

# Neotropical Monogenoidea. 41: New and previously described species of Dactylogyridae (Platyhelminthes) from the gills of marine and freshwater perciform fishes (Teleostei) with proposal of a new genus and a hypothesis on phylogeny

**Delane C. KRITSKY**

Department of Health and Nutrition Sciences, College of Health Professions,  
Campus Box 8090, Idaho State University, Pocatello, Idaho 83209 (USA)  
kritdela@isu.edu

**Walter A. BOEGER**

Department of Biological Sciences,  
Campus Box 8007, Idaho State University, Pocatello, Idaho 83209 (USA)  
Departamento de Zoologia, Universidade Federal do Paraná,  
Caixa Postal 19073, Curitiba, Paraná, 81530 (Brazil)  
Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq)  
wboeger@bio.ufpr.br

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## ABSTRACT

*Euryhaliotrema* n. gen. (Dactylogyridae) is proposed for species having a bulbous base of the copulatory organ. The following are described from the gills of marine and freshwater teleosts of Brazil, Peru, Venezuela and/or Mexico: *Euryhaliotrema chaoi* n. gen, n. sp. (type species), *E. lovejoyi* n. gen, n. sp., *E. potamocetes* n. gen, n. sp., *E. thatcheri* n. gen, n. sp., *E. monacanthus* n. gen, n. sp., and *E. succedaneus* n. gen, n. sp. from *Plagioscion squamosissimus* and *Plagioscion* sp. (Sciaenidae); *E. atlantica* n. gen, n. sp. from *Paralanchurus brasiliensis* (Sciaenidae); and *E. sagmatum* n. gen., n. sp. from *Umbrina xanti* (Sciaenidae). *Euryhaliotrema carbunculus* n. comb. (syn. *Pseudohaliotrema carbunculus* Hargis, 1955) from *Lagodon rhomboides* (Sparidae); *E. bychowskyi* n. comb. (syn. *Haliotrema bychowskyi* Obodnikova, 1976) from *Hapalogenys mucronatus* (Haemulidae); *E. paralanchuri* n. comb. (syn. *Pseudohaliotrema paralanchuri* Luque & Iannacone, 1989) from *Paralanchurus peruanus* (Sciaenidae); and *E. chrysotaeniae* n. comb. (syn. *Haliotrema chrysotaeniae* Young, 1968), *E. fastigatum* n. comb. (syn. *Haliotrema fastigatum* Zhukov, 1976), *E. johni* n. comb. (syn. *Haliotrema johni* [Tripathi, 1959] Young, 1968), *E. longibaculum* n. comb. (syn. *Haliotrema longibaculum* Zhukov, 1976), *E. lutiani* n. comb. (syn. *Haliotrema lutiani* Yamaguti, 1953), *E. para-*

## KEY WORDS

Platyhelminthes,  
Monogenoidea,  
Dactylogyridae,  
*Euryhaliotrema* n. gen.,  
Sciaenidae,  
Lutjanidae,  
Haemulidae,  
Sparidae,  
phylogeny,  
new genus,  
new species.

*canthi* n. comb. (syn. *Haliotrema paracanthi* Zhukov, 1976), *E. torquecirrus* n. comb. (syn. *Haliotrema torquecirrus* Zhukov, 1976), and *E. tubocirrus* n. comb. (syn. *Haliotrema tubocirrus* Zhukov, 1976) all from species of Lutjanidae are proposed. Phylogenetic analysis of 14 species of *Euryhaliotrema* spp. indicates that the genus had a marine origin and that the freshwater species of *Euryhaliotrema* n. gen form a monophyletic clade.

## RÉSUMÉ

*Monogenoidea néotropicaux. 41 : Espèces nouvelles et précédemment décrites de Dactylogyridae (Plathelminthes) des branchies de poissons perciformes (Téléostéens) marins ou d'eau douce, proposition d'un nouveau genre et hypothèse sur la phylogénie.*

Le genre *Euryhaliotrema* n. gen. est proposé pour des espèces qui ont un organe copulateur avec base bulbeuse. Les espèces suivantes, parasites des branchies de téléostéens marins ou d'eau douce du Brésil, du Pérou, Vénézuéla et/ou Mexique sont décrits : *Euryhaliotrema chaoi* n. gen., n. sp. (espèce-type), *E. lovejoyi* n. gen., n. sp., *E. potamocetes* n. gen., n. sp., *E. thatcheri* n. gen., n. sp., *E. monacanthus* n. gen., n. sp. et *E. succedaneus* n. gen., n. sp., parasites de *Plagioscion squamosissimus* et *Plagioscion* sp. (Sciaenidae), *E. atlantica* n. gen., n. sp. de *Paralanchurus brasiliensis* (Sciaenidae) et *E. sagmatum* n. gen., n. sp. de *Umbrina xanti* (Sciaenidae). Des combinaisons nouvelles sont proposées, pour *Euryhaliotrema carbunculus* n. comb. (syn. *Pseudohaliotrema carbunculus* Hargis, 1955) parasite de *Lagodon rhomboides* (Sparidae) ; *E. bychowskyi* n. comb. (syn. *Haliotrema bychowskyi* Obodnikova, 1976) de *Hapalogenys mucronatus* (Haemulidae) ; *E. paralonchuri* n. comb. (syn. *Pseudohaliotrema paralonchuri* Luque & Iannacone, 1989) de *Paralanchurus peruanus* (Sciaenidae) ; et les parasites de Lutjanidae *E. chrysotaeniae* n. comb. (syn. *Haliotrema chrysotaeniae* Young, 1968), *E. fastigatum* n. comb. (syn. *Haliotrema fastigatum* Zhukov, 1976), *E. johni* n. comb. (syn. *Haliotrema johinii* [Tripathi, 1959] Young, 1968), *E. longibaculum* n. comb. (syn. *Haliotrema longibaculum* Zhukov, 1976), *E. lutiani* n. comb. (syn. *Haliotrema lutiani* Yamaguti, 1953), *E. paracanthi* n. comb. (syn. *Haliotrema paracanthi* Zhukov, 1976), *E. torquecirrus* n. comb. (syn. *Haliotrema torquecirrus* Zhukov, 1976) et *E. tubocirrus* n. comb. (syn. *Haliotrema tubocirrus* Zhukov, 1976). Une analyse phylogénétique de 14 espèces d'*Euryhaliotrema* spp. indique que le genre a une origine marine et que les espèces d'eau douce d'*Euryhaliotrema* n. gen. forment un monophylum.

## MOTS CLÉS

Plathelminthes,  
Monogenoidea,  
Dactylogyridae,  
*Euryhaliotrema* n. gen.,  
Sciaenidae,  
Lutjanidae,  
Haemulidae,  
Sparidae,  
phylogénie,  
nouveau genre,  
nouvelles espèces.

## INTRODUCTION

The freshwaters of the Neotropics maintain disproportionately high numbers of animal species that originated comparatively recently from marine environments. Although total diversity of the Monogenoidea is poorly known in South America, marine-derived species in this group of flatworms are already well represented in the

Neotropics. Mayes *et al.* (1981) described *Potamotrygonocotyle tsalickisi* Mayes, Brooks & Thorsen, 1981 (Monocotylidae Taschenberg, 1879) and *Paraheteronchocotyle amazonensis* Mayes, Brooks & Thorsen, 1981 (Hexabothriidae Price, 1942) from freshwater stingrays (Potamotrygonidae) in northwestern Brazil. Kritsky & Thatcher (1984) described five new species of *Diplectanum* Diesing, 1858 (Diplec-

tanidae Bychowsky, 1957) from South American freshwater croakers, *Plagioscion* spp. (Sciaenidae), in Brazil; and Nasir (1983) reported *Cycloplectanum americanum* (Price, 1937) (syn. *Pseudorhabdosynochus americanum* [Price, 1937] Kritsky & Beverley-Burton, 1986) (Diplectanidae) from a freshwater characid and cyprinodontid in Venezuela. Kohn *et al.* (2000) described *Paranaella luquei* (Microcotylidae Taschenberg, 1879) from the freshwater catfishes, *Hypostomus* sp., *H. regani* (Ihering, 1905) and *Rhinelepis aspera* Spix & Agassiz, 1829 (all Loricariidae) in southern Brazil. Finally, new species of *Euryhaliotrema* n. gen. (Dactylogyridae Bychowsky, 1933) are described from South American freshwater croakers in the present study. Members of the Monocotylidae, Hexabothriidae, Diplectanidae and Microcotylidae are typically marine, while the phylogenetic analysis presented herein indicates that *Euryhaliotrema* also had its origin within the marine environment.

## MATERIALS AND METHODS

Fish hosts were collected by hook-and-line, net or purchased at local fish markets in Brazil, Peru, Venezuela and Mexico during 1978-1999. Host gills were removed and placed in vials containing a 1:4000 formalin solution. After approximately half an hour, the vials were vigorously shaken and the formalin solution raised to 3% for fixation. Some helminths were mounted unstained in Gray and Wess' medium or Hoyer medium for study of sclerotized structures. Other specimens were stained with Mayer's carmalum or Gomori's trichrome to determine internal features. Illustrations were prepared with the aid of a camera lucida or microprojector. Measurements, all in micrometers, were made according to the procedures of Mizelle & Klucka (1953) except that those of the coiled copulatory organ include the diameter of the proximal ring and an approximation of total length obtained by using a Minerva curvimeter on camera lucida drawings; direction of the coil (clockwise *vs* counterclockwise) of the

copulatory organ was determined using the procedure suggested by Kritsky *et al.* (1985). Dimensions of organs and other structures represent the greatest measurement in dorsoventral view; lengths of curved or bent structures (anchors, bars, accessory piece) represent straight-line distances between extreme ends; the hook measurement represents the total hook length; the body width is that of the greatest width of the trunk (excluding haptor). The average measurement is followed by the range and the number (n) of specimens measured in parentheses. Numbering (distribution) of hook pairs follows that recommended by Mizelle (1936; see Mizelle & Price 1963). Type specimens are deposited in the collections of the Instituto Nacional de Pesquisas da Amazônia (INPA), Manaus, Amazonas, Brazil; the US National Parasite Collection (USNPC), Beltsville, Maryland, USA; the University of Nebraska State Museum (HWML), Lincoln, Nebraska, USA; the Muséum national d'Histoire naturelle (MNHN), Paris, France; and the Colección Nacional de Helmintos (CNHE), Universidad Nacional Autónoma de México, Mexico City, Mexico, as indicated in the respective descriptions. In addition, the following museum specimens were examined: four paratypes, *Haliotrema bychowskyi* Obodnikova, 1976 (Zoological Institute of the Russian Academy of Sciences [ZIAC 2938, 2945], Saint Petersburg, Russia); two paratypes, *Haliotrema calcaris* Bychowsky & Nagibina, 1971 (ZIAC 2815); holotype, paratype, *Haliotrema chrysotaeniae* Young, 1968 (USNPC 61274, 61275); four voucher specimens, *Haliotrema cornigerum* Zhukov, 1976 (USNPC 91427, 91429, 91430); four paratypes, *Haliotrema cromileptis* Young, 1968 (USNPC 61277); four voucher specimens, *Haliotrema johnei* (Tripathi, 1959) Young, 1968 (USNPC 61272, 61273); two voucher specimens, *Haliotrema longibaculum* Zhukov, 1976 (USNPC 91427, 91428); three paratypes, *Haliotrema longitubocirrus* Bychowsky & Nagibina, 1971 (ZIAC 3012); holotype, five paratypes, *Haliotrema lutiani* Yamaguti, 1953 (Meguro Parasitological Museum [MPM 22640], Tokyo, Japan); two

paratypes, *Haliotrema noncalcaris* Bychowsky & Nagibina, 1971 (ZIAC 2813); paratype, *Haliotrema patellacirrus* Bychowsky & Nagibina, 1971 (ZIAC 3007); three voucher specimens, *Haliotrema torquescirrus* Zhukov, 1976 (USNPC 91432); two voucher specimens, *Haliotrema tubocirrus* Zhukov, 1976 (USNPC 91431); two voucher specimens, *Haliotrema* sp. (unidentified from Zhukov's collection) (USNPC 91433); holotype, *Pseudohaliotrema brevis* Mizelle & Price, 1964 (USNPC 60016); holotype, *Pseudohaliotrema canescens* Mizelle & Price, 1964 (USNPC 60015); holotype, eight paratypes, *Pseudohaliotrema carbunculus* Hargis, 1955 (USNPC 49340, 49341); holotype, nine paratypes, *Pseudohaliotrema fusiforme* Yamaguti, 1953 (MPM 22838, 22839); holotype, seven paratypes, *Pseudohaliotrema mugilinus* Hargis, 1955 (USNPC 49342, 49343); two paratypes, *Pseudohaliotrema paralonchuri* Lugue & Iannacone, 1989 (USNPC 81341); three voucher specimens, *Pseudohaliotrema platycephali* (Yin & Sproston, 1948) Young, 1968 (USNPC 60875, 60876); holotype, several paratypes, *Pseudohaliotrema sigani* Yamaguti, 1953 (MPM 22837); holotype, *Pseudohaliotrema sphincteropus* Yamaguti, 1953 (MPM 22838); two voucher specimens, *Pseudohaliotrema thysanophrydis* (Yamaguti, 1937) Young, 1968 (USNPC 60874); holotype, *Pseudohaliotrema zancus* Mizelle & Price, 1964 (USNPC 60018); and two voucher specimens, *Tetrancistrum fusiforme* (Yamaguti, 1953) Young, 1967 (USNPC 81296).

Eighteen transformation series, representing 38 character states, were used in determining the phylogenetic relationships of *Euryhaliotrema* n. gen. Ingroup taxa included only those (14) species of *Euryhaliotrema* n. gen. for which we had specimens of sufficient quality to determine character states; five species of *Euryhaliotrema* n. gen., originally described by Zhukov (1976) in *Haliotrema* Johnston & Tiegs, 1922, were not included in the analysis. An initial hypothesis on the evolutionary relationships of *Euryhaliotrema* spp. was constructed using Hennigian argumentation (Hennig 1966; Wiley 1981); the topology of the clado-

gram was then subjected to PAUP\* (Phylogenetic Analysis Using Parsimony), Version 4.0b8 for 32-bit Microsoft Windows (Swofford 2001), to confirm that it was a most-parsimonious tree. Polarization of homologous series was determined by outgroup and functional outgroup analyses (Watrous & Wheeler 1981; Maddison *et al.* 1984). *Ligophorus* Euzet & Suriano, 1977, and an apparent monophyletic group of *Haliotrema* species occurring on species of Lutjanidae and Sparidae and which included *Haliotrema calcaris*, *Haliotrema cornigerum*, *Haliotrema gracilihamus* Zhukov, 1976, *Haliotrema heteracantha* Zhukov, 1976, *Haliotrema longihamus* Zhukov, 1976, *Haliotrema longitubocirrus*, *Haliotrema magnigastrohamus* Zhukov, 1976, *Haliotrema mediohamus* Zhukov, 1983, *Haliotrema noncalcaris*, *Haliotrema parvicirrus* Zhukov, 1983, and *Haliotrema patellacirrus* were used as outgroups. All binary homologous series were considered ordered; multistates series were considered unordered. Bootstrap support for the respective nodes (replicates = 1000) was determined using MAXTREE = 100 and was considered supportive when  $\geq 50\%$ ; the tree presented from strict consensus analysis is intended as a measure of support for respective clades and should not be construed to be an evolutionary hypothesis for the dactylogryids.

## SYSTEMATICS

Subclass POLYONCHOINEA Bychowsky, 1937  
Order DACTYLOGYRIDEA Bychowsky, 1937  
Family DACTYLOGYRIDAE Bychowsky, 1933

### Genus *Euryhaliotrema* n. gen.

TYPE SPECIES. — *Euryhaliotrema chaoi* n. gen., n. sp. from *Plagioscion* sp. and *P. squamosissimus* (Heckel, 1840) (Sciaenidae).

SPECIES INCLUDED. — *Euryhaliotrema atlantica* n. gen., n. sp. from *Paralonchurus brasiliensis* (Steindachner, 1875) (Sciaenidae); *Euryhaliotrema bychowskyi* (Obodnikova, 1976) n. comb. from *Hapalogenys mucronatus* (Eydoux & Souleyet, 1850) (Haemulidae); *Euryhaliotrema carbunculus* (Hargis, 1955) n. comb.

from *Lagodon rhomboides* (Linnaeus, 1766) (Sparidae); *Euryhaliotrema chrysotaeniae* (Young, 1968) n. comb. from *Lutjanus carponotatus* (Richardson, 1842) (senior synonym of *Lutjanus chrysotaenia* [Bleeker, 1851]) (Lutjanidae); *Euryhaliotrema fastigatum* (Zhukov, 1976) n. comb.\* from *Lutjanus apodus* (Walbaum, 1792) and *Lutjanus jocu* (Bloch & Schneider, 1801) (Lutjanidae); *Euryhaliotrema johni* (Tripathi, 1959) n. comb. from *Lutjanus johnii* (Bloch, 1792) and *Lutjanus fulviflammus* (Forsskål, 1775) (Lutjanidae); *Euryhaliotrema longibaculum* (Zhukov, 1976) n. comb. from *Lutjanus mahogoni* (Cuvier, 1828) and *Lutjanus synagris* (Linnaeus, 1758) (Lutjanidae); *Euryhaliotrema lovejoyi* n. gen., n. sp. from *Plagioscion squamosissimus* and *Plagioscion* sp. (Sciaenidae); *Euryhaliotrema lutiani* (Yamaguti, 1953) n. comb. from *Lutjanus* sp. (Lutjanidae); *Euryhaliotrema monacanthus* n. gen., n. sp. from *Plagioscion squamosissimus* and *Plagioscion* sp. (Sciaenidae); *Euryhaliotrema paracanthi* (Zhukov, 1976) n. comb.\* from *Lutjanus apodus* (Lutjanidae); *Euryhaliotrema paralonchuri* (Lugue & Iannacone, 1989) n. comb. from *Paralonchurus peruanus* (Steindachner, 1875) (Sciaenidae); *Euryhaliotrema potamoctes* n. gen., n. sp. from *Plagioscion squamosissimus* and *Plagioscion* sp. (Sciaenidae); *Euryhaliotrema sagma-tum* n. gen., n. sp. from *Umbrina xanti* Gill, 1862 (Sciaenidae); *Euryhaliotrema succedaneus* n. gen., n. sp. from *Plagioscion squamosissimus* and *Plagioscion* sp. (Sciaenidae); *Euryhaliotrema thatcheri* n. gen., n. sp. from *Plagioscion squamosissimus* and *Plagioscion* sp. (Sciaenidae); *Euryhaliotrema torquecirrus* (Zhukov, 1976) n. comb. from *Lutjanus synagris* and *Ocyurus chrysurus* (Bloch, 1791) (Lutjanidae); *Euryhaliotrema tubocirrus* (Zhukov, 1976) n. comb. from *Lutjanus analis* (Cuvier, 1828), *L. apodus*, *Lutjanus cyanopterus* (Cuvier, 1828), *L. synagris* and *Rhomboplites aurorubens* (Cuvier, 1829) (Lutjanidae). Species identified by an asterisk are transferred to *Euryhaliotrema* n. gen. without benefit of the present authors' examination of type or voucher specimens.

**ETYMOLOGY.** — The generic name is from Greek (*eury* = wide, broad + *halilo* = sea, salt) appended to the commonly used ending *-trema*. The name refers to the broad saline conditions (freshwater to marine) in which members of the genus occur.

**DIAGNOSIS.** — Body fusiform or flattened dorsoventrally, comprising cephalic region, trunk, peduncle, haptor. Tegument smooth. Two terminal, two bilateral cephalic lobes; three pairs of bilateral head organs; cephalic glands unicellular, lateral or posterolateral to pharynx. Eyes 4; granules small, ovate. Mouth subterminal, midventral; pharynx comprising muscular, glandular bulb; esophagus short; intestinal caeca 2, confluent posterior to gonads, lacking diverticula. Common genital pore midventral near level of intestinal bifurcation. Gonads intercecal, tandem or slightly overlapping; germarium pretesticular. Vas deferens looping left intestinal cecum; seminal vesicle a simple

dilation of vas deferens; one or two prostatic reservoirs. Copulatory complex comprising tubular copulatory organ coiled or meandering, accessory piece; base of copulatory organ expanded to form bulb. Accessory piece serving as guide for distal portion of copulatory organ, with or without articulation process attached to base of copulatory organ. Seminal receptacle pregermarial; vaginal aperture dextral, marginal or submarginal; vagina sclerotized. Vitellaria in trunk, absent from regions of other reproductive organs. Haptor globose, with dorsal, ventral anchor/bar complexes (one species lacking dorsal complex), seven pairs of similar hooks. Hook distribution as described by Mizelle (1936); hook with upright acute thumb, slender shank comprised of one subunit. Bars straight to V-shaped. Parasites of gills of marine and freshwater teleosts.

#### REMARKS

*Euryhaliotrema* n. gen. is distinguished by one synapomorphy (bulbous base on the copulatory organ) and is further diagnosed by dactylogyrids with the combined presence of: 1) tandem or slightly overlapping gonads (germarium pretesticular); 2) the vas deferens looping the left intestinal cecum; 3) the copulatory complex comprising a coiled or meandering tubular copulatory organ and an accessory piece; 4) a dextral (marginal or submarginal) vaginal aperture; 5) ventral and dorsal anchor/bar complexes (dorsal complex absent in *E. monacanthus* n. gen., n. sp.); and 6) 14 hooks, each with an upright acute thumb and a slender shank composed on one subunit. The new genus includes seven new species and 12 species previously included in *Haliotrema* or *Pseudohaliotrema* Yamaguti, 1953. Presence of a bulbous base of the copulatory organ distinguishes *Euryhaliotrema* n. gen. from these latter genera.

#### *Euryhaliotrema chaoi* n. sp.

(Fig. 1)

**TYPE SPECIMENS.** — Holotype (INPA 401); 23 paratypes (INPA 402a-k, USNPC 91369, 91370, 91371, HWML 16423, MNHN 21HG Tg 143-144).

**ETYMOLOGY.** — This species is named for Dr L. N. Chao, INPA, Manaus, Amazonas, Brazil, who provided specimens of *Plagioscion* sp. and in recognition of his research on sciaenid and other Neotropical fishes.

**TYPE HOST AND LOCALITY.** — Gills of *Plagioscion* sp. (Sciaenidae): Igarapé Zamula, Rio Negro near

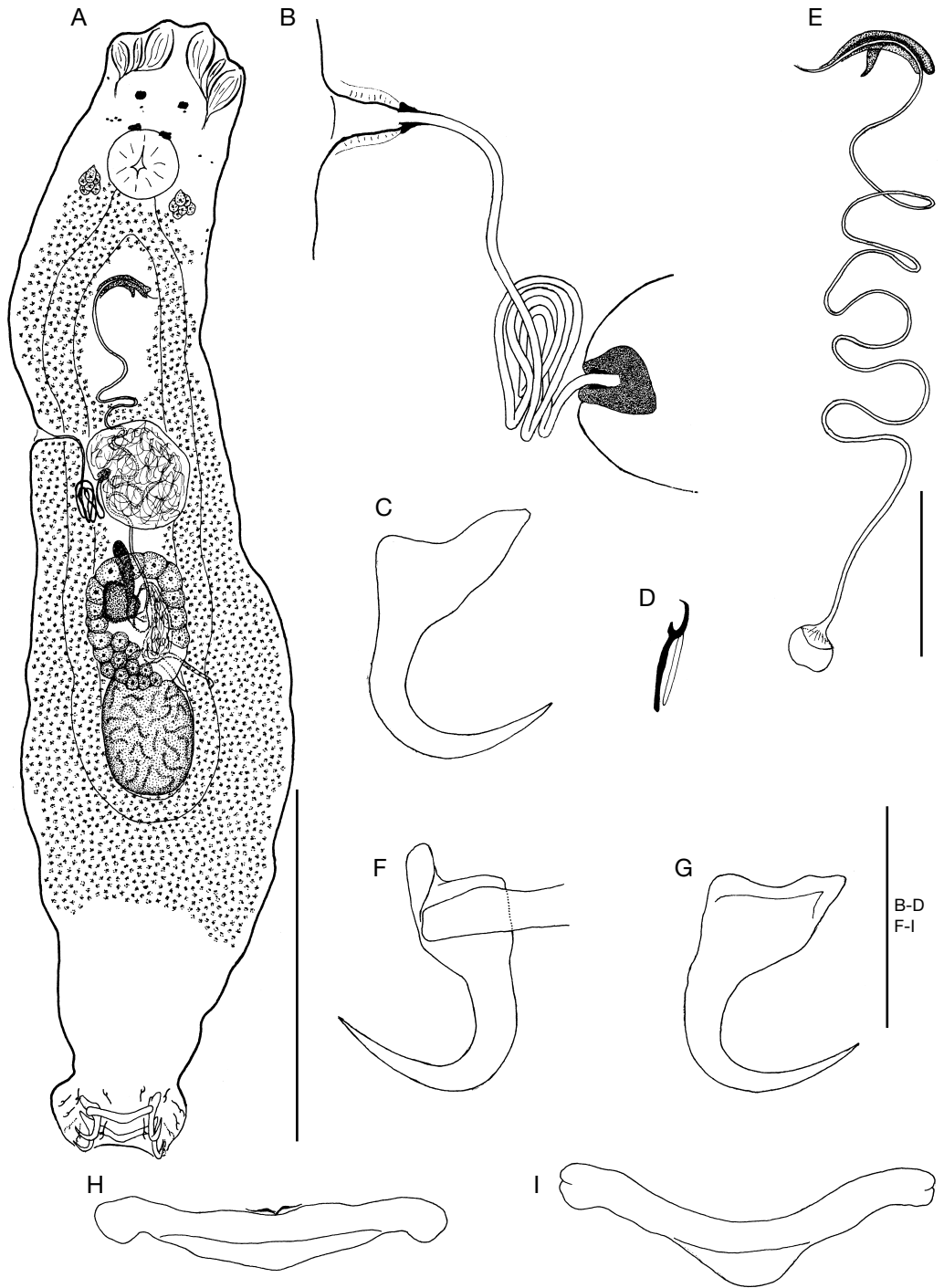


FIG. 1. — *Euryhaliotrema chaoi* n. gen., n. sp.; **A**, whole mount (composite, ventral view; germarium not totally inked in order to show the dorsal male reproductive organs); **B**, vagina (ventral view); **C**, ventral anchor; **D**, hook; **E**, copulatory complex (ventral view); **F**, **G**, dorsal anchors; **H**, ventral bar; **I**, dorsal bar. Scale bars: **A**, 200  $\mu$ m; **B**-**D**, **F**-**I**, 25  $\mu$ m; **E**, 50  $\mu$ m.

Barcelos, Amazonas, Brazil, 00°51'S, 62°46'W, 19.X.1996.

MATERIAL EXAMINED. — *Plagioscion* sp. (Sciaenidae): 12 voucher specimens, Rio Paduairi (southern tributary), downstream from confluence of Rio Unini and Rio Negro above Novo Airão, Amazonas, Brazil, 02°20'S, 61°20'W, 4.X.1989 (USNPC 91374). *Plagioscion squamosissimus* (Sciaenidae): seven voucher specimens, Manaus Fish Market, Manaus, Amazonas, Brazil, 13.IX.1978 (USNPC 91372); four voucher specimens, Belém Fish Market, Iquitos, Loreto, Peru, VII.1999 (USNPC 91375, 91376); 2 voucher specimens, Rio Nanay, Pampa Chica, 4.54 km west of Iquitos, Loreto, Peru, 03°45'09"S, 73°17'00"W, 7.VIII.1999 (USNPC 91373).

#### DESCRIPTION

Body 706 (614-799; n = 10) long, fusiform; greatest width 142 (121-171; n = 10) usually at level of testis. Cephalic region broad; cephalic lobes moderately developed. Members of posterior pair of eyes slightly larger, closer together than members of anterior pair; accessory granules in cephalic, anterior trunk regions. Pharynx spherical, 38 (34-45; n = 10) in diameter. Peduncle broad, tapered posteriorly; haptor subhexagonal, 82 (75-87; n = 10) wide, 67 (55-78; n = 10) long. Anchors similar; each with poorly differentiated short roots, evenly curved to straight short shaft, point extending past level of tip of superficial root; superficial root of dorsal anchor frequently bent around tips of dorsal bar toward body midline (Fig. 11); ventral anchor 32 (31-33; n = 9) long, base 17 (16-19; n = 8) wide; dorsal anchor 30 (28-31; n = 8) long, base 15 (14-18; n = 7) wide. Ventral bar 33 (32-35; n = 8) long, yoke shaped, with thin short shield on posterior margin, delicate anteromedial muscle-attachment plate; dorsal bar 39 (35-40; n = 8) long, broadly U-shaped, ends bent laterally, with small rounded shield on posteromedial margin. Hook 15 (14-16; n = 27) long, shank varying slightly in width along length; filamentous hooklet (FH) loop about shank length. Copulatory organ meandering, 279 (220-344; n = 8) long; base lying dorsal to germarium. Accessory piece 28 (26-32; n = 7) long, comprising variable sheath with subterminal branch, lacking articulation process.

Testis 105 (78-153; n = 7) long, 56 (45-74; n = 6) wide, ovate; seminal vesicle lying dorsal to germarium, pyriform; two prostatic reservoirs, one elongate pyriform, one subpyramidal, both dorsal to germarium. Germarium subovate, 64 (46-90; n = 8) long, 43 (30-51; n = 8) wide, slightly overlapping testis; oviduct, ootype not observed; uterus delicate, ventral. Vaginal aperture marginal; vagina distally funnel shaped, proximal portion an elongate narrow sclerotized tube coiled prior to discharging into large medial seminal receptacle. Vitellaria dense.

#### REMARKS

*Euryhaliotrema chaoi* n. gen., n. sp. is the type species of the genus. It differs from its congenitors in possessing an elongate meandering copulatory organ with its base lying dorsal to the germarium.

#### *Euryhaliotrema lovejoyi* n. sp.

(Fig. 2)

TYPE SPECIMENS. — Holotype (INPA 403); 4 paratypes (USNPC 91377, 91378, INPA 404, HWML 16424).

ETYMOLOGY. — This species is named for Dr Nate Lovejoy, University of Manitoba, Winnipeg, Manitoba, Canada, who kindly provided specimens of *Plagioscion* spp. from Peru and Venezuela.

TYPE HOST AND LOCALITY. — Gills of *Plagioscion* sp. (Sciaenidae): Igarapé Zamula, Rio Negro near Barcelos, Amazonas, Brazil, 00°51'S, 62°46'W, 19.X.1996.

MATERIAL EXAMINED. — *Plagioscion squamosissimus* (Sciaenidae): two voucher specimens, Caicara de Orinoco Fish Market (Orinoco River), Bolivar, Venezuela, IV.1999 (USNPC 91380); voucher specimen, Belém Fish Market, Iquitos, Loreto, Peru, VII.1999 (USNPC 91379).

#### DESCRIPTION

Body 375 (345-387; n = 4) long, fusiform; greatest width 99 (79-111; n = 4) usually at level of testis. Cephalic region broad; cephalic lobes moderately developed. Eyes subequal; members of posterior pair closer together than members of anterior pair; accessory granules uncommon

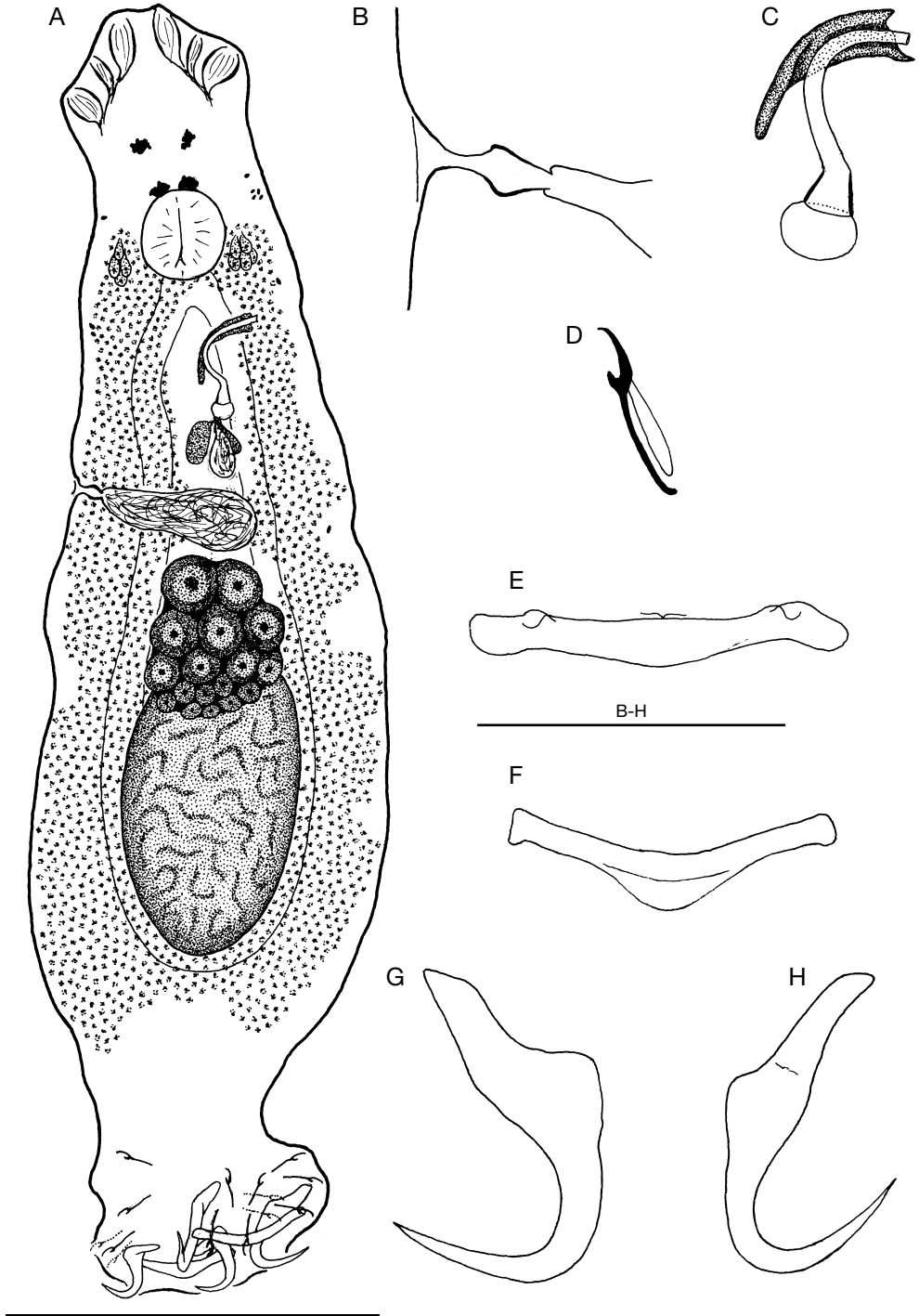


FIG. 2. — *Euryhaliotrema lovejoyi* n. gen., n. sp.; **A**, whole mount (composite, ventral view); **B**, vagina (ventral view); **C**, copulatory complex (ventral view); **D**, hook; **E**, ventral bar; **F**, dorsal bar; **G**, ventral anchor; **H**, dorsal anchor. Scale bars: A, 100 µm; B-H, 25 µm.



in cephalic, anterior trunk regions. Pharynx subspherical, 24 (19-30; n = 4) in diameter. Peduncle tapered posteriorly; haptor subhexagonal, 65 (63-66; n = 3) wide, 56 (40-72; n = 4) long. Anchors similar; each with poorly defined deep root, elongate superficial root, evenly curved short shaft, point extending past level of tip of superficial root; superficial root of dorsal anchor frequently bent around tip of dorsal bar toward body midline; ventral anchor 19 (n = 2) long, base 11 (n = 2) wide; dorsal anchor 23 (n = 1) long, base 17 (n = 1) wide. Ventral bar 32 (n = 1) long, straight to broadly U-shaped, usually with delicate anteromedial muscle-attachment plate, posterior shield absent; dorsal bar 30 (n = 1) long, broadly V-shaped, with small delicate shield on posterior margin. Hook 13-14 (n = 2) long; shank delicate, uniform; FH loop about shank length. Copulatory organ 33 (30-38; n = 3) long, a loosely coiled tube of slightly less than one counterclockwise ring. Accessory piece 18 (16-19; n = 4) long, comprising simple sheath; articulation process absent. Testis 60 (57-62; n = 2) long, 28 (25-30; n = 2) wide, ovate; seminal vesicle fusiform, anterior to seminal receptacle; two saccate prostatic reservoirs. Germarium subovate, 41 (30-54; n = 3) long, 27 (19-32; n = 3) wide; oviduct, ootype not observed; uterus delicate, ventral; vaginal aperture marginal; vagina with small distal funnel-shaped tegumental indentation, short dilated straight tube discharging into large transverse seminal receptacle anterior to germarium. Vitellaria dense.

#### REMARKS

Phylogenetic analyses suggest that the sister species of *Euryhaliotrema lovejoyi* n. gen., n. sp. is *E. monacanthus* n. gen., n. sp. The two species share the following features: a simple accessory piece in the copulatory complex, short vaginal canal, and similarly shaped ventral bars. *Euryhaliotrema lovejoyi* differs from *E. monacanthus* n. gen., n. sp. in having a dorsal anchor/bar complex (absent in *E. monacanthus* n. gen., n. sp.) and a copulatory organ comprising less than one ring (about two rings in *E. monacanthus* n. gen., n. sp.).

#### *Euryhaliotrema potamocetes* n. sp.

(Fig. 3)

TYPE SPECIMENS. — Holotype (INPA 405); 40 paratypes (USNPC 91381, 91382, 91383, 91384, 91385, HWML 16425, INPA 406a-t, MNHN 22HG Tg 145-148).

ETYMOLOGY. — The specific name is from Greek (*potamlo* = river + *cetlo* = monster + *-es* = an agent or doer) and refers to the habitat of this species.

TYPE HOST AND LOCALITY. — Gills of *Plagioscion* sp. (Sciaenidae): Igarapé Zamula, Rio Negro near Barcelos, Amazonas, Brazil, 00°51'S, 62°46'W, 19.X.1996.

MATERIAL EXAMINED. — *Plagioscion* sp. (Sciaenidae): 21 voucher specimens, Rio Paduairi (southern tributary), downstream from confluence of Rio Unini and Rio Negro above Novo Airão, Amazonas, Brazil, 02°20'S, 61°20'W, 4.X.1989 (USNPC 91392). *Plagioscion squamosissimus* (Sciaenidae): four voucher specimens, Manaus Fish Market, Manaus, Amazonas, Brazil, 13.IX.1978 (USNPC 91387); voucher specimen, Puerto Ayacucho Fish Market (Rio Orinoco), Amazonas, Venezuela (according to vendor, the host was imported from Caicara de Orinoco, Bolivar, Venezuela) 24.III.1999 (USNPC 91386); 13 voucher specimens, Belém Fish Market, Iquitos, Loreto, Peru, VII.1999 (USNPC 91388, 91389, 91390, 91391).

#### DESCRIPTION

Body 460 (276-619; n = 15) long, fusiform; greatest width 95 (76-129; n = 23) usually at level of testis. Cephalic region broad; cephalic lobes moderately developed. Eyes infrequently dissociated; members of posterior pair larger, closer together than members of anterior pair; accessory granules in cephalic, anterior trunk regions. Pharynx ovate, greatest width 27 (22-34; n = 20). Peduncle broad, tapered posteriorly; haptor subhexagonal, 71 (62-88; n = 15) wide, 63 (44-77; n = 16) long. Anchors similar; each with poorly defined deep root, elongate superficial root, straight shaft, point extending past level of tip of superficial root; ventral anchor 32 (30-34; n = 16) long, base 15 (13-17; n = 16) wide; dorsal anchor 29 (27-30; n = 13) long, base 14 (12-15; n = 9) wide. Ventral bar 35 (33-37; n = 9) long, straight to broadly U-shaped, ends enlarged, usually with delicate anteromedial muscle-attachment plate, posterior shield absent; dorsal bar 35 (32-38;

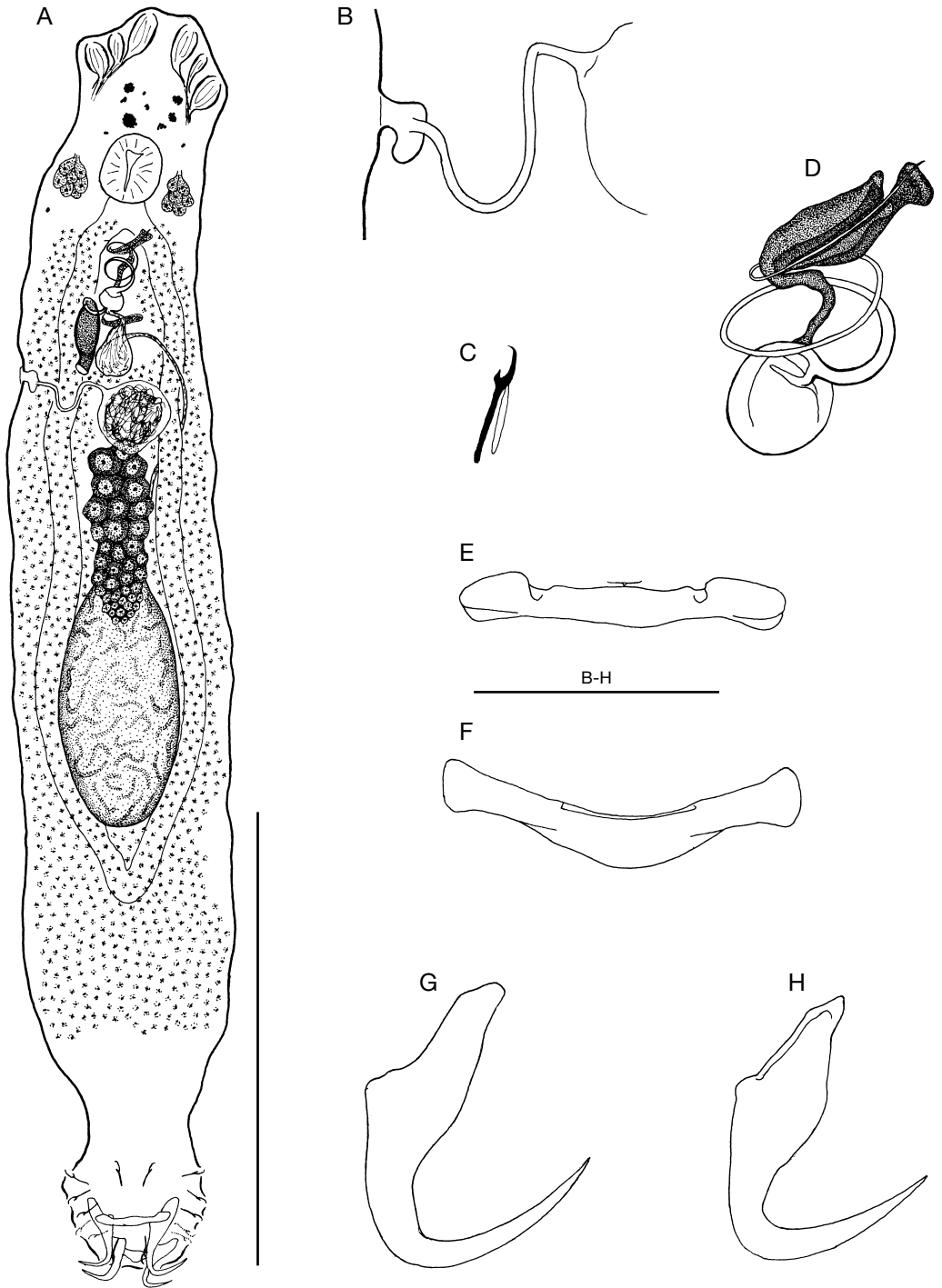


FIG. 3. — *Euryhaliotrema potamocetes* n. gen., n. sp.; **A**, whole mount (composite, ventral view); **B**, vagina (ventral view); **C**, hook; **D**, copulatory complex (ventral view); **E**, ventral bar; **F**, dorsal bar; **G**, ventral anchor; **H**, dorsal anchor. Scale bars: A, 200 µm; B-H, 25 µm.

n = 10) long, broadly U-shaped, with short broad posterior shield. Hook 14-15 (n = 38) long, with uniform shank; FH loop about shank length. Copulatory organ a coil with about two and a half counterclockwise rings, 119 (110-128; n = 5) long, coil diameter 18 (17-20; n = 28); bulbous base large. Accessory piece 19 (16-22; n = 15) long, comprising variable sheath along distal shaft of copulatory organ, articulation process attached to base of copulatory organ. Testis 70 (31-98; n = 12) long, 36 (29-45; n = 12) wide, ovate; seminal vesicle sigmoid, pyriform; two prostatic reservoirs, dextral reservoir with thick wall. Germarium irregular, 56 (24-78; n = 15) long, 29 (23-40; n = 15) wide; oviduct, ootype not observed; uterus delicate, ventral. Vaginal aperture marginal, with small distal vestibule; proximal vaginal canal a narrow sclerotized tube with posterior loop near midlength prior to discharging into large medial seminal receptacle lying anterior to germarium; vitellaria dense.

#### REMARKS

*Euryhaliotrema potamocetes* n. gen., n. sp. is the apparent sister group for the remaining species of the genus found on *Plagioscion* spp. and is the only freshwater species possessing an articulated copulatory organ and accessory piece. In this respect it more closely resembles *E. paralonchuri* n. comb. and *E. atlantica* n. gen., n. sp., both of which form the sister group of the freshwater clade. *Euryhaliotrema potamocetes* n. gen., n. sp. differs from these marine counterparts in lacking a vaginal bulb at the vaginal aperture.

#### *Euryhaliotrema thatcheri* n. sp.

(Fig. 4)

TYPE SPECIMENS. — Holotype (INPA 407); 52 paratypes (USNPC 91393, 91394, 91395, 91396, HWML 16426, INPA 408a-y, MNHN 23HG Tg 149-152).

ETYMOLOGY. — This species is named for our friend and colleague, Dr Vernon Thatcher, retired, INPA, Manaus, Amazonas, Brazil, in recognition of his research on the parasites of fishes in the Neotropical Region.

TYPE HOST AND LOCALITY. — Gills of *Plagioscion* sp. (Sciaenidae): Igarapé Zamula, Rio Negro near Barcelos, Amazonas, Brazil, 00°51'S, 62°46'W, 19.X.1996.

MATERIAL EXAMINED. — *Plagioscion* sp. (Sciaenidae): 10 voucher specimens, Rio Paduairi (southern tributary), downstream from confluence of Rio Unini and Rio Negro above Novo Airão, Amazonas, Brazil, 02°20'S, 61°20'W, 4.X.1989 (USNPC 91405); nine voucher specimens, Janauacá Lake near Manaus, Amazonas, Brazil, 03°25'S, 60°17'W, 20.IV.1979 (USNPC 91407). *Plagioscion squamosissimus* (Sciaenidae): five voucher specimens, Caicara de Orinoco Fish Market (Rio Orinoco), Bolivar, Venezuela, IV.1999 (USNPC 91401); three voucher specimens, Puerto Ayacucho Fish Market (Rio Orinoco), Amazonas, Venezuela (according to vendor, the host was imported from Caicara de Orinoco, Bolivar, Venezuela), 24.III.1999 (USNPC 91402); 13 voucher specimens, Belém Fish Market, Iquitos, Loreto, Peru, VII.1999 (USNPC 91397, 91398, 91399, 91400); voucher specimen, Rio Nanay, Pampa Chica, 4.54 km west of Iquitos, Loreto, Peru, 03°45'09"S, 73°17'00"W, 7.VIII.1999 (USNPC 91403); two voucher specimens, confluence of Rio Amazonas and Rio Tamshiyaca, about 3 km south of Tamshiyacu, Loreto, Peru, 04°01'42"S, 73°08'45"W, 28.VII.1999 (USNPC 91404); voucher specimen, Manaus Fish Market, Manaus, Amazonas, Brazil, 13.IX.1978 (USNPC 91406).

#### DESCRIPTION

Body 303 (233-360; n = 18) long, fusiform; greatest width 85 (65-115; n = 20) in posterior trunk at level of testis. Cephalic region broad; cephalic lobes poorly developed. Members of posterior pair of eyes larger, closer together than members of anterior pair; accessory granules uncommon in cephalic, anterior trunk regions. Pharynx spherical, 20 (15-22; n = 21) in diameter. Peduncle broad, tapered posteriorly; haptor subhexagonal, 66 (57-73; n = 19) wide, 51 (38-69; n = 20) long. Ventral anchor 25 (24-26; n = 11) long, with poorly differentiated short roots, curved short shaft, point extending past level of tip of superficial root; base 13 (12-14; n = 9) wide. Dorsal anchor 22 (21-23; n = 15) long, with elongate superficial root usually bent around dorsal bar toward body midline (Fig. 4H), nonexistent deep root, straight shaft, point extending to level of tip of superficial root; base 15 (14-17; n = 15) wide. Bars similar, broadly U- or V-shaped, with posterior shield-like process

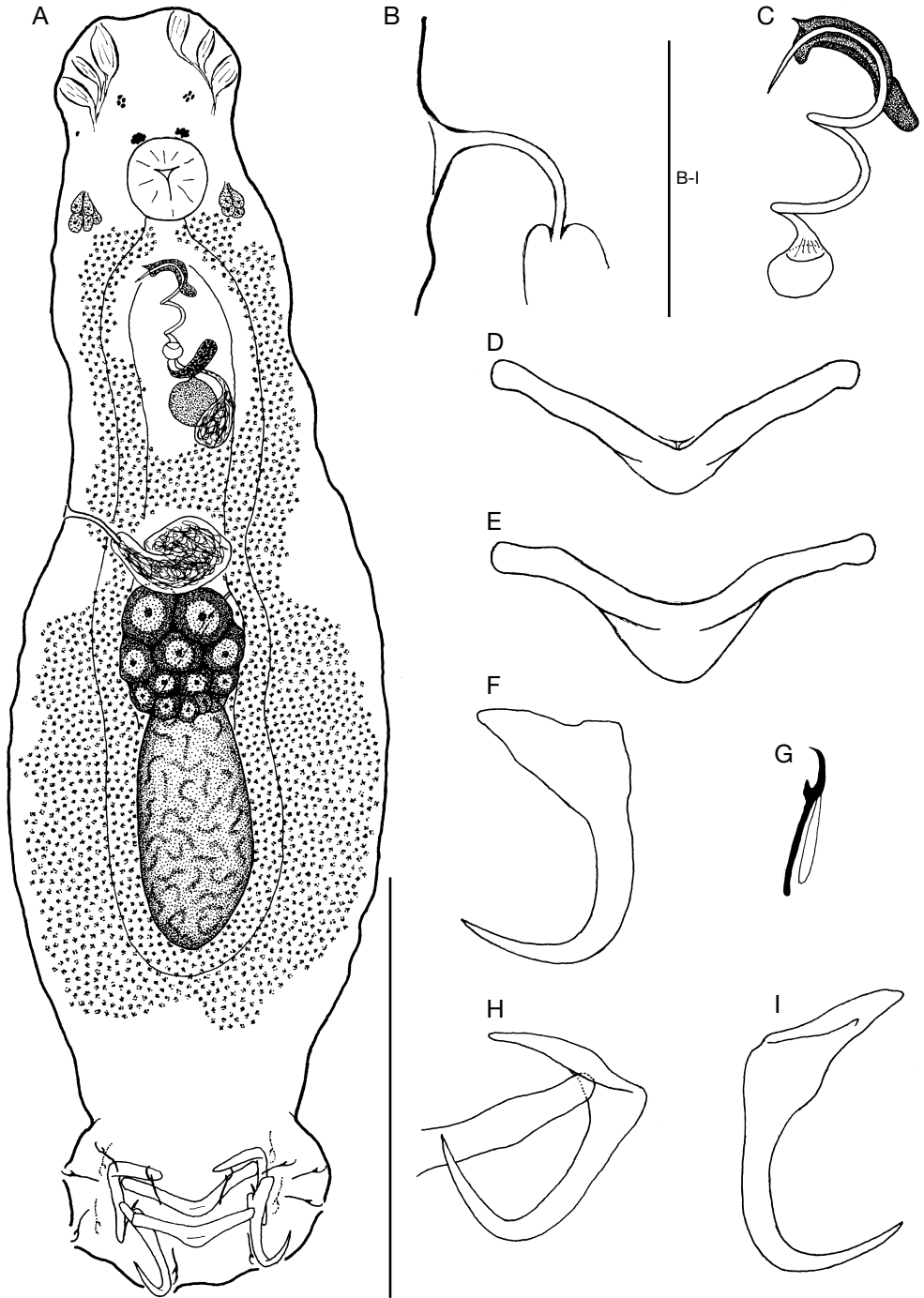


FIG. 4. — *Euryhaliotrema thatcheri* n. gen., n. sp.; **A**, whole mount (composite, ventral view); **B**, vagina (ventral view); **C**, copulatory complex (ventral view); **D**, ventral bar; **E**, dorsal bar; **F**, ventral anchor; **G**, hook; **H**, **I**, dorsal anchors. Scale bars: **A**, 100  $\mu$ m; **B-I**, 25  $\mu$ m.

originating from posterior margin; ventral bar 32 (31-40; n = 12) long, with delicate antero-medial muscle-attachment plate; dorsal bar 35 (33-39; n = 20) long. Hook 14 (13-15; n = 31) long, with uniform shank; FH loop about shank length. Copulatory organ a coil of about two and a half counterclockwise rings, 60 (53-68; n = 12) long, coil diameter 8 (7-9; n = 18). Accessory piece 16 (14-19; n = 7) long, comprising variable sheath along distal shaft of copulatory organ; articulation process absent. Testis 46 (31-63; n = 10) long, 26 (19-37; n = 10) wide, ovate; seminal vesicle pyriform; two prostatic reservoirs. Germarium subspherical to ovate, 37 (26-49; n = 11) long, 27 (20-38; n = 10) wide; oviduct, ootype not observed, uterus delicate, ventral; vaginal aperture marginal, distally funnel shaped; vaginal canal slightly arched anteriorly, sclerotized; seminal receptacle medial, pregermarial; vitellaria dense.

#### REMARKS

*Euryhaliotrema thatcheri* n. gen., n. sp. is sister group to *E. monacanthus* n. gen., n. sp. + *E. lovejoyi* n. gen., n. sp. based on presence of a short vaginal tube lacking a loop. It resembles *E. lovejoyi* n. gen., n. sp. by possessing a dorsal anchor/bar complex and in the morphology of the haptor armament, while it compares to *E. monacanthus* n. gen., n. sp. in the morphology of the copulatory complex. It differs from both species in having a posterior flap on the ventral bar.

#### *Euryhaliotrema monacanthus* n. sp.

(Fig. 5)

TYPE SPECIMENS. — Holotype (INPA 409); 26 paratypes (USNPC 91408, 91409, 91410, HWML 16427, INPA 410a-l, MNHN 24HG Tg 153-154).

ETYMOLOGY. — The specific name is from Greek (*monas* = single + *akantha* = a thorn) and refers to the presence of a single anchor pair in the haptor.

TYPE HOST AND LOCALITY. — Gills of *Plagioscion* sp. (Sciaenidae): Igarapé Zamula, Rio Negro near Barcelos, Amazonas, Brazil, 00°51'S, 62°46'W, 19.X.1996.

MATERIAL EXAMINED. — *Plagioscion* sp. (Sciaenidae): Voucher specimen, Rio Paduairi (southern tributary), downstream from confluence of Rio Unini and Rio Negro above Novo Airão, Amazonas, Brazil, 02°20'S, 61°20'W, 4.X.1989 (USNPC 91414). *Plagioscion squamosissimus* (Sciaenidae): five voucher specimens, Caicara de Orinoco Fish Market (Rio Orinoco), Bolivar, Venezuela, IV.1999 (USNPC 91411); two voucher specimens, Rio Nanay, Pampa Chica, 4.54 km west of Iquitos, Loreto, Peru, 03°45'09"S, 73°17'00"W, 7.VIII.1999 (USNPC 91412); voucher specimen, confluence of Rio Amazonas and Rio Tamshiyaca, about 3 km south of Tamshiyacu, Loreto, Peru, 04°01'42"S, 73°08'45"W, 28.VII.1999 (USNPC 91413).

#### DESCRIPTION

Body 331 (210-515; n = 16) long, fusiform; greatest width 81 (62-94; n = 14) near midlength. Cephalic region broad; cephalic lobes moderately developed. Members of posterior pair of eyes larger, closer together than members of anterior pair; eye granules variable in size; accessory granules uncommon in cephalic, trunk regions. Pharynx spherical, 21 (15-25; n = 17) in diameter. Peduncle broad, relatively long; haptor subhexagonal, 77 (68-86; n = 11) wide, 58 (44-71; n = 15) long. Ventral anchor 32 (30-35; n = 10) long, with elongate depressed superficial root, poorly defined deep root, broadly curved shaft, point extending well past level of tip of superficial root; base 14 (12-16; n = 6) wide. Ventral bar 46 (43-50; n = 14) long, straight, rod shaped, with delicate anteromedial muscle-attachment plate, posterior shield absent. Dorsal anchors, dorsal bar absent. Hook 16-17 (n = 24) long, with shank varying slightly in width; FH loop about shank length. Copulatory organ a loose coil of about two counterclockwise rings, 51 (48-53; n = 4) long, coil diameter 7 (6-8; n = 6). Accessory piece 23 (21-25; n = 5) long, comprising variable sheath terminally paralleling distal shaft of copulatory organ; articulation process absent. Testis 50 (39-60; n = 7) long, 25 (17-30; n = 8) wide, ovate; seminal vesicle pyriform; two prostatic reservoirs, pyriform. Germarium subovate to pyriform, 41 (24-53; n = 10) long, 24 (15-31; n = 10) wide, slightly overlapping testis; oviduct, ootype not observed, uterus delicate, ventral. Vaginal aperture marginal, distally funnel-

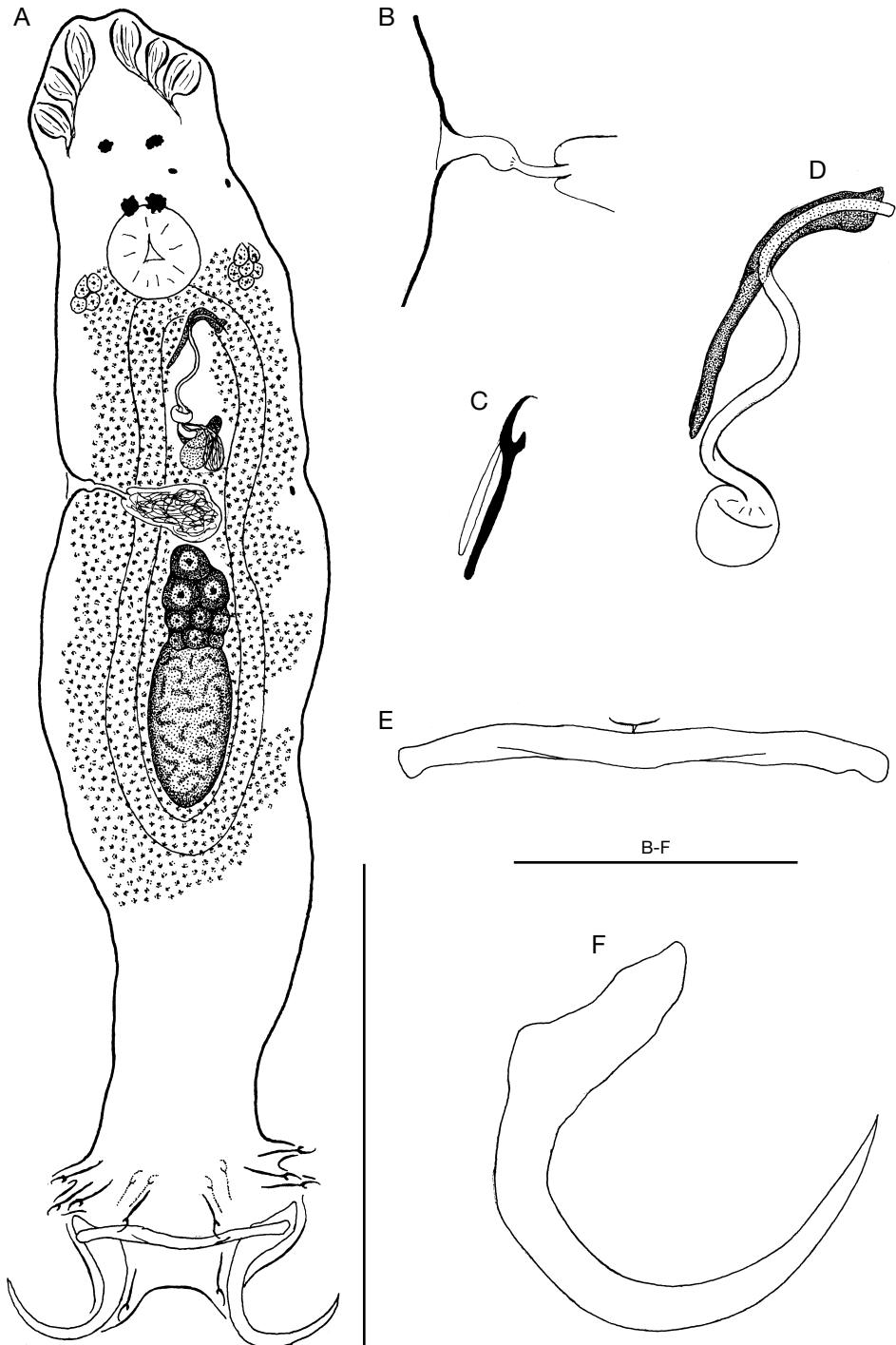


FIG. 5. — *Euryhaliotrema monacanthus* n. gen., n. sp.; **A**, whole mount (composite, ventral view); **B**, vagina (ventral view); **C**, hook; **D**, copulatory complex (ventral view); **E**, ventral bar; **F**, ventral anchor. Scale bars: A, 100 µm; B-F, 25 µm.

shaped; vaginal canal short, straight; seminal receptacle pregermarial, pyriform to irregular; vitellaria dense.

REMARKS

*Euryhaliotrema monacanthus* n. gen., n. sp. differs from all congenitors in lacking a dorsal anchor/bar complex. Phylogenetic analysis suggests that this species originated within the freshwater clade of *Euryhaliotrema* n. gen. species and does not support proposal of a new genus for this unique species. *Euryhaliotrema monacanthus* n. gen., n. sp. is sister species to *E. lovejoyi* n. gen., n. sp. (see Remarks for *E. lovejoyi* n. gen., n. sp. for differentiation).

*Euryhaliotrema succedaneus* n. sp.  
(Fig. 6)

TYPE SPECIMENS. — Holotype (USNPC 91415); 13 paratypes (USNPC 91416, 91417, 91418, 91419, 91420, HWML 16428, MNHN 25HG Tg 155-156).

ETYMOLOGY. — From Latin *succedaneus* = a substitute, refers to the similarity of this species to the type species, *E. chaoi* n. gen., n. sp.

TYPE HOST AND LOCALITY. — Gills of *Plagioscion squamosissimus* (Sciaenidae): Belém Fish Market, Iquitos, Loreto, Peru, VII.1999.

MATERIAL EXAMINED. — *Plagioscion* sp. (Sciaenidae): Voucher specimen, Rio Paduairi (southern tributary), downstream from confluence of Rio Unini and Rio Negro above Novo Airão, Amazonas, Brazil, 02°20'S, 61°20'W, 4.X.1989 (USNPC 91421). *Plagioscion squamosissimus* (Sciaenidae): Voucher specimen, Manaus Fish Market, Manaus, Amazonas, Brazil, 13.IX.1978 (INPA 411).

DESCRIPTION

Body 873 (676-979; n = 8) long, fusiform; greatest width 170 (129-212; n = 8) usually near body midlength or in posterior trunk. Cephalic region narrow; cephalic lobes moderately developed. Members of posterior pair of eyes slightly larger, closer together than members of anterior pair; accessory granules scarce in cephalic region. Pharynx spherical, 42 (35-49; n = 9) in diameter. Peduncle moderate to narrow, gradually tapering posteriorly; haptor subhexagonal, 84 (78-93; n = 5) wide, 67 (59-81; n = 8) long. Anchors sim-

ilar; each with poorly defined deep root, stocky superficial root, short shaft, point extending past level of tip of superficial root; ventral anchor 31 (29-34; n = 9) long, base 17 (14-18; n = 5) wide; dorsal anchor 30 (28-31; n = 5) long, base 15 (14-17; n = 3) wide. Ventral bar 30 (28-32; n = 6) long, yoke shaped, with narrow shield on posterior margin, delicate anteromedial muscle-attachment plate; dorsal bar 32 (30-34; n = 5) long, broadly U-shaped, with small rounded shield on posteromedial margin. Hook 17 (16-18; n = 8) long, shank uniform; FH loop about shank length. Copulatory organ meandering, 207 (200-213; n = 5) long. Accessory piece 26 (23-28; n = 5) long, comprising variable sheath with distal loop enclosing tip of copulatory organ, lacking articulation process. Testis 143 (128-162; n = 6) long, 53 (47-62; n = 6) wide, elongate ovate; seminal vesicle fusiform; two prostatic reservoirs fusiform. Germarium bacilliform, 143 (123-174; n = 4) long, 51 (45-57; n = 4) wide, overlapping anterior end of testis; oviduct short; ootype not observed; uterus delicate, ventral. Vaginal aperture marginal, funnel shaped, with submarginal muscular-appearing bulb; vaginal canal with proximal coil prior to discharging into irregular medial seminal receptacle anterior to germarium. Vitellaria dense.

REMARKS

This species is sister to *E. chaoi* n. gen., n. sp., which it resembles in the general morphology of the copulatory complex and haptoral armament. *Euryhaliotrema succedaneus* n. gen., n. sp. differs from *E. chaoi* n. gen., n. sp. in having a shorter copulatory organ whose base lies anterior to the germarium and a shorter vaginal tube with one proximal loop before entering the seminal receptacle (numerous loops in *E. chaoi* n. gen., n. sp.).

*Euryhaliotrema atlantica* n. sp.  
(Fig. 7)

TYPE SPECIMENS. — Holotype (INPA 412); 13 paratypes (USNPC 91423, 91424, HWML 16430, INPA 413a-e, MNHN 27HG Tg 159).

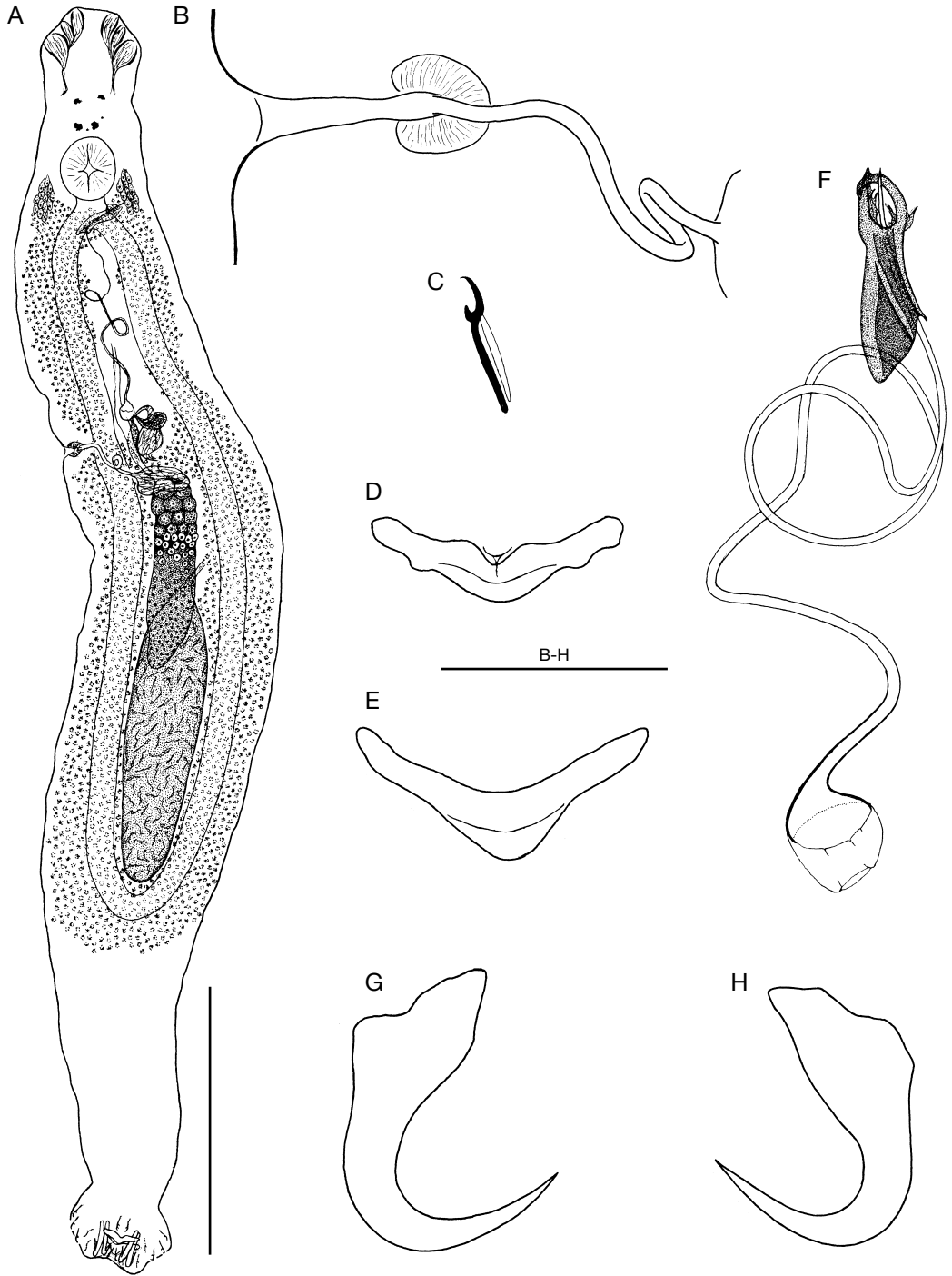


FIG. 6. — *Euryhaliotrema succedaneus* n. gen., n. sp.; **A**, whole mount (composite, ventral view); **B**, vagina (ventral view); **C**, hook; **D**, ventral bar; **E**, dorsal bar; **F**, copulatory complex (ventral view); **G**, ventral anchor; **H**, dorsal anchor. Scale bars: A, 200 µm; B-H, 25 µm.



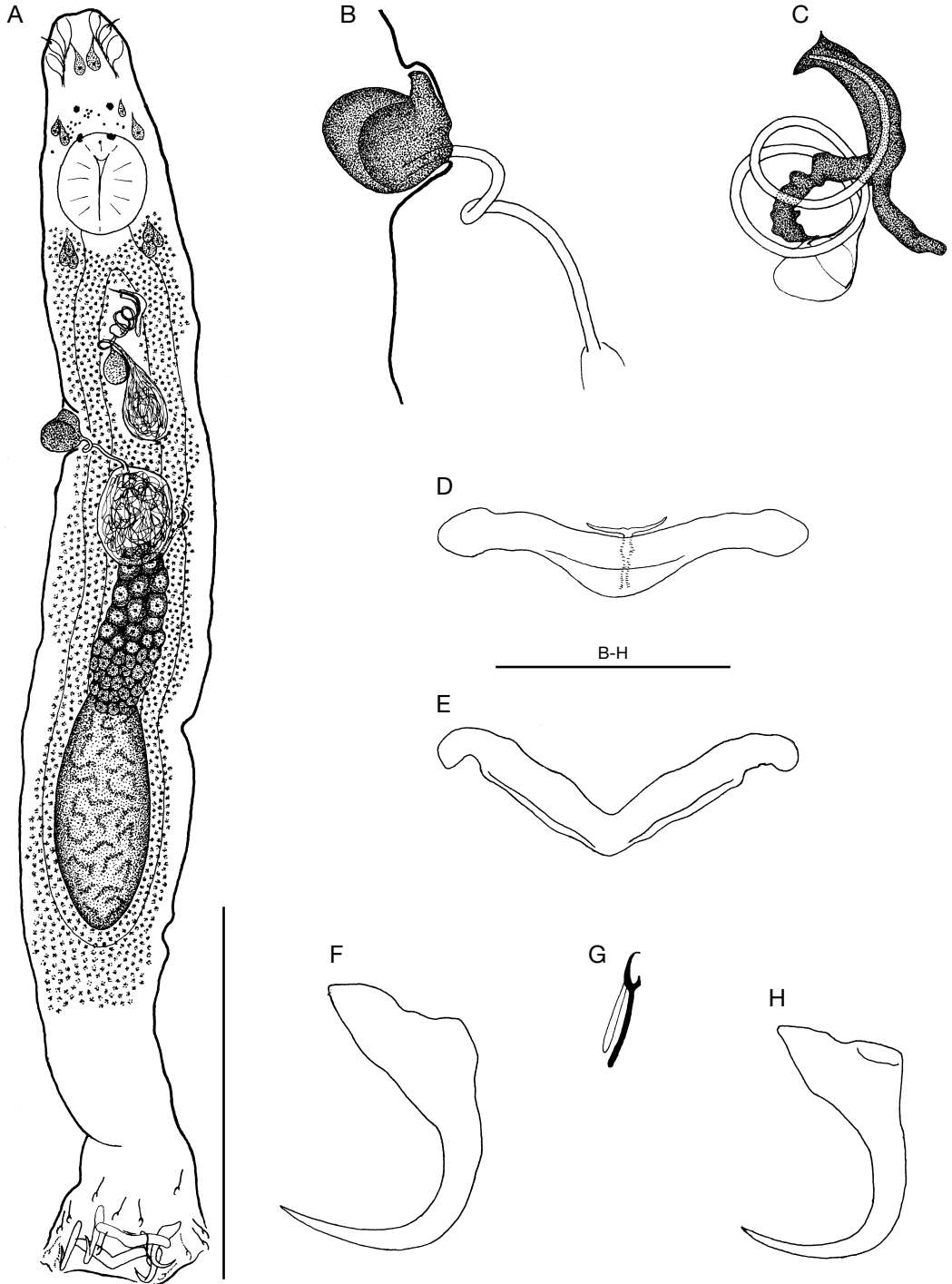


FIG. 7. — *Euryhaliotrema atlantica* n. gen., n. sp.; **A**, whole mount (composite, ventral view); **B**, vagina (ventral view); **C**, copulatory complex (ventral view); **D**, ventral bar; **E**, dorsal bar; **F**, ventral anchor; **G**, hook; **H**, dorsal anchor. Scale bars: A, 200  $\mu$ m; B-H, 25  $\mu$ m.

ETYMOLOGY. — The specific name is derived from Greek (*atlantikon* = the Atlantic [Ocean]).

TYPE HOST AND LOCALITY. — Gills of *Paralanchurus brasiliensis* (Sciaenidae): Baía de Guaratuba, Guaratuba, Paraná, Brazil, 30°50'S, 48°28'W, 15.VII.1996.

MATERIAL EXAMINED. — *Paralanchurus brasiliensis* (Sciaenidae): five voucher specimens, Atlantic Ocean off Rio Grande, Rio Grande do Sul, Brazil, 32°00'S, 51°48'W, 4.III.1996 (USNPC 91425).

#### DESCRIPTION

Body 614 (582-664; n = 6) long, slender, fusiform; greatest width 108 (94-122; n = 6) usually at level of testis. Cephalic region broad; cephalic lobes moderately developed; small spike frequently protruding from second pair of head organs. Eyes subequal, equidistant, infrequently dissociated; accessory granules common in cephalic, anterior trunk regions. Pharynx subspherical to ovate, 43 (36-46; n = 6) in diameter. Peduncle elongate; haptor subhexagonal, 88 (77-98; n = 6) wide, 65 (57-68; n = 5) long. Anchors similar; each with poorly differentiated short roots, evenly curved short shaft, point extending past level of tip of superficial root; ventral anchor 30 (28-32; n = 5) long, base 17 (16-18; n = 4) wide; dorsal anchor 27 (26-29; n = 5) long, base 14 (12-15; n = 4) wide. Ventral bar 42 (40-44; n = 5) long, slightly bent posteriorly near midlength, with slightly expanded ends, small posterior shield, delicate medioanterior cup-shaped projection; dorsal bar 37 (31-41; n = 5) long, V-shaped, with knob-like ends. Hook 13-14 (n = 10) long, with uniform shank; FH loop about shank length. Copulatory organ a coil of about two and a half counterclockwise rings, 109 (100-115; n = 3) long, proximal ring diameter 15 (14-17; n = 8). Accessory piece 26 (24-29; n = 3) long, comprising variable sheath along distal shaft of copulatory organ, with posteriorly directed branch originating near midlength; articulation process attached to base of copulatory organ. Testis 78 (n = 1) long, 31 (n = 1) wide, ovate; seminal vesicle pyriform; 1 prostatic reservoir. Germarium pyriform to elongate ovate, 67 (64-78; n = 4) long, 30 (25-38; n = 4) wide; oviduct, ootype not observed; uterus delicate, ventral. Vaginal aperture on fleshy bulb protruding

from right side of body; vaginal canal with distal loop; seminal receptacle anterior to germarium, large, ovate. Vitellaria dense.

#### REMARKS

This species closely resembles *Euryhaliotrema paralonchuri* n. comb., from which it differs in having smaller and more delicate haptoral sclerites and copulatory complex. The vaginal tube in *E. atlantica* n. gen., n. sp. is narrow and lightly sclerotized, while it has a much larger diameter and apparently lacks sclerotization in *E. paralonchuri* n. gen., n. sp.

#### *Euryhaliotrema carbunculus* (Hargis, 1955) n. comb. (Fig. 8)

*Pseudohaliootrema carbunculus* Hargis, 1955: 189, 190.

*Pseudohaliootrema* (*P.*) *carbunculus* – Yamaguti 1963.

TYPE HOST AND LOCALITY. — Gills of *Lagodon rhomboides* (Sparidae): Alligator Harbor, Franklin Co., Florida (Hargis 1955).

MATERIAL EXAMINED. — Holotype (USNPC 49340); eight paratypes (USNPC 49340, 49341).

#### MEASUREMENTS

Body 362 (338-382; n = 5) long, fusiform; greatest width 64 (52-74; n = 5) at level of testis; pharynx 21 (19-25; n = 7) in diameter; haptor 79 (69-96; n = 6) wide, 65 (59-71; n = 6) long; ventral anchor 38 (36-42; n = 6) long, base 16 (14-17; n = 3) wide; dorsal anchor 50 (48-53; n = 7) long, base 15 (13-16; n = 5) wide; ventral bar 37 (34-41; n = 6) long, dorsal bar 35 (31-39; n = 6) long; hook 13-14 (n = 7) long, FH loop about shank length; copulatory organ 115 (n = 1) long, coil counterclockwise, ring diameter 22 (20-23; n = 2); accessory piece 18 (17-20; n = 2) long; testis 29 (n = 1) long, 14 (n = 1) wide; germarium 36 (32-39; n = 3) long, 18 (14-23; n = 3) wide; vaginal aperture marginal.

#### REMARKS

In the original description of this species as *Pseudohaliootrema carbunculus*, Hargis (1955) did not

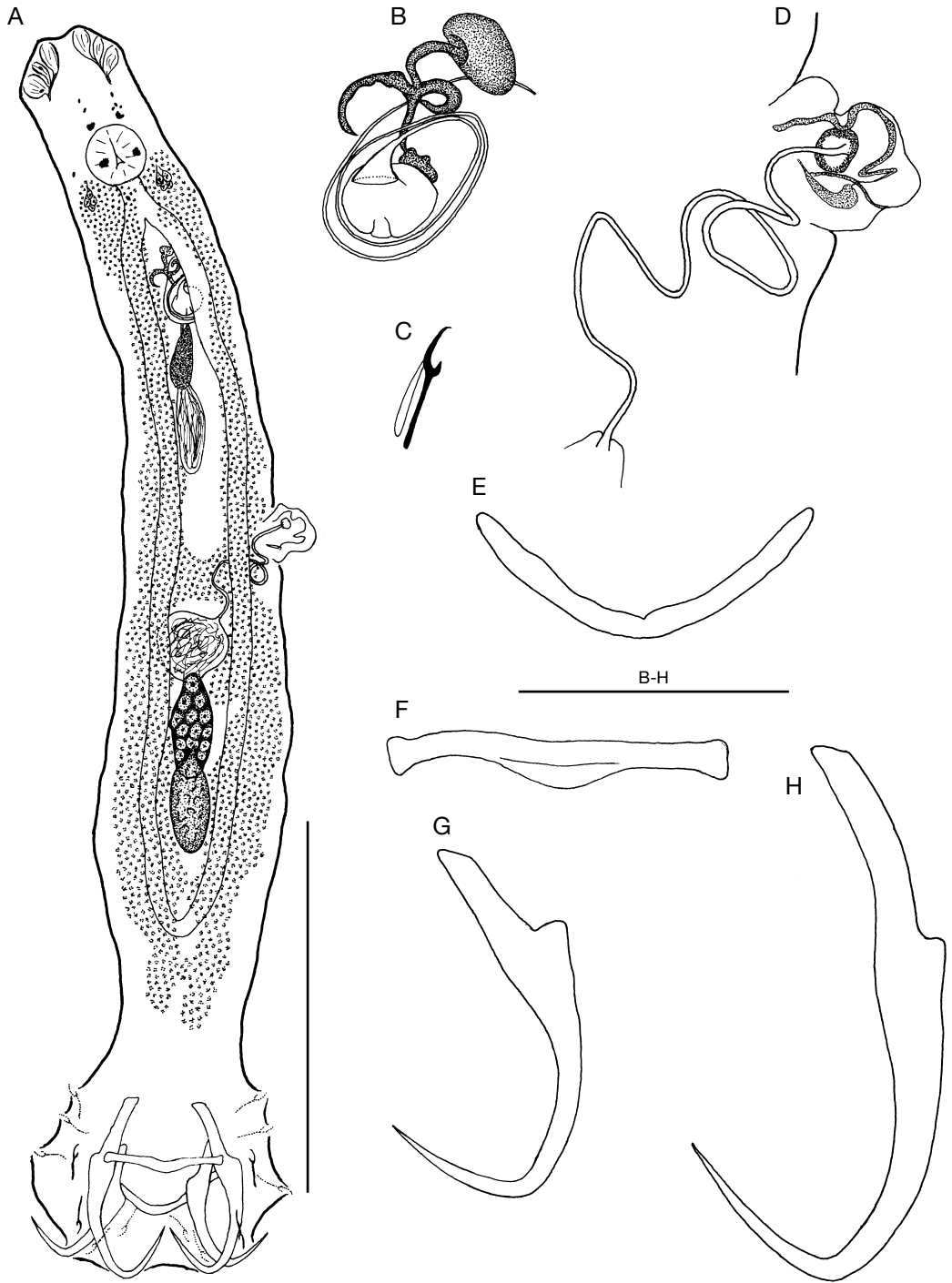


FIG. 8. — *Euryhaliotrema carbunculus* (Hargis, 1955) n. comb.; **A**, whole mount (dorsal view); **B**, copulatory complex (dorsal view); **C**, hook; **D**, vagina (dorsal view); **E**, ventral bar; **F**, dorsal bar; **G**, ventral anchor; **H**, dorsal anchor. Scale bars: A, 100 µm; B-H, 25 µm.

report the presence of an articulated copulatory organ and accessory piece via a short articulation process. The original whole-mount drawing of the holotype (Hargis 1955: fig. 42) suggests that a loop of the vas deferens and the proximal portion of the seminal vesicle lie dorsal to the left cecum. Unfortunately, we could not confirm the course of the vas deferens in available type specimens, but suggest that male duct does loop the left cecum based on findings in other species of *Euryhaliotrema*. All other features of the species support the transfer of *P. carbunculus* to *Euryhaliotrema* n. gen. Thus, *E. carbunculus* n. comb. is proposed.

*Euryhaliotrema sagmatum* n. sp.  
(Fig. 9)

TYPE SPECIMENS. — Holotype (CNHE 4015); 21 paratypes (USNPC 91422, HWML 16429, CNHE 4016, MNHN 26HG Tg 157-158).

ETYMOLOGY. — The specific name is from Greek (*sagmatos* = a saddle) and refers to the germarium forming a saddle over the anterior end of the testis.

TYPE HOST AND LOCALITY. — Gills of *Umbrina xanti* (Sciaenidae): Chamela Bay, Jalisco, Mexico, 19°28'N, 105°08'W, 5.VI.1999.

DESCRIPTION

Body 870 (753-1016; n = 9) long, flattened dorsoventrally; greatest width 244 (194-301; n = 9) usually at level of testis. Cephalic region broad, short; cephalic lobes moderately to well-developed. Eyes subequal, members of posterior pair farther apart than members of anterior pair; accessory granules in cephalic region. Pharynx subspherical, 81 (67-95; n = 11) in greatest width, with posterior circular lobe. Peduncle broad, tapering posteriorly; haptor subovate, 105 (88-117; n = 6) wide, 58 (50-62; n = 6) long. Ventral anchor 26 (24-28; n = 4) long, with large perpendicular superficial root, short deep root, short evenly curved shaft, point reaching level of tip of superficial root; base 20 (18-21; n = 3) wide. Dorsal anchor 20 (19-21; n = 8) long, delicate, with elongate superficial root, short deep root, evenly curved short shaft, point not reaching level of tip of superficial root; base 17 (16-18; n = 8) wide. Ventral bar 30 (28-33; n = 12) long,

yoke shaped, with anteromedial swirled protuberance, posterior shield absent; dorsal bar 37 (35-41; n = 10) long, broadly U-shaped, expanded medially. Hook 12 (11-13; n = 16) long, shank uniform; FH loop about shank length. Copulatory organ 97 (78-105; n = 10) long, a coil of about one and a half counterclockwise rings; coil diameter 18 (17-20; n = 9). Accessory piece 47 (43-53; n = 9) long, comprising rod with complex distal pincher-like termination, lacking articulation process. Testis 144 (122-171; n = 4) long, 74 (65-88; n = 4) wide, ovate; seminal vesicle forming C-shaped loop posterior to base of copulatory organ; one prostatic reservoir lying within loop of seminal vesicle. Germarium 165 (148-187; n = 7) long, 58 (41-65; n = 7) wide, usually proximally bilobed, overlying anterior end of testis; oviduct extending ventral to seminal receptacle; ootype not observed; uterus delicate, ventral. Vaginal aperture dextroventral, with muscular-appearing posterior thickened wall distally; vaginal canal tubular, straight to slightly arced anteriorly, with proximal end indenting seminal receptacle. Seminal receptacle medial, irregular, pregermarial. Vitellaria dense.

REMARKS

*Euryhaliotrema sagmatum* n. gen., n. sp. is sister species to *E. bychowskyi* n. comb. Both species are relatively large dactylogyrids with dorsoventrally flattened bodies, an anteromedial protuberance on the ventral bar, and a vaginal tube that indents the seminal receptacle. They differ in comparative morphology of the dorsal and ventral anchors (small, delicate in *E. sagmatum* n. gen., n. sp.; base massive in *E. bychowskyi* n. comb.).

*Euryhaliotrema bychowskyi*  
(Obodnikova, 1976) n. comb.  
(Fig. 10A-G)

*Haliotrema bychowskyi* Obodnikova, 1976: 89-91.

TYPE HOST AND LOCALITY. — Gills of *Hapalogenys mucronatus* (Haemulidae): Yellow Sea (Chifu, sic) (Obodnikova 1976).

MATERIAL EXAMINED. — Four paratypes (ZIAC 2938, 2945).

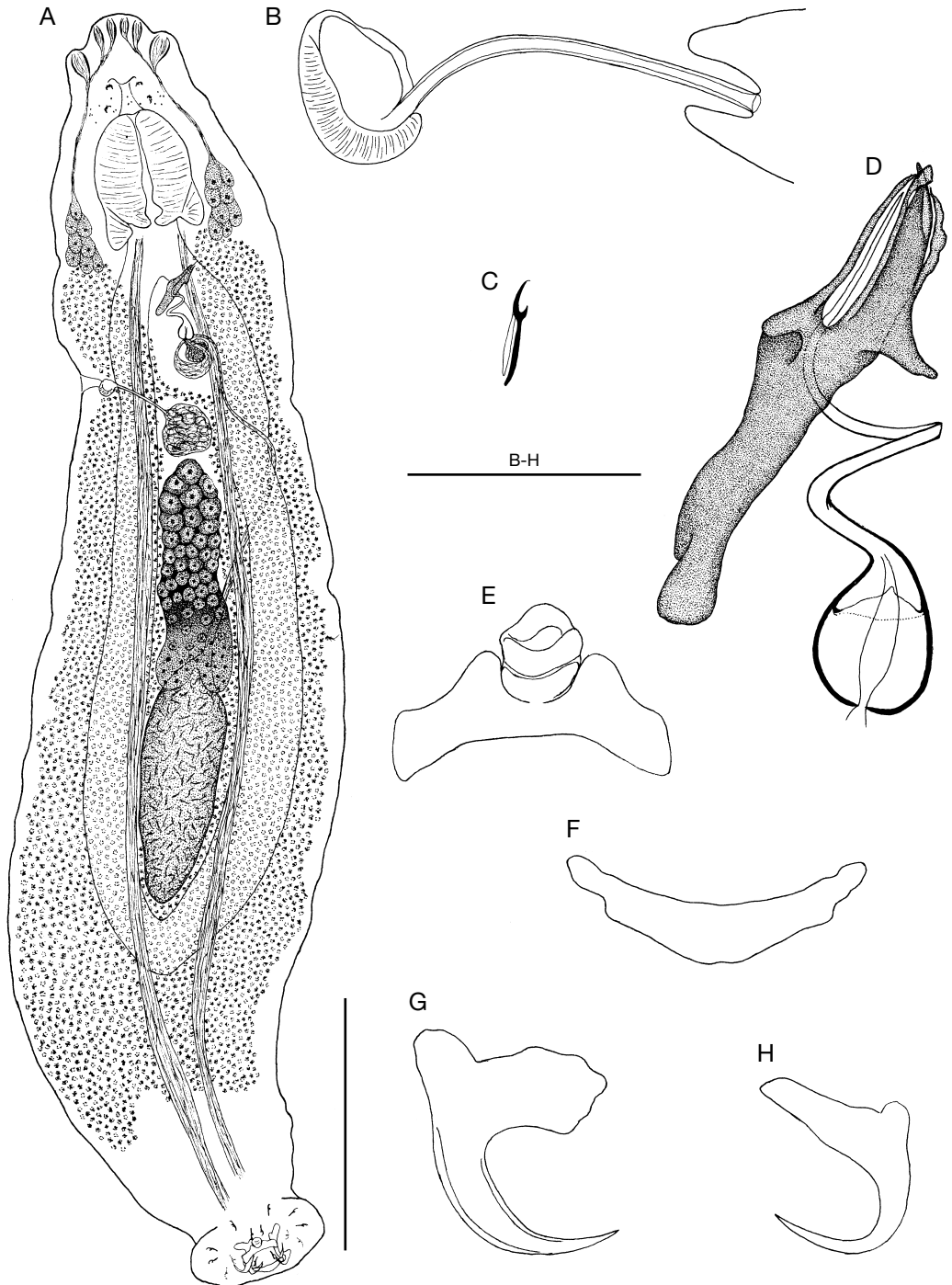


FIG. 9. — *Euryhaliotrema sagmatum* n. gen., n. sp.: **A**, whole mount (ventral view); **B**, vagina (ventral view); **C**, hook; **D**, copulatory complex (ventral view); **E**, ventral bar; **F**, dorsal bar; **G**, ventral anchor; **H**, dorsal anchor. Scale bars: A, 200 µm; B-H, 25 µm.

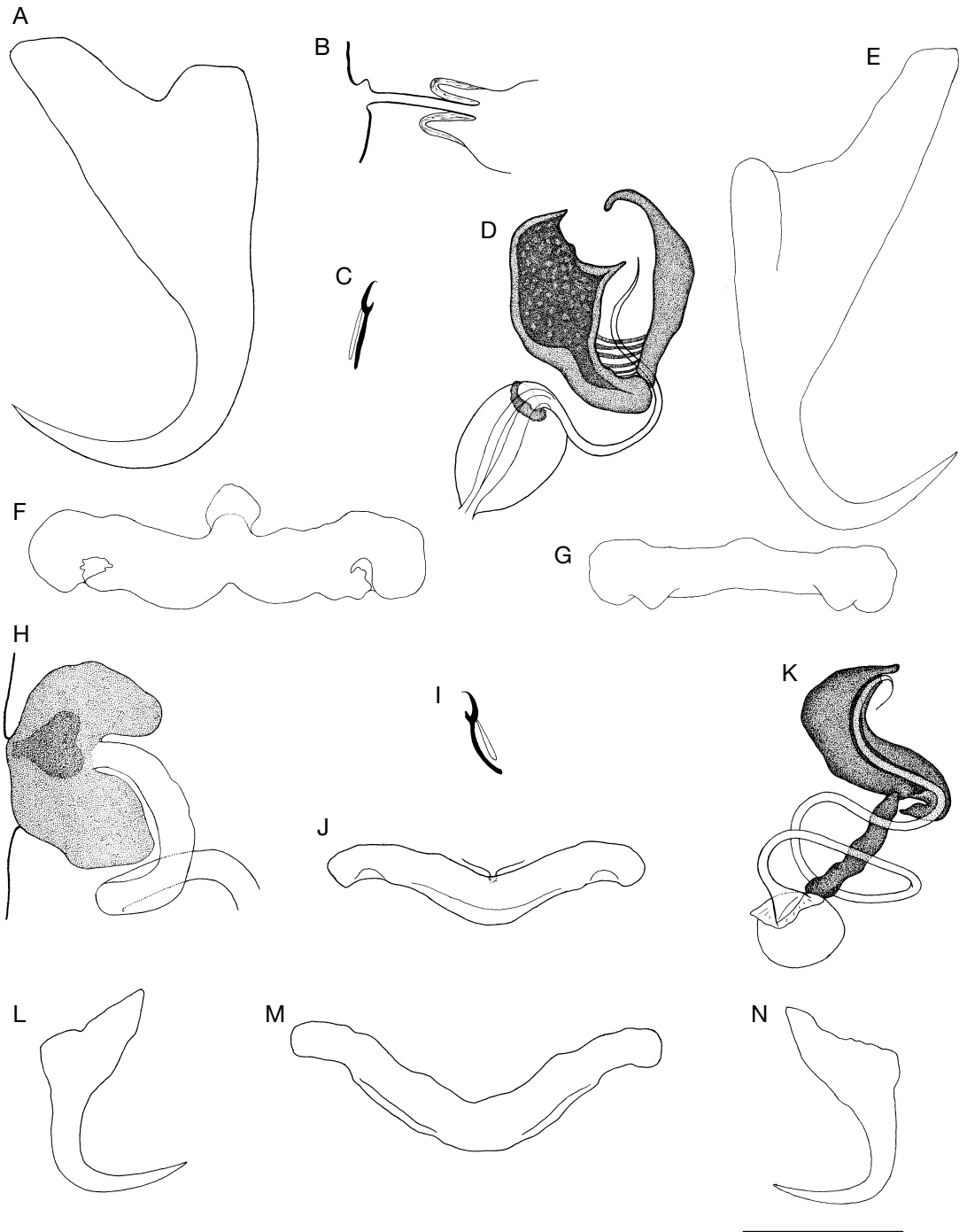


FIG. 10. — Sclerotized structures of *Euryhaliotrema* n. gen. species; **A-G**, *Euryhaliotrema bychowskyi* (Obodnikova, 1976) n. comb.; **A**, ventral anchor; **B**, vagina (ventral view); **C**, hook; **D**, copulatory complex (ventral view); **E**, dorsal anchor; **F**, ventral bar; **G**, dorsal bar; **H-N**, *Euryhaliotrema paralonchuri* (Lugue & Iannacone, 1989) n. comb; **H**, vagina (ventral view); **I**, hook; **J**, ventral bar; **K**, copulatory complex (ventral view); **L**, dorsal anchor; **M**, dorsal bar; **N**, ventral anchor. Scale bar: 25  $\mu$ m.

## REDESCRIPTION

Body 858 (683-1189; n = 4) long, flattened dorsoventrally; greatest width 285 (243-356; n = 4) at level of posterior end of testis. Cephalic region broad; cephalic lobes moderately to well developed. Eyes dissociated; accessory granules in narrow band anterior to pharynx. Pharynx spherical, 63 (54-68; n = 4) in greatest width. Peduncle short, tapering posteriorly; haptor subtrapezoidal, 150 (120-189; n = 4) wide, 106 (82-121; n = 4) long. Ventral anchor 74 (72-75; n = 4) long, with short roots, short evenly curved shaft, point reaching level of tip of superficial root; base 40 (39-41; n = 2) wide. Dorsal anchor 82 (80-83; n = 4) long, with large base, elongate superficial root, short deep root, evenly curved short shaft, point reaching level of tip of superficial root; base 39 (34-43; n = 2) wide. Ventral bar 60 (50-69; n = 4) long, yoke shaped, with anteromedial protuberance, posterior shield absent; dorsal bar 56 (50-62; n = 4) long, straight, with bilateral subterminal posterior bosses. Hook 14 (13-16; n = 7) long, shank uniform; FH loop about shank length. Copulatory organ 75 (72-80; n = 3) long, with coil of about one and a half counterclockwise rings; coil diameter 17 (15-19; n = 4). Accessory piece 35 (32-38; n = 3) long, comprising two subunits forming pincher-like claw, lacking articulation process. Testis 349 (313-386; n = 2) long, 144 (138-149; n = 2) wide; seminal vesicle forming C-shaped loop posterior to base of copulatory organ; prostatic reservoir lying within loop of seminal vesicle. Germarium 182 (163-201; n = 2) long, 80 (72-89; n = 2) wide, elongate pyriform, usually proximally lobed, overlying anterior end of testis; oviduct, ootype not observed; uterus delicate, ventral. Vaginal aperture marginal; vaginal canal short, straight, indenting seminal receptacle. Seminal receptacle elongate, extending to near dextral body margin anterior to germarium. Vitellaria dense.

## REMARKS

This species is sister to *E. sagmatum* n. gen., n. sp. Differentiation of these species is provided in the

Remarks for *E. sagmatum* n. gen., n. sp. The present species possesses all of the characters defining *Euryhaliotrema* n. gen. and its transfer as *E. bychowskyi* n. comb. is proposed.

*Euryhaliotrema paralonchuri*

(Lugue & Iannacone, 1989) n. comb.

(Fig. 10H-N)

*Pseudohaliootrema paralonchuri* Lugue & Iannacone, 1989: 545-547.

HOST AND LOCALITY. — Gills of *Paralonchurus peruanus* (Sciaenidae): Litoral de Lima, Peru, 12°30'S, 76°50'W.

MATERIAL EXAMINED. — Two paratypes (USNPC 81341); two voucher specimens (USNPC 91426).

PREVIOUS RECORD. — *Paralonchurus peruanus* (Sciaenidae): Fish Market at Chorrillos, Lima, Peru (Lugue & Iannacone 1989).

## MEASUREMENTS

Measurements of our specimens follow those of the two paratypes in brackets. Body fusiform; ventral anchor 30 (29-31; n = 2) (31 [29-32; n = 3]) long, base 15-16 (n = 2) (19 [18-20; n = 3]) wide; dorsal anchor 31 (30-32; n = 2) (29-30 [n = 3]) long, base 18 (17-19; n = 2) (16 [15-18; n = 3]) wide; hook 14 (13-15; n = 6) (13-14 [n = 6]) long, FH loop about shank length; copulatory organ 149 (145-153; n = 2) (128 [113-143; n = 2]) long; coil counterclockwise, diameter 23 (22-25; n = 2) (30 [28-31; n = 2]); vaginal aperture marginal.

## REMARKS

Our specimens and the paratypes of *E. paralonchuri* n. comb. are unstained and cleared and are unsuitable for redescription of the species. Lugue & Iannacone (1989) originally placed this species in *Pseudohaliootrema*. Based on the presence of a bulbous base of the copulatory organ, however, it is clearly a member of *Euryhaliotrema* n. gen., where it serves as sister species to *E. atlantica* n. gen., n. sp. Thus, *E. paralonchuri* n. comb. is proposed. Differentiation of *E. paralonchuri* n. comb. and *E. atlantica* n. gen., n. sp. is provided in the Remarks for the latter species.

*Euryhaliotrema chrysotaeniae*

(Young, 1968) n. comb.

(Fig. 11A-G)

*Haliotrema chrysotaeniae* Young, 1968: 55, 56.

TYPE HOST AND LOCALITY. — Gills of *Lutjanus chrysotaenia*, a junior synonym of *L. carponotatus* (Lutjanidae): Heron Island, Queensland, Australia (Young 1968).

MATERIAL EXAMINED. — Holotype (USNPC 61274); paratype (USNPC 61275).

MEASUREMENTS

Body 529 (485-574; n = 2) long, fusiform; greatest width 146 (124-168; n = 2); pharynx 35 (32-39; n = 2) in diameter; haptor 93 (85-101; n = 2) wide, 70 (61-79; n = 2) long; ventral anchor 41 (39-43; n = 2) long, base 18 (17-19; n = 2) wide; dorsal anchor 35-36 (n = 2) long, base 16-17 (n = 2) wide; ventral bar 25 (24-26; n = 2) long, dorsal bar 37-38 (n = 2) long; hook 13-14 (n = 4) long, FH loop about shank length; copulatory organ 495 (n = 1) long; coil clockwise; ring diameter 44 (41-47; n = 2); accessory piece 36 (32-39; n = 2) long; testis 80 (69-91; n = 2) long, 83 (70-96; n = 2) wide; germarium 57 (53-61; n = 2) long, 39 (30-48; n = 2) wide; vaginal aperture dextroventral.

REMARKS

This species, originally placed in *Haliotrema* and adequately described by Young (1968), is transferred to *Euryhaliotrema* n. gen. as *E. chrysotaeniae* n. comb. It, *E. johnei* n. comb. and *E. lutiani* n. comb., parasitize lutjanid hosts and form a monophyletic lineage within *Euryhaliotrema* n. gen. *Euryhaliotrema chrysotaeniae* n. comb. differs from *E. johnei* n. comb. and *E. lutiani* n. comb. in possessing a delicate copulatory organ with more than three rings and an elongate meandering vaginal canal (vaginal canal comparatively short in *E. johnei* n. comb. and *E. lutiani* n. comb.).

*Euryhaliotrema lutiani* (Yamaguti, 1953) n. comb.

(Fig. 11H-N)

*Haliotrema lutiani* Yamaguti, 1953: 211, 212.

TYPE HOST AND LOCALITY. — Gills of *Lutjanus* sp. (Lutjanidae): Macassar, Celebes (Yamaguti 1953).

MATERIAL EXAMINED. — Holotype, five paratypes (MPM 22640).

MEASUREMENTS

Body 840 (730-922; n = 4) long, fusiform; greatest width 168 (163-175; n = 3); pharynx 41 (35-46; n = 6) in diameter; haptor 93 (83-111; n = 4) wide, 75 (67-89; n = 4) long; ventral anchor 35 (32-36; n = 6) long, base 18 (16-20; n = 2) wide; dorsal anchor 35 (34-36; n = 6) long, base 19 (16-20; n = 6) wide; ventral bar 28 (24-32; n = 6) long, dorsal bar 40 (38-44; n = 6) long; hook 14 (13-15; n = 9) long, FH loop about shank length; copulatory organ 65 (n = 1) long, coil clockwise, ring diameter 24 (21-27; n = 3); accessory piece 26 (22-28; n = 4) long; testis 232 (218-242; n = 3) long, 111 (106-115; n = 3) wide; germarium 56-57 (n = 1) long, 36-37 (n = 1) wide; vaginal aperture dextroventral.

REMARKS

Yamaguti (1953) described this species as *Haliotrema lutiani* Yamaguti, 1953. His description, while basically adequate, lacks drawings of the haptor armament and copulatory complex, which are provided herein for comparative purposes. The species is transferred to *Euryhaliotrema* n. gen. as *E. lutiani* n. comb. It is most similar to *E. johnei* n. comb. based on the morphology of the copulatory complex. *Euryhaliotrema lutiani* n. comb. and *E. johnei* n. comb. differ in comparative morphology of the haptor armament and vagina.

*Euryhaliotrema johnei* (Tripathi, 1959) n. comb.

(Fig. 11O-U)

*Ancyrocephalus johnei* Tripathi, 1959: 44-46.

*Haliotrema johnii* (Tripathi, 1959) – Young, 1968: 43.

TYPE HOST AND LOCALITY. — Gills of *Lutjanus johnii* (Lutjanidae): River Hooghly at Diamond Harbor, India (Tripathi 1959).

MATERIAL EXAMINED. — Four voucher specimens (USNPC 61273).

OTHER RECORDS. — *Lutjanus johnii* (Lutjanidae): Green Island, Queensland, Australia (Young 1968). *Lutjanus fulviflamma* (Lutjanidae): Heron Island, Queensland, Australia (Young 1968).

MEASUREMENTS

Body 730 (711-747; n = 3) long, fusiform; greatest width 148 (145-153; n = 3); pharynx 44



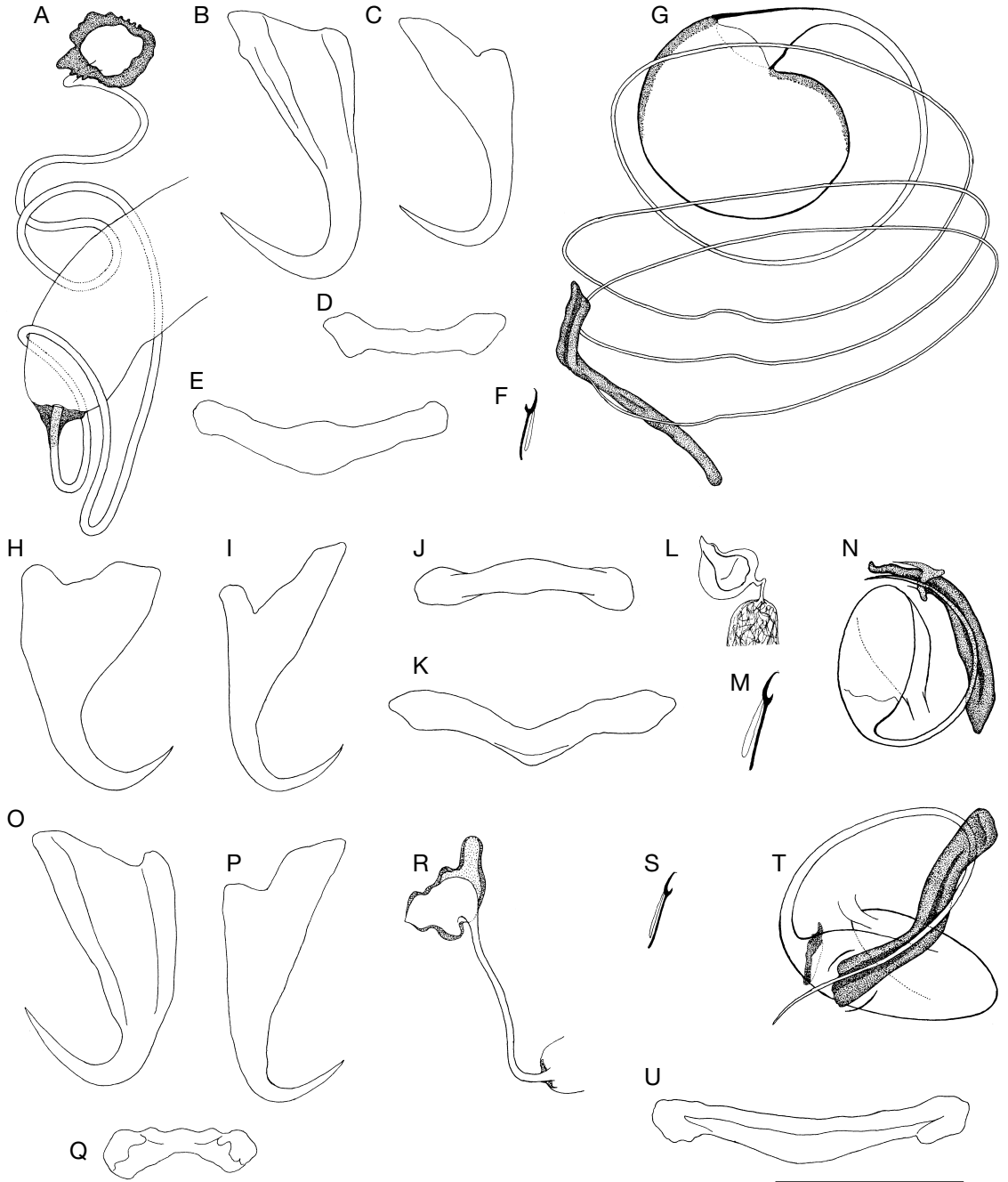


FIG. 11. — Sclerotized structures of *Euryhaliotrema* n. gen. species; **A-G**; *Euryhaliotrema chrysotaeniae* (Young, 1968) n. comb.; **A**, vagina (ventral view); **B**, ventral anchor; **C**, dorsal anchor; **D**, ventral bar; **E**, dorsal bar; **F**, hook; **G**, copulatory complex (ventral view); **H-N**; *Euryhaliotrema lutiani* (Yamaguti, 1953) n. comb.; **H**, ventral anchor; **I**, dorsal anchor; **J**, ventral bar; **K**, dorsal bar; **L**, vagina (ventral view); **M**, hook; **N**, copulatory complex (dorsal view); **O-U**; *Euryhaliotrema johni* (Tripathi, 1959) n. comb.; **O**, ventral anchor; **P**, dorsal anchor; **Q**, ventral bar; **R**, vagina (ventral view); **S**, hook; **T**, copulatory complex (ventral view); **U**, dorsal bar. Scale bar: 25  $\mu$ m.

(41-48; n = 3) in diameter; haptor 93 (82-99; n = 3) wide, 67 (65-69; n = 3) long; ventral anchor 35-36 (n = 2) long, 24-25 (n=1) wide; dorsal anchor 32 (31-34; n = 3) long, 20-21 (n=1) wide; ventral bar 22-23 (n = 2) long, dorsal bar 39 (37-42; n = 2) long; hook 14-15 (n = 8) long, FH loop about shank length; copulatory organ 120 (n = 1) long, coil clockwise, ring diameter 28 (21-32; n = 3); accessory piece 29 (26-31; n = 3) long; testis 232 (218-242; n = 3) long, 111 (106-115; n = 3) wide; germarium 51 (45-57; n = 2) long, 31 (26-36; n = 2) wide; vaginal aperture dextro-ventral.

REMARKS

The original description of this species by Tripathi (1959) as *Ancyrocephalus johni* Tripathi, 1959 is inadequate. Young (1968) redescribed the species and transferred it to *Haliotrema* based on specimens collected in Queensland, Australia. The species is herein transferred to *Euryhaliotrema* n. gen. as *E. johni* n. comb., where it most closely resembles *E. lutiani* n. comb. Differentiation of these two species is accomplished in the Remarks for *E. lutiani* n. comb.

*Euryhaliotrema longibaculum*  
(Zhukov, 1976) n. comb.

*Haliotrema longibaculum* Zhukov, 1976: 39.

MATERIAL EXAMINED. — Voucher specimen from *Lutjanus synagris*, Gulf of Campeche (Gulf of Mexico) (USNPC 91427).

PREVIOUS RECORDS. — Gills of *Lutjanus mahogoni* (type host) and *Lutjanus synagris* (Lutjanidae): Havana and Gulf of Campeche (Gulf of Mexico) (Zhukov 1976). According to Timofeeva (pers. comm.), the holotype of *E. longibaculum* n. comb. was collected from *L. mahogoni*.

MEASUREMENTS

Ventral anchor 27 (25-28; n = 2) long, base 13 (12-14; n = 2) wide; dorsal anchor 45 (43-46; n = 2) long, base 9-10 (n = 2) wide.

REMARKS

The original description of this species as *Haliotrema longibaculum* by Zhukov (1976) indicates

that the body is fusiform and the vaginal aperture is dextroventral in the body, while the direction of the coil of the copulatory organ is uncertain. Although not a part of the type series, the specimen of *H. longibaculum* available to us was collected by Dr Zhukov and was apparently used to complement his description of the species (Timofeeva pers. comm.). The unstained specimen is severely flattened and damaged, and it was not possible to determine many diagnostic features of internal anatomy and of the sclerotized parts of the haptor and copulatory complex. Nonetheless, this species is clearly a member of *Euryhaliotrema* n. gen. as shown by the presence of a bulbous base of the copulatory organ. Zhukov (1976) shows the bulbous base of the copulatory organ in his drawing of the copulatory complex but the bulb was not illustrated in his drawing of the terminal reproductive genitalia (Zhukov 1976: fig. 6). Thus, *Euryhaliotrema longibaculum* n. comb. is proposed. It differs from all other described species of *Euryhaliotrema* n. gen. in having a comparatively broad copulatory tube comprising less than one ring. The accessory piece is articulated to the base of the copulatory organ by a straight stout articulation process. The ventral anchor possesses a narrow base with an elongate superficial root, while the deep root is short to nonexistent.

*Euryhaliotrema torquecirrus*  
(Zhukov, 1976) n. comb.

*Haliotrema torquecirrus* Zhukov, 1976: 41, 42.

MATERIAL EXAMINED. — Three voucher specimens from *Ocyurus chrysurus*, Gulf of Campeche (Gulf of Mexico) (USNPC 91432).

PREVIOUS RECORDS. — Gills of *Lutjanus synagris*, *Ocyurus chrysurus* (type host) (Lutjanidae): Havana and Gulf of Campeche (Gulf of Mexico) (Zhukov 1976). According to Timofeeva (pers. comm.), the holotype of *E. torquecirrus* n. comb. was collected from *O. chrysurus*.

MEASUREMENTS

Copulatory organ ring diameter 31-32 (n = 1); accessory piece 35-36 (n = 1) long; ventral anchor

24-25 (n = 2) long, base 14-15 (n = 1) wide; dorsal anchor 26 (25-27; n = 2) long, base 14-15 (n = 2) wide; ventral bar 30-31 (n = 1) long; dorsal bar 30-31 (n = 1) long; hook 13-14 (n = 8) long.

#### REMARKS

The three vouchers from Zhukov's collection are unstained, flattened and highly cleared and one specimen is badly damaged. While it was not possible to determine features of the internal organ systems from available specimens, the body of *E. torquecirrus* n. comb. is apparently fusiform and the vaginal aperture appears to be dextro-ventral. The copulatory organ has three rings and a large bulbous base, the accessory piece is distally bilobed, and the hook possesses an upright acute thumb and slender shank comprised of one subunit. Although the species requires redescription, these features are sufficient to place it in *Euryhaliotrema* n. gen.; *E. torquecirrus* n. comb. is proposed. Based on the morphology of the copulatory complex, *E. torquecirrus* n. comb. most closely resembles *E. chrysotaeniae* n. comb., from which it differs in having a more robust accessory piece and ventral anchors with well differentiated roots.

#### *Euryhaliotrema tubocirrus* (Zhukov, 1976) n. comb.

*Haliotrema tubocirrus* Zhukov, 1976: 40, 41.

MATERIAL EXAMINED. — Two voucher specimens from *Lutjanus synagris*, Gulf of Campeche (Gulf of Mexico) (USNPC 91431).

PREVIOUS RECORDS. — Gills of *Lutjanus analis*, *Lutjanus apodus*, *Lutjanus cyanopterus*, *Lutjanus synagris* (type host), *Rhomboplites aurorubens* (Lutjanidae): Havana and Gulf of Campeche (Gulf of Mexico) (Zhukov 1976). According to Timofeeva (personal communication), the holotype of *E. tubocirrus* n. comb. was collected from *L. synagris*.

#### MEASUREMENTS

Copulatory organ ring diameter 28-29 (n = 1); accessory piece 27-28 (n = 1) long; ventral anchor 29 (28-31; n = 2) long, base 15-16 (n = 1) wide; dorsal anchor 31-32 (n = 2) long, base 15-16 (n = 1) wide; dorsal bar 33 (31-36; n = 2) long; hook 14-15 (n = 3) long.

#### REMARKS

This species requires redescription. The two specimens from Zhukov's collection, both damaged, flattened and cleared, were unsuitable for determination of internal features. The vaginal aperture is apparently dextro-ventral; the tube of the copulatory organ has a bulbous base and appears to be enclosed within a tissue sheath; the accessory piece is clavate and apparently not articulated to the bulbous base of the copulatory organ; the anchors have well-developed roots; and the hook has an upright acute thumb and slender shank composed of one subunit. Based on these observations, this species is transferred to *Euryhaliotrema* n. gen. as *E. tubocirrus* n. comb. *Euryhaliotrema tubocirrus* n. comb. is similar to *E. torquecirrus* n. comb. but differs from it in having a sheath surrounding the tube of the copulatory organ.

#### *Euryhaliotrema fastigatum* (Zhukov, 1976) n. comb.

*Haliotrema fastigatum* Zhukov, 1976: 43.

PREVIOUS RECORDS. — *Lutjanus apodus* (type host), *Lutjanus jocu* (Lutjanidae): Havana (Gulf of Mexico) (Zhukov 1976). According to Timofeeva (personal communication), the holotype of *E. fastigatum* n. comb. was collected from *L. apodus*.

#### REMARKS

Specimens of this species were not available for study. Our proposed new combination for *Haliotrema fastigatum* is based on details presented in the original description (Zhukov 1976), where figures of the copulatory complex, haptor armament and internal organs are consistent with the diagnosis of *Euryhaliotrema* n. gen. The original two drawings of the copulatory complex are contradictory regarding the direction of the two and a half rings of the copulatory organ (Zhukov 1976: fig. 10). This species requires redescription in order to determine its phylogenetic position within *Euryhaliotrema* n. gen.

TABLE 1. — Character matrix used in reconstruction of evolutionary relationships of *Euryhaliotrema* n. gen. species. Abbreviations: **A-R**, see Character analysis; **?**, refers to an unknown character state; **-**, refers to an inapplicable state.

Taxon	A	B	C	D	E	F	G	H	I	J	K	L	M	N	O	P	Q	R
<i>E. atlantica</i> n. gen., n. sp.	0	0	0	0	1	0	1	1	1	0	1	1	0	1	1	0	1	1
<i>E. succedaneus</i> n. gen., n. sp.	0	1	1	-	0	0	1	0	1	1	1	1	0	1	1	1	1	1
<i>E. monacanthus</i> n. gen., n. sp.	0	1	0	0	0	0	0	0	1	-	-	1	0	1	0	-	1	1
<i>E. thatcheri</i> n. gen., n. sp.	0	1	0	0	0	0	0	0	1	1	1	1	0	1	1	1	1	1
<i>E. potamocetes</i> n. gen., n. sp.	0	1	0	0	1	0	1	0	1	0	1	1	0	1	0	1	1	1
<i>E. lovejoyi</i> n. gen., n. sp.	0	1	0	0	0	0	0	0	1	1	1	1	0	1	0	1	1	1
<i>E. chaoi</i> n. gen., n. sp.	0	1	1	-	0	0	1	0	1	1	1	1	0	1	1	1	1	1
<i>E. carbunculus</i> (Hargis, 1955) n. comb.	0	0	0	0	1	0	1	1	1	0	0	0	0	0	0	0	1	1
<i>E. sagmatum</i> n. gen., n. sp.	1	0	0	0	0	1	0	0	2	0	0	0	0	2	0	0	0	1
<i>E. chrysotaeniae</i> (Young, 1968) n. comb.	0	0	0	1	0	0	1	0	2	0	0	0	1	0	0	0	1	1
<i>E. lutiani</i> (Yamaguti, 1953) n. comb.	0	0	0	1	0	0	1	0	2	0	0	0	0	0	0	0	1	1
<i>E. johni</i> (Tripathi, 1959) n. comb.	0	0	0	1	0	0	0	0	2	0	0	0	1	0	0	0	1	1
<i>E. bychowyski</i> (Obodnikova, 1976) n. comb.	1	-	0	0	0	1	0	0	1	0	0	0	0	2	0	0	1	1
<i>E. paralonchuri</i> (Lugue & Iannaccone, 1989) n. comb.	0	-	0	0	1	0	1	1	1	0	1	1	0	1	1	0	1	1
<i>Ligophorus</i> spp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>H. calcaris</i> group	0	0	0	?	?	?	0	?	1	0	1	0	0	0	0	0	1	0

***Euryhaliotrema paracanthi***  
(Zhukov, 1976) n. comb.

*Haliotrema paracanthi* Zhukov, 1976: 42, 43.

TYPE HOST AND LOCALITY. — *Lutjanus apodus* (Lutjanidae): Havana (Gulf of Mexico) (Zhukov 1976).

REMARKS

While this species requires redescription and specimens were not available for study, *Haliotrema paracanthi* is transferred to *Euryhaliotrema* n. gen. based on the drawings presented in the original description. Zhukov's (1976) drawings are unclear regarding the morphology and position of the basal bulb and the direction of the rings of the coil of the copulatory organ (Zhukov 1976: fig. 9). Details of the internal organ systems and hook morphology in this species are wanting and its phylogenetic position within the genus is uncertain.

CHARACTER ANALYSIS

Homologous series used in the analysis follow. Numbers in parentheses preceding the definition of a character state refer to the coding that state

received in the matrix (Table 1). Bold numbers in brackets following the definition refer to respective evolutionary changes depicted in the cladogram (Fig. 12).

A. Body shape. Plesiomorphy: (0) fusiform. Apomorphy: (1) dorsoventrally flattened [2].

B. Eyes (when present). Plesiomorphy: (0) equidistant or members of posterior pair farther apart than those of anterior pair. Apomorphy: (1) members of posterior pair closer together than those of anterior pair [21].

C. Copulatory organ. Plesiomorphy: (0) coiled. Apomorphy: (1) meandering [25].

D. Coil of copulatory organ. Plesiomorphy: (0) counterclockwise. Apomorphy (1) clockwise [9].

E. Accessory piece. Plesiomorphy: (0) not articulated to base of copulatory organ [24]. Apomorphy: (1) articulated to base of copulatory organ [13].

F. C-shaped loop of vas deferens. Plesiomorphy: (0) absent. Apomorphy: (1) present [4].

G. Vaginal duct. Plesiomorphy: (0) without coils or loops [11, 26]. Apomorphy: (1) coiled or with loops [7].

H. Vaginal bulb. Plesiomorphy: (0) absent. Apomorphy: (1) present [14, 19].

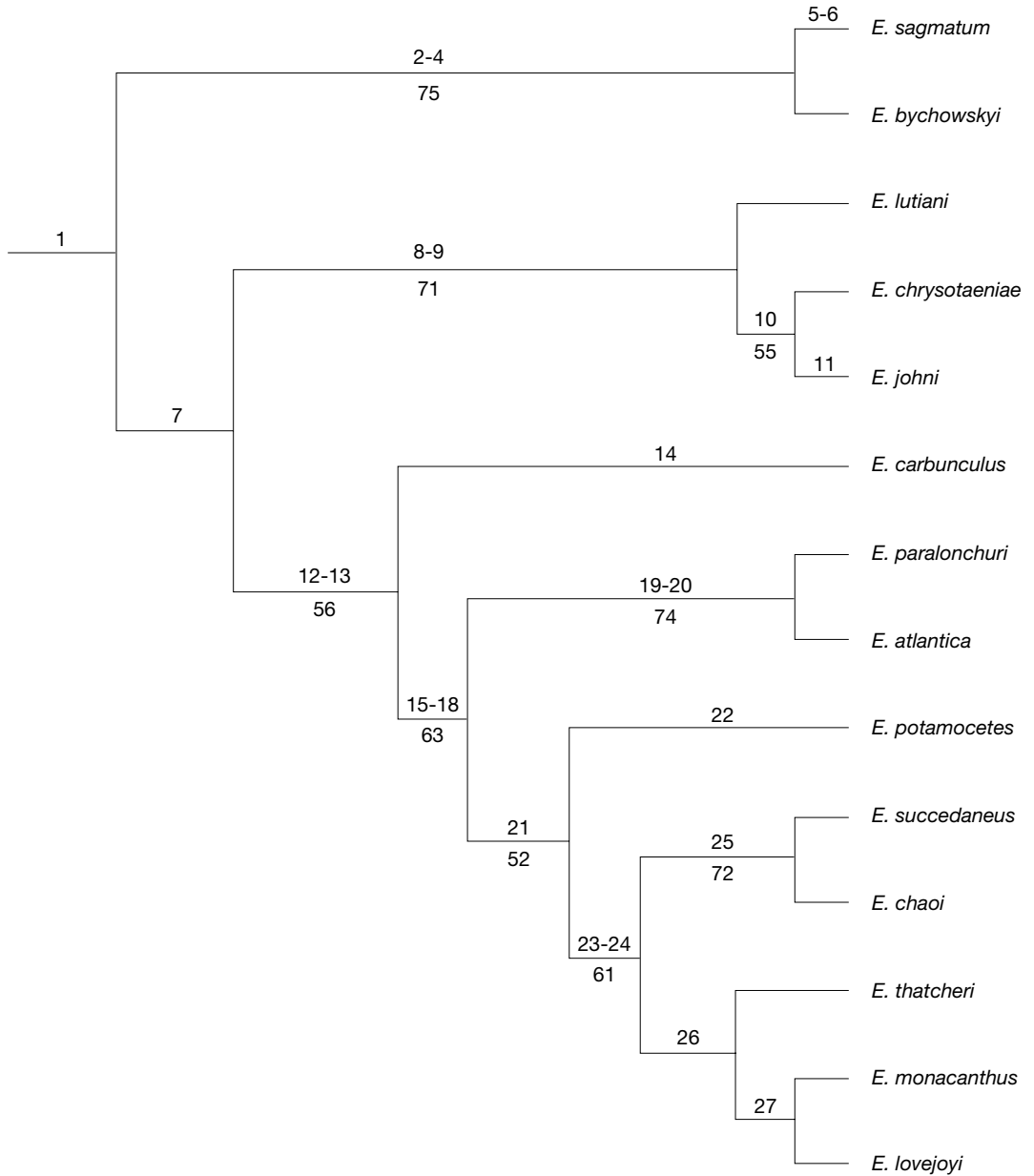


FIG. 12. — Hypothesis for the evolutionary history of 14 species of *Euryhaliotrema* n. gen. based on 18 homologous series of morphological characters. Numbers above each branch refer to postulated evolutionary changes as indicated in the character analysis. Numbers below each branch refer to bootstrap support for 1000 replicates; only values  $\geq 50\%$  are presented. Tree length = 30; Consistency Index = 66.7%; Retention Index = 83.1%.

I. Position of the vaginal aperture. Plesiomorphy: (0) midventral. Apomorphies: (1) dextral; (2) dextroventral [5, 8]. A midventral vaginal aper-

ture is apparently a synapomorphy of *Ligophorus* spp., while a dextral vaginal aperture appears to represent the plesiomorphic state for the ingroup.

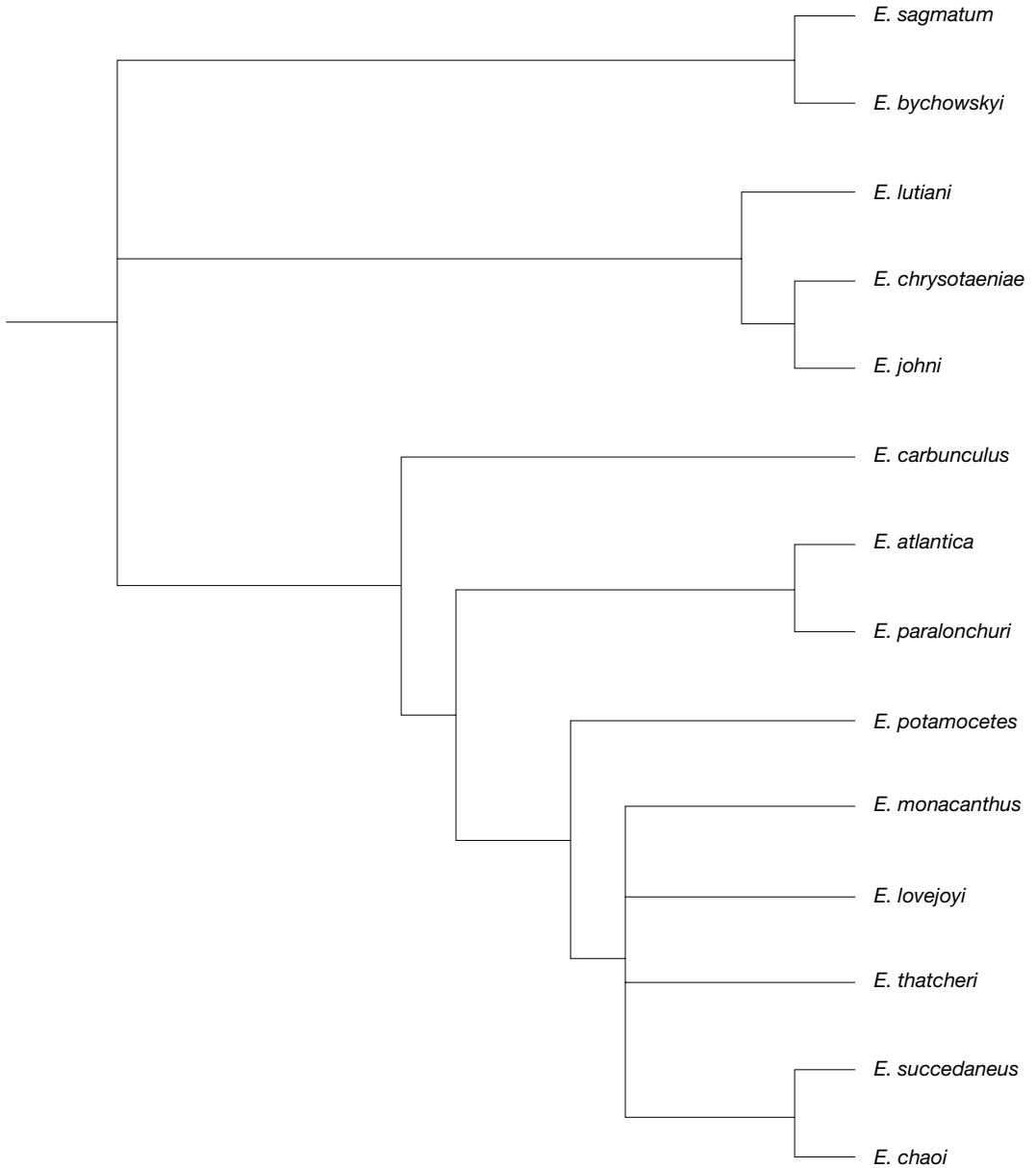


FIG. 13. — Strict consensus tree for sister-group relationships of 14 species of *Euryhaliotrema* n. gen. from eight equally parsimonious solutions obtained with PAUP\*.

J. Superficial root (dorsal anchor). Plesiomorphy: (0) straight. Apomorphy: (1) bent over dorsal bar [23].

K. Deep root (dorsal anchor). Plesiomorphy: (0) well-defined. Apomorphy: (1) poorly defined [18].

L. Deep root (ventral anchor). Plesiomorphy: (0) well defined. Apomorphy: (1) poorly defined [17].

M. Anterior and posterior margins of base of ventral anchor. Plesiomorphy: (0) without ridges. Apomorphy: (1) with heavy ridges [10].

- N. Anteromedial projection (ventral bar). Plesiomorphy: (0) absent. Apomorphies: (1) formed as a delicate plate [16]; (2) knob like [3].  
 O. Shield (ventral bar). Plesiomorphy: (0) absent [22, 27]. Apomorphy: (1) present [15].  
 P. Shield (dorsal bar). Plesiomorphy: (0) absent [20]. Apomorphy: (1) present [12].  
 Q. Submedial anterior projections (ventral bar). Plesiomorphy: (0) present. Apomorphy: (1) absent [6].  
 R. Base of copulatory organ. Plesiomorphy: (0) plate like or cone shaped. Apomorphy: (1) bulbous [1].

## PHYLOGENY

Five species, *Euryhaliotrema fastigatum* n. comb., *E. longibaculum* n. comb., *E. paracanthi* n. comb., *E. torquecirrus* n. comb. and *E. tubocirrus* n. comb., were excluded from analyses because of insufficient information on character states. The phylogenetic hypothesis (length = 30; Consistency Index = 66.7%; Retention Index = 83.1%) for the remaining 14 species of *Euryhaliotrema* n. gen., one of eight most parsimonious trees produced through the PAUP\* analysis using the 18 homologous series, is presented in Fig. 12. The hypothesis shows that the species of *Euryhaliotrema* n. gen., including the aberrant *E. monacanthus* n. gen., n. sp., from the freshwater sciaenids, *Plagioscion* spp., form a monophyletic clade, with *E. paralonchuri* n. comb. + *E. atlantica* n. gen., n. sp. from marine *Paralonchurus* spp. (Sciaenidae) comprising its sister group. *Euryhaliotrema sagmatum* n. gen., n. sp. from a marine sciaenid is sister species to *E. bychowskyi* n. comb. from a haemulid host indicating a possible host-switching event in the evolutionary history of the genus. *Euryhaliotrema* spp. from lutjanid hosts are monophyletic suggesting that they may have coevolved with their hosts. These relationships have variable support from strict consensus (Fig. 13) and bootstrap (Fig. 12). All species infesting marine hosts in the Lutjanidae, Haemulidae, Sparidae and Sciaenidae form the basal lineages suggesting that *Euryhaliotrema* n. gen. originated in the marine environment.

## DISCUSSION

Morphological boundaries of marine dactylogyrid genera are generally not well-established, with many, including *Haliotrema s.l.*, and *Pseudohaliotrema s.l.*, apparently representing polyphyletic taxa (see Klassen 1994; Lim in press). Kritsky & Stephens (2001) state that *Haliotrema (s.l.)* comprises 148 nominal species parasitizing fishes from 33 teleost families. Lim (in press), who restricts *Pseudohaliotrema s.s.* to five species from siganid hosts, lists a total of 16 species (from fishes of 10 host families) that have previously been placed in *Pseudohaliotrema (s.l.)*. *Euryhaliotrema* n. gen. incorporates new species (both freshwater and marine) and some marine species previously included in these genera. The new genus corresponds in part to Young's (1968) group 2 of *Haliotrema* species, which included *Haliotrema caesionis* Yamaguti, 1953, *H. chrysoetaeniae*, *H. johni*, and *H. lutiani*. A total of seven species of *Haliotrema (H. chrysoetaeniae, H. fastigatum, H. johni, H. longibaculum, H. lutiani, H. paracanthi, H. torquecirrus, and H. tubocirrus* from lutjanid hosts), and two species of *Pseudohaliotrema (P. carbunculus* from a sparid host and *P. paralonchuri* from a sciaenid) are transferred to *Euryhaliotrema* n. gen. as new combinations. *Haliotrema caesionis* from *Caesio cuning* (Bloch, 1791) (Caesionidae), a family closely aligned with the Lutjanidae (see Johnson 1975, 1980), is not accommodated in *Euryhaliotrema* n. gen. because it lacks an accessory piece in the copulatory complex and the base of the copulatory organ is disc shaped; it is provisionally retained in *Haliotrema*.

Fish hosts of the Lutjanidae are known to harbor nine other species (*Haliotrema calcaris*, *H. cornigerum*, *H. gracilihamus*, *H. heteracantha*, *H. longihamus*, *H. longitubocirrus*, *H. magnigastrohamus*, *H. noncalcaris*, and *H. patellacirrus*) and those of the Sparidae two species (*H. mediohamus* and *H. parvicirrus*) (see Bychowsky & Nagibina 1971; Zhukov 1976, 1983) that appear to form a monophyletic grouping. These species are characterized in part by having a perforation in the base of the dorsal anchor, shafts of the

ventral and/or dorsal anchors with a subterminal internal projection or expansion, and a copulatory organ lacking an accessory piece. This group of *Haliotrema* species, showing a similar host distribution to that of *Euryhaliotrema* spp., may represent the sister group to the new genus.

Our analysis of morphological characters of *Euryhaliotrema* spp. indicates that the genus is monophyletic based on presence of a bulbous base in the copulatory organ as its synapomorphy. That the marine species of *Euryhaliotrema* n. gen. form basal clades within the phylogenetic hypothesis suggests that the genus is comparatively old and had a marine origin that pre-dates the origins of the respective perciform families containing their hosts. On the other hand, the freshwater species of *Euryhaliotrema* n. gen. comprise a single terminal clade within the hypothesis which indicates that a single "colonization" of freshwater by their common ancestor occurred during historical development of the clade. The latter occurrence apparently occurred comparatively recently and probably corresponds to the concomitant colonization event by its ancestral *Plagioscion* host. Further, the Lutjanidae, Haemulidae, Sciaenidae and Sparidae, all of which contain hosts of *Euryhaliotrema* spp., have been suggested to be related (Chao 1978) indicating that species of *Euryhaliotrema* n. gen. may have coevolved with these host groups. If coevolution represents a significant aspect of the history of the taxon, it could be predicted that other marine perciform families, especially those with phylogenetic affinities with the Lutjanidae, Sciaenidae, Haemulidae and Sparidae, might be parasitized by other members of this genus.

One species, *Euryhaliotrema monacanthus* n. gen., n. sp., possesses a single anchor/bar complex (ventral), while all other species of *Euryhaliotrema* n. gen. possess both dorsal and ventral complexes. Traditionally, absence (representing apparent loss) of such structure has been used to justify proposal of independent higher taxa (genera) to accommodate these "aberrant" forms (i.e., *Schilbetrematoides* by Kritsky & Kulo 1992). In the case of *E. monacanthus* n. gen., n. sp., phylogenetic analysis shows that this species had its ori-

gin within the clade containing all other freshwater species of *Euryhaliotrema* n. gen. and that absence (loss) of the dorsal anchor/bar complex is a secondary event. The analysis does not support proposal of a new genus to accommodate *E. monacanthus* n. gen., n. sp. A comparable example was recently shown by Desdevises (2001), who suggests that *Furnestinia echeueis* (Wagener, 1857), the only member of *Furnestinia* Euzet & Audouin, 1959 (Monogenoidea: Diplectanidae) and which possesses a single lamellocyst (apparently representing secondary loss of one lamellocyst), should be included in *Lamellocystis* because phylogenetic analyses indicate that it had its origin within the latter taxon.

*Plagioscion squamosissimus* apparently has been recently introduced into the Paraná River in southern Brazil by man (Agostinho & Julio 1999). While species of *Euryhaliotrema* n. gen. enjoy a wide distribution on this fish in the Amazon and Orinoco River systems in northern South America, species of the genus were not encountered on this host in southern Brazil (seven specimens of *P. squamosissimus* examined from Itaipu Reservoir, Paraná River). Without discounting potential sampling error, absence of *Euryhaliotrema* spp. from the latter locality could be a result of extinction after introduction of the host into the new habitat.

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## REFERENCES

- AGOSTINHO A. A. & JULIO H. F. JR 1999. — Peixes da bacia do Alto Rio Paraná, in LOWE-MCCONNEL R. H., VAZZOLLER A. E. A. DE M., AGOSTINHO A. A. & CUNNINGHAM P. T. (eds), *Estudos Ecológicos de Comunidades de Peixes Tropicais*. EDUSP, São Paulo, 534 p.
- BYCHOWSKY B. E. & NAGIBINA L. F. 1971. — [New and little known species of the genus *Haliotrema* Johnston & Tiegs, 1922 (Monogeneoidea). 2]. *Zoologicheskii Zhurnal* 50: 25-40 (in Russian).
- CHAO L. N. 1978. — *A Basis for Classifying Western Atlantic Sciaenidae (Teleostei: Perciformes)*. NOAA Technical Report Circular 415, United States Department of Commerce, National Marine Fisheries Service, 64 p.
- DESDEVEISES Y. 2001. — The phylogenetic position of *Furnestinia ebeneis* (Monogenea, Diplectanidae) based on molecular data: a case of morphological adaptation? *International Journal for Parasitology* 31: 205-208.
- HARGIS W. J. JR 1955. — Monogenetic trematodes of Gulf of Mexico fishes. Part II. The Superfamily Gyrodactyloidea. (Continued). *Journal of Parasitology* 41: 185-193.
- HENNIG W. 1966. — *Phylogenetic Systematics*. University of Illinois Press, Urbana, Illinois, 263 p.
- JOHNSON G. D. 1975. — The procurrent spur: an undescribed perciform caudal character and its phylogenetic implications. *Occasional Papers of the California Academy of Sciences* 121, 23 p.
- JOHNSON G. D. 1980. — The limits and relationships of the Lutjanidae and associated families. *Bulletin of the Scripps Institute of Oceanography* 24: 1-114.
- KLASSEN G. J. 1994. — Phylogeny of *Haliotrema* species (Monogenea: Ancyrocephalidae) from boxfishes (Tetraodontiformes: Ostraciidae): Are *Haliotrema* species from boxfishes monophyletic? *Journal of Parasitology* 80: 596-610.
- KÖHN A., BAPTISTA-FARIAS M. F. D. & COHEN S. C. 2000. — *Paranaella luquei* gen. et sp. n. (Monogenea: Microcotylidae), a new parasite of Brazilian catfishes. *Folia Parasitologica* 47: 279-283.
- KRITSKY D. C., BOEGER W. A. & THATCHER V. E. 1985. — Neotropical Monogenea. 7. Parasites of the pirarucu, *Arapaima gigas* (Cuvier), with descriptions of two new species and redescription of *Dawestrema cycloancistrum* Price and Nowlin, 1967 (Dactylogyridae: Ancyrocephalinae). *Proceedings of the Biological Society of Washington* 98: 321-331.
- KRITSKY D. C. & KULO S.-D. 1992. — *Schilbetrematoides pseudodactylogyrus* gen. et sp. n. (Monogeneoidea, Dactylogyridae, Ancyrocephalinae) from the gills of *Schilbe intermedius* (Siluriformes, Schilbeidae) in Togo, Africa. *Journal of the Helminthological Society of Washington* 59: 195-200.
- KRITSKY D. C. & STEPHANS F. 2001. — *Haliotrema abaddon* sp. n. (Monogeneoidea: Dactylogyridae) from the gills of wild and maricultured West Australian dhufish, *Glaucosoma hebraicum* (Teleostei: Glaucosomatidae), in Australia. *Journal of Parasitology* 87: 749-754.
- KRITSKY D. C. & THATCHER V. E. 1984. — Neotropical Monogenea. 6. Five new species of *Diplectanum* (Diplectanidae) from freshwater teleosts, *Plagioscion* spp. (Sciaenidae), in Brazil. *Proceedings of the Biological Society of Washington* 97: 432-441.
- LIM S. L. H. in press. — Three new species of *Pseudohaliotrema* Yamaguti, 1953 (Monogenea: Ancyrocephalidae) from *Siganus* species (Siganidae) and the description of a mechanism for cross-insemination. *Journal of Natural History*.
- LUGUE J. L. & IANNAcone J. 1989. — *Pseudohaliotrema paralonchuri* sp. n. (Monogeneoidea: Dactylogyridae), parasitic on *Paralonchurus peruanus* (Steindachner) (Teleostei: Sciaenidae) from the Peruvian Coast. *Memorias Instituto Oswaldo Cruz* 84: 545-547.
- MADDISON W. P., DONOGHUE M. J. & MADDISON D. R. 1984. — Outgroup analysis and parsimony. *Systematic Zoology* 33: 83-103.
- MAYES M. A., BROOKS D. R. & THORSON T. B. 1981. — *Potamotrygonocotyle tsalickisi*, new genus and species (Monogenea: Monocotylidae) and *Paraheteronchocotyle amazonensis*, new genus and species (Monogenea: Hexabothriidae) from *Potamotrygon circularis* Garman (Chondrichthyes: Potamotrygonidae) in northwestern Brazil. *Proceedings of the Biological Society of Washington* 94: 1205-1210.
- MIZELLE J. D. 1936. — New species of trematodes from the gills of Illinois fishes. *American Midland Naturalist* 17: 785-806.
- MIZELLE J. D. & KLUCKA A. R. 1953. — Studies on monogenetic trematodes. XIV. Dactylogyridae from Wisconsin fishes. *American Midland Naturalist* 49: 720-733.
- MIZELLE J. D. & PRICE C. E. 1963. — Additional haptorall hooks in the genus *Dactylogyrus*. *Journal of Parasitology* 49:1028-1029.

- NASIR P. 1983. — Occurrence and significance of the monogenean *Cycloplectanum americanum* (Price, 1937) Oliver, 1968, on a freshwater host. *Journal of Parasitology* 69: 957-962.
- OBODNIKOVA V. A. 1976. — [A new representative of the genus *Haliotrema* (Dactylogyridae, Ancyrocephalinae) from *Haplochromis mucronatus*], in Fauna, Systematics and Phylogeny of Monogenoidea. *Proceedings, Institute of Biology and Pedology, Far-East Science Centre, Academy of Sciences of the U. S. S. R., New Series* 35: 89-91 (in Russian).
- SWOFFORD D. L. 2001. — *Phylogenetic Analysis Using Parsimony (\*and other methods). Version 4.* Sinauer Associates, Sunderland, Massachusetts.
- TRIPATHI Y. R. 1959. — Monogenetic trematodes from fishes of India. *Indian Journal of Helminthology* 9: 1-149.
- WATROUS L. E. & WHEELER Q. D. 1981. — The out-group comparison method of character analysis. *Systematic Zoology* 30: 1-11.
- WILEY E. O. 1981. — *Phylogenetics. The Theory and Practice of Phylogenetic Systematics.* John Wiley & Sons, New York, 439 p.
- YAMAGUTI S. 1953. — Parasitic worms mainly from Celebes. Part 2. Monogenetic trematodes of fishes. *Acta Medicinæ Okayama* 8: 203-256.
- YAMAGUTI S. 1963. — *Systema Helminthum.* Volume IV: *Monogenea and Aspidocotylea.* Interscience Publishers, New York, 699 p.
- YOUNG P. C. 1968. — Ten new species of *Haliotrema* (Monogenoidea: Dactylogyridae) from Australian fish and a revision of the genus. *Journal of Zoology, London* 154: 41-75.
- ZHUKOV E. V. 1976. — [New monogenean species of the genus *Haliotrema* Johnston and Tiegs, 1922, from the Gulf of Mexico fishes of the Fam. Lutianidae], in Fauna, systematics and phylogeny of Monogenoidea. *Proceedings, Institute of Biology and Pedology, Far-East Science Centre, Academy of Sciences of the U. S. S. R., New Series* 35: 33-47 (in Russian).
- ZHUKOV E. V. 1983. — [New species of monogeneans of the genus *Haliotrema* from gills of fishes belonging to the families Serranidae and Sparidae from the Mexican Gulf]. *Parazitologiya* 13: 57-61 (in Russian).

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