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A new type of haptor in mesoparasitic monogeneans of the genus *Enterogyrus* Paperna, 1963, with a description of *Enterogyrus foratus* n. sp. and *E. coronatus* n. sp, stomach parasites of cichlids in West Africa

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Abstract

Descriptions are given of *Enterogyrus foratus* n. sp., collected from the stomach of *Sarotherodon melanotheron* (Osteichtyes, Cichlidae) in Senegal and the Ivory Coast, and *E. coronatus* n. sp. from the stomach of *Tilapia guineensis* (Osteichtyes, Cichlidae) in the Ivory Coast. The two new species differ from almost all other congeneric species mainly with regard to the novel shape of the haptor. This haptor comprises two segments: an elongated posterior peduncular segment, which deeply penetrates the stomach wall, and a bulbous anterior segment. The posterior segment bears two pairs of hamuli (dorsal and ventral), a transverse V-shaped ventral bar and ventral hooklets I and II. The anterior segment has hooklets III and IV (dorsal) and V to VII (ventral) arranged in an equatorial circle. These two species possess the spiral cirrus characteristic of the genus *Enterogyrus*, but differ with respect to each other and to other members of the genus by the nature of the spirality of the cirrus.

Introduction

The large majority of monogeneans are branchial or cutaneous ectoparasites. Amongst the Dactylogyridea, some show an unusual localisation: oesophagus (*Diplectanotrema* Johnston and Tiegs, 1922), urinary bladder and ureters (*Acolpenteron* Fischthal & Allison, 1940), nasal cavity (*Dactylogyrus nasalis* Strelkov & Kha Ki, 1964), ovipositor (*Dactylogyrus* n. sp. Yukhimenko & Danilov, 1988) and stomach (*Enterogyrus* Paperna, 1963). The adaptation of these monogeneans to mesoparasitism suggests the possibility of studies, particularly comparative research, on gill dactylogyrids, investigating in particular: (i) the functional adaptation of the haptor, tegument, physiology, etc; (ii) specificity for the cichlid host; and (iii) life-cycle and strategy of infestation.

The genus *Enterogyrus* currently includes seven species, which are all parasites of the proximal digestive tract (stomach) in fishes of the family Cichlidae:

Enterogyrus cichlidarum Paperna, 1963, a parasite of *Tilapia zillii* Gervais, 1848 and *Oreochromis niloticus* (L.) (syn. *Tilapia nilotica*). This parasite has been described in Israel and was found in Cameroon in *O. niloticus* by Bilong Bilong *et al.* (1989).

E. globodiscus (Kulkarni, 1969) Gussev & Fernando, 1973 and *E. papernai* Gussev & Fernando,

1973. These two species are parasites of *Etroplus suratensis* Block, 1790 in Sri Lanka.
E. hemihaplochromii Bender, 1979, a parasite of *Hemihaplochromis multicolor* Hilgendorf, 1903 (Cichlidae, originating in East Africa). This parasite, which is described in an unpublished thesis, was discovered in an aquarium in Germany.
E. niloticus Eid & Negm, 1987, a parasite of *O. niloticus* in Egypt. The description and illustration of this species are insufficient, especially with regard to the form of the penis.
E. malmbergi Bilong Bilong, 1988, a parasite of *O. niloticus* in Cameroon. This species may be synonymous with the preceding species.
E. melenensis Bilong Bilong, Birgi & Lambert, 1989, described from *Hemichromis fasciatus* in Cameroon.

It should be noted that *Enterogyrus* sp. reported in *Pomacanthus paru* (Bloch, 1787) by Cone, Gratzek & Hoffman (1987), originating in the Caribbean Sea and raised in an aquarium, is not an *Enterogyrus* but more closely related to the genus *Diplectanotrema* Johnston & Tiegs, 1922 or *Pseudempleurosoma* Yamaguti, 1965, which have previously been described in the pharynx of carangids (see Yamaguti, 1968).

Mesoparasitic (see Euzet, 1989) monogeneans with a very novel haptor shape were found during dissections of the digestive tract of *Sarotherodon melanotheron* Rüppel, 1853 from Senegal and the Ivory Coast and *Tilapia guineensis* Bleeker, 1862 from the Ivory Coast.

Materials and methods

Monogeneans were collected from three West African cichlids: *Sarotherodon melanotheron melanotheron* from the mouth of the Casamance river (Senegal) and both *Sarotherodon melanotheron heudelotii* (Duméril, 1859) and *Tilapia guineensis* from the aquaculture station of Layo in Ebrié Lagoon in the Ivory Coast (run by the "Centre de Recherches Océanographiques d'Abidjan").

Fish were dissected immediately after capture. The digestive tract was removed by two incisions, one at the oesophagus and the other at the rectum, wrapped in aluminium foil, and immediately submerged in liquid nitrogen. Samples were stored in dry ice during transport to France and were placed in a freezer (−80°C) upon arrival in the laboratory. For study, frozen samples were sprayed with Ringer's soluton in a Petri dish. After thawing at room temperature, the digestive tube was cut open lengthwise. *Enterogyrus* specimens, which were firmly fixed to the stomach wall, were carefully detached using a thin quill under a binocular microscope. They were then placed directly between slide and coverslip, either in a mixture of ammonium picrate-glycerine (Malmberg, 1957) or in Berlese's chloral gum, then preparations were sealed.

Some parasites were fixed in 2% glutaraldehyde in 0.1M cacodylate buffer, pH 7.4, and postfixed in 1.3% osmium tetroxide in 0.13M cacodylate buffer for 1 h at 4°C. The samples were then dehydrated, critical point dried, sputter-coated with gold, and observed under a Jeol JSM 35 scanning electron microscope. Small portions of stomach wall with *Enterogyrus* were fixed in Bouin's fluid, embedded in paraffin and sections were stained with malachite green.

Observations were made using a light microscope with an immersion objective, and drawings were made using a camera lucida. Sclerotised parts were measured directly from the drawings, as defined by Gussev (1962) and adapted by Bilong Bilong (1988). The terminology is that of Euzet & Prost (1981). Measurements (in micrometres) are presented in the following order: (number of measurements) mean ± standard deviation (maximum-minimum).

Enterogyrus foratus n. sp.

Host: *Sarotherodon melanotheron melanotheron* (Rüppel, 1853) [type-host] and *S. m. heudelotii* (Duméril, 1859).
Site: Stomach.
Locality: Mouth of the Casamance River, Senegal; Layo station, Ebrié Lagoon, Ivory Coast.
Material studied: 64 individuals (53 from Senegal, 11 from the Ivory Coast), 19 mounted with Berle-

se's gum, 25 with ammonium picrate glycerine, 10 for scanning electron microscopy and 10 for histological sections.
Specimens deposited: One holotype and one paratype at the Museum National d'Histoire Naturelle, Paris, nos 90 HF Tk3 and 90 HF Tk4, and one paratype at the Natural History Museum in London, no. 1990.12.7.1.
Etymology: Based on the attachment of the haptor, which penetrates deeply into the stomach wall.

Description

The body is (17) 602.68 ± 113.10 (849.62–417.29) long by (17) 148.03 ± 22.92 (195.49–101.50) wide. It has a thick tegument, striated transversely. There are 2 pairs of eye-spots: an anterior pair, small and well separated, and a posterior pair that were very close or, in occasional individuals, merged on the median plane. The pharynx is (9) 33.37 ± 6.02 (42.77–25.07) in diameter. A slight constriction marks the division between the body and the haptor, whose tegument is thinner and does not have the transverse striations characterising the body. The unusual haptor (Figs 1–3) comprises 2 segments:
– an elongate posterior peduncular segment bearing 2 pairs of hamuli (dorsal and ventral), a transverse V-shaped ventral bar, and ventral hooklets I and II.
– a bulbous anterior segment that is somewhat wider than the body and twice as wide as the posterior segment, with hooklets III and IV (dorsal) and V to VII (ventral) arranged in an equatorial circle with their tips directed anteriorly (Fig. 3). As in other species of the genus, the hooklets all have a larval form.

Histological sections showed that only the posterior segment penetrates the stomach wall deeply (Figs 1c, 3). The anterior globular segment lies in a small depression formed by a reaction of the stomach epithelium. The tips of hooklets III to VII, which hold it in the depression, penetrate the reactive tissue. The anatomy of the genital complex conforms to that described in other species of the genus. Eggs were seen on several occasions in the uterus. The cirrus is (28) 50.21 ± 3.70 (57.71–41.10) long and forms a continuous spiral as in other species of the genus: from the wide base to the very thin posterior end there are 4 turns, then 2 longer turns, and finally 3 very tight contiguous terminal coils, i.e., a 4-2-3 spiral sequence (Figs. 1d$_1$, 5b).

Measurements of sclerotised part of the haptor (Fig. 2)
Dorsal hamuli (43): a: 12.81 ± 0.86 (15.08–10.93); b: 18.49 ± 1.09 (20.99–15.52); c: 25.90 ± 2.76 (30.39–18.58); d: 8.37 ± 0.78 (10.49–6.56); e: 5.89 ± 0.80 (7.87–3.93). Ventral hamuli (29): a: 14.17 ± 0.79 (15.52–12.24); b: 12.61 ± 0.72 (14.65–11.37); c: 7.63 ± 1.09 (10.06–5.90); d: 5.45 ± 0.70 (7.00–3.06); e: 4.50 ± 0.70 (5.68–2.62). Transverse bar (11): 17.86 ± 1.49 (21.20–15.30). Hooklets (all similar) (50): 14.25 ± 1.11 (16.61–12.24).

***Enterogyrus coronatus* n. sp.**

Host: *Tilapia guineensis* Bleeker, 1862.
Site: Stomach.
Locality: Layo station, Ebrié Lagoon, Ivory Coast.
Material studied: 25 individuals, 3 mounted with Berlese's gum, 22 with ammonium picrate glycerine.
Specimens deposited: One holotype and one paratype at the Museum National d'Histoire Naturelle, Paris, nos. 89 HF Tk1 et 89 HF Tk2, and one paratype at the Natural History Museum in London, no. 1990.12.7.2.
Etymology: Based on the crown arrangement of hooklets III to VII on the bulbous segment of the haptor.

Description

The body is (15) 535.11 ± 55.51 (641.22–454.20) long by (15) 115.01 ± 13.57 (137.40–95.42) wide. It has a thick tegument, striated transversely. There are two pairs of dorsal eye-spots, i.e., an anterior pair, small and well separated, and a

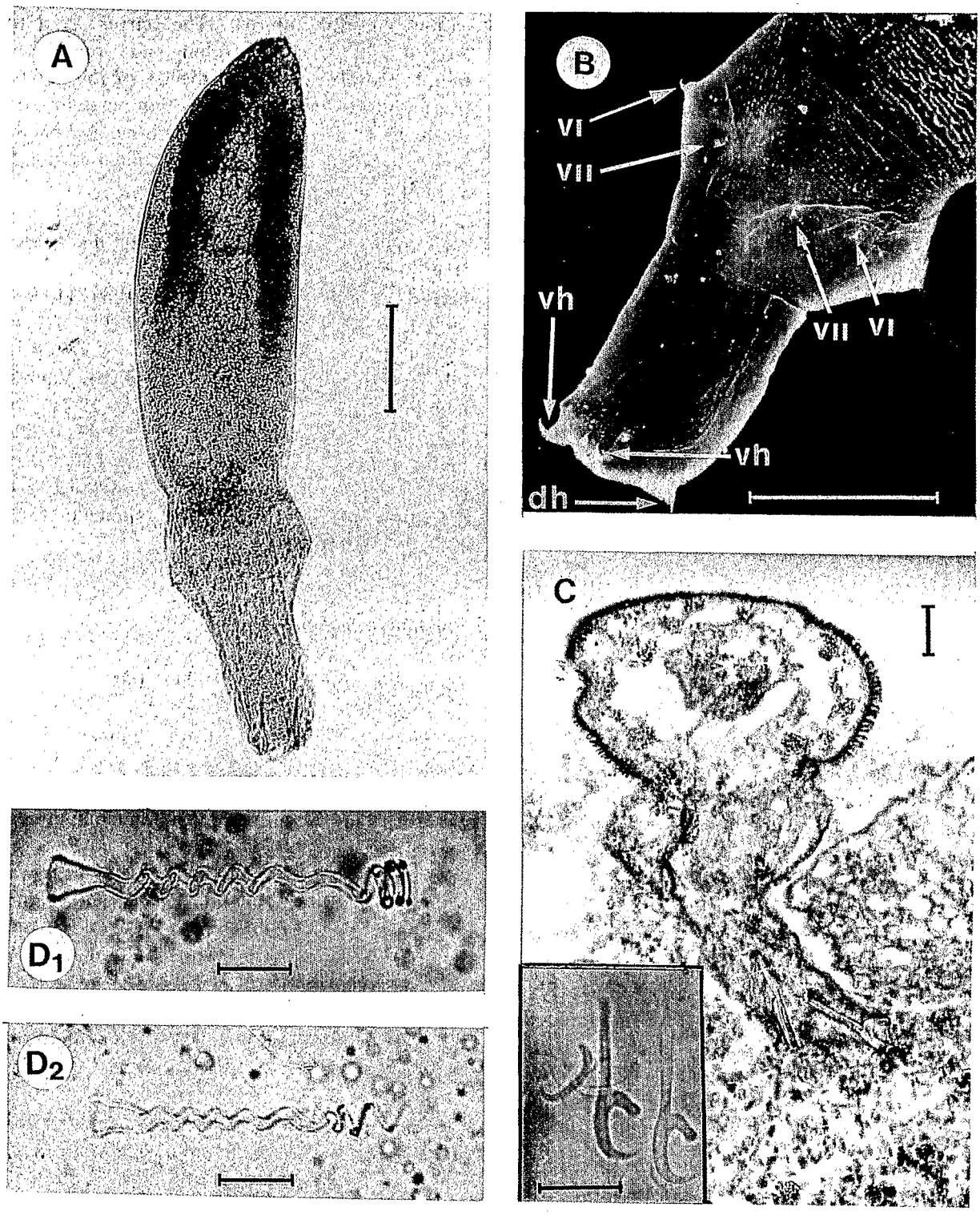

Fig. 1. A. Photomicrograph of *Enterogyrus foratus* (*in toto*); B. SEM photomicrograph of the haptor of *Enterogyrus foratus* (ventral view); C. Photomicrograph of a transverse section of *E. foratus* (*in situ*), with details of sclerotised parts in the posterior segment of the haptor; D. Photomicrograph of the copulatory organ, D_1, *E. foratus*; D_2, *E. coronatus*. *Scale-bars*: 100 μm, A, B; 20 μm, C; 10 μm, D. *Abbreviations*: dh, dorsal hamuli; vh, ventral hamuli; VI and VII, ventral hooks.

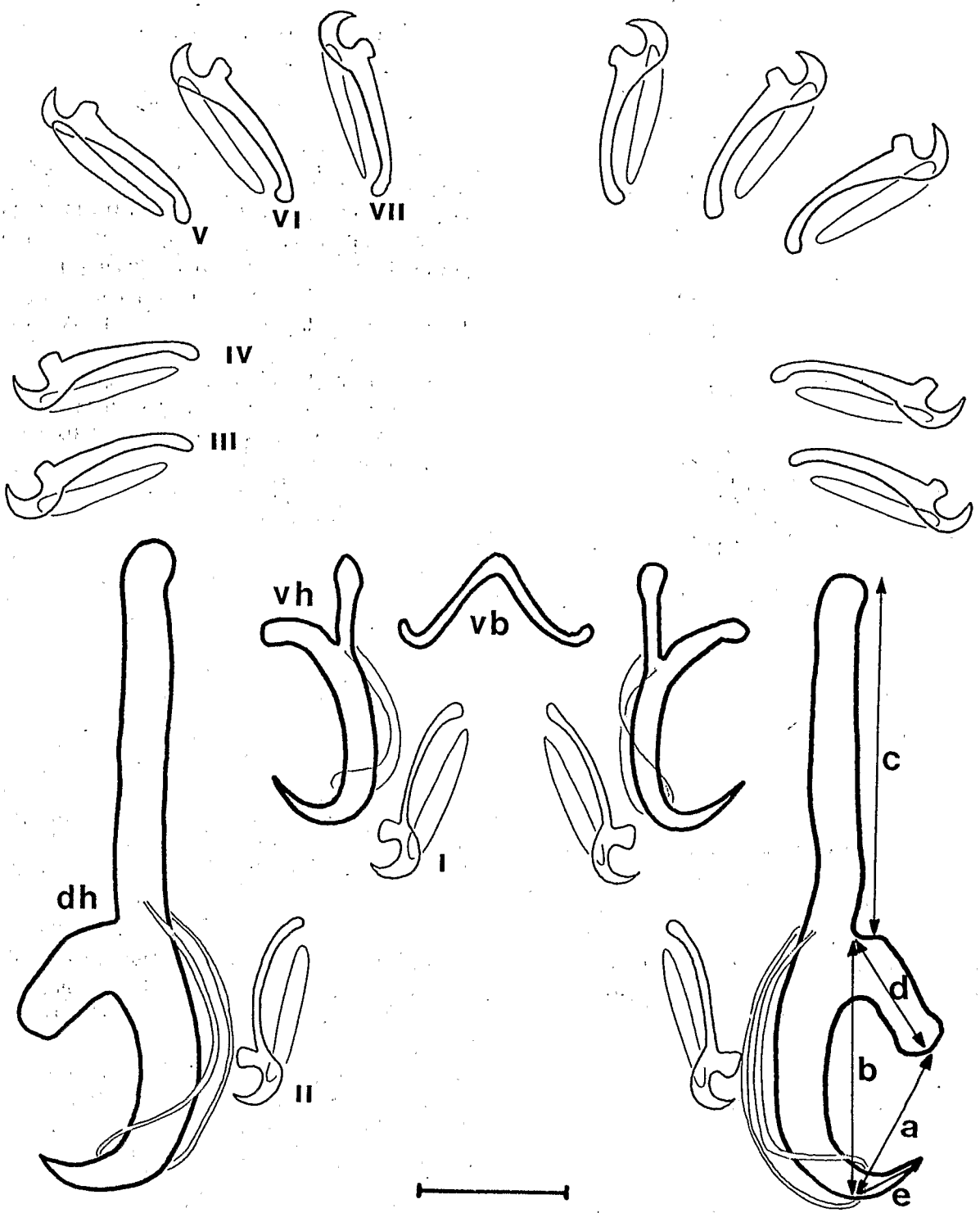

Fig. 2. Sclerotised parts of the haptor of *E. foratus*. *Abbreviations*: dh, dorsal hamuli; vb, ventral bar; vh, ventral hamuli; III to IV, dorsal hooklets; I–II, V to VII, ventral hooklets. Details of measurements used for hamuli: a, anchor length; b, main part; c, handle (outer root); d, inner root; e, point. *Scale-bar*: 10 μm.

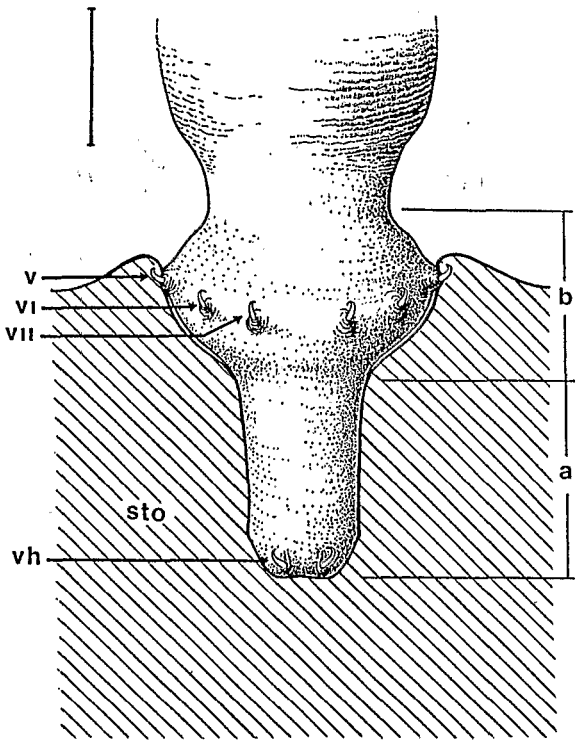

Fig. 3. Diagram of the haptor of *Enterogyrus foratus* and *E. coronatus* (*in situ*, ventral view). A. Posterior segment of the haptor (including ventral hamuli and I–II hooklets); B. Anterior segment (including ventral hooklets V to VII). *Abbreviations*: vh, ventral hamuli; sto, stomach wall (transverse section); V to VII, hooklets. *Scale-bar*: 100 μm.

posterior pair that are very close and even occasionally merged on the median plane in some individuals. The pharynx is (9) 33.37 ± 6.02 (42.77–25.07) in diameter. The form of the haptor is identical to that of the preceding species, with the same arrangement of sclerotised parts, i.e., 2 dorsal hamuli, 2 ventral hamuli, a ventral transverse bar and 2 pairs of hooklets (I and II) on the posterior peduncle and 5 pairs of hooklets (III to VII) on the bulbous anterior segment (Figs 3, 4). The anatomy of the genital complex is similar to that of other *Enterogyrus* species. Uterine eggs were also observed in several individuals. The cirrus (Figs 1d$_2$,5a), measuring (23) 48.60 ± 2.52 (52.46–42.85), forms a continuous spiral as in other species of the genus, with 3 even turns, then 2 longer turns and finally 3 posterior turns (the first very tight and small in diameter, and the other 2 longer and larger in diameter), i.e. a 4-2-1 + 2 spiral sequence.

Measurements of sclerotised part of the haptor (Fig. 4a)

Dorsal hamuli (34): a: 11.38 ± 1.13 (13.12–7.21); b: 16.40 ± 0.91 (18.14–13.99); c: 21.17 ± 1.39 (23.61–18.14); d: 7.14 ± 0.51 (8.09–6.12); e: 5.47 ± 0.90 (8.09–3.94). Ventral hamuli (30): a: 15.00 ± 0.82 (16.40–13.33); b: 12.83 ± 1.04 (15.74–10.71); c: 6.33 ± 0.61 (7.65–5.03); d: 5.67 ± 0.86 (7.21–3.06); e: 4.69 ± 0.80 (7.21–3.06). Transverse bar (3): 18.14 ± 0.93 (18.80–16.83). Hooklets (all similar) (61): 14.18 ± 0.94 (16.18–12.02).

Discussion

Enterogyrus foratus and *E. coronatus* differ from other species described for this genus in the morphology of their haptor. Indeed, in all *Enterogyrus* species so far described, the haptor forms a wide subcircular ventral cupule. The only known exception is *E. globodiscus* which would appear to possess a haptorial morphology similar to that described in the present paper (see Gussev and Fernando, 1973, p. 209, fig. 2A). Other interspecific differences in this genus concern the size of the sclerified structures of the haptor and the spirality of the cirrus. These differences are detailed in Table I.

Although no significant differences can be distinguished between the dimensions of the haptorial structures of *Enterogyrus foratus* and *E. coronatus*, these two species can be distinguished by the spirality of the cirrus (*E. foratus* is a type 4-2-3 and *E. coronatus* of type 4-2-1 + 2 (Figs 1d, 5)). It is considered that this consistent difference might constitute a mechanism for reproductive isolation and can be used as a diagnostic morphological characteristic of the species.

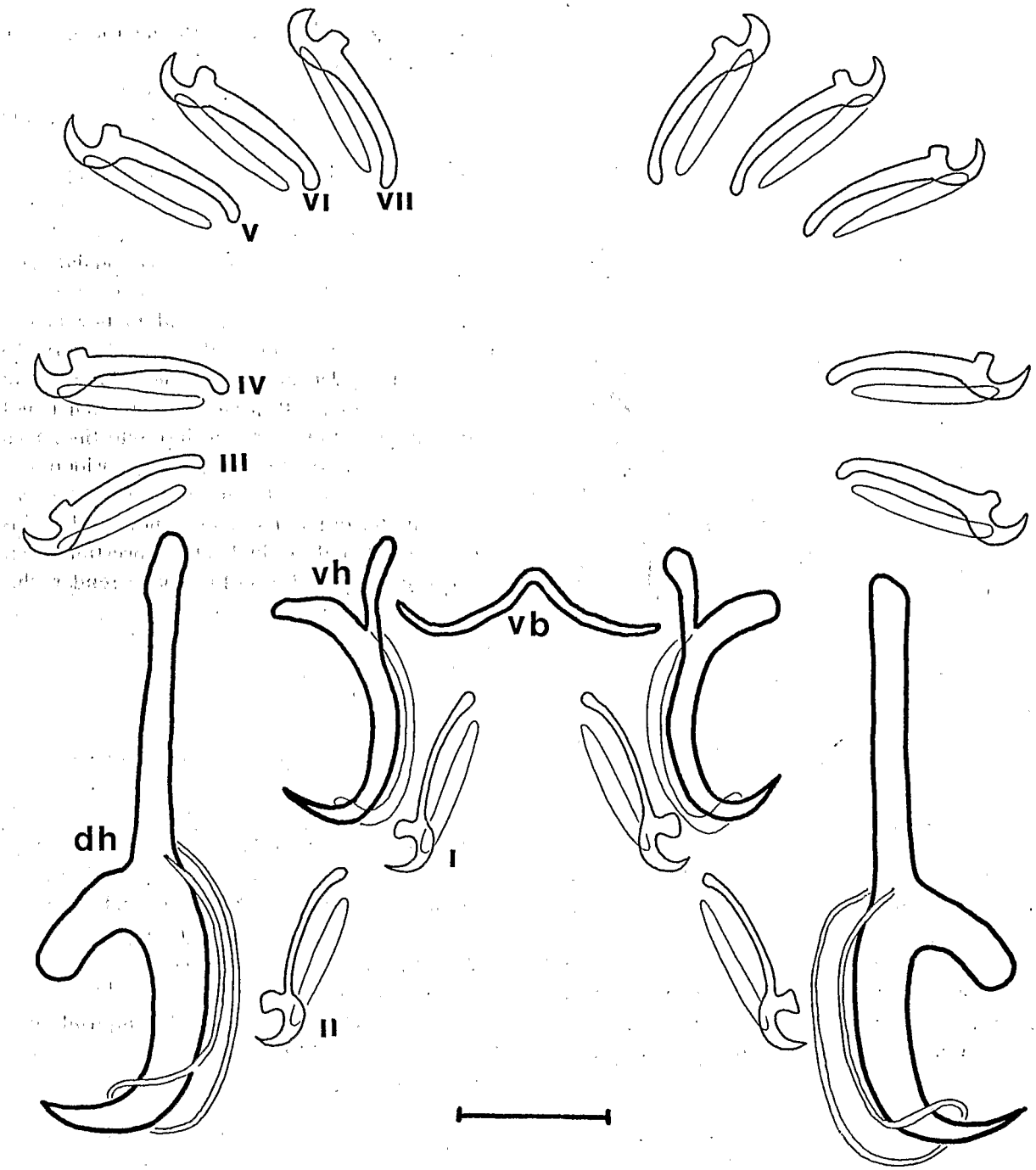

Fig. 4. Sclerotised parts of the haptor of *Enterogyrus coronatus*. *Abbreviations*: dh, dorsal hamuli; vb, ventral bar; vh, ventral hamuli, III to IV, dorsal hooklets; I–II, V to VII, ventral hooklets. *Scale-bar*: 10 μm.

Conclusion

The observed differences, i.e. haptor split into two parts and hooklets III to VII turned backward, could justify the creation of a new genus. With respect to described members of the genus *Enterogyrus*, however, the organisation of the haptor and the morphology of its sclerified struc-

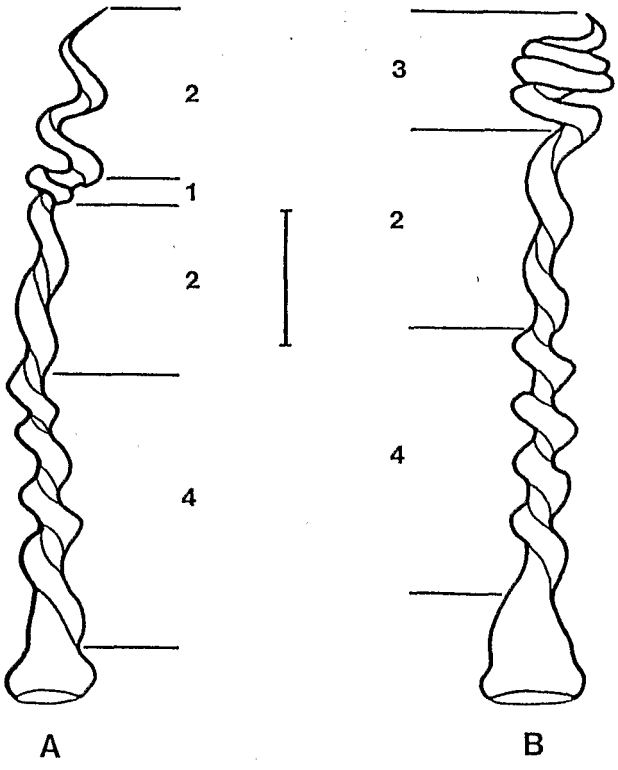

Fig. 5. Comparative drawing of spiral copulatory organs of *Enterogyrus coronatus* (A) and *E. foratus* (B) (see text). *Scale-bar*: 10 μm.

tures remain unaltered. This haptor would, therefore, appear to correspond to a morphological functional adaptation with limited taxonomic importance. The exceptional nature of the copulatory organ, with a penis always of spiral type, demonstrates a taxonomic homogeneity that can be considered to be characteristic of the genus.

Considerable variations in the haptor morphology have been described for branchial ectoparasites (Lambert, 1980a,b), and similar morphological adaptations of this attachment organ could exist in the case of monogenean endoparasites, linked to the structure of the stomach wall.

Questions remain as to the origin and affinities of *Enterogyrus* and whether there exist closely related genera amongst the ancyrocephalid ectoparasites of cichlids. Two genera have been described amongst these branchial monogeneans, i.e. *Cichlidogyrus* Paperna, 1960 and *Onchobdella* Paperna, 1968. The anatomy of the genital system of *Cichlidogyrus*, with a vas deferens that is not wrapped around the left branch of intestine, as in the case of *Enterogyrus*, cannot be considered as being in the same evolutionary lineage. *Onchobdella*, on the other hand, does not display this characteristic and could be the ancestral form, though the atypical form of the penis renders this hypothesis very improbable.

Two other points of note support the hypothesis that the genus *Enterogyrus* is very old. Firstly, *E. globodiscus* and *E. papernai* are stomach parasites of a cichlid that is considered to be primitive (*Etroplus suratensis*, a native species of India and Sri Lanka). Secondly, *Enterogyrus* has a large geographical range.

The specific morphology of the haptor of *Enterogyrus foratus* and *E. coronatus*, and in consequence its mode of attachment, provokes lesions on the gastric epithelium of its host and many cause pathological conditions. This is especially so as the development of the parasite, which would appear to be direct, facilitates its multiplication in intensive cultures of the hosts.

Table I. Comparison of measurements (micrometres) of sclerotised parts in *Enterogyrus* spp.

Enterogyrus spp.	*E. cichlidarum* (1)	*E. globodiscus* (2)	*E. papernai* (2)	*E. hemihaplochromii* (3)	*E. niloticus*	*E. malmbergi*	*E. melenensis*	*E. foratus*	*E. coronatus*
Host	*T. zilli* (*T. nilotica*)	*Etroplus suratensis*	*Etroplus suratensis*	*Hemihaplochromis multicolor*	*Tilapia nilotica*	*Tilapia nilotica*	*Hemichromis fasciatus*	*Sarotherodon melanotheron*	*Tilapia guineensis*
Locality	Israel (Cameroon)	Sri Lanka India	Sri Lanka	Germany (aquarium)	Egypt	Cameroon	Cameroon	Senegal Ivory Coast	Ivory Coast
Authors	Paperna (Bilong Bilong)	Kulkarni	Gussev & Fernando	Bender	Eid & Negm	Bilong Bilong	Bilong Bilong		
Date	1963	1969	1973	1979	1987	1988	1989		
Dorsal hamuli									
a	11.2	25.8	25.3	9.4		23.1	8.8	12.8	11.4
b	16.7	27.4	43.2	12.6	30.2	33.2	13.7	18.5	16.4
c	18.5	10.6	18.9	23.3	20.3	23.3	14.7	25.9	21.2
d	8.1	15.5	20.5	7.1		15.4	7.7	8.4	7.1
e	5.0	10.6	11.6	3.5		6.4	4.7	5.9	5.5
Ventral hamuli									
a	13.0	16.1	20.5	10.9		17.6	12.1	14.2	15
b	11.3	14.2	12.6	12.6	b + c =	14.1	10.9	12.6	12.8
c	6.4	7.1	8.9	5.6	18.4	9.8	6.0	7.6	6.3
d	5.2	7.7	10.5	4.5		8.9	5.5	5.4	5.7
e	4.1	6.8	9.5	2.5		4.8	3.4	4.5	4.7
Transverse bar	16.5	26.4 16.8	23.2 21.0	17.7	41.2	42.9	16.8	17.9	18.1
Hooklets	12.5	14.2	21.0	10.6	12.8	13.6	12.5	14.5	14.2
Copulatory organ	48.6	65.2	113.7	37.7	60.8	44.3	45.7	50.2	48.6
Spiral	1-2-3	2-2	2-2	4-1-(3 or 4)	(2 or 3)-2-2	3-2-3	4-2-3	4-2-1 + 2	

(1) According to Bilong Bilong (1988).
(2) According to the figures of Gussev & Fernando (1973).
(3) According to the figures of Bender (1979).

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