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A Critical Review of Current Data and Hypotheses on Hexapod Phylogeny*

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Abstract

The most problematic fields in the reconstruction of hexapod phylogeny are (1) the very basal splitting events among Collembola, Protura, Diplura, and Insecta (=Ectognatha); (2) the basal relationships in Dicondylia, concerning the position of *Tricholepidion* with respect to Zygentoma *s. str.* and Pterygota as well as the monophyly of Zygentoma *s. str.*; (3) the relationships among the three major pterygotan lineages Ephemeroptera, Odonata, and Neoptera; and (4) the large basal polytomy in Neoptera, which includes Plecoptera, Orthoptera, Dictyoptera, Notoptera (=Grylloblattodea), Mantophasmatodea, Embioptera, Dermaptera, Phasmatodea, Zoraptera, Acercaria, and Endopterygota (=Holometabola). The great amount of new morphological and molecular data accumulated during recent years has so far not provided convincing clarification of any of the abovementioned issues; inconsistence between different characters and analyses has grown in proportion to the data, and this is also reflected in the numerous incongruent phylogenetic hypotheses that have been proposed. Furthermore, the uncertainty about which other subgroup of Mandibulata is phylogenetically closest to Hexapoda (Myriapoda or Crustacea, or some subgroup thereof) and the additional option of hexapod non-monophyly render work on basal hexapod phylogeny a laborious task that should be embedded in broader studies of mandibulatan phylogeny. This paper provides a critical review of previously suggested morphological autapomorphies of putative hexapod clades, and results of recent morphology-based and molecular-based cladistic analyses are embedded in these discussions.

Key words: Hexapoda, Insecta, Pterygota, Neoptera, characters, cladistics, morphology, phylogeny

1. Introduction

Much of our current concepts on the phylogeny of Hexapoda is based on the works of Hennig (1969, 1981), Boudreaux (1979), and Kristensen (1975, 1981, 1991, 1995, 1998). According to Kristensen (1991: Fig. 5), the Hexapoda can be divided into the Collembola, Protura, Diplura, and Insecta (=Ectognatha). In Insecta a basal split between Archaeognatha and Dicondylia is proposed. The Dicondylia include the Pterygota, the Zygentoma, and the isolated species *Tricholepidion gertschi* (formally placed in Zygentoma). The Pterygota fall into the three lineages Ephemeroptera, Odonata, and Neoptera. In Neoptera, which comprise the vast majority of hexapod species, 11 principal lineages are placed in an unresolved basal polytomy: Plecoptera, Embioptera, Orthoptera (=Saltatoria), Dermaptera, Dictyoptera, Mantophasmatodea (described in Klass *et al*., 2002), Phasmatodea, Notoptera (=Grylloblattodea), Zoraptera, Acercaria (hemipteroid orders), and Endopterygota (=Holometabola). Accordingly, the basal relationships of the Hexapoda, the Dicondylia, the Pterygota, and the Neoptera appear as the most severe problems in the reconstruction of hexapod phylogeny. One would ask whether some substantial progress has been achieved after Kristensen's (1991, 1995, 1998) papers.

Recent years have seen a large number of new contributions relevant to phylogenetic work in Hexapoda. Many morphological papers focus on particular character systems such as the circulatory system (*e. g*., Pass, 1991, 1998, 2000; Gereben-Krenn and Pass, 1999, 2000; Pass *et al*., 2006), ovarioles (*e. g*., Büning, 1994, 1998, 2006), spermatozoa (*e. g*., Jamieson *et al*., 1999; Dallai *et al*., 2001, 2002, 2003, 2004), wings and their articulation (*e. g*., Kukalová-Peck, 2008; Haas and Kukalová-Peck, 2001; Béthoux, 2005; Hörnschemeyer and Willkommen, 2007; Willkommen, 2008), tarsal and pretarsal attachment devices (*e. g*., Gorb, ed. 2004), female genitalia (Klass, 1998c, 2001a, 2003a, 2008; Klass *et al*., 2003), mid-abdominal musculature and nervous system (Klass, 1999, 2000; Klug and Bradler,

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2006; Klug and Klass, 2007), visual system (Paulus, 2000; Friedrich *et al*., 2006), head apodemes and mandibular articulations (Staniczek, 2000; Fürst von Lieven, 2000; Koch, 2000a, b, 2001), proventriculus (Klass, 1998a, b), or embryonic development (*e. g*., Ikeda and Machida, 1998, 2001; Machida and Ando, 1998; Machida *et al*., 2002, 2004; Machida, 2006). These contributions substantially improved the knowledge on the character systems in question and partly led to completely new evolutionary interpretations. Extensive phylogenetically based reviews on hexapod relationships were published by Willmann (2003, 2005a), Beutel (2004), and Grimaldi and Engel (2005), partly also including the fossil evidence. Other authors used much of the available morphological data for cladistic analyses either including all hexapod orders (Beutel and Gorb, 2001, 2006) or focussing on the basal splits in Hexapoda (Bitsch and Bitsch, 1998, 2000, 2004). On the other hand, morphological matrices used in the combined analyses of Whiting *et al*. (1997), Wheeler *et al*. (2001), Giribet *et al*. (2004), Terry and Whiting (2005), and Kjer *et al*. (2006) suffer from many shortcomings that render their results spurious.

On the molecular side a rich spectrum of methods for sequence alignment, data selection, tree construction, and estimation of clade support has been developed in recent years. Accordingly, however, there has also been increasing dispute about which are the "right" methods. This is an important aspect, because phylogenetic results drawn from a database can differ strongly depending on the methods applied. The studies by Whiting *et al*. (1997), Wheeler *et al*. (2001), Kjer (2004), Terry and Whiting (2005), and Kjer *et al*. (2006) are relevant for order-level relationships throughout Hexapoda. Carapelli *et al*. (2000), Regier *et al*. (2004), Giribet *et al*. (2004), and Luan *et al*. (2005) focus on the basal splits in Hexapoda. Some further papers are relevant for the position of Hexapoda within the Arthropoda: Regier and Shultz (1997, 1998), Shultz and Regier (2000), Giribet and Ribera (2000), Giribet *et al*. (2001), Cook *et al*. (2001, 2005), Nardi *et al*. (2003a, b), Pisani *et al*. (2004), Regier *et al*. (2004, 2005), Carapelli *et al*. (2005), and Mallatt and Giribet (2006) (see also Delsuc *et al*., 2003). Apart from DNA sequences, mitochondrial gene order has been tested for its phylogentic informativeness (with data currently available for *ca*. 100 hexapod species), but due to the lack of variation it can now be considered very unlikely to yield evidence on interordinal hexapod relationships (Cameron *et al*., 2006a, b). Minor differences in the genetic code are probably neither informative due to strong homoplasy among subgroups of Hexapoda (Abascal *et al*., 2006).

Regarding the fossil evidence, the still widespread non-phylogenetic reasoning as well as the extremely poor record of Hexapoda from the Lower Carboniferous and Devonian are major problems. Morphological and cladistic work on the earliest known Pterygota from the Upper Carboniferous is most relevant in terms of order-level phylogeny. Most notably, there has been substantial progress recently with regard to the huge basal-neopteran assemblage of "Protorthoptera" (*e. g*., Béthoux and Nel, 2002, 2004, 2005; Béthoux *et al*., 2004 on "orthopteroid" taxa) and to the Odonata (Bechly, 1995, 1996, 2005). In both cases pterygotan lineages could be traced back to their early roots at the beginning of the Upper Carboniferous. Some other outstanding findings on fossils are highly disputed. One case is the interpretation of the Devonian marine arthropod *Devonohexapodus* as a stemgroup hexapodan (Haas *et al*., 2003; Haas, 2005 *vs*. Willmann, 2005b). Another case is the descriptions of Carboniferous hexapods by J. Kukalová-Peck (*e. g*., Kukalová-Peck, 1987, 1990, 1991, 1992), which suggest that early hexapods from various lineages possessed many elements absent in all extant relatives (additional podomeres in the limbs of head, thorax, and abdomen; basal podomeres bearing multiple exites and endites).

Despite all these new data, however, hardly any substantial progress has been achieved in the clarification of the most problematic nodes mentioned above; instead, conflicts have grown in proportion to the amount of data, and numerous incongruent hypotheses are now on the market. The present contribution surveys the current state of knowledge on the phylogeny of Hexapoda, focused on the basal splits in Hexapoda, Insecta, Pterygota, and Neoptera. Morphological characters are listed that yield potential synapomorphies of clades (numbered sequentially in bold print), and the results of the various analyses of morphological, molecular, and combined data are compared. In addition, the current evidence regarding the (non-)monophyly of Hexapoda is briefly reviewed.

2. Monophyly and relationships of Hexapoda

Relationships of Hexapoda

Traditionally the myriapods or a subgroup of these (Progoneata or Symphyla) were considered the sister group of Hexapoda (Tracheata or Atelocerata hypothesis). The complete lack of second antennae (limbless "intercalary segment") unambiguously supports this hypothesis, as does the tracheal system, which shows complex similarities in the musculature and innervation of the spiracles between, at least, Insecta and Chilopoda (Klass and Kristensen, 2001). The presence of temporal organs (=Tömösváry's organs) does not support Tracheata, because similar organs occur among crustaceans (Klass and Kristensen, 2001: 270). The case is similar with the tentorial arms, because head apodemes resembling the anterior and posterior tentorial arms of Hexapoda are also found in many Malacostraca (*e. g.*, Marvillet, 1978, 1982; Coleman, 2002).

During the last two decades morphological evidence accumulated that suggests a close relationship of Hexapoda to Crustacea (Tetraconata or Pancrustacea hypothesis; survey in Richter, 2002). One character system taken to support this view was the cellular composition of the ommatidia (*e. g.*, Dohle, 2001), but this has become ambiguous with the discovery of some of the crucial structural details in a scutigeromorph chilopod (Müller *et al.*, 2003). Several characters specifically point to a close relationship between Hexapoda (or perhaps only Insecta) and Malacostraca. In the ontogeny of the nervous system there occur individual neuroblasts (perhaps true for all Crustacea), and these show a particular arrangement on the ventral side of the segments as well as a special sequence of cleavages (Simpson, 2001; Dohle, 2001; Harzsch, 2003). In addition, Malacostraca and Insecta share a similar set of nerve cells transmitting the visual stimulus to the optic ganglia (Nilsson and Osorio, 1997) as well as structural complications in the optic neuropils, such as the presence of a lobula and nerve chiasmata between the neuropiles (Sinakevitch *et al.*, 2003). However, the characters of the visual system are actually ambiguous since the apomorphies are partly absent in the basal taxa Leptostraca and Archaeognatha. In contrast to morphology, molecular analyses predominantly indicate Branchiopoda to be the closest relatives of Hexapoda (as far as Hexapoda appears as a monophylum; *e. g.*, Babbitt and Patel, 2005; Regier *et al.*, 2005; Mallatt and Giribet, 2006).

Monophyly of Hexapoda

Hexapod monophyly is only weakly supported from the morphological side. There is much ambiguity in the interpretation of most of the relevant characters, which is partly due to the uncertainty regarding the sister taxon of Hexapoda (or sister taxa of its principal subgroups; see Klass and Kristensen, 2001).

The most widely known character considered to support hexapod monophyly is [1] the tagmatisation of the trunk into thorax and abdomen. If one compares Hexapoda with Myriapoda, the apomorphy is the formation of an abdomen that lacks walking legs. However, in the four major hexapod lineages the abdominal appendages are differentiated in very different ways: highly specialized (and hardly reduced!), basally fused appendages of segments 1, 3, and 4 in Collembola (ventral tube, retinaculum, manubrium); paired stumps with one or few podomeres on abdominal segments 1–3 in Protura; flat coxal lobes with styli and coxal vesicles on the pregenital (and partly genital) abdominal segments in Diplura and Insecta (coxites in most taxa fused with eusternite into a coxosternite). Consequently, at most a moderate reduction of the abdominal appendages can perhaps be viewed as a hexapod autapomorphy. Comparing Hexapoda with Malacostraca leads to a different result. The pleon of Malacostraca also represents a posterior trunk tagma with modified and more or less reduced appendages, and homologising trunk tagmatisation in Malacostraca and Hexapoda appears tempting. An evolutionary shift of the border between the two tagmata has then to be assumed – surely a plausible transformation. For this issue the segmentation genes (hox genes and others) bear some relevance. The genes *Antp* and *abd-A* are in the plesiomorphic condition expressed in the major part of the trunk, as in Branchiopoda. In an isopod (Malacostraca) *Antp* was found to be largely restricted to the peraeon, while *abd-A* is restricted to the pleon, resembling the limitation of *Antp* to the thorax and of *abd-A* to the abdomen in Insecta (Abzhanov and Kaufman, 2000). In both Insecta and Isopoda the last segment of the posterior tagma (bearing the uropods or cerci) lacks *abd-A* expression. The gene *Ubx*, however, shows no congruence: expression in the isopod peraeon and the insect abdomen. The evidence is thus somewhat contradictory (Hughes and Kaufman, 2002). Whether in case of homology the malacostracan or the hexapodan type of tagmatisation is plesiomorphic would appear ambiguous.

[2] Considering the posterior tentorial apodemes a synapomorphy of the hexapod lineages requires the homology of certain head apodemes in Collembola, Diplura, and Insecta (Manton, 1964; Boudreaux, 1979: 133; Koch, 2000a; Willmann, 2003), which, however, is disputed (Bitsch and Bitsch, 2002). In addition, many Malacostraca have apodemes of very similar location (between the two maxillary segments; Snodgrass, 1951; Lauterbach, 1970: 105; Scheloske, 1977; Marvillet, 1978, 1982; Coleman, 2002), which thus might represent a synapomorphy for Hexapoda (or only Insecta) and Malacostraca. [3] The condition of two corneageneous cells as primary pigment cells in the compound eye ommatidia and [4] the multi-segmented filamentous cerci are not convincing hexapod autapomorphies, because Diplura and Protura lack compound eyes and both Collembola and Protura do not have appendages that can clearly be homologized with the cerci. Other apomorphies shared by the major lineages of Hexapoda are ambiguous because they are also present in myriapod subgroups, such as [5] fusion of the second maxillae into a labium (also in Symphyla and perhaps in the ground plan of Tracheata: Fanenbruck, 2003: 268ff; Bitsch and Bitsch, 2004: 535). When comparing Hexapoda with Myriapoda, one might also assume that [6] the absence of spiracles in the first postcephalic segment could be a hexapod autapomorphy (Fanenbruck, 2003), but this is

also ambiguous (Klass and Kristensen, 2001: 283f).

There is also morphological evidence for non-monophyletic Hexapoda. [7] For instance, Insecta and Malacostraca share flagellate antennae with musculature only in the basal antennomeres (4 in Leptostraca, 2–3 in Eumalacostraca, 1 in Insecta; Claus, 1888; Schmidt, 1915: Fig. 11; Cochran, 1935; Snodgrass, 1935; Lauterbach, 1970). [8] Characters from the optic neuropiles could also be viewed as supporting insect-malacostracan relationships (*e. g.*, presence of a lobula; see data in Sinakevitch *et al.*, 2003).

Many molecular studies support a monophyletic Hexapoda (Regier and Shultz, 1998, 2001; Wheeler *et al.*, 2001; Kjer, 2004; Regier *et al.*, 2005; Kjer *et al.*, 2006; Mallatt and Giribet, 2006). These results are based on data from 18S, 28S, EF-1α, and EF-2, as well as combined analyses of the mitochondrial COI, COII, 12S, and 16S. Non-monophyletic Hexapoda were mainly obtained in analyses of short genes like H3 and snRNA-U2 (Edgecombe *et al.*, 2000) and of subsets of the fast evolving mitochondrial sequences (Nardi *et al.*, 2003a; Cook *et al.*, 2005; Carapelli *et al.*, 2005), and in some POY analyses (Giribet and Ribera, 2000; Giribet *et al.*, 2001, 2004: Fig. 2).

Due to this conflicting evidence from both the morphological and the molecular side, the monophyly of Hexapoda should currently be regarded as uncertain (while the following chapter 3 is based on its preliminary acceptance). The problem can probably only be resolved by phylogenetic work covering the entire Mandibulata, which will require considerable efforts with regard to comparative morphology.

3. Basal relationships in Hexapoda

Monophyly of Diplura

Characters supporting this group are [9] a tongue-and-groove connection of the maxillary galeae with the hypopharyngeal superlinguae (François, 1970: Fig. 10; Kristensen, 1998) and [10] a special type of entognathy (Koch, 1997, 2000a, b, 2001) where the mandibles and maxillae of one side are enclosed in a common pouch. In the ontogenetic development of entognathy in Diplura the labial parts become rotated (Ikeda and Machida, 1998; Machida, 2006; Sekiya and Machida, 2009), and the dorsum of the maxillary segment forms parts (admentum; François, 1970: Ad in Fig. 2; Ikeda and Machida, 1998) that later are placed lateral to the labium; these features might be further apomorphies uniting Diplura. Manton (1972, 1977) proposed that [11] a bipartite and twisted condition of the trochantero-femoral muscle, one bundle of which extends far into the femur is an autapomorphy of Diplura. However, reinvestigations by Szucsich and Pass (2008) let this character appear doubtful. [12] Whether a loss of the anterior tentorial arms is a potential autapomorphy of Diplura is disputed (Koch, 2000a and Fanenbruck, 2003 *vs*. Bitsch and Bitsch, 2000, 2004). [13] The phylogenetic evidence from the 10-segmented dipluran abdomen (Koch, 1997; Machida, 2006) is unclear, because the number of abdominal segments in the hexapod ground plan is unknown (Klass and Kristensen, 2001: 267).

Evidence contradicting dipluran monophyly comes from [14] the structure of the ovaries. In Diplura-Campodeina these are structured as in Collembola and Protura, altogether sac-like and not subdivided, and (as in Collembola) with a meroistic germarium-vitellarium area. The ovaries of Diplura-Japygina resemble those in basal Insecta, with a comb-like division into ovarioles and a panoistic germarium-vitellarium area. (*e. g.*, Štys and Biliński, 1990; Biliński and Szklarzewicz, 1991; Štys *et al.*, 1993; Kristensen, 1997; Bitsch and Bitsch, 1998, 2000; Heming, 2003). Nonetheless, the phylogenetic interpretation of the ovary characters is difficult.

A monophyletic Diplura is found in the morphology-based cladistic analyses by Bitsch and Bitsch (2000) and Giribet *et al.* (2004: Fig. 1), but not in that of Bitsch and Bitsch (2004). The molecular data unequivocally support Diplura (Wheeler *et al.*, 2001; Giribet *et al.*, 2004: Fig. 2; Kjer, 2004; Luan *et al.*, 2005; Kjer *et al.*, 2006). Together with the prevalence of morphological characters in favour of Diplura, this would render the monophyly of this taxon quite well-supported.

Monophyly of Insecta (=Ectognatha)

This taxon is strongly supported by morphological characters (Bitsch and Bitsch, 2004; Beutel and Gorb, 2006) and also widely confirmed by molecular analyses (Wheeler *et al.*, 2001: Fig. 12A; Giribet *et al.*, 2004: Fig. 2; Mallat *et al.*, 2004; Kjer, 2004; Regier *et al.*, 2005; Luan *et al.*, 2005; Kjer *et al.*, 2006; Mallatt and Giribet, 2006).

One striking autapomorphy of Insecta is [15] the female ovipositor ventrally on abdominal segments VIII and IX (see Klass, 2003a: 195ff, 2008 for its basic pattern). It is composed of the coxites of the two segments (valvifers), their gonapophyses (=1st and 2nd valves, derived from coxal vesicles: Bitsch, 1994), the posteriorly prolongated coxal lobes of segment IX (3rd valves or gonoplacs), and several smaller sclerites around the valve bases, among them remnants of the eusternites. The 1st and 2nd gonapophyses of a side are interconnected by a tongue-and-groove system (rhachis + aulax=olistheter). The plesiomorphic position of the female genital opening is likely on the hind margin of segment VII, as in Archaeognatha and Zygentoma (Rousset, 1973; Bitsch, 1974). Another conclusive apomorphy is [16] the restriction of musculature to the basalmost antennomere and the presence of Johnston's organ in the second (while an unmuscled flagellum as such is shared with Malacostraca, see above). [17] The posterior tentorial arms are fused medially to form a transverse tube or beam (while similar – but medially separated – apodemes are shared with many Malacostraca and perhaps other Hexapoda, see above). [18] The tarsus is subdivided into several tarsomeres (*e. g.*, Sturm and Machida, 2001). [19] The claw-bearing praetarsus is reduced, whereby the bases of the claws are in contact with the distal margin of the last tarsomere. [20] The dorsal tip of the abdomen bears a long, articulate terminal filament (=caudal filament, paracercus; reduced in Pterygota other than Ephemeroptera). [21] The antennal vessels are separated from the aorta (Pass, 1991, 1998, 2000; Pass *et al.*, 2006). [22] The labial glands open on the anterior base of the labium and lead into a salivarium enclosed by the labium and hypopharynx (Bitsch and Bitsch, 2004). In the embryo [23] the serosa folds over the ventral side from both sides and after its closure forms a transitional cavity; at least part of the inner fold walls originates from embryonic tissue, thus representing an amnion (Machida and Ando, 1998; Machida *et al.*, 2002; Masumoto and Machida, 2006; Machida 2006). [24] The appendages of abdominal segment 1 transitionally form glandular pleuropodia (Machida, 1981; Sturm and Machida, 2001: 159, 173; Heming, 2003: 134).

Relationships between Collembola, Protura, Diplura, and Insecta

The grouping of Collembola, Protura, and Diplura into a taxon Entognatha (*e. g.*, Hennig, 1969; Boudreaux, 1979) has been based on the reduction of [25] the compound eyes and [26] the Malpighian tubules; nonetheless, under the Tetraconata hypothesis the weak development of the latter is more parsimoniously considered plesiomorphic. [27] The inclusion of the mandibles and maxillae in deep head pouches (entognathy) is a further argument. The structure and ontogeny of the pouches and surrounding parts differ strongly between Ellipura (=Collembola + Protura) and Diplura (Koch, 1997; Kristensen, 1998; Ikeda and Machida, 1998; Machida, 2006): mandibles and maxillae in separate pouches in Ellipura but in a single pouch in Diplura. However, in all entognathans the "mouth tube" is formed by hypertrophied lateral cranial folds that grow over the mandibles and maxillae and fuse with the labrum and labium, and this still constitutes an apomorphy shared among the entognathan taxa.

Other arguments favour a clade Diplura + Insecta: [28] The flagellum of the spermatozoa has an additional outer cylinder of nine microtubuli (Dallai, 1998; Jamieson *et al.*, 1999). [29] In the embryonic development a secondary embryonic sheath is formed (amnion) that grows from the margins of the embryo around the entire egg and displaces the serosa (Ikeda and Machida, 2001; Machida, 2006: Fig. 4; Sekiya and Machida, 2009). [30] Temporal organs are present in Collembola (postantennal organs) and Protura (pseudoculi) but absent in Diplura and Insecta. [31] The rectal ampullae and papillae of the hindgut are perhaps another apomorphy common to Diplura and Insecta (Bitsch and Bitsch, 1998). [32] The similar structure of the abdominal appendages may also support this clade: coxal lobes with coxal sclerites (=coxites, often fused with the eusternite) bearing styli and coxal vesicles. [33] Paired pretarsal claws and [34] the multi-segmented filamentous cerci may provide further support, but the phylogenetic interpretation is ambiguous (Klass and Kristensen, 2001: 268).

A clade Collembola + Protura (=Ellipura) has not been obtained in morphology-based cladistic analyses (Bitsch and Bitsch, 1998, 2000, 2004; Beutel and Gorb, 2001, 2006; Giribet *et al.*, 2004: Fig. 1; see also Koch, 1997, 2000a, b, 2001). Yet, [35] the special form of entognathy (see above) is perhaps a good argument, while it also appears possible that the dipluran-type entognathy is derived from it. Further ellipuran apomorphies are [36] the groove-like "linea ventralis" along the ventral midline of the labium and cervical region (Willmann, 2005a: Fig. A.6) and [37] the transformation of distal parts of the anterior abdominal appendages to vesicle-like structures (apical vesicles of ventral tube in Collembola and of abdominal appendages 1–3 in Protura; see Klass and Kristensen, 2001: 277).

A clade Collembola + Diplura + Insecta is indicated by [38] a character of the primary embryonic sheath (serosa): Protura are the only Hexapoda in which the serosa contributes to the final dorsal wall of the animal, as in Crustacea and Myriapoda, while in the remaining hexapods this feature has become lost (Fukui and Machida, 2006; Machida, 2006).

Most molecular analyses have obtained a clade Diplura + Protura (Wheeler *et al.*, 2001: Fig. 12A; Giribet *et al.*, 2004: Fig. 2; Kjer, 2004; Luan *et al.*, 2005; Kjer *et al.*, 2006; Mallatt and Giribet, 2006), based on a variety of different analytical methods, and often with strong support. Collembola are most frequently found as the sister group to Diplura + Protura (Kjer, 2004; Luan *et al.*, 2005; Kjer *et al.*, 2006; Mallatt and Giribet, 2006), confirming the Entognatha hypothesis; only in Wheeler *et al.* (2001: Fig. 12A) they are sister to Insecta.

In consequence, the relationships among Collembola, Protura, Diplura, and Insecta remain unclear.

4. **Basal relationships in Insecta**

Monophyly of Archaeognatha

This is supported by [39] the very large, dorsally contiguous compound eyes, [40] the bilobed glossa and paraglossa, [42] a triangular projection on the first maxillary palpomere, and [43] the absence of tracheal spiracles on abdominal segment 1 (see Sturm and Machida, 2001: Figs. 8.8, 8.9, 8.62, 8.63). Sturm and

Machida (2001: 189f) and Bitsch and Bitsch (2004) list further potential autapomorphies, most of which, however, appear less conclusive in the one or the other way.

Monophyly of Dicondylia

[44] The median fusion of the anterior tentorial arms appears to be unique to the Dicondylia and clearly supports this group. All other characters are ambiguous to some extent: [45] The additional anterior articulation between mandible and head capsule (Staniczek, 2000; Fürst von Lieven, 2000; Koch, 2001: 153) and [46] the epistomal sulcus (clypeofrontal sulcus; traversing between the anterior bases of the mandibles) are among the most well-known autapomorphies proposed for Dicondylia. The articulation is fairly loose in Zygentoma *s. str.*, *Tricholepidion*, and nymphs of Ephemeroptera (actually two closely adjacent articulations with the base of the anterior tentorial arm and the margin of the clypeus), while Odonata and Neoptera have a tight ball-and-socket joint. However, Collembola also show articulation-like differentiations at the anterior base of the mandible, and in Archaeognatha the membrane between the sclerite margins is very narrow (Koch, 2001). Furthermore, dicondylic mandibles are widespread in Myriapoda (*e. g.*, Rilling, 1968 for Chilopoda) and Malacostraca. In some subgroups of Malacostraca the anterior articulation shows a very similar structure and location (on the head capsule) as in Dicondylia, and is also associated with an epistomal sulcus (*e. g.*, Schmidt, 1915; Snodgrass, 1950; Manton, 1964; Lauterbach, 1970; Marvillet, 1978). [47] The gonangulum-sclerite of the ovipositor is even more doubtful as an autapomorphy of Dicondylia, because its two precursor sclerites (laterocoxite and praecoxite in Bitsch, 1974; Klass, 2003a: Fig. 64) are still separated in ovipositor-bearing Odonata (fused only in *Epiophlebia*) and some basal Dermaptera, as they are in Archaeognatha (Klass, 2003a: 202, 2008).

Regarding some further apomorphies shared by Zygentoma *s. str.* and Pterygota, data on *Tricholepidion* are lacking, and these apomorphies either support Dicondylia, or Dicondylia excluding *Tricholepidion*: [48] The tracheal system has regular connections between the two sides of a segment and between successive segments. Diplura have almost exclusively longitudinal connections (Bitsch and Bitsch, 1998), for which positional correspondence with those in Dicondylia is unclear, and Archaeognatha have at most some scattered longitudinal and transverse connections (Stobbart, 1956; Sturm and Machida, 2001). [49] The egg has a micropyle for fertilization (Sturm and Machida, 2001: 173). [50] In the mature embryo the frons of the head bears an unpaired egg tooth (Sturm and Machida, 2001: 173); however, an egg tooth has so far been reported only for few subgroups of Pterygota (*e. g.*, Matzke and Klass, 2005: 112, references therein). For two further characters the polarity is unclear: [51] The septum that separates the lumen of the cercus from the remaining hemolymph space is non-muscular in Archaeognatha but muscular in Zygentoma *s. str.* and Ephemeroptera (Gereben-Krenn and Pass, 1999, 2000; Pass *et al.*, 2006). [52] Ontogeny starts with a completely superficial cleavage (Kristensen, 1998; Sturm and Machida, 2001: 173; see data in Bitsch and Bitsch, 1998 for ambiguous polarity).

The monophyly of Dicondylia is supported in all morphology-based cladistic analyses (Beutel and Gorb, 2001, 2006; Bitsch and Bitsch, 2004; Giribet *et al.*, 2004: Fig. 1) as well as in most molecular-based analyses (Wheeler *et al.*, 2001: Fig. 12A; Kjer, 2004; Luan *et al.*, 2005; Kjer *et al.*, 2006; Mallatt and Giribet, 2006). On the other hand, Edgecombe *et al.* (2000) did not find a monophyletic Dicondylia using H3 and U2 snRNA sequences. Regier *et al.* (2004) in their combined analysis of EF-1 α, EF-2, and Pol-II found support for Archaeognatha + Zygentoma as sister to Pterygota (based on several analytical methods but with low support). Kjer *et al.* (2006) found that the mitochondrial COI, COII, 12S, and 16S data also support such a clade. Giribet *et al.* (2004: Fig. 2) obtained Archaeognatha + Zygentoma as a subgroup of Pterygota based on nuclear rRNA, COI, 16S, and H3 sequences.

Monophyly of Zygentoma s. str. *(excl.* Tricholepidion*)*

Zygentoma *s. str.* includes the Lepismatidae, Nicoletiidae (incl. Atelurinae), Protrinemuridae, and Maindroniidae (Koch, 2003). Its monophyly is difficult to substantiate. [53] The flat habitus with horizontally orientated, dorsoventrally flattened coxae and femora and with coxal excavations receiving the femora (Koch, 2003; Willmann, 2003, 2005a; Bitsch and Bitsch, 2004; all less distinct in *Tricholepidion*) was a favourable precondition for the evolution of flight (Hasenfuss, 2002) and may thus be plesiomorphic for Dicondylia. [54] The round lenses of the ommatidia (Koch, 2003) are not very conclusive in view of the general reduction of compound eyes in Zygentoma. [55] The loss of ocelli is also not very convincing in view of the multiple independent loss of ocelli in Neoptera. [56] The conjugation of the spermatozoa is structurally inhomogeneous (see below).

A few characters contradict the monophyly of Zygentoma *s. str.*: [57] The fusion of the anterior and posterior parts of the tentorium in Maindroniidae and Pterygota (Koch, 2003) is a potential synapomorphy of these taxa. [58] Winglike processes on the anterior tentorial arms that bear part of the mandibular adductor attachments occur in Lepismatidae and Maindroniidae (Koch, 2003) but also in at least Mantodea and Phasmatodea among the Pterygota (Klass and Eulitz, 2007; see muscle 21 in Levereault, 1938 for Mantodea). Zygentoma *s. str.* vary a lot with regard to [59] the presence of styli and coxal vesicles and the fusion of coxites and eusternite in the pregenital abdomen (*e. g.*, Bitsch, 1979: 344f). Since Pterygota always lack pregenital styli and coxal vesicles, and have coxites and sternites fused, this character complex would include apomorphies shared between Pterygota and subgroups of Zygentoma *s. str.*

Giribet *et al.* (2004: Fig. 2) and Regier *et al.* (2004, 2005) are the only molecular contributions that include more than one family of Zygentoma *s. str.*: Lepismatidae and Nicoletiidae. In their analyses these taxa group together, but one should note that in the same analyses a clade Archaognatha + Zygentoma is obtained.

Monophyly of Pterygota

With the evolution of flight the entire skeletomuscular system of the thorax has undergone extensive structural transformation (Boudreaux, 1979; Hasenfuss, 2002, 2008). The most evident autapomorphy of Pterygota is [60] the presence of wings on the meso- and metathorax. At an early stage of wing evolution all three thoracic segments were involved, as shown by small, winglike, veined lateral lobes on the prothorax of many Carboniferous Pterygota from several major subgroups (*e. g.*, Kukalová-Peck, 1978, 2008; Bechly *et al.*, 2001; Grimaldi and Engel, 2005). The wings constitute a very complex character system comprising many features of the venation and basal articulation that are shared by all Pterygota. Further autapomorphies in the pterothoracic segments of Pterygota (according to Hasenfuss, 2002, 2008) are [61] the fusion of certain sclerites between coxa and wing base that formerly had been discrete podomeres; [62] the extensive sclerotization of formerly membraneous areas; [63] the pleural sulcus; [64] the separation of the basalar sclerite from the other sclerotizations of the most proximal former podomere; and [65] the formation of the subalar sclerite. A further character is [66] the delimitation of a posterior sclerite portion (scutellum) by a curved sulcus. The scutellum also serves as a pump case for the underlying enlarged part of the heart (Pass, 2000). In the circulatory system (Pass, 1991, 1998; Pass *et al.*, 2006), [67] the paired circumoesophageal vessels are absent (present in Collembola, Diplura, Archaeognatha, and Zygentoma). [68] The legs have diaphragms consisting of connective tissue, which separate the distally and proximally directed hemolymph currents. [69] The endoskeleton made from connective tissue, which in apterygote Hexapoda serves for the attachment of many muscles, has been lost almost completely (Birket-Smith, 1974; Boudreaux, 1979: 188; see character [112] for vestiges in Dictyoptera). [70] The lateral parts of abdominal tergite 11 are reduced and fragmented, or absent. Thereby the dorsal base of the cerci is in contact with the hind margin of tergite 10 (Klass, 2001a: Figs. 29–36), and dorsal longitudinal muscles of segment 10 come to act as cercal muscles. [71] The delimitation of lateral cervical sclerites from prothoracic sclerotizations could be a further autapomorphy of Pterygota (Boudreaux, 1979: 189; Weidner, 1982: 154), but a clear interpretation requires a comprehensive evaluation of the published data across Insecta.

On the other hand, [72] the evidence from the fusion of the anterior and posterior parts of the tentorium is ambiguous (see character [57]). [73] The direct transfer of a spermatophore (or sperm) to the female genitalia *via* a male copulatory organ is also an ambiguous pterygotan autapomorphy, because a transfer from the male genital opening to the female is found in Ephemeroptera and Neoptera, whereas in Odonata the sperm is first transferred from the male genital opening to a male copulatory organ on abdominal segments 2 and 3, and only then to the female genitalia.

Most molecular studies confirm the monophyly of Pterygota (Wheeler *et al.*, 2001; Hovmöller *et al.*, 2002; Terry and Whiting, 2005; Kjer *et al.*, 2006; Mallat and Giribet, 2006). Only Giribet *et al.* (2004: Fig. 2) obtain Archaeognatha + Zygentoma as a subgroup of Pterygota, and Giribet *et al.* (2001) find the long branch taxa *Drosophila* and Japygidae in a group with Crustacea, remote from other pterygotans. In Kjer (2004) *Tricholepidion* is, with weak support, nested in Pterygota as sister to Odonata.

Relationships between Tricholepidion, *Zygentoma* s. str., *and Pterygota*

Among the synapomorphies proposed for *Tricholepidion* and Zygentoma *s. str.*, [74] the four-segmented labial palps (Staniczek, 2000) is perhaps the most convincing, as this is apparently neither reported for apterygotes nor for basal Pterygota. All other characters are problematic. Parallel evolution is required for [75] the reduction of the hypopharyngeal superlinguae (also true for most Pterygota), and for [76] the enlarged apical labial palpomere (also found in some Pterygota and Archaeognatha; see Staniczek, 2000; Sturm and Machida, 2001: 86). [77] Some kind of sperm conjugation is present in *Tricholepidion* and all families of Zygentoma *s. str.*, but it is achieved in several different ways that can hardly be considered as including a shared apomorphy (Dallai *et al.*, 2001, 2002, 2004). [78] The hook-like condyle at the dorsal base of the cerci that is articulated upon the free, overhanging hind edge of abdominal tergite 10 (Koch, 2003) could indeed be a precursor structure of the simpler articulation between cercal base and hind margin of tergite 10 in many Ephemeroptera and Neoptera (intercorrelated with character [70]; Klass, 2001a). The articulation could thus as well be an autapomorphy of Dicondylia. *Tricholepidion* and Nicoletiidae share [79] special sensilla on the underside of the terminal filament of males (Wygodzinsky, 1961; Kristensen, 1991); however, a re-examination of this character in a selection of Zygentoma and Ephemeroptera species is advisable.

A clade Zygentoma *s. str.* + Pterygota receives support from [80] the complete loss of lateral genal folds and resulting exposure of the mouthpart bases; [81] the loss of the zygomatic ligament connecting the ventral mandibular adductors of the two sides; [82] the origin of the posteriormost mandibular adductors on the tentorium (Staniczek, 2000 for these head characters); and by [83] the non-segmental arrangement of the ovarioles (Barnhart, 1961: 192; Bitsch and Bitsch, 1998) contrasting the segmental arrangement in Japygina, Archaeognatha, and *Tricholepidion* (Štys *et al*., 1993: Table 1, Fig. 2). Staniczek (2000) proposes [84] the presence of a muscle connecting the mandible and hypopharynx as a further argument, but a similar muscle is found in Archaeognatha and Collembola (Bitsch, 1963: 632).

Among the morphology-based cladistic analyses, *Tricholepidion* is sister to Zygentoma *s. str.* in Giribet *et al*. (2004: Fig. 1), but to the remaining Dicondylia in Beutel and Gorb (2001) and Bitsch and Bitsch (2004). Beutel and Gorb (2006) obtain an unresolved trichotomy of *Tricholepidion*, Zygentoma *s. str.*, and Pterygota. Molecular analyses are also contradictory. 18S data alone let *Tricholepidion* appear as the sister group of Odonata (but with weak support; Kjer, 2004). Kjer *et al*. (2006), including several genes, obtained *Tricholepidion* sister to the remaining Zygentoma. In Giribet *et al*. (2004: Fig. 2) *Tricholepidion* is subordinate in Zygentoma. Terry and Whiting (2005), applying various alignment parameters to 18S, 28S, and H3 sequences, found *Tricholepidion* as the sister group of Zygentoma *s. str.* + Pterygota.

The evidence concerning the relationships between *Tricholepidion*, Zygentoma *s. str.*, and Pterygota is thus extremely contradictory both based on morphological and molecular data. Since the monophyly of Zygentoma excl. *Tricholepidion* is also hardly supported, the basal splitting events in Dicondylia are altogether obscure.

5. Basal relationships in Pterygota

Monophyly of Neoptera

This clade is difficult to argue from a morphological perspective. [85] Neoptery has long appeared as the most evident autapomorphy of this clade. It means the ability to swing both pairs of wings backward horizontally so that they lie on the abdomen, forewings covering hindwings and all anterior wing margins directed (ventro-) laterally. This neopterous condition is based on a special architecture of the 3rd axillary, a special function of the (plesiomorphic) muscle attached to it, a membraneous gap between certain axillary sclerites and their associated wing veins, and flexion lines within the wing base (*e. g*., Hennig, 1969: 151f, Fig. 25A; Boudreaux, 1979: 201; Hörnschemeyer and Willkommen, 2007). Neoptery allows for entering clefts or crevices in order to search for food or shelter, and it furthermore enables adaptation to life in narrow spaces without the need to give up the ability to fly. It often goes along with a hardening of the forewings into tegmina that also protect the more delicate hindwings.

In recent years, however, many leading workers have tended to consider neoptery as the plesiomorphic condition for Pterygota (Brodsky, 1994; Willmann, 1998; Kukalová-Peck, 2008; Willkommen, 2008; Hörnschemeyer and Willkommen, 2007, leave the question of polarity open). Palaeoptery, found in Ephemeroptera, Odonata, and most Palaeodictyopteroidea†, is then regarded as having evolved several times independently; for Ephemeroptera and Odonata it is variously considered homologous (*e. g*., Kukalová-Peck, 2008) or homoplastic (Willkommen, 2008).

[86] The arolium between the praetarsal claws may be an autapomorphy of Neoptera (Beutel and Gorb, 2006), but if so it has been lost so frequently that in the cladistic analysis of Beutel and Gorb (2006) it is not confirmed as such. [87] The gonoplacs of the ovipositor forming a sheath around the two pairs of gonapophyses (*e. g*., Kristensen, 1975; Grimaldi and Engel, 2005: 158) is not a convincing autapomorphy of Neoptera, as this condition is discrete only in a few neopteran subgroups, while others (*e. g*., Dermaptera, Dictyoptera) do not differ distinctly in this respect from Odonata (Ephemeroptera lack an ovipositor).

Neoptera result as monophyletic in nearly all molecular-based phylogenetic analyses, based on a variety of nuclear and mitochondrial genes and different analytical methods (Wheeler *et al*., 2001; Hovmöller *et al*., 2002; Kjer, 2004; Terry and Whiting, 2005; Kjer *et al*., 2006; Mallatt and Giribet, 2006). In some of Cameron *et al*.'s (2006a; mitochondrial genome) analyses, however, the Odonata are subordinate in the Neoptera (close to Orthoptera), though with low support.

Relationships between Ephemeroptera, Odonata, and Neoptera

The relationships between these taxa have long been controversial, and all three possible hypotheses still receive support by part of the data. Characters of the flight apparatus are difficult to apply to this problem, because the basalmost dichotomy in Pterygota is here the issue, and potential outgroup taxa are wingless (wing characters are briefly summarised in Willkommen, 2008: 290ff).

The hypothesis of a Odonata + Neoptera clade (=Metapterygota) appears most convincing from the morphological point of view (Kristensen, 1991; Beutel and Gorb, 2006). [88] The anterior mandibular articulation is a ball-and-socket joint with the ginglymus (acetabulum) on the mandible and the condyle on the head capsule (Staniczek, 2000). In correlation with the resulting limitation of mandibular movements, [89] several mandibular muscles have become lost (Staniczek, 2000). Nonetheless, the very similar articulation in many Malacostraca must be kept in mind (see character [45]). [90] Odonata and Neoptera do not have imaginal moults as Ephemeroptera (from subimago to imago), Zygentoma, and Archaeognatha (frequent imaginal moults, Sturm and Machida, 2001: 175, 185). [91] The meso- and metathoracic legs and also the wings are supplied by two tracheal stems each, which come from the spiracles of the same and of the following segment. In Zygentoma and Ephemeroptera (usually) the legs and paranota or wings are supplied only by one tracheal stem from the same segment (Ander, 1938; Kristensen, 1975). [92] The heart is closed posteriorly and lacks a valve in its abdominal portion; the hemolymph current is thus directed anteriad along the entire heart (Pass *et al*., 2006). In Diplura, Archaeognatha, and Zygentoma the heart is open posteriorly, but it is also closed in Collembola and Protura. [93] Odonata and Neoptera have a nervous connection between the corpora cardiaca and corpora allata, which is absent in Ephemeroptera and in apterygote hexapods. However, for one ephemeropteran species such a nerve has been reported (see Kristensen, 1975). On the other hand, [94] occlusor muscles on the abdominal spiracles (Kristensen, 1991; Beutel and Gorb, 2006) cannot be considered a synapomorphy of Odonata and Neoptera. First, the occlusors of Odonata and Neoptera show a very different spatial arrangement (Miller, 1962; Poonawalla, 1966; Klass, 2008: 101f); second, the zygentoman *Thermobia* has spiracle muscles in the posterior abdominal segments that show positional correspondence with those in many Neoptera (Rousset, 1973; Klass and Kristensen, 2001: Figs. 14, 15). [95] The near-complete reduction of the terminal filament (Beutel and Gorb, 2006) is neither a convincing character, because in some Palaeozoic relatives of Odonata the filament is fairly long and probably jointed (Bechly *et al*., 2001: Fig. 12). At most a moderate reduction could be synapomorphic for Odonata and Neoptera. For [96] the absence of the tentorio-lacinial muscle (present in Archaeognatha and Ephemeroptera, but not reported for Zygentoma) and [97] the absence of superlinguae (present in Archaeognatha and Ephemeroptera, but not in Zygentoma; see Kristensen, 1991: 131) interpretations are ambiguous (Kristensen, 1975 and references therein).

The hypothesis Ephemeroptera + Odonata (Palaeoptera), favoured by *e. g*., Kukalová-Peck (1997, 2008), Bechly *et al*. (2001), and Soldán (2003), has been advocated mainly based on characters from the venation and articulation of the wings, though for such characters polarity is difficult to argue. One character concerns [98] the presence of intercalary veins: parts of the archaedictyon (a network of crossveins between the main wing veins) are rearranged to form long, straight lines in between the main veins. It is noteworthy, however, that the putatively most plesiotypic Odonatoptera (Carboniferous Geroptera) neither had intercalary veins nor an archaedictyon (*e. g*., Willmann, 2005a: 29; Grimaldi and Engel, 2005: 174). [99] A basal brace between the posterior cubital and anterior anal veins (cup–aa1) also occurs in Plecoptera (Béthoux, 2005). [100] A common stem of the anterior and posterior sectors of the media (MA, MP; Haas and Kukalová-Peck, 2001: 494, Table 6A) is also wide-spread in Neoptera (see Kukalová-Peck, 1991; Kristensen, 1991: 131). [101] The short antennae (Hennig, 1969) have likely evolved independently in Odonata and Ephemeroptera, as distinctly longer antennae probably occurred in Palaeozoic relatives of both taxa (Brauckmann and Zessin, 1989; Grimaldi and Engel, 2005: 167). It has been proposed that in nymphs of both Ephemeroptera and Odonata [102] the galea and lacinia are fused. However, the character is ambiguous due to conjectural homologisation of the two terminal maxillary processes in Odonata with the palpus, galea, and lacinia (*e. g*., Matsuda, 1965).

The poor morphological arguments for a clade Ephemeroptera + Neoptera mostly refer to direct sperm transfer and to the flight apparatus, especially which thoracic muscle groups cause the movements relevant to flight (*e. g*., Boudreaux, 1979: 195f). These arguments are strongly weakened by problems with character polarity.

Molecular results are contradictory. All analyses depend much on 18S and 28S rDNA data, and incongruence mainly results from analytical differences. A clade Ephemeroptera + Neoptera is obtained in Kjer (2004: 18S) and favoured by Mallat and Giribet (2006, but with Ephemeroptera and Odonata represented by only one species each). In contrast, Wheeler *et al*. (2001: Fig. 12A) recover Odonata + Ephemeroptera. Such a Palaeoptera clade is also supported in Hovmöller *et al*. (2002: 18S and 28S), but this analysis used an unadjusted Clustal alignment and a gapcost 75 × that of nucleotide changes. The analyses by Kjer *et al*. (2006) find the same relationships using the combined data, while separate analyses of both EF-1 α and the 18S+28S rRNA support Ephemeroptera + Neoptera. Terry and Whiting (2005) did not present a separate molecular hypothesis and support Odonata + Neoptera under inclusion of (dubious) morphological data. Ogden and Whiting (2003) showed that the result of Hovmöller *et al*. (2002) is supported only under a narrow range of alignment parameters; using additional sequence data (18S, 28S, H3) for a broader selection of taxa, and applying a wider range of analytical methodologies, they conclude that their analyses could not clearly resolve relationships among the three taxa.

6. Basal relationships in Neoptera

The basic situation

Kristensen (1991: Fig. 5.5) showed a basal neopteran polytomy including ten lineages: Plecoptera, Dictyoptera, Notoptera, Dermaptera, Orthoptera, Phasmatodea, Embioptera, Zoraptera, Acercaria, and Endopterygota. Later Mantophasmatodea (described in Klass *et al*., 2002) has been added as an eleventh lineage. Efforts to resolve this polytomy on a morphological basis suffer from the vast incompleteness of the database (especially on the musculature, nervous system, and internal organs), and from an extensive inconsistence among characters. Altogether the relationships among the eleven lineages are obscured by such extensive contradictions that shared apomorphies can be found for numerous incongruent groupings. Cladistic analyses such as Beutel and Gorb (2001, 2006) must be seen as very preliminary because of the incomplete data available. The situation is not better with molecular-based analyses. Different data sets usually yield very different results for the basal neopteran relationships (compare *e. g*., nuclear sequences in Terry and Whiting, 2005 and mitochondrial data in Cameron *et al*., 2006b), and strong differences may also occur when the same data are subjected to different methods of alignment and tree construction (see trees in Terry and Whiting, 2005). It is thus not surprising that in recent years a number of mutually incongruent morphology- or molecular-based hypotheses on basal neopteran relationships have been proposed.

Molecular evidence on neopteran relationships

Wheeler *et al*. (2001: Fig. 12A, 18S + 28S) found a basal split between (Phasmatodea + Dictyoptera + Orthoptera + Embioptera + Acercaria) and (Dermaptera + Plecoptera + Zoraptera + Endopterygota). The analyses by Kjer (2004: 18S) and Kjer *et al*. (2006: several genes), both excluding Zoraptera, yielded a sistergroup relationship between Plecoptera + Dermaptera and the remaining Neoptera, which included a monophyletic group containing Notoptera + Mantophasmatodea, Phasmatodea + Embioptera, and Dictyoptera. Terry and Whiting (2005: 18S + 28S, H3) obtained the monophyla Phasmatodea + Orthoptera + Embioptera, Dermaptera + Plecoptera + Zoraptera, and Notoptera + Mantophasmatodea; the relationships among these groups and the remaining neopteran taxa (Dictyoptera, Acercaria, Endopterygota) are very different depending on the alignment parameters used. The conflicts among the mentioned analyses stems mostly from the analytical methods employed. The support values for groupings comprising several principal lineages of Neoptera are very low in most cases. But even for clades with high support values, there can be contradictory evidence. For example, Terry and Whiting (2005) and Kjer *et al*. (2006) found Mantophasmatodea + Notoptera strongly supported by nuclear rDNA, while Cameron *et al*. (2006b) in an analysis of the whole mitochondrial genome, and Kjer *et al*. (2006) using parts of it, found Mantophasmatodea + Phasmatodea distinctly supported.

Morphological evidence on neopteran relationships

First it is noteworthy that several of the principal lineages of Neoptera show features that appear uniquely plesiomorphic at the neopteran or even pterygotan level; the absence of the respective feature would support the monophyly of all neopteran lineages under exclusion of the lineage in question.

Plecoptera show a particularly great number of such plesiomorphies, though for most of these characters the interpretation includes problems. [103] Plecoptera have cercal vessels, which are otherwise found in Diplura, Archaeognatha, Zygentoma, and Ephemeroptera (condition unknown in Odonata) but not in neopterans (Pass *et al*., 2006: characters 10, 11). However, this character cannot be judged in the many taxa with reduced or absent cerci (mainly Phasmatodea, Orthoptera, Acercaria, Endopterygota, Zoraptera). [104] In plecopteran nymphs a strand composed of muscular and connective tissue has been found that connects the upper and lower walls of the maxillary stipes (Moulins, 1968: ts in Fig. 12; "transverse stipital muscle" in Moulins, 1968, Kristensen, 1991, and Beutel and Gorb, 2001, 2006). It shows positional correspondence with ligamentous structures in Zygentoma (Chaudonneret, 1950: dsa in Fig. 42) and Archaeognatha (Bitsch, 1963: maxillary ligaments lmx1 and lmx2 in Fig. 45), and has not been reported for other Pterygota (*e. g*., Rähle, 1970: Table 3). However, these delicate strands may have been overlooked in other studies, and they have been documented only for nymphs of Plecoptera, while there are no studies of the nymphal mouthpart musculature in other lower neopteran taxa. Moreover, Zygentoma and Archaeognatha have additional intrinsic stipital ligaments located further posteriorly, and these have so far been found only in Embioptera (Rähle, 1970: B2 in Table 3 and p. 265). In the abdominal nervous system [105] most Neoptera have a lateral nerve B giving origin to the branches to the ventral body wall and to the mid-segmental lateral (dorsoventral) muscles. In Plecoptera these branches originate from the ventral nerve C and the dorsal nerve A, respectively, as in Zygentoma

(Birket-Smith, 1974) and Ephemeroptera (Birket-Smith, 1971). Nonetheless, innervation of lateral muscles by a branch of nerve A is also sporadically found in Embioptera and Phasmatodea, and the formation of a nerve B is thus an ambiguous autapomorphy of non-plecopteran Neoptera (Klug and Klass, 2007). Plecoptera are the only known Neoptera where [106] the abdominal dorsal nerves A arise from the CNS in front of their ganglia (Klug and Klass, 2007), as in Zygentoma (Heckmann and Kutsch, 1995). However, Ephemeroptera (Klug and Klass, 2007) and Odonata (Klass, 2008: Fig. 16) correspond with the non-plecopteran Neoptera in the origin of nerve A from its ganglion. [107] The segmentally arranged outlet tubes of the testis in many Plecoptera can perhaps also be considered a unique plesiomorphy (Zwick, 1980: 67ff). Altogether, most of the characters supporting a basal position of Plecoptera inside Neoptera are somewhat ambiguous. In Beutel and Gorb (2006) the sistergroup relationship between Plecoptera and the remaining Neoptera was based on character [104], while characters [103] and [105]–[107] were not included.

Potential unique plesiomorphies of Notoptera are [108] the presence of a metathoracic spina (posteromedian ventral apodeme; Walker, 1938: ss3 in Fig. 3); [109] the absence of a closing mechanism (sclerites and muscles) on the abdominal spiracles (Walker, 1943; if this is actually plesiomorphic for Pterygota: see character [94]); and [110] the presence of a median eversible sac on abdominal venter 1, which has been interpreted as the medially fused eversible vesicles of this segment (*e. g.*, Kristensen, 1991: 130) – a view consistent with the presence of paired retractor muscles from coxosternum 1 (Walker, 1943: muscle 141).

Two other unique plesiomorphies occur in Dictyoptera: [111] The proventriculus of many Blattaria is very similar to the complicated proventriculus of lepismatid Zygentoma (Klass, 1998a). However, this issue is ambiguous because the proventriculus is very simple in other Zygentoma and many Pterygota (see Klass, 1998b). [112] Blattaria and Isoptera are the only Neoptera that have in their abdomen simplified vestiges of a tendinous endoskeleton (Klass, 1999; Klug and Klass, 2007): segmental plates within the hyperneural muscle, showing positional correspondence with segmental ligaments of Zygentoma (see Klass, 2001a: Fig. 37).

A unique plesiomorphy on the pterygotan level is [113] the presence in many basal, ovipositor-bearing Dermaptera of coxal lobes in the female genitalic region not only in segment IX (3rd valves=gonoplacs) but also in segment VIII (Klass, 2003a: gl8 in Figs. 18, 23, 41). This complies with the presence of coxal lobes VIII in Archaeognatha and Zygentoma, which are absent in other Pterygota.

One of the few inner-neopteran relationships that in recent years has been increasingly confirmed – though again without some counterevidence – is the sistergroup relationship between Acercaria and Endopterygota (clade Phalloneoptera =Eumetabola). Several potential synapomorphies are reported for the flight apparatus (Haas and Kukalová-Peck, 2001; Kukalová-Peck and Lawrence, 2004; Hörnschemeyer and Willkommen, 2007; see also Beutel and Pohl, 2006: 204): [114] a sclerotization on the jugum of the wing (jugal bar; see also Hamilton, 1972a, b; Kristensen, 1991: 135); [115] a broad, lobate base of the radius; [116] an elongate base of the media; [117] a triangular shape of the 2nd axillary; [118] an additional muscle inserting on the 3rd axillary, which thus has two muscles rather than only one (see also Matsuda, 1970). Note that these wing characters cannot be assessed in the consistently wingless lineages Notoptera and Mantophasmatodea. In addition, [119] the sternites of the meso- and metathorax are infolded along the midline (pterothoracic endosterny; Kristensen, 1991; Willmann, 2005a). [120] The male copulatory organs show a special, probably apomorphic mode of ontogeny: a pair of mesomeres fuses to form an aedeagus, beside which there is a pair of free, lateral parameres (*e. g.*, Boudreaux, 1979: 222). However, the exposed thoracic sternites of some Acercaria and the absence of an aedeagus in Acercaria-Psocodea constitute problems. [121] Structural details of the ovarioles may also support phalloneopteran monophyly (Büning, 1994, 1998; Kristensen, 1995). Moreover, there are some apomorphic features in the female genitalia (Klass, 2003a: 219, Figs. 77, 78): [122] The coxites IX have anterolateral pouches that give rise to long tendons, and [123, 124] the basal sclerotizations of both gonapophyses 8 and 9 form laterally directed arms. Nonetheless, characters [122]–[124] cannot be assessed in a number of acercarian subgroups and in all Endopterygota excl. Hymenoptera, which have a simplified ovipositor.

The molecular analyses in Kjer (2004) and Kjer *et al.* (2006) weakly confirm a clade Acercaria + Endopterygota, while the results of Wheeler *et al.* (2001: Fig. 12A) contradict it, and Terry and Whiting (2005: combined molecular and morphological data) obtain different results depending on alignment parameters.

The only viable alternative to the Phalloneoptera hypothesis is a sistergroup relationship between Acercaria and Zoraptera, which is discussed below.

Another grouping of neopteran lineages apparently accepted by many authors is the "Polyneoptera," which essentially comprises all Neoptera except for Acercaria and Endopterygota, though depending on the author Plecoptera and/or Zoraptera may additionally be excluded (see *e. g.*, Hennig, 1969; Boudreaux, 1979; Grimaldi and Engel 2005; Willmann, 2005a; other names describing groupings of such content are "Paurometabola" and "Pliconeoptera"). However, this assemblage of Orthoptera, Dictyoptera, Phasmatodea, Notoptera, Dermaptera, Embioptera, and Mantophasmatodea is, whether additionally including Plecoptera and Zoraptera or not, hardly supported. Many of the older arguments were already falsified by Kristensen (1975, 1981, 1991, 1995); like some strongly homoplastic apomorphies (*e. g.*, reduction of tarsomeres, loss of ocelli and wings) these characters are no longer mentioned here. An important point to note is that among the "polyneopteran" taxa *s. l.* there are only two for which considerable evidence exists that they might be more closely related to Acercaria and/or Endopterygota than to other "polyneopterans;" these are the Dermaptera and the Zoraptera discussed below.

One character may support a group Plecoptera + Orthoptera + Dictyoptera + Phasmatodea + Dermaptera + Embioptera + Notoptera (while Mantophasmatodea cannot be assessed due to lacking examination): In addition to the usual incurrent ostia, [125] the heart has also excurrent ostia. However, the segmental distribution of these varies strongly, and while in Plecoptera and Embioptera the ostia are unpaired and medioventral, they are paired in Dermaptera, Dictyoptera, Notoptera, Phasmatodea, and Orthoptera (Nutting, 1951; Pass *et al.*, 2006; see Barnhart, 1961 for absence in Zygentoma).

A clade Plecoptera + Orthoptera + Dictyoptera + Phasmatodea + Dermaptera + Notoptera + Mantophasmatodea (*i. e.*, under exclusion of Embioptera) may be indicated by two apomorphies, the first of which, however, is not applicable to the wingless Notoptera and Mantophasmatodea. This is [126] the enlarged hindwing anal field, which in repose is folded several times. However, since the extent to which different main veins contribute to the anal field varies considerably among the taxa (*e. g.*, Haas and Kukalová-Peck, 2001; Béthoux, 2005), it is disputed whether this character can be fully homologized among taxa. In addition, this wing area has often undergone strong secondary reduction (*e. g.*, Isoptera, subgroups of Plecoptera), which further reduces the conclusiveness of this character. [127] Tarsal euplantulae are found in all taxa listed above (*e. g.*, Beutel and Gorb, 2001, 2006; Willmann, 2003, 2005a), but are (secondarily?) absent in several subgroups of these.

Only a single highly doubtful wing character can be mentioned in favour of the narrower grouping Orthoptera + Dictyoptera + Phasmatodea + Dermaptera (+ perhaps Notoptera and Mantophasmatodea, which cannot be assessed): [128] the moderately increased sclerotisation of the forewings (tegmina). One problem is the absence of forewing enforcement in basal Mantodea (Smart, 1956) and its weakness in some members of Dictyoptera and Orthoptera (Kristensen, 1975: 12). Another problem is the presence of tegmina (or even elytra) in many Hemiptera and Coleoptera. As the ability to enter clefts or crevices is one of the putative advantages of neoptery, both the presence of some tegminisation in the common ancestor of Neoptera or even Pterygota (with many instances of secondary loss) and a frequent independent evolution of tegminisation appear plausible.

Several authors favour a clade Phasmatodea + Orthoptera based on wing characters (*e. g.*, Haas and Kukalová-Peck, 2001; Willmann, 2003, 2005a), which again cannot be assessed in Mantophasmatodea and Notoptera. Nonetheless, the characters are problematic anyway due to ambiguous vein homologies. Whether Phasmatodea and Orthoptera share [129] an enlarged praecostal field in the forewing (costa remote from anterior wing margin) is difficult to assess, because extant Phasmatodea lack the costa (Willmann, 2003 derives this hypothesis from fossil Phasmatodea that apparently have retained the costa; see also Béthoux and Nel, 2002 and Béthoux, 2006).

A clade Phasmatodea + Orthoptera + Dictyoptera is supported by [130] a special apomorphic musculature of the basal ampullae of the antennal vessels; this was found in all investigated Dictyoptera (4 species) and Phasmatodea (only *Carausius*) but only in part of the examined Orthoptera (Pass *et al.*, 2006: character 8). This musculature was also reported to be absent for a mantophasmatodean (Baum *et al.*, 2007).

A group of similar (but in detail uncertain) composition is indicated by a rearrangement of sclerotizations in the coxites IX (valvifers IX) of the female genitalia, which includes two apomorphies (Klass, 2003a: 203ff). First, [131] a median fusion of the anteriormost parts of the two coxites IX; it occurs in probably all studied Orthoptera, Dictyoptera, Phasmatodea, and Notoptera (but also Archaeognatha, and not in Mantophasmatodea). Second, [132] a specific transverse division of coxites IX by which the medially fused part becomes a discrete, unpaired anterior sclerite. Transverse divisions of coxites IX occur in different ways across Insecta; they can be distinguished by the distribution of muscle attachments on coxite IX (anterior and posterior tergocoxal muscles, coxogonapophyseal muscles) and the articulation of coxite IX with the gonangulum over the resulting sclerites. The different divisions in Archaeognatha, in Dictyoptera and Orthoptera, and in Dermaptera, Acercaria, and Endopterygota (see below) can be defined by these criteria. The specific subdivision here in question is unambiguously present in many Dictyoptera (but absent in many others) and Orthoptera-Ensifera (Klass, 1998c); conditions in Orthoptera-Caelifera and Phasmatodea, however, are difficult to interpret. In Plecoptera, Embioptera, and Zoraptera (and Ephemeroptera) characters [131] and [132] cannot be assessed due to their lack of the ovipositor and related sclerite differentiations.

A clade Dictyoptera + Notoptera is suggested by a single character: [133] a diaphragm in the cercus that separates the distally and proximally directed hemolymph flows (Pass *et al.*, 2006: character 11). Plecoptera show the more plesiomorphic possession of cercal vessels, while at least Mantophasmatodea, Embioptera, Phasmatodea, and Orthoptera lack both vessels and diaphragms. Of course, the application of the character to taxa with reduced cerci is somewhat problematic (compare character [103]).

A clade Phasmatodea + Embioptera is supported by [134] the presence of an operculum at the anterior pole and a single micropyle on the ventral side of the egg (Jintsu *et al.*, 2007) (an operculum is known for many Plecoptera, but probably not in the ground pattern of this taxon: Zwick, 1980). An apomorphy unique to Phasmatodea and Embioptera is [135] the presence of a special dorsal adductor muscle of the paraglossa; probably an adductor of the praementum has become subdivided by gaining an intermediate insertion (Maki, 1935: 194; Rähle, 1970: 303); the distal part is the muscle here in question. However, only a single species per order has been examined. Notoptera cannot be assessed since neither the undivided nor the divided muscles are present (Rähle, 1970: Table 4). For Mantophasmatodea the plesiomorphic condition has been reported (Baum *et al.*, 2007). The clade Phasmatodea + Embioptera is congruent with the molecular results of Terry and Whiting (2005) and of Kjer *et al.* (2006).

Haas and Kukalová-Peck (2001) propose a clade Plecoptera + Embioptera based on wing morphology. The two taxa also share [136] the unpaired excurrent ostia of the heart (Pass *et al.*, 2006; compare character [125]), but it is not clear whether the unpaired or the paired condition (found in other "polyneopterans") is plesiomorphic for these ostia. The lack of male styli and of the ovipositor, and tarsomere reduction, though found in many Neoptera, may be viewed as additional support for this hypothesis.

Regarding Mantophasmatodea, two molecular studies (Terry and Whiting, 2005; Kjer *et al.*, 2006) as well as the morphology-based analysis of Beutel and Gorb (2006) indicate a sistergroup relationship to Notoptera, while for this clade there is virtually no support from morphology. The shared [137] absence of wings and [138] absence of ocelli (the two synapomorphies in Beutel and Gorb, 2006) are weak arguments, because these structures have been lost many times independently in Neoptera and may be functionally correlated (Friedrich *et al.*, 2006). Notoptera and Mantophasmatodea also have [139] a similar proventriculus (Klass *et al.*, 2002), which is probably apomorphic with respect to, *e. g.*, that of Dictyoptera (Klass, 1998a) and the phasmid *Timema* (Tilgner *et al.*, 1999). However, the presence of a strongly simplified (Plecoptera, Embioptera, and Dermaptera) or modified (Orthoptera) proventriculus (which could be derived from conditions as seen in Notoptera and Mantophasmatodea) in other neopteran lineages strongly limits the phylogenetic conclusiveness of this character. Notoptera and Mantophasmatodea share some embryological features, *i. e.*, the manner of blastokinesis and the structure of the chorion (Uchifune and Machida, 2005: 119f; Uchifune *et al.*, 2006).

On the other hand, there is a strong similarity between Mantophasmatodea and Dictyoptera in [140] the construction of the right half of the asymmetrical male genitalia (Klass *et al.*, 2003: 57). This pattern is absent in other Hexapoda (though a re-examination is needed for Notoptera and Phasmatodea). A second character suggesting this relationship concerns [141] the walls of the antennal vessels, which only in Mantophasmatodea and Dictyoptera have a two-layered basal part, with a peculiar inner layer of transporting cells (Pass *et al.*, 2006: Fig. 17).

A more inclusive clade Mantophasmatodea + Notoptera + Dictyoptera + Orthoptera is supported by [142] the presence of "connecting bands" in the flagellum of the spermatozoa (Dallai *et al.*, 2003, 2005).

A clade Mantophasmatodea + Phasmatodea is supported by the analysis of mitochondrial DNA sequences in Cameron *et al.* (2006b) and Kjer *et al.* (2006). The two taxa share [143] a projecting transverse sclerite behind the male genitalia (vomer resp. vomeroid in Klass *et al.*, 2002, 2003). However, different positional relations contradict the homology of these structures (Klass *et al.*, 2002), and it remains to be tested by a comparative study including the muscular connections whether some postabdominal sclerite in Notoptera is a potential homologue. In both Mantophasmatodea and Phasmatodea [144] the euplantulae are covered with acanthae. In addition, Mantophasmatodea and the phasmatodean genus *Timema* (sister to the remaining Phasmatodea; *e. g.*, Bradler, 2005) share [145] characters of the arolium, such as its enormously large size (Klass *et al.*, 2002) and a ventral coverage with acanthae (Beutel and Gorb, 2008). (The two latter characters cannot be assessed in taxa lacking euplantulae and the arolium, respectively.)

Mantophasmatodea also share an apomorphic similarity with many Plecoptera: [146] a flattened process in the middle of the male subgenital plate (Klass *et al.*, 2002: Fig. 2A), used for drumming on the substrate (Eberhard and Picker, 2008). However, this element is unlikely to belong to the ground pattern of Plecoptera (P. Zwick, pers. comm.).

For Dermaptera a close relationship to Acercaria + Endopterygota (if this is a monophylum) is indicated by [147] a special division of coxites IX of the ovipositor (Klass, 2003a: Figs. 77–79; different from the division in character [132]). However, this cannot be assessed in the many dermapteran, acercarian, and endopterygotan subgroups that have the ovipositor reduced, and the same is true for Zoraptera, Embioptera, and Plecoptera. [148] The occurrence of meroistic ovarioles with branched cell clusters is consistent with a group Dermaptera + Acercaria + Endopterygota, though conditions in basal dermapterans remain unknown, and in both Acercaria and Endopterygota several reversals to panoistic ovarioles ("neopanoistic") must be assumed (Kristensen, 1999; Heming, 2003: 54f). In the meroistic ovarioles of Collembola, Diplura-Campodeina, and Ephemeroptera, cell clusters are linear (*e. g.*, Heming, 2003: 41f, Fig. 2.9.).

Apomorphies indicating a clade Dictyoptera + Dermaptera are [149] the large female subgenital plate formed by the coxosternite of abdominal segment VII (Klass, 1998c, 2003a), and [150] the fusion of abdominal ganglion 7 to the terminal ganglion (neuromeres 8–11; Klass, 2001a; the latter apomorphy also applies to Zoraptera and Acercaria with their extensively fused abdominal ganglia). Characters of the wings and of the exoskeleton and musculature of the wing-bearing segments may confirm this relationship (Boudreaux, 1979; Haas and Kukalová-Peck, 2001: 484). This includes [151] the reduction of the dorsal longitudinal muscles and their main attachment sites (phragmata), and of the tergosternal muscles. While usually in Pterygota these muscles strongly contribute to the down- and upstroke, respectively, the downstroke in Dictyoptera and Dermaptera is effectuated by muscles of the basalare and subalare, and the upstroke is accomplished by tergopleural and tergocoxal muscles (see also Kristensen, 1981).

The Zoraptera have been assigned to various positions in the system of Neoptera, but only two hypotheses are supported considerably (see Engel and Grimaldi, 2000, 2002; Grimaldi and Engel, 2005; Beutel and Weide, 2005; Yoshizawa, 2007): zorapteran-acercarian and zorapteran-embiopteran relationships.

Zoraptera + Acercaria (see Hennig, 1969, 1981) has been obtained in the analysis by Beutel and Gorb (2006) based on [152] an extensive fusion of the abdominal ganglia, [153] the cibarium forming a sucking pump, and [154] the slender, elongate maxillary laciniae that lack mesally directed setae. Willmann (2005a) additionally mentions [155] the areola postica, a special configuration in the wing venation formed by a fork of the cubitus anterior. [156] The large and complex clypeobuccal muscle and [157] a median internal ridge on the praementum could tentatively be added to this list (Beutel and Weide, 2005). Characters of the ovipositor cannot be assessed in Zoraptera due to both its reduction (Weidner, 1969) and lack of detailed descriptions; characters [122]–[124] would thus allow for relationships (Acercaria + Zoraptera) + Endopterygota. (See Yoshizawa, 2007 for further discussions.)

Zoraptera + Embioptera receives support from [158] the very heavy hind-tibial depressor muscles resulting in thickened hind femora (Minet and Bourgoin, 1986), and from characters of the hindwing articulation (Yoshizawa, 2007; not applicable to Notoptera and Mantophasmatodea, and not examined in Orthoptera): [159] the enlarged tegula, [160] the detached posterior notal wing process (see Yoshizawa, 2007 for differences to the similar condition in some Endopterygota), [161] the connection of the latter with the 1st axillary, [162] a special subdivision of the basiradial sclerite, and [163] a far posteriorly located attachment of a ventral wing ligament to the 2nd axillary. Yoshizawa (2007) additionally mentions [164] an enlargement of the anterior part of the 1st axillary, but this appears doubtful due to the highly variable proportions and positional relationships of this part of the 1st axillary across the neopteran taxa. Further synapomorphies proposed for Zoraptera and Embioptera, such as subsociality, reduced number of antennal flagellomeres, and others, are too unspecific or homoplastic as to yield much support (Beutel and Weide, 2005: 133). The report of character [160] for a phasmatodean (Yoshizawa, 2007) indicates a clade Phasmatodea + (Embioptera + Zoraptera). Grimaldi and Engel (2005) assume a clade Plecoptera + (Embioptera + Zoraptera), but their arguments are simple reductions (tarsomeres, ovipositor, male styli) found in many neopterans.

Haas and Kukalová-Peck (2001) place Zoraptera in a group also including Dermaptera, Notoptera, and Dictyoptera, but regard this as poorly supported. Relationships between Zoraptera and Dictyoptera have variously been suggested based on zorapteran-isopteran similarities such as [165] wing shedding and [166] presence of different morphs. These apomorphies, however, are in conflict with dictyopteran autapomorphies (Klass, 2003b), as Isoptera now are strongly supported to be subordinate within Blattaria (Klass, 2001b; Lo, 2003; Terry and Whiting, 2005; Klass and Meier, 2006; Kjer *et al.*, 2006; Pellens *et al.*, 2007; Lo *et al.*, 2007; Inward *et al.*, 2007; Ware *et al.*, 2008). Further characters that had been proposed to support zorapteran-dictyopteran relationships are rejected in Beutel and Weide (2005: 133).

Molecular evidence on the placement of Zoraptera is sparse, and the highly derived rDNA sequences pose analytical problems (branch length effects: Yoshizawa, 2007). Zoraptera have been obtained either as sister to

Dermaptera (high support in Terry and Whiting, 2005) or of Dictyoptera (Yoshizawa and Johnson, 2005). There is no morphological evidence for Zoraptera + Dermaptera; Terry and Whiting (2005) mention the one-segmented cerci, but there are fossil representatives of both taxa that have more cercomeres (see Willmann, 2003, 2005a and Yoshizawa, 2007).

7. Conclusions

In recent years a number of morphological character systems were intensely studied in many taxa. The evidence from old and newly found characters was aptly discussed in specialized contributions, and analyses based on large character matrices were conducted. DNA sequence data were acquired for numerous hexapod species (though with a strong focus on a handful of markers), and methods for the analysis of such data were greatly improved. However, character incongruence has so far grown to the same extent as the amount of data, and there has been hardly any improvement with regard to the unresolved parts of hexapod phylogeny. Yet, only a small fraction of the potentially usable data has been made available by now for purposes of phylogeny reconstruction, and this concerns both molecular and morphological data.

In the reconstruction of hexapod phylogeny the principal problems are still the same as they were decades ago: (1) The relationships among Protura, Collembola, Diplura, and Insecta at the base of Hexapoda. (2) The basal relationships in Dicondylia, where the position of *Tricholepidion* either inside a Zygentoma *s. l.* or as the sister group of Zygentoma *s. str.* + Pterygota is still unclear, as is the monophyly of Zygentoma *s. str.* (3) At the base of Pterygota the relationships between Ephemeroptera, Odonata, and Neoptera have remained unresolved. (4) At the base of Neoptera, a polytomy of eleven taxa still appears to represent current knowledge most adequately: Plecoptera, Embioptera, Notoptera, Mantophasmatodea, Dictyoptera, Orthoptera, Phasmatodea, Dermaptera, Zoraptera, Acercaria, and Endopterygota.

Enormous new problems with regard to basal hexapod relationships have appeared since the time-honored Tracheata-hypothesis has become increasingly outcompeted by the Tetraconata-hypothesis. While there is still some evidence left in favour of Tracheata, the Tetraconata-hypothesis indeed includes two very different offers: morphological data (visual system, ontogeny of nervous system) suggest Malacostraca to be the closest relatives of Hexapoda, whereas molecular data favour Branchiopoda in this position. By this ambiguity, outgroup comparison for phylogenetic work on hexapods is presently an extensive task, and full of character conflicts. The matter is further complicated by the ambiguous evidence on hexapod monophyly, which means that phylogenetic work on basal hexapods can only be convincing if embedded in phylogenetic work on mandibulate arthropods, *i. e.*, it must currently consider much of the morphological and genetic diversity found across myriapods and crustaceans. This also requires extensive renewed evaluation of many morphological character systems as well as a close collaboration among researchers specialized on the major mandibulate taxa.

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