



FIRST REPORT OF LECANICEPHALIDEAN TAPEWORMS (EUCESTODA) FROM FRESHWATER, INCLUDING DESCRIPTION OF THREE NEW SPECIES OF *TETRAGONOCEPHALUM* SHIPLEY AND HORNELL, 1905

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KEY WORDS

ABSTRACT

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The lecanicephalidean cestodes parasitizing the spiral intestine of the endangered giant freshwater whipray, *Urogymnus polylepis* (Bleeker), are investigated for the first time. Eight host specimens were collected between 2002 and 2008 at 2 collecting sites off the eastern coast of Borneo: 6 from the Kinabatangan River (Malaysia) and 2 from a fish market in Tarakan (Indonesia). Two of these individuals were found to be infected with a total of 3 new species of *Tetragonocephalum* Shipley and Hornell, 1905. *Tetragonocephalum georgei* n. sp. and *Tetragonocephalum opimum* n. sp. were recovered from a host specimen from the Kinabatangan River, and *Tetragonocephalum levicorpum* n. sp. was found parasitizing a host specimen purchased at a fish market in Tarakan. Specimens of each of the new species were prepared for light microscopy; specimens of 2 of the new species were prepared for scanning electron microscopy, and histological sections were prepared for 1 of the new species. The 3 new species are distinct from the 9 valid species of *Tetragonocephalum* and the 1 species *inquirendum* based on, for example, total length, number of proglottids and testes, and size of the scolex and acetabula. *Tetragonocephalum georgei* n. sp. and *T. levicorpum* n. sp. are unusual among their congeners in that they are euapolytic (i.e., gravid proglottids were not observed) rather than apolytic. They differ from one another in scolex and acetabula size. *Tetragonocephalum opimum* n. sp. is unusual among its congeners in its possession of vitelline follicles arranged in 2, rather than 3, regions in the proglottid. These new species increase the total number of valid species of *Tetragonocephalum* to 12 and the total number of known cestodes from *U. polylepis* to 13 species across 6 genera in 4 orders. This is the first account of lecanicephalideans reported from freshwater. The taxonomic status of each of the 32 nominal taxa historically associated with *Tetragonocephalum* is re-assessed. Type host identities of all valid species are revised and discussed in light of recent taxonomic efforts in the Dasyatidae Jordan and Gilbert.

The giant freshwater whipray, *Urogymnus polylepis* (Bleeker), better known by its junior synonyms *Himantura chaophraya* Monkprasit and Roberts and *H. polylepis* (Bleeker), has attracted much public attention because of its massive size; it can attain a disk width of up to 2 m and a weight of 600 kg (see Monkprasit and Roberts, 1990 Last et al., 2016b; Vidthayanon et al., 2016). Formal conservation efforts by the International Union for Conservation of Nature (IUCN) have categorized this species as endangered as of 2011 (see Vidthayanon et al., 2016). *Urogymnus polylepis* is known to inhabit river systems in the

Indo-West Pacific region from India to Indonesia, including rivers in eastern India, Thailand, Cambodia, Vietnam, and Lao PDR, as well as throughout the islands of Borneo and Sumatra (Monkprasit and Roberts, 1990; Last and Stevens, 1994; Rainboth, 1996; Sezaki et al., 1999; Manjaji, 2004; Yano et al., 2005; Healy, 2006; Cuny and Piyapong, 2007; Last et al., 2010; IUCN, 2013; Iqbal and Yustian, 2016; Vidthayanon et al., 2016; Gray et al., 2017; Iqbal et al., 2018; Sen et al., 2020). Some debate remains as to the salinity tolerance and thus habitat of the species. *Urogymnus polylepis* has been referred to variously as an obligate freshwater species (e.g., Cavanagh et al., 2003; Martin, 2005), “mainly a freshwater species” (Vidthayanon et al., 2016), a “riverine” species (Compagno and Cook, 2005, p. 216), euryhaline (e.g., Compagno, 2002; Lucifora et al., 2015; Grant et al.,

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2019), and an “estuarine and coastal marine species” (Last and Manjaji-Matsumoto, 2008, p. 289; see also Last et al., 2010).

Ten species of cestodes representing 3 orders have been reported from *U. polylepis*. All of these reports come from the Kinabatangan River, Sabah, Malaysia. They include 5 onchoproteocephalideans in the genus *Acanthobothrium* Blanchard, 1848 (see Fyler and Caira, 2006), 3 rhinebothriideans comprising 2 species of *Rhinebothrium* Linton, 1890 (see Healy, 2006), and a species originally described as *Rhinebothrium* (see Healy, 2006) that was subsequently designated as the type species of *Sungaicestus* Caira, Healy, Marques and Jensen, 2017 by Caira et al. (2017), and 1 species each of the trypanorhynch genera *Prochristianella* Dollfus, 1946, and *Proemotobothrium* Beveridge and Campbell, 2001 (see Schaeffner and Beveridge, 2014). To date, no lecanicephalideans have been reported from this host species.

Our current concept of *Tetragonocephalum* Shipley and Hornell, 1905, is based on the description of its type species, *Tetragonocephalum trygonis* Shipley and Hornell, 1905, by Shipley and Hornell (1905), as well as the revisional treatments of Pintner (1928), Euzet and Combes (1965), Ivanov and Campbell (2000), and Jensen (2005). In the most recent study on lecanicephalidean interrelationships, Jensen et al. (2016) recognized *Tetragonocephalum* as the only member of the Tetragonocephalidae Yamaguti, 1959, and newly circumscribed the family to reflect this more restricted membership. Among the Lecanicephalidea, the Tetragonocephalidae are both one of the most molecularly divergent (see Jensen et al., 2016) and most morphologically distinct families in the order. The possession of the following combination of features easily identify members of *Tetragonocephalum* (see also Jensen et al., 2016): (1) a prominent, muscular, non-retractable, dome-shaped apical organ; (2) proglottids that are acraspedote; (3) a bisaccate uterus; (4) an expansive genital atrium; (5) an ovary that is compact, essentially oval in dorso-ventral view, and C-shaped in cross section; (6) testes that are restricted to the region anterior to the cirrus sac; and (7) vitelline follicles that are arranged in 2 or 3 distinct regions in the proglottid (referred to as “fields” in Jensen et al. [2016], p. 302). All but the first 2 features are unique among the Lecanicephalidea. In contrast, members of the only other 2 lecanicephalidean genera with prominent, muscular apical organs (i.e., *Stoibcephalum* Cielocha and Jensen, 2013 and *Tylocephalum* Linton, 1890) possess proglottids that are craspedote, a saccate uterus, a shallow genital atrium, an ovary that is lobulated, H-shaped in dorso-ventral view, and bilobed in cross section, testes present in fields anterior and posterior to the genital pore, and vitelline follicles arranged in 2 lateral bands or circumcortically in some species (see Ivanov and Campbell, 2000; Jensen, 2005; Cielocha and Jensen, 2013).

Herein, 3 new species of *Tetragonocephalum* are described from *U. polylepis*. This is the first report of lecanicephalideans from *U. polylepis* and the first report of lecanicephalideans from freshwater. To facilitate future work on this group, the taxonomic status of each of the current 32 nominal taxa attributed to the genus is also re-evaluated.

MATERIALS AND METHODS

Eight individuals of the giant freshwater whipray, *Urogymnus polylepis*, were examined for tapeworms. Three males (90.5 cm,

81.2 cm, and 45.8 cm in disc width [DW]) were collected from the Kinabatangan River off Kampung Abai ($5^{\circ}41'10.81''N$, $118^{\circ}23'8.35''E$), Sabah, Malaysia in 2003 and 2004 (host specimen nos. BO-108, BO-496, and BO-497, respectively). Three additional specimens were collected from this locality (host specimen nos. BO-355, BO-356, and BO-358) in 2002; however, their sex and disc widths were not recorded. Two females (99.2 cm and 127.3 cm in DW) were purchased at the Pasar Beringin fish market in Tarakan ($3^{\circ}17'47.04''N$, $117^{\circ}34'57.26''E$), North Kalimantan, Indonesia, in 2008 (host specimen nos. KA-393 and KA-397, respectively). Additional host information is available in the Global Cestode Database (<http://elasmobranchs.tapewormdb.uconn.edu>) and can be retrieved by searching by Collection Code and Collection Number (e.g., “BO-108”).

Each stingray was dissected in the field by a mid-ventral incision to remove the spiral intestine. The spiral intestine was opened with a longitudinal incision and either immediately fixed in 10% formalin buffered with seawater (1:9) or examined for cestodes in the field. In the latter cases, a subset of the cestodes encountered was fixed in 95% ethanol; the remainder of the cestodes, as well as the spiral intestine, were fixed in 10% formalin buffered with seawater (1:9). All spiral intestines were transferred to 70% ethanol for long-term storage. Host identifications of 6 of the 8 individuals were confirmed using NADH2 sequence data (see Naylor et al., 2012).

Cestodes prepared as whole mounts for light microscopy were hydrated in a graded ethanol series, stained with Delafield’s hematoxylin, dehydrated in a graded ethanol series, cleared with methyl salicylate, and mounted in Canada balsam on glass slides. Scoleces for examination with scanning electron microscopy (SEM) were hydrated in a graded ethanol series, transferred to 1% osmium tetroxide for no less than 6 hr at 4 C, dehydrated in a graded ethanol series, and placed in hexamethyldisilizane (HMDS, Electron Microscopy Sciences, Hatfield, Pennsylvania) for 15 min. They were subsequently allowed to air-dry before being mounted on aluminum stubs with double-sided adhesive carbon dots (PELCO tabs, Ted Pella, Inc., Redding, California). Specimens were sputter-coated with 30–35 nm of gold and examined with a FEI Versa 3D Dual Beam field emission scanning electron microscope (Thermo Fisher Scientific, Waltham, Massachusetts) at the Microscopy and Analytical Imaging Laboratory, University of Kansas, Lawrence, Kansas. Specimens for histological sectioning were dehydrated in a graded ethanol series, stained with Fast Green, and cleared in xylene before being embedded in paraffin in plastic block holders. Serial sections of proglottids were cut at 7 μ m intervals using an Olympus Cut 4060 retracting rotary microtome (Triangle Biomedical Sciences, Durham, North Carolina); sections were floated on glass slides using a 2.5% sodium silicate solution and dried on a slide warmer at 40 C or allowed to air-dry for several hours. Sections were stained with Delafield’s hematoxylin, counter-stained with eosin, differentiated in Scott’s solution, dehydrated in a graded ethanol series, cleared in xylene, and mounted on glass slides in Canada balsam. Strobila vouchers of scoleces examined with SEM and scolex vouchers of strobila prepared as histological sections were mounted using the aforementioned protocol for whole-mounted specimens.

Line drawings were made using a camera lucida attached to a Zeiss Axioskop 2 Plus compound microscope (Zeiss, Thornwood, New York). Reproductive organs were measured in the posterior-

most mature proglottid. Measurements are given in micrometers (μm) unless otherwise stated and are reported as ranges followed in parentheses by the mean, standard deviation, number of individual specimens examined, and total number of measurements if more than 1 measurement was taken per worm.

Images of histological sections were taken using a Lumenera Infinity 3 USB camera (Lumenera Corporation, Ottawa, Ontario, Canada) attached to a Zeiss Axioskop 2 Plus compound microscope (Zeiss). Measurements of whole-mounted worms were taken using the image analysis program Leica Application Suite (LAS) Version 3.6.0 (Leica Microsystems, Buffalo Grove, Illinois).

For comparative purposes, specimens of *Tetragonocephalum passeyi* Jensen, 2005, from the personal collection of KJ were examined. Museum abbreviations used are as follows: LRP, Lawrence R. Penner Parasitology Collection, Department of Ecology and Evolutionary Biology, University of Connecticut, Storrs, Connecticut; MZB, Museum Zoologicum Bogoriense, Center for Biology, Indonesian Institute of Science, Cibinong, Jakarta-Bogor, Java, Indonesia; MZUM(P), Muzium Zoologi, Universiti Malaya, Kuala Lumpur, Malaysia; USNM, National Museum of Natural History, Smithsonian Institution, Washington, D.C. Dasyatid taxonomy follows Naylor et al. (2012) and Last et al. (2016a, 2016b). Microthrix terminology follows Chervy (2009). Ovary shape follows Clopton (2004).

RESULTS

Taxonomic status of nominal species of *Tetragonocephalum*

Jensen et al. (2017) assessed the status of 31 nominal taxa historically assigned to *Tetragonocephalum*. They categorized each as a valid species, a *species inquirendum*, an unavailable name (including *nomina nuda*), or a species *incertae sedis*. What follows is a re-assessment of the determinations of the taxonomic status of these names of Jensen et al. (2017) based on the re-interpretation of criteria for each of the categories. In addition, the status of *Tetragonocephalum minutum* (Southwell, 1925) Perrenoud, 1931, which was not included in Jensen et al. (2017), is clarified. A summary is given in Table I. These 32 names are now considered to fall into the following 5 categories: valid species, *species inquirendae*, *nomina dubia*, unavailable names (including *nomina nuda*), and species *incertae sedis*. Nominal taxa assigned to each category are as follows.

(1) Valid species: Only 9 species of *Tetragonocephalum* are recognized as valid here. These are *Tetragonocephalum kazemii* Roohi Aminjan and Malek 2017, *Tetragonocephalum mackenziei* Roohi Aminjan and Malek 2017, *T. passeyi*, *Tetragonocephalum sabae* Roohi Aminjan and Malek 2016, *Tetragonocephalum salarium* Roohi Aminjan and Malek 2016, *Tetragonocephalum simile* (Pintner, 1928) Perrenoud, 1931, *T. trygonis*, *Tetragonocephalum uarnak* (Shipley and Hornell, 1906) Perrenoud, 1931, and *Tetragonocephalum minutum* (Southwell, 1925) Perrenoud, 1931. The last was mistakenly omitted from consideration by Jensen et al. (2017).

(2) *Species inquirendae*: Following Jensen et al. (2017), *Tetragonocephalum yamagutii* Muralidhar, 1988, is considered in this category. Despite the substandard description, a holotype was indicated to have been deposited. The examination of this specimen could allow the morphology of the species to be more

comprehensively re-assessed in the future. However, we were unable to confirm the existence of the holotype at the “Cestodology laboratory, Zoology Department, Marathwada University, Aurangabad” (Muralidhar, 1988, p. 257), India; inquiries sent to several faculty in the Department of Zoology and the Zoological Museum at Marathwada University (Aurangabad, India) remained unanswered.

(3) *Nomina dubia*: In total, 9 species are considered *nomina dubia*. These are *Tetragonocephalum alii* Deshmukh and Shinde, 1979, *Tetragonocephalum aurangabadensis* Shinde and Jadhav, 1990, *Tetragonocephalum bhagawatii* Shinde, Mohekar and Jadhav, 1985, *Tetragonocephalum madhulatae* (Andhare and Shinde, 1994) Jensen, 2005, *Tetragonocephalum madrasense* (Andhare and Shinde, 1994) Jensen, 2005, *Tetragonocephalum raoi* Deshmukh and Shinde, 1979, *Tetragonocephalum ratnagiriensis* Shinde and Jadhav, 1990, *Tetragonocephalum sephenis* Deshmukh and Shinde, 1979, and *Tetragonocephalum shipleyi* Shinde, Mohekar and Jadhav, 1985 (see Deshmukh and Shinde, 1979; Shinde et al., 1985; Shinde and Jadhav, 1990; Andhare and Shinde, 1994). All were originally considered to be *species inquirendae* by Jensen et al. (2017). However, the descriptions of these species are substandard. They include erroneous, internally conflicting, and/or incomplete morphological characterizations, doubtful or uncertain host identifications, comparisons to what appears to be a random assortment of taxa rather than “related or similar taxa” (Recommendation 13A; ICZN, 1999), and incomplete reference to relevant taxonomic literature. Most importantly, type material for these species was never deposited. The designation of these species was thus revised from *species inquirendae* to *nomina dubia* herein (see Schenk and McMasters, 1956; Horton et al., 2017), because, based on the information presented in the original descriptions, it is essentially impossible to attribute any newly collected specimens to any of these species. The *species inquirendum* designation, in contrast, implied that each of these species “may still have extant type specimens or be adequately described, but just not have been reassessed” (Horton et al., 2017, p. 13) (see also Schenk and McMasters, 1956; ICZN, 1999; Jensen, 2005; Clopton et al., 2007). As a result, comparisons between the 9 *nomina dubia* and the new species described herein were not drawn, nor were questions related to type host identities of these species discussed further.

(4) Unavailable names (including *nomina nuda*): Following Jensen et al. (2017), 7 names, *Tetragonocephalum janardane* Wankhede, 1990, “*Tetragonicephalum* [sic] *karachiensis* Bilqees and Fatima, 1982,” “*Tetragonicephalum* [sic] *stegostomai* Bilqees and Fatima, 1982,” “*Tetragonicephalum* [sic] *varium* Bilqees and Fatima, 1982,” *Tetragonocephalum meenae*, “*Tetragonocephalum shindei* Shipley et Hornell, 1906,” and “*Tetragonocephalum marnrle*”, Shipley et Hornell, 1906, all published after 1930 but before 1999, are considered *nomina nuda* because they violate Article 13 of the ICZN (1999) since they were published without accompanying descriptions. The name *T. janardane* was introduced in an abstract by Wankhede (1990) and was thus not validly published (see Article 9; ICZN 1999). The names *Tetragonicephalum* [sic] *karachiensis*, *Tetragonicephalum* [sic] *stegostomai*, and *Tetragonicephalum* [sic] *varium* were included solely in a list of cestodes parasitizing marine fishes in Pakistan by Bilqees (1995). In the cases of all 3 of these names, “Bilqees and Fatima (1982)” (see Bilqees, 1995, p. 75) was given as the authority; however, this citation lacks journal information and

Table I. Current status of nominal taxa of *Tetragonocephalum*, including updated host names and host identifications for valid species, species inquirendae, and species incertae sedis.

	Type host (literal)	Type host (updated)	Country
Valid species			
<i>Tetragonocephalum georgei</i> n. sp.	<i>Urogymnus polylepis</i>	<i>Urogymnus polylepis</i> (Myliobatiformes: Dasyatidae)†	Malaysia
<i>Tetragonocephalum kazemii</i> Roohi Aminjan and Malek, 2017	<i>Pastinachus sephen</i>	<i>Pastinachus sephen</i> (Myliobatiformes: Dasyatidae)†	Iran
<i>Tetragonocephalum levicorum</i> n. sp.	<i>Urogymnus polylepis</i>	<i>Urogymnus polylepis</i> (Myliobatiformes: Dasyatidae)†	Indonesia
<i>Tetragonocephalum mackenzieri</i> Roohi Aminjan and Malek, 2016	<i>Pastinachus sephen</i>	<i>Pastinachus sephen</i> (Myliobatiformes: Dasyatidae)†	Iran
<i>Tetragonocephalum minutum</i> (Southwell, 1925) Perrenoud, 1931	“ <i>Urogymnus</i> sp. (aserrimus?)”	<i>Urogymnus aserrimus</i> or <i>U. granulatus</i> (Myliobatiformes: Dasyatidae)	Sri Lanka (as Ceylon)
<i>Tetragonocephalum optimum</i> n. sp.	<i>Urogymnus polylepis</i>	<i>Urogymnus polylepis</i> (Myliobatiformes: Dasyatidae)†	Malaysia
<i>Tetragonocephalum passayi</i> Jensen, 2005‡	<i>Himantura undulata</i>	<i>Himantura leptodura</i> (Myliobatiformes: Dasyatidae)†	Australia
<i>Tetragonocephalum sabae</i> Roohi Aminjan and Malek, 2016	<i>Himantura randalli</i>	<i>Maculabatis randalli</i> (Myliobatiformes: Dasyatidae)†	Iran
<i>Tetragonocephalum salarii</i> Roohi Aminjan and Malek, 2016	<i>Himantura randalli</i>	<i>Maculabatis randalli</i> (Myliobatiformes: Dasyatidae)†	Iran
<i>Tetragonocephalum simile</i> (Pintner, 1928) Perrenoud, 1931	<i>Trygon walga</i>	<i>Brevitrygon imbricata</i> or <i>B.</i> sp. 1 sensu Fernando et al. (2019) (Myliobatiformes: Dasyatidae)	Sri Lanka (as Ceylon)
<i>Tetragonocephalum tryonis</i> Shipley and Hornell, 1905 type species	<i>Trygon walga</i>	<i>Brevitrygon imbricata</i> or <i>B.</i> sp. 1 sensu Fernando et al. (2019) (Myliobatiformes: Dasyatidae)	Sri Lanka (as Ceylon)
<i>Tetragonocephalum uarnak</i> (Shipley and Hornell, 1906) Perrenoud, 1931	<i>Trygon uarnak</i>	<i>Himantura leoparda</i> , <i>H. tutul</i> , <i>H. uarnak</i> , or <i>H. undulata</i> (Myliobatiformes: Dasyatidae)	Sri Lanka (as Ceylon)
<i>Species inquirendae</i>			
<i>Tetragonocephalum yamaguitii</i> Muralidhar, 1988	<i>Trygon walga</i>	<i>Brevitrygon imbricata</i> or <i>B.</i> sp. 1 sensu Fernando et al. (2019) (Myliobatiformes: Dasyatidae)	India
<i>Nomina dubia</i>			
<i>Tetragonocephalum alii</i> Deshmukh and Shinde, 1979	<i>Trygon sephen</i>		India
<i>Tetragonocephalum aurangabadiensis</i> Shinde and Jadhav, 1990	<i>Trygon zugei</i>		India
<i>Tetragonocephalum bhagawatii</i> Shinde, Mohekar and Jadhav, 1985	<i>Trygon sephen</i>		India
<i>Tetragonocephalum madhulatae</i> (Andhare and Shinde, 1994) Jensen, 2005	<i>Trygon zugei</i>		India
<i>Tetragonocephalum madrasensis</i> (Andhare and Shinde, 1994) Jensen, 2005	<i>Trygon zugei</i>		India
<i>Tetragonocephalum raoi</i> Deshmukh and Shinde, 1979	<i>Trygon zugei</i>		India
<i>Tetragonocephalum ratnagiriensis</i> Shinde and Jadhav, 1990	<i>Trygon zugei</i>		India
<i>Tetragonocephalum sephenis</i> Deshmukh and Shinde, 1979	<i>Trygon sephen</i>		India
<i>Tetragonocephalum shiplei</i> Shinde, Mohekar and Jadhav, 1985	<i>Trygon sephen</i>		India
Unavailable names (including <i>nomina nuda</i>)			
<i>Tetragonocephalum goniini</i> Khamkar and Shinde, 2012			
<i>Tetragonocephalum janardane</i> Wankhede, 1990*			
<i>Tetragoniccephalum [sic] karachiensis</i> Bilqees and Fatima, 1980 or 1982*			
<i>Tetragonocephalum marnie</i> in Mohekar et al. (2002)*			
<i>Tetragonocephalum meenae</i> in Mohekar et al. (2002)*			
<i>Tetragonocephalum panjiensis</i> Kankale, 2011			
<i>Tetragonocephalum pulensis</i> Kankale, 2014			
<i>Tetragonocephalum sepheni</i> Lanka, Hippargi and Patil, 2013			
<i>Tetragonocephalum shindei</i> “Shipley and Hornell, 1906” in Mohekar et al. (2002)*			
<i>Tetragoniccephalum [sic] stegostomai</i> Bilqees and Fatima, 1980 or 1982*			
<i>Tetragoniccephalum [sic] varium</i> Bilqees and Fatima, 1980 or 1982*			
Species incertae sedis in the Cephalobothriidae			
<i>Tetragonocephalum akajeiensis</i> Yang, Liu and Lin, 1995	<i>Aetobatis narina</i>	<i>Aetobatis ocellatus</i> (Myliobatiformes: Myliobatidae)	Sri Lanka (as Ceylon)
<i>Tetragonocephalum aciobatis</i> Shipley and Hornell, 1905	<i>Dasyatis akajei</i>	<i>Hemitrygon akajei</i> (Myliobatiformes: Dasyatidae)	China

* *Nomen nudum*.

† Host specimen identification verified (see Naylor et al., 2012; Roohi Aminjan and Malek, 2016, 2017).

‡ As *Tetragonocephalum* n. sp. 3 in Jensen et al. (2016).

the publication date of the partial citation is inconsistent with the date of the authority. The names *T. meenae* and *T. shindei* appeared in Mohekar et al. (2002) in a list of species collected from the west coast of Maharashtra, India. The former was used by Mohekar et al. (2002) without authority or citation and the original description could not be located. The latter was erroneously attributed to "Shipley et Hornell, 1906" (see Mohekar et al., 2002, p. 98). However, that name does not appear in any publications by Shipley and Hornell that year (see, e.g., Shipley and Hornell, 1906). The name *T. marnrle* was included solely in a list of species of *Tetragonocephalum* by Lanka et al. (2013), who attribute the name to "Shipley et Hornell (1906)" (see Lanka et al., 2013, p. 11). Again, we were unable to locate a publication by these authors describing this taxon.

Four names published after 1999, *Tetragonocephalum govindi* Khamkar and Shinde, 2012, *Tetragonocephalum panjiensis* Khamkar, 2011, *Tetragonocephalum pulensis* Kankale, 2014, and *Tetragonocephalum sepheni* Lanka, Hippargi and Patil, 2013, are unavailable for nomenclatural purposes (see Table I). The authors (Khamkar, 2011; Khamkar and Shinde, 2012; Lanka et al., 2013; Kankale, 2014) neither explicitly fixed a holotype or syntypes nor included a statement of intent that types will be (or have been) deposited in a collection. As a consequence, these descriptions violate Article 16.4 of the International Code of Zoological Nomenclature (ICZN, 1999), and the names are unavailable.

(5) Species *incertae sedis*: As was determined by Jensen et al. (2017), 2 species are likely members of genera in the Cephalobothriidae Pintner, 1928, rather than *Tetragonocephalum*. The description of *Tetragonocephalum aetiobatidis* Shipley and Hornell, 1905, is inconsistent with the current diagnosis of *Tetragonocephalum* in that it was described by Shipley and Hornell (1905) as possessing craspedote rather than acraspedote proglottids, suckers that are directed anteriorly rather than laterally, and lacking a bisaccate uterus. Based on these features, *T. aetiobatidis* is more consistent with the diagnosis of *Adelobothrium* Shipley, 1900, than *Tetragonocephalum*. Due to its possession of craspedote rather than acraspedote proglottids and an ovary that is lobulated rather than compact (see Yang et al., 1995), *Tetragonocephalum akajeinensis* Yang, Liu and Lin, 1995, is most likely a member of *Tylocephalum*. We have refrained from creating new combinations until the generic placement for both of these species has been confirmed. *Tetragonocephalum aetiobatidis* and *T. akajeinensis* are considered to be species *incertae sedis* in the Cephalobothriidae herein.

DESCRIPTIONS

Tetragonocephalum georgei n. sp. (Figs. 1A–C, 2, 3)

Description (based on 16 specimens: 12 whole-mounted specimens [6 immature, 6 mature]; 1 cross-sectional series of mature proglottids and 3 specimens prepared for SEM, and their whole-mounted vouchers): Worms 4.5–7.3 mm (5.8 ± 1.0; 6) long, euapolytic, maximum width at level of scolex, 28–37 (31 ± 3.3; 6) proglottids, acraspedote, non-lacinate (Fig. 1A). Scolex 313–460 (367 ± 43.3; 10) long by 362–473 (408 ± 33.8; 11) wide, consisting of scolex proper, apical modification of scolex proper, and apical organ, widest at level of scolex proper (Fig. 1B). Scolex proper 120–337 (213 ± 59.8; 10) long by 362–473 (408 ± 33.8; 11)

wide, bearing 4 acetabula. Acetabula sucker-like in form, 60–90 (71 ± 7.2; 12; 24) long by 60–88 (73 ± 7.1; 12; 24) wide. Apical modification of scolex proper cylindrical, narrower than scolex proper, bearing apical organ. Apical organ large, globular in form, muscular, non-invaginable, non-retractable, with glandular surface, 149–285 (196 ± 45.2; 9) long by 254–395 (336 ± 35.7; 12) wide, 111–166 (131 ± 20.3; 8) thick at apex.

Surface of apical organ with irregular tubercles (Fig. 2B), suggesting glandular surface. Surface of posterior region of apical organ (Fig. 2C), scolex proper (Fig. 2D), and acetabula (Fig. 2E) covered with aciculae filiriches. Surface of strobila (Fig. 2F) covered with capilliform filiriches.

Cephalic peduncle absent. Immature proglottids 24–34 (28 ± 3.6; 6) in number, initially wider than long, becoming longer than wide with maturity, 1–6 (4 ± 1.9; 6) immature proglottids longer than wide; posterior-most immature proglottid 340–575 (474 ± 94.9; 6) long by 269–349 (304 ± 28.1; 6) wide. Mature proglottids 2–4 (3 ± 0.8; 6) in number, terminal mature proglottid 635–1,048 (839 ± 140.3; 6) long by 269–355 (306 ± 36.2; 6) wide. Gravid proglottids not observed. Testes 27–45 (34 ± 6.0; 12) in number, 16–26 (20 ± 3.1; 6; 18) long by 29–57 (49 ± 7.4; 6; 18) wide, extending from anterior margin of proglottid to anterior margin of cirrus sac (Fig. 1C), arranged in 2 irregular columns in dorso-ventral view, essentially 2 layers deep in cross section (Fig. 3A). Vas deferens minimal, sinuous, visible extending from level of ovary to cirrus sac, entering cirrus sac at its proximal end. External seminal vesicle absent. Internal seminal vesicle not observed. Cirrus sac pyriform, 107–165 (136 ± 20.5; 6) long by 117–141 (132 ± 9.1; 6) wide, oriented along long axis of proglottid, opening into genital atrium at its anterior margin, containing coiled cirrus. Cirrus armed with spiniriches. Genital pores lateral, irregularly alternating, 40–50% (46 ± 4.0; 6) of proglottid length from posterior end. Genital atrium expansive, extending past midline of proglottid. Ovary broadly dolioform (sensu Clopton, 2004) in dorso-ventral view, C-shaped in cross section (Fig. 3B), 88–156 (118 ± 25.4; 6) long by 118–184 (146 ± 27.4; 6) wide; ovicapt in middle of ovary. Mehlis' gland posterior to ovicapt. Vagina thick-walled, weakly sinuous, extending anteriorly from ootype to genital atrium, opening into genital atrium at its proximal end posterior to cirrus sac; vaginal sphincter not observed. Vitellarium follicular; vitelline follicles 6–28 (13 ± 6.9; 6; 18) long by 19–83 (43 ± 21.8; 6; 18) wide, in 3 regions: anterior to genital atrium arranged in 2 irregular columns on each lateral margin, between genital atrium and ovary arranged in single compact field, and posterior to ovary arranged in single compact field. Uterus bisaccate, constricted at level of genital atrium, medial, extending from level of Mehlis' gland to near anterior extent of field of testes. Excretory ducts in 2 lateral pairs. Eggs not observed.

TAXONOMIC SUMMARY

Type and only known host: *Urogymnus polylepis* (Bleeker), giant freshwater whipray (Myliobatiformes: Dasyatidae Jordan and Gilbert).

Type and only known locality: Kampung Abai (5°41'10.81"N, 118°23'8.35"E), Kinabatangan River, Sabah, Malaysia (host specimen no. BO-108).

Site of infection: Spiral intestine.

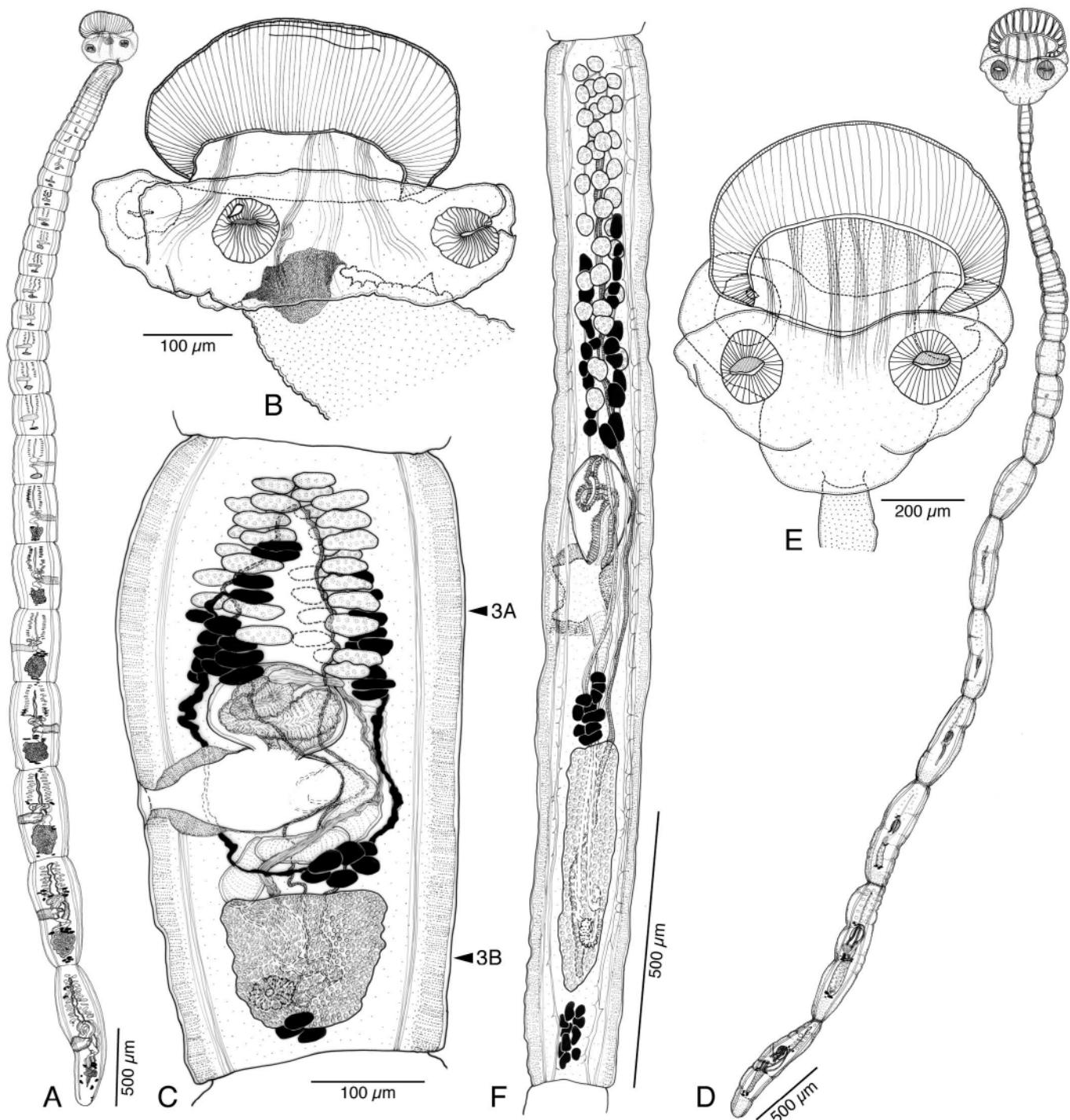


Figure 1. Line drawings of *Tetragonocephalum georgei* n. sp. (A–C) and *Tetragonocephalum levicorpum* n. sp. (D–F). (A) Whole worm (holotype, MZUM[P] 2020.1 [H]). (B) Scolex (paratype, USNM 1620831). (C) Mature proglottid (paratype, USMN 1620830); vitelline ducts connecting vitelline fields anterior and posterior to cirrus sac drawn as thick, solid black lines; arrows indicate level at which sections in Fig. 3 were taken. (D) Whole worm (holotype, MZBCa 209). (E) Scolex (holotype, MZBCa 209). (F) Mature, subterminal proglottid (paratype, USNM 1620836).

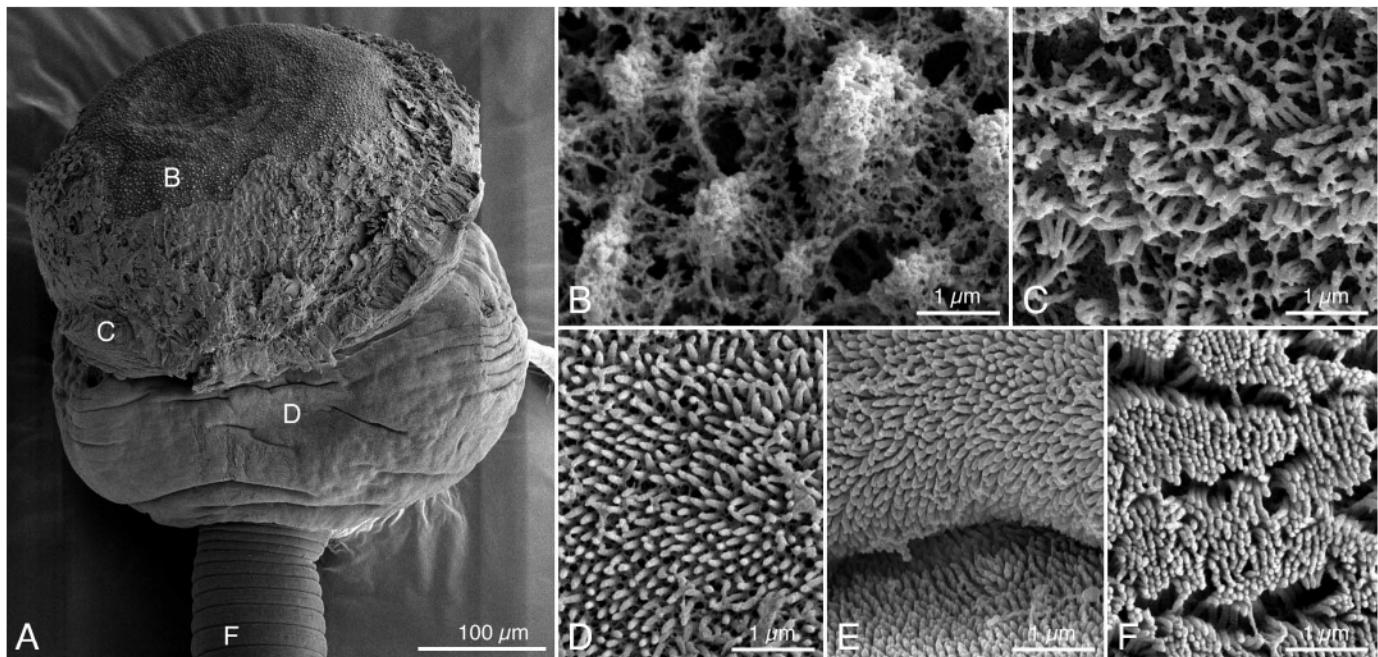


Figure 2. Scanning electron micrographs of *Tetragonocephalum georgei* n. sp. (A) Scolex; small letters indicate location of details shown in B–D, and F. (B) Surface of apical organ. (C) Surface of posterior region of apical organ. (D) Surface of scolex proper at level of acetabula (E) Surface of acetabula. (F) Surface of strobila.

Specimens deposited: Holotype (MZUM[P] 2020.1 [H]) and 3 paratypes (MZUM[P] 2020.2–4 [P]); 5 paratypes (4 whole worms, and 1 cross-sectional series of a mature worm and its whole-mounted voucher; USNM 1620830–1620834); 7 paratypes (4 whole worms and 3 whole-mounted strobila vouchers of scoleces prepared for SEM; LRP 10261–10267); scoleces prepared for SEM retained in the personal collection of KJ at the University of Kansas.

ZooBank registration: urn:lsid:zoobank.org:act:A2BBEF3A-4AC4-4131-AB17-59CBE7EB6EA4.

Etymology: This species honors the second author's father, George Register, who continues to inspire curiosity and wonder of the natural world in each of his children.

Remarks

Tetragonocephalum georgei n. sp. is clearly a member of *Tetragonocephalum*. Its possession of a muscular, non-retractable, dome-shaped apical organ, acraspedote proglottids, a bisaccate uterus, an expansive genital atrium, a compact ovary that is essentially oval in dorso-ventral view and C-shaped in cross section, testes that are restricted to the region anterior to the cirrus sac, and vitelline follicles arranged in 3 distinct regions solidly place it in this genus. Its possession of a euapolytic (i.e., absence of gravid proglottids on the strobila), rather than an apolytic strobila, differentiates it from all 9 of its valid congeners. In addition, *T. georgei* n. sp. is shorter in total length (4.5–7.3 vs. 28.8–36.6, 23.2–32.4, 23.5–35.9, approx. 21 [based on fig. 37 of Pintner, 1928, p. 91], and 20–40 mm) and has fewer proglottids (28–37 vs. 50–65, 42–53, 76–86, “ungefähr 75” [Pintner, 1928, p. 103], and approx. 60 [based on fig. 3 of Shipley and Hornell, 1905, p. 54]) than *T. kazemii*, *T. sabae*, *T. salari*, *T. simile*, and *T. trygonis*, respectively. It is shorter in total length (4.5–7.3 vs. 20

mm) and has a greater number of proglottids (28–37 vs. 11–20) than *T. minutum*. *Tetragonocephalum georgei* n. sp. is also shorter in total length than *T. uarnak* (4.5–7.3 vs. up to 35 mm). Furthermore, this new species has a greater number of testes than *T. mackenziei* (27–45 vs. 10–14) and fewer testes than *T. passeyi* (27–45 vs. 54–73). *Tetragonocephalum georgei* n. sp. also differs from the *species inquirendum*, *T. yamagutii*, in possessing larger acetabula (60–90 wide and 60–88 long vs. 30–40 wide and 40–50 long) and fewer testes (27–45 vs. 54–56).

Tetragonocephalum levicorpum n. sp. (Figs. 1D–F, 4)

Description (based on 13 specimens: 12 whole-mounted specimens [7 immature, 5 mature]; 1 specimen prepared for SEM and its whole-mounted voucher): Worms 5.8–16.5 mm (9.7 ± 4.1; 5) long, euapolytic, maximum width at level of scolex, 17–30 (23 ± 4.7; 5) proglottids, acraspedote, non-laciniate (Fig. 1D). Scolex 542–752 (615 ± 58.6; 12) long by 413–633 (518 ± 73.3; 12) wide, consisting of scolex proper, apical modification of scolex proper, and apical organ, widest at level of scolex proper (Fig. 1E). Scolex proper 355–531 (428 ± 50.5; 11) long by 413–633 (518 ± 73.3; 12) wide, bearing 4 acetabula. Acetabula sucker-like in form, 102–129 (117 ± 7.7; 12; 24) long by 103–125 (111 ± 7.0; 12; 24) wide. Apical modification of scolex proper cylindrical, narrower than scolex proper, bearing apical organ. Apical organ large, globular in form, muscular, non-invaginable, non-retractable, 216–365 (291 ± 42.0; 11) long by 361–515 (457 ± 49.5; 12) wide, 144–267 (193 ± 35.3; 11) thick at apex.

Microtriches not visible on surfaces of apical organ (Fig. 4B), scolex proper (Fig. 4C), acetabula, nor strobila.

Cephalic peduncle absent. Immature proglottids 16–27 (21 ± 4.0; 5) in number, initially wider than long, becoming longer than

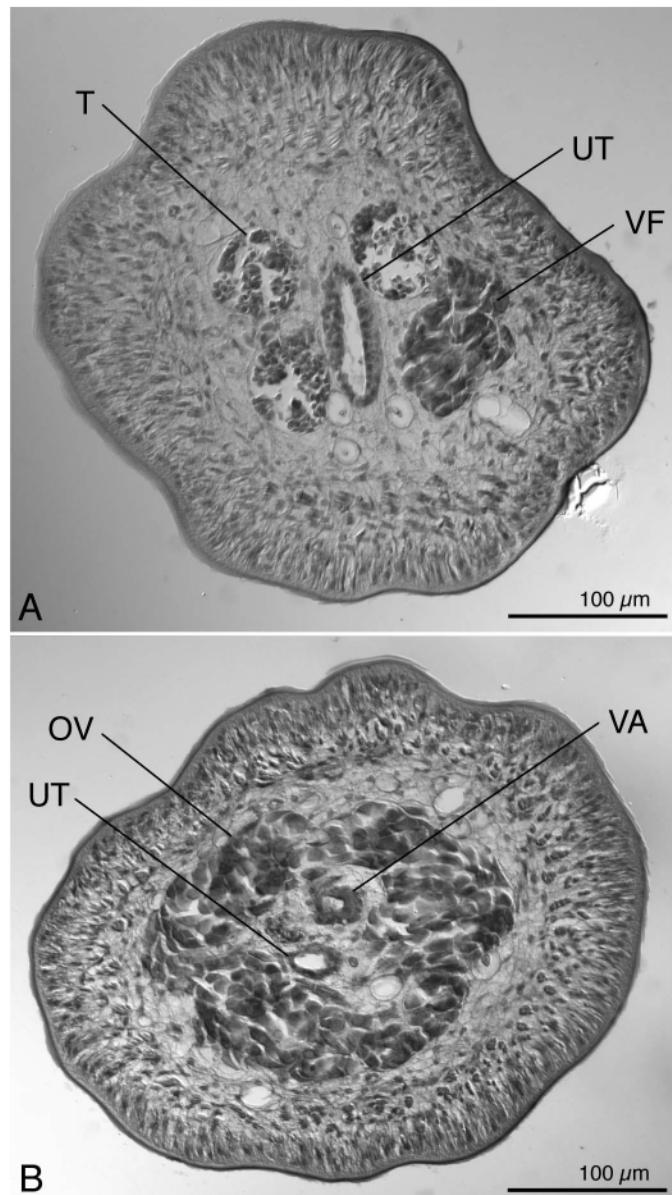


Figure 3. Photomicrographs of cross sections of a mature proglottid of *Tetragonocephalum georgei* n. sp. (paratype, USNM 1620834). (A) At level anterior to cirrus sac. (B) At level of ovary anterior to ovicapt. Abbreviations: OV, ovary; T, testis; UT, uterus; VA, vagina; VF, vitelline follicle.

wide with maturity; posterior-most immature proglottid 810–1,607 (1,012 ± 337.8; 5) long by 179–261 (205 ± 33.4; 5) wide. Mature proglottids 1–3 (2 ± 0.7; 5) in number, terminal mature proglottid 825–1,917 (1,286 ± 431.2; 5) long by 178–238 (199 ± 25.6; 5) wide. Gravid proglottids not observed. Testes 20–33 (24 ± 5.0; 5) in number, 16–43 (26 ± 8.6; 5; 15) long by 18–42 (33 ± 8.0; 5; 15) wide, extending from anterior margin of proglottid to anterior margin of cirrus sac, arranged in 2 irregular columns in dorso-ventral view (Fig. 1F), essentially 2 layers deep in cross section. Vas deferens minimal, essentially straight, visible extending from level of ovary to cirrus sac, entering cirrus sac at proximal end. External seminal vesicle absent. Internal seminal

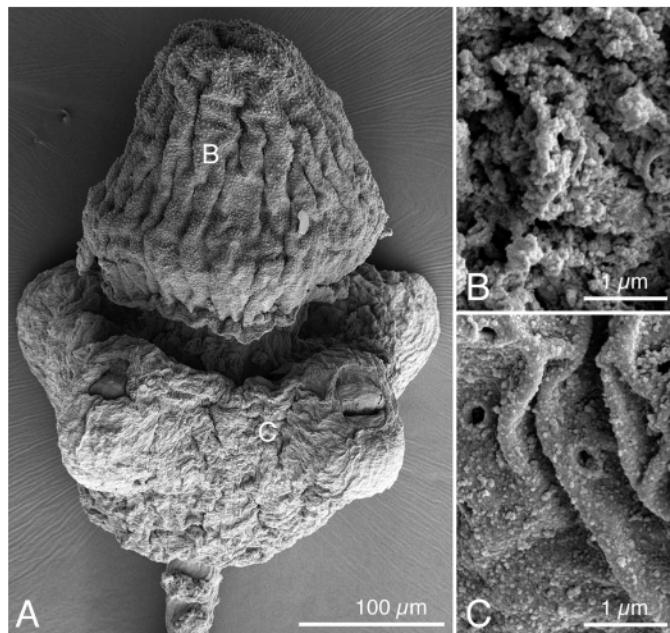


Figure 4. Scanning electron micrographs of *Tetragonocephalum levicorpum* n. sp. (A) Scolex; small letters indicate location of details shown in B–C. (B) Surface of apical organ. (C) Surface of scolex proper.

vesicle not observed. Cirrus sac pyriform, 91–164 (131 ± 28.6; 5) long by 66–107 (90 ± 18.6; 4) wide, oriented along long axis of proglottid, opening into genital atrium at its anterior margin, containing cirrus. Cirrus armed with spinitriches. Genital pores lateral, irregularly alternating, 41–54% (47 ± 5.0; 5) of proglottid length from posterior end. Genital atrium expansive, extending past midline of proglottid. Ovary narrowly dolioform (sensu Clopton, 2004) in dorso-ventral view, C-shaped in cross section, 150–455 (261 ± 133.6; 4) long by 74–93 (86 ± 8.4; 4) wide; ovicapt in posterior third of ovary. Mehlis' gland posterior to ovicapt. Vagina thick-walled, medial, essentially straight, extending anteriorly from ootype to genital atrium, opening into genital atrium at its proximal end posterior to cirrus sac; vaginal sphincter not observed. Vitellarium follicular; vitelline follicles 8–28 (15 ± 6.7; 5; 15) long by 13–36 (18 ± 5.9; 5; 15) wide, in 3 regions: anterior to genital atrium arranged in 1–2 irregular columns on each lateral margin, between genital atrium and ovary arranged in single compact field, and posterior to ovary arranged in single compact field. Uterus bisaccate, constricted at level of genital atrium, medial, extending from posterior margin of ovary to near anterior extent of field of testes. Excretory ducts in 2 lateral pairs. Eggs not observed.

Taxonomic summary

Type and only known host: *Urogymnus polylepis* (Bleeker), giant freshwater whipray (Myliobatiformes: Dasyatidae).

Type and only known locality: Pasar Beringin (03°17'47.04"N, 117°34'57.26"E), Celebes Sea, Tarakan, North Kalimantan, Indonesia (host specimen no. KA-393).

Site of infection: Spiral intestine.

Specimens deposited: Holotype (MZBCa 209) and 1 paratype (MZBCa 210); 5 paratypes (USNM 1620835–1620839); 6 paratypes (5 whole worms and 1 whole-mounted strobila voucher

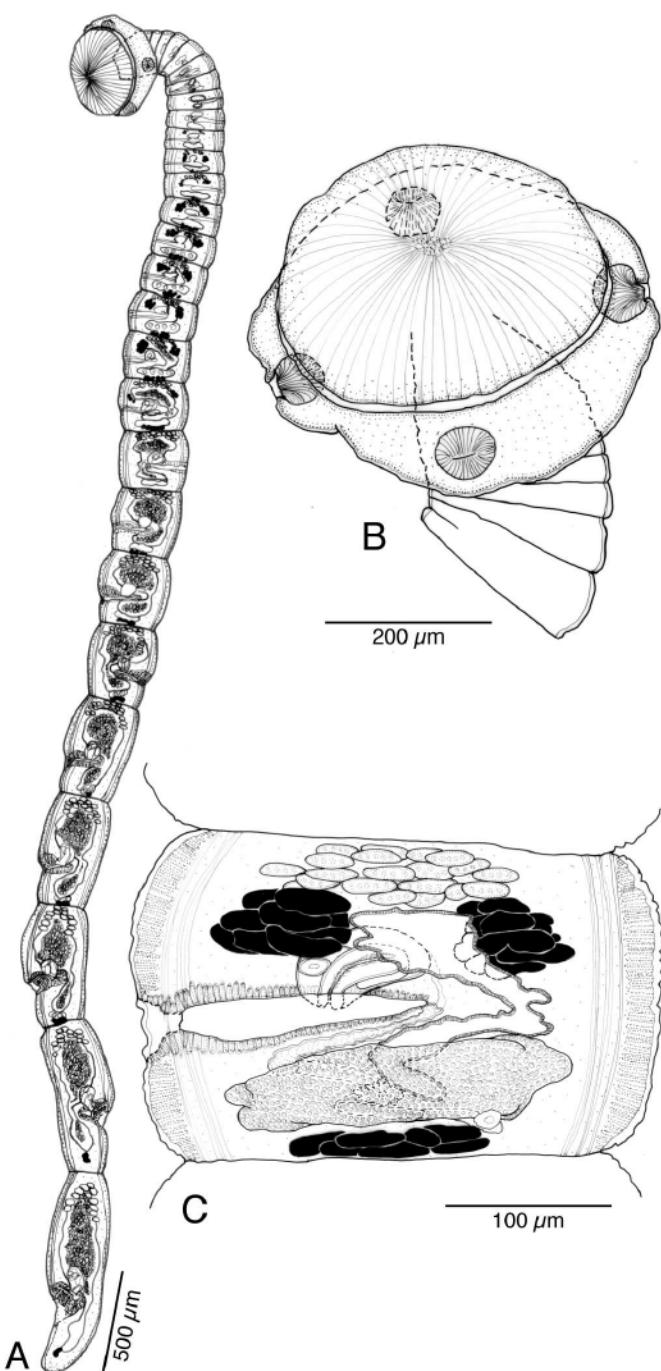


Figure 5. Line drawings of *Tetragonocephalum opimum* n. sp. (holotype, MZUM[P] 2020.5 [H]) (A) Whole worm. (B) Scolex. (C) Mature proglottid.

of scolex prepared for SEM; LRP 10268–10273); scolex prepared for SEM retained in the personal collection of KJ at the University of Kansas.

ZooBank registration: urn:lsid:zoobank.org:act:4F0BF035-761C-4014-9734-404A62FE1C2A.

Etymology: The specific epithet is derived from *levi* (L., slight) and *corpus* (L., body) emphasizing the narrow nature of the strobila of this species relative to its congeners.

Remarks

Its possession of an apical organ that is muscular, non-retractable, and dome-shaped, acraspedote proglottids, a bisaccate uterus, an expansive genital atrium, a compact ovary that is essentially oval in dorso-ventral view and C-shaped in cross section, testes that are restricted to the region anterior to the cirrus sac, and vitelline follicles arranged in 3 distinct regions places *Tetragonocephalum levicorpum* n. sp. as a member of *Tetragonocephalum*. This new species differs from 9 of the 10 valid species (i.e., all except *T. georgei*) in possessing an euapolytic rather than apolytic strobila. It further differs from *T. kazemii*, *T. salarii*, *T. simile*, *T. trygonis*, and *T. uarnak* in its shorter in total length (5.8–16.5 vs. 28.8–36.6, 23.5–35.9, approx. 21 [based on fig. 37 of Pintner, 1928, p. 91], 20–40, and up to 35 mm, respectively) and fewer proglottids (16–27 vs. 50–65, 76–86, “ungefähr 75” [Pintner, 1928, p. 103], approx. 60 [based on fig. 3 of Shipley and Hornell, 1905, p. 54], and 30–40, respectively). In addition, *T. levicorpum* n. sp. has fewer testes than *T. minutum*, *T. passeyi*, and *T. sabae* (20–33 vs. 83–63, 54–73, and 42–50, respectively) and a greater number of testes than *T. mackenziei* (20–33 vs. 10–14). A fewer number of testes further distinguishes *T. levicorpum* n. sp. from the species *inquirendum*, *T. yamagutii* (20–33 vs. 54–56). The new species can be distinguished from *T. georgei*—the only other euapolytic member of the genus—by its larger scolex (542–752 long by 413–633 wide vs. 313–460 long by 362–473 wide) and larger suckers (102–129 long by 103–125 wide vs. 60–90 long by 60–88 wide). The new species also possesses a less conspicuous genital atrium and genital pore, and a narrower strobila than *T. georgei*.

Tetragonocephalum opimum n. sp. (Fig. 5)

Description (based on 1 whole-mounted gravid specimen): Worm 6.9 mm long, apolytic; maximum width at middle of strobila; 34 proglottids, acraspedote, non-laciniate; length to first gravid proglottid 1.9 mm. Scolex 292 long and 477 wide, consisting of scolex proper, apical modification of scolex proper, and apical organ, widest at level of scolex proper. Scolex proper 477 wide, bearing 4 acetabula. Acetabula sucker-like in form, 61–69 (64 ± 3.5 ; 1; 4) long by 69–73 (71 ± 2.8 ; 1; 2) wide. Apical modification of scolex proper cylindrical, narrower than scolex proper, bearing apical organ. Apical organ large, globular in form, muscular, non-invaginable, non-retractable, 174 long by 399 wide.

Cephalic peduncle absent. Immature proglottids 20 in number, wider than long; posterior-most immature proglottid 150 long by 300 wide. Mature proglottids 3 in number; posterior-most mature proglottid 199 long by 330 wide. Gravid proglottids 11 in number; terminal proglottid 1,029 long by 280 wide. Testes 15–20 (17 ± 2.5 ; 1; 3) in number, 8–9 (8 ± 0.6 ; 1; 3) long by 30–33 (31 ± 1.5 ; 1; 3) wide, restricted to anterior region of proglottid, arranged in 4–5

highly irregular columns in dorso-ventral view, 2 layers deep in cross section. Vas deferens minimal, weakly sinuous, visible extending from level of ovary to cirrus sac, entering cirrus sac at proximal end. External seminal vesicle absent. Internal seminal vesicle not observed. Cirrus sac pyriform, 45 long by 89 wide, oriented essentially along the long axis of proglottid, opening into genital atrium at its anterior margin, containing coiled cirrus. Cirrus armed with spinithriches. Genital pores lateral, irregularly alternating, 39% of proglottid length from posterior end. Genital atrium expansive, extending to near midline of proglottid. Ovary very shallowly dolioform (sensu Clopton, 2004) in dorso-ventral view, C-shaped in cross section, 54 long by 209 wide, symmetrical; ovicapt in middle of ovary. Mehlis' gland posterior to ovicapt. Vagina thick-walled, medial, weakly sinuous, extending anteriorly from ootype to genital atrium, opening into genital atrium at its proximal end posterior to cirrus sac; vaginal sphincter not observed. Vitellarium follicular; vitelline follicles 8–14 (10 ± 3.2; 1; 3) long by 37–65 (49 ± 14.6; 1; 3) wide, in 2 regions: anterior to genital atrium arranged in 2–3 irregular columns on each lateral margin and posterior to ovary arranged in single compact field; vitelline follicles between genital atrium and ovary absent. Uterus bisaccate, constricted at level of genital atrium, medial, extending from near posterior margin of ovary to near posterior extent of field of testes. Excretory ducts in 2 lateral pairs. Eggs details not available from single specimen.

Taxonomic summary

Type and only known host: *Urogymnus polylepis* (Bleeker), giant freshwater whipray (Myliobatiformes: Dasyatidae).

Type and only known locality: Kampung Abai (05°41'N, 118°23'E), Kinabatangan River, Sabah, Malaysia (host specimen no. BO-108).

Site of infection: Spiral intestine.

Specimen deposited: Holotype (MZUM[P] 2020.5 [H]).

ZooBank registration: urn:lsid:zoobank.org:act:BA5671F9-0E48-4EC7-874A-6DC15475D0DE.

Etymology: The specific epithet is derived from *optimus* (L., plump, fertile) recalling the width of the proglottids and apolytic nature of this species.

Remarks

The criteria for placing this new species in *Tetragonocephalum* are similar to those for the previous 2 new species. It possesses a muscular, non-retractable, dome-shaped apical organ, acraspedote proglottids, a bisaccate uterus, an expansive genital atrium, a compact ovary that is essentially oval in dorso-ventral view and C-shaped in cross section, testes that are restricted to the region anterior to the cirrus sac, and vitelline follicles arranged in 2 distinct regions. Although only a single specimen of *T. opimum* n. sp. was available for study, this species is easily distinguished from its 11 valid congeners and the *species inquirendum*, *T. yamagutii*, based on the following criteria. With respect to the 11 valid species in the genus, *T. opimum* n. sp. can be distinguished from *T. kazemii*, *T. simile*, and *T. trygonis* based on its shorter total length (6.9 vs. 28.8–36.6, approx. 21 [based on fig. 37 of Pintner, 1928, p. 91], and 20–40 mm, respectively) and fewer proglottids (34 vs. 50–65, “ungefähr 75” [Pintner, 1928, p. 103], and approx. 60 [based on fig. 3 of Shipley and Hornell, 1905, p. 54], respectively). It differs from *T. minutum* in its conspicuously shorter total length

(6.9 vs. up to 35 mm) and greater number of proglottids (34 vs. 11–20). It differs from *T. georgei*, *T. levicorpum*, *T. mackenziei*, *T. passeyi*, *T. sabae*, and *T. salarii* in its possession of vitelline follicles arranged in 2, rather than 3, distinct regions (i.e., vitelline follicles are absent in the region between the genital atrium and the ovary). *Tetragonocephalum opimum* n. sp. further differs from *T. georgei* and *T. levicorpum* in that it is apolytic rather than euapolytic, from *T. mackenziei* in that it has a much wider scolex proper (477 vs. 213–288), and from *T. passeyi*, *T. sabae*, and *T. salarii* in its possession of fewer testes (15–20 vs. 54–73, 42–50, 30–38, respectively). Moreover, *T. opimum* n. sp. is much shorter in total length (6.9 vs. up to 35 mm) and has a shorter terminal gravid proglottid (1,029 vs. 5,000) than *T. uarnak*. It further differs from *T. yamagutii* in bearing larger suckers (61–69 long by 69–73 wide vs. 30–40 long by 40–50 wide) and fewer testes (15–20 vs. 54–56) than *T. yamagutii*.

DISCUSSION

Tetragonocephalum is the sole genus in the Tetragonocephalidae (see Jensen et al., 2016). With the descriptions of *T. georgei*, *T. levicorpum*, and *T. opimum* herein, the number of valid species of *Tetragonocephalum* has increased to 12. Reports of a number of taxa for which morphological data (Caira et al., 2001) or sequence data (Caira et al., 2014; Jensen et al., 2016) have been included in large-scale phylogenetic studies likely represent 2–3 additional, undescribed species. These are *Tetragonocephalum* sp. from *Himantura australis* Last, White and Naylor (as *Himantura* sp.) in Caira et al. (2001), and *Tetragonocephalum* n. sp. 1 (as *Tetragonocephalum* sp. in Caira et al., 2014) from *Urogymnus asperrimus* (Bloch and Schneider) and *Tetragonocephalum* n. sp. 2 from *Pateobatis jenkinsii* (Annandale) (as *Himantura jenkinsii* [Annandale]) in Jensen et al. (2016). As a *species inquirendum*, *T. yamagutii* could be found to be valid if its type material were examined and the species re-described. In total, we estimate the diversity in the genus likely will exceed 15 species.

The morphologies of the 12 valid species are not equally well known. While the original descriptions of the 8 species (see Table I) described within the last 20 yr are comprehensive and detailed, relatively little morphological data were presented in the older descriptions of the other 4 species. Specifically, additional work on the type species, *T. trygonis*, as well as *T. minutum*, *T. simile*, and *T. uarnak*, ideally from their type hosts and as close to the type localities as possible would be highly informative.

Authorities attributable to the names of several of the older species in the genus are somewhat problematic. The confusion centers on the first use of the combinations *Tetragonocephalum minutum*, *Tetr. simile*, and *Tetr. uarnak*. All 3 species were originally described as members of *Tylocephalum* (i.e., *Tylocephalum minutum* Southwell, 1925, *Tylocephalum simile* Pintner, 1928, and *Tylocephalum uarnak* Shipley and Hornell, 1906) during a period when *Tetragonocephalum* was considered to be a junior synonym of *Tylocephalum* (see Shipley and Hornell, 1906; Southwell, 1925). Subsequently, Poche (1926) and Pintner (1928) made only conditional statements about the need to resurrect *Tetragonocephalum* as a valid genus but only after specific features could be confirmed in relevant taxa. As such, Pintner (1928) established *Tylo. simile*, but contrary to Ivanov and Campbell (2000), was not responsible for the combination *Tetr. simile*. Similarly, contrary to Jensen (2005) and Jensen et al.

(2017), he did not create the combination *Tetr. uarnak* (see Jensen, 2005; Jensen et al., 2017). To our knowledge, Perrenoud (1931, p. 551) was the first to use the combinations *Tetr. minutum*, *Tetr. simile*, and *Tetr. uarnak*, and we have indicated these revised authorities in Table I.

The identification of the suite of morphological features unique to members of *Tetragonocephalum* (see above) calls for a re-evaluation of the generic assignment of several species in other lecanicephalidean genera. The illustrations and descriptions of the following 6 species of *Tylocephalum* and 1 species of *Cephalobothrium* Shipley and Hornell, 1906, suggest the presence of 1 or more of these features. *Tylocephalum alii* Andhare and Shinde, 1994, was depicted with what appears to be an expansive genital atrium, testes restricted to the region anterior to the cirrus sac, and a compact ovary in illustrations in the original description (Andhare and Shinde, 1994). *Tylocephalum chiraleensis* Vijayalakshmi and Sanaka, 1995, was described as possessing a bisaccate uterus and testes restricted to the region anterior to the cirrus sac (Vijayalakshmi and Sanaka, 1995). *Tylocephalum choudhurai* Pramanik and Manna, 2007, *Tylocephalum haldari* Pramanik and Manna, 2007, and *Tylocephalum krishnai* Pramanik and Manna, 2007, were described as possessing testes restricted to the region anterior to the cirrus sac (Pramanik and Manna, 2007). Illustrations accompanying the descriptions of *Tylocephalum girindrai* Pramanik and Manna, 2007, and *Cephalobothrium longisegmentum* Wang, 1984, show testes restricted to anterior to the cirrus sac (Pramanik and Manna, 2007, and Wang, 1984, respectively). All 7 species were also illustrated and/or described as possessing proglottids that are acraspedote. However, the descriptions of these species also include features that are inconsistent with some of the features considered characteristic of *Tetragonocephalum*: for example, a shallow or inconspicuous rather than an expansive genital atrium in all 7 species; U- or V-shaped, rather than C-shaped, ovary in *Tylo. chiraleensis*, *Tylo. choudhurai*, *Tylo. girindrai*, *Tylo. haldari*, and *Tylo. krishnai*; a saccate rather than a bisaccate uterus in *Tylo. choudhurai*, *Tylo. haldari*, *Tylo. krishnai*, and *C. longisegmentum*; and vitelline follicles along the lateral margins of the proglottid rather than in 2 or 3 regions in *Tylo. alii*, *Tylo. haldari*, *Tylo. girindrai*, and *Tylo. krishnai*. The combination of features described for these 7 species does not allow any to be definitively assigned to a genus in the Tetragonocephalidae or Cephalobothriidae. The main issue in all 7 cases is that the original descriptions and accompanying illustrations are substandard and, in several cases, internally inconsistent. Thus, *Tylo. alii*, *Tylo. chiraleensis*, *Tylo. choudhurai*, *Tylo. girindrai*, *Tylo. haldari*, *Tylo. krishnai*, and *C. longisegmentum* should be considered species *incertae sedis* in the Lecanicephalidea until the morphology of each is confirmed through examination of type or newly collected material which will allow for more definitive generic assignments.

In *T. opimum*, we describe the first species of *Tetragonocephalum* lacking vitelline follicles in the region of the proglottid between the genital atrium and the ovary. Until now, variation in the arrangement of vitelline follicles in species of *Tetragonocephalum* has received little attention. The arrangement of the vitelline follicles was not reported in the original descriptions of several of the species described early on (i.e., *T. minutum*, *T. trygonis*, and *T. uarnak*; see Shipley and Hornell, 1905, 1906; Southwell, 1925). Similarly, Pintner (1928) did not explicitly describe the arrangement of the vitelline follicles for *T. simile*. The

more recent descriptions of species of *Tetragonocephalum* by Jensen (2005) and Roohi Aminjan and Malek (2016, 2017) describe vitelline follicle arrangement in 3 distinct regions: anterior to the genital atrium, between the genital atrium and the ovary, and posterior to the ovary. Jensen et al. (2016), in their diagnosis of the family Tetragonocephalidae, were the first to suggest that the vitelline follicles between the genital atrium and ovary may be absent, based on observations made on specimens referred to as *Tetragonocephalum* n. sp. 2 for which sequence data were generated in that study. How common this vitelline condition is in the genus remains to be determined.

Compared to that of other lecanicephalideans (see, e.g., Jensen, 2005; Jensen et al., 2011; Mojica et al., 2014, Herzog and Jensen, 2017), the microthrix pattern of *Tetragonocephalum* is rather mundane. Collectively, the 6 species of *Tetragonocephalum* for which microthrix patterns have been characterized to date (see Jensen, 2005; Roohi Aminjan and Malek 2016, 2017; this study) exhibited only filiriches of varying lengths throughout their scolex and strobilar surfaces. Complicating characterization of microthrix patterns in members of this genus is the fact that surfaces of the apical organ and scolex proper often appear disrupted (Fig. 4; see also, e.g., Roohi Aminjan and Malek 2016), host tissue remains attached to the apical organ (see Fig. 2A), and acetabula are recessed, prohibiting examination of these surfaces. As a consequence, we recommend authors refrain from using microtriches to distinguish among species.

Relatively little is known about lecanicephalidean tapeworms parasitizing species of *Urogymnus*. While this is the first report of lecanicephalideans from *U. polylepis*, only 2 of the remaining 5 species of *Urogymnus* (see Last et al., 2016b) have previously been reported to host lecanicephalideans. Southwell (1925, p. 287) described *Tetr. minutum* (as *Tylo. minutum*) from a host he reported as “*Urogymnus* sp. (*asperrimus*?),” and Herzog and Jensen (2017) described 2 species of *Corollapex* Herzog and Jensen, 2017, from *Urogymnus granulatus* (Macleay). In addition, a specimen each of an undescribed species of *Tetragonocephalum* from *U. asperrimus* and *Polypocephalus* Braun, 1878, from *U. granulatus* were included in the phylogenetic analyses of Caira et al. (2014) and Jensen et al. (2016). Whether this is the full complement of lecanicephalidean generic diversity parasitizing species of *Urogymnus* remains to be determined. To date, no lecanicephalideans have been reported from *Urogymnus acanthobothrium* Last, White and Kyne, *Urogymnus dalyensis* (Last and Manjaji-Matsumoto), or *Urogymnus lobistoma* (Manjaji-Matsumoto and Last). With respect to the cestode fauna of *U. polylepis* overall, the description of the 3 new species of *Tetragonocephalum* herein increases the total number of known cestodes from this stingray species to 13 species, representing 6 genera and 4 orders (i.e., Lecanicephalidea, Onchoproteocephalidea, Rhinebothriidea, and Trypanorhyncha (Fyler and Caira, 2006; Healy, 2006; Schaeffner and Beveridge, 2014; Caira et al., 2017).

The substantial amount of revisionary taxonomic work on the identities of stingrays in Southeast Asia that has occurred over the last 2 decades (e.g., Manjaji, 2004; Borsa et al., 2013; Last et al., 2012, 2016a; Fernando et al., 2019) has revealed issues with the true identities of the type hosts of a number of species of *Tetragonocephalum*. This is primarily because it is now clear that type host species of record of many species belong to species complexes. For example, 3 species of *Tetragonocephalum* have been described from hosts originally identified as *Trygon walga*

Müller and Henle in the waters off India (off Chennai [as Madras] Tamil Nadu) and Sri Lanka (Table I). This taxon, assigned to the new genus *Brevitrygon* Last, Naylor and Manjaji-Matsumoto (see Last et al., 2016a; Eschmeyer et al., 2019), is a complex of species consisting of 4 described species (see Last et al., 2016b) and 1 undescribed species referred to as *Brevitrygon* sp. 1 by Fernando et al. (2019). Three of the 5 species occur in India and/or Sri Lanka (see, e.g., Raje et al., 2007; Last et al., 2016a). *Brevitrygon walga* (Müller and Henle) occurs off the northwestern coast of India, *Brevitrygon imbricata* (Bloch and Schneider) occurs off the eastern coast of India, and *Brevitrygon* sp. 1 has been reported from the water of nearby Sri Lanka. Until the full extent of the distribution of *Brevitrygon* sp. 1 is known, the type host of the 3 species of *Tetragonocephalum* described from the eastern coast of India and Sri Lanka (i.e., *T. simile*, *T. trygonis*, and *T. yamagutii*) could be either *B. imbricata* or *Brevitrygon* sp. 1.

Similarly, *Tetragonocephalum uarnak* was described from stingrays identified as “*Trygon uarnak*” from Sri Lanka (Shipley and Hornell, 1906). Last et al. (2016b) considered it also as a complex of species with 3 species occurring off the eastern coast of India: *Himantura leoparda* Manjaji-Matsumoto and Last, *H. uarnak*, and *Himantura undulata* (Bleeker). Complicating matters further is the fact that Fernando et al. (2019) considered the species in this complex found in Sri Lanka to be *Himantura tutul* Borsa, Durand, Shen, Arlyza, Solihin and Berrebi, even though other authors (e.g., Last et al., 2016a; Eschmeyer et al., 2019) consider *H. tutul* to be a synonym of *H. uarnak*. Consequently, the type host for *Tetr. uarnak* off Sri Lanka is 1 of the 4 species but cannot be definitively determined at this time.

Finally, both, *Urogymnus asperimus* and *U. granulatus* have been reported to occur off Sri Lanka (Last et al., 2016b; Fernando et al., 2019). Thus, the identity of the type host species of *T. minutum* from Sri Lanka is also in question. Needless to say, identifications of hosts in all of these groups must be re-evaluated in light of ongoing elasmobranch taxonomic work. The potential for recognition of additional batoid novelty and revisions of geographic distributions for members of each of these complexes is high.

Despite issues with specific identities of hosts, most genera of lecanicephalideans are restricted to a single genus or family of batoid hosts (Jensen et al., 2016). *Tetragonocephalum* fits that pattern. By far the majority of species of *Tetragonocephalum* parasitize members of the stingray family Dasyatidae (Myliobatiformes). The classification of the Dasyatidae was revised most recently by Last et al. (2016a), who recognized 4 subfamilies: the Dasyatinae, the Hypolophinae Stormer, the Neotrygoninae Last, Naylor and Manjaji-Matsumoto, and the Urogymninae Gray. Host records of valid species, the *species inquirendum*, and species not yet formally described of *Tetragonocephalum* (see Table I) include species in 2 of the 4 subfamilies of dasyatids (i.e., the Hypolophinae and Urogymninae). More specifically, species have been reported from the hypolophine genus *Pastinachus* Rüppell (see Roohi Aminjan and Malek, 2017), as well as from the urogymnine genera *Brevitrygon* (see Shipley and Hornell, 1905; Pintner, 1928; Muralidhar, 1988), *Himantura* Müller and Henle (see Shipley and Hornell, 1906; Caira et al., 2001; Jensen, 2005; Jensen et al., 2016), *Maculabatis* Last, Naylor and Manjaji-Matsumoto (see Golestaninasab et al., 2014; Roohi Aminjan and Malek, 2016), *Pateobatis* Last, Naylor and Manjaji-Matsumoto (see Jensen et al., 2016), and *Urogymnus* Müller and Henle (see

Southwell, 1925; Caira et al., 2014; Jensen et al., 2016; this study). Future efforts aimed at discovering additional novel species of *Tetragonocephalum* should focus on the dasyatid host species not previously examined for *Tetragonocephalum*, with emphasis on the more speciose dasyatid genera *Himantura*, *Maculabatis*, *Pastinachus*, *Pateobatis*, and *Urogymnus*.

The distribution of valid species and known but undescribed species of *Tetragonocephalum*, and the *species inquirendum*, currently is restricted to the Indo-West Pacific, including the Gulf of Oman (Golestaninasab et al., 2014; Roohi Aminjan and Malek, 2016, 2017), India and Sri Lanka (Shipley and Hornell, 1905, 1906; Pintner, 1928; Muralidhar 1988), and Australia (Caira et al., 2001; Jensen 2005; Jensen et al., 2016). This study expands the known distribution of *Tetragonocephalum* within that larger region to include Malaysian and Indonesian Borneo.

This is the first report of *Tetragonocephalum* from a host in freshwater. All previous records from the Indo-West Pacific region came from hosts in the marine environment. Of the 2 host specimens found to be parasitized by members of *Tetragonocephalum*, 1 (i.e., BO-108) was definitely collected from freshwater; it was collected in the Kinabatangan River (Sabah, Malaysia) approximately 16 km from the river's mouth. This specimen hosted both *T. georgei* and the single specimen of *T. opimum*. The provenance of the second specimens (i.e., KA-393), host of *T. levicorpum*, is somewhat less certain. This specimen was purchased at the Pasar Beringin fish market in Tarakan, on the island of Tarakan (North Kalimantan, Indonesia). The island is located just east of the mouths of the Sesayap and Sekata Rivers. Thus, this host specimen may have been collected from either of the 2 rivers or their surrounding estuaries. It is also possible that the host was collected from the Celebes Sea. The fact that *U. polylepis* has been characterized as either an obligate freshwater (e.g., Monkolprasit and Roberts, 1990; Compagno and Cook, 1995; Martin, 2005; Last and Manjaji-Matsumoto, 2008) or a euryhaline species (e.g., Last et al., 2010; Lucifora et al., 2015; Grant et al., 2019) leads us to suspect that this second host specimen was collected from 1 of the 2 rivers or their low salinity estuaries. If so, this would make *T. levicorpum* the third lecanicephalidean reported from freshwater. In any case, it would be interesting to examine the other obligate freshwater dasyatids (see Grant et al., 2019) in the Indo-West Pacific (e.g., *Fluvitrygon signifer* [Compagno and Roberts], *Fluvitrygon oxyrhynchus* [Sauvage], *Fluvitrygon kittipongi* [Vidhayanon and Roberts], *Hemitrygon laosensis* [Roberts and Karnasuta], and *Makararaja chindwinensis* Roberts), and other euryhaline species from that region (e.g., *Hemitrygon bennetti* [Müller and Henle] and *U. dalyensis*) for *Tetragonocephalum*.

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