

synapomorphies of Myxophaga and Polyphaga. The interpretation of firmly fused meso- and metaventrites as a synapomorphy of these suborders implies reversal in some groups of Polyphaga (most scirtoids, derodontids, few agyrtids and leiodids, some cantharoids).

A scenario with Archostemata as basal group is better in agreement with the fossil record than the hypothesis of KUKALOVÁ-PECK & LAWRENCE (1993). Archostemata and Adephaga are well represented before the earliest records of Polyphaga.

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## The Basal Relationships of Coleoptera Based on 18S rRNA Sequences

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Together with numerous collaborators, our laboratory has accumulated 18S rRNA sequences which are used here to build a comprehensive tree of the Coleoptera. Sequences were compiled from Genbank and unpublished data. After removal of incomplete and low quality sequences, a total of 795 sequences representing ca. 130 families (of 160–170 total in Coleoptera) were used in the phylogenetic analysis. Sequence alignment was achieved in a stepwise procedure using the ClustalW software, where taxa from undoubtedly monophyletic groups at the level of superfamilies were aligned separately (including some 30 sequences of Histeroidea, 150 sequences of Chrysomeloidea, etc.), prior to aligning them to hierarchically higher groups using the ‘profile alignment’ option in ClustalW. The aligned matrix was subjected to parsimony searches, and yielded shortest trees of 28,950 steps (CI = 0.133, RI = 0.705).

The basal relationships of suborders were consistently found to be Archostemata + (Myxophaga + (Adephaga + Polyphaga)), in accordance with previous findings from a much smaller subset of these data (CATERINO et al. 2002). Rates of change and number of inferred indels were much greater in Adephaga than Polyphaga, and hence both groups were analysed separately. The analysis of adephagan relationships included 220 taxa and a representative sample of all major groups. Parsimony searches yielded a tree of 14,166 steps (CI = 0.221, RI = 0.677). The tree showed the well established (on the basis of 18S rRNA) separation of Geodephaga and Hydradephaga taxa, and the unexpected placement of some presumably basal groups (Cicindelidae, Rhysodidae, Paussidae) within derived carabid groups (SHULL et al. 2001), even with the more comprehensive sampling in this study. Relationships within Hydradephaga included the close relationships of Dytiscidae, Aspidytidae, Hygrobiidae, and Amphizoidae, as described previously (RIBERA et al. 2002).

The analysis of Polyphaga included 575 taxa in over 110 families and produced shortest trees of 14,747 steps (CI = 0.173, RI = 0.651). Among the five Series of families in the suborder, the Elateriformia represented the most basal group, as sister to all other Polyphaga. Within Elateriformia, a clade comprising Eucinetidae (including families Scirtidae, Eucinetidae, Clambidae, Decliniidae)

and the bostrichiform Derodontidae was sister to all other families. The remaining elateriform groups include clearly monophyletic Dascilloidea and Buprestoidea, and larger clades roughly corresponding to Elateroidea and Byrrhoidea of previous authors, with all aquatic families of the latter in close proximity.

The following nodes in the tree correspond to a clade of monophyletic Staphyliniformia plus Scarabaeiformia, and Bostrichiformia paraphyletic with respect to the latter two groups. In the Staphyliniformia we find (weak) evidence for two major lineages, with the Staphylinidae (including several smaller families) as sister to a clade of Hydraenidae, Ptiliidae, Agyrtidae, Leiodidae, Silphidae, plus three families of Histeroidea. The aquatic Hydrophilidae surprisingly showed affinities to the basal Scarabaeiformia.

The Cucujiformia, the largest Series of Polyphaga, was represented in our analysis by 330 taxa of 51 families and clearly recovered as monophyletic. Among the six superfamilies within Cucujiformia, the ecologically diverse Cucujoidea was paraphyletic with respect to Cleroidea. The latter grouped as sister to Kateretidae, with Trogossitidae occupying the most basal node within the Cleroidea. Five clades of 3–5 families each were well supported in Cucujoidea, but one of these (including families Cryptophagidae, Latridiidae, Phalacridae, and Corylophidae) grouped within Tenebrionoidea. This is likely due to long branch attraction, also affecting the placement of Lymexyloidea in this part of the tree. Further we find Curculionoidea plus Chrysomeloidea (the ‘Phytophaga’) to be monophyletic, with basal relationships mainly confirming morphological analyses.

In conclusion, we find that morphological classifications of previous authors, in particular CROWSON (1960) and LAWRENCE & NEWTON (1982), are generally confirmed by the 18S rRNA gene, but our tree needs to be subjected to further testing, using more complete searches, and adding other markers. Methods are needed to assemble large trees from subsets of closely related sequences, and to assess support in very large trees. However, this tree is the most complete phylogenetic hypothesis of basal Coleoptera relationships to date, and can be used to test morphological and ecological diversification of the group.

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## Towards a Consensus: Latest Results from Simultaneous Analysis of the Basal Hymenopteran Lineages

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The phylogeny of the basal hymenopteran lineages has been the subject of intense scrutiny since the groundbreaking work of A.P. Rasnitsyn (summarized in RASNITSYN 1988). Although his phylogenetic hypothesis was derived intuitively, many of the relationships proposed in his paper are upheld by later cladistic analyses, including the reanalysis of his dataset by RONQUIST et al. (1999). VILHELMOSEN (1997, 2001) compiled comprehensive morphological datasets from a number of sources and performed computerized analyses. SCHULMEISTER et al. (2002) and SCHULMEISTER (2003) presented the first simultaneous analyses of basal hymenopteran phylogeny, expanding the morphological dataset of VILHELMOSEN (2001) as well as providing molecular data from five genes (12S, 16S, 18S, and 28S rDNA and COI), including a total of 343 morphological characters and almost 3,000 basepairs, 1,136 of which were phylogenetically informative. More than half of the informative sites were provided by COI.

There is substantial agreement between the results of the latest computerized analyses (Fig. 1). The monophyly of the Hymenoptera is strongly supported by a host of morphological characters (VILHELMOSEN 2001). Prominent autapomorphies are: laterocervicalia fused with propleuron, articulation between propleuron and profurcal arm present, anterior apical protibial spur modified into calcar, cenchrus present, metafurca arising anteriorly on discal vein, forewing anal veins not reaching wing margin, distal hamuli present, abdominal spiracles surrounded by sclerotized cuticle, cordate apodeme on female abdominal tergite 9 present, basal ring and volsella in male genitalia present, and common cornea in larval eye present. Molecular analyses also provide some support (SCHULMEISTER 2003). The monophyly of the order has never really been disputed.

The monophyly of most of the basal superfamilies within the Hymenoptera as currently defined is strongly corroborated. The relationships between them as suggested by the morphology alone and the simultaneous analyses are practically identical, many nodes being well supported. However, in some cases there is conflict between the morphological and the molecular data. Under some circumstances, analysis of the morphological data alone does not place Xyelidae as the sister group to the remaining Hymenoptera. The presence of a separate mesothoracic anepisternum and of an unbranched Rs vein in the forewing provides some support for the monophyly of non-xyelid Hymenoptera, as does the molecular data; however, other

morphological characters contradict this. The Xyelidae always comes out as well supported, autapomorphies being found in the antennal structure (enlarged third segment) and especially in the mouthparts which have the labrum, mandibles and hypopharynx adapted to grind pollen. However, these features are also found in many fossils and in some outgroup taxa, respectively. The difficulties with resolving the basal splitting events within the Hymenoptera might be due to difficulties with polarizing the characters, caused by the highly autapomorphic status of the order.

The Blasticotomidae consistently comes out as the sister group to all other Tenthredinoidea (the Tenthredinoidea s.str.). Otherwise, the phylogeny of this superfamily is poorly resolved and weakly supported, with considerable differences between morphological and molecular hypotheses; it is necessary to sample tenthredinoid diversity much more densely as well as expand the character sets to derive a robust phylogeny. The next superfamily to branch off is the Pamphilioidea, then the Cephoidea. The placement of the family Anaxyelidae is contentious; molecular data supports a sistergroup relationship with Siricidae, whereas the morphological data places it as sister to Siricidae + Xiphydriidae + Orussidae + Apocrita. The latter hypothesis is weakly supported, as substantial character conflict occurs. The sistergroup relationship between Orussidae and Apocrita is very strongly supported by morphology. However, analysis of the molecular data alone fails to retrieve this relationship.

In general, the accumulation of data leads to an increasingly robust phylogeny for the basal hymenopteran lineages. The consensus phylogeny supports the scenario for the evolution of larval lifestyle in basal Hymenoptera depicted in Fig. 2. The larva of the common ancestor of all Hymenoptera was herbivorous. The transition from the herbivorous to the carnivorous/parasitoid lifestyle took place in the common ancestor of Orussidae + Apocrita. Prior to this transition, Hymenoptera had invaded the woody habitat, having wood-boring larvae (as in extant woodwasps: the Anaxyelidae, Siricidae, and Xiphydriidae), a condition that apparently immediately predated the evolution of parasitism. This scenario is corroborated by many basal parasitoid taxa (e.g., Orussidae, Megalyridae, Stephanidae, many Ichneumonoidea) being ectoparasitoids of wood-boring insect larvae, presumably the lifestyle adopted by the ancestral parasitoid. Many of the morphological changes occurring within the basal Hymenoptera can be correlated with the transition to the parasitoid lifestyle. For example, the adult mouthparts