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A New Rock Crawler in Baltic Amber, with Comments on the Order (Mantophasmatodea: Mantophasmatidae)

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ABSTRACT

A new fossil species of the recently described insect order Mantophasmatodea (Polyneoptera: Anartioptera), the “African rock crawlers”, is described and figured from Eocene (Lutetian) Baltic amber. *Adicophasma spinosa*, new genus and species, differs from the only other fossil of this lineage, *Raptophasma*, by the strong spination of the fore- and midlegs, broad abdominal segments, and absence of dorsal carinae on the profemur, resembling in these respects the living African genera *Mantophasma* and *Praedatophasma*. The position of the fossil and of the order among polyneopterous insects is briefly discussed.

INTRODUCTION

The announcement of a new Recent insect order has stirred renewed excitement among entomologists (Klass et al., 2002, 2003; Benenbaum, 2002; Devetak, 2002; Hansen, 2002; Hall, 2002; Chen et al., 2002; Adis et al., 2002; Anonymous, 2003). The order Mantophasmatodea, or African rock crawlers, consists of 14 previously described species in 11 genera (Klass et al., 2002, 2003; Zompro et al., 2002, in press). Ten of these genera occur in sub-Saharan Africa, while the 11th, *Raptophasma*, is known only from mid-Eocene Baltic amber (table 1). Rightly so, the proposal of this new order has stirred debate among entomologists (e.g., Tilgner, 2002; Hamilton, 2003). Indeed, the cohort Polyneoptera includes insects differing dramatically in their morphology and biology, perhaps more so than any other superordinal clade, and this ancient group is today represented by numerous autapomorphic orders with little apparent affinity with one another, like Dermaptera (earwigs) and Grylloblattodea (rock or ice crawlers). The Mantophasmatodea have already been contended to belong within the Orthoptera (Tilgner, 2002), rather than forming a sister group to one of the other lineages. Arillo et al. (1997) recorded the first individual of the order in Baltic amber, but relationships were obscure and it was not until the discovery of Recent species that the phylogenetic affinities of the fossils were clarified (Klass et al., 2002). The order is characterized most notably by the apomorphic absence (loss) of ocelli (although see description of new fossil, below), epistomal sulcus (with the subgenal sulcus looping from the posterior mandibular articulation to the anterior tentorial pit and back to the anterior mandibular articulation), and wings; and by the hypognathous head cap-

sule, enlarged pretarsal arolium with a ventral series of elongate setae (in modern species), presence of a vomer-like process articulating on the apical margin of the tenth sternum (termed “vomeroid” by Klass et al., 2003), and unsegmented cerci (clasping in males; see also Klass et al., 2003).

Herein we present the description of a second species of this order from Lutetian-aged Baltic amber (ca. 45 Ma) and provide some general commentary on the order Mantophasmatodea as a whole. Measurements were made using an ocular micrometer and photomicrographs were prepared using a Microptics ML-1000 digital imaging system.

SYSTEMATIC PALEONTOLOGY

Adicophasma, new genus

TYPE SPECIES: *Adicophasma spinosa*, new species.

DIAGNOSIS: The new species is immediately recognizable by the strong spination of the fore- and midlegs. In this respect *A. spinosa* is apparently more closely related to the living genera *Mantophasma* and *Praedatophasma* than it is to the other “African” rock crawler in Baltic amber, that is, *R. kernegeri*. However, unlike *Mantophasma*, *A. spinosa* has the plesiomorphic retention of enlarged compound eyes which occupy most of the lateral surface of the head, lacks stout spines on the nota, and lacks a row of elongate setae on the ventral surface of the arolium (the latter character erroneously considered an apomorphy for the entire order by Klass et al., 2002). The new genus has spines of the legs more stoutly developed than those seen in *Praedatophasma*, the vertex relatively flattened between the compound eyes (convex in *Praedatophasma*), a transverse head (rounded in *Praedatophasma*), and lacks the spine between the antennae. *Adi-*

TABLE 1
Hierarchical Classification of “African” Rock Crawlers (Mantophasmatodea)

Family AUSTROPHASMATIDAE	Klass, Picker, Damgaard, van Noort, Tojo	
Genus <i>Austrophasma</i>	Klass, Picker, Damgaard, van Noort, Tojo	
	<i>Austrophasma caledonensis</i> Klass, Picker, Damgaard, van Noort, Tojo	South Africa
	<i>Austrophasma gansbaaiensis</i> Klass, Picker, Damgaard, van Noort, Tojo	South Africa
	<i>Austrophasma rawsonvillensis</i> Klass, Picker, Damgaard, van Noort, Tojo	South Africa
Genus <i>Hemilobophasma</i>	Klass, Picker, Damgaard, van Noort, Tojo	
	<i>Hemilobophasma montaguensis</i> Klass, Picker, Damgaard, van Noort, Tojo	South Africa
Genus <i>Karoophasma</i>	Klass, Picker, Damgaard, van Noort, Tojo	
	<i>Karoophasma biedouwensis</i> Klass, Picker, Damgaard, van Noort, Tojo	South Africa
	<i>Karoophasma botterkloofensis</i> Klass, Picker, Damgaard, van Noort, Tojo	South Africa
Genus <i>Lobophasma</i>	Klass, Picker, Damgaard, van Noort, Tojo	
	<i>Lobophasma redelinghuysensis</i> Klass, Picker, Damgaard, van Noort, Tojo	South Africa
Genus <i>Namaquaphasma</i>	Klass, Picker, Damgaard, van Noort, Tojo	
	<i>Namaquaphasma ookiepensis</i> Klass, Picker, Damgaard, van Noort, Tojo	South Africa
Family MANTOPHASMATIDAE	Zompro, Klass, Kristensen, Adis	
Genus <i>Mantophasma</i>	Zompro, Klass, Kristensen, Adis	
	<i>Mantophasma zephyra</i> Zompro, Klass, Kristensen, Adis	Namibia
Genus <i>Sclerophasma</i>	Klass, Picker, Damgaard, van Noort, Tojo	
	<i>Sclerophasma paretensis</i> Klass, Picker, Damgaard, van Noort, Tojo	Namibia
Genus <i>Tyrannophasma</i>	Zompro, <i>nomen nudum</i> ^a	
	<i>Tyrannophasma gladiator</i> Zompro, <i>nomen nudum</i> ^a	Namibia
Family TANZANIOPHASMATIDAE	Klass, Picker, Damgaard, van Noort, Tojo	
Genus <i>Tanzaniophasma</i>	Klass, Picker, Damgaard, van Noort, Tojo	
	<i>Tanzaniophasma subsolana</i> (Zompro, Klass, Kristensen, Adis)	Tanzania
Family Incertae Sedis		
Genus † <i>Adicophasma</i>	n.gen.	
	† <i>Adicophasma spinosa</i> , n.sp.	Baltic amber
Genus <i>Praedatophasma</i>	Zompro and Adis	
	<i>Praedatophasma maraisi</i> Zompro and Adis	Namibia
Genus † <i>Raptophasma</i>	Zompro [= Raptophasmatidae Janzen, 2002, <i>nomen nudum</i> ^b]	
	† <i>Raptophasma kerneggeri</i> Zompro	Baltic amber

† Fossil taxon.

^a These names were first introduced as *nomina nuda* in Dallai et al. (2003) and in Walker (2003) before eventually being made available in Zompro et al. (in press).

^b This name did not include a description or indication that it was proposed as new as now required for all family-group names proposed after 1999 (ICZN, 1999: Arts. 16.1, 16.2). The genus may be sister to all other Mantophasmatodea owing to the absence of tibial spines, a notable plesiomorphy. If this phylogenetic position can be confirmed and any autapomorphies for *Raptophasma* discovered, then Raptophasmatidae may in the future be validated for this taxon (for now it seems unwise to do so).

cophasma further differs from *Raptophasma* by the broad abdomen and absence of dorsal carinae on the profemur. As in the living genera, the course of the subgenal sulcus is unique and arches from the posterior mandibular articulation to the anterior tentorial pit (positioned near the compound eye in *Adicophasma*) before curving back to the an-

terior mandibular articulation (unobserved but presumed present in *Raptophasma*).

ETYMOLOGY: The new genus-group name is a combination of the Greek words *adikos* (meaning “injurious”) and *phasma* (meaning “spirit”). We have chosen not to base the name on *Raptophasma* or *Praedatophasma* since these names are an incorrect combina-

tion of Latin (*raptus*, meaning “seize”, or *praedatus*, meaning “pillage”) and Greek. The new name is feminine.

Adicophasma spinosa, new species

Figures 1–4

Raptophasma kerneggeri Zompro, 2001: 257.
[misidentification of paratype]

DIAGNOSIS: As for the genus (see above).

DESCRIPTION: **Female:** Total body length (excluding antennae) 5.80 mm. Coloration uniformly light brown (figs. 1–2). Maxilla of plesiomorphic orthopteroid form; maxillary palpus five-segmented, basalmost segment smallest, slightly shorter than second segment; third, fourth, and fifth maxillary palpal segments elongate and progressively more slender from base to apex, fifth segment longest; third and fourth segments subequal in length; fifth segment slightly longer than fourth segment, with distinct setae scattered over surfaces; stipes broad, with a few setae; galea apparently with minute fringe of setae at apex, with some short ventral setae; lacinia strongly sclerotized and toothed; two strong spines at apex of cardo (fig. 3). Labium of plesiomorphic orthopteroid construction; labial palpus four-segmented, basalmost segment quadrate and robust; second segment elongate; third segment slightly shorter than second; fourth segment slightly longer than second, with minute fringe of setae at apex, otherwise with scattered, short, simple setae; paraglossa large, with numerous setae; glossa not evident, apparently shorter and hidden by paraglossae. Labrum impunctate, with extensive, faint imbrications, without setae over most of surface; those few setae present simple, sparse, and generally restricted to or near margins; labrum rectangular (width slightly greater than length), apical margin gently convex over entire border except with broad, medioapical extension. Malar space exceedingly short (fig. 4). Clypeus transverse, approximately 2.5 times wider than long, separated from remainder of head by exceedingly shallow depressed line (remnant of vestigial epistomal sulcus: fig. 4). Antennal socket just below facial midlength and near compound eye; sockets separated by about 3 times socket diameter; scape shorter than elongate pedicel; flagellomeres elongate and

with sparse setae (16 flagellomeres); F1 about as long as pedicel but distinctly more slender; distal five flagellomeres with setae that are distinctly less stiff, dense, and shorter than on more proximal flagellomeres. Face with sparse, simple setae; integument faintly imbricate, impunctate. Compound eyes large, extending entire length of head, encompassing almost entire lateral area of head; inner orbits converging below and weakly concave (fig. 4); compound eyes separated dorsally by distance approximately equal to compound eye length, separated ventrally by slightly more than one-half compound eye length; compound eye with a few, simple, short setae. Vertex straight as seen in facial view, with faint scarlike marks perhaps representing vestigial ocelli (fig. 4). Gena impunctate and faintly imbricate. Head transverse (fig. 4).

All podites with scattered long, simple setae except setae of coxae shorter. Procoxae with at least three stout, ventroanterior spines (fig. 3); protrochanter short; profemur noticeably swollen, without dorsal carinae, with two longitudinal rows of stout spines ventrally (distinct ventral surface formed between rows of spines: fig. 3), inner row with spines shorter and more numerous than those spines of outer row; inner surface of protibia with similar stiff, elongate, simple spines as well as more numerous, stout setae on outer surface; tarsus pentamerous, basal four tarsomeres with euplantulae, third tarsomere very weakly bilobed; fourth tarsomere somewhat bilobed so that origin of fifth tarsomere is slightly recessed, fifth tarsomere elongate and slender, bearing simple pretarsal claws and large, broad arolium, without rows of elongate setae (such setae present on arolium in living genera). Midlegs as described for forelegs except mesofemur not as swollen and with fewer stiff setae and spines. Hind legs relatively normal by comparison to pro- and mesothoracic legs (fig. 3), with scattered, simple, stout setae. Coxae elongate; pro- and mesotibiae slightly longer than respective femora; metatibia longer than tibiae of preceding segments.

Pronotum only slightly longer than wide, without setae; integument faintly imbricate and impunctate, narrower than head, about as wide as compound eye length; pronotum



Figs. 1–2. Holotype female of *Adicophasma spinosa*, new species (B-1025). 1. Ventral view. 2. Dorsal view.

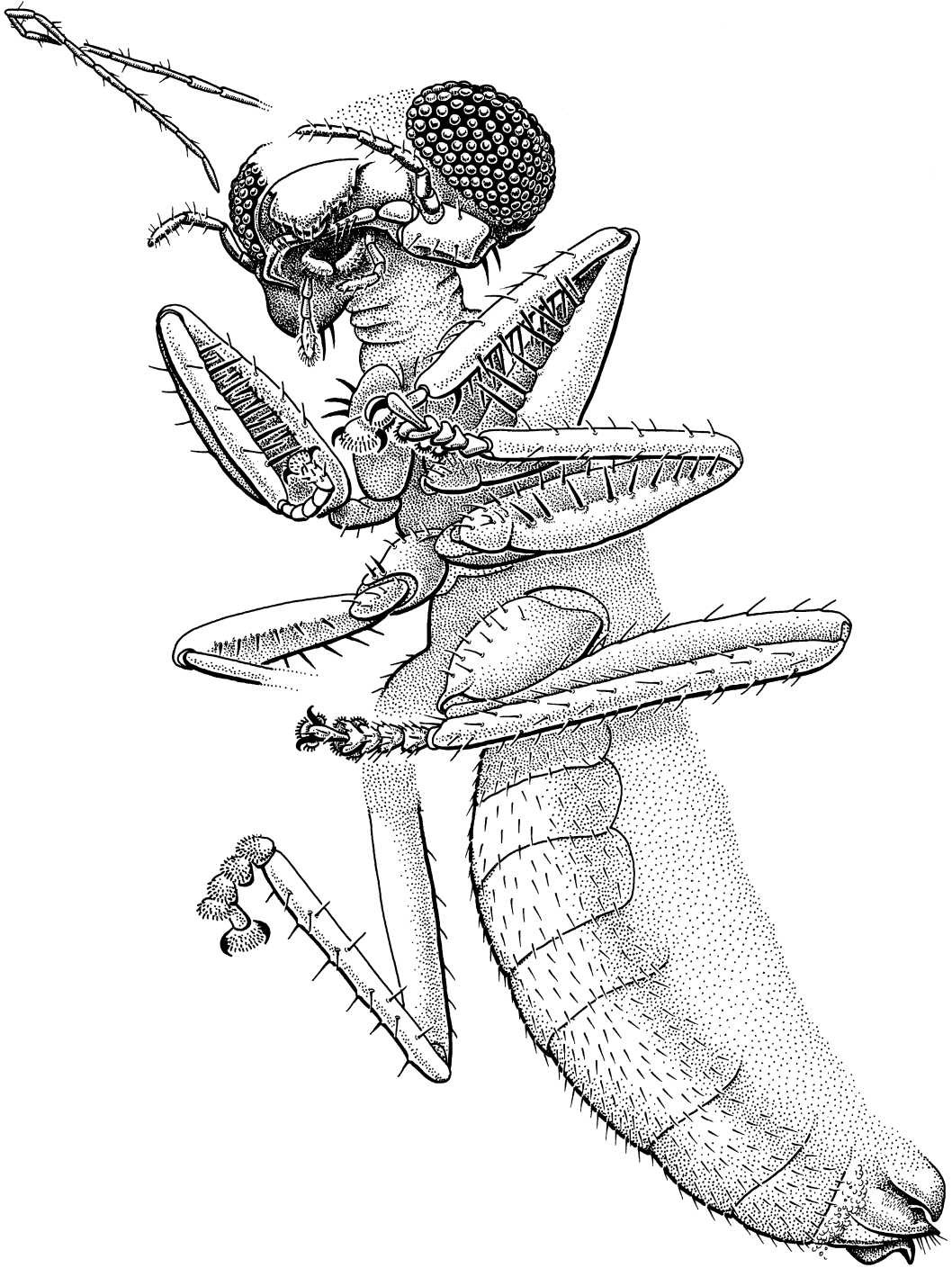


Fig. 3. Ventral illustration of holotype female of *Adicophasma spinosa*, new species (B-1025).

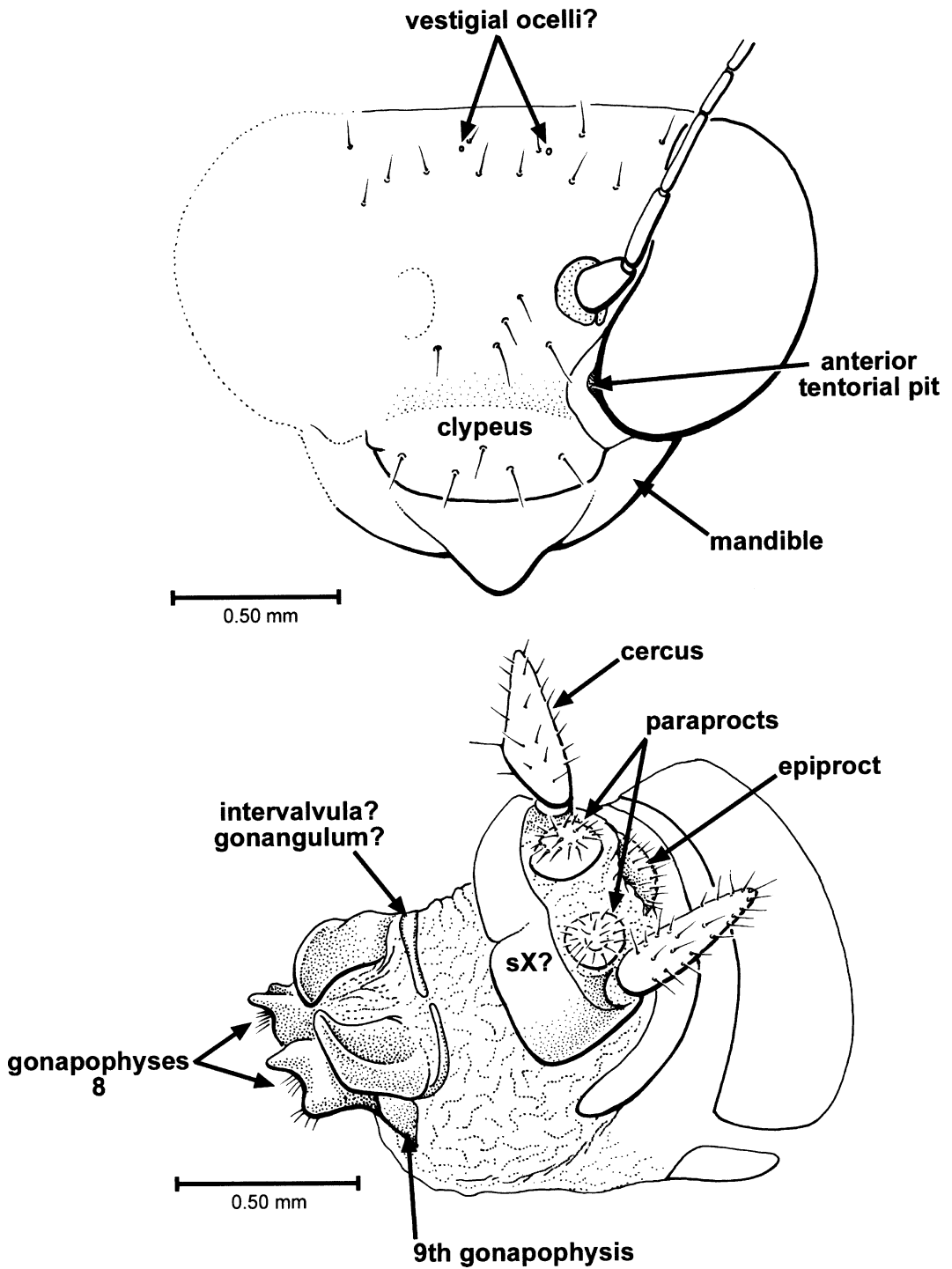


Fig. 4. Face and female terminalia of *Adicopasma spinosa*, new species (B-1025).

only slightly longer than mesonotum. Meso- and metanotum about equal in dimensions, each ca. 1.25 times wider than long; integument faintly imbricate and impunctate.

Abdomen ovoid, with short segments; width of first abdominal segment ca. 6 times length; width of second abdominal segment ca. 7 times length; width of third abdominal segment ca. 7.5 times length; widths of fourth and fifth abdominal segments each ca. 8.5 times length; width of sixth abdominal segment ca. 7 times length; margins of seventh abdominal segment obscured; integument (where observable) faintly imbricate and impunctate. Terga with sparse, erect, simple, setae of moderate length; sterna with such setae more numerous than those on terga. Cerci unsegmented, pointed at apices, longer than wide, with numerous elongate setae (fig. 4). Operculum absent, valvifers exposed (fig. 4).

HOLOTYPE: Female, BALTIC AMBER, *Blau Erde* (B-1025). Deposited in the Amber Collection, Division of Invertebrate Zoology, American Museum of Natural History.

ETYMOLOGY: The specific epithet refers to the stout spines of the fore- and midlegs (*L. spinosus*, meaning “thorny”).

KEY TO DESCRIBED MANTOPHASMATODEA IN BALTIC AMBER

1. Pro- and mesothoracic coxae, femora, and tibiae without spines; profemur with paired, longitudinal carinae dorsally; abdomen elongate and slender (genus *Raptophasma*) *R. kerneggeri* Zompro
- Pro- and mesothoracic coxae, femora, and tibiae with stout spines; profemur without dorsal carinae; abdomen broad (genus *Adicophasma*) *A. spinosa*, n. sp.

DISCUSSION

The first individual of Mantophasmatodea was recorded and described by Arillo et al. (1997) but left unnamed and unassigned as to order. Zompro (2001) subsequently described a series of specimens and named the fossils *R. kerneggeri*, considering them as Orthoptera *incertae sedis*, although he simultaneously provided the first “ordinal” name for the group, Raptophasmatodea. Based on the description, photograph, and drawing of Arillo et al. (1997), their fossil

could be a species of *Raptophasma*, perhaps *R. kerneggeri*.³ However, Arillo (personal commun.) indicates that the forelegs do indeed have spines similar to *Adicophasma* and that it may represent a second species of this genus (the pronotal and abdominal structure differing from *A. spinosa*). Certainly the Arillo et al. (1997) specimen is deserving of further study. The fossil described herein was attributed to and even designated as a paratype⁴ of *R. kerneggeri* (Zompro, 2001), despite its considerable differences. It may eventually prove that additional species of *Raptophasma* and *Adicophasma* also occur in Baltic amber.

The genus *Adicophasma* appears to be more closely related to the living genera *Mantophasma* and *Praedatophasma* (among others) than to *Raptophasma* owing to the spination on the forelegs, as well as elsewhere on the body. The absence of the row of elongate setae on the arolium would appear to exclude *Adicophasma* (and likely *Raptophasma*) from a clade of the living species. The enlarged compound eyes and transverse head are presumably plesiomorphic features shared with *Raptophasma* (and in the case of the eyes, with *Praedatophasma* as well).

It is not surprising to discover Baltic amber relatives of taxa today restricted to sub-Saharan Africa, as is the case with *Adicophasma* and *Raptophasma*. Indeed, this is a common biogeographic connection, with numerous lineages in Baltic amber surviving in southern Africa or Asia (e.g., Larsson, 1978, for summaries). Mantophasmatodea may have been relatively widespread, albeit not common, during the Paleogene, having perhaps experienced significant declines in diversity following the Eocene to arrive at the modern, isolated distributions of the known

³ The specimen reported by Arillo et al. (1997) was originally in the collection of J. Serafin (as noted in that publication) but has recently been acquired by the Museum of Natural Science of Alava, Vitoria, Spain and is accessioned as specimen MCNA10686 (Arillo, personal commun.).

⁴ The current specimen was purchased by the AMNH after the publication of Zompro (2001) and the individual is, therefore, not attributed to the AMNH in that paper. Instead, the AMNH specimen is referenced in Zompro (2001) as “[120]” and is the piece from A. Krylov.

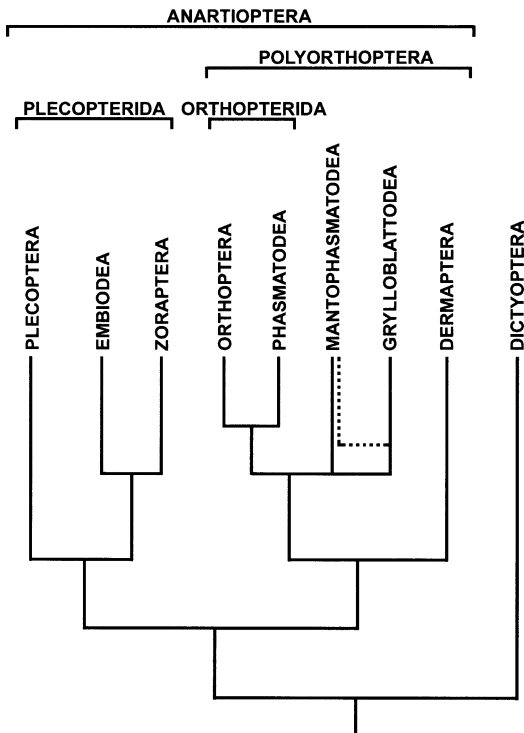


Fig. 5. Hypothesis of relationships among Recent orders of Polyneoptera (modified from Engel and Grimaldi, 2000); dashed lines indicate likely affinity of Mantophasmatodea with Grylloblattodea.

extant members. Although unlikely, Mantophasmatodea may eventually be discovered outside of Africa and species will almost certainly be recovered from other fossiliferous deposits elsewhere in the world.

Building upon the hypothesis of polyneopteran relationships outlined by Engel and Grimaldi (2000; fig. 5), the placement of Mantophasmatodea would indicate a relationship with the Orthopterida (i.e., Phasmatodea and Orthoptera; also the extinct †Titanoptera and †Caloneurodeae, not discussed further herein) within the Anartioptera (= Plecopterida + Orthopterida; fig. 5). The gonoplac is short in Mantophasmatodea but is sclerotized and more developed than the second valvulae. Thus, as in Orthopterida, the gonoplac may act as the functional ovipositor, suggesting a placement near that superordinal complex. Mantophasmatodea possess a vomer-like process on the apex of the

tenth sternum and therefore resemble Phasmatodea among Orthopterida. Dismissed as being nonhomologous with the vomer of Phasmatodea by Klass et al. (2002, 2003), owing to the articulation of this sclerite along its *posterior* margin to the tenth sternum (versus the anterior margin in Phasmatodea, and hence the reason it was termed a “vomeroid”), it is possible that there was an inversion and this rearrangement is merely autapomorphic for Mantophasmatodea. Such placement is intuitively pleasing owing to the superficial similarity of African rock crawlers to plesiomorphic Phasmatodea (i.e., *Timema*) and to possession of a “vomer” (sensu lato) in these orders. Unlike the stick insects, however, African rock crawlers lack a true operculum or micropylar plate in oöcytes but do possess a circular ridge reminiscent of an operculum (Klass et al., 2002). Tilgner (2002) indicated a possible placement of Mantophasmatidae near Proscopiidae in the Orthoptera (Caelifera); however, as noted by Klass (2002), the absence of striking orthopteran synapomorphies (e.g., cryptopleuron, jumping hind legs) and the synsclerotic conditions of the tarsi are not homologous (basal three tarsomeres completely fused to form a single subsegment of the podite in Orthoptera, united but still pentamerous and differentiated by distinct, dorsal grooves in Mantophasmatodea) would seem, for now, to exclude African rock crawlers from Caelifera. The assertion of a relationship between Mantophasmatodea and Mantodea based on sperm ultrastructure (Dallai et al., 2003) is not supported by any other characters, is based on an exceedingly small sampling of derived members of some polyneopteran orders, and includes characters which may be rampantly labile even within some of the lineages under consideration. The African rock crawlers are certainly not dictyopterans, despite the unfortunate similarity in the names of the two taxa considered.

Perhaps more striking is the similarity between Mantophasmatodea and the ice crawlers (i.e., Grylloblattodea). Both lineages share a similar configuration of sclerites in the proventriculus and the structure of the midgut caeca (Klass et al., 2002). In such a case, the African rock crawlers would be in

tantalizing Gondwanan juxtaposition to the Laurasian Grylloblattodea, analogous to the biogeographic split between the suborders of Plecoptera; i.e., Arctoperlaria and Antarcoperlaria (Zwick, 2000). At present there is little justification for a definitive placement of the Mantophasmatodea within Orthoptera near Phasmatodea or, more drastically, within Orthoptera.

Certainly new material of Mantophasmatodea, particularly more ancient fossils and molecular data, will provide improved insight into the phylogenetic placement of these insects. Already our knowledge of the distribution of these insects is expanding with new species and new records from South Africa (e.g., Pennisi, 2002; Picker et al., 2002; Klass et al., 2003), and the further description and study of these taxa will hopefully clarify the validity of the order and its placement in the greater context of polyneopteran insects. It would be very interesting to explore similar plants in Chile to see if mantophasmatodeans are lurking there. Should a Grylloblattodea + Mantophasmatodea clade exist, the two groups could be considered suborders of a single order (Grylloblattaria s.l. or Notoptera). Such a relationship would reflect an apparent Jurassic split between Gondwanan and Laurasian suborders of a single lineage, again analogous to that seen in Plecoptera.

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