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Ultrastructure of attachment specializations of hexapods (Arthropoda): evolutionary patterns inferred from a revised ordinal phylogeny

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Abstract

Attachment devices of representatives of most higher taxa of hexapods were examined. Short descriptions of tibial, tarsal and pretarsal adhesive structures for each order are presented. In their evolution, hexapods have developed two distinctly different mechanisms to attach themselves to a variety of substrates: hairy surfaces and smooth flexible pads. The flexible properties of pad material guarantees a maximal contact with surfaces, regardless of the microsculpture. These highly specialized structures are not restricted to one particular area of the leg. They may be located on different parts, such as claws, derivatives of the pretarsus, tarsal apex, tarsomeres, or tibia. The 10 characters of the two alternative designs of attachment devices – smooth and hairy – were coded and analysed together with a data matrix containing 105 additional morphological characters of different stages and body parts. The analysis demonstrates, that similar structures (arolium, euplantulae, hairy tarsomeres) have evolved independently in several lineages. Nevertheless, some of them support monophyletic groups (e.g. Embioptera + Dermaptera; Dictyoptera + Phasmatodea + Grylloblattodea + Orthoptera; Dictyoptera + Phasmatodea; Hymenoptera + Mecoptera; Neuropterida + Strepsiptera + Coleoptera). Other structures such as claw pads (Ephemeroptera), balloon-shaped eversible pads (Thysanoptera), or fossulae spongiosae (Reduviidae) are unique for larger or smaller monophyletic units. It is plausible to assume that the evolution of flight and the correlated necessity to cling to vegetation or other substrates was a major trigger for the evolution of adhesive structures. Groups with a potential to evolve a great variety of designs of adhesive pads are Hemiptera and Diptera. Even though characters of the adhesive pads are strongly subject to selection, they can provide phylogenetic information. The results of the cladistic analyses are largely congruent with current hypotheses of hexapod phylogeny. A sistergroup relationship between Diplura and Insecta and between Zygentoma (excl. *Tricholepidion*) and Pterygota is confirmed. Plecoptera are probably the sistergroup of the remaining Neoptera. Dermaptera are the sistergroup of Embioptera and Dictyoptera the sistergroup of Phasmatodea. Paurometabola excl. Dermaptera + Embioptera are monophyletic. A sistergroup relationship between Zoraptera and a clade comprising Paraneoptera + Endopterygota is only supported by weak evidence. Coleoptera + Strepsiptera are the sistergroup of Neuropterida and Hymenoptera the sistergroup of Mecoptera.

Key words: adhesion – cuticle – evolution – friction – functional morphology – Hexapoda – locomotion – phylogeny – ultrastructure – scanning electron microscopy (SEM) – transmission electron microscopy (TEM)

Introduction

Flies grasping the under surface of smooth substrates had already fascinated scientists by the nineteenth century (West 1862; Dewitz 1884; Rombouts 1884). Comparative accounts on hexapod pretarsal structures were given by de Meijere (1901) and Holway (1935) and a terminology was presented by Dashman (1953). To date, both the morphological and ultrastructural bases of the ability of hexapods to walk on vertical surfaces have been studied in detail only in representatives of selected groups including Orthoptera (Slifer 1950; Kendall 1970; Henning 1974), Blattodea (Roth and Willis 1952; Arnold 1974), Thysanoptera (Heming 1970, 1972), Hemiptera (Lees and Hardie 1988; Dixon et al. 1990; Gillett and Wigglesworth 1932; Hasenfuss 1977a,b, 1978; Carver et al. 1991), Hymenoptera (Snodgrass 1956; Federle et al. 2000), Diptera (Bauchhenss and Renner 1977; Bauchhenss 1979; Walker et al. 1985; Röder 1986; Gorb 1998c) and Coleoptera (Stork 1980a,b, 1983a,b). Fine structure and functional morphology of attachment or adhesive structures of representatives of other hexapod orders still need attention. Specific information about the general design of hexapod structures adapted to attachment is scattered in the vast systematic literature.

In their evolution, hexapods have developed two distinctly different mechanisms to attach themselves to a variety of substrates: with smooth pads or with setose or hairy surfaces. Due to the flexibility of the material of the attachment structures, both mechanisms can maximize the possible contact area with the substrate, regardless of its microsculpture (Fig. 1).

It is remarkable that these highly specialized structures are not restricted to one particular area of the leg. They may be located on different parts such as claws, derivatives of the pretarsus, tarsal apex, tarsomeres, or tibia. Therefore, it appears obvious, that structures adapted to attachment have evolved several times independently (Breidbach 1980; Schliemann 1983). However, previous authors have discussed this phenomenon considering only members of few hexapod taxa, and have not provided a phylogenetic analyses of the characters in question.

Here, we summarize our ultrastructural studies of the cuticle of hexapod adhesive pads in representatives of most hexapod orders and additional data in the literature. Our principal goal is to provide a concise review of structures adapted to substrate attachment during locomotion and an evolutionary interpretation based on a cladistic analysis of the distribution of adhesive structures and of a broad spectrum of other characters of adults and immature stages. Leg structures specialized for prey-capture and/or copulation, were excluded.

Materials and methods

List of taxa examined

Symphyla, Scutigereidae: *Scutigereilla immaculata* Newport 1845; undetermined species from Mozambique and Costa Rica.
Diplura, Campodeidae: *Campodea* sp.
Archaeognatha, Machilidae: *Machilis* spp.
Zygentoma, Lepismatidae: *Lepisma saccharina* L. 1758
Ephemeroptera, Leptophlebiidae: *Paraleptophlebia* sp.

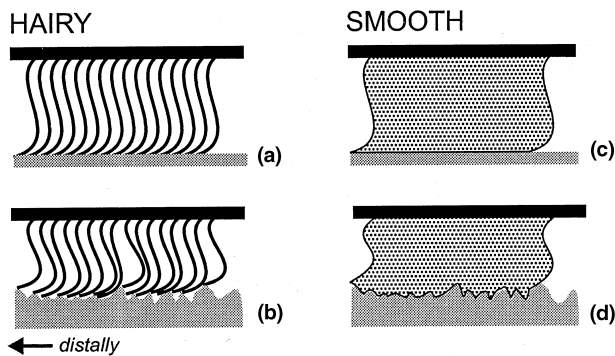


Fig. 1. Scheme of action of the 'hairy' (a, b) and 'smooth' (c, d) pad attachment systems on the smooth (a, c) and structured (b, d) substrates. Both systems are able to adapt to the surface profile

Odonata, Coenagrionidae: *Enallagma cyathigerum* (Charpentier 1840), Lestidae: *Lestes barbarus* (Fabricius 1798), Aeschnidae: *Anax imperator* Leach 1815
 Plecoptera, Taeniopterygidae: *Brachyptera risi* (Morton 1896)
 Blattodea, Blattellidae: *Periplaneta americana* (L. 1758), *Blattella germanica* (L. 1758)
 Ensifera, Tettigoniidae: *Tettigonia viridissima* L. 1758
 Caelifera, Acrididae: *Omocestus viridulus* L. 1758, *Schistocerca gregaria* (Forsk. 1775)
 Zoraptera, Zorotypidae: *Zorotypus hubbardi* Caudell 1918
 Auchenorrhyncha, Cercopidae: *Cercopis vulnerata* Rossi 1807
 Heteroptera, Coreidae: *Coreus marginatus* (L. 1758); Pyrrhocoridae: *Pyrrhocoris apterus* (L. 1758)
 Dermaptera, Forficulidae: *Forficula auricularia* L. 1758
 Megaloptera, Sialidae: *Sialis lutaria* (L. 1758); Corydalidae: *Corydalis* spp. (presumably undescribed species from Bolivia)
 Neuroptera (= Planipennia), Chrysopidae: *Chrysoperla carnea* (Stephens 1836)
 Coleoptera, Cupedidae: *Priacma serrata* LeConte 1861; Gyridae: *Gyrinus substriatus* Stephens 1828; Trachypachidae: *Trachypachus holmbergi* Mannerheim 1853; Noteridae: *Noterus crassicornis* Müller 1776; Dytiscidae: *Dytiscus marginalis* L. 1758; Cantharidae: *Rhagonycha fulva* (Scopoli 1763), *Cantharis fusca* L. 1758; Chrysomelidae: *Leptinotarsa decemlineata* (Say 1824)
 Hymenoptera, Siricidae: *Urocerus gigas* L. 1758; Apidae: *Apis mellifera* L. 1758; Vespidae: *Paravespula* sp.; Argidae: *Abia seriacea* L. 1767
 Mecoptera, Panorpidae: *Panorpa communis* L. 1758; Boreidae: *Boreus hiemalis* L. 1758
 Diptera, Tipulidae: *Tipula* spp.; Bibionidae: *Biblio nigriiventris* Haliday 1833, *Biblio marci* L. 1758; Empididae: *Rhamphomyia* sp.; Syrphidae: *Episyrphus balteatus* (de Geer 1776); Calliphoridae: *Calliphora vicina* Robineau-Desvoidy 1830
 Siphonaptera, Ceratophyllidae: *Ceratophyllus* sp.

Light microscopy and scanning electron microscopy

Most specimens were captured in the field and fixed in alcoholic Bouin or 70% ethanol. Tarsi were dissected, dehydrated in ethanol, and critical point dried. To obtain information about spatial architecture of pad material, some dried specimens were fractured using a razor blade. This material was used for scanning electron microscopy. Air-dried material was also obtained from museum collections. Such specimens were used only in special instances, because vulnerable structures of attachment devices were often deformed.

Some specimens were fixed in 2.5% glutaraldehyde (0.01 M phosphate buffer at pH 7.3), postfixed for 1 h in 1% osmium tetroxide in phosphate buffer at 2°C, washed, dehydrated and embedded in a low-viscosity resin (Spurr 1969). Semi-thin sections (0.5–2.0 µm) of pads embedded in Spurr-resin were sectioned using a diamond knife, were stained with toluidine blue or with triple stain after Cason (Romeis 1989) and studied by light microscopy.

An additional technique was used to obtain information about inner structures. Sections were picked up on pioloform-covered cover-slips,

treated with Maxwell's solution (Maxwell 1978) for 2–5 min in order to remove the resin, washed in absolute ethanol and critical-point dried.

All dried preparations were mounted on holders, sputter-coated with gold-palladium (8–10 nm) and examined in a Hitachi S-800 (Nissei Sangyo GmbH (Deutschland), Ratingen, Germany) or in a JEOL JSM-5400 (JEOL (Germany) GmbH, Eching, Germany) scanning electron microscope at 20 kV.

Cladistic analysis

Computer software (PAUP version 3.1; Swofford 1991) was used to calculate minimum length trees (heuristic search settings: stepwise addition, addition sequence random, 100 replicates, tree bisection-reconnection). Analysis of character evolution was conducted in MacClade (version 3; Maddison and Maddison 1992). Branch support values (Bremer 1988) were calculated using the 'converse approach' (Bremer 1994).

Chilopoda and Symphyla were included as outgroup taxa and treated as were all other groups in the analysis (simultaneous analysis; Nixon and Carpenter 1993). The traditional concept of a monophyletic group comprising myriapods and Hexapoda (e.g. Kraus and Kraus 1994) seems to be supported by a recent, detailed study of head structures (Koch 2000c) and by a comprehensive analysis of a broad spectrum of morphological, developmental, ultrastructural and gene order characters (Edgecombe et al. 2000). Even if tracheates would not be monophyletic as indicated in some studies based on developmental and DNA sequence data, myriapods are certainly members of a monophyletic taxon Mandibulata and therefore still suitable as outgroup. However, hypotheses suggesting closer relationships between Hexapoda and Crustacea or crustacean subgroups (Malacostraca or Branchiopoda) are not consistent (e.g. Adoutte and Phillippe 1993; Averov and Akam 1995; Friedrich and Tautz 1995; Regier and Shultz 1997; Wheeler 1998a,b).

As a first step, phylogenetic relationships between groups of Hexapoda were calculated using characters that were not related to attachment (1–105; Fig. 10). Then all characters were pooled and analysed again (Figs 11, 13). Additional analyses were carried out after successive reweighting (Fig. 12). Finally, evolution of selected attachment structures was analysed in the context of relationships between different groups of Hexapoda.

Glossary

Literature data on particular hexapod groups contain information on leg attachment devices. However, these data are sometimes almost useless, because of confusing terminology. Authors often refer to any attachment structures as pulvilli or just as attachment pads. Below, a glossary on tarsal and pretarsal structures is provided to clarify differences in morphology of attachment devices. The terms used here are largely in accordance with the definitions given by Dashman (1953).

Tarsus: the distal part of a hexapod or myriapod leg. It comprises 1–5 tarsomeres. The proximal tarsomere is often the longest and is called the basitarsus. The most distal tarsomere is often called the terminal tarsomere or distitarsus.

Pretarsus (post-tarsus): the terminal part of the hexapod leg, closely associated with the distal end of the terminal tarsomere. It is represented by a complete annulus in entognathous hexapods and usually consists of two ventral sclerites, the planta and unguis-tractor plate in representatives of other groups.

Dactylopodite: the simple, claw-like, distal leg segment occurring in most arthropods including Crustacea. It is controlled by a pair of muscles (levator and depressor). Dactylopodite-like pretarsi occur in entognathous hexapods, and in larval Lepidoptera and Coleoptera. However, in these taxa it is controlled only by a single depressor muscle (Snodgrass 1935).

Claws (ungues): hollow, multicellular, movable structures which articulate dorsally at the distal end of the tarsus. The claw segment is usually reduced to a small median claw or a lobe-like structure.

Unguifer: a median process of the dorso-distal part of the terminal tarsomere, to which the unguis are articulated.

Depressor muscle: adductor or flexor of the claw (= retractor muscles. Dashman 1953). Its tendon (retractor of the claws) is inserted on the median claw or unguittractor.

Unguitractor (unguitractor plate): median basal plate of the ventral surface of the pretarsus. It is usually invaginated into the end of the terminal tarsomere (Fig. 2).

Planta: distal part of an unguitractor plate which is divided into two sclerites (Fig. 2).

Arcus: elastic, U-shaped band, which embraces the base of the arolium ventrally with its arms extending distally in the lateral walls on either side (Fig. 2).

Manubrium (= Orbicula s. Dashman 1953): Elongate medial sclerite in the dorso-basal region of the arolium. It is articulated proximally on the end of the tarsus between the bases of the claws and by its narrowed distal end it is attached like a handle to the base of the arolium (Fig. 2).

Arolium: the median hollow lobe of the pretarsus. It can be completely membranous or at least partly sclerotized (Figs 2, 3a). The arolium is morphologically and ultrastructurally completely different from a lobular median empodium. Its surface is smooth and its cuticle consists of rod-like chitin crystallites oriented perpendicular or at some angle to the surface. The median empodium is composed of common layered cuticle and its surface is covered by acanthae.

Empodium: a median process between the pulvilli. It arises from the distal end of the unguitractor plate, is spine-shaped or lobe-like and is similar in form to the pulvilli (empodial pulvillus) (Fig. 3b,c).

Auxiliae or auxiliar sclerites (= Basipulvilli s. Dashman 1953): lateral sclerites beneath the bases of the claws (Fig. 2).

Pulvilli: smooth or hairy paired lateral membranous lobes ventral to the claws. They are located on the auxiliae (Fig. 3b,c), which participate in control of pulvilli movements.

Euplantulae: flexible pad-like structures without hairs on the ventral side of one or more tarsomeres (Fig. 3h).

Plantar lobes: specialized, adhesive tarsal thorns (Fig. 3i).

Results (Table 1)

External tarsal morphology

1 Protura (Janitschek 1970)

The tarsus is undivided as in all other entognathous hexapods. A very short, ring-shaped pretarsus is present. It bears a single claw, an unmodified empodial seta and a ventral empodial appendage. The claw is usually knife-shaped. Mid- and hind claws have a navicular shape in protentomids and acerentomids and are equipped with lateral teeth, which are connected by a membrane in members of the latter group (Janitschek 1970). Specialized adhesive structures such as arolia, pulvilli, or dense fields of hairs are absent as in all other apterygote hexapods. However, empodial structures may be potential preadaptations for formation of pulvilli.

2 Collembola (Schaller 1970)

The pretarsus is a very short but separate leg section. On the ventral side, opposed to the single claw a spur-like empodial appendage and an empodial tubercle are present, and in some springtails an accessory empodial appendage. The claw is triangular in cross-section with a median edge – sometimes toothed – and two lateral edges. The lateral edges are equipped with one lateral tooth in most species. Sminthurids (e.g. *Sphyrrotheca* sp.) are characterized by a membranous claw sheath (tunica; Schaller 1970).

3 Diplura (Grassé 1949; Condé and Pagés 1991)

Presence of an empodial median claw and of a pair of larger, lateral claws is probably a groundplan feature of the order. This condition is found in *Anajapyx* and *Lepidocampa* species. The median claw is lost in all other diplurans.

4 Archaeognatha

The tarsus is three- or rarely two-segmented (Watson and Smith 1991). A well-defined, segment-like pretarsus is not developed in archaeognathans and all following groups. The reduced pretarsus bears two simple claws. A median claw or empodium is not developed.

5 Zygentoma

The tarsus is three-segmented in most members of *Zygentoma* (Smith and Watson 1991) but five-segmented in *Tricholepidion gertschi* Wygodzinsky 1961 (Wygodzinsky 1961: Figs 29, 30). The reduced pretarsus bears one median empodial claw and a pair of lateral claws (Fig. 4A).

6 Ephemeroptera

The tarsus is usually four- or five-segmented (Peters and Campbell 1991). The transformation of one of two claws into a thickened attachment organ (claw pad) is a characteristic feature found only in ephemeropterans (Figs 3h, 4B). Other adhesive structures are absent.

7 Odonata

The tarsus is three-segmented and the distal segment is longer than the others. The paired claws are usually armed with a hook (Watson and O'Farell 1991). Specific adhesive structures are absent from dragonflies and damselflies.

8 Plecoptera

The two proximal tarsomeres of the three-segmented tarsus bear euplantulae in the larger species (Zwick 1980). An

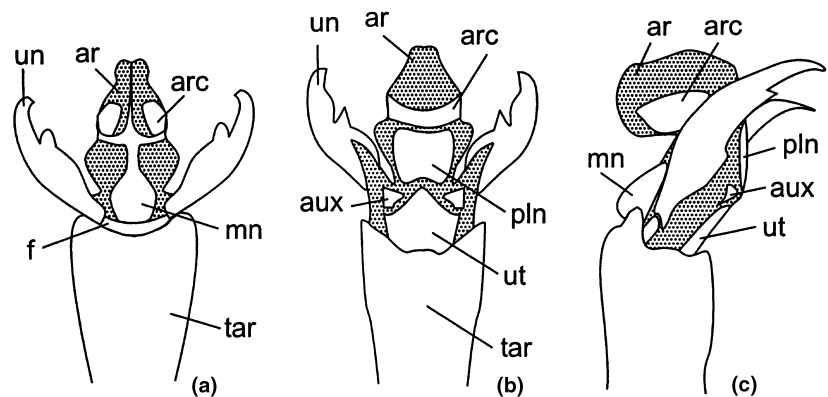


Fig. 2. Terminology of arolium structures (schematized from Snodgrass 1956). (a) Dorsal aspect; (b) ventral aspect; (c) lateral aspect. ar, arolium; arc, arcus; aux, auxillae; f, marginal flange of the terminal tarsomere; mn, manubrium; pln, planta; tar, tarsal segments; un, claw; ut, unguitractor plate

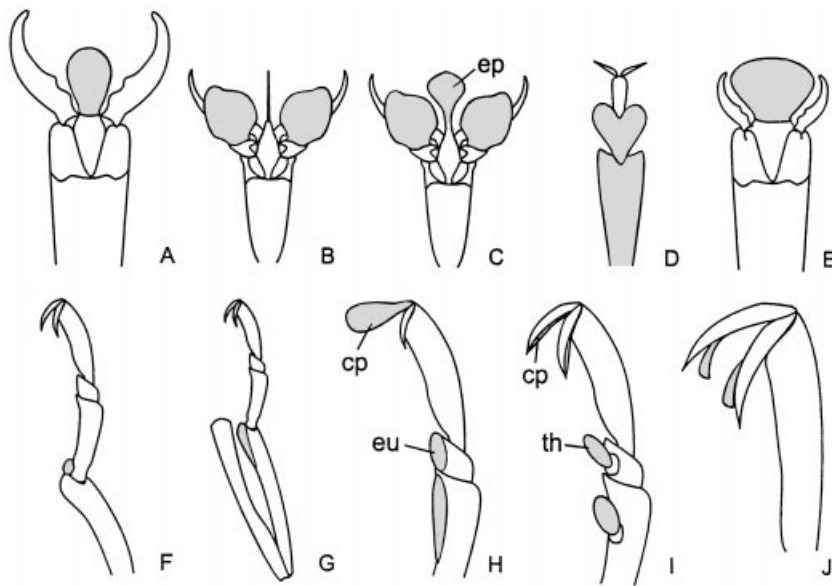


Fig. 3. Diversity of the leg attachment devices (gray-colored areas) in hexapods. (a) Arolium (smooth). (b) Pulvilli (smooth or hairy). (c) Empodial pulvillus (ep) (hairy). (d) Hairy adhesive soles of tarsomeres. (e) Eversible pretarsal bladder (smooth). (f) Eversible structure between tibia and tarsus (smooth). (g) Fossula spongiosa (hairy). (h) Euplantulae (eu) and claw pad (cp) (both smooth). (i) Tarsal thorns transformed into adhesive structures (th), claw pad (cp) (both smooth). (j) Adhesive claw setae

arolium is present between the strong, paired claws (Fig. 3a). The arolium cuticle bears chitinous threads oriented at an angle to the surface (Fig. 4I).

9 Dermaptera

The second tarsomere of the three-segmented tarsus is distinctly shorter than the others in representatives of Dermaptera excluding *Hemimerus* (Günther and Herter 1974; Figs 3d, 7D,E). The two proximal tarsomeres usually bear a dense brush of hairs on the ventral side (Günther and Herter 1974). An arolium is found in hemimerines (Günther and Herter 1974; Haas and Gorb, unpublished data).

10 Blattodea

Tarsi are five-segmented. An arolium is present or absent. Tarsomeres 1–4 are usually equipped with euplantulae (Figs 3a,h, 4C). Reduction of adhesive structures occurs often in cavernicolous forms (Roth 1991). The arolium cuticle bears chitinous threads oriented at some angle to the surface (Roth and Willis 1952).

11 Isoptera

Tarsi are five-segmented in *Mastotermes* species, but four-segmented in other termites (Watson and Gay 1991). An arolium is present in alate adults. Euplantulae are not developed.

12 Mantodea

Tarsi are five-segmented in almost all species (Balderson 1991). Euplantulae are developed on the proximal four tarsomeres. An arolium is missing.

13 Embioptera

Tarsomeres 1 and 2 of the three-segmented middle- and hind leg tarsi are densely covered with hairs. The proximal tarsomere of the proleg is strongly distended due to the presence of silk glands (Ross 1991).

14 Ensifera

Tarsi are three- or four-segmented. Proximal tarsomeres are equipped with euplantulae (Fig. 3h). An arolium is lacking.

15 Caelifera

Tarsi are one-, two- or three-segmented, with euplantulae on the proximal tarsomeres. The cuticle of the arolium has a characteristic inner structure of chitinous threads oriented at some angle to the surface (Fig. 4G,H).

16 Phasmatodea

Tarsomeres 1–4 of the five-segmented tarsus are equipped with euplantulae. An arolium is present.

17 Grylloblattodea (= Notoptera)

The five-segmented tarsi are equipped with euplantulae. An arolium is lacking (Rentz 1991).

18 Zoraptera

Tarsi are two-segmented with strongly shortened basitarsus. A strong, curved bristle is present between the paired claws. Specific adhesive structures are absent.

19 Thysanoptera

The presence of an eversible, balloon-shaped pretarsal adhesive structure at the distal end of a one- or two-segmented tarsus is unique to thysanopterans ('Blasenfüße') (Fig. 3e). Homology of this structure with the arolium is likely as demonstrated by Heming (1970, 1972, 1973).

20 Psocoptera

The tarsus is two- or three-segmented (Weidner 1972). Euplantulae and arolium are lacking. A seta which is slightly extended distally ('saugerartiger Pulvillus'; Weidner 1972) is present on the toothed or simple claws (Fig. 3j).

21 Phthiraptera

Tarsi are one- or two-segmented. A claw pad, dissimilar from that of ephemeropterans, is present in some representatives of Phthiraptera (Amblycera, Ischnocera part.) (Fig. 3i). Euplantulae which allow attachment to smooth surfaces are also present in some mallophagan species.

22 Sternorrhyncha

The tarsus is two-segmented in most representatives of Sternorrhyncha, but one-segmented in coccoids (Strümpel

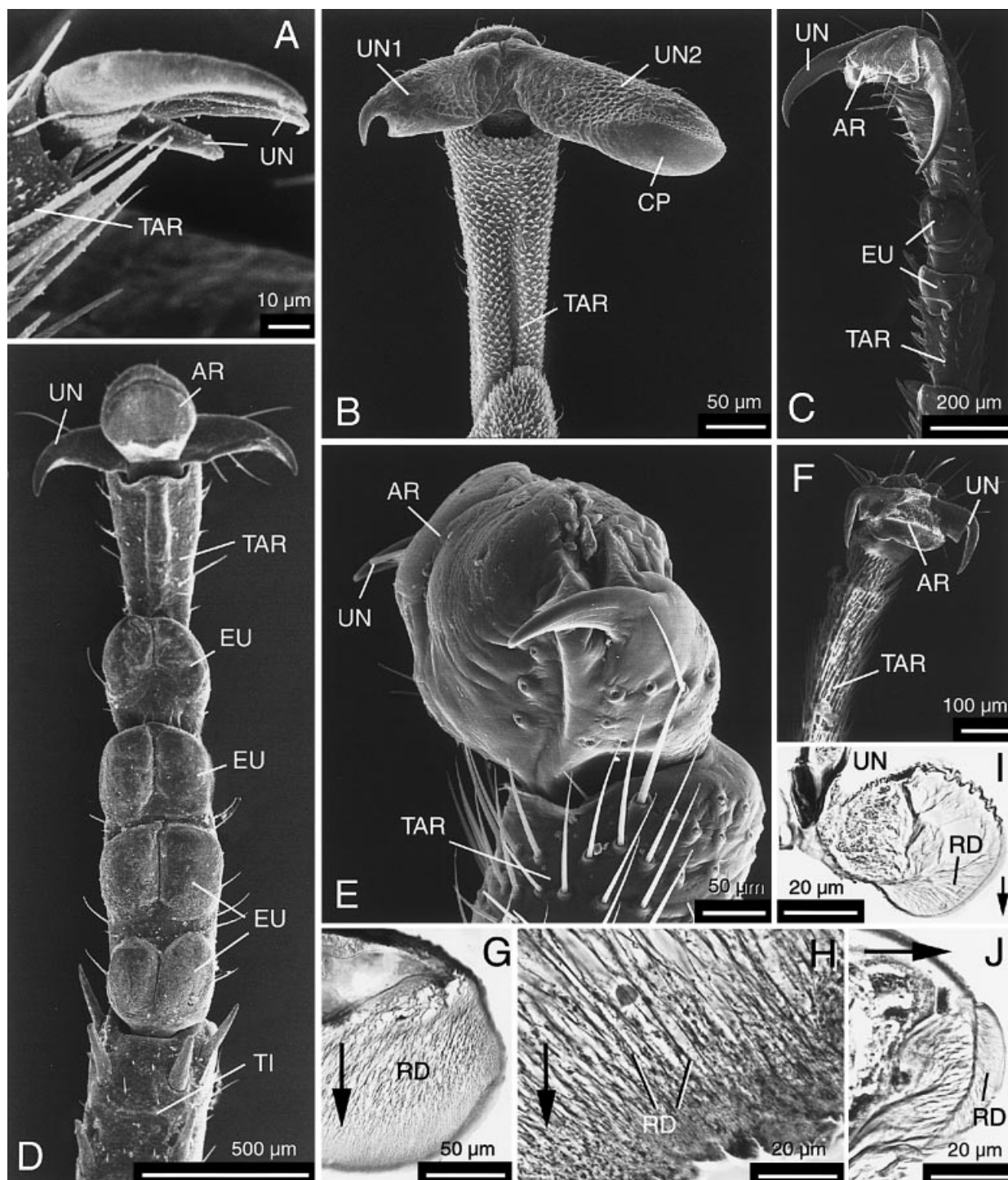


Fig. 4. Details of hexapod tarsi and pretarsi. (A) *Lepisma saccharina* (Zygentoma), foreleg, pretarsus, lateral aspect. (B) *Paraleptophlebia* sp. (Ephemeroptera), midleg, pretarsus, ventral aspect. (C) *Blattella germanica* (Blattodea), midleg, tarsus, ventro-lateral aspect. (D) *Omocestus viridulus* (Caelifera), foreleg, tarsus, ventral aspect. (E) *Cercopis vulnerata* (Auchenorrhyncha), midleg, pretarsus, ventro-lateral aspect. (F) *Chrysoperla carnea* (Neuroptera), pretarsus, ventral aspect. (G, H) *Schistocerca gregaria* (Caelifera), foreleg, arolium sagittal section, triple stain after Cason. (I) *Brachyptera risi* (Plecoptera), midleg, arolium, sagittal section, triple stain after Cason. (J) *Cercopis vulnerata* (Auchenorrhyncha), midleg, sagittal section, triple stain after Cason. Black arrows indicate ventral directions. AR, arolium; CP, claw pad; EU, euplantulae; RD, chitinous threads; TAR, tarsal segments; TI, tibia; UN, claw, UN1, ephemeropteran hook-like claw, UN2, ephemeropteran pad-bearing claw

1983). A cushion-like, simple or bilobed arolium is present in many psylloids. Some representatives of Aphididae possess pulvilli. Other aphidid species examined are characterized by an eversible structure resembling euplantula between tibia and tarsus (Lees and Hardie 1988; Dixon et al. 1990) (Fig. 3f).

23 *Auchenorrhyncha*

Tarsi are three-segmented. An arolium has evolved in cicadids and cercopids (Fig. 4e). The arolium cuticle has a characteristic inner structure of chitinous threads oriented at some angle to the surface (Fig. 4j).

24 Heteroptera

The tarsus is maximally three-segmented. An arolium is present in slaterellines (Lygaeidae), an arolium and smooth euplantulae in mirines (Miridae), smooth pulvilli are present in members of Coreidae, Pentatomidae and Pyrrhocoridae (Figs 3b, 5A), and smooth pulvilli and a fossula spongiosa in reduviids (Carver et al. 1991) (Fig. 3g).

25 Neuroptera (= Planipennia)

The tarsus of the middle and hind legs is almost always five-segmented as in members of other holometabolous groups with the exceptions noted. Modification in number of tarsomeres is only known from the specialized raptorial fore legs of some mantispids (New 1991). No specific adhesive structures are present in members of Sisyridae, Myrmeleontoidea and Ithonidae. An arolium is developed in representatives of other groups (Fig. 4F).

26 Megaloptera

Tarsomeres with a dense ventral brush of hairs are present in members of Chauliodidae (Maki 1936: Fig. 32), Corydalidae and Sialidae. Tarsomere 4 is expanded and bilobed in *Sialis* species (Theischinger 1991; Figs 3d, 5E,I).

27 Raphidioptera

The ventral side of tarsomeres 1–3 is densely covered with hairs. Tarsomere 4 is very short and largely concealed between the two lobes of the heart-shaped tarsomere 3 (Aspöck and Aspöck 1991).

28 Coleoptera

Tarsi are five-segmented in most groups of Coleoptera. However reduction in number of tarsomeres occurs in several lineages (e.g. Chrysomeloidea). The ventral side of the proximal tarsomeres is covered with a very dense layer of hairs in males or both sexes of many coleopteran species (Fig. 3d, 5B,G,H). This is considered as a groundplan feature of the order. Tarsal hairs are transformed into larger or smaller suckers in representatives of some aquatic groups of Adephaga such as Gyriminae and Dytiscinae. In *Priacma serrata* (Archostemata), the hairs are branched in a feather-like pattern (Fig. 5C,D,F). Arolium, pulvilli, and euplantulae are absent from adults and most larvae of Coleoptera. An arolium-like structure is present in larvae of Chrysomelidae (Gannon et al. 1994).

29 Strepsiptera

The full number of five tarsomeres and double claws are present in males of Mengenillidae, Mengeidae and Triozocerinae (Kinzelbach 1971). Tarsomeres are densely covered with hairs (Kinzelbach 1971). Broadened proximal tarsomeres, and loss of claws and the distal tarsomere, is characteristic of males of Stylopiformia (Kinzelbach 1971).

30 Hymenoptera

Four- or three-segmented tarsi are found only in a few representatives of Hymenoptera (e.g. Chalcidoidea part., Platygasteridae, Trichogrammatidae; Naumann 1991). An arolium is generally present (Figs 2, 3a, 6F) and additional, specialized tarsal adhesive thorns in the nonapocritan groups ('Symphyta') (Figs 3i, 6A–C).

31 Trichoptera

Adults of Trichoptera possess either pulvilli or a small arolium.

32 Lepidoptera

An arolium is usually present. Hairy pulvilli are described for *Epiphyas* (Tortricidae; Nielsen and Common 1991: Fig. 41.3D) and *Micropterix* (Kristensen, personal communication). This condition is considered a groundplan feature of the order.

33 Mecoptera

An arolium is absent in boreids and notiothaumids (Mickoleit 1971), but present in other mecopterans (Fig. 6D; Byers 1991). Other specific adhesive structures are lacking. Paired claws are present in members of all groups with the exception of Bittacidae which possess single-clawed raptorial tarsi.

34 Diptera

Less than five tarsomeres are found in few representatives of Diptera. An arolium is present in tipulids (Fig. 6E; Rees and Ferris 1939; Hennig 1973) and hairy pulvilli in adults of other groups (Figs 3b,c, 7A–C,E). A lobe-like, pulvilliform empodium is present as an additional adhesive structure in tabanoids (Brachycera) and representatives of Nematocera excl. Tipulidae (Figs 3c, 7A; Snodgrass 1959).

35 Siphonaptera

Smooth pulvilli are present in siphonapterans (Fig. 7G,H).

Surface characteristics

Hairy systems always contain cuticular protuberances on their surfaces. Protuberances on the hairy pads of Coleoptera, Dermaptera and Diptera belong to different types. Representatives of the first two lineages have socketed setae on their pads. Setae range in length from a few micrometres to several millimetres. Presumably, in these pads, the sensory cells degenerate in the trichoid complex during development. Dipteran protuberances are acanthae: single sclerotized protuberances originating from a single cell (Richards and Richards 1969). Acanthae range in length from a few micrometres to at most 0.5 mm. The key morphological characteristic of acanthae is their lack of a socket and a sensory cell (Richards 1965; Hepburn 1969). Both types of structures can be covered with additional minute outgrowths referred to as microtrichia. Fimbriate setae were found in the beetle *Priacma serrata*, a representative of the basal suborder Archostemata (Beutel and Haas 2000; Fig. 5C,D,F).

The surface of smooth systems appears smooth in the light microscope. However, it may consist of a pattern of hexagonal structures (area $14.7 \mu\text{m}^2$; SD = 1.96; n = 22) as in representatives of Ensifera (Fig. 8A). The hymenopteran (Fig. 8E) and mecopteran (Fig. 8D) arolium may be patterned in lines running perpendicular to the longitudinal axis of the pretarsus. A similar pattern occurs on the surface of attachment thorns in some species of non-apocritan Hymenoptera (Fig. 6C). The surface of a tipulid arolium exhibits a complex pattern of microfolds (Fig. 8F). Microfolds found on the surface of attachment thorns in some species of non-apocritan Hymenoptera are much larger (Fig. 8C). In some specimens, remnants of secretory substances are present on the arolium surface (Fig. 8B). Footprints on glass surfaces were previously reported for both hairy and smooth systems as consisting of round droplets (hairy systems: Coleoptera: Ishii 1987; Diptera: West 1862; smooth systems: Blattodea: Roth and Willis 1952; Orthoptera: Jiao et al. 2000; Sternorrhynchi: Lees and Hardie 1988).

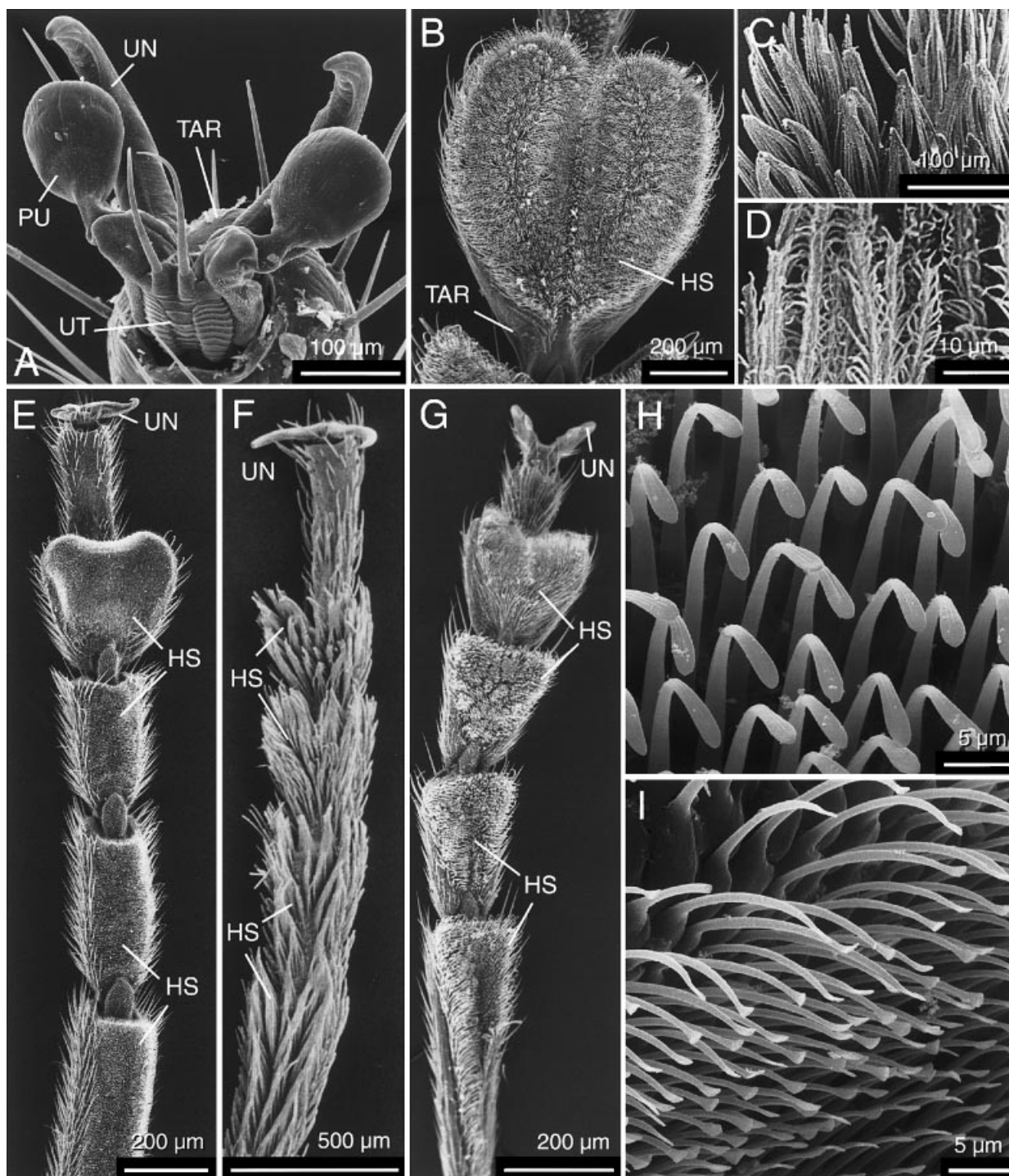


Fig. 5. Details of hexapod tarsi and pretarsi. (A) *Coreus marginatus* (Heteroptera), hindleg, pretarsus, ventro-lateral aspect. (B) *Cantharis fusca* (Coleoptera, Polyphaga), hindleg, first and second tarsomeres, ventral aspect. (C, D, F) *Priacma serrata* (Coleoptera, Archostemata), midleg, tarsus, ventral aspect. (E, I) *Sialis lutaria* (Megaloptera), midleg, tarsus, ventral aspect. (G) *Rhagonycha fulva* (Coleoptera, Polyphaga), midleg, tarsus, ventral aspect. (H) *Cantharis fusca* (Coleoptera, Polyphaga), foreleg, tarsus, adhesive setae. HS, hairy soles; PU, pulvilli; TAR, tarsal segments; UN, claw

Ultrastructural architecture of pad material

Structural features of fly adhesive hairs have been previously reported from the syrphid *Episyrphus balteatus* (Gorb 1998a): the acanthae are hollow inside and some of them contain pores under the end plate (Fig. 7F). This pore presumably delivers an adhesive secretion directly on the contact area. Additional, porous channels at the base of the shaft may

transport secretion to the surface (Bauchhenss 1979). The membranous cuticle of hairy pads is of fibrous composite material with loosely distributed fibres. In coleopterans, the hair bases are embedded in this material (Fig. 9C), which provides flexibility to hairs and adapts them to a variety of substrate profiles. Pores have not been previously reported from beetle hairs.

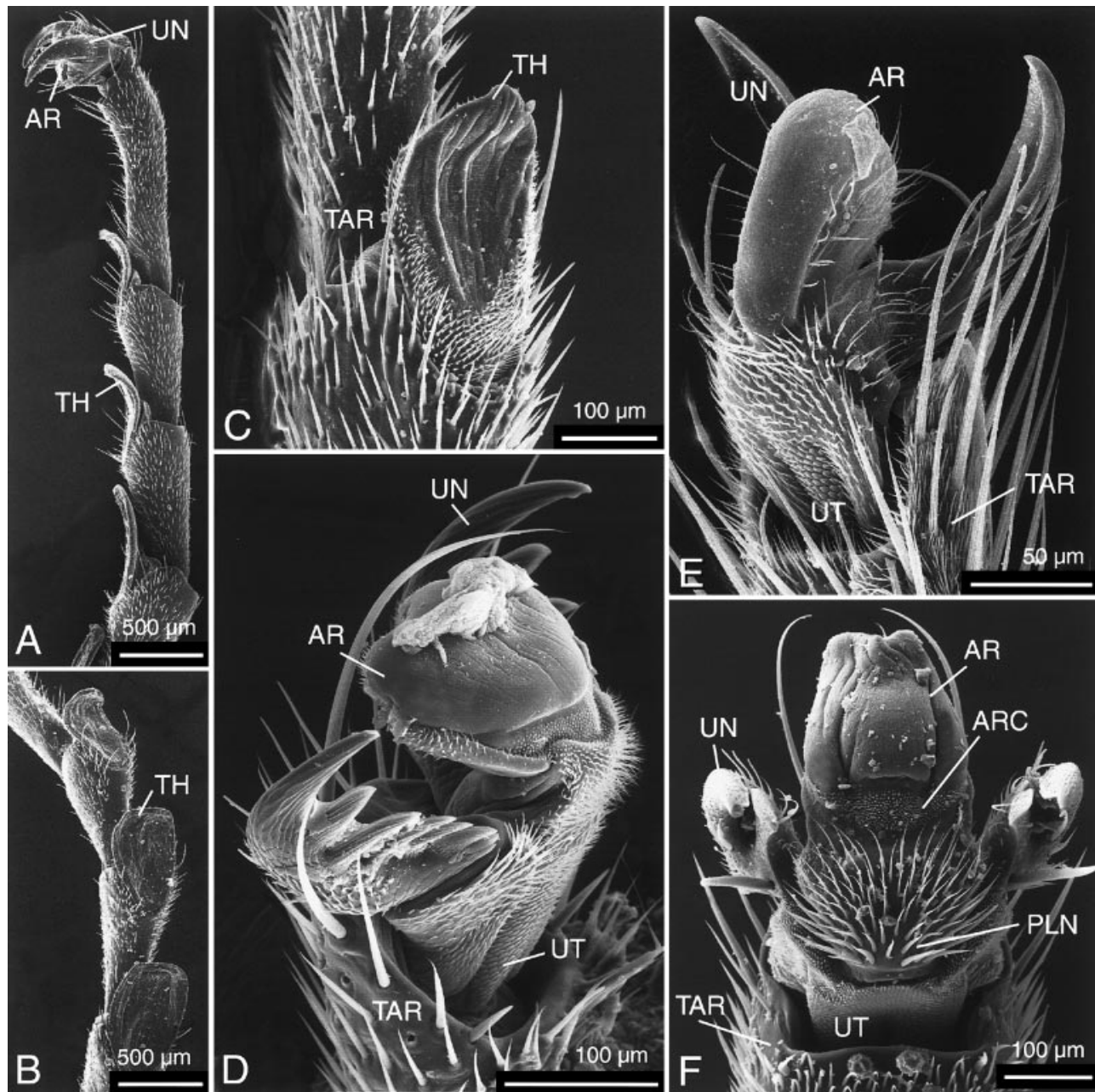


Fig. 6. Details of hexapod tarsi and pretarsi. (A, B) *Urocerus gigas* (Hymenoptera), hindleg, tarsus, lateral aspect. (C) *Abia seriacea* (Hymenoptera), hindleg, ventro-lateral aspect of the single attachment thorn. (D) *Panorpa communis* (Mecoptera), midleg, pretarsus, ventro-lateral aspect. (E) *Tipula* sp. (Diptera), midleg, pretarsus, ventro-lateral aspect. (F) *Apis mellifera* (Hymenoptera), midleg, tarsus, ventral aspect. AR, arolium; ARC, arculus; HS, hairy soles; PLN, planta; TAR, tarsal segments; TH, specialized tarsal adhesive thorns; UN, claw; UT, unguitractor plate

Ultrastructural studies show the cuticle of smooth pads to be of natural friction-active materials with a specific inner structure. In orthopterans, tiny threads of $0.08 \mu\text{m}$ in diameter ($\text{SD} = 0.01$; $n = 25$) are located just under the epicuticle of euplantulae (Fig. 9A). These filaments are branches of thicker threads of $1.12 \mu\text{m}$ diameter ($\text{SD} = 0.09$; $n = 20$) located more deeply in the cuticle (Kendall 1970; Henning 1974). It has been shown that these threads can change their shape under loads (Gorb and Scherge 2000). The arolium of bees contains thinner and longer threads (Fig. 9D), which may provide higher flexibility of the material. Internal architecture of the arolium of cicadas resembles foam, consisting of fluid-filled cells

surrounded by flexible cuticle (Fig. 9B). The diameter of the cells increases in deeper layers of the material.

Character coding of adhesive devices (for character coding of other structures see Appendix)

- 1 (= 106. in data matrix) Arolium: (0) absent; (1) present; (2) transformed into an eversible bladder
- 2 (= 107.) Pulvilli: (0) absent; (1) smooth; (2) hairy
- 3 (= 108.) Euplantulae: (0) absent; (1) present
- 4 (= 109.) Hairy adhesive soles of tarsomeres: (0) absent; (1) present
- 5 (= 110) Fossula spongiosa: (0) absent; (1) present

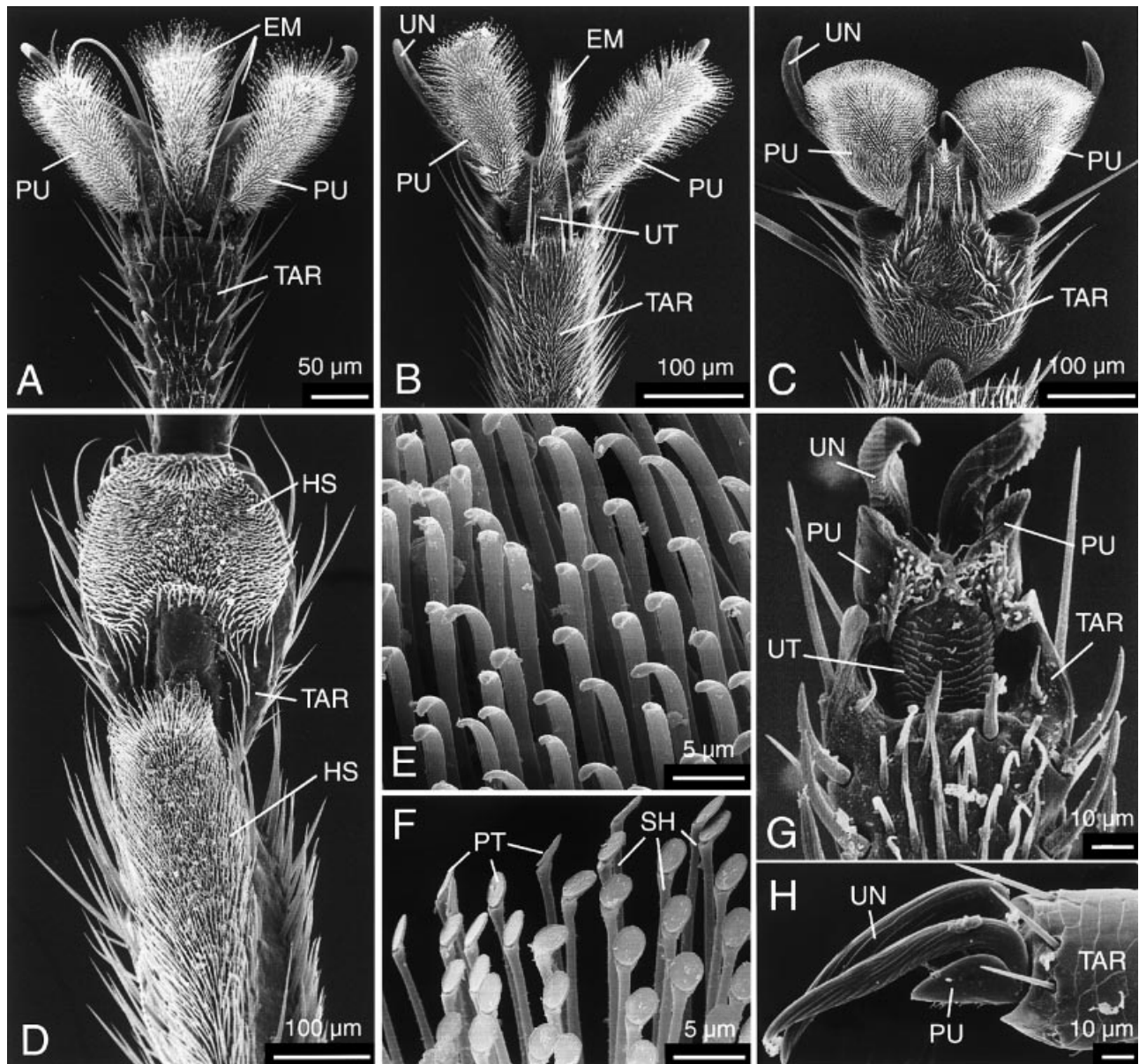


Fig. 7. Details of hexapod tarsi and pretarsi. (A) *Bibio nigriventris* (Diptera), hindleg, pretarsus, ventral aspect. (B) *Rhamphomyia nigripes* (Diptera), hindleg, ventral aspect. (C, F) *Episyrphus balteatus* (Diptera), midleg, pretarsus, ventral aspect. (D, E) *Forficula auricularia* (Dermaptera), hindleg, tarsus, ventral aspect. (G, H) *Ceratophyllus* sp. (Siphonaptera), midleg, pretarsus, ventral (G) and lateral (H) aspects. EM, empodium; HS, hairy soles; PT, hair plate; PU, pulvilli; SH, hair shaft; TAR, tarsal segments; TH, specialized tarsal adhesive thorns; UN, claw; UT, unguitractor plate

- 6 (= 111) Eversible structure between tibia and tarsus: (0) absent; (1) present
- 7 (= 112) Claw pad: (0) absent; (1) present
- 8 (= 113) Specialized adhesive tarsal thorns (plantar lobes): (0) absent; (1) present
- 9 (= 114) Empodium plate-like: (0) no; (1) yes
- 10 (= 115) Adhesive claw setae: (0) absent; (1) present

Results of the cladistic analysis

An analysis of the full set of 115 characters (appendix) results in 24 minimal length trees with 305 steps (CI: 0.675, HI: 0.531, RC: 0.535; Figs 11–13). 48 minimal length trees with 268 steps are obtained, when adhesive pad characters (106–115) are excluded (CI: 0.668, HI: 0.500, RC: 0.538) (Fig. 10). They are largely identical with the previous cladograms.

However, Dermaptera are not the sistergroup Embioptera in all trees (Figs 10, 11). Only three minimal length trees are obtained after successive reweighting (complete data set: Fig. 12).

Discussion

Functional aspects: ‘hairy’ and ‘smooth’ – two alternative designs for adhesive pads

The most interesting result of our literature investigation and comparative ultrastructural study is that diversity of attachment- or adhesive structures of hexapods is generally based on only two basic mechanisms: hairy surfaces or smooth flexible pads. We suggest that a fibrous composite material, such as

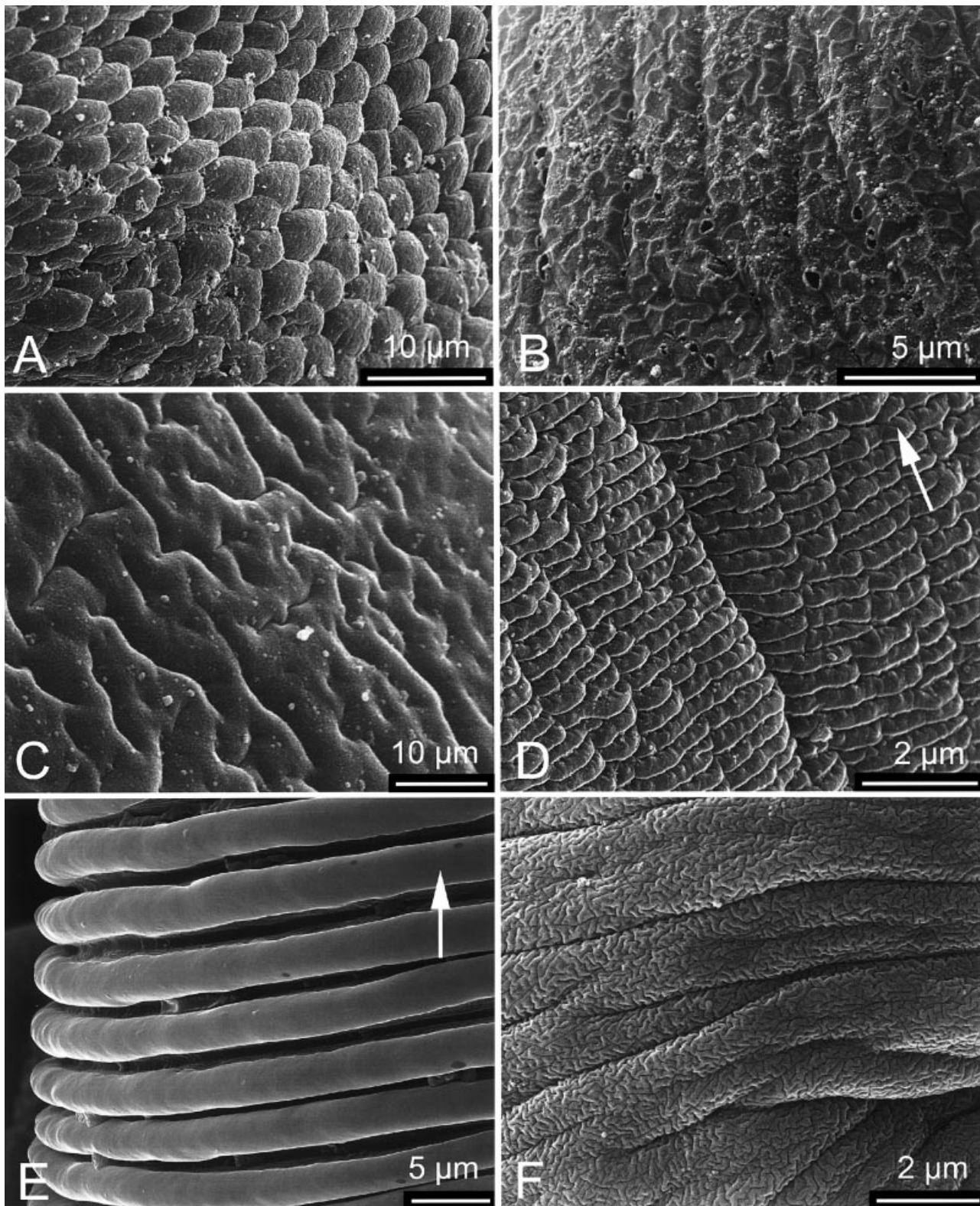


Fig. 8. Surface details of smooth systems of hexapod tarsi. (A) *Tettigonia viridissima* (Ensifera), euplantulae. (B) *Apis mellifera* (Hymenoptera), arolium. (C) *Urocerus gigas* (Hymenoptera), attachment thorn. (D) *Panorpa communis* (Mecoptera), arolium. (E) *Paravespula germanica* (Hymenoptera), arolium. (F) *Tipula* sp. (Diptera), arolium

hexapod cuticle (Neville 1975), is pre-adaptative and may provide limited options for the design of attachment systems.

Data on the hairy pad system of the adult reduviid bug *Rhodnius prolixus* Stal 1859 let previous authors suggest that

mechanical seizure between adhesive setae and substrate irregularities is responsible for attachment to the substratum (Gillett and Wigglesworth 1932). In *Chrysolina polita* (Linnaeus 1758) (Coleoptera, Chrysomelidae), attachment force

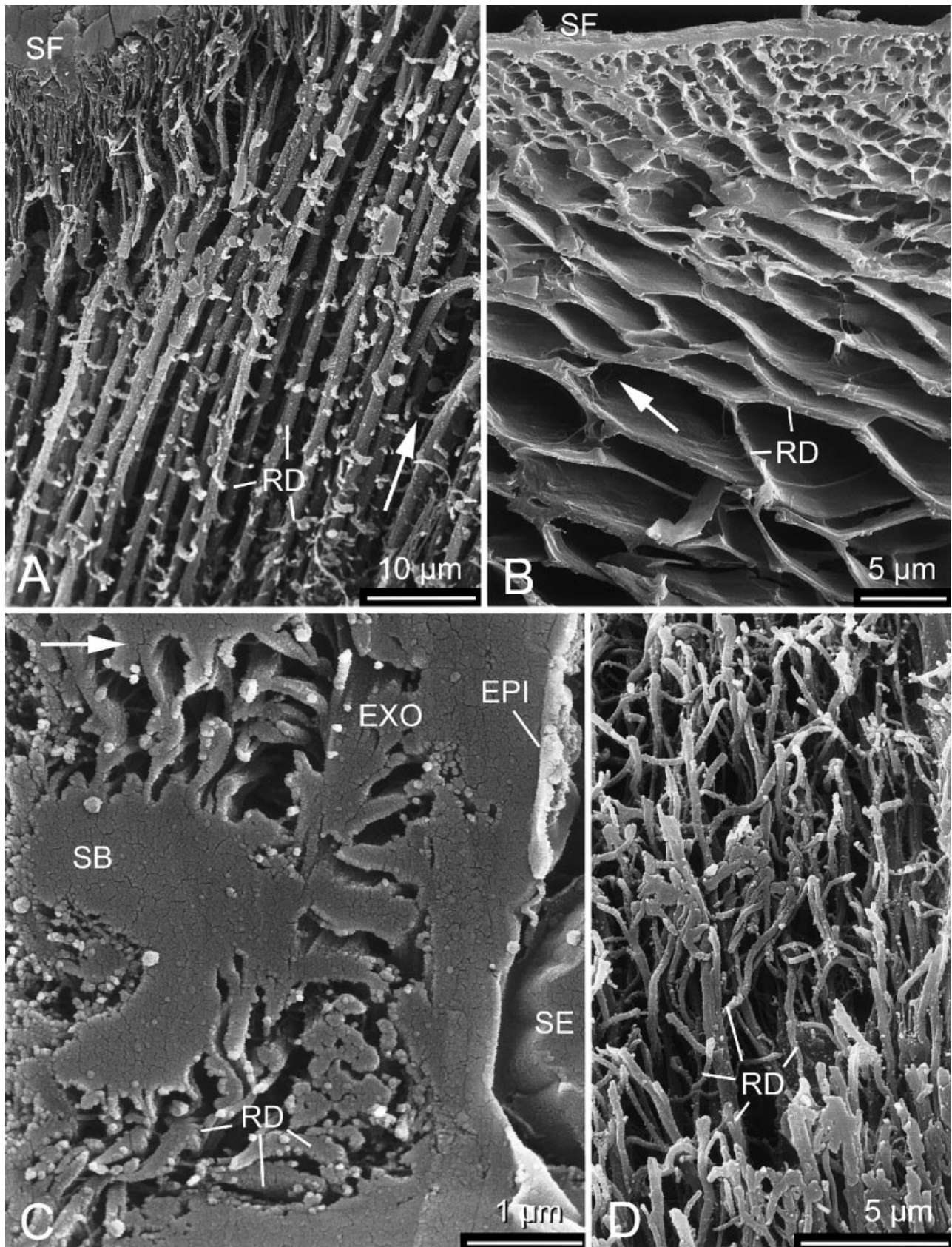


Fig. 9. Inner architecture of the cuticle of smooth systems of hexapod tarsi. (A) *Tettigonia viridissima* (Ensifera), euplantulae. (B) *Cercopis vulnerata* (Auchenorrhyncha), arolium. (C) *Rhagozycha fulva*, ventral part of the tarsus (Coleoptera, Polyphaga). (D) *Apis mellifera* (Hymenoptera), arolium. (A, B, D) fractures. (C) semithin Spurr-section ($\approx 2 \mu\text{m}$) treated with Maxwell's solution. EPI, epicuticle; EXO, exocuticle; basis of the seta; RD, chitinous threads; SB, setal base; SE, seta; SF, surface

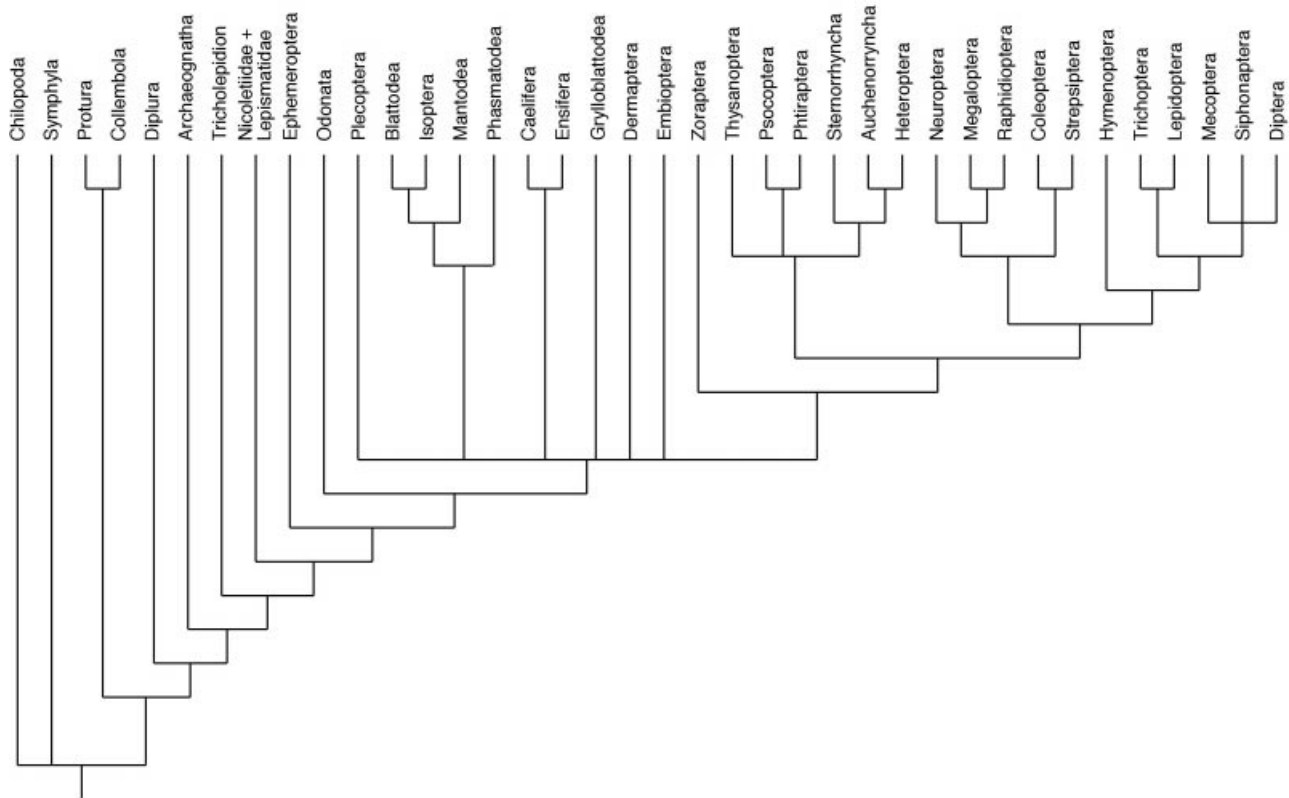


Fig. 10. Strict consensus tree of 48 minimal length trees (268 steps, CI: 0.668, HI: 0.500, RC: 0.538), adhesive pad characters (106–115) excluded

increases with the increase in number of adhesive setae (Stork 1980b). In the beetle hairy system, two main forces contribute to overall attachment: (1) molecular adhesion between setae and substratum and (2) surface tension in a thin layer of epidermal secretion. Molecular adhesion requires very close approximation between contacting surfaces. This means that setae or setal ends have to consist of extremely flexible material. The flexibility of beetle setae has been demonstrated by use of Mallory's single stain (Stork 1983b). For hairy pad systems, there are no data on the dependence of attachment pad material to the substratum with increasing loading force. A similar attachment mechanism has been hypothesized for spatulate hairs on the adhesive pads of geckos (Ruibal and Ernst 1965; Hiller 1968; Russell 1975; Stork 1983a).

The deformable cuticle of the pads has an ultrastructure differing from that of the surrounding cuticle. It consists mainly of the endocuticle (Roth and Willis 1952; Henning 1974) organized as characteristic filaments or as a foam-like network. The filaments are orientated at some angle to the cuticle surface (Dewitz 1884; Slifer 1950). Attachment of smooth systems to a surface is strongly dependent on deformation of the pads (Jiao et al. 2000). Pads can copy the surface to guarantee maximum contact. The mechanical properties of pad material are determined by its composite structure. Sectioned and fractured pad material provides evidence that, when the surface is compressed, the pad cuticle decreases in thickness, and the filaments flatten close to one another against the inner layer. When pressure is released, the filaments return to their previous condition (Slifer 1950). Additionally, euplantulae contain air sacs branching from the tracheal trunk (Henning 1974). Spaces within the tarsus are filled with haemolymph. Air sacs embedded in the fluid may

provide an additional source for flexibility of the pad. For smooth systems, the viscoelastic properties of the pad material have been suggested previously (Brainerd 1994) and recently proved experimentally (Gorb et al. 2000). It was shown that pads deform elastically under rapidly applied force and behave visco-elastically under slowly increasing force (Gorb et al. 2000).

An adhesive secretion is an essential component of attachment in both hairy and smooth systems. Pad fluids have been previously reported from hairy adhesive pads of reduviid bugs (Edwards and Tarkanian 1970), flies (Bauchhens and Renner 1977; Bauchhens 1979; Walker et al. 1985), coccinellid beetles (Ishii 1987), and from the smooth pads of cockroaches (Roth and Willis 1952), aphids (Lees and Hardie 1988; Dixon et al. 1990) and bugs (Hasenfuss 1977a,b, 1978; Ghasi-Bayat and Hasenfuss 1980a,b,c).

Pad secretion is an essential factor for attachment to smooth substrata. For example, the bug *Rhodnius prolixus* with pads treated with lipid solvents, had poorer attachment performance than nontreated pads (Edwards and Tarkanian 1970). Aphids (*Aphis fabae* Scopoli 1763) after some period of walking on silica gel, lost their ability to attach to smooth surfaces (Dixon et al. 1990). The pad secretion of diverse hexapods contains a nonvolatile, lipid-like substance which can be observed in footprints under water (Hasenfuss 1977a; Bauchhens 1979), or in footprints stained by Sudan Black (Lees and Hardie 1988). This fluid adheres well to both hydrophilic and hydrophobic surfaces, such as wax (Roth and Willis 1952) and silanized glass (Dixon et al. 1990). In beetles, the chloroform-soluble part of the pad secretion consists mainly of hydrocarbons, fatty acids and alcohols (Ishii 1987; Kosaki and Yamaoka 1996). However, identity of the water

soluble fraction of the fluid remains unknown. It has been suggested that the fluid contains a kind of surfactant, which would make adhesion less sensitive to the nature of the substrate (Dixon et al. 1990). Information on the adhesive properties of the fluid itself is not available in the literature.

Leg attachment devices are adaptive structures. Their construction and properties may correlate with the preferred substrata usually used by particular hexapod species. Hexapod attachment pads probably evolved to facilitate walking on plant surfaces. Plant surfaces have a wide range of textures: they may be smooth, hairy, and covered with waxes or with moist secretions. As with any integument, plant cuticle is a functional organ reflecting response to a variety of environmental pressures. This results in the particular design, ultra-structure and chemistry of the plant surface. During the long period of co-evolution between flowering plants and hexapods (e.g. Labandeira 1998), plants have not only developed structures attracting pollinators, but also a wide variety of structural and chemical attributes of their surfaces related to defence against herbivores. The co-evolution of plant surfaces and hexapod pads results from a competition between hexapod attachment systems and plant anti-attachment surfaces.

The study of mechanisms of hexapod attachment to plant surfaces remains understudied. Few reports illustrate pad specializations to particular plant surfaces. In oak-feeding aphids, correspondence of attachment structures on legs to host plant surface is an important characteristic of their specialization to this plant substratum. The aphid, *Tuberculatus (Tuberculoides) annulatus* (Hartig 1841), feeding mainly on leaves of *Quercus robur*, has difficulty walking on leaves of *Quercus ilex*. The aphid *Myzocallis schreiberi* Hille Ris Lambers & Stroyan 1959, living on *Q. ilex*, walks more effectively on the surface of this plant (Kennedy 1986). W. Federle and coworkers carried out a series of experiments on ants able to walk effectively on slippery waxy blooms of *Macaranga* ant-plants (Federle et al. 1997: Fig. 14.7). Many hexapods, including other ant species, slip off these plant surfaces. Only the symbiotic partner ants of *Macaranga* are capable of climbing on these plants (*Creumatogaster (Decacrema) msp.1* and *C. msp. 6*).

In spite of the adaptability of pad characters, the phylogenetic analysis performed demonstrates some general evolutionary trends in the structures studied. Structures such as the arolium, euplantulae, and hairy tarsomeres have evolved independently in several lineages. Nevertheless, some of them support monophyletic lineages (e.g. Embioptera + Dermaptera; Paurometabola excl. Dermaptera + Embioptera; Isoptera + Blattodea; Neuropterida + Strepsiptera + Coleoptera; Hymenoptera + Mecopterida). Other structures such as claw pads (Ephemeroptera), balloon-shaped eversible pads (Thysanoptera), or fossulae spongiosae (Reduviidae) are unique to members of larger or smaller monophyletic units. It is plausible to assume that the evolution of flight and the correlated necessity to cling to vegetation or other substrates was a major trigger for the evolution of adhesive pads. Groups with a potential to evolve a great variety of designs in adhesive pads are Hemiptera and Diptera.

The two alternative designs of leg attachment systems used in locomotion, have independently evolved in several groups of arthropods. Smooth pads have been reported in solifugids and pseudoscorpions, and setose pads in spiders. If representatives of a broader number of animal groups were compared, one may reveal other biological fibrous composites such as skin in

amphibians (Ernst 1973a,b; Emerson and Diehl 1980; Green 1981; Linnenbach 1985; Green and Carson 1988; Hanna and Barnes 1990; Emerson 1991) and mammals (Schliemann 1970, 1971, 1974, 1975; Schliemann and Hoerber 1978; Schliemann and Rehn 1980; Thewissen and Etnier 1995). Skin has been selected to form similar smooth attachment structures as described above, whereas keratinized derivatives of lizards (Braun 1878; Dellit 1934; Ruibal and Ernst 1965; Ernst and Ruibal 1967; Hiller 1968; Bauer and Good 1986; Röhl 1995; Irschick et al. 1996) resemble the hairy systems found in hexapods (Stork 1983a). A plausible explanation for the existence of these two principal designs is that leg pads are primarily involved in and adapted to facilitate locomotion. This means that ability to detach from a substrate quickly is of equal importance to fast attachment on a variety of substrates. Other mechanisms such as suckers, hooks, or glue cannot work well, because of their inability to detach rapidly (Nachtigall 1974; Gorb 1998b).

Evolution of pad structures on the background of hexapod phylogeny

Hexapod phylogeny was not the main focus of this paper. An analysis of many characters was carried out principally to allow a more reliable interpretation of the evolution of adhesive pad characters. Phylogenetic conclusions which may be drawn from this analysis are discussed briefly.

Trees obtained are almost congruent with or without consideration of attachment structures (Figs 10–13). However, a sistergroup relationship between Dermaptera and Embioptera is retained in the strict consensus tree when all characters are included (Figs 10, 11; see above). Circularity as a result of inclusion of characters that might be selectively correlated with the evolutionary question (e.g. Coddington 1988) was refuted by Luckow and Bruneau (1997).

Results of our analyses (Figs 10–13) are largely consistent with phylogenies proposed by other authors, especially Kristensen (1975, 1981, 1991, 1997, 1999). This is not surprising as many characters in our data matrix (Appendix) were adopted from these studies and from other works (e.g. Hennig 1969; Jamieson 1987; Pass 1991, 1998; Whiting et al. 1997).

Monophyly of Hexapoda, Ellipura and Insecta (Ectognatha) is confirmed. A sistergroup relationship between Diplura and Insecta, proposed by Kukalová-Peck (1991) and Koch (1997, 2000c), is supported by three unambiguous apomorphies: loss of tömösvary organs (3.1; all apomorphies listed in the following based on tree 1 obtained after successive reweighting; Fig. 12), double claws (40.1) and superficial cleavage (99.1; character state unknown for Protura). Presence of posterior suspensions of the anterior tentorial arms to the cranium may be a further synapomorphy (Koch 2000a). These characters are not fully convincing and the implied paraphyly of Ectognatha should not be ruled out completely (Kristensen 1997). Differences in entognathism (char. 17; Koch 1997; 2000c) do not necessarily mean that the advanced condition found in ellipurans is not derived from from a hypothetical configuration of mouthparts in a common ancestor. Diplura were treated as a terminal, monophyletic taxon in this study, as their monophyly seems well supported by several nonregressive apomorphies listed by Kristensen (1997). Nevertheless, he emphasized that little is known about characters states in representatives of the small families Anajapygidae, Projapygidae and Procampodeidae, and that several, presumably

derived features are shared by members of dipluran subgroups and Ellipura or Insecta, respectively (e.g. absence of spiracles, 71.0 and 1; ovaries divided into ovarioles, 81.0 and 1; Kristensen 1991, 1997). One argument suggesting non-monophyly of Diplura was refuted lately. Japygidae show the usual 9 + 9 + 2 sperm axoneme pattern (Dallai 1998; Koch 2000c). This could be considered as a further character supporting a sistergroup relationship Diplura + Insecta. However, the sperm axoneme pattern varies considerably within orders.

Adhesive structures are not found in entognathous hexapods, which live mainly in soil and leaf litter. However, rather complicated claws and associated structures have evolved in diplurans, collembolans and proturans (see above).

The rise of Insecta (Ectognatha) is a crucial event in hexapod evolution, which is reflected not only in structural changes of the antenna (14.1, 16.1) and in the acquisition of an ovipositor with elongate gonapophyses VIII and IX (72.1) and terminal filament (76.1), but also by distinct changes in leg structure. Subdivision of the tarsus (38.2) and reduction of the ring-shaped pretarsus (39.1), still more or less distinct in Diplura (Kristensen 1997: Fig. 21.2H) and Ellipura, are autapomorphies of this large clade. These changes, especially adaptive flexibility of the tarsus, are probably preconditions for further modification and the appearance of different attachment devices.

Our analysis does not support the monophyly of the Zygentoma. Lepidothrichidae represent the sistergroup of the remaining silverfish + Pterygota. This relationship is supported by characters of the head presented in a detailed morphological study by Staniczek (2000): reduced size of the postoccipt and reduced pleural folds (4.1), ligamentous endoskeleton reduced (11.1), transverse mandibular apodeme

reduced (20.1) and presence of *M. mandibulo-hypopharyngalis* (29.1). Shortened maxillary palps (24.1; accelerated transformation = ACCTRAN), and loss of coxal vesicles (67.1) and styli (at least from segment II; 68.1; ACCTRAN) are further features suggesting a closer affinity of Nicoletiidae and Lepismatidae (Maindroniidae?) with Pterygota. Paraphyly of *Zygentoma* implies parallel evolution of sperm conjugation (95.1), loss of superlinguae (8.1; present in nymphs of Ephemeroptera) and extension of the apical labial palpomere (Kristensen 1997). The latter condition is also found in a number of archaeognathans (Kristensen, personal communication) and ephemeropteran nymphs and in representatives of other hexapod orders (Staniczek 2000). It may have evolved several times independently or represent a symplesiomorphy of the taxa in question.

The basal position of Ephemeroptera within pterygote hexapods, i.e. the sistergroup relationship between Odonata and Neoptera is clearly confirmed (see Figs 11–13). Ephemeropterans are characterized by an unusual, autapomorphic condition of the distal leg: the presence of claw pads.

A sistergroup relationship between Plecoptera and the remaining Neoptera, discussed by Zwick (1981) and Kristensen (1991), was supported in some trees of the initial analyses (with and without pad characters) and in all three trees obtained after successive reweighting (Fig. 12). Presence of *M. mandibulo-hypopharyngalis* (29.1, ACCTRAN), loss of *M. stipitalis transversalis* (31.1) and terrestrial habits of larvae (104.0) are possible synapomorphies of Neoptera excluding Plecoptera.

Orthoptera and Dictyoptera are clearly monophyletic and a lineage comprising Dictyoptera, Orthoptera, Phasmatodea and Grylloblattodea is supported by 2 unambiguous apomor-

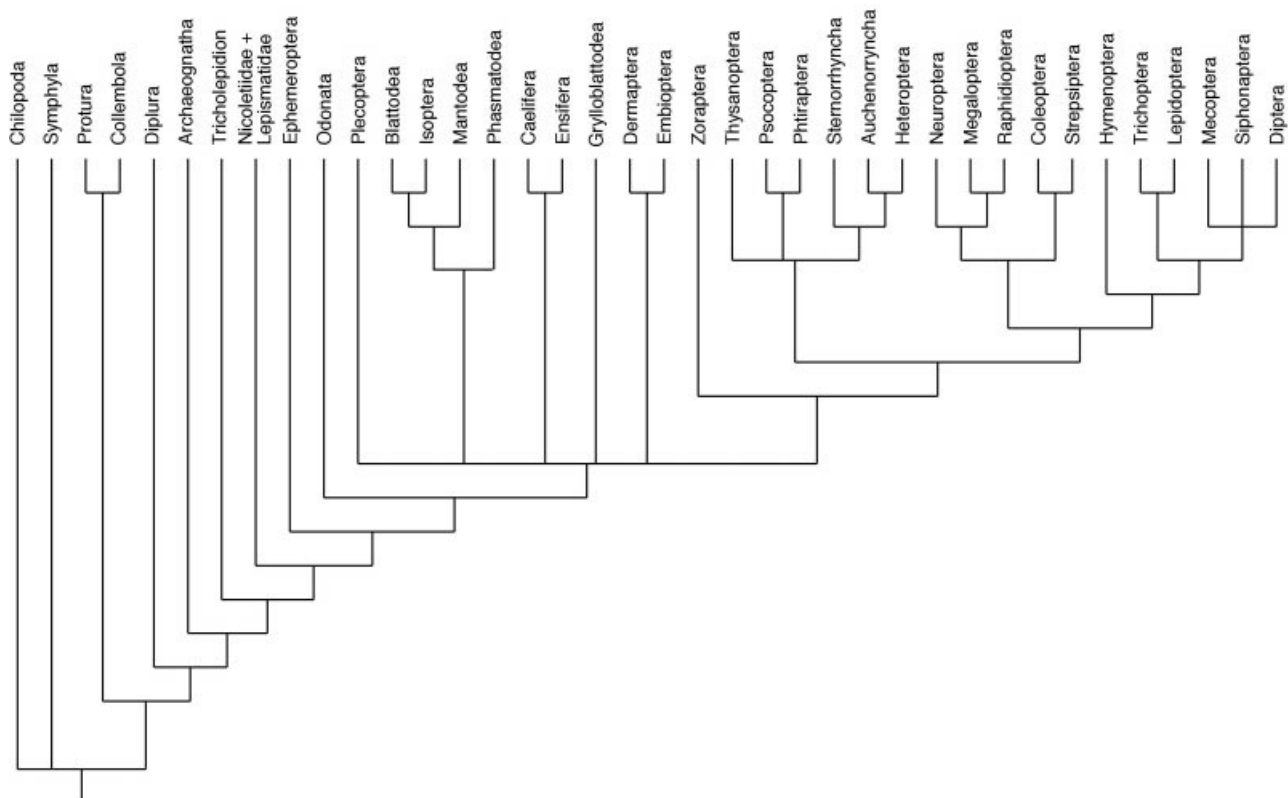


Fig. 11. Strict consensus tree of 24 minimal length trees (305 steps, CI: 0.675, HI: 0.531, RC: 0.535 adhesive pad characters (106–115) included

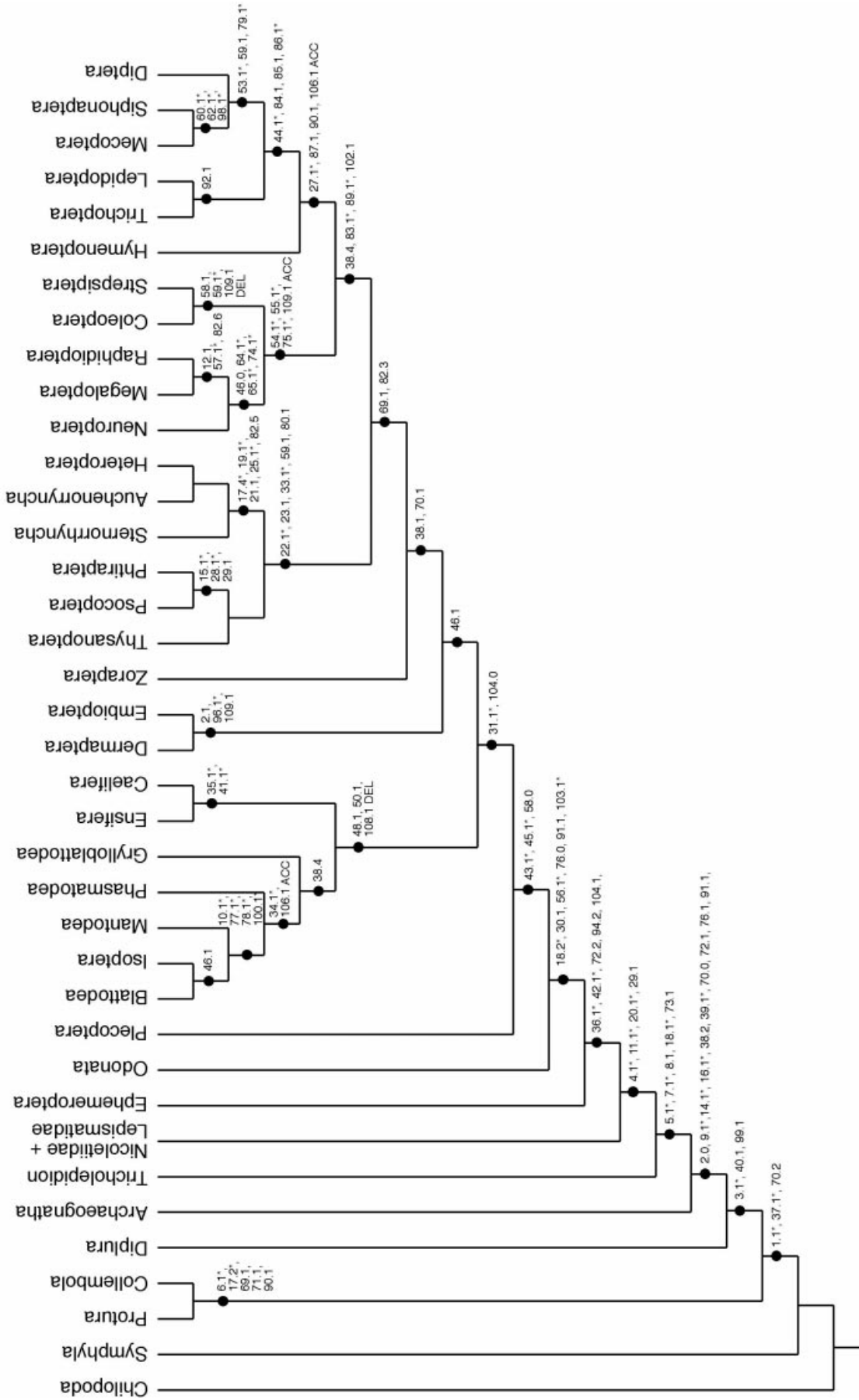


Fig. 12. Tree 1 of three minimum length cladograms obtained after successive reweighting, adhesive pad characters included, unambiguous apomorphies (accelerated and delayed transformation) mapped on trees; asterisks indicate nonhomoplasious changes. Thysanoptera are placed as sistergroup of Hemiptera in tree 2 and as sistergroup of the remaining Paraneoptera in tree 3

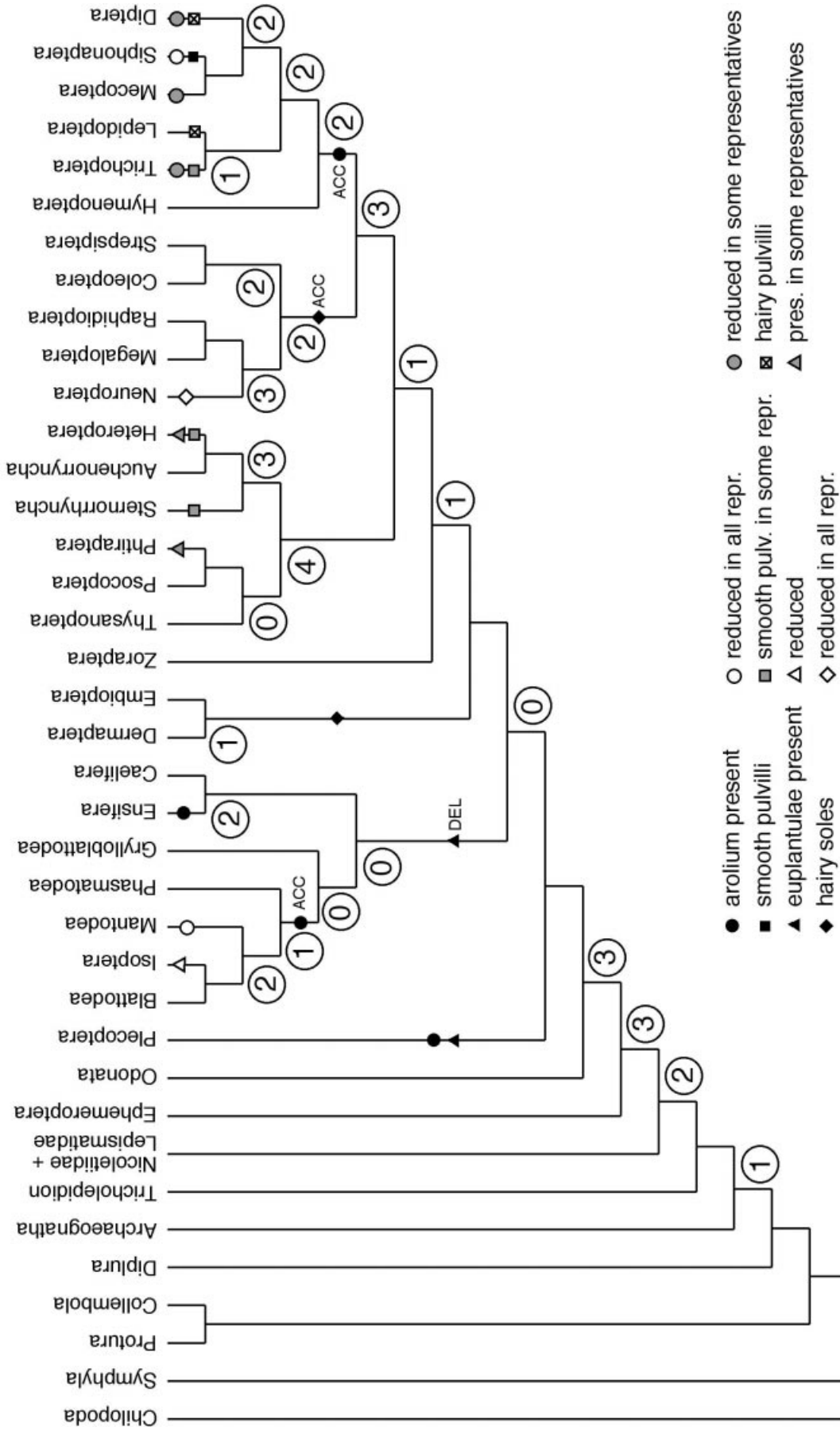


Fig. 13. Selected tree of 24 minimal length trees (pad characters included; topology identical with tree in Fig. 12), adhesive pad characters mapped on cladogram; numbers left of branches are branch support values (Bremer 1988) for selected clades

Table 1. Character state matrix, adhesive pad characters: 105–115; (?) refer to missing character states (–) to inapplicable characters

| | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 | 16 | 17 | 18 | 19 |
|-----------------------|---|-------|---|---|---|---|---|---|---|----|----|----|----|----|----|----|----|----|----|
| Chilopoda | 0 | 1 | 0 | 0 | 0 | 0 | ? | ? | 0 | – | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Symphyla | 0 | 1 | 0 | 0 | 0 | 0 | ? | ? | 0 | – | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Diplura | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | – | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 |
| Protura | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | – | 0 | 0 | 1 | 2 | – | – | 2 | 0 | 1 |
| Collembola | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | – | 0 | 0 | 1 | 0 | 0 | 0 | 2 | 0 | 0 |
| Archaeognatha | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 |
| Lepism.-Nicolet.* | 1 | 0 | 1 | 1 | 1 | 0 | 1 | 1 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 0 |
| <i>Tricholepidion</i> | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 0 |
| Ephemeroptera | 1 | 0 | 1 | 1 | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 0 |
| Odonata | 1 | 0 | 1 | 1 | 1 | 0 | 1 | 1 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 2 | 0 |
| Plecoptera | 1 | 0 | 1 | 1 | 1 | 0 | 1 | 1 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 2 | 0 |
| Dermaptera | 1 | 1 | 1 | 1 | 1 | 0 | 1 | 1 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 2 | 0 |
| Blattodea | 1 | 0 | 1 | 1 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 2 | 0 |
| Isoptera | 1 | 0 | 1 | 1 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 2 | 0 |
| Mantodea | 1 | 0 | 1 | 1 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 2 | 0 |
| Embioptera | 1 | 1 | 1 | 1 | 1 | 0 | 1 | 1 | 1 | 0 | 1 | 1 | 0 | 1 | 0 | 1 | 0 | 2 | 0 |
| Ensifera | 1 | 0 | 1 | 1 | 1 | 0 | 1 | 1 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 2 | 0 |
| Caelifera | 1 | 0 | 1 | 1 | 1 | 0 | 1 | 1 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 2 | 0 |
| Phasmatodea | 1 | 0 | 1 | 1 | 1 | 0 | 1 | 1 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 2 | 0 |
| Grylloblattodea | 1 | 1 | 1 | 1 | 1 | 0 | 1 | 1 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 2 | 0 |
| Zoraptera | 1 | 0 | 1 | 1 | 1 | 0 | 1 | 1 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 2 | 0 |
| Thysanoptera | 1 | 0 | 1 | 1 | 1 | 0 | 1 | 1 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 3 | – | 2 |
| Psocoptera | 1 | 0 | 1 | 1 | 1 | 0 | 1 | 1 | 1 | 0 | 1 | 0 | 0 | 1 | 1 | 1 | 0 | 2 | 0 |
| Phthiraptera | 1 | 1 | 1 | 1 | 1 | 0 | 1 | 1 | 1 | 0 | 1 | 0 | 0 | 1 | 1 | 1 | 0 | 2 | 0 |
| Sternorrhyncha | 1 | 0 | 1 | 1 | 1 | 0 | 1 | 1 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 4 | – | 1 |
| Auchenorrhyncha | 1 | 0 | 1 | 1 | 1 | 0 | 1 | 1 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 4 | – | 1 |
| Heteroptera | 1 | 0 | 1 | 1 | 1 | 0 | 1 | 1 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 4 | – | 1 |
| Neuroptera | 1 | 0 | 1 | 1 | 1 | 0 | 1 | 1 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 2 | 0 |
| Megaloptera | 1 | 0 | 1 | 1 | 1 | 0 | 1 | 1 | 1 | 0 | 1 | 1 | 0 | 1 | 0 | 1 | 0 | 2 | 0 |
| Raphidioptera | 1 | 0 | 1 | 1 | 1 | 0 | 1 | 1 | 1 | 0 | 1 | 1 | 0 | 1 | 0 | 1 | 0 | 2 | 0 |
| Coleoptera | 1 | 0 | 1 | 1 | 1 | 0 | 1 | 1 | 1 | 0 | 1 | 1 | 0 | 1 | 0 | 1 | 0 | 2 | 0 |
| Strepsiptera | 1 | 0 & 1 | 1 | 1 | 1 | 0 | 1 | 1 | – | – | 1 | 0 | 0 | 1 | 0 | 1 | 0 | – | 0 |
| Hymenoptera | 1 | 0 | 1 | 1 | 1 | 0 | 1 | 1 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 2 | 0 |
| Trichoptera | 1 | 0 | 1 | 1 | 1 | 0 | 1 | 1 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | – | 0 |
| Lepidoptera | 1 | 0 | 1 | 1 | 1 | 0 | 1 | 1 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 2 | 0 |
| Mecoptera | 1 | 0 | 1 | 1 | 1 | 0 | 1 | 1 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 2 | 0 |
| Diptera | 1 | 0 | 1 | 1 | 1 | 0 | 1 | 1 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | – | 1 |
| Siphonaptera | 1 | 1 | 1 | 1 | 1 | 0 | 1 | 1 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | – | 1 |

| | 20 | 21 | 22 | 23 | 24 | 25 | 26 | 27 | 28 | 29 | 30 | 31 | 32 | 33 | 34 | 35 | 36 | 37 | 38 |
|-----------------------|----|----|----|----|----|----|-------|----|----|----|----|----|----|----|----|----|----|----|----|
| Chilopoda | 0 | 0 | – | – | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Symphyla | 0 | 0 | 0 | 0 | – | 0 | – | 0 | 0 | ? | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Diplura | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 |
| Protura | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 |
| Collembola | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 |
| Archaeognatha | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 2 |
| Lepism.-Nicolet. | 1 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 2 |
| <i>Tricholepidion</i> | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | ? | 0 | 0 | 0 | 0 | 0 | 1 | 4 |
| Ephemeroptera | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 4 |
| Odonata | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 2 |
| Plecoptera | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 2 |
| Dermaptera | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 2 |
| Blattodea | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 1 | 0 | 1 | 1 | 4 |
| Isoptera | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 1 | 0 | 1 | 1 | 4 |
| Mantodea | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 1 | 0 | 1 | 1 | 4 |
| Embioptera | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 1 | 1 | 2 |
| Ensifera | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 1 | 1 | 3 |
| Caelifera | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 1 | 1 | 2 |
| Phasmatodea | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 0 | 1 | 0 | 1 | 1 | 4 |
| Grylloblattodea | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | – | 1 | 4 |
| Zoraptera | 1 | 0 | 0 | 0 | 1 | 0 | 0 | ? | 0 | 0 | 1 | 1 | 0 | 0 | ? | 0 | 1 | 1 | 1 |
| Thysanoptera | 1 | 0 | 1 | 1 | 1 | 0 | 0 & 1 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | ? | 0 | 1 | 1 | 1 |
| Psocoptera | 1 | 0 | 1 | 1 | 1 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 0 | 1 | ? | 0 | 1 | 1 | 2 |
| Phthiraptera | 1 | 0 | 1 | 1 | 1 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 0 | 1 | ? | 0 | – | 1 | 1 |
| Sternorrhyncha | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 0 | 1 | 1 | 1 |
| Auchenorrhyncha | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 0 | 1 | 1 | 2 |
| Heteroptera | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 0 | 1 | 1 | 2 |
| Neuroptera | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 4 |

Table 1. (Continued)

| | 20 | 21 | 22 | 23 | 24 | 25 | 26 | 27 | 28 | 29 | 30 | 31 | 32 | 33 | 34 | 35 | 36 | 37 | 38 | |
|-----------------------|-------|----|----|----|----|----|-------|-------|----|-------|-------|-------|-------|----|----|-------|----|----|----|-------|
| Megaloptera | 1 | 0 | 0 | 0 | 1 | 0 | 0 & 1 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 4 | |
| Raphidioptera | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | ? | 0 | 1 | 1 | 4 | |
| Coleoptera | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 4 | |
| Strepsiptera | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 4 | |
| Hymenoptera | 1 | 0 | 0 | 0 | 1 | 0 | 0 & 1 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 4 | |
| Trichoptera | 1 | - | - | - | - | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 4 | |
| Lepidoptera | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 4 | |
| Mecoptera | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 4 | |
| Diptera | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 4 | |
| Siphonaptera | 1 | 1 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | - | 1 | 4 | |
| | 39 | 40 | 41 | 42 | 43 | 44 | 45 | 46 | 47 | 48 | 49 | 50 | 51 | 52 | 53 | 54 | 55 | 56 | 57 | 58 |
| Chilopoda | 0 | 0 | 0 | 0 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | ? |
| Symphyla | 0 | 1 | 0 | 0 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | ? |
| Diplura | 0 | 1 | 0 | 0 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 0 | ? |
| Protura | 0 | 0 | 0 | 0 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 0 | ? |
| Collembola | 0 | 0 | 0 | 0 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 0 | ? |
| Archaeognatha | 1 | 1 | 0 | 0 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 0 | ? |
| Lepism.-Nicolet. | 1 | 1 | 0 | 0 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 0 | 1 |
| <i>Tricholepidion</i> | 1 | 1 | 0 | 0 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | ? | ? |
| Ephemeroptera | 1 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 |
| Odonata | 1 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 |
| Plecoptera | 1 | 1 | 0 | 1 | 1 | 0 | 1 | 0 & 1 | 1 | 0 | 0 | 0 & 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 |
| Dermaptera | 1 | 1 | 0 | 1 | 1 | 0 | 1 | 1 | 1 | 1 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 & 1 |
| Blattodea | 1 | 1 | 0 | 1 | 1 | 0 | 1 | 1 | 1 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 |
| Isoptera | 1 | 1 | 0 | 1 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 |
| Mantodea | 1 | 1 | 0 | 1 | 1 | 0 | 1 | 0 | 1 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 |
| Embioptera | 1 | 1 | 0 | 1 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 |
| Ensifera | 1 | 1 | 1 | 1 | 1 | 0 | 1 | 0 | 1 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 |
| Caelifera | 1 | 1 | 1 | 1 | 1 | 0 | 1 | 0 | 1 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 |
| Phasmatodea | 1 | 1 | 0 | 1 | 1 | 0 | 1 | 0 | 1 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 |
| Grylloblattodea | 1 | 1 | 0 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | ? | 0 |
| Zoraptera | 1 | 1 | 0 | 1 | 1 | ? | 1 | 1 | 0 | 0 | ? | 0 | 0 | 0 | 0 | ? | ? | ? | ? | ? |
| Thysanoptera | 1 | 1 | 0 | 1 | 1 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | ? | 0 | 0 | 1 | 0 | 0 |
| Psocoptera | 1 | 1 | 0 | 1 | 1 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 |
| Phthiraptera | 1 | 1 | 0 | - | - | - | - | - | - | - | - | - | - | - | - | 0 | 0 | - | 0 | 0 |
| Sternorrhyncha | 1 | 1 | 0 | 1 | 1 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 |
| Auchenorrhyncha | 1 | 1 | 0 | 1 | 1 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 |
| Heteroptera | 1 | 1 | 0 | 1 | 1 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 |
| Neuroptera | 1 | 1 | 0 | 1 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 2 | 1 | 1 | 0 | 0 |
| Megaloptera | 1 | 1 | 0 | 1 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 & 1 | 1 | 1 | 1 | 0 |
| Raphidioptera | 1 | 1 | 0 | 1 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 0 |
| Coleoptera | 1 | 1 | 0 | 1 | 1 | 0 | 1 | 1 | 0 | 0 | 1 | 3 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 1 |
| Strepsiptera | 1 | 1 | 0 | 1 | 1 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 1 | 1 | 0 | 1 |
| Hymenoptera | 1 | 1 | 0 | 1 | 1 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 & 1 |
| Trichoptera | 1 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 |
| Lepidoptera | 1 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 |
| Mecoptera | 1 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 |
| Diptera | 1 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 0 | 0 | 1 | 0 | 2 | 0 | 1 | 0 | 0 | 1 | 0 | 0 |
| Siphonaptera | 1 | 1 | 2 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 0 | 1 |
| | 59 | 60 | 61 | 62 | 63 | 64 | 65 | 66 | 67 | 68 | 69 | 70 | 71 | 72 | 73 | 74 | 75 | 76 | 77 | |
| Chilopoda | ? | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 1 | - | 4 | 0 | 0 | - | - | - | 0 | 0 | |
| Symphyla | ? | 0 | ? | 0 | ? | 0 | 0 | 0 | 0 | 0 | - | 4 | 1 | 0 | - | - | - | 0 | 0 | |
| Diplura | ? | 0 | ? | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 & 2 | 0 & 1 | 0 | - | - | - | 0 | 0 | |
| Protura | ? | 0 | ? | 0 | ? | 0 | 0 | 0 | 0 | 0 | 1 | 2 | 1 | 0 | - | - | - | 0 | 0 | |
| Collembola | ? | 0 | ? | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 2 | 1 | 0 | - | - | - | 0 | 0 | |
| Archaeognatha | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | |
| Lepism.-Nicolet. | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 & 2 | 0 & 1 | 0 | 1 | 0 | 1 | 1 | 0 | 0 | 1 | 0 |
| <i>Tricholepidion</i> | ? | 0 | ? | ? | 0 | 0 | 0 | ? | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | |
| Ephemeroptera | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 1 | 0 | 0 | 0 | 2 | 1 | 0 | 0 | 1 | 0 | |
| Odonata | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 & 1 | 2 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | |
| Plecoptera | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 2 | 1 | 0 | 0 | 0 | 2 | - | 0 | 0 | 0 | 0 | |
| Dermaptera | 0 & 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 2 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | |
| Blattodea | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 2 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | |
| Isoptera | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 2 | 1 | 0 | 0 & 1 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | |
| Mantodea | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 2 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | |
| Embioptera | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 2 | 1 | 0 | 0 | 0 | 2 | - | 0 | 0 | 0 | 0 | |

Table 1. (Continued)

| | 97 | 98 | 99 | 100 | 101 | 102 | 103 | 104 | 105 | 106 | 107 | 108 | 109 | 110 | 111 | 112 | 113 | 114 | 115 |
|-----------------------|----|----|----|-----|-----|-----|-----|-------|-----|-------|-------|-------|-----|-------|-------|-----|-------|-------|-----|
| Diplura | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Protura | 0 | 0 | ? | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Collembola | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Archaeognatha | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Lepism.-Nicolet. | 0 | 0 | 2 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| <i>Tricholepidion</i> | 0 | 0 | ? | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Ephemeroptera | 0 | 0 | 2 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 |
| Odonata | 0 | 0 | 2 | 0 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Plecoptera | 0 | 0 | 2 | 0 | 1 | 0 | 1 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Dermaptera | 1 | 0 | 2 | 0 | 1 | 0 | 1 | 0 | 1 | 0 & 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 |
| Blattodea | 0 | 0 | 2 | 1 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Isoptera | 0 | 0 | 2 | 1 | 1 | 0 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Mantodea | 0 | 0 | 2 | 1 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Embioptera | 0 | 0 | 2 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 |
| Ensifera | 0 | 0 | 2 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Caelifera | 0 | 0 | 2 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Phasmatodea | 1 | 0 | 2 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Grylloblattodea | 0 | 0 | 2 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Zoraptera | 0 | 0 | 2 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Thysanoptera | 0 | 0 | 2 | 0 | 1 | 1 | 1 | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Psocoptera | 0 | 0 | 2 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 |
| Phthiraptera | 0 | 0 | 2 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 & 1 | 0 | 0 | 0 | 2 | 0 | 0 | 0 |
| Sternorrhyncha | 0 | 0 | 2 | 0 | 1 | 0 | 1 | 0 | 0 | 0 & 1 | 0 & 1 | 0 | 0 | 0 | 0 & 1 | 0 | 0 | 0 | 0 |
| Auchenorrhyncha | 0 | 0 | 2 | 0 | 1 | 0 | 1 | 0 | 0 | 0 & 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Heteroptera | 0 | 0 | 2 | 0 | 1 | 0 | 1 | 0 & 1 | 0 | 0 & 1 | 0 & 1 | 0 & 1 | 0 | 0 & 1 | 0 | 0 | 0 | 0 | 0 |
| Neuroptera | 0 | 0 | 2 | 0 | 1 | 1 | 1 | 0 & 1 | 0 | 0 & 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Megaloptera | 0 | 0 | 2 | 0 | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 |
| Raphidioptera | 0 | 0 | 2 | 0 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 |
| Coleoptera | 0 | 0 | 2 | 0 | 1 | 1 | 1 | 0 & 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 |
| Strepsiptera | 0 | 0 | 2 | 0 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 |
| Hymenoptera | 0 | 0 | 2 | 0 | 1 | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 & 1 | 0 | 0 |
| Trichoptera | 0 | 0 | 2 | 0 | 1 | 1 | 1 | 1 | 0 | 0 & 1 | 0 & 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Lepidoptera | 0 | 0 | 2 | 0 | 1 | 1 | 1 | 0 | 0 | 1 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Mecoptera | 0 | 1 | 2 | 0 | 1 | 1 | 1 | 0 | 0 | 0 & 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Diptera | 0 | 0 | 2 | 0 | 1 | 1 | 1 | 0 & 1 | 0 | 0 & 1 | 0 & 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 & 1 | 0 |
| Siphonaptera | 0 | 1 | 2 | 0 | 1 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |

*Maindroniidae were not included in the data matrix (and tree) as very little morphological information about this small family was available.

phies: folding of the hind wing vannus (48.1) and transformation of the hind wings into tegmina (50.1). The presence of euplantulae is another possible synapomorphy of these orders (108.1, delayed transformation = DELTRAN). Monophyly of Grylloblattodea + Phasmatodea + Dictyoptera is suggested by the presence of five-segmented tarsi (38.4) and a sistergroup relationship between the latter two taxa by the presence of a characteristic muscle apparatus connected with the antennal ampullae (34.1) and by the presence of an arolium (106.1, ACCTAN).

The monophyly of Dermaptera and Embioptera is well supported by the loss of ocelli (2.1), an oblique sperm implantation fossa (96.1) and female broodcare (105.1, ACC-TRAN). Presence of hairy tarsomeres (109.1) is another unambiguous synapomorphy of both orders. This type of adhesive structure evolved for the first time in these hemimetabolous insects. Regression of male genitalia may be another shared derived condition (Kristensen 1991). However, this was not included in the data matrix due to homology problems (see Appendix). Prognathy, which has a different morphological basis in both groups (Kristensen 1991) was also excluded. Dermaptera + Embioptera are placed as sistergroup of a monophyletic unit comprising Zoraptera, Paraneoptera and Endopterygota. The presence of less than five costal crossveins (46.1) is the only unambiguous apomorphy of this lineage.

The placement of Zoraptera, considered a close ally or subgroup of Paraneoptera by some workers (e.g. Hennig 1969), is indicated by a reduced number of tarsomeres (38.2) and a number of four to eight malpighian tubules (70.1). It is clearly weakened by the incompletely known morphology of zorapterans (see matrix). The morphological treatment of the thorax by Rasnitsyn (1998) is insufficient and internal head structures have yet to be investigated in detail.

Monophyly of Paraneoptera and the branching pattern within this group is largely consistent with other studies (monophyly of Psocodea and Hemiptera, e.g. Kristensen 1991). An interesting point is the evolution of a broad variety of attachment structures in members of this lineage. A balloon-shaped eversible structure between the claws is a unique autapomorphy of Thysanoptera (106.2). Distally broadened adhesive setae on the claws have evolved in Psocoptera (115.1). A claw pad (112.2) is present in phthirapterans, probably as an adaptation to ectoparasitism. An arolium (106.1) and smooth pulvilli (107.1) have evolved independently in several lineages of Hemiptera. Euplantulae are present in some mallophagans and mirines (Heteroptera, Miridae; 108.1), but are absent from other heteropterans. A fossula spongiosa is present in piratines (Heteroptera, Reduviidae; 110.1).

Endopterygota are the sistergroup of Paraneoptera, even though this is not well supported (cerci strongly reduced or absent, 69.1; polytrophic branched ovarioles, 82.3; jugal bar,

49.1, DELTRAN). The branching pattern within the largest lineage of Hexapoda is largely consistent with previous studies (e.g. Kristensen 1991, 1999). They are divided into two large monophyletic groups, Neuropterida and Coleoptera + Strepsiptera (enlarged head of axillary I, 54.1; caudal process of axillary II, 55.1; gonocoxite fused with stylus base, 75.1; hairy tarsomeres, 109.1, ACCTRAN) on one hand and Hymenoptera + Mecopterida (fully sclerotized hypopharyngeal floor, 27.1; larval labial silk glands, 87.1; single larval claws, 90.1; arolium, 106.1, ACCTRAN) on the other. Both lineages show distinctly different trends concerning attachment structures. Members of the former group are characterized by hairy adhesive soles (reversal in Neuroptera?). An arolium and hairy or smooth pulvilli are characteristic for representatives of the latter monophyletic taxon.

The sistergroup relationship between Coleoptera and Strepsiptera was confirmed even though posteromotorism and decrease in size of the mesothorax were not included in the data matrix as unspecific character states (see Appendix). Loss of *Mm. furco-pleurocostales* III (58.1) and *M. scutello postnotalis* III (59.1) and secondary loss of dorsal pulsatile organs (63.0, ACCTRAN) are presumed synapomorphies of both groups. Other shared derived features of beetles and strepsipterans are losses of several mesothoracic muscles (see Beutel and Haas 2000). However, these may be correlated with the reduced mesothorax and with formation of elytra or halteres, respectively. They were not included in this analysis. The proposed placement of Strepsiptera is in contrast to a study by Whiting et al. (1997) who consider a sistergroup relationship with Antliophora (morphological characters) or with Diptera ('Halteria'; total evidence). A clade Strepsiptera + Antliophora requires 10 additional steps in our analysis and 11 for a clade Diptera + Strepsiptera. The 'Halteria'-concept proposed by Whiting et al. (1997) is intriguing, but weakened by several problematic characters and character codings in their morphological data matrix (see Appendix: characters not included in the analysis). A monophylum 'Halteria' seems to be supported by rDNA sequence data (Whiting et al. 1997: 18S rDNA, 28S rDNA; Willmann, personal communication). However, more molecular data and additional morphological evidence are desirable. A scenario which involves exchange of thoracic segments as a result of shifts in expression of Hox-genes is interesting but speculative (Kristensen 1999).

Mecopterida (attachment of pleural muscle to axillary I, 44.1; separate larval dististipes, 84.1; larval craniocardinal muscle absent, 85.1; larval *M. craniodististipitalis* present, 86.1), Antliophora (excl. Strepsiptera) (specialized posterior notal wing process with insertion of pleural muscles, 53.1; complex sperm pump, 79.1) and Amphiesmenoptera (female heterogametic sex determination, 92.1) are confirmed as monophyletic lineages. The possible non-monophyly of Mecoptera (Kristensen 1999; Willmann, personal communication) was not addressed in our study. However, Mecoptera form a clade with Siphonaptera in all minimal length trees obtained after successive reweighting. The clades Mecopterida, Antliophora and Amphiesmenoptera are not supported by adhesive pad characters. However, it is evident that development of different types of adhesive structures plays an important role in the diversification of several orders. Hymenopterans have retained an arolium, which is ascribed to the groundplan of a clade comprising Hymenoptera + Mecopterida, and representatives of non-apocritan families

('Symphyta') possess an additional unique type of attachment structure derived from tarsal thorns (plantar lobes). Most Mecopterida have also retained the arolium, however, it is secondarily absent from the ground-living boreids and from notiothaumids (Mickoleit 1971). Most dipterans possess a plate-like empodium (Tabanoidea, Nematocera excl. Tipulidae) and hairy pulvilli. The latter character state was found in all taxa examined with the exception of Tipulidae. The presence of an arolium in members of this family is probably a plesiomorphic condition.

Acknowledgements

We are greatly indebted to Dr B. S. Heming (University of Alberta, Canada) and Dr N. P. Kristensen (Zoologisk Museum, Copenhagen, Denmark) for numerous valuable comments and criticisms. A comprehensive unpublished character state matrix and list of characters was provided by Dr J. C. Carpenter (American Museum of Natural History, New York, U.S.A.) and Dr M. F. Whiting (Brigham Young University, Provo, USA). This is gratefully acknowledged. Only data already published in previous studies were used and commented on in this contribution. We are grateful to Dr C. Carlton (Louisiana State Arthropod Museum), Prof. Dr O. Kraus (Zoologisches Institut und Zoologisches Museum der Universität Hamburg) and Dr H. Dastych (Zoologisches Institut und Zoologisches Museum der Universität Hamburg) for the loan or gift of valuable specimens. Some specimens of Hymenoptera were provided by Dr V. M. Ermolenko (Schmalhausen Institute of Zoology, Kiev, Ukraine). *Forficula auricularia* specimens were kindly supplied by Dr F. Haas (Universität Ulm, Germany) and *Rhamphomyia nigripes* by Professor Dr L. Frantsevich (Schmalhausen Institute of Zoology, Kiev, Ukraine). We also wish to thank Dr Marion Kotrba (Zoologische Staatssammlung, München, Germany) and Barbara Meidl (Institut für Limnologie, FSU Jena, Germany) for the determination of specimens. Permanent support by the Electron Microscopy Unit team (Dr H. Schwarz, J. Berger, I. Zimmermann) at the MPI of Developmental Biology (Tübingen, Germany) is greatly acknowledged. Elke Gretscher (Institut für Spezielle Zoologie und Evolutionsbiologie, FSU Jena, Germany) kindly helped with light microscopic procedures. This project was partly supported by the Federal Ministry of Education, Science and Technology, Germany to SG (Project BioFuture 0311851) and partly by the Deutsche Forschungsgemeinschaft (DFG, grant No. BE 1789/1–2).

Zusammenfassung

Ultrastrukturelle Untersuchungen an Haftapparaten von Insekten (Arthropoda): eine evolutive Interpretation auf der Grundlage einer revidierten Großgruppensystematik der Hexapoda

Tibiale, tarsale und praetarsale Haftstrukturen von Vertretern der meisten höheren Taxa der Hexapoda wurden untersucht und für jede Ordnung kurz beschrieben. Im Laufe ihrer Evolution haben die Insekten zwei deutlich verschiedene Mechanismen entwickelt um sich an unterschiedlichen Unterlagen anzuheften: haarige Oberflächen oder weiche, flexible Polster. Die flexiblen Eigenschaften des Materials der Haftpolster garantiert einen maximalen Kontakt mit Oberflächen, unabhängig von deren Mikrostruktur. Die hochspezialisierten Haftstrukturen sind nicht auf einen Teil des Beines beschränkt. Sie können an Klauen, auf Derivaten des Praetarsus, apikal am Tarsus, auf Tarsomeren oder an der Tibia auftreten. Die 10 Merkmale der beiden alternativen Varianten von Haftstrukturen – weich und haarig – wurden codiert und zusammen mit einer Datenmatrix mit 105 zusätzlichen morphologischen Merkmalen von verschiedenen Lebensstadien und Körperteilen analysiert. Die Analyse zeigt, daß ähnliche Strukturen (Arolium, Euplantulae, haarige Tarsomeren) mehrfach unabhängig entstanden sind. Dennoch können sie monophyletische Gruppen unterstützen (z.B. Embioptera + Dermaptera; Dictyoptera + Phasmatodea + Grylloblattodea + Orthoptera; Dictyoptera + Phasmatodea; Hymenoptera + Mecopterida; Neuropterida + Strepsiptera +

Coleoptera). Andere Strukturen wie z.B. Haftlappen auf Klauen (Ephemeroptera), ballonförmige, ausstülpbare Blasen (Thysanoptera), oder Fossulae spongiosae (Reduviidae) treten nur einmalig bei einer größeren oder kleineren monophyletischen Gruppe auf. Es ist plausibel anzunehmen, daß die Entwicklung des Flugvermögens und die korrelierte Notwendigkeit auf Pflanzen oder anderen Substraten Halt zu finden ein wesentlicher Auslöser für die Evolution von Haftstrukturen war. Gruppen mit dem Potential eine besonders große Bandbreite von Haftstrukturen auszubilden sind die Hemiptera und Diptera. Obwohl Haftstruktur-Merkmale einem starken Selektionsdruck unterliegen, liefern sie phylogenetische Information. Ergebnisse der kladistischen Analyse stimmen weitgehend mit gängigen Hypothesen überein. Ein Schwestergruppenverhältnis zwischen den Diplura und den Insecta, und zwischen den Zygentoma (ohne *Tricholepidion*) und den Pterygota wurde bestätigt. Die Plecoptera sind wahrscheinlich die Schwestergruppe der übrigen Neoptera. Die Dermaptera sind die Schwestergruppe der Embioptera und die Dictyoptera die Schwestergruppe der Phasmatodea. Die Paurometabola ohne Dermaptera + Embioptera sind monophyletisch. Ein Schwestergruppenverhältnis zwischen den Zoraptera und einem Monophylum das die Paraneoptera + Endopterygota umfaßt, ist nur schwach abgesichert. Die Coleoptera + Strepsiptera sind die Schwestergruppe der Neuropterida und die Hymenoptera die Schwestergruppe der Mecopterida.

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Appendix: general list of characters for phylogenetic analysis

The presumably plesiomorphic condition is coded as 0 even though this traditional convention is inconsequential in cladistic analyses with a posteriori polarity assessment.

A. Characters of adults

I. Head

1. Tagmata: (0) caput and body; (1) caput, thorax, abdomen
2. Ocelli, adults: (0) present; (1) absent
Ocelli are absent in all representatives of Progoneata, Chilopoda, Protura, Diplura, Collembola, Dermaptera, Embioptera, Grylloblattodea, Phthiraptera and Siphonaptera. They are probably secondarily absent or reduced in some members of other orders such as Zygentoma (Smith and Watson 1991), Zoraptera, Psocoptera (usually absent in apterous forms; Smithers 1991), Neuroptera, Megaloptera and Diptera. In these cases, the character is coded as (0). The presence of ocelli in beetles (e.g. Sirkotealiniidae, Lafer 1996; Hydraenidae, Derodontidae, Dermestidae, personal observation Beutel) is also considered a groundplan feature of the order and scored as (0). Irregular pigment spots, sometimes divided into two or three groups, are present in early puparia of some representatives of Strepsiptera (Kinzelbach 1971). They are probably vestiges of ocelli (coded as 0 & 1).
3. Temporal organs (Tömösvary's organ): (0) present; (1) absent
This character was tentatively included even though the homology of the structures is unresolved. Absence was considered a possible synapomorphy of Diplura and Insecta by Kukalová-Peck (1987, 1991) and Koch (1997).
4. Postocciput and pleural folds: (0) well developed; (1) reduced
A reduced postocciput and loss of pleural folds was considered a possible synapomorphy of Zygentoma (excl. *Tricholepidion*) and Pterygota (Staniczek 2000). The presumably plesiomorphic condition is found in Archaeognatha and *Tricholepidion* (Staniczek 2000).
5. Postoccipital suture: (0) incomplete; (1) complete dorsally
A complete postoccipital ridge or suture was considered a possible autapomorphy of Dicondylia by Kristensen (1997).
6. Linea ventralis: (0) absent; (1) present
A ventromedian longitudinal furrow of the head capsule or linea ventralis was considered a synapomorphy of Ellipura by Kristensen (1991, 1997) and Koch (1997).
7. Hypopharyngeal fultura: (0) present; (1) absent
Absence of fultura is a possible synapomorphy of Zygentoma (incl. *Tricholepidion*) and Pterygota (Kristensen 1997).
8. Superlinguae: (0) present; (1) absent
The complete absence of superlinguae was considered a possible autapomorphy of Zygentoma by Kristensen (1997). They are still present in nymphs of Ephemeroptera but absent from adults which have degenerate mouthparts (coded as 0).
9. Tentorial bridge: (0) absent; (1) present
Presence of a tentorial bridge (tentorial bar) connecting the posterior tentorial arms was considered an autapomorphy of Insecta by Kristensen (1991, 1997). The possibility that posterior tentorial arms belong to the groundplan of Hexapoda was suggested by Koch (2000a). The tentorium is vestigial in adult males of Strepsiptera (Kinzelbach 1971; coded as -).
10. Perforation of metatentorium: (0) absent; (1) present
The 'perforated corpotentorium' of dictyopterans is not a true perforation but is rather due to the presence of a secondary, anterior transverse bar (Kristensen 1991, personal observation Beutel). The character was coded as (-) for entognathous hexapods and Strepsiptera (incomplete or vestigial tentorium).
11. Ligamentous endoskeleton: (0) present; (1) absent
A ligamentous endoskeleton is absent from all members of Dicondylia except for *Tricholepidion* (Boudreaux 1979; Kristensen 1991, 1997; Staniczek 2000).
12. Gula: (0) absent; (1) present
A sclerotized gula is present in members of Embioptera, Coleoptera, Megaloptera and Raphidioptera (Rähle 1970; Kristensen 1991).
13. Opening of salivary glands on ventral side of head: (0) absent; (1) present (Bitsch and Bitsch 1998)
The presence of a single opening of the salivary gland in a midventral groove of the labium was considered a possible autapomorphy of Entognatha by Bitsch and Bitsch (1998).
14. Antenna: (0) all antennomeres except ultimate muscular; (1) nonmuscular flagellum; (2) absent
The nonmuscular antennal flagellum was considered an autapomorphy of Insecta by Kristensen (1975, 1991, 1997).
15. Rupture-facilitating cuticle modification of antennal flagellum: (0) absent; (1) present
A rupture-facilitating cuticle modification is present in Psocodea (= Psocoptera + Phthiraptera; Seeger 1975). The character is coded as (-) for Protura.
16. Johnston's organ of second antennomere: (0) absent; (1) present
Johnston's organ is an autapomorphy of Insecta (Kristensen 1991, 1997). The character is coded as (-) for Protura.
17. Mouthparts: (0) ectognathous; (1) entognathous, maxillae and mandibles hidden in separate gnathal pouches; (2) entognathous, maxillae and mandibles hidden in single gnathal pouch (Tuxen 1959; Koch 1997, 2000b); (3) left mandible enclosed in a pouch formed by anteclypeal wall, labrum, stipes and hypopharynx; (4) bases of mandibular and maxillary stylets articulate inside head with mandibular and maxillary plates
Differences between the entognathous conditions of Diplura and Ellipura were pointed out by Koch (1997; 2000b). Independent origin in both groups was suggested by this author. Other types of entognathy are found in representatives of some groups of pterygote insects. The left mandible is enclosed in a pouch formed by the anteclypeal wall, labrum, stipes and hypopharynx in thysanopterans (Mickoleit 1963). Bases of the stylet-like mandibles and laciniae articulate inside the head with internal surfaces of plates by means of mandibular and maxillary levers in hemipterans (Carver et al. 1991). Stylets are invaginated in a deep preoral cavity in anoplurans. However, this is not a groundplan feature of Phthiraptera (coded as 0) (Tröster 1990).
18. Mandibular articulation: (0) primary joint only; (1) additional articulation complex; (2) both articulations fully fixed
A fully fixed, secondary mandibular ball-and-socket articulation (Fürst v. Lieven 2000; Staniczek 2000) was considered a synapomorphy of Odonata and Neoptera by Kristensen (1991) and Staniczek (2000). The character is coded as (-) for paraneopteran and endopterygotan groups with secondarily modified or reduced mandibles.
19. Function of mandibles: (0) biting; (1) both mandibles piercing, stylet-like; (2) only left mandible stylet-like, right mandible reduced
Stylet-like mandibles were considered an autapomorphy of Hemiptera by Kristensen (1991). They have presumably evolved independently in Phthiraptera (part.; coded as 0), Diptera and Siphonaptera. Only the left mandible is transformed into a stylet-like structure in Thysanoptera. The right mandible is strongly reduced (Mickoleit 1963; Heming 1978, 1993; Moritz 1982).
20. Transverse mandibular apodeme: (0) present; (1) absent
Absence was considered a possible synapomorphy of Zygentoma (excl. *Tricholepidion*) and Pterygota (Staniczek 2000).
21. Cardo: (0) present; (1) strongly reduced or absent
Absence was considered an autapomorphy of Hemiptera (e.g. Kristensen 1991). A separate cardo is still retained in basal lineages of Thysanoptera and Diptera (Mickoleit 1963; Moritz 1982; Hennig 1973; coded as 0). It is absent in adults of Siphonaptera (Matsuda 1965). The character is scored as (-) for trichopterans, which have strongly reduced mouthparts as adults.
22. Insertion of lacinia: (0) on stipes; (1) detached from stipes
A lacinia detached from the stipes was considered an autapomorphy of Paraneoptera by Kristensen (1991).
23. Lacinia: (0) not elongate and stylet-like; (1) elongate and stylet-like
A stylet-like lacinia was considered an autapomorphy of Paraneoptera by Kristensen (1991). A similar condition is found in dipterans (part.) and siphonapterans.
24. Maxillary palp: (0) as long as thoracic legs; (1) distinctly shorter
Unusually long maxillary palps are characteristic for Archaeo-

- gnatha and *Tricholepidion* (Wygodziński 1961; Kristensen 1997).
25. Labial rostrum: (0) absent; (1) present
Presence was considered an autapomorphy of Hemiptera (e.g. Kristensen 1991).
 26. Labial palps: (0) three-segmented or less; (4) four-segmented
Presence of four palpomeres was considered a possible autapomorphy of Zygentoma by Kristensen (1997). However, four-segmented palps are also found in some representatives of other taxa (Thysanoptera part., Megaloptera part., Hymenoptera part.). This character is apparently miscoded in Whiting et al. (1997).
 27. Fully sclerotized floor of the sucking pump: (0) present; (1) absent (Kristensen 1999)
Presence of a fully sclerotized floor of the sucking pump, formed by a 'sitophore' plate on the hypopharyngeal base, accompanied by loss of the ventral transverse cibarial muscles, is an interesting character state shared by hymenopterans and mecopterids (Kristensen 1999). This condition is not found in strepsipterans. The cibarium is strongly reduced. The externally visible opening is the anatomical mouth (Kinzelbach 1971).
 28. Cibarial water-vapour uptake apparatus: (0) present; (1) absent (Rudolph and Knülle 1982)
Presence was considered an autapomorphy of Psocodea by Kristensen (1991). The water-vapour uptake apparatus is absent in *Zorotypus hubbardi* (Heming, personal communication, personal observation Beutel).
 29. Mandibulo-hypopharyngeal muscle: (0) absent; (1) present
Presence in members of Zygentoma (excl. *Tricholepidion*) and Pterygota was considered a possible synapomorphy of both taxa by Staniczek (2000). However, the muscle is absent in representatives of different groups of Pterygota, especially Endopterygota (e.g. Matsuda 1965). Presence of a small ligament in Lepidoptera, possibly a remnant of the muscle, is coded as (0).
 30. *M. tentoriomandibularis*: (0) composed of several components; (1) only one thin bundle or absent
Reduction or absence of this muscle (Maki 1936; Matsuda 1965; Kinzelbach 1971; Staniczek 2000: M4-M7) was considered a synapomorphy of Odonata and Neoptera by Kristensen (1991, 1997). The muscle is also absent in collembolans (Tuxen 1959).
 31. *M. stipitalis transversalis*: (0) present; (1) absent
Absence of this muscle (Das 1937; Matsuda 1965) was considered a possible autapomorphy of Neoptera excluding Plecoptera by Kristensen (1991).
 32. Dorsal flexor of paraglossa: (0) absent; (1) present
Presence of this unusual muscle in members of Embioptera and Phasmatodea was pointed out by Rähle (1970). It is probably derived from an extrinsic prelabial muscle (Kristensen 1975). It is puzzling that this character was coded two times in a different manner in Whiting et al. (1997) (Dorsal paraglossa flexor. – Normal (0); 'aberrant', 'peculiar' and Dorsal flexor of paraglossa. – absent (0); present).
 33. Cibarial dilators: (0) normally developed; (1) strongly enlarged
A distinctly enlarged postclypeus with unusually strong cibarial dilators (Matsuda 1965) was considered an autapomorphy of Paraneoptera by Kristensen (1991).
 34. Ampullo-ampullary and accessory ampullary muscles attached to aorta: (0) absent; (1) present (Pass 1991, 1998)
A specific muscle apparatus connected with the antennal ampullae was described for members of Dictyoptera and Phasmatodea by Pass (1991, 1998).
- ## II. Thorax
35. Pronotum: (0) not saddle-like; (1) saddle-like
A saddle-like pronotum was considered a possible autapomorphy of Orthoptera by Kristensen (1991).
 36. Scutellum: (0) absent; (1) present (Krenn 1993)
As presence is probably correlated with appearance of pulsatile structures designed for haemolymph supply of wings (Krenn 1993), this character is coded as (–) for secondarily wingless taxa with largely or completely reduced scutellum.
 37. Number of legs: (0) more than three pairs; (1) three pairs
 38. Tarsus: (0) undivided; (1) two tarsomeres; (2) three tarsomeres; (3) four tarsomeres; (4) five tarsomeres
The highest number of tarsomeres found in representatives of Isoptera (*Mastoterme*; Watson and Gay 1991), Ensifera, Caelifera, Phasmatodea and other orders is considered a groundplan character state of the respective taxon.
 39. Pretarsus: (0) retained as a small, separate sclerite and attached claws; (1) separate sclerite reduced
A pretarsal annulus is present in diplurans (Kristensen 1997: Fig. 21.2H), ellipurans and myriapods. It is partly reduced (transformed into planta and unguitactor plate) in all members of Insecta (Kristensen 1991).
 40. Claws: (0) single; (1) double
Presence of double claws is a potential synapomorphy of Diplura and Insecta (e.g. Kristensen 1997). Double claws are also present in symphylans.
 41. Jumping legs: (0) absent; (1) with enlarged femur; (2) with enlarged coxa
 42. Wings: (0) absent; (1) present
 43. Wing base: (0) without folding lines; (1) folding lines present
The presence of folding lines at the wing base and a characteristic arrangement of axillary sclerites enable neopterans to fold back their wings over the abdomen. This and the following wing-related characters are coded as (–) for wingless taxa.
 44. Axillary 1: (0) no attachment of pleural muscle; (1) attachment of pleural muscle (Hennig 1969)
Attachment of a well-defined pleural muscle to axillary 1 (Mickoleit 1969) was considered a possible autapomorphy of Mecoptera by Hennig (1969) and Kristensen (1991: Fig. 5.7A). This muscle is derived from a part of the posterior tergopleural muscle which belongs to the groundplan of Pterygota according to Hennig (1969). The muscle is absent from strepsipterans (Kinzelbach 1971; Kristensen 1999; coded as 0). Only single fibres of *M. pleuro-axillaris anterior* may reach the axillary 1 according to Kinzelbach (1971).
 45. Median plate: (0) undivided; (1) diagonally divided
 46. Costal cross veins: (0) more than five; (1) less than five
Presence of more than five cross veins meeting the anterior margin of the hind wing is a characteristic of some basal lineages of Pterygota and of the neuropteroid orders.
 47. Hind wing vannus: (0) not enlarged; (1) distinctly enlarged
This was considered a possible synapomorphy of the lower neopteran orders by Kristensen (1991).
 48. Folding of vannus: (0) few anal veins, not pleated; (1) pleated (Whiting et al. 1997)
 49. Jugal'bar': (0) absent; (1) present
Presence of a jugal sclerotization (Hamilton 1971–72) was considered a possible synapomorphy of Paraneoptera and Endopterygota by Kristensen (1991).
 50. Sclerotization of fore wings: (0) absent; (1) moderately sclerotized tegmina; (2) strongly shortened, sclerotized tegmina; (3) elytra with epipleurae
The interpretation of forewings in lower Neoptera is difficult and the transformation into tegmina is a gradual modification rather than a clearly defined character state. We consider the presence of moderately sclerotized fore wings as a groundplan feature of Mantodea and Blattodea (coded as 1). However, this issue is not fully clarified at present. Unmodified alae are characteristic for most plecopteran subgroups. However, the pigmented wings encountered in Plecoptera-Antarctoperlaria do somehow resemble tegmina as found in other orthopteroid groups (Kristensen, personal communication; coded as 0 & 1 for Plecoptera).
 51. Halteres: (0) absent; (1) on mesothorax; (2) on metathorax
 52. Pronounced precostal field: (0) absent; (1) present (Whiting et al. 1997)
 53. Posterior notal wing process (0) unspecialized, no insertion of pleural muscles; (1) specialized, insertion of pleural muscles

- A specialized posterior alar process with insertion of specific pleural muscles (Mickoleit 1966, 1969) is a possible autapomorphy of Antliophora (Kristensen 1991: Fig. 5.7A).
54. Head of axillary I: (0) not enlarged; (1) distinctly enlarged and cranially truncate; (2) enlarged with distal process (Hörschemeyer 1998)
A distinctly enlarged, anteriorly truncate axillary I is found in megalopterans (part.), raphidiopterans, many representatives of Coleoptera, and in strepsipterans (Hörschemeyer 1998). A somehow modified character state is present in neuropterans (coded as 2).
55. Caudal process of axillary II: (0) absent; (1) present (Hörschemeyer 1998)
Presence of a caudal process of axillary II is a possible synapomorphy of Neuropterida, Coleoptera and Strepsiptera (Hörschemeyer 1998).
56. Leg- and wing tracheae: (0) not connected with following spiracle; (1) connected with following spiracle
Connection of leg- and wing tracheae was considered a possible synapomorphy of Odonata and Neoptera by Kristensen (1991). The character was coded as (-) for wingless insects.
57. Epimeral apophysis: (0) present; (1) absent
A firm connection of the metepimeron to an apophysis-bearing 'postepimeron' pertaining to abdominal segment I is a possible synapomorphy of Raphidioptera and Megaloptera (Kristensen 1991).
58. Mm. furco-pleurocostales III (Matsuda 1970; p-s 1 III): (0) present; (1) absent (Beutel and Haas 2000)
59. M. scutello-postnotalis III (Matsuda 1970; t 13 III): (0) present; (1) absent (Beutel and Haas 2000)
This character is coded as (-) for primarily wingless taxa. The muscle is present in basal hymenopterans (Vilhelmsen 2000).
60. Proventriculus: (0) absent or without prominently elongated acanthae; (1) with close-set, prominently elongated acanthae (Kristensen 1991)
Presence of a very characteristic proventriculus with acanthae was considered a possible synapomorphy of Siphonaptera and Mecoptera by Kristensen (1991).
61. Mid-ventral ostia: (0) absent; (1) present (Nutting 1951; Kristensen 1991)
Mid ventral ostia are present in the metathorax of plecopterans and embiopterans (Nutting 1951; Kristensen 1991).
62. 'Link plates' adjacent to thoracic spiracles: (0) absent; (1) present
Presence of these unusual structures was considered a possible autapomorphy of a monophylum including mecopterans and siphonapterans (Kristensen 1991). The character was tentatively included in the analysis. More study is desirable according to Kristensen (1991).
63. Dorsal pulsatile diaphragms: (0) absent; (1) paired separate; (2) unpaired separate; (3) attached single (Pass 1998)
Different dorsal pulsatile diaphragms are present in most members of Endopterygota but completely lacking in beetles, strepsipterans and siphonapterans. They are absent from all hemimetabolous insects except for Hemiptera (Pass 1998).
- III. Abdomen*
64. Transverse suture of abdominal tergum I: (0) absent; (1) present
The character states scored as (1) of this and the following character were suggested as autapomorphies of Neuropterida by Ahtelig (1975).
65. Caudally bifid mediolongitudinal suture of tergum I: (0) absent; (1) present
66. Ocluser muscles inserting directly on abdominal spiracular sclerites: (0) absent; (1) present
Presence of these muscles (Miller 1962; Poonawalla 1966) was considered a possible synapomorphy of Odonata + Neoptera by Kristensen (1991). They are absent from some odonates (Kristensen 1991).
67. Abdominal coxal vesicles: (0) present; (1) on ventral tube of segment I; (2) absent
Presence of eversible coxal vesicles in representatives of Diplura, Protura, Archaeognatha, Nicoletiidae and Lepidothrichidae was considered a plesiomorphic feature by Kristensen (1991, 1997). Eversible structures are present on the ventral tube of collembolans.
68. Styli: (0) present; (1) absent from segment II or completely reduced
Pregenital styles are found in representatives of Diplura, Protura, Archaeognatha, Nicoletiidae and Lepidothrichidae (Wygodzinsky 1961; Kristensen 1991). They are at least absent from abdominal segment II in other hexapods (Kristensen 1997).
69. Cerci: (0) present; (1) strongly reduced or absent
Cerci were coded as present in all groups of holometabolous insects by Whiting et al. (1997). However, they are absent in almost all members of Endopterygota.
70. Malpighian tubules: (0) numerous, more than eight; (1) four to eight; (2) strongly reduced malpighian ampullae; (3) three tubules; (4) one pair
This character is miscoded in Whiting et al. (1997). More than six Malpighian tubules are only found in few representatives of Endopterygota. They are not absent in collembolans but represented by shortened ampullae. Presence of three tubules is probably a groundplan feature of Strepsiptera. This condition is found in females of *Mengenilla* (Kinzelbach 1971).
71. Abdominal spiracles: (0) present; (1) absent
Absence of abdominal spiracles and a strongly reduced tracheal system was considered a possible autapomorphy of Ellipura by Kristensen (1975).
72. Ovipositor: (0) absent; (1) with well developed, elongate gonapophyses VIII and IX, ovipositor sheath formed by third valvulae (gonocoxite + stylus IX) present or absent; (2) reduced
Presence of a well developed ovipositor is a groundplan feature of Odonata, Blattodea, Isoptera, Mantodea and Dermaptera (Klass, personal communication). The ovipositor of females of Caelifera is strongly modified but still very distinct (coded as 1).
73. Gonangulum: (0) absent; (1) present
Presence was considered an autapomorphy of Dicondylia (incl. *Tricholepidion*) by Hennig (1969). The character is coded as (-) for taxa with strongly reduced ovipositor. Presence is considered a groundplan feature of Thysanoptera and Hemiptera. The gonangulum is present in species with a well-developed, lacinate ovipositor (Heming-van Battum and Heming 1986). The gonangulum is absent from the ovipositor of females of Odonata (Klass, personal communication).
74. Third pair of valves: (0) not fused; (1) fused, and with internal musculature
Fused third valves with internal musculature (Mickoleit 1973) were considered an autapomorphy of Neuropterida by Kristensen (1975, 1991).
75. Genital appendages IX: (0) gonocoxite not fused with stylus base into a sensory appendage; (1) gonocoxite fused with stylus base into a sensory appendage, gonapophyses absent.
It was pointed out by Mickoleit (1973) that a sensorial appendage formed by fusion of gonocoxite IX with the gonostylus base is characteristic for Coleoptera (vaginal palp) and Neuropterida. It is plausible to assume that an apical appendage is retained as a distal part of the stylus. Gonapophyses IX are completely reduced.
76. Terminal filament: (0) strongly reduced or absent; (1) well developed
77. Genital pocket with large subgenital plate derived from sternum VIII: (0) absent; (1) present
Presence of a large genital pocket was considered an autapomorphy of Dictyoptera (Kristensen 1991). The enlarged subgenital plate is derived from sternum VIII in these orders.
78. Moveable lobes of subgenital plates: (0) present; (1) absent
Presence of these unusual structures was considered a derived groundplan feature of all dictyopterans by Klass (1995) (coded as 1 for Isoptera, Blattodea and Mantodea).
79. Advanced sperm pump: (0) absent or unspecific muscular coat of sperm ducts; (1) present, transfer of liquid sperm
A specific, advanced sperm pump is present in males of Diptera, Mecoptera (Kristensen 1975) and Siphonaptera (Mickoleit, personal communication). A muscle-coated vesicular part of the strepsipteran male duct (Kinzelbach 1971) is different from this

condition (coded as 0; see also Kristensen 1991). A bulbous muscular coat forming an 'ejaculatory pump' is also present in Mecoptera-Amphiesmenoptera (Kristensen 1999).

80. Abdominal ganglia: (0) more than two separate ganglia; (1) two separate ganglia; (2) one single ganglionic mass; (3) ganglia 2–5 form an elongated tractus

Presence of two separate ganglia was considered a possible synapomorphy of Zoraptera and Paraneoptera by Hennig (1969), whereas the presence of a single ganglionic mass is a possible autapomorphy of Paraneoptera (Acercaria) according to Kristensen (1991). A single mass of ganglia is also found in Collembola. Fusions of varying degree also occur in Protura (Bitsch and Bitsch 1998) in which abdominal ganglia 2–5 form an elongate tractus.

81. Ovaries: (0) sac-shaped, not divided into ovarioles; (1) subdivided into ovarioles (Stys and Bilinski 1990)

Undivided, more or less sac- or tube-shaped ovaries are present in females of Protura, Collembola, Campodea (Stys and Bilinski 1990) and Strepsiptera (Kathirithamby 1991). Ovarioles are present in females of Japygina and other hexapods. Traces of original metamerism (Stys and Bilinski 1990) cannot be coded as a well-defined character state.

82. Ovaries/Ovarioles: (0) panoistic; (1) neopanoistic; (2) polytrophic, linear arrangement; (3) polytrophic, branched arrangement; (4) ephemeropteran telotrophic type; (5) hemipteran telotrophic meroistic type; (6) megalopteran-raphidiopteran telotrophic type; (7) coleopteran telotrophic type (Büning 1998)

The tubes break down in third larval instar of Strepsiptera (coded as –). The character is coded as (1 and 6) for Megaloptera. It is likely to assume that the ovarioles of females of Megaloptera-Corydalidae are secondarily (neo) panoistic (Büning 1998; Kristensen, personal communication). Neopanoistic ovarioles are derived from ancestral polytrophic ovarioles according to Stys and Bilinski (1990).

B. Larval characters

I. Head

83. Larval eyes: (0) persist; (1) disintegrate or pulled back proximally into cerebrum

De novo formation of compound eyes and ocelli during metamorphosis was considered an autapomorphy of Endopterygota by Kristensen (1991, 1999).

84. Stipes: (0) undivided; (1) divided into basistipes and dististipes

The division of the larval stipes into proximal and distal portions (Das 1937; Rousset 1966) was considered a possible synapomorphy of the panorpoid orders by Kristensen (1991). Similar conditions occur in larvae of basal representatives of Coleoptera (*Omma*, personal observation Beutel; coded as 0 & 1) and in larvae of Megaloptera and Raphidioptera (Kristensen 1991; coded as 0 & 1). The stipes is undivided in larvae of siphonapterans (Sharif 1937; Elbel 1991).

85. M craniocardinalis: (0) present; (1) absent

Absence of the cardinal promotor (Das 1937) was considered a synapomorphy of the panorpoid orders by Kristensen (1991). However, the muscle is present in larvae of Siphonaptera (Sharif 1937).

86. M. craniodististipitalis: (0) absent; (1) present (Kristensen 1991)

Presence of a cranial extensor muscle of the dististipes was considered a synapomorphy of the panorpoid orders by Kristensen (1991).

87. Larval labial glands: (0) no silk production; (1) silk production (Kristensen 1999)

Silk producing labial glands of larvae were considered a possible synapomorphy of Hymenoptera and Mecoptera. However, they are also present in nonparasitic psocodeans (Kristensen 1999). The possibility that the presence is a plesiomorphic feature within Endopterygota was pointed out by the same author.

II. Thorax

88. Thoracic legs: (0) present; (1) absent

Absence of legs in larvae of Curculionidae is a secondarily derived feature within Coleoptera (coded as 0).

89. External wing buds: (0) present; (1) absent

External wing buds are absent from most strepsipteran larvae (review in Kinzelbach 1971; Kristensen 1991, 1999) and larvae of all other groups of Endopterygota (coded as 0 & 1 for Strepsiptera). The possibility that invaginated wing discs have originated four times independently (Svacha 1992) was discussed in Kristensen (1999). Absence of wing buds in representatives of taxa with secondarily reduced wings is coded as (–).

90. Claws: (0) double; (1) single

Presence of a single claw in many larvae of Coleoptera (Adephaga part., Myxophaga, Polyphaga) is a secondary feature (Beutel and Haas 2000; coded as 0 for Coleoptera). Paired claws are present in larvae of Megenillidae (Kristensen 1999; coded as 0 for Strepsiptera).

III. Abdomen

91. Terminal filament: (0) present; (1) absent

Absence of the terminal filament was considered a possible autapomorphy of Neoptera excluding Plecoptera (Kristensen 1991). The filament is still preserved in a few nymphs of Plecoptera (Kristensen 1991) (coded as 0 & 1).

C. Reproduction and development

92. Heterogametic sex: (0) males (xy); (1) females (zw)

Sex chromosomes zw in females was considered a synapomorphy of Trichoptera and Lepidoptera by Hennig (1969) and Kristensen (1975, 1991).

93. Amniotic cavity: (0) absent; (1) open; (2) at least temporarily closed (Kristensen 1997; Whiting et al. 1997; Larink 1997)

A reduced amnioserosa is present in long germ embryos of 'higher dipterans' (Brachycera and Cyclorapha) and no amniotic cavity is formed (Hartenstein 1993; Campos-Ortega and Hartenstein 1997). This is considered a secondary condition (coded as 2 for Diptera).

94. Sperm transfer: (0) external, spermatophore deposited on substrate or attached to a thread spun by the male; (1) indirect internal sperm transfer; (2) direct internal sperm transfer via an elongate intromittent organ

Males of Collembola, Diplura, Meinertellidae (Archaeognatha; Watson and Smith 1991) and Zygentoma (part.; Smith and Watson 1991) deposit a stalked or flask-shaped spermatophore on the substrate. Other archaeognathans and silverfish (*Lepisma*) attach the spermatophores on a thread. As the specific deposition varies considerably within the apterygote orders, external transfer is only coded as one character state. Different anomalous methods of insemination such as puncturing the external body integument or vaginal wall occur in cimicoids (Carayon 1977). These secondary conditions, which are certainly not a groundplan feature of Heteroptera, are not coded as separate character states.

95. Sperm conjugation: (0) absent; (1) present

Sperm conjugation (Wygodzinsky 1961; Wingstrand 1973; Jamieson 1987) was considered a possible autapomorphy of Zygentoma (incl. *Tricholepidion*) by Kristensen (1991, 1997). A similar condition does also occur in few representatives of Coleoptera (Jamieson 1987). However, this is almost certainly not a groundplan character state of the order (coded as 0).

96. Oblique implantation fossa: (0) absent; (1) present

Presence of this specialized structure was considered a possible synapomorphy of Embioptera and Dermaptera by Jamieson (1987).

97. Double anterior axonemal cylinder: (0) absent; (1) present

Presence of an anterior axonemal cylinder was considered a possible synapomorphy of Phasmatodea and Dermaptera by Jamieson (1987).

98. Sperm axoneme: (0) not coiling around mitochondrial derivative; (1) coiling around mitochondrial derivative (Kristensen 1991)

The presumably derived condition was considered a possible synapomorphy of Siphonaptera and Mecoptera by Kristensen (1991).

99. Cleavage: (0) total and equal; (1) early total cleavage followed by superficial cleavage; (2) superficial cleavage (Bitsch and Bitsch 1998)

Total cleavage is characteristic for symphylans (Tiegs 1940) and collembolans. Archaeognathans, at least in part (Larink 1997), exhibit an early total cleavage, whereas superficial cleavage is

found in other hexapods. Cleavage of proturans is still unknown (Bitsch and Bitsch 1998). Total cleavage is also known in viviparous generations of aphids, in eggs of certain parasitoid hymenopterans and in eggs of some strepsipterans (Ivanova-Kasas 1972). This is probably not a groundplan character state in these orders (coded as 2).

100. Egg cocoon: (0) absent; (1) present
Formation of egg cocoons or oothecae is characteristic for females of Mantodea (Balderson 1991) and Blattodea (Roth 1991) with few exceptions. Compact egg masses are also laid by females of Mastotermidae (Watson and Gay 1991). We consider this a groundplan feature of the order (coded as 1). Single eggs are laid by other termites.
101. Postembryonic development: (0) anamorphic; (1) epimorphic
Proturans are the only hexapods with anamorphic development (Bitsch and Bitsch 1998).
102. Pupal stage: (0) absent; (2) present
Quiescence of the last immature stage and metamorphosis are innovative features only paralleled in some subordinate exopterygote hexapods [Heming 1973; Kristensen 1999; coded as (0) for all exopterygote orders]. However, ancestral pupae, especially of neuropterids, differ strongly from the pupae of 'higher endopterygotes' (e.g. Lepidoptera) and permit considerable activity of the pharate adults (Kristensen 1999).
103. Imaginal moult: (0) present; (1) absent
Absence of the imaginal moult was considered a synapomorphy of Odonata and Neoptera by Kristensen (1991).
104. Larvae: (0) terrestrial; (1) aquatic
105. Maternal broodcare: (0) absent; (1) present
Maternal broodcare is a feature shared by dermapterans, embiopterans and zorapterans (Kristensen 1991; Whiting et al. 1997). It is also known from some hemipterans (e.g. *Tectocoris*; Carver et al. 1991) and thysanopterans (Heming, personal communication) but is almost certainly not a groundplan feature of these orders (coded as 0).

Adhesive pad characters

- 106 (1.). Arolium: (0) absent; (1) present; (2) eversible
- 107 (2.). Pulvilli: (0) absent; (1) smooth; (2) hairy
- 108 (3.). Euplantulae: (0) absent; (1) present
- 109 (4.). Hairy adhesive soles of tarsomeres: (0) absent; (1) present
- 110 (5.). Fossula spongiosa: (0) absent; (1) present
- 111 (6.). Eversible structure between tibia and tarsus: (0) absent; (1) present
- 112 (7.). Claw pad: (0) absent; (1) present
- 113 (8.). Tarsal thorns transformed into adhesive structures: (0) absent; (1) present
- 114 (9.). Empodium plate-like: (0) no; (1) yes
- 115 (10.). Adhesive claw setae: (0) absent; (1) present

Characters not included in this analysis

- Enlarged epipharyngeal ganglia (e.g. Whiting et al. 1997)
The homology of these structures is very uncertain (Koch, personal communication).
- Criss-crossing of mandibles
This character state was interpreted as a possible synapomorphy of Diptera and Mecoptera by Mickoleit (1971). As a similar condition is found in males of Strepsiptera this was discussed as a possible support for a strepsipteran-antliophoran clade by Whiting (1998). However, this presumably derived condition is not found in Diptera and Siphonaptera and has probably evolved independently within different groups of Endopterygota with more or less elongate mandibles (e.g. xyelid sawflies, Kristensen 1999; Cicindelinae, Corydalidae).
- Fusion of premental lobes (Whiting et al. 1997)
This is an unspecific, regressive feature (Kristensen 1999). The premental lobes (i.e. glossa and paraglossa) are reduced or fused with the prementum in plecopterans, embiids, othopteroids, strepsipterans, dipterans and mecopterans (Whiting et al. 1997), but also in coleopterans and members of other groups of hexapods (e.g. Trichoptera).
- Cranial antagonist of the primitive craniolacinal muscle in larvae
The homology of this muscle is rather unclear. It is only described for *Machilis* (Matsuda 1965).
- Fusion of labium and hypopharynx
Different degrees of fusion occur in trichopterans and also in representatives of Coleoptera and other groups of hexapods (e.g. Strepsiptera; Kinzelbach 1971). The formation of an eversible haustellum is a possible autapomorphy of Trichoptera (Kristensen, personal communication).
- Presence or absence of cruciate cervical muscles (Boudreaux 1979; Whiting et al. 1997)
This muscle is absent in members of Endopterygota excl. Coleoptera (Whiting et al. 1997), but also in representatives of other groups of hexapods (e.g. Archaeognatha, Ephemeroptera, Plecoptera; Matsuda 1970).
- Discoid pronotum (Whiting et al. 1997)
Formation of a more or less typical discoidal pronotum (Whiting et al. 1997) is a gradual modification which has obviously evolved independently in different lineages. A discoid pronotum is present in Dermaptera and Blattodea (Whiting et al. 1997), but also in coleopterans and members of other groups of insects.
- Trochantin
The high variability of the trochantin, especially in apterygote hexapods, was pointed out by Kristensen (1997). A 'trochantin-episternal sulcus', which was scored as a shared condition for Embioptera, Dermaptera and Plecoptera in Whiting et al. (1997), could not be identified as a well-defined character state in these taxa.
- Presence or absence of meron (Boudreaux 1979; Whiting et al. 1997)
A meron is present in representatives of Endopterygota excluding Hymenoptera and Coleoptera according to Whiting et al. (1997). However, this is also the case in members of several other groups of insects (Larsén 1945a,b; Kristensen 1999). A meron is also present in the metacoxae of basal representatives of Coleoptera (e.g. *Priacma serrata*; Kristensen 1999).
- Outer tergal remotor (Hennig 1969; Whiting et al. 1997)
The absence was considered as a possible synapomorphy of the panorpoid orders by Hennig (1969) and as a shared feature of Strepsiptera and this unit by Whiting et al. (1997). However, the homology of the muscle in different groups is problematic and the muscle is present in a presumably basal representative of Lepidoptera (*Agathiphaga*; Kristensen 1991, 1999). The presence in this unusual lepidopteran group is arguably a character reversal. The presence in another lower moth has been shown to be due to an observational error (Nielsen and Kristensen 1996).
- Gastric caeca (Kristensen 1981; Whiting et al. 1997)
Different degrees of reduction have almost certainly taken place in different groups of hexapods. In contrast to Whiting et al. (1997), they are retained at least in Corydalidae (Kristensen 1999).
- Ventral muscles of diaphragm inserted on ventral nerve cord (Richards 1963)
The peculiar insertion of these muscles on the dorsal surface of the ventral nerve cord is an autapomorphy of Amphimesmenoptera and sheath enlargement as a true connective tissue formation with copious extracellular material fabricated by the sheath cells an apomorphic ground plan feature of Neolepidoptera (Kristensen and Nielsen 1980). We have excluded the character from this analysis because the ventral diaphragm seems to appear and disappear several times independently, and character states of different hexapod orders are unknown (Richards 1963).
- Metameric or nonmetameric outlet ducts of testis (e.g. Kristensen 1991; Whiting et al. 1997)
Metameric outlet ducts (Zwick 1973, 1980, 1981) were considered a plesiomorphic feature of Plecoptera (Zwick 1981; Kristensen 1991). However, in contrast to Whiting et al. (1997), such a condition is neither found in different, presumably basal groups of hexapods (e.g. Japygidae, Protura) nor in myriapods. Conditions in other groups of apterygote hexapods are distinctly different from what is found in Plecoptera, and should not be considered as a single character state. Metameric outlet ducts are probably not a groundplan feature of Tracheata and Hexapoda.

- **Phallomeres**
The homology of the structures in question in different hexapod orders appears too uncertain, to include this character system in the analysis. Nevertheless, for selected taxa, this character may provide useful information (e.g. characteristic asymmetry in Blattodea and Mantodea; Klass 1997).
- **Male styli suppressed** (Boudreaux 1979; Whiting et al. 1997)
Reduction of male styli has occurred in Plecoptera, Dermaptera and Embioptera (Whiting et al. 1997), but also in other groups of insects (e.g. Coleoptera; Diptera, Colless and McAlpine 1991). The homology of male terminalia is not sufficiently clarified at present.
- **Phallic rudiments produce gonopods** (Boudreaux 1979)
This character was interpreted as a possible synapomorphy of Paraneoptera and Endopterygota by Boudreaux (1979). However, it is not clearly defined and coding as a common character state for all paraneopteran and endopterygote orders is superficial.
- **Sex determination (XX/XY, XX/X0, e.g. Whiting et al. 1997; Thorne and Carpenter 1992)**
This character is highly variable even within hexapod orders or smaller taxonomic units (e.g. Hemiptera, Strümpel 1983; Neuroptera, New 1989; Mecoptera, Kaltenbach 1978; Diptera, Hennig 1973). Therefore it is probably not useful for phylogenetic investigations on the ordinal level. The groundplan of each taxon would have to be established prior to analysis.
- **Sperm axoneme pattern (9 + 2; 9 + 9 + 2 with 4 + 5 or 4 + 3 + 2 arrangement of outer row; 9 + 9 + 2 with regular arrangement of outer row; 12–14 + 0; 9 + 9 + 0)**
Many variations of the typical 9 + 9 + 2 pattern occur in different orders (Jamieson 1987)