

A new genus and new species of microbothriid monogenean (Platyhelminthes) with a functionally enigmatic reproductive system, parasitic on the skin and mouth lining of the largetooth sawfish, *Pristis microdon*, in Australia

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Abstract

Dermopristis paradoxus gen. et sp. nov., a microbothriid monogenean parasite from the skin and mouth lining of the largetooth sawfish, *Pristis microdon* (Elasmobranchii, Pristidae) in Australia, is described. The parasite has 2 juxtaposed testes and differs from other microbothriids in possessing a unique and unusual terminal male reproductive tract comprising a proximal and a distal tube, the latter with a conspicuous opening on the ventral surface and lacking a recognisable male copulatory organ. The smalltooth sawfish, *P. pectinata*, also has a skin-parasitic microbothriid, *Dermophthirioides pristidis* Cheung et Nigrelli, 1983, but this parasite species has a prominent copulatory papilla. *Dermopristis paradoxus* also has parallel ridges with broad tops running in a roughly transverse direction across the ventral surface of the body. The ventral ridges are prominent from the level of the pharynx to the posterior region of the body. The function of the ridges is unknown. Reproductive biology, attachment and feeding in *D. paradoxus* are discussed. In the absence of unmounted parasite specimens for sectioning, a mounted specimen of *D. paradoxus* was released from the slide and successfully processed to provide serial, stained, resin sections. This useful technique is recommended to provide anatomical information in situations where only specimens on slides are available for study.

Keywords

Platyhelminthes, Monogenea, Microbothriidae, *Dermopristis paradoxus* gen. et sp. nov., *Dermophthirioides pristidis*, sawfish, *Pristis* spp., reproductive biology, functional morphology

Introduction

Microbothriid monogeneans are typically found on the skin of elasmobranch fishes (sharks and rays), although there is a record of *Dermophthirius carcharhini* MacCallum, 1926 in the olfactory organs (= nasal fossae) of a shark identified as *Carcharias commersonii* (see Price 1938). Those that live on the skin attach themselves by means of a relatively small haptor to a single host denticle (Kearn 1965; Whittington and Chisholm 2008, Fig. 13.2G). Elasmobranch denticles lack a covering of skin and hence provide a hard substrate. This is reflected in the lack of haptor hooks or sclerites of any kind, apart from vestiges of hooks in the larva (= oncomiracidium) (Kearn and Evans-Gowing 1990, Glennon *et al.* 2006). It has

been shown that the microbothriid skin parasite *Leptocotyle minor* uses an adhesive secretion to cement the haptor to a host denticle (Kearn 1965, Kearn *et al.* 2001).

Little is known of the reproductive biology of microbothriids. Mating was observed in *L. minor* by Kearn (1965) and insemination (possibly mutual) appears to be achieved by insertion of a penis into a spacious vagina. A preliminary examination of the reproductive systems of microbothriids from the skin and mouth lining of the largetooth sawfish, *Pristis microdon*, revealed features that were fundamentally different from those of *L. minor*, demanding a detailed anatomical study. Moreover, parasites from the largetooth sawfish appeared to be undescribed and different both generically and specifically from other microbothriids, including *Dermoph-*

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thirioides pristidis Cheung et Nigrelli, 1983 from the skin of the closely related smalltooth sawfish, *P. pectinata*.

Materials and methods

Shortly after collection, parasites were preserved in 10% formalin. Specimens were later stained with Semichon's carmine or left unstained, dehydrated in an ethanol series, cleared in cedarwood oil and mounted in Canada balsam. One whole mount specimen was soaked in xylene to remove the Canada balsam and to detach it from the slide; the specimen was then embedded in LR white embedding medium (London resin; Agar Scientific). Serial transverse sections cut at a thickness of 1.5 µm were stained in 0.25% toluidine blue in 1% borax. Whole mounts and serial sections were examined using a compound microscope equipped with phase contrast optics. Measurements, made using a calibrated ocular micrometer, are presented in micrometres as the mean followed by the range in parentheses and the number of measurements taken. Where measurements are separated by a multiplication sign, the first dimension is length followed by width. The boundaries of soft parts were sometimes obscure and in these circumstances, measurements were not taken or were recorded as approximations.

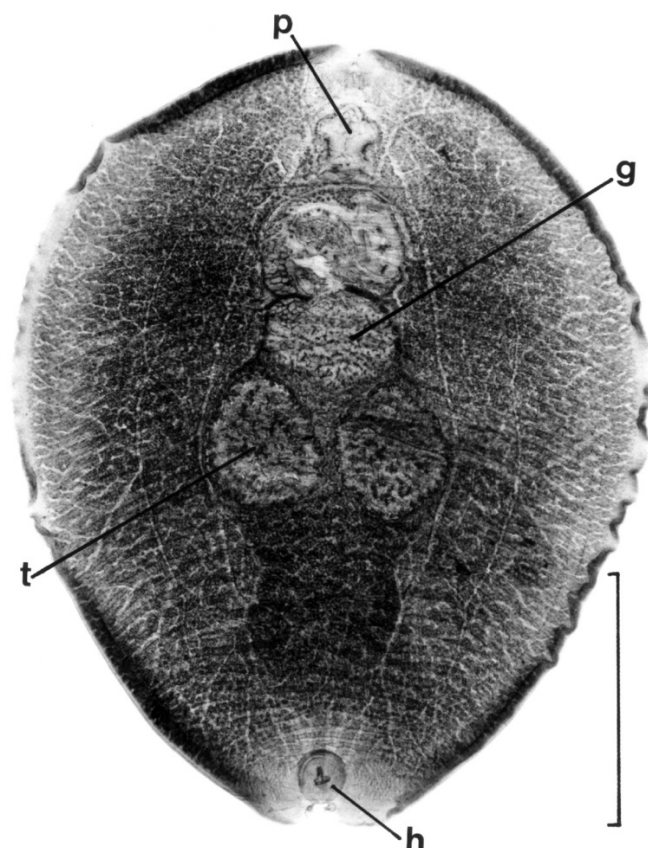


Fig. 1. *Dermopristis paradoxus* gen. et sp. nov.: Whole adult animal. Holotype (SAMA AHC 29783); g – germarium, h – haptor, p – pharynx, t – testis. Scale bar = 2 mm

For comparative purposes, 3 paratype specimens of *Dermophthirioides pristidis* mounted on a single slide, were obtained on loan from the United States National Parasite Collection (USNPC no. 076523.00; storage no. MT22:190; host: the smalltooth sawfish *Pristis pectinata*). In addition, 14 carmine-stained, wholemount specimens (4 slides), identified as *D. pristidis*, host identity uncertain, were available from the collection of IDW but were originally collected by P.J. Cheung from fish material held at the New York Aquarium and passed to IDW by Dr A.D.M. Dove. Specimens of *Leptocotyle minor* and *Pseudocotyle squatinæ* from the collection of GCK and voucher specimens of *Pseudoleptobothrium aptychotremæ* in The Australian Helminthological Collection of The South Australian Museum (SAMA AHC 28917-40) were also studied for comparative purposes.

Type material of the new taxon is deposited in the following curated collections: Parasitic Worms, Department of Zoology, Natural History Museum, Cromwell Road, London SW7 5BD, U.K. (BMNH; contact: Eileen Harris – e.harris@nhm.ac.uk); The AHC, Parasitology Section, SAMA, North Terrace, Adelaide, South Australia 5000, Australia (contact: Leslie Chisholm – leslie.chisholm@samuseum.sa.gov.au); USNPC, United States Department of Agriculture, Agricultural Research Service, Building 1180, BARC-East, 10300 Baltimore Avenue, Beltsville, Maryland 20705-2350, U.S.A. (contact: Eric Hoberg – ehoberg@anri.barc.usda.gov or Pat Pilitt – ppilitt@anri.barc.usda.gov).

Results

Microbothriidae Price, 1936

Microbothriinae Yamaguti, 1963

Dermopristis gen. nov.

Diagnosis: Haptor small, sclerites absent. Ventral body surface with parallel ridges with broad tops orientated in roughly

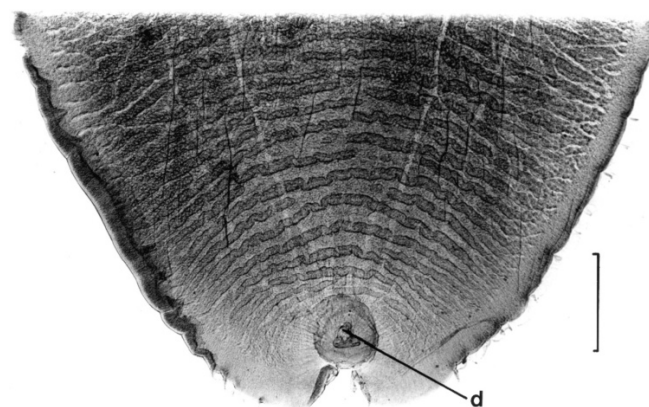


Fig. 2. *Dermopristis paradoxus* gen. et sp. nov.: Ventral surface of posterior region of body of immature individual showing ridges running in a roughly transverse direction. Paratype (SAMA AHC 29784); d – denticle inside haptor. Scale bar = 0.5 mm

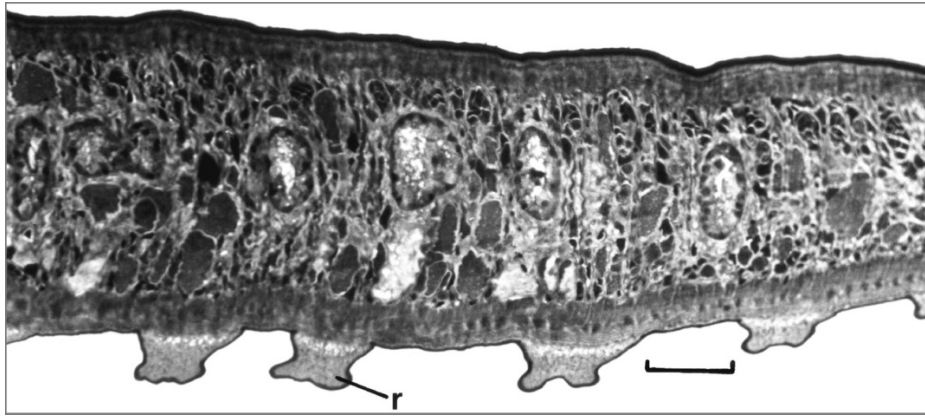


Fig. 3. *Dermoprists paradoxus* gen. et sp. nov.: Light photomicrograph of toluidine-blue-stained resin section through the posterior region of the body; r – ventral ridge in transverse section. Scale bar = 50 μ m

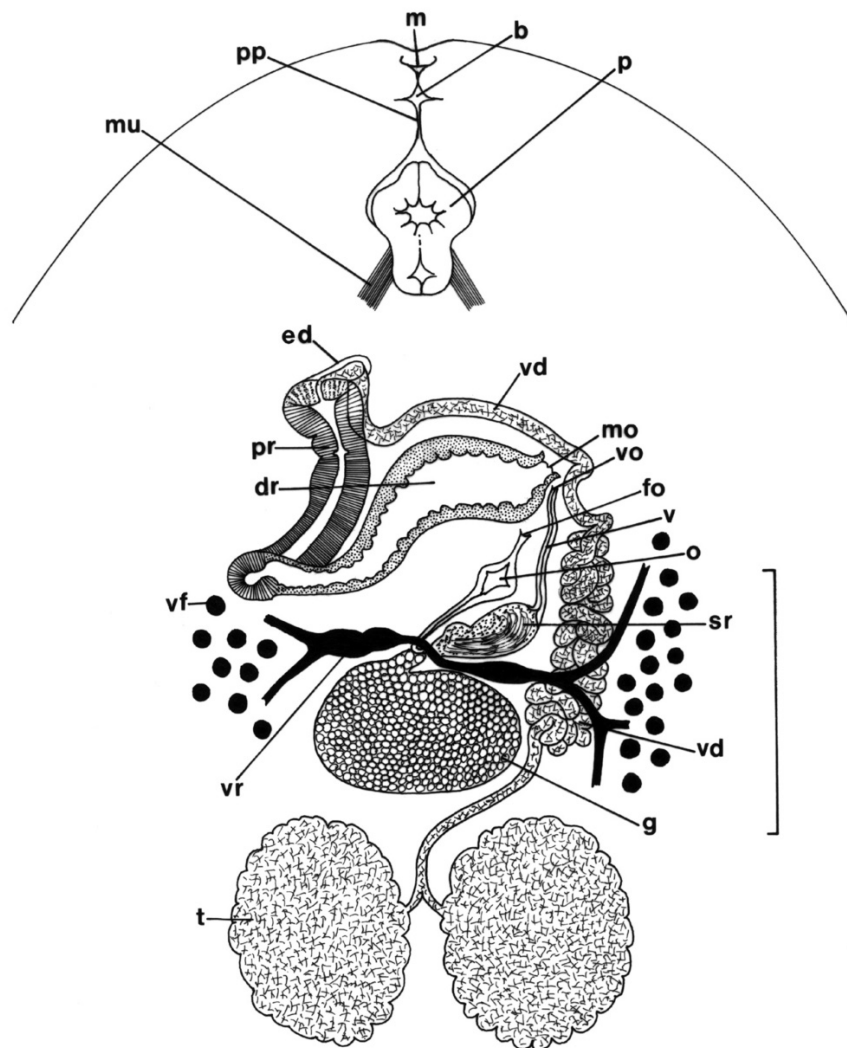


Fig. 4. *Dermoprists paradoxus* gen. et sp. nov.: Ventral view based on holotype showing pharynx and reproductive system; b – buccal cavity, dr – distal tubular region of male reproductive tract, ed – ejaculatory duct, fo – opening of female reproductive system, g – germarium, m – mouth, mo – opening of male reproductive tract, mu – muscle, o – ootype, p – pharynx, pp – pre-pharynx, pr – proximal tubular region of male reproductive tract, sr – seminal receptacle, t – testis, v – vagina, vd – vas deferens, vf – vitelline follicle, vo – vaginal opening, vr – vitelline reservoir. Scale bar = 1 mm

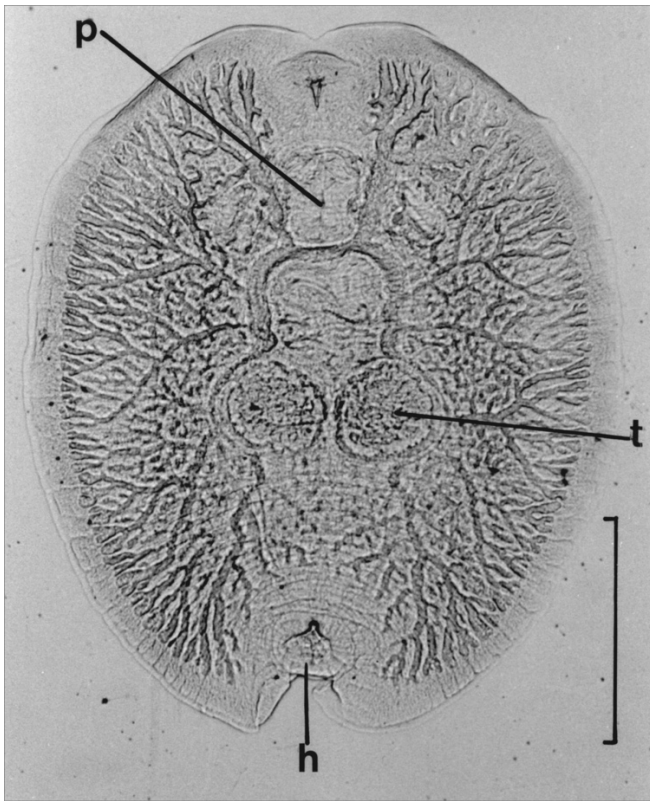


Fig. 5. *Dermopristis paradoxus* gen. et sp. nov.: Whole immature specimen (paratype SAMA AHC 29785). The branched gut is visible as it is not yet obscured by the vitellarium (cf. Fig. 1); h – haptor, p – pharynx, t – testis. Scale bar = 0.5 mm

transverse direction. Ridges prominent from level of pharynx to posterior region of body. Gut dendritic. Testes 2, juxtaposed. Vas deferens highly coiled, communicating with tubular male reproductive tract, divided into 2 distinct regions: proximal region with thick wall, initially glandular, becoming muscular for most of its length; distal region with highly folded, glandular (?) wall and spacious lumen with ventral opening on left side of midline. No readily recognisable male copulatory organ; no sclerites associated with male apparatus. Distal region of vagina narrow, opening ventrally close to male opening; proximally vagina enlarges to form seminal receptacle. Female genital opening ventral, posterior to openings of male system and vagina. Ectoparasitic on elasmobranchs.

Type and only species: *Dermopristis paradoxus* sp. nov.

Etymology: Reflects habitat on skin (Greek *derma* – skin) of largetooth sawfish (*Pristis microdon*).

***Dermopristis paradoxus* sp. nov.** (Figs 1–7)

Type host and locality: *Pristis microdon* Latham, 1794 (Pristidae) (largetooth sawfish) caught in the Gulf of Carpentaria, Queensland, Australia; parasites collected on 15 May 2003 by Mr Julian Baggio, Senior Aquarist, Cairns Marine Aquarium Fish, Cairns, Queensland, Australia.

Site on host: Preferred site reported as skin around mouth and around nasal fossae; some inside mouth cavity and some on skin of dorsal surface (J. Baggio; personal communication).

Infection details: Not recorded.

Etymology: Species name refers to unusual features of reproductive system and related difficulties in understanding how insemination may occur.

Holotype: SAMA AHC 29783 (1 wholemount).

Paratypes: SAMA AHC 29784–29787 (4 wholemounts); BMNH 2009.10.27.1–4 (4 wholemounts); USNPC 102403 (4 wholemounts).

Description: Based on 7 adult (1 damaged) and 6 immature parasites mounted on slides. One adult specimen embedded in resin and sectioned (see Materials and methods; 106 slides of sections through the anterior end and reproductive system, 15 slides of sections through the haptor region. All slides with sections retained in the collection of GCK: Reference numbers 525/1 – 106 and 525/H1–H15). Dimensions based on 6 mounted adults. Whole animal oval (Fig. 1): 4986 (4091–6076) 6 × 4296 (3489–5189) 6. Haptor small (Figs 1, 5): 388 (372–434) 4 × 378 (337–396) 5. Haptor of all wholemount specimens contained a single host denticle (Fig. 2); denticle present in haptor of sectioned adult specimen. Haptor sclerites absent.

Parallel ridges with broad tops, 30 to 65 wide, running in roughly transverse direction across ventral body surface from level of pharynx to posterior region of body (Figs 2, 3); no ridges dorsally. Mouth anterior, sub-terminal, leading to deeply infolded buccal cavity (Fig. 4). Eyes absent. Narrow pre-pharynx (Fig. 4). Anterior region of pharynx accommodated in cavity (Fig. 4). Approximately 9 digitiform papillae project into spacious lumen of anterior region of pharynx; from resin sections no conspicuous gland cells or ducts observed inside papillae or in pharynx wall. Prominent muscles, one on each side, run from external surface of posterior region of pharynx in posterolateral direction (Fig. 4). Approximate pharynx dimensions: 423 (345–517) 6 × 422 (365–463) 6 (estimations only because of indistinct boundaries). Gut highly branched, not uniting posteriorly (Fig. 5). Gut pigment found in only one of 13 specimens – an immature individual with total length 2127.

Testes two, equally sized, juxtaposed, with undulating margins (Fig. 4). Testis dimensions (adults only): 903 (627–1113) 12 × 752 (588–963) 12. Vas deferens highly coiled, communicating with tubular male reproductive tract, divided into 2 distinct regions. Proximal region with roughly longitudinal orientation, with thick wall, initially glandular, becoming muscular for most of its length. Prior to entering proximal male tube, vas deferens acquires thick wall, possibly muscular, creating short ejaculatory duct. Distal region of tubular male tract orientated roughly transversely across body; lumen spacious (Figs 4; 6A, B), with ventral opening on left side of midline (Figs 4, 6B). Wall of distal half of distal tubular region highly folded, staining intensely in resin sections with toluidine blue and possibly glandular (Fig. 6). Contents of distal tubular region granular (Fig. 6). No readily recognisable male cop-

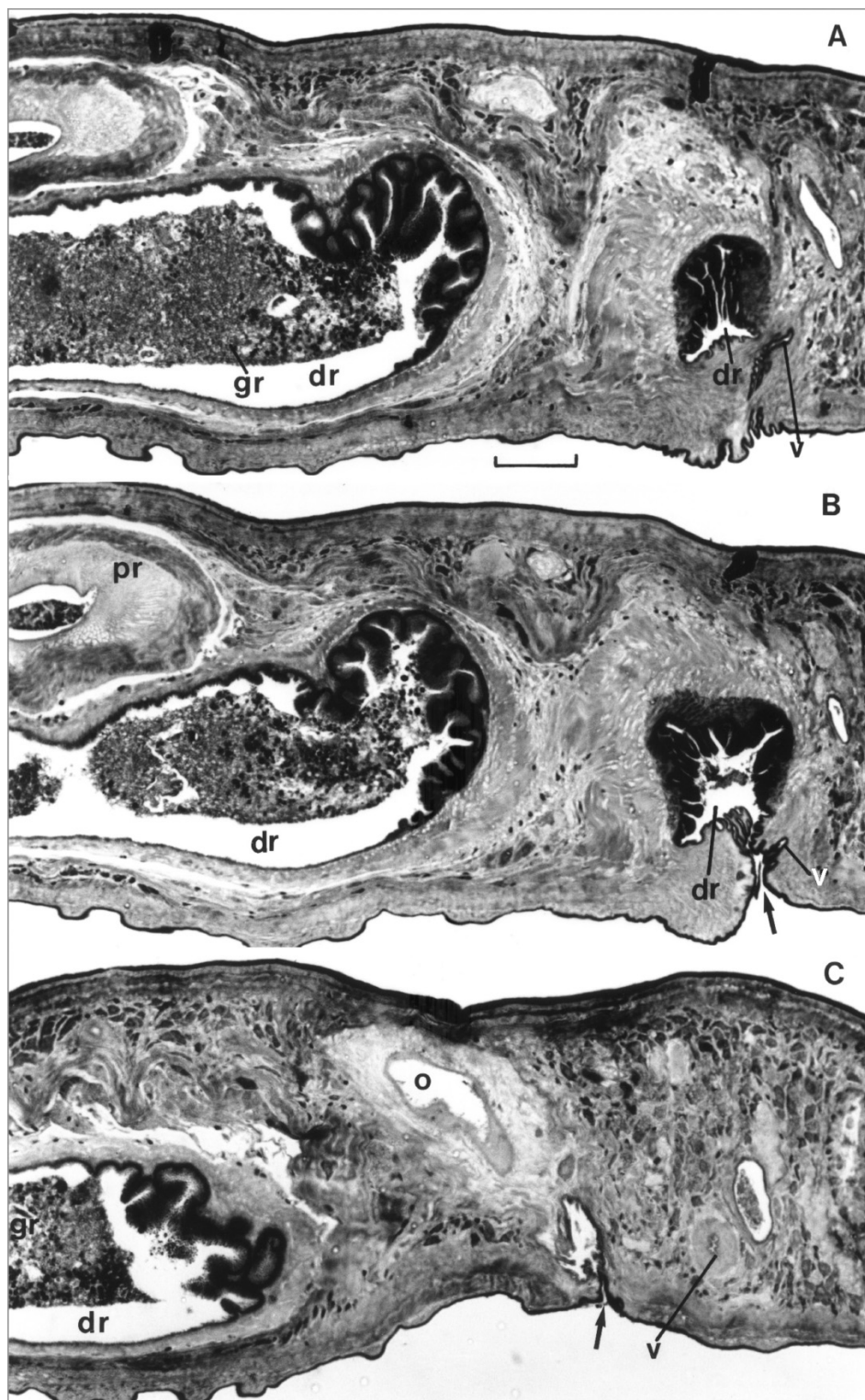


Fig. 6. *Dermopristis paradoxus* gen. et sp. nov.: Light photomicrographs of toluidine-blue-stained sections through the reproductive system. **A** – Section showing close proximity of terminal (distal) region of male reproductive tract (dr) and vagina (v). **B** – Neighbouring section through adjacent opening (arrow) of the distal tubular region of the male reproductive tract (dr) and the vagina (v). **C** – Section through ventral opening of female reproductive tract (arrow). Other lettering: gr – granular contents of male reproductive tract, o – ootype, pr – proximal tubular region of male reproductive tract. Scale bar = 50 μ m

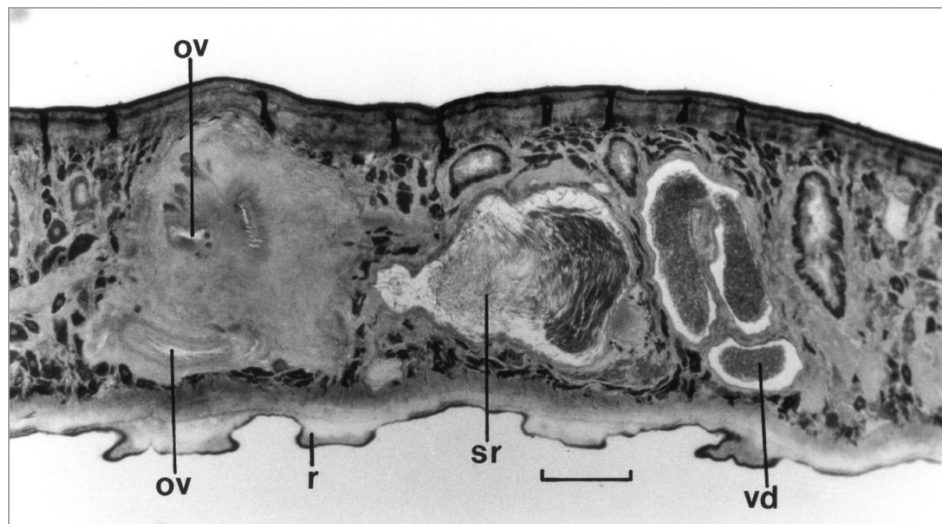


Fig. 7. *Dermopristis paradoxus* gen. et sp. nov.: Light photomicrograph of toluidine-blue-stained section through the seminal receptacle (sr) containing sperm, ov – oviduct (?), r – ventral ridge, vd – coiled vas deferens. Short, darkly stained features running at right angles to the dorsal tegument are artefacts produced by folding of the semi-thin section. Scale bar = 50 µm

ulatory organ; no sclerites in association with terminal male apparatus.

Small vaginal opening adjacent to male genital opening (Figs 4, 6B). Distal portion of vagina with thick wall and narrow lumen (Fig. 6C). Vagina expands proximally to form large seminal receptacle (Fig. 7); contains sperm. Female reproductive system opens ventrally, posterior to male genital opening (Fig. 6C). Uterus absent. No eggs found inside parasites. Shape of ootype indicates tetrahedral egg (needs confirmation). Parasitic on skin and mouth lining of largetooth sawfish, *Pristis microdon*.

Differential diagnosis: *Dermopristis paradoxus*, like *Dermophthirius* spp. and *Dermophthirioides pristidis*, possesses 2 juxtaposed testes and differs from all other known microbothriids, which possess a single testis or multiple testes. *Dermopristis paradoxus*, like *Dermophthirioides pristidis*, has no sclerites associated with the terminal male apparatus, but *D. pristidis* has a large “penis” (regarded as a cirrus by Cheung and Nigrelli 1983), which is absent in *Dermopristis paradoxus*. According to Cheung and Nigrelli (1983), *Dermophthirioides pristidis* has approximately 21 digitiform papillae in the pharynx while *Dermopristis paradoxus* has approximately 9. *Dermopristis paradoxus* is also distinguished from other microbothriids by the presence of roughly transverse parallel ridges with broad tops on the ventral surface from the level of the pharynx to the posterior end of the body.

Discussion

Microbothriid monogenean parasites from the skin and mouth lining of the largetooth sawfish, *Pristis microdon*, represent a new genus and new species, namely *Dermopristis paradoxus*. This species differs from all previously described microboth-

riids, including *Dermophthirioides pristidis* from the small-tooth sawfish, *P. pectinata*, by its unique and highly unusual male reproductive tract. With species of the microbothriid genera *Dermophthirius* and *Dermophthirioides*, *Dermopristis paradoxus* shares the presence of a dendritic gut and 2 juxtaposed testes, and all species within this group, with the exception of *D. paradoxus*, have a papillate male terminal organ.

The male papilla in *Dermophthirius* spp. and the monotypic *Dermophthirioides pristidis* is invariably described as a cirrus, for example by Price (1938) in *Dermophthirius carcharini* and by Cheung and Nigrelli (1983) in *Dermophthirioides pristidis*. However, a cirrus is extended by eversion, as for example in the capsalid monogenean *Neoentobdella garneri* (see Whittington and Kearn 2009, fig. 2) and, at the present time, in the absence of similar evidence for this ability in the microbothriids, it would seem sensible to regard their male terminal papillae as penises (protrusible but not eversible). *Dermophthirioides pristidis* has an unarmed penis papilla, but in *Dermophthirius* spp. the penis is armed with variously arranged spines. *Dermopristis paradoxus* is unique in this respect in possessing no recognisable male copulatory organ and no spines.

The distal region of the male reproductive tract of *D. paradoxus* is a wide tube with a highly folded wall and a spacious lumen (Fig. 4) with a relatively large opening on the ventral surface. It is conceivable that this tube might extend by turning inside out in the manner of a cirrus, but there is no evidence from any of the specimens that this is the case. Even if it were capable of eversion, the vagina has a relatively tiny opening on the ventral surface and a diminutive distal lumen (Fig. 6B, C) and would be incapable of accepting a male copulatory organ of reasonable size. Nevertheless, the expanded proximal region of the vagina functions as a seminal receptacle and frequently contains sperm (Fig. 7).

The proximal tubular region of the male tract is likely to receive sperm from the vas deferens via the ejaculatory duct, but there is also a major glandular contribution to the contents of the male tract (see Fig. 6A, B). This secretion may have two, possibly more, sources – the wall of the proximal end of the proximal male tube and the highly folded lining of the distal male tube. This raises the possibility that *D. paradoxus* assembles a spermatophore in the distal male tube, but, if so, it seems likely to be too large to be accepted by the vagina. However, the capsalid monogenean *Entobdella soleae* is able to withdraw sperm into an extremely narrow distal vagina from the centre of a relatively large jelly-like spermatophore attached superficially to the parasite's ventral surface (Kearn 1970). No externally attached spermatophores were found in any of the specimens of *D. paradoxus*.

The close proximity of the openings of the male tract and the vagina in *D. paradoxus* (Fig. 6B) indicates that self insemination may take place, perhaps as the only means of insemination or as a fall-back position in the absence of a sexually mature neighbour. Self insemination is known to take place in other monogeneans (see for example Kearn and Whittington 1992). Although *D. paradoxus* is cemented to a host denticle, this does not necessarily preclude locomotion to within mating distance of a receptive neighbour – the microbothriid *Leptocotyle minor* is capable of moving from one denticle to another and can cross inseminate (Kearn 1965). Resolution of the many questions raised by the unusual male reproductive system of *D. paradoxus* must await the opportunity to study these parasites alive.

Dermopristis paradoxus has another unusual feature. Parallel ridges with broad tops running in a roughly transverse direction are present on the ventral body surface from the level of the pharynx to the posterior end of the body (Figs 2, 3). There are no reports of similar ridges in previously published descriptions of microbothriids or in specimens of *Dermophthirioides pristidis*, *Leptocotyle minor*, *Pseudocotyle squatiniae* and *Pseudoleptobothrium aptychotremae* examined in the course of this study for comparative purposes. These ridges in *Dermopristis paradoxus* greatly increase the area of the ventral surface of the parasite but the function of this development is obscure.

It is noteworthy that, in each wholmount and in the sectioned specimen of *D. paradoxus*, a single host denticle was lodged in the haptor (Fig. 2). Each of these denticles was most probably torn out of the host's skin when the parasite was dislodged by the collector, indicating that the bond between the parasite and the denticle is stronger than the bond between the denticle root and the host's skin. It seems likely that the cement secreted by the parasite binds the haptor to the denticle as in *L. minor* (see Kearn 1965). The presence of detached denticles in the haptors of all the collected specimens, including those from the mouth, implies that denticles are also present in the mouth lining.

The diet of *L. minor* is host epidermis which can be reached between the host's denticles (Kearn 1965). Presumably other

microbothriids feed in the same way. The epidermis of some fish species contains no pigment and the gut contents of their parasites are colourless, but Kearn (1979) found brown pigment (melanin?) in the epidermis of the shovel-nosed shark, identified as *Aptychotrema banksi* (now *A. rostrata*), and in the gut contents of all adult specimens of the microbothriid *P. aptychotremae* collected from this host. The gut contents of most of the specimens of *D. paradoxus* lack pigment, indicating either that their feeding sites on *Pristis microdon* were pigment free or that any ingested pigment had been egested prior to preservation. The presence of gut pigment in one specimen of *D. paradoxus* indicates that epidermal pigment is present in at least one site on the host.

Superficially, the pharynx of *D. paradoxus* resembles that of another epidermal feeder, namely the capsalid, *Entobdella soleae* (see Kearn 1963). In both parasites the pharynx lies in a cavity inside the head and possesses papillae projecting into the pharyngeal lumen. However, there are few other similarities. In *E. soleae* the mouth is ventrally located at the level of the anterior end of the pharynx, while in *D. paradoxus* there is a lengthy pre-pharynx and buccal cavity leading to the sub-ventral mouth. During feeding *E. soleae* everts its pharynx through the mouth (Kearn 1963). In *D. paradoxus* the cavity enclosing the anterior region of the pharynx indicates that the parasite may do the same, but, if so, the pharynx must travel much further to emerge from the mouth. Powerful muscles attached to the lateral borders of the pharynx of *D. paradoxus* and running in a posterolateral direction appear well-suited to retract a protruded pharynx. In *E. soleae* the wall of the pharynx contains large gland cells, each of which opens at the distal tip of a pharyngeal papilla, but in *D. paradoxus* sections failed to reveal corresponding cells in the papillae, or indeed elsewhere in the wall of the pharynx. Moreover, no prominent gland cells were located in sections of the pre-pharyngeal and buccal regions. Perhaps the gut caeca are the source of any secretions required to dislodge host epidermal cells and commence the process of extracorporeal digestion, if such a process takes place.

In this study it was necessary to use serial resin sections to confirm anatomical details that were not clearly visible in the whole mounts. Unfortunately, no preserved but unmounted specimens were available for embedding and so a mounted specimen was released from the slide by soaking in xylene to remove the mountant (Canada balsam) and subsequently embedded in resin and sectioned. This technique was found to be successful, providing stained serial sections of high quality (see Figs 3, 6, 7). The technique is recommended as an extra source of anatomical information in situations where only specimens on slides are available for study.

Acknowledgements. We are most grateful to Julian Baggio, Senior Aquarist, Cairns Marine Aquarium Fish, Cairns, Queensland, Australia for donating microbothriids. We also thank Dr Pat Pilitt for the loan of specimens of *Dermophthirioides pristidis* from the USNPC. Financial support for this study was provided by Australian Research

Council grant no. DP0556780 (2005-07) awarded to IDW and Professor Steve Donnellan (Evolutionary Biology Unit, South Australian Museum).

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(Accepted January 20, 2010)