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Belonion, a New Genus of Fresh-water Needlefishes from South America

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INTRODUCTION

While preparing the sections on needlefishes and halfbeaks for "Fishes of the western North Atlantic," I examined two collections containing two new species that represent a new genus of needlefishes (Belonidae). One of these collections is from the Río Atabapo, a tributary of the Orinoco River on the Venezuela-Colombia border. The other is from the Rio Madeira, a tributary of the Amazon in Brazil. After completion of the first draft of this manuscript, an additional series of the second new species, recently collected in a tributary of the Rio Madeira in Bolivia near the Brazilian border, became available to me. Until the present time, only three fresh-water species of synentognaths have been known from South America east of the Andes: one halfbeak, *Hyporhamphus brederi* (Fernández-Yépez), and two needlefishes, *Potamorrhaphis guianensis* (Schomburgk) and *Pseudotylosurus angusticeps* (Günther).

Mme. M. L. Bauchot and the late Dr. Paulo de Miranda Ribeiro kindly lent me the original series of both new species. Recently, Dr. Reeve M. Bailey collected a fresh series of one of the new species, and he has graciously permitted me to report on these. This material was collected on the American Museum-Bolivian Expedition of 1964, sup-

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ported by Grant No. DA-MD-49-193-63-G82 of the United States Army Medical Research and Development Command, Office of the Surgeon General, and by the National Geographic Society and the American Museum of Natural History. Drs. E. H. Ahlstrom and Stanley H. Weitzman have assisted me with parts of the osteological work. Specimens were cleared and stained with the trypsin digestion method devised by Dr. W. Ralph Taylor. Messrs. Robert E. Jenkins, Harold Lazard, and Anthony H. Pierce, Jr., made the radiographs. Drs. Daniel M. Cohen, Robert H. Gibbs, Jr., William A. Gosline, John E. Randall, Donn E. Rosen, and Mr. Frederick H. Berry have commented on drafts of the manuscript. The figures of the new species were drawn by Mrs. Mildred H. Carrington. The figures of pharyngeal teeth, caudal skeletons, and interorbital canals were prepared by the author with the aid of a camera lucida and were inked and shaded by Mrs. Carrington. This paper is the fifth in a series on the systematics of synentognath (beloniform) fishes.

MATERIALS AND METHODS

Type materials of the new species are in the following collections:

A.M.N.H., the American Museum of Natural History
M.N.H.N., Museum National d'Histoire Naturelle, Paris
M.N.R.J., Museu Nacional, Rio de Janeiro, Brazil
U.S.N.M., United States National Museum, Smithsonian Institution

The specimens of *Belonion dibranchodon* are very soft; the specimens of *B. apodion* from both series are better preserved but are distorted. Therefore it was difficult to obtain accurate measurements. The body length from the posterior margin of the opercle to the base of the caudal fin is used as the indication of size rather than the standard length which includes the length of the frequently broken upper jaw. In order to emphasize the few morphometric differences, most of the measurements have been converted into per cent of head length for presentation. Head length was measured from the tip of the upper jaw to the posterior margin of the opercle.

In addition to examining the type material of the two new species, many preserved specimens, and radiographs of more than 1000 specimens representing 28 of the approximately 30 genera of synentognaths, I have partially dissected cleared and stained specimens of 24 genera which served as the primary basis for the comparative part of this paper. The number of cleared and stained specimens examined follows the name of the species.

Belonidae
- *Belone belone* (Linnaeus), two
- *Tylosurus crocodilus* (Peron and LeSueur), one
- *Ablennes hians* (Valenciennes), two
- *Platybelone argalus* (LeSueur), one
- *Strongylura notata* (Poey), two
- *Strongylura marina* (Walbaum), five
- *Pseudotylosurus angusticeps* (Günther), one
- *Xenentodon cancila* (Hamilton-Buchanan), one
- *Potamorrhaphis guianensis* (Schomburgk), four
- *Belonion dibranchodon,* new species, one
- *Belonion apodion,* new species, four

Scomberesocidae
- *Scomberesox saurus* (Walbaum), two
- *Cololabis saira* (Brevoort), four
- *Cololabis adocoetus* Böhlke, four

Hemiramphidae
- *Hemiramphus brasiliensis* (Linnaeus), two
- *Hyporhamphus picarti* (Valenciennes), 10
- *Hyporhamphus* species, 10
- *Arrhamphus sclerolepis* (Günther), one
- *Chriodorus atherinoides* Goode and Bean, four
- *Euleptorhamphus velox* Poey, two
- *Zenarchopterus gilli* Smith, three
- *Zenarchopterus buffonis* (Valenciennes), one
- *Dermogenys* species, one
- *Hemirhamphodon pogonognathus* (Bleeker), one
- *Oxyporhamphus micropterus* (Valenciennes), two

Exocoetidae
- *Fodiator acutus* (Valenciennes), one
- *Parexocoetus brachypterus* (Richardson), four
- *Exocoetus obtusirostris* Günther, five
- *Exocoetus volitans* Linnaeus, two
- *Danichthys rondeletii* (Valenciennes), five

This material is, or will be, deposited in the United States National Museum.

To facilitate comparison of *Belonion* with the other synentognath genera, the genera are listed in tables 1–3 in order of what I consider to be increasing specialization, insofar as this can be expressed in a linear sequence. The first two families (Belonidae and Scomberesocidae) form the suborder Scomberesocoidei (superfamily Scomberesocoidea of Rosen, 1964) which differs from the Exocoetoidei (superfamily Exocoetoidea of Rosen), composed of the Hemiramphidae and Exocoetidae, primarily by having the third pair of upper pharyngeal bones completely separate, not fused or closely joined. My ideas for the arrangement of the genera are based partly on my unpublished studies on the Belonidae and Hemiramphidae and partly on the literature (Regan, 1911;

TABLE 1

TOTAL NUMBER OF VERTEBRAE IN GENERA OF SYNENTOGNATHI

	35	37	39	41	43	45	47	49	51	53	55	57	59	61	63	65	67	69	71	73	75	77	79	81	83	85	87	89	91	93	95	97
BELONIDAE																																
Belone	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	x	x	x	x	—	—	—	—	—	—	—	—
Petalichthys	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	x	—	—	—	—	—	—	—	—	—	—	—	—	—
Tylosurus	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	x	x	x	x	x	x	x	x	x	x	x	x	x	x	—	—
Ablennes	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	x	x	x	x	x	x	x	x	x
Platybelone	—	—	—	—	—	—	—	—	—	—	—	—	—	x	x	x	x	x	x	x	x	—	—	—	—	—	—	—	—	—	—	—
Strongylura	—	—	—	—	—	—	—	—	—	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	—	—	—	—	—
Xenentodon	—	—	—	—	—	—	—	—	—	—	—	x	x	x	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Pseudotylosurus	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	x	x	x	—	—	—	—	—	—	—	—	—	—	—	—
Potamorrhaphis	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	x	x	x	x	x	x	—	—	—	—	—	—	—	—	—	—	—
Belonion dibranchodon	—	—	—	—	—	—	—	—	—	—	—	x	x	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Belonion apodion	—	—	—	—	—	—	—	—	x	x	x	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
SCOMBERESOCIDAE																																
Scomberesox	—	—	—	—	—	—	—	—	—	—	—	—	—	—	x	x	x	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
New genus Hubbs and Wisner	—	—	—	—	—	—	—	—	—	—	—	x	x	x	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Cololabis	—	—	—	—	—	—	—	—	—	—	—	—	—	—	x	x	x	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
New genus Hubbs and Wisner	—	—	—	—	—	—	—	—	—	x	x	x	x	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—

TABLE 1—(*Continued*)

	35	37	39	41	43	45	47	49	51	53	55	57	59	61	63	65	67	69	71	73	75	77	79	81	83	85	87	89	91	93	95	97
Hemiramphidae																																
Hemiramphus	—	—	—	—	—	—	—	—	x	x	x	x	x	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Hyporhamphus	—	—	—	—	—	x	x	x	x	x	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Odontorhamphus	—	—	—	—	—	—	—	—	—	x	x	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Arrhamphus	—	—	—	—	—	—	—	—	x	x	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Chriodorus	—	—	—	—	—	—	—	x	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Euleptorhamphus	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	x	x	x	—	—	—	—	—	—	—	—	—	—	—	—
Zenarchopterus	—	x	x	x	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Dermogenys	—	x	x	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Hemirhamphodon	—	—	x	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Oxyporhamphus	—	—	—	—	—	—	—	x	x	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Exocoetidae																																
Fodiator	—	x	x	x	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Parexocoetus	x	x	x	x	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Exocoetus	—	—	—	x	x	x	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Cypselurus	—	—	x	x	x	x	x	x	x	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Prognichthys	—	—	—	x	x	x	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Hirundichthys	—	—	—	—	x	x	x	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Danichthys	—	—	—	—	x	x	x	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—

TABLE 2
NUMBER OF PECTORAL RAYS IN GENERA OF SYNENTOGNATHI

	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
BELONIDAE																
Belone	—	—	—	—	—	—	—	x	x	x	—	—	—	—	—	—
Petalichthys	—	—	—	—	—	—	x	x	—	—	—	—	—	—	—	—
Tylosurus	—	—	—	—	—	—	—	—	x	x	x	—	—	—	—	—
Ablennes	—	—	—	—	—	—	—	x	x	x	x	—	—	—	—	—
Platybelone	—	—	—	—	—	x	x	x	x	—	—	—	—	—	—	—
Strongylura	—	—	—	—	x	x	x	x	x	—	—	—	—	—	—	—
Xenentodon	—	—	—	—	—	x	x	x	—	—	—	—	—	—	—	—
Pseudotylosurus	—	—	—	x	x	x	—	—	—	—	—	—	—	—	—	—
Potamorrhaphis	—	—	x	x	—	—	—	—	—	—	—	—	—	—	—	—
Belonion dibranchodon	x	x	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Belonion apodion	x	x	—	—	—	—	—	—	—	—	—	—	—	—	—	—
SCOMBERESOCIDAE																
Scomberesox	—	—	—	—	—	—	—	—	x	x	—	—	—	—	—	—
New genus Hubbs and Wisner	—	—	—	—	—	x	x	—	—	—	—	—	—	—	—	—
Cololabis	—	—	—	—	—	—	—	—	x	x	—	—	—	—	—	—
New genus Hubbs and Wisner	—	—	—	x	x	x	x	—	—	—	—	—	—	—	—	—
HEMIRAMPHIDAE																
Hemiramphus	—	—	—	—	—	x	x	x	—	—	—	—	—	—	—	—
Hyporhamphus	—	—	—	x	x	x	x	x	—	—	—	—	—	—	—	—
Odontorhamphus	—	—	—	—	—	—	x	x	—	—	—	—	—	—	—	—
Arrhamphus	—	—	—	—	—	—	—	x	x	—	—	—	—	—	—	—
Chriodorus	—	—	—	—	—	—	—	x	x	x	—	—	—	—	—	—
Euleptorhamphus	—	—	x	x	x	—	—	—	—	—	—	—	—	—	—	—
Zenarchopterus	—	—	—	x	x	x	x	—	—	—	—	—	—	—	—	—
Nomorhamphus	—	—	—	—	—	—	—	x	—	—	—	—	—	—	—	—
Dermogenys	—	—	—	—	x	x	x	x	—	—	—	—	—	—	—	—
Hemirhamphodon	—	—	—	x	x	—	—	—	—	—	—	—	—	—	—	—
Oxyporhamphus	—	—	—	—	—	—	x	x	x	—	—	—	—	—	—	—
EXOCOETIDAE																
Fodiator	—	—	—	—	—	—	—	—	x	x	x	x	—	—	—	—
Parexocoetus	—	—	—	—	—	—	—	x	x	x	—	—	—	—	—	—
Exocoetus	—	—	—	—	—	—	—	—	—	x	x	x	x	—	—	—
Cypselurus	—	—	—	—	—	—	—	x	x	x	x	x	x	—	—	—
Prognichthys	—	—	—	—	—	—	—	—	—	—	—	—	x	x	x	—
Hirundichthys	—	—	—	—	—	—	—	—	—	—	x	x	x	x	x	x
Danichthys	—	—	—	—	—	—	—	—	—	—	—	x	x	x	x	x

Nichols and Breder, 1928; Breder, 1932, 1938; Böhlke, 1951; and Parin, 1961). The names used for the Belonidae follow Collette and Berry (1965) rather than Mees (1962, 1964). Only the range of variation is given in tables 1–3 because the tables are intended to show only broad

TABLE 3

NUMBER OF BRANCHIOSTEGAL RAYS IN GENERA OF SYNENTOGNATHI

	6	7	8	9	10	11	12	13	14	15
BELONIDAE										
Belone	—	—	—	—	—	—	x	x	—	—
Petalichthys	—	—	—	—	—	—	x	—	—	—
Tylosurus	—	—	—	—	—	—	—	—	x	x
Ablennes	—	—	—	—	—	—	x	x	—	—
Platybelone	—	—	—	—	x	x	—	—	—	—
Strongylura	—	—	—	—	—	—	x	x	x	x
Xenentodon	—	—	—	—	—	x	—	—	—	—
Pseudotylosurus	—	—	x	—	—	—	—	—	—	—
Potamorrhaphis	—	—	—	—	x	x	—	—	—	—
Belonion dibranchodon	x	x	—	—	—	—	—	—	—	—
Belonion apodion	x	x	—	—	—	—	—	—	—	—
SCOMBERESOCIDAE										
Scomberesox	—	—	—	—	—	—	—	x	x	x
New genus Hubbs and Wisner	—	—	—	—	x	x	x	—	—	—
Cololabis	—	—	—	—	—	—	x	x	x	x
New genus Hubbs and Wisner	—	—	—	x	x	x	—	—	—	—
HEMIRAMPHIDAE										
Hemiramphus	—	—	—	—	—	—	x	x	—	—
Hyporhamphus	—	—	—	—	x	x	x	x	—	—
Odontorhamphus	—	—	—	—	—	x	x	x	—	—
Arrhamphus	—	—	—	—	—	—	x	x	x	—
Chriodorus	—	—	—	—	—	—	x	x	—	—
Euleptorhamphus	—	—	—	—	—	—	—	x	x	—
Zenarchopterus	—	—	x	x	x	x	—	—	—	—
Dermogenys	—	—	—	—	x	—	—	—	—	—
Hemirhamphodon	—	—	x	x	—	—	—	—	—	—
Oxyporhamphus	—	—	—	—	x	x	x	x	—	—
EXOCOETIDAE										
Fodiator	—	—	—	x	x	x	—	—	—	—
Parexocoetus	—	—	—	x	x	x	x	x	—	—
Exocoetus	—	—	—	x	x	x	x	—	—	—
Cypselurus	—	—	—	x	x	x	x	x	—	—
Prognichthys	—	—	x	x	x	x	x	—	—	—
Hirundichthys	—	—	—	x	x	x	x	—	—	—
Danichthys	—	—	—	—	x	x	x	—	—	—

evolutionary trends. The data for these tables are partly original and partly from the literature (Breder, 1938; Bruun, 1935; Parin, 1961).

BELONION, NEW GENUS

TYPE SPECIES: *Belonion apodion,* new species.

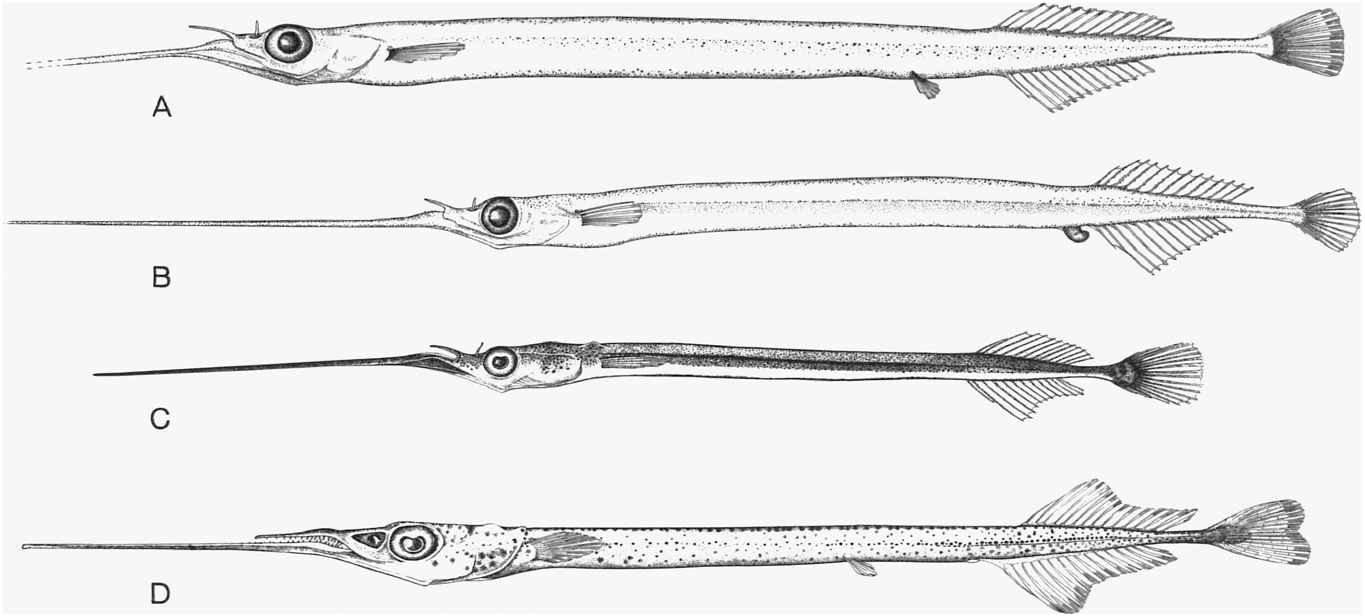

FIG. 1. A. Lateral view of paratype of *Belonion dibranchodon,* new species, U.S.N.M. No. 199463, Venezuela, Río Atabapo, 38.2 mm. in body length. B. Lateral view of paratype of *Belonion apodion,* new species, U.S.N.M. No. 199540, Brazil, Borba, 29.4 mm. in body length. C. Lateral view of holotype of *B. apodion,* new species, A.M.N.H. No. 20805, Bolivia, 3 kilometers southwest of Costa Margues, Brazil, female, 40.1 mm. in body length. D. Lateral view of juvenile of *Strongylura marina,* U.S.N.M. No. 189006, Nicaragua, 23.5 mm. in body length.

Diagnosis: Epipleurals absent (present in all other genera of Synentognathi). Fourth pair of upper pharyngeal bones absent (present in other genera of Scomberesocoidei except *Xenentodon*, absent from all genera of Exocoetoidei). Branchiostegal rays 6 or 7 (as low as 8 only in *Pseudotylosurus*, *Zenarchopterus*, *Hemirhamphodon*, and *Prognichthys*, 9–15 in other genera; table 3). Pectoral rays 5 or 6 (7–8 in *Potamorrhaphis*, 8–10 in *Pseudotylosurus*, 7–9 in *Euleptorhamphus*, 8–19 in other genera; table 2). Pleural ribs attached to second vertebra (on third in all other synentognaths except on second in *Hemirhamphodon*, and on fourth or fifth in *Pseudotylosurus*. Precaudal vertebrae 32–37, caudal vertebrae 19–23, total 52–59 (table 1). An elongate nasal barbel present. Preorbital canal a simple tube with three pores and no branches. Lower jaw very long (50% to 60% of body length) and upper jaw short. Second pair of upper pharyngeal bones present or absent. Principal caudal rays 7+8 or 6+7. Reproductive maturity attained at a small size (about 25 mm. body length).

Description: Head length 18 per cent to 23 per cent of body length. Snout length 29 per cent to 38 per cent of head length; postorbital distance 35 per cent to 45 per cent of head length; length of preopercle 11 per cent to 18 per cent of head length; length of orbit 23 per cent to 29 per cent of head length; interorbital width 17 per cent to 25 per cent of head length; head depth just posterior to orbit 23 per cent to 28 per cent of head length; head width just posterior to orbit 26 per cent to 31 per cent of head length; pectoral fin length 41 per cent to 51 per cent of head length.

Etymology: The neuter diminutive is from the Greek *belone*, needle, in reference to the small size of both species in the genus.

Belonion dibranchodon, new species

Figure 1A

Holotype: M.N.H.N. No. 87-836, 34.0 mm. in body length, 36.9 mm. in standard length; Venezuela, Río Atabapo, a tributary of the Orinoco River on the border between the state of Amazonas, Venezuela, and Vaupes, Colombia; M. Chaffanjon; 1887.

Paratypes: M.N.H.N. No. B.2529 (seven, 30.4–33.1 mm. in body length), U.S.N.M. No. 199463 (seven, 27.1–38.2 mm. in body length), and A.M.N.H. No. 20808 (one, 32.1 mm. in body length); all from the type locality.

Diagnosis: A species of *Belonion* with pelvic fins and pelvic girdle present; 7+8 principal caudal rays; 34–37 precaudal, 22–23 caudal, and 57–59 total, vertebrae; first pair of upper pharyngeal bones absent, second and third toothed; 12–14 dorsal rays, usually 14; 12–15 anal rays, usually 14 or 15. The interorbital canals are joined together (fig. 7D).

DESCRIPTION: Meristic data for *Belonion dibranchodon* are compared with those for *B. apodion* in tables 4 and 5; morphometric data are given in table 6. *Belonion dibranchodon* has a narrower interorbital width (17% to 22% of head length, $\bar{x}$ 18.3, versus 20% to 25%, $\bar{x}$ 21.6); a shorter post-orbital distance (35% to 40% of head length, $\bar{x}$ 37.4, versus 38% to 45%, $\bar{x}$ 40.8), and a slightly longer snout (30% to 38% of head length, $\bar{x}$ 33.8, versus 30% to 34%, $\bar{x}$ 31.4).

TABLE 4
NUMBER OF FIN RAYS IN *Belonion dibranchodon* AND *B. apodion*

	B. dibranchodon	*B. apodion*	
		Brazil	Bolivia
Dorsal fin rays			
11	—	5	—
12	1	24	2[a]
13	3	13	5
14	12[a]	1	—
Anal fin rays			
12	1	10	—
13	2	25	5[a]
14	8[a]	8	2
15	5	—	—

[a]Holotypes.

There are three longitudinal bands of pigment on the dorsum, sides, and venter. The band on the dorsum extends from the head to the base of the caudal fin along the middorsal line. It appears as two lines, because the smallest melanophores on the middorsal line have mostly faded. This pigment band is darker around the dorsal fin base. The lateral band is faint (fig. 1A) and composed of very small melanophores as in the Brazilian series of *Belonion apodion.* The ventral band is moderately wide and is composed of medium-sized melanophores. The band is wider than that of either of the two series of *B. apodion,* and the melanophores are somewhat smaller. The band becomes darker just anterior to the urogenital area, where it divides into two bands that continue on each side of the anal fin base and become lighter.

The pectoral, pelvic, and anal fins lack pigment, but there are a few melanophores on the pectoral fin base. The dorsal fin is mostly immaculate, but there are scattered melanophores on a few of the rays. There is a faint subterminal band on the caudal fin.

LOCALITY: These specimens are part of a collection made by Chaffanjon in the Orinoco and sent to the Paris museum in June, 1887. The exact locality of this collection is not known, but it was in the Río Atabapo which extends only about 70 miles along the Venezuela-Colombia border from the point where smaller streams come together on the south to its junction with the Orinoco proper on the north.

TABLE 5
NUMBER OF VERTEBRAE IN *Belonion dibranchodon* AND *B. apodion*

	B. dibranchodon	*B. apodion*	
		Brazil	Bolivia
Precaudal vertebrae			
32	—	1	—
33	—	10	1
34	1	17	3[a]
35	8[a]	2	3
36	5	—	—
37	2	—	—
Caudal vertebrae			
19	—	10	1
20	—	14	2[a]
21	—	5	4
22	9[a]	1	—
23	7	—	—
Total vertebrae			
52	—	2	1
53	—	15	—
54	—	9	3[a]
55	—	4	2
56	—	—	—
57	4[a]	—	—
58	9	—	—
59	3	—	—

[a] Holotypes.

Pellegrin (1903a, 1908, 1909, 1912) described a number of new species from Chaffanjon's Orinoco collections: a cichlid, *Pterophyllum altum;* three characins, *Hemiodus argenteus, Anastomoides atrianalis,* and *Brycon bicolor;* and a catfish, *Xenocara macrophthalma.* Pellegrin (1903b), in his revision of the Cichlidae, utilized material of five more species from Chaffanjon's collections: *Acaropsis nassa* (Heckel), *Cichla ocellaris* Bloch and Schneider, *Cichla temensis* Humboldt, *Cichlasoma insigne* (Heckel), and *Crenicichla brasiliensis* (Bloch) (three of Heckel's "varieties," *lenticula, lugubris,* and *johanna*).

TABLE 6

COMPARISON OF MORPHOMETRIC CHARACTERS OF *Belonion dibranchodon* AND TWO POPULATIONS OF *Belonion apodion*

(Head length in per cent of body length; other measurements in per cent of head length.)

	B. dibranchodon (N=9)		*B. apodion,* Brazil (N=8)		*B. apodion,* Bolivia (N=7)	
	$\bar{x}$	Range	$\bar{x}$	Range	$\bar{x}$	Range
Body length (mm.)	32.8	28.5–38.2	30.2	26.4–35.3	37.2	33.5–41.8
Standard length (mm.)	39.6	34.0–47.5	36.3	31.5–42.4	45.1	38.2–50.0
Head length	20.5	18.7–22.8	21.4	19.7–22.8	20.6	18.2–22.3
Snout length	33.8	30.5–37.9	31.6	29.8–33.8	31.2	29.2–33.8
Postorbital distance	37.4	35.2–40.0	41.1	37.5–43.7	40.5	39.2–45.0
Preopercle length	14.8	13.8–16.7	14.1	12.3–18.3	12.5	11.2–14.8
Orbital length	26.4	23.9–27.7	26.8	24.7–28.1	25.7	22.8–28.8
Interorbital width	18.3	16.9–21.8	21.3	19.7–23.4	22.0	19.7–25.0
Head depth	25.7	23.3–27.7	26.3	24.7–28.1	25.6	23.6–27.9
Head width	28.6	26.0–30.0	27.9	26.0–29.8	28.1	25.8–30.6
Pectoral length	45.4	41.1–50.9	45.0	43.1–47.4	44.9	41.8–47.5
Pelvic length	12.3	10.5–14.1	No pelvic fins		No pelvic fins	

ETYMOLOGY: From the Greek *di-*, two, *branchos,* gill, and *odontos,* tooth, in reference to the two pairs of toothed upper pharyngeal bones.

Belonion apodion, new species

Figure 1B, C

HOLOTYPE: A.M.N.H. No. 20805, female, 40.1 mm. in body length, 48.2 mm. in standard length; Bolivia, laguna 3 kilometers southwest of Costa Margues, Brazil, Río Guaporé; October 1, 1964; R. M. Bailey field number 64–48.

PARATYPES: A.M.N.H. No. 20806 (three, 34.1–37.1 mm. in body length) and U.S.N.M. No. 199539 (three, 33.5–41.8 mm. in body length), collected with the holotype. M.N.R.J. No. 4490 (82, 22.3–29.7 mm. in body length), U.S.N.M. No. 199540 (28, 21.0–37.9 mm. in body length), M.N.H.N. No. 66–725 (two, 25.3–27.1 mm. in body length), and A.M.N.H. No. 20807 (two, 25.5–30.4 mm. in body length), Brazil, Estado Amazonas, Lago Acara, Borba, Madeira River drainage, a tributary of the Amazon; A. Parko; September, 1943.

DIAGNOSIS: A species of *Belonion* without pelvic fins and pelvic girdle; 6+7 principal caudal rays; 32–35 precaudal, 19–22 caudal, and 52–56 total, vertebrae; first and second pair of upper pharyngeal bones absent, third pair toothed; 11–14 dorsal rays, usually 12; 12–14 anal rays; interorbital canals separate from each other (fig. 7C).

DESCRIPTION: Meristic and morphometric data for *Belonion apodion* and *B. dibranchodon* are compared in tables 4–6. *Belonion apodion* has a wider interorbital distance, a longer postorbital distance, and a slightly shorter snout.

There are three lateral pigment bands on the body of *Belonion apodion* as in *B. dibranchodon.* The Bolivian series is fresher and better preserved than the Brazilian series and differs in pigmentation mainly in having the melanophores more expanded. The Brazilian series has an even band of medium-sized melanophores on the dorsum, about 10 melanophores wide. The melanophores in the dorsal band of the Bolivian series are so expanded that they nearly fuse together to form a black stripe. The lateral band is even on its dorsal edge in the Brazilian series and irregular ventrally. The melanophores are much smaller than in the dorsal band. The lateral band in the Bolivian series is even and well defined ventrally, but the band gradually grades into the dorsal band above. The melanophores are much smaller, and there is more space between individual melanophores than in the dorsal band. The ventral band in both series is quite narrow and consists of medium-sized melanophores. The ventral band passes laterally to the immaculate urogenital region. The band is variable in intensity along the anal base and may become a solid black stripe in some specimens in the Bolivian series.

In the Brazilian series, the pectoral and anal fins lack pigment, but there is a concentration of melanophores surrounding the dorsal half of the pectoral fin base. A few scattered melanophores are present in some specimens on the anterior and posterior surfaces of the dorsal fin rays. In the Bolivian series, pigment around the base of the pectoral fin forms a crescent dorsoposteriorly. Small melanophores outline the pectoral rays. Most of the first three anal rays and the distal two-thirds of the other anal rays have melanophores. Melanophores are present all over the dorsal fin rays, and a few are present on the basal part of the dorsal fin membranes. The rays of the caudal fin are outlined by melanophores.

MATURITY: The Brazilian specimens more than 24.5 in body length are apparently mature. Most are females with small eggs. The smaller Brazilian specimens (22.8–24.5 mm. in body length) are immature. All the Bolivian specimens examined are mature, and the largest two (40.1–41.8 mm. in body length) have much larger (0.3 mm. in diameter) eggs than any of the Brazilian specimens, so may be nearly ripe.

ETYMOLOGY: From the Greek *a,* without, and *podos,* foot, in reference to the absence of pelvic fins and girdle.

DISCUSSION

By definition, *Belonion* belongs to the suborder Scomberesocoidei (superfamily Scomberesocoidea of Rosen, 1964) because it has the third pair of upper pharyngeal bones separate (fig. 2); in the Exocoetoidei (super-

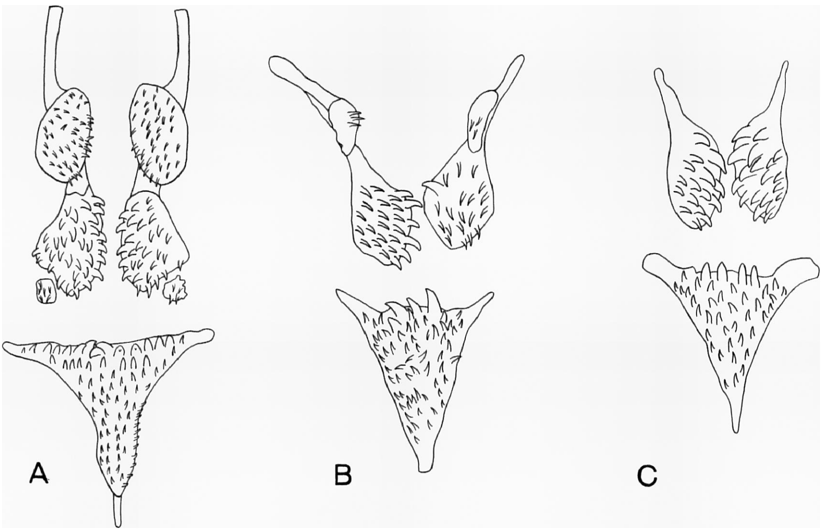

FIG. 2. Pharyngeal teeth. A. *Potamorrhaphis guianensis.* B. *Belonion dibranchodon.* C. *Belonion apodion. Potamorrhaphis* has all three pairs of upper pharyngeal bones; *B. dibranchodon* has the second and third pairs; and *B. apodion* has only the third pair.

family Exocoetoidea of Rosen), these bones are joined together in a manner analogous to the fusion of the lower pharyngeal bones throughout the Synentognathi. *Belonion* lacks the dorsal and anal finlets diagnostic of the Scomberesocidae.

Superficially, *Belonion* resembles a hemiramphid because of its short upper jaw and elongate lower jaw. All Belonidae go through a "halfbeak" stage during ontogeny (fig. 1D), and some, such as *Platybelone argalus,* have a relatively short upper jaw even as adults (Berry and Rivas, 1962, fig. 1a). All known specimens of *Belonion* are small (largest 41.8 mm. in body length, 50.0 mm. in standard length), and they retain the short upper jaw, characteristic of juveniles of other needlefishes, into maturity. Thus, *Belonion* may be considered a paedomorphic or neotenic species with regard to size and retention of a short upper jaw. This is the third case of paedomorphism in the order. Nichols and Breder (1928) suggested that the scomberesocid genus *Cololabis* is a permanently arrested stage in the ontogenetic development of *Scomberesox*. Böhlke (1951) described *Cololabis adocoetus* as having evolved from *C. saira* by the loss of pectoral rays and gill rakers. Hubbs and Wisner (MS) consider *C. adocoetus* to be gener-

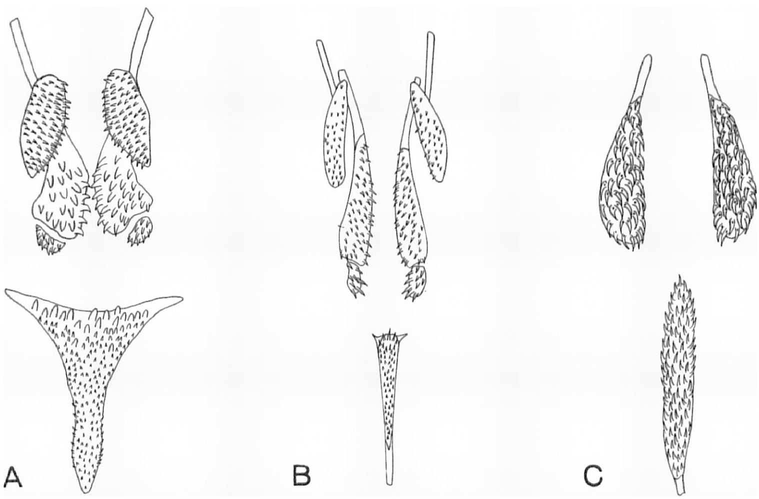

FIG. 3. Pharyngeal teeth. A. *Strongylura notata*. B. *Pseudotylosurus angusticeps*. C. *Xenentodon cancila*. *Xenentodon* has only the third upper pair of pharyngeal bones.

ically distinct from *C. saira* because of its small size and reduced numbers of vertebrae, pectoral fin rays, and branchiostegal rays. They also will describe a new genus and species that has similarly evolved through arrested development from *Scomberesox*.

In its reduced pharyngeal dentition (fig. 2) and in the number of vertebrae (table 1), pectoral rays (table 2), and branchiostegal rays (table 3), *Belonion* shows tendencies similar to those apparent in the three other fresh-water genera of needlefishes (*Potamorrhaphis* and *Pseudotylosurus* from South America, and *Xenentodon* from Asia) and in the specialized, viviparous, brackish and fresh-water Indo-Australian genera of the Hemiramphidae (*Zenarchopterus, Dermogenys,* and *Hemirhamphodon*).

Xenentodon and *Belonion apodion* have the most reduced pharyngeal

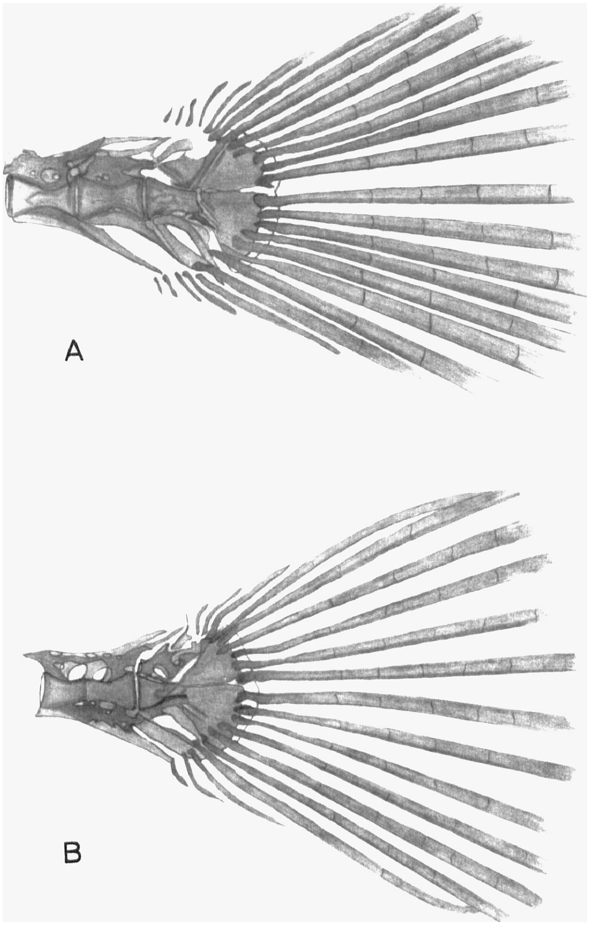

FIG. 4. Caudal skeletons. A. *Belonion dibranchodon* with 7 + 8 principal caudal rays. B. *Belonion apodion* with 6 + 7 principal caudal rays. The penultimate centrum of *B. apodion* is abnormal.

dentition in the order. Both lack all but the third pair of upper pharyngeal bones. The shapes of the tooth patches on these bones in *Xenentodon* (fig. 3C), however, are different from those of all other species of the Belonidae, including *Belonion apodion.* Therefore, it is clear that the loss of teeth was independent in the two genera. The lower pharyngeal plate of *Xenentodon* is also strikingly different from that of any other synentognaths in lacking any trace of the triangular expansion at the posterior

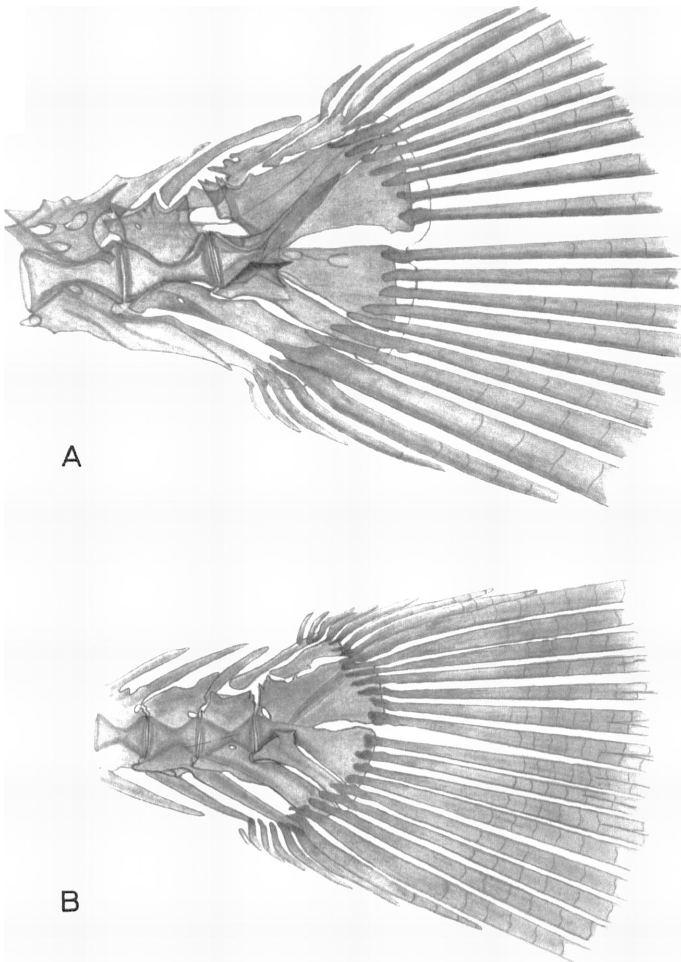

FIG. 5. Caudal skeletons. A. *Strongylura notata.* B. *Xenentodon cancila.*

end of the bone. *Xenentodon* does not show a reduction in number of pectoral or branchiostegal rays (tables 1, 2), and its caudal structure (fig. 5) is typical of most other genera of the Belonidae.

A number of characters show a close relationship between *Belonion* and *Potamorrhaphis.* In pharyngeal dentition, there seems to be a progressive reduction from *Potamorrhaphis* to *Belonion dibranchodon* to *B. apodion.* The shapes of the third upper pharyngeal bones and the lower pharyngeal plate and the teeth on them are very similar in both genera (fig. 2).

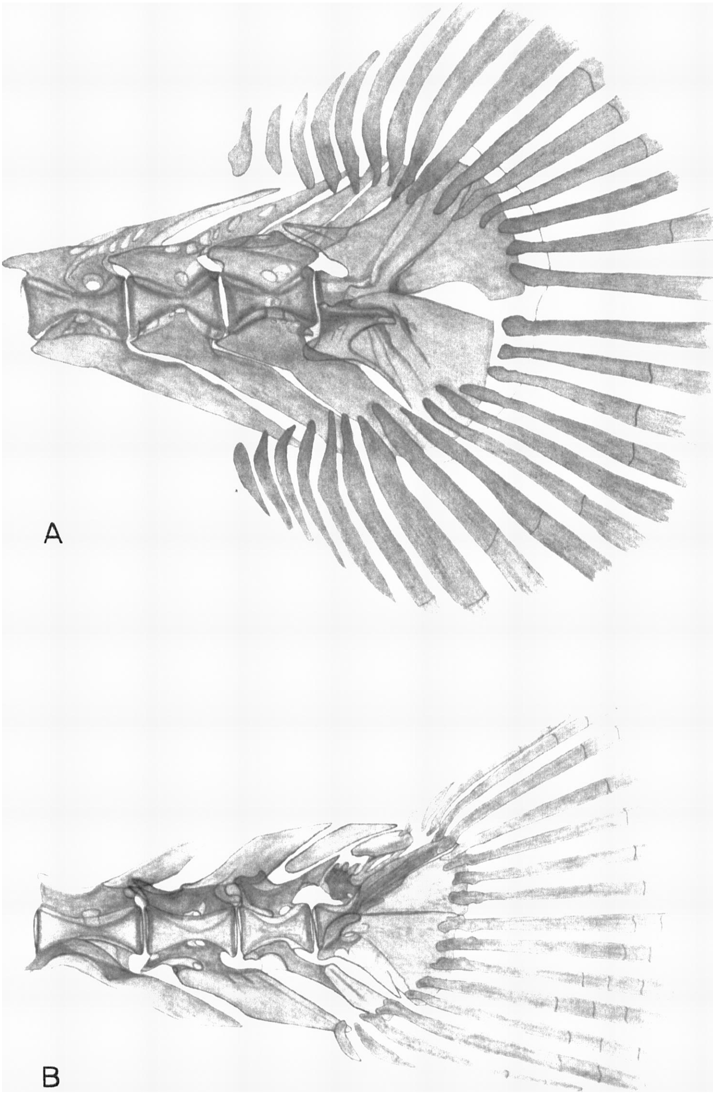

FIG. 6. Caudal skeletons. A. *Pseudotylosurus angusticeps*. B. *Potamorrhaphis guianensis*.

Belonion dibranchodon has lost the small fourth upper pharyngeals present in *Potamorrhaphis* and other needlefishes and has the dentition and size of the second upper pharyngeals reduced. The second pharyngeals have disappeared in *Belonion apodion*.

In both *Belonion* and *Potamorrhaphis* the anterior projection of the flattened first neural spine fits between the prominent flanges of the exoccipital and the paired supraoccipital crests. The position of the first neural spine relative to the supraoccipital crests varies widely in the other genera of synentognaths but none of these variations resemble the condition in *Belonion* and *Potamorrhaphis*. The degree of expansion of the first neural spine varies among the genera. Most synentognaths have two supraoccipital crests, as Rosen (1964, p. 231) noted, but there are a few exceptions. According to Parin (1961, p. 123), *Exocoetus monocirrhus* has only one crest, although *E. volitans* and *E. obtusirostris* have the usual two crests. At least one species of *Hemiramphus* (*H. brasiliensis*) and one species of *Hyporhamphus* (*H. picarti*) have three crests. *Oxyporhamphus* also has three crests, as Parin noted (1961, p. 123).

Potamorrhaphis further resembles *Belonion* in its reduced number of pectoral rays (seven to eight versus five to six) but differs in having more branchiostegal rays (10–11). The most obvious meristic differences between the two genera are the large number of dorsal (29–34) and anal (26–30) rays in *Potamorrhaphis*. *Belonion* has a more usual count for needlefishes (dorsal 11–14, anal 12–15).

The majority of synentognaths have 7 + 8 principal and 6 + 7 branched caudal rays. The eighth principal ventralmost caudal ray frequently inserts over the expanded last haemal spine, and the seventh principal ventral ray does so, at least partially, in some species (figs. 5–6). The fresh-water genera of needlefishes and the brackish-water and fresh-water genera of halfbeaks tend to have rounded tails in contrast to the lobed or forked tails of marine genera. This tendency is correlated with a reduction in the number of principal caudal rays in *Potamorrhaphis* (fig. 6B) and in *Belonion apodion* (fig. 4B).

Within the Belonidae, there is relatively little variation in the pattern of the interorbital canals. *Strongylura notata* (fig. 7A) and *Potamorrhaphis* (fig. 7B) are representative of the family. Not unexpectedly, *Belonion apodion* has the anterior portion of the canal reduced (fig. 7C). However, the canal in *B. dibranchodon* (fig. 7D) is unlike that of any other synentognath. The left and right canals are joined together so that median pores are present as well as the usual lateral pores. Superficially, the canal is similar to that of preserved specimens of *Hemirhamphodon*, but in *Hemiramphodon* this is due to the great reduction of bone in the cranial elements of the anterior portion of the canal, and not to fusion of the left and right canals, as is the case in *B. dibranchodon*.

Within the Synentognathi, two trends in vertebral number are apparent (table 1). The number increases with increasing specialization in the

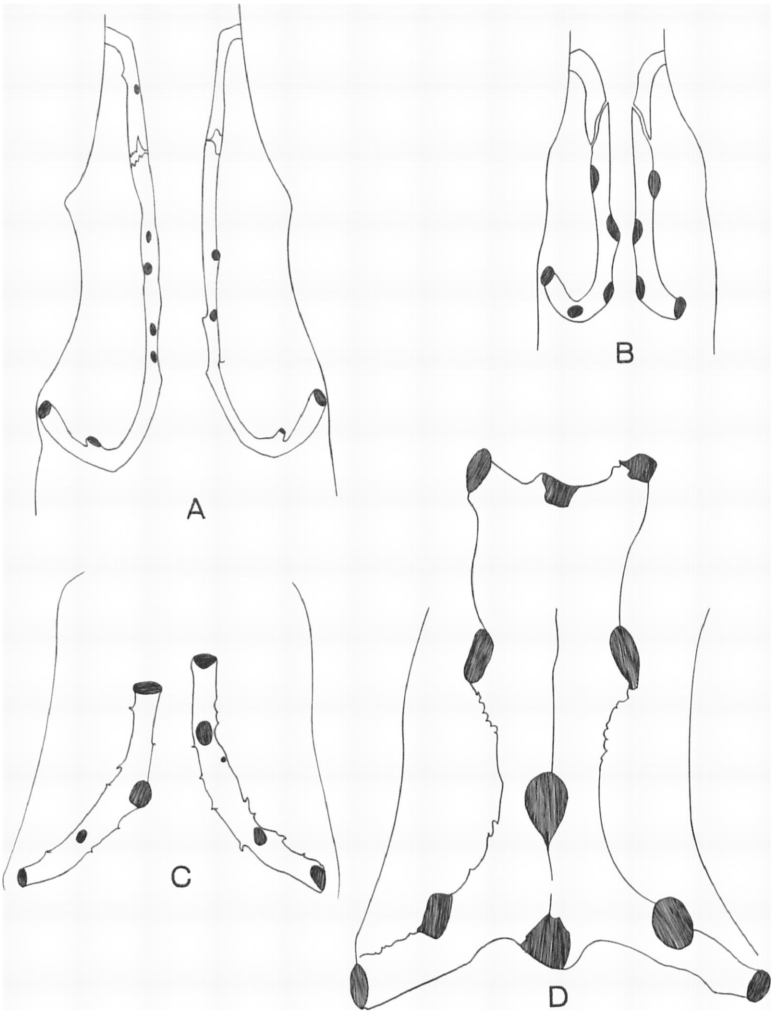

FIG. 7. Interorbital canals. A. *Strongylura notata.* B. *Potamorrhaphis guianensis.* C. *Belonion apodion.* D. *Belonion dibranchodon.*

Exocoetidae. The number is reduced in the two neotenic genera of Scomberesocidae (Hubbs and Wisner, MS). In the Hemiramphidae, both increase and decrease are associated with specialization. The pelagic genus *Euleptorhamphus* has 10–14 more vertebrae than any other genus, whereas *Zenarchopterus, Dermogenys,* and *Hemirhamphodon* have four to eight fewer. The Belonidae also show both trends. *Ablennes* has an increased number and is an ecological parallel of *Euleptorhamphus*. The trend toward reduction is shown in two species of *Strongylura* (*notata* and *urvillii*), *Xenentodon*, and *Belonion*. *Belonion dibranchodon* has about the same number of vertebrae as *Xenentodon*, *S. notata*, and *S. urvillii*. *Belonion apodion* has fewer vertebrae than any other species in the family.

The absence of epipleurals from both species of *Belonion* is a unique character in the Synentognathi. As Rosen (1964, p. 242) noted, most synentognaths have the first pleural rib articulating with the third vertebra. *Belonion* is an exception in having the first pleural rib on the second vertebra. The one cleared and stained specimen of *Pseudotylosurus* has the first pleural rib on the fourth vertebra on one side and on the fifth on the other side. The halfbeak *Hemirhamphodon* is the only other synentognath that has the first pleural rib on the second vertebra.

On the basis of the evidence presently available, I interpret the evolution of *Belonion* as follows: Inshore or neritic marine needlefishes similar to *Strongylura*, with three pairs of toothed upper pharyngeal bones, a moderate number of pectoral rays and vertebrae, a truncate caudal fin, and unforked pelvic fins smaller than the pectoral fins, moved into the fresh waters of South America. There *Pseudotylosurus* evolved, with its peculiar spine-bearing scales, elongate pharyngeal plate, and reduced number of branchiostegal rays. Another line of development from the same stock led to the ancestors of *Potamorrhaphis* and *Belonion*, needlefishes having an association of the expanded first neural spine with the supraoccipital crests and exoccipital flange. The teeth on the pharyngeal bones became larger and fewer, the number of pectoral rays was reduced to seven or eight, and the caudal fin became distinctly rounded. From such a form the ancestors of *Potamorrhaphis* secondarily developed a larger number of caudal vertebrae and dorsal and anal rays, whereas the ancestors of *Belonion* continued to specialize by reduction—in number of vertebrae, branchiostegal rays, and pectoral rays. The small fourth pharyngeal bone disappeared, and the size of the second became greatly reduced. This is the stage reached by *Belonion dibranchodon*. *Belonion apodion* became still more specialized along the same evolutionary line. The number of vertebrae became further reduced, the pelvic fins and pelvic girdle were lost, the caudal fin lost two principal rays, and the small second pharyngeal bone disappeared. These changes resulted in the most specialized of all needlefishes—*B. apodion*.

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