A comparative study of the abdominal trichobothria of Trichophora, with emphasis on Lygaeoidea (Hemiptera: Heteroptera)

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Abstract. Members of the clade Trichophora (Hemiptera: Heteroptera: Pentatomomorpha) have trichobothria on their abdominal sterna. There is no comparative study of the fine structure of abdominal trichobothria in the group and until now the trichobothria of their immatures were virtually unknown. The fine structure of the abdominal trichobothrial complex (= the trichobothrium and its associated structures) of adults of 98 species belonging to 25 families in 5 superfamilies and larvae of 7 species belonging to 7 families in 2 superfamilies of Trichophora were examined using scanning electron microscopy. This study indicates that the fine structure of the abdominal trichobothria is very variable and useful for determining evolutionary lineages within the clade. Six types of bothria, three of trichomes and three of microtrichia are recognized and their evolutionary transformations discussed. Changes in the size of trichomes, and density and size of the microtrichia during the postembryonic development of selected species are discussed.

1. INTRODUCTION

Trichobothria are complex sensory structures usually consisting of a long, slender mechanoreceptive seta (sensillum) set in a depression in the cuticle. They occur on the integument of various arthropods, such as arachnids (Acari, Araneae, Scorpionida, Pseudoscorpionida), myriapods (Pauropoda, Symphyla), entognaths (Collembola, Diplura) and insects (Dahl, 1911, Millot, 1949, Schuh, 1975). Trichobothria occurring on different parts of the body of distantly related groups of arthropods are certainly non-homologous and their remarkably similar morphology is apparently a result of convergent evolution. They most probably act as air current or sound receptors (Drašlar, 1973; Keil, 1997; Yack, 2004) and in spiders they also help in detecting prey (Görner, 1965; Christian, 1971). The functional morphology of trichobothria has been studied using electron microscopy and electrophysiological methods in a few arthropods and insects (Keil, 1997; Barth & Höller, 1999; Yack, 2004).

In insects, trichobothria occur in Thysanura, Archaeognatha, Blattodea, Orthoptera, Psocoptera, Hemiptera and the larvae of certain Lepidoptera (Schuh, 1975; Gaffal,

1976; Mclver & Siemicki, 1984; Keil, 1997). In Hemiptera, the presence of trichobothria is documented in the Fulgoromorpha (Holzinger et al., 2002, Gnezdilov & Wilson, 2007), Coleorrhyncha (China, 1962) and the heteropteran infraorders Gerromorpha, Leptopodomorpha, Cimicomorpha and Pentatomomorpha (Schuh, 1975), but the homology of these morphologically similar structures occurring in different clades is uncertain. Abdominal trichobothria occur in all members of Trichophora (= the infraorder Pentatomomorpha except Aradidae) and in Pachynomidae and Velocipedidae (both belonging to Cimicomorpha) (Carayon & Villiers, 1968; Schuh, 1975; Schuh & Štys, 1991). Strong hairs resembling trichobothria on the pregenital abdominal segments of certain Anthocoridae are documented by Carayon (1972), however, these are probably not homologous with the trichobothria in the above mentioned taxa (Schuh & Štys, 1991). The function of trichobothria in Heteroptera is unclear, but is perhaps multiple and diverse (Davidová & Štys, 1976; Drašlar, 1973; Schaefer, 1975).

The number and disposition of abdominal trichobothria are highly conservative, therefore they have considerable value in the diagnostics of suprageneric taxa

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and morphological phylogenetic studies on Trichophora (Tullgren, 1918; Schaefer, 1975; Henry, 1997a, b; Grazia et al., 2008); they are most thoroughly documented and analyzed in the superfamily Lygaeoidea (Schaefer, 1975). Štys & Davidová-Vilímová (1979) document the intraspecific variability in the number of trichobothria in Pentatomomorpha other than Idiostolidae. Data on trichobothrial patterns in Pentatomoidea are reviewed by Davidová-Vilímová & Štys (1993); morphological diversity in the pentatomid subfamily Podopinae and in the family Cydnidae is recorded and its phylogenetic significance discussed by Davidová-Vilímová & Štys (1993) and Lis & Hohol-Kilinkiewicz (2001a, b; 2002a, b), respectively.

In addition to early microscopic studies (Tullgren, 1918), comprehensive surveys include works on the fine structure of trichobothria occurring on the femora of Miridae (Schuh, 1975) and antennae of Pachynomidae and Reduviidae (Mclver & Siemicki, 1984; Wygodzinsky & Lodhi, 1989; Catalá, 1997; Weirauch, 2003). In spite of the vast literature on the spatial distribution of abdominal trichobothria in Trichophora, there is virtually no data on their individual morphology except for the SEM photographs of a few taxa scattered in the literature (Schuh, 1975; Davidová-Vilímová & Štys, 1993; Schuh & Slater, 1995; Gao & Bu, 2009) and no comparative study of the various taxa. In addition, there is no data on the fine structure of the abdominal trichobothria in immature stages.

The aim of the present study is to document the structural diversity of the abdominal trichobothria and associated structures in Trichophora and evaluate their taxonomic and phylogenetic significance. We dedicate this paper to Thomas J. Henry on the occasion of his 70th birthday, in recognition of his fundamental contribution to the systematics of Trichophora.

2. MATERIALS AND METHODS

2.1 Material examined

The fine structure of the adult abdominal trichobothria (AT) of 98 species of Trichophora (Heteroptera) was studied. The species belonged to the following higher taxa: Lygaeoidea (78 species in 15 families), Coreoidea (5 species in 3 families), Pyrrhocoroidea (2 species in 2 families), Pentatomoidea (12 species in 4 families), Idiostoloidea (1 species in 1 family). The fine structure of the cuticle of the AT of larvae belonging to the Lygaeoidea (6 species in 6 families) and Pentatomoidea (1 species in 1 family) was also studied.

One specimen of each species was examined; multiple specimens were examined when no satisfactory micrographs could be taken using a single specimen. All the specimens examined are preserved in the insect collections of Nankai University, Tianjin, China (NKUM) and Nanjing Forestry University, Nanjing, China (NFU). The taxa included in this study and their depositories are listed in Tables 1 and 2.

2.2 Methods

The abdomens of pinned specimens were removed, cleaned manually, fixed to scanning electron microscope (SEM) stubs using double-sided tape and sputtered with gold in a sputter coater (BAL-TEC SCD 005, Balzers, Switzerland). The fine structure of the cuticle was examined and photographed using a FEI Quanta 200 SEM operated at 15–20 kV.

The family and subfamily level classification used in this paper follows Henry (1997a), and the tribal classification of Rhyparochromidae adopted was from Slater (1964) and Slater & O'Donnell (1995).

3. RESULTS

3.1 Disposition and gross morphology

The ATs are located submedially on sternites III–IV and sublaterally on sternites V–VII in the Lygaeoidea, Coreoidea and Pyrrhocoroidea studied (Fig. 1a–c); all the ATs are located sublaterally in the Pentatomoidea studied.

Each AT is composed of a sensillum (SS) in a bothrium (BO). Further, the AT might be associated with a patch of small cuticular microtrichia, the trichome (TM) (Figs 1–7); the term "trichobothrial complex" is proposed here for the trichobothrium and associated trichome. All the Coreoidea, Pentatomoidea and Idiostoloidea studied have simple ATs composed only of a sensillum and a recessed bothrium (Fig. 3b–e, i). Nevertheless, the trichome in the trichobothrial complex in the species of Lygaeoidea and Pyrrhocoroidea studied is very diverse (Figs 4–5).

3.2 Sensillum

The strong, central mechanoreceptive seta on the AT corresponds to the structure called hair shaft by Gaffal (1976), trichobothrial seta by Weirauch (2003) or simply "hair" by Meßlinger (1987). It is generally circular in cross-section, straight or curved, not twisted and usually with grooves running its whole length (Fig. 4c, j). The base of the sensillum is subcylindrical (Fig. 3a) or slightly constricted (Fig. 3b). If the sensillum is constricted basally, the bothrium usually tends to be recessed. The diameter of the sensillum varied from 1.21 to 4.19 μm in the adult specimens studied.

The lengths of sensilla on different abdominal sternites differ. In Lygaeoidea, the longest sensillum on sternite III or IV is shorter than those on sternites V–VII (Fig. 1a–c); whilst the longest sensilla on sternites V–VII are of subequal length (Fig. 1a–c) in the same individual.

The lengths of sensilla on the same sternite also differ in Lygaeoidea. The shortest sensillum on sternite III can be either (1) the lateralmost one of a triangular group (Fig. 2a); (2) the anteromedian one of a triangular group (Fig. 2d); (3) the lateralmost one of a transverse or oblique row (Fig. 2b); or (4) the middle one of a transverse or oblique row (Fig. 2c). The shortest sensillum is usually the middle one of the three sensilla on sternite IV and the longest sensillum is either the most mesal one or the most lateral one (Fig. 2a).

In Lygaeoidea, the shortest sensillum in the posterior pair on each of the abdominal sternites V–VII is usually the one closest to the midline (Fig. 1d–f), and the longest is usually the anterior one on sternite V (Fig. 1d). The lengths of the anterior one and the more lateral one in the posterior pair on sternite VI are subequal (Fig. 1e), whilst the lateral one is usually longer than the more mesal one on sternite VII in Lygaeoidea (Fig. 1f).

There are two pairs of trichobothria on the lateral portions of each abdominal sternite in the species of Pentatomoidea studied. The sensillum closest to the midline is

Table 1. Taxa included in the analysis of adult abdominal trichobothria.

Superfamily	Family	Subfamily or tribe	Species	Depository
Lygaeoidea	Artheneidae	Artheneini	*Holcocranum diminutum* Horváth, 1898	NKUM
			Artheneis intricata Putshkov, 1969	NKUM
	Berytidae	Metacanthini	*Yemma signatus* (Hsiao, 1974)	NKUM
			Yemma exilis (Horváth, 1905)	NFU
		Metatropini	*Metatropis denticollis* Lindberg, 1934	NKUM
	Blissidae		*Iphicrates spinicaput* (Scott, 1874)	NKUM
	Colobathristidae		*Phaenacantha* sp.	NKUM
	Cryptorhamphidae		*Cryptorhamphus orbus* Stål, 1859	NFU
	Cymidae		*Cymus glandicolor* Hahn, 1832	NKUM
	Geocoridae	Geocorinae	*Geocoris pallidipennis* (Costa, 1843)	NKUM
			Geocoris ochropterus (Fieber, 1844)	NKUM
			Geocoris varius (Uhler, 1860)	NKUM
		Bledionotinae	*Parapamphantus braziliensis* Barber, 1954	NFU
		Henestarinae	*Henestaris oschanini* Bergroth, 1917	NKUM
	Heterogastridae		*Heterogaster chinensis* Zou & Zheng, 1981	NKUM
	Lygaeidae	Ischnorhynchinae	*Pylorgus sordidus* Zheng, Zou & Hsiao, 1979	NKUM
			Kleidocerys resedae (Panzer, 1797)	NKUM
		Lygaeinae	*Lygaeosoma pusillum* (Dallas, 1852)	NKUM
			Lygaeus equestris (Linnaeus, 1758)	NKUM
			Spilostethus hospes (Fabricius, 1794)	NKUM
			Arocatus rufipes Stål, 1872	NKUM
			Tropidothorax sinensis (Reuter, 1888)	NFU
		Orsillinae	*Nysius ericae* (Schilling, 1829)	NKUM
			Ortholomus punctipennis (Herrich-Schäffer, 1838)	NKUM
			Sinorsillus piliferus Usinger, 1938	NKUM
	Malcidae	Malcinae	*Malcus auriculatus* Stys, 1967	NKUM
		Chauliopinae	*Chauliops horizontalis* Zheng, 1981	NKUM
			Chauliops fallax Scott, 1874	NKUM
			Chauliops bisontula Banks, 1909	NKUM
			Chauliops zhengi Xue & Bu, 2004	NKUM
			Chauliops quaternaria Gao & Bu, 2009	NKUM
			Chauliops conica Gao & Bu, 2009	NKUM
	Ninidae		*Ninomimus flavipes* (Matsumura, 1913)	NKUM
			Ninus insignis Stål, 1860	NKUM
			Cymoninus turaensis (Paiva, 1919)	NKUM
	Oxycarenidae		*Oxycarenus lugubris* (Motschulsky, 1859)	NKUM
			Oxycarenus hsiaoi Péricart, 2001	NKUM
	Pachygronthidae	Pachygronthini	*Pachygrontha antennata antennata* (Uhler, 1860)	NKUM
		Teracriini	*Pachyphlegyas modiglianii* (Lethierry, 1888)	NKUM
			Stenophyella macreta Horváth, 1914	NKUM
	Piesmatidae		*Piesma* sp.	NKUM
	Rhyparochromidae	Plinthisinae	*Plinthisus maculatus* (Kiritshenko, 1931)	NKUM
		Antillocorini	*Botocudo marianensis* (Usinger, 1946)	NKUM
		Cleradini	*Harmostica hirsuta* (Usinger, 1942)	NKUM
		Drymini	*Drymus sylvaticus* (Fabricius, 1775)	NKUM
			Drymus orientalis Kerzhner, 1977	NKUM
			Eremocoris sinicus Zheng, 1981	NKUM
			Paradieuches dissimilis (Distant, 1883)	NKUM
			Retoka gibba (Zheng, 1981)	NKUM
		Gonianotini	*Pionosomus opacellus* Horváth, 1895	NKUM
			Trapezonotus arenarius elegantulus Kiritshenko & Scudder, 1973	NKUM
			Emblethis brachynotus Horváth, 1897	NKUM
		Lethaeini	*Neolethaeus dallasi* (Scott, 1874)	NKUM
			Neolethaeus densus Li & Bu, 2006	NKUM
			Diniella sevosa (Distant, 1901)	NKUM
		Megalonotini	*Lamprodema maura* (Fabricius, 1803)	NKUM
			Sphragisticus nebulosus (Fallén, 1807)	NKUM
		Myodochini	*Pachybrachius luridus* Hahn, 1826	NKUM
			Pamerana scotti (Distant, 1901)	NKUM
			Gyndes pallicornis (Dallas, 1852)	NKUM
			Eucosmetus incisus (Walker, 1872)	NKUM
			Horridipamera lateralis (Scott, 1874)	NKUM
			Paromius gracilis (Rambur, 1839)	NKUM
			Pamerarma ventralis (China, 1930)	NKUM
			Pseudopachybrachius guttus (Dallas, 1852)	NKUM
			Ligyrocoris sylvestris (Linnaeus, 1758)	NKUM
		Ozophorini	*Bryanellocoris orientalis* Hidaka, 1962	NKUM
			Prosomoeus brunneus Scott, 1874	NKUM
			Vertomannus emeia Zheng, 1981	NKUM
			Primierus longispinus Zheng, 1981	NKUM
		Rhyparochromini	*Scudderocoris albomarginatus* (Scott, 1874)	NKUM
			Panaorus csikii (Horváth, 1901)	NKUM
			Panaorus albomaculatus (Scott, 1874)	NFU
			Usilanus burmanicus Distant, 1909	NKUM
			Poeantius lineatus Stål, 1874	NKUM
			Peritrechus convivus (Stål, 1858)	NKUM
			Dieuches femoralis Dohrn, 1860	NKUM
			Metochus abbreviatus Scott, 1874	NKUM
Coreoidea	Alydidae	Alydinae	*Riptortus linearis* (Fabricius, 1775)	NKUM
			Riptortus pedestris Fabricius, 1775	NFU
	Coreidae	Coreinae	*Cletus punctiger* (Dallas, 1852)	NKUM
			Homoeocerus striicornis Scott, 1874	NFU
	Rhopalidae	Rhopalinae	*Rhopalus sapporensis* (Matsumura, 1905)	NKUM
Pentatomoidea	Pentatomidae	Pentatominae	*Menida violacea* Motschulsky, 1861	NKUM
			Eysarcoris annamita Breddin, 1909	NFU
			Erthesina fullo (Thunberg, 1783)	NFU
			Plautia fimbriata (Fabricius)	NFU
	Plataspidae		*Megacopta cribraria* (Fabricius, 1977)	NFU
	Scutelleridae	Hoteinae	*Hotea curculionoides* (Herrich-Schäffer, 1836)	NKUM
		Scutellerinae	*Lamprocoris roylii* (Westwood, 1837)	NKUM
			Lamprocoris lateralis (Guérin-Méneville, 1838)	NKUM
	Cydnidae	Sehirinae	*Adomerus notatus* (Jakovlev, 1882)	NKUM
			Sehirus cinctus cinctus (Palisot de Beauvois, 1805)	NKUM
		Cydninae	*Fromundus pygmaeus* (Dallas, 1851)	NKUM
			Adrisa magna (Uhler, 1860)	NFU
Pyrrhocoroidea	Largidae	Physopeltini	*Physopelta cincticollis* Stål, 1863	NKUM
	Pyrrhocoridae		*Pyrrhopeplus posthumus* Horváth, 1892	NKUM
Idiostoloidea	Idiostolidae		*Monteithocoris* sp.	NKUM

NKUM – Nankai University, Tianjin, China; NFU – Nanjing Forestry University, Nanjing, China.

Table 2. Taxa included in the analysis of larval abdominal trichobothria.

Superfamily	Family	Subfamily or tribe	Species	Depository
Lygaeoidea	Malcidae	Chauliopinae	*Chauliops fallax* Scott, 1874	NKUM
	Blissidae		*Dimorphopterus* sp.	NKUM
	Oxycarenidae		*Oxycarenus hsiaoi* Péricart, 2001	NKUM
	Heterogastridae		*Heterogaster chinensis* Zou & Zheng, 1981	NKUM
	Geocoridae	Geocorinae	*Geocoris varius* (Uhler, 1860)	NKUM
	Pachygronthidae	Pachygronthini	*Pachygrontha antennata antennata* (Uhler, 1860)	NKUM
Pentatomoidea	Pentatomidae	Pentatominae	*Menida* sp.	NKUM

NKUM – Nankai University, Tianjin, China.

longer than the more lateral one, which is opposite to the condition in Lygaeoidea (Fig. 1g).

The pairs of the sensilla are usually deflected symmetrically on both sides of the abdomen, but no other regularities were recorded in the direction of the deflection.

3.3 Bothrium

The sensillum is invariably inserted on a small, dome-shaped cuticular protuberance (Fig. 3a, c). Following Weirauch (2003) we call it a dome; it corresponds to the "socket ring" of Meßlinger (1987). The dome is surrounded by a cavity in the cuticle that is recessed to different extents, the bothrium; the inner wall of the bothrium usually protrudes above the surface of the surrounding cuticle, and this rim-like outer wall then blends in with the surrounding flat area of cuticle.

The bothrium can be concave to various extents, but two rather distinct types could be differentiated.

Type A: the bothrium is deeply recessed into the surrounding cuticle, more or less cup- or cavity-like. All the members of Pentatomoidea and Coreoidea studied, and the single member of Idiostoloidea studied have bothria of this type (Fig. 3b–i). Such bothria apparently occur only exceptionally in Lygaeoidea (Artheneidae, Piesmatidae, Cryptorhamphidae, and some Lygaeidae: Lygaeinae).

On the inner wall of the type A bothrium there are various outgrowths of cuticle (OG) (Figs 3; 4a–c). The following five subtypes can be recognized based on the shapes of the rim of the recessed bothrium and the outgrowths inside the cavity (Table 3).

Type A1: the bothrium is surrounded by a thick elevated rim of cuticle; outside of the bothrium the cuticle is distinctly rugose; the wall of its cavity bears short, irregular outgrowths (Fig. 3i). This type was only recorded in the single species of Idiostolidae studied.

Type A2: bothrium is surrounded by a circular, thick, rather elevated rim; the inner wall of the cavity has radially arranged, divergent, ridge-like outgrowths (Fig. 3b–e). This type occurs in Coreoidea and Pentatomoidea.

Type A3: bothrium is surrounded by a circular, thick, rather elevated rim; the inner wall of the cavity has irregularly arranged finger-like, columnar outgrowths that are rather slim and straight (Fig. 3f–g) or geniculate proximal to a broadened tip (Fig. 6d). This type occurs in Piesmatidae and Cryptorhamphidae.

Type A4: the inner wall of the cavity is covered with irregularly arranged cone-shaped, rather stout outgrowths; there are also outgrowths on the rim of the bothrium, which therefore appears serrate (Fig. 3h). This type was recorded

in some of the species of Artheneidae studied (*Artheneis intricata*).

Type A5: the bothrium is deeply recessed and it has a high rim; the wall of the cavity has transverse lamellae which are usually somewhat wavy or sparsely serrate (Fig. 4a–c). This type was recorded in the majority of the Lygaeinae studied (genera *Lygaeus*, *Lygaeosoma*, *Spilostethus*, *Tropidothorax*).

Type B: the bothrium is shallow, the base of the sensillum is not sunk below the surface of the cuticle, therefore the dome-shaped protuberance is very visible (Figs 2; 3a). This is the most common type in the Lygaeoidea and the only type of bothrium in most of the included families studied. The species of Pyrrhocoroidea studied also have this kind of trichobothrium. In some groups (e.g. Orsillinae, Teracriini) it might appear to be somewhat more strongly recessed due to the fusion of surrounding microtrichia, but it never approaches the condition found in type A (Fig. 5d–f).

3.4 Trichome

The trichobothrium is frequently surrounded by a trichome, an area of densely arranged microtrichia (MT) (Figs 4–5). Trichomes are present in all the species of the superfamily Pyrrhocoroidea and the majority of Lygaeoidea studied, whereas all members of Pentatomoidea, Coreoidea and Idiostoloidea, and the lygaeoid families Oxycarenidae, Piesmatidae, Cryptorhamphidae and Berytidae studied lack trichomes (Table 3).

The microstructure of adult abdominal trichomes is complex and diverse. The bases of microtrichia are frequently more or less fused, especially in the region immediately surrounding the insertion of the sensillum. Based on this feature three types can be recognized (Table 3):

Type T1: microtrichia are nearly uniform, distinctly separate from each other (Fig. 4d–h), or at most fused basally, forming a simple linear series (Fig. 4i–j: SR) occurring only in the area immediately surrounding the bothrium or in other areas of the trichome. This type occurs in the majority of the lygaeoid subgroups except for the few exceptions listed below.

Type T2: the bases of microtrichia near the bothrium are broadly fused into a reticulate structure and only their apical portions are free (Fig. 5a–c; g–i). This type occurs in some of the Rhyparochrominae (*Neolethaeus dallasi*, *N. densus*, *Dieuches femoralis*) and all of the Henestaridae, Cymidae, Ninidae and Malcidae (both Malcinae and Chauliopinae) studied.

Type T3: all the microtrichia are fused into a reticulate structure, with the apical portions of the individual micro-
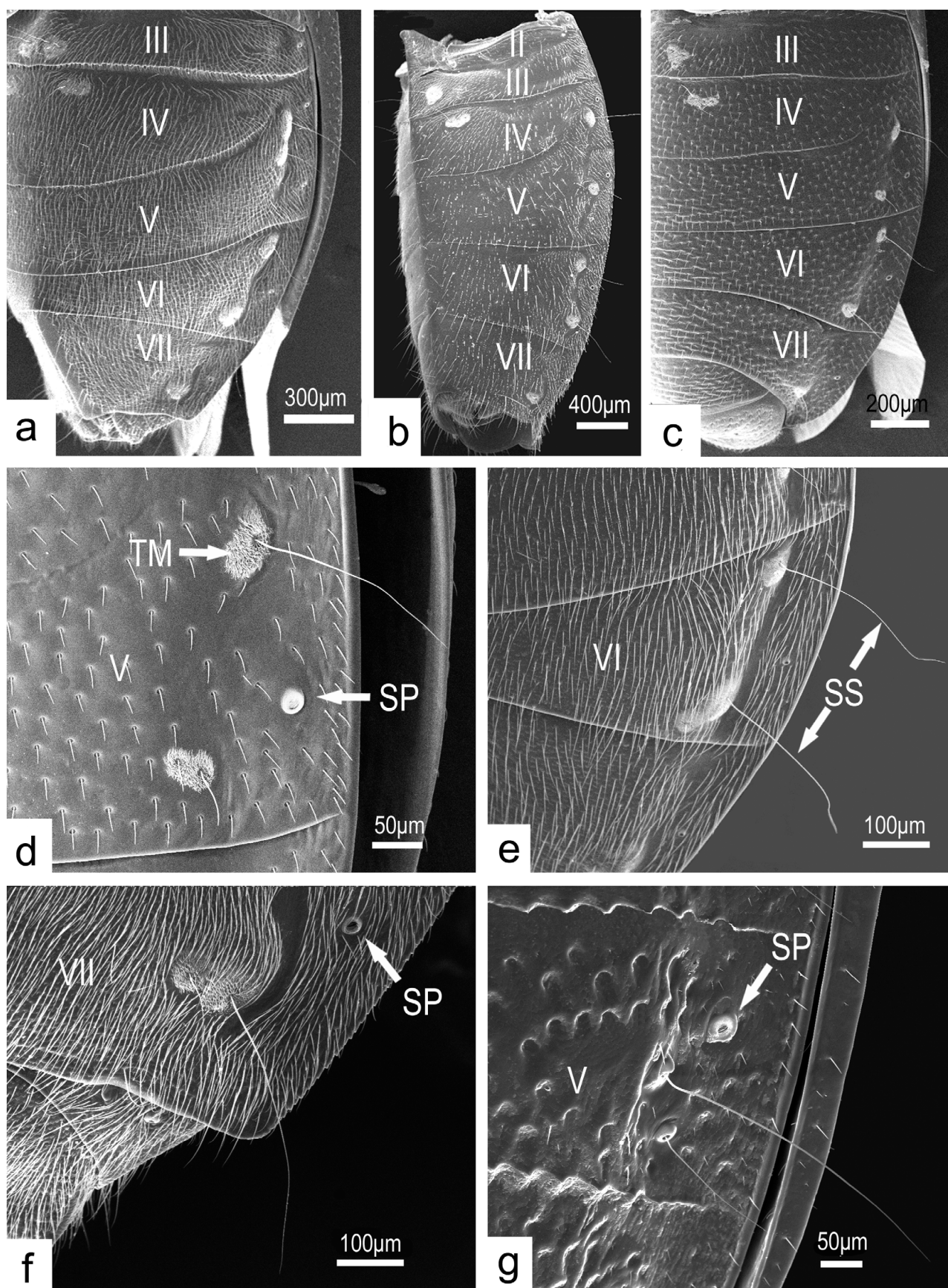
Fig. 1. a–c: Abdomen, ventrolateral view. a – *Drymus sylvaticus* (Rhyparochromidae: Drymini); b – *Harmostica hirsuta* (Rhyparochromidae: Cleradini); c – *Lamprodema maura* (Rhyparochromidae: Megalonotini); d – trichobothria on sternite V of *L. maura*; e – trichobothria on sternite VI of *Botocudo marianensis* (Rhyparochromidae: Antillocorini); f – trichobothria on sternite VII of *Eucosmetus incisus* (Rhyparochromidae: Myodochini); g – trichobothria on sternite V of *Fromundus pygmaeus* (Cydnidae). TM – trichome; SP – spiracle; SS – sensillum. Roman numerals indicate the homologies of the sternites.
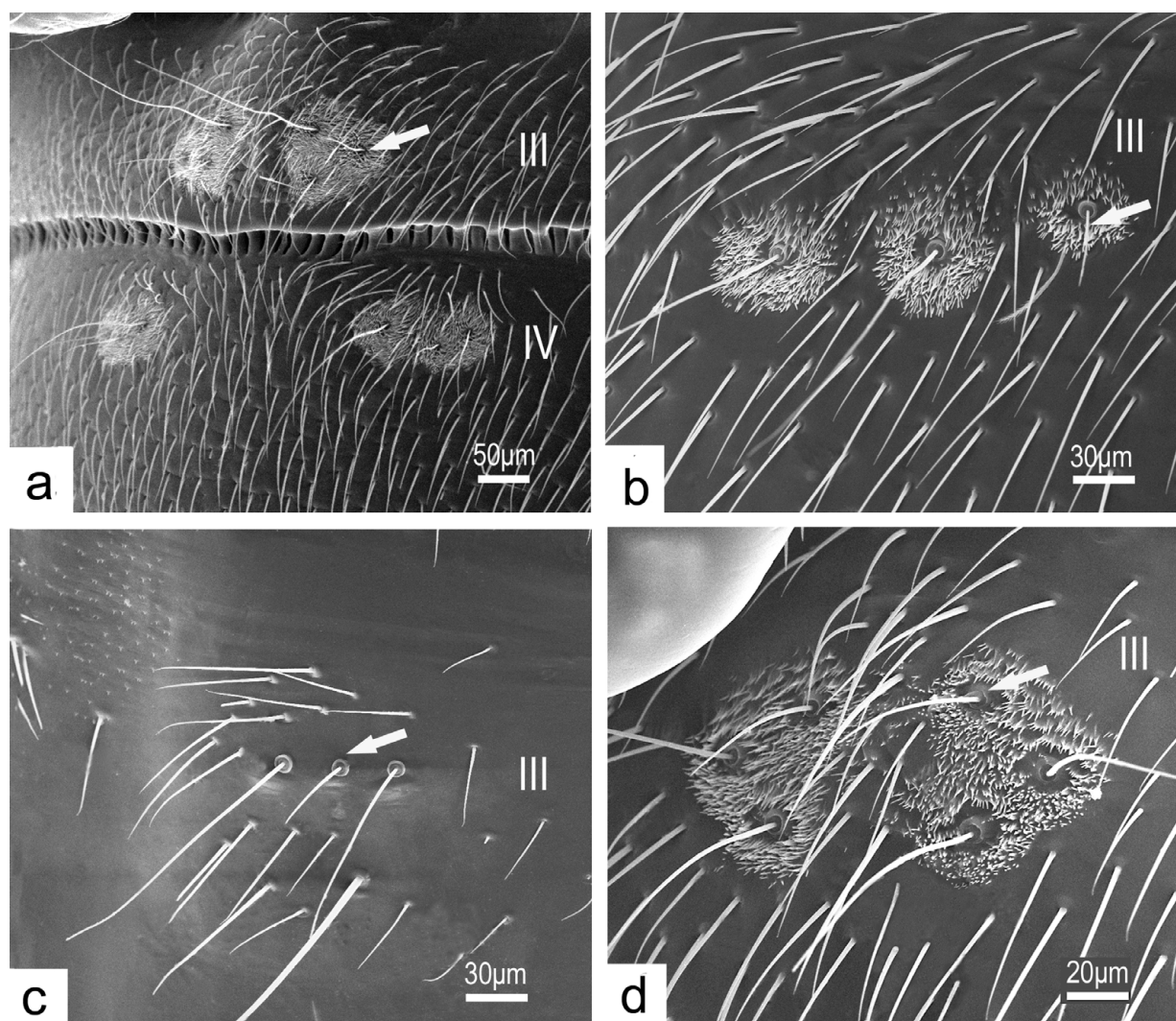
Fig. 2. a – arrangement of trichobothria on sternites III–IV of *Paromius gracilis* (Rhyparochromidae: Myodochini); b–d – arrangement of trichobothria on sternite III. b – *Heterogaster chinensis* (Heterogastridae); c – *Oxycarenus lugubris* (Oxycarenidae); d – *Geocoris pallidipennis* (Geocoridae). Roman numerals indicate the homologies of the sternites. Arrows indicate the position of the shortest sensillum on sternite III.

trichia still separate (Fig. 5d) or completely indistinguishable (Fig. 5e–f). This type occurs in some of the Orsillinae (*Nysius ericae*, *Ortholomus punctipennis*) and in both members of Pachygronthidae: Teracriini studied.

The shape of the individual microtrichia is also diverse. Three types can be distinguished (Table 3):

Type M1: microtrichia hair-, spine- or cone-like, gradually tapering towards apex, straight or slightly curved (Figs 4a–j; 5a–c). The overwhelming majority of the species of Lygaeoidea have such trichobothria.

Type M2: microtrichia subcylindrical, with a very swollen base, apical portion strongly curved, sharply tapering into a pointed tip (Figs 4k, l; 5g, h). This type was present in all the species of Pyrrhocoridae and Blissidae studied.

Type M3: microtrichia flattened, with a very swollen base, apical portion elongate and geniculate immediately proximal of a broadened tip (Fig. 5i–l). This type occurred in all the species of Cymidae and Malcidae (both Malcinae and Chauliopinae) studied.

Some species have a diffuse trichome. In these species sparsely scattered microtrichia occur virtually all over the integument of the respective abdominal sternites and the density of the microtrichia gradually decreases with the distance from the trichobothrium, therefore the trichome is indistinctly delimited. In several cases diffuse trichomes extend over a large area of the abdominal venter. Diffuse trichomes occurred in some of the species of Blissidae, Colobathristidae, Lygaeidae: Lygaeinae and Rhyparochromidae: Drymini studied (Fig. 4k).

The trichome is on a distinct tubercle in Malcidae (Fig. 5k), Lygaeidae: Orsillinae, and Teracriini (Pachygronthidae) (Fig. 5d–f).

In groups with closely spaced trichobothria, the trichomes belonging to the individual trichobothria are commonly confluent, therefore the group of trichobothria appears to be surrounded by a single patch of microtrichia (Figs 2a, d; 4h; 5a, e, i, k). This was recorded on sternites III–VII of a variety of lygeoid taxa, but without a clear taxonomic pattern.
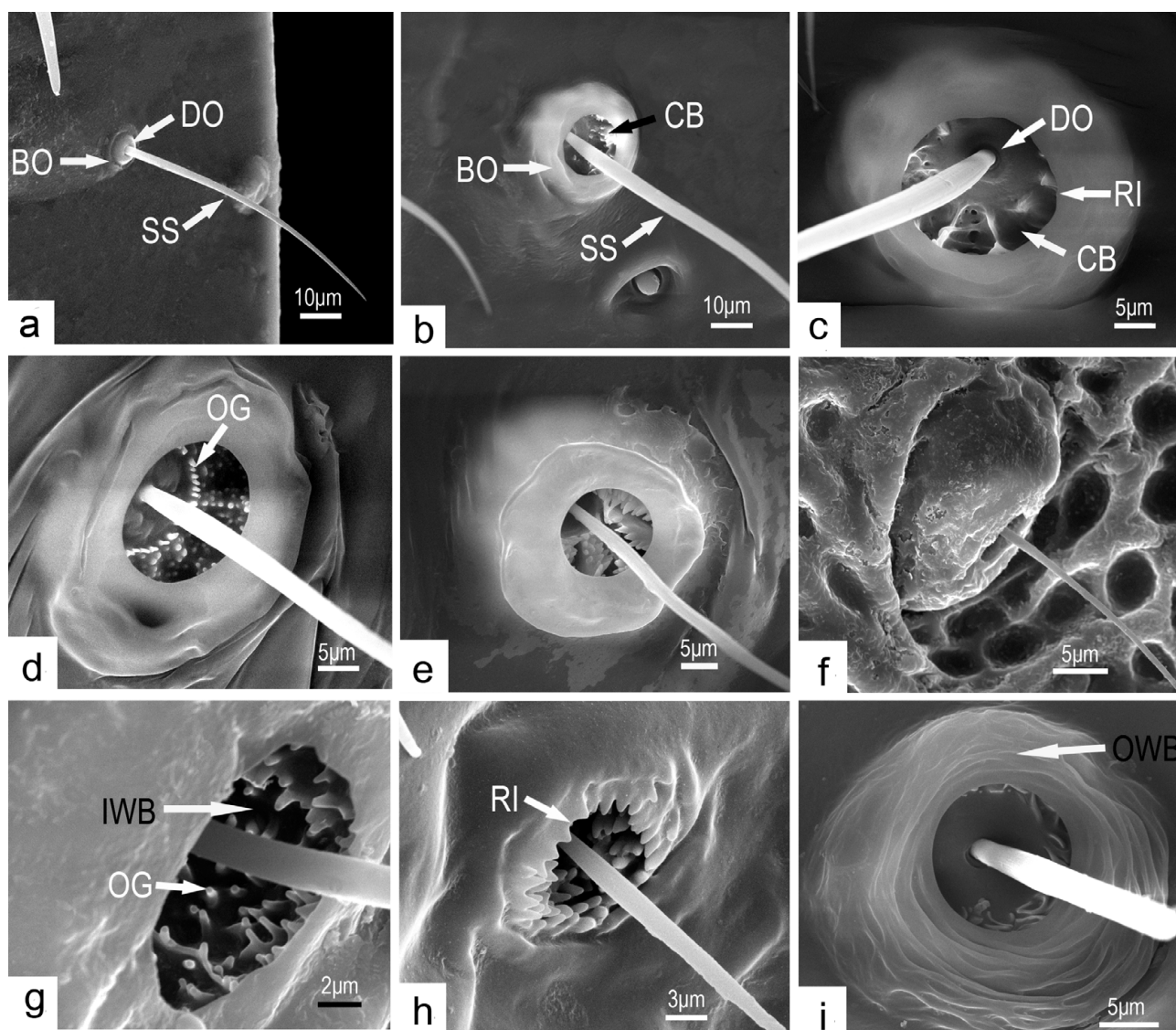
Fig. 3. Trichobothria of species of Pentatomoidea, Coreoidea, Idiostoloidea, and Lygaeoidea. a – on sternite V of *Yemma signatus* (Berytidae); b – on sternite V of *Cletus tenuis* (Coreidae); c – laterally on sternite III of *Riptortus linearis* (Alydidae); d – laterally on sternite IV of *Menida violacea* (Pentatomidae); e – laterally on sternite III of *Adomerus notatus* (Cydnidae); f – on sternite V of *Piesma* sp. (Piesmatidae); g – on sternite VI *Piesma* sp. (Piesmatidae); h – mesal trichobothrium of the posterior pair on sternite VI of *Artheneis intricata* (Artheneidae); i – trichobothrium of *Monteithocoris* sp. (Idiostolidae). BO – bothrium; CB – cavity of bothrium; DO – dome-shaped part of bothrium; IWB – inner wall of bothrium; OG – outgrowth inside the cavity of a recessed bothrium; OWB,– outer wall of bothrium; RI – rim of bothrium; SS – sensillum.

3.5 Trichobothria of larvae of Trichophora

For six species of Lygaeoidea, trichobothria of adults and different larval instars were examined. Conspecific larvae were also examined in an additional lygaeoid and a pentatomid species.

In all the conspecific larvae and adults studied the trichobothria were of the same type in all stages. However, considerable differences were recorded among the developmental stages in the size and density of the trichomes. The microtrichia are generally much smaller and fewer in larvae than in conspecific adults, and the sensilla are also shorter (Fig. 7). In *Chauliops fallax* (Malcidae: Chauliopinae) the size of the trichome and the number and length of the microtrichia increase gradually from the first instar to the adult (Fig. 7a–i).

4. DISCUSSION

4.1 Character polarity

4.1.1 Direction of deflection and disposition of sensilla of different lengths

The AT is innervated by one or several sensory neurons (Keil, 1997; Weirauch, 2003) and the articulation at their base allows deflection of each sensillum in only one exactly defined plane (Keil, 1997). Sensilla of different lengths usually also have different functions (Drašlar, 1973). During this study no clear patterns were detected either in the usual direction of deflection or the arrangement of sensilla of different lengths on each sternite. Accordingly, these characters were not used for analyzing the evolutionary transitions in the trichobothrial complex.
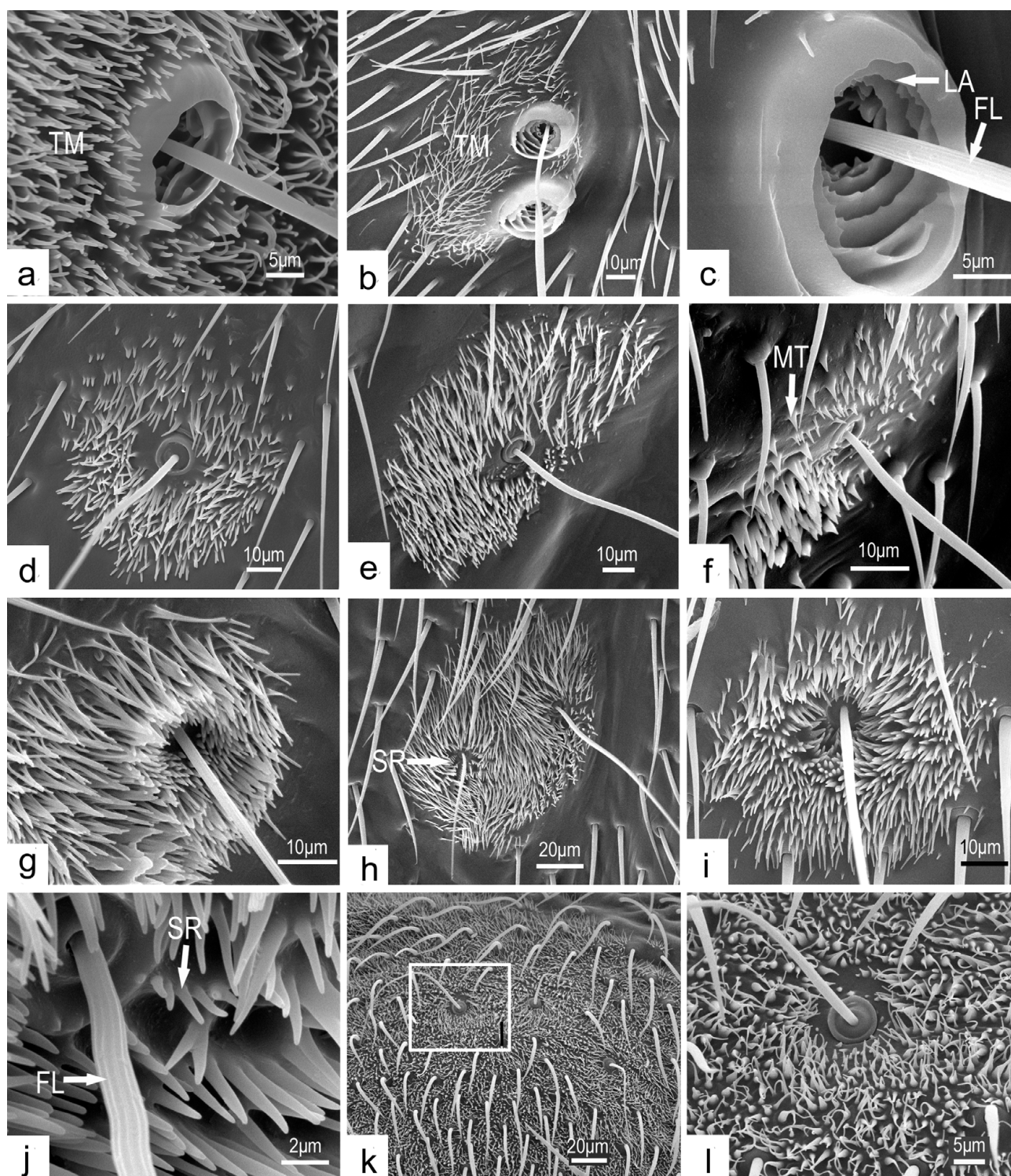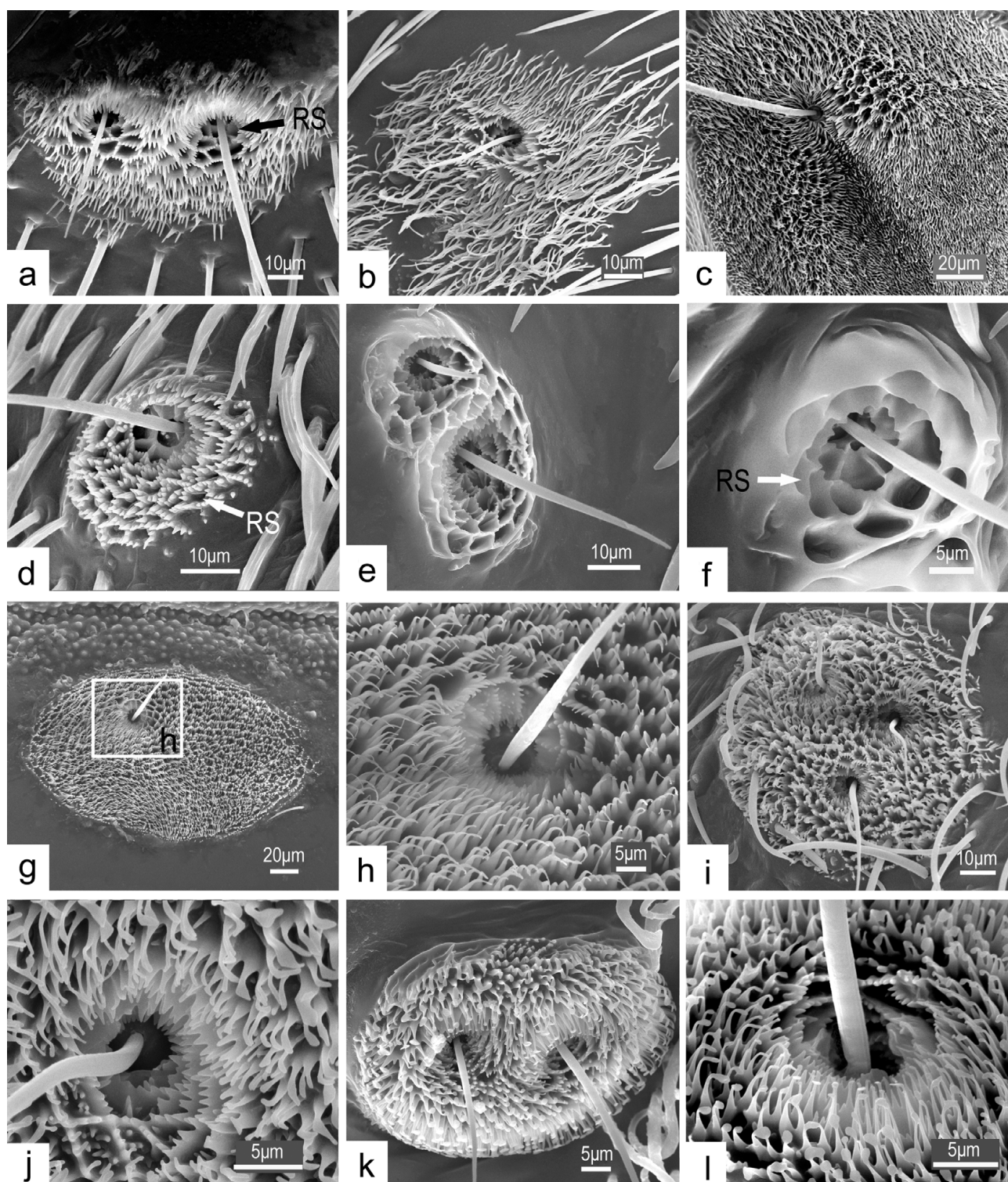
Fig. 4. a – trichobothrium on sternite V of *Spilostethus hospes* (Lygaeidae: Lygaeinae); b – posterior two trichobothria on sternite VI of *Lygaeosoma pusillum* (Lygaeidae: Lygaeinae); c – anterior trichobothrium on sternite V of *L. pusillum*; d – the middle trichobothrium on sternite III of *Heterogaster chinensis* (Heterogastridae); e – anterior trichobothrium on sternite VI of *Geocoris ochropterus* (Geocoridae: Geocorinae); f – lateral trichobothrium of the posterior row on sternite VI *Plinthisus maculatus* (Rhyparochromidae: Plinthisinae); g – lateral trichobothrium on sternite VII of *Arocatus rufipes* (Lygaeidae: Lygaeinae); h – posterior two trichobothria on sternite V of *Drymus sylvaticus* (Rhyparochromidae: Drymini); i – lateral trichobothrium on sternite IV of *Trapezonotus arenarius elegantulus* (Rhyparochromidae: Gonianotini); j – anterior trichobothrium on sternite V of *T. a. elegantulus* (Rhyparochromidae: Gonianotini), enlarged; k – three trichobothria on sternite III of *Iphicrates spinicaput* (Blissidae); l – part of Fig. 4k, enlarged. FL – fluting of sensillum; LA – lamellae of bothrium; MT – microtrichium of trichome; SR – fused simple rows of microtrichia; TM – trichome.

4.1.2 Bothrium

The topographic arrangement of AT in Idiostolidae (documented, among others, by Scudder, 1962; Schaefer, 1966a, b, 1975; Woodward, 1968a, b; Schaefer & Wilcox, 1969) is widely considered to represent the most plesiomorphic character state among Trichophora, although

Fig. 5. a – two trichobothria on sternite VII of *Henestaris oschanini* (Geocoridae: Henestarinae); b – middle trichobothrium on sternite III of *Ninomimus flavipes* (Ninidae); c – anterior trichobothrium on sternite V of *Neolethaeus densus* (Rhyparochromidae: Lethaeini); d – middle trichobothrium on sternite III of *Nysius ericae* (Lygaeinae: Orsillinae); e – two trichobothria on sternite V of *Stenophyella macreta* (Pachygronthidae: Teracriini); f – anterior trichobothrium on sternite VI of *Pachyphlegyas modiglianii* (Pachygronthidae: Teracriini); g – anterior trichobothrium on sternite III of *Pyrrhopeplus posthumus* (Pyrrhocoridae); h – part of Fig. 5g, enlarged; i – three trichobothria on sternite III of *Cymus glandicolor* (Cymidae); j – lateral trichobothrium on sternite VI of *C. glandicolor*; k – posterior two trichobothria on sternite V of *Chauliops quaternaria* (Malcidae: Chauliopinae); l – lateral trichobothrium on sternite III of *Chauliops horizontalis*. RS – reticulate structure.

not directly ancestral to any existing pattern (Štys, 1967; Schaefer, 1966a, b, 1975, 1993; Schaefer & Wilcox, 1969). Because an AT having a recessed bothrium is found not only in Idiostolidae, but also in Pentatomoidea, the group usually considered as the sister group of the rest of Trichophora (Henry, 1997a; Hua et al., 2008; Tian et al., 2011; Yuan et al., 2015; Li et al., 2016, 2017; Wang et al., 2016), and such bothria are also common in many groups
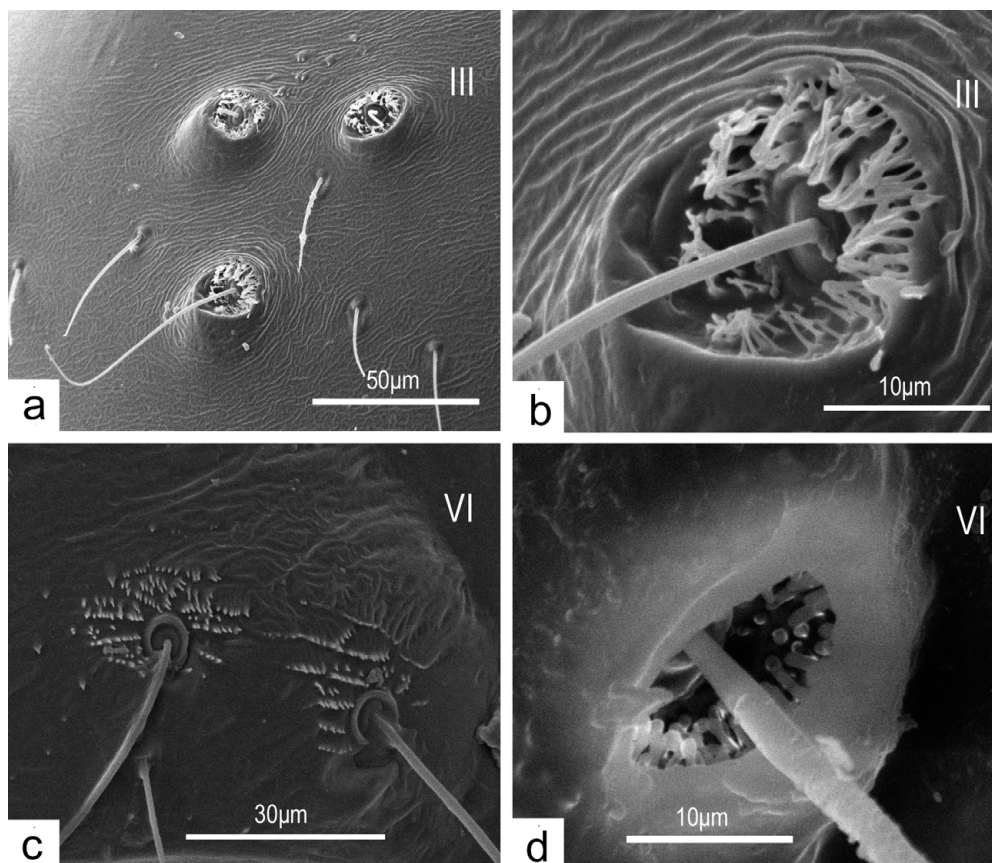
Fig. 6. a – three trichobothria on sternite III of *Parapamphantus braziliensis* (Geocoridae: Bledionotinae); b – posterior trichobothrium on sternite III of *P. braziliensis*; c – posterior pair of trichobothria on sternite VI of *P. braziliensis*; d – trichobothrium on sternite VI of *Cryptorhamphus orbus* (Cryptorhamphidae). Roman numerals indicate the homologies of the sternites.

of arthropods (Millot, 1949; Meßlinger, 1987; Alberti et al., 1994; Miller et al., 2011), we regard the presence of deeply recessed (type A) bothria as plesiomorphic and the shallow (type B) bothria with exposed dome-shaped protuberance as derived within the Trichophora.

A secondary type A bothrium, however, can apparently be derived from the type B by fusion of the microtrichia immediately surrounding the base of the sensillum and uniting into an elevated, cup-like structure. The morphology of such a bothrium is virtually identical to that of the ancestral type A bothria that occurs in early offshoots of Trichophora (Pentatomoidea, Coreoidea). Such bothria are recorded in Piesmatidae (*Piesma*), Cryptorhamphidae (*Cryptorhamphus*) and some of the members of Artheneidae (*Artheneis*) and Lygaeinae studied (genera *Lygaeus*, *Lygaeosoma*, *Spilostethus*, *Tropidothorax*).

The bothrium in the two members of Teracriini studied is of type B, however, it appears more strongly recessed than in other typical species of this group (Fig. 5e–f). The condition of the bothrium found in these taxa can be considered to be between types B and A: the microtrichia surrounding the sensillum are united into a reticulate, lamellar structure superficially resembling the rim of a typical type A bothrium, which is incompletely fused.

4.1.3 Trichome

The AT are not associated with trichomes either in Pentatomoidea, Coreoidea or Idiostolidae; therefore we consider the lack of a trichome as a plesiomorphy and presence of a trichome as an apomorphy.

In the vast majority of the taxa with trichomes, including the basal lineages, the individual microtrichia are simple, straight and more or less hair-like (type M1). Modified microtrichia only occur in a few isolated taxa (type M2 in Pyrrhocoridae and Blissidae, type M3 in Malcidae and Cymidae). Type M1 is therefore considered as the plesiomorphic character state, probably from which both types M2 and M3 are derived.

4.2 Ontogenetic evidence and the evolutionary origin of the trichome

The trichome of the first instar larva of *Chauliops fallax* (Malcidae: Chauliopinae) (Fig. 7f) is compact and the individual microtrichia are densely packed and strongly resemble the elevated rim of a type A trichobothrium. The condition in later instars (Fig. 7g–h) is very similar to the type B trichobothrium of the adult (Fig. 7i). During ontogeny the trichome becomes flattened and the inner microtrichia that immediately surround the sensillum are directed horizontally, but become reflexed and directed more or less perpendicularly to the plane of the integument.

The type A bothrium usually has cuticular outgrowths (types A1, A3–A4) (Fig. 3f–i) or lamellae (types A2 and A5) (Figs 3b–e, 4a–c) on the inner wall of the bothrial cavity. The outgrowths are frequently similar to the microtrichia that make up the trichome. Type A bothrium is not
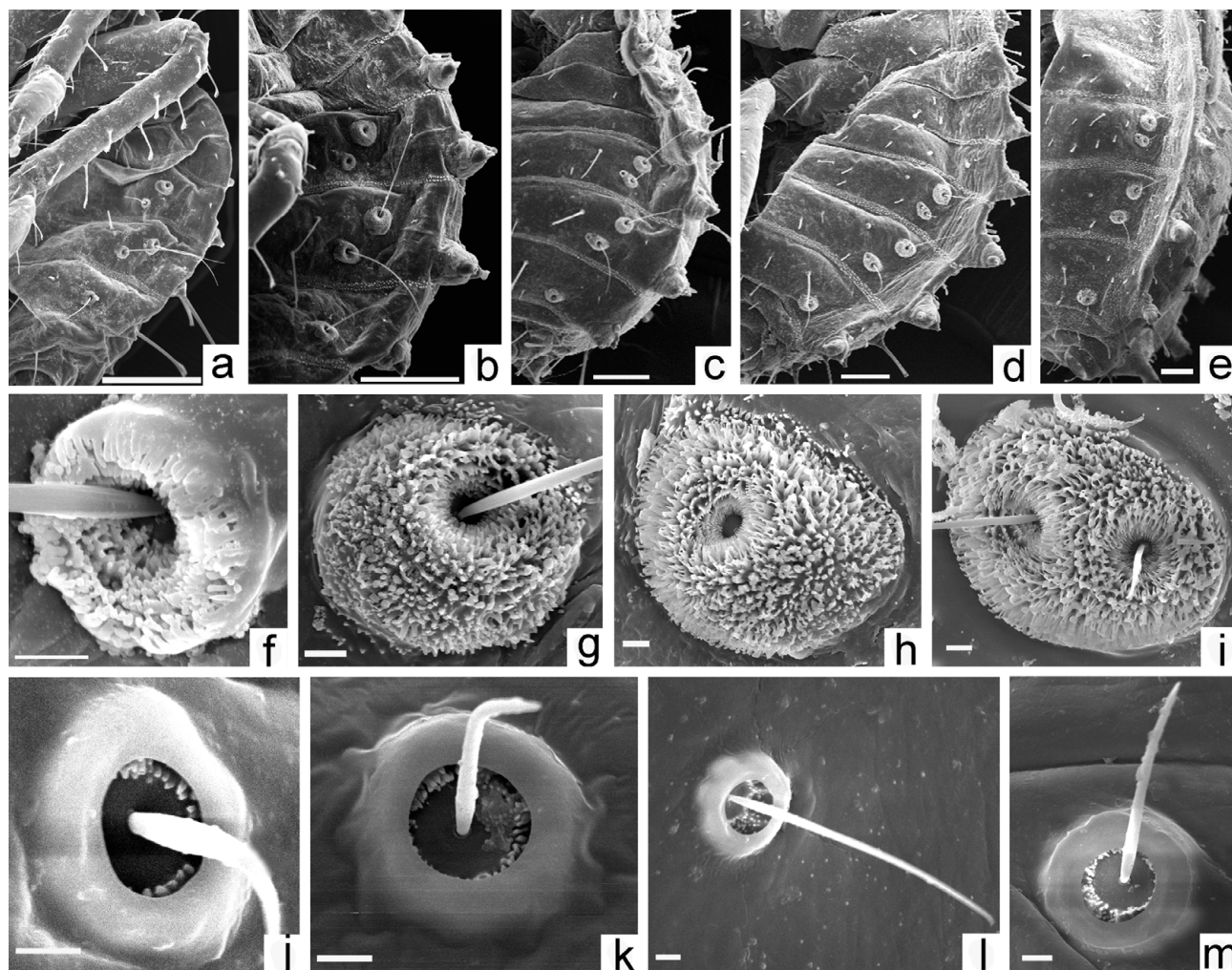
Fig. 7. Abdominal trichobothria of larvae. a–i – *Chauliops fallax* (Malcidae: Chaulopinae). a–e – abdomen, lateral view. a – first instar; b – second instar; c – third instar; d – fourth instar; e – fifth instar; f–i – trichobothria. f – first instar, posterior trichobothrium on sternite VI; g – third instar, anterior trichobothrium on sternite VI; h – fifth instar, anterior trichobothrium on sternite V; i – adult, trichobothrium on sternite III; j–m – *Menida* sp., trichobothria. j – first instar, trichobothrium on sternite VII; k – third instar, trichobothrium on sternite VII; l – fourth instar, trichobothrium on sternite IV; m – fifth instar, trichobothrium on sternite VII. Scales: a–e – 100 μm; f–m – 5 μm.

associated with the trichome in the vast majority of cases. These facts offer a seemingly plausible explanation for the evolutionary origin of the trichome: it is perhaps derived from an eversion of the inner wall of the bothrial cavity and externalization of its cuticular outgrowths. Among the subgroups of the type A bothrium, subtypes A3 (Fig. 3g) and A4 (Fig. 3h) are the most similar to the condition found in the first instar larva of *C. fallax* (Fig. 7f), and these are apparently derived conditions in which the inner wall of the bothrial cavity is partially everted.

In *Parapamphantus braziliensis* (Geocoridae: Bledionotinae) sternites V–VII have typical type T1 trichomes (Fig. 6c), whilst sternites III–IV have trichomes with a shallow concavity immediately surrounding the sensilla (Fig. 6a–b). As the trichobothria on different abdominal sternites are presumably serially homologous, the presence of these different types also seemingly support a derivation of the trichome surrounding a type B bothrium from the cuticular outgrowths on the inner wall of the cavity of a type A bothrium.

4.3 Taxonomic significance of the trichobothrial complex

The fine structure of the cuticle of the trichobothrial complex is rather uniform in the superfamilies Coreoidea and Pentatomoidea: in all the taxa studied the bothrium is of A2 type and is not associated with a trichome. In contrast, the trichobothrial complex is remarkably diverse in Lygaeoidea and Pyrrhocoroidea. A special type of bothrium without a trichome occurs in the single species of Idiostoloidea studied.

A type B bothrium associated with a type T1 trichome composed of a type M1 microtrichia is the most frequently occurring condition in Lygaeoidea: 19 of the 30 subfamilies or tribes studied (species belonging to 7 families of the 15 studied) have this type of AT. We consider this set of character states as the most plesiomorphic condition found in Lygaeoidea and part of the ground plan of the superfamily.

Various other kinds of trichobothria occur in at least some of the species of several families or subfamily rank taxa of Lygaeoidea. In clades where two different con-
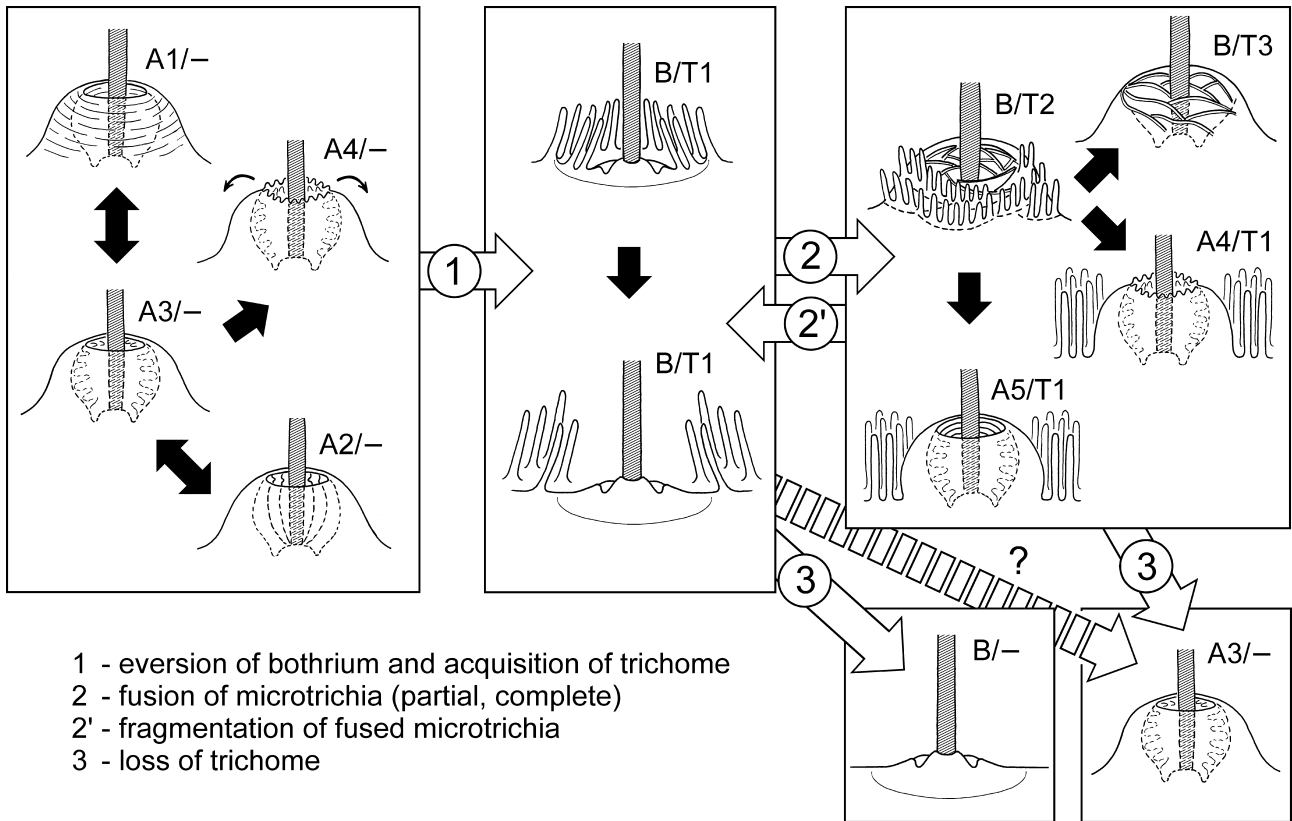
1 - eversion of bothrium and acquisition of trichome
2 - fusion of microtrichia (partial, complete)
2' - fragmentation of fused microtrichia
3 - loss of trichome

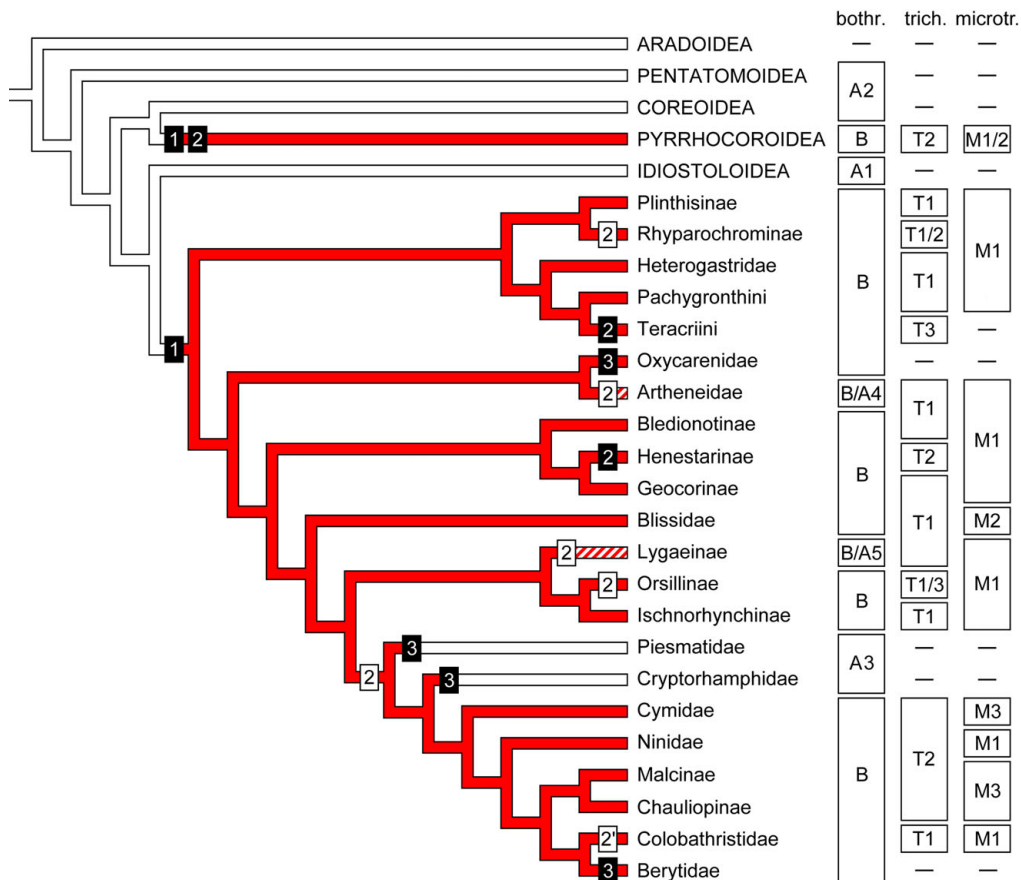**Fig. 8.** The major types of abdominal trichobothria and their hypothesized transitions.

Fig. 9. Trichobothrial characters placed on the cladogram of Pentatomomorpha inferred from the morphological analysis of Henry (1997a). Bothr. – bothrium, trich. – trichome, microtr. – microtrichia. Characters: 1 – everted bothrium, 2 – partial or complete fusion of microtrichia, 2' – fragmentation of fused microtrichia, 3 – loss of trichome; numbers in black box refer to present in all taxa studied, those in white box to part of the taxa studied within the particular clade; red branches indicate presence of type B bothria.

Table 3. Character states of the abdominal trichobothrial complex recorded in different families of Trichophora.

	A1	A2	A3	A4	A5	B	T1	T2	T3	M1	M2	M3
Idiostolidae	+	–	–	–	–	–	–	–	–	–	–	–
Cydnidae	–	+	–	–	–	–	–	–	–	–	–	–
Plataspidae	–	+	–	–	–	–	–	–	–	–	–	–
Scutelleridae	–	+	–	–	–	–	–	–	–	–	–	–
Pentatomidae	–	+	–	–	–	–	–	–	–	–	–	–
Coreidae	–	+	–	–	–	–	–	–	–	–	–	–
Alydidae	–	+	–	–	–	–	–	–	–	–	–	–
Rhopalidae	–	+	–	–	–	–	–	–	–	–	–	–
Largidae	–	–	–	–	–	+	–	+	–	+	–	–
Pyrrhocoridae	–	–	–	–	–	+	–	+	–	–	+	–
Artheneidae	–	–	–	+	–	+	+	–	–	+	–	–
Blissidae	–	–	–	–	–	+	+	–	–	–	+	–
Colobathristidae	–	–	–	–	–	+	+	–	–	+	–	–
Cymidae	–	–	–	–	–	+	–	+	–	–	–	+
Cryptorhamphidae	–	–	+	–	–	–	–	–	–	–	–	–
Geocorinae	–	–	–	–	–	+	+	–	–	+	–	–
Bledionotinae	–	–	–	–	–	+	+	–	–	+	–	–
Henestarinae	–	–	–	–	–	+	–	+	–	+	–	–
Heterogastridae	–	–	–	–	–	+	+	–	–	+	–	–
Ischnorhynchinae	–	–	–	–	–	+	+	–	–	+	–	–
Lygaeinae	–	–	–	–	+	+	+	–	–	+	–	–
Orsillinae	–	–	–	–	–	+	+	–	+	+	–	–
Chauliopinae	–	–	–	–	–	+	–	+	–	–	–	+
Malcinae	–	–	–	–	–	+	–	+	–	–	–	+
Ninidae	–	–	–	–	–	+	–	+	–	+	–	–
Pachygronthini	–	–	–	–	–	+	+	–	–	+	–	–
Teracriini	–	–	–	–	–	+	–	–	+	–	–	–
Plinthisinae	–	–	–	–	–	+	+	–	–	+	–	–
Antillocorini	–	–	–	–	–	+	+	–	–	+	–	–
Cleradini	–	–	–	–	–	+	+	–	–	+	–	–
Drymini	–	–	–	–	–	+	+	–	–	+	–	–
Gonianotini	–	–	–	–	–	+	+	–	–	+	–	–
Lethaeini	–	–	–	–	–	+	+	+	–	+	–	–
Megalonotini	–	–	–	–	–	+	+	–	–	+	–	–
Myodochini	–	–	–	–	–	+	+	–	–	+	–	–
Ozophorini	–	–	–	–	–	+	+	–	–	+	–	–
Rhyparochromini	–	–	–	–	–	+	+	+	–	+	–	–
Berytidae	–	–	–	–	–	+	–	–	–	–	–	–
Oxycarenidae	–	–	–	–	–	+	–	–	–	–	–	–
Piesmatidae	–	–	+	–	–	–	–	–	–	–	–	–

Types of bothrium: A1 – outside wall of the bothrium is rugose, wall of its cavity is ornamented with irregular outgrowths; A2 – rim of the recessed bothrium is smooth, divergent ridge-like ornaments or protuberances present inside the cavity; A3 – rim of the recessed bothrium is smooth, outgrowths that are either columnar or geniculate proximad to broadened tip present inside the cavity; A4 – rim of the recessed bothrium serrate, cone-shaped outgrowths present inside the cavity; A5 – outside wall of the bothrium elevated, its interior wall lamellate; B – bothrium shallow, base of sensillum not sunk below surface of surrounding cuticle. Types of trichome: T1 – microtrichia are nearly uniform, not fused, or fused into simple rows; T2 – microtrichia fused into a reticulate structure near bothrium; T3 – all microtrichia fused into reticulate structure. Types of microtrichia: M1 – spine-like; M2 – curved, base swollen, then sharply tapering into a point; M3 – flattened, bases swollen, then geniculate proximal to a broadened tip. + presence; – absence.

ditions were recorded, in most cases one of them is the ground plan condition of the Lygaeoidea (type B bothrium, type T1 trichome composed of M1 microtrichia) (Rhyparochromidae: Rhyparochrominae; Artheneidae; Lygaeidae: Lygaeinae and Orsillinae).

The following characters are the most constant among family group rank taxa and therefore can be recognized as diagnostic for clades: the presence or absence of a trichome; a strongly recessed (type A) or almost flat (type B) bothrium; and the position of the trichome (on the same level as the integument or on a distinct tubercle).

Trichomes on sternites III–IV and the posterior parts of sternites V–VII might be linked (Figs 2a, d; 4h; 5a, e, i, k) or separated by a more or less broad interspace (Fig. 2b). A great variation at generic and higher levels was recorded in respect of this character, making it impossible to use it for defining higher taxa.

Henry (1997a) provides a phylogenetic analysis of Pentatomomorpha based on morphological characters, including seven characters of trichobothria. The following comments and corrections are offered:

(1) Henry (1997a) claims that Larginae, Pyrrhocoridae, Colobathristidae and Lygaeinae lack a trichome (character 46: trichobothrial "pads"); based on the present study we conclude that all of the above mentioned taxa have trichomes (Figs 4a–c, j; 5g). A re-examination of the taxa studied by Henry (1997a) and a reconsideration of the character coding is necessary.

(2) The species of Piesmatidae (*Piesma* sp.) studied have a single pair of trichobothria located laterally on both sternites V and VI, therefore the character states for characters 47 and 50 need adjustment for this family.

(3) The trichobothria on abdominal segment IV of all the species of Lygaeoidea studied are medioventral (Fig. 1a–

c), and not lateral as claimed by Henry (1997a), therefore character 48 should be modified for all lygaeoid taxa in the above mentioned publication.

4.4 Phylogenetic implications of the abdominal trichobothria in Trichophora

The number and distribution of AT are remarkably constant within families, subfamilies and tribes (Schaefer, 1975). In contrast, the fine structure of AT is very diverse in higher taxa of Trichophora, especially in Lygaeoidea, indicating that the diversification in the fine structure of AT happened after the patterns in the number and disposition were fixed.

As shown above (4.1), the presence of type A bothria is considered to be plesiomorphic within the Trichophora, occurring in the Pentatomoidea (Fig. 3d–e), Coreoidea (Fig. 3b–c) and Idiostoloidea (Fig. 3i). A type A → type B transition (for a possible mechanism see 4.2) occurred at least in the stem group of Pyrrhocoroidea and Lygaeoidea.

The systematic position of Idiostolidae has remained a subject of controversy. The cladistic studies based on morphological data are incongruent; Henry (1997a) regards the Idiostoloidea as the sister group of Lygaeoidea and Yao et al. (2012) the sister group of Coreoidea. The topology suggested by Yao et al. (2012), however, seems unlikely for several reasons (highly polyphyletic Lygaeoidea, Piesmatidae being the sister group of the rest of Trichophora, Rhyparochromidae being the sister group of the rest of Trichophora except for Piesmatidae). Recent molecular studies (Xie et al., 2005; Hua et al., 2008; Tian et al., 2011; Yuan et al., 2015; Li et al., 2016, 2017; Wang et al., 2016) do not include any species of Idiostoloidea.

Pyrrhocoroidea is considered to be the sister group of Coreoidea by Henry (1997a). The monophyly of these two superfamilies is based on the shared occurrence of medioventral abdominal trichobothria (character 48) and "salivary glands" (more precisely, the principal salivary glands) being four-lobed (character 52). The character polarity of various trichobothrial arrangements is not always clear, but the presence of medioventral trichobothria is considered as a plesiomorphy within Trichophora by several authors (Štys, 1967; Schaefer, 1966a, b, 1975, 1993; Schaefer & Wilcox, 1969); furthermore, as pointed out above (4.3), the coding for this character is wrong in the study of Henry (1997a), and the character state exhibited by Coreoidea and Pyrrhocoroidea is also shared by all Lygaeoidea. A monophyletic Pyrrhocoroidea + Coreoidea clade is recovered by some molecular studies (Yuan et al., 2015) and a monophyletic Pyrrhocoroidea + Lygaeoidea clade by others (Li et al., 2016, 2017; Wang et al., 2016); none of these studies include Idiostoloidea. The support for a monophyletic Coreoidea + Pyrrhocoroidea clade is therefore not particularly strong.

The bothrium of *Monteithocoris* sp. (Idiostolidae), the only member of the Idiostoloidea studied, is unique among the trichophora studied (Fig. 3i), therefore it is difficult to use it for speculating about the systematic placement of this superfamily. The presence of type B bothria on the abdominal sternites, however, is a potential synapomorphy

for the clade comprising Pyrrhocoroidea + Lygaeoidea. The phylogenetic relationships of these superfamilies cannot be resolved based on the available data.

The presence of type B bothria, derived from plesiomorphic type A bothria, is a synapomorphy of Lygaeoidea, occurring in the vast majority of its subclades. The type A bothria occurring in various lygaeoid groups (Piesmatidae, Cryptorhamphidae, some Artheneidae and Lygaeinae) can be derived from type B bothria by fusion of the microtrichia immediately surrounding the base of the sensillum (Fig. 8); although the resulting type A bothria are superficially similar to the type A bothria in Pentatomoidea and Coreoidea, they are of different origin. This type B → type A transition independently happened at least within the families Artheneidae and Lygaeinae, and in the stem groups of Piesmatidae and Cryptorhamphidae.

The inner wall of the bothrium can be modified in various ways: short, irregular (subtype A1) or finger-like cuticular projections (subtypes A3, A4), which might fuse to form longitudinal (subtype A2) or transverse (subtype A5) ridges. The character polarity of these states is unclear, perhaps they can easily transform from one to the other (Fig. 8). Some of these types are apparently autapomorphies of particular clades: subtype A3 was only recorded in Piesmatidae and Cryptorhamphidae, subtype A4 only in *Artheneis intricata* (the other species of Artheneidae studied had type B bothria); and A5 in all members of Lygaeinae studied except *Arocatus rufipes*.

As shown above (4.2), the trichome probably originated from the eversion of the inner wall of the bothrial cavity and the microtrichia probably derived from the cuticular projections on the inner wall of the bothrial cavity (Fig. 8). In plesiomorphic forms of type B trichobothria the trichome was probably restricted to the immediate surroundings of the bothrium (as seen in *Parapamphantus braziliensis*, Bledionotinae) (Fig. 6a–b); the extensive trichobothria occupying a large surface around the bothrium occurring in various taxa (e.g. Figs 2a–b, d, 4a–b, d–l, 5a–l, 6c) is probably a derived condition (Fig. 8).

Partial or complete fusion of the microtrichia is a common feature in all Trichophora that have trichomes. The microtrichia are at least partially fused in Pyrrhocoroidea (Fig. 5g–h) and, independently, in several lygaeoid clades, at least in species of Henestarinae (Fig. 5a), Cymidae (Fig. 5i–j), Ninidae (Fig. 5b) and Malcidae (both Malcinae and Chauliopinae) (Fig. 5k–l). T1 → T2 and T2 → T3 transitions are evident; in some cases, the microtrichia immediately surrounding the bothrium might transform into a structure resembling an elevated, cup-like rim resulting in a complex similar to a type A bothrium surrounded by an area of free microtrichia, therefore T2 → T1 transitions are also possible. Complete fusion was recorded in some Orsillinae (*Nysius ericae*, *Ortholomus punctipennis*) (Fig. 5d) and in the two species of Pachygronthidae: Teracriini studied (Fig. 5e–f).

There is little variability in the shape of the individual microtrichia forming the trichome. The vast majority of the taxa have simple, finger-or hair-like (type M1) mi-

crotrichia, which evidently is the plesiomorphic character state in all subclades. Derived microtrichia occur in Pyrrhocoridae, Blissidae (both M2), Cymidae and Malcidae (both Malcinae and Chauliopinae) (all M3). The specialized microtrichia are results of M1 → M2 and M1 → M3 transitions, respectively. The M1 → M2 transitions in the stem groups of Pyrrhocoroidea and Blissidae were evidently independent; the M1 → M3 transitions in Cymidae and Malcidae, two closely related clades, possibly happened in the stem group of the clade uniting both of these families.

Fused microtrichia apparently can fragment again; as indicated by a type T1 trichome in Colobathristidae, a family nested within a clade with the majority of its members having fused (type T2) trichobothria (Cymidae, Ninidae, Malcidae), which can probably be explained by a secondary fragmentation of the fused microtrichia. The secondary loss of the microtrichia occurred in the stem groups of Oxycarenidae and Berytidae, and possibly also in the stem groups of the clade containing the Piesmatidae and Cryptorhamphidae. The lack of a trichome in the Idiostoloidea is potentially a plesiomorphy.

Štys (1967) recognizes the "malcid-line" as a presumably monophyletic clade within Lygaeoidea, comprising the current families Berytidae, Malcidae, Cymidae (including the current Cryptorhamphidae and Ninidae as subgroups) and Colobathristidae; Schaefer (1975) also regards Piesmatidae as a member of this group. Henry (1997a) recovered a monophyletic clade comprising the above families (including Piesmatidae). This clade has considerable support from the morphology of the trichobothria. In all of these families, except the Colobathristidae and Berytidae, the microtrichia around the bothrium are partially fused (the free microtrichia in Colobathristidae is probably a result of reversal, whilst the complete lack of a trichome in Berytidae a result of secondary loss). In addition, both Cymidae and Malcidae (both Malcinae and Chauliopinae) have M3 type microtrichia.

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