

REDESCRIPTION OF *POLYIPNUS FRASERI* FOWLER, 1934
(TELEOSTEI: STOMIIFORMES: STERNOPTYCHIDAE),
WITH REMARKS ON PAEDOMORPHOSIS

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Abstract.—The sternoptychid *Polyipnus fraseri* Fowler, 1934 was described from a single specimen from the Philippine Islands. In recent revisions the species has been synonymized; authors have treated the unusual morphology displayed by Fowler's specimen as an abnormality. Comparison of the holotype with new material from the Philippine Sea reveals that *P. fraseri* is not aberrant and should be recognized as a valid species. Furthermore, this species possesses a unique posterior preopercular spine. The redescription includes a discussion of the characters that have led to systematic confusion. Examination of ontogenetic trajectories of supra-anal photophore addition for all 22 nominal species of *Polyipnus* shows that the juvenile-like features of adult *P. fraseri* are probably a result of some paedomorphic process, but the paucity of material precludes further analysis.

The peculiar species *Polyipnus fraseri* Fowler, 1934 became known, like many deep ocean forms, through the expeditions of R/V *Albatross*. A single specimen was taken in the waters around the Philippines at a maximum depth of just over 1000 m. In his revision of the hatchetfishes, Schultz (1961) provided additional description of Fowler's specimen, and included an improved illustration. The next published work on the group was Baird (1971) in which *P. fraseri* was synonymized with *P. tridentifer* McCulloch, 1914, without comment. Borodulina (1979) placed *P. fraseri* in the synonymy of *P. spinosus* Günther, 1887. Yamamoto (1982) reported a specimen from the Philippine Sea (Kyushu-Palau Ridge) which was ascribed to *P. fraseri*, but the author thought it might represent a "larval form of one of the other species."

Borodulina (1979) did not state whether she had seen the holotype of *P. fraseri* (or any other material) but did comment on some of the unusual characteristics shown by published drawings. In her opinion some

of the features could be explained by "retention of juvenile features," but she continued . . . "this is contradicted by the large size of the specimen" (Borodulina 1979:8). The latter statement is confusing because it was the large size of the specimen that suggested that juvenile features had been retained.

I believe that Borodulina was essentially correct in recognizing that paedomorphic features are apparent in *P. fraseri*. In this paper I compare ontogenetic trajectories (sensu Alberch et al. 1979) for all nominal species of *Polyipnus* (material listed in Appendix) to develop a heterochronic explanation of the problematical photophore features of *P. fraseri*. The solving of such a problem requires a phylogenetic framework (Fink 1982) but an explicit statement of interspecific relationships for *Polyipnus* is not yet available. However, for the present purpose it is sufficient to accept the monophyly of the genus *Polyipnus* (Weitzman 1974) and the *P. spinosus* complex, including *P. fraseri* (Harold 1989).

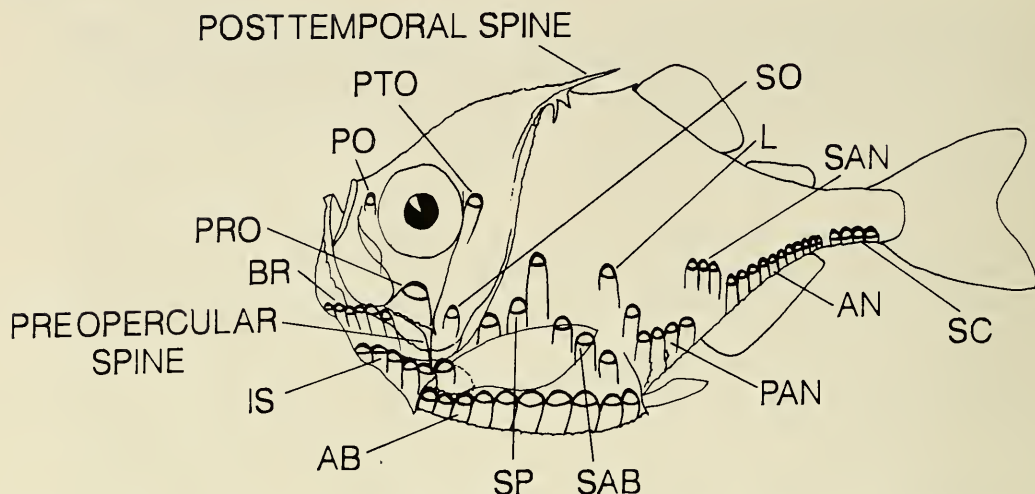


Fig. 1. Locations of spines and photophore clusters in *Polyipnus* species. Abbreviations defined in Methods section. Redrawn from Schultz (1961).

Methods

Measurements and meristics were made following Hubbs & Lagler (1958). Fin-ray counts are the totals, including rudimentary and unbranched elements. All body lengths are SL. Terminology and abbreviations of photophore clusters, which follows Ahlstrom et al. (1984), is illustrated in Fig. 1 and briefly defined here: AB, abdominal; AN, anal; BR, branchiostegal; IS, isthmus; L, lateral; PAN, preanal; PO, preorbital; PRO, preopercular; PTO, postorbital; SAB, supra-abdominal; SAN, supra-anal; SC, subcaudal; SO, subopercular; SP, suprapectoral. Individual photophores of a cluster are referred to by number, counting from the anterior. Institutional abbreviations follow Leviton et al. (1985).

Systematic Section

Polyipnus fraseri Fowler, 1934

Fig. 2

Polyipnus fraseri Fowler, 1934:257–258.—Schultz, 1961:642.—Schultz, 1964:267.—Yamamoto, 1982:327.—Fujii, 1984:47.—Harold, 1989:874–875.

Polyipnus tridentifer.—Baird, 1971:86

(incorrect spelling and year: “*Polyipnus fraseri* Fowler, 1933”).

Polyipnus spinosis [sic].—Borodulina, 1979:7–8 (incorrect spelling of *Polyipnus spinosus*).

Diagnosis.—A member of the genus *Polyipnus* Günther, 1887 with four anal and no supra-anal photophores, and a unique posterior preopercular spine. Eye relatively large, orbit length about one quarter of standard length. Two pigment bars extending down flank from dorsum.

Description of holotype.—Body deep, compressed, anterior body profile round (Fig. 2). Caudal peduncle extremely narrow. Head relatively large. Ventral margin of dentary, and frontal ridges smooth, the latter terminating posteriorly in a spine above center of eye. Parietal ridge reduced, smooth. Posttemporal dorsal arm smooth, posterolateral keel of ventral arm deeply serrated. Dorsal and ventral arms joined by broad web-like ossification, producing extensive armored shield between occiput and dorsal fin origin. Three prominent posttemporal spines: dorsal element longest, reaching beyond dorsal fin origin, ventral and median spines about half length of dorsal spine.

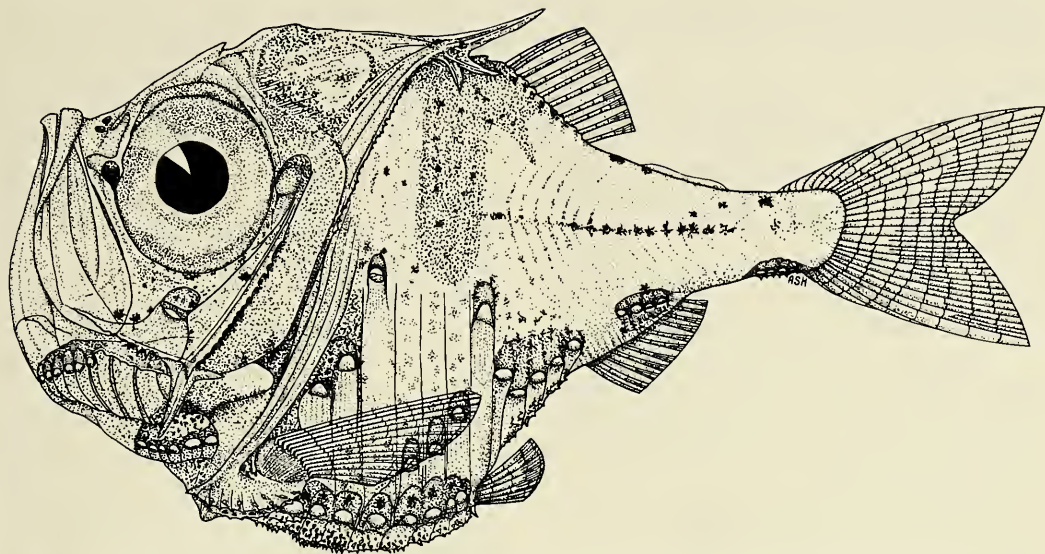


Fig. 2. *Polyipnus fraseri* Fowler, 1934, holotype, 40.4 mm, USNM 92324. Jaws and fin rays reconstructed, after Schultz (1961).

Ventral spine curving slightly towards anterior, median spine curved dorsally. Pectoral shield with many short spines over entire surface and a group of about six spines present on lateral knob adjacent to pectoral fin radials. Preopercular keels on dorsal and anterolateral limbs deeply serrate. Two preopercular spines: ventral spine long, about half orbit length, and narrow; posterior spine about one third length of ventral spine, and directed posteriorly. Dorsal preopercular spine absent. Dorsal blade not visible externally. Adipose fin present. Fin-ray counts: dorsal (10), anal (11), pectoral (14), pelvic (7). Gill rakers 7 + 13. Morphometrics (percent of standard length): head length 38.0; orbit length 23.0; body depth 65.8; caudal peduncle depth 11.3; caudal peduncle length 22.2; dorsal fin length 15.3; anal fin length 16.6; preanal length 70.5; predorsal length 58.7; preventral length 67.1; postdorsal length 48.8; postanal length 38.1; length of SC photophore cluster 5.3; distance between AN and SC photophore clusters 11.9.

Photophore counts typical of *Polyipnus*

species except for AN and SAN series (given below): IS (6); BR (6); PO (1); PTO (1); PRO (1); SO (1); SP (3), stepped dorsally from anterior to posterior, second very slightly above first with third elevated to level of anal fin insertion; SAB (3), stepped dorsally in approximately equal increments from anterior to posterior; AB (10), each photophore scale covered with minute denticles, photophores #1 and #2 small, located under pectoral shield proximal to medial axis, #3 to #10 follow arc of abdominal keel; L (1), at level slightly below SP #3; PAN (5), first well above second, #2 to #5 in line parallel with ventral body margin; SAN (0); AN (4) and SC (4), relatively small, scales denticulate.

Dark dorsomedian pigment present, extending from occiput to mid-point of dorsal fin. Ventral margin of dorsomedian pigment extending down flank as two distinct bars. Anterior bar broad, terminating bluntly at level of photophore SP #3. Posterior bar shorter, tapered, arising at posterodorsal base of anterior pigment bar and extending posteroventrally. Isolated mela-

nophores located on preopercle, dorsal fin base, caudal peduncle and posterior midline.

Distribution.—Philippine Islands and Philippine Sea, to a maximum depth of about 1000 m. Using bathymetric criteria this species should be considered mesopelagic although, like other species of *Polyipnus*, it appears to occur in areas of abrupt sea floor topography (i.e., continental slope and rises), and may be benthopelagic.

Holotype.—PHILIPPINE ISLANDS: Buton Strait, R/V *Albatross* Sta. 5476, 12°56'24"N latitude, 124°25'24"E longitude, open-net tow to 1032 meters, USNM 92324 (40.4 mm SL).

The following non-type specimen was also examined:

PHILIPPINE SEA: Kyushu-Palau Ridge, 26°46.01'N latitude, 135°19.00'E longitude, 322–340 meters, BSKU 29353 (32.4 mm SL).

Remarks.—The examination of new material has contributed to the recognition of *Polyipnus fraseri* as a distinct species that can be distinguished from all congeners by the absence of the supra-anal photophore cluster, and the presence of four anal photophores and a unique posterior preopercular spine. Although it has not been possible to examine the gonads of *P. fraseri*, the specimens possess highly denticulate ventral photophore scales as do adults of other species belonging to the *P. spinosus* complex. Usually only juveniles (up to about 15 mm SL) have as few as 4 anal photophores (see Fig. 3 in which all nominal species of *Polyipnus* are represented). Additions of photophores are usually made at body sizes up to 30 mm SL (lowest AN count in other species at that standard length is 7). Rate of addition is probably quite low in *P. oluolus* Baird, 1971 as well (Fig. 3: 6 AN photophores at 26.9 mm SL, only known specimen). The largest individual of another species with no SAN photophores is 16.9 mm SL (*P. ruggeri* Baird, 1971). With so much interspecific and ontogenetic varia-

tion in photophore number, and only one specimen known, Baird (1971) and Borodulina (1979) believed they were taking a conservative approach in synonymizing *P. fraseri*.

Relative size of various elements of the skull are also atypical and seem to be correlated with enlargement of the eye. As percentages of standard length, *P. fraseri* has an orbital length of 18.0 to 23.0, 13.6 to 19.0 in other species at SL less than 25 mm, and 10.8 to 17.2 in other species at SL greater than 25 mm.

Polyipnus fraseri is a member of the *P. spinosus* complex, a monophyletic group of Indo-Pacific species with denticulate abdominal keel scales and a multispinose posttemporal. Arrangement and shape of posttemporal spines in *P. fraseri* is most similar to that of *P. spinifer*, *P. spinosus* and *P. stereope*, all of which have large dorsal and prominent, but much shorter, basal spines.

Discussion

The specialized Type Alpha photophores of sternoptychids develop and increase in numbers by budding anteriorly from a common gland (Weitzman, in Ahlstrom et al. 1984:195), a mechanism which is thought to be a synapomorphy of the ten genera in the family, as Weitzman (1974) defined it. In general, development of gonostomatids and sternoptychids is protracted and photophores do not reach their full complement until comparatively late in life. Among the more unusual features of *P. fraseri* are the absence of supra-anal photophores and the presence of only four anal photophores. In adults of the other 21 species in the genus there are typically three supra-anal photophores (one per myomere), located between the preanal and anal clusters, and six or more photophores in the anal cluster. Since these two clusters of luminescent organs are the last to appear ontogenetically in this genus, it is reasonable to conclude that their

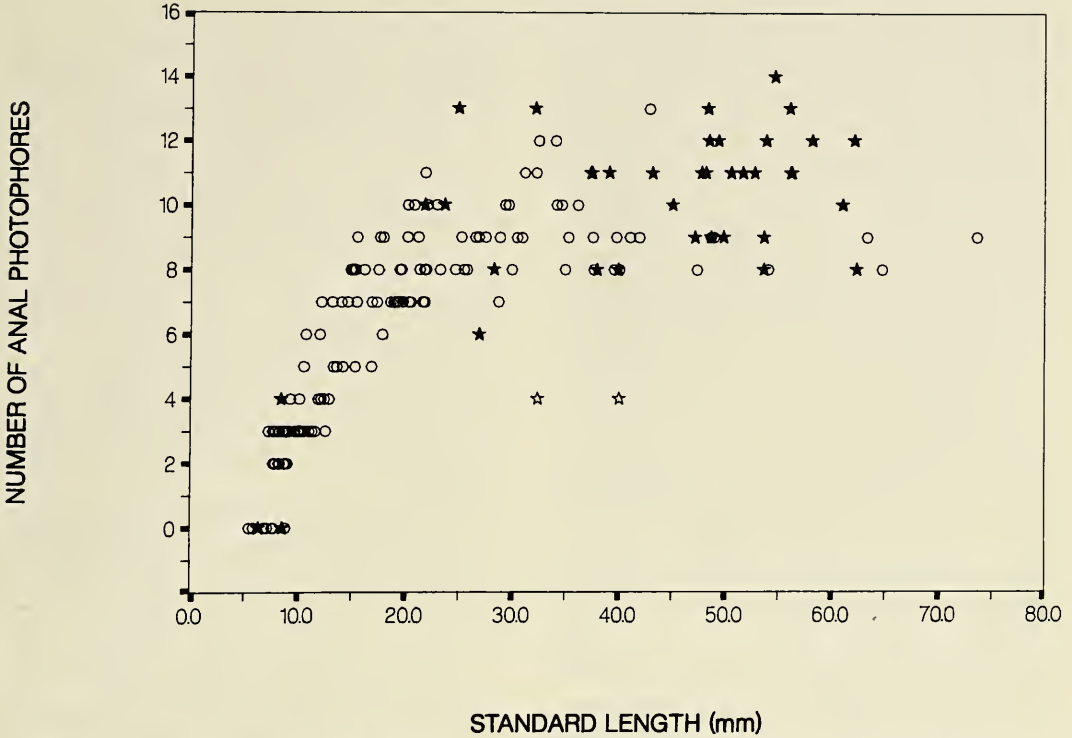


Fig. 3. Number of anal photophores plotted against standard length for 22 *Polyipnus* species. All stars = *P. spinosus* complex; open stars = *P. fraseri*; circles = *P. asteroides* and *P. laternatus* complexes combined (i.e., all other species).

absence or reduced numbers in *P. fraseri* is a result of some process producing paedomorphic development.

The occurrence of species exhibiting paedomorphosis has been noted for a diverse assemblage of fishes (Fink 1981, Weitzman & Vari 1988), including the deep-sea families Gonostomatidae (Ahlstrom et al. 1984), Stomiidae (Fink 1985), and Sternoptychidae (Weitzman 1974). The existence of species or higher taxa with juvenile-like features in adults can be a source of difficulty in systematics. It is now generally accepted that much of observed morphological diversity, including otherwise perplexing morphologies, may result through heterochronic alteration of developmental programs. A framework for interpretation of such cases has been emerging over the past decade (see Alberch et al. 1979, Fink 1982,

Kluge 1988). Figure 3, which compares relative growth of structures among related taxa, can be interpreted as a set of ontogenetic trajectories. Due to unavailability of a growth series of *P. fraseri* it is not possible to compare slopes with other species or to plot sizes at which various events take place. It is clear, however, that rate of photophore addition to the anal cluster is probably lower than in other species. In a form that reaches a body size comparable to possible sister taxa and *Polyipnus* outgroups (*P. asteroides* Schultz, 1938 and *P. laternatus* Garman, 1899 complexes), such development is considered neotenic. Alternatively, the presence of four anal photophores could be the result of late onset of growth with the rate of addition the same as in other species (i.e., postdisplacement). The supra-anal photophore cluster is absent in the two

known specimens but the possibility remains that *P. fraseri* reaches a much larger body size and has unusually protracted development of AN and SAN photophores. In either case, when compared with all known possible immediate outgroups, it appears probable that some process has affected the general ontogenetic program of photophore development. Without material representing the entire size range of *P. fraseri* it is not possible to comment on rate of appearance of the other groups of luminescent organs, or to say which of the possible heterochronic explanations is the more likely. Since *P. fraseri* is a member of the *P. spinosus* complex, then the distribution of ontogenetic photophore characters (absence of SAN, low AN number) is such that their states in *P. fraseri* are most parsimoniously interpreted through outgroup comparison as apomorphic.

Qualitatively, the body shape (e.g., large orbit; narrow caudal peduncle) of *P. fraseri* is very similar to juveniles of other species of the *P. spinosus* complex and the outgroups. The possibility remains that the known specimens of *P. fraseri* are juveniles of a large species. However, this explanation requires very early development of photophore-scale denticles relative to the appearance of typically adult photophore features.

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Literature Cited

- Ahlstrom, E. H., W. J. Richards, & S. H. Weitzman. 1984. Families Gonostomatidae, Sternoptychidae, and associated stomiiform groups: development and relationships. Pp. 184–198 in H. G. Moser, W. J. Richards, D. M. Cohen, M. P. Fahay, A. W. Kendall, Jr., and S. L. Richardson, eds., *Ontogeny and systematics of fishes*. Special Publication Number 1, American Society of Ichthyologists and Herpetologists, 760 pp.
- Alberch, P., S. J. Gould, G. F. Oster, & D. B. Wake. 1979. Size and shape in ontogeny and phylogeny.—*Paleobiology* 5(3):296–317.
- Baird, R. C. 1971. The systematics, distribution, and zoogeography of the marine hatchetfishes (family Sternoptychidae).—*Bulletin of the Museum of Comparative Zoology, Harvard University* 142(1):1–128.
- Borodulina, O. D. 1979. Composition of the “*Polyipnus spinosus* complex” (Sternoptychidae, Osteichthyes) with a description of 3 new species of the group.—*Journal of Ichthyology* 19(2):1–10.
- Fink, W. L. 1981. Ontogeny and phylogeny of tooth attachment modes in actinopterygian fishes.—*Journal of Morphology* 167:167–184.
- . 1982. The conceptual relationship between ontogeny and phylogeny.—*Paleobiology* 8(3): 254–264.
- . 1985. Phylogenetic relationships of the stomiid fishes (Teleostei: Stomiiformes). *Miscellaneous Publications of the Museum of Zoology, University of Michigan*, No. 171, 127 pp.
- Fowler, H. G. 1934. Descriptions of new fishes obtained 1907 to 1910, chiefly in the Philippine Islands and adjacent seas.—*Academy of Natural Sciences of Philadelphia, Proceedings* 85:233–437.
- Fujii, E. 1984. Family Sternoptychidae. Pp. 47–48, pl. 49L in H. Masuda, K. Amaoka, C. Araga, T. Uyeno, and T. Yoshino, eds., *Fishes of the Japanese Archipelago*. Tokai University Press, Tokyo, 433 pp., 370 pl.
- Harold, A. S. 1989. A new species of *Polyipnus* (Stomiiformes: Sternoptychidae) from the Coral Sea, with a revised key to the species of the *P. spinosus* complex.—*Copeia* 1989(4):871–876.
- Hubbs, C. L., & K. F. Lagler. 1958. *Fishes of the Great Lakes region*. The University of Michigan Press, Ann Arbor, 213 pp.
- Kluge, A. G. 1988. The characterization of ontogeny. Pp. 79–81 in C. J. Humphries, ed., *Ontogeny and systematics*. Columbia University Press, New York, 236 pp.
- Leviton, A. E., R. H. Gibbs, Jr., H. Heal, & C. E. Dawson. 1985. Standards in ichthyology and herpetology: Part I. Standard symbolic codes for

- institutional resource collections in herpetology and ichthyology.—*Copeia* 1985(3):802–832.
- Schultz, L. P. 1961. Revision of the marine silver hatchetfishes (family Sternoptychidae).—*Proceedings of the United States National Museum* 112(3449):587–649.
- . 1964. Family Sternoptychidae. Pp. 241–273 in H. B. Bigelow et al., eds., *Fishes of the Western North Atlantic, Part 4, Isospondyli*. Sears Foundation for Marine Research Memoir No. 1, 599 pp.
- Weitzman, S. H. 1974. Osteology and evolutionary relationships of the Sternoptychidae, with a new classification of stomiatoid families.—*Bulletin of the American Museum of Natural History* 53(3):327–478.
- , & R. P. Vari. 1988. Miniaturization in South American freshwater fishes: an overview and discussion.—*Proceedings of the Biological Society of Washington* 101:444–465.
- Yamamoto, E. 1982. Sternoptychidae. P. 327 in O. Okamura, K. Amaoko, and F. Mitani, eds., *Fishes of the Kyushu-Palau Ridge and Tosa Bay*. Japan Fisheries Resource Conservation Association, Tokyo, 435 pp.
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- Appendix
- Comparative material examined.*—*P. aquavitus* Baird, 1971: USNM 298928, 1 (17.5 mm), USNM 298927, 1 (15.4 mm), USNM 298925, 10 (10.6–17.9 mm), AMS I.19761-029, 10 (10.2–34.1 mm), AMS I.16492-008, 3 (12.0–14.9 mm), AMS I.20310-017, 3 (17.6–20.7 mm), AMS I.19762-002, 3 (21.2–34.6 mm), AMS I.20316-005, 3 (20.2–36.1 mm); *P. asteroides* Schultz, 1938: MCZ 66695, 1 (41.9 mm), MCZ 66696, 1 (30.9 mm); *P. elongatus* Borodulina, 1979: AMS I.21975-007, 2 (54.6–65.0 mm); *P. indicus* Schultz, 1961: personal collection, uncatalogued, 3 (53.6–62.3 mm); *P. inermis* Borodulina, 1981: personal collection, uncatalogued, 3 (48.6–49.8 mm); *P. kiwiensis* Baird, 1971: AMS I.15984-002, 1 (48.6 mm), AMS I.24496-001, 1 (73.6 mm); *P. laternatus* Schultz, 1938: USNM 298924, 3 (32.4–42.8 mm), MCZ 40575, 1 (31.1 mm); *P. matsubarai* Schultz, 1961: ORIT 2572–2578, 2580, 2582, 2585, 2587, 11 (18.6–41.0 mm), NMC 79-0009, 1 (97.4 mm); *P. meteori* Kotthaus, 1967: MCZ 64694, 1 (17.9 mm), ZMUC P206931, 1 (37.6 mm), ZMUC P206928, 1 (54.0 mm), ZMUC P206929, 2 (12.2–21.3 mm), SIO 61-541-10, 1 (28.7 mm), USNM 256965, 1 (20.3 mm); *P. nuttingi* Gilbert, 1905: BPBM 24892, 3 (28.3–39.9 mm), BPBM 23779, 1 (47.1 mm); *P. oluolus* Baird, 1971: holotype, USNM 204390, 1 (26.9 mm); *P. omphus* Baird, 1971: USNM 256967, 1 (32.2 mm); *P. parini* Borodulina, 1979: holotype, ZIL 43997, 1 (61.0 mm), illustration (Borodulina, 1979: Fig. 3) and x-radiograph; *P. polli* Schultz, 1961: MCZ 80400, 27 (9.7–34.9 mm); *P. polli?*: MCZ 80401, 13 (5.9–11.0 mm); *P. ruggeri*: USNM 298920, 1 (16.9 mm), USNM 298920, 2 (8.9–12.6), ZMUC P202814, 1 (24.6 mm), ZMUC P206958, 1 (21.6 mm), ZMUC P206956, 1 (63.3 mm), AMS I.27166-004, 1 (64.7 mm), AMS I.20312-007, 1 (21.3 mm), AMS I.20066-014, 1 (48.9 mm), AMS I.21372-006, 1 (25.5 mm); *P. spinifer* Borodulina, 1979: USNM 289176, 3 (21.7–24.9 mm), ORIT 2552, 2555, 2556, 3 (48.1–50.5 mm), AMS I.22808-028, 6 (32.1–51.6 mm), AMS I.22817-014, 6 (50.5–56.2 mm); *P. spinosus* Günther, 1887: holotype, BMNH 1987.12.7.159, 1 (45.0 mm); *P. stereope* Jordan and Starks, 1904: ORIT 2519, 1 (47.7 mm); *P. tridentifer* McCulloch, 1914: AMS I.18711-014, 3 (48.4–62.1 mm); *P. triphanos* Schultz, 1938: ZMUC P206963, 2 (26.5–30.4 mm), AMS I.24338-001, 1 (47.3 mm); *P. unispinus* Schultz, 1938: *Polyipnus* sp. (*P. spinosus* complex): USNM 298929, 1 (6.4 mm), AMS I.27171-007, 1 (8.6 mm), AMS I.27166-003, 1 (8.4 mm); *Polyipnus* sp.: MCZ uncatalogued, field no. RHB 2056, 14 (5.5–10.3 mm), USNM 298929, 1 (9.3 mm), USNM 298926, 1 (7.3 mm), MCZ 80402, 1 (9.2 mm).