

**UC San Diego**  
**Bulletin of the Scripps Institution of**  
**Oceanography**

**Title**

External and internal characters, horizontal and vertical distributions, luminescence, and food of the dwarf pelagic shark, *Euprotomicrus bispinatus*

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**Publication Date**

1967-09-26

Peer reviewed

EXTERNAL AND INTERNAL  
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VERTICAL DISTRIBUTION,  
LUMINESCENCE, AND FOOD OF THE  
DWARF PELAGIC SHARK,  
EUPROTOMICRUS BISPINATUS

BY

CARL L. HUBBS, TAMOTSU IWAI, and KIYOMATSU MATSUBARA

UNIVERSITY OF CALIFORNIA PRESS  
BERKELEY AND LOS ANGELES

1967

BULLETIN OF THE SCRIPPS INSTITUTION OF OCEANOGRAPHY

UNIVERSITY OF CALIFORNIA, SAN DIEGO

LA JOLLA, CALIFORNIA

ADVISORY EDITORS: G. O. S. ARRHENIUS, C. S. COX, E. W. FAGER, C. H. HAND,  
M. B. SCHAEFER, E. L. WINTERER

Volume 10

Approved for publication February 3, 1967

Issued September 26, 1967

Price, \$2.50

UNIVERSITY OF CALIFORNIA PRESS

BERKELEY AND LOS ANGELES

CALIFORNIA



CAMBRIDGE UNIVERSITY PRESS

LONDON, ENGLAND

[CONTRIBUTION FROM THE SCRIPPS INSTITUTION OF OCEANOGRAPHY, NEW SERIES]

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PRINTED IN THE UNITED STATES OF AMERICA

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EXTERNAL AND INTERNAL CHARACTERS,  
HORIZONTAL AND VERTICAL DISTRIBUTION,  
LUMINESCENCE, AND FOOD OF THE DWARF  
PELAGIC SHARK, *EUPROTOMICRUS BISPINATUS*<sup>1</sup>

BY

CARL L. HUBBS, TAMOTSU IWAI,<sup>2</sup> AND KIYOMATSU MATSUBARA<sup>2</sup>

INTRODUCTION

THE OBJECT of this paper is to coordinate and expand knowledge of *Euprotomicrus bispinatus* (Quoy and Gaimard, 1824), the pigmy shark (pl. 1): a most remarkable creature, which until recent years had been known for a century and a quarter on the basis of very few, casual observations at sea and of 8 museum specimens. As a result of increasing emphasis on high-seas research we now have data on 37 specimens, and a much richer fund of information on the species.

The pigmy shark is a strange creature, defying most concepts of a shark. In the first place it is tiny: the largest known example spans only 265 mm (10½ in.) in total length and weighs less than 70 grams (about 2½ ounces)! Males mature at 170 mm, females at 233 mm or less. Its terete body and wee gill openings remind one of a lamprey. Its essentially diphyccercal tail, with large, rounded dorsal and ventral caudal-fin lobes and horizontal termination of the spinal column, little resembles the long-drawn-out, upturned heterocercal tail that is ordinarily associated with a shark. In this, and in some other respects, the appearance of this shark is almost embryonic. Its skeleton is almost devoid of calcification (apparently an adaptation for neutral buoyancy). Its vertebrae are unexpectedly few for a shark, and in radiographs look strangely like those of a bony fish. The teeth are strikingly unlike in the two jaws.

This little shark has been taken only at the sea surface, almost exclusively in the vast, relatively sterile central water masses of the world ocean. Its thousands of tiny light organs can combine to produce a bright blue-green glow. We now learn that it undertakes vertical migrations to considerable depth, where it feeds on bathypelagic squids and fishes.

ACKNOWLEDGMENTS

We owe deep gratitude to the many who in one way or another have assisted us in this investigation: Dr. Shelton P. Applegate, Los Angeles County Museum of Natural History, for advice on replacement of shark teeth; Mrs. Elizabeth S. Ash, Scripps Institution of Oceanography, for assistance in preparing the manuscript; Dr. Marie-Louise Bauchot, Muséum National d'Histoire Naturelle, for information regarding specimens (1-3, in table 1) in Paris Museum; Thomas E. Chase, Scripps Institution, for access to an unpublished bathymetric chart of the East Pacific Rise, and for other information on bathymetry bearing on the finding of sand

<sup>1</sup> Presented at the Eleventh Pacific Science Congress at Tokyo, Japan, August 29, 1966.

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grains in the stomach of one shark (no. 27); William L. Craig, California State Fisheries Laboratory, for information on specimens 29–31, for field observations, and for permission to report on the specimens and observations; Dr. Robert Ph. Dollfus, Laboratoire d'Helminthologie et Parasitologie Comparée, for identification of parasites; Drs. Albert E. J. Engel and Celeste G. Engel, Scripps Institution, for identification of the sand grains, and for advice on the submarine geology of East Pacific Rise; John E. Fitch, California State Fisheries Laboratory, for information regarding specimens 29–31 and for permission to publish thereon; Dr. Abraham Fleminger, Scripps Institution, for identification of copepod from stomach of specimen 27; Dr. W. I. Follett, of the California Academy of Sciences, for information regarding specimen 6 and for loan of specimen 9; Dr. Robert J. Goldstein, University of Texas Southwestern Medical School, for preliminary identification of parasites; Dr. Shigemasa Hattori, Tokai Regional Fisheries Research Laboratory, for placing specimen 25 at our disposal; Mrs. Laura C. Hubbs, for customary assistance in computations and in preparing the manuscript; Bert N. Kobayashi, Scripps Institution, for identification of fishes, especially *Vinciguerrria* and *Argyropelecus*; Dr. Tham Ah Kow, Director, Fisheries Biology Unit, University of Singapore, for information on specimen 22; Dr. Zenjiro Kubota, Shimonoseki College of Fisheries, for placing specimens 24 and 32 at our disposal; Dr. Ernest A. Lachner and staff, United States National Museum, for loan of specimens 11, 12, and 23 and for information on them; Dr. C. C. Lindsey, formerly of the Institute of Fisheries, University of British Columbia, for information regarding specimen 22; Dr. Isao Matui, Shimonoseki College of Fisheries, for placing specimens 24 and 32 at our disposal; Dr. Austin J. MacInnis, University of California, Los Angeles, for preliminary identification of parasites; Dr. John A. McGowan, Scripps Institution, for identification of invertebrate food remains, especially of squids; James R. Moriarty, Scripps Institution, for preparation of figures; Dr. William A. Newman, Scripps Institution, for aid in identification of invertebrate food remains; Dr. N. V. Parin, Instituta Okeanologii, Akademia Nauk (Moscow), for data on four additional specimens (33–36) and for other information, with gracious permission to publish thereon; Joseph L. Reid, Jr., Scripps Institution, for advice on oceanographic patterns bearing on the distribution of *Euprotomicrus*; Mrs. Margaret K. Robinson and staff, Scripps Institution, for pertinent oceanographic data; Dr. Milner B. Schaefer, Institute of Marine Resources, University of California, for information on specimen 11; Dr. William C. Schroeder, Museum of Comparative Zoology, Harvard University, for extracts of older literature; Howard G. Shirley, Scripps Institution, for skill and patience in preparing illustrations; Robert W. Topp, Museum of Comparative Zoology, Harvard University, for data on specimen 37; Dr. Shoji Ueyanagi, Nankai Regional Fisheries Research Laboratory, for placing specimen 24 at our disposal; Peter J. Whitehead, British Museum (Natural History), for measurements and weights of BM(NH) specimens (4, 5, 8, 10) and for other information; Robert L. Wisner, Scripps Institution, for preparing numerous radiographs used in the study and illustration of skeletal features (involving trials and experiments), for assistance in counting vertebrae, and for aid in identifying a lanternfish eaten by *Euprotomicrus*.

The senior author receives support on his ichthyological investigations from the National Science Foundation, currently by grant GB-4672.

#### SYSTEMATIC STATUS

Recent systematic revisions (Hubbs and McHugh, 1951; Bigelow and Schroeder, 1957) place *Euprotomicrus* in the subfamily Dalatiinae, of the spiny-dogfish family Squalidae. Previously these groups had been given higher ranking, as Dalatiidae and Squaloidea. The genus *Euprotomicrus* has been separated from its congeners in the Dalatiinae by reasonably diagnostic, though few and in part hardly paligenetic, characters.

*Euprotomicrus bispinatus* appears to be a single taxonomic unit, quite distinct from any other, on the generic as well as the specific level. There are no indications of specific differentiation within the apparently somewhat disrupted range (fig. 9) of the species. Fowler (1930: 497; 1941: 264-266) did synonymize *Euprotomicrus* with *Squaliolus* Smith and Radcliffe (*in* Smith, 1912: 683-685, fig. 4, pls. 50, 51), a genus later recognized by De Noronha (1926: 385-389, pl. 35). In this lumping interpretation Fowler was followed for two decades (by Belloc, 1937: 370-372; Sigalas, 1939-1940: 70-71; Bigelow and Schroeder, 1948: 450, 500; and Maul, 1948: 139). Hubbs and McHugh (1951: 161-165), taking issue with this action, presented evidence substantiating the generic separation of *Squaliolus*, even in a conservative generic appraisal. They were strongly supported by Bigelow and Schroeder (1957: 112-113, 126-132) in the next treatment of the question, and since then *Squaliolus* has consistently been recognized as distinct (by Teng, 1959: 1-6, 1 pl.; Garrick, 1960: 545; Abe, 1962: 147-151; Teng, 1962: 171, fig. 43; Chen, 1963: 94-95; Garrick and Springer, 1964: 678-679; Springer and Garrick, 1964: 92-93; and Parin, 1964: 174-175, 177-180).

Striking, fundamental differences between *Euprotomicrus* and the supposedly very close relative *Isistius*, in internal as well as external characters, as outlined in this treatise, suggest that a more penetrating study of the dalatiine genera will yield a more adequate taxonomic concept of the group. This, however, is not the object of the present paper. Rather, we proceed at once with the following annotated synonymy.

#### SYNONYMY OF *EUPROTOMICRUS BISPINATUS*

- Scymnus bispinatus*.—Quoy and Gaimard, 1824: 197-198, pl. 44, figs. 1-2 (original description, with name given also in French vernacular, Leiche laborde; "île de France" [= Mauritius]).
- Dalatis (Somniosus) bispinatus*.—Gray, 1851: 77 (synonymy; Isle of France [= Mauritius], Isle of Bourbon [= Réunion]).
- Euprotomicrus bispinatus*.—Regan, 1908: 56 (Indo-Pacific). Waite, 1912: 316 ([erroneously] listed for New Zealand). Garman, 1913: 234-235 (synonymy—except reference to New Zealand; diagnosis). Waite, 1916: 46, 49, 52 (records repeated for Campbell Island, for New Zealand [by error], and for Indian Ocean). Phillipps, 1927*a*: 10 (reference to *Scymnus bispinatus* only; [erroneously] listed for New Zealand); 1927*b*: 11 ([erroneously] listed for New Zealand); 1928: 224-225, fig. 5 (line tracing of type figure; [erroneous] record for New Zealand by Hutton, 1872, doubted; characters). Fowler, 1930: 497 (New Zealand [erroneous], Hawaii, Indian Ocean). Whitley, 1934: 200 (mention of [erroneous] New Zealand record by Hutton based on jaws, now lost, *vide* Phillipps). Bertin, 1939: 76 (synonymy; record of holotype). Whitley, 1940: 150 (Hutton's record to be expunged; Campbell Island record doubted). Fowler, 1941: 264-265 (synonymy



- [except for reference to New Zealand]; description, translated from Quoy and Gaimard). Hubbs and McHugh, 1951: 159-176, pls. 4-6 (detailed description; relationships and classification; 34°57' N. lat., 131°30' W. long.; review of published records). King and Ikehara, 1956a: 17-18, fig. 1 (18°24' N., 175°12' W.; description). Dickens, 1956: 73 23°10' S., 101°58' E.; viviparity; luminescence). Marshall, 1956: 73-74 (same specimen; viviparity; photophores; deep habitat). Bigelow and Schroeder, 1957: 126-128, fig. 16F and pl. 2, lower fig. (references; description; size; luminescence; birth of young). Otsu and Yoshida, 1957: 58 (32°46' N., 176°42' W.). Garrick, 1960: 545 (published records; New Zealand record cannot be substantiated). Garrick and Springer, 1964: 678-679 (wide range in Pacific and Indian oceans). Parin, 1964: 163, 166, 172-184, figs. 2-4 (general review; synonymy in detail; habitat; bioluminescence; embryos). Springer and Garrick, 1964: 78, 92 (number of vertebrae; near Midway Island, W. of Johnson Island, South Pacific Ocean, and off California).
- Scymnus Mauritanus*.—[Quoy and Gaimard], in Audouin, *et. al.*, 1831: pl. 114 (Poissons, pl. 22), fig. 2 (Leiche laborde, *Scymnus bispinatus* renamed, with reference to original figure, obviously on basis of same material and figure; only diagnosis is "remarquable par la petitesse de su dorsale.")
- Scymnus (Laemargus) Labordei*.—Müller and Henle, 1841: 94-95 (original account, attributed to Quoy and Gaimard [obviously because they named the fish "Leiche laborde," and dedicated it to LaBorde, as well as giving it the scientific name of *Scymnus bispinatus*]; Isle de France [= Mauritius] and Isle de Bourbon [= Réunion]; 3 in Paris Museum).
- Scymnus Labordei*.—Gill, 1865: 264n (indicated, by parenthetic inclusion, as type of *Euprotomicrus* [new genus]).
- Laemargus Labordei*.—Duméril, 1865: 457-458 (synonymy; description; Ile Maurice [= Mauritius], Quoy and Gaimard; and 1 from unknown locality).
- Euprotomicrus labordei*.—Günther, 1870: 427-428 (synonymy; diagnosis; 2 specimens, no locality, from J. B. Godfrey, Esq.). Cunningham, 1899: 732-734 (one of several reported to have been washed aboard between 80° and 90° W., in about latitude of Cape Horn; external and visceral characters). Burckhardt, 1900b: 566, fig. 6 (distribution of photophores). Boulenger, 1902: 174 (references; Campbell Island, S. of New Zealand). Waite, 1907: 8 (New Zealand [by error; reference wrongly accredited by Fowler, 1941: 265, to *Scymnus labordei*]).
- Euprotomicrus labordei*.—Sauvage, 1891: 511 (region of Madagascar, between 3° and 26° lat., and between 42° and 65° long.).
- Euprotomicrus*.—Gill, 1865: 264n (diagnosis [new genus], with type indicated, by parenthetic inclusion, as *Scymnus Labordei*). Burckhardt, 1900a: 488-489 (photophores, of *Spinax* [= *Etmopterus*] type, may well be functional). Bigelow and Schroeder, 1948: 450, 500 (comparisons; range [New Zealand included by error]). Aleev, 1963: 24 (bioluminescence [account abstracted by Parin, 1964: 176]). Gilbert, 1963: 295 (nictitans and spiracle). Garrick and Springer, 1964: 678-679 (member of midwater fauna).
- Euprotomicrus sp.*—Hutton, 1872: 81 (New Zealand [based on set of jaws subsequently lost, *fide* Phillipps, 1928: 81; record obviously false]). Parin, 1963: 131 (central part of Pacific Ocean and eastern part of Indian Ocean; dipnetted under light).
- Euprotomyrus* [misspelled].—Andriashev, 1965: 540 (luminescent; one of warm-water forms penetrating into Kerguelen Subregion of Antarctic Region).
- Euprotomicrus hyalinus*.—Eigenmann, 1890: 35 (original description; stranded on ship in heavy sea nearer Honolulu than San Francisco). Garman, 1913: 234-235 (reference; characters; distinctness doubted).
- Dalatiidae*.—Andriashev, 1961: 231 (specimens 13 and 14 of table 1 listed, from Obj. Sta. 421).

#### KNOWN SPECIMENS

Although the species was described in 1824, only 8 specimens of *Euprotomicrus bispinatus* were reported by 1951. As a result of recent, exponentially accelerated

oceanographic exploration, it has become rather well represented in collections. We have traced records of 36 specimens (tables 1, 2; fig. 9). Of these, 8 were collected in the last century, the next 2 in 1948, all 26 others during the past two decades.

The original describers of the species, Quoy and Gaimard (1824: 197-198), listed only one specimen, a male, no. 1 in table 1. They specified the locality as "île de France" (= Mauritius), the length of the type as "sept pouces quatre lignes," which, by computing 1 old *pouce* as 27.07 mm and 12 *lignes* as 1 *pouce*, yields the metric equivalent of 198 mm. Müller and Henle (1841: 94-95) recorded "drei Exemplare in Paris durch Dussumier," mentioned one as 7½ inches (190 mm) long (probably no. 1 of our table), and listed the localities as "Isle de France, Isle de Bourbon" (= Mauritius and Réunion). The three specimens are listed as 1, 2, and 3 in table 1, with specifications in part assumed from the information furnished by Duméril (1865: 457-458), by Burekhardt (1900b: 566), by Bertin (1939: 76), and by Dr. Marie-Louise Bauchot (personal communication, 1966), on specimens, probably the same, in the Paris Museum. Duméril described "deux individus longs de 0<sup>m</sup> .205 et de 0<sup>m</sup> .210, dus à MM. Quoy et Gaimard," (though Quoy and Gaimard mentioned only one). Duméril specified further: "*Habitat*.— Ile Maurice: Quoy et Gaim., et un sujet d'orig. inconnue." We interpret the "205"-mm specimen as the male mentioned by Duméril and as the original type; the "210"-mm one as no. 2, which Müller and Henle attributed to Isle de Bourbon, and the specimen of unknown origin as no. 3. Bertin gave "19 cm" as the length of the holotype (no. 1). Dr. Bauchot has informed us that there are still three specimens in the Paris Museum: the holotype, which she measured as 196 mm; a second specimen, registered also as from "Ile Maurice" and as having been donated by Cuvier, which she measured as 205 mm long (thought, though not without doubt, to be no. 2, as listed in table 1); and one 143 mm long, "de provenance inconnue," thought very probably to be no. 3 of our table. The female treated by Burekhardt and stated to be 200 mm long is probably no. 2.

It seems probable that only the three specimens in Paris had been reported when Günther (1870: 427-428) listed two more, of unknown provenance, but collected by "J. B. Godfrey, Esq." Günther gave the lengths as between 8 and 9 inches (between 203 and 229 mm). According to Peter J. Whitehead (personal communication, 1966) these specimens are BM(NH) 1901.5.26.1 and 2, respectively 206 and 201 mm long. Cunningham (1899: 732-734) and Boulenger (1902: 174) each reported an additional specimen, respectively 7 and 8 (table 1), and Regan (1908: 56) listed three, 200 to 220 mm long. Whitehead listed no. 8 as BM(NH) 1901.11.8.1, 219 mm long. No. 7 has not been located.

Particulars on subsequent specimens (9-37) involve no special queries, and seem to be adequately presented in tables 1 and 2.

For comparison with *Euprotomicrus bispinatus* we have at Scripps Institution of Oceanography a single specimen of *Isistius brasiliensis* Quoy and Gaimard (for synonymy see Bigelow and Schroeder, 1948: 513-514), a mature male 386 mm in total length (SIO 52-413-5A). It was dipnetted under a light at the surface, over a depth of 3,274 m, on the night of August 14, 1952, on Scripps Institution "Shell-back" expedition, by Staff members Cunningham, Richter, and Berner, just on

TABLE 1

DATA ON KNOWN SPECIMENS OF *Euprotomicrus bispinatus*

Repeated accounts of a given specimen are assigned the same number as for the first recording. The numbers in parentheses after "Parin (1964)" are those used in that paper (p. 166). The localities are charted, by specimen number, on fig. 9.

No.	Reference	Museum* or station no.	Date of capture	Locality	How taken	Sex	Length (mm) <sup>b</sup>
1	Quoy & Gaimard, 1824.....	MNHN 1216	1817-20	"Île de France" (Mauritius)	?	♂	(198)
1?	Müller & Henle, 1841.....	{ MNHN 1216?	1817-20	"Isle de France" (Mauritius)	?	♂	(190)
2		{ MNHN 1217?	1817-20	"Isle de Bourbon" (Réunion)?	?	♀?	[205?]
3		{ MNHN 1215	Unknown	Unknown	?	?	[143]
1	Duméril, 1865.....	{ MNHN 1216	1817-20	"Île Maurice" (Mauritius)	?	♂	"200"
2		{ MNHN 1217?	1817-20	Mauritius?; Bourbon?	?	♀?	"205"
3		{ MNHN 1215	Unknown	Unknown	?	?	[143]
4	Günther, 1870.....	{ BM(NH) 1860.5.26.1	Unknown	{ Unknown; from "J. B. God-	?	♀	[206]
5		{ BM(NH) 1860.5.26.2 }			frey, Esq."	?	♀
6	Eigenmann, 1890.....	CAS 12715	Unknown	Nearer Honolulu than San Francisco	Washed aboard	♀	[158]
7	Cunningham, 1899.....	Not located	Unknown	90° to 100° W. long., lat. of Cape Horn	Washed aboard	♀	ca. 250
2?	Burckhardt, 1900b	MNHN 1217?	1817-20?	Isle de Bourbon?	?	♀	"200"
8	Boulenger, 1902.....	BM(NH) 1901.11.8.1	V:4:1899	Campbell Id.	?	♀	(219)
4, 5, 8	Regan, 1908.....	(See above)	(See above)	(See above)	(See above)	♀s	"200 to 220"
1	Phillipps, 1928 <sup>c</sup> .....	[MNHN 1216]	[1817-20]	[Mauritius]	?	♂	[196]
1	Bertin, 1939.....	MNHN 1216	[1817-20]	"Île Maurice" (Mauritius)	?	[♂]	"19 cm."
9	Hubbs & McHugh, 1951.....	CAS 20431	XI:19:1948	34°57' N., 131°30' W.	Dip net	♀	233
10	Dickens, 1956; Marshall, 1956	BM(NH) 1956.6.23.1	Unknown	23°10' S., <sup>d</sup> 101°58' E.	Dip net	♀	234
11	King & Ikehara, 1956a.....	USNM 164176	III:3:1948	18°24' N., 175°12' W.	Dip net	♀	161
12	Otsu & Yoshida, 1957.....	USNM 190031	IV:3:1956	32°46' N., 176°42' W.	Dip net	♀	242
13	{ Andriashev, 1961; }	Obj Sta. 421 <sup>e</sup>	V:3:1958	37°55' S., 109°24' W.	Dip net	{ ♂	202
14	{ Parin, 1964(8) }					{ ?	?
15	Parin, 1964 (1).....	Vitiaz Sta. 3831	I:6:1958	32°00' S., 177°13' W.	Dip net	?	(Lost)
16	Parin, 1964 (2).....	Vitiaz Sta. 4343	II:20:1959	24°03' N., 179°01' W.	Dip net	♀	256

TABLE 2  
SPECIMENS OF *Euprotomicrus bispinatus* USED IN PRESENT INVESTIGATION<sup>a</sup>

Specimen no.	Ship	Agency <sup>b</sup>	Station	Collector	Temperature, °C.		Depth (m)
					Surf.	200 m	
6	Str. Gaelic.....	Comm.	...	Lt. F. A. Gardner	....	....	....
9	U.S.S. Serrano.....	NEL-SIO	118	J. L. McHugh and Robt. F. Huffer	18.3	10.15	4,389-5,121
11	M/V Oregon.....	HBL	...	Milner B. Schaefer	24.8 <sup>o</sup>	....	ca. 1,829
12	Charles H. Gilbert.....	HBL	...	T. Otsu and H. O. Yoshida	16.9	15.0 <sup>d</sup>	ca. 4,755
23	Hugh M. Smith.....	HBL	HMS-15	Thomas S. Hida	26.3	18.4	....
24	Koyo Maru.....	SCF	...	Z. Kubota	25.2 <sup>o</sup>	18.12 <sup>o</sup>	....
25	Soyo Maru.....	TRFL	20	T. Okutani	25.6	14.95	....
26	Unknown <sup>f</sup> .....	NRFL	...	Unknown <sup>f</sup>	....	....	....
27	Horizon.....	SIO	Downwind 40	Edward Brinton	24.3	16.5	3,579
28	Horizon.....	SIO	Capricorn 147	Martin W. Johnson	26.6 <sup>g</sup>	20.5 <sup>g</sup>	....
29	Alaska.....	CSFL	61A4-9	D. J. Mackett	15.6	13.5 <sup>h</sup>	5,304
30	N. B. Scofield.....	CSFL	61S3-14	Wm. L. Craig	15.8	12.5 (125 m)	4,901
31	N. B. Scofield.....	CSFL	65S3-12	J. E. Phelan	16.6	10.9	4,206
32	Koyo Maru.....	SCF	....	Arao Tsuruta	25.6	....	....
33	Vitiaz.....	IOAN	5321	.....	....	....	....
34	Vitiaz.....	IOAN	5333	.....	....	....	....
35	Vitiaz.....	IOAN	5338	.....	....	....	....
36	Vitiaz.....	IOAN	5444	.....	....	....	....
37	Anton Bruun.....	NSF	23 (Cr. 13)	Robert W. Topp	21.2	....	3,550-4,100

<sup>a</sup> Additional data, supplementary to table 1.

<sup>b</sup> Comm. = commercial vessel; CSFL = California State Fisheries Laboratory, Marine Resources Operations, California Department of Fish and Game; HBL = Honolulu Biological Laboratory, U.S. Bureau of Commercial Fisheries (formerly POFI = Pacific Oceanic Fisheries Investigations; the M/V Oregon was operated, in conjunction with the Laboratory, by the Pacific Exploration Company); IOAN = Institut Okeanologii, Akademia Nauk (USSR); NEL = U.S. Navy Electronics Laboratory, San Diego; NRFL = Nankai Regional Fisheries Research Laboratory; NSF = National Science Foundation; SCF = Shimonoseki College of Fisheries; SIO = Scripps Institution of

Oceanography, University of California, San Diego; TRFL = Tokai Regional Fisheries Research Laboratory, Japan.

<sup>o</sup> Taken by BT on March 4, at 18°20' N., 175°44' W.

<sup>d</sup> Taken by BT at 32°47' N., 176°42' W.

<sup>g</sup> Taken at next station at 20°13' N., 158°19.5' W., on December 27, 1961.

<sup>f</sup> Specimen taken by Nankai Regional Fisheries Research Laboratory on cruise of its research vessel.

<sup>g</sup> Taken by BT at 14°19' S., 120°51' W.

<sup>h</sup> Taken by BT at 35°29' N., 137°28' W., at 119 m.

17	Parin, 1964 (3).....	Vitiaz Sta. 4668	XII:12:1959	31°33' S., 110°42' E.	Dip net	♂	216
18	Parin, 1964 (4).....	Vitiaz Sta. 4570	XII:13:1959	31°15' S., 106°36' E.	Dip net	♂	220
19	Parin, 1964 (5).....	Vitiaz Sta. 5101	IX:26:1961	08°26' S., 140°04' W.	Dip net	♂	160
20	Parin, 1964 (6).....	Vitiaz Sta. 5199	VIII:23:1962	26°02' S., 91°38' E.	Dip net	♂	216
21	} Parin, 1964 (7).....	{ Vitiaz Sta. 5200	VIII:25:1962	23°52' S., 99°57' E.	Dip net	{ ♂	206
22							
23	Springer & Garrick, 1964....	USNM 190032	II:2:1957	13°38' S., 110°34' W.	Dip net	♂	112
24	Original.....	FAKU 36370	XII:26:1961	18°07' N., 159°50' W.	Dip net	♀	139.5
25	Original.....	SIO 66-111-5A	VIII:17:1958	29°51' N., 175°00' W.	Dip net	♂	213
26	Original.....	SIO 66-110-5A	VI-VIII:1963	01° to 28° S., 74° to 102° E.	?	♂	200
27	Original.....	SIO 58-309-5A	II:13:1958	14°17' S., 108°52' W.	Dip net	♂	170
28	Original.....	SIO 63-1086-5A	II:1:1963	14°16' S., 120°40' W.	Dip net	♀	109
29	Original.....	LACM 6988	V:20:1961	35°29' N., 137°28' W.	Dip net	♂	211
30	Original.....	LACM 6989	VI:2:1961	35°18' N., 130°36' W.	Dip net	♀	240
31	Original.....	LACM 6990	VI:5:1965	33°11' N., 131°24' W.	Dip net	♀	285
32	Original.....	FAKU 39024	I:3:1966	06°00' S., 25°19.2' W.	Dip net	♀	105
33	Original.....	Vitiaz Sta. 5321	XII:15-16:1964	23°01' S., 60°20' E.	Dip net	♂	168
34	Original.....	Vitiaz Sta. 5333	I:20:1965	32°27' S., 108°03' E.	Dip net	♂	213
35	Original.....	Vitiaz Sta. 5338	II:5-6:1965	17°36' S., 92°13' E.	Dip net	♂	125
36	Original.....	Vitiaz Sta. 5444	VIII:12:1965	22°25' N., 157°55' W.	Dip net	♂	99
37	Original.....	MCZ 45900	I:19:1966	33°48' S., 176°42' W.	Dip net	♂	209

\* BM(NH) = British Museum (Natural History); CAS = California Academy of Sciences; FAKU = Faculty of Agriculture, Kyoto University; LACM = Los Angeles County Museum of Natural History; MNHN = Muséum National d'Histoire Naturelle, Paris; SIO = Scripps Institution of Oceanography, University of California, San Diego; U. Sing = University of Singapore fish museum; USNM = United States National Museum.

<sup>b</sup> Total length transformed into millimeters when otherwise stated (1 old *pouce*, or

French inch, calculated as 27.07 mm); transformed measurements in parentheses; measurements taken subsequently in square brackets.

<sup>c</sup> Line drawing of type (presumably from type figure).

<sup>d</sup> Misstated as 23°0' N. lat. by Parin, 1984: 173.

<sup>e</sup> Also listed by Parin, 1964: 186, as bearing invoice no. 37068 in Akademia Nauk SSSR.

<sup>f</sup> Second specimen donated to fish museum, University of Singapore; now misplaced (Dr. Tham Ah Kow, personal communication).

the equator at 100°00' W. long., where the surface temperature was reduced by upwelling to 23.6° C. In all respects this specimen is typical of *I. brasiliensis*, as contrasted with the recently described *I. plutodus* (Garrick and Springer, 1964).

Another specimen (FAKU 39108) of *I. brasiliensis* has been examined. It was taken in a trawl with 200 m of wire out, on December 22, 1964, in the Peru Current off Peru, at 13°46.0' S., 81°52' W.

#### EXTERNAL CHARACTERS

The brief descriptions of *Euprotomicrus bispinatus* by earlier authors were expanded in considerable detail by Hubbs and McHugh (1951) and supplemented by Parin (1964) and by King and Ikehara (1956a). We now offer a note on the color of the species, a morphometric analysis, and a description of the photophores, the denticles, and the dentition. In addition we treat certain internal characters (its visceral anatomy, in detailed comparison with that of *Isistius brasiliensis*, and its vertebrae and other skeletal parts); also the claspers and the ova and embryos.

#### COLOR

The color pattern (pl. 1, figs. 1, 2) of *Euprotomicrus bispinatus* has been described and figured several times. Mention has not been made, however, of the general color tone. This varies from very light brown to brownish black. For example, of four specimens in the British Museum, 4 and 5 (see table 1) are "light brown," 8 is "slightly darker," and 10 is "black" (Peter J. Whitehead, personal communication). Among four specimens from off California, the ground color grades from light brown to brownish black, in the following sequence of specimens: 30—29—9—31. The variation is great, but gradual.

#### MORPHOMETRIC ANALYSIS

In order to determine whether, and if so how, proportions (1) change with increasing size, (2) differ with sex, and (3) vary geographically, we present as basic data proportional measurements of 21 specimens (table 3). All proportions are expressed as thousandths of the total length. Except for two replacements and a few additions, chiefly to match measurements fully with those listed by Parin (1964: 175), our set of measurements, and our techniques of measuring, follow those utilized by Hubbs and McHugh (1951: 170–171) for one specimen (no. 9 in our series). In general, the methods follow the standards set by Hubbs and Lagler (1964: 19–26, figs. 3–7).

Of the 21 specimens, 14 were measured by us for 73 body parts, plus 2 more on males only, and 7 were measured by Parin (1964) for 29 dimensions. In all, more than 1,200 measurements are listed.

For greater precision, all measurements were taken from point to point, never as projections. Dial calipers were used for smaller dimensions, under magnification as needed. Origins of vertical fins and insertions of paired fins were located by gently pushing one point of the instrument against the anterior base of the fin until slight resistance was felt. Depending on obvious context, either the minimal or the maximal measurement was employed. Most bilateral parts were measured

TABLE 3

MEASUREMENTS OF *Euprotomicrus bispinatus* IN THOUSANDTHS OF TOTAL LENGTH

The 21 specimens are separately arranged by order of size, first under sex, then under major ocean areas. Detailed collecting data are given in tables 1 and 2. Measurements reported by Parin (1964: 175) are indicated by the letter P following the specimen number. Proportions in parentheses, from Parin (1964), are for values that certainly or probably deviated from corresponding measurements by us because of a difference in method. The plus marks for measurements of specimen no. 31 represent low values attributable to shrinkage. Specimen no. 6 is also considerably shrunken. Fins are thus abbreviated: C = caudal, D<sub>1</sub> = first dorsal, D<sub>2</sub> = second dorsal, P<sub>1</sub> = pectoral, P<sub>2</sub> = pelvic. The asterisk indicates a mature male or gravid female; others are immature, spent, or of unknown maturity.

Ocean area	North Pacific Ocean									South Pacific Ocean					Indian Ocean					Atlantic Ocean	
	Male		Female							Male			Female	Male					Female		
Sex.....	29*	25*	24	6	11	9*	30*	12*	16*P	31	23	19P		27*	13*P	28	26*	21*P		17*P	20*P
Specimen no.....	211	213	139.5	158	161	233	240	242	256	265	112	160	170	202	109	200	206	216	216	220	105
1. Predorsal length, to D <sub>1</sub> .....	513	529	500	524	516	527	531	500	546	511	519	530	526	511	524	528	530	533	551	548	523
2. Predorsal length, to D <sub>2</sub> .....	676	699	654	659	667	679	684	679	710	671	666	671	689	663	661	675	689	680	700	685	675
3. Between dorsal origins.....	163	170	154	135	151	152	153	179	164	160	147	150	163	159	137	147	156	157	155	142	152
4. Interdorsal space.....	139	148	134	109	132	122	131	154	..	130	125	..	137	..	107	119	..	..	..	..	124
5. D <sub>2</sub> origin to end, C.....	316	312	353	346	334	314	320	311	..	332	336	..	317	..	347	324	..	..	..	..	343
6. Tip D <sub>2</sub> to C margin.....	189	203	208	203	207	190	179	169	..	185	205	..	196	..	203	177	..	..	..	..	205
7. P <sub>1</sub> insertion to D <sub>1</sub> origin.....	281	283	285	299	289	300	326	294	341	317	268	285	280	275	295	286	290	259	315	291	267
8. Prepectoral length.....	253	262	237	220	245	245	223	224	218	215	259	247	261	249	264	263	255	252	252	266	262
9. Prepelvic length.....	599	613	584	590	583	614	615	611	620	600	603	603	653	595	578	601	628	589	621	612	582
10. D <sub>2</sub> origin to upper C origin.....	182	187	190	188	188	174	173	176	163	189	180	194	184	184	183	196	188	190	169	195	191
11. P <sub>2</sub> insertion to lower C origin.....	238	234	254	228	252	217	228	233	243	236	230	234	236	244	214	255	232	255	229	250	240
12. Between P <sub>1</sub> and P <sub>2</sub> insertions.....	348	346	344	370	355	379	406	389	..	404	330	..	364	..	319	359	..	..	..	..	343
13. Body depth (greatest).....	104	133	114	117	112	116	132	109	126	123	118	103	124	111	131	116	138	107	142	114	124
14. C peduncle depth (least).....	22	21	25	25	22	21	18	19	18	17+	29	21	25	20	23	21	21	19	20	21	29
15. Body width (greatest).....	120	122	102	104	108	117	119	108	101	109	121	112	128	104	123	109	126	117	116	110	116
16. C peduncle width at front C.....	23	20	29	22	22	22	20	..	16+	..	27	..	24	..	27	21	..	..	..	..	29
17. Length to 1st gill slit.....	199	201	193	191	187	189	168	171	158	159	211	190	197	188	211	201	190	191	191	192	209
18. Width between 1st gill slits.....	117	114	122	109	107	111	102	102	..	ca. 94	129	..	114	..	123	119	..	..	..	..	119
19. Snout length (preocular).....	71	68	66	67	66	63	56	58	..	49+	73	..	67	..	69	66	..	..	..	..	76
20. Snout length (preoral).....	103	107	108	95	106	102	89	91	77	87	106	100	105	94	112	106	108	99	103	92	124
21. Snout tip to nostril.....	36	37	44	38	33	34	30	30	(19)	23+	37	(22)	39	(20)	30	41	(28)	(22)	(27)	(22)	38
22. Nostril length (incl. pore).....	32	31	36	28	27	30	25	22	..	20+	31	..	34	..	32	27	..	..	..	..	34
23. Internarial width (least).....	26	23	29	24	22	21	23	21	21	19+	29	22	21	20	23	23	28	26	28	24	27
24. Between dorsal pores, nostrils.....	44	41	45	33	35	40	38	33	..	32+	45	..	45	..	39	42	..	..	..	..	48
25. Between tips of narial flaps.....	57	53	63	52	54	53	50	46	..	41	60	..	55	..	63	55	..	..	..	..	71
26. Nostril to orbit (least).....	37	33	42	30	32	33	28	30	..	28+	35	..	34	..	36	34	..	..	..	..	38
27. Nostril to mouth (least).....	73	73	80	68	72	72	63	67	..	63	79	..	71	..	78	71	..	..	..	..	88

30. Between ends, oral grooves...	101	97	103	87	94	92	90	81	..	72+	99	..	103	..	103	99	..	..	..	..	105
31. Orbit to end, oral groove.....	61	62	57	60	55	64	50	52	..	49+	64	..	63	..	61	61	..	..	..	..	57
32. Orbit notch to same end.....	58	59	50	55	48	60	46	44	..	48	61	..	58	..	53	58	..	..	..	..	52
33. Suborbital width (least).....	25	29	29	22	25	24	17	23	..	22	26	..	26	..	28	28	..	..	..	..	29
34. Orbit length (excl. notches)...	38	41	49	45	35	36	33	31	36	35+	44	38	39	40	50	40	45	42	43	39	46
35. Orbit length (incl. notches)...	47	46	51	52	45	46	45	40	..	41	47	..	55	..	56	50	..	..	..	..	57
36. Orbit height.....	36	33	36	27	25	30	28	24	..	21+	35	..	32	..	37	29	..	..	..	..	39
37. Interorbital width (fleshy)....	90	87	93	81	85	82	73	75	..	63+	96	..	88	..	96	89	..	..	..	..	105
38. Between orbits ventrally.....	71	72	77	71	70	68	62	57	..	50+	83	..	75	..	78	71	..	..	..	..	86
39. Interspiracular distance.....	71	70	73	65	68	69	60	61	..	54+	77	..	75	..	78	74	..	..	..	..	76
40. Postorbital notch to spiracle..	28	31	34	28	26	30	21	23	..	24+	33	..	30	..	31	27	..	..	..	..	36
41. Spiracle length.....	23	22	25	20	21	20	18	19	18	18	28	20	22	17	20	19	24	20	21	22	19
42. Spiracle width.....	11	10	13	15	9	13	13	9	..	14	14	..	10	..	15	11	..	..	..	..	14
43. Spiracle to end, oral groove...	37	34	37	36	36	38	29	32	..	28	42	..	43	..	42	38	..	..	..	..	43
44. Spiracle to P <sub>1</sub> insertion.....	107	120	114	98	115	110	100	102	..	94	123	..	119	..	116	113	..	..	..	..	107
45. Between gill slits 1 and 5.....	54	56	50	53	55	50	54	45	49	49	55	53	60	56	49	59	49	49	53	60	50
46. Length longest gill slit.....	12	11	14	10	13	16	13	10	..	12	12	..	16	..	17	12	..	..	..	..	14
47. Height of 1st gill slit.....	12	11	13	9	13	10	12	9	13	12	12	12	16	14	12	12	14	12	13	11	14
48. Height of 5th gill slit.....	12	10	11	13	9	8	13	10	11	8	12	9	10	9	13	10	10	12	12	9	14
49. D <sub>1</sub> base.....	22	25	22	27	21	29	25	21	(16)	25	28	(19)	24	(28)	28	27	(22)	(20)	(19)	(19)	27
50. D <sub>1</sub> origin to extreme tip.....	47	59	57	54	58	60	49	59	..	55	67	..	61	..	53	65	..	..	..	..	67
51. D <sub>1</sub> upper-posterior edge.....	18	27	32	25	20	31	30	18	..	31	38	..	26	..	33	27	..	..	..	..	33
52. D <sub>1</sub> lower-posterior edge.....	25	35	36	32	34	37	27	37	..	28	38	..	35	..	28	33	..	..	..	..	44
53. D <sub>1</sub> height.....	13	18	23	13	17	20	18	13	19	19	14	13	16	21	14	15	17	19	17	14	24
54. D <sub>2</sub> base.....	96	95	89	97	86	86	99	83	70	99	98	93	92	97	101	107	95	97	86	105	93
55. D <sub>2</sub> origin to extreme tip.....	135	103 <sup>a</sup>	143	133	127	130	136	136	..	128	136	..	137	..	143	139	..	..	..	..	138
56. D <sub>2</sub> upper edge.....	102	81 <sup>a</sup>	111	106	93	104	113	101	..	..	..	..	95	..	123	113	..	..	..	..	114
57. D <sub>2</sub> lower-posterior edge.....	40	21 <sup>a</sup>	44	46	39	50	39	49	..	39	42	..	46	..	41	43	..	..	..	..	55
58. D <sub>2</sub> height.....	18	18	26	13	20	20	15	15	16	..	21	19	21	15	14	18	16	19	17	20	24
59. C upper lobe (extreme).....	138	131	158	157	147	142	144	140	135	138	163	134	145	158	162	135	147	143	136	128	162
60. C lower lobe (extreme).....	118	104	129	119	117	120	113	103	106	115	128	113	119	129	136	119	116	112	112	112	138
61. C upper orig. to end urostyle..	118	118	151	141	143	129	120	118	..	120	147	..	126	..	147	124	..	..	..	..	143
62. Same, to margin (least).....	93	91	115	108	104	102	92	87	..	86	123	..	105	..	129	102	..	..	..	..	124
63. P <sub>1</sub> base (fin appressed).....	41	43	37	48	37	39	42	34	..	38	44	..	44	..	44	40	..	..	..	..	43
64. P <sub>1</sub> length (fin appressed).....	94	99	97	103	98	98	94	95	92	90	96	94	98	99	98	97	88	103	97	96	95
65. P <sub>1</sub> length to lower-rear tip....	99	100	93	88	102	101	100	90	..	94	95	..	108	..	85	99	..	..	..	..	90
66. P <sub>1</sub> posterior edge.....	73	92	57	78	84	85	73	82	..	88	71	..	89	..	89	83	..	..	..	..	76
67. P <sub>1</sub> extreme width.....	77	93	97	81	85	91	73	83	..	88	64	..	89	..	84	85	..	..	..	..	94
68. P <sub>1</sub> lower-posterior edge.....	63	66	64	72	70	71	54	60	..	64	71	..	79	..	57	68	..	..	..	..	64
69. P <sub>2</sub> base.....	53	48	61	59	52	68	59	49	..	68	47	..	53	..	57	47	..	..	..	..	58
70. P <sub>2</sub> length to outer-rear tip....	54	58	52	56	55	55	46	49	..	46	56	..	61	..	45	61	..	..	..	..	46
71. P <sub>2</sub> outer-posterior edge.....	65	63	82	47	57	72	73	51	..	72	56	..	54	..	65	55	..	..	..	..	62
72. P <sub>2</sub> inner-posterior edge.....	16	16	37	41	32	48	43	43	..	45	45	..	14	..	39	16	..	..	..	..	43
73. P <sub>2</sub> insertion to tip, rays.....	94	88	94	91	89	100	97	98	95	103	80	..	99	..	89	89	..	..	..	..	92
74. P <sub>2</sub> insertion to tip, clasper...	118	111	..	..	..	..	..	..	..	..	84	91	127	114	..	107	114	114	113	115	..
75. Genital pore to tip, clasper...	77	79	..	..	..	..	..	..	..	..	42	..	89	..	..	79	..	..	..	..	..

<sup>a</sup> Measurements for second dorsal fin were too low because fin had a rounded tip (injured?).



on each side and averaged (partly to eliminate extremes and partly to compensate for distortion on preservation).

Specifications for certain individual measurements, as made by us, follow in the sequence of numbered headings corresponding to those in the first column of table 3:

2, "Predorsal length, to  $D_2$ ," was computed by us by adding permillage values for item 1 (predorsal length to origin of first dorsal) and item 3 (distance between dorsal origins). Because the whole line is nearly straight, little error is thus involved.

5, " $D_2$  origin to end, C," was taken from extreme front of second dorsal base to farthest point of margin on upper caudal lobe.

6, "Tip  $D_2$  to C margin," from extreme upper-posterior rayed tip of second dorsal fin to farthest point on margin of upper caudal lobe.

13, "Body depth," and 15, "Body width," like other measurements, were made when specimen was manipulated to approximate its normal form in life.

19, "Snout length (preocular)," from front edge of orbit, excluding the anterior notch.

20, "Snout length (preoral)," from the front of the transverse mouth slit, in relaxed position.

21, "Snout tip to nostril," was taken by us from tip of snout on midline (as in other measurements from snout tip) to the definite outer end of the nostril. Since Parin's measurements are all smaller than ours, we assume that he took this measurement to the nearest point of the nostril margin.

24, "Between dorsal pores of nostrils," is the least interspace between the inner walls of the dorsolateral rounded opening in the narial slit.

28, "Mouth length (projection)," from front of mouth groove along mid-sagittal line to a straight edge laid between extreme ends of backward extending grooves of gape. Other measurements to ends of oral grooves were also to the extreme ends.

29, "Mouth width," was taken by us between outer margins of concealed lips.

45, "Between [fronts of] gill slits 1 and 5."

49, "Dorsal base," was taken by us between extreme limits, yielding values averaging higher than Parin's.

50 and 55,  $D_1$  and  $D_2$  "origin to extreme tip," were substituted for the much less precise measurement to upper anterior tip.

51, " $D_1$  upper-posterior edge," and 56, " $D_2$  upper edge," are highly variable, partly because the anterior point of measurement is indefinite.

52 and 57,  $D_1$  and  $D_2$  "lower posterior edge," are more definitive and less variable.

53 and 58,  $D_1$  and  $D_2$  "height," were taken by us, in an effort to match Parin's values, as the vertical height from the solid body to the margin of the fin in natural position, measured at a right angle to the margin of the body proper.

#### TREND OF PROPORTIONS WITH SIZE OF SHARK

By scanning the proportions in sequence of size of shark, giving consideration to possible sexual and areal differences, indications are obtained of either isometry or allometry. These indications were supplemented, for our measurements, by trial

graphs in which the values for the ocean regions and for the sexes were identified by distinctive symbols.

The one small specimen from the Atlantic Ocean (105 mm long) seems to be a bit extreme in many proportions, such as no. 20, snout length (preoral), and no. 25, between tips of narial flaps (table 3 and fig. 3); also in characters 7, 8, 14, 19, 22, 24, 27, 29, 30, 36-40, 43, 52, 57, 59, and 60 (shown in table 3 only). Most of the extreme

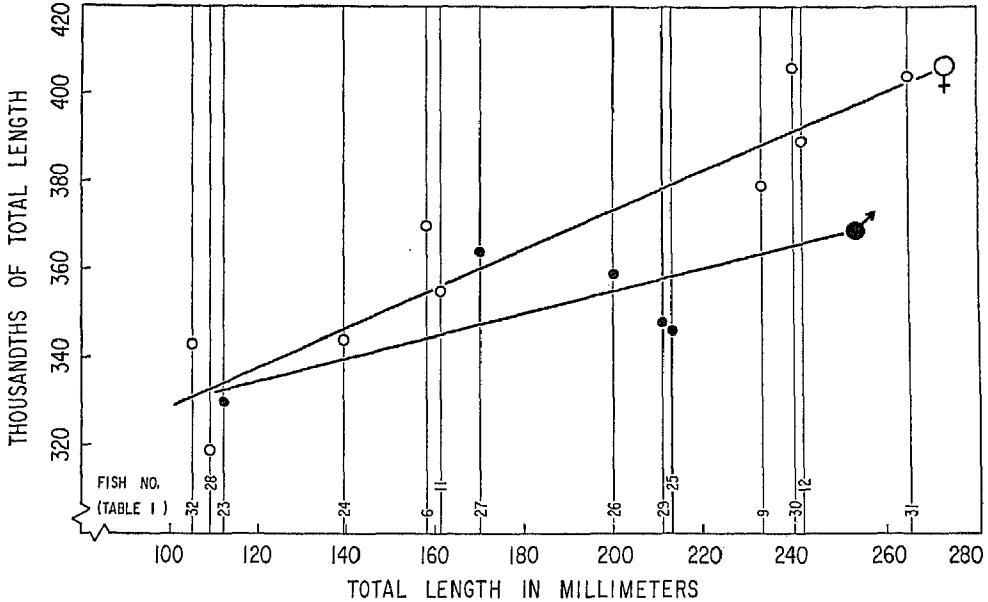


Fig. 1. Positive allometry of distance between insertions of paired fins (dimension 12, table 3) in *Euprotomicrus bispinatus*. Solid dots represent males; hollow dots, females. Lines fitted by eye.

proportions involve the large size of the anterior parts (larger than would be expected from the small size of this shark); a few of the higher than expected values are for fins. But the differences merely exaggerate the normal allometric changes and do not appear to be great enough to warrant taxonomic separation. No other suggestion was obtained of differentiation between major ocean areas. For this reason, all the material is treated as a unit in evaluating allometry and sexual differences in relative growth, which are now considered together.

With the one exception of the length of the abdomen—expressed by character 12, the distance between insertions of paired fins (fig. 1), and, less notably, by the prepelvic length (9), which involves the same part of the body—the growth pattern is isometric or negatively allometric. The females, as would be expected, as an adaptation to fecundity in a dwarfed shark, exhibit strong positive allometry in the length of the abdomen. The males seem to show some, but much less, positive allometry. Thorson, Watson, and Cowan (1966: 395) have indicated that females of a large shark, *Carcharhinus leucas* (Müller and Henle), have relatively longer abdomens than males, and such may well be a common characteristic of sharks. The slightly higher average number of monospondylous vertebrae, but lower average

number of diplospondylous vertebrae in "*Spinax niger*" = *Etmopterus spinax* (Linnaeus), as indicated by Punnett (1904: 318-320), may be related to this morphometric trend. Springer and Garrick (1964: 79), in referring to Punnett's biometric data, erred in stating that Punnett had indicated that the values for "half vertebrae" (diplospondylous units) as well as for "whole vertebrae" (monospondylous units) average higher in females than in males.

Since the abdomen becomes relatively longer with increased size of fish, either the preabdominal or the postabdominal region, or both, must in compensation become relatively shorter. Examination of the data shows that both the head and caudal region do grow with negative allometry.

All measurements of the caudal-fin region (fig. 2) show a progressive decrease in relative size of the parts, in both sexes. This is true not only of the essentially lengthwise measurements, but also of the caudal-peduncle depth and width (characters 14 and 16, table 3).

The anterior parts also grow with negative allometry, as may be seen for four selected characters in figure 3, and for all other head parts, without exception, in table 3. The negative allometry of dimension 17, length to first gill slit (top section of fig. 3), and for some other dimensions, is much stronger in females than in males; the impression given is that the expanded abdomen, more notable in females than in males, has displaced the gill region forward. The preoral snout length (character 20, second unit in fig. 3) shows similar relations, as do some other anterior parts. In other anterior parts, as the spiracle length (41, bottom unit of fig. 3), the sexes differ little, and in a few characters the negative allometry of the males is slight or even dubious. But, considering both sexes, every anterior dimension, of the many measured, becomes relatively smaller with increased size of fish.

Essential isometry is exhibited by body parts other than those of the abdominal, caudal, and cephalic regions. This applies to the predorsal and interdorsal measurements (1-4), pectoral insertion to origin of first dorsal (7), prepectoral length (8), second-dorsal origin to upper caudal origin (10), between pelvic insertion and lower caudal origin (11), body depth and width (13, 15), width between first gill slits (18), measurement of and between gill slits 1 and 5 (45-48), measurements of dorsal, pectoral, and pelvic fins (49-53, 63-75), except, of course, for the sexually modified parts of the pelvic fin.

#### PHOTOPHORES AND LUMINESCENCE OF *Euprotomicrus* AND OTHER SHARKS

Burckhardt (1900a, b) correctly interpreted numerous black specks on *Euprotomicrus Labordii* (= *E. bispinatus*) as luminous organs and figured their distribution on the lower half of the body. He dealt briefly also with minute photophores in other squaloid sharks, referred by him to the Spinacidae and Laemargidae (respectively equivalent to Squalinae, in part, and Dalatiinae). He mentioned observations on the luminescence of *Isistius brasiliensis* as early as that made by Bennett in 1840 (quoted in full by Garman, 1899: 39, by Fowler, 1941: 271, and by Parin, 1964: 169). Dickens (1956) observed strong luminescence in the specimen of *Euprotomicrus bispinatus* that he captured, and wrote: "Attention was first drawn to it by the presence of a greenish glow at a distance of 50 ft. [15 m], a luminosity which was later found to be a natural function, mainly on its underside." Stras-

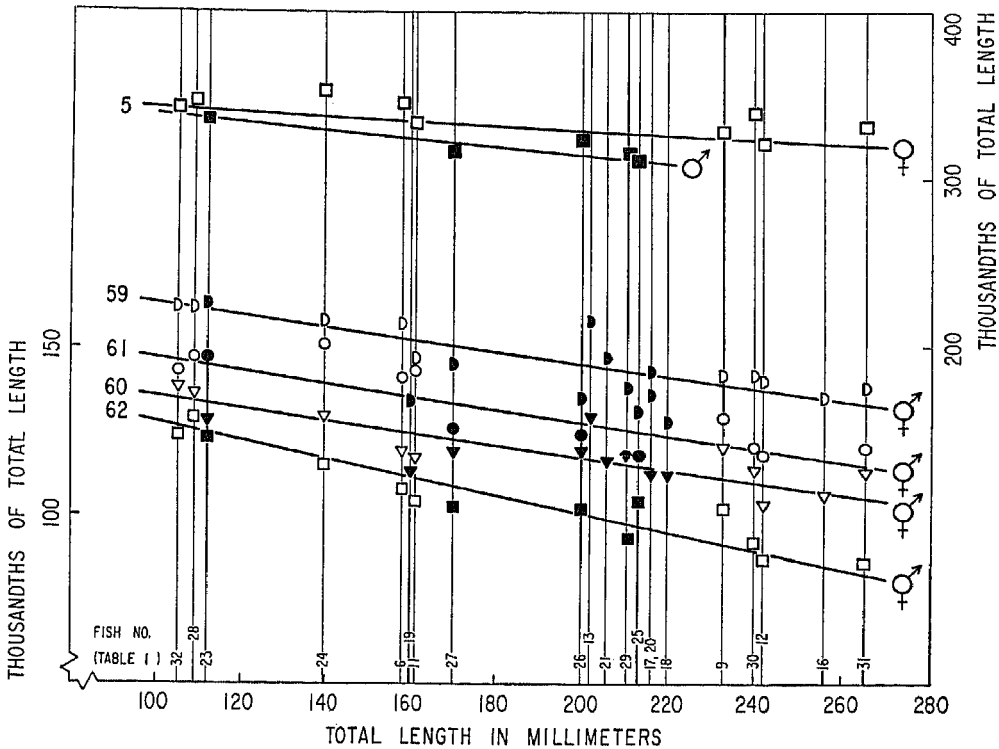


Fig. 2. Negative allometry of five dimensions of caudal fin in *Euprotomicrus bispinatus*. Solid symbols represent males; hollow symbols, females. Lines fitted by eye. From top, five dimensions (numbered at left), as entered in table 3, are graphed: 5, upper squares, origin of second dorsal fin to end of caudal fin; scale on right margin (scale on left margin applies to other dimensions); 59, half-circles, extreme length of upper caudal lobe; 61, circles, upper caudal origin to end of urostyle; 60, triangles, extreme length of lower caudal lobe; 62, lower squares, upper origin to nearest point on caudal margin.

burg (1963: 35) stated that one *Isistius* "emitted a light-blue glow." Parin (1964: 170), after quoting Bennett, gave a field note from the journal of the R/V *Vitiaz*, which reported that a specimen of *I. brasiliensis* radiated a slight greenish luminescence, which faded at times. Parin (p. 176) referred to Dickens' observation and quoted, from field journals of the same ship, observations on the luminescence of three specimens of *E. bispinatus*, indicating that the entire ventral surface and the lower borders of the sides radiated a pale-greenish light, at first on irritation and on sudden movements of the shark, then becoming constant before and for some time after death.

Burckhardt (1900a, b), probably overgeneralizing, thought that all Dalatiinae (his Laemargidae) have luminous organs. They have been described in several squaloid sharks, and luminescence has been observed in some of them.

It is clear from observations on bioluminescence in *Euprotomicrus*, *Isistius*, and certain other squaloid sharks that functional luminous organs occur, chiefly on the ventral surface. The photophores are obviously the thousands of minute bodies that appear under the binocular microscope as black dots, mainly on the lower parts.

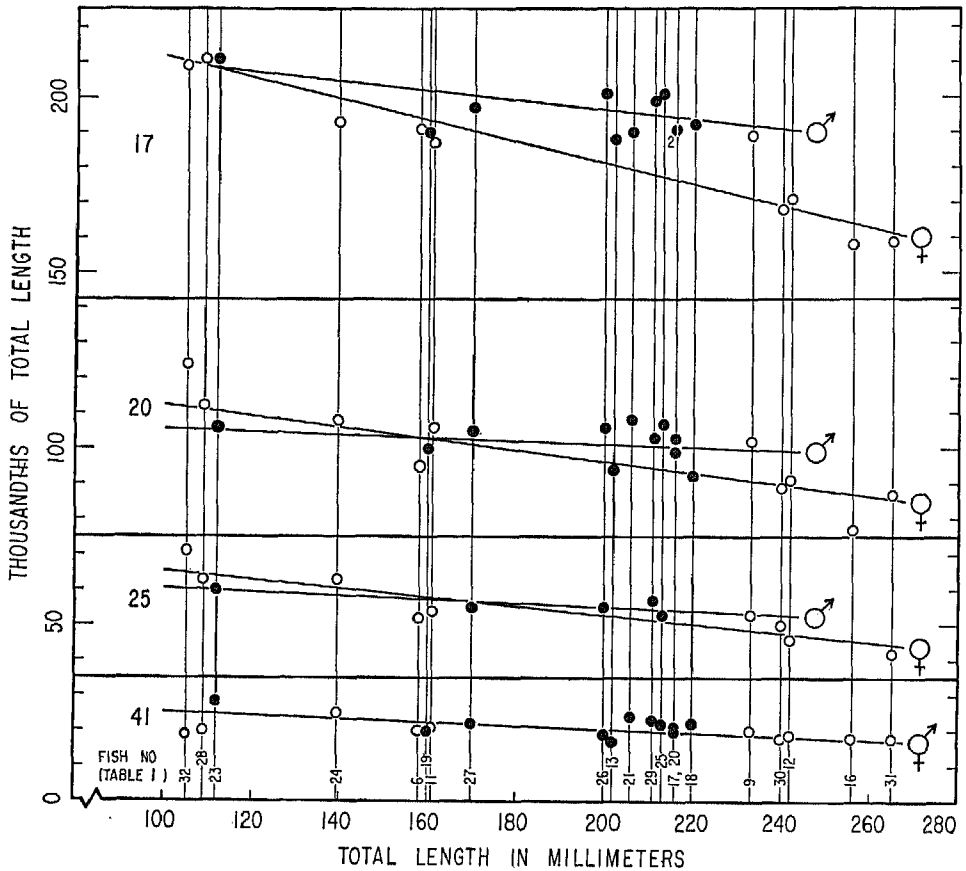


Fig. 3. Negative allometry of *Euprotomicrus bispinatus* in four dimensions. Numbers at left refer to the dimensions, as entered in table 3: 17, length to first gill slit (= head length); 20, preoral length of snout; 25, distance between tips of narial flap of each side; 41, length of spiracle. Solid dots represent males; hollow dots, females. Lines fitted by eye.

Inasmuch as neither Burckhardt nor any other author has described in detail the photophores of *Euprotomicrus* or *Isistius*, and inasmuch as the descriptions of the luminous organs in other sharks have left much to be desired, these structures have been studied by us in a specimen of *E. bispinatus* (no. 24, table 1), and, for comparison, in two specimens of *Etmopterus lucifer* Jordan and Snyder, 157 and 210 mm in total length, and in three specimens of *Centroscyllium ritteri* Jordan and Fowler, 142 to 216 mm long.

Although Burckhardt (1900) and Parin (1964) indicated that the photophores of the various luminescent sharks are very similar in structure, we distinguish two types. The only type heretofore described (by Johann, 1899, Burckhardt, 1900b, Dahlgren and Kepner, 1908, Ohshima, 1911, Iwai, 1960, and others), is characterized by an iris-like structure, formed of dendritic pigment cells capable of covering a group of several photogenic cells. These structures, along with the lens cells and pigment sheath, are not consolidated into compact units, but rather are separated

in the epidermal layer. Such organs are scattered at random in various sharks referable to the subfamily Squalinae, for example *Etmopterus lucifer*, *E. frontimaculatus* Pietschmann, *Centroscyllium ritteri*, *C. granulatum* Günther, and *C. fabricii* Reinhardt.

In contrast, the photophores of *Euprotomicrus bispinatus* form a complicated network, and each is more compact, lacks an iris-like structure, and contains a single photogenic cell. In the main differential features, the type heretofore recognized seems to be the more specialized in respect to the development of the iris-like structure, but the more generalized in other respects. Thus, each type seems to combine specialized and generalized features (which seems to be a very general rule). The distinctness of the types suggests that bioluminescence has evolved independently at least twice in sharks, as it has, repeatedly, in teleosts and in other animals.

We now proceed with a more detailed account of the photophores, first in *Euprotomicrus*, and then in other sharks.

#### PHOTOPHORES OF EUPROTOMICRUS BISPINATUS

In this dwarf pelagic shark the very numerous minute light organs form a rather uniform network over the entire venter and lower sides of body and head (pl. 2, fig. 2; pl. 3, A-C; fig. 4, A; Burckhardt, 1900b: fig. 6). The upper fringe of the eyes, the basal parts of the paired fins, and the posterior tip of the caudal axis bear similar photophores. Each unit of the network is a roughly V-shaped aggregation of photophores paralleling the two posterior oblique sides of each denticle. Where they are densely distributed, as on the belly, more than 25 make up each single V-shaped cluster, and no fewer than 60 may be seen in an area of 1 mm<sup>2</sup>. Each organ is so tiny, about 50 to 90  $\mu$  in diameter, as to be scarcely visible to the unaided eye. The smallest ones are not much larger than an erythrocyte. Under low magnification, each organ appears as a black spot, representing the underlying black sheath.

As is usual among free-moving luminescent animals, the light is directed almost entirely downward. In this species, no luminous organs can be seen on the dorsal surface, and the luminescent area in the trunk region scarcely reaches to the lateral line, or, on the head, to the line from eye to gill openings. Aleev (1963: 24), quoted by Parin (1964: 126), having heard from Andriashev that the ventral side of the body is luminescent, theorized that because the body in *Euprotomicrus* is ventrally flattened for buoyancy (and would thus tend to form a shadow), "the liquidation of the treacherous shadow is, in this case, achieved by a special illumination of the ventral side of the body" (our translation). In view of the considerable depth range of the species, and recalling that Dickens (1956) could see the reflection of the luminescence at 15m, this explanation seems farfetched, though it could be cited as a special case of the general theory advanced by Clarke (1963).

The minute luminous organs of *Euprotomicrus* are enclosed in the epidermis, which is composed of stratified squamous epithelium. Each photophore is spherical and comprises three main elements (pl. 3, D): (1) a single photogenic cell (*ph*), (2) a black sheet of pigment (*ps*) closely embracing the pigment cell ventrally and laterally, and (3) a lens (*l*) made up of a group of small cells overlying the

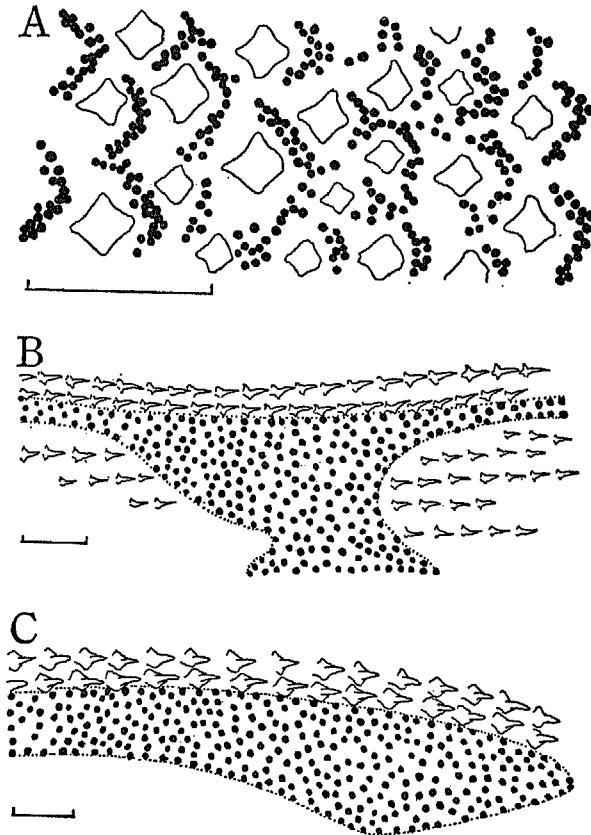


Fig. 4. Arrangement of photophores on ventrolateral part of flank in three luminescent sharks. A, *Euprotomicrus bispinatus*; B, *Etmopterus lucifer*; C, *Centroscyllium ritteri*. Black spots represent photophores. Each scale bar indicates 1 mm.

apical surface of the photogenic cell. Each photogenic cell characteristically contains in the basal part many granules, presumably photogenic, and a large deeply staining mass that seems to be the acidophilic secretion. The large nucleus of the light-producing cell usually lies near the apical margin. Photogenesis seems to be intracellular. Except over the median area of the broadly convex apical border of the photophore, the photogenic cell is surrounded by a cup-shaped sheath of black pigment cells. No iris-like structure of dendritic pigment is discernible. The cells making up the lens contain homogeneous cytoplasm. In external view, in preserved specimens, the lens is seen under due magnification as a white dot surrounded by a black ring. In life, it is presumably transparent.

The photophores of *Euprotomicrus bispinatus* resemble in general features those of *Isistius brasiliensis*, but differ notably from those of *Etmopterus lucifer* and *Centroscyllium ritteri*, both in arrangement and in structure. In the specimen of *I. brasiliensis* from 13°46.0' S., 81°52.0' W. (FAKU 39108), the photophores measure about 60 to 85  $\mu$  in diameter.

## PHOTOPHORES OF ETMOPTERUS AND CENTROSCYLLIUM

In *Etmopterus lucifer* and *Centroscyllium ritteri* the light organs are very irregularly distributed. They are densely concentrated on the ventral surface of the body, where there are no fewer than 12/mm<sup>2</sup>. In these species some isolated organs are scattered along the dorsal side (pl. 3, *E-G*). The photophores are particularly dense over the inky-black areas of the body. In *E. lucifer* these areas are on the ventral surface of the body, in a T-shaped pattern on the flank (pl. 3, *E*; fig. 4, *B*), and in dashlike markings on the caudal peduncle and caudal fin. In *C. ritteri* the black areas are on the basal parts of the paired fins, in longitudinal bands on the two sides of the interspace between the paired fins, in a slender mark on the flank (pl. 3, *G*; fig. 4, *C*), and as a small spot on the posteroventral corner of the caudal peduncle. In this species the photophores are not uniformly distributed, even on the black markings; they are irregularly disposed along the outer sides of the marking on the flank and along the median sides in the ventral bands. Though small, about 100 to 150  $\mu$  in diameter, the photophores in the species of *Etmopterus* and *Centroscyllium* examined are somewhat larger than those of *Euprotomicrus bispinatus*.

The photophores of *Etmopterus lucifer* and *Centroscyllium ritteri* differ from those of *Euprotomicrus bispinatus* also in detailed structure. In those species each organ is an irregularly hemispherical cup composed of four elements: (1) a group of photogenic cells, (2) an iris-like structure formed by dendritic pigment cells, (3) a peripheral cluster of 2 or 3 lens cells, and (4) a pigment sheath directly underlying the mass of photogenic cells. Generally there are 6 to 13 photogenic cells in the bottom of the organ. These cells contain eosinophil secretion. Photogenesis therefore appears to be intracellular. Along the outer surface of the photogenic-cell mass crowded chromatophores extend dendritic processes toward the apex of the luminous complex. It is assumed that by dispersion and contraction this group of pigment-filled cells serves as an iris to regulate the amount of light emitted from the photogenic cells. The lens cells are filled with a homogeneous structure, and the nucleus of each is displaced to the base of its cell.

The type of photophore just described characterizes certain luminescent sharks of the subfamily Squalinae (according to the classification adopted by Hubbs and McHugh, 1951, and by Bigelow and Schroeder, 1957), and these sharks all appear from collection data to be essentially benthonic. In contrast, the other type described above is characteristic of *Euprotomicrus* and *Isistius*, of the subfamily Dalatiinae, and these genera are the only luminescent sharks that are definitely pelagic. Parin (1964: 177) erred, we believe, in his statement that luminescent organs among sharks occur only in bathypelagic species.

## ALLEGED PHOTOPHORES OF SOMNIOSUS

A third type of photophore was described by Burekhardt (1900b) for the sleeper sharks *Laemargus borealis* and *L. rostratus* (*Somniosus microcephalus* (Bloch and Schneider) and *Somniosus rostratus* (Risso) in current usage), but we disbelieve the function unreservedly attributed to these structures by Burekhardt. The organs do not closely resemble structures known to be luminescent in other



fishes, and they occupy incongruous positions for light-giving organs—along the lateral line and on the anterior dorsum. The evidence of luminescence in the sleeper sharks seems to be solely that provided by Burckhardt for specimens of *S.rostratus* which had been collected for him at the Naples Zoological Station. He “was greatly struck at the time by the splendour of the spectral colors that these fishes exhibited.” He was induced by this display to prepare a colored sketch. “A later scrutiny of this sketch convinced me of the fact that I had been able to observe the phosphorescence of these organs by daylight, so strong was their luminous power”: all the more remarkable, since the sharks had apparently died during the preceding night! Despite these more than dubious circumstances, Burckhardt’s claim of luminosity for this shark and his identification of certain dermal structures as photophores have been accepted by later authors, including Tortonese (1956: 188), Bigelow and Schroeder (1957: 117), and, with some apparent reservation, by Parin (1964: 177). Bigelow and Schroeder (1957: 120), however, could detect nothing suggestive of luminescent organs on *Somniosus microcephalus*.

#### DENTICLES

The dimorphic denticles of *Euprotomicrus bispinatus* were described in some detail by Hubbs and McHugh (1951), whose account is now supplemented by several figures (pl. 1, fig. 3; pl. 2; pl. 3, A-C; fig. 4, A). The pits at the four corners of the large denticles may be lacking, or extra ones may be interpolated (pl. 1, fig. 3). Parin’s (1964) figure 3 does not portray pits, but they appear to be a normal feature of the large denticles. Deviations from a regularly quadrate form of the denticles are frequent.

Concerning the denticles on USNM 164176 (our specimen 11, table 1), Bigelow and Schroeder (1957: 127) stated: “We have detected the smaller denticles alone on the specimen we have seen, and only a few of these, here and there. Seemingly its skin has been largely denuded of its armature.” On the contrary, the investment is complete and normal, as is indeed shown in their photograph (pl. 4, lower fig.). The authors were apparently misled in comparing the integument of *Euprotomicrus* with that of *Squaliolus*, which has much coarser denticles.

There are several differences between *Euprotomicrus bispinatus* and *Isistius brasiliensis* in the form of the denticles. Those of *Isistius*, essentially as figured by Bigelow and Schroeder (1948: fig. 98, C), but not quite so regular, are quadrate and deeply pitted medially with raised points at the corners of the surrounding ridge. They vary considerably, but are not definitely dimorphic, either in size or structure. The photophores, numerous on the lower parts and scarce above, generally lie between the denticles, in naked channels that are much narrower than in *Euprotomicrus*, as shown in our plate 1, figure 3, and in Parin’s (1964) figure 3. *Euprotomicrus bispinatus* and *Isistius brasiliensis* differ further in the distribution of denticles on the clasper (table 3, p. 36; fig. 7).

#### DENTITION

*Euprotomicrus*, along with other genera of the Dalatiinae (the Dalatiidae of some authors), agrees with certain other sharks of the family Squalidae (in the broad

sense, equivalent to the suborder Squaloidea of certain authors), in the trenchantly different structure of the teeth in the two jaws (Bigelow and Schroeder, 1948: 449-532; Hubbs and McHugh, 1951: 164-167, fig. 1). The raptorial teeth of the upper jaw are narrowly triangular, needle-pointed, multiserial in function, and, as an extreme feature of this one genus, arranged in quincunx in a subtriangular patch. In strong contrast, the sectorial teeth of the lower jaw are flat, subquadrate platelets, with triangular points strongly deflected laterally. Only the median tooth is erect. In one specimen, among the 14 examined by us for dentition, the median tooth of the series being replaced has an oblique tip—deflected toward the right—but less sharply than the lateral teeth; furthermore, the median tooth in the replacement band is erect. The median teeth in the replacement series, as in specimen 24 (pl. 4, fig. 1), may, however, be deflected to one side. The free edges of the lower teeth are closely aligned to form a single cutting edge, along a gentle arc. The outermost lower tooth of each side is a broad keel with only a trace of the triangular tip (as shown for *Isistius brasiliensis* by Bigelow and Schroeder, 1948: fig. 99 on p. 510).

This whole structure is admirably fitted for securing food. The upper teeth can hold the small prey effectively, while lateral back-and-forth movements of the lower jaw bring the cutting mechanism into play. A relatively sizable ingested lanternfish with the urosome cleanly sheared off (p. 51) bespeaks the efficiency of the dental apparatus.

The two-shouldered median tooth of each series in the lower jaw alone overlaps the next one on either side (pl. 4, fig. 1), as shown for *Isistius brasiliensis* by Bigelow and Schroeder (*op. cit.*). A prominent distolateral shoulder on each of the other lower teeth overlaps the next tooth laterad (pl. 4, fig. 2). The lower teeth are all so flat that the overlap is appreciable with difficulty. In specimen 29 a tooth 2.75 mm high is only 0.40 mm thick. Each root is completely exposed on the outer face, but the inner face adheres closely to the lower jaw. The base is deeply pitted medially. The lower teeth are firmly interlocked by a peg (the "shoulder" mentioned above)-and-socket arrangement: a point not duly stressed in discussions, as by Bigelow and Schroeder (1948: 65-66, fig. 7), and by Strasburg (1963: 35-37, figs. 2-4), of the replacement of the teeth of this uniserial, flat, basally subquadrate structure. In the structure and arrangement of the mandibular teeth *Euprotomicrus* closely resembles *Dalatias licha* (Bonnaterre) (James, 1953: 425, pl. 2). The type of juxtaposition or of overlap, which was particularly stressed by Strasburg, is really of no great significance for teeth of such structure: the sequence of replacement of the individual teeth is immaterial because it has been shown that when the next band has come into use the old, still interlocked single ribbon-like band moves, out of service, downward on the outer face of the essentially transverse lower jaw until the whole unit flakes off. (Pl. 4, fig. 2 shows, still interlocked, the first 8 left lower teeth that had been, a bit prematurely, flicked off the outer face of the mandible of specimen 29.) Bigelow and Schroeder assumed that these teeth, which form a single cutting edge, are simultaneously replaced, because they had never seen gaps in the row being replaced. In dealing with *Isistius brasiliensis*, Strasburg agreed on the same basis and also, more pointedly, because

he found in the stomachs of the shark, teeth of the same species, including what he regarded, properly we believe, to be the entire set of lower teeth that the same individual had recently lost through tooth replacement (p. 52).

Two of the 14 specimens of *Euprotomicrus* studied by us for food were caught in the act of tooth replacement, much as was a specimen of *Isistius* illustrated by Strasburg (1963: fig. 3). The replacement teeth are the larger, but no effort was made to compute, from the differential size of the teeth in the two series, and from the size relation between teeth and fish, the number of tooth replacements in the life span of the shark, as Strasburg (1963: 37, fig. 4) had done for *Isistius*. The overall length of the third tooth from the median one on the right side measures, respectively for the tooth being replaced and for the one newly in service, 2.00 and 2.60 mm in a 161-mm fish (no. 11), and 2.44 and 2.75 mm in one (no. 29) of 211 mm. As for *Isistius brasiliensis* (Strasburg, 1963: 37, fig. 4) the differential size is the greater in the smaller specimen. This size relationship appears to hold also in a longitudinal section (pl. 4, fig. 3) of a 139.5-mm specimen (24).

The transverse rows of replacement teeth are also regularly aligned (pls. 3 and 7, b), as in *Isistius* (pl. 7, a). A sharp radiograph of a 211-mm specimen (29) of *Euprotomicrus bispinatus* (pl. 7, b) shows only two replacement rows plus a third incipient row, on the left side only, whereas a similar radiograph of a 386-mm *Isistius brasiliensis* (pl. 7, a) shows four full rows. However, a 139.5-mm specimen (24) of *Euprotomicrus* shows four rows in surface view (pl. 4, fig. 1) and four rows plus a tooth bud in longitudinal section (pl. 4, fig. 3). Perhaps the number of replacement rows decreases with age. In the longitudinal section the angle between the functional tooth and the first replacement tooth is about  $150^\circ$ . The tooth therefore rotates through a very wide angle. The longitudinal fibers connecting the erupted tooth with its successor are recognizable. The arrangement closely resembles that described for *Dalatias licha* by James (1953: 436, pl. 2).

This longitudinal section illustrates the successive stages of odontogenesis, the elaboration of the dentine, the pulp cavities, and the relation of the mandibular teeth, in the series of replacement ribbons, to the soft tissues and to Meckel's cartilage.

In 14 specimens of *Euprotomicrus* we find the total number of lower teeth to vary from 19 to 23 (table 4), with mean of 21.36. The frequencies of left-right formulas, omitting the constantly present median tooth, are 9—9 (2), 10—9 (1), 10—10 (3), 10—11 (1), 11—10 (5), 11—11 (2). The numbers are bilaterally asymmetrical in 50 percent of the 14 specimens, with the count 1 higher on the left side in 6, 1 higher on the right side in only 1. This discrepancy is surprising, but is probably to be attributed to the small size of the sample.

The relation between total mandibular tooth count and size of fish in the 14 specimens counted is as follows:

<i>Tooth count</i>	<i>Total lengths (mm)</i>
19	105, 139.5
20	213
21	161, 170, 211
22	109, 112, 158, 200, 233, 240
23	242, 265

The fact that 2 of the 4 smallest specimens have the lowest count and that the 2 largest have the highest count might be cited as agreeing with the qualified suggestion for *Isistius brasiliensis* by Garman (1899: 41), and the unqualified assertion for the same species by Bigelow and Schroeder (1948: 511), that the lowers increase in number with growth. The second- and third-smallest sharks, however, have next to the highest count. Strasburg, furthermore, by comparing the number of lower teeth in the functional and replacement dentitions of the same species found that for sharks of total length 237 to 462 mm: "The number of teeth was constant for all dentitions of a particular shark, discrediting the idea that there is an increase in number with growth. Instead, one would deduce a loss with growth,

TABLE 4  
VARIATION IN TOTAL MANDIBULAR TOOTH COUNT OF *Euprotomicrus bispinatus*  
(By major ocean areas)

Major ocean area	Mandibular tooth count				
	19	20	21	22	23
North Pacific Ocean.....	1	1	2	3	2
South Pacific Ocean.....	..	..	1	2	..
Indian Ocean.....	..	..	..	1	..
Atlantic Ocean.....	1	..	..	..	..
Total.....	2	1	3	6	2

for the ratios of total length to tooth count in these sharks are 237/31, 249/31, 292/30, 382/29, 383/29, 446/29, and 462/30. This small sample shows a decline in tooth number with increase in length."

Inasmuch as the outermost tooth of each side in both genera is distinctly specialized in all specimens, it is difficult to understand how the total number may change with age. The published indications of increasing numbers appear to be false, and to be attributable to individual variation and to the small size of the samples.

There is a slight indication (table 4) of areal differentiation in tooth numbers, but we have only a single count each for the Indian and Atlantic oceans, and both come within the range for the Pacific. Between the North Pacific and South Pacific samples there is no evidence of a difference in total number.

The 386-mm specimen of *I. brasiliensis* (SIO 52-413-5A) at hand from the equatorial Pacific has the following tooth formula:

$$\frac{15 + 1 + 15}{14 + 1 + 14} = \frac{31}{29}$$

#### INTERNAL CHARACTERS

A major feature of this investigation has been the discovery that *Euprotomicrus bispinatus* and *Isistius brasiliensis* differ trenchantly in many visceral and skeletal structures. Obviously, the two genera have diverged long and far, and must differ in functions as well as in structure.

TABLE 5

CONTRASTING VISCERAL CHARACTERS IN *Euprotomicrus bispinatus* AND *Istiatius brasiliensis*<sup>a</sup>

Visceral character	<i>Euprotomicrus bispinatus</i> (fig. 5)	<i>Istiatius brasiliensis</i> (fig. 6)
Gastrointestinal tract, general form	Compressed S-shaped	Two straight segments with very short connection
Front end, valvular intestine	Continuous anteroposteriorly with duodenum	A blind sac in advance of duodenal valve
Anterior part (nearly half) of cardiac part of stomach	Free of body wall; largely embraced by liver	Firmly attached to dorsal wall of body cavity
Stomach	J-shaped	Simple tube
Pyloric part of stomach	Well developed	Lacking
Duodenum	Compressed U-shaped	Short, straight tube
Spiral valve	13 narrow turns	8 broader turns
Right arm of spleen	Much elongated	Scarcely produced
Liver	About half mass of rest of viscera	Several times mass of rest of viscera
Liver occupying	Less than half length of body cavity	Nearly full length of body cavity
Anterior end of liver	Truncate	Pointed, conical
Lobes of liver	Each a weakly spiral coil, not coiled together; barely overlapping gut anteriorly; united only at extreme anterior end	Coiled together and against body wall; almost completely encompassing gut; united ventrally, save for deep crease, along anterior half
Point of discharge of bile duct	Anterior bend of duodenum	Anterior tip of blind extension of valvular intestine
Oil in body cavity and often in gut	Hardly evident	Generally profuse
Testes in	Anterior half of body cavity	Largely in posterior part of body cavity

<sup>a</sup> For differential proportional dimensions see table 6.

TABLE 6  
 DIMENSIONS OF PARTS OF VISCERA<sup>a</sup>  
 (In percent of length of main body cavity)

Visceral part	<i>Euprotomicrus bispinatus</i>	<i>Isistius brasiliensis</i>
Gastrointestinal tract (within body cavity)		
Length to outer edge first bend.....	68	62
Length antrorse segment <sup>b</sup> .....	38	11
Posterior straight section (total).....	71	48
Before valvular intestine <sup>c</sup> .....	24	6
Valvular intestine <sup>d</sup> .....	24	32
Behind valvular intestine.....	22	13
Length of rectal gland.....	13	6
Length of spleen (midline).....	10	5
Liver		
Length left lobe.....	37	93
Length right lobe.....	45	89
Length ventral junction.....	8	44
Greatest overall width.....	24	17
Width at end, first 5 percent.....	21	4
Length, right testis.....	33	34
Length, main part, sperm sac.....	32	23

<sup>a</sup> Measurements taken from figs. 5, 6.

<sup>b</sup> In *Euprotomicrus* from outer edges of bends involving pyloric section of stomach and first (antrorse) section of duodenum; in *Isistius* from outer edge of first bend to insertion in valvular intestine.

<sup>c</sup> Including duodenal valve.

<sup>d</sup> Measured from duodenal valve.

VISCERAL ANATOMY OF *EUPROTOMICRUS BISPINATUS*  
 DESCRIBED, AND COMPARED WITH THAT OF *ISISTIUS BRASILIENSIS*

Very brief accounts of the visceral anatomy, based on specimens apparently not well preserved internally, have been given, without illustrations, for *Euprotomicrus* by Cunningham (1899) and for *Isistius* by Strasburg (1963: 35). These accounts, so far as they go, correspond with our observations.

The viscera provide some of the most trenchant characters of *Euprotomicrus bispinatus*, at least in contrast with those of the supposedly very closely related, somewhat less dwarfed *Isistius brasiliensis* (Quoy and Gaimard, 1824: 198). These differences involve the fundamental structural plan (table 5), as well as the proportional size of the parts (table 6). This is especially surprising in view of the similar ranges, habitats, and food of the two species. The differences in the viscera seem even more striking than those in the claspers (p. 34). It is trusted that those ichthyologists who seem preoccupied in lumping genera will keep in mind such fundamental differences, which so obviously indicate prolonged and profound separation.

The following description and comparisons and figures 5 and 6 are respectively based primarily on specimen 29 of *Euprotomicrus bispinatus* (table 1), an adult male 211 mm in total length from the northeastern Pacific, and on an adult male of *Isistius brasiliensis* 386 mm long (SIO 52-413-5A) from the equator at 100° 00' W. Most of the characters for *Euprotomicrus* were checked for at least approx-

imate agreement on the other available adult males, but no comparative material of the *Isistius* was used. Except in gonad structure the females of *Euprotomicrus* were found to agree with the males.

The short *esophagus* of *Euprotomicrus* has thick, muscular walls, the lining of which is raised into nine strong, even, regularly parallel, longitudinal folds.

The *stomach*, also thick-walled, is deflected somewhat to the left side (and is drawn farther deflected in that direction, which is shown to the right, in fig. 5). It passes through a rather narrow collar of the liver near its forward end. It is underlaid for about one-third the length of its cardiac part by the right lobe of the liver, but for only about one-tenth that length by the left lobe. On its right side the stomach fits into a shallow groove on the subvertical inner face of the right lobe of the liver; the thin left lobe of the liver spirals along the dorsal surface of the stomach. The stomach is J-shaped, with the closely appressed lesser (pyloric) arm only about one-fourth as long as the longer (cardiac) arm. In normal position the longer arm lies largely below the shorter. The mucosa of the stomach is elevated in low, thin, irregularly kinked, longitudinal folds. In a section of the stomach the muscular coat is abruptly thickened in the pyloric region.

The antrorse segment of the enteron extends over somewhat more than the middle third of the body cavity. Somewhat less than half of this length comprises the pyloric section of the stomach, which is separated from the *duodenum* by the thick, muscular pyloric valve, which greatly constricts the lumen. The duodenum describes a compressed U, with arms of subequal length. Superficially, the proximal arm of the duodenum is a direct continuation of the pyloric arm of the stomach, but the intervening valve is usually discernible externally. The rather thin walls of the duodenum bear villous mucosa, which contrasts sharply and abruptly with the folds of the stomach. The bend of the duodenum is about opposite the groove separating the left and right lobes of the liver. The proximal section is closely appressed against the cardiac part of the stomach; the distal segment fits for about half its length into a groove along the inner-posterior edge of the right lobe of the liver.

The duodenal and the valvular divisions of the intestine are separated by the thick, muscular duodenal valve, which is more or less discernible externally, just posterior to the pyloric valve. The gut is constricted just behind this duodenal valve, but then expands considerably in the *valvular intestine*. The 13 tight coils of the spiral valve, which occupy about half the length of the gut behind the duodenal valve, nearly occlude the central lumen, which, however, is continuous, as in a spiral staircase. The mucosal lining is villous.

Toward the *colon* the intestine tapers considerably. The firm and conspicuous *rectal gland* extends forward from the dorsal side of the rectum, not far in advance of the *cloaca*, in which the *urogenital papilla* is conspicuous.

The *liver* comprises two thin, short, somewhat spirally curved lobes, which are connected medially by less than one-fifth of their length and by less than one-tenth the length of the body cavity. The right lobe is much the more massive, and occupies about four-fifths of the limited face of the liver that is exposed in ventral view (as in the figure). Topologic relations of liver and enteron are mentioned

above. Some proportional measurements of the liver are listed in table 6. The *gall bladder* occupies the rounded medioventral finger of the left lobe of the liver. The *bile duct* arises on the inner face of the right lobe of the liver at the ventral edge of the groove into which the stomach fits; from here it extends backward and slightly to the left to connect with the front end of the second gastrointestinal bend.

The dark *spleen* is a dorsoventrally depressed, ventrally flattened, triangular bident, which embraces the abrupt turn of the stomach. The rather sharp left horn is confined to the bend, but the right horn extends along the right edge of the pyloric part of the stomach approximately to (sometimes not quite to) the pyloric valve. In one specimen (9) the anterior end of this long arm is broken up into several flattened lobes. The long arm varies considerably in thickness.

The *pancreas*, cream-colored in preservative, appears in ventral view as a flattened, oval mass (doubled in the specimen figured), cuddled in the axil of the second bend of the gut. From this exposed lobe a compressed band extends dorsally, pinched between the tightly appressed arms of the duodenum. On the dorsal side of these appressed arms the pancreas expands into a narrow band that extends forward a short distance and backward along the entire length of the antrorse (reversed) arm of the gut. (This section of the pancreas is very fragile and subject to destruction, and may not always develop fully.) The pancreas was not found in the specimen of *Isistius* particularly studied, but was located in the other example studied (FAKU 39108, see p. 9) and is entered on the drawing; the position, in relation to duodenum and to spleen, is similar to that observed in *Euprotomicrus*.

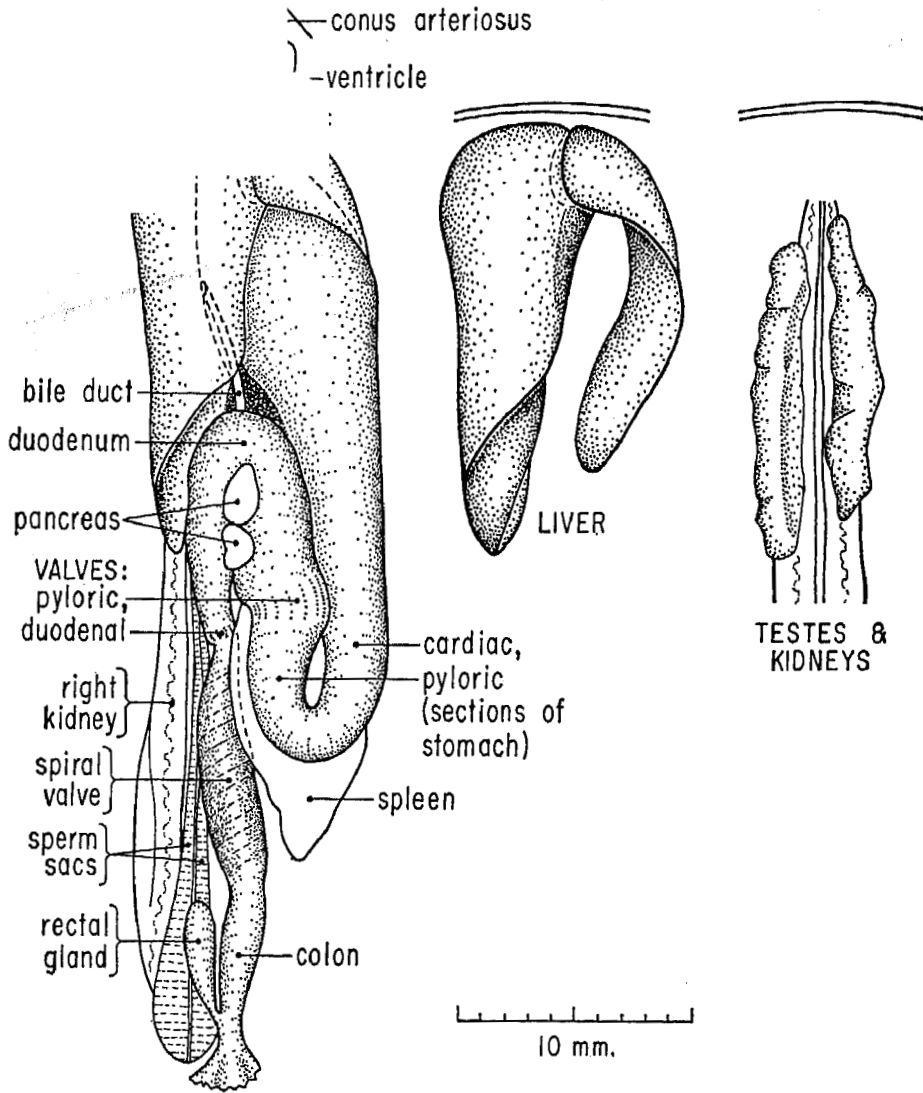
In all mature males examined the right *testis* is well developed, as a band lying against the ventral surface of the kidney, along much of the anterior half of the body cavity. In the specimen (29) illustrated in figure 5, the left testis is nearly as large as the right testis, but lies a little farther forward (as does the ovary in this species). In other males, however, the left testis seems to be much the smaller, and in one, the left testis seems to be replaced by the kinked end of the right testis. However, preservation of the testes was imperfect.

The *ovaries* are described in the section on eggs and embryos (pp. 34-37). In specimen 9, a female 233 mm in total length with ova not yet fully elaborated, the oviducts are large, symmetrically paired bands running forward between kidneys and ovaries almost to the front end of the body cavity.

#### VERTEBRAL COLUMN

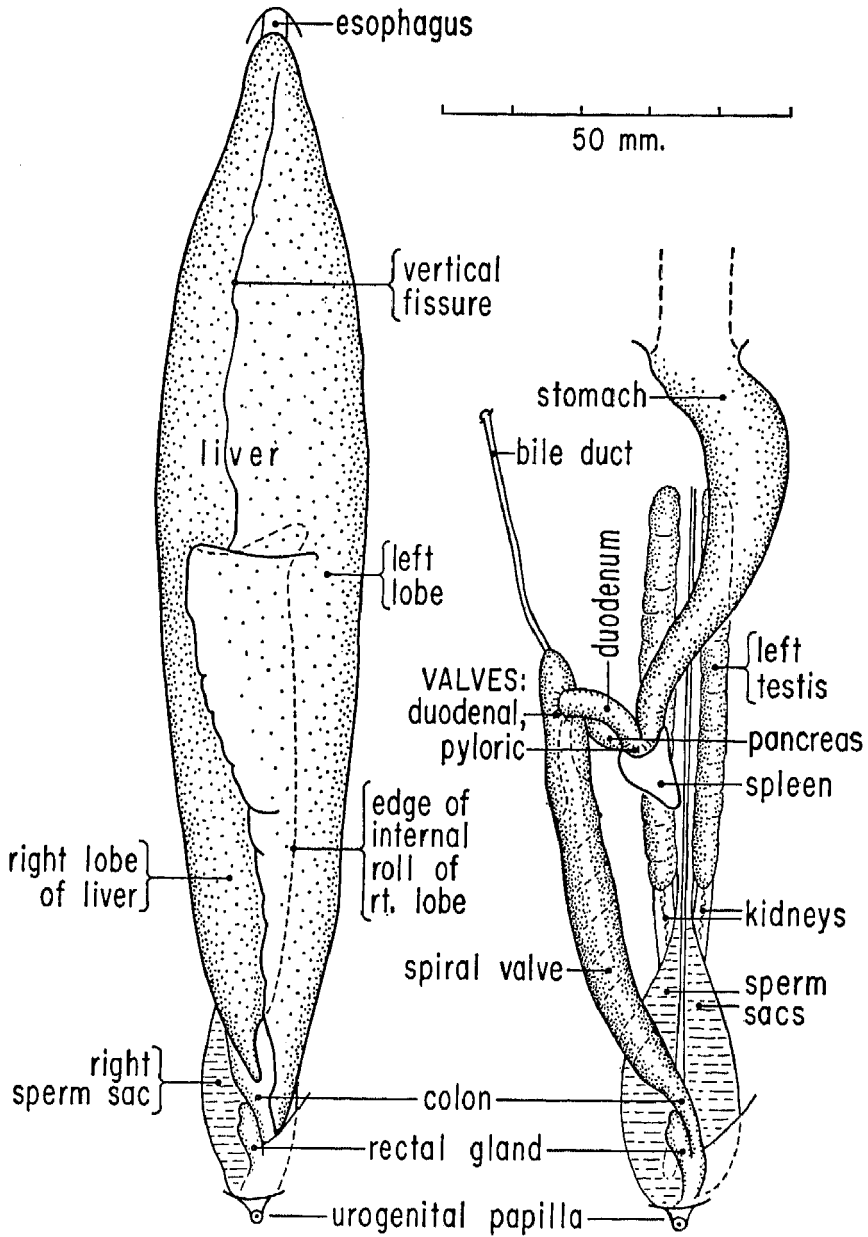
As Hubbs and McHugh (1951: 169, pl. 6) noted, *Euprotomicrus* is characterized among sharks by the remarkably low number of segments. In their extended survey of vertebral numbers in sharks, Springer and Garrick (1964: 92-95) found only one other genus, the related and still more dwarfed *Squaliolus*, to have so low a number. In *Isistius* (see below) the number is considerably higher, though also very low for a shark. Hubbs and McHugh related the low number to dwarfism, but it seems evident now that the low number as well as the elongate, spool-shaped appearance of the vertebrae, as these structures are seen in radiographs (pls. 6-8), is as much or more a group character; for the larger dalatiines (*Dalatis* and





### *EUPROTOMICRUS BISPINATUS*

Fig. 5. Visceral organs of *Euprotomiorus bispinatus*, in ventral aspect. Drawn to scale from specimen 29, a 211-mm adult male. Intestinal tract was deflected to left side (to right in figure), pulling the duodenum out of groove in liver and bringing into view posterior half of the more dorsal urogenital system. Anterior half of urogenital system shown to right of insert depicting intact liver in natural position. Long dorsal arm of pancreas concealed.



### *ISISTIUS BRASILIENSIS*

Fig. 6. Visceral organs of *Isistius brasiliensis*, in ventral aspect. Drawn to scale from a 386-mm adult male (SIO 52-413-5A), from equator at 100°00' W. long. On left, viscera shown as they appear with ventral body wall displaced. On right, liver is deleted and intestinal canal is deflected to right side (to left in figure) posteriorly and to left side anteriorly, to show the more dorsal urogenital system.

*Somniosus*) were shown by Springer and Garrick to have the vertebrae few, intermediate in number between those of *Euprotomicrus* and *Squaliolus* and those of *Isistius*.

We now present (table 7) vertebral counts for 13 specimens of *Euprotomicrus bispinatus*, including recounts for the 3 tallied by Springer and Garrick, and add one count for *Isistius brasiliensis*.

Examination of this table shows possible, but at most only average, differences between the main ocean areas, and no apparent sexual differences.

The number of monospondylous vertebrae is remarkably constant—31 or 32, in about equal frequency. This constancy is ascribable to the low number and to the fixed and definitive anatomical position of the group: in all specimens of *Euprotomicrus* and *Isistius* X-rayed by us monospondylously unmistakably and abruptly changes into diplospondylously at a consistent point, directly over the posterior part of the pelvic-fin base. (According to Springer and Garrick, 1964: 81, the change occurs in most sharks over the pelvic fin, usually over the base of that fin.) No trace of monospondylously recurs in any specimen beyond the point of change. Hence, the count of monospondylous vertebrae is readily obtained and is completely reliable. Finding this to be true, we regard it as unfortunate that Springer and Garrick did not separately tally the monospondylous vertebrae in the many vertebral counts that they made of sharks.

The number of diplospondylous vertebrae is spectacularly less constant. Our frequency counts are 28 (1), 29 (2), 31 (5), 32 (1), 33 (1), 35 (2), 38 (1). It is customary in fishes for the later-formed elements to be more variable than those formed early, but the discrepancy here is greater than usual.

The diplospondylous vertebrae were separately tallied as precaudal and as caudal, on the arbitrary but rather useful criterion adopted by Springer and Garrick, who fixed the point of separation as being opposite the origin of the upper caudal lobe. At first we located this point along the vertebral column on the X-ray negatives, as Springer and Garrick did, by inserting a pin at the upper origin of the caudal. Later we found that sensitive film and proper exposure showed the outline of the caudal well enough to enable the defined point to be discerned more precisely. But even then a possible variation in the count of  $\pm 1$  in each division remains, because the exact point of fin origin is somewhat difficult to fix and may lie approximately over the center of a vertebra (as in pl. 6, *b*). Some judgment remains, but the effect is slight in comparison with the actual variation, in both the precaudal and caudal count of diplospondylous elements.

The 13 counts of diplospondylous precaudal vertebrae range from 15 to 20, compared with the variation of 31 or 32 for the monospondylous precaudals. The difference in coefficient of variation would of course be much greater. Some of the variation may be due to fluctuation in the point of origin of the caudal fin that is unrelated to the vertebral column. (The X rays do show almost no calcified neural arches or processes.) It is probable, however, that much of the variation in number of precaudal diplospondylous vertebrae is inherent in the column itself.

The caudal vertebrae, as defined above, are even more variable, yielding counts ranging from 11 to 19. Even with excellent X-ray equipment and careful exposures the caudal vertebrae are often difficult to count, and variations of 1 to 3 occur on

TABLE 7  
 VERTEBRAL COUNTS FOR *Euprotomicrus bispinatus* AND *Isistius brasiliensis*<sup>a</sup>

Species and oceanic area	Sex	Specimen no. (Table 1)	Precaudals			Caudals	Grand total	
			Monosp.	Diplosp.	Total			
<i>Euprotomicrus bispinatus</i>	M	25	32	19	51	19	70	
	M	29	32	18	50	13	63	
	North Pacific	F	9	32	15	47	13	60
		F	11	31	17	48	14	62
		F	12	31	19	50	12	62
		F	24	32	18	50	14	64
		F	30	31	18	49	15	64
		F	31	32	20	52	15	67
	South Pacific	M	23	31	18	49	13	62
		M	27	32	16	48	13	61
F		28	32	17	49	14	63	
Indian	M	26	31	18	49	17	66	
Atlantic	F	32	31	18	49	11	60	
<i>Isistius brasiliensis</i> Equatorial Pacific	M	SIO 52-413-5A	41	21	62	22	84	
Comparisons of counts for <i>Euprotomicrus</i> by Springer and Garrick (S) and by us (H) on same specimens		11 (S)	..	..	47	14	61	
		11 (H)	31	17	48	14	62	
		12 (S)	..	..	51	13	64	
		12 (H)	31	19	50	12	62	
		23 (S)	..	..	46	15	61	
		23 (H)	31	18	49	13	62	

<sup>a</sup> The counts follow the presentation by Springer and Garrick (1964), in that the precaudal and caudal counts separate the vertebrae lying respectively before and behind the origin of dorsal lobe of the caudal fin. In addition, we separate the monospondylous and diplospondylous precaudals.

repeated counts for some specimens. The main difficulty lies in the circumstance that the terminal vertebrae become not only minute but also irregular in size and shape, and more or less separated from one another; at the very end, one or two may be very difficult to distinguish on the magnified X-ray negatives from one large denticle or a cluster of two to 4 smaller ones (pl. 6, *a*). In the *Isistius* specimen X-rayed (pl. 6, *b*), each of the terminal vertebrae retains its anterior but not its posterior expansion and is otherwise unusually elongated and slender.

Our counts diverge somewhat from those given by Springer and Garrick (1964: 92) for the same specimens (table 7). The divergence of 3 in the count of precaudals of specimen 23 cannot be reconciled readily, for our count of 49 is minimal.

It is the rule among fishes (Hubbs and Hubbs, 1954: 193; Hubbs, 1963: 145) that the numbers of anterior and posterior elements in a meristic series are negatively correlated. This rule appears not to hold for monospondylous vs. diplospondylous vertebrae of *Euprotomicrus*, though the numbers are too few for reliability: in specimens with 31 monospondylous vertebrae the number of diplospondylous precaudals and of total diplospondylous elements averages 18.0 and 31.7, whereas in those with 32 monospondylous vertebrae these averages are 17.6 and 32.0. When we compare precaudal with caudal counts (table 7), the indications favor (though hardly reliably) a positive correlation: the average number of caudals associated with 47 or 48, 49, and 50 to 52 precaudals is 13.3, 14.0, and 14.6.

#### COMPARISON WITH ISISTIUS

The vertebral counts of one specimen of *Isistius brasiliensis* (SIO 52-413-5A) from the equator at 100°00' W., included in table 7, confirm the numbers assigned to this species by Springer and Garrick (1964: 92). The monospondylous vertebrae (41) number about 10 more than in *Euprotomicrus bispinatus*. The number of precaudal diplospondylous vertebrae (21) is 1 higher than the maximum we have counted for the *Euprotomicrus*, which is the minimal count given by Springer and Garrick for *Isistius brasiliensis*. We have counted more caudals (22) in the *Isistius* than in the *Euprotomicrus*, but Springer and Garrick's minimal count (20) for the *Isistius* matches our maximal count for the *Euprotomicrus*. The one recorded specimen of *Isistius plutodus* is reported (Garrick and Springer, 1964: 682; Springer and Garrick, 1964: 92) to have even higher caudal (27) and total (92) counts than *I. brasiliensis*.

There are differences in kind as well as in number in the axial skeleton of *Euprotomicrus bispinatus* and *Isistius brasiliensis*.

In the caudal region of *Euprotomicrus* the neural arches and radials and the hemal arches and spines are seemingly so devoid of calcification and so soft as to fail to show on sensitive X-ray film (pl. 6, a). By dissection of one specimen (25) we find that the neural arches and radials are essentially flat and are almost in contact, and that each hemal arch-spine complex is swollen into a thin-walled bulbous structure seemingly filled with liquid.

In the specimen (SIO 52-413-5A) of *Isistius brasiliensis* X-rayed, the arches, radials, and spines of the caudal region are sufficiently hard and calcified to register well on X-ray film (pl. 6, b). Each neural arch forms a parallelogram directed obliquely upward and backward from the centrum. Together the arches have an even upper edge that appears on the X-ray film to be separated from the bases of the dorsal radials by a narrow, even interspace. Near the origin of the upper caudal lobe the upper parts of adjacent arches are separated by a small, triangular intercalated dorsal platelet. The radials are flat and are narrowly separated along oblique lines. In the specimen X-rayed, the first 5 radials grade from very rudimentary to nearly full size, and their bases lie above caudal vertebrae 3 to 5½. The total number appears to be 21, of which the anterior 6 are abruptly graduated in length and the other 15 become gradually shorter caudad. The base of the last one lies over caudal vertebra 18. Near the posterior end of the series the radials are fewer than the centra, but elsewhere they are more numerous. The lines represent-

ing the approximated posterior and anterior edges of adjacent radials give the false impression on the radiograph of forming a row of spines.

In the *Isistius* specimen, the hemal arches and the apparently inseparably connected hemal spines of the caudal region are flattish cartilages with enough calcification to show faintly on the X-ray film. Each arch is deflected backward from the ventral surface of the elongate centrum to a position below the posterior half or two-thirds of the next-anterior centrum, from which position it is extended downward, with a gentle backward curve.

The weaker calcification of the axial skeleton and the bulbous, seemingly liquid-filled hemal arches of *Euprotomicrus* may be adaptations that were involved in the development of the apparent neutral buoyancy of *Euprotomicrus*, a buoyancy *Isistius* has attained in part at least by its excessive development of liver (see tables 5, 6, pp. 24-25).

Toward the head the vertebrae seem to be abruptly broadened in *Isistius* (pl. 7, a), but not in *Euprotomicrus* (pl. 7, b), and the centra seem to be the more heavily calcified in *Isistius* (pls. 6-8).

#### HEAD REGION

The labial, cranial, and pectoral cartilages of *Euprotomicrus bispinatus* are also so devoid of calcification as to register very weakly and incompletely on a carefully exposed radiograph (pl. 7, b). These structures in *Isistius* appear from a comparable radiograph (pl. 7, a) to be much more heavily, though still weakly, calcified. The jaws of the *Isistius* are the more massive.

The pattern of the head cartilages of *Isistius* shows rather well in the radiograph, but inasmuch as these structures barely show in the radiographs of *Euprotomicrus*, we have not studied or described them.

#### SECONDARY AND PRIMARY SEXUAL FEATURES

Because of their significant bearing on the systematics and life ways of *Euprotomicrus bispinatus*, we have given attention to the secondary and primary sexual features of this species, and, in comparison, those of the supposedly closely related *Isistius brasiliensis*, as represented by one 386-mm adult male specimen (SIO 52-413-5A), dipnetted on the equator at 100°00' W.

#### CLASPER OF EUPROTOMICRUS BISPINATUS DESCRIBED AND COMPARED WITH THAT OF ISISTIUS BRASILIENSIS

Despite the circumstance that claspers (myxopterygia) of elasmobranchs have been found since the pioneering studies of Leigh-Sharpe (1920, 1926, and intervening "memoirs"), Ishiyama (1958), and some others, and despite the accumulating evidence that characters related to reproduction are often of paramount importance in the classification of fishes and other animals, many writers on the Elasmobranchii have neglected to utilize these characters. This is glaringly true of the great treatises on the Chondrichthyes of the western North Atlantic (Bigelow and Schroeder, 1948, 1957).

With these ideas in mind, we have examined (pl. 2, fig. 2; pl. 6, a; pl. 8, a; fig. 7) the claspers of the four available mature males of *Euprotomicrus*, 170 to 213 mm in total length (nos. 25, 26, 27, 29; table 1), and, in comparison, the one male

of *Isistius brasiliensis* mentioned above. Both species agree with squaloid fishes in general as described by Leigh-Sharpe (1920: 259, fig. 8; 1926: 340), who used the unavailable name Spinacidae in the broad sense for which Hubbs and McHugh employed the name Squalidae. Points of apparent family significance are the close adhesion of the claspers to the pelvic fin proper and the inclusion of a knifelike spine (the spur).

Although the general structural plan of the clasper is alike in *Euprotomicrus* and *Isistius*, and probably also in *Squaliolus* (indicating the phyletic value of similarities in clasper structure), we find that *Euprotomicrus* and *Isistius* differ trenchantly in several features in clasper (and pelvic) structure (table 8; fig. 7; pls. 6, a, and 8). These differences, as well as fundamental dissimilarities in visceral anatomy (pp. 25-27), indicate prolonged and profound separation of the phyletic lines.

The internal structure was not determined by dissection, but was examined by X-ray technique. Some features, especially about the tip of the clasper, could not be precisely determined, but seem to be quite different in the two species.

In general, the calcification of the pelvic arch and the pelvic and clasper cartilages is more reduced in *Euprotomicrus* than in *Isistius*. The pelvic radials are invisible in the preparations of *Euprotomicrus*, but are moderately evident (12 counted) on the X-ray films and radiographs of *Isistius*.

#### OVA AND EMBRYOS

The dwarf size and the pelagic habitat of *Euprotomicrus bispinatus* incite interest in its reproduction.

Dickens (1956) reported that a 234-mm female (no. 10, table 1) gave birth, a few hours after he had collected it, to six embryos, each in an imperforated yolk sac. Marshall (1956) located two additional embryos in this shark. Hence the total complement was eight. Peter J. Whitehead (personal communication) has measured the five embryos remaining with this specimen as 22.3, 22.6, 23.0, 24.4, and 24.8 mm in total length.

Parin (1964: 175-176, fig. 3) figured, but did not describe, one of the eight embryos 54-60 mm long which he found, four in each oviduct, in a 256-mm female (no. 16).

None of the specimens at hand has embryos, and only four, nos. 30, 12, 9, and 31 (the largest known specimens of the species), respectively 240, 242, 233, and 265 mm long (table 1), contain well-formed ova. The first two have four ova in each ovary; no. 9 has 3 + 3 in successive stages of development, with the full complement presumably not yet attained; and no. 31 (the largest known specimen of the species) apparently has four rather small ova in the right ovary and one larger one and remnants of others (being resorbed?) in the left ovary. (The gonads in this specimen are not well preserved.)

On the basis of these six observations it appears that the normal complement of fully developed ova and of embryos is  $4 + 4 = 8$ . The very small size of this shark and its limited range in size at maturity (p. 37 and fig. 10) are plausible causes for the seemingly constant number of offspring per brood—a rare phenomenon among ovoviviparous sharks.

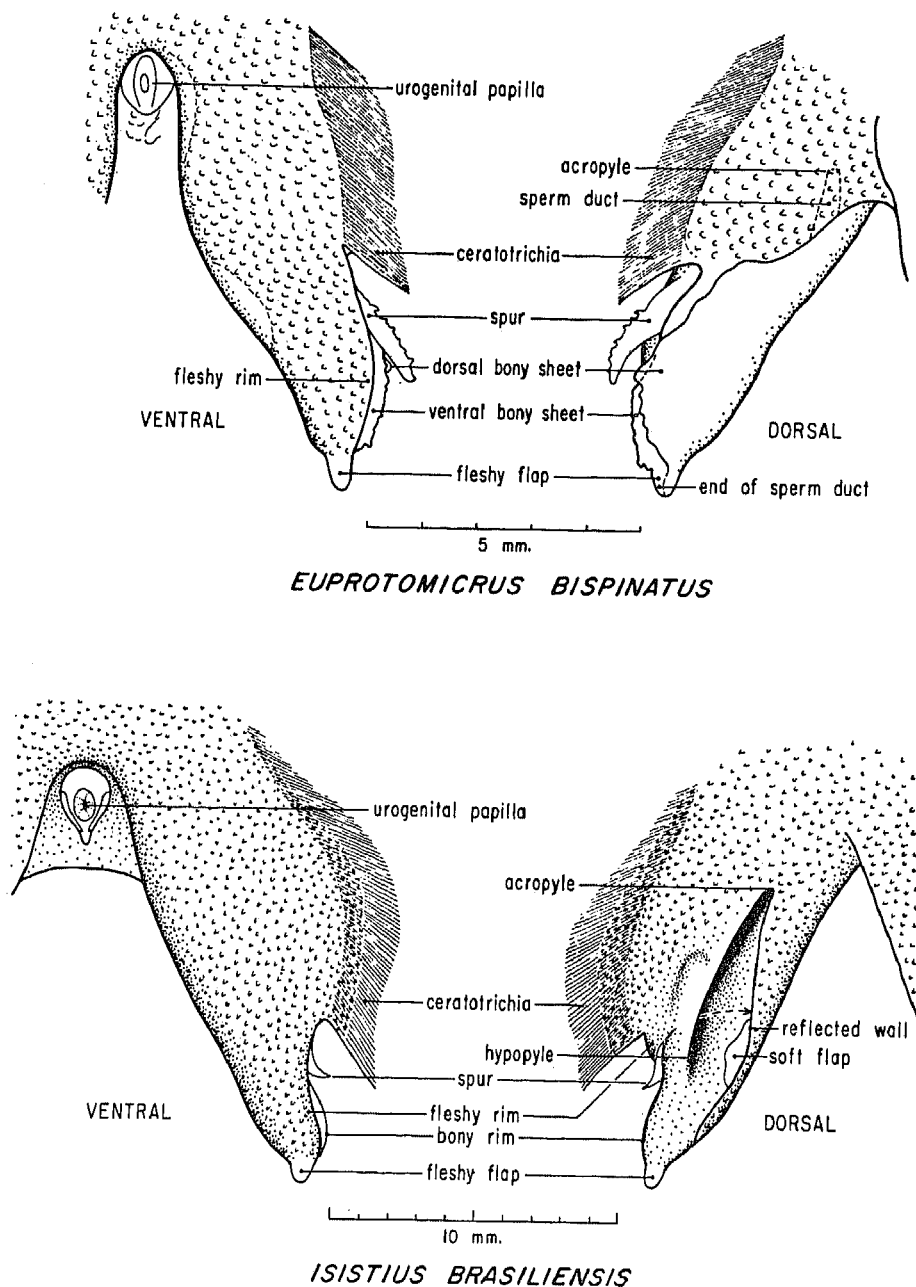


Fig. 7. Left claspers of *Euprotomicrus bispinatus* (above) and *Isistius brasiliensis* (below) in ventral and dorsal aspects, drawn to scale. *Euprotomicrus*: specimen 29, 211 mm in total length. Spur shown partly erected. Skin area where covered with denticles and photophores is shaded by v's. *Isistius brasiliensis*: SIO 52-413-5A, 386 mm in total length, from surface on equator at 100°00' W. long. Spur shown partly erected. Skin area where covered with denticles and photophores is shaded by v's. Fleshy covering of sperm duct is reflected to left, to show duct and fleshy flap.



TABLE 8  
 CONTRASTING CLASPER AND PELVIC CHARACTERS IN *Euprotomicrus bispinatus*  
 AND *Isistius brasiliensis*  
 (Fig. 7 and pl. 8)

Character	<i>Euprotomicrus bispinatus</i>	<i>Isistius brasiliensis</i>
<i>External</i>		
Length of clasper beyond pelvic base as proportion of distance from end of pelvic base to front rim of cloaca	About one-half	About one-third
Basal part of ceratotrichia	Free of flesh and denticles	Concealed beneath flesh and denticles
Inner face and dorsal surface of inside rim of sperm duct	Free of denticles	Covered by denticles
Spur	Long, nearly straight	Short, hooked
Outer edge of spur	Irregularly serrate	Smooth
Spur groove separated from sperm duct by	Narrow bony rim	Wide expanse of dorsal surface of clasper
Distal part of sperm duct	Extended to end of terminal fleshy flap; very deep and narrow	Ending proximal to terminal flap; broad and shallow
Dermal flap on inner mesad wall of sperm duct	Absent	Present
<i>Internal</i>		
Pelvic arch	Slender, slightly convex forward; little expanded medially	Thicker, transverse; markedly expanded midventrally
Basal cartilage	Broader, parallel	Slenderer, convergent backward
Small, intercalated cartilage	Lacking	Developed in front part of caudal fin
Inner median cartilage	Clavate base, pointed tip	Nonclavate base, parallel-sided
Outer median cartilage	Apparently present	Apparently absent
Spur base	T-shaped; outer edge rounded	Pointed; outer edge angulated

The disposition as well as the number of maturing ova seems to be consistent. The ova in the 240-mm specimen (30) are neatly aligned and closely juxtaposed in each ovary to form an even, parallel file. The overall length of the file on the left side (171 per mill of the total length of the shark) is distinctly shorter than the file in the right ovary (223 per mill). There is bilateral asymmetry also in the location of the files: the distance from tip of snout extends from 254 to 425 per mill of the total length on the left side and from 302 to 521 per mill on the right.

In the 242-mm female the ova are similarly aligned, and the file on the left side is the shorter and the farther forward. In this specimen (12), the ova increase in size backward, reflecting the order of development and growth.

In the 233-mm specimen (9) the ova and the ovary are of similar pattern, but are in an earlier stage of maturation. In each ovary the most posterior ovum is about half as long as in specimens 12 and 30 and is preceded by a somewhat smaller one. On the right side a third ovum was definitely starting to enlarge, and there seems to have been a trace of a fourth one on this side and of a third one in the left ovary.

In a 139.5-mm specimen (24), ova were in an early stage of maturation. Some follicles, associated with ova in various stages of maturation, were found in the small ovary. One follicle, enlarged about 400 times, shows a vesicle containing a group of nucleoli in the yolk (pl. 5, fig. 1).

Except for the still huge yolk sac and the filamentous external gills, the advanced embryo pictured by Parin (1964, fig. 3) looks remarkably like the adult—a point seemingly related to the dwarfism of the species (p. 54). The pigmentary pattern on the pectoral and caudal fins was already developing. The eye is relatively much larger than in the adult, and the fins are more rounded and are shorter, especially in basal length. Before birth, the embryos presumably attain more than one-fourth the length of the mother.

By the time they reach total length of about 100 mm, the young are essentially like the adult. As is detailed in the morphometric analysis (pp. 9–14), there is considerable allometry in the differential growth of certain parts of the body.

#### SEX RATIO AND DIFFERENTIAL SIZE OF SEXES

The 33 specimens of *Euprotomicrus bispinatus* for which we have record of sex are about equally divided, 16 females and 17 males.

Data on sex, maturity, and size (fig. 10; table 1) indicate that males mature at a smaller size than females and fail to become as large. A 170-mm male (no. 27) has the clasper almost completely elaborated, and all larger males, measuring 198 to 220 mm in total length, are mature. So far as known, all females smaller than 220 mm are immature, and all larger ones (233–265 mm long) bear either maturing ova or embryos (pp. 34, 37).

#### HORIZONTAL DISTRIBUTION

Enough data are now at hand to draw some conclusions and comparisons regarding the areal distribution of *Euprotomicrus bispinatus* throughout the world ocean, and to correlate its distribution with physical/chemical factors and with the known distribution of some other organisms.

## TEMPERATURE RELATIONS

Inspection of the distributional charts (fig. 9) shows that the surface isotherms of 65° F. (18.3° C.) and 80° F. (26.7° C.) for summer (for August in the northern and February in the southern hemisphere) seem to circumscribe or at least to approach nearly all the 32 plottable records of the species (all 37 listed in table 1 with the exception of 3-5 and 26). The two outstanding exceptions are two presumed strays (specimen 8, from Campbell Island, south of New Zealand, and specimen 7, from west of Cape Horn, both approaching the Antarctic Convergence).

The surface temperatures at or near the place and time of capture varied in rounded figures from 16° to 27° C. for the 21 specimens for which data are available (fig. 8). Since we do not know to what depths *Euprotomicrus* descends by day (p. 42), we cannot plot the temperature-salinity (T-S) values for the depth range of the species, as Ebeling (1962: 120-138, figs. 45-67) effectively did in identifying the water masses in which melamphaid fishes occur, on the basis of the envelopes of T-S curves that characterize the different water masses (Sverdrup, Johnson, and Fleming, 1942: 605-761, figs. 158-212, esp. 739-745, fig. 209; Bradshaw, 1959; Johnson and Brinton, 1963; Dietrich, 1963: 201-202, fig. 81).

Since we can assume, on the basis of food items eaten by *Euprotomicrus* (pp. 45-53), that it does descend well beyond 200 m, we may consider the 200-m temperatures where *Euprotomicrus* occurs. These temperatures ranged from 10° to 21° C (in rounded figures) for the fifteen available records taken at or near the place and time at which the species was dipnetted at the surface (fig. 9).

If we compare the mapped distribution of *Euprotomicrus* with a chart of the temperature of the world ocean at 200 m (such as Chart IV by Sverdrup, Johnson, and Fleming, 1942), we note, except for the apparent strays in the far south, a concentration of the occurrences at points where the 200-m temperatures range from 13° to 21° C. This is notably true in the North Pacific, both central and eastern, and in the southeastern Pacific, and holds also for the cluster of records in the Indian Ocean and for the one record from the Atlantic Ocean. Even more striking is the lack of records from the well-worked bands off the west coasts of North and South America occupied by the California and Peru currents (Wooster and Reid, 1963), where the temperature at 200 m is charted as well below 13°, and in the great eastern wedge of Pacific Equatorial Water (Knauss, 1963), which is also cool at 200 m, and is largely occupied, near the surface, by the Pacific equatorial currents. (For a generalized map of the current systems see Chart VII in Sverdrup, Johnson, and Fleming, 1942.) Furthermore, there are no records from the Kuroshio Current area, where the species is probably absent or extremely rare.

Although the areal distribution of *Euprotomicrus* appears to depend in some way on water temperature, there is much regional variation in the temperature inhabited at given times. For example, in the northern Pacific, the five northernmost locations, from 32°46' to 35°13' N., each for one specimen (9, 12, 29-31 of tables 1 and 2 and fig. 9) registered only 15.6° to 18.3° at the surface, whereas the three specimens from 18°07' to 29°51' N. registered 22.3° to 25.6° at the surface. The northeastern group of specimens (9, 29-31) came from places where the tem-

perature in deep water was unusually low for the species:  $10.15^{\circ}$  and  $10.9^{\circ}$  for nos. 9 and 31, respectively, at 200 m;  $13.5^{\circ}$  and  $12.5^{\circ}$  for nos. 29 and 30, respectively, at 119 m and 125 m (at bottom of BT casts).

In the southeastern Pacific the surface temperature for the four stations (specimens 19, 23, 27, 28) from  $08^{\circ}26'$  to  $14^{\circ}16'$  S. were  $24.3^{\circ}$  to  $26.3^{\circ}$ ; from one station (specimen 15) at  $32^{\circ}00'$  S.,  $21.8^{\circ}$ ; for one station (specimen 37) at  $33^{\circ}46'$  S.,  $21.2^{\circ}$ ; for one station (specimens 13 and 14) at  $37^{\circ}55'$  S., only  $16.8^{\circ}$ . The temperatures at 200 m so far as recorded from these three sets of collections were  $16.5^{\circ}$  to  $20.5^{\circ}$ ,  $17.3^{\circ}$ , and  $12.4^{\circ}$ .

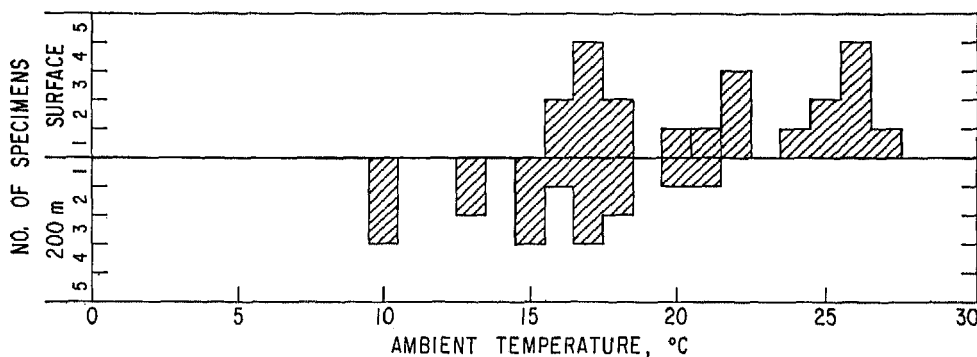


Fig. 8. Frequencies of temperature records for *Euprotomicrus bispinatus* at surface (above horizontal line) and at 200 m (below line). Data, from table 2 and from Parin (1964: table 1 on p. 166), expressed to nearest whole degree C. Some data for a station adjacent in time and place to station of capture.

In the Indian Ocean, the north-south series of temperatures, for specimens (21 and 22), 20, 18, and 17 ranged as follows: at the surface,  $22.1^{\circ}$ ,  $20.1^{\circ}$ ,  $17.0^{\circ}$ , and  $18.4^{\circ}$ ; at 200 m,  $17.4^{\circ}$ ,  $16.2^{\circ}$ ,  $13.5^{\circ}$ , and  $12.8^{\circ}$

Continuing farther south, toward the Antarctic Convergence, we note that the sea-surface temperatures inhabited seem to drop greatly. Basing the estimate on the World Atlas of Sea Surface Temperatures (Scripps Institution of Oceanography, 1948) the temperature for May at Campbell Island, south of New Zealand (for specimen 8) is about  $7^{\circ}$ . The annual range for  $56^{\circ}$  S.,  $90^{\circ}$  W., roughly where specimen 7 was taken (at an unspecified date), is approximately from  $3^{\circ}$  to  $7^{\circ}$ .

It appears that this pelagic shark is not directly and critically delimited in range by either the surface or the deepwater temperature. The relation may well be of an indirect and long-term nature.

#### SALINITY AND DISSOLVED OXYGEN

Other than the possible role of the sharp depletion of oxygen with depth in Pacific Equatorial Water (Wooster and Cromwell, 1958: 179, 180, profiles 1c, 1d; Knauss, 1963: 241-244, figs. 7, 8), chemical factors in the open sea do not seem to limit the distribution of *Euprotomicrus*.

Comparison of the distributional chart of *Euprotomicrus* in the world ocean with a chart of surface salinities (such as Chart VI in Sverdrup, Johnson, and Fleming, 1942) shows that the species occurs throughout the usual range of salinity

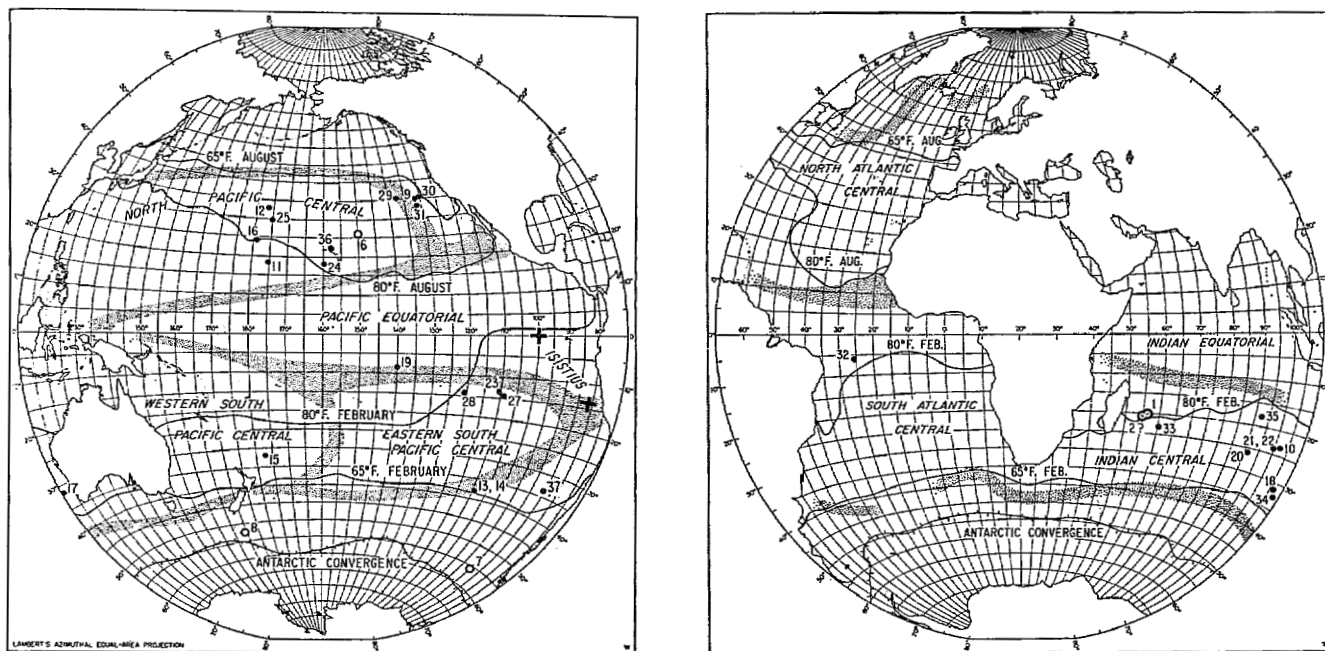


Fig. 9. Known distributional records for *Euprotomicrus bispinatus*. Numbers correspond with entries in table 1. Hollow circles pertain to old records of three specimens (1, 2?, 8) from islands, and for two specimens (6, 7) washed aboard by storm at locations not precisely stated. Black dots are for specimens dipnetted at specified positions on oceanographic cruises. Isotherms replotted from charts prepared by Scripps Institution of Oceanography (1948). Antarctic Convergence replotted from Deacon (1963, fig. 3). Boundaries (shaded) of water masses replotted from chart by Ebeling (1962, fig. 71), which was based on figure 209A accompanying original analysis of water masses by Sverdrup, Johnson, and Fleming (1942). The North Pacific Central Water Mass is represented as a unit, because its separation into western and eastern divisions seems inconsistent with recent evidence (Joseph L. Reid, Jr., personal communication). Only specimens not chartable are nos. 3-5 and 26.

(approximately from 33.0 to 36.5 per mill). Some actual values for surface salinity from stations where the shark was taken are 33.78 for specimen 9 (in the northeast Pacific) and 35.71 to 35.97 for specimens 23, 27, and 32. Salinities at 200 m depth were recorded for stations of capture as 33.75 for specimen 9 and 35.45 and 35.23 for specimens 23 and 27.

Dissolved oxygen (in ml/L) was recorded as 5.35 at the surface and as 4.76 at 203 m for the station in the northeastern Pacific where specimen 9 was taken, and as 4.74 at the surface and 3.51 at 200 m for the station in the southeastern Pacific where specimen 27 was taken.

#### DEPTH OF WATER AT STATION

Ordinarily, *Euprotomicrus* occupies the upper layers over very deep water. The 15 stations for which we have a definite record range in depth of water from about 1,829 to 9,938 m; all but two records are within the range of 3,000 to 6,000 m (table 2 of this work and table 1 in Parin, 1964).

#### RELATION TO WATER MASSES

The correspondence between the known occurrences of *Euprotomicrus* and the pattern of water masses (both illustrated in fig. 9) is in general very close.

All records for the North Pacific are within the bounds of the North Pacific Central Water Mass, with some extension eastward toward California; however, none of the records are for the area of long and intensive survey by the California Cooperative Oceanic Fisheries Investigations (Ahlstrom and Counts, 1955, and 1958; Fleminger, 1964; Alvaríño, 1965). The eastern boundary of the Central Water fluctuates considerably, as is reflected in the pelagic fauna as well as by the physical/chemical data; but the eastward extent of this water mass is blocked by the California Current from reaching close to the North American coast. The records for the southeastern Pacific fall within the accepted limits of the central water masses or their borders, with one exception (off Chile). Those for the Indian Ocean are all within the mapped limits of the Indian Central Water. The one, new Atlantic Ocean record is within the poorly defined South Atlantic Central Water, and apparently well within the limits of the Equatorial Current as charted. In this respect, the Atlantic record diverges from those of the Pacific and Indian oceans, wherein *Euprotomicrus* seems to avoid the areas of major equatorial current flow.

The apparent avoidance by *Euprotomicrus* of the Pacific Equatorial Water, which is notably cold at 200 m, follows a common distributional pattern, for this water mass is definitely the range of some species, but is avoided by others. For fishes, this circumstance has been most notably demonstrated by the Melamphaidae (Ebeling, 1962), but has been determined in greater detail and with much more abundant data for various groups of pelagic invertebrates, for example by Dales (1957), Bieri (1959), Bradshaw (1959), Brinton (1962), and Johnson and Brinton (1963). The apparent avoidance of the Pacific Equatorial Water may be related to the intensification therein of the oxygen-minimum layer.

Reid (1962) has contrasted the high phosphate-phosphorus content and high zooplankton volumes of the Pacific Equatorial Water Mass with the low values in the North Pacific Central Water.

It seems to be assured that *Euprotomicrus*, at least as a surface swimmer, is to be included among the moderately antitropical fishes (Hubbs, 1952; Hubbs, Mead, and Wilimovsky, 1953). Various pelagic invertebrates, for example euphausiid crustaceans (Brinton, 1962), are similarly distributed.

In summary, *Euprotomicrus* inhabits the vast central water masses, chiefly in the great gyres of the North Pacific, South Pacific, southern Indian Ocean, and, we now learn, the South Atlantic. It seems to shun coastal waters, except about such oceanic islands as Oahu, Campbell, Mauritius, and probably Réunion.

In comparison, *Isistius brasiliensis* has been shown to be distinctly more tropical (Bigelow and Schroeder, 1948: 512; Strasburg, 1963: 33-34, fig. 1). There is evidence of a slight overlap in the ranges, near the Hawaiian Islands. Specimen SIO 52-413-5A, taken at the surface on the equator at 100°00' W., links the one record from near the Galápagos Islands (Garman, 1899: 40; Bigelow and Schroeder, 1948: 510) with the 21 localities reported by Strasburg for 22 specimens, all caught by midwater nets. The other specimen examined by us (FAKU 39108) brings the range of the species much closer to the American mainland, as it was taken at 13°46.0' S., 81°52.0' W., in the Peru Current, off Peru.

#### VERTICAL DISTRIBUTION OF EUPROTOMICRUS AND OTHER DWARF DALATIINES

Marshall (1956: 74) wisely concluded that this "deep sea shark probably spends much of its time in the ocean depths at several hundred fathoms below the surface. But from time to time it comes to the surface and there is one other record of its having been washed aboard a merchant ship."

Parin (1964: 176) also concluded, on the basis of strong circumstantial evidence, that *Euprotomicrus bispinatus* without doubt belongs to the bathypelagic fish fauna. He stated (our translation):

VERTICAL DISTRIBUTION.—As mentioned before, all known specimens have been caught at the surface of the water. In spite of this fact there is no doubt that this species belongs to the bathypelagic ichthyofauna. This assumption is also completely confirmed by their bioluminescence, which is lacking, without exception, in all pelagic fishes inhabiting the surface layer. Obviously *E. bispinatus* dwells in the upper layers of the bathypelagic and undertakes regular vertical migrations, rising to the surface during dark hours.

Garrick and Springer (1964: 678-679) also attributed *Euprotomicrus* to the "little known midwater shark fauna, along with *Isistius*, *Squaliolus*, and *Heteroscymnoides*."

By a study (pp. 45-53) of the contents of the intestinal canal of this species we have confirmed Marshall's and Parin's convictions. The hatchetfish *Argyropelecus* cf. *aculeatus*, the lightfish *Vinciguerria nimbaria*, and bathypelagic squids all demonstrate feeding at considerable depth. The hatchetfish suggests descent to at least 300 meters. The finding of volcanic sand grains in the stomach of one specimen taken over very deep water on the side of the East Pacific Rise (p. 52) proves at least occasional descent to, and presumably some feeding on, the bottom, possibly in very deep water.

The frequent capture of *Euprotomicrus bispinatus* at the surface at various times of night (soon after dusk, near midnight, and early morning are all recorded

in field notes) indicates to us that its movements to the surface are regular events, following descents to midwater depths where at least much of the feeding is accomplished. The equal sex ratio among the exclusively surface-caught specimens (p. 37), and the finding of bathypelagic organisms in the intestinal canal of specimens of both sexes, indicate that both males and females partake in the vertical migrations.

#### COMPARISON WITH OTHER DWARF DALATIINES

It is probable that *Isistius brasiliensis*, the somewhat less dwarfed pelagic dalatiine shark, also undertakes vertical migrations, though it very seldom comes to the surface. Evidence on its possible vertical migrations is given in the discussion on activity and reactions to light (p. 45).

The dalatiines of the genus *Squaliolus*, which are the ultimate dwarfs among sharks, seem to have a wide depth range and a diverse habitat. The two specimens described from the Philippine Islands as *S. laticaudus* (by Smith and Radcliffe, in Smith, 1912: 683-685, fig. 4, pl. 54) were taken by beam trawl at depths of 170 and 198 fathoms (311 and 362 m) (Bureau of Fisheries, 1911: 38, 42). The type specimen of *S. sarmenti*, described from Maderia (De Noronha, 1926: 384-389, pl. 35), was taken on a vertical midwater setline with hooks from about 500-800 fathoms (914-1,463 m); the depth was indicated by Maul (1948: 135, 139) on the basis of a report by De Noronha and Sarmiento (1948: 45) as "do altio (além de 650 braças)." The same species was reported by Belloc (1937) and Sigales (1939-1940) as having been taken in a shrimp net in the shallow bassin d'Arcachon, connected with the Bay of Biscay on the coast of France. Teng (1959: 1-6, 1 pl.; 1962: 171, fig. 43) described *S. alii* from the depth of about 180 fathoms (329 m) off Tung-Kang, Taiwan, where it was taken by bottom longline. Abe (1962) reported the capture in Suruga-wan, Japan, along with the bathypelagic shrimp *Sergestes lucens*, of a species of *Squaliolus* identified by him as *S. laticaudus*. Obviously *Squaliolus* species have a wide vertical range, and probably share demersal and pelagic habitats (as various other fishes probably do).

#### BUOYANCY OF EUPROTOMICRUS AND ISISTIUS

The surface-swimming and the vertical migrations of *Euprotomicrus bispinatus* lead one to suspect that its body is of at least approximately neutral buoyancy. Observations under a light on shipboard (p. 17) certainly give this impression. Particularly pertinent is the remark by Dickens (1956): "In swimming it was observed that the top forepart of its head and the middle of its back were awash."

Elasmobranchs as a rule are demersal creatures, which, because they contain no gas and have skeletal and muscular tissue that is denser than seawater, either stay on the sea floor or exert energy to keep off the bottom. Pelagic teleosts that lack a gas bladder, particularly those of the bathypelagic realm, have attained neutral buoyancy through such adaptations as deposition of fat, reduced ossification, weakened musculature, and enlarged lymphatics (Denton and Marshall, 1958; Marshall, 1960).

With these thoughts in mind, it may be conjectured that neutral buoyancy in *Euprotomicrus* and *Isistius* may have been attained through comparable adaptations. No specific-gravity measurements of any whole sharks or parts thereof are



known to us, but we do find indications that these pelagic sharks have become adapted to or toward neutral buoyancy.

In *Euprotomicrus bispinatus* the entire skeleton is extraordinarily weak, is reduced in bulk, and is so devoid of calcification that its different parts vary from only slightly to not at all opaque to the soft X rays used. The results appear in the radiographs of the entire shark (Hubbs and McHugh, 1951: pl. 5), of the head region (pl. 7, *b*), the posterior parts (pl. 6, *a*), and the clasper region (pls. 6, *a* and 8, *a*). Even with carefully worked-out exposures on sensitive film, the small cranium and the pectoral arch are barely visible. The pelvic arch and the clasper cartilages were brought out with difficulty. The vertebral centra show moderately well, apparently because of calcification around the periphery of the notochord, to produce the spoonlike configurations shown on the radiographs (pls. 6-8). The other parts of the centra show very weakly. The centra become greatly reduced in the caudal region, where the neural arches and the hemal arches and spines hardly register and the dorsal radials (basals) produce no trace on the film. On dissection, the hemal arches and spines are seen to be modified into bladder-like structures that are probably filled with lymph (p. 32). The ceratotrichia are extremely delicate and the dermal denticles (pl. 1, fig. 3; pl. 2) are minute. All these conditions presumably contribute to the neutral buoyancy of this shark. The flattened ventral surface (Alevy, 1963: 24) and the small size of the fish no doubt are contributing factors.

The other common small dalatiine, *Isistius brasiliensis*, has a considerably less decalcified skeleton (pls. 6-8), but its spectacularly enlarged liver presumably provides complete compensation (table 5, p. 24; fig. 6).

#### ACTIVITY AND REACTIONS TO LIGHT

The circumstance that *Euprotomicrus bispinatus* has never been captured in mid-water trawls, despite recent frequent use, and despite our demonstration that this fish must engage in vertical migrations, suggests that it is a strong and evasive swimmer. Perhaps it has sufficient light perception to escape capture, by avoiding the luminescence induced by the moving trawl; the gleam reflected from the eye of the related species *Isistius brasiliensis* indicated to Strasburg (1963: 35) the presence of a tapetum lucidum. Or, senses other than vision may be involved.

Published observations on the activities of this shark at the surface have been very limited. Hubbs and McHugh (1951: 159) noted that specimen 9 (table 1) "was cruising slowly at the surface." Dickens (1956) in reporting on the specimen (10) he caught, stated: "The swimming actions were seen to be slow with powerful movements of the tail section and little real body movement [indicating sinuous swimming]," but when disturbed by electric light in a saltwater bath it swam frantically. Parin (1963: 131; 1964: 176) stressed the positive phototaxis of the species to artificial light. Following is our translation of his 1964 statements:

A peculiarity of this species is the positive reaction to artificial light (Parin, 1963). All specimens of *E. bispinatus* were taken while collecting under a light and they were attracted to the ship by the rays of deck lights. According to our data, these sharks usually swim in a lighted zone rather slowly and return to the underwater lamp several times (see also Hubbs and McHugh, 1951). In some observations, however, the sharks moved around more quickly and crossed the lighted area with greater speed.

William L. Craig reports that specimen 30 darted rapidly with sinuous movement of the body through the lighted zone, to disappear under the ship. An hour or so later, a fish, thought to be the same, reentered the lighted area from beneath the ship and was promptly dipnetted. It swam about actively and in apparent good health in a small container for about an hour, until it was preserved.

Comparison of *Euprotomicrus bispinatus* with the other small pelagic shark *Isistius brasiliensis* in respect to activity is somewhat confused. The fact that only one specimen (SIO 52-413-5A) of *Isistius* seems to have been dipnetted under a light may not prove that this more tropical shark reacts differently to light, but rather that it probably avoids the surface. The one specimen referred to was dipnetted just on the equator, where upwelling had reduced the surface temperature to 23.6° C. Strasburg (1963: 34-35) noted that all 22 specimens of *Isistius* that he reported were taken in midwater trawls and in meter-nets, and all at night. These were the largest organisms taken in the trawls, thus evoking the query: Are they slow swimmers, or are they insensitive to the net? That *Isistius* is not sluggish seems obvious from its ability to capture relatively large squids. May not the sharks discussed by Strasburg have been attracted to the luminescence induced by the moving net? Probably this genus also engages in vertical movements, but between lower depths, at each limit, than *Euprotomicrus* traverses. By daylight it may well be below the net tows.

The now known bioluminescence and vertical migrations of *Euprotomicrus bispinatus* render plausible the assumption that this species aggregates, and probably schools, although it, like many other fishes so endowed, may scatter at the surface during night. Parin (1964: 176) stated (our translation) that "occurrence in schools is not so obvious for *E. bispinatus* as it is for *I. brasiliensis* (all specimens of *E. bispinatus* have been caught one by one)." Parin, however, gave some evidence for aggregation, by indicating that two specimens (13 and 14 and 21 and 22 of our table 1, respectively nos. 7 and 8 of Parin's tabulation) were twice taken at one night-light station.

The position of the small dorsal fins of *Euprotomicrus*, well behind the middle of the body, may give the body stability in the yawing plane, as Bertelsen and Marshall (1956: 30) have theorized for the opposed, backward-set dorsal and anal fins of such teleosts as the Stomiidae and the Miropinnati.

In the following discussion of the food of *Euprotomicrus* and, in comparison, that of *Isistius*, it appears that these little sharks are sufficiently active to capture sizable and active fishes and squids and that they are structurally fitted for predatory existence. Their streamlined form certainly suggests speedy swimming, at least in spurts.

#### ITEMS FOUND IN INTESTINAL CANAL OF EUPROTOMICRUS IDENTIFIED, AND CONSIDERED IN REFERENCE TO ITS VERTICAL DISTRIBUTION AND BIOLOGY

A survey of the contents of the stomach and intestines of 12 specimens of *Euprotomicrus bispinatus* was undertaken because, except for one brief mention by Parin (1964: 176), nothing seems to have been published on its food, and, in particular, because it was hoped that such a study would test the hypothesis that this lumines-

cent pelagic shark descends by day to considerable depths. Authorities for identifications are listed in the introduction, under acknowledgments. Circumstances of identification and bearings on distribution and biology are stated below in the discussion of individual food items. In that discussion the gut-content items are listed in the same sequence as under the heading of each specimen in the following empirical tabulation. (See table 1 for data on specimens.)

## SUMMARY BY SHARK SPECIMENS

## Specimen No. 9

*Miscellaneous invertebrates*.—A paper-thin, apparently segmented body suggestive of the abdomen of a phyllosoma larva of *Panulirus* (spiny lobster), with traces of probable appendages seemingly consonant with this identification. Also one stringy piece of (invertebrate?) tissue, with nodular skin.

*Squids*.—One bathypelagic squid, probably a cranchiid, in cardiac section (of stomach). Other seemingly bathypelagic species suggested by traces of black skin.

*Eye lenses* (referring to loose lenses, either of squid or of fish).—One spherical lens, 3 mm in diameter, in pyloric section.

## Specimen No. 11

*Squids (?)*.—Blackish food remains in intestine and what may be remains of a pen suggest some dark bathypelagic squid.

*Fishes*.—One half-grown specimen, 26 mm in standard length, of *Vinciguerria nimbaria*, from cardiac section.

*Parasites*.—One cestode, in cardiac section.

## Specimen No. 12

*Miscellaneous invertebrates (?)*.—Very small amount, unidentifiable.

*Fishes*.—One small, flattened pelvic spine.

## Specimen No. 23

*Squids (?)*.—Some of the very limited food remains suggest cephalopod skin.

*Eye lenses*.—One lens.

*Parasites*.—Four cestodes, in cardiac section.

## Specimen No. 24

*Squids*.—One small squid beak.

*Fishes*.—One vertebral column, 11 mm long, and a piece of digested flesh with scales of a juvenile bramid, *Collybus drachme* Snyder.

*Parasites*.—Fourteen cestodes (pl. 5, fig. 2) in cardiac section.

## Specimen No. 25

*Squids (?)*.—Trace of blackish remains, possibly of squid.

*Fishes*.—One subadult of *Argyropelecus* cf. *sculeatus*.

## Specimen No. 26

*Squids*.—Blackish remains, particularly some skin very thickly set with oval melanophores, almost surely represent a bathypelagic squid.

*Fishes*.—One small fish scale, probably of a myctophid, and one fin ray.

*Parasites*.—One small and one larger cestode, in cardiac section.

Specimen No. 27

*Miscellaneous invertebrates*.—Two very small invertebrates, one a cyclopoid copepod, *Oncaea* sp., of stage VI or VII, and one hyperiid amphipod, apparently of an early stage.

*Squids (?)*.—Much digested squid remains are suggested by fragments of black skin among the unidentified debris.

*Eye lenses*.—One minute lens, possibly from a *Vinciguerria*.

*Fishes*.—One very young specimen, about 12 mm long, almost surely of some species of *Vinciguerria*; also various pieces of several still smaller fish, mostly with photophores like those of *Vinciguerria*; most or all probably of the same species. Also one fish scale of some other genus.

*Sand grains*.—Several small grains, largely of feldspar; all in cardiac section.

*Parasites*.—Two cestodes, in cardiac section.

Specimen No. 28

*Eye lenses*.—Two, one minute and one small (bare trace of other food).

*Parasites*.—Five cestodes of graded size (one minute), in cardiac section.

Specimen No. 29

*Squids (?)*.—Trace of food remains, including fragments suggestive of squids.

Specimen No. 30

*Squids*.—Inclusion of at least one squid in the much digested food remains is shown by the presence of one small squid beak and a pair of semiovoid eye lenses.

*Eye lenses*.—Three spherical lenses, in addition to two just mentioned.

*Fishes*.—Midsection of one lanternfish, *Myctophum nitidulum*, from near shoulder girdle to just behind SAO file of photophores, with some scales attached, in cardiac section; also, in spiral valve, two scales of same type.

*Tooth of Euprotomicrus*.—One, partly digested, in spiral valve.

Specimen No. 31

*Squids*.—Two: one blackish, relatively very large, its twisted strands forming a skein extending from near esophagus through the spiral valve, retaining both beaks and both lenses; the other, smaller and almost black, with lenses largely intact.

*Eye lenses*.—One, intermediate in size between those connected with the two squids.

DISCUSSION OF ITEMS IN INTESTINAL CANAL

We now proceed to discuss the identification and the biological significance of the various items found in the stomach and intestine of *Euprotomicrus bispinatus*.

MISCELLANEOUS INVERTEBRATES

Invertebrates other than squids—all crustaceans so far as recognized—appear from the examination of 12 specimens to play a very minor part in the alimentation

of *Euprotomicrus*. In this respect this shark contrasts sharply with many pelagic teleosts, but resembles large pelagic sharks of the open sea (Strasburg, 1958: 349-350), as well as certain large, voracious teleosts, such as tunas (King and Ikehara, 1956b).

*Panulirus* (?).—What appears to be the remains of a phyllosoma larva of a spiny lobster, in specimen 9 (from off California, at 34°57' N., 131°30' W.) suggests an epipelagic food item. It is from farther offshore than expected, though Johnson (1960) has indicated a considerable offshore drift of these animals along the west coast of North America.

*Minute Crustacea*.—Several minute crustaceans found in the intestinal canal of *Euprotomicrus* seem much too small to have tempted even so small a shark. They more likely were items that had previously been ingested by fish prey, remains of which were in the shark stomachs involved. Shark no. 27 contained a cyclopoid copepod, which Dr. Abraham Fleminger of Scripps Institution of Oceanography has identified as a species of the epipelagic genus *Oncaea*, and a minute amphipod, the identification of which as a hyperiid has been confirmed by Drs. John A. McGowan and William A. Newman, of Scripps Institution of Oceanography.

#### SQUIDS

Cephalopods, presumably squids, but possibly including some pelagic octopi, apparently constitute a considerable proportion of the seemingly meager diet of *Euprotomicrus bispinatus*. Remains of cephalopods (all termed "squids" in the preceding tabulation) were found in the alimentary canal of this shark, certainly in 5 specimens and possibly to probably in at least 5 others, among the 12 examined for food. The types represented are consonant with the fishes eaten in indicating that this shark feeds well below the surface.

Parin's (1964: 176) one mention of the food of this shark concerned finding, in a 216-mm specimen, well-preserved pieces of tentacles of an obviously rather large squid.

*Cranchiid squid*.—Remains in shark no. 9 of a squid, identified as almost certainly one of the Cranchiidae by Dr. John A. McGowan of Scripps Institution of Oceanography, strongly confirms the hypothesis that *Euprotomicrus bispinatus* commonly feeds well below the surface and engages in diurnal vertical migrations. This very pale squid specimen has a greatly expanded, very thin tail fin, connected with the foreparts by a very slender "waist." Both beaks remain. According to Dr. McGowan the cranchiids are rather common at moderate depths in the open sea, but are encountered with extreme rarity at the surface.

*Blackish remains of other squids*.—Nearly all the twelve specimens opened contain at least a trace of much digested blackish to jet-black remains of flesh and/or skin which appear to represent squids. Such material was noted in sharks no. 9?, 11?, 23?, 25?, 26, 27?, 29?, 30, and 31. The better-preserved remnants and even isolated pieces of skin with thickly set oval melanophores (as in specimen 26), little resemble the types of squid that are dipnetted under light, and presumably represent bathypelagic species that the shark had captured during vertical migration.

## EYE LENSES (OF SQUIDS OR FISH)

Isolated eye lenses, which have resisted digestion, were found in specimens 9, 23, 28, 30, and 31. Two lenses, seemingly a pair, in specimen 30 are semiovoid (truncated at one end) and seem to represent a squid, but all the other loose lenses are spherical and are not distinguished as to squid or fish origin.

## FISHES

Fishes are obviously of high importance in the nutrition of this extremely dwarfed pelagic shark, and the species that are eaten reveal something of this shark's distribution and life ways. They indicate that *Euprotomicrus*, as has been suspected, generally feeds well below the very surface where all specimens have been caught, and therefore must engage in vertical migrations (p. 42). At least moderate alacrity is suggested by the species caught. Biting efficiency of the well-aligned and sharp lower teeth (p. 21) is reflected in the clean cut through the body of a lanternfish, *Myctophum nitidulum*.

*Vinciguerria nimbaria* (Jordan and Williams).—The identification of a rather well preserved, half-grown specimen of this lightfish, 26 mm in standard length, from *Euprotomicrus* no. 11, collected in the central North Pacific at 18°24' N., 175°12' W., seems fully assured on the basis of characters used by Ahlstrom and Counts (1958), by Grey (1964: 143–149, figs. 29–34), and by other authors quoted in those articles. Critical characters are the pair of symphyseal photophores and the number of gill rakers (5 in this specimen, with first one reduced + 1 + 12 on each side). The rakers are much more numerous in *V. lucetia* (Garman), but are only slightly fewer in *V. poweriae* (Coeco). Distinction from *poweriae* is clearly established not only by the symphyseal photophores, but also by the relatively small, numerous, and nearly erect mandibular teeth. Half-grown and adult specimens of *V. poweriae*, which we now have from the Pacific Ocean but which was scarcely represented in the material available to the authors just cited, have, as a trenchant character, the few and large mandibular teeth directed first outward, then hooked upward. (The Pacific population may be taxonomically distinct.) The specimen of *V. nimbaria* in question is deposited in the United States National Museum (Cat. No. 200618).

This species is of special significance in connection with the distribution of *Euprotomicrus bispinatus*. It, like *Euprotomicrus*, seems to be largely confined to the central water masses, avoiding the shoreline. The one specimen taken very close to the shore in southern California, and the only other one from the California Current region (see Ahlstrom and Counts, 1958: 406–407, fig. 29) were obviously strays.

The known vertical distribution of *V. nimbaria* renders it almost certain that the specimen of this species under discussion was captured by *Euprotomicrus* well below the surface. Grey (1964: 136) had no study material from the surface and reviewed the vertical distribution of the species as follows:

*Vertical Distribution.* In the North Atlantic, postlarval stages are found chiefly in the upper 50 m, the metamorphosis stages and adults in 30–150 m. There are only a few records of capture over shallow depths: the specimen reported here, taken aboard the CAROLINE in a trawl hauled

in 438-549 m; one specimen in 457 m off West Africa; and possibly the young specimens from Florida. A specimen was once caught at the surface at night in Funchal Harbor, Madeira; and specimens have been found washed ashore in South Africa and onto the deck of a ship in the open Pacific. The vertical distribution in the Pacific is not known, but specimens from the Indian Ocean were all from depths below 400 m. Norman reported 161 specimens, 17-46 mm, taken in the Arabian Sea; 79 of them were from midwater hauls made in depths between 400 and 2000 m (1-39 per haul), and 82 of them were caught in a single bottom haul made in 549-640 m.

Data checked for us by Bert N. Kobayashi on the material of this species in Scripps Institution of Oceanography, mostly from the Pacific Ocean, confirms the virtual certainty that the specimen eaten by *Euprotomicrus* was taken well below the surface. All the 26 cataloged lots, with the exception of the one taken by explosives close to the California shore and of one other from the stomach of the deep-living bigeye tuna, *Thunnus obesus* (Lowe), were captured by midwater trawl. Not one specimen has been secured during hundreds of collections dipnetted by the staff of this institution.

*Vinciguerria* sp.—*Euprotomicrus* no. 27 contained one young *Vinciguerria* of undetermined species, about 12 mm in standard length, along with various pieces, mostly with similar photophores, representing still smaller fish. The freshness of these tiny fish, and the lack in the gut of any animal in fresh enough condition to have been the primary predator, indicates that at times *Euprotomicrus* feeds on very small organisms.

*Argyropelecus* cf. *aculeatus* Valenciennes.—The identification of this hatchetfish (by Bert N. Kobayashi, who has extensively studied the genus) is somewhat tentative because the fish has been broken up considerably. Characters indicative of *A. aculeatus* are anal and subcaudal photophores closely grouped; dorsal blade very high; caudal peduncle slender; ventral-profile scales probably spined.

This food item, from the mid-North Pacific (from shark no. 25), provides particularly strong evidence that *Euprotomicrus* feeds at considerable depths and engages in vertical migrations. None of the hatchetfishes occurs at the surface: 300 m approximates their upper limit.

*Myctophum nitidulum* Garman.—One specimen of this lanternfish, estimated to have been 42 mm in standard length (using measurements between photophores in this example and in net-caught fish), was in the cardiac part of the stomach of shark no. 30. By special good fortune the diagnostic SAO and VLO photophores remain, with a few of the VO, to warrant a firm identification. The relative position of the photophores to one another and to the lateral line corresponds with that figured for *Myctophum affine* (Lütken) by Bolin (1939, fig. 11), and with no other species treated in that paper, which covered the myctophids then known from off western North America: SAO<sub>1-3</sub> form a straight and very steep line, with SAO<sub>2</sub> very close to the lateral line; VLO is slightly below the level of SAO<sub>2</sub> and directly below origin of dorsal fin.

Identification with *Myctophum affine* is correct only to the species group, which is currently under revision and is known to be a complex. Gibbs (1957) has already shown that "*M. affine*" of the Atlantic is a complex of two distinct species, *M. affine* proper and *M. nitidulum* Garman (1899: 266-267, pl. 56, fig. 3), which was

described from the east-central North Pacific. According to Robert L. Wisner of Scripps Institution of Oceanography, an authority on the family, *M. nitidulum* is the only species of the *M. affine* group in the general region from which our specimen came, and no other myctophid with the observed photophore pattern occurs in that area.

The structure of scales still adhering to the specimen, and of two scales found loose in the spiral valve, confirms the identification. They are smoothly rounded on the exposed margin and have a wide and regular fan of radii and strong circuli on the concealed anterior field; some of them have extremely fine, readily denuded vertical lines (circuli?) on the exposed field, which is devoid of ordinary circuli.

This food species is noncommittal in regard to the depth at which the shark had been feeding, because it commonly rises to the very surface at night.

The lanternfish had been clearly bitten in two just behind the SAO file: a demonstration of the effectiveness of the regular knifelike alignment of the thin yet strong and interlocked mandibular teeth (p. 21).

*Collybus drachme* Snyder.—Very slender, vertically elongated scales associated with a vertebral column and a piece of flesh in specimen 24 prove, on comparison with material from the stomach of tunas, to have come from a juvenile of this bramid. Snyder (1904: 526) had material from the stomach of a dolphinfish (*Coryphaena*) at Honolulu, Hawaii, and King and Ikehara (1956b) found this pomfret to be a significant item in the food of yellowfin and bigeye tuna in the tropical Pacific. Gosline and Brock (1960: 180) noted that the young of *Collybus drachme* are taken in nets hauled near Hawaii for offshore plankton. The pomfret, therefore, was probably caught near the surface.

*Unidentified fish remains*.—A single small fish scale from the intestinal canal of shark no. 26, which was taken in the Indian Ocean, closely resembles the scales of *Myctophum nitidulum* just described and probably came from some other species of Myctophidae. It differs chiefly in having ordinary circuli on the basal part of the exposed field, the outer part of which had been digested. A small fin ray came from the same shark.

A single fish scale, found in specimen 27, remains unidentified despite its very distinctive structure. It is described because eventually it should be recognized. The scale is vertically subelliptical,  $0.8 \times 1.3$  mm. Its vertically elliptical nucleus, presumably representing the scale of a prejuvenile stage, is covered by vertical, parallel circuli on the larger posterior field and at most one or two circuli on what was the anterior edge. Outside this nucleus strong circuli ring the anterior field and run obliquely across the lateral fields. On the posterior field, in the rather narrow margin outside the prejuvenile vertical circuli, the surface is unsculptured. The gently curved posterior edge comprises flat, sharply pointed processes. We do not recognize the group of fish represented by this scale. It seems certain that the scale is not that of a young *Vinciguerrria*, because *V. lucetia* (Garman) has more rounded scales without a prejuvenile nucleus, and has a smooth posterior field and even posterior border, coarser circuli, and one foldlike median radius in the anterior field.

The only other unidentified fish remnant found in this study, in shark no. 12,



seems distinctive, but has as yet defied identification. It appears to be a small pelvic spine, with a complex and highly asymmetrical base. It is flattened, and is denticulate along one edge. We do not recall any surface-pelagic fish with such a spine.

#### TOOTH OF EUPROTOMICRUS

The single *Euprotomicrus* tooth recovered in this food study was found in the spiral valve of shark no. 30, the teeth of which were much larger. Much of the basal part of the tooth had been digested. These circumstances, along with Strasburg's findings and conclusions regarding *Isistius* teeth in the intestinal canal of *Isistius*, lead us to believe that *Euprotomicrus* no. 30 had swallowed one of its own lower teeth, presumably as a result of its having been snagged, probably with other teeth, in food being ingested during a previous period of tooth replacement. Perhaps this tooth had long remained trapped in a fold of the spiral valve. As for *Isistius*, cannibalism seems to be a less plausible explanation.

It seems that swallowing its "lowers" is infrequent in *Euprotomicrus*, though probably a common occurrence in *Isistius*. Among 8 specimens of *Isistius* examined for gut contents by Strasburg, 3 contained teeth (respectively 27, 9, and 3) of the same species, whereas among the 12 specimens of *Euprotomicrus* studied for food only one contained a single tooth. Perhaps *Isistius*, which reaches a considerably larger size than *Euprotomicrus*, attacks larger and stronger prey, which more often break off the ribbon of mandibular teeth being replaced (pp. 21-22). Strasburg did comment on the apparent large size of squids eaten by *Isistius*.

#### SAND GRAINS

Several sand grains were a startling constituent of the contents of the cardiac section of the stomach of *Euprotomicrus* no. 27, which was collected at the surface over a point near the eastern edge of the East Pacific Rise, far off northern South America, at 14°16' S., 120°40' W., where the depth was recorded as 3,579 m. Most of these grains are clear-whitish; one is a flattish black grain with undular surface; others are a blackish and a brown flakelet. Dr. Albert E. J. Engel and Celeste G. Engel (personal communication) have identified most of the grains as feldspar and have expressed the opinion that they resemble the sand grains produced by weathering of submarine volcanic rock along the East Pacific Rise, as described by them (Engel and Engel, 1964).

When the inorganic material was found in the stomach of this pelagic shark it was assumed that it had been scooped up, probably during feeding activity, on a nearby guyot or a seamount. Examination of a detailed bottom topography chart being drawn up by Thomas E. Chase for Dr. Henry W. Menard of Scripps Institution of Oceanography, however, shows no guyots closer than a chain along the Easter Island Fracture Zone, close to 25° S., nearly 1,000 miles to the southeast. A cluster of deep seamounts lies considerably closer, along the East Pacific Rim to the westward. Near the point of collection there are some bottom hillocks, but of low relief. It is quite possible that there may be guyots or seamounts in the vicinity, inasmuch as the station where this *Euprotomicrus* was taken is at the southern tip of one leg of "Downwind" expedition and a vast region farther southward remains a bathymetric blank. Because it seems unlikely that this tiny shark

moves far or fast we are prompted to predict the discovery of a major seamount or guyot nearby. There is no proof, however, that the sand grains may not have long remained among the mucosal folds of the stomach. Nor can we be sure that the shark is incapable of very deep dives. Sand derived from the weathering of undersea volcanics does occur in very deep water on the East Pacific Rise, as Engel and Engel have shown.

The evidence that this epipelagic shark descends at times to the bottom, and probably feeds there, is one more link in a long chain of evidence that the distinction between benthonic and pelagic living is not nearly so sharp as has generally been assumed.

#### CESTODE PARASITES

Cestodes were found in 6 of the 12 specimens of *Euprotomicrus* which were examined for food. They appear to represent a single type (pl. 5, fig. 2). They range in size from barely above microscopic to a length (preserved) of 17 mm. All were loose in the cardiac section of the stomach. The number per fish was 1 in specimen 11 (see table 1), 2 each in 26 and 27, 4 in 23, 5 in 28, and 14 in 24. Nos. 11 and 24 came from the north-central Pacific, 23, 27, and 28 from the southeastern Pacific, and 26 from the Indian Ocean.

These parasites were identified by Dr. A. J. MacInnis, University of California, Los Angeles, and Dr. Robert J. Goldstein, University of Texas Southwestern Medical School, as trypanorhynchian cestodes. Dr. Goldstein kindly referred the material to the outstanding authority on the group. Dr. Robert Ph. Dollfus, Laboratoire d'Helminthologie et Parasitologie Comparée, Paris, who, after examining the specimens further, has definitely identified them as *Sphyriocephalus tergestinus* Pintner (1913: 123), particularly on the basis of the diagnostic character of the ova in one adult specimen. Parasites of this group may mature in the spiral intestine of elasmobranchs, but none was found there in *Euprotomicrus*. *Sphyriocephalus tergestinus*, the type species of the genus, was described from "*Alopecias*" [*Alopias*] *vulpinus* (Bonnaterre). Dr. Dollfus informs us that this cestode has been reported from the stomach of *Isurus "glaucus"* [*oxyrinchus* Rafinesque], from Japan, by Yamaguti (1934: 94-95, figs. 145-151), under the name of *Sphyriocephalus viridis* (Wagener).

#### FOOD OF EUPROTOMICRUS AND ISISTIUS COMPARED

There seems to be considerable similarity between *Euprotomicrus* and *Isistius* in respect to their food, which is surprising in view of their sharply contrasting internal anatomy (pp. 23-34). Strasburg (1963: 35) found that the food of *Isistius* commonly consists of squid, as is true for the subject of our study, and of fishes, including *Vinciguerria*, which is likewise eaten by *Euprotomicrus*. *Vinciguerria*, however, may have been caught by *Isistius* in the trawl, as Strasburg suggested. One of the eight specimens of *Isistius* studied by Strasburg contained "three crustaceans which bear some resemblance to caligoid copepods."

In agreement with the findings of Strasburg, the one *Isistius* in the Scripps collection, a 386-mm mature male dipnetted at the surface on the equator at 100° 00' W., contained the following material: in the cardiac section of the stomach, in addition to some food debris, a single squid beak 7.7 mm in longest dimension (con-

firming Strasburg's findings that *Isistius* feeds on surprisingly large squid); in the duodenum, 3 lenses of either squids or fish; and, in the valvular intestine, only some food debris. The suggestion that *Isistius* ingests larger food items than *Euprotomicrus* does is consonant with its larger size and firmer tissue, and with its broader mouth and stronger jaw (p. 33; pl. 7).

The Scripps specimen, in this respect also resembling Strasburg's, contained considerable liquid oil in the body cavity and a small amount within the alimentary canal. The abundance of oil in *Isistius* and the lack of appreciable quantities in *Euprotomicrus* seem to be related to the immense liver of *Isistius* and the much reduced organ in *Euprotomicrus* (pp. 24-26; figs. 5, 6).

#### DWARF SIZE

Except for the still more dwarfed squaloid sharks of the related genus *Squaliolus*, discussed, with references, in the section on systematic status (p. 3), *Euprotomicrus bispinatus* is the smallest known shark. Males are even smaller than females (p. 37). The small size is related to the pelagic habitat, and is interpretable as one of the adaptations toward the attainment of neutral buoyancy (p. 43).

Total lengths, available for 33 of the 36 known specimens of *E. bispinatus* (table 1; fig. 10), range for males from 97 to 220 mm and for females from 105 to 265 mm. Weights, seemingly alike for the sexes, range from 5.3 to 67.6 g.

The two reported sets of embryos, all retaining large yolk sacs, varied from 22.3 to 24.8 and from 50 to 60 mm in total length. We presume that the length at birth is between 70 to 95 mm, because the four smallest known juveniles are 97 to 112 mm long. These are essentially small replicas of the adults. A 170-mm male is almost fully mature, to judge from the almost completely elaborated clasper, and all eleven larger males, 198 to 220 mm long, are fully mature. The three females 140 to 161 mm long are immature, and none of the four females 201 to 219 mm long seems to be gravid. Six females 233 to 265 mm long contain developing ova or embryos. The largest one, the only one longer than 256 mm, may show signs of senility, with some ova possibly being resorbed (p. 34).

The length-weight curve (fig. 10) appears to be of typical exponential form. Because the weights are of preserved specimens of varying condition and treatment, the length-weight relations have not been analyzed in any detail.

The dwarf size of this shark, nicely paralleling the dwarf size of certain melamphaid teleosts discovered by Ebeling (1962), undoubtedly of genetic basis in each group, seems to be correlated with existence in waters of low nutrients and low plankton production (Reid, 1962).

#### CHARACTERS CORRELATED WITH DWARFISM

Many of the distinctive characters of *Euprotomicrus bispinatus* are of the sort that have been correlated with dwarfism in other fishes, particularly by Te Winkel (1935) in her study of *Mistichthys luzonensis*, which was the smallest known vertebrate (Smith, 1902) until the discovery (Herre, 1927: 198-199, pl. 15, fig. 3; 1929) of another still smaller gobioid fish. Among the features of *Euprotomicrus* correlated in other fishes with small size we note the following: Cartilage is re-

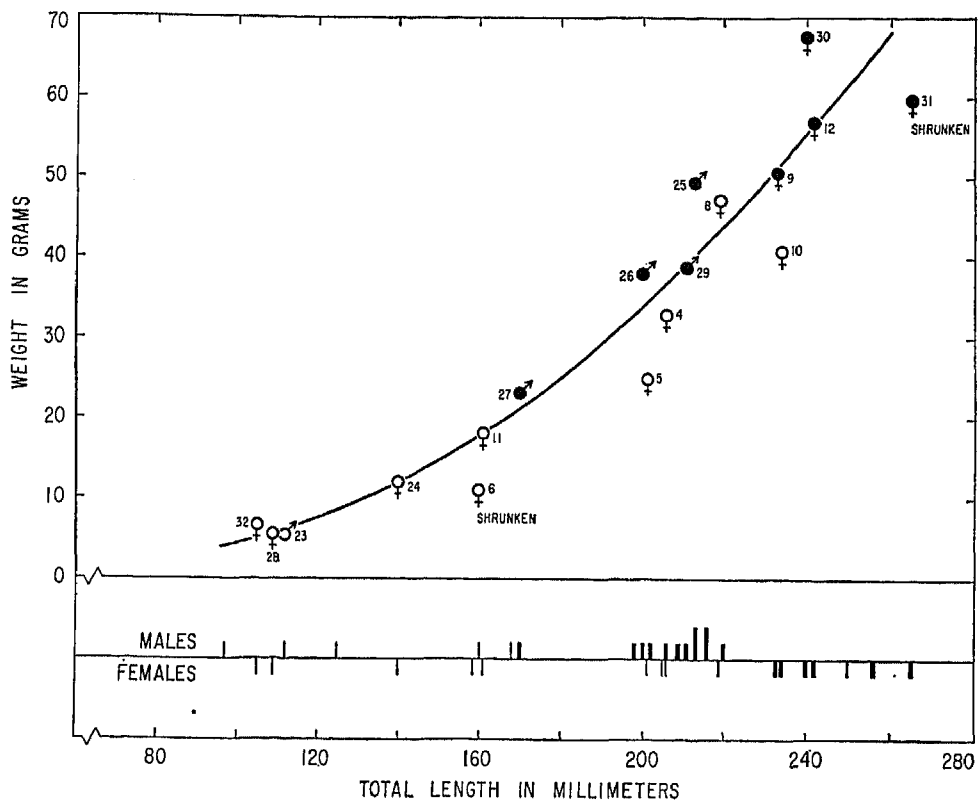


Fig. 10. Length and weight relations of the sexes of *Euprotomicrus bispinatus*. *Above*: length-weight relations; sex indicated by conventional symbols, with circles blackened for mature males and for four females with maturing ova. Numbers correspond with entries in table 1. *Below*: all available total-length data (as in table 1); bars broadened for mature males and for the six known females with maturing ova or embryos. (Narrow lines represent immature males and either immature or unchecked females.)

tained to a marked degree in the skeleton. In *Euprotomicrus* this is paralleled by the very limited calcification of the skeleton, already stressed in the accounts of the vertebral column, the head region, and the claspers and adjacent structures (pp. 27-34; pls. 6-8). However, this feature in *Euprotomicrus* may also be regarded as an adaptation for neutral buoyancy.

Segments and other meristic features are few. As pointed out above (pp. 27, 30), the number of vertebrae in *Euprotomicrus* is fewer than in any other shark, with the exception of the still more dwarfed sharks of the related genus *Squaliolus*. The teeth are also few (pp. 22-23). However, the numbers are few also in relatively large members of the same family (secondarily increased in size?). Certainly the photophores are not few.

Some characters, notably the essentially diphyccercal tail, are interpretable as being juvenile or even embryonic. This feature, shared by the even more dwarfed genus *Squaliolus* and approached by *Isistius*, is perhaps the most definite of the

features related to dwarfism in these sharks, for the larger dalatiines have heterocercal caudals (Bigelow and Schroeder, 1948: 499-532; 1957: 109-136). The relatively large head, large eyes, and large spiracles are interpretable as juvenile characters.

The embryos are few, with a seemingly constant complement of  $4 + 4 = 8$  (pp. 34, 37).

The clasper (pp. 33-36) is much less differentiated from the pelvic fin proper than in most elasmobranchs. This again seems to be in part a group character, rather than being, or in addition to being, a feature related to dwarfism. Perhaps, however, the manifestation of such characters in the larger dalatiines may reflect secondary increase in size of the larger genera.

### SUMMARY

*Euprotomicrus* is treated as a distinct monotypic genus in the subfamily Dalatiinae of the family Squalidae (equivalent to the superfamily or suborder Squaloidea in some classifications). *Squaliolus*, comprising the only smaller sharks, is maintained as a distinct genus. Very trenchant differences in clasper structure, in the skeleton, and even more spectacularly in visceral anatomy indicate that the differentiation of *Euprotomicrus* and *Isistius* has been long and profound.

The species names *mauritanus*, *labordii*, and *hyalinus* are listed as synonyms in the complete synonymy of *Euprotomicrus bispinatus*.

Only 8 specimens of the species were reported prior to 1951. We now list 37.

Color varies from light brown to brownish black.

Detailed morphometric analysis discloses no specific distinctions, but suggests the possible slight differentiation of a race in the Atlantic Ocean, from which the species is now recorded.

The abdomen grows with positive allometry; the caudal and head regions, consistently with compensatory negative allometry. Other regions grow isometrically.

*Euprotomicrus* is luminescent, emitting a blue-green glow from thousands of tiny photophores on the ventral surface. The photophore structure resembles that of *Isistius*, but is different from that of the luminescent squaline sharks *Etmopterus* and *Centroscyllium* in that the light organs of *Euprotomicrus* form a complicated network, lack an iris-like feature, and contain a single photogenic cell. Some features are generalized, some specialized. It is thought that the structures alleged to be photophores in *Somniosus* are not light organs.

Denticles of *Euprotomicrus* are dimorphic. The larger ones are variably pitted.

The upper and lower teeth are profoundly different. The needle-pointed upper teeth are arranged in quincunx. The lower teeth form an even-edged series, locked together and replaced as a unit. The 19 to 23 mandibular teeth seem to remain constant in any individual.

Stomach is J-shaped; duodenum is an inverted U, leading directly into the valvular intestine, which contains about 13 turns. The small 2-lobed liver is restricted to the front of the body cavity. Spleen has a long inner arm. Pancreas is well developed. *Isistius* has a straight stomach; a short duodenum connecting end of

stomach with the valvular intestine behind its blind anterior end; 7 turns in the spiral valve; and an immense, rolled liver filling almost entire body cavity.

Vertebrae are notably few, about as in *Squaliolus*: monospondylous vertebrae are remarkably constant (31 or 32); diplospondylous ones number 28 to 38, of which 15 to 20 are precaudal and 11 to 19 caudal. Calcification is almost wholly confined to region of notochordal sheath (more so than in *Isistius*). In the tail, neural arches and radials seem devoid of calcification, as also the hemal arches, which form thin-walled bulbs. These structures are weakly calcified in *Isistius*.

Cranial and labial cartilages also seem to be virtually devoid of calcification in *Euprotomicrus*, moderately calcified in *Isistius*.

Clasper structure is of the squaloid type, with marked external and internal differences between *Euprotomicrus* and *Isistius*.

*Euprotomicrus* is ovoviviparous with, uniquely, a complement of four embryos in each ovary. Even at a length of 54 to 60 mm embryos closely resemble adults, and young of about 100 mm are essentially adult in appearance.

Sex ratio of 33 sexed individuals is 16:17. Mature male specimens are consistently smaller than mature females.

*Euprotomicrus bispinatus* is known almost exclusively from the relatively sterile central water masses of the North Pacific, South Pacific, South Indian, and South Atlantic oceans. It avoids the major marginal currents, where temperatures are low at the depth of 200 m. It also avoids the great eastern wedge of Pacific Equatorial Water, where the temperature is also low at 200 m and the oxygen minimum layer similarly shallow. Strays have been taken twice not far north of the Antarctic Convergence.

The depth of water where *Euprotomicrus* has been taken, always at the surface, ranges (15 records) from 1,829 to 9,938 m.

The hypothesis that this luminescent shark undertakes vertical, presumably diurnal, migrations has been confirmed by a study of its food, which includes bathypelagic squids and fishes. *Isistius* probably also moves vertically, but has seldom been caught at the surface. *Squaliolus* seems to have a wide vertical range and to be both benthonic and pelagic.

*Euprotomicrus* seems to be neutrally buoyant, apparently as a result of adaptations involving weak tissues, including a delicate skeleton largely devoid of calcification. Small size is no doubt a contributing factor.

This shark is attracted to light and is an active swimmer and a predacious feeder.

Bathypelagic squids and fishes enter prominently, and perhaps chiefly, into the nutrition of this shark. Despite the abundance of crustaceans in the waters presumably traversed by this shark, it seems to rely primarily on fishes and cephalopods, as do some of the largest and most predacious pelagic sharks and teleosts. For such prey the grasping upper teeth and the shearing common edge of the lower teeth seem admirably adapted. The considerable proportion of nearly empty alimentary tracts, the lack of any full stomachs among the 12 studied, and the small size of food commonly taken (such as lightfish, *Vinciguerra* sp., 12 mm and less in standard length) is concordant with the oceanographic evidence that *Euprotomicrus* typically inhabits the oligotrophic central water masses. Occa-

sionally *Euprotomicrus* swallows its lower teeth, probably during replacement, but apparently less often than does *Isistius*. Volcanic grains of sand in one specimen indicate occasional feeding on the bottom, possibly in very deep water (further deemphasizing the sharpness of the contrast between benthonic and pelagic distributions).

Trypanorhynchan cestodes, of one species, *Shyriocephalus tergestinus*, are of frequent occurrence in the cardiac section of the stomach.

Except for the still more dwarfed sharks of the related genus *Squaliolus*, *Euprotomicrus* is the smallest known shark. Lengths range from 97 to 265 mm; weights (of preserved specimens), from 5.3 to 67.6 g. Length at birth is presumably between 70 and 95 mm. Juveniles about 100 mm long essentially resemble adults. Mature male specimens range from 170 to 220 mm; gravid females, 233 to 265 mm. Length-weight curve is of typical exponential form.

Characters correlated with dwarfism include very limited calcification of the skeleton; few vertebrae and few teeth; essentially diphyercal caudal, a neotenic feature; large head, eyes, and spiracles; few embryos; and the less than usual differentiation of the clasper from the pelvic fin.

## LITERATURE CITED

- ABE, TOKIHARU  
 1962. A record of a little squaloid shark, *Squaliolus laticaudus*, from Suruga Bay. Jap. Jour. Ichth., 8 (5/6): 147-151.
- AHLSTROM, ELBERT H., and ROBERT C. COUNTS  
 1955. Eggs and larvae of the Pacific hake *Merluccius productus*. Fish. Bull. 99, U.S. Fish and Wildlife Serv., 56: i-ii, 295-329, figs. 1-25.  
 1958. Development and distribution of *Vinciguerria lucetia* and related species in the eastern Pacific. Fish. Bull. 139, U.S. Fish and Wildlife Serv., 58: i-iv, 363-416, figs. 1-29.
- ALEEV, YU.  
 1963. Funktsionalnyye osnovy vneshnego stroenia ryby (Functional basis of the exterior structure in fishes). M., Izd-vo AN SSSR (Moscow ed. of the Acad. of Sci. USSR). Pp. 1-247, figs. 1-162.
- ALVARIÑO, ANGELES  
 1965. Distributional atlas of Chaetognatha in the California Current region. California Cooperative Oceanic Fisheries Investigations, Atlas no. 3: i-xiii, 7 figs., charts 1-291.
- ANDRIASHEV, A. P.  
 1961. Spisok ikhtologičeskih stantsii s predvaritel'noi kharakteristikoi lovov (List of ichthyological stations with a preliminary characterization of the catches). Trudy Sovetskoi Antarkticheskoj Ekspeditsii, 22: 227-234.  
 1965. A general review of the antarctic fish fauna. In Biogeography and ecology in Antarctica. Ed. P. van Oye and J. van Mieghem. Monogr. Biol., 15: 491-550, figs. 1-18.
- BELLOC, GÉRARD  
 1937. Sur la capture dans le bassin d'Arachon d'un Squale nouveau pour la faune de France; *Euprotomicrus Sarmeniti* Noronha. Bull. Mus. Nat. Hist. Nat. Paris, ser. 2, 9: 370-372.
- BERTENSEN, E., and N. B. MARSHALL  
 1956. The Miripinnati, a new order of teleost fishes. Dana Report no. 42: 1-34, figs. 1-15, pl. 1.
- BERTIN, LÉON  
 1939. Catalogue des types de Poissons du Muséum National d'Histoire Naturelle. 1<sup>re</sup> Partie, Cyclostomes et Sélaciens. Bull. Mus. Nat. Hist. Nat. Paris, ser. 2, 11 (1): 51-98.
- BIERI, ROBERT  
 1959. The distribution of the planktonic Chaetognatha in the Pacific and their relationship in the water masses. Limnol. and Oceanogr., 4 (1): 1-28, figs. 1-26.
- BIGELOW, HENRY B., and WILLIAM C. SCHROEDER  
 1948. Sharks. In Fishes of the western North Atlantic, part one. Mem. Sears Found. Mar. Res., 1 (1): 59-546, figs. 6-106.  
 1957. A study of the sharks of the suborder Squaloidae. Bull. Mus. Comp. Zool. Harvard Coll., 117 (1): 1-150, figs. 1-16, pls. 1-4.
- BOLIN, ROLF L.  
 1939. A review of the myctophid fishes of the Pacific coast of the United States and of Lower California. Stanford Ichth. Bull., 1 (4): 89-156, figs. 1-29.
- BOULENGER, G. A.  
 1902. Pisces. In Report on the collections of natural history made in the antarctic regions during the voyage of the "Southern Cross." British Museum, London. Pp. 174-189, pls. 11-18.
- BRADSHAW, JOHN S.  
 1959. Ecology of living planktonic Foraminifera in the North and Equatorial Pacific Ocean. Contr. Cushman Found. Foraminiferal Res., 10 (2): 25-64, figs. 1-43, pls. 6-8.
- BRINTON, EDWARD  
 1962. The distribution of Pacific euphausiids. Bull. Scripps Inst. Oceanogr., 8 (2): 51-270, figs. 1-126.
- BURCKHARDT, RUD.  
 1900a. Beiträge zur Anatomie und Systematik der Laemargiden. Anat. Anz., 18 (20-21): 488-492, figs. 1-4.



BURKHARDT, RUD.—*Continued*

- 1900b. On the luminous organs of selachian fishes. *Ann. and Mag. Nat. Hist.* ser. 7, 6: 558-568, figs. 1-8.

## BUREAU OF FISHERIES

1911. Dredging and hydrographic records of the U.S. Fisheries Steamer Albatross during the Philippine Expedition, 1907-1910. *Bur. Fish. Doc. no. 741* (included in *Rep. Comm. Fish.*, 1910): 1-97.

## CHEN, JOHNSON T. F.

1963. A review of the sharks of Taiwan. *Dept. Biol., Coll. Sci., Tunghai Univ., Biol. Bull.* 19 (Ichthyol. Ser. no. 1): 1-102, figs. 1-28.

## CLARKE, WILLIAM D.

1963. Function of bioluminescence in mesopelagic organisms. *Nature*, 198 (4887): 1244-1246, figs. 1-2.

## CUNNINGHAM, ROBERT O.

1899. On a few points in the structure of Laborde's shark (*Euprotomiscus labordei*). *Proc. Zool. Soc. London*, 1899: 732-734.

## DAHLGREN, ULRICH, and W. A. KEPNER

1908. A textbook of the principles of animal histology. New York: Macmillan. Pp. i-xiii, 1-515, figs. 1-470.

## DALES, R. PHILLIPS

1957. Pelagic polychaetes of the Pacific Ocean. *Bull. Scripps Inst. Oceanogr.*, 7 (2): 99-168, figs. 1-64.

## DEACON, G. E. R.

1963. The Southern Ocean. *In* *The Sea: Ideas and observations on progress in the study of the sea*. Ed. M. N. Hill. New York and London: Interscience. Vol. 2: pp. 281-296, figs. 1-3.

## DI [= DE] NORONHA, ADOLFO CÉSAR

1926. A new species of deep water shark (*Squaliolus sarmenti*) from Madeira. *Ann. Carnegie Mus.*, 16: 385-389, pl. 35.

## DE NORONHA, ADOLFO CÉSAR, and ALBERTO ARTUR SARBENTO

1948. Vertebrados da Madeira, 2 (Peixes). *Junta Geral do Distrito Autónomo do Funchal*. Pp. i-xii, 1-181.

## DENTON, E. J., and N. B. MARSHALL

1958. The buoyancy of bathypelagic fishes with a gas-filled swimbladder. *Jour. Mar. Biol. Assoc. United Kingdom*, 37: 753-767, figs. 1-3.

## DICKENS, D. A. G.

1956. Deep sea shark: Indian Ocean. *Marine Observer, London*, 26: 73.

## DIETRICH, GÜNTER

1963. General oceanography: An introduction. *Trans. Feodor Ostapoff*. New York and London: Interscience. Pp. i-xv, 1-588, figs. 1-228.

## DUMÉRIL, AUG.

1865. Histoire naturelle des Poissons ou ichthyologie générale. Vol. 1: élamobranches plagiostomes et holocéphales ou chimères. Pt. 1, pp. 1-720.

## EBBLING, ALFRED W.

1962. Melamphaidae. I: Systematics and zoogeography of the species in the bathypelagic fish genus *Melamphaes* Günther. *Dana Report no. 58*: 1-164, figs. 1-73.

## EIGENMANN, ROSA SMITH

1890. Description of a new species of *Euprotomiscus*. *Proc. California Acad. Sci.*, ser. 2, 3: 35.

## ENGEL, A. E. J., and CELESTE G. ENGEL

1964. Igneous rocks of the East Pacific Rise. *Science*, 146 (3643): 477-485, figs. 1-4 and cover fig.

## FLEMINGER, A.

1964. Distributional atlas of calanoid copepods in the California Current region. Pt. I. California Cooperative Oceanic Fisheries Investigations, Atlas no. 2: i-xvi, 6 figs., charts 1-313.

## FOWLER, HENRY W.

1930. A list of the sharks and rays of the Pacific Ocean. Proc. 4th Pac. Sci. Cong., 3: 481-508.  
1941. Contributions to the biology of the Philippine Archipelago and adjacent regions. The fishes of the groups Elasmobranchii, Holocephali, Isospondyli, and Ostariophysi obtained by the United States Bureau of Fisheries Steamer "Albatross" in 1907 to 1910, chiefly in the Philippine Islands and adjacent seas. Bull. U.S. Nat. Mus. no. 100, vol. 13, pp. i-x, 1-879, figs. 1-30.

## GARMAN, SAMUEL

1899. The Fishes. In Reports on an exploration off the west coasts of Mexico, Central and South America, and off the Galapagos Islands, in charge of Alexander Agassiz, by the U.S. Fish Commission Steamer "Albatross," during 1891, Lieut. Commander Z. L. Tanner, U.S.N., Commanding. Mem. Mus. Comp. Zool., Harvard Coll., 24: 1-431, pls. 1-85, A-N.  
1913. The Plagiostomia (sharks, skates, and rays). Mem. Mus. Comp. Zool. Harvard Coll., 36: i-xiii, 1-515, pls. 1-77.

## GARRICK, J. A. F.

1960. Studies on New Zealand Elasmobranchii. Pt. XII: The species of *Squalus* from New Zealand and Australia; and a general account and key to the New Zealand Squaloidea. Trans. Roy. Soc. New Zealand, 88 (3): 519-557, figs. 1-6.

## GARRICK, J. A. F., and STEWART SPRINGER

1964. *Isistius plutodus*, a new squaloid shark from the Gulf of Mexico. Copeia, 1964 (4): 678-682, figs. 1-2.

## GIBBS, ROBERT H., JR.

1957. A taxonomic analysis of *Mycotophum affine* and *Mycotophum nitidulum*, two lanternfishes previously synonymized, in the western North Atlantic. Deep-Sea Research, 4: 230-237, figs. 1-5.

## GILBERT, PERRY W.

1963. The visual apparatus of sharks. In Sharks and survival. Boston: D. C. Heath. Pp. 233-326, figs. 1-30.

## GILL, THEODORE

1865. Synopsis of eastern American sharks. Proc. Acad. Nat. Sci. Philadelphia, 16 (1864): 258-265.

## GOSLINE, WILLIAM A., and VERNON E. BROCK

1960. Handbook of Hawaiian fishes. Honolulu: University of Hawaii Press. Pp. i-ix, 1-372, figs. 1-277, 2 col. pls.

## GRAY, JOHN EDWARD

1851. List of the specimens of fish in the collection of the British Museum. Pt. I., Chondropterygii, pp. i-xi, 1-160, pls. 1-2.

## GREY, MARION

1964. Family Gonostomatidae. In Fishes of the western North Atlantic, pt. 4. Mem. Sears Found. Mar. Res., 1 (4): 78-240, figs. 21-61.

## GÜNTHER, ALBERT

1870. Catalogue of the Physostomi, and of the Chondropterygii, Cyclostomata, Leptocephali, in the British Museum. Cat. Fishes Brit. Mus., 8: i-xxv, 1-549, 3 figs.

## HERRE, ALBERT W. C. T.

1927. Gobies of the Philippines and the China Sea. Monogr. Bur. Sci., Manila, P.I., 23: 1-352, figs. 1-6, frontisp., pls. 1-30.  
1929. The smallest living vertebrate. Science, n.s., 69 (1786): 329-330.

## HUBBS, CARL L.

1952. Antitropical distribution of fishes and other organisms. Proc. 7th Pac. Sci. Cong., 3: 324-339.  
1963. *Chaetodon aya* and related deep-living butterflyfishes: their variation, distribution and synonymy. Bull. Mar. Sci. Gulf and Caribbean, 13 (1): 133-192, figs. 1-14.

- HUBBS, CARL L., and LAURA C. HUBBS  
 1954. Data on the life history, variation, ecology, and relationships of the kelp perch, *Brachyistius frenatus*, an embiotocid fish of the Californias. Calif. Fish and Game, 40 (2): 183-198, figs. 1-3.
- HUBBS, CARL L., and KARL F. LAGLER  
 1964. Fishes of the Great Lakes region. Ann Arbor: University of Michigan Press. Pp. i-xv, 1-213, figs. 1-251, pls. 1-44.
- HUBBS, CARL L., and J. L. MCHUGH  
 1951. Relationships of the pelagic shark *Euprotomierus bispinatus*, with description of a specimen from off California. Proc. Calif. Acad. Sci. ser. 4, 27 (6): 159-176, pls. 4-6.
- HUBBS, CARL L., GILES W. MEAD, and NORMAN J. WILIMOVSKY  
 1953. The widespread, probably antitropical distribution and the relationship of the bathypelagic iniomous fish *Anotopterus pharao*. Bull. Scripps Inst. Oceanogr., 6 (5): 173-198, fig. 1, pls. 2-6.
- HUTTON, FREDERICK WOLLASTER  
 1872. Fishes of New Zealand. Catalogue, with diagnoses of the species. Wellington: Colonial Museum and Geological Survey Department. Pp. i-xxi, 1-93, i-iii, pls. 1-12.
- ISHIYAMA, REIZO  
 1958. Studies on the rajid fishes (Rajidae) found in the waters of Japan. Jour. Shimonoseki Coll. Fish., 7 (2, 3): 193-394, figs. 1-86, pls. 1-3.
- IWAI, TAMOTSU  
 1960. Luminous organs of the deep-sea squaloid shark, *Centroscyllium ritteri* Jordan and Fowler. Pacific Sci., 14 (1): 51-54, figs. 1-4.
- JAMES, W. WARWICK  
 1953. The succession of teeth in elasmobranchs. Proc. Zool. Soc. London, 123 (2): 419-474, figs. 1-11, pls. 1-12.
- JOHANN, LEOPOLD  
 1899. Über eigenthümliche epitheliale Gebilde (Leuchtorgane) bei *Spinax niger*. Zeitschr. Wissensch. Zool., 66: 136-160, pls. 10-11.
- JOHNSON, MARTIN W.  
 1960. Production and distribution of larvae of the spiny lobster, *Panulirus interruptus* (Randall), with records on *P. gracilis* Streets. Bull. Scripps Inst. Oceanogr., 7 (6): 413-461, figs. 1-36.
- JOHNSON, M. W., and E. BRINTON  
 1963. Biological species, water-masses and currents. In *The Sea: Ideas and observations on progress in the study of the sea*. Ed. M. N. Hill. New York and London: Interscience. Vol. 2: pp. 381-414, figs. 1-13.
- KING, JOSEPH E., and ISAAC I. IREHARA  
 1956a. Some unusual fishes from the central Pacific. Pacific Sci., 10 (1): 17-24, figs. 1-5.  
 1956b. Comparative study of food of bigeye and yellowfin tuna in the central Pacific. Fish. Bull. 108, U. S. Fish and Wildlife Service, 57: i-ii, 59-85, figs. 1-12.
- KNAUSS, J. A.  
 1963. Equatorial current systems. In *The Sea: Ideas and observations in progress in the study of the sea*. Ed. M. N. Hill. New York and London: Interscience. Vol. 2: pp. 235-252, figs. 1-11.
- LEIGH-SHARP, W. HAROLD  
 1920. The comparative morphology of the secondary sexual characters of elasmobranch fishes: The claspers, clasper siphons, and clasper glands. Jour. Morph., 34 (2): 245-265, figs. 1-12.  
 1926. The comparative morphology of the secondary sexual characters of elasmobranch fishes: The claspers, clasper siphons, and clasper glands. Memoir X. Jour. Morph. and Physiol., 42 (1): 335-348, 2 diagrs., fig. 1.
- MARSHALL, N. B.  
 1956. Deep sea shark: Indian Ocean. Marine Observer, London, 26: 73-74.  
 1960. Swimbladder structure of deep-sea fishes in relation to their systematics and biology. Discovery Reports, 31: 1-122, figs. 1-47, pls. 1-3.

MAUL, G. E.

1948. Lista sistemática dos peixes assinalados nos mares da Madeira e índice alfabético. Junta Geral do Distrito Autónomo do Funchal. Funchal. Pp. 1-53. Separate, dated 1949, from Vertebrados da Madeira, 2 (Peixes), de Adolfo César de Noronha e Alberto Artur Sarmiento, pp. 135-181.

MÜLLER, J., and J. HENLE

1841. Systematische Beschreibung der Plagiostomen. Berlin: Von Heit & Co. Pp. i-xxii + 4, 1-200, 60 pls.

NORONHA (*see* DE NORONHA)

OHSHIMA, HIROSHI

1911. Some observations on the luminous organs of fishes. Jour. Coll. Sci. Tokyo Imp. Univ., 27 (15): 1-25, figs. 1-4, 1 pl.

OTSU, TAMIO, and HOWARD O. YOSHIDA

1957. Another record of the rare shark, *Euprotomicrus bispinatus*, from the Pacific Ocean. Copeia, 1957 (1): 58.

PARIN, N. V.

1963. Rezulytaty izucheniya pelagicheskoi iktiofauny Tikhogoi Indiiskogo okeanov pri pomoshchi elektricheskogo sveta [Results of studying pelagic ichthyofauna of the Pacific and Indian oceans by use of electric light for attracting fishes]. In Russian with English summary. Trudy Inst. Okeanol., 62: 128-144, 1 map.

1964. Data on the biology and distribution of the pelagic sharks *Euprotomicrus bispinatus* and *Isistius brasiliensis* (Squalidae, Pisces). Trans. Inst. Oceanol. Acad. Sci. USSR. Pp. 163-184, figs. 1-4. Translation by Edith Roden, reviewed and edited by Carl L. Hubbs, published in Fishes of the Pacific and Indian oceans: Biology and distribution, ed. T. S. Rass. (Washington: Smithsonian Institution and National Science Foundation, 1966). Pp. 173-195, figs. 1-40. Translation sponsored by the Israel Program for Scientific Translations (TT 65-50120).

PHILLIPPS, W. J.

- 1927a. Bibliography of New Zealand fishes. New Zealand Mar. Dept. Fish., Bull. no. 1: 1-68.  
1927b. A check list of the fishes of New Zealand. Jour. Pan-Pacific Res. Inst., 2 (1): 9-15.  
1928. Sharks of New Zealand: no. 2. New Zealand Jour. Sci. and Techn., 10 (4): 221-226, figs. 1-8.

PINTNER, THEODOR

1913. Vorarbeiten zu einer Monographie der Tetrarhynchoideen. Sitzungsber. Akad. Wiss. Wien, 122, Abt. 1: 171-254, pls. 1-4.

PUNNETT, R. C.

1904. Merism and sex in "*Spinax niger*." Biometrika, 3 (4): 313-362, pl. 1.

QUOY, [JEAN R. C.], and P. GAIMARD

1824. Description des Poissons, in Zoologie. In Louis de Freycinet, Voyage autour du monde, ... sur les corvettes de S. M. l'Uranie et la Physicienne ... 1817, 1818, 1819 et 1820. Paris: Pillet Aîné. Pp. 192-401, pls. 43-65.  
1831. [Entry on] "Leiche de Laborde, *Scymnus Mauritanus*, Quoy et Gaimard, Voyage de l'Uranie, pl. 44, fig. 2." Dictionnaire classique d'histoire naturelle, by Audouin, *et al.*, vol. 17, p. 131, pl. 114, fig. 2 [reference variously cited].

REGAN, C. TATE

1908. A synopsis of the sharks of the family Squalidae. Ann. and Mag. Nat. Hist., ser. 8, 2: 39-57.

REID, JOSEPH L., JR.

1962. On circulation, phosphate-phosphorus content, and zooplankton volumes in the upper part of the Pacific Ocean. Limnol. and Oceanogr., 7 (3): 287-306, figs. 1-6.

SAUVAGE, H.

1891. Histoire Naturelle des Poissons. In Histoire physique, naturelle et politique de Madagascar publiée par Alfred Grandidier. Paris. Vol. 16: pp. 1-543, pls. 1-50.

SCRIPPS INSTITUTION OF OCEANOGRAPHY

1948. World atlas of sea surface temperatures. 2d ed., 1944 (reprint). U.S. Navy Hydrographic Office, H.O. no. 225. 1 p., 48 charts.

- SIGALAS, R.  
1939-1940. Sur *Euprotomierus sarmenti* Noronha. Act. Soc. Linn. Bordeaux, 91: 70-71.
- SMITH, HUGH M.  
1902. The smallest known vertebrate. Science, n.s., 15 (366): 30-31.  
1912. The squaloid sharks of the Philippine Archipelago, with descriptions of new genera and species. Proc. U.S. Nat. Mus., 41 (1877): 677-685, figs. 1-4, pls. 50-54.
- SNYDER, JOHN OTTERBEIN  
1904. A catalogue of the shore fishes collected by the steamer Albatross about the Hawaiian Islands in 1902. U.S. Fish Comm. Bull., 22, for 1902: 518-533, pls. 1-13.
- SPRINGER, VICTOR G., and J. A. F. GARRICK  
1964. A survey of vertebral numbers in sharks. Proc. U.S. Nat. Mus., 116 (3496): 73-96, fig. A.
- STRASBURG, DONALD W.  
1958. Distribution, abundance, and habits of pelagic sharks in the central Pacific Ocean. Fish. Bull. 138, U.S. Fish and Wildlife Serv., 58: i-iv, 335-361, figs. 1-20.  
1963. The diet and dentition of *Isistius brasiliensis*, with remarks on tooth replacement in other sharks. Copeia, 1963 (1): 33-40, figs. 1-5.
- SVERDRUP, H. U., MARTIN W. JOHNSON, and RICHARD H. FLEMING  
1942. The Oceans: Their physics, chemistry, and general biology. New York: Prentice-Hall, Inc. Pp. i-x, 1-1087, figs. 1-265, charts 1-7.
- TENG, HUO-TU  
1959. Studies on the elasmobranch fishes from Formosa. Pt. IV: Squaliolus alii, a new species of deep sea squaloid shark from Tung-Kang, Formosa. Lab. Fish. Biol. Rept. no. 8: 1-6, 1 pl.  
1962. Classification and distribution of the Chondropterygii of Taiwan. 304 pp., figs. 1-77. (In Japanese, processed.)
- TE WINKEL, LOIS E.  
1935. A study of *Mistichthys luzonensis* with special reference to conditions correlated with reduced size. Jour. Morph., 58 (2): 463-535, pls. 1-13.
- THORSON, THOMAS B., DONALD E. WATSON, and C. MICHAEL COWAN  
1966. The status of the freshwater shark of Lake Nicaragua. Copeia, 1966 (3): 385-402, fig. 1.
- TORTONESE, ENRICO  
1956. Leptocardia, Cyclostomata, Selachii. In Fauna d'Italia. Bologna: Calderini. Vol. 2: pp. 1-332, figs. 1-163.
- WAITE, EDGAR R.  
1907. A basic list of the fishes of New Zealand. Res. Canterbury Mus., 1 (1): 1-39.  
1912. Additions and corrections to the basic list of the fishes of New Zealand. Rec. Canterbury Mus., 1 (4): 313-322.  
1916. Fishes. In Australian Antarctic Expeditions 1911-1914: Scientific Reports, ser. C, 3 (1): 1-92, pls. 1-5, maps 1-2.
- WHITLEY, GILBERT PERCY  
1934. Notes on some Australian sharks. Mem. Queensland Mus., 10 (4): 180-200, figs. 1-4, pls. 27-29.  
1940. The fishes of Australia. Pt. I: The sharks, rays, devil fish, and other primitive fishes of Australia and New Zealand. Roy. Zool. Soc. New South Wales. Aust. Zool. Handbook, Sydney. Pp. 1-280, figs. 1-303.
- WOOSTER, WARREN S., and TOWNSEND CROMWELL  
1958. An oceanographic description of the eastern tropical Pacific. Bull. Scripps Inst. Oceanogr., 7 (3): 169-282, figs. 1-2, profiles 1-36.
- WOOSTER, WARREN S., and JOSEPH L. REID, JR.  
1963. Eastern boundary currents. In The Sea: Ideas and observations in progress in the study of the sea. Ed. M. N. Hill. New York and London: Interscience. Vol. 2: pp. 253-280, figs. 1-17.
- YAMAGUTI, S.  
1934. Studies on the helminth fauna of Japan. Pt. 4: Cestodes of fishes. Japan Jour. Zool., Tokyo, 6: 1-112, figs. 1-187.

## PLATES

PLATE 1

*Euprotomicrus bispinatus* (Quoy and Gaimard)

Fig. 1. Lateral aspect of specimen 27, 170 mm in total length, a male with claspers not quite fully elaborated, from southeastern Pacific Ocean at 14°17' S., 108°52' W.

Fig. 2. Ventral aspect of same specimen.

Fig. 3. Much enlarged view of denticles, but no photophores, on dorsal surface of specimen 24.

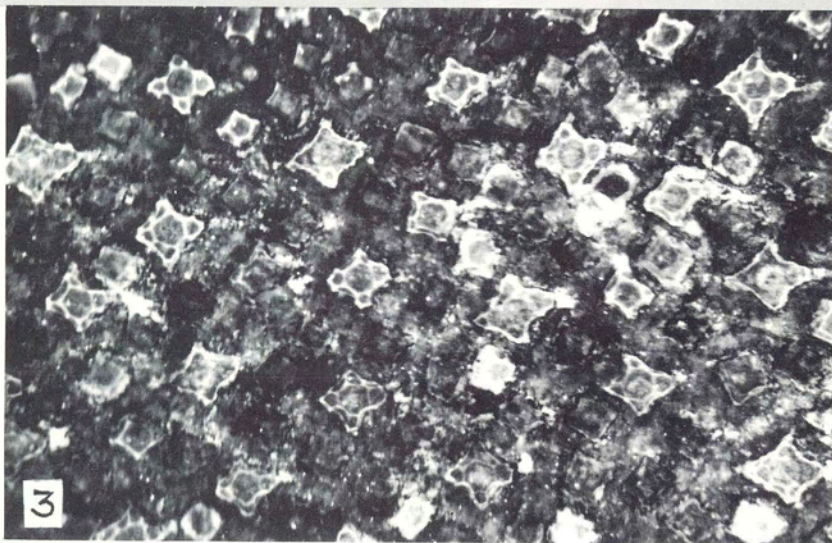
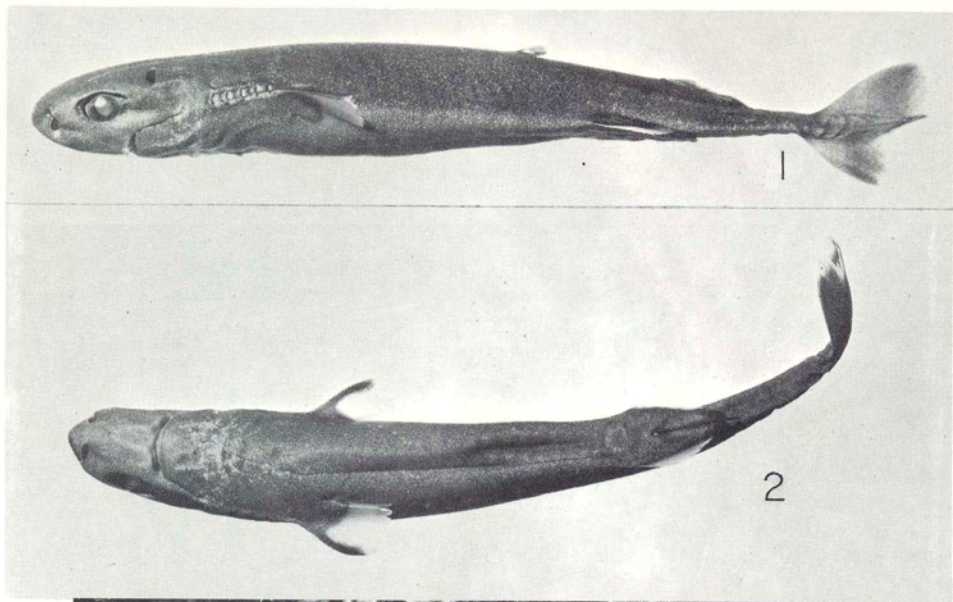




PLATE 2

Enlarged views of skin of *Euprotomicrus*  
*bispinatus*, specimen 27

Fig. 1. Dorsal region in front of first dorsal fin, showing denticles but no photophores.

Fig. 2. Ventral region, including pelvic fins, claspers, and adjacent area with denticles and crescentic groups of photophores.

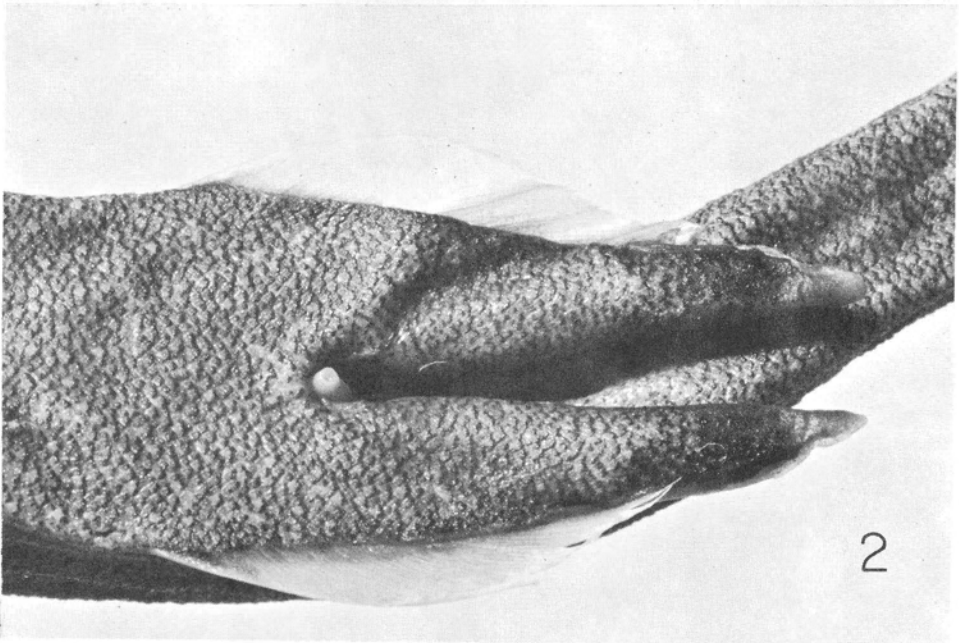


PLATE 3

Photomicrographs of photophores and denticles of three  
luminescent sharks

*Euprotomicrus bispinatus*: *A*, belly, × 45; *B*, preoral part of  
snout, × 45; *C*, ventral surface of caudal peduncle, × 54; *D*,  
longitudinal section of photophore near base of pectoral fin,  
× 630.

*Etmopterus lucifer*: *E*, flank, × 40; *F*, dorsum before first  
dorsal fin, × 45.

*Centroscyllium ritteri*: *G*, flank, × 45.

KEY: *l*, lens; *lo*, light organs; *m*, melanophores; *ph*, photo-  
genic cell; *ps*, pigment sheath; *s*, scale.

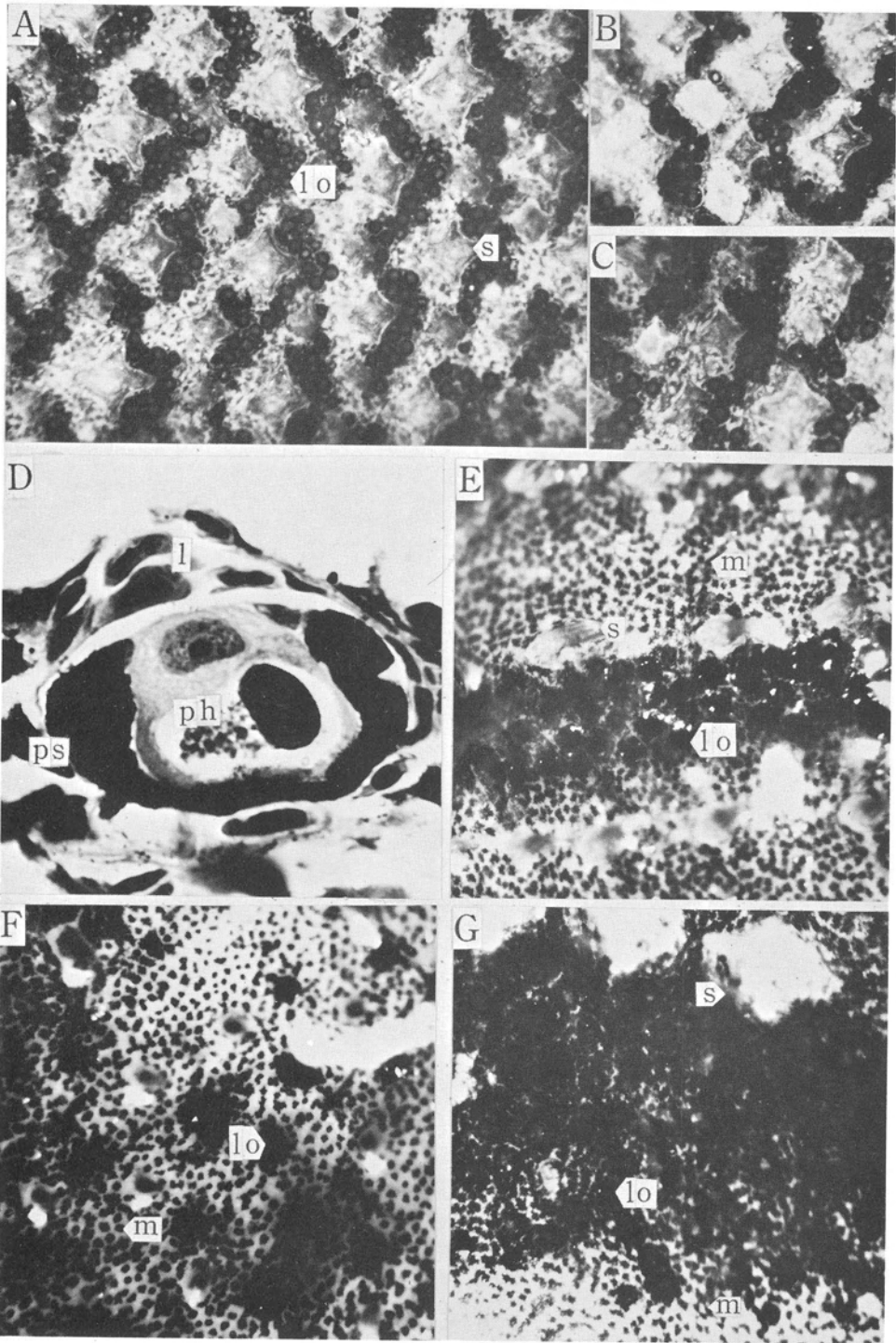


PLATE 4

Mandibular dentition of *Euprotomicrus bispinatus*

Fig. 1. Replacement dentition of specimen 24. Four transverse rows of replacement teeth, showing four longitudinal sets on right side and three on left side of the two-shouldered median tooth in each row. Slightly retouched.

Fig. 2. First eight mandibular teeth of left side, in band being replaced on specimen 29. Band was intact but broke as it was being flicked off a bit prematurely. Scale in millimeters.

Fig. 3. Longitudinal section through mandible and lower teeth of specimen 24. Shown in sequence in the one longitudinal row sectioned are the teeth of 5½ horizontal rows: (1) tooth of erect functional row; (2) teeth of four replacement rows, the first apparently about ready to revolve into position for service, and three more in successive stages of development; (3) a single tooth bud.

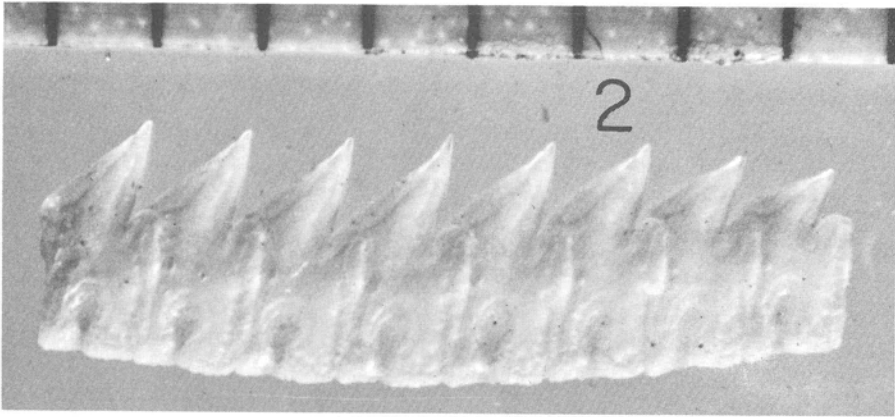
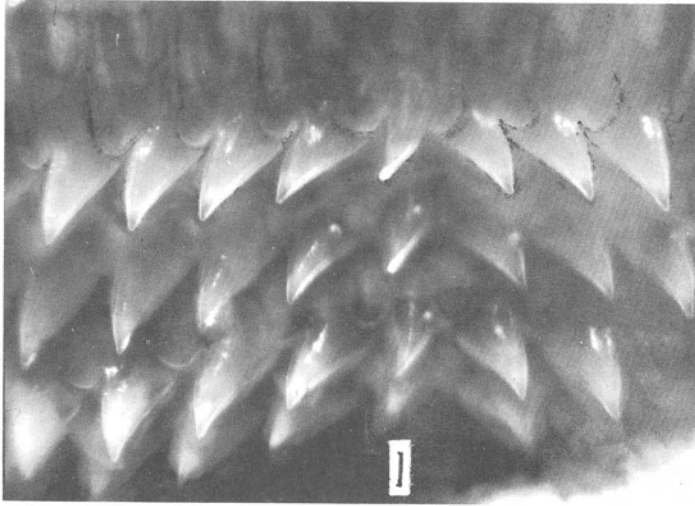
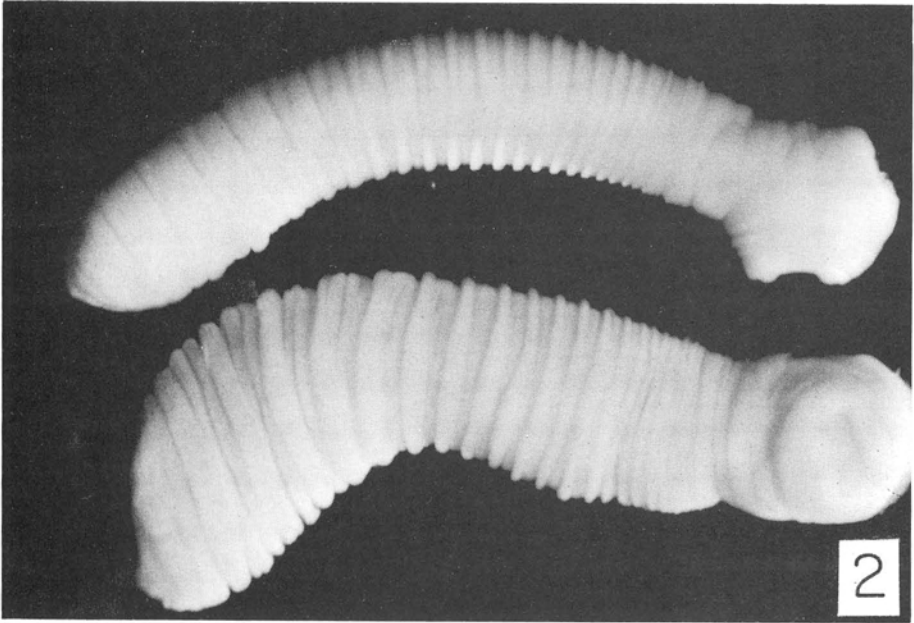


PLATE 5

*Euprotomicrus bispinatus*, specimen 24

Fig. 1. Early-maturing follicle from right ovary. Note group of nucleoli in vesicle. Magnification  $\times ca.$  400.

Fig. 2. Two cestode parasites, *Sphyriocephalus tergestinus* Pintner (1913: 123), each about 10 mm long in preserved state, from cardiac part of stomach.





## PLATE 6

### Radiographs of adult males of two dalatiine sharks

(a). Posterior part of specimen 29, 211 mm long, of *Euprotomicros bispinatus*. Note: (1) abrupt change, marked by arrow, from last monospondylous vertebra to first diplospondylous one; (2) much reduced and very irregular caudal vertebrae (counted as 15 behind upper origin of caudal fin); division between pre-caudal and caudal vertebrae marked by vertical line; (3) lack of register of uncalcified vertebral arches; (4) pelvic and clasper cartilages.

(b). Caudal skeleton of *Isistius brasiliensis*. Specimen (SIO 52-413-5A), 386 mm long, from equator at 100°00' W. long. Caudal vertebrae counted as 22, the last 2 interpreted as much elongated.

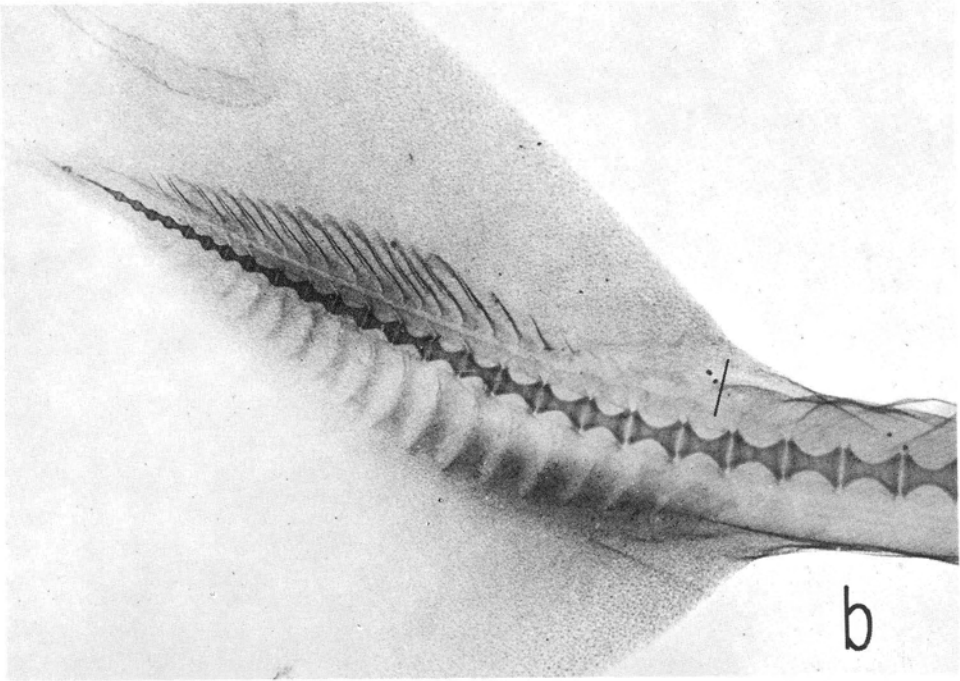
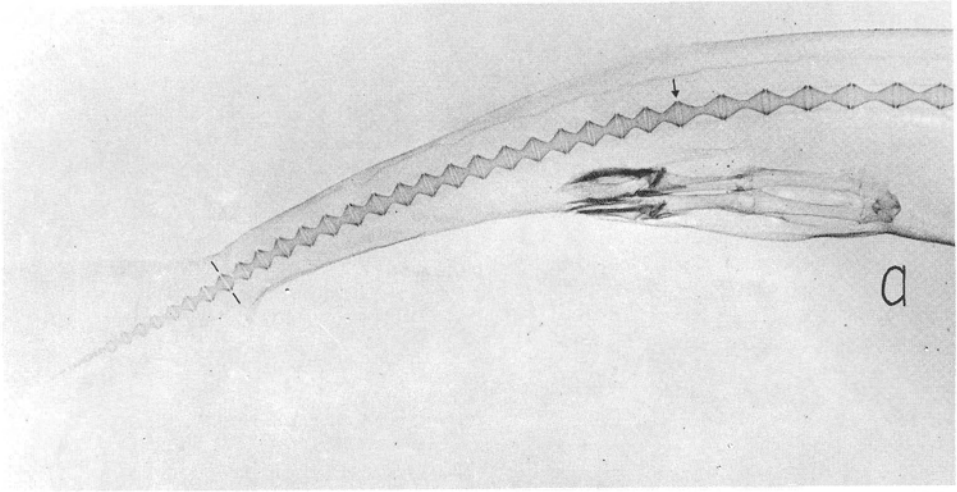


PLATE 7

Radiographs of head region, in dorsal aspect, of  
*Euprotomicrus bispinatus* and *Isistius brasiliensis*

Represented are: (a) a 386-mm example (SIO 52-413-5A) of  
*Isistius*, from equator at 100°00' W. long., and (b) a 211-mm  
specimen (29) of *Euprotomicrus*.

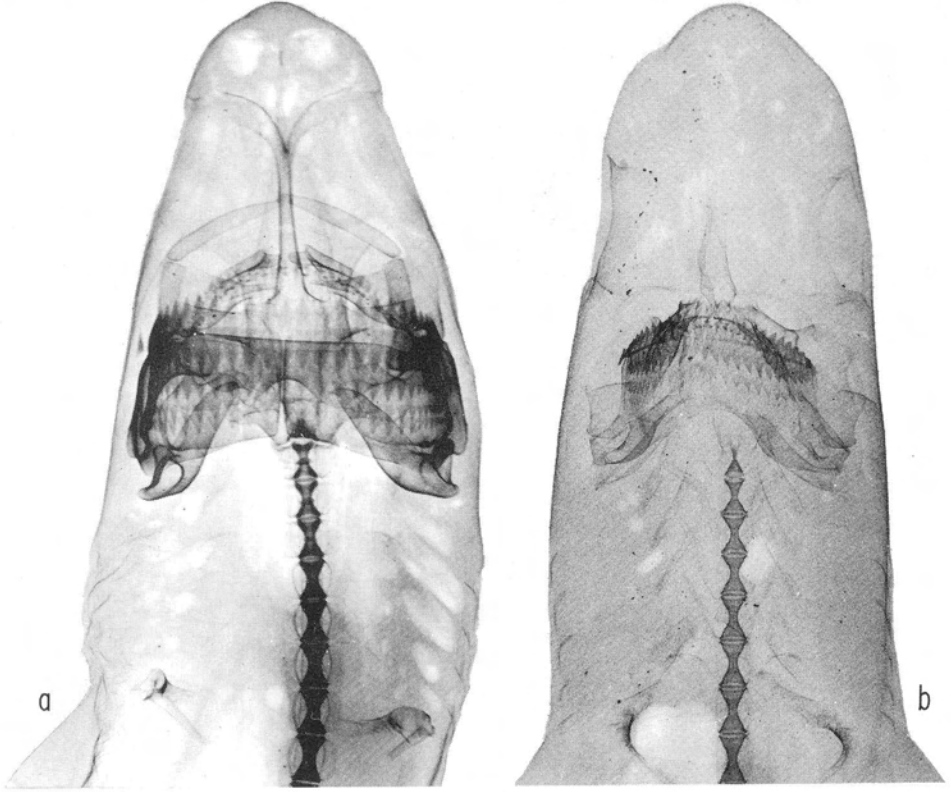


PLATE 8

Radiographs, from above, of claspers and adjacent parts of  
*Euprotomius bispinatus* (a) and *Isistius brasiliensis* (b)

Same specimens as in plate 7. Radiographs somewhat re-  
touched.

