

Proceedings of the 1st Dresden Meeting on Insect Phylogeny: “Phylogenetic Relationships within the Insect Orders” (Dresden, September 19–21, 2003)

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Foreword

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Recent years have seen remarkable progress in reconstructing the phylogenetic relationships of the Insecta, based on a flood of new morphological and molecular evidence and rapid development of analytical methods. Whereas the relationships among the different ‘orders’ are still far from being robustly resolved, hypotheses about the basal relationships within a number of these ‘orders’ are now approaching maturity. Still, this is true to a very different extent for the various orders, and it does not mean that there are no longer disputes about diametrically conflicting hypotheses. Long-standing questions such as the relationships between Zygoptera and Anisoptera in Odonata, between Caelifera and Ensifera in Orthoptera, and between the four suborders of the Coleoptera are cases in point, as are the position of the Isoptera inside or outside the Blattaria, of the Siphonaptera inside or outside the Mecoptera, and of the Phthiraptera inside or outside the Psocoptera.

These basal phylogenetic relationships within the various insect orders were the subject of the meeting the proceedings of which are here presented – a subject that would be laborious to comprehensively access through a search of the literature. The meeting, which took place in the ‘Blockhaus’ in the historical center of Dresden immediately after the annual meeting of the German ‘Society for Biological Systematics’ (GfBS), was designed and organized by Klaus-Dieter Klass, with much support from Matthias Nuss and Niels Peder Kristensen.

In 35 invited talks, 55 speakers (including coauthors) who have been deeply involved in research on the basal phylogenetic relationships of the individual insect ‘orders’ presented the state-of-the-art in their fields; many of them included yet unpublished results from their laboratories. The program also included the recently (in 2002) discovered order Mantophasmatodea, which up to now has grown to include 13 described species, rendering it worthwhile to discuss its intraordinal phylogeny. Unfortunately, on the other hand, both of the announced talks on Odonata had to be cancelled briefly before the meeting; still, a written contribution on Odonata phylogeny by Günter Bechly could be included in these proceedings.

In the talks, evidence from both the morphological and the molecular field was included according to the availability of data, and partly results from the two fields were presented in separate talks by speakers specialized on the evaluation of the one or the other kind of data; conflicts between different data sets were indicated; and it was explained which phylogenetic hypothesis is presently considered to have the strongest support. A particularly impressive aspect was that due to the rapid development of sequencing and analytical methods for some insect orders molecular data sets are meanwhile available that include hundreds of species. In contrast, in some other orders, such as Archaeognatha and Zygentoma, the compilation of molecular data sets is still at a very early stage; and it became also clear that in a number of insect orders there is still a very limited knowledge of morphological data.

Speakers came on their own expenses from various institutions in Germany, Austria, Denmark, France, the United Kingdom, Czechia, Italy, the USA, Australia, Singapore, and Argentina. Including the ca. 50 additional visitors, the meeting was altogether attended by about 100 persons.

A volume presenting the current state of understanding of the basal splitting events in the various insect orders is planned for completion within the next two years (editors: Rudolf Meier, Klaus-Dieter Klass, Niels-Peder Kristensen & Michael Whiting). The team of authors preparing the book chapters is largely congruent with the group of speakers invited to present a talk at the meeting.

Motivated by the great success of this meeting, the organizers are intending to arrange similar meetings on high-rank insect phylogeny in Dresden that should take place every second year. Focal issues of the meeting scheduled for September 2005 should be: (1) morphological und molecular character systems that are particularly relevant in analysing the relationships among the insect orders; (2) the different and partly competing methods used in the analysis of molecular data; and (3) the results of the working groups that have conducted comprehensive analyses on the relationships among the insect orders.



Participants of the 1st Dresden Meeting on Insect Phylogeny (photo: F. Höhler)

For the following talks presented at the meeting no written contributions for the 'Proceedings' were submitted:

"Hemiptera morphological and molecular (18S RNA) phylogenies: real conflict or unfinished work?" by THIERRY BOURGOIN¹, DAVID OUVARD¹ & BRUCE C. CAMPBELL¹

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"The Systematics of the Heteroptera" by WARD C. WHEELER & RANDALL T. SCHUH

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"Molecular phylogenetics in Lepidoptera: resolution and radiation" by BRIAN M. WIEGMANN¹, JEROME C. REGIER² & CHARLES MITTER³

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"Phylogenetic relationships among the Mecoptera based on morphological evidence" by RAINER WILLMANN

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Character Evolution in the Archaeognatha: Consensus and Conflict

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Introduction

The current view on character evolution in the Archaeognatha (= Microcoryphia) is based on a phylogenetic system inferred by STURM & BACH DE ROCA (1993) from an evaluation of "a wider spectrum of characteristics". Cladistic analyses, however, are still missing for the persisting difficulty to compile a reliable data matrix. This is partly due to inappropriate descriptions of many genera and the need for revision of other genera (STURM 1991), partly due to the lack of relevant data especially on internal anatomy as well as molecular sequences, and generally due to the uniformity of archaeognathan external morphology. Differences in reproductive traits accordingly still form the central arguments for phylogenetic conclusions. Main progress in the past decade primarily concerns the description of nearly 150 new species, which increased the number of species known to date to 493 in total (MENDES 2002). STURM & MACHIDA (2001) integrated the new species into the current system under maintenance of a distinction between so-

called paleoforms, remaining Machilidae, and Meinertellidae (Fig. 1A). This concept leaves three major problems unresolved: (i) the integration of the fossil record, (ii) the assessment of the phylogenetic position of the 'paleoforms' and (iii) a high number of parallelisms. Recent insights into early hexapod evolution permit to revise the early branching events.

†Dasyleptidae as extinct sister group of Machiloidea

The extinct Dasyleptidae (= †Monura Sharov, 1957) are generally attributed to the Archaeognatha due to "strong phenetic resemblance" (KRISTENSEN 1998). Support for this view no longer only relates to the (1) presence of long maxillary palps, which seem to be hypertrophic (e.g., BITSCH 1956) and functionally arranged like a second pair of antennae. Comparative analyses of the head morphology in primarily wingless hexapods (KOCH 2001) in addition favour (2) a sucking mode of food uptake, structurally

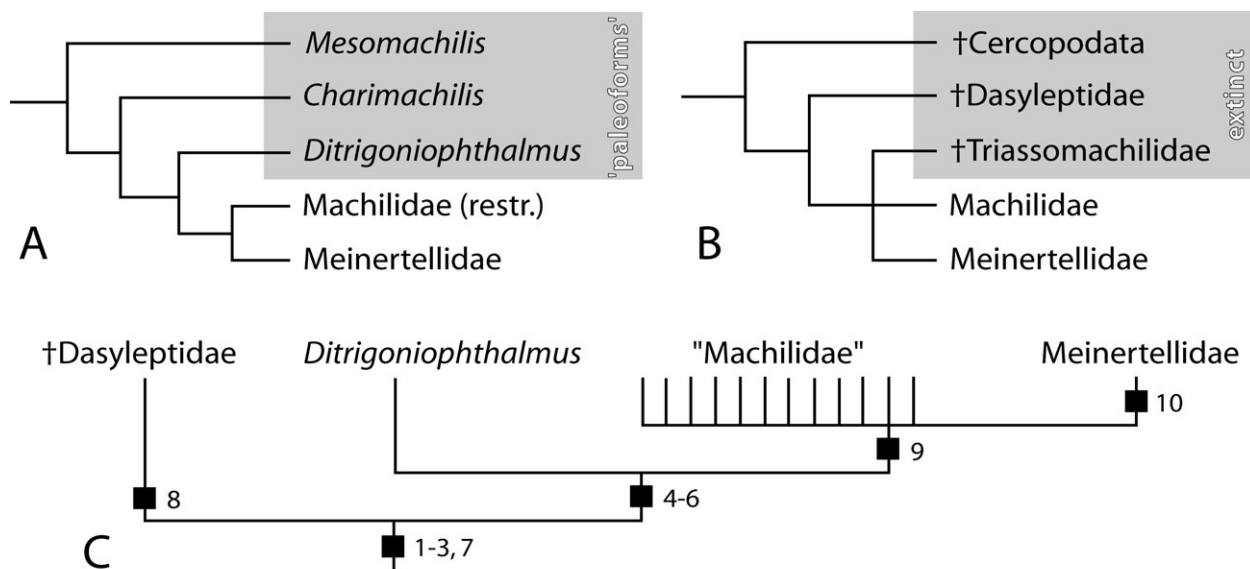


Fig. 1. Current hypotheses on the phylogeny of the Archaeognatha. **A:** After STURM & MACHIDA (2001). **B:** After BITSCH & NEL (1999). **C:** Present conclusions; numbers refer to potential synapomorphies as explained in the text.

based on the presence of narrow, elongate mouthparts forming a feeding cone, as a further potential synapomorphy of †Dasyleptidae and the extant subgroups (commonly united as Machiloidea). The same is true for the mandible morphology: outgroup comparison (Diplura, Zygentoma, Ephemeroptera) dictates the interpretation as the most parsimonious assumption that the inability of biting in extant archaeognathans is a derived state; the (3) monocondylic state of the mandibles shared by †Dasyleptidae and Machiloidea accordingly represents another potential synapomorphy. Previous support of this view by the attribution of an extinct species with allegedly dicondylic mandibles – inappropriately designated as “*Dasyleptus*” sp. (cf. KUKALOVÁ-PECK 1987) – to the Archaeognatha (BITSCH & NEL 1999; Fig. 1B: †Cercopodata), however, seems to be obsolete: according to the revision of this fossil by WILLMANN (2003), its phylogenetic position presently remains as unclear as – among others – the mandible structure of this organism. The same is also true for the extinct, monotypic †Triassomachilidae, which according to RASNITSYN (2002) “proved to be mayfly nymph”. All this presently speaks in favour of a basal splitting of Archaeognatha into †Dasyleptidae and Machiloidea, since the monophyly of the latter is beyond any doubt. The most obvious synapomorphies of the extant species are (4) large compound eyes being contiguous in the midline; (5) the thorax is strongly arched in correlation with the jumping ability; and (6) spiracles are lost on the first abdominal segment. A plenty of further potential synapomorphies were summarized by STURM & MACHIDA (2001), but these suffer from being known from only a few species.

Arguments for the alternative view of a sistergroup relationship between †Dasyleptidae and Archaeognatha + Dicondylia (WILLMANN 2003) are less convincing. Potential synapomorphies of the latter (with the plesiomorphic state presumed to be maintained in †Dasyleptidae) mainly refer to characters showing high variability within basal subgroups of the Ectognatha (subdivision of the tarsus, length of the ovipositor valves, enhancement of the thorax as a tagma) or imply parallel evolution in Diplura (paired pre-tarsal claws), respectively. The latter may also concern the greater reduction of the 11th abdominal segment. This trait seems to correlate with the peculiarity that its paired appendages, the cerci, are moved – if at all – by longitudinal muscles of the 10th abdominal segment. Due to the possibility that this is also true in Diplura (SNODGRASS 1931),

their cerci may be homologous appendages of the 11th abdominal segment, despite its indistinctness both in embryonic and postembryonic stages (for different interpretations see KLASS 2001: 293–294). This tentatively permits to favour the (7) loss of cercal mobility in Archaeognatha (with subsequent (8) loss of the cerci in †Dasyleptidae) as the more parsimonious assumption over the alternative view of an independent gain of cerci and/or cercal mobility in Diplura and Dicondylia. For final decisions, however, the homology of the cercal movers in Diplura and Dicondylia needs to be clarified.

The cuticular head endoskeleton provides the possibility to further test the hypothesis of a sistergroup relationship between †Dasyleptidae and Machiloidea. In the extant species, the metatentorial plate is strongly enlarged in correlation with the jumping ability. The clarification of its shape in †Dasyleptidae accordingly could provide (presently missing) evidence for their jumping ability. With regard to the current view that insects may be terrestrial crustaceans, however, studies on the homology of the muscles involved in jumping in Caridoidea (Crustacea: Malacostraca) and Archaeognatha are required to clarify whether the jumping ability was newly acquired or only optimized in Archaeognatha.

***Ditrioniophthalmus oreophilus* as sister species of the remaining Machiloidea**

Among the so-called paleoforms within Machiloidea, only the basal position of *Ditrioniophthalmus oreophilus* presently seems to be justified: all other extant species are characterized by the (9) loss of the styli on the first abdominal segment. Their presence in *D. oreophilus*, however, still needs to be reconfirmed. The exclusion of the remaining ‘paleoforms’ (*Charimachilis* and *Mesomachilis*) from the Machilidae remains questionable as the monophyly of the latter is still left unsupported by any synapomorphic character. One noteworthy trait restricted to Machilidae within Machiloidea is the carrier-thread method of sperm transfer, but outgroup comparison (Chilopoda, Progoneata, Collembola, Diplura, Zygentoma) indicates that this method as such is the plesiomorphic state within Machiloidea (WITTE & DÖRING 1999; conditions in *D. oreophilus* unknown). Specifics of this method are variable within Machilidae and apparently characteristic for subgroups only (GOLDBACH

2000; STURM & MACHIDA 2001). Sperm transfer via stalked spermatophores in the Meinertellidae, in contrast, correlate with (10) corresponding transformations of the male genitalia (strongly reduced penis length, no 'parameres' = gonapophyses VIII and IX, special glands connected with the vasa deferentia) and maxillary palps (2nd palpomere with hook-like projection).

Conclusions

Based on the available data, the possibility still cannot be excluded that the so-called paleoforms (except *Ditrigoniophthalmus*) and remaining Machilidae form a paraphyletic assemblage with respect to Meinertellidae (Fig. 1C). The high number of parallelisms resulting from the current view on archaeognathan phylogeny may accordingly be artificial. Its explanation by "discontinuously active genes" (STURM 1994) in any case seems to be premature, since the most parsimonious character distribution still remains to be inferred.

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Towards a Phylogenetic System of the Zygentoma

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Introduction

Since ESCHERICH's (1905) monographic treatment of the systematics of the Zygentoma, the taxonomic work in the past 50 years especially by Pedro Wygodzinsky and Luis Mendes provided a much more differentiated view on the phylogenetic relationships among the 470 silverfish species known to date. Yet, however, a considerable number of characters were included into phylogenetic analyses of two subgroups only: Lepismatidae, which comprise most of the 'free-living' representatives, and Nicoletiidae, in which all cave dwellers and deep edaphic forms are subsumed (MENDES 1991, 1994). Their composition and monophyly is traditionally a matter of debate. This especially concerns the uncertainty upon whether the generally myrmeco- or termitophilous representatives of the 'Ateluridae' form a sub-

group of the Nicoletiidae, in as much as nidicolous forms are also known from the Lepismatidae. The character combination in the Maindroniidae also renders a decision difficult upon whether this taxon is more closely related to Nicoletiidae or Lepismatidae.

These uncertainties may hardly surprise as only few morphological characters are presently considered to be significant at high-rank level. MENDES (2002) concluded from his latest analysis that the eyeless representatives (Nicoletiidae and Ateluridae), in contrast to the traditional view, form a paraphyletic assemblage. Data raised from recent studies on the head morphology of *Tricholepidion gertschi*, the only extant species of the Lepidotrichidae, furthermore strengthened previous doubts upon whether the Lepidotrichidae and remaining zygentoman subgroups form a monophylum (STANICZEK 2000; BEUTEL & GORB 2001). Recent revision

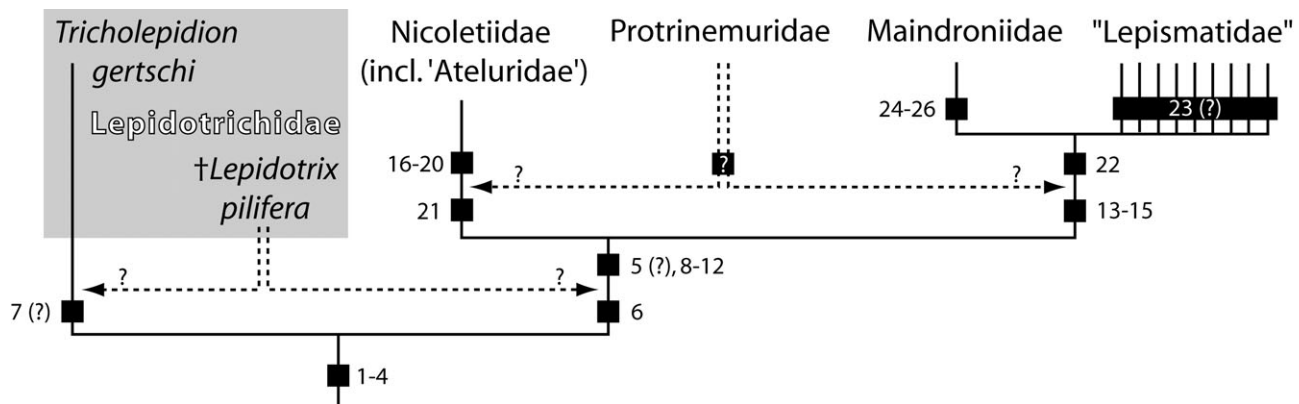


Fig. 1. Present conclusions on the phylogenetic interrelationships among the subgroups of the Zygentoma. Numbers refer to apomorphic characters as explained in the text.

of the structure of the spermatozoa (DALLAI et al. 2001, 2002) in addition rendered the previous view questionable that these provide support for zygentoman monophyly. New data especially on the morphology of the Maindroniidae contribute to a clarification.

New arguments in favour of zygentoman monophyly

Previous arguments unambiguously in support of zygentoman monophyly concern the (1) loss of the superlinguae and (2) certain transformations of the walking legs (horizontal orientation of broadened, dorsoventrally flattened coxa and femur; WILLMANN 2003) that seem to correlate with the (3) dorsoventral depression of the body. New evidence for the monophyly of the Zygentoma (incl. Lepidotrichidae) is derived from the (4) structure of the abdominal cerci: a unique hook-like condyle at their base proved to be present in representatives of all high-ranking subgroups except 'Ateluridae'. Different from what is found in any other insect subgroup, the condyle is formed as a lateral protuberance of the cercal base and articulates with the posterior margin of the 10th abdominal tergum, which bridges the 11th tergum and overhangs the cercal base. The shape of this condyle, however, differs within Zygentoma: it is composed of a single, externally visible hook in *Tricholepidion* and *Nicoletia*, while this hook faces an additional, adjacent hook hidden by the 10th abdominal tergum in *Maindronia neotropicalis* as well as *Lepisma* and *Thermobia* spp. (and *Ctenolepisma longicaudata* as illustrated by ESCHERICH 1905: fig. 41). The absence of this condyle in *Atelura formicaria* ('Ateluridae') may correlate with the great shortening of the cerci. As illustrated by MENDES et al. (1994: fig. 36), however, the condyle seems to be maintained on the likewise shortened cerci of *Trichotriuroides boneti* (Nicoletiidae).

Further new support for zygentoman monophyly is derived from the cuticular head endoskeleton of *Maindronia neotropicalis*. In this zygentoman species, the anterior tentorium is similarly fused with the posterior tentorium as in pterygotes; in *Tricholepidion gertschi* and the lepismatids yet studied, in contrast, these two tentorial components have remained discrete. On the other hand, the paired anterior tentorial apodemes in *M. neotropicalis* share a peculiar feature with those in Lepismatidae: presence of a wing-like protuberance, from which components of the tentorial mandibular 'adductor' muscles originate. This protuberance is a potential synapomorphy of Maindroniidae and Lepismatidae (and Nicoletiidae?) as it is not only missing in *T. gertschi*, in which the homologous muscles still arise from the connective transverse mandibular tendon, but also

seems to be absent in the Pterygota. In this group, the origin of the homologous mandibular muscles at the anterior tentorial apodemes accordingly differs in detail from the state in Maindroniidae and Lepismatidae. All this presently permits to favour the view that (nearly) corresponding transformations of the head endoskeleton and coincident changes of the mandibular musculature happened within Zygentoma and Pterygota in parallel.

Basal splitting events within Zygentoma

Due to missing data on the state in Nicoletiidae and 'Ateluridae', the transformation of the head endoskeleton (5: loss of the connective transverse mandibular tendon and coincident shift of the origin of the individualized bundles of the mandibular 'adductor' muscle to the anterior tentorial apodemes or hypopharynx, respectively) still remains a tentative argument for the view that the Lepidotrichidae form the adelphotaxon of the remaining Zygentoma. Any further support for a sistergroup relationship of this kind concerns a considerable number of reductive traits. Among these, the (6) loss of the median eyes (ocelli) is especially noteworthy. Their apparent absence in the type species of the Lepidotrichidae, the extinct †*Lepidotrix pilifera* (CARPENTER 1992: 17), however, questions the previous view that this species and the extant *Tricholepidion gertschi* form a monophylum. The only potential synapomorphy of these two species concerns the (7) presence of 5 tarsomeres, but this feature may rather already belong to the ground pattern of the Dicondylia (Zygentoma + Pterygota; e.g., MENDES 2002).

Accordingly, the possibility cannot be excluded that the Lepidotrichidae form a paraphyletic assemblage, with *Tricholepidion gertschi* as sister species to a unit composed of all other zygentomans (Fig. 1). According to this view, the extinct †*Lepidotrix pilifera* branches from the stem line of the remaining extant zygentomans characterized by a (8) reduced number of tarsomeres. Further characteristics (with the plesiomorphic state maintained in *T. gertschi* and, as far as known, in †*L. pilifera*) concern the (9) reduced number of ommatidia, the (10) reduced number of pectinate appendages (prostheca) on the lacinia, the (11) reduced number of ovarioles and the (12) reduced size of the abdominal pregenital sterna (KRISTENSEN 1998). The states of these characters (9–12), however, are variable in extant zygentomans, which renders their phylogenetic significance difficult to assess. In this respect, the structure of the male genital coxosterna (KRISTENSEN 1998: character 68) may provide a more reliable argument, but a comparative analysis of their composition is still wanting.

Nicoletiidae (incl. 'Ateluridae') as sister group of Protrinemeridae + Maindroniidae + Lepismatidae?

Based on the available data, the exclusion of the Protrinemerinae (now with family rank) from Nicoletiidae (MENDES 2002) seems to contribute a more parsimonious interpretation of the character evolution within Zygentoma. The current hypothesis that Protrinemeridae are more closely related to Maindroniidae and Lepismatidae is not only supported by the (13) loss of the maxillary protheca and the (14) total absence of abdominal vesicles (MENDES 2002). Protrinemeridae also correspond with Maindroniidae and Lepismatidae in that (15) all coxosternal plates of the pregenital abdomen (I–VII) are no longer subdivided by sutures into a median 'sternite' and lateral 'coxites'. The significance of this potential synapomorphy, however, remains questionable for being paralleled in 'Ateluridae' and Subnicoletiinae within Nicoletiidae as well as in the Pterygota.

The hypothesis of a unit comprising Protrinemeridae, Maindroniidae and Lepismatidae also permits to favour the view that features common to 'Ateluridae' and remaining Nicoletiidae evolved only once within Zygentoma: (16) secondary sexual modification of the male antennal pedicel, (17) transformation of the penial opening into a thin, longitudinal slit, (18) gain of a spinulated area at the inner distal wall of the female gonapophyses IX, and probably also the (19) formation of spermatolophids (MENDES 2002). The (20) presence of a subgenital plate formed by the hind part of venter VII and covering the base of the ovipositor in 'Ateluridae' and Nicoletiidae may also support their close affinity. The polarity of this character, however, remains unclear: a similar plate is formed in the few Pterygota that have retained both a fully developed ovipositor and the original position of the genital opening at the hind rim of segment VII, at least Dictyoptera and Ensifera (KLASS 1998a), which indicates that a subgenital plate may already belong to the ground pattern of the Dicondylia. A small lobe present in Lepismatidae in corresponding position ("languette" in *Thermobia*; ROUSSET 1973) may accordingly represent a remnant of this plate. This presently leaves the hypothesis of a close relationship between 'Ateluridae' and Nicoletiidae mainly based on correspondences in reproductive traits. As a subgroup of the Nicoletiidae, however, the monophyly of the 'Ateluridae' seems to be only supported by the presence of entire coxosterna in the pregenital abdomen (cf. character 15) and hence remains questionable.

Conflicts resulting from the view that Protrinemeridae form a clade with Maindroniidae and Lepismatidae not only concern the implication of a parallel (21) loss of the compound eyes in Nicoletiidae and Protrinemeridae. This hypothesis also strongly weakens the support for the monophyly of the Protrinemeridae, with the absence of eyes being left as the only potential synapomorphy of its two subgroups. In addition, the monophyly of a clade Maindroniidae + Lepismatidae is no longer supported by the available data if these families form a clade with Protrinemeridae. Under this hypothesis, the only potential synapomorphy seems to be the (22) reduction of the compound eyes to (constantly?) 12 ommatidia on each side. Due to the complete reduction of the eyes in the closest relatives (Nicoletiidae and Protrinemeridae), however, the significance of this character is dubious.

The assessment of the phylogenetic relations of the Maindroniidae is further hampered by the persisting difficulty to reason the monophyly of the Lepismatidae. The significance of the (23) presence of a proventriculus in (all?) representatives of this group still remains ambiguous. In part, this is due to claims that denticles are also present in the posteriormost part of the foregut in *Nicoletia* (Nicoleti-

idae) (GRASSI 1886). Detailed structural correspondences of the proventriculi in some Pterygota furthermore indicate that this organ may already belong to the ground pattern of the Dicondylia (KLASS 1998b). The monophyly of the Maindroniidae, in contrast, is beyond any doubt. The unusually large body size and peculiarities of the head and mouthparts – (24) prognathous head posture, (25) mandibular gnathal lobe composed of incisor teeth only (molar plate lost) and the (26) transformation of the maxillary lacinia into a strong hook bare of any appendages – indicate that these may be predators.

Conclusions

While the monophyly of the Zygentoma presently remains a reasonable hypothesis, the interrelationships of its subgroups are still far from being clear. This is due to the deficiency that current conclusions remain based on reductive traits only and/or arguments implying parallelisms within Zygentoma and Pterygota. Unique acquisitions are presently known only from Nicoletiidae (excl. Protrinemeridae, incl. 'Ateluridae') and Maindroniidae. These are accordingly the only high-ranking subgroups that at present can be accepted as monophyla. For any further decisions, available data are insufficient.

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Ephemeroptera Phylogeny and Higher Classification: Present Status and Conflicting Hypotheses

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Ephemeroptera relationships to other insects

The order can be characterized by the following principal characters: (1) bristle-like adult antennal flagellum, (2) specific arrangement of tentorial muscles (STANICZEK 2000); (3) ‘sliding’ articulation of mandibles (KUKALOVÁ-PECK 1991); (4) ‘true’ hypopharyngeal superlinguae; (5) galealacinia fusion; (6) unique arrangement of thoracic tracheal trunks (only a single tracheal trunk coming from the leg trachea, corresponding to the trachea of the paranotal lobes of Zygentoma or Archaeognatha; LANDA 1948); (7) universally lacking occlusor muscles of the abdominal spiracles; (8) well developed, long terminal filament in larvae; (9) retention of winged subimaginal stage; (10) fore wings with prominent basal subcostal brace, and (11) anal brace ending on CuP at a bulla; (12) aquatic mode of life; (13) telotrophic ovarioles.

Apparently, some characters are shared with primitive Neoptera, such as Plecoptera (4, 12), and some with Odonata (e.g., 1, 7, 12, partly 10, 11), and one (6) is sometimes considered neotenic.

Three hypotheses on ephemeropteran affinities are available: (a) Ephemeroptera + Odonata (= Paleoptera, perhaps including extinct paleodictyopteran orders) are the sister group of Neoptera; (b) Ephemeroptera are the sister group of Odonata + Neoptera; (c) Odonata are the sister group of Ephemeroptera + Neoptera. The problem still remains open to a general discussion. From the neontological-morphological point of view, hypothesis (b) seems to be most parsimonious (BEUTEL & GORB 2001), but requires, e.g., parallelism in the antennal flagellum structure, and the non-homology of all neopteran hypopharyngeal lobes with superlinguae is perhaps disputable. In contrast, a detailed study of fossil material does lend support to hypothesis (a); according to my opinion this hypothesis is well corroborated by characters of wing venation (e.g., media always with basal stem) and, in general, by the wing-from-leg-base-exite theory (KUKALOVÁ-PECK 1983). Hypothesis (c) seems to be unlikely (see, e.g., discussions by KUKALOVÁ-PECK 1991 and KRISTENSEN 1991).

Suborder relationships

The original subordinal classification by MCCAFFERTY & EDMUNDS (1979), based mostly on thoracic morphology and wing pad position, comprised the holophyletic Pannota and the paraphyletic suborder Schistonota indicating the retention of certain plesiomorphic traits. Later MCCAFFERTY

(1991) suggested a reasonable re-classification into 3 suborders: Rectracheata (including unchanged original Pannota as an infraorder), Setisura, and Pisciforma. Although he used numerous characters including internal anatomy data by LANDA & SOLDÁN (1985), the Pisciforma still required some revision through abandoning the use of plesiomorphic characters.

Since then some progress has been achieved, but it seems to be extremely difficult to reach a parsimonious solution of this problem because some groups (e.g., the superfamily Siphonuroidea) are defined by plesiomorphies, and new characters are hardly available. Independently, N.Yu. Kluge (see KLUGE 2000 for a complete list of his contributions) defined suborders Costatargalia and Furcatargalia on the basis of presence or absence of certain gill structures (therein called “tergalia” to emphasize wing origin; however, ‘gills’ in mayflies might be of a rather different origin). Later, the same author suggested two suborders again: Anteritorna and Posteritorna based on two-fold emergence of anteromorphy. Although partly including clearly holophyletic taxa (e.g., Posteritorna), both subordinal classifications are essentially based on a single character.

Infraorder relationships

MCCAFFERTY’S (1991) suborders Rectracheata and Pisciforma comprise 3 (namely Vetulata, Lanceolata, and Pannota) and 2 (namely Arenata and Imprimata) infraorders, respectively. This classification seems to be generally accepted, except for the above mentioned parphyly of the Pisciforma and the position of some ‘critical’ genera. For instance, the genus *Oniscigaster* (and the respective monotypic family) requires more attention showing, e.g., dramatic autapomorphic increase in ventral tracheal anastomoses. It is treated in the monotypic infraorder Vetulata by MCCAFFERTY (1991) but is left in the Siphonuridae-like taxa in his Tridentiseta by KLUGE (2000), probably on the basis of the mouthpart “dentisetae” synapomorphy and bordered gills of this genus, which gives to Kluge’s Costatargalia a rather paraphyletic status. Similarly, the genus *Pseudiron* (and the respective monotypic family) deserves further critical evaluation, being treated in the otherwise well defined Setisura-like lineage (KLUGE 2000, his Brachytergaliae) but in Pisciforma-Arenata by MCCAFFERTY (1991). A rather different higher classification using “consistently non-ranking taxonomy” has been developed by KLUGE (2000, see therein for earlier citations, and on

<http://www.bio.pu.ru/win/entomol/KLUGE/EPH/Contents.htm> for more details). I am definitively not in a position to evaluate the scientific invention of this undoubtedly sophisticated classification, but there are some evident restrictions concerning its general acceptance: in many respects, it interferes with the ICZN (for instance, rather arbitrary handling with synonymy, e.g., Arthropleidae Balthasar, 1937 is definitively not a synonym of Heptageniidae Needham, 1901); it is still not applicable to any other insects except for the Ephemeroptera; and it seems to be extremely complicated to be used in other than strictly taxonomic papers (I do not understand why to use “*Turbaniculata Anteropatellata Baetis/fg7 Acentrella/g1*” instead of simply the genus (subgenus) name *Acentrella* of the family Baetidae, e.g., in faunistic lists and ecological papers). Moreover, as many as 20 suprageneric names (7 of them newly erected as “taxon nov.”) are introduced in this treatment (KLUGE 2000) and to trace their relationships to widely used sub- and infraordinal, super- and subfamilial, familial or even generic names requires a long time and maximal concentration.

Superfamily and family relationships

Contrary to the situation in the sub- and infra-ordinal ranks, there is a general consensus in the definition of taxa of (super-)family rank as well as in the application of taxon names. Five superfamilies (namely Leptophlebioidea, Behningioidea, Ephemeroidea, Caenoidea and Neoephe-meroidea) have been introduced by MCCAFFERTY (1991) in addition to the Siphonuroidea, Baetoidea, and Heptagenioidea, approximately corresponding to his infraorders Arenata and Imprimata, and the suborder Setisura, respectively. At present, 37 families have been recognized, which include 376 genera and approximately 3,100 species – contrary to 20 families defined, e.g., by MCCAFFERTY & EDMUNDS (1979). However, taxonomic changes at this level are restricted mostly to formal shifts in rank (from subfamily to family status). As far as I know, only the genus *Siphuriscus* (originally incertae sedis within the Siphonuroidea) will be treated in a separate family soon.

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Phylogeny of Ephemeroptera: Molecular Evidence

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Mayflies are unique among insects by the presence of a non-reproductive winged stage (subimago) that molts to become the reproductive adult. Phylogenetic relationships among mayfly families are poorly known, and current hypotheses are based on untested scenarios of character evolution, which lack any sort of rigorous phylogenetic analysis.

In our ongoing study we use data based on five genes (18S rDNA, 28S rDNA, 16S rDNA, 12S rDNA, and histone 3) to estimate mayfly phylogenetic relationships. Nearly 100 genera of mayflies, representing the majority of lineages, are included. Previous hypotheses for higher-level relationships are discussed and tested in light of these data. In the following explanations the use of taxon names refers to the classification of MCCAFFERTY (1991).

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Our analysis supports the family Baetidae as sister to all other mayflies, though this result is sensitive to outgroup and optimization alignment parameter selection. The pisciform mayflies are supported as grossly paraphyletic. Potamanthidae is nested outside the clade Scaphodonta (= Ephemeroidea + Leptophlebiidae + Behningiidae) and Behningiidae is nested within the Ephemeroidea, rendering this group of burrowing mayflies non-monophyletic. These results suggest that mandibular tusks were gained on multiple occasions with a secondary loss in the lineage Behningiidae. Additionally, the large family Heptageniidae is not supported as monophyletic because the genera *Pseudiron* and *Arthroplea* are nested within this family. The families Baetidae, Leptohiphidae, Nesameletidae, Oligonuridae, Potamanthidae and Ephemerellidae are sup-

ported as monophyletic groups. While our analysis is in its preliminary stages, it represents the first formal cladistic analysis across the major lineages of Ephemeroptera.

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The Phylogenetic Relationships of the Three Extant Suborders of Odonata

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The order Odonata includes three extant suborders (Zygoptera, Anisozygoptera: Epiophlebiidae, and Anisoptera) with totally 5538 described species. The fossil record is relatively well documented with more than 600 fossil species and reaches from Tertiary representatives of extant families back to primitive protodonates of the lowermost Upper Carboniferous (320 mya).

The system of Odonata is still largely based on the typological classification by FRASER (1957), but within the last two decades there have been several attempts towards a phylogenetic system of odonates (CARLE 1982; TRUEMAN 1996; LOHMANN 1996; BECHLY 1999; REHN 2003). Differences between the results of these attempts are based on different selection of characters or even more so on different methodological approaches (e.g., traditional Hennigian Phylogenetic Systematics versus computer-based numerical analysis).

There is a broad consensus that Epiophlebiidae and Anisoptera are both monophyletic, while 'Anisozygoptera' is a paraphyletic assemblage of Epiophlebiidae and fossil stemgroup representatives of Anisoptera.

The monophyly of Anisoptera is supported by numerous morphological autapomorphies (sperm vesicle developed as copulatory organ, wing venation with hypertriangle, triangle, subtriangle and anal loop, larval locomotion by jet-propulsion) and this is also the case for Epiophlebiidae (hamuli posteriores developed as copulatory organ, interocellar lobe, ovoid pedicel, hairy eye tubercle, larval stridulation organs). It is also undisputed that Epiophlebiidae is the sister group of Anisoptera, because there are several good synapomorphies (discoidal cell distally distinctly widened in hindwing, male hindwing with anal angle, males with a secondary epiproctal projection, synthorax with the dorsal portion of the interpleural suture suppressed, larvae with anal pyramid).

Concerning Zygoptera, most recent authors considered them as monophyletic, while TRUEMAN (1996), in a cladistic analysis of wing venational characters, suggested that Zygoptera is a highly paraphyletic group, as already indicated in FRASER (1957). However, the monophyly of Zygoptera is supported by several strong putative autapomorphies, such as the transverse head, the more oblique pterothorax, abdominal sternites with triangular cross-section and longitudinal keel, formation of an ovipositor-pouch by the enlarged outer valves (valvula 3 = gonoplacs) of the 9th abdominal sternite, and of course the highly specialized ligula that is developed as copulatory organ. The presence of caudal gills, even though uniquely present in Zygoptera among extant odonates, has been demonstrated to be a symplesiomorphy by the finding of a fossil dragonfly larva. This larva has wing sheaths that clearly show the characteristic veinal features of the isophlebiid stemgroup representatives of Anisoptera, but still possesses three caudal gills.

A detailed phylogenetic system of fossil and extant odonates with all synapomorphies, based on my results, is available at <http://www.bechly.de/phylosys.htm>.

A recent cladistic study of 122 morphological characters by REHN (2003) basically confirmed this phylogeny; this includes the sistergroup relationship of Tarsophlebiidae and crown-group Odonata, the monophyly of Zygoptera, a lestinoid + coenagrionoid clade which is sister group to Calopterygoidea, the position of the relict damselfly *Hemiphlebia* at the very base of lestinoid zygopteres, the position of Petaluridae at the base of Anisoptera, and the sistergroup relationship of African Coryphagrionidae to the Neotropical Pseudostigmatidae. The only clear differences concern the positions of amphipterygid and megapodagrionid damselflies, which REHN (2003) proposes to represent a paraphyletic basal grade towards the lestinoid + coenagrionoid clade. However, the wide separation of the zygopteran genera *Diphlebia* and *Philoganga* in this phylogeny appears doubtful, because these two genera are united by very strong larval synapomorphies and some synapomorphies of the imagines.

Recent molecular studies on the higher phylogeny of odonates (MISOFF & RICKERT 1999a, b) did not resolve the Zygoptera problem and did partly even conflict with monophyla like Cavilabiata (including Cordulegastridae, Neopetaliidae, Chlorogomphidae and libelluloids) that are very well-established by morphological evidence beyond reasonable doubt. Methodological artefacts like long-branch-attraction and noise seem to be prevalent.

The interpretation of the three different types of secondary copulatory organs as autapomorphies of the three extant suborders respectively is based on a groundplan reconstruction of the male secondary genital apparatus. This ground plan includes small hamuli anteriores and posteriores, a small unsegmented ligula and an undifferentiated vesicula spermalis. This hypothetical reconstruction has been confirmed by the discovery of a well-preserved male specimen of Tarsophlebiidae, the putative fossil sister group of all extant odonates, which shows exactly this type of genitalia (Fig. 1). Consequently, none of the substructures was suited as intromittent organ for sperm transfer in the ground plan, so that there still must have been a mechanism involving external spermatophores. This is confirmed by the finding that the primitive protodonate *Namurotypus sippeli* from the Carboniferous of Germany did not yet possess a secondary male genital apparatus, but primary genitalia that are most similar to those of *Zygentoma*, which deposit spermatophores. The curious odonate mating wheel probably evolved by attaching the spermatophore on the sternites of the basal male abdomen.

Concerning the phylogenetic position of the order Odonata in the tree of insects the evidence is ambiguous. Fossil evidence and some morphological and molecular characters support the monophyly of Palaeoptera (= Palaeodictyopteroidea + Ephemeroptera + Odonata), while rather strong characters of the extant head morphology (STANICZEK 2000) and some molecular data support the monophyly of Metapterygota (= Odonata + Neoptera). Consequently, this issue still has to be considered as more or less unresolved.

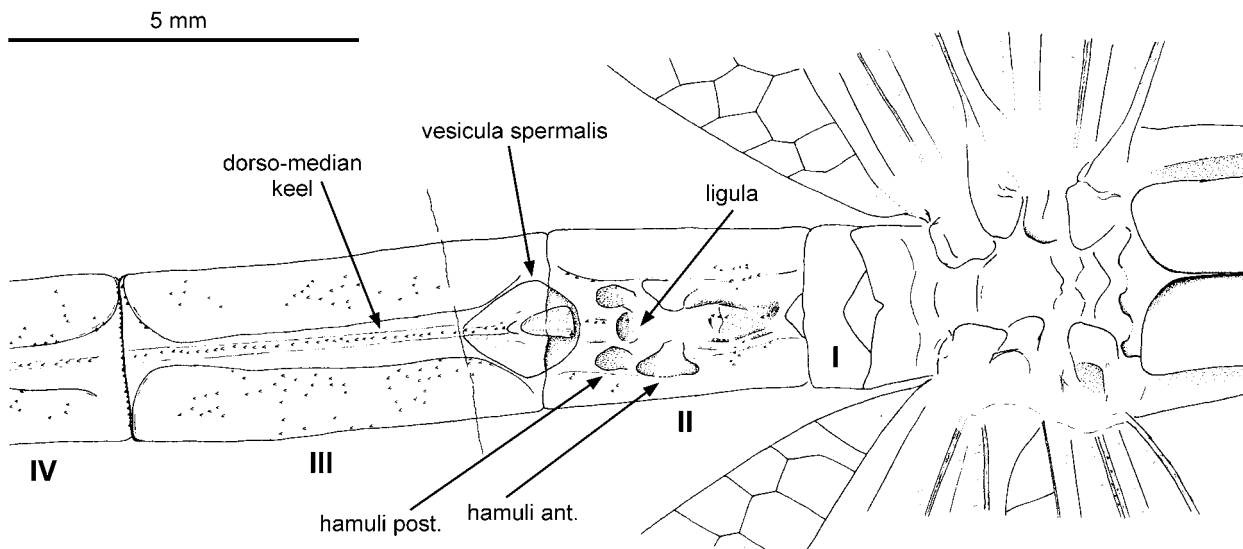


Fig. 1. *Tarsophlebia eximia*, Upper Jurassic Solnhofen Limestone, male specimen no. SOS 1720 at the Jura Museum in Eichstätt (Germany), camera lucida drawing of ventral side of abdomen with secondary genital apparatus.

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Morphological Support of the Major Clades of Plecoptera

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The monophyly of the order Plecoptera is beyond doubt, but the position of Plecoptera among the Neoptera continues to be debated. Ordinal apomorphies are few: the loop-shaped gonads, loop-shaped seminal vesicles, absence of an ovipositor, presence of a cercus heart, and oblique intersegmental musculature supporting the laterally (!) undulating larval swimming movements.

Since the earliest studies, two clades were distinguished within Plecoptera, at various levels between genus (*Perla* versus *Nemoura*) and suborder (Setipalpia versus Filopalpia, or Systellognatha versus Holognatha) (KLAPÁLEK 1905; ENDERLEIN 1909). The competing suborder designations reflect differences of opinion that were actually formalistic and marginal; the disagreement is easily overcome by consistent phylogenetic methodology.

Contemporary systems are based on a large number of characters of external and internal morphology that were studied across all families of the order, and by some cytological and behavioural characters (ZWICK 1973, 2000). The

relationships of the four endemic southern hemisphere families had previously not been satisfactorily recognized. Several of the traditionally recognized major taxa proved to be monophyletic and persist in the present classification.

The Systellognatha are supported, among other, by the reduction of the adult mandibles, by a complex set of gills in particular positions on the thorax, complicated male epi-procts involving numerous movable components, and profound modifications of abdominal tergite 10; variations can be followed across all families. Eggs are hard-shelled, with a suction-disk-like attachment organ, the anchor, at the posterior pole. The first larval instar lives on yolk remains in the gut, only the 2nd instar is actively feeding. The female receptacle carries a number of accessory glands along its stalk-like base. The vast majority of all Systellognatha belong to the Perloidea, which share carnivorous larvae with a modified, slender type of mandible (some adults in this group with secondarily functional mandibles possess the same derived type of mandible), tiny glossae that are

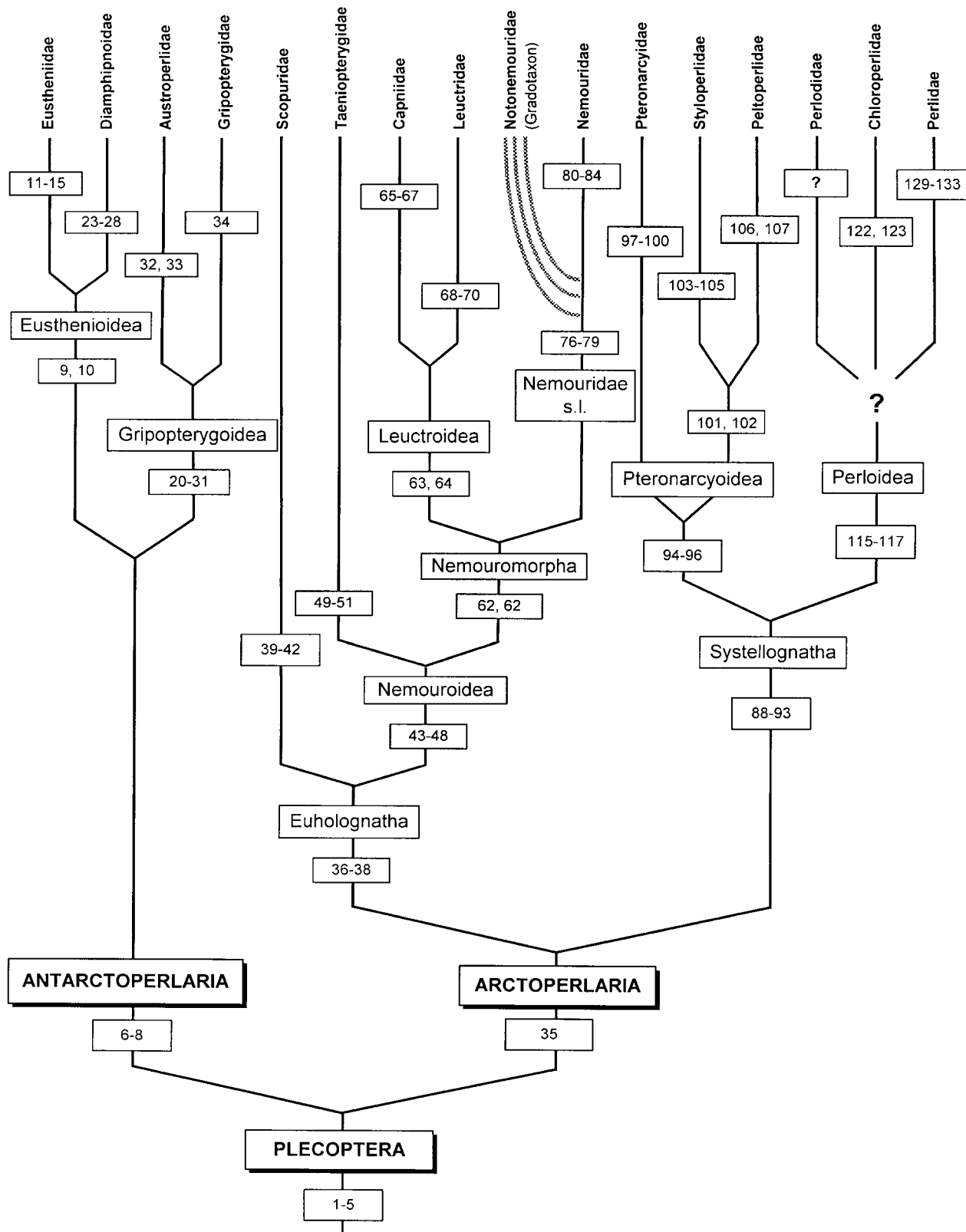


Fig. 1. Cladogram of extant Plecoptera (from ZWICK 2000). Apomorphic characters supporting monophyly of taxa numbered. For character descriptions see the original paper.

much smaller than the paraglossae, and long, slender palpi. The embryo hatches through a defined opercle at the anterior egg pole. The number of free abdominal ganglia is reduced, etc. Within Systemlognatha, the monophyly of the Perlodidae is still weakly supported. Consequently, the relations of Perlodidae with the other two families in superfamily Perloidea are unclear. Only the Perlidae have also colo-

nized large parts of the southern hemisphere, all other Systemlognatha are holarctic endemics. The main apomorphies shared by the Euholognatha are an unpaired corpus allatum fused to the aorta, and the reduction of chorionic sclerotization: euholognathan eggs are soft, with a delicate sticky shell. The Euholognatha include a few wingless species of Scopuridae, and the large com-

plex of the Nemouroidea. The latter are distinguished by numerous modifications of the thorax, especially through a tiny furcasternum on which the furcal bases and spina are located and interconnected by sclerite bridges. There are extra tergo-pleural flight muscles. Also, a number of attachment points of other muscles have shifted away from ancestral positions. Abdominal sternite 10 is reduced, the paraprocts therefore lie directly behind sternite 9. Males have a characteristic pedunculate ventral vesicle with soft surface at the base of sternite 9 that is used in drumming (see below). The mode of sperm transfer via accordingly modified paraprocts, epiprocts, or directly the gonopore on the elongated sternite 9 provide means to convincingly distinguish and group the included families as shown in Fig. 1. Some Nemouridae and Leuctridae advance into the Oriental region but otherwise the Euholognatha are of holarctic distribution, except the disjunct, exclusively southern hemisphere Notonemouridae. These pose presently unsolved problems. In all probability they are a paraphyletic assemblage of ancient surviving lines of early Nemouroidea.

A syndrome of structural and behavioural characters related to sexual communication via substrate vibrations strongly supports the sistergroup relationship between Systellognatha and Euholognatha, which together form the suborder Arctoperlaria.

The southern hemisphere fauna comprises (in addition to the Arctoperlaria: Perlidae and Notonemouridae, both of which occur also in Africa) four endemic monophyletic families (none of them extant in Africa). For a long time, family interrelations were doubtful. Two of the families were for some time regarded as a separate suborder, Archiperlaria, the alleged archaic sister group of all other Plecoptera (ILLIES 1960, 1965), while the other two families were supposedly related to the Filopalpia. However, all four families share unique details of front leg musculature, namely absence of a tergal and presence of an additional sternal depressor of the trochanter. Also, all four families possess the complicated floriform osmoregulatory cells, which occur only in them. Apparently, the four families in question represent a monophylum, the Antartoperlaria (ZWICK 1973, 1980). Since their members show none of the constitutive characters of any of the families or higher-ranked subgroups of the Arctoperlaria, Arctoperlaria and Antartoperlaria are obviously sister groups. They are pre-

sently recognized as the two largely vicariant suborders of Plecoptera (Fig. 1).

Superfamily Eusthenioidea includes the largest Antartoperlaria. They have gills on basal abdominal segments that stand in ventrolateral positions and appear to be a plesiomorphy. Pteronarcyidae and several other relatively primitive Arctoperlaria have similar gills. Details of the structure and musculature of these gills are characteristic of each of the two families, Eustheniidae (carnivorous) and Diamphipnoidae (detritivorous).

Members of superfamily Gripopterygoidea range from very large species with reticulate wing venation to tiny ones with much reduced venation; they are essentially detritivores and lack paired abdominal gills. Gripopterygidae and Austroperlidae instead have gills at the abdominal tip, each family of a characteristic kind. The close relationship of the two families is mainly evidenced by unique modifications of inner genitalia, namely reduction of a seminal receptacle in females, and development of large accessory male glands.

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Phylogeny of Plecoptera: Molecular Evidence and Evolutionary Trends

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Phylogenetic analysis of morphological data (ZWICK 2000) and six molecular markers (12S, 16S, 18S and 28S rDNA; and cytochrome oxidase II and histone 3) including 173 Plecoptera species from all extant families and multiple outgroup exemplars supports a monophyletic Plecoptera basal to all remaining Neoptera. Subordinal relationships within Plecoptera are largely congruent with previous morphological hypotheses with a few notable exceptions (M.D. Terry & M.F. Whiting in prep.: “Phylogeny of Plecoptera: evidence from a combined analysis of six molecular markers and morphology”). Systellognatha and Antartoperlaria are monophyletic; however, Euholognatha is paraphyletic

due to its placement as the first several basal clades within Plecoptera. Under sensitivity analysis this paraphyly is always supported, however, the relationships within Euholognatha vary slightly. Nemouridae form the basal most clade, followed by two clades of the remaining euholognathan families. Notonemouridae (exemplars from Africa, Australia/New Zealand, and South America) are supported as a monophyletic group and not a “gradotaxon” sensu Zwick. Gripopterygidae appear to be paraphyletic with the Austroperlidae nesting within. *Megaleuctra* is not supported as a member of the Leuctridae and deserves recognition as its own family (‘Megaleuctridae’). These results conflict with

several morphological features, particularly the paraphyly of Euholognatha in light of the presence of an unpaired corpus allatum; and future studies will need to more fully examine molecular support for these relationships in light of morphological characters. Patterns of geographical distribution are consistent with early diversification of basal lineages prior to the break up of Pangea, the survival of only two lineages (progenitors of Notonemouridae and Antarcto-

perlaria) on Gondwanaland, and the more recent invasion of South America and sub-Saharan Africa by small groups of Perlidae.

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Phylogenetics of Embioptera (= Embiidina)

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Introduction

Embioptera is an interesting order comprising relatively uncommon, relictual, pseudosocial insects. Phylogenetic studies of the Embioptera are still in their infancy. Despite the small size of the order – with close to 350 described species (ROSS 2001, 2003a, 2003b) – there are no explicit proposals about the relationships between families and there is no reason to believe that currently recognized families are monophyletic units. Rather, a preliminary cladistic study on the classification of the order (SZUMIK 1996) and subsequent analyses at the family level (SZUMIK 1994, 1998) show that many of the currently recognized higher groups are not monophyletic.

Most of the groups in the order have been recognized almost solely on the basis of male terminalia. These display an enormous variety of processes, modified for copulation, and this has kept other potentially informative structures almost completely ignored in traditional classifications of Embioptera.

Given this situation, a morphological and molecular analysis including all the potentially useful characters and many taxa representing all the major groups is strongly needed.

Data and scope

Our morphological analysis includes 57 genera from 8 families, represented by 157 species. This sample represents about 70 % of the described embiid genera, and about 45 % of the known species. 182 morphological characters were scored: 29 cephalic, 53 thoracic and abdominal, and 100 from terminalia. These are characters that vary between apparently distant groups as well as characters that only distinguish genera or groups of genera that seem to be closely related. The molecular data set we analyzed consists of sequences for 16S, 18S and 28S rDNA and COI for 22 species from 6 families and 15 genera. The trees were rooted on the 'primitive' embiopteran *Clothoda*; given this, the monophyly and phylogenetic position of Clothodidae is obviously not tested here.

Results

The resulting trees from the morphological and from the combined data set have well resolved basal clades; in other words, they have a good resolution of the higher groups. In both cases (morphological and combined analyses) only 3

of the 8 families result clearly as monophyletic: Teratembidae, Anisembidae and Australembidae. Notoligotomidae (from Java and Australia) results included in the American-African Archembidae, with these two families together forming a monophyletic group which is ambiguous in the combined data set but supported in the morphological analysis. Embiididae appears non-monophyletic in both analyses; some of its African genera are grouped with the Australembidae.

The major difference between the morphological and the combined analyses is that in the former Teratembidae + Oligotomidae result as the sister group of the remaining non-clothodid Embioptera, while in the latter the Anisembidae take this position.

Conclusion

The results indicate that many non-male-terminalia characters are also very informative; many of them support major groups. Given that some groups (like Archembidae) are not well supported by the molecular data, the combined data set needs to be expanded in several ways (e.g., including more taxa in the DNA data set, and including internal morphology and maternal behavior in the morphological data set).

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Basal Diversification and the Evolution of Wings within Stick Insects (Phasmatodea)

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The stick and leaf insects or Phasmatodea have recently been subject to several phylogenetic analyses, based on both morphological and molecular data. A sistergroup relationship of the wingless Nearctic genus *Timema* (17 described species) to all remaining Phasmatodea (ca. 3000 species), the Euphasmatodea, has appeared uncontroversial including molecular studies (KRISTENSEN 1975; TILGNER et al. 1999; TILGNER 2002; BRADLER 2000, 2003; WHITING et al. 2003). Autapomorphies of the latter are hard-shelled, seed-like eggs, the fusion of metatergum and abdominal tergum 1 and the reduced prothoracic sternal apophysis (furca), while a fusion of the three basal tarsomeres and the presence of a mesal lobe on the right cercus of the male are apomorphies supporting the monophyly of *Timema*.

The primary internal splits of the Euphasmatodea remain debatable (Fig. 1; BRADLER 2000, 2003; TILGNER 2002; WHITING et al. 2003; ZOMPRO 2003). Molecular data suggest that several clades of presumably non-monophyletic 'Diapheromerinae' form the basal lineages of extant euphasmatodeans (Fig. 1B; WHITING et al. 2003). Taking into consideration the basal position of *Timema*, this well supported finding implies that the ancestral phasmid lacked

wings, followed by a long diversification of wingless taxa. Consequently, wings must have been recovered in those clades that contain fully winged or brachypterous species.

Performing a cladistic analysis of morphological characters of the adult female and egg capsule, TILGNER (2002) presents reasonable evidence that the Aschiphasmatinae, which comprise several winged and wingless species and have not been included in any molecular analysis so far, form the most basal branch of extant euphasmatodeans (Fig. 1A). The apomorphic characters supporting the sister group of Aschiphasmatinae are the presence of a galealobulus, the fusion of coxopleurite and anapleurite in the prothorax, and the absence of a pro-spina (character dot = cd 1 in Fig. 1; TILGNER 2002).

Both studies contradict the view of BRADLER (2000, 2003) that the wingless South American genus *Agathemera* is the most basal branch within the Euphasmatodea and sister taxon to the Neophasmatidae (Fig. 1C). *Agathemera* exhibits a number of plesiomorphic characters such as an orthognathous head and relatively short thoracic and abdominal segments with longitudinal musculature spanning the entire segments as in *Timema*. In all Neophasmatidae the longitu-

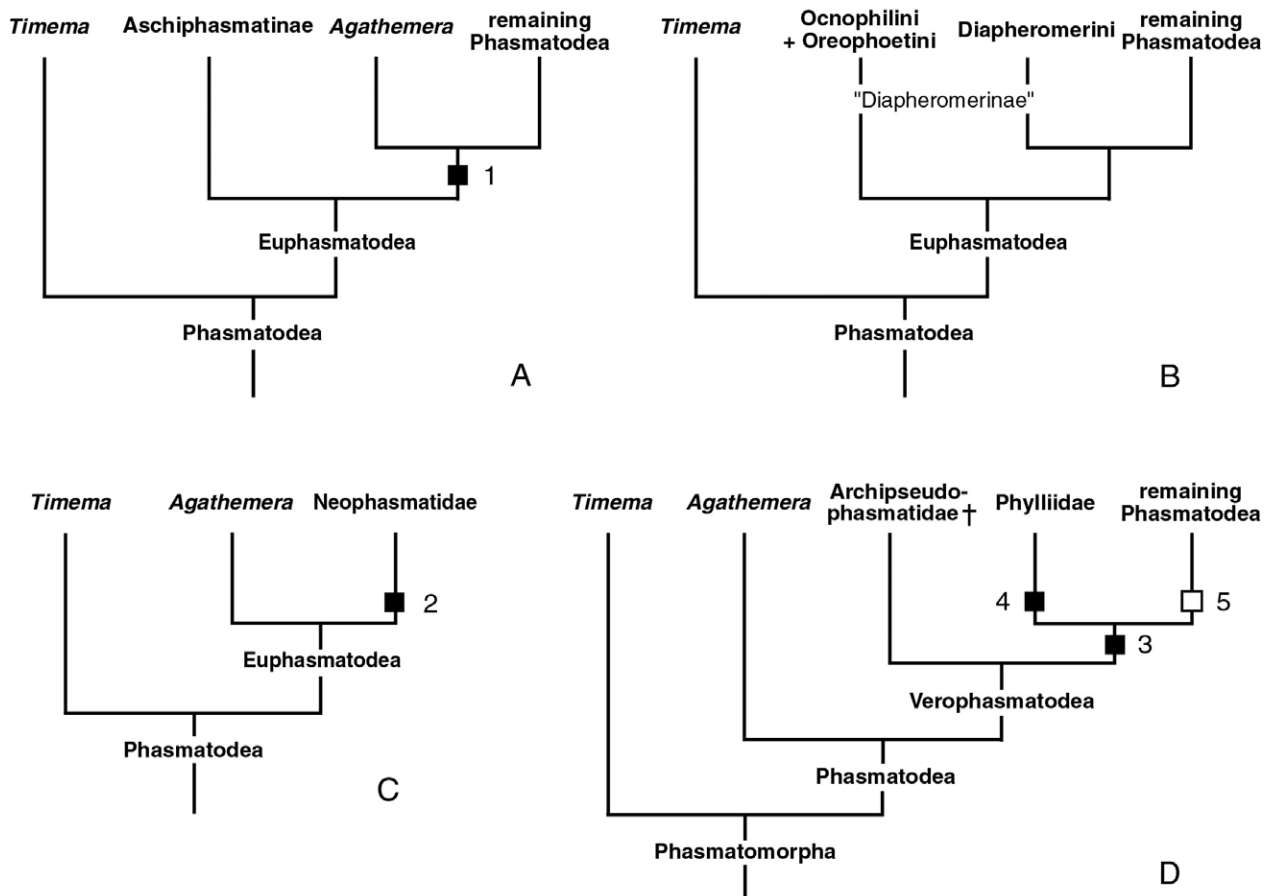


Fig. 1. Alternative hypotheses of the basal splitting events within the Phasmatodea. **A:** After TILGNER (2002). **B:** After WHITING et al. (2003). **C:** After BRADLER (2000, 2003). **D:** After ZOMPRO (2003). The squares represent apomorphic (black) and plesiomorphic (white) characters resp. character dots (cd) referred to in text. Note that in Fig. 1D the name Phasmatodea is replaced by Phasmatomorpha, Euphasmatodea by Phasmatodea, and Neophasmatidae by Verophasmatodea.

dinal muscles do not span the entire length of an abdominal segment but are restricted to the posterior part of each segment (cd 2 in Fig. 1); at least on the ventral side this is likely due to a loss of the internal longitudinal muscles, only the short external ventral muscles remaining (KLASS 1999; BRADLER 2000, 2003). The latter apomorphy is also found in the pregenital abdomen of *Abrosoma festinatum* (Fig. 2), a Bornean member of the Aschiphasmatinae, thus contradicting the basal position of Aschiphasmatinae as proposed by TILGNER (2002).

The mesonotal lobes of *Agathemera* have recently been homologized with wings, incorrectly with hind wings (alae) instead of tegmina (ZOMPRO 2003). As these lobes are positioned dorsally on the hind margin of the mesonotum, lack venation and articulation, they are here not considered homologous with tegmina, in agreement with CAMOUSSEIGHT (1995). Hence, the possible basal placement of *Agathemera* would even strengthen the hypothesis of wing recovery in phasmid evolution since it would form another basal apterous lineage. However, according to molecular data *Agathemera* is a subordinate taxon within the Euphasmatodea (WHITING et al. 2003).

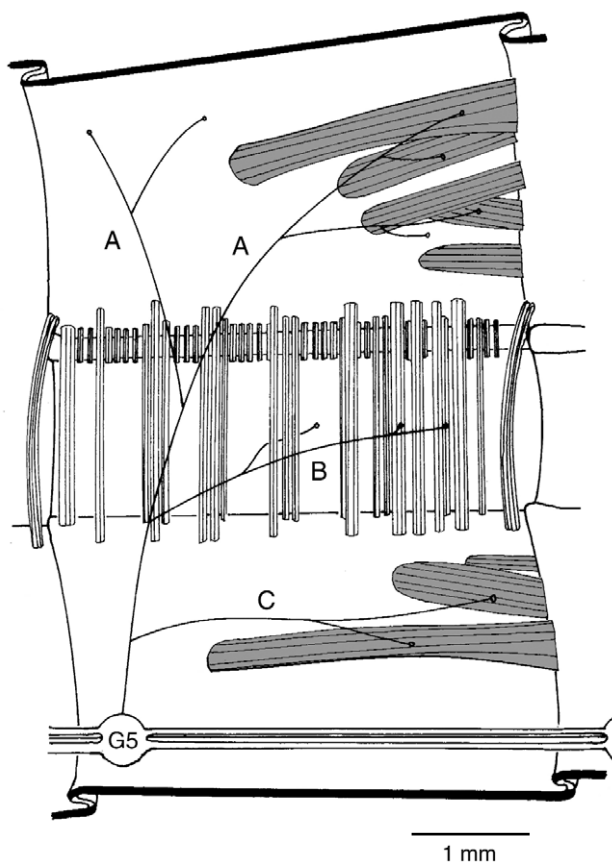


Fig. 2. Muscles and nerves of female abdominal segment 5 of *Abrosoma festinatum* (Euphasmatodea: Aschiphasmatinae). Internal view of right half of abdominal segment 5; orientation: ← anterior, ↑ dorsal. The longitudinal muscles are shaded grey. G5 = abdominal ganglion 5; A = dorsal nerve; B = lateral nerve; C = ventral nerve (R. Klug, original).

ZOMPRO (2003) agrees with BRADLER (2000, 2003) in the position of *Agathemera* (Fig. 1D). In addition, ZOMPRO (2003) presents a phylogeny beyond the level of Neophasmatidae (= Verophasmatodea therein, Fig. 1D). The fossil Archipseudophasmatidae are supposed to be the

sister group of all extant Verophasmatodea (= Phylliidae + remaining Phasmatodea). The only character supporting the latter is the possession of shortened tegmina (cd 3 in Fig. 1). In the majority of (winged) phasmids the tegmina are reduced to small wing pads that cover the base of the hind wings. However, at least in some members, e.g., the male of Malaysian *Heteropteryx dilatata*, the tegmina are almost as long as the hind wings and reach the tip of the abdomen. Hence, the minimal difference in length between fore and hind wings in Archipseudophasmatidae and other phasmids can hardly be considered as a convincing apomorphy.

Within the extant Verophasmatodea ZOMPRO (2003) places the Phylliinae (= Phylliidae sensu Zompro; walking leaves) as the basal side branch (Fig. 1D). While the Phylliinae form a well supported clade based on the presence of a stridulatory organ in the antennae of females and juvenile males, dilated sternites in the abdomen, and laterally fringed micropylar plate of the eggs (cd 4 in Fig. 1), its surmised sister group is only founded on plesiomorphic characters: the absence of a stridulatory organ in the antennae, sternites not dilated, and micropylar plate not fringed laterally (cd 5 in Fig. 1). Hence, the basal placement of the Phylliinae appears unsupported. On the other hand, according to morphological (TILGNER 2002) and molecular data (WHITING et al. 2003) the Phylliinae are a rather subordinate taxon among the Euphasmatodea (= Phasmatodea sensu ZOMPRO).

In summary, the controversial assumptions presented here on basal splitting events in the Euphasmatodea highlight the need for future investigations of phasmid phylogeny. These additional phylogenetic analyses must include a larger selection of taxa, additional molecular markers, and morphological data interpreted via a rigorous phylogenetic analysis. The next step surely is the inclusion of Aschiphasmatinae in molecular studies.

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Relationships among the Principal Lineages of Dictyoptera Inferred from Morphological Data

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Introduction

The Dictyoptera include three major subgroups (usually considered orders), each phenetically distinctive: Blattaria, Isoptera, and Mantodea. While the monophyly of Dictyoptera is generally accepted, phylogenetic relationships within Dictyoptera have been strongly disputed in recent years. This concerns mainly the relationships among the three 'orders' and the basal splitting events in Blattaria.

Monophyly of Dictyoptera

Monophyly is well supported by some striking apomorphies: (1) the perforation in the tentorium through which the ganglionic connectives pass; (2) the formation of a female subgenital plate by coxosternum 7 (as in Dermaptera) that bears a discrete dorsal vestibular sclerite (this is in addition to another, smaller subgenital plate formed by the hind part of venter 7: laterosternal shelf); (3) the packing of the eggs in an ootheca that is built by secretions from morphologically and biochemically asymmetrical accessory glands of abdominal segment 9; and probably (4) the insertion of the abdominal spiracle dilators on the paratergite (rather than on the coxosternum). It should be noted that in the Isoptera (4) has been demonstrated only for *Mastotermes*, and (3) is present only in this genus (see also NALEPA & LENZ 2000).

Important character systems

For reconstructing dictyopteran phylogeny three character systems have been used extensively that are very rich in informative characters: the male genitalia (phallomeres), female genitalia (including the ovipositor), and proventricle (gizzard; the hindmost, cuticulized part of the foregut).

The phallomeres are in all Blattaria and Mantodea very complex (due to their composition of many sclerites, formative elements such as processes, apodemes, tendons, pouches, etc., and muscles) and strongly asymmetrical, and across both groups they show a great structural diversity (especially in Blattaria). This diversity requires – prior to the definition of characters – an extensive analysis aimed at the identification of corresponding parts among taxa (corresponding to alignment in molecular analysis; see KLASS 2001b). Reliable 'alignment' hypotheses require the inclusion of muscles and formative elements into phallomere studies, because these provide additional landmarks for the alignment.

Phallomere characters are not applicable to Isoptera, which have strongly simplified male genitalia (KLASS 2001a; KLASS et al. 2000). There is no outgroup comparison possible for phallomere characters, because corresponding phallomere components could not yet be identified between Dictyoptera and other insects; trees based on phallomere characters can thus only be rooted by including non-phallomere characters.

Phallomere characters were used in three extensive phylogenetic studies: MCKITTRICK (1964; non-numerical; addi-

ons in MCKITTRICK & MACKERRAS 1965), GRANDCOLAS (1994, 1996; numerical), and KLASS (1995, 1997; numerical re-analysis currently in preparation by K.-D. Klass & R. Meier). However, in MCKITTRICK's and especially GRANDCOLAS' contributions the study of cuticular morphology is very superficial, muscles are not considered, and the alignment is tentative (see KLASS 1997, 2001b for a detailed scrutiny). With the more detailed comparative analysis by KLASS, which includes many additional cuticular elements and, partly, the muscles, a very different 'alignment' hypothesis results, which leads to a very different set of informative characters, and eventually to a different phylogenetic hypothesis.

The female genitalia show a complicated pattern of sclerites, articulations, projections (e.g., the gonapophyses and gonopods), apodemes, the spermatheca, and the genital opening. The area lateral to the bases of gonapophyses 8 and 9, where several sclerites contact each other, and the area comprising the laterosternal shelf and the genital opening are especially rich in characters. The numerous muscles of the female genitalia show a fairly constant arrangement and thus help in aligning the sclerites; on the other hand, minor differences in the musculature yield informative characters.

Characters of the female genitalia are fully applicable to *Mastotermes* among the termites, while their application to other termites is limited due to reductions. Outgroup comparison is possible for many female genitalic characters of Dictyoptera but is ambiguous in some of these.

MCKITTRICK (1964) and MCKITTRICK & MACKERRAS (1965) illustrated the female genitalia of many species of Blattaria, partly including the muscles. However, many structural details remain unclear, and the descriptions are altogether too incomplete for composing a reliable character matrix. The more detailed study of the exoskeleton of eight dictyopteran species in KLASS (1998a) allows implications on the relationships among the three 'orders', but for analysing relationships within these groups additional taxa have to be studied.

The proventricle shows a pattern of longitudinal, partly sclerotized folds (plicae) of different rank: wide primary plicae usually bearing heavy sclerites and teeth; much narrower secondary and tertiary plicae. The proventricular plicae are essentially arranged following a hexaradial symmetry, which, however, is overlain by a bilateral symmetry. The distinctness of the bilateral component provides the most obvious point of variation: it varies from very strong (e.g., in Blattidae) to completely absent (e.g., in Isoptera), and several characters can be drawn from this.

It has long been assumed that a complete radial symmetry of the proventricle is plesiomorphic for Dictyoptera, and the bilateral component has developed within the group. However, the proventricle shows a very similar bilateral pattern in many Blattaria and Zygentoma (KLASS 1998b). Using this for outgroup comparison, strongly bilateral proventricles appear plesiomorphic; proventricle characters are then much more congruent with the phallomere characters, so this reversed polarity assumption appears supported.

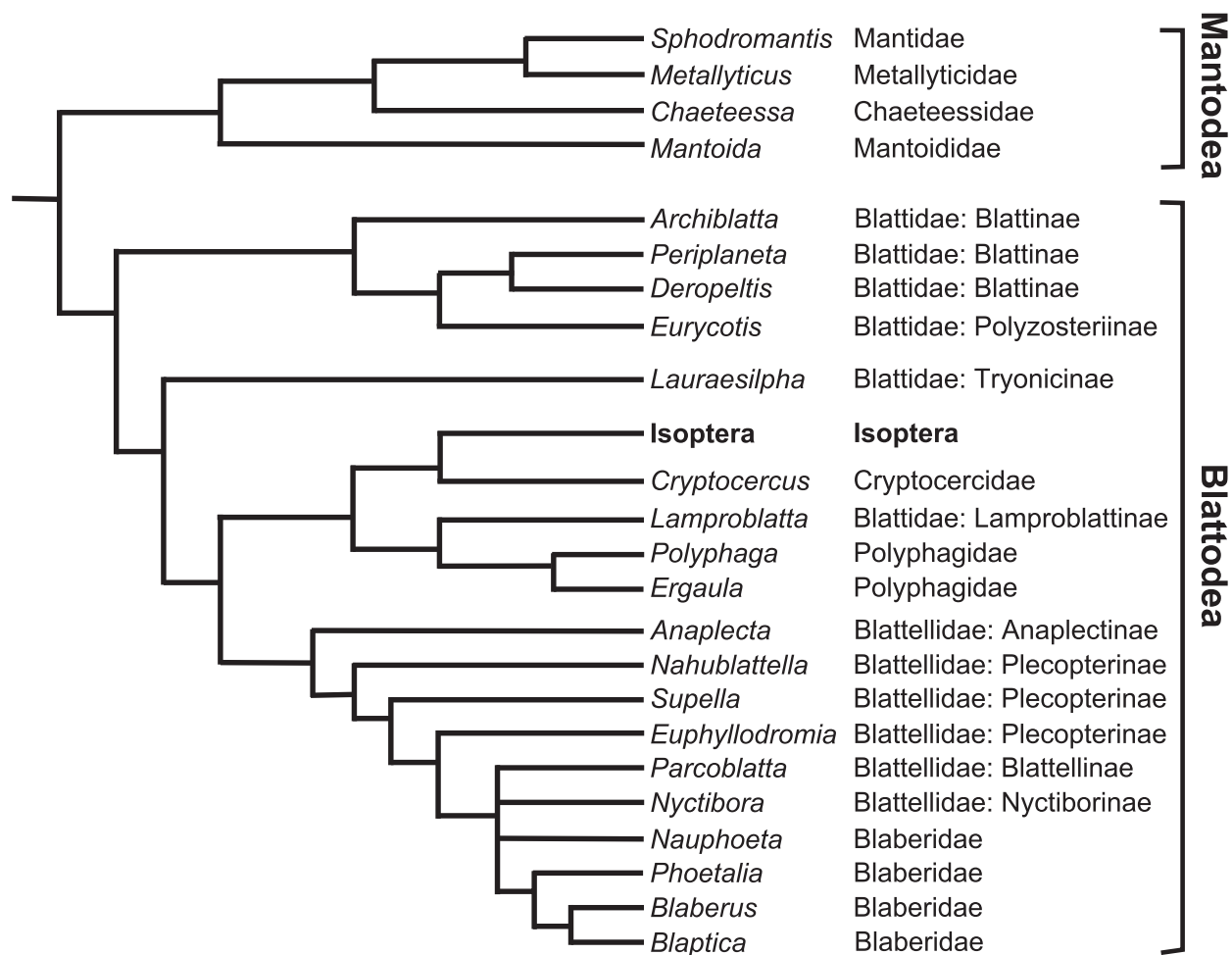


Fig. 1. Phylogenetic relationships in Dictyoptera. Relationships in Blattaria and Mantodea based mainly on phallomere studies (mental analysis by KLASS 1995, 1997 and ongoing numerical analyses by K.-D. Klass & R. Meier). Inclusion of Isoptera based on KLASS (1995) and DEITZ et al. (2003). 'Blattodea' is used for comprising Blattaria and Isoptera.

Phylogenetic relationships among Blattaria, Isoptera, and Mantodea

The point of dispute is here the placement of the eusocial Isoptera as the sister group (1) of Blattaria + Mantodea, or (2) of Blattaria alone, or (3) of the subsocial blattarian genus *Cryptocercus*, which shows many similarities in life history with the termites. A numerical analysis by THORNE & CARPENTER (1992) suggested the topology Isoptera + (Blattaria + Mantodea). However, a recent revision of the same data set by DEITZ et al. (2003) demonstrated that in THORNE & CARPENTER (1992) numerous mis scorings of taxa, disputable polarity assumptions, and cases of misinterpreted literature data were included. DEITZ et al. (2003) obtained Mantodea + (Blattaria excluding *Cryptocercus* + (*Cryptocercus* + Isoptera)), with all nodes strongly supported, thus confirming the hypothesis of KLASS (1995). In DEITZ et al. (2003) seven characters were added to THORNE & CARPENTER's (1992) data set, but the latter topology also resulted using the revised original data set alone.

Due to the vast incompleteness of the available data, in both analyses Blattaria excluding *Cryptocercus* constitute a single terminal, while actually each major blattarian lineage should be included as a separate terminal. This has the effects that the support for a clade *Cryptocercus* + Isoptera may be weakened, and the result cannot tell whether this

clade, if existing, is the sister group or a subgroup of the remaining Blattaria.

The monophyly of Blattaria + Isoptera (= Blattodea) is supported by: (1) the loss of the unpaired ocellus; (2) the fat body harbours symbiotic Eubacteria of the genus *Blattabacterium* (only *Mastotermes* among termites; see LO et al. 2003); (3) the cardiac valve at the transition between proventricle and midgut is strongly elongated; (4) the proventricle bears sclerites on the secondary plicae. Two additional characters from the female genitalia depend on the fact that Blattaria and *Mastotermes* among Isoptera build the ootheca in the vestibulum (space above subgenital plate coxosternum 7), while Mantodea build it on the substrate: (5) the ovipositor in Blattaria and Isoptera is shorter than in Mantodea (ending in the vestibulum); (6) as a casting mould for the ootheca Blattaria and *Mastotermes* have a pair of discrete membranous folds on the subgenital plate.

The monophyly of *Cryptocercus* + Isoptera is supported by characters of the proventricle and life history, e.g.: (1) *Cryptocercus* has the bilateral symmetry component in the proventricle strongly reduced, closely approaching the purely radial conditions in the Isoptera (partly paralleled in some other blattarian lineages); (2) the primary pulvilli (soft cushions formed by the posterior part of the primary plicae) form huge bulbs; (3) the teeth are laterally compressed, ± blade-like; (4) the hindgut harbours a unique diversity of

oxymonadid and hypermastigid flagellates, with several flagellate taxa shared between *Cryptocercus* and basal Isoptera (see KLASS 2001b with regard to GRANDCOLAS & DELEPORTE's 1996 hypothesis on this issue); (5) the flagellates are transfected to the progeny by anal trophallaxis. Further similarities in life history add to this.

The monophyly of Mantodea is mainly supported by: (1) specializations of the raptorial forelegs, including the presence of a femoral brush of setae (cleaning device); (2) some peculiarities in the strongly derived proventricle (e.g., loss of one primary tooth; presence of extensive system of elevated grooves; KLASS 1998b); (3) presence of a transverse apodemal ridge across the pronotum, which externally is usually visible as a 'supracoxal groove'; (4) fusion of the 2nd and 3rd abdominal ganglia to the 1st abdominal and metathoracic ganglia (KLASS 1999).

Basal splitting events in Blattaria and Mantodea

The phylogenetic results in KLASS (1995, 1997) are based on a mental evaluation of phallomere characters. A numerical analysis using the same data set (though with some additions) is presently conducted by K.-D. KLASS & R. MEIER and leads to a nearly identical hypothesis (Fig. 1). In the Blattaria sample (20 species) all 'families' from the classification of MCKITTRICK (1964) are represented (Blattidae, Cryptocercidae, Polyphagidae, Blattellidae, Blaberidae) as well as many 'subfamilies'. In the Mantodea sample (4 species) the three monogeneric families are represented that have been considered most primitive by BEIER (1968) (Mantoididae, Chaeteessidae, Metallyticidae); *Sphodromantis* represents the strongly derived Mantidae, while the remaining families of the system by BEIER (1968) were not included (Eremiaphilidae, Amorphoscelidae, Empusidae, Hymenopodidae). Of the 107 phallomere characters included in the matrix, roughly equal partitions come from the sclerites, formative elements, and muscles. The numerical analyses yielded four most parsimonious trees, of which the strict consensus is shown in Fig. 1 (with resolution lacking only in the clade comprising the Blattellinae, Nyctiborinae, and Blaberidae).

In the Mantodea, *Mantoida* constitutes the most basal clade, followed by *Chaeteessa* (both genera neotropical); both nodes are strongly supported. *Mantoida* shows several 'blattarian' features in its phallomeres that are unique among Mantodea. Two of the autapomorphies of the clade *Metallyticus* + *Sphodromantis* were also consistently found in the phallomeres of various Eremiaphilidae, Amorphoscelidae, Empusidae, Hymenopodidae, and Mantidae described by LAGRECA (1954) (other autapomorphies mostly not visible therein), supporting the view that *Mantoida* and *Chaeteessa* are actually the most basal Mantodea.

In the Blattaria, the Blattidae s.str. (excluding Tryonicinae and Lamproblattinae) is obtained as the sister group of the remaining cockroaches. The next branch is the blattid subfamily Tryonicinae. The remaining Blattaria fall into two clades, Cryptocercidae + (Lamproblattinae + Polyphagidae) and Blattellidae + Blaberidae. In the latter clade, Anaplectinae are basal, followed by paraphyletic Plectopterinae (= Pseudophyllodromiinae) and a clade comprising Blattellinae, Nyctiborinae, and the ovoviparous Blaberidae (and probably Ectobiinae). The placement of the Isoptera in Fig. 1 (as the sister group of *Cryptocercus*) is based on the results of DEITZ et al. (2003).

The phylogenetic hypothesis of GRANDCOLAS (1994, 1996, 1997) differs from that in KLASS (1995, 1997) mainly by a deeply subordinate position (1) of Tryonicinae and Lamproblattinae in Blattidae and (2) of *Cryptocercus* in Polyphagidae, and by (3) monophyletic Plectopterinae (= Pseudophyllodromiidae) and (4) monophyletic Plectopterinae

+ Blaberidae. These issues are comprehensively discussed in KLASS (1997, 2001b).

Future tasks

The most important tasks in the morphology-based reconstruction of dictyopteran phylogeny are the extension of phallomere studies to a larger taxon sample, and the study of the female genitalia in all species sampled for the phallomere studies. Here it is required that morphology is analysed in great detail and that the musculature is also included. This secures a reliable identification of corresponding parts among taxa and also yields a much greater amount of informative characters. The search for new characters in all parts of the body is important with regard to the inclusion of Isoptera, which have strongly reduced genitalia.

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Molecular Phylogenetics of Dictyoptera: Insights into the Evolution of Termite Eusociality and Bacterial Endosymbiosis in Cockroaches

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The Dictyoptera is a well-accepted monophyletic group, consisting of three easily recognized insect types: cockroaches, termites and praying mantids. Cockroaches are well known for their relatively detailed fossil record, though the early roach-like fossils dating back to the Upper Carboniferous (~300 million years ago), which dominated the terrestrial fauna of this ancient era (CARPENTER 1980), were almost certainly stemgroup representatives of the Dictyoptera. Termites have the relatively rare traits among animals of wood-feeding and highly eusocial behaviour, the latter of which is present in all species. Finally, praying mantids are famous for their striking morphological appearance, and their strict predatory diet.

As is the case for many insect groups, relationships within the Dictyoptera have been the subject of controversy for several decades (NALEPA & BANDI 2000; DEITZ et al. 2003), and this controversy has extended into recent molecular studies. The questions of whether praying mantids and termites are each monophyletic have never been in doubt; however, the monophyly of the cockroaches – which might seem reasonable based on the overall uniformity in the body plan of all cockroaches – has been disputed. The two main rival hypotheses of basal dictyopteran relationships have been: (1) a close relationship between praying mantids and all cockroaches, with termites as the outlier (e.g., THORNE & CARPENTER 1992); (2) a close relationship between termites and wood-feeding cockroaches of the genus *Cryptocercus*, with this clade being either separate to, or nested within, other cockroaches. In the latter scenario, Mantodea are considered the outlier to cockroaches and termites (NALEPA & BANDI 2000; DEITZ et al. 2003).

Four genes have now been sequenced from various representatives of all three insect ‘types’: the mitochondrial genes 12S rDNA, 16S rDNA and cytochrome oxidase II, and the nuclear 18S rDNA gene. Initial studies of 12S rDNA and 16S rDNA supported hypothesis (1) above (KAMBHAMPATI 1995). A study of cytochrome oxidase II that did not include *Cryptocercus* indirectly supported hypothesis (2) (MAEKAWA et al. 1999). Following this, a study of 18S rDNA, cytochrome oxidase II as well as endogenous cellulase genes of termites and cockroaches supported hypothesis (2) (LO et al. 2000). In a recent study, all four genes available for mantids, termites and cockroaches were combined and shown to support hypothesis (2) (LO et al. 2003). Included in this study was an examination of the phylogeny of bacterial symbionts present in one primitive termite (*Mastotermes darwiniensis*) as well as all cockroaches. These symbionts are apparently transmitted strictly vertically and are expected to be obligate mutualists, conditions which should lead to phylogenetic congruence between host and symbiont. Evidence for such congruence was indeed found, and the phylogeny of the endosymbionts was shown to support a termite-*Cryptocercus* relationship. Estimates of divergence times between the main lineages of

cockroaches indicated that these occurred at the beginning of the Cretaceous period (~130 mya), not the Carboniferous.

Thus there is now growing molecular evidence that termites are most closely related to the cockroach genus *Cryptocercus*, which would render the cockroaches paraphyletic. There is also some evidence for Mantodea being the most basal lineage of the Dictyoptera, although this is not strong. With regard to the evidence for a termite-*Cryptocercus* grouping, two things should be considered. The first is that for two of the genes that show strong support for this grouping (endogenous cellulases and endosymbiont 16S rDNA), no mantid sequences are available, because their diet does not contain cellulose, and because they do not harbour the relevant endosymbionts. Thus it is conceivable that the absence of mantids in these analyses might lead to incorrect relationships being estimated for termites and cockroaches. The second consideration is taxon sampling for the cockroaches. Although representatives of each of the five traditional families of cockroaches have been examined, it is possible that these morphology-based family classifications are misleading, and that several other important high-level (basal) cockroach lineages exist. Recent morphological studies by KLASS (1995, 1997) indeed suggest that this is the case. Inclusion of extra cockroach taxa in molecular studies may show that one of these is more closely related to termites than *Cryptocercus*, although several shared characteristics between these two groups make this unlikely. One distinct possibility that should be explored in future studies is that mantids are the sister group of another lineage of cockroaches, which would render modern cockroaches polyphyletic with respect to both termites and mantids.

Future molecular studies of basal dictyopteran relationships should focus on deciphering the number of deep branching cockroach lineages that exist, perhaps using genes such as cytochrome oxidase or 18S rDNA. Following this, many additional nuclear genes will likely be required to understand relationships between these main lineages, and between these and termites and praying mantids.

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Phylogeny of Mantodea Based on Molecular Data: Evolution of a Charismatic Predator

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Phylogenetic relationships among mantids are poorly known, and a formal quantitative character analysis has yet to be performed. We inferred phylogenetic relationships for Mantodea from DNA sequence data. Five genes (16S rDNA, 18S rDNA, 28S rDNA, cytochrome oxidase II, and histone 3) were sequenced for 63 taxa representing major mantodean lineages and outgroups. The monophyly of mantodean families and subfamilies was tested under varying parameter settings using parsimony and bayesian analyses.

In regards to the classification of EHRMANN (2002), analyses supported the non-monophyly of Hymenopodidae, Iridopterygidae, Mantidae, and Thespidae and the monophyly of the Amorphoscelidae subfamily Paraoxypilinae. All represented subfamilies of Iridopterygidae and Mantidae appear non-monophyletic. Mantoididae is sister group to the rest of the sampled mantid taxa, and is so placed basally on the topology. The other presumably basal

families (Chaeteessidae, Metallyticidae, and Erempiophilidae) were not represented in our analysis. Lineages congruent with current subfamilial taxonomy include Paraoxypilinae, Hoplocoryphinae, Hymenopodinae, Acromantinae, and Oligoniciinae.

We defined mantid hunting strategy as either generalist, cursorial, or ambush predators. Mapping hunting strategy onto our phylogenetic hypothesis reconstructs the ancestral predatory condition as generalist hunting, with three independent shifts to cursorial hunting and one shift to ambush hunting. The single origin of ambush hunting strategy is associated with the largest radiation of mantodean species.

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The Basal Phylogenetic Relationships in the Dermaptera

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Introduction

The Dermaptera, which include ca. 2000 species, have long been divided into three ‘suborders’ (e.g., HAAS 2003). While the Forficulina comprise the ‘typical’ earwigs (Fig. 2C), the Hemimerina (*Hemimerus*, *Araeomerus*; Fig. 2D,E,F) and Arixeniina (*Arixenia*, *Xeniaria*; Fig. 2A,B) include few, highly specialized species living in close association with certain rats (Muridae) and bats (Molossidae), respectively (NAKATA & MAA 1974). The most primitive Forficulina are comprised in the Karschiellidae (*Karschiella* and *Bormansia*), Diplatyidae (e.g., *Haplodiplatys* and *Diplatys*), and Pygidicranidae, the two latter possibly being paraphyletic, and all three often comprised in a single family,

Pygidicranidae (s.l.) (e.g., KLASS 2003). The Pygidicranidae include a number of ‘subfamilies’: Anataelinae, Challinae, Esphalmeninae (*Esphalmenus*), Blandicinae, Pyragrinae (e.g., *Pyragra*), Pygidicraninae (e.g., *Tagalina* and *Dacnodes*), Cylindrogastrinae, and Echinomatinae (e.g., *Echinotoma*).

Following the classical studies of Burr, Verhoeff and Zacher, dermapteran phylogeny was re-assessed in some contributions by POPHAM (e.g., 1985). He used characters and character state transformation, however, no outgroup and no numerical procedure was used for reconstructing the tree. Both was introduced to the study of Dermaptera by HAAS (1995) and HAAS & KUKALOVÁ-PECK (2001). While the latter authors focus on wing structure, the morphology

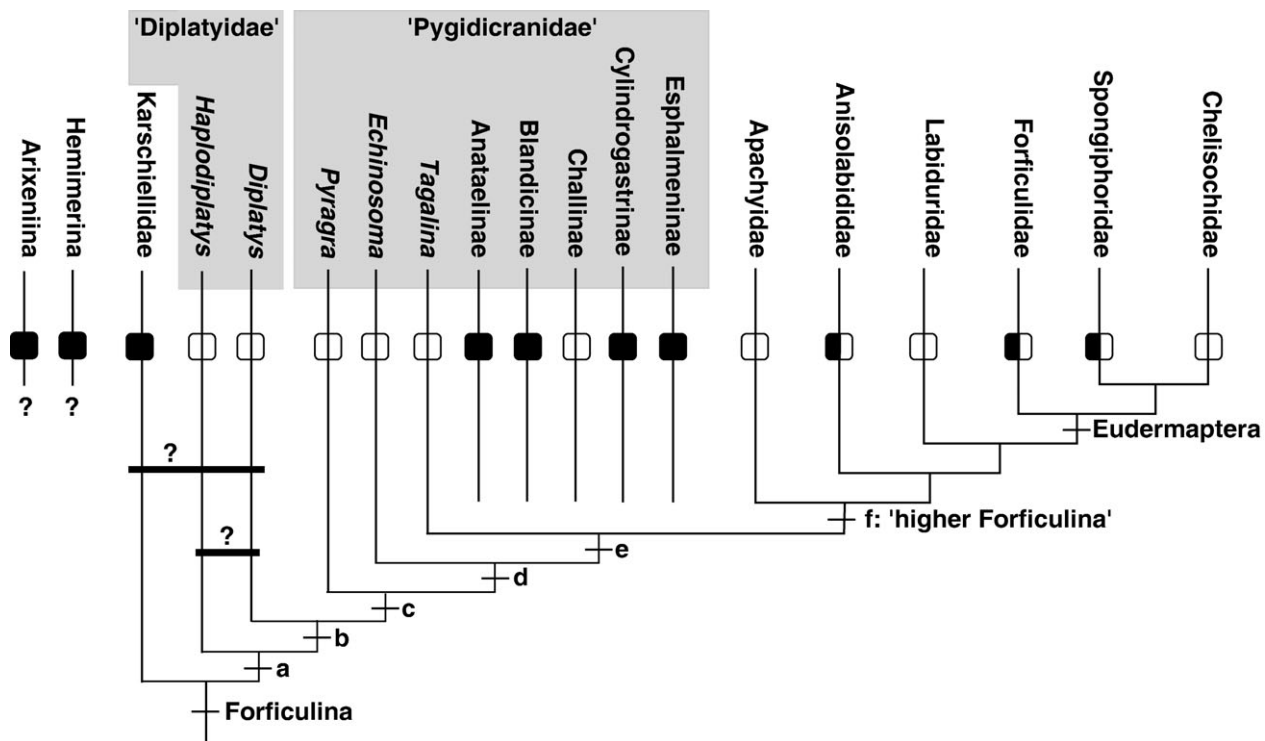


Fig. 1. Cladistic hypothesis of dermapteran relationships, modified after HAAS & KUKALOVÁ-PECK (2001). For the purpose of the discussions in this contribution the Arixeniina, Hemimerina, and Forficulina are regarded as separate higher taxa of Dermaptera, although this view is criticized here. The lack of hind wings is a major issue in the presented discussion, and hence it is mapped onto the tree; filled square: only wingless species in taxon; empty square: only winged species in taxon; filled and empty square: winged and wingless species in taxon.

of the female genitalia (ovipositor and surrounding structures) and other parts of the abdomen (e.g., basis of cerci) was studied by KLASS (2001, 2003). The two character systems most elaborately studied so far (hindwings, ovipositor) have limitations in terms of their evidence on dermapteran phylogeny, because Hemimerina, Arixeniina, and several subgroups of basal and derived Forficulina lack hindwings (Fig. 1), and Hemimerina, Arixeniina, and all 'higher Forficulina' have strongly reduced ovipositors.

Monophyly of Dermaptera

Autapomorphies so far suggested for Dermaptera suffer from many sources of uncertainty. Some apomorphic conditions present throughout Dermaptera, such as the prognathous head, the presence of apodemes on the anterior rim of the abdominal coxosterna, and the formation of a female subgenital plate from coxosternum 7, could as well be (largely conflicting) synapomorphies of Dermaptera and various other Pterygota. The same is true for reductive apomorphies in the female genitalia: gonapophyses 9 (if present) much shorter than gonapophyses 8, without a median fusion, and shifted posteriorly; olistheter absent; fusion of extreme lateral parts of abdominal terga 9 and 10. The reduction to three-segmented tarsi, the lack of ocelli, the one-segmented cerci, and the lack of styli on male abdominal coxosternum 9 (subgenital plate) are likely dermapteran autapomorphies, since five- or four-segmented tarsi, two ocelli, many-segmented adult cerci, and male styli are present in 'Protelytroptera' (close extinct relatives of Dermaptera) and some Jurassic Dermaptera (VISHNYAKOVA 1980; HAAS & KUKALOVÁ-PECK 2001; WILLMANN 2003). However, due to the frequent homoplasy of these reductive traits in Pterygota, their support for dermapteran monophyly is limited. The highly derived condition of both forewings (as short tegmina) and hindwings (with many unique structural adap-

tations serving for folding; HAAS 1995; HAAS & KUKALOVÁ-PECK 2001) in Dermaptera appears as a particularly rich source of ordinal autapomorphies. However, conclusiveness is limited because Hemimerina, Karschiellidae, and several subgroups of Pygidicranidae (i.e., most of the taxa crucial in the issue of dermapteran monophyly) lack hindwings or both pairs of wings. The clasper-shape of the cerci applies to all Forficulina; its absence in Hemimerina (thread-like cerci) and indistinctness in Arixeniina is plausibly explained as a secondary loss resp. reduction (KLASS 2001). Holocentric chromosomes may also be autapomorphic for Dermaptera (including Hemimerina), but data are said to be doubtful for Arixeniina, and only a *Dacnodes* has been studied among the primitive Forficulina (WHITE 1976). The X-shaped invagination on the stipes, peculiar sensory papillae on the maxillary and labial palps, the accessory lateral cervical sclerite, the location of the mesosternal pits on an infolding, a metapleural accessory plate, and the virgae of the male genitalia may be further dermapteran autapomorphies (POPHAM 1985) but have likewise been studied only in a limited sample of basal Forficulina.

The presence of a manubrium on the male coxosternum 9 (subgenital plate) is not a dermapteran autapomorphy (KLASS 2001). The overlapping of the abdominal terga and coxosterna probably is a dermapteran (+ 'protelytropteran') autapomorphy (HAAS & KUKALOVÁ-PECK 2001) though a similar abdominal structure occurs in the distantly related *Zygentoma* (KLASS 2001).

Relationships within Forficulina

The presently most elaborate phylogenetic hypothesis (Fig. 1) is based on HAAS (1995) and HAAS & KUKALOVÁ-PECK (2001), who focus on wing characters: Karschiellidae + ^a(*Haplodiplatys* + ^b(*Diplatys* + ^c(*Pyragra* + ^d(*Echinossoma* +

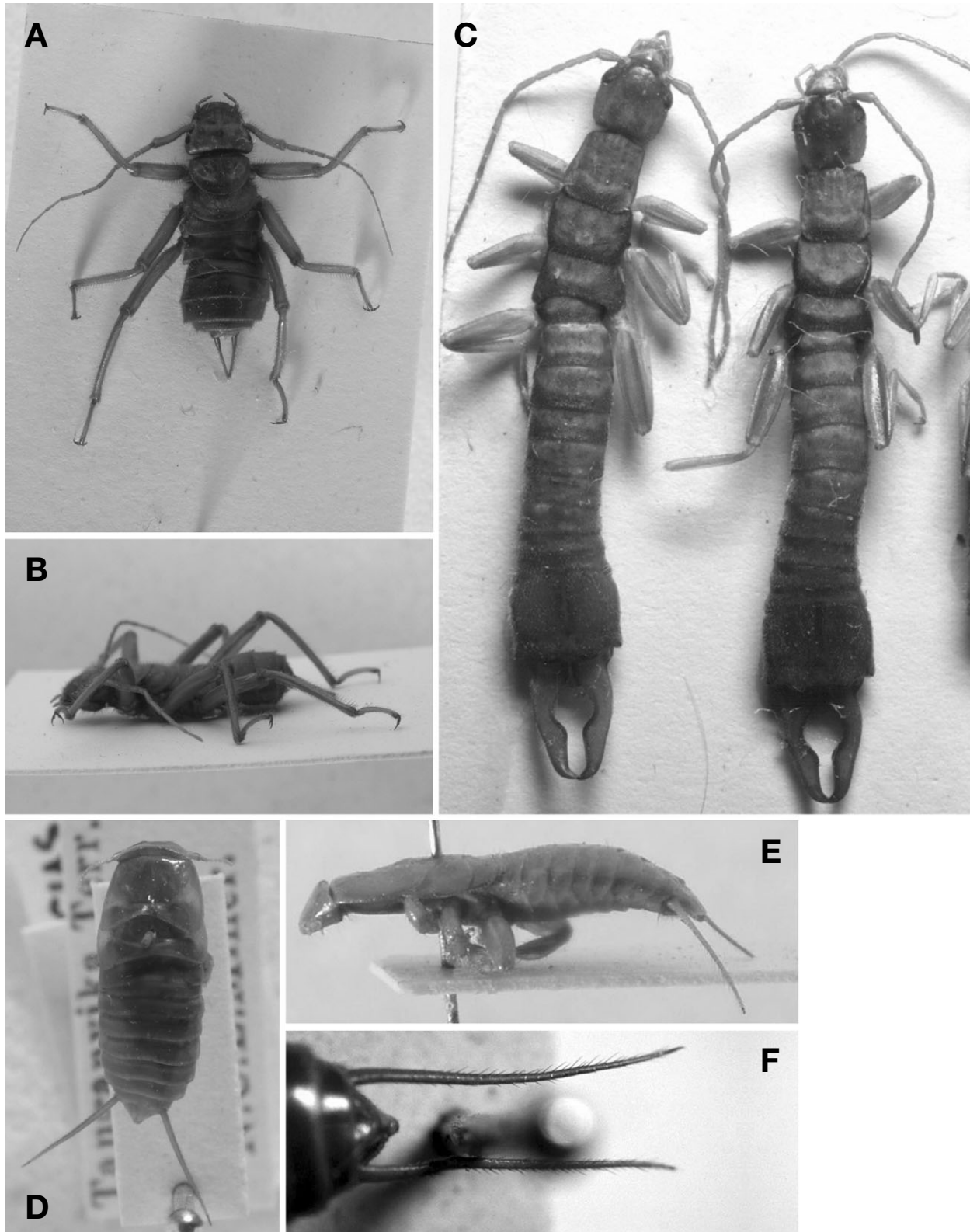


Fig. 2. The three major taxa of the Dermaptera – Arixeniina, Hemimerina and Forficulina – are shown in comparison to demonstrate their different appearance. **A, B:** *Arixenia esau* Jordan, 1909, dorsal view (A) and lateral view (B). **C:** Two specimens of *Anataelia canariensis* Bolivar, 1899, dorsal view. **D, E:** *Hemimerus bouvieri* Chopard, 1934, dorsal view (D) and lateral view (E). **F:** Cerci of *Hemimerus deceptus* Rehn & Rehn, 1936, showing no annulation. Not to scale. Copyright for all images except C at NHM; C taken at ZMUC.

(*Tagalina* + 'higher Forficulina')))). Hemimerina and Arixeniina are not included because of their winglessness, and basal Forficulina are represented by Karschiellidae (*Karschiella*), two genera of Diplatyidae (*Haplodiplatys*, *Diplatys*), and three genera of Pygidicranidae belonging to Pyragrinae, Echinomatinae, and Pygidicraninae, respectively. The 'higher Forficulina' (clade f), comprising all Forficulina not belonging to one of the three latter 'families', is very well supported through 12 autapomorphies, while nodes basal to this clade are less strongly supported and partly ambiguous.

Clade a is supported by the presence of a device locking the tegmina to the thorax (longitudinal groove on metanotum; ridge bearing macrotrichae on tegmen). Clade b, rendering Diplatyidae paraphyletic, is supported by the presence of a spiny ridge on each side of the metanotal groove (another part of the locking device) and the asymmetry of the tegmina. However, evidence from the tegmina locking device is ambiguous, because reductions may have accompanied the loss of the hindwings in Karschiellidae, as indicated by the report of tegminal macrotrichae as well as an indistinct metanotal groove and spiny ridge from some species of *Karschiella* (HAAS & KUKALOVÁ-PECK 2001; VERHOEFF 1902). On the other hand, the species of *Diplatys* and *Haplodiplatys* studied by KLASS (2003) display four apomorphic features in the female genitalia that are quite unique in insects and suggest them to form a monophyletic Diplatyidae: the (paired) spermathecae are strongly branched and are internally widened into bulbs; gonapophyses 9 (2nd valves of ovipositor) are shaped as broad, flat lobes and hug into a membranous mould behind their bases. Moreover, a clade Karschiellidae + Diplatyidae is supported by paired spermathecal openings, which are unambiguously apomorphic by outgroup comparison (for a detailed description of the structures see KLASS 2003).

Autapomorphies (all in the hindwing) of clade c are the specialized fustis area (the antero-basal tenth of the dermapteran hindwing), a short-and-broad or long-and-broad condition of the costal area (instead of long and slender), the position of the end of cubital vein CuA3+4 anterior to the 8th branch of anal vein AP1+2, the flat condition of the tail of the ano-jugal arm FAJ, and the broad separation of the proximal branches of anal vein AP1+2. However, all these hindwing characters are neither applicable to the wingless Karschiellidae nor to the outgroup (Dictyoptera), and therefore with monophyletic Diplatyidae being a reasonable alternative based on new evidence from the female genitalia, the characters here under consideration may prove as yielding additional autapomorphies for Diplatyidae (with the states listed above being the plesiomorphic ones).

Clade d is supported by the presence of two virgae in the male genitalia, and clade e by the small size of the jugal prong of the 3rd axillare of the hindwing articulation. Nonetheless, in these characters there are problems in terms either of character polarity or coding of states, leaving these nodes ambiguous (KLASS 2003).

Incidentally the monophyly of the remaining 'families' of the Dermaptera is not well supported. Notable exceptions are the Apachyidae, which are highly autapomorphic in many characters, while Forficulidae, Chelisochidae and Spongiphoridae are supported by few characters. The Anisolabidiidae, at the moment, appear as an assemblage of superficially similar Dermaptera that can hardly be supported at all, and the Labiduridae proved almost as difficult to support (HAAS & KUKALOVÁ-PECK 2001).

Placement of Hemimerina and Arixeniina

Historically, the Hemimerina and Arixeniina were placed at the same hierarchical level as the Forficulina – usually 'suborders', sometimes 'orders' – because in their structure and

natural history they differ fundamentally from all Forficulina (e.g., HAAS 2003). Both taxa have a strongly modified physical appearance due to their epizoic habits and are not easily recognized as Dermaptera (which apart from these taxa are rather uniform in appearance), and both are viviparous. The related features are unique among Dermaptera and are not found in the Forficulina (with the notable exception of viviparity in *Marava arachidis*), and so, by stressing differences instead of common features in a non-phylogenetic methodology, the Hemimerina and Arixeniina were not perceived as potentially nested in the Forficulina. This view on difference and common features has changed and to date the most likely hypothesis suggests, yet supported only by weak evidence, for Hemimerina and Arixeniina a position deeply within Forficulina. For Hemimerina support comes from some apomorphies shared with higher Forficulina (KLASS 2001): advanced immobilization (not fusion) of the shortened female abdominal terga 8–10 and specific reductions in the female genitalia; a close relationship with Apachyidae is furthermore indicated by the shared absence of a dorsal telson sclerite (or perhaps its fusion with tergum 11) and fusion of terga 10 and 11 in the female postabdomen. For Arixeniina a placement within Forficulina is supported by apomorphies shared with the Spongiphoridae (= Labiidae in POPHAM 1985), mainly the presence of auxiliary sclerites associated with the virga in the male genitalia (POPHAM 1985); the characters concerned, however, need re-examination.

Conclusions

The relationships at the basis of Forficulina are presently only tentatively resolved, and the same is true for the placement of Hemimerina and Arixeniina. Most important for forthcoming morphology-based analyses is the inclusion of representatives of the remaining pygidicranid 'subfamilies' (see above and Fig. 1), including wingless ones. This should be based on detailed studies of male and female genitalia and wing structure. Another requirement is the exploration of new character systems such as the structure of the tarsi and their adhesive devices, investigations on which have been begun by HAAS & GORB (in press). An extensive molecular data set is also presently being established, using sequences of 18S rDNA, 28S rDNA, and histone 3 (manuscript in preparation by K.J. Jarvis, F. Haas & M.F. Whiting). Thus, considerable progress in the analysis of intra-ordinal relationships in Dermaptera is expected for the near future.

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Phylogeny and Evolution of Acoustic Communication in Orthoptera

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Based on morphology and the molecular analyses in FLOOK & ROWELL (1997) and ROWELL & FLOOK (1998), a sistergroup relationship between the suborders Caelifera and Ensifera is presently the best supported hypothesis on the basal splitting event in Orthoptera. Relationships among subgroups of Caelifera are considered in FLOOK & ROWELL (1997) and ROWELL & FLOOK (1998).

The Ensifera (crickets, katydids, and related insects) is usually classified into the families Gryllidae; Gryllotalpidae; Rhaphidophoridae; Haglidae and/or Prophalangopsidae; Schizodactylidae; Stenopelmatidae and/or Anostostomatidae and/or Gryllacrididae; and Tettigoniidae. Representatives of Ensifera are well known for acoustic signals produced in the contexts of courtship and mate recognition. However, there is still controversy regarding the monophyly of major lineages, the relationships between them, and whether the acoustic structures and behaviors of Ensifera are homologous (plesiomorphic) or multiply derived. To address these questions, M. Jost works on a phylogenetic estimate of the Ensifera for a sample of 51 systematically diverse exemplars, using sequences from 18S rRNA, 28S rRNA and 16S rRNA, and three exemplary species of Caelifera as outgroup taxa.

The results support a basal split between monophyletic Grylloidea (comprising Gryllidae, Gryllotalpidae, and *Schizodactylus*) and monophyletic Tettigonioidae (comprising Tettigoniidae, Rhaphidophoridae, *Cyphoderris*, and the 'gryllacridoid' families) (Fig. 1). Support was also found for a monophyletic Tettigoniidae and for a monophyletic 'Gryllacridoidea' including the Gryllacrididae, Stenopelmatidae, Anostostomatidae, and the genus *Lezina*, and the results provide a robust estimate of phylogeny within a monophyletic Gryllidae.

Tree comparison tests with the molecular data using parsimony found Jost's estimate to be significantly better than the phylogenetic hypotheses of SHAROV (1968) and GOROCHOV (1995) although the data could not significantly reject the result of the only numerical analysis of Ensifera to date, GWYNNE (1995), which used morphological data. Conversely, the most parsimonious tree from GWYNNE (1995) was not significantly better than Jost's fully resolved estimate when tested using Gwynne's data matrix and cha-

racter assumptions, although it was significantly better than the estimates from SHAROV (1968) and GOROCHOV (1995).

Molecular data were then used to estimate phylogenetic relationships within the Gryllidae, and the resulting phylogeny was used to test the hypothesis that losses of acoustic structures are usually coupled with flightlessness, microptery, or aptery. Jost presents a phylogenetic estimate for the Gryllidae using 18S rRNA and 16S rRNA sequences for a diverse sample of 49 species, representing 46 genera from 13 subfamilies. Parsimony and Bayesian results strongly support a monophyletic Gryllidae, as well as the monophyly of most recognized subfamilies including the Gryllinae, Podoscirtinae, Oecanthinae, Phalangopsinae, Nemobiinae, and Trigonidiinae. Tree comparison tests using parsimony found Jost's most parsimonious estimate to be significantly better at explaining the molecular data than the phylogenetic hypotheses from two prior studies: GOROCHOV (1984) and DESUTTER (1987). Two tests of character state distributions in the Gryllidae (which accounted for phylogeny) provided significant support for the hypothesis that losses of acoustic traits are usually coupled with hindwing microptery and/or aptery.

Close examination of wings, stridulatory tegmina, and tibial tympana in gryllids reveals a continuum of adult phenotypes that closely resemble the observed stages of mid- to late-instar nymphs. Acoustic structures and wings are strictly adult characters in crickets, and might be coupled through similar post-embryonic developmental constraints. To test the strength and significance of these correlations, character states for hindwings, forewings, and tibial auditory tympana were coded as an ontogenetic series and scored for adults of a diverse sample of gryllid taxa. Felsenstein's method of independent contrasts was used to test the hypothesis that adult-like character states are positively correlated with other adult-like character states, and juvenile-like character states are positively correlated with other juvenile-like character states. Two phylogenetic hypotheses were used to compute node contrasts: one estimated by a Bayesian analysis of 16S and 18S sequence data, and another from a previously published phenetic study (DESUTTER 1987). Regardless of the hypothesis used,

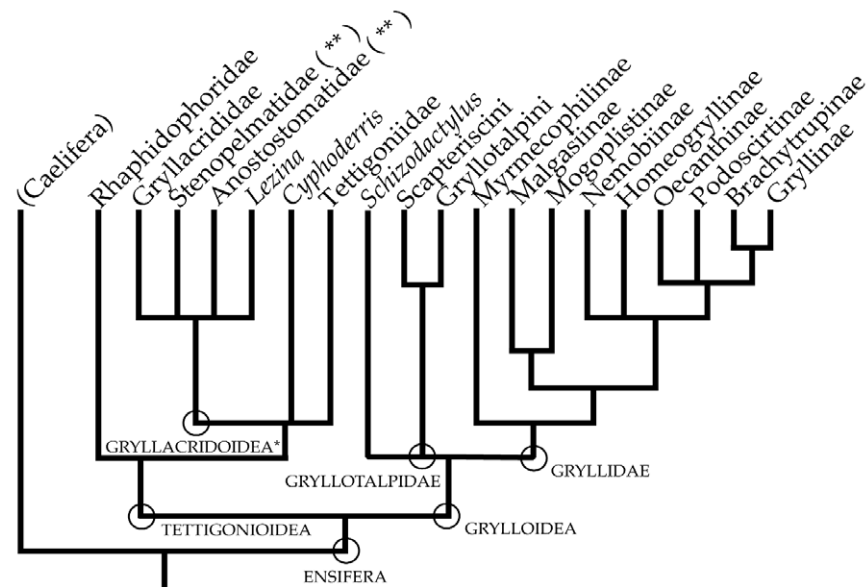


Fig. 1. Phylogenetic relationships among major lineages of Ensifera. From ongoing work by M. Jost based on analyses of 18S rRNA, 28S rRNA and 16S rRNA in 51 ensiferan exemplars, simplified. Caelifera used as outgroup. * Gryllacridoidea resulting as subordinate within Tettigoniidae; ** monophyly of taxon not strongly supported.

Spearman's rank correlation (with ties) on the node contrast values showed that forewing length and hindwing length are significantly correlated with one another, and that forewing length is significantly correlated with tibial tympana development. Hindwing length was significantly correlated with tibial tympana development using Jost's Bayesian estimate, but not using the hypothesis from DESUTTER (1987); however, the sum of wing length scores was significantly correlated with tibial tympana development, regardless of the phylogenetic hypothesis used. It is suggested that this pattern has resulted from a common mechanism such as heterochrony, and that many independent losses of wings and acoustic structures are due to paedomorphosis.

P. Naskrecki's ongoing work relates to the phylogeny and classification of Tettigoniidae, which contains more than 6400 species distributed worldwide. Naskrecki has reconstructed phylogeny in the Tettigoniidae using 195 taxa and 331 morphological characters, many newly identified from informative structures on the head, sternal endoskeleton, ovipositor, and eggs. The strict consensus of most parsimonious trees found most currently recognized tettigoniid subfamilies to be paraphyletic (including the large subfamilies Conocephalinae and Pseudophyllinae) or polyphyletic (including Bradyporinae and Listrosclidinae). Naskrecki is preparing to introduce a new classification based on the monophyletic lineages found in this analysis. He then uses hypotheses on phylogeny to examine the evolution of female stridulation in the Tettigoniidae.

Naskrecki's phylogenetic hypothesis supports at least seven independent origins of female stridulation, which he classifies into several types. In the 'bradyporoid' female stridulatory mechanism (considered to be the most primitive), the male and female sound producing structures are fully homologous. In the 'ephippigeroid' type, male and female sound producing structures are functionally similar, but not homologous. In the 'phaneropteroid', 'polyancistroid', and 'pterophylloid' types, male and female sound producing structures are functionally different and not homologous. In the phaneropteroid type, females have multiple stridulatory files on lateral branches of 2A on the dorsal side of the right tegmen. In the 'polyancistroid' type, the female stridulatory file is on a secondary branch of Cu1 on the dorsal side of the right tegmen. In the 'pterophylloid' type, females have a

stridulatory 'net' on the lateral branches of 2A on the ventral side of the left tegmen, and a multi-tooth scraper on the inner edge of the right tegmen. In all of these except for the phaneropteroid and pteryphylloid types, females are capable of producing calls similar to those of males, and often pure tone calls. The phylogenetic distribution of female stridulation among the Tettigoniidae may suggest that bidirectional phonotaxis between the sexes may evolutionarily precede unidirectional, female-to-male phonotaxis.

The authors also wish to call attention to the Orthoptera Species File online, a complete taxonomic and synonymy database of all Orthoptera described prior to 1998. The URL for this public database is <http://140.247.119.145/Orthoptera/>.

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Species Diversity and Intraordinal Phylogenetic Relationships of Mantophasmatodea

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The description of the new insect order Mantophasmatodea by KLASS et al. (2002) was based on two lines of morphological evidence: (1) these wingless insects lack the sets of apomorphies that characterize the other insect orders; (2) evidence on the sistergroup relationship of Mantophasmatodea to some other insect order was weak and conflicting. The ordinal status of Mantophasmatodea was doubted by TILGNER (2002), but his argumentation was refuted by KLASS (2002). While the assignment of Mantophasmatodea to the Pterygota-Neoptera is supported by several apomorphies (KLASS et al. 2002), the identification of its sister group on a morphological basis has remained doubtful due to character conflicts (KLASS et al. 2003). Molecular studies suggest a sistergroup relationship to the Notoptera (= Grylloblattodea; M.D. Terry & M.F. Whiting, pers. comm.).

Presently 13 extant (all African) and 1 fossil species (European) of Mantophasmatodea are known. The probably earliest report of mantophasmatodeans in the literature is that in ARILLO et al. (1997), which relates to immature Baltic amber specimens that were not formally described therein. The first species to be described (prior to the description of the order!) was *Raptophasma kerneggeri* Zompro, 2001 from Baltic amber, classified as “Orthoptera incertae sedis” (ZOMPRO 2001). *Mantophasma zephyra* Zompro et al., 2002 from Namibia and *Tanzaniophasma subsolana* (Zompro et al., 2002; as *Mantophasma*) from Tanzania were described along with the ordinal description in KLASS et al. (2002); both are known from a single specimen and were probably not recovered since (the species identity of the specimens considered “*Mantophasma zephyra*” in DALLAI et al.’s 2003 study of sperm structure is unresolved, see KLASS et al. 2003: 48). Another Namibian species, *Praedatophasma maraisi* Zompro & Adis, 2002, was described in ZOMPRO et al. (2002).

A short paper by PICKER et al. (2002) was the first to indicate that probably several Mantophasmatodea species occur in western South Africa. Subsequent work by our team led to the description of five new genera including eight new species from this area (KLASS et al. 2003): *Austrophasma* (*A. rawsonvillensis*, *A. caledonensis*, *A. gansbaaiensis*), *Lobophasma* (*L. redelinghuysensis*), *Hemilobophasma* (*H. montaguensis*), *Karoophasma* (*K. biedouwensis*, *K. botterkloofensis*), and *Namaquaphasma* (*N. ookiepensis*). In addition, another new genus and species from Namibia has been described by KLASS et al. (2003), *Sclerophasma* (*S. paresiensis*), and our collecting efforts in 2003 led to finding some additional South African species still waiting for taxonomic treatment. Eventually, a further, spiny Namibian species was mentioned as “*Tyrannophasma gladiator* Zompro, 2003” in DALLAI et al. (2003) and will probably soon be formally described.

Thus, extant Mantophasmatodea are only known from Africa south of the equator, and in South Africa and possibly in Namibia the group shows strong endemism, with at least many species restricted to some limited distribution area. The approximately 45 million year old *Raptophasma* fossils from Baltic amber, however, show that in the early Tertiary mantophasmatodeans also occurred in Europe.

KLASS et al. (2003) discuss characters that support the

monophyly of Mantophasmatodea, and they gave the first detailed description of taxonomically significant and phylogenetically informative character systems in this order, most importantly the exoskeleton of the male and female postabdomen (including the genitalia) and antennae. A formal morphology-based cladistic analysis of phylogenetic relationships within the order, however, has not yet been possible due to problems in outgroup comparison (absence or doubtful identification of many character-bearing structures of Mantophasmatodea in other Neoptera, see KLASS et al. 2003: 57f; influential but doubtful choice of outgroup taxa due to lacking resolution of basal neopteran phylogeny). KLASS et al. (2003) present a phylogenetic tree of Mantophasmatodea based on two mitochondrial genes encoding COI and 16S rRNA; considering the later inclusion in our data set of a specimen that likely belongs to “*Tyrannophasma gladiator*”, our molecular analysis presently includes all abovementioned species except *Mantophasma zephyra*, *Tanzaniophasma subsolana*, *Praedatophasma maraisi*, *Namaquaphasma ookiepensis*, and the fossil *Raptophasma kerneggeri* (Fig. 1). Some of the included species were represented by specimens from different localities.

The molecular and the partly tentative morphological results on Mantophasmatodea phylogeny were our basis for a classification of Mantophasmatodea (KLASS et al. 2003). Apart from the definition of genera this includes a subdivision into three families, Tanzaniophasmatidae, Mantophasmatidae, and Austrophasmatidae, which so far are congruent with Tanzanian, Namibian, and South African Mantophasmatodea, respectively (*Praedatophasma* and *Raptophasma*, with neither genitalia nor molecules then studied, left “incertae sedis”; *Tyrannophasma* then unpublished). With the forthcoming refinement of our molecular tree, we will use the results on basal dichotomies within the order for polarizing morphological characters in order to make these available for cladistic analyses.

The monophyly of Mantophasmatodea is morphologically well-founded by (1) a very specialized structure of the antennae, which are composed of a varied number of basiflagellomeres that have no constrictions between them and have only coarse setation, and the distal ones of which show a secondary subdivision; and of distiflagellomeres that always count seven, the first being very long and the second very short, are separated by discrete constrictions, and have very fine setation in addition; (2) by the strongly angled course of the subgenal sulcus on the head, which depends on a dorsal shift of the origins of the anterior tentorial arms; (3) by a medioventral projection on the male subgenital plate (used for drumming; also present in many Plecoptera); (4) by a conspicuously blunt tip of gonapophyses 8 in the ovipositor; and (5) by a small dorsal projection in the membrane beyond the 3rd tarsomere. Monophyletic Mantophasmatodea are also strongly supported in our molecular analysis, where, however, the apparently basal *Tanzaniophasma* and *Raptophasma* as well as notopterans (as an important outgroup) are lacking.

The monophyly of Austrophasmatidae is strongly supported by the molecular analysis; the inclusion of *Namaquaphasma* in this family is based on its male genitalia being very simi-

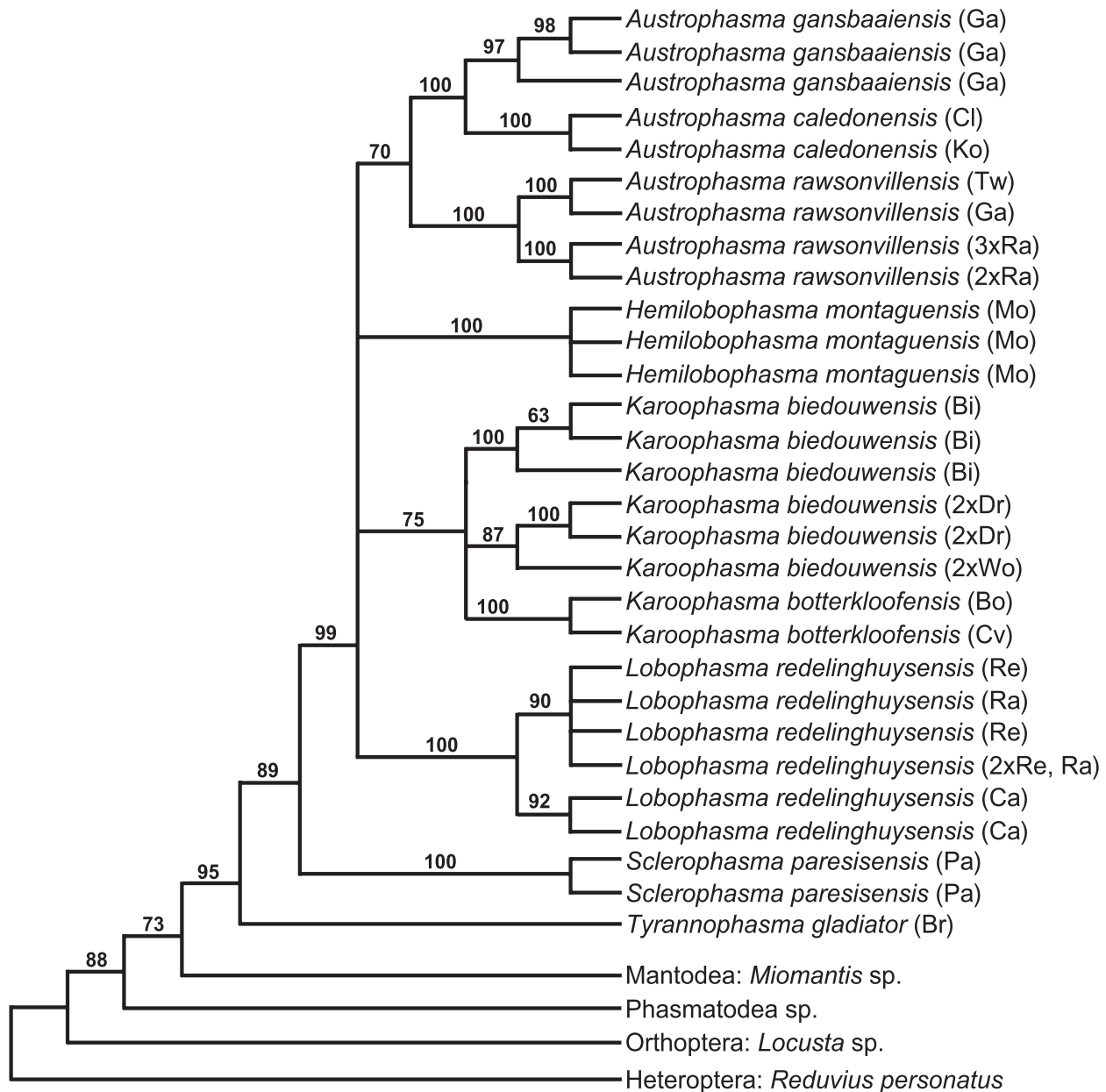


Fig. 1. Molecular-based phylogenetic hypothesis for Mantophasmatodea using mitochondrial COI and 16S rRNA genes; *Namaquaphasma*, *Mantophasma*, *Praedatophasma*, and *Tanzaniophasma* (with 1 species each) not included. All sequenced specimens included. Locality given in brackets behind species name (see KLASS et al. 2003: 11 for abbreviations; Pa, Br in northern Namibia; Bi, Bo, Ca, Cl, Dr, Ga, Ko, Mo, Ra, Re, Tw, Wo in Western Cape Province, and Cv in Northern Cape Province of South Africa), '2x' in front of locality abbreviation means that 2 specimens were studied that had identical sequences.

lar to those in other austrophasmatid genera. The relationships among the five genera of Austrophasmatidae have remained unresolved due to low support values. In our analysis we obtain the Namibian *Sclerophasma* as the sister group of Austrophasmatidae. This taxon has genitalia quite different from all Austrophasmatidae, with, e.g., presence of two additional sclerites but absence of two small sclerotized hooks in the male, and presence of a paired vaginal sclerite and a paired row of strong setae ventrally between the two gonoplocs of the ovipositor in the female. Since in the mentioned female characters *Mantophasma* (males unknown) conforms with *Sclerophasma*, the two genera were tentatively combined in the same family ('Mantophasmatidae' due to nomenclatural priority). Nonetheless, among the characters characterizing Mantophasmatidae, only the setae between the gonoplocs are quite surely apomorphic. *Tyrannophasma* results as the sister group of Austrophas-

matidae + Mantophasmatidae in our molecular analysis and would thus deserve the status of a separate family; genitalia in this taxon have remained unstudied. *Tanzaniophasma* differs fundamentally from the other Mantophasmatodea with male genitalia known by the simple structure and bilateral symmetry of these (very complicated and asymmetrical in others); we thus classified it into a separate family Tanzaniophasmatidae, though it is not entirely certain whether the configuration of its genitalia is actually plesiomorphic for Mantophasmatodea. *Raptophasma*, according to ZOMPRO et al. (2002), lacks the strong tibial spines present in all other species; this is likely to be a plesiomorphic condition, and a position as the sister group of the remaining Mantophasmatodea (making it deserve the status of a separate family) is the best guess at the moment – which would nicely match with the isolated occurrence of this genus in the northern hemisphere.

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New Insights in Grylloblattodean Phylogeny

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Introduction

Grylloblattodea (= Notoptera) is one of the most enigmatic and diverse lineages of extremophile insects. Also known as ice crawlers, this order of 25 species inhabits ice caves, glacial margins, talus slopes, forest floors, and similar habitats. North American grylloblattids generally require temperatures near 0°C for survival, thus the common name ‘ice crawlers’. Populations of *Grylloblatta* are distributed throughout the northern Rockies and Sierra Nevadas in numerous disjunct populations. KAMP (1979) postulated that this distribution is due to post-Pleistocene migration from south of the Pleistocene glaciers.

Order Grylloblattodea is comprised of five genera in a single family (Grylloblattidae). *Grylloblatta* is the most widespread genus (11 spp.), found exclusively in the Pacific Northwestern USA and western Canada. The remaining four genera are found in Asia, with *Galloisiana* (11 spp.), *Grylloblattina* (1 sp., 2 subsp.) and *Namkungia* (1 sp.) in eastern Asia in and around Japan, and *Grylloblattella* (1 sp.) in central Siberia. STOROZHENKO (1996) presented the only hypothesis thus far on the phylogenetic relationships among these genera, based on an informal examination of characters. He proposed that the North American *Grylloblatta* is sister to the Asian grylloblattids and that *Galloisiana* and *Grylloblattella* are sister taxa.

Materials and methods

This phylogenetic analysis includes four *Grylloblatta* species, two *Galloisiana* species and the two subspecies of the only species of *Grylloblattina*. Five additional representatives of undescribed *Grylloblatta* and *Galloisiana* species were also included, and individuals from multiple populations of the same species were included for a total of 15 grylloblattid taxa. Recent analyses of extensive data (in a manu-

script submitted by M.D. Terry & M.F. Whiting) indicate that mantophasmatodeans are sister to grylloblattodeans. Therefore, two mantophasmatodean taxa and one species each from Blattaria, Mantodea and Isoptera were included. Trees were rooted to Mantodea.

Sequence data were generated from cytochrome oxidase II mitochondrial DNA (650 bp), 18S nuclear ribosomal DNA (2000 bp), 28S nuclear ribosomal DNA (2400 bp), and histone-3 nuclear protein-coding DNA (370 bp) for all exemplar taxa. STOROZHENKO (1996) coded a morphological and ecological matrix of 12 characters within Grylloblattodea, which was adapted to the taxon sampling in this analysis. The data were analyzed simultaneously in POY (GLADSTEIN & WHEELER 2001) using direct optimization under a 1:1:1 gap:transversion:transition ratio. TBR branch swapping was performed on 200 random sequence additions. Bootstrap values were calculated in PAUP* (SWOFFORD 2002) using the implied alignment output from POY.

Results

Phylogenetic reconstruction based on these data indicates a Mantophasmatodea + Grylloblattodea relationship with a bootstrap value of 100, and analyses of the genes separately also recover this relationship. These data also support the monophyly of the genera *Grylloblatta*, *Grylloblattina* and *Galloisiana*. Contrary to the only previous hypothesis of grylloblattid phylogeny (STOROZHENKO 1996), our data indicate a basal *Galloisiana*, rather than a basal *Grylloblatta*. This result is supported by a bootstrap value of 100 for the clade *Grylloblatta* + *Grylloblattina*. The phylogeny within the North American grylloblattodeans is somewhat discordant with the distribution of the populations. This indicates that the colonization of modern populations was not a simple dispersion, but rather there may have been multiple migration events.

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Phylogeny of the Zoraptera

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Introduction

Among the 'smaller' insect orders, a few stand out as truly depauperate in number of species within a class famed for its overwhelming diversity. The Zoraptera is one of a few insect orders whose diversity does not exceed 100 described species; 38 living and fossil species are presently known. Zorapterans are minute, enigmatic insects superficially resembling booklice (Psocoptera) and termites (Isoptera). Individuals live gregariously under the bark of decaying logs or within termite nests, where they principally feed on fungal hyphae as well as nematodes or minute arthropods (e.g., mites, collembolans) (ENGEL 2003, in press). Adults occur in two morphs within each species – eyed, winged forms (i.e., alates), which eventually shed their wings, and blind, apterous forms. The order occurs pantropically with only four species found distributed slightly outside of the tropical zone. Six fossil species are known, the oldest being four (only three included in the present study) from Middle Cretaceous (lowermost Cenomanian) amber from Myanmar (ENGEL & GRIMALDI 2002).

Zoraptera monophyly is based on a peculiar wing venation (see figures in ENGEL & GRIMALDI 2002; ENGEL 2003); 2-segmented tarsi (the more elongate 2nd segment probably results from fusion of two segments); peculiar mating via 'mating hook' (also evident in Cretaceous fossils); unsegmented cerci (2-segmented in one derived fossil species); stout metafemoral spines; and moniliform, 9-segmented antennae (additional characters discussed by ENGEL & GRIMALDI 2000; ENGEL in press). Placement of the order among other hemimetabolous insects has been troubling and the Zoraptera have been placed in a plethora of phylogenetic positions (reviewed in ENGEL & GRIMALDI 2002). The placement of the order will not be discussed further herein but to note that outgroup comparisons for polarity matter little whether Embiodea or Psocoptera are used, i.e., whether the Polyneoptera (WHEELER et al. 2001; clade comprising Anartioptera = Plecoptera, Embiodea, Orthoptera, Phasmatodea, Grylloblattodea, Mantophasmatodea, Dermaptera, their extinct allies †Titanoptera, †Caloneurodeae, and various families of the unnatural 'Protorthoptera', and possibly the Zoraptera) or the Eumetabola (HENNIG 1969; KRISTENSEN 1995; clade comprising the hemipteroid orders, Endopterygota, and possibly the Zoraptera) hypothesis for placement is preferred.

Discussion of basal Zoraptera

Overall species of the order are remarkably homogenous. Only one taxon departs from overall plan of zorapteran morphology, albeit, only slightly so. The Middle Cretaceous †*Xenozorotypus burmiticus* plesiomorphically retains an additional vein in the hind wing (M_{3+4}), thereby suggesting that it is sister to all other Zoraptera (the loss of this vein being a putative event that occurred in the common ancestor of all other Zoraptera; Fig. 1). All remaining species of the order are placed in the genus *Zorotypus*.

Basal divisions within *Zorotypus* remain problematic (Fig. 1). The Middle Cretaceous species †*Zorotypus acanthothorax* and †*Z. nascimbenei* (both placed here in *Octozoros* subgen.n., see below) are perhaps basal within the genus, as indicated by the plesiomorphic retention of the strong and slightly expanded empodium of the meta-pretarsus (reduced to a single, slender seta or absent in *Zorotypus* s.str.; Fig. 1). Together these two species form a monophyletic group supported by the apomorphic reduction of the antenna to eight segments (nine in all other *Zorotypus* and in †*Xenozorotypus*) and the presence of jugate setae along the middle third of the posterior border of the forewing (absent in all other Zoraptera).

ENGEL & GRIMALDI (2000, 2002) highlighted a few of the potential character systems that may be of utility in the Zoraptera (e.g., the terminal spine present on the apex of the cerci of some species may eventually unite a clade). However, phylogenetic studies within the order are compromised by the heterogeneity of material and information available for individual species. For instance, of the 38 described living and fossil species merely 13 are known on the basis of both sexes and only 7 are known from both apterous and winged morphs (not including the 6 known only from apterous and dealated individuals, where wing morphology is therefore unknown). Thus, characters from wing structure are available for less than 20 % of the species in the order, and male genitalic characters are available for just less than 45 % of the species. This dramatically limits the amount of comparable data between species. The greatest strides toward resolving phylogenetic relationships within the order will come from intensive fieldwork. Field studies are needed to obtain useful material for molecular studies, additional morphs and/or sexes, and to discover yet unknown species (e.g., the order likely has a much wider

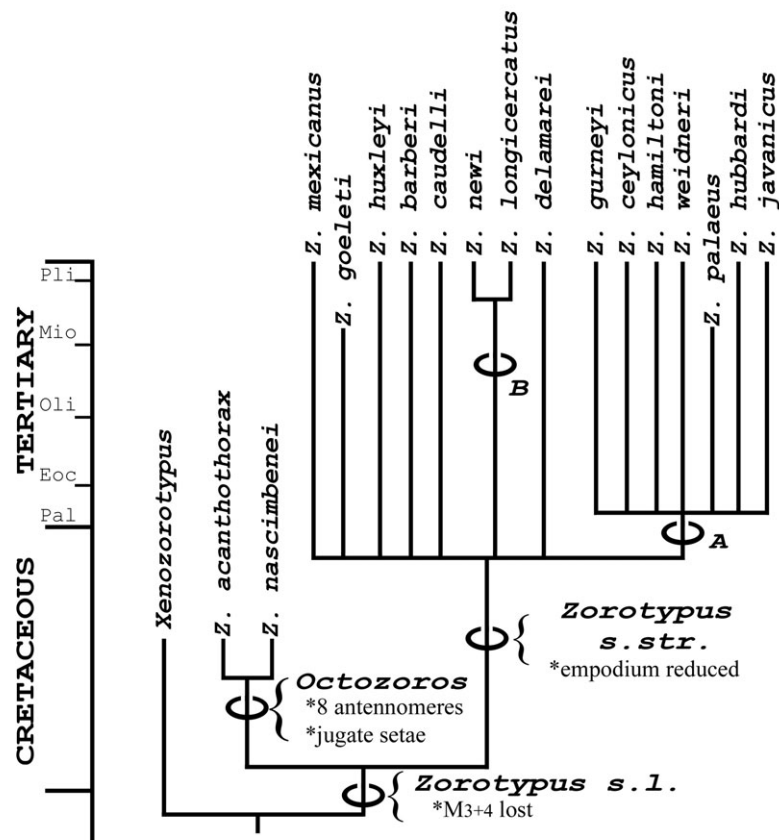


Fig. 1. Preliminary phylogenetic hypothesis for zorapteran relationships (including only a few representatives of *Zorotypus* s.str.), with emphasis on basal divergences. Relationships in *Zorotypus* are difficult to discern owing to paucity of comparable data across species. A putative node “A” is indicated for representative species with uniform series of metafemoral spines; a putative node “B” is indicated for species with elongate cerci. For apomorphies of †*Xenozorotypus* and the entire order refer to ENGEL & GRIMALDI (2002), and ENGEL & GRIMALDI (2000) and ENGEL (2003, in press), respectively.

distribution with additional species in Southeast Asia and tropical Africa). In addition, more data on the biology and ethology of zorapterans are required to thoroughly evaluate the utility of these characters within the order.

†*Octozoros* subgen.n.

Diagnosis. This subgenus is overall similar to *Zorotypus* s.str. but differs by reduction of the antenna to eight segments, presence of jugate setae along middle third of forewing posterior border, and empodium of meta-pretarsus strong and slightly expanded (reduced to a single, slender seta or absent in *Zorotypus* s.str.).

Type species. *Zorotypus nascimbenei* Engel & Grimaldi, 2002.

Other included species. *Zorotypus acanthothorax* Engel & Grimaldi, 2002.

Derivatio nominis. A combination of the Greek ‘okto’ (meaning ‘eight’) and ‘zoros’ (meaning ‘pure’); a reference to the 8-segmented antenna. The name is masculine.

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Phylogenetics of Psocoptera and the Origins of Lice

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The close relationship between Psocoptera (bark lice and book lice) and Phthiraptera (parasitic lice) has long been recognized. Together these two orders comprise the insect group Psocodea. The monophyly of Psocodea is supported on the basis of 18S rDNA sequence data (WHITING et al. 1997) and by several morphological autapomorphies, such as reduction of the ovipositor and development of an atmospheric water-vapor uptake system, among others.

Recent studies of both morphological and molecular data have begun to investigate higher level phylogenetic relationships within Psocodea. LYAL (1985) used morphological characters to show that the chewing lice ('Mallophaga') are not a monophyletic group, but rather form a grade within Phthiraptera; this has been confirmed by recent molecular studies (JOHNSON & WHITING 2002; BARKER et al. 2003; see also the following article by Vincent Smith on Phthiraptera phylogeny). Most importantly, LYAL (1985) identified the psocopteran family Liposcelididae as the sister taxon of Phthiraptera rendering the order Psocoptera paraphyletic. This result was based on the following apomorphic characters shared between Liposcelididae and Phthiraptera: dorso-ventral compression of the head, reduction of the compound eye to two ommatidia, loss of abdominal spiracles I and II, and shortening of legs. Data from the 12S and 16S mitochondrial genes confirm a monophyletic clade Liposcelididae + Phthiraptera (YOSHIZAWA & JOHNSON 2003). With these data, the monophyly of Phthiraptera is uncertain, because in many analyses Liposcelididae tends to fall within the Phthiraptera, albeit with weak support. Liposcelididae also appears to share a dramatically elevated mitochondrial substitution rate with lice, so long branch attraction must be seriously considered as a possible confounding factor. Further molecular data from the nuclear 18S gene (K. Johnson, unpublished) also support a clade uniting Liposcelididae and Phthiraptera, lending independent support to this hypothesis. Analyses of this gene tend to place Liposcelididae as the sister taxon of Amblycera, making both Psocoptera and Phthiraptera paraphyletic. If this relationship is correct, either parasitism evolved twice in lice or was lost in Liposcelididae.

Until recently, the higher level phylogenetic relationships within Psocoptera have received less attention than those in lice. Little attempt has been made to reclassify Psocoptera taking into account its putative paraphyly. Traditionally the order Psocoptera is divided into three suborders: Trogiomorpha, Troctomorpha, and Psocomorpha. An early phylogenetic analysis based on morphology for Psocoptera was conducted by SMITHERS (1972). He suggested that the Psocomorpha is the sister taxon of Troctomorpha based on synapomorphies such as a closed phallosome, loss of the paraproct spine, smooth eggs, and shortened antennae. However, much of the remainder of the classification implied by Smithers' phylogenetic hypothesis has generally been abandoned in favor of more traditional classifications within each suborder.

The phylogeny of the suborder Psocomorpha has received recent attention. Traditionally Psocomorpha is divided into four infraorders: Epipsocetae, Caeciliusetae, Homilopsocidea, and Psocetae. A recent cladistic study of morpho-

logical characters by YOSHIZAWA (2002) suggested that the family Archipsocidae should be removed from the Homilopsocidea, being sister to all other Psocomorpha. In addition, his analysis suggested that Hemipsocidae be removed from Psocetae. In other respects the phylogenetic results of YOSHIZAWA (2002) resembled traditional classification. JOHNSON & MOCKFORD (2003) used data from the nuclear 18S and mitochondrial 16S, 12S, and COI genes to test various classification schemes for Psocomorpha. Using outgroups within Psocoptera, support was found for monophyly of Psocomorpha. They also found support for a basal position of Archipsocidae within Psocomorpha, as suggested by YOSHIZAWA (2002). The family Hemipsocidae, however, was placed within Psocetae with molecular data, contradicting YOSHIZAWA's (2002) study, but consistent with traditional classification. Monophyly of the infraorders Caeciliusetae and Psocetae was supported (JOHNSON & MOCKFORD 2003), but monophyly of Homilopsocidea could not be recovered, even with Archipsocidae excluded. More phylogenetic work is needed to provide a comprehensive classification of Psocomorpha. The phylogenetic relationships within Trogiomorpha and Troctomorpha remain to be investigated in detail.

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Lousy Phylogenies: Phthiraptera Systematics and the Antiquity of Lice

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Phthiraptera (parasitic lice) comprise about 5,000 described species present in four suborders (Fig. 1): Anoplura (colloquially known as sucking lice), Rhynchophthirina (a monogeneric group found on elephants and warthogs), Ischnocera and Amblycera. Phthirapteran monophyly is supported by 19 apomorphies, the most significant of which include haploid reduction in primary spermatogonia, the presence of a basal hydropile in the egg, dorsoventral compression of the head and loss of the dorsal tentorial arms.

Every conceivable relationship between the four phthirapteran suborders has been proposed at some time. Historically the chewing lice (Amblycera, Ischnocera and arguably Rhynchophthirina) had been subsumed under the name 'Mallophaga', which was awarded ordinal status along with the Anoplura. Morphological data supporting the monophyly of 'Mallophaga' was proposed by KIM & LUDWIG (1978, 1982), although these results were controversial (HAUB 1980).

LYAL (1985) conducted a detailed review of the morphological data that define basal louse relationships. His study confirmed the monophyly of all four suborders, although ischnoceran monophyly was the least well supported. The subordinal phylogeny established by LYAL (1985) confirmed that 'Mallophaga' are paraphyletic and form a grade within Phthiraptera. Significant synapomorphies given by LYAL (1985) defining these relationships are (1) for Rhynchophthirina + Anoplura: head 'fixed' in relation to thorax, loss of anterior tentorial pits and partial transfer of antennal muscle attachment site to dorsum of head; (2) for Rhynchophthirina + Anoplura + Ischnocera: development of saucer-shaped antennal sensilla, partial occlusion of occipital foramen by a connective tissue septum and development of spiracular glands.

Recent molecular evidence supports LYAL's (1985) phylogeny. Using nuclear genes CRUICKSHANK et al. (2001), JOHNSON & WHITING (2002) and most recently BARKER et al. (2003) have investigated phthirapteran basal relationships. All but CRUICKSHANK et al.'s (2001) results are completely congruent with those of LYAL (1985), and the discrepancies in CRUICKSHANK et al.'s study are likely to be the result of an over-reliance on a relatively short fragment of the faster evolving EF1- α gene (SMITH et al. in press).

Familial relationships within each of the suborders are slightly less problematic, with the notable exception of the Ischnocera.

Anopluran lice exclusively parasitise mammals and have a significant medical and veterinary importance. In part, this explains why they are the best-studied suborder of Phthiraptera. Between 1920 and 1935 Gordon Ferris provided the foundation for modern taxonomic work on the Anoplura, and when republished as a monograph FERRIS (1951) recognized 6 families. In the light of new species descriptions this was expanded to 15 (KIM & LUDWIG 1978). Apomorphies for Anoplura include the development of piercing stylets from the hypopharynx and labium, fusion of the pronotum to the mesonotum, and reduction of the meso- and metathoracic terga. A generic level morphological phylogeny for Anoplura was proposed by KIM (1988). Molecular studies on anopluran relationships are ongoing, but for the moment BARKER et al. (2003) provides an initial account of anopluran relationships using 18S rRNA.

Rhynchophthirina comprise just three species in a single genus. The subordinal status of this taxon was awarded by

FERRIS (1931) on account of the peculiar morphology of its members. Both monophyly and high rank are supported by morphological (LYAL 1985) and molecular (BARKER et al. 2003) data. Notable apomorphies for Rhynchophthirina include an anterior prolongation of the head into a rostrum with mandibles terminal and rotated 180°, and extension of the pretarsal apodeme into the femur without a tibial muscle bundle.

Amblyceran classification has been the subject of several detailed studies, most notably by CLAY (1970), who did much to stabilise their familial groupings. CLAY (1969) also considered possible relationships of genera in the largest amblyceran family, the Menoponidae. This study has been considerably expanded by MARSHALL (2003), who provides the most comprehensive study of amblyceran relationships to date covering generic level relationships for almost all taxa that parasitise birds and Australasian marsupials. Her study is broadly consistent with the available molecular studies, although the latter are few in number and largely confined to terminal clades of the amblyceran tree. Significant apomorphies for Amblycera include the development of an antennal fossa concealing the antennae and the presence of a pedunculate first flagellar segment.

Ischnocera form the largest suborder of Phthiraptera and their basal systematics is the subject of intense debate. HOPKINS & CLAY (1952) recognize just 3 families while EICHLER (1963) accepts 21. Based on both molecular and morphological data the most recent studies on Ischnocera recognize at least three monophyletic groups (LYAL 1985; MEY 1994; SMITH 2000, 2001; SMITH et al. in press). These are the Trichodectidae (sensu HOPKINS & CLAY 1952) restricted to mammalian hosts, the Heptapsogasteridae (sensu SMITH 2000) present on tinamiform birds and the Gonioididae (sensu SMITH 2000) of Galliformes and Columbiformes. A fourth group, the Philopteridae (sensu EICHLER 1963) comprise some 70 % of ischnoceran species and are present on almost all families of birds. It is generally accepted that this is a miscellaneous collection of genera and is almost certainly para- or polyphyletic. Despite being the subject of several extensive phylogenetic studies there is little consensus about basal ischnoceran relationships (SMITH et al. in press). Indeed, even the monophyly of the Ischnocera is weakly supported with no unequivocal morphological apomorphies defining this clade. Character convergence, multiple substitutions at high divergences, and ancient radiation over a short period of time have contributed to the problem of resolving ischnoceran phylogeny with the data currently available. A monotypic taxon (the Trichophilopteridae) represented by a single species present on Madagascan primates (Lemuridae and Indridae) may be related to the avian 'Philopteridae'. This species bears a number of significant morphological characters that are apparently intermediate between the 'Philopteridae' of birds and the Trichodectidae of mammals. Consequently the affinities of this genus are unclear, and it has been variably placed amongst both these groups or in an independent family within Ischnocera (SMITH 2001).

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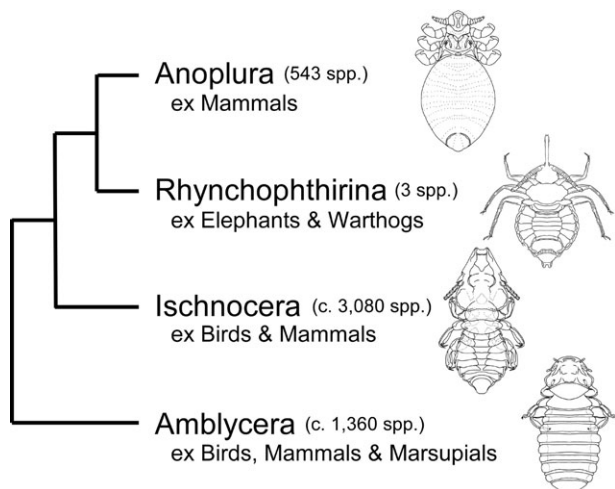


Fig. 1. The four suborders of Phthiraptera and their species content, host range, and phylogenetic relationships.

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The Morphological Background to Thysanoptera Phylogeny

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The order Thysanoptera either forms an unresolved trichotomy with the Hemiptera and Psocodea (Psocoptera + Phthiraptera), or is sister group to the Hemiptera (based on the structure of the wing sclerites: YOSHIZAWA & SAIGUSA 2001) with Psocodea sister to these two. BHATTI (1988), whilst accepting the monophyly of Thysanoptera, considered that the level at which this group is recognised should be raised. He thus stressed the many structural differences between the two traditional suborders, Terebrantia and Tubulifera, and suggested that the Thysanoptera should be considered a superorder with two orders. However, this change in taxonomic levels does not affect our understanding of relationships, based on the synapomorphic structure of the maxillary laciniae and pretarsal arolium in all thrips, and it is not accepted by other workers on the group. In contrast, ZHERIKHIN (2002) reduced the Thysanoptera to subor-

der Thripina and placed this with the fossil suborder Lophioneurina in an order Thripida; this also is not accepted currently, as the fossils have tarsal claws, extra wing veins, no wing fringes, and apparently two mandibles. In proposing such relationships, palaeontologists place great emphasis on the relatively superficial similarities provided by narrow wings with long fringing setae. They thus ignore the great diversity of wing form that occurs in extant Thysanoptera, and take no cognisance of the functional relationships between wing form and the ways in which wings are used in flight and particularly the way in which wings are parked on the abdomen when not in use.

The monophyly of the suborder Tubulifera is uncontested, on the basis of the structure of the wings with no longitudinal veins and the marginal cilia not arising from sockets, also the tubular condition of abdominal segment 10 and the

versible chute-like ovipositor of females. However, relationships between Tubulifera and Terebrantia remain unresolved: Tubulifera is either the sister group of Terebrantia, or it is sister to part of a family within the Terebrantia (MOUND et al. 1980: Panchaethripinae). An extensive summary by BHATTI (1988) of the morphological evidence supports the first hypothesis, all members of the Terebrantia having three well-developed longitudinal wing veins bearing setae, the marginal cilia in figure-of-eight shaped sockets, and abdominal segment 10 fully divided ventrally with the ovipositor comprising four saw-toothed valves.

In the Terebrantia, eight families are recognised, with the four genera comprising the Melanthripidae currently removed from the Aeolothripidae (cf. fig. 1 of following article by D.C. Morris & L.A. Mound), although European workers retain these four genera within the Aeolothripidae (as in the said figure). More recent consideration of the data has resulted in the Aeolothripidae being defined on two synapomorphies (loss of abdominal sternite 8 in females; presence of longitudinal sensilla on antennae), neither of which are present in any of the Melanthripidae. Moreover, melanthripids are all flower-feeding, whereas aeolothripids are either facultative or obligate predators. One problem involving the Melanthripidae is that it cannot be distinguished satisfactorily from the Merothripidae, both groups being defined on plesiomorphies, despite the great difference in their body sizes and feeding associations. Similarly, an analysis of a data matrix for the genera in the Fauriellidae and Adiheterothripidae provided no support for either family (Fig. 1), and genera in both of these groups show a remarkably disjunct distribution between western USA and the Mediterranean (MOUND & MARULLO 1999). The 60 species in the Heterothripidae occur only in the New World, whereas the major Terebrantia family, the Thripidae, with 2000 species and 260 genera, occurs worldwide. The monophyly of this large family has never been questioned, based largely on the presence of slender emergent sensilla on the 3rd and 4th antennal segments. But equally, it has never been adequately demonstrated, and is accepted largely for reasons of tradition. Unfortunately, within this large family there are further systematic problems: 50 % of the genera are monotypic, and the available suprageneric classification has few supporting character states and cannot be applied satisfactorily to the world fauna.

In the Tubulifera, only one family is usually recognised, the Phlaeothripidae, with two subfamilies, Phlaeothripinae and Idolothripinae. In contrast, BHATTI (1994, 1998) has recognised twelve additional families (Fig. 2), whilst retaining 98 % of the 3200 described tubuliferan species within the Phlaeothripidae. The Aleurodothripidae was erected for a single species in which the labro-maxillary complex is amalgamated with the cranium, but this same character state was used to define two further families, the Adurothripidae and the Urothripidae. The Xaniothripidae was erected for a single genus in which the wings are sometimes unusually broad and the abdomen bears many spines. However, this genus is considered, on molecular and behavioural evidence, to be sister to the genus *Koptothrips* in the Phlaeothripidae; the species in these two genera are biologically similar in being kleptoparasitic in the domiciles of other thrips species on *Acacia* in Australia, but are structurally highly divergent (MORRIS et al. 2002). Of the twelve families distinguished from the Phlaeothripidae by BHATTI (1998), nine include only a single genus (four with one species, two with two species), and a tenth includes two genera (each with one species). Finally, the Hydiiothripidae and the Urothripidae each include about 30 species, although both appear to have their closest relatives within the Phlaeothripidae, and both are best considered as informal genus-groups within the Phlaeothripidae.

This recognition of a series of small families does little to promote our understanding of relationships amongst the 2500 described species of Phlaeothripinae. With 50 % of the available genera monotypic, and limited understanding of the biological and genetic significance of the structural polymorphism amongst so many species, development of a suprageneric classification has not proved possible. Currently three lineages that are weakly defined morphologically are recognised in this group, the *Haplothrips*-lineage of flower-feeding species, the *Liothrips*-lineage of leaf-feeding species, and the *Phlaeothrips*-lineage of fungus-feeding species (MOUND & MARULLO 1996).

Within the second of the Tubulifera subfamilies, the Idolothripinae, systematic relationships appear to be more clearly defined (MOUND & PALMER 1983). However, monophyly of this subfamily itself requires further support. Despite the main character state (maxillary stylets more than 4 µm in diameter) appearing to be robust, it is related to the fact that all the species feed by ingesting whole fungus spores. Since feeding habits among thrips are notoriously opportunistic, the possibility of homoplasy must be further investigated.

None of the Phlaeothripidae exhibit any character state that can be considered to be in a plesiomorphic state, whereas within the Terebrantia families there is a progressive series from plesiomorphic to derived character states. Moreover, some fossil Terebrantia exhibit plesiomorphic character states, but no fossil 'proto-Tubulifera' have been described. There can be little doubt that the Thysanoptera is monophyletic, considering the unique structure of the maxillary stylets enclosing a single channel. But at what point the tubuliferan lineage separated from the terebrantian lineage is a problem. If these two suborders are sister groups, then either the proto-Tubulifera did not live in suitable situations to be fossilised, or such fossils have yet to be found. The alternative evolutionary scenario is that the Tubulifera evolved relatively late, arising through neotenic development from larval Panchaethripinae within the most highly derived of the Terebrantia families, the Thripidae, and subsequently radiated rapidly. This suggestion is based on the presence of a tubular abdominal segment 10 in Panchaethripinae larvae, and the presence in many adult Panchaethripinae of sigmoid wing-retaining setae on the abdominal tergites.

The plesiotypic life-style of thrips is considered to be fungus-feeding in detritus, with the small-bodied, fungus-feeding species in the Terebrantia family Merothripidae retaining the largest number of plesiomorphies (antennae 9-segmented; tentorium complete; large pair of trichobothria on abdomen). However, a sistergroup relationship to the remaining Terebrantia families is not clear, and as indicated above the morphology-based family classification owes more to tradition than to phylogenetic character state analysis. Clearly, the future of phylogenetic studies on Thysanoptera must involve alternative sources of data including molecular data.

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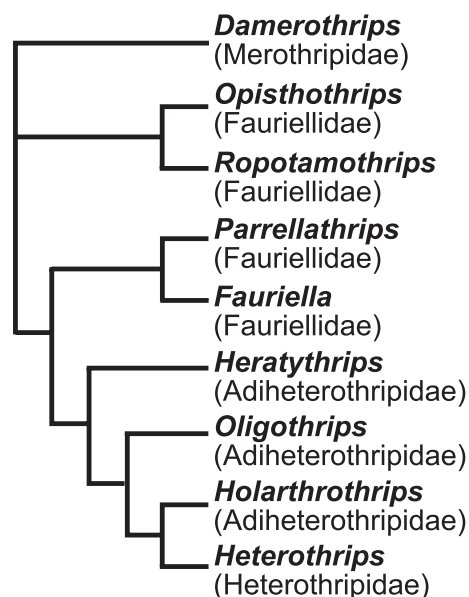


Fig. 1. Relationships among Adiheterothripidae and Fauriellidae according to MOUND & MARULLO (1999), using the 'ie' option in Hennig86.

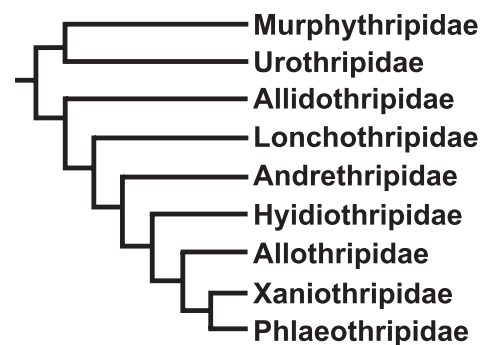


Fig. 2. Tubuliferan families recognised by BHATTI (1994); it is unclear whether tree dichotomies are intended to propose phylogenetic relationships; see BHATTI (1998) for Adurothripidae, Aleurodothripidae, and Habrothripidae.

Thysanoptera Phylogeny – the Molecular Future

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The monophyly of the Thysanoptera is strongly supported by a number of morphological characters including the protrusible arolium on the pretarsus and the asymmetric mouthparts (right mandible is absent). Molecular analyses also strongly support the monophyly of the Thysanoptera (CRESPI et al. 1996).

The current classification of Thysanoptera consists of approximately 5500 species in two suborders, Tubulifera and Terebrantia, and nine families, with Phlaeothripidae alone constituting the Tubulifera. The only recent attempt to assess the phylogeny of the order as a whole (MOUND et al. 1980) raises several questions about the relationships of the families within the order that are unresolved with morphological methods. One such question was that of the evolutionary origins of the Phlaeothripidae, which possesses so

many autapomorphic characters that it could either be sister taxon to the remaining eight families (i.e., to Terebrantia) or it could be derived from the subfamily Panchaethripinae, making the Thripidae paraphyletic (see Fig. 1). The former hypothesis is supported by many apomorphic characters that suggest that Phlaeothripidae may be independently evolved from the Protothysanoptera, and several synapomorphic characters that are shared by all of the Terebrantian families (MOUND et al. 1980). The latter hypothesis is based on a number of apparent synapomorphies uniting Phlaeothripidae and Panchaethripinae to the exclusion of the remaining families (as well as the remaining Thripidae). Some of the questions relating to the relationships of the thysanopteran families were subsequently addressed using molecular methods by CRESPI et al. (1996), who used frag-

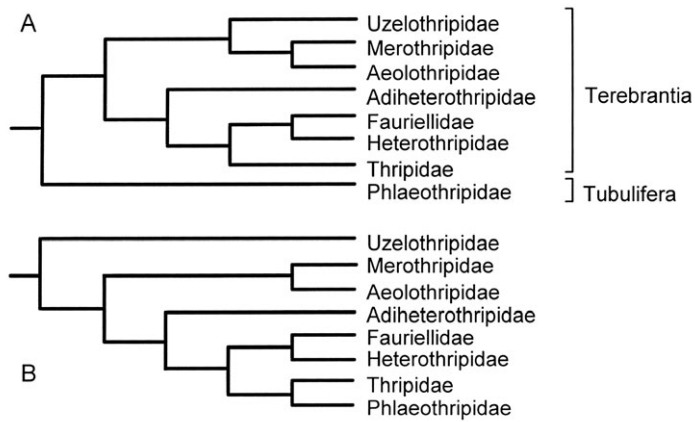


Fig. 1. Two alternative hypotheses for thysanopteran familial relationships based on morphological characters (redrawn from MOUND et al. 1980). **A:** Phlaeothripidae sister to all other families, with the suborders Tubulifera and Terebrantia as sister taxa. **B:** Phlaeothripidae as sister taxon to Panchaetothripinae (a subfamily within Thripidae), making the Terebrantia paraphyletic.

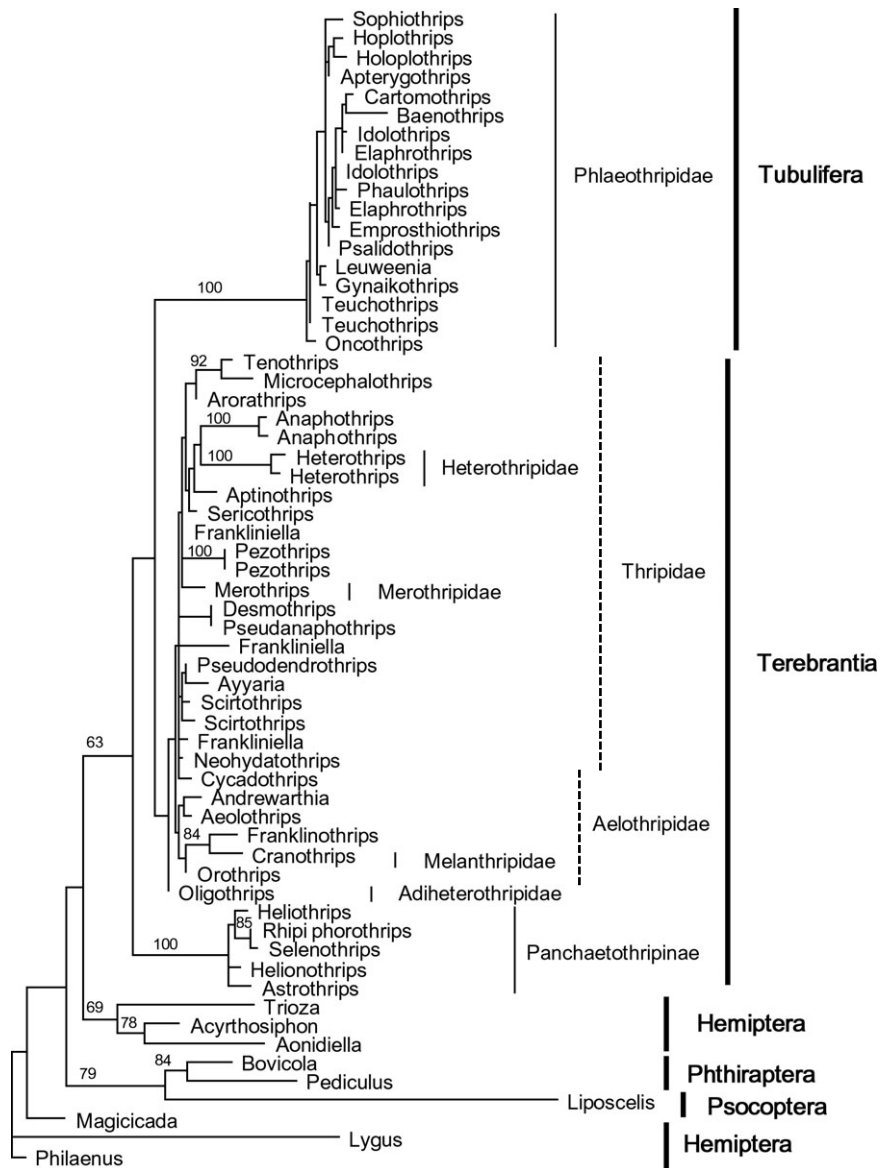


Fig. 2. A phylogenetic hypothesis for the order Thysanoptera based on a maximum likelihood analysis (model TrNef+I+G) of 18S rDNA. Numbers shown above branches are parsimony bootstrap values (10,000 reps using the ‘fast’ stepwise addition algorithm in PAUP* 4.0). Current family-level classification for the genera is shown with slender vertical bars, with broken lines indicating the families whose representatives are not monophyletic in this tree, e.g., Thripidae (which also includes Panchaetothripinae) and Aeolothripidae. The broad, bold vertical bars are indicative of subordinal (in the case of the ingroup Thysanoptera) or ordinal affiliations.

ments of the mitochondrial COI gene and the nuclear ribosomal 18S gene to examine the subordinal and familial relationships within Thysanoptera. Unfortunately, the small number of taxa (approximately 0.1 % of known species) included in that study limited the utility of the results.

In our study we attempt to expand the data set of CRESPI et al. (1996) to incorporate a broader range of thrips species. We obtained sequence data for approximately 600 bp of the 18S gene from 52 species of Thysanoptera representing most of the thysanopteran families. To these data we added a number of 18S sequences (taken from Genbank) for a range of other paraneopteran taxa to serve as outgroups. Maximum likelihood analysis of this data set yielded the tree shown in Fig. 2.

This result is not robust due to a lack of informative characters; however, it does suggest some relationships that are not reflected in the current hypotheses of thysanopteran phylogeny. This analysis recovers only two significant clades with appreciable levels of support among the ingroup taxa. One clade is that containing all Tubulifera, supporting a hypothesis of the monophyly of this suborder (i.e., of Phlaeothripidae), but with no resolution between its two subfamilies (Phlaeothripinae and Idolothripinae). The other

well-supported clade contains all sampled Panchaethripinae. This is an unanticipated result, given that all other terebrantian taxa are unresolved, and no family groupings are recovered. MOUND et al. (1980) noted a number of morphological characters in common between the Phlaeothripidae and Panchaethripinae. Should our results be supported by further data, this would suggest that these characters are plesiomorphic for Thysanoptera, especially because Panchaethripinae and then Phlaeothripidae are presently indicated to be the two most basal clades of Thysanoptera (Fig. 2). Our current results suggest that the present classification may not reflect the phylogeny of the order, but further molecular data is required to confirm this.

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Phylogeny of the Strepsiptera – Morphological Evidence

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Introduction

The Strepsiptera are entomophagous insects. There are about 600 described extant species world-wide and, in a traditional classification, nine or ten families. The minute first instar larvae are free-living and represent the infectious stage. The second instar larvae of all species and the neotenic females of the Stylopodia are endoparasites of representatives of various higher taxa of insects including the Zygentoma, Blattaria, Mantodea, Orthoptera, Hemiptera, Hymenoptera, and Diptera. Due to their parasitism, they have evolved extremely modified morphology and life histories. Conspicuous characters of the males include the reduced forewings, which resemble dipteran halteres, and the fan-shaped hindwings as well as the ‘raspberry’ compound eyes. Females are always wingless and only those of the basal Mengenillidae are free living, and partly leave their larval exuviae. In Stylopodia, only the anterior part of the female body is externally exposed; the females remain enclosed in the exuviae of earlier stages, and form a functional unit with them within the host.

Basal relationships of the Strepsiptera

The phylogeny of the Strepsiptera proposed by KINZELBACH (1990) was based on a non-numerical analysis (Hennigian approach) of morphological characters, mostly of adults, and is generally accepted today (Fig. 1A). KINZELBACH (1990) suggested the division into two major groups, the basal Mengenillidia with free living females (not confirmed for the Baltic amber fossil *Mengea*) and the Stylopodia with endoparasitic females.

POHL (2002) carried out the first cladistic analysis based on morphological characters of the first instar larvae (Fig. 1B). This analysis supported the monophyly of Stylopodia, whereas the monophyly of Mengenillidia could not be verified.

The first instar larvae of the Baltic amber fossil *Mengea* are not known. Discrepancies with the topology based on adults pertain to subtaxa of the Stylopodia, especially the placement of Elenchidae, which are almost certainly not the sister group of Myrmecolacidae as proposed by KINZELBACH (1990), and the paraphyly of Stylopidae. *Xenos* and *Pseudoxenos* turned out as not closely related with other Stylopidae sensu KINZELBACH (1990), and consequently POHL (2002) re-established Xenidae.

Here we summarize our recent results on the basal relationships of the order based on a cladistic analysis of 38 characters of males of 12 ingroup (including a newly discovered Baltic amber fossil) and 3 outgroup taxa (manuscript submitted by H. Pohl, R.G. Beutel & R. Kinzelbach: “Protoxenidae fam.n. from Baltic amber – a ‘missing link’ in strepsipteran phylogeny”) (Fig. 1C).

The monophyly of Strepsiptera s.l., Strepsiptera excl. the newly discovered fossil (= sp. a in Fig. 1C), and Strepsiptera excl. this fossil and Mengeidae (including only *Mengea*) is strongly supported. Important apomorphies of the males of Strepsiptera s.l. are the reduction of the tentorium, distinctly separated ommatidia, eight antennomeres, flabellate antennomeres 3–7, absence of the lacinia, 1-segmented maxillary palps, absence of the labial palps, mesothoracic halteres, and a strongly sclerotized abdominal segment 9. Apomorphies of Strepsiptera excl. the newly discovered fossil are size reduction (less than 7 mm), a dorsomedian frontal impression of the head, a strongly shortened or membranised coronal suture, seven antennomeres or less, absence of the galeae, wings wider than long, an elongated and shield-like metapostnotum, and abdominal sternites more heavily sclerotised than the tergites. Strepsiptera s.str. (i.e., excl. stem lineage) is not supported by many autapomorphies, but one important derived feature is the strongly reduced labrum of males. Strepsiptera s.str. excl. *Eoxenos* is well supported and this implies paraphyly of Mengenillidae,

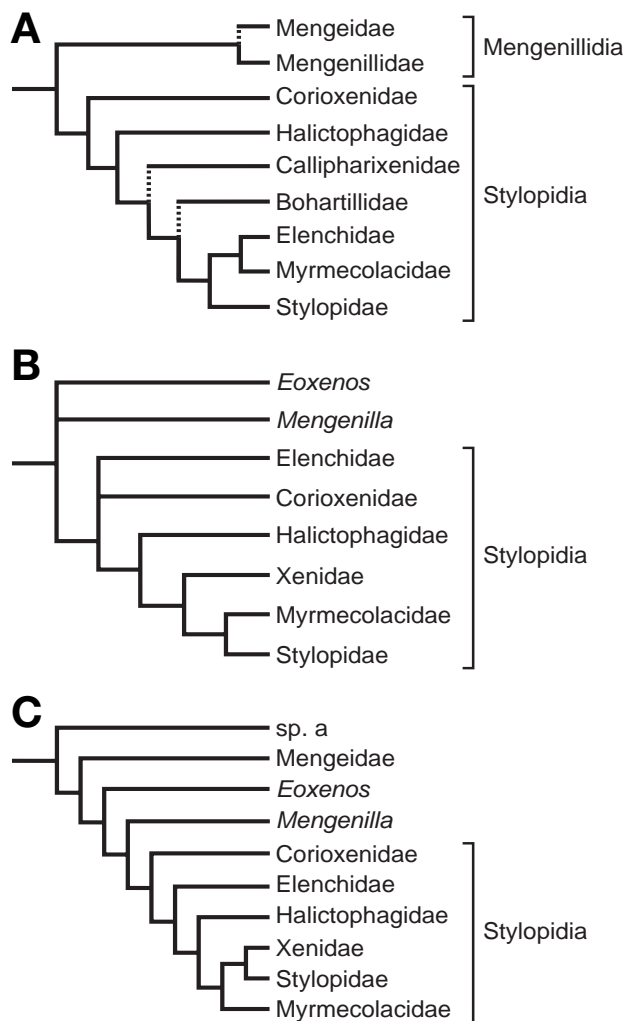


Fig. 1. Hypotheses on strepsipteran phylogeny. **A:** Tree modified from KINZELBACH (1990). Dotted lines indicate uncertain relationships. **B:** Tree based on characters of first instar larvae; strict consensus tree of four minimum length trees (modified from POHL 2002). **C:** Tree based on characters of males; one of two minimum length trees (modified from a manuscript submitted by Pohl et al.); sp. a = newly discovered species from Baltic amber.

which are mainly characterised by one plesiomorphic feature, the free living females.

The major step in the evolution of Strepsiptera is the rise of Stylopidia (97 % of all known species), which are well supported by several character transformations of males (modifications of tarsomeres with specialised adhesive hairs to attach to the host of the parasitic females, loss of abdominal spiracles). The most striking feature however, is the endoparasitism of the adult females, correlated with highly unusual morphological character transformations, such as the formation of a unique type of brood organs and of a secondary birth opening in the cephalothorax.

The 'Strepsiptera problem'

The phylogenetic placement of Strepsiptera is one of the most enigmatic issues of ordinal-level insect systematics ("the Strepsiptera problem"; KRISTENSEN 1981). Strepsiptera was first described by ROSSIUS (1793), who placed it in the Hymenoptera near the Ichneumonidae. At the end of the 19th century, the group had been associated with the

Ephemeroptera, Odonata, Hymenoptera, Lepidoptera, Diptera, and Siphonaptera (PIERCE 1909).

Recently, the phylogenetic placement centered around four major hypotheses: (1) as a subordinate group of polyphagan beetles (CROWSON 1960), (2) as the sister group of Coleoptera (KINZELBACH 1990), (3) as the sister group of Diptera ("Halteria"; WHITING et al. 1997), and (4) as having a position outside of Endopterygota ("Neoptera incertae sedis"; KRISTENSEN 1991).

The first mentioned hypothesis (1) was based on superficial similarities and can be ruled out with reasonable certainty. A non-reductive potential synapomorphy with the Coleoptera (2), the presence of densely setose tarsal attachment devices (BEUTEL & GORB 2001), has evolved within the Strepsiptera (Stylopidia) and does not belong to the ground plan of the order (see above). Another potential synapomorphy, the stronger degree of sclerotisation of the abdominal sternites (compared to the tergites) is also invalid: this condition was absent in the most basal strepsipteran from Baltic amber. Posteromotorism is also a derived feature shared by Coleoptera and Strepsiptera. However, this condition has evolved within several lineages of insects independently (e.g., Orthoptera, Dermaptera).

The 'Halteria' concept (3) is mainly supported by 18S rDNA sequences, but the clade comprising Strepsiptera and Diptera may be due to long-branch attraction (e.g., HUELSENBECK 1997). 5.8S rDNA, 28S rDNA, and the engrailed homeobox gene do not support a sistergroup relationship between these two groups (HWANG et al. 1998; ROKAS & HOLLAND 2000).

The position of Strepsiptera outside of Endopterygota (4) was discussed mainly based on the presence of external wing buds in late instar larvae of the Strepsiptera. Other potential plesiomorphies of Strepsiptera are the formation of compound eyes in the second instar larvae (not in the pupal stage, as in Endopterygota) and the presence of a well developed abdominal segment 11 in the first instar larvae. A sistergroup relationship between Strepsiptera and the remaining Endopterygota should probably be considered as the most viable working hypothesis.

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Phylogeny of the Neuropterida – Morphological Evidence and the Molecular *Advocatus Diaboli*

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Neuropterida

Understanding the phylogeny of this basal holometabolan superorder comprising the orders Raphidioptera, Megaloptera and Neuroptera, is thought-provokingly correlated with hypotheses on general phenomena: evolution of aquatic larvae, evolution of complex larval sucking tubes with extraintestinal digestion, evolution of cryptonephry, production of silk etc. Monophyly of the Neuropterida is based on rather inconspicuous characters concerning thoracic and abdominal sutures, special musculature of the ovipositor, characters of larval stemmata, and specializations at the wing-bases (literature summarized in ASPÖCK 2002; ASPÖCK et al. 2001; KRISTENSEN 1999). A sistergroup relationship with Coleoptera is the preferred hypothesis at present (KRISTENSEN 1999).

Prehennigian and most recent classifications favour Raphidioptera + Megaloptera against Megaloptera + Neuroptera (the concept of Raphidioptera + Neuroptera is out of the main discussion). Argumentations pro Raphidioptera + Megaloptera (summarized in WILLMANN 2003) base on symplesiomorphies (e.g., the gula), or appear to be highly sophisticated (postepimeron-complex, polyintersegmental muscle between abdominal tergites 2–5, reduction of tergite 2, various ovariole-concepts). Overall similarity might have been an inductive factor for this approach. Arguments pro Megaloptera + Neuroptera resulted from a morphological approach mainly comprising larval characters (head capsules, mouthparts, primary aquatic lifestyle; ASPÖCK 1995) and were corroborated by a cladistic computer analysis based on a broad pallet of morphological characters (ASPÖCK et al. 2001). The cladogenesis of this group as deduced from this analysis is summarized in Fig. 1. Additional support comes from unpublished molecular data (Haring & Aspöck in prep.: “Molecular phylogeny of the Neuropterida”). Synapomorphies of Megaloptera + Neuroptera are rosette-like organized trichobothria on the ectoproct, male gonocoxites of segment 9 modified to appendices of the tergite, aquatic larvae, integration of the cardines (basal parts of the maxillae) into the head capsule, and elongation of larval stipites (ASPÖCK et al. 2001; ASPÖCK 2002).

The monophyly of Raphidioptera (including families Raphidiidae and Inocelliidae), which has never been questioned, is reflected by several adult characters: subcosta running into costa, third tarsale enlarged, tergite and sternite of abdominal segment 9 in the male amalgamated to a ring, and ovipositor of the female elongated to form a hose-like structure. Also paraphyly of Megaloptera (including families Corydalidae and Sialidae) is meanwhile no longer discussed. Monophyly of this order is supported by specia-

lizations in the organization of somatic ovarian tissues and the tracheal gills of the larvae. The monophyly of Neuroptera has never been doubted and is mainly based on the complex sucking tubes of the larvae and the silken cocoon of the pupae.

Controversies on splitting events in Neuroptera

The great challenge in Neuropterida are sistergroup relationships within the extremely heterogeneous Neuroptera (17 families). Morphological analyses (commented in ASPÖCK 2002) revealed three monophyletic groups, either (Nevrorthiformia + Myrmeleontiformia) + Hemerobiiformia, or Nevrorthiformia + (Myrmeleontiformia + Hemerobiiformia) (Fig. 1). The controversial hypotheses derived from the above cited cladistic analyses concern Myrmeleontiformia: (Psychopsidae + Nemopteridae) + (Nymphidae + (Myrmeleontidae + Ascalaphidae)) versus Psychopsidae + (Nemopteridae + (Nymphidae + (Myrmeleontidae + Ascalaphidae))) is still unsettled but of minor relevance compared with controversies in Hemerobiiformia. This suborder comprises an assembly of 11 extremely heterogeneous families. Arguments in support for monophyly of the eidonomically primitive basal group Ithonidae (including Rapismatidae) + Polystoechotidae rest on the morphology of their scarabaeiform blind larvae (the larvae of Rapismatidae are, however, unknown) and on the hypothesis of phytosuccivory of these larvae as root suckers. All other families constitute the ‘higher Hemerobiiformia’, with constricted larval cardines as synapomorphy. A sistergroup relationship of Osmylidae + Chrysopidae revealed from the analyses is only weakly supported, and also Coniopterygidae + Sisyridae need corroboration. Only the dilarid clade comprising Dilaridae + (Mantispidae + (Rhachiberothidae + Berothidae)), with strong synapomorphies of the larvae (flattened heads, broad insertions of the cardines, elongation of the postmentum), has never been doubted.

If we accept aquatic larvae as a synapomorphy of Megaloptera and Neuroptera, terrestrial larvae (and their cryptonephries) must have evolved twice in a concept (Nevrorthiformia + Myrmeleontiformia) + Hemerobiiformia, but only once in a concept Nevrorthiformia + (Myrmeleontiformia + Hemerobiiformia). However, in the latter case the terrestrial clade of the Hemerobiiformia contains aquatic Sisyridae. This hypothesis involves secondarily evolved aquatic larvae (with one cryptonephric malpighian tubule as reminiscence of a terrestrial ‘intermezzo’) in this family. The compact specialized larval head capsule (with several autapomorphies concerning the tentorium, and the enormous sucking

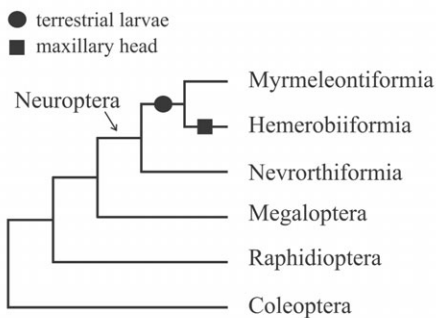


Fig. 1. Simplified preferred cladogram of the Neuropterida based on morphological and biological characters (for details see ASPÖCK et al. 2001 and ASPÖCK 2002).

tubes) of the Myrmeleontiformia apparently evolved from a simple compact head, similar to recent Nevrothidae, and not as a reversal of an open maxillary head, as in recent Hemerobiiformia, which is not compact at all, but predominantly constructed by basal pieces of the maxillae – therefore the term ‘maxillary head’. In the concept of monophyletic Hemerobiiformia the maxillary head is certainly the most important synapomorphy, symbolizing the splitting of the two suborders.

Our molecular analysis corroborates the sistergroup relationship of Megaloptera and Neuroptera, the Nevrothiformia as the sister group of the remaining Neuroptera, and the monophyly of Myrmeleontiformia. A result in conflict with our previous (morphology-based) concept is that the Hemerobiiformia do not turn out as a monophyletic group (Fig. 2). As a consequence we are faced with a parallel evolution of the maxillary head – which is at least not parsimonious at all. Another conflict concerns straight sucking tubes in the larvae, a specialization in correlation with certain food strategies, which were considered as a synapomorphy of certain families. Straight sucking tubes could also have evolved several times independently, which would be the necessary assumption in the context of the molecular analysis and avoiding the interpretation of curved sucking tubes being reversals.

It should be mentioned that in the DNA trees the Ithonidae

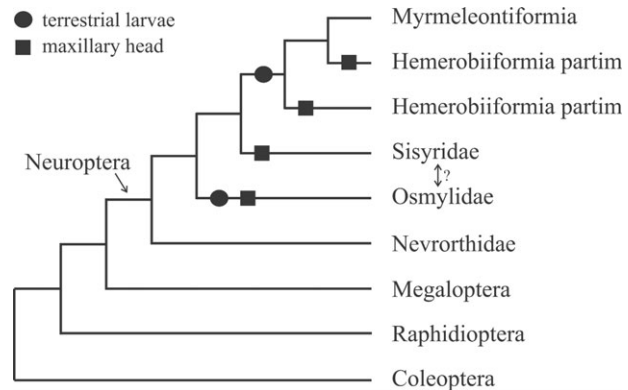


Fig. 2. Simplified preferred cladogram of the Neuropterida based on molecular characters (Haring & Aspöck in prep.).

are not monophyletic. This primitive but nonetheless specialized group as well as the highly specialized Coniopterygidae – usually apostrophized as the ‘early offshoots’ in previous classical as well as in recent nonhennigian concepts – do not emerge basally in the two comprehensive analyses, neither in the morphological nor in the molecular approach, but nevertheless remain enigmatic.

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Molecular Phylogeny of Neuropterida with Emphasis on the Lacewings (Neuroptera)

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The Neuropterida, comprising the orders Megaloptera (dobsonflies, alderflies), Raphidioptera (snakeflies) and Neuroptera (= Planipennia, lacewings), are considered one of the most basal, or ‘plesiomorphic’, groups of Holometabola. While numerically they are a small to medium sized group, there is considerable morphological diversity across the ca. 21 families within the clade. This diversity has made estimates of homology difficult to reconcile across families, and while Neuropterida has undergone numerous taxonomic and morphological studies, little progress has been made towards developing an overarching phylogeny. Indeed, the phylogeny of Neuroptera published

by WITHYCOMBE (1925) has served as the basis for our understanding of the evolution of order until very recently. Recent important morphological studies using cladistic methodology (e.g., ASPÖCK et al. 2001) have proposed new hypotheses of neuropterid relationships. Unfortunately, these hypotheses are based on relatively few characters and have left many unanswered questions (or poorly supported conclusions) regarding the position of several key families and family groups. Moreover, the relationships of the three orders, Megaloptera, Raphidioptera and Neuroptera, are subject to considerable debate.

I am presently examining the phylogeny of Neuropterida,

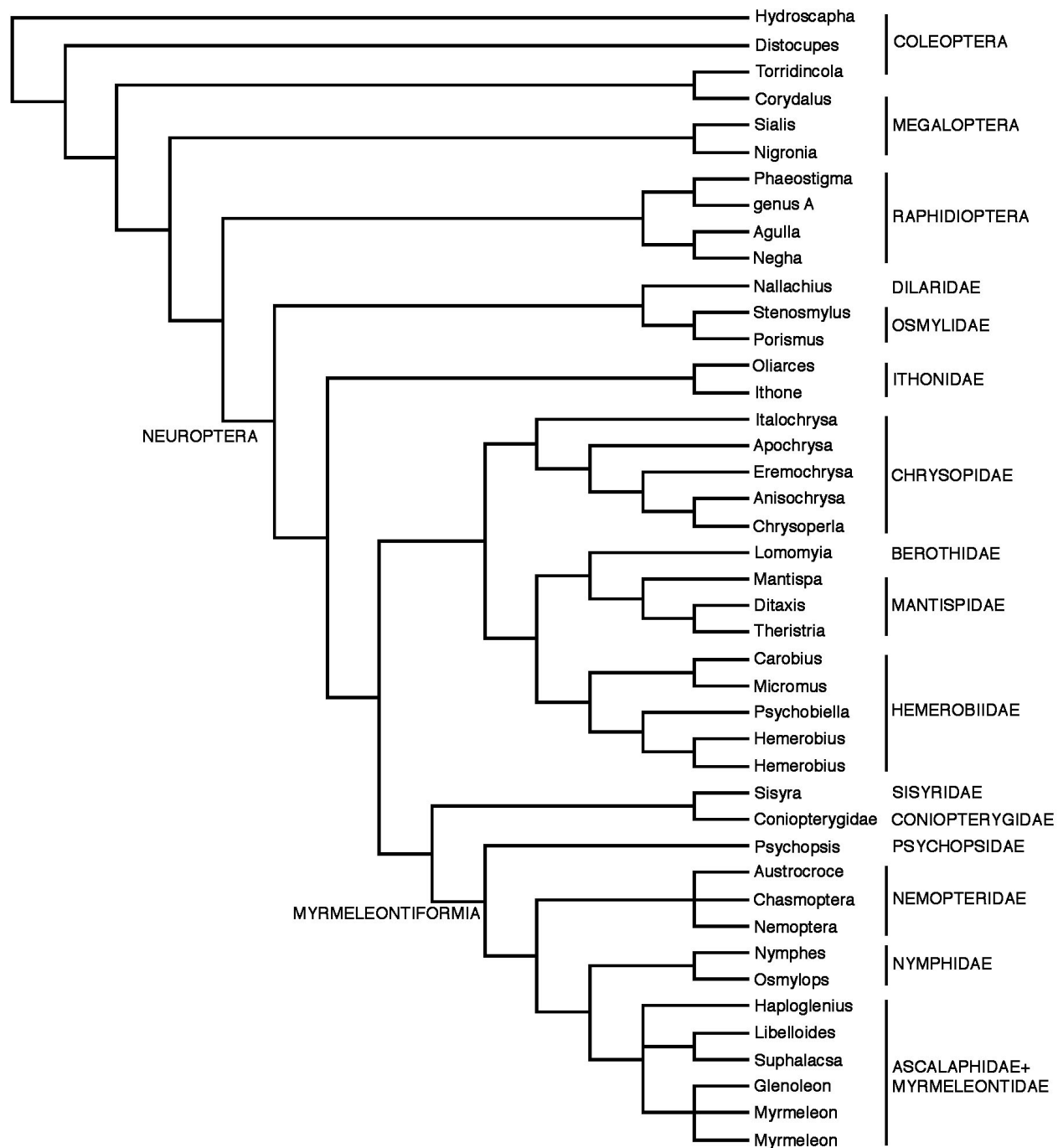


Fig. 1. Phylogeny of Neuropterida: strict consensus tree of 39 most parsimonious trees (length = 1220 steps; CI = 0.62; RI = 0.65) based on combined morphological characters and 18S rDNA gene sequence.

with emphasis on Neuroptera, using data from 18S ribosomal DNA and adult and larval morphology. A phylogeny based on preliminary data of 2.2 kb of 18S rDNA and 56 adult and larval morphological characters from 38 genera of Neuropterida and three coleopteran outgroups is presented in Fig. 1. There is extensive node resolution throughout the Neuroptera, with both the major suborders, Myrmeleontiformia and Hemerobiiformia, being resolved (the third suborder, Nevrothiformia, here not included). Notable exceptions include the positions of Osmylidae, Dilaridae, and Sisyridae + Coniopterygidae. There is general agreement with the morphology-based phylogenetic hypothesis of ASPÖCK et al. (2001) in regard to the placement of various families within each suborder, although with some notable

exceptions. Unfortunately, there are fewer than 30 % of the nodes in the tree generated from the equally weighted analysis that have bootstrap values above 50 %. Moreover, the Megaloptera are not recovered, while the Raphidioptera and Neuroptera are both well supported. Several important taxa are yet to be included in the analysis, such as Nevrothidae, Coniopterygidae, Rhachiberothidae and Polystoechotidae, as well as more genera of Megaloptera. All of these taxa are crucial to the final analysis and will likely influence the final analysis greatly. Therefore, I consider these results as only preliminary and indicative of trends in the data, awaiting the addition of further characters and completed taxon sampling.

Acknowledgements

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Basal Splitting Events in Coleoptera

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Introduction

With more than 360,000 described species Coleoptera are by far the largest group of Metazoa. Considering this unusual diversity, a major issue for coleopterists should be the reasons for this evolutionary success. However, for the development of possible scenarios, a well founded phylogenetic hypothesis for the major groups is needed. Surprisingly the crucial question of the interrelationships of the four suborders is still discussed controversially.

Current hypotheses

KUKALOVÁ-PECK & LAWRENCE (1993) have postulated a sistergroup relationship between Polyphaga and the remaining Coleoptera, and between Archostemata and Myxophaga + Adephaga. This hypothesis was based on characters of the wing venation and articulation and a non-numerical character evaluation. It is confirmed in a hitherto unpublished study of these authors with a cladistic analysis of a similar data set. A phylogenetic scheme which was already proposed by CROWSON (1960) – Archostemata + (Adephaga + (Myxophaga + Polyphaga)) – was supported by a cladistic analysis of 107 characters of adults and immature stages (BEUTEL & HAAS 2001). A basal position of Archostemata was confirmed by an analysis of 18S rDNA sequences presented by CATERINO et al. (2002). However,

Adephaga was placed as the sister group of Polyphaga in this contribution.

Scenario of splitting events

Coleoptera is characterised by many autapomorphies, notably the rigidly connected sclerites, the absence of exposed membranes, elytra with epipleura, folded alae, a prognathous, wedge-shaped head, invaginated terminal abdominal segments, and the loss of several thoracic muscles. The retention of a considerable number of plesiomorphies in adults of Archostemata (e.g., transverse ridge of mesoventrite present, metatrochantin exposed, presence of *M. notosternalis* 2) is most easily explained with a basal position of the group within Coleoptera. The monophyly of the suborder is well supported, however almost exclusively by larval features, which are correlated with wood-boring habits: strongly sclerotised wedge-shaped head, shortened or reduced legs, unsclerotised cylindrical body, and presence of tergal ampullae. Potential synapomorphies of Adephaga, Myxophaga and Polyphaga are the loss of nine homologous thoracic muscles, the absence of an exposed metatrochantinus, the loss of the transverse ridge of the mesoventrite, and the primary absence of the mesothoracic katapisternal joint (similar structure present in some scirtids). The fused tibia and tarsus of larvae, the single larval claw, the prothoracic trochantinopleura, and several muscle losses are potential

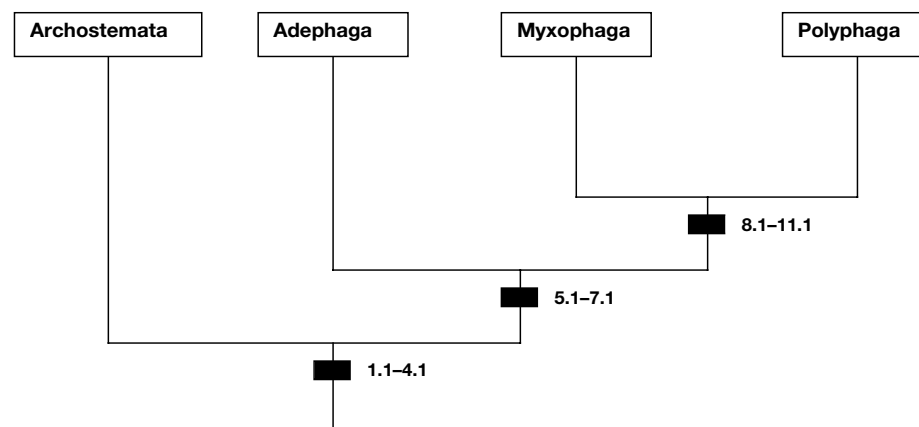


Fig. 1. Hypothesis of basal splitting events in Coleoptera. Apomorphies mapped on cladogram: 1.1 absence of exposed membranes, 2.1 elytra with epipleura, 3.1 wing folding, 4.1 muscle losses; 5.1 loss of nine thoracic muscles, 6.1 external metatrochantinus absent, 7.1 transverse ridge of mesoventrite absent, 8.1 larval tibiotarsus, 9.1 single claw of larvae, 10.1 muscle losses, 11.1 meso- and metaventrites firmly connected.

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 leioidids, 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, Leioididae, 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). VILHELMSSEN (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 VILHELMSSEN (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 (VILHELMSSEN 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 discremen, 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

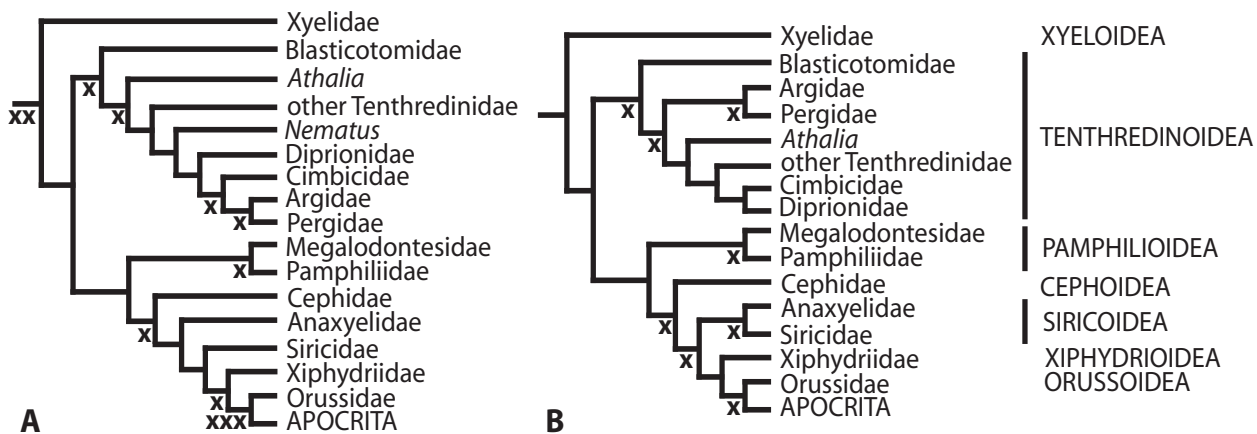


Fig. 1. Phylogeny of the basal lineages of Hymenoptera according to **A:** VILHELMSSEN (2001; only morphological characters); **B:** SCHULMEISTER (2003; simultaneous analysis). Superfamily classification superimposed. Number of X'es below nodes indicates degree of clade support (the more X'es, the stronger the support).

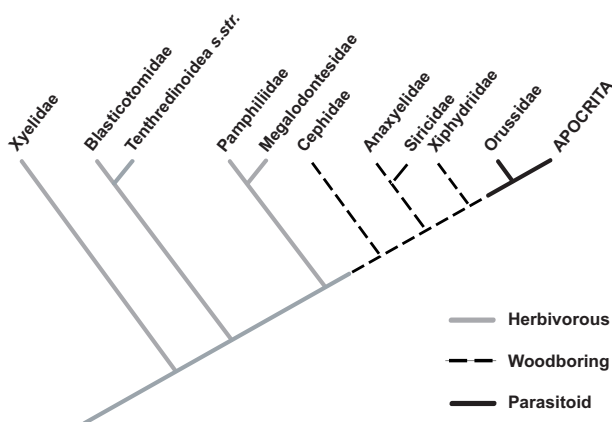


Fig. 2. Early evolutionary history of the Hymenoptera, with the larval lifestyle mapped onto the topology in Fig. 1B.

display posterior displacement and subsequent reduction of the labrum (VILHELMSSEN 1996); these changes permit the mandibles to be employed more efficiently when chewing an escape tunnel from the pupal chamber, which is paramount for taxa pupating in wood. Later in the evolutionary history of the Hymenoptera, the mandibles were used as tools in numerous other circumstances (e.g., many social Hymenoptera; JERVIS & VILHELMSSEN 2000). The ovipositor apparatus is another instance of a character system having undergone extensive modification throughout the order (QUICKE et al. 1999; VILHELMSSEN 2000) in correlation with oviposition in different substrates. A very elongate ovipositor was probably present in the common ancestor of Orussidae + Apocrita; this was useful for penetrating deep into the substrate of its presumably concealed host, but caused problems with handling when used to drill in wood. The internalized ovipositor of the Orussidae and the wasp-waist of the Apocrita, respectively, can be interpreted as different solutions to these problems (VILHELMSSEN et al. 2001). Finally, the extensive reductions in larval anatomy (absence of eyes, laterocervicalia, thoracic and abdominal legs; reduction of antennae and mouthparts; see VILHELMSSEN 2003) that can be inferred to have taken place between the ancestral hymenopteran and the ancestral parasitoid wasp can also be correlated with the transition from an externally living herbivorous lifestyle to ectoparasitism of a con-

cealed host; the latter lifestyle is probably much less demanding of the sensory and locomotory apparatus.

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The Pattern of Relationships among Superfamilies of Apocritan Hymenoptera Derived from Recent Morphological and Molecular Analyses

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Introduction

The Apocrita represent a massive radiation of insects that may comprise 20–25 % of all insect species. This huge diversity is largely due to the evolution of several biological attributes: (1) parasitism where various groups have radiated to exploit other insects and spiders as hosts, (2) eusociality among the higher aculeates, and (3) various forms of specialised predation and phytophagy (e.g., gall-forming, pollen/nectar-feeding). The Apocrita comprise the vast majority of Hymenoptera and they are defined by the unique character of having the first abdominal segment (propodeum) broadly fused to the posterior thorax, and a narrow waist developed between the first and second abdominal segments. The current classification recognises 13 superfamilies and 76 families, and of these the parasitic Ichneumonoidea and Chalcidoidea, and the aculeate Vespoidea (including the ants) and Apoidea constitute the most diverse groups by far.

Morphological studies

While recent studies have made significant headway in resolving the phylogeny among basal Hymenoptera (the ‘Symphyta’, or sawflies), relationships within the Apocrita remain poorly resolved, even though numerous recent studies have focused on this problem. As with sawfly phylogenetic research, RASNITSYN’s (1988) benchmark study is often considered to be the ‘modern’ starting point for phylogenetic research on the Apocrita. The tree presented by RASNITSYN (1988), although generated intuitively, has formed a basis for most subsequent work and initiated substantial interest in hymenopteran phylogeny, resulting in numerous detailed anatomical studies. Although these studies have identified a number of potentially informative character systems, none have yet been incorporated into broad analyses of apocritan relationships.

Overall, two studies stand out as being critically important. RONQUIST et al. (1999) reanalysed RASNITSYN’s (1988) data within a cladistic framework, and revealed a substantially different set of relationships compared with those predicted in the original intuitive tree. For example, this study (Fig. 1) found no support for Ichneumonoidea + Aculeata, or Ceraphronoidea + Evanioidea + Trigonaloidea/Megalyroidea/Stephanoidea (i.e., Rasnitsyn’s Evaniomorpha), but did broadly support the Proctotrupomorpha (i.e., Chalcidoidea + Platygastroidea + Cynipoidea + Proctotrupeoidea, but with quite different internal relationships and the inclusion of Ceraphronoidea) and the non-monophyly of the Proctotrupeoidea. Recently, SHARKEY & ROY (2002), however, have highlighted a number of shortcomings with RASNITSYN’s (1988) original data, and shown that much of the structure in the RONQUIST et al. (1999) tree is due to reductional characters associated with the wings. They revised all wing

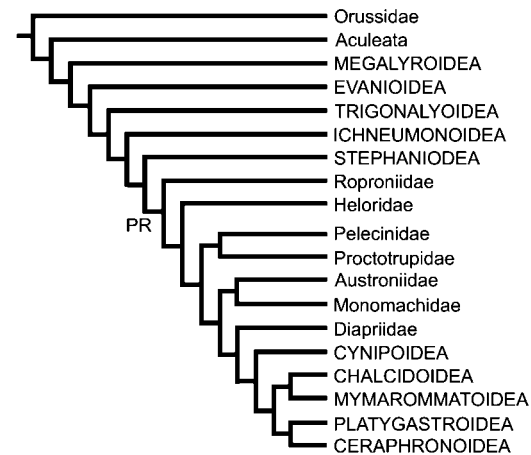


Fig. 1. Apocritan relationships indicated by the RONQUIST et al. (1999) reanalysis of RASNITSYN’s (1988) morphological data (PR = Proctotrupomorpha).

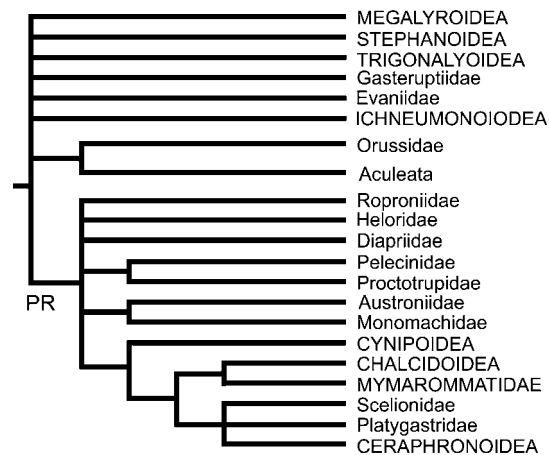


Fig. 2. Apocritan relationships developed by SHARKEY & ROY (2002) following reinterpretation of wing characters and reanalysis of the RONQUIST et al. (1999) data matrix (PR = Proctotrupomorpha).

characters, but the resulting tree (Fig. 2) was largely comb-like, with the exception of a monophyletic Proctotrupomorpha (including Ceraphronoidea).

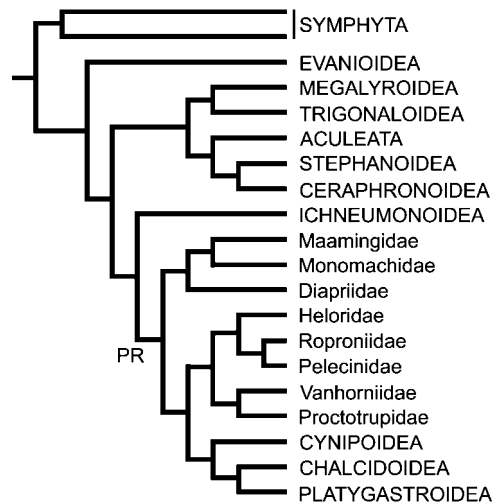


Fig. 3. Apocritan relationships following analysis of sequence data from multiple genes by DOWTON & AUSTIN (2001) (PR = Proctotrupomorpha), using two symphytans as the outgroup.

Molecular studies

Over the last ten years we have undertaken a series of studies employing DNA sequence data in an attempt to resolve relationships within Apocrita, particularly among the nine parasitic superfamilies (DOWTON & AUSTIN 1994, 2001; DOWTON et al. 1997). The most comprehensive of these (2001) employed sequence data from three genes (16S and 28S rDNA and COI) and 84 exemplar taxa representing all apocritan superfamilies. Under different models of analysis a number of relationships were consistently recovered (Fig. 3), including a monophyletic Proctotrupomorpha (excluding Ceraphronoidea), the monophyly of Diapriidae + Monomachidae + Maamingidae (a family recently described by EARLY et al. 2001), Vanhorniidae + Proctotrupidae, and Megalyridae + Trigonalidae. Further, Chalcidoidea + Platygastroidea were recovered as sister groups except under the simplest model, the Proctotrupeoidea was always polyphyletic, and the Ichneumonoidea was often not resolved although this is likely due to very different A-T content between braconid and ichneumonid mitochondrial genes. Like SHARKEY & ROY (2002), what is not evident from this study is a stable backbone to the apocritan tree below the Proctotrupomorpha (i.e., the basal relationships).

To date, all studies on apocritan phylogeny have been limited in some way. Most important limitations are that (1) many of Rasnitsyn's characters (employed by RONQUIST et al. 1999 and in part by SHARKEY & ROY 2002) are not clastic in nature (i.e., states often not properly separated as discrete entities amenable to cladistic analysis, partly discussed by SHARKEY & ROY 2002); (2) numerous morphological characters have been coded for hypothetical ground-plan taxa, not exemplars; (3) morphological nomenclature is often not standardised and the identification of homologous structures is sometimes problematic; (4) data from numerous post-Rasnitsyn anatomical studies on 'new' character systems have not been incorporated; (5) at least 16 apocritan families are thought to be paraphyletic or polyphyletic, 14 of which are contained within just three superfamilies – Proctotrupeoidea, Chalcidoidea and Apoidea; (6) taxon sampling for molecular studies has been minimal

given the species richness and biological diversity of many groups; and (7) there have been general discrepancies/problems in combining and analysing independent datasets (see CARPENTER & WHEELER 1999 for discussion).

Future studies

Where to now? In July 2003 the U.S. National Science Foundation announced the funding of a 'Tree of Life' project whose primary aim is to undertake a large-scale, fully integrated phylogenetic analysis of the Hymenoptera employing more than 500 morphological characters and sequences from five genes for a large number of exemplar taxa. The project will run for five years, will involve 30 research staff and graduate students and will focus on the family level for the whole order and at the subfamily level for the taxon-diverse Aculeata, Chalcidoidea and Ichneumonoidea. This task will require an unprecedented level of scientific cooperation and project management, but the outcome is likely to be a robust phylogeny that will serve as an evolutionary framework to support future research on the Hymenoptera for many years to come.

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Phylogeny of Trichoptera

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Trichoptera (caddisflies) comprise the largest order of aquatic insects and occur in rivers, streams, and lakes around the world. They are known for the remarkable cases and silken nets built by the aquatic larvae. Larvae are integral components of aquatic ecosystems and also key species for assessing water quality in biomonitoring programs. There are some 45 families of Trichoptera, represented by about 12,000 described species.

The monophyly of Trichoptera is well supported by a number of morphological characters such as the modified hypopharynx (= haustellum) of the adult and the apneustic aquatic larvae with reduced antennae and absence of abdominal prolegs (except the terminal pygopods). Monophyly of Trichoptera, as well as its sistergroup relationship to Lepidoptera, also consistently results from molecular analyses. Despite the long interest in the biology and natural history of the order, monophyly of the three trichopteran suborders (Annulipalpia, the fixed-retreat makers; Integripalpia, the portable-case makers; and Spicipalpia, the closed-cocoon makers) and their relative phylogenetic relationships was unsettled, with several quite different hypotheses having been presented.

The crux of the problem centers on the monophyly of Spicipalpia (included families Rhyacophilidae, Hydrobiosidae, Glossosomatidae, and Hydroptilidae) and its relationship to the other suborders (each monophyletic in all hypotheses) as either paraphyletic and allied to Integripalpia (ROSS 1967), monophyletic and allied to Annulipalpia (WEAVER 1984), monophyletic and basal within the order (WIGGINS & WICHARD 1989), or variously polyphyletic (FRANIA & WIGGINS 1997; IVANOV 2002). MORSE (1997) provided a summary of these hypotheses as well as a review of phylogenetic research within the order.

Using combined and partitioned analyses of molecular and morphological data, we previously established the phylogenetic relationships among the three trichopteran suborders as Annulipalpia + (Spicipalpia + Integripalpia) (KJER et al. 2001, 2002), reflecting the hypothesis originally proposed by ROSS (1967). We tested this hypothesis with additional data. Taxa were added to the analysis, and gene fragments that had been missing in our original analysis were completed. Taxa with substantial missing data were removed, as was the EF-1 α data (which was missing for most taxa). The program 'MrBayes 3.0' (HUELSENBECK & RONQUIST 2001) now implements mixed models that permit more realistic combined analyses. We analyzed our data under a combined analysis of the different partitions, each analyzed according to its own model, including the MK model for morphological characters (LEWIS 2001), and a doublet model for paired sites in rRNA (SCHÖNIGER & VON HAESELER 1994). We included data from nuclear rRNA fragments (28S, D1, D3 and 18S, V4-V5), insertions and deletions from the rRNA data, a COI mitochondrial DNA fragment, and morphological characters previously presented by FRANIA & WIGGINS (1997). Analysis of 138 taxa revealed the same relationships among the suborders as we previously reported.

The monophyly of Spicipalpia, while unlikely, is still equivocal. The higher taxa among Integripalpia include monophyletic Plenitentoria and Brevitentoria. Within Brevitentoria, Sericostomatoidea is strongly supported, but

a monophyletic Leptoceroidea is still not recovered, although it cannot be strongly rejected. Relationships within Annulipalpia, when the morphological data of FRANIA & WIGGINS (1997) are included, closely match the higher level structure reported by these authors, with monophyletic Philopotamoidea and Hydropsychoidea; our results differ only in the placement of some of the hydropsychoid families. Thus, the implementation of more realistic models, combined with additional taxa and data, did not substantially alter our original conclusions. For the most part, support indices remained strong where they had been strong, and weak where they had been weak. Support for more apical family groups, particularly among Linnephiloidea, 'Leptoceroidea', and Sericostomatoidea remains low, and will probably require additional characters, rather than a more dense taxon sampling, to resolve these relationships with any degree of confidence.

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Resolving the Basal Phylogeny of Lepidoptera: Morphological Evidence

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Introduction

As many as some 98–99 % of the currently described (ca. 150,000) species of Lepidoptera pertain to the subordinate clade Ditrysia, whose members are structurally overall uniform. In contrast, the lineages constituting the remaining tiny fraction of extant lepidopterans exhibit a remarkable morphological diversity, spanning the gap between the ‘ordinal’ ground plan with overall very generalized endopterygote characters and the ditrysiian ground plan with its considerable ‘derivation load’. The non-ditrysiian grade is currently considered a model case of a ‘Hennigian comb’, the constituent principal extant clades of which apparently arose in several successive splitting events (Fig. 1). Lepidopteran monophyly is strongly supported by 20+ morphological synapomorphies of the order’s basal constituent lineages; this includes the dense scale vestiture of the wings, a protibial epiphysis for antennal grooming, a posteromedian process on the tentorial bridge, an apodemal process issued from the mesothoracic pleural ridge below the wing process, and non-nucleated ‘parasperm’ present in addition to normal ‘eusperm’.

The non-glossatans

Three currently recognized extant moth families, Micropterigidae (150+ species), Agathiphagidae (2 species) and Heterobathmiidae (9 species), have retained short, generalized maxillary galeae, hence they are outside the clade Glossata, which comprises all other Lepidoptera and for which the coilable proboscis formed by linked galeae is the most conspicuous groundplan autapomorphy. In these three families movable mandibles are retained throughout adult life (but it remains uncertain whether adult agathiphagids feed at all).

Morphological evidence bearing on the basal split within the Lepidoptera is ambiguous: either the Micropterigidae or Agathiphagidae are the sister group of the rest of the ‘order’. The former solution is here preferred, because the derived character states shared by non-micropterigids include some noteworthy neoformations (including a muscle-accommodating process of the metafurcal stem, perhaps a double-compartment spermathecal duct, and a unique larval head-flattening muscle), while those shared by non-agathiphagids are regressive traits (loss of vein M4, loss of protibial spur and one pair of mesotibial spurs, reduced ovariole number, small size of testes follicles) exclusively.

Since paraspermatozoa are absent in the examined *Micropterix* the question has been asked whether this genus is actually the sister group of all remaining Lepidoptera, and the family Micropterigidae as currently delimited hence paraphyletic. However, *Micropterix* does possess a suite of apomorphies (including, e.g., antennal ‘ascoïd sensilla’, close-set radial folds around male gonopore and, particularly, a unique larval trunk histology) which seemingly provides strong support for micropterigid monophyly. The absence of parasperm in the genus is therefore in all probability an autapomorphy.

The next split is apparently between agathiphagids and the rest; the sistergroup relationship between heterobathmiids

and Glossata is supported primarily by shared noteworthy specializations of the larval head, such as the adfrontal and hypostomal sulci and the medially opened hypostomal/postgenal bridge. The Heterobathmiidae are the first lepidopteran clade whose members consistently depend on angiosperm plants throughout the life cycle.

Basal Glossata

The restructuring of the adult mouth apparatus in the glossatan ground plan involves, besides the formation of the galeal proboscis, also a suite of regressive traits (loss of mandibular articulations, of the strong epistomal sulcus/ridge, etc). Some noteworthy glossatan groundplan neoformations are unrelated to the adult feeding mode: incorporation of adult’s tritocerebral commissure in suboesophageal mass, and development of larval spinneret.

The first three glossatan splitting events are apparently, in sequence, (1) between Eriocraniidae and the rest (characterized, i.a., by a specialized wing scale vestiture and specialized 1st thoracic spiracles); (2) between Acanthopteroctetidae and the rest (characterized, i.a., by produced meso-‘basisternum’); and (3) between Lophocoronidae and the rest, known as Myoglossata and characterized primarily by the development of an inner musculature in the proboscis. The basal split within the Myoglossata was apparently between the Neopsustidae and the rest, collectively known as the Neolepidoptera and characterized in the ground plan by dissociation of the metathoracic aorta from the ‘wing heart’, by adecticous and obtect pupae, and perhaps by ‘typical’ caterpillars with the crochet-bearing prolegs on III–VI & X (the unknown neopseustid larvae may, of course, prove to be of the same type, but since the adults have retained strong mandibular muscles, the similarly unknown pupae are surely decticous and likely exarate). And the basal split within the Neolepidoptera was apparently between the Exoporia (including the first lepidopteran family-group taxon with several hundreds of species, viz., the Hepialoidea) and the rest, the time-honoured taxon Heteroneura characterized, i.a., by a simplified hindwing radial sector.

The outlined basal phylogeny of the Lepidoptera (KRISTENSEN & SKALSKI 1998; KRISTENSEN 1998a, b) is reasonably well supported, but not without problems (homoplasies). For instance, it requires that neolepidopteran pupal adecticousness must have been paralleled in Lophocoronidae, and some thoracic specializations (proprecoxal bridge, prospinasternum contiguous with meso-basisternum) have been independently evolved in Neopseustidae and stem-lineage Heteroneura.

The basal phylogeny within the Heteroneura has proved difficult to unravel. Recently accumulating morphological evidence (KRENN & KRISTENSEN 2000; KRISTENSEN 2000; LUKHTANOV 2001) supports the monophyly of a clade Eulepidoptera, which excludes the Nepticuloidea (and perhaps the very recently established family Andesianidae). Moreover, this new evidence indicates that at least the Tischeriidae are more closely related to the Ditrysia than the Incurvarioidea are. It must be noted, though, that apomorphies in embryonic development (absence of thickened

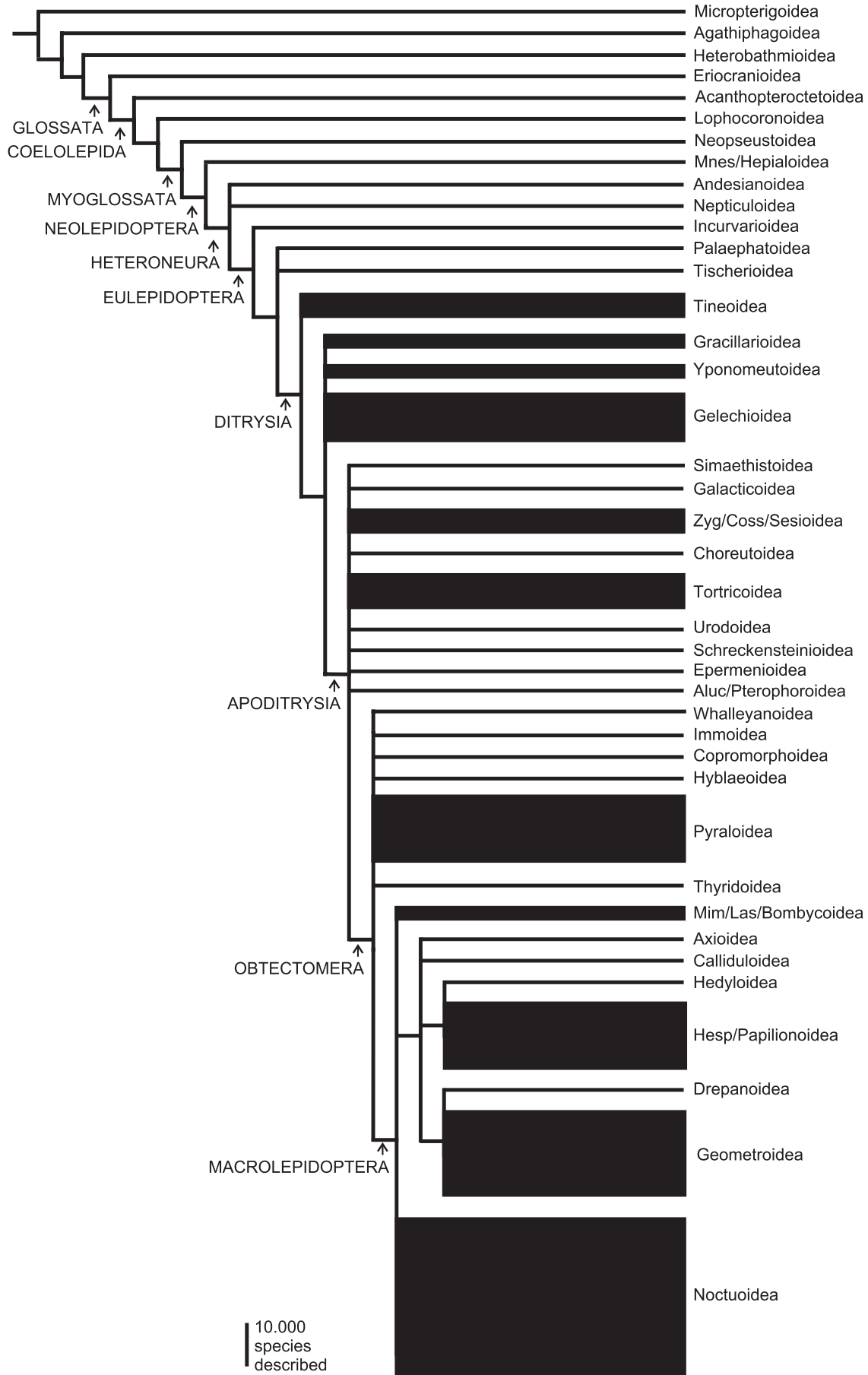


Fig. 1. Phylogeny of extant lepidopteran superfamilies. Width of extant superfamily lines indicate approximate numbers of described extant species (where these numbers exceed 1000). Eulepidopteran monophyly and *all* proposed groupings above superfamily level in the Ditrysia must be considered *very* tentative. Redrawn (updated/corrected) from KRISTENSEN & SKALSKI (1998).

serosal cells, embryo remaining immersed in yolk until immediately before hatching) indicate the monophyly of a nepticuloid/ditrysiian assemblage excluding incurvarioids (KOBAYASHI 1997).

MINET'S (1991) suggestion that three major, successively less inclusive and internally partly/largely unresolved, subordinate clades (Apoditrysia, Obtectomera and Macrolepidoptera) can be recognized within the Ditrysia remains state-of-the-art, its tentative nature notwithstanding. Forthcoming morphological work on selected character complexes will likely add resolution to the heteroneuran family tree in the next few years, and obviously integration with molecular evidence should be the ultimate goal.

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A Comprehensive Phylogeny of Mecoptera and Siphonaptera

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Phylogenetic relationships among Mecoptera and Siphonaptera were inferred from molecular data for a wide range of exemplar taxa and a coded morphological matrix. Every mecopteran family and nearly every mecopteran genus was included in this analysis, for a total of ~125 species representing 1/5 of mecopteran species diversity. Additional taxa representing 11 flea families and outgroups were included. Genes sequenced include 18S rDNA, 28S rDNA, cytochrome oxidase II, and cytochrome B. A morphological matrix consisting of 75 characters coded at the generic level was also generated. These data were analyzed in a total evidence framework via direct optimization on an IBM SP2 supercomputer.

These analyses support the monophyly of every mecopteran family. The clades Nannochoristidae, Boreidae + Siphonaptera, and the remaining Mecoptera are supported as mono-

phyletic groups. However, resolution among these three clades is still under investigation. Boreidae is placed as sister group to Siphonaptera, and this result is congruent with a number of characters associated with ovariole structures and other features. Panorpidae is sister to Panorpididae, and relationships within Panorpidae are partially congruent with the designated species groups. The genera *Panorpa* and *Bittacus* are each grossly paraphyletic. There is overall congruence between the morphological and molecular data partitions. These data support the paraphyly of Mecoptera with regards to fleas, and that Boreidae should be recognized as its own distinct order ('Neomecoptera'). If Nannochoristidae is supported as sister to the clade (Boreidae + Siphonaptera) + remaining Mecoptera, then ordinal designation for Nannochoristidae ('Nannomecoptera') is also warranted.

Preliminary Phylogeny of the Siphonaptera

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Siphonaptera (fleas) is comprised of approximately 3000 described species and subspecies, of which 2525 are considered valid (LEWIS 1998). While it is clear that the order is monophyletic, there has yet to be a formal quantitative analysis of flea phylogenetic relationships. LEWIS (1998) proposed a classification based on 15 families, avoiding a superfamilial classification. MEDVEDEV (1994) performed a mental analysis of morphology for 52 genera based on cha-

acters associated with the head, thorax, and terminalia. We present a robust phylogeny for the order Siphonaptera based on a combination of molecular and morphological data. Our taxon sampling for the molecular work is comprised of ~150 flea species which represent 11 of the 15 families, 23 of 28 subfamilies, and ~5 % of all described species. Genes sequenced include 18S rDNA, 28S rDNA, cytochrome oxidase II, and cytochrome B for a total of ~6425

nucleotides per taxon. The morphological matrix is comprised of 56 discrete morphological characters coded for representatives of all families and subfamilies, and 11 of these were treated as multistate unordered characters. These data were analyzed on an IBM SP2 supercomputer using direct optimization as implemented in POY. The majority of the branches received high bootstrap and Bremer support values.

These data are somewhat equivocal as to which taxon is the basal most flea. Ceratophylloidea (= Ceratophyllidae + Ischnopsyllidae + Leptopsyllidae), Ceratophyllidae, and Ischnopsyllidae are supported as monophyletic groups, but Leptopsyllidae is paraphyletic in regards to Ischnopsyllidae and Ceratophyllidae. Pulicidae is paraphyletic with the enigmatic *Tunga* placed elsewhere on the topology.

Ctenophthalmidae is grossly non-monophyletic with major groups placed in at least four different positions on the topology. In summary, these data suggest that roughly half of the families, a third of the subfamilies, and a fifth of the flea genera which were studied in the analysis constitute non-monophyletic groups.

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Phylogeny of True Flies (Diptera): a 250 Million Year Old Success Story in Terrestrial Diversification

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The insect order Diptera (true flies) is one of the most species rich, anatomically varied and ecologically innovative groups of organisms, making up around 12 % of the known animal species. An estimated 125,000 species of Diptera have been described, however, the total number of extant fly species is many times greater. The living dipteran species have been classified into about 10,000 genera, 150 families, 22–32 superfamilies, 8–10 infraorders and 2 suborders (YEATES & WIEGMANN 1999).

The monophyly of Diptera is well established. HENNIG (1973) lists 37 autapomorphies some of which form morphologically complex structures such as the specialized mouthparts adapted for sponging liquids. Traditionally, the best-known autapomorphy is the transformation of the hind wings into halteres, but this character may now be in need of reinterpretation due to recent phylogenetic research suggesting a sistergroup relationship between Strepsiptera and Diptera (WHITING et al. 1997). This work implies homology between the Diptera halteres and Strepsiptera pseudohalteres. The sister group of Diptera remains unknown. Morphology suggests either Mecoptera, Siphonaptera, or a monophylum consisting of both, but based on the aforementioned molecular evidence the Strepsiptera has to be added to the list of candidate taxa. The first fossils attributable to Diptera are known from the Permian, and a large number of fossil Diptera are known from the Mesozoic (YEATES & WIEGMANN 1999).

Phylogenetic work in the strict sense on Diptera began with HENNIG (1973) and GRIFFITHS (1972). Only recently, numerical analyses have started to address the relationships within higher-level taxa. Although molecular data has been used increasingly to reconstruct dipteran phylogeny, most published analyses to date have focussed on questions at a lower level, generally within particular infraorders. An exception is a recent detailed analysis of Brachycera relationships using over 2 kb of 28S rDNA (B. Wiegmann in prep.). The results of the last 30 years of phylogenetic research on the higher-level relationships of the Diptera using morphological data have been synthesized by us using supertree techniques. This Diptera supertree (Fig. 1) forms the framework for the following discussion.

The supertree generally supports recent research and shows that major dipteran higher categories such as Brachycera, Eremoneura, Muscomorpha, Cyclorrhapha, Schizophora, and Calyptrata are monophyletic. Conversely, a number of traditional higher taxa are paraphyletic based on morphological and molecular data. These include the Nematocera, Orthorrhapha, and Aschiza. We therefore prefer to use the informal terms Lower Diptera, Lower Brachycera and Lower Cyclorrhapha for these groups. They represent evolutionary grades at the base of major radiations of Diptera, Brachycera, and Cyclorrhapha, respectively.

The paraphyly of the Lower Diptera has been suspected for decades, beginning with Hennig, and demonstrated in recent quantitative cladistic analyses using morphological data (OOSTERBROEK & COURTNEY 1995). There have been only a few comprehensive phylogenetic analyses of the relationships between lower dipteran families using morphological and especially molecular data. The position of the tipulids and their relatives has been very unstable; some morphological treatments consider them the basal lineage of Diptera (HENNIG 1973), while others consider them to be closely related to Brachycera (OOSTERBROEK & COURTNEY 1995). The supertree analysis currently favors Ptychopteromorpha + Culicomorpha as the sister group to the remaining Diptera with Blephariceromorpha and Bibionomorpha being the next lineages to emerge from the lower dipteran stem. Close to the grade transition to Brachycera, the lower dipteran infraorders are not monophyletic, with Psychodomorpha and Tipulomorpha forming a paraphyletic grouping, the superfamily Tipuloidea being sister to the Brachycera. The arrangement of Tipulomorpha and Psychodomorpha represents a resolution of the incongruence between input trees.

The Brachycera is certainly a monophyletic group, with a large number of undisputed autapomorphies. The phylogeny of the Lower Brachycera has been scrutinized intensively over the past 15 years. A recent quantitative reanalysis of morphological characters used to define relationships between the lower brachyceran families attempted to summarize and synthesize this research (YEATES 2002). This study revealed weak evidence for the monophyly of a clade

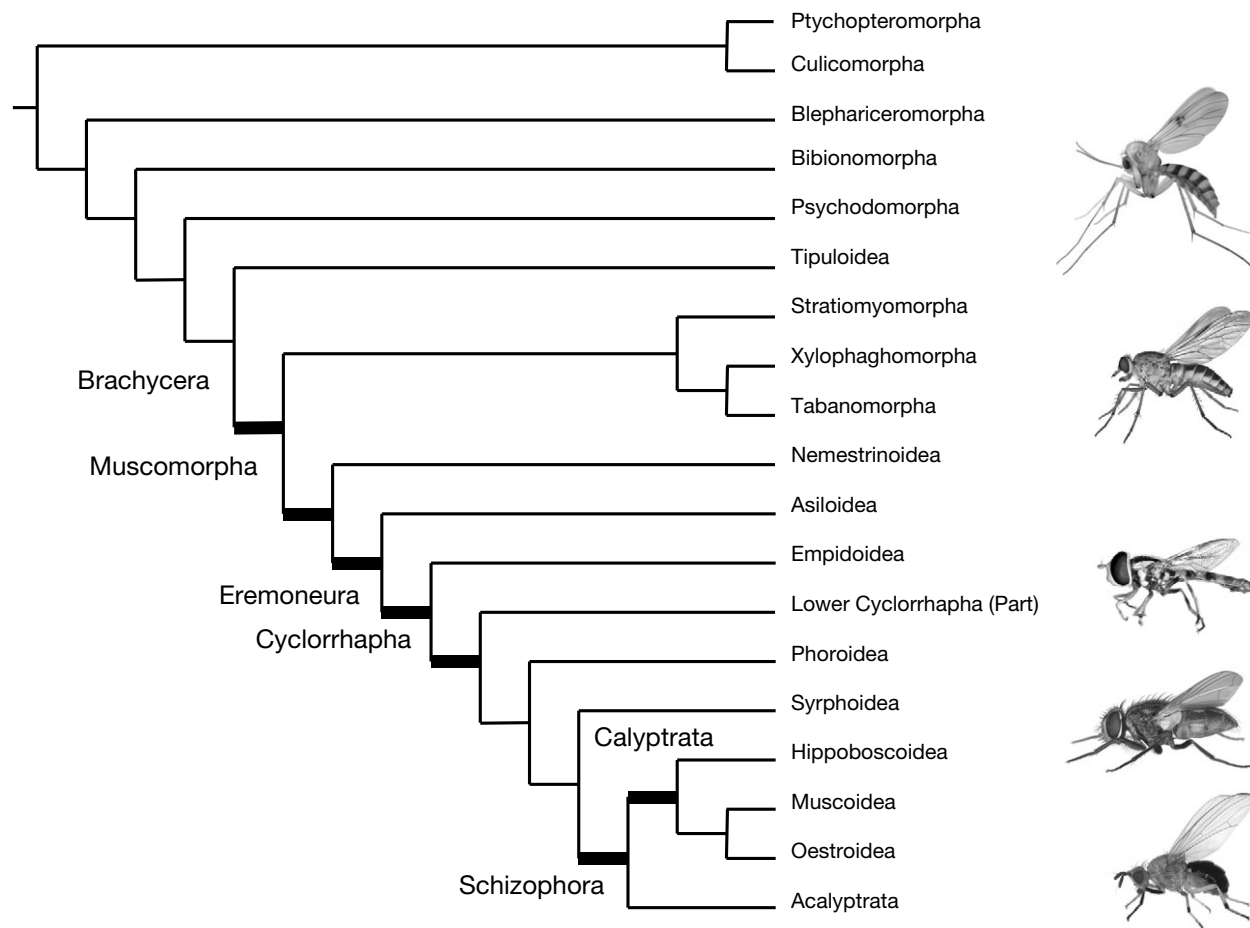


Fig. 1. A phylogenetic tree for Diptera resulting from a supertree analysis of fly families summarized at the infraorder/superfamily level. The analysis was based on an MRP coded matrix of 12 primary source trees including GRIFFITHS (1972), HENNIG (1973), MCALPINE (1989), OOSTERBROEK & COURTNEY (1995) and YEATES (2002). For more details contact the senior author.

containing Xylophagomorpha, Stratiomyomorpha and Tabanomorpha, and these findings are reflected in the supertree. The most basal lineage of Brachycera in the supertree analysis contains Stratiomyomorpha + (Xylophagomorpha + Tabanomorpha), reflecting the results of recent quantitative cladistic analyses.

The infraorder Muscomorpha contains all brachyceran families except those belonging to Stratiomyomorpha, Xylophagomorpha and Tabanomorpha, and is a well-supported clade found on the supertree. The Nemestrinoidea, Asiloidea and Empidoidea are monophyletic, arising from the main stem of the Brachycera in that sequence. Evidence for the monophyly of nemestrinoids and asiloids is not strong, and they appear paraphyletic in some analyses. A number of asiloid families have received critical phylogenetic scrutiny in recent years, partly because of their proximity to Eremoneura.

Eremoneura is the muscomorphan lineage containing Empidoidea + Cyclorrhapha, and is one of the best-supported higher-level brachyceran clades with many autapomorphies. Recent morphological work has emphasized male genitalic characters for phylogenetic reconstruction in Eremoneura, however some analyses of molecular data are beginning to appear. There is strong evidence for the monophyly of the Empidoidea and its subgroups Atelestidae, Hybotidae, Empididae and Microphoridae + Dolichopodidae from both morphological and molecular data.

Cyclorrhaphan monophyly is well supported by characters such as the invagination of the larval head capsule and modifications of the larval mouthparts, as well as pupation within the skin of the last larval instar. These are the most

recognizable features of this landmark in dipteran evolution. Over the last 40 years only three workers have attempted to synthesize phylogenetic evidence on cyclorrhaphan relationships in a comprehensive fashion. All studies were not based on explicit data sets and results differed in many regards (HENNIG 1973; GRIFFITHS 1972; MCALPINE 1989). Exploration of new character systems applied broadly across cyclorrhaphan groups, for example of egg and larval morphology, female genitalia and internal morphology, and nucleotide sequences are urgently needed. There are a number of competing hypotheses regarding the relationships of the families belonging to the lower cyclorrhaphan grade, but the Syrphoidea are generally regarded the sister group to the Schizophora.

The monophyletic Schizophora are classified into at least 80 families and comprise just over half the family-level diversity in Diptera. Major reviews of Schizophora phylogeny are the synthetic revisions by GRIFFITHS (1972) and MCALPINE (1989), which provided new information while building on Hennig's earlier research. GRIFFITHS (1972) provided detailed interpretation and scorings of male genitalic characters along with other morphological features, and MCALPINE'S (1989) fully resolved phylogenetic arrangements draw on most morphological character systems as well as fly biology. Based on calypter morphology the Schizophora have been traditionally subdivided into the Acalyptratae and Calyptratae, but it has long been recognized that the calypter is too variable in both groups to be a reliable phylogenetic marker. Although Acalyptratae is supported on our supertree it is generally regarded as being paraphyletic.

MCALPINE (1989) divided the Acalyptratae into 10 superfamilies and these are found in the supertree: Nerioidae, Diopsoidea, Conopoidea, Tephritoidea, Lauxanioidea, Sciomyzoidea, Opomyzoidea, Sphaeroceroidea, Carnoidea, and Ephydroidea. Only a few superfamilies are uncontentious (e.g., Ephydroidea, Tephritoidea) while the remaining will probably see some major rearrangements after more intensive phylogenetic scrutiny. Generally, MCALPINE's (1989) classification maintains HENNIG's (1973) groupings while GRIFFITHS (1972) proposes a more radical restructuring. In contrast to the Acalyptratae and despite the lack of complex morphological autapomorphies, the Calyptratae appear monophyletic based on molecular and morphological evidence. Of the three superfamily-level taxa, the Hippoboscoidea are monophyletic, the Oestroidea may be monophyletic, while the Muscoidea is likely paraphyletic. Advances in understanding the relationships of flies will accelerate with the increasing use of molecular data and quantitatively analysed data matrices. The most important areas for future phylogenetic research in the Diptera are in the Lower Diptera and Schizophora. In the Lower Diptera, resolving the relationships between the infraorders and the position of the craneflies and their relatives (Tipulidae) are critical tasks. The Schizophora also await more focused phylogenetic scrutiny applied to relationships between, and within, the superfamilies as they are currently defined.

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