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A new species of *Heteronybelinia* (Cestoda: Trypanorhyncha) from *Sympterygia bonapartii* (Rajidae), *Nemadactylus bergi* (Cheilodactylidae) and *Raneya brasiliensis* (Ophidiidae) in the south-western Atlantic, with comments on host specificity of the genus

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Abstract

Adults and plerocercoids of a new species of *Heteronybelinia* (Trypanorhyncha, Tentaculariidae) were recovered from the skate *Sympterygia bonapartii* (Rajiformes: Rajidae) and two species of teleosts, *Raneya brasiliensis* (Ophidiiformes: Ophidiidae) and *Nemadactylus bergi* (Perciformes: Cheilodactylidae), respectively. *Heteronybelinia mattisi* n. sp. differs from its congeners in its possession of a tentacular armature consisting of hooks with slight differences in size and shape on opposite surfaces of the tentacle (uncinate with rounded bases on the bothrial surface and uncinate with elongate bases on the antibothrial surface), without a characteristic basal armature, hooks increasing in size toward the tip of the tentacles, and pars bothrialis slightly overlapping with bulbs. The description of *Heteronybelinia* is emended regarding the distribution of testes to include species without postovarian testes (*H. palliata* and *H. mattisi*), and without testes anterior to cirrus sac on the poral side (*H. robusta* and *H. mattisi*). Host data are summarized for all 15 valid species of *Heteronybelinia.* Host specificity of adults and plerocercoids of *Heteronybelinia* is variable among species, the adults being more host specific than the plerocercoids. With the exception of *H. mattisi*, the definitive hosts of all species of *Heteronybelinia* for which adults are known include carcharhiniform sharks. *Heteronybelinia mattisi* seems to have oioxenous specificity for its definitive batoid host, *S. bonapartii*, and to be more specific for the intermediate hosts than most of its congeners.

Introduction

Heteronybelinia Palm, 1999 is one of the most diverse genera in the Tentaculariidae, represented by 14 valid species (Palm, 2004; Pereira & Boeger, 2005). Palm (1999) erected *Heteronybelinia* for species with homeoacanthous, heteromorphous, metabasal, tentacular armature with or without characteristic basal armature and heteromorphous hooks (Palm, 1999, 2004). At that time, Palm transferred to the genus 14 species that were originally described in *Nybelinia* Poche, 1926 (namely, *N. alloiotica* Dollfus, 1960; *N. cadenati* Dollfus, 1960; *N. elongata* Shah & Bilqees, 1979; *N. estigmena* Dollfus, 1960; *N. eureia* Dollfus, 1960; *N. karachii* Khurshid & Bilqees, 1988; *N. nipponica*

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Table 1. Host associations of adults and/or plerocercoids of *Heteronybelinia* including *H. annakohnae*, *H. australis*, *H. elongata*, *H. estigmena*, *H. eureia*, *H. heteromorphi*, *H. mattisi* n. sp., *H. minima* and *H. nipponica*.

Heteronybelinia annakohnae Pereira & Boeger, 2005			
Plerocercoid	Perciformes		
		Ctenosciaena gracilicirrhus (Metzelaar) (Sciaenidae)* §	Pereira & Boeger, 2005
		Cynoscion guatucupa (Cuvier) (Sciaenidae) §	Pereira & Boeger, 2005
		Cynoscion jamaicensis (Vaillant & Bocourt) (Sciaenidae) §	Pereira & Boeger, 2005
		Menticirrhus americanus (Linnaeus) (Sciaenidae) §	Pereira & Boeger, 2005
Heteronybelinia australis Palm & Beveridge, 2002			
Adult	Carcharhiniformes		
		Carcharhinus amboinensis (Müller & Henle) (Carcharhinidae)*	Palm & Beveridge, 2002
		Carcharhinus brachyurus (Günther) (Carcharhinidae)	Palm & Beveridge, 2002
Heteronybelinia elongata (Shah & Bilqees, 1979)			
Plerocercoid	Aulopiformes		
		Saurida tumbil (Bloch) (Synodontidae)	Palm, 2004
	Clupeiformes		
		Ilisha elongata (Anonymous [Bennett]) (Pristigasteridae)*	Shah & Bilqees, 1979
	Perciformes		
		Nemipterus furcosus (Valenciennes) (Nemipteridae) #	Palm, 2004
		Lepturacanthus savala (Cuvier) (Trichiuridae) #	Palm, 1999
		Pampus argenteus (Euphrasen) (Stromateidae)	Palm, 2004
		Lethrinus lentjan (Lacepède) (Lethrinidae)	Palm, 2004
		Lutjanus kasmira (Forsskål) (Lutjanidae)	Palm, 2004
Heteronybelinia estigmena (Dollfus, 1960)			
Adult	Carcharhiniformes		
		Carcharhinus amblyrhynchoides (Whitley)(Carcharhinidae)	Palm & Beveridge, 2002
		Carcharhinus leucas (Müller & Henle) (Carcharhinidae)	Borucinska & Caira, 2006
		Carcharhinus limbatus Valenciennes (Carcharhinidae)	Palm & Beveridge, 2002
		Carcharhinus obscurus (Lesueur) (Carcharhinidae) #	Palm & Walter, 2000
		Prionace glauca (Linneaus) (Carcharhinidae)	Palm, 2004
	Rajiformes		
		Raja binoculata Girard (Rajidae)	Palm, 2004
		Raja inornata Jordan & Gilbert (Rajidae)	Palm, 2004
		Raja rhina Jordan & Gilbert (Rajidae)	Palm, 2004
Plerocercoid	Perciformes		
		Brama dussumieri Cuvier (Bramidae)	Palm, 2004
		Taractichthys steindachneri (Döderlein) (Bramidae)	Palm, 2004
		Alectis alexandrina (Geoffroy Saint-Hilaire) (Carangidae)*	Dollfus, 1960
		Caranx rhoncus Geoffroy Saint-Hilaire (Carangidae) #	Palm & Walter, 2000
		Selar crumenophthalmus (Bloch) (Carangidae)	Palm, 2004
		Selene setapinnis (Mitchill) (Carangidae)	Dollfus, 1960
		Seriola dumerili (Risso) (Carangidae) #	Palm & Walter, 2000
		Trachurus murphyi Nichols (Carangidae)	Palm, 2004
		Coryphaena equselis Linnaeus (Coryphaenidae) #	Palm & Walter, 2000
		Echeneis naucrates (Linnaeus) (Echeneidae)	Palm, 1999
		Haemulon plumeiri (Lacepède) (Haemulidae) §	Palm, 2004
		Pomadasys incisus (Bowdich) (Haemulidae) #	Palm & Walter, 2000
		Pomatomus saltatrix (Linnaeus) (Pomatomidae)	Palm, 1999
		Epinephelus fasciatus (Forsskål) (Serranidae)	Palm, 1999
		Cynoscion jamaicensis (Sciaenidae) §	Pereira & Boeger, 2005
		Genyonemus lineatus (Ayres) (Sciaenidae)	Palm, 2004
		Otolithes ruber (Bloch & Schneider) (Sciaenidae)	Palm, 2004
		Sarda australis (Macleay) (Scombridae)	Palm & Beveridge, 2002
		Scomberomorus maculatus (Mitchill) (Scombridae)	Palm, 2004
		Thunnus albacares (Bonaterre) (Scombridae)	Palm, 2004
		Boops boops (Linnaeus) (Sparidae)	Dollfus, 1960
		Sphyraena guachancho Cuvier (Sphyraenidae) # §	Palm & Walter, 2000
		Xiphias gladius Linnaeus (Xiphiidae)	Palm, 2004
	Syngnathiformes		
		Fistularia tabacaria Linnaeus (Fistularidae)#	Palm & Walter, 2000
	Tetraodontiformes		
		Aluterus monoceros (Linnaeus) (Monocanthidae)	Palm, 2004
Heteronybelinia eureia (Dollfus, 1960)			
Plerocercoid	Carcharhiniformes		
		Mustelus canis (Mitchill) (Carcharhinidae)*	Dollfus, 1960
	Anguilliformes		
		Paraconger macrops (Günther) (Congridae) #	Palm, 2004

Table 1 – *continued*

Heteronybelinia heteromorphi Palm, 1999			
Adult	Carcharhiniformes		
	Carcharhinus cf. d*ussumieri* (Müller & Henle) (Carcharhinidae)	Haseli *et al.*, 2010	
	Eusphyra blochii (Cuvier) (Sphyrnidae)	Palm, 1999	
	Sphyrna mokarran (Rüppell) (Sphyrnidae)*	Palm, 1999	
Plerocercoid	Perciformes		
	Bothus podas (Delaroche) (Bothidae)	Palm, 2004	
	Nemipterus furcosus (Nemipteridae)	Palm, 2004	
Heteronybelinia mattisi n. sp			
Adult	Rajiformes		
	Sympterygia bonapartii Müller & Henle (Rajidae)* §	Present study	
Plerocercoid	Perciformes		
	Nemadactylus bergi (Norman) (Cheilodactylidae) §	Present study	
	Ophidiiformes		
	Raneya brasiliensis (Kaup) (Ophidiidae) §	Present study	
Heteronybelinia minima Palm, 1999			
Plerocercoid	Aulopiformes		
	Harpodon nehereus (Hamilton) (Synodontidae)*	Palm, 1999	
	Perciformes		
	Polynemus paradiseus Linnaeus (Polynemidae)	Palm, 1999	
	Upeneus moluccensis (Bleeker) (Mullidae)	Palm, 2004	
	Upeneus sulphureus Cuvier (Mullidae)	Palm, 2004	
	Upeneus vittatus (Forsskål) (Mullidae)	Palm, 2004	
	Pleuronectiformes		
	Pseudorhombus arsius (Hamilton) (Paralichthyidae)	Palm, 2004	
	Scorpaeniformes		
	Chelidonichthys obscurus (Walbaum) (Triglidae) #	Palm, 2004	
Heteronybelinia nipponica (Yamaguti, 1952)			
Adult	Carcharhiniformes		
	Sphyrna lewini (Griffith & Smith) (Sphyrnidae) §	São Clemente & Gomes, 1992	
	Rajiformes		
	Rhynchobatus djiddensis (Forsskål) (Rhinobatidae)	Palm, 2004	
Plerocercoid	Beryciformes		
	Hoplostethus mediterranus Cuvier (Trachichthyidae)	Palm, 2004	
	Carcharhiniformes		
	Carcharhinus signatus (Poey) (Carcharhinidae) §	Knoff *et al.*, 2004	
	Sphyrna zygaena (Linnaeus) (Sphyrnidae) §	Palm, 2004	
	Gadiformes		
	Coelorinchus caelorhinchus (Risso) (Macrouridae)	Palm, 2004	
	Ophidiiformes		
	Genypterus brasiliensis Regan (Ophidiidae) §	São Clemente *et al.*, 2004	
	Neobythites macrops Günther (Ophidiidae)*	Yamaguti, 1952	
	Osmeriformes		
	Argentina kagoshimae Jordan & Snyder (Argentinidae)	Yamaguti, 1952	
	Perciformes		
	Menticirrhus americanus (Sciaenidae) §	Pereira & Boeger, 2005	
	Umbrina canosai Berg (Sciaenidae) §	Pereira & Boeger, 2005	
	Pleuronectiformes		
	Paralichthys isosceles Jordan (Paralichthyidae) §	Felizardo *et al.*, 2010	
	Pseudorhombus pentophthalmus Günther (Paralichthyidae)	Yamaguti, 1952	
	Xystreurys rasile (Jordan) (Paralichthyidae) §	Felizardo *et al.*, 2010	
	Tetraodontiformes		
	Sphoeroides pachygaster (Müller & Troschel) (Tetraodontidae)	Dollfus, 1960	

In **bold,** hosts included in the original descriptions.
Hosts reported in redescriptions of species based on type material and newly collected specimens.
§ Host reported in the south-western Atlantic.
*Type host.

Yamaguti, 1952; *N. palliata* [Linton, 1924]; *N. perideraeus* [Shipley & Hornell, 1906]; *N. punctatissima* Dollfus, 1960; *N. robusta* [Linton, 1890]; *N. rougetcampanae* Dollfus, 1960; *N. senegalensis* Dollfus, 1960; and *N. yamagutii* Dollfus, 1960), and described *H. heteromorphi* Palm, 1999, and *H. minima* Palm, 1999. Six of the 14 species originally included by Palm (1999) in *Heteronybelinia* have subsequently been synonymized with other species, four with *H. estigmena* (i.e. *H. alloiotica*, *H. cadenati*, *H. punctatissima* and *H. senegalensis*), one with *H. nipponica* (i.e. *H. rougetcampanae*), and one with *Parotobothrium balli* (Southwell, 1929) (i.e. *H. karachii*) (see Palm, 2004). Four species of *Heteronybelinia* have since been described (namely, *H. australis* Palm & Beveridge, 2002; *H. pseudorobusta* Palm & Beveridge, 2002; *H. overstreeti* Palm, 2004; and *H. annakohnae* Pereira & Boeger, 2005).

Table 2. Host associations of adults and/or plerocercoids of *Heteronybelinia* including *H. overstreeti*, *H. palliata*, *H. perideraeus*, *H. pseudorobusta*, *H. robusta* and *H. yamagutii*.

Heteronybelinia overstreeti Palm, 2004		
Adult	Carcharhiniformes	
	Carcharhinus limbatus (Müller & Henle) (Carcharhinidae)*	Palm, 2004
Plerocercoid	Carcharhiniformes	
	Carcharhinus limbatus (Carcharhinidae)	Palm, 2004
	Perciformes	
	Pseudopeneus maculatus (Bloch) (Mullidae) §	Palm, 2004
Heteronybelinia palliata (Linton, 1924)		
Adult	Hexanchiformes	
	Notorynchus cepedianus (Péron) (Hexanchidae) §	Palm, 2004
	Carcharhiniformes	
	Sphyrna zygaena (Linnaeus) (Sphyrnidae)*	Linton, 1924
Plerocercoid	Aulopiformes	
	Alepisaurus ferox Lowe (Alepisauridae)	Palm, 2004
	Carcharhiniformes	
	Mustelus canis (Triakidae)	Palm, 2004
	Perciformes	
	Cynoscion regalis (Bloch & Schneider) (Sciaenidae)	Palm, 2004
	Pleuronectiformes	
	Paralichthys dentatus (Linnaeus) (Paralichthyidae) #	Palm, 2004
Heteronybelinia perideraeus (Shipley & Hornell, 1906)		
Adult	Carcharhiniformes	
	Glyphis gangeticus (Müller & Henle) (Carcharhinidae)*	Shipley & Hornell, 1906
	Orectolobiformes	
	Nebrius ferrugineus (Lesson) (Gynglostomatidae)	Palm, 2004
	Rajiformes	
	Rhynchobatus djiddensis (Rhinobatidae)	Palm, 2004
	Hexanchiformes	
	Notorynchus cepedianus (Hexanchidae) §	Palm, 2004
Plerocercoid	Perciformes	
	Secutor ruconius (Hamilton) (Leiognathidae)	Palm, 2004
Heteronybelinia pseudorobusta Palm & Beveridge, 2002		
Plerocercoid	Scorpaeniformes	
	Lepidotrigla modesta Waite (Triglidae)*	Palm & Beveridge, 2002
Heteronybelinia robusta (Linton, 1890)		
Adult	Carcharhiniformes	
	Carcharhinus limbatus (Carcharhinidae) #	Palm, 1999
	Mustelus asterias Cloquet (Triakidae)	Palm, 2004
	Rajiformes	
	Dasyatis centroura (Mitchill) (Dasyatidae)*	Linton, 1890
	Raja inornata (Rajidae)	Palm, 2004
	Rajella leopardus (von Bonde & Swart) (Rajidae)	Palm, 2004
Plerocercoid	Anguilliformes	
Heteronybelinia yamagutii (Dollfus, 1960)	*Bassanago albescens* (Barnard) (Congridae)	Palm *et al.*, 1997
	Aulopiformes	
	Saurida undosquamis (Richardson) (Synodontidae)	Palm *et al.*, 1997
	Lophiiformes	
	Lophioides mutilus (Alcock) (Lophiidae)	Palm, 2004
	Lophius piscatorius Linnaeus (Lophiidae)	Palm, 2004
	Perciformes	
	Caranx rhonchus (Carangidae)	Palm, 2004
	Pleuronectiformes	
	Chascanopsetta lugrubris Alcock (Bothidae)	Palm, 2004
	Polymixiformes	
	Polymixia nobilis Lowe (Polymixiidae)	Palm *et al.*, 1997
	Scorpaeniformes	
	Satyrichthys adeni (Lloyd) (Peristediidae)	Palm *et al.*, 1997
Adult	Carcharhiniformes	
	Sphyrna lewini (Carcharhinidae)	Palm, 1999
Plerocercoid	Anguilliformes	
	Derichthys serpentinus Gill (Derichthyidae)	Gartner & Zwerner, 1989
	Nessorhamphus ingolfianus (Schmidt) (Derichthyidae)	Gartner & Zwerner, 1989
	Nemichthys scolopaceus Richardson (Nemichthyidae)	Gartner & Zwerner, 1989
	Aulopiformes	
	Saurida undosquamis (Synodontidae)	Palm *et al.*, 1997

Table 2 – *continued*

Beryciformes	
Beryx splendes Lowe (Berycidae)	Palm, 2004
Carcharhiniformes	
Carcharhinus signatus (Carcharhinidae) §	Knoff *et al.*, 2004
Gadiformes	
Coelorinchus flabellispinis (Alcock) (Macrouridae)	Palm, 2004
Lophiiformes	
Chaunax pictus Lowe (Chaunacidae)	Palm, 2004
Myctophiformes	
Metelectrona ventralis (Becker) (Myctophidae)	Palm, 2004
Perciformes	
Gempylus serpens Cuvier (Gempylidae)	Palm, 2004
Thyrsitoides marleyi Fowler (Gempylidae)	Palm, 2004
Benthodesmus elongatus (Clarke) (Trichiuridae)	Palm, 2004
Polymixiformes	
Polymixia nobilis Lowe (Polymixiidae)	Palm, 2004
Stomiiformes	
Gonostoma elongatum Günther (Gonostomatidae)	Gartner & Zwerner, 1989
Polyipnus polli Schultz (Sternoptychidae)	Palm, 2004
Tetraodontiformes	
Sphoeroides pachygaster (Tetraodontidae)*	Dollfus, 1960
Teuthida	
Loligo pealeii Leseur (Loliginidae)	Palm, 2004
Lycoteuthis springeri (Voss) (Lycoteuthidae)	Palm, 2004
Sthenoteuthis oualaniensis (Lesson) (Ommastrephidae)	Palm, 2004
Todarodes angolensis Adam (Ommastrephidae)	Palm *et al.*, 1997

In **bold,** hosts included in the original descriptions.
Hosts reported in redescriptions of species based on type material and newly collected specimens.
§ Host reported in the south-western Atlantic.
* Type host.

Most species of *Heteronybelinia* have been described on the basis of plerocercoids and adults (tables 1 and 2). The type species, *H. estigmena*, was originally described as plerocercoids from the perciform *Selene setapinnis* (Mitchill, 1815) (see Dollfus, 1960). Later, Palm & Beveridge (2002) redescribed the plerocercoid and added the description of the adult. Only the plerocercoid stage is known for *H. annakohnae*, *H. elongata*, *H. eureia*, *H. minima* and *H. pseudorobusta,* whereas the description of *H. australis* was just based on adult worms (tables 1 and 2).

Seven species of *Heteronybelinia* have been reported from the south-western Atlantic (tables 1 and 2). Among them, adults of *H. palliata* and *H. perideraeus* were recovered from the broadnose sevengill shark, *Notorynchus cepedianus* (Péron, 1807), and *H. nipponica* from *Sphyrna lewini* (Griffith & Smith, 1868) (see São Clemente & Gomes, 1992; Palm, 2004). Other records in the south-western Atlantic, including *H. nipponica*, were found as plerocercoids in a diverse array of hosts (tables 1 and 2).

In a recent survey, several specimens of *Sympterygia bonapartii* Müller & Henle, 1841 (Rajidae) and teleosts, examined for parasites along the Argentine coast, were found to be parasitized by a new species of *Heteronybelinia*. Adults and plerocercoids of this new species are described below.

Materials and methods

Collection and examination of cestodes

During 2008–2011 specimens belonging to 24 species of teleosts and 19 species of elasmobranchs captured along the Argentine Sea were examined for cestodes. These included *Acanthistius brasilianus* (Cuvier, 1828) (Serranidae), *Cottoperca gobio* (Günther, 1861) (Bovichtidae), *Cynoscion guatucupa* (Cuvier, 1830) (Sciaenidae), *Genypterus blacodes* (Forster, 1801) (Ophidiidae), *Merluccius hubbsi* Marini, 1933 (Merlucciidae), *Micropogonias furnieri* (Desmarest, 1823) (Sciaenidae), *Mullus argentinae* Hubbs & Marini, 1933 (Mullidae), *Nemadactylus bergi* (Norman, 1937) (Cheilodactylidae), *Pagrus pagrus* (Linnaeus, 1758) (Sparidae), *Patagonotothen brevicauda* (Lönnberg, 1905) (Nototheniidae), *Patagonotothen ramsayi* (Regan, 1913) (Nototheniidae), *Porichthys porosissimus* (Cuvier, 1829) (Batrachoididae), *Pseudopercis semifasciata* (Cuvier, 1829) (Pinguipedidae), *Prionotus nudigula* Ginsburg, 1950 (Triglidae), *Prionotus punctatus* (Bloch, 1793) (Triglidae), *Raneya brasiliensis* (Kaup, 1856) (Ophidiidae), *Salilota australis* (Günther, 1878) (Moridae), *Serranus auriga* (Cuvier, 1829) (Serranidae), *Stromateus brasiliensis* Fowler, 1906 (Stromateidae), *Trachurus lathami* Nichols, 1920 (Carangidae), *Trichiurus lepturus* Linnaeus, 1758 (Trichiuridae), *Umbrina canosai* Berg, 1895 (Sciaenidae), *Urophycis brasiliensis* (Kaup, 1858) (Phycidae), and *Xystreurys rasile* (Jordan, 1891) (Paralichthyidae), *Atlantoraja castelnaui* (Miranda Ribeiro, 1907) (Rajidae), *Atlantoraja cyclophora* (Regan, 1903) (Rajidae), *Bathyraja magellanica* (Philippi, 1902) (Rajidae), *Carcharhinus brachyurus* (Günther, 1870) (Carcharhinidae), *Discopyge tschudii* Heckel, 1846 (Narcinidae), *Galeorhinus galeus* (Linnaeus, 1758) (Triakidae), *Mustelus schmitti* Springer, 1939 (Carcharhinidae), *Mustelus fasciatus* (Garman, 1913) (Carcharhinidae), *Notorynchus cepedianus* (Péron, 1807) (Hexanchidae), *Psammobatis bergi* Marini, 1932 (Rajidae), *Psammobatis extenta* (Garman, 1913) (Rajidae), *Rioraja* *agassizi* (Müller & Henle, 1841) (Rajidae), *Squalus acanthias* Linnaeus, 1758 (Squalidae), *Squalus mitsukurii* Jordan & Snyder, 1903 (Squalidae), *Squatina guggenheim* Marini, 1936 (Squatinidae), *Sympterygia acuta* Garman, 1877 (Rajidae), *Sympterygia bonapartii* Müller & Henle, 1841 (Rajidae), *Schroederichthys bivius* (Müller & Henle, 1838) (Scyliorhinidae) and *Zearaja chilensis* (Guichenot, 1848) (Rajidae).

The specimens of the new species of *Heteronybelinia* described below were collected from *S. bonapartii*, *N. bergi* and *R. brasiliensis* caught off Puerto Quequén, Buenos Aires Province, Argentina (38°37′S, 58°53′W), with the help of commercial trawlers. Additional specimens of *R. brasiliensis* and *N. bergi* were caught by line on board the Oceanographic Vessel *Puerto Deseado* off Necochea (39°03′S, 59°05′W) and San Clemente del Tuyú (36°09′S, 55°53′W), respectively.

The plerocercoids were removed from the pyloric stomach of two specimens of *S. bonapartii* and the visceral mesentery of *N. bergi* and *R. brasiliensis*. Gravid and mature specimens found in the spiral intestine of *S. bonapartii* were relaxed in seawater.

All cestodes were fixed in 10% formalin and transferred to 70% ethanol for storage. A total of 14 specimens (8 plerocercoids, 1 mature and 5 gravid worms) were prepared for light microscopy, hydrated in a graded ethanol series, stained with Harris' haematoxylin, dehydrated in a graded ethanol series, cleared in methyl salicylate and mounted in Canada balsam. All worms prepared for scanning electron microscopy (SEM) were hydrated in a graded ethanol series, post-fixed in 1% osmium tetroxide overnight at room temperature, dehydrated in a graded ethanol series, and dried using hexamethyldisilazane. After dehydration, the specimens were mounted on a stub with carbon tape, coated with 40 nm of gold/palladium in a Thermo VG Scientific Polaron SC 7630 (Quorum Technologies Ltd, East Grinstead, West Sussex, England) and examined in a Philips XL 30 scanning electron microscope (Fei Company, Eindhoven, The Netherlands). Terminology for the morphology of microtriches follows Chervy (2009). Gravid proglottids were embedded in paraffin and serial cross-sections were cut at a thickness of 8 μm. Sections were stained with Harris' haematoxylin and counterstained with eosin and mounted in Canada balsam. Tentacles were removed from the scolex of five worms (4 plerocercoids and 1 adult) and temporarily mounted in glycerine to study the tentacular armature in detail. Terminology for the morphology of hooks follows Campbell & Beveridge (1994). Whole and temporary mounts and sections were observed and measured using a Zeiss Axioskop and an Olympus BX 51 compound microscope (Olympus Corporation, Tokyo, Japan). Drawings were made with the aid of a drawing tube attached to a Zeiss Axioskop compound microscope. Measurements include the range, followed in parentheses by the mean, standard deviation (when n ≥ 3), number of worms examined (n), and the total number of observations when more than one measurement per worm was taken (*n*). Host specificity categories follow Palm & Caira (2008). Labels AMPD-003, AMPD-012, AMPQ-162, AMPQ-211 and VIPQ-048 refer to individual host specimens in our database. All measurements are in micrometres unless otherwise stated. Museum abbreviations used are as follows: MACN-Pa, Museo Argentino de Ciencias Naturales, Colección Parasitológica, Buenos Aires, Argentina; NHMUK, Natural History Museum, London, United Kingdom. The description below includes only the measurements of the adults, as follows: scolex features were based on mature and gravid specimens; worm length, maximum width and number of immature, mature and gravid proglottids refer only to gravid worms. Measurements of plerocercoids are provided in table 3, measurements and shape of hooks in specimens

Table 3. Measurements of plerocercoids of *Heteronybelinia mattisi* n. sp. from both species of teleosts, *N. bergi* and *R. brasiliensis*, and the skate *S. bonapartii*.

	Measurements in μm; range with mean, standard deviation, number of specimens (n), and number of measurements (*n*) in parentheses
Total length	1287–1725 (1581 ± 77, n = 8)
Scolex length (velum included)	1287–1600 (1567 ± 135, n = 8)
Scolex length (velum not included)	938–1250 (1125 ± 110, n = 8)
Maximum width of scolex	660–910 (822 ± 79, n = 8)
Scolex length to width ratio	1.32–2.10 (1.91 ± 0.24, n = 8)
Bothrium (L × W)	630–770 (713 ± 46, n = 8, *n* = 16) × 340–760 (4200 ± 144, n = 7, *n* = 8)
Pars bothrialis (Pbo) length	650–810 (755 ± 56, n = 8)
Pars vaginalis (Pvag) (L × W)	570–830 (715 ± 81, n = 8) × 195–380 (300 ± 69, n = 8)
Pars bulbosa (Pb) (L × W)	250–355 (320 ± 37, n = 8) × 190–295 (228 ± 31, n = 8)
Pars postbulbosa (Ppb) (L × W)	370–610 (465 ± 80, n = 7) × 420–630 (570 ± 73, n = 7)
Pars postbulbosa: total length (%)	22–39 (30 ± 4, n = 7)
Pbo:Pva:Pb:Ppb	1:0.70–1.03:0.31–0.47:1.28–1.75
Bulbs (L × W)	200–295 (268 ± 27, n = 8, *n* = 17) × 75–115 (97 ± 13, n = 7, *n* = 15)
Bulbs length to width ratio	2.38–3.66 (2.7 ± 0.36, n = 7, *n* = 15)
Velum (L × W)	350–540 (476 ± 79, n = 7) × 420–630 (555 ± 67, n = 7)
Tentacle diameter at base without hooks	37–48 (44 ± 4, n = 5, *n* = 7)
Tentacle diameter at base with hooks	42–56 (51 ± 45, n = 5, *n* = 7)
Distal tentacle diameter without hooks	28–37 (32 ± 4, n = 4, *n* = 7)
Distal tentacle diameter with hooks	42–50 (46 ± 43 n = 4, *n* = 7)

L, Length; W, width.

Table 4. Morphology and measurements of hooks of *Heteronybelinia mattisi* n. sp. from both species of teleosts, *N. bergi* and *R. brasiliensis*, and the skate *S. bonapartii*.

Surface	Shape	Specimen	Row	Length (L)	Base (B)	Height	Toe (T)	T/B ratio (%)
Ab (Ba)	Uncinate with elongate base	Holotype	1–2	7.0–9.3 (8.1 ± 1.1)	7.3–9.5 (8.4 ± 1.1)	7.0–9.5 (8.1 ± 0.9)	4.0–5.5 (4.8 ± 0.6)	52–63 (56 ± 4)
		Paratypes (n = 5)	1–2	5.9–9.5 (7.0 ± 1.0)	6.9–9.5 (8.2 ± 1.0)	5.9–8.5 (6.9 ± 0.9)	3.9–6.9 (5.0 ± 1.1)	50–67 (60 ± 7)
Bo (Ba)	Uncinate with rounded base	Holotype	1–2	5.9–7.5 (6.7 ± 0.7)	5.9–7.8 (6.7 ± 0.6)	5.9–7.0 (6.4 ± 0.6)	3.0–3.4 (3.2 ± 0.2)	43–47 (46 ± 2)
		Paratypes (n = 5)	1–2	5.9–7.5 (6.7 ± 0.5)	6.9–8.3 (7.9 ± 0.5)	5.9–7.8 (6.7 ± 0.6)	3.0–3.9 (3.7 ± 0.2)	43–47 (46 ± 1)
Ab (MBa)	Uncinate with elongate base	Holotype	5	10.3–10.8 (10.7 ± 0.3)	10.8–11.5 (11.0 ± 0.3)	10.0–11.0 (10.5 ± 0.4)	5.3–6.5 (5.9 ± 0.4)	50–54 (55 ± 2)
			10	11.3–12.5 (11.2.0 ± 0.6)	11.3–13.0 (12.4 ± 0.5)	11.5–13.0 (12.11 ± 0.6)	6.0–7.5 (6.7 ± 0.5)	50–57 (54 ± 3)
			15	12.3–13.5 (12.8 ± 0.5)	12.7–13.5 (13.5 ± 0.6)	12.0–13.5 (12.9 ± 0.5)	6.4–7.5 (7.1 ± 0.4)	50–54 (52 ± 1)
		Paratypes (n = 5)	3–20	9.8–15.7 (11.0 ± 1.7)	9.8–15.0 (11.5 ± 1.3)	6.9–13.7 (9.3 ± 1.6)	4.0–7.5 (6.2 ± 0.7)	50–70 (55 ± 4)
Bo (MBa)	Uncinate with rounded base	Holotype	5	8.8–10.0 (9.4 ± 0.5)	8.8–10.0 (9.4 ± 0.6)	8.8–10 (9.2 ± 0.5)	3.9–4.5 (3.9 ± 0.3)	39–45 (42 ± 3)
			10	10.0–10.8 (10.4 ± 0.4)	10.0–11.0 (10.4 ± 0.4)	10.0–11.0 (10.5 ± 0.4)	3.9–5.0 (3.7 ± 0.3)	35–45 (38 ± 2)
		Paratypes (n = 5)	3–20	8.8–14.7 (10.0 ± 2.0)	8.8–13.7 (10.0 ± 1.1)	7.3–11.0 (8.8 ± 1.2)	3.5–5.9 (4.3 ± 0.5)	35–48 (43 ± 3)

Measurements are given in μm as range, with mean and standard deviation in parentheses.
Ab, Antibothrial; Ba, basal; Bo, bothrial; MBa, metabasal armature.

studied (holotype and paratypes) are detailed in table 4, microthrix patterns in adults and plerocercoids are described in table 5.

Heteronybelinia mattisi n. sp

Description

Based on 10 complete plerocercoids and 7 adult specimens prepared as follows: 14 whole mounts (8 plerocercoids and 6 adults) and 3 specimens observed with SEM (2 plerocercoids and 1 adult). Adult worms apolytic, 12.4–23.6 (19.4 ± 5.3, n = 4) mm long, maximum width at level of gravid proglottids; proglottids acraspedote, 67–91 (77 ± 11, n = 5) per worm (fig. 1). Scolex 975–1330 (1120 ± 127, n = 6) long, maximum width at the level of pars bothrialis. Apex of scolex covered with coniform spinitriches (see fig. 17). Four oval bothria, tapering posteriorly, 610–760 (710 ± 43, n = 6, *n* = 10) long, 320–362 (343 ± 19, n = 3, *n* = 3) wide (figs 2, 3, 9, 16), lateral bothrial margins covered with hamulate spinitriches with broad bases (figs 10, 13), posterior bothrial margins covered with elongate hamulate spinitriches with slender bases (figs 10, 12, 14, 18). Proximal bothrial surface covered with coniform spinitriches interspersed with acicular filitriches (fig. 15). Anterior two-thirds of distal bothrial surface covered with coniform spinitriches with ridging surface interspersed with acicular filitriches (figs 10–11), posterior third covered with acicular filitriches only (figs 10, 12, 21). Pars bothrialis 700–830 (762 ± 47, n = 6) long, 510–700 (617 ± 64, n = 6) wide, tentacle sheaths weakly sinuous. Pars vaginalis 610–860 (785 ± 72, n = 6) long, 105–215 (152 ± 41, n = 6) wide; covered with acicular filitriches (fig. 19). Pars bulbosa 250–325 (298 ± 26, n = 6) long, 255–360 (288 ± 31, n = 6) wide; covered with acicular filitriches (fig. 20). Bulbs short, 235–305 (277 ± 23, n = 6, *n* = 18) long, 90–110 (103 ± 7, n = 6, *n* = 18) wide, length to width ratio 2.14–3.39 (2.70 ± 0.32, n = 6, *n* = 18):1. Retractor muscle originates at base of bulb (figs 2, 3). Ratio of pars bothrialis:pars vaginalis:pars bulbosa 1:0.87–1.10:0.33–0.45. Tentacles short and tapered, without basal swelling, up to 550 long, diameter at base without hooks 25–47 (40 ± 7, n = 5, *n* = 6), diameter at base with hooks 33–57 (50 ± 7, n = 5, *n* = 6). Distal diameter of tentacles without hooks, 30–37 (33 ± 3, n = 3, *n* = 5), distal diameter with hooks 42–52 (48 ± 4, n = 3, *n* = 5).

Armature homeoacanthous, weakly heteromorphous; hooks solid, arranged in ascending continuous spiral rows, up to 32 rows. Basal hooks arranged in 1–2 rows, basal antibothrial hooks uncinate with elongate bases (figs 22, 27, 33, table 4), basal bothrial hooks uncinate with rounded bases (figs 23, 26, 31, table 4). Basal hooks begin at very base of tentacle in bothrial and internal surfaces (figs 23, 25); small inverted V-shape area devoid of hooks in basal antibothrial and external surfaces (figs 22–24).

Metabasal armature (from row 3) consists on ascending rows, 6–7 hooks per half row (figs 22–25, 32). Antibothrial surface consists of uncinate hooks with elongate bases (figs 22, 27–29, table 4), bothrial surface with uncinate hooks with rounded bases

Table 5. Microthrix pattern on the surface of the scolex of *Heteronybelinia mattisi* n. sp.

Surface	Microthrix morphology	Adult: Size (L × W at base)	Adult: Density (mt/μm²)	Plerocercoid: Size (L × W at base)	Plerocercoid: Density (mt/μm²)
Apex of scolex (fig. 17)	Coniform spinitriches	2.07–2.46 × 0.51–0.66	1–2	1.90–2.10 × 0.56–0.73	1–2
Proximal bothrial (fig. 15)	Coniform spinitriches	2.62–3.45 × 0.42–0.53	1	2.68–3.06 × 0.76–0.79	
	Acicular filitriches	0.46–0.52 × 0.14–0.16	8–12	0.43–0.63 × 0.13–0.17	9–13
Distal bothrial (fig. 11)	Coniform spinitriches	3.01–3.30 × 0.52–0.58	1	3.11–4.01 × 0.52–0.83	1
	Acicular filitriches	0.35–0.42 × 0.09–0.13	11–14	0.35–0.50 × 0.11–0.13	9–12
Lateral bothrial margin (fig. 13)	Hamulate spinitriches	6.82–9.25 × 7.84–8.97	1	7.74–10.74 × 5.13–8.04	1
Posterior bothrial margin (figs 11, 14, 18)	Hamulate spinitriches	8.74–19.24 × 6.30–7.32	1	10.68–12.78 × 3.44–4.19	1
Pars vaginalis (fig. 19)	Acicular filitriches	0.22–0.25 × 0.15–0.16	28–31	0.38–0.42 × 0.12–0.14	17–21
Pars bulbosa (fig. 20)	Acicular filitriches	0.22–0.33 × 0.10–0.13	15–21	0.29–0.37 × 0.09–0.12	17–23

L, Length; mt, microtriches; W, width. Measurements given in μm.

(figs 23, 26, 34, table 4). Hooks gradually increase in size from bothrial to antibothrial surface of tentacle, showing transitional shape and size of hooks on internal and external surfaces in basal and metabasal armature (figs 24–27).

Immature proglottids wider than long, 48–57 (50 ± 4, n = 5) in number (fig. 1). Mature proglottids wider than long, 260–410 (310 ± 38, n = 4, *n* = 31) long, 710–1000 (856 ± 68, n = 4, *n* = 31) wide, length to width ratio 0.30–0.49 (0.36 ± 0.05, n = 4, *n* = 31):1; 9–14 (11 ± 2, n = 5) mature proglottids per worm. Gravid proglottids wider than long, 325–670 (476 ± 92, n = 4, *n* = 72) long, 860–1350 (1114 ± 128, n = 4, *n* = 72) wide, length to width ratio 0.26–0.61 (0.43 ± 0.08, n = 4, *n* = 72):1; 12–29 (21 ± 7, n = 5) gravid proglottids per worm (figs 1, 4, 5).

Genital pore ventrosubmarginal, 15–26% (23 ± 3, n = 4, *n* = 28) from anterior margin of mature proglottid. Testes spherical, 26–38 (31 ± 3, n = 4, *n* = 24) per proglottid, 50–95 (72 ± 9, n = 4, *n* = 79) long, 33–80 (58 ± 7, n = 4, *n* = 79) wide, extending from level of cirrus sac to posterior margin of proglottid on poral side, throughout entire proglottid on aporal side (fig. 4), overlapping ovary in between dorsal and ventral ovarian lobes, one irregular row deep in cross-section (figs 4, 7, 8). Cirrus sac elongate, slender, 210–280 (239 ± 18, n = 4, *n* = 26) long, 40–80 (56 ± 9, n = 4, *n* = 26) wide, length to width ratio 3.12–6.25 (4.37 ± 0.79, n = 4, *n* = 26):1, containing unarmed cirrus (figs 4, 6). Vas deferens coiled, extending to mid-proglottid (figs 4, 6). Vagina thin walled, opening into genital atrium posterior and dorsal to cirrus sac, running parallel to cirrus sac, descending posteriorly to ootype region (figs 4, 6). Ovary lobulated, two-lobed in dorsoventral view, four-lobed in cross-section at level of ovarian isthmus, 230–325 (280 ± 31, n = 4, *n* = 22) wide (fig. 8). Seminal receptacle present, anterior to ovarian isthmus (figs 4, 7). Vitelline follicles circum-medullary, extending throughout entire proglottid, interrupted dorsally and ventrally at level of ovary and genital atrium (figs 4, 6, 8), follicles 15–37 (28 ± 5, n = 4, *n* = 76) long, 15–30 (23 ± 4, n = 4, *n* = 76) wide. Mehlis' gland 68–105 (84 ± 11, n = 4, *n* = 14) in diameter, posterior to ovarian isthmus (figs 4, 8). Uterus saccate, extending throughout length of gravid proglottids (fig. 5), uterine pore not observed.

Measurements of plerocercoids and adults are similar in most features (figs 1–3, table 3).

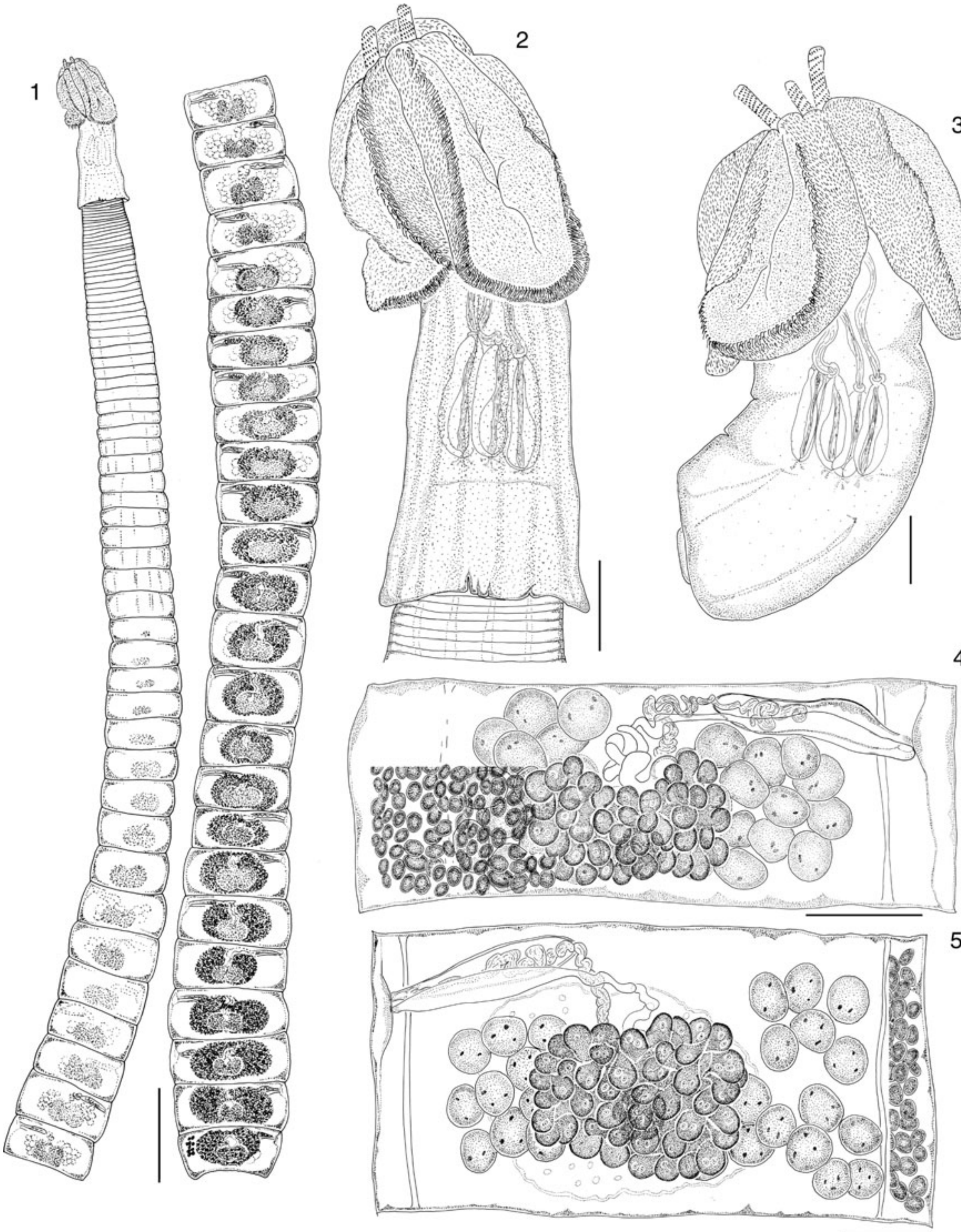
Taxonomic summary

Definitive host. *Sympterygia bonapartii* Müller & Henle, 1841, smallnose fanskate (Rajiformes: Rajidae) (AMPQ-162, VIPQ-048).

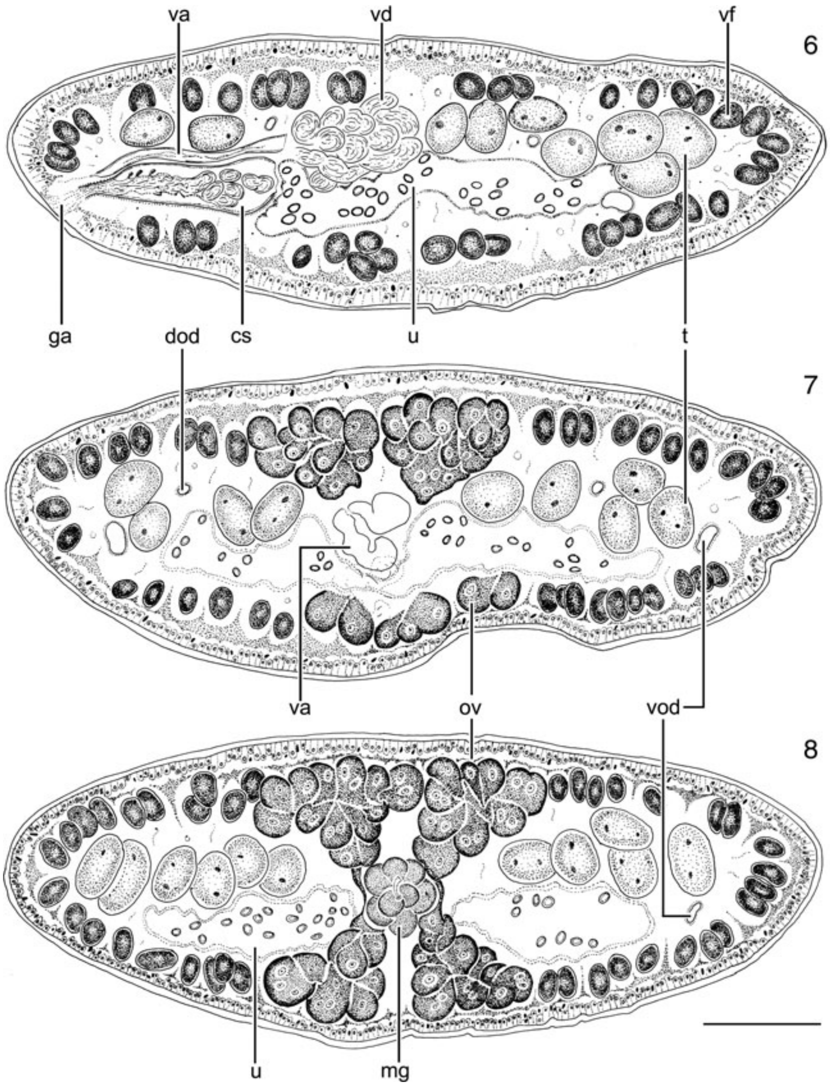
Intermediate hosts. Plerocercoids from *Raneya brasiliensis* (Kaup, 1856), banded cusk eel (Ophidiiformes: Ophidiidae) (AMPD-03), and *Nemadactylus bergi* (Norman, 1937), hawkfish (Perciformes: Cheilodactylidae) (AMPD-012).

Site of infection. Adults in spiral intestine, plerocercoids in pyloric stomach of *S. bonapartii* and visceral mesentery of teleosts.

Type locality. Puerto Quequén, Buenos Aires Province, Argentina (38°37′S, 58°53′W).



Figs 1–5. *Heteronybelinia mattisi* n. sp.: 1, entire worm, circum-medullar vitelline follicles not drawn to allow the view of internal organs (scale bar = 1 mm); 2, scolex of adult worm (scale bar = 200 μm); 3, plerocercoid (scale bar = 200 μm); 4, mature proglottid, dorsal view, circum-medullar vitelline follicles partially drawn (scale bar = 150 μm); 5, gravid proglottid, ventral view, circum-medullar vitelline follicles partially drawn (scale bar = 150 μm).



Figs 6–8. *Heteronybelinia mattisi* n. sp., cross-sections of a gravid proglottid (scale bar = 150 μm): 6, at the level of the genital pore; 7, at level of the ovary, anterior to ovarian isthmus; 8, at level of Mehlis' gland, posterior to ovarian isthmus. cs, Cirrus sac; ga, genital atrium; dod, osmoregulatory duct; mg, Mehlis' gland; ov, ovary; t, testis; u, uterus; va, vagina; vd, vas deferens; vf, vitelline follicles; vod, ventral osmoregulatory duct.

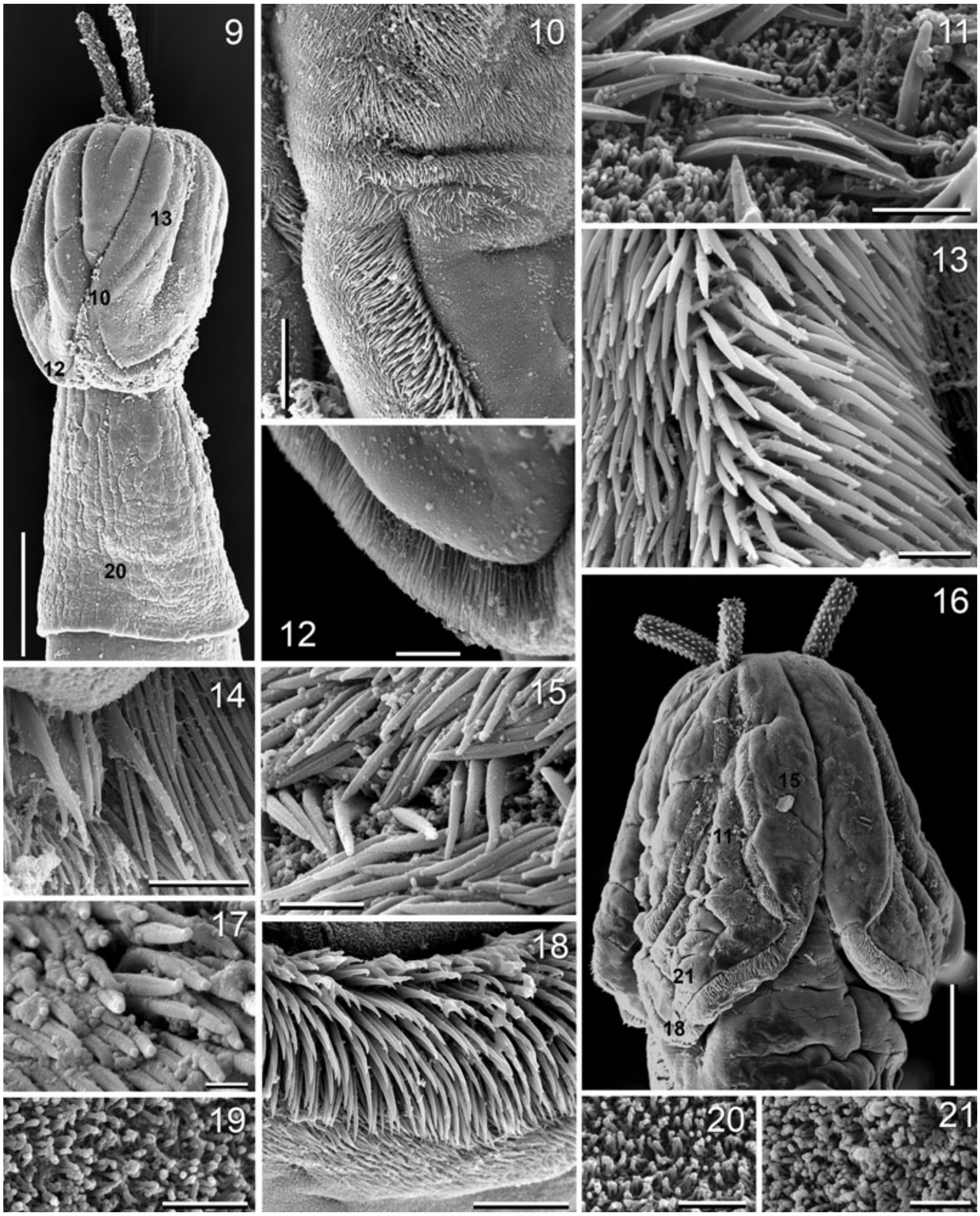
Other localities. Off Puerto Quequén (39°03′S, 59°05′W), off San Clemente del Tuyú (36°09′S, 55°53′W), Buenos Aires Province, Argentina.

Specimens deposited. Holotype (adult) and three paratypes (1 plerocercoid and 2 adults) deposited at MACN-Pa No. 537/1–4, two paratypes (1 plerocercoid and 1 adult) deposited at NHMUK No. 2012.9.11.1-2. Additional specimens (whole mounts, histological sections and specimens prepared for SEM) are retained in the personal collection of the senior author (V.I.).

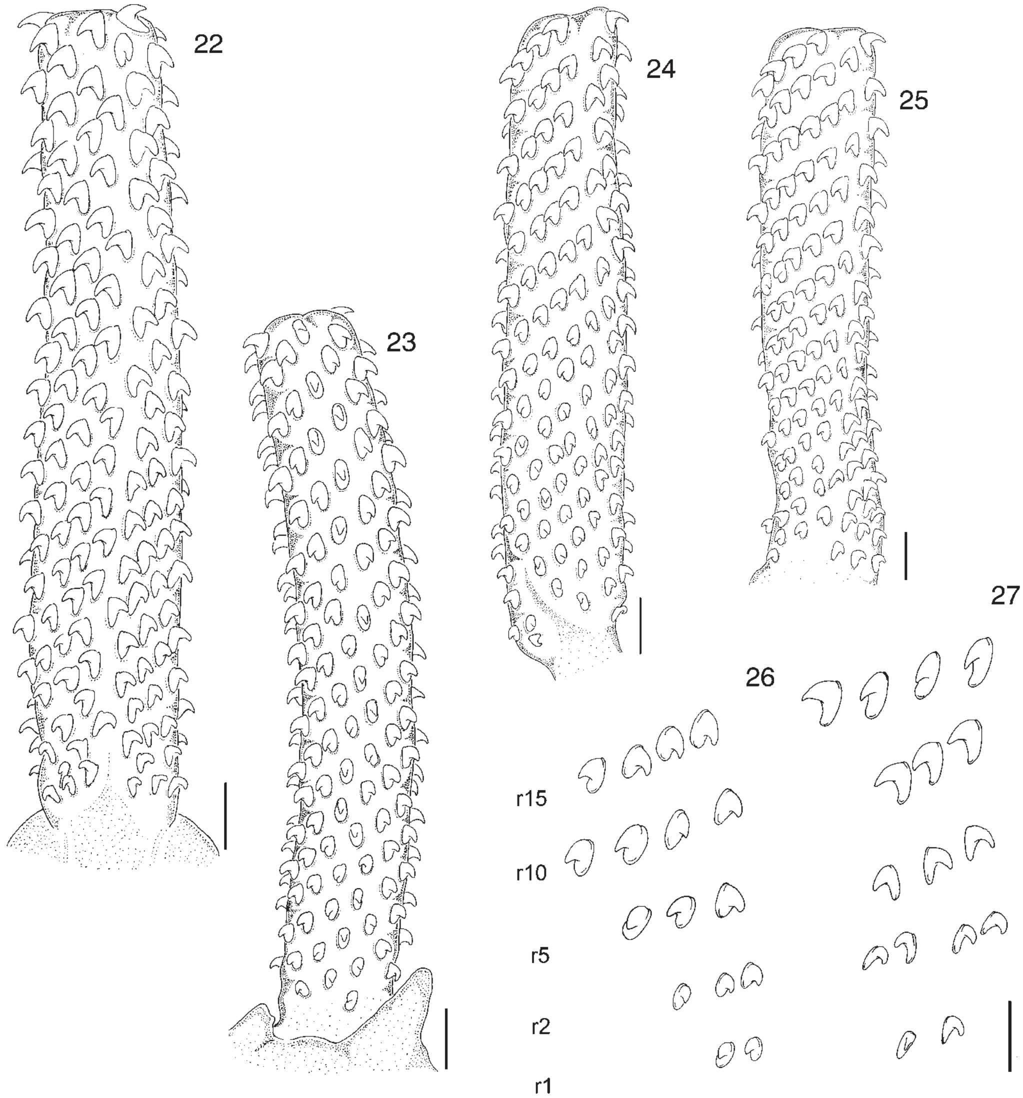
Etymology. The species is named in memory of Tom Mattis, in recognition of his work on the development of trypanorhynchs.

Prevalence and intensity of infection. Adult prevalence 4.8% (2 of 42 skates examined); intensity, 4 worms per host (in each of the 2 infected skates). Plerocercoid prevalence in *R. brasiliensis* 33.3% (1 of 3 specimens examined), in *N. bergi* 20% (1 of 5 specimens examined); intensity, 3 worms per host in *R. brasiliensis*, 5 worms per host in *N. bergi*.

The presence of homeoacanthous, heteromorphous, metabasal armature, basal heteromorphous hooks and the absence of a distinctive basal armature places this new species unequivocally in *Heteronybelinia*. *Heteronybelinia mattisi* n. sp. can be clearly distinguished from *H. yamagutii* and *H. nipponica* in lacking a characteristic basal armature consisting of bill hooks and spiniform hooks. The new species has metabasal armature consisting of uncinate hooks rather than the rosethorn-shaped hooks, as seen in *H. robusta* and *H. pseudorobusta*, or falcate hooks, as seen in *H. eureia*. Whereas in *H. overstreeti*,



Figs 9–21. *Heteronybelinia mattisi* n. sp., scanning electron micrographs. 9, Dorso-ventral view of the scolex, adult (scale bar = 300 μm), small numbers indicate locations of details shown in figs 10, 12, 13 and 20; 10, lateral and posterior bothrial margins, adult (scale bar = 30 μm); 11, distal bothrial surface, plerocercoid (scale bar = 2 μm); 12, posterior margin of bothria, adult (scale bar = 25 μm); 13, detail of lateral bothrial margin, adult (scale bar = 5 μm); 14, hamulate spinitriches on the posterior bothrial margin, adult (scale bar = 10 μm); 15, proximal bothrial surface, plerocercoid (scale bar = 3 μm); 16, lateral view of the scolex, plerocercoid (scale bar = 150 μm), small numbers indicate locations of details shown in figs 11, 15, 18 and 21; 17, apex of scolex, plerocercoid (scale bar = 1 μm); 18, hamulate spinitriches in the posterior margin of bothria, plerocercoid (scale bar = 15 μm); 19, pars vaginalis, plerocercoid (scale bar = 2 μm); 20, surface of pars bulbosa, adult (scale bar = 1.5 μm); 21, distal bothrial surface near posterior margin of bothria, plerocercoid (scale bar = 2 μm).

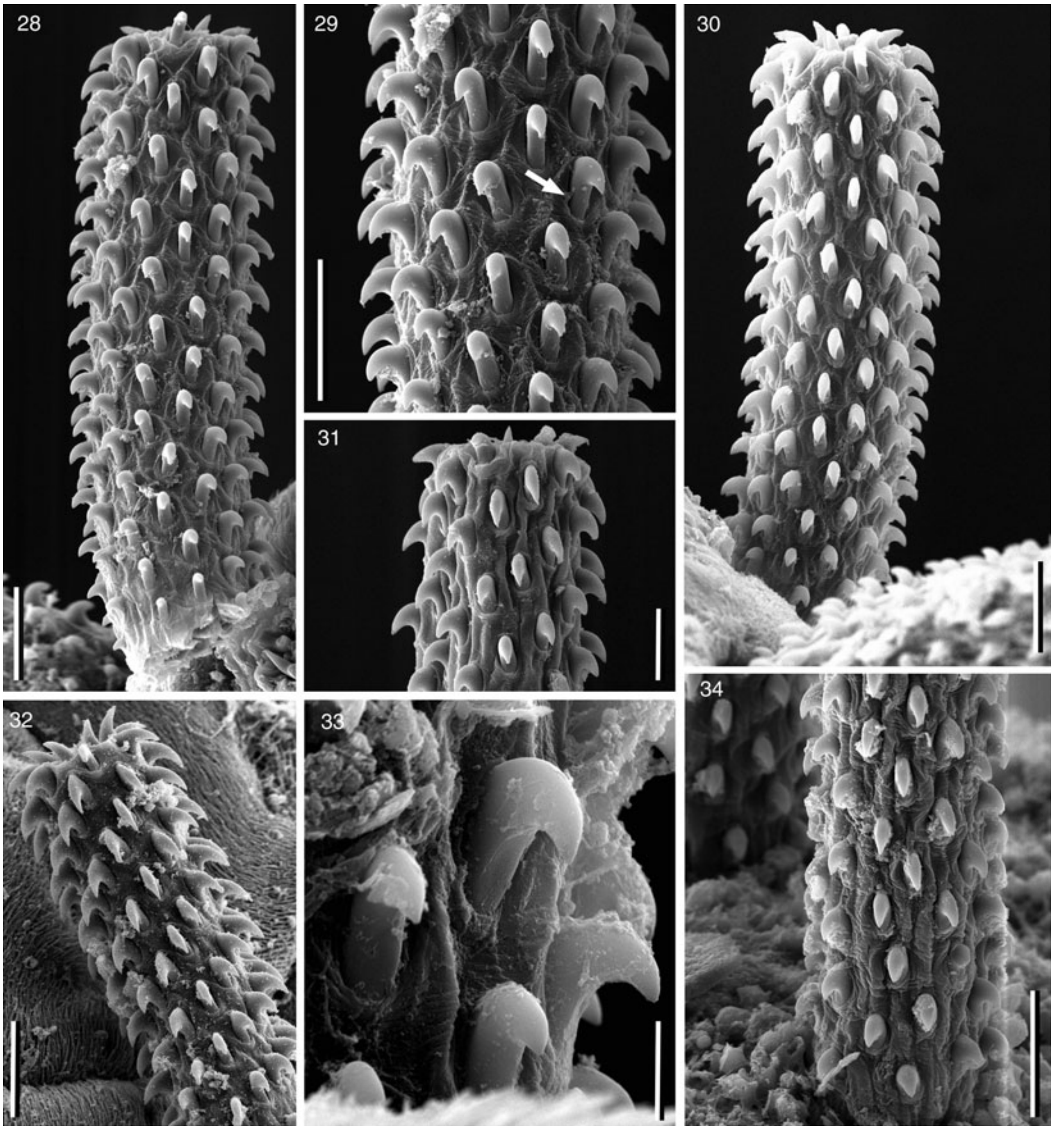


Figs 22–27. *Heteronybelinia mattisi* n. sp., tentacular armature. 22, Antibothrial surface of the tentacle, plerocercoid (scale bar = 25 μm); 23, bothrial surface of the tentacle, plerocercoid (scale bar = 25 μm); 24, external surface of tentacle, plerocercoid (scale bar = 25 μm); 25, internal surface of the tentacle, plerocercoid (scale bar = 25 μm). 26–27, Profiles of hooks of basal and metabasal armature of *Heteronybelinia mattisi* n. sp. (scale bar = 20 μm): 26, bothrial surface, uncinate hooks with rounded bases; 27, antibothrial surface, uncinate hooks with elongate bases. r1, row 1; r2, row 2; r5, row 5; r10, row 10; r15, row 15.

H. estigmena and *H. minima* the metabasal hooks decrease in size toward the tip of the tentacle, in *H. mattisi* n. sp. the hooks increase in size in that direction, thus, the largest hooks are in the distal region of the tentacle. In *H. elongata* and *H. perideraeus* the antibothrial hooks are conspicuously smaller than the bothrial hooks on the basal armature, but in *H. mattisi* n. sp. they differ slightly in shape and size on both surfaces. Whereas the metabasal hooks of *H. palliata* differ in shape on the internal and external surface (rosethorn-shaped and more slender and spiniform, respectively), in *H. mattisi* n. sp. they differ in size and shape on antibothrial and bothrial surfaces (uncinate with elongate bases and uncinate with rounded bases, respectively). Additionally, *H. heteromorphi* has quite larger metabasal hooks than *H. mattisi* n. sp. (21–28 versus. 8.8–15.7).

In *H. annakohnae* the bulbs completely overlap the pars bothrialis, resulting in a very short pars vaginalis (115–125 long), but in *H. mattisi* n. sp. the pars bothrialis only slightly overlaps with the pars bulbosa (0–19%), having a longer pars vaginalis (570–830 long). In addition, there exists a conspicuously long pars postbulbosa in *H. annakohnae* (65% of the plerocercoid length), which is rather shorter in *H. mattisi* n. sp. (22–39% of the plerocercoid length).

Finally, all four tentacles on a scolex have the same armature pattern in *H. mattisi* n. sp., differing far from the unique pattern found in *H. australis*, which



Figs 28–34. *Heteronybelinia mattisi* n. sp., scanning electron micrographs: 28, antibothrial surface of the tentacle, plerocercoid (scale bar = 20 μm); 29, detail of the metabasal armature, antibothrial surface showing an interrupted row of hooks at the level of row 8 (arrow), plerocercoid (scale bar = 7 μm); 30, bothrial surface of the tentacle, plerocercoid (scale bar = 20 μm); 31, metabasal hooks, bothrial surface, plerocercoid (scale bar = 15 μm); 32, metabasal region, antibothrial surface, adult (scale bar = 7 μm); 33, basal hooks, antibothrial surface, plerocercoid (scale bar = 5 μm); 34, bothrial surface of the tentacle, plerocercoid (scale bar = 20 μm).

has the largest hooks on the bothrial surface of two tentacles, and on the antibothrial surface of the other two tentacles.

Discussion

The tegument of all cestodes, including the Trypanorhyncha, is highly specialized and has been considered useful for taxonomic and phylogenetic studies (Palm, 2004; Tyler, 2006; Chervy, 2009). Studies on the ultrastructure of the tegument of trypanorhynchs, using SEM, have demonstrated a high morphological variability in form and size of the microtriches (Palm, 2004; Chervy, 2009). The microthrix pattern of a single species of *Heteronybelinia*, *H. estigmena*, had been examined until now (Palm, 2004; Borucinska & Caira, 2006; Chervy, 2009). The microtriches described in *H. estigmena* are similar in morphology to the pattern observed in *H. mattisi.* Both species have filiform microtriches on all surfaces of the scolex, in addition to coniform spinitriches on the apex and part of the distal bothrial surface (Figs 5 and 7 in Borucinska & Caira (2006); figs 11 and 17 of the present study), and hamulate spinitriches on the bothrial margins (Fig. 7 in Borucinska & Caira (2006); figs 12–14, 18 of the present study). They essentially differ in the distribution of the hamulate spinitriches, which might be absent on the posterior margin of the bothria in *H. estigmena* (see Borucinska & Caira, 2006). More species of *Heteronybelinia* should be examined with SEM to determine whether this pattern is consistent throughout all members of the genus.

The anatomy of the proglottids is consistent in all species of *Heteronybelinia* described as adults, having ventrosubmarginal genital pores, ovary in a central position, elongate cirrus sac, unarmed cirrus and the absence of seminal vesicles (Linton, 1890, 1924; Palm, 1999, 2004; Palm & Overstreet, 2000; Palm & Walter, 2000; Palm & Beveridge, 2002). In the diagnosis of *Heteronybelinia*, Palm (2004) included the presence of postovarian testes and testes anterior to the cirrus sac as a feature of the genus. However, *H. palliata* and *H. mattisi* lack postovarian testes (Fig. 7 in Palm & Overstreet (2000); figs 4 and 5 of the present study), and in *H. robusta* and *H. mattisi* the testes extend anterior to the cirrus sac only on the aporal side of the proglottid (Fig. 8C in Palm & Walter (2000); figs 4 and 5 of the present study). In most species the ovary does not overlap with the testicular field, however, in *H. australis*, *H. estigmena* and *H. mattisi* there are some testes between the dorsal and ventral ovarian lobes (Figs 53H and 55D in Palm (2004); figs 4 and 7 of the present study). As a consequence, Palm's (2004) diagnosis of *Heteronybelinia* should be emended as follows: strobila craspedote or acraspedote, anapolytic; proglottids wider than long or longer than wide; cirrus unarmed; cirrus sac lateral; genital pores ventrosubmarginal, alternating irregularly, in first third of the proglottid; seminal vesicles absent; testes numerous in single or multiple layers, medullary; postovarian testes present or absent on poral side; testes anterior to cirrus sac present or absent; uterine pore present or absent.

It is worth mentioning that even if all species of *Heteronybelinia* have continuous spiral rows of hooks along the tentacle, in some species there are rows interrupted by the absence of a single hook, giving the appearance of discontinuous rows. This was observed on different surfaces of the tentacle in *H. mattisi* (figs 22, 23, 25, 28, 29), and illustrated in the bothrial surface of *H. eureia* (Figs 33 and 35 in Dollfus (1960)), in the internal surface of *H. perideraeus* (Fig. 50G in Palm (2004)), and in the metabasal armature of *H. pseudorobusta* (Fig. 39 in Palm & Beveridge (2002)).

The host specificity of adults of *Heteronybelinia* is widely variable among species, ranging from very high (oioxenous, such as *H. overstreeti* and *H. yamagutii*, which are restricted to a single host species (table 2)), to very low (euryxenous, as *H. robusta*, *H. perideraeus*, *H. estigmena*, *H. nipponica* and *H. palliata*, which have been reported for hosts in different orders (tables 1, 2)). *Heteronybelinia australis*, a mesostenoxenous species, is restricted to a particular host genus (*Carcharhinus* spp.), and the metastenoxenous species *H. heteromorphi* is found in hosts of the same family (Sphyrnidae). Regardless of their degree of host specificity, with the exception of *H. mattisi*, the definitive hosts of all species of *Heteronybelinia* for which adults are known, include carcharhiniform sharks (Sphyrnidae, Carcharhinidae and Triakidae) (tables 1 and 2). Some species are restricted to carcharhiniform hosts (i.e. *H. australis*, *H. heteromorphi*, *H. overstreeti* and H. *yamagutii*), others include either a rajiform (i.e. *H. estigmena*, *H. nipponica* and *H. robusta*) or an hexanchiform host (i.e. *H. palliata*), and *H. perideraeus* has been found in hosts belonging to four different orders of elasmobranchs (Carcharhiniformes, Rajiformes, Orectolobiformes and Hexanchiformes) (tables 1 and 2). So far, adults of *H. mattisi* seem to have oioxenous specificity for their definitive batoid host, *S. bonapartii.* Even though species of some carcharhiniform and hexanchiform genera, reported as hosts for other species of *Heteronybelinia,* have been examined for cestode parasites in the same area (i.e. *M. schmitti*, *M. fasciatus, G. galeus, C. brachyurus*, *S. bivius* and *N. cepedianus*), no specimens of *H. mattisi* have yet been found.

Palm (2004) proposed an oceanic complex life cycle involving at least four hosts for the tentaculariids. These included copepods as first intermediate hosts, euphausiids or schooling fishes as second intermediate hosts, teleosts as third intermediate or paratenic hosts, and oceanic sharks as definitive hosts. In general, the plerocercoids of *Heteronybelinia* have a very low specificity for their third intermediate hosts, being reported from a diverse array of teleosts in 16 orders and in cephalopods (tables 1 and 2). Even so, the specificity is variable among species, from species that were reported from a single host species (i.e. *H. eureia*, *H. perideraeus*, *H. pseudorobusta* and *H. overstreeti*) to species that are parasites of several unrelated hosts (e.g. *H. yamagutti* from hosts in 12 families and nine different orders of teleosts) (tables 1 and 2). *Heteronybelinia mattisi* seems to be more specific for its intermediate hosts than most of its congeners. This new species has only been found in two species of teleosts (*R. brasiliensis* and *N. bergi*) out of the 24 species examined for parasites in the same area. Nineteen species of elasmobranchs, including ten species that have been reported to prey on *R. brasiliensis* and/or *N. bergi*, have been examined for parasites during this survey (Koen Alonso *et al.*, 2001, 2002; Gosztonyi *et al.*, 2007; Belleggia *et al.*, 2008; Barbini, 2011; Froese & Pauly, 2012). However, *H. mattisi* was only found in *S. bonapartii*, reinforcing the idea of a strict specificity for its definitive host.

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References

Barbini, S.A. (2011) Ecología trófica de las rayas (Chondrichthyes, Rajidae) en el ecosistema bonaerense y uruguayo. PhD thesis, Universidad Nacional de Mar del Plata.

Belleggia, M., Mabragaña, E., Figueroa, D.E., Scenna, L.B., Barbini, S.A. & Díaz de Astarloa, J.M. (2008) Food habits of the broad nose skate, *Bathyraja brachyurops* (Chondrichthyes, Rajidae), in the southwest Atlantic. *Scientia Marina* **72**, 701–710.

Borucinska, J.D. & Caira, J.N. (2006) Mode of attachment and lesions associated with trypanorhynch cestodes in the gastrointestinal tracts of two species of sharks collected from coastal waters of Borneo. *Journal of Fish Diseases* **29**, 395–407.

Campbell, R.A. & Beveridge, I. (1994) Order Trypanorhyncha Diesing, 1863. pp. 51–148 *in* Khalil, L.F., Jones, A. & Bray, R.A. (*Eds*) *Keys to the cestode parasites of vertebrates*. Hertfordshire, UK, CAB International.

Chervy, L. (2009) Unified terminology for cestode microtriches: a proposal from the International Workshops on Cestode Systematics in 2002–2008. *Folia Parasitologica* **56**, 199–230.

Dollfus, R. (1960) Sur une collection de Tétrarhynches homeacanthes de la famille des Tentaculariidae, récoltés principalment dans la région de Dakar. *Bulletin de l'Institut Francais d'Afrique Noire* **22**, 788–852.

Felizardo, N.N., Torres, E.J.L., Fonseca, M.C.G., Pinto, R.R., Gomes, D.C. & Knoff, M. (2010) Cestodes of the flounder *Paralichthys isosceles* Jordan, 1890 (Osteichthyes - Paralichthyidae) from the state of Rio de Janeiro, Brazil. *Neotropical Helminthology* **4**, 113–125.

Froese, R. & Pauly, D. (2012) Fishbase World Wide Web electronic publication. www.fishbase.org, version (accessed April 2012).

Gartner, J.V. & Zwerner, D.E. (1989) The parasite faunas of meso- and bathypelagic fishes of Norfolk Submarine Canyon, western North Atlantic. *Journal of Fish Biology* **34**, 79–95.

Gosztonyi, A.E., Kuba, L. & Mansur, L.E. (2007) Estimation of body size using morphometric relationships of head bones, pectoral fin bones and bony precaudal distance in *Raneya brasiliensis* (Kaup, 1856) (Pisces: Ophidiiformes, Ophidiidae) in Patagonian waters. *Revista de Biología Marina y Oceanografía* **42**, 1–5.

Haseli, M., Malek, M. & Palm, H.W. (2010) Trypanorhynch cestodes of elasmobranchs from the Persian Gulf. *Zootaxa* **2492**, 28–48.

Knoff, M., São Clemente, S.C., Pinto, R.M. & Gomes, D.C. (2004) Registros taxonômicos de cestóides Trypanorhyncha/Homeoacanthoidea em elasmobrânquios coletados na costa do Estado do Paranáelasmobrânquios coletados na costa do Estado do Paraná, Brasil. *Parasitologia Latinoamericana* **59**, 31–36.

Koen Alonso, M., Crespo, E.A., García, N.A., Pedraza, S.N., Mariotti, P.A., Berón Vera, B. & Mora, N.J. (2001) Food habits of *Dipturus chilensis* (Pisces: Rajidae) off Patagonia, Argentina. *Journal of Marine Science* **58**, 288–297.

Koen Alonso, M., Crespo, E.A., García, N.A., Pedraza, S.N., Mariotti, P.A. & Mora, N.J. (2002) Fishery and ontogenetic driven changes in the diet of the spiny dogfish, *Squalus acanthias*, in Patagonian waters, Argentina. *Environmental Biology of Fishes* **63**, 193–202.

Linton, E. (1890) Notes of Entozoa of marine fishes of New England, with description of several new species Part II. *Annual Report of the U.S. Commissioner of Fish and Fisheries for 1887*, 719–900.

Linton, E. (1924) Notes on cestode parasites of sharks and skates. *Proceedings of the U.S. National Museum* **64**, 1–114.

Palm, H.W. (1999) *Nybelinia* Poche, 1926, *Heteronybelinia* gen. nov. and *Myxonybelinia* gen. nov. (Cestoda, Trypanorhyncha) in the collections of The Natural History Museum, London. *Bulletin of the Natural History Museum London (Zoology)* **65**, 133–153.

Palm, H.W. (2004) *The Trypanorhyncha Diesing, 1863*. 710 pp. Bogor, PKSPL-IPB Press.

Palm, H.W. & Beveridge, I. (2002) Tentaculariid cestodes of the order Trypanorhyncha (Platyhelminthes) from the Australian region. *Records of the South Australian Museum* **35**, 49–78.

Palm, H.W. & Caira, J.N. (2008) Host specificity of adult versus larval cestodes of the order Trypanorhyncha (Cestoda). *International Journal for Parasitology* **38**, 381–388.

Palm, H.W. & Overstreet, R.M. (2000) New records of trypanorhynch cestodes from the Gulf of Mexico, including *Kotorella pronosoma* (Stossich, 1901) and *Heteronybelinia palliata* (Linton, 1924) comb. n. *Folia Parasitologica* **47**, 293–302.

Palm, H.W. & Walter, T. (2000) Tentaculariid cestodes (Trypanorhyncha) from the Museum National d'Histoire Naturelle, Paris. *Zoosystema* **22**, 641–666.

Palm, H.W., Schwerdtfeger, G. & Reimer, L.W. (1997) *Nybelinia* Poche, 1926 (Cestoda: Trypanorhyncha) from the Mozambique coast, with description of *N. beveridgei* sp. nov. and systematic consideration of the genus. *South African Journal of Marine Science* **18**, 273–285.

Pereira, J. & Boeger, W.A. (2005) Larval tapeworms (Platyhelminthes, Cestoda) from sciaenid fishes of the southern coast of Brazil. *Zoosystema* **27**, 5–25.

São Clemente, S.C. & Gomes, D.C. (1992) Description of the adult form of *Nybelinia* (*Syngenes*) *rougetcampanae* Dollfus, 1960 and new data on *N.* (*N.*) *bisulcata* (Linton, 1889) (Trypanorhyncha: Tentaculariidae). *Memorias do Instituto Oswaldo Cruz* **87**, 251–255.

São Clemente, S.C., Knoff, M., Padovani, R.E.S., Lima, F.C. & Gomes, D.C. (2004) Cestóides Trypanorhyncha parasitos de congro-rosa, *Genypterus brasiliensis* Regan, 1903 comercializados nos municípios de Niterói e Rio de Janeiro, Brasil. *Revista Brasileira de Parasitologia Veterinaria* **13**, 97–102.

Shah, M. & Bilqees, F.M. (1979) *Nybelinia elongata*, new species from the fish *Pellona elongata* of Karachi coast. *Pakistan Journal of Zoology* **11**, 231–233.

Shipley, A.E. & Hornell, F.L.S. (1906) Report on the cestode and nematode parasites from the marine fishes of Ceylon. *Ceylon Pearl Oyster Fisheries Marine Biological Reports* **5**, 43–96.

Tyler, G.A. (2006) Tapeworms of elasmobranchs (Part II). A monograph on the Diphyllidea (Platyhelminthes, Cestoda). *Bulletin of the University of Nebraska State Museum* **20**, 1–142.

Yamaguti, S. (1952) Studies on the helminth fauna of Japan. Part 49. Cestodes of fishes, II. *Acta Medicae Okayama* **8**, 1–76.