Zoodiversity, **56**(4):265–284, 2022
DOI 10.15407/zoo2022.04.265

Fauna and Systematics

UDC 595.133

SEM STUDY OF HOOKS IN THE ACANTHOCEPHALA WITH EMPHASIS ON STRUCTURAL-FUNCTIONAL RELATIONSHIPS

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SEM Study of Hooks in the Acanthocephala with Emphasis on Structural-Functional Relationships. Amin, O. M., Heckmann, R. A. — The retractable proboscis of acanthocephalans is equipped with hooks for attachment to the intestine of the definitive host. Throughout their evolutionary history, acanthocephalans have developed a variety of ways to maximize their anchoring to host gut and to avoid dislodgement. Hooks vary in their size and shape along the longitudinal axis of the proboscis, texture, structure, and hardness as well as in their contribution to the absorption of nutrients. Hooks also vary in their chemical composition, especially calcium, phosphorus, and sulfur, contributing to their hardness. Hook roots are paramount in anchoring them to the cuticular and subcuticular layers of the proboscis. Roots vary in size and shape and are often simple and directed posteriorly but often have anterior manubria or may be vestigial or absent especially posteriorly. The core layer of roots is usually continuous with that of the hook. Hooks often, but not always, maintain a similar pattern in families. Because of the inconsistencies and inadequacies in the description of hooks, especially in line drawings, in various groups of acanthocephalans, we have decided to provide the largest assortment of morphological and anatomical variabilities among the many species that we have studied over the years. We are, thus, reporting the SEM of hooks of 30 selected species of acanthocephalans in 13 families in an attempt to elucidate patterns and trends characteristic of acanthocephalan families.

Key words: Acanthocephala, hook morphology and anatomy, scanning electron microscopy, functional relationships.

Introduction

Acanthocephalans are called “spiny-headed worms” for a reason. Actually, they have no heads. They have a proboscis which is studded with hooks, not spines. Over 1,400 species of acanthocephalans are known to science (Amin, 2013 and new species described since) each of which has developed anchoring hooks on the proboscis for attachment to the gut of the definitive hosts. Cystacanths have also developed proboscis hooks similar to those of adults of the same species. Hooks are usually arranged in longitudinal rows that sometimes assume a spiral arrangement. They are normally smallest apically and posteriorly but occasionally are largest basally. There can be as few as 6 in each of 3 circles on the proboscis as in Neoechinorhynchidae to many as in Rhadinorhynchidae. The chemical composition of hooks, using Energy Dispersive x-ray analysis (EDXA), varies for each species including many measurable elements that contribute to their degree of hardness. This presentation provides a wide coverage of the structural-functional relationships of hooks of many species of acanthocephalans that we have studied over the years, among others.

Material and methods

Collections

All specimens imaged using scanning electron microscopy (SEM) were collected from localities referenced in table 1 where complete names of species of acanthocephalans and hosts, collecting sites, and figure numbers are listed.

Acanthocephalans are listed by families in alphabetical order.

Scanning electron microscopy (SEM)

Specimens that have been fixed and stored in 70 % ethanol were processed for SEM following standard methods (SM) (Lee, 1992). These included critical point drying (CPD) and mounting on aluminum SEM sample mounts (stubs) using conductive double-sided carbon tape. The sample was sputter coated with an 80–20 % gold-palladium target for 3 minutes using a sputter coater Q150T ES (Quorum, www.quorumtech.com) equipped with a planetary stage, depositing an approximate thickness of 20 nm. Sample was placed and observed in an FEI Helios Dual Beam Nanolab 600 Scanning Electron Microscope (FEI, Hillsboro, Oregon). Samples were imaged using an accelerating voltage of 5 kV, and a probe current of 86 pA, at high vacuum using a SE detector.

Used SEM images were sourced from our large stockpile of saved SEM material including those listed in table 1. Published material listed are copyrighted to OMA or modified from original publication. A few other images used were not previously published.

Microscope images

Microscope images were created using 10x or 40x objective lenses of a BH2 light Olympus microscope (Olympus Optical Co., Osachi-shibamiya, Okaya, Nagano, Japan) attached to an Am Scope 1000 video camera (United Scope LLC, dba AmScope, Irvine, California), linked to an ASUS labtop equipped with HDMI high-definition multimedia interface system (Taiwan-USA, Fremont, California). Images from the microscope are transferred from the labtop to a USB and stored for subsequent processing on a computer.

Focused Ion Beam (FIB) sectioning of hooks

A dual-beam SEM with gallium (Ga) ion source (GIS) is used for the Liquid Ion Metal Source (LIMS) part of the process. Hooks were sectioned at two positions (tip and middle) using the FEI Helios Dual Beam Nano lab mentioned above. The dual-beam FIB/SEM is equipped with a gallium (Ga) Liquid Ion Metal Source (LIMS). The hooks of the acanthocephalans were centered on the SEM stage and cross-sectioned using an ion accelerating voltage of 30 kV and a probe current of 2.7 nA following the initial cut. The time of cutting is based on the nature and sensitivity of the tissue. The sample also went through a cleaning cross-section milling process to obtain a smoother surface. The cut was analyzed with an X-ray normally at the tip, middle, and base of hooks for chemical ions with an electron beam (Tungsten) to obtain an X-ray spectrum. The intensity of the GIS was variable according to the nature of the material being cut.

Results were stored with the attached imaging software then transferred to a USB for future use.

Table 1. A listing of acanthocephalan species studied for proboscis hook patterns and their hosts and distribution

Family & species	Type and other hosts	Distribution	Published sources	Fig. nos.
	Arhythmacanthidae			
Heterosentisholos pinus Amin, Heckmannm & Ha, 2011	*Plotosus lineatus* (Thunberg); striped eel catfish	Vietnam; Halong Bay	Amin et al., 2011a & Amin et al., 2019 d	1–3
	Cavisomidae			
Cavisoma magnum (Southwell, 1927) Van Cleave, 1931	*Mugil cephalus* Linn.; flathead grey mullet	Arabian Gulf; Iraq	Amin et al., 2018 a	4–6
Pararhadinorhynchus magnus Ha, Amin, Ngo & Heckmann, 2018	*Scatophagus argus* (Linn.); spotted scat	Vietnam; Hai Phong	Ha et al., 2018	7–9
	Centrorhynchidae			
Centrorhynchus globirostris Amin, Heckmann, Wilson, Keele & Khan, 2015	*Centropus sinensis* (Stephens); pheasant crow	Pakistan; Sind	Amin et al., 2015 b	10–12
Centrorhynchus globocaudatus (Zeder, 1800) Lühe, 1911	*Falco tinnunculus* Linn.; falcon *Buteo buteo* Linn.; buzzard	Italy; Ferrara	Amin et al., 2020 a	13–18
	Echinorhynchidae			
Acanthocephalus parallelcementglandatus Amin, Heckmann & Ha, 2018	*Clarias batrachus* (Linn.); walking catfish. *Odorrana* sp. & *Hylarana* sp. frogs. *Tylosurus* sp.; needle fish	Vietnam; central & Ma River	Amin et al., 2018 b	19–22

Echinorhynchus cinctulus (Porta, 1905) Amin, 2013	*Lota lota* (Linn.); burbot	Russia; Lake Baikal	Amin et al., 2015 a	25–28
Echinorhynchus gadi Zoega in Müller, 1776	*Hippoglossus stenolepis* Schmidt; Pacific halibut	USA, Alaska	Amin et al., 2021 a	29–30
Echinorhynchus salmonis Müller, 1784	*Coregonus lavaretus* (Linn.); whitefish	Russia; Lake Baikal	Amin et al., 2015 a	23
Pseudoacanthocephalus lutzi (Hamann, 1891)	*Chaunus limensis* Werner; Peru coast toad	Peru; Lima	Amin & Heckmann, 2014	24
Gigantorhynchidae				
Intraproboscis sanghae Amin, Heckmann, Sist & Basso, 2021	*Phataginus tetradactyla* Linn.; black-bellied pangolin	Central African Republic	Amin et al., 2021 b	31–34
Mediorhynchus africanus Amin, Evans, Heckmann & El-Naggar, 2013	*Numida meliagris* Linn.; helmeted Guinea fowl & other fowl spp.	South Africa; Limpopo	Amin et al., 2013 a	35–37
Mediorhynchus gallinarum (Bhalerao, 1937)	*Gallus gallus* Linn.; chicken (Isa brown egg-laying hen)	Indonesia; Yogykarta	Amin et al., 2013 b	38
Heteracanthocephalidae				
Aspersentis megarhynchus (von Linstow, 1892) Golvan, 1960	*Notothenia coriiceps* Richardson; rock cod	W. Antarctica; Galindez Island	Amin et al., 2021 c	39–42
Moniliformidae				
Moniliformis cryptosaudi Amin, Heckmann, Sharifdini & Albayati, 2019	*Hemiechinus auratus* (Gmelin); long-eared hedgehog	Iraq; Baquba, Diyala Gov.	Amin et al., 2019 b	43–48
Moniliformis saudi Amin, Heckmann, Mohammed & Evans, 2016	*Paraechinus aethiopicus* (Ehenberg); desert hedgehog	Saudi Arabia; Unaizah	Amin et al., 2016	49–50
Moniliformis kalahariensis Meyer, 1931	*Atelerix frontalis* Smith; South African hedgehog	South Africa; Limpopo	Amin et al., 2014 b	51–54
Neoechinorhynchidae				
Neoechinorhynchus dimorphospinus Amin & Sey, 1966	*Chelon macrolepis* (Smith), *Lizaklunzigeri* (Day) & 4 marine spp. in 4 fish families	Arabian Gulf; Kuwait	Amin et al., 1984 & Amin et al., 2015 c	61–63
Neoechinorhynchus johnii Yamaguti, 1939	*Eleuthero nemate tradactylus* (Shaw), *Johnius carouna* (Cuvier), *Johnius* sp., *Otolithes ruber* (Bloch & Schneider)	Vietnam; along north & south coasts	Amin et al., 2019 a	65–68
Neoechinorhynchus manubrianus Amin, Ha & Ha, 2011	*Johnius carouna* (Cuvier); Caroun croaker, *Nibea albiflora;* yellowdrum, (Richardson), *Pennahia argentata* (Houttuyen); silver croaker	Vietnam; Halong Bay	Amin et al., 2011 b & Amin, Heckmann, 2012	64
Neoechinorhynchus personatus Tkach, Sarabeev& Shvetsova, 2014 *Neoechinorhynchus ponticus* Amin, Sharifdini, Heckmann, Rubtsova& Chine, 2020	*Mugil cephalus* Linn.; flathead grey mullet *Chelon auratus* Risso; golden grey mullet	Mediterranean off Tunisia & Black Sea	Amin et al., 2020 b	55–60
Oligacanthorhynchidae				
Macracanthorhynchus hirudinaceus (Pallas, 1781) Travassos, 1917	*Sus scrofa* Linn.; wild boar	Ukraine; Zhyromyr Region,	Amin et al., 2021 d	69–72
Nephridiacanthus major (Bremser, 1811 in Westrumb, 1821) Golvan, 1962	*Hemiechinus auratus* (Gmelin); Middle Eastern long-eared hedgehog & *Erinaceus concolor* Martin; Eastern European hedgehog	Iran; Mashhad, Khorasan	Heckmann et al., 2013 & Amin et al., 2020 c	73–78
Pachysentis canicola Meyer, 1931	*Chrysocyon brachyurus* (Illiger, 1815); maned wolf	USA, Texas	Amin et al., 2021 e	79–82
Polymorphidae				
Corynosoma strumosum (Rudolphi, 1802) Lühe, 1904	*Pusa caspica* (Gmelin); Caspian seal	Caspian Sea; Mazandaran, Iran	Amin et al., 2011 c	83–84
Neoandracantha peruensis Amin & Heckmann, 2017	*Ocypodegaudi chaudii* Milne-Edwards & Lucas; ghost crab	Peru; Pacific coast at Callao	Amin & Heckmann, 2017 a	85–88
Profilicollis altmani (Perry, 1942) Van Cleave, 1947	*Emerita analoga* (Simpson); mole crab & *Larus belcheri* (Vigors); Belcher's gull	Peru; Lurin& Chorrillos, Lima, Punta, Miraflora, Lima	Amin et al., 2022 a	89–90

Southwellina hispida (Van Cleave, 1925) Witenberg, 1932	*Gillichthys mirabilis* Cooper; longjaw mudsucker	USA; California	Amin et al.; 2022 b	91–96
		Quadrigyridae		
Acanthogyrus (*Acanthosentis*) *kashmirensis* Amin, Heckmann & Zargar, 2017	*Schizothorax plagiostomus* Heckel; snow trout; *S. labiatus* (McClelland), *S. curvifrons* Heckel, *S. esocinus* Heckel	Kashmir; Jhelum & Sandran rivers	Amin et al., 2017 b	97–99
Acanthogyrus (*Acanthosentis*) *fusiformis* Amin, Chaudhary, Heckmann, Ha & Singh, 2019	*Arius* sp.; catfish	Vietnam; Gulf of Thailand	Amin et al., 2019 b	100
Pallisentis (*Brevitritospinus*) *indica* Mital & Lal, 1976	*Channa gachua* Hamilton; dwarf snakehead & *Channa punctatus* Block & Schneider; spotted snakehead	India; Kali Nadi River, Aligarh	Amin et al., 2017 c	101–102
Pallisentis (*Pallisentis*) *nandai* Sarkar, 1953	*Nandus nandus* (Hamilton); Gangetic leaffish	India; Ganga River, Calcutta & Bijnor	Amin et al., 2021 f	103–107
Pallisentis (*Pallisentis*) *paranandai* Amin, Chaudhary, Heckmann, Rubtsova& Singh, 2021	*Channam arulius* (Hamilton); great snakehead	India; Ganga River at Bijnor, Uttar Pradesh	Amin et al., 2021 g	108
		Rhadinorhynchidae		
Leptorhynchoides polycristatus Amin, Heckmann, Halajian, El-Naggar & Tavakol, 2013	*Acipenser stellatus* Pallas; starry sturgeon & *A. nudiventris* Lovetzsky; fringebarbel sturgeon	Iran; Caspian Sea Chaparsararea	Amin et al., 2013c	109
Rhadinorhynchus hiansi Soota & Bhattacharya, 1981	*Ablennes hians* Valenciennes; needlefish & *Sarda orientalis* Temminck Schlegel; striped bonito	Vietnam; Nha-Trang & India; Kerala	Amin et al., 2020 d	113–116
Rhadinorhynchus laterospinosus Amin, Heckmann & Ha, 2019	*Balistes* sp., *Alectis ciliaris* (Bloch), *Auxis rochi* (Lacépède), *A. thazard* (Lacépède) & 5 other spp.	Vietnam; Halong Bay and other Pacific localities	Amin et al., 2011d, Amin et al., 2019 c	117–120
Rhadinorhynchus oligospinosus Amin & Heckmann, 2017	*Scomber japonicus* Houttuyn; chub mackerel & *Trachurus murphyi* Nichols; Chilean Jack mackerel	Peru; Port of Chicama, La Libertad	Amin & Heckmann, 2017 b	110–112
		Transvenidae		
Paratrajectura longcementglandatus Amin, Heckmann & Ali, 2018	*Nemipterus japonicus* Bloch; Japanese threadfin bream & *Otolithes ruber* Bloch & Schneider; tigertooth croaker	Arabian Gulf; Iran & Iraq at Basrah	Amin et al., 2018 c	121–126

Results

The SEM of 30 species of acanthocephalans in 13 families representing the widest morphological and anatomical spectra that we have come across, among the many species that we have studied, are selected for this presentation. The quality and extent of diversity covered is limited to the species that we have sampled for which we have selected SEM images as reported herein. From our experience, this presentation covers most, if not all, morphological and structural diversity of proboscides and hooks in the 13 selected families. The coverage is presented alphabetically by family following the arrangement in table 1, and not by any specific taxonomic order. SEM figures emphasize hook arrangement on the proboscis, hook shape, size, external topography, and internal anatomy. Some of the images are published herein for the first time. The text gives an overview by family.

Arhythmacanthidae

This family is represented by one species only, *H. holospinus*, which characteristically has a small anteriorly globular proboscis with long smooth anterior hooks having a heavy core and thin cortical layer continuing into the roots (figs 1–3). See Legends.

Cavisomidae

Both cavisomid species presented, *C. magnum* and *P. magnus* (figs 4–9) have relatively long proboscides with many uniform hooks in longitudinal rows; smallest hooks apical and posterior. Hooks are without prominent grooves or serrations. Serrations are shallow in *C. magnum* (fig. 5) or nearly absent in *P. magnus* (fig. 8). Structurally, cross sections show a prominent core and narrow to moderate cortical layer (figs 6, 9).

Centrorhynchidae

The two representative species in this family (figs 10–18) have either globular proboscis or cylindrical with two types of hooks (see figs 10 & 13) separated at the insertion point of the anterior end of the receptacle to the inner proboscis wall. Hooks are usually in longitudinal rows elevated or recessed (fig. 15) with either external serrations (fig. 11) or latero-ventral pebble-like surface (fig. 16). Hook core is usually extensive and solid and the cortical layer thin (figs 17, 18).

Echinorhynchidae

Five species in three genera are represented in this family (figs 19–30). In *A. parallelcemenglandatus*, a few similar hooks in longitudinal rows (fig. 19) have extensive micropores for nutritional uptake (fig. 20). They also have an extensive solid core and moderate cortical layer (figs 21, 22). *Pseudoacanthocephalus lutzi* also has hooks with micropores (fig. 24), and some specimens of *E. salmonis* from Lake Baikal have additional apical mini-hooks (fig. 23). Anterior hooks of *E. cinctulus*, also from Lake Baikal, have unique dorsal mini-hooks (spurs) branching off the dorsal side of the original hooks (figs 25–27). Hooks of *E. cinctulus* also have well developed core and slim cortical layer (fig. 28). Most species of *Echinorhynchus* have many similar hooks in longitudinal rows. In *E. gadi*, anterior hooks are usually raised (fig. 29) and posterior hooks are recessed deeper in the proboscis cuticle (fig. 30).

Gigantorhynchidae

Three species in two genera are presented (figs 31–38). *Intraproboscis sanghae* has a large apically flat proboscis (figs 31–33) enclosing the receptacle (fig. 32). Its hooks have serrations on the latero-ventral side (fig. 34). Two species of *Mediorhynchus* from birds have 2-part proboscides with 2 types of smooth hooks each (fig. 35) embedded in elevated cuticular lobes (fig. 36) each with lateral grooves (figs 37, 38).

Heteracanthocephalidae

Aspersentis megarhynchus exhibits the characteristic feature of heteracanthocephalid acanthocephalans of dorso-ventral differentiation of hooks (fig. 39). The sharp posterior angulation of smooth hooks (figs 40, 41) and the relatively thick cortical hook layer (fig. 42) are also characteristic.

Moniliformidae

All species of *Moniliformis* presented were recovered from mammals (hedgehogs). The hooks of *M. cryptosaudi*, a cryptic species (figs 43–48), are distinguished from those of *M. saudi*, its mirror image (figs 49, 50), by having a collagenous spongy texture (figs 43–48) and the virtual absence of calcium and phosphorous in its composition. The normal looking hooks of *M. saudi* (figs 49, 50) have the usual levels of calcium and phosphorous. The hooks of both species are smooth and have no evident special serrations, micropores, or projections. The hooks of adult *M. kalahariensis* (figs 53, 54) however, were similar to those of 2 species of *Mediorhynchus* from birds (figs 37, 38) in having distinct lateral grooves. These lateral grooves appear to manifest developmentally as underdeveloped immature worms in the intermediate cockroach host do not have them (fig. 52) and juveniles show stages in their development (fig. 53).

Neoechinorhynchidae

Five species of *Neoechinorhynchus* were recovered from marine fish in various waters (figs 55–68). Hooks of most species, i.e., *N. dimorphospinus*, *N. personatus,* and *N. ponticus* had solid well-developed core and thin corrugated coat with deep external lamellae (figs 56–60, 62, 63). The hooks of *N. johnii* and *N. manubrianus* also had solid to variably vacuolated core (figs 64, 66–68) and thin cortical layer that did not show evident lamellae, micropores, or branching.

Oligacanthorhynchidae

Macracanthorhynchus hirudinaceus (figs 69–72), *N. major* (figs 73–78), and *P. canicola* (figs 79–82) are parasites of mammals that have developed very similar morphological and structural features. The shape of the proboscis, the rounded heavy hooks deeply set within cuticular elevations, the proximal base of hooks with ventral expansion, and their solid core almost without cortical layer are all features in common. The proboscis armature is clearly designed for strength.

Polymorphidae

The four presented species in four genera (figs 83–96) have been recovered from mammals, birds, and fish as well as from crabs (intermediate hosts) and hooks' morphology offered a corresponding variety of shapes and morphology. The proboscis of all species, except *P. altmani,* enlarges posteriorly (figs 83, 85, 91) and hooks in all proboscides are similar, except in *C. strumosum* where they enlarge considerably at bulge (fig. 83). In addition, anterior hooks of *S. hispida* are more slender (fig. 92) than shorter middle hooks (fig. 93). All hooks are smooth without lamellae but only those of *C. strumosum* that have many micropores (fig. 84). Hook sections of the polymorphid worms that we examined had virtually no cortical layer and either totally solid (fig. 88) or partially vacuolated core (figs 94, 96). Intraspecific variability in degree of vacuolation is noted.

Quadrigyridae

Five species in two genera, all from freshwater fish in India and Vietnam, are presented (figs 97–108). No micropores or longitudinal grooves on the epicuticle of hooks were found in this family. The organization of hooks (figs 97, 100, 101, 103) was comparable except for the additional presence of inter-hook bumps in *P. indica* (fig. 101). The proboscis of *A. fusiformis* is unusual in being narrow anteriorly and with the basal hooks being the largest (fig. 100). Gallium-cut sections show that hooks had a moderate cortical layer and either near solid core as in *P. nandai* (figs 106, 107) or totally vacuolated core as in *A. kashmirensis* (fig. 99) making hooks appearing collapsed (fig. 98). Hooks in this family were smooth except for the presence of noticeable serrations on the basal latero-ventral aspects of hooks as in *P. nandai* and *P. paranandai* (figs 104, 105, 108).

Rhadinorhynchidae

Four species in two genera (figs 109–120) from marine fish in Iran, Vietnam, and Peru are presented. The Proboscis is long with many hooks in longitudinal rows (figs 110, 113, 117). Hooks in all species have epicuticular serrations that vary from prominent (figs 109, 114, 115, 118, 119) to barely noticeable as in *R. oligospinosus* (fig. 111). Hook cortical layer is of moderate thickness and the core varied between solid as in *R. hiansi* and *R. laterospinosus* (figs 116, 120) to partially vacuolated as in *R. oligospinosus* (fig. 112) reflecting on the hooks looking emaciated (fig. 111).

Transvenidae

Only one species of *Paratrajectura*, *P. longcementglandatus*, is known in this family. It has 2 types of hooks, larger elevated anterior hooks (fig. 121) and smaller recessed hooks posteriorly (fig. 122), in longitudinal rows. Longitudinal Gallium-cut sections show hooks of both types to have solid core and thin cortical layer but variations in cross sections show partial vacuolations (fig. 125). Most unusually, some hooks branch (fig. 126).

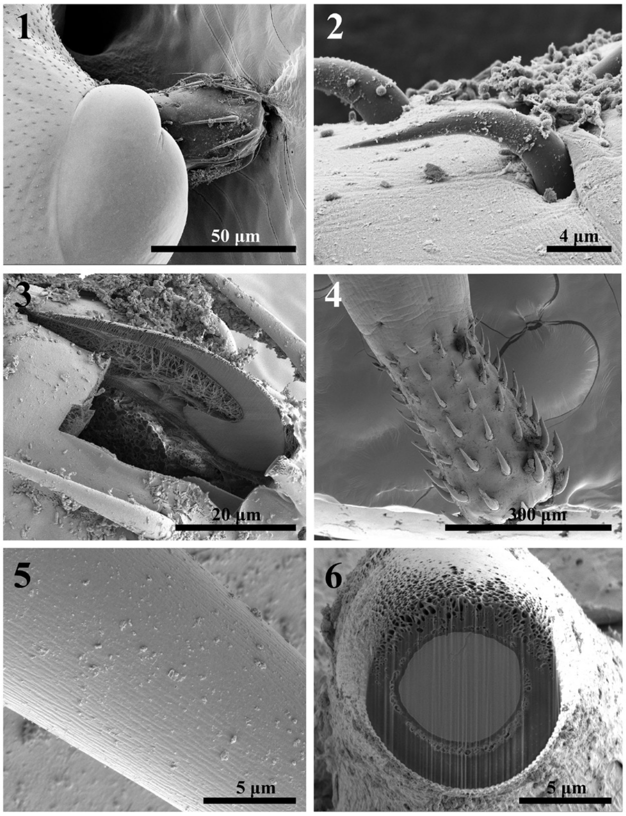
Discussion

The evolutionary significance and value of the various adaptations in hook morphology, surface texture, anatomy, structural strength, and hardness vs. flexibility directly contribute to acanthocephalans' attachment and survival in host gut and avoiding loss once established. Examples include the epicuticular hook lamellae in Neoechinorhynchidae and Rhadinorhynchidae, the deep lateral grooves in hooks of species of *Mediorhynchus* and *Moniliformis*, the solid hook core in Oligacanthorhynchidae and species of *Centrorhynchus*, *Neoandracantha*, and *Rhadinorhynchus.* spurs on the anterior hooks of *E. cinctulus* and double branching hooks in *P. longcementglandatus* also contribute to more efficient attachment. In addition to the solid hook core of acanthocephalans of land mammals such as Oligacanthorhynchidae, hooks are rendered even stronger by having a ventral expansion near their base interfacing with proboscis cuticle and sub-cuticle for additional strength and support. Related metabolic function includes the contribution of hooks of some species to nutrition uptake through a multitude of micropores in the hooks as is commonly the case in the trunk. In our study, we found micropores in hooks of acanthocephalans in 2 families, *A. parallelcemenglandatus*, and *P. lutzi* (Echinorhynchidae), *C. strumosum* (Polymorphidae). In general, we found a relationship between host groups (classes) and proboscis hooks' morphology and anatomy. The energy dispersive X-ray analysis has been used to describe the level of metals that contribute to the hardness and flexibility of hooks in many reported species.

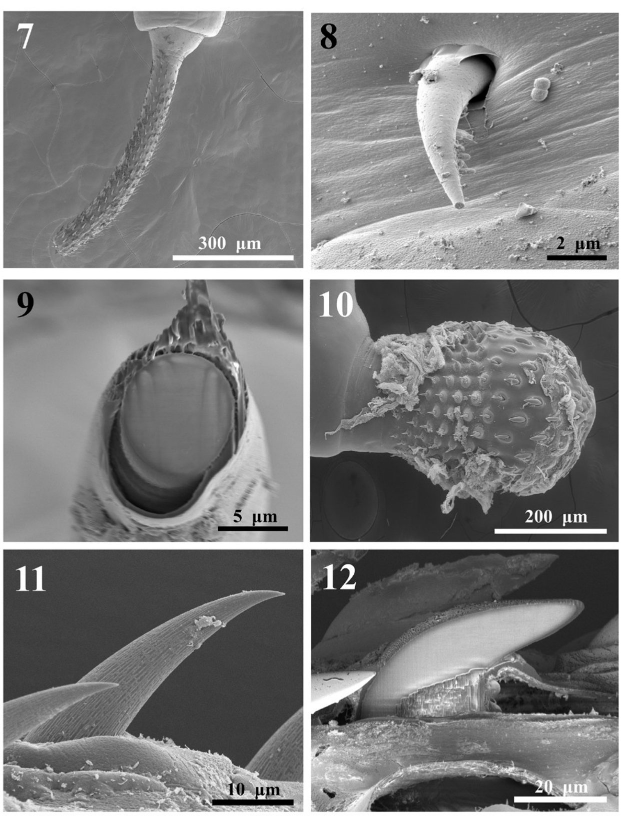
This project was supported in part by the Department of Biology, Brigham Young University (BYU), Provo, Utah, and by the Parasitology Center, Inc. (PCI), Scottsdale, Arizona. We thank Elisabeth Trimble, Bean Museum (BYU) for expert help in the preparation and organization of plates and figures and to Dr. Nataliya Rubtsova (PCI) for additional help. We extend our special appreciation to Michael Standing, Electron Optics Laboratory (BYU), for his technical help and expertise in the creation of the SEM images.

Declarations

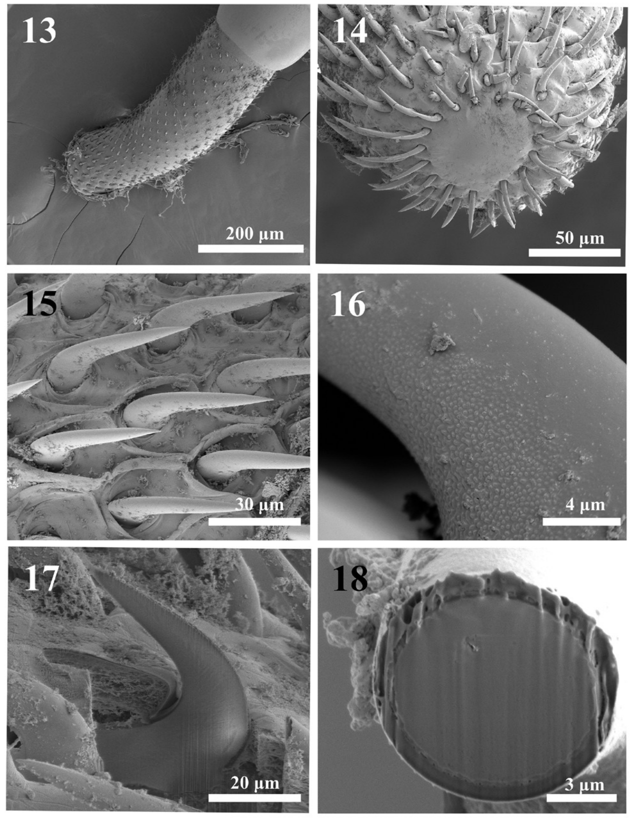
Compliance with ethical standards
Conflict of interest. The authors declare no conflicts of interest or competing interests.
Ethical approval. The authors declare that they have observed all applicable ethical standards.
Availability of data. All presented and related data are available by contacting the senior author especially for previously unpublished images.



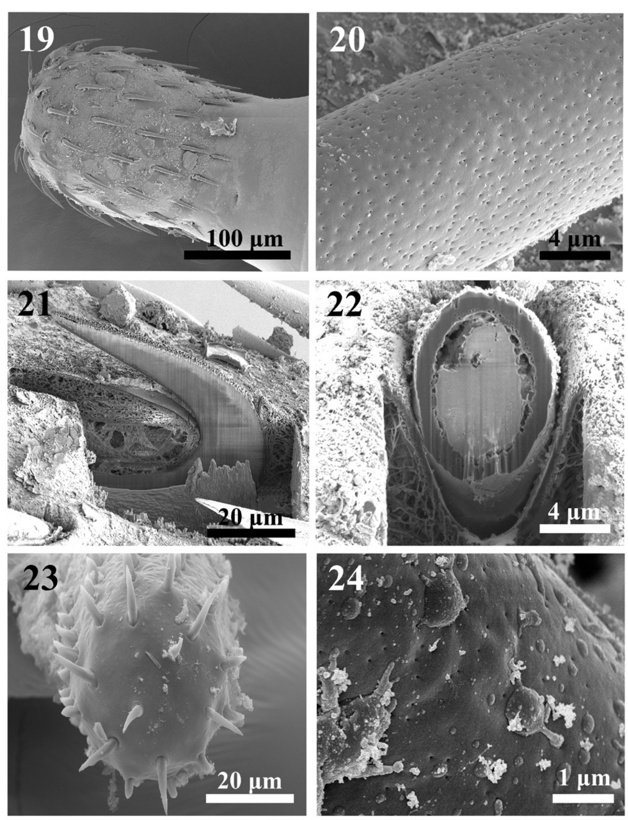
Figs 1—6. SEM of proboscides and hooks of *Heterosentis holospinus* (Arythmacanthidae) (figs 1—3) and *Cavisoma magnum* (Cavisomidae) (figs 4–6): 1 — proboscis of *H. holospinus* with very long anterior hooks and spiny anterior trunk with spine-free anterior cone; 2 — high magnification of posterior spines; 3 — a Gallium-cut longitudinal section of an anterior hook showing thin cortical layer and thick solid core with high levels of calcium and phosphorous; 4 — a partially retracted proboscis of *C. magnum* showing the gradual reduction in hook size posteriorly; 5 — a high magnification of a middle hook showing its shallow serrated surface; 6 — a Gallium-cut cross section of a middle hook showing its moderately thick cortical layer and core with high sulfur content.



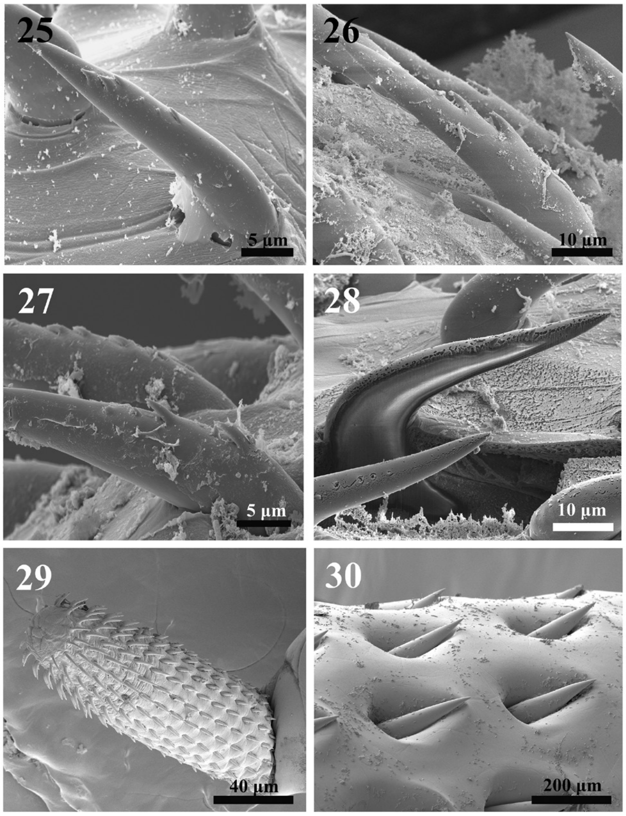
Figs 7–12. SEM of proboscides and hooks of *Parhadinorhynchus magnus* (Cavisomidae) (figs 7–9) and *Centrorhynchus globirostris* (Centrorhynchidae) (figs 10–12): 7 — long cylindrical proboscis with gradually decreasing hook size posteriorly; 8 — a ventral hook; note its curvature and robust base; 9 — a Gallium-cut cross section of a middle hook showing in thick core with high phosphorous and calcium content, and thin cortical layer; 10 — the globular proboscis of *C. globirostris* showing the separation line between the larger anterior hooks and the smaller posterior spine-like hooks where the anterior end of the receptacle inserts; 11 — an anterior hook showing the ribbed surface found on all hooks; 12 — a Gallium-cut longitudinal section of a hook showing its thick core and marginal cortical layer.



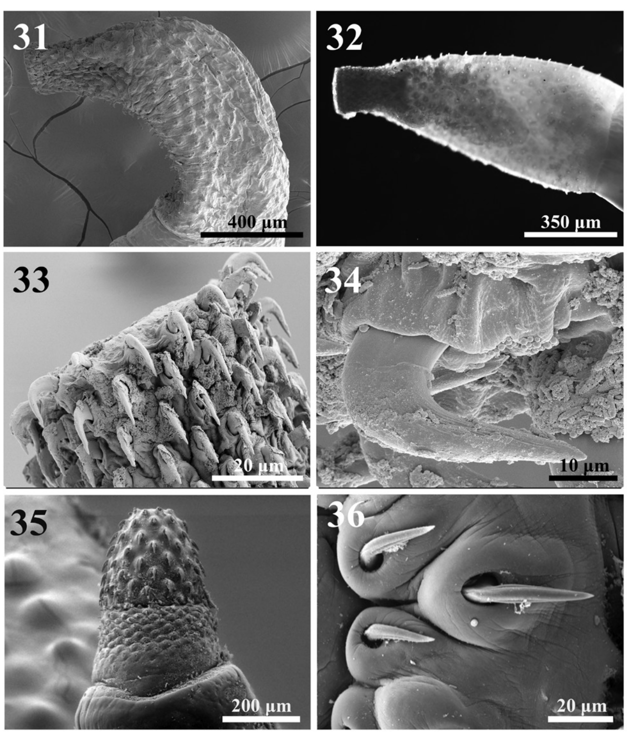
Figs 13–18. SEM of proboscis and hooks of *Centrorhynchus globocaudatus* (Centrorhynchidae): 13 — the proboscis of a female specimen showing the spiral arrangement of longitudinal hook rows; 14 — the prominent bare-apical surface of a proboscis; 15 — near apical and anterior hooks in indentations on proboscis surface; 16 — basal part of hook showing latero-ventral pebble-like protrusions; 17, 18 — a longitudinal and cross Gallium-cut hook sections showing its prominent core and very thin cortical layer with high levels of calcium and phosphorous.



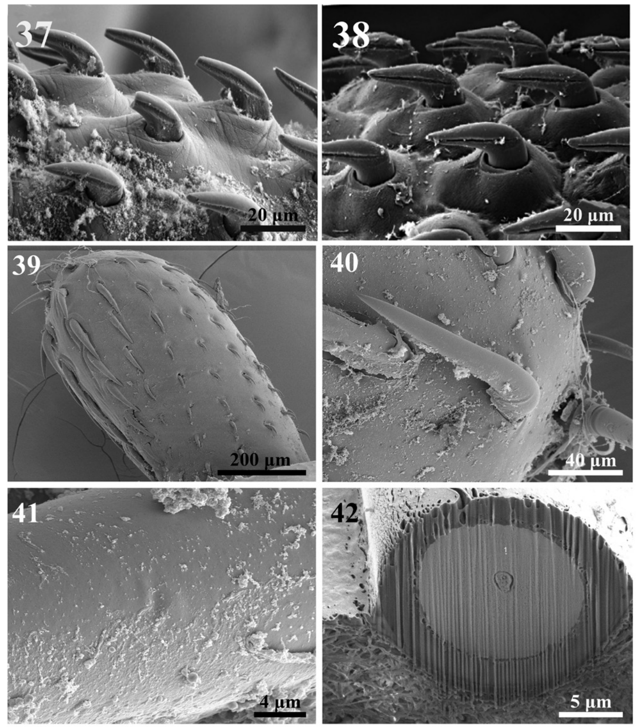
Figs 19–24. SEM of proboscis and hooks of *Acanthocephalaus parallelcemenglandatus* (figs 19–22), *Echinorhynchus salmonis* (fig. 23), and *Pseudoacanthocephalus lutzi* (fig. 24) (Echinorhynchidae): 19 — a typical proboscis *A. parallelcementglandatus* with parallel sides and a sensory pore on the neck; 20 — a high magnification of a hook showing numerous micropores; 21, 22 — a Gallium-cut lateral and cross sections of hooks with solid core extending into the root and a relatively thick cortical layer and with high levels of calcium and moderate levels of phosphorous. Sulfur levels were negligible; 23 — an apical view of a proboscis of *E. salmonis* showing 2 odd mini-hooks; 24 — a high magnification of a hook of *P. lutzi* showing many micropores.



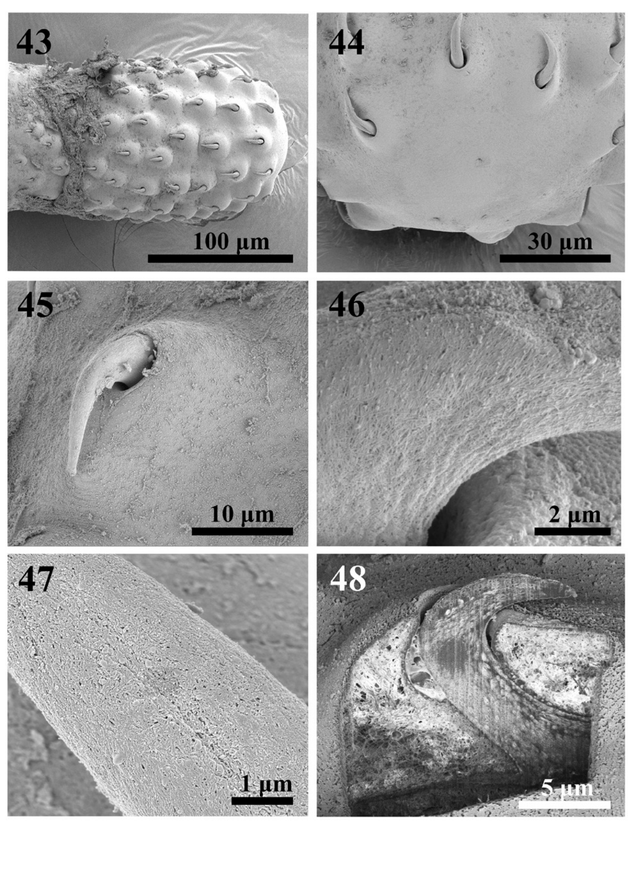
Figs 25–30. SEM of proboscis and hooks of *Echinorhynchus cinctulus* (figs 25–28) and *Echinorhynchus gadi* (figs 29–30) (Echinorhynchidae): 25–27 — anterior hooks in some specimens of *E. cinctulus* with a variety of spines or thorns mostly on the dorsal side of hooks; 28 — the well-developed core and thinner cortical layer of a Gallium-cut longitudinal section of a middle hook; 29 — a proboscis of an *E. gadi* specimen with 15 hooks per row and elevated anterior hooks; 30 — a high magnification of depressed posterior hooks on the same proboscis in fig. 29.



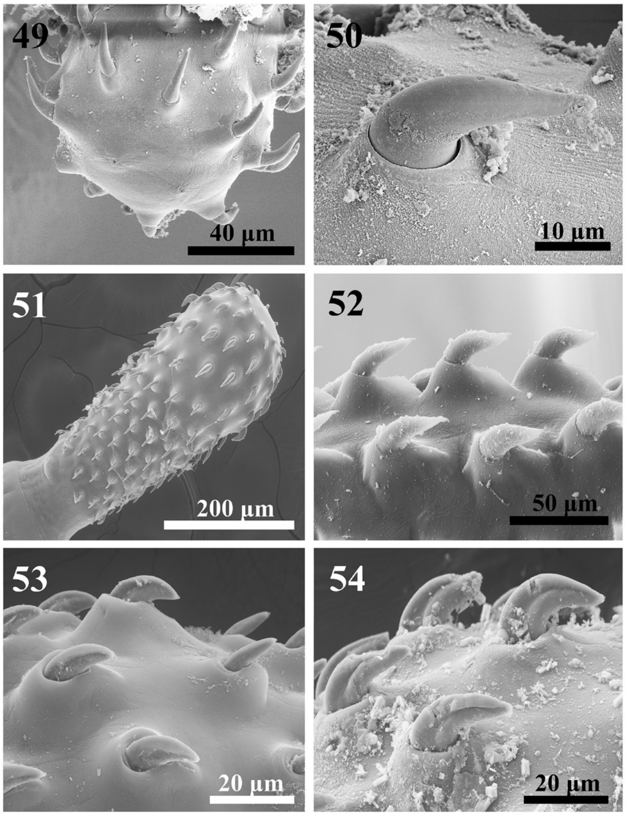
Figs 31–36. SEM and microscope image of proboscis and hooks of *Intraproboscis sanghae* (figs 31–34) and SEM of *Mediorhynchus africanus* (figs 35, 36) (Gigantorhynchidae): 31 — anterior and posterior proboscis of *I. sanghae*; 32 — a microscope black and while image of proboscides showing the dark receptacle within the posterior proboscis; 33 — the flat apical end of the anterior proboscis with hooks; 34 — a higher magnification of an anterior hook showing the lamellar texture of the lateral and ventral surface; 35 — proboscis of *M. africanus* showing the divide between anterior hooks and posterior spine-like hooks; 36 — face view of anterior hooks of *M. africanus* showing proboscis swelling at insertion.



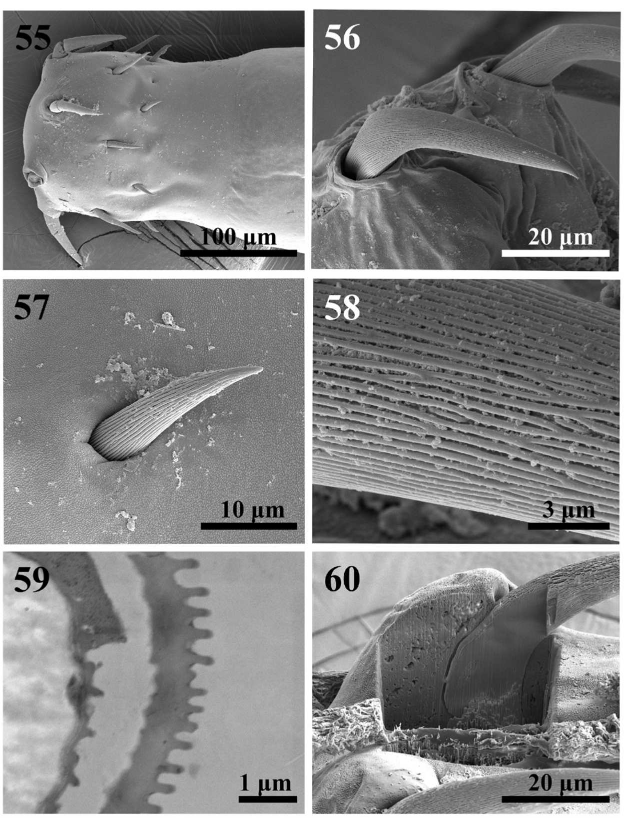
Figs 37–42. SEM of proboscis and hooks of *Mediorhynchus africanus* (fig. 37), *Mediorhynchus gallinarum* (fig. 38) (Gigantorhynchidae), and *Aspersentis megarhynchus* (figs 39–42) (Heteracanthocephalidae): 37 — lateral view of anterior hooks of *M. africanus* showing the lateral grooves; 38 — lateral view of anterior hooks of *M. gallinarum* showing the same type of lateral grooves; 39 — proboscis of *A. megarhynchus* showing the spiral arrangement of hook rows, the gradual decline in hook size posteriorly, and the larger ventral hooks; 40 — anterior hook showing its extreme angular curvature; 41 — high magnification of a hook with very small micropores on its surface; 42 — a Gallium-cut cross section of a large hook exhibiting a large solid core with very high level of Calcium and a relatively thick cortical layer with highest level of sulfur.



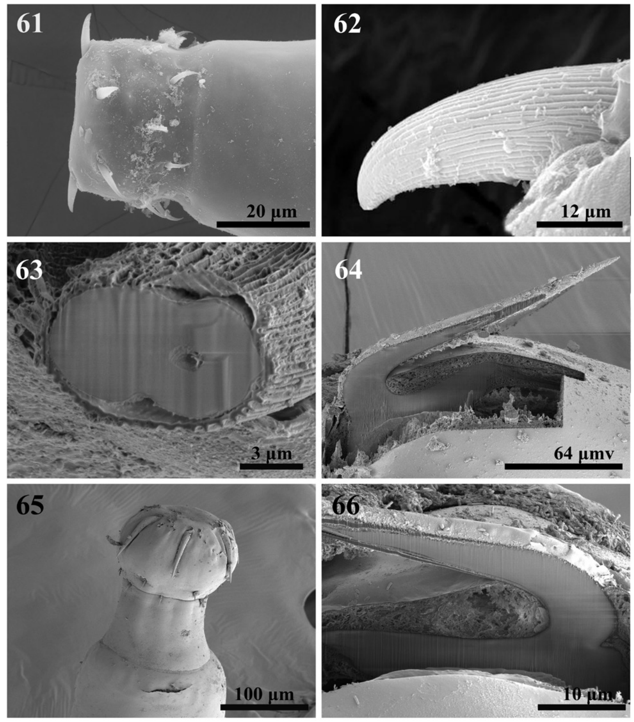
Figs 43–48. SEM of proboscis and hooks of *Moniliformis cryptosaudi* (Moniliformidae): 43 — the proboscis of a male specimen showing the smaller posterior hooks and the dome-shaped proboscis surface at hook insertion site; 44 — the apical end of a proboscis showing 2 sensory pores; 45 — a posterior hook in a dome-like proboscis base at insertion point; 46 — a Gallium-cut hook base showing its collagenous, porous, and spongy composition; 47 — a middle hook showing the porous texture of its collagenous forming elements; 48 — a Gallium-cut section of a posterior hook and root showing the continuity of their collagenous and porous nature. The levels of calcium, sulfur and phosphorous in all hooks were very scarce.



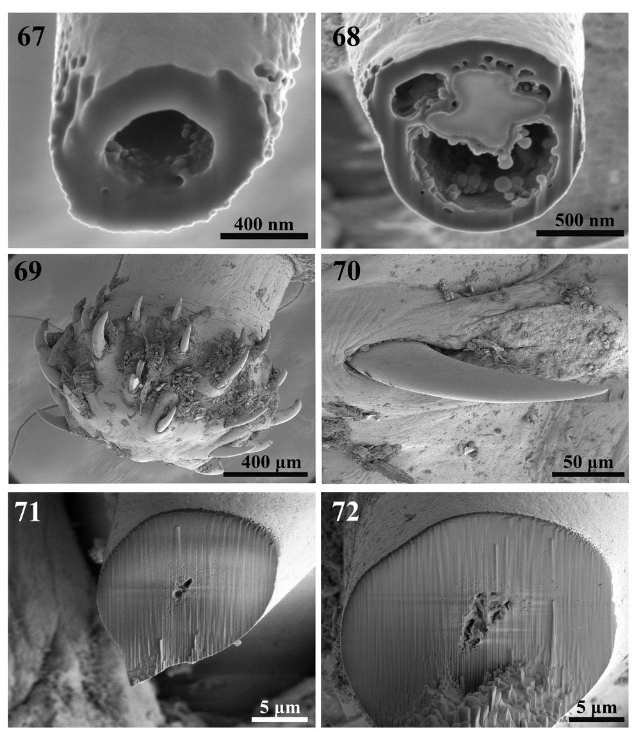
Figs 49–54. SEM of proboscis and hooks of *Moniliformis Saudi* (figs 49–50) and *Moniliformis kalahariensis* (figs 51–54) (Moniliformidae): 49 — apical end of a proboscis of *M. Saudi* also had 2 sensory pores like *M. cryptosaudi*; 50 — a middle hook with high levels of calcium and phosphorous; 51 — the proboscis of *M. kalahariensis*; hooks gradually decrease in size posteriorly; 52 — undeveloped hooks from cockroach; 53 — developing hooks in a juvenile beginning to develop lateral grooves; 54 — fully developed hooks in an adults with completely formed lateral grooves. Hooks of *M. kalahariensis*, also had high levels of calcium and phosphorous like hooks of *M. saudi.*



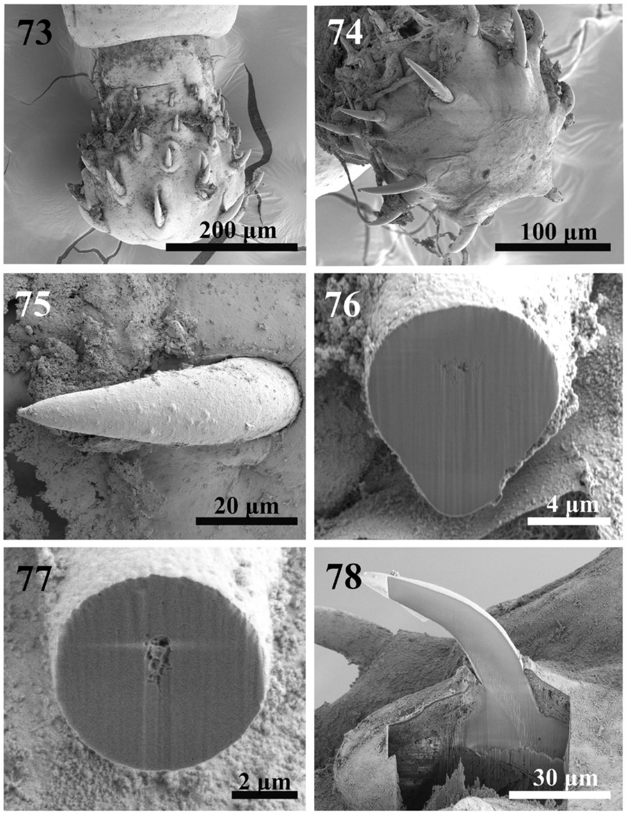
Figs 55–60. SEM of proboscis and hooks of *Neoechinorhynchus ponticus* (figs 55, 56) and *Neoechinorhynchus personatus* (figs 57–60) (Neoechinorhynchidae): 55 — proboscis of *N. ponticus* with a sensory pore at level of posterior hooks; 56 — anterior hook showing angle of projection and external serrations; 57 — posterior hook of *N. personatus* showing serrations; 58 — a high magnification showing pattern of serrations on an anterior hook; 59 — outermost layer of a hook showing detail of longitudinal serrations in cross section; 60 — a part of a Gallium-cut section of an anterior hook showing its thin cortical layer and dense core, and its articulation vs. the root of the same core density.



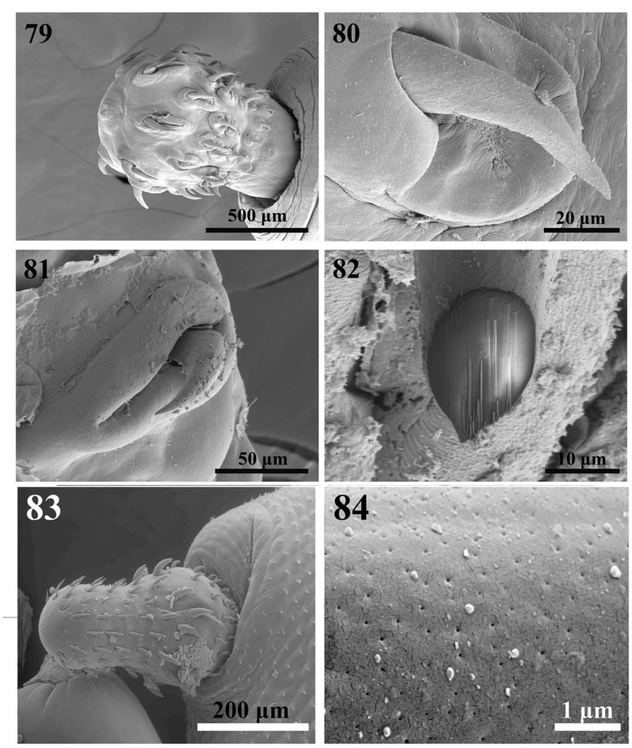
Figs 61–66. SEM of proboscis and hooks of *Neoechinorhynchus dimorphospinus* (figs 61–64) and *Neoechinorhynchus johnii* (figs 65–66) (Neoechinorhynchidae): 61 — the proboscis of a specimen of *N. dimorphospinus* showing the longer lateral hooks (top & bottom); 62 — a longer anterio-lateral hook showing longitudinal serrations; 63 — a Gallium-cut cross section of an anterior hook showing its extensive core and thin serrated cortical layer; 64 — a longitudinal section of an anterior longer hook showing the continuity of its solid core with that of the root; 65 — the globular proboscis and narrow neck of a *N. johnii* male specimen; 66 — a Gallium cut longitudinal section of an anterior hook showing its thick and solid core continuous with that of the root and its thin cortical layer.



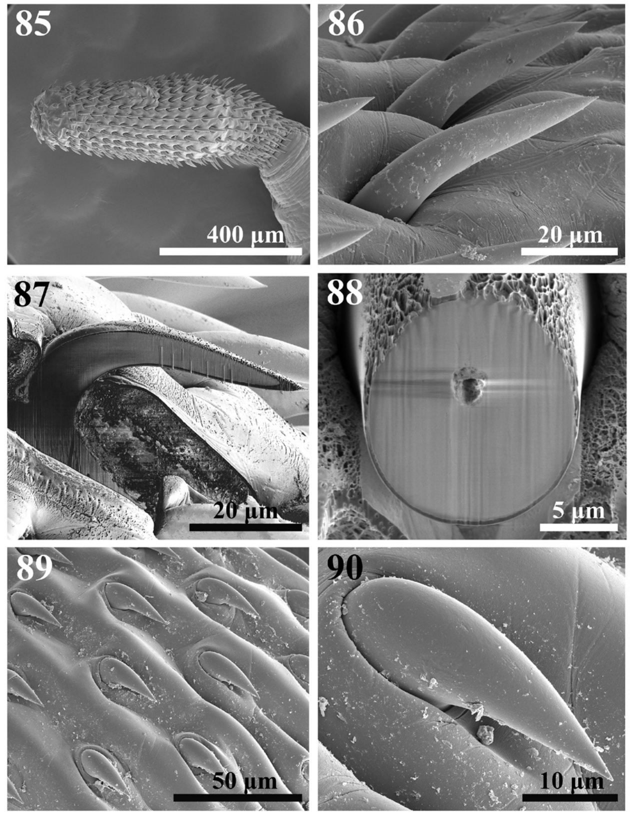
Figs 67–72. SEM of proboscis and hooks of *N. johnii* (Neoechinorhynchidae) (figs 67–68) and *Macracanthorhynchus hirudinaceus* (Oligacanthorhynchidae) (figs 69–72): 67–68 — variations in the degree of vacuolations of partially hollowed hooks of *N. johnii* specimens in Gallium-cut sections; 69 — the girthy proboscis showing the organization of hooks of various sizes antero-posteriorly and the robust neck; 70 — the external shape and curvature of a large hook with smooth surface embedded in a cuticular proboscis distention; 71, 72 — a Gallium-cut cross sections of a small hook near its base showing ventral distention (fig. 71), and of a larger round hook near its terminal end (fig. 72).



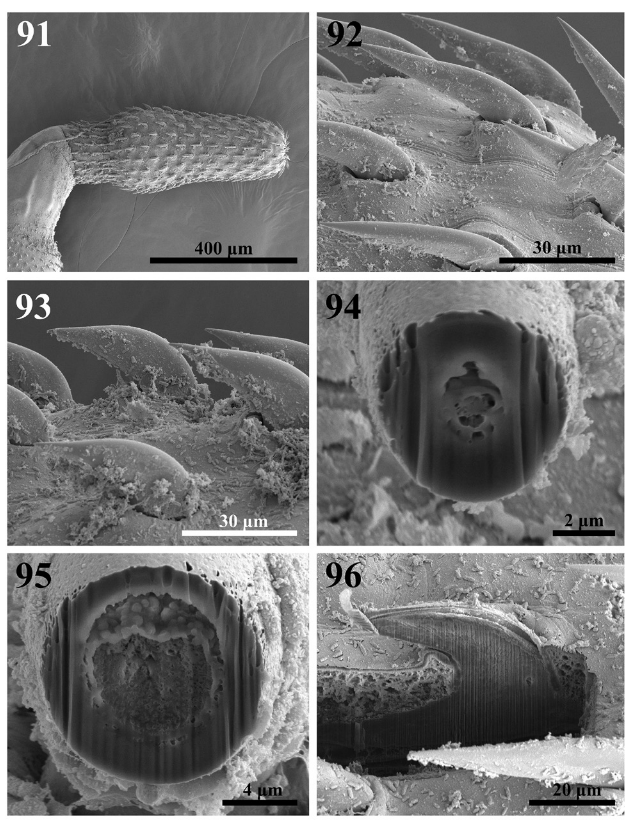
Figs 73–78. SEM of proboscis and hooks of *Nephridiacanthus major* (Oligacanthorhynchidae): 73 — hook arrangement and prominent neck of *N. major*; 74 — a dorso-lateral view of proboscis showing slightly elevated surface of apical organ; 75 — dorsal view of a short posterior hook; 76 — a Gallium-cut section of a hook near its base with prominent ventral expansion similar to that in *M. hirudinaceus* with almost no cortical layer seen; 77 — a perfectly spherical Gallium cut cross section of another hook near its terminal end; 78 — a lateral Gallium-cut section of another hook showing the same core-cortical relationships as in figs 76 & 77. Note the continuity with the elaborate root.



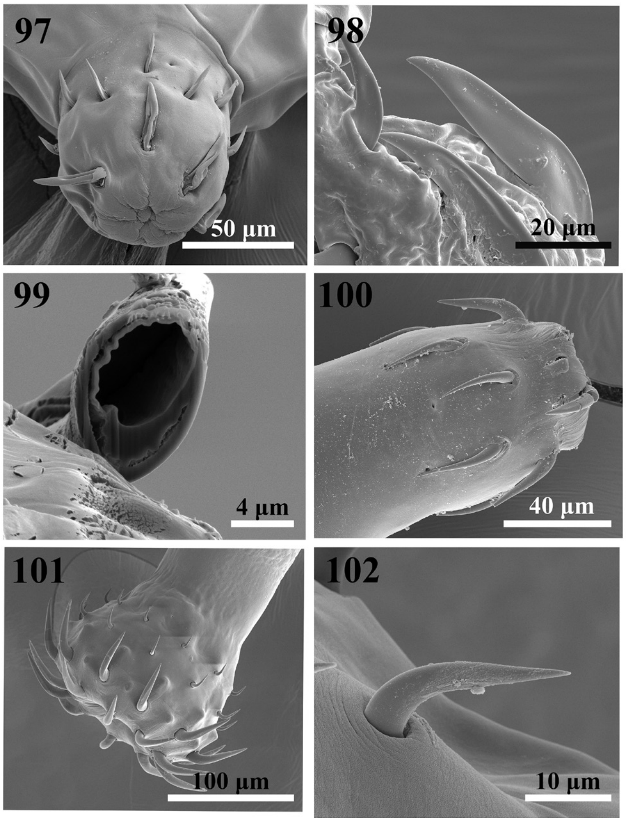
Figs 79–84. SEM of proboscis and hooks of *Pachysentis canicola* (Oligacanthorhynchidae) (figs 79–82) and *Corynosoma strumosum* (Polymorphidae) (figs 83, 84): 79 — the proboscis of a female *P. canicola* showing hook arrangement and sensory pores at posterior proboscis and neck; 80 — an anterior hook deeply recessed in thick cuticular fold; 81 — a posterior hook also deeply recessed in a boat-like cuticular fold; 82 — a Gallium-cut cross section of a hook near its base showing the ventral protrusion as seen in other oligacanthorhynchid genera: *Macracanthorhynchus* and *Nephridiacanthus*; 83 — the proboscis of a specimen of *C. strumosum* showing its bare apical end and larger hooks at the bulge; 84 — a high magnification of a hook showing micropores.



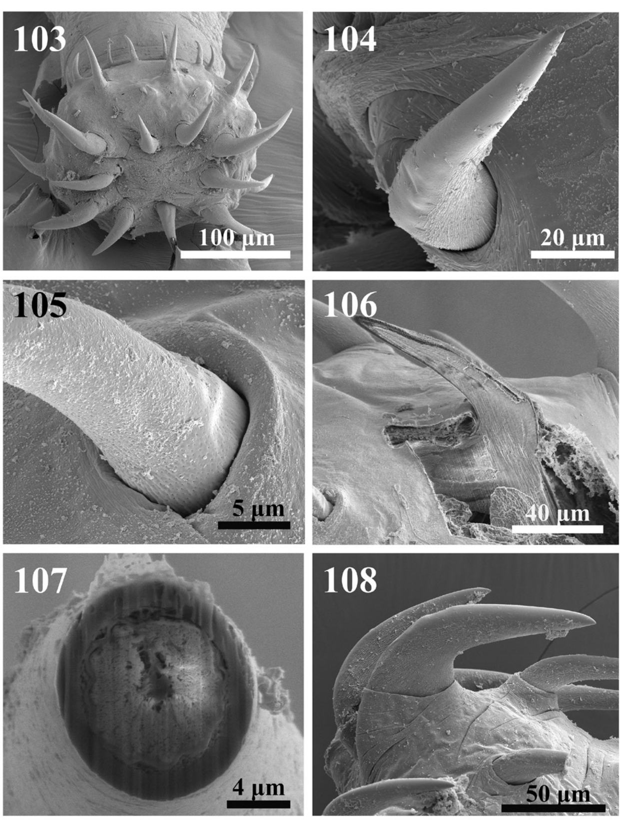
Figs 85–90. Proboscis and hooks of *Neoandracantha peruensis* (figs 85–88) and *Profilicollis altmani* (figs 89–90) (Polymorphidae): 85 — the proboscis of a cystacanth of *N. peruensis* showing the arrangement of hooks on all parts of the proboscis; 86 — a higher magnification of hooks deeply embedded in cuticular folds of proboscis showing their shape and orientation; 87–88 — a Gallium-cut longitudinal and cross sections of hooks showing their solid core and thin cortical layer exhibiting high levels of calcium and phosphorous and miniscule levels of sulfur; 89 — mid-proboscis section in a specimen of *P. altmani* showing deeply embedded hooks in cuticular furrows of the proboscis; 90 — an enlarged hooks from fig. 89 showing its girth being almost as wide at base as it is long. These hooks had high levels of sulfur and low levels of calcium and phosphorous.



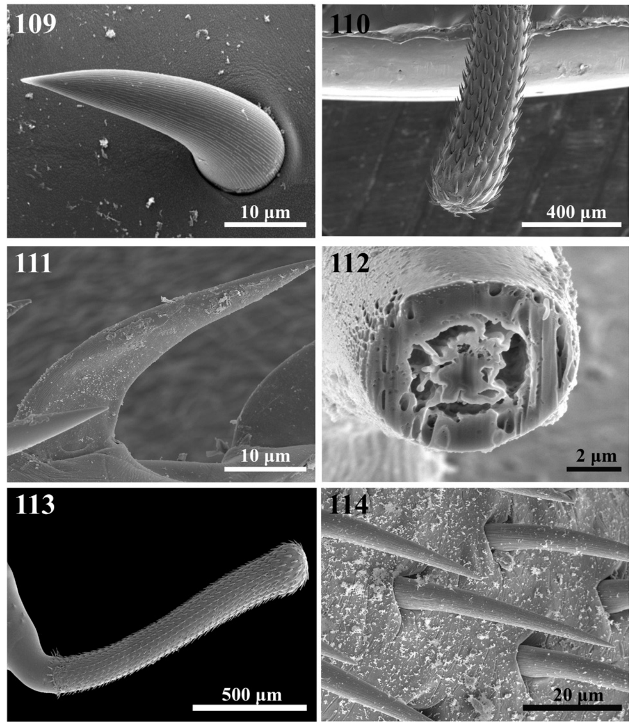
Figs 91–96. Proboscis and hooks of *Southwellina hispida* (Polymorphidae): 91 — a proboscis of a juvenile *S. hispida* showing the long anterior hooks, the shorter and thicker middle hooks at swelling, and the smaller posterior hooks; 92 — a few anterior hooks; 93 — shorter and more robust middle hooks at swelling; 94–95 — variations on the degree of vacuolation of the core of hooks with relatively thick cortical layer; 96 — a Gallium-cut section of a middle hook showing a thin cortical layer and solid core.



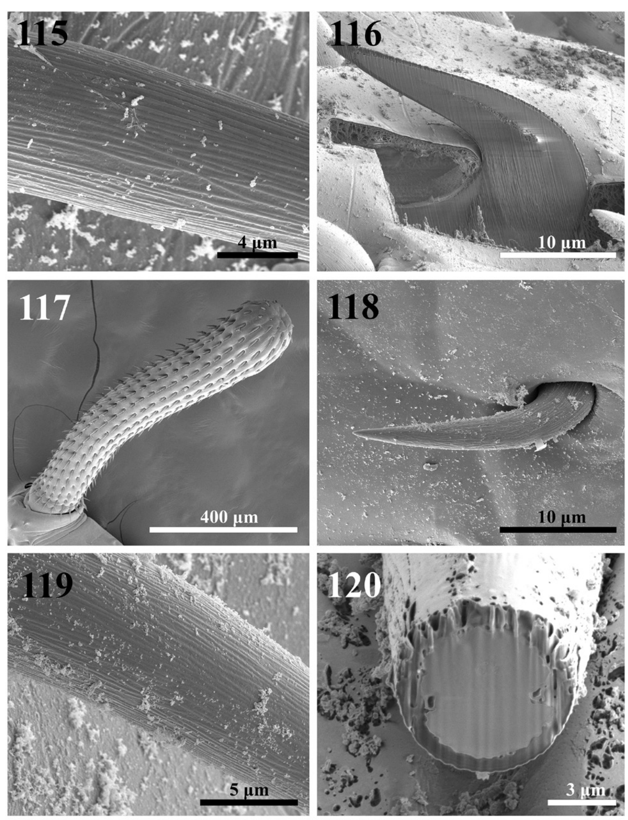
Figs 97–102. Proboscis and hooks of *Acanthogyrus* (*Acanthosentis*) *kashmirensis* (figs 97–99), *Acanthogyrus* (*Acanthosentis*) *fusiformis* (fig. 100), and *Pallisentis* (*Brevitritospinus*) *indica* (figs 101–102)(Quadrigyridae):97—proboscisof *A. kashmirensis* showing hook arrangement and sensory pore at its base; 98 — profile of anterior and middle hooks showing their emaciated appearance; 99 — the appearance of the hooks in fig. 98 is explained by their hollow core; see this figure of a Gallium-cut cross section of an anterior hook; 100 — the unusual shape of the proboscis of *A. fusiformis* with the smaller hooks on the anterior constricted part of the proboscis; 101 — the proboscis of *P. indica* showing proboscis bumps and sensory pore at its posterior end; 102 — a middle hook showing its angle and relative dimensions.



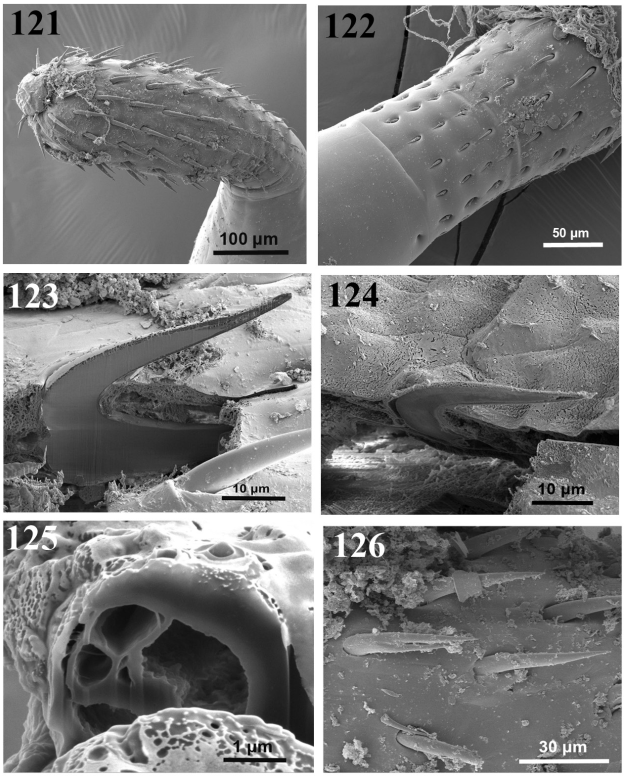
Figs 103–108. Proboscis and hooks of *Pallisentis* (*Pallisentis*) *nandai* (figs 103–107) and *Pallisentis* (*Pallisentis*) *paranandai* (fig. 108) (Quadrigyridae): 103 — an apical view of the proboscis of *P. nandai* showing the hook arrangement and the proboscis bumps; 104 — an anterior hook with latero-ventral serrations; 105 — a higher magnification of the base of an anterior hook at indented insertion in elevated proboscis ring; note the latero-ventral serrations; 106–107 — a Gallium-cut longitudinal and cross sections of anterior hooks showing the proportion of cortical and core layers and continuity with root elements. These hooks had very high levels of calcium and sulfur but negligible levels of phosphorous; 108 — anterior and middle hooks of *P. paranandai* also showing elevated serrations at their base.



Figs 109–114. Proboscis and hooks of *Leptorhynchoides polycristatus* (fig. 109), *Rhadinorhynchus oligospinosus* (figs 110–112), *Rhadinorhynchus hiansi* (figs 113–114) (Rhadinorhynchidae): 109 — the particular pattern of serrations on a middle hook of *L. polycristatus* can be seen; all hooks are similarly serrated; 110–111 — the proboscis and anterior hook of *R. oligospinosus*; note the hook curvature and thickness at base; 112 — a Gallium cut hook showing its thick cortical layer and partially vacuolated core; 113 — a very long proboscis with many hooks of *R. hiansi*; 114 — deeply set almost strait middle hooks barely showing their texture.



Figs 115–120. Proboscis and hooks of *Rhadinorhynchus hiansi* (cont.) (figs 115–116), *Rhadinorhynchus laterospinosus* (figs 117–120) (Rhadinorhynchidae): 115 — a high magnification of a *R. hiansi* hook showing detail of its external striations; 116 — a longitudinal Gallium-cut section of a hook showing a thin cortical layer and a dense core. Whole anterior hooks have high levels of calcium, moderate levels of phosphorous and sulfur; 117 — the proboscis of *R. laterospinosus* with many hooks in longitudinal rows; 118–119 — the angle of a middle hook and the serrated pattern on its surface; 120 — a Gallium cut cross section of another hook showing its dense core and thin cortical layer. These hooks have high levels of sulfur and low levels of calcium and phosphorous.



Figs 121–126. Proboscis and hooks of *Paratrajectura longcementglandatus* (Transvenidae): 121 — proboscis of *P. longcementglandatus* with longer anterior hooks; 122 — shorter and more deeply embedded posterior hooks. Note sensory pore just posterior to basal hooks; 123, 124 — a Gallium-cut longitudinal sections of a middle and a more posterior hook, respectively, showing consistent solid core and thin cortical layers continuous with roots; 125 — a partially vacuolated core of another hook in a Gallium cut cross section; 126 — an unusually branched hook in middle of proboscis.

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Received 4 May 2022
Accepted 3 August 2022