

NOTES ON THE BRITISH SPECIES OF *TRIDIDEMNUM* (DIDEMNIDAE, ASCIDIACEA), WITH A REPORT OF THE OCCURRENCE OF *T. NIVEUM* (GIARD) IN THE PLYMOUTH AREA

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(Text-fig. 1)

Berrill (1950) records two species of *Trididemnum* Della Valle (1881) as occurring in British waters—*T. tenerum* (Verrill, 1871) and *T. alleni* Berrill (1947). A third species, *T. niveum* (Giard, 1872), was reported from Millport by Rankin (1900), but it is impossible to determine whether his species was *T. niveum* or some other species of *Trididemnum* or *Didemnum*. Rankin's identifications are suspect, for he describes as common at Millport species of Polyclinidae and Didemnidae which have not been seen in British waters (or indeed, anywhere) before or since. *Trididemnum niveum* has not been reported since from Millport. The synonymy and distinctness of these three species are confused. Hartmeyer (1924) stated that *T. niveum* is a synonym of *T. tenerum*. This was denied by Harant & Vernières (1933), but without any reasons of weight. Berrill (1947, 1950) claims that *T. alleni* is certainly distinct from *T. tenerum*, but he allows the possibility that it may be synonymous with *T. niveum*, which apparently he had never seen.

In the Plymouth area I have frequently collected *T. tenerum* and *T. alleni*, and I have in my possession colonies of *T. tenerum* from Naples and from Scotland. Recently I collected a colony of a *Trididemnum* species from the Salstone (Salcombe, Devon); it was growing on the test of a specimen of *Polycarpa rustica* (Linnaeus), a few centimetres below the low-water mark of spring tides. I ascribed this colony to *Trididemnum niveum*, and through the kindness of Dr C. Levi I was able to obtain specimens of this species from the type locality at Roscoff, including a portion of a colony from the type collection of that laboratory, determined by Pizon. I was thus able to check that my identification was correct. From the examination of numerous colonies of these three species of *Trididemnum* I have no hesitation in stating that they are all three distinct species.

T. tenerum is found in waters from low tide down to about 200 m. It is commonly found encrusting rocks and stones and on the holdfasts of algae. It is particularly abundant where the substratum is hard mud. *T. alleni* is recorded from a little below low tide down to about 30 m., encrusting gor-

gonians, hydroids and algal holdfasts. It seems to require situations swept by strong currents or tides. *T. niveum* extends from a little below low-tide mark to about 30 m., and is especially abundant on the sargassids which inhabit the *Laminaria* zone. My specimens from Roscoff were all found growing on *Cystoseira*. Giard (1872) states that he never found it on stones or rocks. Like many other ascidians, and especially didemnids, it seems to require an organic surface for settling.

Trididemnum tenerum forms large colonies of several centimetres in extent and 3 or 4 mm. thick. The colour varies through greenish, ochre, brown or grey, and the colonies are very rarely white. The zooids are usually visible through the test; they are arranged in systems which may be obscured by the very abundance of the zooids. *T. alleni* forms much smaller colonies of the same thickness but rarely over 1 cm. in extent. The colonies are usually brilliant white because of the abundance of the spicules, and for the same reason the zooids are not visible. *T. niveum*, growing on *Cystoseira*, is limited in its extent in one direction, but in the other the colonies may extend to 60 or 70 mm.; the thickness is about 5 mm. The test is usually colourless, but the blue pigment of the abdomina combining with the white of the spicules produces the bluish white effect which led Giard to give it the specific name 'niveum' or 'snowy'. In some colonies, however, the surface of the test is streaked with brown, and one group of colonies from Roscoff was in life a dark yellow-ochre. The zooids in all my colonies are visible through the test.

The spicules of *Trididemnum tenerum* are rather irregular in form. Commonly, elongate or needle-like crystals, or plates, are scattered in the test, but these may be aggregated into irregular, or rarely regular, spherical groupings of 20-40 μ diameter; the points of these spherical spicules are usually needle-like and numerous. The spicules in most colonies are few in number and hardly obscure the transparency of the test. In *T. alleni* the spicules are very closely packed, rendering the test completely opaque. They are spherical, of 8-25 μ in diameter and geometrical in form; looking into the sphere, in successive circles of points there are generally 1, 6 and 9 points, but rarely the formula may be 1, 4, 8 or, in the smallest, 4, 8. The rays are usually obtusely pointed but may be rounded or rod-like, even in the same colony. In *T. niveum* the spicules are intermediate in abundance between those of the other two species. They are spherical and geometrical in form with formulae of 1, 6, 12; 1, 4, 8; or 1, 4. I have not found any with the formula 4, 8. They are 20-40 μ in diameter with a few slightly smaller. The points are acute. In all three species they are most abundant in, or confined to, the upper layers of the test.

The thorax of the zooids of *T. tenerum* is at least as large as, or generally larger than, the abdomen and generally separated from it by a very narrow constriction, which is, however, short. The thorax of *T. alleni* is always

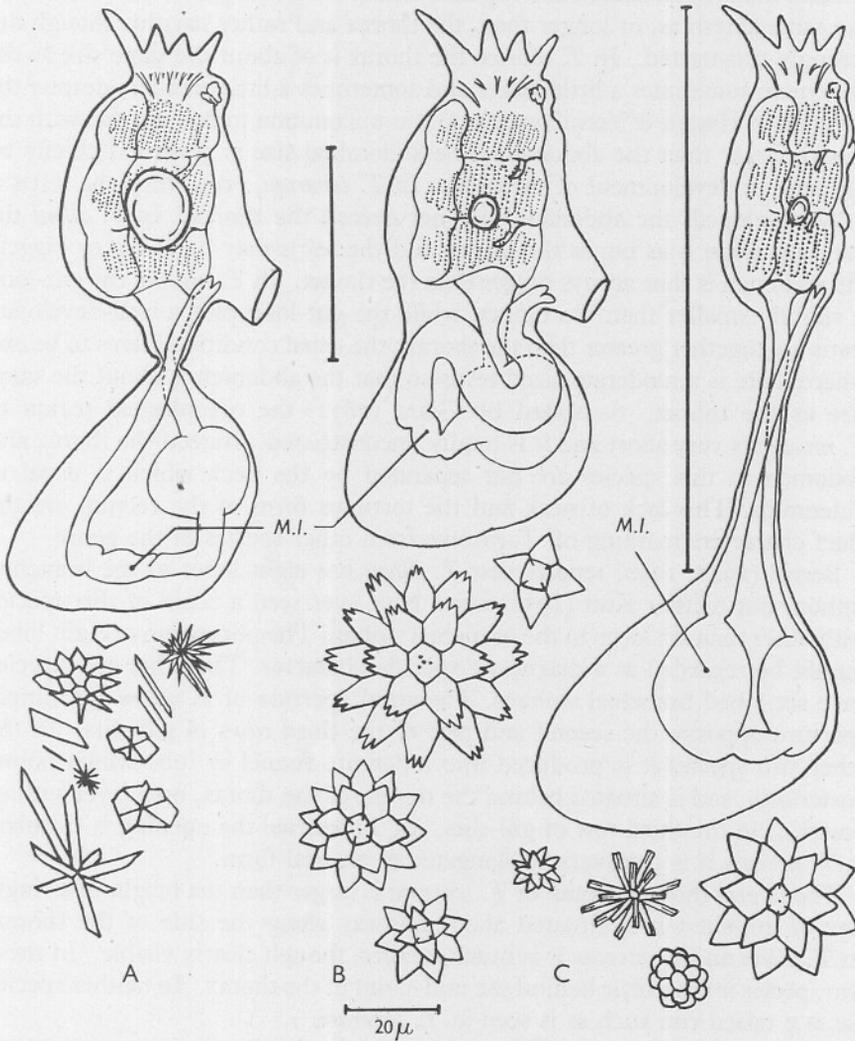


Fig. 1. Drawings from the left side of zooids of A, *T. tenerum*, B, *T. niveum*, and C, *T. alleni*, together with a group of spicules from each of the three species. Each group of spicules is from a single colony. The bottom scale line refers to the degree of magnification of the spicules. The zooids of *T. tenerum* and *T. niveum* are drawn to the same scale, but that of *T. alleni* is enlarged more, so that it may be drawn with the same thorax size; in each case the scale line represents 0.5 mm. The entire genital system and the pyloric gland are omitted, so that the course of the gut—important for identification—may be followed. The buccal lobes and tentacles of the opposite side are omitted, so that one more than half the total number of each are drawn. *M.I.* mid-intestine.

smaller than the abdomen and separated from it by a long neck which is about the same length as, or longer than, the thorax and rather narrow, though not strongly constricted. In *T. niveum* the thorax is of about the same size as the abdomen, sometimes a little larger and sometimes a little smaller; despite the drawing of Harant & Vernières (1933) it is uncommon to find a zooid with the thorax larger than the abdomen. The abdominal size is governed chiefly by the state of development of the testis. In *T. tenerum*, even when the testis is fully developed, the abdomen does not exceed the thorax. In *T. alleni* the gut-loop alone is as big as the thorax and the testis may be as big or bigger; the abdomen is thus always bigger than the thorax. In *T. niveum* the gut-loop is slightly smaller than the thorax, while the gut-loop plus a well-developed testis are together greater than the thorax; the usual condition seems to be one where there is a moderate-sized testis so that the abdomen is about the same size as the thorax. As stated by Giard (1872) the oesophageal region of *T. niveum* is very short and it is totally uncontracted. Indeed the thorax and abdomen in this species are not separated by the neck which is usual in didemnids. This lack of neck and the tortuous form of the rectum are the chief characters marking off *T. niveum* from other species of the genus.

Berrill (1947, 1950) reports that *T. alleni* has eight lobes to the branchial siphon, but neither Kott (1952) nor I have ever seen a zooid of this species with other than six lobes to the branchial siphon. The possession of eight lobes cannot be regarded as a diagnostic specific character. The other two species have six-lobed branchial siphons. The atrial aperture of *T. alleni* is a simple aperture opposite the second and part of the third rows of gill-slits. In the other two species it is produced into a definite funnel or tube which points posteriorly, and is situated behind the middle of the thorax, on a level with or posterior to the third row of gill-slits. In *T. tenerum* the opening is circular; in *T. niveum* it is transversely elongated to an oval form.

The lateral thoracic organ of *T. tenerum* is larger than the height of a single row of gill-slits; it is situated about midway along the side of the thorax. In *T. alleni* and *T. niveum* it is much smaller, though clearly visible. In these two species it lies a little behind the mid-point of the thorax. In neither species has it a raised rim such as is seen in *T. tenerum*.

A thoracic muscular retractor process may be developed in some zooids or colonies of all three species. All three commonly possess eight buccal tentacles, but large zooids of *T. tenerum* may have eight extra smaller tentacles making sixteen in all. *T. tenerum* and *T. niveum* possess nine to twelve stigmata in each half-row, with ten or eleven as the commonest number. *T. alleni* usually has seven or eight in each half-row.

The oesophagus of *T. tenerum* is more than half the length of the thorax, but less than its full length. That of *T. alleni* is longer than the thorax; that of *T. niveum* is less than half the length of the thorax. In all three it is straight and opens into a smooth globular stomach. The post-stomach of *T. tenerum*

runs posteriorly and then turns ventrally. It is separated from the horizontal mid-intestine by an oblique constriction. The mid-intestine in its turn is separated from the ascending rectum by another constriction. The rectum is slightly curved. In *T. alleni* the post-stomach is horizontal and opens after a slight constriction into the ascending, globular mid-intestine which is as large as or larger than the stomach. This passes without much break into the rectum which runs practically straight up to the atrium. In *T. niveum* the post-stomach is horizontal and is separated by an abrupt constriction from the very small mid-intestine which runs almost without constriction into the rectum. This is curved into a tight S, quite unlike the condition usual in didemnids.

Berrill (1947, 1950, p. 118) states that: 'Four or five obvious epidermal ampullae with fairly long stalks and large terminals arise from the abdominal region' in *T. tenerum*, whereas in *T. alleni* they are hardly discernible. In *T. niveum*, Lahille (1890) saw five epidermal ampullae with voluminous terminals. Giard (1872, pl. 22, fig. 1) illustrates *T. niveum* without epidermal ampullae in contradistinction to '*Didemnum cereum*' (= *T. tenerum*) which he illustrates on the same plate (his fig. 3) with large ampullae. Berrill lays great stress on this character, but I believe Van Name (1945, p. 99) is nearer the truth when he writes of *T. tenerum* that, 'at certain stages of growth clavate vascular processes extending into the test from the middle region of the body are found'. These are evidently the epidermal ampullae of Berrill. My own observations indicate a great variability in all three species in the degree of development of these ampullae. While they are never very large in *T. alleni*, they are sometimes clearly visible, and the other two species show all stages between highly developed ampullae and ampullae so small that they are only visible in sectioned material.

The number of turns the vas deferens makes around the testis has some value as a specific character in the Didemninae, although the number is never so rigidly fixed as some authors seem to imply. In *T. tenerum* the number is usually given as twelve, and this is the commonest, but zooids may be found, even in the one colony, with eleven or thirteen turns of the spire. In *T. alleni* there is similar variation between seven and nine with eight turns of spire being most common. In *T. niveum* there are equal numbers of zooids with seven and with eight turns while a very few have six or nine turns.

The larvae of the three species differ. The trunk of the larvae of *T. tenerum* and *T. niveum* is about 0.45–0.5 mm. long; that of *T. alleni* is slightly smaller, being about 0.35 mm. long. The tail of the larva of *T. niveum* is longer than that of *T. tenerum*, for it curves round the trunk even past the sensory vesicle, while that of *T. tenerum* rarely passes the branchial siphon. The tail of *T. alleni* is of the same relative length as that of *T. tenerum*. The larva of *T. alleni* has only two suckers, whereas those of the other two species possess three suckers each.

The three species may be diagnosed as follows:

T. tenerum. Colonies up to 60 mm. across, usually with few spicules. Zooids always visible through test. Spicules chiefly irregular, 20–40 μ diameter. Abdomen never larger than thorax, and separated from it by a short but pronounced constriction. Atrial siphon prolonged to a tube, behind middle of thorax. Lateral thoracic organ near middle of thorax and larger than height of one row of stigmata. About ten or eleven stigmata per half-row. Oesophagus shorter than thorax. Post-stomach behind stomach; mid-intestine horizontal; rectum little curved. Vas deferens with about twelve turns around testis.

T. alleni. Colonies up to 10 mm. across, with abundant spicules. Zooids never visible through test. Spicules geometrical, spherical, about 8–25 μ diameter, with points arranged with formulae: 1, 6, 9; 1, 4, 8; or 4, 8. Abdomen always larger than thorax and separated from it by a narrow neck longer than the thorax. Atrial aperture a simple opening opposite the middle row of gill-slits. Lateral thoracic organ behind middle of thorax and smaller than the height of a single row of stigmata. About seven or eight stigmata per half-row. Oesophagus longer than thorax. Post-stomach ventral to stomach; mid-intestine large and globular, vertical; rectum little curved. Vas deferens with about eight turns around testis. Larva with only two suckers.

T. niveum. Colonies up to 60 mm. long, with sparse spicules. Zooids usually visible through test. Spicules geometrical, spherical, about 20–40 μ diameter, with formulae: 1, 6, 12; 1, 4, 8; or 1, 4. Abdomen larger or smaller than the thorax, and not separated from it by even the slightest constriction or neck. Atrial siphon prolonged into a tube behind middle of thorax. Lateral thoracic organ behind middle of thorax and smaller than the height of a single row of stigmata. About ten stigmata per half-row. Oesophagus shorter than half the length of the thorax. Post-stomach ventral to stomach; rectum curved into a sharp S, with final curve overlying stomach. Vas deferens with about seven or eight turns around testis.

SUMMARY

The presence of *Trididemnum niveum* (Giard) is reported from the Plymouth area. It is compared with the other two British species of *Trididemnum*, *T. tenerum* and *T. alleni*, with which it has in the past been somewhat confused, and all three are shown to be distinct species. A short diagnosis of the three species is given as an aid to identification.

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