STUDIES ON THE FAUNA OF CURAÇAO AND OTHER CARIBBEAN ISLANDS: No. 118.

SPIRORBINAE (POLYCHAETA) FROM THE WEST INDIES

by

JULIE H. BAILEY

(Department of Zoology, University College of Swansea)

The collections studied here were received from Dr. P. WAGENAAR HUMMELINCK, Zoölogisch Laboratorium, Utrecht, Nederland; and from Dr. S. B. HILL, Department of Zoology, University of Reading. They were particularly welcome following the recent discovery that the percentage of Spirorbinae with opercular incubation may be remarkably high in warm seas. Collections from the Mediterranean have shown that over 80% of species have this method of incubation (BAILEY, 1969). Records from Ceylon (PILLAI, 1960; DE SILVA, 1961, 1965) had revealed a similar situation there, so there was an interesting faunistic connection between the two areas. It seemed possible that the link might have been derived from the Sea of Tethys, but it may equally have resulted from similar ecological and physiological selection pressures in two separate regions.

The Caribbean collections dealt with here are from a sea area which has been called the Mediterranean of the New World. It is interesting too in being separated from the Pacific ocean only by the isthmus of Panamá. The Spirorbinae from the Pacific coast of México have been thoroughly described by RIOJA (1942, 1962), which raises the possibility that a comparison of the two areas may throw light on rates of evolution in the subfamily. The isthmus of Panamá has been interrupted during several epochs of the Cenozoic and the history of these events is thought to have been well established (EKMAN, 1967).

RIOJA (1942, 1962) recorded thirteen species of *Spirorbis* from

Present address of author: Dept. of Zoology, Univ. of Hawaii, Honolulu.

western México, but very little has been published about the group from any of the eastern coasts of the Americas, apart from the important paper by CAULLERY & MESNIL (1897), which dealt with seven species from Patagonia. BUSH (1904, 1910) named two species from Bermuda, but the descriptions were inadequate. She gave the name *Spirorbis formosus* to dextral forms, which probably included that subsequently described as *Spirorbis steueri* by STERZINGER (1909), for some of her figures feature the lobed talon characteristic of the latter species. Sinistral forms were named *Spirorbis mutabilis* with some prescience, for the original description specified tube incubation, but a later figure showed an opercular brood chamber. The two widely distributed species, *Spirorbis corrugatus* Caullery & Mesnil and *Spirorbis spirillum* (L.), have been recorded from various places round the Gulf of Mexico (HARTMAN, 1951; RENAUD, 1956; RIOJA, 1959), whilst *Spirorbis corrugatus* and *Spirorbis laevis* Quatrefages have been recorded from Bonaire and Curaçao by AUGENER (1936). He had previously (AUGENER, 1922) given the name *Spirorbis antillarum* to a form collected from St. Thomas, but the description was inadequate and may have related to *S. corrugatus* or *S. steueri*. There were thus only two or three species of *Spirorbis* in those early records from the West Indies.

COLLECTING AREAS AND METHODS OF STUDY

The collections were made from seventeen islands of the Lesser Antilles and Bahamas. These are shown on the map (Fig. 125), where they are numbered consecutively in an arc from north to south. There were several collecting locations on most of the islands, details of which are given in Table 1. There the islands have been listed alphabetically, but each is followed by the reference number which marks its position on the map.

The samples were mostly from shallow water, between 0.25–2 m, in sheltered lagoons and bays around the islands. Many specimens were on plant material, such as calcareous algae (*Halimeda*), eelgrass (*Thalassia*) and mangroves (*Rhizophora*). The rest were from gastropod shells, stones and pieces of coral. Two samples from Puerto Rico were from 10 m and 90 m respectively and were obtained by dredging.

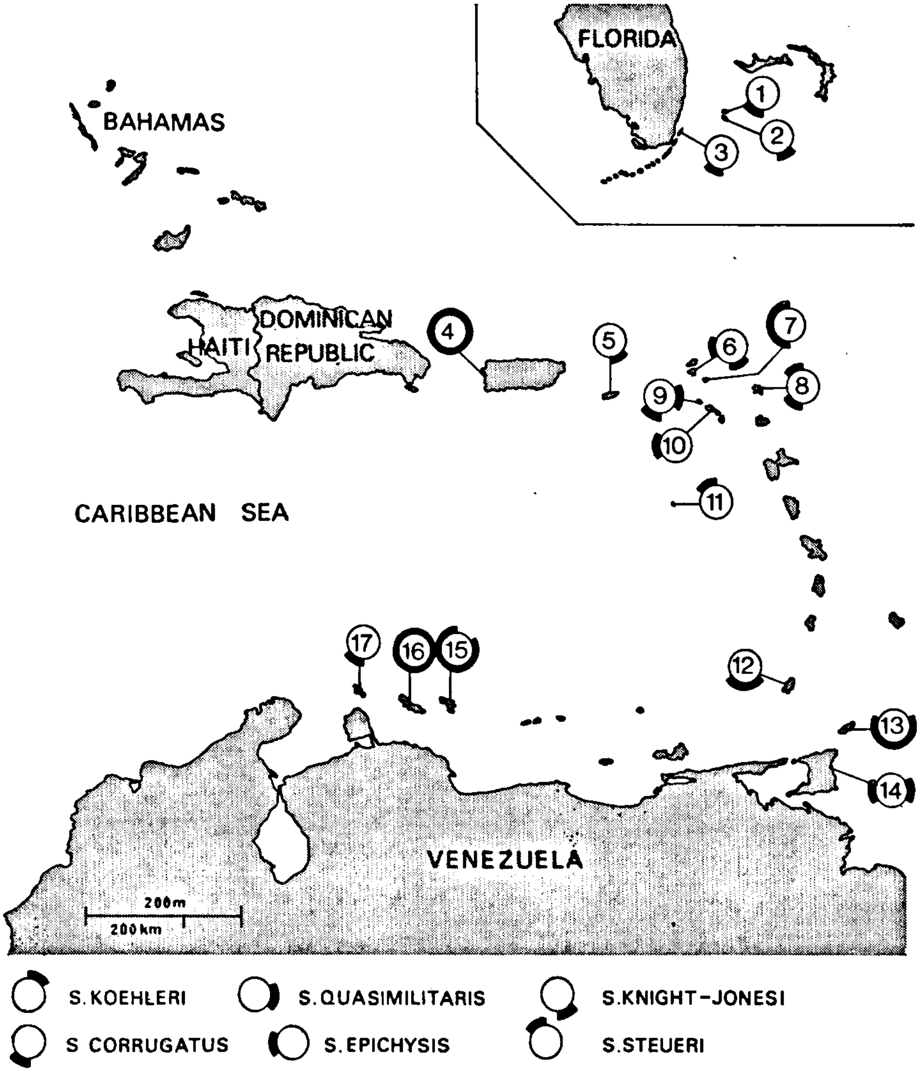


Fig. 125. Map showing the islands of the West Indies from which collections of *Spirorbis* were received. The occurrence of each of the six species is indicated by thickening an appropriate segment of the ring which surrounds each island number: – 1, Bimini (north); 2, Bimini (south); 3, Key Biscayne (Florida); 4, Puerto Rico; 5, St. Croix; 6, St. Martin; 7, La Fourche; 8, Barbuda; 9, St. Eustatius; 10, St. Kitts; 11, Aves; 12, Grenada; 13, Tobago; 14, Trinidad; 15, Bonaire; 16, Curaçao; 17, Aruba.

The specimens were preserved in alcohol. Tube and opercular characters were observed with a low power binocular microscope. The distribution and detailed structure of the setae were best seen in lactophenol whole mounts of specimens removed from their tubes, using phase-contrast objectives.

I am indebted to Dr. P. Wagenaar Hummelinck, on whose collections this work is based; Drs. H. A. ten Hove (also at the Zoölogisch Laboratorium, Utrecht) for carefully sending the material, with much information about the literature dealing with the area; Dr. S. B. Hill for two additional samples; Professor E. W. Knight-Jones for advice on preparing the manuscript; and the S.R.C. for a research studentship.

KEY TO THE SPECIES OF SPIRORBIS OBSERVED

This may help to introduce the reader to the Spirorbinae of the region, but it is based mainly upon the characters of mature opercula. In young individuals the opercula are often different and, to identify juveniles, it will be necessary to make careful comparisons with the figures and descriptions which follow.

1. Coiling sinistral (mouth of tube faces clockwise) 2
Coiling dextral (mouth of tube faces anticlockwise) 4

2. Embryos incubated in a single brood chamber 3
2a. Embryos incubated in two or more brood chambers stacked one above the other (Fig. 126–128). . . *S.* (*Leodora*) *knightjonesi*

3a. Brood chamber formed from two or three interlocking plates (Fig. 129–130) . . . . *S.* (*Pileolaria*) *koehleri*
3b. Domed brood chamber with distally projecting spines (Fig. 139–140) . . . . *S.* (*Pileolaria*) *quasimilitaris*

4a. Opercular talon small or absent, with no more than two lobes 5
4b. Opercular talon large, with three or four lobes 6

5a. Talon bilobed or absent. Opercular plate saucer-shaped (Fig. 131–132) . . . . *S.* (*Janua*) *corrugatus*
5b. Talon peg-like or absent. Opercular plate with marginal projection like spout of a jug (Fig. 149–152) *S.* (*Janua*) *epichysis*

6. Large lobate talon still present in mature form (Fig. 133–135) . . . . *S.* (*Janua*) *steueri*

TABLE

DETAILS OF THE COLLECTING LOCATIONS AND THE

The numbers given to the islands mark their position in Fig. 125.
Some names of algal and other substrate are abbreviated as follows:

Acet. = *Acetabularia*
Bat. = *Batophora*
Batill. = *Batillaria*
Cer. = *Cerithium*
Hal. = *Halimeda*
Rhiz. = *Rhizophora*

L.T. = low tide; A = abundant (more than 10 individuals); P = present (1–10 individuals) tz = tidal zone; depth in meters.

Island	nr.	Sta. nr.	*Location*
ARUBA	17	1003	Boekoeti, lagoon
		1005b	Boekoeti, lagoon
		1309	Seroe Colorado
AVES	11	1114	(East of Dominica)
BARBUDA	8	833	Great Lagoon, Cuffy Creek
		1396	Great Lagoon, Village
BIMINI (N)	1	495	Alice Town, lagoon
BIMINI (S)	2	1150A	lagoon
BONAIRE	15	1071	Boca Onima
		1056Ba	Paloe Lechi
		1062a	Lac, Soerebon
		1065	Lac, Poejito, lagoon
		1066	Lac, Cay, lagoon
		1066a	Lac, Cay, lagoon
		1067	Lac, Cay
		1575	Lac, Puitu, lagoon
		1581	Lac, Awa di Salinja, lagoon
		1591	Lac, Punta di Rancho
		1598A	Lac, Boca Jewfish, lagoon
		1601A	Lac, Palu Grandi, lagoon
		1602A	Lac, Palu Grandi, lagoon
		1609A	Lac, Bacuna, lagoon
		1070C	Lagoen
CURAÇAO	16	1023	Plaja Hoeloe
		1024	Plaja Hoeloe
		1026	Spaanse Put Baai, pools
		1155	St. Marta Baai pool
		1321	St. Marta Baai, lagoon

1

SPIRORBIS SPECIES RECORDED FROM EACH

Sarg. = *Sargassum*
Syr. = *Syringodium*
Thal. = *Thalassia*

			Spirorbis					
Date	*Substratum*	*Depth*	*koehleri*	*quasimilitaris*	*knightjonesi*	*corrugatus*	*epichysis*	*steueri*
18. 6.30	*Thalassia*; mud on rock	½–1	—	—	—	A	—	—
8. 2.49	*Rhizophora*; muddy sand	tz–1	—	—	—	A	—	—
2. 5.55	rocky pools, in surf	tz–1	—	—	—	A	—	—
12. 4.49	cast ashore; sandy		—	—	—	—	—	P
22. 7.67	*Thalassia* cast ashore		—	—	—	A	—	—
4. 7.55	*Bat.*, *Thal.*, *Syr.*; sandy	½–1	—	—	—	—	—	P
18. 8.49	*Thalassia* cast ashore		—	—	—	P	—	—
17. 8.49	*Rhizophora*; sandy mud	tz–1	—	—	P	—	—	—
19. 9.48	on *Nerita*; rock in surf	tz–½	—	—	A	—	—	—
27. 4.49	beachrock	½	—	—	—	—	P	—
17. 4.55	*Rhiz.*, *Thal.*, *Hal.*; sandy	tz–1	—	P	—	—	A	—
17. 9.48	*Thal.*, *Hal.*; mud flat	½–1	—	—	—	—	—	A
1. 9.48	*Thalassia*; mud	tz–1	—	—	—	A	—	A
25. 2.49	*Rhiz.*, *Avicennia*, *Thal.*	tz–1	—	—	P	—	—	—
17. 9.48	*Thalassia*; sand	1½–2	—	—	—	P	—	P
11. 8.67	*Rhiz.*, *Hal.*; mud	tz	—	—	P	—	—	—
9. 9.67	*Bat.*, *Rhiz.*, *Batill.*; mud	½–1	—	—	A	—	—	—
18. 8.67	*Thal.*, *Hal.*; sandy	tz	—	—	—	P	—	—
22. 8.67	*Batillaria*; mud	tz	—	—	A	—	P	—
31. 8.67	*Bat.*, *Thal.*; muddy sand	tz–1	—	—	P	—	—	—
30. 8.67	*Acet.* on *Batophora*	tz–1	—	—	P	—	—	—
15. 8.67	*Batophora*; mud on sand	tz–1	—	—	A	—	—	—
14. 9.48	near *Rhiz.*; muddy sand	tz–1	—	—	—	P	—	—
28.10.48	sandy reef	tz–1	—	P	—	—	—	—
2. 4.49	rock with sand	tz	—	—	—	—	A	—
—. 2.49	*Batill.*; coral debris	¼–½	—	—	A	—	—	—
29. 7.53	on coral	tz–1	—	P	—	P	—	—
3. 3.55	*Rhizophora*, *Batillaria*	½–1	—	P	A	—	—	—

Island	nr.	Sta. nr.	*Location*
		1504A	St. Marie Baai, seepage
		1028	Piscadera Baai, inner bay
		1028A	Piscadera Baai, inner bay
		1458	Piscadera Baai, outer bay
		1460	Piscadera Baai, mouth
		1461	Piscadera Baai, mouth
		1461A	Piscadera Baai, pools
		1463	Piscadera Baai, entrance
		(1463)	Piscadera Baai, entrance
		1487	Piscadera, N.E. lagoon
		1501	Piscadera, N. lagoon
		1334	Caracasbaai, submarine buoy
		1035	Spaanse Water, Kabrietenbaai
		1039	Fuik Baai, Newport Bath
		s.n.	Groot St. Joris
Key Biscayne	3	1410	Bear Cut
Grenada	12	1391	Lagoon St. George
La Fourche	7	453A	Five Island Bay
		1124	Five Island Bay
Puerto Rico	4	1415	Mayagüez, 4 km off P. Cadena
		1416	Mayagüez, 4 km off Añasco R.
		1419	Parguera, Mata de la Gata
		1421	Parguera, Bahía Fosforescente
St. Croix	5	1404	Krausse Lagoon, seaside
St. Eustatius	9	116B	Gallows Bay
St. Kitts	10	1397	Frigate Bay
St. Martin	6	476	Simson Lagoon, Flamingo Pond
		1131	Simson Lagoon, Little Key
		1132	Simson Lagoon, Flamingo Pond
		1428	Étang aux Poissons, mouth
Tobago	13	1388	Scarborough, Red Point
		S. Hill	Swallows
Trinidad	14	1382	Monos Island, Avalon Bay
		S. Hill	Balandra

Date	Substratum	Depth	*Spirorbis* *koehleri*	 *quasimilitaris*	 *knightjonesi*	 *corrugatus*	 *epichysis*	 *steuri*
22.12.63	coral debris	0–¼	—	—	A	P	—	—
2. 2.49	*Rhizophora*; mud	¼–1½	—	—	—	A	—	—
2. 2.49	*Rhizophora*; mud	tz–1	—	—	—	P	—	—
5. 1.64	sandy, rock debris	1–1½	—	—	—	P	—	—
14.12.63	*Rhiz.*; sand (tidal flow)	tz	P	A	—	P	P	—
14.12.63	*Rhiz.*; (tidal flow)	tz	—	—	—	—	P	—
14.12.63	*Rhiz.*; sandy decay	tz	—	—	—	P	—	—
14.12.63	*Rhiz.* (tidal flow)	tz–1	—	—	—	—	P	—
28.11.63	*Rhizophora*, muddy	tz	—	—	—	P	—	—
25.11.63	*Rhizophora*; mud	tz–1	—	—	—	P	—	—
25.11.63	dead *Rhizophora*; mud	tz	—	—	—	P	—	—
9. 2.55	on corals	?10	—	P	—	—	—	—
9.12.30	*Rhizophora*; sandy mud	tz–1	—	—	—	P	P	—
20.11.48	*Thalassia*; mud	½–1	—	P	—	P	—	P
9. 4.49	*Rhizophora*	tz–1	—	—	P	P	—	—
1. 9.63	*Hal.*, *Syr.*, *Thal.*; sandy	¼–1	—	—	—	P	—	—
24. 1.55	on oysters; muddy sand	tz	—	—	A	A	—	—
2. 4.49	cast ashore; *Sarg.*		—	—	—	—	—	P
2. 4.49	sandy, rock debris	½–1½	—	—	—	P	A	—
14. 9.63	shell debris, muddy	90	—	P	—	—	—	—
14. 9.63	sandy mud	10	—	—	—	—	P	P
12. 9.63	*Rhiz.*, *Thal.*, *Hal.*; sand	tz–1	P	—	—	P	—	—
17. 9.63	*Rhiz.*, *Thal.*; sand	½–1½	—	—	P	—	—	—
15. 4.55	*Rhiz.*, *Thal.*, *Bat.*; sandy	tz–2	—	—	A	—	—	—
15. 7.49	rocky beach	1–2	—	P	—	P	—	—
20. 7.55	sandy cliff, on shell	tz	—	—	—	—	P	—
8. 6.49	cast ashore; muddy		—	—	A	—	P	—
2. 8.49	*Rhiz.*, *Thal.*, *Bat.*; sandy	tz–1	—	—	P	—	P	—
8. 6.49	*Rhiz.*, *Bat.*; mud	tz–1	—	—	A	—	A	—
3.10.63	*Rhiz.*, *Cer.*, *Batill.* (flow)	tz–1½	—	—	A	—	P	—
14. 1.55	on cherts, cliff (surf)	tz	—	—	—	—	A	—
5. 6.67	coral/rock	1	—	P	P	A	P	—
10. 1.55	on cherts, sandy	½–1½	—	P	—	—	P	—
17. 6.67	on stones	⅓	—	—	—	—	A	—

DESCRIPTIONS OF SPECIES

It is convenient to retain the genus *Spirorbis* despite the large number of species contained in it, but it may be regarded as comprising a number of subgenera (BAILEY, 1969a), of which three are represented in these collections.

Genus **Spirorbis** Daudin, 1800

Serpulids with a spirally coiled, calcareous tube which lies flat against the substratum. There is an operculum and the number of thoracic segments is never more than four or less than three.

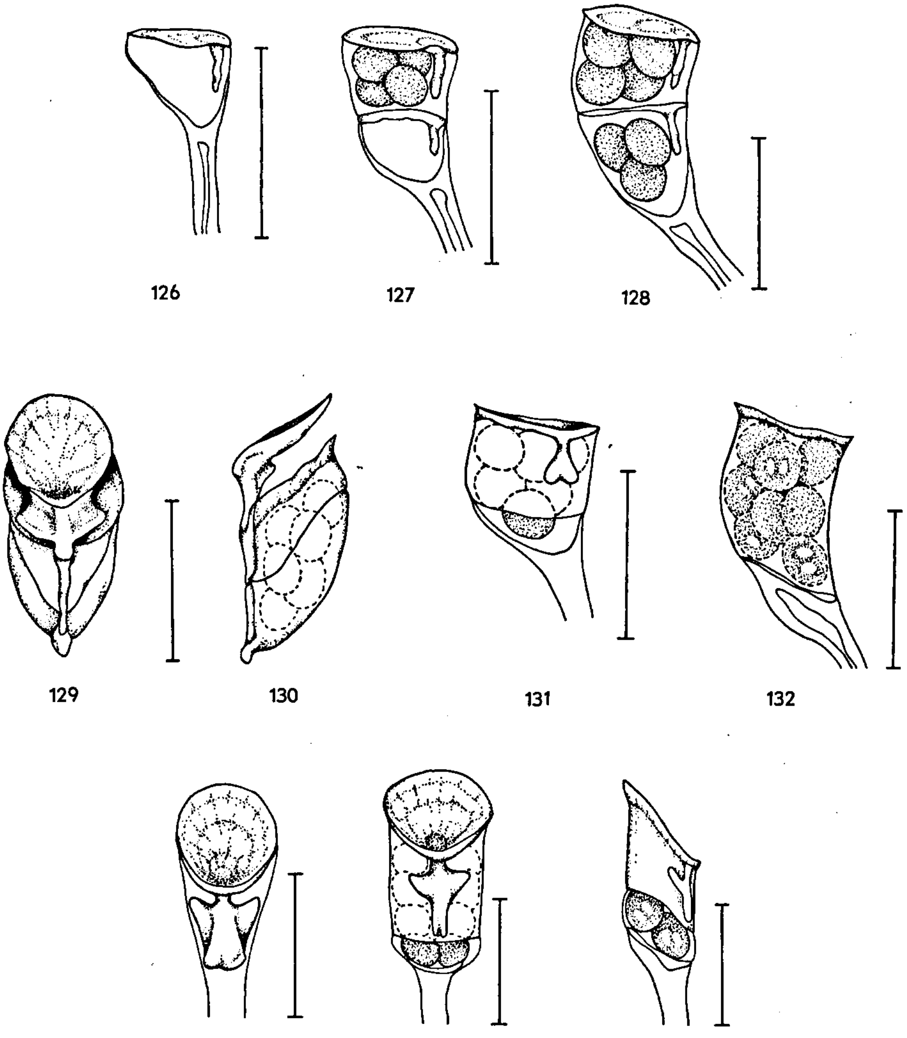
Subgenus **Leodora** Saint-Joseph, 1894

Sinistral coiling; incubation in a opercular brood chamber; three thoracic segments; collar setae without a gap between fin and blade.

1. **Spirorbis (Leodora) knightjonesi** de Silva, 1965

Sinistral, white tube with three well marked longitudinal ridges and faint transverse growth lines. The mouth is round and partially overlaps the last whorl; but may ascend. The diameter across the coil is 1.5 mm.

Opercular incubation in an ampulla, with a flat, distal plate bearing an eccentric peg-talon (Fig. 126–128). Embryos which were fully developed could clearly be seen to have paired thoracic attachment glands (QUIÉVREUX, 1963), like those typical of the subgenus *Janua* (BAILEY, 1969a). Most specimens had a second brood chamber underneath the first one. Some of these contained eggs, which were always at an earlier stage of development than those in the most distal ampulla. The opercular plate of this chamber always possessed a talon and formed the base of the upper chamber.



126 127 128

129 130 131 132

133 134 135

Fig. 126–135. Variations in the operculum of the four species of *Spirorbis* which have been previously described: 126–128, *S.* (*Leodora*) *knightjonesi*; 129–130, *S.* (*Pileolaria*) *koehleri*; 131–132, *S.* (*Janua*) *corrugatus*; 133–135, *S.* (*Janua*) *steueri*. – All scales = 0.25 mm.

The thorax has three thoracic segments with simple collar setae lacking cross striations. The setae of the second and third segments are simple tapered blades.

The abdomen has a long asetigerous region and 6–8 segments with geniculate toothed setae.

It seems likely that the form which AUGENER (1936) studied and identified as *Spirorbis laevis* was really this species. It is very close to *S. laevis*, but differs from it in having multiple brood chambers stacked one above the other, a talon to the opercular plate and a tube that is generally ridged. Some individuals lack these characters and AUGENER had only a few specimens at his disposal. Original material from Curaçao from the collection of P. WAGENAAR HUMMELINCK and labelled *Spirorbis laevis* (1.VIII.1932) by AUGENER, was made available through the kindness of the Hamburg Museum. Those forms have peripheral talons and stacked opercula (Fig. 128 and as described for *S. knightjonesi* by DE SILVA, 1965). The latter constitute a striking character and it seems that DE SILVA was justified in giving the new name, to the form which he found commonly in a coral environment, particularly as the status of *S. laevis* is dubious but rather interesting.

Spirorbis laevis QUATREFAGES (1865) was described from Guéthary, between Biarritz and the Spanish frontier, but was not found off the north coast of Spain by RIOJA (1923). It has been recorded from Roscoff, but it seems that recent investigators have not found it there (L'HARDY & QUIÉVREUX, 1964). CLAPARÈDE (1870) described it from Naples, PIXELL (1913) from the Red Sea, EHLERS (1913) from South Africa, and LAUBIER & PARIS (1962) from Banyuls. In this species the tube may be smooth (France, Naples) or with longitudinal ridges (Red Sea).

The interesting taxonomic position of *Spirorbis laevis* was recently pointed out by ZIBROWIUS (1968). It resembles *Spirorbis pagenstecheri* Quatrefages so closely as to suggest that it may be a sinistral mutant of that dextral and widely distributed form. It seems to have been found sporadically and never abundantly, as might be expected of an abnormal mutant. STERZINGER (1909) and POTSWALD (1967) have recorded *situs inversus* individuals in other species of *Spirorbis*.

S. knightjonesi also resembles *S. pagenstecheri* in the detailed form of the opercular plate and collar setae and, most significantly, in having paired larval attachment glands. These must be regarded as important taxonomically (HÖGLUND, 1951) and their apparent restriction to the two subgenera *Leodora* and *Janua* indicates a close *situs inversus* relationship.

Spirorbis knightjonesi was the most abundant sinistral species and was found on Bonaire, Curaçao, Grenada, Puerto Rico, South Bimini, St. Croix, St. Martin and Tobago. – Distribution elsewhere: Ceylon (DE SILVA, 1965).

Subgenus **Pileolaria** Claparède, 1868-70

Sinistral coiling; incubation in an opercular brood chamber; three thoracic segments; fin and blade collar setae (which may bear cross striations).

2. **Spirorbis (Pileolaria) koehleri** Caullery & Mesnil, 1897

Sinistral, white tube with three well defined longitudinal ridges. Diameter across the coil 1.3–1.5 mm.

The operculum (Fig. 129–130) consists of two or three plates with peripheral talons stacked one above the other. Each interlocks by means of its talon with the plate below. Embryos are incubated below these plates in a calcareous brood sac. The sac hinges with the last-formed (most proximal) talon and eggs can be seen through the transparent walls between the plate and the brood sac (Fig. 130). This structure is exactly like that seen in material from the Mediterranean (BAILEY, 1969).

Three thoracic segments. The collar setae have a proximal fin and a distal toothed blade without cross striations. The second segment has setae with simple blades, whilst the third has some with simple blades and others with recurved hooked blades.

Abdomen with a long asetigerous region and with 10–15 segments, which bear geniculate setae with rounded serrations.

Spirorbis koehleri was found on Curaçao and Puerto Rico. – Distribution elsewhere: La Ciotat, near Marseille (CAULLERY & MESNIL, 1897); Villefranche (ZIBROWIUS, 1968); Chios, Aegean Sea (BAILEY, 1969).

3. **Spirorbis (Pileolaria) quasimilitaris** sp. n.

Sinistral, white tubes, smooth or with three indistinct longitudinal ridges and with a wide, round mouth (Fig. 136). Diameter across the coil 1.5–2 mm.

This species shows opercular dimorphism, but this is less extreme than in *S. militaris* Claparède (ZIBROWIUS, 1967).

The primary operculum consists of a concave plate with a short, slightly eccentric talon (Fig. 137). This is very similar to the primary operculum of *Spirorbis pseudomilitaris* Thiriot-Quiévreux (BAILEY, 1969). Underneath this a domed calcareous brood chamber develops. When fully formed the dome bears two curved rows of distally projecting spines. Calcification of the chamber forms a helmet-shaped structure, as in *Spirorbis militaris* Claparède, and developing embryos with single white attachment glands of the rectal type (QUIÉVREUX, 1963) could be seen through the transparent part of the chamber wall (Fig. 139).

This species agrees with *Spirorbis pseudomilitaris* as far as the primary operculum is concerned, but *S. pseudomilitaris* has a flat-topped chamber with few spines, whereas this species resembles *S. militaris* in being domed with conspicuous spines.

There are three thoracic segments. Collar setae have distal, cross striated blades and proximal fins and are associated with fine capillary setae (Fig. 141–142). The second segment has setae with simple blades (Fig. 143) and the third some with simple blades and others of the recurved hooked type (Fig. 144).

The abdomen has a long asetigerous region and 8–10 segments, which bear geniculate setae with coarse teeth (Fig. 145).

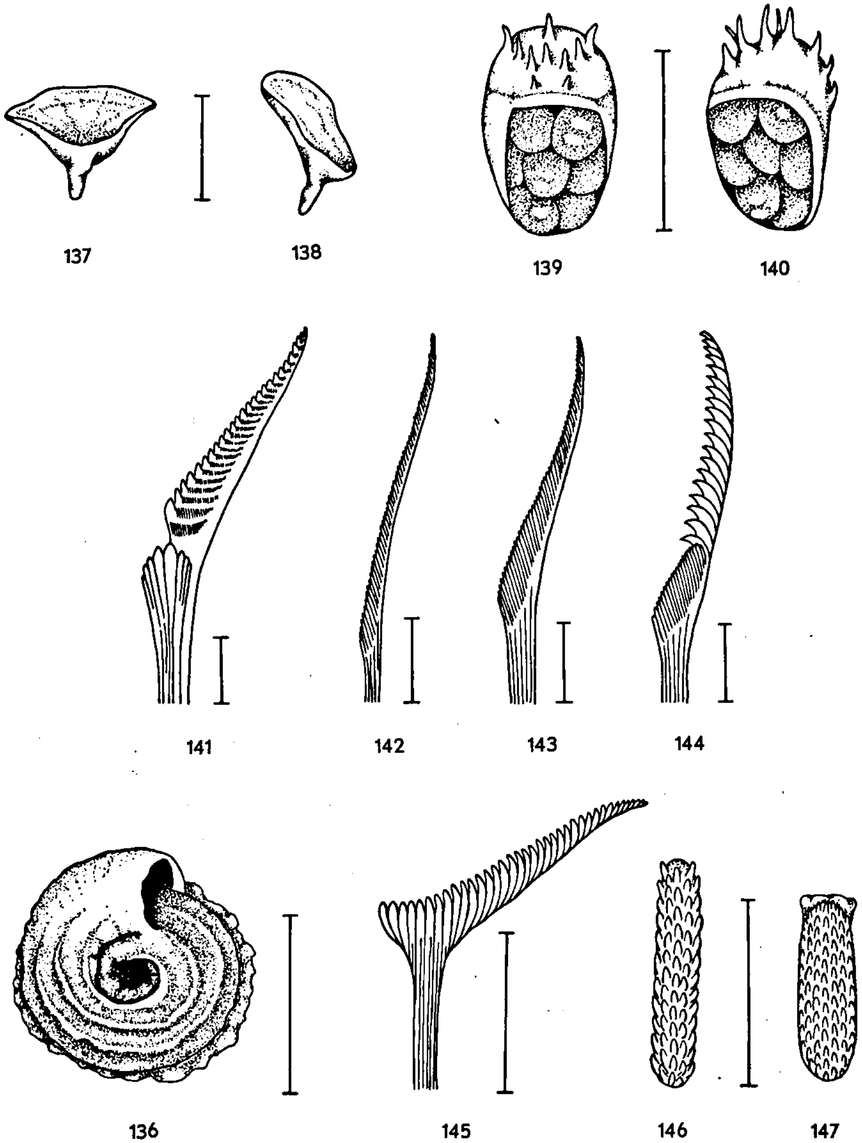


Fig. 136–147. Characters of *Spirorbis* (*Pileolaria*) *quasimilitaris* sp. n. – 136, tube; 137–138, face and side views of primary operculum; 139–140, face and side views of incubatory chamber; 141, collar seta of the first thoracic segment; 142, capillary seta of first thoracic segment; 143, simple seta of second and third thoracic segment; 144, hooked seta of third thoracic segment; 145, abdominal seta; 146, thoracic uncinus; 147, abdominal uncinus. – Scales: 136 = 1 mm; 137–138 = 0.15 mm; 139–140 = 0.25 mm; 141–147 = 0.01 mm.

This species differs from *S. militaris* particularly in the type of primary operculum and the shape of the tube.

Paratypes in B.M. (Nat. Hist.) nos. 1969.484.

Spirorbis quasimilitaris has been collected on Bonaire, Curaçao, Puerto Rico, St. Eustatius, Tobago and Trinidad. – Distribution elsewhere: possibly México, if this may be the species recorded from that country as *S. militaris* by RIOJA (1942).

Subgenus **Janua** Saint-Joseph, 1894

Dextral coiling; incubation in an opercular brood chamber; three thoracic segments; collar setae without a gap between fin and blade, which may or may not bear cross striations.

4. **Spirorbis (Janua) corrugatus** Caullery & Mesnil, 1897

Dextral, white tube with three well marked longitudinal ridges. Round mouth which may partially overlap the previous whorl. Diameter across the coil 1–1.5 mm.

The primary operculum is a slightly concave opercular plate with a peripheral talon, which is characteristically bilobed. This forms the top of a cylindrical brood chamber which develops underneath (Fig. 131). The walls are of transparent calcareous material and a basal plate is present when the operculum is full of eggs (Fig. 132). This forms the next opercular plate and lacks a talon.

There are three thoracic segments. The collar setae are simple blades, those on the convex side being cross striated and larger than those on the concave side, which lack cross striations. The setae of the second and third segments are simple blades.

The abdomen consists of 8–10 segments, bearing geniculate setae with small teeth.

The embryos each have a pair of white attachment glands.

Spirorbis corrugatus is known from Aruba, Barbuda, Bonaire, Curaçao, Florida, Grenada, La Fourche, North Bimini, Puerto Rico, St. Eustatius and Tobago. – Distribution elsewhere: English Channel, Madeira and Naples (CAULLERY & MESNIL, 1897); Adriatic (STERZINGER, 1910); Galicia, N.W. Spain (RIOJA, 1923); Roscoff (L'HARDY & QUIÉVREUX, 1964); Aegean (BAILEY, 1969); closely related or identical forms are known from South Africa, the East Indies and Philippines (ZIBROWIUS, 1968).

5. **Spirorbis (Janua) epichysis** sp. n.

Dextral, white tube with three longitudinal ridges and often a peripheral flange which increases the area of attachment to the substratum. The mouth is round and may partially overlap the previous whorl (Fig. 148). Diameter across the coil 1–1.5 mm.

The opercula show many variations according to the size and breeding condition of the specimens.

The primary plates are flat or slightly convex with a peripheral peg talon (Fig. 149). Some stages were found which lacked the talon revealing an empty ampulla (Fig. 150).

The brood chamber develops below this plate and many intermediate stages were observed about to shed the primary plate (Fig. 151). The plate forming the top of the brood chamber is convex with a distal almost circular rim which projects on the concave side to form an extension like the spout of a jug. In more mature forms this projection from the rim is less obvious; but both types contained developing embryos (Fig. 152).

There are three thoracic segments. The collar setae (Fig. 153) are simple toothed blades without cross striations or any distinction between fin and blade (like that seen in *S. pagenstecheri*). Setae of the second segment are simple (Fig. 155) whilst those of the third are of two types, one simple, and the other with recurved hooked blades (Fig. 156).

The abdomen has 6–8 segments with setae typical of the subgenus *Janua* (Fig. 157).

Each fully developed embryo has a pair of white attachment glands.

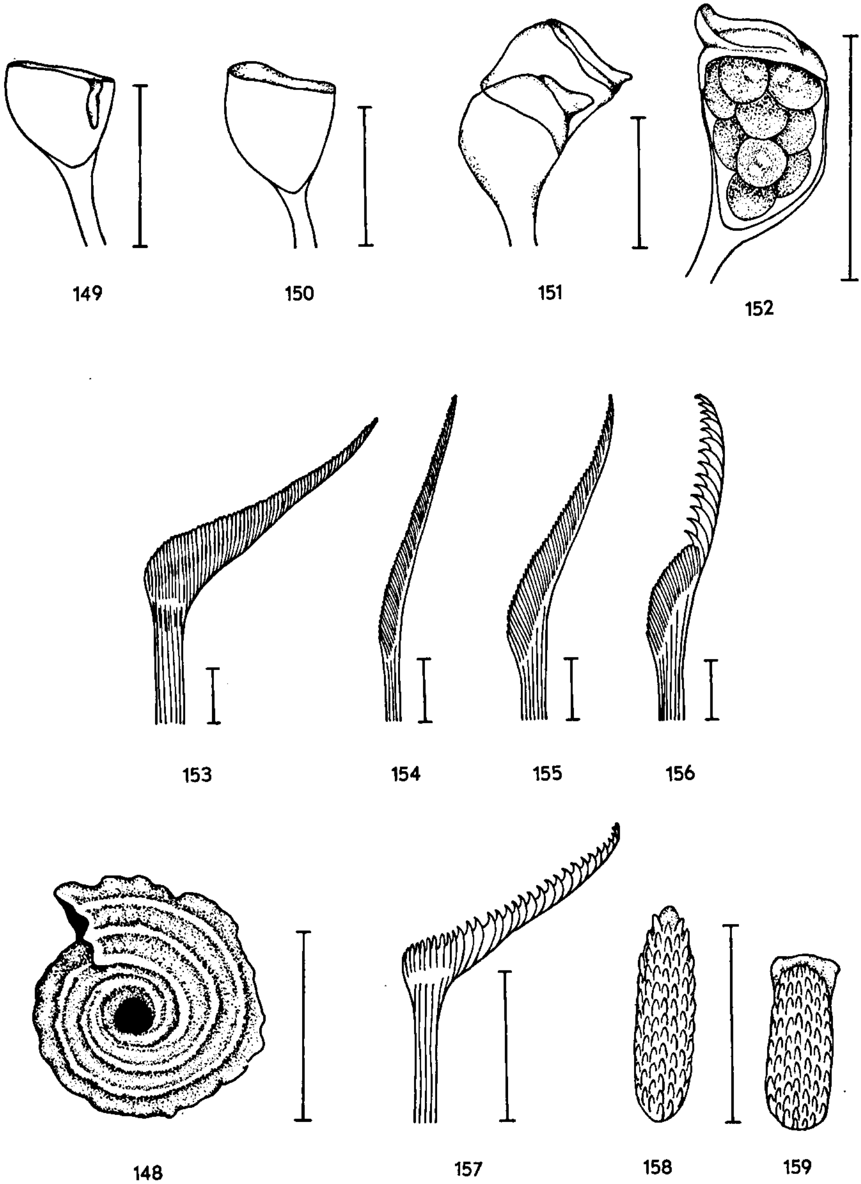


Fig. 148–159. Characters of *Spirorbis* (*Janua*) *epichysis* sp. n. – 148, tube; 149, primary operculum; 150, primary operculum without a talon; 151, intermediate stage in opercular moult; 152, mature brood chamber with embryos; 153, collar seta of first thoracic segment; 154, capillary seta of first thoracic segment; 155, simple seta of second and third thoracic segments; 156, hooked seta of third thoracic segment; 157, abdominal seta; 158, thoracic uncinus; 159, abdominal uncinus. – Scales: 148 = 1 mm; 149–151 = 0.2 mm; 152 = 0.25 mm; 153–159 = 0.01 mm.

Paratypes in British Museum (N.H.) nos. 1969.485.

Spirorbis epichysis was found on Bonaire, Curaçao, La Fourche, Puerto Rico, St. Kitts, St. Martin, Tobago and Trinidad.

6. **Spirorbis (Janua) steueri** Sterzinger, 1909

Dextral, white tube with three well marked longitudinal ridges and transverse growth lines. There is a flange against the substratum and the mouth may partially overlap the previous whorl. Diameter across the coil 1.2–1.5 mm.

The primary operculum consists of a slightly concave plate with an eccentric talon. The talon is quite large and has two lateral wings or lobes (Fig. 133). It unites with the calcareous thickening ot the ampulla wall to form the brood chamber, but is comparatively opaque, so remains easily distinguishable from the rest of the chamber wall. The wall extends only two-thirds of the way down the chamber and the embryos and basal plate can be seen clearly below (Fig. 134–135). Each larva has a pair of white attachment glands.

There are three thoracic segments. The collar setae are simple blades, those on the convex side being cross-striated and larger than those on the concave, which lack cross-striations. Setae of the second and third segments are simple blades.

The abdomen has a long asetigerous region and 6–8 segments bearing geniculate setae with small teeth.

Spirorbis steueri was collected on Barbuda, Bonaire, Curaçao, Islote Aves, La Fourche and Puerto Rico. – Distribution elsewhere: Suez canal (STERZINGER, 1909); probably Bermudas (some figured from these islands as *Spirorbis formosus* by BUSH, 1904, are probably this species, but the description was inadequate).

ZOOGEOGRAPHICAL CONSIDERATIONS

Of the six species of *Spirorbis* recorded here, *S. quasimilitaris* and *S. epichysis* are otherwise unknown, *S. corrugatus* has been recorded from S.W. Europe and the Mediterranean, and the records for *S. koehleri*, *S. steueri* and *S. knightjonesi* are restricted to the Mediterranean, Suez Canal and Ceylon respectively. The species described by DE SILVA (1965) from Ceylon, *S. knightjonesi*, is closely related to *S. laevis*, which was recorded by AUGENER (1936) from the West Indies and is otherwise known from S.W. Europe. CLAPARÈDE (1870) and ZIBROWIUS (1968) give full descriptions of this form, but further study of its status is still needed. It may be either (i) a distinct species, (ii) a coldwater variant of *S. knightjonesi* or (iii) a *situs inversus* mutant *S. pagenstecheri*.

Since the West Indies Spirorbinae thus have quite strong faunistic links with fairly remote sea areas to the east of the region, it is remarkable that they are so different from those on the other side of the isthmus of Panamá. RIOJA (1942, 1962) recorded from west México two species of the subgenus *Spirorbis* (= *Laeospira*), five of *Pileolaria*, one of *Circeis*, three of *Dexiospira* (= *Spirorbella*), one of *Janua* and one of *Marsipospira* (= part of *Paralaeospira* – see BAILEY, 1969a). None of his forms seem to be represented in the West Indies except possibly one which he called *Spirorbis* (*Pileolaria*) *militaris*. That species may be the same as *Spirorbis* (*Pileolaria*) *quasimilitaris*, described here for the first time. It is unlikely that the west Mexican form is in fact *S. militaris* Claparède, for that European species has a remarkable opercular dimorphism, or polymorphism (ZIBROWIUS, 1967; BAILEY, 1969), which has led to the immature individuals being described as distinct and very distinctive species, *S. beneti* and *S. cornuarietis*. If such individuals had occurred in RIOJA's collections, they would scarcely have escaped his notice, but he did not record them. This leads to the conclusion that the west Mexican species is probably not *S. militaris* and deserves further study. With that possible exception, these records reveal no species links between the West Indies and the eastern Pacific.1)

This situation is parallelled in other taxonomic groups and so is

---

1) Drs. H. A. TEN HOVE finds that West Indies Serpulinae, in contrast, have species links with the tropical Pacific side of America which are quite strong, stronger than with the Indian Ocean. These forms may be expected to be more conservative than the Spirorbinae and it seems that the species concerned are probably older than the Pliocene and not restricted to regions dominated by corals.

the link recorded here between the West Indies and Ceylon, which is not shared by west México. EKMAN (1967) writes "The warmwater fauna of Pacific America actually shows a somewhat weaker connection with the Indo-Pacific than does that of Atlantic America". The groups involved, in the link between West and East Indies, include certain Gorgonaria, Holothuria, Crinoidea, decapod crustaceans, Xiphosura, molluscs and ascidians. Various species or twin species of these occur both in the West Indies and off south-eastern Asia or in the Indian Ocean, but not on the west coast of America. "This is doubtless due to the fact that both the West Indian and the Indo-West-Pacific fauna were formerly parts of the same original fauna, namely that of the Tethys Sea". Very few species are common to both sides of the isthmus of Panamá and those that have such a distribution are regarded by EKMAN as very ancient species. The last marine link across the isthmus seems to have been in the lower Pliocene. Since then this land barrier has existed without interruption (EKMAN, 1967, p. 37). Species links between the West Indies and the Mediterranean could probably have been maintained through transport on flotsam, for Spirorbinae are often found attached to floating materials such as *Sargassum* (ALLEE & SCHMIDT, 1951) and small ships (BAILEY, 1969). Spirorbinae would appear to be particularly well adapted for (i) ocean transport and (ii) subsequent colonisation of new areas because (i) they are small and (ii) they are capable of self-fertilisation (GEE & WILLIAMS, 1965) and have larvae which swim only briefly and settle gregariously (KNIGHT-JONES, 1951).

A species link between Europe and Ceylon could have been maintained or established by transport around Africa on old sailing vessels. The Portuguese oyster was probably introduced to Europe in that way (NAYLOR, 1957). In this indirect fashion, the link with Ceylon may be accounted for. It is in fact rather unrealistic to ascribe it to the Sea of Tethys, because the marine connection between the Mediterranean and Indian Ocean is said to have been severed finally in the Miocene (RUGGIERI, 1967). For the spreading of littoral animals, however, the route round South Africa (minimum water temperature about 15°) was no doubt easier than that round Cape Horn (6°) or the Aleutians (3°). Intershore distances are generally less in the Old World than in the Pacific and were presumably still less at earlier stages of continental drift. Given rates of evolution sufficient to ensure that few species have remained unchanged since the early Pliocene, the zoogeographical picture that emerges seems quite acceptable. The warm-temperate shores of the western Atlantic have maintained some faunistic unity with those of the Old World, but the warm-temperate coastal fauna of this immense region has been cut off from that of the east Pacific, on the one hand by the complete barrier of the American continents, on the other by the immense expanse of the Pacific Ocean itself.

The fact that all the species recorded here have opercular incubation is remarkable and must be physiologically significant. This method of brood protection presumably helps respiration of the embryos and it may therefore be regarded as an adaptation to warm conditions with little water movement. The proportion of *Spirorbis* species showing it tends to fall off in higher latitudes (BAILEY, 1969) and appears to be zero in Patagonia (CAULLERY & MESNIL, 1897), which suggests that rough conditions favour the alternative methods of incubation within the protection of the parent's tube. It is interesting to consider, however, why only 50% of *Spirorbis* species from west México have opercular incubation, in spite of the fact that the water temperatures there are similar to those of the West Indies, whilst the Gulf of California provides sheltered conditions.

This difference in the proportion of species with opercular incubation, between the two sides of the isthmus of Panamá, may stem from the fact that the American west coasts in general are mostly more open and exposed than those of the Caribbean, Mediterranean and Indo-Pacific, whilst the length of coastline with high water temperatures is comparatively short, because of the cold currents from the north and south. The east Pacific has therefore only compact and restricted littoral areas of the kind that would be expected to favour opercular incubation in Spirorbinae. The West Indies would appear to be quite different in this respect, but it seems likely that some tube-incubatory Spirorbinae may be found there, if more samples are taken from deeper water. *Spirorbis spirillum*, for instance, is known from the Gulf of Mexico (HARTMAN, 1951; RENAUD, 1956; RIOJA, 1959).

SUMMARY

Six species of *Spirorbis* were recorded from seventeen islands in the Caribbean. All are opercular incubators. Two, *S.* (*Pileolaria*) *quasimilitaris* and *S.* (*Janua*) *epichysis*, were new and two others, *S.* (*P.*) *koehleri* and *S.* (*J.*) *steueri*, were previ-

ously recorded only from the Mediterranean, the latter only from Suez. The most abundant species were S. (*J.*) *corrugatus* and S. (*Leodora*) *knightjonesi*, of which the latter was previously known only from Ceylon, but is closely related to the European species S. (*L.*) *laevis*. – The zoogeographical picture shows isolation from the Pacific, as there are no species links with W. México or the Galápagos. It seems that evolution of species has been active since the early Pliocene and that transport has occurred readily along warm-temperate coastlines and across the Atlantic, perhaps on flotsam with the trade winds.

REFERENCES

ALLEE, W. C. & SCHMIDT, K. P., 1951. *Ecological animal geography*. 2nd ed. John Wiley: New York.

AUGENER, H., 1922. Ueber litorale Polychaeten von Westindien. *Sitz. ber. Ges. Naturf. Freunde Berlin 1922*: 38–53.

AUGENER, H., 1936. Polychaeten aus den marinen Salinen von Bonaire und Curaçao. *Zool. Jahrb.* (*Syst.*) *67*: 338–352.

BAILEY, J. H., 1969. Spirorbinae (Polychaeta: Serpulidae) from Chios (Aegean Sea). *Zool. J. Linn. Soc. 48*: 363–385.

BAILEY, J. H., 1969a. Methods of brood protection as a basis for reclassification of the Spirorbinae (Serpulidae). *Zool. J. Linn. Soc. 48*: 387–407.

BAILEY, J. H. & HARRIS, M. P., 1968. Spirorbinae (Polychaeta: Serpulidae) of the Galapagos Islands. *J. Zool. Lond. 155*: 161–184.

BUSH, K. J., 1904. Tubicolous annelids of the tribes Sabellides and Serpulides from the Pacific Ocean. *Harriman Alaska Exped. 12*: 169–355.

BUSH, K. J., 1910. Descriptions of new serpulids from Bermuda with notes on known forms from adjacent regions. *Proc. Acad. nat. Sci. Philad. 62*: 490–501.

CAULLERY, M. & MESNIL, F., 1897. Études sur la morphologie comparée et la phylogénie des espèces chez les Spirorbes. *Bull. Soc. Sci. Fr. Belg. 30*: 185–233.

CLAPARÈDE, E., 1868–70. Les Annélides Chétopodes du Golfe de Naples. Tiré des *Mém. Soc. Phys. Hist. Nat. Genève 19 & 20*. H. Georg, Genève & Bâle, 500 pp.

CLAPARÈDE, E., 1870. Les Annélides Chétopodes du Golfe de Naples (Supplement). *Mém. Soc. Phys. Hist. nat. Genève 20*: 365–542.

DAUDIN, F. M., 1800. *Recueil de mémoires et de notes sur les espèces inédites ou peu connues de Mollusques, de Vers et de Zoophytes*. Paris.

DE SILVA, P. H. D. H., 1961. Contribution to the knowledge of the polychaete fauna of Ceylon. Part I. *Spolia Zeylanica 29*: 164–194.

DE SILVA, P. H. D. H., 1965. New species and records of Polychaeta from Ceylon. *Proc. Zool. Soc. London 144*: 463–560.

EHLERS, E., 1913. Die Polychaeten-Sammlungen der deutschen Südpolar-Expedition. *Dt. Südpol-Exped. 13*: 397–598.

EKMAN, S., 1967. *Zoogeography of the sea*. Sidgwick & Jackson: London.

GEE, J. M. & WILLIAMS, G. B., 1965. Self and cross-fertilisation in Spirorbis borealis and S. pagenstecheri. *J. mar. biol. Ass. U.K., 45*: 275–285.

HARTMAN, O., 1951. The littoral marine annelids of the Gulf of Mexico. *Publ. Mar. Inst. Sci. Univ. Texas 2*: 7–124.

HÖGLUND, L. B., 1951. Notes of the morphology and biology of some Spirorbis larvae. *Zool. Bidr. Uppsala, 29*: 261–275.

KNIGHT-JONES, E. W., 1951. Gregariousness and some other aspects of the setting behaviour of Spirorbis. *J. mar. biol. Ass. U.K., 30*: 201–222.

LAUBIER, L. & PARIS, J., 1962. Faune marine des Pyrénées Orientales. IV. Annélides Polychètes. *Vie Milieu 13 (Suppl.)*: 1–80.

L'HARDY, J.-P. & QUIÉVREUX, C., 1964. Observations sur Spirorbis (Laeospira) inornatus et sur le systématique des Spirorbinae. *Cah. Biol. mar. 5*: 287–294.

NAYLOR, E., 1957. Immigrant marine animals in Great Britain. *New Scientist 2* (50): 21–23.

PILLAI, T. G., 1960. Some marine and brackish-water serpulid Polychaeta from Ceylon, including new genera and species. *Ceylon J. Sci. (Bio. Sci.) 3*: 1–40.

PIXELL, H. L. M., 1913. Polychaeta of the Indian Ocean, together with some species from the Cape Verde Islands. The Serpulidae. *Trans. Linn. Soc. Lond. (2) 16*: 69–92.

POTSWALD, H. E., 1967. Observations on the genital segments of Spirorbis (Polychaeta). *Biol. Bull. 132*, 91–107.

QUATREFAGES, M. A. DE, 1865. *Histoire naturelle des Annélides marins et d'eau douce. Annélides et Géphyriens, 2*. Roret: Paris.

QUIÉVREUX, C., 1963. Sécrétion tubipare des larves de Spirorbinae (Annélides Polychètes). *Cah. Biol. mar. 4*: 399–406.

RENAUD, J. C., 1956. A report on some Polychaetous Annelids from the Miami-Bimini area. *Amer. Mus. Novit. 1812*: 1–40.

RIOJA, E., 1923. Estudio sistemático de las especies ibéricas del suborden Sabelliformia. *Trab. Mus. nac. Cien. nat. Madr. (Zool.) 48*: 1–143.

RIOJA, E., 1942. Estudios anelidológicos V. Observaciones acerca de algunos especies del género Spirorbis Daudin, de las costas Mexicanas del Pacífico. *An. Inst. Biol. Méx. 13* (1): 137–153.

RIOJA, E., 1959. Estudios anelidológicos XXII. Datos para el conocimiento de la fauna de anélidos poliquetos de las costas orientales de México. *An. Inst. Biol. Méx. 29*: 219–301.

RIOJA, E., 1962 (publ. 1963). Estudios anelidológicos XXVI. Algunos anélidos poliquetos de las costas del Pacífico de México. *An. Inst. Biol. Méx. 33*:131–229.

RUGGIERI, G., 1967. The Miocene and later evolution of the Mediterranean Sea. In: *Systematics Association Publication 7, Aspects of Tethyan Biogeography*: 283–290.

SAINT-JOSEPH, Le Baron de, 1894. Les annélides polychètes des côtes de Dinard. III. *Ann. Sci. nat. Zool.* (7) *17*: 1–395.

STERZINGER, I., 1909. Einige neue Spirorbis – Arten aus Suez. *Sitz.ber. Akad. Wiss. Wien, Math.-Naturw. 118* (1): 1441–1459.

STERZINGER, I., 1910. Über die Spirorbis – Arten der nordlichen Adria. *Abh. zool.-bot. Ges. Wien 5* (1): 1–13.

ZIBROWIUS, H., 1967. Dimorphisme operculaire et variabilité chez Spirorbis (Laeospira) militaris (Claparède) 1870. *Thalassia Salentina 2*: 138–146.

ZIBROWIUS, H., 1968. Étude morphologique, systématique et écologique des Serpulidae (Annelida, Polychaeta) de la région de Marseille. *Rec. Trav. Stat. Mar. Endoume, Bull. 43* (59): 81–252.