

Syndesmis rubida sp. nov. and *S. albida* sp. nov.
(Turbellaria : Neorhabdozoa : Umagillidae) from
the sea urchin *Echinus esculentus*

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Résumé : Dans *Echinus esculentus*, on trouve deux espèces de *Syndesmis*. L'une, *S. rubida* sp. nov. est typiquement rougeâtre et entièrement ciliée à l'extérieur, ses testicules s'étendent du bord de l'intestin presque jusqu'aux marges latérales, et son stylet pénial, assez court, pénètre librement dans l'antrum mâle. L'autre espèce, *S. albida* sp. nov., est rose pâle ou presque blanche, et manque de cils sur la surface dorsale, sauf dans la partie antérieure du corps. Ses testicules sont concentrés près des marges latérales, et son stylet pénial est très long. La portion distale du stylet ne pénètre pas dans l'antrum mâle. Elle est logée dans un cylindre délimité par deux couches de muscles. La couche externe est en continuité avec la couche musculaire de l'antrum mâle. La forme légèrement spirale de la portion proximale du vagin, et la longue portion sclérotisée, partiellement tortillée, sont d'autres caractéristiques de cette espèce.

Abstract : *Echinus esculentus* is host to 2 species of *Syndesmis*. One of these, *S. rubida* sp. nov., is typically reddish, completely ciliated externally, has testes that extend from the intestine nearly to the lateral margins of the body, and has a short penis stylet that protrudes into the lumen of the male antrum. The other species, *S. albida* sp. nov., is pale pink or nearly white, lacks ciliation on the dorsal surface except near the anterior end, has testes concentrated close to the lateral margins of the body, and has an exceptionally long penis stylet. The distal portion of the stylet does not protrude into the male antrum. It lies within a cylindrical structure that has two sheaths of muscle. The outer sheath is continuous with the muscular sheath of the male antrum. The slightly spiral form of the proximal portion of the vagina of *S. albida*, and the relatively long, sclerotized distal portion, which has many kinks, are other features that separate this species from *S. rubida*.

INTRODUCTION

The type species of the genus *Syndesmis* is *S. echinorum* François, 1886. Because the original description of this umagillid was neither illustrated nor sufficiently detailed to be useful in comparative studies, we prepared a new description (Kozloff & Westervelt, 1987), based on specimens taken from the sea urchin *Paracentrotus lividus* at the type locality, Banyuls-sur-Mer, on the Mediterranean coast of France. Although François stated that he studied worms from both *P. lividus* and *Echinus acutus*, it is likely that the former, readily available in the littoral zone and shallow subtidal habitats at Banyuls, was the source of most of his material ; the umagillid in *E. acutus*, a deepwater urchin, is, moreover, a different species. Worms from *Sphaerechinus granularis*, another urchin common in shallow water at Banyuls, appear to be morphologically identical to those from *P. lividus*, although they are, on the average, slightly larger. It is probable that the robust specimens found by Russo (1895) in *Sphaerechinus* at Naples also belong to *S. echinorum*, as Russo had assumed.

The genus name *Syndesmis* predates François' description of *S. echinorum*, for Silliman (1881) had applied it, without designating a species, to a turbellarian he obtained from the urchin *Echinus esculentus* (*E. sphaera*) at Roscoff, on the Atlantic coast of France. Shipley (1901), working at Plymouth, referred worms from *Echinus* to François' species, although he misspelled the genus name ("*Syndesmus*"). In 1965, one of us (ENK), after studying umagillids in *E. esculentus* at Plymouth and Roscoff, came to the conclusion that there were 2 species in this host. The judgment of Barel and Kramers (1970), who also examined material at Plymouth and Roscoff, was more conservative. They distinguished 2 "types of *S. echinorum*" in *E. esculentus*: one that is brown and oval, the other white and lanceolate. It was not until we worked on specimens from *P. lividus* at Banyuls that we could be sure that both species in *E. esculentus* are distinct from *S. echinorum*. They are described in this paper.

MATERIALS AND METHODS

Specimens of *E. esculentus* were collected by trawling at depths of approximately 40 or 50 m near Plymouth and Roscoff. Many worms taken from the intestine of this host were studied while they were alive. More than 100 were fixed in Bouin's fluid while being flattened under a coverglass, then stained with borax carmine and prepared as whole mounts. For longitudinal and transverse serial sections, specimens were fixed without being flattened, or with only enough pressure from a coverglass to prevent them from curling. Paraffin sections, cut at 6 or 8 μm , were stained with iron hematoxylin.

DESCRIPTIONS

Syndesmis rubida sp. nov. (Figs. 1-7)

Living specimens, viewed in reflected light, are decidedly reddish, sometimes slightly brownish, and tend to cling tightly to the bottom of the dish as they glide. The largest individuals, while extended and in motion, are about 4 mm long and 1.3 mm wide. The length does not often exceed 3.5 mm, however. The width is greatest slightly anterior to the middle. The anterior end is broadly rounded, whereas the posterior part of the body tapers to a nearly acute tip (Fig. 2).

Both the ventral and dorsal surfaces are ciliated. The mouth, on the ventral surface, is about one-seventh of the body length from the anterior edge. The intestine, which succeeds the doliiform pharynx, extends to the beginning of the last one-sixth of the body.

The testes begin at the level of the posterior edge of the pharynx, extend backward to the vitellaria, and occupy much of the area lateral to the gut in this region (Figs. 1, 2). They are extensively branched, each one having about 15 to 20 ultimate lobes. The slender sperm

duct that arises from the medial part of each testis runs anteriorly for a short distance, then turns posteriorly and joins the ejaculatory duct, whose course begins just behind the pharynx. The ejaculatory duct, with an outer layer of prominent circular muscle and an inner layer of less well developed longitudinal muscle, generally has four loops (Fig. 3), and is appreciably longer than the body. Its length, in proportion to body length, is comparable to that of the ejaculatory duct of *S. echinorum*. Extending from the posterior end of the ejaculatory duct is a sclerotized penis stylet, whose length ranges from about 170 to 190 μm . The tip of the stylet protrudes into the male antrum (Figs. 4, 6), whose longitudinal muscles are external to the circular muscles. As in *S. echinorum*, the cells forming the epithelial lining of the male antrum are folded; the slender, crowded folds may give the impression that the epithelium is ciliated.

Each of the 2 vitellaria has several main trunks (Figs. 1, 2). These branch 2 or 3 times, so that there are about 25 ultimate lobes. The ovaries, just behind the vitellaria, have about 8 to 10 lobes. The main trunk of each ovary extends anteromedially for only a short distance before it joins the vitellarium on the same side to form a short ovovitelline duct. This enters the anteriormost part of the seminal receptacle, occupied by large, secretion-filled cells, among which are channels through which sperm pass (Fig. 5, 7). The arrangement of the cells and channels is much like that in the seminal receptacle of *S. echinorum*. The rest of the seminal receptacle is elongated and has a rather spacious lumen, at least when it is filled with sperm. Posteriorly, the seminal receptacle becomes narrowed to a slender sclerotized duct (Fig. 5) that enters the seminal bursa, its opening being located on the nipplelike bursal valve (Fig. 1), as in *S. echinorum*. Also located on the valve is the opening of the slender sclerotized portion of the vagina, which is dorsal to the male antrum. The posterior part of the vagina is much like the male antrum with respect to the arrangement of its musculature and folding of its epithelial cells.

The uterus, also with longitudinal muscle external to circular muscle, is ventral to the male antrum, and when it contains a fully developed egg capsule it may extend anteriorly into the second quarter of the body (Fig. 1). The filament glands, which occupy much of the posterior quarter of the body, are dense; their ducts enter the uterus on both sides. The ductus communis, through which eggs and yolk reach the uterus, originates on the ventral side of the anteriormost part of the seminal receptacle. It lies above and usually to one side of the uterus, and finally enters the dorsal side of the uterus at about the same transverse level as the ducts from the filament glands. Egg capsules are about 150 μm long by 80 μm wide. The common genital antrum, entered by the male antrum, vagina, and uterus, opens to the exterior at the posterior tip of the body.

This species is the "brown, oval form" distinguished by Barel and Kramers (1970), and evidently the one Shipley (1901) studied. Shipley's illustrations of entire specimens show an arrangement of testes and vitellaria corresponding to that of *S. rubida*.

Type specimens: whole mounts, stained with borax carmine, have been deposited in the United States National Museum, Helminthological Collection. Holotype (n° 80872), from the intestine of *Echinus esculentus* Linnaeus, collected offshore from Roscoff, France,

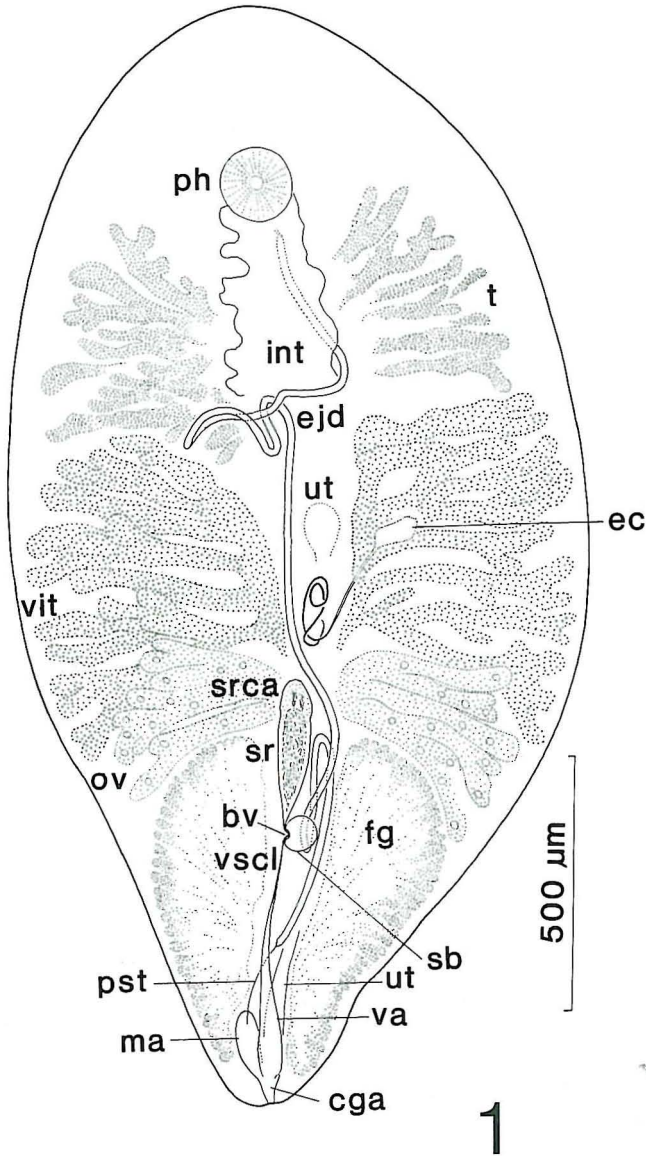
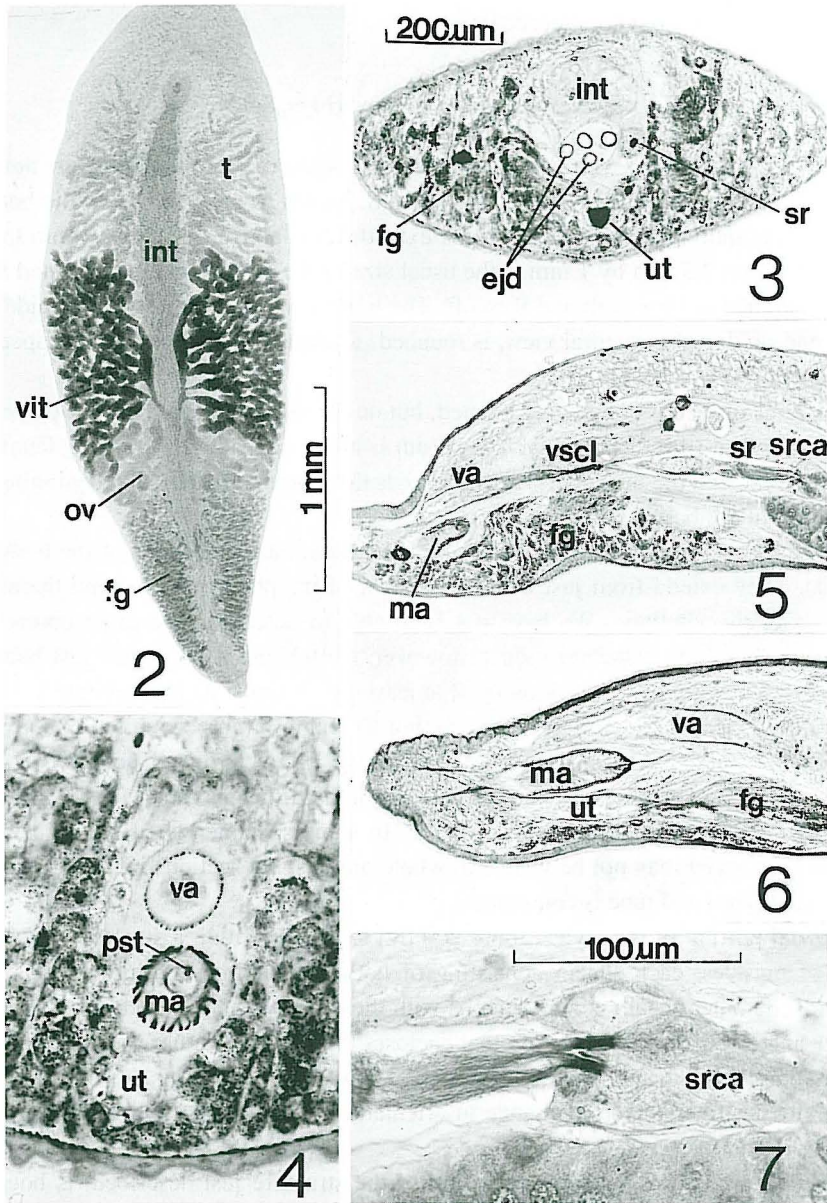


Fig.1 : *Syndesmis rubida* sp. nov. ; holotype, whole mount stained with borax carmine ; camera lucida drawing, dorsal view, somewhat diagrammatic. The specimen was flattened considerably during fixation. This displaced part of the ejaculatory duct toward the left and forced the egg capsule out of the uterus. Abbreviations (for all figures) : bv, bursal valve ; cga, common genital antrum ; dc, ductus communis ; ec, egg capsule ; ejd, ejaculatory duct ; fg, filament glands ; int, intestine ; ma, male antrum ; ov, ovary ; ph, pharynx ; pst, penis stylet ; sb, seminal bursa ; sr, seminal receptacle ; srca, large cells in the anteriormost part of seminal receptacle ; va, vagina ; ut, uterus ; vit, vitellaria ; vscl, sclerotized portion of vagina.



Figs. 2-7: *Syndesmis rubida* sp. nov.; photomicrographs. Figs. 5 and 6 are to the scale shown on Fig. 3; Fig. 4 is to the scale shown on Fig. 7. 2. Paratype, stained with borax carmine, ventral view. This specimen does not have an egg capsule. 3. Transverse section (6 μ m, stained with iron hematoxylin), just posterior to the ovaries. 4. Transverse section through the anterior portion of the male antrum. The vagina and uterus are also shown. 5. Longitudinal section, nearly median, of the posterior portion. 6. Longitudinal section, nearly median, of the posterior portion. 7. Longitudinal section through the anterior part of the seminal receptacle.

depth about 40 m. Paratype (n° 80873), from *E. esculentus*, collected offshore from Plymouth, England (depth not recorded).

Syndesmis albida sp. nov. (Figs. 8-16)

In reflected light, living worms range from nearly white to pale pink ; they are never reddish. Moreover, this species is less inclined than *S. rubida* to cling tightly to the bottom of the dish. Some individuals, measured while extended and active, are about 4 mm long and 1.1 mm wide, but 3.5 mm by 1 mm is the usual size of the largest specimens found in most urchins examined at Plymouth and Roscoff. The body is widest anterior to the middle ; the anterior end, in dorsal or ventral view, is rounded, whereas the posterior end is tapered to a nearly acute tip (Figs. 10, 11).

The ventral surface is completely ciliated, but on the dorsal surface cilia are present only in the anterior one-fifth of the body. The mouth is about one-sixth of the body length from the anterior end, and the intestine, which succeeds the pharynx, reaches the beginning of the last one-fifth of the body.

The testes are distinctive in that they are restricted to lateral portions of the body (Figs. 8, 10, 11). They extend from just behind the level of the pharynx to beyond the anterior-most lobes of the vitellaria. We have not been able to determine the exact course of the sperm ducts. The long ejaculatory duct, however, is obvious. It originates just behind the pharynx and generally bends back on itself at least 4 or 5 times. Its musculature is arranged like that of the ejaculatory duct of *S. rubida*, but its length in proportion to the body length is greater than that in *S. rubida* and *S. echinorum*. The sclerotized penis stylet, which reaches the lumen of the male antrum, is unusual in that it begins rather far anteriorly, near the end of the first third of the body (Fig. 8). In some specimens it is fully 1 mm long. Portions of the stylet may not be visible in whole mounts, but sections invariably show that this delicate sclerotized tube is continuous.

The distal portion of the stylet, about 200 μ m long, lies within a structure that has two sheaths of muscles, each sheath consisting of both longitudinal and circular fibers. The muscles of the outer sheath are continuous with those of the male antrum (Fig. 9). On reaching the anterior end of the structure that encloses the stylet, the outer sheath turns inward, then continues posteriorly as the inner sheath. The longitudinal fibers are more prominent than the circular fibers, and the change in orientation of the former is particularly obvious in sections (Fig. 12).

The stylet, on reaching the posterior end of the structure just described, is bound to a dark-staining and probably sclerotized cup. It does not project into the male antrum, and in this respect it is quite different from the stylet of *S. rubida*, *S. echinorum*, *Syndisyrix franciscanus*, and some other species of the *Syndesmis-Syndisyrix* complex. In the case of *S. albida*, the term penis stylet may even seem to be inappropriate.

The muscle fibers forming the two sheaths that surround the distal part of the stylet are within epithelial cells (or perhaps within a syncytial epithelium). There is only a little space

between these epithelia, and perhaps this is an artifact caused by shrinkage. In the narrow space within which the stylet lies, there are only indistinct fibers ; we have not found any cells.

Each vitellarium has 6 to 8 primary lobes and about 25 ultimate branches (Figs. 8, 10, 11). A few of the more anterior branches do not extend as far laterally as the others ; it is as if their enlargement has been impeded by the posterior portions of the testes. Each ovary has 3 or 4 lobes, and its main stem extends forward for a distance of 150 or 200 μm , then joins the vitellarium on the same side to form a short ovovitelline duct that enters the anteriormost part of the seminal receptacle. This portion of the seminal receptacle is directed slightly downward, but it is similar to that of *S. echinorum* and *S. rubida* in that it contains large secretion-filled cells, between which are channels through which sperm may reach the oocytes (Figs. 13, 14). The posterior portion of the seminal receptacle becomes gradually narrower, finally forming a slender sclerotized duct that opens into the seminal bursa through the nipplelike bursal valve (Figs. 9, 15). The sclerotized anteriormost part of the vagina, whose length (exclusive of numerous closely spaced kinks) is about 190 μm , also enters the bursa through the valve. The rest of the vagina, slightly to the right of the midline and mostly dorsal to the male antrum, has a weakly spiral configuration.

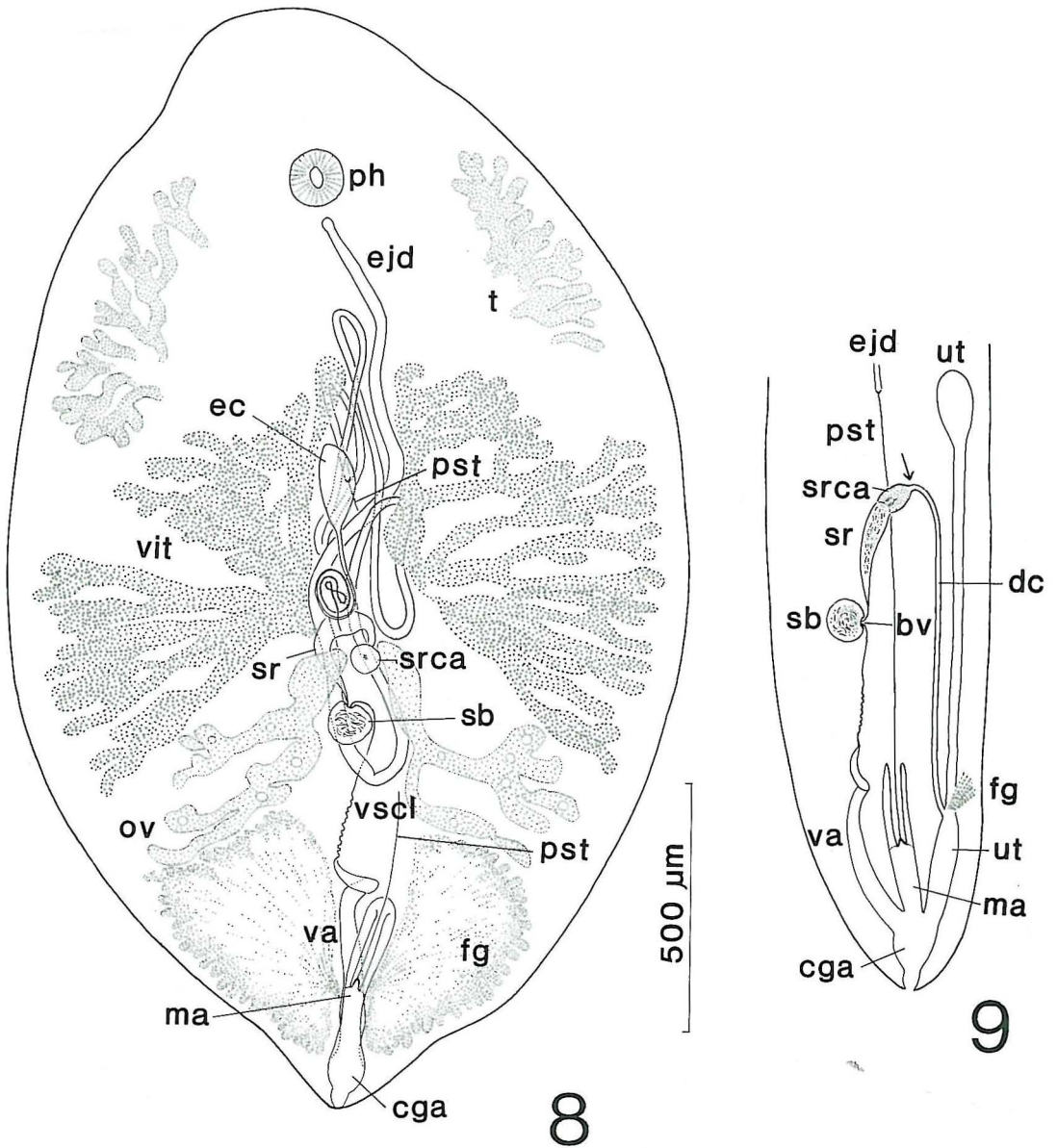
The uterus, ventral to the male antrum, may extend anteriorly nearly to the end of the first third of the body. As in *S. rubida* and *S. echinorum*, the common genital antrum, into which the male antrum, vagina, and uterus open, reaches the exterior at the posterior tip of the body. Egg capsules are usually 180 to 190 μm wide. The filament glands occupy much of the posterior quarter of the body (Figs. 8, 10, 11). The ductus communis, which begins its course on the ventral side of the anteriormost part of the seminal receptacle, joins the dorsal side of the uterus at about the same transverse level as the ducts of the filament glands (Fig. 16).

This species is the "white, lanceolate form" distinguished by Barel and Kramers.

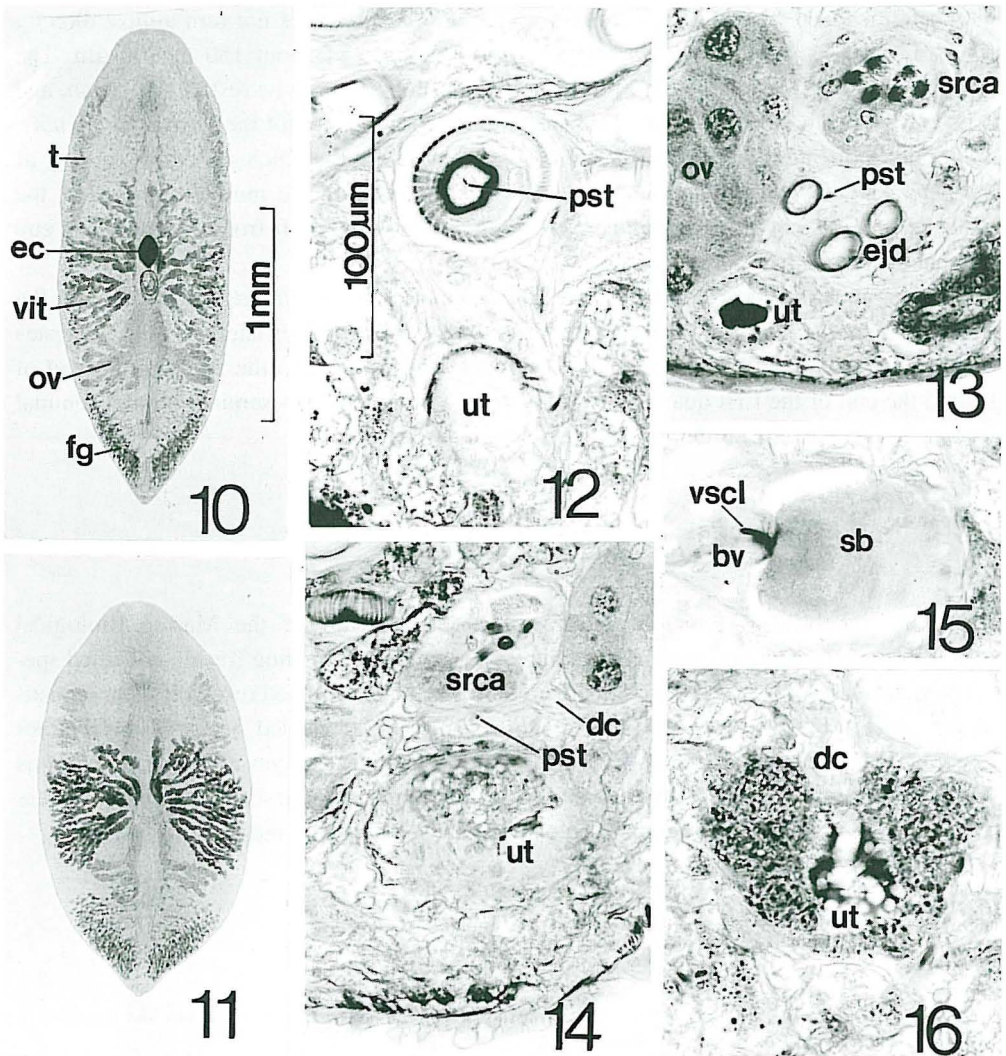
Type specimens : whole mounts, stained with carmine, have been deposited in the United States National Museum, Helminthological Collection. Holotype (n^o 80874), from the intestine of *Echinus esculentus* Linnaeus, collected offshore from Roscoff, France, depth about 40 m. Paratype (n^o 80875), from the intestine of *E. esculentus*, collected offshore from Plymouth, England (depth not recorded).

COMPARISON OF *SYNDESMIS RUBIDA*, *S. ALBIDA*, AND *S. ECHINORUM*

The two species of *Syndesmis* in *Echinus esculentus* may easily be distinguished on the basis of several features. In life, *S. rubida* is decidedly reddish, whereas *S. albida* is pale pink or nearly white. The former, moreover, is completely ciliated externally, while the latter lacks ciliation on most of the dorsal surface. The testes of *S. rubida* extend from the intestine nearly to the lateral margins of the body ; those of *S. albida* are concentrated close to the lateral margins. The sclerotized penis stylet of *S. rubida* is relatively short ; that of *S. albida* is exceptionally long. The anteriormost lobes of the vitellaria of *S. rubida* extend just



Figs. 8-9 : *Syndesmis albida* sp. nov. 8. Holotype ; whole mount stained with borax carmine ; camera lucida drawing, ventral view, somewhat diagrammatic. The specimen was flattened during fixation. This caused the seminal vesicle to be stretched and pushed forward, and part of it to lie transversely. To avoid confusion, the uterus, which is on the observer's side of the male antrum and vagina, is not shown (see Fig. 9). About half of the penis stylet is also omitted. 9. Diagram, based on sagittal sections, showing the arrangement of ducts of the reproductive system in the posterior half of the body. The arrow indicates the level at which the ovovitelline ducts enter the seminal receptacle.



Figs. 10-16 : *Syndesmis albida* sp. nov. ; photomicrographs. Fig. 11 is to the scale shown on Fig. 10 ; Figs. 13-16 are to the scale shown on Fig. 12. 10. Paratype, stained with borax carmine, ventral view. 11. Another specimen, flattened more than the one shown in 10. It has no egg capsule. 12. Transverse section (6 µm, stained with iron hematoxylin) through the anterior part of the tubular structure in which the distal portion of the penis stylet lies. The muscle layer of the outer sheath turns inward to become the muscle layer of the inner sheath ; the longitudinal fibers are more conspicuous than the circular fibers. 13. Transverse section through the anterior part of the seminal receptacle. Some loops of the ejaculatory duct, the penis stylet, and uterus are shown. 14. Transverse section slightly posterior to the one in 13. The penis stylet has diverged away from the ejaculatory duct ; the uterus is also shown. 15. Transverse section through the bursal valve. The anteriormost portion of the sclerotized duct of the vagina is in sharp focus ; the posteriormost portion of the sclerotized duct of the seminal receptacle is beneath it and out of focus. 16. Transverse section through the uterus at the level where the ductus communis and ducts of the filament glands enter.

as far laterally as the more posterior lobes, but in *S. albida* they are obviously shorter than the posterior lobes. The main trunk of the ovary of *S. rubida* does not turn almost directly forward, whereas that of *S. albida* does so for a distance of about 150 or 200 μm . The sclerotized part of the vagina of *S. albida* is long in proportion to the rest of this organ, and it is conspicuously kinked; these attributes are not characteristic of the vagina of *S. rubida*. Another distinctive feature of *S. albida* is the structure that encloses the distal part of the penis stylet. Although its outer sheath is continuous with the muscular sheath of the male antrum, it is not properly part of the antrum, for it is closed off from the latter by a cup of what appears to be sclerotized material.

In general, *S. rubida* resembles *S. echinorum* more than *S. albida* does. Although the testes of *S. rubida* begin farther anteriorly and extend much farther laterally than the testes of *S. echinorum*, and although its ejaculatory duct begins close to the pharynx, instead of behind the end of the first quarter, the penis stylet and the vagina - seminal bursa - seminal receptacle complex are similar in the two species.

ACKNOWLEDGMENTS

We are indebted to directors and members of the staff of the Marine Biological Laboratory, Plymouth, and Station Biologique, Roscoff, for providing freshly collected specimens of *Echinus esculentus* and for other courtesies that facilitated research at these institutions. Most of the morphological work for our study was carried out at Friday Harbor Laboratories of the University of Washington during sabbatical leaves awarded to one of us (CAW) by Chapman College. We acknowledge this support with gratitude. We also express our appreciation to Susan Dryer, who prepared serial sections of some of our material.

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