Proc. 6th Auchen. Meeting, Turin, Italy, 7-11 Sept. 1987, 47-53.

PRELIMINARY THOUGHTS ON THE PHYLOGENY OF FULGOROMORPHA (HOMOPTERA AUCHENORRHYNCHA)[1]

M.ASCHE[2]

ABSTRACT

The Fulgoromorpha forming a large and heterogeneous group within hemipterous insects are subject to a cladistic analysis sensu Hennig. The Fulgoromorpha are most probably monophyletic, some of their currently 20 subunits in family rank which all have been established classificatorically are evidently monophyletic, too: e.g. Tettigometridae, Delphacidae, Meenoplidae, Derbidae, Achilixiidae, Achilidae, Tropiduchidae, Eurybrachidae, Lophopidae, Hypochthonellidae, possibly also Flatidae and Acanaloniidae. The other families still have to be proved to be based on synapomorphic characters. The pairs Delphacidae and Cixiidae, Meenoplidae and Kinnaridae, Dictyopharidae and Fulgoridae most likely form monophyletic groups. The relationships between the monophyla within the Fulgoromorpha (especially the position of the Tettigometridae) and the phylogenetic origin of the whole group are still unclear.

KEY WORDS

Cladistic analysis, monophyla, Tettigometridae.

The phylogenetic relationships of the Fulgoromorpha and of their 20 families have attracted attention of may authors since long ago. Frederic Muir intending a natural classification established already 1923 (with additions and slight modifications in 1930) the classificatorical system which today is still generally in use. The relationships of Fulgoromorpha to other groups of Hemiptera as well as of the subgroups to each other are still unclear, and have never been elucidated by a cladistic analysis.

In the past several authors contributed to the subject (e.g. Cobben, 1965; Evans, 1963; Hennig, 1969; Heslop-Harrison, 1952; Schlee, 1969;), however, most of them included the Fulgoromorpha only by means of comparison with their own group of interest, for example Heteroptera or Sternorrhyncha. In more recent times some morphological and phylogenetic approaches have been published concentrating on Fulgoro-

[1] Research work supported by the DFG, W-Germany, As 52 / 2-1
[2] Fachbereich Biologie-Zoologie, Philipps-University Marburg, W-Germany

morpha or parts of them (e.g. Asche, 1985, Bourgoin, 1985a, b, 1986; Emeljanov, 1979, 1985). Own research was started only few years ago in order to work out ideas on the phylogeny of this group.

These studies concern all recent Fulgoromorpha worldwide based on large material of all subgroups either collected by ourselves, or borrowed from the collections of major museums like Bishop Museum Honolulu and British Museum (N.H.). For reconstructing the phylogeny of Fulgoromorpha the phylogenetic method of Willi Hennig is used, in my opinion currently the only suitable tool for phylogenetic studies.

Some preliminary results

As is assumed in literature (e.g. Hennig, 1969) the Fulgoromorpha are most likely monophyletic. As synapomorphies may be considered, for instance, the special configuration of hind-and middle-coxae, the special position of ocelli and of the antenna-base, the presence of distinct sensory fields (placoids) on the enlarged pedicellus, and perhaps the typical "fulgoromorphan face". However, some of these characters should thoroughly be compared with the situation in other groups, especially in Sternorrhyncha. Some other characters are still unclear in their phylogenetic significance: the presence of tegulae (similar structures are also found in Psyllidae); the absence of a filter-chamber, instead of this in most of the taxa examined so far the presence of a large cephalad directed tube-like process of the mid-gut (cranial diverticle). Also the equipment of muscles in the male genitalia has to be considered for its role in the phylogeny of Fulgoromorpha. As mentioned by Fennah (1945) in Fulgoromorpha in contrast to Cicadelloidea and Cercopoidea a special "unpaired transverse zygomatic abductor muscle" is missing. If this observation can be verified, the lack of the muscle can be interpreted either as reductive synapomorphy for the Fulgoromorpha-taxa, or as symplesiomorphy in case that the presence of that muscle can be valued as synapomorphy for at least Cicadelloidea and Cercopoidea together. Here further studies are necessary.

Within the Fulgoromorpha several monophyletic units could be found. One of the phylogenetically most important groups are the Tettigometridae recently on study by Bourgoin (1985a,b, 1986). They doubtlessly form a monophylum by uniquely derived characters like the very special, almost entire reduction of the female genitalia and a peculiar hindwing-venation. Only about the position of this group within the rest of the Fulgoromorpha different opinions have been published in literature. Muir (1923) considered most of the characters of Tettigometridae primitive, even "pertaining to the Cicadoidea", except for the female genitalia. In 1923 he placed the Tettigometridae below the branches to all other Fulgoromorpha, in 1930, however, he postulated affinities to the "tropiduchid group of families", but without explaining his reasons. Fennah (1952) discussed the possibility that some of the characters appear primitive due to neotenic processes. According to recent morphological studies on the tentorium of Fulgoromorpha by Bourgoin (1985a,b) the Tettigometridae possess a similar disposition

of tentorial
group, the l
have any tee
(Ricaniidae,
nellidae). B
between Flat
however, the
have not yet
synapomorphi
tures reveal
fic variatio
tic group (
tentorial br
different ty
close contex
gently sever
of this cha
be limited.

On the
are highly c
tidae-Tropid
between the
to the conc
which are pr
dae must hav

The
sensory pits
the adult st
of all Tetti
no indicatic
geny in the

The s
ration of th
structures
"Sprungappar
(Emeljanov,
stars of Te
checked so
first insta
characters r
tridae.

Conse
synapomorphi
place the T
as sistergrc

In th
coids could
modified fr
Fulgoromorph
simple placc
Tettigometri

On th
would imply
ters as wel
cond hindta
(the latter
Fulgoromorph
of taxa).

of tentorial branches like Flatidae and the "Ricanoid"-group, the latter comprising the five families which do not have any teeth at the distal margin of the second hindtarsus (Ricaniidae, Eurybrachidae, Lophopidae, Gengidae, Hypochthonellidae). Bourgoin (1985a) places the Tettigometridae in between Flatidae - Tropiduchidae and the Ricanoid-group, however, the phylogenetic relationships between these groups have not yet been proved convincingly by clearly expressed synapomorphies. Own preliminary studies on tentorial structures revealed in some cases a certain degree of intraspecific variation. It also seems that within the same monophyletic group (e.g. Delphacidae) different configurations of tentorial branches are present. I do not exclude that the different types of the tentorium which is functionally in close context with the mouth-parts have been evolved convergently several times. In my opinion the phylogenetic value of this character if considered isolated from others might be limited.

On the other hand the assumption that Tettigometridae are highly derived taxa originating somewhere from the Flatidae-Tropiduchidae-Ricanoid-line (if closer affinities between the members can be proved at all) necessarily leads to the conclusion that some other remarkable characters which are present in all Fulgoromorpha in the Tettigometridae must have been entirely reduced.

The first character is the presence of the complex sensory pits of the nymphs which in some groups persist in the adult stage. These pits could not be found in any instar of all Tettigometrid-nymphs checked so far, therefore I have no indication for any kind of recapitulation of the phylogeny in the ontogenesis.

The second character concerns a very special configuration of the hind-trochanter displaying rib- or teeth-like structures which in literature have been called "Sprungapparat" (Sander, 1950),"coupling apparatus" (Emeljanov, 1979). Also this character is missing in all instars of Tettigometridae-nymphs (in all other Fulgoromorpha checked so far this structure is developed already in the first instar). The alternative would be to interprete both characters not as lost, but as not yet evolved in Tettigometridae.

Consequently these two characters could be valued as synapomorphies for the rest of Fulgoromorpha which would place the Tettigometridae next to the basis, possibly even as sistergroup of all other Fulgoromorpha (fig.1).

In this connection also the more simple antennal placoids could be considered plesiomorphic, if not secondarily modified from a star- or cone-ring-shaped type of the other Fulgoromorpha, in the latter case the superficially more simple placoids were another autapomorphy for the monophylum Tettigometridae.

On the other hand a basal position of Tettigometridae would imply the convergent development of tentorial characters as well as of the reduction of distal spines on the second hindtarsus to only one on the inner and outer side each (the latter character is similarly found in several other Fulgoromorpha-groups, e.g. in the Flatidae- and Issidae-line of taxa).

Further comparative morphological studies (especially of the male genitalia: aedeagus) may provide characters which more significantly determine the position of Tettigometridae.

Within the other Fulgoromorpha more probably monophyletic groups have been recognized:

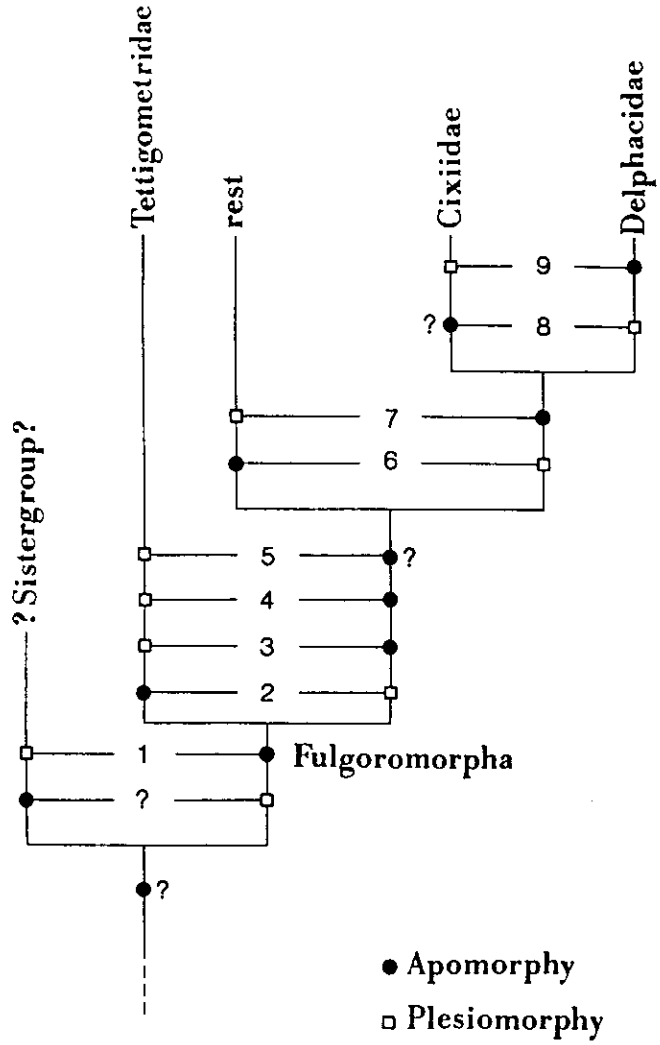
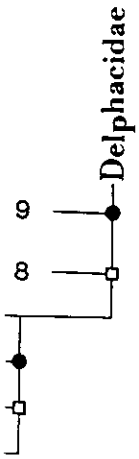


Fig. 1 - Model of a basal position of the Tettigometridae within Fulgoromorpha
1: Fulgoromorpha-synapomorphies 2: Tettigometridae-autapomorphies 3: Larval sensory pits 4: Larval trochanter coupling apparatus 5: Advanced antennal placoids 6: Alteration of the orthopteroid ovipositor 7: Median fusion of 2. valvulae 8: Subterranean life of nymphs 9: movable posttibial spur

.es (especially
ide characters
on of Tettigo-

y monophyletic



hy

rphy

ridae within

tapomorphies
apparatus
thopteroid
ranean life

Cixiidae and Delphacidae together. They may form a monophylum by an entire median fusion of the 2. valvulae (median gonapophyses 9) of the orthopteroid ovipositor to a functional unit. As plesiomorphy is considered a separation of the two parts of the 2. valvula like present in Cicadomorpha (Müller, 1942) and wherever checked in all other Fulgoroidea if not lost by reduction.

Delphacidae by their movable posttibial spur (Asche, 1985).

Cixiidae: Yet no convincing synapomorphic character could be found, perhaps except for the subterranean way of life of the nymphs, if it can be proved that cryptic nymphs in other groups like Achilidae and Derbidae have evolved convergently.

Derbidae by the lack of both a connective and a certain muscle in the male genitalia (Fennah, 1945). According to morphological studies of the alimentary canal by Fick (1984) a highly differentiated double-chamber is present in the endgut of the only species examined so far, *Cedusa funesta* Fowler. Such a chamber was not found in any other Fulgoromorpha-taxon checked. Moreover in contrast to the other Fulgoromorpha *C. funesta* does not possess a cranial diverticle. It is too early for any phylogenetic conclusions, however, the configuration of the alimentary canal may provide characters of high phylogenetic importance.

Meenoplidae and Kinnaridae together by the vertical wax-producing fields on the caudal parts of the tergites 6-8.

Meenoplidae by the obligatorical persistence of the larval sensory pits in the adult stage. Yet for Kinnaridae no significant synapomorphy could be found, perhaps except for the comparatively broad costal field in the tegmen.

Achilixiidae by lateral processes of the abdomen bearing exposed sensory pits.

Achilidae amongst other characters by the shift of the aedeagus-base far cephalad into the abdomen.

At least the last two families are already in the evolutionary line in which the plesiomorphic orthopteroid ovipositor has been modified morphologically and by function. This trend leads to the change of the female genitalia from a piercing apparatus for inserting the eggs into the plant tissue as is found in Delphacidae and plesiomorphic Cixiidae to an excavating-apparatus for covering the eggs with wax and exogeneous material. The eggs are mostly oviposited on or glued to the substrate. If we assume that the alteration of an orthopteroid ovipositor has evolved in only one continuous line to the model of an excavating-apparatus, of which in several cases further changes either by reduction or by modifying it to a secondary piercing-tool has occurred, we could possibly use this alteration as synapomorphy for all Fulgoromorpha except for Cixiidae-Delphacidae and - if decided for a basal position- for Tettigometridae, the latter may represent an independent way leading to the total loss of the ovipositor.

If this assumption is correct, taxa with the plesiomorphic spinulation of the 2. hindtarsus (complete row of spines) should be expected in the more primitive level within this group: Dictyopharidae, Fulgoridae, Achilidae, Achili-

xiidae, Meenoplidae, Kinnaridae and Derbidae, although the latter three families show considerable reductions of the female genitalia, perhaps convergently evolved.

The apparently monophyletic Tropiduchidae have obviously returned to (or retained?) the piercing mode of oviposition on the base of an already modified ovipositor. The parts forming the saw-like mechanism (here the teeth are developed on the 1. valvulae = gonapophyses 8) are different from the orthopteroid type as present in Delphacidae. Moreover all Tropiduchidae checked so far are ditrysic, i.e. the development of a separate canal for inserting the aedeagus during copulation (similar to the ditrysy in Stenocranine Delphacidae).

In the large group with modified female genitalia several more monophyletic units may be found. There is evidence that, for instance, the pair Dictyopharidae-Fulgoridae, Eurybrachidae, Lophopidae, the specialized Hypochthonellidae, and perhaps also Flatidae and Acanaloniidae form monophyletic groups. This has to be verified by further studies.

Future research will focus on:
1. Comparative morphological and biological studies of as many characters as possible both in the different Fulgoromorpha- and the other Hemiptera-taxa;
2. Character-analysis, decision about homology and evolutionary trends on the basis of homologous structures;
3. Testing the monophyly-concept of Fulgoromorpha and the recognized monophyletic subgroups by using additional characters; searching for further monophyla;
4. Reconstructing the organisation of the hypothetical ancestor-species for each monophyletic group;
5. Clearing the relationships between monophyla based on synapomorphic characters in order to get ideas about the sequence of sistergroups; cladogram;
6. Clearing the relationships of Fulgoromorpha to other Hemiptera;
7. Considering consequences for the systematics.

REFERENCES

ASCHE, M. (1985) Zur Phylogenie der Delphacidae LEACH, 1815 (Homoptera Cicadina Fulgoromorpha). Marburger Ent. Publ. 2 (1-2), 1-912.

BOURGOIN, T. (1985a) Morphologie antennaire des Tettigometridae (Hemiptera, Fulgoromorpha). Nouv. Revue Ent. (N.S.) 2 (1), 11-20.

BOURGOIN, T. (1985b) Morphologie comparée, céphalique et genitale des Tettigometridae et autres Fulgoromorpha. Tome I: Texte, Tome II: Planches. Universite de Paris-Sud Centre d'Orsay, These présentée pour obtenir le titre de Docteur III ème cycle, 1-137.

BOURGOIN, T. (1986) Valeur Morphologique de la lame maxillaire chez les Hemiptera; remarques phylogenetiques. Annls Soc. ent. France (N.S.) 22 (4), 413-422.

COBBEN, R.H. (1965) Das aero-mikropylare System der Homoptereneier und Evolutionstrends bei Zikadeneiern (Hom.Auchenorrhyncha). Zool. Beiträge (N.F.) Berlin, 11 (1-2), 13-69.

EMELJANOV, A
betwee
Phylog
Scienc
(Proce

EMELJANOV, A
the fa
(Homop
49-65;
Obozre

EVANS, J.W.
Rev. E

FENNAH, R.G.
dea (E
217-22

FENNAH, R.G.
tridae
Lond.

FICK, W. (19
Fulgor
gleich
441-45

HENNIG, W. (
furt.

HESLOP-HARRI
ancest
of the
12 (5)

MÜLLER, H.J.
der Zi
Tiere

MUIR, F. (19
(Homop

MUIR, F. (19
Ann. I

SANDER, K.
Pyril
Zool.

EMELJANOV, A.F. (1979) The problem of family distinction between the Fulgoridae and the Dictyopharidae. In: Phylogeny and Systematics of insects. Academy of Sciences of the USSR, Trudy Zoologicheskogo Instituta (Proceedings of the Zoological Institute) 82, 3-22.

EMELJANOV, A.F. (1985) A contribution to the knowledge of the families Kinnaridae and Meenoplidae (Homoptera,Fulgoroidea). Entomological Review 64 (1), 49-65; original in Russian: Entomologicheskoye Obozreniye (1984), 3, 468-483.

EVANS, J.W. (1963) The phylogeny of the Homoptera - Ann. Rev. Ent. Palo Alto, 8, 77-94.

FENNAH, R.G. (1945) The external male genitalia of Fulgoroidea (Homoptera). Proc. Ent. Soc. Washington 47 (8), 217-229.

FENNAH, R.G. (1952) On the classification of the Tettigometridae (Homoptera: Fulgoroidea). Trans. R. Ent. Soc. Lond. 103 (7), 239-255.

FICK, W. (1984) Über die Morphologie des Darmtrakts der Fulgoromorpha (Homoptera, Auchenorrhyncha): Ein Vergleich verschiedener Familien. Zool. Jb. Anat. 112, 441-458.

HENNIG, W. (1969) Die Stammesgeschichte der Insekten. Frankfurt. Senckenberg-Buch 49, 1-436.

HESLOP-HARRISON, G. (1952) Preliminary notes on the ancestry, family relations, evolution and speciation of the Homopterous Psyllidae II. Ann. Mag. Nat. Hist. 12 (5), 679-696.

MÜLLER, H.J. (1942) Über Bau und Funktion des Legeapparates der Zikaden (Homoptera Cicadina). Z. Morph. Ökol. Tiere 38, 534-628.

MUIR, F. (1923) On the classification of the Fulgoroidea (Homoptera). Proc. Hawaiian Ent. Soc. 5 (2), 205-247.

MUIR, F. (1930) On the classification of the Fulgoroidea. Ann. Mag. Nat. Hist. 10 (6), 461-478.

SANDER, K. (1956) Bau und Funktion des Springapparates von Pyrilla perpusilla Walker (Homoptera-Fulgoridae). Zool. Jb. Anat. 75 (3), 383-388.