ARTICULATA 2002 17(1): 107 - 111 SYSTEMATIK

Classification of orthopteroid insects - a comment to Rácz

Arne W. Lehmann

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 to 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 *Gryllotalpidae* 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 Euschmidtiinae as an remarkable example of Caelifera are prominent inhabitors 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 livecycle?

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 contrary .....*Orthoptera* ...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.

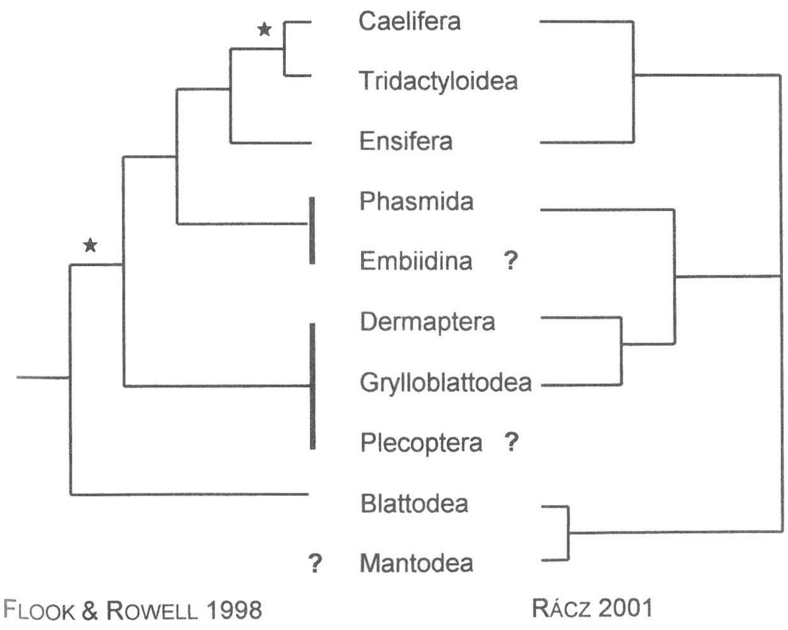

Fig. 1: Proposed cladogram for orthopteroid insects using molecular data (after FLOOK & ROWELL 1998). Two nodes marked by an asterisk are resolved using more extant molecular data (FLOOK et al. 1999). On the right a consensus tree based on the "reanalysed" data after RÁCZ (2001) is represented. Groups indicated by a quotation mark (?) were not included in the analysis.

Author:
Dr. Arne W. Lehmann
Stolper Straße 47
D-16548 Glienicke
Phone: ++49-33056-27940

Acknowledgement

I thank the referee Dr. Köhler, Jena for corrections and some interesting aspects regarding life-forms.

Literature

BEIER, M. (1955): Embioidea und Orthopteroidea. In: WEBER, H. (Ed.): Bronns Klassen und Ordnungen des Tierreichs 5.III.6. (Geest & Portig), Leipzig; 304 pp.

DESUTTER-GRANDCOLAS, L. (1997): A phylogenetic analysis of the evolution of the stridulatory apparatus in true crickets (Orthoptera, Grylloidea). – Cladistics 13: 101-108.

FLOOK, P. K. & ROWELL, C. H. F. (1997a): The phylogeny of the Caelifera (Insecta, Orthoptera) as deduced from mtrRNA gene sequences. – Molecular Phylogenetics and Evolution 8(1): 89-103.j

FLOOK, P. K. & ROWELL, C. H. F. (1997b): The effectiveness of mitochondrial rRNA gene sequences for the reconstruction of the phylogeny of an insect order (Orthoptera). – Molecular Phylogenetics and Evolution 8(2): 177-192.

FLOOK, P. K. & ROWELL, C. H. F. (1998): Inferences about orthopteroid phylogeny and molecular evolution from small subunit nuclear ribosomal RNA sequences. – Insect Molecular Biology 7(1): 163-178.

FLOOK, P. K., KLEE, S. & ROWELL, C. H. F. (1999): A combined molecular phylogenetic analysis of the Orthoptera (Arthropoda, Insecta) and its implications for their higher systematics. – Systematic Biology 48: 233-253.

FLOOK, P. K., KLEE, S. & ROWELL, C. H. F. (2000): Molecular phylogenetic analysis of the Pneumoroidea (Orthoptera Caelifera): molecular data resolve morphological character conflicts in the basal Acridomorpha. – Molecular Phylogenetics and Evolution 15(3): 345-354.

FULLARD, J. H. & YACK, J. E. (1993): The evolutionary biology of insect hearing. – Trends in Ecology and Evolution 8: 248-252.

GOROCHOV, A. V. (1996): Contributions to the systematics and elucidation of the evolution of the order Orthoptera. – Entomological Review 75(5): 156-162. [Originally published in Zoologicheskiy Zhurnal 74(10): 39-45, 1995]

GWYNNNE, D. T. (1995): Phylogeny of the Ensifera (Orthoptera): A hypothesis supporting multiple origins of acoustical signalling, complex spermatophores and maternal care in crickets, katydids, and weta. – Journal of Orthopteran Research 4: 203-218.

HOY, R. R. & ROBERT D. (1996): Tympanal hearing in insects. – Annual Review of Entomology 41: 433-450.

KAMP, J. W. (1973): Numerical classification of the orthopteroids, with special references to the Grylloblattodea. – Canadian Entomologist 105: 1235-1249.

KRISTENSEN, N. P. (1981): Phylogeny of insect orders. – Annual Review of Entomology 26: 135-157.

KUPERUS, W. R. & CHAPCO, W. (1996): Reanalysis of some classic orthopteroid phylogenies. – Journal of Orthoptera Research 5: 205-211.

MAEKAWA, K., KITADE, O. & MATSUMOTO, T. (1999): Molecular phylogeny of orthopteroid insects based on the mitochondrial cytochrome oxidase II gene. – Zoological Science 16: 175-184.

MILLER, J. S. & WENZEL, J. W. (1995): Ecological characters and phylogeny. – Annual Review of Entomology 40: 389-415.

RÁCZ, I. A. (2001): Some problems of the advanced classification of Orthopteroids. – Articulata 16(1/2): 1-10.

RIEDE, K. (1987): A comparative study of mating behaviour in some neotropical grasshoppers (Acridoidea). – Ethology 76: 265-296.

RIEDE, K., KÄMPFER, G. & HÖFLER, I. (1990): Tympana, auditory thresholds, and projection areas of tympanal nerves in singing and silent grasshoppers (Insecta, Acrididae). – Zoomorphology 109: 223-230.

RUST, J., STUMPNER, A. & GOTTWALD, J. (1999): Singing and hearing in a Tertiary bushcricket. – Nature 399: 650.

SHAROV, A. G. (1971): Phylogeny of the Orthopteroidea. – Israel Program for scientific translations, Jerusalem.

STUMPNER, A. & VON HELVERSEN, D. (2001): Evolution and function of auditory systems in insects. – Naturwissenschaften 88: 159-170.

WHEELER, W. C., WHITING, M., WHEELER, Q. D. & CARPENTER, J. M. (2001): The phylogeny of the extant hexapod orders. – Cladistics 17: 113-169.

Zeitschrift/Journal: Articulata - Zeitschrift der Deutschen Gesellschaft für Orthopterologie e.V. DGfO

Jahr/Year: 2002

Band/Volume: 17_1_2002

Autor(en)/Author(s): Lehmann Arne W.

Artikel/Article: Classification of orthopteroid insects - a comment to Racz 107-111