

Mantophasmatodea: A New Insect Order?

Klass *et al.* (1) linked the extinct fossil taxon *Raptophasma* to newly described species of an extant taxon *Mantophasma*, hypothesizing that they form a monophyletic group. This result is interesting and uncontroversial. However, I doubt the claim that *Raptophasma* and *Mantophasma* represent a new order of Insecta, Mantophasmatodea. I feel that these insects are instead aberrant members of the order Orthoptera, which also includes Ensifera (crickets and katydids) and Caelifera (grasshoppers).

Klass *et al.* stated that “[a]lthough wingless and nonjumping Orthoptera . . . can be modified almost beyond recognition, the large prothoracic pleuron concealed by pronotal lobes and the lack of an anterior intervalvula in the ovipositor exclude *Mantophasma* from this clade.” However, presence of a fully formed pleuron does not exclude *Mantophasma* from the order Orthoptera, because this condition is found in at least one family (Proscopiidae) within Orthoptera (2). Furthermore, the presence of anterior intervalvula has never been demonstrated to be a synapomorphy of Orthoptera (some Phasmida, such as *Timema*, also possess it). Even if the absence of the structure were an autapomorphy, it would not exclude *Mantophasma* from Orthoptera. Similar arguments apply to the “lack of longitudinal series of denticles in the proventricule” cited by Klass *et al.* (1).

Klass *et al.* also stated that having five tarsomeres is incompatible with *Mantophasma* being subordinate in the crown-group Orthoptera. However, the first three tarsomeres of *Mantophasma* are synsclerotic, making the tarsi identical to those of the Caelifera family of Orthoptera (3).

If Klass *et al.* had presented a cladistic analysis that included *Mantophasma*, showing that it is not phylogenetically subordinate to an already recognized major monophyletic lineage, it would be a sound basis for these authors to pose the hypothesis that *Mantophasma* and *Raptophasma* are a new order of Insecta. As it appears, support for their hypothesis is in the form of subjective opinions about morphological character polarity, and standard methods of phylogenetic analysis (i.e., simultaneous, unconstrained parsimony analysis performed using a published data matrix) were not used.

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Reference

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2. L. C. Zollessi, *Trans. R. Entomol. Soc. London* **120**, 55 (1968).
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Response: A cladistic analysis testing the placement and ordinal status of Mantophasmatodea would be highly desirable, but demanding it for the present is unrealistic. Even the most elaborate all-insect character matrix to date (1), which uses orders as terminal taxa, is unsatisfactory for two reasons: (i) only a few included characters contribute to resolving relationships among the “lower Neopteran” orders (most relevant for Mantophasmatodea); and (ii) many pertinent characters from the literature (e.g., characters of female genitalic sclerites and muscles, spiracle musculature, and head/thorax and thorax/abdomen transition areas) have not yet been included. It is important to note that testing whether Mantophasmatodea is subordinate within an existing order, as suggested by Tilgner, would require a matrix in which a number of subgroups of each order are scored. Such a matrix is not available at this time.

Composing meaningful matrices will take years of diligent morphological studies. At present, the only feasible way to discuss the phylogenetic position of Mantophasmatodea is by evaluating pertinent characters “mentally,” as we did (2), with assumptions about character polarities based on broad outgroup comparison (not on “subjective opinions,” as stated by Tilgner). The resulting basis for allotting ordinal status to Mantophasmatodea is comparable to that for most other insect orders.

In terms of physical characters and their evidence, Tilgner provides two misinterpretations. First, tarsal structure is not identical in Mantophasmatodea (tarsomeres separated by dorsal grooves) and Caelifera (complete tarsomere fusion without grooves), as suggested in the comment. Second, the anterior intervalvula occurs in Orthoptera, Phasmatoidea, and Dictyoptera;

by comparison with Odonata and Zygentoma, its presence is apomorphic. Its absence would thus exclude Mantophasmatodea from a taxon [Orthoptera + Phasmatoidea + Dictyoptera] whose existence is supported by the intervalvula character but is otherwise uncertain. Thus, our original statement that this character suggests exclusion of Mantophasmatodea from Orthoptera is logically valid.

Can Mantophasmatodea, after all, be placed in Orthoptera? According to the most basic principle of cladistics, all taxa are grouped based on shared apomorphies. Nonetheless, secondary losses of apomorphies (reversals) are common. Tilgner suggests large-scale reversals for Mantophasmatodea (explicitly mentioning the intervalvula, proventricule, and prothoracic pleura characters). However, if insects that, like Mantophasmatodea, lack the known apomorphies of Orthoptera (i.e., have exposed prothoracic pleurae and separated basal tarsomeres, and lack the intervalvula, thickened hind femora, and modifications in the proventricule), are considered subordinate in Orthoptera, these insects must be shown to display other autapomorphies of Orthoptera—or of any of its subgroups—that outweigh the many reversals then to be assumed (due to parsimony, another basic principle of cladistics). I am not aware of apomorphies that in this way could link Mantophasmatodea to Orthoptera, nor does Tilgner suggest any. Instead, Mantophasmatodea share apomorphies with Notoptera and some Phasmatoidea. These circumstances forbid the assignment of Mantophasmatodea to Orthoptera.

Of course, one cannot categorically exclude that future research will reveal Mantophasmatodea to be modified Orthoptera—in the same way that future studies might show that Phasmatoidea are modified Orthoptera, or Coleoptera (beetles) are modified Neuroptera (lacewings and allies). But with present knowledge, these relationships appear very unparsimonious, and proposing them is mere speculation.

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