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New plagioporines (Digenea: Opecoelidae) from deep-sea fishes of the North Atlantic Ocean

Rodney A. Bray[1] and Ronald A. Campbell[2]
[1]*Department of Zoology, The Natural History Museum, Cromwell Road, London SW7 5BD, UK*
[2]*Department of Biology, University of Massachusetts Dartmouth, 285 Old Westport Road, North Dartmouth, MA 02747-2300, USA*

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Abstract

Three new species of digenean are described from demersal fishes taken in deep waters of the northwestern and northeastern Atlantic Ocean: *Podocotyle schistotesticulata* n. sp. from *Antimora rostrata; P. harrisae* n. sp. from *Coryphaenoides (Lionurus) carapinus*; and *Gaevskajatrema halosauropsi* n. sp. from *Halosauropsis macrochir*. The status of the nominal species of the genus *Podocotyle* Dujardin, 1845 is presented in annotated summary, along with a tabulation of the distinctive characteristics of recognised species of the genus. *Gaevskajatrema* Gibson & Bray, 1982 is discussed and its diagnosis amended.

Introduction

Opecoelids are among the more taxonomically confused of digenean groups. Most species have been described from shallow living fishes belonging to host families only distantly related to fishes found in the deep sea. In this paper we describe three new species, two are additions to the genus *Podocotyle* Dujardin, 1845 and one to *Gaevskajatrema* Gibson & Bray, 1982. These new species are recorded, one each from a morid, a macrourid and a halosaur taken in studies of deep-sea fishes from the New York Bight (NW Atlantic) and Rockall Trough and Goban Spur regions (NE Atlantic) mainly at depth in excess of 1,000 metres. Few species of *Podocotyle* and none of *Gaevskajatrema* have been reported from deep-sea hosts.

Materials and methods

Hosts examined from the NW Atlantic were treated as follows (by RAC): freshly caught fish were dissected in sea-water and living worms fixed immediately in alcohol-formalin-acetic acid (AFA) under coverslip pressure at room temperature for approximately 20 minutes. Additional specimens were obtained from data-catalogued hosts preserved in 10% buffered formalin and stored in 70% ethanol. Specimens from the NE Atlantic, collected by RAB, were obtained live during cruises of the NERC RRS *Challenger*, and fixed without flattening in Berland's fluid, for a few minutes, before being transferred to 80% ethanol. Whole-mounts were stained with Mayer's paracarmine, and serial sections were cut at 8–10 μm, stained with haematoxylin and counterstained with eosin. All specimens were mounted in Canada balsam. Hosts were identified by Dr Richard L. Haedrich or Dr Nigel Merrett. Measurements are presented in micrometres as the range (length × width) with the mean in parentheses.

Family Opecoelidae Ozaki, 1925
Subfamily Plagioporinae Manter, 1947

Genus *Podocotyle* Dujardin, 1845

Numerous species of *Podocotyle* have been described, but many have been hived off to other genera during the reorganisation of the group, most notably by Pritchard (1966) (see Table I). We base our concept of the genus on her definition (Pritchard, 1966) and on the concept of Gibson & Bray (1982). The major diagnostic characteristics of the genus are the lobed (usually trilobed) ovary and the (usual) restriction of the vitellarium to the hindbody. Pritchard (1966) pointed out that only

two *Podocotyle* species are from deep water, namely *P. pearsei* Manter, 1934 from *Urophycis chesteri* [Gadiformes: Gadidae] in 250–367 fathoms (457–671 m) off Florida (Manter, 1934) and *P. lanceolata* Price, 1934 from *Polymixia* sp. [Beryciformes: Polymixiidae] from the Puerto Rican Deep (Price, 1934). The latter species was transferred to *Neolebouria* Gibson & Bray, 1982 by Reimer (1987), who recorded the worm from *Polymixia nobilis* from deep waters (500 m) off Mozambique (see also Reimer, 1984). As far as we are aware, no deep-sea species of *Podocotyle* have been described subsequently. Some important characteristics of the recognised species of *Podocotyle* are summarised in Table II.

***Podocotyle schistotesticulata* n. sp.** (Figs 1–2)
Syn: Podocotyle sp.n. of Campbell, Haedrich & Munroe (1980), p. 306.

Material studied
ex *Antimora rostrata* Günther (type-host), Moridae. Intestine and pyloric caeca. New York Bight, NW Atlantic (39° 10′ N, 71°35′ W, 2,481 m (type-locality); 39°11′ N, 71°21′ W, depth 2,603 m, 39°11′ N, 70°12′ W, 2,730 m, 39°13′ N, 71°53′ W, depth 1,947m; 39°11′ N, 71°53′ W, depth 2,603 m). BM(NH) holotype 1995.5.30.1, paratypes 1995.5.30.2-11. USNPC paratypes 84965-7.

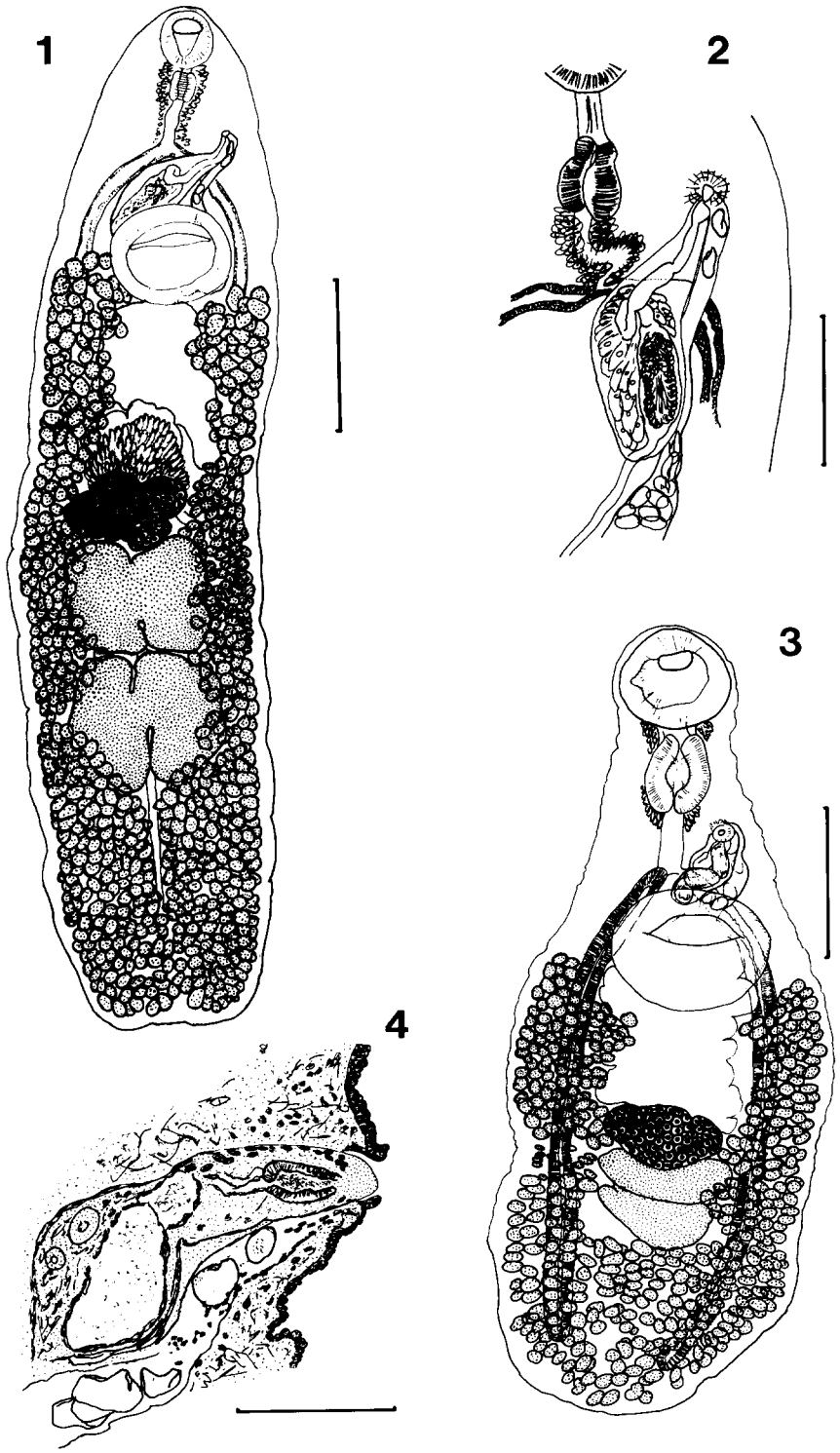
Description

Based on 38 whole-mounts, 10 measured, and one set of serial sections. Body large, elongate oblong, narrowing in forebody; 5,525–8,809 × 1,320–1,860 (7,237 × 1,609); width 18–26 (22)% of body-length. Tegument unarmed. Oral sucker subglobular; subterminal; 334–416 × 312–412 (364 × 348). Ventral sucker transversely oval; muscular; large, 620–859 × 665–876 (714 × 784); aperture transverse, slit-like. Sucker-ratio 1 : 2.06–2.38 (2.26). Forebody 1,033–1,533 (1,293) long; 15–21 (18)% of body-length. Prepharynx usually distinct; 0–135 (51). Pharynx oval; 206–245 × 151–245 (225 × 193). Oral sucker/pharynx width ratio 1 : 1.48–2.07 (1.83). Oesophagus 206–451 (319) long, straight or undulating. Posterior extremity of oral sucker, prepharynx, pharynx and oesophagus ensheathed in gland-cells. Intestinal bifurcation in posterior forebody, 161–477 (350) anterior to anterior margin of ventral sucker. Caeca narrow, widening slightly posteriorly, terminate blindly 174–444 (251) from posterior extremity.

Testes two; tandem, contiguous; in mid-hindbody; both deeply lobate with distinct indentation in median line in both anterior and posterior margins, sometimes almost dividing testis into two parts longitudinally; anterior 644–1,161 × 827–1,097 (868 × 952), posterior 766–1,415 × 795–1,304 (1,064 × 1,081). Post-testicular region 1,288–2,115 (1,610) long; 18–25 (22)% of body length. Cirrus-sac large, 668–1,145 × 261–415 (893 × 334); claviform; just overlapping anterior edge of cirrus-sac. Internal seminal vesicle saccular, reaches about halfway along cirrus-sac, narrows distally, forms small loop or reflexes slightly, then passes distally forming pars prostatica. Pars prostatica thick-walled, ensheathed in numerous gland-cells, which also surround internal seminal vesicle. Ejaculatory duct slightly shorter than pars prostatica, with narrower walls; opens into base of distinct genital atrium. Cirrus not seen. Genital pore near sinistral margin of worm at level of intestinal bifurcation or posterior oesophagus (displaced further forward up to pharynx level by flattening in some specimens); 383–567 (466) from ventral sucker.

Ovary immediately pre-testicular; transversely elongate; anterior margin trilobed, posterior margin irregularly 3–4 lobed, 419–591 × 604–946 (530 × 717). Ventral sucker to ovary distance 827–1,542 (1,154), 13–18 (16)% of body-length. Oviduct leaves from median anterior margin of ovary. Seminal receptacle small; saccular; often empty; immediately anterior to ovary. Mehlis' gland immediately anterior to ovary. Laurer's canal ensheathed in gland-cells; may be moniliform; contains sperm; runs sinistrally in convoluted course opening dorsally close to sinistral margin of ovary. Uterus pre-ovarian, intercaecal, narrows at posterior edge of ventral sucker to form distinct metraterm. Eggs numerous; tanned, not obviously operculate; 68–81 × 38–48 (76 × 41). Metraterm quite thick-walled, ensheathed in gland-cells, opens to genital atrium antero-sinistrally to male duct. Vitellarium follicular; follicles large, numerous; anterior extent of fields usually level with posterior half of ventral sucker, but may be slightly more posterior or anterior; lateral fields dorsal, lateral and ventral to caeca, not encroaching over uterus or gonads; confluent or nearly so ventrally and dorsally in post-testicular region.

Excretory pore terminal. Vesicle I-shaped; reaches to posterior margin of ovary.



Figs 1–4. New species of *Podocotyle* from deep-sea fishes. 1–2. *P. schistotesticulata* n. sp. 1. Ventral view of holotype. 2. Terminal genitalia. 3–4. *P. harrisae* n. sp. 3. Ventral view of holotype. 4. Sagittal section through terminal genitalia. *Scale-bars:* 1, 1.0 mm; 2,3, 400 μm, 4, 100 μm.

Table I. Status list of the nominal species of the genus *Podocotyle* Dujardin, 1845 (valid species in bold).

Species	Comment
abitionis McFarlane 1936	*Podocotyle* (s.s.)–see Pritchard (1966); to *Pellamyzon* see Gibson & Bray (1982).
aeglefini (Müller, 1776) Yamaguti, 1953	Confused situation, partly syn. of *'Apoblema'*, partly probable syn. of *atomon*, see Dollfus (1968).
aegyptiaca Caballero & Caballero, 1970	Renaming of *serrani* Nagaty & Abdel Aal, 1962.
***angulata* (Dujardin, 1845) Dujardin, 1845**	Type-species according to Stiles & Hassall (1898), see Gibson & Bray (1982).
aphanii Paperna, 1964	To *Pseudurorchis*, see Yamaguti (1971).
***apodichthysi* Park, 1937**	*Podocotyle* (s.s.), see Pritchard (1966); Gibson (1986).
***araii* Gibson, 1986**	*Podocotyle* (s.s.), see Gibson (1986).
atherinae Nicoll, 1914	To *Apopodocotyle*, see Pritchard (1966).
***atomon* (Rudolphi, 1802) Odhner, 1905**	Type-species according to Pritchard (1966); but see Gibson & Bray (1982).
atzi Nigrelli, 1939	To *Allopodocotyle*, see Pritchard (1966).
ayu Takahashi, 1928	*Podocotyle* (s.s.), see Pritchard (1966), to *Neoplagioporus*, see Shimazu (1990).
blennicottusi Park, 1937	*Podocotyle* (s.s.), see Pritchard (1966); syn of *enophrysi*, see Nahhas & Krupin (1977).
boleosomi (Pearse, 1924) Yamaguti, 1971	To *Allopodocotyle*, see Kuntz & Font (1984).
***boneti* Caballero & Caballero, 1970**	*Podocotyle* (s.s.).
bongosi Nagaty & Abdel Aal, 1962	To *Apopodocotyle*, see Pritchard (1966).
breviformis Manter, 1940	Syn. of *Apopodocotyle oscitans*, see Pritchard (1966).
caithnessi Manter, 1954	To *Neopodocotyloides*, see Pritchard (1966); *Neopodocotyloides* a syn. of *Podocotyle*, see Gibson & Bray (1982)
californica Park, 1937	*Podocotyle* (s.s.) see Pritchard (1966), Gibson (1986).
capecoastensis (Fischthal & Thomas,1970) Yamaguti, 1971	Originally *Pedunculotrema*, not *Podocotyle* (s.s.).
chloroscombri (Fischthal & Thomas, 1970) Yamaguti, 1971	Originally *Podocotyloides*, not *Podocotyle* (s.s.); see Bray & Cribb (1989).
contortum (Rudolphi, 1819) Stossich,1898	Now in *Accacoelium*.
dorabi Gupta & Puri, 1981	Originally in new subgenus *(Indopodocotyle)*, not *Podocotyle* (s.s.), see Gibson & Bray (1982).
elongata Park, 1937	*Podocotyle* (s.s.) see Pritchard (1966); syn. of *californica* see Nahhas & Krupin (1977).
***enophrysi* Park, 1937**	*Podocotyle* (s.s.), see Pritchard (1966); Gibson (1986).
epinepheli Yamaguti, 1942	To *Allopodocotyle*, see Pritchard (1966), Bray & Cribb (1989).
fractum (Rudolphi, 1819) Stossich, 1898	To *Robphildollfusium*, see Paggi & Orecchia (1963).
furcata Bremser in Rudolphi, 1819	To *Opecoeloides* or *Poracanthium*, see Bartoli & Gibson (1991).
ghanensis (Fischthal & Thomas, 1970) Yamaguti, 1971	Originally *Pedunculotrema*, not *Podocotyle* (s.s.).
***gibbonsia* Johnson, 1949**	*Podocotyle* (s.s.), see Pritchard (1946), Gibson (1986).

Discussion

The deeply incised testes are distinctive features in this species, hence the name. Three species listed in Table II have lobed testes, namely *P. apodichthysi* Park, 1937, *P. californica* Park, 1937 and *P. gibbonsia* Johnson, 1949: these are all shallow-water forms from the NE Pacific Ocean (Gibson, 1986). *P. apodichthysi* has weakly lobate testes, a smaller sucker-ratio and the vitelline fields are usually interrupted at testes level. *P. gibbonsia*, which according to Gibson (1986) may be a synonym of *P. apodichthysi*, also has relatively weakly lobed testes and a smaller sucker-ratio. *P. californica* has fairly deeply lobed testes (the lobation is not of the consistent pattern seen in *P. schistotesticulata* n. sp.), the body is squat and relatively small and the eggs are smaller.

The species originally designated *P. lanceolata* Price, 1934 (now *Neolebouria*) is an Atlantic deep-sea form with lobate testes, but it differs from *P. schistotesticulata* in its size, lanceolate shape, the pattern of testicular lobation, egg-size and vitelline distribu-

Table I. Continued.

Species	Comment
gracilis Yamaguti, 1952	To *Podocotyloides*, see Pritchard (1966).
gurnardi Agrawal, 1965	*Nomen nudum*
***harrisae* n. sp.**	
indica (Dayal, 1944) Yamaguti, 1958	Originally in *Neopodocotyle*, in Allocreadiidae, see Pritchard (1966)
indistincta (Baer, 1959) Yamaguti, 1971	Originally in *Allocreadium*, not *Podocotyle* (s.s.).
israelensis Fischthal, 1980	To *Allopodocotyle*, see Bray (1987)
jaffensis Fischthal, 1980	To *Allopodocotyle*, see Bray (1987); Bartoli *et al.* (1989).
kofoidi Park, 1937	*Podocotyle* (s.s.), see Pritchard (1966); syn of *californica*, see Nahhas & Krupin (1977)
koshari Nagaty, 1973	Renaming of *Podocoyle* sp. of Nagaty & Abdel Aal (1962); not *Podocotyle* (s.s.).
lacustris Paperna, 1964	To *Pseudurorchis*, see Yamaguti (1971)
lanceolata Price, 1934	*Podocotyle* (s.s.), see Pritchard (1966), to *Neolebouria*, see Reimer (1987).
lepomis (Dobrovolny, 1939) Yamaguti, 1954	To *Allopodocotyle*, see Pritchard (1966).
lethrini Yamaguti, 1942	To *Allopodocotyle*, see Pritchard (1966).
***levinseni* Issaitschikov, 1928**	*Podocotyle* (s.s.), see Pritchard (1966).
lutiani Shen, 1990	Probably *Hamacreadium*; new observation, fits all criteria in Bray & Cribb (1989), including host.
macrocotyle (Diesing, 1858) Stossich, 1898	Now in *Accacladocoelium*
mecopera Manter, 1940	To *Allopodocotyle*, see Pritchard (1966).
mehrai Rai, 1972	*Nomen nudum*
mehsena (Nagaty, 1941) Yamaguti, 1971	In *Apopodocotyle*, see Pritchard (1966).
morone MacCallum, 1913	Monogenean, lapsus for *Pedocotyle*.
musculometra Bravo-Hollis & Manter, 1957	To *Apopodocotyle*, see Pritchard (1966).
mycteropercae Sogandares-Bernal, 1959	To *Peracreadium*, see Pritchard (1966).
odhneri Issaitschikov, 1928	*Podocotyle* (s.s.), see Pritchard (1966), but Issaitschikov (1928) described the vitelline fields as uniting at the level of the intestinal bifurcation, may be *Neolebouria*.
olssoni Odhner, 1905	*Podocotyle* (s.s.), see Pritchard (1966); syn. of *reflexa*, see Brinkmann (1975).
oscitans (Linton, 1910) Amato, 1983	To *Apopodocotyle*, see Pritchard (1966)
pachysomum (Eysenhardt, 1829) Stossich, 1898	Now *Haplosplanchnus*.
pacifica Park, 1937	Syn. of *blennicottusi*, see Pritchard (1966); syn. of *enophrysi*, see Nahhas & Krupin (1977).
parupenei Manter, 1963	To *Podocotyloides*, see Pritchard (1966).
***pearsei* Manter, 1934**	*Podocotyle* (s.s.), see Pritchard (1966).
pedicillatum (Stossich, 1887) Stossich, 1898	To *Allopodocotyle*, see Pritchard (1966); Bartoli *et al.* (1989).
pedunculata Park, 1937	To *Neopodocotyloides*, see Pritchard (1966), syn. of *californica* – see Nahhas & Krupin (1977).
pennelli Leiper & Atkinson, 1914	To *Macvicaria*, see Zdzitowiecki (1987).
petalophallus (Yamaguti, 1934) Park, 1937	Type-species of *Podocotyloides*.

tion. The contents ofthe cirrus-sac were not described by Price (1934), but, as far as one can tell from his illustration, they are similar to that of *P. schistotesticulata*.

The allocreadiid *Megalogonia ictaluri* Surber, 1928 has testes similarly divided longitudinally, which in some instances can appear as four testes (Hopkins, 1934). Caira's (1989) cladistic analysis of the Allocreadiidae has indicated that this feature should not separate *Megalogonia* Surber, 1928 from *Crepidostomum* Braun, 1900. Similarly, we do not consider this feature to be of generic value in this instance, but we do believe that, as it is a unique condition in the genus *Podocotyle*, the erection of a new species is justified.

Table I. Continued.

Species	Comment
planci Stossich, 1899	Now in *Orophocotyle*.
plectropomi Manter, 1963	To *Allopodocotyle*, see Pritchard (1966)
polymorpha (Layman, 1933) Yamaguti, 1971	To *Baikalotrema*, see Koval (1966).
producta (Stafford, 1904) Yamaguti, 1953	Syn. of *reflexa*, see Miller (1941).
***radifistuli* (Acena, 1941) Gibson & Bray, 1984**	*Podocotyle* (s.s.), see Gibson & Bray (1984), Gibson (1986).
***reflexa* (Creplin, 1825) Odhner, 1905**	*Podocotyle* (s.s.), see Pritchard (1966), Køie (1981), Gibson & Bray (1982).
retroflexum (Molin, 1859) Barbagallo & Drago, 1903	Now in *Steganoderma*
***schistotesticulata* n. sp.**	
***scorpaenae* (Rudolphi, 1819) Bartoli & Gibson 1991**	*Podocotyle* (s.s.), see Bartoli & Gibson (1991).
serrani Nagaty & Abdel-Aal, 1962	Preoccupied – syn. of *Allopodocotyle epinepheli*, see Pritchard (1966); renamed *aegyptiaca* Caballero & Caballero, 1970 and *yamagutii* Nagaty, 1973; but see Bray & Cribb (1989).
serrani Yamaguti, 1952	To *Allopodocotyle*, see Pritchard (1966).
shawi McIntosh, 1939	To *Plagioporus*, see Margolis (1972), Gibson (in press).
simhai Gupta & Sayal, 1979	Originally in new subgenus *(Indopodocotyloides)*, not *Podocotyle* (s.s.), see Gibson & Bray (1982); probably *Podocotyloides*; new observation.
simplex (Rudolphi, 1809) Stafford, 1904	Rudolphi's name was a renaming of *Fasciola aeglefini* see *P. aeglefini*.
***sinusacca* Ching, 1960**	To *Neopodocotyloides*, see Pritchard (1966); *Podocotyle* (s.s.), see Gibson (1986).
skrjabini (Layman, 1930) Yamaguti, 1971	Originally *Cainocreadium*, looks somewhat like *Podocotyle*, but a spiny tegument is figured by Layman (1930).
spinipora (Sircar & Sinha, 1969) Yamaguti, 1971	Originally in *Neopodocotyle*, in Allocreadiidae, see Pritchard (1966).
staffordi Miller, 1951	Syn. of *atomon*, see Pritchard (1966); syn. of *angulata* according to Gibson & Bray (1982).
***syngnathi* Nicoll, 1913**	*Podocotyle* (s.s.), see Pritchard (1966).
tamane Yamaguti, 1942	to *Allopodocotyle*, see Pritchard (1966).
***temensis* Fischthal & Thomas, 1970**	*Podocotyle* (s.s.).
***theragrae* (Lloyd, 1938) Gibson & Bray, 1984**	*Podocotyle* (s.s.), see Gibson & Bray (1984), Gibson (1986).
umbrinae (Stossich, 1885) Yamaguti, 1971	To *Pycnadenoides*, see Gibson & Bray (1989).
unica (Molin, 1859) Stossich, 1886	*Species inquirenda*.
virens (Sinitsin, 1931) Yamaguti, 1953	To *Allopodocotyle*, see Pritchard (1966).
yamagutii Nagaty, 1973	Renaming of *serrani* Nagaty & Abdel Aal., 1962.

The data incorporated into this table were derived mainly from the Host-Parasite Catalogue and Data-Base in the Parasitic Worms Division, The Natural History Museum, London.

***Podocotyle harrisae* n. sp.** (Figs 3–4)

Syn: *Plagioporus* sp.n. of Campbell, Haedrich & Munroe (1980), p. 305.

Material studied

ex *Coryphaenoides (Lionurus) carapinus* (Goode & Bean) (type host), Macrouridae. Intestine and pyloric caeca. NW Atlantic (39°12′ N, 71°47′ W, 2,293 m (type-locality); 39°45′ N, 70°44′ W, depth 653 m, 39°45′ N, 70°43′ W, 1,926 m; 39°10′ N, 71°35′ W, depth 2,481 m). BM(NH) holotype 1995.5.30.12, paratypes 1995.5.30.13–18. USNPC paratypes 84968-70.

Description

Based on 14 whole-mounts, 10 measured, and one set of serial sections. Body pyriform, narrowing in forebody; 1,741–2,735 × 547–1,046 (2,124 × 793); width 29–43 (38)% of body-length. Tegument unarmed. Oral sucker subglobular; subterminal; 200–270 × 193–290 (244 × 245). Ventral sucker transversely oval; muscular; 251–376 × 334–457 (311 × 400); aperture transverse. Sucker-ratio 1 : 1.33–1.88 (1.65). Forebody 490–906 (642) long; 24–34 (30)% of body length. Prepharynx usually distinct; 0–90 (28). Pharynx oval; large, 148–238 × 135–180 (205 × 165). Oral sucker/pharynx width ratio 1 : 1.25–1.67 (1.48). Oesoph-

Table II. Some morphological characters of species of *Podocotyle* Dujardin, 1845 (*sensu stricto*).

Species	Body-shape	Anterior extent of vitellarium	Shape of ovary	Shape of testes	Length of cirrus-sac	Sucker-ratio
angulata	Elongate	Post. edge VS	Campaniform trilobed	Oval, entire	Well into hindbody	1 : >2
apodichthysi	Elongate	Post. edge VS	Campaniform trilobed	3–6 irregular lobes	Just overlaps VS	1 : <1.1–1.3
araii	Elongate	Post. edge VS	Campaniform weekly trilobed	Oval, entire	Just overlaps VS	1 : 1.8–3.6 (length)
atomon	Elongate	Post. edge VS	Campaniform trilobed	Oval, entire	Just into hindbody	1 : c.2
boneti	Elongate	Post. edge VS	Heart-shaped	Irregular oval	Well into hindbody	1 : 2.5.–2.7
caithnessi	Elongate	Rarely reaching VS	Trilobed	oval, entire	To mid-VS	1 : 1.7–2.0
californica	Oval	Mid-VS	4 unequal lobes	Deeply, irregularly lobate	To mid-VS	1 : 2.0–2.5
enophrysi	Elongate, oval	To VS level	4 lobes	irregularly oval	Well into hindbody	1 : 1.6–1.9
gibbonsia	Elongate	Post. edge VS	Campaniform trilobed	Deeply lobed	Anterior to VS	1 : 1.7
harrisae	Pyriform	Post. part VS	Weakly trilobed	Irregularly oval	Just overlaps VS	1 : 1.3–1.9
levinseni	Oval, narrow forebody	Mid VS	Trilobed (occ. oval)	Irregularly oval	To mid VS	1 : 2.0–2.1
pearsei	Oval	Post. edge VS	Distinctly trilobed	Entire to slightly irregular	c. mid VS	1 : 1.6–2.1
radifistuli	Elongate	Just post. to VS	Campaniform trilobed	Irregularly oval	Well into hindbody	1 : 2.0
reflexa	Elongate	Just post. to VS	Campaniform trilobed	Irregularly oval	Well into hindbody	1 : c.2
schistotesticulata	Elongate oblong	About mid VS	Distinctly 3–4 lobed	Deeply lobed	Just overlaps VS	1 : 2.1–2.4
scorpaenae	Elongate	To post. edge VS	Pyriform, campaniform	Oval, entire	Well into hindbody	1 : 2.0–2.5
sinusacca	Elongate	Well post. to VS	Campaniform trilobed	Irregularly oval	Well into hindbody	1 : 1.4
syngnathi	Elongate	Well post. to VS	Campaniform trilobed	Oval, entire	To mid VS	1 : 1.4
temensis	Elongate oval	Well post. to VS	4–5 lobed	Oval, entire	Well into hindbody	1: 1.8–2.1
theragae	Elongate	Well post. to VS	Campaniform trilobed	Oval, entire or irregular	Well into hindbody	1 : <2

Abbreviations: post., posterior; VS, ventral sucker.

agus 64–264 (163) long. Prepharynx and anterior oesophagus ensheathed in gland-cells. Intestinal bifurcation in posterior forebody or dorsal to anterior half of ventral sucker, between 142 anterior to anterior margin of ventral sucker and 142 posterior to anterior margin of ventral sucker (mean 7 anterior to ventral sucker) Caeca narrow; terminate blindly 97–296 (184) from posterior extremity.

Tested two; tandem, contiguous, in mid-hindbody; transversely elongate, irregularly oval; anterior 71–206 × 213–425 (130 × 312), posterior 77–193 × 206–399 (134 × 310). Post-testicular region 374–728 (507) long; 21–27 (24)% of body length. Cirrus-sac small, 193–290 × 74–109 (246 × 95); claviform; just overlapping anterior edge of ventral sucker. Internal seminal vesicle long, tubular, coiled, filling much of cirrus-sac, reaches close to distal end of cirrus-sac before reflexing back to about mid-cirrus-sac, where it reflexes again running distally as narrow duct surrounded by gland-cells. Pars prostatica oval, vesicular, thick-walled, ensheathed in numerous gland-cells. Ejaculatory duct very short, opens into base of distinct genital atrium. Cirrus not seen. Genital pore sinistral at level of pharynx or anterior oesophagus.

Ovary immediately pre-testicular; transversely elongate, weakly trilobed; 103–216 × 200–412 (172 × 314). Ventral sucker to ovary distance 187–356 (247). Oviduct leaves ovary from mid-dorsal surface. Seminal receptacle small; oval; dorsal to ovary. Mehlis' gland antero-dorsal to ovary. Laurer's canal long, coiled, ensheathed in gland cells; passes laterally and opens dorsally at level of ovary just median to left caecum. Uterus pre-ovarian, intercaecal, overlaps posterior half of ventral sucker. Eggs numerous; tanned, not obviously operculate; 51–63 × 31–45 (57 × 36). Metraterm opens into genital atrium sinistrally to male duct. Vitellarium follicular; anterior extent of fields level with posterior half or posterior margin of ventral sucker; lateral fields lateral and ventral (not dorsal) to caeca, encroaching slightly over gonads; confluent ventrally and dorsally in post-testicular region.

Excretory pore distinctly dorsally subterminal. Vesicle I-shaped, reaches to ovary.

Discussion

This new form shares the characteristic short cirrus-sac, just overlapping the ventral sucker, with several other *Podocotyle* spp., namely *P. apodichthysi* Park, 1937, *P. araii* Gibson, 1986, *P. californica* Park, 1937, *P. gibbonsia* Johnson, 1949, *P. levinseni* Issaitschikov, 1928 and *P. syngnathi* Nicoll, 1913 (Tables I and II). *P. araii*, from *Sebastes* spp. [Scorpaenidae: Scorpaeniformes] off British Columbia, has a quoted sucker-ratio of 1 : 1.8–3.6 (mostly 1:2.0–3.03), with the measurements mainly of depth, rather than width, taken from laterally mounted worms. *P. araii* also differs in its relatively narrow, elongate body, its larger eggs (76–96 × 33–47) and its separated testes with vitelline follicles encroaching between (Gibson, 1986). *P. californica*, from Stichaeidae [Perciformes] and Cottidae [Scorpaeniformes] from off California and Oregon, has a sucker-ratio of 1 : 1.54–2.50 (calculated from the measurement ranges given by Park, 1937, for this species and its synonyms, see Gibson, 1986). When contracted *P. californica* can appear superficially similar to *P. harrisae* n. sp., but in all conditions the gonads are more deeply lobed, the deeply lobate shape of the ovary being 'remarkably consistent' (Nahhas & Krupin, 1977). When extended the testes separate and the vitelline follicles encroach between, and there is 'typically' a gap in the vitelline fields at the testicular level (Nahhas & Krupin, 1977). *P. levinseni*, reported from Scorpaeniformes, Pleuronectiformes and Gadiformes in the Arctic Ocean, has a sucker ratio of 1 : 2.07–2.08 (calculated from the measurement range in Issaitschikov, 1928) and the eggs are large (80–95 × 40–59). *P. apodichthysi*, from *Apodichthys* [Pholidae: Perciformes] from off California, is a relatively elongate worm, with suckers of similar size (ratio 1 : 1.19–1.28 – calculated from range in Park, 1937) and with vitelline follicles encroaching between separated testes. The gonads are deeply lobate, particularly the ovary. *P. gibbonsia*, from Scorpaeniformes, Gobiesociformes, Pleuronectiformes, Salmoniformes and Perciformes from off the western coast of North America, is a relatively elongate worm, with deeply lobed gonads (Johnson, 1949). *P. syngnathi*, from pipe-fishes [Syngnathidae: Gasterosteiformes] in the English Channel (Nicoll, 1913; Baylis & Jones, 1933; Baylis, 1939; Sproston, 1939) differs in its more elongate body-shape, greater egg-size, the saccular seminal vesicle (verified on specimen, BM(NH) 1932.11.28.29), more posterior genital pore, the separated gonads and the vitellarium not reaching to the ventral sucker.

P. harrisae differs from the deep-sea species *P. pearsei* Manter, 1934 in its smaller sucker-ratio, more anterior genital pore, shorter cirrus-sac and much smaller eggs (Manter, 1934). *P. pearsei* is said to lack prostate cells (other details of the cirrus-sac contents are not given).

Etymology. This species is named for Mrs Eileen Harris of The Natural History Museum, London.

Genus *Gaevskajatrema* Gibson & Bray, 1982

This genus was erected by Gibson & Bray (1982) to include *Plagioporus*-like species with 'short caeca, reaching only to the level of the testes, a restricted vitelline distribution, extending back only to the level of the testes, a very large cirrus-sac'. They placed only two species in the genus definitely, the type-species *G. perezi* (Mathias, 1926) and *G. lethrini* (Nagaty, 1942) (Table III). The genus was originally restricted to marine fish parasites.

Gaevskajatrema halosauropsi n. sp. (Figs 5–7)

Syn: *Plagioporus* sp. n. of Campbell, Haedrich & Munroe (1980), p. 306.

Material studied

ex *Halosauropsis macrochir* (Günther) (type-host), Halosauridae. Intestine. NE Atlantic, Goban Spur (49°54′ N, 13°03′ W (type-locality), depth 2,570 m, 8.7.1994). BM(NH) holotype 1995.5.30.19, paratypes 1995.5.30.20–21. NE Atlantic, Rockall Trough (56°56′ N, 09°50′ W, depth 1,908 m, 21.2.1991), collector M.E. Spencer Jones. BM(NH) paratypes 1992.7.1.182–185. NW Atlantic (39°12′ N, 71°47′ W, depth 2,293 m). BM(NH) paratypes 1995.5.30.22–24. USNPC paratypes 84971.

Description

Based on 9 flattened whole-mounts from the NW Atlantic and 13 unflattened whole-amounts and one set of serial sections from the NE Atlantic; for measurements see Table IV. Body pyriform. Tegument unarmed. Oral sucker subglobular; subterminal. Ventral sucker transversely elongate oval to rounded; larger than oral sucker. Prepharynx short; usually within posterior cavity of oral sucker. Oesophagus distinct. Intestinal bifurcation in posterior forebody. Caeca terminate laterally to posterior testis, occasionally just beyond. Numerous gland-cells embedded in forebody parenchyma.

Testes two; irregularly lobate, oblique; filling much of hindbody; anterior testis adjacent to posterior edge of ventral sucker (may be displaced posteriorly by flattening). Cirrus-sac long; claviform, overlapping ventral sucker. Internal seminal vesicle about half length of cirrus-sac; saccular, narrows abruptly to form long, narrow pars prostatica with fairly thick wall; pars prostatica merges imperceptibly into narrow, thin-walled ejaculatory duct. All of internal male duct surrounded by prostatic gland-cells. Cirrus not seen. Genital atrium small. Genital pore at about level of mid-oesophagus and halfway between median line and sinistral margin.

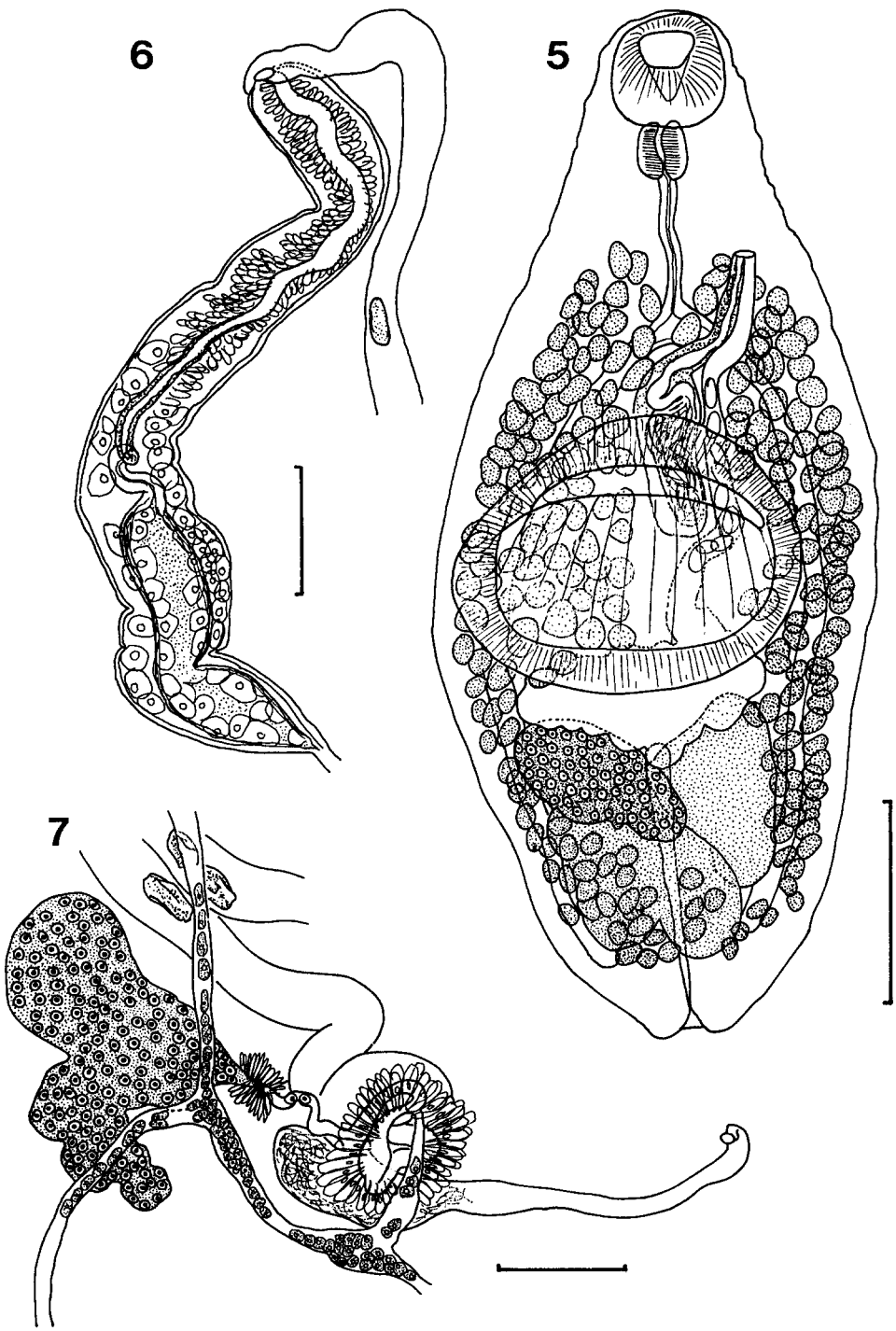
Ovary dextro-lateral to anterior testis, adjacent to ventral sucker (may be displaced posteriorly by flattening); deeply, irregularly lobate. Seminal receptacle dorsal to anterior testis. Laurer's canal runs from sinistral edge of seminal receptacle laterally, opening dorsally to left caecum or just median. Mehlis' gland dorsal to anterior testis. Uterus coiled dorsally to ventral sucker, widest dorsally to posterior half of ventral sucker (may be displaced posteriorly by flattening), narrows anteriorly, passing to left of cirrus-sac as metraterm. Eggs tanned, not obviously operculate. Vitellarium follicular; anterior limit at level of pharynx or oesophagus, lateral fields dorsal, lateral and ventral to caeca, confluent dorsally and almost confluent ventrally at level of intestinal bifurcation; dorsal fields encroach towards uterus and over gonads, ventral fields delimited by ventral sucker and gonads; fields reach just posteriorly to posterior testis, not confluent in post-testicular region.

Excretory pore terminal. Vesicle I-shaped, narrow, thick-walled initially, widens dorsally to posterior testis; terminates dorsally to anterior testis.

Discussion

Table III lists the species which have been considered members of this genus, as well as some putative members and some recently described forms which may belong in the genus. New combinations have not been made, pending more detailed study of the individual species. The form described here is considered a new species because none of the other marine species listed on Table III have deeply lobate ovaries and testes. The four freshwater species listed each have a lobate ovary, but have entire testes; they have all been placed in the new genus *Neoplagioporus* by Shimazu (1990).

This new species has two major characteristics similar to those associated with *Gaevskajatrema*, i.e. the caeca terminate laterally to the posterior testis, and the vitelline fields just pass the posterior testis and are not confluent in the post-testicular region. These characters, however, differ slightly from those given by



Figs 5–7. Gaevskajatrema halosauropsi n. sp. 5. Ventral view of holotype. 6. Terminal genitalia. 7. Detail of female reproductive system showing Mehlis' gland, seminal receptacle and Laurer's canal. *Scale-bars:* 5, 400 μm; 6,7, 100 μm.

Table III. Status list of species of *Gaevskajatrema* Gibson & Bray, 1982.

Recognised species:
Gaevskajatrema perezi (Mathias, 1926) Gibson & Bray, 1982 – type-species
Gaevskajatrema lethrini (Nagaty, 1942) Gibson & Bray, 1982
Gaevskajatrema halosauropsi n. sp.

Following marine species may belong in *Gaevskajatrema* but have small eggs:
Caudotestis neopercis Yamaguti, 1938
Caudotestis thalassomatis Yamaguti, 1942

Possible species of *Gaevskajatrema:*
Plagioporus spari Yamaguti, 1951 (see Gibson & Bray, 1982)
Plagiosporus longicirratus Manter, 1963 (see Bray, 1985)
Plagioporus parathalassomatis Wang, 1982 (see Bray & Cribb, 1989)

Following freshwater species have been considered putative members of *Gaevskajatrema* and have a lobed ovary; Shimazu (1990) placed them in *Neoplagioporus*:
Caudotestis orientalis Yamaguti, 1934 (syn. of *N. elongatus*)
Caudotestis gnathopogonis Yamaguti, 1934 (syn. of *N. zacconis*)
Caudotestis zacconis Yamaguti, 1934 (now *N. zacconis*)
Lebouria elongata Goto & Ozaki, 1930 (now *N. elongatus*)

Gibson & Bray (1982) such that an amended diagnosis of the genus is desirable:

Gaevskajatrema Gibson & Bray, 1982
Opecoelidae, Plagioporinae. Body fusiform to pyriform. Tegument unarmed. Oral sucker ventrally subterminal. Ventral sucker in anterior half of body, larger than oral sucker. Prepharynx distinct, small. Pharynx oval to globular. Caeca unbranched, terminate blindly at about level of posterior testis. Excretory vesicle I-shaped, extends to level of testes. Testes two; tandem to nearly symmetrical; near posterior end of body; entire to lobate. Cirrus-sac variable in size; contains convoluted tubular or saccular seminal vesicle, pars prostatica and ejaculatory duct. Genital atrium small, distinct. Genital pore sinistral at level of oesophagus. Ovary rounded, entire or lobed; antero-dextral to dextro-lateral to anterior testis. Canalicular seminal receptacle and Laurer's canal present. Uterus pretesticular. Eggs large; variable in number. Vitellarium follicular; lateral fields extend from level of pharynx or oesophagus to level of posterior testis or just beyond; fields confluent dorsally in forebody, not confluent in post-testicular region. In marine fishes.

Gaevskajatrema perezi (syn. *Plagioporus pontica* Koval, 1966) is known from labrids [Perciformes] in shallow waters of the NE Atlantic (Gibson & Bray, 1982) and the Black Sea (Gaevskaya & Solonchenko, 1989), and *G. lethrini* is known from lethrinids [Perciformes] in shallow waters of the Red Sea (Nagaty, 1942). Similarly, most of the putative species of *Gaevskajatrema* are from perciforms in marine shallow-water or from cypriniforms in freshwater. *Plagioporus longicirratus* is from a balistid [Tetraodontiformes] from Fiji (Manter, 1963). *G. halosauropsi* n. sp. is biologically most distinct, in that it comes from Notacanthiformes in deep-waters of the northern Atlantic Ocean.

The dimensions of the specimens of *G. halosauropsi* from the different sides of the north Atlantic are distinctly different (Table IV), the overall length measurements not overlapping. We believe that some of these distinctions are due to the different fixation techniques, in particular, the flattening of the NW Atlantic specimens. Most of the important ratios are similar, most notably the sucker-ratio, and the egg sizes have similar ranges.

Table IV. Measurements of *Gaevskajatrema halosauropsi* n. sp. from northwestern and northeastern Atlantic.

Locality	NW Atlantic	NE Atlantic
Condition	flattened	unflattened
n	5	9
Length	2,274–2,800 (2,528)	1,084–1,964 (1,497)
Width	938–1,380 (1,106)	639–874 (763)
Width as % of length	38–49 (44)	42–60 (52)
Oral sucker	233–277 × 238–280 (251 × 292)	180–238 × 180–241 (204 × 210)
Ventral sucker	531–684 × 585–747 (606 × 664)	270–584 × 419–612 (443 × 519)
Sucker-ratio	1 : 1.95–2.62 (2.31)	1 : 2.13–2.79 (2.47)
Forebody	715–828 (779)	380–786 (552)
Forebody as % of body-length	27–35 (31)	34–42 (37)
Prepharynx	0–19 (6)	0
Pharynx	103–131 × 140–169 (124 × 149)	90–129 × 84–116 (111 × 102)
Oral sucker/pharynx width ratio	1 : 1.60–2.57 (1.97)	1 : 1.87–2.21 (2.06)
Oesophagus	206–293 (253)	80–245 (157)
Intentinal bifurcation to ventral sucker	64–232 (150)	57–216 (124)
Caecal terminations to posterior extremity	386–670 (540)	145–335 (202)
Anterior testis	277–451 ×290–514 (375 × 398)	193–386 × 187–348 (289 ×248)
Posterior testis	296–477 × 451–554 (358 × 508)	206–364 × 193–367 (276 × 272)
Post-testicular region	207–367 (291)	53–254 (121)
Post-testicular region as % of body-length	9–13 (11)	4–14 (8)
Cirrus-sac	535–686 × 103–167 (602 × 131)	354–560 × 84–151 (418 ×126)
Anterior extremity to genital pore	386–477 (430)	258–467 (325)
Ovary	193–283 × 316–438 (238 × 379)	155–283 × 187–322 (206×246)
Ventral sucker to ovary	190–374 (281)	[−19]–55 (15)
Ventral sucker to ovary as % of body-length	8–14 (11)	[−1]–3 (1)
Anterior extremity to anterior limit of vitellarium	374–502 (422)	187–425 (275)
Eggs	64–76 × 29–38 (70 × 33)	68–80 × 34–38 (64 × 36)

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