Goezia bangladeshi n. sp. (Nematoda: Anisakidae) from an anadromous fish Tenualosa ilisha (Clupeidae)

M. Akther¹, A. Alam¹, J. D'Silva¹, A.I. Bhuiyan¹, G.A. Bristow^{2*} and B. Berland²

¹Department of Zoology, University of Dhaka, Dhaka, Bangladesh: ²Department of Zoology, University of Bergen, Allégaten 41, N-5007 Bergen, Norway

Abstract

A total of 1432 hilsa shad, *Tenualosa ilisha* (= *Hilsa ilisha*) from 11 fresh water, brackish water and marine localities in Bangladesh yielded 13 adult *Goezia bangladeshi* n. sp., all specimens being found in the intestine of a single fish host caught in the lower Ganges. A total of 2372 *Goezia* juveniles were recovered from 490 infected fish (prevalence 34.2%). This is the first *Goezia* species recorded from Bangladesh, and it differs from other valid species by the number of caudal papillae (pre 7–9, para 3, post 6); encircled by tiny spines, the position of double papillae, the arrangement of body spines, and the length ratio of the intestinal caecum and the ventricular appendix (1: 3.33–4.72). Juveniles were free in the gut, embedded in the gut wall and encapsulated in mesenteries. *Tenualosa ilisha* serves as the definitive host, but the predominance of juveniles may indicate that piscivorous hosts may also serve as such. A list of the nominal *Goezia* species with important characters is provided.

Introduction

The clupeid fish *Tenualosa ilisha* (= *Hilsa ilisha*) – hilsa shad or hilsa for short – is a very important food fish in Bangladesh, providing a major portion of animal protein. During a 'NUFU-Hilsa Parasite Project' to study its parasites (Bhuiyan, 2002) nematodes of the genus *Goezia* Zeder, 1800 were recovered from the stomach, intestine and pyloric caeca, and embedded in the gut wall and encapsulated in mesenteries. Seven species of *Goezia* from fishes of the Indian sub-continent are listed by Soota (1983). Six of these species, *G. aspinolosa*, *G. chitali*, *G. heteropneusti*, *G. pakistanica*, *G. pseudoascaroides* and *G. taunsai* were recorded and partly redescribed by Arya (1980), Zaidi & Khan (1975), Bilqees et al. (1977), Rehana & Bilqees (1972), and one was identified as *G. ascaroides*

(Goeze, 1782) by Khan & Yaseen (1969) from Bangladesh (then East Pakistan). Only one of these species, *G. pseudoascaroides*, is widely accepted as valid. De & Day (1992) added another new species, *G. moraveci*, to the list from India. Another Indian species, *G. gavialidis* Maplestone, 1930, was described from a reptilian host. Thus, there are only three nominal species of *Goezia* on the Indian sub-continent, with no valid species reported from Bangladesh.

Of 1432 specimens of *T. ilisha* examined, only one fish, collected from fresh water (Chandpur, Oct. 1999), was infected with adult *Goezia* specimens (seven males and six females) and two juveniles. The adult specimens collected do not fit descriptions of any valid species of *Goezia*. The specimens are unique in the number, disposition and structure of the caudal papillae, the ratio of intestinal caecum length and ventricular appendix, and the arrangement of cuticular spines. Therefore, we consider the specimens studied as a new species, which we describe in this communication.

^{*}Author for correspondence

Fax: 55 58 96 73

E-mail: Glenn.Bristow@zoo.uib.no

Materials and methods

From January 1997 to August 2000 a total of 1432 *T. ilisha* were collected from 11 sites in Bangladesh, they were grouped in four length categories 17.1–27.4, 27.5–37.7, 37.8–48.0 and 48.1–58.3 cm. Four sites were fresh-water, four were brackish and three were marine localities in the Bay of Bengal. Fish were measured (total length) and dissected immediately after capture, and the alimentary tract was removed quickly, fixed and stored in 4% formaldehyde solution. On return to the laboratory in Dhaka, the alimentary tract of each fish was examined and any parasites found were washed and conserved in glycerol-ethanol.

For light microscopy parasite specimens were cleared in lactophenol and examined as wet whole mounts, identified, washed in 70% ethanol and returned to glycerol-ethanol for storage. Drawings were made by camera lucida and all measurements are given in millimetres. Some of the intestines and pyloric caeca were processed for histology.

For scanning electron microscopy (SEM), *Goezia* juveniles were fixed in 70% ethanol, dehydrated in an ethanol series and acetone, critical point dried, coated with gold and examined with a JEOL, JSM-6400 scanning electron microscope, at 20 kV. Adult *Goezia* were not studied by SEM, due to the scarcity of material.

Results

Of 1432 *T. ilisha* examined, 13 adult *Goezia bangladeshi* specimens were found in the intestine of a single fish host, and a total of 2372 *Goezia* juveniles from 490 fish. Juveniles were free in the gut, embedded in the gut wall and encapsulated in the mesenteries of the fish. This is the first *Goezia* species recorded from Bangladesh.

Goezia juveniles were present in hilsa in all 11 sampling localities and in all size groups. The prevalences for the four size groups varied between 30 and 40%, whereas the prevalences for the sampling localities varied between 27 and 45%, with one locality (Barisal) reporting a value of 14.7% prevalence. *Goezia* juveniles are thus widespread in *T. ilisha* in Bangladesh, in fresh, brackish and salt water.

The descriptions of the adults and juveniles are given below.

Goezia bangladeshi n. sp.

(figs 1–12)

Description. The nematode is typical of the genus (fig. 1). Body stout, cuticle with conspicuous transverse rings or annuli with posteriorly directed spines. Spiny annuli, starting behind the lips, are congested anteriorly, and become gradually separated in the posterior direction. Largest distance between annuli, 0.018–0.03 mm, at level of ventricle. Spines largest towards end of oesophagus. Abruptly, after 17.68–49.71% of body length, rows of spines become very congested and overlap each other. Spines also become smaller and fewer posteriorly, but again become prominent in the cloacal region, tail also with transverse rings with very small, irregular spines; tail also bears small terminal spines. Lips small, one dorsal and two sub-ventral (figs 1, 2 and 7–9) separated from the body by a deep transverse constriction. Dentigerous ridges and inter-labia absent. Cuticle of lips extend as postero-lateral flanges overlapping each other. Dorsal lip with two double papillae, each sub-ventral lip with one double and one single papilla and one lateral amphid; each lip with two distinct conical ridges on the anterior inner face, giving the impression of pointed teeth (fig. 2). Oesophagus clavate, 10.6-15.92% of body length, with ventricle. Ventricular appendix very long and slender, about 3.5 times as long as wide; intestinal caecum appears simple but is composed of two parallel rods. Excretory pore anterior to nerve ring, at level of 7th ring of spines (fig. 3), deirids on 17th–19th rings (fig. 4).

Male (fig. 5). Slender and smaller than female. Body 1.71-2.61 mm long and 0.28-0.45 mm wide. Cuticular rings of spines start at 0.039-0.042 mm from the anterior extremity. Distance between the annuli gradually increases posteriorly, reaching 0.02-0.022 mm at midbody or near posterior end of appendices. Distance between, and the number of, spines on each ring decrease abruptly between 31.79 and 49.71% of body length. Spines are totally absent on ventral surface between anterior level of spicules and last pair of papillae, spines again become prominent near base of the digitiform tail, and around caudal papillae. Nerve ring at 0.11–0.48 mm from anterior. Oesophagus 0.22–0.33 mm long, 0.084–0.112 mm wide; 12.26–17.54% of body length. Ventricle 0.022-0.030 mm long, 0.046-0.058 mm wide. Intestinal caecum and ventricular appendix 0.12-0.18 and 0.60-0.62 mm long, respectively. 16-18 pairs of caudal papillae; on each side 7–9 precloacals in a row, lateral to these are 3 posterolaterals, followed by 3 lateral paracloacals. The postcloacal papillae number 6; two median in a row, two form a double papilla just behind the angle of the cloaca, and two are lateral. All caudal papillae encircled by several small spines giving each the appearance of a sunflower. Spicules alate, sub-equal in length; left spicule (0.15–0.168 mm) slightly longer than right (0.14–0.16 mm).

Female (fig. 1). Larger than male. Body stout, 2.01– 3.96 mm long and 0.34–0.55 mm maximum breadth. Rings with spines present throughout body, starting at 0.048–0.058 mm from the anterior tip. Maximum distance between rings 0.016–0.034 mm at 17.68–34.83% of body length, decreasing anteriorly and posteriorly. Oesophagus, 0.32–0.42 by 0.1–0.124 mm, 10.61–15.92% of body length. Nerve ring at 0.12–0.13 mm from anterior. Ventricle 0.03 by 0.078 mm. Intestinal caecum and ventricular appendix 0.18–0.30 and 0.85–1.26 mm long, respectively. Eggs 0.032 by 0.022 mm.

Juveniles (figs 6–10). Specimens were found free in gut, embedded in the gut wall and encapsulated in the mesenteries. Histological sections show that pyloric caeca were also infected. Very small and slender (fig. 6), length of free larvae 0.72–1.03 mm, maximum diameter 0.072– 0.1 mm. Morphology similar to adults, head with three moderately developed lips (figs 7, 8 and 9), and the entire body, except for the tail region, covered with cuticular rings with posteriorly directed spines (fig. 6). Spines on anterior first three rings very small, spines on 4th–10th rings 0.006 mm long. Tip of tail occasionally with few



Figs 1–6. *Goezia bangladeshi* n. sp. 1, Female, entire; 2, head, lateral view; 3, excretory pore between 6th and 7th spine circles; 4, deirid on 17th spine ring; 5, male, tail ventral view, note circles of tiny spines at base of papillae; 6, juvenile, entire.

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Figs 7–10. Goezia bangladeshi juveniles. 7, Anterior, lateral view; 8 and 9, en face views of head; 10, tail, ventral view. Bars 10 µm.

minute spines (fig. 10). Length of oesophagus, intestinal caecum and ventricular appendix 0.096–0.108 mm, 0.020–0.024 mm and 0.32–0.57 mm, respectively. The capsules containing juveniles are thick-walled, and the juvenile itself is coiled (fig. 12). Its morphology is similar

to that of free juveniles. Histological sections of the fish intestine/pyloric caeca show that free larvae are present in the gut lumen, and some are also embedded in the intestinal wall (fig. 11). The SEM morphology of the sexually immature juveniles is shown in figs 7–9.

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Figs 11 and 12. 11, Section of gut wall of *Tenualosa ilisha* with embedded *Goezia bangladeshi* juveniles, drawn from a photograph; 12, *Goezia bangladeshi* juvenile embedded in capsule, drawn from a photograph.

Type host. Tenualosa ilisha (= *Hilsa ilisha*) (Clupeidae), local name hilsa.

Type locality. River Meghna (GPS reading: N 23°14.401, E 90°40.734) Chandpur, October 1999; fresh water).

Material examined. 13 adults - 7 males and 6 females.

Deposition of type specimens. Type material deposited in the Natural History Museum, London, UK. Holotype, female, no. 2003.5.14.1, paratypes, males on slides and spirit material nos. 2002.5.14.2–6. Remaining type specimens in museum collections, Department of Zoology, University of Dhaka, Bangladesh.

Etymology. Being the first *Goezia* species reported from Bangladesh.

Discussion

Twenty-nine species of *Goezia* have been described worldwide so far. Of these Rasheed (1965) excluded *G. onchorhynchi* Fujita, 1940. Lèbre & Petter (1983) advised that the following five species from India and Pakistan – *G. aspinulosa* Arya, 1978, *G. chitali* Rai, 1967, *G. taunsai* Zaidi & Khan, 1975, *G. heteropneusti* Zaidi & Khan, 1975 and *G. pakistanica* Bilqees *et al.*, 1977 – be excluded because the first four species lack the characteristic cuticular spines, whereas *G. pakistanica* has interlabia, which is not a generic character. The remaining 23 valid species, plus the one described in the present study, are listed in table 1. Only three species of *Goezia* are described from the Indian sub-continent, with two of them from piscine hosts.

Khan &Yaseen (1969) identified the only *Goezia* species reported from Bangladesh as *G. ascaroides*, from a marine fish, *Thrissocles hamiltonii*. However, these specimens have interlabia, and do not fit the generic diagnosis of *Goezia*; the same argument applies to *G. pakistanica*, which also does not show a characteristic double ventricular appendix. Bashirullah (1973) reported a *Goezia* sp. from a freshwater fish *Wallago attu*, and Ali (1968) reported a *Goezia* sp. in the coelom of *Sciaenoides pama* (*Pama pama*), a marine fish. But descriptions of these species were not given.

Most of the valid species differ from *G. bangladeshi* n. sp. in the number of pre-, para- and postcloacal papillae (table 1). There is little information available on *G. annulata*, *G. ascaroides*, *G. kollary* and *G. trichurata* and the male of *G. gavialidis* is unknown. The precloacal papillae number 7 to 9 in the present species. Only *G. fluviatilis*, *G. holmesi* and *G. nankingensis* have comparable numbers; all the other valid species have more than 9 precloacal papillae.

The original description of *G. ascaroides* (Goeze, 1782) in Zeder, 1800 is considered insufficient by many authors. Dollfus (1935) and Punt (1941) redescribed the female of *G. ascaroides* from *Salmo irideus* (= *Oncorhynchus mykiss*) and *Trachinus vipera*, respectively. Although they gave a detailed description of the form they did not indicate the dimensions of the intestinal caecum and ventricular appendix. In any case, the attribution of these two females to *G. ascaroides* is without good foundation according to Lèbre & Petter (1983).

There are 6 pairs of postcloacal papillae in *G. bangladeshi*, the anteriormost two forming a double papilla. Except for *G. alli* (5–6) and *G. spinolosa* (6) all other valid species have fewer than 6 postcloacal papillae. The number of paracloacal papillae, 3 in *G. bangladeshi*, is similar to that of *G. nankingensis*. Only *G. holmesi* has a greater number (5). All other species have less than 3.

The present species possesses pairs of laterally disposed precloacal papillae near the level of the cloaca, similar to *G. pelagia, G. moraveci* and *G. lacerticola,* but these three species do not have laterally disposed postcloacal papillae which are present in *G. bangladeshi*.

The present species resembles G. moraveci De & Day, 1992 described from a freshwater fish, Mastacembalus armatus from India, only in the structure of the caudal papillae which are encircled by spines and in the laterally dispersed postcloacal papillae. The 'sunflower' caudal papillae in *G. bangladeshi* are very striking (fig. 5), but the main differences between the two species are the number of pre-, para- and postcloacal papillae, which are 9–11, 2 and 3 in G. moraveci and 7-9, 3 and 6 in G. bangladeshi, respectively. In addition, the spicules are almost twice as long in G. bangladeshi compared with G. moraveci, as a percentage of body length. In G. moraveci the spicules are of equal length but in G. bangladeshi the left spicule is slightly larger than the right one. The intestinal caecum/ventricular appendage ratio is 1/6.15 in G. moraveci, and 1/3.75 in \hat{G} . bangladeshi. The position of the excretory pore is on the 14th–17th ring in *G. moraveci*, and on the 7th ring in G. bangladeshi.

The body dimensions of *G. bangladeshi* may have been affected by formalin fixation, which tends to cause shrinkage. If fixed live in hot ethanol or in Berland's fluid (Gibson, 1979), nematodes die immediately and become extended. However, as little is known as to how other *Goezia* species were fixed, body dimensions are considered to be less important than morphological characters in defining new species.

Goezia juveniles were present in hilsa in all 11 sampling localities and in all fish size groups in the length categories 17.1–27.4, 27.5–37.7, 37.8–48.0 and 48.1–58.3 cm. For each locality and fish length group prevalence values between 9.1 and 100% were recorded. The total prevalences for each of the four size groups were between 30 and 40%, and likewise the total prevalence for each sampling locality varied between 27 and 45%, with one locality (Barisal) showing a prevalence of 14.7%. *Goezia* juveniles are thus widely present in the *T. ilisha* in Bangladesh, in fresh, brackish and salt water.

The general biology and life cycle of *G. bangladeshi* is likely to be similar to other *Goezia* species. Both Hartwich (1975) and Moravec (1994) refer to the work of Mozgovoy *et al.* (1971) who experimentally found that larvae of *G. ascaroides* develop in eggs shed in water, hatch, grow and, when ingested by a copepod, develop to the third stage. Infected copepods transfer the larvae to fishes, in which they become encapsulated or embedded in the gut wall. Definitive fish hosts acquire larvae either directly from copepods or from paratenic fish hosts containing encapsulated larvae.

Hartwich (1974) placed the subfamily Goeziinae with Anisakinae and Raphidascaridinae in the family Anisakidae. Gibson (1983) saw no reason to retain Goeziinae distinct from Raphidascaridinae, and hence the life cycle of *Goezia* is more comparable with genera and species in Raphidascaridinae, which includes the genus *Hysterothylacium*. The species *H. aduncum* (Rudolphi, 1802) occurs in a large number of teleosts in the North Atlantic, where large, mature specimens live free in the stomach and intestine of their fish host. Larvae develop in eggs shed in the water, hatch and become ingested by copepods, in which they develop to infective third stage larvae each with a boring tooth. When copepod intermediate hosts are eaten by susceptible fish, the larvae - depending upon their size (Køie, 1993) – either bore through the gut wall and become encapsulated in the viscera, or remain in the fish gut, where they grow, moult twice and become adults. The fourth stage larva has 'adult' external morphology, i.e. three typical adult lips, cervical alae and a 'cactus' tail. It is very difficult to distinguish fourth stage larvae from recently moulted, young immature fifth stage 'adults' (Berland, 1961). Thus any fish may harbour free third and fourth stage larvae and young and adult fifth stage specimens as well as encapsulated third stage larvae (Berland, 1998). Young free H. aduncum juveniles may remain as such in the fish gut during the winter months (B. Berland, personal observations).

According to Mozgovoy et al. (cited by Moravec, 1994) infective third stage larvae of G. ascaroides in the copepod intermediate hosts have transverse striae on the cuticle, a rounded cephalic end with a boring tooth. In the present study, larvae found free in the gut of T. ilisha and embedded/encapsulated in gut wall and mesenteries do not have a boring tooth, but have three lips, a cuticle with transverse annuli and conspicuous spines, all of which are seen in the adults. The free larvae, initially assumed to be third stage, must be either fourth stage or young fifth stage, or both. The similarity in the life cycle to Hysterothylacium would lead us to expect third stage larvae with a boring tooth to be present, but no third stage larvae were found in T. ilisha. Consequently, all specimens had probably moulted beyond the third stage, and thus these larvae with 'adult morphology' are noted as juveniles in the text and illustrations; note that the intestinal caecum is poorly developed in juveniles (fig. 6).

However, fixation in formaldehyde solution tends to make the capsules so hard that they are impossible to 'crack', hence it is possible that some capsules contained third stage larvae, but this question can only be answered by further studies on fresh material in the field, or on chilled/frozen material. According to Moravec (1994) *G. ascaroides* becomes localized in swellings in the stomach. If adult specimens in the genus tend to burrow or 'hide' in cavities in stomach wall, the presence of *G. bangladeshi* specimens embedded or 'hiding' in the gut wall, and even in mesenteries, may be quite normal.

The presence of sexually mature G. bangladeshi specimens show that *T. ilisha* serves as a definitive host. Many fourth and fifth stage juveniles may be available to resume final development to maturity. It is not known whether juveniles encapsulated in the viscera return to the host's digestive tract to mature there, become immobilized by the host's immune system and die in situ, or survive until they reach a fish-eating predator in which final development to maturity may take place. It is possible that T. ilisha and G. bangladeshi reproduce at the same time, so that when the young fish fry start to feed, copepods infected with newly formed third stage larvae may be available. Being anadromous, T. ilisha spawns in fresh water, and returns to the sea for some months every year. Goezia bangladeshi is probably a fresh-water species that survives in fish in sea water. It is worth noting that De & Day (1992)

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			No. of ca	iudal pa	pillae		Spic	cule		
Species	Author(s), year	Type host, locality	pre	post	para	Length ratio f IC/VA	as % of body length	Right/left	Oesophagus % of body length	Body length (mm)
G. annulata	(Molin, 1859)	Morone labrax, Italy	I	I	I	I	I	I	I	3-4
G. ascaroides	(Goeze, 1782)	Silurus glanis, Europe	I	I	I	I	I	I	18.4	8.1
G. fluviatilis	Johnston & Mawson, 1940	– South Australia	ß	3-4	б	1:3.9	10-20	1:1	13.6 - 17	2–8
G. gavialidis	Maplestone, 1930	Gavialis gangeticus, India				1:1-7.5	I	I	11.3	9.9
G. holmesi	Sprent, 1978	Crocodylus porosus, North Australia	ß	ю	Ŋ	1:2.8-8.6	7-12	$1\!:\!1$	10.4–14.2	2.6–6.7
G. intermedia	Rasheed, 1965	Cichlaocellaris, British Guiana	22-23	4	0	1:4-7	3-4	1:1.1	9.6 - 10.9	9-15.5
G. kliksi	Deardorff & Overstreet, 1980	Pogonias cromis, Louisiana	10-16	ß	7	1:1.9-3.3	8 - 14	1:1-1.2	8-10	6-14
G. kollari G. lacerticola	(Molin, 1859) Deardorff &	Chrysophrys aurita, Europe Alliyator mississimiensis.	- 22-26	۱ 4	- 6	- 1:2.1–4.6	- 8-16	-1:0.8-1	$^{-}7-15$	8-11 3.9-8.2
	Overstreet, 1979	Florida		•	I)			
G. minuta	Chandler, 1935	Bagre marinus, Texas	16	4	2*	1:4.4	11	L	10	3.1
G. nankingensis	Hsü, 1933	-, China	6-7	3-4	n	I	I	1:1	7.6 - 8.2	5.5 - 9.3
G. pelagia	Deardorff & Overstreet. 1980	Rachycentron canadus. Mexico	12–19	4	7	1:2-4.4	6 - 10	1:.09 - 1.1	10 - 17	3.4-14.5
G. pseudoascaroides	Rehana & Bilgoos 1077	Mastacembalus punctatus,	29	7	0	I	I	I	11-15	3.6-7.8
	Dudges 17/2	T_{m-1}	0110	¢	c	1 0 0 7		1.000	000	- / 0 c
G. signust G. sinamora	Deardorff &	Tructurus araco, prazu Tilapia aurea, Florida	$\frac{3}{13}-16$	4 ‰	5 64	1:1.6-5.7	10-20 3	1:1	8–18 8–18	1.4 - 16.0
	Overstreet, 1980									
G. spinolosa	Diesing, 1839	Arapaima gigas, Brazil	13	9	0	1:1.5-5.3	ŝ	1:1	3.1-8.7	16.3 - 24.8
G. tricirrata	Osmanov, 1940	Onos tricirrata, Black Sea	I :	I i	1	1:2.1-2.5	11	1:1	12.5-21	6-7
G. anguillae	Lèbre & Petter, 1983	Anguilla anguilla, Vaccaris Lake	15	ů.	2	1:3.09	12.2	1:1	10.37 - 10.87	10 - 14
G. brasiliensis	Moravec <i>et al.,</i> 1994	Brycon hilarii, Pseudoplatystoma coruscans Brazil	10	4	0	1:5.4	7.2	1:1	7–9	11.14–15.67
G hrenicaeca	Moravec et al	R hilarii Brazil	20	4	I	$1 \cdot 37$	7 1	1.1	с С	17 15-22 58
	1994		1	•			i	•		
G. nonipapillata	Osorio-Sarabia, 1982	Cichalsoma istlanum, Satherodon aureus, S mossamhirus, Mexico	ß	7	7	1:1.6	13	1:1.03-1.1	11.47–19.63	6.9-12.5
G. alii	Kaur & Khera, 1001	Channa striatus, India	12	5-6	7	1:12-14		$1\!:\!1$		4.88-7.60
G. moraveci	De & Dav. 1992	<i>Mastacembalus armatus</i> India	9–11	ж С	2	1:6-15	6.31 - 9.25	1:1	7.25 - 15.05	2.06 - 3.70
G. bangladeshi n. sp	Akther <i>et al.</i> 2002	Tenualosa ilisha, Bangladesh	7-9	.*9	IΩ	1:3.33-4.72	11.33-13.33	1:1.05-1.07	10.6 - 15.92	1.71-3.96

Table 1. List of valid species in the genus Goezia (males only), including G. bangladeshi n. sp.

Goezia bangladeshi n. sp. from Tenualosa ilisha

reported G. moraveci from the freshwater fish Mastacembelus armatus in neighbouring West Bengal, India.

In the present case, T. ilisha may, of course, not be the normal definitive host, but an intermediate or transport host. Carnivorous teleosts or reptiles, which feed on T. ilisha in the vast fresh-water river maze in Bangladesh, may act as definitive hosts. Another, less likely, possibility is that G. bangladeshi is a marine parasite that is transported into fresh water. An alternative explanation might be precocity. In accidental hosts parasites might develop to the adult stage but do not reach sexual maturity. In the present case, female G. bangladeshi were gravid, suggesting that the infection was not accidental, but neither was it the result of cannibalism, as T. ilisha is a filter feeder. If, on the other hand, T. ilisha is a transport or intermediate host, the presence of mature specimens may be a case of precocity. According to Anderson (1988) precocity in the intermediate host is an important feature of transmission for many ascaridoids by which the nematodes become adults in what was formerly the intermediate host, eventually leading to the elimination of the original definitive host.

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