

Mantophasmatodea: A New Insect Order with Extant Members in the Afrotropics

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A new insect order, Mantophasmatodea, is described on the basis of museum specimens of a new genus with two species: *Mantophasma zephyra* gen. et sp. nov. (one female from Namibia) and *M. subsolana* sp. nov. (one male from Tanzania). This is the first time since 1914 that a newly described extant insect taxon has proved unplaceable within a recognized order. Mantophasmatodeans are apterous carnivores. Their closest phylogenetic relationships may be to Grylloblattodea (ice-crawlers) and/or Phasmatodea (stick insects), but the morphological evidence is ambiguous. *Raptophasma* Zompro from Baltic amber is assigned to the Mantophasmatodea, demonstrating a wider previous range for the lineage.

All of the currently recognized orders of extant insects have been known throughout most of the 20th century. While several high-rank clades of marine animals have been discovered during the last fifty years, the numerous new insects described in that period have all been referable to known orders [with the possible exception of the apterygote *Tricholepidion gertschi* Wygodzinsky, 1961, whose assignment to the Zygentoma remains disputable (1–3)]. The recognized insect order based on the most recently discovered extant taxon is the Grylloblattodea (= Notoptera, ‘ice-crawlers’), the first of whose 26 presently known species was described in 1914. We here report the finding (4) of a new Afrotropical insect genus that cannot be placed within any recognized extant order, and whose phylogenetic relationships to extant or extinct orders remain unclarified. A new order is therefore established to accommodate these insects as well as *Raptophasma kerneggeri* Zompro, 2001 from Baltic amber, hitherto classified as ‘Orthoptera incertae sedis’.

Classification (5): Order Mantophasmatodea Zompro, Klass, Kristensen & Adis, ord. nov.. Family Mantophasmatidae Zompro, Klass, Kristensen & Adis, fam. nov.. Type genus: *Mantophasma* Zompro, Klass, Kristensen & Adis, gen. nov., with two species (extant), known from one ethanol-preserved female specimen (Fig. 1, B and C) and one dried, shriveled, teneral adult male specimen (Fig. 1A), respectively. Other included genus: *Raptophasma* Zompro, 2001, with one species (from Baltic amber).

Etymology: *Mantis* was the Linnean name for mantises (including stick insects), and *Phasma* a classical generic name in the stick insects; the name alludes to the superficial similarity of all the insects in question.

Order and family description (6): Development of the external genitalia indicates that both available specimens of *Mantophasma* are adults. Head hypognathous (Fig. 1, D to F) with generalized mouthparts. Mandibles only with 3 small

teeth in molar area. Palps 5- (maxillae) or 3-segmented (labium). Antennae long, filiform, multisegmented. Ocelli absent. Tentorium without perforation, anterior pit far above anterior mandibular articulation. Epistomal sulcus lacking. Subgenal sulcus with unusual course, extending from posterior mandibular articulation directly to anterior tentorial pit and thence downwards/backwards to anterior mandibular articulation (Fig. 1E). Head capsule posteroventrally closed by weak submentum (no gula).

Thorax with each tergum narrowly overlapping the following. Prothoracic pleuron large, fully exposed (Fig. 1F). Wings entirely lacking. Metathorax without spinal apodeme. Coxae elongate. Tarsi (Fig. 1, G and H) with 5 tarsomeres, 4 basal with euplantulae. 3 basal tarsomeres synscleritous, borders distinctly indicated by grooves. Dorsal membrane beyond 3rd tarsomere with triangular process (Fig. 1I). Pretarsal arolium very large, with row of long setae (Fig. 1J).

In abdomen, tergum I and coxosternum I distinct but short, both free from metathorax; coxosternum without midventral sac. Small spiracles I–VIII located in pleural membrane, with intrinsic occlusor and extrinsic (coxosternal) dilator muscle. Male: Coxosternum IX (Fig. 2A) not subdivided, forming subgenital lobe with median spatulate process; styli absent. Phallic region (Fig. 2, B and C) with membranous lobes around gonopore and transverse, medially asymmetrically produced sclerite articulating with anterolateral corners of tergum X. Cerci one-segmented, prominent, clasping, not forming differentiated articulation with tergum X. Female: Ovipositor projecting markedly beyond short subgenital lobe formed by coxosternum VIII (Fig. 2D). Gonoplags short, strongly sclerotized. Gonapophyses VIII markedly blunt distally. Gonapophyses IX largely fused with gonoplags; composite formation with ventral keel interlocking with dorsal groove on gonapophyses VIII. Gonangulum with usual 3 articulations. One-segmented cerci much shorter than in male.

Foregut with large proventricle (Fig. 2, E and F) armed with weak, papillose (Fig. 2, G and H) sclerites that terminate in three successive whorls of weakly sclerotized lobes. Midgut caeca a pair of short and wide lateral pouches; no pyriform appendices detected. Heart lacking lateral arteries in mid-abdomen. Abdomen with ventral diaphragm. Abdominal ganglion VII free from terminal ganglion (VIIIff). Egg lacking micropylar plate and (defined) operculum, but with circular ridge (Fig. 2, I and J); chorion with hexagonal pattern of grooves traversed by delicate bars (Fig. 2, K and L).

Genus and species descriptions: *Mantophasma* Zompro, Klass, Kristensen & Adis, gen. nov.: Eyes moderately sized, less high than gena. Fore-femora distinctly thickened, mid- and (particularly) hind-femora more slender. Fore- and mid-femora with ventral rows of short spines. Type species by

present designation: *Mantophasma zephyra* Zompro, Klass, Kristensen & Adis, sp. nov. Etymology: Latin for westwind. Holotype: Female (Fig. 1, B and C). Label data: D. S. W. Afr. [Namibia] S. G. Seewald 'JR. No. 827/09' [possibly meaning specimen 827 from 1909]. Museum für Naturkunde, Humboldt University, Berlin, Germany. Length (frons – epiproct apex) 22.5 mm. Colour (as preserved) uniformly light brown. Head (Fig. 1E) rounded, 3 low tubercles between antennae, no tubercle behind antennae, eyes weakly convex. Other included species: *Mantophasma subsolana* Zompro, Klass, Kristensen & Adis, sp. nov.. Etymology: Latin for eastwind. Holotype: Male (Fig. 1A). Label data: Tanganyika [Tanzania] Ufipa Dish, L. Kwela, 22.iii.1950, H. O. Backlund. Zoological Museum, University of Lund, Sweden. Length (frons – epiproct apex, specimen shrivelled) 17.5 mm. Colour light reddish brown with red spots. Head (Fig. 1D) distinctly angular in anterior view, 3 prominent tubercles between antennae, a small tubercle behind each antenna, eyes strongly convex. It cannot at present be categorically excluded that the *M. zephyra* and *M. subsolana* specimens are conspecific, since the small differences noted could reflect sexual dimorphism. But considering also the wide geographical separation of the findings we consider an assumption of conspecificity to be rasher than one of specific distinctness.

Raptophasma Zompro, 2001 from Baltic Eocene amber (7, 8) bears considerable phenetic similarity to *Mantophasma* and shares with it the apomorphic median projection on the male subgenital plate (Fig. 2A) and the small dorsal process beyond the 3rd tarsomere (Fig. 1, G to I); the arolium is also very similar in the two. *Raptophasma* differs from *Mantophasma* by its larger eyes (higher than gena) and stouter, spineless legs. While these Tertiary fossils can have no bearing on dating the origin of the mantophasmatodean stem lineage (which surely must be much older, since there are records of several lower neopteran orders from at least the Permian), they are zoogeographically significant as proof that the clade once also occurred in northern Europe.

Ordinal diagnostic characters: Mantophasmatodeans are phenetically 'orthopteroid' insects, but autapomorphies characterizing known orders in this assemblage ['Polyneoptera' or 'lower Neoptera'; (2, 9, 10)] are lacking. They differ from Phasmatodea (stick insects) by the hypognathous head, lack of prothoracic repellent glands (11), different composition of female subgenital lobe (12) which forms no large operculum (in Phasmatodea covering much of the ovipositor from below), separation between sternum thorax 3 and abdomen I, and lack of micropylar plate and operculum in eggs (13). They differ from Dictyoptera (mantis-cockroach-termite clade) by, e.g., the unperforated tentorium, lack of female subgenital lobe from coxosternum VII, coxosternal [rather than tergal (14, 15)] origins of abdominal spiracle dilator muscles, and discrete abdominal ganglion VII (15). They differ from Grylloblattodea and Dermaptera (earwigs) by hypognathous head; from the former also, e.g., by lack of metaspina (plesiomorphy or apomorphy?), lack of membranous sac on abdominal venter I, and presence of muscled closing devices of abdominal spiracles (16); from the latter also, e.g., by elongate coxae and lack of female subgenital lobe from coxosternum VII. While wingless and non-jumping Orthoptera (grasshoppers and their relatives) can be modified almost beyond recognition, the large prothoracic pleuron unconcealed by pronotal lobes and the lack of an anterior intervalvula in the ovipositor exclude *Mantophasma* from this clade. The lack of longitudinal series

of denticles in the proventricle and the full number of tarsomeres (five) are incompatible with *Mantophasma* being subordinate in crown-group Ensifera or Caelifera (long- resp. short-horned grasshoppers). The well-developed ovipositor and discreteness of basal tarsomeres exclude *Mantophasma* from Plecoptera (stoneflies).

The small process beyond the 3rd tarsomere (Fig. 1, G to I) and the distinctive course of the subgenal suture (Fig. 1E; not known in *Raptophasma*) are putative autapomorphies of the Mantophasmatodea.

Ordinal relationships: Pterygota (winged insects) share the apomorphic absence of a non-cuticular trunk endoskeleton and of the lateral parts of abdominal tergum XI [epiproct remaining (17)]. Mantophasmatodea exhibit the same features, and the valve-like shape of the gonopods, their lack of styli, and the apodemes of the abdominal spiracles (17) suggest a position in the Pterygota-Neoptera. We have found no evidence for a close relationship of Mantophasmatodea to the Acercaria or Endopterygota. Some apomorphies of Mantophasmatodea are recurrent in various Neoptera, but are strongly homoplastic; these include, e.g., lack of epistomal sulcus, ocelli, and male styli, cutting mandibles, basal tarsomere immobilization, and one-segmented cerci. Evidence for the closest relationship being with Phasmatodea and/or Grylloblattodea appears to deserve particular attention, but it too is ambiguous.

The very large arolium of Mantophasmatodea (Fig. 1J) strikingly resembles that in the basal phasmatodean *Timema* (11). However, arolia are smaller in other stick insects, hence the enlargement may not be the ordinal groundplan state. *Mantophasma* (Fig. 2E) and Grylloblattodea (18) display a similar configuration of sclerites and lobes in the proventricle, but the ambiguous identification of the lobes as teeth or pulvilli (19) and homoplasies in the insect proventricle armature hamper conclusions. If the lobes are pulvilli, as indicated by their far posterior position, the complete lack of teeth in front of them is apomorphic. If the lobes are the 'teeth', as suggested by their shape, their far posterior position is apomorphic. In both cases the occurrence of sizeable lobes upon plicae of 3 different ranks is apomorphic within insects. However, all these potentially apomorphic conditions are paralleled in other taxa. The condition of the midgut caeca is another possible synapomorphy of Mantophasmatodea and Grylloblattodea (18) but is paralleled in, e.g., many Ensifera. The produced transverse sclerite on segment X in male *Mantophasma* (Fig. 2, B and C) resembles the 'vomer' of Phasmatodea (11, 20). However, while in *Mantophasma* the morphologically posterior rim of the sclerite articulates with tergum X, in phasmids this is true for the anterior rim of the vomer sclerite. Also the Grylloblattodea have a process-bearing sclerite on venter X; it is, however, restricted to the right side (16).

The phylogenetic position of Mantophasmatodea thus remains unclear. A stronger hypothesis will perhaps emerge from anatomical and molecular study of the new material (21).

Bionomics: The gut contents of the first discovered museum specimens show the Mantophasmatodea to be carnivores: the midgut and proventricle of both specimens were filled with pieces of arthropod cuticle. As indicated by the rows of short spines along the fore- and midleg femora and tibiae prey is captured by means of these legs, as it is also done by some Orthoptera (22). The chorion structure suggests that the egg is capable of plastron respiration (23), as in many insects.

References and Notes

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4. In June 2001 Ms J. Marshall (Natural History Museum, London) showed O. Zompro a male insect from Tanzania, which had been submitted for an opinion 16 years ago. Shortly afterwards O. Zompro received from Mr F. Kernegger a male Baltic-amber insect (subsequently described as *Raptophasma kerneggeri*), whose close similarity to the Tanzania specimen was immediately obvious. In July 2001 O. Zompro discovered in the unsorted alcohol collection of Phasmatodea in the Museum für Naturkunde (Berlin) an adult female of a similar insect from Namibia.
5. According to one school of thought among contemporary systematists, naming of higher taxa, which only contain a single genus is “empty formalism”; we accept the logical merits of this stand. Pragmatically we believe, however, that any recognized genus should be assigned to a “family” and an “order”, because these categories play an important role in the way biologists communicate and biological knowledge is systematized.
6. The description includes many characters presently known only from a single specimen, because genitalic characters can only be observed in a specimen of the respective sex and muscle characters only in the ethanol-preserved female, and only few characters can be judged in the *Raptophasma* fossils.
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21. Since the completion of the work described here, additional (including live) material of further mantophasmatodean taxa has been observed and collected in Namibia by O. Zompro and colleagues during an international expedition supported by the Max-Planck-Institute for Limnology in Plön/Germany, the National Museum of Namibia in Windhoek/Namibia, and Conservation International in Washington, D.C./USA.
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24. We thank the Museum für Naturkunde, Humboldt-University, Berlin (M. Ohl, I. Dorandt), the Natural History Museum, London (J. Marshall), and the Zoological Museum, University of Lund (R. Danielsson) for assistance and permission to study the *Mantophasma* specimens. G. Brovad and R. Meier (Zoological Museum, Copenhagen) are appreciated for help in photographic documentation, and Prof. O. Kraus (Zoologisches Institut und Zoologisches Museum, Universität Hamburg), Prof. W. Dohle (Institut für Zoologie, Freie Universität Berlin), Prof. S. Golovatch (Russian Academy of Sciences, Moscow), Prof. H. Enghoff (Zoological Museum, Copenhagen), and Dr T. L. Erwin (Smithsonian Institution, Washington, D. C.) for comments on the manuscript. This publication is dedicated to Prof. W. J. Junk (MPI Limnologie Plön).

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Fig. 1. *Mantophasma* specimens and their heads and tarsi. (A) *M. subsolana*, male. (B and C) *M. zephyra*, female. (D) Anterior view of head of *M. subsolana*. (E) Same of *M. zephyra*. (F) Lateral view of head and prothorax of *M. zephyra*. (G) Dorsal view of tarsomeres 1-4 of *M. zephyra*. (H) Same of *M. subsolana*. (I) Dorsal view of process beyond 3rd tarsomere of *M. subsolana*. (J) Arolium of *M. zephyra*. Abbreviations: 1-4: tarsomeres 1-4; ar: arolium; cl: claw; dp: process beyond 3rd tarsomere; ma: anterior articulation of mandible; P1: pleuron of prothorax; sg: subgenal sulcus; T1: tergum of prothorax; tp: anterior tentorial pit.

Fig. 2. *Mantophasma* postabdomen, proventricle, and eggs. (A) Lateral view of male postabdomen of *M. subsolana*, with subgenital plate (coxosternum IX). (B) Same without subgenital plate and with genitalia expanded. Ejaculatory duct opening in between phallic lobes. (C) Posterodorsal view of vomer-like element: sclerite, asymmetrical median projection, and lateral articulations with tergum X. (D) Lateral view of female postabdomen of *M. zephyra*. (E) Exoskeleton of proventricle of *M. zephyra*, viewed from gut cavity. Proventricle cut longitudinally and spread in a plane, posterior end down. (F) Part of proventricle as seen by SEM. (G and H) Details of proventricle wall of *M. zephyra*, showing papillose sculpture of proventricle sclerites; papillae in (H) probably abraded by use. (I) Egg of *M. zephyra*, upper end located distally in ovary. (J) Chorion around circular ridge. (K and L) Details of chorion, showing hexagonal grooves with traversing bars. Abbreviations: al, ml, pl: anterior, middle, and posterior lobes of proventricle; C9: coxa IX; cc: cerci; cv: cardiac valve (entrance into midgut); ed: ejaculatory duct; ep: epiproct; er: circular ridge of egg; gc: gonoplac; gp8,9: gonapophyses VIII and IX; iv: posterior intervalvula; ke: keel inserted into dorsal groove of gonapophysis VIII; ph: phallic lobes (male genitalia s.s.); pp: paraproct; re: rectum; S8,9: abdominal coxosterna VIII and IX (subgenital plates); sp: spatulate process of subgenital plate; si8: spiracle VIII; T8,9,10: abdominal terga VIII, IX, and X; vo: vomer-like element.



