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Review of the Rhopalothylacidae Guiart, 1935 (Cestoda: Trypanorhyncha), with a description of the adult of *Pintneriella musculicola* Yamaguti, 1934 and a redescription of *P. gymnorhynchoides* (Guiart, 1935) comb. n.

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Abstract. The family Rhopalothylacidae (Cestoda: Trypanorhyncha) is reviewed. The type species, *Rhopalothylax gymnorhynchoides* Guiart, 1935, is redescribed from the type specimens and belongs within the genus *Pintneriella* Yamaguti, 1934, previously described only from the plerocercus. *Rhopalothylax* therefore becomes a junior synonym of *Pintneriella*. The adult of *Pintneriella musculicola* Yamaguti, 1934 is described for the first time, from the shark *Carcharias taurus* Rafinesque from Australia. *Pintneriella* is characterised by two bothridia, a typical heteroacanthous armature, a unique, bipartite external seminal vesicle and a uterus deviated porally, terminating at a uterine pore. It belongs within the Heteracanthoidea but is distinguishable both from the Eutetrarhynchidae and the Gilquiniidae, the two families which it most closely resembles. Cladistic analyses align *Pintneriella* within the clade containing the families Gilquiniidae, Gymnorhynchidae and Molicolidae rather than with the Eutetrarhynchidae. The family Rhopalothylacidae is therefore retained provisionally to accommodate *Pintneriella* within the Heteracanthoidea. The second genus of the Rhopalothylacidae, *Clujia* Guiart, 1935, is unrecognisable from its description and cannot be redescribed from its holotype. It is therefore considered a *genus inquirendum*.

The trypanorhynch cestode family Rhopalothylacidae was erected by Guiart (1935) to accommodate two new genera, *Rhopalothylax* and *Clujia*, which he described from plerocerci collected from fishes in the Atlantic Ocean (Guiart 1935). The descriptions of both genera are poor with no details of the tentacular armature, such that Dollfus (1942, p. 426) was unable to place either the genera or the family within the classification he developed. Yamaguti (1959), Schmidt (1986) and Campbell and Beveridge (1994) subsequently treated the family and both of its constituent genera as *incertae sedis*.

In this paper, the type specimens of both of the type species, *Rhopalothylax gymnorhynchoides* Guiart, 1935 and *Clujia racovitzai* Guiart, 1935 were re-examined to determine whether or not their taxonomic positions could be determined. The holotype of *Clujia* proved to be in poor condition and its taxonomic position could not be determined. However, the type material of *Rhopalothylax gymnorhynchoides* proved to be similar to but distinct from *Pintneriella musculicola* Yamaguti, 1934, recently redescribed from plerocerci by Beveridge and Campbell (2000). The adult of *P. musculicola* is described here for the first time from an Australian shark; *R. gymnorhynchoides* is redescribed. The detailed descriptions of two species of *Pintneriella* allow further investigation of the taxonomic position of the genus, which was considered a *genus incertae sedis* by Beveridge and Campbell (2000). In addition, the validity and taxonomic position of the Rhopalothylacidae is evaluated.

MATERIALS AND METHODS

Type specimens of *Clujia racovitzai* Guiart, 1935 and *Rhopalothylax gymnorhynchoides* Guiart, 1935 were borrowed from the Musée Océanographique de Monaco (MOP). Paratype and additional material of *Pintneriella musculicola* Yamaguti, 1934 from the Meguro Parasitological Museum, Tokyo (MPO) have previously been examined by the authors (Beveridge and Campbell 2000).

Adult specimens of *P. musculicola* were collected from the spiral valve of a captive grey nurse shark, *Carcharias taurus* Rafinesque, which died following transportation from the Mooloolaba Aquarium in Queensland, Australia, to the Melbourne Aquarium. Although born in captivity, the shark had been fed on fish collected in the Mooloolaba region. Cestodes collected were relaxed briefly in tap water and fixed in AFA solution (Pritchard and Kruse 1982). Cestodes were stained in Celestine blue, dehydrated in ethanol, cleared in methyl salicylate and mounted in Canada balsam. Tentacles were removed from individual scoleces using a scalpel blade, mounted in glycerine jelly and manipulated until appropriate

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orientations of the armature were obtained. Serial longitudinal and transverse sections of segments were prepared by embedding in paraffin, cutting at a thickness of 5 µm and staining with haematoxylin and eosin. Drawings were made using a drawing tube fitted to an Olympus BH-2 microscope. Measurements were made with an ocular micrometer and, unless otherwise stated, are presented in µm as the range followed by the mean of 10 specimens. If fewer specimens were available, the number of measurements is indicated. New material described has been deposited in the South Australian Museum, Adelaide, South Australia (SAM) as follows: 16 slides of whole mounts, AHC 28416, 5 slides of tentacles in glycerine jelly, AHC 28415, and 60 slides of serial sections, AHC 28414.

The phylogenetic relationships of the genus *Pintneriella* were investigated based on the preliminary cladistic study of the Trypanorhyncha by Beveridge et al. (1999). Morphological features of *P. musculicola* were coded using the characters and coding procedures of Beveridge et al. (1999) and the analysis re-run with the additional genus. Polymorphisms were coded using the option for coding polymorphism available in PAUP 3.1 and an heuristic search was conducted using PAUP 3.1, with tree-bisection-reconnection branch swapping, MULPARS option in effect and topological restraints not enforced, following identical methods to those employed by Beveridge et al. (1999). The coding for *Pintneriella* was based on the type species *P. musculicola* and used the 44 characters of Beveridge et al. (1999) listed in the order in which they were employed in that paper: 01010000112000001000101111111110000000001001. The 50% consensus of all of the most parsimonious trees was compared with that obtained in a previous study (Beveridge et al. 1999) and that clade containing the Rhopalothylacidae was examined, as well as the percentage of all trees containing a particular branch and the synapomorphic characters which determine each branch.

RESULTS

Pintneriella musculicola Yamaguti, 1934 Figs. 1–17

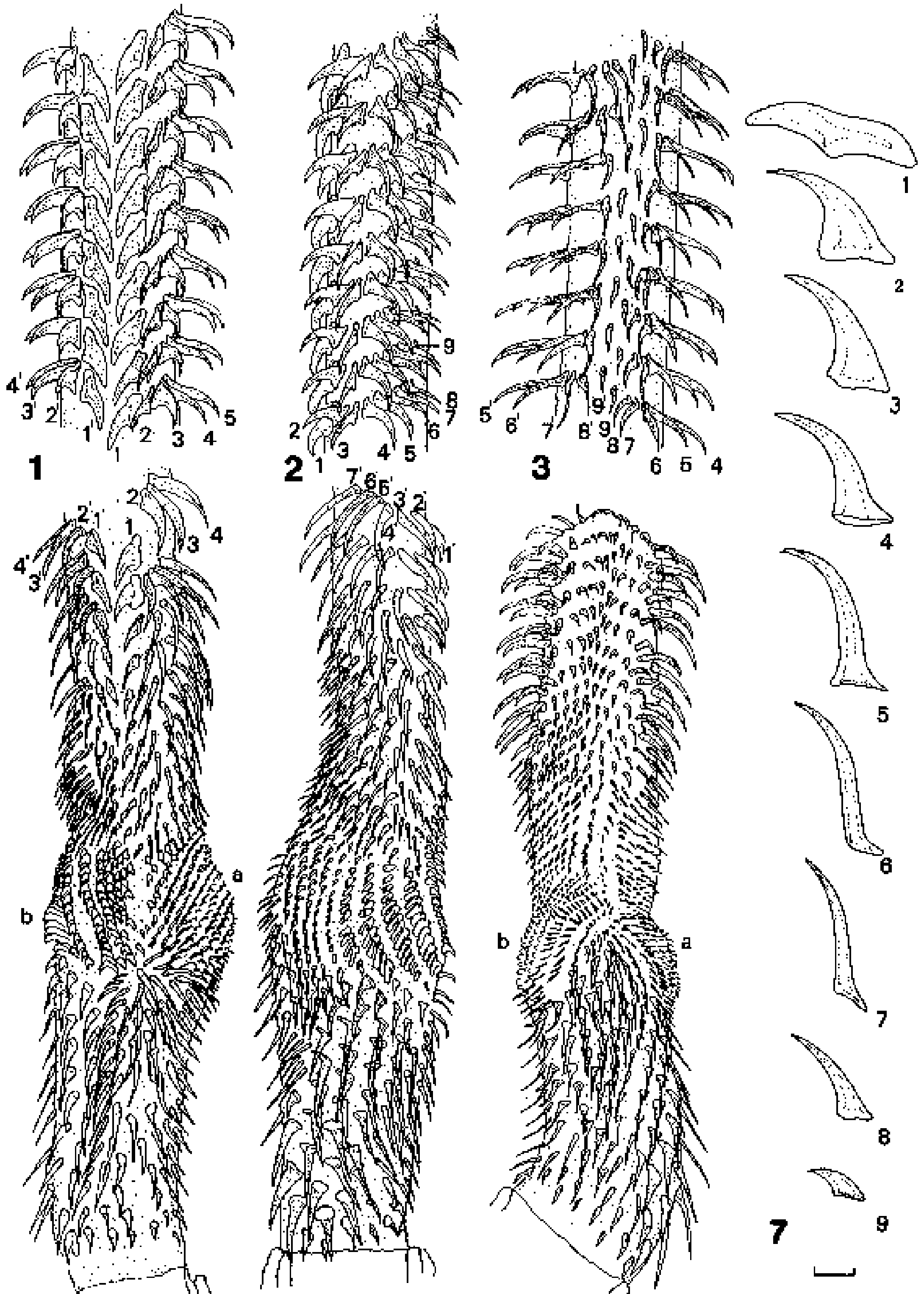
Description. Fragile cestodes; maximum length of intact specimens 25 mm. Scolex acraspedote, 3.85–5.00 (4.14) mm long (Fig. 8), maximum width in pars bulbosa 0.61–0.80 (0.67) mm. Pars bothridialis 1.20–1.65 (1.40) mm; bothridia elongate, without distinct margin, 0.56–0.82 (0.74) (n = 8) mm in width. Pars vaginalis 2.65–3.80 (2.96) long; tentacle sheaths sinuous. Bulbs short, ovoid (Fig. 9), 0.75–0.95 (0.80) mm long, 0.21–0.30 (0.25) mm wide; bulb length to width ratio 2.59–4.52 (3.27); prebulbar organ absent; retractor muscle originates at base of bulb; gland cells absent within bulb; nuclei prominent within retractor muscle. Pars post-bulbosa 0.15–0.28 (0.21) mm. Scolex ratio: 1 : 2.1 : 0.57 : 0.15.

Tentacles elongate, 1.90–3.86 (2.97) (n = 5) mm when everted; tentacles emerge from sleeve-like extension of bothridial tegument, 200–250 long; tentacle diameter 80–100 (88) at level of basal swelling, 40–70 (52) in metabasal and distal regions of tentacle.

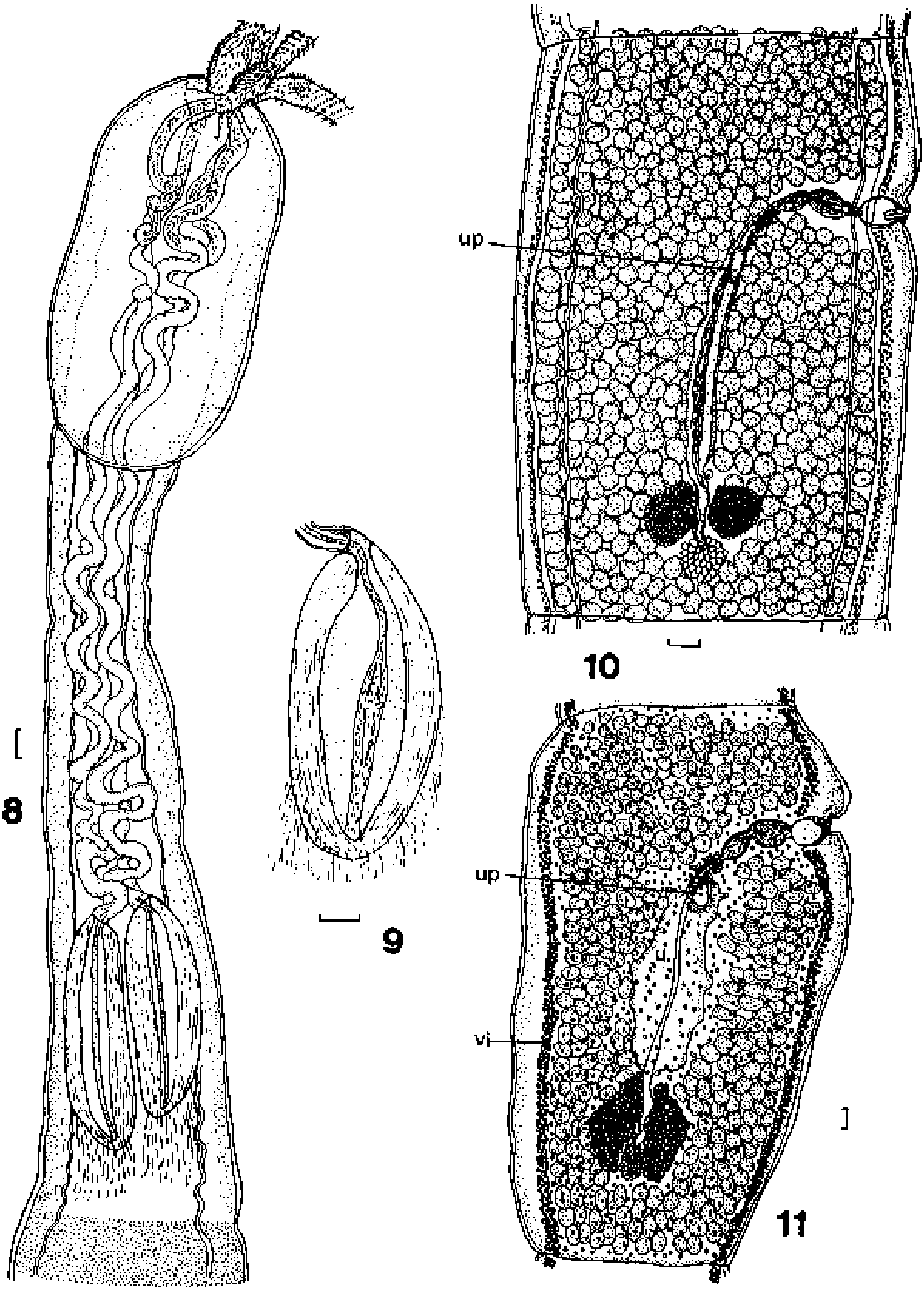
METABASAL ARMATURE (Figs. 1–3). Armature heteroacanthous, heteromorphous; hooks hollow; hooks arranged in ascending half spirals beginning on internal surface of tentacle, terminating on external surface, with 9 hooks per row. Space present between hooks 1 and 1' on internal surface of tentacle (Fig. 1). Hooks 1(1') uncinate, with broad blade and elongate, laterally thickened base, 35–45 (41) long, base length 20–25 (21). Hooks 2(2') uncinate with erect, less robust blade and shorter base, 30–43 (35) long, base length 15–20 (18). Hooks 3(3') erect, uncinate, 33–38 (35) long, base length 15–20 (16). Hooks 4(4') falcate with relatively broad base, 33–48 (38) long, base length 10–20 (14). Hooks 5(5') falcate with narrower base, 30–48 (40) long, base length 10–15 (13). Hooks 6(6') falcate, with narrow base, 33–48 (41) long, base length 10–18 (14). Hooks 7(7') falcate, shorter, 30–43 (36) long, base length 8–13 (11). Hooks 8(8') shorter, more strongly recurved, 25–40 (31) long, base length 8–12 (10). Hooks 9(9') uncinate, with relatively broad base, 18–33 (25) long, base length 5–10 (8). Band of hooks or chainette absent on external surface; slight space present in midline separating hook files 9 and 9'.

BASAL ARMATURE (Figs. 4–6). First or proximal row of hooks deltoid to uncinate, 15–23 (18) long, base length 5–10 (8). Succeeding 10 rows of hooks beginning as slender, elongate hooks on internal surface, enlarging to hastate hooks with broad base on bothridial and antibothridial surfaces, length 22–38 (30), base length 5–13 (9), becoming slender with narrower base on external surface. On basal swelling, hooks arranged in ascending half rows beginning on internal surface. Hooks on bothridial aspect with initial files of hooks robust, erect, almost bill-hook in shape, with broad bases and sharply rebated tips, 8–18 (13) long, base length 3–4 (3), transforming into short, deltoid hooks on external surface. Hook files on antibothridial surface composed of slender hooks with rebated tips, 10–25 (20) long, base length 4–5 (5). On distal aspect of basal swelling, hooks slender, elongate, almost homeomorphous, arranged in ascending half spirals. On antibothridial surface of base, triangular array of tightly packed hooks present, apex of triangle at anterior end of basal swelling. Space between hook files 1 and 1' apparent 5–6 rows anterior to basal swelling on internal surface, not apparent before 25th row on external surface.

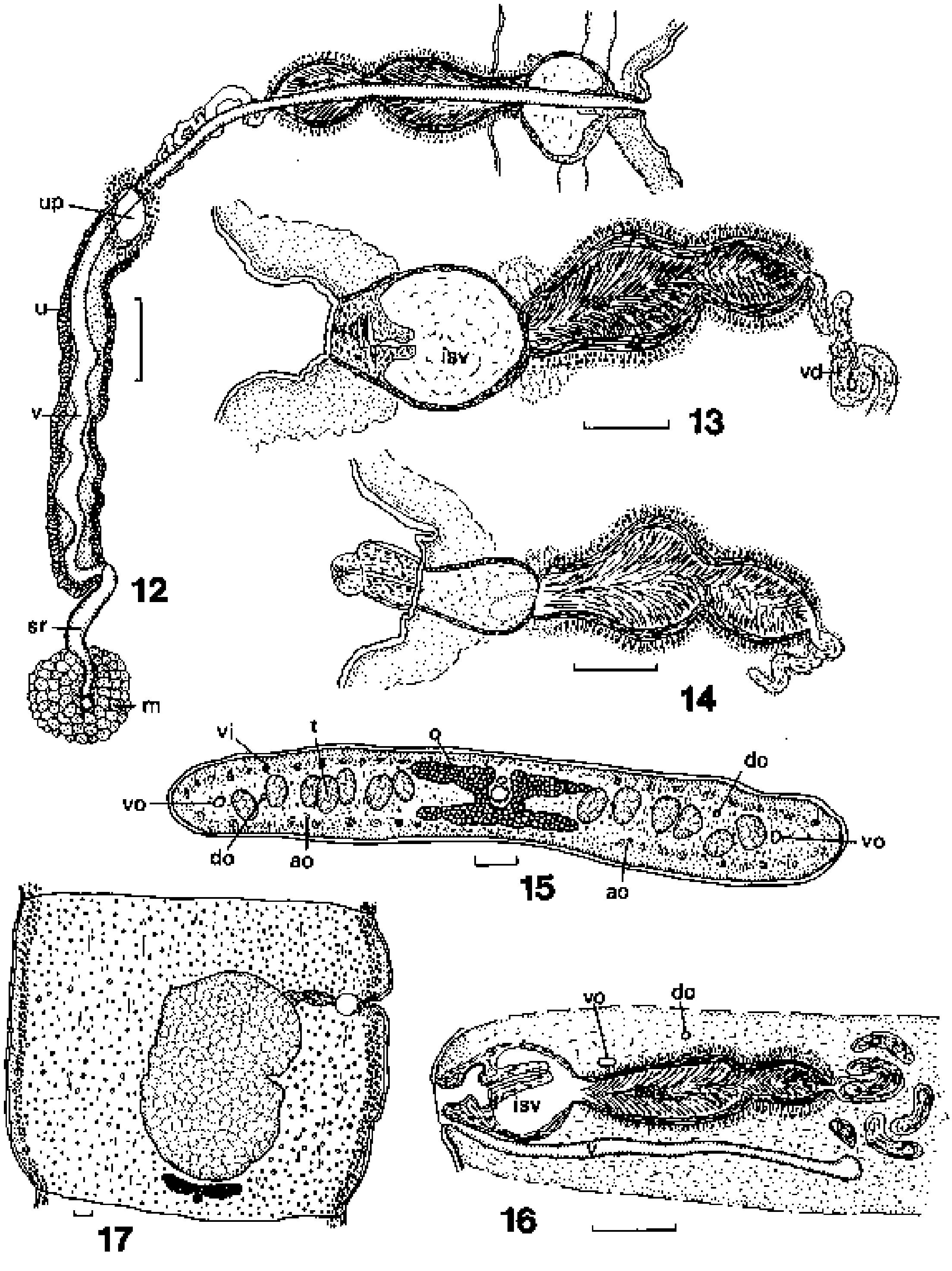
STROBILA. Unsegmented neck region 0.25–0.50 (0.37) mm long. Immature segments much wider than long, 0.12–0.46 (0.30) mm long by 0.72–1.35 (0.98) mm wide. Mature segments acraspedote, 1.30–2.15 (1.71) mm long by 1.35–1.72 (1.51) mm wide. Genital pores alternate irregularly, in anterior third of segment margin, 0.34–0.60 (0.47) mm from anterior end. Genital atrium shallow, surrounded by thickened tegument (Fig. 13). Cirrus sac sub-globular, small, 150–200 (170) long by 120–170 (150) wide, length : width ratio 1 : 0.88,



Figs. 1–7. *Pintneriella musculicola* Yamaguti, 1934. Tentacular armature. **Fig. 1.** Metabasal armature, internal surface of tentacle. **Fig. 2.** Metabasal armature, antibothridial surface of tentacle. **Fig. 3.** Metabasal armature, external surface of tentacle. **Fig. 4.** Basal armature and origin of metabasal armature, internal surface of tentacle. **Fig. 5.** Basal armature and origin of metabasal armature, bothridial surface of tentacle. **Fig. 6.** Basal armature and origin of metabasal armature, external surface of tentacle. **Fig. 7.** Profiles of hooks of principal row, 1–9. Abbreviations: a – antibothridial, b – bothridial. Scale bars: Figs. 1–6 = 0.1 mm; Fig. 7 = 0.01 mm.



Figs. 8–11. *Pintneriella musculicola* Yamaguti, 1934. **Fig. 8.** Scolex. **Fig. 9.** Tentacular bulb. **Fig. 10.** Mature segment; vitelline follicles shown on lateral margins of segment only. **Fig. 11.** Post-mature segment showing enlargement of uterus and patent uterine pore. Abbreviations: u – uterus, up – uterine pore, vi – vitelline follicles. Scale bars = 0.1 mm.



Figs. 12–17. *Pintneriella musculicola* Yamaguti, 1934. **Fig. 12.** Vagina, uterus and uterine pore. For the sake of clarity, the dorso-ventral relationships of the vagina and uterus have not been preserved. **Fig. 13.** Cirrus sac and seminal vesicles, lateral view, cirrus inverted. **Fig. 14.** Cirrus sac and seminal vesicles, lateral view, cirrus everted. **Fig. 15.** Transverse section of mature segment at level of ovary showing four-lobed ovary and single layer of testes. **Fig. 16.** Transverse histological section through genital atrium and terminal genitalia showing vagina opening to atrium independently of cirrus sac and genital ducts passing ventrally to osmoregulatory canals. **Fig. 17.** Gravid segment with grossly distended uterus filled with eggs. Abbreviations: ao – accessory osmoregulatory canal, do – dorsal osmoregulatory canal, esv – external seminal vesicle, isv – internal seminal vesicle, m – Mehlis' gland, o – ovary, sr – seminal receptacle, t – testis, u – uterus, up – uterine pore, v – vagina, vd – vas deferens, vi – vitelline follicles, vo – ventral osmoregulatory canal. Scale bars = 0.1 mm.

thin-walled; cirrus sinuous, unarmed; in retracted state, cirrus projects internally into voluminous internal seminal vesicle (Fig. 13). External seminal vesicle elongate, bipartite, with thick, muscular wall; distal chamber longer than wide, 130–230 (180) long, 90–130 (110) wide; proximal chamber ovoid, shorter than distal chamber, 70–180 (110) long, 70–130 (90) wide. Both chambers of external seminal vesicle lined with elongate, distally-directed, cilia-like projections (Figs. 13, 14). In histological sections (Fig. 16), each cilium-like process with nucleus near base. Entire external seminal vesicle surrounded by prominent layer of glandular cells (Fig. 13). Vas deferens enters external seminal vesicle at proximal pole, thin-walled, greatly coiled, coils extend medially and posteriorly along aporal side of vagina. Testes numerous, approximately 500 per segment, filling entire medullary space; testes arranged in single layer although margins of adjacent testes overlap. Testes extend beyond dorsal osmoregulatory canals but not lateral to ventral canals: confluent at both anterior and posterior margins of segment.

Vagina thick-walled, tubiform, opens independently to genital atrium ventral to cirrus sac (Fig. 16). Vagina runs ventral to cirrus sac and external seminal vesicle, then turns posteriorly to pass dorsal to uterus, towards ovarian isthmus; vagina sinuous, dilating to form diminutive but thick-walled seminal receptacle immediately anterior to ovarian isthmus. Ovary bilobed in dorso-ventral view, four-lobed in transverse section (Fig. 15). Ovarian lobes 200–340 (290) long by 130–250 (180) wide. Oviduct passes posteriorly from isthmus to Mehlis' gland; Mehlis' gland circular, 110–190 (150) in diameter. Uterine duct runs anteriorly from Mehlis' gland, entering uterus at level of anterior margin of ovary. Uterus initially tubular, linear, directed anteriorly, curving slightly porally to terminate at uterine pore, posterior to level of cirrus sac. Uterine pore evident even in immature segments as circular array of cells on ventral aspect, becomes patent in most segments as they achieve maturity. In post-mature segments, uterus expands laterally as testes begin to involute; in most segments, uterine pore remains patent and eggs are discharged into environment; in some segments (Fig. 17), pore apparently not patent and eggs accumulate in uterus causing gross distension. Egg tanned, ovoid 38–45 (43) long by 25–35 (30) wide; operculum not seen. Vitelline follicles small, 25–40 (35) in diameter, scattered, scarcely visible in mature segments except at margins (Fig. 10). Clearly visible in post-mature segments (Fig. 11) and most prominent in gravid segments (Fig. 17) in which testes have degenerated, scattered uniformly across dorsal and ventral aspects of cortico-medullary junction of segments. Ventral osmoregulatory canals slightly sinuous, at lateral margins of medulla, 10–45 (27) in diameter, with commisure at posterior margin of each segment. Dorsal osmoregulatory canals slender, medial to ventral canals, slightly sinuous, 5–10 (9) in diameter. Additional tiny accessory ventral canals detected in transverse sections (Fig. 15); not seen in whole mounts. Genital ducts cross osmoregulatory canals ventrally (Fig. 16).

Material examined: 12 adult cestodes from spiral valve of *Carcharias taurus* Rafinesque, 1810, Mooloolaba Aquarium, Mooloolaba, Queensland, Australia, coll. I. Beveridge (SAM AHC 28414-6).

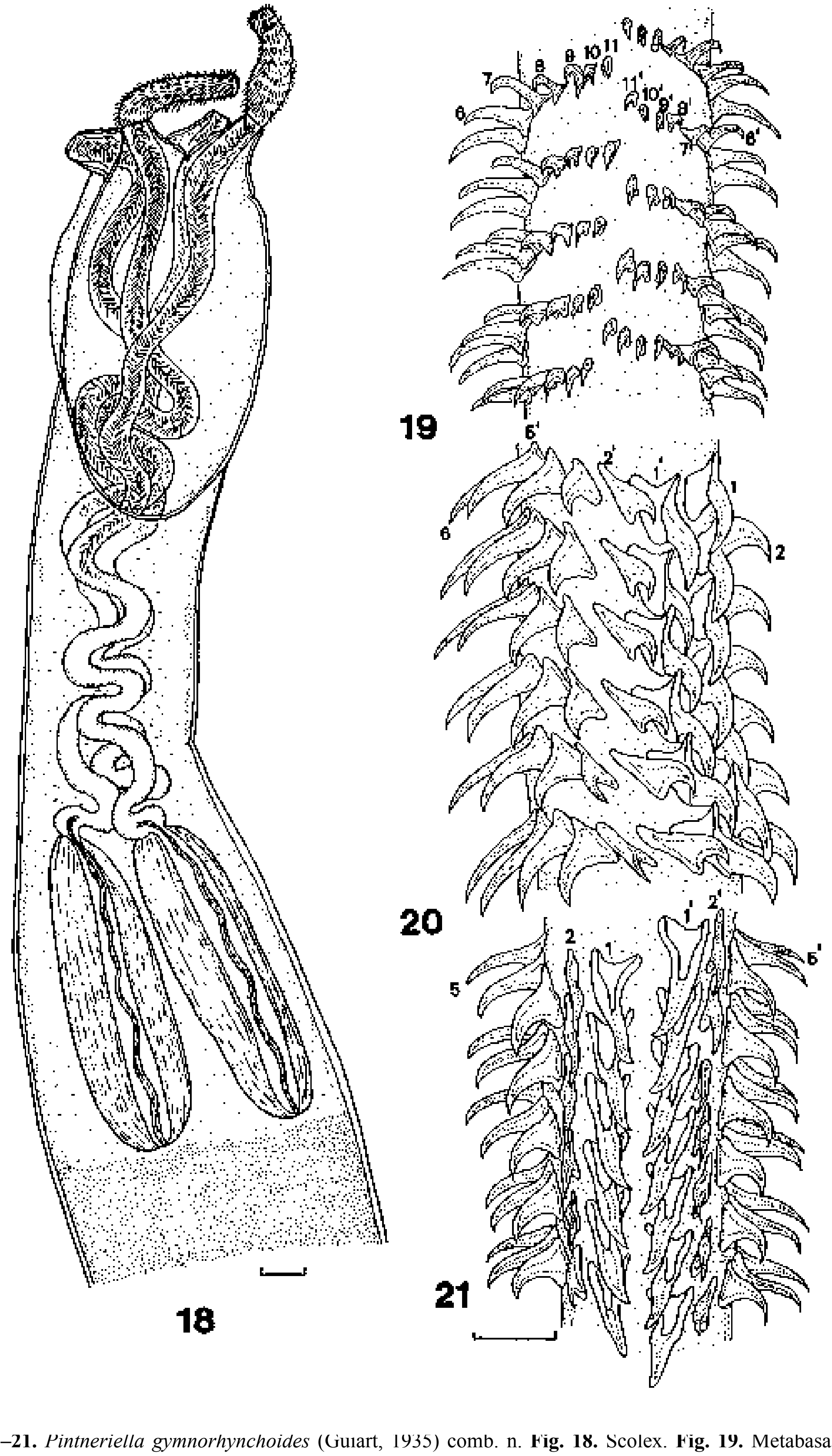
Pintneriella gymnorhynchoides (Guiart, 1935) comb. n. Figs. 18–25

Synonyms: *Rhopalothylax gymnorhynchoides* Guiart, 1935, pp. 36–39, figs. 5A–C, 44–49.

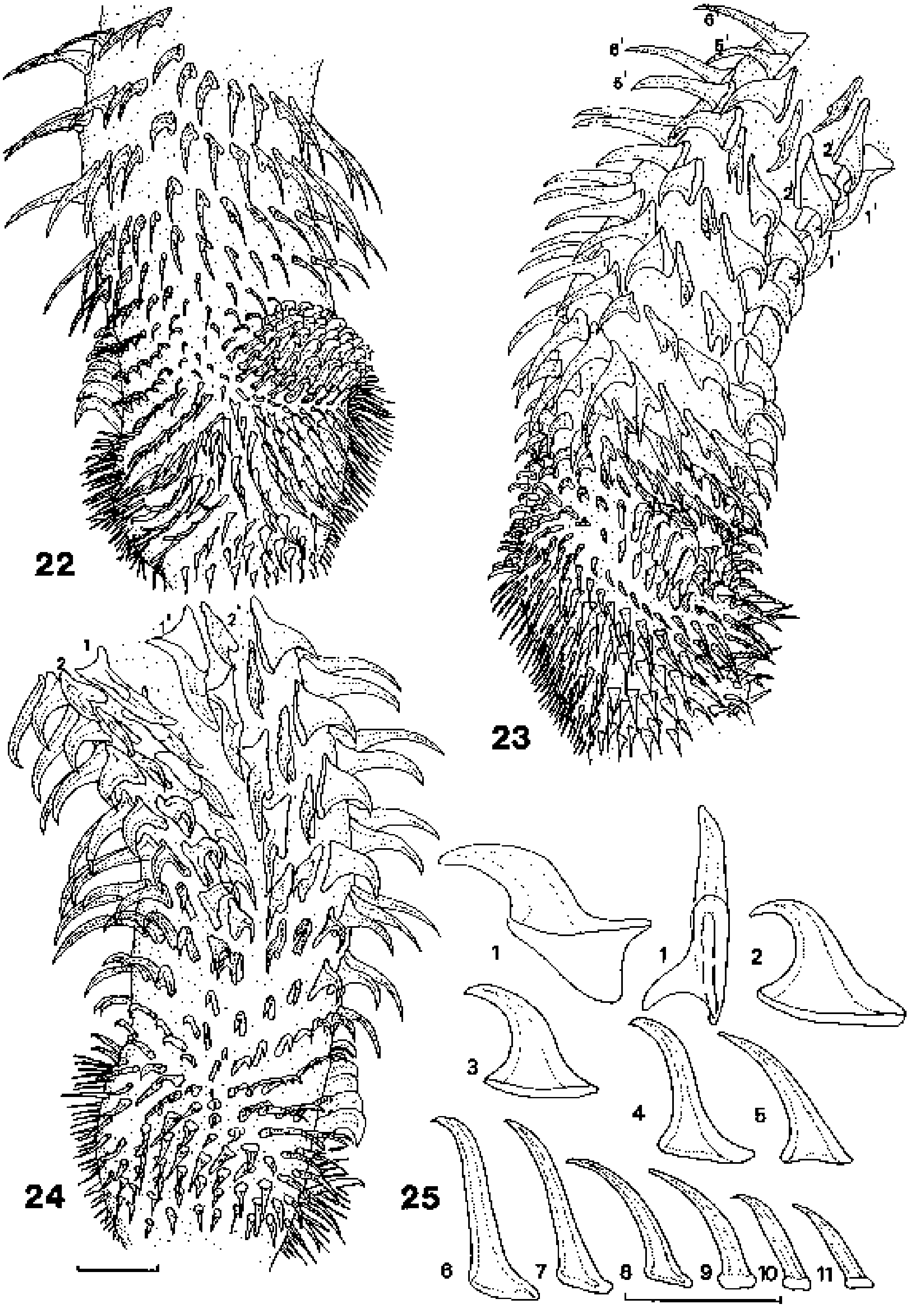
Description. Scolex acraspedote, 8.3 mm long; maximum width in pars vaginalis 1.50 mm, width in pars bulbosa 2.65 mm (Fig. 18). Pars bothridialis 3.2 mm. Bothridia elongate, oval, without thickened margins, 1.9 wide; pars vaginalis 6.2 mm long; tentacle sheaths sinuous; bulbs short stout, 2.9 mm long, 0.85 mm wide. Scolex ratio 1 : 1.94 : 1.10. Retractor muscle originates at base of bulb. Prebulbar organ and gland cells associated with retractor absent. Pars post-bulbosa absent. Tentacles elongate 200–230 (220, n = 5) in diameter in metabasal region; basal swelling present, diameter 230–350 (280, n = 5); tentacles emerge from sleeve-like extension of bothridial tegument.

METABASAL ARMATURE. Armature heteroacanthous, heteromorphous. Hooks arranged in ascending half spirals of 11 hooks, beginning on internal surface of tentacle and terminating on external surface (Figs. 19–21). Distinct space present between commencement of half-spirals on internal surface of tentacle. Hooks 1(1') robust, uncinate, 100–145 (135) long, base length 65–95 (85), with distinctive "keel" 45–55 (47, n = 5) deep (Fig. 25). Hooks 2(2') broadly uncinate, 90–130 (110) long, base length 70–95 (90). Hooks 3(3') uncinate, 80–115 (100) long, base length 65–85 (70). Hooks 4(4') falcate, 105–135 (120), base length 50–75 (65). Hooks 5(5') falcate with narrower base, 90–125 (110) long, base length 45–65 (50). Hooks 6(6') falcate, 105–135 (130) long, base length 45–55 (50). Hooks 7(7') falcate, slender, 115–140 (125) long, base length 40–50 (45). Hooks 8(8') falcate, smaller, 70–120 (100) long, base length 20–40 (30). Hooks 9(9') falcate with narrow base, 70–105 (90) long, base length 20–35 (25). Hooks 10(10') 75–100 (85) long, base length 20–30 (25). Hooks 11(11') filiform, 60–70 (65) long, base length 25–30 (28). Hook rows do not overlap on external surface.

BASAL ARMATURE. (Figs. 22–24). Hooks hollow. First 6 rows of hooks deltoid in shape, 40–65 (52) long, base length 15–25 (19), becoming filiform on external surface, 40–100 (69) long, base length 10–20 (14). On antibothridial surface, 9th row of hooks contains 5



Figs. 18–21. *Pintneriella gymnorhynchoides* (Guiart, 1935) comb. n. **Fig. 18.** Scolex. **Fig. 19.** Metabasal tentacular armature, external surface of tentacle. **Fig. 20.** Metabasal tentacular armature, bothridial surface of tentacle. **Fig. 21.** Metabasal tentacular armature, internal surface of tentacle. Scale bars: Fig. 18 = 0.4 mm; Figs. 19–21 = 0.1 mm.



Figs. 22–25. *Pintneriella gymnorhynchoides* (Guiart, 1935) comb. n. **Fig. 22.** Basal tentacular armature, antibothridial surface. **Fig. 23.** Basal tentacular armature, bothridial surface. **Fig. 24.** Basal tentacular armature, internal surface. **Fig. 25.** Hook profiles of hooks of principal row, 1–11. Scale bars = 0.1 mm.

enlarged, unciform hooks on internal aspect, 50–65 (59, n = 5) long, base length 30–60 (47, n = 5). Quadrangular array of bill hooks, total of 6 rows present, 4–8 hooks per row, on external aspect of swelling, hooks 45–65 (60) long, base length 15–25 (23). Strobila unknown.

Material examined: types, slide of single mounted scolex (MOM INV 19968), slides of dissected tentacles (MOM INV 19966, 19967), from liver of *Centroscymnus coelolepis* Bocage et Capello, 1864 (Squalidae), Azores, 1911 (depth of 1095–3675 m).

Clujia rakovitzai Guiart, 1935

Material examined: holotype, plerocercus, from gastric submucosa of *Prionace glauca* (Linnaeus, 1758) (= *Galeus glaucus*), Cape Verde, MOM INV 19960.

Remarks: The single specimen of this species conforms with the description given by Guiart (1935). Two bothridia are present, the pars vaginalis is long and the bulbs are relatively short. The tentacles are partially everted but are coiled in such a manner as to prevent any detailed examination of the type of armature present. In the absence of such data the taxonomic position of the genus cannot be determined.

Cladistic analysis of the position of *Pintneriella*

Addition of the genus *Pintneriella* resulted in no substantial changes to the phylogenetic tree of genera of the order presented by Beveridge et al. (1999, fig. 3). In the new tree, the consistency index was 0.28, the homoplasy index 0.72 and the rescaled consistency index 0.19, values identical with, or scarcely different from the values achieved in the original analysis. *Pintneriella* was placed unequivocally in clade 8 of Beveridge et al. (1999) and a revised arrangement of this clade with the added genus is shown in Fig. 26. The clade formerly contained members of the families Gilquiniidae, Gymnorhynchidae and Molicolidae.

DISCUSSION

Previously, *Pintneriella musculicola* was known only from the plerocercus (Beveridge and Campbell 2000) and was placed as a genus of uncertain position within the Heteracanthoidea. Beveridge and Campbell (2000) suggested that knowledge of the anatomy of the adult could possibly resolve the taxonomic position of the genus. Here, the adult is described for the first time. Although obtained from a captive shark, the host was born at Mooloolaba, Queensland, and throughout its captive life was fed with teleosts from the Mooloolaba region (N. Kirby, pers. comm.). It is likely therefore that it became infected from the teleosts with which it was fed. A full redescription is provided in part as evidence that the specimens described herein are indeed *P. musculicola*. The type specimens have invaginated tentacles and the redescription of the species by Beveridge and Campbell (2000) was based on plerocerci from the same locality as the type specimens which had been identified by Yamaguti (1952) as *P. musculicola*. The features of the scolex and armature of the new specimens agree closely with those reported from plerocerci by Beveridge and Campbell (2000) and thereby provide compelling evidence for the identification made herein. The sole apparent differences are in the shape of hooks 9(9'), which are shorter and more uncinate in the new material and in the array of hooks on the antibothridial surface of the basal swelling of the tentacle. The array is clearly shown in fig. 8 of Beveridge and Campbell (2000), but is not clearly depicted in the orientations of the basal armature presented in the current paper. This feature is however clearly discernible on the new specimens.

Beveridge and Campbell (2000) suggested that the scolex and armature of *Pintneriella* was intermediate between the characters exhibited by the families Eutetrarhynchidae and Gilquiniidae. The heteroacanthous armature and paired bothridia indicated similarities with the Eutetrarhynchidae (see Beveridge 1990b), while details of the armature, particularly the form of hooks 1(1') and the form of the basal armature as well as the short bulbs lacking prebulbar organs and gland cells suggested similarities with the Gilquiniidae. The space between hooks 9 and 9' on the external surface of the tentacle is present only in the family Shirleyrhynchidae, another heteroacanthoid family with four bothridia (Beveridge and Campbell 1988, Campbell and Beveridge 1994). A number of features of the mature segment of *P. musculicola* present similarities with those of the Gilquiniidae. The cirrus sac is typical of gilquiniid cestodes in having a large internal seminal vesicle, with the retracted cirrus protruding into the vesicle (Fig. 13). This character occurs in all gilquiniid species (Beveridge 1990a) as well as in the gymnorhynchid genus *Chimaerarhynchus* Beveridge et Campbell, 1989. The external seminal vesicle of *Pintneriella* is unique within the Trypanorhyncha in being distinctly bilobed and being lined with numerous cilia-like projections each with a nucleus near its base (Fig. 16). The precise nature of the projections will have to be determined using ultrastructural methods. Unlike all members of the Gilquiniidae, *Pintneriella* lacks an accessory seminal vesicle.

The uterus of *Pintneriella* is deviated porally in its anterior half and terminates in a preformed structure which may develop into a uterine pore (Figs. 10, 11). This arrangement resembles many species of the Gilquiniidae (Beveridge 1990a), as well as *Molicola* (Molicolidae) (Dollfus, 1942), while in *Chimaerarhynchus*, the uterus is similarly deviated, but a preformed pore is absent (Beveridge and Campbell 1989) as is the case for *Gymnorhynchus isuri* Robinson, 1959, based on the redescription by Caira and Bardos (1996). A curious feature of the specimens of

Pintneriella studied here was that although a patent uterine pore was present in many segments, in others it was not functional and the uterus was grossly distended with eggs (Fig. 17). Whether or not these were segments in which the pore failed to develop completely or was not yet open could not be determined. The features of the mature and gravid segments of *P. musculicola* therefore provide further evidence of similarities with the Gilquiniidae as well as a number of features such as the external seminal vesicle which are most probably autapomorphic in these species. Segment morphology provides no evidence in favour of an association of *Pintneriella* with the Eutetrarhynchidae.

Although Guiart's (1935) description of *Rhopalothylax gymnorhynchoides* is uninformative (Dollfus 1942), the type material does consist of a slide of an entire plerocercus with partially everted tentacles as well as two slides of fully everted tentacles dissected from another plerocercus. From these specimens, a full description of the plerocercus has been made. This material reveals that the scolex of *R. gymnorhynchoides* resembles that of *P. musculicola* in having two elongate bothridia, an elongate pars vaginalis and short bulbs with a retractor muscle originating at the base and with the bulbs lacking prebulbar organs and gland cells. However, the dimensions of the scolex of *R. gymnorhynchoides* are larger than those of *P. musculicola*. The basal and metabasal armatures of *R. gymnorhynchoides* resemble those of *P. musculicola* in general features. There is a distinctive basal armature with an array of closely packed hooks on the antibothridial surface. Hooks 1 and 1' are similar in having an enlarged base and the hooks diminish in size gradually along each row. Significant differences between the two species are the sizes of the hooks in each row, the presence of 11 hooks in each principal row of *R. gymnorhynchoides* compared with nine in *P. musculicola* and the absence of any space between the hook rows on the external surface of the tentacle of *R. gymnorhynchoides*. The strobila of *R. gymnorhynchoides* is unknown, but on the basis of the scolex structures this species belongs to the genus *Pintneriella*, described by Yamaguti (1934) one year before *Rhopalothylax.* Consequently, *Rhopalothylax* is suppressed as a synonym of *Pintneriella*, with its type species representing an independent species within the genus, now *P. gymnorhynchoides* comb. n.

The type and only specimen of *Clujia racovitzai* was re-examined and the proportions of the scolex with short bars bulbosa and bulbs and elongate pars vaginalis were confirmed (Guiart 1935). Although the tentacles were everted, they were coiled upon themselves making description of the armature impossible. As a consequence, *Clujia*, which is a monotypic genus, is regarded as a *genus inquirendum* and may not necessarily be related to *Pintneriella* (syn. *Rhopalothylax*). It is therefore excluded from further consideration.

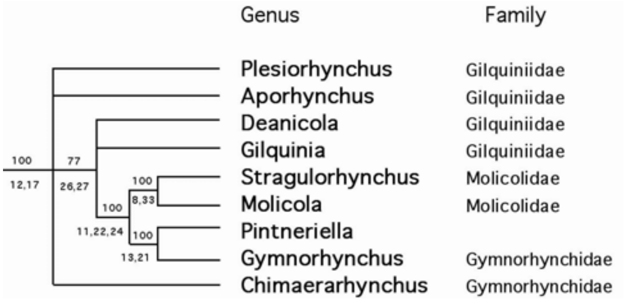


Fig. 26. Clade 8 of the cladistic analysis of the order Trypanorhyncha from Beveridge et al. (1999) showing the position of the added genus *Pintneriella*. Figures above branches indicate the percentage of equally parsimonious trees in which a particular branch occurred; figures below branches indicate the synapomorphic characters defining each particular branch. Numbering of characters follows Beveridge et al. (1999). Character 8: origin of retractor muscle; 11: presence of internal seminal vesicle; 12: presence of external seminal vesicle; 13: presence of accessory seminal vesicle; 17: uterus deviated porally; 21: pars postbulbosa present; 22: bothridial margins thickened; 26: basal tentacular swelling present; 27: distinctive basal armature present.

The addition of morphological data for the adult stage of *Pintneriella* provides novel information on its morphological associations, but does not resolve the position of the genus within the Heteracanthoidea. Consequently, the genus was added to the cladistic analysis of genera of the order reported by Beveridge et al. (1999) in order to further elucidate its phylogenetic affiliations. The analysis, in spite of its limitations (Beveridge et al. 1999), unequivocally placed *Pintneriella* in the clade containing the families Gilquiniidae, Gymnorhynchidae and Molicolidae (Fig. 26). This particular branch occurred in 100% of all equally parsimonious trees and was based on the presence of an internal seminal vesicle and the porally deviated uterus. *Pintneriella* was closest to *Gymnorhynchus* and its addition to the analysis rendered the formerly monophyletic Gymnorhynchidae (*Gymnorhynchus* + *Chimaerarhynchus*) paraphyletic (Fig. 26). The addition of *Pintneriella* to this clade altered the characters defining the clade, which formerly included the possession of an accessory seminal vesicle (except in *Gymnorhynchus*) and the possession of four bothridia. The analysis suggests that *Pintneriella* is more closely aligned with the Gilquiniidae than with the Eutetrarhynchidae, the only similarities it shared with the latter family being paired bothridia (Beveridge et al. 1999). However, in the phenetic classifications of Campbell and Beveridge (1994) and Palm (1997), as well as in the classification of Dollfus (1942), the number of bothridia is given family ranking. Thus in these classifications, the Rhopalothylacidae lies closer to the Eutetrarhynchidae as defined by Dollfus (1942) and Campbell and Beveridge (1994) or to the Lacistorhynchidae in the classification of Palm (1997) even though the latter family contains genera characterised by the possession of chainettes and bands of hooks (Palm 1997). Although the use of the number of bothridia as a family characteristic may need to be revised in the future, in order to incorporate the insights of recent cladistic studies, to maintain stability in the current classification, *Pintneriella* is retained within the existing family Rhopalothylacidae, as redefined below, pending changes to the family structure within the order. Retention of the family name follows article 40 of the International Code for Zoological Nomenclature (synonymy of the type genus).

Rhopalothylacidae Guiart, 1935

Diagnosis: Heteracanthoidea. Scolex acraspedote, two elongate bothridia. Tentacles elongate. Armature heteroacanthous, heteromorphous; hooks hollow. Tentacle sheaths sinuous. Bulbs short, stout, without prebulbar organs; retractor muscle originates at base of bulb. Pars postbulbosa present. Strobila acraspedote. Genital pores marginal, alternate irregularly. Internal and bilobed external seminal vesicles present. Testes medullary, in single layer. Ovary four-lobed. Vitelline follicles encircling medulla. Uterus median, saccate, with ventral pore poral to midline. In elasmobranchs; plerocerci in teleosts and elasmobranchs. Type genus: *Pintneriella* Yamaguti, 1934.

Pintneriella Yamaguti, 1934
(Syn. *Rhopalothylax* Guiart, 1935)

Diagnosis: Scolex acraspedote. Two, elongate bothridia. Margins thick but indistinct. Pars vaginalis much longer than pars bulbosa, tentacle sheaths sinuous. Bulbs short, without prebulbar organ or gland cells. Retractor muscle originates at base of bulb. Tentacles elongate. Basal swelling and distinct basal armature present. Metabasal armature heteroacanthous, heteromorphous; hooks hollow; hook rows do not overlap on external surface. Strobila acraspedote. Genital pores marginal, alternate irregularly. Internal and bilobed external seminal vesicles present. Testes scattered, in single layer, confluent anterior to uterus and posterior to ovary. Ovary four-lobed. Uterus tubular, deviated towards genital pore; uterine pore present; gravid uterus saccate; egg tanned. Vitelline follicles circum-medullary. Adults in sharks; plerocerci in teleosts and elasmobranchs. Type species: *Pintneriella musculicola* Yamaguti, 1934. Other species: *P. gymnorhynchoides* (Guiart, 1935) comb. n. (syn. *Rhopalothylax gymnorhynchoides*).

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