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New species and a new subgenus of Spirorbinae (Serpulidae: Polychaeta) from Kenya

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(With 7 figures in the text)

Four species were collected, all attached to marine angiosperms, *Pileolaria daijonesi* **sp.n.** being the most abundant. The other three have the collar folds fused dorsally, as is characteristic of *Dexiospira* (= *Neodexiospira* Pillai), which is here regarded as a subgenus of *Janua*. *Janua* (*Dexiospira*) *formosa* (Bush) and *Janua* (*Dexiospira*) *steueri* Sterzinger are distinguished clearly from one another for the first time and shown to be widely distributed in warm seas. *Janua* (*Fauveldora*) *kayi* **subgen. et sp. n.** is a very closely related sinistral form, which extends to the Persian Gulf and Ceylon.

Reviewing serpulids, it seems that the primitive position of the operculum in Serpulinae and Spirorbinae was sinistral. The most recent changes involving this character, however, have been *situs inversus* back-mutations, from stocks which are dextral and presumably more labile.

Contents

Introduction

The collections on which the following account is based were made during August 1969 in Turtle Bay, Watamu district, mostly on the north-east side of the mouth of Mida Creek (Isaac & Isaac, 1968). They were brought back by Dr Q. O. N. Kay and Dr D. A. Jones, members of an expedition organized by the Marine Sciences Laboratory, Menai Bridge, U.K. All Spirorbinae collected were on leaves of marine angiosperms, which had been growing in shallow water.

The material was preserved in 5% formaldehyde in sea-water and examined about six months later. Some colours remained and are recorded here, by comparison with the handbook of Kornerup & Wansher (1967), but had no doubt changed from the fresh state. Tubes were broken open by mounted entomological pins and the details of the opercula were distinguished by reflected light. Setae were examined in polyvinyl-lactophenol preparations (Knox, 1951; Gee, 1964; Harris, 1969) and viewed by phase contrast with quartz-iodide illumination. Three of the species found had collar folds fused dorsally, forming a membranous roof over the dorsal groove of the thorax, which is thus converted to a tunnel. This character, which was recently discovered by Pillai (1970), is difficult to see in animals preserved in their tubes, but was demonstrated conclusively by probing with the thin end of a human eyelash, the thick end of which had been stuck to a needle. Drawings were made on squared paper with the help of squared eyepiece graticules, the largest setae and uncini of each type and species being selected for illustration. The species found were compared with type material kindly provided by the Smithsonian Institution of Washington and the British Museum (Natural History).

In treating the taxonomy of Spirorbinae, some authors (Harris, 1969; Bailey, 1969*b*), recognizing that knowledge of this group is still remarkably incomplete, treat it provisionally as mainly comprised of a single genus, *Spirorbis*. Pillai (1970), however, regards it as a separate family, ranking equally with the Serpulidae and containing many genera. This trend is followed here, but more cautiously. Since there are many species of this group still to be described, it seems best at present to regard some of the genera recognized by Pillai as subgenera, reserving the rank of genus for what may be regarded as major subdivisions of the subfamily Spirorbinae. The diagnoses of genera and subgenera are here amended or extended using the criteria summarized by Bailey (1969*b*).

Diagnoses and descriptions

The Kenyan material contained only opercular incubators, as is usual in shallow tropical waters (Bailey, 1969*a*, 1970; Harris, 1969). In the following account *Pileolaria* is treated first, since it is taxonomically closest to the oldest genus *Spirorbis*.

Genus *Pileolaria* Claparède 1868 amended

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 the abdominal setae (Fig. 7(a)); sickle setae may or may not be present; thoracic uncini very slender, with one to three longitudinal rows of teeth; pegs of thoracic uncini about as broad as rest of uncinus and not pointed in surface view; largest abdominal tori lie in the posterior half of the setigerous region (Fig. 6a); larvae have single, white, mid-dorsal attachment glands.

Type: *Pileolaria militaris* Claparède (1868).

Pileolaria daijonesi **sp.n.** British Museum (Nat. Hist.) reg. no. 1971: 4a

Tube sinistral, loosely coiled (evolute), nonporcellanous, with fine irregular growth rings. These meander slightly, to give a faint suggestion of longitudinal ridges (Fig. 1(a)).

Operculum. The brood chamber is capped by a dome-shaped calcified helmet without any ornamentation (Fig. 1(b), (c), (d)). In two specimens this dome was slightly bilobed distally, but in the great majority it was more or less hemispherical. The juvenile opercular plate is concave and transparent, with a peg-shaped talon in a slightly eccentric position (Fig. 1 (e)).

Colour (preserved). Tentacles (seven), thorax, abdomen and embryos dull yellow-orange (4B8 in Kornerup & Wanscher), stomach dark orange (5B8).

Thorax. Collar setae with fin and strongly cross-striated blade (Fig. 1(f)). A few capillary setae occur in the same fascicles. Setae of the second fascicles bear simple blades which are about the same size as those of the collar setae (Fig. 1(g)). In the third fascicles some setae are simple and slender and others are sickles (Fig. 1(h)). Uncini with small teeth behind the anterior peg, followed by paired larger teeth and finally by single teeth. The single teeth which cover most of the length of each uncinus appeared to be arranged diagonally, but this may have been due to the uncini showing some degree of tilt one way or the other, perhaps under coverslip pressure (Fig. 1(k)).

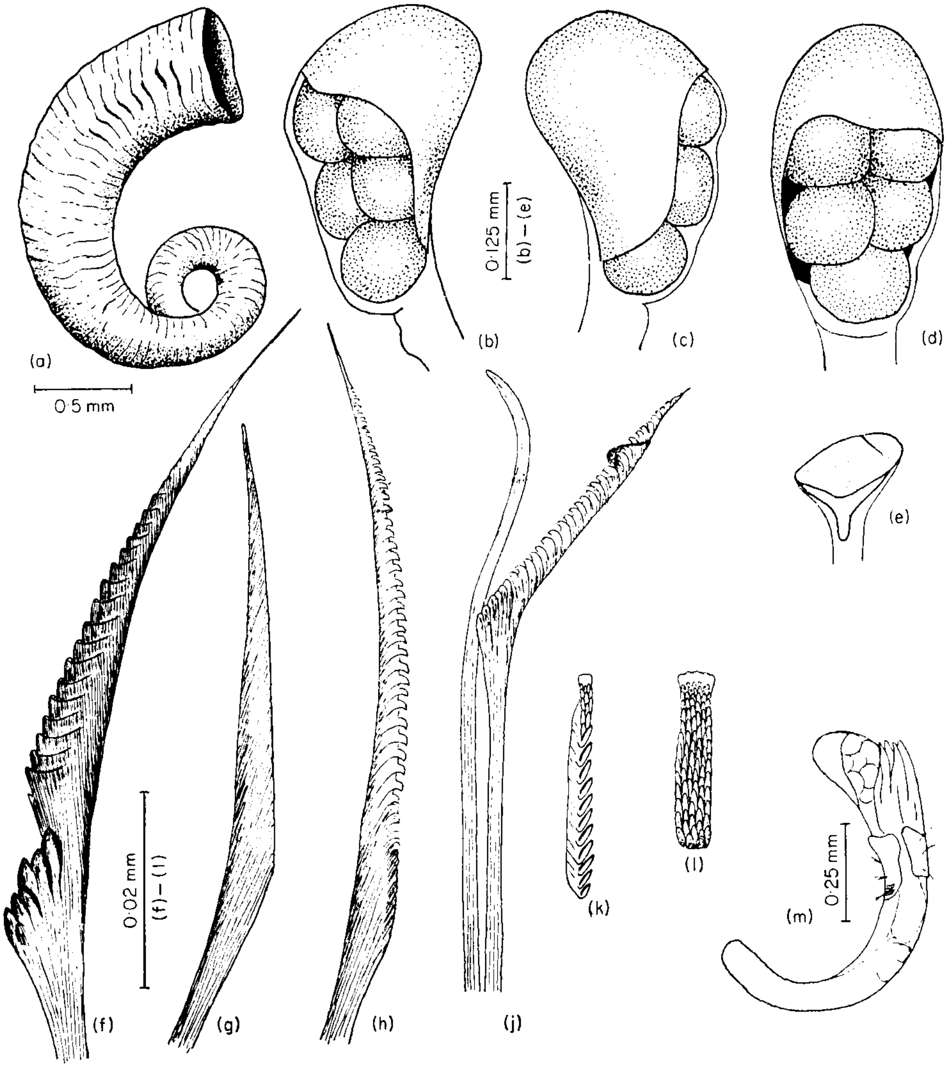

FIG. 1. *Pileolaria daijonesi:* (a) tube; (b), (c) side views of the adult operculum; (d) ventral view of adult operculum; (e) juvenile operculum; (f) fin and blade collar seta; (g) simple seta of the 2nd and 3rd fascicles; (h) sickle-seta of the 3rd fascicle; (j) a pair of abdominal setae, one of which is a simple capillary; (k) thoracic uncinus; (l) abdominal uncinus; (m) whole animal, showing the dorsal collar margins free and unfused.

Abdomen. Setae geniculate, slender and often paired, particularly on the convex side. A few of the more posterior setae may be simple capillaries (Fig. 1(j)). About ten rows of uncini each with a broad, faintly fluted anterior peg, which projects slightly beyond the anterior teeth (Fig. 1(l)). The teeth are arranged in approximately five rows.

Incubation is in the operculum, which usually contains about ten embryos.

Setation. The distribution of uncini (Fig. 6(a)) and relative sizes of setae (Fig. 7(a)) agree with the generic diagnosis given above.

Distribution. Kenya, Watamu district, numerous on leaves of *Enhalus acoroides*, at depths of about 2 m.

Remarks. This species somewhat resembles the form from the Antarctic described by Harris (1969) as *Spirorbis moerchi* Levinsen (1883). The operculum differs, however, in being hemispherical without any rim, whilst the tube is evolute and the sickle setae lack the extraordinarily broad blades figured for the Antarctic species.

In fact the name *moerchi* has most frequently been used for forms from British Columbia (Bush, 1904; Pixell, 1912; Berkeley & Berkeley, 1952; Potswald, 1965). Material identified by Berkeley and loaned by the Smithsonian Institution was found to have an operculum somewhat like that figured by Harris (1969), but the distal margin was bilobed ventrally as the result of a shallow cleft, and in some specimens the rim was emphasized by the presence of tubercles. Moreover this material had collar setae with only faint cross-striations and lacked sickle setae, thus differing markedly from most species of *Pileolaria*. The only other *Pileolaria* species described as lacking sickle setae are, so far as I am aware, *Pileolaria berkeleyana* Rioja (1942), *P. pseudomilitaris* (Thiriot-Quévreux, 1965) and *P. regalis* (Bailey & Harris, 1968). This absence of sickle setae agrees with earlier descriptions of *P. moerchi*, from the Pacific coast of America, including Mexico (Rioja, 1942). Clearly it would be best not to give the name *P. moerchi* to forms with sickle setae, pending examination of material from the type locality (West Greenland).

The Kenyan form somewhat resembles the Ceylon species *P. grandis* Pillai (1970) and the West Indian *P. quasimilitaris* (Bailey, 1970), except that the adult opercula of both are richly ornamented with spines. The young opercula of the former, however, are fig-shaped and without spines, and may contain eggs, according to Pillai. They are quite transparent, however, and thus differ from both adult and juvenile opercula of *P. daijonesi*, but it is interesting to note the similarity of the tubes.

The operculum of *P. daijonesi* strongly resembles that of a Plymouth form referred to by Stebbing (1970) as *P. heteropoma* (Zibrowius, 1968) although it lacks the characteristic single spine seen in Mediterranean specimens of this species. *P. heteropoma* differs from *P. daijonesi*, however, in having a tightly coiled tube with three distinct longitudinal ridges; collar setae with blades much larger than the blades of the other thoracic setae; abdominal setae more strongly geniculate and with blades relatively broader; abdominal uncini with more rows of longitudinal teeth (about eight); and about double the number of thoracic uncini.

The form of the thoracic uncini of *P. daijonesi* is characteristic of many species of *Pileolaria* e.g. *P. heteropoma*, *P. militaris*, *P. quasimilitaris*, *P. clavus* (Harris, 1968), *P. pseudomilitaris*, *P. regalis* and *P. moerchi* (from British Columbia). Pillai similarly describes the thoracic uncini of *P. grandis* as having a single row of teeth.

Genus *Janua* Saint-Joseph 1894 redefined

Mostly with dextral coiling; incubation 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; collar setae without a toothed fin; abdominal setae with blades as big as or bigger than those of the collar setae (Fig. 7(b), (c) and (d)) and often accompanied by secondary setae, with rudimentary shafts (Vine, in press); thoracic uncini with anterior pegs narrow and more or less pointed (in surface view); largest abdominal tori lie in the anterior half of the setigerous region (Fig. 6 (b), (c), and (d)) larvae have paired white attachment glands in thoracic region.

Subgenus *Janua*

Dextral coiling; talon when present a simple peg; sickle-setae present in the third thoracic fascicles; collar not forming a tunnel dorsally.

Type: *Janua* (*Janua*) *pagenstecheri* (Quatrefages, 1865).

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

Coiling usually dextral; talon when present flattened and often bifid; sickle-setae absent; margins of the collar usually fused to form a tunnel over the mid-dorsal thoracic groove.

Type: *Janua* (*Dexiospira*) *pseudocorrugata* Bush (1904) (= *Spirorbis corrugatus* Caullery & Mesnil, 1897).

It is regrettable that the rule of priority makes it necessary to use for this well-defined subgenus a name which has had a chequered history. Caullery & Mesnil proposed it as a subgenus of *Spirorbis*, to include a heterogenous group of dextrally coiling species, the first of which was *S. spirillum* L. and the second *S. armoricanus* (St-Joseph), but these two closely related species are best placed in the genus *Circeis* St-Joseph (1894). Chamberlain (1919) first restricted the name *Dexiospira* to what would appear to be a natural group of species, assigning *Dexiospira pseudocorrugata* (Bush) as the genotype. Bush (1904) gave this name to the species from France and S. Europe which is well known under the name of *S. corrugatus* Montagu. She did so on the grounds that the name *corrugatus* was first given to a sinistral form from Britain, and the grouping of species in Montagu's account (1803) shows that she was right, in spite of what Fauvel (1914) has written to the contrary.

Pillai (1970) first described the fused collar folds of these forms, but grouped them in a new genus *Neodexiospira*. He separated them from *Dexiospira* because he found no collar-fold fusion in specimens which Fauvel had identified as *Spirorbis corrugatus* and deposited in the British Museum (Nat. Hist.). This material (only one intact specimen) has been re-examined and Pillai's observation was confirmed, but the species is not *Janua pseudocorrugata* (see p. 8). Examination of numerous specimens of *J.*(*D.*) *pseudocorrugata* from Roscoff, Lisbon, Corsica, Chios and Malta has shown that the collar folds are fused dorsally. In view of this it seems inevitable that the definition of *Dexiospira* must be extended to include Pillai's important addition to knowledge of Spirorbinae.

Janua (*Dexiospira*) *formosa* (Bush, 1904)

Tube is dextral, nonporcellanous, with about one and a half whorls showing, and with three (sometimes four) longitudinal ridges. There are transverse markings between and outside the ridges (Fig. 2(a)).

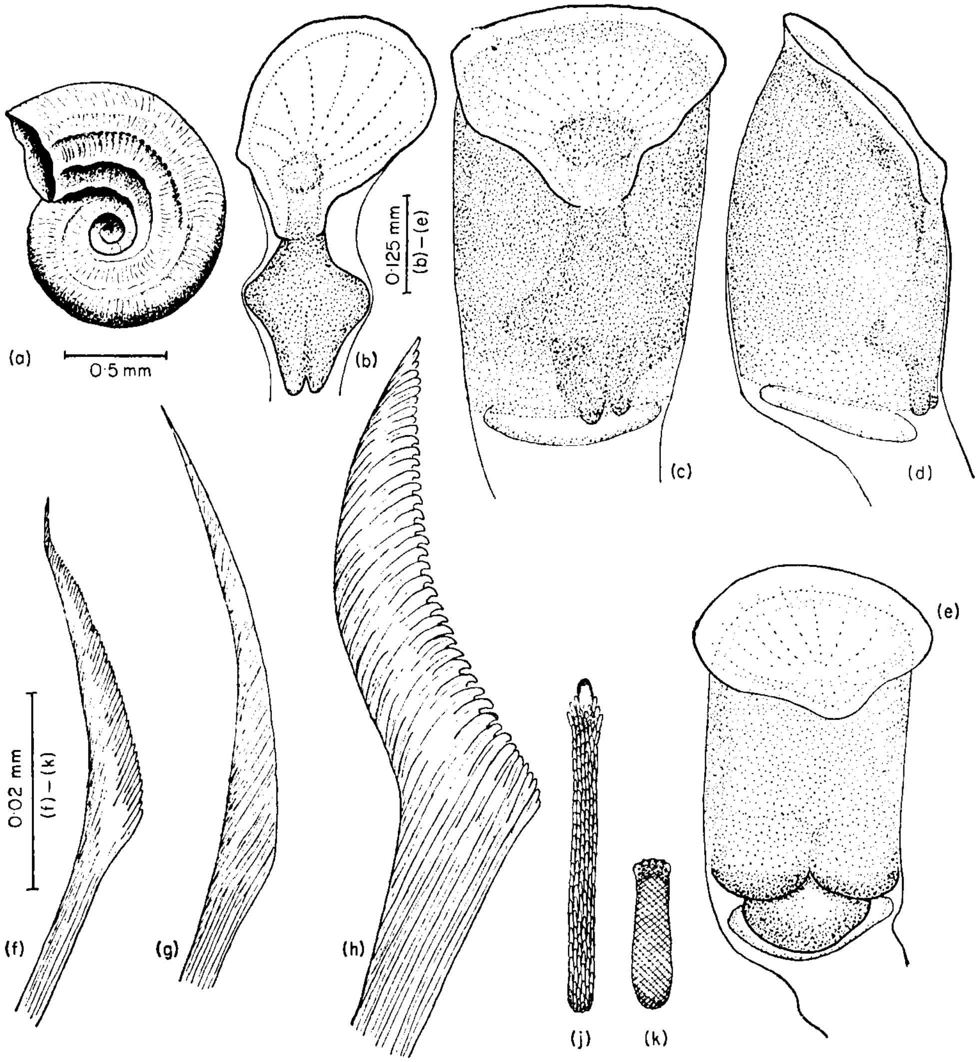

FIG. 2. *Janua* (*Dexiospira*) *formosa:* (a) tube; (b) dorsal view of a juvenile operculum; (c) dorsal view of a first stage adult operculum not yet filled with embryos; (d) side view of (c); (e) dorsal view of mature adult operculum containing embryos; (f) simple collar seta from the convex side; (g) simple seta as found in the 2nd and 3rd fascicles; (h) abdominal seta; (j) thoracic uncinus; (k) abdominal uncinus—cross hatching represents teeth too small to be seen distinctly.

Opercular plate is oblique, elliptical, flat or slightly concave with the rim depressed dorsally (sometimes quite sharply), where it is closely associated with a heavily calcified talon. There is some variation between specimens but the talon always has two terminal and two lateral lobes (Figs. 2(b), (c)). The distal plate is somewhat wider than the incubatory chamber which develops in mature specimens, so that it forms a rim which is prominent on the ventral side but scarcely distinguishable dorsally. The cylindrical wall of the chamber is strongly calcified and appears granular. The granules tend to be arranged in longitudinal rows, but are difficult to distinguish when embryos are present. The talon is closely associated with the wall, but is more opaque and can therefore be easily distinguished. The secondary plate forms in due course a little below the base of the cylinder and does not seem to produce a talon in later brood chambers (Fig. 2(e)).

Colour (preserved). Tentacles (seven in number), thorax, abdomen and embryos, pale dull yellow (3B3); stomach pale olive brown (4C5).

Thorax. Collar fused dorsally as in related species (see Fig. 5). Collar setae with very small simple blades which have finely serrated margins on the convex side (Fig. 2(f)) and almost smooth margins on the concave, both types without cross-striations. Capillary setae also present. Setae of the second and third fascicles larger and with smooth margins (Fig. 2(g)). Uncini with about five rows of teeth, of which the anterior ones tend to splay out on each side of the narrow anterior peg (Fig. 2(j)).

Abdomen. A long asetigerous region is followed by 10–11 rows of uncini, each uncinus with approximately 8–9 rows of teeth covering a broad, faintly fluted anterior projection (Fig. 2(k)). Abdominal setae geniculate and massive compared with the thoracic setae (Fig. 2(h)). In fact the widths of the blade and the top of the shaft are unusually large when compared with other *Janua* species. These setae are often paired, but one of the pair may be little more than a full-sized but more or less shaftless blade, which lies alongside the shaft of the main setae, as though still embedded in a follicle. These secondary setae are also seen in *J.* (*D.*) *steueri* (Fig. 4(k)) and are indeed rather characteristic of the genus *Janua* (Vine, in press).

Incubation is in the operculum, with about 12 embryos.

Setation. The distribution of uncini (Fig. 6(c)) and relative sizes of setae (Fig. 7(c)) are as in the generic diagnosis above (p. 5).

Distribution. Bermuda, numerous on *Sargassum* and also said to occur on stones (Bush, 1904 & 1910); Bonaire, West Indies, sparsely on *Thallasia* at Im (p. 8); Mida Creek, Kenya, sparsely on *Cymodocea aliata*, mainly attached between the ligule and the

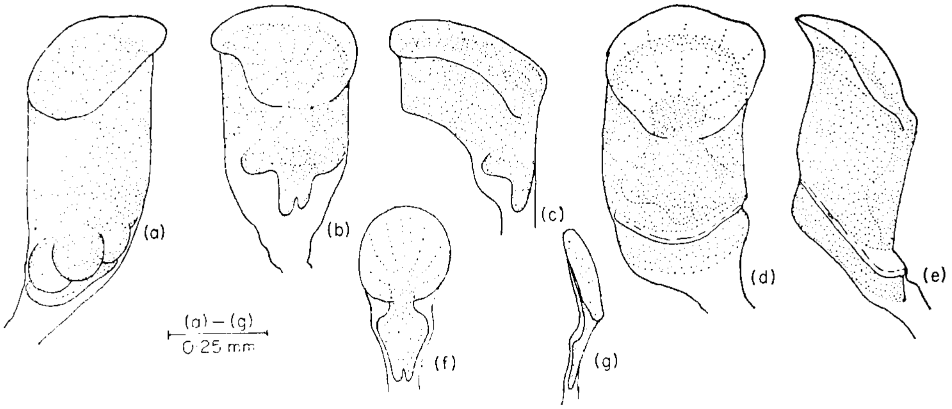

FIG. 3. *Janua* (*Dexiospira*) *formosa* from Bermuda, identified by K. H. Bush, showing range of opercular variation: (a) mature operculum of lectotype; (b) dorsal view of a partially formed first stage mature operculum; (c) side view of (b); (d) dorsal view of a first stage mature operculum (talon present) with a partially formed later stage operculum beneath (talon absent); (e) side view of (d); (f) dorsal view of a juvenile operculum; (g) side view of (f).

blade, at 0·5 m; Ceylon, numerous on a marine angiosperm from a lagoon between Palavi and Kalpitiya at 0·2–2 m (below); south-east Australia, numerous on the kelp *Ecklonia radiata* (pers. obs.).

Remarks. This material agrees closely with some on *Sargassum* from Bermuda kindly supplied by the Smithsonian Institution that had been collected by G. B. Goode and identified by Dr K. H. Bush. It also agrees with the original description (Bush, 1904) which was of material from that region. A lectotype and paralectotypes (Fig. 3) were selected, since no types had previously been designated. Paratypes of *Neodexiospira fauveli* Pillai (1970) from the British Museum (Natural History) were found to consist of 39 dextral and 19 sinistral forms. Five of the dextral forms were extracted from their tubes for examination and all proved to be *J.* (*D.*) *formosa*. Some of the sinistral forms were examined and found to be the same species as that described here later (p. 11). The description of *N. fauveli* fits the characters of *J.*(*D.*) *formosa* except for the setae, which are like those of the sinistral form.

Material from Atlantic *Sargassum* (Station 2103, Campagne 1905, Fauvel, 1914) which was identified as *Spirorbis corrugatus* by Fauvel (see p. 5), is possibly this species, for the only intact specimen available has the characteristically broad-bladed abdominal setae. This specimen had the collar folds separated dorsally, so it seems that collar fusion may be a somewhat variable character in *Dexiospira*, as it is said to be in *Mercierella* (Straughan, 1966). However, several specimens of *J.* (*D.*) *formosa* from Atlantic *Sargassum* 39° 07′ N, 70° 24′ W (200 miles from New York, 500 miles from Bermuda), which were kindly provided by Dr Scheltema, were examined carefully and were found to have fused collar folds. Similar material sent by the Smithsonian Institution, 34° 01′ N, 76° 05′ W (250 miles from C. Hatteras, 550 miles from Bermuda) also proved to be *J.* (*D.*) *formosa*.

In the Kenyan collection this species occurred intermixed with another form, *Janua* (*Dexiospira*) *steueri* (Sterzinger, 1909). These two forms are easily confused. Material from the West Indies labelled *Spirorbis steueri* by Bailey (1970) was re-examined and was found to contain both species. The original descriptions of both were brief and no comparison between them has been made before. A summary of the differences between them is given on page 15.

Janua (*Dexiospira*) *steueri* (Sterzinger, 1909)

Tube is dextral, non-porcellanous, with about one and a half whorls showing and with three to four longitudinal ridges. The tubes were somewhat decalcified (Fig. 4(a)) and indistinct pits occurred between the ridges, in the position of what may once have been transverse furrows (p. 10).

Opercular plate is elliptical, oblique and concave. The talon shows some variation, but arises dorso-eccentrically. It bears four lobes, two terminal and two lateral, and is indeed very similar to that of *J. formosa* except that the lateral wings tend to be transparent (Fig. 4(b), (c)). Mature specimens develop a cylindrical brood chamber of less diameter than the opercular plate, which thus forms a distal peripheral rim. Although the walls of the chamber are calcified and granular, they are sufficiently translucent to allow the opaque areas of the closely associated talon to be distinguished. The secondary plate forms a little way below the chamber and does not seem to produce a talon in later brood chambers (Fig. 4(d)).

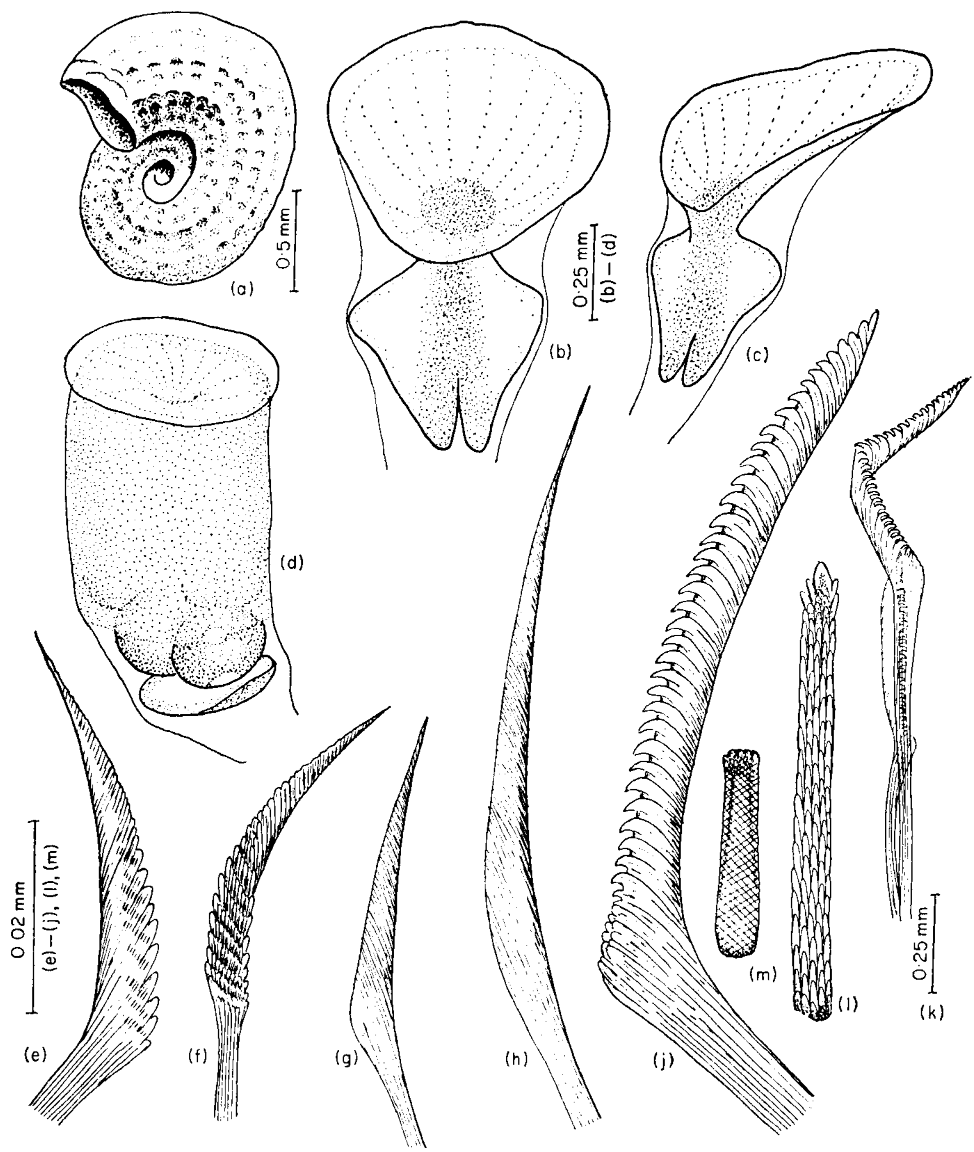

FIG. 4. *Janua* (*Dexiospira*) *steueri:* (a) tube; (b) dorsal view of a juvenile operculum; (c) dorso-lateral view of (b); (d) dorso-lateral view of a mature operculum; (e) side view of a simple faintly cross-striated collar seta from the convex side; (f) another collar seta (convex side) showing edge view proximally and side view distally; (g) simple seta, with smooth margins from the concave side; (h) simple seta as found in 2nd and 3rd fascicles; (j) abdominal seta; (k) abdominal seta (lower magnification) showing a secondary seta in the typical position alongside the shaft; (l) thoracic uncinus; (m) abdominal uncinus—cross-hatching represents teeth too small to be seen distinctly.

Colour (preserved). Tentacles, thorax, abdomen and embryos pale dull yellow (3B3), stomach pale olive brown (4C5).

Thorax. Collar folds fused dorsally. Collar setae, which are accompanied by capillaries, with very small simple blades, those on the concave side having very coarsely serrated margins and cross striations, which may be rather indistinct from certain viewpoints (Fig. 4(e), (f)). Those on the concave side similar to those of the second and third fascicles, in having simple blades with more or less smooth margins (Fig. 4(g), (h)). Uncini with about five longitudinal rows of teeth, of which the anterior ones tend to splay out on each side of a narrow peg (Fig. 4(l)).

Abdomen. Setae geniculate and with recurved teeth on long slender blades (Fig. 4(j)), which can be twice as long as the blades of the collar setae. Secondary setae, with shafts reduced or absent (p. 7), are often associated with these setae (Fig. 4(k)). Long asetigerous region followed by about ten rows of uncini, each uncinus with about eight or nine longitudinal rows of teeth and a wide blunt anterior peg with a scalloped margin (Fig. 4 (m)).

Incubation in the operculum, with about 12 embryos.

Setation (Figs 6 and 7) agreeing with others in this genus.

Distribution. Suez harbour (Sterzinger, 1909) on *Cystoseira*, corals and shells; Curacao, West Indies (Bailey, 1970) on *Thallasia*; Kenya, Mida Creek, sparsely on *Cymodocea* at 0·5 m; South Australia, Kangaroo Island on *Sargassum* (pers. obs.).

Remarks. This material agrees quite well with Sterzinger's original description, except that the opercular rim is smaller and the tube is pitted. Australian material of *J.* (*D.*) *steueri* has an arrangement of four very distinct longitudinal ridges on the tubes, which is like that figured by Sterzinger. It seems likely that the pits are the result of decalcification (which has undoubtedly occurred, since the tubes are quite soft). The original figures from Suez material show the characteristically elongated blade of the abdominal setae and indicate rather distinct cross-striations on the collar setae. The cross-striations in the Kenyan material, however, are seldom as conspicuous. Sterzinger did not make any comparison with or reference to the closely similar species *J. formosa.* In spite of the similarity of opercular structure, the differences in setation show that *J. steueri* is distinct from *J. formosa* (p. 15).

S. treadwelli Pillai (1965) from the British Museum (Nat. Hist.) was examined and found to have indistinctly cross-striated collar setae like those of *J. steueri*, with which it may tentatively be synonymized.

Subgenus *Leodora* (St Joseph, 1894)

Sinistral coiling; sickle setae may or may not be present; collar not forming a tunnel dorsally.

Type: *Janua* (*Leodora*) *laevis* (Quatrefages, 1865).

This type species is a little-known, sporadically occurring form which is closely related to *J.* (*J.*) *pagenstecheri* and might even be regarded as a *situs inversus* mutant of that species. Zibrowius (1968) found sickle setae on the forms he examined. *J.* (*L.*) *knightjonesi* (de Silva, 1965) is closely related (Bailey, 1970) but lacks sickle-setae. Re-examination of the latter species confirmed that it lacks the fused collar folds characteristic of the subgenus *Dexiospira. Leodora* was regarded as a distinct genus by some authorities, when undue weight was given to direction of coiling as a major taxonomic character, but further knowledge shows that these two forms fall clearly into the genus *Janua*, as defined above.

To use a subgenus for them, as a sinistral equivalent to the subgenus *Janua*, seems to be a good compromise.

Subgenus *Fauveldora* nov.

Sinistral coiling; sickle-setae absent; margins of the collar fused to form a tunnel over the mid-dorsal thoracic groove.

The following type species cannot very well be placed in *Leodora* since it is closer to *Dexiospira* (see p. 5).

Janua (*Fauveldora*) *kayi* **sp. n.** British Museum (Nat. Hist.) reg. no. 1971: 2, 3

Tube is sinistral, non-porcellanous, tightly coiled in one plane (Fig. 5(a)) or with the last whorl loosely coiled (Fig. 5(b)), bearing a faint median longitudinal ridge on the inner whorls and irregular transverse growth rings throughout.

Operculum. The distal plate is lightly calcified, covered with a translucent brown membrane and markedly domed, with the dorsal margin inclined proximally, where it gives rise to an almost peripheral talon. The talon is flattened and approximately diamond-shaped, but bilobed terminally (Fig. 5(c), (d)). It is very like those of the two preceding forms, but shows greater variation (e.g. Fig. 5(g)). As in *J.* (*D.*) *formosa* it often develops somewhat asymmetrically, so that one side extends further than the other. In this sinistral species, the longer side of the talon is on the right, when the operculum is viewed dorsally, which is the mirror-image equivalent of the situation in the dextral species *J.* (*D.*) *formosa.* Young specimens about to breed develop fairly opaque, finely granular walls to the broodchamber, around which the wholly membranous margin of the domed plate forms a narrow brown rim (Fig. 5(e)). The more opaque parts of the talon can be distinguished through the broodchamber wall (Fig. 5(e)–(j)). A frail secondary plate develops to form a subsequent brood chamber which is usually indented distally (Fig. 5(k), may or may not have a vestigial brown membranous rim, and never seems to bear a talon. Occasionally a second brood chamber develops before the preceding one has been entirely shed (Fig. 5(j)).

Colour (preserved). Tentacles, thorax, abdomen and embryos dull yellow (4B5), stomach yellow-brown (5D8).

Thorax. Collar setae on the convex side simple and finely serrate (Fig. 5(m)). Those of the concave side, like those of the second and third fascicles, simple and with nearly smooth margins (Fig. 5(n), (o)). Uncini with a narrow somewhat pointed anterior peg and about six longitudinal rows of teeth (Fig. 5(q)).

Abdomen. Setae geniculate, with slender elongated blades (Fig. 5 (p)) of similar proportions to those of *J.* (*D.*) *steueri* (length: breadth ratio about 10:1). Secondary setae, with rudimentary shafts, are often associated with them, as in other species of *Janua* (e.g. Fig. 4 (k)). About nine rows of uncini, each uncinus with a fluted anterior peg and about eight to nine rows of longitudinal teeth (Fig. 5(r)).

Incubation in the operculum. Nine to 19 embryos, each with paired thoracic attachment glands.

Setation as in other species of *Janua* (Figs 6 and 7).

Distribution. Kenya, Mida Creek (five specimens on leaves of *Enhalus acoroides* 2 m); Ceylon, from a lagoon between Palavi and Kalpitiya (numerous on a marine angiosperm at 0·2–2 m); Kuwait (few on algae).

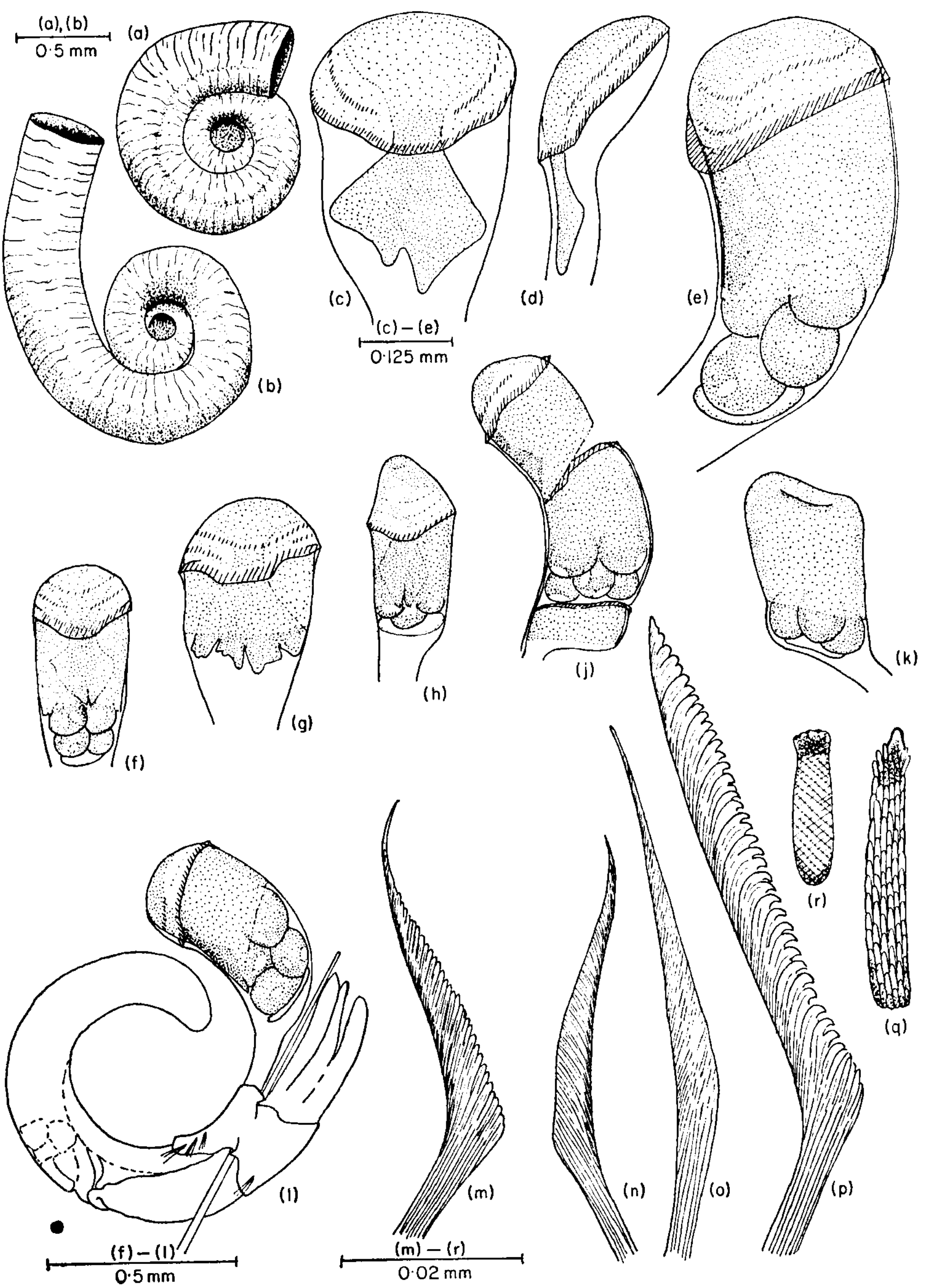

FIG. 5. *Janua* (*Fauveldora*) *kayi:* (a), (b) coiled and evolute tubes; (c) dorsal view of juvenile operculum; (d) side view of (c); (e) side view of first stage incubatory chamber with embryos; (f) dorsal view of (e); (g) dorsal view of another operculum, showing variation in talon; (h) dorsal view of operculum of a specimen from Kuwait (all other illustrations on this page from Kenya); (j) side view of three united opercular chambers, the most distal a first stage

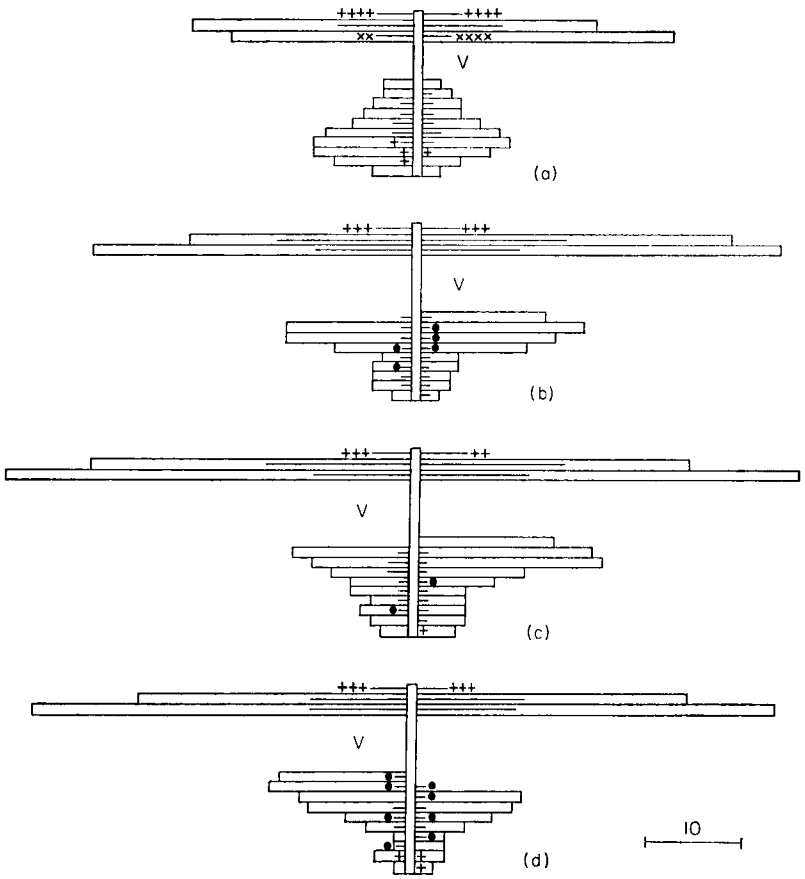

FIG. 6. Distribution of setae and uncini in (a) *Pileolaria daijonesi*, (b) *Janua* (*Fauveldora*) *kayi*, (c) *Janua* (*Dexiospira*) *formosa*, (d) *Janua* (*Dexiospira*) *steueri*.

The histograms indicate the numbers of uncini per segment, the short lines the numbers of main setae and the symbols the numbers and types of ancillary setae, viz. +, long thoracic capillaries and shorter abdominal capillary or hooked setae; ×, sickle setae; ●, secondary setae, with rudimentary shafts.

The relative lengths of the asetigerous regions are indicated and the V's mark the concave sides of the coiled animals.

The figures represent typical specimens, but three distribution counts were made of each species and the variations revealed were small.

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mature form with talon, showing the proximal margin dehisced ventrally where the embryos have been released, next, a mature operculum with ripe embryos, vestigial and membranous brown distal collar and no talon, and proximally a partially formed incubatory chamber also without a talon; (k) side view of a mature operculum without a membranous collar or talon; (l) whole specimen with the dorsal tunnel (below fused collar margins) shown by an exploratory eyelash (see introduction); (m) collar seta from convex side; (n) collar seta from concave side, (o) seta as found in the 2nd and 3rd fascicles; (p) abdominal seta; (q) thoracic uncinus; (r) abdominal uncinus, with cross-hatching to denote teeth too small to be seen distinctly. Diagonal hatching represents the more distinct areas of the brown membranous covering of the opercular plate.

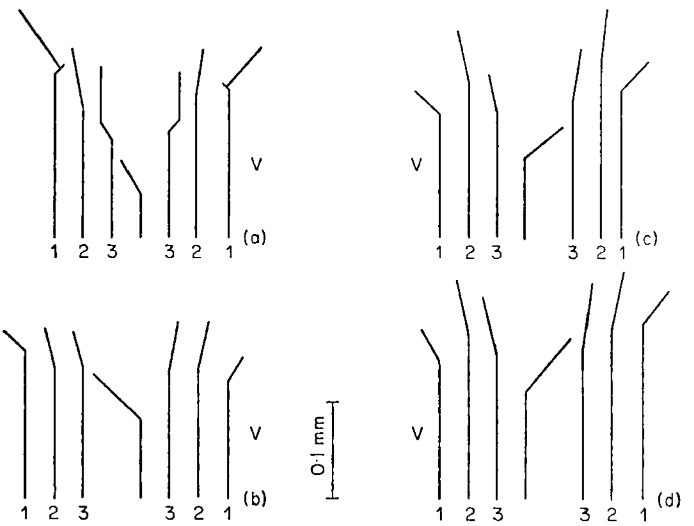

FIG. 7. Diagrams to indicate the relative lengths of setal shafts and blades in (a) *Pileolaria daijonesi*, (b) *Janua* (*Fauveldora*) *kayi*, (c) *Janua* (*Dexiospira*) *formosa*, (d) *Janua* (*Dexiospira*) *steueri*.

The central seta in each figure is abdominal. No difference in size was noted between those of the concave and convex sides, although there was a tendency for the seta to be slightly larger towards the anterior part of the setigerous abdomen and those shown here were the largest. In the thorax, however, the sizes of setae are usually different on the concave and convex sides and therefore both are shown. V denotes the concave side in each figure. 1, 2 and 3 represent setae of the collar, 2nd and 3rd fascicles respectively.

Remarks. Four Spirorbinae on a piece of alga from Kuwait collected by Dr M. Mohammed and presented to the British Museum (Nat. Hist.) in 1969 were examined and proved to be this species, differing from the Kenyan material only in that the doming of the operculum was more exaggerated (Fig. 5(h)). Further specimens on a marine angiosperm from Puttalavi Lagoon, Ceylon, presented to the British Museum (Nat. Hist.) by Dr Pillai were like the Kenyan forms except that the tubes showed no tendency to become uncoiled. Similar uncoiling characterizes *S. evolutus* Bush (1904), which was therefore re-examined but found to lack strong affinities with *Dexiospira* (it has sickle setae) or indeed with *Janua* (the thoracic uncini and abdominal setae are very different).

J. (*F.*) *kayi* seems quite distinct from both *J.* (*D.*) *steueri* and *J.* (*D.*) *formosa.* It differs in that the opercular plate is domed and the talon more variable in form and sometimes multilobed. The tube seems to retain throughout life a juvenile form, with a single longitudinal ridge, and does not develop the additional ridges seen in the other two species. The abdominal setae are unlike those of *J.* (*D.*) *formosa* and the collar setae are unlike those of *J.* (*D.*) *steueri.* The three forms are evidently very closely related but, to judge from their known distribution, it is unlikely that they are mere polymorphic variants of a complex throughout which interbreeding is still taking place. The limited information available shows the sinistral form as coexisting with both the dextral ones only off Kenya. Off Ceylon it was found coexisting just with *J.* (*D.*) *formosa.* It has not been seen off Australia or the West Indies, where the two dextral forms are common.

Discussion

On first encountering the forms described above, the chief difficulty seems to be distinguishing between the two species of *Dexiospira*. To do this it is necessary to have microscopical preparations which show the setae well, particularly the blades of the abdominal setae. In *J.* (*D.*) *steueri* those blades are slender and elongated. Their teeth are relatively large, with lengths about half the width of the blade that bears them. Excluding the teeth, the length : breadth ratio of the blade is at least 10 : 1. In *J.* (*D.*) *formosa* these blades have small teeth but are massive, with a length-breadth ratio of about 5 : 1.

J. (*D.*) *steueri* further differs from *J.* (*D.*) *formosa* in that the teeth of the collar setae are larger and the blades appear faintly cross-striated (it is interesting to note that such cross-striations seem to be always associated with larger marginal teeth), the lateral wings of the talon are usually translucent and the rim of the opercular plate is regularly oval, without any dorsal depression. To judge from the Australian material, furthermore, the fourth ridge of the tube is prominent and fairly peripheral, whereas in *J.* (*D.*) *formosa* the fourth longitudinal ridge is usually rudimentary, even in the most mature specimens. These differences seem in total to be quite significant and the similarity in opercular structure may be regarded as comparatively superficial. It is perhaps somewhat less clear that *J.* (*D.*) *steueri* is specifically distinct from *J.* (*D. pseudocorrugata* (p. 5). Zibrowius (1968) suggested that these two forms are conspecific and the similarities are indeed very detailed. A careful comparison of their setae reveals no striking differences, but it seems best to regard them provisionally as separate species, mainly because of the differences between juvenile talons. In *J.* (*D.*) *pseudocorrugata* the talon is short and blunt, at most bilobed and often not lobed at all. The wall of the adult brood chamber, furthermore, is usually less strongly calcified than that of *J.* (*D.*) *steueri*; it can even be transparent, revealing the embryos within. However, the later opercular chambers of *J.* (*D.*) *steueri* (and also of *J.* (*D.*) *formosa*), lacking any talon, differ from those of *J.* (*D.*) *pseudocorrugata* only in the greater degree of calcification, and the more extensively projecting rim of the opercular plate. The specimens misidentified by Fauvel (p. 8) were of this mature stage.

The close relationship of *Janua* (*Fauveldora*) *kayi* to these forms raises the question of whether *Dexiospira* should be redefined to include sinistral species, but it seems best to retain this group, at subgeneric level, for species which have appropriate characters, and are *usually* dextral. We must continue to place here the sinistral forms of *J.* (*D.*) *steueri*, which were discovered at Suez by Sterzinger (1909) and have been found by Vine (in press) in other Red Sea localities: but it seems inconvenient to multiply the number of sinistral forms in this group, by placing in it a species which seems to be widely distributed and predominantly or exclusively sinistral. Creation of the new subgenus *Fauveldora* may therefore be generally acceptable, particularly since direction of coiling is usually held to be a very useful character in the taxonomy of Spirorbinae. Taking this view, Pillai (1970) and others made *Leodora* a separate genus, but without giving any recognition to its close relationship to *Janua*. It should not stand alone and *Fauveldora* seems still less worthy of full generic status. To make these two groups genera would require creation of a higher taxon, presumably a subfamily Januinae, within which they could be grouped with their dextral relatives. That, in turn, would mean that the Spirorbinae must become a full family, the Spirorbidae. Pillai (1970) takes that final step, but it seems premature to join him whilst we have so few details of these forms, knowledge of which is now increasing rapidly.

We also need a clearer conception of the major groupings involving other serpulids, for their taxonomy too is overdue for revision.

As Bailey's (1969*b*) review showed, the taxonomic value of direction of coiling in Spirorbinae derives largely from its convenience. Reversal of coiling may follow from simple mutations and the character does not necessarily indicate a major division in a natural system of classification. The close relationship of *Janua* (*Fauveldora*) *kayi* to the two species of *Dexiospira* confirms Bailey's conclusion. Apart from being so easily observed, direction of coiling would appear to be no more important in taxonomy than is any other single character.

Since this relationship is so close, the dichotomy in evolution which separated *Fauveldora* and *Dexiospira* must have been relatively recent and hence probably involved the origin of sinistral forms from a dextral stock. It is very unlikely that the change proceeded in the reverse direction, because the large number of species of *Dexiospira* (see *Neodexiospira* in Pillai, 1970) shows that the dextral group has been in existence for a long time. If, as Bailey (1970) suggested, *Janua* (*Leodora*) *laevis* and *J.* (*L.*) *knightjonesi* have a fairly close *situs inversus* relationship to *Janua* (*Janua*) *pagenstecheri*, then *Leodora* too probably evolved from dextral forms, but on a separate occasion, since the event involved forms in which the collar folds do not fuse. It is interesting to note that no sinistral Spirorbinae have yet been described as producing abnormally *situs inversus* strains, though such have been described from three dextral species, *Circeis spirillum* (Linnaeus) (Bock, 1953), *Paradexiospira vitreus* (Fabricius) (Potswald, 1965) and *J.* (*D.*) *steueri* (Sterzinger, 1909; Vine, in press). As Bailey (1969*b*) wrote, "Looking at the genus as a whole, dextral species are somewhat less numerous than sinistral ones, but seem to be more liable to undergo reversals of coiling. The sinistral direction thus appears to be more stable and hence is probably primitive." Basically, it would appear that the dextral forms are the most progressive. They were derived from forms which were more liable to changes, than were most of the sinistral stock, and are hence themselves particularly liable to change back again. Hence the emergence of *Fauveldora* is probably a recent reversion to a primitive condition.

This suggestion that the most primitive Spirorbinae were sinistral prompts examination of Serpulinae. In some genera (*Hydroides*, *Serpula*, *Vermiliopsis*), sinistral and dextral opercula occur in about equal numbers, but this seems to be due to the habit in these forms of regenerating opercula throughout life, from alternate sides. Initially, at least in *Hydroides*, the operculum develops on the left side (Nelson-Smith, 1967). The operculum remains sinistral in *Pomatoceros*, *Placostegus* and *Ditrupa* (McIntosh, 1923), *Chitonopoma* (Hartman, 1948), *Pomatoleios* and *Neopomatus* (Pillai, 1970), and mostly sinistral in *Spirobranchus* (ten Hove, 1970). Only in *Conopomatus*, amongst the Serpulinae studied by Pillai (1960), was the operculum dextral. In *Spirobranchus polytrema* (Phillipi) the operculum develops on the left side with remarkable constancy (Zibrowius, 1968) and the tube is often regularly coiled, the direction of coiling being always towards the opercular side, so that this species might easily be confused with an abnormally large sinistral species of *Spirorbis* (Nelson-Smith, 1967). The adaptive value of this arrangement is that the operculum is on the side adjoining the previous whorls of the tube, so that the other side is clear of anything that would obstruct the expansion of the branchial crown. The preponderance of sinistral forms amongst these other serpulids supports Bailey's (1969*b*) tentative conclusion, that this was the primitive direction of coiling in Spirorbinae.

Summary

Four species from Kenya were all opercular incubators and attached to marine angiosperms, *Pileolaria daijonesi* **sp.n.** being much the most numerous. The other three all have the collar folds fused dorsally, but should be placed in the redefined genus *Janua*, two falling indisputably into the redefined subgenus *Dexiospira* (= *Neodexiospira* Pillai). These two, *J.* (*D.*) *formosa* Bush and *J.* (*D.*) *steueri* Sterzinger, are redescribed and distinguished clearly from one another for the first time, the easiest distinction being that the blades of the abdominal setae are broad in the former and narrow in the latter. Both are shown to be widely distributed in warm seas. The remaining species, *Janua* (*Fauveldora*) *kayi* **subgen. et sp.n.**, which extends to the Persian Gulf and Ceylon, is closely related to *Dexiospira*, but its operculum and related coiling are sinistral. Reviewing these characters in serpulids generally, it seems clear that the primitive position of the operculum in Serpulinae and Spirorbinae was sinistral, that many Spirorbinae have become dextral and that the most recent evolutionary changes, involving this character, have been back-mutations from such dextral stocks.

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