A new genus and two new species of Anteroporidae (Cestoda: Lecanicephalidea) from the darkspotted numbfish, *Narcine maculata* (Torpediniformes: Narcinidae), off Malaysian Borneo

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Abstract: The cestode fauna of the darkspotted numbfish, *Narcine maculata* (Shaw) (Torpediniformes: Narcinidae), from Malaysian Borneo was examined for the first time. This work resulted in the discovery of a new genus and two new species of Anteroporidae (Lecanicephalidea). *Sesquipedalapex comicus* gen. n., sp. n. was erected on the basis of the peculiarities of its scolex, in particular its possession of an extremely long apical modification of the scolex proper, which readily distinguishes it from the other genus in the family. The genus is also distinct in its possession of acetabula that are in the form of suckers, rather than bothridiate in form. This species was found to deeply embed its elongate apical structure for much of its length within the intestinal mucosa, provoking a papilliform expansion of the outer wall of the spiral intestine at the site of attachment. The second new species, *Anteropora klosmamorphis* sp. n., is readily distinguished from its congeners on the basis of testis number and bothridial shape. Both new species are hyperapolytic. The diagnosis of Anteroporidae is amended to accommodate both new taxa. This increases the total number of genera in the family to two, and the total number of species to five.

Keywords: Cestoda, Lecanicephalidea, *Narcine*, new genus, Malaysian Borneo

The darkspotted numbfish, *Narcine maculata* (Shaw), was examined for cestodes for the first time. A remarkably large number of detached proglottids was observed upon examination of the contents of the spiral intestine. Closer investigation revealed that these detached proglottids represented two different hyperapolytic species, both belonging to the lecanicephalidean family Anteroporidae Euzet, 1994. The scolices and strobilae of one of these species were subsequently found deeply embedded in the mucosa of the spiral intestine. The latter species was determined to represent a new genus; the other a new species of *Anteropora* Subhadrach, 1955. These new taxa are described herein and the familial diagnosis is emended to include this, the second genus of Anteroporidae.

MATERIALS AND METHODS

A female specimen of *Narcine maculata* measuring 35.5 cm in total length, was collected using a bottom trawl by the Kuching Fisheries vessel K. K. Manchong, off the coast of southern Sarawak in Malaysian Borneo (02°49'01.2"N, 110°52'47.16"E), in the South China Sea in April, 2004. The spiral intestine was

removed, opened with a longitudinal incision, fixed in 10% buffered formalin in the field, and subsequently transferred to 70% ethanol for storage. Images of the host (No. BO-408) can be viewed in the elasmobranch host component (<http://tapeworm-db.uconn.edu/hosts.php>) of the Global Cestode Database (<http://tapeworms.uconn.edu>). Tapeworms were removed from the spiral intestine in the laboratory. Entire worms, scolices, strobilar fragments, and detached proglottids were prepared as whole mounts for light microscopy as follows. Specimens were stained with Delafield's haematoxylin, dehydrated in a graded ethanol series, cleared in methyl salicylate, and mounted on glass slides in Canada balsam. Specimens for serial sectioning were dehydrated in a graded ethanol series, stained with fast green, cleared in xylene, and embedded in paraffin. Serial sections were cut at 6 µm intervals with an Olympus CUT4060 retracting rotary microtome, and were subsequently attached to glass slides with 10% sodium silicate, stained in Delafield's haematoxylin, counterstained in eosin, cleared in xylene, and mounted in Canada balsam. Semi-permanent egg mounts were prepared as follows: gravid proglottids were placed in lactophenol for 1 h, transferred to glass slides, broken open with insect pins, and mounted in lactophenol under a coverslip ringed with clear nail polish. Specimens for scanning electron microscopy (SEM) were transferred

to distilled water, post-fixed in 1% osmium tetroxide overnight, dehydrated in a graded ethanol series, transferred to hexamethyldisilazane (Ted Pella, Inc., Redding, California) and, after removal of the latter, allowed to air dry. Specimens were subsequently mounted on aluminium stubs on double-sided carbon tape, and sputter coated with 35 nm of gold/palladium and examined with a LEO/Zeiss 1550 field emission scanning electron microscope.

All aspects of light microscopy were conducted using a Zeiss Axioskop 2 compound microscope. Illustrations were prepared with the aid of a drawing tube. Photographs were taken using a Leica DFC 480 digital camera. Measurements were made using an ocular micrometer or the image analysis software OpenLab Demo 4.0.4 and are given in micrometres unless otherwise stated. For each measurement, the range is followed in parentheses by the mean, standard deviation, number of worms measured, and number of measurements taken if more than one measurement was taken per worm.

Museum abbreviations used are as follows: IPCAS, Institute of Parasitology, Academy of Sciences of the Czech Republic, České Budějovice, Czech Republic; LRP, Lawrence R. Penner Parasitology Collection, University of Connecticut, Storrs, Connecticut, USA; MZUM(P), Muzium Zoologi, Universiti Malaya, Kuala Lumpur, Malaysia; SBC, Sarawak Biodiversity Center, Kuching, Sarawak, Malaysia; USNPC, United States National Parasite Collection, Beltsville, Maryland, USA. Microthrix terminology follows Chervy (2009). Scolex terminology follows Caira et al. (1999).

RESULTS

Sesquipedalapex gen. n.

Diagnosis: Worms hyperapolytic. Scolex with 4 acetabula and apical modification of scolex proper housing apical organ; acetabula simple, sessile, sucker-like, facially unmodified; apical modification of scolex proper highly elongated, with apical aperture, expanded at apex to house apical organ; apical organ muscular and glandular, non-eversible; posterior portion of scolex posterior to acetabula elongate, containing glandular tissue. Proglottids craspedote; detached proglottids with conspicuous anterior, vacuous spherical region, anterior fifth of surface covered with gladiate spinitriches. Testes 6, in single column anterior to ovary. Vas deferens extending from near oötype to cirrus-sac. External and internal seminal vesicles absent. Cirrus-sac elliptical; cirrus armed. Ovary irregularly lobed in frontal view, irregular in cross-section; each lobe consisting of ~3 sublobes. Vagina extending from oötype along poral side of proglottid to enter genital atrium posterior to or at same level as cirrus-sac. Genital pores marginal to submarginal, irregularly alternating. Uterus saccate, extending along median line of proglottid to anterior margin of field of testes. Vitellarium follicular; follicles in 2 lateral fields; each field consisting of 1 to 2 irregular columns of follicles, extending from near posterior margin proglottid to level of genital pore. Excretory ducts 4, arranged in 1 dorsal and 1 ventral pair, branched, opening to outside at multiple points along

length of scolex and in velum at posterior of proglottids. Eggs single, spherical, with numerous small regularly spaced surface protuberances, without filaments. Parasites of numbfishes (Narcinidae) in the South China Sea. Anteroporidae, Lecanicephalidea. Type and only known species: *Sesquipedalapex comicus* sp. n.

E t y m o l o g y: From *sesquipedalis* (adj., L., one and one-half feet in length) and *apex* (noun, masc., L., apex or tip), referring to the excessively long apical modification of the scolex proper.

Remarks. The fact that *Sesquipedalapex* is hyperapolytic and bears proglottids with few testes (4 or 6) arranged in a single column, places the genus in the Anteroporidae. It differs conspicuously from *Anteropora*, the only other genus in the family, in its possession of an extremely long apical modification of the scolex proper, rather than one that is small and cone-like. In addition, its acetabula are entirely sessile (rather than free posteriorly) and it exhibits a concentration of glandular tissue in the scolex proper posterior to the acetabula that is not seen in *Anteropora*. Furthermore, *Anteropora* does not appear to exhibit excretory ducts that open to the outside throughout the length of the scolex, as is seen in *Sesquipedalapex*. However, while these criteria serve to distinguish *Sesquipedalapex* from *Anteropora japonica* (Yamaguti, 1934) Euzet, 1994 and *Anteropora leelongi* Jensen, 2005, the fact that *Anteropora indica* Subhadrappa, 1955 is known only from detached proglottids, limits the application of these criteria with respect to this species at this time.

Sesquipedalapex comicus sp. n.

Figs. 1–3

Description (Based on 1 complete strobila with scolex without apical organ, 6 incomplete worms with scolices, 3 incomplete worms with scolices without apical organ, 3 apical organs, 10 strobilar fragments, 10 detached mature and 10 detached gravid proglottids; cross-section series of 2 detached mature and 1 detached gravid proglottid; 4 scolices, 1 strobila, 2 detached proglottids, and 1 gravid proglottid disrupted to reveal eggs examined with SEM; 4 lactophenol preparations of eggs).

Worms up to at least 47.4 mm long; maximum width at terminal proglottid; proglottids up to 372 in number, hyperapolytic. Scolex with 4 acetabula, highly elongated apical modification of scolex proper and apical organ, 727–4,668 ($3,091 \pm 1,411$; 7) long by 143–221 (187 ± 25 ; 10) wide at level of acetabula; scolex proper posterior to acetabula extensive, 220–862 (455 ± 202 ; 10) long by 69–221 (173 ± 49 ; 10) wide, containing intensely-staining glandular tissue. Acetabula in form of suckers, round to oval, 68–117 (93 ± 13 ; 10; 25) long by 62–96 (74 ± 10 ; 10; 23) wide. Apical modification of scolex proper elongate, 420–4,317 ($3,051 \pm 1,486$; 6) long by 94–308 (143 ± 60 ; 11) wide, muscular, with aperture at apex, housing apical organ. Apical organ variable in shape, 102–209 (143 ± 34 ; 9) long by 140–230 (183 ± 29 ; 9)

Fig. 1. Line drawings of *Sesquipedalapex comicus* sp. n. **A** – scolex; **B** – apical modification of scolex proper and apical organ; **C** – posterior region of scolex proper; **D** – whole worm; **E** – detached proglottid (arrowheads indicate location of sections in Fig. 3K and L).

wide, non-eversible, muscular, with dispersed glandular tissue. Cephalic peduncle absent.

Scolex proper (Fig. 2D, E, K), suckers (Fig. 2G, H), and apical modification of scolex proper (Fig. 2C) with acicular to capilliform filitriches; sucker rims also with rostrate spinitriches with irregular, broad bases (Fig. 2G, H); anterior-most region of apical modification of scolex proper also with narrow rostrate spinitriches with inconspicuous bases (Fig. 2C). Proglottids with capilliform filitriches (Fig. 2L–N), and gladiate spinitriches restricted to anterior spherical region (Fig. 2L) and scolopate spinitriches restricted to posterior margins (Fig. 2M, N).

Proglottids craspedote, non-lacinate; immature proglottids initially wider than long, becoming longer than wide, maximum width 200–350 (289 ± 45 ; 10). Terminal immature proglottids 331–787 (594 ± 130 ; 10) long by 173–305 (260 ± 48 ; 10) wide. Detached mature and gravid proglottids conical or teardrop-shaped, with conspicuous anterior vacuous spherical region; detached mature proglottids 891–1,362 ($1,133 \pm 179$; 10) long by 357–427 (387 ± 26 ; 10) wide; detached gravid proglottids 1,147–1,622 ($1,399 \pm 171$; 10) long by 408–574 (466 ± 47 ; 10) wide; anterior spherical region 304–545 (429 ± 86 ; 10) long by 341–427 (380 ± 27 ; 10) wide in detached mature proglottids, 317–611 (477 ± 104 ; 10) long by 384–515 (453 ± 39 ; 10) wide in detached gravid proglottids. Testes 6 (6 ± 0 ; 31) in number, arranged in single column anterior to ovary, 56–169 (94 ± 23 ; 20; 79) long by 84–223 (161 ± 32 ; 20; 79) wide in detached mature and gravid proglottids; anterior-most testis often largest, conspicuously separated from remaining testes. Vas deferens sinuous, extending along poral side of proglottid from oötype to enter cirrus-sac at anterior margin. External and internal seminal vesicles absent. Cirrus-sac elliptical, anterior to or overlapping with second anterior-most testis, oriented perpendicular to proglottid or angled slightly anteriorly, 105–185 (140 ± 29 ; 10) long by 30–59 (47 ± 9 ; 10) wide in detached mature proglottids, 140–200 (172 ± 24 ; 10) long by 55–75 (63 ± 7 ; 10) wide in detached gravid proglottids. Cirrus coiled, armed with spinitriches. Genital pores marginal to submarginal, irregularly alternating, 45–54% ($50\% \pm 3$; 10) from posterior end of proglottid in detached mature proglottids, 45–55% ($52\% \pm 3$; 10) from posterior end in detached gravid proglottids; genital atrium at level of second anterior-most testis. Ovary irregularly lobed in shape in frontal view, irregular in cross-section, 59–122 (90 ± 20 ; 10) long by 92–228 (148 ± 45 ; 10) wide in detached mature proglottids, 57–147 (103 ± 27 ; 10) long by 178–323 (257 ± 48 ; 10) wide in detached gravid proglottids; each lobe consisting of ~3 lobules. Vagina weakly sinuous, initially thick-walled with layer of large, intensely staining cells, extending from oötype along poral side of proglottid to enter genital atrium posterior to, or at same level as, cirrus-sac; seminal receptacle not observed; vaginal sphincter absent. Uterus thick-walled, extending from level of ovarian bridge along median line of

proglottid to anterior extent of field of testes; uterine duct entering uterus at approximately midlevel; uterine pore absent. Vitellarium follicular; vitelline follicles in 2 lateral fields, 13–57 (32 ± 10 ; 20; 60) long by 10–34 (21 ± 7 ; 20; 60) wide in detached mature and gravid proglottids; each field consisting of 1 to 2 irregular columns of follicles, extending from near posterior margin of proglottid to genital pore in anti-poral field and stopping well short of genital pore in poral field. Excretory ducts 4, lateral, in 1 dorsal and 1 ventral pair, with lateral branches, opening to outside at multiple points throughout length of scolex (Fig. 3I, J) and at proglottid velum. Eggs single, spherical, 14–16 (15 ± 0.6 ; 15) in diameter (Fig. 3F, G), with numerous small, regularly spaced surface protuberances, without polar filaments, released by eversion of uterus through dehiscence at mid-level of proglottid.

Type and only known host: *Narcine maculata* (Shaw), the darkspotted numbfish (Torpediniformes: Narcinidae) (Host No. BO-408).

Type and only known locality: South China Sea off southern Sarawak (02°49'01.2"N, 110°52'47.16"E), Malaysia.

Site of infection: Spiral intestine.

Type material: Holotype (complete strobila with scolex without apical organ) (MZUM[P] 2010.34[H]), 6 paratypes (1 incomplete worm with scolex, 1 incomplete worm with scolex without apical organ, 1 strobilar fragment, 1 detached mature and 1 detached gravid proglottid; 1 lactophenol preparation of eggs) (MZUM[P] 2010.35[P]–40[P]); 5 paratypes (1 incomplete worm with scolex, 1 strobilar fragment, 1 detached mature and 1 detached gravid proglottid; 1 lactophenol preparation of eggs) (SBC P-00036–00040); 4 paratypes (1 incomplete worm with scolex, 1 strobilar fragment, 1 detached mature and 1 detached gravid proglottid) (IPCAS C-595); 20 paratypes (2 incomplete worms with scolices, 1 incomplete worm with scolex without apical organ, 2 apical organs, 4 strobilar fragments, 4 detached mature and 4 detached gravid proglottids; cross-section series of 1 detached mature and 1 detached gravid proglottid; 1 lactophenol preparation of eggs) (USNPC 104126); and 14 paratypes (1 incomplete worm with scolex, 1 incomplete worm with scolex without apical organ, 1 apical organ, 3 strobilar fragments, 3 detached mature and 3 detached gravid proglottids; cross-section series of 1 detached mature proglottid; 1 lactophenol preparation of eggs) (LRP 7508–7523); 8 paratypes prepared for SEM retained in senior author's personal collection.

Etymology: This species is named for its comically elongated scolex (i.e., *comicus*, L., comical).

Remarks. Given that *Anteropora indica* is known only from free proglottids, and most of the characters given above to distinguish *Sesquipedalapedex* from *Anteropora* rely on scolex morphology, some treatment of the differences between *Sesquipedalapedex comicus* and *A. indica* is in order. The new species differs conspicuously from *A. indica*, as illustrated by Subhadrachha (1955; fig. 1), in its possession of 6, rather than 4 testes per proglottid. However, it is important to note that Subhadrachha also

Fig. 2. Scanning electron micrographs of *Sesquipedalapex comicus* sp. n. **A** – apical organ; **B** – scolex; **C** – surface of apical modification of scolex proper with narrow rostrate spinitriches without broad bases and acicular filitriches; **D** – surface of scolex proper immediately anterior to acetabula with acicular to capilliform filitriches; **E** – surface of scolex proper slightly posterior to apical organ with acicular filitriches; **F** – scolex at level of acetabula; **G** – surface of sucker rims with rostrate spinitriches with broad bases and acicular filitriches; **H** – anterior surface of sucker rims with rostrate spinitriches with broad bases and acicular filitriches; **I** – detached proglottid; **J** – strobila of immature proglottids; **K** – surface of scolex proper posterior to acetabula with acicular filitriches; **L** – surface of anterior spherical region of detached proglottid with gladiate spinitriches and capilliform filitriches; **M** – surface of posterior margin of immature proglottid (velum) with scolopate spinitriches and capilliform filitriches; **N** – surface of posterior margin of detached proglottid (velum) with scolopate spinitriches and capilliform filitriches. Small letters indicate location of details shown in the referenced figure. Scale bars: A, E, F, J = 50 µm; B = 500 µm; C, G, H, K, L = 1 µm; D, M = 2 µm; I = 100 µm; N = 10 µm.

Fig. 3. Light (A–E, G, I–L) and scanning electron (F, H) micrographs of *Sesquipedalapex comicus* sp. n. **A** – scolex (arrowheads indicate location of light micrographs in Fig. 3I and J); **B, C** – variation in form of apical organ; **D** – scolex at level of acetabula; **E** – scolex at level of acetabula, showing intensely staining glandular tissue and excretory vessels; **F** – egg, showing regularly spaced surface protuberances; **G** – eggs; **H** – spermatocytes with developing spermatids; **I** – excretory vessels in scolex proper anterior to acetabula (arrowheads indicate branching); **J** – excretory vessels in scolex proper posterior to acetabula (arrowheads indicate opening to the outside); **K** – cross-section of detached mature proglottid at level of ovary; **L** – cross-section of detached mature proglottid between ovary and cirrus-sac. *Abbreviations:* MG – Mehlis' gland; O – ovary; T – testis; U – uterus; VA – vagina; VD – vas deferens; VI – vitelline follicles.

reported that 6 of the 60 proglottids she examined had 3, 5, or 6 testes. The proglottid of *S. comicus* bears a poral field of vitelline follicles that is shorter than the anti-poral field, whereas the poral and anti-poral fields of vitelline follicles are symmetrical in *A. indica*. Finally, the uterine duct also joins the uterus much more posteriorly in *A. indica* than it does in *S. comicus*.

The remarkably elongate scolex of *S. comicus* appears to function particularly effectively in attachment to the surface of the mucosa of the spiral intestine of its host. Specimens of this cestode were extremely difficult to remove intact from host tissue as they were found to embed their entire scolex deeply within the mucosa. While insufficient material was found to allow for the histological work required for description of the pathology associated with this species in detail, on a gross morphological level, attached worms were found to provoke conspicuous papilliform expansions of the outer wall of the spiral intestine at the site of attachment (Fig. 4). Given that one scolex with a short (400 μ m) apical modification of the scolex proper was found and that the scolices excised from the host spiral intestine exhibited extensively long apical modifications of the scolex proper (2.6–4.3 mm), it appears that the apical modification of the scolex proper grows into the intestinal mucosa as the worm matures. The scolices of worms that had been detached from the surface of the mucosa were completely encased in a relatively inflexible fibrous sheath, presumably of host origin.

Anteropora klosmamorphis sp. n. Figs. 5–7

Description (Based on 16 complete and 1 incomplete worm, 14 detached mature and 10 detached gravid proglottids; cross-section series of 2 detached mature proglottids; 1 scolex, 1 strobila, 2 detached proglottids, and 1 gravid proglottid disrupted to reveal eggs examined with SEM; 3 lactophenol preparations of eggs).

Worms 2.6–20.8 (8.1 ± 4.0 ; 16) mm long, maximum width at scolex; proglottids 87–274 (178 ± 50 ; 16) in number, hyperapolytic. Scolex with 4 acetabula, apical modification of scolex proper and apical organ, 238–310 (276 ± 26 ; 14) long by 270–362 (333 ± 27 ; 10) wide. Acetabula in form of bothridia, with free posterior margins, notched posteriorly (Figs. 5B, 7A), 185–257 (217 ± 21 ; 15; 27) long by 105–183 (160 ± 20 ; 15; 26) wide. Apical modification of scolex proper dome-shaped, with aperture at apex, housing apical organ. Apical organ spherical, 53–67 (60 ± 5 ; 15) long by 51–68 (60 ± 6 ; 17) wide, in form of conical muscular and glandular pad, non-eversible. Cephalic peduncle absent.

Scolex proper (Fig. 6D) and bothridia (Fig. 6B, C) covered with capilliform filitriches and gladiate spinitriches. Apical modification of scolex proper with capilliform filitriches and hastate spinitriches (Fig. 6E, F). Proglottids with capilliform filitriches (Fig. 6I) throughout, with gladiate spinitriches restricted to anterior spherical region

Fig. 4. Photo of the outer wall of the spiral intestine showing conspicuous papilliform expansions (arrowheads) at the points of attachment of scolices of *Sesquipetalapex comicus* sp. n. to the intestinal mucosa (asterisks indicate strobilae of attached specimens).

(Fig. 6J), with small scolopate spinitriches restricted to posterior margins of velum (Fig. 6K).

Proglottids craspedote, non-lacinate; immature proglottids initially wider than long, becoming longer than wide with maturity, with conspicuous anterior spherical region (Fig. 5D). Immature proglottids 72–109 (92 ± 11 ; 16) wide; terminal immature proglottids 152–346 (228 ± 60 ; 16) long by 61–99 (81 ± 9 ; 16) wide; anterior spherical region containing large, oval cells and anterior-most testis. Detached mature proglottids 457–767 (622 ± 95 ; 14) long by 154–227 (188 ± 21 ; 14) wide; detached gravid proglottids 726–1,122 (850 ± 127 ; 10) long by 175–338 (260 ± 51 ; 12) wide; anterior spherical region 113–194 (148 ± 25 ; 12) long by 134–183 (162 ± 17 ; 10) wide in detached mature proglottids, 140–285 (180 ± 43 ; 10) long by 144–226 (199 ± 26 ; 10) wide in detached gravid proglottids. Testes 4 (4 ± 0 ; 40) in number, arranged in single column anterior to ovary, 34–124 (64 ± 19 ; 24; 81) long by 60–134 (91 ± 18 ; 24; 81) wide in detached mature and gravid proglottids. Vas efferens visible in detached proglottids, forming 2 lateral ducts that extend posteriorly to level of posterior ovarian margin, uniting medially to form vas deferens (Fig. 5C, 5D). Vas deferens sinuous, extensive, extending along poral side of proglottid from oötype to enter cirrus-sac at medial margin. External and internal seminal vesicles absent. Cirrus-sac pyriform or elliptical, tilted anteriorly, anterior to, or overlapping with, second anterior-most testis, 55–113 (80 ± 16 ; 20) long by 30–55 (39 ± 7 ; 22) wide in detached mature and gravid proglottids. Cirrus coiled, armed with spinitriches. Genital pores marginal to submarginal, irregularly alternating, 53–74% ($53\% \pm 5$; 24) from posterior end, at level of second

Fig. 5. Line drawings of *Anteropora klosmamorphis* sp. n. **A** – whole worm; **B** – scolex; **C** – oötype; **D** – detached gravid proglottid (arrowheads indicate location of sections in Fig. 7E–G).

Fig. 6. Scanning electron micrographs of *Anteropora klosmamorphis* sp. n. **A** – scolex; **B** – distal acetabular surface with gladiate spinitriches and acicular filitriches; **C**, **D** – proximal acetabular surface with gladiate spinitriches and acicular to capilliform filitriches; **E**, **F** – surface of apical modification of scolex proper with hastate spinitriches and acicular to capilliform filitriches; **G** – immature proglottid of strobila; **H** – detached proglottid; **I** – surface of posterior margin of immature proglottids with capilliform filitriches; **J** – surface of anterior region of detached proglottids with gladiate spinitriches and capilliform filitriches; **K** – surface of posterior margin of proglottid (velum) with scolopate spinitriches and capilliform filitriches. Small letters indicate location of details shown in the referenced figure. Scale bars: A, G = 50 µm; B–F, J = 1 µm; H = 100 µm; I, K = 2 µm.

Fig. 7. Light (A, C–G) and scanning electron (B) micrographs of *Anteropora klosmamorphis* sp. n. **A** – scolex; **B** – egg with bipolar filaments (inset shows corrugated surface of egg and filaments); **C** – apical organ; **D** – eggs with bipolar filaments of unequal length; **E** – cross-section of detached proglottid at constriction between proglottid proper and anterior spherical region; **F** – cross-section through testis in anterior spherical region (posterior); **G** – cross-section through testis in anterior spherical region (anterior), showing vacuous nature of spherical region.

anterior-most testis. Ovary essentially H-shaped in frontal view, consisting of 3 lobes on each side, irregular in cross-section, 32–98 (70 ± 20 ; 14) long by 58–126 (96 ± 20 ; 12) wide in detached mature proglottids, 69–173 (114 ± 35 ; 9) long by 85–253 (184 ± 61 ; 9) wide in detached gravid proglottids. Vagina sinuous, initially thick-walled, extending from oötype region along poral side of proglottid to enter genital atrium posterior to, or at same level as, cirrus-sac;

vaginal sphincter absent. Uterus thick-walled, extending along median line of proglottid from posterior-most vitelline follicles to proglottid constriction; when gravid, uterus occupying entire posterior region of proglottid; uterine duct joining uterus posteriorly to genital atrium; uterine pore absent. Vitellarium follicular; vitelline follicles in 2 lateral fields, 9–59 (26 ± 10 ; 23; 69) long by 5–35 (17 ± 7 ; 23; 69) wide in detached mature and gravid

proglottids; each field consisting of 1–2 irregular columns of follicles; extending from posterior to ovary to genital pore in anti-poral field and to cirrus-sac in poral field. Excretory ducts 4, lateral, arranged in 1 dorsal and 1 ventral pair. Eggs spherical, 12–14 (13 ± 1 ; 15) in diameter, with corrugated surface and bipolar filaments (Fig. 7B, D) unequal in length; shorter filament 23–37 (30 ± 4 ; 15) long; longer filament 117–162 (140 ± 12 ; 15) long; eggs apparently released by eversion of uterus through dehiscence at mid-level of proglottid.

Type and only known host: *Narcine maculata* (Shaw), the darkspotted numbfish (Torpediniformes: Narcinidae) (Host No. BO-408).

Type and only known locality: South China Sea off southern Sarawak (02°49'01.2"N, 110°52'47.16"E), Malaysia.

Site of infection: Spiral intestine.

Type material: Holotype (MZUM[P] 2010.27[H]), 6 paratypes (2 complete worms, 2 detached mature and 1 detached gravid proglottid; 1 lactophenol preparation of eggs) (MZUM[P] 2010.28[P]–33[P]); 5 paratypes (2 complete worms, 2 detached mature and 1 detached gravid proglottid) (SBC P-00031–00035); 5 paratypes (2 complete worms, 2 detached mature and 1 detached gravid proglottid) (IPCAS C-596); 16 paratypes (5 complete and 1 incomplete worm, 4 detached mature and 4 detached gravid proglottids; cross-section series of 1 detached mature proglottid; 1 lactophenol preparation of eggs) (USNPC 104127), 13 paratypes (4 complete worms, 4 detached mature and 3 detached gravid proglottids; cross-section series of 1 detached mature proglottid; 1 lactophenol preparation of eggs) (LRP 7494–7507); 4 paratypes prepared for SEM retained in senior author's personal collection.

Etymology: This species is named for the unusually elongate and slender form of its strobila (i.e., *klosma*, n., Gr., thread; *morphe*, f., Gr., form).

Remarks. *Anteropora klosmamorphis* conspicuously differs from *A. japonica* and *A. leelongi* in its possession of 4, rather than 6, testes per proglottid, in its possession of acetabula that are notched, rather than intact posteriorly, and in that its apical organ is narrower than those of both species (53–67 vs. 160 and 134–145, respectively). In addition, the vitelline fields extend much more anteriorly in *A. klosmamorphis* than they do in either of the other two species (i.e., to posterior margin of anterior-most testis vs. to level of posterior-most testis and to midlevel of testicular field, respectively).

With respect to *A. indica*, comparisons were hampered by the fact that this species is known only from detached proglottids, misinterpreted by Subhapradha (1955) to represent a cestodian body, and also because the original description provides little morphometric detail. Nonetheless, no proglottids with fewer or greater than 4 testes were seen in *A. klosmamorphis*, whereas Subhapradha (1955) reported finding a few specimens with 3, 5 or 6

testes in *A. indica*. In addition, the spinitriches on the anterior regions of detached proglottids of *A. klosmamorphis* were slightly smaller than those seen in *A. indica* (5–6 vs. 9), as were the eggs (12–14 vs. 15). Whereas Subhapradha (1955) reported the uterus of *A. indica* to have a ventral extension posterior to the ovary in a few specimens, we found this to be the case in all of the proglottids examined here. At this time, we consider *A. klosmamorphis* to be sufficiently distinct from *A. indica* as to justify its recognition as a new species; examination of complete specimens of *A. indica*, and the scolex in particular, would be particularly illuminating. It should be noted that Tian et al. (2008) used the name “*Anteropora xiamenensis* sp.nov.” for a specimen they included in their phylogenetic analysis. *Anteropora xiamenensis* should be considered a *nomen nudum* since the species does not appear to have been described by Tian et al. (2008); nor, as the paper implies for other taxa given new taxon designations, was it described elsewhere.

DISCUSSION

The somewhat unconventional history of Anteroporidae was reviewed by both Euzet (1994) and Jensen (2005). However, the descriptions of *Anteropora japonica* (as *Discobothrium japonicum* Yamaguti, 1934) by Yamaguti (1934) and of *Anteropora leelongi* by Jensen (2005), have done much to stabilize this genus, and thus also the family. The descriptions here of two additional species and a second genus, provide further insight into the morphology of the family. However, in order to accommodate these new taxa, the most recent diagnosis of the genus, provided by Jensen (2005; p. 71), requires slight modification. The distribution should be emended to read “Western Pacific Ocean (Japan, Australia, and Borneo)”, and the list of hosts should be updated based on current elasmobranch classification (Froese and Pauly 2010) to read “Parasites of numbfishes (Narcinidae) and the epaulette shark, *Hemiscyllium ocellatum* (Hemiscylliidae).” In addition, the diagnosis of the family, as presented by Euzet (1994), should be revised to incorporate the scolex apical structure terminology suggested by Caira et al. (1999, 2001) and adopted by Jensen (2005) for the Lecanicephalidea in general, as well as to accommodate the new taxa described here. The revised diagnosis is as follows:

Anteroporidae Euzet, 1994

Diagnosis: Scolex with short or extremely long apical modification of scolex proper, apex expanded to accommodate muscular and/or glandular apical organ, with 4 acetabula in the form of bothridia or suckers. Strobila craspedote, hyperapolytic. Genital pores marginal or submarginal, irregularly alternating. Testes few (usually 4 or 6) aligned along median axis of proglottid. Ovary lobate, with 2–3 lobed on each side, posterior. Vagina opening

into genital atrium posterior to, or at same level as, cirrus-sac. Vitellarium follicular; vitelline follicles arranged in 2 lateral bands; bands extending from posterior to ovary to near genital pore. Uterus saccate. Eggs with or without bipolar filaments; surface of eggs corrugated or with papilliform protuberances. Type genus: *Anteropora* Subhapradha, 1955. Additional genus: *Sesquipedalapex* gen. n. Parasites of numbfishes (Narcinidae) and the epaulette shark, *Hemiscyllium ocellatum* (Bonnaterre) (Hemiscylliidae).

This brings the total number of genera of Anteroporidae to two, and the total number of species in the family to five. The host associations of this family are intriguing. Collectively, four of the five species have been described from three species in two of the nine genera of numbfishes (Narcinidae). It also suggests that the remaining 21 species and seven genera of Narcinidae may be likely sources of additional species of Anteroporidae. The two genera and 14 species of the second family of Torpediniformes (i.e., Torpedinidae, electric rays) would also be interesting to explore. Although cestode records from some of the other members of both families of electric rays exist (e.g., Monticelli 1893, Linton 1900, Alexander 1963, Campbell and Carvajal 1987, Caira and Burge 2001), such reports do not include lecanicephalideans. However, in all but the latter case, it is not clear if this is because no lecanicephalideans were found, or if lecanicephalideans were merely not the focus of such studies.

Although the report of the remaining species in the family, *Anteropora leelongi*, by Jensen (2005), from the epaulette shark, *Hemiscyllium ocellatum*, seems incongruous given the host associations of the other species of Anteroporidae, this association has been confirmed by the third author from new material collected in Cairns, Australia in 2001. Clearly, any of the six other species of *Hemiscyllium* Müller et Henle, none of which have been examined for cestodes, would be particularly interesting to explore.

Sesquipedalapex comicus exhibits intriguing variations in several morphological attributes that have not been observed in any of the five species of *Anteropora*. For example, not only do the ducts of the excretory system of *S. comicus* exhibit lateral branching, but these ducts appear to open to the outside of the worm at numerous points, particularly along the length of the scolex of the worm. These openings are clearly visible with SEM as pores surrounded by capilliform filitriches (Fig. 2E). The implications of these modifications for the functioning of the excretory system are unclear, but would suggest fairly major differences in the operation and/or performance of this system between members of these two genera.

Also intriguing are the modes of attachment seen among members of the Anteroporidae. The proglottids are hyperapolytic and bear dense concentrations of gladiate spinitriches on an anterior, spherical expansion of free

proglottids of all ages in all five species in both genera. As noted by several authors previously (e.g., Subramanian 1939, Rees and Williams 1965, McCullough and Fairweather 1983), it seems likely that the gladiate spinitriches on the anterior expanded region of the free proglottids may serve to aid in attachment of these tiny entities to the gut of their host. Hundreds of free proglottids of *S. comicus* and *A. klosmamorphis* were found in the contents of the spiral intestine of the specimen of *Narcine maculata* examined here. In fact, given the morphological similarities between these two cestode species, the determination of specific identities of these free proglottids was particularly challenging. These results lend support to McCullough and Fairweather's (1983) hypothesis that hyperapolysis may serve to allow the accumulation of reproductive proglottids in the gut, without overburdening the strobila of their respective worms with proglottids. *Sesquipedalapex comicus* and *Anteropora klosmamorphis* join *Trilocularia acanthiaevulgaris* Olsson, 1866 (see McCullough and Fairweather 1983), *Yorkeria salputium* Caira, Jensen et Rajan, 2007 (see Caira et al. 2007), and *Acanthobothrium margiae* Fyler, 2011 (see Fyler 2011) as the fourth and fifth species of elasmobranch-inhabiting cestodes that exhibit what was termed extreme hyperapolysis by Fyler (2011).

Sesquipedalapex comicus is further unusual among the members of its family in the method the worm itself employs to attach to the mucosal surface of the spiral intestine. As noted above, these worms appear to induce a host response in the form of a blister-like/papilliform expansion of the outer wall of the spiral intestine. The fact that their attachment to the internal mucosal surface is manifested on the external surface of the spiral intestine, suggests that these worms have a rather substantial impact on their host. Unfortunately, dissection of these mucosal papillae was required to remove intact worms for study and thus it was not possible to examine the nature of this host response using histology. However, within each papilliform expansion, multiple worms were found, intertwined around one another. Although the mode of attachment has not been studied in species of *Anteropora*, a conspicuous host response has never been reported at the site of attachment of any of the four species and it was certainly not seen in specimens of *A. klosmamorphis* examined here.

Not much information exists about variation in egg morphology in lecanicephalideans in general, since only individual records exist for individual species in some genera. For example, Jensen (2001) described the eggs of *Paraberrapex manifestus* Jensen, 2001 as being grouped in a cocoon, while Jensen (2005) described the eggs of *Polypocephalus helmuti* Jensen, 2005 as single with bipolar filaments in younger gravid proglottids, and contained in a fibrous matrix in older gravid proglottids. With the description of the two new species of Anteroporidae in this study, egg morphology has now been described for

four of the five species in the family. Interestingly, egg morphology varies remarkably between genera. Three of the four species of *Anteropora* (i.e., *A. japonica*, *A. leelongi* and *A. klosmamorphis*) have eggs with polar filaments of unequal length (Yamaguti 1934, Jensen 2005), while the eggs of *Sesquipedalapedes comicus* do not have polar filaments and are perfectly spherical. In addition, the egg surface of *A. klosmamorphis* is corrugated, while the egg surface of *S. comicus* is covered by small protuberances. Investigation of egg morphology in the Lecanicephalidea more broadly might reveal surprising diversity.

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