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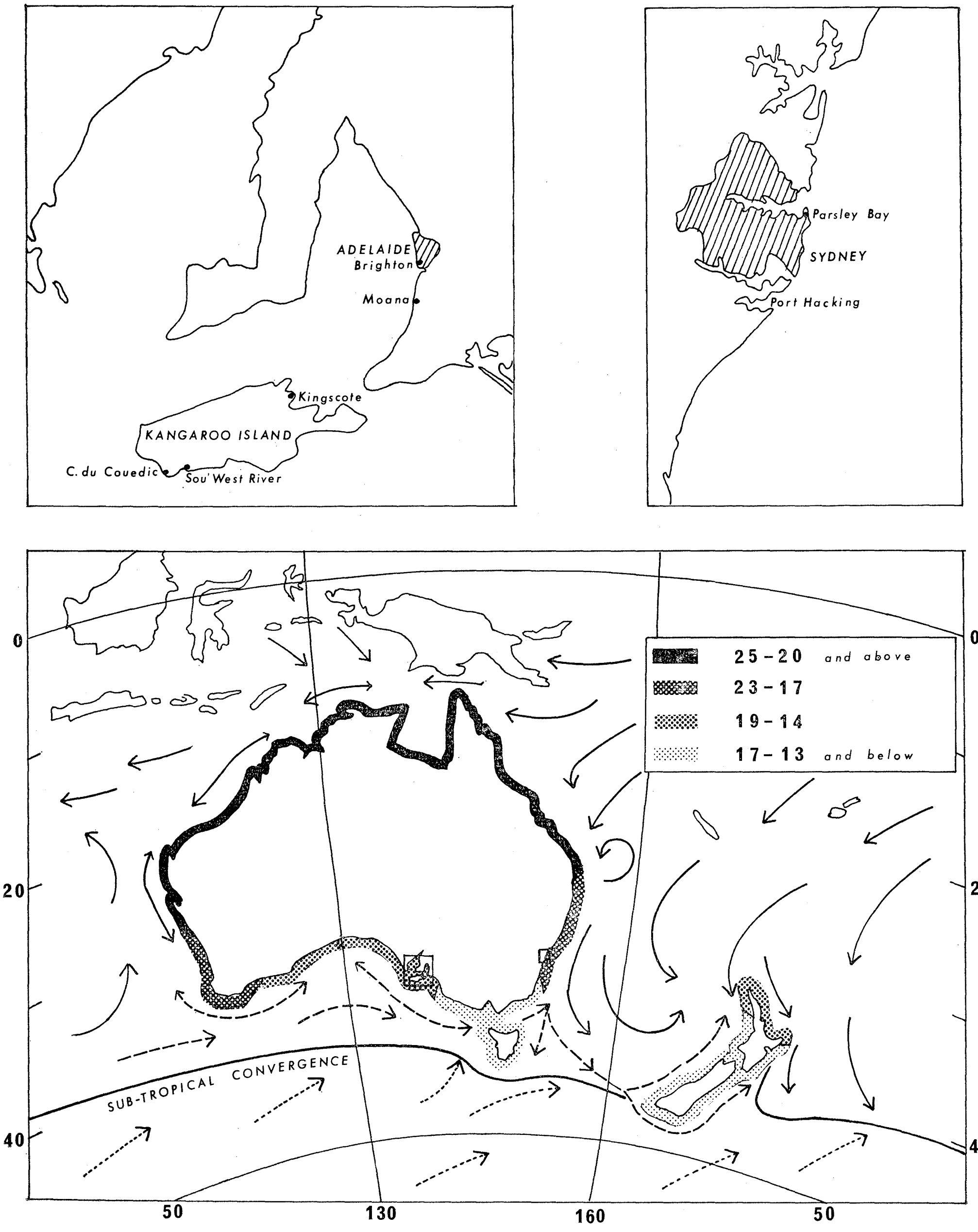

Figure 1.—Top left, collecting sites near Adelaide; top right, ditto near Sydney; bottom, collecting locations inset, showing also currents of warm, cool (interrupted lines) and cold water (dotted lines). A second smaller arrow-head indicates that the current occasionally reverses. Coastal water types and the mean position of the subtropical convergence (see p. 147) modified from Knox (1963), with mean summer (February) and winter (August) temperatures in degrees C.

SPIRORBINAE (POLYCHAETA: SERPULIDAE) FROM SOUTHEASTERN AUSTRALIA.

Notes on their Taxonomy, Ecology, and Distribution

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Figures 1–14 Manuscript received, 1st September, 1972

SUMMARY

Fifteen species belonging to seven genera are described, with pictorial and dichotomous keys to identification and notes on their distribution in other regions. All occur on or adjoining the shore, or on seaweeds cast ashore. Seven species are always attached to algae or *Amphibolis*. The predominant species are: near Sydney, *Eulaeospira convexis*, *Pileolaria pseudomilitaris*, *Janua formosa* and *J. pseudocorrugata;* near Adelaide (on cast weed), *Metalaeospira tenuis* and *Janua steueri;* and on Kangaroo Island, *Romanchella quadricostalis*, *Janua pagenstecheri* and (less commonly found) *Protolaeospira canina* and *Protolaeospira triflabellis*. *Janua lamellosa*, *J. fenestrata* and *J. trifurcata* seem scarcer, whilst only one specimen was found of the remarkable *Amplaria spiculosa*, which is now known from New Zealand.

Of these species, most of the opercular incubators are widespread in warm seas, but those which incubate in their tubes may be endemic and mostly belong to genera centred in the Southern Hemisphere, round which they may perhaps have been distributed by drifting kelp.

CONTENTS

INTRODUCTION

Collections were made by one of us (L. C. Llewellyn) at Brighton and Moanna, near Adelaide; at Kingscote, Sou-West River and Cape du Couedic on Kangaroo Island in January 1967; and at Parsley Bay, Vaucluse, Sydney in July 1967 (fig. 1). Seven of the species found were new and have now been described (Knight-Jones, 1973); two had been previously described from Port Hacking near Sydney by Wisely (1962), but the remaining six species are new records for Australia.

We now redescribe these eight previously known forms and offer a key for the identification of all fifteen species. The recent record by Straughan (1967) probably relates to one of these (p. 141). Earlier authors (Lamark, 1818; Mörch, 1863; Bush, 1904) who have dealt with Australian Spirorbinae have offered a few inadequate descriptions, several based on empty tubes and none including characters sufficiently distinctive for identification.

TECHNIQUES AND DIAGNOSTIC FEATURES

The best preservative is 5% formaldehyde made up with sea water, but plant substrata should not be included because they eventually produce acid conditions which decalcify tubes and opercula. Although 70% alcohol is excellent for observing the general morphology, the setae may thereafter be difficult to see, for specimens which have spent a few years in alcohol do not clear so readily after mounting (p. 112).

Identifications of Spirorbinae cannot be based on tubes alone, for these tend to vary with age, substratum and local conditions. There may be, for instance, only one longitudinal ridge on a young tube and three on an adult (p. 130). On rock the periphery of the tube may spread to form a flange, whereas the same species on algae may lack this. In crowded populations the last whorl may cover the previous whorls or form an ascending spiral instead of coiling flush with the substratum. Such tubes are often seen on filamentous algae where the area for attachment is limited. Some species have characteristically sculptured tubes (e.g., figs 2c and d), but such sculpturing may vary (p. 135). Direction of coiling seems to be constant for each species in the Australian material, but one of these, *Janua* (*Dexiospira*) *steueri*, occurs with both dextral and sinistral coiling in certain Red Sea locations (Sterzinger, 1909; Vine, 1972).

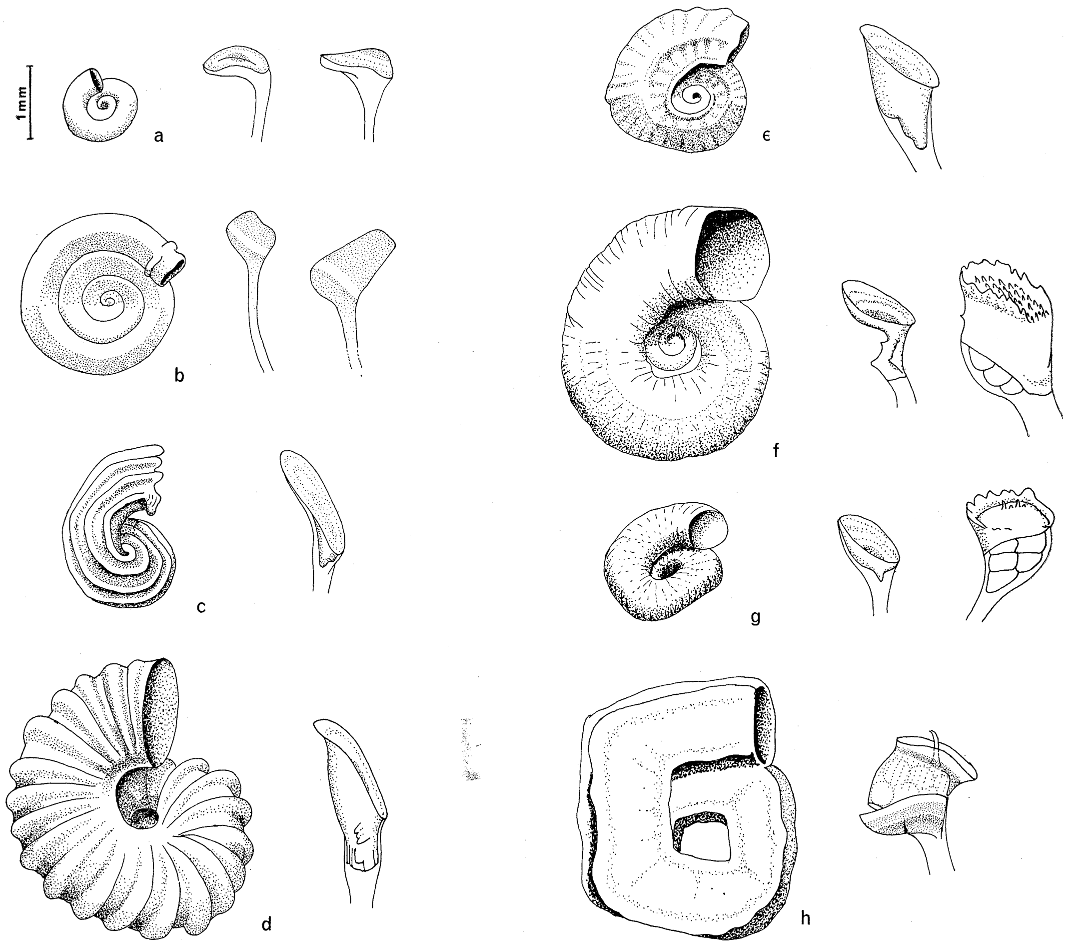


Figure 2.—Tubes (left) and opercula of eight sinistral species of Spirorbinae from southeast Australia: a, *Eulaeospira convexis;* b, *Metalaeospira tenuis;* c, *Romanchella quadricostalis;* d, *Protolaeospira triflabellis;* e, *Protolaeospira canina;* f, *Pileolaria militaris;* g, *Pileolaria pseudomilitaris;* h, *Amplaria spiculosa.* The tubes are all drawn to the scale shown, but the opercula are drawn to various larger scales. In a and b some opercular variations are illustrated, whilst f and g show juvenile forms in the centre and mature forms on the right.

Nevertheless, a few Australian Spirorbinae can be identified simply by inspecting the tube and the operculum, so pictorial keys showing these characters are given here for the eight sinistral species which we have found (fig. 2) and the seven dextral ones (fig. 3). All tubes are drawn to the same scale, but the opercula are more enlarged, to scales varying between species. Incubation within opercular brood-chambers is characteristic of three genera, *Pileolaria*, *Janua* and *Amplaria*, but not all adults contain embryos, whilst juveniles have opercula which are markedly different in form. The remaining Spirorbinae incubate within the tube and certain genera have characteristic ways of anchoring their embryos (Knight-Jones, Knight-Jones and Vine, 1972). A particularly characteristic feature is the special attachment stalk of *Protolaeospira* (fig. 4a), which may be seen in non-brooding adults.

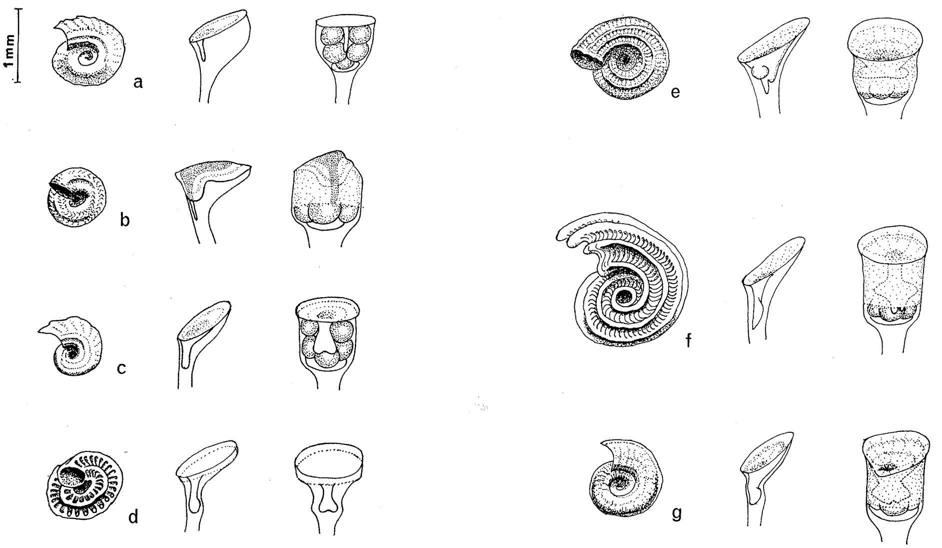


Figure 3.—As figure 2f, but illustrating dextral species. a, *Janua* (*Janua*) *pagenstecheri;* b, *Janua* (*Pillaiospira*) *trifurcata;* c, *Janua* (*Dexiospira*) *pseudocorrugata;* d, *Janua* (*Dexiospira*) *fenestrata;* e, *Janua* (*Dexiospira*) *lamellosa;* f, *Janua* (*Dexiospira*) *steueri;* g, *Janua* (*Dexiospira*) *formosa.* The tube g is only about 0.8 of the average mature size, but the others are typical for the species concerned. The juvenile opercula show the talons in side view, as they would appear in opercula protruding from their tubes. The others, which show the talons in face view, are newly mature. Old brood chambers of *Janua* species usually lack talons (e.g., figures 10d, 11h, 12g, 14f) and are not illustrated here because they are of little use in distinguishing species.

For certain identification the worm should be extracted by chipping away the tube with mounted needles under a dissecting microscope. The shape of the operculum (p in fig. 4a) can usually be studied in sea water or preservative by reflected light with a x5 binocular objective. In some species, however, the talon is large and characteristically sculptured (e.g., figs 2d and e), yet its finer details may be obscured by the ampulla wall, unless this is cleared in clove oil (after alcohol dehydration). Even then the opercula of several dextral species appear closely similar and these species can be distinguished only by examination of other characters.

One of the diagnostic features shared by five out of seven of the dextral forms is fusion of the margins of the thoracic collar on the dorsal side, i.e., the side which is next to the substratum (fig. 4k). This character is difficult to see in preserved material but the tunnel formed by the fusion can be demonstrated by inserting a mounted eyelash (Knight-Jones, 1972). One sinistral species in this collection also shows this feature (fig. 5). The remainder of the species have collar margins that are free dorsally (e.g., fig. 4a).

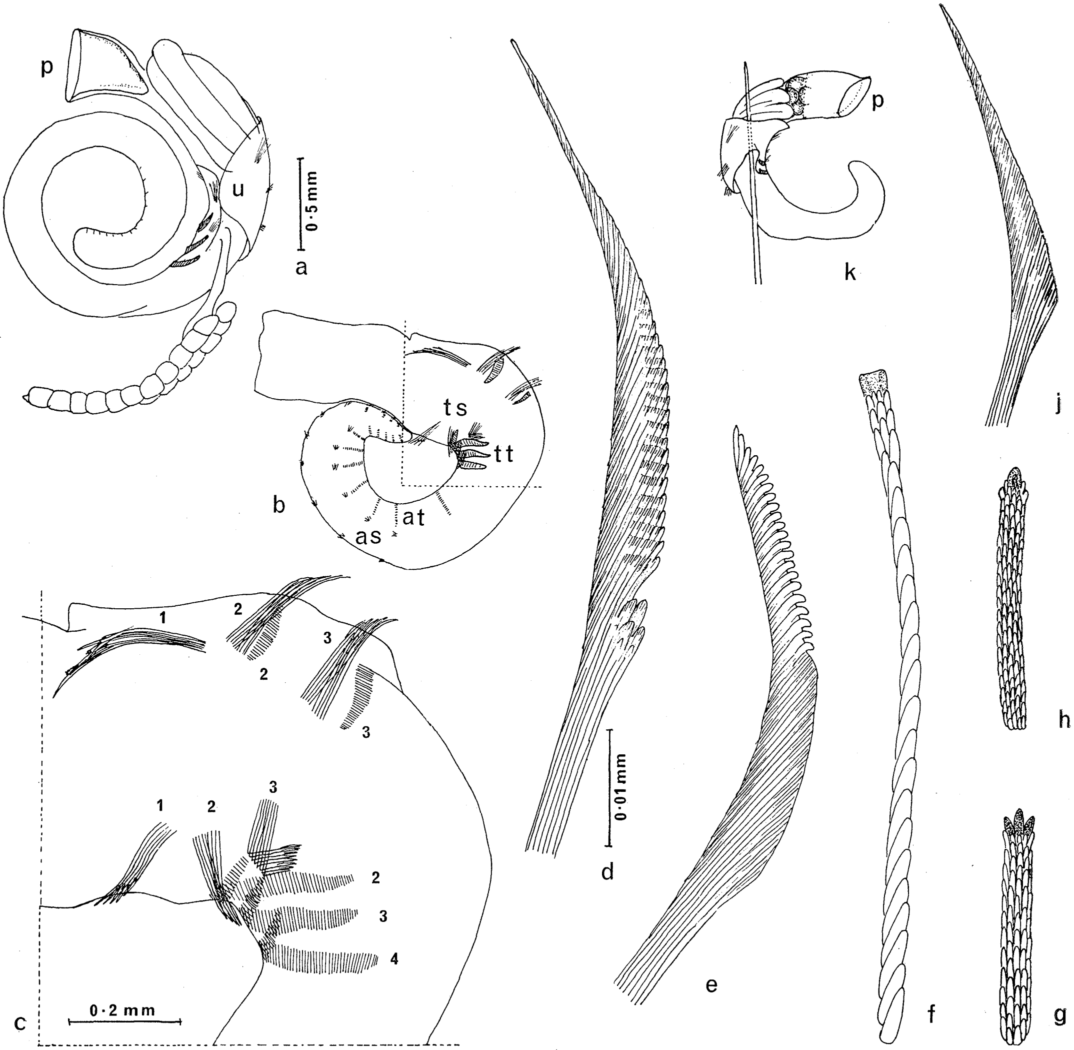


Figure 4.—a to f, *Protolaeospira canina;* g, *Janua* (*Dexiospira*) *trifurcata;* h to k, *Janua* (*Dexiospira*) *formosa.* a, dorsal view of whole animal as seen by reflected light, showing p, opercular plate with proximal talon and u, unfused dorsal margins of thoracic collar. b, dorsal view of animal with operculum removed, mounted in polyvinyl-lactophenol and viewed by transmitted light, showing as, abdominal setae; at, abdominal tori; ts, thoracic setae; tt, thoracic tori. c, as b, but more magnified, showing the setae and uncini of thoracic "segments" 1–4. d, seta from the first fascicles (a collar seta), showing proximal fin of large teeth and distal blade with a serrated outer margin and associated cross-striations. e, sickle seta from third fascicles. f, uncinus from a thoracic torus. g, thoracic uncinus with three-pronged anterior peg. h, ditto with pointed peg. j, simple seta. k, whole animal with collar folds fused dorsally, to form a tunnel demonstrated by an eye-lash probe; the opercular plate (p) surmounts a brood chamber which has the proxima walls less calcified, showing the embryos within.

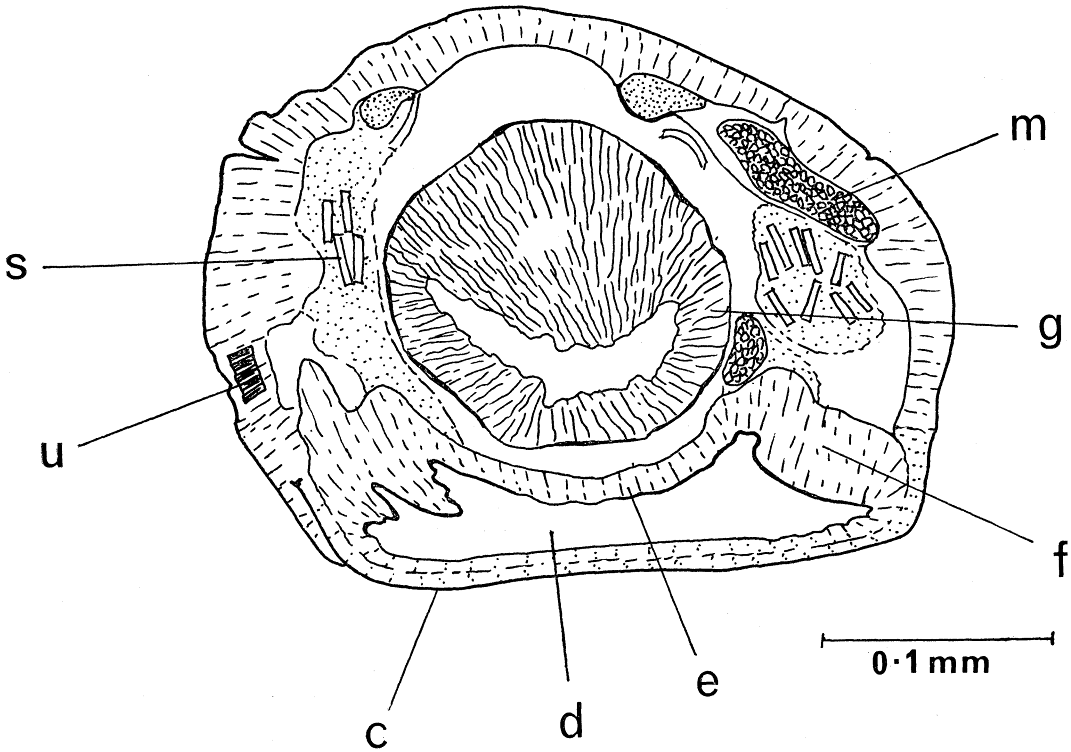
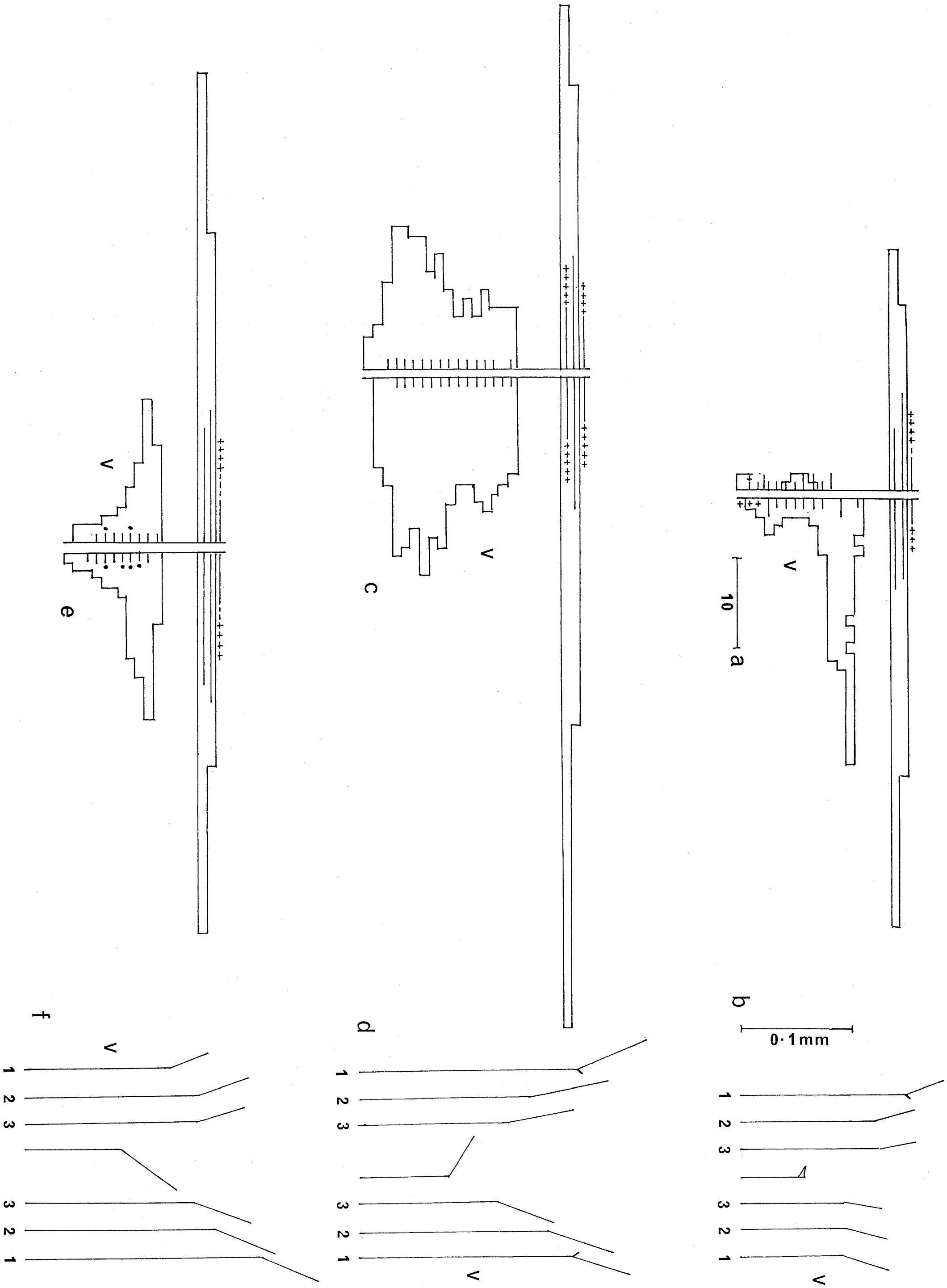


Figure 5.—*Romanchella quadricostalis.* Transverse section through midthoracic region, showing c, collar folds fused to enclose d, the dorsal (faecal) groove; e, epidermis of dorsal body-wall; f, thickened epidermis fringing dorsal groove; g, gut; m, longitudinal muscle on concave side; s, shafts of setae; u, uncini on convex side. The dorsal side is orientated downwards, because this is the side which adjoins the substratum.

OPPOSITE

Figure 6.—a and b, *Eulaeospira convexis;* c and d, *Pileolaria pseudomilitaris;* e and f, *Janua* (*Dexiospira*) *lamellosa.* On left, numbers of uncini per segment can be judged by applying the scale to histograms a, c and e. Each of these represents a worm straightened out, anterior end upwards, concave side marked "V", following the conventions of Bailey (1969b). The gap between thorax and abdomen represents the length of the asetigerous region relative to the length of the nearest abdominal segment. Numbers per segment of collar setae and simple setae (including abdominal setae) are represented to the same scale by straight lines. Indeterminate setae are shown by short dashes, whilst crosses denote capillary setae in thorax and hooked capillaries in abdomen; spots indicate the secondary setae found in the abdomen of *Janua.* On right, the relative length of shafts and blades are shown for different types of setae, all to same scale, following the conventions of Knight-Jones *et al.* (1973). In the centre of each diagram the largest abdominal seta is represented, whilst 1, 2 and 3 mark thoracic setae of the collar, 2nd and 3rd fascicles respectively, with V indicating those on the concave side of the body.

The number of thoracic tori on the concave side (e.g., two, three or four) is a useful generic character, often visible by reflected light at low magnifications. But high power examination of setae is necessary for conclusive specific identification, particularly of most dextral forms. For this the specimen should be mounted in the clearing agent polyvinyl-lactophenol (Knox, 1951) and viewed by transmitted light, preferably with high-power phase contrast. The preparation is improved if the


a
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operculum is detached prior to mounting, to avoid the formation of CO_2 bubbles. Alternatively, covering may be delayed for a few hours, to allow bubbles to disappear. Warming the mount gently on a hot plate for about 48 hr improves the clearing of the tissues (Gee, 1964). Fig. 4b shows typical positions of the uncinigerous tori and fascicles of setae in such a mount. The collar setae differ from the other setae in that they point anteriorly. Since they are pivoted about the point of emergence through the skin, their deeply embedded setal sacs are displaced posteriorly, which may give the false impression that they originate in the second setigerous segment. Behind the collar setae all Spirorbinae may be said to have second and third thoracic segments, each represented by a pair of tori and a pair of fascicles. Some genera (e.g., *Metalaeospira* and *Protolaeospira*) have a fourth thoracic segment represented at least partially, by an extra torus on the concave side. Since there are no tori associated with the collar setae, the fascicles and tori of the concave side then seem to be out of phase (fig. 4c). In several species, including *Protolaeospira triflabellis* (p. 122), the fourth segment is represented on the convex side too, by an extra fascicle and/or torus. Exceptionally (in *Amplaria* and *Anomalorbis*—see pp. 129 and 143) the fourth segment is represented by all four setigerous rudiments and there are rudiments of a fifth thoracic segment, the most conspicuous of these being a fourth thoracic torus on the concave side. Fig. 4 also illustrates a few of the types of setae and uncini which are useful in identifying Spirorbinae. Collar setae are often of the fin and blade type (fig. 4d), but some genera (e.g., *Janua*) lack the proximal fins (fig. 4j). Either type of collar setae may be with or without cross-striations on the blades (e.g., fig. 4d), a useful character in separating some species. Sickle setae (fig. 4e) are characteristically found in the third fascicles, but are lacking in certain groups, such as the genus *Eulaeospira* (p. 118) and the subgenera *Simplicaria* (p. 126) and *Dexiospira* (p. 132). The thoracic uncini in two genera (*Protolaeospira* and *Pileolaria*) are characteristically elongated and thin, mostly bearing only a single row of teeth and with a blunt, indistinctly bifid peg (fig. 4f). In species of *Janua*, however, these uncini are shorter, but with several longitudinal rows of teeth and pointed anterior pegs (figs 4g and h).

Finally, the distribution of abdominal uncini and the relative lengths of abdominal setae, though not very useful in distinguishing species, can be important in characterising genera. All tube-incubating genera centred in the southern hemisphere (Knight-Jones, Knight-Jones & Vine, 1972) have a bilaterally asymmetrical distribution of abdominal uncini, those on the convex side being sparse or absent (fig. 6a), whilst the blades of their abdominal setae are relatively short (fig. 6b) and in *Protolaeospira* vestigial. The opercular incubating genera, on the other hand, have the uncini more symmetrically distributed. The sinistral genus *Pileolaria* is peculiar in having the largest abdominal tori towards the posterior end (fig. 6c), whereas the mainly dextral genus *Janua* (like most Spirorbinae) has the largest tori in the anterior half of the abdomen (fig. 6e). In *Janua* the blades of the abdominal setae are characteristically long, usually longer than those of the collar setae (fig. 6f).

The following key deals only with the species actually found in our material, yet it is likely that additional species are present in southeastern Australia, particularly below tide-marks, to judge from collections made in the region of the Great Barrier Reef (Vine, personal communication) and New Zealand (Vine, 1974). We have therefore thought it advisable to include, in the subsequent taxonomic section, diagnoses of the other genera and subgenera that may possibly be encountered off Australia. It should be noted that, although all species of *Janua* in the key are dextral, this group includes two sinistral subgenera (p. 142), at least one of which (*Leodora*) is likely to be encountered in this area.

The classification into genera used in this paper is mostly a compromise between the views of Bailey (1969b) and Pillai (1970), with amendments explained previously (Knight-Jones, 1972 and 1973). Diagnoses of the genera *Circeis* Saint-Joseph (1894), *Paradexiospira* Caullery and Mesnil (1897), *Prodexiospira* Pillai (1970), *Helicosiphon* Gravier (1907) and a few lesser-known taxa have not been included, because they seem to have restricted distributions, in the northern hemisphere or the Antarctic, and are unlikely to be represented in Australian waters.

KEY TO SPECIES FOUND IN SOUTH-EASTERN AUSTRALIA

1. Tube sinistral (mouth faces clockwise) 2

— Tube dextral 11

2 (1). Tube smooth, or with one obtuse longitudinal ridge 3

— Tube with distinct ridges 5

3 (2). Opercular plate or cap without proximal talon and not forming a brood chamber 4

— Opercular plate with proximal talon or forming a brood chamber 6

4. Tube round in cross section, lacking any ridges (figs 2a and 7a), opercular plate flat or slightly convex, some collar setae of the fin and blade type, no sickle setae, two thoracic tori on the concave side .... *Eulaeospira convexis* Wisely (p. 118)

— Tube almost triangular in cross section, with one obtuse longitudinal ridge (fig. 2b), opercular plate usually forming a truncated cone, collar setae simple, sickle setae in the 3rd fascicle, three thoracic tori on the concave side .... *Metalaeospira tenuis* Knight-Jones (p. 121)

5 (2). Tube with four very distinct longitudinal ridges (fig. 2c), collar setae simple, two thoracic tori on the concave side .... *Romanchella quadricostalis* Knight-Jones (p. 123)

— Tubes with transverse folds or less than four longitudinal ridges. Fin and blade collar setae 6

6 (3). Tube with transverse folds (fig. 2d) or with two longitudinal ridges, and a peripheral flange (fig. 2e). Opercular talon massive, three thoracic tori on the concave side, a thin stalk extends posteriorly from the thoracic region and embryos, if present, lie attached to this within the tube .... Genus *Protolaeospira* 7

— Tube rather round in cross section with indistinct longitudinal ridges or transverse growth striae (figs 2f and g), or rather square in cross section due to peripheral longitudinal ridges (fig. 2h). Operculum with talon (not massive) or forming a brood chamber 8

7 (6). Tube massive with conspicuous transverse folds, opercular talon blunt and with fluted sculpturing (fig. 2d) *Protolaeospira triflabellis* Knight-Jones (p. 122)

— Tube with two longitudinal ridges and a well developed peripheral flange, opercular talon pointed without distinct sculpturing (fig. 2e) .... *Protolaeospira canina* Knight-Jones (p. 122)

8 (6). Tube round in cross section, with indistinct longitudinal or transverse ridges; two thoracic tori on the concave side, juvenile opercular plate concave and with proximal talon, mature operculum forming a brood chamber .... Genus *Pileolaria* 9

— Tube rather square in cross section (having peripheral longitudinal ridges); four thoracic tori on the concave side, operculum forming a brood chamber 10

9 (8). Tube massive with indistinct longitudinal ridges, juvenile opercular talon with lateral wings and a centripetal spur, adult opercular brood chamber a deep 'helmet', which is rather bilaterally symmetrical and bears distal spines (fig. 2f), sickle setae present in third fascicles, a distinctive brown-black spot lies just behind the thorax .. *Pileolaria militaris* Claparède (p. 124)

— Tube with indistinct transverse growth striae, juvenile operculum with a short 'peg' talon, adult operculum a shallow spiny bilaterally asymmetrical helmet (fig. 2g), no sickle setae and no black spot .... *Pileolaria pseudomilitaris* Thiriot-Quiévreux (p. 126)

10 (8). Opercular plate with a flared continuous rim and a single distal spine (fig. 2h), thorax with the rudiments of five "segments" .... *Amplaria spiculosa* Knight-Jones (p. 129)

11 (1). Collar setae simple, juvenile opercular plate bears a somewhat peripheral talon, adult operculum forms a cylindrical brood chamber, a secondary plate develops below the embryo, forms the next distal plate and does not usually bear a talon. (It is difficult to identify some *Janua* species when the talon is absent) .... Genus *Janua* 12

12 (11). Sickle setae in third fascicles, collar margins separate dorsally, talon if present a simple peg (fig. 3a), not closely associated with the transparent wall of the brood chamber .... *Janua pagenstecheri* Quatrefages (p. 130)

— No sickle setae 13

13 (12). Collar margins separate dorsally, opercular plate bilaterally asymmetrical; young forms bear a peg talon, which is rather flattened and closely associated with the opaque wall of the brood chamber (fig. 3b); thoracic uncini with a three-pronged anterior peg (fig. 4g) .... *Janua (Pillaiospira) trifurcata* Knight-Jones (p. 142)

— Collar margins fused dorsally .... Subgenus *Dexiospira* 14

14 (13). Brood chamber with transparent walls, talon small and often bilobed terminally, but without distinct lateral wings or lobes 15

— Brood chamber with opaque walls, talon with distinct lateral wings or lobes 16

15 (14). Talon flat, somewhat triangular (fig. 3c) or subquadrangular in shape, tube bears 3 poorly defined ridges with indistinct transverse furrows between them .... *Janua (D.) pseudocorrugata* Bush (p. 132)

— Talon with two bulbous terminal lobes, tube bears three longitudinal ridges (one peripheral) which are separated and often tunnelled through by deep transverse furrows (fig. 3d) ...... *Janua (D.) fenestrata* Knight-Jones (p. 135)

16 (14). Talon large with bulbous lateral lobes formed by extensions of a transverse bar (fig. 3e). The bifid terminal part of the talon not in close association with the wall of the brood chamber (fig. 13e) .... *Janua* (*D.*) *lamellosa* Lamarck (p. 139)

— Talon, with flat angular lateral wings and terminal "lobes", all of which are closely associated with the walls of the brood chamber (figs 3f and g) 17

17 (16). Collar setae on the convex side with coarsely serrated and cross-striated blades, abdominal setae extremely long and narrow (fig. 14l), tube large with about four well defined ridges and intercostal furrows (fig. 3f) .... *Janua* (*D.*) *steueri* Sterzinger (p. 141)

— Collar setae with finely serrated blades lacking cross-striations, abdominal setae with fairly long but very wide blades (fig. 12m), tube small and often with rather indistinct ridges (fig. 3g) ...... *Janua* (*D.*) *formosa* Bush (p. 136)

SYSTEMATICS

Genus **Spirorbis** Daudin, amended

Coiling usually sinistral (see below); thorax with two pairs of tori; embryos incubated in an "egg string", which is attached posteriorly by a filamentous thread to the inside of the tube wall; collar folds separate dorsally; collar setae of fin and blade type, the blades with or without cross-striations; sickle setae present in the third fascicle; thoracic uncini with blunt anterior peg; abdominal setae obliquely geniculate, with fairly long tapering blades; distribution of abdominal uncini more or less bilaterally symmetrical, with the largest tori towards the anterior end of the setigerous region; larvae with a single white attachment gland.

Type: Serpula spirorbis Linnaeus, 1758.

Representatives of this genus are mainly confined to the northern hemisphere (Knight-Jones, Knight-Jones and Vine, 1972) and indeed to the north Atlantic. They have not yet been found in south-eastern Australia, but one, *Spirorbis* (*Spirorbis*) *bidentatus* Bailey (Bailey & Harris, 1968), which has been recorded at a depth of 50 metres off northern New Zealand (Vine, 1974), was originally described from shallow water in the Galapagos and may be expected to occur in Australian waters. Its tube (up to 1.5 mm across coil) bears 3 longitudinal ridges. Its opercular plate is slightly convex, with a massive talon which in side view shows a distinct almost terminal notch. Collar setae with a small gap separating a well defined fin from a blade that is not cross-striated.

Subgenus **Spirorbella** Chamberlain, 1919

As above for *Spirorbis*, but coiling dextral.

Type: Spirorbis marioni Caullery and Mesnil, 1897.

The range of variation of this species includes the forms *S. bushi* Rioja and *S. tricornigerus* Rioja (Vine, Bailey-Brock and Straughan, 1972). It is known from Panama, Hawaii and the Galapagos, so may possibly extend to northern Australia. It seems to be a close dextral relative of *Spirorbis* (*Spirorbis*) *cuneatus* Gee (1964), having a fairly massive talon, cross-striated collar setae and the teeth of the thoracic uncini arranged in transverse and longitudinal rows (most Spirorbinae have these teeth in diagonal and longitudinal rows).

Genus **Eulaeospira** Pillai, 1970, amended

Sinistral coiling; two pairs of thoracic tori; embryos incubated in the faecal groove; collar setae with blades lacking cross-striations, some with a basal fin; sickle setae absent; marked asymmetry in the distribution of abdominal uncini (fig. 6a); larvae probably lack white attachment glands.

Type: Spirorbis orientalis Pillai, 1960.

Eulaeospira convexis (Wisely, 1962)

Material

Holotype Australian Mus. W.3749; our material Australian Mus. W.4479.

Description

Tube small (under 1mm across coil), smooth, porcellaneous and thin-walled, round in cross section, sinistrally coiled in one plane or with the last whorl lying over the previous ones. The mouth of the tube may bear a thickened rim and occasionally a nearby additional thickening, probably denoting a period of renewed growth (fig. 7a).

Operculum with a thin, lightly-calcified distal plate, which varies in shape from convex (fig. 7d) to slightly concave (fig. 7e), but is usually of an intermediate shape with an asymmetrical depression (figs 7b and c).

Thorax. Collar margins not fused dorsally. Collar setae mostly of the fin and blade type (fig. 7g). The curvature of the region between the fin and blade (after which Wisely named the species) is not always apparent, as the distance between the fin and blade may be very small. The blades of other collar setae may have coarse teeth proximally, but with no gap separating them from the rest of the blade (fig. 7f), giving the appearance of simple setae. These occur more frequently on the concave side, but both types of setae have been found on each side. The setae of the second and third fascicles are simple, with blades almost smooth throughout their length (fig. 7h). Two pairs of tori. Each uncinus with a blunt, fluted anterior peg and four or more longitudinal rows of teeth, the rows more numerous in the smallest uncini at the end of a torus (figs 7k and l).

Abdomen. Asetigerous region about three times as long as the distance between the 1st and 2nd abdominal tori. About fourteen setigers with most of the uncini on the concave side (fig. 6a). Each uncinus has a blunt fluted anterior peg (fig. 7m). Setae strongly geniculate, with a short tapered blade bearing ovate teeth (fig. 7j). Hooked capillary setae may be present in some fascicles (figs 6a and 7j).

Incubation

In close association with the faecal groove but, owing to the small size of this species (and in spite of its abundance) the method of attachment was difficult to establish. Usually it seemed that the embryo mass (up to about 20 eggs) did not lie freely in the groove but adhered to the area between the third thoracic and second abdominal setiger. The egg mass could usually be dislodged intact, but there was often more resistance to detachment near the posterior position. In one specimen there seemed to be a tenuous attachment filament at about the second abdominal segment (fig. 7n). It would be interesting to see whether these attachments are present in fresh material.

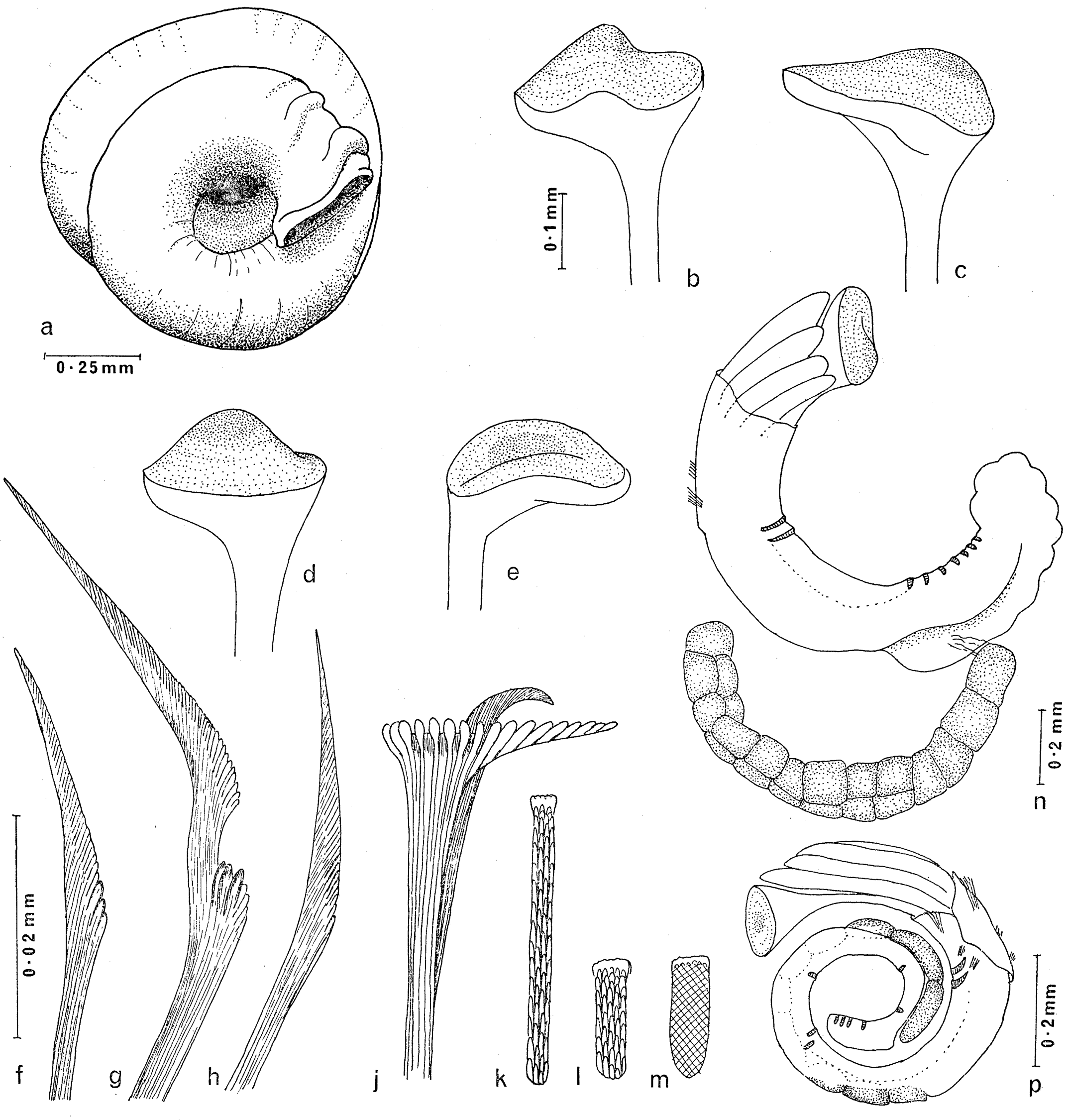

Figure 7.—*Eulaeospira convexis:* a, tube; b and c, typical operculum; d and e, extremes of opercular form; f, "simple" collar seta; g, fin and blade collar seta; h, seta of the second and third fascicles; j, abdominal seta and associated hooked capillary seta; k and l, largest and smallest thoracic uncini; m, abdominal uncinus (cross-hatching denotes longitudinal rows of teeth too small to depict); n, whole animal viewed from the ventral side, showing embryo mass which has been removed from the faecal groove, with what may be a posterior attachment filament. p, *Eulaeospira orientalis* paratype, whole animal (prior to mounting, slide deposited in B.M. Nat. Hist. showing typical flat opercular plate, long opercular stalk and embryos adhering along the faecal groove). Scales: c, d and e as b; g to m as f.

Locations

Previously found at Port Hacking, Sydney (Wisely, 1962). Abundant and widely distributed on marine plants in the Sydney and Adelaide areas (table 1, p. 144). Not recorded outside Australia.

Remarks

Pillai (1970) raised a new genus *Eulaeospira* for species which had the characteristics of *Spirorbis sensu stricto* but lacked sickle setae in the third thoracic fascicles. Paratypes of *Eulaeospira orientalis* Pillai and *E. convexis* (Wisely) were kindly loaned by the British Museum (Nat. Hist.) and compared with the above material. *E. orientalis* also shows marked bilateral asymmetry in the distribution of abdominal uncini (cf. Knight-Jones, Knight-Jones and Bregazzi, 1973), and embryonic masses "adhering" to the faecal groove (fig. 7p). The method of anchoring the embryos differs markedly from that known in *Spirorbis sensu stricto* and indeed from the methods known in all other genera of the Spirorbinae, except perhaps *Metalaeospira* (see p. 121).

Both *E. convexis* and *E. orientalis* show great variations in the size of the gaps between the fin and blade of the collar setae (there is often no gap at all). Another peculiarity is that both have many hooked abdominal capillary setae. Indeed, these were the *only* type present in the abdomen of one specimen of *E. orientalis* studied by Vine (1972). *E. orientalis* differs from *E. convexis* mainly in having a tube with a median ridge, a flat opercular plate, a remarkably long opercular stalk (fig. 7p), and uncini (both thoracic *and* abdominal) with four distinct anterior teeth, all similar in size.

Pillai also includes *E. variabilis* (Bush, 1904) in this genus. We have not examined this species, but it is interesting to note that Bush described it as incubating strings of eggs "along the back of the posterior segments".

Genus **Paralaeospira** Caullery & Mesnil, 1897, amended

Sinistral coiling; three thoracic tori on the concave side; embryos incubated in the region of the faecal groove but attached neither to the body nor to the tube; collar setae with fin and blades usually without cross-striations; thoracic uncini slender and with a blunt anterior peg; thoracic and abdominal uncini much more numerous on the concave side; largest abdominal tori occur towards the anterior end of the setigerous region; abdominal setae about half the length of the collar setae, with fairly short tapering blades.

Type: Spirorbis (*Paralaeospira*) *aggregatus* Caullery & Mesnil, 1897.

This is predominantly a southern genus with only one species known from the northern hemisphere (Knight-Jones, Knight-Jones and Vine, 1972) but it has not yet been found in Australia. It seems quite likely, however, that *Paralaeospira levinseni* Caullery and Mesnil (1897) may occur in the cooler waters of S. Australia and Tasmania, for this species is widespread in the southern ocean (Knight-Jones and Walker, 1973), occurring in South Africa, Chile (personal observations), New Zealand (Vine, 1974) and various Antarctic locations. It is found mainly on stones, shells and serpulid tubes, but sometimes on algae. The tubes are smooth (up to 2.5 mm) and may form aggregations. Many of them are then coiled irregularly. The operculum of the young form is a flat, lightly calcified disc, with a shallow ampulla, set rather asymmetrically on the opercular stalk. A small eccentric talon, variable in shape, develops later beneath the plate, which becomes asymmetrically convex. The collar setae are without cross-striations.

Genus **Metalaeospira** Pillai, 1970, amended

Sinistral coiling; three rows of thoracic tori on the concave side; embryos incubated in and attached to the faecal groove by tenuous threads (Knight-Jones, Knight-Jones and Vine, 1972); collar setae simple (without fins); thoracic uncini slender and with a blunt anterior peg; thoracic and abdominal uncini much more numerous on the concave side; tori large throughout most of the setigerous region; abdominal setae less than a quarter of the length of the collar setae and with vestigial brush-like blades.

Type: Spirorbis pixelli Harris, 1969 *nom. nov. pro Spirorbis antarcticus* Pixell (1913).

Metalaeospira tenuis Knight-Jones, 1973

Material

British Mus. (Nat. Hist.) holotype 1971:8; paratypes 1971:9; Australian Mus. paratypes W.4473.

Remarks

The specific name of this Australian species refers to the attenuated body and opercular "cap". The operculum is fragile and usually has a prominent distal cone in mature specimens, but the cone is truncated or even rather flat in younger specimens. The tube is thin-walled, porcellaneous and triangular in cross section, due to a single obtuse ridge. It has a large number of whorls which usually lie flat against the substratum (algae or marine angiosperms). The whorls increase regularly in size and height so that the central region forms a shallow dish-like depression (fig. 2b). A full description can be found in a recent paper (Knight-Jones, 1973).

Locations

Particularly abundant on *Jeannerettia* cast ashore on Brighton Beach, Adelaide. Also at Moanna and Kangaroo Island (table 1, p. 144).

Genus **Protolaeospira** (Pixell, 1912), redefined

Coiling usually sinistral (see below); three rows of tori on the concave side of the thorax; other traces of a fourth thoracic segment may or may not be present; embryos attached to a stalk which arises dorsally from the floor of the faecal groove in the thoracic region and towards the left side (fig. 4a); collar setae with separate fins and blades which are usually cross-striated (not in *Dextralia*—see below); sickle setae present in the third fascicle; thoracic and abdominal uncini much more numerous on concave side; thoracic uncini usually very long and slender, with a blunt, bilobed anterior peg; abdominal setae less than a quarter the length of the collar setae and with vestigial brush-like blades; opercular talon massive and usually bearing lateral projections; single white larval attachment glands may be present.

Type: Protolaeospira ambilateralis Pixell (1912).

This genus, of which *Marsipospira* Bailey (1969b) is a synonym, includes *Pixellia* Pillai (1970) and seems to be centred in the Southern Hemisphere, though a few species are found in the tropics and the north. Detailed comparison (Knight-Jones, Knight-Jones and Bregazzi, 1973) shows that it is very closely related to the Antarctic genus *Helicosiphon* Gravier.

Protolaeospira triflabellis Knight-Jones, 1973

Material

British Mus. (Nat. Hist.) holotype 1971:10, paratypes 1971:11; Australian Mus. paratypes W.4474.

Remarks

The opaque tube is easily distinguished from tubes of all other Australian Spirorbinae, by its large size and prominent transverse ridges (fig. 2d). The opercular talon is massive and opaque. It bears three irregular fluted projections which appear fan-like in dorsal view. The terminal "fan" is thick in profile and fluted on both sides.

Locations

On stones and *Ecklonia* holdfasts to the south-west of Kangaroo Island (table 1, p. 144).

Protolaeospira canina Knight-Jones, 1973

Material

British Mus. (Nat. Hist.) holotype 1971:12, paratype 1971:13; Australian Mus. paratypes W. 4475.

Remarks

The tube has two longitudinal ridges (the inner one the most prominent), with slight transverse grooves between them. A wide striated flange slopes down from the outer ridge and projects a little in front of the mouth, which may or may not ascend (fig. 2e). The opercular talon is large and in side view somewhat like a canine tooth, but a face view shows faint bulges on each side (one higher than the other) and an indistinct median longitudinal ridge.

Locations

On stones, to the south-west of Kangaroo Island (table 1, p. 144).

Subgenus **Dextralia** Knight-Jones, 1973

As above, for *Protolaeospira*, but with dextral coiling and lacking cross-striations on the blades of the collar setae.

Type: Spirorbis falklandicus Pixell (1913).

Only two species known, both from the south Atlantic (Knight-Jones and Walker, 1973).

Genus **Romanchella** Caullery & Mesnil, 1897

Sinistral coiling; incubation in an egg mass attached anteriorly by a stalk which arises dorsally, level with the thoracic tori and in the left side of the faecal groove; dorsal margins of the collar fused to form a tunnel over the faecal groove (fig. 5); simple collar setae; only two pairs of thoracic tori; sickle setae present in the third fascicles; abdominal setae strongly geniculate, with small tapered blades, less than a quarter the size of the collar setae, and usually paired (though one of a pair is often a hooked capillary setae); thoracic uncini with a blunt anterior peg which is gouge-shaped and may therefore appear bilobed; abdominal uncini numerous on the concave side of the abdomen and sparse on the convex, with the largest tori near the anterior end of the setigerous region; white larval attachment glands probably not present.

Type: Spirorbis perrieri Caullery & Mesnil, 1897.

This species is widespread in the Southern Ocean. Other species are known from Tristan da Cunha (Harris, 1969) and New Zealand (Vine, 1974). This narrow definition of *Romanchella* excludes little known northern forms, such as "*Spirorbis*" *evolutus* Bush, which have collar margins separate dorsally and a rather symmetrical distribution of uncini. These are perhaps best placed in the genus *Sinistrella* Chamberlain (1919) and the taxon *Bushiella* Knight-Jones (1973) should lapse.

Romanchella quadricostalis Knight-Jones, 1973

Material

British Mus. (Nat. Hist.) holotype 1971:14, paratypes 1971:15; Australian Mus. W.4476.

Description

The tube is often irregularly coiled, with four or five high smooth longitudinal ridges, three of which form prominent teeth at the mouth. There are no intercostal markings. The concave opercular plate bears a shallow broad peripheral talon which is cleft terminally (fig. 2c). Sometimes the outer surface of the plate shows incipient delamination and occasionally two lobed plates may be seen, one above the other.

Locations

Common on marine plants south-west of Kangaroo Island (table 1, p. 144).

Genus **Pileolaria** Claparède, 1868; amended

Sinistral coiling; two pairs of thoracic tori; incubation in the operculum; collar margins not fused dorsally; each collar seta with a fin, separate from a blade which is usually coarsely serrated and cross-striated; sickle setae may or may not be present; thoracic uncini very slender with one to three longitudinal rows of teeth and a blunt anterior peg; abdominal setae obliquely geniculate (with tapering blades) and usually about half the size of the collar setae (fig. 6d); abdominal uncini fairly symmetrical in bilateral distribution (fig. 6c); larvae have single white, mid-dorsal attachment glands.

Subgenus **Pileolaria**

Opercular dimorphism between juveniles and adults; juvenile operculum usually more or less flat or even concave and with a proximal talon; adult operculum usually helmet-shaped, bilaterally symmetrical and forming a brood chamber; brood chamber lacks a talon, unless that term is applied to the calcified wall which forms the back of the helmet; there is no separate secondary plate or cup beneath the embryos; collar setae cross-striated; sickle setae always present in the third fascicle; the largest thoracic uncini usually with a single row of teeth for most of their lengths.

Type: Pileolaria militaris Claparède (1868).

Pileolaria (Pileolaria) militaris Claparède

Material

Australian Mus. W.4480.

Description

Tube sinistral, large, often loosely coiled (sometimes ascending) with irregular growth rings and sometimes three faint longitudinal ridges (fig. 8a).

Opercular plate of the juvenile form is concave and has an eccentric talon, with lateral wings and a central spur (figs 8b and c). The helmet-shaped form of operculum may have an encircling symmetrical distal rim (fig. 8e), but usually the rim is absent or vestigial on the side away from the branchial crown (figs 8d and f) and may bear distal papillae (figs 8e and f). In well-developed opercula there are numerous spines within the rim and often one or two outside it (fig. 8d).

Thorax. Collar setae with fin and coarsely serrated, cross-striated blade (fig. 8g) accompanied by capillary setae. The second and third fascicles have simple setae (fig. 8h), with additional sickle setae (fig. 8j) in the third fascicles. Each thoracic uncinus has a blunt anterior peg followed by a few small teeth, but a single row of large teeth for most of its length (fig. 8k).

Abdomen with characteristic black patch in the position of the asetigerous region. The latter is relatively short, measuring about three times the length of the distance between the 1st and 2nd abdominal tori. It is followed by about nineteen setigers, bearing uncini which have approximately five longitudinal rows of teeth and a blunt anterior peg (fig. 8l). The setae are obliquely geniculate with sharply tapering blades (fig. 8m).

Incubation

In the operculum.

Locations

On stones and shells from Kangaroo Island and Sydney (see table 1, p. 144).

Remarks

This material was compared with *S. superbus* Pillai (1960), kindly made available by the British Museum of Natural History, and with specimens of *P. militaris* from Malta and Plymouth, U.K. The main difference between the Australian material and that from other locations is the presence of faint longitudinal ridges on the earlier whorls of the Australian tubes.

This difference seems insignificant, for tube variability is often associated with local conditions (Gee, 1964–see also pp. 108 and 135). The range of opercular variation of the material examined tends to confirm the suggestion of Zibrowius (1967 and 1968) that *Spirorbis beneti* Marion (1879), *S. cornuarietis* Phillipi in Marion & Bobretzky (1875), *S. serratus* Bush (1910), *S. mendosus* Bush (1910), *S. papillatus* Pixell (1913) and *S. superbus* Pillai (1960) are synonymous with this species.

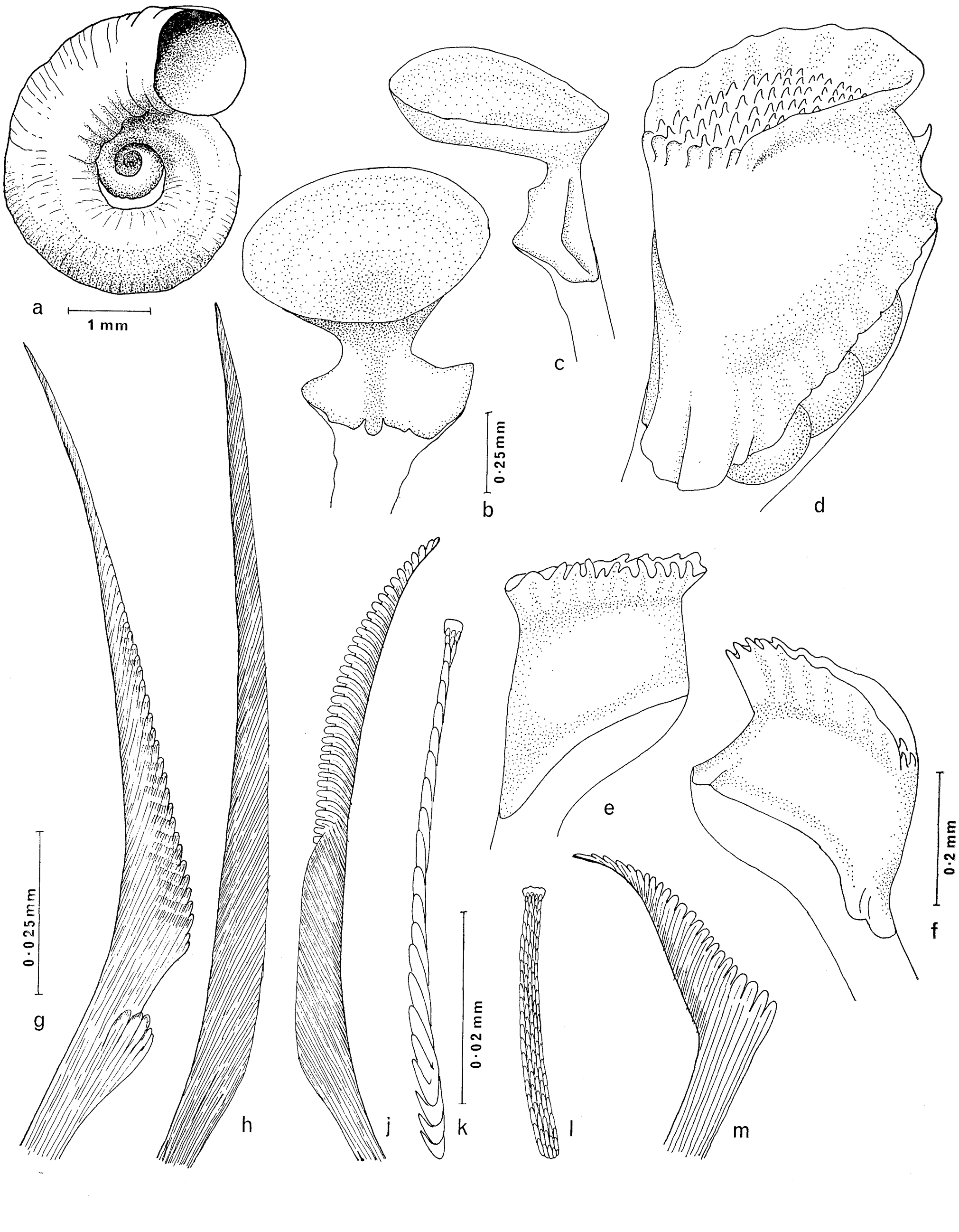

Figure 8.—*Pileolaria* (*Pileolaria*) *militaris:* a, tube; b and c, juvenile operculum, face and side views; d, typical adult operculum with embryos; e and f, variations of adult opercula; g, collar seta; h, simple seta of second or third fascicles; j, sickle seta from third fascicles; k, thoracic uncinus; l, abdominal uncinus; m, abdominal seta. Scales: c and d as b; e as f; h, j and m as g; l as k.

It is interesting to note that the "black spot", first described by Zibrowius (1967), is always found in the wide-spread populations of this species, but has not been found so far in other species, not even in closely related forms, such as *Pileolaria quasimilitaris* (Bailey, 1970). Several other species of *Pileolaria* have red or orange patches in this region, but these tend to disappear in preserved material.

Distribution

Very wide-spread on stones and algae in warm and temperate water. Zibrowius (1968) gives a comprehensive review of previous records from the Mediterranean, north coast of France, west coast of Spain, Madeira, Azores, Mexico, Suez, Zanzibar and Ceylon. It has also been found at Senegal (Sourie, 1954); Aegean (Bailey, 1969a); Red Sea (Vine, 1972); Hawaii (Vine, Bailey-Brock and Straughan, 1972); Malta, Plymouth (U.K.), south-west Ireland, West Indies, Mozambique and Cape Verde Is. (personal observations).

Subgenus **Simplicaria** Knight-Jones, 1973

Mature operculum somewhat helmet-shaped, but shallow, elliptical and bilaterally asymmetrical; sickle setae absent; otherwise like *Pileolaria sensu stricto.*

Type: Spirorbis pseudomilitaris Thiriot-Quiévreux (1965).

Pileolaria (Simplicaria) pseudomilitaris (Thiriot-Quiévreux)

Material

Australian Mus, W.4481.

Description

Tube sinistral, often irregularly coiled and with transverse growth rings which may meander to give an impression of faint longitudinal ridges (figs 9a and b).

Operculum. Plate of the juvenile form is asymmetrically concave with a small eccentric peg (fig. 9c). The mature operculum is an asymmetrical elliptical cap with a partially encircling distal rim which seems to be always absent on the side nearest the substratum. The rim is entire in a newly mature operculum (fig. 9f) but usually with serrations or papillae in older specimens (figs 9d and e). There may also be several spines within this rim.

Thorax. Collar setae with fin and blade with coarse serrations and cross-striations (fig. 9g). Capillary setae are also associated with these fascicles. The setae of the second and third fascicles are simple and slender, with almost smooth margins (figs 9h and j). There are no sickle setae. Two rows of tori. Each uncinus small and slender, the largest having a single row of teeth along most of its length and finer more numerous teeth just behind the blunt anterior peg (fig. 9m).

Abdomen. Length of asetigerous region about five times the distance between the 1st and 2nd abdominal tori. About seventeen abdominal segments. Each uncinus with a blunt anterior peg (fig. 9l). Setae have fairly long, obliquely geniculate blades with large blunt distal teeth (fig. 9k).

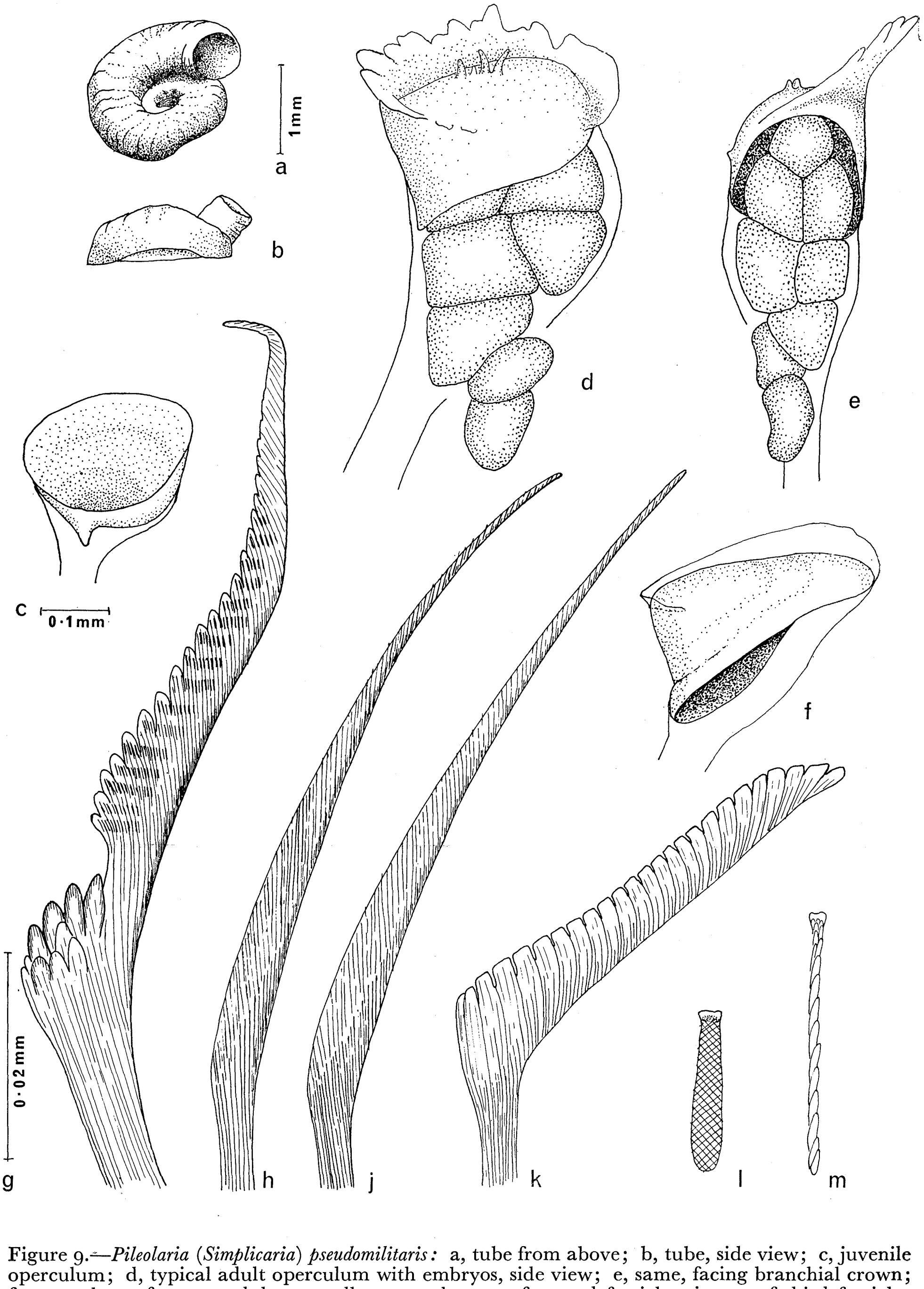

Figure 9.—*Pileolaria* (*Simplicaria*) *pseudomilitaris:* a, tube from above; b, tube, side view; c, juvenile operculum; d, typical adult operculum with embryos, side view; e, same, facing branchial crown; f, operculum of young adult; g, collar seta; h, seta of second fascicle; j, seta of third fascicle; k, abdominal seta; l, abdominal uncinus (cross-hatching represents rows of teeth too small to depict); m, thoracic uncinus. Scales: b as a; d, e and f as c; h to m as g.

Incubation

About eight to twelve eggs in the operculum. One specimen had apparently been fixed in the process of filling the operculum with eggs (figs 9d and e), assuming that this is done through a basal aperture, in the manner outlined by Potswald (1968) and Bailey (1969b). A perforation could be seen in the ampulla, facing a position between the centre of the branchial crown and the distal part of the dorsal groove (figs 9d and e). The eggs had not developed larval rudiments, so that it is unlikely that this specimen was releasing eggs, though there is no reason to suppose that the larvae are not released from the same position. Nevertheless, other specimens showed no sign of such an aperture, so it can be no more than transitory.

Locations

On stones and shells at Kangaroo Island and Sydney (table 1).

Remarks

This material agreed well with material from Malta, with Thiriot-Quiévreux's original description from southern France (1965) and with those of Bailey (1969a) from Chios and Harris (1968) from Naples. Harris called his material *Spirorbis berkeleyana* Rioja, but Rioja (1942) figured a mature operculum completely encircled by a distal rim and with the walls heavily calcified on one side but lightly calcified round the whole of the remaining periphery. This lies outside the range of variation in the different collections that we have examined. Another Galapagos form, *S. regalis* Bailey, is now considered to be synonymous with *P. pseudomilitaris* (Vine, Bailey-Brock & Straughan, 1972).

Distribution

Galapagos; Mediterranean (see above and also Zibrowius, 1968); Hawaii (Vine, Bailey-Brock and Straughan, 1972); New Zealand (Vine, 1974); Malta, Mozambique, Angola, Cape Verde Is. and Japan (personal observations).

Subgenus **Duplicaria** Vine, 1972

Opercula without distinct dimorphism between juveniles and adults, and may have two or more opercular plates stacked one above the other; embryos brooded in a lightly calcified cup below the opercular plates; collar setae not cross-striated; thoracic uncini may bear more than one longitudinal row of teeth for most of their lengths; the anterior abdominal torus on the concave side is often split into two unequal parts.

Type: Pileolaria (*Duplicaria*) *koehleri* (Caullery and Mesnil, 1897).

The type species has a world-wide distribution in warm waters and occurs on the Great Barrier Reef (Vine, personal communication) and New Zealand (Vine, 1974). It could well extend to south-eastern Australia, but was not found in our material. The tube has three irregular ridges, the outer of which is peripheral. Opercular plates (two or three) tend to stack and are joined to one another by a peripheral winged talon, the proximal point of which fits into a socket in the plate below. When brooding, the eggs lie between the lower plate and a delicate, slightly opaque proximal "cup". A good description was given by Bailey (1969a).

Genus **Amplaria** Knight-Jones, 1973

Sinistral coiling; concave side of thorax bears four tori and four fascicles of setae, convex side bears three tori and five fascicles; incubation in the operculum; fin and blade collar setae without cross-striations; sickle setae present in the third, fourth and fifth fascicles; thoracic uncini slender and with blunt anterior peg; abdominal setae geniculate, less than a quarter the size of the collar setae, with a prominent indentation at the "heel" and with short tapering blades; abdominal uncini somewhat asymmetrical in bilateral distribution with the largest tori about halfway along the setigerous region of the abdomen.

Type: Amplaria spiculosa Knight-Jones, 1973.

Amplaria spiculosa Knight-Jones

Material

British Mus. (Nat. Hist.) holotype 1971:16.

Description

The tube is somewhat square in cross section on account of two peripheral longitudinal ridges (fig. 2h). The opercular plate has a peripheral depression, which forms a sharp "V". It is encircled by a high transparent collar, the distal edge of which may be yellow and perhaps horny. From the centre of the plate arises a strong, slender, horny and somewhat hooked spine. The incubatory chamber below the plate is lightly calcified, with faint longitudinal granulations through which the embryos can be seen. The base of the chamber is formed by a calcified "cup". Vine (1974) has recently found this species in New Zealand.

Location

Kangaroo Island on stone (table 1).

Genus **Janua** Saint-Joseph, 1894, amended

Mostly with dextral coiling (pp 141 & 142); incubation in an opercular brood chamber below which a secondary plate (rudiment of the next opercular plate) is formed soon after spawning; only two pairs of thoracic tori; collar setae without a toothed fin; abdominal setae have elongated blades, as big as or more usually bigger than those of the collar setae (fig. 6f), and are often accompanied by secondary setae, with rudimentary shafts (Vine, 1972); thoracic uncini with anterior pegs narrow and more or less pointed in surface view; a bilaterally symmetrical distribution of abdominal tori (fig. 6e), the largest of which lie in the anterior half of the setigerous region; larvae have paired white attachment glands in the thoracic region.

Subgenus **Janua** Saint-Joseph, 1894

Dextral coiling; sickle setae present in the third thoracic fascicles; collar not forming a tunnel dorsally.

Type: Spirorbis pagenstecheri Quatrefages (1865) = *Spirorbis pusillus* St. Joseph, 1894 and *Spirorbis pusilloides* Bush, 1904.

Janua (**Janua**) **pagenstecheri** (Quatrefages)

Material

Australian Mus. W.4482.

Description

Tube usually coiled in one plane, with a single median longitudinal ridge in small specimens and up to three in larger ones; the median ridge being the most prominent. The outside of the coil may bear a large flange spreading over the substratum and extending to a position a little in front of the aperture (fig. 10a).

Opercular plate in the juvenile form is fairly flat and rather transparent except for an eccentric lightly calcified "disc" below which extends an almost peripheral peg-like talon (fig. 10b). On reaching maturity embryos are incubated below the plate and can be seen through the swollen walls of the ampulla. A secondary plate develops below the embryos which eventually becomes the distal plate of the next brood chamber. This and subsequent plates seem to lack talons (fig. 10c). They are usually slightly convex, with the highest point towards the edge where the talon used to be, but there is often a central depression. Fig. 10d shows the typical appearance at this stage, but the eccentric peak may be more prominent.

Thorax. Collar setae simple with finely serrate margins (fig. 10e) and accompanied by capillary setae. The setae of the second and third fascicles are simple, slender and rather straight, with almost smooth margins (fig. 10f). Sickle setae are also present in the third fascicles (fig. 10g). Uncini with about five rows of longitudinal teeth and a pointed anterior peg (fig. 10k).

Abdomen. The length of the asetigerous region is about three times the distance between the 1st and 2nd abdominal tori. There are about five setigers. Uncini with a broad fluted anterior peg (fig. 10l). Setae with long slender obliquely geniculate blades (fig. 10h). Their shafts may be accompanied by the blades of secondary setae (fig. 10j).

Incubation

About eight embryos in the operculum.

Locations

On stones and shells south-west of Kangaroo Island (table 1).

Remarks

Although the type species, this is in fact atypical of most species of *Janua*, which fall within the next subgenus. Previous descriptions contain some noteworthy anomalies. The collar setae, for instance, were said to have proximal fins (Caullery and Mesnil, 1897; Rioja, 1923; Fauvel, 1927; Gee, 1964; Bailey, 1969b) but Zibrowius (1968) found no such fins and examination of numerous mounted specimens from U.K., France, Chios and Malta, has tended to confirm his observations. Occasionally, however, a seta may be found to show the proximal differentiation seen in the figures of some of the above authors. A few specimens of *J.* (*J.*) *pagenstecheri* were viewed by stereoscan electronmicroscopy and the "blades" of the collar setae were shown to be, as in most Spirorbinae, subcircular in cross section and tapering distally. One seta, however, was rather bulbous proximally (fig. 10n) and a three-quarter view of this gives the appearance of an indented "margin" (fig. 10m). The "blades" are composed of numerous rods which show as fine teeth in profile. These are slightly larger on the proximal part of the blade than on the distal part, but there

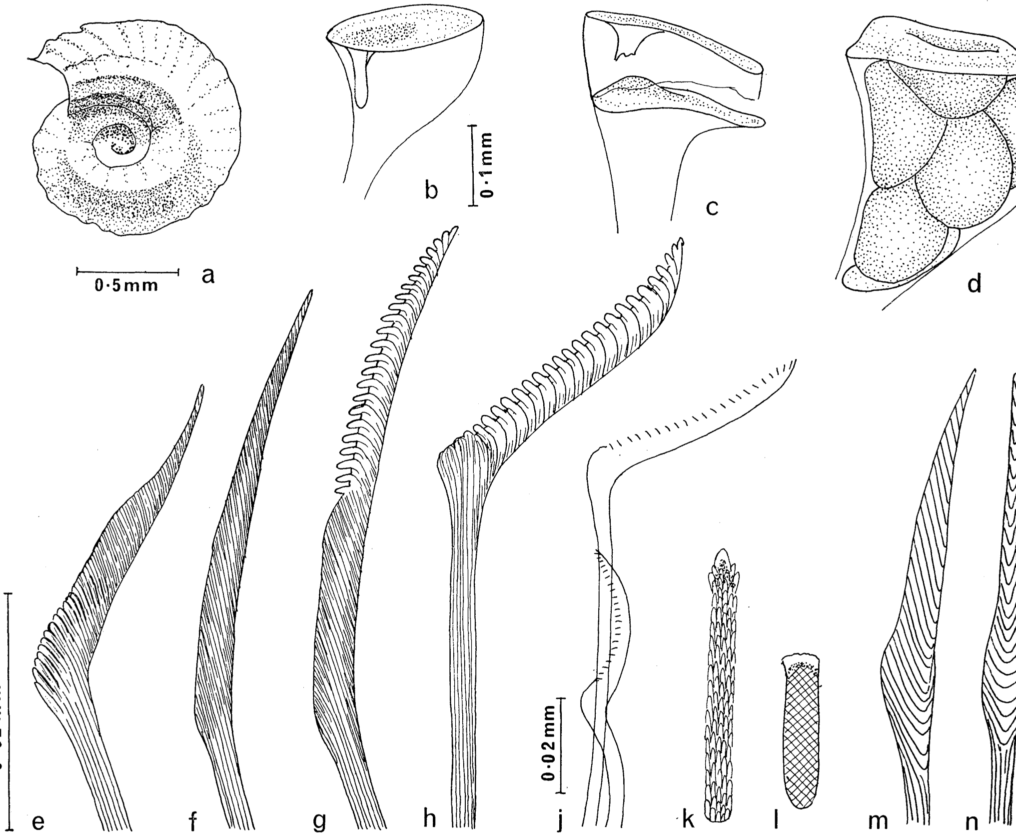

Figure 10.—*Janua* (*Janua*) *pagenstecheri:* a, tube; b, juvenile operculum, side view; c, adult operculum developing below damaged juvenile operculum; d, adult operculum with embryos; e, collar seta; f, simple seta from second or third fascicles; g, sickle seta from third fascicle; h, abdominal seta; j, secondary seta developing alongside shaft of a typical abdominal seta; k, thoracic uncinus; l, abdominal uncinus (cross-hatching denotes rows of longitudinal teeth too small to depict); m, diagrammatic drawing of a collar seta in three-quarter view, as it appears in a stereoscan electron micrograph; n, same showing view of the concave "edge". Scales: c and d as b; f to h and k to n as e.

is a zone of gradual transition between the two sizes. The appearance of a "fin" in some polyvinyl-lactophenol mounts may be due merely to individual setae being viewed at such an angle as to emphasise, in partial profile, any swelling of the proximal region. Zibrowius (1968) also comments on the occurrence at Marseille of specimens in which the opercula are without talons and markedly convex. Our examinations of Mediterranean and Australian forms confirm this, though we find that the strongly convex form is comparatively rare in populations from south-west Britain. Perhaps it is associated with warmer waters, more frequent breeding and therefore more frequent opercular moults. Thus we would agree with Vine, Bailey-Brock and Straughan (1972) that "*Spirorbis*" *epichysis* Bailey (1970) from the West Indies is probably synonymous with this species. Indeed, the range of opercular variation of *J.* (*J.*) *pagenstecheri* also includes *J.* (*J.*) *gnomonicus* (Bailey, 1969a) from the Aegean.

Distribution

Zibrowius (1968) has reviewed records of this species (including '*pusilloides*') from the Mediterranean, north and West Europe, Madeira, Canary Islands, Cape Verde Islands, Brazil, west coast of North America, Mexico, Tuamotu Islands, Gambia and the Persian Gulf. Other records are from Senegal (Sourie, 1954); Ceylon (de Silva, 1961); Galapagos Islands (Bailey and Harris, 1968); Aegean (as *Spirorbis gnomonicus* Bailey, 1969a); West Indies (as *Spirorbis epichysis* Bailey, 1970); Hawaii (Vine, Bailey-Brock, Straughan, 1972); New Zealand (Vine, 1974); South Africa and Angola (personal observations).

Subgenus **Dexiospira** Caullery and Mesnil 1897, amended

=*Neodexiospira* Pillai, 1970; see Knight-Jones, 1972. Coiling usually dextral; margins of the collar fused to form a tunnel over the mid-dorsal thoracic groove; sickle setae absent.

Type: Spirorbis pseudocorrugatus Bush (1904) *nom. nov. pro Spirorbis corrugatus* Caullery and Mesnil 1897 and most recent authors, *non* Montagu 1803, *non* Langerhans 1880 (see Knight-Jones, 1972 and 1973).

Janua (**Dexiospira**) **pseudocorrugata** (Bush)

Material

Australian Mus. W.4483.

Description

Tube dextral, with up to three ridges (the median one most prominent), either coiled flat against the substratum with a peripheral sloping flange extending to a position a little in front of the aperture (figs 11a and b), or with the last whorl ascending and round in cross-section. *Opercular plate* of juvenile flat or concave, often oblique and with a rather flat peripheral talon that may be somewhat triangular with a terminal cleft (fig. 11c, d), or subquadrangular in shape (fig. 11e, f). Specimens about to breed develop below the plate a transparent cylindrical chamber, which is very lightly calcified. Closely spaced granules may be seen in longitudinal rows on the calcified wall (fig. 11g), particularly when the chamber is empty and embryos do not obstruct the light. A secondary plate develops below the embryos and this eventually becomes the distal plate of the next chamber. This and subsequent plates are concave and do not bear talons (fig. 11h).

Thorax. Collar setae simple. Those of the convex side are fairly coarsely serrated with about six teeth and cross-striations per 8μ (fig. 11j). The cross-striations are more distinct in face view than in the more usual view from the side. The collar setae of the concave side have almost smooth margins and thus no cross-striations (fig. 11k), resembling those of the second and third fascicles (fig. 11l). Capillary setae are present in all fascicles. Uncini five to six teeth wide, each bearing a single pointed anterior peg (fig. 11n).

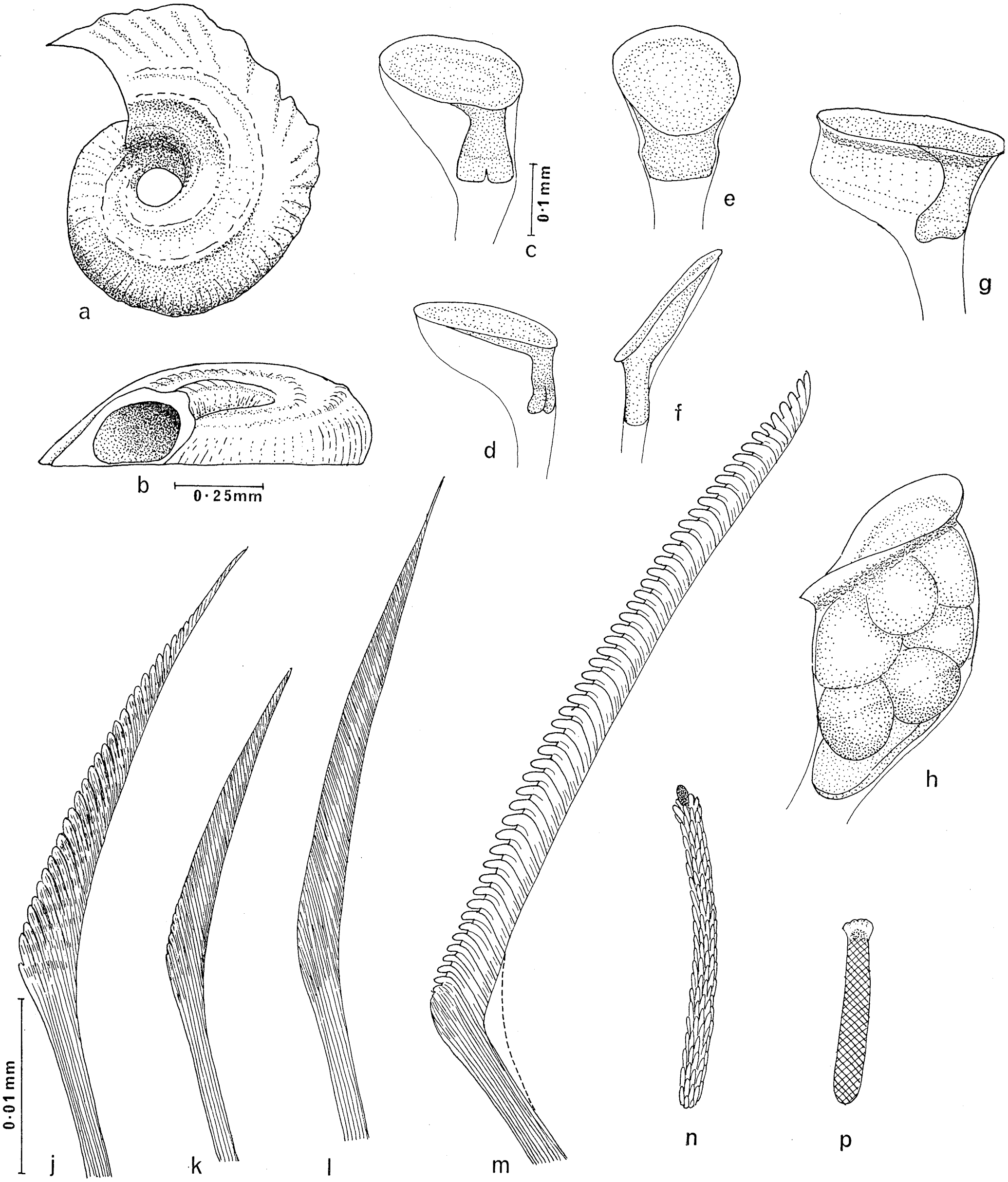

Figure 11.—*Janua* (*Dexiospira*) *pseudocorrugata* var. *ainu:* a, tube from above; b, tube from side; c, d, e and f, juvenile opercula, d and f side views of c and e; g, adolescent operculum with developing brood chamber; h, adult operculum; j, collar seta of convex side; k, collar seta of concave side; l, seta from second or third fascicles; m, abdominal seta (the dotted line represents the widening of the shaft found in *J.* (*D.*) *pseudocorrugata* from the type locality); n, thoracic uncinus; p, abdominal uncinus (cross-hatching represents rows of teeth too small to depict). Scales: a as b; d to h as c; k to p as j.

Abdomen. Asetigerous region fairly long (about five times the distance between the 1st and 2nd abdominal tori) and followed by about ten setigers. Uncini with a broad fluted anterior peg (fig. 11p). Blades of the setae obliquely geniculate and very long and slender (fig. 11m). The length/breadth ratio of the largest can be up to about 13:1. Blades of secondary setae may be found lying along the shafts of these setae.

Incubation

About eight embryos in the operculum.

Locations

On stones near Sydney and more sparsely at Kangaroo Island (table 1).

Remarks

This species shows considerable variation in the shape of the talon (Zibrowius, 1968), which is generally like a flattened pin in material found on algae in regions near the type locality (NW. France). The original description (Caullery and Mesnil, 1897) lacked any figure but could well apply to material with a slender talon, as in some that we have examined from SW. England, SW. Ireland, Roscoff and Malta, and in some Spanish and Mediterranean material figured by Rioja (1923), Sterzinger (1910) and Harris (1969). The somewhat triangular form (fig. 11c) is found particularly commonly on both stones or algae in the Mediterranean, West Indies, Hawaii (Zibrowius, 1968; Bailey, 1969 and 1970; Vine, Bailey-Brock and Straughan, 1972), Portugal, Corsica, Malta, Mozambique and Japan (personal observations). The subquadrangular form figured by Bailey (1969a) is also represented in material from Australia (fig. 11e) and particularly from Japan (kindly sent by Dr Tatuo Kawahara). Uchida (1971) describes a similar talon in a Japanese species which he named *Dexiospira ainu*, but we cannot clearly separate this from *J.* (*D.*) *pseudocorrugata*. The only difference which we can find is that the Australian and Japanese material has abdominal setae with shafts that do not widen noticeably towards the "heel", as they do in specimens from other locations (see fig. 11m). This does not seem enough to separate species, but it may be useful to regard the Australian material as *J.* (*D.*) *pseudocorrugata* var. *ainu*. Paratypes of *Neodexiospira mannarensis* Pillai and *N. benhami* Pillai (1970) from Ceylon were examined and are considered to be indistinguishable from this species, the abdominal setae having broad heels unlike those of var. *ainu*.

Zibrowius (1968) suggests that four other species may be conspecific with *J.* (*D.*) *pseudocorrugata*. They are indeed closely related and most are discussed later.

Distribution

Zibrowius (1968) also reviewed previous records of *J.* (*D.*) *pseudocorrugata* (as *Spirorbis corrugatus*) from France, Spain, Morocco, Azores, Mexico, Suez and various Mediterranean locations. However, the records from the open Atlantic (Fauvel, 1914) and from Madeira (Langerhans, 1880) are now considered to be species other than *J.* (*D.*) *pseudocorrugata* (Knight-Jones, 1972 and 1973). Other records: Naples (Harris, 1968), Aegean and W. Indies (Bailey, 1969a and 1970), Japan (as *Dexiospira ainu*, Uchida, 1971), Hawaii (Vine, Bailey-Brock and Straughan, 1972), SW. England and SW. Ireland, Corsica, Malta, Portugal, Mozambique and Japan (personal observations).

Janua (Dexiospira) fenestrata Knight-Jones, 1973

Material

British Mus. (Nat. Hist.) holotype 1971:17, paratypes 1971:18; Australian Mus. paratypes W.4477.

Description

Tube may coil in one plane or the last whorl may ascend. Three very prominent longitudinal ridges, the outer of which is peripheral and projects as far as, or beyond the area of attachment to the substratum. Between the ridges are deep transverse furrows, which in many specimens extend to form holes (tunnels) through the two outer ridges, giving a "lacy" appearance from above (fig. 3d).

Opercular plate has a central calcified disc surrounded by an upturned brown rather membranous rim. A cylindrical talon, bulbous and bilobed terminally, extends proximally from the dorsal edge of the plate (fig. 3d). Mature opercula which may not bear talons, develop calcified walls through which the embryos can be seen.

Collar setae on the concave side have simple blades with margins coarsely serrated (about four teeth and cross-striations per 8μ). Those of the convex side have almost smooth margins and thus no cross-striations. The asetigerous region was originally described as being remarkably long, but this is not typical of this species.

Location

Known only from rocks and *Ecklonia* holdfasts at Kangaroo Island (table 1). This species was separated mainly because of the sculpturing of the tube, but we now consider this to be a rather unreliable character. For instance, *J.* (*D.*) *nipponica* Okuda (1934) from Japan (kindly collected by Dr. Kawahara) may have ordinary tube ridges in certain habitats and very prominent perforated ridges in others. Nevertheless at Cape du Couedic *J.* (*D.*) *fenestrata* and its extremely close relative *J.* (*D.*) *pseudocorrugata* occurred together in circumstances indicating that the differences involved distinct strains and were not associated with differences in habitat or age. Besides the intricate sculpturing, the tubes of the former differ from most forms of *J.* (*D.*) *pseudocorrugata* in that the third ridge of the tube is always markedly peripheral (cf. figs 3d and c). Moreover *J.* (*D.*) *fenestrata* also differs from the Australian and Japanese form of *J.* (*D.*) *pseudocorrugata* in having the abdominal setae with shafts widening towards the "heel" at the base of the blade, although in this respect it resembles *J.* (*D.*) *pseudocorrugata* from other locations (see p. 134 and fig. 11m). The collar setae of the convex side, furthermore, have coarser serrations, resembling those of *J.* (*D.*) *lamellosa* and *J.* (*D.*) *steueri* rather than *J.* (*D.*) *pseudocorrugata* from any location.

These differences though constant are so slight that both the Australian forms may be no more than varieties of a basic stock of *J.* (*D.*) *pseudocorrugata*, which have nevertheless diverged sufficiently to remain separate from one another, at least on Kangaroo Island. They undoubtedly deserve further study.

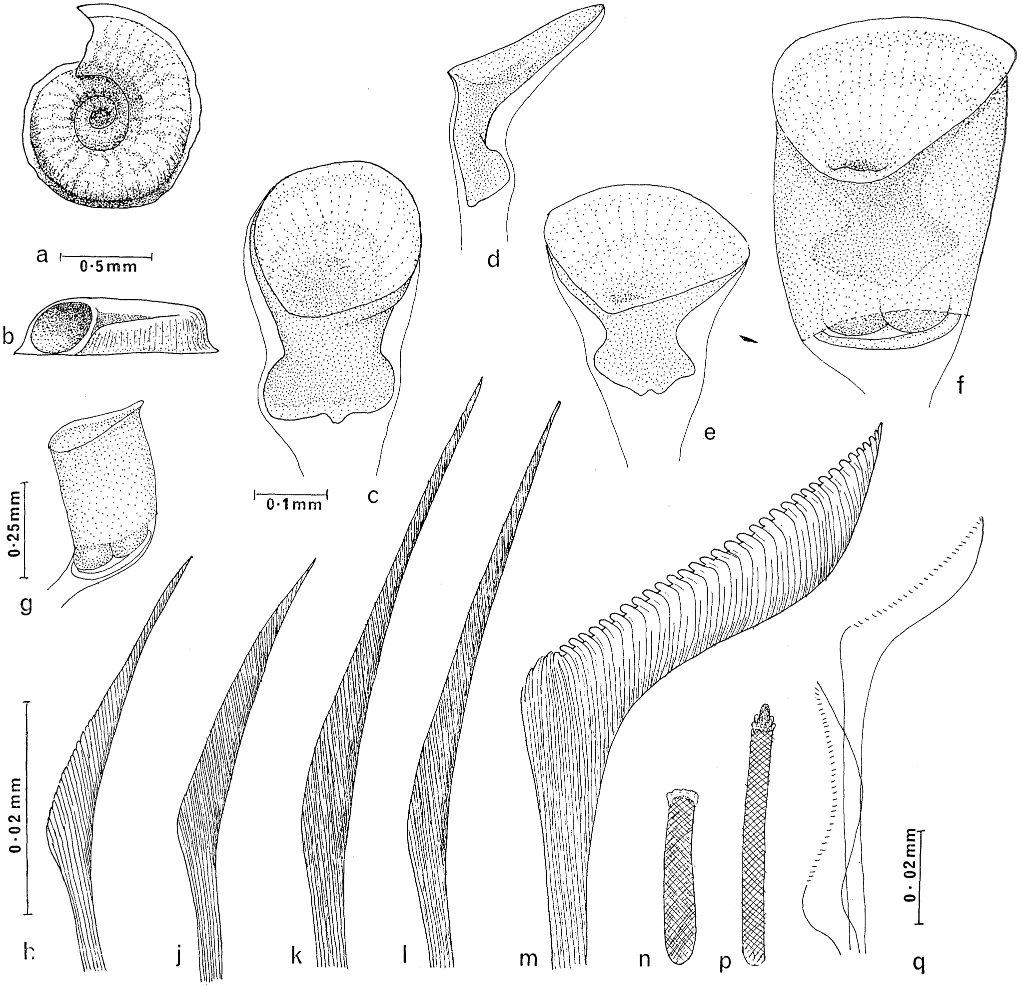

Figure 12.—*Janua* (*Dexiospira*) *formosa:* a, tube from above; b, same side view; c, d and e, juvenile opercula, d side view of c; f, operculum with brood chamber and embryos; g, fully adult operculum; h, collar seta of convex side; j, collar seta of concave side; k, seta of second fascicles; l, seta of the third fascicles; m, abdominal seta; n, abdominal uncinus (cross-hatching represents rows of teeth too small to depict); p, thoracic uncinus; q, secondary seta developing alongside shaft of a typical abdominal seta. Scales: b as a; d, e and f as c; j to p as h.

Janua (Dexiospira) formosa

Bush (1904) var. *australis*

Material

Australian Mus. W.4484.

Description

Tube dextral, rather round in cross section, with a very small peripheral flange and indistinct longitudinal ridges on the upper surface (figs 12a and b). Most of the tubes were very decalcified, making it difficult to study the range of variation.

Opercular plate asymmetrically concave, the deepest part closely associated with a flat winged talon (figs 12c, d, e, and f) which is usually faintly bifurcate terminally. Specimens about to breed develop a brood chamber, the walls of which are calcified heavily enough to hide the embryos but not the closely associated talon (fig. 12f). A secondary plate develops below the embryos and, as in the previous species, this and subsequent plates seem to lack talons (fig. 12g).

Thorax. Collar setae on both sides (figs 12h and j) resemble the setae of the second and third fascicles (figs 12k and l) in being simple with almost smooth margins and consequently without cross-striations. Uncini seem to have about ten longitudinal rows of fine teeth, with larger teeth bordering a pointed anterior peg (fig. 12p).

Abdomen. Asetigerous region long, about six times the distance between the 1st and 2nd abdominal tori. About ten setigers. Uncini with a broad fluted anterior peg (fig. 12n). Setae with obliquely geniculate blades, which are unusually wide, the length/breadth ratio being about 4.5:1 (fig. 12m). Blades of secondary setae may be found lying along the shafts in some fascicles (fig. 12q).

Incubation

About eight to ten embryos in the operculum.

Location

On *Ecklonia radiata* near Sydney (table 1).

Remarks

The talon of this Australian form may resemble that of *J.* (*D.*) *pseudocorrugata* (cf. figs 11c and 12c) and in these waters to a lesser degree that of *J.* (*D.*) *steueri* (fig. 14c). The collar setae and the abdominal setae, however, are distinct from both these species. The bilateral asymmetry of the concave plate is characteristic, but differs somewhat from material of *J.* (*D.*) *formosa* identified by Bush from Bermuda (kindly loaned by the Smithsonian Institute) and that from Kenya, West Indies and Ceylon (Knight-Jones 1972), in which (1) the concavity of the plate is situated more symmetrically, (2) the terminal lobes of the talon are longer and more like those of *J.* (*D.*) *steueri* from most locations (p. 141) and (3) the longitudinal rows of teeth on the thoracic uncini seem to be only about 6 or 7 instead of 10. Details of the setae, particularly the distinctive shape of the abdominal setae, are similar in all locations. We regard the Australian material as *J.* (*D.*) *formosa*, but tentatively separate it from the type by naming it var. *australis*.

Distribution

Bermuda (Bush, 1904, 1910); Ceylon, Kenya, West Indies and on floating *Sargassum* at two locations between U.S.A. and Bermuda (Knight-Jones, 1972); Mozambique (personal observations).

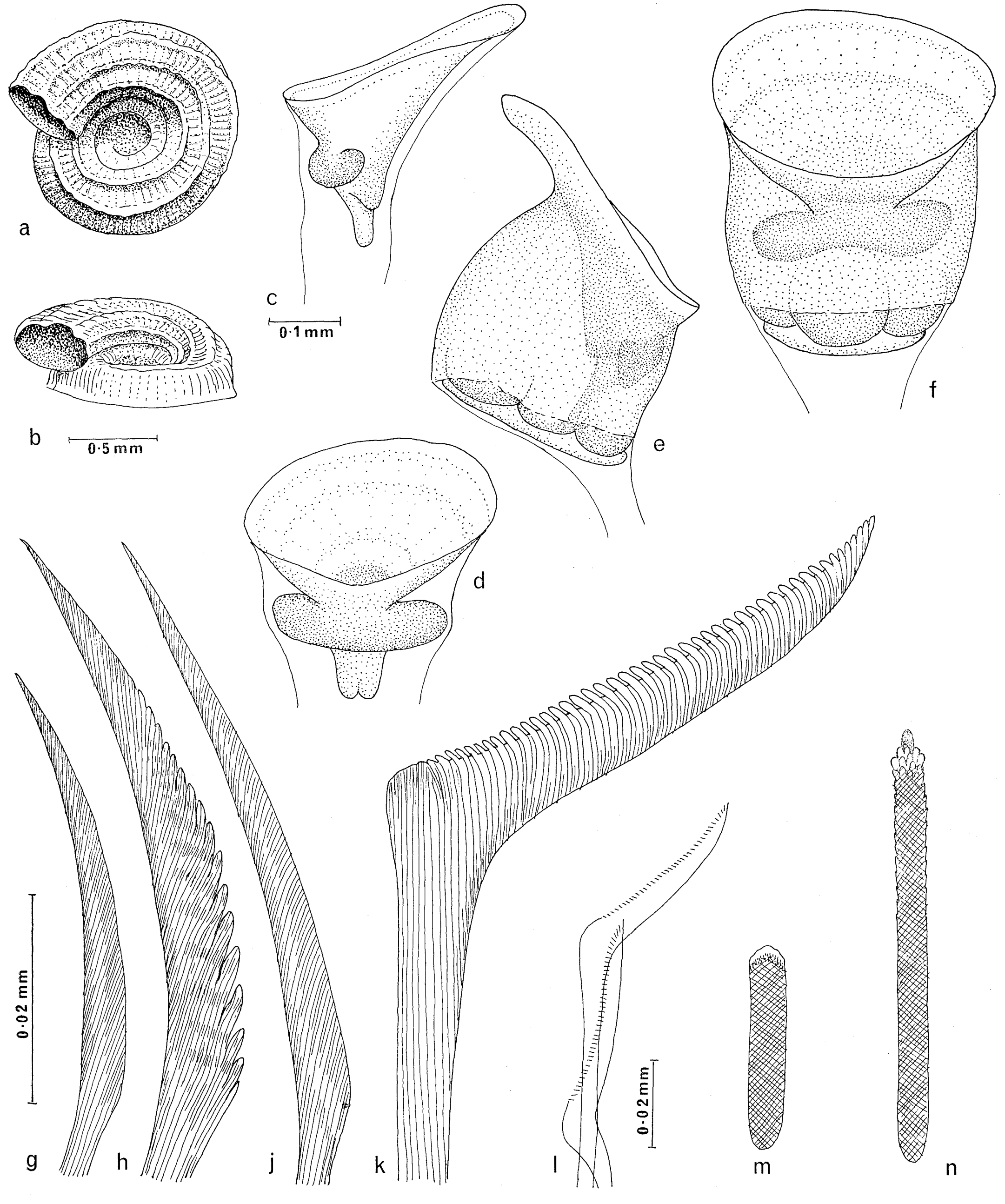

Figure 13.—*Janua* (*Dexiospira*) *lamellosa:* a, tube from above; b, same side view; c, juvenile operculum from side; d, same facing away from branchial crown; e and f, side and face views of an operculum with brood chamber and embryos; g, collar seta from concave side; h, collar seta from convex side; j, seta of second or third fascicles; k, abdominal seta; l, secondary seta developing alongside partner, which is a typical abdominal seta; m, abdominal uncinus; n, thoracic uncinus (cross-hatching represents rows of teeth too small to depict). Scales: a as b; d to f as c; h to k, m and n as g.

Janua (**Dexiospira**) **lamellosa** Lamark, 1818 (Wisely, 1962)

Material

Australian Mus. W.3751.

Description

Tube dextrally coiled, rather round in cross section, but with three or four distinct longitudinal ridges between which are fine transverse furrows (figs 13a and b).

Opercular plate funnel-shaped and bilaterally symmetrical. The dorso-dextral face of the funnel bears a large transverse rounded bar, the ends of which form bulbous lateral lobes. A small bilobed talon extends proximally from the apex of the "funnel" (figs 13c and d). A brood chamber develops in such a way that the plate forms a markedly projecting rim opposite the talon complex (fig. 13e). The chamber walls are heavily calcified, but the more opaque transverse bar can still be seen, though the terminal part of the talon may be obscured by embryos (figs 13e and f).

Thorax. Collar setae simple, those of the convex side coarsely serrated, with about three teeth (or cross-striations) per 8μ (fig. 13h), whilst those on the concave side have almost smooth margins and thus no cross-striations (fig. 13g) and are similar to those of the second and third fascicles (fig. 13j) Uncini seem to have about 8 longitudinal rows of teeth of which the anterior ones are larger and border a pointed anterior peg (fig. 13n).

Abdomen. A fairly long asetigerous region, followed by about eleven setigers (fig. 6e). Uncini with a rounded scalloped anterior peg (fig. 13m). Setae with long, fairly broad, obliquely geniculate blades (fig. 13k). Blades of secondary setae are sometimes found lying along the shafts of these setae (fig. 13l).

Incubation

About eight embryos in the operculum.

Location

On the marine angiosperm *Amphibolis antarctica* at Brighton, near Adelaide (table 1).

Distribution and remarks

Lamarck erected this species merely on the form of the tube (1818), which Chenu figured at a later date (1843). The type locality in Australia is unknown. Wisely (1962) gave the first adequate description of this species, basing his identification on Chenu's figure, which agrees very well with ours, though it must be admitted that such tube characters are not very distinctive. Our Australian material also agrees with Wisely's specimens from *Posidonia* sp., Port Hacking, which had been deposited in and were kindly loaned by the British Museum (Nat. Hist.). The slit in the operculum mentioned by Wisely would appear to be the line of dehiscence during release of embryos. We did not find a brood-chamber without a talon, though secondary plates showed no sign of developing talons. It seems to be very unusual amongst *Dexiospira* species, however, for late stage opercular plates to bear talons.

This species is probably closest to the Japanese form *J.* (*D.*) *foraminosa* (Moore & Bush, 1904), the proportions of the abdominal setae being very similar. It differs from that species in having a prominent cross-bar to the talon, a less slender and more opaque brood chamber and larger marginal teeth (coarser cross-striations) on the collar setae. It may well be endemic to Australia.

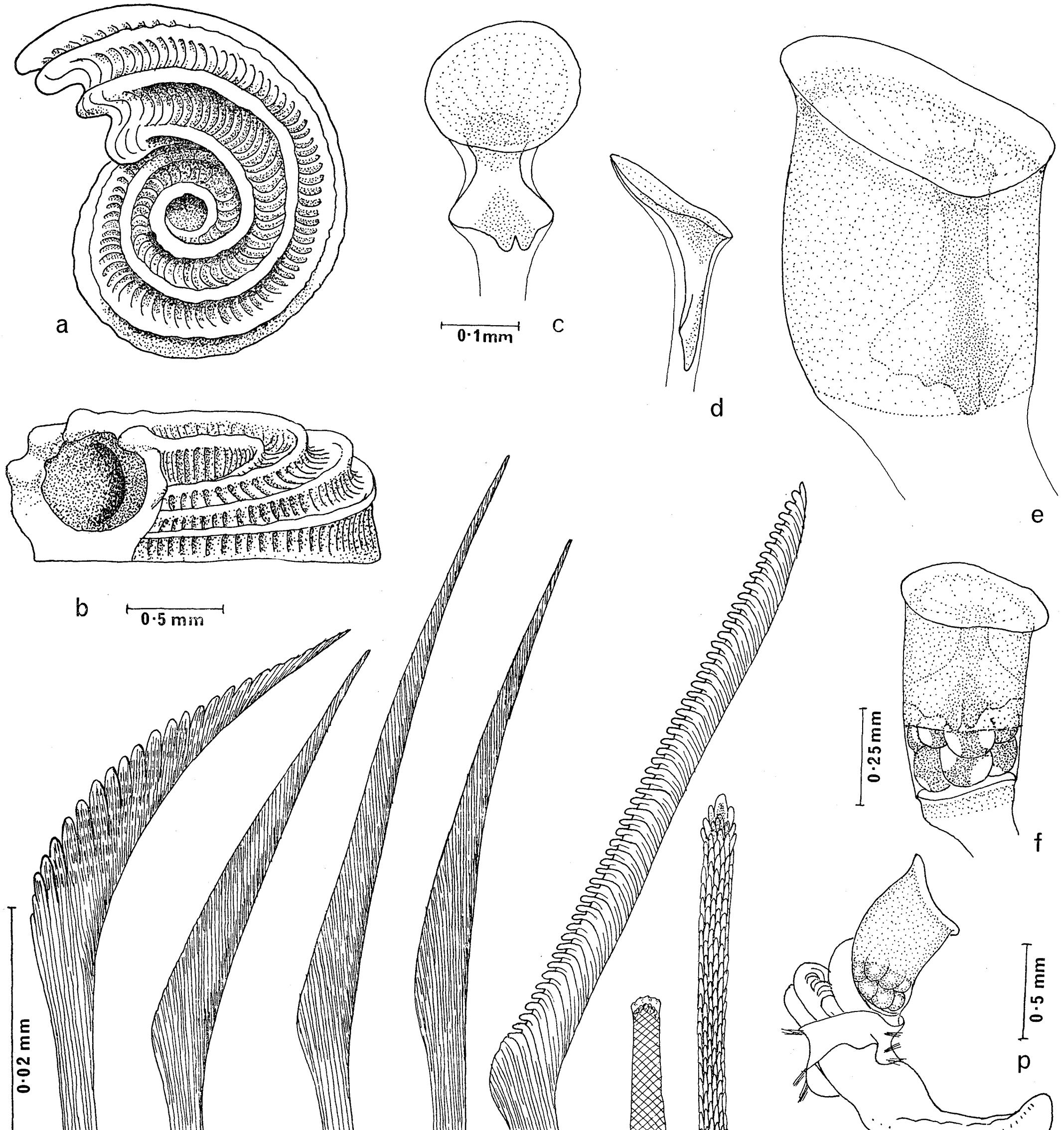

Figure 14.—*Janua* (*Dexiospira*) *steueri:* a, tube from above; b, same side view; c, juvenile operculum showing face of talon; d, same showing side; e, operculum with developing brood chamber; f, operculum with embryos, showing an adult brood chamber developing beneath the secondary plate; g, collar seta from convex side; h, collar seta from concave side; j, seta of second fascicles; k, seta of third fascicles; l, abdominal seta; m, abdominal uncinus (cross-hatching represents rows of teeth too small to depict); n, thoracic uncinus; p, whole animal showing adult operculum and collar margins fused over the dorsal groove. Scales: a as b; d and e as c; h to n as g.

Janua (Dexiospira) steueri (Sterzinger, 1909)

Material

Australian Mus. W.4485.

Description

Tube dextrally coiled, thick walled, with up to four rough prominent longitudinal ridges which usually terminate as three projections at the aperture. Between the ridges are fine curved transverse furrows (figs 14a and b).

Opercular plate slightly concave, bilaterally symmetrical, and bearing towards the dextro-dorsal edge a long talon, with flat transparent angular lateral wings and two white flat terminal lobes (figs 14c and d). A calcified chamber develops beneath the plate leaving a distal collar-like rim. The more opaque parts of the talon can be seen through the wall of the chamber (figs 14e and f). A secondary plate develops below the embryos and later chambers seem to lack talons (fig. 14p).

Thorax. Collar setae simple, those of the convex side coarsely serrated, with about four teeth (and cross-striations) per 8μ (fig. 14g), whilst those on the concave side have almost smooth margins and no cross-striations (fig. 14h) and are similar to those of the second and third fascicles (figs 14j and k). Uncini with about six longitudinal rows of teeth, of which the anterior ones are larger and flank a pointed anterior peg (fig. 14n).

Abdomen. Asetigerous region fairly long, about seven times the distance between the first and second abdominal tori, followed by about eleven setigera. Uncini with a blunt fluted anterior peg (fig. 14m). Setae with long and very slender obliquely geniculate blades (fig. 14l). Blades of secondary setae are sometimes found lying along the shafts of these setae.

Incubation

About 1–14 embryos in the operculum.

Location

On various algae (table 1) in the Adelaide and Kangaroo Island regions.

Remarks

The similarity between this and *J.* (*D.*) *formosa* (p. 136) is superficial and certain identification can be made by examining the collar setae and abdominal setae (cf. figs 12 and 14). Sterzinger's discovery of both sinistral and dextral forms of *J.* (*D.*) *steueri* (on both algae and stones) has been confirmed by recent collections from the Red Sea (Vine, 1972), but the Australian specimens that we have examined have all been dextral.

This species is particularly closely related to *J.* (*D.*) *pseudocorrugata,* but differs in being larger, with a more intricately sculptured tube, a brood chamber with more opaque walls and a more prominent distal rim, a talon with lateral wings and terminal pointed lobes and collar setae that are somewhat more coarsely serrated (cf. figs 11 and 14). "*Spirorbis*" *treadwelli* Pillai (1965) is probably the mature form of this species (Knight-Jones 1972), particularly because of the coarseness of the serrations of the collar setae.

Distribution

Suez (Sterzinger, 1909); West Indies (Bailey, 1970); Philippines (as *S. treadwelli,* Pillai, 1965); E. Australia (as *S. treadwelli,* Straughan, 1967); Kenya (Knight-Jones, 1972); Hawaii (Vine, Bailey-Brock and Straughan, 1972); Red Sea (Vine, 1972); New Zealand (Vine, 1974); Mozambique (personal observations).

Subgenus **Pillaiospira** Knight-Jones (1973)

Lacking sickle setae and in other respects too like *Dexiospira*, but with collar folds not fused dorsally.

Type: Janua (Pillaiospira) trifurcata Knight-Jones (1973).

Janua (**Pillaiospira**) **trifurcata** Knight-Jones

Material

British Mus. (Nat. Hist.) holotype 1971:19, paratypes 1971:20; Australian Mus. paratypes W.4478.

Description

Tube dextral, the last whorl usually coiling over the previous whorls, round in cross section and bearing three longitudinal ridges, with "chevron" sculpturing between (fig. 3b).

Opercular plate in juvenile specimens (fig. 3b) is convex with the dextro-dorsal edge folded downwards to form a deep U-shaped depression, with which a flattened "peg" talon is associated. The folding is asymmetrical and flanked on the right side by a peripheral protrusion. When the first incubatory chamber is formed, by the development of finely granular calcified walls, it is as wide as or wider than the plate, so there is no protruding distal rim. A secondary plate develops below the embryos and forms the distal part of the next brood chamber. This chamber lacks a talon and is more symmetrical, with a flat distal plate surrounded by a thick undulating rim. The wall of an empty chamber in reflected light shows widely spaced longitudinal markings. When damaged the chamber tends to break in the position of these markings, which seem to be lines of weakness, from which the intervening sections of wall splay out like the staves of a barrel.

Thorax. The collar setae of both fascicles are simple with almost smooth margins and no cross-striations. The uncini are distinctive in having a dense strongly trifurcate anterior peg and about 5 longitudinal rows of teeth.

Locations

Adelaide and Kangaroo Island, on algae (Table 1).

Subgenus **Fauveldora** Knight-Jones 1972

As for *Dexiospira*, but with sinistral coiling.

Type: Janua (Fauveldora) kayi Knight-Jones (1972).

The type was found off Kenya. Its talon resembles that of *J.* (*D.*) *steueri*, but the distal plate is strongly domed. *J.* (*F.*) *anticorrugata* Vine (1972), the only other species in this subgenus, occurs in the Red Sea. Its talon resembles that of *J.* (*D.*) *pseudocorrugata*. Neither of these species of *Fauveldora* have yet been found in Australian waters and they are likely to be confined to tropical latitudes. Both species have collar setae (on both sides) with margins that are finely serrated and without cross-striations.

Subgenus **Leodora** Saint-Joseph (1894)

Sinistral coiling; thoracic collar folds unfused; sickle setae absent (see Vine, Bailey-Brock and Straughan, 1972).

Type: Spirorbis laevis Quatrefages (1865).

This species appears to be a *nomen nudum*. It was recorded by Ehlers (1913) at Simonstown, S. Africa (the only record in the southern hemisphere) but his material, deposited in the Hamburg museum, has proved on examination to be a dextral form, in spite of Ehler's figure to the contrary (Zibrowius, 1973). This subgenus however includes another species *Janua* (*Leodora*) *knightjonesi* de Silva (1965) which has a widespread distribution in warm latitudes: Ceylon (de Silva, 1965); West Indies (Bailey, 1970); Hawaii (Vine, Bailey-Brock and Straughan, 1972); and Red Sea (Vine, 1972). This species has been found recently in the region of the Great Barrier Reef (Vine, personal communication). The tube has three well defined ridges. The operculum usually bears two and occasionally three brood chambers one above the other. The talon is peg-like as in *J.* (*J.*) *pagenstecheri*, but peculiar in that it is always developed in each of the successive chambers.

Genus **Anomalorbis** Vine (1972)

Tube probably dextral; rudiments of five thoracic segments; collar setae simple with smooth margins (no fins), resembling the setae of the other thoracic segments; sickle setae absent; development of embryos probably in the operculum.

Type: Anomalorbis manuatus Vine (1972).

Known from only a single specimen, collected from a depth of 30 metres near Port Sudan. It may possibly extend into the warmer waters of the southern hemisphere. The tube and operculum probably resemble those of the juvenile form of *J.* (*D.*) *steueri*. There are four tori and five fascicles of setae on the concave side and three tori and four fascicles on the convex side of the thorax. Each thoracic uncinus has a large pointed anterior peg and a number of associated finger-like projections, looking like the thumb and fingers of a hand. The number of longitudinal rows of teeth on a thoracic uncinus varies from one on the larger uncini of the convex side, to about five on the smaller uncini.

ECOLOGICAL NOTES

All the collections were made by L C L, at the localities listed in table 1. Parsley Bay, South Head, Vaucluse (33° 52′ S., 151° 17′ E.), visited 22 July 1967, is a narrow inlet with rocky sides, sheltered within the Sydney Heads. Five Spirorbinae were found at various levels between tidemarks, the most abundant being *Eulaeospira convexis* and *Janua formosa*, both from fronds of *Ecklonia*. The other species, of which the most common was *J. pseudocorrugata*, were scraped from stones and shells.

The remaining collections were made between 1 and 15 January, 1967. Brighton beach, Adelaide (35° 00′ S., 138° 28′ E.) is sandy without rocky outcrops, but there were plenty of Spirorbinae on plants floating in the surf. These had presumably been washed in from sublittoral reefs and they bore five species, of which the most abundant was *Metalaeospira tenuis*. Similar collections were made at Moanna, a sandy beach 24 miles south of Adelaide, from a large pile of algae probably washed in from a sublittoral reef. There were also Spirorbinae on *Sargassum* attached to rocks on the lower shore at Moanna (13 January, 1967), but these were not kept separate, in the collecting jar, from those that had been drifting.

The greatest variety of Spirorbinae was found on Kangaroo Island (35° 55′ S., 136° 58′ E.), where the exposure to wave action of various shores has been described thoroughly by Womersley (1947). Kingscote, on the sheltered north-east coast, was

Table 1

Distribution of species between site samples. M, L & U & S = middle, lower & upper shore & sublittoral respectively

Locality	Substratum	Tidal level	*E. convexis*	*M. tenuis*	*P. triflabellis*	*P. canina*	*R. quadricostalis*	*P. militaris*	*P. pseudomilitaris*	*A. spiculosa*	*J. pagenstecheri*	*J. pseudocorrugata*	*J. fenestrata*	*J. formosa*	*J. lamellosa*	*J. steueri*	*J. trifurcata*
Sydney,	Stones and molluscs	M	..	..	..	..	..	..	3+	..	..	25+	..	..	..	..	..
Parsley	Stones and molluscs	L	..	..	..	..	..	4	14	..	..	24	..	..	..	..	..
Bay	Stones and molluscs	S	..	..	..	..	..	..	6+	..	..	24+	..	..	..	..	..
	Ecklonia holdfasts	S	..	..	..	..	..	..	..	..	..	22	..	..	..	..	..
	Ecklonia fronds	L & S	100+	..	..	..	..	..	..	..	..	..	..	200+	..	..	..
	Sargassum	L & S	13	..	..	..	..	..	..	..	..	..	..	1	..	..	..
Adelaide,	*Amphibolis*	S	10	19	..	..	..	..	..	..	..	..	..	..	9	8	..
Brighton	*Jeannerettia*	S	4	200+	..	..	..	..	..	..	..	..	..	..	..	..	..
Beach	*Hypnea*	S	..	..	..	..	..	..	..	..	..	..	..	..	..	17	19
Moanna	*Sargassum*	S	19	40	..	..	..	..	..	..	..	..	..	..	..	50	..
Kingscote	Stones and molluscs	L	..	..	..	..	..	..	40	1	84	..	..	..	..	..	..
Sou-West	Stones	M	..	..	..	..	..	..	..	..	10	..	..	..	..	..	..
R.		L	..	..	3	6	..	..	..	..	20+	..	..	..	..	..	..
	Amphibolis	S	2	4	..	..	..	..	..	..	..	..	..	..	..	..	..
	Epiphyte on *Amphibolis*	S	..	..	..	..	28	..	..	..	..	..	..	..	..	..	..
	Hypnea	S	..	..	..	..	..	..	..	..	..	..	..	..	..	..	9
	Sargassum	S	7	..	..	..	..	..	..	..	..	..	..	..	..	16	..
Cape du	Stones and rocks	U	..	..	6	..	..	38	..	..	..	..	1	..	..	..	..
Couedic	Stones	M & L	..	..	2	27	..	61	8	..	23	4	13	..	..	..	..
	Amphibolis	L	..	10	..	..	..	..	..	..	..	..	..	..	..	..	..
	Pterocladia	L	..	..	..	..	100+	..	..	..	..	..	..	..	..	..	..
	Ecklonia holdfasts	S	100+	..	6	..	4	..	..	..	..	..	1	..	..	4	..

visited on 3 Jan. The intertidal zone was searched and three species were scraped from loose rocks and mussels. Spirorbinae were common there, but generally confined to shaded under-surfaces. This collection included the extraordinary opercular incubator, *Amplaria spiculosa*, and the largest numbers of *Pileolaria pseudomilitaris* and *Janua pagenstecheri*.

The south coast of Kangaroo Island, which is very exposed to wave action, was sampled more intensively. At Sou-West River (visited 5 and 6 Jan.) three species were scraped from stones which were jammed under larger boulders and five more were found on unattached plants that had been washed up in heavy surf, apparently from a sublittoral reef about 100 metres off shore. At Cape du Couedic (visited 8 Jan.) eleven species were found, the most remarkable being *Romanchella quadricostalis*, attached to the alga *Pterocladia*, which formed a distinct zone on the shore. This was the sole locality for *Janua fenestrata* and the best for *Pileolaria militaris* and the two species of *Protolaeospira*.

Frequent exchanges of silt-free water undoubtedly favour most Spirorbinae, but it should not be supposed, from their abundance and variety at Cape du Couedic, that they are particularly favoured by exposure to wave action. Most of the collections there were taken from areas of local shelter, particularly in *Ecklonia* holdfasts and shore pools. Practically all species from pools, moreover, were scraped from the undersides of stones or rocky overhangs, whilst the *Romanchella* occurred on the more sheltered basal parts of *Pterocladia* plants. Littoral Spirorbinae generally do best where the sand-table is low and there is consequently less abrasion by wave-borne particles (Gee and Knight-Jones, 1962). They reach their greatest variety in cool latitudes, to judge from the number of species in New Zealand (Vine, 1974). Such factors probably contribute to the variety at Cape du Couedic.

The shore levels at which collections were made are indicated roughly in table 1. Most collections of stones and shells came from between tidemarks, where Spirorbinae were generally common, but confined to pools or damp and shady places. *Pileolaria militaris* seemed to be favoured by conditions in pools quite high on the shore at Cape du Couedic. One might expect this pantropical species to benefit from raised temperatures due to insolation of such pools, yet at Plymouth U.K. (latitude 50° N.) it seems to be confined to the sublittoral, presumably because of the harder winter conditions at higher latitudes. In many warm parts of the world the most generally abundant littoral species are *Pileolaria militaris*, *P. pseudomilitaris*, *Janua pagenstecheri* and *J. pseudocorrugata*.

To judge from experience elsewhere, several more Australian Spirorbinae could be discovered by collecting stones and bryozoa from rocky sublittoral areas, particularly off the southern coasts. In our collections *Janua lamellosa*, *J. steueri* and *J. trifurcata* were found only on drifting plants, that had probably come from sublittoral situations. The other four species which were always attached to plants seemed to occur both sublittorally and at low levels between tidemarks. We thus found seven species which were invariably attached to plants, whilst six species seemed to shun them. Only two species, *Protolaeospira triflabellis* and *Janua fenestrata*, were found both on stones and on algae, and those algae were *Ecklonia* holdfasts, which offer a special environment, with more shelter and less mucus than algal fronds provide.

The species of plants providing substrata were kindly identified by Dr H. B. S. Womersley (table 2). Reference back to table 1 will show that choice by the settling larvae of most of these Spirorbinae cannot be highly specific. Only *Janua trifurcata* may perhaps be confined to a single alga, a species of *Hypnea*. This *Janua*, moreover,

Table 2

Marine plants bearing Spirorbinae (see also Table 1):

Angiospermae
Amphibolis antarctica (Labillardiere) Sonder & Aschers

Phaeophyceae
Ecklonia radiata (C. Agardh) J. Agardh
Sargassum linearifolium (Turner) C. Agardh

Rhodophyceae
Pterocladia capillacea (Gmelin) Bornet & Thuret
Erythroclonium angustatum Sonder
Hypnea musciformis (Wulfen) Lamouroux?
Spyridia biannulata J. Agardh
Polysiphonia cancellata Harvey
Jeannerettia pedicellata (Harvey) Papenfuss
Echinothamnion hystrix (Hooker & Harvey) Kylin

was sparse in our collections and may prove to favour other substrata too, when its main populations are found. Of the other species that may perhaps be endemic, *Janua lamellosa* and *Eulaeospira convexis* were originally described from a marine angiosperm at Port Hacking and occurred in our collections mostly on *Amphibolis*, an angiosperm referred until recently to *Cymodocea*. *E. convexis*, however, also occurred on a variety of algae and so did *Romanchella quadricostalis* and *Metalaeospira tenuis*, though the former particularly favoured *Pterocladia* and the latter *Jeanerettia*. Both the remaining species have been found throughout their geographical range mostly attached to plants. *Janua formosa*, indeed, is almost or entirely confined to plants (Knight-Jones, 1972), though *J. steueri* occurs on a variety of substrata in the Red Sea (Vine, 1972).

Of the other species, which were here confined to rocks and shells, *Pileolaria pseudomilitaris* is now known to have a wide distribution, but has never been recorded from plants, nor have any *Protolaeospira* species so far as we are aware, apart from a single record of *P. racemosa* on kelp holdfasts (Rioja, 1962). *Pileolaria militaris* and *Janua pseudocorrugata*, however, occur on plants in the Mediterranean and seem to be confined to algae in a few British localities where we have found them recently (Plymouth and south-west Ireland), whilst *J. pagenstecheri* occurs very commonly on British coastal algae. *Janua* species, indeed, are particularly abundant on algae, probably because they are small and have short life cycles which would fit them to colonise ephemeral substrata.

ZOOGEOGRAPHICAL COMPARISONS

Of the fifteen species found, six (both *Pileolaria* and all the non-endemic *Janua* species) are wide-spread in warm seas. Some of these often attach themselves to *Sargassum* and may thus drift great distances. Only *P. pseudomilitaris* seems invariably to shun algal substrata and this may perhaps be carried about by shipping.

If the general distributions of these six species are examined, it would appear that *Janua formosa* is particularly adapted to high temperatures, for it has not been recorded from the Mediterranean, Hawaii or New Zealand. *J. pagenstecheri*, in contrast, can tolerate a wide temperature range for it extends from Norway and New Zealand to tropical locations such as Brazil, Angola and Ceylon. The absence of *J. formosa* from the Adelaide area agrees with its distribution elsewhere, but it is surprising that *J. pagenstecheri* was not found at Parsley Bay.

Most species of the pantropical group were represented at Parsley Bay, however, and if we include the original description of *J. lamellosa* from Port Hacking it now appears that there are at least six species of Spirorbinae in the area of Sydney. Five of these are opercular incubators, helping to confirm that this method of brood protection is favoured where the water is warm (Bailey, 1969a; Harris, 1969). The remaining species, *Eulaeospira convexis*, may be endemic to Australia, but appears to represent an unusual genus of tube incubators, which is otherwise represented (so far as is certainly known) by a single tropical species (p. 120) originally described from Ceylon and now known from the Red Sea (Vine, 1972). This genus, however, would seem to have affinities with other tube-incubators of the southern hemisphere, to judge from the asymmetrical distribution of its abdominal uncini (fig. 6a; see also Knight-Jones, Knight-Jones and Bregazzi, 1973).

It may seem remarkable that the species links so far discovered, between the Spirorbinae of Australia and New Zealand, do not involve members of these southern genera. A recent study in New Zealand (Vine, 1974) has resulted in nineteen species being recorded from there, but these include only five of those described here and all five are opercular incubators. One is the extraordinary *Amplaria spiculosa*, whilst the others belong to the pantropical group mentioned above. The majority of New Zealand Spirorbinae, however, have southern affinities, only one being a species of *Spirorbis sensu stricto*. There are at least six *Protolaeospira*, one *Paralaeospira*, one *Metalaeospira* (close to *M. tenuis*), and two *Romanchella*, including at least three species links with Cape Horn and two with the Cape of Good Hope.

Since the Australian representatives of these genera are different from those known elsewhere, it seems unlikely that their spread around the southern hemisphere has been helped much by shipping. Some older dispersal agency must have been involved, such as the buoyant kelp plants which drift in the roaring forties, with epiphytes, stones and shells attached to their holdfasts. Considering the pattern of currents and land masses (fig. 1), it might be expected that species distributed in such a system would colonise New Zealand readily without divergent speciation, but would more rarely succeed in colonising Australia. Subantarctic organisms could be stranded on the south coast of New Zealand in water temperatures low enough for their easy establishment. Subsequent spread could take place gradually and could involve strains adapted to higher temperatures. There need be no sudden temperature change to constitute a barrier to further spreading or to gene flow. Tasmania, however, is north of the subtropical convergence and subantarctic organisms drifting there would meet a considerable increase in temperature. Only very occasionally would a temperature-tolerant strain be able to establish itself and such a strain would then tend to diverge into an endemic species, gene flow from the south being nil or negligible.

The biogeographical data available generally conform with this prediction. Considering the algae as a whole, it seems that the degree of endemism in South Australia is probably higher than in any other part of the world (Womersley, 1960). Drift plants of the buoyant fucacean *Durvillea antarctica* are recorded from the west coast of Tasmania, having presumably come from Kerguelen 3,000 miles away (Knox, 1963). Nevertheless this species does not become established in Australia, though it occurs in New Zealand at water temperatures higher than those in Tasmania (Womersley, 1960). *Durvillea potatorum*, however, is endemic to south-east Australia. Considering the Spirorbinae, those most likely to be transported on southern kelp would be *Paralaeospira levinseni* and *Romanchella perrieri*. Both are often found attached to algae and the ranges of both appear to agree with that of *Durvillea antarctica*, except that *Paralaeospira levinseni* also extends to South Africa, where we have seen it abundantly on *Ecklonia*. Careful search off South Africa, however, revealed no species of *Romanchella* or *Metalaeospira*. There again the subtropical convergence has probably been an effective barrier. It would now be interesting to search Tasmanian shores, for representatives of these southern genera other than the species recorded here, which seem likely to be endemic.

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