

A Revised Interpretation of the Evolution of Attachment Structures in Hexapoda with Special Emphasis on Mantophasmatodea

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> Abstract

Characters of hexapod attachment structures were analysed cladistically together with 110 additional morphological characters of immatures and adults. The results suggest the monophyly of Hexapoda, Ellipura, Diplura + Ectognatha, and Dicondylia. Lepidothrichidae is either the sister group of the remaining Dicondylia or part of a clade Zygentoma. Odonata is the sister group of Neoptera, and Plecoptera possibly the sister group of the remaining neopteran orders. Pliconeoptera are paraphyletic. Embioptera were placed as sistergroup of a clade comprising the remaining Pliconeoptera, Paraneoptera and Endopterygota. The branching pattern of the majority of the “lower neopteran” groups is Dermaptera + ((Dictyoptera + (Orthoptera + Phasmatodea)) + (Grylloblattodea + Mantophasmatodea)). The sister group relationship between Mantophasmatodea and Grylloblattodea is only weakly supported. Zoraptera were placed as sister group of Acercaria (Paraneoptera). The monophyly of Psocodea and Hemiptera was confirmed. Paraneoptera are the sister group of Endopterygota. Strepsiptera were placed as sister taxon to the remaining Endopterygota. Coleoptera + Neuropterida is weakly supported statistically. They are placed as sister group of Hymenoptera + (Amphiesmenoptera + Antliophora). The interrelationships within Antliophora remain uncertain. Attachment devices that have evolved in an apterygote lineage are the tufts of curved hairs on the apical tarsus of archaeognathan species (scopulae). Attachment pads were absent in the groundplan of Pterygota. The arolium is likely a derived groundplan feature of Neoptera, with secondary loss in several groups. It is usually smooth on its surface. The hairy surface of the greatly enlarged arolium and the hairy surface of the euplantulae are autapomorphies of Mantophasmatodea. Pad-like euplantulae are a potential synapomorphy of the clade comprising Dictyoptera, Phasmatodea, Orthoptera, Grylloblattodea (strongly reduced in size) and Mantophasmatodea. Hairy or smooth pulvilli have evolved several times independently. Hairy soles of tarsomeres are present in Embioptera, Dermaptera, Megaloptera, Raphidioptera, Coleoptera (groundplan) and Stylopida (absent in the groundplan of Strepsiptera). The phylogenetic interpretation of this character is ambiguous. An eversible pretarsal vesicle is autapomorphic for Thysanoptera and a fossula spongiosa for Piratinae (Reduviidae). An extended empodium occurs in Nematocera excl. Tipulomorpha and in Tabanoidea. The presence of hairy pulvilli and the loss of the arolium are potential apomorphies of Diptera excl. Tipulomorpha. Plantar lobes are a derived groundplan feature of Hymenoptera and partly or completely reduced in Apocrita.

> Key words

SEM, TEM, cuticle, friction, attachment, ultrastructure, locomotion, Hexapoda, phylogeny, evolution, functional morphology.

1. Introduction

The first comprehensive study on the evolution of hexapod attachment structures based on a cladistic analysis of a broad spectrum of morphological characters was published by BEUTEL & GORB (2001). Since then the available information has increased considerably, mainly thanks to a special volume on

insect attachment devices edited by GORB (2004). It has turned out that insufficient taxon sampling for some groups in BEUTEL & GORB (2001) has led to problematic entries for orders (Dermaptera, Strepsiptera), which were treated as terminal taxa in the data matrix (see HAAS & GORB 2004; POHL & BEUTEL

2004). Consequently, we have changed entries in the matrix presented in this study, and have also added or replaced taxa. Different representatives of Mantophasmatodea, which were recently erected as a new insect order (KLASS et al. 2002), were examined in detail and added to the data matrix. Plecopteran species from the Southern Hemisphere were studied (Antarcoperlaria), legs of *Grylloblatta* sp., alate specimens of Zoraptera, species of two subfamilies of the basal hymenopteran family Xyelidae (VILHEMSEN 2001; SCHULMEISTER 2003), representatives of two genera of the basal strepsipteran family Mengenillidae (POHL & BEUTEL 2005), and species of *Nannochorista* and *Boreus* from Mecoptera (s.l.). New insights on the phylogeny of antliophoran groups (WHITING 2002) induced us to treat Boreidae, the potential sister group of fleas, as a terminal taxon, and also Panorpidae and the enigmatic Nannochoristidae. Diptera are also represented by two separate nematoceran groups, the Tipulidae and Bibionidae.

The major aim of this study is to gain new insights on the evolution of attachment structures in the light of new data. The analysis may also give new impulses to the investigation of hexapod systematics. However, we are aware that more data and other strategies are necessary for a solid and detailed reconstruction of the phylogeny of such an extremely species rich and diverse group.

2. Material and methods

2.1. Additional taxa examined

Only the taxa examined in addition to BEUTEL & GORB (2001) are listed here; for the remaining taxa see that publication.

Archaeognatha: *Meinertellus* sp.

Plecoptera: Gripopterygidae: *Trinotoperla irrorata* Tillyard, 1924; Austroperlidae: *Acruroperla atra* (Šámal, 1921).

Mantophasmatodea: *Karoophasma* sp., *Austrophasma* sp., *Mantophasma zephyra* Zompro, Klass, Kristensen & Adis, 2002.

Grylloblattodea: *Grylloblatta* sp. (legs).

Zoraptera: Zorotypidae: *Zorotypus hubbardi* Caudell, 1918 (alate specimens).

Hymenoptera: Xyelidae: *Macroxyela ferruginea* (Say, 1824), *Xyela julii* (Brébisson, 1818).

Mecoptera: Nannochoristidae: *Nannochorista dipterooides* Tillyard, 1917; Boreidae: *Boreus westwoodi* Hagen, 1866.

Strepsiptera: Mengenillidae: *Mengenilla* spp., *Eoxenos laboulbenei* de Peyerimhoff, 1919.

2.2. Light microscopy and scanning electron microscopy

Most specimens were fixed in 70 % ethanol, but specimens of Xyelidae were preserved in Bouin and specimens of Strepsiptera in FAE.

Legs of *Meinertellus* sp., *Grylloblatta* sp. and *Macroxyela ferruginea* were critical point dried, sputter coated and examined with an FEI XL 30 ESEM and a Hitachi S-4800 SEM.

The tarsi of *Mantophasma zephyra* (Mantophasmatodea) were cut off the body of anaesthetized insects, mechanically mounted on brass stubs, and frozen in melting liquid nitrogen, in order to prevent building of a gaseous phase on the surface during the shock-freezing process. In the prechamber of the cryostage Gatan ALTO 2500, the frozen tarsi were longitudinally and transversally fractured using a razor blade cooled down to the temperature of -140°C. After a short sublimation (freeze-etching) procedure (3 min at the temperature difference -120°C and -90°C), samples were sputter-coated in the frozen condition (-140°C) with gold-palladium (6 nm film thickness) and observed in the frozen condition (-120°C) in the SEM Hitachi S 4800 at accelerating voltage of 1–3 kV. This method has allowed us to study the surface and material of both arolium and euplantulae with high resolution in a condition with a minimum of artefacts.

2.3. 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, 500 replicates, tree bisection-reconnection). Analysis of character evolution was conducted in MacClade (version 3; MADDISON & MADDISON 1992). Branch support values (BREMER 1994) were calculated using the “converse approach” for selected branches.

3. Results

The morphology of attachment structures of groups not or insufficiently treated in BEUTEL & GORB (2001) is described briefly in the following.

3.1. Archaeognatha

A unique brush-like attachment device is present on the apical tarsomere of *Meinertellus* and related genera

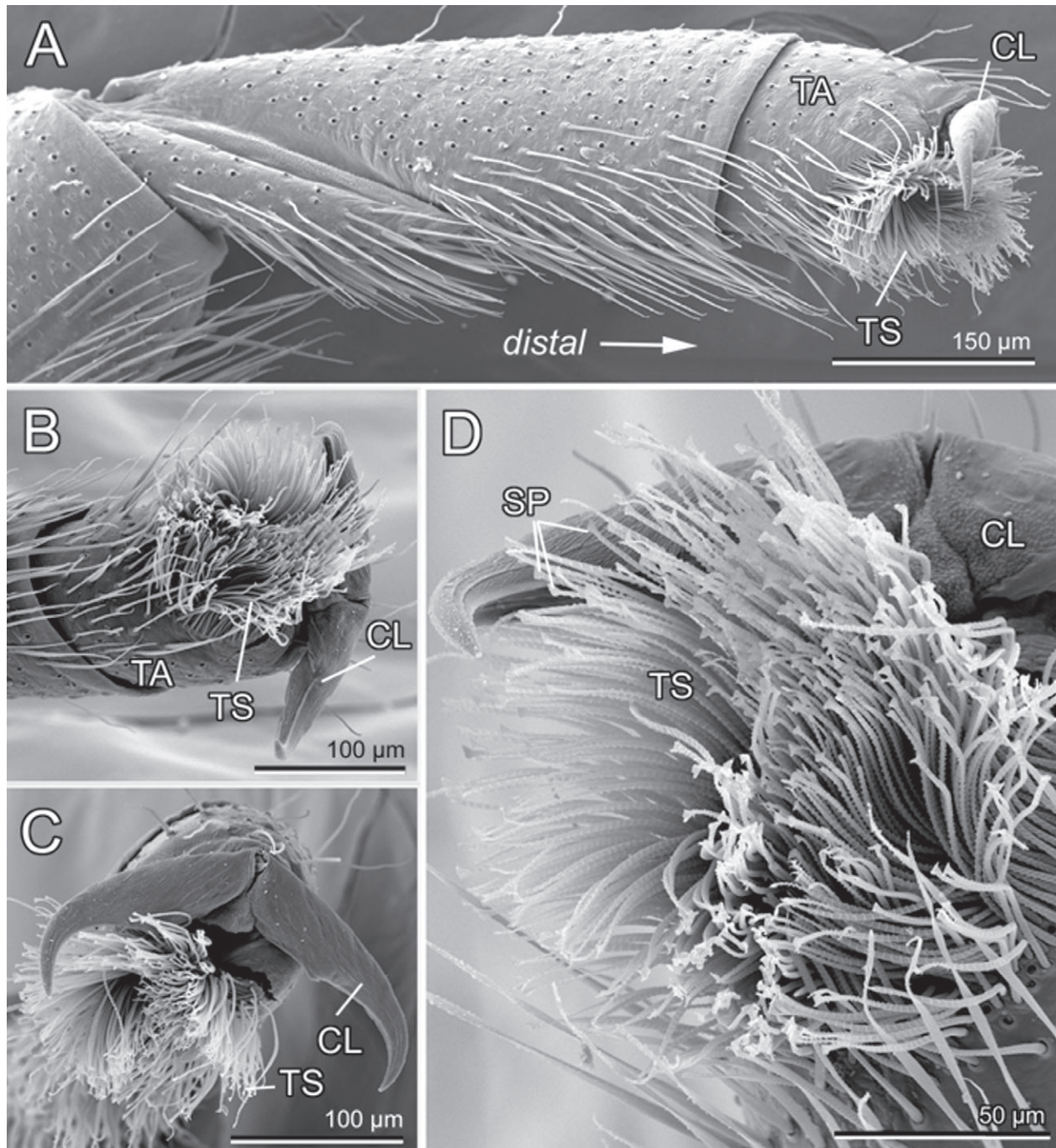


Fig. 1. SEM micrographs of *Meinertellus bogotensis* tarsus. **A:** Lateral aspect of the tarsus. **B,C:** Anteroventral aspects of the pretarsus. **D:** Tenent setae of the tarsus. CL, claw; SP, spatulae; TA, terminal tarsomere; TS, tenent setae. Arrow indicates distal direction in A.

(Fig. 1; M. Koch pers. comm.; STURM & MACHIDA 2001: fig. 8.16). The tenent setae bear spatula-like structures at their tips. The surface of the side walls of the setae is uneven (Fig. 1D). This might be interpreted as a mechanism preventing conglutination of setae, which have a rather high aspect ratio. Attachment structures are absent in most genera of the group.

3.2. Plecoptera (Antarctoperlaria)

A narrow longitudinal unsclerotized zone is distinctly recognizable on the ventral side of the two proximal tarsomeres of the 3-segmented tarsus of larger species (ZWICK 1980). Pad-like euplantulae are not developed. A well developed arolium is present.

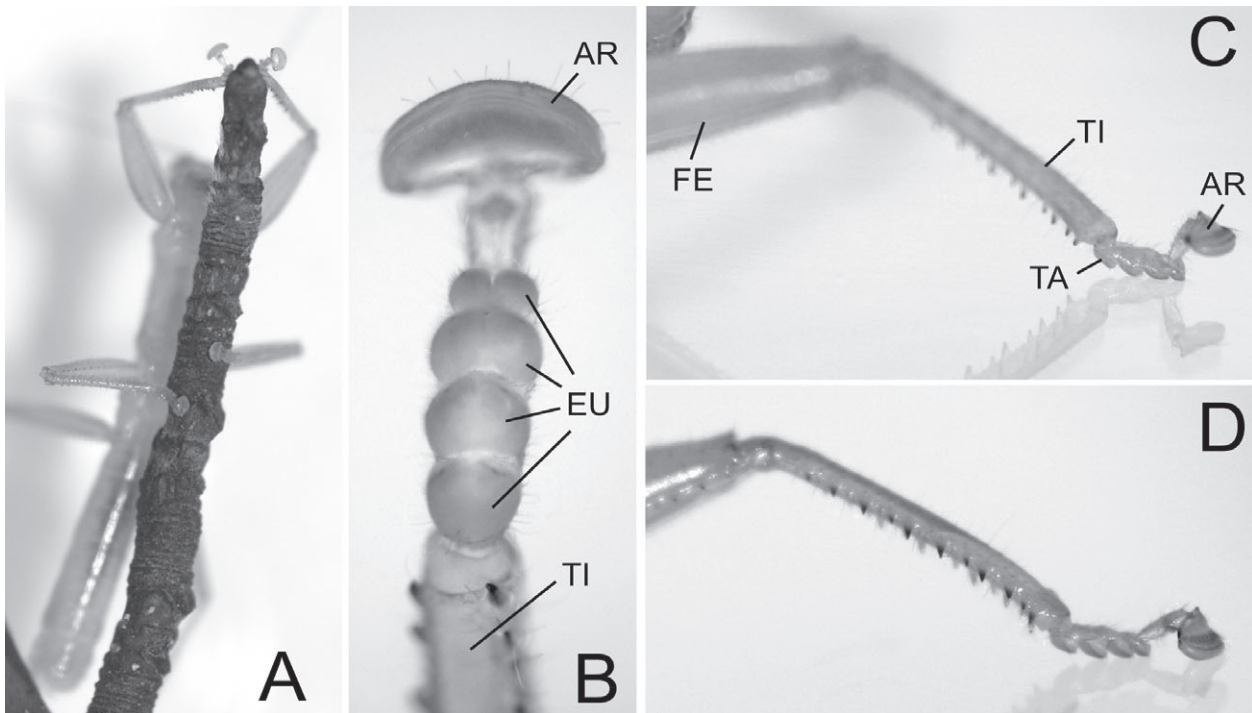


Fig. 2. *Mantophasma zephyra*. **A:** Male climbing on branch. Note that the arolia of the first legs are not in contact with the substrate (only euplantulae), whereas those of the second leg are in contact. **B:** Ventral aspect of tarsus. **C:** Regular position of arolium during walking (not in contact with the substrate). **D:** "Emergency" position of the arolium (in contact). Note that euplantulae are always in contact (A, C, D). AR, arolium; EU, euplantulae; FE, femur; TA, tarsus; TI, tibia.

3.3. Mantophasmatodea

The arolium of *Mantophasma zephyra* is strongly enlarged and only used on smooth surfaces (R. Predel pers. comm.) and only in emergency cases (while carrying additional loads such as prey or a copulating male, during sudden wind pulses, during strong vibrations of the substrate) (Fig. 2). The arolium is bent upwards, together with the terminal tarsomere, and can be brought in contact with the substrate using a very fast reflex (Fig. 2C,D). Euplantulae are well developed on tarsomeres 1–4. The presence of scattered acanthae on the surface of the arolium and a dense layer of long thin acanthae on the surface of the euplantulae are unique features in hexapods (Fig. 3). Acanthae of the arolium have no spatulae, whereas those of the euplantulae possess flattened terminal spatulae at their apices. Interestingly, the cuticle of the euplantulae (Fig. 3G,H) resembles foam-like materials of smooth pads previously described in Ensifera, Caelifera, and Auchenorrhyncha (GORB 2001).

3.4. Grylloblattodea

The euplantulae on the 5-segmented tarsi are recognizable but very small (Fig. 4). Arolium and pulvilli are not developed. The euplantulae of the 5th

tarsomere resemble flattened hemispheres (Fig. 4A,B), whereas those on tarsomeres 1–4 are rather elongate cylindrical structures (Fig. 4C–E,G,H). All euplantulae contain striated patterns of microgrooves on their surface. The microgrooves are oriented perpendicular to the leg segment axis. It cannot be fully excluded that the structures interpreted as partly reduced euplantulae here are in fact transformed tarsal spines.

3.5. Dermaptera

The arolium is absent in most representatives of Dermaptera, but is present in Apachyidae, Diplatyidae, Karschiellidae (partim), Pygidicranidae (partim), and Spongiphoridae (HAAS & GORB 2004). As the latter condition is likely a groundplan feature of the order we code the arolium as present (0). Hairy tarsomeres occur in the large family Forficulidae and in Chelisodidae and Pygidicraninae (coded as 0&1). Euplantulae (plantulae) are only present in 2 species examined by HAAS & GORB (2004) (coded as 0&1).

3.6. Zoraptera (alate specimens of *Zorotypus hubbardi*)

Attachment structures are not only absent in wingless morphs but also in alate specimens of *Zorotypus hubbardi*.

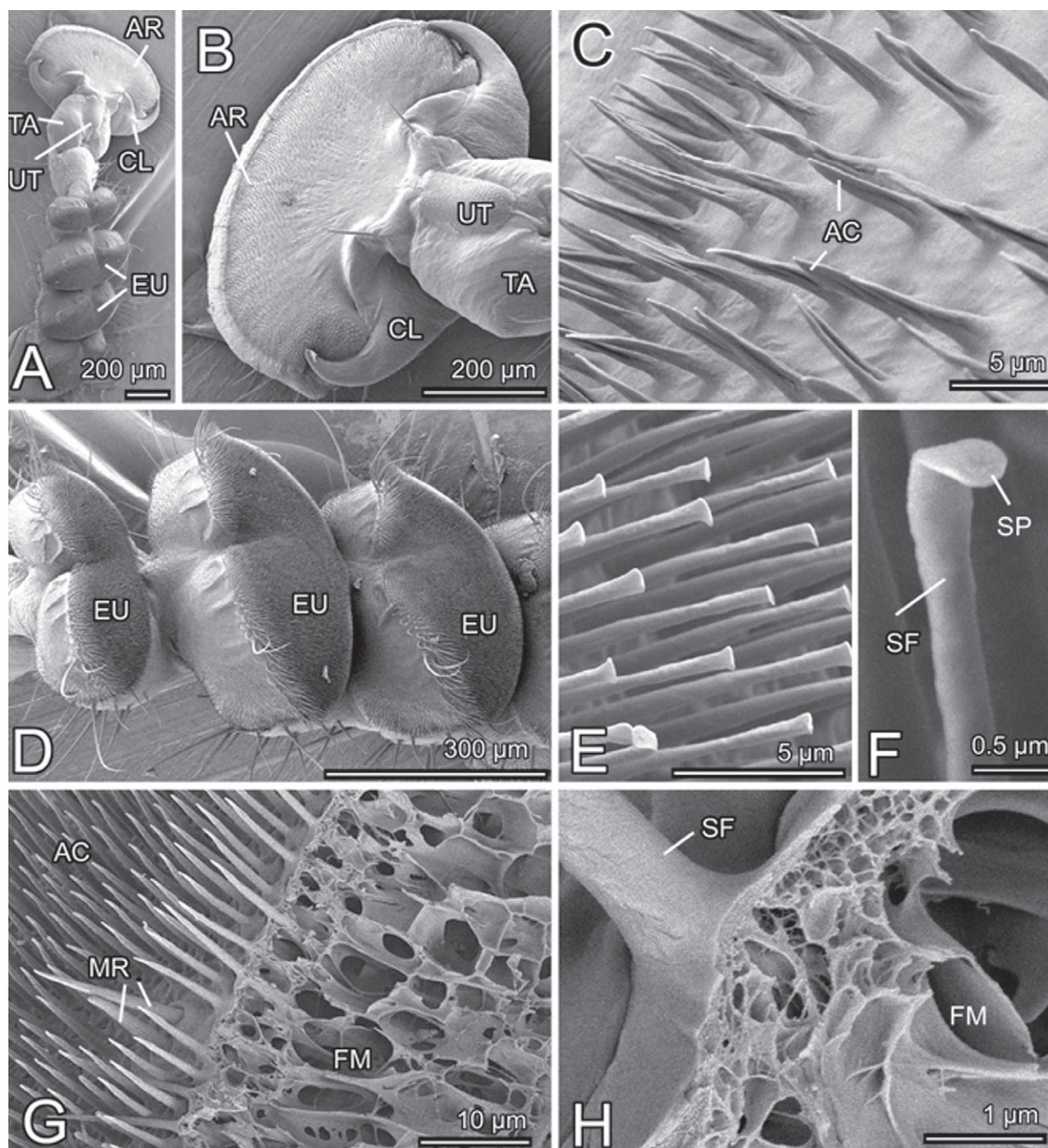


Fig. 3. Cryo-SEM micrographs of *Mantophasma zephyra* tarsi. **A:** Ventral surface of the tarsus. **B,C:** Ventral surface of the arolium. **D:** Euplantulae. **E,F:** Tenent setae of euplantulae with terminal elements. **G,H:** Inner structure of the material of the euplantula (freezing-fracture). AC, acanthae; AR, arolium; CL, claw; EP, euplantulae; FM, foam-like cuticle of the euplantula; MR, mechanoreceptors; SF, shaft of the acantha; SP, spatula; TA, tarsomeres; UT, unguitactor plate.

3.7. Hymenoptera (Xyelidae)

The structure of the plantar lobes of Xyelidae strongly suggests that they are just flat outgrowths of the tarsal cuticle (Fig. 5) and not derived from tarsal thorns as suggested in BEUTEL & GORB (2001). The xyelid plantar lobes are structurally completely different from euplantulae and very likely not homologous with these structures. They are distally elongated

and smooth without any pattern on their surface (Fig. 5A–D). An arolium is present in Xyelidae as in other representatives of Hymenoptera (Fig. 5E–F).

3.8. Strepsiptera (Mengenillidae)

Specialized tenent setae on tarsomeres are absent in males of Mengenillidae (POHL & BEUTEL 2004). This

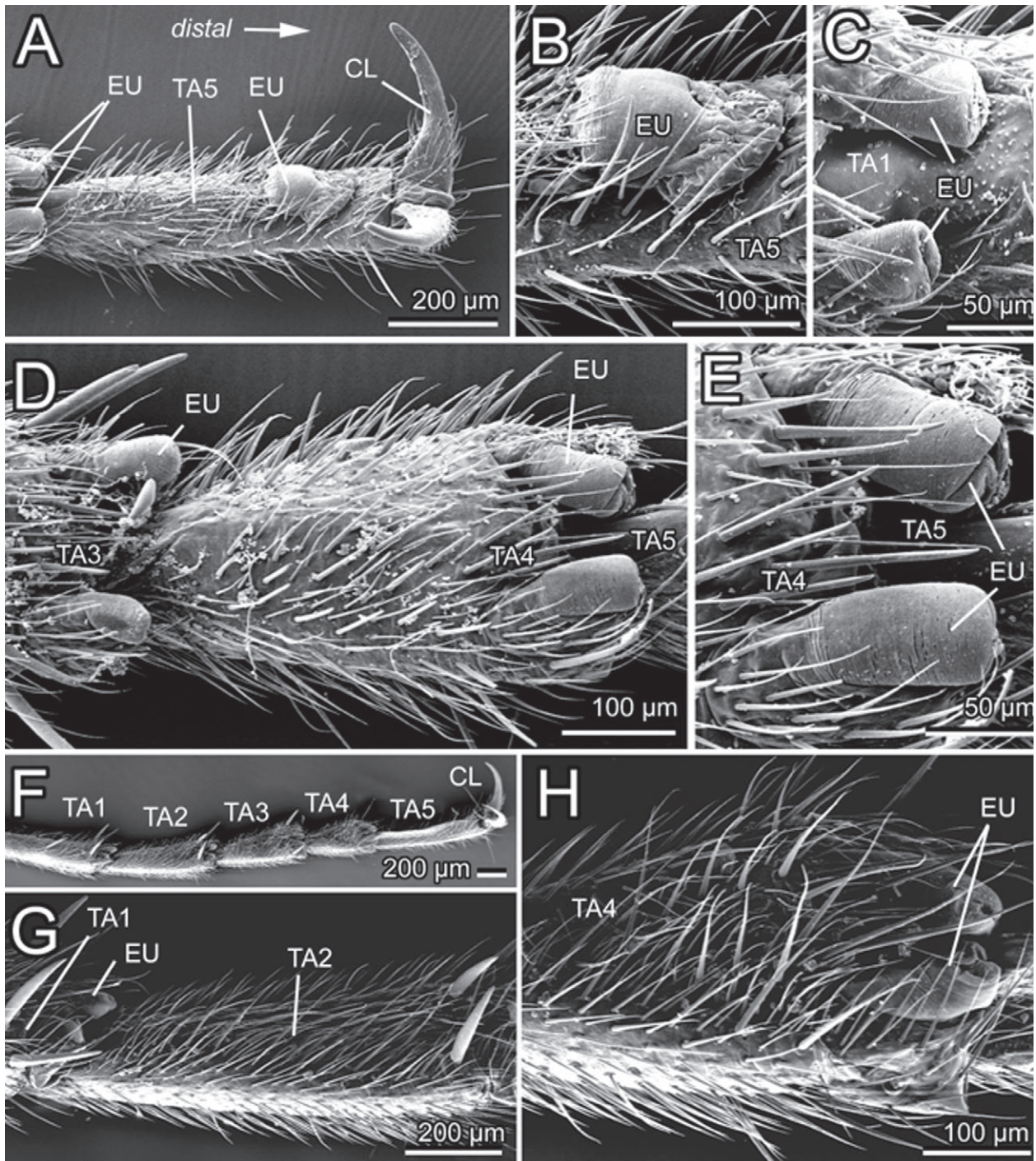


Fig. 4. SEM micrographs of *Grylloblatta* sp. tarsi. **A–E:** Male. **F–H:** Female. **A:** Ventro-lateral aspect of the distal part of the tarsus. **B:** Euplantula of the 5th tarsomere. **C:** Ventral aspect of tarsomere 1. **D:** Ventral aspect of tarsomeres 3 and 4. **E:** Ventral aspect of tarsomere 4. **F:** Ventrolateral aspect of tarsus. **G:** Ventro-lateral aspect of tarsomeres 1 and 2. **H:** Ventro-lateral aspect of tarsomere 4. Arrow indicates distal direction in A–H. CL, claws; EU, euplantulae; TA1–TA5, tarsomeres.

is very likely a groundplan feature of the order (coded as absent). As in Stylopodia, arolium, euplantulae and pulvilli are also absent in Megenillidae (POHL & BEUTEL 2004).

3.9. Mecoptera (Nannochoristidae, Boreidae)

A well developed arolium is present in *Nannochorista*. Other attachment structures are absent. Attachment devices are completely lacking in *Boreus*.

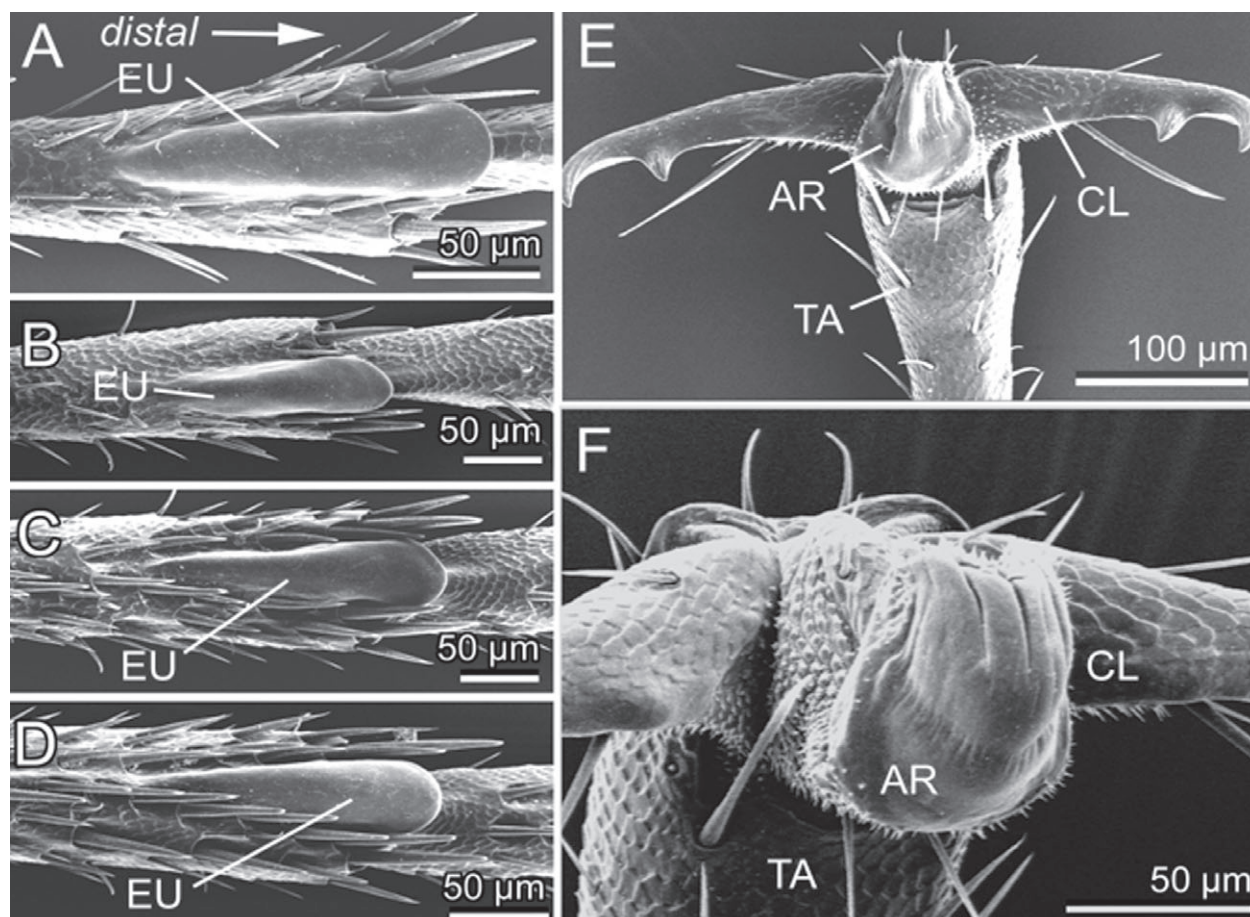


Fig. 5. SEM micrographs of *Macroxyela ferruginea* tarsi. **A–D:** Euplantulae on the ventral side of the tarsus. **E,F:** Pretarsus. **A:** Leg 1, tarsomere 1. **B:** Leg 3, tarsomere 3. **C:** Leg 3, tarsomere 2. **D:** Leg 3, tarsomere 1. **E:** Arolium and claws of leg 3. **F:** Arolium of leg 1. Arrow indicates distal direction in A–D. AR, arolium; CL, claws; EU, euplantulae; TA, terminal tarsomere.

4. Character coding for attachment structures

Only the coding for tarsal attachment structures is given here; for the coding of all other characters used herein see Appendix 1.

01. (= 111. in data matrix) Arolium: (0) absent; (1) present; (2) transformed into an eversible bladder.

02. (= 112.) Pulvilli: (0) absent; (1) smooth; (2) hairy.

03. (= 113.) Euplantulae: (0) absent; (1) present as longitudinal membranous area; (2) present as very small pads (*Grylloblattodea*); (3) present as well developed pads.

04. (= 114.) Hairy adhesive soles of tarsomeres: (0) absent; (1) present.

05. (= 115.) Fossula spongiosa: (0) absent; (1) present.

06. (= 116.) Eversible structure between tibia and tarsus: (0) absent; (1) present.

07. (= 117.) Claw pad: (0) absent; (1) present.

08. (= 118.) Plantar lobes: (0) absent; (1) present.

09. (= 119.) Empodium plate-like: (0) no; (1) yes.

10. (= 120.) Adhesive claw setae: (0) absent; (1) present.

5. Results of the cladistic analysis

The analysis of the full set of 120 characters (Appendix 1 and chapter 4) resulted in 48 minimal length trees with 280 steps (consistency index 0.55; rescaled consistency index: 0.4254; Fig. 6: strict consensus tree with branch support values for selected branches). The three trees obtained after successive reweighting differ only in the relationships among the dictyopteran subgroups.

In the following, apomorphies of selected clades are listed. The consistency index of single characters (abbreviated as ci in the following) is 1.000 and unam-

biguous [characters in bold face] unless otherwise noted. Characters related to attachment structures are underlined. BSV = branch support value (or Bremer support; BREMER 1994); ACCTTRAN = character state optimisation: accelerated transformation; DELTRAN = character state optimisation: delayed transformation.

Diplura + Insecta (Cercophora) (BSV: 1): **3.(1)** Temporal organs absent; 42.(1) Double claw (ci: 0.5); 103.(1) Axoneme pattern 9 + 9x2 + 2 (ci: 0.333).

Zygentoma incl. Lepidothrichidae (not confirmed in all trees): 9.(1) Superlinguae absent (ci: 0.5); 28.(1) Labial palps 4-segmented (ci: 0.667); **69.(1)** Specific articulation of cerci; **99.(1)** Sperm conjugation.

Zygentoma (excl. Lepidothrichidae) + Pterygota (not confirmed in all trees): **4.(1)** Postocciput and pleural folds reduced; **13.(1)** Ligamentous endoskeleton reduced; **22.(1)** Transverse mandibular apodeme absent; 66.(1) Not more than 2 posterior coxal vesicles (DELTRAN, ci: 0.667); 67.(1) Styli absent from abdominal segment II or completely reduced (DELTRAN, ci: 0.333).

Odonata + Neoptera (Metapterygota) (BSV: 3): 20.(2) Secondary mandibular joint developed as ball-and-socket articulation (ci: 0.667); 31.(1) M. tentoriomandibularis with only one bundle or absent (ci: 0.5); **57.(1)** Leg- and wing tracheae connected with following spiracle; 65.(1) Abdominal spiracles with occlusor muscle (ci: 0.5); 76.(0) Terminal filament absent (ci: 0.5); **108.(1)** Subimago absent.

Neoptera excl. Plecoptera (BSV: 1): **32.(1)** M. stipitalis transversalis absent; 109.(0) Larvae terrestrial (DELTRAN, ci: 0.167).

Neoptera excl. Plecoptera and Embioptera (BSV: 1): 40.(4) Tarsus with 5 tarsomeres (polarity doubtful) (ci: 0.444); 60.(0) Mid-ventral ostia absent (polarity doubtful) (ACCTTRAN, ci: 0.5); 94.(1) Segment XI absent in larvae (implies reversal in several groups) (ci: 0.143).

Dermaptera + Dictyoptera + Orthoptera + Phasmatodea + Grylloblattodea + Mantophasmatodea (BSV: 1): 49.(1) Hind wing vannus distinctly enlarged (DELTRAN, ci: 0.5); 50.(1) Hind wing vannus pleated (ci: 0.5); 51.(1) Tegmina (ACCTTRAN, ci: 0.75); 72.(1) Ovipositor with well developed, elongate gonapophyses VIII and IX, ovipositor sheath formed by 3rd valvulae (polarity doubtful) (ci: 0.286); 111.(1) Arolium present (ACCTTRAN, ci: 0.2).

Dictyoptera + Orthoptera + Phasmatodea + Grylloblattodea + Mantophasmatodea (BSV: 1): 48.(1) Less than 5 costal crossveins (polarity doubtful) (ACCTTRAN, ci: 0.25); 113.(2) Well developed pad-like euplantulae (ci: 0.5).

Dictyoptera + Orthoptera + Phasmatodea (BSV: 1): **36.(1)** Ampullo-ampullary muscle present and accessory ampullary muscles attached to aorta.

Orthoptera + Phasmatodea (BSV: 2): 51.(1) Tegmina (DELTRAN, ci: 0.75); **53.(1)** Pronounced precostal field.

Grylloblattodea + Mantophasmatodea (BSV: 1): 2.(1) Ocelli absent (ci: 0.143); 44.(0) Wings absent (ci: 0.4).

Zoraptera + Acercaria (Paraneoptera) (BSV: 1): 23.(1) Lacinia elongate and slender, mesally directed setae absent (ci: 0.5); 34.(1) Cibarial dilator (M. clypeopalatalis) very large (ci: 0.5); 40.(1) Number of tarsomeres reduced (reversal from 40.(4)) (ci: 0.444); 81.(1) Two abdominal ganglionic masses (ACCTTRAN, ci: 0.75).

Paraneoptera + Endopterygota (Eumetabola) (BSV: 1): 49.(0) Hind wing vannus not enlarged (polarity doubtful) (ACCTTRAN, ci: 0.5); 68.(1) Cerci strongly reduced or absent (ACCTTRAN, ci: 0.2); 70.(1) Number of Malpighian tubules distinctly reduced (ci: 0.8); 83.(3) Ovarioles polytrophic, branched arrangement (ACCTTRAN, ci: 0.667).

Endopterygota excl. Strepsiptera (BSV: 1): 62.(1) Dorsal pulsatile diaphragm unpaired separate (ACCTTRAN, ci: 0.250); 85.(1) Appearance of compound eyes in ultimate immature stage (pupa).

Coleoptera + Neuropterida (BSV: 0): 14.(1) Gula present (ACCTTRAN, ci: 0.2); 55.(1) Head of axillary I enlarged with distal process (DELTRAN, ci: 0.667); 56.(1) Caudal process of axillary II present (DELTRAN, ci: 0.5); **75.(1)** Gonocoxite IX fused with stylus base into a sensory appendage, gonapophyses absent; 114.(1) Hairy soles of tarsomeres present (reversal in Neuroptera) (ACCTTRAN, ci: 0.333).

Hymenoptera + Mecopterida (BSV: 2): **29.(1)** Sitophore plate present; 55.(1) Head of axillary I not enlarged (ACCTTRAN, ci: 0.667); 56.(1) Caudal process of axillary II absent (ACCTTRAN, ci: 0.5); 90.(1) Labial silk glands of larvae (ci: 0.5); 93.(1) Larvae with single claws; (ci: 0.333); 111.(1) Arolium present (polarity doubtful) (ACCTTRAN, ci: 0.2).

Mecopterida (BSV: 1): **46.(1)** Axillary I with attachment of pleural muscle; 87.(1) Larval stipes divided into basistipes and dististipes (ci: 0.5); 88.(1) M. craniocardinalis absent (ci: 0.333); **89.(1)** M. craniodististipitalis present.

Antliophora (BSV: 1): **54.(1)** Posterior notal wing process specialized, with insertion of pleural muscle; 59.(1) Proventriculus with close-set, prominently elongated acanthae (ACCTTRAN, ci: 0.5); 61.(1) 'Link plates' adjacent to thoracic spiracles present (ACCTTRAN, ci: 0.5); 102.(1) Sperm axoneme coiling around mitochondrial derivative (ACCTTRAN, ci: 0.5).

Mecoptera (BSV: 1): **5.(1)** Rostrum present (short in some subgroups); **79.(1)** Dorsal and ventral fusion of basistyli; 84.(0) Stemmata absent in larvae (compound eyes) (ci: 0.333).

6. Discussion

6.1. Phylogeny

Hexapod phylogeny was not the main focus of this study. The analysis of a broad character set was mainly carried out to allow an interpretation of the evolution of adhesive pad characters. Therefore, the phylogenetic conclusions, which may be drawn from this analysis, are only discussed briefly.

The basal branching pattern within Hexapoda is in agreement with most current hypotheses (see, e.g., KRISTENSEN 1997; BITSCH & BITSCH 1998, 2000, 2004; BITSCH et al. 2004). In contrast to molecular studies by NARDI et al. (2003a,b) and GIRIBET et al. (2004) the monophyly of Hexapoda is confirmed, and also the monophyly of Ellipura and a clade comprising Diplura and Ectognatha (see, e.g., KUKALOVÁ-PECK 1991; KRISTENSEN 1997; KOCH 1997, 2000a,b; BEUTEL & GORB 2001; WHEELER et al. 2001). It was pointed out in BITSCH et al. (2004) that analyses of combined data sets provide more reliable results concerning basal hexapodan branching events than molecular data alone. The monophyly of Insecta (= Ectognatha) (BSV: 9) and of Dicondylia (BSV: 3) is strongly supported. In contrast to BEUTEL & GORB (2001), the placement of *Tricholepidion* is ambiguous, like in a study largely based on molecular data by GIRIBET et al. (2004). Lepidothrichidae (*Tricholepidion*) may be the sister group of the remaining Dicondylia or part of a clade Zygentoma. A new argument for the latter option is the presence of a specific articulation of the cerci (M. Koch pers. comm.). However, this potential zygentoman autapomorphy appears questionable. The different conditions in Zygentoma and Pterygota may be simply the result of the reduced condition of tergite XI in the latter taxon (K.-D. Klass pers. comm.; KLASS 2001).

The monophyly of Pterygota is well supported in our analysis (BSV: 4) and also the monophyly of a clade comprising Odonata and Neoptera (Metapterygota) (BSV: 3) as suggested by KRISTENSEN (1991) (see also BEUTEL & GORB 2001; WILLMANN 2003, 2005). This is in contrast to the monophyly of Palaeoptera (Odonata + Ephemeroptera) proposed by HAAS & KUKALOVÁ-PECK (2001) and others (see also HENNIG 1969; KUKALOVÁ-PECK 1991). The Palaeoptera hypothesis is weakened by the fact, that it is largely or exclusively based on characters of the wings. An outgroup comparison is not possible for wing characters of the basal pterygote lineages and a formal character analysis was not carried out by HAAS & KUKALOVÁ-PECK (2001). The alternative hypothesis is supported by a broad spectrum of morphological characters (see KRISTENSEN 1991; BEUTEL & GORB 2001; STANICZEK 2000) and also by

the results of analyses mainly based on molecular data (WHEELER et al. 2001). However, a clade Palaeoptera was obtained in an analysis of molecular data by KJER et al. (2006).

The monophyly of Neoptera was confirmed (BSV: 2). The placement of Plecoptera as sister group of the remaining Neoptera (ZWICK 1980; KRISTENSEN 1991; BEUTEL & GORB 2001) is only weakly supported (transverse stipital muscle lost, terrestrial larvae; BSV: 1). Alternative hypotheses are a close relationship of Plecoptera with Embioptera (WHEELER et al. 2001), with Orthoptera + Phasmatodea (Orthoneoptera) (HAAS & KUKALOVÁ-PECK 2001), or with a clade comprising Zoraptera and Dermaptera (TERRY & WHITING 2005) (see discussions in KRISTENSEN 1991; WILLMANN 2003; BEUTEL & WEIDE 2005). Pliconeoptera turned out as paraphyletic in our analysis, as Embioptera are placed as sister group of the remaining neopteran orders (excl. Plecoptera). It is possible that this as an artefact partly due to secondary wing modifications. It is very likely that the reduced anal field of males (wings are absent in females) is a secondary modification in Embioptera (see Ephemeroptera, Plecoptera), and this is likely also true for the membranous condition of the fore wings. Similar reductions occur in Isoptera, which use the wings only for short mating flights. A condition which is very likely autapomorphic for Embioptera is the desclerotisation of the longitudinal wing veins (GRIMALDI & ENGEL 2005). This modification, which allows the wings to collapse among themselves when not in use, would make no sense if the fore wings would be typical tegmina. The monophyly of Neoptera excl. Plecoptera and Embioptera is weakly supported statistically (BSV: 1) and the potential apomorphies (tarsus 5-segmented, mid-ventral ostia absent, segment XI of larvae reduced) are not convincing. In BEUTEL & GORB (2001) the presence of hairy tarsomeres was interpreted as a synapomorphy of Embioptera and Dermaptera. The results of the present analyses imply that this condition has evolved independently in Embioptera and within Dermaptera (HAAS & GORB 2004). The position of Embioptera remains enigmatic. In contrast to the dermapteran affinities proposed in BEUTEL & GORB (2001; see also JAMIESON 1987) or a close relationship with Plecoptera (WHEELER et al. 2001; see above), a sister group relationship with Phasmatodea was proposed by RÄHLE (1970) and also in a recent study based on sequences of different genes (18S, 28S, H3) and morphological characters (TERRY & WHITING 2005). Another alternative is a sistergroup relationship between Embioptera and Zoraptera (see below).

A large clade supported by our analysis comprises Dermaptera, Dictyoptera, Orthoptera, Phasmatodea, Grylloblattodea and Mantophasmatodea. Sclerotized

forewings and fan-like folding of the enlarged hind wing vannus are derived groundplan features, with secondary modifications in some groups (e.g., shortened, sclerotised tegmina in Dermaptera, loss of wings in Phasmatodea [absent in the groundplan with secondary recovery in the group according to WHITING et al. 2003], Grylloblattodea and Mantophasmatodea, simplified wings in Isoptera [similar condition as in Embioptera]). The typical pad-like euplantulae are interpreted as a potential automorphy of this lineage excluding Dermaptera (see below).

In contrast to BEUTEL & GORB (2001), Phasmatodea were not placed as sister group of Dictyoptera, but as sister group of Orthoptera (= Orthopterida; WILLMANN 2003). This is mainly supported by the presence of a strongly developed precostal field (unless wings are reduced) (WILLMANN 2003, 2005). Additional potential synapomorphies are the increased number of cervical sclerites and the shortened and simplified cercus (not included in this analysis; see WILLMANN 2003). An unpaired transverse muscle connecting the antennal ampullae is a potential synapomorphy of Orthopterida and Dictyoptera. The muscle is not only present in Phasmatodea and Dictyoptera (see BEUTEL & GORB 2001), but does also occur in Ensifera and Caelifera (e.g., *Prosarthria*, E. Baum pers. comm.).

The sister group relationship between Mantophasmatodea and Grylloblattodea is only weakly supported statistically (BSV: 1) in our analysis, whereas the support for this clade is high under multiple analytical methodologies in a combined analysis presented by TERRY & WHITING (2005). A formal analysis of more morphological data is desirable, but a clade comprising Mantophasmatodea and Grylloblattodea (Xenomonia; TERRY & WHITING 2005), which is also tentatively supported by similarities of the proventriculus (KLASS et al. 2002, 2003), should be considered as a serious working hypothesis. Apomorphies shared with different other neopteran groups (e.g., Phasmatodea: vomer/vomeroid) were discussed by KLASS et al. (2003). The results of an analysis of mitochondrial gene sequences suggest a sister group relationship between Mantophasmatodea and Phasmatodea (CAMERON et al. 2006). A sister group relationship between Mantophasmatodea and Orthoptera was suggested by ZOMPRO (2005). However, any formal character analysis is lacking in that study.

In contrast to BEUTEL & GORB (2001), Zoraptera were placed as sister group of Acercaria as already proposed by HENNIG (1969) and KRISTENSEN (1975, 1981). Acercarian affinities of Zoraptera were supported by a study of head structures of alate and wingless specimens (BEUTEL & WEIDE 2005). A slender lacinia without any mesally directed spines or setae and a very strongly developed *M. clypeopalatalis* are new arguments for the monophyly of Paraneoptera (incl.

Zoraptera) (BEUTEL & WEIDE 2005). This hypothesis is also in contrast to a sister group relationship between Dermaptera and Zoraptera proposed by TERRY & WHITING (2005) based on an analysis of molecular data (18S, 28S rDNA, Histone 3). In that study, the clade Haplocercata (= Dermaptera + Zoraptera) is strongly supported statistically (bootstrap value 100). Another hypothesis supported by morphological data is a sistergroup relationship between Zoraptera and Embioptera (see above; ENGEL & GRIMALDI 2000; GRIMALDI 2001; GRIMALDI & ENGEL 2005). This option was recently supported by the results of a detailed investigation of the wing base of Zoraptera and potentially related groups (K. Yoshizawa unpubl. results).

The branching pattern we obtained within Acercaria is consistent with BEUTEL & GORB (2001) and other current hypotheses (see, e.g., WILLMANN 2005), i.e., a sister group relationship between Thysanoptera and Psocodea (Micracercaria) and between Auchenorrhyncha and Heteroptera (Euhemiptera). The monophyly of Micracercaria, which is in contrast to the Condylgnatha hypothesis (HENNIG 1969; KRISTENSEN 1981; YOSHIZAWA & SAIGUSA 2001), is massively supported by molecular data (WHEELER et al. 2001).

Our analyses have largely confirmed traditional views of endopterygote interrelationships, i.e., a close relationship between Coleoptera and Neuropterida (only in all trees after successive reweighting) (e.g., MICKOLEIT 1973), a sister group relationship between Hymenoptera and Mecopterida (BSV: 2), and the monophyly of Mecopterida (BSV: 1), Amphiesmenoptera (BSV: 2) and Antliophora (excl. Strepsiptera) (BSV: 1) (see KRISTENSEN 1999; WILLMANN 2005). Interestingly, in our new analysis Strepsiptera were placed as sistertaxon to the remaining Endopterygota (BSV: 1) (see POHL & BEUTEL 2003). This option is in contrast to BEUTEL & GORB (2001: Strepsiptera + Coleoptera) and the Halteria-concept proposed by WHITING et al. (1997), WHITING (1998) and WHEELER et al. (2001) mainly based on 18S rDNA sequences. The hypothesis presented here was already discussed by KRISTENSEN (1991). It is suggested by the presence of a well developed abdominal segment XI and cerci in primary larvae of Strepsiptera, by the presence of external wing buds in secondary larvae of Mengenillidae, and by the appearance of compound eyes before the pupal stage. An important result regarding Strepsiptera is the absence of hairy soles on the tarsomeres in the groundplan. This weakens the case of a potential clade comprising Coleoptera and Strepsiptera ("Coleopterida"; WILLMANN 2005). Hairy soles are clearly an autapomorphy of a strepsipteran subgroup, the Stylopodia (POHL & BEUTEL 2005). They are also a potential synapomorphy of Coleoptera and Neuropterida. However, this implies secondary loss in Neuroptera, and the secondary acquisition of an

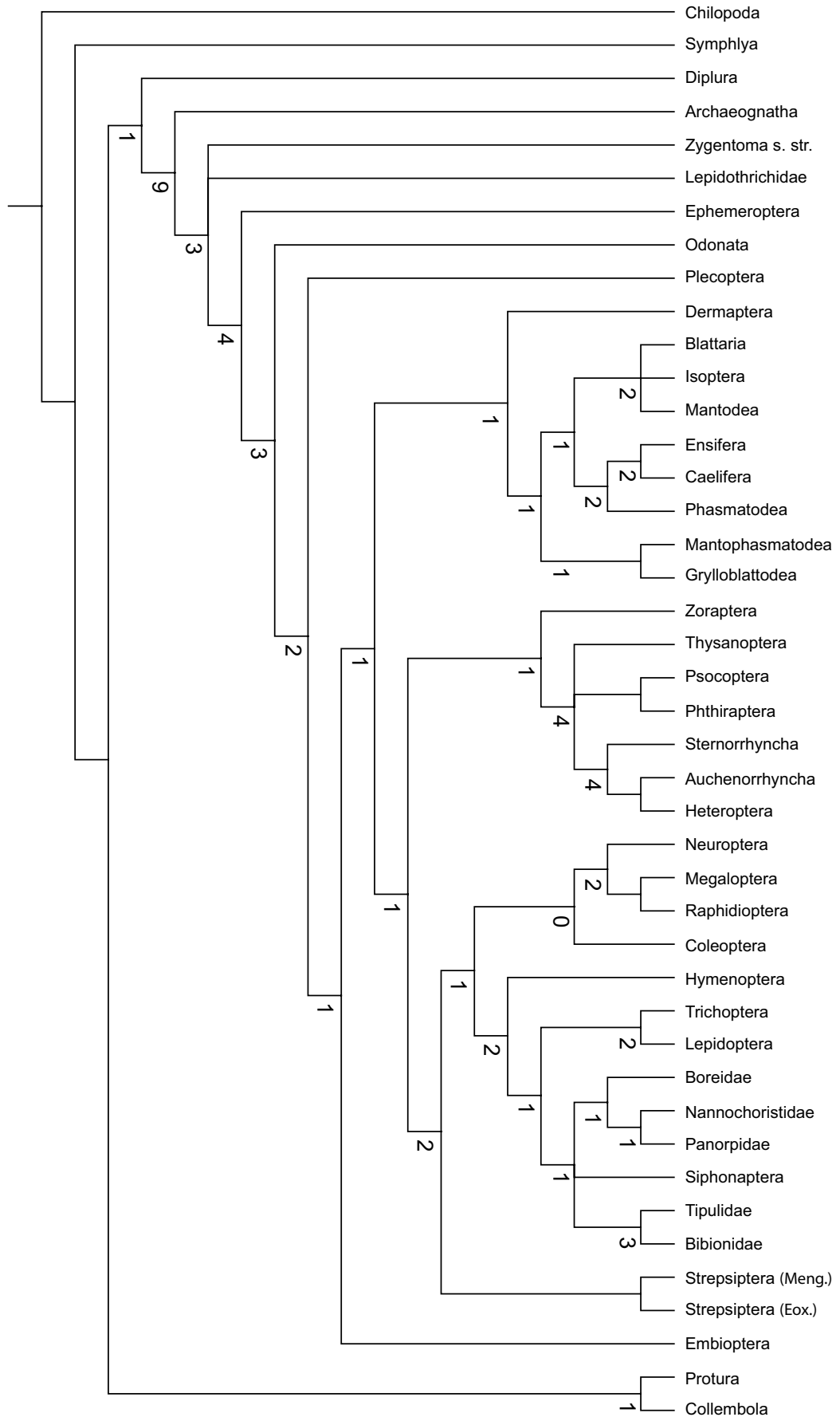


Fig. 6. Strict consensus cladogram of 48 minimal length trees with 180 steps. Branch support values (= Bremer support; BREMER 1994) for selected branches mapped on tree.

arolium, which appears not very likely. The microtrichia on the hairy soles differ in Coleoptera (pedestal present) on the one hand, and Megaloptera and Raphidioptera on the other (pedestal absent). The condition found in the latter groups should be considered as a potential synapomorphy. This would be in agreement with an earlier hypothesis (ACHTELG 1975, 1978; ACHTELG & KRISTENSEN 1973), but is in contrast to a sister group relationship between Neuroptera and Megaloptera proposed by ASPÖCK (2002).

In contrast to a study based on sequences of different genes (18S, 28S rDNA, COII, Elongation factor 1- α) (WHITING 2002), where a sister group relationship between Boreidae and Siphonaptera is supported (bootstrap value: 60; BSV: 10), Siphonaptera were placed as sister group of a clade Mecoptera in our analysis. More morphological data (e.g., larval morphology of Boreidae and Nannochoristidae) are clearly desirable. The taxon sampling and selection of characters in the present study is not sufficient for a full resolution of antliophoran relationships.

Many branches in the presented cladogram (Fig. 6) are weakly supported statistically. One option for a more solid reconstruction of hexapod phylogeny would be to break down the group into several well defined monophyletic units (e.g., Acercaria or Endopterygota), and to reconstruct the phylogeny and the groundplan of these lineages based on cladistic character evaluations. The phylogenetic relationships of the 'last common ancestors' (represented by the hypothesized groundplans) would then follow in a second step. In the first part of the procedure, several basal representatives of each order should be chosen as terminal taxa (e.g., genera of Xyelidae and Tenthredinoidea for Hymenoptera). A well documented and detailed morphological data set for such a specific taxon sampling is still lacking, despite a large number of older and more recent morphological studies. Cladistic studies often suffer from a lack of transparency in the presentation of the morphological data, and the results of analyses are sometimes compromised by inappropriate generalisations or assumptions, without real data for some of the taxa under consideration. These problems could be overcome by a better coordination of teams of systematic entomologists. Total evidence analysis including a broad variety of morphological character systems and DNA sequence data of different genes may lead to a truly solid reconstruction of the phylogeny of hexapods in the near future.

6.2. Evolution of attachment devices

Attachment devices are usually absent in apterygote insects and in the groundplan of Hexapoda (see BEUTEL & GORB 2001). However, scopulae, tufts of

curved hairs with disc-like apices are present in few archaeognathan genera (Fig. 1; e.g., *Meinertellus*, *Graphitarsus*, *Corethromachilis*; STURM & MACHIDA 2001). At least species of *Meinertellus* are able to walk on vertical glass walls with these attachment structures (STURM & MACHIDA 2001). The presence is probably a synapomorphy of the genera in question and not a groundplan feature of the order.

As pointed out in BEUTEL & GORB (2001) it is likely that the acquisition of flight organs was an important trigger for the evolution of attachment structures. Nevertheless, they were almost certainly absent in the groundplan of Pterygota. The claw pads, which occur in Ephemeroptera are likely autapomorphic for this group, and attachment devices are absent in Odonata. Claw pads of a different type have evolved in Amblycera and Ischnocera (partim). In contrast to the condition in Ephemeroptera (BEUTEL & GORB 2001: fig. 4B) they are paired and not simple membranous extensions of the claws, but distinctly separated from them (BEUTEL & GORB 2001: fig. 3J).

The most widespread attachment device in insects is the arolium. It occurs in Plecoptera and most other lineages of non-palaeopteran Pterygota. Nevertheless, the presence was not assigned to the groundplan of Neoptera in our analysis. In contrast to a strict interpretation following parsimony, we assume that it is a derived groundplan feature of this clade, and was reduced several times (e.g., Blattaria partim, Mantodea, Grylloblattodea) or replaced by tarsal hairy soles (e.g., Embioptera, Dermaptera partim, Coleoptera, Megaloptera, Raphidioptera). Several parallel losses appear more plausible (especially in ground oriented or flightless forms, e.g., Embioptera, Zoraptera, Boreidae, Siphonaptera) than 3–11 independent gains, depending on character state optimization. The arolium is usually smooth on its surface, but interestingly it is densely covered with microtrichae in Mantophasmatodea.

In contrast to BEUTEL & GORB (2001) we assume that the presence of the arolium is a plesiomorphic groundplan feature of Endopterygota. It was reduced several times independently, i.e., in Coleoptera, Strepsiptera, Megaloptera, Raphidioptera (present in Neuroptera), Siphonaptera and Diptera excl. Tipulomorpha. The arolium is sometimes distinctly modified in endopterygote insects, especially within Hymenoptera (BEUTEL & GORB 2001: fig. 6F). The eversible pretarsal vesicle of thrips is also likely derived from an arolium.

The euplantulae are the attachment structures typical for several lower neopteran groups, i.e., Dictyoptera (secondarily lost in Isoptera), Phasmatodea, Orthoptera, Grylloblattodea (strongly reduced in size) and Mantophasmatodea. Like the arolium, the euplantulae of mantophasmatodeans are densely covered with microtrichiae, which is also a very atypical condition.

It is unclear whether the absence of euplantulae in Embioptera is a secondary feature. The plantulae of Dermaptera (partim) differ distinctly from the euplantulae of the other lower neopteran groups (longitudinal distally extended membranous fields; HAAS & GORB 2004: fig. 2A,C), and the presence is possibly not a groundplan feature of the order (HAAS & GORB 2004: fig. 15). Dermaptera is one of the groups with a remarkable diversity of attachment devices (plantulae, hairy tarsomere 2, tenent setae, arolium; see HAAS & GORB 2004: fig. 14). Whether the condition found in plecopterans, i.e., a narrow longitudinal membranous bulge is a preceding stage of typical pad-like euplantulae is open to question. This interpretation would be plausible if Plecoptera were the sister group of Pliconeoptera (see above).

Structures more or less closely resembling euplantulae occur in some mallophagan species, in some species of Aphididae (between tibia and tarsus), and some Mirinae (BEUTEL & GORB 2001). The phylogenetic branching pattern shows clearly that they have evolved independently several times and that they are not homologous with the typical smooth tarsal attachment pads of lower neopteran insects. Euplantulae do not occur in any group of Endopterygota.

Different types of pulvilli have obviously evolved in different lineages of Neoptera. Smooth pulvilli are present in some representatives of Aphididae and Heteroptera, in Trichoptera and in Siphonaptera, whereas hairy pulvilli occur in Lepidoptera and Diptera (partim) (BEUTEL & GORB 2001).

The broad variety of attachment structures (e.g., arolium, euplantulae, claw pads, pulvilli, fossula spongiosa, eversible pretarsal vesicle) occurring in different lineages of the well founded clade Acercaria (BSV: 4) was already emphasized in BEUTEL & GORB (2001). This is likely related to ectoparasitism in Phthiraptera and to a close association with plants in Thysanoptera and hemipteran groups. The fossula spongiosa (Piratinae) and the eversible pretarsal vesicle (Thysanoptera) (HEMING 1970) are unique structures within Hexapoda.

Hairy soles of tarsomeres are another major type of attachment device. As already pointed out above, they have doubtlessly evolved several times independently. They occur in the lower neopteran groups Embioptera and Dermaptera, arguably as a result of convergency. They have evolved within Strepsiptera. The presence in males of Stylopodia (see above) is likely related to the necessity to attach to females parasitising pterygote hosts (POHL & BEUTEL 2005). Hairy soles are also widespread in Coleoptera. They are also present in two of the three neuropterid orders, but are absent in Neuroptera. Whether they belong to the groundplan of a Coleoptera-Neuropterida clade is open to question.

Another hairy attachment device, which does only occur in Nematocera excl. Tipulomorpha and in Tabanoidea (BEUTEL & GORB 2001) is an extended empodium. Structurally it resembles the hairy pulvilli of Diptera excl. Tipulomorpha (BEUTEL & GORB 2001: fig. 7A) and it is likely that it functions in very similar manner.

Plantar lobes are an unusual type of smooth tarsal attachment structure occurring only in Hymenoptera. They are likely an autapomorphy of the order with secondary reduction in Apocrita (BEUTEL & GORB 2001). The condition in Xyelidae (Fig. 5) shows that they are probably not homologous with tarsal thorns (or "lower neopteran" euplantulae), but have formed de novo as broad cuticular duplicatures of the ventral side of the tarsomeres.

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Appendix 1: general list of characters for phylogenetic analysis

For complete references see BEUTEL & GORB (2001); for attachment pad characters see chapter 4. The presumably plesiomorphic condition is coded as 0 even though this traditional convention is inconsequential in cladistic analyses with a posteriori polarity assessment. Characters added to those used in BEUTEL & GORB (2001) are indicated by (N [= new]); omitted characters are in brackets; character numbers from BEUTEL & GORB (2001) corresponding with new character numbers here are marked as B&G.

A. Characters of adults

A.1. Head

1. (1. B&G) Tagmata: (0) caput and postcephalic body; (1) caput, thorax, abdomen.
2. (2. B&G) Ocelli: (0) present; (1) absent. Present in Collembola (maximum 6) and stem-lineage representatives of Dermaptera. Absent in Mantophasmatodea.
3. (3. B&G) Temporal organs (Tömösvary's organ): (0) present; (1) absent.
4. (4. B&G) Postocciput and pleural folds: (0) well developed; (1) reduced.
5. (N) Proboscis (rostrum) formed by elongation of clypeal region: (0) absent; (1) present. Present in the mecopteran taxa under consideration. Only slightly elongated in some representatives of the order (e.g., *Nannochorista* [coded as 1], *Brachypanorpa*; HEPBURN 1969).
6. (5. B&G) Postoccipital suture: (0) incomplete; (1) complete dorsally.
7. (6. B&G) Linea ventralis: (0) absent; (1) present.
8. (7. B&G) Hypopharyngeal fultura: (0) present; (1) absent.
9. (8. B&G) Superlinguae: (0) present; (1) absent. Coded as inapplicable for Strepsiptera (BEUTEL & POHL 2005).
10. (9. B&G) Tentorial bridge: (0) absent; (1) present. Present in Mantophasmatodea. Absent in Diptera (0) (HENNIG 1973) and inapplicable in Strepsiptera (BEUTEL & POHL 2005).
11. (10. B&G) Perforation of metatentorium: (0) absent; (1) present. Absent in Mantophasmatodea. Inapplicable for Diptera and Strepsiptera.
12. (N) Ventral head retractor with origin from proxoca: (0) absent; (1) present. Present in Amphimenoptera (KRISTENSEN 1991).
13. (11. B&G) Cephalic ligamentous endoskeleton: (0) present; (1) absent (KRISTENSEN 1991, 1997). The ligamentous endoskeleton of *Tricholepidion* does not only comprise a lamellar tendon connecting the transverse mandibular muscle (see character 22) but also elements associated with maxillary muscles (KRISTENSEN 1997).

- 14.** (12. B&G) Gula: (0) absent; (1) present. Absent in Mantophasmatodea and in the groundplan of Phasmatodea.
- 15.** (13. B&G) Opening of the salivary glands in a midventral groove of the labium: (0) absent; (1) present (BITSCH & BITSCH 1998).
- 16.** (14. B&G) Antenna: (0) all antennomeres except ultimate muscular; (1) non-muscular flagellomeres; (2) absent.
- 17.** (15. B&G) Rupture-facilitating cuticle modification of antennal flagellum: (0) absent; (1) present.
- 18.** (16. B&G) Johnston's organ of second antennomere: (0) absent; (1) present.
- 19.** (17. B&G) Mouthparts: (0) ectognathous; (1) entognathous, maxillae and mandibles hidden in separate gnathal pouches; (2) entognathous, maxillae and mandibles hidden in single gnathal pouch (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.
- 20.** (18. B&G) Mandibular articulation: (0) primary joint only; (1) secondary joint present as a gliding device; (2) secondary articulation present as ball-and-socket joint (FÜRST VON LIEVEN 2000; STANICZEK 2000). Secondary joint present and developed as a ball and socket joint in basal Strepsiptera (coded as 2). Mandibles reduced in Trichoptera and transformed into sucking stylets in several groups (coded as -).
- 21.** (19. B&G) Function of mandibles: (0) biting; (1) both mandibles piercing, stylet-like; (2) only left mandible stylet-like, right mandible reduced; (3) not involved in feeding. Not involved in feeding in Strepsiptera, probably used for opening the puparium.
- 22.** (20. B&G, modified; see STANICZEK 2000) Transverse mandibular muscle (*M. tentorio-mandibularis externus ventralis*) without connection to anterior tentorial arms: (0) present; (1) absent or origin shifted to anterior tentorial arms.
- 23.** (21. B&G) Cardo: (0) present; (1) strongly reduced or absent. Absent in Strepsiptera (e.g., BEUTEL & POHL 2005).
- 24.** (22. B&G) Insertion of lacinia: (0) on stipes; (1) detached from stipes. Inapplicable for Strepsiptera.
- 25.** (23. B&G) Lacinia: (0) not distinctly elongated and slender, with mesally directed hairs; (1) elongate and slender, mesally directed setae absent. Slender, acuminate and without mesally directed setae in Acercaria and Zoraptera (BEUTEL & WEIDE 2005).
- 26.** (24. B&G) Maxillary palp: (0) as long as thoracic legs; (1) distinctly shorter.
- 27.** (25. B&G) Labial rostrum: (0) absent; (1) present.
- 28.** (26. B&G) Labial palps: (0) 3-segmented or less; (1) 4-segmented; (2) absent.
- 29.** (27. B&G) Fully sclerotized floor of the sucking pump: (0) present; (1) absent (KRISTENSEN 1999)
- 30.** (28. B&G) Cibarial water-vapor uptake apparatus: (0) present; (1) absent (RUDOLPH & KNÜLLE 1982). [29. B&G: Mandibulo-hypopharyngeal muscle: (0) absent; (1) present. The character is omitted as the muscle was obviously lost several or many times independently in pterygote insects.]
- 31.** (30. B&G) *M. tentoriomandibularis*: (0) composed of several components; (1) only one bundle or absent. Only one bundle in Zoraptera (BEUTEL & WEIDE 2005) and Mantophasmatodea.
- 32.** (31. B&G) *M. stipitalis transversalis*: (0) present; (1) absent. Absent in Zoraptera (BEUTEL & WEIDE 2005) and Mantophasmatodea.
- 33.** (32. B&G) Dorsal flexor of paraglossa: (0) absent; (1) present. Absent in Zoraptera (BEUTEL & WEIDE 2005) and Mantophasmatodea.
- 34.** (33. B&G) Cibarial dilators (*M. clypeopalatalis*): (0) normally developed; (1) large. Normally developed in Mantophasmatodea and unusually large in Zoraptera (BEUTEL & WEIDE 2005) and Acercaria.
- 35.** (N) Subcomponent of *M. clypeopalatalis* with single median tendon attached to epipharynx: (0) absent; (1) present. Present in Thysanoptera (MICKOLEIT 1963) and Psocodea (BADONELL 1943; RISLER 1954; BUCKUP 1957).
- 36.** (34. B&G) Ampullo-ampullary and accessory ampullary muscles attached to aorta: (0) absent; (1) present (PASS 1991, 1998, 2000). Absent in Zoraptera (BEUTEL & WEIDE 2005) and Mantophasmatodea.

A.2. Thorax

- 37.** (35. B&G) Pronotum: (0) not saddle-like; (1) saddle-like.
- 38.** (36. B&G) Scutellum: (0) absent; (1) present (KRENN 1993). Not recognisable as a separate sclerite in Mantophasmatodea.
- 39.** (37. B&G) Number of legs: (0) more than 3 pairs; (1) 3 pairs.
- 40.** (38. B&G) Tarsus: (0) undivided; (1) 2 tarsomeres; (2) 3 tarsomeres; (3) 4 tarsomeres; (4) 5 tarsomeres.
- 41.** (39. B&G) Pretarsus: (0) retained as a small, separate sclerite and attached claws; (1) separate sclerite reduced.
- 42.** (40. B&G) Claws: (0) single; (1) double.
- 43.** (41. B&G) Jumping legs: (0) absent; (1) with enlarged femur; (2) with enlarged coxa.
- 44.** (42. B&G) Wings: (0) absent; (1) present.
- 45.** (43. B&G) Wing base: (0) without folding lines; (1) folding lines present.
- 46.** (44. B&G) Axillary I: (0) no attachment of pleural muscle; (1) attachment of pleural muscle (HENNIG 1969).
- 47.** (45. B&G) Median plate: (0) undivided; (1) diagonally divided.

- 48.** (46. B&G) Costal cross veins: (0) more than 5; (1) less than 5.
- 49.** (47. B&G) Hind wing vannus: (0) not enlarged; (1) distinctly enlarged.
- 50.** (48. B&G) Folding of vannus: (0) few anal veins, not pleated; (1) pleated (e.g., WHITING et al. 1997). It was pointed out by K.-D. Klass (pers. comm.) that a pleated vannus does also occur in representatives of Plecoptera. The character was coded as 0 for the order in this contribution.
- [**49.** B&G: Jugal bar (0) absent; (1) present. The jugal bar or sclerite, a potential synapomorphy of Paraneoptera (or Acercaria) and Endopterygota, is not well documented. It is therefore excluded from the analysis.]
- 51.** (50. B&G) Sclerotization of fore wings: (0) absent; (1) moderately sclerotized tegmina; (2) strongly shortened, sclerotized tegmina; (3) elytra with epipleurae.
- 52.** (51. B&G) Halteres: (0) absent; (1) on mesothorax; (2) on metathorax.
- 53.** (52. B&G) Pronounced precostal field: (0) absent; (1) present (WHITING et al. 1997).
- 54.** (53. B&G) Posterior notal wing process: (0) unspecialized, no insertion of pleural muscles; (1) specialized, insertion of pleural muscle.
- 55.** (54. B&G) Head of axillary I: (0) not enlarged; (1) distinctly enlarged and cranially truncate; (2) enlarged with distal process (HÖRNSCHEMEYER 1998).
- 56.** (55. B&G) Caudal process of axillary II: (0) absent; (1) present (HÖRNSCHEMEYER 1998).
- 57.** (56. B&G) Leg- and wing tracheae: (0) not connected with following spiracle; (1) connected with following spiracle.
- 58.** (57. B&G) Epimeral apophysis: (0) present; (1) absent.
- [**58.** B&G: Mm. furco-pleurocostales III (MATSUDA 1970: p-s 1 III): (0) present; (1) absent (BEUTEL & HAAS 2000). This character is not documented for basal strepsipterans and several other taxa and parallel losses have obviously taken place. The character is therefore excluded.]
- [**59.** B&G: M. scutello-postnotalis III (MATSUDA 1970: t 13 III): (0) present; (1) absent (BEUTEL & HAAS 2000). See previous character.]
- 59.** (60. B&G) Proventriculus: (0) absent or without prominently elongated acanthae; (1) with close-set, prominently elongated acanthae (KRISTENSEN 1991). Acanthae are absent in Mantophasmatodea (KLASS et al. 2005).
- 60.** (61. B&G) Mid-ventral ostia: (0) absent; (1) present (NUTTING 1951; KRISTENSEN 1991). Unknown for Mantophasmatodea and basal Strepsiptera.
- 61.** (62. B&G) 'Link plates' adjacent to thoracic spiracles: (0) absent; (1) present.
- 62.** (63. B&G) Dorsal pulsatile diaphragms: (0) absent; (1) paired separate; (2) unpaired separate; (3) attached single (PASS 1998, 2000).

A.3. Abdomen

- 63.** (64. B&G) Transverse suture of abdominal tergum I: (0) absent; (1) present.
- 64.** (65. B&G) Caudally bifid mediolongitudinal suture of tergum I: (0) absent; (1) present.
- 65.** (66. B&G) Occlusor muscles inserting directly on abdominal spiracular sclerites: (0) absent; (1) present.
- 66.** (67. B&G) Abdominal coxal vesicles: (0) present on segments II–VII; (1) on ventral tube of segment I; (2) not more than 2 posterior coxal vesicles.
- 67.** (68. B&G) Styli: (0) present; (1) absent from segment II or completely reduced.
- 68.** (69. B&G) Cerci: (0) present; (1) strongly reduced or absent.
- 69.** (N) Specific articulation of cerci: (0) absent; (1) present. Present in *Zygentoma* (incl. *Tricholepidion*; M. Koch pers. comm.).
- 70.** (70. B&G) Malpighian tubules: (0) numerous, more than 8; (1) 4–8; (2) strongly reduced Malpighian ampullae; (3) 3 tubules; (4) one pair. More than 8 in Hymenoptera. Numerous in Mantophasmatodea (KLASS et al. 2005).
- 71.** (71. B&G) Abdominal spiracles: (0) present; (1) absent.
- 72.** (72. B&G) Ovipositor: (0) absent; (1) with well developed, elongate gonapophyses VIII and IX, ovipositor sheath formed by 3rd valvulae (gonocoxite + stylus IX) present or absent; (2) reduced. Well developed in Mantophasmatodea (KLASS et al. 2003). The coding as either absent (0) or reduced (2) is arguably problematic (K.-D. Klass pers. comm.). Even though it is very likely that the ovipositor is secondarily lost in Ephemeroptera (coded as 2 here), the complete absence in females of this order is structurally not different from the absence in dipturans or proturans. The character was coded as 1&2 for some polymorphic taxa (e.g., Thysanoptera, Heteroptera) but as 1 for others (e.g., Isoptera). In the case of termites it is very likely that an ovipositor is present in the groundplan considering the subordinate position within Blattaria (KLASS 1997; KLASS & MEIER 2006).
- 73.** (73. B&G) Gonangulum: (0) absent; (1) present. Present in Mantophasmatodea (KLASS et al. 2003).
- 74.** (74. B&G) Third pair of valves: (0) not fused; (1) fused, with internal musculature.
- 75.** (75. B&G) Genital appendages IX of female: (0) gonocoxite not fused with stylus base into a sensory appendage; (1) gonocoxite fused with stylus base into a sensory appendage, gonapophyses absent (MICKOLEIT 1973).
- 76.** (76. B&G) Terminal filament: (0) strongly reduced or absent; (1) well developed.
- 77.** (77. B&G) Genital pocket with large subgenital plate derived from sternum VIII: (0) absent; (1) present.

[78. B&G: Moveable lobes of subgenital plates: (0) present; (1) absent. This character was excluded as it is only applicable for taxa with a subgenital plate formed by sternite VII, i.e. Dictyoptera and Dermaptera.]

78. (N) Asymmetric phallomere complex with phallomere gland only on left side: (0) absent; (1) present. The presumably derived condition is found in Dictyoptera (KLASS 1997).

79. (N) Dorsal and ventral fusion of basistyli: (0) absent; (1) present. The fusion of basistyli was considered as a potential autapomorphy of Mecoptera by WILLMANN (2005).

80. (79. B&G) Sperm pump with sclerotised elements: (0) absent or unspecific muscular coat of sperm ducts; (1) present, pistilliform type; (1) present, of dipteran type; (2) present, of siphonapteran type (see HÜNEFELD & BEUTEL 2005). It was demonstrated in HÜNEFELD & BEUTEL (2005) that the sperm pumps of Mecoptera (excluding Boreidae and Nannochoristidae) (= pistilliform type), Diptera (absent in Culicomorpha) and Siphonaptera are not homologous. The sperm transmission apparatus of Strepsiptera lacks any sclerotised parts.

81. (80. B&G) Abdominal ganglia: (0) more than 2 separate ganglia; (1) 2 separate ganglia; (2) one single ganglionic mass; (3) ganglia 2–5 form an elongated tractus; (4) partly fused with thoracic ganglia, rest of abdominal ganglia form one complex. The anterior abdominal ganglia are fused with the thoracic ganglia in Strepsiptera. The rest forms one undivided complex (POHL 2005).

82. (81. B&G) Ovaries: (0) sac-shaped, not divided into ovarioles; (1) subdivided into ovarioles (ŠTYS & BILIŃSKI 1990).

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

B. Larval characters

B.1. Head

84. (83. B&G, modified) Stemmata: (0) absent; (1) present. True stemmata are present in the endopterygote orders excluding basal Hymenoptera (coded as 0) and Mecoptera (MELZER et al. 1994; KRISTENSEN 1999).

85. (N) Appearance of compound eyes: (0) before ultimate immature stage; (1) in ultimate immature stage. The compound eyes appear before the penultimate life stage (pupa) in non-endopterygote insects and in Strepsiptera (H. Pohl pers. comm.).

86. (N) Ocelli: (0) present; (1) absent. The larval ocelli are absent in all endopterygote larvae (KRISTENSEN 1991) and also in immature stages of Acercaria (ROSS 1955; HENNIG 1969) (ocellar Anlagen present in Psocoptera; MOCKFORD 1987). According to GURNEY (1938) they occur in nymphal Zoraptera, but are absent in nymphs of the wingless morphs (coded as 0). They are also absent in immature stages of Zygentoma (excl. *Tricholepidion*), Isoptera, Grylloblattodea, Phasmatodea (partim), Dermaptera and Embioptera, and in some representatives of Orthoptera.

87. (84. B&G) Stipes: (0) undivided; (1) divided into basistipes and dististipes.

88. (85. B&G) *M. craniocardinalis*: (0) present; (1) absent.

89. (86. B&G) *M. craniodististipitalis*: (0) absent; (1) present (KRISTENSEN 1991).

90. (87. B&G) Larval labial glands: (0) no silk production; (1) silk production (KRISTENSEN 1999).

B.2. Thorax

91. (88. B&G) Thoracic legs: (0) present; (1) absent.

92. (89. B&G, modified) External wing buds: (0) present; (1) absent. External wing buds are absent from most strepsipteran larvae (KINZELBACH 1971a,b; KINZELBACH & POHL 2005; KRISTENSEN 1991, 1999) and larvae of all other groups of Endopterygota, but are present in the secondary larvae of the basal strepsipteran family Mengenillidae (coded as 0 for Strepsiptera).

93. (90. B&G) Claws: (0) double; (1) single.

B.3. Abdomen

94. (N) Segment XI: (0) present; (1) absent. Present in some groups of hemimetabolous insects (e.g., Embioptera, Orthoptera, Phasmatodea) and well developed in first instar larvae of Strepsiptera (POHL 2000). Absent in all other groups of Endopterygota. Arguably, the character should be only used for either hemimetabolous nymphs or holometabolous larvae, as the comparability between these immature stages is not unproblematic (see, e.g., GRIMALDI & ENGEL 2005). Besides this, it is often difficult to decide, which parts of the posterior abdomen belong to segment X or XI (K.-D. Klass pers. comm.; KLASS 2001).

95. (N) Cerci: (0) present; (1) absent. Present in most groups of hemimetabolous insects and in first instar larvae of Strepsiptera (POHL 2000). Absent in all other groups of Endopterygota.

[91. B&G: Terminal filament: (0) present; (1) absent. It is likely that this structure was reduced in the adult and larval stage simultaneously. Therefore the character is excluded.]

C. Characters of reproduction and development

96. (92. B&G) Heterogametic sex: (0) males (xy); (1) females (zw).

97. (93. B&G) Amniotic cavity: (0) absent; (1) open; (2) at least temporarily closed (KRISTENSEN 1997; WHITING et al. 1997; LARINK 1997).

98. (94. B&G) 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.

99. (95. B&G, modified) Sperm conjugation: (0) absent; (1) head-to-head fusion (binucleated); (2) paired; (3) sperm aggregates. This character was recoded for *Zygentoma* in agreement with DALLAI et al. (2004).

100. (96. B&G) Oblique implantation fossa: (0) absent; (1) present (JAMIESON 1987).

101. (97. B&G) Double anterior axonemal cylinder: (0) absent; (1) absent (JAMIESON 1987).

102. (98. B&G) 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).

103. (N) Additional outer singlets of sperm axoneme: (0) absent; (1) present. The $9 + 9 \times 2 + 2$ pattern occurs in Diplura (BACETTI & DALLAI 1973; DALLAI 1988), Archaeognatha, *Zygentoma* (DALLAI et al. 2004) and Ephemeroptera (central microtubule absent) and in most other pterygote lineages (JAMIESON 1987). They are absent in Siphonaptera and Mecoptera (examined in *Panorpa* and *Bittacus*), and some representatives of Trichoptera and Diptera (e.g., Tipulomorpha) (JAMIESON 1987).

104. (99. B&G) Cleavage: (0) total and equal; (1) early total cleavage followed by superficial cleavage; (2) superficial cleavage (BITSCH & BITSCH 1998). Superficial cleavage in Collembola after the 8 cell stage.

105. (100. B&G) Egg cocoon: (0) absent; (1) present.

106. (101. B&G) Postembryonic development: (0) anamorphic; (1) epimorphic.

107. (102. B&G) Pupal stage: (0) absent; (2) present.

108. (103. B&G) Imaginal moult: (0) present; (1) absent.

109. (104. B&G) Larvae: (0) terrestrial; (1) aquatic.

110. (105. B&G) Maternal broodcare: (0) absent; (1) present. MATZKE & KLASS (2005) compared broodcare in Embioptera and basal Dermaptera and came to the conclusion that the conformities are unspecific and that homology in the two taxa is questionable.

Appendix 2: Character state matrix (continued)

Table with columns labeled 81-120 and rows labeled with taxa names like Chilopoda, Symphyla, Diptera, etc. The cells contain numerical values or symbols representing character states.

