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SUBSPECIES OF THE WESTERN ATLANTIC CAT SHARK, *SCYLIORHINUS RETIFER*

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The cat sharks of the genus *Scyliorhinus* (family Scyliorhinidae) in the western Atlantic are a morphologically homogeneous group readily separable into six categories by differences in color pattern. Five forms have been described. Our purpose in this report is to describe a sixth and to review the status of the group based on newly collected specimens from the West Indies and the coast of South America.

Of the six highly distinctive forms of *Scyliorhinus* we recognize two at the species level but divide one species into five subspecies. We follow Hubbs (1943) to differentiate subspecies from species. Thus, we regard incompleteness versus completeness of differentiation as the main test by which subspecies may be distinguished from species. We consider geographically contiguous but not greatly overlapping ranges as typical of subspecies. All except a few of our specimens in which color pattern remains after preservation are identifiable as one form or another by pattern but the pattern varies moderately in each species or subspecies. Intergradation of pattern is represented in our material only by the tendency for pattern elements of subspecies to blend in a few areas where ranges meet or possibly overlap. Such areas of intergradation are off the Colombia-Venezuela border and around oceanic banks of the northwestern Caribbean Sea. Our series of specimens is not large enough to demonstrate details

TABLE 1. Frequency of occurrence of various numbers of monospondylous vertebrae in species and subspecies of western Atlantic *Scyliorhinus*.

Species	Number of monospondylous vertebrae																			
	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49
Scyliorhinus torrei	1	3	2	3	2															
S. retifer retifer										4	13	14	9	5						
S. retifer meadi														1			1		2	1
S. retifer boa										2	4	2		1	1					
S. retifer haeckelii									1	1	7	1	1	1						
S. retifer besnardi								1	3											

of intergradation of pattern between all subspecies with contiguous ranges—if, in fact, it always does occur.

Scyliorhinus torrei Howell Rivero (1936) differs from S. *retifer retifer* and the other forms considered here to be subspecies of S. *retifer* in color and pattern. S. *torrei* is also much smaller than any of the subspecies of *retifer*. It differs without overlap in the number of monospondylous vertebrae from all the subspecies of S. *retifer* (see Table 1). The distance between a transverse line across the anterior ends of the nasal openings and the tip of the snout is less in our series of S. *torrei* than in any of the subspecies of S. *retifer*. Although our series show some overlap in other proportional measurements with one subspecies or another of S. *retifer*, S. *torrei* usually has a proportionally shorter snout, smaller pectoral fins, and smaller dorsal fins.

Characters other than color pattern separate many specimens of the five subspecies of S. *retifer* but variation within subspecies is substantial; we have found no morphological feature consistently present without overlap, at least between forms occupying contiguous geographical ranges. Since western Atlantic *Scyliorhinus* are demersal and probably non-migratory except for movements of short distances, an analysis of quantifiable characters should provide a good basis for estimates of relationships of populations. It does not appear likely, however, that either sufficient numbers of *Scyliorhinus* or samples properly comparable and representative for statistical treatment of populations can be assembled in the foreseeable future. Morphometrics as traditionally used in shark classification are of limited value as applied to scyliorhinid sharks for delineation of categories in which differences are small. Difficulties follow not only because of variability and allometry inherent in the scyliorhinids but also because unpredictable shrinkage or stretching in preservation and necessarily vague reference points make precise and reproducible measurement impractical.

Color pattern is the most practical character in western Atlantic *Scyliorhinus* identification and is the primary character used in the key that follows. Pattern is best described by

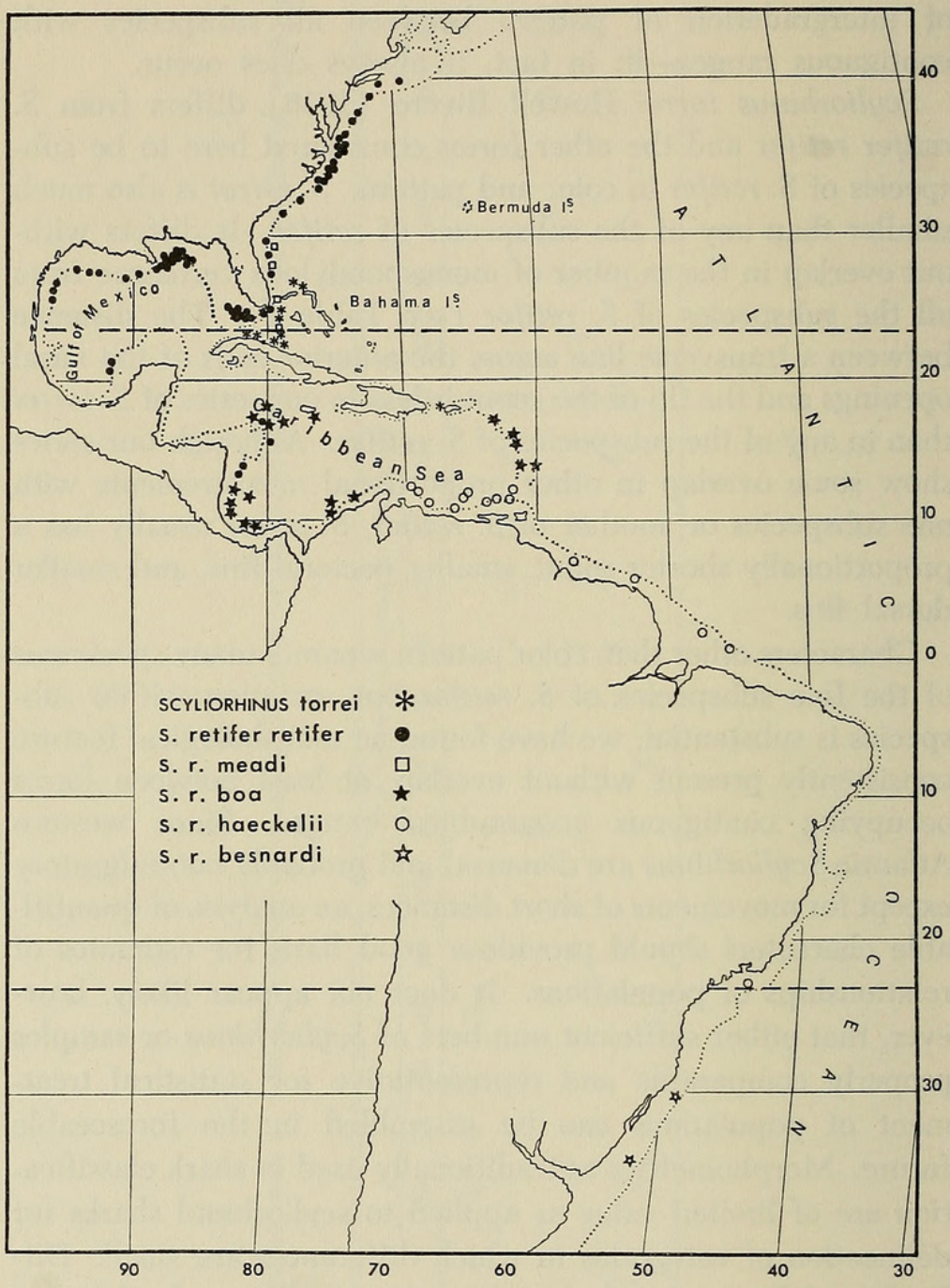

FIG. 1. Chart showing known distribution of western Atlantic *Scyliorhinus*. Details probably are biased because specimens have been collected only by trawling and because *Scyliorhinus* appears to occur most abundantly in areas of rough bottom that may preclude effective trawling. The range of S. *r. haeckelii* probably is continuous along the coast of Brazil between the mouth of the Amazon River and the offing of Rio de Janeiro, where little trawling has been done. The new subspecies, S. *r. besnardi* is to be expected off the coast of northern Argentina.

illustrations. Good drawings of all except the one newly described subspecies (Figure 2) are listed in references under each subspecies.

KEY TO WESTERN ATLANTIC *SCYLIORHINUS*

1A Color pattern of randomly distributed, round or somewhat irregularly shaped, white or cream colored spots, about the size of the dark-adapted pupil or smaller, on brown or light tan ground color over all dorsal surfaces; ventral surfaces white; a series of seven or eight diffuse saddle-blotches of slightly darker brown which may be indistinct; size small, adults mature at about 29 cm and probably do not reach lengths greater than 32 cm ..... *Scyliorhinus torrei* Howell-Rivero, 1936.

(Note: Color patterns in *Scyliorhinus torrei* and *Schroederichthys maculatus* may be identical but *torrei* has a much shorter tail section. In *torrei* the distance from the anus to the tail tip is from 57 to 63 percent of total length whereas in *Schroederichthys* it is from 64 to 72 percent).

1B Color pattern various, but white or light-colored spots, if present, are either irregularly shaped flecks of white in melanistic specimens or are incorporated as parts of saddle-blotches and are not distributed over all of the dorsal surface; dorsal ground color usually gray in life but may become brown after preservation in alcohol; ventral surfaces usually white but may be irregularly suffused with darker color; size moderate, length at maturity 35 cm or more ..... 2A or 2B.

2A Color pattern of dorsal surfaces a network of narrow and solid dark lines which are usually most prominent where they outline 7 or 8 dorsal saddlelike areas, dark lines frequently but not always reticulating along flanks ..... *Scyliorhinus retifer retifer* (Garman, 1881).

2B No continuous, narrow and solid lines of darker color outlining saddle-blotches ..... 3A or 3B.

3A Series of seven or eight saddle-blotches (including two on caudal fin) with indistinct edges; some blotches may be absent in the larger specimens; no small black or

white spots present in color pattern ..... *Scyliorhinus retifer meadi* Springer, 1966.

3B Small black spots, small white spots or both black and white spots present in color pattern ..... 4A or 4B.

4A White spots usually present, usually but not exclusively incorporated in saddle-blotches; melanistic forms from off Colombia-Venezuela border may not have white spots ..... *Scyliorhinus retifer boa* Goode and Bean, 1896.

4B No white spots on dorsal surfaces ..... 5A or 5B.

5A Pattern of numerous small black spots, most of them much smaller than the diameter of expanded pupil; some spots may outline a series of seven or eight saddle-blotches ..... *Scyliorhinus retifer haeckelii* Miranda Ribeiro, 1907. (Note: Color patterns in *Scyliorhinus retifer haeckelii* and *Schroederichthys tenuis* may be identical but *Schroederichthys* differs in having a very long tail section, its length from anus about two times distance from anus to snout tip).

5B Pattern of moderately large black spots, most of them as large as expanded pupil or larger; spots arranged in approximate bilateral symmetry; some spots partly enclosing a center of lighter color or occurring as very closely adjacent pairs; distance between spots or spot-pairs usually greater than diameter of the smaller spot ..... *Scyliorhinus retifer besnardi* new subspecies.

Scyliorhinus retifer retifer (Garman, 1881)

Scyllium retiferum Garman, 1881, p. 233 (type locality, 38°22′35″N, 73°33′40″W, off Delaware Bay in 89 fathoms).

Scylliorhinus retifer: Goode and Bean, 1896, part, pp. 16–17, figs. 14–15.

Scyliorhinus retifer: Regan, 1908, p. 457; Bigelow and Schroeder, 1948, pp. 207–211, fig. 33; Bigelow, Schroeder and Springer 1953, pp. 213–214; Springer, 1966, pp. 602–603, figs. 2, 6, 8.

Study material and records of capture: Museum of Comparative Zoology (MCZ) 825, holotype of *Scyllium retiferum*; USNM 187076 and more than 125 other specimens in United States National Museum (USNM) collection; records from 22 trawling stations (Springer and Bullis, 1956), from 49 trawling stations (Bullis and Thompson, 1965), and from additional trawling stations occupied after 1960 (unpublished data, Bureau of Commercial Fisheries).

Diagnosis: The reticulate pattern of narrow black lines sets this subspecies off from all other Atlantic sharks. The closest resemblance is to halfgrown specimens of *Cephaloscyllium fasciatum* from the vicinity of Hainan Island, China (see Chan, 1966, fig. 5). The reticulated pattern in S. *r. retifer* is well developed by the time the young leave the egg cases. It is remarkably persistent after preservation and in the very large series examined shows only moderate variation. Examples that show extremes in pattern variation are illustrated in Springer's review (1966) of western Atlantic cat sharks. The specimens we have seen fail to show either consistent pattern differences between small and large individuals or between samples from the northern and southern ends of the geographical range.

In S. *r. retifer* chromatophores in the skin produce some of the background color but pigment diffused within the hard material of dermal denticles is a major component of the dark reticulating lines. Excepting two specimens (USNM 75023, from R/V *Albatross* collections made off the coast of South Atlantic states in 1883–1885), all of the series that we have seen are easily and definitely identifiable by pattern. The two specimens have partly disintegrated and denticles are no longer in place.

Size: Males may reach sexual maturity at about 350 mm; the largest specimen seen, a female and probably not sexually mature, was 480 mm long. The length of the young at hatching is probably about 100 mm as indicated by young apparently newly hatched.

Distribution: S. *r. retifer* occurs along the continental shelf and slope from the southwestern edge of Georges Bank, Massachusetts, to Nicaragua. In the extreme northern part of its range it has been taken at depths of as little as 73 m but its habitat becomes deeper southward to 550 m off Nicaragua. The subspecies has not been recorded from the eastern or southern side of the Straits of Florida. Its range is either slightly overlapping or contiguous with the ranges of *Scyliorhinus torrei* and *Scyliorhinus retifer meadi* off the south-central and south-eastern coast of Florida. The geographical ranges of S. *r. retifer* and S. *r. boa* overlap on the continental slope of the northwestern Caribbean Sea but in this area S. *r. retifer* has been found usually at a greater depth than S. *r. boa.*

All of the specimens of western Atlantic *Scyliorhinus* that we find recorded were collected with otter trawls or dredges. Records of capture of S. *r. retifer* along the coast of the United States are especially concentrated off the Virginia Capes, off Dry Tortugas, Florida, and off Pensacola, Florida, in areas with considerable growth of sessile invertebrates of moderate size. Research vessels have collected less than two dozen mature specimens among more than a thousand taken in spite of continued efforts to collect large specimens of S. *r. retifer* over several years. Seventeen of the adults, eleven males, 365 to 410 mm, and five females, 360 to 420 mm long, were taken in a single net haul from about

180 m off North Carolina, July 19, 1960. Most of the locality records are based on captures of immature specimens taken singly. From fishing results we deduce that S. *r. retifer* adults prefer very rough bottom habitats that are generally considered untrawlable and that the immature sharks scatter to some extent over areas with fewer bulky obstructions.

Natural history notes: Several identifiable egg cases of S. *r. retifer* have been recovered that show cross bands similar to those illustrated by Springer (1966, fig. 8). One egg case measures 60 mm long between indented ends and 27 mm at the widest part.

Scyliorhinus retifer boa Goode and Bean, 1896

Scylliorhinus boa Goode and Bean, 1896, p. 17, fig. 6 (type locality, Barbados in 200 fathoms).

Scyliorhinus boa: Bigelow and Schroeder, 1948 (part, pertains only to type specimen), p. 204.—Springer, 1966 (part, reference only to type specimen), p. 601.

Scyliorhinus hesperius Springer, 1966, p. 603–604, fig. 15B.

Study material: MCZ 1335, holotype of *Scylliorhinus boa*; USNM 187732, holotype of *Scyliorhinus hesperius*; USNM 187728 and 26 other specimens.

Diagnosis: Scyliorhinus retifer boa is a subspecies in which differentiation appears to be far from complete, and, as defined here, probably includes several more or less distinct geographical races. The 26 specimens we have seen vary widely in color pattern. The subspecies is characterized by the presence of white or light-colored spots about the size of the dark-adapted pupil or smaller, the white spots usually scattered within dark dorsal saddle blotches. Specimens from the Antilles and the coast of eastern Colombia are darker than those from the coasts of Honduras, Nicaragua, and Panama. In the more melanistic specimens the dorsal pattern is irregular and obscure and dark color extends irregularly onto ventral surfaces. In S. *r. boa* the dorsal saddle areas or dorsal blotches of darker color are not outlined by continuous, reticulating narrow lines of black as they are in S. *r. retifer* and are usually not outlined by small black dots or interrupted series of black dashes as they are in S. *r. haeckelii*. Newly hatched specimens of S. *r. boa* and S. *r. haeckelii*, however, may not always be separable. The only very young ones available to us for examination are from the Lesser Antilles and the Guianas. Some have small, white spots as well as numerous small, black spots. Evidently, the white spots become more prominent with growth in S. *r. boa* but disappear in S. *r. haeckelii*.

The holotype of *Scylliorhinus boa*, a juvenile 6-inches long collected by the R/V *Blake* in about 365 m depth off Barbados, is now in poor condition (Bigelow and Schroeder, 1948). It was named and a diagnosis was given by Goode and Bean (1896) as a variant of S. *retifer*. A dual numbering system for some of the R/V *Blake* material accounts for the

station number CVII given by Goode and Bean and number 291 given by Springer (1966). In this instance the two numbers refer to the same station (see Dick, 1969).

The holotype (MCZ 1335) now shows neither the scarcely visible reticulations noted by Goode and Bean nor the white spots which are apparently intended but not clearly shown in Goode and Bean's illustration (1896, fig. 6). Specimens recently collected off Barbados and off nearby St. Vincent are adults and do have white spots, although a reticulate pattern is not present. *Scyliorhinus* from other areas in the Lesser Antilles and the southern coasts of Hispaniola are also the white-spotted form. We conclude that the white-spotted form should be considered *Scyliorhinus retifer boa* and that *Scyliorhinus hesperius* Springer, 1966 described from the Caribbean off Panama is a junior synonym of *S. boa.*

One melanistic specimen, USNM 204378, from the Colombia-Venezuela zone of intergradation is the only example without white spots in our series that we refer to *S. r. boa.* It has relatively few black spots, larger than those of typical *S. r. haeckelii.* It might be identified as *S. r. besnardi* in the key given here except that the spots are slightly smaller than the dark-adapted pupil and have no light-colored centers.

Size: A sexually mature male from Barbados is 540 mm long. Although the specimens in our small series of *S. r. boa* are large in comparison with specimens in the very large series of *S. r. retifer*, we doubt that this size relation is significant. Because most of the slopes around the smaller islands of the West Indies are rough-bottom areas, exploratory fishing vessels were forced to attempt to get samples from or very near rocky or rough bottom if they were to get them at all. Thus, for *S. r. boa* we have a proportionally larger sample of the full grown specimens which, we postulate, prefer rough-bottom habitats.

Distribution: *S. r. boa* ranges from its type locality at Barbados northward through the Lesser Antilles, and along the southern coasts of Hispaniola and Jamaica. It occurs off the Central American coast southward from Honduras and is represented on the Caribbean coast of Colombia by melanistic variants. The specimens seen were trawled from depths of 274 to 676 m.

Natural history notes: One melanistic Colombia specimen of *S. r. boa* (USNM 204378) was alive when brought on the deck of the R/V *Oregon* and was placed in a drum of sea-water where it was observed to exhibit luminescence (Harvey R. Bullis, Jr., personal communication). He described the light as a diffuse glow from the ventral surfaces but noted two distinct light-producing spots on the dorsal midline between the tip of the snout and the origin of the first dorsal fin. Subsequent examination of this specimen in the laboratory failed to reveal photophores, which suggests that the luminescence may have been of bacterial origin. This appears to be the only report of bioluminescence from a galeoid shark.

Scyliorhinus retifer meadi Springer, 1966

Scyliorhinus meadi Springer, 1966, pp. 600–601, fig. 14B (type locality, off Cape Kennedy, Florida, 28°21′N, 79°51′W).

Study material: USNM 188049, the holotype, and five other specimens.

Diagnosis: Scyliorhinus retifer meadi has a color pattern of seven or eight dorsal saddles but no reticulating dark lines, no black spots, and no white spots, and thus differs from other subspecies of S. *retifer*. It has a greater average number of monospondylous vertebrae than other subspecies but overlaps S. *r. retifer* and S. *r. boa* (see Table 1). The six known specimens have appreciably longer denticle points than other subspecies of S. *retifer* of equal size.

Size: Mature and newly hatched specimens are not known.

Distribution: Specimens have been taken only at the type locality in 329 m depth off Cocoa Beach near Cape Kennedy, from the same depth off St. Augustine, in 457–622 m off Bimini, Bahamas, and in 549 m in the Santaren Channel between the Cay Sal and Bahama Banks. As shown in Figure 1, the known geographical range of S. *r. meadi* lies within and very near the range of S. *r. retifer*. This is in apparent conflict with an expected distribution of a subspecies as outlined earlier. The extent of the range of S. *r. meadi* cannot be well represented, however, by records of six immature specimens from four locations.

The contact between the two subspecies seems insubstantial. The area of geographical overlap lies off the Florida coast between St. Augustine and Fort Pierce. That both subspecies are rare in this area is shown by the capture of only four or five immature specimens of each subspecies in very thorough exploratory trawling operations carried out over several years.

Much less information is available from the side of the Gulf Stream adjacent to the Bahama Banks where less than two percent as much trawling effort has been made. The two records of capture of S. *r. meadi* on the Bahama side of the Gulf Stream thus seem more important and lead to the belief that it is primarily a Bahamian subspecies. In its color pattern S. *r. meadi* resembles some specimens of S. *r. boa* except for the absence of white spots but none of the six immature specimens show any trace of the reticulate pattern that characterizes S. *r. retifer*.

Scyliorhinus retifer haeckelii (Ribeiro, 1907)

Catulus haeckelii Ribeiro, 1907, pp. 163–165, pl. 8 (type locality off Rio de Janeiro in 80 m).

Scyliorhinus boa: Bigelow and Schroeder, 1948, (part, type of *C. haeckelii* depicted in illustration and incorporated in account of species, pp. 204–207, fig. 32).—Springer 1966, (part, except type of S. *boa*, pp. 601–602, fig. 15A).

Scyliorhinus fernandezi Weibezahn, 1953, pp. 3–7, fig. 1.

Study material: Museum Nacional Brasil (MNB) 494, the holotype; USNM 188060 and 20 other specimens.

Diagnosis: Scyliorhinus retifer haeckelii has a color pattern of very small black spots smaller than the dark-adapted pupil, the spots usually distributed generally over the dorsal surfaces and in many examples outlining the seven or eight dark colored dorsal saddles. In three of our specimens the dorsal saddles are only faintly represented and the black spots are smaller, more numerous, and more evenly distributed over the dorsal surfaces than in the more typical form.

None of the available specimens show any trace of reticulating narrow lines except as series of discrete black spots, but three newly hatched specimens have bands of slightly darker color (less strong than the color of dorsal saddles) that are similar to bands on anterior lateral surface of immature western Caribbean S. *r. boa*. The illustrations of the holotype and other illustrations noted in the synonymy above depict very well the color pattern that is characteristic of most of our specimens of S. *r. haeckelii*.

Size: S. *r. haeckelii* may be slightly smaller than S. *r. boa* or S. *r. retifer*, as previously suggested by Springer (1966, p. 602) because a 346-mm male S. *r. haeckelii* is apparently sexually mature.

Distribution: Our material indicates that S. *r. haeckelii* ranges along the continental slope of South America from western Venezuela to the vicinity of Rio de Janeiro, although the only specimen recorded from south of the equator is the holotype. Depths recorded for S. *r. haeckelii* are from 37 to 402 m. The holotype of *Catulus haeckelii* was taken off Rio de Janeiro from 80 m and the holotype of *Scyliorhinus fernandezi* was from 37 m. These records suggests the possibility that S. *r. haeckelii* frequents somewhat shallower water than S. *r. boa* and (in the tropical segment of its range) S. *r. retifer*.

Natural history notes: A series of 9 egg cases with 3 newly hatched young permits positive identification of the egg cases of S. *r. haeckelii*. The egg cases are light amber, transparent, and do not have transverse bands such as has been noted for egg cases of S. *r. retifer* that carry developing eggs. Each egg case has a pair of well-developed tendrils at each end. The upper and lower surfaces are smooth except for very faint longitudinal striae and the lateral edges are thickened and reenforced much as in egg of *Scyliorhinus stellaris* and S. *r. retifer*. The egg cases of the series are 62 to 66 mm long measured along the axis (not including horns and tendrils) and are from 24 to 27 mm at their widest parts. The young obtained with, but not directly from, the egg cases are 100, 102, and 130 mm long. Seven of the cases contain yolk without indication of developing embryos. The series was collected by the UNDP/FAO vessel *Calamar* at its station 413 off Surinam in 137 m—(coral and "sea-fan" bottom) at 07°28′N; 56°24′W.

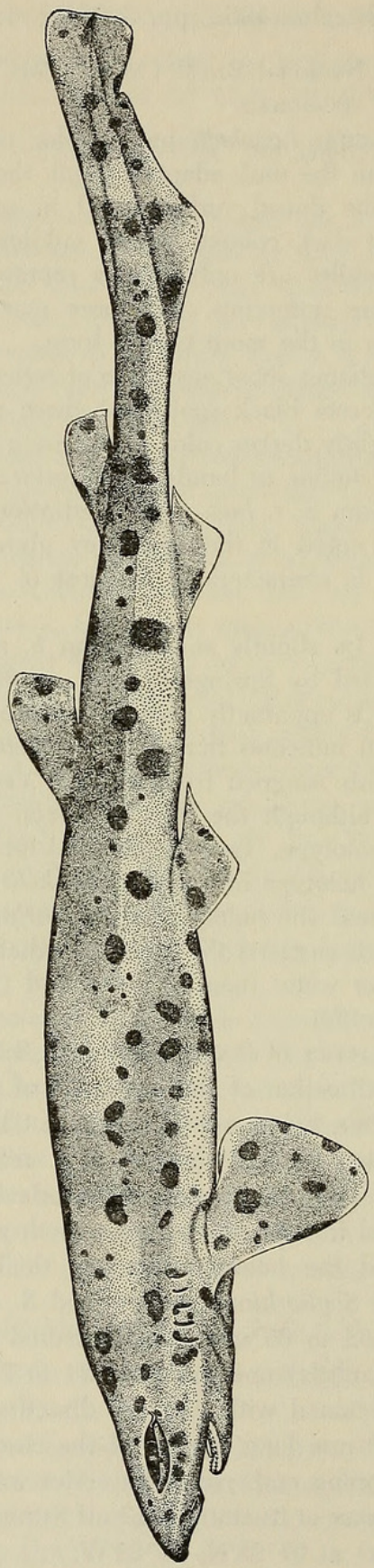

FIG. 2. Drawing of *Scyliorhinus retifer besnardi*, paratype, a 366-mm male, USNM 204377.

Scyliorhinus retifer besnardi new subspecies
(Figure 2)

Holotype: A 385-mm female (USNM 204376) trawled at station 419 the R/V *Prof. W. Besnard* of the Instituto Oceanográfico de la Universidade de São Paulo, from a depth of 190 m, temperature 15.67° C, salinity 35.726‰ at the trawling depth, at 33°26′S, 51°21′S, near the continental shelf edge off northern Uruguay, 2 November 1968.

Paratypes: A 470-mm adult male, Instituto Oceanográfico São Paulo (IOSP 81BS), partially dissected; a 338-mm female (IOSP 82BS); and a 366-mm male (USNM 304377); all from the same haul as the holotype.

Other Material: A 356-mm male (IOSP 83BS) from R/V *Prof. W. Besnard* station 436 from a depth of 140 m, temperature 15.77° C, salinity 35.702‰ at the trawling depth, at 30°15′S, 49°00′W, off Porto Alegre, Brazil.

Diagnosis: *S. r. besnardi* has the diagnostic characters of the genus *Scyliorhinus*; that is, chondrocranium with a supraorbital crest, lower labial furrow developed but upper labial furrow absent, and upper lip slightly overlapping lower lip near mouth corners.

The color pattern of *S. r. besnardi* is somewhat like the color pattern of *Halaelurus buergeri* of Japanese waters but *H. buergeri* lacks supraorbital crests. The color pattern of *S. r. besnardi* also resembles that of some specimens of *Scyliorhinus caniculus* and *S. stellaris* from the west coast of Africa but in the two latter species the nasal flaps extend nearly or quite to the upper lip and sometimes overlap it.

S. r. besnardi may be readily distinguished from other western Atlantic *Scyliorhinus* by the color pattern differences already set forth in the key. In addition, of the five specimens of *S. r. besnardi* for which we have vertebral counts, four have 38 monospondylous vertebrae and one has 37, whereas in 12 specimens of *S. r. haeckelii* only one has as few as 38. Other subspecies of *retifer* have somewhat higher counts, from 39 to 49 (see Table 1).

Description: Following are proportional measurements of the holotype in percentages of total length except as indicated. The range is given in parentheses for the holotype, two paratypes (excepting the 470-mm male), and the 356-mm specimen listed above. Measurements were made as outlined in Bigelow and Schroeder (1948).

Tip of snout to: front of mouth, 4.2 (4.1–5.4); eye, 4.2 (4.2–5.5); spiracle, 10.1 (9.6–10.6); first gill opening, 14.5 (14.5–15.6); last gill opening, 19.0 (18.9–19.2); origin pectoral, 18.2 (17.8–18.5); origin first dorsal, 48.1 (48.1–49.7); origin pelvics, 39.5 (39.5–41.6); origin second dorsal, 66.0 (66.0–67.2); origin anal, 58.5 (58.5–60.9); origin upper caudal lobe 79.2 (77.5–79.3); anterior end cloacal opening, 41.8 (41.8–45.2).

Greatest width of: head, 11.2 (11.2–11.5); trunk at pectorals, 8.6

(8.6–11.0); trunk at pelvics, 6.2 (6.0–6.4); trunk at caudal origin, 2.1 (2.1–2.8).

Greatest height of: head at spiracles 7.3 (6.1–7.3); trunk at pectorals, 9.9 (9.8–9.9); trunk at pelvics, 8.6 (8.4–8.7); trunk at caudal origin, 3.4 (3.3–3.6).

Eyes: horizontal diameter 3.6 (2.9–3.6); distance between supraorbital crests of chondrocranium 3.5 (3.5–3.8); distance between upper eyelids 6.2 (6.2–6.3).

Spiracles: greatest diameter 0.5 (0.5–0.7); least distance from eye, 0.8 (0.8–1.2); distance between, 7.5 (7.5–7.9).

Mouth: width, 6.5 (6.5–7.9); length, 3.9 (3.6–4.2); upper labial furrow absent; length lower labial furrow, 1.2 (1.2–1.7).

Nasal apertures: level of anterior ends to tip of snout, 2.5 (2.5–3.2); level of posterior ends to front of mouth, 0.6 (0.5–1.0).

Gill slits: height of first, 1.8 (1.5–1.9); height of fifth, 1.0 (1.0–1.2).

First dorsal fin: length base, 5.7 (5.7–6.9); length posterior tip (posterior inner margin), 2.6 (2.6–3.1); height, 4.4 (4.5–5.1); length anterior margin, 9.1 (9.1–10.7).

Second dorsal fin: length base, 5.2 (5.2–5.7); posterior tip (posterior inner margin), 2.6 (2.6–2.8); height, 2.9 (2.7–3.8); length anterior margin, 7.5 (7.5–8.2).

Pelvic fins: origin to posterior tip, 9.9 (7.4–10.2).

Caudal fin: upper margin, 20.8 (20.8–22.5); anterior margin lower lobe, 9.6 (9.6–10.4); tip to notch, 6.5 (6.5–7.1).

Distance between fin bases: first to second dorsal, 12.5 (10.4–12.5); pectoral to pelvic, 16.4 (16.1–18.2); pelvic to anal 11.7 (11.7–13.7); anal to lower caudal, 9.9 (7.9–9.9); second dorsal to upper caudal, 9.1 (4.8–9.1).

Teeth: number of upper, 23 plus 23 in holotype to 25 plus 26 in one paratype; number of lower 21 plus 1 plus 23 in holotype to 22 plus 3 plus 23 in one paratype.

Vertebrae: in holotype and in three paratypes from radiographs, in 470-mm male paratype from dissection, total number 125 (122–129); number monospondylous 38 (37–38).

Gill rakers: one about 1 mm high on each side of gill bars plus a second smaller gill raker on some gill bars of holotype; one paratype has only one on each side of gill bars without second smaller gill raker.

Color pattern of holotype (see fig. 2), gray above flecked with a few very small white specks which are incompletely formed replacement denticles; dorsal surface with seven or eight indistinct saddles only slightly darker than background color and marked with black, round or ovoid spots, some paired or double, some forming lunate or ocelluslike markings, most spots as large or larger than pupil, pairs or single spots separated from one another by distances greater than the diameter of spots, a series of eight spots on dorsal midline, three of which are double, spots present on dorsal surface of paired fins and on dorsals and

caudal; ventral surfaces white but somewhat irregularly suffused with darker color.

Paratypes with a similar pattern of spots arranged in approximate bilateral symmetry, as in holotype.

Teeth of upper and lower jaws not differing greatly in size or shape; largest about 1 by 1 mm in holotype; typically with long central cusp flanked by one short cusp on each side but some with additional cusps, usually one extra on the inner side, but a few with extra cusps on both sides of central cusp; bases of teeth striate; symphysis of upper jaw distinct, without median tooth, but first tooth on each side of symphysis small; lower jaw without well-marked symphyseal separation and with 3 small medial teeth.

Dermal denticles 3-pointed on lateral surfaces, the central point longest, with three prominent ridges.

Pelvic fins of males united along inner margins for about two-thirds the distance to their tips, pelvic fins of females united by membrane only at base.

Claspers of the 470-mm male extend well beyond the tips of the pelvics, whereas claspers of the 366-mm paratype do not nearly reach the pelvic tip. This suggests that maturity in the male may be reached at lengths near 470 mm or less.

Etymology: The new subspecies is named in honor of Professor Wladimir Besnard, founder of the Oceanographic Institution of the University of São Paulo.

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