STUDIES ON THE FAUNA OF CURAÇAO AND OTHER CARIBBEAN ISLANDS: No. 139.

SERPULINAE (POLYCHAETA) FROM THE CARIBBEAN: II - THE GENUS SCLEROSTYLA

by

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The genus *Sclerostyla* is better known from fossil records than from recent material (WRIGLEY, 1951; MÜLLER, 1970). This is not surprising, since *Sclerostyla ctenactis* is difficult to find, the tube usually being imbedded in the substrate. Such material was studied only by MÖRCH (1863) in the Zoologiske Museum, København; by AUGENER (1922) in the zoological museums of Berlin and Hamburg; by TREADWELL (1929) in the American Museum of Natural History and by WRIGLEY (1951) in the Allan Hancock Foundation, Los Angeles. The specimens have been reexamined.

Additional specimens were collected by Dr. P. WAGENAAR HUMMELINCK (1955, 1963–64) and by the author (1970). This material, as a rule, was preserved with formaldehyde and, after a short period, transferred to alcohol. These specimens are deposited mainly in the Rijksmuseum van Natuurlijke Historie, Leiden (Nrs. 04466–04476) or in the author's collection (tHU 119, and tHU 121–127). Single specimens have been presented to the Zoologisches Museum, Berlin, D.D.R. (ZMB), to the Zoologisches Museum, Hamburg (ZMH), to the Zoologiske Museum, København (ZMK), to the British Museum Natural History, London (BMNH ZB. 1971. 228–231), to the Allan Hancock Foundation, Los Angeles (AHF), to the Station Marine d'Endoume, Marseille (SME), to the American Museum of Natural History, New York (AMNH) and to the National Museum of Natural History, Washington (USNM).

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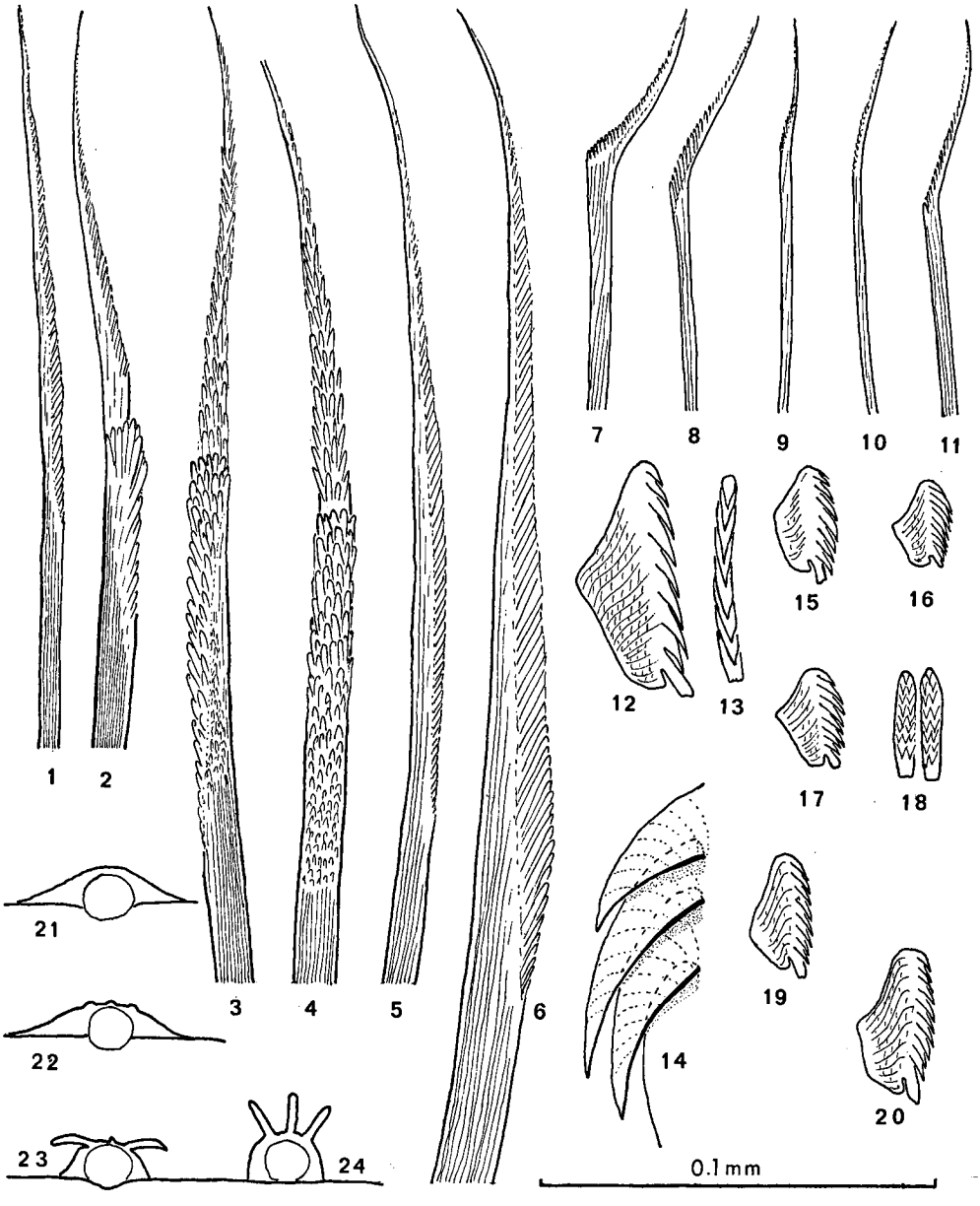
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(WOTRO) enabled the author to collect and to study living specimens in the Netherlands Antilles.

He wishes to express his thanks for the loan of specimens to Dr. K. FAUCHALD (AHF), Dr. Gesa HARTMANN-SCHRÖDER (ZMH), Dr. G. HARTWICH (ZMB), Dr. J. B. KIRKEGAARD (ZMK), Dr. E. KIRSTEUER (AMNH), Dr. W. VERVOORT, Dr. J. VAN DER LAND (RMNH) and Dr. S. WARE (BMNH). Dr. H. ZIBROWIUS (SME) not only sent serpulids, but provided valuable information and comments too. Dr. Marian H. PETTIBONE (USNM) helped by her suggestions and by the critical reading of the English text.

Plates I–IV and Figures 36–37 have been executed by Mr. H. VAN KOOTEN and his staff at the Zoölogisch Laboratorium, Rijksuniversiteit, Utrecht.

Drawings of opercula were made by using a screen in one ocular of the stereomicroscope and screened paper. Drawings of setae and uncini were made with a camera lucida. Measurements (unless stated otherwise) are given in mm. Given are the extremes, the 95% confidence limits of the mean (computed with STUDENT's t-test) and the mean; n stands for number of measurements. The normal distribution of various data was plotted on normal probability paper; dubious normal distributions are given in italics.

LIST OF LOCALITIES

with Station numbers of WAGENAAR HUMMELINCK (*1334*, etc.) and TEN HOVE (*2041*, etc.)

PUERTO RICO

1415 Mayagüez, 4 km off Punta Cadena, ca. 90 m deep, muddy sand, dredge, 14.IX.1963.

2136A 8 mi. off Isla Matei, near La Parguera, 17°53.4′ N, 66°59.8′ W, 95–110 ft, vertical reef, not sandy, 2.X.1970.

BARBADOS

1442 ½ mi. off Holetown, 100 m, muddy sand, shell debris, sponge bottom, dredge, 19.II.1964.

SURINAM

H 57 Shelf off Surinam, 07°35.7′ N, 56°52.6′ W, 94–97 m, fragment of calcareous coral rock with some solitary corals, dredge, 11.V.1966. [H.NL.M.S. "Snellius" 1966]

Fig. 1–24. *Sclerostyla ctenactis, differens* and *semiannulata* nov. spec. — *Scl. ctenactis* from CURAÇAO (Jan Thiel, RMNH 04470: 1–2; Piscaderabaai, RMNH 04469: 3; Boca Hulu, tHU 124: 4, 7, 20). – *Scl. differens* from SURINAM (RMNH 04472: 5–6, 8–10, 12–18). – *Scl. semiannulata* from BARBADOS (off Holetown, tHU 127: 11, 19). — 1–4, collar-setae in side-view and front view; 5–6, thoracic setae; 7–11, abdominal setae from anterior (7), middle (8, 11) and posterior (9–10) regions, various views; 12–14, thoracic uncini, 14 scheme of implantation of teeth; 15–20, abdominal uncini from last ten segments, except 17–18, which are from the middle; 21–24, series of schematic cross-sections through tubes of *Scl. ctenactis*.

BONAIRE

2111Ea Barcadera, Piedra Altu, 60 ft, vertical reef, not sandy, 12.VII.1970.
2112Ge Santa Barbara (near Hato), 40–50 ft, vertical sandy reef, 5.VII.1970.
2112Ja Santa Barbara (near Hato), 135 ft, vertical sandy reef, 25.VI.1970.
2117B 250 m N of Witte Pan, 150 ft, sandy bottom below reef, scarce limestone, 3.VII.1970.

KLEIN BONAIRE

2105B NW coast near Westpunt, 160 ft, sandy bottom below reef, scarce limestone and living corals, 1.VII.1970.

CURAÇAO

1334 Caracas Baai, sub marine iron buoy, 10 m or more deep, 9.II.1955.
1334A Caracas Baai, on chain, about 15 years under water, 22.IV.1955.
2041C Boca Hulu, E, 90–100 ft, sloping reef, little sand, 14.IX.1970.
2046 Portomaribaai, in front of W cliff, 75–85 ft, vertical reef, limestone, little sand, 23.V.1970.
2049B Vaarsenbaai, in front of E cliff, 50–60 ft, vertical reef, some sand, 27.IV. 1970.
2054B Piscaderabaai, outer bay, near entrance, 125 ft, vertical reef, muddy sand, 9.VI.1970.
2070 Jan Thiel, between Jan Thielbaai and Lijhoek, 100 ft, vertical reef, limestone, 3.VI.1970.

Genus **Sclerostyla** Mörch, 1863

Type species: *Serpula* (*Sclerostyla*) *ctenactis* Mörch, 1863, designated by BUSH, 1905 (p. 224). Gender feminine.

Diagnosis. – Thoracic segments seven, first usually achaetous. Thoracic setae unilimbate; collar setae, if any, finely limbate capillaries and special setae. Thoracic uncini saw-shaped, with 8–9 teeth, including rounded anterior tooth. Posterior three pairs of parapodia almost united ventrally. No "*Apomatus*-setae". Abdominal setae almost capillary, with short geniculate tips. Abdominal uncini rasp-shaped with 2–3 rows of teeth, 8–11 teeth in profile. Anterior abdominal pairs of notopodia converging dorsally.

Operculum, as well as opercular stalk or peduncle, entirely calcareous. Operculum funnel-shaped, more or less smooth on outside, with numerous radial ridges on inner side. Collar with large, bilobed ventral part and two lateral "tonguelets." Thoracic membranes very wide anteriorly, narrowing at third or fourth segment, and united ventrally on first abdominal segment. Branchial filaments united by membrane for 1/4–1/2 of their length, surrounding pair

of well-developed palpi. Thorax with pair of comma-shaped glands ventrally.

KEY TO THE RECENT SCLEROSTYLA

1. Tube with very thick transverse ribs of increasing size; entirely adnate, semicircular in cross-section (Pl. II C). Opercular funnel deep (Pl. III D, IV D) . . . . . *Scl. semiannulata*
1a. Tube with longitudinal ridges 2

2. Tube completely adnate, sunken in substrate, semicircular in cross-section, with 3 (exceptionally 0, 2 or more) more or less regular ridges of varying shape and size (Pl. I A, B). Opercular funnel deep (Pl. III A, B) . . . . . *Scl. ctenactis*
2a. Tube adnate only in oldest part, free for greater part; trapezoidal and circular in cross-section. Adult specimens with 6–12 irregular ridges, those of young specimens, 2 (Pl. II A, B). Opercular funnel shallow . . . . . *Scl. differens*

To identify specimens without tubes, it will be necessary to compare them carefully with the figures and descriptions below. Even then it may be impossible to identify single specimens.

DISCUSSION

Sclerostyla differs from all Recent serpulid genera by its operculum being entirely calcareous. Apart from the Spirorbinae, there are only a few genera having a calcareous operculum and talon or peduncle, viz. *Pomatoleios* Pixell, 1913, *Neomicrorbis* Rovereto, 1904, and the exclusively fossil genera *Turbinia* Michelin, 1845 and *Hamulus* Morton, 1834. In addition to the very different setae and uncini, the opercular talon of *Pomatoleios* is very short compared to that of *Sclerostyla* (Fig. 34). Differences with *Neomicrorbis* are to be discussed extensively by ZIBROWIUS (in press). *Turbinia* shows a more or less smooth talon, with the upper surface of the operculum consisting of concentrically raised discs, instead of radial ridges (WRIGLEY, 1951: figs. 49–50). An interesting "intermediate"

form is *Serpula* sp. (WRIGLEY, 1951: fig. 51), in which the upper part of the operculum is *Sclerostyla*-like and the lower part is smooth and *Turbinia*-like. The operculum of *Hamulus* rather resembles that of a *Sclerostyla* but a deficiency of figures prevents settling the question of a possible synonymy.

It will be noted that certain morphological features, i.e. the absence or presence of tonguelets (collar) and the development of mouth-palps, are included, even though they are generally left out of a generic diagnosis. These characteristics may be distinctive and useful in gaining an insight in the higher taxonomy. For instance, short mouth-palps are found in *Pomatoceros triqueter* (Linnaeus) (THOMAS, 1940, text-fig. 2, HANSON, 1949: 230), as well as *Spirobranchus tetraceros* (Schmarda) and possibly *Placostegus tridentatus* (Fabricius). They were not found in the following species: *Ditrupa arietina* (O. F. Müller), *Hydroides elegans* (Haswell), *Mercierella enigmatica* Fauvel, *Pomatoleios kraussii* (Baird), *Pomatostegus stellatus* (Abildgaard), *Serpula vermicularis* Linnaeus, and *Vermiliopsis infundibulum* (Philippi). Tonguelets have been observed in *Spirobranchus* (TEN HOVE, 1970), *Pomatoceros* (THOMAS, 1940, pl. I fig. 5), *Pomatoleios* and *Placostegus*, but n o t in *Ditrupa*, *Hydroides*, *Mercierella*, *Pomatostegus*, *Serpula* and *Vermiliopsis*.

Uniting two genera as different as *Ditrupa* Berkeley and *Sclerostyla* in a separate subfamily Ditrupinae, as done by REGENHARDT (1961: 69), is rather peculiar in the eyes of a neontologist.

Sclerostyla ctenactis (Mörch, 1863)

Serpula (*Sclerostyla*) *ctenactis* MÖRCH, 1863, p. 386. [St. Thomas. – Material studied, ZMK.]

Serpula (*Sclerostyla*) *clenactis* [sic]: QUATREFAGES, 1865, p. 552. [Diagnosis of MÖRCH.]

Sclerostyla ctenactis: BUSH, 1905, p. 224. [Name only.]

p.p. *Sclerostyla differens* AUGENER, 1922, p. 50. [Panamá O., Colón; not Barbados. – The Barbados specimens belong to *Scl. differens*. Material studied, ZMH, ZMB.]

Serpula (*Sclerostyla*) *ctenactis*: AUGENER, 1925, p. 12–15. [St. Croix, St. Thomas, "Westindien". – Redescription of Mörch's material.]

Placostegus calciferus TREADWELL, 1929, p. 12–13, fig. 34–36. [Puerto Rico. – Material studied, AMNH.]

Spirodiscus calciferus: TREADWELL, 1939, p. 301–303, fig. 113. [Same specimen as above.]
Sclerostyla ctenactis: WRIGLEY, 1951, p. 184–185, fig. 38. [Octavia Bay, Colombia. – Material studied.]
Sclerostyla ctenactis: HARTMAN, 1956, p. 299–300. [TREADWELL's & WRIGLEY's specimens.]
Sclerostyla ctenactis: REGENHARDT, 1961, p. 84. [Name only.]

CURAÇAO. – Sta. *1334* (1 specimen in tube, AMNH); *1334A* (tube with operculum, RMNH 04468); *2041C* (2 spec. in tubes, tHU 124); *2046* (7 spec. in tubes, 4 empty tubes, RMNH 04471); *2049B* (1 spec. in tube, ZMB); *2054B* (1 spec. in tube, RMNH 04469); *2070* (3 spec. in tubes, 2 empty tubes, RMNH 04470).
BONAIRE. – Sta. *2111Ea* (1 spec. in tube, ZMH); *2112Ge* (5 spec. in tubes, USNM 45486); *2112Ja* (2 spec. in tubes, BMNH ZB. 1971. 230); *2117B* (3 spec. in tubes, tHU 122).
KLEIN BONAIRE. – Sta. *2105B* (2 spec. in tubes, tHU 123).
ST. CROIX. – "*Trichopoma* n.g. *ctenactis* Mörch, Ørsted (coll.)", relabelled *Sclerostyla ctenactis* (by Augener?) (1 spec., *paralectotype*, ZMK); "*Serpula ctenactis* Mörch" (empty tubes, ZMK).
ST. THOMAS. – "*Trichopoma* n.g. *ctenactis* Mörch, Krebs 1860 (coll.)", relabelled *Sclerostyla ctenactis* (by Augener?) (1 spec., *lectotype*); "*Serpula ctenactis*, O. Mörch (det.?), Krebs 1867, 1872, 1873" (1 dry spec. in tube, 2 opercula in tubes); all ZMK.
PUERTO RICO. – Sta. *1415* (6 eroded opercula, RMNH 04467); *2136A* (2 tubes, RMNH 04476); JULIA COVE, Guánica Harbor, 23.VI.1915 (holotype of *Placostegus calciferus*, AMNH 1996); ROOSEVELT ROADS, pierside (U.S. Navy Oceanographic Office, 3 spec., 3 opercula, 2 tubes, USNM); LA PARGUERA, Enrique reef, windward side. Under overhang, 17 m, coll. J. Rees, April 1969 (1 tube with operculum, tHU 121); Sunken reef off LA PARGUERA, 25 m, underside of *Agaricia* (as *Leptoseris*) *fragilis*, 5.IV.1968 (3 tubes with opercula, RMNH 04466).
TORTUGAS. – LOGGERHEAD KEY, W. L. Schmitt coll., 4. VIII.1930 (1 spec., sub *Scl. ctenactis*, Zibrowius det., USNM 43241).
HONDURAS. – N. coast just south of ISLA ROATAN, on *Phyllangia americana*, 132 ft. (1 tube, Univ. of Miami).
PANAMÁ. – COLÓN, Napperschmidt coll. (1 spec. in tube, syntype of *Scl. differens*, ZMH 1876).
WEST INDIES. – "*Trichopoma* n.g. *ctenactis* Mörch, Svenson legit., Vestindien", relabelled *Scl. ctenactis* (by Augener?) (1 spec. without operculum, *paralectotype*, ZMK).
COLOMBIA. – OCTAVIA BAY, 6°50′ N, 77°41.10′ W, coral, shallow water (1 spec., AHF 002389).
?LOCALITY. – "*Trichopoma* n.g. *ctenactis* Mörch, Krøyer legit.", relabelled *Scl. ctenactis* (by Augener?) (1 spec., *paralectotype*, ZMK).

Tube: Although variable in shape, nearly all tubes and tube-fragments (ca. 40) abruptly increase in diameter, have three longitudinal keels, and were sunken in the substrate. The most simple tube is subfusiform in cross-section with its lower half sunken in the

substrate (10 spec., Fig. 21). Another form has three very faint longitudinal ridges (10 spec., Fig. 22, Pl. I B). The rest of the specimens show a median ridge, flanked by a pair of keels, irregularly scalloped in a more or less horizontal plane (Fig. 23, Pl. I A, B). The teeth of the keels are longitudinally flattened and may be rounded or triangular. Finally there are a few specimens with three irregularly toothed keels (Fig. 24); the specimen from Colón has along one side another 3 or 4 additional ridges and a faint one along the other side. The different forms of the tubes may occur in a single locality, or even in a single tube.

The diameters of the operculum and tube are equal, the operculum being extremely close-fitting. The oldest parts of the tube may be partitioned by "tabulae", as shown in Pl. I C.

In five specimens with a tube-length of 10–40 mm, the ratio of the tube-length to the length of the animal is roughly 1.7, 1.8, 2.0, 2.2, 2.6.

About half of the tubes are pinkish, the others white; both colours may occur in one tube.

Branchiae: Pairs of branchial filaments $13–20 \leqslant \overline{25} \leqslant 31–38$ (n = 29), arranged in a pair of nearly complete circles. The branchial membrane extends 1/3 (1/4–1/2) the length of the filaments. There are two rows of pinnules becoming shorter towards the end of the filaments, which may or may not be devoid of pinnules.

The mouth is bordered by two transverse membranes, the dorsal one extending in a pair of mouth palps (in the center of the circle of filaments), and the ventral one continuing in two short membranes along the bases of the filaments.

Operculum: The operculum is inserted medially. The operculum and peduncle are completely calcified, enclosed by a thin fleshy layer, ending at the brim of the funnel in a number of glandular areas, more or less corresponding to the number of marginal teeth (Fig. 30). The calcified part of the operculum is funnel-shaped, usually smooth on the outside, with toothed radial ridges on the inner side (Fig. 30, Pl. III A, B). The margin of the cup has a number of sharply pointed teeth, corresponding to the radial ridges.

The numbers of components – the radial ridges, marginal teeth, and glandular fields – are not always identical even in the same

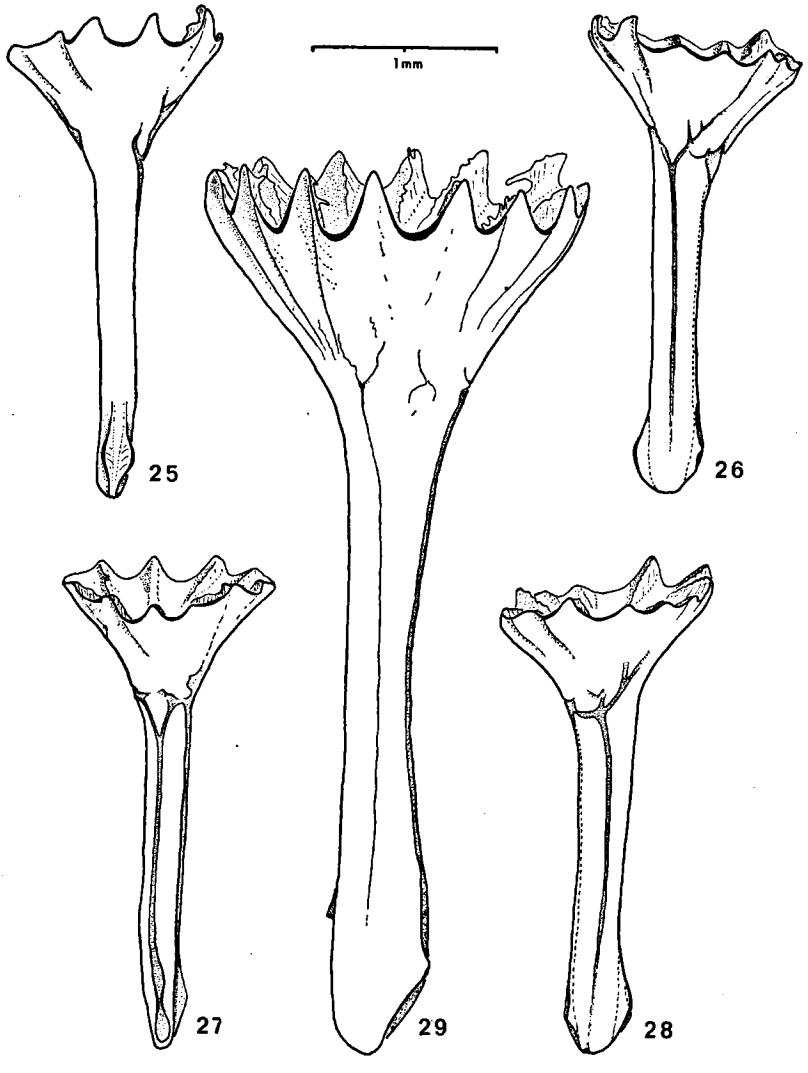


Fig. 25–29. *Sclerostyla ctenactis*, opercula. — 25–28, dorsal, right lateral, ventral and left lateral views of same specimen from BONAIRE (Barcadera, ZMH); 29, right lateral view from CURAÇAO (Portomaribaai, RMNH 04471).

specimen, e.g. 15–18–19, 14–14–16 or 10 (14)–14–14. Generally it is difficult to count all three in a single operculum as it may partly be damaged or overgrown with calcareous algae. The numbers of these components have been compiled in a minimum and maximum series: 8–13 $\leqslant \overline{14.5} \leqslant$ 16–20 and 11–13 $\leqslant \overline{15.1} \leqslant$ 17–23 (n = 33).

The cup is deep, the radial ridges usually well developed and relatively high, with many irregular teeth. Usually these teeth are short, exceptionally they are very long and slender. The marginal teeth are in some instances grooved or indented on the outside (Fig. 29). The base of the cup may be irregularly grooved (Fig. 25–28), as may be the entire outside of the cup (cf. WRIGLEY, 1951, fig. 38). The shaft of the funnel (peduncle) is usually inserted somewhat ventrally or eccentrically to the cup (Fig. 28, 30) and is laterally compressed. The peduncle has 4 longitudinal grooves: a dorsal one, extending from its base to 1/3 of its length, two shallow lateral ones and a deep ventral one along its entire length. The latter three grooves usually continue as branches into the basal grooves of the cup (Fig. 26–28). The base of the peduncle is figured in Figure 31.

The diameter of the operculum is 0.8–2.2 $\leqslant \overline{2.6} \leqslant$ 3.0–4.3, its length, including the peduncle, 1.9–5.2 $\leqslant \overline{6.2} \leqslant$ 7.1–12.0, with a ratio of 1.86–2.26 $\leqslant \overline{2.38} \leqslant$ 2.49–3.00 (n = 29).

Collar and thoracic membranes: The collar is usually well developed, but short, appearing trilobed, with a square ventral lobe, which is indented medially, and two large latero-dorsal lobes. There are two tonguelets between the lateral and ventral "collar-flaps" (see Fig. 35). These tonguelets are perhaps lateral parts of the collar, while the latero-dorsal lobes are the thoracic membrane (cf. SEGROVE 1941, p. 482). The latter is very wide anteriorly, narrowing at the third to fourth segment, and united ventrally, forming a narrow "apron" across the first abdominal segment.

Collar setae were present as very small bundles (4–9 setae) in 4 specimens only. Occasionally they were indicated by a small pit. Usually they were absent altogether. When present, the setae are mostly unilimbate (Fig. 1); the remaining ones have a distal wing and a more or less separate proximal denticulate zone (Fig. 2–4).

Thorax: The thorax includes seven segments, usually six of

them are setigerous. The setae are unilimbate, of two different sizes and slightly different forms (cf. Fig. 5–6). The uncini are saw-shaped with 9–10 teeth including the anterior tooth; the latter seems to be bifurcate, but upon close examination is found to be blunt with some irregularities in front (cf. Fig. 12–13).

Abdomen: The number of segments is variable: *35–53* $\leqslant \overline{58.3} \leqslant$ *63–81* (n = 27). The setae have geniculate tips (Fig. 7); those of the posterior segments may be simple, capillary (cf. Fig. 10). The uncini are rasp-shaped, with 2 (anterior segments) to 4 (posterior) rows of teeth, with 9–10 teeth when seen in profile, including the anterior blunt one (Fig. 20). The anterior first five (or so) abdominal segments lack uncini.

Total length: The length, including operculum, is 5.3–13.2 $\leqslant \overline{15.9} \leqslant$ 18.6–30.0 (n = 27), the breadth of the thorax is generally 1–2 mm.

The colours of the living animal (taken from notes on 5 specimens) vary to some extent, and are apparently of no diagnostic value. Predominant colours are shades of red and orange (anteriorly), white and cream (abdominal). Most striking are the bright red glandular fields on the operculum, the peduncle, which is red dorsally and white ventrally, and the white tonguelets of the collar.

Discussion

In the Zoological Museum of Copenhagen (ZMK) four specimens from the Virgin Islands, which apparently were studied by Mörch (unpublished label *Trichopoma* n.g. *ctenactis*) are present. Augener (1925) reported five specimens, labelled with this *nomen nudum*. Although all the specimens are more or less damaged and without tubes, it seems best to indicate one of them as the LECTOTYPE (St. Thomas) and the other three (from "Vestindien," St. Croix and ?) as PARALECTOTYPES.

The remaining dried material from St. Thomas was identified by Mörch, but, since it is only present in the Museum since 1867–73, it does not belong to the type material. The empty tubes from St. Croix, labelled *Serpula ctenactis*, belong for the greater part to *Hydroides* (*alatalateralis*?) and only a few are *Sclerostyla ctenactis*.

Although it is impossible to identify specimens without tubes

with absolute certainty, the sum-total of measurements, form of operculum and locality renders it very likely that the specimens from Puerto Rico (among which *Placostegus calciferus*) and Tortugas belong to this species, as does the type-material (see also REMARKS). With the proper reserves, the Colombia specimen may be attributed to *Scl. ctenactis*.

The author tried in vain to find a connection between form of tube (as given in Fig. 21–24) and e.g. locality or habitat.

MÖRCH (1863: 386) gives as questionable synonyms "*Die Seeschlange* Schröt. Einl. 2. p. 569, t.VI. f.18" and "Serpula denticulata" Gmelin (1791, 3746), which is a short diagnosis of SCHRÖTER's (1783) material. Although SCHRÖTER's figure of a tube indeed has a certain resemblance to the tubes of Plate I A (but also to a tube of *Crucigera websteri* Benedict), it is not probable that his East Indian specimen belongs to *Sclerostyla ctenactis*.

DISTRIBUTION

Caribbean Sea. In 13 to 53 meters.

Sclerostyla differens Augener, 1922

p.p. *Sclerostyla differens* AUGENER, 1922, p. 50. [Barbados; NOT "Panama O., Colon". – The specimen from Colón belongs to *Scl. ctenactis*. Material studied, ZMB and ZMH.]

BARBADOS. – "Auf toten Seeigelschalen, 15 Faden, Kükenthal & Hartmeyer, 27.II.1907", 2 *syntypes* (ZMB 6411); Sta. *1442* (9 spec. in tubes, ca. 50 tubes, mainly RMNH 04473, tHU 126).
SURINAM. – Sta. *H57* (4 spec. in tubes, 3 tubes, RMNH 04472, tHU 125).

Tube: The tube consists of a small adnate and a large free part (Pl. II B). The adnate part is smooth, trapezoidal in cross-section, with the two edges generally extended in smooth lamelliform keels; laterally 2–6 ridges may or may not be present. The area where the tube is becoming free from the substrate is more or less circular in cross-section, with 4–8 faint, irregular, longitudinal ridges. The free part of the tube is rugose, with 8–13 faintly indicated ridges, giving the tube a polygonal appearance (Pl. II A).

The operculum is so close fitting that in order to remove the

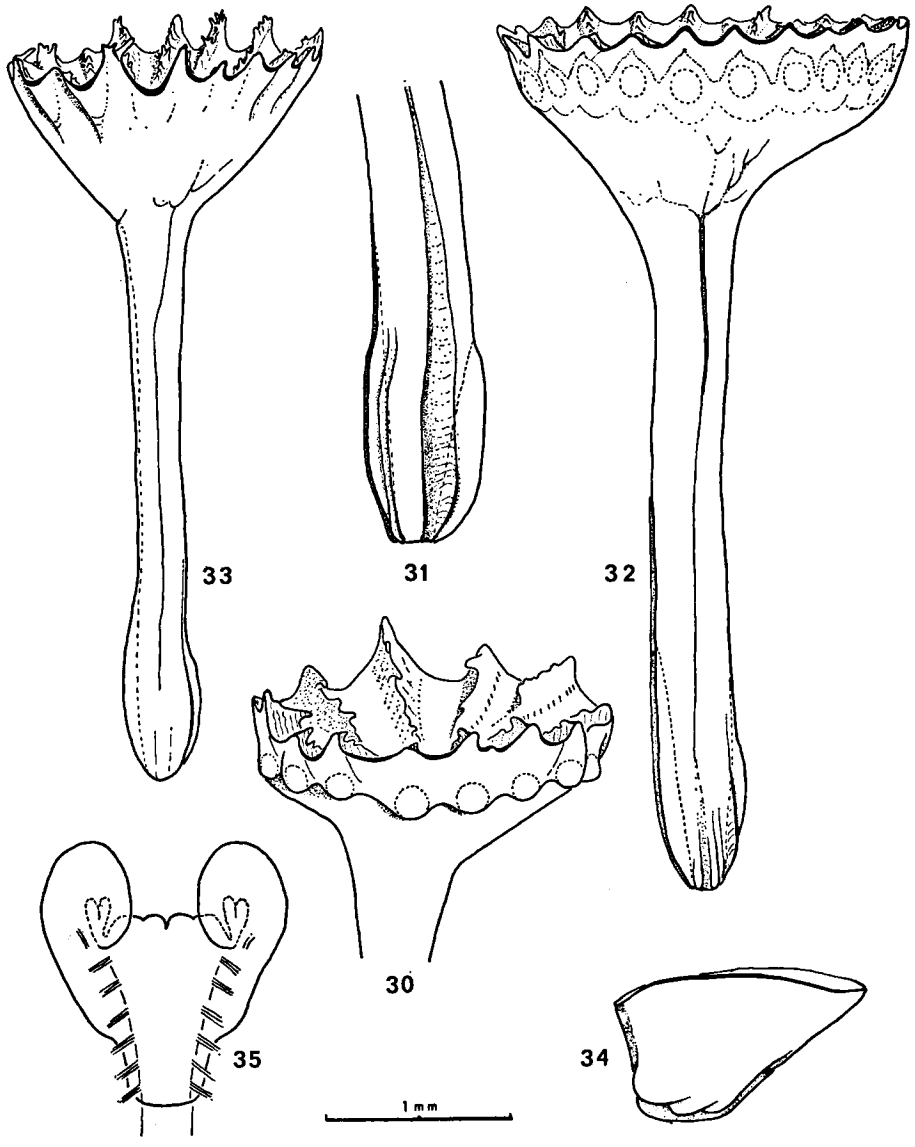


Fig. 30–31. *Sclerostyla ctenactis*, opercula; 30, right antero-lateral view from Bonaire (N. of Witte Pan, tHU 122); 31, base of peduncle, left lateral view from Puerto Rico (Roosevelt Roads, USNM).

Fig. 32. *Sclerostyla differens*, operculum, left lateral view from Surinam (RMNH 04472).

Fig. 33. *Sclerostyla semiannulata* n. sp., operculum, left lateral view from Barbados (off Holetown, USNM).

Fig. 34. *Pomatoleios kraussii*, operculum, right lateral view from Madagascar (Tuléar).

Fig. 35. *Sclerostyla*, scheme of collar and thoracic membranes.

All opercula same scale.

specimen undamaged from the tube, it is necessary to saw a small slit near the opening of the tube and to push the operculum from behind. The oldest parts of the tube may be partitioned by several tabulae in a row, having more or less the same shape as those figured on Pl. I C.

The tube is made up of two clearly different layers, an inner transparent one and an outer opaque one.

In five specimens with a tube-length of 10–48 mm, the ratio of the tube-length to the length of the animal is roughly 1.4, 1.5, 1.6, 1.8, 2.2. The diameter of the tube is up to 5.4 mm, with a lumen of 4.0 mm.

Tubes may be white and/or pinkish (red).

Branchiae: Pairs of branchial filaments are 8–18 $\leqslant \overline{25} \leqslant$ 33–36 (n = 8). The branchial membrane extends 1/4–1/3 the length of the filaments. Otherwise same as *Scl. ctenactis*.

Operculum: The operculum has the general appearance of *Scl. ctenactis* but differs in the following respects. The cup of the operculum is shallow, in some cases nearly flat (Fig. 32). The marginal teeth are generally smaller than those of the preceding species, the radial ridges less expressed, smoother, with very small rounded teeth (Pl. IV A, B, C). Minimum and maximum series of radial components are *18–19* $\leqslant \overline{21.1} \leqslant$ *23–31* and *19–18* $\leqslant \overline{25.0} \leqslant$ *32–43* (n = 8).

The diameter of the operculum is 1.0–1.9 $\leqslant \overline{2.8} \leqslant$ 3.6–3.9, its length, including the peduncle, *2.1–4.4* $\leqslant \overline{6.2} \leqslant$ *8.0–9.2*, with a ratio of *1.91–2.01* $\leqslant \overline{2.32} \leqslant$ *2.44–2.69* (n = 8).

Collar and thoracic membranes: The collar and thoracic membranes resemble those of the preceding species, but are slightly smaller. No collar setae have been observed.

Thorax: The thorax resembles that of *Scl. ctenactis*. Setae and uncini, with 8–9 teeth, are shown in Figure 5–6, 12–14.

Abdomen: The number of segments is variable: 24–38 $\leqslant \overline{44.2}$ $\leqslant$ 50–56 (n = 8). The setae are shown in Figure 8–10; the uncini are rasp-shaped with 2–3 rows of teeth, with 9–11 teeth when seen in profile (Fig. 15–18). The anterior 5–13 abdominal segments lack uncini; the number of uncini in a row slowly increases to 1/3–1/4

from behind, then quickly decreases again. The number of setae per bundle decreases from anterior to posterior.

Total length: The length, including operculum is 4.0–10.1 $\leqslant \overline{15.1} \leqslant$ 20.2–22.1 (n = 8), the breadth of the thorax is generally 2–3 mm.

DISCUSSION

Although AUGENER (1925: 13–14) stated that *Scl. differens* was a synonym of *Scl. ctenactis*, matters are more complicated. The specimen from Colón, indeed belongs to *ctenactis*, based on its measurements, the form of the operculum and tube. The two specimens from Barbados, however, lack tubes and thus can not be identified with absolute certainty. However, it seems best not to introduce a new name for this second species of *Sclerostyla*. The sum-total of the measurements, ratios, form of operculum, and locality renders it very likely that two of AUGENER's syntypes, as well as the other material from Barbados and Shelf of Surinam, belong to a single species.

The measurements of the two syntypes are: branchiae 21, 26; radial components: 20, 21–27; diameter and length of operculum: 2.3 × 4.4, 3.0 × 6.8; ratio of both: 1.91, 2.27; number of abdominal segments: 40, 50; total length: 14.4, 15.5 mm. These measurements are included in the totals given above.

Some of the tubes had been bored (by a snail?) in the same way as figured by MÜLLER (1969) for fossil Ditrupinae.

When examined superficially, the tubes may easily be mistaken for Scaphopoda.

DISTRIBUTION

Barbados, Shelf of Surinam. In 27 to 100 meters.

Sclerostyla semiannulata nov. spec.

BARBADOS. – Sta. *1442* (18 spec. in tubes, 1 operculum in tube, ca. 40 tubes, 4 spec., mainly RMNH 04474, 04475).

Holotype: BMNH ZB.1971.228.
Paratypes 11: 3 BMNH ZB.1971.229, 3 RMNH 04474, 3 USNM 45488, 1 tHU 127, 1 SME.

Tube: The tube is entirely adnate, quickly increasing in diameter. Most striking are the large tori or transverse cushions, giving the tube its characteristic appearance (Pl. II C). There may be 3 (–5) more or less distinct longitudinal ridges between the tori. The oldest part of the tube is circular in cross-section, with three very faint longitudinal ridges and may be partitioned by tabulae. The interspaces between the tori may vary. The tori are of varying thickness, complete tubes have 7 (1 spec.), 8 (4 spec.) and 10 (1 spec.) tori.

The tube is formed of two different layers: an inner firm one, circular in cross-section, and an outer porous one, semicircular in cross-section.

In four specimens with a tube-length of 11–20 mm, the ratio of the tube-length to the length of the animal is roughly 1.3, 1.7, 1.9, 2.5.

The diameter of the tube is up to 7.4 mm, with a lumen of 3.0 mm.

The colour of the tube is whitish.

Branchiae: Pairs of branchial filaments are 9–14 $\leqslant \overline{20} \leqslant$ 25–31 (n = 9). The branchial membrane extends about 1/3 (1/4–1/2) the length of the filaments. Otherwise same as *Scl. ctenactis*.

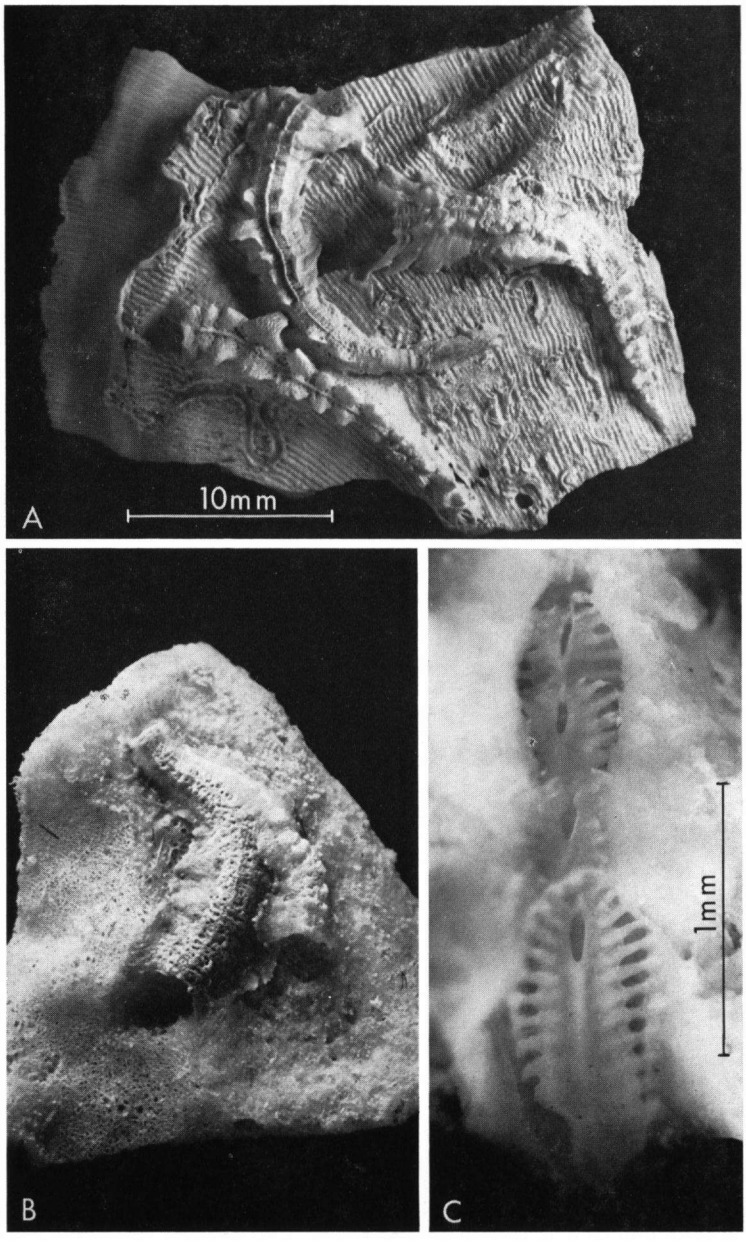
Operculum: The operculum is similar to that of *Scl. ctenactis* (Fig. 33, Pl. III C, D, IV D). Minimum and maximum series of radial components are *15–16* $\leqslant \overline{17.8} \leqslant$ *19–19* and *17–17* $\leqslant \overline{19.9} \leqslant$ *23–25* (n = 10).

The diameter of the operculum is *1.1–1.7* $\leqslant \overline{2.2} \leqslant$ *2.7–3.1*, its length, including the peduncle, is 2.6–4.0 $\leqslant \overline{5.3} \leqslant$ 6.6–8.0, with a ratio of 1.81–2.09 $\leqslant \overline{2.32} \leqslant$ 2.56–2.89 (n = 10).

Collar and thoracic membranes: The collar and thoracic membranes resemble those of *Scl. ctenactis* except for the medio-ventral indentation, which is usually lacking. No collar setae have been observed.

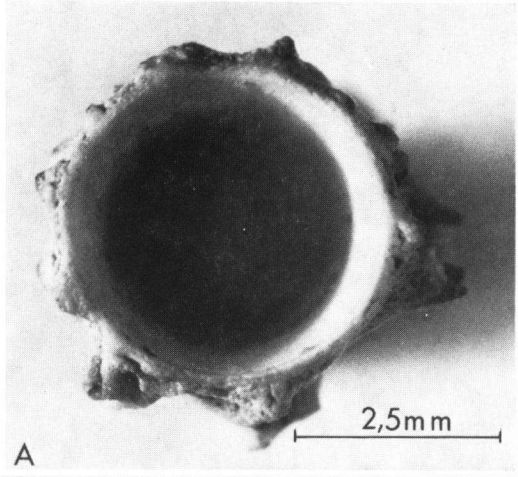
Thorax: The thorax resembles that of *Scl. ctenactis*. The uncini have 7–8 teeth.

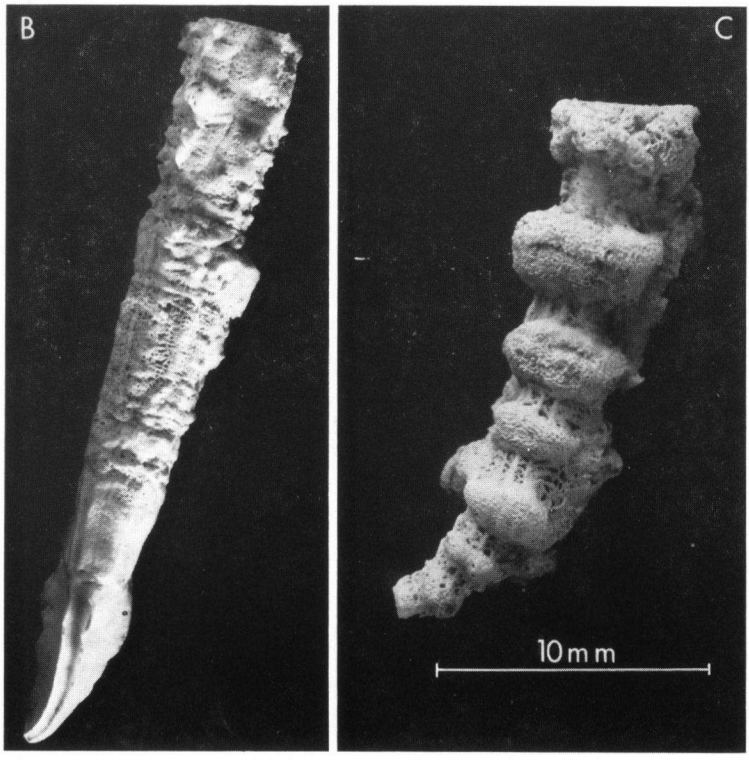
Abdomen: The number of segments is variable: *32–30* $\leqslant \overline{33.8}$ $\leqslant$ *37–40* (n = 8). The setae are shown in Figure 11; the uncini are rasp-shaped, with two rows of teeth, with 9–10 teeth when seen



I. *Sclerostyla ctenactis*. — A. Tubes on underside of *Agaricia fragilis*, from PUERTO RICO (off La Parguera, RMNH 04466). — B. Tubes on sponge, from BONAIRE (Witte Pan, tHU 122; same scale). — C. Transverse tube elements or "tabulae", in older part of tube, from BONAIRE (Santa Barbara, BMNH).

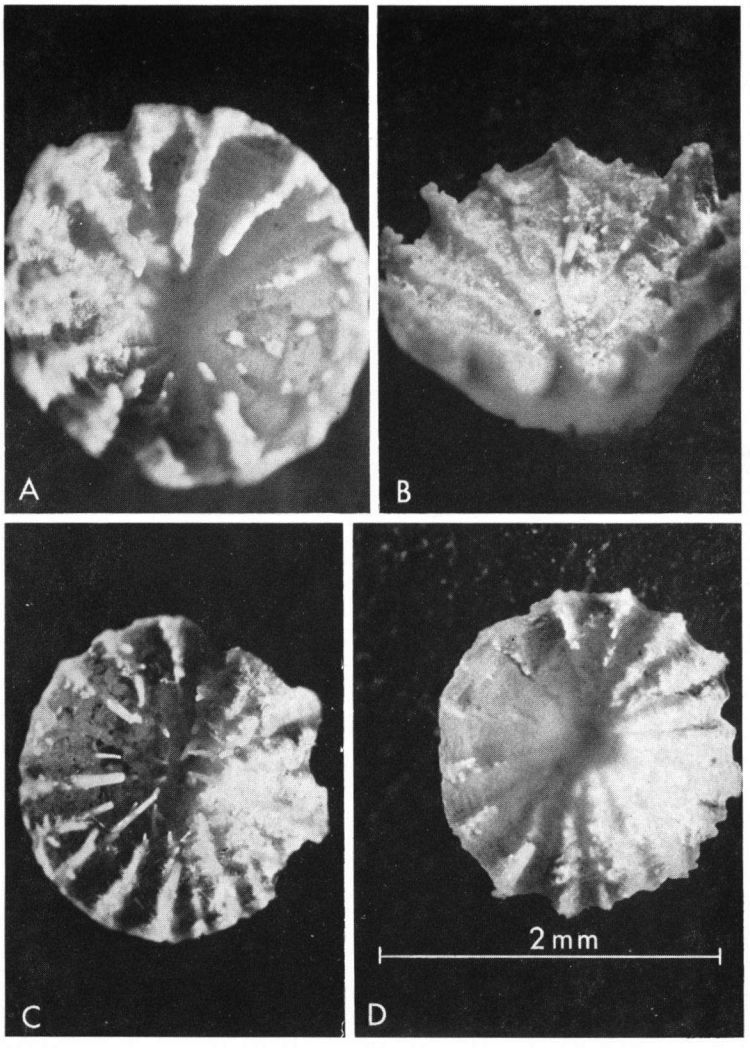
Plate II





II. A–B. *Sclerostyla differens*. — A. Mouth of tube, B. Entire tube from Shelf of SURINAM (RMNH 04472; same scale as C).

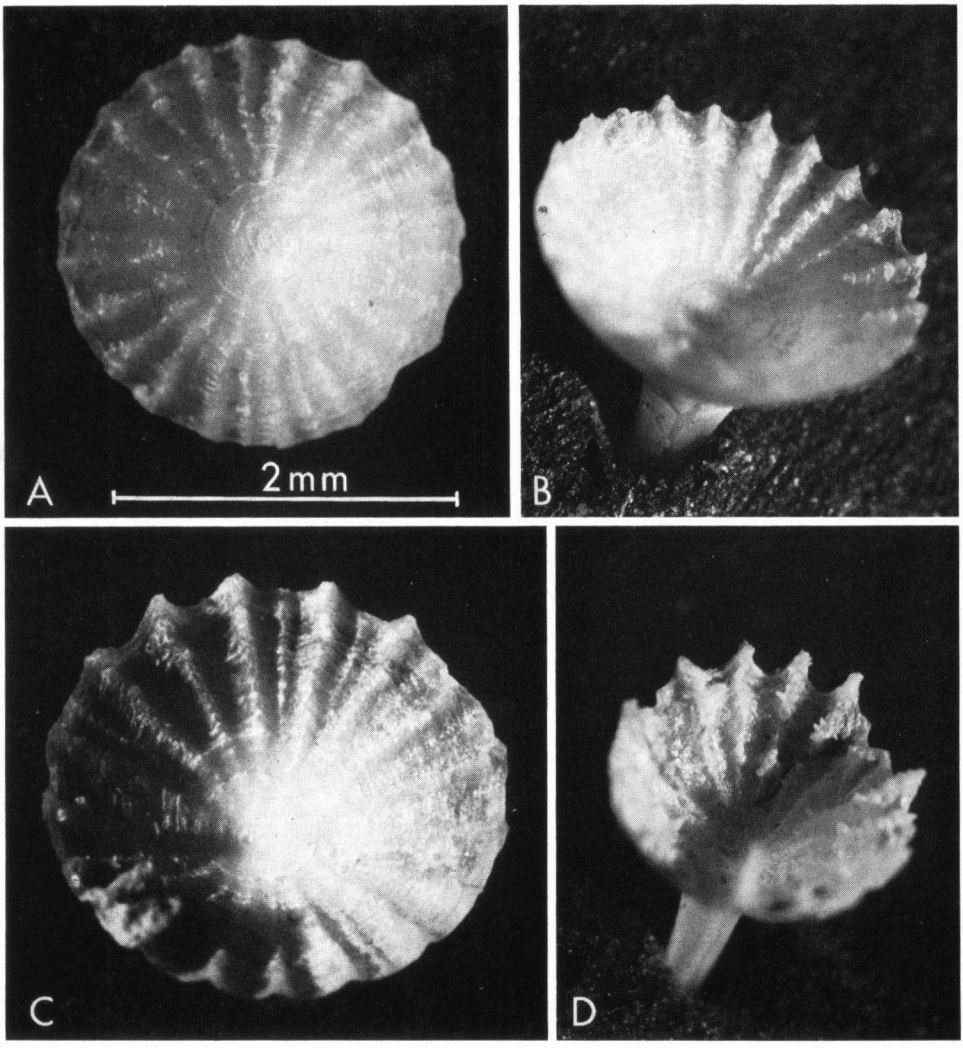
II. C. *Sclerostyla semiannulata*. — Tube from BARBADOS (off Holetown, RMNH 04474).



III. A–B. *Sclerostyla ctenactis.* — A. Operculum, frontal view, from PUERTO RICO (off La Parguera, RMNH 04466). — B. Operculum side-view, from CURAÇAO (Portomaribaai, RMNH 04471).

III. C–D. *Sclerostyla semiannulata.* — Opercula in frontal view, both specimens from BARBADOS (off Holetown, paratypes, RMNH 04474 and USNM 45488). All opercula on same scale.

Plate IV



IV. A–C. *Sclerostyla differens*. — A–B. Operculum in frontal and side-view, same specimen from Shelf of SURINAM (RMNH 04472). C. Operculum in frontal view, from BARBADOS (off Holetown, RMNH 04473).

IV. D. *Sclerostyla semiannulata*. — Operculum in side-view, same specimen as Pl. III. D (USNM 45488). All opercula on same scale.

in profile (Fig. 19). The abdomen is short, with few segments only. Nevertheless at least two specimens were mature and had eggs or sperm in their tubes.

Total length: The length, including operculum is 4.7–6.5 $\leqslant \overline{9.6} \leqslant$ 12.6–16.0 (n = 9), the breadth of the thorax is generally 1.5 mm.

DISCUSSION

Scl. semiannulata differs from *Scl. ctenactis* by its very characteristic tube and from *Scl. differens* by its tube and operculum. The opercula of *semiannulata* and *ctenactis* cannot be distinguished by their form, although the former generally appears to have more radial ridges.

Etymology: The name *semiannulata* has been chosen because of the semi-annular tori of the tube.

DISTRIBUTION

Barbados. In 100 meters.

REMARKS ON THE GENUS SCLEROSTYLA

As indicated above, it is extremely difficult to identify a specimen without tube. Disregarding the fact that some of the figures have a doubtful normal distribution, the 95% confidence limits of the three species exclude each other for the number of abdominal segments only (respectively 30–37, 38–50, 53–63 for *semiannulata*, *differens* and *ctenactis*). Since the actual range of the number of abdominal segments is considerably wider, single specimens thus cannot be identified with certainty. The same holds for all other values, though some of them nearly or partly exclude each other.

Based on all mean values, it appears that generally *Scl. semiannulata* is the smallest species, while the other two are of nearly the same size. *Scl. ctenactis* and *differens* differ in the number of radial ridges on the operculum, being generally higher in the latter. However, if measurements and values are arranged in various ways, the species will usually aggregate in three different groups, illustrated

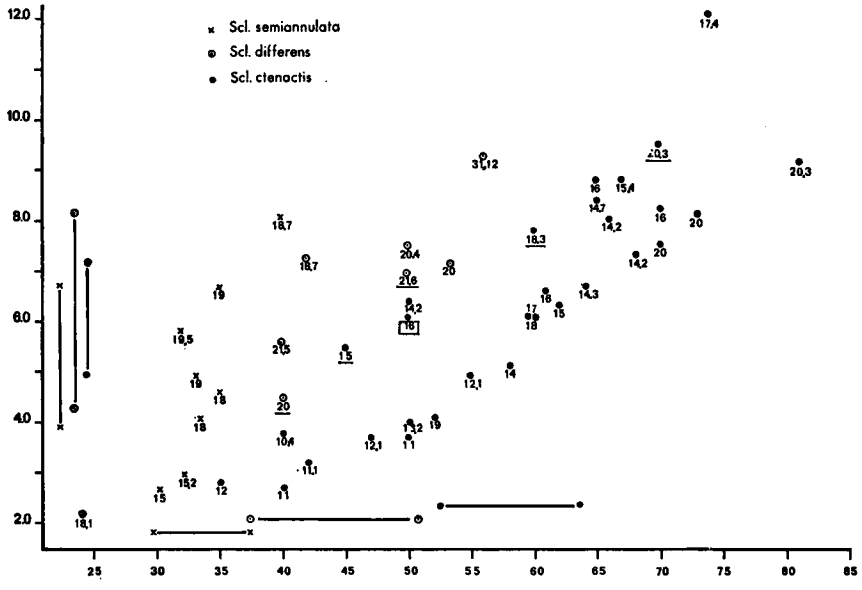


Fig. 36. *Sclerostyla semiannulata* (×), *differens* (⊙) and *ctenactis* (•) Horizontal axis: number of abdominal segments. Vertical axis: lengths of opercula. Lines near the axis give the 95% confidence limits of the mean. 18.7 means minimally 18, maximally 25 radial components. The two syntypes of *Scl. differens* and the lectotype and 1 paratype of *ctenactis* are underlined; [16] = type of *Placostegus calciferus*; 15 = Puerto Rican specimen without tube.

in Figure 36–37. In the overlap, they can be distinguished by the number of radial components of the operculum.

As indicated in Figure 36, a specimen with 35–45 abdominal segments may belong to any of the three species; but if it has 10–15 radial components, it is bound to belong to *Scl. ctenactis*, since the other two species have 18–26 radial components in this area. The latter two species can be distinguished by the form of the opercula. The same holds *mutatis mutandis* for Figure 37. However, it must be kept in mind that these differences in measurements of the various species also may be caused by the different habitats and/or localities.

NESTLER (1963) and MÜLLER (1970) described "tabulae" in the tubes of fossil *Sclerostyla*. Although the form of the tabulae (Pl. I C) may be caused by the segmental structure of the specimens (and

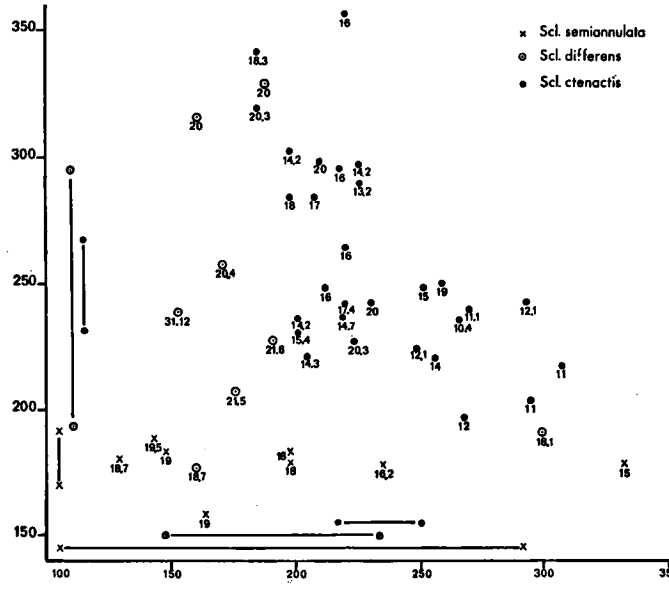


Fig. 37. As Fig. 36. Horizontal axis: ratio of number of abdominal segments/ number of branchial filaments. Vertical axis: ratio of lengths of animals/lengths of opercula.

perhaps by the abdominal glandular fields known from many species), the meaning of the fistula in the center is not clear. Similar tabulae have been observed in *Spirobranchus. Pomatoceros triqueter* (THOMAS, 1940: 7, fig. 4; HEDLEY, 1958: 319–321, fig. 11–15), *Mercierella enigmatica* and *Ditrupa* [= *Serpula*?] *crenata* Ehlers (fide ZIBROWIUS, personal communication) also may have tabulae.

By its operculum and tube *Scl. differens* resembles closely some of the fossil species of *Sclerostyla*, i.e. *Scl. mellevillei* Nyst & le Hon (ROVERETO, 1904: 24–25; WRIGLEY, 1951: 185) and *Sclerostyla trochoides* (Nyst) (ROVERETO, 1904: 25, as variety of foregoing species; WRIGLEY, 1951: 188). Fossil material in the author's collection [No. 119, sub *Scl. mellevillei*?, should be *trochoides*?, Oligocene, mineshaft Hendrik IV, Brunssum (Limburg, S. Netherlands), coll. & don. H. Sipman 1962] shows opercula like those of *Scl. differens*, with a flat cup with numerous (30–60) radial ridges; the diameter is nearly the same (2–4 mm). The general shape of the

peduncle is similar to Figures 27–33. Differences with the Recent material might be found in the outside of the cup and the base of the peduncle, which are more grooved in the fossil material (cf. GERTH, 1941: 161 fig. 2; REGENHARDT, 1961: 15 fig. 5).

Sclerostyla crassa (J. Sowerby), though provided with a smooth triangular tube only, certainly belongs to this group too (type-material studied, BMNH A. 6722). In three of the tubes there are faint indications that the younger part of the tube (broken) has been erect and free, polygonal in cross-section. The opercula have 24 and 29 radial ridges, a third operculum is damaged.

The distribution of the Cretaceous opercular forms of the genus *Hamulus* (of which *Sclerostyla* might be a synonym as stated before) is North America and Palestina according to WADE (1922) and AVNIMELECH (1941). Opercular fossil forms of *Sclerostyla* have been found in Southern England, The Netherlands, Belgium, Northern France and Germany (NYST, 1845; ROVERETO, 1904; SCHMITT, 1927; GERTH, 1941, and WRIGLEY, 1951). This differs markedly from the Recent distribution in the tropical seas of America only. It is remarkable that no representatives of *Sclerostyla* have been found as yet in other tropical seas.

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