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The Fossil Planipennia – a Review

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ABSTRACT

Systematics, palaeontology and stratigraphy of the orders of the Neuropteroidea are briefly discussed and previous work is summarized. From different authors 33 families have been established (19 existent and 14 extinct) within the order Planipennia and are presented in a phylogenetic tree which is mainly based on the classification outline of WITHYCOMBE (1924). Many questions on the phylogenetic relationships remain open since only the usefulness of morphologically recognizable characters provides palaeontological evidence in a stratigraphic context.

1. THE PHYLOGENETIC RELATIONSHIPS OF THE NEUROPTEROIDEA

The Neuropteroidea are doubtlessly the most archaic group of the Holometabola, but up to now it is not clearly evidenced if the 3 recent orders Megaloptera, Raphidioptera and Planipennia (i. e. Neuroptera s. str.) really represent higher categories with a common ancestor, i. e. if they are of monophyletic origin. Phylogenetic interpretations mainly based on morphological characters of the living species have been given by ACHTELIG (1975 and 1981), HENNIG (1969), ASPÖCK et. al. (1980), important former authors are HANDLIRSCH (1906 - 1908), TILLYARD (1926), WITHYCOMBE (1924), CARPENTER (1943 and 1954) and O. MARTYNOVA (1952 and 1962). Generally the Megaloptera, Raphidioptera and Planipennia are well accepted as monophyletic groups and treated as orders within the Neuropteroidea, but only a few - often cryptic - characters indicate so.

However, the phylogenetic relationships of these orders became even more confused when in 1980 RODENDORF & RASNITSYN published their book on "The historical development of the class insecta" (in Russian) and the extinct group Glosselytrodea (synonymous with Jurinida) was added. The Glosselytrodea represent a taxon stratigraphically well distributed mainly in palaeozoic times which was formerly assigned to the Paurometabola. The opinion of RODENDORF & RASNITSYN on the phylogenetic relationships of the Neuropteroidea is here given in figure 1 and should be valid as an arbitrary scheme pending further discussions.

2. INTERPRETATION OF FOSSILS

Fossil Neuropteroidea are mainly preserved in sedimentary rocks as wing or, rarely, as almost complete specimen impressions or, in an often much better state of preservation, in fossiliferous resins; the former evidenced the stratigraphic record from Upper Permian upwards, the latter since early Cretaceous. Unfortunately not any derived groundplan characters are recognizable in the wing venation, hence it follows that especially Palaeozoic fossils that agree in the wing venation with recent Neuropteroidea should not automatically be assigned to one of their subgroups. For instance the determination of fossil Planipennia by their comb-like proliferation of branches of the radial sector is only tentative, since ACHTELIG (1980) gave evidence of this character in species of the extinct Palaeodictyoptera and Megasecoptera. "On the other hand, the non-pectinate radial sector, the fusion of the bases of M and Cu, and the distal fusion of the anal veins are not characters of the Neuropteroidea, let alone of the Planipennia" (ACHTELIG 1980).

3. STEMGROUP - PLANIPENNIA

There are some fossils from late Palaeozoic (Upper Permian) which presumably belong to the Planipennia, but "the most striking similarity between the wings of several of "... these ..." Permian Planipennia and a number of recent families is the presence of trichosors (small thickenings of the wing margin between the tips of the veins and veinlets)" (ACHTELIG 1980). Different families (Palaeomerobiidae, Sialidopseidae, Permithonidae, Archeosmylidae and some synonymous names exist) from the Upper Permian of Australia, Siberia, South Africa and South America habe been established, but actually we do not know whether they belong to the stemgroup or to more advanced recent subgroups of the Planipennia. These families are formally classified due to the amount of branches in the radial sector, the running position of the subcosta either into the costa or into the radius, and the size of the forewings. Probably all of these characters do not have significant value in a phylogenetic interpretation of the whole order, but they are sufficient for a palaeontological (more typological) classification outline, which, naturally, is based only on morphological peculiarities.

Possibly the Palaeomerobiidae and the Sialidopseidae are closer related, forming a superfamily Hemerobiidea (sensu MARTYNOVA 1962), whereas the Permithonidae and the Archeosmylidae, which survived up to the Triassic, are forming another superfamily Polystoechotidea (sensu MARTYNOVA 1962). CARPENTER (1954) considered the Lower Permian Permoberothidae to be the oldest Planipennia, but these are now generally assigned to the Glosselytrodea (RODENDORF & RASNITSYN 1980).

4. PROPOSALS FOR PHYLOGENETIC TREES OF THE PLANIPENNIA

Another arbitrary or perhaps a working hypothesis is the assumption that all the categories in the rank of the recent families are monophyletic since we do not know the exact sister-group relationships between these families. Detailed classification outlines have been given already by HANDLIRSCH (1906 - 1908) and TILLYARD (1962), but WITHYCOMBE's phylogenetic tree published in 1924, in which he showed the presumed sister-group relationships within the order Planipennia, has been adopted in its main emphasis by later authors as FRIEDRICH (1953), and slightly modified by ASPÖCK et al. (1980) and SCHLÜTER (1984). Some objections against it came from the Russian school of Palaeoentomology, expecially by Olga MARTYNOVA (1952) and more specified in 1962 (see RODENDORF et al. 1962). W. HENNIG compared and discussed both opinions in his famous book "Die Stammesgeschichte der Insekten" (1969) and figured the two different phylogenetic trees (fig. 2) proposed by MARTYNOVA and WITHYCOMBE. Later some additional extinct taxa in the rank of new families have been established and their relationships

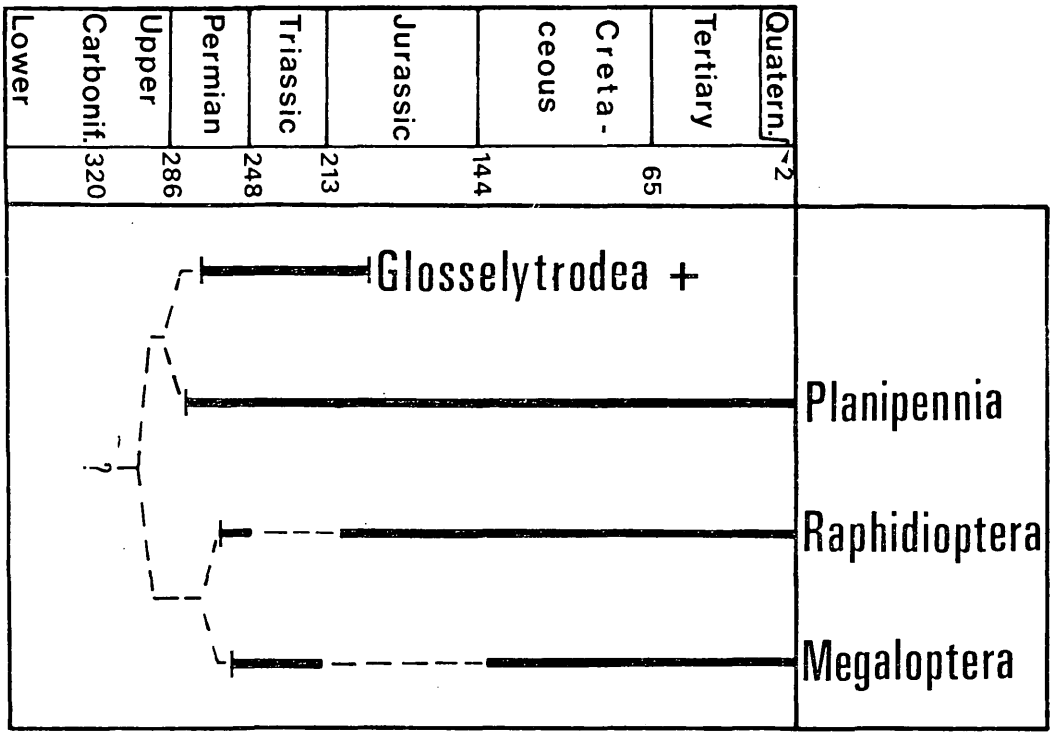

Fig. 1: The phylogenetic relationships of the orders of the Neuropteroidea, as presumed and presented by RODENDORF & RASNITSYN (1980). Slightly modified especially in the nomenclature.

discussed. However, a main agreement in the classification of the superfamilies as shown here in table 1 is clearly recognizable. Obviously the comparison leads to the following still open questions:

1. The position of the Mantispoidea:
   a. They are derived from early Hemerobioidea after MARTYNOVA.
   b. They are derived or at least closely related to the Osmyloidea after WITHYCOMBE.

2. The position of the Sisyridae:
   a. They belong to the Hemerobioidea after MARTYNOVA.
   b. They belong to the Osmyloidea after WITHYCOMBE, RODENDORF & RASNITSYN and other authors.

5. THE STRATIGRAPHIC RECORD OF THE FAMILIES OF THE PLANIPENNIA

The framework of the phylogenetic tree given in figure 3 is generally a modified version of that already published in WITHYCOMBE (1924). Virtually all the systematic categories in the rank of families established by later authors are incorporated herein. Yet this scheme is not wholly satisfactory, but for the moment the scheme here given, in which the order Planipennia is subdivided into 33 families (19 living and 14 extinct), appears to be reasonable in the light of consideration of both living and extinct groups in a joint lineage diagram.

MARTYNOVA (1962)	WITHYCOMBE (1924) and later authors
Myrmeleontidea	**Myrmeleontoidea**
Solenoptilidae	Solenoptilidae
Nymphitidae	Nymphitidae
not mentioned	Nymphidae
Myrmeleonidae	Myrmeleonidae
not mentioned	Stilbopterygidae
Ascalaphidae	Ascalaphidae
Nemopteridae	Nemopteridae
Hemerobiidea	**Hemerobioidea**
Psychopidae	Psychopsidae
not mentioned	Brucheiseridae
Kalligrammatidae	Kalligrammatidae
Brongniartiellidae	ancestors of Rapimatidae after RIEK
Palaeomerobiidae	Palaeomerobiidae
Sialidopseidae	Sialidopseidae
Hemerobiidae	Hemerobiidae
Sisyridae	belonging to Osmyloidea
Chrysopidae	Chrysopidae
Mesochrysopidae	belonging to Chrysopidae
not mentioned	**Mantispoidea**
not mentioned	Dilaridae
Berothidae	Berothidae
not mentioned	Mantispidae
Prohemerobiidae	not mentioned
Proberothidae	not mentioned
Osmylopsychosidae	belonging to Osmyloidea
Polystoechotidea	**Osmyloidea**
Permithonidae	Permithonidae
Archeosmylidae	Archeosmylidae
Osmylidae	Osmylidae
Osmylitidae	Osmylitidae
belonging to Hemerobiidea	Osmylopsychopsidae
Mesopolystoechotidae	Mesopolystoechotidae
not mentioned	Polystoechotidae
not mentioned	Neurorthidae
belonging to Hemerobiidea	Sisyridae
Coniopterygidea	**Coniopterygoidea**
Coniopterygidae	Coniopterygidae
not mentioned	**Ithonoidea**
not mentioned	Ithonidae
not mentioned	Rapismatidae (incl. Brongniartiellidae)

Table 1: Comparison of the systematic classification outlines presented by MARTYNOVA (1962) and WITHYCOMBE (1924) for the families of the order Planipennia.

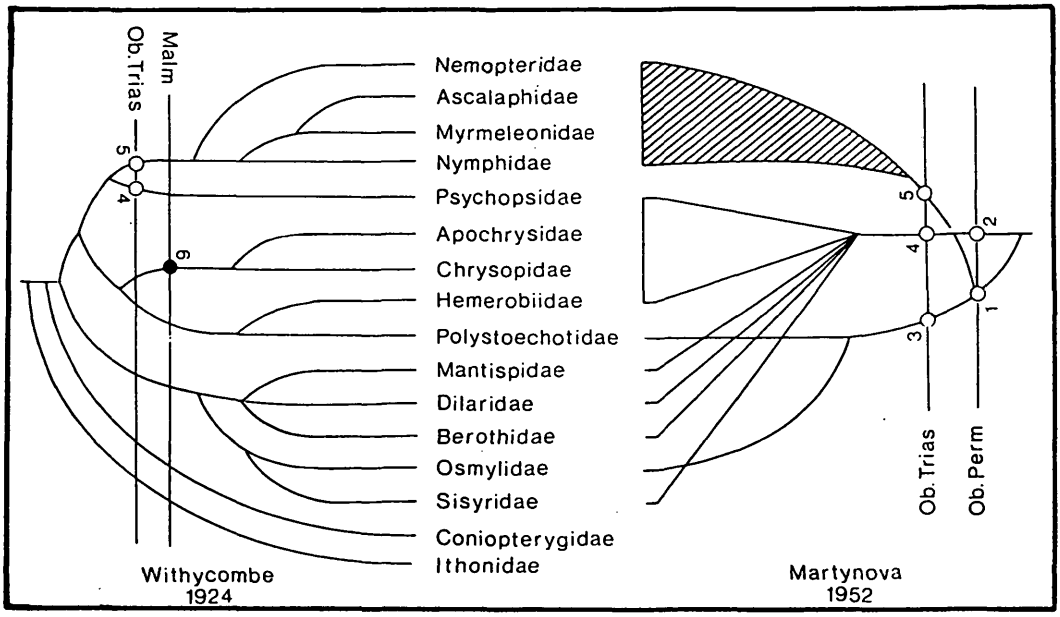

Fig. 2: Proposals of phylogenetic trees of the families of the Planipennia as given in MARTYNOVA (1952) and WITHYCOMBE (1924). Circles indicate the following taxa: 1: Permithonidae (incl. Permegalomidae) and Archeosmylidae from the Upper Permian of Australia and the USSR; 2: Palaemerobiidae from the Upper Permian of the USSR; 3: Petrushevskia borisi MARTYNOVA from the Upper Triassic of Issyk-Kul; 4: Triassopsychops superba TILLYARD from the Upper Triassic of Ipswich (Australia); 5: Sogjuta speciosa MARTYNOVA from the Upper Triassic of Issyk-Kul; 6: Mesypochrysa latipennis MARTYNOVA from the Upper Jurassic of Karatau (Kasachstan).

But similarly as presented in the book of HARLAND et al. (1967), another object of figure 3 lies essentially in the documentation of published records of fossil Planipennia in their stratigraphic context. First- and last-known fossil records of the respective families were to be related as precisely as possible to the standard scheme of the stratigraphic divisions and units. Such a compilation should be a valuable information for a variety of uses, e. g. such as to draw attention to the deficiencies of our present knowledge.

Particularly, more research on the known ranges of the living families is necessary, as opposed to the hypothetical ranges often ascribed to taxa in phylogenetic and other interpretations. Another aim of this paper is to provide a documentation of time ranges of the families of the Planipennia easily accessible to the non-palaeontologically informed and experienced neuropterologist.

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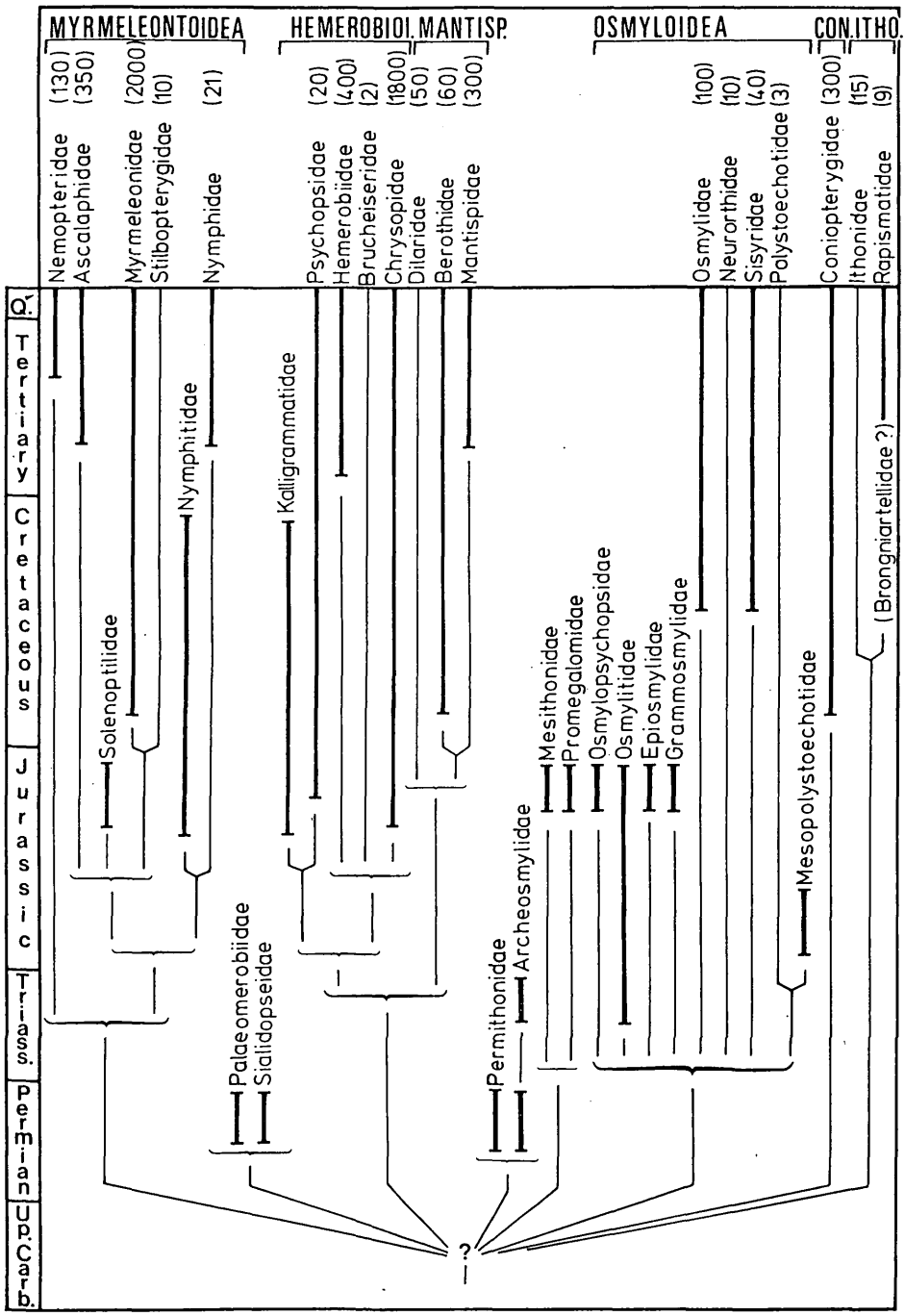

Fig. 3: The stratigraphic range of the families of the order Planipennia. 19 existent (in brackets the number of living species) and 14 extinct families are given. Wide beams give a more or less continuous fossil record for the respective family, thin lines indicate fossil gaps but presumable ranges. Lines connected by brackets give possible relationships.

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