REVIEW

Eur. J. Entomol. **91**: 257–275, 1994
ISSN 1210-5759

Phylogeny and classification of extant Arthropoda: Review of hypotheses and nomenclature

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Phylogeny, classification, nomenclature, Arthropoda, Hexapoda, Insecta

Abstract. Recent contributions to extant arthropod phylogeny are reviewed with particular reference to the Hexapoda. Approaches based on morphology, embryology, and paleontology are compared with those derived from molecular data. A new formal classification of the Arthropoda and Hexapoda, based on strict morphological-molecular consensus, is suggested – Arthropoda: 1. Onychophora, 2. Euchelicerata, 3. Pycnogonida, 4. Crustacea, 5. Myriapoda, 6. Hexapoda: 6.1. Parainsecta, 6.2. Campodeina, 6.3. Japygina, 6.4. Ectognatha. Nomenclature of higher-taxa names used as valid in the literature since 1945 is reviewed and commented upon.

CONTENTS

INTRODUCTION

The Arthropoda, the largest animal phylum, are a subject of intense phylogenetic research. The major problem of many of these studies is that few have been able to encompass, critically, this diversified taxon. The pioneering studies of S.M. Manton and D.T. Anderson in comparative arthropod morphology/embryology and evolution should be emphasized. However, our utilization of a different methodology, viz., cladistic, has led us to quite different conclusions.

It is intended to review recent developments and the present state of knowledge of the phylogeny and classification of the Arthropoda, with special reference to the Hexapoda (=

Insecta s. lat.). Our intention is (a) to summarize the many scattered hypotheses based on new information (we do not attempt to provide a new character analysis and to discuss various formal approaches to arthropod classification), (b) to compare and concile the results of morphological and molecular investigations, and make necessary and possibly unorthodox conclusions upon classification, and (c) to provide a check-list of the numerous names of higher taxa (or often informal phylogenetic concepts) used recently. Extant taxa are discussed only and, consequently, many well known concepts are not included.

Our suggested classification of the Arthropoda is based on strict consensus (see Forey et al., 1992: 77–80) of morphological and molecular data. Most higher taxa, such Mandibulata or Uniramia, are mutually exclusive and they cannot be included in such a consensus. Some of these concepts (viz., Mandibulata) appear to be more credible than others (viz., Uniramia). Nevertheless, it is intended that an equivocality of almost all traditional higher taxa is emphasized, rather than our personal beliefs.

Methodological differences between individual authors need to be accentuated. Results of phylogenetic studies are strongly biased by epistemological approaches of their authors. Thus, those who sought morphological or embryological **differences** to indicate multiple origin of arthropods (e.g., Tiegs, Manton, Anderson, Bergström, Jamieson) have found them. Likewise, **synapomorphies** (i.e., uniquely derived evolutionary novelties of "classic cladists", or set-defining characters of "pattern-cladists") have been found by those who sought evidence of the monophyletic status of the Arthropoda. Moreover, Manton and her co-workers and adherents, if they were indeed right, have shown, only, that the common and exclusive ancestor of the Arthropoda was not yet arthropodized (i.e., indicating a multiple origin of the "arthropod" form within the Arthropoda), believing that this demonstrated that the ancestor did not exist (i.e., that the Arthropoda were polyphyletic).

ARTHROPOD PHYLOGENY

Traditional zoologists have never reached general agreement concerning the basic phylogenetic structure of the Arthropoda. They only agree that Atelocerata (Myriapoda + Hexapoda), Hexapoda, Crustacea (see below), and Euchelicerata (Chelicerata excl. Pycnogonida) represent monophyletic taxa. Their interrelationships have never been established, and all possible hypotheses of these have been formulated. This review could be complicated further by the inclusion of extinct arthropods, Tardigrada (where there is no unambiguous information about their systematic position; see, e.g., Willmer, 1990; Meglitsch & Schram, 1991; Eernisse et al., 1992), and Pentastomida (which have been considered as an independent group, related to the onychophorans and/or tardigrades, but, recently, found to be modified crustaceans; see below). The following basic hypotheses are considered:

(A) Arthropoda are monophyletic, with two extant evolutionary lines, chelicerate (Euchelicerata + Pycnogonida) and mandibulate (Crustacea + Atelocerata; see, e.g., Weygoldt, 1978, 1986; Boudreaux, 1979; Wägele, 1993; Fig. 1). These traditional opinions were also derived from the morphological part of the morphological-molecular "combined approach" (Wheeler et al., 1993).

With regard to interrelationships of the Atelocerata, almost all possible hypotheses have been formulated (for reviews of major hypotheses see Sharov, 1966; Anderson, 1973; Boudreaux, 1979; Jamieson, 1987; Dohle, 1988; Enghoff et al., 1993; Fig. 1). Almost full

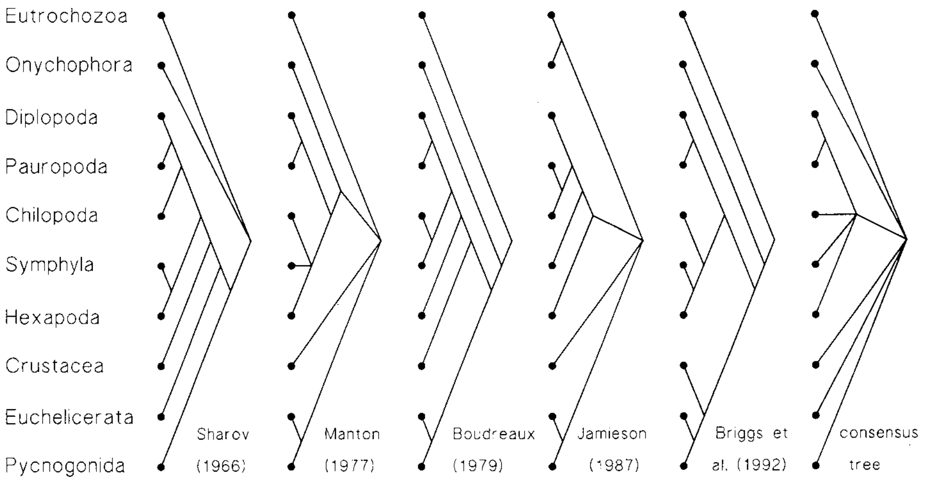

Fig. 1. Examples of published phylogenies of extant Arthropoda (slightly simplified). Manton's (1977) phylogeny was not published in the cladogram form and she did not believe in monophyly of the Hexapoda. Boudreaux's (1979) phylogeny exemplifies the most widely accepted hypothesis. Briggs et al. (1992) explicitly declared their cladogram as "one of six equally parsimonious". Consensus tree does not include the exceptional spermatological view on phylogeny of the Atelocerata (see Jamieson, 1987). Eutrochozoan clade includes Annelida, Mollusca, Sipuncula, etc. (for a review see Eernisse et al., 1992; Conway Morris, 1993); usually, it is represented only by Annelida in traditionally oriented phylogenies. Pentastomida are not included in this scheme.

agreement has been reached on the monophyly of the Dignatha (Diplopoda + Pauropoda; but see below).

Usually, Onychophora and Tardigrada were treated as the arthropod sister groups, and Tardigrada, sometimes, as an independent metazoan clade, perhaps of aschelminth affinities (for a review see Eernisse et al., 1992). Usually, the Annelida (sometimes, including the Echiura, Sipuncula, Lobatocerebrida, Vestimentifera, and/or Pogonophora s.str.: see Conway Morris, 1993) were interpreted as the sister group of the arthropod-onychophoran-(tardigrade?) clade.

(B) Arthropoda are monophyletic, but the atelocerate sister group is the Onychophora (both forming the Uniramia; see Meglitsch & Schram, 1991; Schram, 1991). In other words, Arthropoda plus Onychophora (i.e., Lobopodia sensu Boudreaux, 1979) represent a monophyletic group while the "arthropodized Arthropoda" do not (Budd, 1993).

(C) Arthropoda (either including or excluding the Onychophora) are monophyletic; the Atelocerata are an ancestral offshoot, while Crustacea + Euchelicerata + Pycnogonida represent a monophyletic taxon (Cisne, 1974; Bergström, 1979, 1992; Briggs & Fortey, 1989; Schram & Emerson, 1991; Briggs et al., 1992; Budd, 1993; see Fig. 1).

(D) Arthropoda are polyphyletic. The Onychophora are the sister-group of the Atelocerata (both forming the Uniramia, often including Tardigrada; a traditional

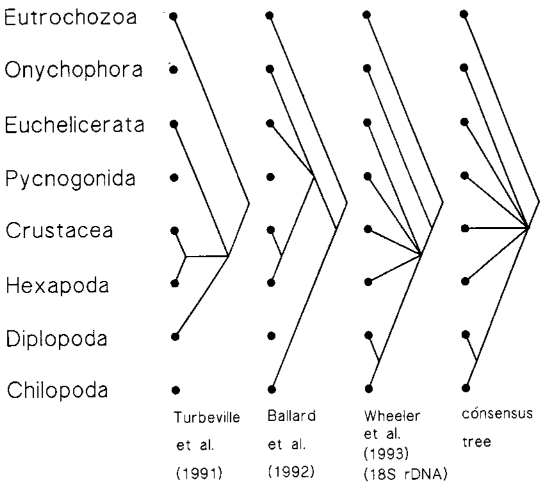

Fig. 2. Phylogeny of Arthropoda based on molecular data. Pauropoda, Symphyla, and Tardigrada have never been studied. Lake's (1990) hypothesis on arthropod paraphyly in terms of the Eutrochozoa is not included in the consensus tree.

polyphyleticist's view shared by Manton, 1972, 1977; Anderson, 1973; Schram, 1978, 1991; Willmer, 1990; and others; Fig. 1).

The arthropod body organization was then evolved from an (unspecified) annelid-like ancestor: either, at least three times, in Euchelicerata + Pycnogonida, Crustacea, and Atelocerata (Manton, 1972, 1977; Anderson, 1973); or twice in Euchelicerata + Pycnogonida? + Crustacea and Atelocerata (Hessler & Newman, 1975; Bergström, 1979, 1992; Budd, 1993: with the position of the Hexapoda unspecified).

(E) Arthropoda are polyphyletic, similarly as in D but, according to Sawyer (1984) and Jamieson (1987; Fig. 1), the Onychophora represent a sister group of (some) clitellate Annelida.

(F) Generally, molecular cladistic studies (Fig. 2) agree that the Arthropoda are monophyletic (Field et al., 1988; Turbeville et al., 1991; Ballard et al., 1992; Wheeler et al., 1993), that they are not related to annelid clade (see below), and that the Arthropoda include Pentastomida (as modified branchiuroid crustaceans: Abele et al., 1989, 1992). Sometimes, the Arthropoda include the Onychophora (Ballard et al., 1992; see Patterson et al., 1993), or, according to Wheeler et al. (1993), Arthropoda and Onychophora are probable sister groups. Exceptionally, Lake's (1990) reanalysis of Field's data, by another numerical algorithm, suggested that arthropods are paraphyletic in terms of the Eutrochozoa (= "protostome eucoelomates", i.e., a mollusc-annelid clade): 1. Diplopoda, 2. Hexapoda, 3.1. Euchelicerata + Crustacea, 3.2. Eutrochozoa.

Molecular cladists never obtain the Atelocerata as a monophyletic group; usually, they agree that the Crustacea + Hexapoda form a monophyletic taxon, excluding myriapods. Only Wheeler et al. (1993) suggest basic pentatomy Pycnogonida-Euchelicerata-Crustacea -Myriapoda-Hexapoda (18S rDNA), which permits many dichotomous solutions (including a monophyletic Atelocerata but also a monophyletic Crustacea + Hexapoda); their combined 18S rDNA-polyubiquitin cladogram appears to prefer the crustacean-hexapod hypothesis.

Unfortunately, Tardigrada, Pauropoda, Symphyla, and some significant taxa of lower rank, such as many chelicerates, crustaceans (namely, Remipedia), and hexapods (Protura, Collembola, Campodeina, Japygina), have yet to be analysed.

(G) There are two recent attempts at a synthesis of morphological and molecular phylogenies (for a general discussion see Patterson et al., 1993). Budd (1993) declares his phylogeny as being based on recent morphological and molecular data (however, not including those by Wheeler et al., 1993); in fact, no published molecular phylogeny accords well with Budd's concept. Seeking a generally acceptable tree, he circumvented the most important molecular conclusions by excluding Hexapoda from his tree "because of uncertainty about their position" (p. 711). His proposed phylogeny (Myriapoda + Onychophora vs. Crustacea + Euchelicerata + Pycnogonida?) can indeed be deduced from the molecular data, published by Ballard et al. (1992), **after this treatment**. However, evaluation of many characters used as apomorphic in Budd's proposed cladogram strongly depend upon where the Hexapoda are placed. Any two taxa (e.g., Crustacea and Euchelicerata, but also Crustacea and Mammalia) can be interpreted as sister groups if the others are excluded selectively from analysis.

Wheeler et al. (1993) attempted a combination of their morphological and molecular data into a, mostly traditionally-ordered, cladogram (p. 14: 1. Onychophora, 2.1. Euchelicerata + Pycnogonida, 2.2.1. Crustacea, 2.2.2. Myriapoda + Hexapoda). However, their **purely molecular cladograms** never unite Myriapoda + Hexapoda as a monophyletic taxon, and strict consensus derived from their morphological and molecular cladograms (pp. 10 and 13: 1. Onychophora, 2.1. Euchelicerata + Pycnogonida, 2.2.1. Myriapoda, 2.2.2. Crustacea + Hexapoda, perhaps with hexapods paraphyletic in terms of crustaceans) does not agree with their "combined" cladogram.

Monophyly of Articulata

According to molecular phylogeneticists (see Field et al., 1988; Lake, 1990; Turbeville et al., 1991; Ballard et al., 1992), the Annelida are related more closely to molluscs and related protostome-eucoelomate groups (forming the Eutrochozoa) than to the Arthropoda. The Arthropoda appear to be an independent clade; yet there is no molecular information as concerns the Tardigrada.

Also, numerical-cladistic analyses based on morphological and developmental data have shown two more or less independent clades, the **Eutrochozoa** Ghiselin, 1988 (sometimes paraphyletic; including at least Annelida, Lobatocerebrida, Mollusca, Pogonophora, Vestimentifera, Echiura, Sipuncula) and **Lobopodia** Snodgrass, 1938 (Tardigrada, Arthropoda incl. Pentastomida, Onychophora); for reviews of diverse opinions see Brusca & Brusca (1990), Willmer (1990), Meglitsch & Schram (1991), Schram (1991), Eernisse et al. (1992), Backeljau et al. (1993), and Conway Morris (1993). However, no agreement has been reached upon a more detailed position of the Onychophora: whether they are arthropod sister group (according to most morphologists and Wheeler et al., 1993) or an ingroup (recently advocated by Meglitsch & Schram, 1991; Ballard et al., 1992; Budd, 1993; see Fortey & Thomas, 1993; Patterson et al., 1993). The traditional taxon Articulata (Annelida, Arthropoda, Onychophora, Tardigrada, Pentastomida, sometimes even Sipuncula and Echiura) is undoubtedly artificial (Fig. 2). This result is supported also by fundamental morphogenetic differences between annelids and arthropods (Minelli & Bortoletto, 1988; Shankland, 1991; Lans et al., 1993).

Monophyly of Arthropoda

Despite the many discussions concerning the monophyly or polyphyly of the Arthropoda proper (for reviews see Manton, 1972, 1977; Anderson, 1973; Schram, 1978; Bergström, 1979; Jamieson, 1987; Lake, 1990), there is no clear evidence against the monophyly of this group (see Paulus, 1979; Weygoldt, 1979, 1986; Field et al., 1989; Kukalová-Peck, 1991; Schram & Emerson, 1991; Turbeville et al., 1991; Wheeler et al., 1993). It appears probable that these discussions are based upon an incomplete understanding of basic phylogenetic concepts: the polyphyleticists (Manton, 1972, 1977; Anderson, 1973) regard some basic arthropod features to have been evolved convergently and, consequently, they consider the Arthropoda to be polyphyletic. The hypothesis of independent origin of arthropod "phyla" is based upon a belief that it is impossible to hypothesize sister-group relationships between those taxa whose putative ancestor would be inviable functionally (if its body plan would be an intermediate between those of their modern representatives), or whose modern structures are not capable of being derived from a modern situation in another related extant taxon (for fundamental criticisms of this approach see, e.g., Kristensen, 1975, 1981, 1991; Ax, 1984; Weygoldt, 1986; Štys & Biliński, 1990).

Approximately, there are twenty morphological and developmental synapomorphies of the Arthropoda (listed in Boudreaux, 1979; Weygoldt, 1986; Brusca & Brusca, 1990; Zrzavý & Štys, in prep.), and also molecular phylogenetics appears to reach a basic consensus about the monophyly of Arthropoda (Fields et al., 1988; Turbeville et al., 1991; Wheeler et al., 1993), or Arthropoda + Onychophora (Ballard et al., 1992).

Monophyly of Mandibulata, Crustacea + Hexapoda, Schizoramia, and Uniramia

Monophyly of the Mandibulata (Atelocerata + Crustacea) has been challenged by Mantonian concept of the Uniramia (Atelocerata + Onychophora). Also molecular data obtained by Field et al. (1989), Turbeville et al. (1991), and Ballard et al. (1992; see Lake, 1990; Erwin, 1991) show no close crustacean-myriapod-hexapod relationships within the Arthropoda. Instead, close relationships of the crustaceans and hexapods are suggested by molecular studies (Fig. 2); only Wheeler et al. (1993; see above) conclude that the mandibulate clade exists (in myriapod vs. crustacean-hexapod version in their molecular cladogram). However, strong morphological and physiological arguments for monophyly of Mandibulata is presented by Wägele (1993).

Some crustacean-hexapod morphological similarities have been suggested although considered convergent or primitively mandibulate (action of mandibles, structure of hypopharynx, structure of eye ommatidium, presence of the embryonic neuroblasts, perhaps also full complement of trunk-differentiating homeotic genes: Crampton, 1921; Manton, 1977; Paulus, 1979; Weygoldt, 1979, 1986; Willmer, 1990; Scholtz, 1992; Averof & Akam, 1993; see Zrzavý & Štys 1994).

The Schizoramia, a taxon uniting Euchelicerata, Pycnogonida, Crustacea (plus some trilobitomorph forms), are recognized, predominantly, by paleontologists (Cisne, 1974; Hessler & Newman, 1975; Bergström, 1979, 1992; Briggs & Fortey, 1989; Schram & Emerson, 1991; Briggs et al., 1992; Budd, 1993). This concept challenges any close relationships among mandibulate groups (recognized by most neontologists), and is based, predominantly, on Mantonian concept of unbranched vs. branched limbs (for morphological discussion see Kukalová-Peck, 1991, 1992; Shear, 1992; Wägele, 1993), and it finds no support in molecular phylogenetics.

Manton's and Anderson's hypothesis of the Uniramia (supported by many zoologists and, ironically, in particular by those working on other animal groups) is based upon a presumed sister-group relationship between the "pararthropod" Onychophora and "euarthropod" Atelocerata (Fig. 1). The concept of Uniramia has been rejected by some morphologists as well as some paleontologists (see e.g. Boudreaux, 1979; Weygoldt, 1986; Kukalová-Peck, 1987, 1991, 1992; Schram & Emerson, 1991; Shear, 1992; Wägele, 1993), and it appears dubious also when confronted with the available molecular data (Field et al., 1989; Turbeville et al., 1991; Wheeler et al., 1993). Regardless of placement of the Onychophora, which cannot be regarded as definitive (compare Ballard et al., 1992, and Wheeler et al., 1993), the Uniramia-concept appears to be outdated.

Monophyly of Euchelicerata + Pycnogonida

Generally, the Pycnogonida are classified as the sister group or even an in-group of (eu)chelicerates (for various opinions see, e.g., Sharov, 1966; Manton, 1977; Boudreaux, 1979; Schram, 1986; Brusca & Brusca, 1990; Willmer, 1990; Bergström, 1992; see Fig. 1). However, their arthropod nature proper has been doubted (for reviews see Brusca & Brusca, 1990; Willmer, 1990). Molecular analysis (Wheeler et al., 1993) shows pycnogonids as an in-group of the Arthropoda, perhaps as a sister group of the Euchelicerata.

The Euchelicerata are regarded as a monophyletic group and molecular data support this view (Turbeville et al., 1991; Ballard et al., 1992; Wheeler et al., 1993).

Monophyly of Crustacea and position of Pentastomida

Carcinologists appear to have serious difficulties with the phylogenetic definition of the Crustacea (see, e.g., Schram, 1986; for a review see Wägele, 1993). An alternative explanation is that the Crustacea are paraphyletic in relation to the Atelocerata (Lauterbach, 1983; see also Zrzavý & Štys, 1994), or to Chelicerata + Trilobitomorpha (Briggs & Fortey, 1989).

A hypothesis about sister-group relationships between Branchiura (Crustacea) and Pentastomida (= Linguatulida), based primarily on sperm structure and spermatogenesis (Wingstrand, 1972; for further references see Brusca & Brusca, 1990: embryogenesis, larval development, structure of cuticle and nervous system), is supported by the molecular studies (Abele et al., 1989, 1992).

Monophyly of Atelocerata and Myriapoda

As stated above, the molecular studies tend to show the myriapod groups (viz., Diplopoda and Chilopoda) as rather early offshoots of the arthropod tree and not necessarily related to the Hexapoda. It is probably the most unexpected conclusion of molecular phylogeneticists, because monophyly of the Atelocerata has never been doubted seriously by morphologists (see Fig. 1).

The Myriapoda proper were often thought to be paraphyletic in relation to the Hexapoda (exact relationships often not specified, e.g., Hessler & Newman, 1975; McNamara &

Trewin, 1993), and strict monophyly of the Myriapoda was defended rarely. Three basic hypotheses were proposed:

(A) Myriapoda paraphyletic: 1. Dignatha (= Diplopoda + Pauropoda), 2. Chilopoda, 3. Symphyla + Hexapoda; see Tiegs & Manton, 1958; Sharov, 1966; Manton, 1972, 1977; Anderson, 1973); this hypothesis is based predominantly on the structure of the head and mouthparts (labium) and is not supported widely in recent literature.

(B) Myriapoda paraphyletic: 1. Chilopoda, 2.1. Hexapoda, 2.2. Symphyla + Dignatha; monophyly of the Hexapoda + Symphyla + Dignatha (see Dohle, 1988) is supported by presence of eversible vesicles and spinnerets and by some embryological characters (total cleavage as a ground pattern, embryonic dorsal organs).

(C) Myriapoda monophyletic (with various interrelationships among individual groups; only monophyly of the Dignatha is accepted generally, except for the spermatological literature; Baccetti, 1979; Jamieson, 1986; Pauropoda and Chilopoda as sister groups). Many possible synapomorphies of the myriapods are listed in Boudreaux (1979) and Brusca & Brusca (1990); according to Kristensen (1991), at least the architecture of the head endoskeleton may represent a true autapomorphy of the clade. Also molecular data collected by Wheeler et al. (1993) suggest monophyly of centipede-millipede clade (pauropods and symphylids have not been studied).

Monophyly of Hexapoda

Modern students of the phylogeny of Hexapoda almost universally regard the group as monophyletic (see, e.g., Boudreaux, 1979; Kukalová-Peck, 1987, 1991; Štys & Biliński, 1990; Kristensen, 1991; Biliński, 1993; Štys et al., 1993). However, some hexapods (Entognatha: Protura, Collembola, Campodeina, Japygina) have never been tested by any non-morphological method and their hexapod affinities need re-analysis (for doubts concerning the hexapod nature see Yin, 1984; François et al., 1992; Xué et al., 1993). Exceptionally, the Entognatha are thought to be closer, cladistically, to the Myriapoda in general (e.g., Handschin, 1956; Rasnitsyn, 1980: 19), or to the Symphyla in particular (Remington, 1955; Sharov, 1966; and references to similar hypotheses therein). Also Manton (1972, 1977) and Anderson (1973) derived Protura, Collembola, Diplura (Campodeina + Japygina), "Thysanura" (Archaeognatha + Zygentoma), and Pterygota independently from an unknown (hexapod?) ancestor. Based on sperm ultrastructure, Jamieson (1987: 285; see also Mackerras, 1970) is ready to suggest monophyletic taxa containing Campodeina + Japygina + Archaeognatha + Zygentoma (but not Pterygota), Campodeina + Archaeognatha, and/or Campodeina + Archaeognatha + Zygentoma + Pterygota (but not Japygina) as alternatives. The supporting evidence for such opinions was probably based on shared symplesiomorphies or convergent homoplasies, and no such hypothesis has been corroborated by the cladistic studies mentioned further in the text. However, some myriapod-parainsect similarities may be true synapomorphies, that define a monophyletic arthropod taxon Parainsecta + Myriapoda (part.?), with marked "diplosegmentation" trends (Zrzavý & Štys, 1994; but see Enghoff et al., 1993). For example, the Tömösváry's organ of the Myriapoda appears to be homologous to the postantennal organ of the springtails and to the pseudoculus of the proturans (see Kukalová-Peck, 1991). Marcus (1949, fide Paclt, 1956) reported presence of the postantennal organ also in Japygina; its homology should be subjected to a new study in light of Kukalová-Peck's (1987) discussion of compound

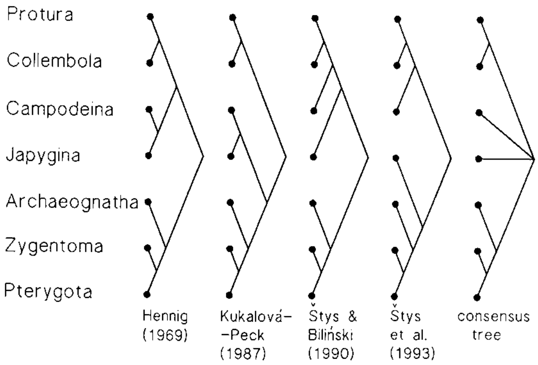

Fig. 3. Phylogeny of extant Hexapoda. Jamieson's (1987) "alternative hypotheses" (monophyletic taxa Campodeina + Japygina + Archaeognatha + Zygentoma, Campodeina + Archaeognatha, Campodeina + Archaeognatha + Zygentoma + Pterygota) are not included in the consensus tree.

eyes in some fossil Japygina (*Testajapyx*) and hypothesis on a sister-group relationship between Japygina and Ectognatha (= Insecta s.str.) by Štys et al. (1993). So, monophyly of Hexapoda should be re-examined critically (see also Yin, 1984).

Regardless of these doubts, there are several modern cladogenetic hypotheses concerning basic dichotomies of the **monophyletic** Hexapoda (see Table 1; Fig. 3):

(A) Traditional hypothesis (e.g., Hennig, 1969; Kristensen, 1975, 1981; Boudreaux, 1979; based predominantly on morphological evidence): 1.1. Parainsecta; 1.2. Campodeina + Japygina; 2. Ectognatha (= Archaeognatha + Zygentoma + Pterygota).

(B) Hypothesis by Kukalová-Peck (e.g., 1987, 1991; based predominantly on fossil records and still unpublished morphological studies by E.L. Smith): 1. Parainsecta; 2.1. Campodeina + Japygina; 2.2. Ectognatha.

(C) Hypothesis by Štys & Biliński (1990; see also Biliński, 1993): 1.1.1. Parainsecta; 1.1.2. Campodeina; 1.2. Japygina; 2. Ectognatha.

(D) Hypothesis by Štys et al. (1993; the last two hypotheses based on morphological evidence, especially on structure and development of gonads and germ cells): 1.1. Parainsecta; 1.2. Campodeina; 2.1. Japygina; 2.2. Ectognatha.

Considering that "the reticulate distribution of apomorphies linked the Diplura with other hexapods", Kristensen (1991: 129) suggests that the Hexapoda be treated as an unresolved trichotomy (Parainsecta, Diplura, Ectognatha), all ranked as classes (see Uemiya & Ando, 1991). Moreover, he regards the monophyly of Diplura as "not immediately obvious, but seemingly justified by the unique leg features" (see Manton, 1972, 1977). Štys & Biliński (1990) and Štys et al. (1993) do not consider their phylogenetic hypotheses (Fig. 3) as a sufficient basis for a new classification (with formal taxa proposed for Parainsecta + Campodeina and Japygina + Ectognatha clades).

Some alternative concepts could be derived from other sources of information which have not yet been explicitly interpreted as phylogenetically relevant: for instance, Archaeognatha **and** Zygentoma share a unique (synapomorphic?) pattern of midgut endocrine cells (see Žitňan et al., 1993). Moreover, monophyly at least of two "elementary taxa", viz., Japygina (incl. Projapygoidea) and Zygentoma (incl. Lepidotrichidae) is disputable (see Kristensen, 1981, 1991; Štys & Biliński, 1990; Štys et al., 1993; for basic data on the Projapygoidea and Lepidotrichidae see Pagés, 1959, and Wygodzinsky, 1961, respectively).

TABLE 1. List of published synapomorphies of the atelocerate taxa. Only the ground-pattern apomorphies linking several of the present elementary taxa and published **explicitly** as synapomorphies are chosen (however, the synapomorphies published by various authors may be in conflict). The additional data concerning head endoskeleton, segmentation and articulation of head, thoracic, and abdominal limbs, abdominal musculature, presence of ovipositor, sperm ultrastructure, and midgut histology should be re-assessed and usually are not covered here. H – Hennig (1969); B – Boudreaux (1979); K_1 – Kristensen (1975, 1981); K_2 – Kristensen (1991); K-P – Kukalová-Peck (1987, 1991); J – Jamieson (1987); Š&B – Štys & Biliński (1990); P – Pass (1991); Š&Z&W – Štys et al. (1993); square parentheses – synapomorphy doubted by author(s) himself (themselves).

- **(1) Protura + Collembola (Parainsecta)**
  - (a) Cerci absent: H, B, K_1, K_2, K-P, Š&B
  - (b) Anamorphosis: [K_2] (cf. 5f)
  - (c) Tarsus non-segmented: K-P, Š&B
  - (d) Claws unpaired: [K_1], [K_2], K-P, Š&B (cf. 4b)
  - (e) Antennal vessels reduced: P
- **(2) Protura + Collembola + Campodeina**
  - (a) Abdominal spiracles absent: Š&B
  - (b) Ovary non-metameric: Š&B (cf. 6a)
  - (c) Ovariole with linear meroism: Š&B, Š&Z&W
  - (d) Embryonic ovary non-metameric: [Š&Z&W]
  - (e) Compound eyes absent or desintegrated: Š&B (cf. 3d)
  - (f) High degree of entognathy: K-P, Š&B (cf. 3a)
- **(3) Protura + Collembola + Campodeina + Japygina (Entognatha)**
  - (a) Mouthpart entognathous: H, B, K_1, [K_2], Š&B
  - (b) Palpi reduced: H, [K_1], B, Š&B
  - (c) Malpighian tubules reduced: H, K_1, [K_2], Š&B
  - (d) Eyes reduced: K_1 (cf. 2e)
  - (e) Ocelli reduced or lost: B, Š&B
  - (f) Sperm centriole adjunct lost: J, [K_2]
- **(4) Campodeina + Japygina (Diplura)**
  - (a) Unique femoro-tibial articulation: K_2
  - (b) Claws paired (convergent to Ectognatha): B (cf. 1d)
- **(5) Campodeina + Japygina + Ectognatha** ("Insecta" according to Kukalová-Peck, 1991)
  - (a) Eyes shifted from head segments 2 + 3 to segment 4: K-P
  - (b) Anterior ocelli fused: K-P
  - (c) Antennae annulated: K-P (as autapomorphy of the Ectognatha: H, K_1, K_2, B, Š&B, [Š&Z&W])
  - (d) Tömösvary's organ reduced: K-P, [K_2]
  - (e) Abdominal limbs articulated by femur: K-P, [K_2]
  - (f) Epimorphosis: K-P (cf. 1b)
- **(6) Japygina + Ectognatha**
  - (a) Ovary metameric: [Š&Z&W] (cf. 2b)

PROPOSAL OF A FORMAL CLASSIFICATION

It is possible to suggest some conclusions:

(A) The Arthropoda, including Pentastomida (as crustaceans related to the Branchiura) and perhaps also Onychophora, represent a monophyletic group.

(B) The Arthropoda are not a sister group of annelids. Phylogenetic relationships of the Tardigrada remain enigmatic (Rieger & Rieger, 1976; Willmer, 1990), but they may belong to the arthropod clade (Brusca & Brusca, 1990; Meglitsch & Schram, 1991; Eernisse et al., 1992).

(C) Neither Uniramia (i.e., onychophoran-myriapod-hexapod assemblage), nor Schizoramia (i.e., pycnogonid-euchelicerate-crustacean assemblage) appear to represent monophyletic taxa. The Atelocerata (Myriapoda + Hexapoda) and perhaps also Mandibulata (Myriapoda + Hexapoda + Crustacea; Fig. 2) may not be monophyletic; the Crustacea and Hexapoda may be unexpectedly closely related (a revival of Börner's "crustacean theory"; see Crampton, 1921; Tiegs & Manton, 1958).

(D) Crustacea, Myriapoda, Dignatha, and Hexapoda should be – **for the present** – considered monophyletic taxa.

So, based on strict consensus of the present phylogenetic data and considering the weakly supported monophyly of the Pycnogonida + Euchelicerata, Atelocerata, Mandibulata, and especially of Crustacea + Hexapoda, and deep phenetic gaps within these assemblages, we suggest the following classification of the recent Arthropoda. To facilitate its understanding we express it in terms of formal categories of the Linnean hierarchy though we are fully aware of its inadequacy and potential harmfulness (de Queiroz & Gauthier, 1992) for the purposes of the phylogenetic systematics. Phylogenetic structure of Euchelicerata (see Weygoldt & Paulus, 1979; Van der Hammen, 1989; Shultz, 1991; Turbeville et al., 1991; Evans, 1992; Wheeler et al., 1993) and Crustacea (see Bowman & Abele, 1982; Schram, 1986; Starobogatov, 1988; Abele et al., 1989, 1992; Brusca & Brusca, 1990; Evans, 1992; Wilson, 1992; Huys et al., 1993) are not included.

(For synonymics see Appendices 1 and 2; sed. mut. – sedis mutabilis, inc. sed. – incertae sedis; [?] – monophyly of the taxon is disputable; convention of the "cladistic sequencing" [see Forey et al., 1992] is not applied.)

Superphylum LOBOPODIA Snodgrass, 1938 (s. lat.) [?]
  Phylum TARDIGRADA Spallanzani, 1777 inc. sed.
  Phylum ARTHROPODA Siebold, 1845 (s. lat.) [?]
    (Sub)phylum ONYCHOPHORA Grube, 1853 inc. sed.*
    Subphylum PYCNOGONIDA Latreille, 1810 sed. mut.
    Subphylum EUCHELICERATA Weygoldt, 1986 sed. mut.
    Subphylum CRUSTACEA Pennant, 1777 sed. mut. (incl. Pentastomida)
    Subphylum MYRIAPODA Latreille, 1796 sed. mut. [?]
      Superclass SYMPHYLA Ryder, 1880 inc. sed.
      Superclass CHILOPODA Leach, 1814 sed. mut.
      Superclass DIGNATHA Tiegs, 1947 sed. mut.
        Class PAUROPODA Lubbock, 1866
        Class DIPLOPODA Blainville-Gervais, 1844
    Subphylum HEXAPODA Latreille, 1825 sed. mut.
        Class PARAINSECTA Kukalová-Peck, 1987 sed. mut.
          Subclass PROTURA Silvestri, 1907
          Subclass COLLEMBOLA Lubbock, 1873
        Class CAMPODEINA Handlirsch, 1903 sed. mut.
        Class JAPYGINA Štys & Biliński, 1990 (incl. Projapygoidea) sed. mut. [?]
        Class ECTOGNATHA Stummer, 1891 sed. mut.
          Subclass ARCHAEOGNATHA Börner, 1904
          Subclass DICONDYLIA Hennig, 1957
            Infraclass ZYGENTOMA Börner, 1904 (incl. Lepidotrichidae) [?]
            Infraclass PTERYGOTA Brauer, 1883

* We suggest to classify the Onychophora as an arthropod subphylum because this classification is compatible with their position as arthropod sister-group as well as their in-group. We propose to use a formal name **Euarthropoda** Cuenot, 1949, for the monophyletic Arthropoda excluding Onychophora. The Lobopodia would then be split into three phyla, Tardigrada, Onychophora, and (Eu)arthropoda.

NOMENCLATURE OF THE ARTHROPOD HIGHER TAXA

The nomenclature of taxa recognized at highest hierarchical levels within the Arthropoda, and within the Hexapoda in particular, is chaotic. There are several reasons for the confusion: new names created arbitrarily (as the Code does not apply and the principle of priority need not be observed); belief that the names should be typified, or refer to the "most characteristic" and inclusive attribute; new names created for newly ranked taxa and for redundant hierarchical levels; new names created for differently defined taxa (though often only moderately different in scope); old names applied to vastly different concepts.

Considering the Onychophora, Euchelicerata, Pycnogonida, Crustacea, Diplopoda, Pauropoda, Chilopoda, Symphyla, and Hexapoda (viz., Protura, Collembola, Campodeina, Japygina, Archaeognatha, Zygentoma, Pterygota) as "elementary taxa", we have prepared two lists of their synonyms and higher rank names, and defined all these names by enumeration of the elementary taxa included (Appendix 1: Arthropoda; Appendix 2: Hexapoda). Under "elementary taxa" we understand such consensual subordinate monophyla of high rank which are necessary for construction of a complete cladogram of a superordinate taxon concerned. However, there are three exceptions:

(A) scutigeroid centipedes (Notostigmophora = Scutigeromorpha) were sometimes classified as independent class Schizotarsia coordinated with other centipedes (see Appendix 1);

(B) concept of Plagioptera vs. Opisthoptera (see Matsuda, 1972; Boudreaux, 1979), based on presumed diphyletic origin of insect wings, simply denied the existence of traditional taxon Pterygota (see Appendix 2);

(C) Merostomata (= Xiphosura = Limulida) and Arachnida are sometimes classified as independent classes, denying the existence of the traditional taxon (Eu)chelicerata (Alexander, 1979; see Appendix 1).

In general, the list is limited to names and their concepts used as valid in the second half of this century; however, some names and some idiosyncratic interpretations have not surely been included. Names differing only in the spelling or suffix (e.g., Ectotropha, Ectotrophi, Ektotropha) are entered only once in the most common and/or simplest form (and the others are listed and marked by "\"). Names of taxa combining a fraction of hexapods with some non-hexapod taxa are included both in Appendices 1 and 2.

Extinct groups and their names are omitted. Omission of the extinct taxa contributes in some cases to the impression of more extensive synonymy than actually exists. For instance, both the Chelicerata s. lat.-Cheliceromorpha-Cheliceriformes-Chelicerophora, and Arachnata-Arachnomorpha-Amandibulata-Cephalogradi are defined in the original sense as being formed by the Euchelicerata and Pycnogonida. However, the latter set of names was always intended for conceptions including both the Euchelicerata-Pycnogonida and the extinct Trilobitomorpha (trilobites and their potential relatives).

The author and year of publication of those names for which it was able to find these data in primary or reliable secondary (marked by "ex") sources are cited (not necessarily in References). Reference to any particular conception of a name is not provided.

Altogether, there are **sixty-nine** names of the higher taxa (excluding variant spellings!) for hierarchical classification of **ten** elementary taxa of the Arthropoda (Appendix 1), and **forty-seven** names of the higher taxa for classification of **seven** elementary taxa of the Hexapoda (Appendix 2). Whereas in the arthropod higher taxa prevail unnecessary synonyms for taxa of the same content of subordinate extant taxa (e.g., Antennata = Atelocerata = Myriapodomorpha = Tracheata), the names of hexapod higher taxa are often equivocal in scope, including different subordinate taxa according to different authors. Hence, the meaning of some names is nowadays always equivocal unless explained by enumeration of included/excluded taxa. Particularly the names "Aptera-Apterygogenea-Apterygota", "Ectognatha-Ectotropha", "Entognatha-Entotropha", "Insecta", and "Thysanura" (Appendix 2) belong to such a category.

Some of the names in both appendices indicate concepts rejected by modern phylogenetics; no name is needed for, e.g., an artificial taxon "Onychophora + Tardigrada + Pentastomida". As concerns Arthropoda in general, most hypothesized clades combining two or more of the elementary taxa have been named. Only some of the higher taxa suggested by molecular phylogenetics (e.g., Crustacea + Hexapoda) bear no name for formal classification.

It is not intended to suggest the most suitable, new, or "correct" names in this review, but it is necessary to caution against new applications of the old names (e.g., Insecta "s. nov." for Japygina + Ectognatha) and against using names discredited by excessive confusion of meaning. The latter applies particularly to the name **Insecta**, but a consensus to use it for the ectognathans only appears to be emerging. Concerning the vernacular names, it is recommended that "hexapods" be used (although it is most probable that the usage of "insects", in a broad sense, will continue) but only "true insects" when the ectognathous taxa are concerned.

ACKNOWLEDGEMENTS. We thank J. Kukalová-Peck (Ottawa), P. Švácha (České Budějovice), and two referees for critical comments on the manuscript drafts. However, this does not necessarily imply their endorsement of all our conclusions. The illustrations were kindly executed by O. Nedvěd (České Budějovice).

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APPENDIX 1. LIST OF NOMENCLATURE OF ARTHROPOD HIGHER TAXA

(1) Ony – Onychophora; (2) Euc – Euchelicerata (incl. Xiphosura; excl. Pycnogonida); (3) Pyc – Pycnogonida; (4) Cru – Crustacea; (5) Pen – Pentastomida (position often unspecified explicitly); (6) Dip – Diplopoda; (7) Pau – Pauropoda; (8) Chi – Chilopoda; (9) Sym – Symphyla; (10) Hex – Hexapoda (Pro, Col, Cam, Jap – see Appendix 2). Extinct taxa omitted.

1. **Amandibulata** Kaestner, 1956
   Euc Pyc
2. **Antennata** Lang, 1888
   Ony Dip Pau Chi Sym Hex
   Cru Dip Pau Chi Sym Hex
   Dip Pau Chi Sym Hex
3. **Arachnata** (ex Paulus, 1979, and Weygoldt, 1979)
   Euc Pyc
4. **Arachnida** Lamarck, 1801 (\Arachnoidea)
   Euc (part.: excl. Xiphosura)
5. **Arachnomorpha** Heider, 1913
   Euc Pyc Cru
   Euc Pyc
   Euc
6. **Arthropoda** Siebold, 1845
   Ony Euc Pyc Cru Dip Pau Chi Sym Hex
   Ony Euc Cru Dip Pau Chi Sym Hex
   Euc Pyc Cru Dip Pau Chi Sym Hex
   Euc Cru Dip Pau Chi Sym Hex

7. **Articulata** Cuvier, 1812
   Ony Euc Pyc Cru Pen Dip Pau Chi Sym Hex (+ Tardigrada + Annelida; or even: + Echiura + Sipuncula)
8. **Atelocerata** Heymons, 1901
   Dip Pau Chi Sym Hex
9. **Atelopoda** Boudreaux, 1978
   Chi Sym
10. **Biantennata** (ex Bergström, 1979)
    Cru
11. **Branchiata** Lang, 1888
    Cru Pyc Euc (part.: Xiphosura)
    Cru
12. **Cephalogradi** Crampton, 1928
    Euc Pyc
13. **Chelicerata** Heymons, 1901
    Euc Pyc
    Euc
14. **Cheliceriformes** Schram, 1978
    Euc Pyc
15. **Cheliceromorpha** Boudreaux, 1979
    Euc Pyc
16. **Chelicerophora** (ex Dubinin, 1959)
    Euc Pyc
    Euc
17. **Chilopoda** Leach, 1814
    Chi
18. **Collifera** Boudreaux, 1978
    Dip Pau
19. **Cormogradi** Crampton, 1928
    Cru Dip Pau Chi Sym Hex
20. **Crustacea** Pennant, 1777
    Cru Euc (part.: Xiphosura)
    Cru Pen
    Cru
21. **Crustaceomorpha** (ex Dubinin, 1959)
    Cru
22. **Crustaciformia** Boudreaux, 1978
    Cru
23. **Diantennata** Weber, 1933
    Cru
24. **Dignatha** Tiegs, 1947
    Dip Pau
25. **Dimalata** Sharov, 1966
    Sym Hex
26. **Diplopoda** Blainville-Gervais, 1844
    Dip
27. **Euarachnida** Lankester, 1881
    Euc
28. **Euarthropoda** Cuenot, 1949
    Euc Pyc Cru Dip Pau Chi Sym Hex (+ Pen?)
    Euc Cru Dip Pau Chi Sym Hex
29. **Euchelicerata** (ex Weygoldt, 1986)
    Euc Pyc
    Euc
30. **Eutracheata** Grobben, 1925
    Dip Pau Chi Sym Hex
31. **Gnathomorpha** Boudreaux, 1978
    Cru Dip Pau Chi Sym Hex
32. **Hexapoda** Latreille, 1825
    Hex
33. **Homopoda** Pocock, 1893
    Chi Sym
34. **Labiata** Tiegs, 1947
    Sym Hex
    Sym Hex (Pro Col Cam Jap)
35. **Linguatulida** Van Beneden, 1849
    Pen
36. **Lobopodia** Snodgrass, 1938
    Ony Euc Pyc Cru Pen Dip Pau Chi Sym Hex (+ Tardigrada)
    Ony Euc Pyc Cru Dip Pau Chi Sym Hex (+ Pen?)
    Ony Pen (+ Tardigrada)
    Ony (+ Tardigrada)
    Ony
37. **Malacopoda** Claus-Grobben, 1892 (?)
    Ony
38. **Mandibulata** Snodgrass, 1938
    Cru Dip Pau Chi Sym Hex
39. **Megadenopoda** Brinck, 1957
    Sym
40. **Merostomata** Dana, 1852 (\Merostomoidea)
    Euc (part.: Xiphosura + Scorpiones)
    Euc (part.: Xiphosura)
41. **Monognatha** Manton, 1973
    Ony
42. **Monomalata** Sharov, 1966
    Dip Pau Chi
43. **Myocerata** Remington, 1955
    Dip Pau Chi Sym Hex (part.: Pro Col Cam Jap)
44. **Myriapoda** Latreille, 1796 (\Myriopoda)
    Dip Pau Chi Sym
45. **Myriapodomorpha** Boudreaux, 1978
    Dip Pau Chi Sym
46. **Oncopoda** Weber, 1954
    Ony Pen (+ Tardigrada)
47. **Onychophora** Grube, 1853
    Ony
48. **Opisthogoneata** Pocock, 1893
    Chi Sym Hex
    Chi Hex
49. **Panchelicerata** Wägele, 1993 (\"Pan-chelicerata" as technical term)
    Che (+ Pyc?)

50. **Panmandibulata** Wägele, 1993 (\"Panmandibulata" as technical term)
Cru Dip Pau Chi Sym Hex
51. **Pantopoda** Gerstaecker, 1863
Pyc
52. **Pararthropoda** Cuenot, 1949
Ony Pyc Pen (+ Tardigrada)
Ony Pen (+ Tardigrada)
Ony (+ Tardigrada)
53. **Pauropoda** Lubbock, 1866
Pau
54. **Pentastomida** Leuckart, 1860 (\Pentastomata, Pentastoma)
Pen
55. **Proboscifera** Sharov, 1966
Pyc
56. **Progoneata** Pocock, 1893
Dip Pau Sym
Dip Pau
57. **Protarthropoda** (ex Wägele, 1993)
Ony (+ Tardigrada)
58. **Protracheata** Bütschli, 1910
Ony
59. **Pycnogonida** Latreille, 1810
Pyc
60. **Schizoramia** Hessler & Newman, 1975
Euc Pyc Cru
Euc Cru
61. **Schizotarsia** Brandt, 1841
Chi (part.: Notostigmophora = Scutigeromorpha; interpreted as a group coordinated with Chilopoda and other myriapods)
62. **Stelechopoda** von Graff, 1877
Pen (+ Tardigrada + Myzostomida)
Pen (+ Tardigrada)
63. **Symphyla** Ryder, 1880
Sym
64. **Syngnatha** Latreille, 1802
Chi
65. **Tracheata** Lang, 1888
Ony Euc (part.) Dip Pau Chi Sym Hex (+ Tardigrada)
Ony Euc Dip Pau Chi Sym Hex
Ony Dip Pau Chi Sym Hex
Dip Pau Chi Sym Hex
66. **Trignatha** Tiegs, 1947
Chi Sym Hex
Chi Sym Hex (part.: Pro Col Cam Jap)
67. **Trilobitomorpha** Størmer, 1944
Euc Pyc Cru
Euc Pyc
Euc
68. **Uniramia** Manton, 1972
Ony Pen Dip Pau Chi Sym Hex (+ Tardigrada)
Ony Dip Pau Chi Sym Hex (+ Tardigrada)
Ony Dip Pau Chi Sym Hex
Dip Pau Chi Sym Hex
69. **Xiphosura** Latreille, 1802 (\Xiphosurida)
Euc (part.)

APPENDIX 2. LIST OF NOMENCLATURE OF HEXAPOD HIGHER TAXA

(1) Pro – Protura; (2) Col – Collembola; (3) Cam – Campodeina; (4) Jap – Japygina; (5) Arc – Archaeognatha; (6) Zyg – Zygentoma; (7) Pte – Pterygota. Dip, Pau, Chi, Sym – see Appendix 1. Extinct taxa omitted.

1. **Amyocerata** Remington, 1955
Arc Zyg Pte
2. **Anamerentoma** Prell, 1912
Pro
3. **Anamorpha** Tillyard, 1930
Pro
4. **Aptera** Linnaeus, 1758 (\Apterata)
Pro Col Cam Jap Arc Zyg Pte
Cam Jap Arc Zyg
Arc Zyg
Zyg
5. **Apterygogenea** Brauer, 1885
Pro Col Cam Jap
Arc Zyg Pte
Arc Zyg
Zyg
6. **Apterygota** Lang, 1889
Pro Col Cam Jap Arc Zyg
Cam Jap Arc Zyg
Arc Zyg
Zyg
7. **Archaeognatha** Börner, 1904 (\Archaeognathata)
Arc
8. **Campodeina** Handlirsch, 1903
Cam
9. **Cercofilata** Kukalová-Peck, 1987
Zyg Pte
10. **Collembola** Lubbock, 1873
Col
11. **Dicellurata** Cook, 1896
Jap

12. **Dicondylia** Hennig, 1953 (\Dicondylata)
    Zyg Pte
13. **Diplura** Börner, 1904 (\Diplurata)
    Cam Jap
14. **Ectognatha** Stummer, 1891 (\Ectognathata)
    Arc Zyg Pte
15. **Ectotropha** Grassi, 1890 (\Ectotrophi, \Ektotropha, \Ektotrophi)
    Arc Zyg Pte
    Arc Zyg
    Zyg
16. **Ellipura** Börner, 1910 (\Ellipurata)
    Pro Col
17. **Entognatha** Hennig, 1953 (\Entognathata)
    Pro Col Cam Jap
    Cam Jap
18. **Entotropha** Grassi, 1888 (\Entotrophi)
    Pro Col Cam Jap
    Cam Jap
19. **Euentoma** Berlese, 1909 (\Euentomata)
    Cam Jap Arc Zyg Pte
    Arc Zyg Pte
20. **Hexapoda** Latreille, 1825
    Pro Col Cam Jap Arc Zyg Pte
21. **Holomerentoma** Prell, 1912
    Col Cam Jap Arc Zyg Pte
22. **Insecta** Linnaeus, 1758
    Pro Col Cam Jap Arc Zyg Pte (+ Dip Pau Chi Sym)
    Pro Col Cam Jap Arc Zyg Pte
    Col Cam Jap Arc Zyg Pte
    Cam Jap Arc Zyg Pte
    Arc Zyg Pte
    Pte
23. **Japygina** Štys & Biliński, 1990
    Jap
24. **Labiata** Tiegs, 1947
    Pro Col Cam Jap Arc Zyg Pte (+ Sym)
    Pro Col Cam Jap (+ Sym)
25. **Lepismatida** Leach, 1815 (\Lepismatoidea, \Lepismatona)
    Arc Zyg
    Zyg
26. **Machilida** Handlirsch, 1903 (\Machiloidea)
    Arc
27. **Microcoryphia** Verhoeff, 1904
    Arc
28. **Monocondylia** Hennig, 1953 (\Monocondylata)
    Arc
29. **Myocerata** Remington, 1954
    Pro Col Cam Jap (+ Dip Pau Chi Sym)
30. **Myrientoma** Berlese, 1909 (\Myrientomata)
    Pro
31. **Oligoentoma** Berlese, 1809 (\Oligoentomata)
    Col
32. **Opisthoptera** Lemche, 1940
    Pte (part.: Ephemeroptera + Neoptera; interpreted as a group coordinated with apterygote taxa and Plagioptera)
33. **Parainsecta** Kukalová-Peck, 1987
    Pro Col
34. **Plagioptera** Lemche, 1940
    Pte (part.: Odonata; interpreted as a group coordinated with apterygote taxa and Opisthoptera)
35. **Podura** Bei-Bienko, 1962 (\Podurata)
    Col
36. **Polyentoma** Grandi, 1969
    Cam Jap
37. **Protomorpha** Handschin, 1956
    Col
38. **Protura** Silvestri, 1907 (\Proturata)
    Pro
39. **Pterygogenea** Brauer, 1885
    Pte
40. **Pterygota** Brauer, 1885
    Pte
41. **Rhabdura** Cook, 1896
    Cam
42. **Scarabaeoda** Rohdendorf, 1977
    Arc Zyg Pte
43. **Scarabaeona** Rohdendorf, 1977
    Pte
44. **Thysanura** Lubbock, 1869 (\Thysanurata)
    Cam Jap Arc Zyg
    Arc Zyg
    Zyg
45. **Uratochelia** Ashmead, 1896
    Jap
46. **Zygentoma** Börner, 1904
    Zyg
47. **Zygoentomata** (ex Brusca & Brusca, 1990)
    Arc Zyg

Received October 1, 1993; accepted December 30, 1993