenbergh, 1874 as the valid name for the fossils previously known as *Chresmoda* Germar, 1839 and mentions a paper by himself (in press, 1992) that should allegedly reveal that the holotype of *Chresmoda* is a locust and was

only later confused with the fossil 'water striders'. Therefore, Carpenter (1992: 181) classified *Chresmoda* within Orthoptera-Caelifera as a 'little-known genus probably related to Acrididae', while he considered *Propygolampis* to be related to Phasmatodea. However, the cited paper of Carpenter that should have appeared in 1992 in the journal *Psyche* was never published (Furth, 1994) and the manuscript has to be considered as lost because it is neither archived at the intended publisher nor could it be found it in Carpenter's archives in his laboratory at MCZ. These taxonomic problems will be discussed in detail in a future publication. Here the suggestion of Rasnitsyn (2002), to retain the oldest available generic name *Chresmoda* and the family name Chresmodidae as valid names for the fossil 'water striders', is followed, especially as the holotype of *Chresmoda obscura* is lost so that it is no longer possible to verify the taxonomic decisions of Carpenter (1992).

Fossil record

The history of this exclusively fossil taxon was discussed by Handlirsch (1906–1908), Esaki (1949), Ponomarenko (1986), Martínez-Delclòs (1989), Carpenter (1992), Rasnitsyn (2002), Nel *et al.* (2004) and Grimaldi and Engel (2005).

There are seven fossil species which range from the Upper Jurassic of Germany (*Chresmoda obscura* = *Propygolampis giganteus*), the Lower Cretaceous of Mongolia (*Chresmoda* sp. nov. and *Saurophthirodes mongolicus*, which could be a nymph of *Chresmoda*), China (*Chresmoda orientalis*), Brazil (*Chresmoda* sp. nov.) and Spain *(Chresmoda aquatica*), to the Upper Cretaceous of Lebanon (*Chresmoda libanica*).

Crato Formation chresmodids

Bechly (1998b: 155; 1999b: 9) was first to note the occurrence of chresmodids in the Crato Formation. Bechly *et al*. (2001a: 55, figure 44) discussed and figured a beautiful fossil *Chresmoda* from the Crato limestones. This female with ovipositor, seems to be the best preserved specimen from this locality of all (Plate 15d), and is deposited with preliminary no. 0134 (old number H56) at SMNS. Another example (AMNH specimen) was figured by Grimaldi and Engel (2005: figure 7.5), and four further specimens (e.g. specimen no. G88; Plate 15e) have been studied by the present author and will be described by Heads and Engel.

All six specimens of the new *Chresmoda* species from the Crato Formation are alate adults with long wings (wing length 27–28 mm). The body length from head (without antennae) to abdomen (without terminalia) is about 21–25 mm, and the mesofemora are about 20–22 mm long. The head has large globular compound eyes

and large prognathous mandibles (similar to tiger beetles), and the antennae are 9–11 mm long. Distinct one-segmented cerci (3 mm long) and a prominent ovipositor are visible in one specimen. All other characters agree with the general diagnosis above.

Being surface striders on saline water that mainly fed on other insects that were trapped on the water surface, the chresmodids most probably represented the only autochthonous aquatic insects in the palaeohabitat of the Crato lagoon.

11.11 Orthopterida: grasshoppers, crickets, locusts and stick insects

Sam W. Heads and Rafael G. Martins-Neto

Phasmatodea: stick insects

The stick insects are an exclusively phytophagous group of orthopterids famous for their remarkable morphological and behavioural crypsis as mimics of sticks and leaves (Bedford, 1978; Key, 1991; Grimaldi and Engel, 2005). So extreme is the mimicry of Recent stick insects that it even extends to their eggs, which often resemble seeds (Sellick, 1997, 1998) and in some cases bear prominent capitula that, like the elaiosomes of many seeds, encourage their dispersal and burial by ants (Compton and Ware, 1991; Hughes and Westoby, 1992): a process known as myrmecochory.

Phasmatodea are rare as fossils, often occurring only as isolated wings (Gorochov and Rasnitsyn, 2002), with very few complete and articulated individuals recorded (e.g. Gorochov, 1994, 2000; Ren, 1997). Fossil stick-insect eggs are also rare but have been reported by Sellick (1994) and are distinguished by their unique detachable anterior operculum and distinctive mycropylar plate. Although the monophyly of Recent Phasmatodea is well established based on a suite of robust morphological characters, their relationship to fossil forms is somewhat controversial. Most workers recognize a number of Mesozoic families (e.g. Carpenter, 1992; Gorochov and Rasnitsyn, 2002; Willmann, 2003) but their assignment to Phasmatodea is questioned by others (notably Tilgner, 2000). However, it is generally accepted by most palaeoentomologists that the Mesozoic forms represent stem group stick insects (Willmann, 2003; Grimaldi and Engel, 2005), although a detailed phylogenetic analysis of Phasmatodea incorporating fossil forms is still lacking and is hindered by the paucity of their fossil record and the fragmentary nature of most specimens.

In the Crato Formation, Phasmatodea are represented by a single species, *Cretophasma araripensis* Martins-Neto, 1989b, known from a single forewing (Figure 11.27). *Cretophasma* was originally placed in its own family (Cretophasmatidae) by Sharov (1968) when he described *Cretophasma raggei* from the Early Cretaceous

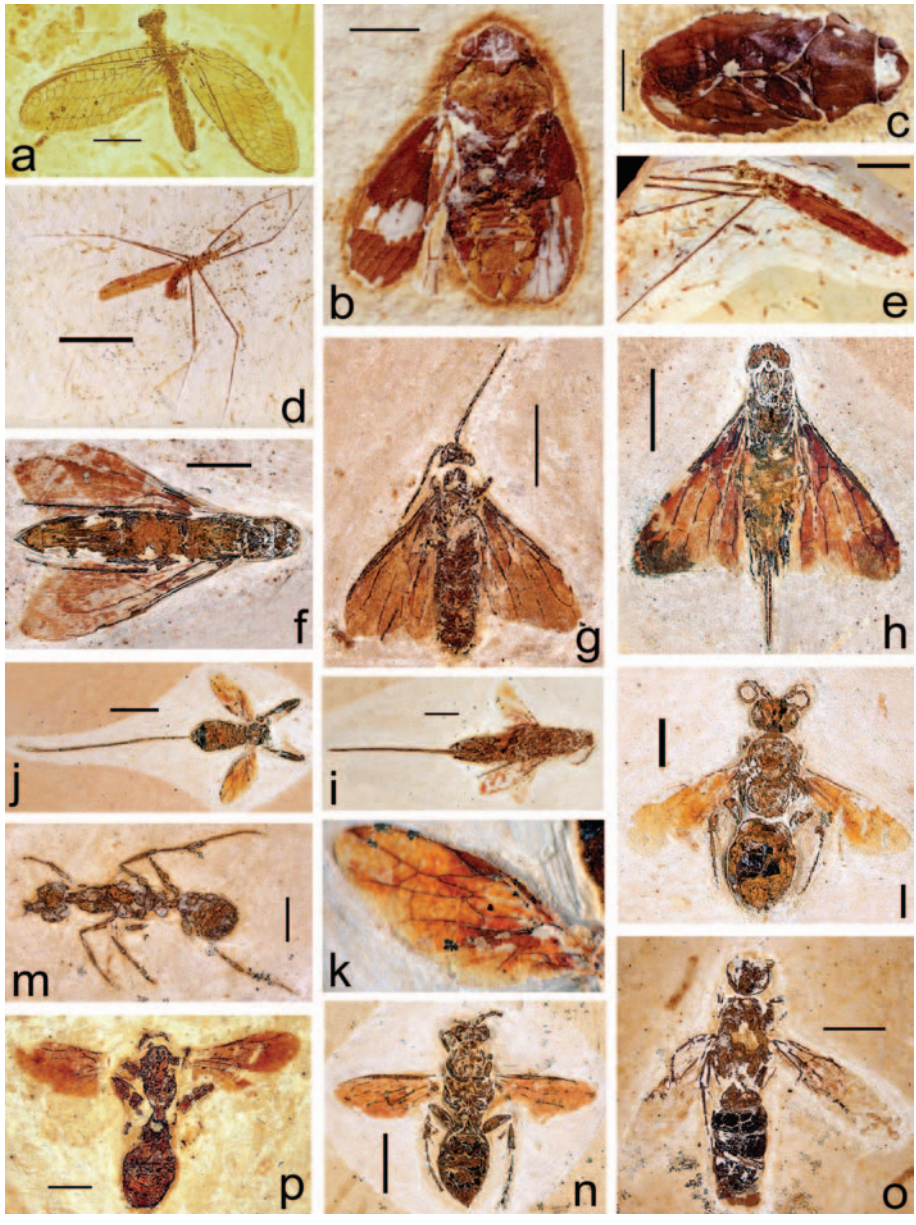

Plate 15. Crato insects: (a) Neuroptera, Hemerobiiformia, Mesochrysopidae gen. et sp. nov., priv. coll.; scale bar, 5 mm; (b) Coleorrhyncha, Progonocimidae gen. et sp. nov. SMNS 66423; scale bar, 2 mm; (c) Coleorrhyncha, Progonocimidae gen. et sp. nov. SMNS 66431; scale bar, 2 mm; (d) Chresmododea, Chresmodidae, *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, Myrmeciinae, *Cariridris bipetiolata*, SMNS 66565; scale bar, 2 mm; (n) Tiphiidae, *Architiphia rasnitsyni*, MURJ without number; scale bar, 5 mm; (o) Tiphiidae,?Myzininae, SMNS 66303; scale bar, 5 mm; (p) Vespidae, ?Eumeninae, SMNS 66295; scale bar, 2 mm.