

SYSTEMATICS AND ZOOGEOGRAPHY OF THE PORCUPINEFISHES (*DIODON*, DIODONTIDAE, TETRAODONTIFORMES), WITH COMMENTS ON EGG AND LARVAL DEVELOPMENT¹

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ABSTRACT

The porcupinefish genus *Diodon* is composed of five species: *D. hystrix* Linnaeus and *D. eydouxi* Brissout de Barneville are closely related species, each of which has a relatively elongate body, spines on the caudal peduncle, and high dorsal and anal fin ray counts; *D. holocanthus* Linnaeus and *D. liturosus* Shaw form a second species pair, each of which has a round body, no caudal peduncle spines, and moderate dorsal and anal fin ray counts; *D. nichthemerus* Cuvier is a round-bodied species but differs from *D. holocanthus* and *D. liturosus* in meristic characters and spination.

Diodon hystrix, *D. holocanthus*, and *D. eydouxi* are distributed circumtropically. The Atlantic population of *D. holocanthus* has diverged from the Indo-Pacific (including eastern Pacific) populations. *Diodon eydouxi* is pelagic, and both *D. hystrix* and *D. holocanthus* have pelagic juvenile stages. *Diodon liturosus* is found in the Indo-West Pacific, and *D. nichthemerus* is limited to Tasmania and southern Australia. It is not known whether the latter species have pelagic stages.

The egg and larval stages of *D. hystrix* and *D. holocanthus* (the latter identified by rearing) are similar. The pelagic eggs are 1.6-2.1 mm in diameter and hatch in about 5 days at 25°C. The larvae metamorphose to spiny juveniles at ca. 4 mm in about 3 wk. Both species have pelagic juvenile stages of long duration: *D. hystrix* remains pelagic to ca. 200 mm standard length, thus providing ample time for dispersal. Eggs and larvae of the other species are unknown.

The identities of the species of the genus *Diodon* have been confused since the time of Linnaeus. The most recent description of a valid "new" species was in 1846, but, unfortunately, time has done little to clarify the situation. Twenty-eight nominal species attributable to *Diodon* have been described since 1758, and most contemporary authors recognize two or three species. However, Le Danois (1959), in the only recent review of the genus as a whole, recognized six species.

The present study grew out of attempts to identify juvenile *Diodon* that resulted from rearing of pelagic eggs taken in Kaneohe Bay, Oahu, Hawaii (Watson and Leis 1974). These juveniles could not be identified using existing keys. While current literature recognized only two species of *Diodon* in Hawaiian waters, examination of museum specimens revealed that three were present there. This discovery, together with the encouragement of J. E. Randall of the Bernice P. Bishop Museum, led to the present study clarifying the identities of all of the species of *Diodon* and the description of their

development. An attempt was made to obtain information on existing type-specimens and this, along with the examination of a large number of specimens, has led to the conclusion that the genus is composed of five species, three of which are distributed circumtropically. Further, it is shown that the present taxonomic confusion is attributable to inadequate original descriptions, reliance on poor characters for differentiation, the close similarity of several of the species, and unusual aspects of the life histories of the species of *Diodon*. All of the nominal species could be distinguished with some certainty with two exceptions: the type of *Diodon echinus* Rafinesque 1810 could not be located and the original description provides no clue to its identification; the holotype of *Trichocyclus erinaceus* Günther 1870 (BMHN 1976.2.23.1) is a small fish in especially poor condition, giving the appearance of having been obtained from a stomach of some predator, and, while it is certainly a *Diodon*, more specific identification could not be made. *Diodon dussumieri* Bibron (see Le Danois 1959, 1961) is a nomen nudum, but examination of the "type" (MNHN 1306) by J. E. Randall of the Bernice P. Bishop Museum indicates that Le Danois was correct in placing *D. dussumieri* in synonymy with *D. holocanthus*.

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Although basically shorefishes, the diodontids (at least *Diodon* and *Chilomycterus*) are strongly tied to the pelagic environment through pelagic eggs and well-developed pelagic juvenile stages. In *Diodon* these juveniles remain pelagic for weeks or months (judging from size) and are often found far from shore. In fact, juvenile *Diodon* spp. are commonly encountered in the stomachs of such pelagic predators as dolphins (Gibbs and Collette 1959), and one species, *D. eydouxi*, is apparently pelagic throughout its life cycle.

The eggs of diodontids are poorly known. Nichols and Breder (1926) described the unfertilized eggs of *Chilomycterus schoepfi* from New Jersey as demersal, nonadhesive, transparent, and about 1.8 mm in diameter. However, Breder and Clark (1947) suggested that the eggs of *C. schoepfi* may be normally pelagic. The pelagic eggs of *D. holocanthus* and *D. hystrix* from Hawaii were briefly described as *Diodon* sp. and "diodontid II," respectively, by Watson and Leis (1974). Sanzo (1930) described the development of what are apparently the pelagic eggs of *D. hystrix* (identified as *Crayracion* sp.?) from the Red Sea. Wolfsheimer (1957) reported an aquarium spawning of *D. holocanthus* (identified by him as *D. hystrix*), but provided little descriptive information on the eggs. The eggs mentioned by Wolfsheimer sank, but did not adhere, to the bottom of the aquarium. They did not develop, so it is likely that they were not fertilized.

Larval and juvenile *Diodon* are no better known than the eggs. Blanco and Villadolid (1951) illustrated a juvenile "*Diodon bleekeri*," but this fish is clearly a juvenile tetraodontid. Many juvenile tetraodontids have prominent spines, particularly on the ventral surfaces. Fowler (1928) illustrated a juvenile *Diodon*, identified as *D. hystrix*, but the figure does not show spines on the caudal peduncle (see below), so this identification is apparently incorrect (assuming the drawing is accurate). No locality or other descriptive data are given by Fowler, so a specific identification cannot be made. Sanzo (1930) illustrated two larvae that resulted from rearing of his *D. hystrix* eggs and a juvenile *Diodon* captured in a plankton tow. The illustration of this latter fish shows no peduncle spines, but in other respects it resembles *D. hystrix*. Mito (1966) illustrated a larval and a juvenile *Diodon*, both identified as *D. holocanthus*. The pigmentation and the relatively small eye shown in Mito's illustrations more closely resemble the specimens of *D. hystrix* studied here. At least four species of

Diodon occur in Japanese waters, and Mito's specimens could be any of these, because he gives no information as to how the identifications were made. Nishimura (1960) reported on juvenile *Diodon* cast ashore in the Sea of Japan, but did not provide specific identifications.

MATERIALS AND METHODS

Measurements and counts are as defined by Hubbs and Lagler (1958:19-28) unless otherwise stated. Measurements routinely were made with needle point dividers to the nearest 0.5 mm. Fish <10 mm and all eggs were measured under a dissecting microscope to the nearest division of the ocular micrometer (± 0.02 mm at 50 \times , the power normally used). All measurements are from preserved specimens.

Unspecified lengths are in millimeters standard length. Caudal peduncle length was measured from the posterior base of the dorsal fin to the end of the hypural plate. Head width was measured immediately behind the eyes. Body width was measured at the base of the pectoral fin. Width of the eye was taken horizontally across the clear cornea. Measurements are given as proportions of standard length.

Dorsal and anal fin ray counts included all rays, branched and unbranched. The last two rays were counted separately because they have separate bases. Pectoral fin ray counts excluded the upper ray. This ray, although well developed in small (<30 mm) juveniles, is a rudiment in adults and is often not visible because it is embedded. In large specimens, the fin bases are especially fleshy and accurate fin ray counts are difficult to make without dissection or radiography.

Body measurements are given as range, mean (\bar{x}), and standard deviation (SD). The sample size for the measurements is given in parentheses at the beginning of the description of each species. Morphometrics are included only from individuals >50 mm. Fin ray counts are included for all specimens on which counts could be made (Table 1). In most cases, rays in both pectoral fins were counted. Fin rays were not counted on specimens with fin damage or on specimens that had rays obscured due to the thick bases of the dorsal and anal fins. Radiography was tried unsuccessfully to obtain vertebral counts: the dermal spines and their bases obscured the vertebrae, and made accurate counts impossible. The vertebral counts

TABLE 1.—Fin ray counts of *Diodon* species.

Dorsal fin rays	12	13	14	15	16	17	18	\bar{x}
<i>D. eydouxii</i>								
Atlantic					3		1	17.25
Indo-Pacific				4	25		6	17.06
<i>D. hystrix</i>								
Atlantic			2	7		1		15.90
Indo-Pacific		2	20	8				15.20
<i>D. holocanthus</i>								
Atlantic			22	4				14.15
Indo-Pacific	9	39	7					13.96
<i>D. liturosus</i>			1	12	15			15.50
<i>D. nichthemerus</i>	1	10						12.91
Anal fin rays	12	13	14	15	16	17	18	\bar{x}
<i>D. eydouxii</i>								
Atlantic					3		1	17.25
Indo-Pacific				2	22		11	17.26
<i>D. hystrix</i>								
Atlantic			3	7				15.70
Indo-Pacific		1	15	6				15.23
<i>D. holocanthus</i>								
Atlantic		9	18					13.67
Indo-Pacific		26	27	1				13.54
<i>D. liturosus</i>			10	17	1			14.68
<i>D. nichthemerus</i>	3	5	2					12.80
Pectoral fin rays	19	20	21	22	23	24	25	\bar{x}
<i>D. eydouxii</i>								
Atlantic			5	3				21.38
Indo-Pacific	7	58	17					20.12
<i>D. hystrix</i>								
Atlantic			1	10	10		1	23.50
Indo-Pacific		2	16	34	6			22.76
<i>D. holocanthus</i>								
Atlantic			7	31	20			22.22
Indo-Pacific		1	17	57	27	5		22.17
<i>D. liturosus</i>			2	11	24	17	2	23.11
<i>D. nichthemerus</i>	2	9	9					20.35

given for *D. holocanthus* were made on cleared and stained material.

The dermal spines require special terminology and measurements, as given below. Measurements, except for shaft length, were taken on dissected spines (Figure 1).

The spine shaft is that portion bearing the pointed tip, but excluding the shaft extension. The length of the spine (= shaft length) was taken from the lower portion of the lateral arm to the tip of the shaft. The starting point for this measurement can be found most easily by probing around the base of the spine.

The shaft extension is the portion of the shaft extending past the lateral arms of the base, and its length was measured from the lower portion of the lateral arm to the tip of the extension.

The lateral arms of the base are the subdermal portions of the spine upon which the spine pivots during erection. The length of the spine base was the straight line distance from tip to tip of the lateral arms.

The frontal spines are those of the anteriormost row on the head between the eyes. The pectoral axil spines are the spines immediately posterior to the base of the pectoral fin.

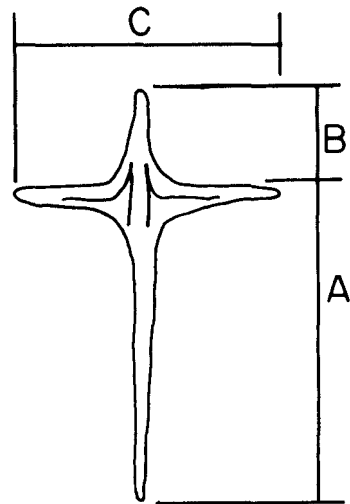


FIGURE 1.—Typical *Diodon* body spine: (A) spine (or shaft) length, (B) length of the shaft extension, (C) length of the spine base. The tip of the spine shaft points caudad.

The number of spines in a longitudinal row over the dorsum from the snout to the dorsal fin base (S-D spines) and the spines in a longitudinal row over the ventrum from the lower jaw to the anus (S-A spines) were counted. These rows of spines are irregular and difficult to follow, so the counts should be considered approximate. With practice, repeated counts of ± 1 can be achieved consistently. The numbers of spines between pectoral fins, both over the dorsum (P-D-P spines) and ventrum (P-V-P spines), were also counted, but these counts are even less reproducible than the longitudinal counts.

Repeated reference is made to the spines on the caudal peduncle. In some species the only spines in the region of the caudal peduncle are some rather large spines associated with the dorsal and anal fin bases. Although these spines extend over the peduncle, their subdermal bases (lateral arms and shaft extension) are at least partially anterior to a line between the base of the posteriormost rays of the dorsal and anal fins, and they are considered not to be on the peduncle. In other species, there are relatively small spines which are wholly posterior to the line defined above on the dorsal and dorsolateral surfaces of the peduncle; these spines are considered to be on the peduncle (Figure 2).

Larvae were obtained from plankton samples (field specimens) and rearing experiments using eggs from plankton tows (reared specimens). All eggs and larvae were captured around the Hawaiian island of Oahu. Rearing took place in

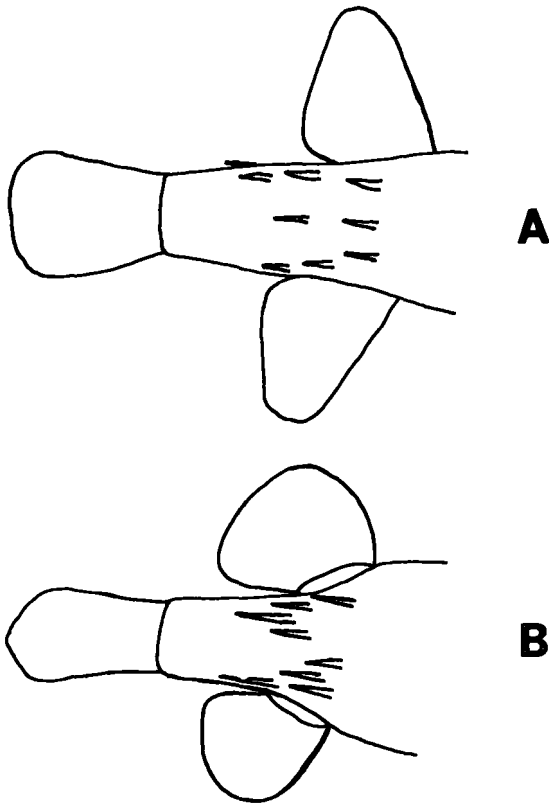


FIGURE 2.—Semidiagrammatic lateral view of the caudal peduncle and posteriormost spines of (A) a slender-bodied, long peduncled species (*Diodon eydouxi*) and (B) a round-bodied, short peduncled species (*D. holocanthus*).

the laboratory under ambient temperature (ca. 25°C) and a variety of conditions. Generally, the eggs were hatched in unaerated 4-l beakers filled with seawater from the collection area. Hatched larvae were transferred to 10-20 l containers and provided with overhead illumination. The containers were wrapped in black plastic. Wild zooplankton (ca. 60-200 μm) from a plankton pump were added on alternate days; this was later supplemented with *Artemia* nauplii. Water was changed twice a week and specimens were removed periodically for preservation. Many rearing attempts were made, but since fewer than 20 eggs usually were available per attempt, few of the attempts were successful.

Some larvae were cleared and stained using the KOH-alizarin red method of Hollister (1934). Measurements and definitions of stages generally follow those of Leis (1977), unless otherwise noted. All drawings of eggs and larvae were made with the aid of a camera lucida.

The institutions housing the examined specimens are as follows: Academy of Natural Sciences of Philadelphia (ANSP); Australian Museum, Sydney (AMS); Bernice P. Bishop Museum, Honolulu (BPBM); British Museum (Natural History) (BMNH); California Academy of Sciences (CAS); Gulf Coast Research Laboratory and Museum (GCRL); George Vanderbilt Foundation (GVF), deposited in CAS; Hawaii Institute of Marine Biology (HIMB); Los Angeles County Museum of Natural History (LACM); Museum National d'Histoire Naturelle, Paris (MNHN); National Marine Fisheries Service, Honolulu, Hawaii (NMFS H), La Jolla, Calif. (NMFS LJ), and Miami, Fla. (NMFS M); Naturhistorisches Museum, Vienna (NMV); J. L. B. Smith Institute of Ichthyology at Rhodes University, South Africa (RUSI); Scripps Institution of Oceanography (SIO); Tulane University (TU); National Museum of Natural History, Smithsonian Institution (USNM); University of Arizona (UA). A catalog number is given when available; many GVF specimens were uncataloged and therefore the register or station number is given.

The synonymies include all known original usage of names. In addition, references of systematic or zoogeographic interest are included. If the identification of a nominal species is questionable, it is preceded by a question mark (?). Pre-Linnaean literature is cited in the text if appropriate, but is omitted from the synonymies.

GENUS *DIODON* LINNAEUS

Diodon Linnaeus 1758:334, after Artedi 1738. Type-species *D. hystrix* Linnaeus by subsequent designation of International Commission on Zoological Nomenclature, opinion 77.

Paradiodon Bleeker 1865:49. Type-species *D. hystrix* Linnaeus by original designation.

Trichodiodon Bleeker 1865:49. Type-species *D. pilosus* Mitchill by original designation.

Trichocyclus Günther 1870:316. Type-species *T. erinaceus* Günther by monotypy.

Diagnosis.—Body rotund, width 0.25-0.54, depth varies greatly depending on degree of inflation. Eyes large, 0.05-0.17. Swim bladder bilobed. Teeth in each jaw fused into a single beaklike unit without a median suture dividing upper or lower jaws into right and left halves. Gill opening a short, vertical slit immediately anterior to the

pectoral fin base. Approximately 20 vertebrae. Dorsal and anal fins usually rounded, set far back on body, with 12-18 rays. Caudal rounded, with 9 rays (there are no secondary rays). Pectoral fin slightly emarginate, with 19-25 rays, the uppermost ray (not counted) greatly reduced in adults. No pelvic fins. Body covered with long spines, all but a few (around the gill opening, dorsal fin base, and caudal peduncle) of which are erectile. Erectile spines consisting of a long pointed shaft, two subdermal lateral bases lying in nearly the same plane as the shaft, and usually a shaft extension which is shorter than the shaft. The shaft extension may be greatly reduced. Nasal organs consisting of a short tentacle with a pair of lateral openings near the tip. In larger individuals of some species the tissue closing the end of the tentacle may be absent, giving rise to a bifid nasal tentacle without nostrils. Both species whose reproductive habits are known (*D. hystrix* and *D. holocanthus*) spawn pelagic spherical eggs of 1.6-2.1 mm in diameter.

Remarks.—Only Bleeker's (1865) proposal of *Paradiodon* for the species here considered to belong in *Diodon* (because of page priority, he believed *Diodon* should apply to those species usually referred to *Chilomycterus*) has disturbed the stability of the usage of the name *Diodon*. *Trichodiodon* and *Trichocyclus* are names applied to juvenile stages of *Diodon*.

Although subgeneric status seems unwarranted, *Diodon* can be broken into two groups on the basis of body width, caudal peduncle length, and squamation. The species of the slender-bodied group, *D. eydouxii* and *D. hystrix*, have a rather narrow body (Figure 3, Table 2), long caudal peduncle (Figure 3, Table 2), and several small spines in the dorsal and dorsolateral surfaces of the peduncle. The species of the round-bodied group, *D. holocanthus*, *D. liturosus*, and *D. nichthemerus*, have a wider body, shorter caudal peduncle (Figure 3), and lack spines on the caudal peduncle (although there are strong spines, projecting over the peduncle, at the base of the dorsal and anal fins). Upon inflation, the dorsal and anal fins are engulfed by the expanding skin. In the round-bodied group, the caudal peduncle and fin are also largely obscured in inflated specimens and the large spines mentioned above provide added protection. In the slender-bodied group, the peduncle remains largely uncovered and is protected only by the relatively small spines on its

upper surfaces. *Diodon nichthemerus*, although clearly a member of the round-bodied group, appears to have undergone a reduction in spine number and base size, and is thus separable from *D. holocanthus* and *D. liturosus*.

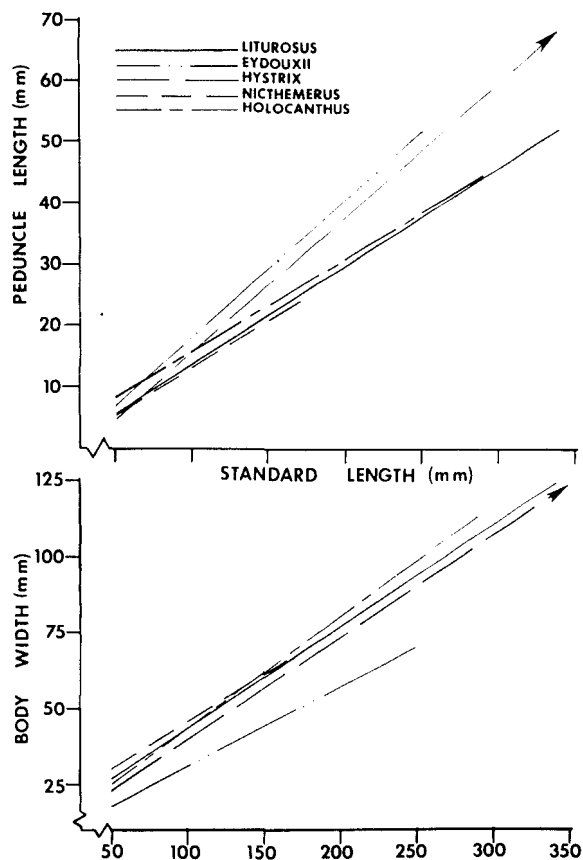


FIGURE 3.—Plotted regression lines of (top) caudal peduncle length vs. standard length and (bottom) body width vs. standard length for the five species of *Diodon*. Lines plotted only over size range of specimens examined. The line with arrow head for *D. hystrix* extends to 571 mm SL. Regression data in Table 2.

TABLE 2.—Regression equations for caudal peduncle length (PL) and body width (BW) vs. standard length (SL) in the five species of *Diodon* (see also Figure 3).

Species	Regression equation	r	t _{slope}	df
<i>D. hystrix</i>	PL = 0.189 SL - 2.79	0.97	21.16	31
<i>D. eydouxii</i>	PL = 0.226 SL - 4.79	0.95	17.44	33
<i>D. liturosus</i>	PL = 0.159 SL - 2.40	0.96	17.88	26
<i>D. nichthemerus</i>	PL = 0.151 SL - 1.38	0.94	7.85	8
<i>D. holocanthus</i>	PL = 0.152 SL + 4.69	0.90	15.86	61
<i>D. hystrix</i>	BW = 0.338 SL + 6.01	0.97	23.41	31
<i>D. eydouxii</i>	BW = 0.262 SL + 5.27	0.88	10.45	33
<i>D. liturosus</i>	BW = 0.333 SL + 10.29	0.90	10.58	26
<i>D. nichthemerus</i>	BW = 0.313 SL + 13.11	0.93	6.44	6
<i>D. holocanthus</i>	BW = 0.368 SL + 6.29	0.96	25.75	62

KEY TO THE SPECIES OF
THE GENUS *DIODON*

- 1a Two or more small spines wholly on the dorsal or dorsolateral surfaces of the caudal peduncle (Figure 2A); color pattern of adults dominated by small (smaller than eye) spots; at least D, P, and C fins of adults with dark spots 2
- 1b No spines wholly on the caudal peduncle (Figure 2B); color pattern of adults dominated by large dorsal and lateral bars or blotches; fins of adults without spots except in some cases at base 3
- 2a P 19-22, both D and A 16-18; D and A of adults falcate; S-A spines ≤ 14 ; head width less than 30% SL *D. eydouxi*
(circumtropical, oceanic)
- 2b P 22-25 (rarely 21), D 14-17, A 14-16; D and A of adults rounded; S-A spines ≥ 14 ; head width greater than 30% SL *D. hystrix*
(circumtropical, shore fish but juveniles pelagic)
- 3a No small, fixed, tribase spine immediately above the gill opening; no small, flat spines on the anterior border of the depression surrounding the gill opening (Figure 4); S-A spines ≤ 11 ; adult color pattern dominated by four large lateral bars, dorsum uniformly dark *D. nichthemerus*
(Australia)

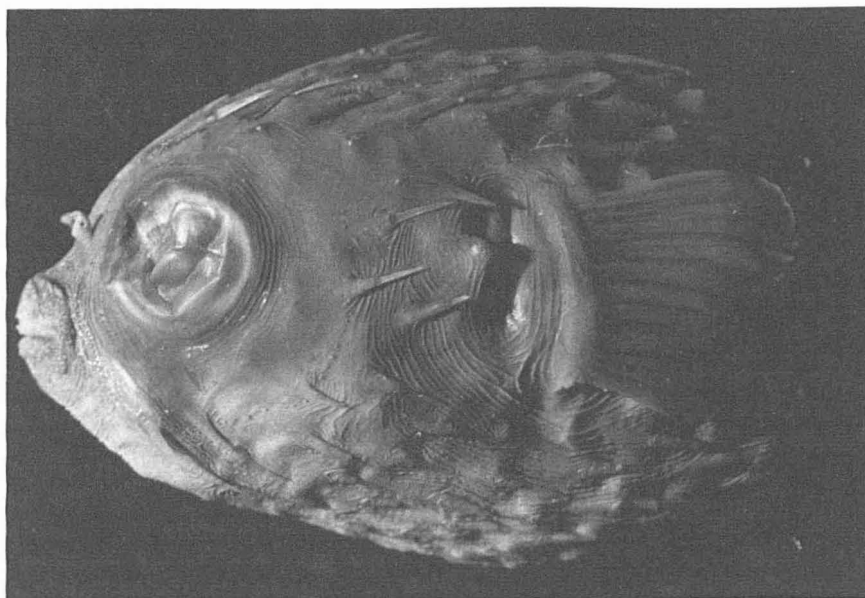


FIGURE 4.—Head of *Diodon nichthemerus* (AMS I.16990-004) showing arrangement of spines in the region of the gill opening. Note that spines anterior to gill opening are not flattened. Also note tubular nostril.

- 3b One or two small, fixed, tribase spines above the gill opening; three or four small, flat spines forming the anterior border of the depression surrounding the gill opening (Figure 5); S-A spines ≥ 12 ; adult color pattern dominated by several dorsal blotches 4

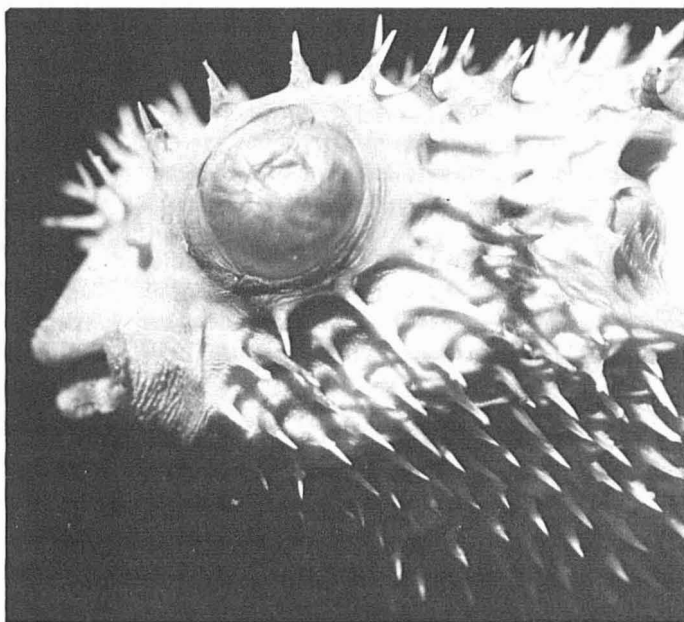


FIGURE 5.—Head of *Diodon liturosus* (CAS 30967) showing arrangement of spines in the region of the gill opening. Note that spines on anterior border of opening are short and flattened. Also note the small downward-pointing spine below the anterior border of the eye.

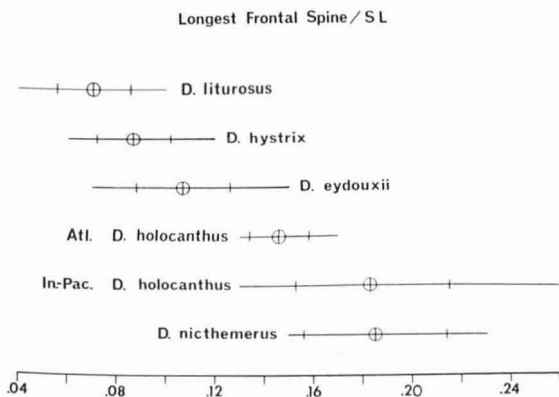


FIGURE 6.—Ratio of frontal spine length to standard length for the five species of *Diodon*. Line indicates range, circle and bar indicate mean, and vertical bars alone denote ± 1 SD. Note difference of spine length between Atlantic and Indo-Pacific specimens of *D. holocanthus*. Number of specimens given in description for each species.

- 4a Frontal spines 0.04-0.10 (Figure 6), much shorter than pectoral axil spines; 17-22 S-A spines; a small downward-pointing spine below the anterior margin of the eye present; dorsal blotches with a distinct light border; a dark gular band from eye to eye under the lower jaw *D. liturosus* (Indo-Pacific)
- 4b Frontal spines 0.13-0.28 (Figure 6), slightly shorter to much longer than pectoral axil spines; 12-15 S-A spines; a small downward-pointing spine below the anterior margin of the eye absent (Indo-Pacific specimens) or present (most Atlantic specimens); dorsal blotches without a distinct light border; no gular band *D. holocanthus* (circumtropical)

DIODON EYDOUXII BRISSOUT DE
BARNEVILLE

Pelagic Porcupinefish (Figure 7)

Diodon eydouxi Brissout de Barneville 1846:142 (eastern Pacific); Troschel 1847:364; Duméril 1855:278.

Diodon melanopsis Kaup 1855:228 (no locality given).

Diodon spinosissimus (not of Cuvier): Günther 1870:307 (Cape of Good Hope, Siam).

Diagnosis.—A slender-bodied *Diodon*, head width 0.25-0.30, peduncle length 0.16-0.22. Caudal peduncle armed dorsally with short spines. Body spines long and slender, moderate in number, S-D spines 13-17, S-A spines 10-14. Pectoral axil spines 0.11-0.16, usually longer than longest frontal spines. A short, fixed tribase spine immediately above gill opening. D 16-18, A 16-18, P 19-22. Nasal tentacle with a pair of lateral openings. No barbels or fleshy tentacles. Dorsal and anal fins falcate (rounded in juveniles). Color pattern dominated by small (ca. = to pupil) dark spots dorsally and laterally. These often associated with the spine axils. A dark gular band starting from below the eyes and continuing under the chin, usually with a branch extending dorsally between eye and gill opening.

Description.—(35 specimens) D 16-18, A 16-18, the first two or three rays unbranched; P 19-22. Head width 0.25-0.30 (\bar{x} = 0.27; SD = 0.01), body width

0.25-0.35 (\bar{x} = 0.30; SD = 0.02), peduncle length 0.16-0.22 (\bar{x} = 0.19; SD = 0.02), eye 0.05-0.10 (\bar{x} = 0.08; SD = 0.01). Dorsal and anal fins falcate, not rounded. Nasal tentacles with a pair of lateral openings.

S-D spines 13-17, S-A spines 10-14, about 12 spine rows over the dorsum between pectoral fin bases, about 21 spine rows over the ventrum between pectoral fin bases. Four or five frontal spines. Longest frontal spine 0.07-0.15 (\bar{x} = 0.11; SD = 0.05), pectoral axil spines 0.11-0.16 (\bar{x} = 0.14; SD = 0.01). Pectoral axil spines usually the longest on the body, 0.61-1.03 (\bar{x} = 0.78; SD = 0.11) in frontal spines. Spines long and slender. Frontal, middorsal, and ventral spines of about the same length. Pectoral axil spines and those dorsolateral spines from over eye to over pectoral fin among the longest on body (ca. 0.8 in frontal spines). Spines on caudal peduncle short (ca. 1.5 in frontal spines) and fixed due to a rather long shaft extension (ca. 2 in shaft). Shaft extension on other spines reduced, never more than 15% of the shaft length. Subdermal bases moderate in extent, and, except for spines around fin bases and caudal peduncle, always shorter than shaft. No spines markedly reduced other than on caudal peduncle; the latter spines generally arranged in one or two bilateral pairs along the dorsolateral edge of the peduncle. Approximately 40% (14 of 36) of the specimens examined also possess a single dorsomedial spine on the caudal peduncle. A short, fixed tribase spine immediately above the gill opening and a second slightly posterior to it above the pectoral base. Three short, flat spines

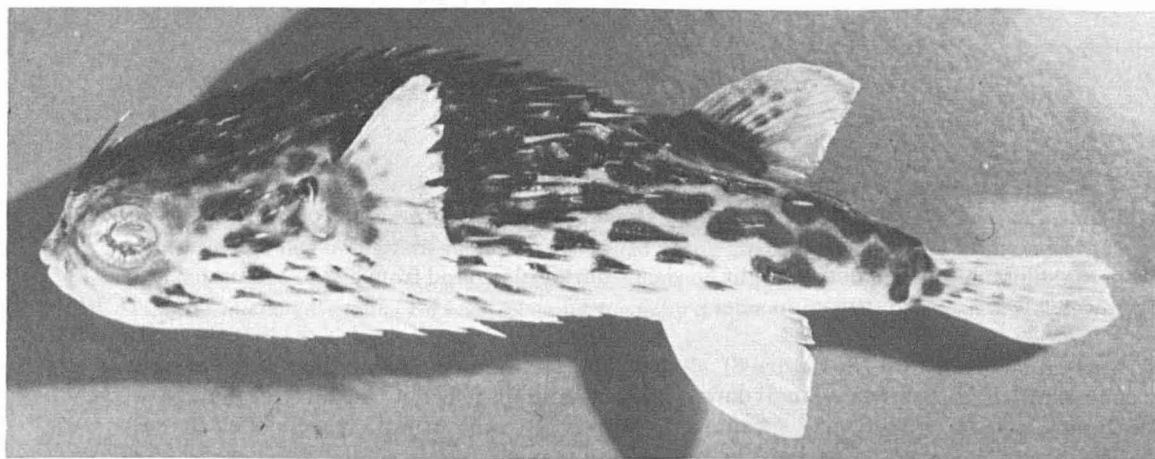


FIGURE 7.—*Diodon eydouxi*, 128 mm SL, central Pacific (NMFS H CHG 55-71).

with broad lateral bases form the anterior border of the gill opening. No spines on the snout.

No barbels or fleshy tentacles.

Dorsally the ground color is light grey to brown grading to white ventrally. Dorsal and lateral surfaces marked with dark ovoid spots (<eye diameter in length) most of which are associated with the spine axils, particularly on the sides posterior to the pectoral fin. Caudal peduncle usually mottled dorsally. Round spots (often diffuse) present on dorsal, pectoral, and caudal fins (caudal spots first seen on 100-mm fish, other fin spots begin to form between 30 and 100 mm). The pectoral spotting is limited to two vertical rows of four to six spots each. The anal fin is often dusky but never spotted. A dark gular band extends from the eye downward and forward, generally paralleling the ventral outline of the head. Usually a branch of this band extends dorsally between the eye and gill opening and is often discontinuous with the gular band. Specimens <100 mm usually have four opposed spots on the iris.

In life the dorsal ground color is medium to dark blue while the dorsal and lateral spots and gular band are dark blue to black. The ventral surfaces are silvery-white and the fins greyish (from a color transparency provided by R. Rosenblatt, SIO).

The largest specimen examined is 252 mm, but the next largest is only 177 mm, apparently a fairly small species. Twelve specimens (125-153 mm) were sexed although none were ripe: 7 males and 5 females.

Eggs, larvae, and pelagic juvenile stages.—No information is available on eggs or larvae. The smallest specimen available is 4.5 mm and is in very poor condition. The fish is almost completely round (inflated?); the spines are short (ca. 0.25 mm) and of uniform length over most of the body. By 13 mm the frontal and pectoral axil spines are ca. 2.5 mm—noticeably longer than the rest of the spines. In the smallest specimen the spines are all erect and the bases resemble small tripods; they may well be fixed at this stage. However, by 8.5 mm the spines are erectile and the fish is definitely capable of inflation. In the 4.5-mm specimen the fin rays are fully formed, as are the nostrils.

The fins remain unpigmented until at least 30 mm except for a small dusky area at the pectoral fin base which forms by 13 mm. In both dorsal and caudal fins, spots gradually spread over the fin from the base. The first row of pectoral fin spots form by 100 mm and the second at about 150 mm.

The smallest fish are uniformly dark to medium brown dorsally with a light area at the base of each spine due to the unpigmented spine sheath. Laterally, distinct black spots (0.25-0.50 mm in diameter) are found. These continue across the white ventral surface. By 8.5 mm the white area at the spine bases has disappeared and spots similar to those on the ventral surface have developed on the dorsal surfaces. The spots are now ca. 1 mm in diameter. The ventral spotting is less conspicuous due to the loss of individual spots by 13 mm, and by 20 mm the belly is white and devoid of spots. The dorsal and lateral spots persist and become associated with the spine bases by 100 mm.

Syntypes.—MNHN 2153, two specimens (101 and 108 mm) taken (apparently speared) in the Pacific between Guayaquil and Hawaii.

Distribution.—*Diodon eydouxi* is a pelagic, oceanic species which is found circumtropically (Figure 8) and seems particularly abundant in the eastern Pacific, but this may be an artifact of collecting effort.

Remarks.—In Brissout de Barneville's (1946:142) description, the total mention of *Diodon eydouxi* is as follows: "Mentionnons encore le *Diodon Eydouxi*, Souleyet (Bibron, Coll. Mus. Paris, et Monographie inedite des Diodoniens) remarquable par ses nageoires dorsale et anale subfal-ciformes." As noted by Brissout de Barneville, Bibron in his unpublished manuscript (MNHN Library MS#867) cited Souleyet as the author of this species. However, Souleyet, insofar as I can determine, never published anything regarding this species. In fact, Bibron's (MS, p. 96) citation refers to the "Voyage de la Bonite. Zool. p. . . .," i.e., he gave no page number, as if in anticipation of publication by Souleyet. There is no mention of *D. eydouxi* in "Voyage de la Bonite" (Eydoux and Souleyet 1841). Because Brissout de Barneville was the first person to use this name in a published work and because he included descriptive information—albeit limited, *Diodon eydouxi* should be attributed to him.

Kaup's (1855) description of *D. melanopsis* is inadequate, but one of his syntypes (BMNH 1852.3.2.7) is extant. Information provided by A. C. Wheeler (pers. commun., BMNH, 29 October 1975) is sufficient to place *D. melanopsis* in the synonymy of *D. eydouxi*. Günther (1870) incorrectly placed *D. melanopsis* in synonymy with *D.*

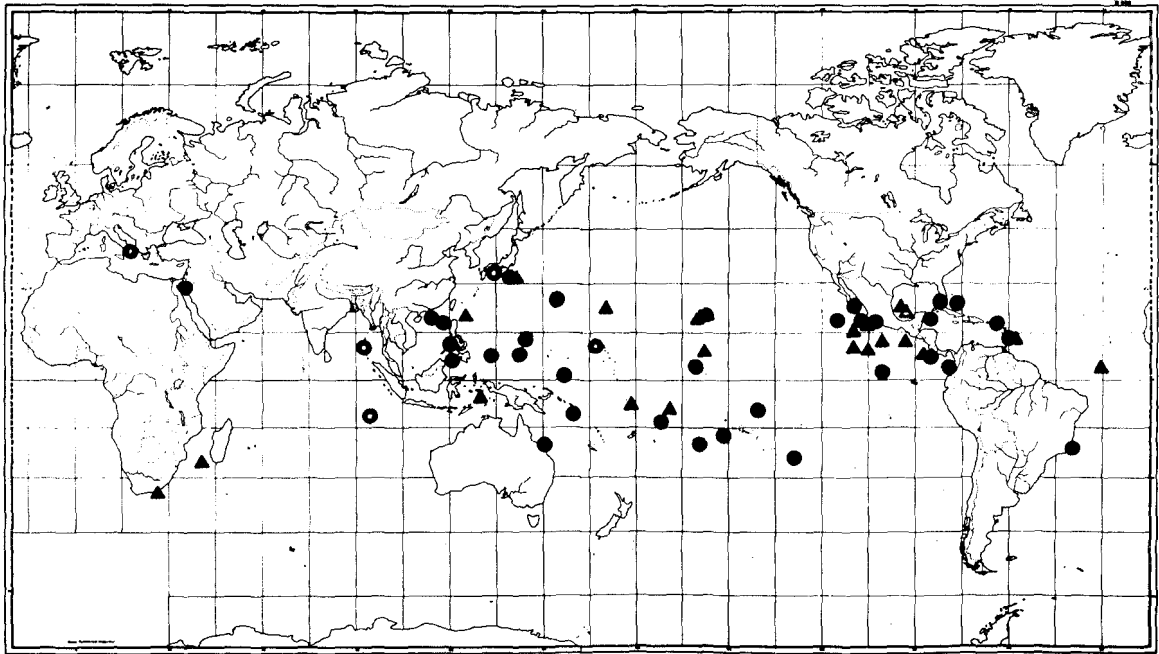


FIGURE 8.—Distribution of *Diodon eydouxi* (triangles) and *Diodon hystrix* (circles). Solid symbols denote specimens examined by me; hollow symbols denote acceptable literature records, photographs, or specimens examined for me by colleagues. Some overlapping records omitted.

spinosissimus Cuvier (see discussion under *D. hystrix*). Le Danois (1959), without comment, incorrectly placed *D. eydouxi* in synonymy with *D. holocanthus*.

The above citations, and those of Troschel (1847) and Duméril (1855) which were essentially reviews of Brissout de Barneville's 1846 paper, constitute the entire literature on *D. eydouxi*.

Diodon eydouxi has undoubtedly been confused in the past with the similar *D. hystrix*. Adaptations to pelagic life by *D. eydouxi* include a lighter, smaller, and more fusiform body compared with *D. hystrix*. The blue color and falcate dorsal and anal fins are also probable adaptations to the pelagic environment. Aside from these characters, *D. eydouxi* differs from *D. hystrix* primarily in its higher dorsal and anal fin ray counts and lower pectoral fin ray counts. *Diodon hystrix* juveniles are pelagic up to a rather large size, and it is tempting to speculate that *D. eydouxi* evolved from this pelagic phase.

All captures of *D. eydouxi* have been at sea (except for one found dead in a South African harbor). Most captures were made under night-lights, and field notes occasionally mention large schools of *Diodon* under the light. Occasional (mostly

small) specimens have been taken in plankton, neuston, or midwater trawl hauls.

As a pelagic member of an otherwise slow-swimming, inshore family apparently specialized to feed on heavy-shelled reef animals (e.g., Randall 1967; Hobson 1974), *D. eydouxi* is unusual. However, a well-developed but relatively unspecialized pelagic stage is present at least in *D. hystrix* and *D. holocanthus*. The tetraodontiform fishes, none of which are noted for a combination of rapid and sustained swimming ability and many of which are specialized for feeding on heavy-shelled benthic invertebrates, have a number of pelagic representatives, e.g., *Lagocephalus lagocephalus* (Tetraodontidae) and *Canthidermis maculatus* (Balistidae). In addition, many other species of Tetraodontiformes have pelagic juvenile stages of moderate to long duration. At least 16 of the 22 tetraodontiform genera known to occur in Hawaii, e.g., have an extended pelagic life history stage (no information is available for the other six genera—pers. observ.). The extremely specialized Molidae, a totally pelagic tetraodontiform family, have retained a beaklike jaw structure similar to that of diodontids and tetraodontids. The utility of such jaws in the pelagic environment where the

external shells and exoskeletons of invertebrates are, in general, greatly reduced is difficult to understand.

The stomach contents of three *D. eydouxi* were examined. The two Pacific specimens (BPBM 10551 and NMFS H CHG55-71) examined had fed on a wide variety of large zooplankton: amphipods, crab zoeae, sergestid shrimps, and fish larvae (*Ranzania laevis*, *Acanthocybium solandri*, and a myctophid were identifiable). The Atlantic specimen (ANSP 138122) had eaten approximately 23 small (25-30 mm) fish of the genus *Polydactylus*; these were in a moderately advanced state of digestion.

Material examined.—52 specimens, 4.5-252 mm.

EASTERN PACIFIC: MNHN 2153 (2:101-108), between Guayaquil and Hawaii; SIO 69-394 (1:13) 15°N, 110°W; SIO 69-483 (1:40) 19°36'N, 105°16'W; SIO 64-176 (1:138) 13°30.9'N, 92°02.2'W; SIO H52-346 (1:121) 13°11'N, 102°07'W; SIO 64-174 (1:151) 10°01'N, 115°55'W; SIO 64-213 (1:132) 08°24'N, 87°37'W; SIO 73-348 (1:148) 10°25'N, 108°50'W; SIO H52-422 (3:118-131) 11°00'N, 105°29'W. CENTRAL PACIFIC: NMFS H CHG55-71(7:125-147) 11°11'S, 179°13'E; SIO 68-480 (5:100-115) 22°02.8'N, 171°34.0'E; BPBM 10551 (1:143) 12°20'S, 169°44'W; NMFS H TC32-32,34,36, & 47 (4:14.5-26.0) 21°59'N, 158°29'W; NMFS H TC32-66,70,71,73 (6:4.5-17.0) 19°31'N, 156°06'W; SIO 60-264 (3:33-165) 7°53'N, 157°29'W; SIO uncat. *Climax II* (4:144-177) between 25°S-30°N along 155°W. WESTERN PACIFIC: AMS I.B. 2746-7 (2:156-168) 5°21'S, 131°17'E; SIO 61-551 (1:153) 20°35.6'N, 126°33.2'E; SIO 73-106 (2:10) 33°17'N, 138°08'E. INDIAN OCEAN: RUSI 3712 (1:252) Pt. Elizabeth, South Africa; LACM 30138-1 (1:145) 27°41'S, 33°22'E. ATLANTIC OCEAN: SIO 63-565 (1:29) 03°21'N, 30°51'W; NMFS M ORI 39-01 (1:ca. 27) 13°00'N, 60°00'W; ANSP 138122 (1:166) 19°28.8'N, 95°27'W; TU 16864

(1:147) 19°35'N, 95°28'W; TU 12766 (1:152) 20°45'N, 93°15'W. NO DATA: SIO uncat. (1:176).

DIODON HYSTRIX LINNAEUS

Porcupinefish (Figure 9)

Diodon hystrix Linnaeus 1758:335 ("Habitat in India") after Artedi 1738; Bloch 1785:68-73, pl. 126 (American seas); Günther 1870:306, 1910:474 (worldwide); Klunzinger 1871:647-648 (Red Sea); Day 1878:708, pl. 179 (Andaman Is.); Herre 1924:504-505 (Philippine Is.); Meek and Hildebrand 1928:827-829 (Panama; largest specimen only); Le Danois 1959:229-230 (worldwide); de Beaufort 1962:412-413 (East Indies).

Diodon atinga (not of Linnaeus): Bloch 1785:67-69, pl. 125 (American seas); Lacepède 1798:1, 3, pl. 25 (no locality given); Kaup 1855:227 (East and West Indies).

?*Diodon plumierii*? Lacepède 1798:10, pl. 30 (tropical eastern America).

Diodon brachiatus Bloch and Schneider 1801:513 (no locality given).

Diodon punctatus Cuvier 1818:132-133 (no locality given).

Diodon spinosissimus Cuvier 1818:134-135 (Brazil).

Paradiodon hystrix Bleeker 1865:56-57, pl. 207 (East Indies).

Diodon hystrix var. *hystrix* Eigenmann 1885:298-306 (American seas).

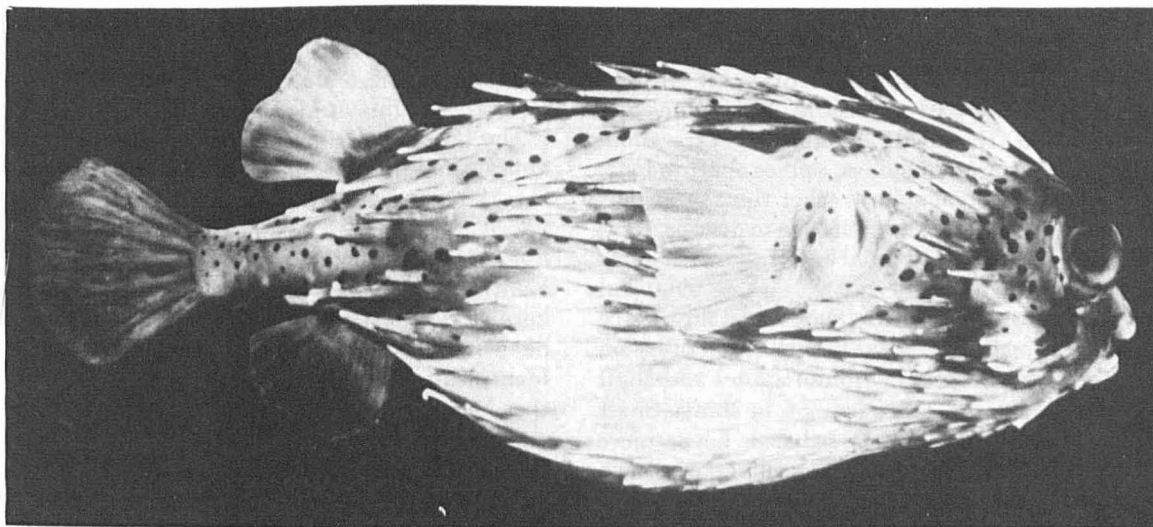


FIGURE 9.—*Diodon hystrix*, 273 mm SL, Oahu, Hawaiian Islands (BPBM 11656). Photo by J. E. Randall.

Diodon nudifrons Jenkins 1904:488-489 (Hawaii).
Diodon armillatus Whitley 1933:107-108, pl. 12,
 15 (Australia).
Diodon totara Curtiss 1938:132-133 (Tahiti).

Diagnosis.—A slender-bodied *Diodon*, head width 0.29-0.42, peduncle length 0.14-0.21. Caudal peduncle armed dorsally with short spines. Body spines short to long, slender, and numerous. S-D spines 15-19, S-A spines 14-19. Pectoral axil spines 0.13-0.19, longest on body. A short, fixed tribase spine immediately above gill opening. D 14-17, A 14-16, P 21-25. Nasal tentacle with a pair of lateral openings. No barbels or fleshy tentacles on body. No short, downward-pointing spine below the anterior border of the eye. Dorsal and anal fins rounded. Color pattern dominated by small (<pupil) dark spots dorsally and laterally, these extend onto all fins in adults. A dark gular band starting below the eyes and continuing under the lower jaw, often with a branch extending dorsally between eye and gill opening.

Description.—(34 specimens) D 14-17, A 14-16, the first two rays in each unbranched; P 21-25. Head width 0.29-0.42 (\bar{x} = 0.33; SD = 0.03), body width 0.30-0.51 (\bar{x} = 0.37; SD = 0.04), peduncle length 0.14-0.21 (\bar{x} = 0.17; SD = 0.02), eye 0.05-0.14 (\bar{x} = 0.08; SD = 0.02). Dorsal and anal fins rounded. Nasal tentacles with a pair of lateral openings.

S-D spines 15-19, S-A spines 14-19, about 15 spine rows over the dorsum between pectoral fin bases, about 25 spine rows over the ventrum between pectoral fin bases. Five frontal spines. Longest frontal spine 0.06-0.12 (\bar{x} = 0.09; SD = 0.02), pectoral axil spines 0.13-0.19 (\bar{x} = 0.15; SD = 0.02). Pectoral axil spines the longest on the body, 0.45-0.78 (\bar{x} = 0.58; SD = 0.09) in frontal spines. Spines short to long, and slender. Dorsal spines, other than those dorsolateral spines from over the eye to over pectoral fin, are approximately equal and of about the same length as the ventral spines. The dorsolateral spines immediately above the pectoral fin may be nearly as long as pectoral axil spines. Spines on peduncle short (ca. 2 in frontal spine) and shaft extension not very large (ca. 2.5 in shaft). Shaft extension on other spines reduced, never more than 16% of shaft length. Subdermal bases moderate to very long. In ventral and lateral spines the bases may be 1.5× or more the length of the shaft. In an ovoid area extending from the interorbital to

the occipit the spines may be greatly reduced or even embedded, particularly in large individuals. Caudal peduncle with one to three dorsolateral pairs of relatively small spines and one or more unpaired spines located either medially or dorsolaterally. Usually one or two ventrolateral spines on peduncle. A short, fixed tribase spine immediately above the gill opening and a second slightly posterior to it (above the pectoral base), both may be embedded. Three short, flat spines with broad lateral bases form the anterior border of the gill opening. No snout spine.

No barbels or fleshy tentacles.

Dorsally in preserved specimens, the ground color is light grey to dark tan grading to white ventrally. Dorsal and lateral surfaces marked with dark brown to black round spots (<pupil). The spots not generally associated with spine axils. Fins unspotted in small specimens (<50 mm), but all fins become covered with spots in adults. The anal fin is not marked except by a dusky area at its base, and in very large individuals by spots.

A dark gular band extends from the eye down and forward generally paralleling the ventral outline of the lower jaw. Often a branch of this band extends dorsally between the eye and gill opening. These bands may be absent in pelagic specimens.

In life the coloration is essentially as described above, but there may be dorsal blotches (similar to those of *D. holocanthus*). These blotches can rapidly appear and disappear. The blotches are particularly evident during feeding but disappear immediately if the fish is disturbed, e.g., by the approach of a diver. I have never seen these blotches retained in a preserved specimen (for examples of these blotches see Clark and Gohar 1953 and Bagnis et al. 1972:225).

The largest specimen examined was 571 mm, but much larger examples have been reported (e.g., 900 mm, de Beaufort 1962).

Eggs, larvae, and pelagic juvenile stages.—The identification of the eggs and larvae described here as *D. hystrix* is tentative because the larvae have not been reared through metamorphosis. Identification is based on the close similarity of these eggs and larvae to those of *D. holocanthus* and the fact that *D. hystrix* and *D. holocanthus* are the only diodontids that commonly occur inshore in Hawaiian waters. *Diodon eydouxi* has not been taken closer than 30 mi from shore around Hawaii, and *Chilomycterus affinis* is very rare

(pers. observ.; J. E. Randall, pers. commun.). The material available for descriptive purposes is limited, 20 eggs (Figure 10) and 7 larvae.

The eggs of *D. hystrix* are similar to those of *D. holocanthus* (see section on the latter species for characters useful in distinguishing the two types of eggs). *Diodon hystrix* eggs are pelagic, spherical, and 1.9-2.1 mm in diameter ($\bar{x} = 2.01$; SD = 0.06; $n = 20$) with 30-50 yellowish oil droplets of 0.03-0.15 mm in diameter. The incubation period is about 5 days at 25°C, but hatching occurs at the end of the late stage (i.e., there is no 'final' stage as defined by Leis 1977; see section on development of *D. holocanthus* for comparison and definition of stages); otherwise, these eggs are similar to *D. holocanthus* eggs.

Development is generally similar to *D. holocanthus* and, aside from hatching at the end of the late stage (i.e., before full eye pigmentation), the only substantive difference is the pigment. Early in the late stage, orange and, to a lesser extent, red chromatophores develop on the dermal sac. The oil droplets tend to be more scattered in *D. hystrix* eggs than they are in *D. holocanthus*. Watson and Leis (1974) illustrated a late stage *D. hystrix* egg (figure A21, p. 115) identified as diodontid II.

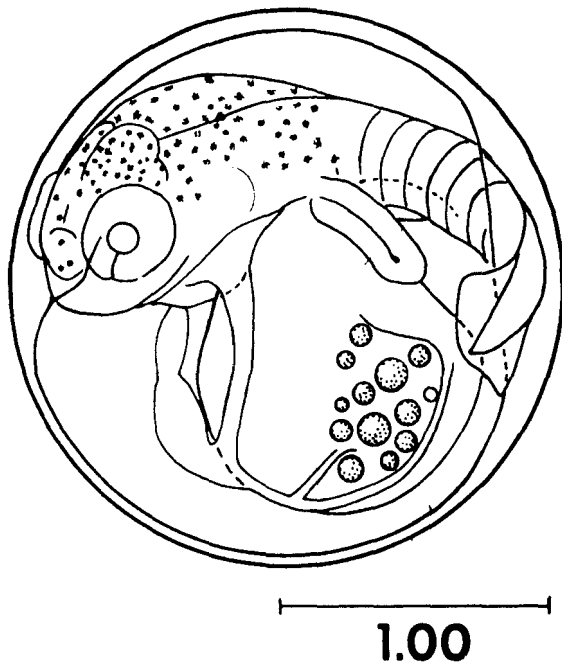


FIGURE 10.—Egg tentatively identified as *Diodon hystrix* just prior to hatching. After Watson and Leis (1974), scale in millimeters.

The newly hatched larvae of *D. hystrix*, ca. 2.6 mm SL (Figure 11), have only slight eye pigment, an open but apparently nonfunctional mouth, and a large amount of yolk. The eyes become fully pigmented by the second day when the mouth apparently becomes functional. The oldest *D. hystrix* larvae available is a 5-day-old individual of 2.60 mm SL. Aside from some shrinkage during the first 2 days after hatching, development is similar to *D. holocanthus*. Table 3 summarizes morphometric data for the larvae.

Melanophores are sparse at hatching, but soon become abundant dorsally and, except for a more caudad extension of melanophores on the caudal peduncle, pigment is essentially the same as that of *D. holocanthus*. The larvae are orange, rather than the yellow background of *D. holocanthus*.

The eggs and larvae described by Sanzo (1930) and tentatively attributed by him to *Crayracion* sp. (Tetraodontidae) closely resemble those here identified as *D. hystrix*. These specimens were clearly not tetraodontids; marine tetraodontids apparently spawn demersal eggs (Breder and Rosen 1966) and their larvae do not resemble those illustrated by Sanzo (pers. observ.). The eggs studied by Sanzo were larger (2.4 mm) and hatched in a shorter period (3 days at 25°C) than *D. hystrix* eggs, but in all other respects they were similar. It is not known how many species of

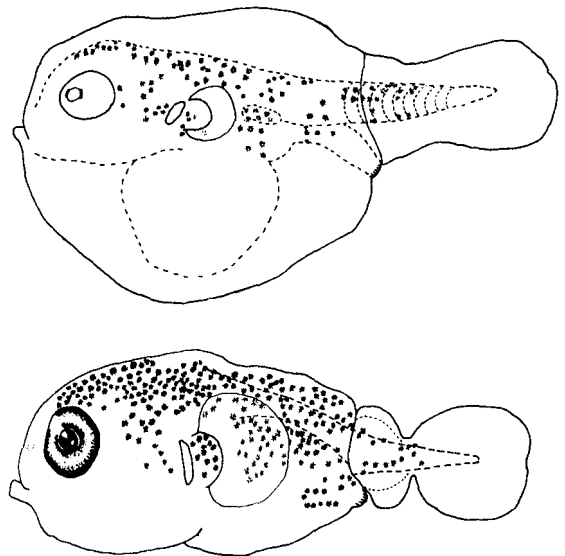


FIGURE 11.—Reared larvae tentatively identified as *Diodon hystrix*: (top) newly hatched larva, 2.57 mm SL, and (bottom) 5-day-old larva, 2.60 mm SL. Hawaiian material.

TABLE 3.—Morphometric and meristic data for larval and juvenile *Diodon hystrix* (measurements in mm). ? indicates individuals of unknown age caught in plankton samples; × indicates damaged.

Age (days) of reared fish	Notochord or standard length	Snout to anus length	Width of eye	Head length	Head width	Mouth width	Fin ray counts		
							D	A	P
Larvae:									
1	2.6	2.0	0.3	0.9	1.0	0.4	0	0	0
3	2.1	1.7	0.3	0.8	1.1	0.7	0	0	0
?	2.4	1.7	0.4	0.9	1.4	0.5	0	0	0
?	2.4	1.9	0.4	1.0	1.5	0.7	0	0	0
?	2.4	1.8	0.3	0.8	1.3	0.5	0	0	0
?	2.4	1.8	0.4	0.8	1.4	0.7	0	0	0
5	2.6	1.8	0.4	0.9	1.2	0.7	0	0	0
Juveniles:									
?	5.1	4.5	1.0	1.6	3.2	1.1	×	×	23
?	11.1	9.0	2.1	5.1	7.0	2.5	15	15	22

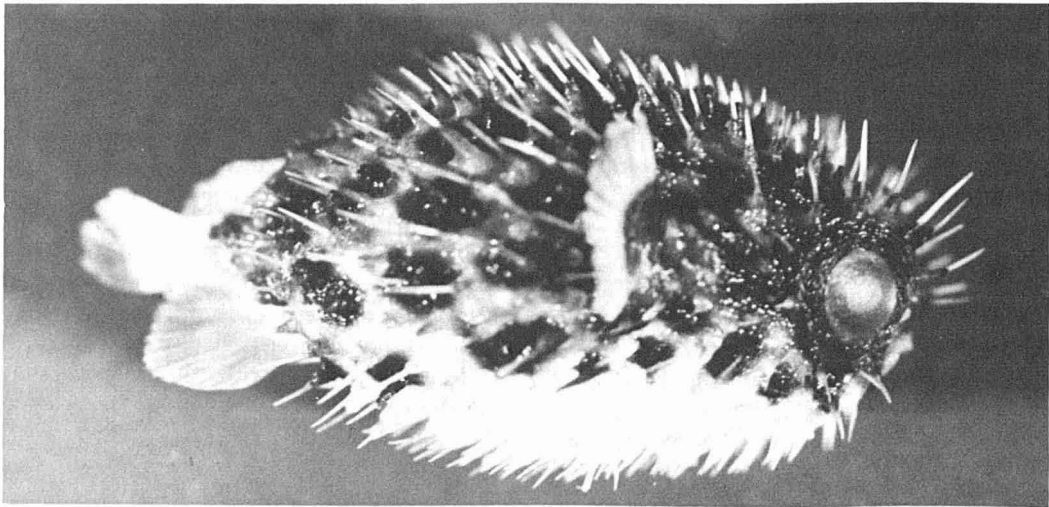


FIGURE 12.—Pelagic juvenile of *Diodon hystrix*, 26 mm SL, western Atlantic (NMFS M Oregon II 72-39-36).

Diodon occur in the Red Sea where Sanzo obtained his specimens; only *D. hystrix* is reported to occur there (e.g., Clark and Gohar 1953).

Metamorphosis to the spiny juvenile stage occurs before 5 mm SL. Juveniles of *D. hystrix* are similar in shape, development, and pigmentation to *D. holocanthus* except that the spines of the former are shorter and its snout is more heavily pigmented (Figure 12). *Diodon hystrix* juveniles remain pelagic for an unknown time, but the largest pelagic individual seen was 180 mm while the smallest individual taken inshore was 191 mm.

Holotype.—No holotype or type-series is known to exist. Linnaeus based his description on that of Artedi (1738).

Distribution.—*Diodon hystrix* is found circumtropically (Figure 8) and often in temperate areas, especially in the western boundary currents. This species apparently is the only member of the genus in the Mediterranean (Torchio 1963).

Remarks.—Linnaeus provided very little diagnostic data in his brief description, the useful information consisting of a mention of long spines, chiefly on the sides. This could apply to *D. hystrix*, as described above, *D. liturosus*, or *D. eydouxi*. Bloch (1785) was the first to use recognizably the name *hystrix*. His illustration of "*D. hystrix*" is clearly of the species here considered as *D. hystrix*.

Several authors have incorrectly applied the name *Diodon atinga* Linnaeus to this species (see synonymy), but it is clear from the original de-

scription that *D. atinga* is a *Chilomycterus* (sensu lato).

Diodon plumierii Lacepède is included in the synonymy of *D. hystrix* with some doubt. The description is not very helpful, but the illustration by Plumier (Lacepède 1790, plate 30), while not immediately recognizable as *D. hystrix*, is probably of that species. The relatively elongate body, short spines, and the three spines on the dorsal surface of the peduncle all indicate *D. hystrix*. The description stated that the fish was blue with white spots; this coloration is not found in any known species of *Diodon*. Lacepède's description was based solely on Plumier's illustration.

Diodonbrachiatus Bloch and Schneider is based at least in part on the "Erizo" of Parra (1787) whose illustration is clearly of *D. hystrix*.

Cuvier's *D. punctatus* is attributable to *D. hystrix* on the basis of his description, and examination of the syntypes (MNHN A.8369, A.8373, and A.8367) by M.L. Bauchot (pers. commun. MNHN, 20 May 1975).

Diodon spinosissimus Cuvier has been a source of confusion. This stems at least in part from the presence of two species in Cuvier's syntypic series (M. L. Bauchot, pers. commun., MNHN, 20 May 1975). The larger specimen (MNHN B.1294) is a *D. hystrix* from Brazil, while the smaller syntype (MNHN B.1294) is a *D. liturosus* from Vanikoro, Santa Cruz Islands, in the western Pacific. Le Danois (1961) referred to the above specimen of *D. hystrix* as the holotype, while there is no evidence that Cuvier recognized it as such, I follow Le Danois' lead and designate MNHN B.1294 as the lectotype of *D. spinosissimus*.

Since the publication of Günther (1870), relative unanimity has prevailed, with most authors applying only the name *D. hystrix* to this species. The three exceptions, barring misidentification of *D. holocanthus*, are *D. nudifrons* Jenkins, *D. armillatus* Whitley, and *D. totara* Curtiss. These are easily referred to *D. hystrix* solely on the basis of the published descriptions (S. Karnella, pers. commun., USNM, 28 January 1976, reports that Jenkins' holotype cannot be located at USNM even though it was cataloged as USNM 50854).

The apparent long pelagic stage of *D. hystrix* has undoubtedly contributed to its wide distribution and to the relative uniformity among populations (Table 1).

Little is known of the ecology of *D. hystrix*. Randall (1967) and Hobson (1974) gave information on

feeding and diel activity patterns. *Diodon hystrix* is a nocturnal predator on hard-shelled invertebrates such as gastropods, hermit crabs, and sea urchins. Eger (1963) reported toxic dermal secretions in *D. hystrix*. This species is eaten by people in Hawaii (pers. observ.) and Tahiti (Curtiss 1938; Bagnis et al. 1972) without apparent ill effect, although it is frequently classified as poisonous (e.g., Halstead 1967).

Material examined.—43 specimens, 5.5-571 mm.

EASTERN PACIFIC: SIO 64-214 (1:128) 7°47'N, 85°45'W; SIO H52-415 (1:180) 2°50.5'N, 101°28'W; UA 73-83-21 (1:236) Cabo San Lucas, Baja California Sur, Mexico; UA 68-59-11 (1:199) Punta Mal Paso, Manta, Ecuador; CAS 1244 (1:209) Clarion I., Revillagigedos; CAS H46-241 (2:191-202) Acapulco, Guerrero, Mexico; CAS uncat. (1:215) La Paz, Baja California Sur, Mexico; NMFS LJ N-49, 67-2 (1:5.5) 18°N, 107°W. CENTRAL and WESTERN PACIFIC: HAWAIIAN IS.—HIMB (1:311) Kaneohe Bay, Oahu; NMFS H-243 (1:135) off Kailua, Hawaii; NMFS H-241 (1:142) 10 mi. W. Keahole Pt., Hawaii; BPBM 11656 (1:272.5) Moku Mana, Oahu. LINE IS.—BPBM 9798 (1:338) Washington I. MARQUESAS IS.—BPBM 12139 (1:290) Nuku Hiva. PITCAIRN I.—BPBM 16821 (1:278), 16717 (1:282). SOCIETY IS.—GVF stn 22 (1:211) Maiao I. COOK IS.—GVF M-37 (1:327) Mangaia I. MARCUS I.—BPBM 8403 (1:403). MARIANA IS.—BPBM 5122 (1:200) Guam. SOLOMON IS.—CAS 6003 (1:107) Bellona I. CAROLINE IS.—GVF stn 29 (1:258) Ifaluk Atoll; GVF stn 12 (1:220) Palau Is.; GVF 176 (1:571) Kapingamarangi Atoll. PHILIPPINE IS.: CAS 26419 (1:199) Jolo I.; CAS 26418 (1:286) Culiion I. SOUTH CHINA SEA: SIO 70-342 (1:49.5) 18°14.4'N, 119°45.2'E; GVF 1748 (1:196) 20°46'N, 116°53'W. JAPANESE WATERS: SIO 73-106 (1:ca. 10) 33°17'N, 138°08'E. AUSTRALIA: AMS IA.6105 (1:263) Hayman I., Queensland. INDIAN OCEAN: RED SEA—CAS HV-1661 (1:235) Eylath, Gulf of Aqaba. WESTERN ATLANTIC: CAS BMN-7526 (1:465) Vitória, Brazil; CAS 23805 (1:307) Harbour I., Bahamas; GCRL V66:1703 (1:328) St. Thomas, Virgin Is.; CAS 19210 (1:335) Key West, Fla., USA; NMFS M *Bowers* 1-10 (1:29.2) 26°00'N, 70°30'W; NMFS M *Oregon II* 72-39-58 (1:30.0) 21°01'N, 80°14'W; NMFS M *Oregon II* 72-43-146 (2:16.0-18.9) Caribbean; NMFS M *Oregon II* 72-39-36 (1:26.2) 17°08'N, 69°58'W; NMFS M *Oregon II* 72-39-136 (1:25.0) 23°45'N, 84°20'W; NMFS M *Oregon II* 76-66-19791 (1:40.0) 17°50'N, 74°47'W.

In addition, a number of specimens (CAS, NMFS M, material) were identified, but not examined in detail. These fish form the basis for some of the points plotted in Figure 8.

DIODON NICTHEMERUS CUVIER

Globefish (Figures 4, 13)

Diodon nictemerus Cuvier 1818:135 pl. 2 (Australia).

Diodon nictemerus: Kaup 1855:228 (no locality given).

Diodon nictemerus: Duméril 1855:278 (no locality given).

Atopomychtherus nychthemerus: Günther 1870:315 (South Australia, Tasmania).

Diodon spinosissimus (not of Cuvier): Castelnau 1872:290 (Australia).

?*Diodon blochii*? Castelnau 1872:210 (Australia).

Atopomychtherus nichthemerus: Waite 1923:229 (South Australia, Tasmania).

Dicotylichthys nychthemerus: Fraser-Brunner 1943:17 (Australia).

Atopomychtherus nichthemerus: Scott 1957:154 (Tasmania).

Diodon nychthemerus: Le Danois 1959:227 (Australia).

Atopomychtherus nichthemerus: Scott 1962:299 (West Australia, South Australia, Tasmania).

Diagnosis.—Round-bodied *Diodon*, head width 0.34-0.43, peduncle length 0.12-0.16. Caudal peduncle without spines. Body spines long and narrow, but relatively few in number, S-D spines 9-12, S-A spines 10-11. Pectoral axil spines shorter than longest frontal spines. No short, fixed tribase spine immediately above gill opening. Fin ray counts low, D 12-13, A 12-14, P 19-21. Nasal tentacle with a pair of lateral openings which are separated by a thin membrane; this is often absent (more often in larger individuals) resulting in the nostrils appearing "confluent, each nasal organ appearing as a bifid tentacle" (Fraser-Brunner

1943:16). Fins without dark spots. Individuals 100 mm and greater with four dark bars on the sides and lacking dark spots on the body.

Description.—(10 specimens) D 12-13, the first unsegmented; A 12-14, the first unsegmented; P 19-21; vertebrae 9 + 12 = 21 (Günther 1870). Head width 0.34-0.43 (\bar{x} = 0.39; SD = 0.03), body width 0.39 - 0.52 (\bar{x} = 0.45; SD = 0.05), peduncle length 0.12-0.16 (\bar{x} = 0.14; SD = 0.01), eye 0.09-0.17 (\bar{x} = 0.12; SD = 0.02) greatest in smaller specimens. Dorsal, anal, and caudal fins all rounded, middle rays longest. Nasal tentacles with a pair of lateral openings which are separated by a thin membrane which is often broken or resorbed, especially in larger individuals, resulting in the nasal organ appearing as a bifid tentacle.

S-D spines 9-12, S-A spines 10-11, about 9 spine rows over dorsum between pectoral fin bases, about 15 spine rows over ventrum between pectoral fin bases. Five frontal spines. Longest frontal spines 0.15-0.23 (\bar{x} = 0.19; SD = 0.03), greatest in smaller specimens, pectoral axil spines 0.11-0.20 (\bar{x} = 0.15; SD = 0.03). Frontal spines longest on body; 1.12-1.35 (\bar{x} = 1.25; SD = 0.08) times pectoral axil spines, although many dorsal spines nearly as long. Ventral spines shorter than dorsal spines (ca. 1.4 in dorsal spines). Lateral spines

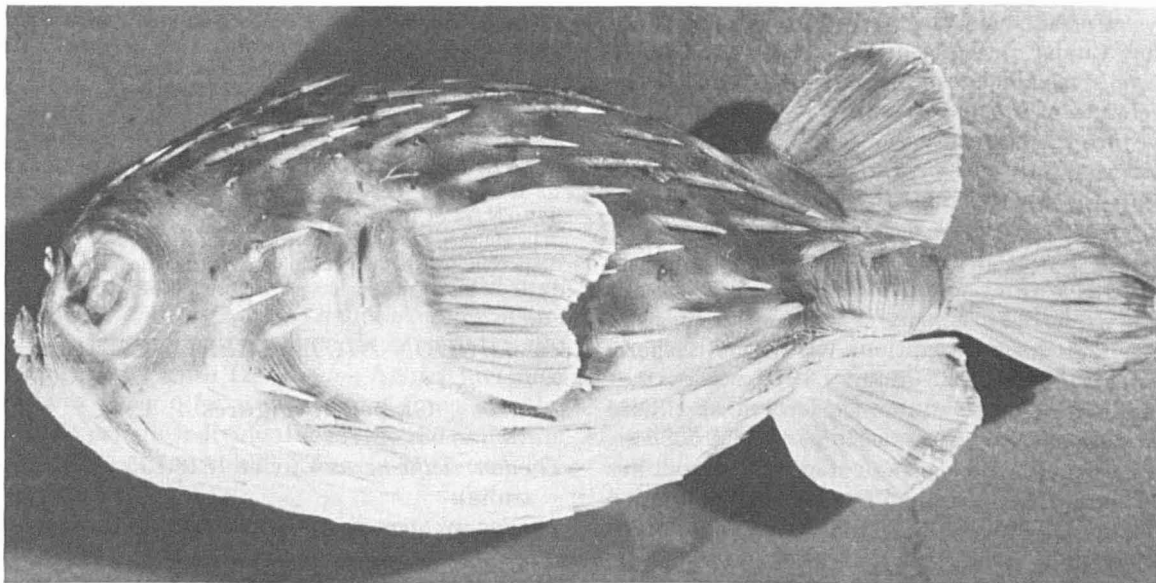


FIGURE 13.—*Diodon nichthemerus*, 110 mm SL, Victoria, Australia (AMS I.16990-004).

nearly as long as dorsal spines (ca. 1.2 in dorsal spines). Spines long and narrow. Subdermal lateral bases short (1.5-5 in shaft length) and the shaft extension reduced or lacking. No spines on caudal peduncle, but along base of both dorsal and anal fins there is a spine whose shaft extends onto the peduncle. No short fixed spine with three subdermal bases immediately above the gill opening. One or two spines originating between eye and gill opening which extend over the depression surrounding the gill opening. No spines on the snout, but a broad spineless area around the eye. Aside from nasal organs, no barbels or tentacles.

Upper parts in preserved specimens uniformly dark brown to grey with four dark bands descending onto the sides: the first below the eye, the second between the eye and gill opening, the third behind pectoral fin, and the fourth below dorsal fin. The first two bars are swept back and the third swept forward. The second and third bars sometimes meet below the pectoral fin to form a ring about its base and the gill opening. White to light grey below a level even with the mouth (except the bars) with no ventral spotting. Fins somewhat dusky but unspotted. In specimens of about 100 mm the uniformly dark dorsum is broken up into

large blotches which appear as continuations of the lateral bars. In smaller fish the dorsal blotches are broken up into small diffuse dark spots (ca. one-half of eye diameter): some of the spots in association with spine bases. Belly is unspotted at all sizes. Le Danois (1959) stated that the bars become lighter in color in large specimens.

Scott (1962:299) gave the following information on live coloration: greenish indigo above, white to silvery below, four dark bars on the sides with several large yellowish spots incorporated in the bars, fins plain yellowish-green and the spines lemon-yellow. An excellent color photograph was provided by Coleman (1974:99).

The largest specimen examined was 158 mm SL. However, both Le Danois (1959) and Scott (1962) reported specimens of 280 mm. A 111-mm specimen was sexable as a male, but may not have been mature.

Eggs, larvae, and pelagic stages.—No information.

Syntypes.—MNHN B.1313 (75 mm) and MNHN 51 (100 mm) taken by Peron and Lesueur in Australia. M.L. Bauchot examined these specimens and provided notes and photographs. Le Danois

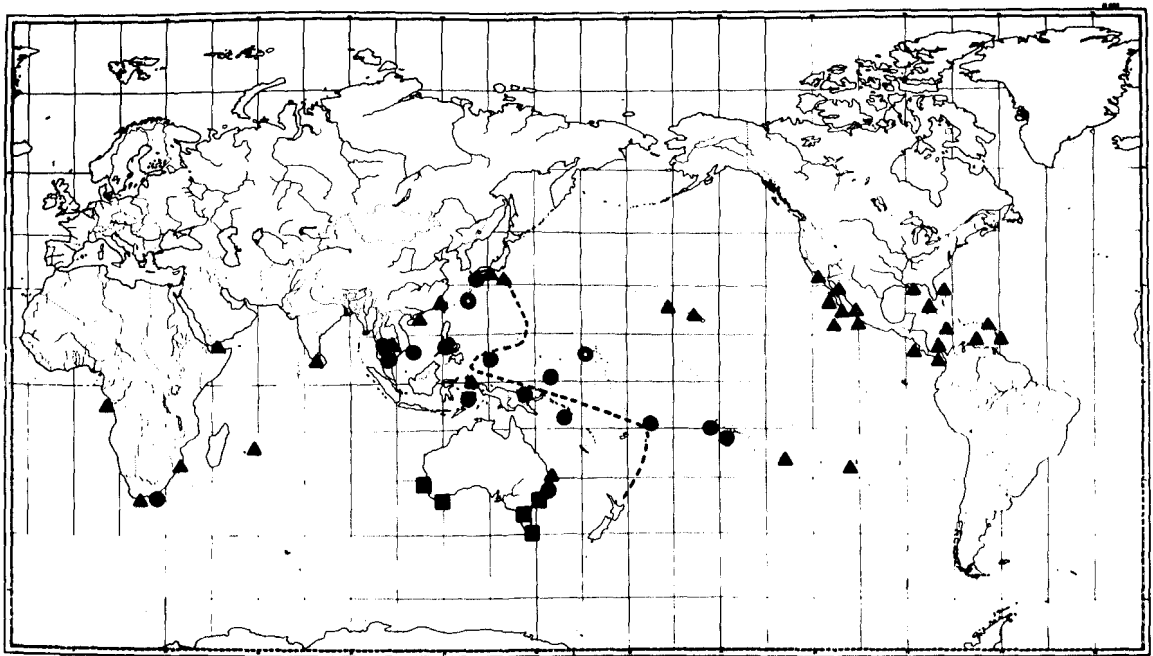


FIGURE 14.—Distribution of *Diodon nictemerus* (squares), *D. lituosus* (circles), and *D. holocanthus* (triangles). Solid and hollow symbols as in Figure 8. Dashed line indicates position of the Andesite line.

(1961) referred to MNHN B.1313 as the holotype of *D. nichthemerus*. There is no evidence that Cuvier regarded it as such, and I prefer not to regard Le Danois' statement as constituting a lectotype designation.

Distribution.—Apparently confined to the southern half of Australia and Tasmania (Figure 14).

Remarks.—Günther (1870) was the first to place this species in *Atopomycterus*, apparently on the basis of Bleeker's (1865) diagnosis of *A. diversispinus*, the type of the genus, as possessing a bifid nasal tentacle and slender spines with long double roots. However, as indicated above, the double spine roots of *D. nichthemerus* are relatively short and the bifid nasal tentacle is not a consistent character. Bleeker (1865) in the first published usage of the name *Atopomycterus diversispinus*, based his brief description on an unpublished description of a specimen (NMHN 2159) by Verreaux. M. L. Bauchot (pers. commun., MNHN, 23 June 1975) reports that Le Danois (1959) was correct in stating that only the ventral and prepectoral dorsal spines have two bases. The postpectoral dorsal spines are tribased and fixed.

Fraser-Brunner (1943) followed Günther (1870) in placing *D. nichthemerus* in *Atopomycterus* (as a subgenus of *Dictylichthys*), apparently solely on the basis of the bifid nasal tentacle. Fraser-Brunner and Günther regarded the condition of the nasal tentacle to be of more importance than the character of the spines, but this does not seem tenable to me. Of the 11 specimens of *D. nichthemerus* for which I have data, 6 (41-111 mm) had tubular nostrils on both nasal tentacles, 1 (84 mm) had one tubular and one bifid tentacle, and 4 (100-158 mm) had a pair of bifid nasal tentacles. This indicates that the bifid nasal tentacle is an ontogenetic character that cannot be used in generic classification. The spines of *D. nichthemerus*, aside from their reduced lateral roots and anterior shaft extension, are no different from those of the other species of *Diodon*.

Diodon blochii Castelnau is placed in synonymy with *D. nichthemerus* with some doubt. The type cannot be found in MNHN, AMS or in the National Museum of Victoria, Australia. The description is incomplete and does not fit exactly any of the five species considered here, but of those, it matches *D. nichthemerus* most closely, particularly in meristic characters.

The distribution of *D. nichthemerus* is unusual for a *Diodon* in both its limited range and its location in a temperate rather than tropical area. This limited range might indicate a pelagic stage that is less well developed than that of other members of the genus, but if this species requires a temperate environment it may have colonized all the available habitat within a reasonable dispersal range (although in a personal communication of 4 February 1976, J. Moreland reports that there were no specimens of any *Diodon* sp. in the collections of the National Museum of New Zealand).

Coleman (1974) reported that *D. nichthemerus* inhabits areas of sand or mud bottom and feeds on molluscs, crustaceans, and echinoderms.

Material examined.—Nine specimens, 41-158 mm.

All specimens from the Australian Museum: I.13619 (41 mm) Swan R., West Australia; I.12840 (67) Fremantle, West Australia; I.A.629 (78.5) King George's Sound, West Australia; I.16899-003 (84.5) Jervis Bay; I.A.5829 (104) Port Franklin, Victoria; I.16990-004 (110) Port Phillip Bay, Victoria; I.16894-001 (111) Jervis Bay; I.6240 (111) Tamar R., Tasmania; I.17564-001 (158) Snug Beach, Tasmania.

DIODON LITUROSUS SHAW

Short-spine Balloonfish (Figures 5, 15, 16)

Le Diodon Tacheté Lacepède 1798:13-15 ("New Cythere").

Diodon liturosus Shaw 1804:436 (Indian Seas); Masuda et al. 1975:140, 335 (southern Japan).

Diodon maculatus Duméril 1855:278 (Latinization of Le Diodon Tacheté Lacepède) after Bibron MS.

Paradiodon novemmaculatus (not of Cuvier): Bleeker 1865:57-58, pl. 206 (East Indies).

Diodon maculatus var. B: Günther 1870:308 (East Indies).

Diodon bleekeri Günther 1910:475-476, pl. 179 (Society Is.); Herre 1924:506-507 (Philippine Is.); Orsi 1974:176 (Vietnam).

Diodon holacanthus (not of Linnaeus): de Beaufort 1962:410-412 (Indo-Australian archipelago); Bagnis et al. 1972:227 (French Polynesia).

Dictylichthys punctulatus (not of Kaup): Grant 1972:472 (Australia).

Diagnosis.—Round-bodied *Diodon*, head width 0.33-0.42, peduncle length 0.12-0.18. Caudal peduncle without spines. Body spines short and

numerous. S-D spines 16-21, S-A spines 17-22. Frontal spines 0.04-0.10, much shorter than pectoral axil spines. A short, fixed tribase spine immediately above gill opening. A short, downward-pointing spine below the front border of eye. Five frontal spines. D 14-16, A 14-16, P 21-25. Nasal tentacle normally with a pair of lateral openings. Usually two small barbels on the chin. A fleshy tentacle may be present over each eye. Color pattern dominated by large, light-edged dorsal, and dorsolateral blotches. The lateral postpectoral surfaces with small spots associated with the spine axils. A dark gular band starting from below the eye and continuing under the chin. Fins without spots except at bases.

Description.—(27 specimens) D 14-16, A 14-16, the first two rays undivided; P 21-25. Head width 0.33-0.42 (\bar{x} = 0.36; SD = 0.03), body width 0.35-0.51 (\bar{x} = 0.41; SD = 0.04); peduncle length 0.12-0.18 (\bar{x} = 0.15; SD = 0.01), eye 0.08-0.15 (\bar{x} = 0.10; SD = 0.02). Dorsal, anal, and caudal fins rounded, middle rays longest. Nasal tentacles normally with a pair of lateral openings; occasionally, the end of the tentacle is split, giving rise to a bifid nasal tentacle without nostrils. When split, the bifid arms tend to become thickened and papillose.

S-D spines 16-21, S-A spines 17-22, about 14 spine rows over the dorsum between pectoral fin bases, about 26 spine rows over the ventrum between pectoral fin bases. Five frontal spines. Longest frontal spine 0.04-0.10 (\bar{x} = 0.07; SD = 0.02), pectoral axil spines 0.10-0.15 (\bar{x} = 0.12;

SD = 0.01). Pectoral axil spines longest on body, 0.40-0.78 (\bar{x} = 0.61; SD = 0.09) in frontal spines. Spines generally short. The only markedly elongate dorsal spines are those above the pectoral fin (ca. 0.60 in frontal spines). Frontal, middorsal, and lateral (excluding pectoral axil spines) spines all of about the same length. Ventral spines somewhat shorter (ca. 1.3 in frontal spines). The spines of the interorbital region and nape often reduced or buried, especially in individuals larger than 150 mm, but, in any case, shorter than frontal spines. The shaft extension is variably developed, its size positively correlated with the size of the lateral bases. No spines on caudal peduncle, but along the base of both dorsal and anal fins there is a spine whose shaft extends onto the peduncle. In two of the specimens examined these spines were on the peduncle, but they were still clearly associated with the fin bases. A short, fixed tribase spine immediately above the pectoral base. Three short, flat spines with broad lateral bases form the anterior border of the gill opening. A short, downward-pointing spine below the anterior border of the eye.

Two small barbels on the chin. A fleshy tentacle above each eye present in about one-third of the specimens. Rarely, a more extensive set of tentacles along the ventrolateral edge of the body similar to that described for *D. holocanthus*.

Background color in preserved specimens varies from dark brown to light buff. The color pattern is dominated by several large dark brown to black blotches on dorsal and lateral surfaces. These blotches edged in a color lighter than background

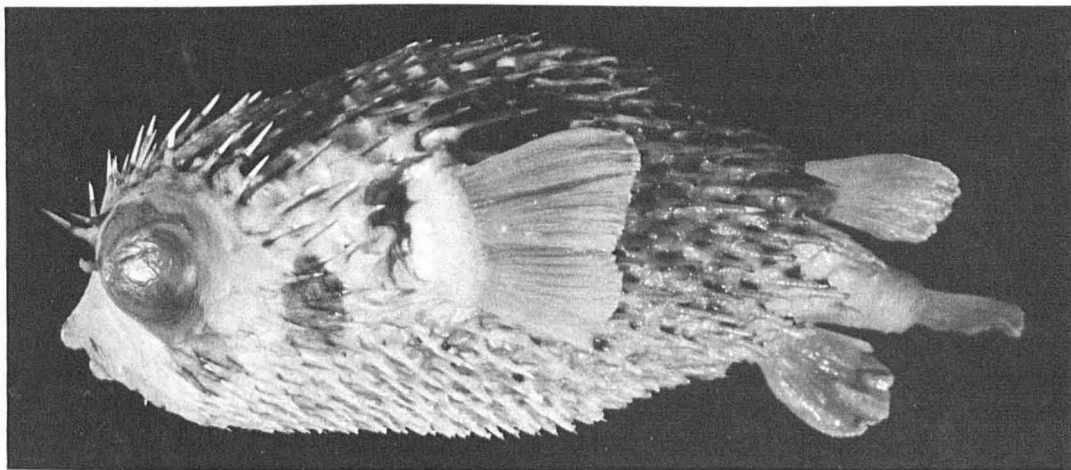


FIGURE 15.—*Diodon liturosus*, 142 mm SL, Ko Samet, Thailand (CAS 30967).

color (usually white). The blotches are located as follows: (Figure 16): 1) one round blotch around the base of the dorsal fin; 2) one round blotch middorsally about midway between the dorsal fin and pectoral base; 3) one round blotch above each pectoral fin along the dorsolateral surface just posterior to the fin base; 4) a broad transverse bar across the occipital region; 5) an irregularly shaped blotch immediately below the occipital blotch, between the eye and pectoral fin; and 6) a bar which crosses each eye downward and usually connects with a broad gular band across the ventral surface just behind the mouth (the bar which crosses the eye does not extend across the interorbital). The chin barbels are located within the gular band, but are light in color. Postpectorally the lateral surfaces are marked with small (<pupil diameter) spots associated with the spine axils. No spots dorsally or ventrally (except in specimens <50 mm). Specimens of 100 mm may be mottled on the caudal peduncle and often have four spots on the iris. Ventrums white and fins unmarked except at bases. A 24.5-mm specimen is light brown dorsally and covered everywhere (except fins) with small (ca. = pupil) dark spots. The spots are less dense on the belly and are not associated with the spine bases. Color in life essentially the same as above but fins yellow.

The largest specimen examined was 349 mm. However, de Beaufort (1962) reported specimens of 500 mm, and Masuda et al. (1975) reported a specimen of 600 mm total length.

Eggs, larvae, and pelagic stages.—No information. However, the 24.5-mm specimen mentioned above

which has "pelagic spotting" may be a pelagic juvenile (the collection data are incomplete). The smallest specimen definitely found inshore was 94 mm.

Holotype.—Shaw (1804) based his description on that of Lacepède (1798), who in turn had based his on a manuscript description by Commerson. The fish illustrated by Commerson is apparently lost.

Distribution.—*Diodon liturosus* ranges throughout the Indo-West Pacific (Figure 14) from South Africa to Japan and the Society Islands, but is absent from Hawaii. Areas of overlap with the closely related *D. holocanthus* are along the edges of the Pacific and Indian Oceans.

Remarks.—*Diodon liturosus* usually has been considered a junior synonym of *D. holocanthus* (e.g., Le Danois 1959) but if recognized as a distinct species has generally been called *D. bleekeri*. Shaw's (1804) description is short and based almost totally on color. However, several details clearly indicate which species is involved. The distribution and number of spots, particularly the "two transverse ones, the first situated beneath the eye and the second between the eye and pectoral fin" (Shaw 1804:436, emphasis mine), and the "dusky cloud" marking the throat clearly eliminate *D. holocanthus*, and apply only to *D. liturosus* as described above. In addition, Lacepède (1798) gave a pectoral fin ray count of 24 which is rare for *D. holocanthus* (Lacepède did not provide a Latin binomial in his description of Le Diodon Tacheté).

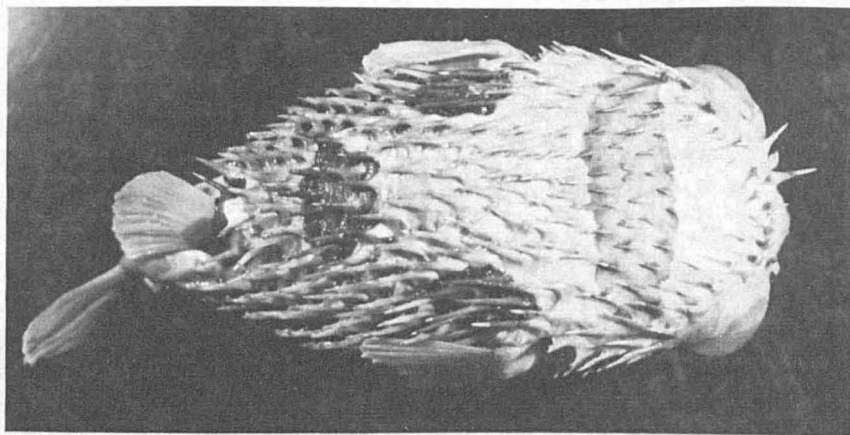


FIGURE 16.—Dorsal view of *Diodon liturosus*, note lack of interorbital bar. Same specimen as in Figure 15.

Günther (1910) did not designate a holotype or syntypic series for *D. bleekeri*, but his description, along with the included plate by Garrett, provide sufficient information to synonymize this nominal species with *D. liturosus*.

In large part the confusion between *D. holocanthus* and *D. liturosus* has resulted from the limited geographical overlap in the distributions of these two species. Because comparative material of both species is rarely available from a given area, it is not surprising that these similar species have been confused, especially considering the less than detailed descriptions available.

Nothing is known of the ecology of this species.

Material examined.—30 specimens, 24.5–340 mm.

INDIAN OCEAN: RUSI 3707 (1:124) Port Elizabeth, South Africa. AUSTRALIA: AMS B.1349 (1:128) Port Jackson, New South Wales. EAST INDIES: AMS B.7810 (1:114) Malay Archipelago; CAS 28225 (3:105–116) Madang, New Guinea; BPBM 19239 (1:132) Ambon, Molucca Is. PHILIPPINE IS.: CAS 38383 (1:130) Panay. GULF OF THAILAND: CAS 30967 (4:107–162) Ko Samet, Thailand; GVF stn 135 (1:186) Goh Proet I. Thailand; GVF stn 8 (1:201) Goh Kram I. Thailand; GVF 2646 (1:264) Goh Luem I. Thailand; GVF 2067 (4:94–152) Bangkok. JAPAN: CAS 6987 (1:24.5) Misaki. PALAU IS.: GVF stn 57–45 (1:155); GVF stn 61 (2:133–139); GVF stn 57–43 (1:217). KAPIN-GAMARINGI: GVF stn 51 (1:125). SOLOMON IS.: CAS 6004 (1:123) Bellona I. AMS B.1350 (1:112) Solomon Is. SOCIETY IS.: GVF (no station data) (1:340) Moorea; GVF stn 39 (1:195) Bora Bora; BPBM 8745 (1:313) Tahiti.

DIODON HOLOCANTHUS LINNAEUS

Balloonfish or Spiny Puffer (Figures 17, 18)

Diodon holocanthus Linnaeus 1758:335 ("Habitat in India") after Artedi 1738; Marshall 1965:500–501, pl. 63 (Queensland, Australia); Orsi 1974:176 (Vietnam).

Diodon pilosus Mitchill 1815:471, pl. 6 (New York); De Kay 1842:326, pl. 55 (New York).

Diodon novemmaculatus Cuvier 1818:136, pl. 6 (no locality given).

Diodon sexmaculatus Cuvier 1818:136–137, pl. 7 (no locality given).

Diodon quadrimaculatus Cuvier 1818:137, pl. 6 (Tahiti? - see text).

Diodon multimaculatus Cuvier 1818:137–138, pl. 7 (no locality given).

?*Diodon maculifer*? Kaup 1855:229 (Cape of Good Hope).

Paradiodon quadrimaculatus: (Bleeker 1865:57–58, pl. 212 (East Indies).

Trichodiodon pilosus: Bleeker 1865:49; Günther 1870:316 (both after Mitchill 1815).

Atopomycterus bocagei Steindachner 1866:447–478, pl. 6 (Port Jackson, Australia).

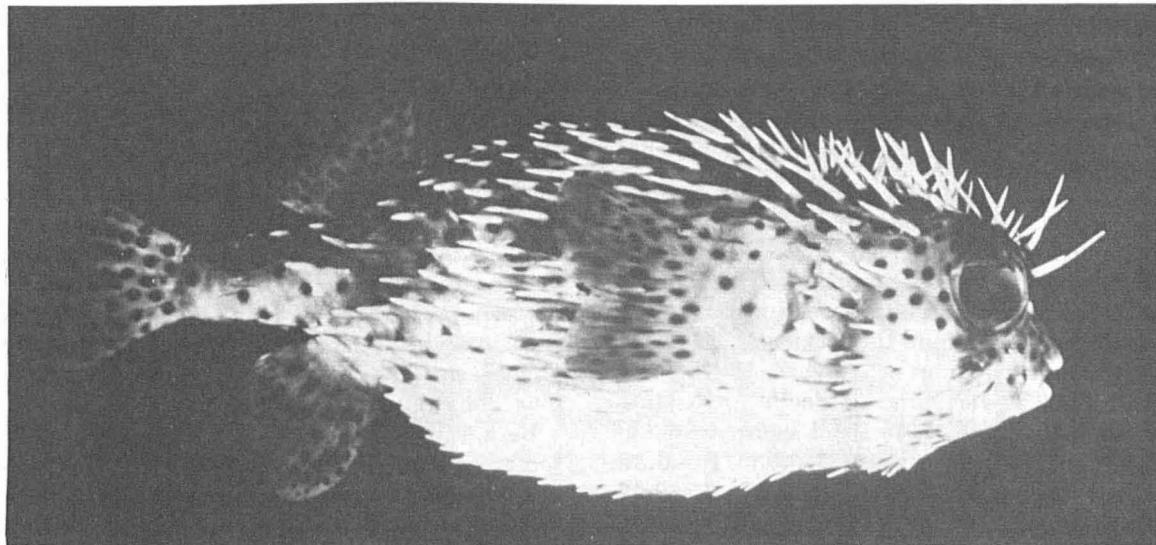


FIGURE 17.—*Diodon holocanthus*, 195 mm SL, Wolmar, Mauritius (BPBM 20255). Photo by J. E. Randall.

Diodon maculatus var. A (not of Lacepède):
Günther 1870:307-308, 1910:475 (various
localities).

Diodon liturosus (not of Shaw): Jordan and Gil-
bert 1883:377 (Panama); see Eigenmann (1885)
for other references.

Diodon hystrix var. *holocanthus* Eigenmann
1885:298-306 (American seas).

Diodon holacanthus (alternate spelling): Jordan
and Evermann 1891:1746 (American seas),
1905:436-437 (Hawaii); Jordan and Snyder
1902:257 (Japan); Herre 1924:505-506 (Philip-
pines); Meek and Hildebrand 1928:829-831
(Panama); Le Danois 1959:231 (in part) (various
localities); Randall 1968:282 (Caribbean).

Diodon hystrix (not of Linnaeus): Meek and Hil-
debrand 1928:827-829 (in part) (Panama); Poll
1959:354-355 (West Africa).

Diagnosis.—Round-bodied *Diodon*, head width 0.26-0.46, peduncle length 0.09-0.20. Caudal peduncle without spines. Body spines rather long, moderate in number. S-D spines 12-16, S-A spines 12-15. Frontal spines 0.13-0.28, from slightly shorter to much longer than pectoral axil spines. A short, fixed tribase spine immediately above the gill opening. A short, downward-pointing spine below the front border of the eye may be present in Atlantic specimens, but is absent in Indo-Pacific specimens. D 13-15, A 13-15, P 21-24. Nasal tentacle with a pair of lateral openings. Two small barbels on chin. On inshore specimens sets of short, fleshy tentacles: one over each eye, a pair in the middle of the back, six along the ventrolateral edge of body, and one on the dorsolateral edge of body posterior to pectoral fin. Some or all of the tentacles often lacking. Color pattern dominated by large dorsal and dorsolateral blotches. Small spots often quite profuse between large blotches. Fins without spots.

Description.—(45 Indo-Pacific and 28 Atlantic specimens) Numbers given are those for Indo-Pacific specimens, those in brackets are for Atlantic specimens. The latter are given separately only if they differ from the former. D 13-15 [14-15], the first two unbranched; A 13-15 [13-14]; P 20-24 [20-23]; vertebrae (2 Pacific, 1 Atlantic specimens) 12 + 9 = 21. Head width 0.26-0.46 (\bar{x} = 0.36; SD = 0.04) [0.33-0.43 (\bar{x} = 0.38; SD = 0.03)], body width 0.33-0.51 (\bar{x} = 0.42; SD = 0.05) [0.38-0.48 (\bar{x} = 0.45; SD = 0.03)], peduncle length 0.09-0.20 (\bar{x} = 0.15; SD = 0.03) [0.12-0.17 (\bar{x} = 0.14; SD = 0.02)], eye 0.07-0.17

(\bar{x} = 0.11; SD = 0.02) [0.08-0.15 (\bar{x} = 0.12; SD = 0.02)]. Dorsal, anal, and caudal fins rounded, middle rays longest. Nasal tentacles with a pair of lateral openings.

S-D spines 12-16 [13-15], S-A spines 12-15, about 11 spine rows over the dorsum between pectoral fin bases, about 24 spine rows over the ventrum between pectoral fin bases. Four or five frontal spines. Longest frontal spine 0.13-0.28 (\bar{x} = 0.18; SD = 0.03) [0.13-0.17 (\bar{x} = 0.146; SD = 0.012)], pectoral axil spines 0.11-0.22 (\bar{x} = 0.16; SD = 0.03) [0.11-0.17 (\bar{x} = 0.144; SD = 0.013)]. Frontal spines generally longest on the body. Pectoral axil spines 0.89-1.38 (\bar{x} = 1.12; SD = 0.11) [0.90-1.23 (\bar{x} = 1.00; SD = 0.07)] in frontal spines. Dorsal, dorsolateral, and lateral spines about equal in length (ca. 1.1 in frontal spines). Ventral spines somewhat reduced (ca. 1.5 in frontal spines). Spines at base of dorsal fin moderate (ca. 1.5 in frontal spines) and extend over the peduncle, but no spines wholly on the peduncle. The subdermal lateral bases moderate (1.4-2.3 in shaft length) except in ventral spines where they may equal the shaft length. Shaft extension short, but present on all spines except those on the top of the head. No spines markedly reduced. A short, fixed tribase spine immediately above the gill opening and usually a second slightly posterior to it above the pectoral base. Three or four flat spines with broad lateral bases forming the anterior border of the gill opening. All but one of 86 Indo-Pacific specimens examined without a short, downward-pointing spine below the anterior border of the eye. However, Atlantic specimens usually have this spine on at least one side (52 of 58 examined).

Two small barbels on the chin. Specimens taken pelagically (5-86 mm) lack these as well as the fleshy tentacles described next. A set of fleshy tentacles is variably present; absence may be due to damage or poor preservation. The full set of tentacles consists of the following: 1) one over each eye, 2) one pair middorsally (ca. one-third of the way between pectoral fin base and dorsal fin), 3) two along each postpectoral dorsolateral edge, 4) two along each postpectoral ventrolateral edge, and 5) four along ventrolateral edge of head.

Background color in preserved specimens light tan or grey to medium brown. The color pattern dominated by several large dark brown to black blotches on dorsal and lateral surfaces. Blotches usually lack a distinct light colored border. Blotches arranged as follows (Figure 18): 1) one

round blotch around the base of the dorsal fin, 2) one middorsal blotch of variable shape about midway between the dorsal fin and pectoral base, 3) a round to squarish blotch above each pectoral fin along the dorsolateral surface just posterior to the fin base, 4) a broad transverse bar across the occipital region, 5) a bar beginning below each eye and extending on to the interorbital (in Indo-Pacific specimens this bar is usually continuous across the interorbital, but in Atlantic specimens it is often not), 6) occasionally, a rather diffuse lateral bar between eye and gill opening. The dorsal and lateral surface with scattered small (<pupil diameter) spots the same color as the blotches; these are variable in number and size and rarely may be entirely lacking; they are not associated with the spine axils. Ventral surfaces white, but may be marked with spots which tend to be larger than the dorsal spots. This "pelagic spotting" (Figure 19) of the belly (see section on Eggs, larvae, and pelagic stages) is always found on specimens taken pelagically, but is often retained on specimens collected inshore (60-200 mm); this seems to be the case particularly with eastern

Pacific specimens. Pelagic spotting may extend dorsally to the level of the pectoral fin. No dark band on the underside of the head. Fins unspotted, except for some small clusters of melanophores associated with the fin rays. Color in life essentially the same as above, but fins may be yellowish and there may be yellowish areas around the spine bases.

The largest specimen examined was 289 mm. There are literature reports of much larger specimens, but these may be based on misidentifications. However, it is clear that *D. holocanthus* does not reach the size of *D. hystrix*.

Eggs, larvae, and pelagic stages.—The eggs and larvae of *D. holocanthus* were initially identified by rearing eggs from plankton tows. Three larvae were successfully reared through metamorphosis. These fish lived 25-33 days after hatching before being preserved. One was cleared and stained.

The eggs of *D. holocanthus* are spherical, with 10-30 clear, yellowish oil droplets of 0.05-0.25 mm in diameter. The eggs are pelagic, with a narrow perivitelline space, unsegmented yolk, and a

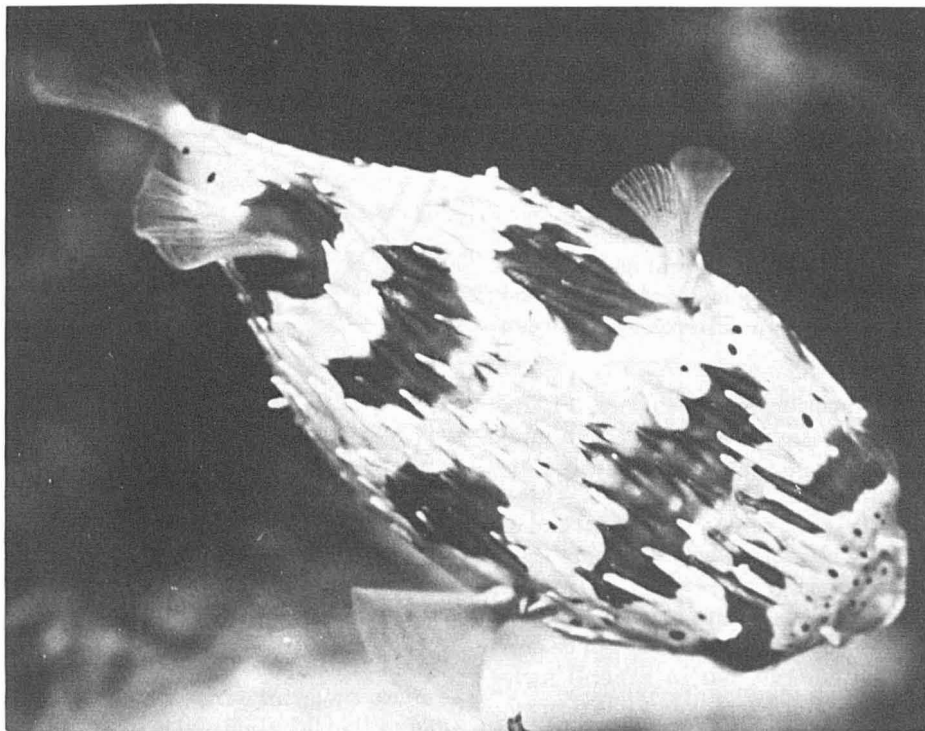


FIGURE 18.—Dorsal view of *Diodon holocanthus*, note interorbital bar. Oahu, Hawaiian Islands, 150 mm SL (HIMB, uncataloged).

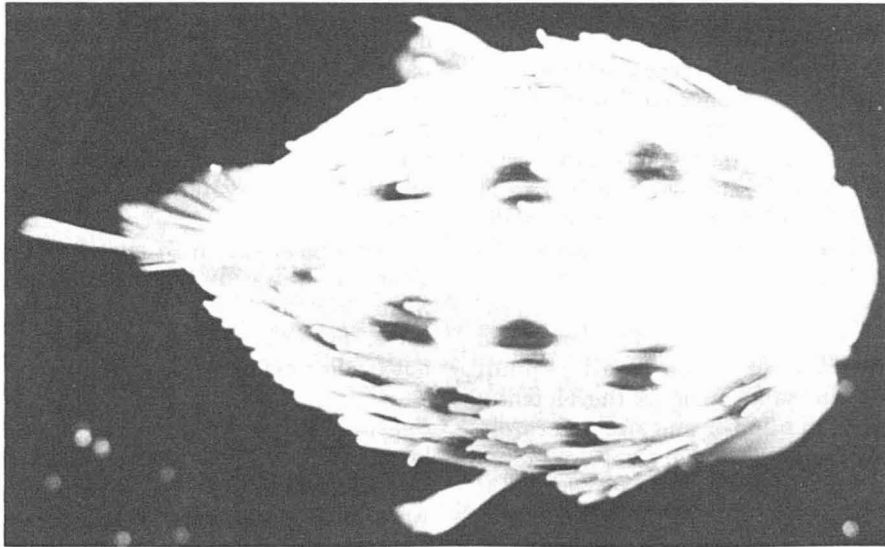


FIGURE 19.—Ventral view of pelagic juvenile of *Diodon holocanthus*, 14.5 mm SL, Hawaiian waters (HIMB, uncataloged). Note pelagic spotting.

clear, unornamented chorion. The diameter of the live eggs is 1.7-1.8 mm ($\bar{x} = 1.74$; SD = 0.03; $n = 16$) and of preserved eggs is 1.6-1.8 mm ($\bar{x} = 1.69$; SD = 0.06; $n = 191$). These means are significantly different at the 5% level (t -test) and a shrinkage of about 4% upon preservation in 5-10% seawater-Formalin³ is indicated. Rearing experiments indicate that the eggs are spawned in the early evening and hatch in 4-5 days at about 25°C. In rearing containers, the eggs sink to the bottom 12-24 h before hatching.

Embryonic Development: The development of *D. holocanthus* eggs is similar to that of *Ranzania laevis* (see Leis 1977). Development is described here with emphasis on differences between these two species.

Early stage (preclosure of blastopore, Figure 20). The earliest eggs collected were in mid-gastrulation. The oil droplets are tightly clustered opposite the embryonic axis. These move with the germ ring to the caudal end of the embryo by blastopore closure where they subsequently start to disperse. The elapsed time between midgastrulation and blastopore closure is 3 h. Some segmentation can be perceived on the embryo, but in general little structure is evident. No pigment has formed.

Middle stage (blastopore closure to separation of the tail bud from the yolk, Figure 21). The oil droplets remain scattered over the caudal one-fourth of the yolk sac. The eyes, heart, brain lobes, and otic vesicles are formed within 18 h of blastopore closure. The head is broad and no pigment is visible.

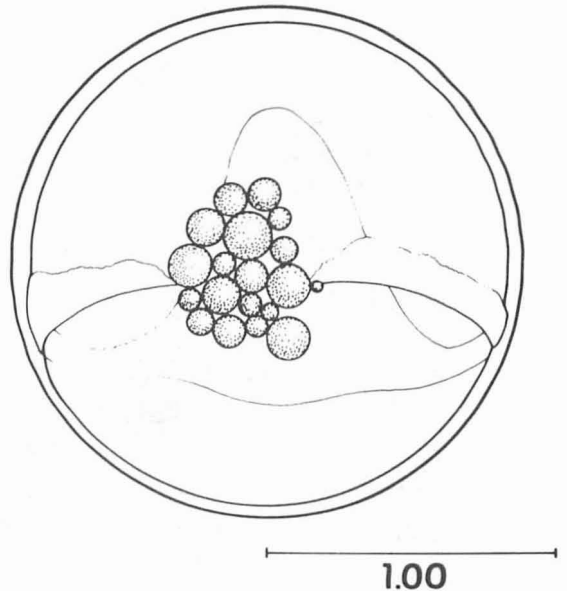


FIGURE 20.—Early stage egg of *Diodon holocanthus*. After Watson and Leis (1974), scale in millimeters.

³Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

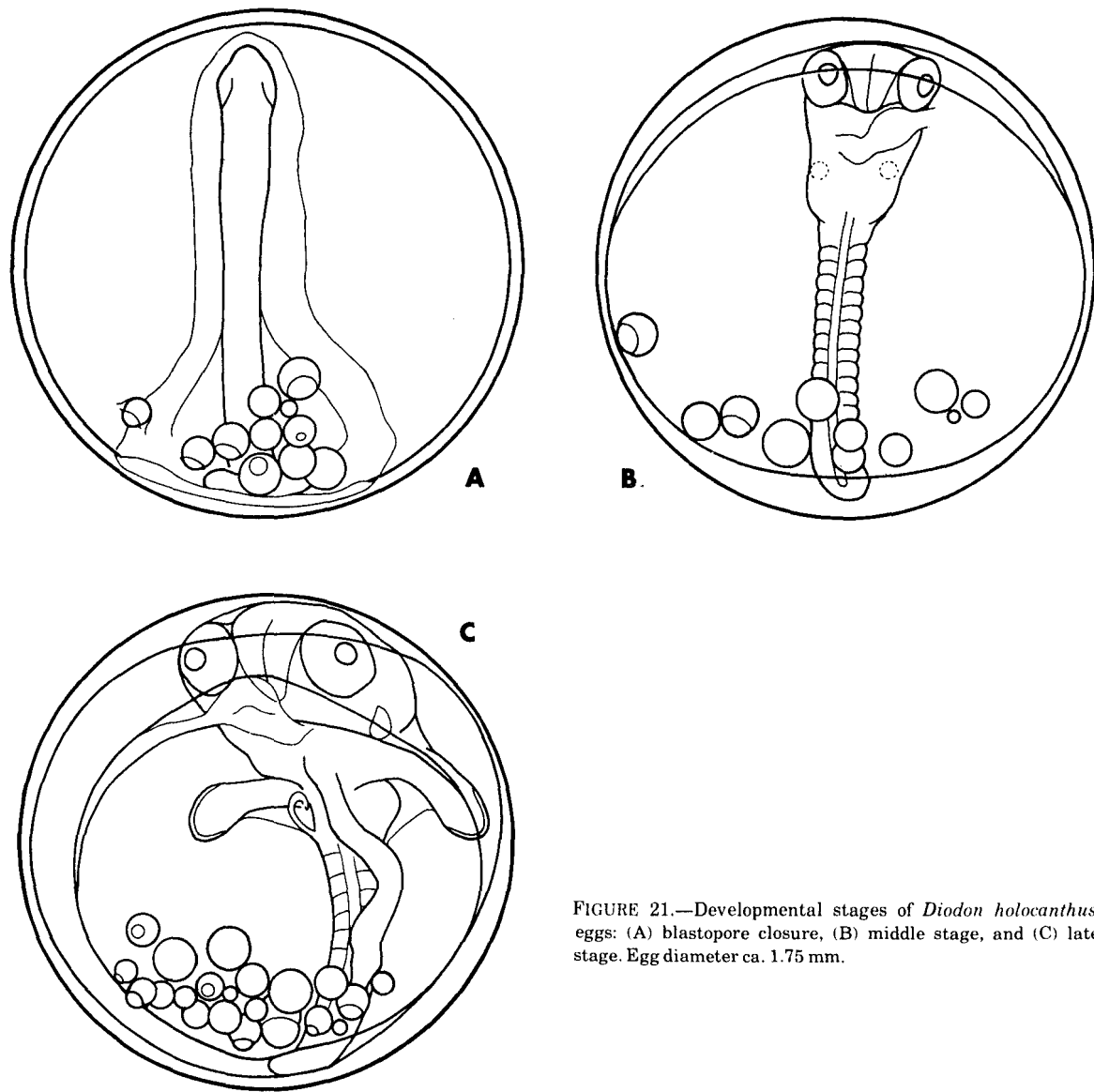


FIGURE 21.—Developmental stages of *Diodon holocanthus* eggs: (A) blastopore closure, (B) middle stage, and (C) late stage. Egg diameter ca. 1.75 mm.

Late stage (tail bud completion to first eye pigmentation and melanophores on body, Figure 21). The oil droplets are on the ventral surface of the yolk sac. The head becomes very broad and enclosed by an inflated vesicular dermal sac which eventually expands to enclose the entire body by the end of this stage. The pectoral fins are well-formed and are occasionally moved by the embryo. An odd hooklike structure which seems to be the incipient pectoral girdle can be seen in live material in the vicinity of the base. The gut forms a long, straight tube. The eyes develop their first pigment dur-

ing this stage, and a few melanophores appear on the head and dorsal surfaces. At about this time red chromatophores appear, scattered throughout the dermal sac and on the fin buds and folds.

Final stage (acquisition of full eye pigmentation through hatching). The oil droplets are no longer visible, being enclosed with the yolk sac within the abdomen. The mouth apparently becomes functional now, and the exhalant gill openings are visible. The eyes are completely, if lightly, pigmented. Body melanophores have spread over most of the

dorsal surfaces. No melanophores are present on the postanal myomeres or on the dermal sac.

Identification of Eggs: The combination of size (>1.5 mm) and numerous oil droplets serves to distinguish the eggs of *D. holocanthus* from those of all other pelagic eggs except those of other tetraodontiform species. The eggs of the molid *Ranzania laevis* have been described by Leis (1977). *Ranzania laevis* eggs may be distinguished from *D. holocanthus* eggs by the former's smaller size (1.4-1.65 mm) and by the extensive pigment which develops on the ventral surface of the yolk sac of *R. laevis* in the middle stage.

Hawaiian ostraciid eggs (*Ostracion* and *Lactoria*) may be distinguished by their slightly oblong shape, fewer oil droplets (<10), but most reliably by a patch of bumps on the chorion surrounding the micropyle. This "rough patch" is easily overlooked.

Diodon hystrix eggs are the only other *Diodon* eggs known (see section on *D. hystrix*). They can be distinguished from those of *D. holocanthus* by their larger size (>1.9 mm), greater number of oil droplets (>30), and the orange (rather than red) pigment.

Larval Development: Fifteen reared and 12 field-collected larvae in good enough condition for descriptive purposes were available. Morphometric data are summarized in Table 4.

The newly hatched larva has well-developed, apparently functional eyes, jaws, and gas bladder (Figure 22). The pectoral fins are quite large, although no rays are formed. The larvae are 1.9-2.1 mm SL at hatching and the body is rotund. Development in reared larvae is slow. Dorsal and anal fin anlagen form by day 10 (2.4 mm, Figure 22); the olfactory pit also forms by this time and the eyes have become proportionally larger. The oldest reared larva available was 16 days old, but it was smaller than the

TABLE 4.—Morphometric and meristic data for larval and juvenile *Diodon holocanthus* (measurements in mm). ? indicates individuals of unknown age, from plankton samples; × indicates damaged.

Age (days) of reared fish	Notochord or standard length	Snout to anus length	Width of eye	Head length	Head width	Mouth width	Fin ray counts		
							D	A	P
Larvae:									
1	2.0	1.5	0.3	0.9	1.1	0.5	0	0	0
1	2.1	1.5	0.3	0.8	1.2	0.5	0	0	0
1	2.0	1.5	0.3	0.8	1.2	0.4	0	0	0
1	2.0	1.4	0.3	0.8	1.2	0.4	0	0	0
1	1.9	1.4	0.3	0.7	1.2	0.5	0	0	0
?	1.9	1.5	0.3	0.8	1.1	0.6	0	0	0
?	1.9	1.4	0.3	0.9	—	0.4	0	0	0
?	1.9	1.6	0.4	0.9	1.2	0.6	0	0	0
?	1.9	1.0	0.3	0.6	—	—	0	0	0
?	2.0	1.6	0.4	0.8	1.1	0.6	0	0	0
?	2.0	1.6	0.3	0.7	1.1	0.3	0	0	0
5	1.8	1.4	0.3	0.8	1.2	0.6	0	0	0
6	1.8	1.4	0.4	0.8	1.0	0.6	0	0	0
7	1.9	1.4	0.3	0.8	1.0	0.5	0	0	0
8	2.1	1.4	0.4	0.9	1.1	0.6	0	0	0
8	2.2	1.7	0.5	0.9	1.4	0.7	0	0	0
8	2.1	1.5	0.4	0.8	1.1	0.6	0	0	0
9	2.0	1.4	0.4	0.8	1.0	0.5	0	0	0
?	2.2	1.5	0.3	0.8	1.2	0.5	0	0	0
?	2.3	2.0	0.5	0.8	1.5	0.6	0	0	0
?	2.3	1.5	0.3	0.8	1.1	0.5	0	0	0
10	2.4	2.0	0.5	0.9	1.5	0.8	0	0	0
10	2.2	1.7	0.5	0.9	1.3	0.6	0	0	0
?	2.5	2.1	0.5	0.7	—	0.4	0	0	0
?	2.6	2.0	0.5	0.7	0.8	0.4	0	0	0
?	2.7	2.2	0.5	0.7	—	—	0	0	0
16	1.9	1.5	0.5	1.0	1.2	0.7	0	0	0
Juveniles:									
?	3.8	3.4	0.8	1.9	2.6	1.0	×	×	22
25	4.8	4.0	1.0	2.3	3.5	1.9	14	14	23
?	5.5	4.8	1.1	2.8	3.3	1.6	—	—	—
?	6.0	5.3	1.2	3.3	3.5	1.8	—	—	—
33	6.7	5.2	1.4	2.9	4.3	1.7	15	×	21
?	7.2	5.5	1.5	3.4	3.7	1.7	14	14	23
ca. 30	8.1	6.7	1.8	3.9	4.8	1.8	14	14	21
?	11.0	9.0	2.0	5.5	6.3	2.7	—	—	—
?	14.1	10.9	2.7	6.3	7.6	3.2	15	14	23

¹Fish in emaciated condition.

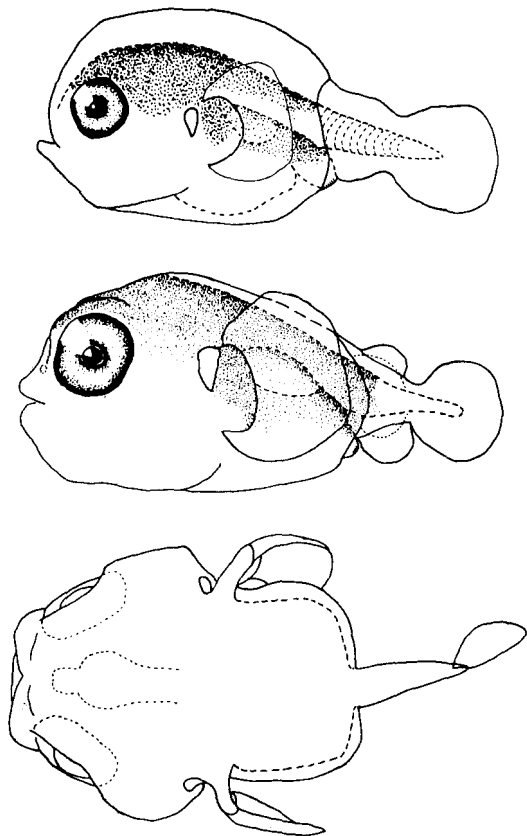


FIGURE 22.—Rearred larvae of *Diodon holocanthus*: (top) newly hatched larva 2.0 mm, (middle) 10-day-old larva 2.4 mm, and (bottom) dorsal view of 10-day-old larva with pigment omitted.

day-10 larvae and appeared emaciated. There are incipient fin rays and bases visible in the fins of the 16-day-old larva, but it otherwise is not obviously advanced over the 10-day-old specimen. There is no sign of development of the caudal fin complex. The largest larva available is a 2.7-mm field-collected specimen which is no more advanced than the day-16 larva. The dermal sac is inflated in young larvae (Figure 22), but the subdermal space is virtually gone by day 10 (Figure 22).

The larvae are more or less uniformly pigmented with scattered melanophores on the dorsal surfaces at all stages. The pigment spreads laterally, but there is little below the level of the pectoral fin and the ventral surfaces remain devoid of melanophores until metamorphosis. The newly hatched larvae have no melanophores posterior to the anus (Figure 22), but by day 10 postanal pigment has spread to

the middle of the dorsal fin anlage. In life, the newly hatched larva is covered with widely scattered red chromatophores on the dermal sac and fins. The red pigment persists through the larval stage and on about day 2 it is supplemented by a yellow background pigment covering all the body surfaces (not the dermal sac), but being most obvious ventrally due to a lack of melanophores there.

A 2.0-mm field-collected specimen was cleared and stained. The only ossified structures were the cleithrum, coracoid, and six branchiostegals.

Juvenile Development: Metamorphosis apparently occurs at ca. 3 mm at an age of about 3 wk. The smallest juvenile available is 3.8 mm and resembles Mito's (1966) illustration of a 3.7-mm juvenile except that Mito's fish had smaller eyes. The caudal, dorsal, anal, and pectoral fins are all formed as are the teeth, and the body is covered with small spines. The spines do not appear to be erectile, but the fish is capable of inflation. The spines are covered with a sheathlike tissue. They elongate rapidly with growth and by 4.8 mm SL (Figure 23) they are obviously erectile. The nostrils are formed in the 3.8-mm fish, although the nasal tentacle with two lateral openings is not formed until 4.8 mm SL, and in fish as large as 6.0 mm, it may be open at the ends. The 4.8-mm fish is in all respects a miniature adult with all external structures formed and functional. External changes to the adult stage involve only changes in proportion; the spines in particular elongate, the body becomes less rotund and the eye relatively smaller. Morphometric and meristic data are summarized in Table 3.

A 33-day-old juvenile of 6.7 mm was cleared and stained. The vertebral column and skull are incompletely ossified but all other structures are ossified. The vertebral formula is $12 + 9 = 21$ and the vertebral column is strongly arched. There are 11 dorsal and 11 anal pterygiophores which are associated with vertebrae 12-16 and 13-17, respectively.

At metamorphosis, pigment changes radically. The background color in live material is still predominantly yellow with scattered red chromatophores but this does not persist. Dorsally, the melanophores are scattered fairly uniformly, with a concentration at the pectoral base and very little pigment on the caudal peduncle.

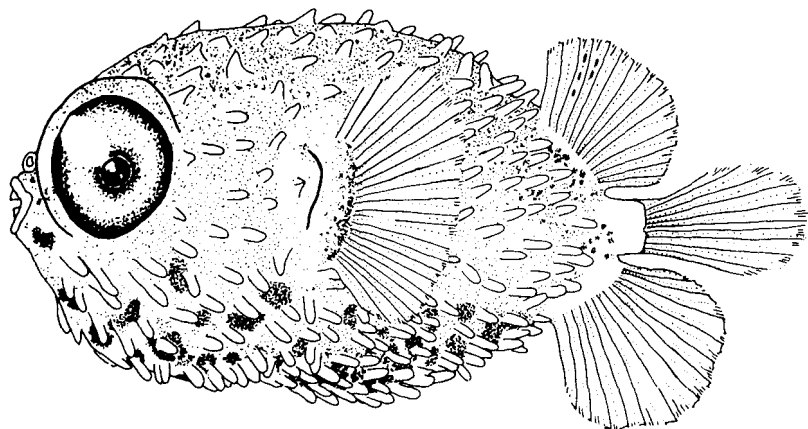


FIGURE 23.—Reared juvenile of *Diodon holocanthus*, 4.8 mm SL, 25 days old. Note pelagic spotting. Hawaiian material.

Ventrally, however, a number of distinct spots have formed that cover the belly (Figure 23). The spots (pelagic spotting) are at first close together but become less numerous and proportionately larger, aligning in rows with growth (Figure 19). Dorsal spotting (always more diffuse than ventral spotting) begins to form at around 10 mm and the characteristic dorsal blotch pattern is generally visible by 30 mm, although in pelagic specimens the contrast with the background color is not great. The pelagic spotting is retained in all pelagic individuals examined (to 86 mm) and in some specimens collected inshore. The fins remain unpigmented except for a few melanophores along the fin rays of the dorsal fin.

Identification of Larvae and Juveniles: Diodontid larvae are likely to be confused only with the rotund, heavily pigmented, sac enclosed ceratioid larvae and other tetraodontiform larvae. Reference to Bertelsen's (1951) work should allow ceratioid larvae to be distinguished as such. Rotund tetraodontiform larvae may be distinguished from diodontid larvae as follows: molids by their body spination and early forming pectoral rays; ostraciids by their pigmentation and early forming pectoral rays; tetraodontids by their relatively more elongate body shape and early forming fin rays. *Diodon* larvae are heavily pigmented only on dorsal surfaces, do not develop fin rays until near or at metamorphosis, have very wide heads and bodies (>body depth), and have very wide mouths.

The larvae of *D. holocanthus* can be distinguished from the putative *D. hystrix* larvae, the only other larval diodontid known, by the less

well-developed condition at hatching of the latter (see section on *D. hystrix*). In addition, *D. hystrix* larvae are predominantly orange upon hatching while those of *D. holocanthus* are yellow. Melanophores of *D. holocanthus* do not extend onto the postanal myomeres past the middle of the dorsal and anal fin anlagen; the postanal myomeres of *D. hystrix* are moderately pigmented. Lastly, the eyes of *D. hystrix* larvae are smaller than those of *D. holocanthus* larvae (Tables 2,3).

Once the spines form, the lack of caudal peduncle spination, fin ray counts and spine placement serve to distinguish *D. holocanthus* from all other *Diodon* species (see Key).

The duration of the pelagic stage is unknown, but judging from reared specimens, metamorphosis occurs about 3 wk after hatching at about 4 mm SL. The largest individual captured pelagically was 86 mm while the smallest captured inshore was 60 mm. A certain amount of plasticity in the duration of the pelagic stage is indicated, but its length clearly must be measured in terms of months. No special adaptations for pelagic life are evident in these juvenile stages except, perhaps, in color. In the tetraodontiform fishes (except the molids) the larval stage is short and relatively unspecialized, while a relatively unmodified pelagic juvenile stage may be quite long (see Remarks under *D. eydouxi*). This strategy (for dispersal?) is in marked contrast to that in many advanced perciform shorefishes (e.g., Acanthuridae, Chaetodontidae) where bizarrely modified and long-lived larval and pelagic prejuvenile stages are developed which subsequently undergo marked (and rapid) metamorphosis upon becoming benthic.

Diodon holocanthus eggs and larvae have been found in Hawaiian waters from February through September, with an apparent peak in abundance in May-June, although they are never common. Larvae usually occurred singly in plankton tows (volume filtered 200-1,000 m³). Although as many as 30 eggs/1,000 m³ have been taken, 1-5 eggs/1,000 m³ were more usual, and most tows contained none. Eggs were usually found close to shore, but larvae rarely were found closer than 1 km from shore (pers. observ.).

Holotype.—No holotype or type-series is known to exist. Linnaeus based his description on that of Artedi (1738).

Distribution.—*Diodon holocanthus* is circumtropical in distribution, but is seemingly absent in the southwest and central Pacific east of the andesite line (the separation of continental from oceanic rocks, Figure 14). However, it reappears in Hawaii, Pitcairn, and Easter Islands. Cuvier's holotype of *D. quadrimaculatus* was allegedly collected by Peron in Tahiti (see Le Danois 1961). Inasmuch as it is known that much of the locality data accompanying Peron's specimens are incorrect (associated with a shipwreck, see Whitley 1931:25) this record is questionable. There is evidence of divergence of the Atlantic population(s) from those of the Indo-Pacific (see Remarks).

Remarks.—I follow the spelling *holocanthus* (rather than *holacanthus* of many authors) which was used consistently by both Linnaeus and Artedi (see also Bailey et al. 1970), and is thus not considered to be a misprint as maintained by Jordan and Evermann (1891). Linnaeus' description is brief; the only useful information being the statement that the spines are terete and extremely long on the head and nape. However, this can apply only to *D. nichthemerus* or *D. holocanthus*. Assuming that "Habitat in India" means India as understood today, and not the entire Indo-Pacific, *D. nichthemerus* is eliminated. However, even if "Habitat in India" means the entire Indo-Pacific, it is unlikely that specimens of *D. nichthemerus*, a species apparently confined to southern Australia, could have reached Artedi by 1738. In any case, subsequent usage and stability demand that the name *D. holocanthus* apply to the species described above.

Diodon pilosus is synonymized with *D. holocanthus* on the basis of Mitchill's observation that no spines were present between the dorsal and caudal fins of his small (ca. 38 mm) New York specimen. *Diodon holocanthus* is the only Atlantic species that lacks peduncle spines. Mitchill distinguished *D. pilosus* on the basis of its flexible spines, but this is the usual condition in small specimens. No holotype is known to exist.

Cuvier's types are extant. Information and photographs of these specimens (catalog numbers and other information are given by Le Danois 1961) provided by M. L. Bauchot (pers. commun., MNHN, 20 May 1975) clearly establish *D. novemmaculatus*, *sexmaculatus*, *quadrimaculatus*, and *multimaculatus* (all of Cuvier) as junior synonyms of *D. holocanthus*. Inasmuch as Cuvier's (1818) descriptions are relatively clear, only his *D. novemmaculatus* requires comment. The holotype of *D. novemmaculatus* (MNHN A.9928, 107 mm) is *D. holocanthus*, apparently from the Atlantic (no locality data are available for this specimen). A spine is present below the anterior margin of the eye and the eye bar is discontinuous over the interorbital. Unfortunately, Cuvier's figure resembles *D. liturosus* as much as *D. holocanthus* (the figure shows the frontal spines shorter than they actually are). This probably led Bleeker (1865) to apply the name *D. novemmaculatus* to *D. liturosus*.

Diodon maculifer Kaup (1855) is included here with some questions. Kaup's description is of little help, and no type material can be found in the British Museum where it would be expected to reside. The holotype may have been part of Kaup's lost personal collection (A. C. Wheeler, pers. commun.). Examination of one of the South African (Kaup's type-locality) specimens of "*Diodon maculifer*" listed by Günther (1870) (BMNH 1845.7.3.103, 100 mm, loaned by A. C. Wheeler) reveals it to be an inflated, dried *D. holocanthus*. In this specimen, inflation is so great (an artifact of stuffing and drying?) that the subdermal spine bases project through the dried skin. Thus, the base of the spines appear to be expanded and transversely compressed. The only characteristic feature of Kaup's description is the compressed nature of the spines, and it seems likely that his description was based on a dried, inflated *D. holocanthus*.

Steindachner's *Atopomycterus bocagei* can be placed in the synonymy of *D. holocanthus* on the basis of information on the holotype (NMV 63848)

provided by P. Kähnsbauer (pers. commun., NMV, 1975). Steindachner's (1866) description is essentially correct and unquestionably refers to *D. holocanthus*. The placement of this specimen in *Atopomycterus* was apparently based on the split nasal tentacle (see section on *D. nichthemerus*). A single split nasal tentacle was present on only 3 of the more than 100 specimens of *D. holocanthus* examined, so this condition is rare but not unprecedented.

Both *D. liturosus* Shaw and *D. maculatus* Lacepède (the Latinized version of Le Diodon Tacheté) have been incorrectly applied to *D. holocanthus* by various authors (see section on *D. liturosus*).

For about the past 50 yr the chief sources of confusion on the identity of *D. holocanthus* have been confusion with *D. hystrix* by some (mostly American) authors and the lumping of *D. liturosus* under *D. holocanthus* by nearly all authors. The latter problem is discussed under *D. liturosus*.

The confusion between *D. hystrix* and *D. holocanthus* stems primarily from three sources. Many authors (e.g., Gosline and Brock 1960) have conjectured that *D. holocanthus* is the young of *D. hystrix* because the former does not reach a large size, and few, if any, small specimens of the latter were available. However, as discussed under *D. hystrix*, this species is pelagic to ca. 200 mm and is thus unavailable to inshore collecting. Inasmuch as *D. holocanthus* does not commonly exceed 200 mm, the confusion was perhaps understandable.

Second, many early descriptions are poor and keys often rely solely on the size of frontal spines relative to the pectoral axil spines to distinguish the two species. Especially in Atlantic specimens of *D. holocanthus*, the frontal spines are likely to be approximately the same size or even shorter than the pectoral axil spines.

Finally, as noted by Clark and Gohar (1953) (see also Bagnis et al. 1972:225), living *D. hystrix* often display a dorsal blotch pattern not unlike that of *D. holocanthus*. I have not observed this color pattern in preserved *D. hystrix*.

The apparent divergence of the Atlantic and Indo-Pacific populations of *D. holocanthus* mentioned above is of interest. At present, since *D. holocanthus* is apparently absent from the Red Sea and the Mediterranean, gene flow could occur only around southern Africa. Evidence that this is apparently not happening comes from the Indian Ocean specimens which lack a snout spine and have very long frontal spines in contrast to the Atlantic specimens (Table 5). In addition, Poll's (1959) description (as *D. hystrix*) of a west African specimen is typical of the specimens from the western Atlantic examined by me. The apparent increase in frontal spine length from the Atlantic to the Pacific to the Indian Oceans is curious. Based on studies of other groups (Ekman 1967) affinities might be expected between the Atlantic and eastern Pacific populations, but no extension to Hawaii and Easter and Pitcairn Islands would be expected. The lack of the snout spine in all but the Atlantic population and one Hawaiian specimen may indicate that the Atlantic population is distinct. Fin ray counts are of little help in resolving this question. Because all the characters which appear to differ between the Atlantic specimens and those from other areas are rather variable (although some are significantly different in a statistical sense), I choose not to distinguish formally the populations nomenclaturally at the subspecific level. If future study shows this split to be desirable, the proper name for the Atlantic specimens would be *Diodon holocanthus pilosus* Mitchill.

Le Danois (1954) reported sexual dimorphism in *D. holocanthus*, but her illustration of a female *D. holocanthus* (p. 2355:fig. 3) appears to be *D. liturosus*.

Material examined.—141 specimens, 5-289 mm.

EASTERN PACIFIC: NMFS LJ (1:18.5) 18°56'N, 104°10'W; NMFS LJ D31-133.25 (1:64.5) 26°04.5'N, 112°48.0'W; NMFS LJ TO-5801 (1:85.5) 5°29.5'N, 77°57'W; NMFS LJ (1:73.5) "350 mi. west of Costa Rica"; NMFS LJ B-5011 157.40 (2:41-41.5) 21°32.5'N, 111°14.5'W; UA 66-39-18 (1:242) San Agustin Bay, Sonora, Mexico; UA 69-35-25 (1:245) Guaymas, Sonora, Mexico;

TABLE 5.—Comparison of selected characters of *Diodon holocanthus* from five regions (see also Figure 6). *n* = number of individuals examined for snout spine.

Area	<i>n</i>	No. with snout spine	Frontal spine/SL	Fin rays (\bar{x})		Interorbital bar
				D	P	
Atlantic	58	52	0.146	14.15	22.15	Usually discontinuous
E. Pacific	11	0	0.154	13.80	22.10	Usually continuous
Hawaii, Pitcairn, and Easter Is.	24	1	0.174	14.44	22.57	Usually continuous
W. Pacific	29	0	0.205	14.11	22.17	Usually continuous
Indian	6	0	0.200	13.80	21.92	Usually continuous

UA 71-63-8 (1:145) Puerto Vallarta, Jalisco, Mexico; UA 71-65-9 (1:126) Isla Jaltamba, Jalisco, Mexico; SIO 59-373 (1:ca. 200) La Jolla, Calif.; SIO 63-82 (1:ca. 90) Cape Marco, Columbia. HAWAIIAN IS.: HIMB (3:135-289), HIMB 67-58 (1:67) Kaneohe Bay, Oahu; HIMB (1:181) Punaluu, Oahu; BPBM 10635 (1:63), BPBM 6977 (1:167) Diamond Head, Oahu; BPBM 5124 (1:129) French Frigate Shoals; NMFS H TC32-6,9,11,14 (6:12.5-30) 21°22'N, 158°14'W; NMFS H TC32-23 (1:14) 21°00'N, 158°30'W; NMFS H TC32-73 (1:7.0) 19°31'N, 156°06'W. SOUTHEAST PACIFIC: (all BPBM) 16459 (2:144-168), 13251 (1:135), 16455 (1:122) Pitcairn I.; 6797 (1:150.5), 6798 (1:185), 6799 (1:158), 6800 (1:156.5) Easter I. WESTERN PACIFIC: GVF stn HK91 (2:85-109) 19°38'N, 111°30'E; GVF 2269 (1:128) Gulf of Thailand; CAS 29126 (1:32) Ternate, Moluccas; CAS 6987 (1:41) Misaki, Japan; CAS 6752 (3:100-114) Wakanoura Kii, Japan; CAS 53402 (1:225) Hachijo I., Japan; CAS 15849 (10:90-125) Taiwan Strait. AUSTRALIA: AMS I.17228-001 (10:67-91) New South Wales. INDIAN OCEAN: RUSI 2782 (1:47.5) Knysna, South Africa; RUSI 3709 (1:60.5) East Cape, South Africa; RUSI 3710 (1:65) Inhaca, Mozambique; BPBM 19022 (2:173-188) Negombo, Ceylon; BPBM 20255 (1:195) Wolmar, Mauritius. WESTERN ATLANTIC OCEAN: CAS 4761 (1:150) Jamaica; CAS 54039 (1:94) Havana, Cuba; CAS 18182 (2:50.5-57.5) 29°14'N, 88°19'W; CAS 17184 (1:91) Pine I., Fla.; GCRL VTS:11184 (1:113) San Blas, Panama; LACM 1463 (1:84.5) Key Biscayne, Fla.; LACM 6281, 6282, 6283, 6284, 5781, 5872 (23:64-159) southern Jamaica; NMFS LJ *Gill* 3-64 (1:59) 33°29'N, 76°40'W; NMFS LJ *Silver Bay* 3458 (1:60) 29°03'N, 78°04'W; NMFS M *Oregon II*-72-39-144 (1:12.5) 23°34'N, 82°22'W, 39-73 (1:13) 21°31'N, 86°14'W, 39-50 (1:24) 16°50'N, 80°13'W, 39-48 (1:24.5) 17°26'N, 79°26'W, 39-58 (1:30) 21°01'N, 80°14'W, 39-63 (2:10-40) 19°41'N, 84°13'W, 39-01 (1:23) 13°00'N, 60°00'W, 39-39 (1:45) 18°00'N, 73°00'W, 39-11 (1:56.5) 17°25'N, 63°00'W; NMFS M *Bowers* 75-126-8 (1:28) 26°00'N, 79°30'W; NMFS M *Oregon II*-76-66-19786 (2:23-32) 18°18'N, 75°22'W, 66-19789 (2:20-30) 18°49'N, 74°44'W, 66-19790 (6:27-34) 19°22'N, 75°44'W, 66-19791 (18:19-33) 17°50'N, 74°47'W.

Note.—Since this paper was accepted for publication, NMFS H and most HIMB specimens were transferred to BPBM.

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