

RESEARCH PAPER

Scanning the Hyocephalidae: details of their external morphology with respect to phylogenetic relationships within Eutrichophora (Hemiptera: Heteroptera)*

Petr KMENT¹⁾, Vladimír HEMALA²⁾ & Igor MALENOVSKÝ²⁾

¹⁾ Department of Entomology, National Museum, Cirkusová 1740, CZ-193 00 Praha – Horní Počernice, Czech Republic; e-mail: sigara@post.cz

²⁾ Department of Botany and Zoology, Faculty of Science, Masaryk University, Kotlářská 2, CZ-611 37 Brno, Czech Republic; e-mails: vladimir.hemala@gmail.com, malenovskyy@sci.muni.cz

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Abstract. Hyocephalidae (Hemiptera: Heteroptera: Pentatomomorpha) is a small family of true bugs containing two genera and three species endemic to Australia. For the first time, we examine here selected structures of their external morphology using scanning electron microscopy – the external structures associated with the metathoracic and dorsoabdominal scent glands, the strainer organ on the sternite III, as well as the trichobothrial pattern and ultrastructure. The following character states are confirmed (i, ii, iii) or newly recognised (iv, v) as autapomorphies of Hyocephalidae: i) apically projected scimitar-shaped peritreme of the metathoracic scent glands; ii) presence of a strainer organ on sternite III in both sexes; iii) trichobothria on sternite V placed immediately ventrad of spiracle, iv) trichobothria on each of abdominal segments III–VII all grouped together within a common trichome, and v) presence of crocus-like structures within the trichome. Of particular interest is the presence of a shallow open bothrium (type B) surrounded by a trichome in Hyocephalidae, a probably derived character state shared with Pyrrhocoroidea and most Lygaeoidea, while Stenocephalidae (previously considered to be closely related to Hyocephalidae and used here for comparison) and the remaining Coreoidea possess a recessed bothrium of type A2, lacking the trichome. The morphology of trichobothria in Hyocephalidae may thus suggest either their closer relationship to Lygaeoidea + Pyrrhocoroidea than to Coreoidea, or a parallel evolution of the open bothrium with trichome in Eutrichophora. We highlight the importance of Hyocephalidae for a better understanding of the phylogeny of Eutrichophora and the urgent need to obtain phylogenomic data for future research. A taxonomic catalogue of Hyocephalidae is supplemented. The neotype designation for *Hyocephalus aprugnus* Bergroth, 1906 made by ŠTYS (1964) and supported by GRANT & ŠTYS (1970) is found invalid.

Key words. Hemiptera, Heteroptera, Trichophora, Coreoidea, Lygaeoidea, Pyrrhocoroidea, Hyocephalidae, Stenocephalidae, morphology, scent glands, strainer organ, trichobothria, ultrastructure, phylogeny, catalogue, invalid neotype designation

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Introduction

Hyocephalidae (Figs 1, 2A) is one of the smallest families of Heteroptera, including only two described genera and three species restricted to Australia (BRAILOVSKY 2002,

CASSIS & GROSS 2002, HENRY 2017). The first taxon of current Hyocephalidae, *Maevius indecorus*, was described based on a brachypterous female and placed in Rhyparochromidae: Lethaeini (Lygaeoidea) by STAL (1874). This systematic placement was revealed as mistaken only much later by SCUDDER (1962b), who transferred *Maevius* to Coreidae. Finally SCHAEFER (1972) reclassified it into Hyocephalidae. The latter taxon was based on another genus and species, *Hyocephalus aprugnus*, originally described from

* We dedicate this paper to the memory of the late Prof. RNDr. Pavel Štys, CSc. (1933–2018), an eminent expert in Hemiptera systematics and morphology. His immense knowledge, precise observations and sharp analyses, which he never hesitated to share, will always remain a great inspiration for us.



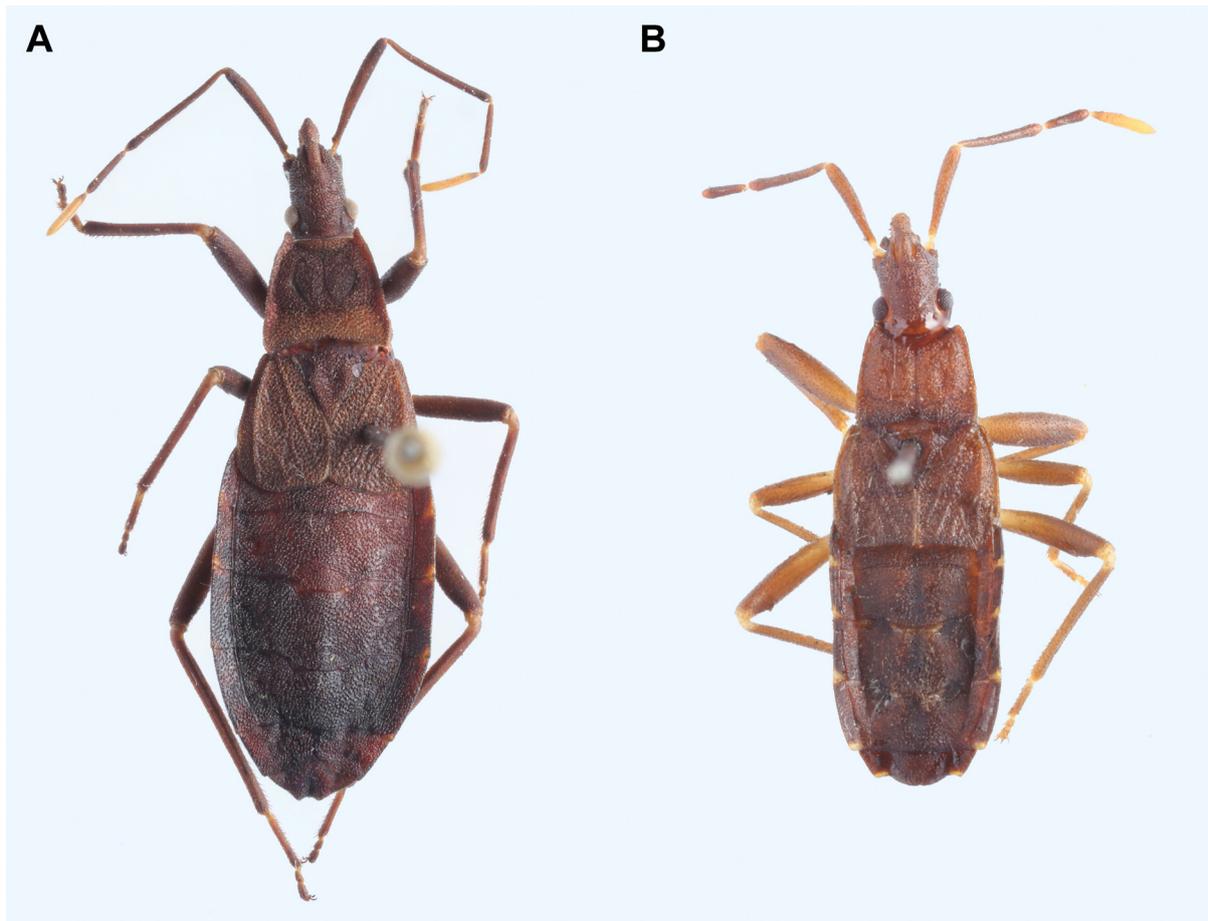


Fig. 1. Dorsal habitus of Hoyocephalidae. A – *Hoyocephalus aprugnus* Bergroth, 1906, female (15.4 mm); B – *Maeivius luridus* Brailovsky, 2002, male (8.7 mm).

a macropterous female from South Australia (BERGROTH 1906); description of a brachypterous female was supplemented by BERGROTH (1912). BERGROTH (1906) established a new subfamily for his new genus, Hoyocephalinae, placed within Coreidae, but later he re-evaluated it only as a tribe within Coreinae (BERGROTH 1912, 1913). However, REUTER (1912), based on BERGROTH's (1906, 1912) descriptions, raised the status of Hoyocephalidae to a family within Coreoidea, an opinion accepted by most subsequent authors, even though none of them had the possibility to examine specimens of Hoyocephalidae directly (for references see ŠTYS 1964 and Appendix). ŠTYS (1964) provided a detailed and richly illustrated morphological study of Hoyocephalidae, based on a series of macropterous females of *H. aprugnus* discovered in the Hungarian Natural History Museum, Budapest, compared it with other families of Coreoidea, Lygaeoidea and Pyrrhocoroidea, and supported the status of Hoyocephalidae as a distinct family. Besides the general external morphology, ŠTYS (1964) described and depicted also the details of the external scent efferent system of the metathoracic and dorsoabdominal scent glands, the unique 'strainer' organ on sternite III, the pattern of abdominal trichobothria, as well as the female genitalia including the ovipositor and spermatheca. WATERHOUSE & GILBY (1964) supplied a description of the metathoracic scent gland, and KUMAR (1966) provided descriptions of the egg and larval instars I–V of '*Hoyocephalus* sp. nov.',

a taxon later identified with *Maeivius indecorus* (SCHAEFER 1981, BRAILOVSKY 2002). Another important step towards the knowledge of Hoyocephalidae was the morphological study by SCHAEFER (1981), who examined *M. indecorus* and described the morphology of its external metathoracic scent efferent system and abdomen, including trichobothrial pattern, and for the first time in Hoyocephalidae, the male genitalia. Finally, BRAILOVSKY (2002) described a third species, *Maeivius luridus*, and provided drawings of habitus, genital capsules and parameres for all known hoyocephalid species. The male genitalia of Hoyocephalidae were also examined and compared to other Coreoidea, Lygaeoidea and Pyrrhocoroidea by YANG (2007).

Hoyocephalidae belong to the true bug infraorder Pentatomomorpha, which has traditionally been divided into five or six superfamilies: Aradoidea, Idiostoloidea, Lygaeoidea, Coreoidea, Pyrrhocoroidea, and Pentatomoidea (e.g. SCHUH & SLATER 1995, HENRY 1997a, WEIRAUCH et al. 2019). Within Pentatomomorpha, Aradoidea, lacking abdominal trichobothria, are traditionally considered a sister group to the remaining superfamilies, the Trichophora, possessing trichobothria on abdominal sternites III–VII (SCUDDER 1962a, SCHAEFER 1966a, HENRY 1997a). The status of Idiostolidae remains controversial as this group has been classified either as a family within Lygaeoidea (e.g. SCUDDER 1962a; SCHAEFER 1966a,b; SCHAEFER & WILCOX 1969; SCHUH & SLATER 1995) or as a separate superfamily

Idiostoloidea (ŠTYS 1964, ŠTYS & KERZHNER 1975, CASSIS & SCHUH 2010), including also Henicocoridae according to HENRY (1997a). The most recent studies are in favour of the latter hypothesis and tend to place Idiostoloidea as the most basal group of Trichophora (GAO et al. 2017, WEIRAUCH et al. 2019). Concerning the remaining trichophoran super-families, phylogenetic studies unequivocally recognize Pentatomoidea as the sister group of Eutrichophora, i.e. Coreoidea + Pyrrhocoroidea + Lygaeoidea (e.g. XIE et al. 2005; LI et al. 2016a; ZHAO et al. 2018; WANG et al. 2016, 2019; LIU et al. 2018, 2019). However, the relationships within Eutrichophora remain obscure, and three competing hypotheses have been suggested:

- (1) Lygaeoidea + (Coreoidea + Pyrrhocoroidea): HENRY (1997a), YANG (2007), CASSIS & SCHUH (2010), TIAN et al. (2011), YUAN et al. (2015), LI et al. (2016b), JOHNSON et al. (2018), ZHAO et al. (2018), SONG et al. (2019), WANG et al. (2019);
- (2) Pyrrhocoroidea + (Coreoidea + Lygaeoidea): XIE et al. (2005), HUA et al. (2008), GORDON et al. (2016), FORTHMAN et al. (2019), WEIRAUCH et al. (2019);
- (3) Coreoidea + (Pyrrhocoroidea + Lygaeoidea): LI et al. (2016a, 2017), WANG et al. (2016), LIU et al. (2018, 2019).

The last hypothesis receives morphological support from the ultrastructure of the bothrium (the cuticular pit of the trichobothrium): Pyrrhocoroidea and most Lygaeoidea share its apomorphic state (an open bothrium surrounded by a trichome), while Coreoidea share the plesiomorphic condition with Idiostoloidea and Pentatomoidea (a recessed bothrium lacking the trichome; GAO et al. 2017, HEMALA et al. in prep. a). However, there are still some gaps in the knowledge of the bothrium type and other ultrastructural characters for some taxa of Eutrichophora, particularly the rare Hyocephalidae, hindering their correct systematic placement. Any detailed examination of these characters requires scanning electron microscopy, a method so far never applied for Hyocephalidae. Recently, we serendipitously discovered a series of specimens among the materials borrowed by the late Professor Pavel Štys, which included representatives of all known genera and species of Hyocephalidae. This material allowed us to describe and illustrate the ultrastructure of the external scent efferent systems of the metathoracic and dorsoabdominal scent glands, the unique strainer organ on the third abdominal ventrite, and of the trichobothria. We compare and interpret our findings in the context of morphology and phylogeny of Eutrichophora.

Material and methods

The specimens were examined without coating under a Hitachi S-3700N environmental scanning electron microscope (= ESEM) at the Department of Palaeontology, National Museum, Prague. Habitus photographs in Fig. 1 were taken using a Canon MP-E 65 mm macro lens attached to a Canon EOS 550D camera and stacked from multiple layers using the Helicon Focus 5.1 Pro software. External observations, body length measurements and line

drawing were made under a Leica MZ75 stereomicroscope provided with an ocular micrometer and a camera lucida. The measurements of ultrastructural details were traced from the ESEM micrographs.

Morphological terminology follows TSAI et al. (2011), KMENT et al. (2016) and RÉDEI (2017), special terms are adopted from KMENT & VILÍMOVÁ (2010a) for the metathoracic scent gland efferent system, VILÍMOVÁ & KUTALOVÁ (2012) for the dorsoabdominal scent gland efferent system, and GAO et al. (2017) for the trichobothrium structure. The individual trichobothrial positions are named in concordance with a parallel detailed study on the abdominal morphology of Pyrrhocoroidea (HEMALA et al., in prep. a) as AT3–7a–c, with AT standing for abdominal trichobothrium, the first numeral indicating the number of the sternite, and the letters a, b and c indicating the relative position of the particular trichobothrium on that sternite, from the median to the lateral positions (for AT3 and AT4) or from the anterior to the posterior positions (AT5, AT6, AT7) (Fig. 7).

The material of Hyocephalidae examined and its depositories are listed in the Appendix. In addition, we used the following specimens of Stenocephalidae (Coreoidea) for comparison: *Dicranocephalus agilis* (Scopoli, 1763): Czech Republic, Moravia mer., Hryzlacké Mlýny, 48°53'10"N 17°36'08"E, 450 m a.s.l., Malaise trap, 7.iv.–12.v.2009, 1 ♀, P. Chvojka, J. Ježek & J. Macek lgt., P. Kment det. (NMPC) [ESEM: trichobothria]; Slovakia, Čenkov near the town of Štúrovo, 19.v.1959, 1 ♀, J. L. Stehlík lgt. et det. (MMBC) [ESEM: metathoracic scent glands]. Stenocephalidae were considered to be closely related to Hyocephalidae by several authors (e.g. ŠTYS 1964, SCHAEFER 1981) but the structure of their metathoracic external scent efferent system and trichobothrium in Stenocephalidae has never been studied in detail (cf. GAO et al. 2017).

Results and discussion

External scent efferent system of the metathoracic scent gland

Description. External scent efferent system (Figs 3A, B) composed of vestibular scar, ostiole, peritreme and evaporatorium. Vestibular scar short, about as long as ostiole (Fig. 3E), extending from anterior margin of metacoxal cavity towards proximal margin of ostiole. Ostiole situated ventrally between meso- and metacetabulum, large, drop-shaped, narrowing proximally and closing gradually towards vestibular scar, widely opening laterad; both mycoid and peritremal surface (the latter as narrow, channel-like stripe) visible at its bottom. Anterior margin of ostiole with raised, C-shaped patch of peritreme-like cuticle, without mycoid microsculpture. Peritreme in form of narrow, sharply emarginated stripe issuing from ostiole and produced as sharply pointed, more or less curved scimitar-shaped projection, not connected with surrounding metapleuron (supporting projection not developed) (Figs 3C–E, G–H), directed posteriad (*Maevius*, Figs 3F–H) or posterolaterad (*Hyocephalus*, Figs 3A–D), lacking median furrow, smooth superficially (Figs 3D, H). Evaporatorium well developed on metapleuron,

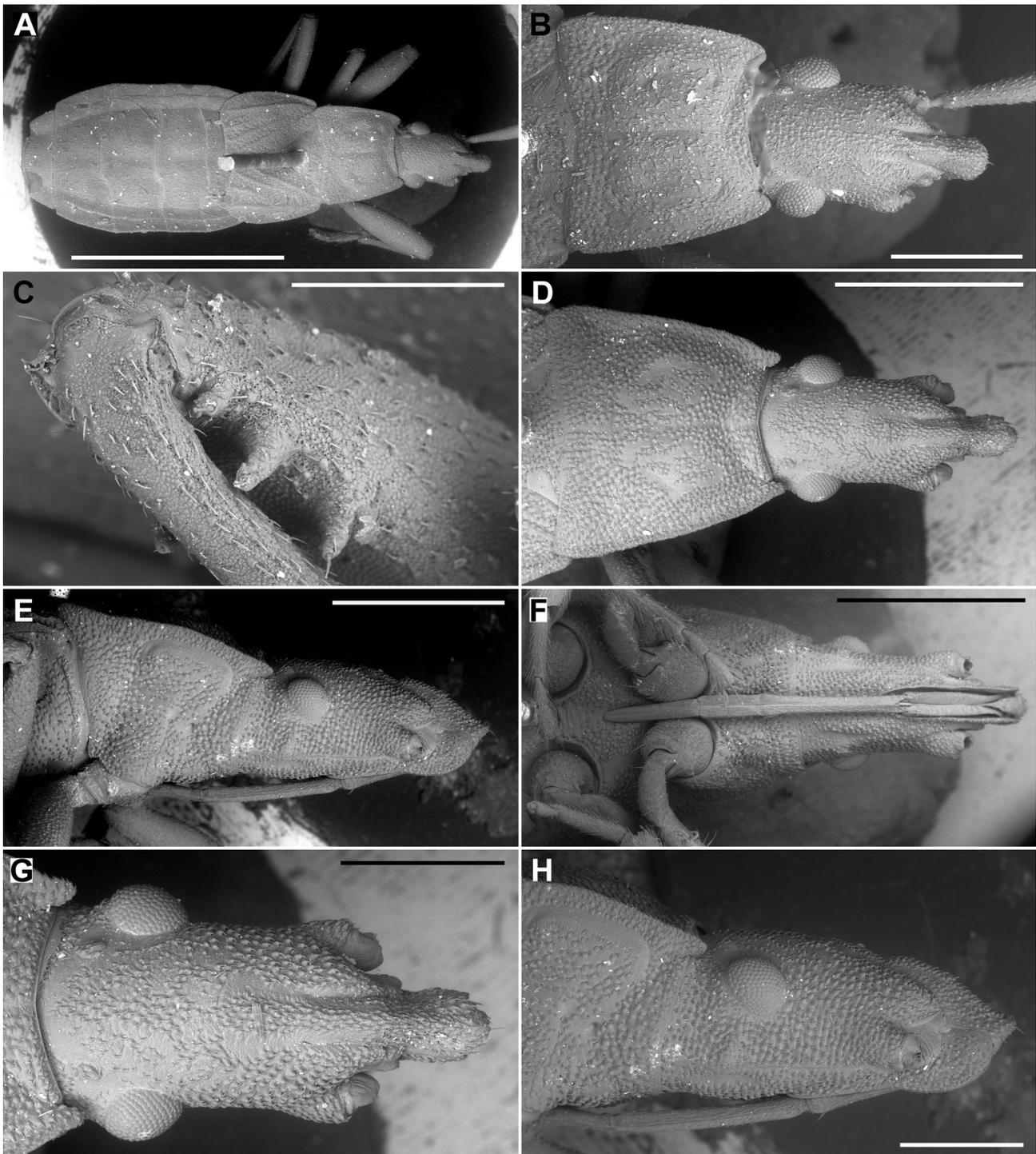


Fig. 2. Head and prothorax of Hoyocephalidae. A–C – *Maevius luridus* Brailovsky, 2002, male: A – dorsal habitus (magnification 13 \times); B – head and pronotum, dorsal view (32 \times), C – apex of profemur with spines (130 \times). D–H – *Hoyocephalus aprugnus* Bergroth, 1906, female: D–F – head and prothorax (D – dorsal view, 23 \times ; E – lateral view, 21 \times ; F – ventral view, 23 \times); G–H – head (G – dorsal view, 40 \times ; H – lateral view, 30 \times). Scale bars: 0.4 mm (C), 1 mm (B, G–H), 2 mm (D–F), 4 mm (A).

surrounding ostiole (Figs 3C, G), forming wide lobe posterolaterad of ostiole (Figs 3C–D, F–G), and narrow stripe on anterior margin of metapleuron reaching lateral end of metathoracic spiracle (Figs 3B, F); evaporatorium consisting of mycoid surface with distinct elongate (in outer parts of ostiole, Figs 3D, G, H) to polygonal mushroom bodies (in the rest of evaporatorium, Figs 3D, G, H), mycoid surface not developed along vestibular scar (Fig. 3E). Mesopleural

evaporatorium developed as narrow stripe on posterior margin of mesopleuron anteriorly of metathoracic spiracle (Figs 3B, F). Metathoracic spiracle long and narrow, slit-like (Figs 3B, F, 4B–D), with opening protected on both anterior and posterior margins by mycoid filter processes in form of unmodified (Fig. 4D) or little-modified mushroom bodies with caps bearing denticles (Fig. 4C). Filter processes absent at entrance to mesothoracic spiracle (Fig. 4A).

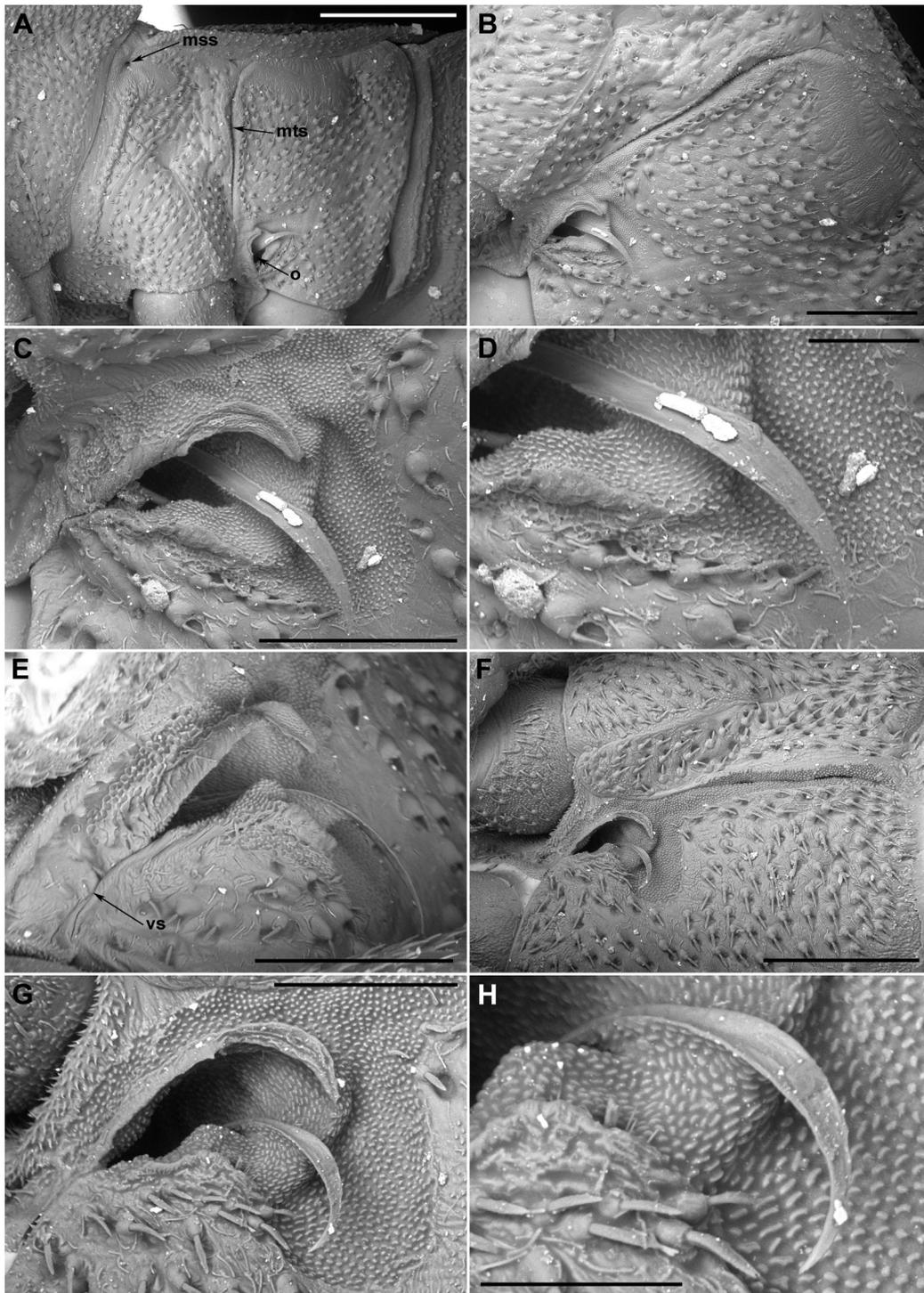


Fig. 3. External scent efferent system of metathoracic glands in Hymenoptera. A–E – *Hyocephalus aprugnus* Bergroth, 1906 (A–D – male, E – female): A – meso- and metathorax, lateral view (magnification 37×); B – external scent efferent system, lateral view (60×); C – ostiole and peritreme, lateral view (180×); D – peritreme, lateral view (300×); E – ostiole and peritreme, ventral view (180×). F–H – *Maevius luridus* Brailovsky, 2002: F – external scent efferent system, lateral view (85×); G – ostiole and peritreme, lateral view (250×); H – peritreme, lateral view (550×). Abbreviations: mss – mesothoracic spiracle, mts – metathoracic spiracle, o – ostiole, vs – vestibular scar. Scale bars: 0.1 mm (D, H), 0.2 mm (G), 0.3 mm (C, E), 0.5 mm (B, F), 1 mm (A).

Discussion. The metathoracic external scent efferent system of Hymenoptera includes all principal components, i.e. the vestibular scar, ostiole, peritreme and evaporatorium formed by mushroom bodies, without conspicuous reductions. The presence of a vestibular scar, the basal position of the ostiole, and the moderately developed evaporatorium are plesiomorphic conditions within Pentatomomorpha

as well as Coreoidea (SCHAEFER 1981; KMENT & VILÍMOVÁ 2010a,b; HEMALA et al., in prep. b). The large, widely opened ostiole, with a narrow stripe of peritremal surface on its bottom, is a derived condition, similar to the situation in Largidae: Physopeltinae (STEHLÍK 2013; STEHLÍK & KMENT 2014; STEHLÍK et al. 2016; HEMALA et al., in prep. b). The peculiar shape of the peritreme in Hymenoptera, which

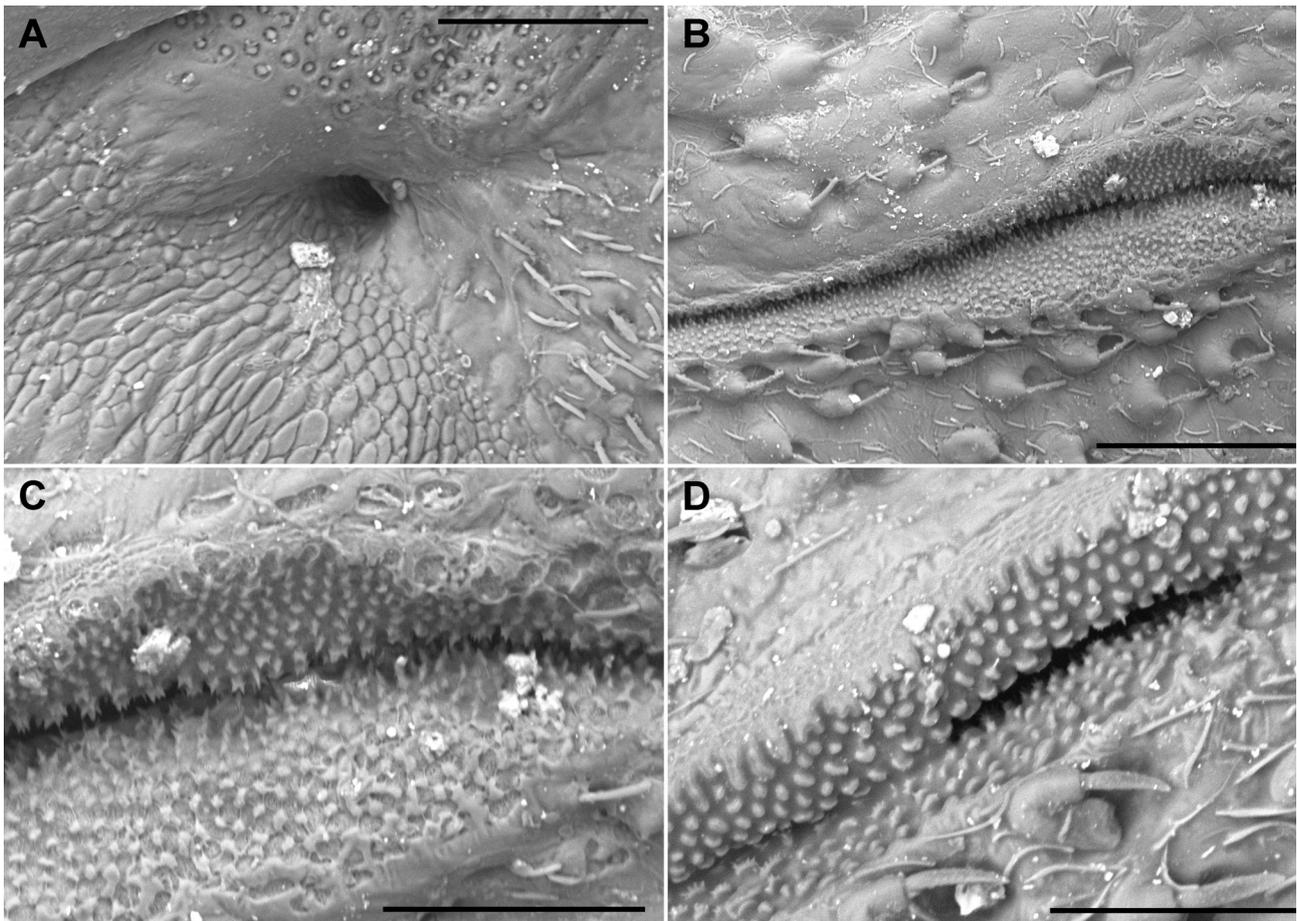


Fig. 4. Ultrastructure of thoracic spiracles in Hoyocephalidae. A–C – *Hyocephalus aprugnius* Bergroth, 1906, male: A – mesothoracic spiracle (magnification 400 \times); B–C – metathoracic spiracle (B – 200 \times , C – 500 \times). D – *Maevius luridus* Brailovsky, 2002: metathoracic spiracle (500 \times). Scale bars: 0.1 mm (A, C–D), 0.2 mm (B).

forms a scimitar-shaped projection not connected with the surrounding metapleuron, has already been described by ŠTYS (1964: fig. 19), SCHAEFER (1981), and CARVER et al. (1991: fig. 30.76 C). This character state is unique among Pentatomomorpha and Heteroptera (e.g. USINGER & MATSUDA 1959; CARAYON 1971; SCHAEFER 1966b; HEPBURN & YONKE 1971; SLATER 1979; PACKAUSKAS 1994; HENRY 1997b,c; KMENT & VILÍMOVÁ 2010a,b; KMENT et al. 2012; PARVEEN et al. 2014; BARÃO et al. 2017; WEILER et al. 2017; HEMALA et al., in prep. b; and many references included) and is used to distinguish Hoyocephalidae in keys for identification of heteropteran families (CARVER et al. 1991, SCHUH & SLATER 1995). SCHAEFER (1981) pointed out the similarity of the scimitar-shaped projection of Hoyocephalidae with the spinously projected peritreme of Berytidae, though he correctly doubted their homology. The peritreme of Berytidae, the spout, is always composed of peritremal surface and a supporting projection of the surrounding metapleuron (KMENT & VILÍMOVÁ 2010a); thus, the supporting projection is present in Berytidae (SCHAEFER 1981; see also CARAYON 1971 and HENRY 1997b,c) but missing in Hoyocephalidae. For comparison, the peritreme of Stenocephalidae is bilobate (Fig. 9E; see also LANSBURY 1965 and SARODE et al. 2017), similar to the situation in many Coreidae and some Alydidae (e.g. SCHAEFER 1965, 1981; HEPBURN & YONKE

1971). The absence of evaporatorium in *Maevius indecorus* mentioned by SCHAEFER (1972) was an error, corrected already by SCHAEFER (1981).

The morphology of the metathoracic spiracle and associated filter processes has received little attention (except KITAMURA et al. 1984, CARVER 1990, KMENT & VILÍMOVÁ 2010a, PARVEEN et al. 2014, BARÃO et al. 2017, WEILER et al. 2017) and has never been used in the systematics of Pentatomomorpha so far. Only recently ZHANG et al. (in prep.) and HEMALA et al. (in prep. b) have documented the metathoracic spiracles and filter processes in about 150 species of Pentatomomorpha. The entrance to the metathoracic spiracle of Hoyocephalidae is protected by mycoid filter processes in form of unmodified or little-modified (denticulate) mushroom bodies (mycoid type sensu ZHANG et al., in prep.). This condition is present also in various representatives of Lygaeoidea (Cymidae, Lygaeidae, Malcidae, Ninidae, Oxycarenidae, some Rhyparochromidae), Pyrrhocoroidea (some Pyrrhocoridae), Aradoidea, and Pentatomoidea (Cydnidae, Dinidoridae, Scutelleridae), and is most probably plesiomorphic, though secondary reductions of more complicated structures cannot be excluded, e.g. in Pyrrhocoridae (ZHANG et al., in prep.; HEMALA et al., in prep. b). On the other hand, all (few) examined members of Stenocephalidae, Coreidae, Alydidae and Rhopalidae,

as well as Largidae and many Pyrrhocoridae, share another pattern of mycoid filter processes: mushroom bodies on the anterior margin of the spiracle with caps modified into a more or less long, conical projection bearing smaller spines, which may be anastomosing into a hedge- or lace-like structure (ZHANG et al., in prep.; HEMALA et al., in prep. b).

External scent efferent system of the dorsoabdominal scent glands

Description. In adult *Hyocephalidae*, external scent efferent systems of two pairs of dorsoabdominal scent glands (DAGs) present between abdominal terga IV–V and V–VI, situated at posterolateral margins of median truncate processes of tergites IV and V, respectively. External scent efferent systems rudimentary without apparent ostioles (Figs 5A–C, G, I, J), represented only by remnants of ear-shaped structures (term according to VILÍMOVÁ & KUTALOVÁ 2012) in form of flat, smooth, drop-shaped areas at posterolateral angles of median projections of terga IV and V (Figs 5D–F, K). Evaporatoria not developed (Figs 5D–F, K).

Discussion. KUMAR (1966) reported the presence and figured two pairs of dorsoabdominal scent efferent systems in larvae of *Maevius indecorus* (instars I–V). ŠTYS (1964: fig. 22) and SCHAEFER (1981) found paired openings of DAGs between tergites IV–V and V–VI in adult *Hyocephalus aprugnus* and *Maevius indecorus*, respectively. SCHAEFER (1981) believed that ostioles of his specimens were not occluded and that the glands were functional in adult *M. indecorus*. Our study did not find any open ostioles in either *Hyocephalus* or *Maevius*, which suggests non-functional DAGs in adult *Hyocephalidae*.

The presence of three pairs of larval DAGs is considered a plesiomorphy within Pentatomomorpha, occurring in Aradoidea, Pentatomoidea, Pyrrhocoroidea, Lygaeoidea (Artheneidae, Colobathristidae, Heterogastridae, Lygaeidae: Ischnorrhynchinae, Malcidae: Malcinae, Ninidae, most Rhyparochromidae); various reductions in number of DAGs then should be regarded as derived character states (ŠTYS 1964, COBBEN 1978, SCHUH & SLATER 1995, HENRY 1997a, DAVIDOVÁ-VILÍMOVÁ & PODOUBSKÝ 1999, DAVIDOVÁ-VILÍMOVÁ 2006, VILÍMOVÁ & KUTALOVÁ 2012). Reduction of the anterior pair between terga III and IV, with only the middle (IV/V) and the posterior (V/VI) pair of DAGs developed, occurs besides *Hyocephalidae* also in the remaining Coreoidea (Alydidae, Coreidae, Rhopalidae, and Stenocephalidae), Idiostoloidea and many families of Lygaeoidea (Blissidae; Cryptorhamphidae; Geocoridae; Lygaeidae: Lygaeinae, Orsillinae; Malcidae: Chauliopininae; Oxycaenidae; Pachygronhidae) (e.g. ŠTYS 1964, COBBEN 1978, OETTING & YONKE 1978, SCHUH & SLATER 1995, HENRY 1997a, DAVIDOVÁ-VILÍMOVÁ et al. 2000). Because of this, the state of development of DAGs is probably of little help in tracing the phylogenetic relationships of *Hyocephalidae*.

Strainer organ

Description. Sternite III posterolaterally (near posterior margin of segment) with flat, slightly raised, nearly circular (*Maevius* spp.) to widely elliptical (*Hyocephalus*

aprugnus) area called *strainer*, emarginated by shallow groove and surrounded by slightly depressed cuticle (Fig. 6A). Strainer bearing number of small pores, either open, each encircled by cuticular ring (Figs 6D,E: op), or closed, apparent externally as spots on thin cuticle (best seen in Fig. 6E: cp). The following measurements and numbers are traced from ESEM micrographs (a single individual of each sex examined): Diameter of strainer: *Hyocephalus aprugnus*: male (Fig. 6B) – 392–458 µm (corresponding to 2.65–3.10% of body length), female (Fig. 6C) – 388–457 µm (2.87–3.38%); *Maevius indecorus*: female (Fig. 6F) – 302–321 µm (3.11–3.31%); *Maevius luridus*: male – 209–213 µm (2.37–2.41%). Number of open pores: *Hyocephalus aprugnus*: male – 238, female – 276, *Maevius indecorus*: female – at least 121, *Maevius luridus*: male – at least 74 (Fig. 6E). Diameter of pores: *Hyocephalus aprugnus*: male – 3.0–6.0 µm, female – 3.8–6.2 µm; *Maevius indecorus*: female – 3.8–5.7 µm; *Maevius luridus*: male – 1.25–4.0 µm.

Discussion. The rounded, flat and smooth spot bearing miniature pores on ventrite III was first noticed in *Hyocephalus aprugnus* by BERGROTH (1906). It was described in detail by ŠTYS (1964) from a female of the same species as a sharply delimited, finely granulated circular area, placed in a depression, bearing a number of small pores (332 in the specimen figured by ŠTYS 1964: fig. 20). ŠTYS (1964) called this structure a ‘strainer’ and interpreted it as an outlet of some internal glandular organ. KUMAR (1966) described the paired strainer in the third larval instar of *Maevius indecorus*. SCHAEFER (1981) mentioned the presence of strainer also in males of *Hyocephalidae*. SLATER (1982) and CARVER et al. (1991) referred to this structure alternatively as ‘a pore-bearing plate’.

We confirm the presence of the strainer in both sexes of *Hyocephalus aprugnus* as well as *Maevius* spp. The few examined specimens do not allow any solid conclusions about sexual dimorphism and/or intraspecific variability of the strainer size and number of pores, but it seems that the number of pores is somewhat higher in females. The strainer organ is a unique feature of *Hyocephalidae* useful for the family diagnosis (CARVER et al. 1991, SCHUH & SLATER 1995, HENRY 1997a). ŠTYS (1964) made a comment that this structure ‘is comparable only to the porose areas in some Megalotinae’ [i.e. Rhyparochromidae]. Cuiqing Gao (pers. comm. 2019) observed similar microscopic pores scattered on sternite IV of *Riptortus linearis* Fabricius, 1775 (Alydidae: Alydinae). However, function of these porose structures in *Hyocephalidae*, Rhyparochromidae and Alydidae remains unknown and hypotheses on their possible homology still have to be tested.

Ventriles of the pregenital abdomen and abdominal trichobothria

Description. Abdomen, in dorsal view, oval, somewhat parallel-sided in middle (Figs 5A, G); in lateral view, parallel-sided (Figs 6A, 7), more or less convex ventrally (Fig. 8A). Ventriles III–VI approximately as long medially as laterally, not produced anterolaterally; intersegmental sutures between all ventrites straight (Figs 6A, 7). Ventrite

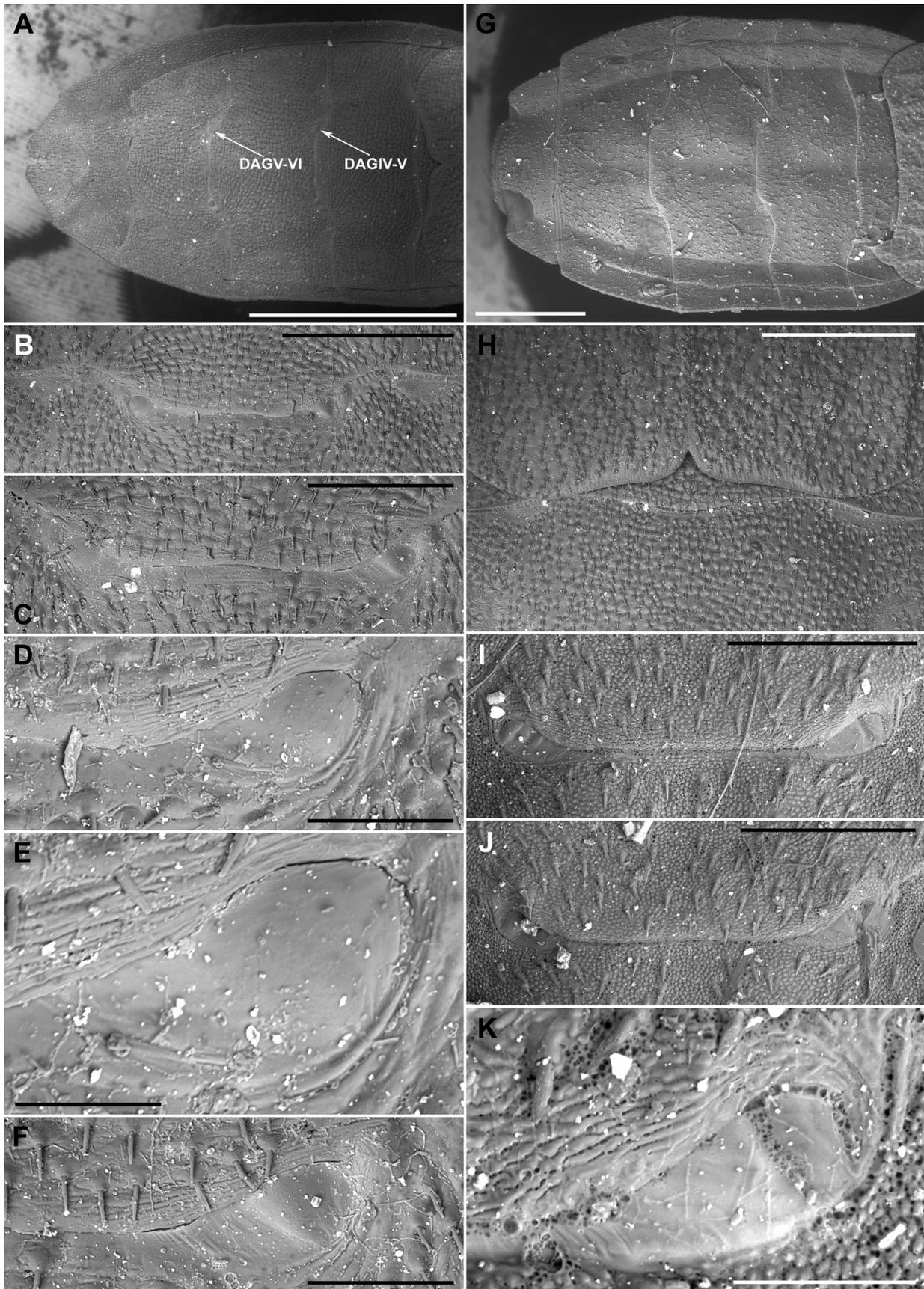


Fig. 5. External scent efferent system of dorsoabdominal glands in Hyocephalidae. A–F – *Hyocephalus aprugnus* Bergroth, 1906, female: A – abdomen, dorsal view (magnification 19×); B, D, E – dorsoabdominal scent efferent system on tergites IV–V (B – 47×, D – 200×, E – 400×); C, F – dorsoabdominal scent efferent system on tergites V–VI (C – 80×, F – 200×). G–K – *Maevius luridus* Brailovsky, 2002, male: abdomen, dorsal view (30×); H – suture between tergites III and IV (42×); I, K – dorsoabdominal scent efferent system on tergites IV–V (I – 130×, K – 500×); J – dorsoabdominal scent efferent system on tergites V–VI (120×). Abbreviations: DAGIV–V, DAGV–VI – scent efferent system of dorsoabdominal scent glands on tergites IV–V and V–VI, respectively. Scale bars: 0.1 mm (E, K), 0.2 mm (D, F), 0.4 mm (I–J), 0.5 mm (C), 1 mm (B, G–H), 3 mm (A).

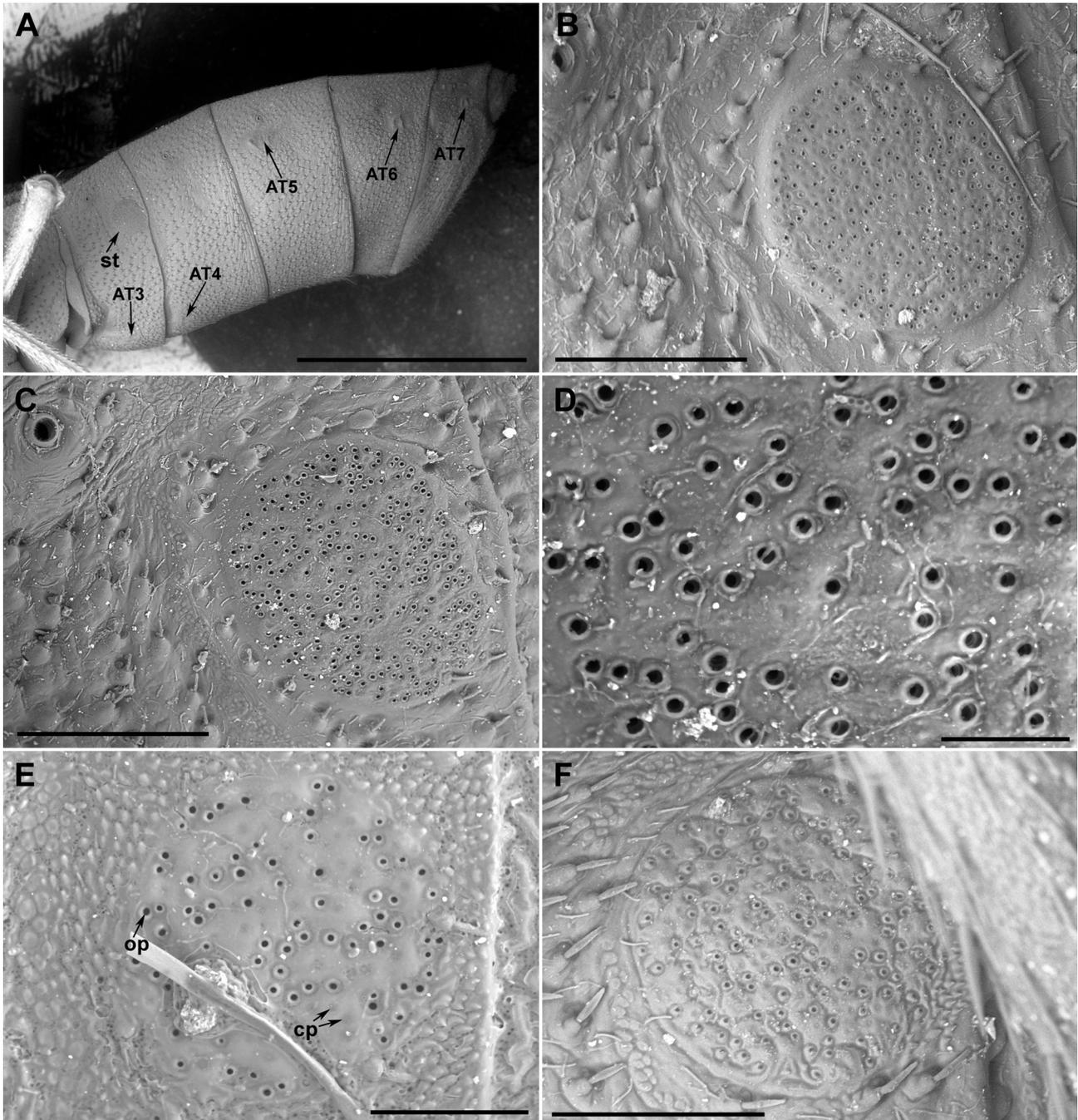


Fig. 6. Strainer organ in Hyocephalidae. A–D – *Hyocephalus aprugnus* Bergroth, 1906: A – female, abdomen, lateral view (magnification 18×); B–D – strainer (B – male, 150×; C – female, 150×; D – female, 600×). E – *Maevius luridus* Brailovsky, 2002, male, strainer (370×). F – *Maevius indecorus* (Stål, 1874), female, strainer (250×). Abbreviations: AT3–7 – abdominal trichobothria on sternites III–VII; cp – closed pore; op – open pore; st – strainer. Scale bars: 50 μ m (D), 0.1 mm (E), 0.2 mm (F), 0.3 mm (B–C), 3 mm (A).

II completely covered by metathorax. Ventrite III with submarginal depressed line near anterior margin (Fig. 7: sml; ŠTYS 1964: fig. 23). Ventrite VII in females split medially into two halves (ŠTYS 1964: fig. 25). Ventral laterotergites developed, tergo-sternal sutures apparent as narrow impressed line (Fig. 7: tss; ŠTYS 1964: fig. 23), abdominal spiracles always situated on ventral part of abdomen (Fig. 7: sp).

Trichobothrial pattern (Fig. 7) with three trichobothria on each of sternites III–VI and only two trichobothria on sternite VII (trichobothrial formula 3-3-3-3-2). Positions

of trichobothria on each sternite not significantly different between *Hyocephalus aprugnus* (ŠTYS 1964: fig. 23) and *Maevius* species (*M. indecorus*: SCHAEFER 1981: Fig. 2B; *M. luridus*: Figs 6A, 7). Abdominal trichobothria AT3–7 clustered (Figs 6A, 7: AT3–7; 8A–H, 9A–D). AT3 and AT4 located submedially, either near anterior margin (AT4) or slightly anterior of centre of segment (AT3) (Figs 6A, 7: AT3 and AT4; 8A). AT3a–c forming transverse (*Hyocephalus aprugnus*, ŠTYS 1964: fig. 23) or slightly skewed row directed anteromedially (*Maevius*, Figs 7: AT3; 8A, B). AT4 arranged transversely (Figs 7: AT4; 8A, C; ŠTYS

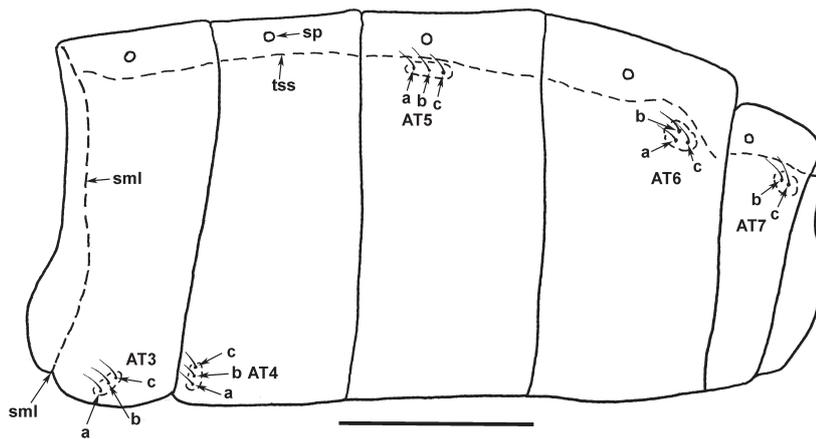


Fig. 7. Schematic drawing of abdomen of *Maevius luridus* Brailovsky, 2002, male, in lateral view. Scale bar: 1 mm. Abbreviations: AT3–7a–c – particular positions of abdominal trichobothria on sternites III–VII; sml – submarginal depressed line; sp – spiracle; tss – tergosternal suture.

1964: fig. 23). AT5–AT7 located on lateral margins of sternites slightly ventrad of tergosternal sutures (Figs 6A, 7). AT5a–c forming longitudinal line (Figs 6A, 7: AT5; 8E, F; 9C) ventrally of spiracle, AT5b situated immediately below spiracle (Figs 6A, 7, 8E). AT6a–c and AT7b–c postspiracular (Figs 6A, 7), AT6a–c forming triangle (Figs 7: AT6; 8H, 9D), AT7b–c in skewed line similarly to AT6b–c (Figs 7: AT7; 9B).

Trichobothria with sensillum always long and easily recognisable (Figs 8B–H, 9A–D). Bothrium shallow, open, of type B according to GAO et al. (2017), base of sensillum not sunken below surface of cuticle, with visible dome-shaped protuberance (Figs 8D, G, 9A). Bothrium surrounded by large circular trichome; trichomes of AT3a–c, AT4a–c, AT5a–c, AT6a–c and AT7b–c always fused into single circular or oval patch on each segment (Figs 7, 8B–H, 9A–D). Microtrichia of trichomes completely fused into reticulate, comb-like structure spread all over trichome (trichome type T3 according to GAO et al. 2017). Inner walls of combs with fine ridges possibly representing remnants of fused microtrichia (Figs 8G, 9A). Trichomes of AT3a–c and AT4a–c anteriorly (Figs 8B–D), of AT5a–c, AT6a–c and AT7b–c dorsally (Figs 8E–H, 9A–D), in *Hyocephalus aprugnus* also medially between AT6a and AT6b–c (Fig. 8H), with several [4 (Fig. 9C) to 14 or 15 (Figs 8F, H)] small (14–21 µm long), cuticular, funnel-shaped structures with irregularly undulate apical margins and nested at base of combs (Figs 8D, G, 9A, B). Because of their resemblance to flowers of *Crocus* plants (Asparagales: Iridaceae), we name them ‘crocus-like structures’.

In contrast, *Dicranocephalus agilis* (Stenocephalidae) has deeply recessed bothria of type A2 according to GAO et al. (2017) without any trichome. Trichobothria of Stenocephalidae are placed on small patch of elevated, smooth cuticle (Figs 9F–H).

Discussion. The pregenital abdomen of Hoyocephalidae features several plesiomorphic character states, shared with other representatives of Eutrichophora: i) all abdominal spiracles situated ventrally [shared with most Trichophora except for a major part of Lygaeoidea, in which at least one spiracle is shifted dorsad (apomorphy); SCUDDER 1962a, 1963a; SCHAEFER 1964, 1966b; ŠTYS 1964, 1967; LANSBURY 1965; SWEET 1967, 1981; WOODWARD 1968a,b; HENRY

1997a]; ii) the presence of complete, straight intersegmental sutures on the whole abdominal venter reaching the lateral margins (shared with Coreoidea, most Lygaeoidea, Largidae: Larginae, and a few genera of Pyrrhocoridae; in contrast, the intersegmental sutures IV/V or IV/V and V/VI are strongly sinuate and incomplete in Rhyparochromidae, Geocoridae: Geocorinae, Largidae: Physopeltinae, and majority of Pyrrhocoridae; SCUDDER 1962a, 1963a; ŠTYS 1964; LANSBURY 1965; SWEET 1967; WOODWARD 1968a,b; HEMALA et al., in prep. a); iii) ventral laterotergites delimited from sternites by a tergosternal suture – a character state largely misinterpreted in previous literature (HEMALA et al., in prep. a), shared with Largidae, majority of Pyrrhocoridae, and several groups of Lygaeoidea (Blissidae, Colobathristidae, Heterogastridae, Lygaeidae: Orsillinae, Pachygronthidae, Rhyparochrominae); in contrast, in the remaining Coreoidea, ventral laterotergites are fused with sternites and tergosternal sutures obliterated (SWEET 1967, WEIRAUCH et al. 2019; HEMALA et al., in prep. a); iv) ventrite VII sexually dimorphic, split medially to retain a xiphoid ovipositor in female (within Trichophora shared with Largidae, Lygaeoidea, Stenocephalidae, †Yuripopoviniidae, most Coreidae, and some fossil genera assigned to Rhopalidae, while a derived plate-like ovipositor developed several times independently in recent Rhopalidae, Alydidae, some Coreidae, Berytidae and Pyrrhocoridae, as well as in Pentatomoidea; TOWER 1913; SCUDDER 1957, 1962a, 1963a; ŠTYS 1962, 1964, 1967; SCHAEFER 1965, 1966b; LANSBURY 1965; WOODWARD 1968a,b; HENRY 1997a; YAO et al. 2006a,b; AZAR et al. 2011; HEMALA et al., in prep. a).

The trichobothrium of Hoyocephalidae features a bothrium of the type B, accompanied by a trichome. This character state occurs only in Hoyocephalidae, all Pyrrhocoroidea and most Lygaeoidea (GAO et al. 2017; HEMALA et al., in prep. a). The comb-like trichome with completely fused microtrichia is quite unusual, but a similar pattern was observed in the tribe Teracriini of Pachygronthidae (Lygaeoidea), including the fine ridges on inner walls of the combs, but without the crocus-like structures (GAO et al. 2017: figs 5e, f). The crocus-like structures, observed in all examined hoyocephalid taxa, have not been reported from any other Heteroptera and may thus represent another autapomorphy of Hoyocephalidae. Their function is unknown to us; most probably, they represent some sensilla. In contrast

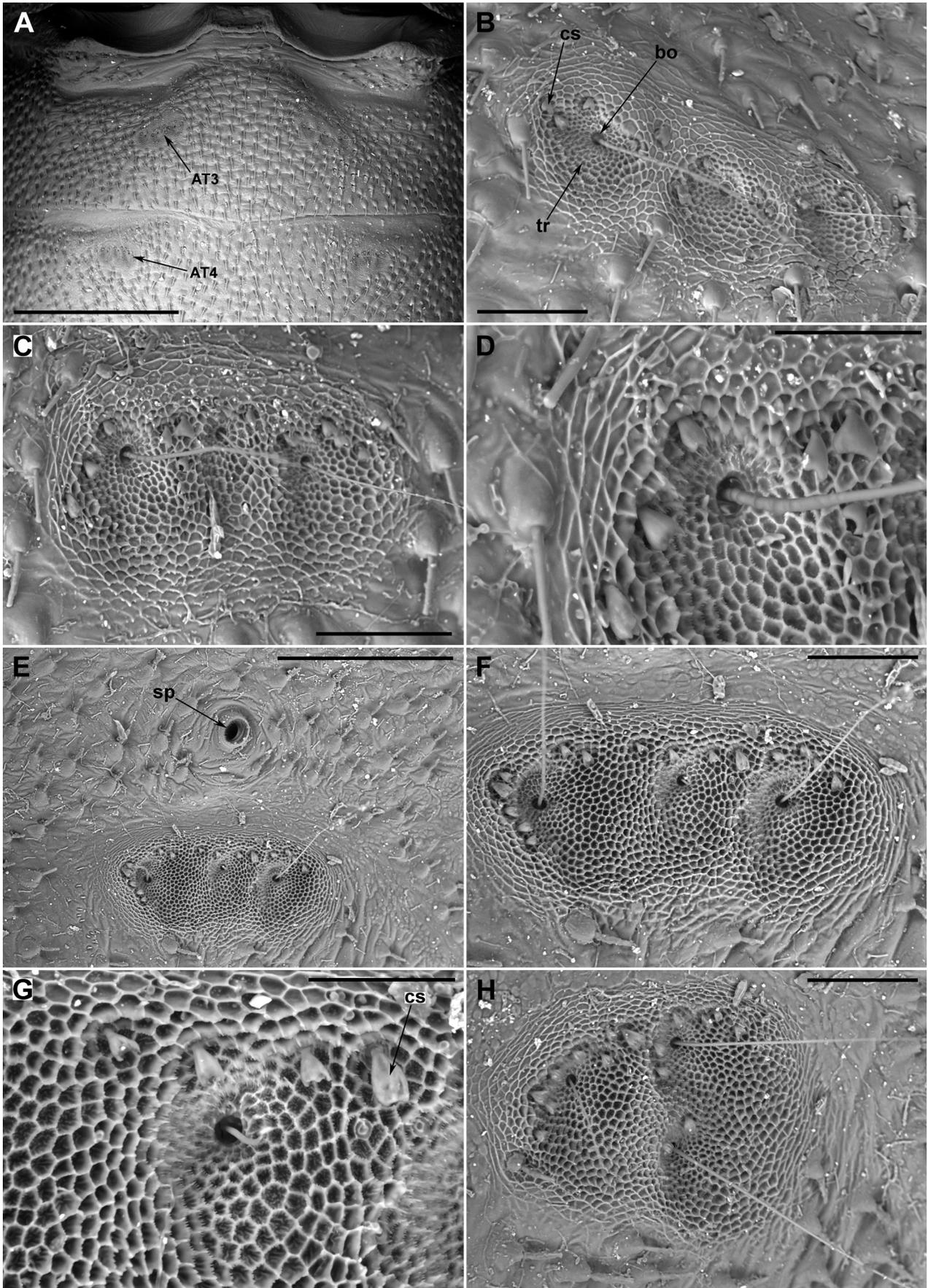


Fig. 8. Abdominal trichobothria in *Hyocephalus aprugnus* Bergroth, 1906, female: A – position of trichobothria on sternites III and IV (AT3 and AT4) (magnification 45×); B – AT3 (300×); C–D – AT4 (C – 400×, D – 800×); E–G – AT5 (E – 160×, F – 300×, G – 800×); H – AT6 (300×). Abbreviations: AT3–4 – abdominal trichobothria on sternites III to IV; bo – bothrium; cs – crocus-like structure; sp – spiracle; tr – trichome. Scale bars: 50 μm (D, G), 0.1 mm (B–C, F, H), 0.3 mm (E), 1 mm (A).

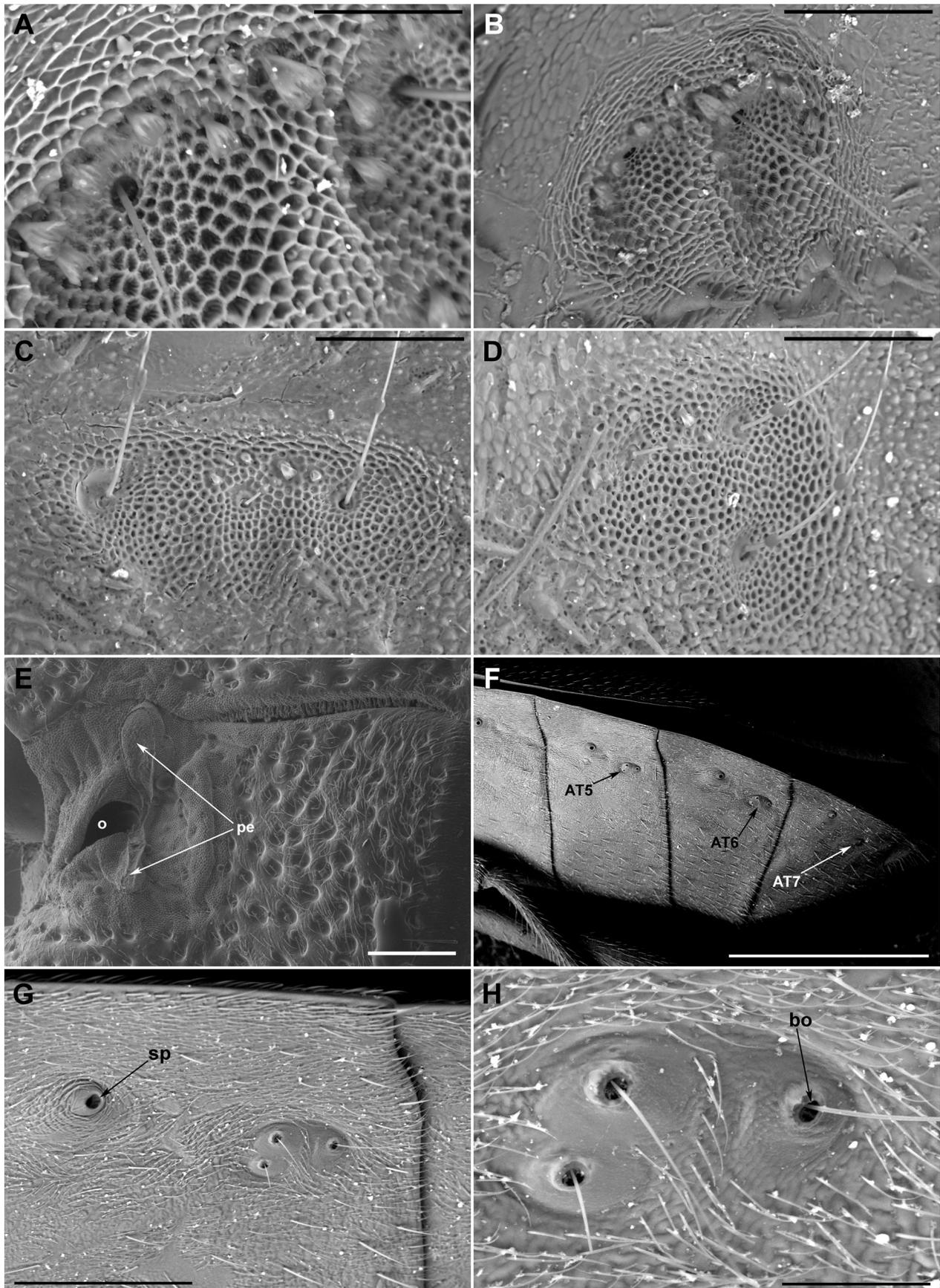


Fig. 9. Details of abdomen and thorax in Hoyocephalidae and Stenocephalidae. A–B – *Hyocephalus aprugnus* Bergroth, 1906, female: A – abdominal trichobothria on sternite VI (AT6) (magnification 800×); B – AT7 (400×). C–D – *Maevius luridus* Brailovsky, 2002, male: C – AT5 (400×), D – AT6 (400×). E–H – *Dicranocephalus agilis* (Scopoli, 1763): E – external scent efferent system (261×); F – abdomen in lateral view (27×); G–H – abdominal trichobothria on sternite VI (G – 120×, H – 400×). Abbreviations: AT5–7 – abdominal trichobothria 5–7; bo – bothrium; o – ostiole; pe – peritreme; sp – spiracle. Scale bars: 50 µm (A), 0.1 mm (B–D).

to Hyocephalidae, in Stenocephalidae we found deeply recessed bothria (type A2) without trichomes. The deeply recessed bothria seem plesiomorphic within Trichophora, occurring in Idiostoloidea (type A1), Pentatomoidea and Coreoidea (Coreidae, Alydidae, Rhopalidae, and Stenocephalidae) (GAO et al. 2017; HEMALA et al., in prep. a).

The trichobothrial formula 3-3-3-2 of Hyocephalidae is shared with all Eutrichophora. AT3 and AT4 placed submedially and AT5–7 situated laterally represents the “lygaeoid type” according to ŠTYS (1962) and SCUDDER (1963a), which is present also in Stenocephalidae, Pyrrhocoroidea, and Lygaeoidea. The “coreoid type” with AT5–7 situated sublaterally occurs in Coreidae, Alydidae, and Rhopalidae (TULLGREN 1918; SCUDDER 1957, 1963a,b; ŠTYS 1962, 1964, 1967; SCHAEFER 1964, 1965, 1966a,b, 1975, 1981; LANSBURY 1965; SWEET 1967; see Table 1 for summary). Also the Lower Cretaceous †Yuripopoviniidae have AT5–7 in lateral position, while AT3–4 are in unusual sublateral position, which, however, may be an artefact in the unique fossil specimen contained in amber (or its illustration). On the other hand, the fact that both Stenocephalidae (SCHAEFER 1975) and Hyocephalidae (KUMAR 1966) bear the full set of trichobothria (3-3-3-2) already in the first larval instar links these two families with other Coreoidea, Largidae, and Heterogastridae, while in Pyrrhocoridae and the remaining lygaeoid families the full set of trichobothria appears

only in the second or later larval instars (SCHAEFER 1975, 1981). The trichobothrial pattern of Hyocephalidae differs from all remaining Eutrichophora in the position of AT5 immediately below the spiracle; in the rest of Coreoidea all AT5a–c are postspiracular, while in Pyrrhocoroidea and most Lygaeoidea at least AT5a (in Pyrrhocoridae all AT5a–c) is prespiracular (ŠTYS 1964; SCHAEFER 1964, 1965, 1975, 1981; HEMALA et al., in prep. a). SCHAEFER (1981) considered the position of AT5 in Hyocephalidae autapomorphic. Also, the condition with all trichobothrial groups narrowly clustered within a common trichome on each segment is a unique apomorphy of Hyocephalidae.

Comments on the phylogenetic relationships of Hyocephalidae

BERGROTH (1906), establishing Hyocephalinae as a new subfamily within Coreidae, mentioned that it is distinguished from all other Coreidae by the antennae inserted on the head ventrally (infericorn; like in Lygaeidae) and the membrane with only four veins (like in Aradidae or Lygaeoidea). For these reasons, REUTER (1912) elevated Hyocephalidae to family rank within Coreoidea. ŠTYS (1964) in his fundamental morphological redescription of *Hyocephalus aprugnus* pointed out a number of characters shared among Hyocephalidae and other families of Coreoi-

Table 1. Trichobothrial formula and relative positions of abdominal trichobothria on sternites III–VII. AT3–7 – abdominal trichobothria on sternites III to VII (after SCHAEFER 1966a,b, 1975, HEMALA et al. in prep. a, etc.).

		trichobothrial formula	AT3	AT4	AT5	AT6	AT7
Idiostoloidea	Idiostolidae	7(6)-7(6)-5(4,3)-4-4(3)	submedially, sublaterally, laterally	submedially, sublaterally, laterally	submedially, sublaterally, laterally; pre- and postspiracular	laterally; pre- and postspiracular	laterally; pre- and postspiracular
Pentatomoidea		2-2-2-2-2	laterally	laterally	laterally; postspiracular	laterally; postspiracular	laterally; postspiracular
Lygaeoidea		3-3-3-3-2	submedially	submedially	laterally; pre- and postspiracular	laterally; pre- and postspiracular	laterally; postspiracular
Pyrrhocoroidea	Largidae	3-3-3-3-2	submedially	submedially	laterally; pre- and postspiracular	laterally; pre- and postspiracular	laterally; postspiracular
	Pyrrhocoridae	3-3-3-3-2	submedially	submedially	laterally; prespiracular	laterally; pre- and postspiracular	laterally; postspiracular
Coreoidea	Hyocephalidae	3-3-3-3-2	submedially	submedially	laterally; at spiracle level	laterally; postspirac- ular	laterally; postspirac- ular
	Stenocephalidae	3-3-3-3-2	submedially	submedially	laterally; postspiracular	laterally; postspiracular	laterally; postspiracular
	Yuripopoviniidae	3-3-3-3-2	sublaterally	sublaterally	laterally; postspiracular	laterally; at spiracle level	laterally; postspiracular
	Coreidae	3-3-3-3-2	submedially	submedially	sublaterally; postspiracular	sublaterally; postspiracular	sublaterally; postspiracular
	Alydidae	3-3-3-3-2	submedially	submedially	sublaterally; postspiracular	sublaterally; postspiracular	sublaterally, postspiracular
	Rhopalidae	3-3-3-3-2	submedially	submedially	sublaterally; postspiracular	sublaterally; postspiracular	sublaterally; postspiracular

dea, Pyrrhocoroidea, and Lygaeoidea (i.e. Eutrichophora of XIE et al. 2005), including many symplesiomorphies, some synapomorphies, as well as a few autapomorphies, such as a unique combination of head characters, which we illustrate here in Figs 2A, B, D–H (porrect head, infericorn antennae, prolonged clypeus, short mandibular plates, large and long bucculae, labial groove on gula, gular sulcus, and occipital sulcus), the structure of the peritreme, and the presence of the strainer on sternite III (ŠTYS 1964). He concluded that Hoyocephalidae form an evolutionary lineage together with Stenocephalidae and Coreidae, being more closely related to Stenocephalidae, because of an identical (sic!, see below) trichobothrial pattern and the structure of the female genitalia shared by Hoyocephalidae and Stenocephalidae. Furthermore, Hoyocephalidae share sulcate tibiae with most Coreidae and resemble externally some taxa of Colpurini, a tribe of Coreinae (ŠTYS 1964). WATERHOUSE & GILBY (1964) described metathoracic scent glands of *Maevius indecorus*, finding them similar to Coreidae but having three pairs of glands. However, HEPBURN & YONKE (1971) considered this difference in the number of glands important and confirmed its uniqueness within Coreoidea. KUMAR (1966) pointed out that Hoyocephalidae differ from all other coreoids in having elongated, lygaeoid-like eggs and a U-shaped ecdysial line remote from the eyes.

SCHAEFER (1981) mostly confirmed the results of ŠTYS (1964) but he correctly noticed the difference in the position of AT5 between Hoyocephalidae (situated at the level of spiracle) and Stenocephalidae (postspiracular). He concluded that Hoyocephalidae were closely related to Stenocephalidae and supposed that these two families were more closely related to the Alydidae-Rhopalidae-Coreidae complex than to any other taxa of Eutrichophora. According to SCHAEFER (1981), the autapomorphies of Hoyocephalidae include the scimitar-shaped projection of the peritreme, the presence of the strainer on sternite III, the arrangement of the abdominal trichobothria on sternite V, and the lack of vesica and sperm reservoir. However, the last character was rejected by YANG (2007: figs 9, 10 – aedeagus = Schaefer's vesica, ejaculatory reservoir = Schaefer's sperm reservoir). The synapomorphies of Hoyocephalidae and Stenocephalidae according to SCHAEFER (1981) include suturing between sternites III and IV, connection between the rims of the genital capsule and the cup-like sclerite, dorsal opening of the genital capsule, and asymmetries of the flange(s) of the spermathecal duct.

Thus, since ŠTYS (1964) and SCHAEFER (1981), Hoyocephalidae have been regarded as a basal group within Coreoidea, closely related to Stenocephalidae. HENRY (1997a) recognised Rhopalidae as the sister-group to the remaining Coreoidea, the latter consisting of two clades, Stenocephalidae + Hoyocephalidae and Coreidae + Alydidae, both sharing shortened bucculae and separate openings of DAGs. According to him, Stenocephalidae and Hoyocephalidae share the infericorn position of the antennae (symplesiomorphy) and paratergite VIII articulated with the first valvifer (interpreted as a synapomorphy in HENRY 1997a, but occurring also in Largidae). In subsequent morphological studies, AZAR et al. (2011) revealed a polytomy

of Rhopalidae, Coreidae, Alydidae, †Yuripopoviniidae and Stenocephalidae + Hoyocephalidae, while YAO et al. (2012) received the following topology of Coreoidea: (Coreidae + Alydidae) + (Rhopalidae + (Hoyocephalidae + Stenocephalidae)). However, YANG (2007), based on the structure of the male genitalia, recovered a trichotomy of Pyrrhocoroidea + Hoyocephalidae + remaining Coreoidea, this clade being sister to Lygaeoidea. Unfortunately, the molecular evidence which would help to find the phylogenetic position of Hoyocephalidae is still poor. LI et al. (2006, 2012) performed phylogenetic analyses based on single (18S rDNA) or several genes (18S rDNA, 28S rDNA, 16S rDNA, and COI), which included also *Maevius indecorus*, but their resulting trees were somewhat incongruent and did not recognise monophyletic superfamilies within Eutrichophora; in combined analyses by LI et al. (2012), *Maevius* was poorly supported as a sister taxon to *Liorhyssus* (Rhopalidae). GORDON et al. (2016) analysed phylogenetic relationships in Eutrichophora with emphasis on Pyrrhocoroidea, based on two mitochondrial protein-coding genes (COI and COII) and three rDNA genes (16S, 18S, and 28S). They recovered monophyletic Coreoidea with a basal position of Hoyocephalidae (represented by *Maevius indecorus*) + Stenocephalidae, this clade being sister to Rhopalidae + (Alydidae + Coreidae); this topology, however, received only low bootstrap support. WEIRAUCH et al. (2019) performed combined analyses of morphological and molecular (16S rDNA, 18S rDNA, and 28S rDNA) characters, recognising *Maevius indecorus* mostly as a member of poorly supported Coreoidea, but with detailed relationships not well resolved, also because of a limited taxon sampling. The phylogenetic position of Stenocephalidae based on molecular characters is better established: Stenocephalidae were recognised as sister to the remaining Coreoidea (LI et al. 2016a, WANG et al. 2016, LIU et al. 2019), or as more closely related to Coreidae + Alydidae (LI et al. 2017). However, none of those analyses included Hoyocephalidae.

Our results bring more detailed information on several morphological characters of Hoyocephalidae, which have never been documented by electron microscopy. We can confirm that Hoyocephalidae share many symplesiomorphies with other groups of Pentatomomorpha (e.g. general structure of the external metathoracic scent efferent system with a vestibular scar) or Eutrichophora (trichobothrial formula 3-3-3-2), a putative synapomorphy/homoplasy (loss of the anterior pair of dorsoabdominal scent glands, shared with the remaining Coreoidea, Idiostoloidea, and part of Lygaeoidea), as well as several autapomorphies defining the family. The unique autapomorphies include the scimitar-shaped peritreme without contact with the surrounding pleuron, the strainer organ on sternite III, the trichobothria on sternite V placed immediately ventrad of the spiracle, the trichobothrial pattern with all trichobothria on each of abdominal segments III–VII grouped within a common trichome, and the presence of crocus-like structures within the trichome (the last two characters are documented here for the first time). Of particular interest is the presence of a shallow open bothrium (type B) surrounded by a trichome

in Hyocephalidae. This character was so far known only in Pyrrhocoroidea and most Lygaeoidea (GAO et al. 2017, HEMALA et al. in prep. a) and may represent a synapomorphy of these two superfamilies and Hyocephalidae. In contrast, Stenocephalidae share a recessed bothrium of type A2 and the absence of a trichome with the remaining Coreoidea, which was considered plesiomorphic (GAO et al. 2017). The presence of these structures in Hyocephalidae may thus suggest either a closer relationship of Hyocephalidae to Lygaeoidea + Pyrrhocoroidea than to Coreoidea or a parallel evolution of the open bothrium with trichome in Eutrichophora. Interestingly, Hyocephalidae are epigeic seed-predators (KUMAR 1966), like most Pyrrhocoroidea, many Lygaeoidea, and some Coreoidea (e.g. Pseudophloeinae). This might be an ancestral lifestyle within Eutrichophora, in contrast to most Coreoidea dwelling on plants (see WEIRAUCH et al. 2019, although their reconstruction of the evolution of feeding types and microhabitat associations in Heteroptera is partly based on inaccurate data, e.g. they treated *Maevius indecorus* as plant-dwelling). The traditional classification and hypotheses on the phylogeny of Coreoidea have recently been challenged by the phylogenomic study by FORTHMAN et al. (2019), focusing on the relationships within Alydidae and Coreidae. The relationships of Hyocephalidae and Stenocephalidae (not included in the dataset of FORTHMAN et al. 2019) with other Coreoidea and Eutrichophora and the traditional concept of Coreoidea still have to be tested using a representative taxon and character sampling. We must highlight here the importance of Hyocephalidae for a better understanding of the phylogeny of Eutrichophora and the urgent need to obtain also phylogenomic data to properly include this taxon in the “tree of life” of Heteroptera.

APPENDIX

Taxonomic catalogue of Hyocephalidae

The following collection acronyms are used:

ANIC	Australian National Insect Collection, Canberra, Australia;
HNHM	Hungarian Natural History Museum, Budapest, Hungary;
MMBC	Moravian Museum, Brno, Czech Republic;
MZHF	Zoological Museum, University of Helsinki, Helsinki, Finland;
NHRS	Naturhistoriska Riksmuseet, Stockholm, Sweden;
NMPC	National Museum, Prague, Czech Republic;
SAMA	South Australian Museum, Adelaide, Australia.

Hyocephalidae Bergroth, 1906

Hyocephalinae (subfamily of Coreinae): BERGROTH (1906): 649 (diagnosis).

Hyocephalaria (division [= tribe] of Coreidae: Coreinae): BERGROTH (1912): 343–344 (systematic placement); BERGROTH (1913): 126, 146 (catalogue); KIRITSHENKO (1916): 10, 12 (classification, generic composition).

Hyocephalidae: REUTER (1912): 38–41, 47, 59 (family status, diagnosis, key to families); KIRITSHENKO (1916): 6–7 (classification); HANDLIRSCH (1925): 1042, 1076–1077 (key to families, diagnosis); BRUES & MELANDER (1932): 19, 149 (classification in Lygaeoidea, key to families); CHINA (1933): 195 (phylogeny); BEIER (1938) (key to families, diagnosis); KIRITSHENKO (1951): 72, 74 (classification); POISSON (1951): 1791 (diagnosis); BRUES et al. (1954): 20, 178 (classification in Lygaeoidea, key to families); CHINA (1955): 368 (phylogeny); CHINA & MILLER (1955): 259 (list, key to families); MILLER (1956): 4, 57–58 (diagno-

sis); IMMS (1957): 458, 464 (key to families, diagnosis); OBNBERGER (1958): 112, 180 (key to families, diagnosis); CHINA & MILLER (1959): 7 (list of families); PUTSHKOV (1961): 1393–1394 (phylogeny); PUTSHKOV (1962): 10, 13 (classification, phylogeny); ŠTYS (1962): 38, 42, 43 (classification in Coreoidea s. l.); ŠTYS (1964): 229–231, 248–260 (morphology, diagnosis, classification, phylogeny); KUMAR (1965): 87 (phylogeny); KUMAR (1966): 898–907, 965–972, 974, 976 (immatures, life cycle); COBBEN (1968): 351, 353, 354 (egg morphology); GRANT & ŠTYS (1970): 113–114 (nomenclature); JORDAN (1972): 34, 35: fig. 74, 41 (key to families, diagnosis, habitus figure); SCHAEFER (1972): 814, 817 (morphology); SCHAEFER (1975): 234, Table 9; COBBEN (1978): 128, 129, 141, 209 (morphology, life habits); SCHAEFER (1981): 83–94 (morphology, phylogeny); SLATER (1982): 439 (diagnosis); SCHAEFER & MITCHELL (1983): 592–593, 609 (host plants); CARVER et al. (1991): 447, 503–504 (key to families, morphology); SCHUH & SLATER (1995): 40, 279–281 (key to families, diagnosis); HENRY (1997a): 278–279, 288, 291–296 (phylogeny); BRAILOVSKY (2002): 41–50 (review, key to genera and species); CASSIS & GROSS (2002): 132–134 (diagnosis, catalogue); LI et al. (2006): 308, 310, 312–314 (phylogeny); YANG (2007): 15, 18: fig. 9, 19: fig. 10, 57, 151, 153, 156, 157 (morphology, phylogeny); HENRY (2009): 226, 242 (diagnosis, biodiversity); AZAR et al. (2011): 638–640 (phylogeny); YAO et al. (2012): 3, 4 (phylogeny); GORDON et al. (2016): 7128, 7130–7131 (phylogeny); HENRY (2017): 283, 301–303 (diagnosis, biodiversity); WEIRAUCH et al. (2019): 71, 74, 78, 81 (phylogeny).

Hyocephalini: KIRITSHENKO (1951): 61 (classification).

Hyocephalus Bergroth, 1906

Hyocephalus Bergroth, 1906: 647–648 (original description). Type species: *Hyocephalus aprugnus* Bergroth, 1906, by monotypy.

Hyocephalus: BERGROTH (1913): 146 (catalogue); ŠTYS (1964): 231 (catalogue); GRANT & ŠTYS (1970): 113–114 (nomenclature); BRAILOVSKY (2002): 50 (key to genera and species); CASSIS & GROSS (2002): 134 (catalogue).

Hyocephalus (subsequent incorrect spelling): YANG (2007): 19 (morphology).

Hyocephalus aprugnus Bergroth, 1906

Hyocephalus aprugnus Bergroth, 1906: 648–649 (original description, illustrations of head in lateral view and wing membrane, distribution). HOLOTYPE: ♀ (macropterous): Australia: South Australia, Yorketown (MZHF; see Note on p. 438).

Hyocephalus aprugnus: BERGROTH (1912): 343–344 (description of brachypterous female); GROSSBECK (1912): 360 (list of type specimens, erroneously listing brachypterous female described by BERGROTH 1912 as type); BERGROTH (1913): 146 (catalogue); ŠTYS (1964): 231–248 (redescription of macropterous female, illustrations of habitus and morphological structures, neotype designation, distribution, parasites); GRANT & ŠTYS (1970): 113–114 (nomenclature); EYLES (1971): 77 (nomenclature); JORDAN (1972): 35: fig. 74 (habitus figure); SCHAEFER (1981): 83 (deposition of non-type material); BRAILOVSKY (2002): 43, 47–50 (illustrations of habitus, genital capsule in posterior view and paramere; distribution; host plant; key to species); CASSIS & GROSS (2002): 134 (catalogue, distribution); YANG (2007): 15, 19: fig. 10, 156 (morphology); YAO et al. (2012): 3, 4 (phylogeny); WEIRAUCH et al. (2019): 78 (habitus photo).

Hyocephalus aprugnus (subsequent incorrect spelling): YANG (2007): 19 (morphology).

Material examined. AUSTRALIA: WESTERN AUSTRALIA: 8 miles SW of Mt. Ragged, 22.iii.1968, 1 ♀ (brachypterous), I. F. B. Common & M. S. Upton lgt. (ANIC); 16 miles N of Collie, 7.iv.1968, 1 ♀ (macropterous), I. F. B. Common & M. S. Upton lgt. (ANIC); Deepdene, 22.iii.1971, 1 ♂ 3 ♀♀ (brachypterous), E. F. Riek lgt. (ANIC, 1 ♂ → MMBC, 1 ♀ → NMPC); Deep Dene, Karridale, 25.iii.1964, 1 ♀ (brachypterous), 28.xii.1964, 1 ♀ (brachypterous), L. M. O’Halloran lgt. (ANIC); Manjimup (Parup Block), pitfall trap, 12–18.iii.1976, 1 ♂ (brachypterous), J. D. Majer lgt. (ANIC); Prevelly Pk., 8 km W Margaret R., 33.58°S 114.59°E, 30.x.–1.xi.1984, 1 ♂ 1 ♀ (brachypterous), J. & N. Lawrence lgt. (ANIC, 1 ♂ → NMPC) [1 ♀ habitus photo, 1 ♂ ESEM]; Sorrento

Beach, 14.–15.vi.1967, 2 ♂♂ 2 ♀♀ (brachypterous), B. Humphries lgt. (ANIC, 1 ♀ → MMBC); Thomas R., 23 km NW by W of of Mt. Arid, 33.515°S 123.00°E, 4.–7.xi.1977, 1 ♀ (brachypterous), M. S. Upton & I. Freehan lgt. (ANIC) [ESEM]. All P. Kment det.

Distribution. Australia: New South Wales (BERGROTH 1912), South Australia (BERGROTH 1906, ŠTYS 1964, BRAILOVSKY 2002, CASSIS & GROSS 2002), Western Australia (BRAILOVSKY 2002, CASSIS & GROSS 2002).

Note. BERGROTH (1906) described *H. aprugnus* based on a single macropterous female, the holotype, but that specimen became missing since then. ŠTYS (1964: 232) redescribed the species based on a series of macropterous females he discovered in HNHM and designated one of them as neotype. However, the original holotype was later recognised among unidentified Coreidae from MZHF (see GRANT & ŠTYS 1970: 113). GRANT & ŠTYS (1970) applied to the International Commission on Zoological Nomenclature for retention of the neotype in preference to the rediscovered holotype, and placing the names *Hyocephalidae*, *Hyocephalus*, and *Hyocephalus aprugnus* on the Official Lists of Names in Zoology. The neotype designation was accepted in the catalogue of CASSIS & GROSS (2002). However, EYLES (1971) argued against the proposal by GRANT & ŠTYS (1970), finding it pointless. We found no Opinion of the ICZN published in the *Bulletin of Zoological Nomenclature* regarding this case, and none of the three names is included in the Official Lists (ICZN 2012; G. Lim, pers. comm. 2019). According to Article 75.8 (ICZN 1999), the designated neotype is set aside on publication of the discovery of the original name-bearing type which retains its validity.

Maevius Stål, 1874

Maevius Stål, 1874: 163, 165 (key to genera, original description, distribution, placed in Lethaeria [= Rhyarochromidae]). Type species: *Maevius indecorus* Stål, 1874, by monotypy.

Maevius: SCUDDER (1962b): 369 (transferred to Coreidae); BRAILOVSKY (2002): 50 (key to genera and species); CASSIS & GROSS (2002): 134 (catalogue).

Macius (subsequent incorrect spelling): YANG (2007): 57 (morphology).

Maevius indecorus Stål, 1874

Maevius indecorus Stål, 1874: 165 (original description, distribution). HOLOTYPE: ♀ (brachypterous), Australia: Queensland, Moreton Bay (NHRS).

Maevius indecorus: SCHAEFER (1972): 814, 817 (morphology of external metathoracic scent efferent system); SCHAEFER (1981): 85–90 (morphology and illustrations of external scent efferent system, pregenital abdomen, and male and female genitalia); SCHAEFER & MITCHELL (1983): 592–593, 609 (host plants); CARVER et al. (1991): 504 (habitus drawing, morphology of thorax and abdomen); BRAILOVSKY (2002): 43–45, 47–48, 50 (differential diagnosis; illustrations of habitus, genital capsule in posterior view and paramere; distribution; host plant; key to species); CASSIS & GROSS (2002): 134 (catalogue, distribution); LI et al. (2006): 310, 312–314 (phylogeny); YANG (2007): 15, 18: fig. 9, 57, 156 (morphology); LI et al. (2012): 6–13 (phylogeny); GORDON et al. (2016): 7128, 7131 (phylogeny); WEIRAUCH et al. (2019): 74, 78, 81, 82, 93, 94 (phylogeny).

Hyocephalus sp. nov.: WATERHOUSE & GILBY (1964): 979–980, 983–986 (metathoracic scent gland morphology, figure, chemical composition of scent secretion); KUMAR (1966): 898–907, 965–972, 974, 976 (morphology and figures of egg and larval instars I–V, life cycle, host plant association, habitat, bionomics, distribution); SCHAEFER (1975): 234, Table 9.

Macius indecorus (subsequent incorrect spelling): YANG (2007): 57 (morphology).

Material examined. AUSTRALIA: QUEENSLAND: Biggenden, Bluff Range, 15.viii.1972, 1 ♀ (brachypterous), H. Frauca lgt., P. Kment det. (ANIC) [ESEM]; S. Queensland, 7.i.1964, 1 ♂ 1 ♀ (brachypterous), R. Kumar lgt. & det. (ANIC, 1 ♀ → NMPC).

Distribution. Australia: New South Wales (BRAILOVSKY 2002), Queensland (STÅL 1874, KUMAR 1966, BRAILOVSKY 2002, CASSIS & GROSS 2002, YANG 2007, this paper), Western Australia (BRAILOVSKY 2002).

Maevius luridus Brailovsky, 2002

Maevius luridus Brailovsky, 2002: 42–44, 46, 50 (original description; differential diagnosis; illustrations of habitus, genital capsule in posterior view and parameres; distribution; key to species). HOLOTYPE: ♂ (brachypterous), Australia: South Australia, Eyre Penn., near Caralue Bluff (SAMA).

Maevius luridus: CASSIS & GROSS (2002): 134 (catalogue, distribution).

Material examined. AUSTRALIA: WESTERN AUSTRALIA: 12 km SW of Donnybrook, 33.40°S 115.44°E, 3.x.1981, 1 ♂, I. D. Naumann & J. C. Cardale lgt. (ANIC); 20 miles W. of Coolgardie, 27.iv.1968, 2 ♂♂ (brachypterous), I. F. B. Common & M. S. Upton lgt. (ANIC, 1 ♂ → MMBC); Thomas R., 23 km NW by W of of Mt. Arid, 33.515°S 123.00°E, 4.–7.xi.1977, 2 ♂♂ (brachypterous), M. S. Upton & I. Freehan lgt. (ANIC, 1 ♂ → NMPC) [1 ♂ habitus photo, 1 ♂ ESEM]. All P. Kment det.

Distribution. Australia: South Australia (BRAILOVSKY 2002, CASSIS & GROSS 2002), Victoria (BRAILOVSKY 2002, CASSIS & GROSS 2002), Western Australia (new record).

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