

Trimusculotrema heronensis sp. nov. (Monogenea, Capsalidae) from the skin of the pink whipray Himantura fai (Elasmobranchii, Dasyatidae) from Heron Island, Queensland, Australia

Ian D. Whittington^{1,2*} and Graham C. Kearn³

¹Monogenean Research Laboratory, Parasitology Section, The South Australian Museum, North Terrace, Adelaide, South Australia 5000, Australia; ²Marine Parasitology Laboratory, School of Earth and Environmental Sciences (DX 650 418), The University of Adelaide, North Terrace, Adelaide, South Australia 5005, Australia; ³School of Biological Sciences, University of East Anglia, Norwich, Norfolk NR4 7TJ, UK

Abstract

Trimusculotrema heronensis sp. nov. is described from the skin of the pink whipray, *Himantura fai*, caught at Heron Island on the Great Barrier Reef, Queensland, Australia. The parasite differs from its closest relative, *T. uarnaki*, by its greater size and by features of the cirrus. There is evidence that the haptor of *T. heronensis* secretes cement. The living parasite is unable to swim. Whether *Trimusculotrema* spp. are benedeniines or entobdellines is discussed.

Keywords

Platyhelminthes, Monogenea, Capsalidae, Trimusculotrema, subfamilial status, ectoparasites of rays

Introduction

In February 1991, examination of the skin surfaces of a stingray identified as a pink whipray, Himantura fai Jordan et Seale (Dasyatidae), from Shark Bay, Heron Island, Queensland, Australia revealed a single specimen of a capsalid monogenean in Trimusculotrema Whittington et Barton, 1990. There are no previous records of species in this genus from fishes off Heron Island. A total of 33 specimens of H. fai was examined by IDW between 1987 and 1991, during five separate visits to Heron Island, but only a single specimen of the monogenean described in this paper was found. Since 1991, another 32 specimens of *H. fai* at Heron Island have been examined for Monogenea by IDW during on-going parasitological studies (e.g. collaborations with Drs L.A. Chisholm, B.W. Cribb and P.R. Last; teaching Parasitology to undergraduate students in field courses). Despite these activities, no further specimens of *Trimusculotrema* have been recovered from Heron Island. We appreciate that a descriptive study based on a single parasite specimen is not ideal. It was possible, however, to conduct a detailed study of the anatomy of this living specimen using phase contrast microscopy and photomicrography. Furthermore, its anatomy is distinctive. Brief reference has already been made to this parasite as *Trimusculotrema* sp. in the following: Kearn (1994, see his Fig. 4E); Whittington and Last (1994, see their page 288); Kearn (1998, see pages 99–100 and his Fig. 5.7e), Kearn (1999, see his page S70); Whittington and Cribb (2001, see their page 164).

Materials and methods

During many visits to the Heron Island Research Station of the University of Queensland, Australia between 1987 and 2002, live specimens of *Himantura fai* (wingspans 51–87 cm) were captured by beach seine or hand line on a rising tide at Shark Bay. Fish were identified from descriptions in Grant (1987), by consultation with Dr Peter Last (CSIRO Marine and Atmospheric Research, Hobart, Tasmania) and by reference to Last and Stevens (1994) and Whittington and Last (1994). Immediately after capture, live stingrays were placed in a large concrete pool (capacity: 7500 l) containing flow-through sea water for no longer than five days before examination for monogeneans. Rays were killed by pithing. Using a scalpel blade, skin scrapings from dorsal and ventral surfaces of ray specimens were placed in separate glass Petri dishes containing filtered sea water (FSW; filtered through two sheets of Whatman No. 1 filter paper) and examined for parasites using

a stereomicroscope with transmitted illumination. The anatomy of the single specimen found was studied alive while partially flattened beneath a coverslip and viewed using bright field and phase contrast microscopy. Extensive use was made of bright field photomicrography. When studies of the live parasite were complete, the specimen was flattened and preserved beneath a coverslip in 10% buffered neutral formalin at room temperature (24°C), stained with Ehrlich's haematoxylin, dehydrated in an ethanol series, cleared in methyl salicylate and mounted in Canada balsam. The flattened whole mount was examined using a compound microscope equipped with phase contrast optics and a drawing tube. Measurements were made using a computerised digitising system similar to that described by Roff and Hopcroft (1986). Unless otherwise indicated, measurements are presented in micrometres. For paired structures (e.g. posterior hamuli, anterior attachment organs, testes), measurements of each structure are given separately, followed by the mean in parentheses. Where measurements are presented in paired sets separated by a multiplication sign, the first figure is length, the second width. Haptor terminology for capsalids follows Whittington et al. (2001).

Comparison was made with 7 specimens of *Trimusculotrema uarnaki* from the personal collection of Dr Ian Whittington (7 of the 11 paratypes given by Whittington and Barton 1990 as in the 'collection of senior author'; these slides are etched as CAP 39–41; CAP 43–45; CAP 48). This material is now deposited as paratypes in The Australian Helminthological Collection, Parasitology Section, The South Australian Museum, North Terrace, Adelaide 5000, South Australia, Australia (SAMA AHC; contact: Dr Ian Whittington) as AHC 29482–AHC 29488 (7 slides, 1 specimen per slide). The single specimen (holotype) of the proposed new species is also deposited in the Australian Helminthological Collection (AHC 29481).

Results

Capsalidae Baird, 1853 Benedeniinae Johnston, 1931 (but see Discussion)

Trimusculotrema heronensis sp. nov. (Figs 1–7)

Type host and locality: *Himantura fai* Jordan and Seale (Dasyatidae) (pink whipray); Heron Island (23°27′S, 151°55′E), Great Barrier Reef, Queensland, Australia.

Site on host: Ventral skin surface.

Infection details: One of 65 stingrays infected (prevalence 1.54%) between November 1987 and November 2002; intensity 1 adult specimen. The only specimen of this new taxon was collected on 26 February 1991 from a female *H. fai* with a wingspan of 69 cm.

Origin of name: The species name refers to the type-locality, Heron Island, a small coral cay at the southern end of the Great Barrier Reef, Queensland, Australia.

Holotype: SAMA AHC 29481 (1 whole mount).

Description (Figs 1-7): Trimusculotrema sensu Whittington et Barton, 1990. Based on single, sexually mature specimen studied alive (Fig. 1) and following preservation as wellflattened whole mount (Fig. 2); measurements from well-flattened, preserved whole mount. Total length including haptor 5.753 mm; maximum breadth at level of testes 3.754 mm (Figs 1 and 2). Haptor oval 1.677 × 1.422 mm, aseptate; notch in haptor margin (see Figs 1, 2 and 3A) considered abnormal. Ventral surface of haptor bearing radially arranged papillae, circular (diameter 24–46) or oval $(38 \times 24–56 \times 38)$ (Figs 1, 2 and 3A), lacking associated sclerites or petal-like extensions. Papillae tend to increase in size and adopt a more oval shape from margin of haptor towards centre, but papillae absent in region of peduncular connection (Fig. 3A). Lengths of median haptoral sclerites as follows: accessory sclerite (one of pair absent, Figs 2 and 3A; considered abnormal) 78 (n = 1), proximal bifid notch ill-defined (Fig. 3B), no tendons observed associated with accessory sclerite; two anterior hamuli 56, 56 (56, n = 2) respectively (Fig. 3C); two posterior hamuli 46, 48 (47, n = 2) respectively (Fig. 3D). Fourteen hooklets distributed around haptor periphery (Fig. 3A, E); posterior-



Fig. 1. *Trimusculotrema heronensis* sp. nov. in ventral view. Composite image of nine bright field photographs of the live single specimen reported here. Scale bar = 1 mm

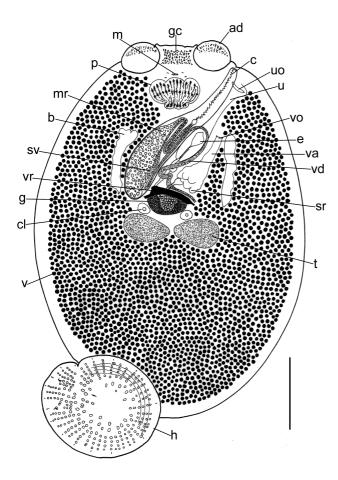


Fig. 2. *Trimusculotrema heronensis* sp. nov. in ventral view. Drawn from the single specimen (holotype): ad – adhesive disc, b – excretory bladder, c – cirrus, cl – cell resembling gland of Goto, e – egg in ootype, g – germarium, gc – gland cells, h – haptor (see Fig. 3 for detail), m – mouth, mr – male accessory gland reservoir, p – pharynx, sr – seminal receptacle, sv – seminal vesicle, t – testis, u – uterus, uo – uterine opening (dorsal), v – vitellarium, va – vagina, vd – vas deferens, vo – vaginal opening (ventral), vr – vitelline reservoir. Scale bar = 1 mm

most pair (hooklets II, see Llewellyn 1963 for numbering system) between posterior hamuli. Distances between adjacent hooklets increase in posterior-anterior direction. Hooklets located at a distance from haptor margin, posterior hooklets approximately 38 from haptor edge, anterior hooklets approximately 62 from edge. Hooklets in line with rows of papillae (Fig. 3A). Most hooklets not flat, hence unsuitable for length measurements; lengths of two flat hooklets about 15 (Fig. 3E). Marginal valve absent; no marginal ribs on haptor. Three narrow circular muscle bands visible on right side only of haptor (Figs 2 and 3A); extra (fourth) band created for short distance by branching of inner band. Peduncle from body joining haptor centrally.

Two anterior attachment organs as saucer-like discs, almost circular 457×525 , 478×557 (468×541 , n = 2) respectively; anterior region of each disc glandular. Gland cells with weak affinity for Ehrlich's haematoxylin in anterior region of body between attachment discs (Fig. 2); because of opacity, these

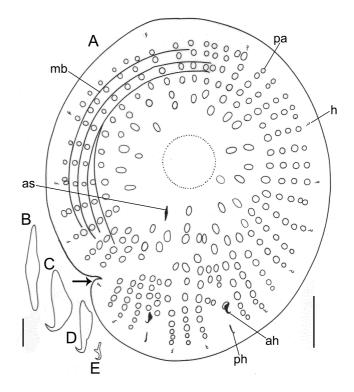


Fig. 3. Haptor and sclerites of *Trimusculotrema heronensis* sp. nov. **A.** Enlarged ventral view of haptor rotated into antero-posterior orientation. Broken circle: position of peduncle joining haptor to body. Arrow: notch in haptor margin, considered abnormal; ah – anterior hamulus, as – accessory sclerite (one of pair missing), h – hooklet, mb – muscle band, pa – papilla, ph – posterior hamulus. **B.** Accessory sclerite. **C.** Anterior hamulus. **D.** Posterior hamulus. **E.** Hooklet. Scale bars = 250 μm (A), 25 μm (B-E)

gland cells are conspicuous in the living animal viewed by transmitted light (Figs 1 and 4); ducts not observed. Ventral surface underlying gland cells bears narrow convoluted ornamentations (ridges?) resembling human fingerprint (Fig. 5). Eyes two pairs, dorsal, pigment shielded, immediately anterior to pharynx; no lens remnants observed. Mouth ventral, median, at level of eyes. Pharynx 494 × 810. Intestinal caeca dendritic anteriorly laterally and medianly; posterior confluence not determined. Excretory bladders conspicuous (Figs 1, 2 and 4), orientated along longitudinal body axis at level of male copulatory apparatus, ootype and vagina.

Reproductive system shown in Figure 2 and enlarged in Figure 6; general plan clear in live specimen (Fig. 1). Arrangement of reproductive organs and associated ducts as in other *Trimusculotrema* spp. (e.g. see Whittington and Barton 1990). Testes ovoid, juxtaposed, relatively small, 331×577 , 354×600 (342×588 , n = 2) respectively. Glands of Goto not observed in posterior angle between testes but two large conspicuous, uninucleated cells resembling glands of Goto located one on each side of germarium, immediately anterior to each testis (Fig. 2); no ducts observed from these cells. Vasa efferentia not observed in whole mount. Vas deferens narrow proximally following course shown in Figure 6. Male copu-

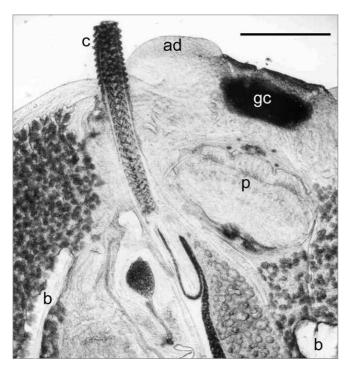


Fig. 4. Anterior region of *Trimusculotrema heronensis* sp. nov. photographed alive (bright field optics) in dorsal view, showing gland cells (gc) between anterior adhesive discs (ad); b – excretory bladders, c – cirrus, p – pharynx. Scale bar = 500 μ m

latory organ a cirrus (see below). Vas deferens enters double-walled cirrus sac dorsally, travels proximally, widening to form narrow reservoir (seminal vesicle?) containing droplets ranging in diameter from 3 to 9, together with finer granular material in places; sperm not identified in seminal vesicle. Cirrus sac also contains capacious elongate male accessory gland reservoir (termed 'spermatophore matrix reservoir' by Whittington and Barton 1990), containing prominent droplets (16 to 53 in diameter) and granular matrix; receives narrow

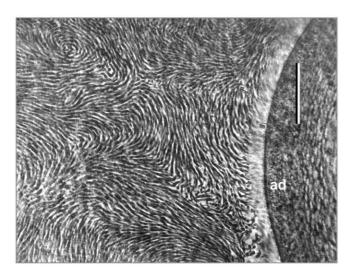


Fig. 5. Ornamentation (ridges?) on ventral surface of *Trimusculotrema heronensis* sp. nov. between anterior adhesive discs (ad). Phase contrast image. Scale bar = $50 \mu m$

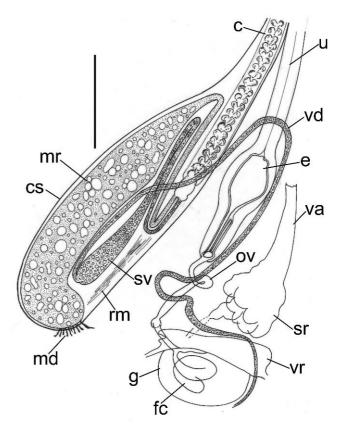


Fig. 6. Semi-diagrammatic, enlarged ventral view of most of the reproductive system of *Trimusculotrema heronensis* sp. nov.: c – cirrus in uneverted position, cs – cirrus sac, fc – fertilisation chamber, md – ducts of male accessory gland, ov – ovo-vitelline duct, rm – cirrus retractor muscle (?). Other lettering as in Figure 2. Scale bar = 500 μm

ducts from presumed male accessory glands entering cirrus sac proximally but gland cells not observed. Ducts from seminal vesicle and accessory gland reservoir run parallel and enter short chamber communicating with proximal end of cirrus (Fig. 6). Male pore through which cirrus everts ventral, submarginal, near left body margin (Fig. 2). Lining of uneverted cirrus bears ridges (Figs 1 and 6); as cirrus everts, ridges transported to outer surface of cirrus where they appear roughly transversely orientated with respect to cirrus (Fig. 7A); ridges project from everted cirrus in proximal direction, like eaves of roof or posterior margins of segments of craspedote tapeworm (Fig. 7A). There are indications that ridges are spirally arranged and continuous (Fig. 7A). Diameter of everted cirrus 152; length of everted region of cirrus bearing ridges 998.

Germarium with large, central fertilisation chamber containing at least 75 ripe oocytes giving rise to oviduct, receiving common vitelline duct to become ovo-vitelline duct (Figs 2 and 6). Vitelline reservoir immediately anterior to germarium. Ootype at level of excretory bladders. Uterine pore separate from male pore, capacious in whole mount and opening dorsally near left body margin, just posterior to male pore at level of eyes and mouth (Fig. 2). No distinct sphincter ob-

served in association with uterine pore. Vagina thick walled, with voluminous proximal region bearing seven roughly spherical seminal receptacles in living animal (Figs 2 and 6); receptacles less distinct in whole mount. Single short duct connects proximal region of vagina with anterodorsal region of vitelline reservoir. From large proximal region, vagina runs anterolaterally for short distance, narrows before opening ventrally between mid-line and left body margin at level of ootype (Fig. 2). Vitelline follicles extend from level of pharynx to posterior end of body proper; not extending anterior to eyes (Figs 1 and 2).

No free eggs observed; one egg in ootype of flattened whole mount seen in side view; roughly triangular; total capsule length 198, capsule breadth 126; appendage folded back on itself, total length 499 (Figs 1 and 6).

Observations on the living parasite (Fig. 1): *Trimusculotrema heronensis* attached itself to a glass surface by means of the haptor. When the edge of the haptor was lifted using a fine needle, the haptor did not detach immediately from the glass. It was necessary to peel off the haptor, which was still firmly attached when about one third of the haptor surface was free of the substrate.

There were no indications that the fully detached parasite could swim.

Differential diagnosis: *Trimusculotrema heronensis* is significantly larger (total length 5.753 mm) than the four other species of *Trimusculotrema*, namely *T. micracantha* (Euzet et Maillard, 1967) Whittington et Barton, 1990 (total length 2–3 mm; see Euzet and Maillard 1967), *T. leucanthemum* (Euzet et Maillard, 1967) Whittington et Barton, 1990 (also described from a single specimen; total length 1.65 mm; see Euzet and Maillard 1967), *T. uarnaki* Whittington et Barton, 1990 (total length 1.432–2.661 mm; see Whittington and Barton 1990)

and T. schwartzi Dyer et Poly, 2002 (total length 0.9-3.425 mm; see Dyer and Poly 2002). Trimusculotrema heronensis is readily distinguished from T. micracantha by the vagina, which in the former opens at the level of the ootype and in the latter opens close to the left anterior adhesive disc (Euzet and Maillard 1967). Each haptor papilla of T. leucanthemum is surmounted by a central circular sclerite and surrounded by 11–13 thin petal-like extensions, creating the appearance of a flower (Euzet and Maillard 1967). The haptor papillae of T. heronensis have no sclerites or petal-like extensions. Moreover, the haptor margin of T. leucanthemum has equally spaced radial ribs, not present in T. heronensis. Trimusculotrema schwartzi is readily distinguished from T. heronensis by the following features: the anterior hamuli of T. schwartzi are longer (mean 114, range 60–205) compared with 56 in T. heronensis; T. schwartzi has no pigment shields associated with the eyes; in T. schwartzi, the two large cells resembling glands of Goto occupy a more median position between the testes and germarium; no ridges were described on the cirrus of T. schwartzi. Trimusculotrema heronensis is most similar to T. uarnaki but, with the exception of the lengths of the haptor sclerites, anatomical measurements of the former parasite are significantly larger. The everted cirruses of *T. heronensis* and T. uarnaki bear transverse ridges, but those of T. heronensis appear to be continuous and spirally arranged and resemble the overlapping posterior margins of the segments of a craspedote tapeworm (Fig. 7A), whereas no spiral pattern was detected on the cirrus of T. uarnaki and the transverse ridges are narrow and appear to be incomplete (Fig. 7B, C). Trimusculotrema heronensis is parasitic on the ventral skin surface of the stingray, *Himantura fai* (Dasyatidae), known as the pink whipray.

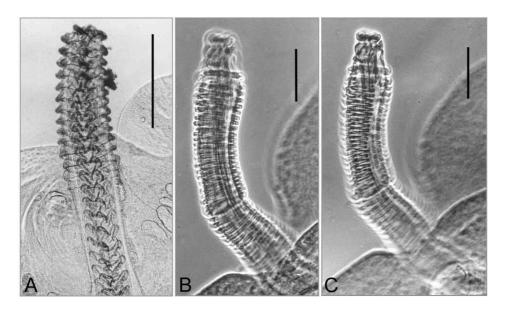


Fig. 7. The everted cirruses of A – *Trimusculotrema heronensis* sp. nov. photographed alive (bright field optics) in dorsal view and of B and C – T. uarnaki Whittington et Burton, 1990, and for comparison also in dorsal view, photographed from a preserved and mounted specimen viewed with phase contrast optics in two different focal planes. Scale bars = 250 μ m (A), 50 μ m (B, C)

Discussion

In spite of an intensive search of many individual specimens of the pink whipray, *Himantura fai*, at Heron Island over a period of 15 years, only one adult specimen of the skin parasitic monogenean *Trimusculotrema heronensis* has been found. However, this single parasite specimen was alive and in excellent condition (Fig. 1). It not only has a different host species but is significantly larger than the four other known species of *Trimusculotrema*, namely *T. micracantha* (Euzet et Maillard, 1967) Whittington et Barton, 1990, *T. leucanthemum* (Euzet et Maillard, 1967) Whittington et Barton, 1990 (also known only from one specimen), *T. uarnaki* Whittington et Barton, 1990 and *T. schwartzi* Dyer et Poly, 2002. Moreover, other features, particularly of the vagina, cirrus and haptor papillae, readily distinguish *T. heronensis* from the other species of *Trimusculotrema*.

There is uncertainty as to whether *Trimusculotrema* spp. belong to the Benedeniinae Johnston, 1931 or to the Entobdellinae Bychowsky, 1957. Whittington and Barton (1990) regarded them as benedeniines but the possibility that Trimusculotrema spp. may belong to the Entobdellinae was mentioned by Kearn et al. (2007). The reason for this systematic uncertainty relates to the absence of what is regarded as the most reliable difference between benedeniines and entobdellines, namely the route taken by the two tendons running into the haptor from extrinsic muscles at the posterior end of the body. In benedeniines and entobdellines, each of these tendons passes through a posterior notch in an accessory sclerite, but in benedeniines the tendon runs out into the haptor and attaches to the base of the ventral haptor tegument, while in entobdellines this tendon typically attaches to the anterior end of the anterior hamulus. In Trimusculotrema spp., all of the median haptor sclerites (accessory sclerites, anterior and posterior hamuli) are greatly reduced in size (e.g. Figs 2 and 3), the notch in the accessory sclerite is barely discernible and there is no trace of tendons associated with the accessory sclerites. The problem is exacerbated by other anatomical features: anterior attachment discs are generally regarded as features of benedeniines while the presence of haptor papillae is a feature of entobdellines. In addition, benedeniines are primarily, possibly exclusively, parasites of teleosts (Yamaguti 1963, Whittington 2004), while elasmobranchs are the principal hosts for entobdelline monogeneans except for Entobdella spp. which mostly parasitise teleost flatfishes (Kearn et al. 2007). As pointed out by Whittington and Barton (1990), the similar anatomy of benedeniines and entobdellines could reflect their similar life styles leading to convergent evolution, and features such as adhesive discs could have evolved independently in entobdellines as well as in benedeniine monogeneans. The application of molecular techniques may be the only way to solve this dilemma.

In entobdellines, the fully developed extrinsic body muscles and their tendons serve to generate suction by lifting the anterior ends of the anterior hamuli and thereby raising the roof of the cup-shaped haptor in which the shafts of the hamuli are embedded (Kearn 1964). A valve around the margin of the haptor prevents any influx of seawater into the cup when its roof is lifted. Presumably the haptor of a benedeniine functions in a similar way, except that the haptor roof is lifted directly by the muscle/tendon system. Trimusculotrema has abandoned this system, having lost the tendons and their muscles and has greatly reduced median haptor sclerites. It is known that Entobdella soleae has a second method of generating haptor suction using the intrinsic muscles of the haptor rather than the extrinsic muscle/tendon/sclerite system (Kearn 1988). As suggested by Whittington and Barton (1990), Trimusculotrema spp. may have become dependent on the intrinsic muscles of the haptor to generate suction, permitting a reduction of the extrinsic muscle/tendon/sclerite system. However, the absence of a marginal valve suggests that the haptor of Trimusculotrema does not generate suction for attachment and the notch (regarded as abnormal) in the haptor margin of T. heronensis also seems likely to prevent an adequate seal at this point. Our observations on the single healthy living specimen of *T. heronensis* indicate that an adhesive secretion may be used for haptor attachment. The use of adhesive secretion for haptor attachment, with associated reduction of haptor sclerites has also been adopted by other monogeneans, such as Leptocotyle minor (see Kearn 1965), Hamatopeduncularia spp. (see Kearn and Whittington 1994) and Neocalceostomoides brisbanensis (see Kearn et al. 1995).

Within the cirrus sac of *T. heronensis*, the male accessory gland reservoir and the seminal vesicle contain droplets and finely granular material. The droplets in the accessory gland reservoir were mostly larger than those in the seminal vesicle (Fig. 1). Granular material is described by Whittington and Barton (1990) in the 'spermatophore matrix reservoir' (= male accessory gland reservoir) of T. uarnaki and is visible in their fig. 13, a photograph of a living animal. Bullard et al. (2004) found similar material in the male accessory gland reservoir of the capsalid monogenean *Listrocephalos corona*. The origins and function of this material are obscure. In T. heronensis, the gland ducts entering the proximal end of the cirrus sac and communicating with the male accessory gland reservoir are too narrow to accommodate droplets of the size found in the reservoir, indicating perhaps that the droplets condense after the male accessory secretion enters the reservoir. The droplets in the seminal vesicle are small enough to enter via the vas deferens but none were found here. Like the droplets in the male accessory gland reservoir, they may condense after entering the seminal vesicle from material produced by the testes. It is also possible that handling the living animal may result in reflux into the seminal vesicle of some of the contents of the accessory gland reservoir and the partial trituration of the larger droplets from the reservoir.

It is known that juveniles and adults of the entobdelline monogenean *Neoentobdella natans* Kearn et Whittington, 2005 from the skin of the stingray *Pastinachus sephen* (Dasyatidae) and of *N. parvitesticulata* Kearn et Whittington, 2005 from the skin of *H. fai* at Heron Island are able to swim freely by undulating the body when fully detached from the host (Kearn

and Whittington 1991, as *Entobdella* sp. for *N. natans*; Kearn and Whittington 2005 for *N. parvitesticulata*). There were no indications that the fully detached living specimen of *T. heronensis* could swim.

Acknowledgments. We are indebted to Di Barton, Leslie Chisholm, Marnie Horton, Margaret Kearn, Sally and Ray Roth and numerous undergraduate students enrolled between 1994 and 2001 in Parasitology Field Studies at The University of Queensland for help with collecting rays at Heron Island. We appreciate the access to infrastructure and facilities at the Heron Island Research Station (HIRS) of The University of Queensland. Financial support for this investigation was provided by Australian Research Council (ARC) grant no. A191941 awarded to both authors in 1991, grant nos. A18716336 (1988-89), A19130175 (1992-94) and A19231545 (1993-95) awarded to IDW and grant no. DP0556780 (2005-07) awarded to IDW and Professor Steve Donnellan (Evolutionary Biology Unit, South Australian Museum). The visit by GCK to Queensland, Australia in 1990-91 was supported jointly by an Overseas Study Visit Grant from The Royal Society (UK) and a Travel Grant from The University of Queensland. GCK also gratefully acknowledges financial assistance from the Browne, Hill and Murray Committee of The Royal Society (UK) for a visit to HIRS.

References

- Bullard S.A., Payne R.R., Braswell J.S. 2004. New genus with two new species of capsalid monogeneans from dasyatids in the Gulf of California. *Journal of Parasitology*, 90, 1412–1427.
- Dyer W.G., Poly W.J. 2002. Trimusculotrema schwartzi n. sp. (Monogenea: Capsalidae) from the skin of the stingray Dasyatis zugei (Elasmobranchii: Dasyatidae) off Hong Kong, China. Systematic Parasitology, 51, 217–225. DOI: 10.1023/A:10 14538529942.
- Euzet L., Maillard C. 1967. Parasites de poissons de mer ouestafricaines, récoltés par J. Cadenat. VI. Monogènes de sélaciens. Bulletin de l'Institut Fondamental d'Afrique Noire, 29, 1435–1493.
- Grant E. 1987. Fishes of Australia.: E.M. Grant Pty Ltd., Scarborough, Australia, 480 pp.
- Kearn G.C. 1964. The attachment of the monogenean *Entobdella soleae* to the skin of the common sole. *Parasitology*, 54, 327–335.
- Kearn G.C. 1965. The biology of *Leptocotyle minor*, a skin parasite of the dogfish, *Scyliorhinus canicula*. *Parasitology*, 55, 473–480.
- Kearn G.C. 1988. Orientation and locomotion in the monogenean parasite *Entobdella soleae* on the skin of its host (*Solea solea*). *International Journal for Parasitology*, 18, 753–759. DOI: 10.1016/0020-7519(88)90115-4.
- Kearn G.C. 1994. Evolutionary expansion of the Monogenea. *International Journal for Parasitology*, 24, 1227–1271. DOI: 10.1016/0020-7519(94)90193-7.
- Kearn G.C. 1998. Parasitism and the Platyhelminths. Chapman and Hall, London, U.K., 544 pp.
- Kearn G.C. 1999. The survival of monogenean (platyhelminth) parasites on fish skin. *Parasitology*, 119, S57–S88.

- Kearn G.C., Whittington I.D. 1991. Swimming in a sub-adult monogenean of the genus *Entobdella*. *International Journal for Parasitology*, 21, 739–741. DOI: 10.1016/0020-7519(91) 90090-T
- Kearn G.C., Whittington I.D. 1994. Ancyrocephaline monogeneans of the genera *Chauhanellus* and *Hamatopeduncularia* from the gills of the blue catfish, *Arius graeffei*, in the Brisbane River and Moreton Bay, Queensland, Australia, with descriptions of four new species. *International Journal for Parasitology*, 24, 569–588. DOI: 10.1016/0020-7519(94)90149-X.
- Kearn G.C., Whittington I.D. 2005. Neoentobdella gen. nov. for species of Entobdella Blainville in Lamarck, 1818 (Monogenea, Capsalidae, Entobdellinae) from stingray hosts, with descriptions of two new species. Acta Parasitologica, 50, 32–48.
- Kearn G.C., Whittington I.D., Evans-Gowing R. 1995. Use of cement for attachment in *Neocalceostomoides brisbanensis*, a calceostomatine monogenean from the gill chamber of the blue catfish, *Arius graeffei*. *International Journal for Parasitology*, 25, 299–306. DOI: 10.1016/0020-7519(94)00142-B.
- Kearn G.C., Whittington I.D., Evans-Gowing R. 2007. A revision of *Entobdella* Blainville in Lamarck, 1818, with special emphasis on the nominal (type) species "*Entobdella hippoglossi* (Müller, 1776) Blainville, 1818" (Monogenea: Capsalidae: Entobdellinae) from teleost flatfishes, with descriptions of three new species and a new genus. *Zootaxa*, 1659, 1–54.
- Last P.R., Stevens J.D. 1994. Sharks and Rays of Australia. CSIRO Australia, Melbourne, Australia, 513 pp.
- Llewellyn J. 1963. Larvae and larval development of monogeneans. *Advances in Parasitology*, 1, 287–326.
- Roff J.C., Hopcroft R.R. 1986. High precision microcomputer based measuring system for ecological research. *Canadian Journal* of Fisheries and Aquatic Sciences, 43, 2044–2048.
- Whittington I.D. 2004. The Capsalidae (Monogenea: Monopisthocotylea): a review of diversity, classification and phylogeny with a note about species complexes. *Folia Parasitologica*, 51, 109–122.
- Whittington I.D., Barton D.P. 1990. A new genus of monogenean parasites (Capsalidae: Benedeniinae) from stingrays (Rajiformes: Dasyatidae) with a description of a new species from the long-tailed stingray *Himantura uarnak* Forsskål from Queensland, Australia. *Journal of Natural History*, 24, 327–340. DOI: 10.1080/00222939000770241.
- Whittington I.D., Cribb B.W. 2001. Adhesive secretions in the Platyhelminthes. Advances in Parasitology, 48, 101–224. DOI: 10.1016/S0065-308X(01)48006-7.
- Whittington I.D., Deveney M.R., Wyborn S.J. 2001. A revision of Benedenia Diesing, 1858 including a redescription of B. sciaenae (van Beneden, 1856) Odhner, 1905 and recognition of Menziesia Gibson, 1976 (Monogenea: Capsalidae). Journal of Natural History, 35, 663–777. DOI: 10.1080/002229301 52023090.
- Whittington I.D., Last P.R. 1994. Himantura fai Jordan & Seale (Myliobatiformes: Dasyatidae), from Heron Island and its monogenean parasite fauna. Memoirs of the Queensland Museum, 35, 285–289.
- Yamaguti S. 1963. Systema Helminthum. Vol. IV. Monogenea and Aspidocotylea. InterScience Publishers, New York, USA, 699 pp.