

Some problems of the advanced classification of Orthopteroids

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Abstract

The author by reviewing the most important literature of the topic, and reconsidering some of the old, numeric taxonomic analysis and taking into account the latest facts of molecular biology, comes to the conclusion - in agreement with the Orthopterologists of the Canadian school and contrary to the conservative researchers -, that it is better to consider the Orthoptera taxon as a superorder (Orthopteroida) with two orders (Ensifera and Caelifera).

Zusammenfassung

Der Autor hat die wichtigste Literatur des Themas gesichtet, dabei einige alte numerische taxonomische Analyse revidiert und die neuesten molekularbiologischen Fakten in Betracht gezogen. Er kommt zur Schlussfolgerung, dass es richtiger ist die Orthoptera Gruppe als Superordo (Superordo: Orthopteroida) betrachten, die über zwei Ordnungen verfügt: Ordo: Ensifera und Caelifera. Diese Meinung stimmt mit der von den Orthopterologen der Kanadaschule überein, bzw. widerspricht der Meinung der konservativ denkenden Autoren.

Outlines (Review)

The expression *Orthoptera* has been used with different meanings in the past, for example the present orders of *Polyneoptera* sectio had alternately been classified into the taxon *Orthoptera* several times. The name "Orthoptera" has been used first by DEGEER (1778) (CIT. V. KÉLER 1963). OLIVIER (1789) was able to characterise this taxon in that form which really considers the main criteria of 'orthopteroids' group nowadays as well. It is LATREILLE, a pioneer in classifying the *Orthoptera* taxon, who first used the term *Saltatoria*, which is still a bit confusing (LATREILLE 1817). At the beginning of the 19th century the scholarly activities of BURMEISTER (1838) and AUDINET-SERVILLE (1838) - however, they do not really surpass LATREILLE - outline the debate between conservative and modern tendency, which is still exists in the higher classification of the *Orthopteroids*.

To the influence of GERSTAECKER (1863) who significantly expanded the "Orthoptera" order by classing the *Thysanoptera* and *Thysanura* taxa and the present *Paraneoptera* taxon as well into this group - merging is the main feature of the conservative trend.

These contradictions has been mostly resolved by HANDLIRSH (1903, 1906-1908, 1925, 1929) with the full knowledge of paleontology data, however in respect of the jumper *Orthopteroids* he is conservative, even if he acknowledges the significant differences between the suborders *Locustoidea* and *Acridoidea*. Many

authors from the end of the 19th and the beginning of the 20th century represent the same view (WALKER, STAL, SCUDDER, BRUNNER VON WATTENWYL, REDTENBACHER, SAUSSURE, KRAUSS, KARSCH, BOLIVAR, GRIFFIN, KARNY, GIGLIO-TOS, E.M. WALKER, RHEN, UVAROV, CHOPARD).

One of the representative of the modern trend is CRAMPTON (1915), who gave a similar approach to the classification of insects as the recent one, based on his comparative insect-morphological research. In his papers between 1915-1938 by emphasising the differences he points it out, that the two taxa (Ensifera and Caelifera) are not only developing in a parallel direction, but they have significant differences among their exterior and interior anatomy, onthogenetics and cytology. This view is reflected by creating the *Orthoptera* (*Panorthoptera*) super-order. He is also noted for first introducing that Acridoidea and *Phasmatoda* are relatives, well before SHAROV (SHAROV 1968).

BLACKITH and BLACKITH (1968), in their numeric taxonomic paper, raised the possibility, that the *Ensifera* and the *Caelifera* suborders should be seen as orders. They compared the orthopteroid groups from the point of view of their exterior morphological differences, and found on the bases of cluster diagrams, that the distance between the two suborders are bigger than e.g. between *Blattodea* and *Mantodea*. HENNIG (1969) proves this proposal in his cladistic system based on philogenetics results, however he does not name the groups, as in other cases as well. KEVAN in his paper in 1973 go further, and regarding those sharp features which make the distinctions between the two suborders known since CHOPARD (1949), he ranks *Ensifera* to the order *Grylloptera*, while the *Caelifera* to the order *Orthoptera* (KEVAN 1973).

The numeric taxonomic results of KAMP (1973) based partly on the data of the two BLACKITH, and of himself proved the above. Nonetheless, he only takes a stand on the total distinction of *Phasmatoda* order, or on the similarities of the *Blattodea* and *Mantodea*. He leaves the *Orthoptera* order unchanged, however notes that *Caelifera* differs more from the *Ensifera* as it is expected.

KRISTENSEN (1975) first critically revise the interpretation of *Hexapoda* orders by HENNIG (HENNIG 1969), in which by qualifying the previous synapomorf features into convergent autapomorf features, he does not regard the *Phasmatoda* to be the sistergroup of *Caelifera*.

However, in case of *Orthoptera* order - regarding the highly important synapomorfisms (kryptopleurit on the prethorax, the jumperleg with a typical interior anatomy, the rotation of wing-initiatives on older larvae), which are the proof of monofiletic origin - he emphasises the uniformity of the order. This is strengthen in his paper on the phylogenesis of insects (KRISTENSEN 1981)

KEVAN (1977, 1986) expounds his views in details on the existence of the orders *Grylloptera* and *Orthoptera* (*s.str.*). Especially in his later work (KEVAN 1986) he details partly those synapomorf features which proves the two taxa monofiletic characteristics, partly the importance of the distinctive features (20 characteristic features) in contrary to the views of both KRISTENSEN (1981) and GOROCHOV (1984).

SZIRÁKI (1996) - in agreement with KAMP (1973), KRISTENSEN (1975, 1981) and GOROCHOV (1995) - again states that the *Orthoptera* order is uniform, since it forms a natural monofiletic unit, the synapomorphistics of which are more

important than, its differentiating characteristics (e.g. organ of hearing, organ of sounds). Finally INGRISCH & KÖHLER (1998) considere again the Ensifera and Caelifera's taxon is a definitely separated order, which is basically based on the determination of KEVAN (1986).

Recent results and discussion

Reappraisal of Kamp results

KAMP in his paper uses a merged database, in which he gives a numeric taxonomic analysis of orthopteroid insects based on 164 unweighted marks. One of the shortcomings of this database is that it does not contain neither the *Embioptera*, nor the *Isoptera* group. Nonetheless, his results are remarkable. Kamp's results can be confirmed - except small differences -one the bases of two dendrograms obtained by reappraising the database unchanged ((Fig.1 and Fig. 2) (KAMP 1973, PP 1238-1243). On the other hand, the interpretations of them are more unambiguous, since not only the similarities between the ((*Dermaptera-Grylloblattodea*)-*Phasmatoda*) taxa are more clear, or the sistergroup feature of *Blattodea* - *Mantodea* groups, but it clearly shows the difference between the *Ensifera* and *Caelifera* groups. The difference found in case of both methods, are significantly bigger, than in between the *Ensifera* and *Caelifera* groups. That is, in case of accepting the existence of *Dermaptera* and *Grylloblattodea* taxa as separate orders, than we have to accept to have order status of the taxa *Ensifera* and *Caelifera*.

Does not change this view the opinion of KRISTENSEN (1975, 1981), who, however, in contrary to HENNIG (1969) finds good synapomorphies for the whole of the jumper orthopteroids (kryptopleurit on the prethorax, the jumperleg with a typical interior anatomy, the rotation on the longitudinal axis of wing-initiatives on older larvae) which prove the monofiletic origin of the group examined, but at the same time he refuses the view of HENNIG on that the *Ensifera* and *Caelifera* are individual monofiletic units, respectively. Thus, actually he comes into conflict with himself, when he finally proves of the ranking these groups to the same order with the monofiletic origin of jumper orthopteroids. Tough, it is true, that for developing filogenetic taxonomic units one of the necessities is the monofiletic characteristic, but not enough, if the given monofiletic unit consists of more, different units which are monofiletic as well.

Realising this, KEVAN established the *Orthopteroida* superorder with the highly different (20 characteristic features) but monofiletic *Grylloptera* (*Ensifera*) and *Orthoptera* (*str.*) (*Caelifera*) orders (KEVAN 1973, 1977, 1986: 63-64).

Life-form types

The *Orthoptera* order can be characterised by the forms of life of the given species. Typifying the life-forms in their nomenclature and fine division are different in case of different authors (NAGY 1944, 1947, BEI-BIENKO 1950, KALTENBACH 1962, SCHIEMENZ 1969, KIS 1970, PRAVDIN 1978, RÁCZ 1998). However, basically they can trace back to two main types of life-forms, the phytophilous ones which prefer plant communities and the geophilous ones preferring free soil and stone surfaces. The given life-form types are showing morphological differences, which manifest not only in builds, but in colouring, which are more explicit

at *Caelifera*, than *Ensifera* (PRAVDIN, 1978). Phytophilouses are represented by the thamnobionts (mainly tettigonoids, e.g. *Meconema* Serv., *Leptophyes* Fieb. genera) and chortobionts (mainly acridoids, e.g. the species of *Chorthippus* Fieb., *Stenobothrus* Fisch. genera). A transition towards the geophilouses is the optional geobionts, which like to live in plants and on soil as well, so it is better to use the term geo-chortobiont. Geophilouses consist of - besides the geobionts and geo-psammobionts (the following acridoid species belong to these life-forms: e.g. *Calliptamus italicus* (L. 1758), *Celes variabilis* (Pall. 1771), *Acrotylus longipes* (Charp. 1845)) - the digger and cavity-living crickets.

Thus, one can think, that the life-form is such genetic determination, which evolved in different period of the evolution of *Orthoptera*. The thamnobiont life-form morphology at the more ancient *Ensifera*, remains at those species that turn to be chortobiont (e.g., *Tesselana vittata* (Charp. 1825)). While the later adaptive radiation of *Caelifera* in open association resulted in different life-form types. This strengthens the view, that the uniform *Orthoptera* or *Saltatoptera* order can not sustain.

Phylogenetic and Genetic research

KUPREUS and CHAPCO (1996) reconsidering the numeric taxonomic results of previous authors by using the new boot-step analysis – practically confirming them -, obtained such consensus tree, which were basically in agreement with the former cladograms.

FLOOK and ROWELL (1997) compared the fragments of the mitochondrial rRNA gene of 32 *Caelifera* taxa and 6 other orthopteroid groups with the help of the evolutionary analysis of the sequences. By analyzing the data it appeared, that however complicated the evolution of *Caelifera* group (FLOOK and ROWELL 1997a) they can be regarded as monophyletic, and the "original" *Caelifera* families and family series as well. It was also proved that the *Grylloblatta* (*Notoptera*) are definitely separated from the jumper *Orthoptera*, and that the *Phasmatoda* is not a sistergroups of *Caelifera*. Finally - however too many *Ensifera* taxa were involved in the research - there is a significant difference between the *Ensifera* and *Caelifera*, which let us conclude, that these are really two taxa with order status (FLOOK and ROWELL 1997a, b).

Some authors by proving the existence of a uniform *Orthoptera* order on one hand make a mistake by taking the opinion of those who argue for the uniformity without any critics, and on the other hand they do not use the rules of cladistics. Third, they only try to disprove 2 major features of KEVAN 20 most important differentiating features. One of them is the problem of the location of the organs of hearing, the other is the way of sound making (SZIRÁKI 1996).

The differences found in the location of the organs of hearing being less important, he explains by that in case of both groups, the organs of hearing evolved by associating to the so-called auditorial trachea, in case of *Ensifera* on the tibiae of forelegs, while in case of the *Caelifera* on the first abdominal segment. In other insect groups, actually this so-called auditorial trachea is the one, connection to which the organs of hearing are evolving (e.g. *Hemiptera*:

Cicadidae, *Lepidoptera*: *Noctuidae*) so this seems to be general at insects (BUSNEL 1963). On the other hand the fact, that the organ of hearing at the *Ensifera* is evolved in connection with an organ of vibration-sensing, which can be found in the legs of all *Orthoptera*, while in case of *Caelifera* the organ of hearing is evolved independently of it, which strengthen the difference between the two groups (BEIER 1972).

Regarding the differences existing in sound making, SZIRÁKI notes, that similar system than the femoro-elytral sound making which is general at the *Caelifera*, can be found at some species of the *Stenopelmatoidea* family series as well, which belongs to the *Ensifera*. In his opinion this refers to that this feature is less differentiated.

Also noted, that in one of the families of a family series which include lots of specialist forms (*Prophalangopsidae*), where the males have more-or-less developed wings, the sound-making is elytro-elytral, while others have no organ of sound-making (e.g. *Raphidiophoridae*).

In families in which most forms have no wings (e.g. *Stenopelmatidae*) femoro-abdominal sound-making may occur, however there are no chirp-pins, but sound is making by the bristles of the hind legs and the special sideplate of the first few abdomen section. This can be seen as a convergent feature, so this is rather support the basic difference.

Finally his statement on if a scientific fact is true or not, depend on whether the scientific community accept it or not, cannot really be believable (DARWIN, WEGENER).

Conclusions

We can state the followings by summarizing KEVAN's and the newer results:

1. The *Phasmatoda* (*Cheleutoptera*) taxon is not a sistergroup of the *Caelifera* taxon.
2. The origin of the *Grylloblattodea* (*Notoptera*) taxon has not been clarified yet. They are considered to be close to the *Dermaptera* and the *Phasmatoda*.
3. The *Ensifera* and *Caelifera* taxa are sistergroups on the basis of the present synapomorphies.
4. 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).
5. In contrary to the conservative view, since the existence of the synapomorphisms is necessary but not enough condition of the uniformity of the given taxon, accepting the standpoint of KEVAN, two suborders of the traditional *Orthoptera* order should be treated as the order *Grylloptera*, (*syn. Ensifera*) and *Orthoptera* (*(s.str.)*, *syn Caelifera*) of the *Orthopteroid* superorder.

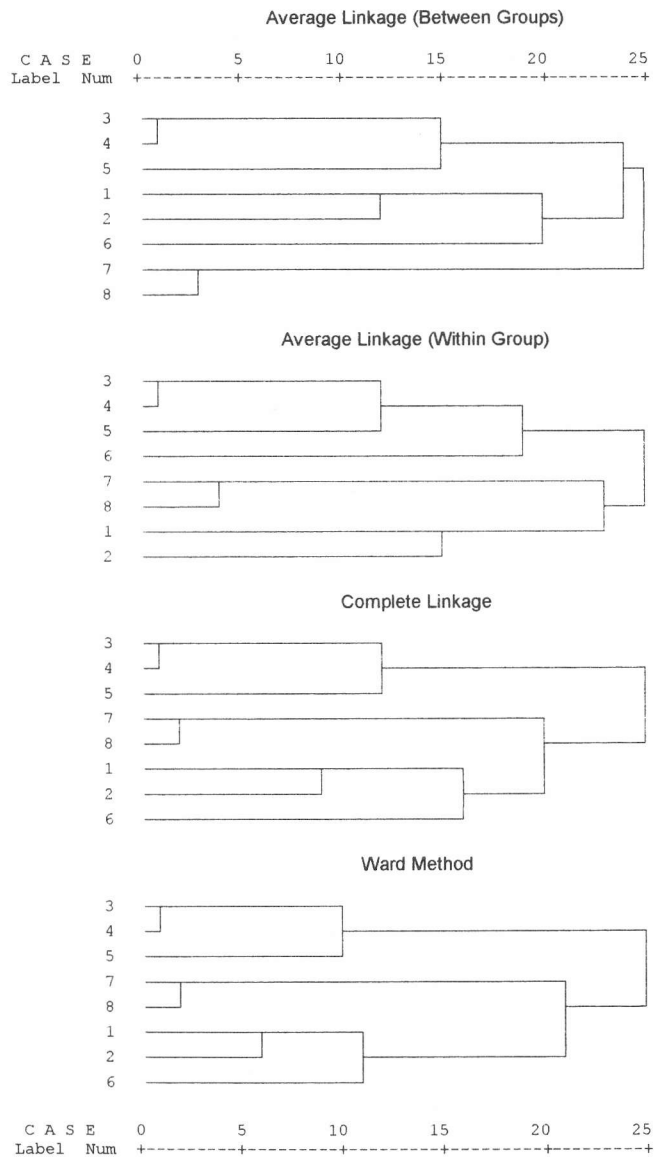


Fig. 1: Hierarchical cluster analysis with SPSS for Windows (Squared Euclidean Distance – dissimilarities) (1 Dermaptera, 2 Grylloblattodea, 3 Tettigoniidae, 4 Gryllidae, 5 Acrididae, 6 Phasmatoda, 7 Blattodea, 8 Mantodea)

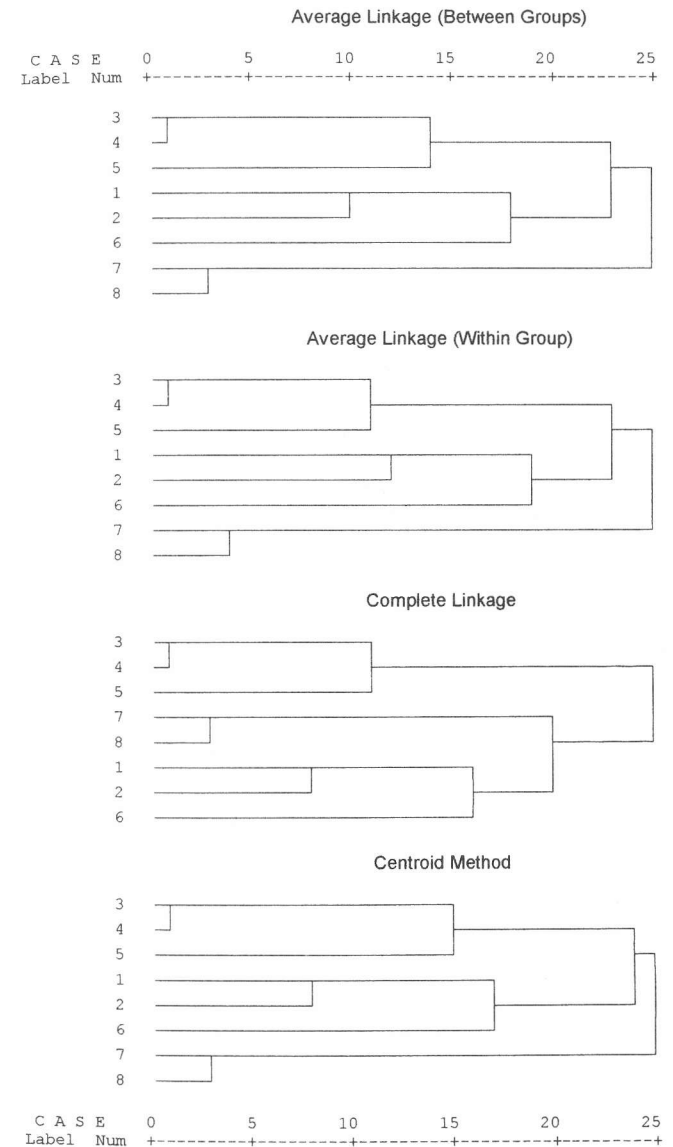


Fig. 2: Hierarchical cluster analysis with SPSS for Windows (Pearson correlation - similarities) (1 Dermaptera, 2 Grylloblattodea, 3 Tettigoniidae, 4 Gryllidae, 5 Acrididae, 6 Phasmatoda, 7 Blattodea, 8 Mantodea)

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