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Rock Crawlers in Baltic Amber (Notoptera: Mantophasmatodea)

ANTONIO ARILLO[1] AND MICHAEL S. ENGEL[2]

ABSTRACT

A fourth species of rock crawler (Notoptera: Mantophasmatodea: Mantophasmatidae) is described and figured from an individual preserved in middle Eocene (Lutetian) Baltic amber. ***Adicophasma grylloblattoides*** Arillo and Engel, new species, is distinguished from its close relative, *A. spinosum* Engel and Grimaldi (reinstated), by the reduced pedicel, absence of spines on the maxillae, absence of mesofemoral spination, and proportions of the thoracic segments. The fossil shares with *A. spinosum* the presence of profemoral spination (confirmed by a new photograph of the holotype) and absence of the dorsal profemoral carina, characters that differentiate *Adicophasma* from the monotypic *Raptophasma*; it shares with all Baltic amber Notoptera the absence of the setal fan on the arolium. As noted by previous authors, the former order Mantophasmatodea is related to modern Grylloblattodea, whereas Mesozoic and Paleozoic grylloblattodeans represent a stem group to both. As such, Grylloblattodea and Mantophasmatodea are considered suborders of a single order, Notoptera Crampton (sensu novum), following the recommendation of Engel and Grimaldi (2004). The names for three rock crawlers are emended in order that the specific epithet may match the gender of the generic name: *A. spinosum*, *Mantophasma zephyrum* Zompro et al., and *Tanzaniophasma subsolanum* (Zompro et al.) (*nomina emendata*). Raptophasmatinae and Ensiferophasmatidae are new synonyms of Mantophasmatidae, while Tanzaniophasmatidae and Austrophasmatidae are newly demoted in rank to a subfamily and tribe of Mantophasmatidae, respectively. A hierarchical classification of Polyneoptera is appended.

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INTRODUCTION

The recent proposal of a new order of modern insects (Klass et al., 2002; Klass, 2004) has stirred a great deal of attention in entomology (e.g., Hall, 2002; Hansen, 2002; Anonymous, 2003; Walker, 2003) as well as controversy (e.g., Tilgner, 2002; Klass, 2002). The first mention of these insects appears to have been by Arillo et al. (1997), who provided the description of an enigmatic insect in Baltic amber, but did not name it. Understandably, Arillo et al. left the fossil unassigned as to order, discussing its apparent affinities to Phasmatodea and other lineages. Zompro (2001) later described, albeit inadequately, additional material that was clearly allied to Arillo et al.'s species, assigning the taxon to the then new genus *Raptophasma*.[3] Although Zompro (2001) formally considered *Raptophasma* as Orthoptera incertae sedis, he noted that the acquisition of modern species similar to the fossil indicated the possibility of distinct ordinal assignment and even provided a name for the group as Raptophasmatodea (thus, technically the Mantophasmatodea was not a new order in 2002 as it had already been named!). More recently, a third species was established and placed in a new, putatively basal family (Zompro, 2005).

Careful study of the modern material by Klaus-Dieter Klass revealed numerous additional characters, providing greater clarity into the affinities of the insects than was possible from the fossil material (Klass et al., 2002). At that time two Recent species were described and assigned to the genus *Mantophasma*, and the order was formally proposed (this time as Mantophasmatodea); the genus was described from species residing in Namibia and Tanzania (Klass et al., 2002; Zompro et al., 2002, 2004), but was shortly thereafter recorded from the Karoo in South Africa (Picker et al., 2002). Engel and Grimaldi (2004) described a second fossil of the order from Baltic amber, *Adicophasma spinosum* (see appendix 1), and discussed the phylogenetic affinities of the group as a whole. Klass et al. (2002) were inconclusive in regard to the affinities of the Mantophasmatodea, although they noted some similarities with the ice crawlers of the Northern Hemisphere (order Grylloblattodea). Engel and Grimaldi (2004) further elaborated upon the affinity of Mantophasmatodea and Grylloblattodea and even demonstrated the strong possibility that the two were sister groups. These same authors later further indicated that Paleozoic and Mesozoic "grylloblattodeans" represented stem groups to modern Mantophasmatodea + Grylloblattodea and that features such as the loss of wings and ocelli were, in fact, additional synapomorphies of the two "orders" (Grimaldi and Engel, 2005). Indeed, more recent molecular studies have further supported the phylogenetic relationship between Grylloblattodea and Mantophasmatodea[4] (Terry and Whiting, 2005). Following the recommendation of Engel and Grimaldi (2004) we here combine the Mantophasmatodea and Grylloblattodea into a single order, employing the name Notoptera as proposed by Crampton (1915) for the composite lineage. The classification of Notoptera is summarized in table 1 (a classification of Polyneoptera is briefly outlined in appendix 2).

Herein we provide a new and formal description of the "first" rock crawler (i.e.,

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[3] A re-examination and detailed descriptions of the various paratypes of *R. kerneggeri* should be undertaken to ascertain whether they have been correctly assigned or represent other species.

[4] Enigmatically Terry and Whiting (2005) stated that the molecular data supported the ordinal rank for Mantophasmatodea. The application of ranks is semantic and used as a reference point for relative inclusiveness of particular taxa. As such the data neither support nor refute the application of any particular rank for a taxon. The data simply indicate that modern Mantophasmatodea and Grylloblattodea (regardless of rank) are sister taxa. It is most conservative and rational, given that the Mesozoic and Paleozoic fossils are basal to the combined rock crawler and ice crawler clade, to consider these taxa as suborders of a single order encompassing the fossil and modern species (thereby avoiding the unnecessary proliferation of orders to accommodate the stem-group species). These same authors superfluously provided another name for this clade, Xenonomia, an unfortunate name that refers to the malformation of the subordinal names Mantophasmatodea and Grylloblattodea rather than any anatomical trait uniting the groups. As noted in the text, we follow the earlier proposals by Engel and Grimaldi (2004) and Grimaldi and Engel (2005) of expanding the far more apt name Notoptera for this order of insects and use the common name "crawler" ("rock crawlers" for the suborder Mantophasmatodea and "ice crawlers" for the suborder Grylloblattodea).

TABLE 1
Hierarchical Classification of Notoptera
(Interfamilial classification provided only for Mantophasmatodea)

ORDER NOTOPTERA CRAMPTON, 1915

- Family †Tillyardembiidae Zalessky, 1938
- Family †Blattogryllidae Rasnitsyn, 1976
- Suborder Grylloblattodea[1] Brues & Melander, 1932
  - Family Grylloblattidae Walker, 1914
- Suborder Mantophasmatodea Zompro et al. *In* Klass et al., 2002, stat. nov.
  - Family Mantophasmatidae[2] Zompro et al. *In* Klass et al., 2002
    - Genus †*Raptophasma* Zompro, 2001
    - Genus †*Adicophasma* Engel & Grimaldi, 2004
    - Genus †*Ensiferophasma* Zompro, 2005
    - Subfamily Tanzaniophasmatinae Klass et al., 2003, stat. nov.
      - Genus *Tanzaniophasma* Klass et al., 2003
    - Subfamily Mantophasmatinae Zompro et al. *In* Klass et al., 2002, stat. nov.
      - Tribe Tyrannophasmatini Zompro, 2005
        - Genus *Praedatophasma* Zompro & Adis *In* Zompro et al., 2002
        - Genus *Tyrannophasma* Zompro *In* Zompro et al., 2004
      - Tribe Mantophasmatini Zompro et al. *In* Klass et al., 2002, stat. nov.
        - Genus *Mantophasma* Zompro et al. *In* Klass et al., 2002
        - Genus *Sclerophasma* Klass et al., 2003
      - Tribe Austrophasmatini Klass et al., 2003, stat. nov.
        - Genus *Austrophasma* Klass et al., 2003
        - Genus *Hemilobophasma* Klass et al., 2003
        - Genus *Karoophasma* Klass et al., 2003
        - Genus *Lobophasma* Klass et al., 2003

[1] Brues and Melander (1915) originally considered this group at the ordinal rank but employed a superfamilial suffix (as Grylloblattoidea). These same authors later emended the name to Grylloblattodea, and we have used this subsequent date for the origin of the name.

[2] The usage of the family-group name Raptophasmatidae by Janzen (2002) is a nomen nudum (see also Engel and Grimaldi, 2004). The name was validated by Zompro (2005), but is herein newly synonymized, as it was based solely on plesiomorphies and is paraphyletic (see Comments).

the specimen studied by Arillo et al., 1997: fig. 1). The age and origin of Baltic amber is reviewed in Weitschat and Wichard (2002). The format for the description and morphological terminology follows that employed by Engel and Grimaldi (2004).

SYSTEMATIC PALEONTOLOGY

Adicophasma grylloblattoides, new species

figures 1–4

Diagnosis: The new species differs from its congener, *A. spinosum* Engel and Grimaldi (see appendix 1), by the shortened pedicel that is about as long as wide, the absence of mesofemoral spination, the absence of spines on the cardines, the proportions of the thoracic nota, and the more elongate abdomen (see also Key to Baltic Amber Notoptera, below).

Description: **Female.** Total body length (excluding antennae) 6.0 mm (additional metrics provided in Arillo et al., 1997). Coloration uniformly light brown. Head transverse. Face with sparse, simple setae; integument impunctate. Compound eyes large, extending entire length of head, encompassing almost entire lateral area of head; ommatidia small and numerous. Vertex straight. Gena impunctate. Malar space exceedingly short. Antennal socket apparently just below facial midlength and near compound eye; scape about equal in size to pedicel; pedicel about as long as wide; 16 flagellomeres elongate and with sparse setae. Maxillary palp five-segmented, basalmost palpomere smallest, approximately equal in

Fig. 1. Photomicrograph of holotype of ***Adicophasma grylloblattoides*** Arillo and Engel, new species (MCNA 10686).

size to second palpomere; third, fourth, and fifth maxillary palpomeres elongate; third palpomere longest; combined lengths of fourth and fifth palpomeres slightly longer than length of third palpomere; distinct setae scattered on apical palpomeres; stipes broad; cardo without spines. Coxae elongate; trochanters short; pro- and mesotibiae slightly longer than respective femora; metatibia longer than tibiae of preceding segments. Procoxa with three stout spines; profemur noticeably swollen, without dorsal carinae, with two longitudinal rows of stout spines ventrally (distinct ventral surface formed between rows of spines as in *A. spinosum*); inner surface of protibia with similar stiff, elongate, simple spines as well as elongate setae on outer surface (figs. 2–4); tarsi pentamerous, basal four tarsomeres with euplantulae; tarsomere IV weakly bilobed such that origin of tarsomere V slightly recessed, tarsomere V elongate and slender, bearing simple pretarsal claws and large, broad arolium (fig. 4); arolium without fans of elongate setae. Middle and hind legs similar in construction and with sparsely scattered, simple setae; mesofemur not as swollen as profemur and lacking spination. Thoracic nota longer than wide and each of approximately equal length and width, with exceedingly sparse, simple setae; integument impunctate; thorax about as broad as posterior width of head; pronotum only slightly longer than mesonotum. Abdomen elongate with sides relatively

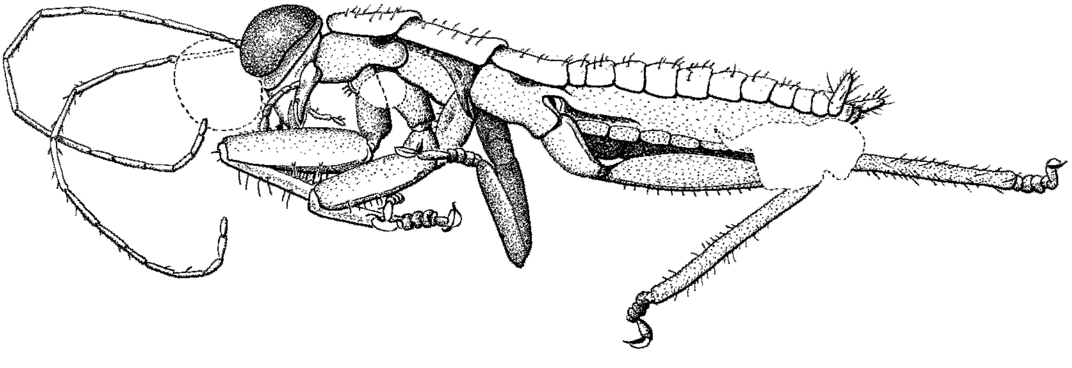

Fig. 2. Illustration of holotype of ***Adicophasma grylloblattoides*** Arillo and Engel, new species (MCNA 10686).

Fig. 3. Photomicrograph of holotype foreleg of ***Adicophasma grylloblattoides*** Arillo and Engel, new species (MCNA 10686).

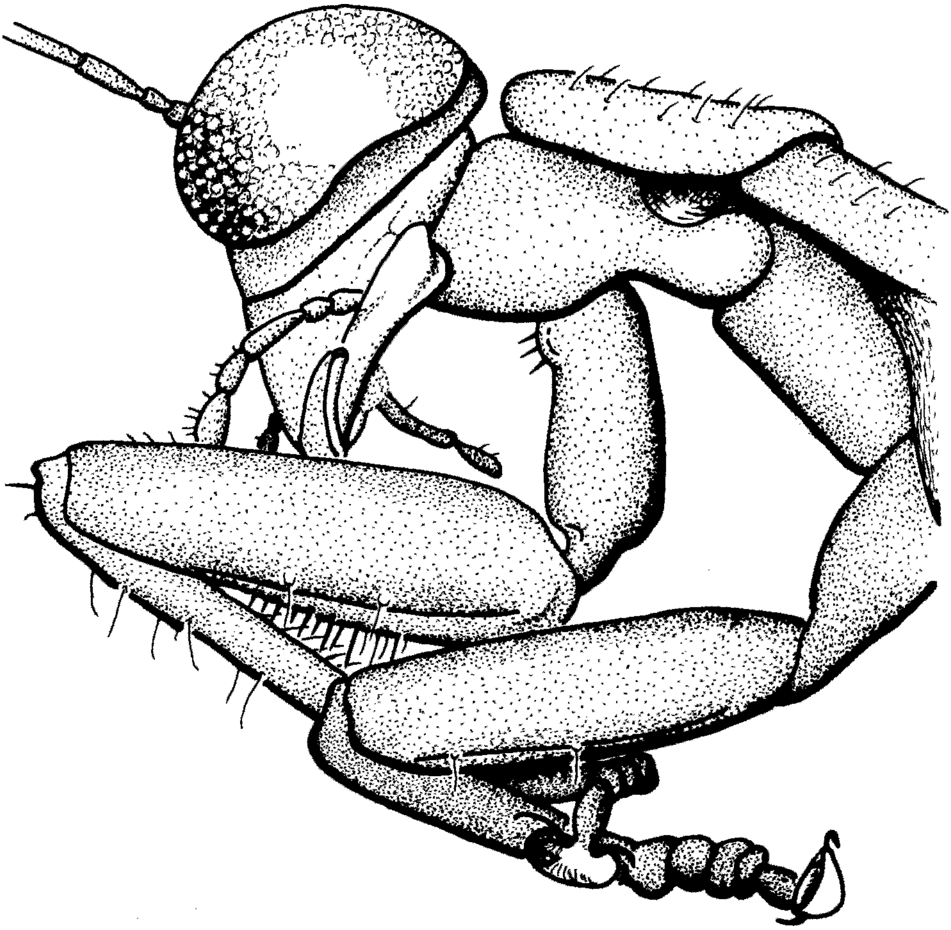

Fig. 4. Illustration of head and pro- and mesothoracic segments of ***Adicophasma grylloblattoides*** Arillo and Engel, new species (MCNA 10686).

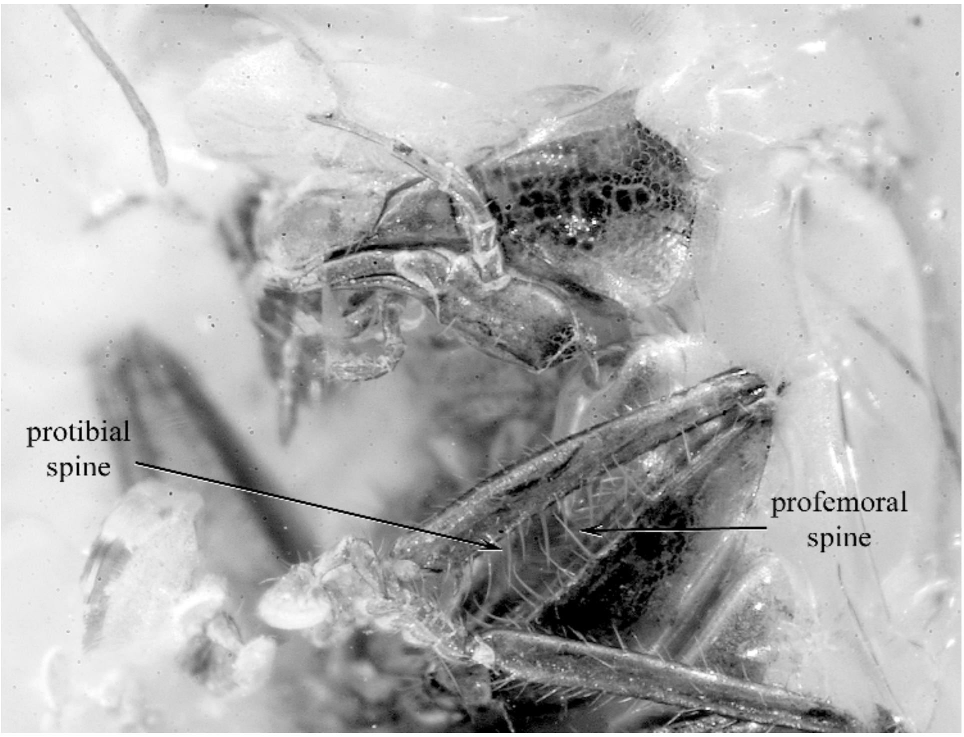

Fig. 5. Photomicrograph of holotype of *Adicophasma spinosum* Engel and Grimaldi showing detail of forelegs, particularly the presence of profemoral and protibial spination (similar, albeit shorter and less stout, spines are also present on the midlegs; see Engel and Grimaldi, 2004).

parallel, segments short, terga and sterna broader than long; terga and sterna with scattered, simple setae. Cerci short, unsegmented, gently tapering to apices, covered with numerous erect to suberect elongate setae.

Holotype: Female, Baltic amber (middle Eocene), MCNA 10686 (fig. 1), deposited in the Museo de Ciencias Naturales de Álava (Vitoria, Spain).

Etymology: The specific epithet is a reference to the similarity and phylogenetic affinity of rock crawlers to the ice crawlers (suborder Grylloblattodea).

Comments: The new species, like all fossil Notoptera, lack the setal fan on the arolium, a feature synapomorphic for the modern, African species of Mantophasmatodea. like *Raptophasma kerneggeri* Zompro the new species lacks mesofemoral spination but otherwise has all of the features of the genus *Adicophasma* as characterized by Engel and Grimaldi (2004).

Zompro (2005) considered the holotype of *A. spinosum* as a nymph solely on its smaller body size. However, *A. spinosum* has fully developed genitalia indicative of an adult and has numerous significant features distinguishing it from *R. kerneggeri* as noted in the original description (Engel and Grimaldi, 2004) and in the following key. Perhaps most notably the adult of *Raptophasma* is supposed to lack femoral spines, while they are exceptionally well developed in *Adicophasma*. Zompro's statement to the contrary is entirely erroneous as the photograph in Engel and Grimaldi (2004) was not taken in the focal plane of the legs, yet the out-of-focus spines on at least one leg can nonetheless be discerned; similar, albeit slightly weaker, spines are obvious on *A. grylloblattoides* (fig. 3). That the spines are indeed present in *A. spinosum* is evidenced by a new photograph of the holotype taken in the focal plane of the legs (fig. 5), demonstrating that statements as to the absence of these structures are meant to mislead. Nymphal forms of rock crawlers can have spines in the latest of nymphal stages, but only when such features are similarly present in the adult (i.e., the latest nymphal stages acquire adult-like femoral spination). Thus, even if the holotype of *A. spinosum* were a nymph (which the terminal structures indicate is not the case), it could scarcely be considered conspecific with *R. kerneggeri,* which is supposed to lack such features entirely in the adult stage [as evidenced by the fact that the adult holotype male lacks such characters, as do, apparently, the paratypes; since spines in at least one paratype were entirely overlooked (fig. 5), the series should be re-examined]. The same can be said for the dorsal profemoral carinae present in *R. kerneggeri* but lacking in *Adicophasma,* among other generic features (see Engel and Grimaldi, 2004). Most descriptions and figures of Baltic amber rock crawlers are inadequate (e.g., Zompro, 2001, 2005) as evidenced by the oversight of obvious features such as the presence/absence of femoral spination among paratypes and should not be relied upon. For more extensive descriptions and figures refer to Engel and Grimaldi (2004) and Grimaldi and Engel (2005). As the subfamily Raptophasmatinae and the family Ensiferophasmatidae are based entirely on plesiomorphies, they are herein newly synonymized with Mantophasmatidae (**new synonymies**). The Tyrannophasmatini is also suspicious and thus is only tentatively retained (table 1). Indeed, the recognition of multiple subfamilies or tribes within this remarkably small and relatively homogeneous family is unwarranted.

Key to Baltic Amber Notoptera

1. Compound eyes occupying major portion of head; antennae shorter than body; arolium projecting beyond pretarsal claws 2
– Compound eyes placed in posterior half of head; antennae several times longer than body; arolium not projecting beyond pretarsal claws (Genus *Ensiferophasma*) . . . . *E. velociraptor* Zompro
2. At least some femora with distinct, ventral spination; profemur without dorsal carinae (Genus *Adicophasma*). 3
– Femora without spination; profemur with paired, dorsal, longitudinal carinae (Genus *Raptophasma*) . . . . . *R. kerneggeri* Zompro
3. Mesofemur with distinct, ventral spination; pedicel elongate, at least three times longer than wide; cardo with two stout, apical spines; pronotum slightly longer than wide, meso- and metanota each wider than long; lateral margins of abdomen convex (i.e., abdomen roughly ovoid); compound eyes with large ommatidial facets (see Engel and Grimaldi, 2004) . . . . *A. spinosum* Engel and Grimaldi
– Mesofemur without ventral spination; pedicel short, about as long as wide; cardo without spines; all thoracic nota longer than wide and each of approximately equal size; abdomen elongate; compound eyes with smaller and more numerous ommatidial facets. . . . . *A. grylloblattoides,* n.sp.

DISCUSSION

The new species described herein attests to the as yet unstudied diversity of polyneopteran (particularly of the Orthopterida, sensu Grimaldi and Engel, 2005) insects in Tertiary ambers, even from those faunae as intensively studied as Baltic amber. In addition, the amber Notoptera further highlight the importance of fossils for understanding the phylogenetic relationships, biogeographic patterns, and other evolutionary phenomena of modern taxa. For example, the Tertiary amber Notoptera indicate that the suborder Mantophasmatodea is of bipolar distribution rather than a strictly Gondwanan group that might be a relic of the rifting of the southern continents. Indeed, the presence of such amber fossils indicates that the suborder Mantophasmatodea had a much wider distribution as recently as the middle Eocene, perhaps becoming extirpated from the Northern Hemisphere by the dramatic climatic shifts of the Eocene-Oligocene transition. It is probable that Mantophasmatodea survived not only in southern Africa but in southern South America and Asia as well. If the habitat preferences of the southern African species are any indication, then suitable environmental conditions may also be found in regions such as Chile or Argentina. Indeed, given that nymphs of rock crawlers may be generally mistaken for immature Orthoptera or

Phasmatodea, it is possible that the lineage may eventually be discovered outside of Africa. Similarly, rock crawlers may also be found in other fossiliferous ambers. It would be particularly exciting to discover such taxa in Cretaceous ambers as these would undoubtedly provide powerful insights on the early history of Mantophasmatodea and perhaps also their sister Grylloblattodea as they differentiated from stem-group families such as Blattogryllidae in the Jurassic or Early Cretaceous.

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APPENDIX 1

A NOMENCLATURAL NOTE

As we were rightly reminded by our colleague Dr. Bernd Hauser (Muséum d'histoire naturelle, Geneva), *Phasma* is of neuter gender in Greek, and accordingly those names based upon this generic stem should also be neuter (i.e., all of the currently recognized genus-group names in Mantophasmatodea). This correction in gender necessitates the emendation of several specific epithets for rock crawlers in order to bring the specific and generic names into alignment. The following emendations are thus required (in alphabetical order):

Adicophasma spinosum Engel and Grimaldi, *nomen emendatum*

Mantophasma zephyrum Zompro et al., *nomen emendatum*

Tanzaniophasma subsolanum (Zompro et al.), *nomen emendatum*

APPENDIX 2

Hierarchical Classification of Polyneoptera

The following table briefly summarizes the hierarchical classification of polyneopteran insects (details within the Dictyoptera are not outlined). Much work remains on the higher classification of this group and so changes are to be expected, particularly with respect to the various fossil lineages. For example Protorthoptera presently comprises taxa that are stem-group forms of various lineages across the Polyneoptera (e.g., many are stem-group Orthopterida, some stem-group Plecopterida, &c.). Similarly, older taxa such as Permoplecoptera, Protelytroptera (in part), and Aeroplanoptera are grades to modern lineages such as Plecoptera, Dermaptera, and Phasmatodea, respectively.

- Supercohort Polyneoptera Martynov
  - "†Protorthoptera" Handlirsch, *partim*
  - Cohort Dictyoptera Leach
  - Cohort Anartioptera Engel
    - Magnorder Polyplecoptera, *novum*
      - Superorder Plecopterida Boudreaux
        - "†Permoplecoptera" Martynov
        - Order Plecoptera Burmeister
        - Mirorder Mystroptera Engel
          - Order Zoraptera Silvestri
          - Order Embiodea Kusnezov
    - Magnorder Polyorthoptera Engel & Grimaldi
      - Superorder Dermapterida Boudreaux
        - "†Protelytroptera" Tillyard, *partim*
        - Order Dermaptera De Geer
      - Superorder Orthopterida Boudreaux
        - Grandorder Notopterodea, *novum*
          - Order Notoptera Crampton[a]
        - Grandorder Panorthoptera Crampton
          - *+various extinct stem group lineages*
          - Order †Glosselytrodea Martynov
          - Order †Caloneurodea Handlirsch
          - Order †Titanoptera Sharov
          - Order Orthoptera Olivier
          - Mirorder Holophasmatodea Grimaldi & Engel
            - "†Aeroplanoptera" Tillyard
            - Order Phasmatodea Brunner van Wattenwyl

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[a] The clade consisting of the suborders Mantophasmatodea and Grylloblattodea, excluding the stem-group families (e.g., Tillyardembiidae), is termed **Neonotoptera** Engel, *novum.*