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Phylogeny of the Heelwalkers (Insecta: Mantophasmatodea) based on mtDNA sequences, with evidence for additional taxa in South Africa

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Abstract

We examined the phylogeny of Mantophasmatodea from southern Africa (South Africa, Namibia) using approx. 1300 bp of mitochondrial DNA sequence data from the genes encoding COI and 16S. The taxon sample comprised multiple specimens from eight described species (*Namaquaphasma ookiepense*, *Austrophasma rawsonvillense*, *A. caledonense*, *A. gansbaaiense*, *Lobatophasma redelinghuysense*, *Hemilobophasma montaguense*, *Karoophasma botterkloofense*, *K. biedouwense*) and four undescribed species of Austrophasmatidae; three specimens of *Sclerophasma paresisense* (Mantophasmatidae); and two specimens of *Praedatophasma maraisi* and one of *Tyrannophasma gladiator* (not yet convincingly assigned to any family). For outgroup comparison a broad selection from hemimetabolous insect orders was included. Equally weighted parsimony analyses of the combined COI + 16S data sets with gaps in 16S scored as a fifth character state supported Austrophasmatidae and all species and genera of Mantophasmatodea as being monophyletic. Most species were highly supported with 98–100% bootstrap/7–39 Bremer support (BS), but *K. biedouwense* had moderate support (87/4) and *A. caledonense* low support (70/1). Mantophasmatodea, Austrophasmatidae, and a clade *Tyrannophasma gladiator* + *Praedatophasma maraisi* were all strongly supported (99–100/12–25), while relationships among the two latter clades and Mantophasmatidae remain ambiguous. Concerning the relationships among genera of Austrophasmatidae, support values are moderately high for some nodes, but not significant for others. We additionally calculated the partitioned BS values of COI and 16S for all nodes in the strict consensus of the combined tree. COI and 16S are highly congruent at the species level as well as at the base of Mantophasmatodea, but congruence is poor for most intergeneric relationships. In forthcoming studies, deeper relationships in the order should be additionally explored by nuclear genes, such as 18S and 28S, for a reduced sample of specimens.

Keywords: Mitochondrial DNA; Parsimony; Nuclear mitochondrial copies; Endemism; Mantophasmatodea

1. Introduction

1.1. Discovery and diversity of Mantophasmatodea

The Mantophasmatodea (Heelwalkers) was described as a new extant insect order by Klass et al. (2002), thereby succeeding—after almost a century—the last discovery of a taxon today rightfully assigned ordinal rank: the Grylloblattodea (Walker, 1914). The description of Mantophasmatodea was based on morphological studies that failed to identify characters suggestive of a phylogenetic position within any of the other ten high-rank taxa comprising the Neoptera (Plecoptera, Phasmatodea, Embioptera, Grylloblattodea = Notoptera, Dermaptera, Orthoptera, Dictyoptera, Zoraptera, Acercaria = hemipteroid orders, and Endopterygota = Holometabola; see Kristensen, 1991; Klass, 2007). Although the original description did not

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include a phylogenetic analysis, it did point to some anatomical details suggesting a sister-group relationship with either Grylloblattodea or Phasmatodea.

The discovery of Mantophasmatodea stimulated further investigations, which revealed a fairly rich extant fauna restricted to Southern Africa (see list of taxa in Appendix A). The original description in Klass et al. (2002) was based on a female *Mantophasma zephyrum* from Namibia and a male *M. subsolanum* from Tanzania, both collected decades ago and then stored in museum collections. Shortly thereafter, *P. maraisi* and *T. gladiator* were described from Namibia (Zompro et al., 2002, 2003). However, most of the new species showed up in South Africa (Picker et al., 2002; Klass et al., 2003a,b), which resulted in the description of five genera and eight species from the Western and Northern Cape Provinces: *A. caledonense*, *A. gansbaaiense*, *A. rawsonvillense*, *Lobophasma redelinghuysense*, *Hemilobophasma montaguense*, *Karoophasma biedouwense*, *K. botterkloofense*, and *Namaquaphasma ookiepense*. In addition, four further species from Namibia have been described: *Sclerophasma paresisense* in Klass et al. (2003a), and *Mantophasma gamsbergense*, *M. kudubergense*, and *M. omatakoense* in Zompro and Adis (2006). However, the assignment of the three latter species to the genus *Mantophasma*, as well as their species status appears questionable due to the limited documentation of the genitalic structures and the absence of molecular studies. The species identity of the Namibian Erongo Mts. specimens listed as "*Mantophasma zephyra*" in Zompro et al. (2003) and Dallai et al. (2003) has remained unclear, as the similar-appearing *S. paresisense* was described after these studies (Klass et al., 2003a). Zompro and Adis (2006) assign these specimens to *Mantophasma kudubergense*. None of the material so far examined could be convincingly associated with *M. zephyrum*.

Klass et al. (2003a) provided the first detailed description of the male and female abdominal terminalia and genitalia. This approach also revealed pronounced differences between the various species in the presence and shape of genitalic sclerites, cerci and posterior tergites. In the same paper the first molecular based phylogenetic analysis of Mantophasmatodea that comprised a dense taxon sampling was presented, using approximately 1300 bp DNA sequence data from the mitochondrial genes encoding *cytochrome c oxidase subunit I* (COI) and the *large mitochondrial ribosomal subunit* (16S). Based on the post-abdominal characters reinforced with molecular phylogenetic studies a classification of Mantophasmatodea was proposed. This resulted in the erection of the above-mentioned new genera and of two new families: Tanzaniophasmatidae comprising the single Tanzanian specimen from the original description (now assigned to *Tanzaniophasma subsolanum*), and Austrophasmatidae comprising all the South African species. *M. zephyrum* and *S. paresisense* were retained in Mantophasmatidae, even though the evidence for monophyly of this taxon was poor. The phylogenetic analysis by Klass et al. (2003a) showed a monophyletic and well resolved Austrophasmatidae. Subsequent inclusion of *T. gladiator* in the molecular data set (Klass et al., 2003b) indicated that this taxon was the sister-group to Austrophasmatidae + Mantophasmatidae (the latter represented by *S. paresisense*).

Klass et al.'s (2003a,b) concept of erecting families for the small number of Heelwalker taxa has been criticized, and a replacement with subfamilial, tribal (or lower) ranks has been proposed instead (Grimaldi and Engel, 2005; Arillo and Engel, 2006). Zompro (2005) and Zompro and Adis (2006) even formally combine all genera of Austrophasmatidae, Mantophasmatidae, and Tanzaniophasmatidae into the first-described genus *Mantophasma*, leaving only *Praedatophasma* and *Tyrannophasma* as separate genera. However, such a down-ranked classification does not avoid any problems with regard to the systematics of the taxon, and widely accepted rules for choosing particular ranks of classification do not exist anyway. Since we consider the diversity in genitalic morphology significant, we prefer to maintain the taxonomic framework established by Klass et al. (2003a). We also emphasize that the different suggestions for classification of Mantophasmatodea do not reflect different hypotheses on phylogeny: Phylogenetic reasoning is virtually absent in the contributions of O. Zompro and J. Adis (e.g., 2006); and Arillo and Engel (2006) accept the relationships proposed by Klass et al. (2003a).

Shortly after the discovery of Mantophasmatodea a dispute started about the phylogenetic relationships of this taxon. Tilgner (2002) suggested that it is subordinate to Orthoptera, which sometimes are specialized almost beyond recognition, but this idea was immediately refuted by Klass (2002). Sperm characters were used to argue a sister-group relationship between Mantophasmatodea and Mantodea (Dallai et al., 2003). Klass et al. (2003a) mentioned conflicting morphological apomorphies that point to a relationship either to Dictyoptera or Phasmatodea. Relationships to Dictyoptera were confirmed later by a character from the antennal vessels (Pass et al., 2006). Molecular studies predominantly based on nuclear markers yielded a clade Mantophasmatodea + Grylloblattodea (Terry and Whiting, 2005; Kjer et al., 2006), which was also obtained in the morphology based cladistic analysis of Beutel and Gorb (2006). On the other hand, using sequence data from the entire mitochondrial genome, Cameron et al. (2006) found a strongly supported clade Mantophasmatodea + Phasmatodea.

1.2. Scope of present study

The molecular studies by Klass et al. (2003a,b) lacked several important species, including *T. subsolanum*, *P. maraisi*, *M. zephyrum* and *N. ookiepense*. In the present study we have been able to include DNA sequence data from *P. maraisi* and *N. ookiepense* as well as from four recently discovered but as yet undescribed South African species; this allows us to expand our hypothesis on intraordinal phylogenetic relationships of Mantophasmatodea. In addi-