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A NEW SPECIES AND A REVIEW OF THE DEEP-SEA FISH GENUS *POROGADUS* (OPHIDIIDAE) FROM THE WESTERN NORTH ATLANTIC

H. Jacque Carter and Kenneth J. Sulak

ABSTRACT

A new species of deep-sea ophidiid, *Porogadus silus*, is described from deep water off the Bahamas. It differs from its congeners chiefly in having a relatively shorter and deeper head, absence of preopercular and frontal spines and relatively large scales covering the body. A partial osteological description of *P. silus* is given. *Porogadus* is reviewed and a provisional key to species from the western North Atlantic is presented. The species group containing *Porogadus* that lack well developed head spines and armature is partially revised on the basis of a study of specimens collected from the Atlantic and Pacific oceans. Of the seven nominal species of *Porogadus* with poorly developed head spines, five are recognized: *P. catena* (with *P. promelas* and *P. breviceps* as synonyms), *P. abyssalis, P. gracilis, P. longiceps* and *P. silus* n. sp.

The circumglobal neobythitine ophidiid genus *Porogadus* includes long and slender benthopelagic fishes inhabiting bathyal and abyssal depths beneath tropical and temperate seas. The 14 nominal species referred to *Porogadus* are much in need of revision (Cohen and Nielsen, 1978). *Porogadus* is presently distinguished from other neobythitine genera by a combination of the following characters (Cohen and Nielsen, 1978): presence of a single median basibranchial tooth patch, V-shaped vomerine tooth patch, 13 to 20 developed rakers on first arch, six caudal fin rays, 17–20 pectoral fin rays, one or two rays in each pelvic fin, eight branchiostegal rays, 16–18 precaudal vertebrae, a row of modified scales dorsally behind the head, a body depth (at vent) that goes into its standard length 10 or more times, prominent cephalic lateralis pores beneath eye and along posterior margin of preopercle, body lateral line arranged in three parallel rows (pores large and prominent in some species).

The generic diagnosis given above appears to best accommodate *Porogadus* species with strongly developed head spines, typified by *Porogadus miles*. Members of the genus with poorly developed head spines are highly variable or wanting in several characters presently used to define the genus. For example, in the new species described herein, there is no median basibranchial tooth patch in more than half the specimens examined; the vomerine tooth patch is occasionally irregular in shape; and three lateral line rows are not evident. Such deviations from the generic diagnosis were also observed in other species of *Porogadus* with poorly developed head armature. We urge caution in discussing relationships until there is a better understanding of generic characters. Unfortunately, taxonomically important species of *Porogadus* described from the Indian and western Pacific oceans are still quite rare in collections and a world-wide revision is not now possible.

The genus *Porogadus* was established by Goode and Bean (1886) for *Porogadus miles*, based on a single specimen collected in the Atlantic Ocean off the east coast of North America; thirteen additional species have been described. Norman's (1939) synopsis of oceanic genera, with a list of described species, represented an early attempt to arrange "brotulid" genera in accordance with their supposed relationships and was based in part on the prior work of Smith and Radcliffe (1913). Nybelin (1957) reviewed the genus *Porogadus* and provided comments

on 14 nominal species which he placed in three species groups based on the relative development of head armature. According to Nybelin (1957), with whom we agree, *Porogadus gracilis* Günther (1878), *P. catena* (Goode and Bean, 1886), *P. longiceps* Garman (1899), *P. atripectus* Garman (1899), *P. breviceps* Garman (1899) and *P. promelas* Gilbert (1891) comprise a species group distinguished by a relative lack of head armature; *P. miles* Goode and Bean (1886), *P. nudus* Vaillant (1888), *P. trichiurus* (Alcock, 1890), and *P. melanocephalus* Wood-Mason and Alcock (1891) comprise a second species group characterized by strongly developed head spines; and *P. guentheri* Jordan and Fowler (1902), *P. subarmatus* Vaillant (1888), and *P. melampeplus* Alcock (1896) comprise a third species group which is characterized by moderately developed head spines intermediate between those of the other two groups.

With the substantial increase in the amount of material of *Porogadus* taken during the last 10 years, we have been able to re-evaluate the species living in the western North Atlantic, Caribbean and Gulf of Mexico. We recognize three species among our study specimens, including *P. miles* and *P. catena* and a new species from Tongue-of-the-Ocean, Bahamas. The new species differs chiefly from its allies in possessing a relatively shorter and deeper head, smaller body size, and relatively large scales (Table 1). A provisional key to species of *Porogadus* occurring in the western North Atlantic is provided. We include in this key the ophidiid, *Penopus macdonaldi,* as young individuals are frequently confused with species of *Porogadus.*

Methods and Materials

Counts and measurements follow those of Hubbs and Lagler (1958). Head length is measured to the posterior tip of the bony opercle. Measurements were made using dial calipers to the nearest 0.1 mm and are expressed as percent of gnathoproctal length. Measurements less than 0.5 mm were made with the aid of an ocular micrometer. Minimum values, maximum values and arithmetic means are presented in tables to supplement the accounts of each species. Analysis of covariance (ANCOVA) procedure was used to test differences between regression of head length versus gnathoproctal length among species of *Porogadus.* Student Newman-Keuls multiple range test (MRT) was used to test differences among regression lines for the species. Statistical tests were performed on a Primos 450 computer at VIMS using programs following the statistical methods presented by Zar (1974).

Vertebral and fin-ray counts were determined from radiographs and from cleared and stained specimens following procedures presented by Taylor (1967). Gill-raker counts (anterior arch) include small rakers (indicated in lower case Roman numerals). All anatomical illustrations except Figure 1 were drawn with the aid of a camera lucida.

Comments and brief systematic accounts of several other species of *Porogadus* present in the northwestern Atlantic are presented below based on materials examined, which are listed under species accounts. Abbreviations used are: USNM, National Museum of Natural History, Smithsonian Institution (Washington, DC); BMNH, British Museum of Natural History (London); FMNH, Field Museum of Natural History (Chicago); MCZ, Harvard Museum of Comparative Zoology (Cambridge); UMML, University of Miami, Rosentiel School of Marine and Atmospheric Science (Miami); VIMS, Virginia Institute of Marine Science (Gloucester Point); SIO, Scripps Institution of Oceanography (La Jolla); ZMUC, Zoological Museum of the University of Copenhagen (Denmark); CAS, California Academy of Sciences (San Francisco); IOS, Institute of Oceanographic Sciences (Surrey, England); MNHN, Museum National d'Histoire Naturelle Paris.

Systematics

Key to *Porogadus* and *Penopus* in the Western North Atlantic

1A. Operculum with a strong, curved spine dorsally and 2 or 3 weak, flattened projections at lower angle; two median basibranchial tooth patches ..... *Penopus macdonaldi* Goode and Bean

1B. Opercular spine poorly ossified; broad, flattened and flap-like; incorporated in angle of the opercle or absent; if present, one median basibranchial tooth patch 2

Table 1. Diagnostic characters for species of *Porogadus* with weakly developed head armature

Characters	*P. silus* (N = 50)	*P. catena* (N = 50)	*P. longiceps* (N = 4) Syntypes	*P. abyssalis* Holotype	*P. gracilis* Holotype	*P. atripectus* (N = 3) Syntypes
No. of pectoral fin rays	17–19 (18)	15–17 (15)	19–20 (20)	18	14	16–18 (16)
Lateral line scales to level of vent	14–20 (17)	24–36 (31)	36–44 (42)	40	U/A	40–48 (42)
Head depth expressed as % head length	60–75 (70)	49–59 (56)	39–42 (42)	51	56	58–62 (61)
No. of spinelets on inner-outer preopercle margins (mode)	(0-0)	(4-0)	(3-4)	(4-0)	(4-0)	(3-0)
Shape of vomerine tooth patch						
Maxillary length expressed as % GNP	30–37 (35)	26–30 (29)	27–32 (30)	63	58	29–32 (30)
Gill raker formula (mode)	(iii-16-iv)	(iii-16-iii)	(ii-12-0)	iii-14-0 (holotype)	v-17-0 (holotype)	(iii-16-0)
No. of neural spines in advance of 1st dorsal fin pterygiophore	2	3	U/A	U/A	U/A	U/A
Three lateral line rows prominent	no	no	yes	yes	no	no
Head depth expressed as % gnathoproctal length	30–35 (34)	25–28 (26)	18–22 (20)	30	50	24–29 (26)
Eye diameter expressed as % head length	7–10 (8)	15–23 (18)	8–12 (11)	16	16	13–16 (14)
Opercle spine	flat, weakly developed	flat, weakly developed	strong, keeled, well developed	flat, usually weakly developed	flat, weakly developed	flat, weakly developed
Modified scales along lateral line	no	no	yes	no	no	yes

U/A = Data unavailable.

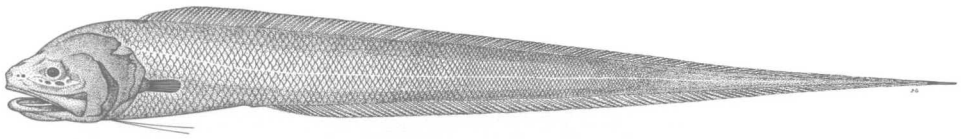


Figure 1. *Porogadus silus*, USNM 238801, holotype, 45.8 mm SN-V.

2A. Head depth 60–75% of head length; frontal spine above eye absent; margins of preopercle smooth; lateral line scales to level of vent 14–20 ..... *Porogadus silus* n. sp.
2B. Head depth less than 60% of head length; frontal spine above eye present; margins of preopercle with scalloped edges or spines; lateral line scales to level of vent 20 or more 3
3A. Spines on top and sides of head well developed; frontal spine above eye conical, sharp and strongly recurved; lateral line scales to level of vent 40 or more; head depth 37–42% of head length; three prominent lateral line rows; margins of preopercle with 3–7 spines ..... *Porogadus miles* (Goode and Bean)
3B. Spines on top and sides of head poorly developed; frontal spine above eye flattened, compressed and slightly recurved; number of lateral line scales to level of vent 28–36; head depth 49–59% of head length 49–59; lateral line absent; margins of preopercle with 3–4 spines ..... *Porogadus catena* (Goode and Bean)

Porogadus silus new species
(Figures 1, 6a, 7, 10–17)

Holotype.—USNM 238801 (45.8 mm SN-V), female, R/V Columbus Iselin, Cruise 7511, Station 387, 24°16'N, 76°16'W, 1962 m, 29 August 1975, 41 ft semi-balloon otter bottom trawl.

Paratypes.—UNSM 238802 (2: 35–45 mm GPL), R/V Columbus Iselin, Cruise 7511, Station 378, 24°21'N, 76°04'W, 1761 m; ZMUC P77729–730 (2: 32–40 mm GPL), R/V Columbus Iselin, Cruise 7511, Station 387, 24°16'N, 76°16'W, 1762 m; UMML 34130 (3: 43–46 mm CPL), R/V Columbus Iselin, Cruise 7406, Station 276, 24°21'N, 76°10'W, 1772 m; MCZ 58994 (41 mm GPL), R/V Columbus Iselin, Cruise 7305, Station 72, 24°00'N, 75°44'W, 1884 m; FMNH 94508 (2: 39–40 mm GPL), R/V Columbus Iselin, Cruise 7305, Station 72, 24°00'N, 75°44'W, 1884 m; CAS 51437 (40 mm GPL), R/V Columbus Iselin, Cruise 7402, Station 191, 24°10'N, 75°56'W, 1810 m; SIO 82-80 (38 mm GPL), R/V Columbus Iselin, Cruise 7402, Station 191, 24°10'N, 75°56'W, 1810 m; BMNH 1982.10.28.37 (38 mm GPL), R/V Columbus Iselin, Cruise 7402, Station 191, 24°10'N, 75°56'W, 1810 m.

Additional Material Examined.—UMML 34131 (40 mm GPL); UMML 34132 (3: 22–32 mm GPL); UMML 34133 (9: 23–46 mm GPL); UMML 34134 (8: 23–46 mm GPL); UMML 34135 (8: 16–40 mm GPL); UMML 34136 (8: 26–46 mm GPL); UMML 34137 (3: 22–33 mm GPL); VIMS 07090

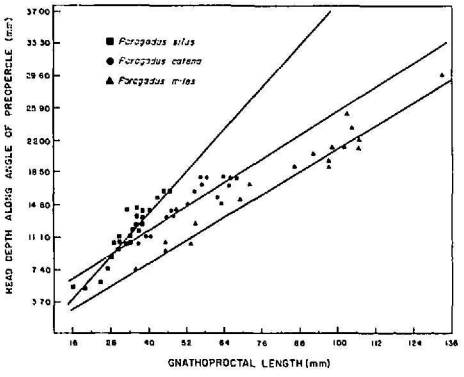


Figure 2. (Left) Regression of head depth on GPL length in three species of *Porogadus*.

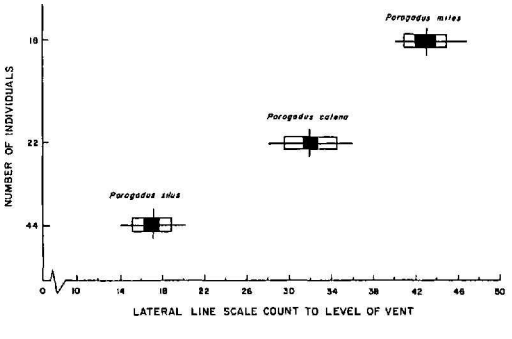


Figure 3. (Right) Lateral line scales to level of vent.

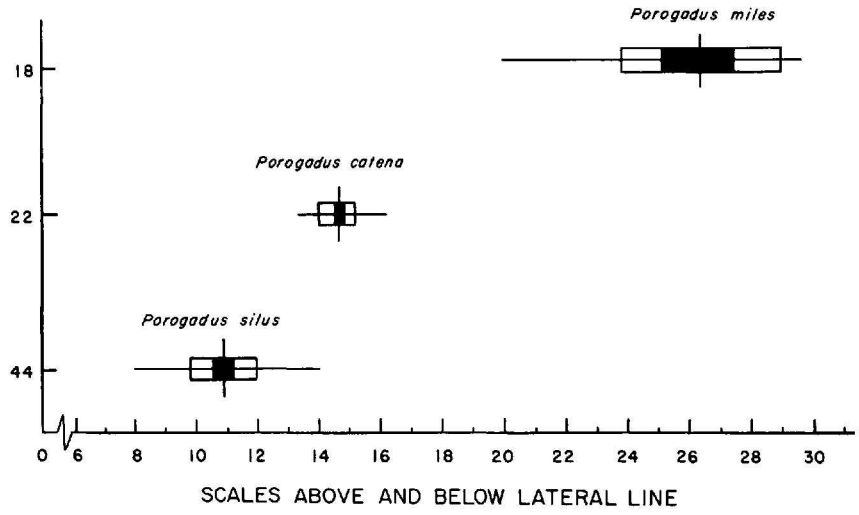


Figure 4. Scale above and below lateral line.

(6: 30–42 GPL); VIMS 07092 (36 mm GPL), VIMS 07091 (15: 30–41 mm GPL); VIMS 07093 (45 mm GPL); VIMS 07483 (25: 32–48 mm GPL).

Diagnosis.—A species of *Porogadus* having the following combination of characters: margins of preopercle smooth; head depth 65–70% of head length; lateral line scales to level of vent 14–20; first dorsal fin pterygiophore originating between second and third neural spines.

Morphometrically, *P. silus* differs from its two closest relatives in the western North Atlantic in having a relatively shorter and deeper head, relatively larger and fewer scales along the body, and an absence of frontal and preopercular spines (Figs. 2–6a). The slope of the regression line of head depth versus gnathoproctal length of *P. silus* was different from the other two species at the 0.01 level of significance (Table 2). In addition the elevations of the regression lines of all three species are significantly different ($P > 0.01$). Morphometric and meristic characters of *P. silus, P. catena* and *P. miles* are presented in Table 3.

Etymology.—From the Latin "silus" (pugnose). A masculine noun in apposition.

Description.—Body dark brown; head, belly and opercular flap darker, almost black. Branchial and oral cavity lining dark brown. Dorsal and anal fin rays short,

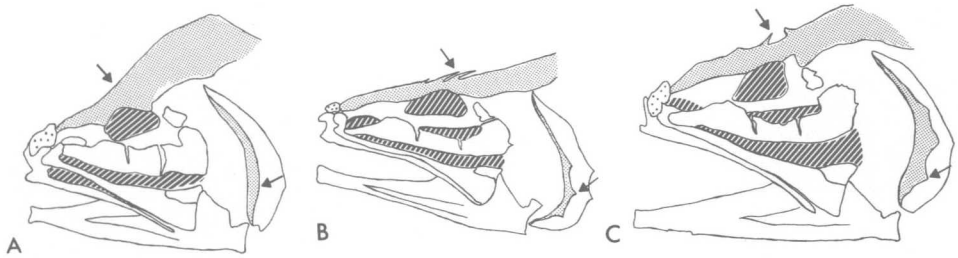


Figure 5. Frontal and preopercular spine development among three species of *Porogadus*. Lateral aspect: A, *Porogadus silus*; B, *Porogadus miles*; C, *Porogadus catena*.

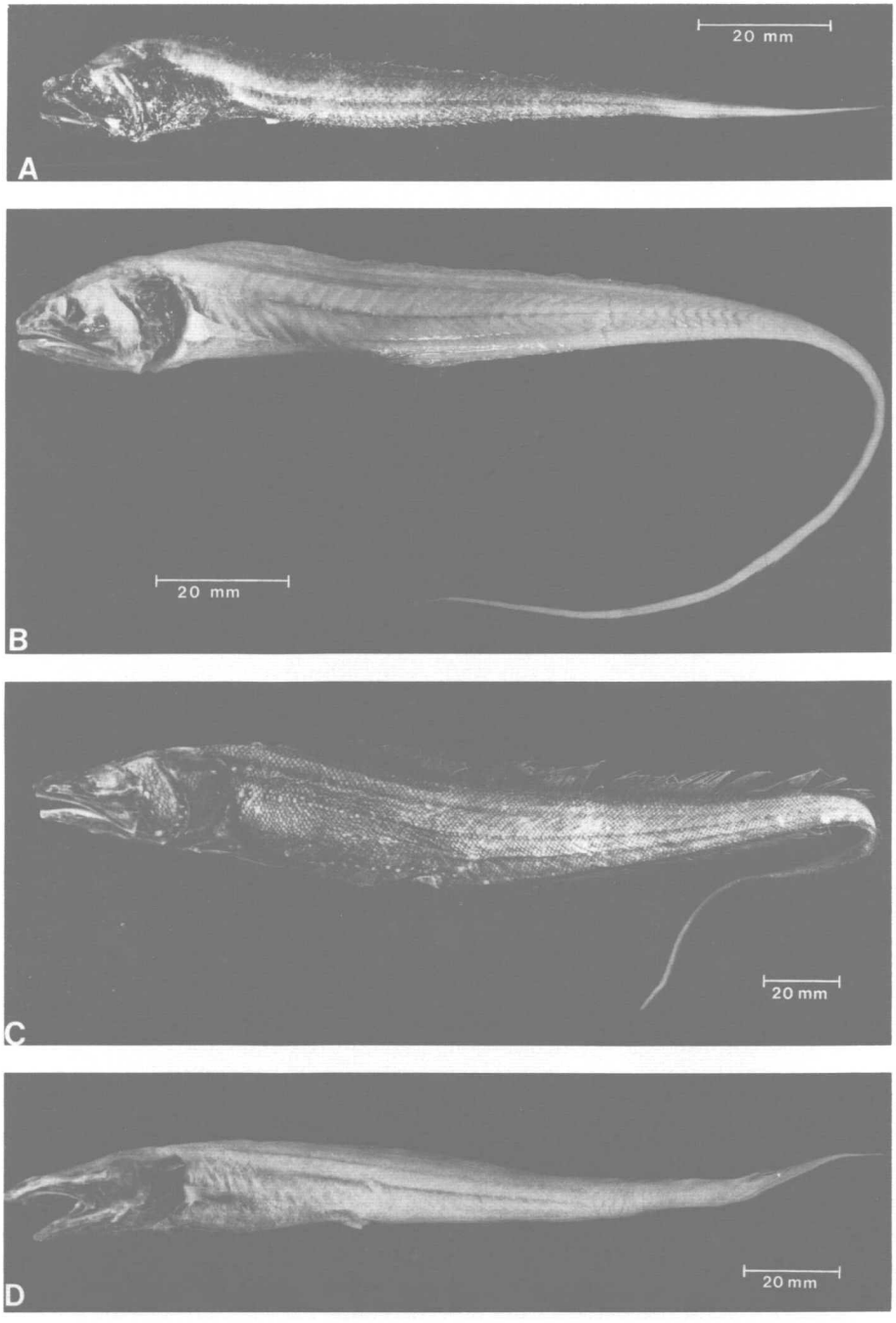


Figure 6. Species of *Porogadus* and *Penopus* living in the Western North Atlantic, Caribbean Sea and Gulf of Mexico: a, *Porogadus silus,* USNM 238802, paratype; B, *Porogadus catena,* USNM 037341, syntype; C, *Porogadus miles,* VIMS 07089; D, *Penopus macdonaldi,* VIMS 03530.

Table 2. Regression equations of greatest depth of head on gnathoproctal length for three species of *Porogadus*

Species	N	Y Intercept	Slope	Coefficient of Determination (r^2)
P. silus	44	−2.4310	0.39045	0.89313
P. catena	22	2.3297	0.23329	0.80844
P. miles	18	−0.1479	0.21717	0.95865

uniform in height, and confluent with caudal fin rays. Pectoral fins entire, narrow and short. Head lacking spines, cavernous and not compressed; head depth much greater than in *P. miles* and *P. catena*. Mouth sub-terminal with wide gape, maxilla extending well beyond eye and much expanded posteriorly. Eyes well developed. Body lateral lines indistinct or absent. Prominent cephalic lateralis pores beneath eye and from the posterior margin of preopercle forward along the ventral surface of the dentary.

Dentition.—Teeth minute, numerous and villiform on all tooth plates. Palatine tooth patch narrow and ellipsoidal. Vomerine tooth patch roughly triangular. Dentition continuous across the jaw symphyses. The single median basibranchial tooth patch variously developed; sometimes absent. Three upper pharyngeal tooth plates present and opposing oval counterparts on the lower pharyngeal plates.

Gill Cavity.—Anterior first gill arch with 3–4 rudimentary knob-like rakers on the upper limb, 1 developed on the angle plus 15–17 developed rakers and 3–4 (mode 3) rudimentary rakers on the lower limb (Fig. 7). Second through fifth branchial arches bearing only rudimentary rakers. Gill filaments small, not much longer than width of arches. Pseudobranch with two short filaments. Externally developed thymus absent.

Integument.—Body except for fin membranes completely covered with relatively large subrectangular cycloid scales. Scales frequently missing on trawled specimens; however, scale pockets distinct.

Viscera.—Esophagus short with muscular walls. Stomach tube-like, longer (2.5 mm) than wide (7.5 mm), slightly swollen posteriorly. Intestine with a compact S-shaped coil immediately following pylorus. Intestine slightly expanded in the pyloric region and decreasing in diameter posteriorly. It continues posteriorly a short distance (7.5 mm) whereupon it forms another S-shaped coil. Lumen white and provided with small numerous villi. Liver yellowish triangular covering the anterior portion of the alimentary tract. Pancreas diffuse, occurring as nodules scattered throughout mesentery. Gall bladder partially surrounded by liver, opening anteriorly into intestine via bile duct.

Swimbladder.—Swimbladder small thin walled, elongated sac-like structure overlying anterior portion of the stomach. Well developed gas-gland and resorbent capillary network investing floor and lateral walls of sac. In males a pair of extrinsic drumming muscles appear to originate on the ventral surface of the prootic region of either side of the skull and extend posteriorly to insert to an attachment site on the anterior pleural ribs.

Gonads.—Mature ovaries horseshoe shaped, completely coalesced along mid-line and closely attached to abdominal wall. Testes in mature individuals milky white, ribbon-shaped, borders slightly scalloped and coalesced along mid-line.

Table 3. Meristic and morphometric characters of species of *Porogadus*

	P. silus (N = 50)			*P. catena* (N = 22)			*P. miles* (N = 18)		
	Types	Range	Mean	Types	Range	Mean	Types	Range	Mean
MORPHOMETRIC CHARACTERS									
Greatest depth of head	37.5	29.5–43.4	37.6	30.0	27.5–34.7	30.0	28.5	24.5–30.9	27.2
Depth of head at angle of lower jaw	36.5	23.5–35.0	31.9	29.0	23.6–30.6	27.6	22.5	19.2–23.0	21.31
Predorsal distance	51.3	45.4–56.6	51.3	45.3	42.5–56.8	52.4	57.5	55.0–64.0	58.9
Preanal distance	—	—	—	—	—	—	—	—	88.7
Gnathoproctal length	—	—	—	—	—	—	—	—	84.1
Dist. from pelvic fin origin to vent	49	45.7–60.3	54.7	54.9	53.5–63.2	57.7	58.1		
Dist. from lower jaw symphysis to angular	37.5	11.1–45.4	37.5	33.4	28.3–38.1	33.8	29.7	28.6–36	33.23
Head length	52.4	4.2–6.2	50.9	47.3	46.2–51.4	48.5	56.7	47.9–56.7	52.8
Snout length	37.1	12.4–18.1	15.0	14.6	12.5–16.9	15.0	16.2	13.9–18.0	15.9
Length of upper jaw	36.0	28.4–41.8	34.9	30.2	26.2–32.3	30.2	34.3	28.0–33.6	31.0
Dist. from snout to innermost edge of preopercle	41.4	33.1–47.7	40.5	37.5	21.6–48.4	37.6	43.7	36.4–44.3	40.7
Length of orbit	8.7	6.6–10.5	8.32	9.0	6.8–12.0	9.1			
Horizontal diameter of orbit							10.5	7.7–15.4	10.9
Head width	24.6	12.1–19.3	15.2	22.0	12.3–25.9	21.1	21.5	17.4–25.1	21.1
Post orbital length	31.8	20.3–33.3	26.1	23.6	20.9–29.9	25.4	30.5	22.5–30.8	26.7
Depth of body at anus	26.2	15.6–30.4	24.3	21.2	19.2–26.6	23.1	28.0	25.1–30.9	27.8
MERISTIC CHARACTERS									
No. pectoral fin rays	18	17–19	17.96	16	15–16	15.65	16	14–16	15.6
Lateral line scales to level of vent	18	14–20	17.0	31	28–36	31.9	42	40–47	43.0
Circumference scale count	10	8–14	10.92	15	14–16	14.6	24	20–29	26.5
Gill rakers anterior arch	iii-17-iv	(iii-15-iii)–(iv-18-iv)	(mode) iii-16-iv		(iii-15-iii)–(iv-17-v)	(mode) iii-16-iii	iii-15-0	(iii-15-0)–(iii-15-0)	mode iii-15-0
Preopercle spines							4-5	(3-4)–(7-7)	mode 5-5
Pelvic fin rays	2—joined		2—joined			2—joined	2—joined		2—joined

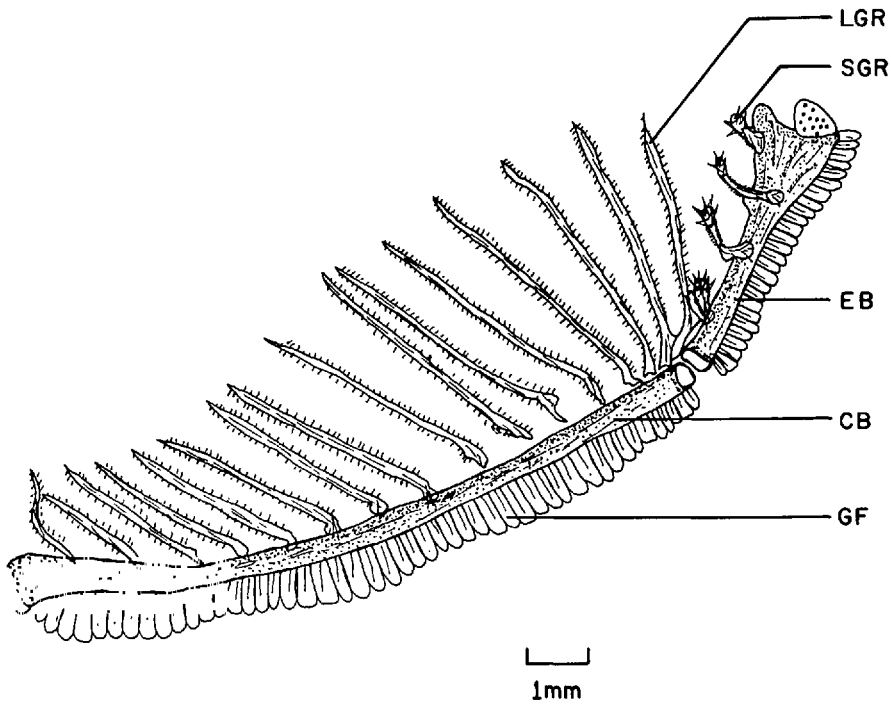


Figure 7. *Porogadus silus*, UMML 34142, First branchial arch from right side.

Distribution.—All specimens of *Porogadus silus* n. sp. were collected between 18°25′–26°15′N, 75°24′–78°12′W in the Bahamas region beneath tropical seas (Figs. 8, 9).

Osteology

This account is based on a single, cleared and stained specimen of *P. silus* (UMML 34142). Terminology follows Cohen (1982).

Cranium (Figs. 10, 11)

Viewed laterally, the cranium is deepest posteriorly and descends steeply in the ethmoid region to the snout. The dorsal outline over the orbital region is relatively smooth and lacks spines so prominent in other species of *Porogadus*.

Ethmoid Region.—A prominent median rostral cartilage lies between the heads of the maxillary elements and is bound to the ascending processes of the premaxillaries. The oval-shaped dermethmoid is overlapped by the anteromedial ends of the frontal. Lateral ethmoids lie posterior to the posterolateral margins of the vomer, lateral to the dermethmoid and the anterior portion of the frontals. Each lateral ethmoid bears a ventrally and laterally-directed articulating head.

Vomer.—A single median anchor-shaped bone with a tapering posterior extension. Ventrally the head bears a patch of small teeth.

Frontals.—Paired bones that are tightly joined medially and articulate anteriorly with the nasals and dermethmoid. In the postorbital region the frontals expand

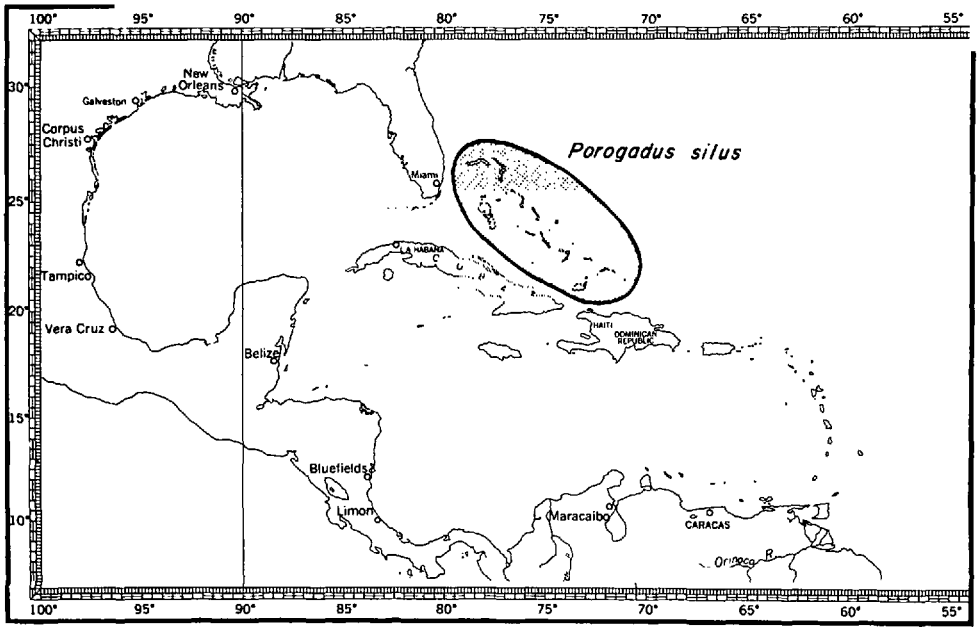


Figure 8. The known distribution of *Porogadus silus*.

into plates which articulate with the parietals posteriorly and the sphenotics pterotics posterolaterally.

Parietals.—The paired parietals are bordered laterally by the pterotics, posteriorly by the epiotics and are separated medially by the intervening supraoccipital.

Supraoccipital.—A single median bone with lateral wings and a median ridge posteriorly.

Exoccipitals.—Paired bones that meet at the midline dorsal to the foramen magnum. Each provides a concave surface that serves as an area of epaxial muscle attachment. Each exoccipital is bordered dorsomedially by the supraoccipital, anteroventrally by the epiotic, ventrally by the basioccipital and capped by the intercalar.

Epiotics.—A pair of concave bones that form the posterior corner of the cranium. They lie posterior to the parietal, lateral to the supraoccipital, medial to the pterotic and anterior to the exoccipital.

Intercalars.—A pair of thin small bones bordered by the exoccipital posteriorly, the pterotic ventrolaterally and the prootic anteriorly. A small distal process ligamentously attaches to the lower arm of the posttemporal.

Basioccipital.—A median bone which forms the posteroventral part of the cranium. It is bordered anteriorly by the prootic, laterally by the intercalar dorsally by the exoccipital, and is ventrally fused to the parasphenoid.

Pterotics.—A pair of elongate bones that form a prominent posterolateral corner of the cranium. Each is posterior to the sphenotic, lateral to the parietal and frontal, and anterior to the epiotic. Anteriorly a lateral fossa receives the posterior arm of the hyomandibula.

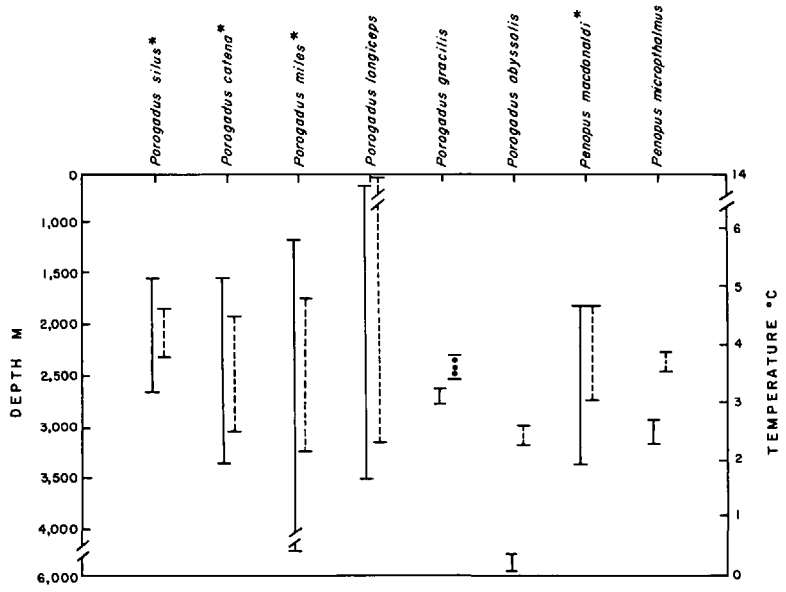


Figure 9. A comparison of the known depth (solid lines) and temperature (dashed lines) ranges of species of *Porogadus* and *Penopus*. In some cases temperature limits have been estimated by correspondence of capture locality with independent temperature data.

Sphenotics.—Paired bones that articulate posteriorly with the pterotics, dorsomedially with the frontals, ventrally with the parasphenoid and anteriorly with the pterosphenoid. A fossa on the ventral surface of the sphenotic accepts the articular facet of the anterior arm of the hyomandibula.

Prootics.—Paired bones that form the anterolateral portion of the otic capsule. A prominent foramen occurs in the center of each bone. Centrally positioned, the prootics contact the parasphenoid, intercalar, pterotic, sphenotic, basioccipital and pterosphenoids.

Pterosphenoids.—Paired bones extending posteroventrally from the ventral surface of the frontal to the prootic and sphenotic.

Parasphenoid.—An elongate median bone which anteriorly lies dorsal to the shaft of the vomer and ventral to the lateral ethmoids. It supports the pterosphenoids along the midlength and posteriorly forms part of the base of the otic capsule.

Opercular Series (Fig. 12)

Preopercle.—A vertically elongate bone, its leading edge with a pronounced ridge nearly completely enclosed by a thin bony shelf. Dorsally, the preopercle lies lateral to the hyomandibula; anteroventrally it is attached to the quadrate.

Interopercle.—A roughly triangular bone with its anterodorsal edge lying medial to the preopercle. A strong ligament connects the anterior angle of the interopercle to the angular.

Opercle.—A three pronged, roughly triangular bone. A slight ridge extends parallel and slightly ventral to the dorsal margin of the bone. The posterior dorsal corner of this bone forms a weak spine observed in fresh specimens.

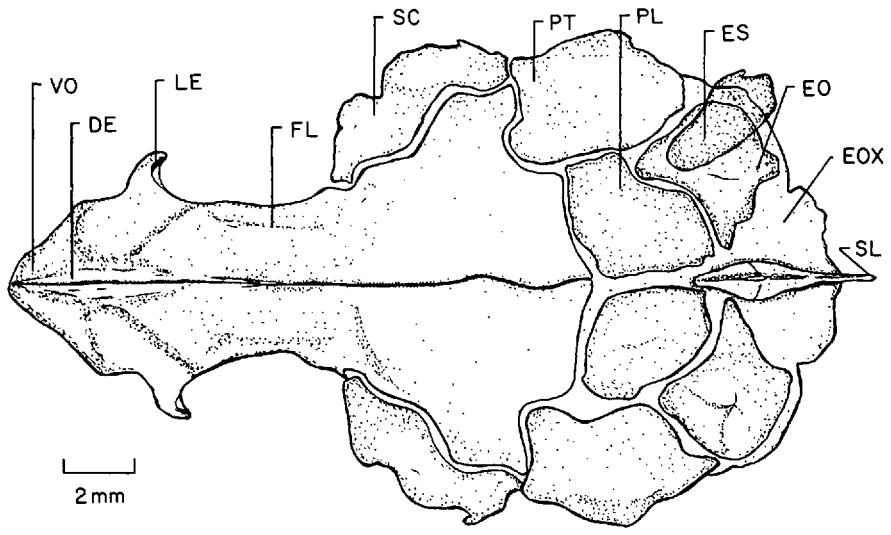


Figure 10. *Porogadus silus*, UMML 34142, Dorsal aspect of neurocranium.

Subopercle.—A fragile, partially ossified, crescent-shaped bone that comprises the rear margin of the opercular flap.

Superficial Dermal Bones (Fig. 12)

Nasals.—Very delicate paired hourglass shaped bones; each lies lateral to the ascending process of the premaxillary.

Circumorbital Series.—There are six pairs of circumorbital bones; the lacrymal extending from the nasal region to mid orbit. Each bone is folded to form a thin shelf.

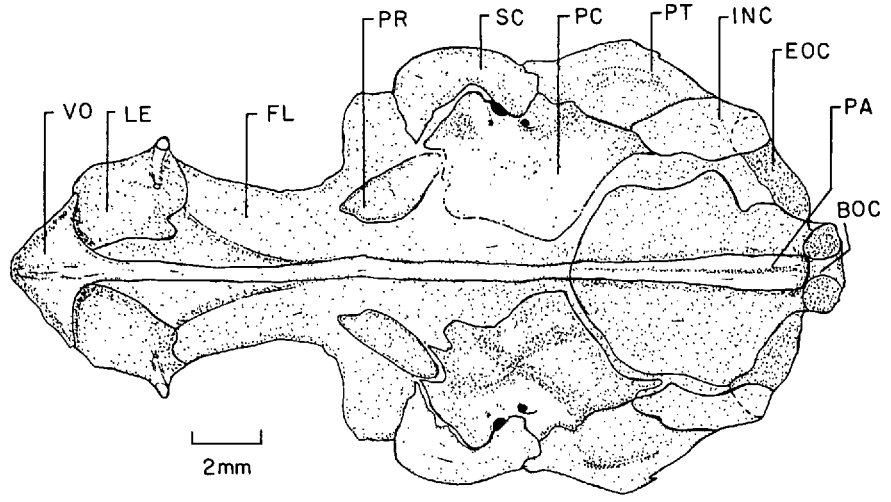


Figure 11. *Porogadus silus*, UMML 34142, Ventral aspect of neurocranium.

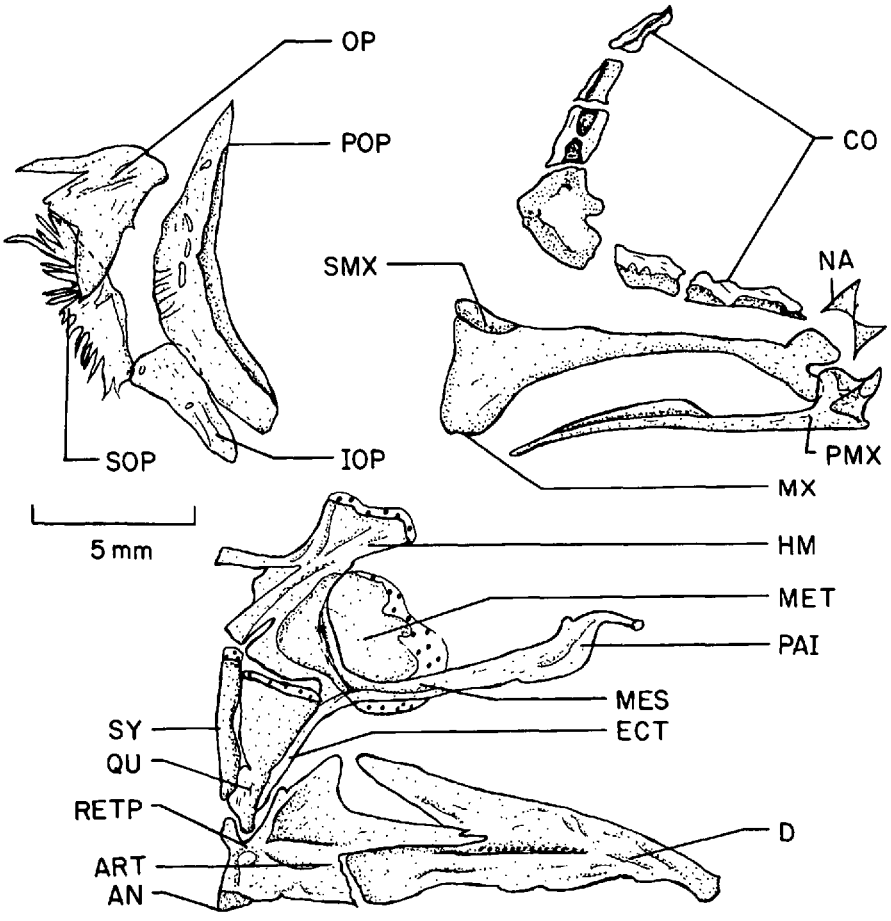


Figure 12. *Porogadus silus*, UMML 34142, Lateral aspect: superficial dermal bones and upper jaw; palatine arch, part of hyoid arch and lower jaw; opercular apparatus.

Mandibular Arch (Fig. 12)

Premaxilla.—This bone consist of an elongate alveolar process extending nearly to the end of the maxilla and bears a single row of teeth; the ascending processes of the premaxillae are tightly joined at the symphysis. Behind the ascending process lies the articular process which articulates with the head of the maxilla.

Maxilla.—A large complex bone broadly expanded posteriorly and with a concave rear margin. The head of the maxilla is specialized to articulate movably with the premaxilla and palatine in the region of the lateral ethmoid.

Supramaxilla.—A single oval-shaped splint of bone lying over the posterior expanded part of the maxilla.

Dentary.—A complex, V-shaped bone joined medially to its fellow and bearing a row of teeth on the thickened dorsal margin. Along the flattened ventral surface lie the tubes and associated pores of the mandibular branch of the cephalic canal system.

Articular.—This bone forms the posterior half of the mandible and is rigidly wedged into a deep notch of the dentary. The bone expands posteriorly. The retroarticular process is a strongly reinforced saddle that receives the articulating head of the quadrate.

Angular.—A small bone located at the lower rear corner of the mandible.

Palatine Arch (Fig. 12)

Metapterygoid.—A broad thin bone of irregular outline expanded into a shelf anteriorly and tightly joined to the hyomandibula posterodorsally. Ventrally it borders on the quadrate and anteriorly overlaps the dorsal arm of the mesopterygoid.

Mesopterygoid.—An L-shaped bone tightly joined along its ventral surface to the ectopterygoid.

Ectopterygoid.—A sickle shaped bone bordered posteromedially by the quadrate; tightly joined anterodorsally to the mesopterygoid and ligamentously joined to the ascending margin of the articular.

Palatine.—A complex bone that gives rise anteriorly to an elongated and cylindrical maxillary process. Dorsomedially the palatine forms a rounded process that articulates with the lateral ethmoid wing. Ventrally it bears a single row of small teeth, and meets the anterior extension of the ectopterygoid posteriorly.

Hyoid Arch (Figs. 12, 13, 14)

Hyomandibula.—A flat bone with four thickened areas, each leading to an articulating head. Anterodorsally it articulates with the sphenotic and pterotic; posteriorly a slender head articulates with the opercle; ventrally it articulates with the symplectic and interhyal. Medially the hyomandibula broadly meets the metapterygoid.

Symplectic.—A slender splint bone joined dorsally by cartilage to the hyomandibula and ventrally extending along the medial surface of the quadrate.

Quadrate.—A flat triangular bone which lies ventral to the metapterygoid, with its anterior margin lateral to the ventral arm of the ectopterygoid. Ventrally the quadrate forms a thickened process that articulates with the medial surface of the articular.

Interhyal.—A flattened rod that connects the ventral articulating process of the hyomandibula with the epihyal.

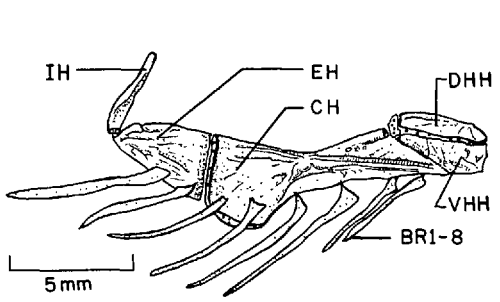
Epihyal.—A triangular shaped bone with its anterior margin lying lateral to the posterior end of the ceratohyal.

Ceratohyal.—An elongate bone which is expanded posteriorly into a broad shelf; a slender anterior shaft lies ventromedially to the ventral hypohyal.

Hypohyals.—A pair, dorsal and ventral, are present on each side. These bones are firmly united to each other and to the ceratohyal. The hypohyals form a fossa to accommodate the basihyal and urohyal.

Urohyal.—A long flattened bone rigidly attached to the anterior ends of the hyoid bars; medially it lies beneath the basibranchials.

Basihyal.—A median compressed rod extending anteroventrally from the first basibranchial, to which it is attached.



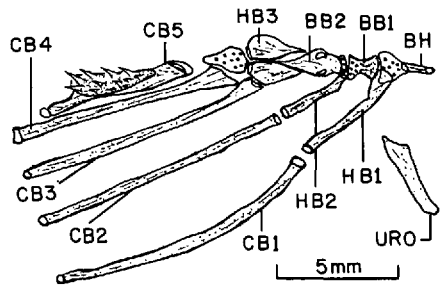


Figure 13. (Left) *Porogadus silus,* UMML 34142, Lateral aspect of portion of the hyoid apparatus with branchiostegals attached.

Figure 14. (Right) *Porogadus silus,* UMML 34142, Dorsal aspect of branchial arches and associated median elements of left side.

Branchial Arches (Figs. 14, 15)

Basibranchials.—These bones comprise two median ossifications; the first of which bears a small hood of cartilage anteriorly. The first basibranchial is hourglass shaped and supports the first arch anteriorly and part of the second arch posteriorly. The second element is elongate and supports part of the second arch anteriorly; its posterior end supports the distal end of the third hypobranchial. The fourth and fifth arch are supported by what appears to be a single median cartilage. The basibranchials bear small teeth in about half the specimens examined.

Hypobranchials.—The first and second pair of the three paired elements each have an expanded anterior section; posteriorly each tapers to a slender rod. The third hypobranchial expands to a broad shelf posteriorly and narrows anteriorly to overlie the posterior surface of the second basibranchial.

Ceratobranchials.—Four pairs of elongate rod-like bones, each bearing multiple patches of teeth. The smaller fifth ceratobranchial bears a prominent tooth plate.

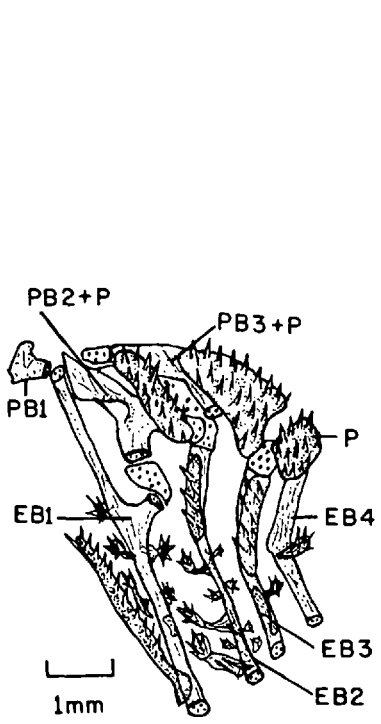
Epibranchials.—Four pairs, the first distinctly forked dorsally and articulating with the first pharyngobranchial cartilage. The second epibranchial is a curved bone which bears a coalesced tooth plate and dorsally supports the second pharyngobranchial. The third epibranchial is similar in shape to the preceding; it bears a coalesced tooth plate and dorsally supports the third pharyngobranchial. The fourth epibranchial lacks a tooth plate; it connects dorsally with the fourth pharyngobranchial tooth plate.

Pharyngobranchials.—Four pairs, the first of which is a roughly triangular plate lacking teeth. The second and third are each a bony plate bearing a patch of small teeth. The fourth is much reduced, cartilaginous and bears a distinct tooth plate which is adjacent to the tooth plate of the third, pharyngobranchial. Pharyngobranchial teeth have coalesced bases and do not originate in clusters.

Pectoral Girdle (Fig. 16a)

Posttemporal.—A flattened scale-like bone. A tapered rod extends anteromedially and articulates with the intercalar.

Supracleithrum.—An elongate triangular bone overlain dorsally by the posttemporal and itself overlays the cleithrum ventrally.



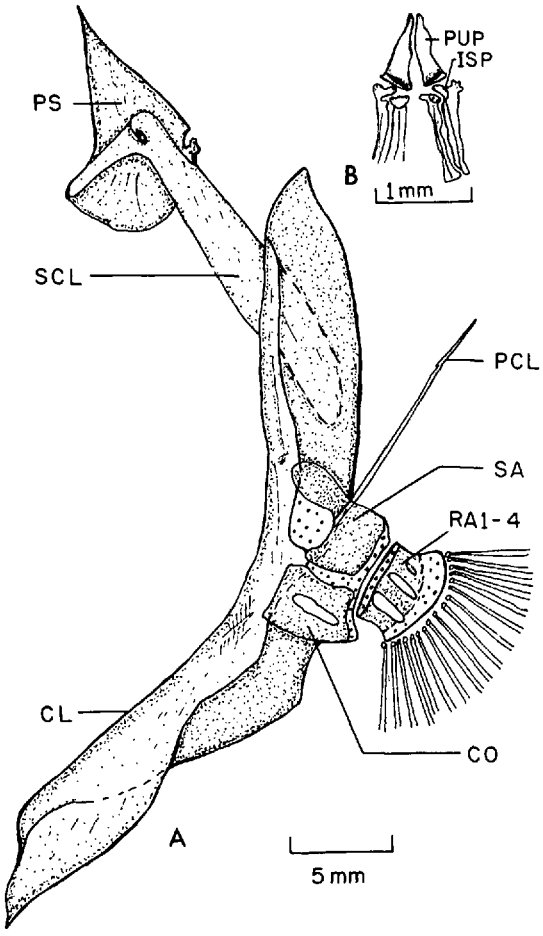


Figure 15. (Left) *Porogadus silus*, UMML 34142, Dorsal aspect of upper portion of branchial arches with associated pharyngeal branchials.

Figure 16. (Right) *Porogadus silus*, UMML 34142, Lateral aspect: A, left pectoral girdle; B, Dorsal aspect: pelvic girdle.

Cleithrum.—A large sickle shaped bone tightly bound to its fellow anteriorly by connective tissue; its leading edge folded back medially to form a partially enclosed canal.

Scapula.—A thin fan shaped bone lying dorsomedially to the cleithrum; its posterior section supporting several pectoral fin rays.

Coracoid.—A thin roughly triangular shaped bone pierced by a single small foramen near the center of the bone.

Pectoral Radials.—Four, flattened hourglass shaped radials, which together with the scapula support the pectoral fin rays.

Postcleithrum.—An elongate splint of bone lying median to the scapula and coracoid.

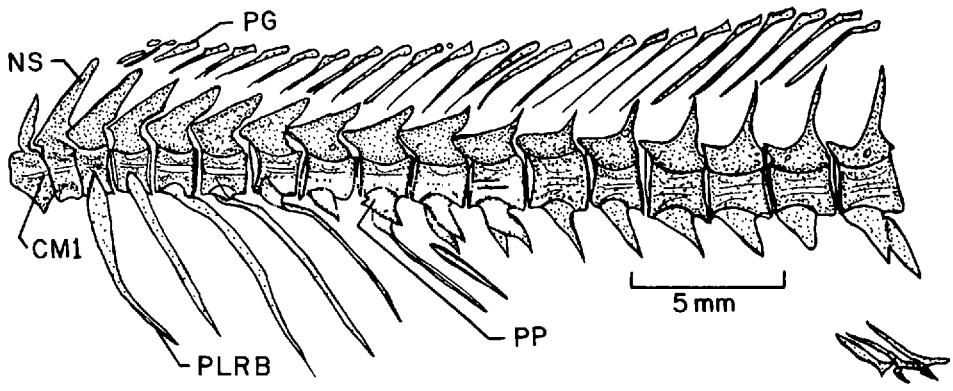


Figure 17. *Porogadus silus*, UMML 34142, Lateral aspect of vertebral column and associated structures.

Pelvic Girdle (Fig. 16b)

The paired pelvic bones are slightly cone shaped and lie vertically between the anterior tips of the cleithrum; each with broad ventral processes which support two long filamentous segmented rays, each bilaterally divided at its bone.

Axial Skeleton (Fig. 17)

The neural spine on the first centrum is shorter than those on subsequent centra; the two halves are joined in the midline. The first two centra lack ribs; centra three to five bear slender pleural ribs; subsequent centra bear well developed parapophyses. The base of the first proximal dorsal fin pterygiophore originates over centra two and three; the anal fin originates under centra 15, 16 and 17.

Porogadus catena (Goode and Bean, 1885)
Figure 6b

Bathyonus catena Goode and Bean, 1885: (8), 603, pl. 11, Fig. A (original description, two specimens, syntypes NMNH 330642, 23.4, 17.5 mm, ALBATROSS stn. 2379, 28°00'N, 87°42'W, 2934 m); Günther, 1887:22, 111 (description, after Goode and Bean, 1885).

Bassozetus catena Goode and Bean, 1895: 323, Fig. 286; Jordan and Evermann, 1898: 47, 2509, 1900, op. cit., Figs. 876, 876a (catalogue description, after Goode and Bean, 1895).

Porogadus catena Norman, 1939: 7(1) 87; Grey, 1956: 212 (synonymy, distribution); Nybelin, 1957: 287–292 (comparison with all known material, Table XIV); Cohen and Nielsen, 1978: 38 (generic synonymy, distribution and list of all nominal species).

Porogadus promelas Gilbert, 1891: (14)546 (original description, five specimens, syntypes, ALBATROSS stn. 3010, 27°N, 111°W, 2010 m); Norman, 1939: (7)87 (description, after Gilbert, 1891); Böhlke, 1953: (5)102 (catalog of Stanford types); Grey, 1956: 214 (synonymy, distribution); Nybelin, 1957: 287–292 (comparison with all known material); Cohen and Nielsen, 1978: 38 (generic synonymy, distributions, and list of all nominal species).

Moebia promelas Jordan and Evermann, 1898: (47)2511; Townsend and Nichols, 1925: (52)1b (mentioned).

Porogadus breviceps Garman, 1899: (24)155–156, (original description, two syntypes, MCZ 3450, 2670; 22–98 mm SN-V, ALBATROSS stn. 3435, 3436, 26°48'N, 110°45'W; 27°34'N, 110°53'W, 1718, 1810 m); Norman, 1939: (7)87–88 (mentioned, after Garman, 1899); Nybelin, 1957: 287–292 (comparison with all known material), Cohen and Nielsen, 1978: 38 (generic synonymy, distribution, and list of all nominal species).

Material Examined.—Syntypes USNM 37341, 28°00'N, 87°42'W, 2934 m, ALBATROSS stn. 2379 (2: 57.5–58.1 GPL); UMML 21632 (20: 37–68 mm GPL); IOS uncatalogued (5: 29–49 mm GPL); UMML

Table 4. Abbreviations used in text and figures

AN	angular	MET	metapterygoid
ART	articular	MX	maxilla
BB	basibranchial	NA	nasals
BH	basihyal	NS	neural spine
BOC	basioccipital	OP	opercle
BR	branchiostegals	PA	parasphenoid
CB	ceratobranchial	PAL	palatine
CH	ceratohyal	PB	pharyngeobranchials
CL	cleithrum	PC	prootic
CM	centrum	PCC	postcleithrum
CO	coracoid	PG	pterygiophore
COB	circumorbital	PL	parietal
D	dentary	PLRB	pleural rib
DE	dermethmoid	PMX	premaxilla
DHH	dorsal hypohyal	POP	preopercle
EB	epibranchial	PP	parapophysis
ECT	ectopterygoid	PR	pterosphenoid
EH	epihyal	PS	posttemporal
EO	epiotic	PT	pterotic
EOC	exoccipital	PUP	pubic plate
ES	extrascapular	RA	radials
FL	frontal	RETP	retroarticular process
GF	gill filaments	SC	sphenotic
HB	hypobranchial	SCC	supracleithrum
HM	hyomandibula	SGR	short gill raker
INC	intercalary	SL	supraoccipital
IH	interhyal	SMX	supramaxilla
IOP	interopercle	SOP	subopercle
ISP	ischial process	SY	symplectic
LE	lateral ethmoid	VHH	ventral hypohyal
LGR	long gill raker	VO	vomer
MES	mesopterygoid	URO	urohyal

34138 (2: 65–67 mm GPL); MCZ 28655 (syntype, 69 mm GPL); MCZ 28658 (syntype, 61 mm GPL); VIMS 04961 (39 mm GPL); USNM 48265 (syntypes, 2: 39–69 mm GPL); USNM 125002 (66 mm GPL).

Diagnosis.—Refer to Table 1 and Key presented above.

Description.—Counts and measurements are presented in Table 3. Body very long, slender and much compressed; tail attenuate and whip-like. Dorsal fin origin slightly posterior to base of pectoral fin. Anal fin origin from tip of snout greater than twice the head length, its rays are shorter than dorsal. Pectoral fin shorter than head and placed rather low on the body, closer to belly than dorsum; its base directed slightly downward. Pelvic fins immediately adjacent to each other at their bases, extending beyond pectoral fin but before vent; each fin comprised of two joined rays.

Head one-half or more preanal length, not much compressed, with about four spines along preopercle margin. Spines few and poorly developed on top and sides of head. Pores of cephalic lateralis system prominent beneath orbital region and on posterior margin of preopercle. Mouth slightly sub-terminal with wide gape; maxilla extending well beyond eye, its length about equal to body depth. Jaws, vomer and palatine with small bands of villiform teeth. Single median basibranchial tooth patch. Eye well developed, its diameter goes about 6 times in head length. Nostrils paired, separated by a small space and closer to eye than

snout. Opercle spine weak, flattened and incorporated in opercle bone. Body lateral lines indistinct. Gill rakers on first arch long with three rudimentary rakers on upper limb, one developed raker at the angle plus 15 developed rakers on lower limb.

Body except for fin membranes completely covered with small subrectangular cycloid scales. Scales frequently missing on trawled specimens; however, scale pockets distinct. In alcohol specimens body is pale yellowish-brown, head and belly slightly darker.

Distribution.—Circumglobal beneath tropical and temperate seas at depths between 1500–3500 m (Fig. 9).

Remarks.—The following account reduces *Porogadus promelas* and *P. breviceps* to junior synonyms of *P. catena.* We believe that the holotype of *P. catena* and the types of *P. promelas* and *P. breviceps* represent a single species. Gilbert's (1891) and Garman's (1899) original descriptions of *P. promelas* and *P. breviceps* respectively were based on only a few rare specimens and did not account for variation. We found upon examination of additional material of *P. catena* that counts and measurements reported in the literature for all three nominal species either fell within the observed range for those characters or were not substantiated upon re-examination of type material. The occurrence of *P. catena* in the western Atlantic and eastern Pacific Oceans is an interesting zoogeographic pattern that provides a useful basis for a comparison of populations on both sides of the Isthmus.

Grey (1956) mistakenly reported the occurrence of two specimens of *P. subarmatus* from the Gulf of Mexico. Upon re-examination, these specimens were found by us to be indistinguishable from the holotype of *P. catena.* The holotype of *P. subarmatus* which we have examined is very similar to *P. catena* and differs primarily in the relative development of the head armature, the former possessing strongly retrorse lateral ethmoids.

Porogadus miles Goode and Bean, 1885
Figure 6c

Material Examined.—Holotype USNM 35625, 38°27'N, 73°02'W, 2125 m, ALBATROSS stn. 2230 (40 mm GPL); VIMS 04817 (2: 88–89 mm GPL); VIMS 03529 (100 mm GPL); MCZ 57611 (3: 100–140 mm GPL); USNM 214666 (4:39–55 mm GPL); USNM uncatalogued (2: 58–71 mm GPL); USNM 214672 (2: 74–112 mm GPL); USNM uncatalogued (103 mm GPL); UMML 34139 (72 mm GPL); UMML 34140 (10: 75–145 mm GPL); VIMS 03531 (95 mm GPL); VIMS 07089 (2: 92–96.0 GPL).

Diagnosis.—Refer to Table 3 and key above.

Description.—Counts and measurements are presented in Table 3. Body very long, slender and highly compressed; tail attenuate and whip-like. Dorsal-fin origin slightly posterior to base of pectoral, its rays much longer than anal. Anal-fin origin from tip of snout about equal to twice head length. Pectoral fin about two-thirds head length and placed rather low on the body, closer to belly than dorsum; its base parallel to the vertical. Pelvic fins immediately adjacent to each other at their bases, origin well in advance of pectorals; each fin comprised of two joined rays (sometimes separate in large adult specimens).

Head one-half or more preanal length with four to five well developed spines along preopercle margins. Mouth large with wide gape, depressed snout projecting slightly over mouth. Spines on top and sides of head numerous and strongly developed. Pores of cephalic lateralis system prominent beneath orbital region and on posterior margin of preopercle. Maxilla expanded posteriorly and extend-

ing well beyond eye. Jaws, vomer and palatines with bands of villiform teeth. Single median basibranchial tooth patch. Eye large, its diameter four and one-half times in head length. Anterior nostrils small, separated by a narrow space, closer to tip of snout than eye; posterior nostrils widely spaced and placed immediately in front of eye. Opercular spine well developed and incorporated in opercle bone. Sides of body with three prominent lateral line rows. Gill rakers on first arch long, with three prominent lateral line rows. Gill rakers on first arch long, with three rudimentary rakers on upper limb, one developed raker at the angle plus 14 developed rakers on the lower limb.

Body except for fin membranes completely covered with very small subrectangular cycloid scales. In life, specimen's body is dark brown, head and belly bluish-black; specimens in alcohol similarly colored but paler.

Distribution.—Circumglobal beneath tropical and temperate seas at bathyal and abyssal depths (Fig. 9).

Remarks.—Substantial morphological variation exists among specimens examined from the western North Atlantic that cannot be attributed to sexual dimorphism. The majority of specimens examined conform to the above description; however, a few specimens of *P. miles* have a narrower interorbital distance, more strongly depressed snout and greater dorsal fin height.

Penopus macdonaldi (Goode and Bean, 1896)
Figure 6d

Material Examined.—Holotype USNM 39433, 38°29'30"N, 70°57'W, 2935 m, ALBATROSS stn. 2716 (315 mm SL); USNM 238803 (45 mm GPL); IOS uncatalogued (39 mm GPL); IOS (101 mm GPL); VIMS 07084 (40 mm GPL); VIMS 03530 (73 mm GPL); UMML 341341 (49–94 mm GPL).

Diagnosis.—Refer to key above.

Description.—Body long and slender. Dorsal fin origin about equal to interorbital distance beyond base of pectoral fin. Anal fin origin from tip of snout equal to or less than twice head length, its rays shorter than dorsal. Pectoral fin placed low on body and about equal to snout length. Pelvic fins separated from each other by a narrow space at their bases and not extending beyond pectorals; each fin comprised of two joined rays.

Head depressed anteriorly with four or five spines at lower angle of preopercle margins. Snout long; projecting over mouth. Opercle with a strong curved spine dorsally and two or three flattened spines incorporated in lower angle. Spines on top and sides of head very poorly developed or lacking. Pores of cephalic lateralis system not visible beneath orbital region and on posterior margin of preopercle. Mouth inferior with large gape; maxilla extending well beyond eye; its length equal to about one-half head length. Jaws, vomer and palatines with villiform teeth. Two median basibranchial tooth patches, the posterior one small. Eye minute, its diameter more than 10 times in head length. Anterior nostril opening is a narrow slit, the posterior larger and oblong in shape. Body lateral line represented by three rows. Gill rakers on first arch long with 3–4 rudimentary rakers on upper limb, 1–2 developed rakers at the angle plus six–eight developed raker on lower limb.

Body except for fin membranes completely covered with small subrectangular cycloid scales. In alcohol specimen's body is yellowish-brown, head and belly bluish-black, specimen's body in life is dark brown, head and belly almost black.

Distribution.—Tropical Atlantic at bathyal and abyssal depths (Fig. 9).

Remarks.—Although there are two nominal species of *Penopus* only one, *Penopus microphthalmus,* described from the eastern Atlantic by Vaillant (1888) appears valid. Nybelin (1957) examined the holotype of *P. microphthalmus* and concluded "the only difference of importance between the two species seems to be the relative greater length of the maxilla in *P. microphthalmus.*" We ourselves have found no differences in meristic or morphometric characters including the maxilla length between *P. macdonaldi* collected from the western Atlantic and *P. microphthalmus* collected off the west coast of Africa (Merrett and Marshall, 1981). We believe further comparison of *Penopus* populations from both sides of the Atlantic Ocean will eventually result in the synonymy of the two nominal species.

Comparative Material Examined

Porogadus atripectus.—MCZ 28654 (syntype, 69 mm SN-V); MCZ 28656 (syntype, 96 mm GPL); MCZ 28657 (syntype 76 mm GPL).

Porogadus longiceps.—Holotype MCZ 28660, 4°56'N, 8°52'30"W, 3240 m, ALBATROSS stn. 3381 (130 mm GPL); MCZ 28662 (syntype, 38 mm GPL); MCZ 28661 (syntype, 83 mm GPL); MCZ 28659 (syntype 155 mm GPL); USNM 57850 (65 mm GPL).

Porogadus subarmatus.—MNHN 86529 (syntype, 51.0 mm GPL); MNHN 86535 (syntype, 56.0 mm GPL); MNHN 86534 (syntype, 52.0 mm GPL).

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