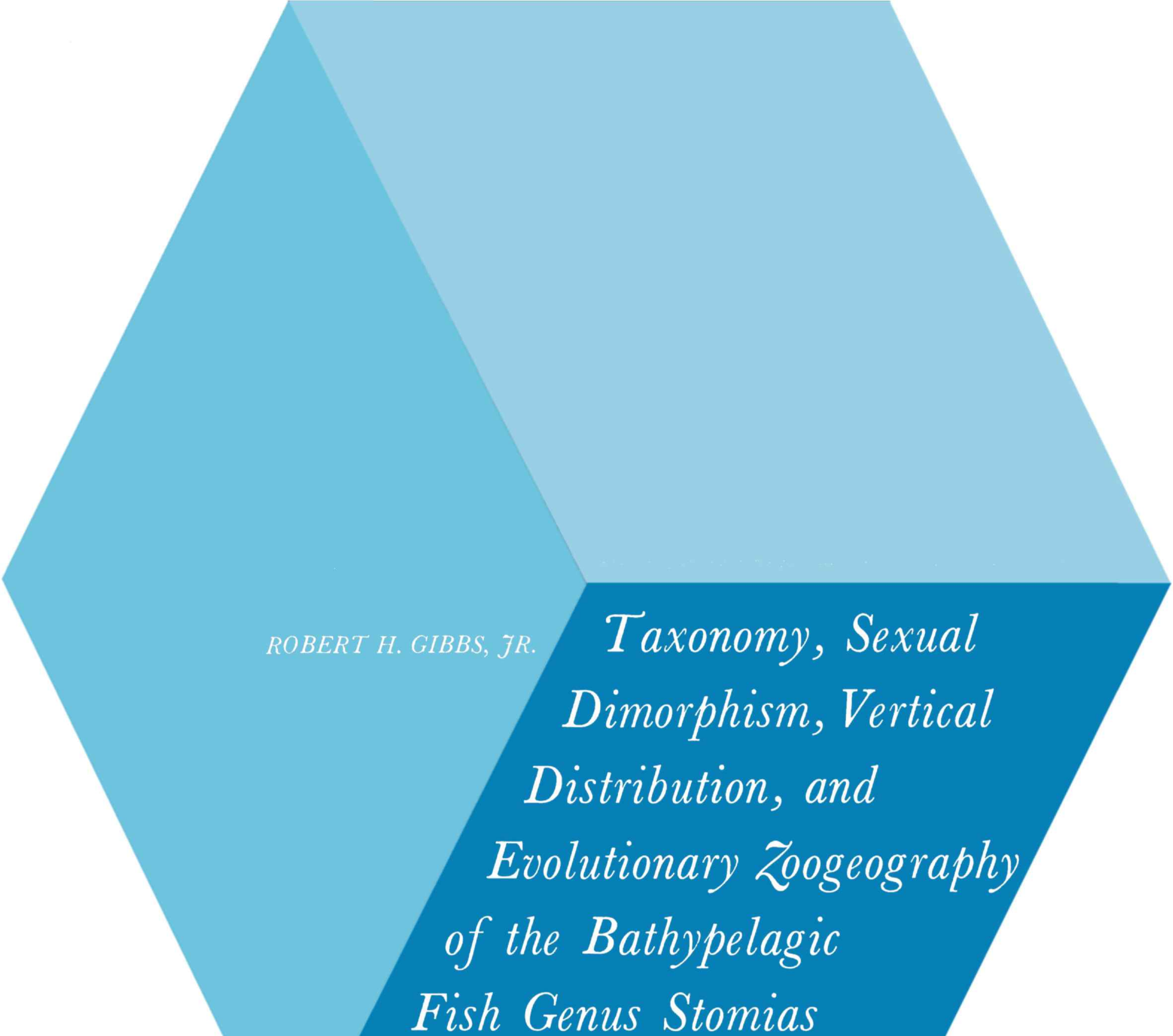

ROBERT H. GIBBS, JR.

Taxonomy, Sexual Dimorphism, Vertical Distribution, and Evolutionary Zoogeography of the Bathypelagic Fish Genus Stomias (Stomiatidae)

SMITHSONIAN CONTRIBUTIONS TO ZOOLOGY • 1969 NUMBER 31

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ABSTRACT

Gibbs, Robert H. Jr. Taxonomy, Sexual Dimorphism, Vertical Distribution, and Evolutionary Zoogeography of the Bathypelagic Fish Genus *Stomias* (Stomiatidae). *Smithsonian Contributions to Zoology,* 31:1–25. 1969.—New information on the characters and geographic distribution and a key for identification are presented for the ten recognized species and subspecies of *Stomias,* of which one, the eastern Atlantic subspecies *S. colubrinus orientalis* Blache, is considered a full species and is redescribed. The name *orientalis,* a junior homonym, is replaced by *lampropeltis.* External sexual dimorphism is demonstrated for all species in three characters: males are smaller than females and have larger eyes and larger postorbital photophores. The magnitude of the dimorphism varies among the species, the most extreme differences in eye and postorbital organ occurring in species in which males attain the least maximum size. Vertical distributions of all except *S. danae* are estimated by comparing numbers of specimens caught in nonclosing nets with the number of meter-hours of trawling at depth in the known geographic range of each form. All appear to migrate from deeper to shallower depths at night. Most species for which data approach adequacy occur in the greatest abundance between 500–1000 meters during daylight and in the upper 200 meters at night, although concentrations of *S. gracilis* are deeper than 200 meters at night. In *S. colubrinus,* however, greatest daytime catches are below 1000 meters and at night below 600 meters. The apparent phylogenetic trends of morphological characters, together with present geographical distributions, suggest that *S. brevibarbatus* and *S. danae* represent the earliest evolved stock of *Stomias,* from which, perhaps simultaneously, the *colubrinus-lampropeltis* group and *S. nebulosus* arose. The *S. boa* group probably arose from *nebulosus*-like ancestors, with the almost circumtropical *S. affinis* the earliest and giving rise to *S. atriventer* in the eastern Pacific and *S. boa boa* in the Subtropical Convergence, and the latter giving rise to *S. gracilis* in subantarctic and Antarctic waters and, most recently, to *S. boa ferox* in the North Atlantic as well as a Mediterranean population that has retained *boa boa* characteristics.

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Robert H. Gibbs, Jr

Taxonomy, Sexual Dimorphism, Vertical Distribution, and Evolutionary Zoogeography of the Bathypelagic Fish Genus Stomias (Stomiatidae)

Introduction

The genus *Stomias* includes elongate stomiatoid fishes with five to six rows of closely spaced hexagons on the sides (each hexagon apparently occupied by a scale), with the dorsal and anal fins set far back toward the caudal fin, with a barbel that is shorter to slightly longer than the head, and rarely with more than 100 photophores in the ventral series. The only other species in the family Stomiatidae is *Macrostomias longibarbatus,* which is much more attenuate than any *Stomias* species, has a barbel several times as long as the head, and has about 150 or more photophores in the ventral series. *Macrostomias,* relatively rare in collections although it has been reported from the Atlantic, Pacific, and Indian oceans, is not treated in this study.

The studies of Ege (1918, 1933, 1934) provided a solid foundation for the systematics of the genus *Stomias.* Based on specimens collected by several Danish oceanographic expeditions, Ege recognized all but one of the taxonomic entities that are currently recognized and reduced many nominal forms to synonymy. The rank of some of Ege's taxa was questioned by Morrow (1964a), who considered some of the subspecies as deserving species status, and I concur. The only valid new entity described since 1934 is *S. colubrinus orientalis* Blache (1964) which I consider a full species. Fowler (1934) described two new genera and species, *Microdontostomias orientalis* and *Pseudeustomias myersi,* which are synonyms of *Stomias nebulosus* and *S. affinis,* respectively (Morrow, 1964a). Fowler's use of the name *orientalis* necessitates the renaming of the entity described by Blache.

Ege's studies and all that followed were hampered by a lack of specimens of several species and by gaps in geographic coverage. In recent years, while engaged primarily in revisionary studies of other stomiatoid families, I have examined numerous specimens of *Stomias* in or from many collections around the world. This paper presents data on the meristic characters of all species that indicate ranges of variation, for the first time in those species formerly considered rare (*danae, atriventer,* and *gracilis*), and redescribes and renames the form that was inadequately described by Blache. Sexual dimorphism is described for the first time in this genus. Geographic and vertical distributions are determined and analyzed, and from these and the morphological information a hypothesis is

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Robert H. Gibbs, Jr., Division of Fishes, Smithsonian Institution, Washington, D.C. 20560

derived that explains the evolutionary zoogeography of *Stomias* species.

METHODS.—In those species for which adequate data are already published (*S. affinis, S. nebulosus, S. boa ferox, S. brevibarbatus*) most counts and measurements were taken on only a few specimens. For *S. atriventer, S. boa boa, S. colubrinus, S. lampropeltis, S. danae,* and *S. gracilis,* data were taken on many specimens.

In the dorsal and anal fins, the last two rays almost invariably are separated by a considerable gap. Examination of cleared and stained material indicates that each of these rays has its own pterygiophore, so these are counted separately, not as one. Pectoral and pelvic rays in most species deviate only rarely from a count of six and five, respectively, and are not considered further except in *S. danae* and *S. brevibarbatus,* where the pectoral rays are seven to nine.

Counts of the large photophores in the ventral and lateral series are expressed in the terminology recently modified slightly from that customarily used for stomiatoids, omitting the hyphen and more clearly designating the sections between pelvic and anal fins (see Morrow, 1964b, p. 276).

In the vental row:

IP,	from anterior isthmus to before pectoral insertion.
PV,	from between pectoral insertions to before pelvic (ventral) insertions.
VAV,	from between pelvic insertions to before anal origin.
AC,	from above anal origin to end of row on posterior caudal peduncle.
IC,	the entire row.

In the lateral row:

OV,	from behind operculum to before pelvic (ventral) insertion.
VAL,	from above pelvic insertion to end of row, usually before anal origin, but occasionally slightly behind it.
OA,	the entire row.

Vertebral counts were made from radiographs or from cleared and stained specimens and comprise all ossified centra including the urostylar; the small unossified space between the first vertebra and the skull, however, is not included.

Sex determination was made by gross microscopic examination of gonads or by use of squash preparations of gonad material stained with aceto-orcein.

MATERIALS.—The following colleagues and institutions have very generously extended to me the use of their collections and facilities or loaned me specimens used in this study: *Dana* Collection (Dr. E. Bertelsen, Miss Esther Hansen); Universitetets Zoologiske Museum, Copenhagen (Dr. Jørgen Nielsen); Centre de Recherches Océanographiques, Abidjan, Cote d'Ivoire, R/V *Reine Pokou* (Dr. P. Rancurel); South African Museum, Cape Town, (Michael J. Penrith); Victoria University of Wellington, New Zealand (Dr. J. A. F. Garrick); New Zealand Oceanographic Institution (Dr. E. W. Dawson); Zoologisches Museum der Humboldt Universität, Berlin (Dr. Kurt Deckert); Institut für Seefischerei, Hamburg, R/V *Walther Herwig* (Dr. Gerhard Krefft); Shimonoseki College of Fisheries (Dr. Reizo Ishiyama); University of Southern California (Dr. Hugh H. DeWitt, Dr. John R. Paxton, Robert J. Lavenberg, Richard F. McGinnis); Scripps Institution of Oceanography (Dr. Carl L. Hubbs, Dr. Richard H. Rosenblatt, Joseph Copp), Stanford University (Dr. Warren C. Freihofer); Museum of Comparative Zoology, Harvard University (Dr. Giles W. Mead, Mrs. Myvanwy M. Dick); Institute of Marine Science, University of Miami (Dr. C. Richard Robins); Bureau of Commercial Fisheries Biological Laboratory, Honolulu (John C. Marr, Dr. Donald W. Strasburg); Bureau of Commercial Fisheries, Tropical Atlantic Biological Laboratory, Miami (Frederick H. Berry, Dr. William J. Richards); Bureau of Commercial Fisheries, Exploratory Fishing and Gear Research Base, Pascagoula, Mississippi (Harvey R. Bullis); Naval Oceanographic Office, Washington, D.C. (Bernard Zahuranec); General Motors Defense Research Laboratory, Santa Barbara, California (Dr. William Aron); Smithsonian Oceanographic Sorting Center (Dr. Leslie W. Knapp).

The only abbreviations used for institutions at which collections are housed are the following: SIO, Scripps Institution of Oceanography; SU Stanford University; USNM, United States National Museum.

Stomias affinis Günther, 1887

Most of my counts fall within the range recorded by Ege (1934), with the exception of VAV, OV, and IC, where some slightly higher counts were found.

Ege had no records of *S. affinis* between the longitudes of New Caledonia (about 178°E) and 116°W.

Key to the Species and Subspecies of *Stomias*

1\. A single tooth on anterior end of each palatine.......... 2

Two teeth on anterior end of each palatine.......... 3

2\. Premaxillary teeth on one side 7 or fewer (rarely 8); mandibular teeth on one side 15 or fewer (rarely 16); combined number of premaxillary and maxillary teeth 21 or fewer (rarely to 23) on each side; no teeth on posterior end of palatine (east tropical Pacific).......... ***S. colubrinus*** Garman

Premaxillary teeth usually 8 or more (6–7 not unusual); mandibular teeth almost always 16 or more (rarely 14–15); combined number of premaxillary and mandibular teeth 22 or more (rarely to 20) on each side; a tooth on posterior end of each palatine (east tropical Atlantic).......... ***S. lampropeltis,*** new name

3\. Most mandibular teeth longer than longest premaxillary teeth; mandibular teeth fewer (9–16) than premaxillary teeth (16–25) (tropical Indo-Pacific).......... ***S. nebulosus*** Alcock

Longest mandibular tooth shorter than longest premaxillary teeth; mandibular teeth more numerous (7–18) than premaxillary teeth (4–12).......... 4

4\. Five rows of hexagonal areas dorsal to lateral series of photophores; barbel length (without terminal filaments) 75 percent of head length or less; premaxillary teeth usually 10 or more; pectoral rays 7 or more.......... 5

Six rows of hexagonal areas dorsal to lateral series of photophores; barbel length (without terminal filaments) usually about equal to head length, rarely less than 67 percent of head length; premaxillary teeth 8 or fewer; pectoral rays 6.......... 6

5\. Bulb of barbel without filaments; 2 slender filaments at base of barbel stem; 6 or fewer photophores in any hexagonal area in the 3 rows above lateral series of photophores; vertebrae fewer than 64 (Indo-Pacific and South Atlantic central waters).......... ***S. danae*** Ege

Bulb of barbel with 4 filaments; no filaments at base of barbel stem; 7 or more photophores in any hexagonal area in the 3 rows above lateral series of photophores; vertebrae 64 or more (North Atlantic between about 20°–40°N).......... ***S. brevibarbatus*** Ege

6\. Total photophores in ventral series (IC) more than 90 (94–102); in lateral series (OA) 65 or more; PV 53 or more; OV 52 or more; vertebrae 86 or more (subantarctic and Antarctic waters).......... ***S. gracilis*** Garman

Total photophores in ventral series (IC) 90 or fewer (73–90); lateral series (OA) 64 or fewer; PV 51 or fewer; OV 50 or fewer; vertebrae 83 or fewer.......... 7

7\. VAV photophores 5–8 (rarely 9); VAL 4–8 (circumglobal in warmer waters).......... ***S. affinis*** Günther

VAV photophores 10–14 (rarely 9); VAL 10–15.......... 8

8\. OV photophores 39–43; OA photophores 52–55; IC photophores 77–82; vertebrae 69–74 (east Pacific).......... ***S. atriventer*** Garman

OV photophores 43–50; OA photophores 57–64; IC photophores 79–90, usually 83 or more; vertebrae 74–83.......... ***S. boa***.... 9

9\. IC photophores 79–88, usually 83–86; vertebrae 74–80 (Mediterranean Sea, northwest African waters, southwest African waters, Subtropical Convergence)..... ***S. boa boa*** (Risso)

IC photophores 85–90, usually 87–89; vertebrae 77–83 (north Atlantic north of about 30°N).......... ***S. boa ferox*** Reinhardt

The present material fills a portion of this distributional gap in equatorial waters between 160°W and 120°W. There is only one record for the entire area of the western Pacific occupied by the Polynesian and Micronesian island groups—a small specimen taken in the Samoan region on *Eltanin* cruise 31. Norman (1939) reports of *S. affinis* from the southern Red Sea, and Aron and Goodyear (1969) now record it from the Gulf of Eilat (Aqaba) and adjacent northern Red Sea.

Stomias atriventer Garman, 1899

Until recently, the holotype and eight additional specimens (Parr, 1931) of this species had been recorded. Ege (1934) regarded it as a subspecies, *S. boa atriventer,* but, as Morrow (1964a) indicated, there is little or no overlap in certain meristic characters between this and any other form closely related to *S. boa.* Counts of OA photophores so far afford complete separation of *S. atriventer* from *S. boa boa,* the most similar species, and OV, PV, and IC photophore counts and vertebral counts show very slight overlap. Thus *S. atriventer* should be regarded as a full species.

The geographic range of *S. atriventer* comprises two separate areas (Figure 5). One comprises the lower Gulf of California and the California Current off southern California and Baja California (Lavenberg and Fitch, 1966; Lavenberg and Ebeling, 1967; Berry and Perkins, 1967). A single specimen was taken in a deep haul by Scripps Institution's Tethys expedition at 13°N, 127°W, indicating possible occasional westward transport by the extension of the California Current.

The second portion of the range is at or below the equator from the Galapagos Islands south to 23°S in the influence of the Humboldt Current.

In both areas frequency distributions of most meristic characters are quite similar, but in the southern portion numbers of dorsal and anal rays and vertebrae average higher than in the northern portion. Differentiation has thus been slight, in spite of the wide separation between the geographical ranges.

Ege (1934) records a single small transitional specimen from west of the Galapagos as *S. boa boa*. I have not seen this specimen, but it is almost certainly *S. atriventer*.

Stomias boa boa (Risso), 1810

The geographic range of *S. boa boa* is divided into two disjunct parts. One part includes the Mediterranean Sea (including the Sea of Marmora; Demir, 1958) and waters under the influence of its outflow off northwestern Africa. The other part is the Subtropical Convergence and southern Humboldt and Benguela currents.

Ege (1934) found no noteworthy differences between samples from various parts of the range, but the present data offer some suggestions that invite future study. In vertebral numbers and in photophores of the PV, IA, IC, and OA groups, specimens from the vicinity of New Zealand have the lowest counts, while those from the central South Pacific (mostly from *Eltanin* cruise 24) have the highest. Specimens from the western Indian Ocean and from the southeastern Pacific are intermediate, but tend to approach the New Zealand and central South Pacific samples, respectively, in their counts. These trends are illustrated by the PV counts in Table 1. The probability that southern *S. boa boa* consists of more than a single subpopulation is indicated also by the flatness of the combined frequency distributions and the wide ranges of meristic characters, especially when compared with the strongly modal distributions of the same data from the Mediterranean population taken from Ege (1934) and included in Tables 8–11.

TABLE 1.—Stomias boa boa: *frequency distribution of PV photophores in the southern population*

Region	*Number of PV photophores* 44	45	46	47	48	49	50
Western Indian Ocean	–	–	5	9	3	2	–
New Zealand	1	4	5	5	1	–	–
Central South Pacific	–	–	–	1	3	4	2
Southeast Pacific	1	–	1	5	6	3	1

Stomias gracilis Garman, 1899

Five specimens of this species have been reported previously (Günther, 1887; Ege, 1934). Several recent expeditions, especially those of the *Eltanin*, have found *S. gracilis* abundant in Antarctic and subantarctic waters.

In numbers of vertebrae and some photophore counts (PV, OV, IC, OA), *S. gracilis* is widely separated from its congeners, justifying Morrow's (1964a) contention that it should be regarded as a full species.

Stomias lampropeltis, new name

FIGURES 1, 2

Stomias colubrinus orientalis Blache, 1964 [no holotype designated; syntypes in Museum National d'Histoire Naturelle, Paris].

This species has been called *S. colubrinus* by previous authors (Brauer, 1906; Ege 1934). Blache (1964), for the first time, compared southeastern Atlantic specimens with Ege's (1934) data for eastern Pacific specimens. Using a statistical test of the differences between means, he found that his sample differed significantly from that from the eastern Pacific in numbers of dorsal rays, anal rays, and PV photophores, although in each case the modes were the same. On this basis he described the eastern Atlantic population as a new subspecies, *Stomias colubrinus orientalis*.

If the differences between two nominal subspecies are so slight that they cannot be determined by inspection of specimens or data, then I do not accept the validity of the subspecies. The use of a statistical test

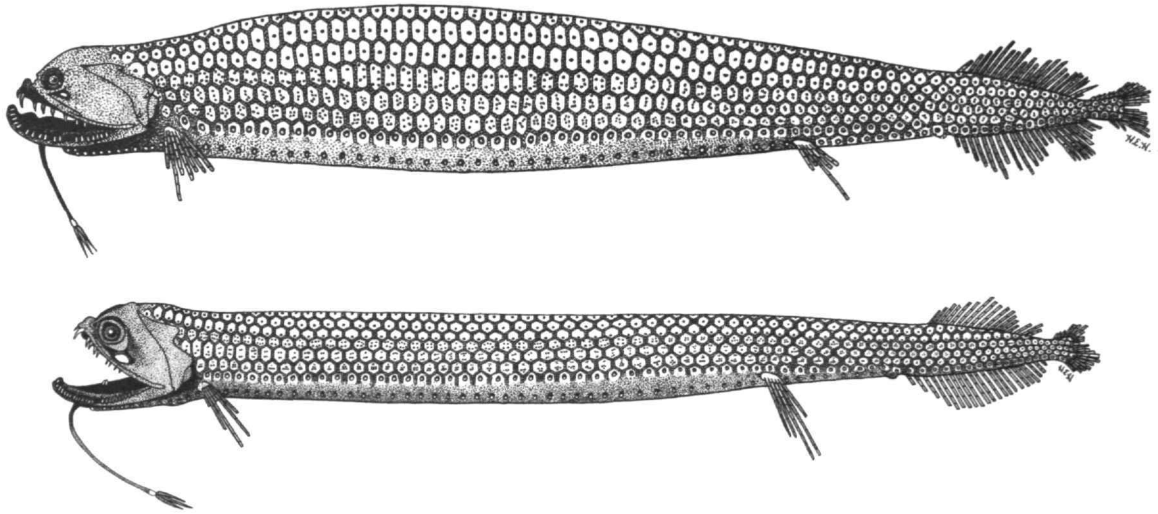

FIGURE 1.—*Stomias lampropeltis.* Top: female, 233 mm, *Dana* station 4003(1). Bottom: male, 95.8 mm, *Reine Pokou* station 540. Drawn by Howard E. Hamman.

of significance between means, when it is the only criterion for naming a subspecies, is unacceptable, to me at least. In the case of Blache's new subspecies, not only were such tests the only criterion, but the basic assumption of a normal distribution was not present in the frequencies of some characters. To indicate the impropriety of using such criteria, I employed Blache's statistical tests using two different samples of the same form, *S. colubrinus* from the eastern Pacific. My own data were tested against those of Ege (1934) that had been used by Blache. The two samples from the eastern Pacific were just as significantly different as were those tested by Blache from the Pacific and Atlantic.

Despite the fact that the characters and criteria used by Blache were inadequate to show that two subspecies should be recognized, comparison of the dentition of the two populations (Figure 2) convinced me that they are, indeed, separate entities. I choose, furthermore, to recognize them as full species.

The name *orientalis,* applied by Blache, is not available for this species, because it is a homonym of *Microdontostomias orientalis* Fowler, 1934, which is a synonym of *Stomias nebulosus* Alcock (Morrow, 1964a). I propose the new specific name *lampropeltis* for the eastern Atlantic species of *Stomias* related to *S. colubrinus* of the eastern Pacific. The name is a noun in apposition, *Lamppropeltis* being a genus of colubrid snakes.

COMPARATIVE DIAGNOSIS.—*Stomias lampropeltis* is closely related to *S. colubrinus* and distinct from all other species in the genus in the following combination of characters: a single tooth on the head of each palatine; premaxillary teeth fewer and longer than mandibular teeth; barbel, exclusive of end filaments, at least two-thirds of head length; six rows of hexagonal (scale) areas on each side of body; in the space ventral to each photophore in the lateral row, an arcuate group of 20 to 30 small diffuse photophores.

Compared with *S. colubrinus, S. lampropeltis* has more and generally shorter teeth (Figure 2; Table 2). The longest premaxillary tooth of *S. lampropeltis* goes 4.6–7.2 times into the length of the premaxilla, in *S. colubrinus* 3.8–6.0 times. The number of premaxillary teeth in *S. lampropeltis* is 6–14, in *S. colubrinus* 5–8. There are 14–26 mandibular teeth in *S. lampropeltis,* 8–16 in *S. colubrinus.* The total tooth count (both premaxillary and mandibular teeth) is 20–37 in *S. lampropeltis,* 13–23 in *S. colubrinus.* In *S. lampropeltis,* there is a small tooth on the posterior end of each palatine; such a tooth has not been observed in *S. colubrinus.*

Meristic characters show only minor differences. *S. lampropeltis* has, on the average, more vertebrae and fewer photophores in both ventral and lateral rows (Tables 8–10), but overlap is almost complete in every case.

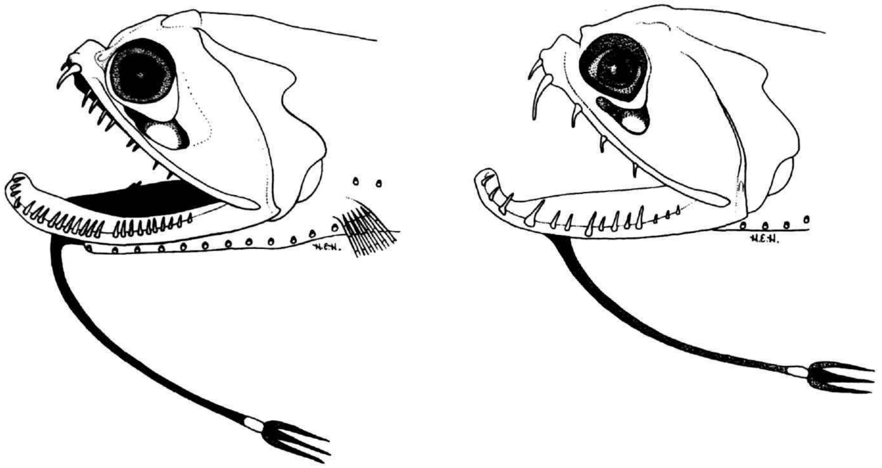

FIGURE 2.—Heads of male *Stomias lampropeltis*, 95.8 mm (left) and *S. colubrinus*, 144.4 mm (right), showing differences in size and number of jaw teeth. Drawn by Howard E. Hamman.

TABLE 2.—Stomias colubrinus (*count in italics*) *and* S. lampropeltis: *frequency distribution of premaxillary and mandibular teeth*

Number of premaxillary teeth	*Number of mandibular teeth*																				
	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28
5	*1*	*2*	*3*	*4*	*3*	*5*	*4*	–	*1*												
6	–	–	*3*	*4*	*3*	*6*	*2*, 1	*2*, 1	–	–	1										
7	–	–	–	*4*	*2*	*1*	*1*	–	*1*, 2	–	*2*	*1*	*2*	–	–	1					
8	–	–	–	*1*	–	–	1	–	2	3	4	7	4	4	1	2					
9	–	–	–	–	–	–	–	–	2	2	3	3	3	5	2	–	1	–	1		
10	–	–	–	–	–	–	–	1	2	5	2	4	2	2	1	2	1	1			
11	–	–	–	–	–	–	–	–	–	–	1	2	3	1	–	1	–	1			
12	–	–	–	–	–	–	–	–	–	–	–	1	–	–	1	1	1	1			
13	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	3					
14	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1						

DESCRIPTION.—Meristic characters given in Tables 8–15. Morphometic characters, as percent of standard length unless otherwise stated, as follows:

Predorsal length: 80.7–86.0.

Preanal length: 78.7–84.7.

Prepelvic length: 66.6–72.6.

Depth behind head: 5.6–9.8.

Head length: 10.2–13.9.

Barbel length (excluding filaments): females: 5:5–12.0 (60–192 percent of head length); males: 10.2–17.1 (77–165 percent of head length).

Fleshy orbit length: females: 1.5–2.8 (15–29 percent of head length); males: 2.1–4.1 (21–34 percent of head length).

Postorbital organ length: females: 21–47 percent of fleshy orbit; males: 40–91 percent of fleshy orbit.

Upper jaw length: 9.1–11.2.

Premaxilla lengh: 7.3–9.3.

Longest premaxillary tooth: 13.8–21.5 percent of premaxilla length.

Snout to bony orbit: 1.3–2.6.

Premaxillary and mandibular tooth counts shown in Table 2. Vomerine teeth: 1 on each side. Palatine teeth: 1 on anterior end, 1 on posterior end. Replacement teeth often present and contiguous to vomerine and palatine teeth. Three widely spaced groups of basibranchial teeth, each composed of 1 to 3 teeth, on each side of midline. Pharyngobranchial teeth in two groups on each side of roof of mouth. Groups of short teeth present on 1st 4 gill arches, eight to ten groups on 1st arch; none on last, attached arch.

DISTRIBUTION.—*S. lampropeltis* has been taken only in the eastern Atlantic Ocean off the west coast of Africa from 21°40′N (*Dana* station 4008) to 14°55′S (*Ombango* station 350).

Stomias colubrinus Garman, 1899

Stomias colubrinus was formerly known from the Gulf of Panama and adjacent waters in the eastern Pacific. The collections reported here extend the known geographic range of the species farther to the west and south than Ege (1934) reported, and Bussing (1965) has published the southernmost locality at about 32°S, 73°W. Meristic and morphometric characters either fall within the ranges given by Ege or extend these ranges slightly.

The record of *S. colubrinus* from Hudson Canyon (Beebe, 1929) is almost certainly in error. This specimen (SU 43286) has been reexamined, and is definitely referable to eastern Pacific *S. colubrinus,* not to *S. lampropeltis* from the eastern South Atlantic. Two other bathypelagic species found in the eastern Pacific but not in the Atlantic were misidentified and recorded by Beebe (1929) among the Hudson Canyon fauna. One is *Idiacanthus antrostomus* (SU 57328, listed by Beebe as *I. fasciola*); the other is an undescribed species of *Astronesthes* (SU 57460, listed by Beebe as *Astronesthes martensi*). All three questioned species were labeled as taken at *Arcturus* station 113, which was the last station following an expedition that made several midwater collections in the eastern tropical Pacific. I strongly suspect that a mixup in labeling occurred, either during or after the *Arcturus* expedition.

Borodin (1931, p. 65) recorded *S. hexagonatus,* a synonym of *S. colubrinus,* from 47°40′N, 37°20′W in the North Atlantic. These specimens (MCZ 31606, 3 specimens, 100, 200, 230 mm) were reexamined and proved to be *S. boa ferox.*

Stomias nebulosus Alcock, 1889

Counts were made on only four central Pacific specimens of this distinctive species. Numbers of dorsal and anal rays were at the low extreme of the ranges given by Ege (1934). Other counts are nearer the center of these ranges. Ege noted differences in VAV and IC photophores in populations of *S. nebulosus.* The few central Pacific specimens agree most closely in VAV counts with Ege's South China Sea specimens (modally eight).

Two specimens taken off southeast Africa at *Galathea* station 203 (25°36′S, 35°21′E, 21 February 1951, maximum depth 730 m) were far south of the otherwise known range of the species. Possibly this extension is due to the warm Agulhas Current.

Stomias danae Ege, 1933

This species was described by Ege from a single South Pacific specimen, and no others have since been reported. I have examined four additional specimens, two from near Hawaii (SIO 60–249; USNM 201739) and two from the western Indian Ocean (USNM 201829, USNM 201830). Another specimen was taken in the South Atlantic by the *Walther Herwig* (Dr. Gerhard Krefft, in litteris, see Figure 6). Meristic and morphometric data for five of the six known specimens are given in Table 3.

The new specimens confirm the characters used by Ege (1933, 1934) to distinguish *S. danae* from the closely related but allopatric *S. brevibarbatus.* In *S. danae* no filaments arise from the end of the bulb of the barbel; two long filaments arise from the base of the barbel stem. The small photophores in the three ventralmost rows of hexagonal areas are few; usually two to three in the third row from the dorsum; usually three to five in the fourth row; usually three to five in the fifth row (the upper two rows have one photophore per hexagon). The number of vertebrae, reported here for the first time, is less than in any other *Stomias* except *nebulosus.* The postorbital organ is apparently smaller in *S. danae* than in *S. brevibarbatus.* In two male *S. danae* this organ is about 39 percent of the fleshy orbit diameter, and in one of undetermined sex it is 50 percent. In two small female *S. brevibarbatus* the organ is 62–75 percent of the eye diameter, and in a 110-mm male, it is 84 percent.

The characters that set *S. danae* and *S. brevibarbatus* apart from all other species of *Stomias* are also confirmed. There are five, rather than six, rows of hexagons. The numbers of premaxillary and mandibular teeth in both species are similar and high for *Stomias.* The barbel is shorter than in other *Stomias* at any given size. In *S. brevibarbatus* it is about one-

TABLE 3.—Stomias danae *counts and measurements* [1]

Character	*Specimen*									
	USNM 201829		*DANA 3583*		*USNM 201739(♂)*		*SIO 60–249*		*USNM 201830(♂)*	
Dorsal rays	18		18		16		17		18	
Anal rays	20		21		20		20		21	
IP	11		11		11		-		11	
PV	31		32		31		30		31	
VAV	13		13		14		12		13	
OV	30		32		31		30		31	
VAL	13		12–13		14		12		13	
AC	13		15		14		14		15	
Vertebrae	60		-		62		61		62	
Premaxillary teeth	10		12		10		10		11	
Mandibular teeth	11+		17		16–17		15		20	
Gill-raker patches	3+7		-		-		3+7		3+7	
Branchiostegal photophores	18		-		17		-		15	
Standard length	48. 9		68. 0		139. 1		145. 2		155. 9	
Predorsal length	41. 2	*84. 3*	58. 5	*86. 0*	118. 5	*85. 2*	122. 3	*84. 2*	134. 2	*84. 6*
Preanal length	41. 0	*83. 8*	58. 0	*85. 3*	117. 3	*84. 3*	123. 2	*84. 8*	132. 6	*83. 7*
Prepelvic length	30. 1	*61. 6*	42. 0	*61. 8*	84. 2	*60. 5*	92. 5	*63. 7*	97. 9	*61. 8*
Head length	5. 5	*11. 2*	8. 2	*12. 1*	16. 2	*11. 6*	16. 6	*11. 4*	18. 0	*11. 4*
Barbel length*	1. 5	*27. 3*	4. 0	*48. 8*	10. 6	*65. 4*	12. 0	*72. 3*	11. 9	*66. 1*
Barbel bulb length**	0. 7	*70. 0*	—	—	1. 4	*50. 0*	1. 6	*66. 7*	1. 3	*34. 2*
Snout to bony orbit*	1. 6	*29. 1*	[2] 2. 5	*30. 5*	3. 9	*24. 1*	2. 5	*15. 1*	3. 9	*21. 7*
Fleshy orbit*	1. 0	*18. 2*	1. 5	*18. 3*	2. 8	*17. 3*	2. 4	*14. 5*	3. 8	*21. 1*
Postorbital organ**	0. 5	*50. 5*	—	—	1. 1	*39. 3*	—	—	1. 5	*39. 5*
Upper jaw length	4. 9	*10. 0*	—	—	16. 1	*11. 6*	14. 7	*10. 2*	16. 5	*10. 6*
Premaxilla length	4. 5	*9. 2*	—	—	12. 5	*9. 0*	12. 1	*8. 3*	14. 1	*9. 0*
Longest premaxillary tooth***	0. 8	*17. 8*	—	—	2. 4	*26. 7*	—	—	2. 1	*14. 9*
Longest mandibular tooth***	0. 4	*8. 9*	—	—	1. 5	*12. 0*	—	—	1. 5	*10. 6*
Depth at pectoral insertion	3. 6	*7. 4*	—	—	11. 1	*8. 0*	11. 2	*7. 7*	11. 3	*7. 2*
Greatest depth (distorted)	3. 6	*7. 4*	4. 7	*6. 9*	12. 8	*9. 2*	14. 6	*10. 0*	13. 4	*8. 6*
Caudal peduncle depth	1. 0	*2. 0*	1. 6	*2. 4*	3. 1	*2. 2*	—	—	3. 4	*2. 2*
Length dorsal base	4. 5	*9. 2*	5. 7	*8. 4*	12. 0	*8. 6*	—	—	15. 1	*9. 5*
Length anal base	5. 1	*10. 4*	8. 3	*12. 2*	16. 1	*11. 6*	—	—	20. 7	*13. 1*

[1] Proportions in italics are in percent of standard length except where the character is marked with asterisks: *percent of head length; **percent of fleshy orbit diameter; ***percent of premaxilla length.

[2] Ege probably measured snout to fleshy orbit.

third of the head length (Ege, 1934), although in two small specimens that I examined it was approximately 40 percent. In *S. danae* the barbel appears to increase in relative length, from 27 percent to 72 percent (Table 3). The pelvic fins are inserted more anteriorly than in other *Stomias:* prepelvic length in *S. brevibarbatus* is 59–63 percent of standard length (Ege, 1934), in *S. danae* 60–64 percent; other species of *Stomias* range from 65–76 percent.

Sexual Dimorphism

Sexual dimorphism in the genus *Stomias* is manifested externally in at least three ways: (1) males are smaller than females; (2) males tend to have larger eyes; (3) males have larger postorbital organs. The sexes have not been determined in previous accounts of the genus, and the literature is useful only for the maximum size of females. The data presented here for *S.*

nebulosus, S. brevibarbatus, and *S. danae* are inadequate and need further amplification.

The maximum size attained by females varies greatly among the species (Table 4). Largest of all are the closely related species *S. colubrinus* and *S. lampropeltis.* Next in order is the group of species related to *S. boa,* in which maximum size is correlated roughly with numbers of serial photophores and vertebrae. Data from Ege (1934) and Morrow (1964a) are sufficient to establish that *S. nebulosus* and *S. brevibarbatus* are small species, the former less than 200 mm, the latter less than 150 mm. No females of *S. danae* have yet been recognized, but if the size of the largest male is taken as an indication, females probably become larger than 200 mm.

TABLE 4.—*Maximum known standard length of* Stomias *species*

Species	*Maximum standard length (mm)* ♀	♂
colubrinus	309	191
lampropeltis	[1] 297	116
gracilis	[2] 290	257
boa ferox	[3] 289	256
boa boa	298	239
atriventer	238	144
affinis	[3] 204	130
nebulosus	176	93
brevibarbatus	[2] 150	111
danae	?	159

[1] Information from Norman (1939).

[2] Information from Ege (1934).

[3] Information from Morrow (1964a).

Males in the *S. boa* group parallel the females in maximum size. Those of *S. gracilis, S. boa ferox,* and *S. boa boa* reach a length that is only about 10–20 percent shorter than the largest females. The largest male *S. atriventer,* however, is almost 100 mm (40 percent) shorter than the largest female. Not only do the smaller species apparently show this trend of the males being smaller in size than the females, but also the males of the largest species, *S. colubrinus* and *S. lampropeltis,* are much smaller than the females, markedly so in *S. lampropeltis.*

Data on eye size are inadequate for *S. nebulosus, S. brevibarbatus, S. danae,* and *S. boa ferox.* In the other six forms there is overlap between males and females, but males, on the average, have larger eyes than females of the same species at any given size. Fleshy orbit diameter relative to head length is given in Table 5. Relative to standard length, the eyes of females are not greatly different among the species. Because head length differs, however, the eye size is inversely correlated with head length, those species with the longest heads having the smallest relative eye size. In males, the head length-eye size relationship does not follow that of the females, although the relative head lengths are similar. These relationships are shown graphically in Figure 3, for *S. lampropeltis,* in which species the dimorphism is most extreme.

TABLE 5.—*Fleshy orbit diameter as percent of head length of* Stomias *species, showing that males have relatively larger eyes than females* [1]

Species	*Fleshy orbit percent of head length* ♀	♂
colubrinus	11.9–22.1	9.8–31.4
lampropeltis	15.0–29.4	20.5–34.1
gracilis	23.7–28.9	24.6–35.0
boa ferox	24.0–27.1	–
boa boa	21.6–26.5	21.3–36.6
atriventer	11.8–26.3	19.4–28.5
affinis	14.9–28.6	19.1–28.6
nebulosus	20.5–24.5	24.5–29.3
brevibarbatus	15.2–19.2	19.1
danae	–	17.3–21.1

[1] Original data only.

As in many stomiatoids, the postorbital organ is the most striking sexually dimorphic character, always larger in males. Its size relative to eye size is shown in Figures 3 and 4. Because the eyes are larger in males than females of each species, the differences in postorbital organ size are even more obvious than indicated by this relationship. In those species in which males become almost as large as females, the postorbital organ is relatively small in both males and females, and the distinction between males and females is not as pronounced. This is shown in Figure 4 for *S. gracilis,* and *S. boa* is quite similar. In *S. atriventer* and *S. nebulosus,* the organ in females is about the same relative size as in *S. gracilis* and *S. boa,* but in males it is relatively larger and hardly overlaps the female size range. This trend is continued in *S. affinis,* in which the female

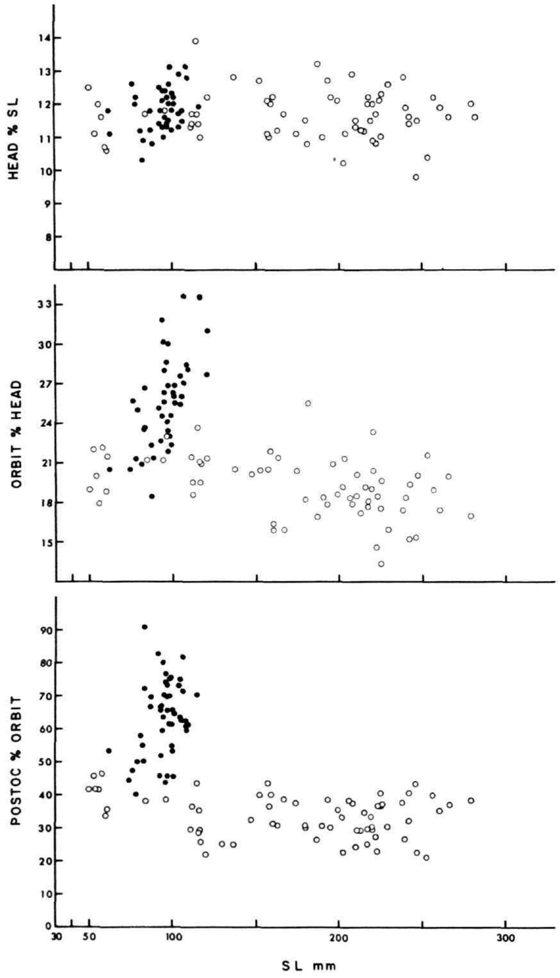

FIGURE 3.—*Stomias lampropeltis.* Graphs showing relationships of head length, fleshy orbit diameter, and postorbital organ. Open circles=females. Dots=males.

postorbital organ becomes somewhat larger, and that of the males is still larger and does not impinge upon the female size range. In females of *S. colubrinus* the postorbital organ is relatively larger than in females of the preceding five species. Males of *S. colubrinus,* however, reach an intermediate size, and the organ is similar in relative size to that of *S. affinis,* still considerably larger than in females. Females of the related species, *S. lampropeltis,* have a postorbital organ that is similar in size, but the males, which do not become as large as those of *S. colubrinus,* have an organ that may be al-

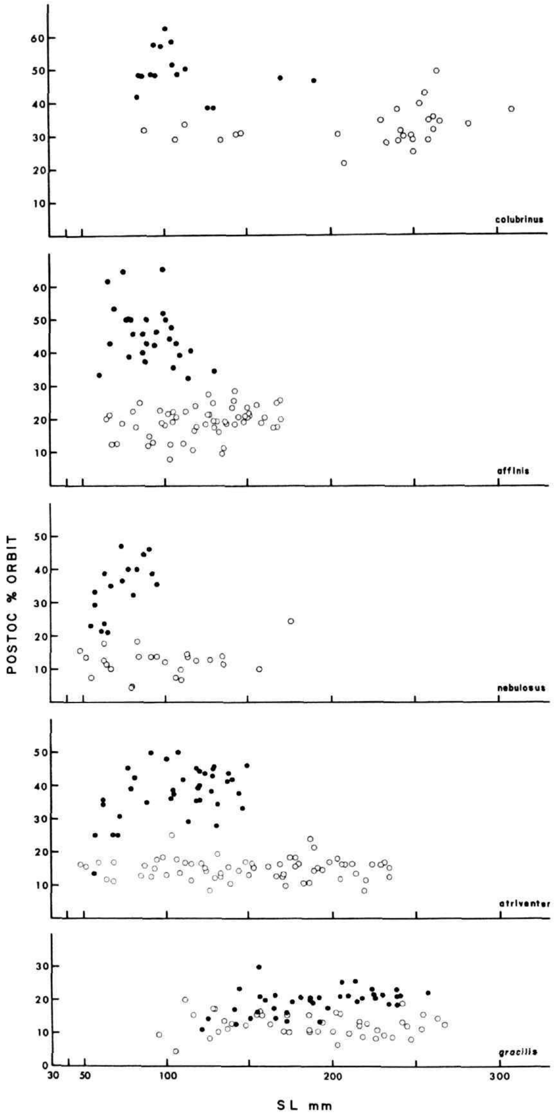

FIGURE 4. Graphs showing relative size of postorbital organ in five species of *Stomias* (see Figure 3 for *S. lampropeltis*). Open circles=females. Dots=males.

most as large as the eye. Two male *S. danae* (Table 3) have postorbital organs about 40 percent of fleshy orbit, while in one small specimen of undetermined sex the organ is 50 percent. This suggests that, in postorbital organ size, *S. danae* may prove similar to *S. atriventer* or *S. nebulosus.* The largest postorbital organ appears to be that of *S. brevibarbatus*. In two females, 60–70 mm SL, its is 62–75 percent of fleshy orbit; in a single male, 111 mm SL, it is 84 percent. The general rule within *Stomias*, then, is that a larger postorbital organ is associated with males that attain the least maximum size. In those species in which the size attained by males and females differs the most, the separation in size of male and female postorbital organs is the greatest.

Vertical Distribution

METHODS.—Because all available collections of *Stomias* were made with nonclosing nets, an analytic procedure was devised, similar to that used by William H. Krueger (unpublished manuscript), for determining depths of capture of *Idiacanthus*. Each species was considered separately. Data were used from expeditions from which all specimens of any species were examined. Only those stations *within the geographic range* of a species were used. Daylight (0700–1700 hours) and night (1900–0500 hours) tows were used, but those that included the usual periods of vertical migration (0500–0700, 1700–1900) were not considered. Collections made by the *Dana* using 100, 200, and 300 cm nets with circular openings were analyzed separately from Isaacs-Kidd midwater trawl (IKMT) collections. *Dana* depths were considered to be one-half the meters of wire out.

For each tow, the number of hours *at depth* (excluding up-down time) was multiplied by the area encompassed by the mouth of the net. For ring trawls of 100, 200, and 300 cm, the areas are 0.785, 1.766, and 7.065 square meters, respectively; for 3-foot, 6-foot, and 10-foot IKMT's, areas of 1, 4, and 9 square meters were used. The number of meter-hours for each depth interval, and the number of specimens caught at each depth interval were tabulated and reduced to percent of total for comparison (Tables 6 and 7). Much of the calculation was done on a time-share computer, using a program devised by Richard H. Goodyear.

In addition to providing the shallowest depth of capture during day or night, the reduced data remove some of the influence of the up-down component, and, therefore, indicate the depths at which concentrations of a species occur. When the percentage of specimens caught at any depth is considerably greater than the percentage of meter-hours at that depth, it may be assumed that this represents a real region of concentration. The reverse indicates that specimens recorded for that depth probably were caught while the net was bing lowered or raised.

GENERAL OBSERVATIONS.—When *Dana* data are used, results usually are biased by the paucity of shallow tows during daylight and of deep tows at night. Furthermore, the number of meter-hours logged by the *Dana* at night within various species ranges is two to eight times the number during daylight. Thus while interpretations of night distributions may be fairly reliable, daytime distributions are seldom so. The IKMT data that combine numerous Scripps Institution or USNS *Eltanin* collections provide the most reliable estimates.

No specimen of any species was taken above 300 m during daylight, and the data suggest that the bulk of most species populations occur between 400 and 1000 m. Two species, *S. colubrinus* and *S. lampropeltis*, appear to inhabit mainly depths below 1000 m during the day. Most species apparently migrate to the upper 100 or 200 m at night; *S. gracilis* remains mostly deeper than 200 m and *S. colubrinus* mostly below 600 m. These generalized vertical distributions place most species in the intermediate water masses during the day, and in subsurface water masses during the night. Some species have apparent peaks of night distribution, in addition to the upper concentration, at depths at which they occur in daytime. This suggests either that a part of the population does not migrate vertically, or that deeper populations become concentrated at somewhat shallower levels at night (see *S. atriventer, S. gracilis*, Tables 6 and 7).

Stomias atriventer. IKMT station data for the northern population are from Clarke (1963). Trawling time is relatively equally distributed among depth categories both day and night. During daylight, *S. atriventer* is most abundant at 500–600 m, with lesser peaks at 800–900 and 1250–1500 m. At night populations are concentrated in the upper 100 m, with lesser peaks at 500–600 and 700–800 m. Lavenberg and Ebeling (1967) indicate a vertical distribution between 500–700 m in the San Pedro basin. Data for the southern population do not allow speculation.

Stomias boa boa. Only the southern population has been analyzed. IKMT station data are from my own records for *Anton Bruun* cruise 14; from Humes (1967) and field notes of Leslie W. Knapp for *Anton Bruun* cruise 18; from the original data sheets for *Eltanin* cruise 21; and from Savage and Caldwell (1965, 1966, 1967) for *Eltanin* cruises 4–6, 9–11, 13–16, 19,

TABLE 6.—*Daytime vertical distributions of* Stomias *species, based on midwater trawls (IKMT) and ring trawls (Dana)*[1]

			southern				*northern*					
Depth (m)	*gracilis*		*boa boa*				*atriventer*		*colubrinus*			
	IKMT		*IKMT*		*DANA*		*IKMT*		*IKMT*		*DANA*	
	M-hr.	*Spec.*	*M-hr.*	*Spec.*	*M-hr.*	*Spec.*	*M-hr.*	*Spec.*	*M-hr.*	*Spec.*	*M-hr.*	*Spec.*
0–100	8. 5	0	0	–	2. 5	0	0. 9	0	27. 1	0	3. 9	0
101–200	1. 3	0	0	–	0	–	13. 5	0	0	–	0	–
201–300	8. 5	0	5. 2	0	0	–	2. 1	0	0	–	0	–
301–400	8. 1	0	2. 4	0	0	–	9. 7	0	33. 9	22. 2	0	–
401–500	3. 0	4. 7	6. 3	0	13. 7	0	0. 8	0	35. 6	22. 2	12. 2	0
501–600	*4. 7*	*14. 2*	4. 8	10	0	–	*11. 8*	*62. 5*	0	–	0	–
601–700	*3. 3*	*29. 3*	3. 6	10	3. 4	0	3. 2	0	*1. 7*	*44. 4*	2. 0	3. 8
701–800	*6. 1*	*31. 1*	4. 8	0	0	–	7. 1	7. 5	0	–	0	–
801–900	5. 0	0	8. 3	10	0	–	*5. 1*	*10. 0*	0	–	0	–
901–1000	3. 9	0. 9	2. 4	10	12. 6	14. 2	7. 7	0	0	–	11. 0	10. 0
1001–1250	8. 5	4. 7	7. 4	10	*6. 8*	*42. 9*	7. 9	0	1. 7	22. 2	*15. 5*	*21. 2*
1251–1500	4. 5	3. 8	2. 4	0	*23. 2*	*42. 9*	*7. 9*	*15. 0*	0	–	*11. 1*	*20. 0*
1501–2000	12. 5	4. 7	2. 7	0	11. 9	0	12. 2	0	0	–	44. 3	45. 0
2001–3000	16. 3	5. 6	20. 4	20	25. 9	0	10. 2	5. 0	0	–	0	–
>3000	5. 9	0. 9	29. 3	30	0	–	0	0	0	–	0	–
Number of specimens		106		10		7		40		9		80
Number of meter-hrs.	2445		746		313		1199		53		159	
Number of nets	140		40		48		59		6		21	

	lampropeltis		*nebulosus*		*affinis*	*brevibarbatus*		*boa ferox*	
	DANA		*DANA*		*DANA*	*DANA*		*DANA*	
	M-hr.	*Spec.*	*M-hr.*	*Spec.*	*Spec.*	*M-hr.*	*Spec.*	*M-hr.*	*Spec.*
0–100	0	–	0	–	–	18. 9	0	14. 1	0
101–200	0	–	0	–	–	16. 0	0	6. 7	0
201–300	0	–	0	–	–	15. 0	0	4. 1	0
301–400	0	–	0	–	–	9. 4	0	3. 2	0
401–500	11. 1	0	6. 2	0	4. 8	13. 6	0	7. 9	0
501–600	0	–	0	–	–	0. 4	0	0	–
601–700	0	–	1. 6	0	0	1. 5	0	2. 4	0
701–800	0	–	0	–	–	0. 9	0	0	–
801–900	0	–	0	–	–	0. 8	0	0	–
901–1000	11. 1	15. 4	*17. 3*	*80*	*61. 9*	3. 1	0	8. 0	50
1001–1250	*8. 3*	*15. 4*	9. 8	0	4. 8	2. 1	0	0	–
1251–1500	11. 1	0	23. 4	15	23. 8	0. 4	100	8. 0	50
1501–2000	*44. 5*	*61. 5*	25. 9	5	0	6. 3	0	8. 0	0
2001–3000	13. 9	7. 7	15. 8	0	4. 8	11. 5	0	37. 6	0
>3000	0	–	0	–	–	0	–	0	–
Number of specimens		13		20	21		1		2
Number of meter-hrs.	127		685			842		221	
Number of nets	24		57			207		44	

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[1] Methods of calculation given in text (page 11). Meter-hours (M-hr.) and specimens (Spec.) expressed as percent of total.

TABLE 7.—*Night vertical distributions of* Stomias *species* [1]

			southern				northern					
Depth (m)	*gracilis*		*boa boa*				*atriventer*		*colubrinus*			
	IKMT		*IKMT*		*DANA*		*IKMT*		*IKMT*		*DANA*	
	M-hr.	*Spec.*	*M-hr.*	*Spec.*	*M-hr.*	*Spec.*	*M-hr.*	*Spec.*	*M-hr.*	*Spec.*	*M-hr.*	*Spec.*
0–100	13.4	4.7	*10.2*	*35.7*	*32.7*	*84*	*4.6*	*51.6*	0	–	24.9	2.4
101–200	4.9	0	3.1	2.4	14.2	4	17.2	0	6.4	0	10.7	7.1
201–300	*3.8*	*10.6*	3.4	2.4	12.0	0	1.3	0	4.7	1.4	14.5	4.8
301–400	6.2	4.7	5.6	4.8	0.9	0	8.8	6.3	12.7	8.1	2.5	0
401–500	3.5	4.7	*8.3*	*26.2*	39.8	12	3.5	6.3	21.6	10.8	*29.6*	*35.7*
501–600	*4.2*	*17.6*	2.7	0	0	–	7.6	14.1	23.5	6.8	5.5	0
601–700	6.1	3.5	6.7	7.1	0	–	2.6	0	*22.1*	*55.4*	*1.4*	*2.4*
701–800	8.3	4.7	3.4	0	0	–	*1.2*	*4.7*	0	–	0	–
801–900	1.5	1.2	3.7	4.8	0	–	9.9	3.1	*0.5*	*10.8*	0	–
901–1000	*4.7*	*9.4*	1.4	2.4	0.4	0	7.2	0	0	–	2.7	7.1
1001–1250	*5.9*	*16.5*	3.4	0	0	–	8.2	1.6	0	–	*2.7*	*28.6*
1251–1500	6.6	2.3	9.2	2.4	0	–	6.1	4.7	0	–	*5.5*	*11.9*
1501–2000	11.7	9.4	12.3	0	0	–	3.6	3.1	0	–	0	–
2001–3000	11.8	9.4	18.0	4.8	0	–	13.9	3.1	6.0	1.4	0	–
>3000	7.5	1.2	8.7	7.1	0	–	4.3	1.6	2.4	5.4	0	–
Number of specimens......		85		42		25		64		74		42
Number of meter-hours.....	2743		1335		799		1261		671		256	
Number of nets............	163		76		99		58		31		49	

	lampropeltis		*nebulosus*		*affinis*	*brevibarbatus*		*boa ferox*	
	DANA		*DANA*		*DANA*	*DANA*		*DANA*	
	M-hr.	*Spec.*	*M-hr.*	*Spec.*	*Spec.*	*M-hr.*	*Spec.*	*M-hr.*	*Spec.*
0–100	32.9	0	38.4	27.3	*50.6*	58.2	15.0	*61.5*	*75.0*
101–200	*15.8*	*71.4*	*27.9*	*46.5*	*35.7*	*19.2*	*65.0*	*20.3*	*22.0*
201–300	15.8	14.3	14.4	16.8	7.0	5.3	10.0	4.4	1.5
301–400	0	–	0.7	0.6	0.8	1.9	2.5	1.4	0.9
401–500	35.5	14.3	15.7	8.2	5.5	11.2	7.5	10.2	0.6
501–600	0	–	0	–	–	1.1	0	0	–
601–700	0	–	0.6	0.6	0	0.9	0	0	–
701–800	0	–	0	–	–	0.1	0	0	–
801–900	0	–	0	–	–	0	–	0	–
901–1000	0	–	0.7	0	0	0.1	0	0.2	0
1001–1250	0	–	0.2	0	0	0.5	0	0.4	0
1251–1500	0	–	0.7	0	0.4	0.3	0	0.4	0
1501–2000	0	–	0.7	0	0	0.6	0	0.2	0
2001–3000	0	–	0	–	–	0.4	0	0.4	0
>3000	0	–	0	–	–	0.3	0	0.6	0
Number of specimens.......		6		333	253		40		545
Number of meter-hours.....	278		2963			7021		3361	
Number of nets............	36		500			1318		537	

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[1] See explanations to Table 6.

24, and 26. Data for *Dana* stations from Carlsberg Foundation (1934).

The meager daytime IKMT catches suggest that *S. boa boa* lives below 500 m, but allow no further limitation of its vertical range. At night this species shows concentrations in the upper 100 m and at 400–500 m. *Dana* collections tentatively indicate daytime concentrations at 900–1500 m, and confirm the night range by IKMT data.

Stomias boa ferox. Dana station data are from Schmidt (1929) and Carlsberg Foundation (1934), catch records are from Ege (1934). Despite reasonable daytime sampling, only two specimens are recorded, between 900–1500 m. The only real conclusion to be drawn is that this species seems to occur below 500 m during daylight hours. At night, it is abundant in the upper 200 m but sampling below 500 m is inadequate to indicate possible deeper concentrations.

Stomias gracilis. Data are from Savage and Caldwell (1965, 1966, 1967) for the same *Eltanin* cruises used for *S. boa boa,* and from Fisher (1964) for Scripps Institution's Expedition "Monsoon."

Although it occurs between 400–500 m in daytime, *S. gracilis* is clearly concentrated between 500–800 m. It occurs in the upper 100 m at night, but the peaks of abundance are found at 200–300 m, 500–600 m, and 900–1250 m. This species remains throughout its vertical migration almost entirely in intermediate water of Antarctic origin (see Reid, 1965).

Stomias affinis and *Stomias nebulosus.* Depth relations of these two species have been analyzed only in the broad area where they occur sympatrically. This includes a relatively narrow band from off southeastern Africa, curving northward to Ceylon, and south of the Indonesian Islands, the South China Sea, Celebes Sea, and closely adjacent areas. Data are from the 1928–30 *Dana* expedition (Carlsberg Foundation, 1934). These data are strongly biased toward night collections, and toward deep daytime and shallow night collections. All daytime stations were used in the calculations, but only every second night station.

A primary objective was to seek some difference in the vertical distribution of these two geographically sympatric species that might explain their apparent coexistence. None was found. The data suggest that, in a general way, *S. affinis* tends to occur at shallower depths than *S. nebulosus,* but the overlap is great. Both species were taken together commonly in the same net by the *Dana.*

At the shallowest daytime depths sampled, 400–500 m, *S. affinis* was taken, but not *S. nebulosus.* Both species appear most abundant at 900–1000 m but this is probably an artifact due to collecting bias and small sample size. At night both species clearly are most abundant in the upper 200 m, with *S. affinis* concentrated in the upper 100 m and *S. nebulosus* at 100–200 m.

In contrast to the sympatry exhibited by these two species throughout the entire range of *S. nebulosus* in the Indian Ocean and Southeast Asian seas, their geographic ranges in the only other region of *S. nebulosus* occurrence, the Central Pacific, are almost completely separated (Figures 5 and 6). Most of these captures were made in the upper 400 m at night (specimens examined by me at the Bureau of Commercial Fisheries Biological Laboratory, Honolulu, and reported, in part, by King and Iversen, 1962).

Stomias colubrinus. Dana data are from Schmidt (1929), the stations being in or near the Gulf of Panama. IKMT data, all from cruises of the *Anton Bruun,* are from my own records for cruise 14, from Chin (1966) for cruise 16, and from Humes (1967) and field notes of Leslie W. Knapp for cruise 18. These stations are all between 2°N and 32°S in the eastern Pacific.

Little collecting has been done in the upper 400 m during daylight, and no catches are recorded in this upper stratum. The vast majority of specimens were caught in nets fished between 900–2000 m, which is where the *Dana* placed most of its nets. Night captures have been made in the upper 100 m, with peaks at 500–600 m (*Dana*), 600–700 m (IKMT), and 1000–1500 m (*Dana*). It seems probable, then, that *S. colubrinus* remains largely at considerable depths, both day and night, perhaps avoiding the oxygen-poor layer. The southern population of *S. atriventer,* on the other hand, may be associated with the oxygen-poor water, if depth data for the northern population can be extrapolated.

Stomias lampropeltis. Data from *Dana* stations 3999–4009 were used, and these are too few to allow reasonable conclusions. They suggest that, like *S. colubrinus, S. lampropeltis* may inhabit depths from 900–2000 m during the day, and at night are found up to 100–200 m, but not in the upper 100 m. In the numerous collections of the *Reine Pokou,* most of them made at night, *S. lampropeltis* was taken at 375–750 m (750–1500 m of wire out), shallower than *Dana*

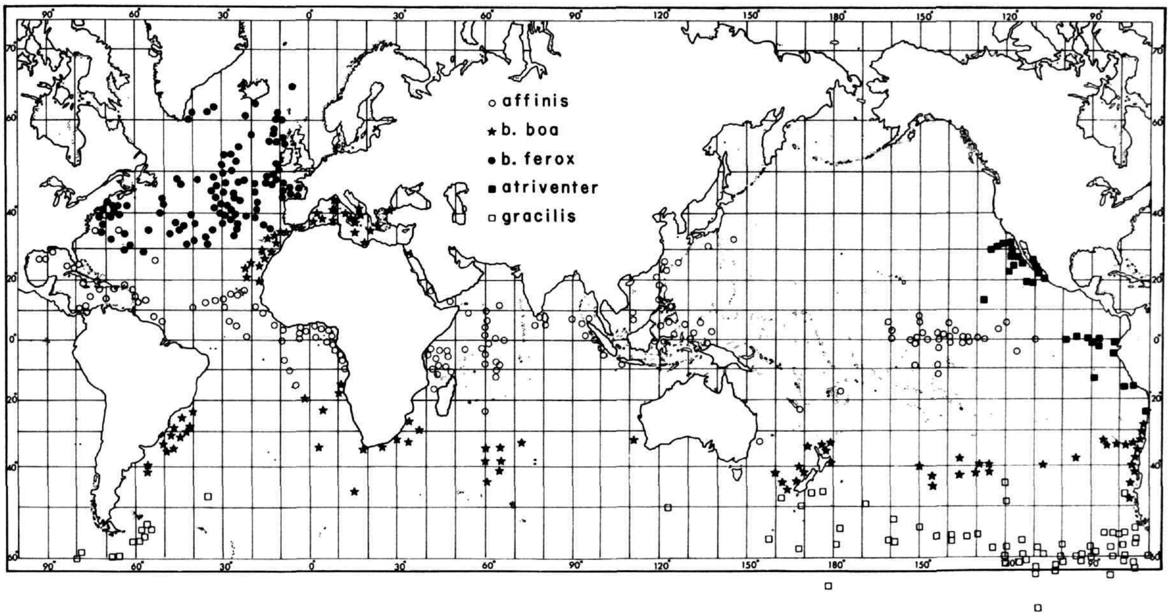

FIGURE 5.—Distributions of the five members of the *Stomias boa* species group. Original data and records from the literature (Ege, 1934; Demir, 1958; Berry and Perkins, 1967; Norman, 1939; Aron and Goodyear, 1969; Blache, 1964).

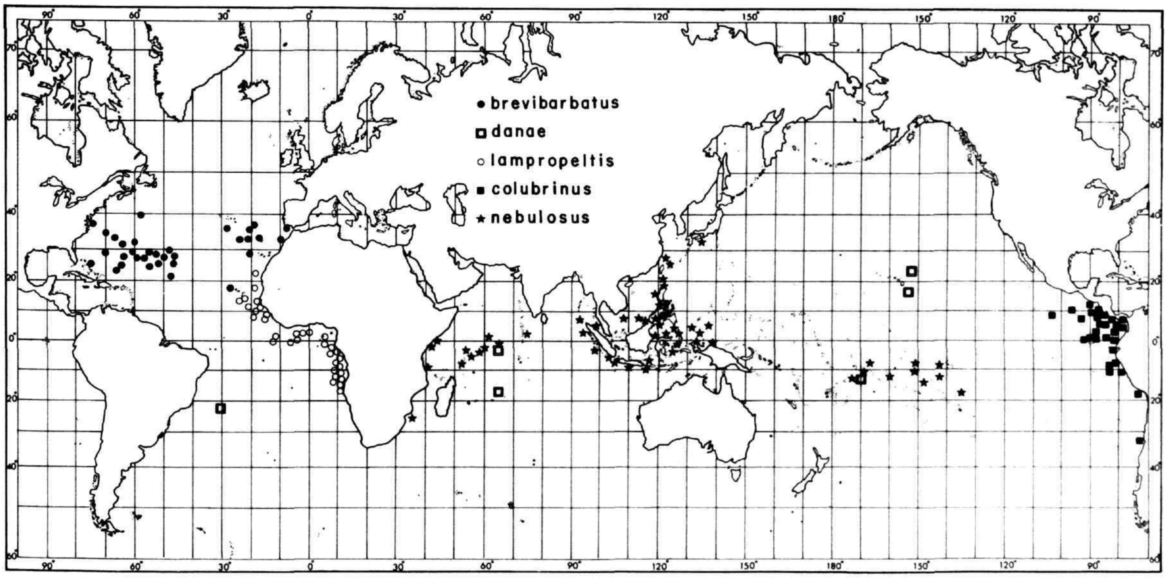

FIGURE 6.—Distributions of species in the *Stomias brevibarbatus, colubrinus,* and *nebulosus* species groups. Original data and records from the literature (Ege, 1934; Blache, 1964; Pieper, 1967; Bussing, 1965).

data suggest. Unfortunately, these were virtually the only depths sampled.

Stomias brevibarbatus. The abundant *Dana* collections in the North Atlantic (Schmidt, 1929; Carlsberg Foundation, 1934) were used in conjunction with specimen data reported by Ege (1934). Despite reasonable effort during the day between 0–500 m and 1500–3000 m, only one specimen was caught. This suggests that the daytime occurrence of *S. brevibarbatus* is between 500–1500 m, where relatively little effort was expended.

A tremendous amount of fishing was done at night from the surface to 500 m but little deeper than 500 m. This clearly shows the greatest night concentrations at 100–200 m.

Stomias danae. Only six specimens are known. The *Dana* specimen from the South Pacific was taken in a trawl fished at 300 m during twilight. One of the two specimens from near Hawaii was taken in a discrete-depth sampler at 317–451 m during daytime (Pieper, 1967); the other was taken in a long trawl at 2671 m covering both night and day hours. One of the two Indian Ocean captures was in a similarly inconclusive night and day trawl to 2500 m; it was, however, in the deep fraction of a Foxton catch divider, and was probably taken below about 250 m. The other was taken in a shallow Foxton fraction during a day-night tow.

Zoogeography and Evolution

Four species groups are apparent within the genus *Stomias*. Group one (the *brevibarbatus* group), comprising *S. brevibarbatus* and *S. danae,* has only five lateral rows of hexagonal areas, the hyoid barbel shorter than the head, seven or more pectoral rays, and the pelvic fins inserted anteriorly, at 59–65 percent of standard length. Group two (the *colubrinus* group), including *S. colubrinus* and *S. lampropeltis,* has only a single tooth at the anterior end of each palatine. Group three, including only *S. nebulosus,* has 16–25 premaxillary teeth, all of which are short, and 9–16 mandibular teeth, most of which are longer than any of the premaxillary teeth. Group four (the *boa* group) contains the four remaining species—*S. atriventer, S. boa* (with two subspecies), *S. gracilis,* and *S. affinis.* All usually have five fanglike premaxillary teeth and eight to ten mandibular teeth, of which the first two or three are short, the posterior ones fanglike and grading from long to moderate toward the rictus. All four groups are distinguished by combinations of other characters, as may be seen in the key to species.

Many morphological characters of the species and species-groups show trends that I interpret as evolutionary trends. The *brevibarbatus* group has many characters, some of them different in the two species of that group, that are changed and stabilized in all the other species-groups. For example, the barbel is short in the *brevibarbatus* group, with either no filaments arising from its tip or with four filaments. In all other groups the barbel is longer, quite similar in length in all species, and has three terminal filaments. There are seven to nine, usually eight pectoral rays in the *brevibarbatus* group, six in all others. The number of lateral rows of hexagons is five in the *brevibarbatus* group, six in all others. I regard this as evidence that the *brevibarbatus* group is phylogenetically the oldest, its species being the survivors of a stock that was considerably more variable in its morphology than are the more recently evolved groups.

The *colubrinus* and *nebulosus* groups are next in order of phylogenetic age, and I believe that the former evolved earliest. About the only primitive character that they retain is a relatively large number of fairly small teeth, and *S. colubrinus* shows signs of reduction in number and enlargement of individual teeth.

Most recently evolved is the *boa* group, with four species that have stable morphological characters, with the exception of somite and photophore numbers.

The trend among and within all groups is toward elongation of the body and higher numbers of vertebrae, somites, and photophores. The lowest counts are seen in the *brevibarbatus* and *nebulosus* groups, followed by the *colubrinus* group. Within the *boa* group, *S. affinis* is quite similar to the *colubrinus* group, followed by *S. antriventer, S. boa boa, S. boa ferox,* and *S. gracilis,* in that order.

Another such trend is seen in postorbital organ size in males. This light organ is largest in *S. brevibarbatus* and the *colubrinus* group, while in *S. nebulosus* it is intermediate in size and resembles some of the *boa* group. Within the *boa* group, the reduction in size of the postorbital organ follows the increase in photophore counts from *S. affinis,* with the largest postorbital organ, to *S. gracilis* with the smallest.

The number of small photophores in the hexagonal areas and in the interspace between the lateral and ventral rows of large photophores show apparent evolutionary trends toward reduction. In *S. brevibarbatus* there are 14–20 photophores in the hexagons of the ventralmost (fifth) row, 12–18 in the fourth row, and 7–10 in the third. These numbers in *S. danae* are 4–6, 4–5, and 2–4, respectively. The three lower hexagon rows in the two species of the *colubrinus* group have 5–9 in the sixth, 4–6 in the fifth, and 4–6 in the fourth rows. The *boa* group has 3–5, 3–4, and 2–4 photophores in these rows, except for *S. affinis,* which has 3, 2–3, and 2, respectively. The greatest reduction is seen in *S. nebulosus,* with 1–3, 1, and 1. The uppermost rows (two in the *brevibarbatus* group, three in all others) have 1 photophore per hexagon. The small photophores between the lateral and ventral rows of serial photophores form a concave arc below each lateral photophore in the series. In the *brevibarbatus* and *colubrinus* groups, these arcs are composed of wide bands of very small photophores. In *S. nebulosus* the arcs are irregular and composed of about 6, somewhat larger photophores, and in the *boa* group the arcs are quite regular and formed primarily by 3–5 larger photophores.

The geographic distribution patterns of the species support the contention that the *boa* group is the most recently evolved. The species of that group occupy complementary ranges in the more productive waters of the world (Figure 5). *Stomias affinis* is found in equatorial or adjacent tropical waters of the Atlantic, Indian, and Pacific oceans, except for the eastern tropical Pacific. It apparently occupies the areas of the cen-

TABLE 8.—Stomias *species: frequency distribution of photophores in ventral row (IC)*[1]

Species	*Number of photophores in ventral row (IC)*																		
	66	67	68	69	70	71	72	73	74	75	76	77	78	79	80	81	82	83	84
atriventer (S)	–	–	–	–	–	–	–	–	–	–	–	–	2	3	9	7	1	–	–
atriventer (N)	–	–	–	–	–	–	–	–	–	–	–	3	5	6	3	3	2	–	–
boa boa (Med)	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	2	12	34
boa boa (S)	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	3	1	9	13
boa ferox	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
gracilis	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
affinis	–	–	–	–	–	–	–	2	5	24	53	74	45	13	5	1	1	–	–
colubrinus	–	–	–	–	–	–	–	–	1	3	22	49	40	23	5	2	–	–	–
lampropeltis	–	–	–	–	–	–	–	2	6	22	32	31	20	5	2	–	–	–	–
brevibarbatus	–	–	–	–	–	–	2	7	15	5	1	–	–	–	–	–	–	–	–
danae	–	–	1	1	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–
nebulosus	X	2	9	19	35	44	13	2	–	–	–	–	–	–	–	–	–	–	–

	Number of photophores in ventral row (IC)																	
	85	86	87	88	89	90	91	94	95	96	97	98	99	100	101	102	N	x̄
atriventer (S)	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	22	80. 1
atriventer (N)	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	22	79. 2
boa boa (Med)	54	29	6	2	–	–	–	–	–	–	–	–	–	–	–	–	139	84. 9
boa boa (S)	25	19	6	6	–	–	–	–	–	–	–	–	–	–	–	–	83	85. 0
boa ferox	1	8	27	37	24	3	X	–	–	–	–	–	–	–	–	–	100	87. 8
gracilis	–	–	–	–	–	–	–	4	6	10	10	7	3	3	1	1	45	96. 9
affinis	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	223	76. 9
colubrinus	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	145	77. 5
lampropeltis	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	120	76. 5
brevibarbatus	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	30	73. 9
danae	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	3	69. 0
nebulosus	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	124	70. 3

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[1] In addittion to original observations, data are included from Ege (1934), Morrow (1964a), and Blache (1964). Where frequency distributions were not given in the literature, the extensions are indicated by an X.

tral water masses in the South Atlantic and Indian oceans, but large areas in these oceans have not been adequately sampled. The two subspecies of *S. boa* meet the northern boundary of *S. affinis* range in the Atlantic, with *S. boa boa* found only in the Mediterranean and its outflow off the northwest coast of Africa and *S. boa ferox* throughout practically the entire North Atlantic. The southern population of *S. boa boa,* in the Subtropical Convergence around the world and northward in the Benguela and Humboldt current regions, abuts the southern boundary of the range of *S. affinis*. In turn, *S. gracilis* occupies subantarctic and Antarctic waters south of the *S. boa boa* range. Two populations of *S. atriventer* are found in the northeastern Pacific and southeastern Pacific, with a wide gap between them. The southern population meets the northward extension of *S. boa boa* along the coast of Chile south of Antofagasta. The only region that has been well collected and where the *boa* group is not represented is the central North Pacific. Whether or not the group is represented in the central South Pacific is still open to question.

The remaining three species groups, in contrast to the *boa* group, have relatively limited ranges, all of them at least partly confluent with members of the *boa* group. This fact alone suggests that the *boa* group has superimposed itself on the others. In most cases, the older groups show evidence of retracted distributions and limitation to relatively unfavorable or specialized environments. The most extreme example is the

TABLE 9.—Stomias *species: frequency distribution of photophores in lateral rows (OA)*[1]

Species	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56
atriventer (S)	–	–	–	–	–	–	–	–	–	–	–	–	3	9	7	4	–
atriventer (N)	–	–	–	–	–	–	–	–	–	–	–	–	4	6	6	5	–
boa boa (Med)	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
boa boa (S)	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
boa ferox	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
gracilis	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
affinis	–	–	–	–	–	–	–	–	X	X	1	1	X	2	–	–	–
colubrinus	–	–	–	–	–	–	2	9	13	7	1	–	–	–	–	–	–
lampropeltis	–	–	–	–	–	4	14	40	22	13	2	1	–	–	–	–	–
brevibarbatus	–	–	–	–	–	–	1	X	X	1	X	–	–	–	–	–	–
danae	–	–	1	1	2	(1)	–	–	–	–	–	–	–	–	–	–	–
nebulosus	X	X	X	X	X	X	–	–	–	–	–	–	–	–	–	–	–

Species	57	58	59	60	61	62	63	64	65	66	67	68	69	70	71	N	$\bar{x}$
atriventer (S)	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	23	53. 5
atriventer (N)	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	21	53. 6
boa boa (Med)	X	X	X	X	X	–	–	–	–	–	–	–	–	–	–	–	–
boa boa (S)	1	10	17	6	3	1	–	–	–	–	–	–	–	–	–	38	59. 1
boa ferox	X	X	X	X	X	X	X	X	–	–	–	–	–	–	–	–	–
gracilis	–	–	–	–	–	–	–	–	1	1	6	16	11	7	3	45	68. 5
affinis	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
colubrinus	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	32	47. 9
lampropeltis	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	96	47. 4
brevibarbatus	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
danae	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	4	43. 3
nebulosus	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–

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[1] In addition to original observations, data are included from Ege (1934), Morrow (1964a), and Blache (1964). Where frequency distributions were not given in the literature, the extensions are indicated by an X.

colubrinus group, of which *S. colubrinus* inhabits the eastern tropical Pacific, with its apparent center of abundance between the equator and 10°N, and *S. lampropeltis* inhabits the eastern tropical Atlantic, also apparently most abundant between 0° and 10°N. There is no question that these two species are closely related and that they are distinct from all others. Their present geographic distributions could only have resulted from reduction of a much wider range that included, at one time, at least the eastern Pacific and the width of the Atlantic. In all probability *S. affinis* displaced the representative of this group in the tropical Atlantic, and *S. lampropeltis* now occupies only the region off west Africa that is characterized by seasonal upwelling, high productivity, and the presence of an oxygen-poor layer (Bubnov, 1966). These two species coincide in the west African area and are able to coexist, presumably, by virtue of having different vertical distribution patterns, although the available data are not sufficient to establish this. In the eastern tropical Pacific, *S. colubrinus* occupies an area that is largely separate from the southern population of *S. atriventer,* but the two occur together in abundance at the Galapagos Islands and along the coasts of Ecuador and Peru, areas within which an oxygen-poor layer occurs. In this case, the vertical distribution data suggest that *S. colubrinus* tends to remain below the oxygen-minimum layer, while *S. atriventer* inhabits this layer (about 100–700 m according to Wooster and Cromwell, 1958), and ver-

TABLE 10.—*Vertebral counts of* Stomias *species: frequency distribution* [1]

Species	*Number of vertebrae*																
	59	60	61	62	63	64	65	66	67	68	69	70	71	72	73	74	75
atriventer (S)	–	–	–	–	–	–	–	–	–	–	1	4	6	12	7	2	–
atriventer (N)	–	–	–	–	–	–	–	–	–	–	1	8	18	5	1	1	–
boa boa (Med)	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1
boa boa (S)	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	6
boa ferox	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
gracilis	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
affinis	–	–	–	–	–	–	–	3	19	39	35	19	4	X	–	–	–
colubrinus	–	–	–	–	–	–	–	1	1	14	33	29	14	3	–	–	–
lampropeltis	–	–	–	–	–	–	1	2	9	15	12	5	–	–	–	–	–
brevibarbatus	–	–	–	–	–	X	X	X	X	X	–	–	–	–	–	–	–
danae	–	1	1	2	–	–	–	–	–	–	–	–	–	–	–	–	–
nebulosus	X	1	8	17	16	8	1	–	–	–	–	–	–	–	–	–	–

Species	*Number of vertebrae*																
	76	77	78	79	80	81	82	83	86	87	88	89	90	91	92	N	$\bar{x}$
atriventer (S)	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	32	71.8
atriventer (N)	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	34	71.0
boa boa (Med)	10	26	9	7	1	–	–	–	–	–	–	–	–	–	–	54	77.3
boa boa (S)	7	11	7	9	4	1	1	–	–	–	–	–	–	–	–	47	77.5
boa ferox	–	1	16	49	70	56	17	3	–	–	–	–	–	–	–	212	80.1
gracilis	–	–	–	–	–	–	–	–	2	7	9	7	5	1	1	32	88.4
affinis	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	119	68.2
colubrinus	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	95	69.5
lampropeltis	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	44	68.1
brevibarbatus	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	14	–
danae	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	4	61.3
nebulosus	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	51	62.5

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[1] In addition to original data, counts are included from Ege (1934); where Ege did not give frequencies, his data are represented by an X.

tically migrates within it. Even the northern population of *S. atriventer,* which does not occur together with *S. colubrinus,* apparently has its main vertical distribution (see Tables 6 and 7) within the oxygen-poor layer (about 300–800 m according to Reid, 1965).

The two species of the *brevibarbatus* group are restricted to the North Atlantic (*S. brevibarbatus*) and the central waters of the Indo-Pacific and South Atlantic (*S. danae*). These are regions of low productivity, and the populations of both species are relatively sparse, as indicated by trawling success. More day or night meter-hours of trawling are recorded within the distributional limits (mainly the Sargasso Sea) of *S. brevibarbatus* than for any other species, yet only 41 specimens were caught during these hours (this does not include trawls during dawn, twilight, or both night and day). This is an average of only one fish per 176 meter-hours at night, a figure not approached by any of the other species that were computed for Tables 6 and 7. The rarity of *S. danae* is attested to by the existence of only six known specimens. The species is known to occupy waters that are inhabited by *S. affinis* (Indian Ocean) and *S. nebulosus* (South Pacific), and it also occurs in the North Pacific near the Hawaiian Islands, where it is the only recorded species of *Stomias.* Probably it was formerly more abundant throughout a large part of the Indo-Pacific, but has diminished in numbers through competition with *S. affinis.* It seems that *S. danae* may even be on the verge of extinction.

TABLE 11.—Stomias *species: frequency distribution of photophores in PV portion of ventral row* [1]

Species	*Number of photophores in PV portion of ventral row*														
	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44
atriventer (S)	–	–	–	–	–	–	–	–	–	–	–	3	7	9	6
atriventer (N)	–	–	–	–	–	–	–	–	–	–	1	6	7	6	3
boa boa (Med)	–	–	–	–	–	–	–	–	–	–	–	–	–	–	X
boa boa (S)	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1
boa ferox	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
gracilis	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
affinis	–	–	–	–	–	–	–	–	–	–	–	1	3	4	1
colubrinus	–	–	–	–	–	–	2	15	42	65	29	3	1	–	–
lampropeltis	–	–	–	–	–	–	1	3	20	59	38	17	5	1	–
brevibarbatus	–	–	4	11	10	3	–	–	–	–	–	–	–	–	–
danae	1	3	1	–	–	–	–	–	–	–	–	–	–	–	–
nebulosus	–	–	–	X	X	1	X	X	X	–	–	–	–	–	–

	Number of photophores in PV portion of ventral row														
	45	46	47	48	49	50	51	52	53	54	55	56	57	N	x̄
atriventer (S)	–	–	–	–	–	–	–	–	–	–	–	–	–	25	42.7
atriventer (N)	1	–	–	–	–	–	–	–	–	–	–	–	–	24	42.3
boa boa (Med)	X	X	X	X	X	–	–	–	–	–	–	–	–	–	–
boa boa (S)	6	10	10	8	6	2	–	–	–	–	–	–	–	43	47.0
boa ferox	–	X	X	X	X	X	X	–	–	–	–	–	–	–	–
gracilis	–	–	–	–	–	–	–	–	3	16	13	9	4	45	54.9
affinis	9	1	–	–	–	–	–	–	–	–	–	–	–	19	43.9
colubrinus	–	–	–	–	–	–	–	–	–	–	–	–	–	157	38.7
lampropeltis	–	–	–	–	–	–	–	–	–	–	–	–	–	144	39.4
brevibarbatus	–	–	–	–	–	–	–	–	–	–	–	–	–	28	33.4
danae	–	–	–	–	–	–	–	–	–	–	–	–	–	5	31.0
nebulosus	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–

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[1] In addition to original observations, data are included from Ege (1934), Blache (1964), and Morrow (1964a). Where frequency distributions were not given in the literature, the extensions are indicated by an X.

The distribution pattern of *S. nebulosus* is interesting. Across the Indian Ocean, it occurs in a narrow band, which apparently is not owing to the fact that most collections were made by the *Dana*. Two north-south transects made by the *Anton Bruun* along 60° and 65° (cruises 3 and 6, 1963 and 1964) took *S. affinis* at ten stations from 12°N to 23°S, but *S. nebulosus* was captured only at three stations, all within a few degrees of the equator (Gibbs, manuscript unpublished). Among the islands of southeast Asia, *S. nebulosus* is common in the Celebes, Sulu, Flores, and South China seas and adjacent waters of the western Pacific, in which areas it is also found together with *S. affinis*, the two species having been taken commonly in the same net (see Ege, 1934 for data). The vertical distribution computations (Tables 6 and 7) suggest that *S. affinis* tends to concentrate at somewhat shallower depths, both day and night, than *S. nebulosus*, but the difference is not striking. The *Dana* data (Ege, 1934) indicate that, in the region of mutual occurrence, *S. nebulosus* is generally more abundant than *S. affinis* (see Tables 6 and 7). Apparently, then, *S. nebulosus* is holding its own against *S. affinis*, but within a limited range. In the central Pacific, a different situation is evident. There, *S. affinis* inhabits the equatorial waters, while *S. nebulosus* occurs separately in a band between about 8° and 18°S (Figures 5 and 6). One factor appears to clarify the situation. Virtually all collections of *S. nebulosus* have been made in the vicinity of land masses or islands. Thus, again, this more primi-

TABLE 12.—Stomias *species: frequency distribution of photophores in OV portion of lateral row* [1]

Species	*Number of photophores in OV portion of lateral row*														
	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44
atriventer (S)	–	–	–	–	–	–	–	–	–	–	–	10	6	7	–
atriventer (N)	–	–	–	–	–	–	–	–	–	1	3	9	4	5	–
boa boa (Med)	–	–	–	–	–	–	–	–	–	–	–	–	–	–	X
boa boa (S)	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1
boa ferox	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
gracilis	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
affinis	–	–	–	–	–	–	–	–	–	–	X	X	1	2	2
colubrinus	–	–	–	–	–	–	X	6	25	6	3	X	–	–	–
lampropeltis	–	–	–	–	–	–	1	8	36	35	14	4	–	–	–
brevibarbatus	–	–	X	X	X	X	–	–	–	–	–	–	–	–	–
danae	2	2	1	–	–	–	–	–	–	–	–	–	–	–	–
nebulosus	–	–	X	X	X	X	X	X	X	–	–	–	–	–	–

	Number of photophores in OV portion of lateral row													
	45	46	47	48	49	50	51	52	53	54	55	56	N	x̄
atriventer (S)	–	–	–	–	–	–	–	–	–	–	–	–	23	41.9
atriventer (N)	–	–	–	–	–	–	–	–	–	–	–	–	22	41.4
boa boa (Med)	X	X	X	X	–	–	–	–	–	–	–	–	–	–
boa boa (S)	7	7	12	3	2	–	–	–	–	–	–	–	32	46.5
boa ferox	X	X	X	X	X	X	–	–	–	–	–	–	–	–
gracilis	–	–	–	–	–	–	–	5	19	12	7	2	45	53.6
affinis	X	X	–	–	–	–	–	–	–	–	–	–	–	–
colubrinus	–	–	–	–	–	–	–	–	–	–	–	–	40	38.2
lampropeltis	–	–	–	–	–	–	–	–	–	–	–	–	98	38.7
brevibarbatus	–	–	–	–	–	–	–	–	–	–	–	–	–	–
danae	–	–	–	–	–	–	–	–	–	–	–	–	5	30.8
nebulosus	–	–	–	–	–	–	–	–	–	–	–	–	–	–

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[1] In addition to original observations, data are included from Ege (1934), Blache (1964), and Morrow (1964a). Where frequency distributions were not given in the literature, the extensions are indicated by an X.

tive species is surviving in a relatively specialized habitat, while *S. affinis* inhabits the open seas as well.

The conjectural zoogeographic-evolutionary picture that emerges, then, starts with a species resembling one of the *brevibarbatus* group that eventually occupied the Atlantic and the Indo-Pacific, probably via tropical waters of the former Tethys Sea. This species was separated, perhaps by the closing off of Tethys connections, and diverged in the two regions to give rise to *S. brevibarbatus* in the Atlantic and *S. danae* in the Indo-Pacific. Next, perhaps essentially simultaneously, the precursors of the *colubrinus* and *nebulosus* groups developed, the former probably in the Atlantic, the latter probably in the Indian Ocean or the southeast Asian area, and both proceeded to occupy the richer equatorial waters, excluding therefrom the original occupants of the *brevibarbatus* group. The ancestral form of the *S. boa* group was *S. affinis* or something similar to it, since this species is at the base of the morphological trends previously described for the group. The ancestral form probably arose from *S. nebulosus* in the Indo-Pacific for they are quite similar in most respects except tooth structure, and spread to the Atlantic, probably around South Africa. From *S. affinis,* two species apparently were generated. A stock became isolated in the eastern Pacific to give rise to *S. atriventer.* At one time *S. atriventer* probably occupied most of the eastern Pacific between about 33°N

TABLE 13.—Stomias *species: frequency distribution of photophores in VAV portion of ventral row and VAL portion of lateral row* [1]

Species	*Number of photophores in VAV portion of ventral row*													
	5	6	7	8	9	10	11	12	13	14	15	16	N	x
atriventer (S)	–	–	–	–	–	3	16	8	–	–	–	–	27	11.2
atriventer (N)	–	–	–	–	X	3	8	12	4	–	–	–	27	11.6
boa boa (Med)	–	–	–	–	–	3	29	52	13	3	–	–	100	11.8
boa boa (S)	–	–	–	–	–	3	19	14	8	1	–	–	45	11.7
boa ferox	–	–	–	–	–	11	47	36	6	–	–	–	100	11.4
gracilis	–	–	–	–	–	–	–	1	13	13	15	3	45	14.1
affinis	13	146	94	18	1	–	–	–	–	–	–	–	272	6.4
colubrinus.	–	–	1	11	77	57	8	1	–	–	–	–	155	9.4
lampropeltis	–	–	1	17	72	51	7	1	–	–	–	–	149	9.3
brevibarbatus	–	–	–	–	–	–	–	1	5	17	4	1	28	14.0
danae	–	–	–	–	–	–	–	1	3	1	–	–	5	13.0
nebulosus	2	35	52	43	4	–	–	–	–	–	–	–	136	7.1

	Number of photophores in VAL portion of laterval row															
	4	5	6	7	8	9	10	11	12	13	14	15	16	17	N	x̄
atriventer (S)	–	–	–	–	–	–	–	10	13	1	–	–	–	–	24	11.6
atriventer (N)	–	–	–	–	–	–	1	7	6	8	1	–	–	–	23	12.0
boa boa (Med)	–	–	–	–	–	–	–	X	X	X	X	X	–	–	–	–
boa boa (S)	–	–	–	–	–	–	–	2	10	14	1	1	–	–	28	12.6
boa ferox	–	–	–	–	–	–	–	X	X	X	–	–	–	–	–	–
gracilis	–	–	–	–	–	–	–	–	–	6	11	15	13	2	47	14.9
affinis	1	–	1	43	90	13	–	–	–	–	–	–	–	–	148	7.8
colubrinus	–	–	–	X	7	26	6	3	–	–	–	–	–	–	42	9.1
lampropeltis	–	–	–	9	23	52	14	–	–	–	–	–	–	–	98	8.7
brevibarbatus	–	–	–	–	–	–	–	X	X	X	X	X	X	X	–	–
danae	–	–	–	–	–	–	–	–	2	2	1	–	–	–	5	12.8
nebulosus	–	X	X	1	X	X	–	–	–	–	–	–	–	–	–	–

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[1] In addition to original observations, data included from Ege (1934), Blache (1964), and Morrow (1964a). Where frequency distributions were not given in the literature, the extensions are indicated by an X.

and 24°S, but the closing of the Central American isthmus, setting up the present set of oceanic conditions, may have made the habitat more favorable for *S. colubrinus,* but unfavorable for *S. atriventer.* It is well established that the permanent thermocline becomes very shallow in this region. Combined with the upwelling that occurs, this might be expected to make suitable habitat for *S. colubrinus,* which lives at greater depths in adjacent areas, leaving no niche for *S. atriventer.*

To the southward, populations of *S. affinis* occupied the Subtropical Convergence and gave rise to *S. boa boa.* In turn, *S. boa boa* derivatives populated the subantarctic and Antarctic intermediate waters and reached species status there as *S. gracilis.*

Probably during one of the Pleistocene glacial periods, *S. boa boa* was able to extend its range through the tropical Atlantic into the North Atlantic and Mediterranean Sea. Fluctuations of up to 9°C have been postulated for the surface waters of the Atlantic

TABLE 14.—Stomias *species: frequency distribution of photophores on isthmus (IP) and in AC portion of ventral row* [1]

Species	*Number of photophores on isthmus (IP)*					*Number of photophores in AC portion of ventral row*									
	9	10	11	12	13	13	14	15	16	17	18	19	20	N	x̄
atriventer (S)	–	–	20	5	–	–	3	16	5	–	–	–	–	24	15.1
atriventer (N)	–	1	20	3	–	5	8	7	1	–	–	–	–	21	14.2
boa boa (Med)	–	X	X	–	–	–	X	X	X	X	X	–	–	–	–
boa boa (S)	1	2	31	4	–	2	4	20	10	1	–	–	–	37	15.1
boa ferox	–	X	X	X	X	–	–	X	X	X	X	X	X	–	–
gracilis	–	2	41	1	–	–	1	3	14	17	6	3	2	46	16.9
affinis	X	3	11	2	–	–	2	3	6	3	3	–	–	17	16.1
colubrinus	–	9	109	38	–	–	–	11	15	26	59	25	5	141	17.6
lampropeltis	3	42	47	2	–	–	–	2	31	33	17	1	–	84	16.8
brevibarbatus	X	–	16	12	–	–	3	18	7	–	–	–	–	28	15.1
danae	–	–	4	–	–	1	2	2	–	–	–	–	–	5	14.2
nebulosus	–	X	X	X	–	–	X	X	2	X	X	–	–	–	–

[1] In addition to original observations, data are included from Ege (1934) and Morrow (1964a). Where frequency distributions were not given in the literature, the extensions are indicated by an X.

TABLE 15.—Stomias *species: frequency distribution of dorsal and anal fin-ray counts* [1]

Species	*Number of dorsal rays*											*Number of anal rays*												
	15	16	17	18	19	20	21	22	23	N	x̄	16	17	18	19	20	21	22	23	24	25	26	N	x̄
atriventer (S)	–	1	4	12	4	2	–	–	–	23	18.1	–	–	2	5	6	8	3	–	–	–	–	24	20.2
atriventer (N)	–	6	16	4	1	–	–	–	–	27	17.0	1	2	12	9	2	1	–	–	–	–	–	27	18.4
boa boa (Med)	–	–	X	X	X	X	–	–	–	–	–	–	–	X	X	X	X	X	–	–	–	–	–	–
boa boa (S)	–	–	6	13	7	3	–	1	–	30	18.4	–	–	5	3	9	6	6	–	–	–	–	29	20.2
boa ferox	–	–	X	X	X	X	X	–	–	–	–	–	–	–	X	X	X	X	X	–	–	–	–	–
gracilis	–	–	2	6	7	14	5	2	1	37	19.6	–	2	6	7	14	5	2	1	–	–	–	37	19.6
affinis	–	1	21	92	87	18	1	–	–	220	18.5	–	–	X	1	6	36	88	84	22	2	–	239	22.3
colubrinus	–	–	6	24	66	44	14	3	–	157	19.3	–	–	–	–	–	9	33	55	41	16	–	154	23.1
lampropeltis	–	–	14	46	49	32	7	2	–	150	18.9	–	–	–	–	7	26	51	51	17	2	–	154	22.3
brevibarbatus	–	X	–	X	X	X	–	–	–	–	–	–	–	–	X	X	X	X	–	–	–	–	–	–
danae	–	1	1	3	–	–	–	–	–	5	17.4	–	–	–	–	3	2	–	–	–	–	–	5	20.4
nebulosus	4	X	X	X	X	X	–	–	–	–	–	–	–	1	2	1	X	X	X	X	X	X	–	–

[1] In addition to original observations, data are included from Ege (1934), Blache (1964), and Morrow (1964a). Where frequency distributions were not given in the literature, the extensions are indicated by an X.

(see Briggs, 1966). If this cooling extended to the midwaters, this should have been sufficient to create temperature conditions similar to those in the areas now occupied by *S. boa boa*. This same cooling would have restricted the range of *S. affinis*, which is a tropical species, preventing competitive exclusion. The relative recency of the invasion of North Atlantic waters by *S. boa boa* is indicated by the development in cooler North Atlantic waters of the subspecies, *S. boa ferox*. At the same time, the stock of *S. boa boa* in the Mediterranean has undergone no apparent change.

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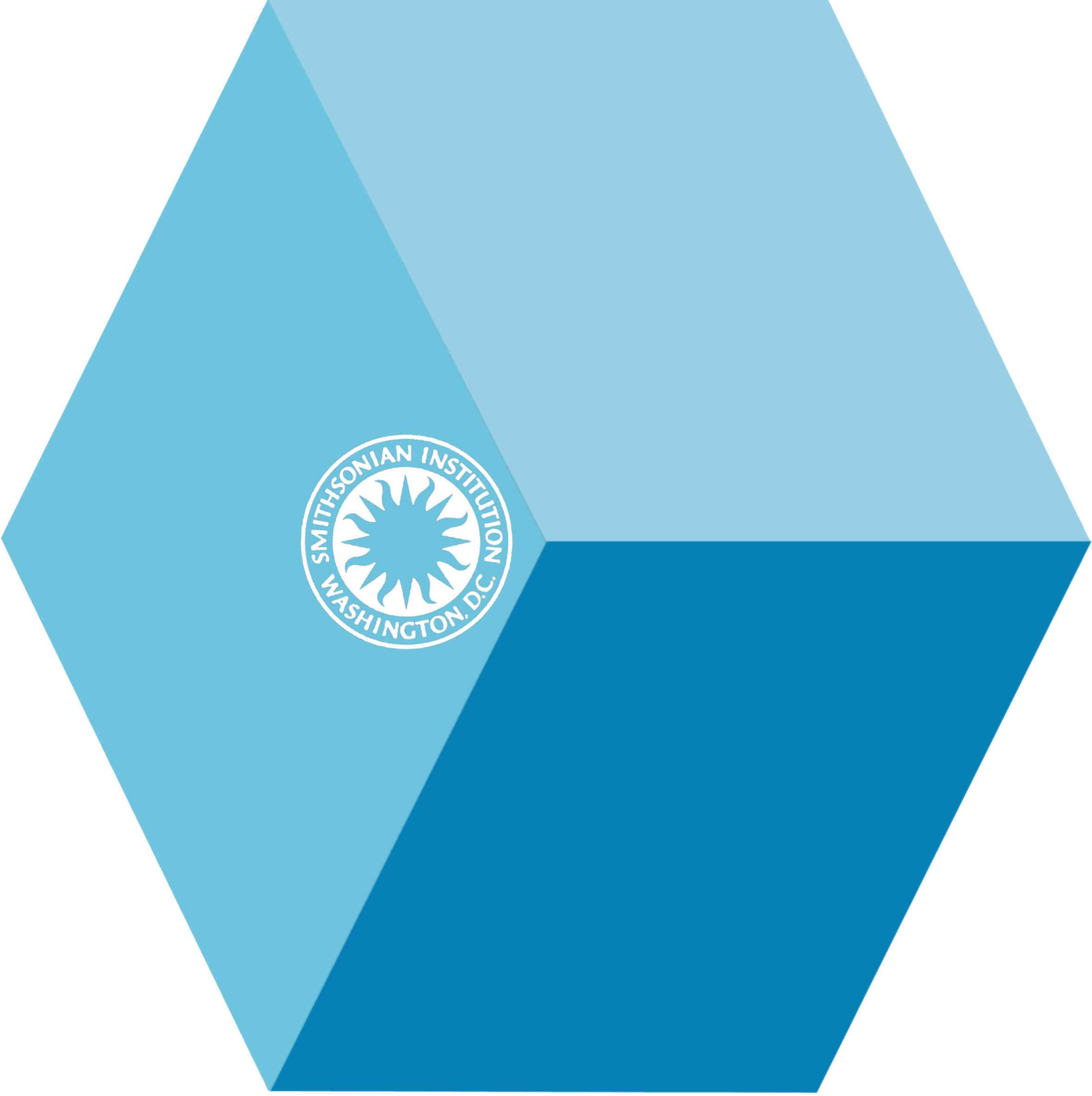
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