

Evolution of attachment structures in the highly diverse Acercaria (Hexapoda)

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Running title: Evolution of Attachment Structures

Abstract

Acercaria display an unusually broad array of adhesive devices occurring on different parts of the legs. Attachment structures of all major subgroups are described and illustrated. Nineteen characters of the distal leg region were combined with a data matrix containing 99 additional morphological characters of different body parts. The results of the cladistic analysis are largely congruent with current hypotheses. Zoraptera are not retrieved as close relatives of Acercaria. The monophyly of the entire lineage and of the major subgroups Psocodea, Phthiraptera, and Hemiptera is confirmed. Our data also support the monophyly of Auchenorrhyncha and a sistergroup relationship between Thysanoptera and Hemiptera (Condylognatha). In contrast to other lineages of insects the hairy type of adhesive devices is only present in one group within the Acercaria (Heteroptera, Cimicomorpha). The arolium is present in the groundplan but missing in several groups (e.g., Psocodea, Cicadoidea, Aphidoidea). Pretarsal pulvilli evolved several times independently. Tarsal euplantulae and different specialized clasping devices have evolved within Phthiraptera, whereas pretarsal attachment devices are missing in this ectoparasitic group. The potential to modify pretarsal attachment devices in their structural details has likely contributed to the very successful diversification of the predominantly phytophagous Hemiptera.

Introduction

Acercaria was introduced by Börner (1904) for a hemimetabolous lineage comprising “Psocoptera” (bark lice), Phthiraptera (true lice), Thysanoptera (thrips) and Hemiptera (bugs). Hennig (1969) considered Zoraptera (ground lice, angel insects) as its sister taxon and referred to the more inclusive lineage as Paraneoptera. Today, polyneopteran affinities of Zoraptera become more and more evident (e.g., Wheeler et al., 2001; Blanke et al., 2012; see also Trautwein et al., 2011), and Aceraria (e.g., Börner, 1904; Seeger, 1975; Kristensen, 1981) and Paraneoptera (e.g., Yoshizawa and Saigusa, 2001; Grimaldi and Engel, 2005) are used for the “hemipteroid assemblage” by different authors. To avoid confusion we will consistently use the former term, which is also less ambiguous.

With more than 100.000 described species Acercaria are an extremely diverse and successful lineage of insects. The group is characterized by a very broad spectrum of feeding habits. It comprises detritovores (mainly “Psocoptera”), highly specialized ectoparasites (Phthiraptera), miniaturized forms feeding on fungi or algae (Phlaeothripidae), numerous species feeding on plant saps (major part of Thysanoptera and Hemiptera), and also predators (which are restricted to several lineages of Heteroptera). Blood feeding on vertebrates evolved twice in Acercaria. Once in Phthiraptera (Anoplura and Rhynchophthirina) and at least three times in Heteroptera (Cimicidae, Reduviidae and Rhyparochromidae (Schuh and Slater, 1995)). Acercaria are also extremely versatile in their habitat choices. Numerous species move efficiently on plant surfaces (e.g., Gorb et al., 2001) but there are also highly specialized semiaquatic and aquatic lineages (Gerromorpha, Nepomorpha), groups specialized on leaf litter and soil or subcortical habitats, and ectoparasites adapted to feathers or hairs of their warm-blooded vertebrate hosts (e.g., Weber, 1969; Grimaldi and Engel, 2005).

With the necessity to cope with a broad spectrum of different surfaces a tremendous variety of attachment devices has evolved in Acercaria. Within the group the structure and function of attachment devices have been investigated in detail for a few selected species, such as

the planthopper *Lycorma delicatula* (Frantsevich et al., 2008), several aphids (e.g., Carver and White, 1971; Lees and Hardie, 1988; Dixon and Croghan, 1990), the true bug *Pameridea roridulae* (Voigt and Gorb, 2008), and the head louse *Pediculus humanus* (Cruz and Mateo, 2009). A systematic investigation of the pretarsal and tibial structures of Reduviidae and Miridae (Heteroptera) has been carried out by Weirauch (2005, 2007) and Schuh (1976), respectively. For summary of cimicomorphan attachment devices see Schuh et al. (2009).

So far adhesive devices of basal representatives of the subgroups of Acercaria have received little attention. A comprehensive comparative study of pretarsal structures of all major lineages is still missing. Especially the subgroups of Sternorrhyncha and Psocoptera have been largely neglected. In most available studies only one representative of one of the four lineages of Sternorrhyncha was included, even though these groups are morphologically highly heterogeneous.

Information on the tarsal and pretarsal morphology of Acercaria is scattered in the literature. An additional problem is the inconsistent nomenclature. Some authors refer to any kind of pretarsal attachment structure as arolium. For *Lygus hesperus* (Miridae), for instance, Shrestha (2007) disregards the commonly used nomenclature (see e.g., Beutel and Gorb, 2001) and refers to the attachment structures as arolia. However, his figures show clearly that these paired structures are in fact pulvilli. Another inappropriate term that persists is “dorsal arolium” (e.g.; Cobben, 1978; Schuh and Slater, 1995; Schuh and Polhemus, 2009) even though this structure is clearly not an attachment device, but a peg-like or trichiform structure, and most likely a sensillum (=dorsomedian sensillum after Weirauch, 2005).

The monophyly of Acercaria seems to be well supported by morphological characters (Beutel and Gorb, 2001, 2006; Hennig 1969; Kristensen, 1981, 1991), even though it is frequently rejected by molecular data (e.g, Yoshizawa and Johnson, 2005; Ishiwata et al., 2011). The monophyly of the major subgroups Psocodea (parasitic Phthiraptera and free living “Psocoptera”) (Seeger, 1975; Rudolph and Knülle, 1982; Lyal, 1985) and Hemiptera (e.g.,

Kristensen 1981; Cryan and Urban, 2012) is also well supported. A sistergroup relationship between Liposcelididae and the true lice appears also well established based on morphological (Lyal, 1985) and molecular data (Yoshizawa and Johnson, 2003; Johnson et al. 2004). However, what is still disputed is the monophyly of the true lice (Amblycera, Ischnocera, Rhynchophthirina and Anoplura) (Barker et al. 2003 (small subunit rDNA); Johnson et al., 2004 (18S rDNA)), the placement of Thysanoptera (Condylognatha vs Micracercaria; e.g., Yoshizawa and Saigusa, 2001; see also Willmann (2005) and Grimaldi and Engel (2005)), the interrelationships of the hemipteran subgroups, and the monophyly of Auchenorrhyncha (e.g., Campbell et al., 1995; Cryan and Urban, 2012).

Despite considerable recent progress in the phylogenetic investigation of Acercaria (e.g., Cryan and Urban, 2012; Johnson et al., 2004, Yoshizawa and Johnson, 2003), a phylogenetic study covering all major lineages and a broad spectrum of morphological characters was still wanting. It is one aim of this study to provide a character set allowing a formal analysis of acercarian relationships, independent from molecular data which are already available (e.g., Johnson et al., 2004 [focused on Phthiraptera]; Cryan and Urban, 2012 [focused on Hemiptera]) or will be available in the near future (see Acercaria subproject of 1KITE: www:1KITE.org). However, the main focus lies on the evolution of attachment structures in Acercaria. Our goal is to describe and document the attachment devices of representatives of all the major lineages and to develop an evolutionary scenario for the relevant structures based on a cladistic analysis of characters of all body parts (see appendix 1). Taxa were chosen for their (presumably) basal phylogenetic position. All figures show the attachment structures of females. Future phylogenetic analyses based on extensive molecular data (transcriptomes; see www:1KITE.org) will provide a robust basis for testing the hypotheses we present in this study.

Methods

Scanning electron microscopy (SEM)

For scanning electron microscopy (Philips XL30 ESEM), specimens were completely dehydrated with ethanol (100%) over several stages, dried at the critical point (Emitech K850; Emitech) or treated with HMDS (Hexamethyldisilazane; Brown, 1993), sputter-coated with gold (Emitech K500, Ashford, Kent, UK), and fixed on a rotatable specimen holder (Pohl, 2010). Scandium software (Soft Imaging System, Münster, Germany) was used for obtaining high resolution images.

Cladistic analysis

We analyzed 118 characters of the head, thorax, abdomen and attachment structures (of the midlegs) of 25 representatives of *Acercaria* plus 8 outgroup taxa. Winclada 1.00.08 (Nixon, 1999) was used for entering the data in a matrix and NONA (Goloboff, 1999) and TNT (Goloboff et al., 2008) for calculating minimum length trees (Ratchet, search settings: 1000 replicates, characters non-additive, non-weighted). Branch support values (Bremer, 1994) were calculated with the function implemented in TNT.

Glossary The terms used here are in accordance with the definitions of Dashmann (1953) and Beutel and Gorb (2001).

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.

Arolium: the median lobe between the claws of the pretarsus. It can be completely membranous or at least partly sclerotized.

Auxiliae: lateral sclerites beneath the bases of the claws.

Claws: hollow, multicellular, movable structures which articulate dorsally at the distal end of the tarsus.

Empodium: a median process between the pulvilli. It arises from the distal end of the of the unguitactor plate, is spine-shaped or lobe-like and is often similar in form to the pulvilli.

Euplantulae: flexible pad-like structures without hairs on the ventral side of one or more tarsomeres.

Manubrium: 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.

Parempodia: bristle-like or fleshy appendages of the distal part of the unguitactor plate.

Planta: distal part of an unguitactor plate which is divided into two sclerites.

Pretarsus: the terminal part of the hexapod leg, closely associated with the distal end of the terminal tarsomere.

Pulvilli: smooth or hairy paired lateral membranous lobes ventral to the claws. They are located on the auxiliae, which participate in control of pulvillar movements.

Tarsus: the distal part of a hexapod leg.

Unguitractor plate: median basal plate of the ventral surface of the pretarsus to which the unguitactor apodeme is attached. It is usually invaginated into the end of the terminal tarsomere. Its surface is highly variable.

Examined Taxa:

Auchenorrhyncha:

Cicadomorpha:

Cercopidae, *Philaenus spumarius* (L., 1758), *Cercopis vulnerata* (Rossi, 1807).

Cicadoidea: Cicadidae, *Cicadetta montana* Scopoli 1772.,

Membracoidea: Membracidae, *Centrotus cornutus* (L., 1758). Cicadellidae, *Cicadella viridis* (L., 1758)

Fulgoromorpha:

Cixiidae, *Cixius* sp., Delphacidae, *Javasella* sp., *Dictyophora europaea* (L. 1767)

Coleorrhyncha:

Peloridiidae, *Hackeriella veitchi* (Hacker 1932).

Heteroptera

Dipsocoromorpha: Dipsocoridae, *Ceratocombus australiensis* Gross, 1950, Schizopteridae, *Corixidea* sp.

Enicocephalomorpha: Enicocephalidae, *Systelloderes* sp.

Pentatomomorpha: Pentatomidae, *Graphosoma lineatum* (L., 1758), *Pentatoma rufipes* (L., 1758)

Psocodea

“Phthiraptera”:

Amblycera: Menoponidae, *Trinoton anserinum* (Fabricius (J.C.), 1805)

Anoplura: Pediculidae, *Pediculus humanus capitis* L., 1758, *Pediculus humanus corporis* L., 1758; *Phthirus pubis* L., 1758.

Ischnocera: Trichodectidae, *Trichodectes melis* (Fabricius (J.C.), 1805); Philopterae, *Columbicola* sp.

Rhynchophthirina: Haematomyzidae, *Haematomyzus elephantis* (Piaget, 1869)

“Psocoptera”:

Psocomorpha: Caeciliidae, *Caecilius flavidus* (Stephens, 1830)

Troctomorpha: Liposcelididae, *Liposcelis* sp., *Embiopsocus* sp.

Trogiomorpha, Trogidae, *Cerobasis* sp.

Sternorrhyncha

Aleyrodoidea: Aleyrodidae, *Aleyrodes* sp.

Aphidoidea: Drepanosiphidae, *Drepanosiphum plantanoides* (Schrank, 1801). Aphididae, *Microsiphum* sp.

Coccoidea: Pseudococcidae, *Pseudococcus* sp. Coccidae, *Coccus* sp.

Psylloidea: Psyllidae, *Cacopsylla* sp.

Thysanoptera

Terebrantia: Thripidae, *Frankliniella* sp.

Zoraptera

Zorotypidae: *Zorotypus weidneri* New, 1978

Outgroups:

Hymenoptera, Xyelidae: *Xyela* sp.

Neuroptera, Nevrorthidae, *Nevrorthus* sp.

Orthoptera, Caelifera, Acridiidae: *Locusta migratoria* (L., 1758)

Orthoptera, Ensifera, Tettigoniidae: *Tettigonia viridissima* (L., 1758)

Odonata, Gomphidae, *Ictinus angulosus selys*, Selys, 1854.

Plecoptera, Nemouridae, *Nemoura cinerea*, Latreille 1796

Results

Tarsal morphology

Auchenorrhyncha (Figs. 1, 2)

Fulgoromorpha, Cixiidae and Delphacidae (Figs. 1C, J, K)

The tarsi of all examined species are 3-segmented and an arolium (ar, Fig. 1C) is present. In delphacids two strong bristles (Weirauch, 2005: guard setae) are inserted dorsally on the distal part of the tarsus.

In *Cixius* sp. the distal tarsomere of the fore- and midlegs is slightly longer than the others, whereas in the hindleg the proximal tarsomere is almost three times as long as the two distal ones. The apices of the two basal segments each bear two thick bristles. The unguitactor plate of *Cixius* sp. (Fig. 1J) and *Javasella* sp. (Fig. 1K) is characterized by a washboard-like

surface. It is subdivided into small sclerotized platelets in 3 columns and 16 rows in *Cixius* sp., whereas they are arranged in 2 columns and 7 rows in *Javasella* sp..

Cicadomorpha

Membracoidea, Membracidae and Cicadellidae (Figs. 1B, D, G, H.)

The tarsi are 3-segmented. The proximal segment is the smallest. The dorsal side of the pretarsus appears scaly. A bilobed arolium (bar, Figs. 1B, D) is present. The arolium is largely fused with the claws. Only the tip of the claw is free. The surface of the unguitactor plate appears scaly (Figs. 1G, H). In *Centrotus* the entire dorsolateral region of the pretarsus is strongly sclerotized (dls, Fig. 2C). Medially adjacent to this sclerotized area is a large plate-like sclerite (ms, Fig. 2C). A sensillum (sen, 1D) protrudes at the inner distal corner of this structure. No sclerites are present on the ventral side of the pretarsus. In *Cicadella* the dorsolateral regions of the arolium are also heavily sclerotized. The medial sclerites (ms, Fig. 2D) are present, but triangular and much smaller than those of *Centrotus*. These sclerites also bear a sensillum (sen, Fig. 1B). The sensilla in *Cicadella viridis* appear more delicate than those of *Centrotus cornutus*.

Cicadoidea, Cicadidae (Fig. 1A)

The tarsi are 3-segmented. No specific attachment structures are present in *Cicadetta montana*. A single sensillum is present between the claws. Whether this sensillum is homologous with the “dorsal arolium” of enicocephalids is unclear. Three thick bristles are arranged in a row on the ventral base of the claws. Ventrally the tarsomeres are densely covered with short setae. Additionally, a long and thin sensillum is present on the ventral side of the first and third tarsomere.

Cercopoidea, Cercopidae (Figs. 1E, F; 2A, B)

The tarsi are 3-segmented. An arolium is present. It is medially distinctly incised. A protrusion with a vestiture of microtrichia (mt, Figs. 1E, F) is present on the distolateral region of the

arolium, directly below the claws. A sclerotized bar bearing 3 to 4 thick bristles (sb, Figs. 1I, 2A) is present ventrolaterad of the arolium on each side of the pretarsus. Dorsally a long sclerite (dls, Fig. 2B) is directly adjacent to the claws. These dorsolateral sclerites enclose a V-shaped medial sclerite (ms, Fig. 2B). Three setae are inserted on each side of the distal part of the arms of the “V”. There are no differences between the pretarsi of *Philaenus* and *Cercopis*.

Sternorrhyncha (Fig. 3)

Coccoidea, Pseudococcidae and Coccidae (Fig. 3A)

In *Pseudococcus* and *Coccus* the tarsus is composed of one segment. Only one claw is present. On each side of the base of the claw a capitate fleshy structure (termed “claw digitule” by Cockerell [1893] and Kondo [2006]) is present. Dorsally two long slender setae with capitate ends (=tarsal digitules, tadi) are present. The structure of the claw digitules strongly suggests that they are homologous with pulvilli.

Aphidoidea, Drepanosiphidae and Aphididae (Figs. 3B, C)

The tarsi are 2-segmented. An eversible, cushion-like pad (tip, Fig. 3B) is present between the tarsus and tibia in *Microsiphum* sp. and *Aphis sambuci*. Additionally, setiform parempodia are located on the pretarsus. The pad between tibia and tarsus is absent in *Drepanosiphum* sp., but fleshy pulvilli (referred to as “empodial pads” in Kennedy [1986]) are present (pu, Fig. 3C). There is no difference in the attachment structures between winged and wingless morphs. Some species of *Neophyllaphis* bear two eversible adhesive vesicles on the posterior abdominal sternites (Carver and White, 1971).

Psylloidea, Psyllidae (Fig. 3D)

The tarsi of *Cacopsylla* are 2-segmented. A bilobed arolium (ar) is present. Three strong guard setae (gs) are present on the dorsal side of the tarsus. The distal part of the arolium is smooth, whereas the proximal part shows a rippled surface structure. Ventrally two setiform parempodia (par) arise from the unguitactor plate.

Aleyrodoidea, Aleyrodidae (Fig. 3E)

The tarsi of the examined species are 2-segmented and covered with small wax platelets like the rest of the body. Dorsally one long guard seta is present. The two claws are largely covered with microtrichia from their bases to the middle region. They are thin and their tip remains glabrous. Between them a spine-like empodium (em) approximately as long as the claws is present. The base of this structure is also covered with microtrichia. The tip is flattened and glabrous with lamellae.

Most authors follow Quaintance and Baker (1913) by referring to this medial structure as “paronychium”. However, Deshpande (1933) suggested to “treat the paronychium as an empodium rather than as a pulvillus.”

Heteropteroidea (Fig. 4)

Coleorrhyncha, Peloridiidae (Fig. 4C)

The tarsi of *Hackeriella* are 2-segmented. An arolium is present between the claws.

Enicocephalomorpha (Fig. 4A, F)

The tarsi are 2-segmented in *Systelloderes*. The distal tarsomere is about four times longer than the proximal one, and densely covered with long setae on all sides. There are no specific attachment structures. Two setiform parempodia (par, Fig. 4A) arise from the distal part of the unguitactor plate (ut). An alveolus is not recognizable. The unguitactor plate bears rectangular scales on its lateral side. The ventral distal rim of the distal tarsomere

bears a row of microtrichia (=ventral brush after Weirauch [2005]). Dorsally between the claws a so called “dorsal arolium” (ds, Fig. 4F) is present. This name is misleading, since the structure is clearly not an arolium, but a sensillum (= dorsomedian sensillum after Weirauch, 2005). The foreleg in enicocephalids is distinctly modified for capturing prey. The tarsus comprises only one segment and the distal part of the tibia bears an armature consisting of spiniform setae.

Dipsocoromorpha, Dipsocoridae and Schizopteridae (Fig. 4B)

The tarsi are 2-segmented in the examined species. The distal tarsomere is about three times longer than the proximal one. No specific pretarsal attachment structures are present in *Ceratocombus australiensis*. The lateral part of the unguitactor plate bears rectangular ridges. A ventral brush and setiform parempodia are missing, but two minute protuberances are present at the distal part of the unguitactor plate where the parempodia normally arise. These structures likely represent strongly reduced parempodia. It is very unlikely that this is an artifact as the same condition is found on all legs and a line of fracture is never recognizable. In the males of *Corixidea* there is an arolium present on the midlegs. There are no parempodia present on the midlegs, only on the hind- and forelegs. According to Stys (1983) metacoxal adhesive pads are present in Dipsocoromorphs. However, they were absent in all examined species.

Pentatomomorpha, Pentatomidae (Fig. 4D, E)

The tarsi are 3-segmented in pentatomids. The ventral distal rim of the distal tarsomere bears a row of microtrichia, referred to as ventral brush (Weirauch, 2005). A small seta is present at the lateral end of the row. Two long setiform parempodia (par, Fig. 4D) arise from an alveolus on the distal part of the unguitactor plate. The ventral and lateral surfaces of the unguitactor plate bear distinct ridges. Large pulvilli (pu, Fig. 4D) are present. Their dorsal side is lamellate (Fig. 4E) and the ventral side more or less concave (variable among species).

Psocodea (Fig. 5)

Troctomorpha, Liposcelididae (Fig. 5A)

The tarsi are 3-segmented in *Liposcelis*. Adhesive structures are absent. The claws are serrate. The femur is distinctly enlarged. All tarsomeres as well as the lateral and dorsal sides of the claws are densely covered with microtrichia

Psocomorpha, Caeciliidae (Fig. 5B)

The tarsi are 2-segmented in *Caecilius*. Paired, flap-like pulvilli are present. Two guard setae are inserted on the dorsal side of the distal tarsal segment.

Trogiomorpha, Trogidae (Fig. 5C)

Tarsi are 2-segmented in *Cerobasis*. Paired fleshy pulvilli are present. Two smooth claws are present (in other species claw teeth can be present [Yoshizawa, 2005]). Three long, strong guard setae are located on the dorsal side of the distal tarsal segment. Directly proximad the pulvilli additional adhesive hairs (adh, Fig. 5C) are present (called “Basalhaare” in Weidner [1972, p. 50]). They arise from the claws, not from the unguitactor plate.

Amblycera, Menoponidae (Fig. 5D,G)

The tarsi are 2-segmented in *Trinoton*. The proximal tarsomere is smaller than the distal one and both bear smooth, slightly concave euplantulae (eu, Fig. 5D). The proximal surface of the euplantulae is covered with tubercles (tu, Fig. 5G). Two sensilla with a flag-like appearance (sen, Fig. 5D) are located at the ventral base of the proximal tarsomere. Two claws are present.

Ischnocera, Trichodectidae and Philopteridae (Fig. 5E)

The tarsus is one-segmented and only one claw is present in *Trichodectes melis* (Trichodectidae). Three to five stout, cone-like hyaline structures (hyc) are present on the apex of the tibia. In ischnoceran species parasitizing birds (*Columbicola* sp., Philopteridae) two claws are present.

Anoplura, Pediculidae (Fig. 5F)

The tarsus comprises only one segment and only one large claw is present. A thumb-like process (thp) is present at the distal part of the tibia. It is opposed to the claw and combined both structures enclose the hairshaft of the host. At the ventral side of the tarsus a round, pad-like euplantula (eu) is present. A claw-shaped apophysis (apo) arises from it. At the base of the claw a fingerlike process, possibly with sensory function (Cruz and Mateo, 2009), is present.

Rhynchophthirina, Haematomyzidae (Fig. 5H)

The tarsus comprises only one segment. There is one main claw and directly above is a smaller accessory claw ("Nebenkrallen" after Weber, 1969). The accessory claw (acl) is only present on the mid- and hindlegs. No specific attachment structures are present.

Thysanoptera, Terebrantia, Aeolothripidae (Fig. 6A, B)

The tarsi are 2-segmented in *Frankliniella*. An eversible, balloon-shaped pretarsal structure is a modified arolium (ar, Fig. 6B). In retracted condition it is encased by two spoon-shaped valves (va, Fig. 6A). Those valves are reduced claws (see Heming, 1971). Distally these valves are covered with teeth-like microtrichia (mt).

Character coding of tarsal structures (for character coding of other structures see Appendix II)

Coding as (0) or (1) does not imply a priori polarity assessment. We do not follow the convention of coding presumably plesiomorphic character as (0). We consistently coded the adhesive structures of the middle leg.

99. Parempodia on unguitactor plate: (0) absent; (1) elongate and setiform, inserted in an alveolus.
100. Number of tarsal segments: (0) one; (1) two; (2) three; (3) more than three.
101. Arolium: (0) absent; (1) present; (2) eversible; (3) bilobed.
102. Sticky terminal lip of arolium: (0) absent; (1) present.
103. Pulvilli: (0) absent; (1) present.
104. Euplantulae: (0) absent, (1) present.
105. Number of claws: (0) one; (1) two; (2) reduced; (3) main claw plus accessory claw.
106. Claw teeth: (0) absent; (1) present.
107. Protuberance with microtrichia on distolateral side of the pretarsus: (0) absent; (1) present.
108. Sensorial setae on mesal side of arolium: (0) absent; (1) present.
109. Adhesive claw setae: (0) absent; (1) present.
110. Eversible structure between tibia and tarsus: (0) absent; (1) present.
111. Tibial thumb-like process: (0) absent; (1) present.
112. Empodial paronychium: (0) absent; (1) present.
113. Tarsal apophysis on the ventral side of the tarsus: (0) absent; (1) present.
114. Two dorsal capitate setae: (0) absent; (1) present.
115. Flag-like sensilla on the 1st tarsal segment: (0) absent; (1) present.
116. Fingerlike process below claw: (0) absent; (1) present.
117. Ventral brush: (0) absent; (1) present.

Cladistic analysis

The analysis of 118 characters yielded three most parsimonious trees (195 steps, Ci: 68, Ri: 84). The strict consensus tree is shown in Fig. 7. Adhesive pad characters are mapped on the tree in Fig. 8. Apomorphies of ingroup taxa (character optimization: unambiguous) are

listed in the following. Homoplasious changes are in italics. Further information about the characters can be found in Appendix I and II.

Acercaria (Bremer support [BS]: 4)

Lacinia stylet-like (7/1), single complex formed by abdominal ganglia (12/2), anterior region of 2nd axillary sclerite inflated (26/1), *fusion of gonangulum with tergum IX (44/1)*, number of Malpighian tubules reduced (93/2), *two tarsal segments (100/1)*.

Psocodea (BS: 5)

Rupture-facilitating modification at base of antennal flagellum (0/1), cardo and stipes fused (4/2), cibarial water-vapour uptake apparatus (10/1), two axonemes in spermatozoa (43/2), *arolium absent (101/1)*.

Liposcelididae + True Lice (BS: 4)

Head and body dorsoventrally flattened (86/1), *hindfemora enlarged (87/1)*, meso- and metanotum fused (88/1), *compound eyes reduced (89/1)*.

True Lice („Phthiraptera“, BS: 2)

Number of antennal flagellomeres reduced (58/1), ovipositor simplified (80/1).

True Lice excl. Amblycera (BS: 2)

Maxillary palps absent (41/1), broad basal apodeme (63/1) and partly fused ventral plates (64/1) of the male genitalia, *only one tarsal segment (100/0)*, *single claw (105/0)*.

Rhynchophthirina + Anoplura (BS: 5)

Mandible stylet-like (3/1), lacinia absent (5/0), *cibarial water-uptake apparatus absent (10/0)*, *articulations between the mesomere, anterodorsal extension of ventral plate and posterior end of basal plate of the genital absent (59/0)*, *mesomere of the aedeagus pointed posteriorly (66/1)*, posteromedian part of basal plate of male genitalia sclerotized (67/1), *proboscis present (77/2)*, pronotum and procoxae fused (83/1), anterior tentorial pits absent (84/1), *hind femora not enlarged (87/0)*.

“Condylgnatha” (Hemiptera + Thysanoptera; BS: 1)

Mandibles stylet-like (3/1), distal median plate of forewing positioned next to second axillary sclerite and articulating along convex hinge (33/1), *maxillary palps absent or reduced to less than four segments* (41/1), *proboscis present* (77/2), dorsal shift of anterior tentorial pits (84/2), labrum narrowed (94/1).

Hemiptera (Auchenorrhyncha, Heteropteroidea and Sternorrhyncha; BS: 3)

Cardo absent (4/1), labial rostrum present (8/1), anterior axillary folding-line forked around distal end of second axillary sclerite, proximal branch running through distal portion of 2Ax (27/1), tubular labium comprising 3 segments (55/1).

Auchenorrhyncha (BS: 4)

Proximal median plate of the forewing membranous (31/1), *Evan’s organ present* (73/1), complex tymbal acoustic system present (91/1), *antennal flagellum aristate* (92/1), *three tarsal segments present* (100/2).

Fulgoromorpha (BS: 4)

Tegulae enlarged with broad extension encircling entire margin (20/1), pretentorium unites internal extremities of mandibular lever and corpotentorium (45/1), sensory plate organs of pedicel present (72/1), *arolium with sticky terminal lip* (102/1).

Cicadomorpha (Bremer support: 1)

Gut with filter chamber containing Malpighian tubules (97/1).

Heteropteroidea (Coleorrhyncha +Heteroptera; BS: 3)

Tegulae of forewing absent (19/1), cephalic trichobothria (53/1), , tubular labium comprising 4 segments (55/2), *number of flagellomeres of the antenna reduced* (58/1).

Heteroptera (BS: 3)

metathoracic scent gland system (54/1), labial proboscis inserted anteriorly on head (56/1),

dorsal abdominal glands present in immature stages(57/1), *parempodia on pretarsus present* (99/1), *arolium absent* (101/0).

Sternorrhyncha (BS: 2)

Proboscis shifted posteriorly between procoxal bases (77/1), posterior parts of head capsule membranous (78/1).

Psyllidae + Aleyrodidae (BS: 4)

Ductus ejaculatorius modified as sperm pump (74/1), abdomen narrowed by reduction of segments I and II (75/1), hind coxae broad and closely adjacent (76/1), eggs pedunculate (96/1).

Aphidoidea + Coccoidea (BS: 2)

Arolium absent (101/0), *Pulvilli present* (103/1).

Discussion

Phylogenetic aspects

The phylogenetic relationships of Acercaria were discussed informally in Hennig (1969), in several review studies by Kristensen (e.g., 1981, 1991), and also briefly in Trautwein et al. (2012). The placement and phylogeny of the entire lineage were addressed in several studies based on molecular data sets (e.g., Wheeler et al., 2001; Kjer, 2004, 2006) and also the phylogenetic relationships of the subgroups (e.g., Wheeler et al., 1993; Yoshizawa and Johnson, 2010; Cryan and Urban, 2012). Aside from studies covering the entire Hexapoda (Beutel and Gorb, 2001, 2006) the first numerical analysis of morphological data including all

orders of Acercaria was conducted by Yoshizawa and Saigusa (2001), based on characters of the base of the forewing. In the present study we attempted to compile and analyse a more extensive morphological data set, including characters of all body parts. In the following, the results of the analyses are compared to those obtained in earlier studies based on different data, and especially with respect to the evolution of attachment structures, the primary focus of this study.

Acercaria

The monophyly of Acercaria is well supported by our data set (Bremer support: 4). The Psocodea, Thysanoptera and Hemiptera share a set of synapomorphic features of different body regions, such as for instance a stylet-like lacinia, arguably a predisposition for specialized sucking-piercing feeding habits, an inflated anterior region of the 2nd axillary sclerite, an extremely compacted abdominal ganglionic chain, and a reduced number of Malpighian tubules (shared with Holometabola excl. Hymenoptera; Beutel et al., 2011). The analysis based on our taxon sampling yielded a 2-segmented tarsus as an additional acercarian autapomorphy. This interpretation appears questionable as 3-segmented tarsi occur in several lineages (e.g., Psocoptera [partim], Heteroptera [majority of groups]). Parallel loss of the 3rd tarsomere appears more plausible than a secondary acquisition in different groups. The slow optimization yielded strongly reduced labial palps and the absence of the abdominal sternite 1 as additional apomorphies of the Acercaria.

Our results do not support a placement of Zoraptera as the sistergroup of Acercaria (e.g., Hennig, 1969; Beutel and Weide, 2005). The precise position of this small and enigmatic order is not settled yet. However, there is an increasing consensus that they should be placed among the lower neopteran lineages (e.g., Kukalová-Peck and Peck, 1993; Wheeler et al., 2001; Yoshizawa, 2007; Yoshizawa and Johnson, 2005; Ishiwata et al., 2011; Yoshizawa, 2011; see also Trautwein et al., 2012).

The placement of Acercaria as sistergroup of Holometabola is widely accepted even though poorly supported by morphological data (e.g., loss of larval ocelli; e.g., Beutel and Gorb, 2001, 2006). A clade including Acercaria and Holometabola (Eumetabola) is also tentatively supported by our data (with a very limited holometabolan taxon sampling) and by molecular studies (e.g., Kjer, 2004; Ishiwata et al., 2011). However, this requires further confirmation. An arrangement with paraphyletic Acercaria and Psocodea as sistergroup of Holometabola as shown in Ishiwata et al. (2011) appears very unlikely considering the morphological evidence.

Psocodea

A clade Psocodea is well supported by unique morphological features (Fig. 7, 8; Rudolph and Knülle, 1982; Seeger, 1975) as well as molecular data (Cryan and Urban, 2011; Ishiwata et al., 2011; Murrell and Barker, 2005). A highly unusual apomorphic groundplan feature identified by Seeger (1975) is the cibarial water uptake apparatus. An additional apomorphy likely present in the groundplan of Psocodea is the mortar-and-pestle apparatus of the cibarium (e.g., Tröster, 1990). It is still retained in the groundplan of Phthiraptera but is reduced in the majority of its subgroups (e.g., Tröster, 1990).

The relationships within Psocodea are still not fully clarified. However, a sistergroup relationship between Liposcelididae and the true lice seems to be well supported by morphological characters such as for instance enlarged hindfemora and fused pterothoracic nota (Figs 7, 8; see also Lyal, 1985) and also by analyses of molecular data (Yoshizawa and Johnson, 2003 [12S, 16SrDNA]). This renders the “Psocoptera” paraphyletic. The Phthiraptera (true lice) were weakly supported as a monophyletic unit (Bremer support: 2) in our analyses. Potential apomorphies are the reduced number of antennal flagellomeres, a condition also occurring in Heteroptera and Coleorrhyncha, and the simplified ovipositor (well developed in the psocodean groundplan). An entire series of apomorphies was suggested by Königsmann (1960), such as for instance the absence of ocelli in all stages, the posteriorly

tilted protocerebrum (see also Tröster, 1990), and a fusion of the metathoracic ganglion with the abdominal complex. Moreover, the complete reduction of the flight organs (absent or distinctly reduced in Liposcelididae), a dorsoventrally flattened body (also in Liposcelididae), and ectoparasitic habits were considered as obvious candidates for phthirapteran autapomorphies (see e.g., Grimaldi and Engel, 2005). Despite of this seemingly strong morphological evidence, the monophyly of the true lice was questioned with respect to Amblycera in recent studies based on molecular data. Analyses of 18SrDNA (Johnson et al. (2004; Murrell and Barker, 2005) yielded a clade Amblycera + Liposcelididae on one hand, and the remaining true lice as its sistergroup. This hypothesis implies that parasitism in this lineage has evolved twice independently and also a series of features characterizing the four ectoparasitic groups. In an analysis using 5 different genes (nuclear 18S rDNA, Histone 3, wingless, mitochondrial 16S rDNA and COI; Yoshizawa and Johnson, 2010) those result were supported. However, the results of the study by Murrell and Barker (2005) also include the unlikely paraphyly of Hemiptera and an unorthodox placement of Coleorrhyncha as sistergroup of Auchenorrhyncha. Considering the morphological data and the specialized ectoparasitism on mammals and birds, we consider a clade Phthiraptera as more likely, but further confirmation by more extensive molecular data is required.

The obtained branching pattern within the true lice corresponds with the phylogenetic hypotheses suggested in earlier morphological studies (Lyal, 1985; Tröster, 1990) and a study based on 18SrRNA (Barker et al., 2003). The basal placement of Amblycera (Königsmann, 1960; Lyal, 1985; Tröster, 1990; see also Grimaldi and Engel, 2005) was confirmed in our analyses. Unambiguous synapomorphies of Ischnocera, Rhynchophthirina and Anoplura (Fig. 7) are modifications of the male genital apparatus, i.e. the presence of broad basal apodemes and partly fused ventral plates. The sistergroup relationship between Rhynchophthirina and Anoplura (e.g., Lyal, 1985; Tröster, 1990) is supported by an entire series of synapomorphies (Fig. 7), such as for instance stylet-like mandibles (like in Hemiptera), loss of the lacinia, secondary absence of the cibarial water-uptake apparatus, the fusion of the procoxae with the pronotum, and the absence of anterior tentorial pits.

Species of Anoplura and Rhynchophthirina exclusively feed on liquid like the hemipterans. The food substrate is exclusively blood of birds or mammals in the former group, whereas this is a rare exception in the case of the Hemiptera (e.g., Cimicidae and some Reduviidae). The underlying structural modifications differ fundamentally in both lineages (Weber, 1929; Tröster, 1990).

Condylognatha

The placement of Thysanoptera is a matter of longstanding controversy (e.g., Kristensen, 1991). The characters we analyzed support a clade Condylognatha (Fig. 7; Bremer support 1), i.e. a sistergroup relationship between Thysanoptera and Hemiptera. Potential synapomorphies include the stylet-like mandibles (right mandible vestigial in thrips), a specifically articulated distal median plate of the forewing, the reduction of the maxillary palps (absent in Hemiptera, less than four segments in thrips), and a dorsal shift of the anterior tentorial pits. The same result was obtained in several studies using different morphological character sets (e.g., Kristensen, 1981; Yoshizawa and Saigusa, 2001; Wheeler et al., 2001: fig. 10; see also Hennig, 1969) and was also tentatively supported by molecular data analysed by Ishiwata et al. (2011). The alternative hypotheses, a clade Micracercaria (Thysanoptera + Psocodea) is suggested by the presence of an enlarged dorsal cibarial muscle with an unpaired median tendon (e.g., Willmann, 2005). A sistergroup relationship between Thysanoptera and Psocodea was also tentatively supported by analyses of 18S rDNA and 28S rDNA (Wheeler et al., 2001) and a study using seven gene regions (Cryan and Urban, 2012). Like in Ishiwata et al. (2011) the sampling of psocodeans and thrips was very limited in Cryan and Urban (2012), a study focused on hemipteran relationships. The results in Wheeler et al. (2001) have to be taken with caution. Neither the analyses of 18SrRNA nor those of 28SrRNA (Wheeler et al., 2001: figs. 13, 14) supported a clade only containing the psocodean and thysanopteran terminals. Moreover, the analytical procedure

(POY, simultaneous alignment and parsimony analyses) has been shown to be less reliable than other approaches (Kjer et al., 2007; Ogden and Rosenberg, 2007; Yoshizawa, 2010).

Hemiptera

There is no doubt about the monophyly of Hemiptera (Auchenorrhyncha, Heteropteroidea and Sternorrhyncha; e.g., Hennig, 1969; Kristensen, 1981, 1991). The most conspicuous autapomorphy is the characteristic labial rostrum, with reduced palps and endite lobes. This finding was clearly supported by our own data (Fig. 7) and also in molecular studies using different data sets and analytical approaches (Cryan and Urban, 2012; Ishiwata et al., 2011; Kjer et al., 2006). The paraphyly of Hemiptera and an unlikely sistergroup relationship between Thysanoptera and Sternorrhyncha was suggested in a study based on SSUrDNA (Murrell and Barker, 2005). However, the focus was on the relationships within Psocodea, and the sampling of outgroups (in this case Thysanoptera and Hemiptera) was limited.

Our data turned out as insufficient for resolving the interrelationships of the three hemipteran subgroups. Schuh (1979) suggested Sternorrhyncha as the sistergroup of the remaining three lineages, thus rendering „Homoptera“ paraphyletic. The same conclusion was reached by Popov (1981 [palaeontological data]), Zrzavy (1992 [morphological and ecological data]) and Cryan and Urban (2012 [extensive molecular data]). A taxon consisting of Heteropteroidea (=Prosorrhyncha) and Auchenorrhyncha was referred to as Euhemiptera. This was also supported in several studies analyzing different partial sequences of 18SrDNA (Campbell et al., 1995; Dohlen and Moran, 1995; Sorensen et al., 1995).

Auchenorrhyncha

A clade Auchenorrhyncha (Bremer support: 4) was well supported by our data (Figs 7, 8). The presence of complex tymbal acoustic system appears as a convincing argument for this clade. Within the group, Fulgoromorpha were also clearly confirmed as a monophyletic unit (Bremer support: 4). The monophyly of Auchenorrhyncha was also supported by analyses of sequences of a broad array of genes (Urban and Cryan, 2007 [18S rDNA, 28S rDNA,

Histone 3, Wingless]) and in an even more extensive study using seven gene regions (Cryan and Urban, 2012 [18S rDNA, 28S rDNA, histone H3, histone 2A, wingless, cytochrome c oxidase I, NADH dehydrogenase subunit 4]). However, it was challenged in other studies. A sistergroup relationship between Cicadomorpha and Aphidoidea was suggested based on characters of the head capsule by Hamilton (1981), and a closer relationship between fulgorids and true bugs was proposed by von Dohlen and Moran (1995). The latter study was only based on 18SrRNA and the taxon sampling was very limited, with only nine species of Auchenorrhyncha included. Similarities in the morphology and histology of the digestive tract of Fulgoromorpha and Heteroptera were pointed out by Goodchild (1966) (for a summary see Forero, 2008), arguably a result of parallel evolution. A sistergroup relationship between Cicadomorpha and Heteropteroidea (Heteroptera + Coleorrhyncha) appears as a serious alternative to the monophyly of Auchenorrhyncha. This was suggested in an evaluation of combined paleontological, molecular and morphological data (Bourgoin and Campbell, 2002) and also supported by a recent study based on transcriptomes (Letsch et al., 2012). Considering the conflicting hypotheses, the issue of the monophyly of Auchenorrhyncha should be considered as an unsolved question.

Heteropteroidea (=Prosorrhyncha, Coleorrhyncha + Heteroptera)

Coleorrhyncha are clearly placed as the sistergroup to Heteroptera (Fig. 7; Bremer support: 3). The same result was supported by Urban and Cryan, 2012 and in other studies (Wheeler et al., 1993; Ouvard, 2000; see also Schlee, 1969), and also by a detailed comparative study of head structures (Spangenberg et al., *subm.*). Furthermore, the wing-coupling structure of moss bugs is very similar to that of Heteropterans (d'Urso, 1993). Considering the overwhelming evidence from different sources previous placements of Coleorrhyncha as a subordinate group within Heteroptera (Breddin, 1897) or Auchenorrhyncha (China, 1962; Murrell and Barker, 2005) can be regarded as obsolete. Structural affinities of Coleorrhyncha and members of Auchenorrhyncha include features of the heart (occupying six abdominal

segments and with six sets of alary muscles; Pendergast, 1962) and the presence of an arolium. We assume that these similarities are either symplesiomorphic (e.g., arolium) or results of parallel evolution.

The monophyly of Heteroptera was clearly confirmed (Bremer support: 3), whereas the relationships within the group remained unresolved. This is mostly due to the very fragmentary knowledge of the morphology of supposedly basal groups such as Enicocephalomorpha and Dipsocoromorpha (Wheeler et al., 1993; Xie et al., 2008; summarized in Weirauch and Schuh [2011]). The basal branching events in Heteroptera are not fully clarified yet. A recent analysis of multiple genes yielded a basal position of Nepomorpha (Li et al., 2012). The position of Enicocephalomorpha and Dipsocoromorpha varied in the Li et al. (2012) study depending on the method applied (Maximum likelihood versus Maximum Parsimony). The placement of Nepomorpha at the base of Heteroptera would be consistent with findings of Mahner (1993, p. 15ff), who considered the reduction of the tentorium as an autapomorphy of Heteroptera excl. Nepomorpha. The tentorium of enicocephalids is largely reduced (R. Spangenberg, pers. obs.), but the condition in dipsocoromorphans is unknown yet. The fast optimization search yielded one additional apomorphy for the Heteroptera: the presence of a ventral brush on the ventral distal rim of the distal tarsomere. However, it is absent in the examined members of Dipsocoromorpha.

Sternorrhyncha

Sternorrhyncha were clearly confirmed as a clade (Fig. 7). Autapomorphies are the posterior shift of the proboscis between the procoxal bases and the membranous posterior parts of the head capsule. A sistergroup relationship between Psyllidae and Aleyrodidae (Psyllomorpha) was also well supported (Bremer support: 4), which is not surprising as most characters were taken from Schlee (1969), who proposed this hypothesis. Synapomorphies are the ductus ejaculatorius modified as a sperm pump, the constriction of the abdominal base, the broad and closely adjacent hind coxae, and the pedunculate eggs. The only potential

synapomorphy of aphids and coccids is the loss of the arolium. However, the arolium is lost several times within Acercaria.

In several studies based on 18S rDNA (Campbell et al., 1994; Sorensen et al., 1995) Psyllidae were placed as the sistergroup of the remaining Sternorrhyncha, and Aleyrodidae as the sistergroup of a clade comprising of Aphidoidea and scale insects. The same relationships were inferred from DNA nucleotid sequence data from 7 gene regions (Cryan and Urban, 2012). White flies share at least some morphological features with aphids and scale insects, such as the reduced wing venation, sedentary or sessile nymphs, and antennae reduced to 6 or fewer segments (e.g., Grimaldi and Engel, 2005). Apparently, the interrelationships of the sternorrhynchan subgroups require further investigation.

Evolution of attachment structures

Despite of a very broad spectrum of structural variations, there are only two basic designs of attachment pads on insect legs: hairy and smooth (Beutel and Gorb, 2001). Interestingly, hairy structures which occur in different lineages of Polyneoptera and Holometabola (Beutel and Gorb, 2001, 2006) are lacking on the tarsus and pretarsus of the acercarian subgroups. An interesting exception is the hairy fossula spongiosa in several subgroups of Cimicomorpha. This is the only case of a hairy pad in Acercaria and apart from tibial elements of some specialised clasping devices of true lice the only tibial attachment structure occurring in the entire Hexapoda. The exact function of the fossula spongiosa is still unclear. It is possibly a tool for capturing prey or alternatively a device involved in locomotion (Weirauch, 2007). It was pointed out in Beutel & Gorb (2001) that the function of adhesive devices of insect legs is generally not restricted to attachment. Easy detachment is equally important in order to guarantee efficient locomotion on a specific substrate.

The location of different attachment devices within Acercaria varies considerably. They occur on the pretarsus as an unpaired pad-like arolium, as paired pulvilli, or as an unpaired sclerotized empodium, on the tarsus as smooth euplantulae, and as pointed out above even on the distal tibia as a fossula spongiosa. This and the incompletely resolved relationships within Hemiptera impede the reconstruction of the evolutionary pathways. However, it is apparent and noteworthy that pretarsal attachment structures are mainly present in the primarily phytophagous Hemipterans, whereas tarsal and tibial attachment devices occur mostly in the ectoparasitic lice (Phthiraptera). In these taxa they are essential for anchoring on the hairs or feather shafts of the host.

Some groups lack attachment devices completely, e.g. the ground-dwelling Zoraptera (Beutel and Gorb, 2006). They are also absent in Enicocephalomorpha, female Dipsocoromorpha, Gerromorpha, Nepomorpha, Leptodomorpha, Rhynchophthirina and Troctomorpha. With the exception of the ectoparasitic Rhynchophthirina and the semiaquatic and aquatic Gerromorpha and Nepomorpha all of these taxa are ground-oriented and live in leaf litter, i.e. in similar microhabitats as the zorapterans. The elephant lice do not attach to hairs in the typical case, but stay directly on the skin surface or in skin creases, respectively (Fowler and Mikota, 2006, p. 458). Their main anchoring mechanism seems to be the proboscis, which is firmly embedded in the skin of the host (Weber, 1969).

Arolium

Arolia are widely spread within Acercaria and a groundplan feature of this lineage. They are generally present in the examined Auchenorrhyncha (with the exception of Cicadidae), in Coleorrhyncha, and in Thysanoptera. An arolium is also present in the males of *Corixidea* and several other male members of the Schizopteridae (Emsley, 1969, p. 20). The females of Dipsocoromorpha lack specific adhesive structures. The distinctly bilobed arolium of membracids and leafhoppers (Membracidae and Cicadellidae; Figs 1B, D; 2C, D; and Psylloidea; Fig. 3D) has apparently evolved independently in these groups, as potential

autapomorphies of these lineages. A unique and apparently autapomorphic feature is the eversible, balloon-like arolium of Thysanoptera. In its retracted position it is enclosed between two valves. This is not the case in fulgorids, where the arolium is also eversible to a certain degree (Frantsevich, 2008).

The arolium was considered as a potential autapomorphy of Neoptera by Beutel and Gorb (2001, 2006). However, whether the unpaired pretarsal attachment pads occurring in different insect lineages are homologous is questionable. The sclerotisation of the arolium of sawflies (Gladun, 2008), for instance, is completely different from the pattern found in the arolia of members of Cicadomorpha. The sclerotized Y-shaped ridge on the ventral side of the arolium in cercopoids may represent strongly modified planta, but this would imply that the auxillae and the arcus are reduced. The V-shaped sclerite on the dorsal side of the pretarsus of cercopids could be a modified manubrium. However, this interpretation is also uncertain. Due to the uncertain assessment of homologies, it is presently not possible to decide whether the differences between arolia occurring in acercarian and holometabolan lineages are due to secondary modifications of substructures or to non-homology of the unpaired pretarsal pads as a whole.

In contrast to this, there is little doubt that the unmodified arolium of cercopoids and the bilobed arolium in membracids are homologous. This is clearly indicated by specific conformities in the inner structure and sclerotisation of these devices. In both cases the cuticle is thickened and composed of branched chitinous rods. A modification characterizing the examined Membracoidea is the loss of the ventral Y-shaped sclerite. A characteristic feature of membracids is the division of the medial sclerite into two separate elements (ms, Fig. 2C). It is V-shaped but undivided in cercopoids. In cicadellids these sclerites are greatly reduced in size (ms, Fig. 2D), arguably an autapomorphy of the family.

The homology of the attachment device of White flies is still unclear. In this study we reluctantly labeled it as an empodium. Most authors, however, follow Quaintance and Baker (1913) in referring to this structure as “paronychium” (=arolium). An arolium is defined as a

median hollow lobe of the pretarsus (Dashman, 1953; Beutel and Gorb, 2001). The structure in the examined Aleyrodidae is not hollow, but resembles a spine-like empodium with a flattened tip. Median empodia are usually covered with acanths (Beutel and Gorb, 2001). This applies only to the base of the structure occurring in Aleyrodidae. This and the absence of empodia in related groups suggests, that this is rather a *de novo* formation and autapomorphy, than a structure homologous to the empodia occurring in several holometabolan lineages (e.g., Diptera).

The results of our analysis suggest the secondary loss of the arolium in several lineages. This includes Heteroptera, Aphidoidea, Coccoidea and Psocodea. In all these groups they were apparently functionally replaced by other kinds of attachment devices, in most cases by paired pulvilli. Considering the relationships indicated by our analysis (Fig. 8) and other studies, it appears that the loss of the arolium is an autapomorphy of each of the taxa listed above. However, as a complete reduction of this structure also occurs in many other lineages of insects (Beutel and Gorb, 2001, 2006), this feature is obviously of minor phylogenetic significance.

Pulvilli

Pulvilli have evolved at least twice independently within Acercaria – in Psocoptera and in the “higher” Heteroptera, respectively (Fig. 7). Interestingly, pretarsal or tarsal adhesive pads are absent in most of the presumably basal taxa of examined Heteroptera, the Enicocephalomorpha, the semi-aquatic and aquatic lineages Gerromorpha, Nepomorpha, and also in Saldidae (Leptopodomorpha), predaceous and ground-dwelling bugs and arguably the sistergroup of the remaining secondarily terrestrial heteropteran lineages (Wheeler et al., 1993). An arolium is present in Coleorrhynchans and some male members of the Schizopteridae (Dipsocoromorpha) and this is certainly a groundplan condition in Heteropteroidea (and Acercaria). The loss of this unpaired pretarsal pad is likely a

groundplan feature and autapomorphy of Heteroptera. Interestingly, in the megadiverse heteropteran subgroups Pentatomomorpha (ca. 14.500 spp.) and Cimicomorpha (more than 20.000 spp., Weirauch and Schuh, 2011) a novel type of attachment device occurs: paired pretarsal pulvilli. The presence of these adhesive structures is arguably related with a close association between those bugs with plants. As pointed out above, pretarsal and tarsal adhesive devices are absent in saldids. There is however one noteworthy exception. A structure resembling an empodium, similar to that of white flies, occurs in the genus *Aepophilus*. Interestingly this attachment device considered as a “true” arolium by Cobben (1978, p. 114 ff) is only present in 5th instar nymphs but is completely lacking in all other stages. However, a “dorsal arolium” occurs in the adults of *Aepophilus bonnairei* (Schuh and Polhemus, 1980) and other members of the saldids. Therefore it seems likely that Cobben misinterpreted this structure. He also stated the presence of arolia in Gerromorpha. However, the structures he described rather resemble paired accessory claws, and they were absent in species of *Gerris* we examined.

Pulvilli are also present in aphids and coccoids, apparently a result of parallel evolution. The pulvilli of coccoids are usually fleshy and thick and therefore similar to those of the examined pentatomids. In contrast, the pulvilli of aphids are flattened like the ones found in trogiomorphs and psocomorphs (Psocodea). The shape of pulvilli can be very variable. This is particularly obvious in the Miridae (Schuh, 1976). However, the characteristic thickened cuticle with chitinous rods found in arolia is absent in the examined pulvilli.

Euplantulae and tibial pads

Within Phthiraptera no pretarsal attachment structures occur. The complete reduction of the arolium is likely related with ectoparasitic habits and a potential autapomorphy of true lice. Within the group different tarsal and tibial devices have evolved. A specific type of euplantulae is present in amblycerans, especially in species specialized on birds as hosts.

They occur on both tarsomeres in Menoponidae, but only on the proximal segment in Laemobothriidae. Interestingly, euplantulae of the proximal tarsomere are also present in species of the genus *Paraheterodoxus* (Boopidae) (Marshall, 2003), even though these amblycerans do not live on birds, but in the fur of the rufous rat-kangaroo. This is an example of how attachment devices of the same type can adapt to different surfaces or structures.

In Ischnocera and Amblycera the mandibles seem to play a more important role as grasping devices than the specialized structures on the legs (Bush et al., 2006). In specimens preserved in ethanol we observed that the hair shaft was not in contact with the legs anymore, but was still firmly anchored between the mouthparts. In anoplurans the thumb-like process on the distal part of the tibia and the opposing claw enclose the hair. It is plausible to assume that the grasping mechanism is enhanced by the tarsal euplantulae. The same function is conceivable for the thick hyaline cones on the apex of the tibia in the examined Ischnocera. These cones on the tibial apex are apparently typical for many ischnoceran species specialized on birds (Smith, 2001).

Conclusions

As pointed out in Beutel and Gorb (2001) attachment devices can provide phylogenetic information despite functional constraints. In our study, the impact on the branching pattern was limited to an improved resolution within Psocodea. However, additional apomorphies of adhesive devices strengthened the support for different lineages (Psocodea, Fulgoromorpha, Heteroptera). Linked with a remarkable versatility in habitat choice, a very wide spectrum of attachment devices has evolved in Acercaria, with the notable exception of hairy pretarsal adhesive structures. Several acercarian subgroups can be characterized by features of the distal leg elements related to attachment and efficient locomotion on different substrates. The phylogenetic hypothesis presented here was based on a relatively limited character system and taxon sampling. In the near future, an extensive molecular data set will likely provide a robust phylogenetic framework for Acercaria and other hexapod lineages (see:

www.1KITE.org). This will be an ideal basis for reconstructing the evolution of attachment structures and other character systems.

Acknowledgement

We would like to thank Christiane Weirauch (University of California, Riverside), Eberhard Mey (Naturhistorisches Museum Schloss Heidecksburg), Viktor Hartung (Museum für Naturkunde, Leibniz-Institut für Evolutions- und Biodiversitätsforschung, Berlin) and the staff of the Zoo Leipzig for providing valuable specimens. We are also indebted to Eric Anton (FSU Jena) for his help with the determination of specimens. We are grateful to Benjamin Wipfer (FSU Jena) for his helpful comments on the manuscript. We also thank Hans Pohl for kindly providing the specimen holder for SEM and the picture of the extended arolium of a thrips (Fig. 6B).

This project was funded by the IMPRS (International Max Planck Research School for the Exploration of Ecological Interactions with Molecular and Chemical Techniques) of the Max-Planck-Institute for Chemical Ecology, Jena.

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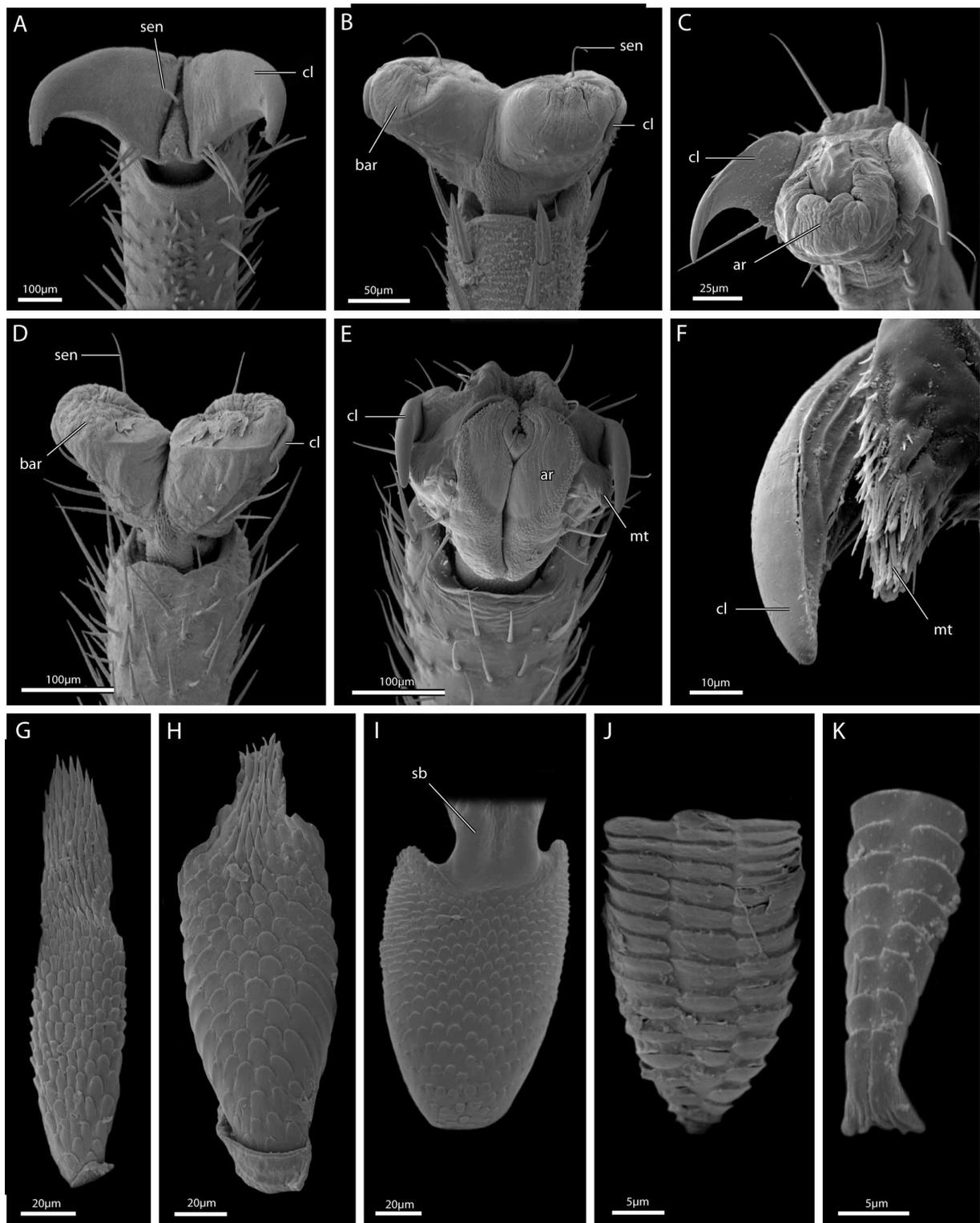


Fig. 1: Tarsi of Auchenorrhyncha. (A) *Cicadetta montana* (Cicadoidea), ventral view. (B) *Cicadella viridis* (Membracoidea), ventral view. (C) *Cixius* sp. (Fulgoromorpha), frontal view. (D) *Centrotus cornutus* (Membracoidea), ventral view. (E) *Cercopis vulnerata* (Cercopoidea), ventral view. (F) *Cercopis vulnerata*, detail view of the protrusion covered in microtrichia. (G-K) unguitractor plates. (G) *Cicadella viridis*. (H) *Centrotus cornutus*. (I) *Cercopis vulnerata*. (J) *Cixius* sp. (K) *Javasella* sp.

Abbreviations: ar – arolium, bar – bilobed arolium, cl – claw, mt – microtrichia, sb – sclerotized bar, sen – sensillum.

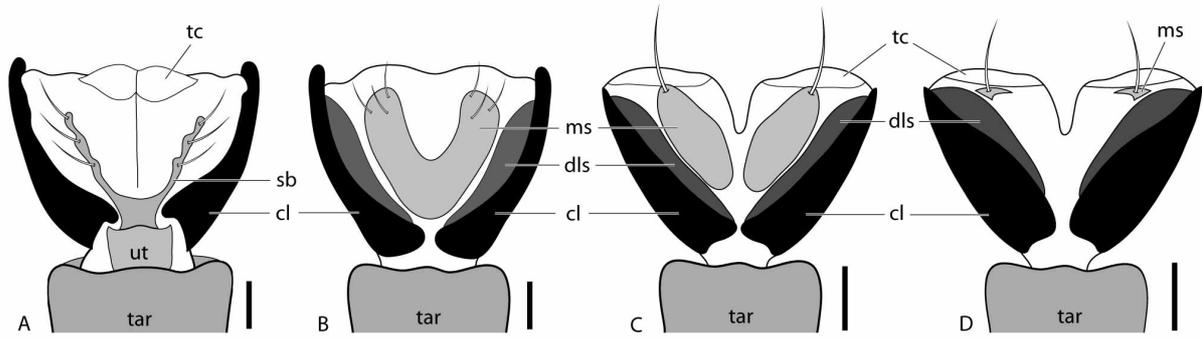


Fig. 2: Sclerites of pretarsi of Auchenorrhyncha. (A) *Cercopis vulnerata*, ventral view. (B) *Cercopis vulnerata*, dorsal view. (C) *Centrotus cornutus*, dorsal view. (D) *Cicadella viridis*, dorsal view. Abbreviations: cl – claw, dls – dorsolateral sclerite, ms – medial sclerite, sb – sclerotized bar, tar – tarsus, tc – area of thickened cuticle, ut – unguitractor. Scale bars: 50 μm.

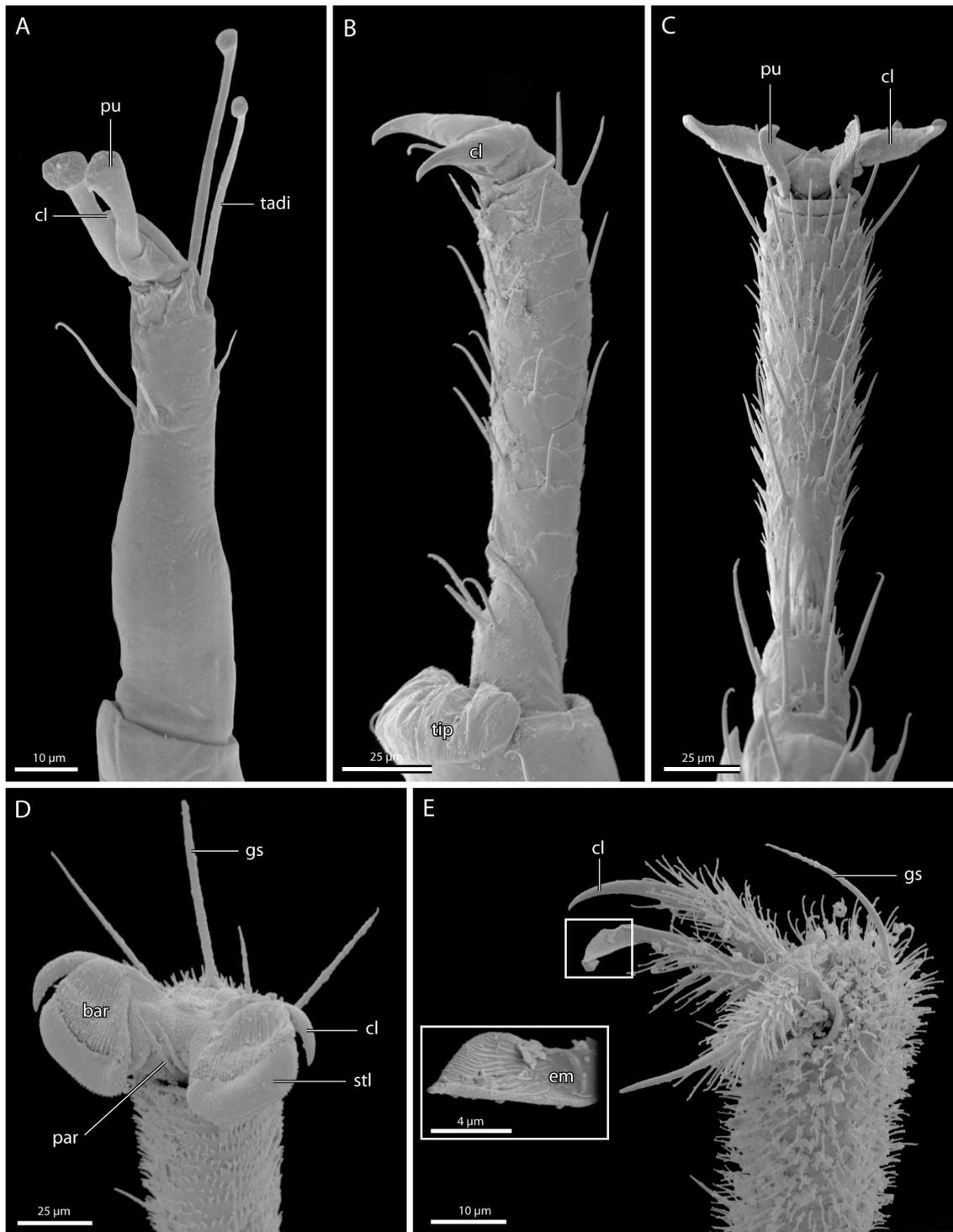


Fig. 3: Tarsi of Sternorrhyncha. (A) *Pseudococcus* sp. (Coccoidea), lateral view. (B) *Aphis sambuci* (Aphidoidea), lateral view. (C) *Drepanosiphum* sp. (Aphidoidea), ventral view. (D) *Cacopsylla* sp. (Psylloidea), frontal view. (E) *Aleyrodes* sp. (Aleyrodidae), lateral view. Abbreviations: bar – bilobed arolium, cl – claw, em – empodium, gs – guard seta, par – parempodia, pu – pulvillus, stl – sticky lip of the arolium, tadi – tarsal digitules, tar – tarsus, ti – tibia, tip – tibial pad.

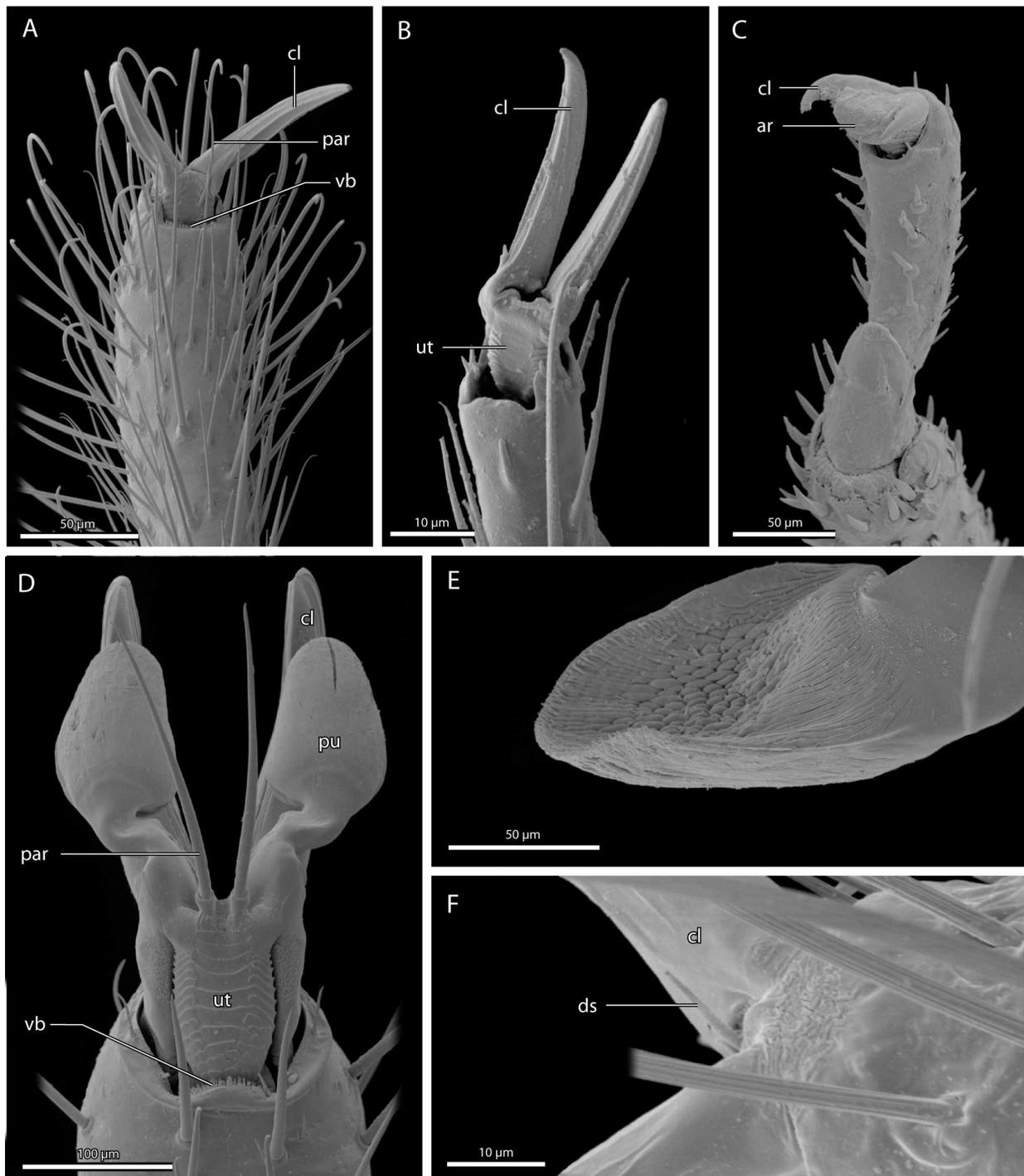


Fig. 4: Tarsi of Prosorrhyncha. (A) *Systelloderes* sp. (Enicocephalomorpha), ventral view. (B) *Ceratocombus australiensis* (Dipsocoromorpha), ventrolateral view. (C) *Hackeriella veitchi* (Coleorrhyncha), ventrolateral view. D *Graphosoma lineatum* (Pentatomorpha), ventral view. (E) *Graphosoma lineatum* (Pentatomorpha), dorsal surface of the Pulvillus. (F) *Systelloderes* sp. (Enicocephalomorpha), dorsal view of the pretarsus.

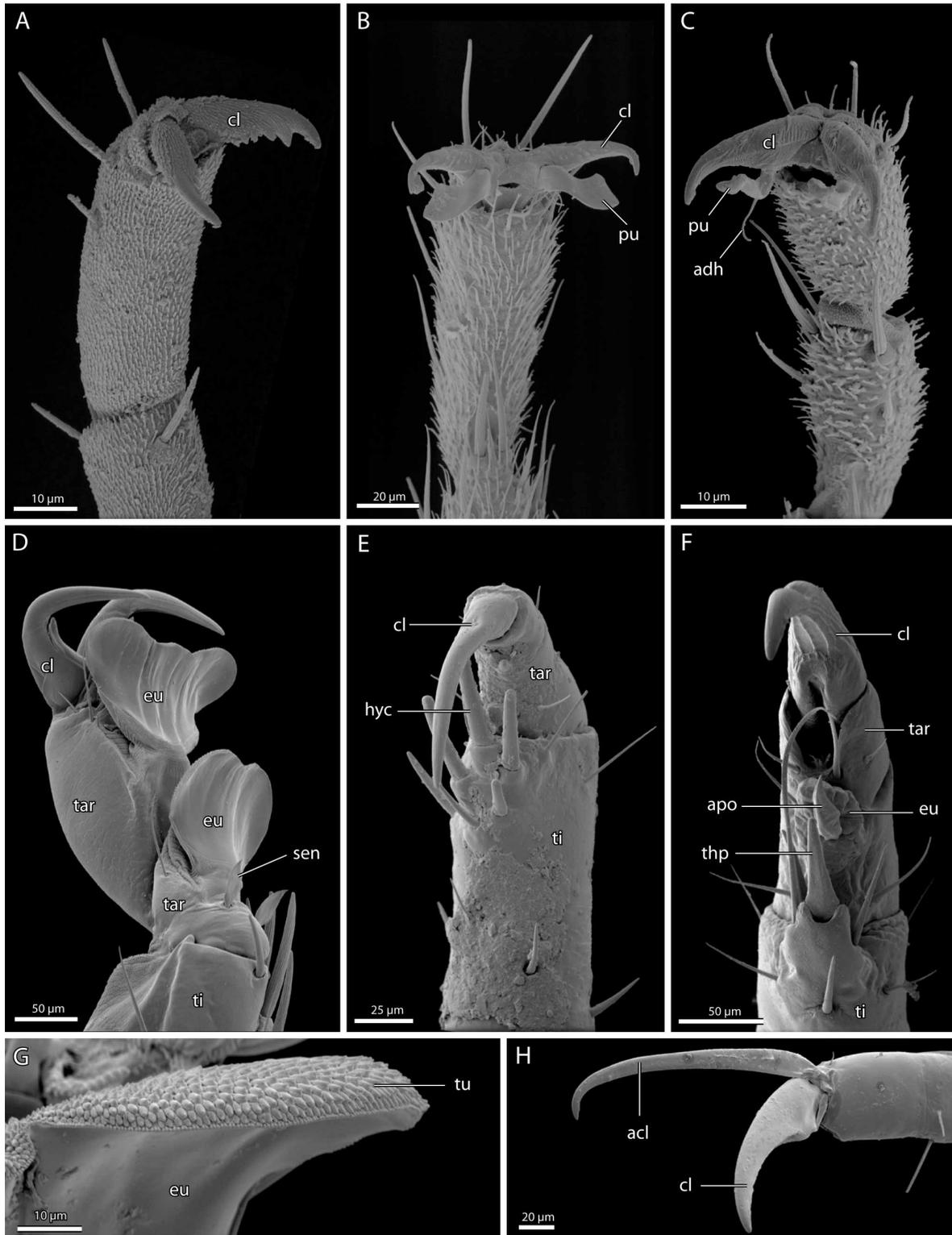


Fig. 5: Tarsi of Psocodea. (A) *Embiopsocus* sp. (Troctomorpha), lateral view. (B) *Caecilius flavidus* (Psocomorpha), ventral view. (C) *Cerobasis* sp. (Trogliomorpha), ventral view. (D) *Trinoton anserinum* (Amblycera), lateral view. (E) *Trichodectes melis* (Ischnocera), ventral view. (F) *Pediculus humanus corporis* (Anoplura), ventral view. (G) *Trinoton anserinum* (Amblycera), detail of the dorsal surface of the euplantulae. (H) *Haematomyzus elephantis* (Rhynchophthirina), lateral view. Abbreviations: acl – accessory claw, adh – adhesive hair, apo – apophysis of the euplantulum, cl – claw, eu – euplantulae, hyc – hyaline cones, pu – pulvillus, tar – tarsus, thp – thornlike process, ti – tibia, tu – tubercle.

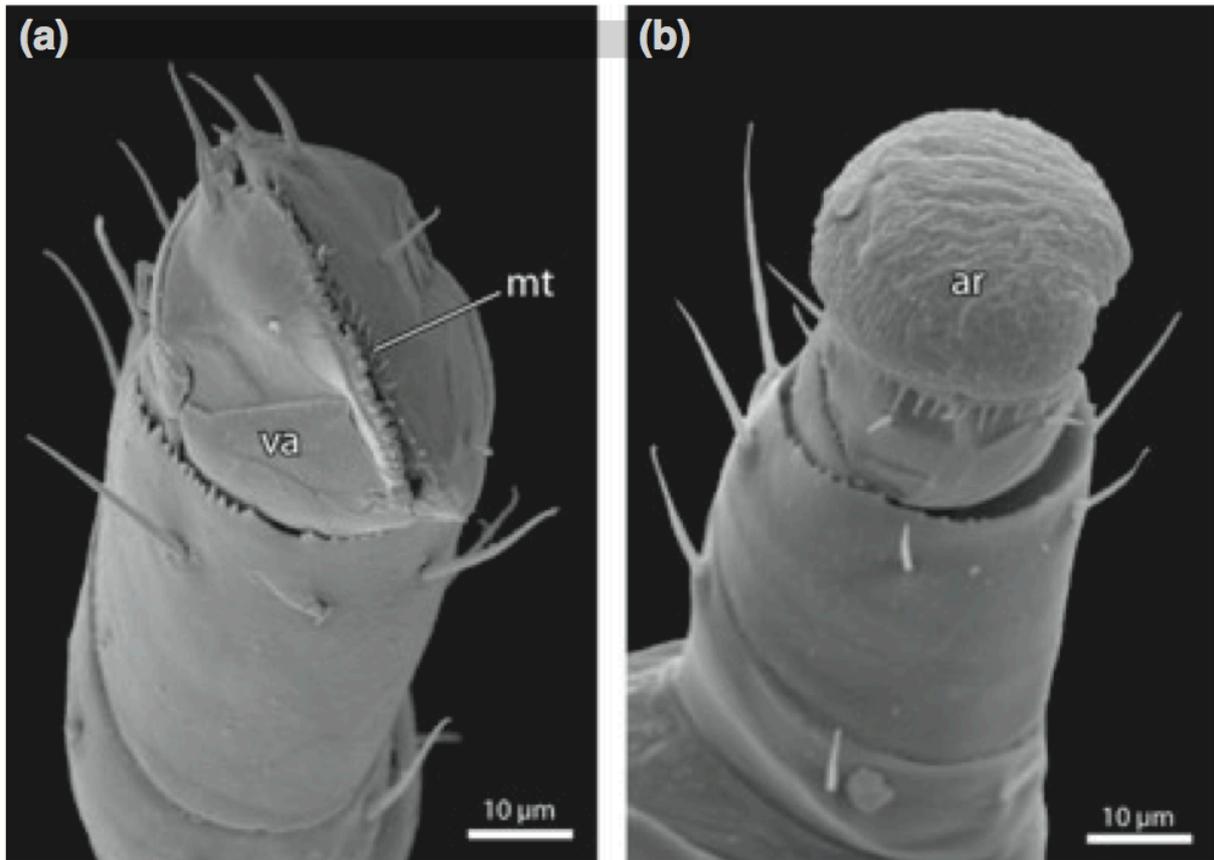


Fig. 6. Tarsi of Thysanoptera. (a) *Frankliniella* sp. Valves closed around the resting arolium. (b) *Frankliniella* sp. Arolium fully extended. ar, arolium; mt, microtrichia; va, valves.

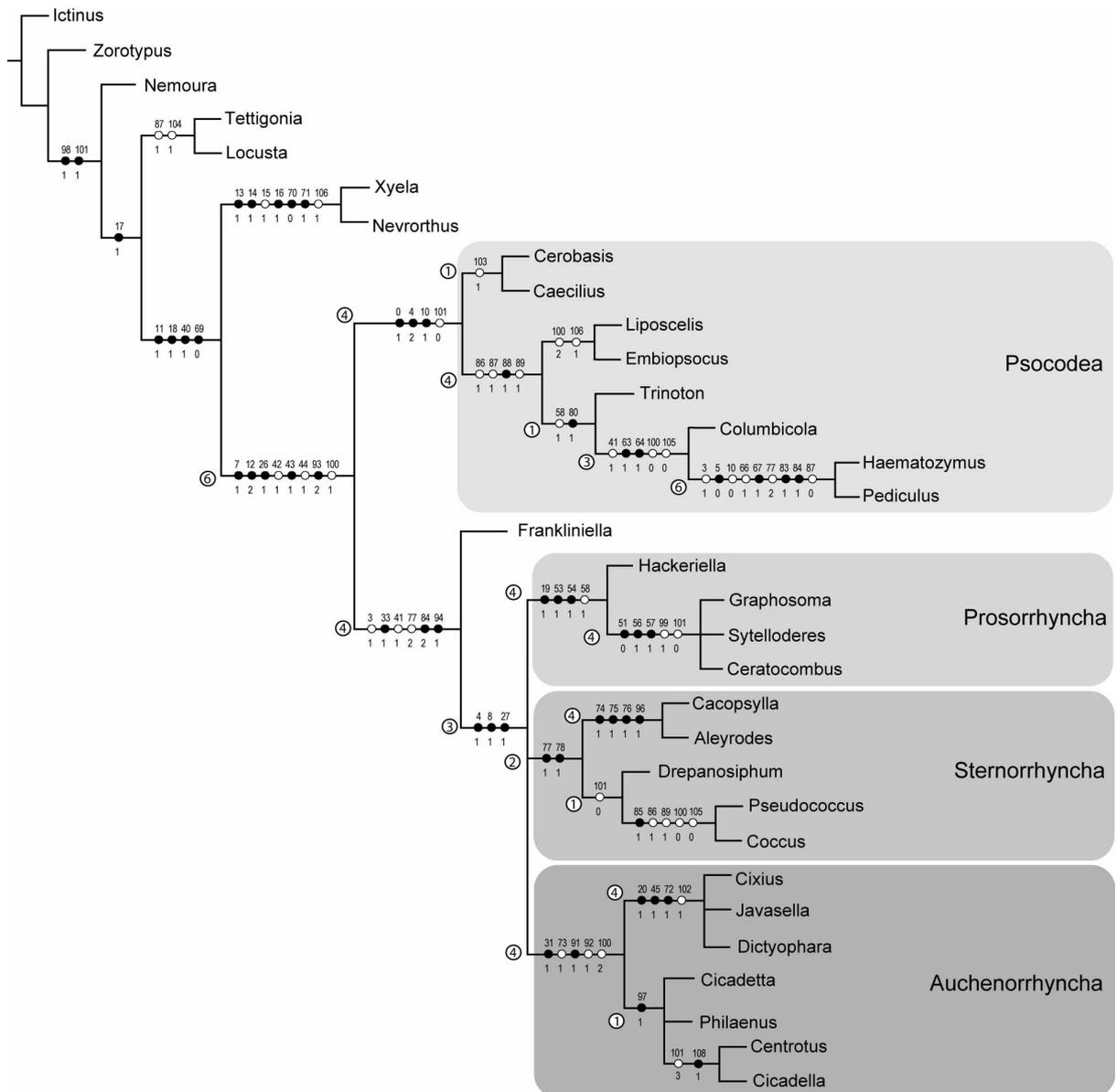


Fig. 7: Strict consensus cladogram of 118 characters (188 steps, Ci: 70, Ri: 86). Black circles indicate non-homoplasious apomorphies, white circles homoplasious ones. Encircled numbers indicate Bremer Support values.

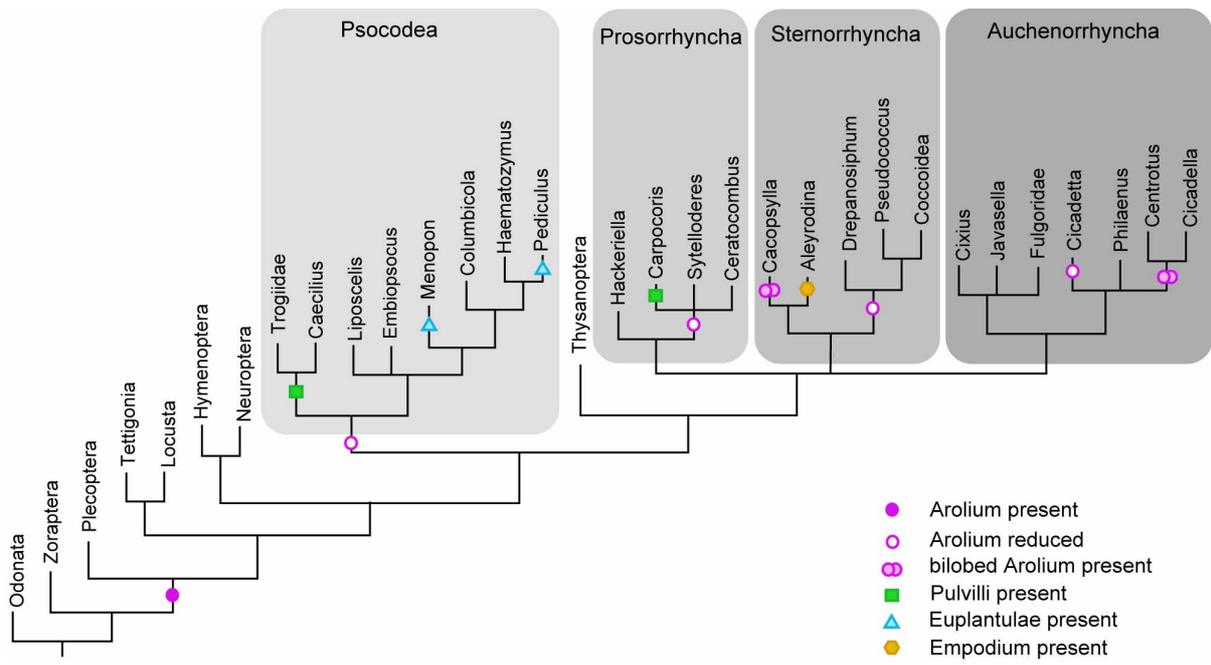


Fig. 8: Strict consensus cladogram of 118 characters, adhesive pad characters mapped on cladogram.