N. Jb. Geol. Paläont. Abh.
2008, vol. 247/3, p. 353–381, Stuttgart, March 2008, published online 2008

The enigmatic Mesozoic insect taxon Chresmodidae (Polyneoptera): New palaeobiological and phylogenetic data, with the description of a new species from the Lower Cretaceous of Brazil

Xavier Delclòs, Barcelona, **André Nel,** Paris, **Dany Azar,** Fanar-Matn, **Günter Bechly,** Stuttgart, **Jason A. Dunlop,** Berlin, **Michael S. Engel,** Lawrence, and **Sam W. Heads,** Portsmouth

With 10 figures

Delclòs, X., Nel, A., Azar, D., Bechly, G., Dunlop, J. A., Engel, M. S. & Heads, S. W. (2008): The enigmatic Mesozoic insect taxon Chresmodidae (Polyneoptera): New palaeobiological and phylogenetic data, with the description of a new species from the Lower Cretaceous of Brazil. – N. Jb. Geol. Paläont. Abh., **247**: 353–381; Stuttgart.

Abstract: The morphology of the enigmatic, Mesozoic, aquatic insect family Chresmodidae is redescribed and its phylogenetic affinities among the polyneopterous orders discussed. Study of the complete venation of both fore- and hind wings observed in some specimens from the Spanish Barremian, permit us to postulate the hypothesis that the family belongs to the Archaeorthoptera, thus to the orthopteroid lineage rather than to crown-group Phasmatodea or to the more inclusive group Holophasmatodea (*sensu* Grimaldi & Engel, 2005). New specimens from Spain, Lebanon, Brazil, and Germany permit a new re-description of some chresmodid body structures with concomitant implications for the phylogenetic position of the family. *Chresmoda neotropica* n. sp. is described from the Aptian-Albian of the Crato Formation (northeast Brazil). The functional morphology proposed for some of their specialized structures suggest a new hypothesis of *Chresmoda* palaeobiology, and related to this some implications for the localized palaeoenvironment as well as global palaeoclimate.

The problematic *Sternarthron* spp. from the Upper Jurassic of Solnhofen were described as probable palpigrades (Arachnida: Palpigradi), based on type material originally thought to be fossil insects. The affinities of *Sternarthron* Haase, 1890 have been questioned. Our restudy of Haase's types clearly confirmed earlier assumptions that these fossils represent nymphal specimens of chresmodids. Consequently, *Sternarthron* has to be considered as an invalid junior synonym of the fossil insect genera *Propygolampis* Weyenbergh, 1874 and *Chresmoda* Germar, 1839.

Key words: Insecta, Polyneoptera, Archaeorthoptera, Sternarthronidae, Chresmodidae, Palpigradi, Functional Morphology, Phylogeny, Paleoecology, Mesozoic, Crato Formation, Solnhofen Lithographic Limestones.

1. Introduction and historical context

Chresmodids are large fossil insects with a water-strider-like habitus. They have short and thick antennae and prognathous chewing mouthparts with strong mandibles, and large compound eyes. The legs are extremely prolonged with very long femora, shorter tibiae, and long, multi-segmented, flagellate tarsi with more than 40 tarsomeres (Fig. 7.2), a feature which is unique within Insecta (Nel et al. 2004). The forelegs are usually directed anteriorly, while the middle and hind legs are directed latero – posteriorly. They 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, typical of polyneopterous insects (Figs. 6.3, 8). There are long,

DOI: 10.1127/0077-7749/2008/0247-0353

0077-7749/08/0247-0353 $ 7.25

© 2008 E. Schweizerbart'sche Verlagsbuchhandlung, D-70176 Stuttgart

monomerous, lancelolate cerci at the end of the abdomen (similar to Phasmatodea), and females have a prominent orthopteroid ovipositor. Males seem to be apterous. The nymphs are similar to the adults except for a much smaller size, a distinctly shorter abdomen, and the absence of wings. Consequently the development of chresmodids was heterometabolous as in orthopterans and other polyneopterous insects. Chresmodids probably lived on the surface of lakes and lagoons (contra Baudoin 1980 who did not know the true structure of chresmodid legs), and fed on insects and other small animals at the water surface, just like the unrelated, but superficially similar, modern Gerridae. Because of their significant larger size and weight it cannot be excluded that chresmodids might have needed floating water plants near the shore to support their heavy bodies on the water surface. The group is exclusively Mesozoic and may have suffered extinction during the Late Cretaceous greenhouse climate.

Since Germar (1839) named *Chresmoda obscura* for an insect found in the Upper Jurassic of Solnhofen-Eichstätt, the taxonomic placement of this enigmatic species has been dramatically reinterpreted several times. Germar (1839) originally established the species for a "flattened-like shaped insect, with a pronotum and with long hind legs", and placed it among the mantises (Mantodea). In the same paper he established also the species *Pygolampis gigantea*, which was a larger insect, similar to *C. obscura*, but with forelegs shorter than the mid- and hind legs. Germar believed *P. gigantea* was a hemipteran similar to the living water-strider *Gerris*. This paper introduced an immediate nomenclatural problem since Germar actually ascribed both species names to his compatriot, Münster, although Münster was not an author on this paper and the work is clearly that of Germar. Subsequent authors (e.g. Carpenter 1992) have correctly treated Germar as the author of these taxa. Weyenbergh (1869: 27) listed "*Pygolampis gigantea* Germ." and mentioned three beautiful fossils of this species from the Teyler Museum in Haarlem, of which he figured one (pl. 2, fig. 21) with the catalogue number 6395. Subsequently, a similar fossil hemipteran genus *Propygolampis* Weyenbergh, 1874 was created for a new Solnhofen species, *Propygolampis bronni* Weyenbergh, 1874. Meanwhile, Assmann (1877) synonymised *P. gigantea* with *C. obscura*, regarding them as orthopterans. Oppenheim (1888) later synonymised *P. gigantea, C. obscura*, and *P. bronni* under the name *Halometra gigantea* (Germar, 1839). He considered the types of both *P. bronni* and *C. obscura* to be unusable, since the original fossils had been painted in (a 'bemalter Artefact'), but gave no justification for rejecting *Propygolampis* as a valid name and substituting his own name, *Halometra*; now regarded as a junior synonym of *Propygolampis* (e.g. Carpenter 1992). Oppenheim, like Germar, thought *H. gigantea* was a semiaquatic hemipteran, referring the genus to the family Hydrometridae. In addition to this, he described a further Solnhofen species, *Halometra* ? *minor* Oppenheim (1888) based on three smaller fossils in the Bayerische Staatssammlung für Paläontologie und Geologie, Munich. Although Oppenheim (1888) was uncertain about the generic affinities of *H.*? *minor*, he specifically noted that the overall shape and number of legs (i.e., six) meant that they could not be crustacean larvae or arachnids. Carpenter (1992) propagated the younger synonym *Propypolampis* Weyenbergh, 1874 as the valid name for the fossils previously known as *Chresmoda* Germar, 1839, and mentions a paper by himself (listed as "in press" for 1992) that allegedly revealed the holotype of *Chresmoda* to be 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 was supposedly "in press" 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 with the intended publisher nor could it be found among Carpenter's archives in his laboratory at the MCZ (GB and MSE, pers. obs.).

Handlirsch (1906-1908) proposed that *Pygolampis gigantea* was a junior synonym of *Chresmoda obscura*, and established the new family Chresmodidae and providing a discussion about its inclusion in Phasmatodea or Orthoptera. Subsequently, Handlirsch (1925, 1926-1930) considered chresmodids as aquatic phasmatodeans. Unfortunately, the holotype of *C. obscura* is missing, whereas the holotype of *P. gigantea* is housed in the Munich Museum (Fig. 2.1). Handlirsch (1906-1908) placed *Gryllidium oweni* Westwood, 1854 into *Chresmoda.* The latter is an isolated forewing with longitudinal veins and with dense crossveins and basal archaedyction, the holotype of which is now lost (SWH pers. obs.).

Martynov (1928) placed the suborder Chresmododea into the Phasmatodea, including four families related by their wing venation: Chresmodidae (Triassic-Cretaceous), Aeroplanidae (Triassic), Necrophasmatidae, and Aerophasmidae (both Jurassic). ESAKI (1949) established the species *Chresmoda orientalis* for an insect with short body (24 mm), but with long legs and antennae (11 mm), from a specimen found in the Upper Jurassic of Ta-hsing-fang-tzu, Jehol in China (this specimen is also missing today).

SHAROV (1968) considered that chresmodids were phasmatodeans and elevated the group to superfamily rank, as Chresmodidaea, including therein the Mesozoic Chresmodidae and Recent Phasmatidae and Phyllidae. POPOV (1980) considered chresmodids as aquatic gerromorphs (Hemiptera: Heteroptera) and PONOMARENKO (1985) as an unusual lineage of paraplecopterans. MARTÍNEZ-DELCLÒS (1991) supported the attribution to 'Paraplecoptera' in the absence of information from the new material presented herein.

Contrary to MARTYNOVA (1962, 1991) we here restrict the Chresmododea to the family Chresmodidae, thus excluding the extinct families Aerophasmatidae, Necrophasmatidae and Aeroplanidae. It cannot yet be totally excluded that some of these taxa might be more closely related to Chresmododea than to Orthoptera or Phasmatodea (see below), but currently there are hardly convincing arguments for such a placement. However, WILLMANN (2003), followed by GRIMALDI & ENGEL (2005), polarized several wing venation characters and proposed a cladogram of putative stem-group members belonging to the extant Phasmatodea, which included Aerophasmatidae. This supports our restriction of the Chresmododea to include only the family Chresmodidae.

The phylogenetic relationship of chresmodids was long disputed and they have been attributed to Hemiptera (Heteroptera: Gerromorpha), Paraplecoptera ('Grylloblattodea' in some systems), Mantodea, Orthoptera, Polyneoptera of uncertain affinity, and most often to Phasmatodea. Most recently they have been considered "unplaced within Gryllones" (RASNITSYN & QUICKE 2002) or within the Orthopterida (GRIMALDI & ENGEL 2005). NEL et al. (2005) placed chresmodids among the monophyletic clade Archaeorthoptera BÉTHOUX & NEL, 2002, which do not correspond exactly to the Orthopterida *sensu* GRIMALDI & ENGEL, 2005, as these authors included the modern Phasmatodea in their Orthopterida. The Recent Phasmatodea show no visible evidence of the pattern of cubito-median veins typical of the Archaeorthoptera, although this could be interpreted as an independent, secondary derivation from within Orthopterida (i.e., secondarily autapomorphic for Phasmatodea). Some authors place them close to the Embiodea, or even with modern Grylloblattodea and Mantophasmatodea (see discussion below). More critical work on the phylogenetic relationships of Phasmatodea and putative relatives is required.

Numerous discoveries in the Upper Jurassic of Germany and Lower Cretaceous of Mongolia, China, Brazil, Spain, and Upper Cretaceous of Lebanon, provide new evidence for the phylogenetic placement of the Mesozoic family Chresmodidae, questioning some of the traditional views.

2. The enigmatic genus *Sternarthron* HAASE, 1890

Some specimens of *Chresmoda* from Solnhofen were previously placed in other groups of arthropods. A restudy of some of them demonstrate close relationships with different ontogenetic stages of *Chresmoda.* This is most notably the case for the genus *Sternarthron* (Fig. 1.1.-1.3).

Palpigrades are a rare order of small arachnids (CONDÉ, 1996 for a recent review), which resemble whip scorpions and which are usually thought of as rather primitive arachnids. Palpigrades are weakly sclerotized and the only reliable fossils are from the Cenozoic (ROWLAND & SISSOM 1980). There is, however, a much older genus, *Sternarthron* HAASE (1890b) from the Upper Jurassic of Germany which was described as an arachnid; most probably a palpigrade. Despite being created from fossils described as insects (OPPENHEIM 1888), and soon being placed back among the insects (HANDLIRSCH 1906), HAASE's palpigrade interpretation for *Sternarthron* was accepted by a number of authors (see below), but was not accepted by HARVEY (2003) in his catalogue of the smaller arachnid orders. With a body length of around 17 mm, *Sternarthron* is much larger than any living palpigrade and HAASE's drawings of it appear somewhat stylised. *Sternarthron* was recently placed back among the insects (CARPENTER 1992) (see below), although it is not clear that anyone since HANDLIRSCH (1906) actually restudied HAASE's type specimens, one of which was clear depicted with four pairs of legs by HAASE (1890b: pl. 31, figs 5-6). Meanwhile, other *Sternarthron* fossils have been compared to harvestmen (Opiliones) and sea spiders (Pycnogonida or Pantopoda) (FRICKHINGER 1999: 37, fig. 54). To address this confusion, we have reviewed the nomenclatural history of this material and present a restudy of Haase's types of this very problematic fossil taxon.

Haase (1890 a) disagreed with the previous attributions and considered *H.*? *minor* as an arachnid. Subsequently, Haase (1890 b) redescribed and figured both Oppenheim's Munich material (one of which he figured with eight legs) plus another Solnhofen fossil housed in the Dresden Mineralogical Museum. He named these *Sternarthron,* a new genus of fossil arachnid, recognising two taxa: *S. zittelii* Haase, 1890 b and *S. zittelii* var. *minus* Oppenheim, 1888, basing this variation on the specimen originally figured by Oppenheim (1888: pl. 31, fig. 4) which Haase regarded as having a broader, less pointed opisthosoma. The name *minor* became *minus* to correspond with the gender change in the generic name. Haase (1890 b) compared *Sternarthron* to various extant arachnids. Haase's spelling *zittelii* has to be considered as an incorrect original spelling and is here formally emended to *zitteli*, even though it was mostly already used with this correct spelling Haase suggested that *Sternarthron* should not be raised to a new order, because there was so little material known, and based primarily on his interpretation of a ventral prosoma with a series of divided sternites and an opisthosoma with a terminal flagellum, he felt that it was better to place *Sternarthron* in Thorell's (1888) then recently recognized arachnid order Palpigradi. Finally, although Haase (1890 b: 653) entitled the last section of his paper '*Eine neue Arthrogastren-Familie...*', and concludes (p. 657) with a remark about the sternal and palpal morphology characterising the family, at no point in the text, footnotes or figure legends did he actually propose a family name!

Handlirsch (1906: 525) placed *Sternarthron* back among the insects, specifically placing *Propygolampis bronni, Halometra gigantea, Halometra*? *minor,* and *Sternarthron zitteli* as junior synonyms of Germar's *Chresmoda obscura*. Handlirsch (1906) therefore considered Germar's 'mantid' and 'bug' to be conspecific, though he figured (Handlirsch 1906: pl. 44, fig. 17) a '*Chresmoda*' with long, slender legs, which resembles Germar's figure of the original *P. gigantea* far more than it resembles Germar's figure of the type of *C. obscura*. Furthermore, Handlirsch rejected the interpretation of these fossils (a combination of *Chresmoda* and *Propygolampis* material) as hemipterans (and specifically Hydrometridae) on the grounds of the presence of well developed cerci, multi-segmented antennae, pattern of wing venation, homeomorphic legs, coxal position, lack of a sucking apparatus and shape of the thorax. Handlirsch (op. cit.) accepted that these fossils belonged to the broad group of insects that were at that time included under 'orthopteroids' and after discussing why they could not belong to groups such as grasshoppers, roaches, and mantises, he concluded that they were most similar to the phasmatodeans (currently placed in their own order Phasmatodea). Handlirsch (op. cit.) noted phasmid features in these fossils such as antennal shape, a thin body, homeomorphic limbs and short, undivided cerci. Although interpreting them as *relatives* of phasmatodeans, and not phasmatodeans in the strict sense themselves, Handlirsch still thought that these fossil insects lived on the surface of the water, (erroneously) noting that some extant phasmatodeans live underwater. Handlirsch (op. cit.) also studied Haase's *Sternarthron* specimens in Munich that he referred to as 'Haase's Spinne' (which implies a spider, but which can, in a broader sense, translate as arachnid). He noted that it had six legs and the characteristic cerci and antennae of *Chresmoda*. On these grounds Handlirsch (op. cit.) interpreted the relatively small *Sternarthron* as a nymphal form of what he believed to be a fossil relative of stick insects.

Handlirsch's study and his synonymy of *Sternarthron* with *Chresmoda* appears to have been widely overlooked, at least among arachnologists and reviewers of the Solnhofen fauna. Roewer (1934) did not accept *Sternarthron* as a palpigrade, noting the differences in size and the number of prosomal sternites and opisthosomal segments, compared to living palpigrades. He regarded *Sternarthron* as an isolated form among the arachnids and discussed evolutionary aspects of its morphology. Meanwhile, *Sternarthron* was occasionally mentioned as a fossil palpigrade in zoological text-books of the period (e.g. Kästner 1941; Millot 1949). In his fossil arachnid monographs Petrunkevitch (1949, 1953, 1955) mentioned *Sternarthron* and accepted it as a palpigrade. It appears that around this time the family name Sternarthronidae was introduced. The oldest record we could find was Petrunkevitch (1949: 261) who gave neither an author nor a diagnosis for it. Subsequently, Petrunkevitch (1955: 115) incorrectly attributed Sternarthronidae to Haase (1890) and diagnosed this family on: 'Thoracic sternites 2 and 3 separated from each other by intersegmental membrane'.

Crowson et al. (1967) included *Sternarthron* as the oldest known palpigrade. In reviews of the Solnhofen

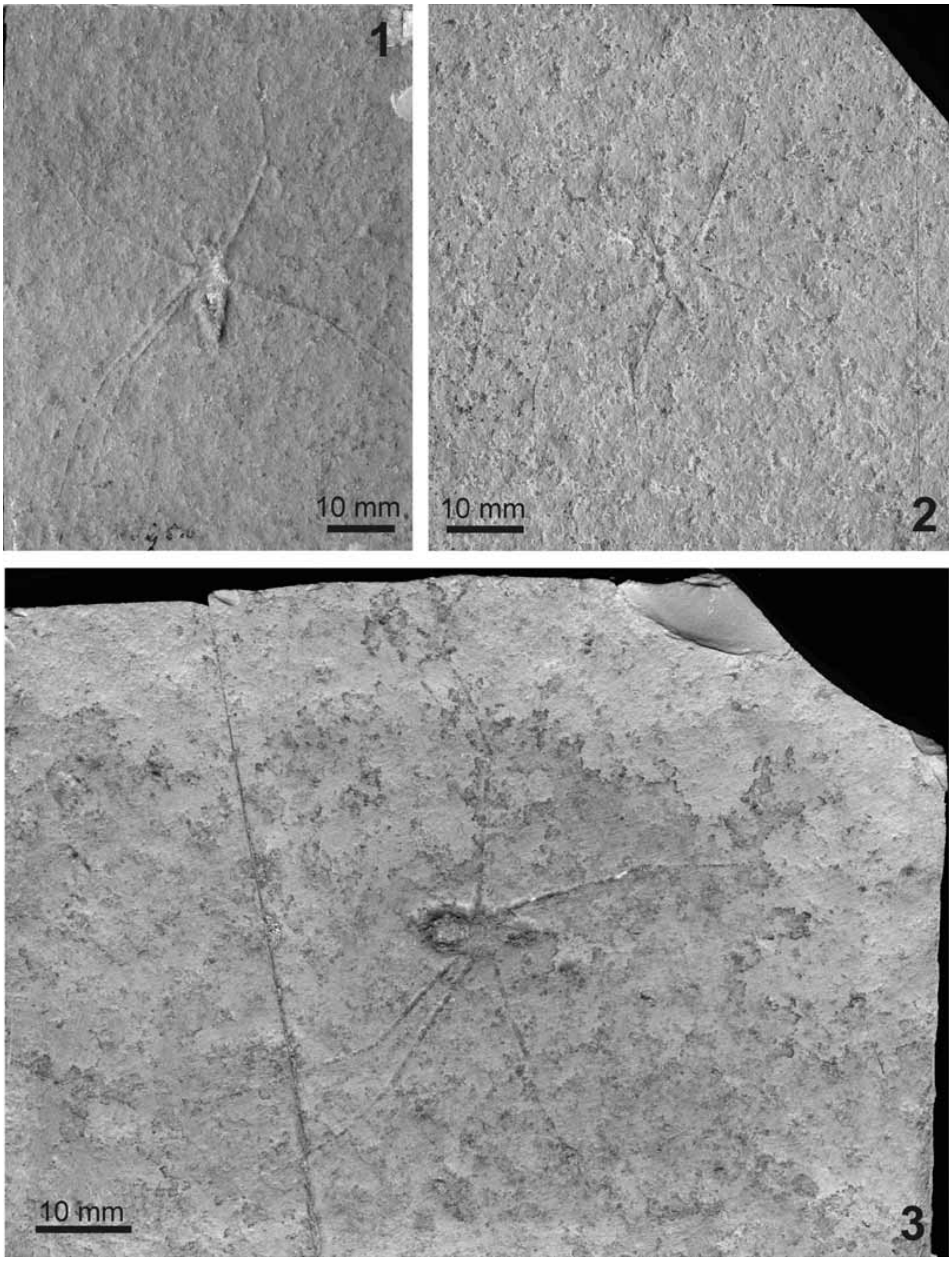

Fig. 1. 1: 413.1870.VII.45; *Sternarthron zitteli* (holotype), Upper Jurassic (Tithonian) of Eichstätt (Germany); Bayerische Staatssammlung für Paläontologie und Geologie Museum (BSPGM), Munich. **2:** 1964.XXIII.164; *Sternarthron zitteli*, Upper Jurassic (Tithonian) of Schernfeld (Germany). **3:** AS.I.822; *Sternarthron zitteli*, Upper Jurassic (Tithonian) of Eichstätt.

fauna, both Kuhn (1961, 1977) and Barthel (1978) accepted *Sternarthron* as an arachnid. Savory (1971) also accepted *Sternarthron* as a palpigrade, reproduced one of Haase's figures and based on the slender legs, inferred that it lived in shallow water (a nonsensical argument given that many fully terrestrial arachnids also have slender legs). Rowland & Sissom (1980: 79) included *Sternarthron* in a synopsis of the

Palpigrada and followed Petrunkevitch's diagnosis of Sternarthronidae. However, they suggested that overall *Sternarthron* looked more like a water strider (Hemiptera, Gerridae) than a living palpigrade and that a re-examination of the original material was required to confirm its identity. Barthel et al. (1990), in a revised translation of his original review, regarded *Sternarthron* as a rather dubious palpigrade.

Carpenter (1992) noted that *Chresmoda* was in fact, under his interpretation, an orthopteran and that it was often confused with *Propygolampis* (as in Handlirsch's synonymy list). Nonetheless, Carpenter (op. cit.) placed both *Halometra* and *Sternarthron* as junior synonyms of *Propygolampis* and figured (Carpenter 1992: 121) a slender-legged *Propygolampis* specimen of the form that Oppenheim (op. cit.) called *Halometra gigantean*, and that Handlirsch (incorrectly) called *C. obscura*. However, following Handlirsch (1906-1908), Carpenter (1992) placed *Propygolampis* and its synonyms (i.e. *Sternarthron*) in an uncertain family of the Phasmatodea, despite the fact that *Propygolampis* has the overall appearance of a semiaquatic, gerromorph hemipteran. Also, misinterpreting Handlirsch (1906-1908), Carpenter (op. cit.) incorrectly stated that Haase placed *Sternarthron* in the Araneae.

As with Handlirsch (1906-1808), Carpenter's (op. cit.) work was initially overlooked and in his review of fossil arachnids, Selden (1993a) regarded *Sternarthron* as a doubtful palpigrade while in *The Fossil Record 2*, Selden (1993b) included Sternarthronidae as palpigrades, while reaffirming the need for restudy. In his review of the Solnhofen fauna, Frickhinger (1994) figured a *Sternarthron* [sic.] specimen from a private collection, referring to it as an arachnid; although in the accompanying English text the German word 'Spinnentiere' (= arachnid) is mistranslated as 'spider'. Meanwhile, *Sternarthron* was not included by Condé (1996) in his review and catalogue of palpigrades. Selden & Dunlop (1998) noted Carpenter's synonymy in their review of the arachnid orders, but miscited Carpenter's systematics by calling *Propygolampis* a heteropteran insect. Frickhinger (1999) corrected the spelling to *Sternarthron,* while noting that the specimen he figured previously (Frickhinger 1994: 159) was not *Sternarthron,* but an unknown arachnid possibly similar to opilionids. A further '*Sternarthron*' from a private collection was figured by Frickhinger (1999) who cites a pers. comm. by G. Bechly (SMNS) that the fossil in question may be either a pycnogonid or a new arachnid order. Consequently, a restudy of the types of *Sternarthron* is long overdue and here provided.

Remarks. – The genera *Sternarthron, Propygolampis, Pygolampis*, and the species *C. obscura* comes from the Upper Jurassic (Tithonian) of Solnhofen, Southern Franconian Alb, in Germany. The geological setting of which was reviewed by Barthel et al. (1990). The fossils are preserved in a fine-grained limestone, usually as simple impressions of the animals, which are sometimes secondarily orange-colored by iron-oxide. The three type specimens of *Sternarthron zitteli* (and *Halometra minor*) are housed in the Bayerische Staatssammlung für Paläontologie und Geologie in Munich (BSPGM), and are re-described below:

Re-description. – Specimen BSPGM labeled "413. 1870. VII. 45. Eichstaett" (Fig. 1.1): body 16 mm long; abdomen cone-shaped (length 9 mm) and apically pointed, with an apparent short "terminal filum" (length 1.5 mm), which is most probably either an artifact or an imprint of the cerci or an ovipositor; no details of head or body visible, except for traces of large eyes, short antennae (length 2 mm), and maybe large biting mouthparts (mandibles); on both sides of the head there is a short appendage visible (length 5 mm left side, right side only 2.5 mm visible length) that apparently originates close to the procoxa (left side) (most probably these appendages are palpi of the mouthparts, or artifacts); only three pairs of legs (profemur 15 mm, protibia only 4 mm, protarsus 10.5 mm; mesofemur 17.5 mm, mesotibia 8 mm, mesotarsus about 8 mm; metafemur 13 mm; metatibia 9 mm); a very distinct kink distal of profemur due to the very short protibia (forelegs); distance between procoxa and mesocoxa 2 mm, between mesocoxa and metacoxa only 1 mm (middle legs and hind legs closely parallel and directed backwards, and forelegs widely separated from them and directed forwards, exactly as in all adult chresmodids!). This was specimen 413 of Haase (1890: pl. 31, figs. 5-6), but his drawings prove to be extremely imprecise when they are compared to the original fossil. This specimen should be designated as the lectotype.

Specimen BSPGM labeled "1964 XXIII 164 Schernfeld" (plate and counterplate) (Fig. 1.2): body 11 mm long; abdomen cone-shaped and apically pointed, but without "terminal filum"; no details of head or body visible, except faint traces of abdominal segmentation and a pair of short antennae (length

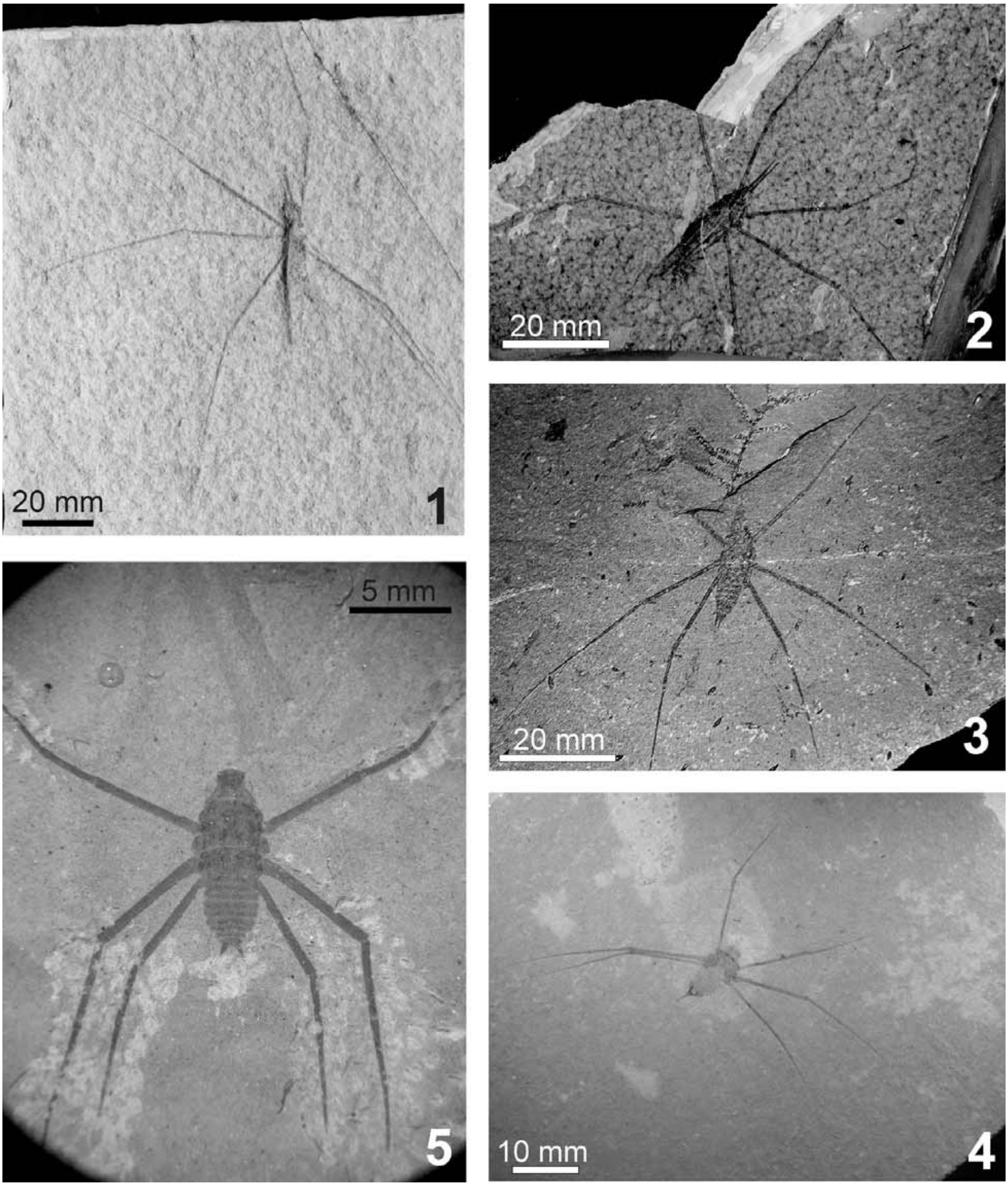

Fig. 2. 1: AS.VII.499, specimen studied and figured by GERMAR (1839) as *Pygolampis gigantea* (= *Chresmoda obscura*), Upper Jurassic (Tithonian) of Solnhofen (Germany); (BSPGM). **2:** LP-94-IEI, *Chresmoda aquatica* (holotype), Lower Cretaceous (Barremian) of El Montsec (Spain). **3:** LH-23300, *Chresmoda* sp., Lower Cretaceous (Barremian) of Las Hoyas (Spain). **4:** NI 3a-b, *Chresmoda libanica* (holotype), Upper Cretaceous (Cenomanian) of Nammoura (Lebanon). **5:** PIN 3149/1711, *Saurophthirodes mongolicus* (holotype) (*Chresmoda mongolica* comb. nov.), Lower Cretaceous of Gurvan-Ereniy-Nuru (Mongolia).

about 3 mm); only three pairs of legs (profemur 15 mm; mesofemur 17.5 mm, mesotibia 8 mm, mesotarsus 8.5 mm; metafemur 14 mm; metatibia 9 mm); a distinct kink distal of profemur (forelegs); distance between procoxa and mesocoxa 2 mm, between mesocoxa and metacoxa only 1 mm. This specimen might eventually be the same as the original Dresden specimen of HAASE (1890: pl. 31, fig. 4), but this is very uncertain and just an assumption.

Specimen BSPGM labeled "AS I 822" (Fig.1.3): body about 14 mm long; abdomen broad and without "terminal filum"; no details of head or body visible, maybe except traces of a pair of short antennae; only three pairs of legs (profemur 15 mm, protibia only 4 mm, protarsus 10.5 mm; mesofemur 17.5 mm, mesotibia 8 mm, mesotarsus about 8 mm; metafemur 13 mm; metatibia 9 mm); a very distinct kink distal of profemur due to the very short protibia (forelegs); distance between procoxa and mesocoxa 2 mm, between mesocoxa and metacoxa only 1 mm. This specimen seems to be the type of *Halometra minor* OPPENHEIM (1888: pl. 31, fig. 4), and is most probably also the same as specimen 414 of HAASE (1890: pl. 31, figs 1, 3).

Discussion. – CARPENTER (1992) already correctly recognized that the fossil arthropods from Solnhofen, known under the name *Sternarthron zitteli*, are not Chelicerata at all, but clearly represent the nymphal stage of *Chresmoda obscura* from the same locality. Our re-examination of the type specimens from the collection of the Museum in Munich (BSPGM no. 1870 VII 45 and AS I 822) confirmed that the description and drawings of HAASE (1890) are completely erroneous, very freely drawn and "reconstructed" (which also explains the dissimilarity to the drawing of OPPENHEIM, 1888), and incorrectly interpreted. These fossils clearly are hexapods with only three pairs of legs, and with leg structures that are very similar to adult *Chresmoda* (contra BECHLY 1999: 9).

3. The genus *Chresmoda* GERMAR, 1839

The family Chresmodidae includes, besides *Chresmoda obscura* GERMAR, 1839 from the Tithonian lithographic limestones of Solnhofen (Fig. 2.1), the similar *C. aquatica* MARTÍNEZ-DELCLÒS, 1989 from the Barremian lithographic limestones of Montsec (Fig. 2.2) and Las Hoyas (Fig. 2.3) in Spain, the quite different *C. orientalis* ESAKI, 1949 from the Lower Cretaceous of Lingyuan in China, and *C. libanica* NEL et al., 2004 from the Cenomanian lithographic limestones of Lebanon (Fig. 2.4). Copious specimens have been discovered from the Upper Jurassic of Inner Mongolia (China), probably representing three different species (HUANG, pers. comm.). Other undescribed species are known from the Middle or Upper Jurassic of Bakhar in Mongolia (RASNITSYN & QUICKE 2002), and from the Aptian – Albian of Santana do Cariri in Brazil (see below). *Saurophthirodes mongolicus* PONOMARENKO, 1986 from the Lower Cretaceous of Gurvan-Ereniy-Nuru, in Mongolia (Fig. 2.5) could be also included in *Chresmoda.* This shows that the genus *Chresmoda* has almost a biostratigraphic range Tithonian to Cenomanian with worldwide, mainly Laurasiatic, distribution. *Sternarthron zitteli*, are not Chelicerata – Pantopoda, but represent the nymphal stage of *C. obscura* from the same locality. The holotype of *C. obscura* is missing today, but the holotype of *P. gigantea* is housed in the Bayerische Staatssammlung für Paläontologie und Geologie, Munich, labelled AS.VII.499 (figured by GERMAR, pl. 22, fig. 8) (Fig. 2.1).

3.1. A new species of *Chresmoda* from the Crato Formation limestones of Brazil

BECHLY (1998: 155) and BECHLY (1999: 9) briefly mentioned the discovery of chresmodid fossils from the Crato Formation for the first time. BECHLY et al. (2001: 55, fig. 44) discussed and figured a beautiful fossil *Chresmoda* from the Crato limestones. This female specimen with ovipositor, which seems to be the best preserved specimen from this locality, is housed with preliminary no. 0134 (old number H56) in the Staatliches Museum für Naturkunde Stuttgart in Germany. Another specimen from the American Museum of Natural History in New York was figured by GRIMALDI & ENGEL (2005: fig. 7.5) (Figs. 3-5). Four further specimens have been studied by the present authors.

BECHLY (2007) discussed the chresmodids from the Crato Fm in more detail and provided a brief description, however without formally naming the new species.

All six of the known specimens of *Chresmoda neotropica* n. sp. from Crato are adults and alate with long wings (wing length 27-28 mm). The body length from head (without antennae) to abdomen (without distal appendages) 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 is visible in one specimen. All other characters agree with the general diagnosis of the lineage.

Being surface striders on superficial fresh- or brackish water (see also MARTILL et al. 2007) that mainly fed on other insects that have been trapped on the water surface, the chresmodids and hydrometrids (NEL & POPOV 2000) most probably represented the only autochthonous aquatic insects in the paleohabitat of the Crato lagoon.

Chresmoda neotropica ENGEL & HEADS, n. sp.

Figs. 3-5

1998	Chresmodidae. – BECHLY, p. 155.
1999	Chresmodidae. – BECHLY, p. 9.
2001	*Chresmoda.* – BECHLY et al., p. 55, fig. 44.
2005	Chresmodidae. – GRIMALDI & ENGEL, p. 193, fig. 7.5.
2007	*Chresmoda.* – BECHLY, pp. 262-265, pl. 15d-e.

Etymology: Specific epithet derived from ‘neotropical’; in reference to the biogeographical provenance of the species.

Type material: Holotype: Macropterous adult female, SMNS 66000-13 (old no. H56); housed in the Staatliches Museum für Naturkunde, Stuttgart (Germany); Paratype: Macropterous adult AMNH SA-46446; housed in the American Museum of Natural History, New York (USA).

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

Type horizon: Lower Cretaceous, upper Aptian, Nova Olinda Member (limestones) of the Crato Formation (previously included in the Santana Formation sensu lato).

Additional material: Incomplete adult (sex indeterminate), UMB K25547 (Pl. 3, fig. 2); housed in the Ulster Museum, Belfast (Northern Ireland, UK); and a specimen with no. G88 in coll. ms-fossil, Sulzbachtal, Germany (featured in BECHLY 2007: pl. 15e).

Diagnosis: Interantennal (supraclypeal?) area swollen; thorax elongate, metacoxae meeting at posterior margin of metasternum, protibia relatively short (30% of profemur length), tibial spines absent, abdomen more elongate and narrow, margins subparallel for majority of their length.

Description of holotype SMNS 66000-134 (Figs. 3.1, 5): Adult macropterous female preserved in ventral aspect; body form slender. Head wider than long (3.21 mm long; 2.26 mm wide); antennae inserted anteriorly and immediately adjacent to one another; scape swollen, approximately 1.5–2.0 times wider than pedicel, approximately as wide as long; pedicel much smaller than scape, approximately as wide as long; proximal flagellar articles as wide as scape; subsequent flagellar articles decreasing in width gradually toward apices of antennae; total number of flagellar articles indeterminate as margins between articles are not discernable; mouthparts not preserved. Thorax moderately broader than head, approximately 1.6 times longer than wide (approximately 6.85 mm long; 4.24 mm wide), with prominent median keel; prothoracic basisternum 2.26 mm long, 1.85 mm wide; mesothoracic basisternum 1.16 mm long at median keel, 3.08 mm wide; metathoracic basisternum approximately 3.29 mm long, 2.61 mm wide; pro–mesosternal intersegmental suture v-shaped towards posterior; meso-metasternal intersegmental suture v-shaped towards anterior. Legs without spination; coxae robust, laterally directed; meso- and metacoxae markedly larger than procoxae; pro- and mesocoxae widely seperated; metacoxae apparently meeting at posterior margin of metathoracic sternum; protibia relatively short (approximately 5.50 mm long), slightly recurved, approximately 30% of profemur length (18.92 mm); tarsi elongate, composed of between 8 and 12 tarsal articles; meso- and metathoracic legs longer than prothoracic legs; prothoracic leg 75% of mesothoracic leg, 80% of metathoracic leg. Only right forewing preserved; well developed, approximately 27.80 mm long, at least 2.0 times as long as abdomen (excluding ovipositor); venation largely indistinct; most veins simple and parallel–subparallel; SC long, simple, reaching wing margin before apex; subcostal area proximally filled with dense, apically directed crossveins at least as far as midwing; RA and RP simple, branching proximally of midwing; MA with two simple branches; ?cubital area with dense pattern of crossveins forming minute cells, some of which lack pigmentation. Abdomen of similar width to thorax, total length (excluding valvulae of ovipositor) approximately 13.88 mm long; abdomen apparently rotated somewhat postmortem to expose lateral surfaces of terga; subgenital plate triangular; valvulae of ovipositor elongate, forcep-like, approximately 3.87 mm long; no serrations are discernable on the valvulae, though the distalmost part of the abdomen and the terminalia have been damaged somewhat during preparation of the specimen.

Description of paratype AMNH SA-46446 (Fig. 5.1-5.4): Adult macropterous female, body form slender. Head wider than long; antennae apparently positioned high on face, with interantennal (supraclypeal?) area slightly raised between antennal toruli, toruli separated by less than scape width; scape swollen, approximately 1.5 times wider than pedicel or flagellar articles, length approximately 2.75 times width; pedicel about as wide as long; first flagellar article elongate, about three-fourths length of scape; total number of flagellar articles indeterminate as antennae are incomplete; mandibles and other mouthparts not discernable. Thorax only slightly broader than head; thorax longer than wide, about 1.8 times longer than wide. Legs without spination; coxae widely separated and laterally directed; protibia relatively short, 30% of profemur length (protibia 5.8 mm, profemur 19.2 mm); tarsi elongate, with at least eight tarsal articles (total number cannot be ascertained in AMNH SA-46446); pretarsus (and its associated claws) either absent or modified into unit resembling a distalmost, apically-rounded tarsal article; tarsi of preserved legs conspicuously surrounded or partially covered by black crystalline material found no where else in the matrix or on the compression. Wings fully developed, folded flat over abdomen when in repose, well surpassing abdominal apex. Abdominal base broadly articulated with thorax and of equivalent width; abdominal terga wider than long (total number of abdominal segments not discernable), lateral margins subparallel, with terga becoming slightly and progressively narrower toward apex, quickly tapering in width in distalmost segments. Cerci and ovipositor are not visible, and the thoracic nota are not well preserved.

3.2. The body structures of *Chresmoda*

Previous publications described accurately the structures of different species of the genus *Chresmoda* (Handlirsch 1906-1908; Esaki 1949; Martínez-Delclòs 1989; Nel et al. 2004; Nel et al. 2005). Here we include and comment on the more interesting features relevant to the phylogenetic placement of the family.

3.2.1. Head

Chresmoda has a prognathous head, completely covered by short, fine setae. The antennae are thick, with 17 setaceous flagellar articles, with fine, short setae (in some specimens of *C. obscura* the antennal setation is long and obscures the antennal segmentation); the scape is long, the pedicel is 1/3 as long as scape and the third segment is the longest. The total length of the antenna is quite variable depending of the species and with respect to the body length, around 8 mm in *C. aquatica*, >12 mm in some specimens of *C. obscura,* and 9-11 mm in Crato specimens; perhaps longer in *C. orientalis* with respect to body length of other species.

The presence of maxillary palpi, a short two- or three-segmented labial palpus without setae, and long and strong mandibles bearing a row of small obtuse teeth, and several short but sharp spines in the mouth suggest that the species of *Chresmoda* were predatory, consuming small animals living at the water surface or trapped by water surface tension (insects), or planktonic or nektonic animals when they came to the surface.

3.2.2. Legs

The legs are very long and narrow, covered with very short setae arranged in rows. These small setae likely assisted in the ability of individuals to rest on the water surface without penetrating, at least when being supported by floating water plants. As preserved, as likely also in life, the forelegs are projected forward, while the mid and hind legs are projected backwards (Fig. 9.3). The general structure is similar in the three legs but the tibial length is variable in respect to the femur for all species. The femora have different length respect to the tibia, which modifies the length of the leg. For example, in adults of *C. aquatica* the pro- and metafemora are equal in length while the mesofemora are longer; in *C. obscura* the meso- and metafemora are equal in length, and longer than the profemora. These differences are not so evident in the tibiae, but *C. libanica* have fore tibiae shorter than other studied species (nevertheless, all Lebanese specimens are nymphs). Tarsi are usually difficult to see but in some individuals it is possible to observe numerous small apical tarsomeres of progressively decreasing lengths (Fig. 7.2). Presumably when these tarsomeres were positioned on the water they created depressions in the surface without penetrating it owing to the backward curvature of the tarsi. The surface tension acted on the whole length of those tarsomeres that were in contact with the water surface to support the weight of these insects. All species studied have more than 40 tarsomeres that are superficially quite similar to antennal articles and have oblique, sigmoidal apices in both nymphal stages and adults (Nel el al. 2004), presumably acting as a locking mechanism to prevent the complete distortion of the legs during rest (Martínez-Delclòs 1991).

The procoxa – protrochanter articulation orients the protrochanter and more distal podites of the leg anteriorly. The mesocoxa – mesotrochanter articulation typically orients the leg perpendicular with respect to the length of the body but the midlegs are capable of being shifted widely forward and, presumably, backward as well (e.g., the preserved position of AMNH SA-46446 – *Chresmoda neotropica* n. sp. – has the midlegs projected forward nearly parallel with the forward-projecting forelegs). This same articulation in the hind legs projects the legs posteriorly. The morphology of the coxa – trochanter articulation suggests that their movement was oar-like. The mobility of the tibia with respect to the femur was weak because in all studied *Chresmoda* the angle between femur and tibia was 100-110 degrees. The angle

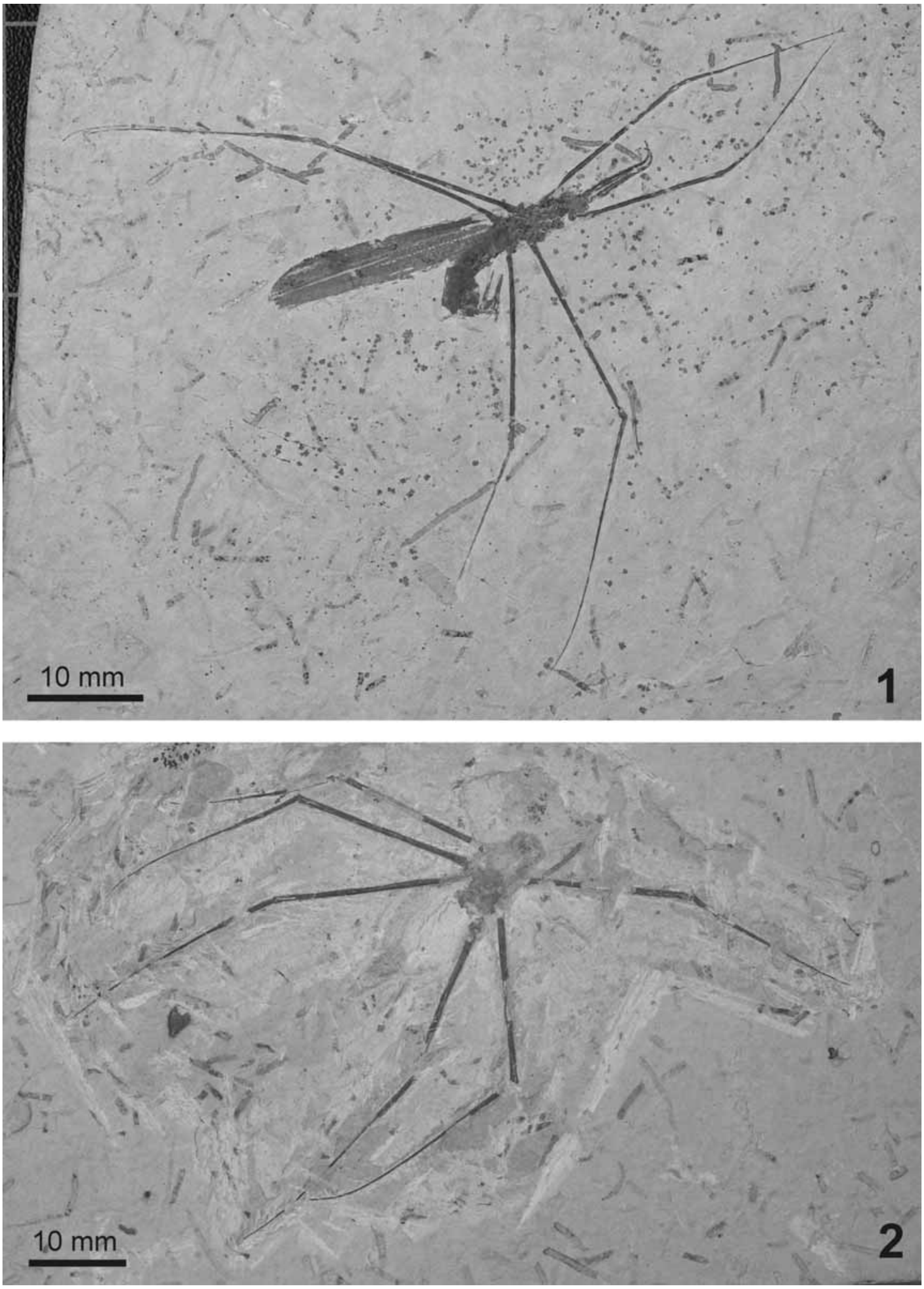

Fig. 3. 1: SMNS 66000-134; *Chresmoda neotropica* Engel & Heads n. sp. (holotype), Lower Cretaceous (Aptian-Albian) of Santa Ana area (Brazil); housed in the Staatliches Museum für Naturkunde Stuttgart (Germany); general habitus of the species. **2:** UMB K25547; *Chresmoda neotropica* Engel & Heads n. sp.; housed in the Ulster Museum, Belfast (Northern Ireland, UK).

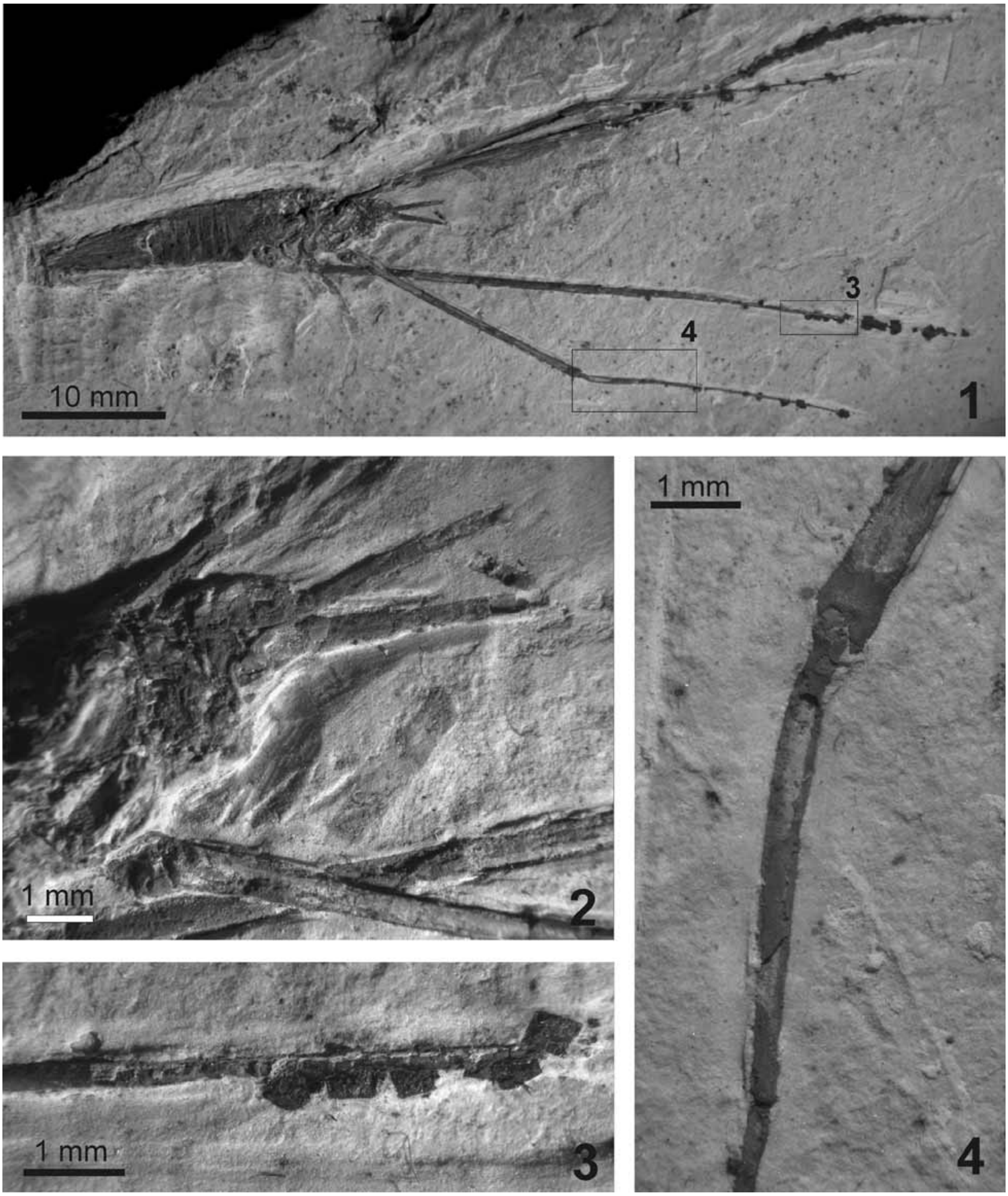

Fig. 4. 1: AMNH SA-46446; *Chresmoda neotropica* Engel & Heads n. sp. (paratype), Lower Cretaceous (Aptian-Albian) of Santa Ana area (Brazil); American Museum of Natural History; general habitus of the macropterous species. **2:** Head, basal part of the antenna and forelegs. **3:** Distal part of the hind leg showing numerous small apical tarsomeres, and original pyrite cubes precipitate during the early diagenetic stages of fossilization. **4:** Distal part of the femur and shorter tibia of the foreleg.

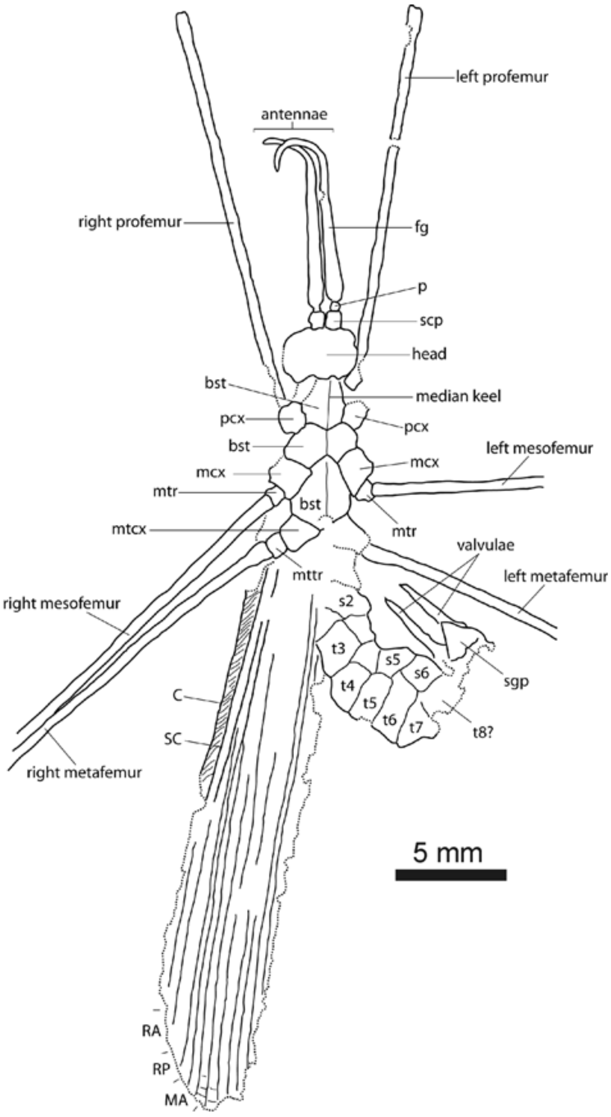

Fig. 5. 1: SMNS 66000-134; *Chresmoda neotropica* Engel & Heads n. sp.; camera lucida drawing of the holotype. bst: basisternite, C: cubital vein, fg: flagellomere, mcx: mesocoxa, mtcx: metacoxa, mtr: mesotrochanter, mttr: metatrochanter, p: pedicel, pcx: procoxa, scp: scape, s: sternite, SC: subcostal vein, sgp: subgenital plate, t: tergite.

between the tibia and tarsus was more constant, around 180 degrees (Fig. 4.4). We consider that all skating effort was done by the basal part of the legs (coxa through tibia).

This dramatic specialization, unique among aquatic Hexapoda, may be perhaps the product of a homeotic mutation affecting genes that participate in leg development, resulting in the transformation of the distal podites of the legs into antenna-like structures (see below). Current evidence indicates that this transformation probably took place during the Upper Triassic or Lower Jurassic, eventually becoming fixed in this lineage, and persisted for more than 65 Ma, disappearing along with the chresmodids during the Cenomanian (Nel et al. 2004).

4.3. Wings

Hitherto now, individuals of *Chresmoda* were always found with their wings folded over the abdomen. Ponomarenko (1985) attributed this taphonomic feature to their special mode of life at the water surface. Some individuals of *C. obscura* with unfolded wings was found in Solnhofen (i.e. JM.1958a and JM.1964.2, both from the Juras-Museum in Eichstätt), although its degree of preservation prevented detailed study of the wings. Usually terrestrial insects that have flown to water and have been trapped by the surface tension of the water die by asphyxiation and unfold their wings (Martínez-Delclòs et al. 2004). One exception is the wings of orthopterans that are typically folded at rest owing to the nature of their articulation. Because chresmodids are broadly related to orthopterans, they may have had a similar form of articulation that promoted their post-mortem retention in a folded position. It was not possible to accurately compare the methods of articulation between chresmodids and other lineages of insects, most notably the Orthoptera.

Two new specimens of *Chresmoda* sp. with preserved fore- and hind wings (LC-1123-IEI, Barremian of El Montsec, and LH-26.546 of Las Hoyas) were recently discovered in Spain. The pattern of venation of LC-1123-IEI (Fig. 8.1-8.3) is nearly identical to those of the Mesozoic “stick insect-like” taxa of the order “Phasmatodea” *sensu* Gorochov (1994). It has elongate wings (Fig. 8.3), straight radial, median and cubital veins, all parallel, with numerous straight cross-veins between them; few elongate intercalary longitudinal veins; ScP ending on the wing margin not far from the wing apex; MA with two simple branches; RA, RP, MP, CuA, and CuP simple; an apical anastomosis between the median veins in the hind wing; a broad anal area in the forewing; and a very large and broad vannus in the hind wing. The pattern of venation of LH-26.546 (Fig. 6.2-6.4) is even more interesting as its forewing base shows for the first time the exact structure of the median and cubital veins. Its concave CuP has a very short concave anterior branch CuPa that extends towards the

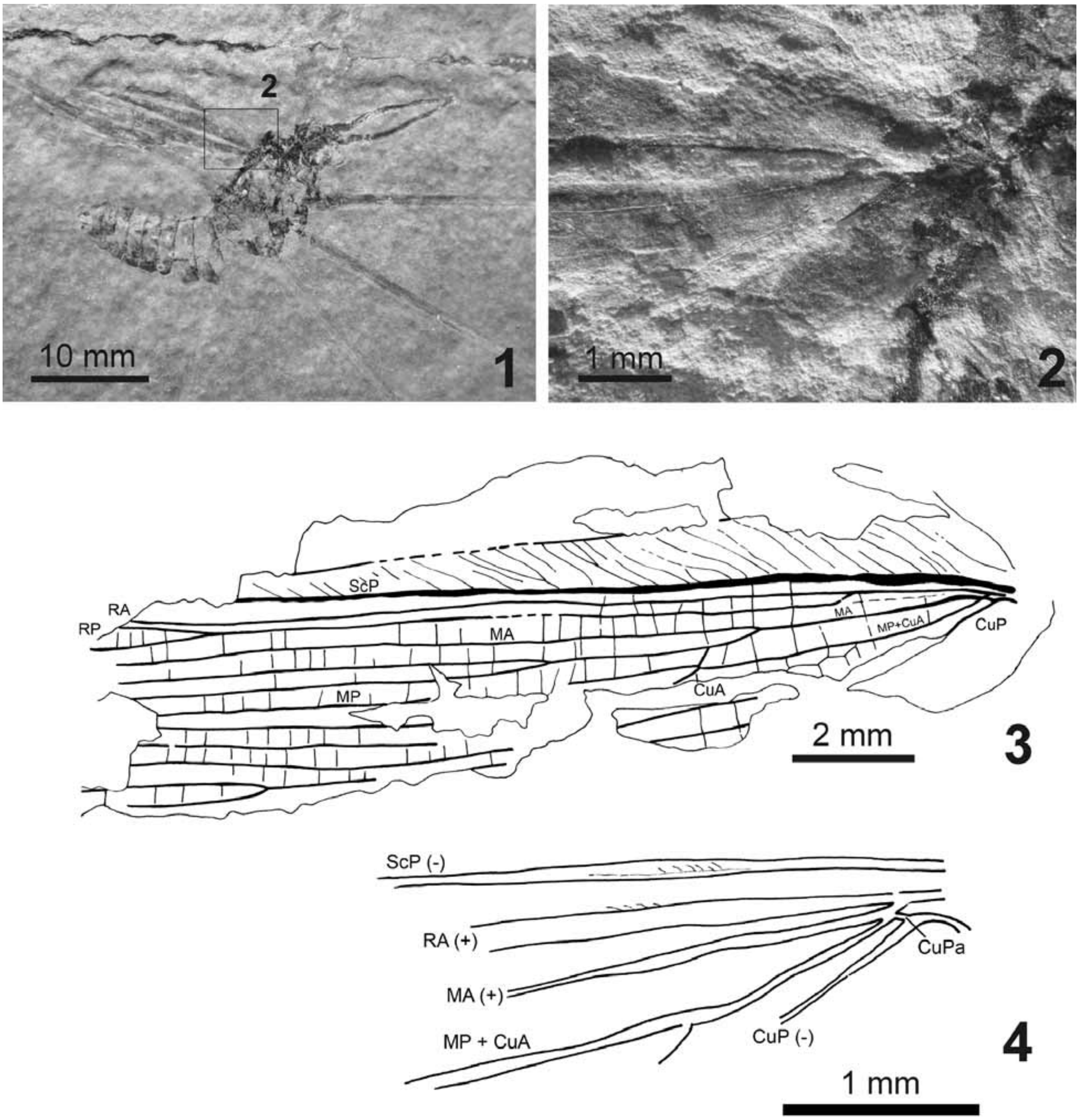

Fig. 6. LH-26.546; *Chresmoda aquatica*, Lower Cretaceous (Barremian) of Las Hoyas. **1:** General habitus of the specimen. **2:** Base of the forewing. **3:** Camera lucida drawing of the forewing. **4:** Camera lucida drawing of a detail of the base of the same forewing.

base of the convex M+CuA. This last vein separates at the same point into a convex anterior MA and a convex posterior branch MP+CuA. MP separates from CuA significantly more distally. This pattern is typical of polyneopteran insects of the Archaeorthoptera (Béthoux & Nel 2002). Veins CuPb, CuA and MP are straight and simple, MA has three long and parallel branches, RP separates from RA in a very distal position, and the preserved part of RA is simple and straight. Nearly all of the longitudinal veins are parallel and straight (see Figs. 5.1, 6.3-6.4, and 8.3).

Some specimens from Solnhofen also have long wings, overlapping the abdomen, similar to the specimen LC-1123-IEI from El Montsec, and are thus

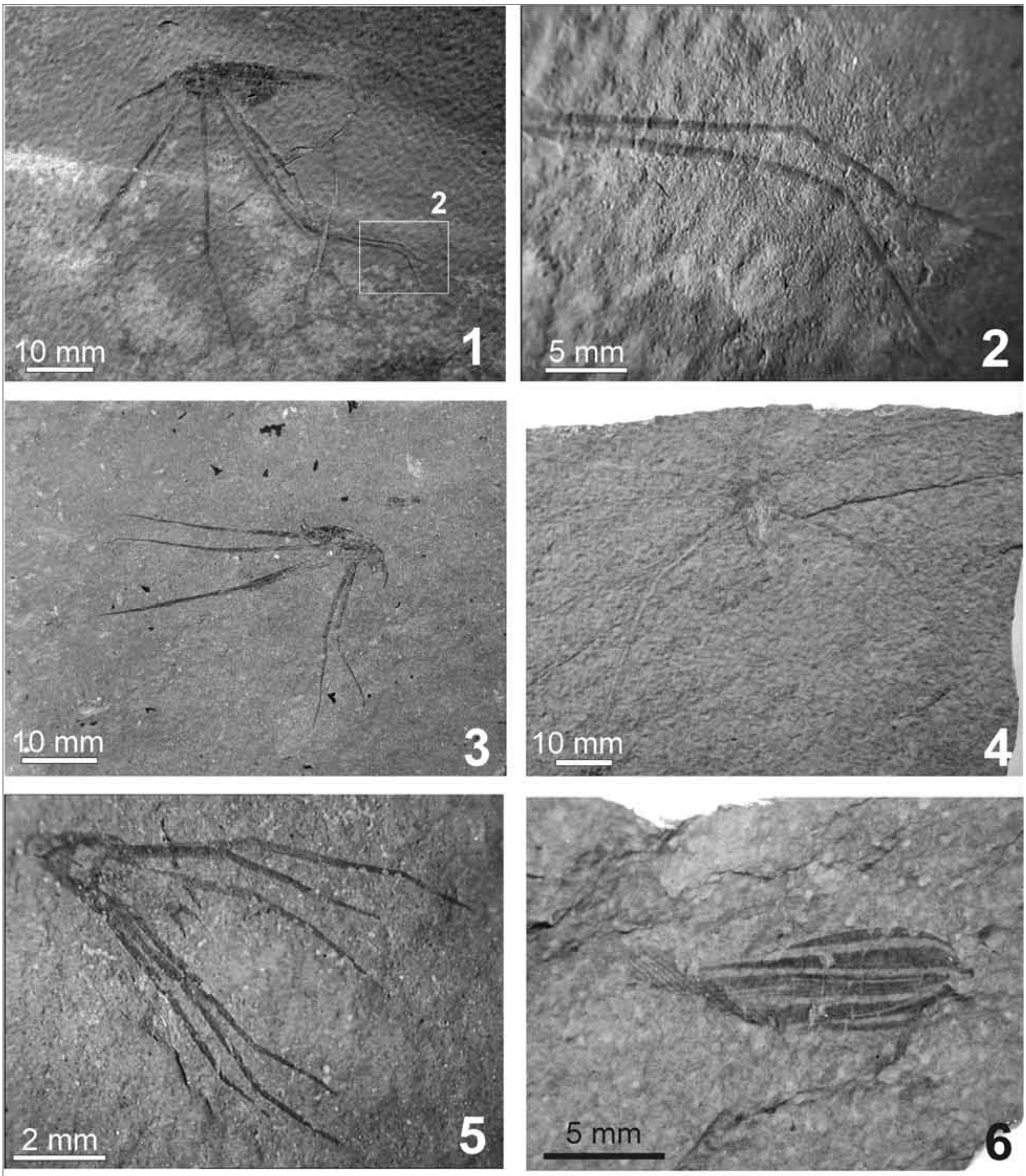

Fig. 7. *Chresmoda aquatica*, Lower Cretaceous of Las Hoyas. **1:** LH-13826, brachypterous female specimen. **2:** distal part of the mid and hind legs; see the numerous small apical tarsomeres that compound the leg. **3:** LH-13574, apterous male specimen preserved in organic rich mudstones. **4:** LH-92AM102, brachypterous female preserved in non-organic rich mudstone level. **5:** MCCM-LH 18023, nymph that shows the numerous small apical tarsomeres. **6:** MCCM-LH 18024, isolated forewing highly sclerotized, possibly from a brachypterous female specimen. All specimens housed in the Museo de las Ciencias de Castilla-La Mancha in Cuenca (Spain).

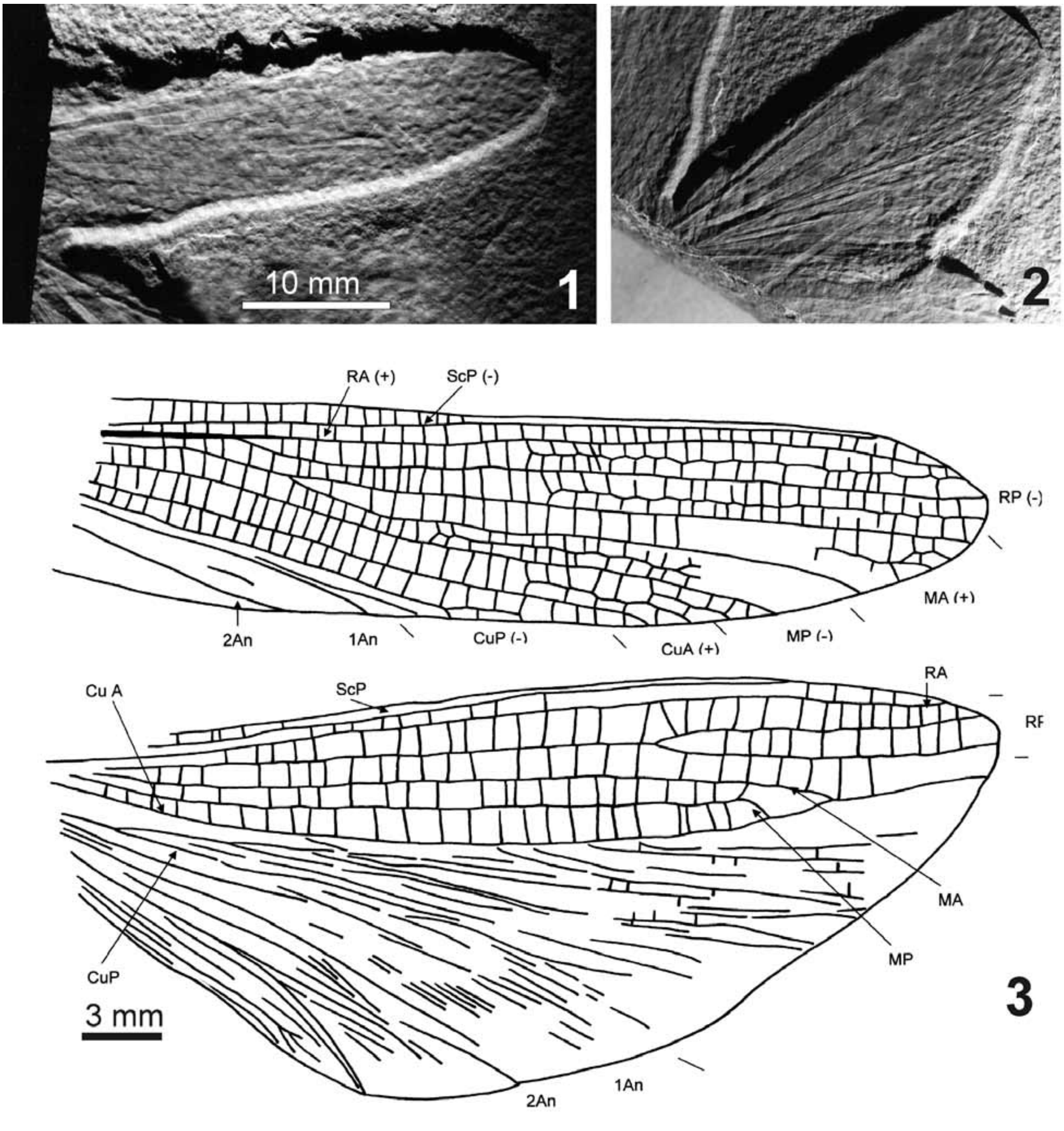

Fig. 8. LC-1123-IEI, *Chresmoda aquatica*, Lower Cretaceous of El Montsec. La Cabrua outcrop. **1:** Right forewing. **2:** Right hind wing with a developed vanus. **3:** Camera lucida from the fore- and hind wing of the specimen, showing the vein pattern distribution. Housed in the Institut d'Estudis Ilerdencs in Lleida (Spain).

macropterous. But some specimens from Solnhofen, Las Hoyas, and El Montsec have distinctly shorter wings relative to the length of the abdomen, just scarcely overlapping the abdomen, with the forewing hairy and probably heavily sclerotized (Fig. 7.1, 7.4). All adult females (large specimens with ovipositor) were winged (Fig. 9.1), whereas adult males (large specimens without ovipositor), and nymphs (smaller specimens, with or without ovipositor) were apterous (Figs. 3.2, 7.5). This contrasts with the usual secondary

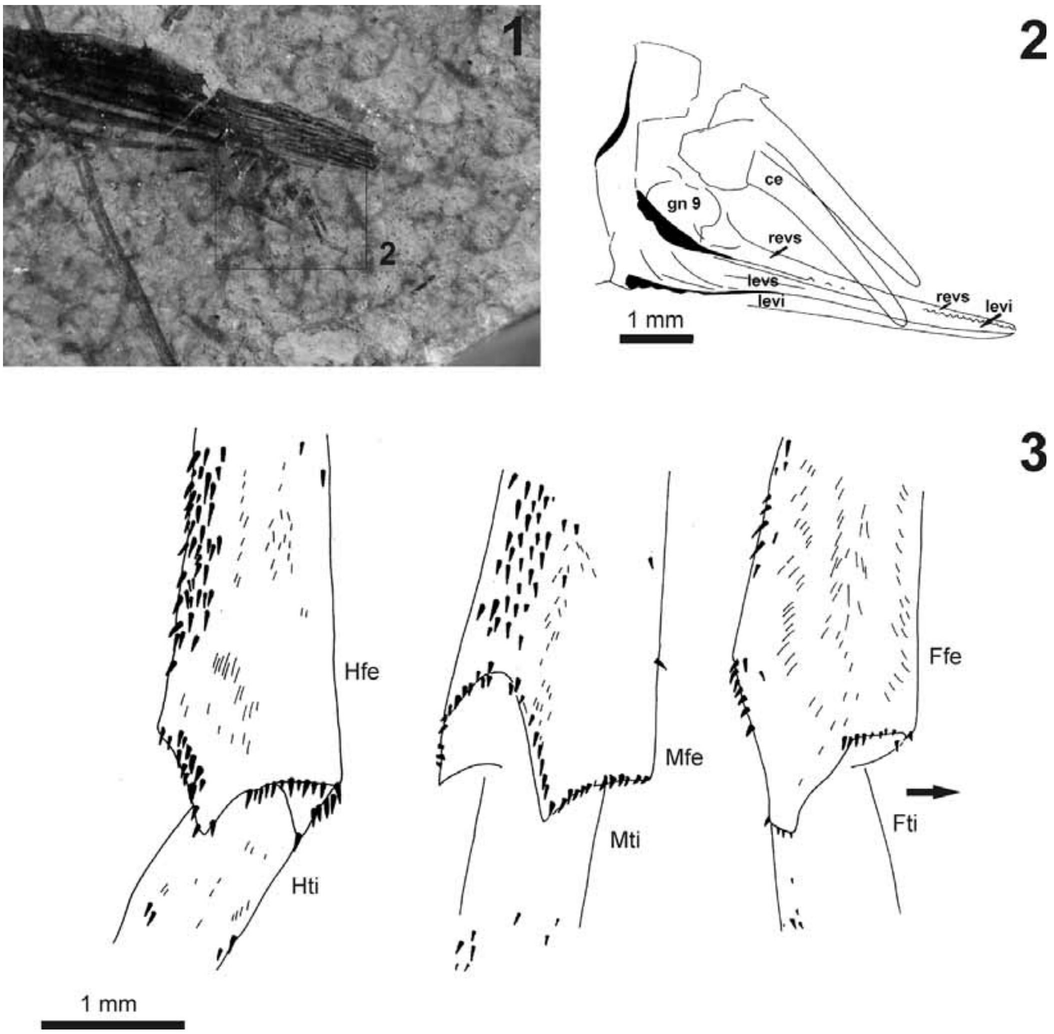

Fig. 9. LP-94-IEI. *Chresmoda aquatica*, holotype; brachypterous specimen, Lower Cretaceous of El Montsec. **1:** distal part of the abdomen showing the ovipositor and cerci. **2:** reconstruction of the distal part of the abdomen; see the unsegmented cerci and serrate ovipositor. **3:** apices of the fore- (right) mid- and hind femur (left) in connection with the tibia; please note the blocking structure between femur and tibia that restricts anterior or posterior movements of the legs (forelegs cannot be moved backwards, while mid- and hind legs cannot be moved forwards). The arrow indicates the anterior orientation in direction of the head. Housed in the Institut d'Estudis Ilerdencs in Lleida (Spain).

apterous females and alate males, in some orthopteroid and phasmatodean species. Perhaps the well-developed wings of *Chresmoda* females increase their possibility to escape from other predaceous insects, or to disperse to new aquatic environments during dry seasons.

4.4. Abdomen

The abdomen seems to be 8- or 9-segmented and distally possesses two small, sharp, pilose, one-segmented cerci (Fig. 9.1.-9.2). The ovipositor is long with two valvulae and an "orthopteroid" gonoplac. The valvulae and gonoplac bear serrations (Fig. 9.2) that might be correlated with endophytic egg-laying, perhaps in floating plants (Nel et al. 2004) or into helophytic ones, such as *Frenelopsis.* The ovipositor sheath is also present in young nymphs from Lebanon and Las Hoyas. The brachypterous females have shorter and stronger abdomens than macropterous specimens (Fig. 7.4). The presence of wings in *C. orientalis* suggests, in relation with other species of

Chresmoda, that it is a female, but no ovipositor is described nor observed. The presence of cerci, among other characters, definitively excludes placement among the Paraneoptera and historical attributions to Hemiptera can be accordingly dismissed.

4. Phylogenetic relationships

4.1. Wing venation

In the last years significant progress was achieved in the basal phylogeny of Recent Phasmatodea (Bradler 2003; Klug & Bradler 2006). However, the phylogenetic position of the crown-group Phasmatodea is still very controversial. The order has been considered as the sister-group of Dermaptera (Kamp 1973), Embioptera (Rähle 1970; Tilgner 2001; Whiting et al. 2003; Zompro 2004; Kjer 2006), Grylloblattodea + Dictyoptera (Maekawa et al. 1999, who did not include Embioptera in their analysis), Dictyoptera (Beutel & Gorb 2001), Orthoptera (Ali & Darling 1998; Flook et al. 1999; Wheeler et al. 2001; Gorochov 2001; Beutel & Gorb 2006), as an 'orthopteroid' order (Kukalová-Peck 1991; Grimaldi 2001; Grimaldi & Engel 2005), as sister to all other Polyneoptera (Dallai et al. 2005), or as a paraphyletic group, viz. one group 'Timematodea' sister to the Embioptera, together representing the sister of the Plecoptera, and the whole set [(Timematodea + Embioptera) + Plecoptera], as the sister-group of 'Phasmatodea' s. str. (Zompro 2005). Dallai et al. (2003, 2007) studied the sperm ultrastructure and failed to support a sister-group relationship of Phasmatodea with Embioptera. Dallai et al. (2005) proposed a polytomic [Mantophasmatodea + Mantodea + (modern) Orthoptera + (modern) Grylloblattodea] supported by a single, unique apomorphy, i.e., 'three connecting bands' in sperm structure. These authors indicated that the situation in Orthoptera is polymorphic going from total absence to one, two, or three such bands, and that they *a priori* chose the above state as the ancestral condition for Orthoptera because it is 'the most frequent one in the group'. This method of estimation of an 'ancestral state' is utterly unfounded, without merit, and should be rejected. Analysis with Orthoptera coded as polymorphic for this character leads to a clearly much less resolved tree. As such, this analysis must be entirely reconsidered. Like Zompro (2004), Kjer et al. (2006) placed the modern Phasmatodea as paraphyletic group near Embioptera, and together as sister-group of [Grylloblattodea + Mantophasmatodea]. Cameron et al. (2006) proposed a relationship [Grylloblattodea (Mantophasmatodea + Timematodea)], but neither included the Phasmatodea s.str. (= Euphasmatodea or Euphasmida) nor the Embioptera in their analysis. A paraphyly of Phasmatodea (= Timematodea + Euphasmatodea) is clearly contradicted by the results of Whiting et al. (2003), and Terry & Whiting (2005).

The *Chresmoda* hind wing LC-1123-IEI from El Montsec (Fig. 8.2-8.3) shows some similarities with those of the Cenozoic and Recent Phasmatodea (true stick- and leaf-insects), especially in the expanded anal area and mains veins simple, straight and parallel. The forewings of the majority of Recent Phasmatodea are reduced or absent, with a strongly sclerotized wing base. Such a character state was recently also described from an Early Tertiary leaf insect by Wedmann et al. (2007). If this reduced state of the wings is a groundplan feature of Phasmatodea is still a matter of debate (Whiting et al. 2003; Trueman et al. 2004; Whiting & Whiting 2004).

Tilgner (2001) discussed the position of the "pre-Tertiary Phasmatodea" attributed to the "Phasmoptera" *sensu* Gorochov (1994) [Susumanioidea + Prochresmodoidea + Aeroplanoidea + Xiphopteroidea], and concluded that they are probably not related to the Recent and Cenozoic Phasmatodea. As no phylogenetic analysis of the "Phasmoptera" or "pre-Tertiary Phasmatodea" is available, the few characters that could be potentially used are not polarized (but see Willmann 2003). At least some representatives (*Orephasma* Ren, 1997; *Aeroplana* Tillyard, 1918) of these "pre-Tertiary Phasmatodea" have specialized structures of the forewing cubito-median veins: a basal fusion of convex CuA with M into a common stem, CuA re-emerging from M a short distance from wing base, and separating from a convex MA and a concave MP, and a concave CuP divided into branches, one of them reaching M+CuA, or MP+CuA. These structures are putative synapomorphies of the "orthopteroid" lineage. Ragge (1955) did not observe them in Recent Phasmatodea. These structures are as difficult to observe in the Recent Phasmatodea as in the modern Orthoptera owing to the strong sclerotization of the wing bases and basal displacement of the stems of the median and cubital veins. But they are very clearly visible in the Palaeozoic and Mesozoic Orthoptera and in some Mesozoic "Phasmatodea". It would, however, be necessary to re-examine all pre-Tertiary "Phasmatodea" to determine their exact patterns of venation. Some of these insects may well have been related to modern phasmatodeans while others were unplaced members of Archaeorthoptera (such as *Orephasma* and *Aeroplana*).

Fortunately, the area of the branches of CuP and base of M+CuA is preserved in the forewing of the *Chresmoda* LH-26.546 from Las Hoyas (Fig. 6.3-6.4). It corresponds exactly to the venational pattern of the Clade Archaeorthoptera [= Orthopterida] and, therefore, supports the attribution of Chresmodidae to the "orthopteroid" rather than to the modern "phasmatodean" lineage.

Comparison of *Chresmoda* with the Mesozoic "Phasmatodea" (Holophasmatodea). – The great majority of Mesozoic "Phasmatodea" (Holophasmatodea *sensu* Grimaldi & Engel, 2005) are known only from isolated forewings. *Chresmoda* differs from the Susumaniidae Gorochov, 1988 in its simple RP, branching from R in the middle of the wing (Gorochov 1988, 2000). Gorochov (1994) characterized the Xyphopteroidea Sharov, 1968 by the pectinate MP in the forewing, quite unlike that seen in *Chresmoda.* The Necrophasmatidae also have a posteriorly pectinate MP (Sharov 1968). The Aeroplanoidea Tillyard, 1918 have RP, MP, or CuA with several branches, unlike that state seen in *Chresmoda.* Within the Prochresmodoidea Vishniakova, 1980, the Permophasmatidae Gorochov, 1992 has RP forked and a zigzagged intercalary vein between RA and RP (Gorochov 1994). *Chresmoda* shows the greatest similarities with Prochresmodidae Vishniakova, 1980 in its simple RP, MP, and CuA, and forked MA (Nel et al. 2004).

4.2. Other characters compared

Some of the characters listed below are difficult to polarize. The pattern of forewing venation remains the best evidence supporting an attribution of *Chresmoda* to the Archaeorthoptera.

Comparison with Mantodea. – Mantises are orthognathous whereas chresmodids were prognathous. In the antennae of mantises, the third antennomere is the longer, not observed in *Chresmoda,* which is equal in length. In most mantises the pronotum is elongate, with a central sulcus, unlike the more or less rounded pronotum of nymphs and adults of *Chresmoda.* However, a short pronotum is still present in basal Recent mantid taxa like *Chaetessa, Mantoida,* and *Metallyticus.* As in *Chresmoda* that had more prominent stiff, stout hairs (or spines) on the rear of the legs, mantids have evident spines in the same position. Mantis tegmina are more or less hard and coriaceous (Fig. 7.6). Some brachypterous species of *Chresmoda* had coriaceous tegmina (with more or less evident venation), whereas in other individuals the wings are completely membranous. The abdomen of mantises is wider in females than in males, while in chresmodids the abdomen is morphologically different depending on whether the individual was apterous, brachypterous, or fully winged. Female mantises have largely vestigial valvulae owing to the deposition of eggs in oothecae. All Cretaceous stem-group mantises are obvious Mantodea (Grimaldi 2003) and bear no relationship to Chresmodidae, which also lack predatorial forelegs, contrary to all known fossil and extant mantises.

Comparison with Phasmatodea. – Phasmatodea and *Chresmoda* are prognathous insects with monofiliform to filiform antennae. They have a short prothorax. Many species are apterous or brachypterous. Phasmatodeans have the posterior wings with a sclerotized anterior region and small, widely-separated coxae, as in *Chresmoda.* The trochanter of Euphasmatodea is considerably smaller than of Chresmodidae, usually fused to the femur, which can be autotomized at its boundary (see also Wedmann et al. 2007). The femora and tibiae are long in both groups. Nonetheless, in *Chresmoda* a notable reduction of the tibiae is present. Phasmatodeans have pentamerous tarsi (the plesiomorphic condition for Insecta), but some regenerate legs can have tetramerous tarsi. In male chresmodids there are no sclerotized structures visible that resemble the vomer of Recent Phasmatodea. Contrary to chresmodids, Recent female phasmatodeans have a reduced ovipositor composed of the standard orthopteroid form (i.e., two valvulae and a gonoplac that assumes a valve-like form and function). In the huge majority of phasmatodean species, the ovipositor is concealed by the abdominal sternum 8 (operculum), thus being internal (see Bradler, 2003: fig. 16.3). According to Bedford (1978), phasmatodeans have 5-7 nymphal instars, according to Bradler (2003) 4-8 instars, with females usually having more (!) instars than conspecific males.

The number of nymphal instars in *Chresmoda* is unknown. Some species of phasmatodeans are parthenogenetic (e.g., *Bacillus, Clonopis,* etc.) with many females and few to no males. It might have been the same for *Chresmoda,* as we found in the fossil record more female than male specimens, but this could also be due to other reasons.

Wedmann et al. (2007) described a fossil leaf insect including the temporal sequence of character evolution that led to the extant crown-group. Characters such as the basally curved fore femora, which are adaptations for camouflage and catalepsy at daylight in Recent Phasmatodea, are obviously not developed in Chresmodidae, suggesting that these insects were not nocturnal.

Comparison with Orthoptera. – *Chresmoda* shares with the Orthoptera their long, tripartite ovipositor (composed of two valvulae and the valve-like gonoplac). The relatively short antenna of *Chresmoda* could be an adaptation to aquatic environments. In Orthoptera the scape and pedicel are larger than the flagellar articles, whereas the pedicel is the shortest article in *Chresmoda.* Macropterous, brachypterous, or apterous taxa are known in Orthoptera, as in *Chresmoda.* Orthopteran ovipositors show denticulate inferior valvulae, as in *Chresmoda.* In addition, the robust metacoxae meeting at the midline of the sternum in *Chresmoda neotropica* are atypical for Orthoptera, which usually have small, well-separated metacoxae.

The *Chresmoda* also have one-segmented cerci. Monomerous cerci are present in Orthoptera and most Recent Phasmatodea, while the cerci tend to be polymerous in most dictyopterans. Although Zompro (2005) proposed unsegmented cerci as a synapomorphy of his 'Orthopteriformia' (= Mantophasmatodea + Orthoptera), the exact phylogenetic value of this character remains uncertain because it is widely homoplastic across Polyneoptera (Tilgner et al. 1999; Tilgner 2001; Grimaldi & Engel 2005). The female terminalia of the Phasmatodea are of a typical orthopteroid type, as is also the case for Grylloblattodea (Deuve 2001), and thus apparently of little interest for our purposes. Palaeozoic and some Mesozoic stem-group dictyopterans (the so-called "roachoids": Grimaldi 1997; Grimaldi & Engel 2005) had long, external ovipositors similar to that observed in *Chresmoda.* Zompro (2005) also proposed the saltatorial hind legs as a synapomorphy of the 'Orthopteriformia', but Béthoux & Nel (2002) demonstrated that saltatorial legs are not present in the most basal lineages of Archaeorthoptera [= Orthopterida]. Thus, if the Mantophasmatodea were actually related to the Orthoptera *sensu stricto*, they would presumably be more derived than many other Archaeorthoptera [= Orthopterida]. The Mantophasmatodea are increasingly understood to be the sister taxon to Grylloblattodea [in Notoptera = Grylloblattodea + Mantophasmatodea] (Engel & Grimaldi 2004; Grimaldi & Engel 2005; Terry & Whiting 2005; Arillo & Engel 2006; Kjer et al. 2006), although the definitive placement of the group remains controversial (Cameron et al. 2006). The absence of saltatorial legs in *Chresmoda* is certainly related to its mode of life and indicates nothing about its phylogenetic affinities as this could merely be autapomorphic.

4.3. Other arthropods with multisegmented tarsi

Until now, no other hexapod has been known to have super-multiarticulate legs, with an extreme subdivision of an individual podite as is seen in *Chresmoda* (Nel et al. 2004). Hexapods have had since the Late Carboniferous, and likely since the Devonian, five or fewer tarsal articles.

Chresmoda have the last two tarsomeres of all legs subdivided into more than 40 minute articles. Some Recent and fossil groups of terrestrial arthropods show multi-segmented legs. Usually these modifications are only present in the forelegs, and are related to sensorial functions. Such is the case in arachnids like Amblypygi, Uropygi and Schizomida, in which the first leg ends in a subdivided, antenniform tarsus with a sensorial function. This is particularly apparent in the slender forelegs of amblypygids. Fossils of Amblypygi and Uropygi are found in the Carboniferous and Cretaceous; Schizomida in the Pliocene (e.g., see Selden & Dunlop 1998). Forelegs of Palpigradi have their first pair of legs multi-articulated with a sensorial function. In palpigrades the first pair of legs never touches the ground, in contrast with the arachnid groups mentioned above. Fossils of this group have been found but are exceptionally rare (Rowland & Sissom 1980). Opiliones have in all four pair of legs a multi-segmented tarsus (up to 100, that permit tarsi to roll around plant axes) and with distal claws on pretarsi, and their functionality are only for walking; the earliest harvestmen are found in the Devonian of Rhynie, but mainly in Tertiary ambers. All of these groups of terrestrial arachnids have a scarce fossil record. No continental aquatic arthropod has either analogous or homologous leg modifications.

5. Palaeobiology of *Chresmoda*

Prior to this work it was supposed that the number of tarsomeres increased along the evolution of the genus *Chresmoda* during the Mesozoic. *Chresmoda* was presumed to have pentamerous *(C. obscura* in Ponomarenko 1985) or tetramerous tarsi (*C. aquatica* in Martínez-Delclòs 1989). Martínez-Delclòs (1991), studying new material from the Barremian of Spain, proposed that the last tarsal article was subdivided into almost eight subsegments that increased in length apically. A pretarsus with claws could not be discerned and instead in *C. aquatica* the apex of the leg is apically rounded, either terminating with the last, subdivided tarsal article (and thereby entirely lacking the pretarsal podite which bears the claws) or in an apically-rounded pretarsal podite with ungues lost.

Nel et al. (2004) studied a then new species of *Chresmoda* from the Cenomanian of Lebanon. That species had the three basal tarsomeres unsegmented but the distal parts of the legs are divided into more than 40 exceptionally small subtarsal articles, decreasing apically in length in the mid and hind legs, and with 15 such units in the forelegs. Subsequent to their work new material from Lebanon, new specimens from the Barremian of Las Hoyas and El Montsec (housed in Spanish museums), and from the Tithonian of Solnhofen (housed in the Natural History Museum, London and the Muséum national d'Histoire Naturelle, Paris) demonstrate that both *C. aquatica* and *C. obscura*, respectively have more than 40 distal subtarsal articles (DA and XD pers. obs.). The same is true for *C. neotropica* n. sp., reported herein from the Crato Formation. This extremely rare segmentation of tarsi is observed also in minute nymphs from Las Hoyas.

Excluding Chresmodidae, the legs of insects are typically composed of six podites (the next to last of which, the tarsus, is divided into a maximum of five articles, or tarsomeres, giving a total apparent number of nine units in the leg) from proximal (closest to the body wall) to distal (tip of the leg) they are the coxa, trochanter, femur, tibia, tarsal articles 1-5, and the pretarsus (Fristrom & Chihara 1978; Grimaldi & Engel 2005). The pretarsus bears the claws which are frequently and quite erroneously called "tarsal claws" but are, in fact, "pretarsal claws" or "ungues". Each podite is separated from the next by a more or less flexible joint composed of arthrodial membrane (the trochanter-femur joint is frequently immobilized) and controlled by musculature originating inside of the body or within the preceding podite (the subdivisions of the tarsus, the tarsomeres, are not true podites and there is no intrinsic musculature operating them; muscles only move the entire tarsus as a unit), with the exception of the pretarsus which is controlled by muscles that extend back through the tarsus to the apex of the tibia or the femoral base. Most of the studies on segmentation and development in insects have been undertaken on the fruit fly *Drosophila.* Segmentation is a developmental mechanism common to a large number of animal lineages. Segmentation subdivides a tissue into a series of repeating units, whereupon each basic unit can then be further elaborated upon during development (Rauskolb 2001). The podites of the legs are not segments in the sense of body segmentation (i.e., developmental metameres) but are instead subdivisions of metamere appendages. Nonetheless, the development and control of the formation of these subdivided appendages has been studied in detail only within model organisms such as *D. melanogaster*, with cursorial examinations for others like *Gryllus, Oncopeltus*, or *Apis,* and the development of most hexapods remains utterly unstudied. Although the molecular basis of segmentation and regional growth during morphogenesis of insect legs is poorly understood, early steps in insect leg development have been elucidated, and some key genes involved in leg segmentation have been identified (Bishop et al. 1999; de Celis et al. 1998; Rauskolb & Irvine 1999). It is now well established that *four-jointed* (*fj*) interacts with *dachs* (*d*), *abelson* (*abl*) and *enabled* (*ena*) and feeds back onto the Notch (N) pathway involving the N ligands Serrate (Ser) and Delta (Dl) to affect growth and segmentation in the *Drosophila* leg (Buckles et al. 2001). Concerning tarsal segmentation, most of the tarsus of insect legs derives from cells expressing Distal less (DLL). The studies of Rauskolb (2001) demonstrated that DLL represses N ligand expression and that *spineless-aristapedia* (*ss*) regulates the expression of *bric-à-brac* (*bab*) which is also required for the subdivision of the tarsus into individual subsegments. Herke et al. (2005) confirmed that in *Oncopeltus fasciatus*, tiptop is a selector gene that is required for the segmentation of the distal leg and is also required to switch appendage development from antenna to leg. For some authors antennae and legs are considered to be serially homologous structures as both are metameric appendages (Grimaldi & Engel 2005) and because they can be interconverted through the action of homeotic genes (Emerald et al. 2003). One could conclude that the leg and tarsal subsegmentation is a complex, polygenic trait. For most of the above cited genes induced mutations generating loss of function result in a reduction of tarsomere number, and yet, it remains unclear how a repeating segmental pattern is generated during leg development, but one could imagine that over-expression of these same genes could induce a multiplication of tarsomere number. Of course this kind of increase in tarsomere number must be followed by subsequent modification of associated tissues requiring the action of additional structural genes. Since the tarsus lacks intrinsic muscles, this would not require modified musculature but would require a great elongation of the pretarsal depressor (the pretarsus lacks a levator muscle) or unguitractor tendon, assuming that the pretarsus was retained in *Chresmoda* in some modified form (perhaps resembling an apicalmost tarsomere), something we cannot confirm. It is possible that during the evolution of the lineage that gave rise to Chresmodidae there were mutations involving homeotic genes for leg segmentation that resulted in increasing the tarsomere number in the family. This mutation was fixed and successful for at least 65 Million years. However, we must also note that any dramatic anatomical change (i.e., most synapomorphies) represents mutations of one form or another that become fixed and successful in the clades that they define. While we have highlighted the peculiar leg morphology of *Chresmoda,* other mutations across the insects gave rise to the eventual origin of wings, various wing-folding mechanisms, the modification of wings into a variety of structures of varying functions (e.g., halteres, elytra, blood sinuses), among innumerable others, and several of them, but not all, has led to a successful diversification of hexapods.

The densely pilose tarsi in *Chresmoda* seem to be a specialization for skating across water surfaces (Martínez-Delclòs 1991; Nel et al. 2004) but surely not in the same manner as in the modern Gerridae (Hemiptera: Heteroptera) owing to their overall different leg structures. The pressure of a leg produces a trough-shaped depression (meniscus) on the water surface, and the surface tension of the water easily supports the weight of the insect. The weight of *Chresmoda* was probably held up by the surface curvature that developed around the legs (impermeable and pilose). Although they possessed different apical leg structures, it is possible that like Recent gerrids *Chresmoda* made whirlpools that affected levels in the water surface and with backward movements propelled the insect forward (Hu et al. 2004). Gerrids transfer quantity of movement to the fluid surface with the help of hemispheric whirlpools produced by their propulsive mid and hind legs. It is possible that *Chresmoda* could have developed similar hemispheric whirlpools (U-shaped) but with all three pairs of legs. Hu et al. (2003) showed that for 342 species of water strider the length of the leg in contact with the water surface increases relative to the body weight and thus the force due to surface tension increases with the force due to body weight. It was apparently the same in *Chresmoda,* as the largest species, *C. obscura*, has legs proportionally longer than in other species.

Chresmoda aquatica, C. mongolica comb. nov., and *C. orientalis* lived in lacustrine environments, while *C. obscura* and *C. libanica* apparently lived in brackish-marine waters. The new species from Crato (Brazil) lived in a saline lagoon (Grimaldi & Engel 2005; Nel et al. 2005). Data concerning the sensitivity of *Chresmoda* species to increased salinity levels of other forms of environmental changes are not available. In general, Gerridae are moderately tolerant to salinity levels (Gooderham & Tsyrlin 2002; Chessman 2003). Pseudomorphs of salt cubes are usually found in the laminated limestones of Crato (Martinéz-Delclòs et al. 2004: 42, fig. 7C) but perhaps the lagoon of Crato was solely saline in its bottom or in its water table (see also Martill et al. 2007), and the water surface itself was fresh such that chresmodids could skate there upon.

Hitherto now, it seems that the more ancient and earliest species of *Chresmoda* lived in brackish or marine water surfaces, while the Early Cretaceous species are found only in lacustrine environments. Owing to the absence of an accurate cladistic phylogenetic position of the genus *Chresmoda* solidly placing the group among the orthopterids (although certainly more closely related to the Orthoptera than the Phasmatodea), it is impossible to know when the homeotic mutation that promoted this hyperspecialized leg structure took place. Nevertheless, we can hypothesize that this transformation likely took place during the Late Triassic or Early Jurassic, favoured by the decreasing of water density as a result of a high global temperature during the Triassic (Fig. 10).

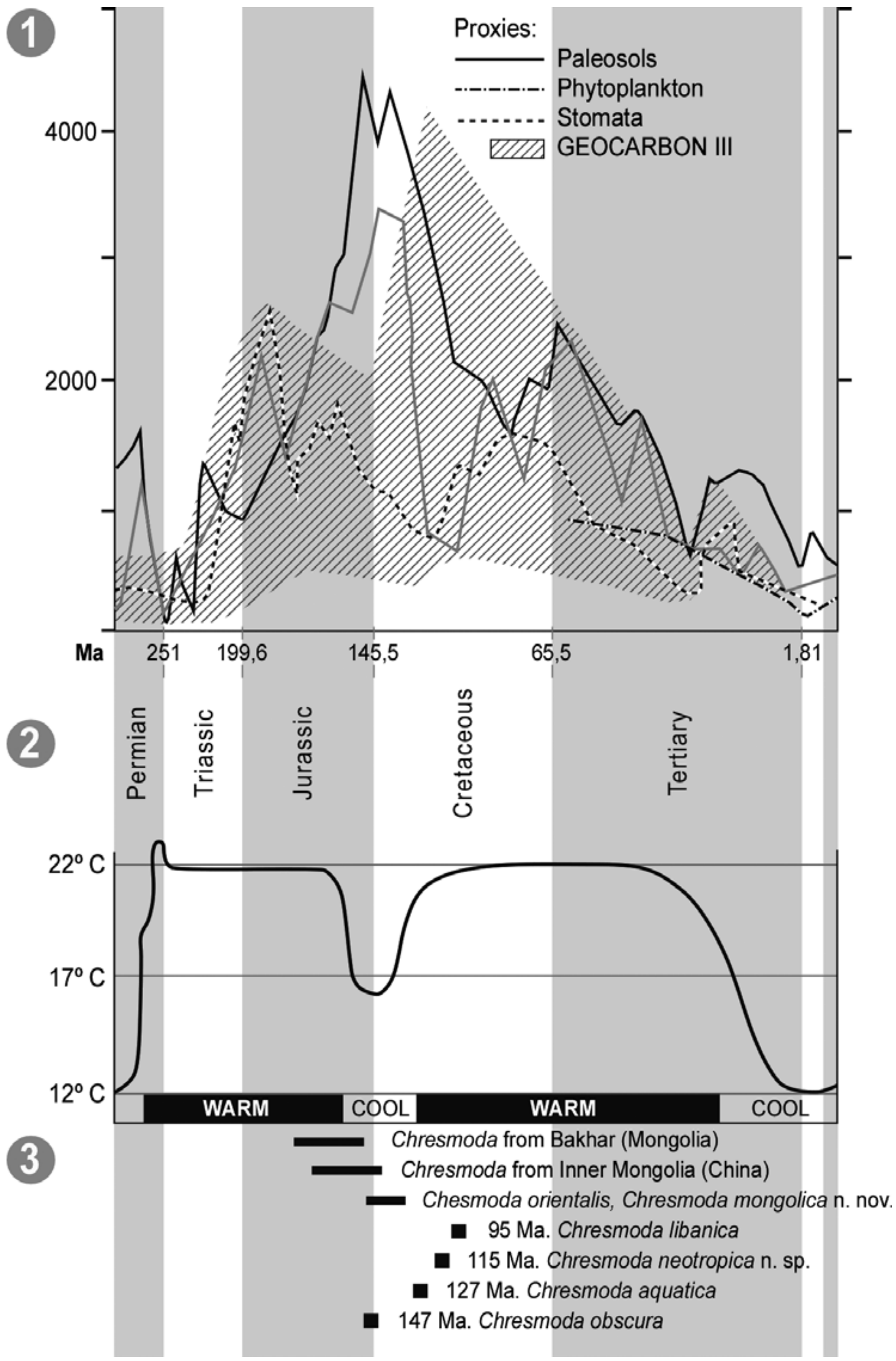

Fig. 10. Period of appearance of chesmodid species in relation with the atmospheric CO_2 average, and global climatic situation. **1:** Graphic showing the details of CO_2 proxy data set (Four-point running averages for individual proxies: Paleosols, Phytophacton, Stomata, and GEOCARB III), and combined atmospheric CO_2 concentration record as determined from proxies (Grey curve represents average values in 10 My (after Royer et al. 2004). **2:** Average of the global temperature, and distribution of the "Ice House" – "Green House" situation in the Earth between Today since the Permian (after Scotese Paleomap 2003 web). **3:** Distribution of the *Chresmoda* species during the Jurassic-Cretaceous.

During the Late Jurassic the global climate changed due to the break up of Pangea. The oldest studied species of *Chresmoda* comes from the Tithonian of Solnhofen, at 40º of latitude, living under a warm temperate climate (SELLWOOD et al. 2000), but during an otherwise global icehouse period (BERNER 1998; VEIZER et al. 2000; LABANDEIRA 2006). The climate was more stable and uniform than today and in low latitudes no evidence of tropical rainforest exists (REES et al. 2000, 2004). Except for *C. libanica*, all species of *Chresmoda* are found in rocks formed under warm temperate climates with moderate humidity and driven by monsoonal seasons in low-mid latitudes (TAJIKA 1998). BARRON et al. (1989, fig. 13) suggest that a globally warm climate meant high precipitation and evaporation rates, predicting high seasonal rainfall focused on the northern and southern borders of Tethys, where diverse species of *Chresmoda* lived. The youngest species, *C. libanica*, is found in the Cenomanian (under warm greenhouse global climate). Its extinction is difficult to explain but we can hypothesize that it was perhaps due to the extreme global warming during the Turonian (BICE et al. 2003; ROYER et al. 2004; JENKYNS et al. 2004). This is not a wholly satisfactory hypothesis because the global climate changed considerably between the Tithonian and the Cenomanian, evolving in middle latitudes from warm temperate to very warm intertropical.

The largest known species of *Chresmoda* (*C. obscura*) lived during the Tithonian, when the water surface temperature was low, with a consequent increase in water density. During the late Early Cretaceous and the Late Cretaceous, a “greenhouse climate” was globally established (GALE 2001, LARSON et al. 1993). In order to float in lacustrine environments, *Chresmoda* species were “obliged” to decrease their dimensions. During the Cenomanian it was necessary for species of *Chresmoda* to occupy brackish or marine environments with a higher water density in order to float. Perhaps *Chresmoda* were also aided by the large development of shelf areas in marine environments caused by a global transgression (HALLAM 1992). The Cenomanian was a period of overall sea-level rise.

It is not possible to correlate the disappearance of *Chresmoda* with the origin and rise of other water-striding insects, such as species of Gerridae or Hydrometridae, since these families of aquatic heteropterans were already established during the Cretaceous [e.g., Albian amber of Peñacerrada, Spain (DELCLÒS et al. 2007), Aptian-Albian laminate limestones of Crato, Brazil (NEL & POPOV 2000), latest Albian amber of Burma (ANDERSEN & GRIMALDI 2001; GRIMALDI et al. 2002; CRUICKSHANK & KO 2003), or in the Cenomanian amber of Charente-Maritime, France (PERRICHOT et al. 2005). From the available evidence it does not appear as though gerrids and/or hydrometrids were competitors excluding chresmodids from the same ecological niche.

6. Conclusions

The Jurassic-Cretaceous genus *Chresmoda* is morphological and phylogenetical restudied. After critical revision we include the genus *Sternarthron* from the Upper Jurassic of Solnhofen which was previously placed among the arachnids, principally the palpigrades.

We also review the principal morphological characters of *Chresmoda* in order to elucidate their phylogenetic relationships with other groups of orthopteroids and arthropods, and we describe the new species *Chresmoda neotropica* ENGEL & HEADS n. sp. from the Aptian-Albian lithographic limestones of the Crato Formation in Brazil. The new specimens of *Chresmoda* found in the Barremian of Spain with well preserved fore- and hind wing venation permit us to determine that the venational pattern follows that of the Archaeorthoptera (= Orthopterida) and presently supports attribution of Chresmodidae to the “orthopteroid” rather than to the modern “phasmatodean” lineage.

One of the more impressive characters is the specialized structured legs adapted for skating across water surfaces. During the evolution of the *Chresmoda* lineage a mutation involving homeotic genes promote leg segmentation that resulted in increasing the tarsomere number in the family. This mutation was fixed and successful for at least 65 Ma. A new hypothesis about their spatial and environmental distribution thorough time based on the climate evolution is proposed. Their extinction during the Late Cretaceous remains unresolved, but likely was not a result of competition for “ecospace” with the semi-aquatic heteropterans.

Acknowledgements

This research was made possible thanks to the active help of ALAIN WALLER, CHRISTIANE AMEDEGNATO, and SIMON POULAIN (Entomology, MNHN, Paris). We thank BILL SHEAR and ANDY ROSS for valuable discussions and DAVE UNWIN for comments on the Solnhofen locality. Participation of M. S. ENGEL was made possible by a Guggenheim Fellowship from the John Simon Guggenheim Memorial Foundation (New York) and National Science Foundation (USA) grant DEB-0542909. We are also grateful to HERBERT AXELROD for donating his large collection of Crato Formation fossils to the American Museum of Natural History (New York). We thank HELMUT TISCHLINGER (Stammham, Germany) for numerous helpful comments of an early draft of this manuscript and for providing important literature, and GÜNTER VIOHL (Jura-Museum, Eichstätt, Germany) and HELMUT MAYR (BSPGM, München, Germany) for give us the possibility to study the *Chresmoda* material housed in their museums. Thanks to DIMITRI E. SHCHERBAKOV (Laboratory of Palaeoentomology, Moscow, Russia) for give us the photograph of *Saurophthirodes mongolicus*. Research was carried out with the support of the Spanish Ministry of Science and Technology CGL2005-00046/BTE. We thank SVEN BRADLER (University of Göttingen, Germany), DAVID GRIMALDI (AMNH, New York) and GÜNTER SCHWEIGERT (SMNS, Stuttgart, Germany) for carefully reviewing this manuscript and for providing numerous very useful comments and corrections.

References

ALI, D. W. & DARLING, D. C. (1998): Neuroanatomy and neurochemistry: implications for the phylogeny of the lower Neoptera. – Canadian Journal of Zoology, **76** (9): 1628-1633.

ANDERSEN, N. M. & GRIMALDI, D. (2001): A fossil water measurer from the mid-Cretaceous Burmese amber (Hemiptera: Gerromorpha: Hydrometridae). – Insect Systematics & Evolution, **32**: 381-392.

ARILLO, A. & ENGEL, M. S. (2006): Rock crawlers in Baltic amber (Notoptera: Mantophasmatodea). – American Museum Novitates, **3539**: 1-10.

ASSMANN, A. (1877): Ueber die von Germar beschriebenen und im palaeontologischen Museum zu München befindlichen Insecten aus dem lithographischen Schiefer in Bayern. – Amtlicher Bericht der 50. Versammlung deutscher Naturforscher und Aerzte, München, p. 191-192.

BARTHEL, K. W. (1978): Solnhofen: Ein Blick in die Erdgeschichte. – 393 pp.; Basel & Thun (Ott).

BARTHEL, K. W., SWINBURNE, N. H. M. & CONWAY-MORRIS, S. (1990): Solnhofen: a study in Mesozoic palaeontology. – 235 pp.; Cambridge (Cambridge University Press).

BAUDOIN, R. (1980): Sur les Gerris des miroirs d'eau actuels et les *Chresmoda* des lagunes post-récifales portlandiennes de Solnhofen. – Annales de la Société national de Zoologie, **2**: 111-116.

BECHLY, G. (1998): Santana – Schatzkammer fossiler Insekten. – Fossilien, **1998** (2): 95-99; **1998** (3): 148-56.

– (1999): Notices. – Meganeura, **4**: 9.

– (2007): Chresmododea – fossil "water striders". – In: MARTILL, D., BECHLY, G. & LOVERIDGE, R. (Eds.): The Crato fossil beds of Brazil: Window into an ancient world, p. 262-265; Cambridge (Cambridge University Press).

BECHLY, G., HAAS, F., SCHAWALLER, W., SCHMALFUSS, H. & SCHMID, U. (2001): Ur-Geziefer – Die faszinierende Evolution der Insekten. – Stuttgarter Beiträge zur Naturkunde, (C), **49**: 96 pp.

BEDFORD, G. O. (1978): Biology and ecology of the Phasmatodea. – Annual Review of Entomology **23**: 125-149.

BÉTHOUX, O. & NEL, A. (2002): Venation pattern and revision of Orthoptera *sensu nov.* and sister groups. Phylogeny of Palaeozoic and Mesozoic Orthoptera *sensu* nov. – Zootaxa, **96**: 1-88.

BERNER, R. A. (1998): The carbon cycle and CO_2 over Phanerozoic time: the role of land plants. – Philosophical Transactions of the Royal Society of London, (B), **353**: 75-82.

BEUTEL, R. G. & GORB, S. N. (2001): Ultrastructure of attachment specializations of hexapods (Arthropoda): evolutionary patterns inferred from revised ordinal phylogeny. – Zeitschrift für Zoologische Systematik und Evolutionforschung, **39** (4): 177-207.

– (2006): A revised interpretation of the evolution of attachment structures in Hexapoda (Arthropoda), with special emphasis on Mantophasmatodea. – Arthropod Systematics & Phylogeny, **64** (1): 3-25.

BISHOP, S. A., KLEIN, T., MARTINEZ-ARIAS, A. & COUSO, J. P. (1999): Composite signalling from *Serrate* and *Delta* establishes leg segments in *Drosophila* through Notch. – Development, **126**: 2993-3003.

BOUCOT, A. J. & GRAY, J. (2001): A critique of Phanerozoic climatic models involving changes in the CO_2 content of the atmosphere. – Earth-Science Reviews, **56**: 1-159.

BRADLER, S. (2003): Phasmatodea, Gespenstschrecken. – In: DATHE, H. H. (Ed.): Lehrbuch der Speziellen Zoologie, Vol. 5, p. 251-261. – Heidelberg (Spektrum & Gustav Fischer).

BICE, K. L., HUBER, B. T. & NORRIS, R. D. (2003): Extreme polar warmth during the Cretaceous greenhouse?: The paradox of the Late Turonian Record at DSDP Site 511. – Paleoceanography, **18** (2): 1031.

BUCKLES, G. R., RAUSKOLB, C., VILLANO, J. & KATZ, F. N. (2001): *Four-jointed* interacts with *dachs, abelson*, and *enabled* and feeds back onto the *Notch* pathway to affect growth and segmentation in the *Drosophila* leg. – Development, **128**: 3533-3542.

CAMERON, S. L., BARKER, S. C. & WHITING, M. F. (2006): Mitochondrial genomics and the new insect order Mantophasmatodea. – Molecular Phylogenetics and Evolution, **38** (1): 274-279.

CARPENTER, F. M. (1992): Superclass Hexapoda. – In: MOORE, R. C. & KAESLER, R. L. (Eds.): Treatise on Invertebrate Paleontology, R, Arthropoda 4, 3/4. – xxii + 655 pp.; Boulder & Lawrence (Geological Society of America & University of Kansas).

CHESSMAN, B. (2003): SIGNAL 2 – A Scoring System for Macroinvertebrate ('Water Bugs') in Australian Rivers, Monitoring River Heath Initiative Technical Report no 31, Commonwealth of Australia, Canberra. http://www.deh.gov.au/water/rivers/nrhp/signal/

CONDÉ, B. (1996): Les Palpigrades, 1885-1995: acquisitions et lacunes. – Revue Suisse de Zoologie, hors série: 87-106.

Crowson, R. A., Rolfe, W. D. I., Smart, J., Waterston, C. D., Willey, E. C. & Wooton, R. J. (1967): Arthropoda: Chelicerata, Pycnogonida, *Paleoisopus,* Myriapoda and Insecta. – In: Harland, W. B., et al. (Eds.). The Fossil Record, p. 499-534; London (The Geological Society of London).

Cruickshank, R. D. & Ko, K. (2003): Geology of an amber locality in the Hukawng Valley, Northern Myanmar. – Journal of Asian Earth Sciences **21**: 441-455.

Dallai, R., Frati, F., Lupetti, P. & Adis, J. (2003): Sperm ultrastructure of *Mantophasma zephyra* (Insecta, Mantophasmatodea). – Zoomorphology, **122**: 67-76.

Dallai, R., Machida, R., Uchifune, T., Lupetti, P. & Frati, F. (2005): The sperm structure of *Galloisiana yuasai* (Insecta, Grylloblattodea) and implications for the phylogenetic position of Grylloblattodea. – Zoomorphology, **124**: 205-212.

Dallai, R., Machida, R., Jintsu, Y., Frati, F. & Lupetti, P. (2007): The sperm structure of Embioptera (Insecta) and phylogenetic considerations. – Zoomorphology, **126**: 53-59.

de Celis, J. F., Tyler, D. M., de Celis, J. & Bray, S. J. (1998): Notch signaling mediates segmentation of the *Drosophila* leg. – Development, **125**: 4617-4626.

Delclòs, X., Arillo, A., Peñalver, E., Barròn, E., Soriano, C., Lòpez Del Valle, R., Bernárdez, E., Corral, C. & Ortuño, V. M. (2007): Fossiliferous amber deposits from the Cretaceous (Albian) of Spain. – Comptes Rendus Palevol, **6**: 135-149.

Deuve, T. (2001): The epipleural field in hexapods. – In: Deuve, T. (Ed.): Origin of the Hexapoda. – Annales de la Société Entomologique de France, (N.S.), **37**: 195-231.

Emerald, B. S., Curtiss, J., Mlodzik, M. & Cohen, S. M. (2003): Distal antenna and distal antenna related encode nuclear proteins containing pipsqueak motifs involved in antenna development in *Drosophila.* – Development, **130**: 1171-1180.

Engel, M. S. & Grimaldi, D. A. (2004): A new rock crawler in Baltic amber, with comments on the order (Mantophasmatodea: Mantophasmatidae). – American Museum Novitates, **3431**: 1-11.

Esaki, T. (1949): The occurrence of the Mesozoic insect *Chresmoda* in the Far East. – Insecta Matsumarana, **17**: 4-5.

Flook, P. K., Klee, S. & Rowell, C. H. F. (1999): Combined molecular phylogenetic analysis of the Orthoptera (Arthropoda, Insecta) and implications for their higher systematics. – Systematic Biology, **48** (2): 233-253.

Frickhinger, K. A. (1994): Die Fossilien von Solnhofen. – 336 pp.; Korb (Goldschneck).

– (1999): Die Fossilien von Solnhofen, Vol. 2. – 190 pp.; – Korb (Goldschneck).

Fristrom, D. & Chihara, C. (1978): The mechanism of evagination of imaginal discs of *Drosophila melanogaster.* V. Evagination of disc fragments. – Developmental Biology, **66**: 564-570.

Furth, D. G. (1994): Frank Morton Carpenter (1902-1994): academic biography and list of publications. – Psyche, **101**: 127-144.

Germar, E. F. (1817): Reise nach Dalmatien und in das Gebiet von Ragusa. – xii + 323 pp.; Leipzig & Altenburg.

– (1839): Die versteinerten Insekten Solenhofens. – Nova Acta Leopoldina Carolina Akademia, Halle, **19** (1): 187-222.

Gooderham, J. & Tsyrlin, E. (2002): The Waterbug Book: a guide to the freshwater macroinvertebrates of temperate Australia. – CSIRO Publishing.

Gorochov, A. V. (1988): [On the classification of fossil orthopterans of the superfamily Phasmomimoidea (Orthoptera) with a description of new taxa.]. – Trudy Zoologicheskogo Instituta Akademii nauk SSSR, St. Petersburg, **178**: 32-44. [In Russian]

– (1992): [New fossil Orthoptera and Phasmoptera from the Mesozoic and Paleozoic of Mongolia.] In: Rozanov, A. Yu. (Ed.): Novye vidy iskopaemykh bespozvonochnykh Mongolii [New taxa of fossil invertebrates from Mongolia.]. – Trudy Sovmestnaya Sovetsko-Mongol'skaya Paleontologicheskaya Ekspeditsiya, Moscow, **41**: 117-121. [In Russian]

– (1994): Permian and Triassic walking sticks (Phasmatodea) from Eurasia. – Paleontological Journal, **28** (4): 83-97.

– (2000): Phasmomimidae: are they Orthoptera or Phasmatoptera? – Paleontological Journal, **34** (3): 295-300.

– (2001): On the higher classification of the Polyneoptera (short course). 1 Simposio Brasileiro de Paleoarthropodologia and 1rst International Meeting on Paleoarthropodology, Universidade de Vale do Rio dos Sinos. – Acta Geologica Leopoldensia, Estudos Tecnologicos, **24** (52/53): 11-56.

Grimaldi, D. A. (2001): Insect evolutionary history from Handlirsch to Hennig, and beyond. – Journal of Paleontology, **75**: 1152-1160.

– (2003): A Revision of Cretaceous Mantises and Their Relationships, Including New Taxa (Insecta: Dictyoptera: Mantodea). – American Museum Novitates, **3412**: 47 pp.

Grimaldi, D. A. & Engel, M. S. (2005): Evolution of the insects. – xv + 755 pp.; Cambridge (Cambridge University Press):

Haase, E. (1890a): Bemerkungen zur Paläontologie der Insecten. – Neues Jahrbuch für Mineralogie, Geologie und Palaeontologie, **1890** (2): 1-33.

– (1890b): Beiträge zur Kenntnis der fossilen Arachniden. – Zeitschrift der Deutschen Geologischen Gesellschaft, **42**: 629-657.

Handlirsch, A. (1906-1908): Die fossilen Insekten und die Phylogenie der rezenten Formen. Ein Handbuch für Paläontologen und Zoologen. – 1430 pp.; Leipzig (Engelmann).

– (1925): Palaeontologie. – In: Schröder, C. (Ed.), Handbuch der Entomologie, Band 3: Geschichte, Literatur, Technik, Paläontologie, Phylogenie, Systematik, p. 117-306; Jena (G. Fischer).

– (1926-1930): Insecta. – In: Kükenthal, W. & Krumbach, T. (Eds.): Handbuch der Zoologie, **4**: 403-892; Berlin.

Harvey, M. S. (2003): Catalogue of the smaller Arachnida orders of the world. – xi + 385 pp.; Collingwood (CSIRO Publishing).

Herke, S. W., Serio, N. V. & Rogers, B. T. (2005): Functional analyses of *tiptop* and *Antennapedia* in the embryonic development of *Oncopeltus fasciatus* suggests an evolutionary pathway from ground state to insect legs. – Development, **132**: 27-34.

Hu, D. L., Chan, B. & Bush, J. W. M. (2003): The hydrodynamics of water strider locomotion. – Nature **424**: 663-666.

Huber, B. T., Norris, R. D. & MacLeod, K. G. (2002): Deep-sea paleotemperature record of extreme warmth during the Cretaceous. – Geology, **30** (2): 123-126.

Jenkyns, H. C., Forster, A., Schouten, S. & Damste, J. S. (2004): High temperatures in the Late Cretaceous Arctic Ocean. – Nature, **432**: 888-892.

Kamp, J. W. (1973): Numerical classification of the orthopteroids, with special reference to the Grylloblattodea. – The Canadian Entomologist, **105**: 1235-1249.

Kästner, A. (1941): Ordnung der Arachnida: Palpigradi, Thorell. – In: Kükenthal, W. & Krumbach, T. (Eds.): Handbuch der Zoologie, Vol. 3, 2 (2): 77-98; Berlin (de Gruyter & Co.).

Kjer, K. M., Carle, F. L., Litman, J. & Ware, J. (2006): A molecular phylogeny of Hexapoda. – Arthropod Systematics & Phylogeny, **64** (1): 35-44.

Klug, R. & Bradler, S. (2006): The pregenital abdominal musculature in phasmids and its implications for the basal phylogeny of Phasmatodea (Insecta: Polyneoptera). – Organisms Diversity & Evolution, **6** (3): 171-184.

Kuhn, O. (1961): Die Tier- und Pflanzenwelt des Solnhofener Schiefers. – Geologica Bavarica, **48**: 68 pp.

– (1977): Die Tierwelt des Solnhofener Schiefers, 5th edition. – 318 pp.; Wittenberg (Ziemsen).

Kukalová-Peck, J. (1991): Fossil history and the evolution of hexapod structures. – In: Naumann, I. D. (Ed.): The insects of Australia, a textbook for students and research workers (2nd edition), p. 141-179; Melbourne (Melbourne University Press).

Maekawa, K., Kitade, O. & Matsumoto, T. (1999): Molecular phylogeny of orthopteroid insects based on mitochondrial cytochrome oxydase II gene. – Zoological Science, **16** (1): 175-184.

Martill, D. M., Loveridge, R. & Heimhofer, U. (2007): Halite pseudomorphs in the Crato Formation (Early Cretaceous, Late Aptian-Early Albian), Araripe Basin, northeast Brazil: further evidence for hypersalinity. – Cretaceous Research, **28** (4): 613-620.

Martínez-Delclòs, X. (1989): *Chresmoda aquatica* n. sp. insecto Chresmodidae del Cretácico inferior de la Sierra del Montsec (Lleida, España). – Revista Española de Paleontología, **4**: 67-74.

– (1991): Insectes hemimetàbols del Cretaci inferior d'Espanya. Tafonomia i Paleoautoecologia. – Doctoral Thesis, University of Barcelona. – 784 pp.

Martínez-Delclòs, X., Briggs, D. E. G. & Peñalver, E. (2004): Taphonomy of insects in carbonates and amber. – Palaeogeography, Palaeoclimatology, Palaeoecology, **203**: 19-64.

Martinov, A. V. (1928): A new fossil form of Phasmatodea from Galkino (Turkestan), and on Mesozoic phasmids in general. – Annals and Magazine of Natural History, **10**: 319-328.

Martynova, O. M. (1962/1991): Order Phasmatodea. – In: Rohdendorf, B. B. (Ed.): Fundamentals of Paleontology, **9**: 213-215. – Washington, D.C. (Smithsonian Institution Libraries & The National Science Foundation).

Millot, J. (1949): Ordre des Palpigrades. – In: Grassé, P.-P. (Ed.): Traité de Zoologie, Tome VI, p. 520-532; Paris (Masson).

Nel, A., Azar, D., Martínez-Delclòs, X. & Makhoul, E. (2004): A new Upper Cretaceous species of *Chresmoda* from Lebanon – a latest representative of Chresmodidae (Insecta: Polyneoptera inc. sed.): first record of homeotic mutations in the fossil record of insects. – European Journal of Entomology, **101** (1): 145-151.

Nel, A., Delclòs, X., Béthoux, O. & Azar, D. (2005): *Chresmoda,* an enigmatic Mesozoic insect that is finally placed. – 3rd International Congress of Palaeoentomology (FossilsX3) Abstracts, Pretoria, South Africa: 48.

Nel, A., Marchal-Papier, F., Béthoux, O. & Gall, J.-C. (2004): A "stick insect-like" from the Triassic of the Vosges (France) (Insecta: "pre-Tertiary Phasmatodea"). – Annales de la Société Entomologique de France, **40** (1): 31-36.

Nel, A. & Popov, Y. A. (2000): The oldest known fossil Hydrometridae from the Lower Cretaceous of Brazil (Heteroptera: Gerromorpha). – Journal of Natural History, **34** (12): 2315-2322.

Oppenheim, P. (1888): Die Insectenwelt des lithographischen Schiefers in Bayern. – Palaeontographica, **34**: 215-247.

Pantel, J. (1917): A propósito de un *Anisolabis* alado. Contribución al estudio de los órganos voladores y de los esclerites torácicos en los Dermápteros; datos para la interpretación del macropterismo excepcional. – Memorias de la Real Academia de Ciencias y Artes de Barcelona, (3), **14** (1): 1-160.

Perrichot V., Nel, A. & Neraudeau, D. (2005): Gerromorphan bugs in Early Cretaceous French amber (Insecta: Heteroptera): first representatives of Gerridae and their phylogenetic and palaeoecological implications. – Cretaceous Research, **26** (5): 793-800.

Petrunkevitch, A. I. (1949): A study of Palaeozoic Arachnida. – Transactions of the Connecticut Academy of Arts and Sciences, **37**: 69-315.

– (1953): Paleozoic and Mesozoic Arachnida of Europe. – Memoirs of the Geological Society of America, **53**: 1-128.

– (1955): Arachnida. – In: Moore, R. C. (Ed.): Treatise on Invertebrate Palaeontology, Part P, Arthropoda 2, p. 42-162; Lawrence (Geological Society of America & University of Kansas Press).

Ponomarenko, A. G. (1985): Fossil insects from the Tithonian "Solnhofener Plattenkalke" in the Museum of Natural History, Vienna. – Annalen des Naturhistorischen Museums in Wien, **87A**: 135-144.

Ponomarenko, A. G. (1986): Scarabaeiformes *incertae sedis*. – In: Rasnitsyn, A. P. (Ed.): Nasekomye v rannemelovykh ekosistemakh Zapadonoy Mongolii [Insects in the Early Cretaceous Ecosystems of West Mongolia.] – Trudy Sovmestnaya Sovetsko-Mongol'skaya Paleontologicheskaya Ehkspeditsiya, **28**: 110-112.

Popov, Y. A. (1980): Superorder Cimicidea Laicharting, 1781. Order Cimicina Laicharting, 1781. – In: Rohdendorf, B. B. & Rasnitsyn, A. P. (Eds.): Historical development of the class of insects. – Trudy Paleontologicheskogo Instituta, Akademiya Nauk S.S.S.R., **175**: 58-69.

Rähle, W. (1970): Untersuchungen an Kopf und Prothorax von *Embia ramburi* Rimsky-Korsakov 1906 (Embioptera, Embiidae). – Zoologische Jahrbücher (Anatomie), **87**: 248-330.

Ragge, D. R. (1955): The wing-venation of the order Phasmida. – Transactions of the Royal Entomological Society, London, **106** (9): 375-392.

Rasnitsyn, A. P. & Quicke, D. L. J. (2002): History of Insects. – xii + 517 pp.; Dordrecht (Kluwer).

Rauskolb, C. (2001): The establishment of segmentation in the *Drosophila* leg. – Development, **128**: 4511-4521.

Rauskolb, C. & Irvine, K. D. (1999): Notch-mediated segmentation and growth control of the *Drosophila* leg. – Developmental Biology, **210**: 339-350.

Rees, P. M., Noto, C. R., Parrish, J. M. & Parrish, J. T. (2004): Late Jurassic Climates, Vegetation, and Dinosaur Distributions. – Journal of Geology, **112**: 643-653.

Rees, P. M., Ziegler, A. M. & Valdes, P. J. (2000): Jurassic phytogeography and climates: new data and model comparisons. – In: Huber, B. T., MacLeod, K. G., Paul, C. R. C. (Eds.): The adequacy of the fossil record, p. 133-163; New York (Wiley).

Roewer, C. F. (1934): Solifugae, Palpigradi. – In: Bronn, H. G. (Ed.): Klassen und Ordnung des Tierreichs, Vol. 5, 4 (4): 609-723; Leipzig (Akademische Verlagsgesellschaft).

Rowland, J. M. & Sissom, W. D. (1980): Report on a fossil palpigrade from the Tertiary of Arizona, and a review of the morphology and systematics of the order (Arachnida, Palpigradida). – Journal of Arachnology, **8**: 69-86.

Royer, D. L., Berner, R. A., Montañez, I. P., Tabor, N. J. & Beerling, D. J. (2004): CO_2 as a primary driver of Phanerozoic climate. – GSA Today, **14** (3): 4-10.

Savory, T. H. (1971): Evolution in the Arachnida. – 42 pp.; Watford (Merrow Monographs).

Selden, P. A. (1993a): Fossil arachnids – Recent advances and future prospects. – Memoirs of the Queensland Museum, **33**: 389-400.

– (1993b): Arthropoda (Aglaspidida, Pycnogonida and Chelicerata). – In: Benton, M. J. (Ed.): The Fossil Record, 2: 297-320; London (Chapman & Hall).

Sellwood, B. W., Valdes, P. J. & Price, G. D. (2000): Geological evaluation of multiple GCM simulations of Late Jurassic palaeoclimate. – Palaeogeography, Palaeoclimatology, Palaeoecology, **156**: 147-160.

Sharov, A. G. (1968): Filogeniya ortopteroidnykh nasekomykh. – Trudy Paleontologicheskogo Instituta, Akademiya Nauk S.S.S.R., **118**: 1-216, Moskva. [in Russian, Translated in English in 1971: Phylogeny of the Orthopteroidea. Israel program for scientific translations, Keter Press, Jerusalem: 1-251.]

Stone, G. & French, V. (2003): Evolution: have wings come, gone and come again? – Current Biology, **13**: R436-R438.

Tajika, F. (1998): Climate change during the last 150 million years: Reconstruction from a carbon cycle model. – Earth and Planetary Science Letters, **160**: 695-707.

Terry, M. D. & Whiting, M. F. (2005): Mantophasmatodea and phylogeny of the lower neopterous insects. – Cladistics, **21**: 240-257.

Thorell, T. (1888): Pedipalpi e Scorpioni dell Arcipelago Malese. – Annali del Museo Civico di Storia Naturale di Genova, Series 2, **26**: 327-428.

Tilgner, E. (2001): The fossil record of Phasmida (Insecta: Neoptera). – Insect Systematics and Evolution, **31** (4): 473-480.

Tilgner, E., Kiselyova, T. G. & McHugh, J. V. (1999): A morphological study of *Timema cristinae* Vickery. Implications for the phylogenetics of Phasmida. – Deutsche Entomologische Zeitschrift, **46** (2): 149-162.

Tillyard, R. J. (1918): Mesozoic insects from Queensland. 3. Odonata and Protodonata. – Proceedings of the Linnean Society of New South Wales, **43**: 417-435.

Trueman, J. W. H., Pfeil, B. E., Kelchner, S. A. & Yeates, D. K. (2004): Did stick insects *really* regain their wings? – Systematic Entomology, **29** (2): 138-139.

Veizer, J., Godderis, Y. & François, L. M. (2000): Evidence for decoupling of atmospheric CO_2 and global climate during the Phanerozoic eon. – Nature, **408**: 698-701.

Vishniakova, V. N. (1980): Order Phasmatida. – In: Rohdendorf, B. B. & Rasnitsyn, A. P. (Eds.): Istoricheskoe rasvitie klassa nasekomukh [Historical development of the class Insecta], pp. 171-173. – Trudy Paleontologicheskogo Instituta Akademii nauk SSSR, **175**: 269 pp. [In Russian]

Wedmann, S., Bradler, S. & Rust, J. (2007): The first fossil leaf insect: 47 million years of specialized cryptic morphology and behavior. – Proceedings of the National Academy of Sciences of the USA, **104** (2): 565-569.

Weyenbergh, H. (1869): Sur les Insects Fossiles du Calcaire Lithographique de la Bavière, qui se trouvent au Musée Teyler. – Extraits des Archives du Musée Teyler, Tome II, 48 pp.; Harlem.

– (1874): Varia zoological et paleontologica. – Periodico zoologico, Sociedad entomologica Argentina, **1**: 77-111.

Wheeler, W. C., Whiting, M., Wheeler, Q. D. & Carpenter, J. M. (2001): The phylogeny of the extant hexapod orders. – Cladistics, **17**: 113-169 + 404 (erratum).

Whiting, M. F., Bradler, S. & Maxwell, T. (2003): Loss and recovery of wings in stick insects. – Nature, **421**: 264-267.

Whiting, M. F. & Whiting, A. S. (2004): Is wing recurrence *really* impossible?: a reply to Trueman et al. – Systematic Entomology, **29** (2): 140-141.

WILLMANN, R. (2003): Die phylogenetischen Beziehungen der Insecta: Offene Fragen und Probleme. – Verhandlungen Westdeutscher Entomologentag, **2001**: 1-64.

ZOMPRO, O. (2001): The Phasmatodea and *Raptophasma* n. gen., Orthoptera *incertae sedis*, in Baltic amber (Insecta: Orthoptera). – Mitteilungen aus dem Geologisch-Paläontologischen Institut der Universität Hamburg, **85**: 229-261.

– (2004): Review of the genera of the Areolatae, including the status of *Timema* and *Agathemera* (Insecta, Phasmatodea). – Abhandlungen des Naturwissenschaftlichen Vereins in Hamburg, (N.F.), **37**: 327 pp.

– (2005): Inter- and intra-ordinal relationships of the Mantophasmatodea, with comments on the phylogeny of polyneopteran orders (Insecta: Polyneoptera). – Mitteilungen aus dem Geologisch-Paläontologischen Institut der Universität Hamburg, **89**: 85-116.

Manuscript received: September 21st, 2007.
Revised version accepted by the Stuttgart editor: December 14th, 2007.

Addresses of the authors:

Dr. X. DELCLÒS (to whom reprint requests should be addressed), Departament Estratigrafia, Paleontologia i Geociències marines, Faculty of Geology, 08028 Barcelona, Spain;
e-mail: xdelclos@ub.edu

Dr. A. NEL, CNRS UMR 5202, CP 50, Entomologie, Muséum National d'Histoire Naturelle, Paris, France;
e-mail : anel@mnhn.fr

Dr. D. AZAR, Department of Biology, Faculty of Sciences II, Lebanese Univ., Fanar-Matn, Lebanon;
e-mail: azar@mnhn.fr

Dr. G. BECHLY, Staatliches Museum für Naturkunde Stuttgart, Rosenstein 1, D-70191 Stuttgart, Germany;
e-mail: bechly.smns@naturkundemuseum.bw.de

Dr. J. A. DUNLOP, Museum für Naturkunde der Humboldt-Universität zu Berlin, D-10115, Berlin, Germany;
e-mail: jason.dunlop@museum.hu-berlin.de

Dr. M. S. ENGEL, Division of Invertebrate Zoology, American Museum of Natural History, Central Park West at 79th Street, New York, NY 10024-5192, and Division of Entomology (Paleoentomology), Natural History Museum, and Department of Ecology & Evolutionary Biology, 1501 Crestline Drive – Suite 140, University of Kansas, Lawrence, KS 66049-2811, USA;
e-mail: msengel@ku.edu

S. W. HEADS, Palaeobiology Research Group, School of Earth and Environmental Sciences, University of Portsmouth, Burnaby Road, Portmsouth PO1 3QL, United Kingdom;
e-mail: sam.heads@port.ac.uk