

STUDIES ON POLYZOA (BRYOZOA) FROM
THE *ENDEAVOUR* EXPEDITION, 1909-1914

I. A NEW LUNULITIFORM POLYZOAN (ASCOPHORA)
FROM SOUTH-EAST AUSTRALIA

II. COLONY FORMATION IN *SELENARIA NITIDA*
MAPLESTONE

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Plates 1 and 2. Figure 1

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II. Colony Formation in *Selenaria nitida* Maplestone

ABSTRACT

Selenaria nitida, known only from the Peronian faunal province in Recent seas, is refigured from one of Maplestone's syntypes. Evidence suggests that the New Zealand material that Livingstone (1929) assigned to *S. nitida* Maplestone belongs to *S. squamosa* Tenison-Woods instead. The astogeny of *S. nitida* is discussed, with particular reference to the mode of ancestrular budding, and comparisons are made with *S. cupola* (Tenison-Woods) var. *spiralis* (Chapman) from the Victorian Tertiary. It is considered that this taxon should be given specific status in view of its spiral mode of budding. The budding mechanism in *Selenaria nitida* was found to be substantially similar to that of multiserial encrusting cheilostomes, being initiated by two distal first-generation zooecia which bud off lateral-proximal successors to surround the ancestrula. These zooecia then bud off serially, giving rise to the radial arrangement of zooecia in the adult colony. The same budding mechanism is exhibited by *S. cupola* (Tenison-Woods), another Victorian Tertiary fossil, and also *S. squamosa* Tenison-Woods, an Australasian species.

INTRODUCTION

The writer became aware of the abundance of *Selenaria nitida* Maplestone whilst sorting through bulk collections of Polyzoa dredged by the *Endeavour* Expedition (1909-1914) from 30-50 fathoms off Twofold Bay, New South Wales, and deposited in the Australian Museum.

A check with Maplestone's syntypes (Australian Museum Cat. No. U.196) confirmed the identity of the *Endeavour* material (A.M. Cat. No. E.6802), but revealed substantial differences from fragmentary material from Little Barrier Island, New Zealand (Mortensen Collection A.M. Cat. No. U.2716), which Livingstone (1929: 62) assigned to Maplestone's species. The larger dimensions of the zoarial fragments (Livingstone p. 62) and the zooecia, as well as the elongated opesia, suggest that Livingstone's specimens should be referred to *S. squamosa* Tenison-Woods instead. (For description and figs. of *S. squamosa* see Brown 1952: 145).

Several juvenile zoaria of *S. nitida* from the *Endeavour* material show various stages of development, and placed in an ontogenological sequence they provide useful information on the early phases of astogeny. Stach (1936: 65, plate 3, figs. 1, 2, text-figs. 1, 3) described in some detail the early stages of colony formation in *S. spiralis* (Chapman) from the Victorian Tertiary. This taxon was formerly regarded as a variety of *S. cupola* (Tenison-Woods). Stach concluded (p. 66) that *S. cupola* exhibited a similar mode of budding. It will be shown, however, that ancestrular budding in Chapman's species is genetically distinct from that in *S. cupola*. Information on a rather different type of budding as demonstrated by *S. nitida* Maplestone is supplied.

SYSTEMATIC DISCUSSION

Genus **Selenaria** Busk, 1854

Type species (by monotypy): *Selenaria maculata* Busk, 1854. Recent: Bass Strait.

Selenaria nitida Maplestone plate 1, figs. 1, 2, 3, 5, 6, 7.

1909 *Selenaria nitida* Maplestone, p. 271, plate 77, fig. 8.

1921 *Selenaria nitida* Maplestone: Waters, p. 407.

Not 1929 *Selenaria nitida* Maplestone: Livingstone, p. 62 (= *S. squamosa* Tenison-Woods).

1952 *Selenaria nitida* Maplestone: Brown, p. 142, text-figs. 87-89. (New Zealand fossil material).

- Distribution:* (a) Recent: 22 miles east of Port Jackson, N.S.W., 80 fathoms (Maplestone). 30-50 fathoms off Twofold Bay, N.S.W. (*Endeavour* material).
 (b) Fossil: Weka Pass (Waiuan, Middle Miocene), New Zealand (Brown).

Remarks: The smaller dimensions of the mature colony of *S. nitida* and of the average size of the individual zooecia, as well as the correspondingly shorter opesia, are the chief features distinguishing Maplestone's species from *S. squamosa* Tenison-Woods. Furthermore, the basal surface of the colony is flattened in the former species, but concave in the latter. It was not possible to examine all of Livingstone's New Zealand material, but he inferred (p. 62) that the zoaria were larger in size than those of the type material of *S. nitida* Maplestone and would appear therefore to belong to *S. squamosa*.

Maplestone's (1909: plate 77, fig. 8) original figure is so unsatisfactory that it could apply equally well to *S. squamosa*. I have photographed a calcined adult specimen of one of Maplestone's five U.196 syntypes (plate 2, fig. 1) to ensure that his species is clearly established.

Astogeny: Ancestrular budding is evidently established soon after metamorphosis of the larva, for no trace of a solitary ancestrula was found, a point which Lagaaij (1963: 182) also observed in *Cupuladria canariensis* (Busk). The earliest stage represented in the *Endeavour* material is a five-cell zoarium (plate 2, fig. 2), encrusting a fragment of a pelecypod valve. It comprises the ancestrula and a distal and proximal vibraculum, with four zooecia situated distal-laterally. The distal pair abut against the distal-lateral walls of the ancestrula and constitute the first generation [cf. *Cupuladria canariensis* (Busk) Lagaaij 1963: text-fig. 10b]. The adjacent pair appear to have been budded laterally from these and are to be interpreted as the second generation. Brown (1952: text-figs. 93, 94) figured an identical juvenile zoarium in *S. squamosa* Tenison-Woods, and erroneously considered (p. 147) that all four zooecia were directly produced from the ancestrula. The juvenile fan-shaped colony is bilaterally symmetrical in both *S. nitida* and *S. squamosa* and a prominent fold of tissue or basal kenozoecium (Brown 1952, caption to text-fig. 93) is exposed along the proximal margin over which the third generation, budded off from the preceding pair, is later formed. A further pair, i.e., fourth generation, is budded from the third generation zooecia to complete the circlet of zooecia around the ancestrula (plate 2, fig. 5).

To summarize: Colony formation in *S. nitida* is initiated by two first-generation zooecia, the right member budding off clockwise lateroproximally, while the left member buds in an anti-clockwise direction, thereby establishing a circlet of eight periancestrular zooecia.

I should like to emphasize that the development of the periancestrular zooecia has not been directly observed. It is well established, however, that not all the several zooecia surrounding the ancestrula in the multi-serial cheilostomes are produced as its buds (Harmer 1931: 159, 160).

Confirmation of this is provided by *Electra pilosa* (Linnaeus), an encrusting cheilostome, whose budding mechanism has been studied by Waters (1924) and Marcus (1926), and summarized by Harmer (1931: 122). Here three distal buds arise from the ancestrula, representing the first generation of zooecia. Successive generations are budded off distally, forming the young fan-shaped colony, the distal-lateral edges of which are soon reflected proximally and meet on the proximal margin of the ancestrula. The writer (in part I of these studies) has documented a closely

similar budding pattern in the new ascophoran *Australiana bifenestrata* from south east Australia. As Harmer (p. 162) noted, the actual number of zooecia surrounding the ancestrula is not constant for a species. In *S. nitida*, for example, it may vary from seven to nine.

I have examined a juvenile colony of *S. spiralis* (Chapman) from Caldwell's Cliff, south-west Victoria (Pliocene) (plate 2, fig. 4). This fossil specimen is of particular interest because the stage of development is almost equivalent to that of *S. nitida* (plate 2, fig. 3), except that both fourth-generation zooecia are wanting. Useful comparisons can, however, be drawn between the two.

Stach (1936: 65) has shown that budding in *S. spiralis* (Chapman) is initiated simultaneously from the right side of the distal half of the ancestrula as well as the left side of its proximal half to form two first-generation zooecia, and three successive pairs are budded off in a clockwise direction laterally. The fourth pair (i.e., B₄, A₄ components in Stach's terminology), normally situated at the distal and proximal margins of the ancestrula, are not developed in the present fossil specimen (plate 2, fig. 4) and its symmetry at this stage is analogous to the two-fold crystallographic symmetry axis.

Essentially the budding mechanism in *S. nitida* and *S. spiralis* is the same in that the eight zooecia surrounding the ancestrular region are formed by the budding of two first-generation zooecia. The important difference concerns the spiral mode of budding in the latter species, resulting from the oblique position of the two first-generation components both of which bud off laterally in a clockwise direction (plate 2, fig. 4).

Once the circlet of zooecia is completed, further budding in *S. nitida* commences from the two first-generation zooecia, each of which produces one distal successor (plate 2, fig. 5). Budding is then initiated from the lateral and proximal margins as well, until the circular outline of the colony is attained (plate 2, fig. 6). A tendency towards radial growth now becomes apparent (plate 2, figs. 6, 7), the semi-mature colony having eight primary rows, corresponding to the number of zooecia encircling the ancestrula. The secondary branches, however, are established between these when some members of the circlet bud off two distal successors. During later stages of development (plate 2, fig. 1), new branches are intercalated when space permits.

Discussion: Stach (1936: 66, text-figs. 2, 4, 5, 6) considered that the ancestrular region of *S. cupola* from the Victorian Tertiary showed spiral development similar to *S. spiralis*. Careful examination of the photograph of the plesiotype from the "Glycimeris Beds" (Stach: plate 3, fig. 3) which appears to correspond to his figured specimen (i.e., text-fig. 2; the magnified ancestrular region in fig. 4 seems to have been taken from a different specimen), does not substantiate Stach's opinion. The periancestrula zooecia are bilaterally symmetrical as in *S. nitida* (fig. 5), and comprise two distal, four medial and two proximal members; the B₄ components at the extremity of the distal vibraculum in Stach's text-figs. 2, and probably also in 4 and 5, are not analogous to the fourth-generation component in *S. spiralis* as it is budded from either the left or right first-generation zoecium proximally. The A₄ component, positioned in Stach's figure 2, at the extremity of the proximal vibraculum is misplaced; it does not abut on the distal wall of the vibraculum as shown, but is situated to one side of it and comprises one of the members of the proximal or fourth-generation pair as in *S. nitida* (plate 2, fig. 5). Through the kindness of Professor M. F. Glaessner, Geology Department, University of Adelaide, I was able to examine the syntypic material of *S. cupola* (Tension-Woods) from Muddy Creek (Middle Miocene). Only in syntype G (Stach, text-fig. 6) is the apical region intact, and the periancestrula zooecia show the same orientation as in plate 3, fig. 3 of Stach.

From the foregoing observation it follows that the mode of budding in *S. cupola* is not the same as in *S. spiralis* as Stach maintained, but is allied to *S. nitida* instead. It now becomes evident that the important difference between *S. cupola* (Tenison-Woods) and *S. spiralis* (Chapman) is the radial growth of the former species built up from the serial budding of eight zooecia, in contrast to the spiral growth in the latter, which is initiated by the clockwise budding of two first-generation zooecia, and continued as two spiral whorls. Clearly, the mode of budding in Chapman's species constitutes an important genetic distinction.

Conclusions: The maintenance of strict bilateral symmetry during the earliest stages of colony formation in *S. nitida* and radial growth during the later stages of development achieves an even disposition of zooecia within the colony, demanded presumably by the feeding requirements of the individual polypides, as well as the need to preserve the equilibrium of the colony in its free mode of life.

Some lunulitiform species attain their equilibria by developing spiral growth; these are *Heliodoma implicata* Calvet, *Setosellina goësi* (Silén), *Setosella spiralis* Silén and *Selenaria spiralis* (Chapman). The phenomenon of spiral growth has received particular attention by Silén (1942). He has shown that the spiral series may either be derived from two first-generation buds as in *Heliodoma* (and demonstrated by Stach for *Selenaria spiralis*), or as in *Setosella spiralis*, where either one or two spiral series are formed; the second series is derived from the bifurcation of the single first-generation bud and not from the ancestrula. In some of the species, however, which Silén used to demonstrate spiral growth, e.g., *Setosella constricta* Harmer and *Setosella vulnerata* Busk, the zooecia often bifurcate during budding and concentric spiral whorls are not developed. Lagaaij (1963: 182, 184) has also shown that Silén's theory of spiral growth is not valid for *Cupuladria*.

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EXPLANATION OF PLATE 2

- Fig. 1: *Selenaria nitida* Maplestone Syntype x 30. A.M. Cat. No. U.196. Locality: 22 miles East of Port Jackson, 80 fathoms. Mature colony.
- Fig. 2: *Selenaria nitida* Maplestone x 30. Five-cell zoarium. Comprising the median ancestrula with distal and proximal vibraculum and two first-generation zoecia distally, each of which has budded off a second-generation zoecium laterally (cf. Brown 1952, text-fig. 93, *S. squamosa* Tenison-Woods).
- Fig. 3: *Selenaria nitida* Maplestone x 30. Eight-cell zoarium. One fourth-generation zoecium is yet to be intercalated at the proximal margin.
- Fig. 4: *Selenaria spiralis* (Chapman) x 30. Locality: Caldwell's Cliff, South West Victoria (Pliocene), Brown Collection. Seven-cell zoarium. This stage is almost equivalent to fig. 3. Note, however, that the zoecia are budded off in two discrete series resulting in the formation of double spiral whorls in the mature colony (Stach 1936, text-fig. 1).
- Fig. 5: *Selenaria nitida* Maplestone x 30. The circlet of zoecia around the ancestrula is complete and the two first-generation zoecia have commenced serial budding distally.
- Fig. 6: *Selenaria nitida* Maplestone x 30. Budding is well advanced on the distal margin of the colony, less so laterally and proximally. Note the incipient radiate growth.
- Fig. 7: *Selenaria nitida* Maplestone x 30. The semi-mature colony has attained its circular shape. (Figs. 2, 3, 5-7 all from A.M. Cat. No. E.6802, off Twofold Bay, N.S.W.)

