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Phylogeny of endopterygote insects, the most successful lineage of living organisms*

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Abstract. The monophyly of the Endopterygota is supported primarily by the specialized larva without external wing buds and with degradable eyes, as well as by the quiescence of the last immature (pupal) stage; a specialized morphology of the latter is not an endopterygote groundplan trait. There is weak support for the basal endopterygote splitting event being between a Neuropterida + Coleoptera clade and a Mecopterida + Hymenoptera clade; a fully sclerotized sitophore plate in the adult is a newly recognized possible groundplan autapomorphy of the latter. The molecular evidence for a Strepsiptera + Diptera clade is differently interpreted by advocates of parsimony and maximum likelihood analyses of sequence data, and the morphological evidence for the monophyly of this clade is ambiguous. The basal diversification patterns within the principal endopterygote clades ("orders") are succinctly reviewed. The truly species-rich clades are almost consistently quite subordinate. The identification of "key innovations" promoting evolutionary success (in terms of large species numbers) is fraught with difficulties.

INTRODUCTION

Pie-charts depicting the proportional representation of the principal taxa of living organisms are routinely presented by entomologists who want to get the message across that "speaking about biodiversity is essentially equivalent to speaking about arthropods" (Platnick, 1991). Haldane's recognition of the Creator's "inordinate fondness for beetles" is an oft-repeated anecdote (see, e.g. Farrell, 1998), and indeed Platnick's statement could be followed up by saying that speaking about arthropod diversity is essentially equivalent to speaking about endopterygote insects. This would be equally true whether one refers to estimates of the actually known species, or to the considerably more uncertain estimates of the number of species which are actually present out there. For example, in Hammond's (1992) conservative estimates of the figures in question the endopterygotes account, respectively, for more than 70 and 80% of all arthropods, and more than 45 and 60% of all living organisms.

It is the purpose of the present contribution to review succinctly the present state of understanding of the phylogeny of the basal lineages of the Endopterygota/Holometabola and thereby tracking the evolutionary pathways which have led to the greatest bursts of speciation in the living world.

The names Endopterygota and Holometabola are both in very widespread use; I have myself used both in writing at different times. Arguably Endopterygota should be preferred for referring very specifically to a principal autapomorphy of the taxon in question. Martynov's "Oligoneoptera" seems on the way out, although it is still used at least in some palaeontologists' writings. As to Kukalová-Peck & Brauckmann's (1992) "Endoneoptera", I believe the entomological community will find the introduction of yet another name for the same taxon little helpful. The same is true for the "typified" names for higher insect taxa introduced by the "Rohdendorf school" in Russia (see e.g. Rohdendorf & Rasnitsyn 1980; under their scheme the Endopterygota are "Scarabaeiformes").

ARE THE ENDOPTERYGOTA A MONOPHYLUM?

The endopterygotes comprise 11 taxa conventionally ranked as "orders" (a term retained here in a non-committal sense, while acknowledging that current arguments against applying formal ranks to entities in the biological system are overall well taken; see e.g., Ax, 1987): the Neuroptera (= Planipennia), Megaloptera, Raphidioptera, Mecoptera, Siphonaptera, Diptera, Trichoptera, Lepidoptera, Hymenoptera, Coleoptera, and the enigmatic Strepsiptera. Apart from the latter (of which more below), the monophyly of this assemblage has remained largely uncontested for more than a half-century. It is also not contested here, but it must be emphasized that the so far identified potential groundpattern autapomorphies of the Endopterygota are not numerous, and perhaps not particularly weighty either.

Much has been written on "the origin of the insect pupa", but this expression, as well as text-book statements such as "the evolution of a pupal stage in the life history has made holometabolous development possible" (Gillot, 1995) arguably turn things upside down: the last immature instar of ancestral endopterygotes *retained* the morphology of its counterpart in the closest exopterygote

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Fig. 1. Pharate adult raphidiid snakefly, *Phaeostigma notata* (F., 1781). The pupal integumental structure of such generalized endopterygotes is overall very similar to that of comparable last-instar exopterygote nymphs, and it similarly permits considerable activity on the part of the pharate adult insect. (Courtesy of professor E. Wachmann.)

relatives; its quiescence is indeed an innovation that is incidentally paralleled in some very subordinate exopterygote lineages which are not under discussion as potential endopterygote sister groups). This "retention" view of the pupa was actually emphasized by Hinton (Hinton & Mackerras, 1970 being one example), though he still addressed the issue under "origin" headings. The commonplace concept of the pupal stage as being a notable innovation is largely due to the fact that the only widely known insect pupae are the highly autapomorphic obtect/adecticous kinds characteristic of higher Lepidoptera, as well as those of cyclorrhaphan flies in which the true pupal structure, of course, is concealed by a hardened larval skin. Pupae of the ancestral type whose exarate/decticous structure permits considerable activity of the pharate adult (particularly striking in some Neuropterida, Fig. 1), are unfamiliar objects, even to most biologists.

The principal innovation of the endopterygotes is, then, the *larval* stage, which unlike the nymphs of non-endopterygotes (1) consistently lacks external wing buds (and genital-appendage buds), and (2) is equipped with special larval eyes which are extensively degraded and reconstructed at metamorphosis. But how "strong" are even these apomorphies? The delay in the appearance of external wing buds until the penultimate, i.e. larval/pupal, moult (and in the case of genital appendages *at least* to this moult, sometimes until the ultimate one) gave name to the "Endopterygota": the wing anlage resides *inside* the larval body, i.e., the rudiment is an epidermal fold below the larval cuticle. However, it has been emphasized by Švácha (1992, see also Sehnal et al., 1996) that these subcuticular wing-rudiment folds are not always invaginated into epidermal pockets, as they usually are in the examples illustrated in textbook diagrams. Furthermore, the wing discs may appear indiscernible in dissections of pre-final, and "usually also in active final", larvae of taxa which one would a priori consider to represent basal endopterygotes, such as neuropterids, Mecoptera and non-apocritan Hymenoptera. Švácha therefore concluded that invaginated wing discs in pre-final instars originated probably at least four times independently in the Endopterygota: within the Coleoptera, within the Diptera, within the Hymenoptera, and in the Amphiesmenoptera. Available evidence bearing on this interesting issue is ambiguous. For example, Sundermeier (1940) reported invaginated wing discs from quite young larvae of *Myrmeleon* (Neuroptera: Myrmeleontidae). I believe that invaginated wing rudiments in the final larval instar can tentatively be upheld as an endopterygote groundpattern autapomorphy. Such formations are also well developed in the active larva of a nannochoristid scorpionfly (Fig. 2) which represents one of the most basal mecopterid lineage (see below), and they have also recently been documented from tenthredinid sawflies (Barlet, 1994); incompletely invaginated wing rudiments may therefore prove to represent secondary modifications.

The eyes of endopterygote larvae are believed consistently to be broken down at metamorphosis and subsequently replaced by the adult insects' compound eyes (which in subordinate lineages among nematoceran Diptera may develop precociously already in the larva, Paulus, 1979); remnants of the larval eyes are often identifiable in the adult's optic lobe. These eyes themselves are almost always scattered simple eyes ("stemmata"). Scorpionflies are an exception. In well-studied Mecoptera-Pistillifera the larval eye has all the structural characteristics of a compund eye, and it has been interpreted to represent indeed a formation of this kind (Paulus, 1986a, b; Suzuki & Nagashima, 1989; Melzer et al. 1994); it differs, however, from the compound eye in exopterygote immatures in that the ommatidia number re-

Fig. 2. Horizontal section of thorax of active last-instar larva of the nannochoristid scorpionfly *Nannochorista philpotti* Tillyard, 1917. The thick-walled wing bud (wi) is enclosed in a thin-walled epidermal pocket (arrows).

mains constant throughout larval life (Paulus, 1986a). The larval eye of nannochoristid scorpionflies (Melzer et al., 1994) is similarly a compound eye, but the ommatidia are devoid of corneal lenses, which may be related to the aquatic life-style of the insect. Also in the hymenopteran larval eye (retained only in the non-apocritan grade) are the ommatidia contiguous. While this may be a genuine plesiomorphy, the ommatidia are derived in being covered by a communal corneal lens and in being devoid of crystalline cones (Paulus, 1979). All other endopterygote larvae have the lateral eyes dispersed. In larval Lepidoptera-Micropterigidae the stemmata are densely clustered but can hardly be said to form a compound eye as stated by previous authors (Tillyard, 1923; Lorenz, 1961); however, their histology remains unstudied.

Reduction of the larval ocellus complement is apparently yet another (but evidently "weak", as a regressive trait) endopterygote groundpattern autapomorphy. To my knowledge the only record of ocelli in larval endopterygotes is that of the median ocellus in Mecoptera-Bittacidae (Byers, 1991), so at least lateral larval ocelli were probably lost in the endopterygote stem lineage; the median ocellus in bittacids is actually most parsimoniously explained as an autapomorphic character reversal.

It remains to be ascertained whether other derived features of the vast majority of endopterygote larvae (particularly the reduction of sclerotized areas on trunk segments) can actually be ascribed to the endopterygote ground pattern. Reliable ground pattern autapomorphies in adult structure similarly remain to be established. I have (Kristensen, 1981, 1991/94) tentatively ascribed such derived states as pterothoracic mera (cf. below) and endosterny with concomitant mediad shift of coxae to the endopterygote ground pattern. However, these apomorphies are too homoplasious (endosterny paralelled in many Paraneoptera and apparently secondarily obliterated in some Hymenoptera-Apocrita; mera non-developed in Hymenoptera and on coleopteran mesocoxae) to be operational even if they may prove to be valid. As already noted, however, the described larval characters have sufficed to establish a near-consensus among entomologists about the monophyly of the Endopterygota. The molecular analysis with the so far most extensive taxon sampling (Whiting et al., 1997, 18 and 28S rDNA) also does support endopterygote monophyly.

"The Strepsiptera problem"

The "stylopids" deserve special attention in the context of endopterygote monophyly. These highly autapomorphic insects have larvae which in the second and following instars always are endoparasites of other insects. However, the prevalent developmental mode in which all post-1st-instar immatures as well as the adult female are apodous and remain within the host does not represent the ground pattern condition of the "order": In the rather poorly known family Mengenillidae, generally considered to be the sister group of all other Strepsiptera, the thoracic legs are retained throughout larval life, and the last instar as well as the apterous adult female are free-living.

A couple of pharate pre-pupal instars with external wing buds have been recorded from the better studied higher Strepsiptera (review in Kinzelbach, 1971), and moreover strepsipteran larval eyes have been stated to be carried over unchanged to the adult (see e.g. Paulus, 1979: 352). On this basis I have previously (Kristensen, 1981, 1991/94) questioned the assignment of the Strepsiptera to the Endopterygota. However, as noted by Sehnal et al. (1996), the accounts by Parker & Smith (1933, 1934) of the development of a mengenillid make no reference to such "exopterygote" pre-pupal juveniles which therefore might represent a secondary modification characterizing a subordinate strepsipteran group. But Sehnal et al. also suggest an alternative interpretation which would obviate the need for postulating this kind of instars altogether, namely that two of the alleged juvenile cuticles which envelop the developing adult are "ecdysial

membranes" (formed after the pupal and adult apolysis respectively) rather than genuine exuviae.

Interesting, but also perplexing, are the indications emerging from a suite of molecular analyses (Whiting & Wheeler, 1994; Chalwatzis et al., 1995, 1996; Whiting et al., 1997; Hwang et al., 1998) that the Strepsiptera are the closest relatives of the Diptera. The principal problem with this hypothesis is that the Strepsiptera appear to be devoid of some of the apparently strong Mecoptera/Diptera synapomorphies in pterothorax structure (Kristensen, 1995). Also, the paired claws on the thoracic legs of mengenillid larvae as well as the absence of a pleural muscle insertion on the first axillary sclerite are incompatible with a position within the next higher taxon, the Mecopterida.

Morphological evidence for the assignment of the Strepsiptera to the Antliophora (hitherto circumscribed as Mecoptera/Siphonaptera + Diptera, cf. below) was discussed by Whiting (1998a). Most noteworthy is perhaps the structure of the adult's mandibles with their slender blade-like shape and regressed anterior articulation; the criss-crossing of the mandibles, considered a possible Mecoptera/Diptera synapomorphy by Mickoleit (1971, 1981) is similarly characteristic of strepsipterans, but it also occurs in e.g. xyelid sawflies and hence is questionably apomorphic. Other imaginal character complexes supporting this placement of the Strepsiptera are purely regressive, such as the loss of prelabial lobes plus ligula and associated musculature. The reduction of labial palp segments to two or less would be an additional character in the same category: the Strepsiptera have only a single segment (Kinzelbach, 1971), and the flea palp is obviously secondarily multisegmented. The complete loss of the outer pterothoracic tergo-coxal remotor in Strepsiptera is shared with the Mecopterida, and Whiting also counted the absence of an ovipositor among potential strepsipteran/mecopterid synapomorphies. A suite of other currently recognized autapomorphic characters of the Antliophora or Mecopterida are either unknown or inapplicable in Strepsiptera. Altogether the available morphological evidence bearing on a possibly close Strepsiptera/Antliophora relationship is highly ambiguous.

Two additional putative strepsipteran/antliophoran synapomorphies are mentioned by Whiting, but one must be discarded, and the other is very problematical. The former is "Male abdominal segment IX ring-like, enlarged and fused on the pleuron". Whiting's following text reads: "Kristensen (1991) treats the fusion of the gonopod bases above and below the phallic aparatus as an autapomorphy of the order Mecoptera, but it clearly is also present in the Strepsiptera (Kinzelbach, 1971). All nematocerous Diptera have this character, which is probably the basal condition in Diptera (Wood & Borkent, 1989), although Kristensen (1995: 104) contends that "it remains uncertain whether the male segment IX was "ring-like" in the dipteran ground plan". There is here an inadvertent confusion of two separate phenomena: the lateral fusion of the tergal and sternal sclerotizations of IX into a ring-like structure, and a fusion of the gonopod bases around the phallic apparatus. The latter character state was first recognized as a mecopteran autapomorphy by Mickoleit (1971; see also Willmann, 1987, 1989); a similar condition is widespread in Diptera also, but at least the ventral fusion is apparently not a groundpattern trait of that order. However, the issue is of no consequence for the Strepsiptera, whose males are actually devoid of gonopods (Kinzelbach, 1971). A synscleritous segment IX ring, such as is seen in Strepsiptera, is commonplace in all "orders" of the Mecopterida and is ascribed to the ground pattern of the Trichoptera + Lepidoptera lineage (Kristensen, 1984); discrete dorsal and ventral sclerotizations were still attributed to the ground pattern of the Diptera by Hennig (1973), but if they turn out to be secondary even here (as, e.g., believed by Blaschke-Berthold, 1994), the ring-configuration can at most support an assignment of the Strepsiptera to the Mecopterida, not to any subordinate taxon thereof.

The problematical character is the male sperm pump. Whiting stated that "Strepsiptera ... possess a sperm pump", and considered this to be another synapomorphy with the Antliophora which owe their name to the possession of a formation of this kind. However, a hypothetical ancestral apparatus from which the various kinds of complex sperm-extrusion devices recorded from Mecoptera (including fleas) and Diptera can be derived still remains to be worked out. While the muscle-coated vesicular part of the strepsipteran male duct (e.g. Kinzelbach, 1971) can indeed appropriately be called a sperm pump, it is questionable whether it will prove to have any specific similarities with antliophoran pumps. A bulbous muscular coat forming an "ejaculatory pump" is also present in the Mecopterida-Amphiesmenoptera.

Whiting & Wheeler (1994; see also Whiting, 1998a, Whiting et al., 1997) have advanced the intriguing idea that the Strepsiptera arose from ancestors which already had a Diptera-type thorax structure, and that their origin was mediated by a homoeotic mutation which effectively reversed the pterothoracic segments. In these terms the strepsipteran forewing halters and the dipteran hindwing halters are considered homologous, and the name "Halteria" was introduced for the putative monophylum comprising the two taxa. I have previously (Kristensen, 1995) noted that this idea would seem more easily reconcilable with a subordinate position of the Strepsiptera within the crown-group Diptera than with a position as their sister group. Expression of the *Ubx* ("Ultrabithorax") gene has been found to be "dramatically modified" in the Strepsiptera (Whiting, 1998a); it remains to be seen whether this line of inquiry will prove phylogenetically informative. In any case the suggestion of this developmental scenario for the sister-group relationship must be kept separate from the evidence for the relationship itself. Carmean & Crespi (1995), Huelsenbeck (1997, 1998) and recently Hwang et al. (1998) have challenged the conclusiveness of the molecular evidence. This debate reflects the current controversy over performance of parsimony versus probabilistic (maximum likelihood) analyses of sequence data in retrieving the correct relationships of "long branched" taxa (i.e., taxa with high substitution rate in the genes examined). Whiting (1998b), Siddall (1998) and Siddall & Whiting (1999) have countered important aspects of the criticism, but the case may not be closed yet (Friedrich & Tautz, in press).

The "Halteria" hypothesis is obviously incompatible with previous suggestions that the Strepsiptera are the closest relatives of the Coleoptera, but while this place-

ment, and perhaps even more Crowson's proposal of the Strepsiptera being subordinate within the beetles (see e.g. Lawrence & Newton, 1995), are a priori attractive ideas, it has long been argued that the evidence is problematical (Kinzelbach, 1971; Kinzelbach & Pohl, 1994; Kristensen, 1981, 1991; Whiting, 1997b). Newer support for a Strepsiptera/beetle sister group relationship from wing characters (Kukalová-Peck & Lawrence, 1993) has been challenged by Whiting & Kathirithamby (1995), and Kukalová-Peck's rebuttal (1997) appears inconclusive to me.

Two additional Strepsiptera/Coleoptera similarities were identified here. One, a unique condition within the endopterygotes ("non-stemmed" alleged Rs branches), is expressly characterized as being "ultra-primitive, plesiomorphic"; hence it cannot possibly support the sister group relationship. Another newly identified similarity is a direct wing muscle, arising on the pleuron and inserting on or just behind the third axillary; it is said by Kukalová-Peck to be "old, complex and unique, it represents a convincing synapomorphy of Strepsiptera + Coleoptera". But it is not explained how this muscle in any "complex and unique" way differs from its homologue in other neopterans, i.e., the commonplace wing flexor.

In conclusion I believe that Hwang et al. (1998) are correct in considering the question of strepsipteran affinities to remain unanswered. If forthcoming additional evidence really will continue to support the Strepsiptera/Diptera sister group relationship, this hypothesis will become ranked among the most spectacular contributions of molecular characters to systematic zoology; however, it is early days yet. A trustworthy placement of the Strepsiptera will have to be achieved from a quantitative analysis of endopterygote inter-relations based on a truly comprehensive character set, the procurement of which will require a substantial amount of work. Sequence data from additional genes are highly desirable, as is more information about pertinent morphological characters; the need for detailed accounts of mengenillid juveniles must be particularly emphasized.

ENDOPTERYGOTE AFFINITIES AND AGE

The phylogenetic position of the Endopterygota within the pterygote insects remains uncertain. They are usually grouped together with the Paraneoptera (= the "hemipteroid" orders, Psocodea + Thysanoptera + Hemiptera), and the composite taxon is then referred to as the "Eumetabola" or "Phalloneopterata". Putative Paraneoptera + Endopterygota autapomorphies have been identified in wing structure (a jugal sclerotization according to Hamilton 1972; R+MA fusion, short-stemmed forewing M and Cu, presence of MP-CuA crossvein/brace according to the interpretations of Kukalová-Peck, 1991) and in the developmental mode of male genitalia (longitudinal division of phallic anlage usually followed by fusion of median lobes into intromittent organ, lateral lobes forming clasping organs; Boudreaux, 1979). However, the validity of most if not all of these characters are debatable and dependent on ad hoc explanations of conditions in some subordinate taxa. Another potential groundpattern autapomorphy of the "Eumetabola" may be a polytrophic ovariole structure from which telotrophic and secondarily panoistic types were developed in a number of lineages (Büning, 1998). The Paraneoptera + Endopterygota clade also emerged in Whiting et al.'s (1997) total evidence (morphology plus molecules) tree, but not in their molecular-only trees, none of which retrieved a monophyletic Paraneoptera. Their tree based on all molecular characters had a Dictyoptera + (Dermaptera + Plecoptera) clade as endopterygote sister-group, while the tree based on 18S rDNA had the Hemiptera in this position (several pertinent taxa are missing in the 28S data set).

The absence of any known operational endopterygote groundpattern autapomorphies in external features will obviously impede recognition of the earliest endopterygotes in the fossil record. Kukalová-Peck (1991/1994) has identified an apterous arthropod from the Upper Carboniferous (Pennsylvanian) as an endopterygote larva, and while I share Willmann's (1997) reluctance in accepting this identification, the timing is very plausible. Labandeira & Phillips have recently (1997) provided evidence that a similarly Pennsylvanian gall in a tree-fern frond was caused by an endopterygote larva. Most of the splitting events in which endopterygote "orders" arose had taken place by the end of the Permian, though the Hymenoptera, whose stem lineage must be at least of Permian age, if any of the current endopterygote phylogenies is correct, are unrecorded until the Middle Triassic (Jarzembowski & Ross, 1996), and the Trichoptera/Lepidoptera split is undocumented before the Lower Jurassic (Kristensen, 1997). Unsurprisingly, the Strepsiptera and Siphonaptera are not documented until much later still (Lower Cretaceous).

BASAL SPLITTING EVENTS IN THE ENDOPTERYGOTA

A few "supraordinal" entities have long been recognized within the Endopterygota, viz., the Neuropterida (= Neuropteria), comprising the Neuroptera, Megaloptera and Raphidioptera, and the Mecopterida (= Mecopteria, = Panorpida; the "panorpoid orders") comprising two lower-rank "supraordinal" entities, Antliophora (Mecoptera, Siphonaptera, Diptera – and perhaps Strepsiptera?) and Amphiesmenoptera (Trichoptera and Lepidoptera).

There is no consistency in the current use of the supraordinal names Neuropteria/Neuropterida and Mecopteria/Mecopterida/Panorpida. I submit that the use of Neuropterida is now most likely to promote stability, because of the adoption of this name in the impact-rich 2nd edition of *Insects of Australia* (CSIRO ed., 1991) and its student-text successor *Systematic and Applied Entomology* (I.D. Naumann ed., 1994). While the same argument may now be used to discard Mecopteria, the issue is less clear with respect to Panorpida versus Mecopterida, since both are used in the books in question (in the chapters by Kristensen and Kukalová-Peck respectively). However, I believe Mecopterida is preferable after all, because the name Panorpida might be construed as a scorpionfly taxon centred on the family Panorpidae.

The basal relationships within the Endopterygota remain questionable, however. Hennig (1969/1981) proposed that the basal phylogeny can be represented as (Coleoptera + Neuropterida) + (Hymenoptera + Mecopterida), and I have myself (Kristensen, 1975, 1981, 1991, 1995) considered this to be the arrangement best supported by available morphological information. The modest previous evidence for a Coleoptera + Neuropterida monophyly (summarized in Kristensen, 1991/1994) has recently been supplemented by putative synapomorphies in wing base structure (Hörnschemeyer, 1998).

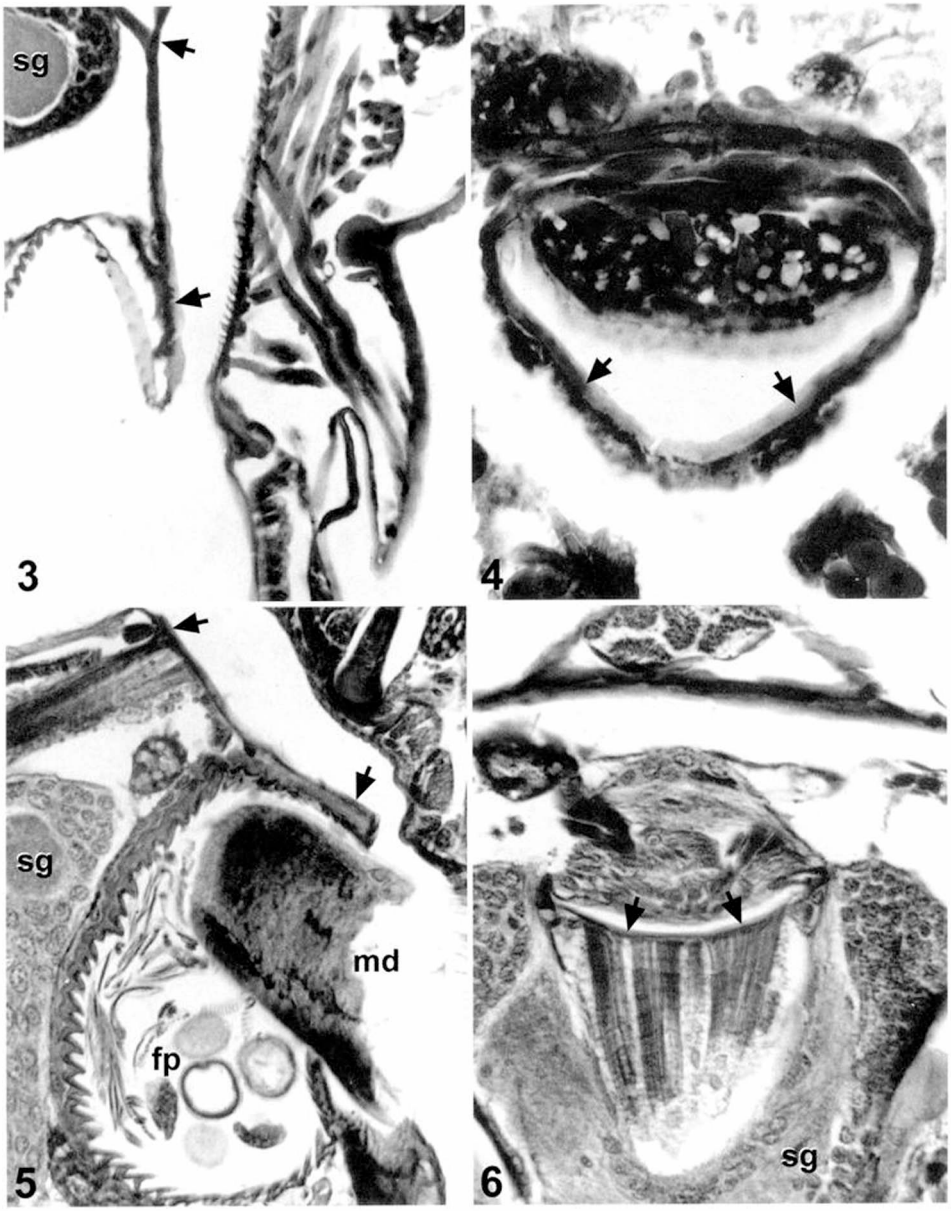
The presence in one of two examined members of the Coleoptera-Myxophaga of a highly specialized kind of telotrophic ovariole has led Büning & Maddison (1998) to suggest that the genetic potential for its formation was developed already in the last common ancestor of Neuropterida and Coleoptera. The character distribution in question could be construed as supporting the notion that this ancestor was not ancestral to other endopterygote clades, from which the ovariole type in question is unknown. However, the legitimacy of this line of reasoning is at least highly controversial.

The sister group relationship between the Hymenoptera and the Mecopterida has so far been supported by two larval characters. One is the single-clawed pretarsus; this is undoubtedly an apomorphic state, but as a regressive character it carries only modest weight. The parallelism in Coleoptera-Polyphaga (+ Myxophaga) is well known, and the incompatibility with a placement of the Strepsiptera within the Mecopterida is already mentioned. The other putative Hymenoptera/Mecopterida synapmorphy is the cocoon-spinning with labial-gland silk rather than with a secretion from the malpighian tubules as in the Coleoptera and Neuropterida. However, while Hennig's interpretation of the labial-gland silk as derived has not been questioned by later authors it *is* debatable: The non-parasitic Psocodea ("Psocoptera") similarly use labial-gland secretion for silk production, and if the Paraneoptera (the "hemipteroid orders") are indeed the closest relatives of the endopterygotes, labial silk could indeed well be plesiomorphic. It has long been known that in some chalcidoid wasps an apparent malpighian-tubule secretion provides cocoon material (review in Quicke, 1997). Are conditions here and in the Coleoptera/Neuropterida independently derived, or is this particular condition in subordinate Hymenoptera-Apocrita an autapomorphic character reversal to a spinning-mode that was ancestral at the endopterygote level?

Königsmann (1976) suggested that the "eruciform" larval type is a potential synapomorphy of Hymenoptera and Mecopterida (see also Whiting et al., 1997). An eruciform ("caterpillar-like") larva is characterized by being hypognathous and having abdominal prolegs. I have questioned (Kristensen, 1991/94) the significance of this, referring to the prognathous larvae of nannochoristid scorpionflies and primitive Amphiesmenoptera. Moreover, prolegs can most probably not be ascribed to the ground pattern of the Mecopterida (except, perhaps, the "anal feet" on X). Simple, non-musculated prolegs in some scorpionfly larvae do resemble those of larval *Micropterix*, but are most likely parallel neoformations in the two cases.

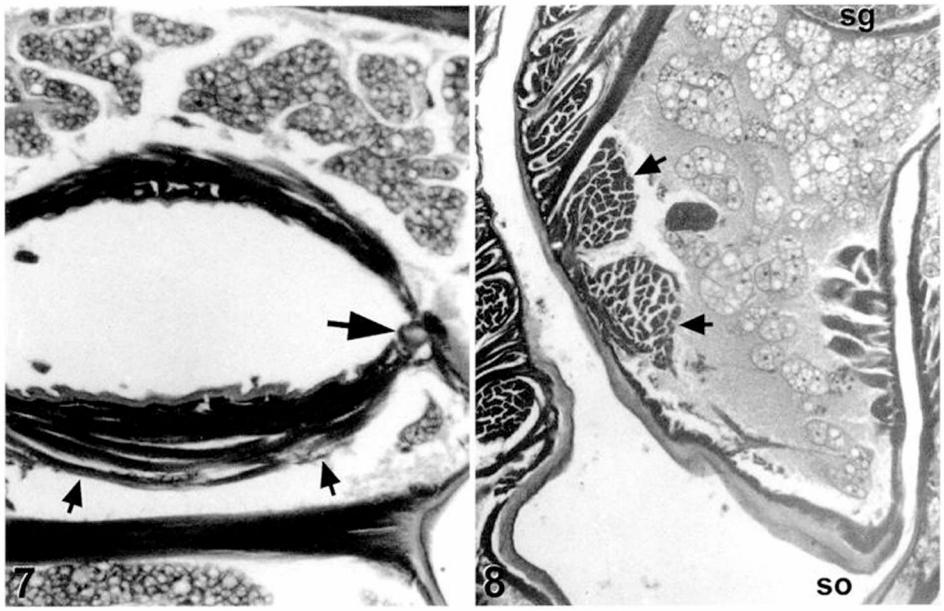
Prolegs are absent in nannochoristids and in the putative boreid + flea lineage within the Mecoptera; they are similarly absent ("anal feet" excepted) in Trichoptera. It is important to note that within the Lepidoptera-Micropterigidae prolegs are *only* present in the Palaearctic genus *Micropterix* and its putative southern hemisphere sistergroup (the "*Sabatinca*" *zonodoxa* group of species), but lacking in the known larvae of other members, which currently are believed to be paraphyletic in terms of the aforementioned genera (Kristensen, unpubl.). Prolegs are also absent (non-crochet-bearing anal feet in Heterobathmiidae and Acanthopteroctetidae excepted) from all other known larvae of non-neolepidopteran moths, and while this could be attributed to their endophagous life-style, it must be recalled that heterobathmiid larvae are not overall strongly modified for the leaf-mining habit; for example, they have retained the full amphiesmenopteran set (seven) of stemmata and very generalized thoracic legs, and they can move from one leaf to another to initiate new mines (Kristensen & Nielsen, 1983). The "typical lepidopteran" preanal proleg complement (musculated, crochet-bearing and restricted to segments III–VI) is an autapomorphy of the Neolepidoptera or a more inclusive taxon comprising also the Lophocoronidae and/or Neopseustidae whose larvae are so far unknown (Nielsen & Kristensen, 1996). The very numerous proleg types recorded from various dipteran larvae are also neoformations (Hinton, 1955).

An interesting additional potential synapomorphy for Hymenoptera and Mecopterida is a fully sclerotized floor of the sucking pump in the adult insect, formed by a "sitophore" plate on the hypopharyngeal base (Figs 3–6), and accompanied by a loss of transverse ventral cibarial muscles. The plesiomorphic condition in insects with a closed preoral cavity is that the latter is laterally strengthened by oral arms, rod-like sclerites which pertain to the complement of hypopharyngeal suspensoria (and on the proximal apices of which the mouth angle retractor muscles insert), whereas the median part of the cavity floor remains membranous and transverse ventral cibarial muscles are retained. This condition is retained in the Neuropterida (Denis & Bitsch, 1973; Vilhelmsen & Kristensen, unpubl., Figs 7–8), and it can arguably also be ascribed to the coleopteran ground pattern: In the Archostemata the oral arms are broad sclerotized zones but the median area of the sucking pump floor remains membranous, and ventral transverse cibarial muscles are present (Vilhelmsen & Kristensen, unpubl.; Beutel, 1997 and pers. comm.). In other beetles the oral arms are often united by a narrow sclerotized bridge; this may well pertain to the ground pattern of the "Pantophaga" but has, then, been evolved independently of the Hymenoptera + Mecopterida sitophore. Unlike the latter it only stiffens a small strip of the sucking pump floor (Dorsey, 1943; Evans, 1961; R.G. Beutel, pers. comm.). As noted by Vilhelmsen (1996) the presence of an extensive sitophore plate obviously facilitated development of specialized sucking mouthparts, which have been evolved on several occasions in adult Hymenoptera and Mecopterida, while they are rare elsewhere among endopterygotes. Outside the Endopterygota a sclerotized sitophore in the Paraneoptera, but since the clearly plesiomorphic hypopharynx configuration is retained in an endopterygote assemblage this is considered a parallelism.



Figs 3–6. Sucking pumps of adult hymenopterans (3–4) and a mecopterid (5–6), in medial sagittal (3, 5; epipharynx to the right) and transverse (4, 6) sections. 3 – Hymenoptera: Xyelidae: *Xyela julii* (Brébisson, 1818); 4 – Hymenoptera-Tenthredinidae: *Athalia* sp.; 5–6 – Lepidoptera: Micropterigidae: *Micropterix calthella* (L., 1761). The full width of the sucking pump floor is strengthened by the sclerotized sitophore (arrows) for a considerable distance, and there are no ventral transverse cibarial muscles. fp – food particles (pollen grains) in "infrabuccal pouch" (= "triturating basket"); md – mandible; sg – suboesophageal ganglion.

One of the principal alternative phylogenetic hypotheses (Boudreaux, 1979) can be represented as Coleoptera (plus Strepsiptera) + (Hymenoptera + "Meronida"), while in another (Ross, 1965; Rohdendorf & Rasnitsyn, 1980) the basal endopterygote dichotomy is between the Hymenoptera and the remaining "orders". I have previously (Kristensen, 1981, 1991/94) reviewed the problems with the evidence for these phylogenies. Here I would like to add that mesenteric caeca, the loss of which was considered a possible synapomorphy of the non-coleopterans by Boudreaux, are actually retained in at least the Megaloptera: Corydalidae (New & Teischinger, 1993). Boudreaux's "Meronida", comprising the Neuropterida + Mecopterida, are characterized primarily by a strong suture demarcating a prominent posterior portion of each pterothoracic coxa (the meron), hence apparently dividing the segment ("Spalthüfte"). However, well demarcated coxal mera probably belong to the ground pattern of the Endopterygota or even a more inclusive clade, also comprising the Paraneoptera and perhaps even some "lower neopterans", where they accommodated coxosubalar and large inner tergocoxal muscles. In any case a distinct meron can be ascribed to the metacoxa of Coleoptera. It is well developed in the archostematan *Priacma* (Baehr, 1975) and its absence or weak development in the coleopteran mesothorax as well as in the Hymenoptera is most probably due to reduction or loss of the inner tergocoxal muscle (Larsén, 1945a).



Figs 7–8. Sucking pump of an adult neuropterid, Neuroptera: Ithonidae: *Ithone fusca* Newman, 1838, in transverse (7) and medial sagittal (8, epipharynx to the left) sections. The floor of the pump consists of soft cuticle only. Notice the ventral transverse cibarial muscles (small arows). The sclerotized oral arm which provides lateral support for the pump is indicated (large arrow) in 7. sg – suboesophageal ganglion; so – salivary orifice.

According to Larsén the inner tergocoxal muscle is absent in the Hymenoptera, and I have repeated this statement (Kristensen, 1975; also Kristensen 1991 where the "inner" was inadvertently omitted). However, Daly (1963) has identified it in *Xyela* and *Sirex*, and in an ongoing large-scale study (Vilhelmsen, unpubl.) of the metathoracic muscles in non-apocritan families it is recorded also from the Tenthredinidae (*Athalia*), Megalodontesidae and Cephidae. The muscle is never strongly developed and consistently inserts on the coxal rim. It is worth noting that in a secondarily flightless moth Larsén (1945b) recorded a similar displacement of the insertion of a regressed inner tergocoxal muscle from the meral surface to the coxal rim.

Molecular studies have not so far provided strong support for any basal endopterygote phylogeny. In the most comprehensive molecular analysis published to date Whiting et al. (1997, based on 18 and 28S rDNA data) found the Hymenoptera placed as sister group of all other endopterygotes, while these authors' total-evidence analysis (combining molecular and morphological data) retrieved a paraphyletic (Coleoptera + Neuropterida) assemblage and a (Hymenoptera + Mecopterida-including-Strepsiptera) clade. Both analyses intriguingly indicated a coleopteran non-monophyly which was subsequently revealed as being due to DNA contamination (Wheeler, pers. comm.), and a reanalysis of the corrected data set is now anticipated with some interest. The 18S rDNA datasets analyzed by Chalwatzis et al. (1996), Pashley et al. (1993) and Carmean et al. (1992) all are based on much less extensive taxon sampling; they never retrieve a basal dichotomy between a Coleoptera + Neuropterida and a Hymenoptera + Mecopterida clade, but their results are little consistent and dependent on outgroup choice and analytical procedure. Both Pashley et al. and Carmean et al. conclude that the endopterygote "orders" were differentiated within a short time span, allowing for but few apomorphies to accumulate on the internodes of the phylognetic tree.

BASAL DIVERSIFICATION MODES WITHIN THE ENDOPTERYGOTE LINEAGES: AN OUTLINE

The basal diversification patterns in the major endopterygote lineages are presently resolved to quite variable degrees. The differences are unquestionably partly due to different research efforts, but most likely also reflect real differences in diversification patterns, i.e., in rates of succession of splitting events.

A summary cladogram of the endopterygotes is presented in Fig. 9; this includes some indications of species richness of the principal clades. Unless otherwise stated, figures for species numbers are taken from Parker (1982) and therefore on the low side of present-day counts. They are estimates of *described* species.

Neuropterida

Though the Neuropterida have long been considered a systematic entity, strong morphological evidence for their monophyly was first provided with Mickoleit's important 1973 study of ovipositor structures. There is accumulating morphological evidence for a monophyletic Megaloptera + Raphidioptera lineage (Achtelig, 1981; Kristensen, 1991), and this monophyly has received strong support from rDNA data (Whiting et al., 1997); see, however, the Neuroptera section below.

Raphidioptera

The smallest (< 200 species, Aspöck et al., 1991) and most homogeneous endopterygote "order" comprising a single pair of families (Inocelliidae and Raphidiidae) whose status as monophyla appears well founded.

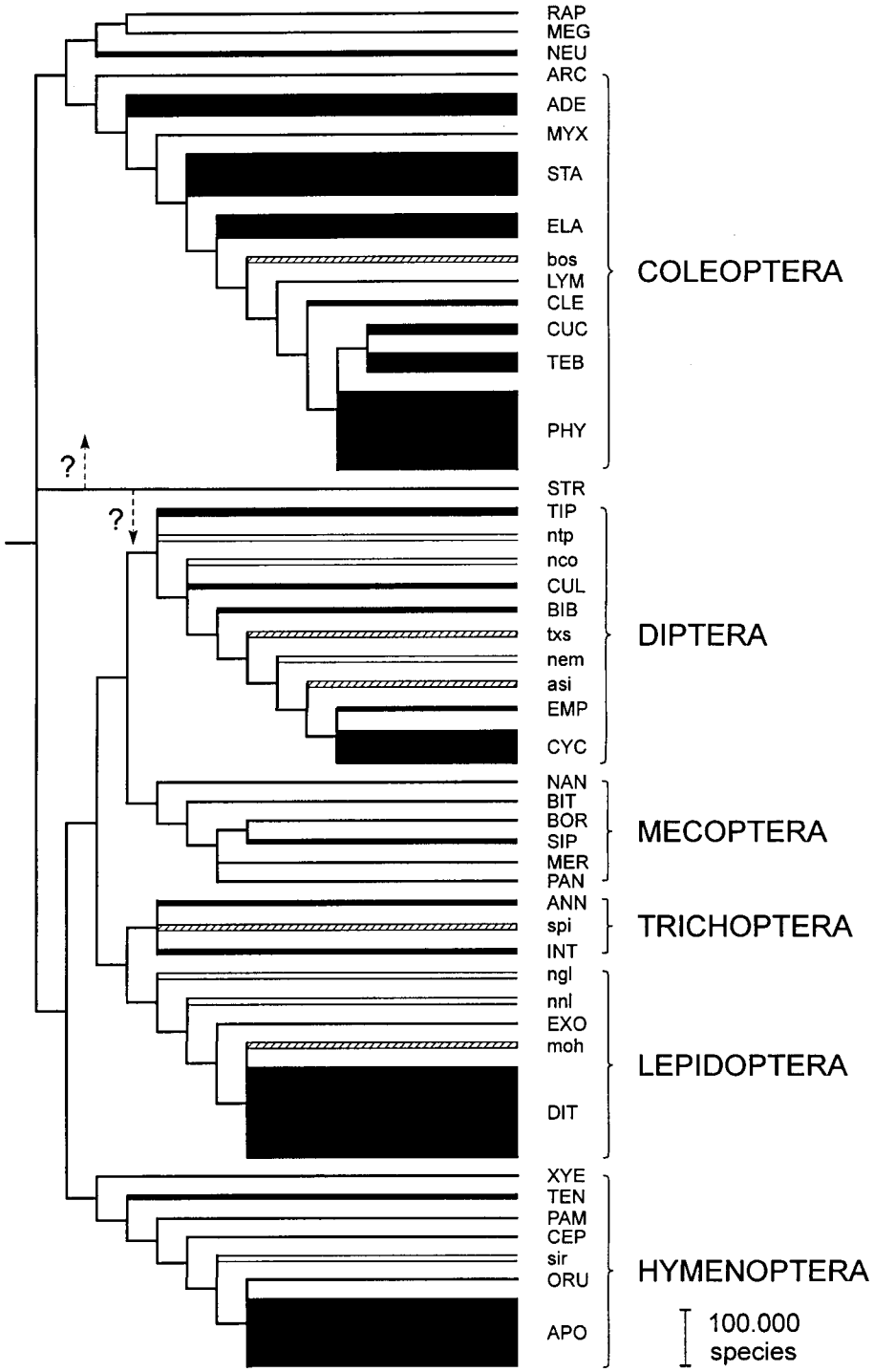


Fig. 9. Summary cladogram of the principal endopterygote lineages. For sources of phylogenetic information see text; dipteran phylogeny from Yeates & Wiegmann (1999), with nematoceran grade modified according to Michelsen (1996). Thin single and double lines indicate, respectively, monophyla and paraphyletic assemblages with < 1000 described species; bold and shaded lines indicate, respectively, monophyla and paraphyletic assemblages with 1,000–10,000 species. For clades with > 10,000 described species the approximate species number is indicated by the width of the clade line; scale in lower right corner. ADE – Adephaga; ANN – Annulipalpia; ARC – Archostemata; APO – Apocrita; asi – asiloid assemblage; BIB – Bibionomorpha; BIT – Bittacidae; BOR – Boreidae; bos – bostrichiform assemblage; CEP – Cephoidea; CLE – Cleroidea; CUL – Culicomorpha; CUC – Cucujoidea; CYC – Cyclorrhapha; DIT – Ditrysia; ELA – Elateriformia; EMP – Empidoidea; EXO – Exoporia; INT – Integripalpia; LYM – Lymexylonoidea; MEG – Megaloptera; MER – Meropeidae; moh – monotrysian Heteroneura; MYX – Myxophaga; NAN – Nannochoristidae; nco – non-culicomorph oligoneuran non-neodipterans; nem – nemestrinoid assemblage; NEU – Neuroptera; ngl – non-glossatan assemblage; nml – non-neolepidopteran Glossata; ntp – non-tipuloid polyneuran nematocerans; ORU – Orussoidea; PAM – Pamphilioidea; PAN – Panorpomorpha; PHY – "Phytophaga" (=chrysomeloid/curculionoid assemblage); RAP – Raphidioptera; SIP – Siphonaptera; sir – siricoid assemblage; spi – spicipalpian assemblage; STA – Staphyliniformia; STR – Strepsiptera; TEB – Tenebrionoidea; TEN – Tenthredinoidea; TIP – Tipuloidea; txs: tabanomorph/xylophagomorph/stratiomyomorph assemblage; XYE – Xyeloidea.

Megaloptera

The phylogeny of this small (< 300 species, New & Teischinger, 1993) group has recently been debated because of the intriguing diversity in its members' ovariole structure. Arguably the best founded solution is that the two currently recognized families, the Sialidae and Corydalidae indeed do constitute a monophylum, as conventionally suggested on the basis of their aquatic larvae with lateral abdominal tracheal-gill appendages and more or less extensive spiracle closure in early instars (Achtelig & Kristensen, 1973; Kristensen, 1995).

Strikingly similar specializations in the telotrophic ovariole type shared by Sialidae and Raphidioptera led Štys & Biliński (1990) and Kubrakiewicz et al. (1998) to suggest a sistergroup relationship between the two; hence Megaloptera would be paraphyletic. Büning (1998) agrees that the specialized telotrophic ovarioles in Sialidae and Raphidioptera are a genuine synapomorphy, but he considers specializations in the organization of somatic ovarian tissues shared by Sialidae and Corydalidae to support megalopteran monophyly; this necessitates the assumption that the secondarily panoistic ovarioles in Corydalidae are derived from the telotrophic type.

Preliminary observations by Kubrakiewicz et al. (1998) on the ovarioles of Corydalidae: Chauliodinae indicate that these are secondarily panoistic like those of the better-known Corydalinae.

Neuroptera (=Planipennia)

Relationships within the Neuroptera are among the principal contemporary challenges in basal endopterygote phylogenetics. In conventional arrangements the poorly known Rapismatidae and Ithonidae as well as the Coniopterygidae are excluded from an assemblage comprising the remaining families. The use of cladistic thechniques to basal neuropteran systematics was pioneered by Aspöck (e.g. 1992, 1995) and eventually led to the following scheme: (Sisyridae + ((Ithonidae + Polystoechotidae) + hemerobioid assemblage – the latter including the Coniopterygidae in a quite subordinate position) + (Neurorthidae + myrmeleontoid assemblage)); the Rapismatidae (whose immatures remain unknown!) remain unplaced. This tree of a major clade is unusually symmetrical: the two lineages that are inferred to have arisen in the basal splitting event both account for very close to one-half of the ca 5,500 described neuropteran species.

A noteworthy innovation in Aspöck's 1995 contribution is the revival of the suggestion that the Neuroptera are the closest relatives of the Megaloptera, that their last common ancestor was aquatic, and that this life-style in putatively primitive representatives within the two basal clades (Sisyridae and Neurorthidae respectively) hence is primary. While interesting, this hypothesis does entail serious problems. Thus, the several apparent raphidiopteran/megalopteran synapomorphies (morphological and molecular) have to be interpreted as homoplasies.

Aspöck's suggestion that the cryptonephridia encountered in representative neuropteran larvae should be particularly easily explicable as a result of a secondarily terrestrial life-style is debatable; similar explanations certainly cannot be invoked in the parallel cases in Coleoptera and Lepidoptera. And while Aspöck's proposal of the maxillary stylet in neuropteran larvae being of stipital origin can be partly supported by myology and innervation (since the stylet includes a stipital component along with at least a lacinial one), there is also evidence that elongation of the maxilla in megalopteran and neuropteran larvae had been independently evolved (Rousset 1966: 162).

It must be stressed that Aspöck's family groupings (based on larval cephalic structure in particular) are largely independent of the Neuroptera/Megaloptera sistergroup theory, and they are a good starting point for future work. Conflicting evidence is already forthcoming: recent studies on ovariole structure do support a more conventional (basal) placement for the Coniopterygidae (Kubrakiewicz et al., 1998) within the Neuroptera. A strongly supported basal Neuroptera phylogeny will evidently require much additional information on a number of key taxa, including the stout-bodied Rapismatidae and Ithonidae.

Coleoptera

Four basal beetle lineages have been recognized for several decades now, and at least three of the fifteen possible phylogenies have for a while been en vogue. The currently best supported is Archostemata + (Adephaga + (Myxophaga + Polyphaga)), as advocated by Klausnitzer (1975), Beutel (1997), and particularly strongly by Beutel & Haas (1998 and in press) on the basis of a sizable data set drawing on a broad spectrum of morphological characters. In the last mentioned analysis the monophyly of the "Pantophaga" (= Adephaga + (Myxophaga + Polyphaga)) is supported by 20 potential synapomorphies of its constituent lineages, including nine non-homoplasious ones.

The principal alternative basal phylogenies are (Archostemata + Adephaga) + (Myxophaga + Polyphaga), as advocated by Baehr (1979), and Polyphaga + (Archostemata + (Adephaga + Myxophaga)), as advocated by Kukalová-Peck & Lawrence (1993). In addition to being best supported by morphology the Archostemata + Pantophaga phylogeny has the attraction of being in good accordance with the reasonably good record of early beetle fossils, which are overall Archostemata-like, yet apparently form an assemblage which is paraphyletic in terms of the still-extant lineages (Beutel, 1997).

The Archostemata and Myxophaga combined comprise a tiny fraction (<< 1%) of the described extant beetles, while the Adephaga account for more than one-tenth, namely some 35,000 species. According to present understanding (Lawrence & Newton, 1995; Hansen, 1996) the basal split within the Polyphaga is between two very species-rich clades, viz., the Staphyliniformia s. l. (70,000+ species; including the Scarabaeoidea: Hansen, 1997) and all other taxa, constituting the so-called "eucinetoid lineage" of Kukalová-Peck & Lawrence (1993). Within the latter there may be a sister group relationship between an "elateriform" and a considerably larger "bostrichiform + cucujiform" clade. Within the latter the Chrysomeloidea and Curculionoidea together with a Tenebrionoidea + Cucujoidea clade probably constitute a

monophylum, of which the Cleroidea and Lymexylonidea are successively more distant relatives. The Chrysomeloidea and Curculionoidea are sometimes talked of collectively as the "Phytophaga"; this overwhelmingly species-rich assemblage comprises some 130,000 described species, but it remains debatable whether it is actually monophyletic (Hansen, pers. comm.).

Farrel's recent (1998) study of the phylogeny and host associations of Polyphaga: "Phytophaga" led to the conclusion that repeated shifts from primitive-grade seed plants to angiosperms has promoted major radiations, as evidenced from the numerical dominance of extant angiosperm-feeding lineages as compared to their gymnosperm-/cycad-feeding sister groups. Angiosperm feeding was consequently seen as being the principal explanation for coleopteran species richness.

Mecopterida: Antliophora (=Mecoptera + Diptera + ?Strepsiptera) + Amphiesmenoptera (=Trichoptera + Lepidoptera)

The above mentioned "Strepsiptera problem" apart, the monophyly of the "panorpoid orders" (a less inclusive assemblage than Tillyard's typologically circumscribed "panorpoid complex") continues to be accepted; while this assemblage is not consistently retrieved in available molecular analyses, its morphological support appears adequate (Kristensen, 1991). The constituent high-rank subgroups Antliophora and Amphiesmenoptera are similarly accepted, the latter is indeed clearly the most strongly supported of all supraordinal groupings within the Hexapoda.

Mecoptera s. l.

Scorpionfly phylogeny was revolutionized during the 1970s and 1980s when studies by Mickoleit and Willmann (see comprehensive reviews by Willmann, 1987, 1989) on the female and male genital segments respectively provided evidence for non-basal positions of earlier authors' "protomecopterans", viz., Eomeropeidae (= Notiothaumidae) and Meropeidae. Instead the attention was focused on the circumantarctic Nannochoristidae whose genital morphology suggests a sister group relationship to the remaining mecopterans and whose aquatic larvae also differ markedly from previously known mecopteran larvae. Hinton's (1981) establishment of a separate "order" Nannomecoptera for these insects has not won general acceptance, nor has Wood & Borkent's (1989) proposal that they may be the sister group of the Diptera or the Diptera + Siphonaptera. The state-of-the-art phylogeny of the families within a conventionally circumscribed Mecoptera (with altogether about 500 species) is Nannochoristidae + (Bittacidae + (Boreidae + Meropeidae + Panorpomorpha)); the Panorpomorpha comprise the Eomeropeidae + (Apteropanorpidae + (Choristidae + (Panorpidae + Panorpodidae))).

An apparent second revolution of mecopteran phylogeny comes with the accumulating evidence that the Siphonaptera (fleas, some 1,700+ species), are not just the sister group of the scorpionflies, but actually subordinate within them. The evidence for a sister group relationship between fleas and the mecopteran family Boreidae ("snow fleas") comes from a suite of derived characters of their secondarily panoistic ovariole structure (Büning, 1998; Biliński & Büning, 1998), rDNA data (Chalwatzis et al., 1996; Whiting et al., 1997) and newly acquired information on the adult insects' mouth parts (V. Michelsen, pers. comm.). This position of the fleas would also resurrect the loss of the outer "singlets" in the sperm axoneme as a genuine synapomorphy of fleas and higher scorpionflies. According to Gassner et al. (1972) these tubules are retained in bittacid scorpionflies (nannochoristid sperm structure remains to be studied).

Acceptance of this position of the fleas will, then, bring the number of endopterygote "orders" down from 11 to 10. It may necessitate some ad hoc assumptions concerning some larval characters of which fleas have retained plesiomorphic states believed to be lost in mecopterans, according to information by Hinton (1958; this is the basis of Kristensen's subsequent accounts). However, there is inadequate information on the larvae of many mecopterans, including bittacids and nannochoristids. In any case a position of the fleas subordinate within the primitively winged scorpionflies, as sister group of the already flightless snow fleas, appears to make excellent sense in an evolutionary context: invasion of mammal nests from a habitat like that attributable to moss-feeding boreid ancestors appears a highly plausible ecological scenario.

Diptera

Among the megadiverse endopterygote "orders" it is the Diptera whose basal diversification pattern has so far appeared most difficult to resolve. Oosterbroek & Courtney (1995) reviewed earlier work and analyzed an extensive matrix comprising morphological characters of all stages of the basal lineages, while important subsequent contributions by Michelsen (1996) and Friedrich & Tautz (1997) draw on substantial original studies on imaginal cervico-thoracic anatomy and 28S rDNA, respectively. A comprehensive overview of the morphological and molecular evidence bearing on the high-rank phylogeny of flies is given by Yeates & Wiegmann (1999).

There is general agreement on the nematoceran assemblage being paraphyletic in terms of a monophyletic Brachycera and on the monophyly of a major "culicomorph" family-group among the nematocerans. A basal dichotomy between a tipuloid clade and the remaining Diptera is weakly supported in Friedrich & Tautz' maximum likelihood analysis of the molecular data (but not in their parsimony analyses in which, respectively, the culicomorphs and a psychodoid + trichoceroid clade come out as the sister group of the remaining Diptera). This is in accordance with a suite of earlier proposals and is also compatible with Michelsen's hypothesis, which implies that the Tipuloidea, Trichoceroidea, Tanyderoidea and Ptychopteroidea are outside a clade "Oligoneura" comprising all other Diptera. The Oosterbroek & Courtney analysis surprisingly assigned a tipuloid + trichocerioid clade a quite subordinate position, viz., as sister group to an anisopodoid + Brachycera clade inside the Bibionomorpha s. l. This arrangement is contradicted by Michel-

sen's findings which strongly support a monophyletic clade "Neodiptera" comprising the Brachycera + Bibionomorpha s. l. inside the Oligoneura, and hence excluded the tipuloids and trichoceroids. The Neodiptera are not retrieved in any of Friedrich & Tautz' molecular analyses, but the taxon is also not contradicted in these author's cautious general conclusion, viz., that the examined dipteran taxa can be grouped into six well supported basal clades (Culicomorpha, Trichoceridae, Tipulomorpha s. str., Psychodidae, Bibionomorpha s. l., and Brachycera); current molecular evidence does not permit a grouping beyond the unresolved hexatomy. They note that the "small amount of phylogenetic information documenting the earliest splits in the Diptera at both the molecular and morphological level is ... consistent with the rapid diversification of the major lineages".

While the basal phylogeny of the orthorrhaphan-grade lineages within Brachycera also remains unclarified, there is accumulating morphological and molecular evidence supporting the sister group relationship between the Empidoidea and the extremely species-rich clade Cyclorrhapha, which comprises >40% of all described Diptera.

Trichoptera

The basal diversification pattern of the caddisflies remains problematical; it is sobering that the recent comparative study by Frania & Wiggins (1997), while presenting a wealth of comparative morphological data, did not disclose characters that are decisively informative with respect to the basal splits; see also Morse (1997), Kristensen (1997), Ivanov (1997) and Wichard et al. (1997). There is general agreement on the monophyly of two high-rank taxa, the Annulipalpia (larvae net spinners, retreat makers, etc., 2,000+ species) and the Integripalpia (larvae tube-case makers, 2,800+ species) which together comprise the bulk of the "order". Outside these clades are four overall primitive families: Hydroptilidae (larvae free-living, except in purse-case making final instar), Glossosomatidae (larvae saddle-case makers), Rhyacophilidae and Hydrobiosidae (larvae "free-living", actually ambushers as pointed out by Ivanov, 1997). The assemblage (some 1,600+ species) comprising these families have by some been considered a monophylum ("Spicipalpia"), but it is most likely paraphyletic in terms of Annulipalpia, Integripalpia or both, as was expressly suggested by Ivanov (1997), whose proposed phylogeny (Rhyacophilidae + Hydrobiosidae + Annulipalpia) + ((Glossosomatidae + Hydroptilidae) + Integripalpia) awaits evaluation.

Lepidoptera

The basal sector of the lepidopteran phylogenetic tree is currently considered to be a highly resolved "Hennigian comb"; principal references are Kristensen (1984), Nielsen & Kristensen (1996), Kristensen & Skalski (1998), Krenn & Kristensen (in press). Applying the conventions ("phylogenetic sequencing" etc.) of "the annotated Linnean hierarchy" (Wiley, 1981) the relationships can be presented as:

Micropterigidae
Agathiphagidae
Heterobathmiidae
Glossata
  Eriocraniidae
  Coelolepida
    Acanthopteroctetidae
    Lophocoronidae
    Myoglossata
      Neopseustidae
      Neolepidoptera
        Exoporia
        Heteroneura
          Nepticuloidea
          Incurvarioidea
          Eulepidoptera
            Palaephatidae sedis mutabilis
            Tischeriidae sedis mutabilis
            Ditrysia sedis mutabilis

While the Ditrysia comprise >98% of the described ca. 150,000 Lepidoptera species, the bulk of the morphological diversity of the "order" resides in the small non-ditrysian grade. Ditrysian groupings above superfamily level remain quite tentative. Following Minet (benchmark review: 1991) one can now recognize three successively more inclusive clades: Macrolepidoptera (principal components Noctuoidea, Geometroidea, Hesperioidea/Papilionoidea, Bombycoidea), nested within Obtectomera (principal additional component Pyraloidea), nested within Apoditrysia (principal additional components Tortricoidea, Zygaenoidea, Sesioidea). The non-apoditrysian grade comprises such major superfamilies as the Gelechioidea, Yponomeutoidea, Gracillarioidea and Tineoidea; the last-mentioned are most likely the sister group of, or paraphyletic in terms of, all other Ditrysia.

Ecologically the Lepidoptera are far more homogeneous than any other insect clade of comparable species richness. Only two non-glossatan families (Micropterigidae and Agathiphagidae, comprising <0.01% of the described Lepidoptera) are likely primarily non-dependent on angiosperms.

Hymenoptera

The phylogeny of the Hymenoptera is largely reminiscent of that of the Lepidoptera, with a highly pectinate basal sector and a strongly autapomorphic and exceedingly species-rich subordinate clade, the "waist wasps", Apocrita (Vilhelmsen, 1997, 1999). Few clades above superfamily rank are currently named; using the "phylogenetic sequencing" convention the basal diversification can be represented as:

Xyeloidea
Tenthredinoidea
Pamphilioidea*
Cephoidea
"Siricoidea"
Vespina
Orussoidea
Apocrita

There is some uncertainty about the basalmost split, inasmuch as the Xyeloidea: Xyelidae as usually delimited (Macroxyelinae + Xyelinae) is not with certainty monophyletic. A hypothesis of the Xyelinae only being the sister group of all remaining Hymenoptera is supported by scale-like microtrichia on the paraglossa surface, and some homoplasious characters. The monophyly of Xyelidae s. l. is supported primarily by strongly asymmetrical adult mandibles; this, however, is a questionably apomorphic state. The "Siricoidea" as usually circumscribed are apparently paraphyletic, since the Anaxyelidae, Siricidae and Xiphydriidae seem to have arisen in three consecutive splitting events in the lineage leading to the Orussoidea + Apocrita.

An Orussoidea + Apocrita clade appears strongly supported; > 30 potential synapomorphies of the two have been identified, including seven non-homoplasious ones (Vilhelmsen, 1999). In contrast, the relationships between the major lineages within the Apocrita are largely unresolved in a recent quantitative-cladistic analysis of a sizable data matrix (Ronquist et al., 1999); for example, an Ichneumonoidea + Aculeata clade which has been repeatedly proposed in recent years (see, e.g., Sharkey & Wahl, 1992; Dawton & Austin, 1994), was not retrieved in the shortest trees.

The non-apocritan grade comprises 6,000+ species (Gaston, 1993), which is just about 5% of the described Hymenoptera and almost certainly an even much smaller proportion of those actually existing: being predominantly extra-tropical and mostly medium sized (never minute) insects, non-apocritans are overall better-studied than the "Parasitica" superfamilies which comprise the bulk of the Apocrita. The vast majority (5,300+ species) of the non-apocritans are tenthredinoid sawflies. This superfamily is thereby larger than any of the aforementioned basal lepidopteran clades by almost an order of magnitude; the parallelism between the two orders' diversification patterns thus has its limits.

PHYLOGENETIC PATTERNS AND THE ENDOPTERYGOTE SUCCESS STORY

"When the evolution of any group of animals is well known, it is usual to find that the acquisition of its characteristic structures and habits occurred slowly and progressively up to a certain critical point, when, some acquisition being now perfected, the group was able to radiate rapidly because it could now exploit its environment more fully or because it could now invade environments from which it was previously barred. These critical points in evolution may be called nodal points." In the eloquent address (Hinton, 1977) opened by this paragraph the origin of endopterygote metamorphosis was identified as one of the "nodal points" in insect evolution. Hinton emphasized that the absence of external wing buds facilitates movements (particularly *backwards*) of endopterygote juveniles in dense substrates, and it was argued that this facilitation has paved the way for that high degree of differential utilization of the environment by juveniles and adults to which endopterygote success has been repeatedly attributed.

But just how precisely can "nodal points" actually be identified? While this contribution opened by emphasizing the immense species richness of the Endopterygota as such, it is apparent from the preceding survey and the summary cladogram in Fig. 9 that the truly extraordinary species numbers are attributable to just a small number of quite subordinate endopterygote taxa, namely the staphyliniform and (particularly phytophagan) cucujiform beetles, the cyclorrhaphan flies, the ditrysian Lepidoptera and the apocritan wasps. Arguably, therefore, the bases of each of the said taxa could be labelled "nodal points" more justifiably than the base of the Endopterygota as a whole. However, a closer look at the intrinsic phylogeny of each of these taxa usually reveals an unsurprising repetition of the higher-level pattern: a taxonomic hierarchy with the bulk of the constituent species pertaining to just a small set of subordinate taxa. Iteration of the process in most cases seemingly renders the quest for "nodal points" a quest for the rainbow's end.

The "nodal point" issue is closely linked to the quest for "key innovations", which is a controversial theme in evolutionary biology; for a recent exchange see Hunter (1998a, b), Masters & Rayner (1998), and references therein. Hunter warns against construing key innovations as "characters originating at the base of a radiation", noting "the possibility that traits occurring earlier in the history of a lineage are in fact the ones necessary for radiation to occur". This stand agrees with the difficulty repeatedly encountered in attempts of identifying plausible causes for the success of species-rich clades among their groundpattern autapomorphies. Exceptions do occur, such as the "wasp-waist" of Hymenoptera-Apocrita, which may have enhanced postabdominal manoeuvrability during oviposition in insect hosts, and perhaps the protective puparium of cyclorrhaphan flies (admittedly paralleled elsewhere within the Diptera). But generally it seems that the degree of success of any given taxon is to be explained by the *unique combinations* of apomorphies that have been acquired in its stem lineage, including those acquired on tree internodes that were shared with increasingly distant relatives. The most species-rich organismal clades owe their success partly to suites of apomorphies added relatively recently on top of the endopterygote ground pattern complement, but also to the pterygote-type locomotor apparatus *and* a hexapod-type cuticle, etc.

* Megalodontoidea auct. (Springate, in press).

As noted above, Farrell (1998) has argued that the capacity for herbivory (understood as angiosperm feeding) is the principal cause for the success of beetles. The same capacity may similarly explain lepidopteran success; in fact the Lepidoptera "above" the Agathiphagidae constitute the most species-rich clade of primarily angiosperm-feeders in the animal kingdom (Powell et al., 1998). These success stories are special cases of a general pattern which Mitter et al. disclosed a decade ago (1988): That herbivorous clades with non-herbivorous sister-groups are more species-rich than the latter. The same authors have subsequently (Wiegmann et al., 1993) examined, by a similar methodology, whether the same is true for parasitic (in a broad sense, including parasitoids) carnivores; they found that it is not.

Sister group comparisons are one set among a suite of approaches to reconstructing shifts in diversification rates (e.g. Sanderson & Donoghue, 1996). But while the conclusiveness of the procedure in adaptation studies of this kind remains debatable (also Coddington, 1994, Zrzavý, in prep.), probably few biologists would contest the notion that the diversity of neopteran insects is indeed linked to the rich and varied resource that became available with angiosperm radiation. Herbivorous insects, in turn, constitute themselves a rich resource, and while diversity promotion of carnivorous parasitism may not hold as a general principle among insects, it is certainly true for the largest clades of the largely endopterygote-parasitizing endopterygotes, viz., the Hymenoptera: Orussoidea + Apocrita and the Diptera: Tachinidae. These clearly outnumber their non-parasitic sister groups, and extrapolating from species numbers in the best inventoried area of the World (NW Europe) one may actually hypothesize that the Hymenoptera: Apocrita will eventually prove to be a group for which the Creator had an even greater fondness than for Haldane's beetles. The failure of these radiations to comply with a general (i.e., recurrent) pattern is unsurprising. The emphasis on organismal diversity being the result of innumerable sequences of *unique* historical events is a hallmark of evolutionary biology.

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