CONDITIONS INDUCING POLYMORPHISM IN *THALAMOPORELLA ROZIERI* (AUDOUIN) (POLYZOA, ANASCA).

by

N.A. Powell

National Museum of Canada, Ottawa

and

P.L. Cook

British Museum, Natural History.

Résumé

L'auteur essaie de déterminer les facteurs qui induisent le développement de l'aviculaire de *Thalamoporella rozieri* (Audouin). Les facteurs du développement des kénozoécies sont d'abord réexaminés. Ces structures résultent toujours d'une nette insuffisance de place à l'intérieur du zoarium, rompant la disposition normale des zoécies. Des aviculaires apparaissent toujours au début de la ramification des rangées de zoécies, comme le bourgeon disto-latéral d'une paire inégale formée à partir de la zoécie-mère proximale ; le bourgeon distal devient zoécie. L'irrégularité dans la distribution des aviculaires, aussi bien que leur position définie dans le zoarium, s'explique dans les conditions du mécanisme suivant d'une inhibition de la croissance. Le développement du bourgeon-fils distal se produit toujours plus rapidement que celui du bourgeon disto-latéral ; il occupe, de ce fait, un plus grand espace et devient une zoécie-fille. En rapport avec la compression due au manque de place, le développement du bourgeon disto-latéral en zoécie est inhibé et il se transforme en un aviculaire plus petit. Les taux de croissance égaux de deux bourgeons-fils produisent deux zoécies de dimensions à peu près égales. Ce mécanisme de croissance est frappant chez *T. evelinae* Marcus, espèce sans aviculaire, dont les bourgeons disto-latéraux, au début des nouvelles rangées se transforment en kénozoécies.

Introduction

The sporadic distribution of the vicarious avicularium among thalamoporellid zoaria is well known, but with the exception of Silén's (1938:223) study of *Thalamoporella liotica* (Ortmann), no explanation for this irregularity has been advanced (1).

The recent findings of Soule and Soule (1964:194, 195, 198, 199) are of special interest in this regard, as they confirmed the total absence of avicularia in material of *T. evelinae* Marcus, obtained from St. Helena Island. They pointed out (p. 194) that the absence of avicularia is a unique character in that species since these structures

(1) Harmer (1909:725), suggested that genetical research might produce information on the evolution and occurrence of vicarious avicularia generally.

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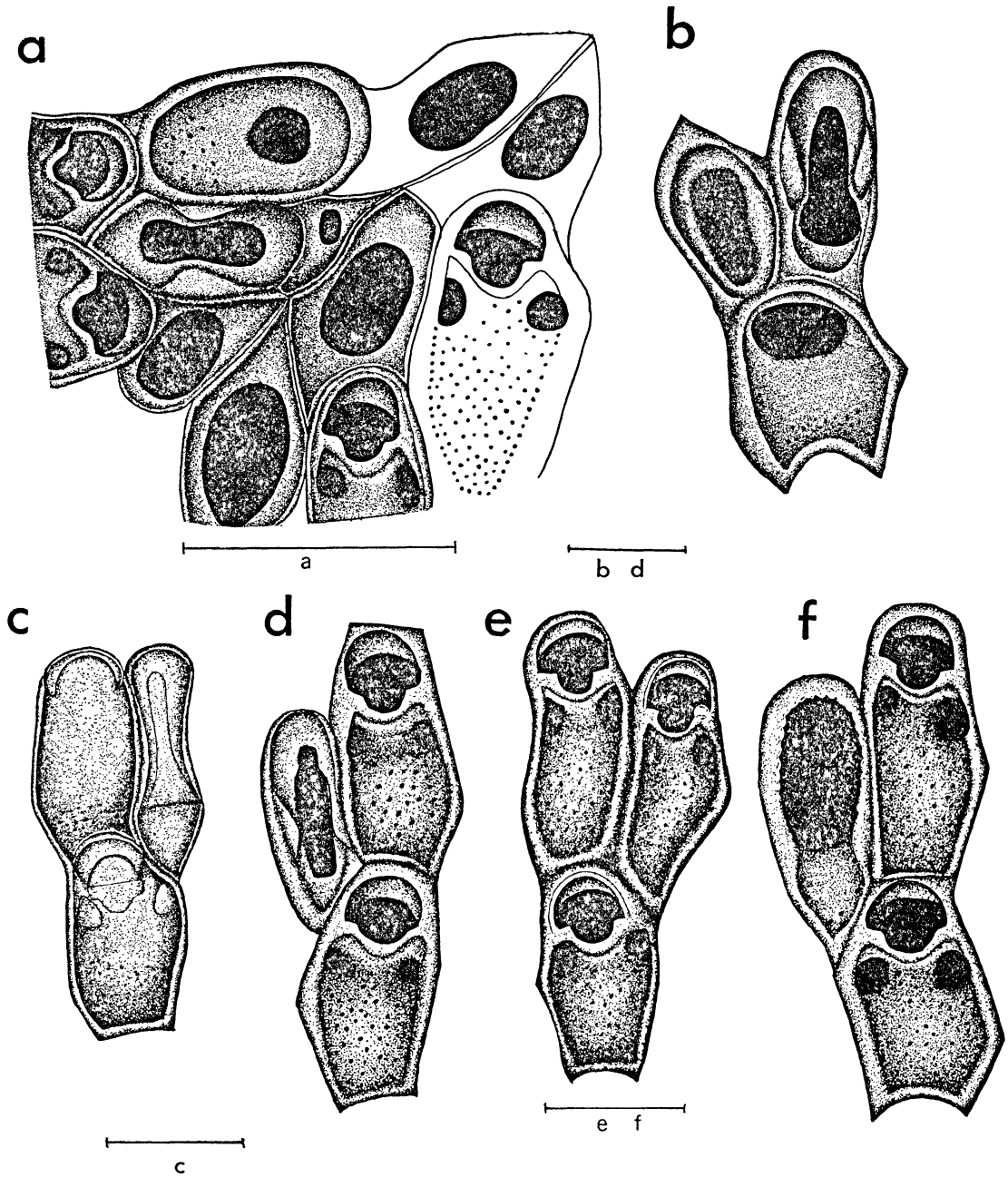

TEXT-FIG I

a. — Showing a deformed area within a zoarium, at the intersection of two opposing directions of zoarial growth. The diagnolly thickened wall denotes the area of impact. Note the avicularium and sister-kenozooecium. The several other kenozooecia represent zooecial buds whose development has been prematurely arrested (Scale = 1 mm).

b. — Three individuals situated in close proximity to an obstruction enveloped by the zoarium: comprising a proximal mother-kenozooecium from which has developed a kenozooecium and an avicularium (Scale = 0.5 mm).

are present in all other recent Thalamoporellidae. This intra- as well as inter-specific variation assumes considerable significance, in view of the important diagnostic value (Harmer, 1926:291-2) attribued to the avicularium, particularly the mandible, as a criterion for species differentiation.

An attempt is made in the present paper to evaluate the conditions that influence polymorphism in the type-species of *Thalamoporella, T. rozieri* (Audouin), with special regard to the avicularium. It is believed that the conclusions reached here may also be applicable to certain other Anascan and Ascophoran species.

This study is based on extensive non-breeding material collected from the sub-littoral zone of Massawa Harbour, South Red Sea.

Observations

Like most other species of *Thalamoporella* (with the notable exception of *T. evelinae*), budding in *T. rozieri* produces three types of individuals: *Zooecia,* the largest and dominant type, which under normal conditions of zoarial growth, are arranged in alternate parallel rows. *Avicularia,* vicarious and substantially smaller than zooecia, being randomly distributed through the zoarium. Each is derived from a proximal mother-zooecium, as a distal-lateral bud of an unlike pair (the distal bud always becomes a zooecium), and thereby initiates a new zooecial row. *Kenozoocia,* which are reduced individuals without a polypide and orifice, are the least common type represented.

In *T. rozieri,* kenozooecia are very common in disturbed or deformed areas of the zoarium, where the normal arrangement of zooecia has been disrupted; for example at the intersection of two opposing directions of growth within the same zoarium or between two different zoaria (Text-Fig. 1, a), or in close proximity to obstructions encountered by the growing zoarium. An instance was observed in which one kenozooecium situated near an obstruction had generated two daughter-buds. The distal bud was a kenozooecium, the distal-lateral bud was developed as an avicularium (Text-Fig. 1, b). Silén (1938:224) attributed the development of kenozooecia in *T. liotica* to similar disturbances: ["Diese Zoide sind oft im Äusseren sehr deformiert und treten an solchen Stellen auf, wo die den Zoarienbau störende Kraft besonders start einwirkt... Bezirke mit solchen

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c. — Three individuals situated near the growing edge of the zoarium: comprising a mature mother-zooecium, a distal immature zooecium (the cryptocyst is only partly developed), and a small or distal-laveral avicularium with mandible intact (Scale = 0.5 mm).

d. — To show the differences in dimensions between unlike daughter-individuals, i.e. small distal-laveral avicularium and the larger sister-zooecium (Scale = 0.5 mm).

e. — To show the similarity in dimensions between sister-zooecia (Scale = 0.5 mm).

f. — Three individuals, the bud of the left daughter-member has aborted to form a kenozooecium. (cf. Soule and Soule 1964: text-fig. 1) (Scale = 0.5 mm).

All figures are camera lucida drawings of material collected from the littoral zone of Massawa Harbour. Canada balsalm preparations.

Abnormitäten in der Zoidbildung usw. kommen z. B. im Zusammenhang mit Unregelmässigkeiten der äusseren Zoarienform vor so beispielsweise bei dem hier als Excempel gewählten Zoarium am Boden der Längswellen, in denen das Zoarium gebrochen ist."]. "These zooids are often strongly deformed in their external shape and they are present in such places where the force disturbing the structure of the zoaria acts particularly strongly... Regions where the zooids are abnormally developed etc., occur for example in connection with irregularities in the external shape of the zoaria. In the zoarium which we have discussed as an example, they occur at the base of the longitudinal waves where the zoarium is broken". Kenozooecia in *Thalamoporella* therefore represent partly-formed zooecia, the buds of which have aborted because of an acute lack of space necessary for their full development. Zooecial abortion according to Marcus (1939:130) and Soule and Soule (1964:198) frequently occurs in *T. evelinae,* producing "aberrant zooecia" (i.e. kenozooecia). The phenomenon is especially common at the beginning of a bifurcating row—the position of avicularial formation in other Thalamoporellidae. Rare instances of this condition were also observed in *T. rozieri* (Text-Fig. 1, f). A very similar process occurs in the cribrilinid, *Figularia spinea* Brown (Powell, in press), but in that species the kenozooecia sometimes regenerate into avicularia.

The following points should now be considered before interpreting the conditions inducing the development of avicularia in *T. rozieri:*

1) the occurrence of avicularia is initially determined at the growing edge of the colony when the walls of the various individuals are first laid down, prior to the formation of the frontal cryptocyst (Text-Fig. 1, c). They are usually inconsistently distributed in the zoarium at the commencement of branching rows of zooecia, being abundant in some, but rare or wanting in others. Because of the spasmodic development of avicularia, new zooecial rows are very frequently initiated by zooecia.

2) In some instances an avicularium may attain the same length as its adjacent sister-zooecium, but normally the length of the avicularium as well as the width, is substantially reduced, i.e. the sister-zooecium occupies more space in the zoarium compared to the avicularium (Text-Fig. 1, d). On the other hand, the two daughter-zooecia generated from a mother-zooecium, always have approximately the same dimensions, each occupying an equal amount of space within the zoarium (Text-Fig. 1, e).

3) The bud which forms an avicularium is potentially zooecial, as it is derived together with that of the adjacent daughter-zooecium, from a proximal mother-zooecium; two avicularia are never budded off from the same mother-zooecium.

4) In the large amount of material of *T. rozieri* examined, avicularia were never seen to occur among uniserial rows of zooecia. Silén (1938:224, 225) however, observed atypical instances in *T. liotica* where some avicularia were found in such positions, in association with localised disturbances in the zoaria which had upset the quincuncial arrangement of the zooecia; a large number of the individuals being deformed kenozooecia, particularly where the disturbances were strong. We quote from Silén (p. 304): ["Auffalend ist, ... dass

hier die Avicularienbildung mit deutlichen Störungen im Zoarienwachstum und seiner Quincunanordnung zusammentrifft, sowie dass solche Störungen stärkerer Art mit der Ausbildung von Kenozoiden einhergeben".] "It is striking... that here the formation of the avicularia coincides with distinct disturbances in the growth of the zoarium and its quincuncial arrangement, and that such disturbances of a stronger nature occur simultaneously with the formation of kenozooida".

Comparable instances of avicularia-kenozooecia associations in relation to strong zoarial deformation were also observed in *T. rozieri*, but in every case the avicularia were numerically few, each being derived as a distal-lateral bud from the proximal mother-zooecium (Text-Fig. 1, a). Silén's observations are very significant in that they show that under certain conditions of stress imposed by disturbances on the zoarium, some buds within uniserial rows which are primarily zooecial, may become modified as avicularia. Where these disturbances are very pronounced, the buds are largely developed as kenozooecia (Silén:225). ["wo diese Störungen sehr stark sind, sind die Zoide in grossem Ausmass als Kenozoide ausgebildet."]

Conclusions

1. The three types of individuals in *T. rozieri* are derived from potentially polymorphic buds: *Zooecia* are the largest and dominant individuals and therefore occupy the greatest amount of area within the zoarium. *Avicularia* replace zooecia but are substantially smaller and haphazardly distributed throughout the zoarium; when present they are nearly always confined to the bifurcation of new zooecial rows. *Kenozooecia* are the least common individuals present and are more commonly associated with deformed areas in the zoarium, where acute lack of space has prevented their full maturation as zooecia or avicularia.

2. Of the two daughter-buds generated from the mother-zooecium at the growing edge of the zoarium, one (i.e. the distal bud) develops at a faster rate and therefore assumes a greater amount of space to become a daughter-zooecium; the other, owing to the resultant pressure brought about by restriction in available room, becomes modified into a smaller avicularium. Equal growth rates of two daughter-buds on the other hand, produces two zooecia, each having approximately the same dimensions. Such an inhibiting mechanism explains (a) the restriction of avicularia to the bifurcation of the zooecial rows, in this as well a the several other species of *Thalamoporella*; (b) their rather spasmodic distribution in many thalamoporellid zoaria. Striking evidence of this mechanism is very apparent in *T. evelinae*, where avicularia are absent. Instead, the lateral daughter-buds generated from a proximal mother-zooecium (corresponding precisely to the position of the avicularium in *T. rozieri*), frequently become modified as kenozooecia (Soule and Soule: text-fig. 1).

3. Based on the foregoing observations it seems reasonable to postulate that the restriction of vicarious avicularia to the bifurcation of the zooecial rows in *T. rozieri*, stems directly from some localised

inhibiting influence, namely, lack of space, which presents the lateral daughter-bud of a mother-zooecium becoming a zooecium; and an avicularium is developed instead.

4. The results of this study are probably applicable to other Anascan and Ascophoran species where the avicularia are similarly confined to the bifurcation of the zooecial rows (see Group 1 of Silén 1938:288).

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Summary

An attempt is made to evaluate the conditions inducing development of the avicularium in *Thalamoporella rozieri* (Audouin). The conditions causing the development of the kenozooecia were first reviewed. These structures always result from severe shortages of space localised within the zoarium, disrupting the normal arrangement of the zooecia. Avicularia always occur at the beginning of a bifurcating row of zooecia, as the distal-lateral bud of an unlike pair generated from the proximal mother-zooecium; the distal bud becomes a zooecium. Both the irregularity in avicularial distribution as well as their consistent positioning in the zoarium is explained in terms of the following growth-inhibiting mechanism. Development of the distal daughter-bud always proceeds at a faster rate than the distal-lateral bud, it thereby occupies a greater amount of space and becomes a daughter-zooecium. Owing to pressure brought about by insufficient space, development of the distal-lateral bud as a zooecium is inhibited and it becomes modified as a smaller avicularium. Equal rates of growth of two daughter-buds produces two zooecia of approximately similar dimensions. Striking evidence of this growth mechanism is to be found in *T. evelinae* Marcus, a species without avicularia, the distal-lateral buds at the beginning of new rows becoming modified as kenozooecia instead.

Zusammenfassung

Man hat versucht, die Bedingungen zu ermitteln, die die Entwicklung des Avikulariums bei *Thalamoporella rozieri* (Audouin) auslösen. Es wird zuerst eine Uebersicht der Bedingungen gegeben, die eine Entwicklung der Kenozooecien verursachen. Diese Strukturen sind immer eine Folge einer starken Reduktion des Raums im Zoarium, die die normale Anordnung der Zooecien stört. Avikularien treten immer an der Wurzel einer abzweigenden Reihe von Zooecien auf, als distal-laterale Knospe eines ungleichen Paars, das vom proximalen Mutterzooecium gebildet wird. Die distale Knospe entwickelt sich zu einem Zooecium. Sowohl die unregelmässige Verteilung der Avikularien als auch ihre Lage im Zoarium können durch den folgenden Mechanismus der Wachstumshemmung erklärt werden. Die Entwicklung der distalen Tochterknospen ist immer rascher als diejenige der distal-lateralen Knospen. Sie nimmt deshalb mehr Raum ein und wird zum Tochterzooecium. Der durch den Platzmangel bedingte Druck führt zu einer Hemmung der Entwicklung der distal-lateralen Knospe zu einem Zooecium, die sich deshalb zu einem kleineren Avikularium abwandelt. Wenn die Wachstumsgeschwindigkeit von zwei Tochterknospen die gleiche ist, entwickeln sich zwei Zooecien von ungefähr der gleichen Grösse. Dieser Wachstumsmechanismus ist besonders deutlich bei *T. evelinae* Marcus, einer Art die keine Avikularien besitzt, bei der die an der Wurzel neuer Reihen sitzenden distal-lateralen Knospen als Kenozooecien ausgebildet werden.

REFERENCES

HARMER, S.F., 1909. — Presidential Address to the Zoological Section. *Rep. Brit. Ass.*, 78 (Dublin, 1908), *pp.* 715-731.

HARMER, S.F., 1926. — Polyzoa of the Siboga Expedition II, Cheilostoma Anasca. *Rep. Siboga Exped.*, 28 b, Leiden, *pp.* 181-501.

MARCUS, E., 1939. — Briozoarios Marinhos Brasileiros III. *Bol. Fac. Filos Ciênc. S. Paulo, Zool.* 3, *pp.* 113-356.

POWELL, N.A. — Note on the Relationship between Kenozooecia and Avicularia in some Cribrilinidae (Polyzoa). *Trans. Roy. Soc. New Zealand* (in press).

SILÉN, L., 1938. — Zur Kenntnis des Polymorphismus der Bryozoen. Die Avicularien der Cheilostomata Anasca. *Zool. Bidrag. Uppsala*, 17, *pp.* 140-366.

SOULE, J.D. and D.F., 1964. — Clarification of the Family Thalamoporellidae (Ectoprocta). *Bull. So. Calif. Acad. Sci.* 63, 4, *pp.* 193-200.