Four chapters about the monophyly of insect 'orders': A review of recent phylogenetic contributions

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Abstract. Recent phylogenetic analyses, both morphological and molecular, strongly support the monophyly of most insect 'orders'. On the contrary, the Blattaria, Psocoptera, and Mecoptera are definitely paraphyletic (with respect of the Isoptera, Phthiraptera, and Siphonaptera, respectively), and the Phthiraptera are possibly diphyletic. Small relictual subclades that are closely related to the Isoptera, Phthiraptera, and Siphonaptera were identified (Cryptocercidae, Liposcelididae, and Boreidae, respectively), which provides an enormous amount of evidence about the origin and early evolution of the highly apomorphic eusocial or parasitic ex-groups. Position of the enigmatic 'zygentoman' *Tricholepidion* Wygodzinsky, 1961, remains uncertain. Possible non-monophyly of the Megaloptera (with respect of the Raphidioptera) and the Phasmatodea (with respect of the Embioptera) are shortly discussed.

Key words. Insecta, Zygentoma, *Tricholepidion*, Blattaria, Isoptera, *Cryptocercus*, Psocoptera, Phthiraptera, Liposcelididae, Mecoptera, Siphonaptera, Boreidae, Nannochoristidae, *Timema*, phylogeny, monophyly

Introduction

The goal of modern systematics is twofold: to provide a biological '*lingua franca*' that facilitates an exchange of information among researchers, and to provide a hierarchical system that is meaningful in the context of our understanding of phylogenetic history. However, both goals are often in conflict. Phylogenetics is about a nested hierarchy of *clades*, without any privileged 'rank' (like 'order' or 'family'). Traditional Linnean hierarchy, though superficially similar, is about *names* and *ranks* of the selected taxa which are 'so important' to deserve formal designation. However, there are no absolute ranks (a 'genus' of flies is not comparable in any way with a 'genus' of mammals), and the recent developments in systematic biology are

evidently directed towards the rankless phylogenetic classification. On the contrary, biology textbooks are still contaminated by 'orders' and 'classes', however they are scientifically misleading and hated by students. Consequently, some taxa are somewhat 'more equal than others': it seems to be more important to discover a new insect 'order' (e.g., the Mantophasmatodea; KLASS et al. 2002) than a new insect 'family' (e.g., the Meruidae; SPANGLER & STEINER 2005). It is much more interesting if an 'order' is found unnatural (i.e. non-monophyletic) than a 'superorder' or a 'suborder' (compare the emotional distress concerning the non-monophyly of, e.g., the Blattaria, Polyneoptera, and Troctomorpha, respectively).

There are about 30 'orders' of the true insects, the Ectognatha, in the recent literature (note that there are no 'orders' in the nature). They are the Archaeognatha, Zygentoma, Ephemeroptera, Odonata, Plecoptera, Dermaptera, Zoraptera, Mantodea, Blattaria, Isoptera, Grylloblattodea, Mantophasmatodea, Orthoptera, Phasmatodea, Embioptera, Psocoptera, Phthiraptera, Thysanoptera, Hemiptera, Neuroptera, Megaloptera, Raphidioptera, Coleoptera, Strepsiptera, Mecoptera, Siphonaptera, Diptera, Trichoptera, Lepidoptera, and Hymenoptera.

In the present paper, recent contributions concerning the phylogenetic position of several important insect groups will be discussed, with a special emphasis to taxa whose phylogeny-based placements seem to cause disintegration of some of the conventional textbook 'orders' (namely the Zygentoma, Blattaria, Psocoptera, Phthiraptera, and Mecoptera).

I dedicate the present review to my friend Professor Pavel Štys in recognition of his outstanding contribution to our knowledge of insect morphology and phylogeny. He was probably the first worker who inserted cladistic reasoning in general and the insect phylogenetics in particular to the Czech (Czechoslovak) literature and thus inspired the birth of the Czech phylogenetic school in the early 1990s.

Archaeognatha, Euzygentoma, and *Tricholepidion*: one more insect 'order'?

As both groups of the primarily wingless true insects, the bristletails (Archaeognatha) and the silverfish (Zygentoma), are superficially similar morphologically, they were united in one group ('Thysanura'). It has long been known, however, that the bristletails are in general more basal and that the silverfish are more closely related to the winged insects (together forming the Dicondylia) than to the bristletails.

It may be that things are not that simple. The apparently primitive zygentoman family Lepidotrichidae was originally described from the mid-Eocene Baltic amber genus *Lepidotrix* Menge, 1854, and is now represented by a single living species, *Tricholepidion gertschi* Wygodzinsky, 1961, from northern California. The family Lepidotrichidae itself may not be monophyletic, since *Tricholepidion* Wygodzinsky, 1961 (the only zygentoman with distinct ocelli) may be more primitive than *Lepidotrix* and less closely related to the Euzygentoma (= Nicoletiidae s. lat. + Lepismatidae + Maindroniidae). The Lepidotrichidae possess large abdominal sterna with posteriorly attached coxopodites, and a large number of pregenital abdominal styli and eversible sacs. Five characters have been proposed to support intra-zygentoman position of *Tricholepidion* (see GRIMALDI & ENGEL (2005) and references therein).

They include (i) unique sensillar structures on the terminal filament (shared by *Tricholepidion* and the Nicoletiidae), (ii) a widened apical segment of the labial palp, (iii) obliteration of the superlingua, (iv) mating behaviour (the male deposits a spermatophore on a web which he has spun during the final phase of foreplay; the female picks up the spermatophore using her ovipositor; see STURM (1997)), and (v) sperm conjugation (putatively shared by *Tricholepidion* and the Lepismatidae). However, even in the nicoletiids (*Atelura* Heyden, 1855), sperm bundles are stored in the proximal part of the testes, intermingled with dense granules and forming the so called 'spermatolophids'. Sperm aggregation in the Zygentoma is, therefore, quite diverse (DALLAI et al. 2001a,b, 2002) and its phylogenetic interpretation is uncertain.

Tricholepidion has five-segmented tarsi, which is the presumed plesiomorphic condition for Pterygota, while both the Archaeognatha and the Euzygentoma have two- or three-segmented tarsi. Moreover, *Tricholepidion* ovaries are clearly primitive and archaeognath-like, being composed of seven metamerically arranged ovarioles (compare three or five non-metameric ovarioles in the Euzygentoma and the highly variable number and arrangement of ovarioles but no ovary metamerism in the Pterygota; ŠTYS et al. 1993) and including opaque granules in early vitellogenic oocytes (SZKLARZEWICZ et al. 2004).

A possible sister group relationship between *Tricholepidion* and the Euzygentoma + Pterygota has been raised by KRISTENSEN (1981), based on the retention of the intergnathal connective ligament in the Archaeognatha and *Tricholepidion*. A detailed analysis of the mandibles and mandibular musculature also corroborated the view that *Tricholepidion* is a basal dicondylian (STANICZEK 2000). BITSCH & BITSCH (1998, 2000, 2004) in their numerical analyses of morphological characters did not find any resolution of the representatives of the Zygentoma and of the Pterygota. BEUTEL & GORB (2001) performed a numerical analysis of 115 morphological characters and concluded that *Tricholepidion* represents a sister group of the Euzygentoma-Pterygota clade, the latter supported by a reduced size of the postocciput and reduced pleural folds, reduced ligamentous head endoskeleton, reduced transverse mandibular apodeme, presence of *musculus mandibulo-hypopharyngalis*, shortened maxillary palps, and reduced or absent pregenital vesicles and styli.

In molecular analyses, the position of *Tricholepidion* was highly unstable, ranging from conventional placement as a sister group of the Euzygentoma (MISOF et al. (2007): 18S ribosomal DNA) to an unorthodox intra-pterygote position next to the Odonata (KJER (2004), using the same molecular marker). Mitochondrial genomes have not yet been conclusive, evidently owing to poor taxon sampling, but they seem to support zygentoman monophyly (see COOK et al. 2005, CAMERON et al. 2006, CARAPELLI et al. 2006). GIRIBET et al. (2004) analyzed relationships among basal hexapods on the basis of a cladistic analysis of five genes and 189 morphological characters in a simultaneous analysis. Morphological characters solely corroborated monophyletic Zygentoma (*Tricholepidion* vs. Euzygentoma) but with very low support; the same applied to the multigene molecular analysis. Using a sensitivity analysis approach and testing for stability within the combined morphological-molecular analysis, the most congruent parameters resolved *Tricholepidion* as a sister group to the remaining Dicondylia (with very low support again), whereas most suboptimal parameter sets grouped *Tricholepidion* with the Euzygentoma. Finally, in the combined analysis by KJER et al. (2006), using eight gene sequences and 170 morphological characters, *Tricholepidion* appeared as a

sister group of the Euzygentoma.

The position of the enigmatic *Tricholepidion* remains controversial as none of the data sets provides substantial support for either of the two competing hypotheses (i.e. monophyletic or paraphyletic Zygentoma). It seems only clear that a sister-group relationship between *Tricholepidion* and the Nicoletiidae has not yet been supported by morphology and molecular analyses. By all means, *Tricholepidion* is the most promising candidate for a new insect 'order' (or, in other words, the only insect species whose ordinal classification remains uncertain), either as a sister group of the Euzygentoma, or of the Euzygentoma-Pterygota superclade.

Blattaria and Isoptera: the origin of eusociality

Termite societies are large, extended families with a characteristic division of labor and with only a few reproducing individuals within a colony. Termites (Isoptera) are the earliest-evolved eusocial insects, with their complex societies dating back to the Cretaceous (130 million years ago). They are closely related to the cockroaches (Blattaria) and mantids (Mantodea), forming a well-established clade, the Dictyoptera, uniquely defined by having a 'perforated' tentorium, proventriculus with six internal longitudinal plicae, asymmetrical male genitalia (in details of uncertain homology – see disputes of, e.g., GRANDCOLAS (1996) versus KLASS (2001)), and reduced ovipositor, and by enclosing their eggs with secretions from the colleterial glands within an ootheca (lost in most termites; see NALEPA & LENZ (2000), COURRENT et al. (2008); for termite phylogeny see INWARD et al. (2007a,b), LEGENDRE et al. (2008)). Within the Dictyoptera, there is agreement that both termites and mantids are monophyletic groups. Although the relative positions of these lineages is somewhat debated, the weight of the evidence strongly suggests that the termites are nested within the Blattaria, being just 'highly modified, social, myopic, wood-eating roaches', or 'citizen roaches' (GRIMALDI & ENGEL 2005). It is then clear how misleading it was to use termites as an outgroup in previous analyses of the blattarian phylogeny, which excluded them *a priori* from nesting within the cockroaches.

The morphology-based phylogeny of blattarian families was explored, e.g., by GRANDCOLAS (1996), GRANDCOLAS & D'HAESE (2001), KLASS (2001), and KLASS & MAIER (2006). The major contributions agree that the basalmost divergence is between the Blattidae (possibly paraphyletic; see KLASS (2001), KLASS & MAIER (2006) and references therein) and the rest of roaches, and that the Blattellidae and the Blaberidae form a clade. The Polyphagidae are placed somewhere between basal blattids and the blattelid-blaberid clade; the genus *Cryptocercus* Scudder, 1862, is the subject of the greatest disparity between the published phylogenies. By all means, it is related to the Polyphagidae, either as its deeply nested member (and consequently not related to the termites; see GRANDCOLAS (1993), GRANDCOLAS & DELEPORTE (1996)), or forming together with the termites a sister group of the polyphagids (see KLASS & MAIER 2006).

The relict wingless, long-lived, and social 'woodroach' *Cryptocercus* is then one of the most intriguing insect genera. There are several species living in forests of North America and East Asia. Usually a pair of parents and about 20 offspring inhabit galleries in a soft, rotten log, remaining together for at least three years (the brood care probably lasts until the death

of the adults), with larvae maturing in approximately six years (see NALEPA & BANDI (2000), KAMBHAMPATI et al. (2002) and references therein). The juveniles are pale, termite-like, with highly reduced eyes, and they feed on liquids exuded by an adult from the anus (proctodeal trophallaxis) for approximately their first year (1st and 2nd instars). This behaviour allows them to acquire symbiotic oxymonadid and hypermastigid protists, required for the digestion of wood. Young larvae actively groom older juveniles and adults.

An overwhelming molecular evidence from recent years (LO et al. 2000, 2003, 2007; TERRY & WHITING 2005; KJER et al. 2006; PELLENS et al. 2007; INWARD et al. 2007a; LEGENDRE et al. 2008; WARE et al. 2008) shows that the Isoptera are a sister group of *Cryptocercus*. The most comprehensive molecular analysis by INWARD et al. (2007a) included 107 species of the Dictyoptera (five of the 15 mantid families, all six cockroach families as well as 22 of the 29 cockroach subfamilies, and all termite families and subfamilies), along with 11 outgroups, and five gene loci (two mitochondrial: 12S rDNA and cytochrome oxidase II, three nuclear: 28S rDNA, 18S rDNA, and histone 3). The Isoptera-*Cryptocercus* clade was found as sister to the Blattidae, and that combined clade as sister to the Blattellidae + Blaberidae. The Polyphago-idea (Polyphagidae + Nocticolidae) are then sister to all the other cockroaches (including the termites). Similar phylogenetic patterns have been received from an analysis of the bacterial intracellular symbionts (*Blattabacterium* Mercier, 1906) that reside in specialized cells of cockroaches and the basalmost termite *Mastotermes* Froggatt, 1897; the analysis found a close relationship between endosymbionts from termites and woodroaches (LO et al. 2003).

WARE et al. (2008) showed, using four gene loci (cytochrome oxidase II, 16S rDNA, 18S rDNA, and 28S rDNA) and morphological data for 62 species (including eight outgroups), that the choice of both outgroup and ingroup taxa as well as data partition greatly affects tree topology. Depending on the outgroup selection, the most basal splitting event within the Dictyoptera is either between the Mantodea and the Blattodea (cockroaches and termites), or between the Polyphagoidea and the rest of the Dictyoptera (including mantids). Within the non-polyphagoid Blattodea, the next problematic issue is the relationship among the Blattellidae + Blaberidae, Blattidae, and *Cryptocercus* + Isoptera (probably a sister group of the blattids).

This is in strong contrast to earlier hypotheses that assumed a position of the Isoptera outside a monophyletic Blattaria (THORNE & CARPENTER 1992) and a subordinate position of *Cryptocercus* inside the cockroach family Polyphagidae (GRANDCOLAS 1996). In all molecular analyses all included species of the Polyphagidae (LO et al. 2003, 2007; KJER et al. 2006; INWARD et al. 2007a,b; KLASS et al. 2008; LEGENDRE et al. 2008; WARE et al. 2008) clustered together unambiguously, while the whole polyphagid clade is remote from the *Cryptocer-cus*-Isoptera clade. Consequently, the hypothesis of *Cryptocercus* being deeply nested in the Polyphagidae (close to *Therea* Billberg, 1820) should eventually be dismissed. The only evidence that may still contradict a *Cryptocercus*-Isoptera clade is the analysis of hypertreha-losaemic neuropeptides from *corpora cardiaca* (GÄDE et al. 1997), but this is based on very few informative characters.

Morphologically, the sister-group relationship between *Cryptocercus* and Isoptera is based on the morphology of the proventriculus, dentition of the mandibles, possibly also detailed structure of the antennal segments, relatively small genome size (KOSHIKAWA et al. 2008), and

predominantly on numerous behavioural and ecological characters (see KLASS et al. (2008) for a review). They include shared (and unique) ability to nest in and ingest fairly recalcitrant dead wood sources that may take decades to degrade. All studied cockroach and termite species have endogenous cellulase genes, which suggests a widespread ability to use cellulose-based materials as food. Only *Cryptocercus* and lower termites, however, have an additional specific type of cellulose digestion that involves hindgut symbiotic flagellates, requiring vertical intergenerational transmission. *Cryptocercus* and lower Isoptera share many flagellates of the Oxymonadida and Hypermastigida (both Excavata) in their hindgut that are unique to them, such as the Spirotrichosomidae, Hoplonymphidae, Staurojoeninidae, and Eucomonymphidae. GRANDCOLAS (1999a,b) and GRANDCOLAS & DELEPORTE (1996) assumed that xylophagy and intestinal symbiosis in the Isoptera and *Cryptocercus* was a matter of convergence and/or horizontal transfer (gut flagellates could have been passed from termites to *Cryptocercus*). Interestingly, several groups of the hindgut flagellates are shared exclusively between *Cryptocercus* and different isopteran subgroups (*Leptospironympha* Cleveland, 1934 and the Spirotrichosomidae shared with the Stolotermitinae; *Oxymonas* Janicki, 1915, Hoplonymphidae and Staurojoeninidae shared with the Kalotermitidae, and the Eucomonymphidae shared with the Rhinotermitidae). The differences in hindgut flagellate faunas of the various termite subgroups have probably been caused by mosaic-like losses from the ancestrally complete set of oxymonadids and hypermastigids (even recent, intraspecific losses have been reported; see KLASS & MEIER (2006)). According to the lateral-transfer hypothesis, *Cryptocercus* should have obtained its gut fauna either through several additive tranfers from a variety of termite groups, or through a single transfer from the termite ancestor. If *Cryptocercus* were of Cenozoic origin (GRANDCOLAS 1999a,b), its physical contact with the isopteran stem lineage would be impossible; several parallel contacts between cryptocercids and termites leading to sequential collection of the *Cryptocercus* hindgut fauna are unparsimonious at best. Recently, OHKUMA et al. (2008), based on18S ribosomal DNA and glyceraldehyde-3-phosphate dehydrogenase sequences of the woodroach and termite trichonymphid symbionts (Hypermastigida), found that the symbionts of *Cryptocercus* were always robustly sister to those of termites. It strongly suggests that this set of symbiotic flagellates was already present in the common ancestor of *Cryptocercus* and the Isoptera.

As concerns their social behaviour, *Cryptocercus* and the Isoptera share monogamy, extended biparental care, allogrooming, and proctodeal trophallaxis. The *Cryptocercus*-like biparental sociality is also present in dealated pairs of termites during the early stages of colony foundation; the family switches to eusociality with the appearance of workers or pseudergates. The crucial difference in the sociality of *Cryptocercus* and termites is that only in the latter is the care and feeding of young brood taken over by older brood in the family. However, as a result of asynchronous hatching and the quick growth of neonates, both trophically dependent (1st and 2nd instars) and trophically independent nymphs (3rd and subsequent instars) can be contemporaneous even in young families of *Cryptocercus* (KLASS & MEIER 2006).

The finding that the termites are nested within the cockroaches causes a classificatory problem. INWARD et al. (2007a) proposed that the 'Isoptera' should no longer be used and that the species should be classified within the family Termitidae as part of the order Blattodea. This would mean that the existing termite taxa need to be downgraded by one taxonomic

rank (i.e. families become subfamilies, subfamilies become tribes etc.), a taxonomical acti-on that provoked strong counteraction ('Save Isoptera!'; Lo et al. 2007). In fact, there is no reason why not to preserve the well-known and widely used name 'Isoptera' regardless of its phylogenetic position; naturally, this problem is a direct consequence of using the basically non-phylogenetic Linnean rank hierarchy in the phylogeny-dominated modern systematics.

On the origin of lice: non-monophyletic Phthiraptera within non-monophyletic Psocoptera

Lice (Phthiraptera: Amblycera + Ischnocera + Rhynchophthirina + Anoplura) are permanent ectoparasites of birds and mammals that spend their entire life cycle on the body of the host. To understand the origins of parasitism and related morphological, physiological and behavioural specializations in lice, a reliable phylogenetic hypothesis of lice and related insects is required. The closest relatives of lice are book- and barklice (Psocoptera), the two groups comprising the clade Psocodea. The monophyly of Psocodea is supported by the specialized water vapour uptake system with a unique sclerotization of esophagus (sitophore sclerite), fusion of the cardo with the stipes, a modification of the basal part of their antennal flagellomeres to faci-litate rupture (Lyal 1985, Yoshizawa & Saigusa 2003), and molecular data (Wheeler et al. 2001, Yoshizawa & Johnson 2003, Johnson et al. 2004). Psocoptera are free-living insects, but there are many records of various species of the Psocoptera in the plumage of birds and pelage of mammals, as well as in their nests. This association is thought to be a short-term commensalism, which may have given rise to a permanent association in lice.

However, if so, the Psocoptera have to be paraphyletic with respect of the Phthiraptera. Monophyly of the Psocoptera has been usually doubted but Seeger (1979) found embryo-logical and egg structure characters suggesting that it is a natural taxon. Thus there are two competing hypotheses: (i) monophyletic Psocoptera are the sister group of the Phthiraptera or (ii) the Psocoptera are paraphyletic, and the sister group of the Phthiraptera must be placed somewhere within the Psocoptera. Each hypothesis was weakly supported morphologically and/or embryologically, and this problem has not been resolved prior to molecular phyloge-netics. The advent of the molecular phylogenetics has, however, also heavily complicated phylogeny of the Phthiraptera itself.

The monophyly of lice has long and widely been assumed because of their highly spe-cialized modifications for parasitism. Lyal (1985) described 19 character states which may support the monophyly of lice (see also Grimaldi & Engel 2005); however, 13 are losses strongly linked to the ectoparasitism on homeothermic vertebrates (e.g., the reductions of the labial palpi, antennal flagellum and compound eyes). Therefore such apomorphies may have easily evolved independently as a result of specialization to the parasitic lifestyle (but even if the Phthiraptera were polyphyletic, their 'subgroups' would be supported by the putatively 'convergent' autapomorphies, which means they, in fact, are good phylogenetic characters at some level). Six gain character states were identified as possibly supporting the monophyly of lice, but one (cementing of eggs to host pelage using glue-like spumaline that is secreted from the female accessory gland) is also correlated with the parasitic lifestyle. Dorsoventral compression of the head (and its partial to complete fusion to the thorax as well) is considered

to be a gain autapomorphy of lice, but this character state is shared by some psocopterans and thus cannot unequivocally support the Phthiraptera. The posteriad movement of the supraesophageal ganglion is considered to be strongly linked to the compression of the head. The other spermatological and developmental characters putatively supporting monophyly of the Phthiraptera (e.g., egg with a hydropile and operculum, and loss of the 4th larval instar) have not yet been studied in the 'louse-like psocopterans'. Only one character state, the development of a lacinial gland (present in the Amblycera, Ischnocera and Anoplura but absent in the Rhynchophthirina), may possibly support the monophyly of lice, if the putative homoplasies were to be *a priori* excluded from phylogenetic discussions. However, a weakly developed lacinial gland is observed in *Lepinotus* Heyden, 1850 (Psocoptera: Trogiomorpha), and the glands of the Liposcelididae and Pachytroctidae (both Psocoptera: Troctomorpha) have not been examined in detail. In summary, although the monophyly of lice has been accepted on the basis of many morphological characters, all apomorphies observed in lice are either correlated with parasitism or do not unambiguously support louse monophyly.

The Phthiraptera have traditionally been classified into two suborders, the biting lice (Mallophaga) and the sucking lice (Anoplura). Both morphological (Lyal 1985) and molecular (Cruickshank et al. 2001, Johnson & Whiting 2002, Barker et al. 2003) analyses support non-monophyly of the Mallophaga as well as monophyly of all phthirapteran suborders, i.e. the Amblycera, Ischnocera, Anoplura, and monogeneric Rhynchophthirina. Phylogenetic relationships among the four suborders of lice inferred from gene sequences are roughly the same as those inferred from their morphology: the Amblycera are the most distant group, the Rhynchophthirina are a sister group to the Anoplura, and the rhynchophthirine-anopluran clade is sister to the Ischnocera.

Yoshizawa & Johnson (2003) sequenced the 12S and 16S rDNA for five species of *Liposcelis* Motschoulsky, 1853, and found that the genus was embedded within lice. Johnson et al. (2004), based on sequences from the 18S rDNA (see also Barker et al. 2003, Murrell & Barker 2005), proposed that lice are actually polyphyletic, specifically that the Amblycera are closely related to the Liposcelididae and Pachytroctidae, and that all other lice are a sister group to these. It requires either a loss followed by re-development of free-living habits and traits such as wings, fully developed eyes, and ocelli in the liposcelids and pachytroctids, or – more probably – an independent origin of the parasitism in the Amblycera and in the Ischnocera-Rhynchophthirina-Anoplura clade.

The morphology of male genitalia in the Psocodea has been investigated in detail by Yoshizawa & Johnson (2006). They found that the Amblycera form a clade together with the Pachytroctidae and Liposcelididae, and are separated from the Ischnocera, Rhynchophthirina and Anoplura. Monophyly of the Ischnocera-Rhynchophthirina-Anoplura clade was supported by a partial fusion of the ventral plates and a broadened basal apodeme. In the Pachytroctidae, Liposcelididae and Amblycera, the posterodorsal corner of the basal plate, mesomere and ventral plate articulate at a point. In contrast, no apomorphic feature in the phallic organ which potentially supports the monophyly of lice was identified.

Both morphology and molecules thus seem to converge to a single phylogeny. Four groups of the Psocodea, namely, the Pachytroctidae (probably paraphyletic; see Johnson et al. (2004)), Liposcelididae, Amblycera, and the Ischnocera-Rhynchophthirina-Anoplura

clade, are closely related and together form a clade nested within the 'psocopteran suborder' Troctomorpha (which is basally split into 'infraorders' Amphientometae and Nanopsocetae, the latter including basal Sphaeropsocidae and the pachytroctid-liposcelidid-lice superclade). The other 'psocopteran' groups, Trogiomorpha and Psocomorpha, are probably monophyletic (YOSHIZAWA 2002, JOHNSON & MOCKFORD 2003, YOSHIZAWA et al. 2006), the former being a sister group of all other Psocodea, the latter a sister group of the 'Troctomorpha'-Phthiraptera clade.

LYAL (1985) pointed to the similarities between the Phthiraptera and the Liposcelididae that might indicate sister group relationships between them but concluded that they are most probably convergencies linked with the reduction or loss of the wings in both groups (like loss of ocelli, great reduction of eyes, reduction of the pterothorax, shortening of the antennae, reduction or loss of ctenidiobothria on the tarsi, and trichobothria on the genitalia). Liposcelidid wings are short and with vestigial venations; many liposcelidids are apterous. They inhabit tight spaces under bark and stones and amongst leaf litter; some commonly occur in mammal and bird nests or even amongst the feathers and fur. There are also features shared by the liposcelidids and lice that appear not to be convergently correlated with wing reduction. They include dorsoventrally flattened bodies, a prognathous head with greatly reduced or lost epicranial sutures, reduced labial palps, lost abdominal spiracles 1 and 2, and enlarged hind femora. The Amblycera and the Liposcelididae diverged at least 100 Mya, in which case the hosts of lice would have been early mammals, early birds, and possibly other feathered theropod dinosaurs as well as haired pterosaurs (GRIMALDI & ENGEL 2006). The Phthiraptera (mono- or diphyletic) probably did not significantly diversify until the large radiations of placental mammals and passerine birds that took place in the Tertiary.

Recent phylogenetic analyses have pointed out the possibility that both the Psocoptera and the Phthiraptera are not monophyletic. There are two possibilities to reclassify the Psocoptera and the Phthiraptera to reflect monophyletic groups: to divide them into several independent 'orders', or to recognize the monophyletic Psocodea as a single 'order'. However, to establish stable (sub)ordinal divisions within the Psocodea, more molecular and morphological analyses are required.

Mecoptera and Siphonaptera: death of one more, parasitic 'order'

Mecoptera (scorpion flies) are a small holometabolous insect 'order' (approximately 600 extant described species in nine 'families'). The living species of the Mecoptera represent a vestige of a long and diverse evolutionary history begining from the Permian period. Mecopterans have been defined by a medially divided 1st abdominal sternite, the female genital chamber formed by an invagination behind sternum 9, the bulbous male genital capsule with complex genitalia and large gonocoxites, a distinctive proventriculus lined with spicule-like acanthae, the fusion of clypeus and labrum, and the loss of some mouthpart muscles. The monophyly of each mecopteran family is well established by morphological characters. Relationships among the extant families have been analysed by WILLMANN (1987) and WHITING (2002a). Major areas of agreement include basal positions of the Nannochoristidae and Boreidae, and close relationships between the Panorpidae and Panorpodidae. The major

difference between the two hypotheses concerned the Bittacidae (either closely related to the Panorpodidae, or one of the most basal clades). The phylogenetics of Mecoptera has centered around two problematic families, the Nannochoristidae and Boreidae (= Neomecoptera).

The Boreidae ('snow fleas') is a small group of 26 species distributed throughout North America and Eurasia. Adults emerge in winter and are associated with mosses. Their wings are reduced to small flaps in females and to hooks in males, which function to clasp the female during mating.

The Nannochoristidae (eight species from Australia, New Zealand and temperate South America) have unusual, aquatic larvae, a pigmented larval 'eye spot', and unique wing venation characteristics. A possible sister group relationship with the Diptera was proposed (see KRISTENSEN (1999) and references therein; BEUTEL & BAUM (2008)), though most evidence (see below) indicates that nannochoristids are basal mecopterans and their resemblance to flies is based largely on plesiomorphies.

A clade comprising Mecoptera and Siphonaptera (fleas) seems to be well supported (e.g., BEUTEL & GORB 2001, WHITING 2002a,b). A presumably derived feature is the absence of the outer group of microtubuli in the sperm flagellum. Another potential synapomorphy is the specific configuration of the acanthae in the proventriculus. Other features supporting this hypothesis are unspecific reductions, such as, for example, the absence of the extrinsic labral muscles or the absence of labial endite lobes (for detailed analyses of head structures see BEUTEL & BAUM (2008) and BEUTEL et al. (2008)). However, the monophyly of the traditional order Mecoptera has been challenged recently. A sister group relationship between the Boreidae and the Siphonaptera is strongly supported by molecular data (WHITING 2002a,b) and a comprehensive combined analysis (75 morphological characters, 18S rDNA, 28S rDNA, cytochrome oxidase II, and cytochrome *b* (WHITING et al. 2003)). Once the molecular data suggested this relationship, a reevaluation of morphology demonstrated that this is a highly plausible hypothesis (see BEUTEL & POHL (2006) for reviews).

The process of resilin secretion in fleas (pleural arch) and *Boreus* Latreille, 1816 (wing base) is similar, and different from that of the locust and the dragonfly. Both groups share the ability to jump when disturbed (probably via a similar mechanism) and both often feign death after their leaps. The proventricular spines in fleas and boreids have similar morphology. Other features are the absence of extrinsic labral muscles, absence of arolium, elongation of the labrum and maxillolabium, reduced or lost ocelli, reduced or lost larval legs, and sexual dimorphism in the ventral nerve cord (males having more ganglia than females). Among mecopteroids, only fleas and boreids form silken pupal cocoons. Phylogenetic analysis of long-wavelength opsins from the three lineages (flea, snow flea, panorpid) revealed a high degree of similarity between flea and boreid opsins (TAYLOR et al. 2005). Both groups have multiple sex chromosomes and sperm axoneme coiling around the mitochondrion. On the contrary, some spermatological similarities of *Panorpa* Linnaeus, 1758, and *Boreus* (two longitudinal extra-axonemal rods and a glycocalyx consisting of longitudinal parallel ridges or filaments; see DALLAI et al. 2003) suggest either monophyly of the conventional Mecoptera (quite improbable if confronted with the huge amount of conflicting evidence), or homoplasy.

The most convincing morphological evidence comes from research on ovarioles, which demonstrates that boreid ovaries are fundamentally different from those in other Mecoptera (Štys & Biliński 1990, Biliński & Büning 1998, Biliński et al. 1998). Fleas and boreids share the secondary loss of nurse cells ('neopanoism'), completion of initial stages of oogenesis during postembryonic development, occurrence of rDNA amplification and resulting appearance of multiple nucleoli, differentiation of the late previtellogenic ooplasm into two clearly recognizable regions, and presence of accumulations of membrane-free, clathrin-like cages.

These data suggest that the Mecoptera, as currently constituted, are a paraphyletic assemblage. While it seems certain that the Boreidae and the Siphonaptera are sister groups, their placement relative to the other Mecoptera is not that well supported by the data. Moreover, while it seems clear that the Nannochoristidae should occupy a basal position, it is not clear whether it is a sister group to the flea-boreid clade or the whole Mecoptera (including the Siphonaptera). The most comprehensive, morphology and four-gene molecular analysis (Whiting et al. 2003) supports a major division of the Mecoptera into two clades: the Nannochoristidae-(Boreidae-Siphonaptera) and the Eumecoptera (= remaining Mecoptera). This pattern is strongly supported also by the histology of nannochoristid ovaries (Simiczyjew 2002). They are (neo)panoistic, with multiple nucleoli in the oocyte nucleus, which suggests an extrachromosomal amplification of the ribosomal DNA. The structure of the ovarioles and the course of oogenesis in nannochoristids thus share derived features with boreids and fleas, but differ significantly from all eumecopterans.

Beutel & Baum (2008) have recently proposed a possible clade comprising the Nannomecoptera, Siphonaptera, and Diptera, supported by the presence of a labral food channel, the absence of the galea, a sheath for the paired mouthparts formed by the labium, very strongly developed labial palp muscles and cibarial dilators, and the presence of a well-defined postcerebral pharyngeal pumping chamber. Moreover, close affinities of the Nannomecoptera with the Diptera are suggested by the presence of a unique sensorial groove on the third maxillary palpomere, the elongate and blade-like lacinia, and possibly by the presence of a frontal apodeme and a primarily lamelliform mandible without teeth. The presence of a salivary channel on the laciniae and a subdivided labrum are shared derived features of *Nannochorista* and Siphonaptera. On the contrary, the secretion with a strongly developed intrinsic muscle of the salivary duct might be a possible synapomorphy of the Mecoptera including the Boreidae but excluding the Nannomecoptera. By all means, it seems that the Nannomecoptera, Neomecoptera, and Siphonaptera are closely related, and that the precise position of the Diptera within the mecopteroid complex requires more investigation.

The new phylogeny of the mecopteroid complex (= Eumecoptera, Nannomecoptera, Neomecoptera, Siphonaptera) provides a plausible ecological scenario of the origin of fleas, a situation highly reminiscent of the proposed relationships between liposcelidid psocopterans and the lice. The transition from mosses into mammal nests and dens (during the Mesozoic period, as evidenced by the Late Jurassic-Early Cretaceous boreid *Palaeoboreus* Sukatcheva & Rasnitsyn, 1992, and by the early Cretaceous stem-lineage flea *Tarwinia* Jell & Duncan, 1986 (see Grimaldi & Engel (2005) and references therein) was followed by the Mesozoic/

Cenozoic radiation of the mammals (and their parasites) and by multiple, relatively recent colonizations of birds by the fleas. The fleas (2,380 described species) are by far the most speciose group of the otherwise relictual Mecoptera, a good example of the relatively recent radiation correlated with their parasitism (WHITING et al. 2008).

Conclusions and perspectives

It could be concluded that the present-day phylogenetic analyses, based on both morphological and molecular characters, strongly support the monophyly of most insect 'orders', namely, the Archaeognatha, Ephemeroptera, Odonata, Plecoptera, Dermaptera (including the Arixeniidae and Hemimeridae), Zoraptera, Mantodea, Grylloblattodea, Mantophasmatodea, Orthoptera, Embioptera, Thysanoptera, Neuroptera, Raphidioptera, Strepsiptera, Diptera, Trichoptera, Lepidoptera, and Hymenoptera.

On the contrary, the Blattaria, Psocoptera, and Mecoptera are definitely paraphyletic (with respect of the Isoptera, Phthiraptera, and Siphonaptera, respectively), and the Phthiraptera are possibly polyphyletic. Within the Mecoptera sensu lato, a new phylogenetic subordinal classification can be presented (1. Eumecoptera, 2.1. Nannomecoptera, 2.2. Neomecoptera, 2.2. Siphonaptera). Unfortunately, the internal phylogeny of the Blattodea (including the *Cryptocercus*-Isoptera clade) and the Psocodea (including the Pachytroctidae-Liposcelididae-'Phthiraptera' clade) is too unstable to establish a new subordinal classification of these 'orders'.

The monophyly of the Coleoptera and Hemiptera has been doubted by molecular phylogeneticists several times as well (see, e.g., WHITING et al. 1997, WHEELER et al. 2001, KJER 2004, TERRY & WHITING 2005, KJER et al. 2006; see KRISTENSEN (1999) for a comment); both groups are, however, so obviously monophyletic from the morphological point of view that some molecular tree-building artefacts seem to be a better explanation of these results.

The monophyly of the Megaloptera has been questioned repeatedly (see ŠTYS & BILIŃSKI 1990, KUBRAKIEWICZ et al. 1998) on the basis of similar oogenesis in the Raphidioptera and the Sialidae (Megaloptera). BÜNING (1998), however, considered the Megaloptera monophyletic based on the nearly identical organization of somatic tissues of the ovaries (see also BÜNING 2005). The eversible sacs on segment 11 are another possible synapomorphy of the Megaloptera (ASPÖCK 2002). Monophyly of the Megaloptera is also supported by most molecular and combined analyses (WHEELER et al. (2001): two genes + morphology; HARING & ASPÖCK (2004): four genes; KJER et al. (2006): eight genes + morphology). Moreover, both morphological and molecular analyses tend to support sister-group relationships between the Raphidioptera and the Megaloptera-Neuroptera complex as a whole (ASPÖCK 2002, HARING & ASPÖCK 2004, ASPÖCK & ASPÖCK 2008; but see BEUTEL & GE (2008)), which would furthermore exclude the possible sialid-raphidiopteran affinity.

Recently, molecular and combined morphological-molecular analyses agree that the Embioptera and Phasmatodea are closely related (forming 'Eukinolabia'; see, e.g., TERRY & WHITING (2005)), and the most comprehensive combined analysis (KJER et al. 2006) even suggests that embiids are nested within the Phasmatodea as a sister group of the Euphasmida,

leaving the west Nearctic phasmatodean genus *Timema* Scudder, 1895, as a sister group of the whole Euphasmida-Embioptera complex. Because of the highly apomorphic morphology and behaviour of the embiids, it is difficult to exclude almost any hypothesis about their origin, and the possible reclassification of the Phasmatodea requires more detailed (and more broadly sampled) analyses.

In conclusion, there are 25-28 monophyletic 'orders' in the true insects (Ectognatha). They are the Archaeognatha, *Tricholepidion*-Euzygentoma (?), Ephemeroptera, Odonata, Plecoptera, Dermaptera, Zoraptera, Mantodea (?), Blattodea s. lat. (possibly including also the Mantodea), Grylloblattodea, Mantophasmatodea, Orthoptera, Phasmatodea-Embioptera (?), Psocodea, Thysanoptera, Hemiptera, Neuroptera, Megaloptera, Raphidioptera, Coleoptera, Strepsiptera, Mecoptera s. lat., Diptera, Trichoptera, Lepidoptera, and Hymenoptera. The Californian silverfish *Tricholepidion* and the (largely) Californian stick insect *Timema* are at present probably the most problematic insects, both possibly deserving 'ordinal' reclassification. Go west, young entomologist!

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