POLYNEOPTERA OR “LOWER NEOPTERA” - NEW LIGHT ON OLD AND DIFFICULT PHYLOGENETIC PROBLEMS

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Introduction

Polyneoptera is a group with uncertain monophyly and strongly disputed interordinal phylogenetic relationships. Consequently it is often referred to with the neutral term “lower Neoptera” which does not imply a monophyletic origin and underlines that the subgroups are mainly characterized by plesiomorphic features. Together with Acercaria (Psocodea, Thysanoptera, Hemiptera; = Paraneoptera excl. Zoraptera) and Holometabola the “lower Neoptera” form a very large monophyletic unit Neoptera, which is mainly characterized by the ability to fold back the wings over the abdomen, one of the major innovations in the evolutionary history of insects. Compared to the hemipterans and their relatives and especially the extremely successful holometabolan orders (ca. 800,000 spp.) the “lower Neoptera” have retained plesiomorphic conditions in their development (hemimetabolism) and also in the morphology of different body regions (e.g., largely unmodified orthopteroid mouthparts).

The monophyly of Polyneoptera was considered as unconfirmed by HENNIG (1969) in his groundbreaking “Die Stammesgeschichte der Insekten”. He emphasized the isolated position of Plecoptera (HENNIG, 1969: fig. 40) and the lacking support for a sistergroup relationship between this group and all remaining orders combined in a unit Paurometabola. Ground-oriented habits, leathery forewings ( tegmina), and botryoid male accessory glands were considered as potential paurometabolan groundplan apomorphies by Hennig (1969). KRISTENSEN (e.g., 1975, 1991) underlined the very uncertain monophyly of the “lower neopterans” and presented a cladogram showing the entire lineage as a completely unresolved comb, with Dictyoptera as the only supraordinal terminal taxon (Kristensen, 1991: fig. 5.5). The monophyly of the entire group is presently not supported by a single convincing morphological autapomorphy. “Typical” features are forewings modified as leathery tegmina, hind wings with an enlarged anal field, and pad-like tarsal euplantulae (e.g., KRISTENSEN, 1975; BEUTEL & GORB, 2006, 2008). However, none of these features occurs in all groups. Wings are completely lacking in Mantophasmatodea and Grylloblattodea and they are distinctly simplified in Embioptera, Isoptera and Zoraptera. The attachment devices of the distal leg are atypical in Embioptera and Dermaptera, largely reduced in Grylloblattodea (minute euplantulae, aorlum absent), and completely missing in Zoraptera.

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In recent years, partly triggered by the spectacular discovery of Mantophasmatodea (Klass et al., 2002; see also Klass et al., 2003; Daamgård et al., 2008), the interest in the phylogenetic relationships of the polyneopteran orders increased. However, studies based either on morphology in a wide sense (e.g., Dallai et al., 2003, 2005, 2007; Beutel & Gorb, 2006, 2008; Yoshizawa, 2007, 2011;
Wipfler et al., 2011) or on molecular data (Terry & Whiting, 2005; Yoshizawa & Johnson, 2005; Cameron et al., 2006, Ishiwata et al. 2011; Wang et al., 2013) resulted in an astonishing “diversity” of different branching patterns and did not converge upon a stable systematic concept (see also Trautwein et al., 2012; fig. 1).

In the present contribution short introductions of all orders presently assigned to Polyneoptera are presented. The morphological approach of the Entomology Group at the Phyletisches Museum (Institut für Spezielle Zoologie und Evolutionsbiologie, FSU Jena) is discussed briefly. The main aim is to outline recent developments in the investigation of the phylogenetic relationships. This comprises preliminary results from a morphology-based project (DFG, BE1789/10-1) mainly conducted by the Entomology group at the Phyletisches Museum and T. Hörnschemeyer and co-workers (University of Göttingen), but also results of a cooperation with the Research group of R. Machida (Sugadaira Montane Research Center, Tsukuba University) and first results of the 1KITE project (www:1KITE.org) based on analyses of transcriptomes.

THE ORDERS OF POLYNEOPTERA OR “LOWER NEOPTERA”

Plecoptera

Plecoptera are a medium sized group with ca. 3,500 described species and a worldwide distribution. Their placement in Polyneoptera was often disputed (see above, e.g., Hennig, 1969; Kristensen, 1975, 1991). They are mostly characterized by plesiomorphic features, such as for instance largely unmodified mouthparts, long filiform antennae, unscerotized forewings, inconspicuous tarsal euplantulae (Beutel & Gorb, 2006), and multisegmented cerci. Plecoptera are the only polyneopteran group with aquatic larvae. As the aquatic immatures (“naiads”) of Ephemeroptera, Odonata and Plecoptera differ very distinctly in their morphology and specific adaptations, it appears unlikely that this is a preserved groundplan condition of Pterygota. Plecopteron larvae usually live in oxygen-rich rivers (Zwick, 1980) and can be used as indicators of water quality. They are highly diverse in their breathing organs (e.g., gills on the cervical membrane, the leg bases, or the abdominal apex) and their feeding habits. Feeding plays only a minor role (if at all) in adults of some plecopteran groups. Two membranous pairs of wings are almost always present. The anal field of the hind wings is enlarged and a fan-wise folding pattern is found in larger species. The fore- and hindwings are not coupled in flight (functional quadrupletism) and the flying abilities are modest. Plecoptera are supported as a clade by an unusual intersegmental musculature of the larvae and by some features of the internal genitalia (Zwick, 1980), notably by testes and ovaries of both sides connected anteriorly and forming a closed loop. An additional derived character complex is the greatly reduced condition of the external male and female genitalia.

Fig. 1

Tyrannophasma gladiator. Foto courtesy Reinhard Predel.
Mantodea (praying mantises)

Mantodea are a medium sized group with ca. 2,300 known species. They occur in warmer regions, with only one species reaching Central Europe. Mantodeans or praying mantises are specialized carnivores with raptorial forelegs, in the typical case ambush predators. Camouflage mechanisms are frequently found in the group. They are also known for females devouring the male during copulation. Autapomorphic features are mostly linked with the specialized predacious habits. This includes the very movable triangular head with large compound eyes and very long and thin multisegmented antennae and the raptorial forelegs. The forewings are typical leathery tegmina as they also occur in other lower neopteran groups (“Blattaria”, Orthoptera, Phasmatodea, Dermaptera) and the anal field of the hind wings is enlarged and folded fan-wise.

“Blattaria” (roaches)

Insects similar to roaches were already very successful in the Carboniferous (e.g., Grimaldi & Engel, 2005). Roaches comprise approximately 4,600 species which are mainly found in tropical and subtropical areas. Relatively few species occur in the temperate regions and few species are economically important cosmopolitan pest insects (e.g., Periplaneta americana, Blatta orientalis) which can cause great damage, especially to stored products. Roaches are usually omnivorous but specialized wood-feeding habits have evolved within the group (e.g., Cryptocercus). Typical roaches are ground oriented and running very efficiently. The forewings, if present, are leathery tegmina. In the ground plan a large anal field of the hindwing is present and folded in a fan-wise manner. The flying abilities are modest at best and many species are brachypterous or wingless, especially as females. The roaches (“Blattaria”) are not monophyletic but Isoptera are a subordinate group within a clade Blattodea (e.g., Deitz et al., 2003; Lo et al., 2000).

Isoptera (termites)

Isoptera are the sistergroup of the roach genus Cryptocercus (e.g., Deitz et al., 2003). They are highly specialized wood-feeding insects (e.g., Weidner, 1970). Like roaches they mainly occur in tropical and subtropical areas. They can cause extreme damage to wooden constructions in the widest sense and are a serious problem in many countries. The termites have evolved highly developed social systems with distinctly different castes. Both pairs of wings are membranous and the hind wings lack an enlarged anal field. The venation is simplified and a zone of weakness is present at the base. The wings are discarded after a short wedding flight. Some groups establish their colonies simply in rotting wood (ground-plan) whereas others build sophisticated termite mounds. Largely immobilized physogastric females can produce enormous numbers of eggs.

Embioptera (web spinners)

Embioptera are a small group with ca. 360 described species. They occur in warmer regions also including the Mediterranean area. The relatively small insects are characterized by a conspicuous dimorphism, with males with simplified dehiscent wings and larger completely wingless females (e.g., Kaltenbach, 1968). The presence of greatly enlarged protarsomeres 1 with numerous spinning gland subunits is a unique autapomorphy. With silk formed by the gland secretions they produce galleries under stones or wood. In this protected environment they move very efficiently forwards and backwards with their cylindrical body. Embioptera live in colonies and female broodcare is an additional apomorphic feature of the order. The external genitalia are strongly modified. The ovipositor is missing.

Dermaptera (earwigs)

Dermaptera are another medium sized group with ca. 2000 spp. species, mainly but not only occurring in warmer regions. Autapomorphies are the strongly shortened sclerotized forewings (sometimes erroneously referred to as elytra) and the one-segmented cerci forming a pincer-like apparatus at the tip of the abdomen (e.g., Günther & Herter, 1974). The hindwings are excessively folded and stored under the shortened forewings at rest. Dermapterans are mostly omnivorous and have a preference for narrow spaces. Some species are highly specialized ectoparasites of mammals including bats. Like Embioptera they are characterized by female broodcare and the external genitalia are also strongly modified. The ovipositor is very thin and not suitable for the deposition of eggs.

Orthoptera (grasshoppers, locusts, katyids)

With ca. 20,000 described species Orthoptera are by far the most successful group of Polyneoptera (Beier, 1972). They reach the greatest diversity in tropical and subtropical areas but occur also in the temperate regions. The monophyly is well supported by the presence of a saddle-shaped pronotum, hing legs modified as jumping legs, and longitudinally twisted wing buds of the nymphs. Orthoptera are subdivided
in two well-founded suborders, Ensifera with long antennae and ovipositor, and Caelifera with the antennae and ovipositor greatly shortened. Many species of Ensifera are carnivorous, whereas caeliferas generally feed on plants. The remarkable acoustic communication systems, which have likely contributed to the evolutionary success, have apparently evolved several times independently. Locusts are already mentioned in the Bible as one of the plagues. Locusta migratoria and some other species can occur in extreme numbers of individuals and cause tremendous damage in agriculture.

Phasmatodea (stick insects, walking leaves)

Phasmatodea are a medium sized group with ca. 3,000 described species. They are mainly restricted to tropical and subtropical regions but also occur in warmer European areas including Italy (Bacillus and Clonopsis). In contrast to Orthoptera they are exclusively phytophagous (BEIER, 1968). Phasmatodea were considered as close relatives of Orthoptera (or even as a subgroup) by different authors (e.g., WILLMANN, 2005). Autapomorphies are defense glands with openings on the pronotum and a pectinate appendage of the midgut. The elaborate camouflage mechanisms commonly found in the group do not belong to the ground plan (BRADLER, 2009). Most species either resemble twigs or leaves (Phyllium), but the basal Timematodea have a simple cigar-shaped body. Most species are wingless but well developed wings occur within the order. It was suggested that wings re-evolved within Phasmataodea (WHITING et al., 2003) but this hypothesis is strongly debated.

Grylloblattodea (ice crawlers)

Grylloblattodea are one of the smallest groups of insects with presently 32 described extant species (SCHOVILLE, 2012). They occur in western North America and in northern Asia including the Altai in the west and Japan in the east (BAI et al., 2010; SCHOVILLE, 2012). All species are completely wingless. A remarkable feature is that they only occur in cold areas, usually in mountain regions. In the typical case they feed on dead or dying insects along snow fields or glaciers. Grylloblatta campodeiformis dies at temperatures above 15°C, but some species occur in lower elevations and even in areas with relatively warm climatic conditions, as for instance the southeastern Japanese main island Shikoku. The group is mostly characterized by plesiomorphic features such as for instance largely unmodified orthopteroid mouthparts, filiform antennae, five-segmented tarsi, and multisegmented antennae. The strongly asymmetric genitalia are probably autapomorphic for the group.

The fossil record shows that the few extant grylloblattodean species are only a relic of a more widely distributed and moderately successful group (e.g., VRSANÝ et al., 2001; ENGEL & GRIMALDI, 2004; BAI et al., 2011). However, the assignement of fossils preserved only as wings is problematic.

Mantophasmatodea (beelwalkers)

The discovery of the order Mantophasmatodea (Fig. 1) about ten years ago (Klass et al., 2002) was a highlight in systematic entomology. The group is restricted to southern Africa. The first two specimens were not discovered in the field but in museums in Berlin and Lund, respectively. Like Grylloblattodea they are completely wingless. They are night active predators and they are usually found in lower vegetation. The monophyly is supported by unique features of the filiform antennae (DRILLING & Klass, 2010) and by a very large pan-shaped arolium densely covered with acanths. A similar arolium occurs in basal lineages of Phasmataodea (BEUTEL & GORB, 2008). However, in Mantophasmatodea it is only in contact with the substrate in specific situations, for instance when they carry large prey or when they walk on steep and smooth surfaces. The name “HEELWALKER” refers to the elevated position of the arolium during normal locomotion.

Zoraptera (groundlice, angel insects)

Zoraptera is one of the smallest insect orders with presently 39 described species placed in one monogeneric family Zorotypidae (Mashimo et al., 2013). The group occurs in tropical and subtropical regions (Fig. 2) but is missing on the Australian mainland. The occurrence of Zorotypus burrardi in the northern U.S.A. is an artifact. The position of Zoraptera is one of the most disputed issues in insect phylogenetics. HENNG (1969) placed the small order as the sistergroup of Acercaria (Paraneoptera) but recent results strongly suggest a placement among the polyneopteran orders (see below). The monophyletic origin is undisputed. The most conspicuous autapomorphy is the dimorphism, with unpigmented morphs without wings and eyes, and more or less dark brown individuals which have compound eyes and ocelli and two pairs of simplified but functioning wings. Both pairs of wings are membranous with a distinctly reduced venation and an enlarged anal field is missing. In contrast to earlier statements (e.g., BOUDREAU,
1979) the thoracic muscle system is well developed and probably close to the neopteran groundplan (FRIEDRICH & BEUTEL, 2008a). All known species are very small (2 mm or less) and cryptic. They are mostly found in humid conditions (Fig. 2), especially under bark.

THE MORPHOLOGICAL APPROACH OF THE ENTOMOLOGY GROUP AT THE PHYLETISCHES MUSEUM

The Entomology Group was established at the Phyletisches Museum (Jena) in 2004. Its research is focused on innovative morphological techniques and high level insect phylogeny. In the last ten years strong efforts were made to optimize morphological methods (e.g., BEUTEL et al., 2011; FRIEDRICH et al., 2013; BEUTEL et al., 2013). Depending on the species under study different combinations of traditional and innovative techniques were applied. This includes dissections in some cases. This simple technique can yield results very rapidly, especially an overview of general anatomical configurations, but is only suitable for larger specimens with a body size above 10 mm. Histology, i.e. microtome sectioning is a well-established technique with a long tradition in human anatomy. It was greatly improved in the last decades by the use of new embedding materials (e.g., Araldit, Spurr) and glass or diamond knives. This makes microtome sectioning much more suitable for organisms with a hardened exoskeleton (BEUTEL et al., 2013; FRIEDRICH et al., 2013). Scanning electron microscopy is extremely useful for the documentation of external surface structures. With a specifically designed rotatable specimen holder (POHL, 2010) it is possible to obtain all standard views with a single specimen and to reduced charging. Confocal laser scanning microscopy can be useful for examining very small (or flat) specimens or also isolated parts such as for instance genitalia (e.g., SCHAWAROCH et al., 2005). Micro-computed tomography (µ-CT) has turned out as extremely useful in insect morphology in the last 10 years. Since its first
application in entomology (HÖRNSCHEMEYER et al., 2002) this technique was distinctly improved (e.g., FRIEDRICH & BEUTEL, 2008b; FRIEDRICH et al., 2013). Moreover, desktop μ-CT scanners are meanwhile available at many institutions. Micro-computed tomography has several advantages. It is largely artifact free and the images are perfectly aligned for reconstruction. As it is a non-invasive method it is also suitable for scanning very rare specimens and even type material. The maximum resolution is distinctly below 1 µm. It depends on the size of the specimen and the specific equipment (see FRIEDRICH et al., 2013). Visualization and animation of external and internal structures has also greatly improved since computer-based reconstruction was introduced in the 1990ties (e.g., BEUTEL & HAAS, 1998). A combination of Imaris (or Amira) with Maya turned out as highly efficient, combining advantages of both software programs, automatic surface reconstruction and implied surface smoothing functions (FRIEDRICH et al., 2013).

The optimized combination of the techniques outlined here and an efficient work-flow make it possible to compile large and well documented morphological data sets within an relatively short time frame. In the morphology-based Polyneoptera-project a matrix with 369 characters (also including developmental features and sperm morphology) was compiled within approximately two years. Presently analyzed molecular data sets obviously dwarf even sizable morphological matrices (e.g., BEUTEL et al., 2011). Nevertheless, the accelerated data acquisition greatly strengthens the morphological part in projects with a broad spectrum of approaches (e.g., 1KITE [www:1KITE.org]: transcriptome analyses, bioinformatics, morphology, embryology, palaeontology) and aiming at complex evolutionary scenarios.

RECENT DEVELOPMENTS IN POLYNEOPTERAN SYSTEMATICS

As pointed out above, recent studies based on morphological characters (e.g., BEUTEL & GORB, 2006, 2008; YOSHIZAWA, 2007, 2011; WIPFLER et al., 2011) or on different molecular data sets (e.g., WHEELER et al., 2001; TERRY & WHITING, 2005; LETSCH, et al., 2012) did not yield consistent results (Fig. 3). Nevertheless, several issues in polyneopteran systematics appear clarified or at least close to a stable solution.

Dictyoptera were the only widely accepted supraordinal polyneopteran group for a long time (e.g., HENNIG, 1969). The clade comprising Mantodea, roaches and termites is mainly characterized by an accessory anterior tentorial bridge formed by a medially connected laminatentoria (sometimes erroneously referred to as “perforated corpotentorium”), by a specific armature of the proventriculus, a female genital atrium, and by the production of robust egg cocoons, the oothecae (secondarily lost in some roaches and in Isoptera excluding Mastotermidae).

An important breakthrough was the discovery that termites are only a subordinate subgroup of Blattodea, with the subsocial and wood-associated genus Cryptocercus as its sister taxon. This was confirmed by morphological characters (e.g., DEITZ et al., 2003) and by molecular data (LO et al., 2000) and is also supported by the presence of endosymbionts – flagellates – which do not occur in other groups of insects including other roaches.

In the last years, the situation in polyneopteran systematics has further improved. Studies based on transcriptomes (LETSCH et al., 2012; LETSCH & SIMON, 2013) tentatively suggest a monophyletic origin of Polyneoptera including Plecoptera, but both studies did not include all orders.

Soon after the discovery of Mantophasmatodea (KLASS et al., 2002) this new group was identified as the sistergroup of the long disputed Grylloblattodea (e.g., KLASS et al., 2003; TERRY & WHITING, 2005; UCHIFUNE & MACHIDA, 2005; BEUTEL & GORB, 2006; BAUM et al., 2007; WIPFLER et al., 2011). Both completely wingless taxa were united in a clade Xenonomia. Whether the loss of wings occurred in a common ancestor or independently is the topic of current investigations. Another breakthrough was the placement of Phasmatodea. As mentioned above they were considered as close relatives of Orthoptera by most insect systematists (e.g., WILLMANN, 2005). This hypothesis was not confirmed by recent studies based on morphology (e.g., WIPFLER et al., 2011; FRIEDEMANN et al., 2012) or molecular data (TERRY & WHITING, 2005; YOSHIZAWA & JOHNSON, 2005; ISHIWATA et al., 2011; WANG et al., 2013). Phasmatodea are very likely the sistergroup of Embioptera, both groups forming a clade which is called Eukinolabia (e.g., TERRY & WHITING, 2005; YOSHIZAWA & JOHNSON, 2005; ISHIWATA et al., 2011; WIPFLER et al., 2011).

A very important result is the placement of Zoraptera within Polyneoptera. This implies that apomorphies of Paraneoptera (Zoraptera + Acercaria) suggested by HENNIG (1969) and others (e.g., BEUTEL & WIEDE, 2005) are due to parallel evolution, possibly partly related with size reduction (Zoraptera, Psocodea, Thysanoptera). This includes the reduced number of tarsomeres
Fig. 3
Cladograms showing hypothesized relationships of Polynopteran orders.
within the group, which obviously go back to the rapid radiation in the Carboniferous (see above).

Preliminary results of analyses of transcriptomes of more than hundred terminal taxa representing all hexapod orders (1KITE; B. Misof & K. Meusemann, pers. comm. to R.G. Beutel & B. Wipfler) also support the monophyletic origin of Polyneoptera including Plecoptera and Zoraptera. A weakly supported clade Zoraptera + Dermaptera forms the sistergroup of all the remaining polyneopteran orders. Plecoptera is placed as the sister taxon of a large clade comprising Orthoptera, Dictyoptera, Xenonomia and Eukinolabia (see also DALLAI et al., 2005). The last three groups form a monophyletic unit, and Xenonomia and Eukinolabia are sistergroups.

OUTLOOK

The phylogeny and evolution of the “lower neopteran” orders will be investigated intensively in the Polyneoptera-subproject of 1KITE, and the Dictyoptera in more detail in another subproject focussed on this monophyletic polyneopteran subunit. Transcriptomes will be analysed for an extensive sampling of all polyneopteran orders. The obtained phylogenies will be used as the basis for further detailed investigations of different aspects of the group. This will include the dating of important evolutionary events and phylogenetic splits, but also the reconstruction of morphological and embryological character transformations. This approach will probably not only yield a stable phylogenetic hypothesis but also a complex and well-founded evolutionary scenario for this difficult but fascinating lineage of Hexapoda.

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BIBLIOGRAFIA


Baum E., Dressler C., Beutel R.G., 2007 – Head struc
tures of Karoophasma sp. (Hexapoda, Mantophasmatodea) with phylogenetic implications. - Journal of Zoological Systematics & Evolutionary Research, 45: 104-119.


Klass K.D., Picker M.D., Damgaard J., Noort S.V., Tojo K., 2003 – The taxonomy, genitalic morphology,
Wippler B., Machida R., Müller B., Beutel R.G., 2011 – On the head morphology of Gryllolbattoidea (Insecta) and the systematic position of the order - with a new nomenclature for the head muscles of Neoptera. - Systematic Entomology, 36: 241-266.