

CESTODES FROM HECTOR'S BEAKED WHALE (*MESOPLODON HECTORI*) AND SPECTACLED PORPOISE (*PHOCOENA DIOPTRICA*) FROM ARGENTINEAN WATERS

Pavel N. Nikolov, H. Luis Cappozzo*, Bárbara Berón-Vera†, Enrique A. Crespo†, J. Antonio Raga‡, and Mercedes Fernández‡§

Central Laboratory of General Ecology, Bulgarian Academy of Sciences, 2 Gagarin Street, 1113 Sofia, Bulgaria.
e-mail: mercedes.fernandez@uv.es

ABSTRACT: Single individuals of 2 little-known cetacean species, *Mesoplodon hectori* and *Phocoena dioptrica*, stranded and died on the coast of Argentina (Buenos Aires and Chubut provinces, respectively) and were studied for the presence of helminths. The cestodes found were described and illustrated using light microscopy. The following cestode taxa were recovered: *Tetrabothrius (Tetrabothrius) hobergi* n. sp. (several fragmented specimens, at least 1 gravid) and *Tetrabothrius (s.l.)* sp. 1 (several fragmented immature specimens) from *M. hectori*, and *Tetrabothrius (s.l.)* sp. 2 (single fragmented immature specimen) and 2 morphotypes of tetraphyllidean larvae from *P. dioptrica*. *Tetrabothrius (T.) hobergi* n. sp. can be distinguished from *Tetrabothrius (T.) forsteri* by the greater number of testes and larger eggs and oncospheres, from *Tetrabothrius (T.) curilensis* by the smaller testes and vitellarium, the shape and size of the ovary, and the larger oncospheres and longer embryonic hooks, and from *Tetrabothrius (T.)* sp. from *Ziphius cavirostris* by the narrower strobila, smaller scolex, and smaller number of testes. The generic designations of *Tetrabothrius (s.l.)* sp. 1 and *Tetrabothrius (s.l.)* sp. 2 were based on the scolex morphology. *Tetrabothrius (s.l.)* sp. 1 is closest to *Tetrabothrius (T.) forsteri* and *Tetrabothrius (Biamniculus) innominatus* based on the number of testes, while the scolex size of *Tetrabothrius (Tetrabothrius) sp. 2* is within the variability range reported for *Tetrabothrius (T.) forsteri*. More definite identification of the 2 species was not possible due to the condition of the available material. The present study provides the first descriptions of cestodes from *M. hectori* and *P. dioptrica*, thus enriching the knowledge regarding the helminths of insufficiently studied marine mammals.

The Hector's beaked whale *Mesoplodon hectori* (Gray, 1871) (Ziphiidae) and the spectacled porpoise *Phocoena dioptrica* Lahille, 1912 (Phocoenidae), occurring in the Southern Hemisphere only, are among the less known cetaceans (Goodall, 2009; Pitman, 2009). The available information on these mammals has been gathered from stranded animals, which are categorized as "Data Deficient" according to the IUCN Red List (2001). Parasitological data for these species are also scarce. Baker et al. (2001) reported larval *Anisakis* sp. from the stomach and *Tetrabothrius forsteri* from the intestine of a *M. hectori* off New Zealand. For *P. dioptrica*, 3 records of parasites are known. Gallardo (1913) found nematodes in the blowhole and nasal sacs of the type specimen, Goodall and Schiavini (1995) reported nematodes from 3 stomachs of spectacled porpoises off Tierra del Fuego, and Berón-Vera et al. (2008) collected nematodes, cestodes, and acanthocephalans from the digestive tracts of 2 hosts. Previous records of cestodes from mesoplodont whales could be summarized to "*Tetrabothrius* sp." from *Mesoplodon bidens* (Sowerby, 1804) and *M. densirostris* (de Blainville, 1817) (Gibson et al., 1998), and *T. forsteri* and "*Tetrabothrius* sp." from *M. hectori* (Baker et al., 2001, and Cappozzo et al., 2005, respectively). However, the systematic diversity of the cestodes from beaked whales remains virtually unknown because the above studies did not improve the data regarding the morphology of the cestodes or provide sufficient information for their identification. Moreover, the complicated taxonomy, wide morphological

variability, and the host range reported for *T. forsteri* (Baer, 1932; Delyamure, 1955; Temirova and Skryabin, 1978) require further confirmation of the records of this species in beaked whales.

Single specimens of *M. hectori* and *P. dioptrica* stranded on the coast of Argentina were examined for helminths. The cestodes found in the 2 hosts were independently identified as "*Tetrabothrius* sp." by Cappozzo et al. (2005) and Berón-Vera et al. (2008), respectively. The present study on the same materials revealed the presence of 2 tetrabothriid species from the Hector's beaked and 1 from the spectacled porpoise. The condition of the cestodes collected did not allow detailed taxonomic descriptions for all of them; only 1 of the species from *M. hectori* was described as a new species. Since *Tetrabothrius* sp. was already reported from the same host specimen, we consider both the former (Berón-Vera et al., 2008) and the present record (based on an immature specimen) the first finding of a tetrabothriid cestode in the spectacled porpoise, from which we also report the occurrence of tetraphyllidean larvae.

MATERIALS AND METHODS

An adult female (3.84 m long) Hector's beaked whale was found at Puerto Quequén, Argentina (38°37'S, 58°50'W), on 3 September 2002 (see Cappozzo et al., 2005). The animal stranded was alive (Code 1 sensu Geraci and Lounsbury, 2005) and died 2 hr later. The intestine (1,850 cm long) was kept frozen until necropsy, then split length-wise and cut longitudinally. The content of each section was washed through a 0.2-mm mesh sieve. The solid contents were collected in a Petri dish and examined using a stereomicroscope.

A pre-mature female (1.94 m long) spectacled porpoise (referred to as Pd2 by Berón-Vera et al., 2008) was stranded on El Doradillo beach, Argentina (42°39'S, 64°59'W), on 17 March 2007. The animal was in good condition (Code 2 sensu Geraci and Lounsbury, 2005). The intestine (1,205 cm long) was processed as described above for the beaked whale.

Cestodes were washed in physiological saline, then fixed and preserved in 70% ethanol and stained with iron acetocarmine (Georgiev et al., 1986). Mature proglottids were hand-sectioned by a razor blade transversely (following Hoberg, 1987) to facilitate examination of the genital ducts. The designated syntypes were deposited at the Natural History Museum of Geneva (MHNG), Switzerland, and the voucher specimens were retained in the helminthological collection of the Marine Zoology Unit

Received 13 May 2009; revised 14 September 2009, 27 February 2010; accepted 29 March 2010.

*Laboratorio de Ecología, Comportamiento y Mamíferos Marinos, Museo Argentino de Ciencias Naturales "Bernardino Rivadavia" (CONICET), Av. Angel Gallardo 470, C1405DJR-Buenos Aires, Argentina.

†Laboratorio de Mamíferos Marinos, Centro Nacional Patagónico-CONICET, Blvd. Brown 3600, 9120-Puerto Madryn, Chubut, Argentina.

‡Unidad de Zoología Marina, Instituto Cavanilles de Biodiversidad y Biología Evolutiva and Fundación General de la UVEG, Universidad de Valencia, P.O. Box 22085, 46071-Valencia, Spain.

§To whom correspondence should be addressed.

DOI: 10.1645/GE-2200.1

(ICBIBE), University of Valencia, Spain. The cestodes were studied and illustrated using a light microscope with drawing apparatus. Measurements (length \times width) and counts are given as the range, with the mean and the number of measurements made (n) in parentheses. Unless otherwise stated, measurements are in micrometers.

DESCRIPTIONS

Tetrabothrius (Tetrabothrius) hobergi n. sp.

(Figs. 1–5)

Description (based on 4 scolices and numerous strobilar fragments, including 5 syntypes): Cestodes fragmented; with maximum width at gravid proglottids. Longest fragments available measured 3.1 cm, including scolex, neck, and 212 juvenile proglottids; 3.6 cm with 118 juvenile and pre-mature proglottids; 2.4 cm with 69 pre-mature proglottids; 3.5 cm including 82 mature proglottids; and 4.2 and 3.4 cm with 60 and 43 pre-gravid proglottids, respectively; then 1.2, 0.9, 0.3, and 0.3 cm for 10, 11, 2, and 4 gravid proglottids, respectively.

Scolex massive, rounded (Fig. 1), with maximum width at level of posterior part of bothridia 600–670 (640, n = 3); scolex in lateral position 620 (n = 1) wide. Bothridia oval, cup-shaped, strongly muscular, 375–490 (415, n = 16) long and 270–330 (300, n = 4) wide. Each bothridium provided with single muscular digitiform auricle, 210–295 (237, n = 5) long and 55–80 (69, n = 5) wide; anterior parts of bothridia and auricles forming concave apical organ. Neck 19.9–31.8 mm (24.6 mm, n = 3) long and 320–490 (410, n = 4) wide.

Proglottids craspedote, rectangular; pre-mature proglottids wider than long, 183–377 \times 715–814 (307 \times 759, n = 20); mature (hermaphroditic) and pre-gravid proglottids wider than long, 337–589 \times 800–1,145 (461 \times 977, n = 49); gravid proglottids wider than long or as long as wide, 472–1,076 \times 1,151–2,469 (738 \times 1,809, n = 21). Genital pores unilateral. Genital ducts passing between longitudinal osmoregulatory canals. Genital atrium tubular, 33–80 (49, n = 16) long and 35–83 (58, n = 16) wide. Osmoregulatory canals 2 pairs; ventral osmoregulatory canals 70 wide, connected by transverse anastomosis near posterior proglottid margin, 30 wide; dorsal osmoregulatory canals 35 wide. Testes elliptical, 38–57 (45, n = 61) in number, measuring 38–80 \times 13–54 (57 \times 34, n = 150), dorsal and surrounding female organs anteriorly and posteriorly (Fig. 2). Cirrus sac rounded to elliptical, 70–103 (84, n = 24) long and 55–88 (75, n = 24) wide; wall consisting of circular musculature 6–14 (9, n = 20) thick (Fig. 3). Internal vas deferens thin-walled, coiled, with diameter of 9–24 (16, n = 20). External vas deferens with maximum diameter 8–24 (15, n = 20), strongly coiled, dorsal to vagina. Male canal straight, with size 23–55 \times 15–33 (37 \times 24, n = 20), its lumen 3–8 (5, n = 20) wide; sphincter lacking. Everted cirri not observed. Withdrawn cirrus 43–68 (56, n = 6) long, with strongly folded walls, leading into globular expansion with diameter 30–38 (33, n = 8), followed by thick-walled convoluted canal connecting it to internal vas deferens; cirrus spines absent. Ovary transversely elongate or arcuate, with its lateral ends directed posteriorly, 250–426 (330, n = 20) wide, consisting of 2 lateral wings connected by isthmus 66–137 (107, n = 20) wide, and occupying 29.1–39.3% (35.1%, n = 20) of total proglottid width (Fig. 2); ovary posterior to vitellarium and developing uterus, anterior to seminal receptacle and Mehlis' gland. Vitellarium bilobed, elliptical to arcuate, with size 52–118 \times 109–187 (85 \times 136, n = 19), anterior to ovary and uterus; vitelline duct passing ventrally to uterus and ovary. Mehlis' gland rounded, 25–50 (42, n = 20) in diameter, median, located between ovarian wings. Distal part of vagina tubular to funnel-like when entering genital atrium, with diameter of lumen 22–40 (31, n = 24), ventral to male orifice; sharply expanded, coiled, and with maximum diameter of lumen 15–25 (23, n = 21) at level of poral osmoregulatory canals, ventral to cirrus sac; in proximal direction, vagina as narrow duct dorsal to ovary and developing uterus, entering thin-walled pyriform seminal receptacle with maximum width 38–68 (54, n = 20), located between ovarian wings and adjacent to Mehlis' gland. Externally, all parts of vagina and anterior portion of seminal receptacle covered by layer of intensely stained cells; no armament observed along copulatory part of vagina. Uterus (Fig. 4) transversely elongate, consisting of 2 lateral sac-like lobes connected by wide isthmus and dorsal to ovary in mature proglottids, with anterior and posterior diverticula in pre-gravid proglottids and occupying gravid proglottids entirely; uterine duct dorsal to ovary in mature proglottids. Eggs (Fig. 5) with maximum diameter 58–90 (69, n = 8), with outer envelope of irregular shape.

Oncospheres rounded to elliptical, with maximum diameter 37–50 (42, n = 16). Embryophore with even thickness of 1 μ m. Embryonic hooks with minor differences in shape and length: hooks from extralateral pair 20 (n = 2) long, hooks from intralateral pair more massive, 19–20 (n = 13) long; hooks from central pair 20–21 (n = 4) long.

Taxonomic summary

Type host: *Mesoplodon hectori* (Gray, 1871), Hector's beaked whale.

Additional hosts: None.

Site: Intestine.

Type locality: Puerto Quequén, Argentina (38°37'S, 58°50'W).

Specimens deposited: MHNG INVE 67081 (5 syntypes including scolex with neck, mature fragment, pre-gravid fragment, gravid fragment, and cross sections of the genital atrium).

Etymology: The species is named in honor of Dr. Eric P. Hoberg for his contributions to the systematics of the tetrabothriid cestodes.

Remarks

The material described here as *Tetrabothrius (Tetrabothrius) hobergi* n. sp. was identified as belonging to the nominotypical subgenus of the genus *Tetrabothrius* on the basis of the structure of the genital atrium (Temirova and Skryabin, 1978; Hoberg, 1994). Temirova and Skryabin (1978) listed 8 species in the subgenus, with 2 species reported from cetaceans: *T. (T.) curilensis* Gubanov in Delyamure (1955) and *T. (T.) forsteri* (Kreff, 1871) Fuhrmann, 1904. More recently, Fernández et al. (2004) reported *Tetrabothrius (T.)* sp. from *Ziphius cavirostris* Cuvier, 1823. Our material can be distinguished from *T. (T.) curilensis* by the smaller number of testes (88–96 in *T. curilensis* vs. 38–57 in our material), the shape (wide digitiform processes of the lobes in *T. curilensis* vs. simple lobes in our material) and size of the ovary (680 wide vs. 250–426 wide), the smaller vitellarium (180 \times 320 vs. 52–118 \times 109–187), the larger oncospheres (maximum 29–35 vs. 37–50), and the longer embryonic hooks (12–13 vs. 19–20 for the lateral pairs and 17 vs. 20–21 for the central pairs). From *T. (T.) forsteri*, our material can be distinguished by the greater number of testes (15–25 in *T. forsteri* vs. 38–57 in our material), larger eggs (40–48 vs. 58–90), and oncospheres (24–27 vs. 37–50). From *Tetrabothrius* sp. in *Z. cavirostris* (see Fernández et al., 2004), our specimens can be differentiated by the narrower strobila (maximum width at pre-gravid proglottids 4.9–5.2 mm vs. 0.8–1.2 mm in our material), the smaller scolex (in dorsoventral position, 0.96–1.09 mm wide vs. 0.6–0.67 mm wide) and bothridia (608–688 \times 436–504 vs. 375–490 \times 270–330), the smaller number of testes (55–78 vs. 38–57), the smaller cirrus sac (178–196 \times 143–162 vs. 70–103 \times 55–88), and the narrower ovary (590–662 vs. 250–426) and vitellarium (179–262 vs. 109–187).

Tetrabothrius (s.l.) sp. 1

(Fig. 6)

Diagnosis (based on 2 scolices and several immature strobilar fragments from Mesoplodon hectori): Scolex (Fig. 6) quadrangular, with maximum width 490–660 (n = 2) at posterior part of bothridia. Bothridia 220–340 \times 220–305 (298 \times 263, n = 4); each bothridium bearing single auricle 220 (n = 1) long. Neck at least 4.25–4.74 mm (n = 2) long and 120–130 (n = 2) wide. Longest strobilar fragment available 31.3 mm long. Juvenile proglottids wider than long, with size 90–260 \times 180–320 (90 \times 180, n = 20). Primordial testes numbering 19–30 (23, n = 10), with size 6–28 \times 5–20 (15 \times 11, n = 164).

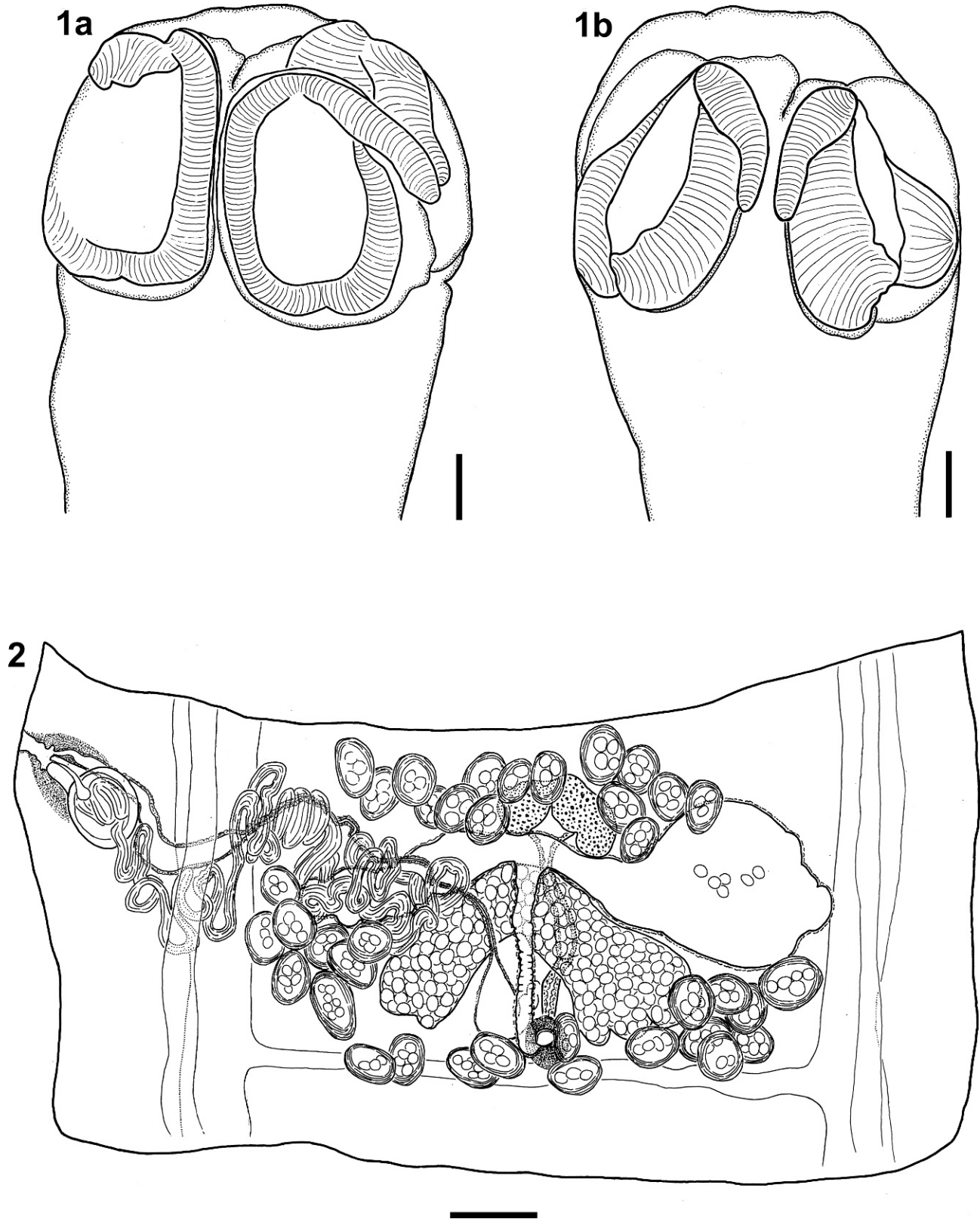
Tetrabothrius (s.l.) sp. 2

(Fig. 7)

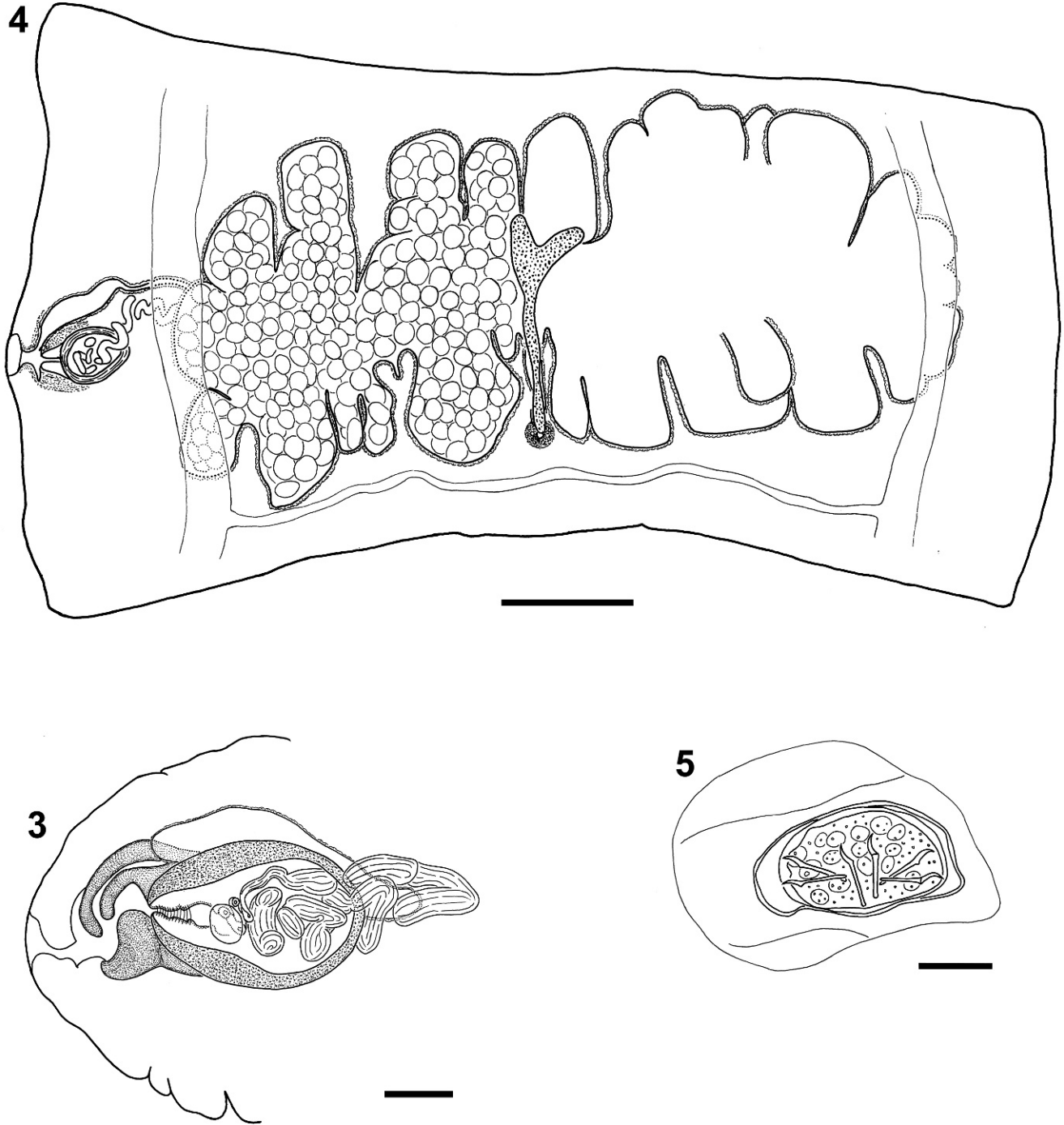
Diagnosis (based on single fragmented immature specimen from Phocoena dioptrica): 3 strobilar fragments (1 with scolex) with length 5.98 (including the scolex), 15.4 and 4.9 mm. Scolex (Fig. 7) quadrangular, with maximum width 1,300 (n = 1) at posterior part of bothridia. Bothridia rounded, with size 550–750 \times 570–640 (660, n = 4), provided with single strongly muscular auricles with size 460–525 \times 75–95 (488 \times 86, n = 4); each auricle continuing into single protuberance on proximal side of bothridium. Neck 3.1 mm (n = 1) long and 570 (n = 1) wide. Proglottids wider than long; first proglottid with genital primordia 70 \times 840.

Remarks

In total, 4 helminth taxa were recovered from 2 host species: *Tetrabothrius (Tetrabothrius) hobergi* n. sp. and *Tetrabothrius (s.l.)* sp. 1



FIGURES 1–2. (1) *Tetrabothrius (Tetrabothrius) hobergi* n. sp. from *M. hectori*: (a) Scolex, dorsoventrally; (b) Scolex, laterally. Scale bar = 100 μ m. (2) Mature proglottid, dorsally. Scale bar = 100 μ m.

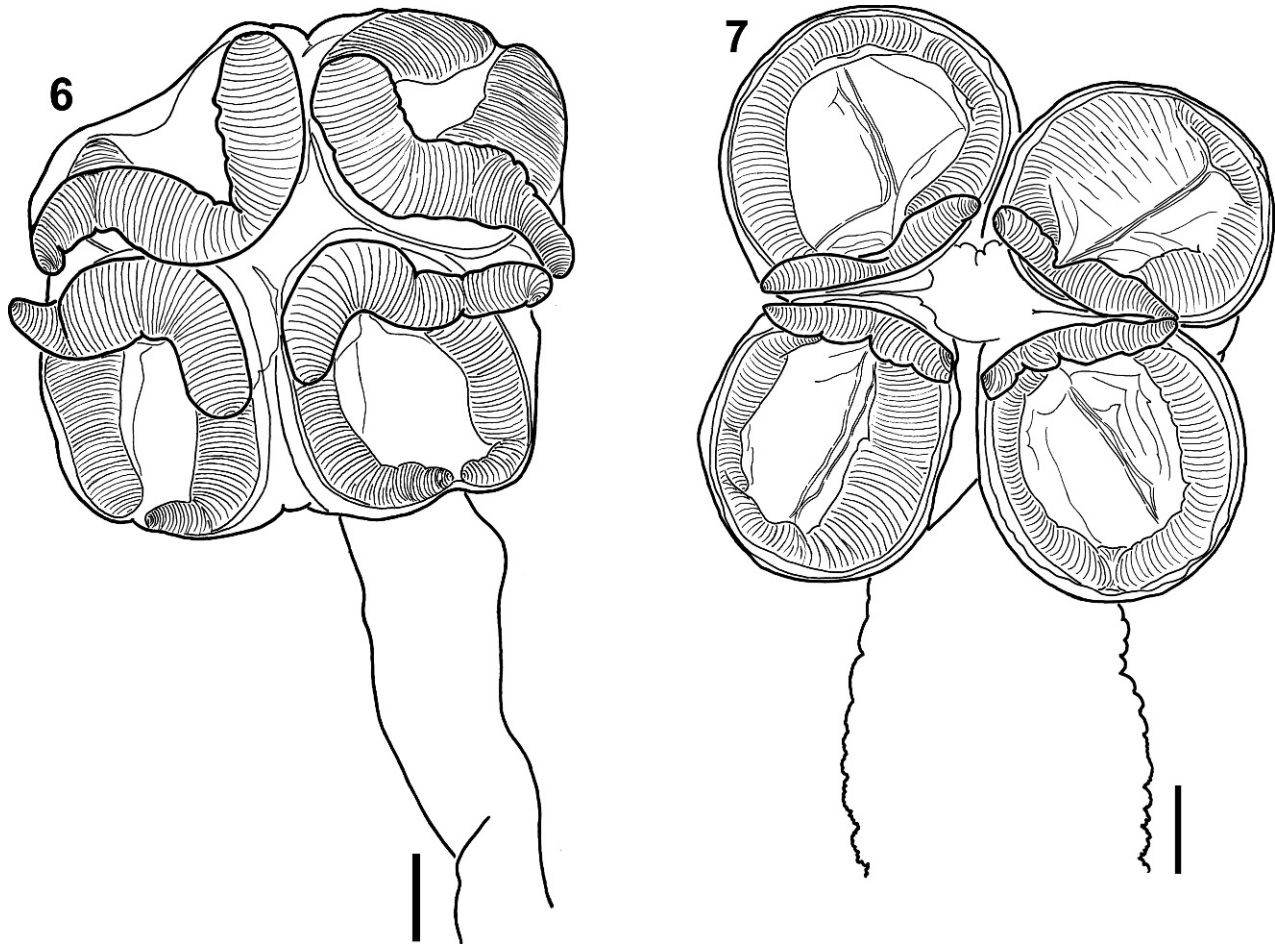


FIGURES 3–5. *Tetrabothrius (Tetrabothrius) hobergi* n. sp. from *M. hectori*. (3) Genital atrium. Scale bar = 50 μ m. (4) Gravid proglottid, ventrally. Scale bar = 200 μ m. (5) Egg. Scale bar = 20 μ m.

from *Mesoplodon hectori*; *Tetrabothrius (s.l.)* sp. 2 and tetraphyllidean larvae (2 of “small” and 4 of “large” morphotype as determined by Aznar et al. [1994], Fernández et al. [2004], and Agustí et al. [2005]) from *Phocoena dioptrica*. These data, along with those by Cappozzo et al. (2005) and Berón-Vera et al. (2008) as discussed above, represent the first descriptions of cestodes from *M. hectori* and *P. dioptrica*.

The generic allocations of *Tetrabothrius (s.l.)* sp. 1 and *Tetrabothrius (s.l.)* sp. 2 were identified on the basis of the scolex morphology. Based on the number of testes, *Tetrabothrius (s.l.)* sp. 1 is closest to *Tetrabothrius (T.) forsteri* (Kreff, 1871) and *Tetrabothrius (Biannicu-*

lus) innominatus Baer, 1954 (with 15–25 and 24–26, respectively). However, the scolex width reported for these species make any identification insufficiently supported: wide variability of 0.28–1.5 mm (along with extensive host and geographical range) for *Tetrabothrius (T.) forsteri* (see Temirova and Skryabin, 1978) and 320 for *Tetrabothrius (B.) innominatus* (Baer, 1954). The scolex width of *Tetrabothrius (Tetrabothrius) sp. 2* also falls within the variability range of *Tetrabothrius (T.) forsteri* (see see Temirova and Skryabin, 1978), but there is no support for its identification with any of the known tetrabothriids from cetaceans.



FIGURES 6–7. (6) *Tetrabothrius* (s.l.) sp. 1 from *M. hectori*. Scolex, dorsoventrally. Scale bar = 100 μ m. (7) *Tetrabothrius* (s.l.) sp. 2 from *P. dioptrica*. Scolex, dorsoventrally. Scale bar = 200 μ m.

ACKNOWLEDGMENTS

We are very grateful to Dr. B. B. Georgiev (Central Laboratory of General Ecology, Sofia, Bulgaria) for his valuable comments on an early version of the manuscript. M.F. was granted a long-term research visit to the Central Laboratory of General Ecology, Bulgarian Academy of Sciences (Sofia), by the Valencian Government and benefits from an I3 Contract from the Ministry of Science and Innovation of Spain. H.L.C. held a Marie Curie grant for senior researchers. The study was partially funded by the (U.S.) National Science Foundation, PBI grants DEB 0818696 and DEB 0818823, and grant CGL2009-07465 (MICINN).

LITERATURE CITED

- AGUSTÍ, C., F. J. AZNAR, AND J. A. RAGA. 2005. Tetrabothriid plerocercoids from western Mediterranean cetaceans and other marine mammals around the world: A comprehensive morphological analysis. *Journal of Parasitology* **91**: 83–92.
- AZNAR, F. J., J. A. BALBUENA, AND J. A. RAGA. 1994. On the identity and emigration of *Scolex pleuronectis* larvae (Cestoda) in the striped dolphin. *European Research on Cetaceans* **8**: 243–246.
- BAER, J.-G. 1932. Contribution à l'étude des Cestodes de Cétacés. *Revue Suisse de Zoologie* **39**: 195–228.
- . 1954. Revision taxinomique et étude biologique des Cestodes de la famille des Tetrabothriidae, parasites d'oiseaux de haute mer et de mammifères marins. Secrétariat de l'Université, Neuchâtel, France, 121 p.
- BAKER, A., P. J. DUIGNAN, R. J. NORMAN, AND A. VAN HELDEN. 2001. A juvenile Hector's beaked whale, *Mesoplodon hectori* (Gray, 1871), without functional throat grooves, plus notes on endoparasites (Cetacea: Ziphiidae). *Marine Mammal Science* **17**: 171–175.
- BERÓN-VERA, B., E. A. CRESPO, AND J. A. RAGA. 2008. Parasites in stranded cetaceans of Patagonia. *Journal of Parasitology* **94**: 946–948.
- CAPPOZZO, H. L., M. F. NEGRI, B. MAHLER, V. V. LÍA, P. MARTÍNEZ, A. GIANGGIOBE, AND A. SAUBIDET. 2005. Biological data on two Hector's beaked whales, *Mesoplodon hectori*, stranded in Buenos Aires province, Argentina. *Latin American Journal of Aquatic Mammals* **4**: 113–128.
- DELYAMURE, S. L. 1955. Helminthofauna of marine mammals (ecology and phylogeny). Izdatel'stvo Akademii Nauk SSSR, Moscow (Israel Program of Scientific Translations, Jerusalem, Israel, 1968), 522 p.
- FERNÁNDEZ, M., F. J. AZNAR, F. E. MONTERO, B. B. GEORGIEV, AND J. A. RAGA. 2004. Gastrointestinal helminths of Cuvier's beaked whales, *Ziphius cavirostris*, from the western Mediterranean. *Journal of Parasitology* **90**: 418–420.
- GALLARDO, A. 1913. Notas sobre la anatomía del aparato espiracular, laringe y hioides de dos delfines, *Phocaena dioptrica* Lahille y *Lagenorhynchus fitzroyi* (Waterhouse) Flower. *Anales del Museo de Historia Natural de Buenos Aires* **24**: 235–245.
- GEORGIEV, B., V. BISERKOV, AND T. GENOV. 1986. *In toto* staining method for cestodes with iron acetocarmine. *Helminthologia* **23**: 279–281.
- GERACI, J. R., AND V. L. LOUNSBURY. 2005. Marine mammals ashore: A field guide for strandings, 2nd ed. National Aquarium in Baltimore, Baltimore, Maryland, 371 p.
- GIBSON, D. I., E. A. HARRIS, R. A. BRAY, P. D. JEPSON, T. KUIKEN, J. R. BAKER, AND V. R. SIMPSON. 1998. A survey of the helminth parasites of cetaceans stranded on the coast of England and Wales during the period 1990–1994. *Journal of Zoology* **244**: 563–574.

- GOODALL, R. N. P. 2009. Spectacled porpoise *Phocoena dioptrica*. In Encyclopedia of marine mammals, 2nd ed., W. F. Perrin, B. Würsig, and J. G. M. Thewissen (eds.). Elsevier, Burlington, Massachusetts, p. 1087–1091.
- , AND A. C. M. SCHIAVINI. 1995. On the biology of the spectacled porpoise, *Australophocaena dioptrica*. Reports of the International Whaling Commission, Special Issue **16**: 411–453.
- HOBBERG, E. P. 1987. *Tetrabothrius shimmi* sp. nov. (Eucestoda) from *Phalacrocorax atriceps bransfieldensis* (Pelecaniformes) in Antarctica with comments on morphological variation, host-parasite biogeography, and evolution. Canadian Journal of Zoology **65**: 2969–2975.
- . 1994. Order Tetrabothriidea Baer, 1954. In Keys to the cestode parasites of vertebrates, L. F. Khalil, A. Jones, and R. A. Bray (eds.). CAB International, Wallingford, U.K., p. 275–304.
- IUCN. 2001. IUCN Red List categories and criteria: version 3.1. IUCN Species Survival Commission. IUCN, Gland, Switzerland, 30 p.
- PITMAN, R. 2009. Mesoplodont whales (*Mesoplodon* spp.). In Encyclopedia of marine mammals, 2nd ed., W. F. Perrin, B. Würsig, and J. G. M. Thewissen (eds.). Elsevier, San Diego, California, p. 721–726.
- TEMIROVA, S. I., AND A. S. SKRYABIN. 1978. Suborder Tetrabothriata (Ariola, 1899) Skrjabin, 1940. In Osnovy Tsestodologii, vol. 9, K. M. Ryzhikov (ed.). Izdatel'stvo Nauka, Moscow, USSR, p. 7–117.