

Spirorbinae (Polychaeta, Serpulidae) of the Hawaiian Chain

Part 2, Hawaiian Spirorbinae¹

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NO TAXONOMIC STUDY of tubeworms in the subfamily Spirorbinae has been made previously in Hawaii except for a recent description of three new species (Vine, 1972). This second paper deals with 10 other species, previously described from elsewhere, which were collected around Oahu and Hawaii.

Collections have been made by each of the authors and preliminary studies were made independently. Settlement plates have been used by two of us (Bailey-Brock and Straughan) and it was found that several species settled very readily on these. Most of the collections were littoral or from shallow water and it is likely that other species will be found at greater depths.

The descriptions and drawings presented here are the work of one of us (Vine) although each author has contributed to the ecological data.

Spirorbinae were usually removed from their substrates by slicing them off with a sharp scalpel and were then preserved in 5 percent sea-

water formalin or 70 percent ethyl alcohol. It was found that those preserved in formalin were easier to study in detail than the others, which soon became hardened and colorless. Details of setation were studied in polyvinyl-lactophenol mounts, with the phase microscope, using quartz-iodide illumination. The presence of dorsally fused collar folds in some species was confirmed by probing with an eyelash (Knight-Jones, 1972).

SPECIES ENCOUNTERED

Taxonomy of Spirorbinae has been recently reviewed by Gee (1964), Bailey (1969b), and Pillai (1970). Important advances are now being made, however (Knight-Jones, 1972, in press; Vine, in press), and the arrangement used here follows that adopted by Phyllis Knight-Jones (1972), which represents a slight modification of that proposed by Bailey (1969b).

KEY TO SPECIES OBSERVED

1. Eggs incubated in tube 2
Eggs incubated in operculum 3
2. Tube dextral (mouth faces anticlockwise) ... *Spirorbis* (*Spirorbella*) *marioni* (p. 151)
Tube sinistral (mouth faces clockwise) *Protolaeospira* species *A* (p. 155)
3. Collar setae have a distinct fin and blade (tubes all sinistral) 4
Collar setae lack a distinct proximal fin (all except one are dextral) 7
4. Operculum has spines 5
Operculum without spines 6
5. Sickie setae present in third thoracic fascicle
Tube lacks longitudinal ridges *Pileolaria* (*Pileolaria*) *militaris* (p. 157)
Tube has three longitudinal ridges *Pileolaria* (*Pileolaria*) *semimilitaris* (p. 140)

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- Sickle setae absent from third thoracic fascicle
 *Pileolaria (Simplicaria) pseudomilitaris* (p. 158)
6. Tube has two or three irregular longitudinal ridges
 *Pileolaria (Duplicaria) koebleri* (p. 161)
- Tube has four narrow longitudinal ridges
 *Pileolaria (Duplicaria) dalestraughani* (p. 143)
7. Tube dextral (mouth faces anticlockwise) 8
 Tube sinistral (mouth faces clockwise) 11
8. Tube has three longitudinal ridges and lacks any other distinctive pattern
 *Janua (Janua) pagenstecheri* (p. 163)
- Tube has transverse as well as longitudinal ridges 9
9. Collar setae are not cross-striated 10
 Collar setae are cross-striated
- Operculum has transparent walls and short spade-shaped talon
 *Janua (Dexiospira) pseudocorrugata* (p. 166)
- Operculum has calcified walls and bifid talon with lateral wings
 *Janua (Dexiospira) steueri* (p. 168)
- Operculum has transparent walls and long, asymmetrical, pointed talon
 *Janua (Dexiospira) turrita* (p. 145)
10. Operculum has transparent walls and a short spade-shaped talon; thoracic uncini have
 trifurcate anterior pegs *Janua (Dexiospira) nipponica* (p. 170)
11. Opercular chambers may be stacked and each one has a short talon
 *Janua (Leodora) knightjonesi* (p. 172)

Genus *Spirorbis* Daudin, 1800 (amended)

The genus is described as follows: coiling usually sinistral; thorax with two pairs of tori; collar folds normally unfused; collar setae with basal fin and distal blade which may be cross-striated; sickle setae present in third fascicles; thoracic uncini with several longitudinal rows of teeth and broad anterior pegs; abdominal tori without any marked bilateral asymmetry; abdominal setae smaller than collar setae; embryos incubated in an egg string attached posteriorly to the tube; larvae usually have a single attachment gland.

Type

Spirorbis spirorbis (Linnaeus) = *S. borealis* Daudin.

Subgenus *Spirorbella* (Chamberlin, 1919)

This subgenus may be described as above, except that it is coiled dextrally.

Type

Spirorbis (Spirorbella) marioni (Caullery & Mesnil, 1897).

The genus *Spirorbella* was originally separated by Chamberlin and has recently been recognized by Pillai (1970). Here it is given subgeneric status as the only feature dividing it from the subgenus *Spirorbis* is its direction of coiling (and, in certain Spirorbinae, this may vary, even within the same species; see Bailey, 1969b, and Vine, in press).

Spirorbis (Spirorbella) marioni
 Caullery & Mesnil

Fig. 1, 2a, 3a

Material

Twenty-four specimens.

Location

Nanakuli, Oahu, Hawaii.

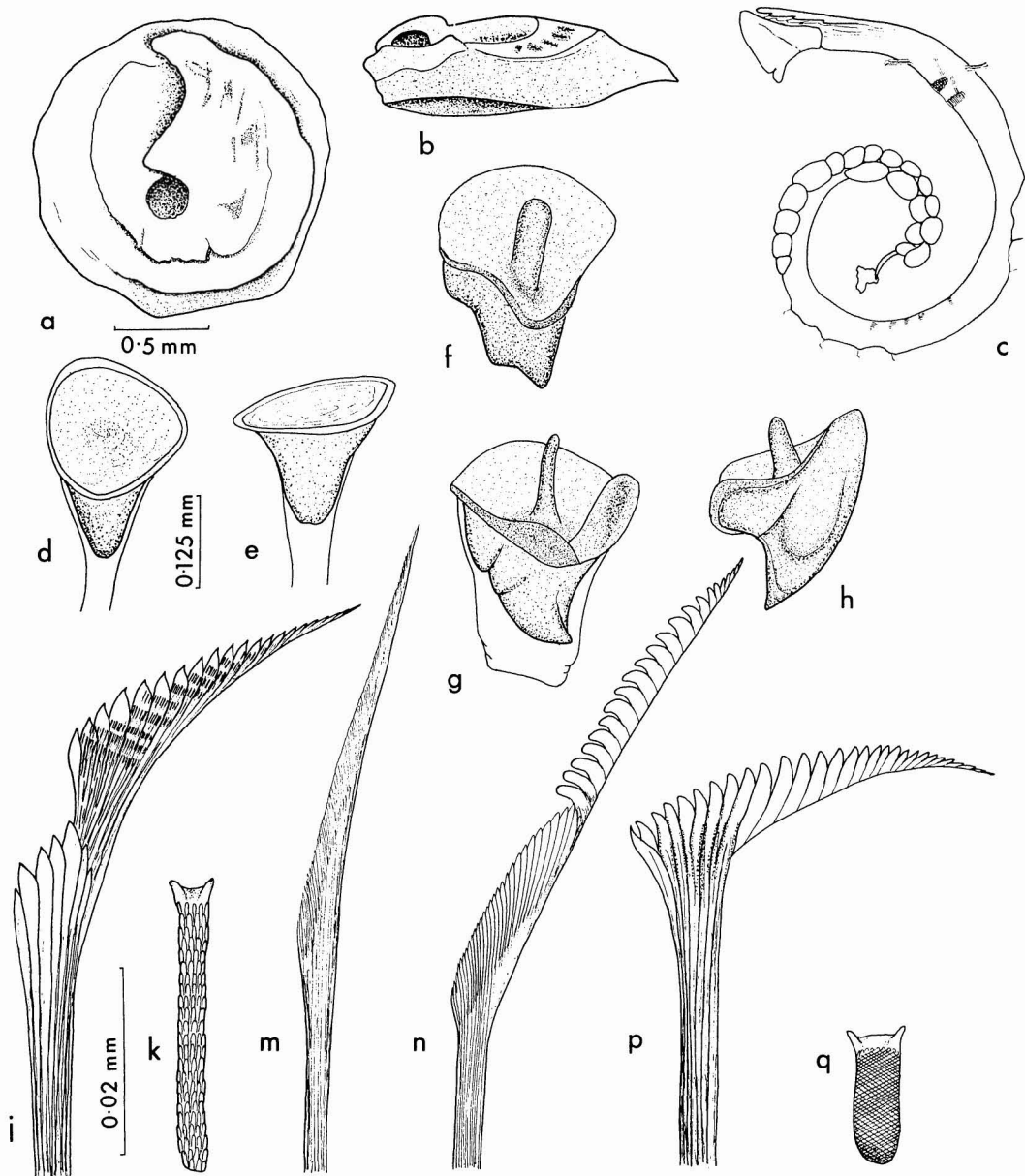


FIG. 1. *Spirorbis* (*Spirorbella*) *marioni*. *a*, Tube viewed from above; *b*, side view of tube; *c*, dorsal view of whole animal showing eggstring attached posteriorly to a fragment of the tube (the specimen was hardened and collar folds could not be distinguished); *d*, dorsal view of juvenile operculum; *e*, side view of juvenile operculum; *f*, later stage of operculum; *g*, dorsal view of fully developed operculum; *h*, side view of fully developed operculum; *i*, collar seta; *j*, thoracic uncinus; *k*, thoracic uncinus; *m*, simple seta from third thoracic fascicle; *o*, abdominal seta; *p*, abdominal uncinus; *q*, abdominal uncinus.

SCALE: *b* and *c* as *a*; *e*, *f*, *g*, and *h* as *d*; *k*, *m*, *n*, *o*, and *p* as *j*.

Habitat

The species is found in the intertidal zone on igneous rocks.

Description of Species

TUBE: Tube is dextral and characteristically flattened against the substrate. An outer longitudinal ridge demarcates the indented flat top from the oblique sides. It is tightly coiled with the terminal portion and mouth overlapping the previous whorl, making the tube almost round when viewed from above. In adult specimens two whorls can be seen on the underside of the tube (Fig. 1a). Coil diameter is 1.5 to 2.0 mm.

OPERCULUM: As Berkeley and Berkeley (1941) have commented, the operculum has a variable structure. In the past this has given rise to descriptions of three separate species: *S. marioni* Caullery & Mesnil, 1897; *S. bushi* Rioja, 1942; and *S. tricornigerus* Rioja, 1942. Study of opercula of *S. marioni* collected in Hawaii shows that, as they grow, they develop an increasingly complex structure. The plate and talon are always lightly calcified and more or less transparent. The earliest operculum (Figs. 1d, e) has a slightly concave plate and a massive cone-shaped talon. At this stage the operculum is reminiscent of an ice-cream cone with the dome licked off. The next stage is for the concavity to deepen, whilst a central peg develops from the plate and a slight depression appears on the dorsal edge of the plate (Fig. 1f). Finally, the edge of the plate thickens on each side of this depression (Fig. 1g).

THORAX: The thorax has two pairs of tori. The dorsal folds of the collar do not appear to be fused, but the specimens are hardened and the collar is difficult to distinguish. Collar setae have rather broad blades with coarse, pointed teeth and fine cross-striations. A proximal fin has several large teeth centrally and smaller teeth on each side of these. Capillary setae are associated with the collar setae on the convex side. The second and third fascicles have simple, finely serrated setae and the third fascicles also have sickle setae. The blades of the latter have their proximal and distal portions about equal in length. Uncini have fine teeth arranged

in approximately four longitudinal rows and many transverse rows, which are unusual in being mostly perpendicular to the long axis. Each uncinus has a broad peg at the anterior end, which appears bifid.

ASETIGEROUS REGION: This is long, being approximately equivalent to eight times the distance between the first two abdominal tori.

ABDOMEN: This structure has approximately nine segments and the largest tori are toward the middle segments of the abdomen. Setae are geniculate with blunt-ended teeth; they appear to have a fan of more pointed teeth, but stereo-microscope study shows that this effect is due to sculpturing of the gaps between the larger teeth (Phyllis Knight-Jones, personal communication). The first tooth of the blade is recurved and prominent. Some fascicles contain paired setae. Uncini have approximately nine longitudinal rows of fine teeth (illustrated by cross-hatching in Fig. 1p) and an apparently bifid anterior end similar to that of the thoracic uncini.

INCUBATION: Incubation occurs in an egg string attached posteriorly to the tube (Fig. 1c).

Distribution Elsewhere

Species has been found in Panama (Caullery and Mesnil, 1897); Mexico (Rioja, 1942); Galápagos (Bailey and Harris, 1968); southern California (Berkeley and Berkeley, 1941).

Remarks

Specimens intermixed on the same substrate and having similar tubes and setation showed enough opercular variation to indicate clearly that the two species described by Rioja (1942) as *S. bushi* and *S. tricornigerus* are the same as *S. marioni*. In having cross-striated collar setae and thoracic uncini with straight transverse rows of teeth, this species resembles *Spirorbis* (*Spirorbis*) *cuneatus* Gee, but differs from most species of *Spirorbis sensu stricto*. This arrangement of teeth is indeed very unusual amongst Spirorbinae in general (Phyllis Knight-Jones, personal communication).

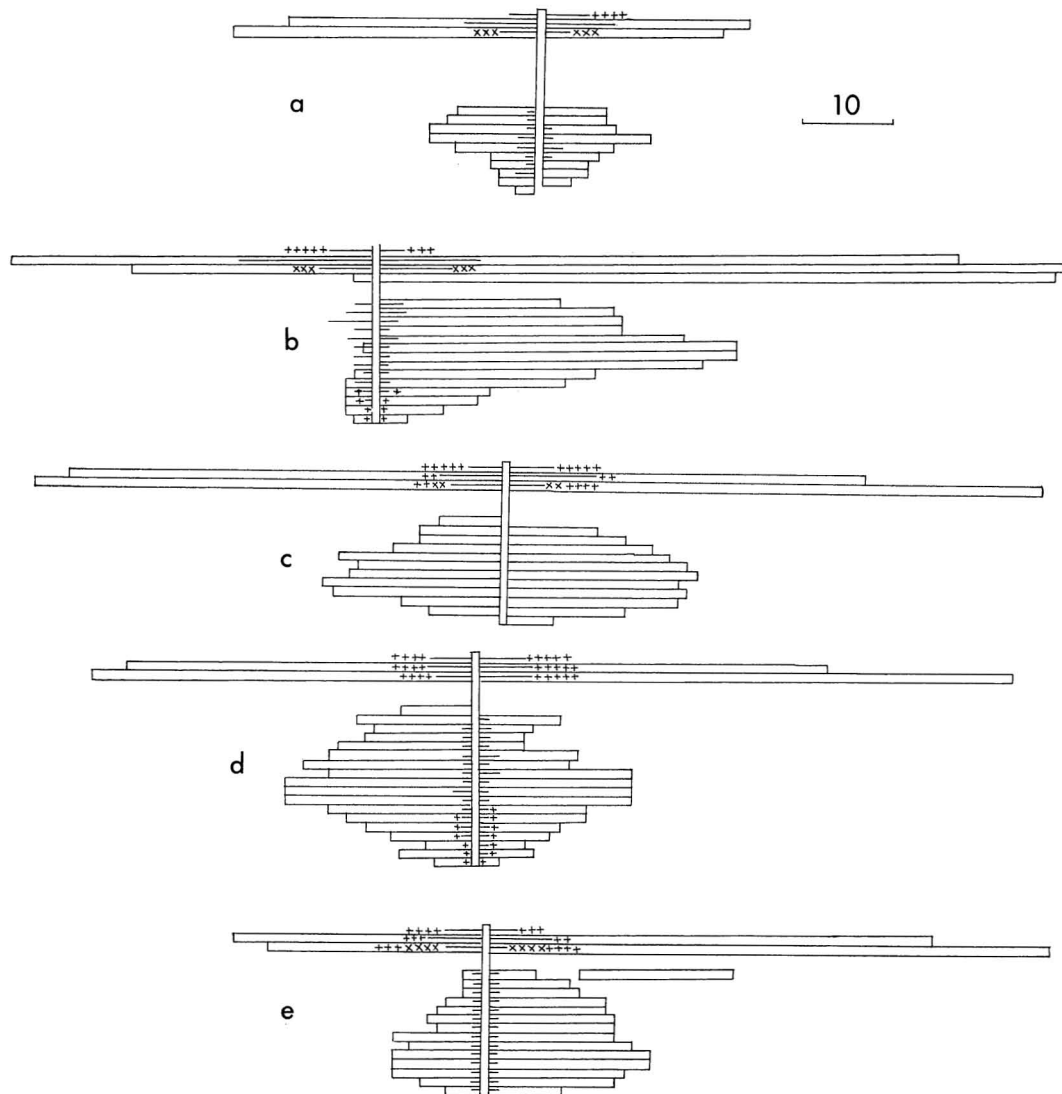


FIG. 2. Chart showing distribution of setae and uncini in: *a*, *Spirorbis* (*Spirorbella*) *marioni*; *b*, *Protolaeospira* sp. *A*; *c*, *Pileolaria* (*Pileolaria*) *militaris* (abdominal setae could not be counted on the single slide of this species); *d*, *Pileolaria* (*Simplicaria*) *pseudomilitaris*; *e*, *Pileolaria* (*Duplicaria*) *koebleri*.

The histograms indicate the number of uncini per torus on the concave and convex sides of the animal. Continuous lines within these indicate the number of setae in each fascicle and symbols represent various kinds of ancillary setae, viz.:

- + = long thoracic capillaries and shorter abdominal capillaries or hooked setae
- X = sickle setae
- * = secondary setae with rudimentary shafts

Species are shown as they appear *in situ*. Thus, in sinistral species the concave side is on the reader's right, whereas in dextral ones the concave side is on the reader's left.

The length of the asetigerous region is represented as a multiple of the distance between the first and second abdominal tori on the concave side. The distance between tori on the histograms is standardized and, thus, the histograms do not necessarily give a true indication of the length of the asetigerous region in relation to that of the whole animal. In some species the anterior abdominal tori are themselves unusually far apart and this will result in the asetigerous region appearing relatively shorter in the histogram.

The figures represent single typical specimens but, where sufficient material was available, three counts were made of each species and the variations were small. The exact distribution of paired setae and capillary setae in the abdomen was not constant. Generally speaking, it is the overall pattern of the histogram which characterizes a particular species rather than separate details which vary with age and show slight variation within a species, even between individuals of the same size.

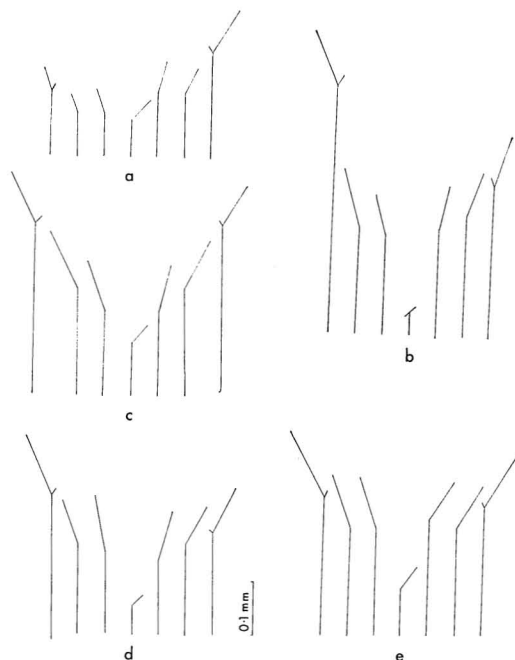


FIG. 3. Relative sizes of setal shafts and blades in: a, *Spirorbis* (*Spirorbella*) *marioni*; b, *Protolaeospira* sp. A; c, *Pileolaria* (*Pileolaria*) *militaris*; d, *Pileolaria* (*Duplicaria*) *koehleri*; e, *Pileolaria* (*Simplicaria*) *pseudomilitaris*.

The stick diagrams represent relative lengths of setal shafts and blades. The numbers in Fig. 3a represent the arrangement of setae in all the diagrams. The central seta is abdominal. Numbers 1, 2, and 3 represent setae from the collar, second and third fascicles on each side. *Spirorbis* (*Spirorbella*) *marioni* (Fig. 3a) is dextral and in this case the concave side is on the observer's left, whereas all the other species in Fig. 3 are sinistral and the concave side is represented by the stick setae on the observer's right.

Genus *Protolaeospira* Pixell (1912) redefined
(= *Marsipospira* Bailey, 1969b; includes
Pixellia Pillai, 1970)

Coiling is usually sinistral. Three rows of tori occur on the concave side of the thorax; other traces of a fourth thoracic segment may or may not be present. Embryos are attached to a stalk which arises dorsally from the floor of the fecal groove, approximately level with the first thoracic torus. Collar setae have separate fins and broad cross-striated blades; sickle setae are present in the third and fourth fascicles. Thoracic and abdominal uncini are much more numerous

on the concave side; thoracic uncini are usually very long and slender, with a blunt anterior peg. Abdominal setae are less than a quarter the length of the collar setae and have vestigial brushlike blades. The opercular talon is massive and usually bears lateral projections. A single white larval attachment gland may be present.

Type

Protolaeospira ambilateralis (Pixell, 1912).

Protolaeospira sp. A

Fig. 2b, 3b, 4

Material

A single specimen has been preserved as a polyvinyl-lactophenol mount. Fragments of the tube are preserved in alcohol and the operculum is in clove oil.

Location

Coconut Island, Oahu, Hawaii.

Habitat

The animal was found on a settlement plate in shallow water.

Description of Species

TUBE: Tube is sinistral with thick bulging transverse ridges, translucent, and vitreous. In some gaps between the ridges the tube is transparent. Terminal section of tube widens out to form a broad mouth. Coil diameter is approximately 3.5 mm.

OPERCULUM: The operculum is translucent except for a median densely calcified rod on the dorsal side of the asymmetrically lobed talon, which lacks a central spur. The plate is slightly concave. The whole operculum is notable for its extremely light calcification.

THORAX: The thorax has three tori on each side, but the third torus on the convex side has only two uncini. There are no setae associated with the third tori. Collar setae are large, particularly those on the convex side. The longer shafts of the latter originate behind the first torus on the convex side and behind the origin of the second thoracic fascicle on that side. They

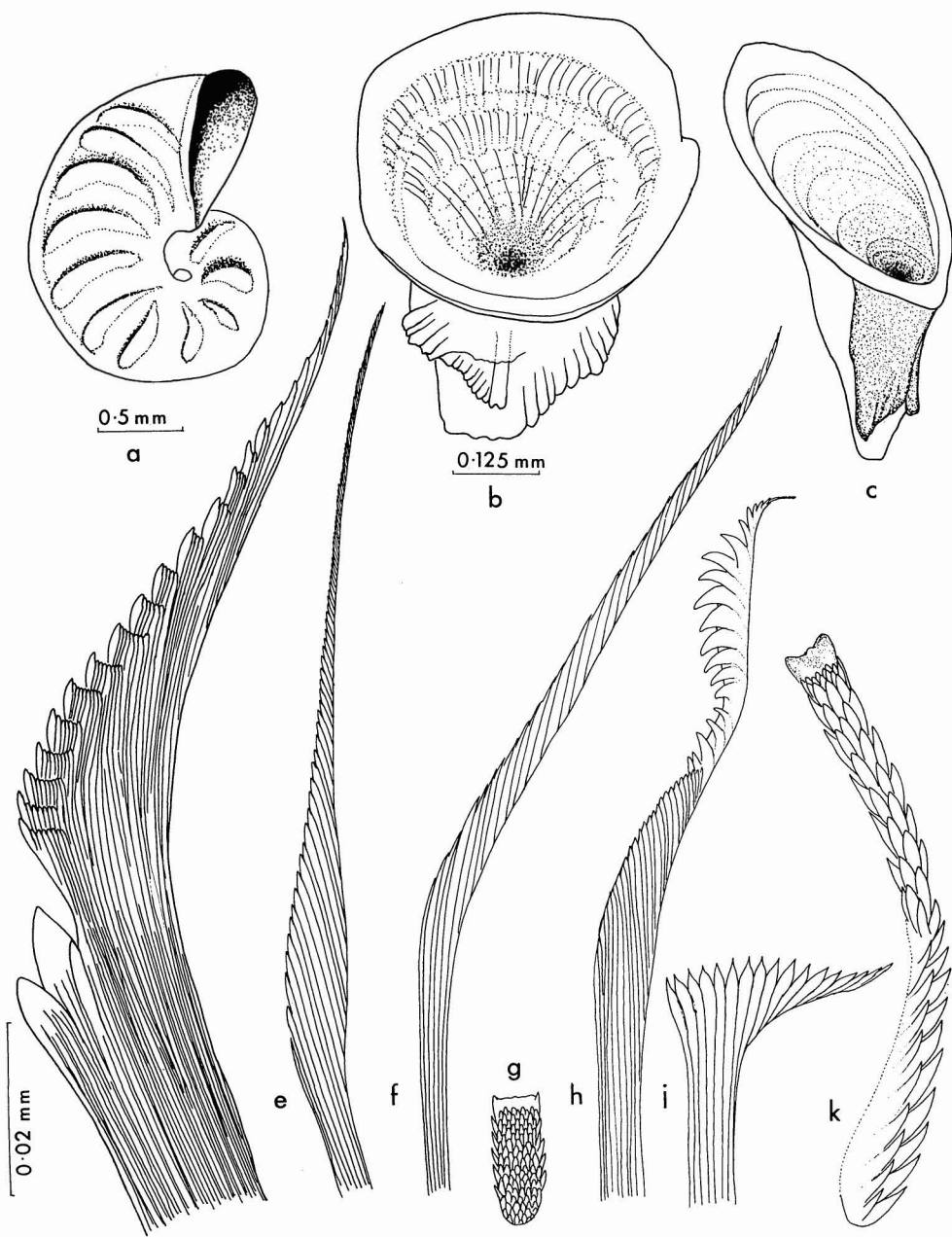


FIG. 4. *Protolaeospira* sp. A. a, Tube; b, dorsal view of operculum; c, side view of operculum; d, collar seta; e, seta from second thoracic fascicle; f, seta associated with collar setae; g, abdominal uncinus; h, sickle seta from third thoracic fascicle; i, abdominal seta; j, thoracic uncinus.

SCALE: c as b; e, f, g, h, j, and k as d.

have a proximal fin with three or four large teeth and a broad distal blade which has coarse teeth and cross-striations across the narrow width of the blade. The section between the fin and blade is unusually broad. Capillary setae associated with the collar setae bear minute teeth. Simple setae in the second and third fascicles are numerous and have smooth blades lacking any distinct striations. Capillary setae are also present in these fascicles except for the third fascicle on the convex side. The third fascicles also have sickle setae with a proximal smooth blade and a distal portion bearing relatively large recurved teeth. Uncini have three or four longitudinal rows of teeth and a blunt gouged anterior end lacking teeth. In some cases the anterior end appears to have an irregularly indented edge, possibly a result of convolutions.

ASETIGEROUS REGION: This region is short, approximately 1.5 times the length between the first and second abdominal tori.

ABDOMEN: The abdomen has approximately 14 segments. Setae have short, brushlike blades with pointed teeth. Anteriorly they may be in groups of three and, in one fascicle on the convex side, five were counted. More posteriorly they are paired or single. The most posterior segments also have simple finely serrated non-geniculate setae. Uncini are unusually widely spaced within tori on the concave side. They have approximately seven longitudinal rows of small teeth and are short and broad with blunt anterior ends. Many segments on the convex side lack uncini but have setae. Thus the distribution of uncini is very asymmetrical.

INCUBATION: Embryo mass is born on a stalk originating from the dorsal side of the thorax close to the first thoracic torus.

Remarks

Inasmuch as only a single specimen has been found, it is not yet possible to state whether this should be regarded as a new species. It appears to be closely related to, or perhaps the same as, *S. translucens* Bailey & Harris (1968) from the Galápagos Islands. The opercular structure of other *Protolaeospira* species tends to be somewhat variable, and it is difficult to be sure how significant are the differences between this oper-

culum and that of *S. translucens*. This specimen resembles *S. translucens* in having three or four rows of teeth on each thoracic uncinus; most *Protolaeospira* species have single rows of teeth on their thoracic uncini. It also bears some resemblance to a species from southern Australia (Knight-Jones, in press), but that species has a densely calcified opaque tube, a slightly different operculum, and thoracic uncini with single longitudinal rows of teeth.

Genus *Pileolaria* Claparède, 1868
(amended Knight-Jones, 1972)

The genus is described as follows: sinistral coiling; incubation in the operculum; only two pairs of thoracic tori; fin and blade collar setae, with the blades usually bearing large teeth and distinct cross-striations and greatly exceeding in length the blades of abdominal setae; sickle setae may or may not be present; thoracic uncini very slender, often with only one longitudinal row of teeth; pegs of thoracic uncini about as broad as rest of uncinus and not pointed in surface view; arrangement of abdominal tori almost bilaterally symmetrical and with the largest tori lying toward the posterior end; larvae with single, white, middorsal attachment glands.

Subgenus *Pileolaria*

Opercula of juvenile and adult are morphologically different from one another; the opercular plate is single with embryos brooded under it. Collar setae are cross-striated. Thoracic uncini are usually found with single rows of teeth.

Type

Pileolaria (Pileolaria) militaris Claparède, 1868.

Pileolaria (Pileolaria) militaris
Claparède, 1868

Fig. 2c, 3c, 5

Material

One specimen.

Location

Coconut Island, Oahu, Hawaii.

Habitat

Animal was found in the intertidal zone, on an oyster.

Description of Species

TUBE: Tube is sinistral, with indistinct wavy transverse growth thickenings, the terminal portion ascending. Coil diameter is 3.0 mm.

OPERCULUM: The operculum formed a brood chamber containing eggs. The plate is slightly convex and covered with spines. A rim of spines almost surrounds it, but is discontinuous on the dorsal side where the rim dips. Walls of the chamber are densely calcified and opaque. On the ventral side at the base of the wall are five short spines; and a number of eggs can be seen clearly from this side, where the wall does not extend as far down as it does on the dorsal side.

THORAX: The thorax has two pairs of tori and the collar folds are not fused. A dark granular region partially obscures the tori on the concave side and extends into the asetigerous region. Collar setae have fins and distinctly cross-striated blades. Capillary setae are associated with all the thoracic fascicles. Second and third segments have simple setae, and sickle setae are found in the third fascicles. Uncini usually have a single longitudinal row of teeth and a bifid anterior end.

ASETIGEROUS REGION: This is rather long and equivalent to approximately four times the distance between the anterior abdominal tori.

ABDOMEN: The abdomen has about 12 segments and the longest tori are toward the posterior end. Setae are geniculate with rounded teeth. Uncini have about six longitudinal rows of teeth and a bifid anterior end.

INCUBATION: Incubation occurs in operculum.

Distribution Elsewhere

The distribution of this species has been reviewed in considerable detail by Zibrowius (1968). It is a widely distributed species with many records in the Mediterranean Sea and Atlantic and Pacific oceans. Recently it was found near Plymouth, England (Phyllis Knight-Jones, personal communication), in the Red Sea

(Vine, in press), and off southern Australia (Phyllis Knight-Jones, in press). It thus appears to show a worldwide distribution in tropical, subtropical, and warm temperate waters.

Remarks

The description agrees closely with those of previous authors. The operculum of the species described here differs slightly from that of specimens recently described from the Red Sea (Vine, in press) in that the rim of the plate has a definite depression on the dorsal side and lacks spines there. Zibrowius (1967) studied this species in the Mediterranean and showed that its operculum exhibits quite considerable variation in structural detail. Recent research tends to suggest that some widely distributed Spirorbinae such as *P. (P.) militaris* should be treated as superspecies, but there is not yet enough information to characterize geographical races.

Subgenus *Simplicaria* Knight-Jones, in press

This subgenus resembles *Simplicaria*, but lacks sickle setae.

Type

Pileolaria (Simplicaria) pseudomilitaris (Thiriot-Quévieux, 1965).

Pileolaria (Simplicaria) pseudomilitaris

Fig. 2d, 3e, 6

Material

Thirty specimens.

Locations

Oahu, Hawaii: Sand Island in Kaneohe Bay and Koko Head.

Habitat

Animals were taken in the intertidal zone, to 3 m, on stones.

Description of Species

TUBE: Tube is sinistral, with transverse growth thickenings; terminal section often ascends and coiling may be helical. Coil diameter is 2.0 mm.

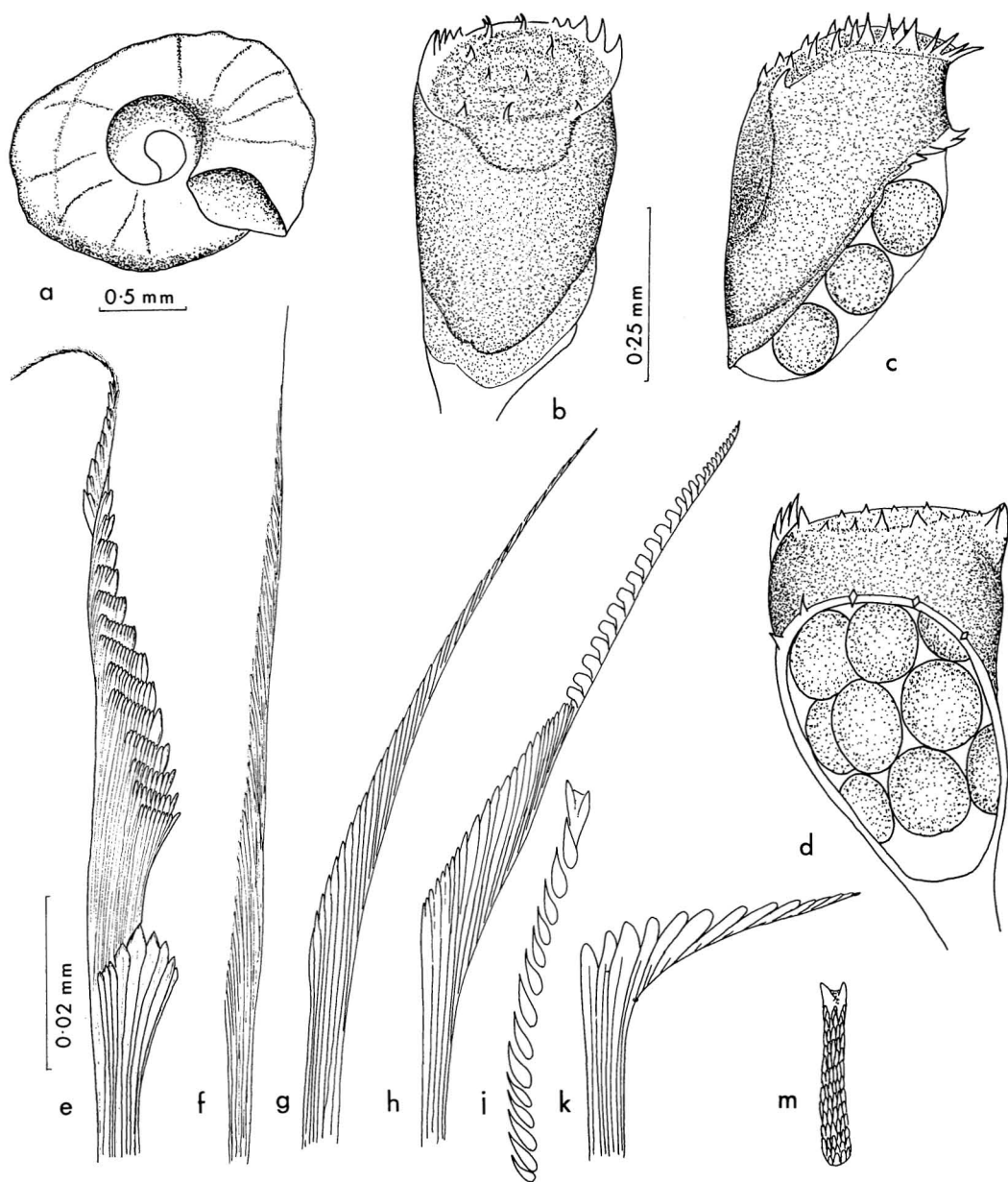


FIG. 5. *Pileolaria (Pileolaria) militaris*. a, Tube; b, dorsal view of operculum; c, side view of operculum; d, ventral view of operculum, showing eggs; e, collar setae; f, seta associated with collar setae; g, seta from second thoracic fascicle; h, sickle seta from third thoracic fascicle; i, thoracic uncinus; j, abdominal seta; m, abdominal uncinus.

SCALE: c and d as b; f, g, h, j, k, and m as e.

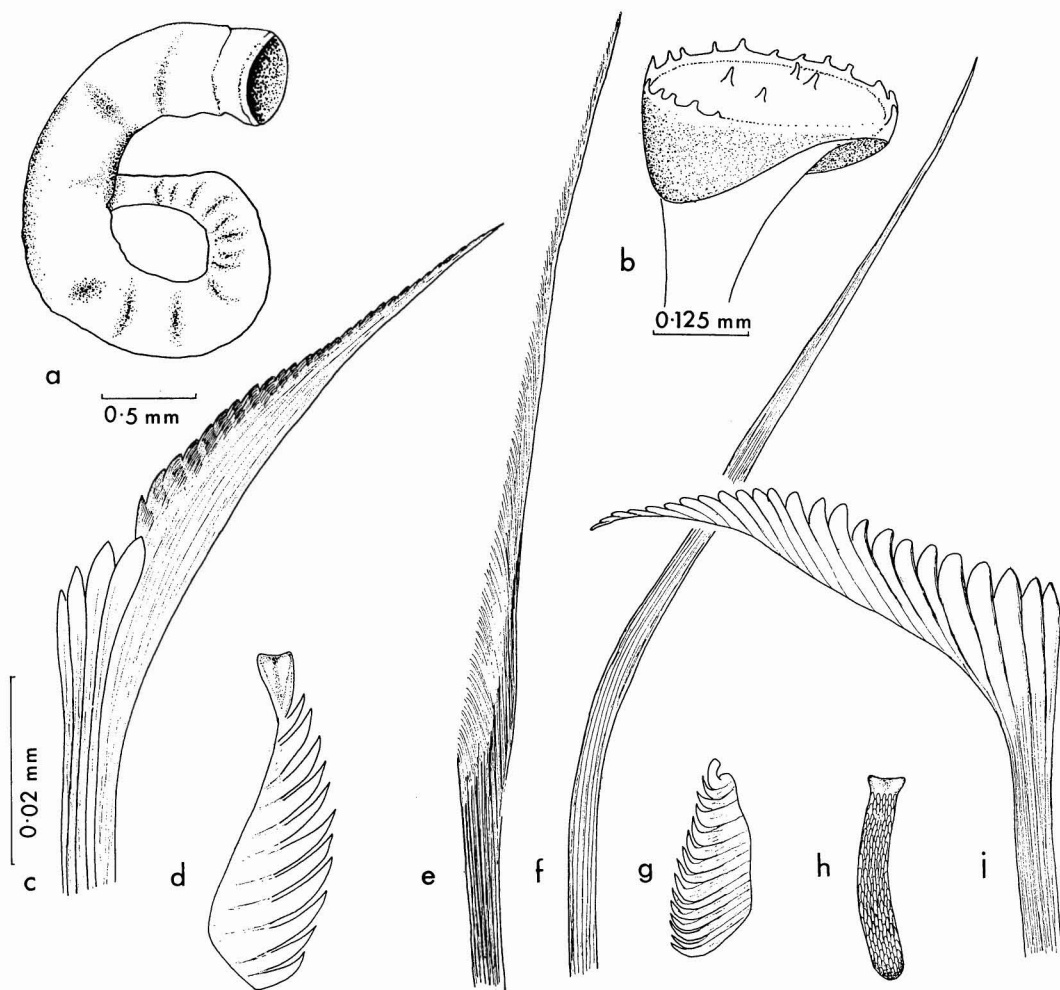


FIG. 6. *Pileolaria (Simplicaria) pseudomilitaris*. a, Tube; b, mature operculum; c, collar seta; d, thoracic uncinus; e, simple seta from second thoracic fascicle; f, capillary seta associated with collar setae; g, side view of abdominal uncinus; h, edge-on view of abdominal uncinus; i, abdominal seta.

SCALE: d, e, f, g, b, and i as c.

OPERCULUM: Juveniles had a slightly concave plate and an eccentric fingerlike talon. Adults have a helmet-shaped calcified chamber with a slightly convex plate bearing several spines and an incomplete rim bearing short spines.

THORAX: The thorax bears two pairs of tori. Each collar seta has a proximal fin and a distal toothed blade, with fairly distinct cross-striae. Capillary setae are associated with these and are present in all the thoracic fascicles. The second and third fascicles bear simple setae and

lack sickle setae. Uncini have a somewhat bifid gouged anterior end and a single row of teeth.

ASETIGEROUS REGION: This region is fairly long, equivalent to four times the distance between the first two abdominal tori.

ABDOMEN: The abdomen has approximately 17 segments. Setae are geniculate with blunt recurved teeth. Uncini have four or five longitudinal rows of distinct teeth and a blunt anterior end lacking teeth.

INCUBATION: Incubation takes place in opercular brood chamber.

BODY COLORS: Tentacles are pale pink or orange; gut is nut brown; eggs in ovary are green-blue.

Distribution Elsewhere

The species has been taken from the Mediterranean Sea (Thiriot-Quievreux, 1965; Zibrowius, 1968; Harris, 1968, as *S. berkeleyanus*); Aegean Sea (Bailey, 1969a); Galápagos Islands (Bailey and Harris, 1968, as *S. regalis*); West Indies (Bailey, 1970); southern Australia (Knight-Jones, in press); northeastern Australia (personal observations by P.J.V.); New Zealand (unpublished, P.J.V.).

Remarks

S. regalis from the Galápagos Islands is almost certainly the same as *Pileolaria* (*Simplicaria*) *pseudomilitaris*. Bailey and Harris (1968) separated these two species on the basis of the former's having a domed opercular plate with several spines and a smooth tube lacking longitudinal ridges. More recent studies have shown that *P. (S.) pseudomilitaris* often has a relatively smooth tube and the opercular plate may be flat or slightly domed.

Subgenus *Duplicaria* Vine, in press

Subgenus resembles *Pileolaria*, except that adult operculum in *Duplicaria* develops from juvenile form without sharp dimorphism and has two or more opercular plates stacked one above the other; embryos are brooded below them in a chamber with lightly calcified, rather delicate walls; collar setae not distinctly cross-striated; thoracic uncini have several longitudinal rows of teeth; anterior abdominal torus on concave side is usually split into two unequal portions.

Type

Pileolaria (*Duplicaria*) *koehlerii* Caullery & Mesnil (1897).

Pileolaria (*Duplicaria*) *koehlerii*

Fig. 2e, 3d, 7

Material

One hundred fifty-one specimens were preserved in tubes and five were mounted in polyvinyl-lactophenol.

Location

Maili Point, Oahu, Hawaii; Hilo, Hawaii.

Habitat

Animals were found off Oahu at 8 m on stones. They were taken off the island of Hawaii from the intertidal zone and shallows and were found to be abundant on lava rocks.

Description of Species

TUBE: Tube is sinistral, somewhat porcelainous, and tightly coiled. Outer longitudinal ridge projects almost horizontally from the top outer edge of tube. Mouth is often wider than rest of tube. Irregular vertical ridges occur on sides. It is often colored brown by algal growth. Coil diameter is 1.5 mm.

OPERCULUM: This structure has two or three slightly concave plates interlocking by peg and socket arrangement and is also supported by lateral wings on talon. Underneath these plates brood chambers develop with lightly calcified, rather delicate, walls, through which eggs can be distinguished.

THORAX: The thorax has two pairs of tori. Collar folds are not fused. Collar setae have a broad fin with many narrow teeth at the outer edge and approximately five larger teeth toward the opposite side. There is hardly any gap between this and the distal blade, which is fairly coarsely serrated but lacks cross-striations. Smooth-edged, flexible, capillary setae are associated with these and are also present in the second and third fascicles. Simple setae are the main setae in the second fascicles and are also present in the third, although sickle setae tend to be more numerous there. The proximal portion of each sickle blade is only a quarter of the length of the whole blade. Uncini have two or three longitudinal rows of teeth and a broad anterior end which lacks teeth.

ASETIGEROUS REGION: This is rather short, approximately 1.5 times the distance between the first two abdominal tori.

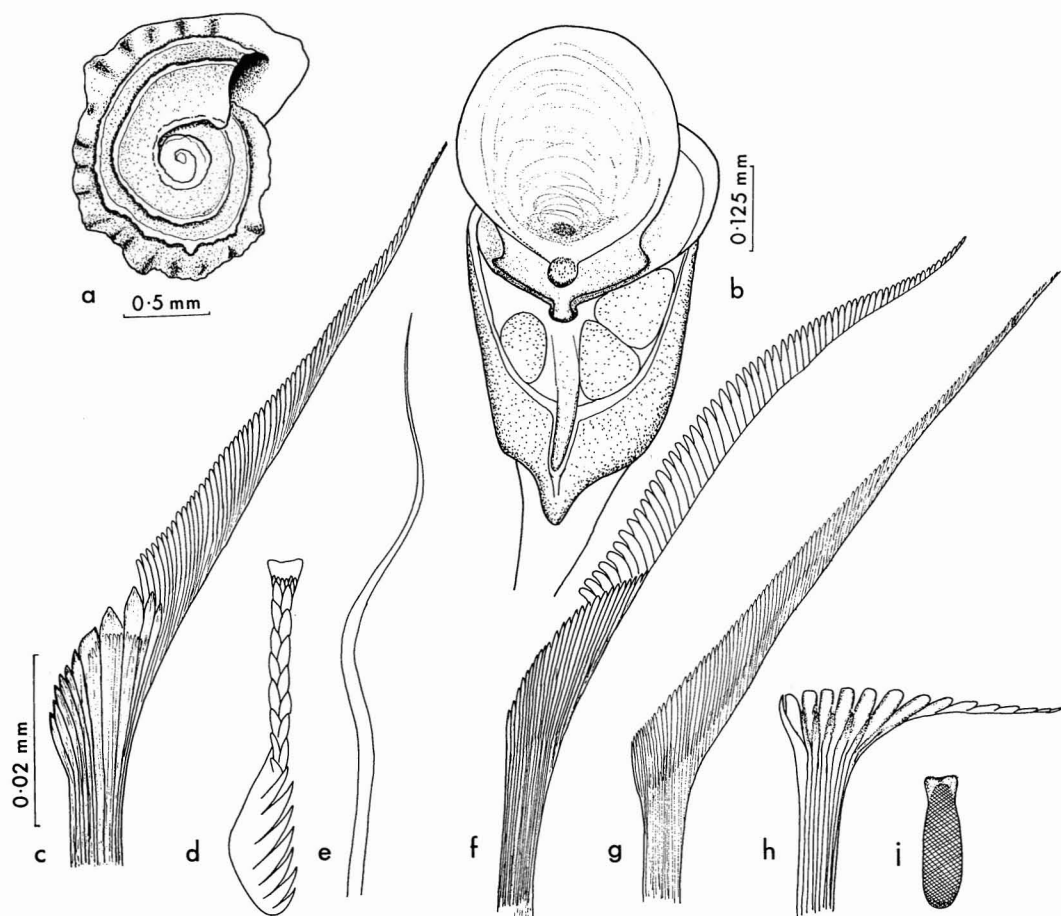


FIG. 7. *Pileolaria (Duplicaria) koebleri*. *a*, Tube; *b*, mature opercular brood chamber; *c*, collar seta; *d*, thoracic uncinus; *e*, capillary seta associated with collar setae; *f*, sickle seta from third thoracic fascicle; *g*, simple seta from second thoracic fascicle; *h*, abdominal seta; *i*, abdominal uncinus.

SCALE: *d*, *e*, *f*, *g*, *h*, and *i* as *c*.

ABDOMEN: The abdomen consists of about 14 segments. Setae are geniculate with rather blunt, deeply gouged teeth. The first tooth of the blade is large and slightly recurved, partially overlying the next tooth. Uncini have about nine longitudinal rows of fine teeth and a broad anterior end lacking teeth. The anterior torus on the concave side is split into two unequal sections, of which the one nearest the concave edge bears more uncini than the other and is out of line with the other tori on this side.

INCUBATION: Incubation occurs in opercular chamber.

Distribution Elsewhere

This species has been taken from the Mediterranean Sea (Caullery and Mesnil, 1897; Zibrowius, 1968); Aegean Sea (Bailey, 1969*a*); West Indies (Bailey, 1970); Red Sea (Vine, in press); New Zealand (unpublished, P.J.V.); Australia (personal observations, P.J.V.).

Remarks

It is possible that *Spirorbis (Pileolaria) polyoperculata* Straughan (1969) from Eniwetok in the Marshall Islands is the same as *P. (D.) koebleri*. Straughan separated the two species on

the basis of *S. (P.) polyoperculata* having a smooth tube and lacking wings to its talon. The tube of *P. (D.) koeblersi* is variable, however, and the wings of the talon are often almost transparent and may be partly obscured by secondary plates. Recent studies which have extended the distribution of *P. (D.) koeblersi* to the Red Sea, New Zealand, and Australia (as well as to Hawaii) tend to support this suggestion. Further studies are needed to show if these two species are synonymous.

Genus *Janua* de Saint-Joseph, 1894
(redefined Knight-Jones, 1972)

Most species of this genus have dextral coiling. Incubation is in an opercular brood chamber, below which a secondary plate (rudiment of next opercular plate) is formed soon after spawning. Only two pairs of thoracic tori are present. Collar setae are without a toothed fin; abdominal setae have blades as big as, or bigger than, those of the collar setae, and often are accompanied by secondary setae with rudimentary shafts. Thoracic uncini have anterior pegs narrow and more or less pointed in surface view. The largest abdominal tori lie in the anterior half of the setigerous region. Larvae have paired white attachment glands in thoracic region.

Subgenus *Janua sensu stricto*

This subgenus exhibits dextral coiling. The talon when present is a simple peg. Sickie setae are present in the third thoracic fascicles. The collar does not form a tunnel dorsally.

Type

Janua (Janua) pagenstecheri Quatrefages, 1865.

Janua (Janua) pagenstecheri
Fig. 8a, 9

Material

Three specimens are preserved in tubes and two are mounted in polyvinyl-lactophenol.

Location

Sand Island, Oahu, Hawaii.

Habitat

J. pagenstecheri was found in the intertidal zone, on stones.

Description of Species

TUBE: The tube shows dextral coiling with three longitudinal ridges. Terminal section usually partly overlies previous whorl and is sometimes upturned. Coil diameter is 1.3 mm.

OPERCULUM: The operculum has a lightly calcified, partly concave, opercular plate which is somewhat convex but has a central concavity like an inverted saucer. The walls of the chamber are more or less transparent and two or three embryos, with white attachment glands, can be distinguished inside the cup-shaped operculum. A secondary plate forms the basal plate and this gives rise to the terminal plate of a later chamber. The opercula studied lacked talons, probably because the chambers were not primary ones.

THORAX: The thorax has two pairs of tori. Collar folds are not fused dorsally. Collar setae have a proximal "fin" of fine teeth and this is followed immediately by the distal blade with slightly narrower teeth. The splayed "fin" is quite distinct on the two slides prepared of these Hawaiian specimens but has proved less clear on specimens from some other areas. The fin is not like those of most other fin and blade collar setae, however, and it appears to be due to slightly larger proximal teeth tending to splay when squashed whereas the finer distal teeth lie flat. The fin is less distinct on the smaller collar setae of the concave side. Several capillary setae are associated with the collar setae. The second and third fascicles have simple, finely serrated setae and the third fascicle also possesses sickle setae. Uncini have two or three longitudinal rows of teeth and a tapering peg at the anterior end around which several teeth are splayed.

ASETIGEROUS REGION: The asetigerous region is fairly long, approximately five times the distance between the first and second abdominal tori.

ABDOMEN: This structure has about six segments. Setae are geniculate with slightly re-

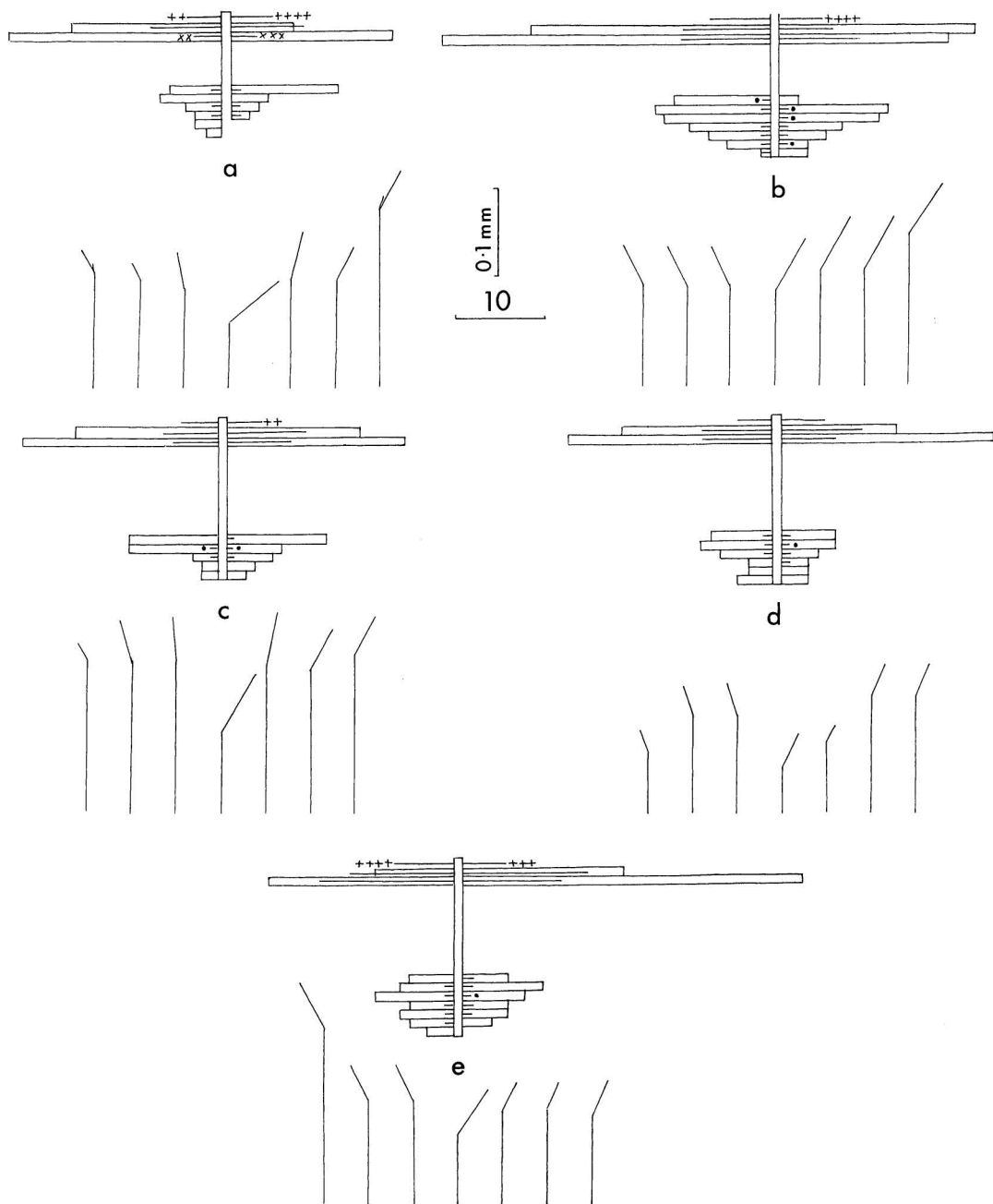


FIG. 8. Distribution of setae and uncini and comparative sizes of setal shafts and blades in: a, *Janua* (*Janua*) *pagenstecheri*; b, *Janua* (*Dexiospira*) *pseudocorrugata*; c, *Janua* (*Dexiospira*) *steueri*; d, *Janua* (*Dexiospira*) *nipponica*; e, *Janua* (*Leodora*) *knightjonesi*.

For explanation of histograms and setal stick diagrams see legend for Figs. 2 and 3.

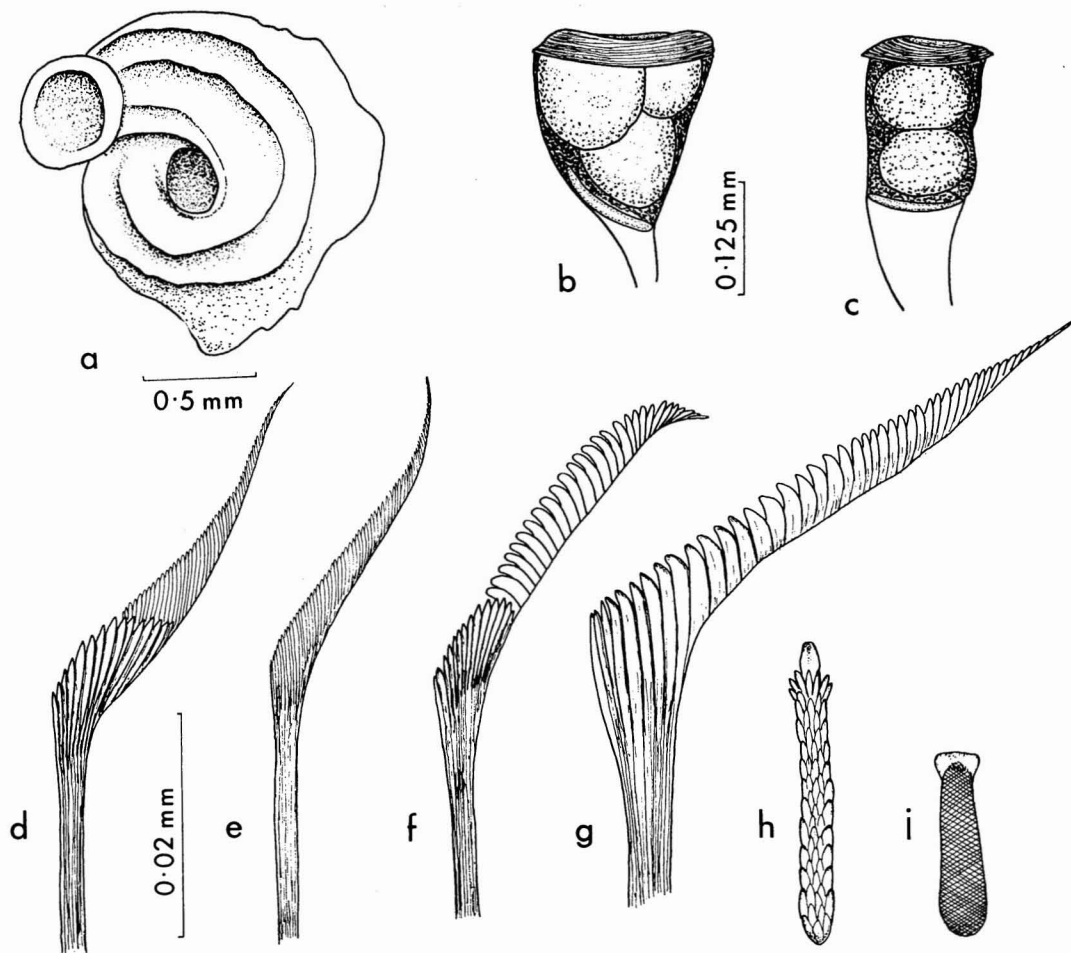


FIG. 9. *Janua (Janua) pagenstecheri*. a, Tube; b, side view of adult operculum; c, dorsal view of adult operculum; d, collar seta with rudimentary fin; e, simple seta from second thoracic fascicle; f, sickle seta from third thoracic fascicle; g, abdominal seta; h, thoracic uncinus; i, abdominal uncinus.

SCALE: c as b; e, f, g, h, and i as d.

curved teeth. Uncini have approximately 10 longitudinal rows of teeth and a rather broad anterior fan lacking teeth.

INCUBATION: This occurs in the operculum.

Distribution Elsewhere

Zibrowius (1968, p. 201–203) reviewed in some detail the taxonomic history and present zoogeographic knowledge concerning this species. It is widely distributed in the Mediterranean Sea and Atlantic Ocean and, in addition to the locations listed by Zibrowius, has been found off the Galápagos Islands (Bailey and

Harris, 1968) and off Chios in the Aegean Sea (Bailey, 1969a). *S. epichysis* Bailey, 1970, from the West Indies is probably conspecific, because the main difference noted by Bailey was the absence of a proximal fin in the collar setae. This feature has recently been shown to be frequently absent from *J. (J.) pagenstecheri* (see Zibrowius, 1968, p. 202). *J. (J.) pagenstecheri* has recently been found in southern Australia (Phyllis Knight-Jones, in press) and in New Zealand (unpublished, P.J.V.).

Other records from the Pacific show that the species is found off North America as *S. pusil-*

loides (Pixell, 1912; see Zibrowius, 1968, for discussion); from Mexico (Rioja, 1941, 1942); from the Tuamotu atolls (Fauvel, 1919, 1947). In the Indian Ocean it is known from Ceylon (de Silva, 1961).

J. (J.) pagenstecheri thus appears to have a worldwide distribution. The recent records from southern Australia and New Zealand, together with the present one from Hawaii, tend to support the record from Ceylon by de Silva (which has been questioned by Pillai) and also that from the Tuamotu atolls by Fauvel. Thus the species appears to display an Indo-Pacific, as well as Atlantic, Caribbean, and Mediterranean, distribution. Zibrowius (1968) stated that *S. pusilloides* and *S. pagenstecheri* are conspecific, and this extends its distribution to the west coasts of Mexico, the United States, and Canada.

Remarks

J. (J.) pagenstecheri differs slightly from all other species in the genus by having the rudiments of a proximal fin in the collar setae. The rudimentary fin has been observed by some authors and not by others. It is not a prominent feature and its appearance partially depends on how the setae are orientated and to what extent they are squashed, in a polyvinyl-lactophenol mount.

This species may also be unique amongst *Janua* species in possessing sickle setae. It seems possible that the sinistral forms with sickle setae, described by Zibrowius (1968) as *Spirorbis laevis*, may have been *situs inversus* of *J. pagenstecheri*. The puzzling status of *Spirorbis laevis* is discussed later.

Subgenus *Dexiospira* Caullery & Mesnil, 1897
(= *Neodexiospira* Pillai, 1970)

Subgenus is like *Janua*, with coiling usually dextral, but sickle setae are absent and the margins of the collar usually are fused to form a tunnel over the middorsal thoracic groove.

Type

Janua (Dexiospira) pseudocorrugata (Bush, 1904).

Janua (Dexiospira) pseudocorrugata

Fig. 8b, 10

Material

More than 100 specimens comprise the material.

Location

Coconut Island, Oahu, Hawaii.

Habitat

Species was found on settlement plates in shallows.

Description of Species

TUBE: Tube is dextral, with three longitudinal ridges formed by rows of calcified "knobs" on top of the tube. The central ridge is the most prominent. Rather narrow transverse ridges pass through these "knobs." The sides of the tube slant outward and are vertically ridged. Two whorls can be distinguished from above, and the terminal section of the tube partially overlies the previous whorl.

OPERCULUM: The operculum has a bifid calcified talon which is almost peripheral. In some cases it dips under the rim of the lightly calcified plate whereas, in others, it overlaps the edge of the plate. Walls are more or less transparent. A basal plate is present in some forms and secondary (or later) opercula lack talons.

THORAX: Thorax has two pairs of tori. The collar folds are fused to form a tunnel dorsally. Collar setae on the convex side lack a proximal fin and are coarsely toothed with indistinct cross-striations. Collar setae in the fascicle on the concave side lack cross-striations and are like the simple setae of the second and third fascicles. Uncini have a single anterior peg and approximately three longitudinal rows of teeth.

ASETIGEROUS REGION: This region is rather long, approximately six times the distance between the first two abdominal tori.

ABDOMEN: This has approximately six segments. Setae are geniculate with long, rather narrow blades and recurved teeth. Secondary setae are present in some fascicles (see Vine, in

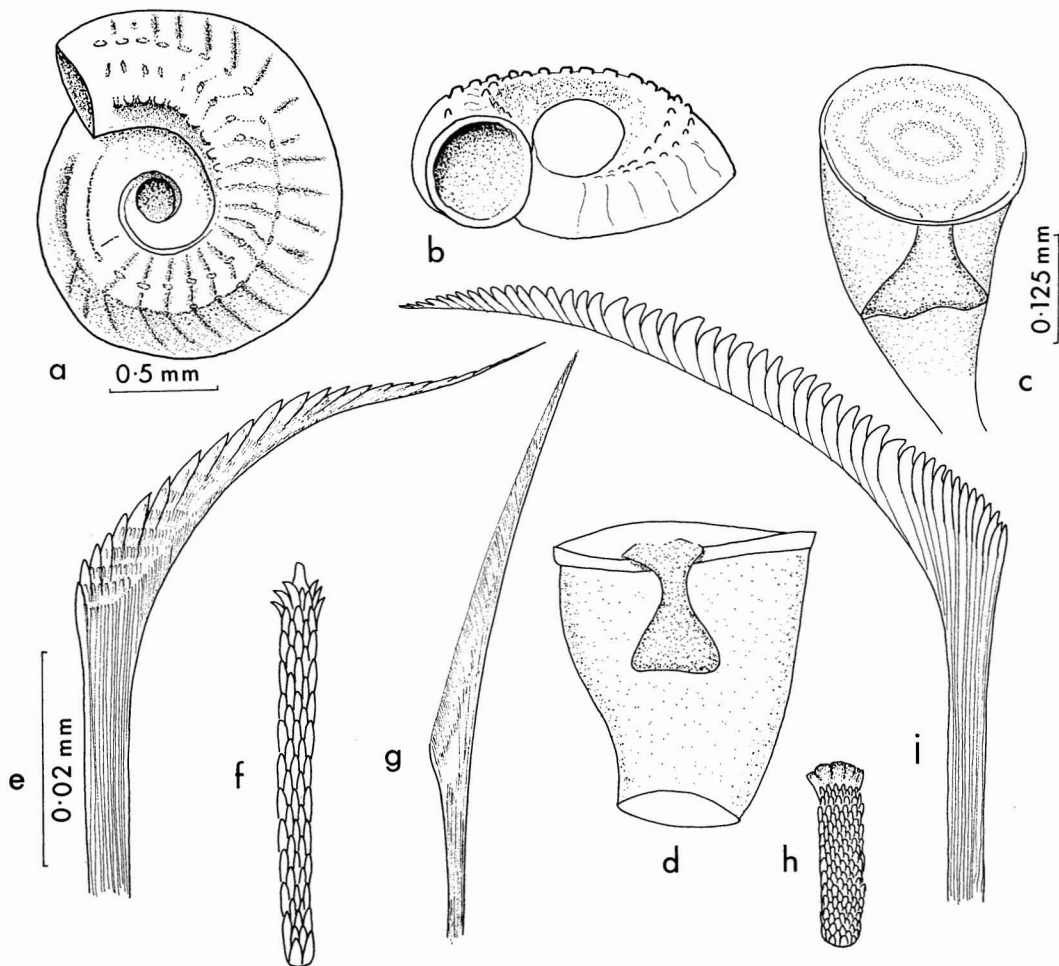


FIG. 10. *Janua* (*Dexiospira*) *pseudocorrugata*. *a*, Tube; *b*, side view of tube; *c*, juvenile form of operculum; *d*, mature form of operculum without eggs; *e*, collar seta; *f*, thoracic uncinus; *g*, simple seta from second thoracic fascicle; *h*, abdominal uncinus; *i*, abdominal seta.

SCALE: *b* as *a*; *d* as *c*; *f*, *g*, *h*, and *i* as *e*.

press). Uncini have five to seven longitudinal rows of fine teeth and have an anterior, somewhat convoluted, fan.

INCUBATION: This takes place in the operculum.

Distribution Elsewhere

Zibrowius (1968) reviewed the distribution of this species in detail (under the name *Spirorbis corrugatus*), but he considered that several

other species were synonymous with it (see remarks below).

It seems likely that some of the species listed by Zibrowius, though closely related, are not conspecific and the distribution discussed here relates only to *J. (D.) pseudocorrugata*.

It is widely distributed in the Atlantic Ocean and Mediterranean Sea: English Channel (Caulery and Mesnil, 1897); Roscoff (L'Hardy and Quiévreux, 1964); northwestern Spain (Rioja, 1923); Morocco (Fauvel, 1936); Madeira

(Langerhans, 1880⁵); Azores (Fauvel, 1909, 1914); Sargasso Sea (Fauvel, 1909, 1914); Mexico (Rioja, 1959); Mediterranean Sea (Caullery and Mesnil, 1897; Sterzinger, 1909, 1910; Fauvel, 1911; Casanova, 1954; Bellan, 1959; Zibrowius, 1968; Bailey, 1969a); West Indies (Bailey, 1970). The only previous record from the Pacific of which we are aware is that of Knight-Jones (in press) from southern Australia.

Remarks

There are a number of *Janua* species which show slight variations in structure of tubes, opercula, and details of setation. The mature operculum of *J. (D.) pseudocorrugata*, which lacks a talon, is difficult to distinguish from a number of other species. Zibrowius (1968) considered *S. steueri* Sterzinger (1909), *S. heideri* Sterzinger (1909), *S. foraminosa* Moore & Bush (1904), and *S. treadwelli* Pillai (1965) to be conspecific with *J. (D.) pseudocorrugata*. Recent study in the Red Sea (Vine, in press) suggests that *J. (D.) steueri* may be a distinct species and that *S. heideri* should perhaps be considered as a subspecies of the latter. The tube of *J. (D.) steueri* usually has three longitudinal ridges with deep indentations between them, forming a crisscross network of ridges and indentations. Its juvenile operculum has a bifid talon with wings (which are sometimes transparent) and the mature chamber has rather heavily calcified, almost opaque, walls. *J. (D.) pseudocorrugata* has a less distinctive crisscross pattern on its tube and the talon of the juvenile operculum has its broadest section distally. In addition, the walls of the brood chamber are more or less transparent. Pillai's description of *S. treadwelli*, in details of tube and operculum, resembles *J. (D.) steueri* rather than *J. (D.) pseudocorrugata*, but he failed to compare his material with either of these closely related species.

The situation with regard to *J. (D.) foraminosa* is slightly more confusing since a recent description by Day (1961) probably referred to another species. This problem is discussed more fully elsewhere, but it seems likely that

J. (D.) foraminosa is an acceptable species with a distribution that may be very limited.

Phyllis Knight-Jones (1971) discussed the taxonomic history of *J. (D.) pseudocorrugata* and established that Bush was correct in renaming, as *S. pseudocorrugata* Bush (1904), the species called *S. corrugatus* Montagu by Caullery and Mesnil (1897), since the latter name had been first applied to a sinistral form.

Janua (Dexiospira) steueri Sterzinger, 1909
(= *J. (D.) foraminosus*)

Fig. 8c, 11

Material

Three specimens were preserved in tubes and one mounted in polyvinyl-lactophenol.

Location

Maili Point, Oahu, Hawaii.

Habitat

Animals were found on an alga, at approximately 8 m deep.

Description of Species

TUBE: Tube is dextral with three longitudinal ridges on the top and one on the side. The outer ridge on top of tube has outwardly projecting blunt processes. There are deep indentations between the ridges and the two outer ridges are actually perforated where indentations on opposite sides connect. Tube has one or two whorls. Coil diameter is 1.5 to 2.0 mm.

OPERCULUM: In the juveniles, a slightly concave plate has a bifid talon with calcified wings. The bifid ends bend sharply and project ventrally. The talon persists in the primary brood chamber of the mature worm and the wings tend to be lightly calcified or even completely transparent. The chamber walls are rather lightly calcified and developing embryos can be distinguished, but not as clearly as in *J. (D.) pseudocorrugata*. Secondary brood chambers lack a talon and are then more difficult to distinguish from those of *J. (D.) pseudocorrugata*.

THORAX: Thorax has two pairs of tori. Collar folds are fused to form a tunnel dorsally. Collar

⁵ These records probably do not refer to the same species as that described above.

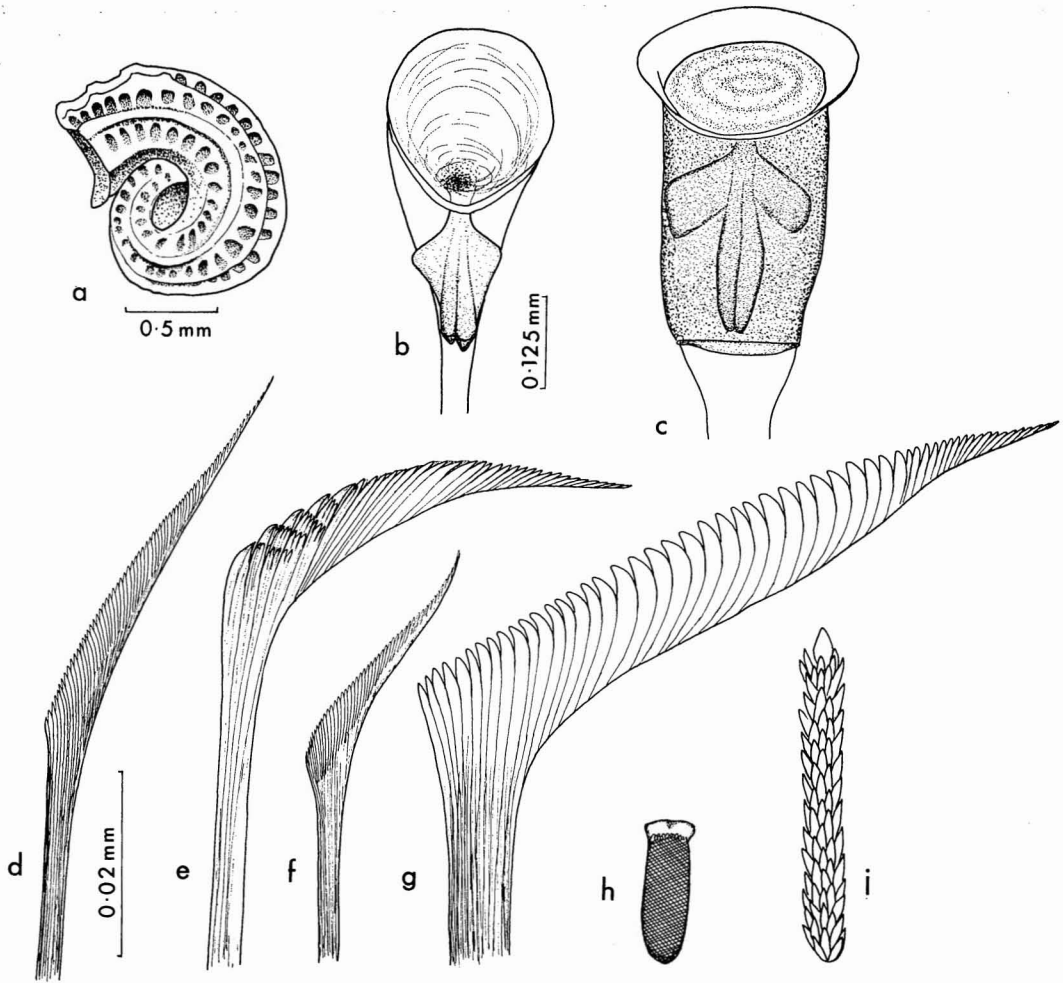


FIG. 11. *Janua (Dexiospira) steueri*. *a*, Tube; *b*, juvenile operculum; *c*, mature operculum; *d*, thoracic seta from second fascicle on convex side; *e*, collar seta from convex side; *f*, collar seta from concave side; *g*, abdominal seta; *h*, abdominal uncinus; *i*, thoracic uncinus.

SCALE: *c* as *b*; *e*, *f*, *g*, *h*, and *j* as *d*.

setae on the convex side have simple blades, with coarse teeth and rather faint cross-striations, whereas those on the concave side have smaller blades, narrower teeth, and no cross-striations. Second and third fascicles have finely striated simple setae and there are no sickle setae in the third fascicles. Uncini have three or four longitudinal rows of teeth and these splay out around a triangular peg at the anterior end.

ASETIGEROUS REGION: This area is long, approximately 10 times the distance between the first two abdominal tori.

ABDOMEN: The abdomen has about 14 segments. Setae are geniculate with a rather broad blade and small teeth. Uncini have about six longitudinal rows of teeth and a broad fan at the anterior end.

INCUBATION: This occurs in operculum.

Distribution Elsewhere

J. (D.) steueri, of which this is probably a variety, is rather widely distributed. It was first recorded by Sterzinger (1909) in the Red Sea, at Suez, and has recently been found farther

south in the Red Sea, near Port Sudan (Vine, in press). Phyllis Knight-Jones (1972) has recorded it from Kenya and in discussing this species she tentatively suggested, after studying original material, that *S. treadwelli* is synonymous. This has been recorded from the Philippines (Pillai, 1965) and at Heron Island on the Great Barrier Reef of Australia (Straughan, 1967). *J. (D.) steueri* was also found in southern Australia by Phyllis Knight-Jones (in press), and off northeastern Australia and South Island, New Zealand, by Vine (personal observation). In addition to these records in the Indo-Pacific, Bailey (1970) recorded *J. (D.) steueri* in the Caribbean Sea. It is, therefore, rather remarkable that it has not been discovered elsewhere in the Atlantic or in the Mediterranean.

Remarks

J. (D.) steueri has, until recently, been a rather doubtful species. Zibrowius (1968) considered it to be synonymous with *J. (D.) pseudocorrugata* but material studied from Kenya (Phyllis Knight-Jones, 1972) and the Red Sea (Vine, in press) has indicated several differences between these closely related species. The tube of *J. (D.) steueri* is usually more intricately patterned with three or four longitudinal ridges and deep transverse indentations. The juvenile opercula differ, that of *J. (D.) steueri* having asymmetrical lateral wings arising from the middle of a long, bifid, densely calcified, central talon. The other species has a more fan-shaped talon with the broadest section distally, and the walls of the mature opercular brood chamber are less densely calcified and almost transparent. *J. (D.) steueri* varies in different areas, but there is considerable variation in tubes and talons of specimens from the same area, so it seems sensible for the present to regard these slight geographical variants as belonging to the same species.

The Hawaiian variety described here differs in several points from the forms found in the Red Sea area (Vine, in press). Only dextrally coiling specimens were found. The tube has four longitudinal ridges (compared with three on the Red Sea species) and perforations between the ridges are often complete. Collar

setae are not so clearly cross-striated as those of the Red Sea form. The asetigerous region is longer in the Hawaiian form and the blades of the abdominal setae are broader, approaching in width those of *J. (D.) foraminosa* or *J. (D.) formosa*.

The Hawaiian variety of *J. (D.) steueri* bears some striking resemblances to *J. D. foraminosa* Moore & Bush, 1904, from the Sea of Japan. The original material has since been reexamined by Phyllis Knight-Jones who finds that the tentacles are particularly long, their ends reaching the outer rim of the opercular brood chamber. The species also differs from *J. (D.) steueri* in that the blades of the abdominal setae are shorter and broader, approaching those of *J. (D.) formosa*. The species differs from the latter, however, in having cross-striated collar setae. It seems best at present to regard *J. (D.) steueri* as being distinct from *J. (D.) foraminosa*.

It now seems clear that this Hawaiian material is really *J. (D.) foraminosa* (Bush, in Moore and Bush, 1904). This species was inadequately described, but Phyllis Knight-Jones (personal communication) has examined the type from the Smithsonian Institution and fresh material from Japan. She found that it usually differs from the true *J. (D.) steueri* in the pattern of pitting between ridges on the tube, and always differs in having more transparent walls to the brood chamber and wider blades on the abdominal setae. (In the last character, which is easily seen, it is intermediate between *J. [D.] steueri* and *J. [D.] formosa*.)

Janua (Dexiospira) nipponica Okuda, 1934

Fig. 8d, 12

Material

Eight specimens.

Location

Nanakuli, Oahu, Hawaii.

Habitat

J. nipponica was found in the littoral zone on a red alga.

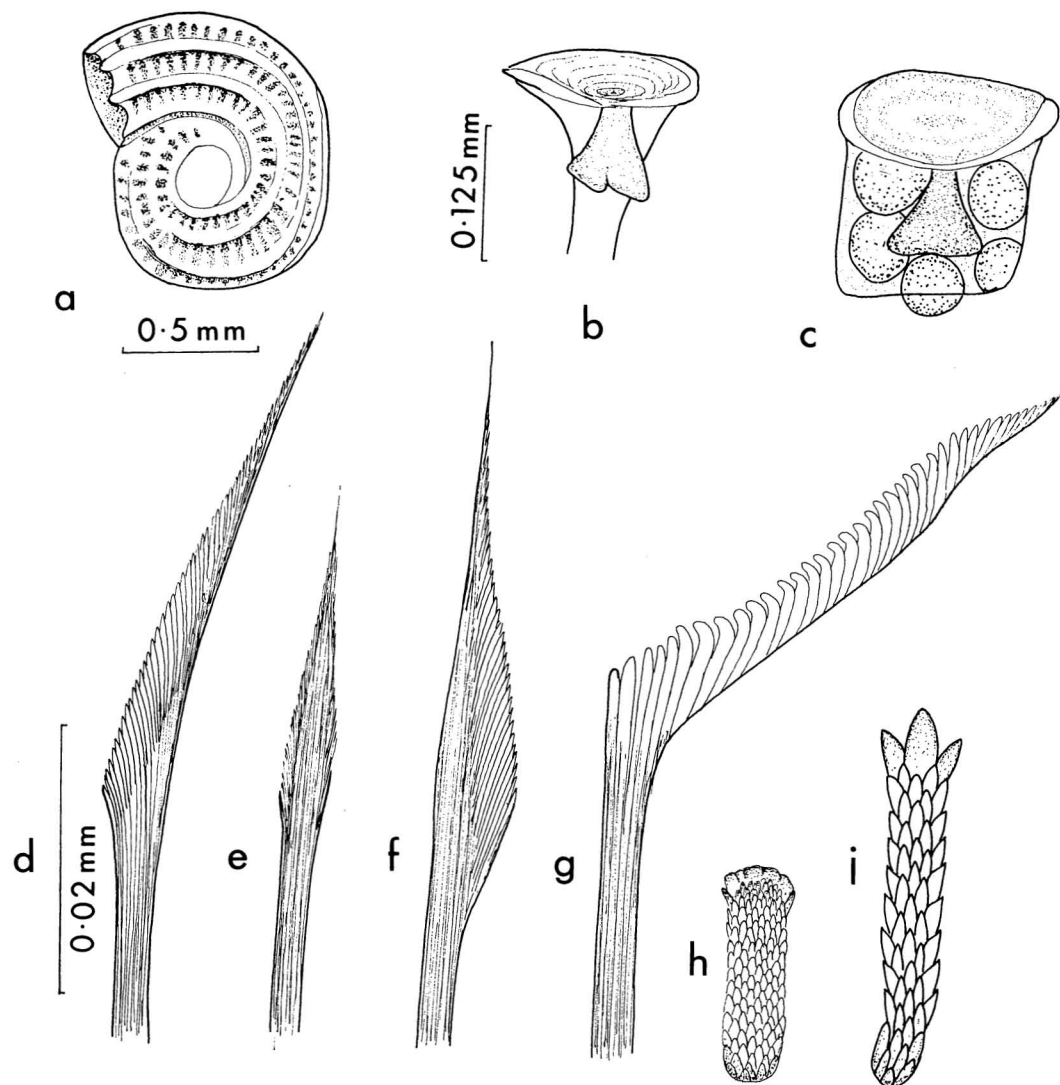


FIG. 12. *Janua (Dexiospira) nipponica*. *a*, Tube; *b*, juvenile operculum; *c*, adult operculum; *d*, collar seta from convex side; *e*, collar seta from concave side; *f*, simple seta from second thoracic fascicle; *g*, abdominal seta; *h*, abdominal uncinus; *i*, thoracic uncinus.

SCALE: *c* as *b*; *e*, *f*, *g*, *h*, and *j* as *d*.

Description of Species

TUBE: Tube is dextral, with three longitudinal ridges on top and one on side of tube. Transverse bars between these ridges create an appearance of deep oblong indentations in the surface of the tube. Two whorls are present. Terminal section sometimes ascends. Coil diameter is 1.5 to 2.0 mm.

OPERCULUM: The operculum is small and has a flat or slightly concave calcareous plate with a wedge-shaped talon. An indentation may be present creating a slightly bifid appearance. Brood chamber has a narrow transparent rim around a more or less flat calcified plate. The walls are almost transparent and the calcified talon is usually less bifid than in *Janua pseudo-corrugata* Bush (1904).

THORAX: Thorax has two pairs of tori. Dorsal collar folds are fused. Collar setae are simple, finely serrated blades, not coarsely toothed or cross-striated on either side. Second and third fascicles have similar simple setae and there are no sickle setae in the third segment. Uncini have at the anterior end a broad peg and two large teeth, one on each side, creating a distinctly trifid appearance. Teeth of the uncini are arranged rather irregularly, in approximately four longitudinal rows.

ASETIGEROUS REGION: Region is long, approximately equivalent to 10 times the distance between the first two abdominal tori.

ABDOMEN: This structure has six rows of uncini on each side. Setae are geniculate and have their blades relatively shorter than in many *Janua* species. Secondary setae are present in some segments. Uncini are broad and have approximately six longitudinal rows of fine teeth. The anterior end lacks teeth and appears somewhat fluted.

INCUBATION: This occurs in the operculum.

Distribution Elsewhere

Species is known in Japan as *S. nipponicus* (Okuda, 1934, 1937) and as *S. alveolatus* (Imajima and Hartman, 1964). In South Africa it is known as *S. foraminosus*.

Remarks

It has been suggested by Ushakov (1955), Imajima and Hartman (1964), and Pillai (1965) that *J. (D.) nipponica* is synonymous with *J. (D.) alveolata* Zachs (1933). Although the description by Zachs lacks diagrams and does not satisfactorily describe the operculum or details of setation, it nevertheless seems to refer to a species quite different from *J. (D.) nipponica*. The tube of *J. (D.) alveolata* is semi-transparent and Zachs mentions that incubation probably takes place in the tube. Although he drew a loose comparison between it and *J. (D.) foraminosa* based on both having smooth collar setae and foramina in their tubes, he dismissed the possibility that they could be the same because the opercula were not similar.

Imajima and Hartman follow the suggestion of Ushakov and list *S. nipponica* as a homonym

of *J. (D.) alveolata*. Their description clearly refers to *J. (D.) nipponica* rather than to *J. (D.) alveolata*.

Day (1961) described a species from South Africa which he identified as *J. (D.) foraminosa* and kindly made available for examination. It clearly has trifurcate thoracic uncini (as Day described) and is apparently the same as the species described above as *J. (D.) nipponica*. In type material of *J. (D.) foraminosa* Bush, kindly supplied by the Smithsonian Institution, the thoracic uncini have single pointed pegs.

The shape of the talon suggests close affinity with *J. (D.) pseudocorrugata* (also described above), but it can be easily distinguished from this species because it lacks cross-striations on the collar setae and has trifid pegs on the thoracic uncini.

Subgenus *Leodora* de Saint-Joseph (1894), amended

Sinistral coiling is present; collar folds are unfused; collar setae are not coarsely toothed or cross-striated; sickle setae are absent.

Type

Janua (Leodora) laevis (Quatrefages, 1865).

Janua (Leodora) knightjonesi (de Silva, 1965)

Fig. 8e, 13

Material

Eight specimens are preserved in tubes and three mounted in polyvinyl-lactophenol.

Location

Sand Island in Kaneohe Bay, Oahu, Hawaii.

Habitat

Species was found in the intertidal zone on stones.

Description of Species

TUBE: This is sinistral, with three well-defined longitudinal ridges. Mouth of tube is sometimes upturned away from the substrate. Coil diameter is 1.5 mm.

OPERCULUM: Operculum often bears one, two, or occasionally three brood chambers in se-

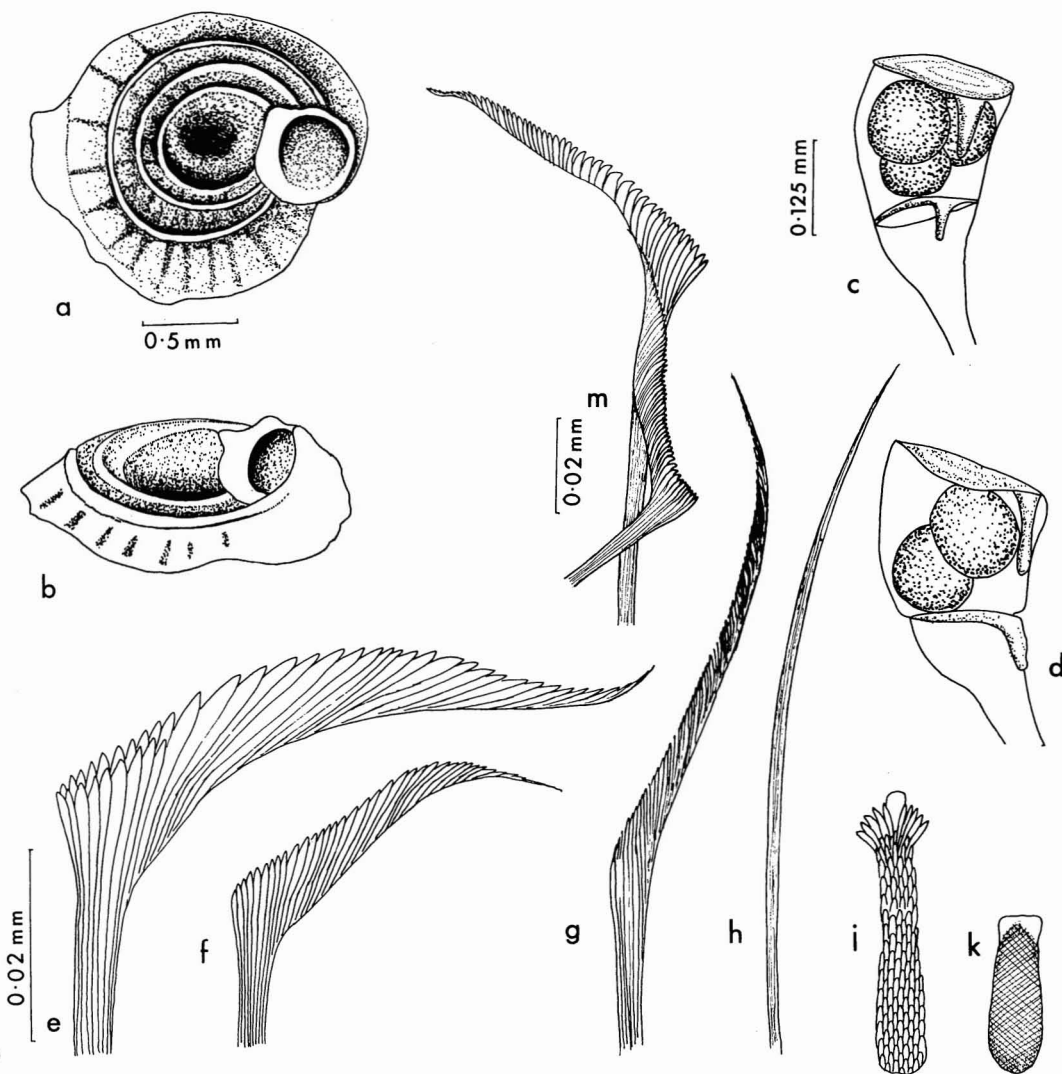


FIG. 13. *Janua (Leodora) knightjonesi*. *a*, Tube; *b*, side view of tube; *c*, dorsal view of adult operculum; *d*, side view of adult operculum; *e*, collar seta from fascicle on convex side; *f*, collar seta from fascicle on concave side; *g*, simple seta from third thoracic fascicle; *h*, capillary seta from third thoracic fascicle; *i*, thoracic uncinus; *j*, abdominal uncinus; *k*, abdominal uncinus; *m*, primary and secondary abdominal setae.

SCALE: *b* as *a*; *d* as *c*; *f*, *g*, *h*, *j*, and *k* as *e*.

ries, each with very lightly calcified, transparent walls, and a more or less flat plate bearing a white calcified talon, which is approximately round in cross section. Each chamber contains developing embryos, those in the distal chamber being more developed. The basal plate of the distal chamber is also the terminal plate of the chamber immediately underneath.

THORAX: This structure has two pairs of tori. Collar setae are rather geniculate and broad proximally. Those on the convex side have blades almost twice as long as those of the concave side, but the basic structure of the collar setae on both sides is similar, each having blades with jagged edges, the teeth being somewhat coarser proximally than distally. The blade is

constructed of several layers of teeth and in some cases these have peeled back (on the polyvinyl-lactophenol mounts) to reveal the multi-layered structure of the blade. There are no distinct cross-striations, however, inasmuch as the rows of teeth on the edge of the blade are too few and too irregularly arranged. Associated with the collar setae on each side are several capillary setae. Setae of the second and third fascicles have extremely narrow, finely striated blades and are accompanied by some capillary setae. There are no sickle setae in the third thoracic fascicles. Each uncus has a blunt anterior peg and on each side of this there are several teeth which tend to fan out, giving the anterior end a shape reminiscent of a tapering spade. This is rather characteristic of this species and has not been mentioned by previous authors.

ASETIGEROUS REGION: This is long, approximately seven times the distance between the first and second abdominal tori.

ABDOMEN: The abdomen has approximately six segments. Setae are geniculate with rather long narrow blades and slightly recurved teeth. Secondary setae are present in several abdominal segments. These have already been noted in other members of the genus *Janua* (Vine, in press; Knight-Jones, 1972). They have rudimentary shafts and blades approximately the same length as those of the primary abdominal setae. Uncini have approximately 10 longitudinal rows of fine teeth and a broad, somewhat convoluted fan.

INCUBATION: Incubation in *Janua knightjonesi* takes place in opercular brood chambers.

Distribution Elsewhere

Species is found in Ceylon (de Silva, 1965); West Indies (Bailey, 1970); Australia (personal observation by one of us, P.J.V.). As *S. laevis*, it is found in Curaçao (Augener, 1936).

Remarks

De Silva (1965) described *Janua* (*Leodora*) *knightjonesi* from Ceylon. He recognized its affinities with the subgenus *Leodora* and the type "*S. laevis*" Quatrefages (1865). He listed other species which he believed should be included in this subgenus. They were: *S. verruca*

Fabricius (1780); *S. valida* Verrill (1874); *S. perrieri* Caullery & Mesnil (1897); *S. abnormis* Bush (1904), and *S. coronatus* Zachs (1933). These were grouped on the basis of their sinistral coiling and simple collar setae and, in several cases, the mode of brood protection had not been recorded.

Bailey (1969b) reviewed the taxonomy of Spirorbinae and emphasized the importance of methods of brood protection. On this basis the subgenus *Leodora* is separated from the genus *Romanchella* Caullery & Mesnil (1897) (see Knight-Jones, in press). Recent studies have shown that the latter genus includes *R. perrieri* and probably *R. coronata*. Of the remaining little-known species which de Silva grouped in the subgenus *Leodora*, only *S. laevis* has opercular details somewhat similar to those of *J. (L.) knightjonesi*.

The status of *J. (L.) laevis* was recently discussed by Bailey (1970) who found that material identified by Augener (1936) as *S. laevis* was the same species as that described by de Silva (1965) from Ceylon as *S. knightjonesi*. In view of the taxonomic history of *J. (L.) laevis* it was correct of de Silva to apply a new name to the species which had already been described by Augener because it was clearly different from that first described by Quatrefages as *S. laevis* (see below). *J. (L.) knightjonesi* differs from every adequate description of material identified as *S. laevis* (except for that of Augener) in at least some of the following characters: its sinistral tube with three distinct longitudinal ridges; its stacked opercula, every chamber of which possesses a talon; unfused collar; broad geniculate collar setae which lack a proximal fin or cross-striations; the shape of the anterior end of the thoracic uncini; and the absence of sickle setae from the third thoracic fascicles.

J. (L.) knightjonesi has now been found in Ceylon (de Silva, 1965); West Indies (Augener, 1936; Bailey, 1970); Australia (personal observation, P.J.V.), and Hawaii. It thus appears to have an Indo-Pacific and Caribbean distribution. It has not been recorded on the west coast of the Americas or in Europe, and Bailey (1970) offered a possible explanation for these apparent gaps in its distribution. It is pos-

sible, however, that some records of *S. laevis* in Europe have referred to this species and further research may show that these gaps are more apparent than real.

THE PROBLEM OF "SPIORBIS LAEVIS"

The original description by Quatrefages (1865) of a species from Guettary was inadequate. It did not refer even to the direction of coiling, but some later authors appear to have regarded the name as indicating sinistral coiling, because the Latin *laevis* means on the left side. In fact, the Latin *laevis* means smooth and it is uncertain whether the species which Quatrefages described was sinistral or dextral. He was clearly referring to smoothness of the tube in the name *laevis*, because he placed his species under the heading "Spirorbe lisse." His description covered several other important characters. The animal had only four branchiae and the cylindrical operculum had a narrow rim around the distal plate. He described the operculum as containing red cells which were presumably eggs. He completed this short description (which did not include the setae) with the comment: "Je regret de n'avoir pas pris de notes étendues sur cette petite Annélide."

Claparède (1870) provided a much more complete description of a sinistral species from Naples which he considered fitted the important points in Quatrefages' description of *S. laevis*. At that time taxonomists were not aware of the large number of species of Spirorbinae present in the Mediterranean and N. Atlantic and Claparède was probably justified in guessing that his Naples species tallied with Quatrefages' completely inadequate description of a species from the Bay of Biscay.

Claparède described a sinistral smooth tube and illustrated a rather more cylindrical operculum than that figured by Quatrefages. He described the setae in some detail but made no mention of sickle setae. In fact, he inferred that these were absent: "Les soies dorsales des deux autres segments thoraciques sont filiformes, lancéolées à l'extrémité." He gave drawings of all the setae and his study appears to have been a careful one, so there is no reason to suppose that the species he described had sickle setae in the third thoracic fascicles. His drawing of the

whole animal is perhaps the best drawing from life of any of the Spirorbinae and the best known, having been reproduced in several major textbooks of invertebrate zoology. It seems doubtful, however, if there has been any record since that time of a mature form with only two pairs of tentacles.

Since the work of these two early authors, almost every mention in the literature of *S. laevis* has been either (1) a reference to these first descriptions, without any new material (de Saint-Joseph, 1894; Caullery and Mesnil, 1897; Rioja, 1923; Fauvel, 1927; Prenant, 1927; Cornet and Rullier, 1951; Laubier and Paris, 1962; L'Hardy and Quiévreux, 1964; Cabioch, L'Hardy, and Rullier, 1968) or (2) records of its occurrence usually comprising just a single sentence, not supported by drawings or a description or any note of material deposited in a museum (Pruvot, 1897). Pixell (1913) recorded this species at Suez but her brief description referred to a form with three longitudinal ridges. That may well have been the sinistral form of *Janua steueri*, which was recorded there by Sterzinger (1909) and was recently rediscovered in the Red Sea (Vine, in press). Ehlers (1913) described a species from South Africa as *S. laevis* but this had a characteristically ridged tube with deep indentations, and his drawing is also somewhat reminiscent of the sinistral form of *J. (D.) steueri* found in the Red Sea (Sterzinger, 1909; Vine, in press) and of a sinistral species on pearl oysters in the Tuamotu atolls (Fauvel, 1919).

Augener (1936) was the first taxonomist since Claparède to provide an adequate description of material from the Caribbean Sea, which he called *S. laevis*. His specimens differed from earlier descriptions in that they had three distinct longitudinal ridges and often had multiple opercular chambers, each with a talon (see Bailey, 1970). De Silva (1965) discovered the same species as this in Ceylon and, recognizing that it differed from *S. laevis*, called it *S. knight-jonesi*. Although Augener had already provided an almost adequate description of de Silva's species there was good reason for de Silva to rename it inasmuch as it was clearly different from *S. laevis* Quatrefages, and there is a possibility that later authors may discover a species

which tallies closely with that recognized by Claparède as *S. laevis*.

Zibrowius (1968) described a few sinistral opercular-incubating specimens which he obtained from a submarine cave near Marseille; he mentioned a tube with three longitudinal ridges, an operculum like that of *J. (J.) pagenstecheri*, and sickle setae in the third thoracic fascicles. In fact, his description differs from that of *J. (J.) pagenstecheri* only in direction of coiling. In three important details it differs from the species described by Quatrefages and Claparède. Its tube was not smooth, its operculum was more cup-shaped than cylindrical (like Quatrefages' drawing), and there were sickle setae in the third fascicles (not found by Claparède, Fauvel, Pixell, Augener, or any other author).

Direction of coiling may be reversed both within a single species (see Sterzinger, 1909; Bock, 1953; Potswald, 1965; and also Vine, in press) and within a genus (see Knight-Jones, 1971 and Vine, in press), so that it appears possible that the few specimens described by Zibrowius and identified as *S. laevis* were, in fact, sinistral mutants of *J. (J.) pagenstecheri* which he recorded from the same locality and habitat.

If one discounts these records by Augener (1936) and Zibrowius (1968), no record of *S. laevis* has been supported by an adequate description or drawings, since that of Claparède (1870).

In view of the recent rediscovery of the sinistral variety of *J. (D.) steueri* in the Red Sea (Vine, in press) and of the sinistral species within the subgenus *Fauveldora* Knight-Jones (1972), it seems quite probable that some records of sinistral opercular incubators with simple collar setae may have been attributed to *S. laevis* without close investigation of details of tube structure, opercular structure, or setation.

In view of the inadequacy of the original description by Quatrefages and the subsequent failures to find anything that is comparable in detail with the figures of Claparède, it seems that *S. laevis* should be regarded as a *nomen dubium*. It is unfortunate that de Saint-Joseph (1894) selected such a doubtful species when he established the genus *Leodora*.

ECOLOGICAL OBSERVATIONS

The majority of species collected were present in the intertidal zone settling on lava rock, dead corals, and molluscan valves, especially oysters (*Isognomum* sp.), or algae (see Table 1). Only *Pileolaria* (*Pileolaria*) *semimilitaris*, *Pileolaria* (*Duplicaria*) *dalestraughani*, and the *Protolaeospira* sp. were absent from the intertidal collections.

Shallow rock pools in the upper shore and splash zone contained the tube-incubating species *Spirorbis* (*Spirorbella*) *marioni* which is presumably better adapted to avoid desiccation and salinity fluctuations than are most of the opercular-brooding species. The other species which can apparently tolerate the conditions in the upper shore is the opercular incubator *Janua* (*Dexiospira*) *pseudocorrugata* which often settles on valves of the oyster (*Isognomum* sp.) and on lava rock.

Most other species could be found in shallow pools of the middle and lower shore under stones and on algae.

The rather large species *Pileolaria* (*Pileolaria*) *militaris* settles on a calcareous red alga which encrusts the undersides of platelike coral structures. *Pileolaria* (*Simplicaria*) *pseudomilitaris* is an abundant intertidal species usually found on the undersides of stones on the lower shore and in the shallow sublittoral zone. *Pileolaria* (*Duplicaria*) *koehleri* was found intertidally on stones in rock pools but appears to favor settlement below tidemarks and can live in the intertidal zone only when it is permanently covered by water. *Pileolaria* (*Duplicaria*) *dalestraughani* settles on bryozoa encrusting dead corals in deeper water (such as McVey's artificial reef off Oahu, 15 m).

Janua (*Janua*) *pagenstecheri* occurred sparsely on the underside of stones in the intertidal zone and Bailey and Harris (1968) suggested that it may be more sublittoral in tropical conditions. *Janua* (*Dexiospira*) *pseudocorrugata*, *J. (D.) steueri*, and *J. (Leodora)* *knightjonesi* all settle on hard substrate on the middle and lower shore. *J. (D.) steueri* also settles on algae whilst *J. (D.) nipponica* and *J. (D.) turrita* were found exclusively on algae.

Settlement plates lowered at various times into shallow water at Coconut Island, off Oahu, col-

TABLE 1
SPECIES AND NUMBERS OF SPIRORBINAE COLLECTED, BY INTERTIDAL AND SUBTIDAL ZONES

SPECIES	INTERTIDAL		SUBTIDAL	
	ON STONES, DEAD CORALS, OR SHELLS	ON ALGAE	ON STONES, DEAD CORALS, OR SHELLS	ON ALGAE
<i>Spirorbis (Spirobella) marioni</i>	abundant (24)	—	—	—
<i>Protolaeospira</i> sp. <i>A</i>	—	—	rare (1)	—
<i>Pileolaria (Pileolaria) militaris</i>	uncommon (1)	—	—	—
<i>Pileolaria (Pileolaria) semimilitaris</i>	—	—	uncommon (2)	—
<i>Pileolaria (Simplicaria) pseudomilitaris</i>	abundant (19)	—	abundant (11)	—
<i>Pileolaria (Duplicaria) koehleri</i>	abundant (156 +)	—	abundant (+)	—
<i>Pileolaria (Duplicaria) dalestraughani</i>	—	—	probably common (7)	—
<i>Janua (Janua) pagenstecheri</i>	possibly locally common (3)	—	—	—
<i>Janua (Dexiospira) pseudocorrugata</i>	abundant (100 +)	—	abundant in shallows	—
<i>Janua (Dexiospira) steueri</i>	—	present	—	probably common (3)
<i>Janua (Dexiospira) turrita</i>	—	abundant (14)	—	—
<i>Janua (Dexiospira) nipponica</i>	—	probably common (8)	—	probably present
<i>Janua (Leodora) knightjonesi</i>	common (11)	—	—	—

NOTE: Numbers in parentheses indicate number of specimens collected. + indicates large numbers of individuals—not quantitative. Comments are results of observations by authors.

lected many of the species described here. *Pileolaria pseudomilitaris* and *Janua (Dexiospira) pseudocorrugata* were particularly abundant on the plates. After approximately a month's settlement, plates had many fully mature adults of these two species, with well-developed embryos in their opercula.

The paucity of species collected on the island of Hawaii (in comparison with Oahu) and the absence of species from the upper littoral zone, such as *Spirorbis (Spirobella) marioni*, may perhaps be explained by active volcanic action, for a massive lava flow had occurred in the collecting region several years prior to our study. Frequent rises in coastal sea temperature asso-

ciated with these flows must have resulted in repeated reconstruction of the littoral zone. The only possibly endemic species which was found in the littoral zone, *Janua (Dexiospira) turrita*, came from this region, suggesting that the disruptive influence of lava flows may have promoted invasion of the littoral zone by an endemic, but normally sublittoral, species, through the removal of more successful and widely distributed competitors. It must be admitted that this species was not found sublittorally, but then the sublittoral collections were not very extensive.

There is considerable scope for the study of the ecology of Hawaiian Spirorbinae, and it is

hoped that the present taxonomic study will provide a good basis for further work in this area.

ZOOGEOGRAPHICAL DISCUSSION

The species described here show several characteristics typical of tropical and subtropical Spirorbinae. The two dominant genera, *Pileolaria* and *Janua*, are both opercular incubators. Only two out of 13 Hawaiian species incubate their embryos in their tubes. It appears that opercular incubators are generally favored in warm waters, to judge from recent research elsewhere in the tropics (Bailey, 1970; Pillai, 1970; Knight-Jones, 1972; and Vine, in press). Although the opercular brood chambers seem more exposed to predation, they must help embryonic respiration, which may present problems to tube incubators in warm waters.

The affinities between Spirorbinae of the Hawaiian chain and those from other regions at similar latitudes where adequate studies have been carried out are summarized in Table 2. Closest affinity is with the western Pacific (eight out of nine spp.). Spirorbinae from the Indian Ocean (six out of nine), Mediterranean (five out of nine), and Caribbean (six out of nine)

also show close affinities with the Hawaiian species. Although geographically closest to Hawaii, the west coast of America shows least similarity in its assemblage of Spirorbinae (only three out of nine species in common with Hawaii), and the east Atlantic has a similarly low number of species in common with Hawaii.

Ekman (1967, p. 19) has drawn attention to the high percentage of endemic species around Hawaii, citing molluscs, crustaceans, echinoderms, and fish, but Spirorbinae differ from many of these forms in being easily transported as adults and, indeed, as breeding colonies. Such transport of adults is likely to be much more effective in dispersal than the transport by currents of comparatively ephemeral planktonic larvae.

Considering the ease with which many adult Spirorbinae species may be transported on floating algae and the stones or shell fragments associated with these, and on crustacean carapaces, turtle shells, driftwood, ships' bottoms, and perhaps on algae or barnacles attached to cetaceans, the differences in distribution of species is unlikely to be explained by differential transport to various regions. It seems more likely that there are a number of species (approxi-

TABLE 2
SPECIES OF SPIRORBINAE AND AREAS IN WHICH THEY WERE COLLECTED

HAWAIIAN SPECIES	AREA 1	AREA 2	AREA 3	AREA 4	AREA 5	AREA 6
<i>Spirorbis marioni</i>	X	—	—	—	—	—
<i>Pileolaria militaris</i>	X	X	X	X	X	X
<i>Pileolaria pseudomilitaris</i>	—	X	—	—	X	—
<i>Pileolaria koebleri</i>	—	X	X	—	X	X
<i>Janua pagenstecheri</i>	X	X	X	X	X	X
<i>Janua pseudocorrugata</i>	—	X	—	X	X	X
<i>Janua steueri</i>	—	X	X	—	—	X
<i>Janua nipponica</i>	—	X	X	—	—	—
<i>Janua knightjonesi</i>	—	X	X	—	—	X
Percentage similarity of species assemblage with that found around Hawaii	33%	89%	67%	33%	56%	67%

KEY: X, species has been recorded; —, species has not been recorded.

AREAS: 1, Eastern Pacific; coast of U.S.A.; 2, western Pacific; Australia, and New Zealand; 3, Indian Ocean and Red Sea; 4, western Atlantic; Spain and North Africa; 5, Mediterranean Sea; 6, Caribbean Sea.

mately eight) which show a widespread distribution throughout regions with water warm enough for growth of hermatypic corals. Although at similar latitudes to Hawaii, the west coasts of California and of North Africa do not have coral reefs. Cold coastal currents lower surface sea temperatures in these regions. The most widespread warm-water Spirorbinae appear to be *Pileolaria militaris*, *P. pseudomilitaris*, *P. koehleri*, *Janua pagenstecheri*, *J. pseudocorrugata*, *J. steueri*, *J. nipponica*, and *J. knightjonesi*. Of these eight species, *Pileolaria militaris*, *Janua pagenstecheri*, and *J. pseudocorrugata* appear to be eurythermal, also occurring widely in temperate regions.

Not enough Spirorbinae from deeper water localities elsewhere in the Pacific have been studied to establish whether the three new species from the Hawaiian Islands are endemic. The most likely endemic species is perhaps *J. (D.) turrita*, which was abundant on red alga in the intertidal zone on Hawaii but not found on Oahu. It is remarkable that the Hawaiian list of Spirorbinae does not contain more endemic species. Evidently there have been continuous invasions of species from other regions.

SUMMARY

Collections from the Hawaiian chain included 13 Spirorbinae, three of which are new. Eleven species belong to the opercular-incubating genera *Pileolaria* or *Janua*, whereas two tube-incubating genera, *Spirorbis* and *Protolaeospira*, are each represented by single species. Most of the species are widely distributed in coral reef areas and close links exist between Hawaii, the western Pacific, Indian Ocean, Mediterranean, and the Caribbean, whereas links with the west coast of America seem to be slighter. The low numbers of endemic Spirorbinae in the Hawaiian chain and the widespread distribution of species can perhaps be explained by the ease with which adults may be transported. Distribution of species appears to reflect hydrological conditions and physiological tolerances of species rather than greatly different transport.

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