

Classification of orthopteroid insects - a comment to Rácz

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In Articulata 16, Rácz (2001) has nicely outlined some historical facts about the classification of the diverse group of orthopteran insects. This group has developed early on earth compared to many other insects, leading to units of quite distant relatedness. Furthermore, the modern Caelifera rapidly radiated in concordance with the establishing of vast grassland habitats in the tertiary period (GOROCHOV 1996). This fact causes problems for their accurate classification (FLOOK & ROWELL 1997a,b, FLOOK et al. 2000). Conclusions (1) – (3) of Rácz (2001) agree well with current hypothesis of hexapod evolution (WHEELER et al. 2001). In contrast, conclusions four and five might be complemented for the general reader by comments in the field of molecular genetics and the evolution of sound and hearing.

Conclusion 4 of Rácz (2001). The early division of *Ensifera* and *Caelifera* (perm, trias, 225 million years ago), than their parallel evolution resulted in significant morphological and behavioural differences (e.g., organs of hearing, sound-making, life-form types).

Hearing and sound-making

Hearing in insects has evolved independently several times and has led to an enormous biodiversity of auditory systems (FULLARD & YACK 1993, HOY & ROBERT 1996). In any case, hearing seems to be a very ancient invention in Orthoptera (SHAROV 1971), with bushcricket fossils from the tertiary reveal very modern tympanic structures (RUST et al. 1999). For the *Ensifera* it is likely that acoustic signalling and hearing developed from vibratory communication in a co-evolutionary process for mate finding (STUMPNER & VON HELVERSEN 2001). In the *Caelifera* it is quiet obvious that the ability to hear was developed first and acoustic signalling evolved later (RIEDE et al. 1990, FLOOK et al. 2000). The original function of tympana in the *Caelifera* may have been related not to conspecific communication but predator detection. However, recent phylogenetic analyses have suggested that song-producing mechanisms have multiple origins within the *Ensifera* (GWYNNE 1995, DESUTTER-GRANDCOLAS 1997). The comparison of morphological characters in the Acridoidea leads to similar conclusion about grasshopper stridulation (RIEDE 1987). It is true that the *Caelifera* and the *Ensifera* use quite different modes of hearing, but it is also true that hearing (and sound-producing) is too diverse in the Orthoptera to serve as a single character dividing the *Ensifera* clade from the *Caelifera*.

Life-forms

Whether the so called life-forms reflect orthopteran phylogeny is speculative at the moment. In my opinion ecological parameters, which are part of the life-forms, are too adaptable to be used in orthopteran classification. They have evolved in concordance with habitat requirements. Gwynne (1995) provided evidence, that the evolution of maternal care, reduction of the ovipositor and ground digging in Ensifera is of multiple origin. Such multiple origin must also be proposed for mole like life-forms, which have developed under similar adaptive pressure in connection with digging in the ground; this has taken place in the *Gryllootalpidae* as a group of the Ensifera, and in the *Tridactyliidae* and *Cylindrachaetidae* within the Caelifera. Therefore multiple times have the adaptation to a special way of live changed the groundplan in a very similar matter, transforming the homologous forelegs into digging shovels (BEIER 1955). It is true that species belonging to either Ensifera or Caelifera differ remarkable in morphological traits and this distinction give way to different habitat requirements. Nonetheless the life-form concept is based largely on the situation in Europe and Asia, dominated by orthopteran assemblages adapted to grassland and deserts, which does not cover the worldwide diversity. The Euschmidtinae as an remarkable example of Caelifera are prominent inhabitants of the understory in the tropical forest with the majority of the species brightly coloured, hardly fitting into the life-forms proposed for grasshoppers.

Life-forms as defined by RÁCZ (2001) can also change during ontogeny: (a) The phytophilous larvae of *Aiolopus thalassinus* live in grassy habitats, whereas adults change to open places exhibiting an "oedipodine-like" geophilous behaviour. (b) The bushcricket *Tettigonia viridissima* lives as larvae in the grass, feeding on flowers (chortobiont), changes as adults to trees (thamnobiont) and returns to the ground for egg-deposition (geobiont) – three "life-forms" during a lifecycle?

In conclusion, it is doubtful whether ecological parameters can reflect the phylogeny of the Orthoptera (compare MILLER & WENZEL 1995).

Conclusion 5 of RÁCZ (2001). In contraryOrthoptera ...should be treated as the order *Grylloptera*, (syn. *Ensifera*) and *Orthoptera* ((s.str.), syn. *Caelifera*)....

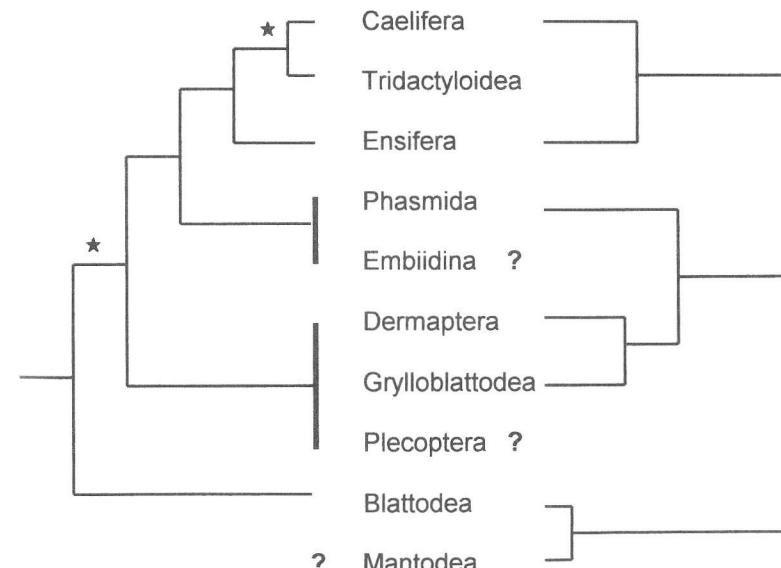
Using the arguments by RÁCZ (2001) this is simply a formal question of classification (splitter-lumper problem). If we like to point on the differences between the sistergroups Ensifera and the Caelifera we easily can accept this splitting. If we on the other hand like to point on the common ancestor of all living Orthoptera, we might like to stay with one order and two suborders. It must be mentioned that both classifications based on the same tree of life and that this is only a down- or up-grade of a formal class. Both ways are identical in their interpretation of the relationships!

RÁCZ (2001) arguments for two distinct orders based on the reanalysis by KUPERUS & CHAPCO (1996) of the data from KAMP (1973). They cited a large number of characters to support the separation of the Ensifera from the Caelifera. However, the palaeontological records suggest that Caelifera are derived

from Ensifera or, as a minimum, that both orders are derived from some common trunk (GOROCHOV 1996). While the orthopteran progenitor is often thought of as ensiferan-like (KRISTENSEN 1981), there are speculations that the Ensifera may actually be paraphyletic with respect to the Caelifera (SHAROV 1971). Paraphyly of the Ensifera would either necessitate the creation of several orders or retention of the existing hierarchy!

Furthermore, the phylogenetic signal in the database of RÁCZ (2001) seems to be weak. The clade of Caelifera/Ensifera is grouped in four cases with the Blattodea /Mantodea clade, in the remaining four cases it is grouped with the (Dermaptera /Grylloblattodea) /Phasmida clade. Therefore, the position of the Orthoptera is not resolved using his analysis. Molecular data (FLOOK & ROWELL 1998, FLOOK et al. 1999, MAEKAWA et al. 1999, WHEELER et al. 2001) in comparison prove that Ensifera and Caelifera can be grouped into a single clade, distinct from the other orthopteroid groups (Fig. 1).

We must await further data, especially including more of the diverse Ensifera into the molecular analysis, until we can draw a full picture on the evolution and splitting of the Orthoptera.



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