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Tenarea tessellatum (Lemoine) Littler, comb. nov., an unusual crustose coralline (Rhodophyceae, Cryptonemiales) from Hawaii

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New information concerning the development of *Tenarea tessellatum,* an unusual member of the crustose Corallinaceae, is presented. The morphological features that distinguish it from other species of *Tenarea* are: spiral manner of growth and the regular manner in which younger parts of the thalli grow over older parts; secondary pit connections that occur either singly or paired in localized regions connecting palisade cells in three directions; and the development of conceptacles several thallus layers beneath the surface, and the subsequent sloughing of the upper layers. Cell divisions occur only in planes parallel to the palisade cell long axes except during the formation of cover cells and conceptacles.

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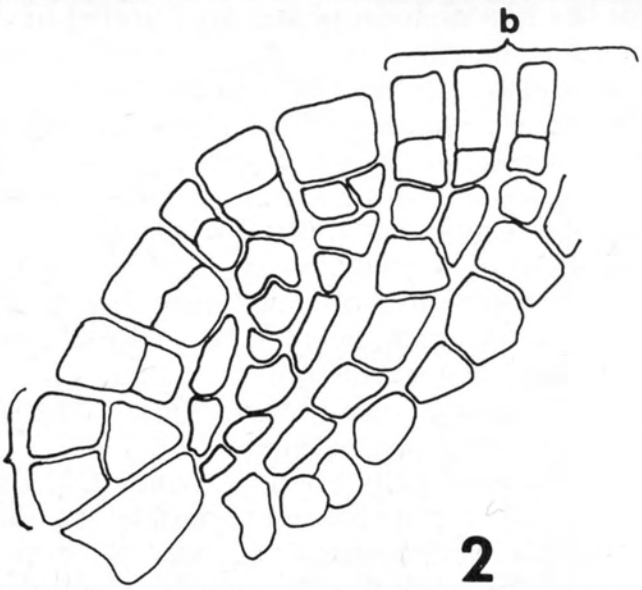
The alga treated here was first described by Lemoine (1929) as *Lithophyllum tessellatum* from two samples taken in the Galapagos Islands. Since then, collections of this alga have not been reported. Subsequently, Setchell and Mason (1943) placed this alga in the genus *Goniolithon.* The author collected large quantities of *Tenarea tessellatum* from 1968 to 1970 during SCUBA studies of reef-forming organisms. Represented by herbarium numbers ML 424, 508, 554, 581, 616, 622, 1021, 1034 and 1082, *T. tessellatum* was found only below 10 m, becoming increasingly abundant to the maximum depth (30 m) where collections were made. It occurs only on consolidated calcium carbonate substrata and, because of its distinctive external morphology, it is easily recognizable in the field.

A tetrasporangial specimen, ML 1082, has been placed in the herbarium of the U.S. National Museum, Washington, D.C. Other specimens have been deposited in the M. S. Doty Herbarium, Department of Botany, Honolulu, Hawaii; the G. M. Smith Herbarium, Hopkins Marine Station, Pacific Grove, California; and the Herbarium of the University of California, Berkeley, California.

Only saxicolous specimens of *T. tessellatum* have been found. These thalli are characterized by spiraled knob-like excrescences, the surfaces of which appear slightly glazed. The living specimens range in colour from Rhodonite Pink to Rocellin Purple (Ridgeway, 1913).

The most striking external feature of *T. tessellatum* is the spirally sculptured growth pattern. This surface pattern (Fig. 1) results from the clockwise and counterclockwise spiral development of the thallus from a single apical cell. The spiral (Fig. 2) is derived from the apical palisade cell and all other palisade cells dividing in planes parallel to their long axes. Following the lengthwise apical cell division, the first daughter cell divides twice. Whereas these last two division planes are parallel to the long cell axes, they are in planes at right angles to each other (*"a"* in Fig. 2). The two apicals of the three resultant cells then divide, forming more dichotomies, and elongate toward the thallus margin. The dichotomous branching and unequal elongation of the cell walls of the horizontal palisade-cell filaments (*"b"* in Fig. 2) act in a wedge-like manner resulting in the spiral form. There appears to be an equal probability that the spiral will turn clockwise or counterclockwise since the two kinds of spirals occur in about equal numbers.

The marginal cells of the expanding thallus (*"a"* in Fig. 3) divide only parallel to their long axes. The daughter palisade cell cut off from each marginal cell divides periclinally (*"b"* in Fig. 3) producing a small cover cell that is triangular in side view (Fig. 3, 4) but



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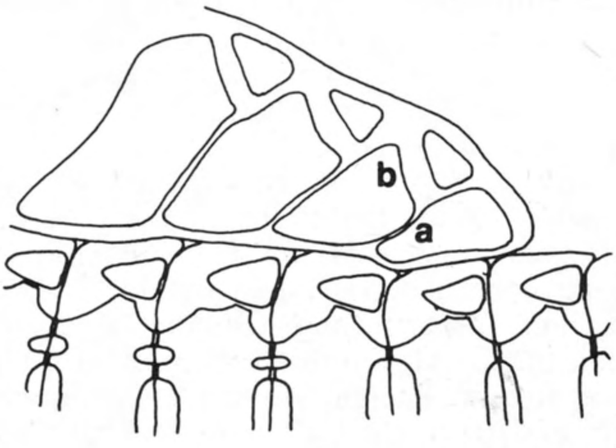

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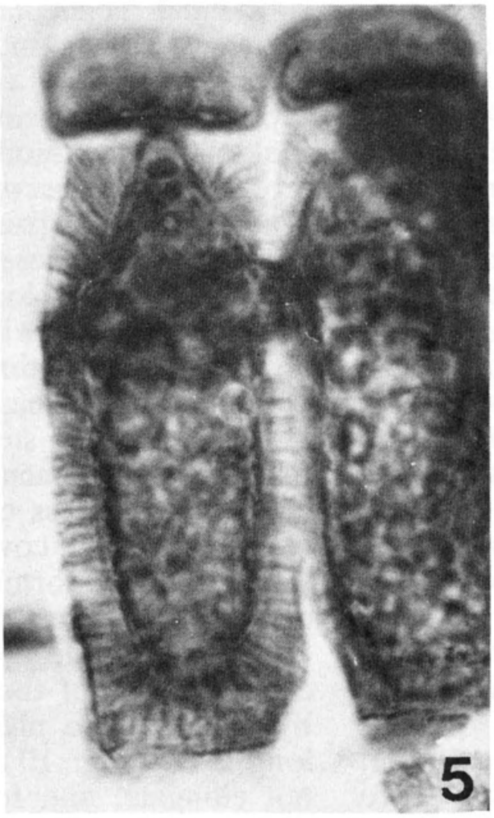
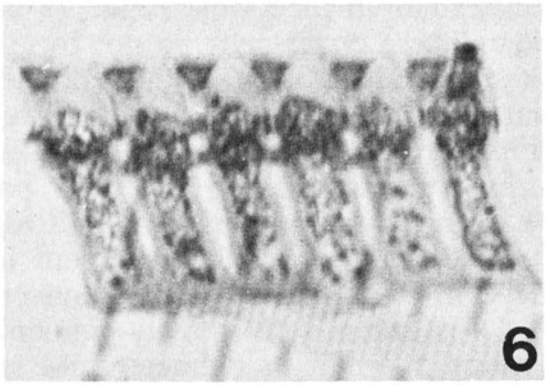
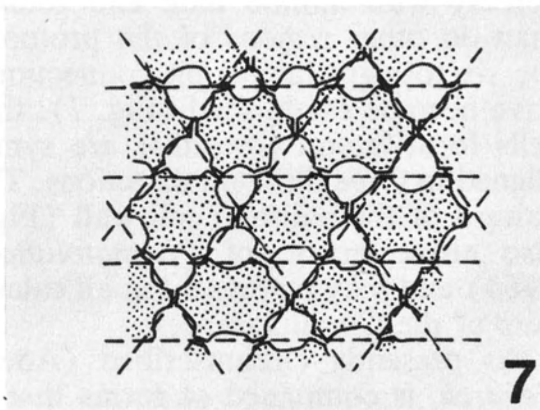
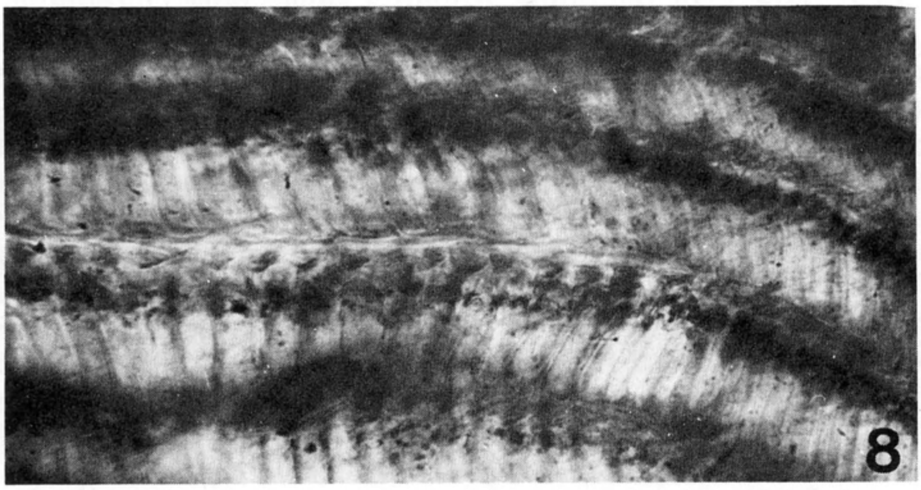
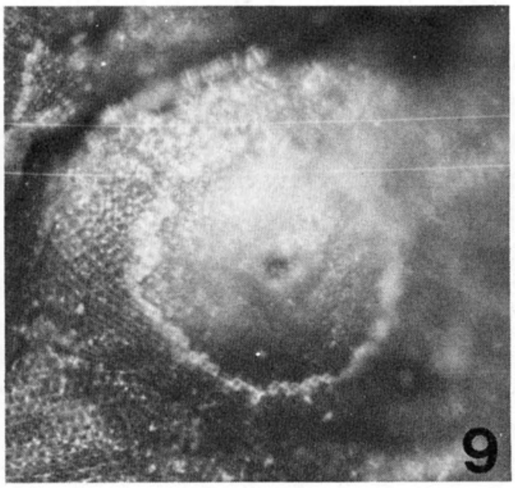
FIG. 1–3. *Tenarea tessellatum*. Fig. 1. Surface view of the knobbed excrescences showing the unique spirally-sculptured growth pattern; × 7. Fig. 2. Surface view of the cells comprising one counter-clockwise spiral, showing the large apical cell at the lower left, the apical cell derivatives (*a*) and derived dichotomous branches (*b*), which extend the thallus margin differentially in a spiral; × 430. Fig. 3. Vertical section (at right angles to the plane of Figure 2) showing the first plane of division (*a*) of a marginal cell followed by division of the daughter palisade cell (*b*) at right angles; half of an underlying thallus layer is included; × 640.











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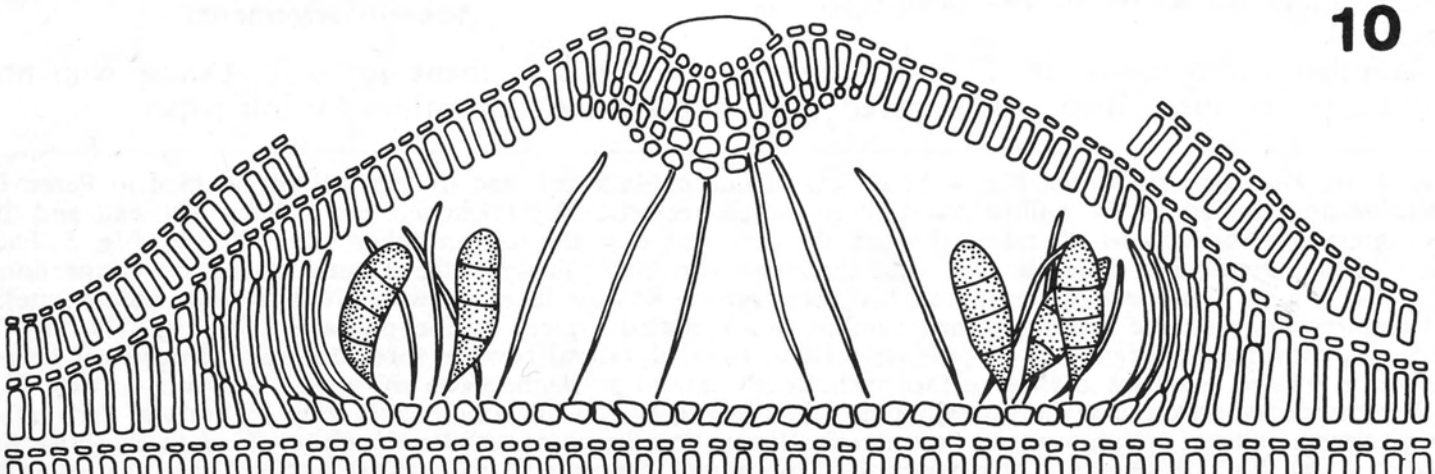

rectangular in face view (Fig. 5) and surface view. These cover cells do not form secondary pit connections nor do they divide. As they mature, the palisade cells elongate vertically (Fig. 3) to about 40–60 μm in height and form large, single (Fig. 4, 5) or paired (Fig. 6) secondary pit connections in a region about three-fourths of the distance from the base of the cell. This region of pit connections (Fig. 5, 6) is laden with heavily-pigmented, round plastids 3–5 μm in diameter and stains more densely with aniline blue and toluidene blue than do other regions of the protoplast. Once the six to eight lateral pit connections per cell have become established (Fig. 7), the palisade cells form lateral rows that are symmetrically aligned in three different directions. The striated pattern of the palisade cell wall (Fig. 5, 6) is also characteristic of *Phymatolithon* (Adey, 1964) and may be present in all calcified members of the Corallinaceae.

As presently circumscribed (Adey, 1970), *Tenarea,* is comprised of forms that show two types of vegetative development: (*1*) those that are bi-stromatic consisting of a single layer of palisade cells, each of which has a single cover cell (*e.g., T. prototypum* [Fosl.] Adey); and (*2*) those that form a perithallium of vertical filaments by means of cell divisions that occur at right angles to the long axes of the palisade cells (*e.g., T. bermudense* [Foslie & Howe] Adey). *T. tessellatum* is a representative of the first type and most closely approximates *T. prototypum* (Lemoine, 1917; Foslie, 1897), differing in the features described above. Also, *T. tessellatum* forms its knob-like excrescences by the spiral piling-up of thalli (Fig. 1, 8); other crustose corallines that form excrescences do so by means of upright filaments.

Another characteristic of *T. tessellatum* is the nature of the convex, single-pored tetrasporangial conceptacles (Fig. 9, 10), each about 400–475 μm in diameter. These structures arise from a single older thallus 1–5 layers below the surface. They are usually in the lower and more shaded portions of excrescences. Conceptacle development is initiated by a localized elongation of a lens of palisade cells. These cells divide twice perpendicular to their long axes, producing three daughter cells of which the middle cell elongates to about six times the length of a normal vegetative cell. These elongated cells then degenerate forming sterile paraphyses within the resulting conceptacular cavity (Fig. 10). This elongation process causes the uppermost layer of palisade and cover cells to be driven upwards thereby forming the dome of the conceptacle. The superficial thalli are sloughed-off. The palisade cells near the center of the conceptacle roof then produce additional cells by dividing in a plane at right angles to their long axes (Fig. 10). These daughter cells do not elongate, and form a lining at the center of the dome around a single pore containing a plug (Fig. 10). The plug appears to have been secreted during maturation of the paraphyses. This last assumption is based on the observation that many of the paraphyses from the floor of the conceptacle radiate toward this plug (Fig. 10).

The zonate tetrasporangia measure about 80 μm × 25 μm (Fig. 10) and are located on the periphery of the conceptacle floor. They arise from the lowest layer of cuboidal to rectangular cells forming the conceptacle floor after the paraphyses have developed. Sexual conceptacles have not been found.

Acknowledgements

I wish to thank my wife, Diane, who prepared the illustrations for this paper.

FIG. 4–10. *Tenarea tessellatum*. Fig. 4. Side view of one palisade cell and its cap cell (decalcified in Perenyi's Solution and stained in 1% aniline blue); note the characteristically thickened and striated cell wall and the two lateral pit connections extending through the cell wall near the top on either side; × 1850. Fig. 5. Face view of two decalcified, palisade cells, and their two cap cells, showing the nature of the pit connections; × 1850. Fig. 6. Side view of one decalcified, bi-stromatic thallus layer showing, in this case, paired lateral pit connections; note the densely-stained (aniline blue) region typical of the palisade cells; × 430. Fig. 7. Diagram showing the alignment of palisade cells in parallel, lateral rows in three different directions (*dashed lines*), as viewed from the thallus surface; usually six lateral pit connections are present per cell; × 640. Fig. 8. View of cross-section of several overlapping, bi-stromatic thallus layers; × 280. Fig. 9. Surface view of a single-pored, convex, tetrasporangial conceptacle illustrating the characteristic sloughing-off of thalli above the dome; × 60. Fig. 10. Diagram of a young tetrasporangial conceptacle in vertical section; *note* the stepwise sequence of elongation and formation of three daughter cells from the palisade cells at the periphery of the conceptacle; × 140.

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