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Otobothrium cysticum (Cestoda: Trypanorhyncha) from the muscle of butterfishes (Stromateidae)

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Abstract On the basis of the tentacular armature, surface ultrastructure, and morphological measurements of plerocerci obtained from the musculature of butterfishes (Stromateidae), we corroborate an earlier proposal that *Otobothrium crenacolle*, a commonly reported trypanorhynch cestode from the northwestern Atlantic coast, is a junior synonym of *O. cysticum*. This action exemplifies at least an Atlantic Ocean and Indian Ocean distribution for *O. cysticum*. The infection in commercially important butterfishes shows that an otobothriid trypanorhynch may heavily infect fish flesh and influence the market value of some fish species yet also be restricted to the body cavity of other fish intermediate hosts. Infections of *O. cysticum* in the flesh of *Peprilus burti* (Gulf butterfish) and *P. alepidotus* (harvestfish) in the Gulf of Mexico has varied annually since 1970, with samples ranging in prevalence between 20% and 100% and in mean intensity between 1 and 3,500 or more plerocerci per fish. Comparative infections in *P. burti* from the Gulf of Mexico and *P. triacanthus* (butterfish) from the Atlantic Ocean demonstrate a present geographic difference in infections. The prevalence and mean intensity in 4 collections of butterfishes ranged from 9% to 98% of the fish and from 1 to 678 plerocerci in a subsample of tissue, respectively, with prevalent and heavy infections being observed in the Gulf of Mexico fish and relatively few individuals being infected with few worms in the Atlantic fish. A slight host response in the butterfishes involving some fatty infiltration and inflammatory infiltration was associated with the metacestode. In some larger fish, encapsulations were yellow, and in a few cases, worms had degenerated. This finding and an increase in intensity with fish weight suggest a continual accumulation of the worms in association with little host resistance.

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Introduction

Otobothrium crenacolle Linton, 1890 is one of the most abundantly reported trypanorhynch cestodes off the North American Atlantic coast. Since its original description by Linton (1890) from the smooth hammerhead shark, *Sphyrna zygaena*, from Woods Hole, Massachusetts, the plerocerci of this trypanorhynch have been reported from numerous teleosts, elasmobranchs, and a squid, and the adult is reported to infect several elasmobranch hosts (e.g., Linton 1924; Dollfus 1942; Stunkard 1977; Reimer 1984). Linton (1907a, 1910, 1913) directed special attention to the muscle infection of the butterfish, *Peprilus triacanthus* (as *Rhombus triacanthus* and *Poronotus triacanthus*) but included infections from other sites in various other fishes from Woods Hole, the Dry Tortugas, and Bermuda (Linton 1901, 1905, 1907a, b, 1909). Heavy infections affected the market for this food fish because of the unappetizing appearance and presumed poor quality of infested specimens and due to the prejudice against eating wormy meat (Linton 1907a, 1913; Smith and Youngberg 1982).

During recent investigations on trypanorhynch cestode fauna from West African and Brazilian localities, Palm et al. (1994) and Palm (1997a) collected specimens from the mesentery of ten teleost species and identified them as *O. cysticum* (Mayer, 1842) Dollfus, 1942. *O. cysticum* is known only in the larval form and was redescribed from the type host *Chelonia mydas* (green turtle) off the African coast by Dollfus (1942). On the basis of similar scolex and hook morphology, Palm

(1995) proposed in a dissertation that *O. crenacolle* was a junior synonym of *O. cysticum*. However, he did not examine plerocerci of *O. crenacolle* from butterfishes, which Linton considered to be the main intermediate hosts for the species.

The purpose of the present study was to compare plerocerci reported as *O. crenacolle* and *O. cysticum* and to reconsider the synonymy of *O. crenacolle* with *O. cysticum* on the basis of an ultrastructural investigation of muscle-dwelling specimens from butterfishes. Data on the occurrence of *O. cysticum* in butterfishes from different localities in the Gulf of Mexico and the United States Atlantic seaboard are reported, and the meaning of this important flesh parasite for United States fisheries is discussed.

Materials and methods

From February 1970 to May 1998, plerocerci of *Otobothrium cysticum* were collected from stromateid fishes, *Peprilus alepidotus* (harvestfish), *P. burti* (Gulf butterfish), and *P. triacanthus* (butterfish). In the northern Gulf of Mexico, *P. burti* and, in some cases, *P. alepidotus* were caught either from inshore and near-shore (as far as 10 km south of Horn Island) waters in Mississippi in trawls or offshore with trawls and purse seines along the continental shelf and slope by the National Marine Fisheries Service (NMFS) using RV OREGON II or commercial fishing boats conducting butterfish surveys for the NMFS. The latter samples came from various offshore locations throughout the Gulf off the coasts of Florida, Mississippi, and Texas, some locations being at least 145 m deep. Two trawl collections (July 1988, May 1989) were made south of the area between the Mississippi River and Mobile Bay. Fishes from inshore Mississippi waters were maintained alive until examined; those from offshore waters were quick-frozen aboard vessels. Samples of *P. triacanthus* from the New England United States Atlantic coast came from a commercial dealer in Point Judith, Rhode Island, and from a groundfish survey conducted by the NMFS Northeast Fisheries Center, Woods Hole Laboratory, in September 1988. Fish from that survey included grouped samples from an area extending from the Gulf of Maine to Cape Hatteras. Parasite counts for the four NMFS samples represent the number counted in four combined 1-cm^2 sites per fish near the vertebral column, two above and two below. As based on photographs and representative counts in several fish, the number of parasites from the four sites represents about 30% of the total number of worms per fish (therefore, counts can be multiplied by 3.3 for approximate total values). The condition [length-weight relationship expressed as the fork length (FL) in millimeters and the weight (W) in grams: $K = W \times 10^5/FL^3$] of *P. burti* was determined for 18 pairs of heavily and lightly infected fish having nearly identical lengths as well as for 9 pairs of lightly infected and noninfected individuals of *P. triacanthus* from the United States Atlantic coast.

Trypanorhynch specimens isolated from butterfishes were killed in hot water or cold 5% buffered formalin. Paraffin sections were cut to a thickness of 4 μm and then stained in hematoxylin and eosin (H&E). The scolices of eight specimens fixed in Karnovsky's solution were transferred to 0.1 *M* sodium cacodylate (NaCaC) buffer, postfixed in 1% osmium tetroxide for scanning electron microscopy (SEM), transferred to distilled water, and dehydrated in a graded ethanol series. They were then critical-point-dried and mounted with double-sided adhesive tape onto SEM stubs, sputter-coated with gold-palladium in an argon atmosphere, and examined under a Zeiss DSM 940 scanning electron microscope operating at 15 kV.

In addition to morphometric data on specimens obtained from *P. burti* and *P. triacanthus*, those on specimens identified as *O. crenacolle* from the United States National Parasite Collection (USNPC, Beltsville, Md.), namely, USNPC 7695 (adult from *Sphyrna zygaena*, coll. E. Linton) and 35923 (larva from *P. triacanthus*, coll. G.A. MacCallum), were examined for purposes of comparison. The orientation of bothridial surfaces follows that of Richmond and Caira (1991), and the terminology follows that of Palm (1997b). We used the following abbreviations: scolex length, SL; scolex width at the level of the pars bothridialis, SW1; scolex width at the level of the pars bulbosa, SW2; pars bothridialis, pbo; pars vaginalis, pv; pars bulbosa, pb; and appendix, app. Measurements are given in micrometers unless otherwise indicated; ranges are given in parentheses.

▶

Figs. 1–5 Scanning electron micrographs of *Otobothrium cysticum*
Fig. 1 Scolex. *Bar* 50 μm
Fig. 2 External surface of an evaginated tentacle, showing the metabasal armature (*M*) and the basal armature with strongly recurved (*B*) and spiniform (*S*) hooks. Note the relatively large basal hooks on the external surface (*arrow*). *Bar* 10 μm
Fig. 3 External surface of the metabasal armature. *Bar* 2.5 μm
Fig. 4 Antibothridial surface of the metabasal armature. *Bar* 50 μm
Fig. 5 External surface of the basal armature. Note the rows of strongly recurved hooks. *Bar* 50 μm0

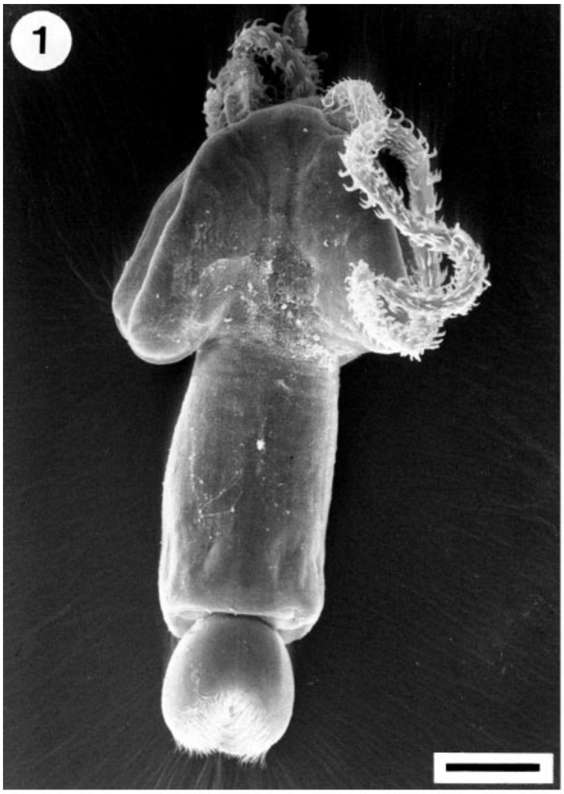
Results

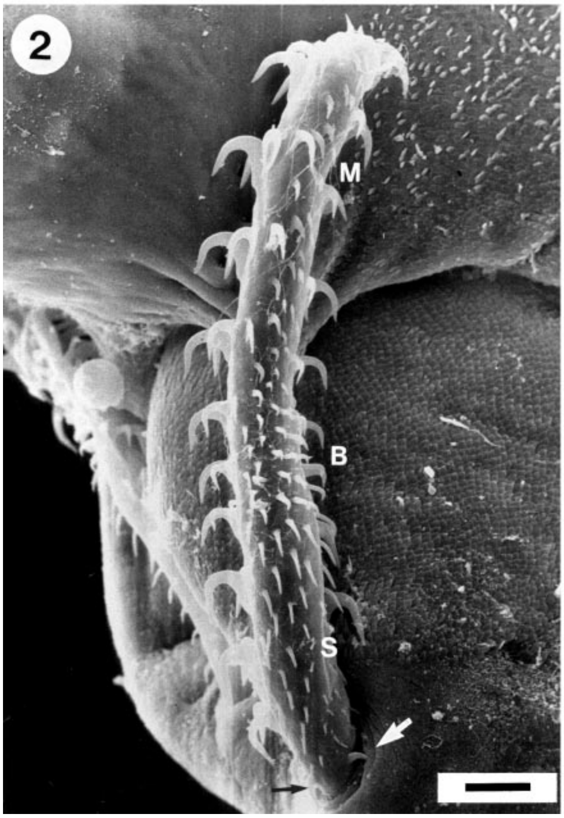
Description

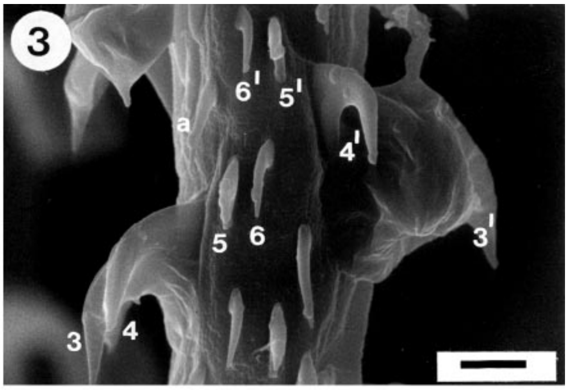
Otobothrium cysticum (Mayer, 1842)

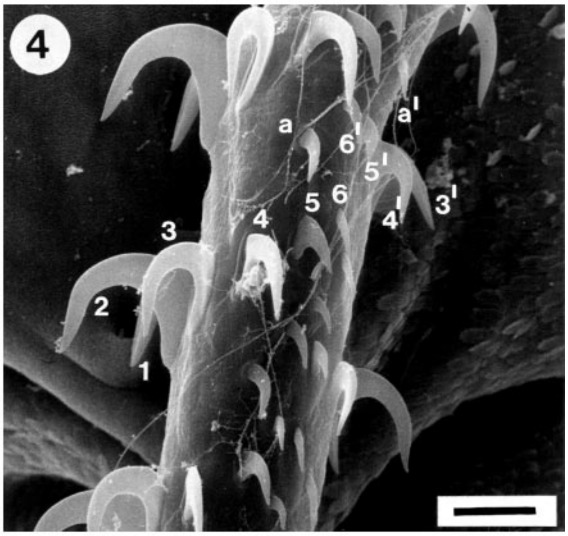
1. Synonyms: *Tetrarhynchus cysticus* Mayer, 1842; *Echinococcus corollatus* Mayer, 1842 (*alterum nomen*); *Tetrarhynchus* sp. Wagener, 1851; *T. uranoscopi scabri* (Wagener, 1851) Diesing, 1863; *T. lychias vadigo* (Wagener, 1854) Diesing, 1863; *Otobothrium crenacolle* Linton, 1890; *Tetrarhynchus* sp. Linton, 1897, in part; *T. crenacolle* (Linton, 1890) Vaullegeard, 1899; *T. testudinis* (Meyer, 1840) Vaullegeard, 1900; *Rhynchobothrium* sp. Linton, 1901; *R. curtum* Linton, 1909; *O. crenacolle* Linton, 1890 [= type species of genus]; *O. curtum* (Linton, 1909) Dollfus, 1942; and *O. cysticum* (Mayer, 1842) Dollfus, 1942 (also see Dollfus 1942; Palm 1995).

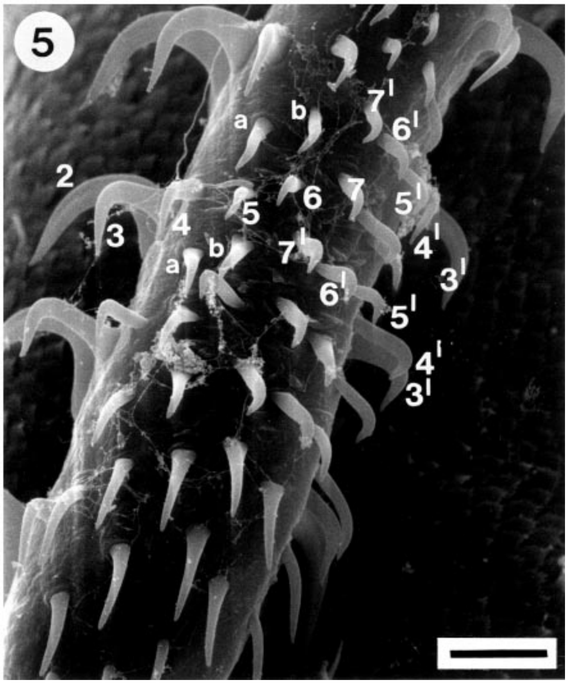
2. Supplemental data (based on eight specimens from *Peprilus burti* and two from *P. triacanthus*): scolex and tentacle features correspond to descriptions by Dollfus (1942), Palm et al. (1994), and Palm (1995) for *O. cysticum*. The SL ($n = 5$) is 478 (415–583), the SW1 ($n = 8$) is 245 (201–291), the SW2 ($n = 6$) at its narrowest is 114 (81–139) and at its widest is 130 (94–161). There are two elongated bothridia, which occupy nearly half the length of the scolex (Fig. 1). The pbo ($n = 8$) is 234 (193–278), with a posterior notch, the bothridial margins are not fused with the scolex peduncle. The pv is variable in size ($n = 5$), measures 408 (316–522) and contains spirally coiled tentacle sheaths. The tentacle bulbs are ovoid and extend to the posterior margin. The bulbular length ($n = 7$) is 77 (74–83), the width ($n = 7$) is 55 (44–65), and the bulb length: width ratio is 1.4:1. The scolex proportions correspond to pbo:pv: pb = 3:5.3:1; the app ($n = 8$) length is 92 (774–114) and the width is 138 (121–165).











The tentacular armature is differentiated into the metabasal and the characteristic basal armature, the latter consisting of two distinct regions (Fig. 2). The metabasal part displays 6 principal hooks ($n = 4$) with a length of 1 (1′) = 7.5–8; 2 (2′) = 7.5–8; 3 (3′) = 7–7.5; 4 (4′) = 3.5–4.8; 5 (5′) = 2.4–3.0; 6 (6′) = 2.0–2.8, alternating with a single intercalary hook (1.7–2.1); the basal length of hooks 1–2 (1′–2′) is 6.7–7.0. On

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the external tentacle surface, the principal hooks, 5–6 (5′–6′), form 2 files of alternating hooks (Fig. 3); internal hooks, 1–4(1′–4′), larger than the external ones [5–6 (5′–6′), and intercalary hooks] (Fig. 4), rose-thorn-shaped along the internal tentacle surface (Fig. 6). The basal armature (Figs. 2, 5) has its upper region arranged in files of 7 principal hooks alternating with 2–3 intercalary hooks. The external tentacle surface displays strongly recurved hooks with a slender shaft (Fig. 7), unlike all other hooks along the tentacle. The basal part of the tentacle at the entrance of the sheath has spine-like hooks (3.4–4.2) with a short base (0.5–1.0). Basal hooks with larger ones are visible on both the external (Fig. 2, arrow) and internal tentacular surfaces; internal hooks of rows 2 and 3 are the largest, with a hook length of 9.7–10.5 and a basal length of 7–7.7.

In all, 4 bothridial pits, whose appearance is sphere-like when they are completely protruded (diameter 22; Fig. 9), occur at the posterior margins of bothridia (Fig. 17) and are capable of protruding far above the bothridial surface (Figs. 8, 9), forming half circles (diameter 15; Fig. 8) during the process of evagination. Protruded pits form a pair of papilla-like structures (Fig. 9) adorned with hook- or spine-like microtriches, measuring approximately 4.0–6.5 in length and 1.0 in width at the base and positioned in pairs.

The scolex surface is covered with 4 kinds of microtriches (palmate, filamentous, hair-like, and cilia-like). The distal bothridial surface is adorned with 3–5 fingered palmate microtriches (Fig. 10); the proximal bothridial surface is densely covered with 5–6 fingered palmate microtriches that are approximately 2 long and 1.2 wide at the base (Fig. 11). The pv is covered with similar, more widely spaced palmate microtriches along most of its length (Fig. 12), with the surface between the palmate microtriches being covered with filamentous microtriches. The posterior pb contains filamentous microtriches only. The app is covered with a field of hair-like microtriches measuring approximately 10 in length and 0.5 in width at the base (Fig. 13), with the anterior portion being distinct and smooth without microtriches.

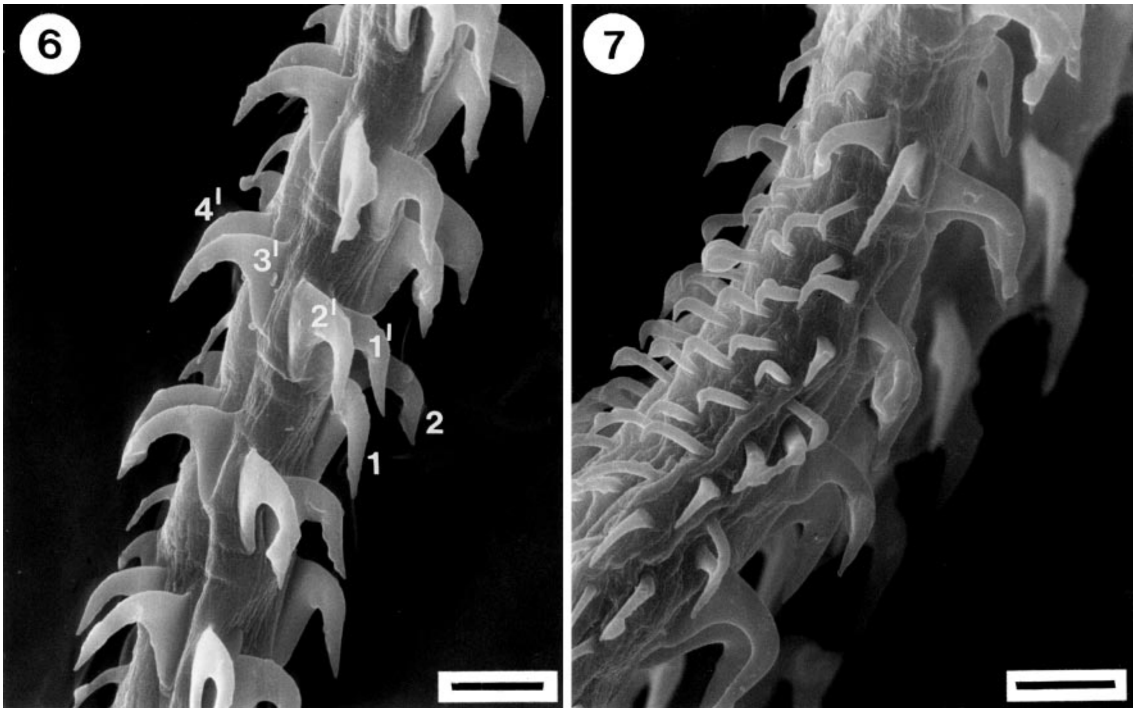
Figs. 8–13 *O. cysticum*
Fig. 8 Partly evagina1ted bothridial pit. *Bar* 2 μm
Fig. 9 Completely evaginated bothridial pits. *Bar* 2 μm
Fig. 10 Three-fingered palmate microtriches on the distal bothridial surface. *Bar* 1 μm
Fig. 11 Six-fingered palmate microtriches on the proximal bothridial surface. *Bar* 1 μm
Fig. 12 Five- to six-fingered palmate and filamentous microtriches on the scolex surface. *Bar* 1 μm
Fig. 13 Microtriches on the posterior end of the appendix. *Bar* 5 μm

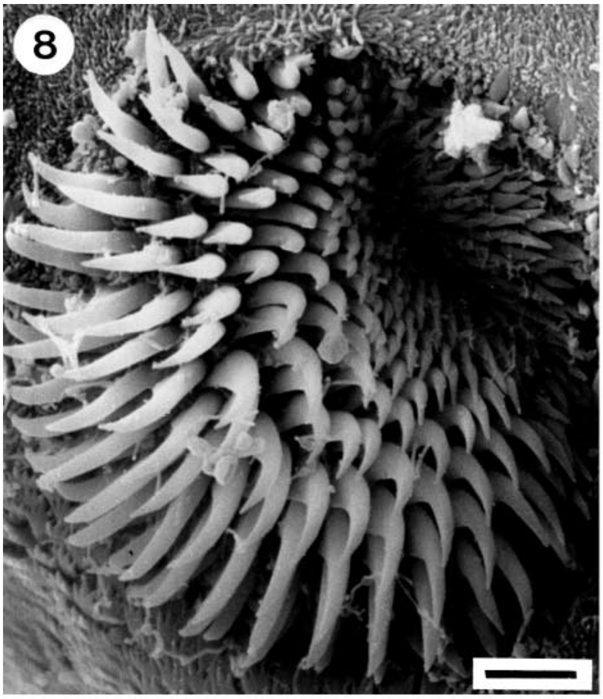
Taxonomic summary

Type host: *Testudo mydas* [= *Chelonia mydas* (Linnaeus, 1758), green turtle] (Cheloniidae) for *Tetrarhynchus cysticus*

1. Plerocerci and host material examined: plerocerci from the musculature of *P. burti* Fowler, 1944 (Gulf of Mexico, off Mississippi), *P. alepidotus* (Linnaeus, 1766) (Gulf of Mexico, off Mississippi, Florida to Texas), and

Figs. 6, 7 *O. cysticum. Bars* 5 μm
Fig. 6 Internal surface of the metabasal armature
Fig. 7 Bothridial surface of the basal armature

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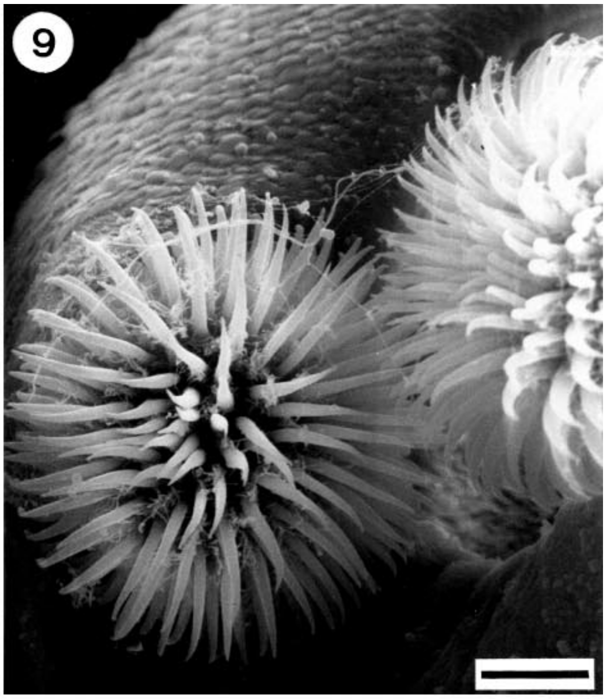
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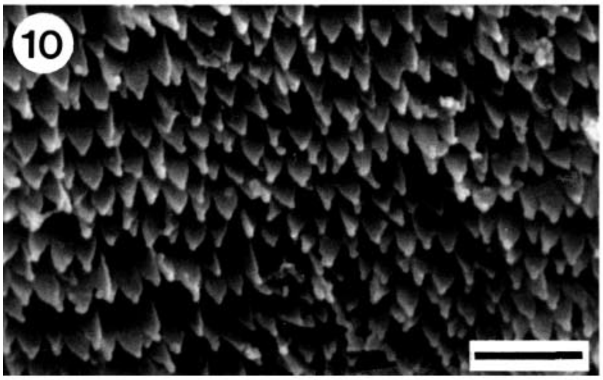
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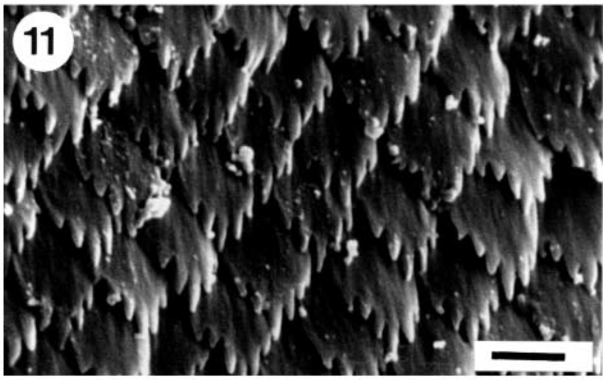
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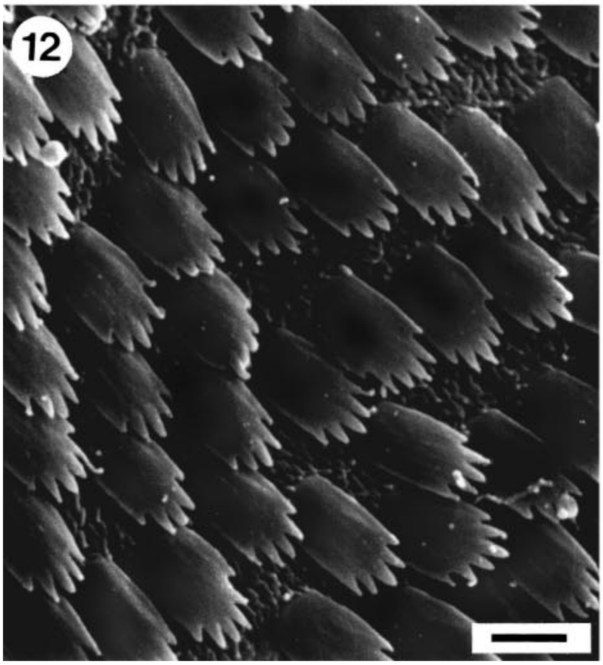
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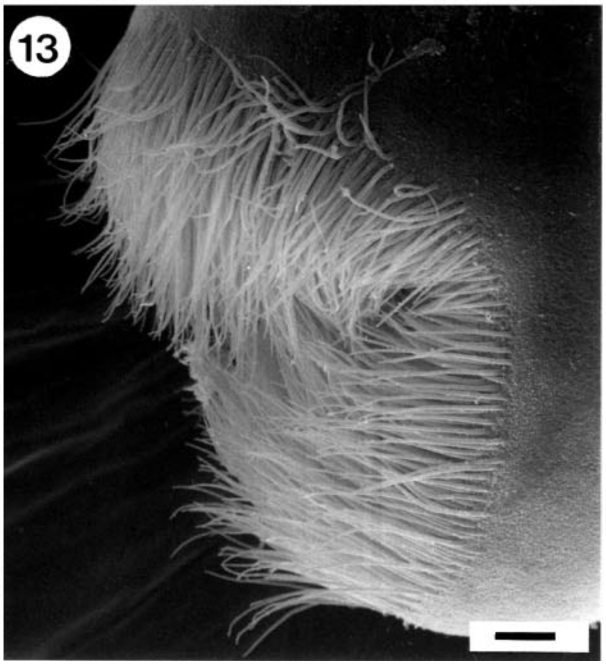
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P. triacanthus (Peck, 1804) (Atlantic Ocean between the Gulf of Maine and Cape Hatteras) (Stromateidae).

2. Additional museum cestode specimens examined: *O. crenacolle*, USNPC 7695 (adult from the spiral valve of *Sphyrna zygaena*, Woods Hole, 7 August 1914, coll. E. Linton) and USNPC 35923 (cysts in the flesh of *Prionotus triacanthus*, 13 May 1915, coll. MacCallum).

3. Other hosts of the plerocercus listed in the literature: if one considers the synonyms of hosts, the plerocercus infects at least 56 fishes, 1 turtle, and 1 squid species as listed by Linton (1924), Dollfus (1942), Rees (1969), Stunkard (1977), Reimer (1984), Palm (1995, 1997a), and Palm et al. (1994).

4. Hosts of the adult stage: *S. zygaena* (Linnaeus, 1758), the smooth hammerhead shark (Sphyrnidae); *Carcharhinus melanopterus* (Quoy and Gaimard, 1824), the blacktip reef shark (as *C. melanopterus*); *C. obscurus* (Lesueur, 1817), the dusky shark; *C. leucas* (Valenciennes, 1841), the bull shark (as *C. platyodon*); *Galeocerdo cuvier* (Peron and Lesueur 1822), the tiger shark (as *G. tigrinus*); *Rhizoprionodon terraenovae* (Richardson, 1836), the Atlantic sharpnose shark (as *R. terrae-novae* and *Scoliodon terrae-novae*) (Carcharhinidae), with all the above-mentioned species being reported from the western North Atlantic Ocean; and *Dasybatis margarita* (Günther, 1870), the daisy stingray (as *D. margar.*) (Dasyatidae), from West Africa (see Dollfus 1942; Palm 1995).

5. Deposited specimens: USNPC 87938, two voucher specimens from the muscle tissue of *P. burti*.

Plerocercus infections

Encapsulated plerocerci of *O. cysticum* (called "cysts" in most of the literature) are chalky white and translucent in most inshore infections and in small fish (Figs. 14, 15). The plerocercus with its holdfast is withdrawn within the receptaculum of the blastocyst. "Blastocyst" defines the posterior bladder-like region (Fig. 16). Calcareous corpuscles are visible within the scolex (Fig. 18). The plerocercus is surrounded by a parasitically derived cyst (Fig. 19, arrow), which is encapsulated by a thin host connective-tissue layer a few cells thick (Fig. 19, arrowhead). Many of the capsules in larger fish from offshore collections had a yellow pigmentation. Some fish also contained necrotic areas encapsulated by a thick layer of connective tissue (Fig. 20) that appeared to be degenerated cestodes or clusters of cestodes.

In all 3 stromateid species infected with up to about 250 plerocerci, most plerocerci occurred close to the vertebral column, immediately above the trunk kidney (Fig. 14). In heavier infections, plerocerci occurred throughout the muscle tissue, but at a higher density near the vertebral column. A few specimens also occurred on the viscera and in the mesentery and submucosa of the alimentary tract, but muscle tissue was the primary site.

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Figs. 14–20 *O. cysticum* from *Peprilus burti*

Fig. 14 Thawed, filleted, infected specimen of *P. burti*

Fig. 15 Moderately high degree of infection with plerocerci in muscle along the vertebral column of *P. burti*

Fig. 16 Plerocercus with blastocyst as visualized under coverslip pressure

Fig. 17 Nonextruded bothridial pit in a live specimen

Fig. 18 Calcareous corpuscles in the scolex

Fig. 19 Histology section (H&E) showing an encapsulated plerocercus, the host capsule (*arrowhead*), the parasite cyst (*arrow*), and the blastocyst (*B*) as well as the associated lipid deposition (*L*) and slight inflammatory response

Fig. 20 Histology section (H&E) of degenerated necrotic specimens

Prevalence and intensity of infections

In the Gulf of Mexico, both *P. burti* and *P. alepidotus* contained plerocerci in their muscle tissue. In inshore and near-shore (10 km south of Horn Island) waters of Mississippi, small individuals of *P. burti* (standard length 46–98 mm, a value slightly lower than the FL) were infected. During the examination of irregularly collected samples of butterfish for parasites since 1970 (sample sizes: $n = 3\text{–}10$) the prevalence of *O. cysticum* ranged from 20% to 100%, with 2–100 individuals being counted per infected fish. Similar samples from offshore localities revealed a prevalence of infection varying from 78% to 100%, with mean intensity values ranging from 4 to about 3500 worms per fish and with median values being about 20 in the most lightly infected sample and about 2000 in the most heavily infected sample.

The condition (K) of the NMFS collections of *P. burti* in the Gulf of Mexico was not affected (as determined by Wilcoxon signed-rank test) by heavy infections (mean $K = 2.30$ versus 2.23 in lightly infected counterparts of 18 pairs). Among the 18 pairs (FL 120–180 mm) of both heavily [mean 446 (341–678) worms per sample, estimated as 30% of the total number of worms per fish] and lightly [mean 14 (0–38) worms per sample] infected fish, each having the same length, 10 fish with heavy infections weighed more than their equal-length counterpart, and the mean weight was slightly but not significantly (88.1 versus 86.0 g) higher for heavily infected ones. When 9 similarly matched pairs of *P. triacanthus* [mean FL 136 mm] (105–166 mm) from the United States Atlantic coast were compared using the Wilcoxon signed-rank test, infected ones [mean 30 (12–70) worms per sample] showed a nonsignificantly lower K value ($K = 2.07$, range 1.42–2.47) than did the noninfected fish ($K = 2.39$, range 1.56–3.08).

There was an obviously patchy distribution of infections among samples (standard length 130–174 mm, slightly longer if presented as the FL). A specimen of the harvestfish (standard length 143 mm) from offshore waters had 20 worms, but 4 smaller specimens (FL 43–51 mm) from inshore Mississippi localities were not infected. The specimens of *P. triacanthus* from Atlantic Ocean collections were lightly infected, with the mean intensity ranging from 6 to <100. No difference in the


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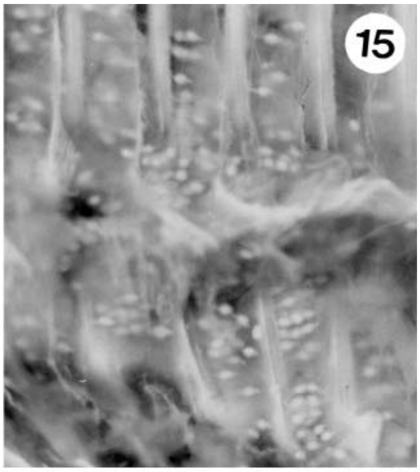
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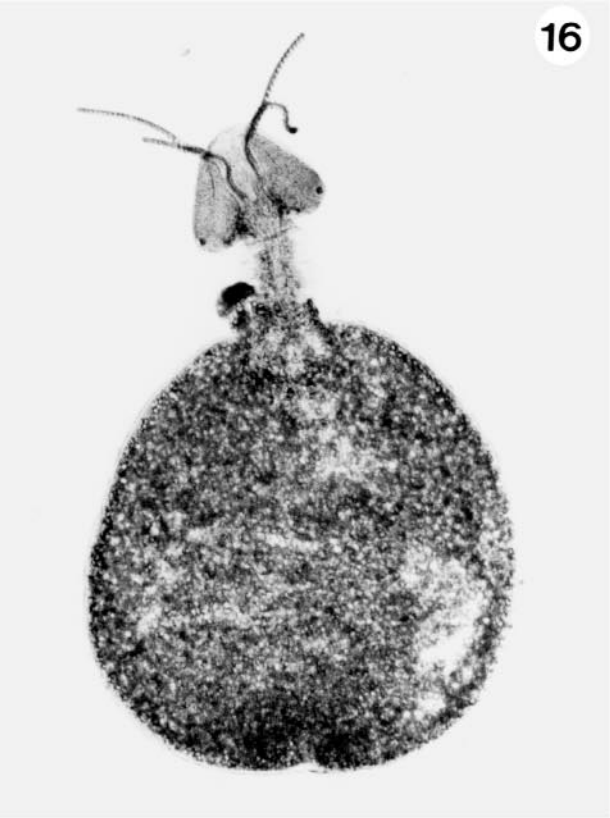
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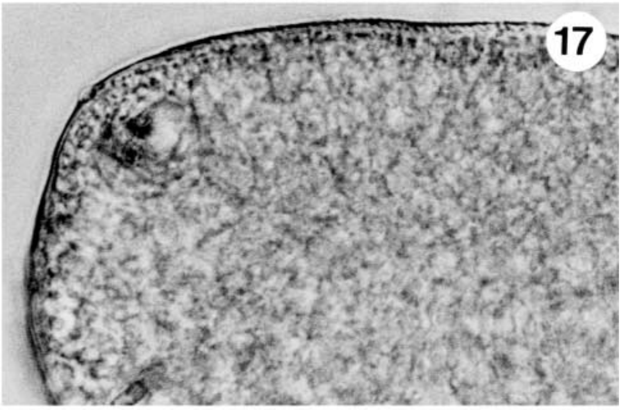
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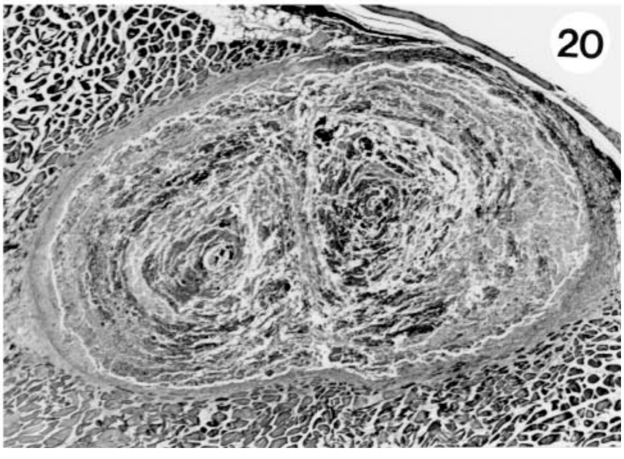
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general appearance of the host-parasite relationship occurred among these infections or between infections in these fish and those in *P. burti* from the Gulf of Mexico.

Data on the 4 major NMFS collections of butterfishes from the Gulf of Mexico and the Atlantic Ocean, totaling 2176 individuals, and their corresponding infections are presented in Table 1. Infections were more prevalent and the mean intensity was greater in *P. burti* from the North-central Gulf of Mexico than in *P. triacanthus* from the western North Atlantic. Differences for the 2-year period occurred in mean intensity in Gulf fish (104 versus 59 worms), where nearly every fish (96.8%) was infected, and the prevalence of infection in the Atlantic fish differed between collections (38% versus 9%). Most dramatically, the difference in levels of infections in the Gulf *P. burti* (mean intensity 76.1 worms in 96.8% of the fish) as compared with the Atlantic *P. triacanthus* (mean intensity 0.8 worms in 16.1% of the fish) indicates the strong geographic difference. The frequency distribution of the intensity of infection in the Gulf butterfish showed an increase in intensity with increasing fish size as measured by weight in 10-g fish groups (Fig. 21). A similar relationship was not evident in the Atlantic butterfish, but the prevalence of infection was higher in larger June 1988 samples of *P. triacanthus* than in the relatively smaller September 1988 samples (Table 1).

Discussion

Taxonomy

Dollfus (1942) described plerocerci from the type host *Chelonia mydas* (green turtle) from the West African coast. His specimens of *Otobothrium cysticum* and those illustrated by Linton (1890, 1907a) as well as Linton's material deposited at the USNPC correspond in terms of scolex morphology and morphometry to those described in the present study (Table 2). The comparison with

Table 1 *Otobothrium cysticum* from *Peprilus burti* and *P. triacanthus* collected by or for the National Marine Fisheries Service, Southeast Fisheries Center, Pascagoula, Mississippi

Collection	*P. burti* in the North-central Gulf of Mexico		*P. triacanthus* in the western North Atlantic	
	July 1988, off area from Mississippi River to Mobile Bay	May 1989, off area from Mississippi River to Mobile Bay	about June 1988, off NE U.S. coast	September 1988, from Gulf of Maine to Cape Hatteras
Number of fish	405	640	273	858
FL in mm, mean (range)	146 (85–189)	133 (33–165)	140 (98–181)	89 (19–180)
Mean weight (range) in g	73.7 ± 1.1 (12–134)	67.9 ± 0.6 (11–119)	62.4 ± 1.9 (15–138)	21.7 ± 0.8 (1–124)
Prevalence of infection in %	95.6	97.7	38.1	9.1
Mean number of plerocerci[a]	104.4 ± 5.7	58.6 ± 3.2	1.1 ± 0.2	0.4 ± 0.1
Range of plerocerci[a]	0–678	0–521	0–32	0–70
Median of plerocerci[a]	65	22	0	0

[a] Values represent subsamples, and the total estimated number of plerocerci per fish is approximately 3.3 times the table value

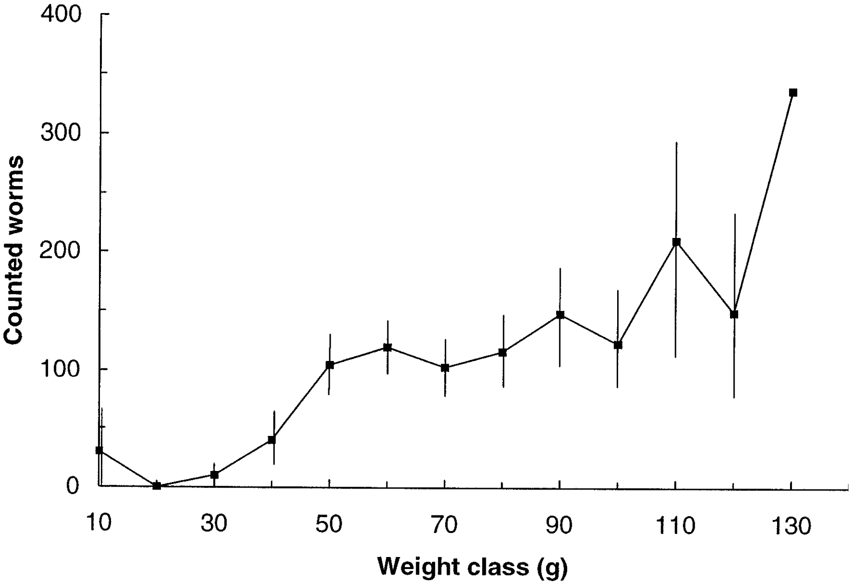

Fig. 21 Counts of *O. cysticum* in samples of *P. burti* caught in the Gulf of Mexico off the Mississippi coast, estimated to be 30% of the total number of worms as a function of the host weight in grams. A total of 384 fish in a July 1988 collection were pooled into 10-g weight groups

Table 2 Morphometric measurements recorded for *O. cysticum* by different authors

Characters	Present study (*O. cysticum*)	Linton (1890) (*O. creanacolle*)	E. Linton (*O. creanacolle*) USNPC 7695	Dollfus (1942) (*O. cysticum*) ex-*Chelonia mydas*	Dollfus (1942) (*O. cysticum*) ex-*C. melanopterus*	Palm et al. (1994b) (*O. cysticum*)/in Palm (1995)	Palm (1995) (*O. cysticum*)
Scolex length	478 (415–583)	320–360	453	452–458	414	375	387
Scolex width (SW 1)	245 (201–291)	300–320	293	178–184	142	–	233
Pars bothridialis	234 (193–278)	170–222	179	194–210	200	150	175
Pars vaginalis	408 (316–522)	–	355	242–259	291	225	286
Bulb length	77 (74–83)	60–100	79 (73–84)	99	66	50	69
Bulb width	55 (44–65)	40–50	40 (38–43)	50	46	–	–
Bulb ratio	1.4:1	1.5–1.6:1	1.4:1	2:1	1.44:1	1.4:1	1.55:1
Scolex proportions	3:5.3:1	2.2, 2.5, 3.6:–:1	2.1:4.2:1	2.1:–:1	3:4.4:1	3:4.5:1	2.5:4.1:1
Appendix	92 (774–114)	–	–	–	–	50	–
Hook length 1 (1́)	7.5–8	7–8 (length of hooks)	7.7–9	–	–	–	6–8
Hook length 2 (2́)	7.5–8		7–7.7	–	–	–	6–7
Hook length 3 (3́)	7–7.5		6.3–7	–	–	–	7–9
Hook length 4 (4́)	3.5–4.8		3.5–4.9	–	–	–	6
Hook length 5 (5́)	2.4–3		1.4–2.4	–	–	–	2–3
Hook length 6 (6́)	2–2.8		1.4–2.4	–	–	–	1–2
Hook length a (á)	1.7–2.1		2.3–3	–	–	–	1–3

material collected by MacCallum (USNPC 35923) provided the same result; the morphometrical data involving the scolex and hooks correspond to those described for the present specimens.

Mayer (1842) and Dollfus (1942) gave no precise description of the tentacular armature of *O. cysticum*; however, their descriptions correspond to the findings recorded during the present study. Both authors reported 8 large, sharply recurved principal hooks, corresponding to hooks 1–4 and 1′–4′ in Fig. 6. The small hooks on the external surface were numerous, according to Mayer (1842), and totaled 8 (4 on each surface) as described by Dollfus (1942). Figure 154 of Dollfus (1942) clearly illustrates the arrangement of the hooks in a single intercalary row, with 1–2 hooks standing between each principal row, similar to the occurrence of 6 principal hooks (4 large and 2 small ones) and 1 intercalary hook in the metabasal part of the tentacle (Figs. 3, 4) and of 2–3 intercalary hooks per row in the upper part of the basal armature (Fig. 5). Additionally, a larger basal hook on the internal surface together with spiniform hooks on the external surface can be seen as shown in Fig. 3d of Palm et al. (1994) and in Figs. 150 and 152 of Palm (1995). Thus, we consider the present specimens from butterfishes to be conspecific with *O. cysticum*.

Linton (1890) described specimens of *O. crenacolle* from the butterfish in the Atlantic Ocean as possessing scolex measurements as well as hook sizes of the tentacular armature (see p. 851, Linton 1890; Table 2) similar to those reported by Dollfus (1942) and by us for *O. cysticum*. For example, the length of larger hooks was reported to be 7–8 by Linton (1890), 6–9 in Figs. 154–155 of Dollfus (1942), and 7–8 in the present study, and the smaller hooks ranged between 3 and 4. The length/width bulb ratio was 1.5–1.6:1 as described by Linton (1890), 1.4–2:1 as reported by Dollfus (1942), 1.4–1.6:1 as described by Palm (1995), and 1.4:1 in the present study, whereas, the values recorded for the pars bothridialis/pars bulbosa were 2.2–3.6, 2.1–3.1, 1.5–2.5, and 3.0, respectively. We found no difference between our material from the Gulf of Mexico and that from the Atlantic Ocean. Thus, we conclude that *O. crenacolle* Linton, 1890 is a junior subjective synonym of *O. cysticum* (Mayer 1842), but *O. crenacolle* Linton, 1890 is still the type species for *Otobothrium* Linton, 1890. Genetics studies could establish how much, if any, material of *O. cysticum* from different oceans differ.

Surface morphology

Richmond and Caira (1991) and Palm (1995) have concluded that microtriches of trypanorhynchs are taxonomically useful. The present study indicates that the microtriches on the scolex of *O. cysticum* show similarities with those of other otobothrioid species as well as with those of members of the Lacistorhynchidae sensu Palm (1997b). In contrast to *O. insigne*, *Poecilancistrium* *caryophyllum*, *Poeciloacanthum oweni*, and *Pseudotobothrium dipsacum* (Palm 1995), all of which bear three-fingered microtriches on the distal bothridial surface and filamentous microtriches on the rest of the scolex, *O. cysticum* has nearly the entire scolex covered with palmate microtriches having more than three fingers. This arrangement is characteristic for representative species in several genera within the Lacistorhynchidae (see Palm 1995). This finding suggests that the formation of microthrix forms and patterns has developed differently within otobothrioid trypanorhynchs. This is not astonishing, since microtriches are multifunctional and, as proposed by Palm et al. (1998), the palmate microtriches with a different number of fingers apparently do not change their general architecture. However, on the basis of the microthrix pattern, *O. cysticum* seems to display more similarities to lacistorhynchid trypanorhynchs than to other congeneric species.

The organ we call a "bothridial pit" was earlier termed a "ciliated pit" or "sensory fossette" by Campbell and Beveridge (1994) and other investigators. We call it a bothridial pit because it is a pocket incorporating structures resembling microtriches rather than cilia, and its actual function remains to be shown. When completely protruded, the structure in *O. cysticum* is either nearly spherical, resembling a tuft of microtriches protruding far above the bothridial surface, or hemispherical, depending on the degree of evagination. This form is different from the typically horseshoe-shaped pits of *O. penetrans* (see Palm et al. 1993) and *P. oweni* (see Palm 1995), both of which are in the superfamily Otobothrioidea Dollfus, 1942, in the sense both of Campbell and Beveridge (1994) and of Palm (1995). However, the posterior location of the pits on the bothridia of all three species is similar, in contrast to the lateral location in other species such as *O. balli* Southwell, 1929 and *O. propecysticum* Dollfus, 1969 (see Shields 1985). Pintner (1934) proposed a relationship between these retractile organs and the bothridial borders ("Sinneskante") of other trypanorhynchs such as *Heterotetrarhynchus institatum* Pintner, 1931 and *Callitetrarhynchus speciosus* (Linton, 1897) (see Fig. 121 in Palm 1995). Similarly, they could be related to sensory papillae resembling "haystacks," which are regularly arranged on the entire bothridial surface of *Bombycirhynchus sphyraenaicum* (Pintner, 1930) (see Palm et al. 1998). Interestingly, the microtriches on the evaginated bothridial pits of *O. cysticum* appear hook- or spine-like (Figs. 8, 9), similar to the hooklets and spine-like microtriches on the bothridial borders and surface of *Nybelinia edwinlintoni* Dollfus, 1960 (see Palm 1997a). However, the real relationships between these bothridial structures cannot be decided at present.

Zoogeography

In the present study, *O. cysticum* includes the synonyms *O. crenacolle* and *O. curtum* Linton 1909, the latter also being considered a synonym by Pintner (1913) and Dollfus (1942). *O. cysticum* is widely distributed along the coasts of the Atlantic (Linton 1905, 1907b, 1909, 1924; Palm 1997a; Palm et al. 1994) and the Indian Ocean (Shipley and Hornell 1906; Reimer 1984). This is not surprising, since its final hosts are widely distributed migrating sharks, including *Carcharhinus* spp. and *Sphyrna* spp., and plerocerci have been found in different species of widely distributed teleost genera such as *Coryphaena*, *Scomberomorus*, and *Sphyraena*. Moreover, several hosts of *O. cysticum* are the same as those described for different species of *Nybelinia* Poche, 1926, to which Palm (1999) and Palm et al. (1997) recently attributed a transoceanic to worldwide zoogeographic distribution.

Together with *C. gracilis* (Rudolphi, 1819), *O. cysticum* appears to be one of the most recorded trypanorhynch species (Palm 1995). These two species have a similarly wide host range in coastal areas together with a narrow host specificity in some restricted localities (Palm et al. 1994; Palm 1997a). Similarly, both species demonstrate a similar site preference, encapsulating on the viscera of many host species. However, *C. gracilis* occurs in the muscle of few host species (Overstreet, unpublished observations), and Palm (1997a) reported only a single accidental musculature infection for *C. gracilis*. In contrast, the musculature is clearly the preferred site of *O. cysticum* in butterfishes. The present study shows that one otobothriid trypanorhynch may heavily infect the flesh of one fish host species but be restricted to the body cavity of other fish intermediate hosts.

Plerocercus infections

The yellowish appearance of the encapsulation around plerocerci in some larger fish may be an indication of worm longevity in the host. Whereas specimens in the fish muscle often have associated yellowish ceroid or other pigmentation, plerocerci discussed by Linton (e.g., 1924) from the viscera of different fish, such as *Trichiurus lepturus*, often demonstrated a blackish or amber melanin-like pigmentation in the capsule. Also, some species of serranids as well as a few lutjanids commonly respond to parasites and other foreign bodies with a fibrotic encapsulation associated with what appears to be ceroid, lipofuscin, and melanin pigmentation (Overstreet and Thulin 1989). Yellowish encapsulations have also occurred in muscle infections of *P. caryophyllum* (Diesing 1850) in spotted seatrout (*Cynoscion nebulosus*) suspected to be at least 2 years old (Overstreet 1977). Specimens older than that became necrotic, similar to the necrotic samples we observed in *P. burti*. However, degeneration of *O. cysticum* in *P. burti* was rare, probably because the host is short-lived (1.5–2.5 years, according to Murphy and Chittenden 1991), at least less so than *P. caryophyllum* in the spotted seatrout (Overstreet 1977).

In the case of the seatrout, the fish appears to develop premunition (concomitant immunity), an immune condition inhibiting further infections as long as a live specimen remains present (Overstreet 1977). Whether infections can build up in butterfishes or whether the infection level becomes established from an initial base infection is not known. However, heavy infections were never seen in young inshore butterfish, even though some contained a few individuals, and the observed increase in numbers of plerocerci with increasing fish weight suggests a continual accumulation of worms in association with little host resistance.

With the exception of prior reports of *O. crenacolle* from butterfishes and a filefish (Linton 1924), this is the first report to show *O. cysticum* from the flesh of its fish host (Palm et al. 1994). Reimer (1984) and Palm et al. (1994), however, encountered another stromateid infection in West Africa involving an unidentified species of *Otobothrium* in the muscle (see Fig. 2K of Obiekezie et al. 1992). As indicated above, individuals of *O. cysticum* are also reported to be common on the viscera, including the mesentery, and in the submucosa of the stomach and intestine of numerous teleost and elasmobranch species. We have not undertaken a concerted effort to identify all small encapsulated metacestodes in the mesentery and on the viscera of fishes in the northern Gulf of Mexico, but many such metacestodes occur.

Prevalence and intensity of infections

There exists variability in infections among butterfishes and, presumably, year-classes. Data from the Gulf of Mexico in Table 1 suggest that infections are much greater in the Gulf than along the United States Atlantic seaboard. This widespread difference may not be real. First, sampling was not conducted over the entire Gulf or along all different areas in the Atlantic where butterfish occur, indicating a potential sampling bias. Second, and more important, historic samples from offshore New England, where we found low levels of infection in 1988, have shown heavy ones during many years in the past. As indicated above, some samples of *P. burti* from the Gulf of Mexico demonstrated fewer than 100 worms per fish, whereas other specimens from different localities and from similar areas during different years displayed considerably heavier infections amounting to a few thousand parasites per fish. Whereas we did not see such high levels in *P. triacanthus* from the western Atlantic Ocean in 1988, Linton (e.g., 1924) noted examples both of high prevalence and of many fish containing heavy infections from 1899 through 1920. In 1911, 86% of the fish were infected, with a heavy infection occurring in 67% of those infected. In 1922, however, only 45% were infected, and they had few plerocerci per fish.

The mean intensity of *O. cysticum* can be high. Whereas we estimated 3500 worms in a heavily infected 174-mm (standard length) Gulf butterfish, Linton (1907a) estimated "several thousands" in some heavily infected Atlantic butterfish. He (1901) reported 40 in a 4-mm^2 piece of tissue and 400 in a single interspinous space (Linton 1907a). Linton (1907a, 1910) explained such heavy infections by a direct life cycle, whereby the butterfish had to have become infected by feeding on a gravid segment filled with embryonated eggs. We, however, assume that a crustacean is required as a first intermediate host. Atlantic butterfish are known to feed on a variety of invertebrates, including amphipods, copepods, and annelids (e.g., Linton 1901; Murawski and Waring 1979). Small crustaceans probably feed on the larvae and become infective to the butterfish, sometimes in large numbers. These crustaceans could be available to infect some stocks of butterfish during a specific period in a specific habitat. The chalky white and translucent appearance of encapsulated specimens in most inshore infections and in small fish as opposed to the yellowish appearance in some larger fish from offshore collections suggests that infections probably originate in shallow waters in young fish. There is a similarly high abundance of *O. cysticum* in commercial inshore fishes from the Cross River Estuary, Nigeria (Palm et al. 1994). The reason for the temporal and spatial differences among infective intermediate hosts is probably related to differences in the abundance of elasmobranch definitive hosts and to natural fluctuations in environmental conditions.

Infections relative to fisheries

Regardless of intensity, the cestode does not appear to have an effect on the condition of Gulf butterfish. Linton (1907a) added up the difference in the weights of 12 pairs of Atlantic *P. triacanthus* with identical lengths, 1 specimen being heavily infected and its counterpart containing few plerocerci. He noted a mean decrease in weight of 4.8% in the heavily infected fish, with each heavily infected member being lighter than its lightly infected counterpart. In our similar calculations involving 18 heavily and lightly infected specimens of *P. burti* from the Gulf of Mexico we did not find the same difference. Indeed, 10 of the fish with heavy infections weighed more than their equal-length counterpart, the mean fish weight (and, therefore, total fish weight) was slightly higher for the heavily infected group, and there was no statistical difference in K. We did not find heavily infected individuals of *P. triacanthus*, but in a comparison of lightly infected versus noninfected counterparts the difference was not significant.

All three stromateid fishes support important fisheries (e.g., Vacchione 1987). At least during the late 1980s the Gulf butterfish drew a lower market value, especially from the Japanese, than did the Atlantic butterfish. The butterfishes have a high value in Japan, but the reported relatively low fat content and recent high intensity of *O. cysticum* in specific Gulf butterfish stocks have generated a lower market acceptability and price for these stocks than for their Atlantic counterparts (C. Gledhill and M. Grace, NMFS, personal communication).

The biology of all three butterfishes is poorly understood, and this lack of knowledge results in inefficient exploitation of their stocks. The Gulf butterfish appears to live for 2.5 years in the North-central Gulf but has been stated to live for only 1.5 years in the northwestern Gulf (Murphy and Chittenden 1991). There appear to be spring and autumn spawning peaks, with marketable stocks being captured from patchy distributions in the relatively deep water on the outer continental shelf (Vacchione 1987). The Gulf species has also been reported along the Atlantic seaboard from Virginia to northeastern Florida (Robins et al. 1986), where they occur along with the similar-appearing Atlantic butterfish (Collette 1963). Murawski and Waring (1979) consider marketable stocks of the Atlantic butterfish in the northwestern Atlantic (from Nova Scotia to the south of Cape Hatteras), which reach a 25 cm FL, to comprise > 3-year-old stocks. The harvestfish occurs in Chesapeake Bay and from the northern Gulf of Mexico to Argentina (Robins et al. 1986) and has been marketed along the Atlantic United States coast and in Japan, with potential existing for further sales (Smith and Youngberg 1982). After 1986 a small fishery directed to both Gulf and Atlantic butterfish for human consumption followed the arrival of New England freezer trawlers. By 1990 the maximal sustainable yield had not been reached, but fishing of 0-year-class fish was not recommended (Gledhill, unpublished 1991 NMFS report). With knowledge about the current prevalence and intensity of *O. cysticum* infections in subsamples from different localities, one may be capable of providing a general biological indicator of stock origin for the stock identification of butterfishes. Consequently, parasite data can be an economically important indicator for seafood dealers or brokers as well as fishery managers.

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References

Campbell RA, Beveridge I (1994) Order Trypanorhyncha Diesing 1863. In: Khalil LF, Jones A, Bray HW (eds) Keys to the cestode parasites of vertebrates. CAB International, Wallingford, pp 50–148

Collette BB (1963) The systematic status of the Gulf of Mexico butterfish, *Poronotus burti* (Fowler). Copeia 1963: 582–583

Dollfus RP (1942) Études critiques sur les Tétrarhynques du Museum de Paris. Arch Mus Nat Hist Nat (Paris) 19: 1–466

Linton E (1890) Notes on Entozoa of marine fishes of New England. 2. Cestodes. Annu Rep US Comm Fish 1887: 718–899

Linton E (1901) Parasites of fishes of the Woods Hole region. Rep US Fish Comm 1899: 405–492

Linton E (1905) Parasites of fishes of Beaufort, N. C. Bull US Fish Comm 24: 321–428

Linton E (1907a) A cestode parasite in the flesh of the butterfish. Bull US Bur Fish 26: 111–132

Linton E (1907b) Notes on parasites of Bermuda fishes. Proc US Nat Mus 33: 85–126

Linton E (1909) Helminth fauna of the Dry Tortugas. I. Cestodes. Carnegie Inst Wash Publ 102: 157–190

Linton E (1910) Notes on the flesh parasites of marine food fishes. Proceedings of the 4th International Fishery Congress, Washington, 1908. Bull US Bur Fish 28: 1195–1209

Linton E (1913) Cestode cysts in the flesh of marine fish and their bearing on food values. Trans Am Fish Soc 42: 119–127

Linton E (1924) Notes on cestode parasites of sharks and skates. Proc US Nat Mus 64: 1–114

Mayer AFJK (1842) Über einen Eingeweidewurm von *Testudo mydas*, *Tetrarhynchus cysticus*. Arch Anat Physiol Wiss Med Berl Jahrg 1842: 213–217

Murawski S, Waring GT (1979) A population assessment of butterfish, *Peprilus triacanthus*, in the northwestern Atlantic Ocean. Trans Am Fish Soc 108: 427–439

Murphy MD, Chittenden ME Jr (1991) Reproduction, age and growth, and movements of the Gulf butterfish *Peprilus burti*. Fish Bull 89: 101–116

Obiekezie AI, Anders K, Lick R, Möller H, Palm HW (1992) External lesions and flesh parasites in commercial fishes of Nigerian inshore waters. Aquat Liv Res 5: 173–183

Overstreet RM (1977) *Poecilancistrium caryophyllum* and other trypanorhynch cestode plerocercoids from the musculature of *Cynoscion nebulosus* and other sciaenid fishes in the Gulf of Mexico. J Parasitol 63: 780–789

Overstreet RM, Thulin J (1989) Response by *Plectropomus leopardus* and other serranid fishes to *Pearsonellum corventum* (Digenea: Sanguinicolidae), including melanomacrophage centres in the heart. Aust J Zool 37: 129–142

Palm HW (1995) Untersuchungen zur Systematik von Rüsselbandwürmern (Cestoda: Trypanorhyncha) aus Atlantischen Fischen. Ber Inst Meereskd Kiel 275: 1–238

Palm HW (1997a) Trypanorhynch cestodes from commercial fishes from North-East Brazilian coastal waters. Mem Inst Oswaldo Cruz 92: 69–79

Palm HW (1997b) An alternative classification of trypanorhynch cestodes considering the tentacular armature as being of minor importance. Syst Parasitol 37: 81–92

Palm HW (1999) *Nybelinia* Poche 1926, *Heteronybelinia* gen. nov. and *Mixonybelinia* gen. nov. (Cestoda: Trypanorhyncha) in the collections of The Natural History Museum, London. Bull Nat Hist Mus Lond (Zool) 65: 133–153

Palm HW, Möller H, Petersen F (1993) *Otobothrium penetrans* (Cestoda; Trypanorhyncha) in the flesh of belonid fish from Philippine waters. Int J Parasitol 23: 749–755

Palm HW, Obiekezie AI, Möller H (1994) Trypanorhynchid cestodes of commercial inshore fishes of the West African coast. Aquat Liv Res 7: 153–164

Palm HW, Walter T, Schwerdtfeger G, Reimer LW (1997) Trypanorhynch cestodes of the genus *Nybelinia* Poche, 1926 from coastal waters off Mozambique with systematic consideration on the genus. S Afr J Mar Sci 18: 273–285

Palm HW, Poynton SL, Rutledge P (1998) Surface ultrastructure of *Bombycirhynchus sphyraenaicum* (Pintner, 1930) (Cestoda: Trypanorhyncha). Parasitol Res 84: 195–204

Pintner T (1913) Vorarbeiten zu einer Monographie der Tetrarhynchoideen. Sitzungsber Oesterr Akad Wiss Math Naturwiss Kl 122: 171–253

Pintner T (1934) Bruchstücke zur Kenntnis der Rüsselbandwuermer. Zool Jahrb Abt Anat Ontog Tiere 58: 1–20

Rees G (1969) Cestodes from Bermuda fishes and an account of *Acompsocephalum tortum* (Linton 1905) gen. nov. from the lizard fish *Synodus intermedius* (Agassiz). Parasitology 59: 519–548

Reimer LW (1984) Investigations of shallow and deepwater prawns and fishes on parasites and a short note on biomass of plankton of the coast of the P.R. of Mozambique. Fisch Forsch Wiss Schriftenr 22: 27–35

Richmond C, Caira JN (1991) Morphological investigations into *Floriceps minacanthus* (Trypanorhyncha: Lacistorhynchidae) with analysis of the systematic utility of scolex microtriches. Syst Parasitol 19: 25–32

Robins RC, Ray GC, Douglass J, Freund R (1986) A field guide to Atlantic coast fishes of North America, the Peterson Field Guide Series. Houghton-Mifflin, Boston

Shields JD (1985) Surface morphology and description of *Otobothrium kursi* new species (Cestoda: Trypanorhyncha) from a hammerhead shark, *Sphyrna lewini*. Int J Parasitol 15: 635–643

Shipley AE, Hornell FLS (1906) Report on the cestode and nematode parasites from the marine fishes of Ceylon. Rep Gov Ceylon Pearl Oyster Fish Gulf Mannaar R Soc Lond 5: 43–96

Smith ME, Youngberg P (1982) The gateway to oriental markets for Gulf and South Atlantic fishery products. US Dept Commerce NOAA Nat Mar Fish Serv 1982: 1–62

Stunkard HW (1977) Studies on tetraphyllidean and tetrarhynchidean metacestodes from squids taken on the New England coast. Biol Bull 153: 387–412

Vacchione M (1987) Commercial fishing for Gulf butterfish, *Peprilus burti*, in the Gulf of Mexico. Mar Fish Rev 49: 14–22