

Monocotylids (Monogenoidea) infecting elasmobranchs in Moreton Bay, Queensland, Australia, with descriptions of *Calicotyle cutmorei* n. sp. (Calicotylinae) and *Dendromonocotyle raiae* n. sp. (Monocotylinae)

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Received: 27 July 2020/Accepted: 25 September 2020/Published online: 31 October 2020 © Springer Nature B.V. 2020

Abstract Eighteen monocotylid species were collected from elasmobranchs during surveys of the parasites of fishes of Moreton Bay, Queensland, Australia. Two new species, *Calicotyle cutmorei* n. sp. (Calicotylinae) from *Carcharhinus sorrah* (Valenciennes) (Carcharhiniformes) and *Dendromonocotyle raiae* n. sp. (Monocotylinae) from *Hemitrygon fluviorum* (Ogilby) and *Neotrygon trigonoides* (Castelnau) (both Myliobatiformes) are described and illustrated. Six new faunal records for Moreton Bay are reported: *Thaumatocotyle australensis* Beverley-Burton &

This article was registered in the *Official Register of Zoological Nomenclature* (ZooBank) as

urn:lsid:zoobank.org:pub:6D54922D-954B-4DC9-B9C2-9BE63DF1A164. This article was published as an Online First article on the online publication date shown on this page. The article should be cited by using the doi number. This is the Version of Record.

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Williams, 1989 (Merizocotylinae) from Maculabatis toshi (Whitley) (Myliobatiformes); Monocotyle corali Chisholm, 1998 (Monocotylinae) from Pastinachus ater (Macleay) (Myliobatiformes); Neoheterocotyle rhynchobatis (Tripathi, 1959) Chisholm, 1994 (Heterocotylinae) from Glaucostegus typus (Anonymous [Bennett]) and Aptychotrema rostrata (Shaw) (both Rhinopristiformes); and Decacotyle elpora Marie & Justine, 2005 (Decacotylinae), Dendromonocotyle torosa Chisholm & Whittington, 2004 (Monocotylinae), and Clemacotyle australis Young, 1967 (Monocotylinae) from Aetobatus ocellatus (Kuhl) (Myliobatiformes). Maculabatis toshi is a new host record for T. australensis, and A. rostrata is a new host record for N. rhynchobatis. Ten species previously recorded from Moreton Bay were collected: Monocotyle caseyae Chisholm & Whittington, 2005 (Monocotylinae) and Heterocotyle whittingtoni Chisholm & Kritsky, 2020 (Heterocotylinae) from M. toshi; Monocotyle sp. A of Chisholm (1998a) (Monocotylinae) from H. fluviorum; Dendromonocotyle kuhlii Young, 1967 and Monocotyle kuhlii Young, 1967 (both Monocotylinae) from *N. trigonoides*; *Thaumatocotyle* cf. pseudodasybatis Hargis, 1955 (Merizocotylinae), Empruthotrema kearni Whittington, 1990 (Merizocotylinae) and Decacotyle octona Young, 1967 (Decacotylinae) from A. ocellatus; and Mycteronastes icopae (Beverley-Burton & Williams, 1989) Kearn & Beverley-Burton, 1990 (Merizocotylinae) and *Troglocephalus rhinobatidis* Young, 1967 (Dasybatotreminae) from *G. typus*.

Introduction

During January 2016, the senior author along with other specialists participated in a survey of the parasites infecting the fishes of Moreton Bay, Queensland, Australia. Previously, the occurrences of monogenoids infecting some beloniforms (Kritsky, 2018a), gerreids (Kritsky, 2018b), lutjanids and monodactylids (Kritsky 2019), and scorpaeniforms (Kritsky & Nitta, 2019) in the bay were published. The present paper, the fifth installment, examines the monocotylid fauna collected from elasmobranchs during the 2016 survey and during studies conducted by Dr Scott Cutmore during 2003 and 2005. In addition, unpublished host and geographical records of Neoheterocotyle rhynchobatis (Tripathi, 1959) Chisholm, 1994 (Monocotylidae: Heterocotylinae) in Moreton Bay are included.

Materials and methods

Elasmobranchs were collected from Moreton Bay, Queensland, Australia, by various methods during 2003, 2005 and 2016. The fishes were transported alive to the Moreton Bay Research Station located in Dunwich, North Stradbroke Island, Queensland, where they were euthanised, identified using Johnson (2010), and necropsied for parasitic infections. Methods for collection, preparation, illustration, and measurement of monogenoidean specimens were those of Kritsky (2018a). In the following species accounts, helminths indicated as infecting the "external surface" of their respective hosts were collected from body washes using hot ($\sim 60^{\circ}$ C) water; the specific infection site of these helminths on their hosts was not determined unless location was verified by direct observation. Measurements, all in micrometres, represented straight-line distances between extreme points and were expressed as the range followed by the mean and number (n) of structures measured in parentheses; body length included that of the haptor. Descriptions of the new species were based solely on designated type-specimens, except fragments of dissected specimens mounted in Gray & Wess medium (Humason, 1979) were occasionally used to obtain drawings of haptoral and copulatory sclerites. Scientific and common names of hosts were determined and verified in Froese & Pauly (2019) and Fricke et al. (2020), respectively. Type- and voucher specimens of helminths were deposited in the Queensland Museum (QM), Brisbane, Queensland, Australia; the Australian Helminthological Collection (AHC), South Australian Museum, Adelaide, South Australia; the Invertebrate Zoology Collection (USNM), National Museum of Natural History, Smithsonian Institution, Washington, D. C.; and the University of Nebraska State Museum, Harold W. Manter Laboratory (HWML), Lincoln, Nebraska.

Results

Current and previous records of monocotylids in Moreton Bay are presented in Table 1. Eighteen species of Monocotylidae were collected and reported in the present study. Two new species, six new faunal records for Moreton Bay, and two new host records were revealed. Descriptions of the two new species and additional data for the other 16 species follow.

Subclass Polyonchoinea Bychowsky, 1937 Order Monocotylidea Lebedev, 1988 Monocotylidae Taschenberg, 1879 Calicotylinae Monticelli, 1903

Calicotyle cutmorei n. sp.

Type-host: Carcharhinus sorrah (Müller & Henle) (Carcharhiniformes: Carcharhinidae), spot-tail shark. *Type-locality:* Moreton Bay near St. Helena Island, Queensland, Australia (27°22'S, 153°13'E), 11.iv.2003, 24.ii.2005.

Site on host: External surface near cloacal aperture. *Type-material*: Holotype, QM G238514; 2 paratypes, QM G238512, G238513; 2 paratypes, AHC 36752, 36753; 2 paratypes, USNM 1618964, 1618965. All adult specimens.

ZooBank registration: To comply with the regulations set out in Article 8.5 of the amended 2012 version of the International Code of Zoological Nomenclature (ICZN, 2012), details of the new species have been submitted to ZooBank. The Life Science Identifier (LSID) for Calicotyle cutmorei n. sp. is

Table 1 Monocotylids infecting elasmobranchs in Moreton Ba	ay, Queensland, Australia		
Parasite species	Host ^a	Site of infection	Reference
Calicotylinae Monticelli, 1903			
Calicotyle australis Johnston, 1934	Aptychotrema rostrata	Unknown	Young (1970)
	Glaucostegus typus	Ventral skin, cloaca, rectum	Whittington et al. (1989)
Calicotyle cutmorei n. sp.	Carcharhinus sorrah	External surface near cloacal aperture	ex nobis
Dasybatotreminae Bychowsky, 1957			
Troglocephalus rhinobatidis Young, 1967	Glaucostegus typus	Gills	Whittington et al. (2004); Kearn (1978); <i>ex nobis</i>
Decacotylinae Chisholm, Wheeler & Beverley-Burton, 1995			
Decacotyle elpora Marie & Justine, 2005 ^b	Aetobatus ocellatus	Gills	ex nobis
Decacotyle octona (Young, 1967)	Aetobatus ocellatus	Gills	Chisholm & Whittington (1998b); ex nobis
Euzetinae Chisholm & Whittington, 2001			
Euzetia occultum Chisholm & Whittington, 2001	Rhinoptera neglecta	Gills	Chisholm & Whittington (2001)
Heterocotylinae Chisholm, Wheeler & Beverley-Burton, 1995			
Heterocotyle chinensis Timofeeva, 1983	Hemitrygon fluviorum	Gills	Chisholm & Whittington (1996a)
	Himantura uarnak	Gills	Chisholm & Whittington (1996a)
Heterocotyle granulatae Young, 1967	Urogymnus granulatus	Gills	Young (1967)
	Himantura uarnak	Gills	Chisholm & Whittington (1996a)
Heterocotyle whittingtoni Chisholm & Kritsky, 2020	Maculabatis toshi	Gills	Chisholm & Kritsky (2020)
Neoheterocotyle rhinobatidis (Young, 1967)	Glaucostegus typus	Gills	Kearn (1978); Whittington et al. (2004)
Neoheterocotyle rhynchobatis (Tripathi, 1959) ^b	Glaucostegus typus	Gills	ex nobis
	Aptychotrema rostrata ^c	Gills	ex nobis
Merizocotylinae Johnston & Tiegs, 1922			
Empruthotrema dasyatidis Whittington & Kearn, 1992	Hemitrygon fluviorum	Nasal tissue	Whittington & Kearn (1992)
Empruthotrema kearni Whittington, 1990	Aetobatus ocellatus	Nasal tissue	Whittington (1990); ex nobis
Mycteronastes icopae (Beverley-Burton & Williams, 1989)	Glaucostegus typus	Nasal tissue	Kritsky et al. (2017a); Whittington et al. (2004a); Cribb et al. (2004); ex nobis
Thaumatocofyle australensis Beverley-Burton & Williams, 1989 ^b	Maculabatis toshi ^c	Nasal tissue	ex nobis
Thaumatocotyle cf. pseudodasybatis Hargis, 1955	Aetobatus ocellatus	Nasal tissue	Whittington (1990); ex nobis
Monocotylinae Taschenberg, 1879			
Clemacotyle australis Young, 1967 ^b	Aetobatus ocellatus	Gills	ex nobis
Dendromonocotyle kuhlii Young, 1967	Neotrygon trigonoides	Skin	Young (1967); ex nobis
Dendromonocotyle lasti Chisholm & Whittington, 2005	Maculabatis toshi	Dorsal skin, gills	Chisholm & Whittington (2005)
Dendromonocotyle raiae n. sp.	Hemitrygon fluviorum	External surface	ex nobis
	Neotrygon trigonoides	External surface	ex nobis
Dendromonocotyle torosa Chisholm & Whittington, 2004 ^b	Aetobatus ocellatus	External surface	ex nobis

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Parasite species	Host ^a	Site of infection	Reference
Monocotyle caseyae Chisholm & Whittington, 2005	Maculabatis toshi	Gills	Chisholm & Whittington (2005); ex nobis
	Himantura uarnak	Gills	Chisholm (1998a)
Monocotyle corali Chisholm, 1998b	Pastinachus ater ^c	Gills	ex nobis
Monocotyle granulatae Young, 1967	Urogymnus granulatus	Gills	Young (1967)
Monocotyle kuhlii Young, 1967	Neotrygon trigonoides	Gills; external surface	Young (1967); ex nobis
Monocotyle spiremae Measures, Beverley-Burton & Williams, 1990	<i>Himantura</i> sp.	Gills	Chisholm & Whittington (2005)
Monocotyle tritestis Young, 1967	Neotrygon trigonoides	Gills	Young (1967)
Monocotyle sp. A of Chisholm (1998)	Hemitrygon fluviorum	Gills	Chisholm (1998a); ex nobis
^a Scientific names of hosts are current and follow Fricke et al. (2020) ^b New faunal record for N	Moreton Bay; ^c New host record	

Table 1 continued

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Etymology: The species is named for our colleague and friend Dr Scott Cutmore, University of Queensland, in appreciation of his support of our studies on Australian monogenoids and who provided the specimens on which the description of the new species was made.

Description

[Based on 7 specimens; Figs. 1–7.] Body including haptor 3,870-4,050 (3,950; n = 5), dorsoventrally flattened; body proper with oval outline (Fig. 1), 3,530-3,910 (3,700; n = 5) long, greatest width 1,600-1,900 (1,720; n = 5) at level of testicular mass. Peduncle infrequently extended (Fig. 2). Cephalic region tapered anteriorly, terminally rounded, with large subterminal concavity having weak muscular rim. Cephalic lobes and cephalic-gland pores not observed. Eye-spots absent. Mouth located within subterminal cephalic concavity, flanked by 2 bilateral rounded lobes. Pharynx subspherical, 243-281 (264; n = 5) long, 265–299 (278; n = 5) wide, lying dorsoposterior to cephalic concavity; 2 bilateral groups of oesophageal-gland cells posterolateral to pharynx. Oesophagus short to absent. Caecal bifurcation immediately posterior to pharynx. Intestinal caeca 2, narrow, lacking diverticula, extending posteriad along internal margin of vitellarium, ending blindly posterior to testicular mass.

Haptor subcircular in outline, 955-1,540 (1,130; n = 7) in diameter, with 7 peripheral loculi (single interhamular peripheral loculus) and central loculus, each delimited by muscular septa; 1 pair of anchors; wide marginal valve delicate, folded ventrally toward center of haptor, with smooth undulating margin. Hooks absent in adult. Anchor 93–141 (120; n = 8) long, with short tapered recurved point arising perpendicularly from short robust tapered shaft, variably flattened superficial root, elongate rectangular and striated deep root (Figs. 3, 4).

Common genital pore midventral, immediately anterior to uterus (Fig. 7). Testicular mass 1,900–3,000 (2,300; n = 7) long, 1,200–1,600 (1,300; n = 5) wide, intercaecal, subovate, with truncate anterior margin. Origin of vas deferens from testicular mass not observed; seminal vesicle a simple dilation of distal vas deferens, forming an inverted U



Fig. 1 Whole-mount illustration of *Calicotyle cutmorei* n. sp. (composite, ventral view)

or J, with thick wall, giving rise distally to ejaculatory duct; ejaculatory duct entering base of proximal ejaculatory bulb, extending into distal ejaculatory bulb. Proximal ejaculatory bulb 70–80 (75; n = 5) wide, with 2 juxtaposed internal chambers; distal ejaculatory bulb 36–48 (42; n = 6) wide, capped by expanded base of male copulatory organ (MCO)

(Fig. 7). Prostates and prostatic reservoirs not observed. MCO 151–225 (193; n = 6) long, an inverted J-shaped sclerotised tube with expanded proximal end (Figs. 5, 6); proximal portion of MCO enclosed in cone-shaped compartment (Fig. 7).

Germarium convoluted, dorsoventrally looping right intestinal caecum (Fig. 1). Oviduct extending sinistrally to oötype where duct from seminal receptacle and common vitelline duct (not seen) presumably enter. Oötype proximal to uterus, apparently lacking glandular components. Mehlis' gland not observed. Uterus lying along body midline just posterior to common genital pore, 121-149 (135; n = 4) long, 110-134 (123; n = 4) wide, pestle or club shaped, with thick muscular wall. Bilateral vaginal pores unarmed, ventral just lateral to uterus. Paired vaginae delicate; each arising from respective lateral end of reniform vaginal chamber (Fig. 7). Vitellarium dense, comprising 2 wide dense bilateral bands along lateral margins of intestinal caeca; vitelline ducts present within vitellarium, departing from medial margins of vitellarium to form transverse vitelline duct; common vitelline duct not observed. Egg(s) absent in all specimens.

Remarks

Calicotyle cutmorei n. sp. is differentiated from all of its congeners, except *C. californiensis* Bullard & Overstreet, 2000 and *C. ramsayi* Robinson, 1961, by having haptoral anchors, each with comparatively slender deep roots and protruding superficial roots. In the remaining congeners, the deep root of the anchor is broad and generally stout, the superficial root is incorporated into the anchor base from which it only slightly protrudes, or anchors are absent. *Calicotyle cutmorei* with a comparatively short J-shaped MCO is easily differentiated from *C. ramsayi* which has an elongate coiled MCO with about 2 ¹/₂ rings (Robinson, 1961) and from *C. californiensis* which has an elongate coiled MCO with about two rings (Bullard & Overstreet, 2000).

Woolcock (1936) reported that *C. inermis* lacked haptoral "hooks." Assuming Woolcock (1936) was referring to the haptoral anchors rather than the 14 hooks, *C. inermis* was the only congener reported to lack anchors at that time. Chisholm et al. (1995) were unable to locate the type-specimens of *C. inermis* to confirm this observation, and as such they considered



Figs. 2–6 *Calicotyle cutmorei* n. sp. 2, Whole-mount specimen with folded haptor showing peduncle (ventral view); 3, 4, Anchors from 1 paratype showing variability; 5, Male copulatory organ (lateral view); 6, Male copulatory organ (ventral view). Parallel lines on Figs. 5 and 6 indicate respective limits of the dimension measured

C. inermis a valid species with uncertain generic assignment. Anchors were not described or depicted in the original description of *C. ramsayi* (see Robinson,

1961), but Chisholm et al. (1997) confirmed their presence in the holotype. Recently, *C. japonica* was described by Kitamura et al. (2010), who reported that



Fig. 7 Distal components of the reproductive system of *Calicotyle cutmorei* n. sp. (ventral view). *Abbreviations*: AVD, anterior vitelline duct; C, cone-shaped compartment enclosing the male copulatory organ; DEB, distal ejaculatory bulb; GP, common genital pore; MCO, male copulatory organ; OO, oötype; OV, oviduct; PEB, proximal ejaculatory bulb; PVD, posterior vitelline duct; SR, seminal receptacle; SV, seminal vesicle; TVD, transverse vitelline duct; U, uterus; V, vagina; VC, vaginal chamber

anchors were absent in adults of the species, suggesting that Woolcock's (1936) observations on *C. inermis* might be factual. Presence of anchors in members of the Monogenoidea is plesiomorphic and their absences in some species clearly represents secondary losses (Boeger & Kritsky, 1993, 2001).

Nybelin (1941) proposed *Gymnocalicotyle* Nybelin, 1941 as a subgenus of *Calicotyle* to accommodate *Calicotyle*-like species such as *C. inermis* that lacked an anchor pair, while Yamaguti (1963) subsequently elevated the taxon to full generic rank. However, no evidence currently exists to suggest that *Gymnocalicotyle* is valid, and a phylogenetic analysis of species comprising *Calicotyle* is currently lacking to support the division of *Calicotyle* as proposed by Nybelin (1941).

Chisholm et al. (1997) indicated that presence of 14 haptoral hooks in part served as a diagnostic feature of the Calicotylinae and confirmed their presence in several species of *Calicotyle* for which the hooks were not mentioned in the respective original descriptions. However, Kitamura et al. (2010) indicated that hooks were not evident in the single immature and five adult specimens comprising the type-series of *C. japonica*, and Rohde et al. (1992) reported that the 14 hooks

were seen only in immature specimens of *C. australiensis*. Hooks were not observed in our specimens (all adults) of *C. cutmorei*, suggesting that the absences of hooks in adults of *C. australiensis*, *C. japonica*, *C. cutmorei*, and possibly *C. inermis* represent one or more secondary losses, which would not justify a separate genus or subgenus to accommodate these species.

Dasybatotreminae Bychowsky, 1957

Troglocephalus rhinobatidis Young, 1967

Type-host: Rhinobatos batillum Whitley [now *Glaucostegus typus* (Anonymous [Bennett])] (Rhinopristiformes: Glaucostegidae), giant shovelnose ray.

Type-locality: Off Heron Island (23°27′S, 151°55′E), Queensland, Australia.

Previous records: G. typus (as *R. typus* or *R. batillum*): off Heron Island, Queensland, Australia (Young, 1967; Kearn, 1978; Chisholm & Whittington, 1996b, 2000, 2002; Chisholm, 1998b; Chisholm et al., 2001; Beverley-Burton in Lester & Sewell, 1989; Cribb et al., 2001; Watson, 1997; Mollaret et al., 1997); Moreton Bay off Dunwich, North Stradbroke

Island, Queensland Australia (27°30′S, 153°25′E) (Whittington et al., 2004b). *Present records: G. typus:* Moreton Bay off Peel Island

(27°30'S, 153°20'E), Queensland, Australia, 13–15. i.2016; Moreton Bay off Wynnum North (27°25'S, 153°11'E), Queensland, Australia, 18–22.i.2016. *Site on host*: Gills.

Specimens studied: 11 vouchers, QM G238457-G238461, G238463-G238466, G238471, G238472; 7 vouchers, AHC 36754-36756; 6 vouchers, USNM 1618958-1618960; 3 vouchers, HWML 216332, 216333.

Remarks

Although frequently recorded from the giant shovelnose ray off eastern Australia, the present finding of *T. rhinobatidis* on *G. typus* represents only the second faunal record of the species in Moreton Bay.

Decacotylinae Chisholm, Wheeler & Beverley-Burton, 1995

Decacotyle elpora Marie & Justine, 2005

Type-host: Aetobatus cf. *narinari* (Euphrasen) of the Indo-West/Central Pacific Ocean [now *Aetobatus ocellatus* (Kuhl), see White et al., 2010] (Myliobatiformes: Aetobatidae), ocellated eagle ray.

Type-locality: Off Ilôt Maître (near 22.34°S, 166.40°E), Nouméa, New Caledonia.

Previous records: There have been no published records of this parasite other than that of the original description by Marie & Justine (2005).

Present record: *A. ocellatus*: Moreton Bay near Port of Brisbane (27°23′S, 153°11′E), Queensland, Australia, 19.i.2016.

Site on host: Gills.

Specimens studied: Voucher, QM G238456; 2 vouchers, AHC 36757.

Remarks

The finding of *D. elpora* is a new faunal record for Moreton Bay.

Decacotyle octona (Young, 1967) Chisholm & Whittington, 1998

Syn. Papillicotyle octona Young, 1967

Type-host: Aetobatus narinari (Euphrasen) of the Indo-West/Central Pacific Ocean [now *Aetobatus ocellatus* (Kuhl), see White et al., 2010] (Myliobati-formes: Aetobatidae), ocellated eagle ray.

Type-locality: Off Heron Island, Queensland, Australia. *Previous records*: *A. ocellatus* (all as *A. narinari* of the Indo-West/Central Pacific Ocean): off Heron Island, Queensland, Australia (Young, 1967 as *P. octona*), Chisholm & Whittington, 1998b); off Ilôt Maître, Nouméa, New Caledonia (near 22.34°S, 166.40°E) (Marie & Justine, 2005); Moreton Bay, Queensland, Australia (Chisholm & Whittington, 1998b).

Present records: A. ocellatus: Moreton Bay near the Port of Brisbane (27°23'S, 153°11'E), Queensland, Australia, 19.i.2016; Moreton Bay off Green Island (27°25'S, 153°14'E), Queensland, Australia, 24.vi.2016. *Site on host:* Gills.

Specimens studied: 4 vouchers, QM G238467-G238470; 4 vouchers, AHC 36758, 36759; 3 vouchers, USNM 1618961.

Remarks

Decacotyle octona appears to be restricted to *A. ocellatus* in the western Pacific Ocean. Although two other monocotylids, *D. floridana* (Pratt, 1919) Chisholm & Whittington, 1998 and *Thaumatocotyle pseudodasybatis* Hargis, 1955 are recorded from eagle rays in both Pacific and Atlantic Oceans, *D. octona* has not been reported from the latter environs.

Heterocotylinae Chisholm, Wheeler & Beverley-Burton, 1995

Heterocotyle whittingtoni Chisholm & Kritsky, 2020

Type-host: Maculabatis toshi (Whitley) (Myliobatiformes: Dasyatidae), black-spotted whipray.

Type-locality: Moreton Bay near Dunwich, North Stradbroke Island (27°15′S, 153°15′E), Queensland, Australia.

Previous records: M. toshi: Moreton Bay near Dunwich, North Stradbroke Island (27°15′S, 153°15′E), Queensland, Australia; Moreton Bay off Peel island (27°30′S, 153°20′E), Queensland, Australia; Gulf of Carpentaria, near Weipa (12°35′11″S, 141°42'34″E), Queensland, Australia (all Chisholm & Kritsky, 2020).

Site on host: Gills.

Specimens studied: 3 paratypes, QM G238334-G238336.

Remarks

The three paratypes listed above were collected during the 2016 survey and are part of the type-series of the recently described *H. whittingtoni* Chisholm & Kritsky, 2020.

Neoheterocotyle rhynchobatis (Tripathi, 1959) Chisholm, 1994

Syns Horricauda rhynchobatis Tripathi, 1959; Horricauda rhynchobatidis of Kearn (1978) (lapsus)

Type-host: Rhynchobatus djiddensis (Forsskål) (Rhinopristiformes: Rhinidae), giant guitarfish.

Type-locality: Bay of Bengal, India.

Previous records: R. djiddensis: Bay of Bengal, India (Tripathi, 1959). *Glaucostegus typus:* off Heron Island, Great Barrier Reef Queensland, Australia (Chisholm & Whittington, 1997).

Current records: *G. typus*: Moreton Bay off Dunwich, North Stradbroke Island (27°30'S, 153°25'E), Queensland, Australia, 26.viii. 2002, 30.viii.2002, 29.vi.2005. Eastern shovelnose ray *Aptychotrema rostrata* (Shaw) (Rhinopristiformes: Trygonorrhinidae): Moreton Bay off Dunwich, North Stradbroke Island (27°30'S, 153°25'E), Queensland, Australia, 5.vii.2005. *Site on host*: Gills.

Remarks

The specimens of *N. rhynchobatis* reported here were collected from the gills of three *G. typus* and one *A. rostrata* from Moreton Bay by Chisholm during 2002 and 2005 and donated to colleagues for studies on the biology of monogenoids. Results of these studies and the geographical and host records were never published. The finding of *N. rhynchobatis* in Moreton Bay by Chisholm is first recorded here, and *A. rostrata* represents a new host record for the helminth. Unfortunately, voucher specimens of the species were not retained, but identification of the helminths was confirmed by Chisholm.

Chisholm & Whittington (1997) indicated that Kearn (1978) had previously recorded *N. rhynchobatis* on *G. typus* in Moreton Bay, but no such mention of the helminth was made by Kearn (1978) in this regard. Kearn (1978) only mentioned Tripathi's species as *Horricauda rhynchobatidis* (sic) in the discussion of his paper and in reference to Tripathi (1959) recording spines on the dorsal surface of the haptor.

Merizocotylinae Johnston & Tiegs, 1922

Empruthotrema kearni Whittington, 1990

Type-host: Aetobatus narinari (Euphrasen) of the Indo-West/Central Pacific Ocean [now *Aetobatus ocellatus* (Kuhl), see White et al., 2010] (Myliobati-formes: Aetobatidae), ocellated eagle ray.

Type-locality: Moreton Bay (27°10′S, 153°15′E), Queensland, Australia.

Previous record: There have been no other records of *E. kearni* since its original description by Whittington (1990).

Present record: A. ocellatus: Moreton Bay near the Port of Brisbane (27°23'S, 153°11'E), Queensland, Australia, 19.i.2016.

Site on host: Nasal tissue.

Specimens studied: 2 vouchers, QM G238486, G238487; voucher, AHC 36760.

Remarks

The three specimens collected during the present study were identified as *E. kearni* based on comparison of their MCOs with figure 3 in Whittington (1990). In addition, lengths of the MCO in the three specimens [98 (95–99; n = 3)] fell within the range (91–103) for those reported by Whittington (1990). The whole-mount drawing in the original description is stylised and does not conform to the general morphology of the helminth, although the overall description is adequate. In our specimens, the testis has a third lobe posterior to the two lobes shown in figure 1 of the original description. Whittington (1990) described the testis as "single, folded, U-shaped with deep median cleft" but apparently missed the posterior lobe lying beneath (or within) the posterior field of the vitellarium.

Based on published accounts of the species of *Empruthotrema*, Kritsky et al. (2017b) provided five diagrammatic representations of the patterns of the loculi, septa and hook distributions in the haptors of the described species. *Empruthotrema kearni* was shown to be the lone species where hook pairs 1 and 2 were associated with the single interhamular marginal

loculus (figure 6 in Kritsky et al., 2017b). Examination of present specimens, however, revealed that the pattern shown by Whittington (1990) in figure 1 of the whole mount was incorrectly depicted. Instead, the pattern in this species (based on present specimens) is that presented in figure 5 of Kritsky et al. (2017b) for four other described species (*E. chisholmae* Hernández-Orts, Ahuir-Baraja, Raga, & Montero, 2010, *E. dasyatidis* Whittington & Kearn, 1992, *E. stenophallus* Chisholm & Whittington, 2005, and *E. tasmaniensis* Chisholm & Whittington, 1999), where hooks of pair 2 are associated with the haptoral septa separating the interhamular loculus from the remaining marginal loculi.

Mycteronastes icopae (Beverley-Burton & Williams, 1989) Kearn & Beverley-Burton, 1990

Syn. *Merizocotyle icopae* Beverley-Burton & Williams, 1989

Type-host: Rhinobatos batillum Whitley [now *Glaucostegus typus* (Anonymous [Bennett])] (Rhinopristiformes: Glaucostegidae), giant shovelnose ray.

Type-locality: Off Heron Island (23°27′S, 151°55′E), Queensland, Australia.

Previous records: See Mollaret et al. (1997) and Kritsky et al. (2017a).

Present records: G. typus: Moreton Bay off Peel Island (27°30'S, 153°20'E), Queensland, Australia, 15.i.2016; Moreton Bay off Wynnum North (27°25'S, 153°11'E), Queensland, Australia, 18.i.2016.

Site on host: Nasal tissue.

Specimens studied: 13 vouchers, QM G238473-G238485; 9 vouchers, AHC 36761-36763; 7 vouchers, USNM 1422259-1422265; 9 vouchers, HWML 216334, 216335.

Remarks

Mycteronastes icopae is one of the more prevalent species infecting the giant shovelnose ray, having been reported repeatedly from this host off eastern Australia, including Moreton Bay. The species also has been found on the nasal tissues of *Glaucostegus thouin* (Anonymous [Lacépède]) occurring in Indonesian waters (Chisholm & Whittington, 2012).

Thaumatocotyle australensis Beverley-Burton & Williams, 1989

Syn. *Merizocotyle australensis* (Beverley-Burton & Williams, 1989) Chisholm, Wheeler & Beverley-Burton, 1995

Type-host: Himantura uarnak (Forsskål) (Myliobatiformes: Dasyatidae), honeycomb stingray.

Type-locality: Off Heron Island (23°27′S, 151°55′E), Great Barrier Reef, Queensland, Australia.

Previous records: H. uarnak: off Heron Island (23°27'S, 151°55'E), Great Barrier Reef, Queensland, Australia (Beverley-Burton & Williams, 1989); Buffalo Creek, Darwin, Northern Territory (as M. australensis) (Chisholm & Whittington, 1999). Himantura fai Jordon & Seale [now Pateobatis fai (Jordon & Seale)] (Myliobatiformes: Dasyatidae), pink whipray: Shark Bay, Heron Island, Queensland, Australia (as M. australensis) (Watson, 1997; Chisholm & Whittington, 1999). Himantura gerrardi (Gray) [now Maculabatis gerrardi (Gray)] (Myliobatiformes: Dasyatidae), sharpnose stingray: off Sematan, Sarawak (01°48'15.45"N, 109°46′47. 17"E), Malaysia (as M. australensis) (Chisholm & Whittington, 2012). Himantura cf. gerrardi (now Maculabatis gerrardi): off Sarawak (02°00'00.45"N, 110°37′60.00″E), Malaysia (as M. australensis) (Chisholm & Whittington, 2012).

Present records: Maculabatis toshi (Whitley) (Myliobatiformes: Dasyatidae): Moreton Bay off Green Island (27°25'S, 153°14'E), Queensland, Australia, 15.i.2016; Moreton Bay off Peel Island (27°30'S, 153°20'E), Queensland, Australia, 15.i.2016.

Site on host: Nasal tissue.

Specimen studied: Voucher, QM G238455; voucher, AHC 36764.

Remarks

This species was originally described as *T. australensis* by Beverley-Burton & Williams (1989). In their revision of the Monocotylidae, Chisholm et al. (1995) synonymised *Thaumatocotyle* Scott, 1904 and *Mycteronastes* Kearn & Beverley-Burton, 1990 with *Merizocotyle* Cerfontaine, 1894 and transferred *T. australensis* along with other species as new combinations to the latter genus based on a phylogenetic analysis of morphological characters. The synonymy of *Thaumatocotyle* with *Merizocotyle* was rejected by Neifar et al. (2000), who argued that haptoral morphology was important in defining genera within

the Monocotylidae. Chisholm et al. (2001) suggested that these genera could be resurrected in the future when their analysis based on 28S rDNA sequences showed Merizocotyle (sensu lato) to be paraphyletic. Nonetheless, Chisholm & Whittington (2012) continued to place Thaumatocotyle-like species in Merizocotyle. Although not directly challenging the synonymy of Thaumatocotyle with Merizocotyle, Kritsky et al. (2017a) resurrected Mycteronastes after their reanalysis of some of the characters used by Chisholm et al. (1995) to justify their proposed synonymies, which suggested that the patterns of loculi in species of the three genera might provide synapomorphies for each genus. Thus, the decision of Neifar et al. (2000) regarding the acceptance of Thaumatocotyle is followed here.

The finding of *T. australensis* on the nasal tissues of *M. toshi* in Moreton Bay represents a new host record for the parasite and a new fauna record for the bay.

Thaumatocotyle cf. *pseudodasybatis* Hargis, 1955 Syn. *Merizocotyle pseudodasybatis* (Hargis, 1955) Chisholm, Wheeler & Beverley-Burton, 1995

Type-host: Aetobatus narinari (Euphrasen) (Myliobatiformes: Aetobatidae), whitespotted eagle ray.

Type-locality: Alligator Harbor, Franklin County, Florida.

Previous Indo-Pacific records: Aetobatus ocellatus (Kuhl) (all as A. narinari of the Indo-West/Central Pacific Ocean), ocellated eagle ray: Moreton Bay (27°10'S, 153°15'E), Queensland, Australia (Whittington, 1990); off Heron Island, Queensland, Australia (Whittington in Lester & Sewell, 1989; Marie & Justine, 2006); off Ilôt Maître (near 22.34°S, 166.40°E), Nouméa, New Caledonia (Marie & Justine, 2005, 2006); off Ranguiroa, French Polynesia (Marie & Justine, 2006); Makassar Strait, Kota Baru (03°14′44.80″S, 116°13′23.80″E), South Kalimantan, Merizocotyle pseudodasybatis) Indonesia (as (Chisholm & Whittington, 2012). The records listed above are only for those of T. pseudodasybatis from the Indo-Pacific Ocean.

Present records: A. ocellatus: Moreton Bay near Port of Brisbane (27°23'S, 153°11'E), Queensland, Australia, 19.i.2016; Moreton Bay off Green Island

(27°25′S, 153°14′E), Queensland, Australia, 24.vii.2016.

Site on host: Nasal tissue.

Specimens studied: 6 vouchers, QM G238515-G238520.

Remarks

Until recently, the host of *T. pseudodasybatis* in the western Pacific Ocean was identified as *Aetobatus narinari*, which was considered to have a circumglobal distribution. Phylogenetic analyses using molecular data, however, suggested that *A. narinari* constituted a species complex comprising three distinct clades: a western and central Pacific clade, an eastern Pacific clade and a central Atlantic clade (Richards et al., 2009). White et al. (2010) then recognised *A. ocellatus* as a valid species representing the form occurring throughout much of the western Pacific Ocean, including eastern Australia. The phylogenetic hypotheses in White et al. (2010) also suggested that *A. narinari* (*sensu stricto*) represented the eagle ray occurring in the western Atlantic Ocean.

Two monocotylid species, Decacotyle floridana (Pratt, 1910) Chisholm & Whittington, 1998 and T. pseudodasybatis, were originally described from A. narinari from the western Atlantic Ocean and subsequently recorded from eagle rays (now A. ocellatus) in the western Pacific Ocean (Whittington, 1990; Chisholm & Whittington, 1998b; Marie & Justine, 2005, 2006, among others). Other than access to the holotype of T. pseudodasybatis, the latter authors did not have specimens from the western Atlantic for comparison and determination of variation between the Atlantic and Pacific forms. In 2007, Dr Stephen A. Bullard, Auburn University, and the senior author collected several specimens of a monocotylid off Ship Island (Gulf of Mexico), Mississippi, that were identified as T. pseudodasybatis from A. narinari. Comparison of these specimens with those from A. ocellatus from Moreton Bay revealed potentially important morphological differences in the MCOs of specimens from the two populations, suggesting that like their hosts, T. pseudodasybatis may currently represent a species complex. Because further study will be required to determine relationships between these parasite populations, the specimens from Moreton Bay are here tentatively identified as *Thau*matocotyle cf. pseudodasybatis.

Monocotylinae Taschenberg, 1879

Clemacotyle australis Young, 1967

Type-host: Aetobatus narinari (Euphrasen) of the Indo-West/Central Pacific Ocean [now *A. ocellatus* (Kuhl), see White et al., 2010] (Myliobatiformes: Aetobatidae), ocellated eagle ray.

Type-locality: Heron Island, Queensland, Australia.

Previous records: A. *ocellatus* (as *A. narinari*): off Heron Island, Queensland, Australia (Young, 1967; Chisholm, 1998b; Chisholm et al., 2001); Shark Bay off Heron Island, Queensland, Australia (Beverley-Burton & Whittington, 1995); off Ilôt Maître (near 166.40°E, 22.34°S), Nouméa, New Caledonia (Marie & Justine, 2005).

Present record: A. *ocellatus*: Moreton Bay off Green Island (27°25′S, 153°14′E), Queensland, Australia, 5.vii.2016.

Site on host: External surface (specimen obtained from a body wash; specific site on host undetermined). *Specimen studied*: Voucher, QM G238462.

Remarks

One specimen of *C. australis* was collected and identified based on the original description provided by Young (1967). Its occurrence in Moreton Bay is a new faunal record for the bay.

Janse & Borgsteede (2003) found high numbers of worms in the skin scrapings of *A. narinari* (now *A. ocellatus*) from the Maldives and identified them as *C. australis*. Whittington & Chisholm (2008) noted that the worms were likely *Dendromonocotyle torosa* Chisholm & Whittington, 2004 but did not detail the reasons for this supposition. Since *C. australis* is a gill parasite, it is unlikely the worms collected by Janse & Borgsteede (2003) would be found in large numbers on the skin of the host. Thus, we concur with Whittington & Chisholm (2008) that the worms collected by Janse & Borgsteede (2003) were likely *D. torosa*.

Although the single specimen reported herein as coming from the external surface of the host, its likely site of infection was the gills. The procedure involved in skin washings is not specific, and gill parasites are often found in the ensuing sediments.

Dendromonocotyle kuhlii Young, 1967

Type-host: Dasyatis kuhlii (Müller & Henle) of eastern Australia [now *Neotrygon trigonoides* (Castelnau)] (Myliobatiformes: Dasyatidae), New Caledonian maskray.

Type-locality: Moreton Bay, Queensland, Australia. *Previous records*: *N. trigonoides* [as *Dasyatis kuhlii* or *Amphotistius kuhlii* (Müller & Henle)]: Moreton Bay, Queensland, Australia (Young, 1967; Kearn, 1979). *Neotrygon kuhlii* (Müller & Henle): Burger's Zoo Aquarium, Arnhem, The Netherlands (host originally obtained from Jakarta, Indonesia) (Vaughan & Chisholm, 2009).

Present records: N. trigonoides: Moreton Bay, Wanga Wallen Bank (27°25′21″S, 153°25′46″E), Queensland, Australia, 3.iii.2005; Moreton Bay off Garden Island (27.61°S, 153.33°E), Queensland, Australia, 28.vi.2016.

Site on host: External surface.

Specimens studied: 4 vouchers, QM G238490-G238493; 4 vouchers, AHC 36765-36766.

Remarks

Dendromonocotyle kuhlii can be distinguished from all other described species of the genus by having an exceptionally long MCO that extends posteriorly to the level of the anterior region of the haptor and by the presence of keyhole-shaped sclerites at the tips of the haptoral papillae (see Young, 1967). The parasite appears to be restricted to the dorsal surface of rays comprising the Neotrygon kuhlii complex of six species from the Indo-West Pacific Ocean (see Last et al., 2016b). Dendromonocotyle kuhlii is currently known from N. trigonoides from eastern Australia (Young, 1967) and N. kuhlii from the waters off Jakarta, Indonesia (Vaughan & Chisholm, 2009). However, Last et al. (2016b) described Neotrygon orientale Last, White & Séret, a member of the N. kuhlii complex from the environs of Jakarta, which suggests that the host of D. kuhlii reported by Vaughan & Chisholm (2009) as *N. kuhlii* may be *N. orientale*.

Dendromonocotyle raiae n. sp.

Type-host: Hemitrygon fluviorum (Oligby) (Myliobatiformes: Dasyatidae), estuary stingray.

Type-locality: Moreton Bay, Wanga Wallen Bank off North Stradbroke Island (27°25′21″S, 153°25′46″E), Queensland, Australia, 2–4.iii.2005.

Other records: Neotrygon trigonoides (Castelnau), New Caledonian maskray: Moreton Bay, Wanga Wallen Bank off North Stradbroke Island (27°25'21"S, 153°25'46"E), Queensland, Australia, 3.iii.2005.

Site on host: External surface (specimens obtained from body washes; specific location on body unknown).

Type-material: Holotype, QM G23850; 11 paratypes, QM G238494-G238504; 6 paratypes, AHC 36767–35772; 5 paratypes, USNM 1618962; 2 paratypes, HWML 216337.

Other material: 18 slides with fragments of dissected specimens, HWML 216336 (these specimens were used to determine morphology of hard parts of the haptor and MCO); 2 vouchers (from *N. trigonoides*), QM G238506, G238507; 1 voucher (from *N. trigonoides*), AHC 36773.

ZooBank registration: To comply with the regulations set out in Article 8.5 of the amended 2012 version of the *International Code of Zoological Nomenclature* (ICZN, 2012), details of the new species have been submitted to ZooBank. The Life Science Identifier (LSID) for *Dendromonocotyle raiae* n. sp. is urn:lsid: zoobank.org:act:BE84E661-5724-4913-A0F5-FA7E18C96BEC.

Etymology: The specific name, a cognomen derived from Latin (*raia* = ray, skate), identifies the species as a parasite of a ray.

Description

[Based on 25 specimens; Figs. 8–20.] Body including haptor 1,150–3,270 (1,980; n = 21) long. Body proper tear-drop shaped, 922–2,740 (1,620; n = 23) long; greatest width 475–1,960 (1,120; n = 24) posterior to germarium (Fig. 8). Cephalic region tapered anteriorly, broad, terminally rounded, with subterminal concavity having weak rim. Cephalic lobes absent; cephalic glands not observed; 6 bilateral pairs of marginal putative gland-duct pores at level of cephalic concavity (Fig. 8); secretion type undetermined. Eye-



Fig. 8 Whole-mount illustration of *Dendromonocotyle raiae* n. sp. (composite, ventral view)

spots 2 pairs; members of anterior and posterior pairs shaped as apostrophes, tandem, often in contact. Mouth located within subterminal cephalic concavity. Pharynx 147–326 (216; n = 19) long, 113–210 (159; n = 19) wide, composed of 2 indistinct tandem bulbs, lying posterior to cephalic concavity; cephalic and oesophageal glands not observed or apparently absent. Oesophagus short to absent. Caecal bifurcation immediately posterior to pharynx. Intestinal caeca 2, narrow, with lateral and medial diverticula, ending blindly in posterior portion of body proper; caecal diverticula blind, dendritic, heavily pigmented.

500µm



Figs. 9–19 Dendromonocotyle raiae n. sp. 9, Male copulatory organ; 10, Distal end of male copulatory organ; 11, Hook; 12, 13, Anchors showing variability among specimens; 14, Typical sclerite of radial septa; 15, Typical sclerite of inner-circle septum; 16, Typical terminal papillary sclerite; 17, Typical subterminal papillary sclerite; 18, 19, Two variations of sclerites on outer-circle septum. Parallel lines on Fig. 9 indicate respective limits of the dimension measured

Haptor circular in outline, 545-1,720 (993; n = 23) in diameter, with 8 peripheral loculi (2 interhamular) and single central loculus, each delimited by muscular septa. Haptoral rim with 56 marginal papillae, each with 3 or 4 butterfly- or V-shaped (Fig. 17) and single terminal ram's-horn-shaped sclerites (Fig. 16). Anterior haptoral loculi with 6 marginal papillae each; anterolateral and posterolateral loculi with 7 marginal papillae each; interhamular loculi with 8 papillae each. Each radial septum with 13-15 butterfly-shaped sclerites (Fig. 14); inner and outer rings with variable number of comma or butterfly shaped sclerites (Figs. 15, 18, 19). Marginal haptoral valve narrow, delicate, with smooth margin. One pair of anchors; anchor 45–88 (71; n = 9) long, with tapering point, short shaft, tapering blunt superficial root, elongate deep root comprising 2 zones; distal zone of deep root variable in length (compare Figs. 12, 13). Hooks 14; each 15-17(16; n = 22) long, with short tapered point, slightly arced shaft, base with shelf and terminally tapered, elongate uniform shank; filamentous hook (FH) loop (domus) nearly shank length (Fig. 11).

Common genital pore, testis, proximal portion of vas deferens not observed, obscured by heavily pigmented intestinal caeca and diverticula. Distal portion of vas deferens ventral to ejaculatory bulb, dilating to form fusiform seminal vesicle lying to right of ejaculatory bulb; seminal vesicle with slightly thickened wall; ejaculatory duct entering ejaculatory bulb; ejaculatory bulb spherical, 151-242 (198; n = 19) in diameter, with thick wall. Prostates and prostatic reservoirs not observed. MCO 221-306 (263; n = 16) long, a straight to slightly undulating or arching tube originating from dorsal surface of ejaculatory bulb; proximal end of MCO slightly expanded, shaft uniform in diameter (Fig. 9); distal end of MCO lacking filaments, with delicate acute tip with fine circumambient ridges (Fig. 10). Distal portion of MCO enclosed within thick muscular phallic-like organ with attenuated tip; phallic-like organ 129-166 (148; n = 13) long; proximal portion of MCO and phallic-like organ enclosed within delicate membranous sheath (Fig. 20).

Germarium intercaecal near mid-length of body proper, convoluted, dorsoventrally looping right intestinal caecum. Oviduct extending toward body midline. Oötype obscured by vagina and vitelline ducts; Mehlis' gland not observed. Uterus lying on body midline just posterior to ejaculatory bulb, ventral to MCO, pestle- or club-shaped, with thick muscular wall, distally enclosing a maximum of 1 egg. Seminal receptacle spherical (Fig. 20). Vagina extending anterolaterally from body midline toward left side of body, comprised of delicate tube lying within 2 thick muscular layers; outer muscular layer coiled around inner layer and vaginal canal; subspherical to ovate spermatophore frequently present just internal to vaginal pore. Vitellarium comprising delicate cells scattered between caecal diverticula throughout lateral regions of body proper; transverse vitelline duct arising from medial margins of vitelline fields, extending medially ventral to MCO complex and dorsal to vagina; common vitelline duct not observed. Egg collapsed, tetrahedral, with proximal filament.

Remarks

Dendromonocotyle currently contains 21 species, including D. raiae n. sp. The presence or absence of anchors and the number and distribution of marginal papillae relative to the haptoral loculi are easily seen characters that can be used as a first step in distinguishing species of the genus. Vaughan et al. (2008) recognised two groups of Dendromonocotyle species that have 56 marginal papillae. These groups were defined by the pattern of associations of the haptoral papillae and loculi. Dendromonocotyle raiae belongs to Group 1 (6-7-7-8), where six papillae are associated with each anterior loculus, seven papillae with each anterolateral and posterolateral loculus, and eight with each posterior loculus. The only described species of Dendromonocotyle that possess anchors and the Group-1 arrangement of papillae are D. akajeii Ho & Perkins, 1980 (anchors first reported in this species by Chisholm & Whittington, 1995) and D. ukuthena Vaughan, Chisholm & Christisen, 2008. Dendromonocotyle raiae n. sp. can easily be distinguished from D. akajeii by having an unsclerotised vagina encircled by two relatively thick muscular layers (vagina bare, distally sclerotised in D. akajeii) and from D. ukuthena by the vagina lacking spination (vagina with distal inner-ring of sclerotised spines in D. ukuthena) (see Ho & Perkins, 1980; Vaughan et al., 2008).

During the present study, numerous specimens of *D. raiae* n. sp. were found infecting *H. fluviorum*, which appears to be the parasite's natural host. The finding of *D. raiae* n. sp. on *N. trigonoides*, however, may have been a result of host transfer. The new species has never been reported from the latter host,



Fig. 20 Distal components of the reproductive system of *Dendromonocotyle raiae* n. sp. (ventral view). *Abbreviations*: C, intestinal caecum; EB, ejaculatory bulb; MCO, male copulatory organ; MPO, muscular phallic-like organ; OV, oviduct; S, outer sheath of MCO; SP, spermatophore; SR, seminal receptacle; SV, seminal vesicle; TVD, transverse vitelline duct; U, uterus; V, vagina; VD, distal vas deferens

even though the ray had been previously examined from Moreton Bay for external parasites. For the present study, *H. fluviorum* and *N. trigonoides* were both collected during the same time period in 2005, and the possibility exists that transfer of this external parasite could have occurred during transportation or holding of the live rays. Nothing was stated in the field notes available to the present authors to indicate that the two species of rays were held in separate containers prior to necropsy.

Dendromonocotyle torosa Chisholm & Whittington, 2004

Type-host: Aetobatus narinari (Euphrasen) of the Indo-West/Central Pacific Ocean [now A. ocellatus

(Kuhl), see White et al., 2010] (Myliobatiformes: Aetobatidae), ocellated eagle ray.

Type-locality: Underwater World, Mooloolaba, Queensland, Australia.

Previous records: A. ocellatus (as *A. narinari*): Underwater World, Mooloolaba, and Cairns Marine (aquarium supplier), Queensland, Australia (Chisholm & Whittington, 2004). The recorded occurrence of *Clemacotyle australis* on *A. ocellatus* by Janse & Borgsteede (2003) may have been *D. torosa* (see above Remarks for *C. australis*).

Present record: A. ocellatus: Moreton Bay off Wynnum North (27°25′S, 153°11′E), Queensland, Australia, 5.vii.2016.

Site on host: External surface.

Specimens studied: 2 vouchers, QM G238488, G238489; voucher, AHC 36774; 2 vouchers, USNM 1618963.

Remarks

The infection by *D. torosa* on *A. ocellatus* in Moreton Bay represented a new faunal record for the bay. As noted above, the worms identified as *C. australis* from the skin of *A. ocellatus* by Janse & Borgsteede (2003) were likely *D. torosa* (see also Whittington & Chisholm, 2008). The latter record requires confirmation.

Monocotyle caseyae Chisholm & Whittington, 2005 Syn. *Monocotyle* sp. B of Chisholm (1998a)

Type-host: Himantura sp. [now *Maculabatis toshi* (Whitley)] (Myliobatiformes: Dasyatidae), black-spotted whipray.

Type-locality: Moreton Bay near Dunwich (27°15'S, 153°15'E), North Stradbroke Island, Queensland, Australia.

Previous records: M. toshi (as *Himantura* sp.): Moreton Bay near Dunwich (27°15'S, 153°15'E), North Stradbroke Island, Queensland, Australia (Chisholm & Whittinton, 2005). Honeycomb stingray *H. uarnak* (Gmelin) [as *H. uarnak* (Forsskål)]: Moreton Bay, Queensland, Australia (as *Monocotyle* sp. B) (Chisholm, 1998a).

Present records: M. toshi: Moreton Bay near Green Island (27°25'S, 153°14'E), Queensland, Australia, 17.i.2016; Moreton Bay near Peel Island (27°30'S, 153°20'E), Queensland, Australia, 15.i.2016. *Site on host:* Gills.

Specimens studied: 2 vouchers, QM G238510, G238511; voucher, AHC 36775.

Remarks

This species was first reported as *Monocotyle* sp. B from the gills of *H. uarnak* in Moreton Bay by Chisholm (1998a), who provided drawings of its anchor and copulatory complex. The species was subsequently described and named by Chisholm & Whittington (2005) from Moreton Bay on the gills of four of five unidentified rays named only as *Himantura*

sp. Chisholm & Whittington (2005) could not identify their rays because color variations on their dorsal surfaces and features of their mouths and nostrils did not match any of the diagnosed species in Last and Stevens (1994) for Australian rays. Chisholm & Whittington (2005) mentioned, however, that a personal communication from Dr Peter Last suggested that some of their rays were closest to *H. toshi* (now *Maculabatis toshi*). Chisholm & Kritsky (2020) have since provided additional evidence that the hosts identified as *Himantura* sp. by Chisholm & Whittington (2005) and the whiprays collected for the present study were *M. toshi*.

The sclerite pattern on the haptoral septa and marginal papillae and the general morphology of the copulatory complex and haptoral anchor of the three monocotylids we collected corresponded closely with the respective features originally described for *M. caseyae* by Chisholm & Whittington (2005). Chisholm & Whittington (2005) described and illustrated 20 rings in the coil of the MCO, but 30 and 32 rings were observed in present specimens. This difference in the number of rings in the coil of the MCO is not considered sufficient to exclude the present specimens from *M. caseyae*, as ring number may vary depending on the extent or tightness of the coil and on the age of the helminth specimen (see Chisholm, 1998a).

Monocotyle corali Chisholm, 1998

Type-host: Pastinachus sephen (Forsskål) of eastern Australia [now *Pastinachus ater* (Macleay)] (Myliobatiformes: Dasyatidae), cowtail stingray.

Type-locality: Shark Bay, Heron Island, Queensland, Australia.

Previous records: P. ater (as *P. sephen*): Shark Bay off Heron Island, Queensland, Australia (Chisholm, 1998a); off Heron Island (23°27'S, 151°55'E), Queensland, Australia (Chisholm & Whittington, 1998a; Chisholm et al., 2001).

Present record: *P. ater*: Moreton Bay near Peel Island (27°30'S, 153°20'E), Queensland, Australia, 15.i.2016.

Site on host: Gills.

Specimens studied: Voucher, QM G238509; voucher, AHC 36776.

Remarks

The finding of *M. corali* represents a new faunal record for Moreton Bay, and the specimens conform well to the original description. The type-host of *M. corali* was identified by Chisholm (1998a) as *P. sephen*, which at the time was believed to have a widespread distribution within the Indo-Pacific Region. However, *P. sephen* has recently been shown to be restricted to the northwestern Indian Ocean (Last et al., 2016a). A similar species, *P. ater*, is more widespread in the Indo-Pacific and apparently represents the ray previously considered *P. sephen* off eastern Australia. Tazerouti et al. (2011) stated that *M. corali* occurs on *Myliobatis australis* (Macleay), but no published record was found establishing such.

Monocotyle kuhlii Young, 1967

Type-host: Dasyatis kuhlii (Müller & Henle) of eastern Australia [now *Neotrygon trigonoides* (Castelnau)] (Myliobatiformes: Dasyatidae), New Caledonian maskray.

Type-locality: Moreton Bay, Queensland, Australia.

Previous records: N. trigonoides (as *D. kuhlii*): Moreton Bay, Queensland, Australia (Young, 1967); East China Sea (Zhang et al., 1999; locality as given in Zhang et al., 2003).

Present records: N. trigonoides: Moreton Bay, Wanga Wallen Bank (27°25′21″S, 153°25′46″E), Queensland, Australia, 3.iii.2005; Moreton Bay off Garden Island (27.61°S, 153.33°E), Queensland, Australia, 28.vi.2016.

Site on host: Species of *Monocotyle* are generally parasites of the gills of their hosts; the 2 specimens collected during the present surveys were obtained from body washes; the specific site on the host was undetermined (see Remarks for *Clemacotyle australis*).

Specimen studied: Voucher, QM G238508; voucher, AHC 36777.

Remarks

The specimens were identified as M. kuhlii based on the morphology of the haptoral and copulatory sclerites. The only observed difference between the current specimens and the description of the species provided by Young (1967) was that the length of the anchor was shorter in our specimens [65-75 (n = 4)] compared with that originally reported in the original description (130–146).

Monocotylesp. A of Chisholm (1998a)

Previous record: Dasyatis fluviorum Ogilby [now *Hemitrygon fluviorum* (Ogilby)] (Myliobatiformes: Dasyatidae), estuary stingray: Moreton Bay, Queensland, Australia (Chisholm, 1998a).

Present record: H. fluviorum: Moreton Bay off Wynnum North (27°25'S, 153°11'E), Queensland, Australia, 21.i.2016.

Site on host: Gills.

Specimen studied: Voucher, AHC 36778.

Remarks

The specimen was tentatively identified as Monocotyle sp. A of Chisholm (1998a) based on the morphology of the copulatory complex and presence of comparatively large anchors. The egg is tetrahedral in shape with a short filament at its proximal pole. The copulatory complex is comprised of a coiled MCO and a small accessory piece at the distal end of the MCO. The loose coil of the MCO had approximately 8 rings, and the proximal end of the shaft was minimally expanded. The distal tip of the MCO was tapered to a fine point and was inserted into a relatively nondescript accessory piece. The anchors were not oriented such that their morphology could be determined. Nonetheless, Chisholm (1998a) characterised the anchors of Monocotyle sp. A as being large and provided measurements of 504-544 in length. Anchors in the present specimen measured 782 and 845 long, respectively, suggesting that a significantly wide range in anchor length could be expected in a larger series of specimens of this species.

Comparison of the few morphological details presently known for *Monocotyle* sp. A with those of currently described species of *Monocotyle* suggested that the two specimens of Chisholm (1998a) and the specimen reported here represented an undescribed species, the description of which must await further collections of the helminth from *H. fluviorum*.

Acknowledgments The collection of monocotylids during 2016 were made as part of a survey of the parasites of the fishes of Moreton Bay and supported by an Australian Biological

Resources Study Grant (RF215-40) awarded to Drs Tom Cribb and Scott Cutmore. Specimens of *Neoheterocotyle rhynchobatis* were collected in Moreton Bay during field trips funded by the Australian Research Council large grants A00104635 (2001–2003) and DP0557697 (2005–2007) awarded to Dr Ian Whittington. We are especially grateful to Scott Cutmore who provided the specimens of *Calicotyle cutmorei* n. sp. and *Dendromonocotyle raiae* n. sp. and to Tom Cribb for the invitation extended to the senior author to participate in the survey of parasites of the fishes in Moreton Bay.

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Ethical approval The authors assert that all applicable institutional, national, and international guidelines for the care and use of animals were followed.

References

- Beverley-Burton, M., & Whittington, I. D. (1995). Clemacotyle australis (Monogenea: Monocotylidae) from the whitespotted eagle ray Aetobatus narinari (Rajiformes: Myliobatididae) on the Great Barrier Reef: redescription, emended generic diagnosis, and oncomiracidium. Journal of Parasitology, 81, 616–625.
- Beverley-Burton, M., & Williams, A. (1989). Merizocotyle icopae, sp. nov., and Thaumatocotyle australensis, sp. nov., (Monogenea: Monocotylidae) from the nasal cavities of rajiform elasmobranchs of the Great Barrier Reef. Australian Journal of Zoology, 37, 25–35.
- Boeger, W. A., & Kritsky, D. C. (1993). Phylogeny and a revised classification of the Monogenoidea Bychowsky, 1937 (Platyhelminthes). Systematic Parasitology, 26, 1–32.
- Boeger, W. A. & Kritsky, D. C. (2001). Chapter 10. Phylogenetic relationships of the Monogenoidea. In: Littlewood, D. T. J. & Bray, R. A. (Eds), *Interrelationships of the Platyhelminthes* (pp. 92–102). London: Taylor & Francis.
- Bullard, S. A., & Overstreet, R. M. (2000). Calicotyle californiensis n. sp. and Calicotyle urobati n. sp. (Monogenea: Calicotylinae) from elasmobranchs in the Gulf of California. Journal of Parasitology, 86, 939–944.
- Chisholm, L. A. (1998a). A revision of *Monocotyle* Taschenberg, 1878 (Monogenea: Monocotylidae) with descriptions of three new species from Australia. *Journal of Natural History*, 32, 1259–1290.
- Chisholm, L. A. (1998b). Ciliated cells and chaetotaxy of the larvae of seven species of monocotylid monogeneans (Platyhelminthes) from Heron Island, Great Barrier Reef, Australia. *Parasitology Research*, 84, 828–834.
- Chisholm, L. A., Hansknecht, T. J., Whittington, I. D., & Overstreet, R. M. (1997). A revision of the Calicotylinae Monticelli, 1903 (Monogenea: Monocotylidae). Systematic Parasitology, 38, 159–183.
- Chisholm, L. A., & Kritsky, D. C. (2020). *Heterocotyle whittingtoni* n. sp. (Monogenea: Monocotylidae) from the gills

of the black-spotted whipray, *Maculabatis toshi* (Myliobatiformes, Dasyatidae), collected in coastal waters of Queensland, Australia. *Systematic Parasitology*, 97(6). https://doi.org/10.1007/s//1230-020-09939-z.

- Chisholm, L. A., Morgan, J. A. T., Adlard, R. D., & Whittington, I. D. (2001). Phylogenetic analysis of the Monocotylidae (Monogenea) inferred from 28S rDNA sequences. *International Journal for Parasitology*, 31, 1537–1547.
- Chisholm, L. A., Wheeler, T. A., & Beverley-Burton, M. (1995). A phylogenetic analysis and revised classification of the Monocotylidae Taschenberg, 1879 (Monogenea). Systematic Parasitology, 32, 159–191.
- Chisholm, L. A., & Whittington, I. D. (1995). A revision of Dendromonocotyle Hargis, 1955 (Monogenea: Monocotylidae) with a description of a new species from Pastinachus sephen (Forsskål) (Myliobatiformes: Dasyatididae) from the Great Barrier reef, Australia. Journal of Natural History, 29, 1093–1119.
- Chisholm, L. A., & Whittington, I. D. (1996a). A revision of *Heterocotyle* (Monogenea: Monocotylidae) with a description of *Heterocotyle capricornensis* n. sp. from *Himantura fai* (Dasyatididae) from Heron Island, Great Barrier Reef, Australia. *International Journal for Parasitology*, 26, 1169–1190.
- Chisholm, L. A., & Whittington, I. D. (1996b). Descriptions of the larvae of six species of monocotylid monogeneans from *Himantura fai* (Dasyatididae) and *Rhinobatos typus* (Rhinobatidae) from Heron Island, Great Barrier Reef, Australia. *Systematic Parasitology*, 35, 145–156.
- Chisholm, L. A., & Whittington, I. D. (1997). A revision of *Neoheterocotyle* (Monogenea: Monocotylidae) with descriptions of the larvae of *N. rhinobatis* and *N. rhynchobatis* from Heron Island, Great Barrier Reef, Australia. *International Journal for Parasitology*, 27, 1041–1060.
- Chisholm, L. A., & Whittington, I. D. (1998a). Morphology and development of the haptors among the Monocotylidae (Monogenea). *Hydrobiologia*, 383, 251–261.
- Chisholm, L. A., & Whittington, I. D. (1998b). Revision of Decacotylinae Chisholm, Wheeler & Beverley-Burton, 1995 (Monogenea: Monocotylidae), including the synonymy of *Papillicotyle* Young, 1967 with *Decacotyle* Young, 1967 and a description of a new species from Australia. *Systematic Parasitology*, 41, 9–20.
- Chisholm, L. A., & Whittington, I. D. (1999). A revision of the Merizocotylinae Johnston and Tiegs, 1922 (Monogenea: Monocotylidae) with descriptions of new species of *Empruthotrema* Johnston & Tiegs, 1922 and *Merizocotyle* Cerfontaine, 1894. *Journal of Natural History*, 33, 1–28.
- Chisholm, L. A., & Whittington, I. D. (2000). Egg hatching in 3 species of monocotylid monogenean parasites from the shovelnose ray *Rhinobatos typus* at Heron Island, Australia. *Parasitology*, 121, 303–313.
- Chisholm, L. A., & Whittington, I. D. (2001). Euzetia occultum n. g., n. sp. (Euzetiinae n. subf.), a monocotylid monogenean from the gills of *Rhinoptera neglecta* (Rhinopteridae) from Moreton Bay, Queensland, Australia. Systematic Parasitology,48, 179–183.
- Chisholm, L. A., & Whittington, I. D. (2002). Efficacy of praziquantel bath treatments for monogenean infections of the *Rhinobatos typus*. Journal of Aquatic Animal Health, 14, 230–234.

- Chisholm, L. A., & Whittington, I. D. (2004). Two new species of *Dendromonocotyle* Hargis, 1955 (Monogenea: Monocotylidae) from the skin of *Taeniura meyeni* (Dasyatidae) and *Aetobatus narinari* (Myliobatidae) from aquaria in Queensland, Australia. *Systematic Parasitology*, 57, 221–228.
- Chisholm, L. A., & Whittington, I. D. (2005). Dendromonocotyle lasti n. sp. from the skin and Monocotyle caseyae n. sp. (Monogenea: Monocotylidae) from the gills of Himantura sp. (Dasyatidae) in Moreton Bay, Queensland, Australia. Systematic Parasitology, 60, 81–89.
- Chisholm, L. A., & Whittington, I. D. (2012). Three new species of *Merizocotyle* Cerfontaine, 1894 (Monogenea: Monocotylidae) from the nasal tissues of dasyatid rays collected off Malaysian and Indonesian Borneo. *Systematic Parasitology*, 82, 167–176.
- Cribb, B., Armstrong, W., & Whittington, I. (2004). Simultaneous fixation using glutaraldehyde and osmium tetroxide or potassium ferricyanide-reduced osmium for an assessment for *Merizocotyle icopae*. *Microscopy Research and Technique*, 63, 102–110.
- Cribb, B. W., Gould, R. J., & Whittington, I. D. (2001). A comparison of anterior adhesive areas and secretions in *Troglocephalus rhinobatidis* and *Neoheterocotyle rhinobatidis* (Monogenea: Monocotylidae) from the gills of the shovelnose ray, *Rhinobatos typus* (Rhinobatidae). Australian Journal of Zoology, 49, 577–587.
- Fricke, R., Eschmeyer, W. N., & Van der Laan, R. (Eds). (2020). Eschmeyer's Catalog of Fishes: Genera, Species, References. http://researcharchive.calacademy.org/research/ ichthyology/catalog/fishcatmain.asp. Accessed 26 March 2020.
- Froese, R., & Pauly, D. (Eds). (2019). FishBase. Available at https://www.fishbase.se/search.php (12/2019). Accessed 26 March 2020.
- Ho, J-s, & Perkins, P. S. (1980). Monogenea from fishes of the Sea of Japan. Part I. Order Monopisthocotylea. Annual Report of the Sado Marine Biological Station, Niigata University, 10, 1–10.
- Humason, G. L. (1979). Animal Tissue Techniques (4th ed.). San Francisco: W. H. Freeman and Company, 661 pp.
- ICZN (2012). International Commission on Zoological Nomenclature: Amendment of articles 8, 9, 10, 21 and 78 of the International Code of Zoological Nomenclature to expand and refine methods of publication. Bulletin of Zoological Nomenclature, 69, 161–169.
- Janse, M., & Borgsteede, F. H. M. (2003). Praziquantel treatment of captive white-spotted eagle rays (*Aetobatus narinari*) infested with monogenean trematodes. *Bulletin of the European Association of Fish Pathologists*, 23, 152–156.
- Johnson, J. W. (2010). Fishes of the Moreton Bay Marine Park and adjacent continental shelf waters, Queensland, Australia. *Memoirs of the Queensland Museum – Nature*, 54, 299–353.
- Kearn, G. C. (1978). Early development and microhabitat of the monogenean *Horricauda rhinobatidis*, with observations on the related *Troglocephalus rhinobatidis*, from *Rhinobatos batillum* from Queensland, Australia. *International Journal for Parasitology*, 8, 305–311.
- Kearn, G. C. (1979). Studies on gut pigment in skin-parasitic monogeneans, with special reference to the monocotylid

Deringer

Dendromonocotyle kuhlii. International Journal for Parasitology, 9, 545–552.

- Kitamura, A., Ogawa, K., Shimizu, T., Kurashima, A., Mano, N., Taniuchi, T., et al. (2010). A new species of *Calicotyle* Diesing, 1850 (Monogenea: Monocotylidae) from the shortspine spurdog *Squalus mitsukurii* Jordan & Snyder and the synonymy of *Gymnocalicotyle* Nybelin, 1941 with this genus. *Systematic Parasitology*, 75, 117–124.
- Kritsky, D. C. (2018a). Dactylogyrids (Monogenoidea) infecting the gill lamellae of some beloniform fishes from Moreton Bay, Queensland, Australia, with a redescription of *Hareocephalus thaisae* Young, 1969 and descriptions of six new species of *Hemirhamphiculus* Bychowsky & Nagibina, 1969. *Systematic Parasitology*,95, 33–54.
- Kritsky, D. C. (2018b). Species of Monogenoidea infecting the gill lamellae of the common silver-biddy *Gerres oyena* (Forsskål) and the common silver belly *Gerres subfasciatus* Cuvier (Perciformes: Gerreidae) in Moreton Bay, Queensland, Australia. *Systematic Parasitology*, 95, 499–525.
- Kritsky, D. C. (2019). Euryhaliotrema spp. (Monogenoidea: Dactylogyridae) parasitic on the gill lamellae of perciform fishes in Moreton Bay, Queensland, Australia, with the description of Euryhaliotrema solenophallus sp. nov. from the silver moony Monodactylus argenteus (Linnaeus) (Monodactylidae). Acta Parasitologica, 64, 223–227.
- Kritsky, D. C., Bullard, S. A., Bakenhaster, M. D., Scharer, R. M., & Poulakis, G. R. (2017a). Resurrection of *Myc*teronastes (Monogenoidea: Monocotylidae), with description of *Mycteronastes caalusi* n. sp. from olfactory sacs of the smalltooth sawfish, *Pristis pectinata* (Pristiformes: Pristidae), in the Gulf of Mexico off Florida. *Journal of Parasitology*, 103, 477–485.
- Kritsky, D. C., Bullard, S. A., Ruiz, C. F., & Warren, M. B. (2017b). *Empruthotrema longipenis* n. sp. (Monogenoidea: Monocotylidae: Merizocotylinae) from the olfactory sacs of the smooth butterfly ray *Gymnura micrura* (Bloch & Schneider) (Myliobatiformes: Gymnuridae) in the Gulf of Mexico. *Systematic Parasitology*, *94*, 777–784.
- Kritsky, D. C., & Nitta, M. (2019). Dactylogyrids (Platyhelminthes: Monogenoidea) infecting the gill lamellae of flatheads (Scorpaeniformes: Platycephalidae), with proposal of *Platycephalotrema* n. gen. and descriptions of new species from Australia and Japan. *Diversity*, 11, 132.
- Last, P. R., & Stevens, J. D. (1994). Sharks and rays of Australia. Melbourne: CSIRO Publishing, 513 pp.
- Last, P. R., Naylor, G. J. P., & Manjaji-Matsumoto, B. M. (2016a). A revised classification of the family Dasyatidae (Chondrichthyes: Myliobatiformes) based on new morphological and molecular insights. *Zootaxa*, 4139, 345–368.
- Last, P. R., White, W. T., & Séret, B. (2016b). Taxonomic status of maskrays of the *Neotrygon kuhlii* species complex (Myliobatoidei: Dasyatidae) with the description of three new species from the Indo-West Pacific. *Zootaxa*, 4083, 533–561.
- Lester, R. J. G., & Sewell, K. B. (1989). Checklist of parasites from Heron Island, Great Barrier Reef. *Australian Journal* of Zoology, 37, 101–128.
- Marie, A. D., & Justine, J.-L. (2005). Monocotylids (Monogenea: Monopisthocotylea) from Aetobatus cf. narinari off

New Caledonia, with a description of *Decacotyle elpora* n. sp. *Systematic Parasitology*, *60*, 175–185.

- Marie, A. D., & Justine, J.-L. (2006). Thaumatocotyle pseudodasybatis Hargis, 1955 (Monogenea: Monocotylidae) from Aetobatus cf. narinari, with a comparison of specimens from Australia, French Polynesia and New Caledonia. Systematic Parasitology, 64, 47–55.
- Mollaret, I., Jamieson, B. G. M., Adlard, R. D., Hugall, A., Lecointre, G., Chombard, C., et al. (1997). Phylogenetic analysis of the Monogenea and their relationships with Digenea and Eucestoda inferred from 28S rDNA sequences. *Molecular and Biochemical Parasitology*, 90, 433–438.
- Neifar, L., Euzet, L., & Ben Hassine, O. K. (2000). New species of the Monocotylidae (Monogenea) from the stingray *Dasyatis tortonesi* Capapé (Euselachii, Dastyatidae) off the Tunisian coast, with comments of host-specificity and the specific identities of Mediterranean stingrays. *Systematic Parasitology*, 47, 43–50.
- Nybelin, O. (1941). Dictyocotyle coeliaca n. g. n. sp. Ein Leibeshöhlebewohnender monogenetischer Trematode. Göteborgs Kunglig Vetenskaps- och Vitterhets-Samhälles Handlingar, Series B, 1, 1–19.
- Richards, V. P., Henning, M., Witzell, W., & Shivji, M. S. (2009). Species delineation and evolutionary history of the globally distributed spotted eagle ray (*Aetobatus narinari*). *Journal of Heredity*, 100, 273–283.
- Robinson, E. S. (1961). Some monogenetic trematodes from marine fishes of the Pacific. *Transactions of the American Microscopical Society*, 80, 235–266.
- Rohde, K., Heap, M., Hayward, C. J., & Graham, K. J. (1992). Calicotyle australiensis n. sp. and Calicotyle sp. (Monogenea, Monopisthocotylea) from the rectum and rectal glands, and Rugogaster hydrolagi Schell, 1973 (Trematoda, Aspidogastrea) from the rectal glands of holocephalans off the coast of southeastern Australia. Systematic Parasitology, 21, 69–79.
- Tazerouti, F., Neifar, L., & Euzet, L. (2011). Redescription of *Monocotyle myliobatis* (Monogenea, Monocotylidae) from the type host *Myliobatis aquila* (Elasmoranchii, Myliobatidae) off the Algerian coast. *Acta Parasitologica*, 56, 274–279.
- Tripathi, Y. R. (1959). Monogenetic trematodes from fishes of India. Indian Journal of Helminthology, 9 [1957], 1–149.
- Vaughan, D. B., & Chisholm, L. A. (2009). Three Dendromonocotyle species (Monogenea: Monocotylidae) reported from captive rays, including D. lotteri sp. n. from Himantura gerrardi (Elasmobranchii: Dasyatidae) in the public aquarium at the Atlantis resort, Dubai. Folia Parasitologica, 56, 99–106.
- Vaughan, D. B., Chisholm, L., & Christison, K. (2008). Overview of South African *Dendromonocotyle* (Monogenea: Monocotylidae), with descriptions of 2 new species from stingrays (Dasyatidae) kept in public aquaria. *Zootaxa*, 1826, 26–44.
- Watson, N. A. (1997). Spermiogenesis and sperm ultrastructure in *Troglocephalus rhinobatidis*, *Neoheterocotyle rhinobatidis* and *Merizocotyle australensis* (Platyhelminthes, Monogenea, Monopisthocotylea, Monocotylidae). *International Journal for Parasitology*, 27, 389–401.
- White, W. T., Last, P. R., Naylor, G. J. P., Jensen, K., & Caira, J. N. (2010). Clarification of *Aetobatus ocellatus* (Kuhl,

1823) as a valid species, and a comparison with *Aetobatus* narinari (Euphrasen, 1790) (Rajiformes: Myliobatidae). In: Last, P. R., White, W. T. & Pogonoski, J. J. (Eds), Descriptions of new sharks and rays from Borneo. CSIRO Marine and Atmospheric Research Paper 032. Hobart, Tasmania, Australia: CSIRO Marine and Atmospheric Research, pp. 141–164.

- Whittington, I. D. (1990). Empruthotrema kearni n. sp. and observations on Thaumatocotyle pseudodasybatis Hargis, 1955 (Monogenea: Monocotylidae) from the nasal fossae of Aetobatus narinari (Batiformes: Myliobatidae) from Moreton Bay, Queensland. Systematic Parasitology, 15, 23–31.
- Whittington, I. D., Armstrong, W. D., Chisholm, L. A., & Cribb, B. W. (2004a). A comparison of the anterior adhesive system in the oncomiracidium and adult of the monogenean parasite *Merizocotyle icopae* (Monocotylidae). *Parasitology Research*, 93, 223–229.
- Whittington, I. D., Armstrong, W. D., & Cribb, B. W. (2004b). Mechanism of adhesion and detachment at the anterior end of *Neoheterocotyle rhinobatidis* and *Troglocephalus rhinobatidis* (Monogenea: Monopisthocotylea: Monocotylidae). *Parasitology Research*, 94, 91–95.
- Whittington, I. D., Barton, D. P., & Lester, R. J. G. (1989). A redescription of *Calicotyle australis* Johnston, 1934 (Monogenea: Monocotylidae) from a new host, *Rhinobatos batillum* (Batifomes: Rhinobatidae), from Moreton Bay, Queensland. *Systematic Parasitology*, 14, 145–156.
- Whittington, I. D., & Chisholm, L. A. (2008). Chapter 13. Diseases Caused by Monogenea. In: Eiras, J. C., Segner, H., Wahli, T. & Kapoor, B. G. (Eds.), *Fish diseases*. Enfield, New Hampshire: Science Publishers, pp. 683–816.
- Whittington, I. D., & Kearn, G. C. (1992). Empruthotrema dasyatidis n. sp. (Monogenea: Monocotylidae) from the olfactory sacs of Dasyatis fluviorum (Rajiformes: Dasyatidae) from Moreton Bay, Queensland. Systematic Parasitology, 22, 159–165.
- Woolcock, V. (1936). Monogenetic trematodes from some Australian fishes. *Parasitology*, 28, 79–91.
- Yamaguti, S. (1963). Systema Helminthum. IV. Monogenea and Aspidocotylea. New York: John Wiley & Sons, 699 pp.
- Young, P. C. (1967). A taxonomic revision of the subfamilies Monocotylinae Gamble, 1896 and Dendromonocotylinae Hargis, 1955 (Monogenoidea: Monocotylidae) *Journal of Zoology, London, 153*, 381–422.
- Young, P. C. (1970). The species of Monogenoidea recorded from Australian fishes and notes on their zoogeography. Anales del Instituto de Biologia, Universidad Nacional Autónoma de México. Serie Zoología (Número Único), 41, 163–176.
- Zhang J., Qiu Z., Ding, X., et al. (1999). *Parasites and parasitic disease of fishes*. Beijing: Science Press, 790 pp (In Chinese).
- Zhang, J., Yang, T., Liu, L., & Ding, X. (2003). A list of monogeneans from Chinese marine fishes. *Systematic Parasitology*, 54, 111–130.

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