

Cladistic analysis of Neuroptera and their systematic position within Neuropterida (Insecta: Holometabola: Neuropterida: Neuroptera)

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Abstract. A phylogenetic analysis of Neuroptera using thirty-six predominantly morphological characters of adults and larvae is presented. This is the first computerized cladistic analysis at the ordinal level. It included nineteen species representing seventeen families of Neuroptera, three species representing two families (Sialidae and both subfamilies of Corydalidae) of Megaloptera, two species representing two families of Raphidioptera and as prime outgroup one species of a family of Coleoptera. Ten equally most parsimonious cladograms were found, of which one is selected and presented in detail. The results are discussed in light of recent results from mental phylogenetic cladograms. The suborders Nevrothiformia, Myrmeleontiformia and Hemerobiiformia received strong support, however Nevrothiformia formed the adelphotaxon of Myrmeleontiformia + Hemerobiiformia (former sister group of Myrmeleontiformia only). In Myrmeleontiformia, the sister-group relationships between Psychopsidae + Nemopteridae and Nymphidae + (Myrmeleontidae + Ascalaphidae) are corroborated. In Hemerobiiformia, Ithonidae + Polystoechotidae is confirmed as the sister group of the remaining families. Dilaridae + (Mantispidae + (Rhachiberothidae + Berothidae)), which has already been proposed, is confirmed. Chrysopidae + Osmylidae emerged as the sister group of a clade comprising Hemerobiidae + ((Coniopterygidae + Sisyridae) + (dilarid clade)). Despite the sister-group relationship of Coniopterygidae + Sisyridae being only weakly supported, the position of Coniopterygidae within the higher Hemerobiiformia is corroborated. At the ordinal level, the analysis provided clear support for the hypothesis that Megaloptera + Neuroptera are sister groups, which upsets the conventional Megaloptera + Raphidioptera hypothesis.

Introduction

Neuroptera, with about 6000 species in seventeen families, is an ancient order of insects that exhibit an exceptionally broad range of morphological and biological diversity. The monophyly of the group has not been in doubt and is mainly based on morphological characters of the larvae. 'The sucking tubes of the larvae are not only their most spectacular autapomorphy but also the magic formula for a rich evolutionary aquatic and terrestrial diversification...' (Aspöck, 1992). Together with

Megaloptera (270 species, two families) and Raphidioptera (205 species, two families), they constitute superorder Neuropterida, which is commonly considered to be the most primitive Holometabola. The comparatively small number of species, heterogeneity of taxa, vicariant distribution patterns and rich fossil record all suggest that the golden age of Neuropterida has long expired. The extant fauna is but a remnant of that of former times and many groups can be characterized as living fossils (Aspöck, 1998; Aspöck & Aspöck, 1994, 1999).

The monophyly of Neuropterida and their systematic position within Holometabola as the sister group of Coleoptera are generally accepted. These hypotheses are established by numerous arguments that are to some extent cryptic and sophisticated (Hennig, 1969, 1981; Mickoleit, 1973; Aspöck *et al.*, 1980; Paulus, 1986; Aspöck *et al.*, 1991;

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Cordially dedicated to Horst Aspöck on the occasion of his 60th birthday (21 July 1999).

Kristensen, 1991, 1995; Whiting *et al.*, 1997). Strong persuasive characters are lacking, but there are no convincing alternatives. Thus, the monophyly of Neuropterida awaits verification or falsification, but this is not the aim of the present analysis.

Until recently, the favoured arrangement for the internal relationships of Neuropterida had Neuroptera as the adelphotaxon of Megaloptera + Raphidioptera (arguments summarized in Aspöck *et al.*, 1980, 1991) and was based on the hypothesis of the monophyly of each of the three orders. Only the monophyly of Neuroptera and the homogeneous Raphidioptera have not been questioned. Although the monophyly of Megaloptera has not been fully worked out, it is an operational hypothesis of the present analysis. It should be mentioned, however, that two versions of a paraphyletic Raphidioptera have been previously proposed. One ((Raphidiidae + Corydalidae) + Chauliodidae) + Sialidae, was proposed by Achtelig (1967), but then rejected by Achtelig & Kristensen (1973). The other, Sialidae + Raphidioptera, was based on wing characters (Hennig, 1953) and supported by Stys & Bilinsky (1990) on the basis of specialized telotrophic ovarioles. The 'ovariole' approach (Stys & Bilinsky, 1990; Büning, 1994; Kubrakiewicz, 1998) advocates conservatism of the ovary complex as phylogenetically meaningful. Another argument, which stresses the evolutionary conservatism of certain structures, is Sziraky's (1996a,b, 1998) female internal genitalia (FEIG) concept. The comparative morphology of FEIG structures in diverse representatives of Neuroptera should be subjected further to strict cladistic analysis.

The presence of aquatic larvae has always been the chief argument for the monophyly of Megaloptera. Yet, in another context, aquatic larvae have been considered plesiomorphic within Neuropterida, and the tracheal gills of the larvae of Megaloptera regarded as an autapomorphy of this group (Aspöck, 1995).

The idea that Megaloptera + Neuroptera have a sister-group relationship is not a resurrection of Bodreaux's (1979) concept, which was based on wing venation, but a new hypothesis based on the presence of aquatic larvae as a synapomorphy for these orders (Aspöck, 1995). Another larval feature supporting this relationship is the elongation of the stipes, which served as a pre-adaptation for the evolution of the sucking mouthparts (Aspöck, 1995).

Classification of Neuroptera has a long history and was centred primarily on palaeontological criteria (Handlirsch, 1906–1908) and, later, predominantly the wing venation of recent species and fossil material (Comstock, 1918; Tillyard, 1919). Withycombe (1925), ahead of his time, was first to focus on early developmental stages and internal anatomy as phylogenetic criteria. Although pre-Hennigian, his otherwise classical phylogenetic tree has entered modern monographs (e.g. Aspöck *et al.*, 1980; New, 1989).

MacLeod's (1964) excellent study of the larval head capsule included representatives of nearly all neuropteran families, although not Nevrothidae. Two groups clearly emerged from that morphological study: Hemerobiiformia, with a more primitive larval head, and Myrmeleontiformia with a highly specialized head. Thereafter, only Myrmeleontiformia

received further cladistic investigation (Henry, 1978; Mansell, 1992). The first modern approach toward systematization of Hemerobiiformia and, consequently, also of Neuroptera, was catalysed by a new interpretation of Nevrothidae that resulted in a triple-suborder concept: Nevrothiformia, Myrmeleontiformia and Hemerobiiformia (Aspöck, 1992, 1993, 1995). The phylogenetically isolated position of Nevrothiformia and the hitherto overlooked derived state of the head capsule of Hemerobiiformia ('maxillary-head') were the most important traits supporting this concept.

Several familial clades have been examined using computerized cladistic methods: Chrysopidae (Brooks & Barnard, 1990), Psychopsidae (Oswald, 1993b), Hemerobiidae (Oswald, 1993a), Myrmeleontidae, Brachynemurini (Stange, 1994) and Berothidae (Aspöck & Nemeschkal, 1998). Except for a preliminary abstract (Aspöck & Nemeschkal, 1999), no computerized cladistics on Neuroptera have been published. The present study reports such an analysis and aims to establish a systematization (*sensu* Ax, 1984, 1988; Lincoln *et al.*, 1988; Sudhaus & Rehfeld, 1992) of Neuroptera, which confronts phylogenetic relationships derived from previous mental analyses (Aspöck, 1992, 1993, 1995) and a systematization of Neuropterida with the sister group Megaloptera + Neuroptera as opposed to the previously regarded sister group Megaloptera + Raphidioptera.

Materials and methods

Nineteen taxa of Neuroptera were chosen to represent all seventeen families. An eighteenth family, Rapismatidae, most probably belongs to Ithonidae (see Penny, 1996, below). It was excluded, however, because the larvae of this taxon are unknown. Species were selected, as far as possible, by data availability for males, females and larvae. In two families, Ithonidae and Psychopsidae, we were constrained by a lack of material to examine the adults and larvae of disparate species (see Table 1).

Species examined are listed in Table 1. Most were obtained from the Naturhistorisches Museum, Wien (NHMW) and Horst & Ulrike Aspöck collection (HUAC). Adults and larvae of *Zabrus tenebrioides* (Goeze) (Carabidae, Coleoptera) are from the Klausnitzer collection (Dresden), the larva of *Nemoptera coa* (Linnaeus) from the Tröger collection (Freiburg) and the larva of *Sisyra fuscata* (Fabricius) from the Weißmair collection (Wolfers, Austria). Data for several larvae were available only from accounts in the literature: Ithonidae, Polystoechothidae, Psychopsidae, Nymphidae (MacLeod, 1964), and Dilaridae, Rhachiberothidae, Berothidae, Mantispidae (Minter, 1990; 1992).

Additional material studied included the following. Coleoptera: adults and larvae of Cleridae (coll. Klausnitzer), Elmidae (NHMW); Neuropterida: larvae of Nemopteridae (coll. Mansell, Pretoria; coll. Monserrat, Madrid), Ascalaphidae and Chrysopidae (coll. Stelzl, Graz). All available adults of Corydalidae from the NHMW and

Table 1. Species examined.

Species	Family, order
<i>Zabrus tenebrioides</i> (Goeze, 1777)	Carabidae, Coleoptera
<i>Atlantoraphidia maculicollis</i> (Stephens, 1836)	Raphidiidae, Raphidioptera
<i>Chauliodes pectinicornis</i> (Linnaeus, 1763)	Chauliodinae & Corydalidae, Megaloptera
<i>Corydalus cornutus</i> (Linnaeus, 1758)	Corydalinae & Corydalidae, Megaloptera
<i>Parainocellia resslis</i> (H. Aspöck & U. Aspöck, 1965)	Inocelliidae, Raphidioptera
<i>Sialis lutaria</i> (Linnaeus, 1758)	Sialidae, Megaloptera
<i>Acanthaclisis baetica</i> Rambur, 1842	Myrmeleontidae, Neuroptera
<i>Chrysopa pallens</i> (Rambur, 1838)	Chrysopidae, Neuroptera
<i>Drepanopteryx phalaenoides</i> (Linnaeus, 1758)	Hemerobiidae, Neuroptera
<i>Helicoconis lutea</i> (Wallengren, 1871)	Coniopterygidae, Neuroptera
<i>Libelloides macaronius</i> (Scopoli, 1765)	Ascalaphidae, Neuroptera
<i>Mantispa styriaca</i> (Poda, 1761)	Mantispidae, Neuroptera
<i>Megalithone tillyardi</i> Riek, 1974 (adults), <i>Ithone fusca</i> Newman, 1838 (larvae)	Ithonidae, Neuroptera
<i>Microberotha vesicaria</i> Tjeder, 1968	Rhachiberothidae, Neuroptera
<i>Nallachus krooni</i> Minter, 1986	Dilaridae, Neuroptera
<i>Nemoptera coa</i> (Linnaeus, 1758)	Nemopteridae, Neuroptera
<i>Nevrorthus fallax</i> (Rambur, 1842)	Nevrorthidae, Neuroptera
<i>Nymphes myrmeleonoides</i> Leach, 1814	Nymphidae, Neuroptera
<i>Osmylus fulvicephalus</i> (Scopoli, 1763)	Osmylidae, Neuroptera
<i>Podallea vasseana</i> (Navás, 1910)	Berothidae, Neuroptera
<i>Polystoechotes punctatus</i> (Fabricius, 1793)	Polystoechotidae, Neuroptera
<i>Cabralis gloriosus</i> Navás, 1912 (adults), <i>Psychopsis elegans</i> (Guérin-Ménéville, 1844) (larvae)	Psychopsidae, Neuroptera
<i>Sisyra fuscata</i> (Fabricius, 1793)	Sisyridae, Neuroptera

HUAC, and of Nevrorthidae from the National Science Museum, Tokyo, were examined.

Finally, it should be emphasized that the present work relied greatly on the wealth of information in two monographic works: *Neuroptera of Europe* (Aspöck *et al.*, 1980) and *Raphidioptera of the World* (Aspöck *et al.*, 1991), which are largely cited for the figures of genitalia, although the terminology and figure labels may have changed in the meantime. Illustrations of larval head capsules largely refer to the work of MacLeod (1964). Terminal structures of adult abdomen and larvae were cleared in cold KOH solution and embedded in glycerine for study.

Cladistic relationships were determined using Hennig86 (version 1.5; Farris, 1988). The dataset comprised thirty-six characters (Table 2). Of eighteen adult characters, eleven were specific to male genitalia and five to female genitalia. Of the sixteen larval characters, thirteen concerned the head capsule and the mouthparts. Several characters, although earnestly considered, were rejected as unsuitable for this study. For example, all wing characters but one were omitted as they ultimately proved too heterogeneous at this level. However, certain wing characters have been extensively analysed and employed at the family level, e.g. Hemerobiidae (Oswald, 1993a).

Nineteen characters are binary and seventeen multistate. Normally, it is desirable to code each described state of a character separately and not combine character states by including one in the definition of another. In characters 6–10, we have coded the apparent, secondary loss of that structure

with the character state (0), instead of awarding it its own apomorphic character state. We consider in these specific cases that it would be a weaker hypothesis to code these losses as if they were primary and homologous than to assume that the losses are secondary.

At an earlier stage in the analysis (Aspöck & Nemeschkal, 1999), the internal relationships of Neuroptera were compared using Raphidioptera and Megaloptera as outgroup taxa. The taxa base was subsequently expanded and Coleoptera and Raphidioptera were selected as outgroup taxa. Coleoptera are generally considered to be the sister group to Neuropterida. *Zabrus* Clairville (Carabidae) was chosen to represent Coleoptera as the primary outgroup, in part, because it is possible to recognize homologies in the genital structures as well as in the larval head capsule and mouthparts with respect to Neuropterida.

In Hennig86, we used the command sequence 'mh*; bb' as well as 't; bb*' to rapidly examine the behaviour of the data. The taxa were input in the order given in Table 2, but the order was not varied experimentally to search for shorter cladograms. All character states were treated as unordered and we did not *a priori* assign differential weights to characters.

Several variations of implicit enumeration commands containing 'ie' and 'ie*' were employed also (despite very high time consumption), the results of which are certain to contain the most parsimonious cladograms. The cladograms were examined by manually plotting out the proposed synapomorphies.

Table 2. Data matrix used in cladistic analysis.

Taxa	Characters																																								
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36					
Outgroup																																									
<i>Zabrus tenebrioides</i>	0	0	1	2	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0				
<i>Atlantoraphidia maculicollis</i>	1	0	1	0	0	0	0	0	0	0	0	0	0	0	1	2	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0				
<i>Chaulioides pectinicornis</i>	2	1	0	1	1	0	0	0	0	0	0	0	0	0	2	2	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	1	0	0	0				
<i>Corydalus cornutus</i>	2	1	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	1	0	0				
<i>Parainocellia ressi</i>	1	0	1	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0				
<i>Sialis lutaria</i>	3	0	0	1	1	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	1	2	1	0	2	0	0	0	0	0	0	0	1	0	1	0			
Neuroptera																																									
<i>Acanthaclisis baetica</i>	3	1	0	1	2	0	0	1	0	0	0	0	1	1	0	0	0	0	1	0	1	0	1	1	0	1	0	0	2	0	0	0	0	0	0	1	2	0			
<i>Chrysopa pallens</i>	2	0	0	1	2	0	0	0	0	0	0	1	0	1	2	0	0	0	1	0	0	1	2	1	1	1	1	0	1	0	0	0	0	0	2	2	0	0			
<i>Drepanopteryx phalaenoides</i>	2	1	0	2	2	0	0	1	0	1	0	0	0	1	2	0	0	0	1	0	0	1	2	1	2	2	1	0	1	0	0	0	0	0	2	2	0	0			
<i>Helicoconis lutea</i>	3	1	1	1	3	2	0	0	0	0	3	0	1	2	0	1	0	1	1	0	1	2	1	2	2	1	1	2	0	0	0	0	2	0	0	0	2	0			
<i>Libelloides macaronius</i>	3	1	0	1	2	0	0	1	0	0	0	0	1	1	2	1	0	0	1	0	1	0	1	1	0	1	0	0	2	0	0	0	0	1	0	0	0	1	0		
<i>Mantispa styriaca</i>	3	1	0	1	2	0	0	0	1	1	1	0	0	0	2	0	0	0	1	1	0	1	2	1	2	2	0	0	1	1	1	0	0	2	0	0	2	0	1		
<i>Megalithone tillyardi</i> (adults)																																									
& <i>Ithone fusca</i> (larvae)	2	1	0	1	2	0	0	0	0	0	0	0	0	1	2	0	0	0	1	0	0	1	1	1	2	1	0	0	0	0	0	1	0	2	0	0	0				
<i>Mucroberotha vesicaria</i>	2	1	0	1	2	0	0	0	1	1	1	1	2	1	2	2	0	0	1	1	0	1	2	1	2	2	0	0	1	1	1	0	0	2	0	0	2	0	0		
<i>Nallachus krooni</i>	2	1	0	1	2	0	0	0	0	1	0	0	0	0	1	0	0	0	1	1	0	1	2	1	2	2	0	0	0	1	1	0	0	2	0	0	2	0	0		
<i>Nemoptera coa</i>	2	1	0	1	2	0	1	2	0	0	0	0	0	1	2	1	0	1	1	0	0	0	1	1	0	1	0	0	2	0	0	0	0	1	0	0	0	1	0		
<i>Nevrorthus fallax</i>	2	0	1	1	2	0	2	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0	1	1	0		
<i>Nymphes myrmeleonoides</i>	2	0	0	1	2	0	1	1	1	0	0	0	0	1	2	0	0	0	0	1	2	0	1	0	1	1	0	0	2	0	0	0	0	0	0	1	0	0	1	0	
<i>Osmylus fulvicephalus</i>	2	1	0	1	2	1	0	0	0	0	0	0	0	0	0	0	0	0	1	2	0	1	2	1	1	1	0	0	0	0	0	0	0	0	2	2	0	0	2	0	
<i>Podallea vasseana</i>	2	0	0	1	2	0	0	0	1	1	1	1	0	1	2	0	0	0	1	1	0	1	2	1	2	2	0	0	0	1	1	0	0	2	0	0	1	0	0	2	0
<i>Polystoechotes punctatus</i>	2	0	0	1	2	1	0	1	1	0	0	0	0	0	2	0	0	0	1	0	0	1	1	1	2	1	0	0	0	0	0	1	0	2	0	0	1	0	2	0	
<i>Cabralis gloriosus</i> (adults) & <i>Psychopsis elegans</i> (larvae)	2	1	0	1	2	0	0	1	0	0	0	1	0	1	0	0	0	1	1	0	0	0	1	1	0	1	0	0	2	0	0	0	0	1	0	0	0	1	0		
<i>Sisyra fuscata</i>	2	0	0	1	2	0	0	0	0	0	0	0	0	0	0	0	1	0	1	1	0	1	2	1	2	3	1	1	3	0	0	0	0	2	3	0	0	2	3	0	

The analysis is based on species. However, the comments and observations in the following section refer to species within their respective genus or family.

Characters and observations

Male terminalia

1. *Trichobothria*: (0) absent; (1) loosely forming a band (Aspöck *et al.*, 1991: Fig. 1036); (2) organized in a rosette (Aspöck *et al.*, 1980: Fig. 341); (3) reduced (Aspöck *et al.*, 1980: Fig. 792).

The accumulation of trichobothria, as found in Neuropterida, seems to be restricted to this group (Tuxen, 1970; Torre-Bueno, 1989) and is a synapomorphy of Neuropterida. Primary absence is thus plesiomorphic (0); a band-like formation (1) is apomorphic and serves as an autapomorphy for Raphidioptera. Formation of a rosette is a derived state (2) and synapomorphic for Megaloptera and Neuroptera. Reduction must have occurred independently several times (as evidenced by diverse modifications of the ectoprocts) and is autapomorphic for *Sialis* Latreille, *Acanthaclisis* Rambur, *Helicoconis* Enderlein, *Libelloides* Schäffer and *Mantispa* Illiger.

The trichobothria rosette is an important landmark in the homology of the anal segment in Megaloptera. It is interpreted

as tergite 10 + callus cerci + 9th gonocoxites (Acker, 1960: Figs 27, 29, 31, 33; Glorioso, 1981: Figs 22, 23; New & Theischinger, 1993: Fig. 37d). However, the sclerite that carries the trichobothria, the ectoproct, which Tjeder (1954) considered as tergite 10 or tergite 10 + 11, is not fused with the gonocoxites. In Megaloptera, the ectoproct may be divided, apparently secondarily, into dorsal and ventral parts.

2. *Ectoproct*: (0) unpaired (Aspöck *et al.*, 1980: Fig. 359); (1) paired (Aspöck & Mansell, 1994: Figs 7, 8, 39, 40).

Irrespective of its composition (tergite 10 + 11 or tergite 10 only), the unpaired ectoproct appears to be the primitive state (0). In the analysis, paired ectoprocts (1) emerged as an autapomorphy of Corydalidae and a synapomorphy of Myrmeleontiformia + Hemerobiiformia, although, with several reversals.

Tjeder (1954, 1970) apparently interpreted the lateral process of the ectoprocts in 'primitive Corydalidae' as the primitive condition and the fusion of these processes in lateral plates and their further dorsal fusion in a half-ring as derived in Neuroptera. However, Corydalidae do not appear primitive in this respect; on the contrary, the divided ectoproct is probably secondary.

Acker (1960) interpreted the ectoproct of Megaloptera as an amalgamation (thus a derived condition) of tergite 10 and the 9th gonocoxites (his Figs 27, 28, 'coxopodite 9'). Glorioso (1981: Fig. 22) attributed the lateral process of the ectoproct to gonostylus IX.

The supraanale of Dilarinae (Aspöck *et al.*, 1980: Figs 425, 428, 429, 446–449), which was suspected to represent the modified ectoproct (Aspöck *et al.*, 1980), may be confidently homologized with this structure, as evidenced by the ‘transitional’ ectoprocts of Nallachiinae (Adams, 1970: Figs 5A, 7, 8A, 9B, 9D; Penny, 1994: Figs 3, 4).

3. *Tergite and sternite of segment 9*: (0) free (Aspöck *et al.*, 1980: Fig. 561); (1) forming a ring (Aspöck *et al.*, 1980: Figs 256, 346, 347).

Tergite 9 and sternite 9 fused to a ring is apomorphic (1) and appears to be an independent autapomorphy for Nevrothidae and Coniopterygidae (parallelism). Since all representatives assigned to the outgroup have the apomorphic state, the character emerged in the analysis as a reversal uniting Megaloptera and Neuroptera. Although it cannot be refuted that our outgroup, Coleoptera and Raphidioptera, share the derived ring-like segment 9, a more realistic course of evolution is to assume independent acquisitions of the ring and to interpret free tergite 9 and sternite 9 as a symplesiomorphy of Megaloptera and Neuroptera.

4. *Ninth gonocoxites, size*: (0) large lateral plates, covering internal genitalic sclerites (Aspöck *et al.*, 1991: Fig. 2440); (1) small appendix-like sclerites (Aspöck *et al.*, 1980: Fig. 383, *cp*); (2) absent.

Large 9th gonocoxites are primitive (Weidner, 1982), their modification into smaller appendage-like sclerites is apomorphic (1) and a synapomorphy of Megaloptera and Neuroptera. *Zabrus*, a member of the outgroup, is apomorphic (2) with respect to the 9th gonocoxites.

State (2) also occurs in *Drepanopteryx phalaenoides* (Linnaeus). However, the loss of the 9th gonocoxites cannot be interpreted as an autapomorphy of Hemerobiidae, since state (1) is found in the primitive genus *Carobius* Banks which still possesses small 9th gonocoxites (New, 1988; Oswald, 1993a).

In Megaloptera, the 9th gonocoxites may be fused. They were interpreted as parameres by Acker (1960: Figs 27, 28) and as gonocoxite X in *Acanthacorydalis orientalis* (McLachlan) by Glorioso (1981: Fig. 22), but as the tenth sternite in *Protohermes* Van der Weele, *Neoneuromus* Van der Weele, *Chloronia* Banks, *Corydalus* Latreille and *Platyneuromus* Van der Weele (his Figs 38–42). Penny & Flint (1982: Figs 13, 14, 19, 20) also regarded what we consider to be the 9th gonocoxites as the tenth gonocoxites in *Chloronia* species.

5. *Ninth gonocoxites, position*: (0) along the caudal margins of tergite 9 and sternite 9 (Aspöck *et al.*, 1991: Fig. 1195); (1) at or near the base of tergite 9 (Aspöck *et al.*, 1980: Fig. 6, *cp*); (2) associated with the gonarcus (Aspöck *et al.*, 1980: Fig. 358, *cp*); (3) associated with the ectoproct (Aspöck *et al.*, 1980: Figs 256, 257, *gs*).

The shifting of the bases of the 9th gonocoxites to the base of the tergite 9 is apomorphic (1) and a synapomorphy of Megaloptera. The association of the 9th gonocoxites with the gonarcus (2) is a strong synapomorphy of Neuroptera. In *Helicoconis lutea*, the 9th gonocoxites are associated with the ectoproct, an autapomorphy (3) of Coniopterygidae. In this

family, the 9th gonocoxites are known as the *gonarcus*, e.g. Tjeder (1954: Fig. 5A).

6. *Gonapophyses of the ninth gonocoxites*: (0) sclerites at the base of the 9th gonocoxites, closing the genitalia ventrally and externally (Aspöck *et al.*, 1991: Figs 1035, 1036, *h*), or sclerites (secondarily) absent (this state includes two descriptions, see Material and methods for coding); (1) small internal sclerites (Aspöck *et al.*, 1980: Fig. 341, at base of *cp*, not indicated); (2) small sclerites, visible externally (Aspöck *et al.*, 1980: Figs 256, 257, *ap*).

Large 9th gonapophyses are plesiomorphic (0) and have only been retained in Raphidioptera, where they are known as hypovalva (in Raphidiidae) or as pseudostyli when they are present in Inocelliidae. Reduced 9th gonapophyses in Osmyliidae, Polystoechotidae and Coniopterygidae are apparently apomorphic in two states (1, 2) and they serve as autapomorphies for these families.

In Raphidiidae, the 9th gonapophyses (= hypovalva) have secondarily undergone high diversification. In Osmyliidae and Polystoechotidae, the 9th gonapophyses have not been previously considered. In Coniopterygidae, they were misinterpreted as an appendage of the gonarcus in *Helicoconis*, e.g. *H. lutea* (Aspöck *et al.*, 1980: Figs 256, 257), or as an entoprocessus of the gonarcus in *Coniopteryx* Curtis, e.g. *C. loipetsederi* H. Aspöck (Aspöck *et al.*, 1980: Figs 271, 272).

7. *Gonarcus*: (0) unpaired plate, situated medially (Aspöck *et al.*, 1980: Fig. 359), or (secondarily) absent (this state includes two descriptions, see Material and methods for coding); (1) paired sclerites, situated laterally, connected medially (Aspöck *et al.*, 1980: Fig. 769, not labelled; Oswald, 1998: Figs 13, 15); (2) paired sclerites, situated laterally, not connected medially (Aspöck *et al.*, 1980: Fig. 349).

The more or less connected lateral sclerites are apomorphic (1) and convergent in Nemopteridae and Nymphidae, whereas the separated sclerites (2) are an autapomorphy of Nevrothidae.

Actually, we do not know what the gonarcus is. Tjeder (1954, 1970) introduced the gonarcus as an ‘invention’ (in the sense of an autapomorphy) of Neuropterida. However, the gonarcus more likely represents an old derivative of the eleventh segment. It could be the fused 11th gonocoxites. The eversible sacs of the gonarcus in Sialidae, a character not used in the analysis, may represent a synapomorphy of Megaloptera. In *Dysmicohermes ingens* Chandler (Chauliodinae, U.S.A.), the eversible sac provides some evidence for a lost gonarcus.

8. *Arcessus*: (0) paired sclerites (Aspöck *et al.*, 1980: Fig. 359, *pa*), or (secondarily) absent (this state includes two descriptions, see Material and methods for coding); (1) unpaired sclerite (*Drepanopteryx algida* (Erichson); Aspöck *et al.*, 1980: Fig. 463, *med*); (2) greatly enlarged sclerite (*Nemoptera coa*, Aspöck *et al.*, 1980: Figs 768–770).

An unpaired arcessus is apomorphic (1) and a synapomorphy of Myrmeleontiformia and apparently occurs convergently in both Polystoechotidae and Hemerobiidae. A greatly enlarged arcessus is an additional apomorphic state (2) and is an autapomorphy of Nemopteridae.

The term arcessus was coined by Tjeder (1954), who defined it as restricted to the flexible appendages attached to the gonarcus. However, he also referred to the same structure as the mediuncus, and subsequent authors applied the term to any processus-like amalgamation to the gonarcus. The term mediuncus, however, should be used for structures associated with the parameres and is certainly not homologous with the arcessus. To avoid introducing new terminology, the words arcessus and mediuncus are retained, but arcessus is restricted to the gonarcus-appendix and mediuncus (see also comments to ch. 10) is restricted to the sclerite(s) associated with the parameres. If we interpret the gonarcus as derived from the 11th gonocoxites, then the arcessus could be interpreted as derived from the styli of the 11th gonocoxites.

9. *Parameres*: (0) paired sclerites (Aspöck *et al.*, 1980: Figs 658, 659), or (secondarily) absent (this state includes two descriptions, see Material and methods for coding); (1) sclerites fused (Aspöck *et al.*, 1980: Fig. 466).

Paired parameres are plesiomorphic and still exist among representatives of Coleoptera, Raphidioptera and in the neuropteran families Hemerobiidae, Coniopterygidae, Chrysopidae, Dilaridae and Osmylidae, where they may be retained in single species only. Fused unpaired parameres are apomorphic and evolved several times independently but serve as a synapomorphy for the Mantispidae-Rhachiberothidae-Berothidae clade. The loss of parameres is most certainly secondary and always apomorphic.

The parameres are highly controversial structures. Our primary hypothesis is that the parameres are homologous in Coleoptera and Neuropterida. But it must be emphasized that in neuropterological literature the term parameres has been used differently and certainly not always for homologous structures.

In a cladistic analysis of Hemerobiidae, Oswald (1993a) referred to the parameres by a new name, the parabacula, and, in order to avoid confusion, followed Adams (1969) in homologizing the 'parameres' of male Neuroptera with the 9th gonocoxites of most other insects. The interpretation of Oswald that the parabaculum is a unique evolutionary novelty of Hemerobiidae is not adopted here. As we understand it, the parabacula of Hemerobiidae are not an autapomorphy of the family, and the parameres are not homologous with the 9th gonocoxites.

It is noteworthy that extant Megaloptera appear to lack parameres. Whether this is an autapomorphy of the order, or whether the parameres became lost several times independently, remains open.

What do plesiomorphic paired parameres look like? There is an amazing similarity of the parameres of *Italochrysa* Principi (Chrysopidae: Neuroptera; Aspöck *et al.*, 1980: Figs 658, 659) with those of certain Raphidioptera (Aspöck *et al.*, 1991: Figs 561, 713–730) and Coleoptera (Lawrence & Britton, 1991: Fig. 35.8). They are all paired, stick-like sclerites that are basally widened and connected to soft tissue. In Coleoptera, they are associated with the aedeagus, in Raphidioptera with the endophallus, in *Helicoconis* (Coniopterygidae: Neuroptera) with a large mediuncus (interpreted as the penis by all other investigators of the group). In *Drepanopteryx* Leach &

Brewster (Hemerobiidae), they are linked to a tiny sclerite that most certainly is the mediuncus, but which has not attracted any notice so far. In *Osmylus* Latreille (Osmylidae), the reduced parameres are associated with a pair of sclerites that have also not received special attention until now, and are interpreted here as the mediuncus. In Nallachiinae (Dilaridae), the paired parameres are associated with the Y-shaped mediuncus; in Dilarinae, the parameres have shifted to the gonarcus-gonocoxite-complex, and the mediuncus is lost. The New World genus *Nallachus* Navás shows the evolutionary pathway of the parameres from mediuncus to gonarcus.

10. *Mediuncus*: (0) paired (Aspöck *et al.*, 1980: Fig. 270, *p*), or (secondarily) absent (this state includes two descriptions, see Material and methods for coding); (1) unpaired, as in Minter (1986: Fig. 10, *mu*), where it is a small median sclerite located apically between elongate sclerites, or as a small sclerite above parameres (Aspöck *et al.*, 1980: Fig. 465, not labelled).

An unpaired mediuncus is apomorphic (1) and a synapomorphy of the dilarid-mantispid-rhachiberothid-berothid clade and convergent in Hemerobiidae and Coleoptera (penis).

Since the inception of the terms mediuncus and arcessus (Tjeder, 1954), the two have been confounded with each other (see comments under ch. 8, and Tuxen, 1970). Here, the term mediuncus is only applied to the sclerites that are connected with the parameres (see also comments under ch. 9, and in Aspöck *et al.*, 1980: Fig. 257, 'penis' of *Helicoconis*; Fig. 342, 'parameres' of *Osmylus*) or to sclerites that are incorporated into the paramere-mediuncus complex.

11. *Paramere-mediuncus complex*: (0) absent; (1) present (Aspöck *et al.*, 1980: Fig. 402; Aspöck & H. Aspöck, 1988: Fig. 14).

The fusion of the parameres and the mediuncus into an unpaired structure is apomorphic (1) and considered as a robust synapomorphy of Mantispidae, Rhachiberothiae and Berothidae.

Female terminalia

12. *Ectoproct*: (0) free (Aspöck *et al.*, 1980: Fig. 362); (1) fused with tergite 9 (Aspöck *et al.*, 1980: Fig. 760); (2) reduced (Aspöck *et al.*, 1980: Fig. 8); (3) absent.

A free ectoproct is plesiomorphic (0), fusion with the tergite 9 is apomorphic (1) and a synapomorphy of Rhachiberothidae and Berothidae, but also occurs independently in Chrysopidae and Psychopsidae.

13. *Tergite 9*: (0) simple sclerite (Aspöck *et al.*, 1980: Fig. 344); (1) divided ventrolaterally (Aspöck *et al.*, 1980: Figs 895, 896, not labelled); (2) sclerite with pseudohypocaudae (Aspöck & Mansell, 1994: Figs 13, 14).

A simple tergite 9 is plesiomorphic (0), ventrolateral separations are apomorphic (1) and emerged as a synapomorphy of Myrmeleontidae and Ascalaphidae. The phenomenon of a divided tergite 9 occurs independently in *Spermophorella* Tillyard (Berothidae) and is scattered among several other taxa as well. The pseudohypocaudae, which are digitiform processes, represent an autapomorphy (2) of

Rhachiberothidae, although, similar processes exist in *Austroberothella* U. Aspöck & H. Aspöck and *Protobiella* Tillyard (Protobiellinae: Berothidae).

14. *Ninth gonocoxites (attachment to tergite 9)*: (0) by a narrow 'articulation' (Aspöck *et al.*, 1980: Fig. 344); (1) broad connection (Aspöck *et al.*, 1980: Fig. 596).

A narrow 'articulation' is plesiomorphic (0) and belongs to the groundplan of, at least, Coleoptera and Neuropterida (Mickoleit, 1973; Kristensen, 1991: Fig. 5.6). The broad connection is apomorphic (1) and a synapomorphy of Myrmeleontiformia, but evolved independently in several families of Hemerobiiformia, appears autapomorphic in Ithonidae, Chrysopidae and Hemerobiidae, and as a synapomorphy of Rhachiberothidae and Berothidae.

15. *Ninth gonocoxites (ovipositor), length and shape*: (0) club-shaped (Aspöck *et al.*, 1980: Fig. 344); (1) elongate, tube-shaped (Aspöck *et al.*, 1991: Fig. 51, *gl*); (2) shortened, broadly oval (Aspöck *et al.*, 1980: Fig. 568, *gl*).

The medium-sized, club-shaped gonocoxites are plesiomorphic (0) and evolved divergently in two directions: the elongate ovipositor (1), on the one hand, and the shortened but often broadened sclerites of most neuropterans (2) on the other. The long ovipositor is apomorphic for Raphidioptera and Dilaridae. A long ovipositor also occurs in the mantispid subfamily Symphrasinae (not included in the study). In a previous study (Aspöck & Mansell, 1994), the long ovipositor was interpreted as a synapomorphy of the whole dilarid clade with reversals in Berothidae + Rhachiberothidae and the rest of Mantispidae, which may be an alternative hypothesis.

The short and broad ovipositor emerged as a synapomorphy of Hemerobiiformia and Myrmeleontiformia, with a reversal to club-shaped 9th gonocoxites in Psychopsidae, Myrmeleontidae, Osmylidae and Sisyridae. This result lacks plausibility for Osmylidae and Sisyridae since their ovipositor, with respect to shape and articulation, is most likely plesiomorphic.

16. *Sternite 8*: (0) unpaired (Lawrence & Britton, 1991: Fig. 35.9B, Aspöck *et al.*, 1980: Fig. 2, *sg*; 353); (1) paired (Aspöck *et al.*, 1980: Fig. 772); (2) absent.

An unpaired sternite 8 is certainly plesiomorphic (0), but modification and reduction of this unpaired sclerite must have occurred several times independently. A paired sternite 8 is apomorphic (1) and convergent in Nemopteridae and Ascalaphidae. Sternite 8 is lost (2) independently in Chauliodinae and Rhachiberothidae.

Remaining adult characters

17. *Labial palps, terminal segment*: (0) not enlarged; (1) enlarged.

The enlargement of the terminal segment of the labial palps is apomorphic (1) and emerged here as a synapomorphy of Coniopterygidae and Sisyridae. However, this character may have easily evolved independently and should not be interpreted as a strong argument for this sister-group relationship.

18. *Vena triplica of hindwing*: (0) absent; (1) present (Tjeder, 1960: Figs 327, 329, 331, 333; Tjeder, 1967: Fig. 1936, however, *M* should be read as *Rs*).

The vena triplica of the hindwing is apomorphic (1) and a synapomorphy of Psychopsidae and Nemopteridae. The phylogenetic usefulness of this character with respect to Psychopsidae was devaluated by Oswald (1993b), but he did not discuss Nemopteridae.

Larval characters

19. *Mandibular function*: (0) chewing; (1) sucking, in cooperation with the maxillae.

Sucking jaws in larvae, constructed by specialized mandibles and maxillae forming a tube, are apomorphic (1). This unique trait is a strong and classical synapomorphy of Neuroptera.

20. *Shape of mandibles*: (0) curved; (1) straight, without fracture line; (2) straight, with fracture line.

Curved mandibles are plesiomorphic (0), straight ones are apomorphic (1) and serve as an apomorphy of (Coniopterygidae + Sisyridae) + (the dilarid clade). Straight mandibles with a fracture line independently evolved as an autapomorphy (2) of Osmylidae.

Straight mandibles, although sometimes interpreted as primitive, are most likely a secondary adaptation to stationary prey. Curved mandibles are more efficient for catching and holding movable prey.

21. *Mandibles, grasping teeth*: (0) absent (New, 1989: Fig. 145); (1) present (New, 1989: Figs 146, 147).

Mandibles with grasping teeth are apomorphic (1) and a synapomorphy of Nymphidae + (Myrmeleontidae + Ascalaphidae).

22. *Head capsule, ventral aspect*: (0) closed, with or without gula (Aspöck, 1993: Figs 1–3); (1) open, mainly constructed by parts of the maxillae (Aspöck, 1993: Figs 4, 5).

A ventrally closed compact head capsule is plesiomorphic (0), an open head capsule, constructed mainly from elements of the maxillae ('maxillary head'), is apomorphic (1) for Hemerobiiformia and Sialidae.

23. *Gula*: (0) forming a large plate (Aspöck, 1993: Figs 1, 2); (1) reduced to small triangle (Aspöck, 1993: Fig. 3); (2) absent (U. Aspöck, 1993: Figs 4, 5).

A reduced gula is apomorphic (1) and a synapomorphy of Hemerobiiformia and Myrmeleontiformia, with a further apomorphic change (2) in higher Hemerobiiformia. There is an independent loss of the gula in Coleoptera.

The interpretation of the evolution of the gula is controversial. Kaestner (1973), for example, considered the gula of Neuropterida as apomorphic, which is certainly erroneous.

24. *Cardines*: (0) situated beyond apical boundary of head capsule (Aspöck *et al.*, 1991: Fig. 55); (1) integrated with the head capsule, so that it forms a large part of the ventral surface of the structural head.

The apical position of the cardines is plesiomorphic (0), integration with the head capsule is apomorphic (1) and a synapomorphy of Megaloptera and Neuroptera. Although

Zabrus shows the plesiomorphic state, it should be noted that integration of cardines with the head has evolved independently in many Coleoptera (Lawrence & Britton, 1991: Fig. 35.17).

Generally, the maxillary part of the sucking jaws are considered derived from the galea or lacinia (Withycombe, 1925). Whichever, there is no trace of a palpus. The basal parts of the maxilla, which are withdrawn into the head capsule, are interpreted as stipes and cardo (Withycombe, 1925; MacLeod, 1964). That no larva has been found with mouthparts intermediate between those of Megaloptera and those of Neuroptera was emphasized by Withycombe (1925). However, the large stipes in Megaloptera (Corydalidae), with a tiny palpus, gave rise to the hypothesis that the maxillary part of the jaws should be interpreted as stipes (Aspöck, 1995). As a consequence the basal parts should be the cardines only, irrespective of whether they are divided or undivided (divided cardines are known from Coleoptera, too). It is worth mentioning that Rousset (1966) interpreted the maxillary stylet to be composed of the stipes and lacinia.

25. *Cardines, length*: (0) shorter than one-third of the head capsule (Aspöck *et al.*, 1991: Fig. 55); (1) shorter than half of the length of the head capsule (Aspöck, 1993: Figs 2, 4); (2) longer than half of the length of the head capsule (Aspöck, 1993: Fig. 5).

Apomorphic states (1) and (2) are elongations: state (2) emerged as synapomorphy of Hemerobiiformia and state (1) as a synapomorphy of Chrysopidae and Osmylidae. The chrysopid-osmylid clade is only weakly supported by this character.

26. *Cardines, direction*: (0) horizontal (Aspöck *et al.*, 1991: Figs 55, 59); (1) oblique, directed proximally (Aspöck, 1993: Figs 3, 4); (2) parallel (Aspöck, 1993: Fig. 5); (3) oblique, directed distally (MacLeod, 1964: Fig. 28).

Horizontal cardines are plesiomorphic (0), proximally directed, oblique cardines are apomorphic (1) and a synapomorphy of Megaloptera and Neuroptera. In another evolutionary step, the cardines bend downward becoming parallel to each other. This is a synapomorphy (2) of Hemerobiidae, Coniopterygidae, Sisyridae and the dilarid clade; it is also an autapomorphy of Sialidae. The distally directed cardines signify another apomorphic state change (3) and are autapomorphic for Sisyridae.

In previous studies (Aspöck, 1992, 1993), the different character states of the cardines were characterized as curved (*Bogen-maxillen* type) or parallel (*Parallel-maxillen* type).

27. *Cardines, terminal constriction*: (0) absent (Zwick, 1967: Fig. 4, *St*); (1) present (Gaumont, 1976: Fig. 12A, *st*).

The broad insertion of the cardines without a constriction is plesiomorphic (0), constricted is apomorphic (1) and a synapomorphy of higher Hemerobiiformia (all Hemerobiiformia with the exception of Ithonidae + Polystoechotidae), although there is a reversal to broad insertion state in the dilarid clade.

28. *Cardines, narrowing to slender sclerites*: (0) absent; (1) present (MacLeod, 1964: Fig. 59, *St*).

Narrowing of the cardines is apomorphic (1) and emerged as a synapomorphy of Coniopterygidae and Sisyridae.

29. *Prementum*: (0) undivided; (1) divided (Minter, 1990: Fig. 7); (2) labial palp segment-like (MacLeod, 1964: Fig. 67); (3) absent.

A divided prementum is apomorphic (1) and evolved independently in Chrysopidae, Hemerobiidae, Mantispidae and Rhachiberothidae. The labial palp segment-like prementum is apomorphic (2) for Myrmeleontiformia and for Coniopterygidae.

30. *Postmentum*: (0) not elongated; (1) elongated (Minter, 1990: Fig. 16, *me*).

An elongation of the postmentum is apomorphic (1) and a strong synapomorphy of the dilarid clade.

31. *Flatness of the 'maxillary-head'*: (0) absent; (1) present (MacLeod, 1964: Fig. 41).

Ventrally, the 'maxillary-head' (Aspöck, 1992) is characterized mainly by elements of the maxillae. It is an autapomorphy of Hemerobiiformia. Within this group the flat head condition is apomorphic (1) and a synapomorphy of the dilarid clade.

32. *Phytosuccivorous habits of larvae*: (0) absent; (1) present.

Phytosuccivorous nutrition is apomorphic (1) and a synapomorphy of Ithonidae and Polystoechotidae. The hypothesis of phytosuccivorous nutrition (sucking of roots) in Ithonidae is based on *Oliarces clara* Banks and *Ithone fusca* Newman (literature summarized in Faulkner, 1990). A further hypothesis mentioned by Faulkner indicates that both genera of Polystoechotidae, *Polystoechotes* Burmeister and *Platystoechotes* Carpenter, have phytophagous larvae. The assumption that larval Ithonidae and Polystoechotidae have similar feeding habits is strengthened by the morphology of the dorsoventrally enlarged head capsules and the short, stout sucking tubes (MacLeod, 1964). The larvae of all other Neuroptera, Raphidioptera and Megaloptera are carnivorous. Phytosuccivorous larvae thus appear to be apomorphic.

33. *Tracheal gills of the first instar*: (0) absent; (1) present.

Tracheal gills in the first instar are apomorphic (1) and emerged as a synapomorphy of Megaloptera. In Sisyridae, the first instar lacks gills, only the second and third instars have tracheal gills.

34. *Cervix*: (0) ribbon-like (Aspöck *et al.*, 1991: Fig. 55, *cv*); (1) neck-like, articulating (Zwick, 1967: Fig. 3, MacLeod, 1964: Figs 66, 67); (2) cushion-like (MacLeod, 1964: Figs 14–16).

The inconspicuous ribbon-like cervical sclerite is plesiomorphic (0), a neck-like, somewhat articulating cervix is apomorphic (1) and a synapomorphy of Neuroptera. A cushion-like cervix that covers the base of the open 'maxillary-head' is a further apomorphic change (2) and a synapomorphy of Hemerobiiformia.

The neck-like cervix has been previously interpreted as a synapomorphy of Nevrothidae/Nevrorthiformia and Myrmeleontiformia (Aspöck, 1992, 1993, 1995).

35. *Cryptonephry*: (0) terrestrial larvae without cryptonephry, all malpighian tubules ending free; (1) aquatic larvae without cryptonephry, all malpighian tubules ending free; (2) terrestrial larvae with cryptonephry, 2 malpighian

tubules ending free; (3) aquatic larvae with only one cryptonephric malpighian tubule, others ending free.

A terrestrial life style of larvae with the malpighian tubules ending free is plesiomorphic (0), aquatic larvae with all malpighian tubules ending free is apomorphic (1) and a synapomorphy of Megaloptera and Neuroptera. Terrestrial larvae with cryptonephry and with only two free malpighian tubules is apomorphic (2) and a synapomorphy of Myrmeleontiformia and Hemerobiiformia. Aquatic larvae with all malpighian tubules but one free is a further apomorphic state change and emerged as an autapomorphy (3) of Sisyridae.

The cryptonephry of larval Neuroptera was studied and illustrated by Gaumont (1976; see Figs 41, 44, 46, 48, 49). Sisyridae were interpreted as primarily aquatic (Aspöck, 1995). However, the single cryptonephric malpighian tubule is problematic. In the larvae of Nevrothidae, which are also aquatic, all malpighian tubules end free. The present result corroborates the previous hypothesis of aquatic larvae as a synapomorphy of Megaloptera and Neuroptera (Aspöck, 1995), the terrestrial life style as apomorphic (not primitive as previously assumed), and the development of cryptonephry as an adaptive step toward life in a new physiological environment. In this context, the aquatic larvae of Sisyridae must be a reversal, and the single remaining cryptonephric malpighian tubule is evidence of ancestral cryptonephry.

36. *Hypermetamorphosis*: (0) absent; (1) present.

Hypermetamorphosis is an apomorphic development characterized by additional metamorphoses in the life cycle (1). It is a synapomorphy of Mantispidae, Rhachiberothidae and Berothidae, based on studies of Mantispidae and Berothidae, but only hypothesized for Rhachiberothidae.

Results and discussion

For the data matrix in Table 2, Hennig86 always recovered the same ten cladograms using any commands. The number of steps measured in these cladograms (L) was 107, consistency index (CI) 0.55 and retention index (RI) 0.69. We rejected cladograms containing unsupported nodes (Kitching *et al.*, 1998). One cladogram was selected as preferred and is shown in detail (Fig. 1). Two cladograms were obtained by successive weighting. Except that the relationships within Megaloptera are unresolved, the topology of one of these is identical with the preferred equally weighted cladogram. In the other successively weighted cladogram, Berothidae form the basal branch of Mantispidae + Rhachiberothidae + Berothidae clade. The strict consensus cladogram (Fig. 3) calculated from the ten equally weighted cladograms using the Hennig86 command 'nelsen' is five steps longer than the most parsimonious cladograms and revealed the following two polytomies. In Hemerobiiformia, there is a polytomy consisting of Chrysopidae, Hemerobiidae, Osmylidae and Coniopterygidae + Sisyridae. In the dilarid clade, Mantispidae, Rhachiberothidae and Berothidae form a trichotomy.

Systematization of Neuropterida

One concern of this analysis was to elucidate the relationships of the three Neuropteridan orders: Raphidioptera, Megaloptera and Neuroptera. The sister-group relationship of Megaloptera and Neuroptera is strongly supported by five synapomorphies: (1) trichobothria organized in a rosette; (2) reduction of the 9th gonocoxites to appendage-like structures; (3) integration of larval cardines with head capsule; (4) their proximally curved direction; and (5) aquatic life style of larvae. This result confirms a previous hypothesis of Aspöck (1995). The argument that the sucking jaws of Neuroptera may have evolved by an elongation of the stipites in the common ancestor of Megaloptera and Neuroptera rather than from a plesiomorphic state represented by Raphidioptera additionally supports the present result.

The traditional grouping of Raphidioptera + Megaloptera was based on criteria concerning the connection of the thorax with the abdomen and differentiation in larval stemmata (Achtelig, 1978; Achtelig in Hennig, 1981; Paulus, 1986; summary in Aspöck *et al.*, 1991). It should be mentioned that the Raphidioptera + Megaloptera relationship was recently supported (but not the monophyly of Neuropterida) by molecular data (Whiting *et al.*, 1997) in a broad study of the phylogeny of Holometabola, addressing, in particular, the Strepsiptera problem. The results are interesting but seem exploratory as far as Neuropterida are concerned.

Systematization of Neuroptera

Within Neuroptera, three suborders clearly emerged: Nevrothiformia, Myrmeleontiformia and Hemerobiiformia. A sister-group relationship of Myrmeleontiformia and Hemerobiiformia is well supported by at least two robust synapomorphies: drastically reduced gula and terrestrial larvae with cryptonephry. The previous hypothesis of Nevrothiformia and Myrmeleontiformia as adelphotaxa (Aspöck, 1992, 1993, 1995) remains as an alternative and was supported by Güsten (1996).

The well established monophyly of Myrmeleontiformia is re-confirmed, which is not surprising, as they are a relatively homogenous group. The hypothesis of a sister-group relationship between Nemopteridae and Psychopsidae (Aspöck, 1995) is corroborated. In addition to the apomorphy presented in the cladogram (vena triplica of hindwing), there are other traits that most likely also support the sister-group relationships, such as male genitalia (cf., e.g., Aspöck *et al.*, 1980: Figs 765–767 and Oswald, 1993b: Figs 21–31), larval head and habitus (cf. Aspöck & Aspöck, 1999: Fig. 52, and Tröger, 1993: Fig. 4). All other relationships within Myrmeleontiformia are confirmed by the current interpretation.

The monophyly of the more heterogeneous Hemerobiiformia is confirmed. Two groups emerged within this suborder: Ithonidae + Polystoechotidae (synapomorphy: hypothesis of phytosuccivory of larvae, arguments see ch. 32), and the 'higher Hemerobiiformia', a clade comprising the remaining families. A sister-group relationship of Ithonidae and

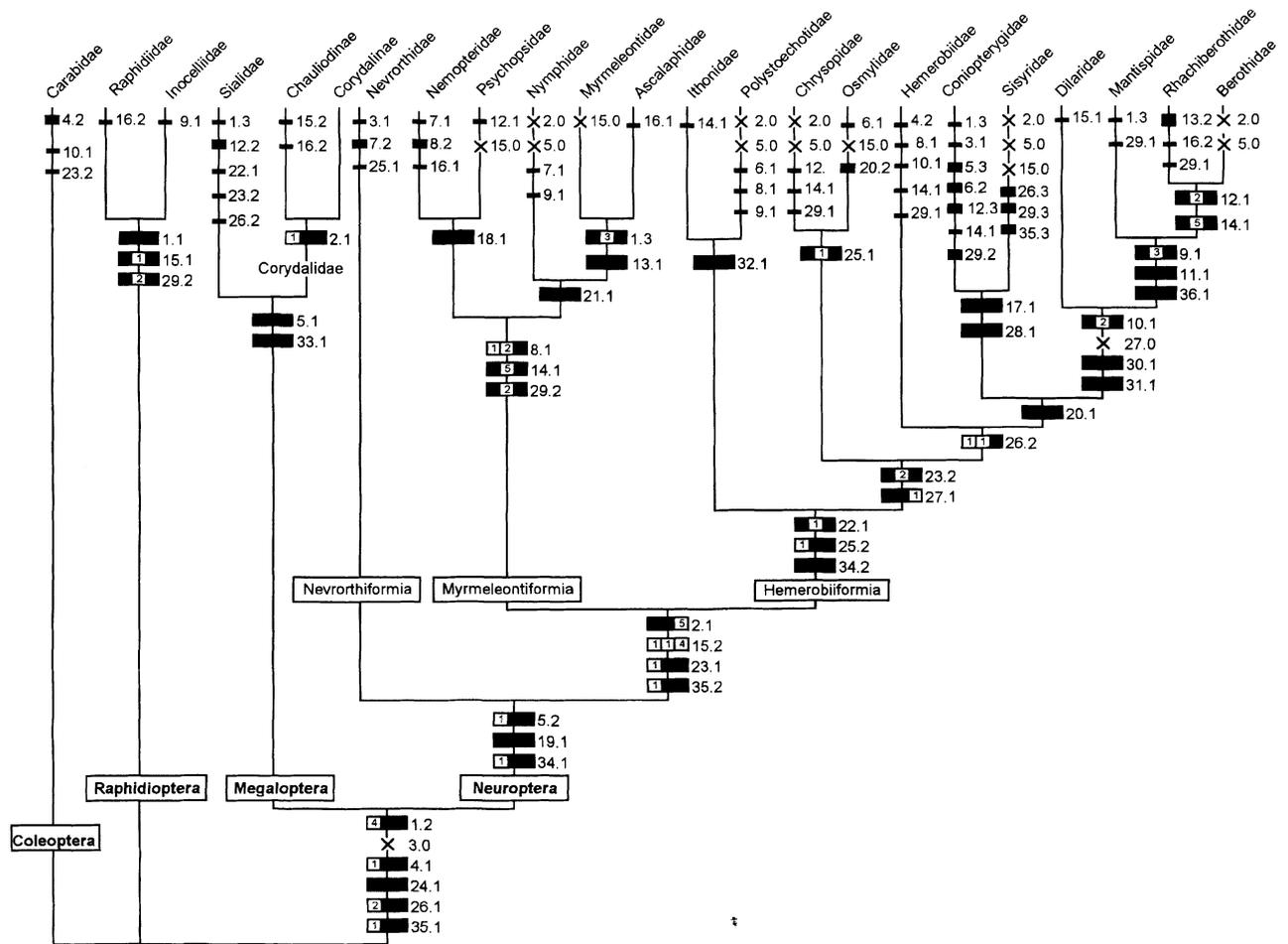


Fig. 1. Preferred cladogram of Neuropterida, selected from a set of ten cladograms, each with 107 steps. Numbers to the right of the symbols refer to characters and their character states, as described in the text. To display the relative strengths and weaknesses of proposed synapomorphies, three components were considered: (1) how many steps required to account for reversions occurring within the supported clade for the particular character is given by the number, if any, on the right side of the cross-bar; (2) how many apomorphic state changes occur within the supported clade for the particular character (further evolution) is given by the number, if any, on the left side of the cross-bar; (3) how often the character state occurs elsewhere, outside the supported clade (convergency), is given by the number, if any, in the middle of the cross-bar. Solid cross-bars represent synapomorphies that are unique, unreversed and have not evolved to other apomorphic states within the supported clade. X=reversal; dash=convergency; solid square=autapomorphy.

Polystoechotidae based on the morphology of larval heads of these families was already postulated by MacLeod (1964). In connection with the Ithonidae + Polystoechotidae clade, Rapismatidae, an enigmatic taxon hitherto placed near this group, should be mentioned. Only recently was the ithonid genus, *Adamsiana*, described (Penny, 1996). It shows character states intermediate between Ithonidae and Rapismatidae, making the family status of Rapismatidae questionable. However, because the larvae have not yet been identified, Rapismatidae were excluded from the present analysis.

Synapomorphies of the extremely heterogeneous 'higher Hemerobiiformia' include the complete loss of larval gula and the terminal constriction of cardines. Within this group, the clade Dilaridae + (Mantispidae + (Rhachiberothidae + Berothidae)) received strong support from the synapo-

morphies: unpaired mediuncus, elongation of postmentum and ventrally flat 'maxillary head', but the positions of the other families remain debatable.

The internal relationships in the dilarid clade have been a subject of conflict. In one study, Rhachiberothinae were interpreted as a subfamily of Mantispidae (Willmann, 1990), but in another, as well as here, they are treated as the adelphotaxon of Berothidae (Aspöck & Mansell, 1994).

The sister-group relationship of Chrysopidae and Osmylidae is based on larval head characters. Although the length of the cardines is not a strong argument, it is plausible. Additional support for the group may come from the possession of special prothoracic glands (Güsten & Dettner, 1992). However, the presence of these glands has not been investigated in other families.

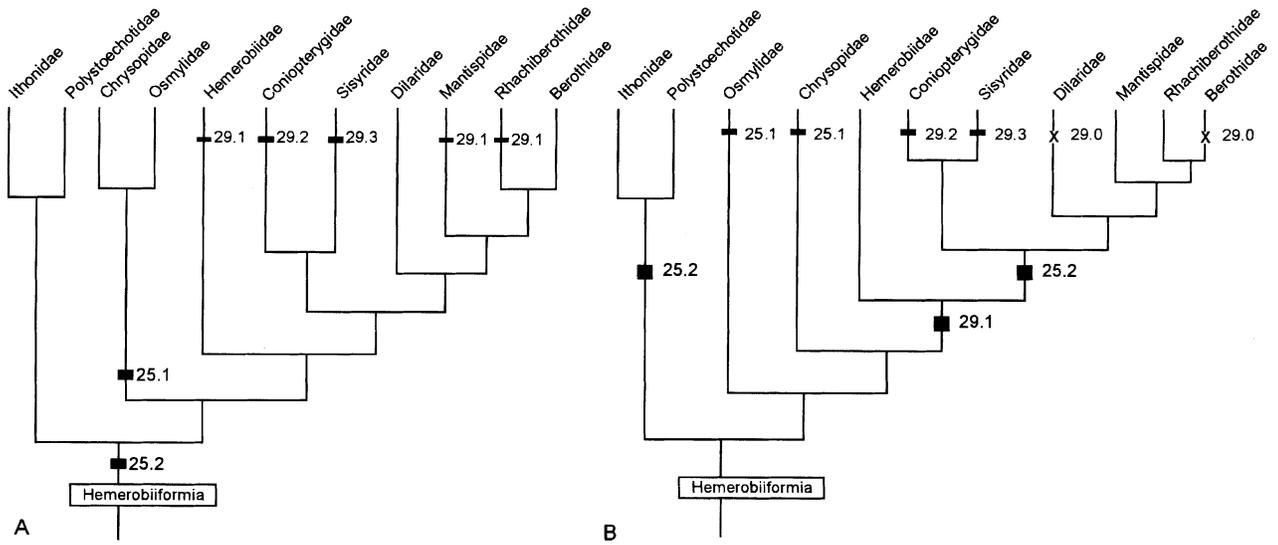


Fig. 2. Cladograms of Hemeroptera, with characters 25 (larval cardines) and 29 (larval prementum) mapped on (A) the preferred cladogram and (B) an alternative. Remaining character transformations are as in Fig. 1. Solid square = synapomorphy; solid dash = autapomorphy; X = reversal.

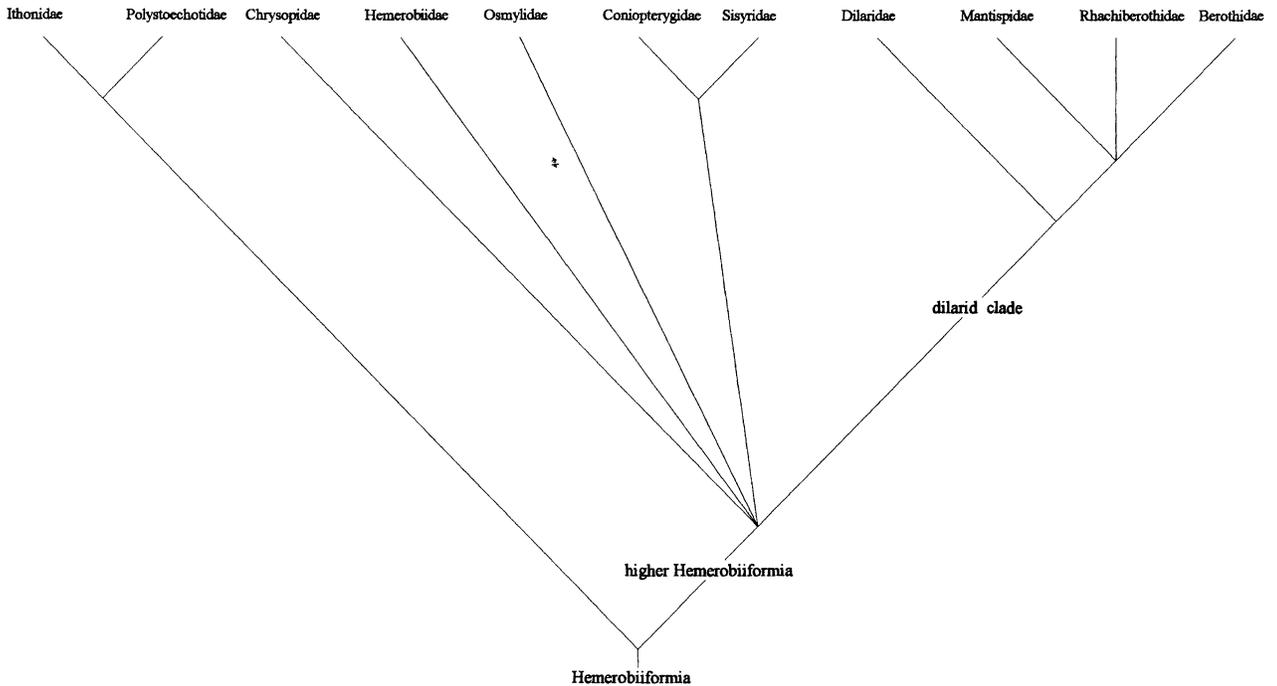


Fig. 3. Part of strict consensus cladogram, showing Hemeroptera. The remainder of the cladogram is structured as in Fig. 1.

In an alternative cladogram (Fig. 2B), Osmyliidae emerged as the adelphotaxon of all other higher Hemeroptera. Initially, it seems preferable to have the primitive Osmyliidae basal to the other families, but there is only one weak synapomorphy supporting this arrangement. The Hemeroptidae + (Coniopterygidae + Sisyridae) + dilarid clade

is strongly supported by the presence of parallel formation of the cardines (ch. 26).

The sister-group relationship of Coniopterygidae and Sisyridae is well supported by characters 17 and 18, and had already emerged in a preliminary cladogram using only Raphidioptera and Megaloptera as outgroup taxa (Aspöck &

Nemeschkal, 1999). Separate branching of each family would, however, appear more plausible because these characters may be independently developed. The most important result concerning Coniopterygidae is its new position within Hemerobiiformia. Former concepts (Withycombe, 1925; Meinander, 1970) considered Coniopterygidae (and, independently, also Ithonidae) to be an early offshoot to all other Neuroptera. With respect to Coniopterygidae, the high number of autapomorphies may have been the reason for this interpretation.

It is also important that Sisyridae, judging from their position in the cladogram, must have had secondarily aquatic larvae. The stem-species of Neuroptera + Megaloptera apparently evolved aquatic larvae as an autapomorphy, and such larvae are still retained by all Megaloptera and Nevrothidae. The larvae of the stem-species of Myrmeleontiformia + Hemerobiiformia was likely to be terrestrial and acquired cryptonephry as an osmotic adaptation. Under this scenario, sisyrid larvae reverted back to an aquatic habit, yet they retained one malpighian tubule, which is fixed to the rectum and interpreted as evidence for terrestrial ancestry.

Suggestions for future research

One of the phylogenetically most interesting characters examined here is cryptonephry in larvae. Our knowledge of this condition is derived from the study of Gaumont (1976) on *Myrmeleon formicarius* (Linnaeus), *Chrysoperla carnea* (Stephens), *Drepanopteryx phalaenoides*, *Sisyra fusca* and *Nevrothus fallax* (Rambur). Further investigations should focus on the malpighian tubules of all families, or at least on the more ecologically diverse families, e.g. Osmyliidae, which have strictly terrestrial larvae (Stenosmylinae), in addition to many well known 'semi-aquatic' representatives.

The evolutionary origin of sucking jaws in larvae is still unknown. There is no known transition stage linking chewing and sucking mouthparts. Comparative anatomical studies of larval mouthparts, especially of Megaloptera, could shed light on the evolutionary changes of the maxilla with respect to the nature of the maxilla blade, whether it is derived from the stipes or the lacinia. Finally, enigmatic relict groups, such as Nevrothidae, Ithonidae, Rapismatidae and Polystoechotidae, may prove crucial in future interpretation of morphological structures and biogeographic patterns.

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