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NEW ZEALAND
DEPARTMENT OF SCIENTIFIC AND INDUSTRIAL RESEARCH

BULLETIN 154

Flabellum rubrum (Quoy and Gaimard)

by
DONALD F. SQUIRES

The U.S. National Museum
Smithsonian Institution

New Zealand Oceanographic Institute
Memoir No. 20

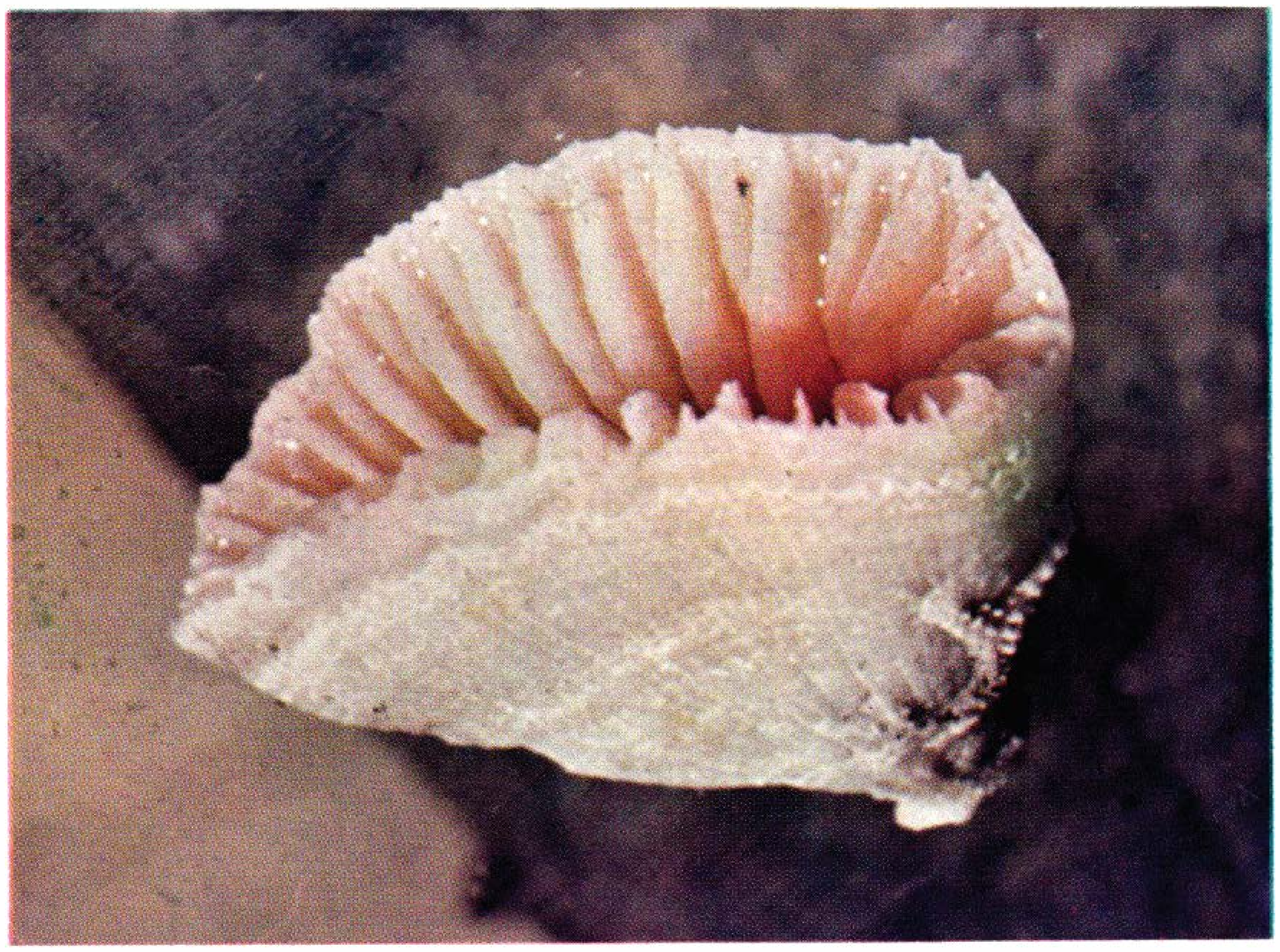

Photo: H. O. Kane

Flabellum rubrum (Quoy and Gaimard) taken at N.Z O.I. Station C 190 in Cook Strait, New Zealand.

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FOREWORD

The New Zealand cup coral, *Flabellum rubrum*, is a common component of faunas on the New Zealand shelf. The coral is of considerable importance in palaeontological and zoogeographic studies, and Dr Squires in this monograph, as well as removing the systematic confusion hitherto existing between this and similar corals, gives valuable accounts of its morphology, development, and ecological relationships.

The preliminary editing of the manuscript has been carried out by Mrs P. M. Cullen. Mr M. O'Connor (Information Bureau, D.S.I.R.) has been responsible for final editing.

J. W. Brodie,
Director,
N.Z. Oceanographic Institute.

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Flabellum rubrum (Quoy and Gaimard)

By DONALD F. SQUIRES,

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ABSTRACT

Flabellum rubrum (Quoy and Gaimard) is the common cup coral of New Zealand. Through misapplication of the name, the concept of the species has been warped so that a variety of flabellid corals are often placed in it. History of the taxonomy of the species is reviewed, the original description and figures reproduced, and a complete synonymy is given. A description, based upon recently collected topotypic specimens from Cook Strait, includes not only the corallum morphology but the gross anatomy of the polyps. Ecology and faunal associations of the species are discussed. Statistical studies show the systematic relationships between *F. rubrum* and related species as well as allometry. Fossil distribution and paleoecology of the species are considered.

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*Formerly of the American Museum of Natural History.

INTRODUCTION

The first described coral from New Zealand waters is probably also the most common species of coral on the New Zealand shelf. Unfortunately, its systematic position has been greatly confused and the specific appellation has been misapplied for the last 50 years. Because of the frequency with which the coral is encountered, in dredgings and as a fossil, and because it is an important species from both systematic and zoogeographic aspects, a comprehensive review is desirable.

Because some of the earlier literature pertaining to the species is not readily available, the original description and illustrations are reproduced here. One volume of the atlas of Quoy and Gaimard (1833) Zoophytes of the "Voyage de découvertes de *l'Astrolabe*" is present at the Dominion Museum, Wellington. I am unaware of the existence of the accompanying text in any library in New Zealand although several libraries hold sections dealing with Mollusca.

Materials forming the basis for this study include the ample collections of the New Zealand Geological Survey, the New Zealand Oceanographic Institute, and the various universities and museums of New Zealand. These were studied several years ago (Squires, 1958a) and more recently during 1959. Comparative materials include large suites of southern ocean corals housed in the American Museum of Natural History, collected by the Lamont Geological Observatory (R/V *Vema*), New Zealand Oceanographic Institute and the U.S. "Deepfreeze" program of Antarctic research. Other materials include specimens generously loaned for study by Dr W. J. Rees, British Museum (Natural History), from the *Discovery* collections. Living specimens of *Flabellum rubrum* from Cook Strait were collected from the M.V. *Viti* of the New Zealand Oceanographic Institute. This sample, N.Z.O.I. Sta. A 489, was taken in 55 fm of water at 41° 27′ S, 174° 50·8′ E, and contained over 90 specimens of *F. rubrum*.

ACKNOWLEDGMENTS

This study was begun during the tenure of a Fulbright Research Fellowship in New Zealand during 1959. Through the cooperation of Mr James Brodie and Dr Henry Pantin, New Zealand Oceanographic Institute, I was able to participate in a cruise of the m.v. *Viti* in Cook Strait during which the specimens here recorded were collected. For discussions regarding the occurrence, ecology, and systematics of *F. rubrum*, I am grateful to: Dr Patricia Ralph, Zoology Department, Victoria University; Dr A. W. B. Powell, Auckland Institute and Museum; Dr Richard Dell, Dominion Museum; Dr C. A. Fleming, Geological Survey; and Dr J. W. Wells, Cornell University, U.S.A.

Dr Gilbert Ranson, Muséum National d'histoire Naturelle, Paris, furnished photographs of the cotypes of *F. rubrum* preserved in the collections of that museum. I am grateful to him also for measurements and other data concerning the specimens. Mr G. Robert Adlington made the photographs other than those of the cotypes. Drafting of charts and illustrations was done by Mr W. Holmquist and R. Gartland of the American Museum of Natural History.

THE ARGUMENT AND CONCLUSIONS

It is the argument of this paper that *F. rubrum* has been confused with species which differ greatly morphologically, ecologically, biologically, and zoogeographically. The group of *Flabellum* characterised by reproduction (?) by transverse fission, as for example, *Flabellum stokesii* or *F. aculeatum* (Semper, 1872, Milne-Edwards and Haime, 1857) is actually a distinct species group, if not genus, and has been wrongfully included with *F. rubrum* from about 1900. It is the principal object of this memoir to substantiate the need for this separation.

While being grossly lumped together with tropical species, *F. rubrum* has simultaneously been divided excessively within its "home" range. Thus, it is also my contention that *F. rubrum* and *F. rugulosum* are one and the same together with numerous synonymic names applied to these two "species".

In the course of gathering data for the systematic study outlined above it became apparent that there was a wealth of disseminated information about *F. rubrum*, which, if placed together in context, would provide the basis for many additional investigations. Thus, inquiry has extended to areas of biologic associations and such other ecologic data as are available on *F. rubrum* and the scattered information brought together. It is hoped that the obvious gaps in biological and ecological data will stimulate interest among zoologists for further study.

SYSTEMATICS

SYNONYMY

Family FLABELLIDAE Bourne, 1905

Genus **Flabellum** Lesson

1831. Illust. Zool., pl. 14.

Type Species: Flabellum pavoninum Lesson (Lectotype, Milne-Edwards and Haime, 1850)

Flabellum rubrum (Quoy and Gaimard, 1833)
(pl. 1, fig. 1-10)

1830. *Caryophyllia compressa* Blainville, Dictionnaire des Sciences Naturelles, Paris, 60 :310. (*Nomen nudum.*)

1833. *Turbinolia rubra* Quoy and Gaimard, Voyage de découverte de *l'Astrolabe*. Zoologie, Vol. 4, Zoophytes, 188, pl. 14, fig. 5–9.

1834. *Caryophyllia compressa* Blainville, Manuel d'Actinologie ou de Zoophytologie, Paris, 344. (*Nomen nudum*).

1836. *Turbinolia rubra;* Milne-Edwards, *in* Deshayes and Milne-Edwards, Histoire Naturelle des Animaux sans Vertèbres, Ed. 2, Paris, 2 :360.

1849. *Turbinolia rubra;* Milne-Edwards, in Cuvier, Le Règne Animal . . . Edition Accompagnée de Planches Gravées. ["Disciples Edition"], Paris, 20: pl. 82, fig. 5.*

1846. *Euphyllia rubra;* Dana, United States Exploring Expedition. Vol. 7, Zoophytes, 161.

1848. *Flabellum rubrum;* Milne-Edwards and Haime, Ann. Sci. nat., Ser. 3, 9 : 280.

1857. *Flabellum rubrum;* Milne-Edwards and Haime, Hist. Nat. Corall. ii, Paris, 2 : 97.

1859. *Euphyllia rubra;* Dana, Synopsis of the Report on Zoophytes of the U.S. Exploring Expedition, Privately Printed, 14.

? 1862. *Flabellum campanulatum* Holdsworth, Proc. zool. Soc. Lond.: 198, pl. 28, fig. 1–3.

1862. *Flabellum nobile* Holdsworth, ibid: 198, pl. 28, figs. 4, 5.

1870. *Flabellum rubrum;* Duncan, Quart. J. geol. Soc. London 26 :311.

1878. *Flabellum latum* Studer, Monatsb. preuss. Akad. Wiss. für 1877 : 630, pl. 1, fig. 3a, b.

1878. *Flabellum rubrum;* Tenison-Woods, Proc. Linn. Soc. N.S.W. 2 : 311.

1879. *Cylicia vacua*, Tenison-Woods, Proc. Linn. Soc. N.S.W. 3 : 134, pl. 12, fig. 4, 4a, 4b.

1880. *Flabellum rugulosum* Tenison-Woods, (Col. Mus. Geol. Surv. Dep.) Palaeontology of New Zealand, Pt. 4 : 12, fig. 8a, b.

1880. *Flabellum rubrum;* Tenison-Woods, ibid:13.

1881. *Flabellum rubrum;* Quenstedt, Petrefactenkunde Deutschlands, 6 : 953, pl. 180, fig. 7.

Not 1902. *Flabellum rubrum;* Gardiner, Proc. Camb. phil. Soc. 11 : 463.

? 1902. *Flabellum latum;* . Alcock, Siboga-Exped., Monogr. 16a : 31.

1904. *Flabellum rubrum;* Hutton. Index Faunae Novae Zelandiae: 315.

Not 1904. *Flabellum rubrum;* Gardiner, Mar. Invest. So. Africa, 2 : 125, pl. 4, fig. 22–34.

Not 1905. *Flabellum rubrum;* Bourne, Ceylon Pearl Fisheries, Suppl. Rep., 29 : 198, pl. 1, fig. 4.

Not 1905. *Flabellum rubrum;* Gardiner, Fauna and Geography of the Maldive and Laccadive Archipelagos, 2 : 954.

1906. *Flabellum rugulosum;* Suter, Trans. N.Z. Inst. 38 : 334.

Not 1907. *Flabellum pavoninum* var. *latum;* Vaughan, Bull. U.S. nat. Mus. 59 : 55, pl. 2, fig. 2a, b.

Not 1909. *Flabellum rubrum;* Harrison and Poole, Proc. zool. Soc. London for 1909 : 899.

1910. *Flabellum rugulosum;* Park, Geology of New Zealand, Wellington : 164.

1911. *Flabellum rugulosum;* Morgan, N.Z. geol. Surv. Bull., n.s. 13 : 75.

Not 1913. *Flabellum rubrum;* Felix, Palaeontographica 60 : 311.

Not 1918. *Flabellum rubrum;* Folkeson, K. Svensk. Vet. Akad. Handl. 59 : 4.

1923. *Flabellum* [*sic*]; Oliver, Trans. N.Z. Inst. 54 : 530.

Not 1924. *Flabellum rubrum;* Hickson, An Introduction to the study of Recent Corals, Manchester: 41, fig. 12.

Not 1927. *Flabellum rubrum;* Faustino, Mon. Bur. Sci. Philippines 22 : 50, pl. 3, fig. 1–9.

1929. *Flabellum harmeri* Gardiner, Nat. Hist. Rep. Brit. Ant. *Terra Nova* Exped. 1910, Zoology, 4 : 122, pl. 1, fig. 19, 20.

Not 1933. *Flabellum rubrum;* Stephenson and Marshall, Sci. Rep. Great Barrier Reef Exped. 3, 8 : 222.

1934. *Flabellum rugulosum;* Powell, Rec. Auckland Mus., 1, 5 : 263.

1937. *Flabellum rugulosum;* Powell, Trans. roy. Soc. N.Z. 66 : 386.

Not 1938. *Flabellum rubrum;* Umbgrove, Zoöl. Meded. 20 : 264.

Not 1938. *Flabellum rubrum;* Gardiner and Waugh, Sci. Rep. *John Murray* Exped., Zoology, 5, 7 : 174.

Not 1939. *Flabellum harmeri;* Gardiner, *Discovery* Rep. 18 : 326.

Not 1942. *Flabellum rubrum;* Yabe and Eguchi, Sci. Rep. Tohoku Univ. Ser. 2, Geol. 22 : 96, pl. 8, fig. 6–30.

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*Dr J. W. Wells, Cornell University, U.S.A., has informed me that pp. 129–60 and pl. 81–5 of this volume were published in 1849. There is no internal evidence of this date, the series being published during the period of 1836 to 1849.

Not 1942. *Flabellum rubrum;* Yabe and Eguchi, ibid,: 132, pl. 9, fig. 15.
1947. *Flabellum rubrum;* Powell, Native Animals of New Zealand, Auckland: 8.
1947. *Flabellum rugulosum;* Powell, ibid,: 8, fig. 16.
1948. *Flabellum rubrum;* Ralph, N.Z. Sci. Rev. 6, 6 : 108.
1948. *Flabellum rugulosum;* Ralph, ibid: 108, fig. 1.
? 1950. *Flabellum sp.;* Fleming, N.Z. J. Sci. Tech. B31 (5) : 36.
Not 1950. *Flabellum rubrum;* Umbgrove, J. Paleont. 24 : 641, pl. 81, fig. 5-12.
Not 1952. *Flabellum rubrum;* Crossland, Sci. Rep. Great Barrier Reef Exped., 6, 3 : 105.
Part 1958. *Flabellum rubrum rubrum;* Squires, N.Z. Geol. Surv. Pal. Bull. 29 : 65, pl. 12, fig. 1-9.
Part 1958. *Flabellum rubrum campanulatum;* Squires, ibid; 67, pl. 14, fig. 1-8.
? 1958. *Flabellum* sp.; Skerman, N.Z. J. Sci. 1 : 229.
1960. *Flabellum campanulatum;* Squires, N.Z. J. Geol. Geophys. 3 : 1.

TYPE SPECIMENS

Lectoholotype (here designated): The specimen illustrated as fig. 5 and 6 on pl. 14, Quoy and Gaimard (1833). Syntype: A second specimen illustrated as fig. 8 and 9, pl. 14, by Quoy and Gaimard (1833). Both specimens dry. Repository of type specimens: Laboratoire de Malacologie, Muséum National d'histoire Naturelle, Paris, France.

Type Locality: Cook Strait, New Zealand Depth: 25 fm. Collector: d'Urville, 1829.

ORIGINAL DESCRIPTION

The original description of this species given by Quoy and Gaimard, 1833, p. 188 is as follows.

TURBINOLIE ROUGE*

> **Turbinolia rubra**, nob.
>
> *Turbinolia, triangularis, compressa, cuneiformis; stella oblonga, sublutea et rubra; lamellis regularibus inaequalibus. Animale rubro; tentaculis longis, albis, verucosis.*
>
> Nous décrivons ce Zoophyte comme un genre à part, en attendant qu'on le réunisse aux Caryophyllies, dont il ne paraît vraiment être qu'un individu, vivant isolé. Cette espèce, haute d'environ un pouce, a beaucoup de rapports avec la Turbinolie comprimée de M. de Lamarck, laquelle est fossile. Elle est toujours fixée, de forme triangulaire, comprimée, élargie un peu à la base. Son ouverture, ovalaire se déjette légèrement en dehors. Son contour en est régulier, un peu arqué, garni en dedans d'environ cinquante lamelles alternativement grandes et petities, ne débordant point. Les moins longues atteignent à peine le fond de l'entonnoir, qui est profond et rétréci. Les parois extérieures sout à peine striées, et de couleur rougeâtre. L'étoile est d'un jaunâtre clair avec six bandes rouges. L'animal est d'un rouge très-vif. Sa bouche est ovalaire, grande, plissée, de coleur rosée, avec quelques taches blanchâtres, garnie dans son contour de plusieurs rangées d'assez longs tentacules déliés, blancs, diaphanes et tuberculeux sur leur longueur.
>
> Ce Zoophyte provient de la Nouvelle-Zélande dans le détroit de Cook; il était seul adhérent à une Valve de Vénus, et fut pris par vingt-cinq brasses de profondeur.

NOTES ON SYNONYMY

In the following notes, references cited are given in the synonymy and are not repeated in the bibliography. The discussion is arranged under the headings: Historical Period, Period of Changing Concepts, and Modern Period. References cited under the Historical Period are largely those in which the original description of the species was followed, to which no additional specimens have been referred. The second group of citations include those in which the original concept of *Flabellum rubrum* became altered in several different ways. The final group includes references which follow the various interpretations of *F. rubrum* brought forth in the previous period. There is much compromise, or attempt at reconciliation, in these references.

Historical Period

Blainville (1830, 1834) cited *Caryophyllia compressa* after the Quoy and Gaimard manuscript as stated by him (see also the footnote in Quoy and Gaimard, 1833, p. 188, quoted above). Citations of *F. rubrum* by Milne-Edwards (1836, 1849) are reiterations of the original definition. The illustration in the "Disciples" edition of "Le Règne Animal" is a reproduction of fig. 5 of Quoy and Gaimard. Dana (1846, 1859) correctly noted inaccuracies of the original figures which show only a single row of tentacles, while in reality there are several rows. His diagnosis is otherwise a restatement of the original description. Dana (1846) clearly makes a distinction between fixed species (*Euphyllia rubrum* [*sic*]) and transversely dividing ones (*E. spheniscus* [*sic*]).

Milne-Edwards and Haime (1848) were the first to add information to that contained in the original description, although no new specimens or localities were involved. It is not apparent from the

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*C'est la même que N. de Blainville a indiquée sous le nom de Caryophyllie aplatie, Dict., Zooph. tome LX, page 530, d'après nos manuscrits, dénomination que nous avons cru devoir rectifier.

discussion in Quoy and Gaimard (1833) that there were several specimens in the original collection although two corals are figured. Milne-Edwards and Haime (1848) record the existence of two specimens, giving the measurements of one.

Measurements made by Milne-Edwards and Haime (1848, p. 281) of a cotype of *F. rubrum*:*

Height of corallum	18 mm
Maximum diameter of calice ..	28 mm
Minimum diameter of calice ..	11 mm
Depth of the fossa	8 mm

In this same study Milne-Edwards and Haime introduce the threefold grouping of species of *Flabellum* enlarged upon later in 1857. Distinguished were "Flabellines pédicellées", "Flabellines tronquées", and "Flabellines fixées", the latter including only *F. rubrum*. This classification is significant not only for the introduction of a needed scheme of organisation for the already multitudinous species of *Flabellum*, but also because it clearly demonstrates the recognition by these authors of the differences between the group typified by, say, *F. stokesii* and that of *F. rubrum*, a difference later obscured.

In 1857, Milne-Edwards and Haime enlarged upon their species groups, defining them with greater precision. Of the "Flabella fixa" they said: "Polypier restant toujours fixé par une large base" (1857, p. 96). Included in the group were two species: *F. rubrum*, still known only from the two original specimens of Quoy and Gaimard; and *Monomyces anthophyllum* Ehrenberg. This latter species had been removed from the genus *Monomyces* by Milne-Edwards and Haime and placed in *Flabellum* with *F. rubrum* because it is fixed to the substrate, although attached by stout tubular rootlets, rather than by cementation of the pedicel. Current opinion (Vaughan and Wells, 1943; Wells, 1956) maintains the distinction between *Monomyces* (type species *M. anthophyllum*) and *Flabellum*.

Tenison-Woods (1878) recognised the fixed nature of the corallum, stating in his description " . . . corallum always attached." He recorded seeing specimens reputedly from Australia in New Zealand collections, but considered that these data were faulty.

Period of Changing Concepts

In two papers discussing the coral fauna of the Cape of Good Hope, Gardiner (1902, 1904) was the first to enlarge the concept of *Flabellum rubrum*. In his description (1904, p. 128) Gardiner says of the specimens before him: "Although there are only three specimens in the collection, which appear to be absolutely the same as *F. rubrum*, this name has the priority. All the young corallites are, of course, fixed. They break off generally when their calicles have attained a length in their long axes of about 9 mm, the free corallites being about 5 mm high. Some, however, are attached considerably longer, the largest attaining a height of 23 mm. Three of the specimens could not ever have become free, the central stalk being still perfect and surrounded on all sides by rootlets, numbering 7, 8, and 9." Gardiner (1904) clearly indicates the inclusion into *F. rubrum* of specimens described by Semper (1872) under a variety of other specific names.

It is presumed that Gardiner likened the bases of the corals he included under the heading of *F. rubrum* to the illustrations of *F. rubrum* taken from New Zealand, although the latter specimens (those of Quoy and Gaimard) were somewhat larger. The large numbers of specimens of *F. rubrum* taken from New Zealand waters in recent years show conclusively that transverse fission of the corallum such as that attributed to the species by Gardiner does not occur in New Zealand populations. The basal portions of the coralla of both types (those remaining attached and those becoming free) are similar in appearance, being of a rather generalised form, and both are fixed to the substrate by cementation of the basal disc. The similarities between the two types end when the corallum attains a height of approximately 25 mm, at which stage transverse fission of the corallum usually occurs in the species group of the "Flabellines tronquées," while among *F. rubrum* from New Zealand, no transverse fission occurs. Introduced, then, with these two papers of Gardiner, is the concept of *F. rubrum* as an attached species which becomes free of the attachment in the adult stage by transverse fission of the corallum; that is, a merging of the species groups separated by Milne-Edwards and Haime as the "Flabella truncata" and "Flabella fixa".

Bourne (1905) was strongly influenced by Gardiner (1902, 1904) in his conclusions regarding the identity of the genus *Flabellum*, and in particular of the species *F. rubrum*. Bourne (1905, p. 197–8) states:

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*These measurements correspond closely to those made by Dr. Gilbert Ranson, Muséum National d'Histoire Naturelle, of the specimen illustrated by fig. 5 and 6 of Quoy and Gaimard (1833) (see p. 39).

> These Ceylonese specimens are so similar in all respects to the figures and description of Semper's *F. irregulare* that there can be no doubt of their identity. According to Gardiner . . . [1904], *F. irregulare*, Semper = *F. rubrum*, Quoy and Gaimard, and there is certainly some resemblance between his (not wholly satisfactory) fig. 26, 30, 31 and the Ceylonese specimens, while the latter can certainly be included in the amended definition of *F. rubrum* given by Gardiner on p. 28. It is further stated that *F. variable*, Semper, is connected with *F. rubrum* by individuals, Semper's species being identified by Moseley [1881] with *F. stokesi*, M. Edwards and H., which in turn is identical with *F. oweni*, *aculeatum*, *spinosum*, *debile*, *sumatrense* and *candeanum*. I must take leave to doubt whether these identifications are correct. That *F. variable*, Semper, is identical with *F.* (*Turbinolia*) *rubrum*, Quoy and Gaimard, I have no doubt. The characters of the corallum are similar and a comparison of Semper's figure of the expanded polyps (. . . [Semper, 1872], plate xviii, fig. 1) of *F. variable* with Quoy and Gaimard's figure of *F. rubrum* (. . . [Quoy and Gaimard, 1833], plate xiv, fig. 5 to 9) show a very close correspondence in the coloration of the living animal; in both there are the same six alternating radial bands of deeper red and lighter red or yellow.
>
> On the other hand, *F. irregulare*, as described by Semper, is red with as many radial white lines as there are principal septa. The colour, no doubt, is variable to some degree, but it must be taken into account, and what I wish to point out here is, that Semper is the only author who has paid special attention to the colour of the living polyp; that he had at least as many specimens for comparison as Gardiner; that he found a constant colour difference between his *F. variable* and *F. irregulare*, and that the colour of the former, and not that of the latter, corresponds to Quoy and Gaimard's figure of *F. rubrum*. It follows, therefore, that *F. variabile* = *F. rubrum*, and as Semper showed beyond all cavil, *F. stokesi*, *oweni*, *aculeatum*, *spinosum*, *debile* and *sumatrense*, all M. Edw. and H., are synonyms of *F. variabile*.

Bourne (1905, p. 200) was not entirely satisfied with Gardiner's (1902, 1904) treatment of *F. rubrum* for he states: "I differ, with some hesitation, from Mr Gardiner, but I feel bound to point out that his reasons for uniting nearly all the described species of *Flabellum* under *F. rubrum* are not satisfactory."

Bourne continues, stating that the basis of Gardiner's work, largely statistical, was premature, and should await a fuller understanding of the variability of *Flabellum*. That Bourne (op. cit.) was impressed by the occurrence of transverse fission, and similarly unaware of the existence of attached forms which did not undergo transverse fission, is indicated by his definition of the Family Flabellidae (Bourne, 1905, p. 195): "Simple corals, multiplying asexually by transverse fission from a fixed nurse-stock . . ." [It is not my intention to discuss the family or the genus here.] Reference to Semper (1872) made by both Gardiner and Bourne indicate the persuasive nature of the work of the former. The results of his studies on transverse fission are considered in detail below.

Bourne's statements in regard to the colour of the living polyp are still valid. There is, in general, insufficient data available on the variation of colour in any of the solitary corals to make an assessment of this important character. Indeed, polyp colours of many species are not recorded and data of considerable value is not preserved.

A second concept of *Flabellum rubrum* was added by interpretation of species of *Flabellum* occurring in New Zealand waters. Suter (1906, p. 334) mentioned living specimens of *Flabellum* dredged from 50 fm from between Cuvier and Mokohinau Islands, Hauraki Gulf, New Zealand. These specimens were allied with Pliocene fossils named *F. rugulosum* by the Rev. J. E. Tenison-Woods (1880), a very apt relationship. Suter makes two statements which are of considerable interest: "Unfortunately, the animal had already been removed, but Captain Bollons told me that it was beautifully banded with white and scarlet." and later, "This interesting addition brings the New Zealand species of the genus up to two, *F. rubrum*, Q. and G., being the other species. This latter is not uncommon on rocks at low-water mark in Hauraki Gulf, and is very conspicuous by its scarlet animal." Thus introduced was the dichotomy between the deep water species, *F. rugulosum* Tenison-Woods, and the shallow water, nearly intertidal species *F. rubrum* (Quoy and Gaimard).

Powell (1947, p. 8) again utilised both names, making the following interpretation: "*F. rugulosum* is found attached to rock and old shells at moderate depths in the Hauraki Gulf. The coral base is pure white and the animal scarlet. An intertidal relative, *F. rubrum*, is not uncommon, attached to the underside of stones in North Auckland waters. The coral base is dull brownish and the animal salmon to dull vermillion." The separation between the two species was now firmly established in a popular handbook, not only on the basis of the different occurrences of the species, but upon colour of the animal as well.

Ralph (1948) continued the scheme, indicating that *F. rugulosum* is usually found in moderate depths, but interestingly stating (1948, p. 108) ". . . may live free or attached to small rocks and shells. Generally speaking, young specimens are attached and older specimens are free." *F. rubrum* was indicated as the related species which was usually to be found nearly intertidally.

Squires (1958) not only followed Gardiner (1902, 1904) in uniting forms reproducing asexually by transverse fission with *F. rubrum* (largely through ignorance of the significance of the basal scar and misinterpretation of the modern forms), but combined this erroneous and complex relationship with that introduced by Suter (1906). The result was a definition of *F. rubrum* which included forms with either a pedicel or a broad basal scar. *F. rubrum rubrum* included forms reproducing by transverse fission, as well as modern forms of cylindrical shape with a broad basal scar of attachment. It was given a geological range of Whaingaroan (Oligocene) to Recent and an Indo-Pacific distribution. *F. rubrum campanulatum* Holdsworth was constructed to include the forms previously known as *F. rugulosum* Tenison-Woods. Although not stated, it was implicit that this was a deeper water subspecies or variety of *F. rubrum rubrum.*

Stephenson and Marshall (1933), who restate the physiologic conclusions of Gardiner (1904), Gardiner and Waugh (1938), and Yabe and Eguchi (1942a, b) follow Gardiner's usage of *F. rubrum*, applying it widely, but none of the citations appear to be correctly made.

Both Umbgrove (1950) and Crossland (1952) utilised the name *F. rubrum* in the sense of Gardiner. Umbgrove, however, went to some pains to differentiate between *F. rubrum* and *F. stokesii.* The morphologic character selected by Umbgrove to display the differentiation between these two "species" was the angle formed by the lateral edges. That angle in *F. rubrum* was characteristically about 30° while in *F. stokesii*, the angle was about 70°. Although there was overlap, the decided bimodality of the distribution warrants strong consideration in the separation of the populations, but the species having the narrower angle between the two lateral edges is not *F. rubrum,* but a member of the truncate group probably referable to the *F. owenii*, *debile*, *variabile* complex.

Subjective Synonyms

F. rugulosum Tenison-Woods was erected to accommodate specimens from the lower Pleistocene of New Zealand. Tenison-Woods (1880, p. 12) was aware of *F. rubrum* for he states, "This coral has some points of resemblance to *F. rubrum* (Quoy and Gaimard), at present living in the New Zealand seas. It is, however, larger, and the costa are different, besides its general form." The specimens described by Tenison-Woods are slightly abraded so that the distal ends of the septa are seen through the thinned epitheca, accounting for the costae he describes. The form of the corallum of *F. "rugulosum"* is different from the shallow-water *F. rubrum* when seen only from the series available to Tenison-Woods.

F. latum Studer was described from a single specimen taken off North Cape, New Zealand, from a depth of 45 fm. Alcock (1902) also recorded it from the Sulu Sea, but as the specimen was not described or illustrated, it cannot be evaluated. Vaughan (1907), discounting the importance of the attachment of the corallum, allied *F. latum* with his *F. pavoninum* group, an alliance based largely upon the angle formed by the lateral edges of the corallum. The specimen illustrated by Vaughan is not *F. latum* as interpreted here, as the pedicel is worn and is clearly of the *F. pavoninum* type, as is also indicated by the septa.

F. harmeri Gardiner (1929) was described from near Great King Island at a depth of 300 fm, and allied closely with *F. curvatum* Moseley from the Patagonian region and *F. transversale* Moseley described from Australia. Gardiner (1939) also recorded *F. harmeri* from the Palmer Peninsula, but these have been placed in *F. impensum* by Squires (1962).

Holdsworth (1862) named two species of *Flabellum: F. campanulatum* and *F. nobile*. The former, a small specimen, slightly over an inch in height, is heavily ornamented and probably is related to the "Flabella truncata" group. *F. nobile*, founded upon badly worn specimens probably from New Zealand, is quite definitely the same as *F. rugulosum.* Squires (1958a) unfortunately considered the two species of Holdsworth as identical, thus introducing another name into the literature on New Zealand *Flabellum.*

Summary of Systematic History

F. rubrum carries two concepts today which are of questionable validity. (1) That the species is identical with forms which undergo transverse fission, a concept introduced by Gardiner (1902). Of this, more will be said, and it is hoped, a conclusive demonstration of the differences between these two groups provided. (2) A dual nomenclature of *F. rubrum* and *rugulosum* initiated perhaps through Suter (1906) but brought into prominence by Powell (1947) which suggests that *F. rubrum* is a shallow-water species (subspecies, var., facies) and *F. campanulatum* is the deeper-water species (subspecies, var., facies). The concept was continued by Squires (1958) and was hopefully, but incorrectly, extended to include *F. latum* as a still deeper species (subspecies, var., facies) for the system.

NOTES ON THE TYPE SPECIMENS

There are in the Laboratoire de Malacologie, Muséum National d'histoire Naturelle, Paris, two specimens bearing the notice "*F. rubrum* (Quoy and Gaimard), Nouvelle Zealande. Expedition d'Urville, 1829". For over 30 years these were the sole representatives of the species known to science, and for nearly 125 years the only specimens of the species accurately identified and illustrated. To a certain extent, the somewhat misleading aspect of the original drawings may have led to some confusion in interpretation of the species.

Photographs of the type specimens furnished by Dr G. Ranson are reproduced in this paper as pl. 1, fig. 1–4. The specimen selected as lectoholotype (fig. 5 and 6 of Quoy and Gaimard, pl. 1, fig. 1, 2, 5, 6 of this paper) is incorrectly represented in the original drawings as having two strongly rugose talons. Actually, the base is broadly expanded, asymmetrically, in a fashion described below. This type of attachment involves the deposition of sheets of epithecal material more or less vertically disposed. Seldom are these talons rugose, never to the extent figured. The other specimen (fig. 8, 9 of Quoy and Gaimard, pl. 1, fig. 3, 4, 8, 9, of this study) is illustrated in the photograph from the side opposite that represented in the drawing. The expanded nature of the base is more clearly represented as are the vertically arranged talons of epithecal material. This specimen is firmly attached to a shell, identified by Quoy and Gaimard (1833) as *Venus*.

Measurements of the two specimens as determined by Dr Ranson are given in the following table.

Measurements (in millimetres) of the cotypes of *F. rubrum* as determined by Ranson (in Litt., 13 May 1961).

	Lectoholotype	*Paratype*
Height of Corallum ..	17	18
Maximum diameter of Calice	28	21
Minimum diameter of Calice	11	10

It is interesting to note that although Quoy and Gaimard (1833) speak of a single specimen, "... il étaitseul adhérent à une Valve de Vénus ..." two specimens are illustrated. Dr Ranson has noted the attachment of one specimen to a shell and says of the other, "... L'autre était fixe sur un support mais ne l'est plus, il en a est detache." (in Litt., 13 May 1961).

MORPHOLOGY OF THE CORALLUM

Corallum cuneiform, arising from a narrow pedicel, and having evenly rounded narrow ends lacking aliform appendages or spines. Sides of corallum gently undulating, formed by a fine epitheca showing numerous, finely spaced growth lines. The calice is elliptical in section with axial ratio of about 1·5 : 1·0. The upper margin of the calice is nearly in a plane, the lateral portions (the ends of the major axis of the calice) are slightly lower than the central calice (the shorter axis). The fossa is deep, the proximal edges of the septa nearly vertical. The fossa is floored by thickened ends of the septa and trabecular offshoots of the septa which form a dense columella. Septa are non-exsert, and are not notched adjacent to the wall. Proximal edges of the septa, particularly of the first two cycles of septa, are usually thickened and almost rope-like. Minor cycle septa are thin, those of the last cycle are frequently wavy on the proximal edge. Laterally, the septa are spinose, the spines being approximately a millimetre in length, and bear ridges parallel to the proximal edge. Lower cycle septa are thin and often wavy, the spines on the proximal edge being alternate in position and corresponding to the undulations of the edge of the septa.

Coralla found in shallow or turbulent waters are more cylindrical in form, the basal or pedicel region having several concentric rings of epitheca extending from the corallum to the substrate. These projections of the epitheca may be hollow and root-like or may be concentric.

Variation in Form

Lateral ornamentation of the septa is quite variable but appears to be correlated with the thickness of the septa. This latter feature has not yet been associated with any single environmental factor but seems to be characteristic of certain populations and with size as in the larger members of any given population. In this respect, thickening and subsequent coarsening of septal ornamentation may be a reflection of decelerated upward growth. When septa are thin, the spines are relatively long. A fossil population from the Castlecliffian of Te Piki, East Cape (Wanganuian, Pleistocene), is particularly notable for the light construction of the coralla.

Similarly, the development of ridges parallel to the proximal and upper edge of the septa may be more pronounced in some specimens than in others. A suite of specimens from Gannet Island, off the eastern end of Waiheke Island, Hauraki

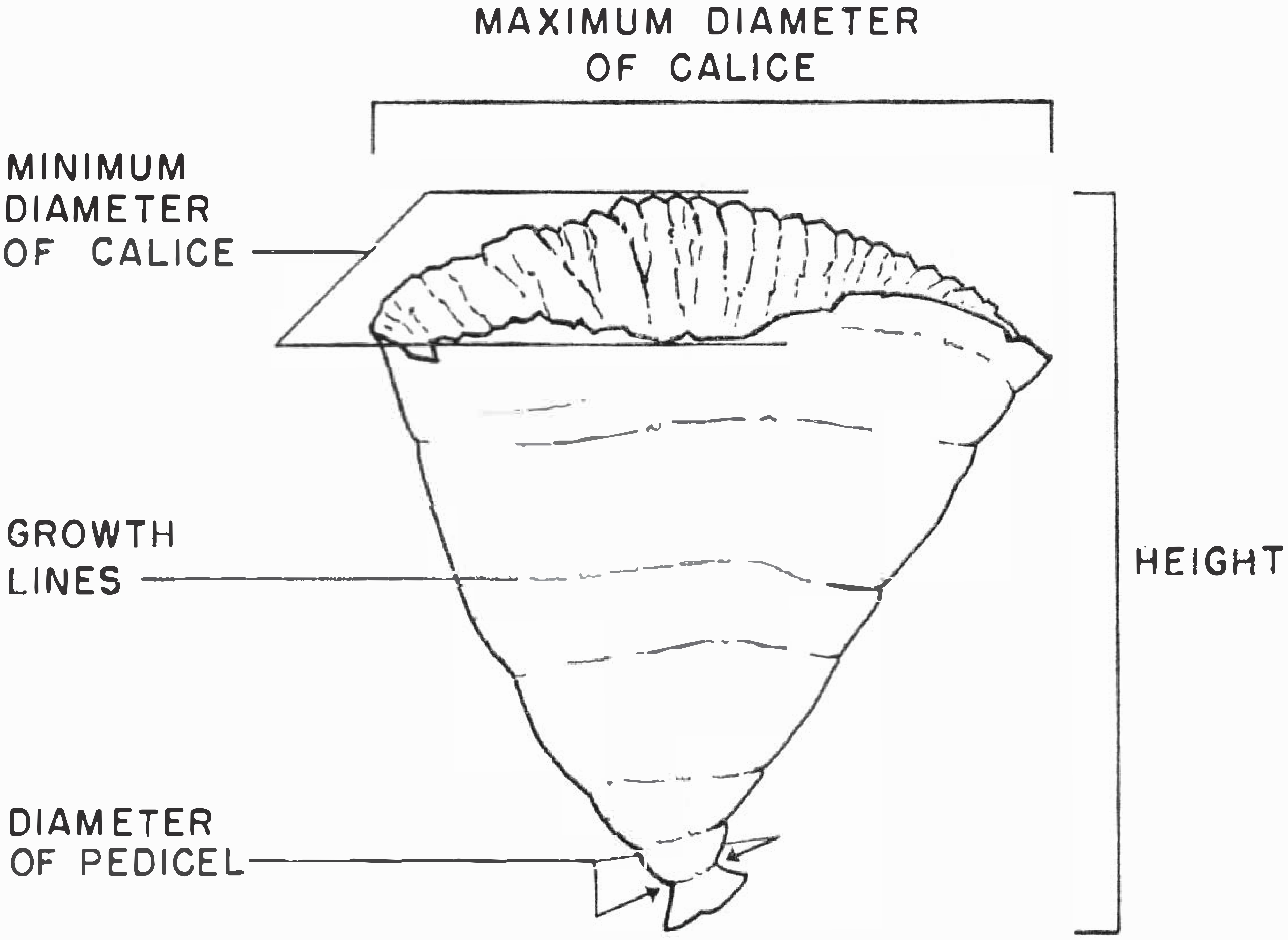

Fig. 1. Schematic drawing of *F. rubrum* (Quoy and Gaimard) showing some of the measurements used in this study.

Gulf, from a depth of 12–15 fm (Auckland Museum), has pronounced parallel "ridges" formed of very closely spaced, delicate septal granules which completely dominate the aspect of the lateral face of the septa.

A number of specimens from 2 miles south of the North Cape, North Island, from a depth of 55 fm (Dominion Museum) differ from the more typical form in that the basal attachments are broad and in many instances have well developed talons of epithecal material. The entire growth of the coralla of this population suggests that some factor in the local ecology was responsible for distortion of growth characters, perhaps a soft substrate or spatial competition. A single specimen from the Hen and Chicken Islands, 26–30 fm (Auckland Museum), also shows strong talon development.

Pathology of the coral may induce any number of abnormalities. One of the more interesting developments was observed in a corallum in the collections of the Dominion Museum taken in Cook Strait, which showed damage to the calice, with subsequent regrowth of the corallum, but with the polyp divided into two parts. There is no evidence of subsequent settlement of secondary larvae. Umbgrove (1950, pl. 81, fig. 3, 4) illustrates a similar phenomenon for *F. stokesii* [*sic*].

Perhaps the most significant variation in the form of the corallum is that displayed in the basal region. A generalisation to the effect that specimens taken in shallow water are cylindrical, while those from deep waters are pedicellate-cuneiform is substantially correct, but not invariable. Squires (1958a, pl. 12, fig. 2) (pl. 2, fig. 12 of this paper) illustrated specimens from an unknown depth, but not "shallow", which were nearly cylindrical. It is the hypothesis of this study that the diameter of the base of the coral is strongly affected, *in this species*, by the character of the substrate. On an unstable substrate, or in areas of turbulent water, additional strength of attachment is obtained by the coral through the secretion of additional skeletal material. The mechanism of this secretion will be developed in detail in a later section.

Variation in lateral angle has been investigated from several aspects. Both Dr P. Ralph (Victoria University) and I have independently investigated the possible correlation between the angle formed by the lateral edge of the corallum and the depth of occurrence (Ralph and Squires, 1962). In neither study could a definite correlation be attributed to the variation with respect to environmental factors.

As increase in the angle formed by the lateral edges reflects increased length (and breadth) of the oral surface of the coral, it might be presumed that such an increase would enhance the food gathering propensities of the polyp. Increase in length of the calice is also directly correlated with increase in numbers of septa, mesenteries, and tentacles, as well as enlargement of the oral surface. It is not known which of the two major feeding methods employed by corals (capture of food by tentacles or ingestion of small particles entrapped in mucous on the polyp surface) predominates in *F. rubrum*, but both would become more efficient as a result of these changes resulting from greater calice length. Enlargement of the oral surface of the polyp would favour mucous feeding although the effectiveness of the increase is not easily ascertained for most corals expand greatly out of the calice, the volume of the expanded polyp being several times that of the corallite. An increase in the number of tentacles would surely favor food capture by these structures. As a result, one might postulate that increase in lateral angle would be a positive selective factor in deeper, less turbulent waters, and in areas of negligible bottom currents. The absence of a positive correlation between lateral angle and environment may well reflect the inadequacy of the samples available for study to represent these variables.

If one accepts the concept of a gradational increase in the angle formed by the lateral edges of the corallum as a response to increasing depth of occurrence, one must consider the placement of *F. latum* Studer, the type of which has an angle formed by the lateral edges of 112° and yet was taken in only 45 fm. Specimens from 60 fm in Hauraki Gulf have an angle of about 45° rather consistently, and Gardiner's specimens from 300 fm have an angle of 45°. As the hypothesis is unsound, a more profitable line of preliminary investigation would be to ascertain the variation in angle within various populations as compared to interpopulation variation in the same parameter. From general observation, it would appear that interpopulation variation is great, intrapopulation variation small.

To be considered also is the effect of the environment upon individual specimens. As an example, the specimen figured by Squires (1958a, pl. 14, fig. 1, 2) was taken in 25 fm of water, but is distorted through growth. It is apparent that the initial corallum was developed upon a vertical surface and that the distortion of the corallum results from differential growth as the polyp attempted to attain a vertical orientation. The concavity of the face shown in pl. 2, fig. 1 and corresponding convexity of the other face (pl. 2 fig. 2) is a primary result. Lengthening of the maximum diameter of the calice to abnormal proportions and curvature of this axis are other normal responses to this type of stress, which has been observed in other *Flabellum*.

DEVELOPMENT OF THE CORALLUM

The youngest stage of corallum development found in the N.Z.O.I. Sta. A 489 collection* consists of six low protosepta which appear as low ridges on the substrate, in this instance a valve of *Chlamys gemmulata*. The basal plate is present only as an extremely thin deposit of calcium carbonate, largely concentrated in the region to be occupied by the protocolumella. From this central area, more or less bounded by a circle, the perimeter of which is defined by the inner or proximal edges of the protosepta, the basal plate thins laterally. Apparently it does not extend to the distal ends of the septa in the earliest stages, appearing to feather out two-thirds of the distance to the distal ends of the protosepta. The basal plate subsequently thickens until it extends to the ends of the protosepta; its growth direction is then reflexed upward as the wall, the epitheca. In all specimens observed at this stage, the basal plate appears to be of a granular material with no conspicuous structure.

With the development of an appreciable thickness of basal disc, and at a stage when the wall has a vertical height of about one millimetre, spines may be seen along the surface of the basal disc. At first, these seem to be related in position to prominences of the substrate; thus, on *C. gemmulata*, an elongate fan of spines, usually simple, will grow above the area where the growth lamellae cross the radial ribs. Spines are also found concentrated in two other areas, these becoming the predominant areas later in the development of the corallum when the irregularities of the substrate have been smoothed by continued deposition of stereome on the basal disc: (1) The interseptal loculi; and (2) the site of the columellar ring (See Durham, 1949, for a discussion of this structure). Spines

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*Unless otherwise noted, all references are to specimens from N.Z.O.I. Sta. A 489.

in the interseptal loculi are more prominent along the site of the developing second cycle septa which have not as yet taken form, than elsewhere on the basal disc. There is considerable variability, some specimens, however, having rows of radial spines in a position approximating that of the third cycle septa. Other specimens may have spines in the interseptal loculi which are without apparent orientation or relationship to subsequent structures. In general, these spines are usually simple, although they may be fused at their base in a blade-like form.

From the time of deposition of the first epitheca, until the corallum has a height of between one and two millimetres, the diameter of the calice is steadily reduced, until it is about 70 per cent that of the original protosepta. From this stage, the polyp and corallum begin to increase in diameter again, but still retain their cylindrical form. The period of contraction of diameter may represent that time during which the polyp is not feeding, but utilising stored food.

When the corallum is between one and two millimetres in height, rudimentary second-cycle septa can be seen on the walls of the corallum. These first appear as spines in most instances and may be found in various unequal stages of development in the loculi between first-cycle septa. It is not uncommon to find septa of the third cycle in approximately the same stage of development as those of the second, in coralla of this size, but later development of third-cycle septa is most generally retarded as corallum growth proceeds. A common development in loculi at this stage of growth is the appearance on the wall of horizontal lappets of considerable size which are directed in a gentle downward fashion towards the centre of the calice. The proximal edges of the lappets are usually spinose. The radial length of a lappet is generally about one-half of its width (as measured tangent to the circumference of the corallum). It is apparently composed of compound spinules developed from the internal stereome.

When the corallum is two millimetres high, first-cycle septa are well developed, and show some thickening on the proximal edge. Second-cycle septa then are low, about one-third to one-half the length of those of the first cycle, while third-cycle septa are present as low striae on the wall. Widely spaced erect spines appear on the walls, in the loculi between septa. The axial area of the corallum at this stage is extremely variable, ranging from the development of a strong columellar ring to complete absence of structures. In forms with an open fossa, the primary septum of the first cycle is joined by other septa to form a tangled mass. In still others, a pronounced columellar ring is developed. All septa and the columellar structures are laterally spinose.

As introduction of the third cycle of septa is completed, a sharply defined change occurs in the development of the corallum. Cylindrical growth ceases, one axis becoming established as the major, and expanding at a faster rate than the other. The relationship between this axis and the directive mesenteries is not known. On the exterior of the corallum this change is marked by the division of the broad epithecal bands corresponding to the first two cycles of septa. It is probable that the change in growth habit is gradual, but it becomes apparent rather consistently at this stage.

Increase in height beyond this stage results in increase in the greater diameter of the calice. This relationship between height and the major diameter appears to be more or less an isometric function after the first few millimetres of height and has a calculated growth index of 1·0755,* that is, the ratio of maximum diameter of the calice to height of the corallum is, on the average, 0·929, and is apparently a constant at this figure throughout the life of the coral (fig. 2). On the other hand, the relationship between the diameters of the calice measured along the two principal axes is allometric, the ratio changing as the corallum increases in height. Fig. 3 is a scattergram showing this allometry.

As the corallum grows upward, thickness of the basal disc increases through deposition of stereome. With the development of the columella, the axial space, or fossa, is filled more and more completely until, in mature *F. rubrum*, approximately the lower third of the corallum is more or less solid calcium carbonate. The infilling of the interseptal loculi seems to be a result both of deposition of stereome on the basal plate and of addition of stereome to the sides of the septa. The columellar structures are also plastered with a thick layer of stereome, but some vacuities remain. The polyp seals off the lower portion of the corallum as upward growth proceeds, but infilling of cavities in the lower portion takes place at a slower rate than upward growth. This is presumably a reflection of the lesser ability of the basal portion of the polyp to secrete carbonate in comparison with cells adjacent to the oral disc. Similarly, the columella is situated, relatively, progressively deeper in the calice as the margins of the corallum grow upward at a faster rate.

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*All statistical data are based upon measurements of specimens from N.Z.O.I. Sta. A 489 unless otherwise noted.

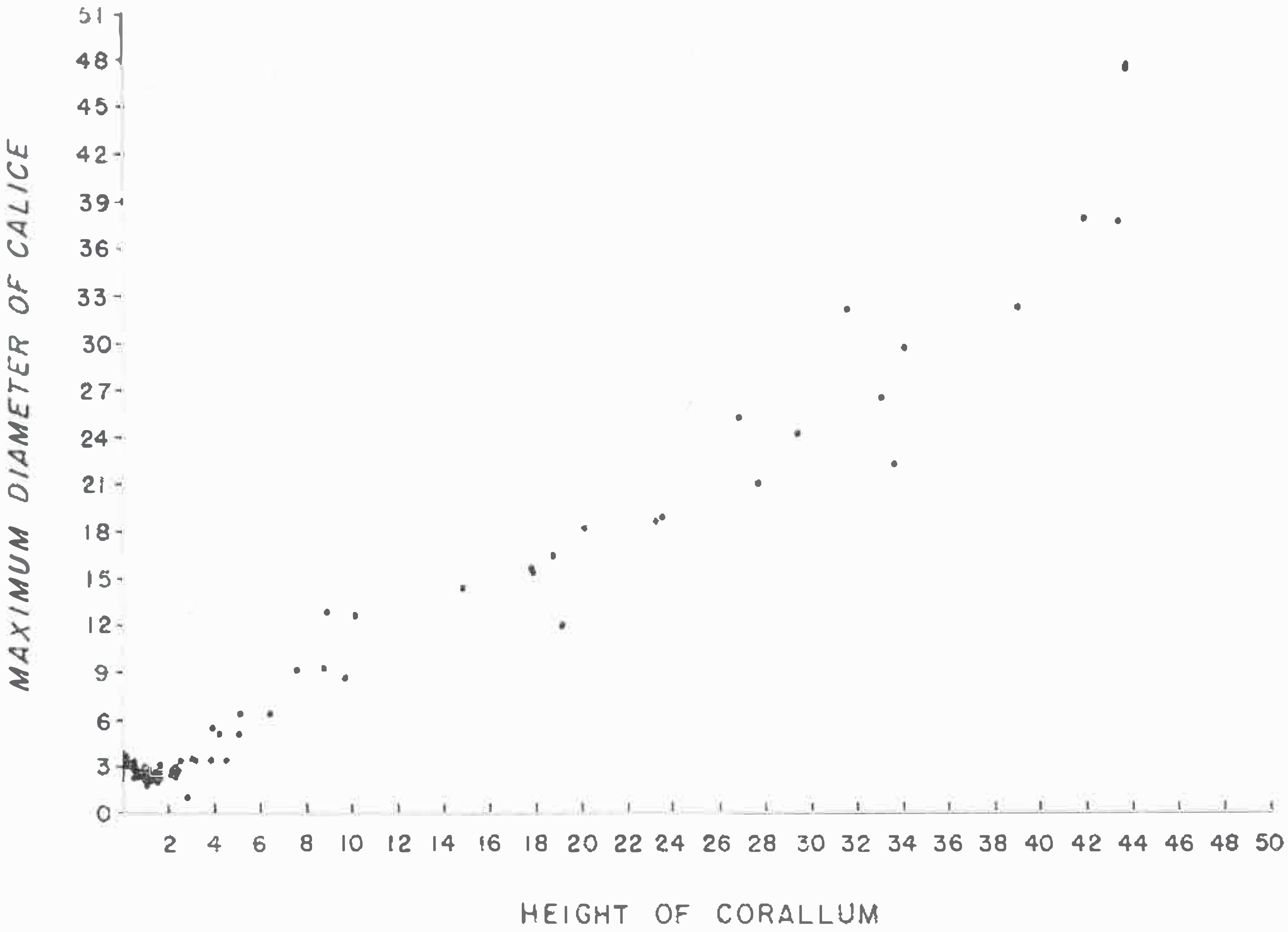

Fig. 2. Scattergram showing the relationship between height of corallum and maximum diameter of the calice in *F. rubrum* as represented in N.Z.O.I. Sta. A 489. The points are grouped about a straight line after the initial cluster, suggesting that there is no allometry in this relationship.

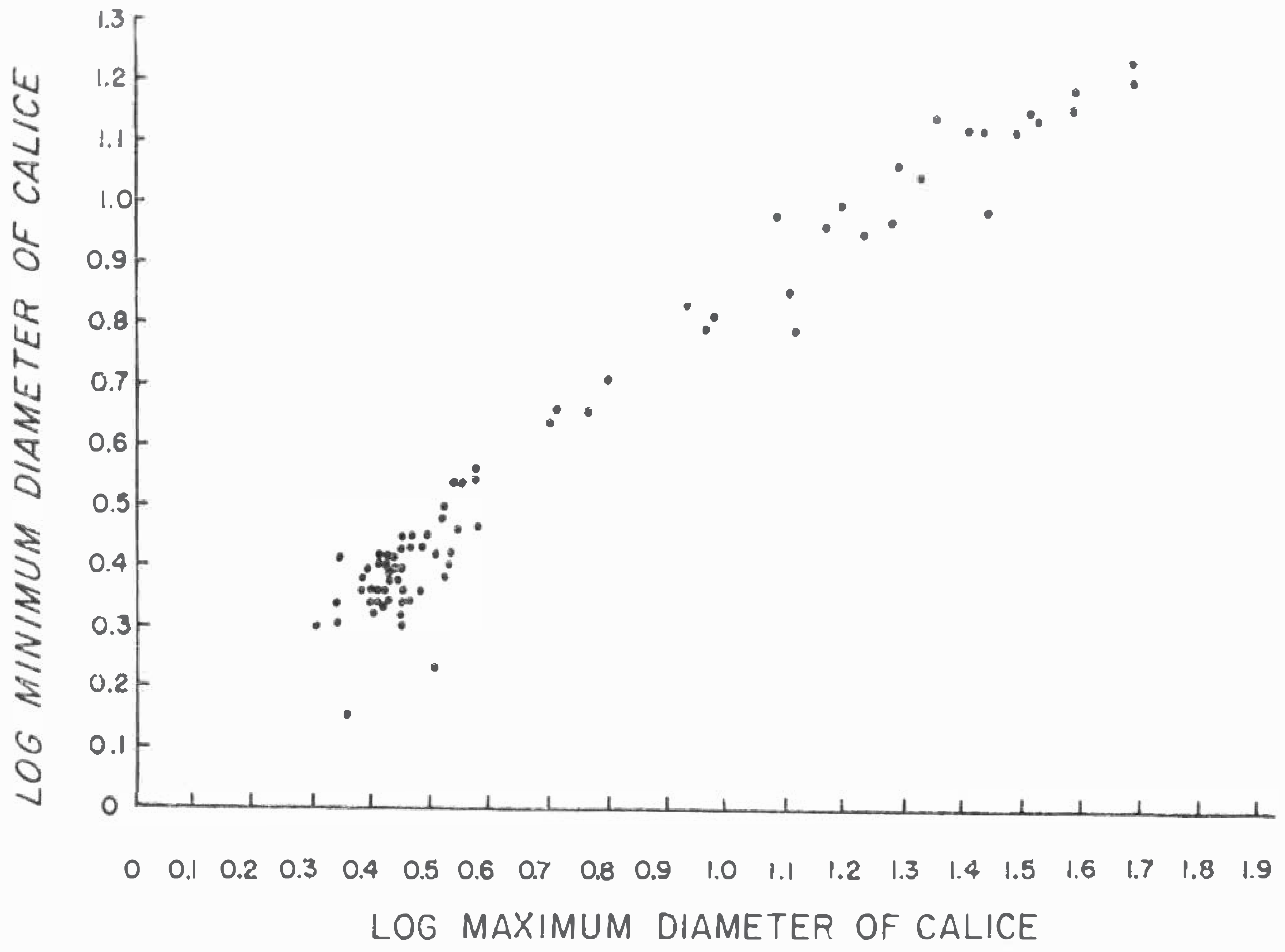

Fig. 3. Scattergram showing the allometric relationship between the longer and shorter axes of the calice of *F. rubrum*. The plot is of the logarithms of the measurements so that the points are grouped about a straight line. Measurements of specimens from N.Z.O.I. Sta. A 489 are the basis for the graph.

The relationship between number of septa and maximum diameter of the calice is illustrated in fig. 4. As shown, this function is allometric, the number of septa increasing more slowly than the diameter of the calice. Although not directly expressed, what is indicated by this allometry is the increasing width of the interseptal loculi with age (as indirectly measured by the height of the corallum). This decreasing width of interseptal loculi is not apparent visually and is probably compensated for by an increase in the thickness of the septa. The high correlation (r) of 0·982 between maximum diameter of the calice and the number of septa and the tight clustering of plotted points for these parameters indicates that this character may be of some significance in specific determinations. The variation in measurements from youngest to oldest stages is slight, and variation in width of loculi within individual coralla is usually greater than that found between young and old coralla. Because of this, a more sophisticated means of analysis is required than simple averages based upon a few measurements for valid utilisation of this character in specific differentiation.

MORPHOLOGY OF THE POLYP

Of the three polyps taken alive in N.Z.O.I. Sta. A 489, and preserved for study, two polyps were decalcified for dissection, the third polyp left in the corallum. Only gross anatomy was considered as more detailed studies require more suitable material and larger numbers of specimens.

The expanded polyp is quite different from the contracted and preserved specimen in appearance as has been noted for most anthozoans. Observations on the expanded polyps were made on shipboard where specimens were kept alive for several hours despite the primitive temporary arrangements utilised for their maintenance. The polyps were apparently not fully expanded, although the tentacles were long and in motion. Exposure to light had little immediate effect upon

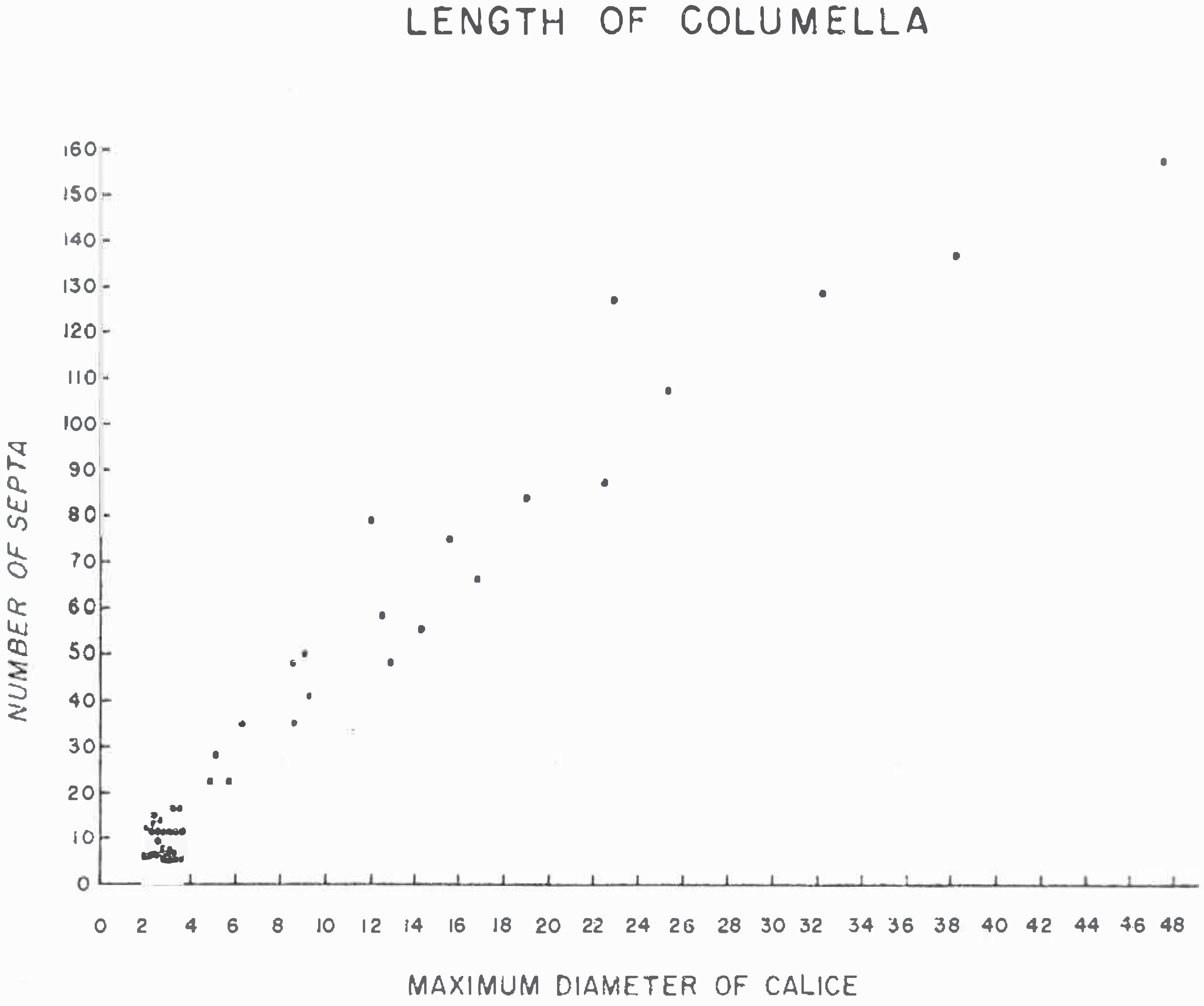

Fig. 4. Scattergram showing the allometric relationship between number of septa and maximum diameter of the calice of *F. rubrum*. Measurements are of specimens from N.Z.O.I. Sta. A 489. As illustrated by this plot, as the diameter of the calice increases, the number of septa increases, but not as rapidly as the diameter.

the polyps, although continued exposure induced slow contraction. Death of the polyps was preceded only by slow contraction of the tentacles and gradual relaxation and enlargement of the mouth.

In life, the polyps observed were variously a dull orange, a salmon, and a light yellow in colour; the lesser colour intensities were associated with the larger specimens. Tentacles of all three specimens were a translucent pale yellow having some yellow-green hues near the base. All tentacles bear white, knobbed, nematocyst batteries, some having large terminal batteries. The mouths, which were strongly ridged, were yellow, but in varying shades.

In the partially expanded condition, the tentacles are long, up to three centimeters in length, the shorter ones being equal to about the minimum diameter of the calice in their length. The bases of the tentacles were quite broad and formed two broadly defined circlets about the mouth. The mouth itself is long and slit-like, in the expanded condition it was about two-thirds the length of the long diameter of the calice.

An examination of the preserved specimens shows the tentacles arranged in a double circlet about the mouth (pl. 2, fig. 7). The inner circlet is formed by large, stout tentacles which are situated over the larger septa constituting the first septal group and partially embraces the outer circlet. The outer circlet of tentacles is situated over the second and third groups of septa. Tentacles corresponding to the last cycle of septa are present, suggesting that all septa are entocoelic.

All tentacles are knobbed with nematocyst batteries. In general, the distal end of the tentacles is a large, smoothly rounded tip, somewhat larger in diameter than the adjacent lower portions. In the contracted state, the tentacles are roughly conical, but when expanded, the mid-portion is narrowest with the diameter at the base always larger than that at the terminal end.

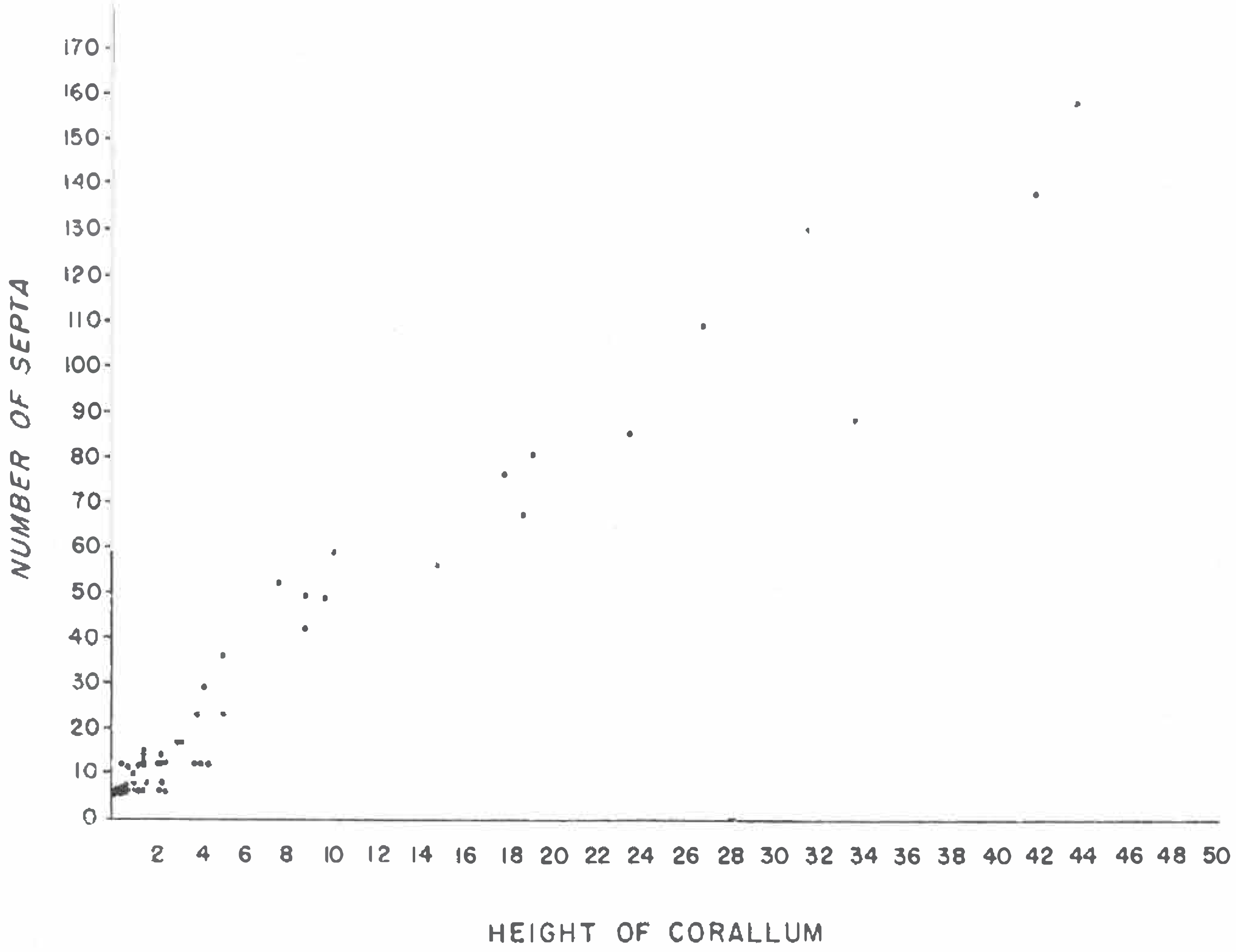

Fig. 5. Scattergram showing the relationship between number of septa and height of the corallum of *F. rubrum*. Measurements are of specimens taken in N.Z.O.I. Sta. A 489. The slight curvature of the trend of the points indicates that some allometry may be present in the relationship. Septa are not added as rapidly in later growth as in younger stages. See also fig. 4.

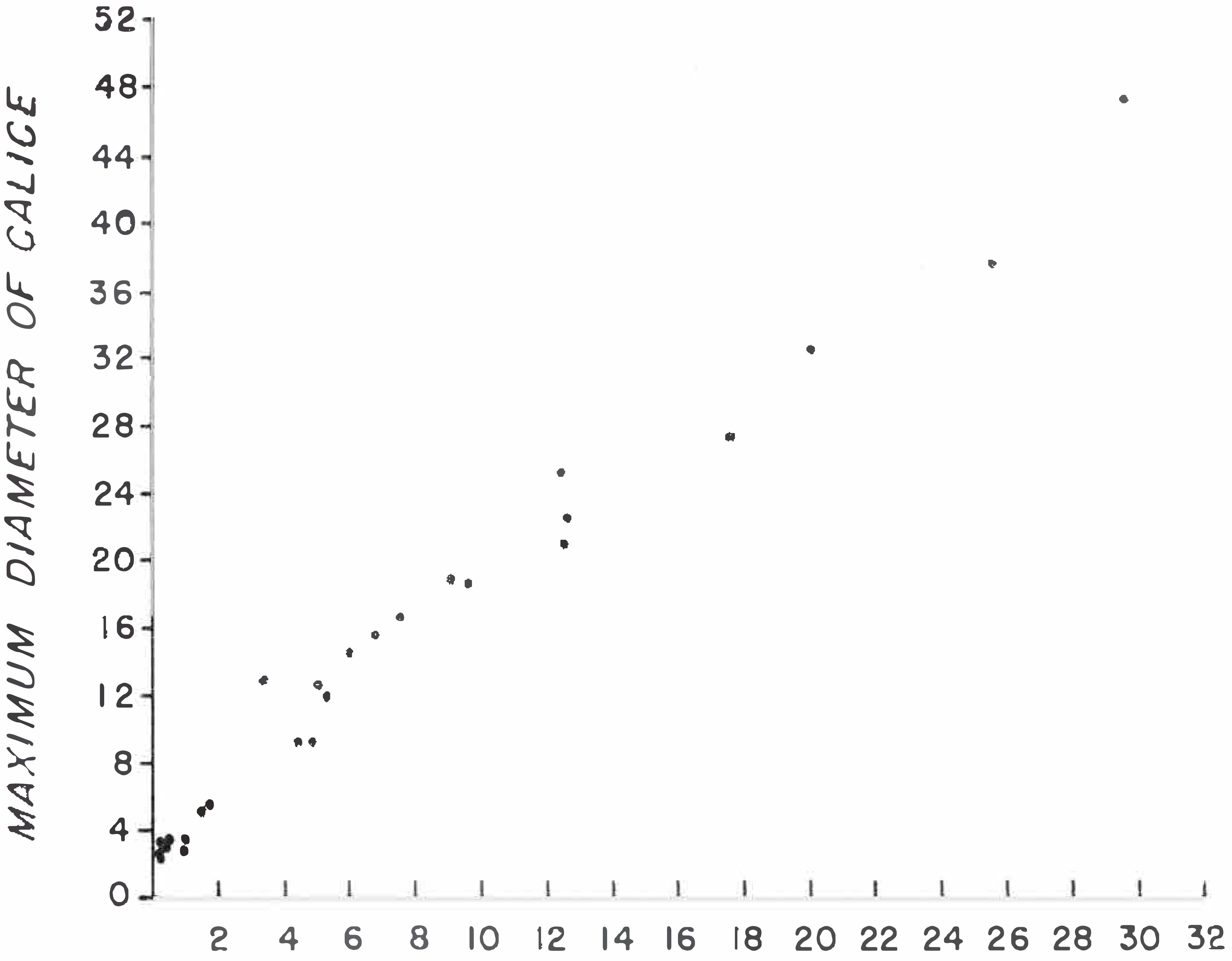

Fig. 6. Scattergram showing the relationship between the maximum diameter of the calice and the length of the columella of *F. rubrum*. Measurements are of specimens from N.Z.O.I. Sta. A 489. Although depth of the columella increases with upward growth (see text), the length of the columella remains proportionately the same as the calice becomes longer.

The ridged stomadeum is up to two-thirds of the longest diameter of the calice in length. It is not known to what extent this measurement reflects unusual contraction of the oral disc, for there was continual and gradual lengthening of the mouth during the time the live corals were under observation and presumably dying. None of the mesenteries of the polyps examined bore conspicuous gonads, although one poorly developed testis was observed, but its nature not confirmed by histological sections.

In comparing these observations with those of other authors, the most conspicuous discrepancy is that concerning colour. As noted above, Powell (1947) gives the colour of the polyp of *F. rugulosum* [*sic*] from Hauraki Gulf as scarlet, and that of *F. rubrum* [*sic*] as salmon to dull vermillion. Suter (1906) gives the colour of the animal (as reported to him) as being banded scarlet and white. Dr A. W. B. Powell (in Litt., Jan. 17, 1961) states that the ". . . littoral *Flabellum* is solid coloured salmon-pink to orange and that of the deep-water (25–30 fathoms) form is striped alternately (radially) bright pink and white in approximately ¼ inch stripes." The importance of these colour records is discussed again with regard to the systematic conclusions.

The observation made here that in *F. rubrum* tentacles are present over all septa is contrary to that made by Gardiner who says (1904, p. 133) with regard to *F. rubrum* [*sic*, = *F. stokesii*], "The tentacles arise over the entocoelic septa alone, and are accordingly half as numerous as the whole body of septa." That all septa of *F. rubrum* are entocoelic has not been verified by sectioning, but it is assumed that the condition exists in the specimens examined because tentacles were borne above each septum. Gardiner (1904) noted the presence of a complete complement of tentacles over septa in *F. pavoninum* and concluded that they were all entocoelic.

Knowledge of the anatomy of the polyps of many corals, particularly the deeper water species is poor. As a result, one cannot state the distribution of the character noted above. If it is true of all species of the *F. rubrum* type, the significance would be considerable, and could in addition to other biological factors, be taken as a basis for the separation of the species group into another genus.

THE SYSTEMATIC ARGUMENT

As stated in the introduction, one of the primary purposes of this study is to establish the identity of *F. rubrum* (Quoy and Gaimard) with respect to two common mis-usages of the name in past literature; to differentiate *F. rubrum* from the species which apparently undergo transverse fission, commonly referred by authors to the group of *F. stokesii*, and from the two depth "facies" of *Flabellum* often recognised in New Zealand. A table of comparisons has been prepared (table 1) which shows relationships in several pertinent characters between the various taxa under consideration. In the following discussion, the taxa are referred to as in the headings of the table.

TABLE 1: COMPARISON OF POPULATIONS ASSIGNED TO THE SPECIES *F. rubrum* (Q. AND G.)

	F. rubrum (Type)	*F. rubrum* (Littoral)	*F. rugulosum* (Auct.)	*F. rubrum* (A 489)	*F. rubrum* (Gardiner)	*F. Stokesii* (M.E. and H.)
Size of Corallum ..	Small	Small	Large	Large	Small	Medium
Shape of Corallum ..	Cuneiform	Subcylindrical	Cuneiform	Cuneiform	Cuneiform	Cuneiform
Ratio of Axes of Calice ..	2·5 : 1·0	1·0 : 1·3	?	1·5 : 1·0	2·0 : 1·0	?
Base	Attached	Attached	Attached	Attached	Attached	Attached
Ephebic Attachment ..	Attached	Attached	Attached	Attached	Free	Free
Presence of "wings, or spines"	Absent	Absent	Absent	Absent	Present	Present
Basal Rootlets	Present	Present	Present	Present	Absent	Absent
Basal Stereome	?	Present	Present	Present	Absent	Absent
Colour of Polyp ..	Yellow with red bands	Salmon to dull vermillion	Red and white radial stripes	Pale yellow, dull orange	Red and white striped	Red and white striped
Tentacles	?	?	?	Entocoelic	Entocoelic	?
Septa	?	?	?	Entocoelic	Ento- and Exocoelic	?
Distribution	Cook Strait	New Zealand	New Zealand	Cook Strait	South Africa	Philippines

Morphology of the Corallum

In general, *F. rugulosum* (Auct.) is the largest of the corals observed. The type of *F. rubrum* is a small individual (cf. pl. 1, fig. 5) being about half the size of the largest of the specimens described by Gardiner (1904) and only slightly larger than one-third the height of the largest specimen taken at Sta. A 489. *F. rubrum* (littoral) is the only group lacking the strongly compressed corallum and elliptical calice; all specimens of this *Flabellum* known to me are only slightly compressed. Axial ratio, that is, the relationship between the larger and small diameter of the calice is variable and measurements of single specimens are not significant.

Great differences are to be found among the characters of the base of the corallum. In *F. rubrum* (littoral), *F. rubrum* (A 489) and the type specimen, wings, aliform "appendages", or supplementary hollow rootlets are absent. These structures, usually interpreted as supports for the coral to keep it in an upright position, are common occurrences in the *F. stokesii* group (cf. Gardiner, 1904, and Semper, 1872). Supplementary epithecal material may be deposited on and near the pedicel in an apparent strengthening of the basal attachment of *F. rubrum*, or, as a result of the stimulation of overturning of the corallum. As illustrated by Quoy and Gaimard (1833, pl. 14, figs. 3, 3e), (pl. 1, fig. 1, 5, of this paper), additional epithecal material may be present on the side of the corallum and one figure (fig. 3), shows what might be interpreted as a double pedicel. *F. rubrum* (littoral), *F. rubrum* (A 489) and *F. rugulosum* (Auct.), have thick deposits of stereome in the basal portions of the corallum. It would seem that deposits such as these are absent in the bases of the *F. stokesii* group coralla, and that the interseptal loculi remain open, even after separation of the upper portion of the corallum from the lower (Gardiner, 1904, p. 148, footnote). The basal portion of the upper segment of *F. stokesii* is sealed with stereome, but the time of the deposition of this material is not known, and it may occur after separation.

Morphology of the Polyp

Among the most conspicuous differences between the three groups are the discrepancy in colours. Two general colour types have been described: Striped with white or yellow and red or scarlet alternating bands; and, solid orange, yellow, salmon, or vermillion polyps. Bourne (1905) and Semper (1872) were prone to place considerable significance upon constancy and similarity in colour pattern. Evidence from collections in New Zealand is contradictory. Until more is known of the distribution of colour patterns of *F. rugulosum* (Auct.), there is not much point in pursuing the argument. The possibility of change of colour according to sexual stage or local ecology is still present and must be solved.

Also to be considered are the differences in tentacular and septal arrangement. In *F. rubrum* (Gardiner) the tentacles are half the number of the septa. For *F. rubrum* (A 489) the number of tentacles and septa are equal. Further, it has been shown that *F. rubrum* (A 489) probably has only entocoelic septa, while in *F. rubrum* (Gardiner), the last group of septa inserted are exocoelic.

Perhaps the most important argument pertinent to the discussion is the nature of transverse fission. It is difficult to utilise this argument effectively, for too little is known about transverse fission and its significance. The only instance of fission which has been observed was that reported by Semper (1872) who saw it only in a specimen in the process of maceration. It is undeniable, however, that the majority of specimens in his and Gardiner's populations exist without a normal base. Whether the phenomena of transverse fission represents a mode of asexual reproduction, or whether it is a complex mechanism involving a change from a fixed to a free life, is not known. It is more or less invariable that the majority of specimens of the *F. stokesii* type will lack bases, while on the contrary, no specimen of *F. rubrum* has been seen which was severed from the base! The only conclusion which can be drawn is that there is a fundamental difference in the biology of the species.

Ecology

All of the species considered here, with the exception of *F. rubrum* (Gardiner), are similar, being attached throughout the life of the polyp. It is presumed that the specimens also remain upright throughout their life. *F. rubrum* (Gardiner) and all members of the flabellid corals which undergo transverse fission, must, because of their severance from the base, be free. None of the specimens belonging to this species group shows any indication of being attached. Spines, struts, and other prop-like structures are often present on the corallum before fission occurs, and presumably, therefore, have supportive value only before fission.

Distribution

F. rubrum (Gardiner) and *F. stokesii* (Auct.) is distributed in a band along the tropics extending from the Philippines to the Cape of Good Hope. North of this, the species distribution follows the warm current of the Kuro Sivo to the southern islands of Japan, and to the south, the warm, South Equatorial Current to the Great Barrier Reef. *F. rubrum* (s.s.) is, on the other hand, restricted in distribution to New Zealand. A single record of *F. latum* from the Indian Ocean is of questionable validity.

Paleontology

In sediments of Waitakian age (Middle Oligocene) through Altonian (lower Miocene) in New Zealand, occur a suite of six, as yet undescribed, species all assignable to the *F. rubrum* (Gardiner) species group (see Squires, 1958a, pl. 12, fig. 7, 6). All have the typically truncate base, and indeed, some are associated with small "stumps" which possibly are the bases of the coral before truncation. These species became extinct in New Zealand before *F. rubrum* appeared. The *F. stokesii* type seem to be typically associated with warm water faunas in the New Zealand fossil record, while *F. rubrum* (s.s.) is associated with colder waters and the invasion of New Zealand by southern faunas. It is not likely that *F. rubrum* (s.s.) is derived from a lineage of *F. stokesii*, for there is a considerable gap in time represented, as well as rather different faunal associations and temperatures as indicated by the faunas.

Conclusions

On the basis of the evidence cited above, it is my contention that *F. rubrum* is a distinct entity from the species which undergo transverse fission commonly referred to as *F. rubrum*, but more properly belonging to the *F.* "*stokesii*" species group. The weight of biological evidence is such that it is probable that separation into distinct genera would be justified. Until more is known of the circumstances of the transverse fission, its possible nature as a reproductive mechanism, and its general biology, such a step should not be taken.

ECOLOGY

From an examination of the occurrence of *F. rubrum* in New Zealand waters, it becomes apparent that temperature is not the only primary factor in affecting the distribution of the species. When associations of other benthos and *Flabellum* are considered, one generalised community, largely controlled by substrate in its spatial occurrence, is suggested. Although there are many blank areas in the distribution records, such evidence as is available indicates that the coral occurs in all three of the New Zealand faunal subprovinces, that is the Aupourian, Cookian, and Forsterian, and within these subprovinces exists through a wide range of temperature and salinity conditions (see fig. 7).

SUBSTRATE AND FAUNAL ASSOCIATIONS

Since Powell's (1937a) pioneer studies on benthic marine communities in Auckland and Manukau Harbours, several analogous communities have been found over a wide range of New Zealand shores. Powell (1937a) originally defined the *Tawera* + *Glycymeris* formation, one subdivision of which is the *Flabellum* + *Notocorbula* association. The *Tawera* + *Glycymeris* formation is characteristic of the outer harbour of Auckland, particularly in main channels and around the shores of islands in exposed areas. The most striking characteristic of the formation is its location on hard substrates which contain a low percentage of silt and sand and frequently are composed of shell debris. It is therefore not a primary immigrant association, but rather emerges as a replacement of a previous association on the *in situ* debris of that community or follows development of an accumulation of debris from a neighbouring community. Powell (1937a, p. 397) states that the substratum is composed mostly of worn bivalve shells and comminuted shell with finer grades of sediment (fine sand and silt) composing less than 2·81 per cent of the dry weight of the sample.

In the *Flabellum* + *Notocorbula* association, neither *Tawera* or *Glycymeris* (both characteristic genera of the formation according to Powells' definition) are found living, but their shells are the largest contributors to the accumulation of debris forming the substrate. An average of 19 species were identified from this association, the maximum number occurring at any one station being 31. The fauna is reduced in systematic diversity in comparison to other associations recognised by Powell, and as would be expected, is dominated by suspension and filter-feeding animals microfauna and infauna are almost entirely absent.

Fleming (1950) recognised *Flabellum* sp. from several stations in the fiords of western Southland in "Brachiopod – *Chlamys*" association. Although these specimens have not been seen,* it is more than probable that they represent *F. rubrum* for the species has been identified from other localities in the same fiord system†. The association of animals in these occurrences is dominated by the occurrence of large numbers of brachiopods, including *Neothyris*, *Liothyrella*, *Tegulorhynchia*, and *Terebratella*, as well as the bivalve *Chlamys radiata*. Associated were numbers of mollusca and the echinoid *Pseudochinus huttoni*. Again, the fauna was found where currents were strong and bypassing of sediment occurred. Bottom samples from these localities showed a coarse substrate formed of pebbles, dead molluscan shells, and lesser amounts of fine sediment.

Specimens from N.Z.O.I. Sta. A 489 were attached to pebbles and shells which at this locality compose a muddy shingle. Of the 95 specimens recorded, 66 were still attached to an object as listed on page 28.

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*Through the courtesy of Dr C. A. Fleming, I have recently been able to examine certain of the corals from the *New Golden Hind* expedition. *Flabellum* sp. from stations 2, 81, and 82 prove to be a species of *Caryophyllia*. The larger of the three specimens is rather abnormally developed and shows signs of having been injured, with resulting abnormalities in septal and palar arrangement. Specimens of "small branching coral" from stations 2, 49, and 82 prove to be small, distal fragments of the hydroid Stylasterine coral *Conopora*. As not all of the holdings of these stations are in one repository, it is possible that *Flabellum* sp. is present, but more question must be placed upon its presence.

†Dominion Museum collections contain four dead specimens of *F. rubrum* from Goal Passage, Doubtful Sound, coll. W. H. Dawbin, 8-5-50.

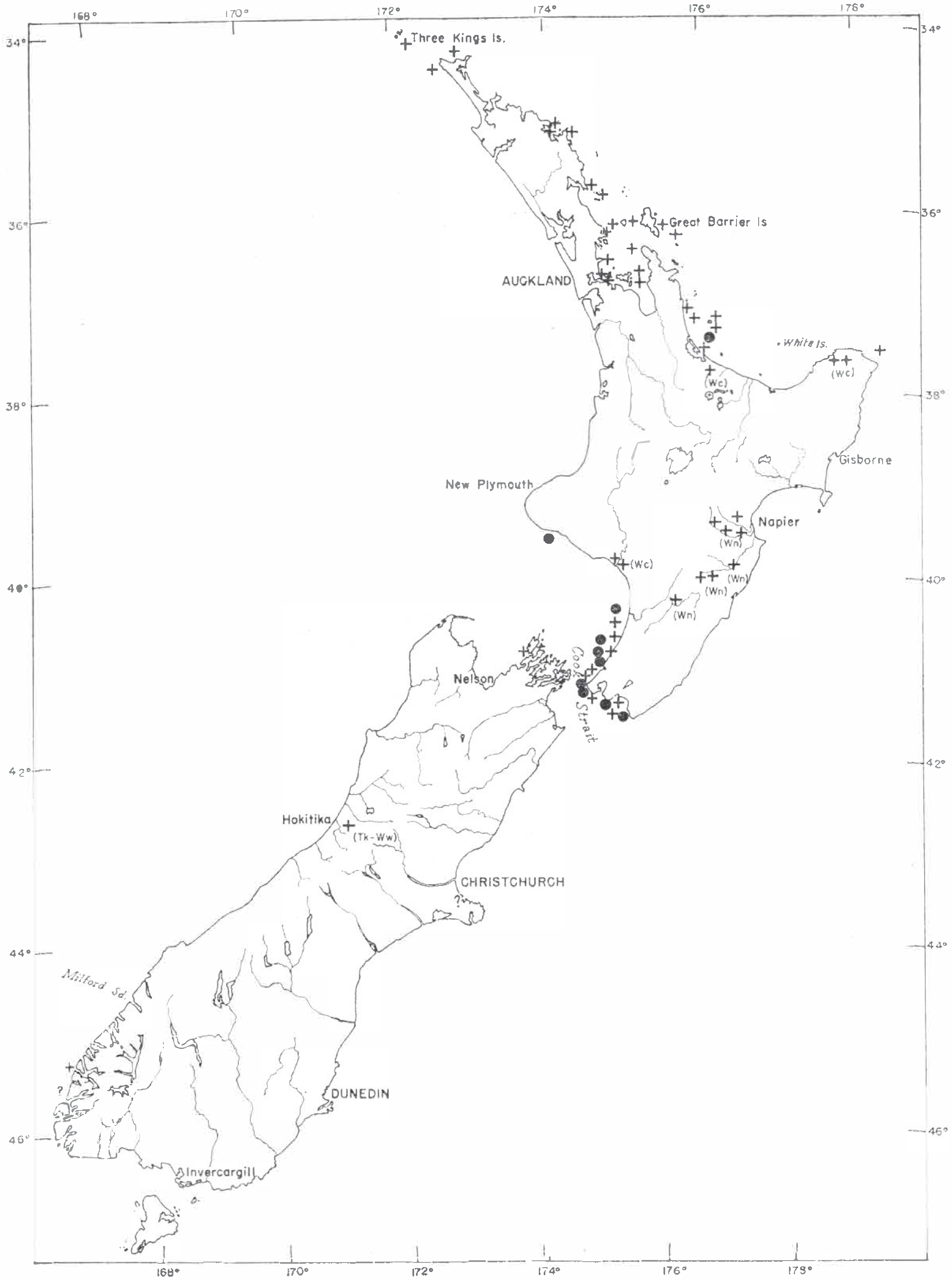

Fig. 7. Distribution of *F. rubrum* (Quoy and Gaimard). Crosses mark occurrences of living specimens. Open circles are records based upon dead specimens only. Crosses on land areas are records of fossil *F. rubrum*. Letters in parentheses beside these crosses are the abbreviations of the stratigraphic stage in the N.Z. Geological Survey system.

Number of Coralla	*Attached to*
27	*Flabellum rubrum* (Quoy and Gaimard)
16	Polyzoa (dead)
5	*Chlamys gemmulata* (Reeve)
5	*Barbatia novazelandiae* Smith
3	*Venericardia difficilis*
3	Pebbles
2	*Modiolus areolatus* Gould
2	Shell fragments (indet.)
1	*Mesopeplum convexum* (Quoy and Gaimard)
1	*Ostrea sinuata*
1	Brachiopod fragment

Because of the manner in which the sample was sorted, and because only larger corals were retained by me, there is a high bias in this record towards young coralla which had settled on larger coralla. Only a few shells and pebbles which obviously had smaller corals on them were kept with the large coralla. Other shells and pebbles undoubtedly had corals on them, but they were not apparent in the unwashed sample. However, this does not negate the general concept that larvae apparently are successful in development only when attached to a solid substrate at least a centimeter in diameter. There is no evidence in the collection that this attachment of the corallum ever is broken during the life of the coral, for those 29 coralla for which no attachment is recorded, were either broken off above the pedicel during collecting or were dead coralla which were very badly worn. The significance of the attachment of the corallum will be considered in greater detail below.

Although the community structure for the region N.Z.O.I. Sta. A 489 is not established, there are several aspects which strongly suggest that it is analogous to the *Tawera* + *Glycymeris* formation and the Brachiopod + *Chlamys* associations discussed above.

Dell (1951) recognised a Brachiopod + *Chlamys* formation in Queen Charlotte Sound, typically developed where strong currents cause bypassing of sediments and in some instance winnowing of finer material. Analysis of the substrate (Dell, 1951, p. 20) showed that 59·2 per cent of the sediment was coarser than 2 mm, but also present were appreciable percentages of all the finer grades, including 9·3 per cent sediment finer than 0·06 mm. Dell notes that this distribution of constituent particles is similar to that Powell (1937a) found for the *Maoricolpus* formation, but that the fauna is closer to the *Tawera* + *Glycymeris* formation. In fact, Dell (1951, p. 21) suggests that the Brachiopod + *Chlamys* formation is superimposed upon the *Tawera* + *Venericardia* association. This community then could be considered as intermediate between that record by Fleming from the Southland fiords and the Auckland provinces of Powell (1937a). A similar association to that described as the Brachiopod + *Chlamys* formation by Dell (1951) has been illustrated by Hurley (1959) from several localities in Cook Strait. It is probable that this sort of association is common in Cook Strait for it is an area which in many places is subjected to strong tidal flow. Hurley (1959, p. 144) mentions bottom currents (two inches above the bottom) of the range of one-quarter to one-half knot.

Although *F. rubrum* is recorded from Queen Charlotte Sound, its faunal association there is not known. The species is extremely abundant in Cook Strait and seems to be associated in every instance with the Brachiopod + *Chlamys* formation, although more work is needed to be certain of the invariability of this relationship. Similar faunal communities have been recognised for several other areas of New Zealand. The Foveaux Strait oyster beds (Fleming, 1952a) are a faunal community closely analogous to the *Tawera* + *Glycymeris* formation of Auckland. As would be expected, the infaunal elements are more closely allied to those of the Auckland association, while the structure of the epifauna differs. No corals have been recorded from Foveaux Strait but few attempts have been made to collect them. Although Fleming (1952a) notes that Coelenterata were observed in the course of that investigation, he has written (pers. comm., 21 February 1961) that no corals were found in the unsorted collections although the habitat would suit *Flabellum*. Powell (1950) has described a *Chlamys delicatula* + *Fusitron* community from eastern Otago typically developed in areas subjected to severe tidal flow and which have a substrate consisting of hard sand, shell, or gravel. Except for the fact that it is apparently best developed in the depth range of 50 to 70 fm, this community would be a likely one for *Flabellum*. Powell (1950), however, does not record the species.

Practically nothing is known of the ecology of the shallow-water occurrences of *F. rubrum*. Powell (1947) has stated that the species occurs under boulders slightly below the low-tide line in the Auckland region. Its presence there now is problematical as pollution has had a strong influence upon the fauna of Auckland Harbour (Powell, pers. comm.). The only other citation of shallow water *F. rubrum* of which I am aware is that of Oliver (1923) in his study of the littoral communities of New Zealand. *Flabellum* [*sic*] occurs in the *Corella* association of the "Coriaceous-Coated-Animals Formation" on the rocky coast of Long Beach, Bay of Islands. Among the collections of the Dominion Museum are 12 specimens of *F. rubrum* collected alive by Oliver from this locality on 4 December 1911, so that the reference of 1923 is accurate. The Corella association is found under stones near the low-tide mark where light does not penetrate and is often encountered in rock pools. Common associates are tunicates, sponges, tubicolous worms, chitons, mollusca, and Polyzoa. It is apparent that many of the organisms of this community are exposed during portions of the low tide. Many reef corals, of course, are exposed daily and some species are able to survive prolonged exposures without great damage.

BREEDING HABITS AND GROWTH RATES

Skerman (1958a) recorded "*Flabellum* sp." from settling plates set out in Port Lyttelton. Data based upon these records are presented with all diffidence because of the uncertain nature of the identification. Skerman (pers. comm., 1959) states that he has been unable to relocate the specimens and as neither Dr. Patricia Ralph (pers. comm., 1960) nor I have seen corals from Lyttelton Harbour, the identification lacks verification. If the generic identification is accepted as correct (and the most likely source of confusion would be with *Culicia*, an astrangiid coral which Mr Skerman has recognised), then *F. rubrum* is the probable species. A number of specimens of "small solitary corals" were taken from a settlement panel immersed during the month of October 1953, according to Skerman (1958a, p. 236), who also records "six further specimens of a similar size (0·5 cm in overall height)" on a panel immersed during the six-month period of June through November 1954. A third panel submerged from August 1953 to May 1954 (nine months) held " . . . an extensive establishment of coral colonies (1·0 to 2·0 cm height) . . . " From these occurrences of corals Skerman concludes that settlement of their larvae took place in the spring and early summer.

Collections of *F. rubrum* made at N.Z.O.I. Sta. A 489 during the middle of October 1959 contained numerous small (less than 1 cm height) live corals attached to shells and other objects (see p. 26 and table 1) indicating recent settlement of larvae. A histogram derived from the occurrence of living corals at this station in Cook Strait shows a pronounced skewness towards the younger classes but also shows a sprinkling of members in each height class through the size range of the sample. The largest corals of this collection are comparable to the usual larger-sized individuals observed in other collections, and can be assumed therefore, to represent most age classes.

Two fundamental hazards in this analysis are believed to be unimportant. First, the decision of what constitutes a live coral is difficult for almost all specimens were deeply imbedded with blue clay. Removal of this material, implanted during the dredging, frequently also resulted in removal of the polyp from the corallum. Hence, in many cases "recently dead" coralla must be included in the data. For purposes of comparison, this latter group have been graphed separately in fig. 8. A second source of error was introduced at the time of collection. Not all larger material was examined carefully for smaller corals, as the sample was not washed before removal of the corals for study. As a result, there is undoubtedly a bias towards the larger individuals, hundreds of smaller coralla having been overlooked.

Data given by Skerman (1958a) and information derived from the N.Z.O.I. collection are consistent with a breeding period of spring or early summer for *F. rubrum*. If Skerman's species is accepted as *F. rubrum*, then it becomes apparent that there is only one breeding period per year. This is not at variance with the data derived from collection A 489. If more than one breeding period had occurred during the year, one would expect a bimodal distribution in an age-dependent variable such as corallum height, while in the collections there is no conclusive evidence of such a situation (fig. 8). On the other hand, the absence of conspicuous high points other than the initial one might be taken as evidence of the existence of only one age class in the population. Such an instance is unlikely, and the small size of the sample probably accounts for the apparent absence of other modes. Growth rates for *Flabellum* sp. may be derived from the data given by Skerman (1958a). In the table below, the settling of larvae is assumed to have occurred in the months of October or November, and the age of the corals is calculated from that date.

Age of Panel	*Age of Specimens*	*Height of Specimens*	*Growth Rate*
1 month	1 month	0·5 cm	0·5cm/mo
6 months	1 month	0·5 cm	0·5cm/mo
9 months	6 months	1·0–2·0 cm	0·16–0·4cm/mo

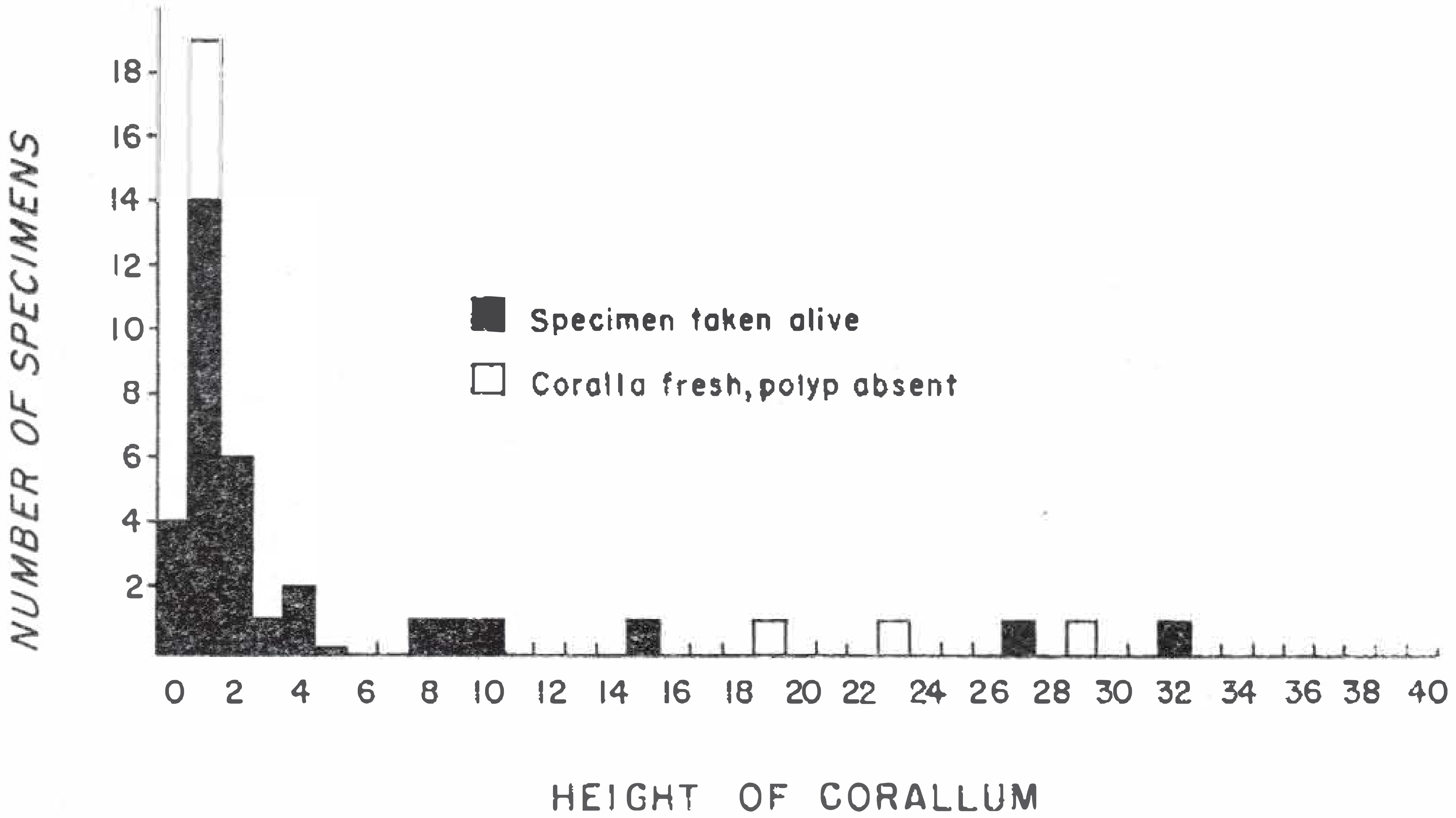

Fig. 8. Size distribution of specimens of *F. rubrum* taken in N.Z.O.I. Sta. A 489. The distribution is biased in favour of the larger specimens because collection of smaller individuals was incomplete.

If height is assumed to be non-allometric, then the largest living specimens in collection A 489, some 43·8 mm high, are less than one year in age. Growth rugosities, a highly speculative means of estimating age, if considered as annual, indicate a life span of a dozen years, and for a sample of 18 specimens, a growth rate of 2·5 mm per year. Both of these indirect means of determining growth rates are highly speculative and have little value except as a mental exercise. Most growth rates are allometric, and as there is evidence in many solitary corals that upward growth decreases in rate with age, the assumption that this measurement is non-allometric is speculative.

It is of some interest that fouling experiments conducted at the Port of Auckland from 1954 to 1956 (Skerman, 1959) did not produce records of any coral although *F. rubrum* has been recorded from there in very shallow waters.

BIOLOGY OF ATTACHMENT

Larvae of *F. rubrum* usually settle upon a solid object which is at least a centimeter in diameter. Although there is no direct evidence to suggest that larvae are discriminatory in this respect, there is probably selection against those which settle upon smaller objects. Upon settling and fixation, formation of protosepta and basal plate is begun, and as shown above, this involves a number of steps, all, in general, oriented towards obliteration of the topography of the substrate beneath the polyp. Vertical growth of the wall (as the epitheca) commences almost immediately upon completion of the basal disc. As *Flabellum* does not have an edge zone, the polyp is in contact only with the upper margin of the calice; no tissues extend down the outside of the corallum, or through perforations in the wall. As a result, the initial attachment of the species is final unless specific later adjustments are made by the polyp. This contrasts strongly with corals in which an edge zone is present and in which large, spreading, mat-like attachments are formed (e.g., *Caryophyllia*). A number of specimens of *F. rubrum* have been observed in which supplementary attachment structures are developed on the base. These are of two distinct types: Those which are formed early in the life of the coral and which show several concentric widely-spaced walls on the attachment, and those which are formed later and are more directional, most commonly appearing in the form of "talons". Structures of the first type have been observed in both shallow and deep water *F. rubrum* and are, in general character of the base, polycyclic (Durham, 1949), that is, a series of concentric walls united by distal extensions of the septa within each of the enclosures. This type of attachment has been illustrated (Squires, 1958a, pl. 12, fig. 5) and is not uncommon among shallow-water *F. rubrum*, among which rather perfect specimens of polycyclic development can be found. It is apparent that, from the onset of growth, external conditions in the environment have stimulated lateral extension of the polyp at the expense of upward growth.

The lateral growth can only proceed at the expense of upward growth, and must follow the period of initial contraction of the polyp at a height of one or two millimetres. As a result, growth, rather than following the normal allometric pattern towards calicular compression and resulting expansion of the polyp along one axis, forms a low, spreading polyp and corallum. Epithecal material, rather than being deposited as a vertical wall, extends along the substrate as a continuation of the basal disc.

This growth form, were it invariable, would be excellent morphologic grounds for the erection of a separate species, but it is not invariable within a population, nor does it always follow the same course. In some instances, as in the specimen illustrated (Squires, op. cit.), polycentricity may be asymmetrical. Stimulation of growth in this case was directional.

The second type of supplemental attachment structures are talons (Squires, 1958a, pl. 14, fig. 1, 2, 5), developed at a later stage of growth, when the polyp has abandoned the lower portion of the corallum. This structure must be formed by the polyp extending down over the wall of the corallum. Deposition of calcium carbonate by the polyp is more rapid on the basal portion than in the mid-regions of the corallum, for although there is a thin layer of epitheca on the wall adjacent to the talon, it is insignificant in volume of carbonate in comparison to the talon. As an example, a specimen figured (Squires, 1958a, pl. 14, fig. 5) shows five strong rugosities in its profile, representing five unknown intervals of time. Formation of the talons developed on the lower portion of the corallum took place when the corallum had a height about equal to the height of the third rugosity, and continued for some time resulting in several layers of stereome being deposited. Note that this specimen lacks pedicel and the base is worn. It is not known whether this is a primary or secondary feature resulting from wear of the corallum.

Identification of the stimulus for formation of accessory supporting structures is not easy. It is tacitly assumed that *F. rubrum* is negatively geotrophic, for there is abundant evidence that the polyp will distort a normal growth pattern of the corallum to avoid contact with the substrate. *F.rubrum* have been noted in which the corallum is bent either in, or at right angles to, the plane of major compression. If such bending of the corallum is associated with supplementary attachment structures, the stimulus for both could be assumed to be the result of contact with the substrate, but both reactions are not always associated.

As none of the observations serve to suggest a stimulus for the secretion of basal material, other than that it is apparently associated with instability of the corallum, it is only possible to hypothesise concerning its origin. A most probable conjecture is that the bending of the corallum and the deposition of accessory basal talons are resultants of departure from vertical growth sufficient to stimulate the polyp to corrective measures. If the stimulation is strong, as if caused by rapid departure from the vertical, the response may be secretion of talons. More gradual overturning, which does not exceed growth rate and does not cause death of the polyp, results in curvature of the corallum. Most of the instances of talon formation are associated with attachment to objects above the sea floor, such as antipatharian branches, or branches of other colonial corals, where increasing weight of the corallum may result in bending or breaking of the substrate, a relatively rapid stimulus. Curvature of the corallum reflects slower rectification of overturn, and could be brought about either through slow change in the axial direction of growth, or by falling to a recumbent position under fortuitous circumstances which would not result in death of the polyp. If the base of attachment is sufficiently small, the stable orientation of the overturned corallum, that is, recumbent on one of the flat faces, will be taken and curvature in growth will then be in a plane at right angles to these faces. Should the object to which the corallum is attached be of a nature to prohibit the corallum from assuming this orientation, then curvature of the corallum would be in a plane other than that at right angles to the two faces.

Implicit in this discussion is the assumption that *F. rubrum* will not live successfully while the corallum is lying laterally on the substrate, and that the coral has a relatively rapid growth rate. Both of these assumptions are subject to confirmation. Deposition of secondary basal structures are observed, as is curvature of the corallum. While the latter is general condition and is found among most free-living solitary corals, the former is directive and in difficulty approaches the feat of deposition of scalariform processes in *Goniocorella* (Squires, 1960a, p. 197).

Deposition of stereome in the basal regions of the corallum, resulting in a heavy "ballast", is not compatible with an attached mode of life, particularly when the focus of the attachment is small or unstable. Free-living forms, negatively geotrophic, could effectively utilise a mechanism such as "ballast" for the maintenance of position in a soft substrate when subjected to low-current activity. Analogy with *Manicina areolata* (Linnaeus) is apt, for this reef coral customarily inhabits sandy environments which permit penetration of the basal portion of the corallum. In an unpublished study, I have found that stability of *Manicina* is responsible for the development pattern of the meandrine calicular valleys, sideways falling of the corallum (occurring when the base is prevented from penetration into the substrate) resulting in distortion of this pattern. Certain specimens collected from a soft, muddy sand patch (Squires, 1958b, p. 255, pl. 37, fig. 2, 3) were not typical in form, but were cuneiform in shape, a reflection of rapid upward growth as the corallum subsided steadily into the substrate. Had a hard layer been present to stop subsidence, undoubtedly the corallum would have continued growth upward and lateral extension of the calice would have continued, but as the point of instability was reached (that point at which the mass of corallum above the substrate exceeds the equilibrium values for stability in comparison to the mass below the substrate) the corallum would have overturned, with a resulting stimulus for growth of a different form.

Goreau (1961) suggests that the decreasing rate of carbonate deposition with age, which has been shown for *M. areolata*, is an adaptive mechanism to prohibit the sinking of the corallum into the substrate as the mass increases. This view is not inconsistent with that stating that deposition of basal stereome in coralla is a stabilisation mechanism, for stability will depend upon the type of substrate and the nature of the coral.

F. rubrum, which abandons both wall and interior of the corallum with upward growth, could have the basal corallum submerged in the substrate without injury to the polyp. However, attachment to a broad object does not permit subsidence, particularly on shingle or pebble bottoms characteristic of *F. rubrum* communities. The "ballast" represented by the stereome must then be a weight upon the attachment substrate which functions as an anchor to hold the attachment substrate against the bottom. Once the attachment is broken, or the corallum is overturned, only arching of the corallum can correct the situation, otherwise the polyp dies.

Once overturned, ballast in the basal portions of the corallum will permit the polyp to be free of sediment as the lip of the corallum is reflected upward, for it will counterbalance the extension of the corallum. Speculation of this sort can be misleading, however, for deposition of stereome such as seen in *F. rubrum* may result from physiologic processes only and not reflect primary adaptations.

Squires (1961) has reported the decay of attachment in *F. curvatum* from the Patagonian Continental Shelf, attributing the process to destruction of the basal pedicel by attrition and chemical corrosion by attaching organisms settling around the basal portion of the corallum. A different mechanism is here postulated to provide an organism-free base as has been observed for most specimens of *F. rubrum*. Most observers consider the communities in which the species occurs are subject to scour activity which not only removes substrate, but also removes all but the most hardy benthos. The answer is not complete, and considerable attention is needed on the questions of coral attachment.

TEMPERATURE

The distribution of *F. rubrum* (fig. 7) may be broken into two discrete units (a third unit could be based upon unverified records) separated by large gaps resulting from either absence of the species or ignorance of its occurrence. The northern range of *F. rubrum* is wholly within the subtropical Aupourian Subprovince, and extends from North Cape to East Cape on the north-eastern side of the North Island, New Zealand. The area has a yearly surface-water temperature range of 68–58°F (Garner, 1954) and is directly under the influence of the Tasman or East Australian Current. The fauna of the Aupourian Subprovince is characteristically subtropical and contains many Peronian elements (Powell, 1937b).

A second distribution region is that in western Cook Strait, on the northern side of the Strait, extending from Palliser Bay on the east to Kapiti Island and South Taranaki Bight on the west. On the southern coast of Cook Strait, the species is known only from the vicinity of D'Urville Island (B. Waterhouse, pers. comm., has reported the species from this region, but I have not seen specimens).

This distribution is approximately in the centre of the Cookian Subprovince and has a yearly surface-water temperature range of 67–56°F (Garner, 1954). This region, considered as a belt of mixed waters by Fleming (1944, 1952b), is characterised by a mixed fauna of both cold and warm water derivations although some stenozonal species are present. Some deeper-water species extend further to the south than littoral species of this zone, indicating that at depth, on the shelf, there may be more southerly penetration of the warm waters from the north.

A third area of occurrence of *F. rubrum* is represented only by the records given by Skerman (1958a) and Fleming (1950), which have not been verified. Fleming (1950) states that a number of species of mollusca have been recorded from the fiords that are not known elsewhere in southern New Zealand and suggests that bottom waters in the fiords may be appreciably warmer than the surface water though not verified by actual measurements. Warm-water species in the fiords would be isolated from other occurrences by cold, upwelling waters on the west coast. Data given by Skerman (1958b) indicates that water temperatures in Port Lyttelton are from about two degrees lower than outside (open water) temperatures in the winter to almost three degrees warmer in the summer. The seasonal surface-water temperature range of Lyttelton Harbour is about 42–70°F (Skerman, 1958b), providing a potential for possible breeding of *F. rubrum* in the temperature range of the northern occurrences of the species, if survival during the winter was possible. Garner (1954) indicates a range in temperature of approximately 50–58°F for the area about Doubtful Sound.

Accounting for this divided distribution pattern is not difficult because of the scanty evidence available. More complete knowledge of the distribution of the species and of ecological conditions in areas of non-occurrence will undoubtedly complicate the picture. Fleming (1952b) and Garner (1953, 1954) have shown that the warm, south flowing East Cape Current, a southward, near-shore extension of the Tasman Current, penetrates deep to the south along the eastern coast of the North Island. In the region of Cook Strait this current has a profound effect, creating contrasts in surface temperature between Cape Campbell and Palliser Bay of as much as 9°F. A current such as the East Cape Current provides a distributional mechanism for warm-water species into the "zone of mixed waters". More recently, Wyrtki (1960) has shown the West Wind Drift to be a more significant contributor to New Zealand surface-water circulation, particularly during the winter months. Wyrtki places the boundary between the northern Subtropical Water mass and the southern Subantarctic Water, which is generated by the confluence of the East Australian and West Wind Drift, well to the north. During most of the year, the Subtropical Convergence lies in a north-easterly position, extending from Tasmania to the North Cape or even more northerly positions. Although the West Wind Drift is shown to be a strong feature on the west coast of North Island, Wyrtki states (1960, p. 34) that only minor transport of Subantarctic Water occurs around the North Cape. To balance transport, Wyrtki (1960) suggests convergence along the western region of both the North and South Islands at the shelf edge. Upwelling along the coasts of both the North and South Islands may contribute significantly to the lower temperatures encountered there. Upwelling of cold sub-surface is apparently not a significant factor in the Taranaki Bight, for surface temperatures there are considerably higher than at corresponding latitudes on the east coast.

DEPTH RANGE

F. rubrum inhabits the Littoral and Sub-littoral zones of the New Zealand shelf. Documented records of living *F. rubrum* extend in an almost continuous series of depths from intertidal to a maximum of 85 fm. As the shallow occurrences are of some importance because of the potential of raising and maintaining these animals for experimental purposes in the laboratory, all authentic records known to me are listed below:

Leigh, Cape Rodney; Karewa Island, and Whangamata, Bay of Plenty; Whangamumu and Long Beach, Bay of Islands; Takapuna – North Head, Auckland; Milford Reef, Auckland; and between Wade Heads and Arkles Bay, south side of Whangaparoa Peninsula. Abundance of specimens in these localities is unknown. But this distribution and the widespread occurrences of the coral in deeper water should make it a suitable animal for either detailed ecological or physiological or biological studies.

The greatest depth from which living *F. rubrum* has been taken is 80–85 fm off East Cape, an occurrence noted by Dr A. W. B. Powell (in litt. 17 Jan. 1961). Specimens recorded from greater depths are dead and worn. A fragment of a columella probably of this species collected from 550 fm in Cook Strait is the deepest record of even dead material. Specimens described by Gardiner (1929) as *F. harmeri* were taken off Great King Island in 300 fm but of the four specimens listed, it is clearly stated that three were dead. The fourth, the largest specimen (and the one illustrated) also appears to have been dead, so that the record has been discounted in the establishment of the total range of the species.

The shallow habitats of the species have been described by Powell (1954) and are generally small coralla found on the underside of boulders near the low-tide mark. This type of occurrence has been described for dendrophyllid corals as a negative response to the increased illumination and the same reasoning is probably valid for *F. rubrum.*

PALEOECOLOGY

Squires (1960b) discussed Plio-Pleistocene occurrences of *F. campanulatum* [=*F. rubrum*] in particular relation to the paleoecological analysis of faunas of the Wanganui Basin made by Fleming (1953). A suggestion was then made that scarcity of *F. rubrum* in the Wanganui Basin during Plio-Pleistocene time was a result of shallowness of the water during deposition of now exposed sediments. Further, it was postulated that worn specimens of *F. rubrum* commonly taken in dredgings in Cook Strait might, in part, be derived from Pleistocene sediments outcropping below sea level and representing deep-water deposits of the Wanganui region. Since then, I have been able to obtain a date for one sample of dead and worn specimens of *F. rubrum* by a Carbon-14 isotope analysis made by the Institute of Nuclear Sciences, D.S.I.R. These "derived" specimens have an apparent age of approximately 600 years. As a result, one must assume that these specimens are of recent origin and are subjected to considerable wear *in situ.*

Unanswered still is the question of the absence of *F. rubrum* from shallow-water deposits of the Wanganui Basin, even though environments comparable to those in which the species lives today existed there. For example, *F. rubrum* has not been recorded from the Hautawa Shell Bed although Fleming (1953, p. 132) has indicated the similarity between this fossil assemblage and the Brachiopod-*Chlamys* association of southern New Zealand as well as the hard-bottom communities of Auckland Harbour. Similarly, the more sandy upper portion of the Shakespeare Cliff Siltstone contains a fauna very similar in character to the *Tawera* + *Venericardia* Community of Powell (1937d), but *F. rubrum* is not recorded in the fauna. Fleming (1953, p. 236) makes direct comparisons between the conditions of deposition of the Upper Shakespeare Cliff Sand and the *Tawera* + *Glycymeris* formation, even postulating formation in tidal channels in part. Again, in the Castlecliff Shell Bed, the faunas indicate a succession of hard-bottom associations. Where *F. rubrum* is present in the Wanganui Basin, such as in the Lower Castlecliff and Tainui Shell Beds, sediments and fossils are indicative of a hard-bottom environment with bypassing of sediment in depths of 15 to 30 fm of water.

It is apparent from certain well known fossil associations that the community structure of fossil occurrences of *F. rubrum* are quite similar to modern situations. Less well known (ecologically) are the occurrences of *F. rubrum* in the Hauraki Gulf and Cook Strait, where the species occurs in large numbers on muddy-shingle bottoms. These situations are at least grossly comparable to fossil environments of Hawke's Bay region during Wanganui time.

DISTRIBUTION AND HISTORICAL RELATIONSHIPS

The first known appearance of *F. rubrum* in the fossil record of New Zealand is in the Kapitean-Waitotaron (Upper Miocene-Pliocene) sediments of Kanieri, Westland. It is abundant in North Island Nukumaruan through Castlecliffian sediments (Pleistocene) in most areas of outcrop of these horizons. This distribution is suggestive of a northward spread of the species from late Pliocene time onwards, but the pattern of distribution is strongly biased by the occurrences of fossiliferous sediments of these ages and by the bias in past collecting for selection of only molluscan fossils. It has been suggested by many authors that cold-water faunas began immigration into New Zealand during the late Pliocene, a consideration followed by Squires (1956, 1958a) in stating that Wanganui coral faunas reflect the extinction in New Zealand of earlier warmer water types and subsequent replacement by cooler water faunas from the south.

As presently interpreted systematically, *F. rubrum* is a member of a closely knit species group of *Flabellum*, including *F. impensum* Squires, *F. thouarsii* Milne-Edwards and Haime, *F. antarcticum* Gravier, *F. gracile* Studer, and *F. serpuliforme* Gravier (Squires 1961,1962).* With the exception of the last two species listed, the distribution of this group is solely within the confines of the Southern Ocean, on shelf areas of Antarctica, New Zealand, and Argentina. *F. serpuliforme* is found only from the Atlantic, while *F. gracile* Studer is recorded by two specimens from two New Zealand localities. The morphological relationships between the most similar of these species has already been considered in some detail (Squires, 1961b).

The origin of the *Flabellum rubrum* group is not known for the fossil record of attached *Flabellum* is not rich. In the collections of the Museo La Plata, La Plata, Argentina, is an undescribed species of *Flabellum* which probably represents an ancestral member of the group. These coralla, from the Julicnse Group (Oligocene) of Santa Cruz, Argentina, are up to 27 mm in height, but are not as wide in calicular diameters as *F. rubrum* or *F. thouarsii*, tending to the *F. antarcticum-serpuliforme-gracile* type of corallum. Calice diameters for the largest specimen were 12·4 and 7.2 mm, the septa were relatively widely spaced and rather coarsely granular laterally. In all respects, the specimens seemed closely related to *F. antarcticum.*

It appears then, on the scanty evidence available, that the phylogeny of the *F. rubrum* group consists of an attached species similar to *F. antarcticum* from which *F. antarcticum*, *F. gracile*, and *F. serpuliforme* may have been derived. *F. thouarsii*, *F. rubrum*, and *F. impensum* represent shallow-water equivalents of those species and are derived from the same ancestral stock. The appearance of *F. rubrum* at the time of invasion of New Zealand by cold-water faunas suggests a southern origin for the species, but to suggest that *F. impensum* is the progenitor would be unwise for that species may itself be a post-Pleistocene immigrant into Antarctica.

If one assumes a northward distribution from the colder waters of the Southern Ocean during a period when New Zealand coasts were under a cooler hydrologic regime, one must account for the apparently disjunct distribution today. Fig. 7 shows the distribution (fossil and recent) of the species in New Zealand. The density of records in and around the North Island may reflect more common occurrence of the species, or more probably, more intensive collecting attempts. Dredgings on the coasts of the South Island have been very few. Powell (1940) records the Mollusca *Kidderia*, *Scalaronoba*, *Striatestea*, and *Venustilifer* from the Aupourian (Auckland) Province, noting that they are more common constituents of the southern faunal subprovinces but that they are absent from the Cookian (see also Fleming, 1944, 1950). Such disjunct ranges are probably relatively recent occurrences. The invasion of *F. rubrum*, on the other hand, if the southern origin for the species is accepted, began relatively early and the range became disjunct before the close of the Pleistocene.

**F. patagonichum* Moseley, from the Chilean Coast, *F. curvatum* Moseley from the Argentine Shelf, and several species of Atlantic *Flabellum* are attached through a sufficiently long period of growth so that the corallum bears a distinct scar of attachment. However, these species represent a divergence from the phylogenetic line represented here by *F. thouarsii* and *F. impensum* because their ephebic stages are free.

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PLATE 1

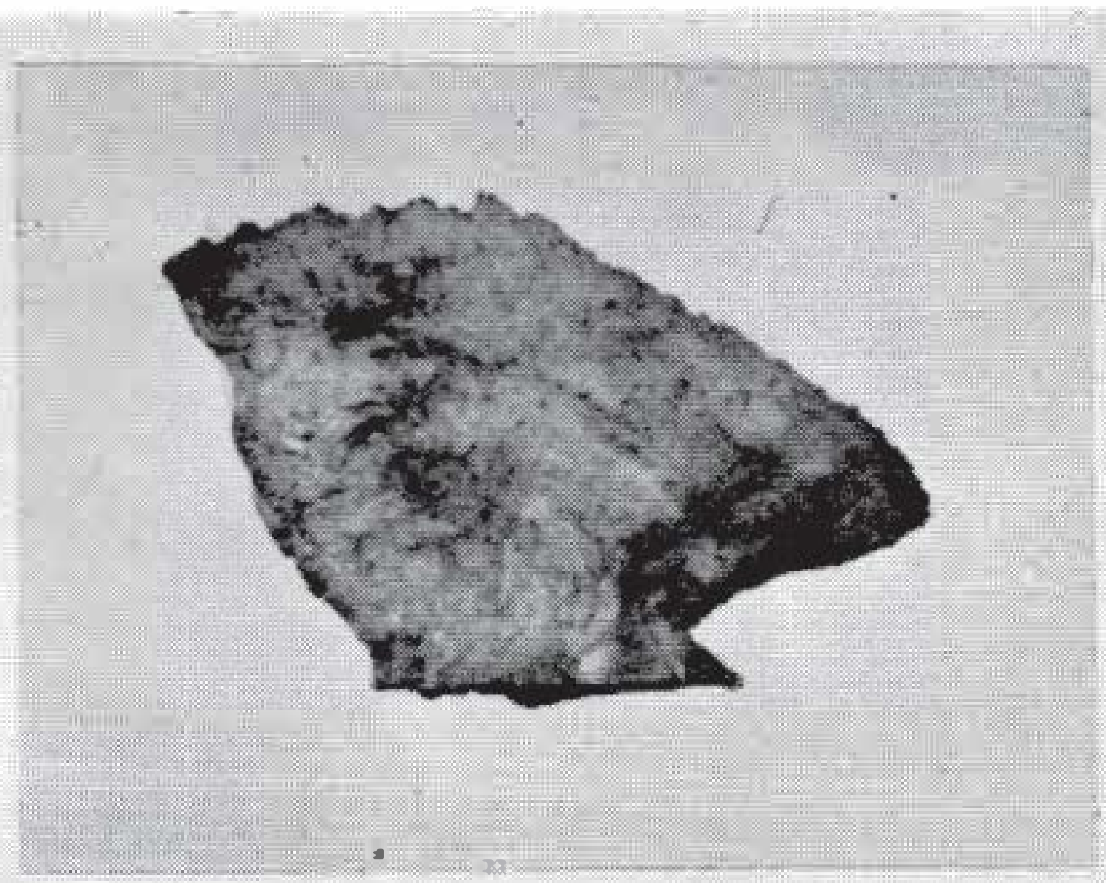
Fig. 1, 2. *Flabellum rubrum* (Quoy and Gaimard). Lectoholotype × 1·4 (approx.), side and calicular views. This specimen is the basis for fig. 5 and 6 of Quoy and Gaimard, reproduced below.

Fig. 3, 4. Paratype of *F. rubrum* (Quoy and Gaimard), × 1·4 (approx.), side and calicular views. This specimen is the basis for fig. 8 and 9 of Quoy and Gaimard, reproduced here.

Fig. 5–9. *F. rubrum* (Quoy and Gaimard) as originally illustrated (Quoy and Gaimard, 1833, pl. 14, fig. 5–9).

Fig. 10. The caption for fig. 5–9 as given by Quoy and Gaimard (1833, pl. 12).

Tubinolie [sic] rouge (Nouv-Zelande)



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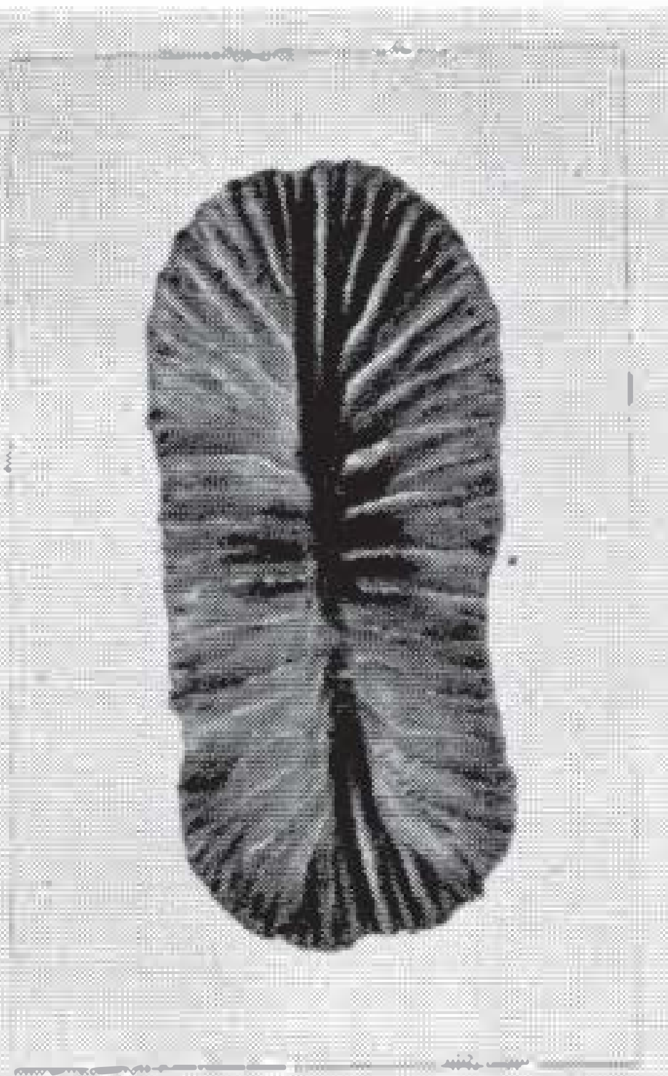

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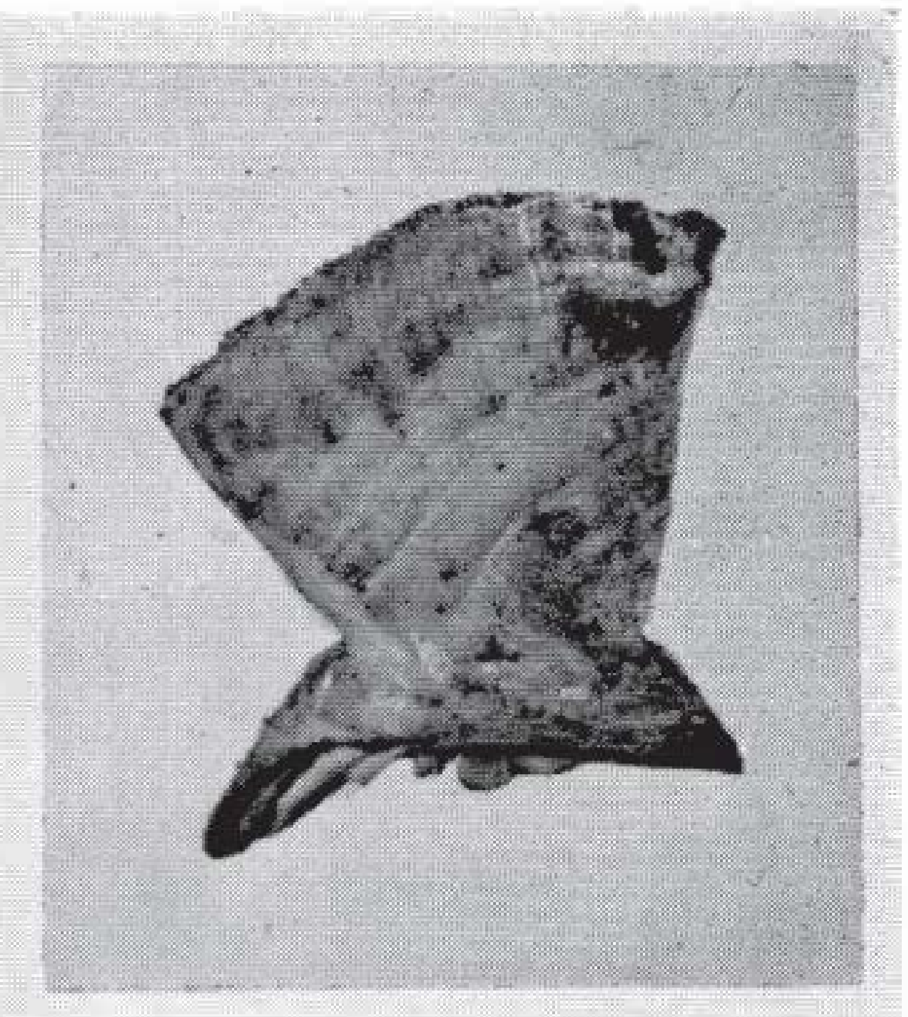

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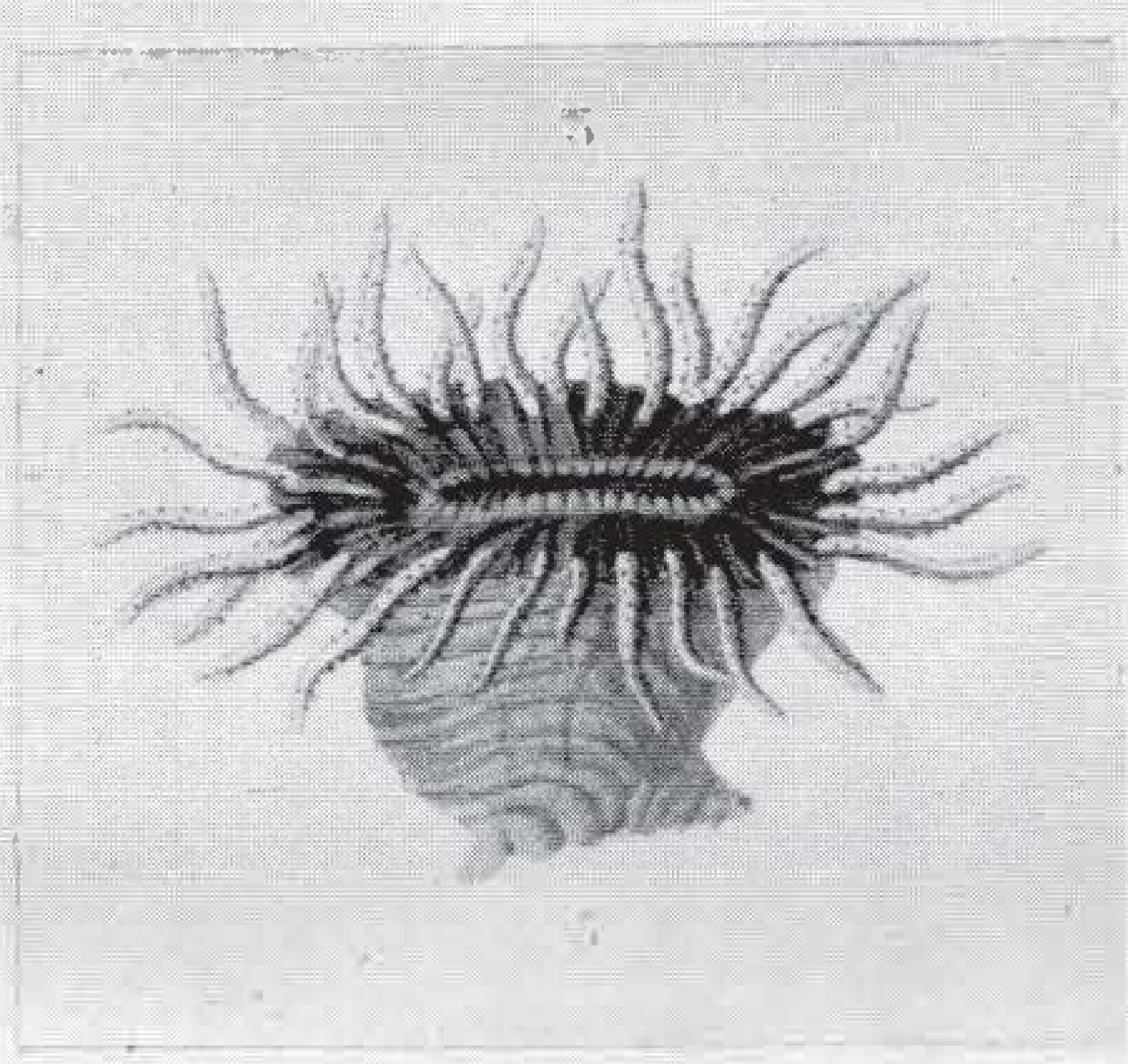

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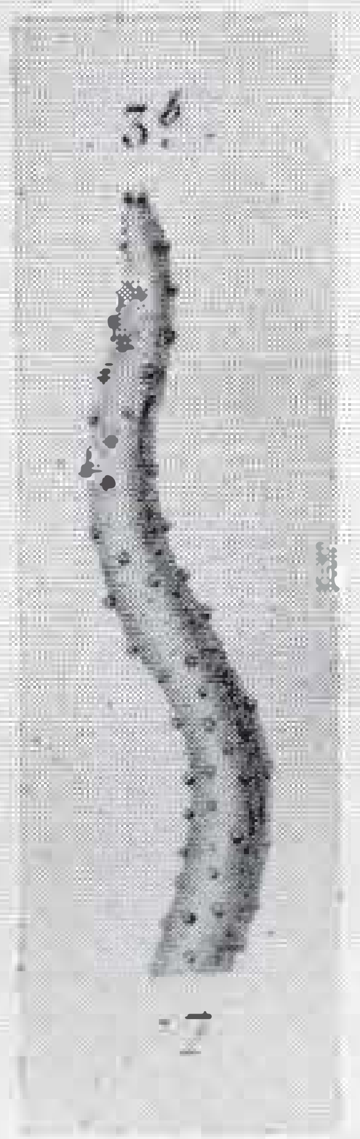

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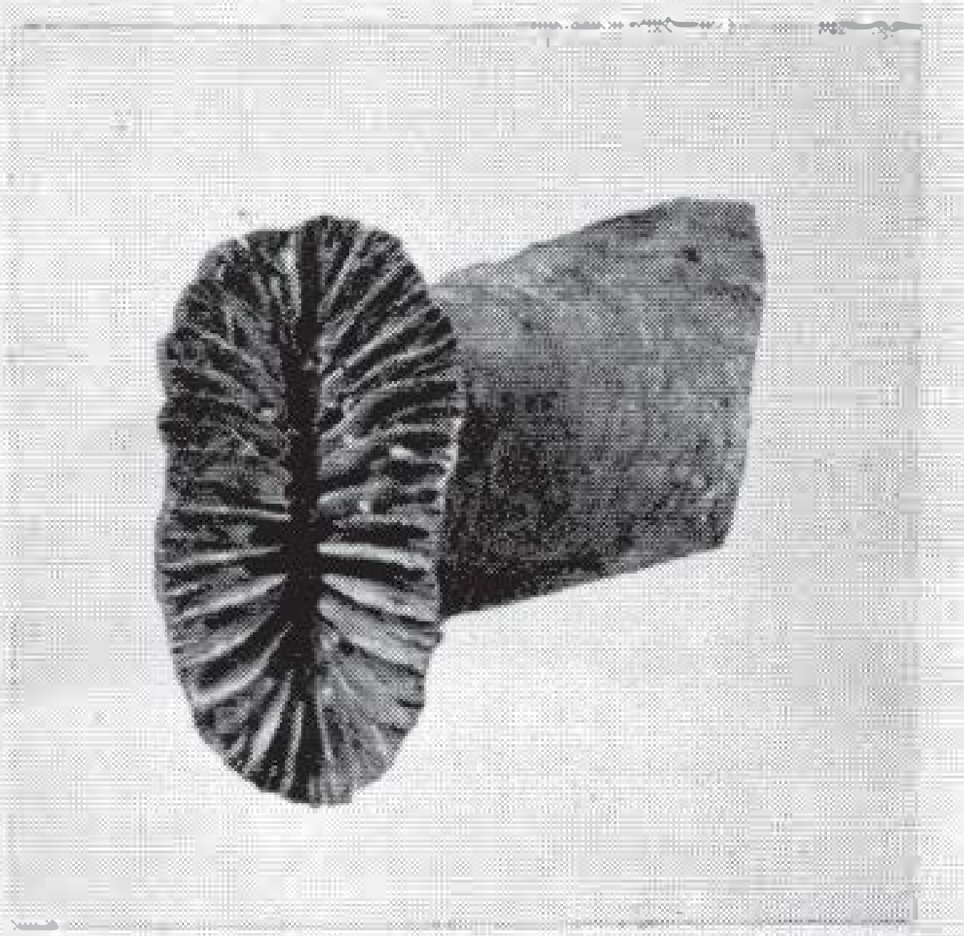

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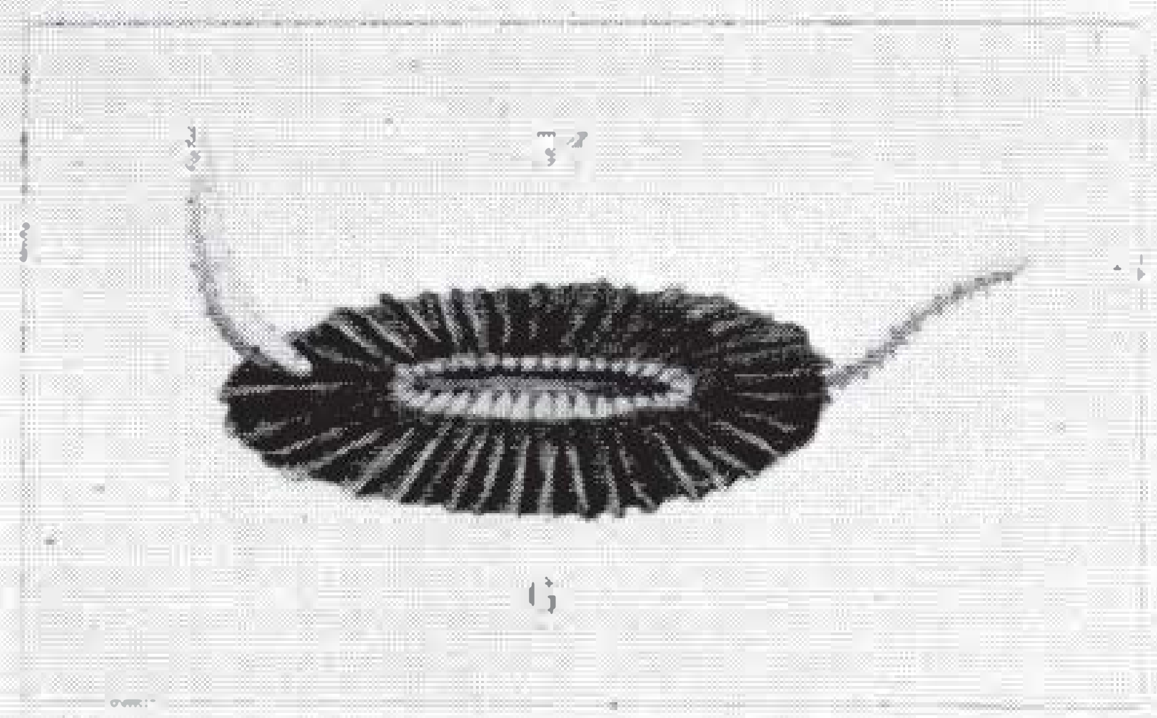

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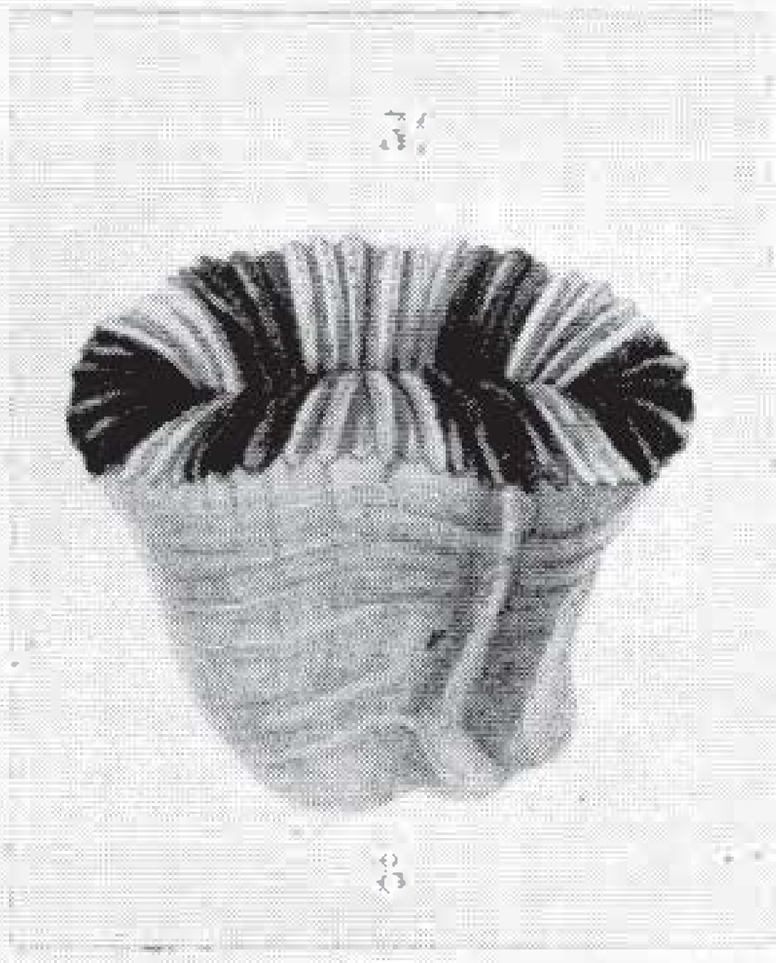

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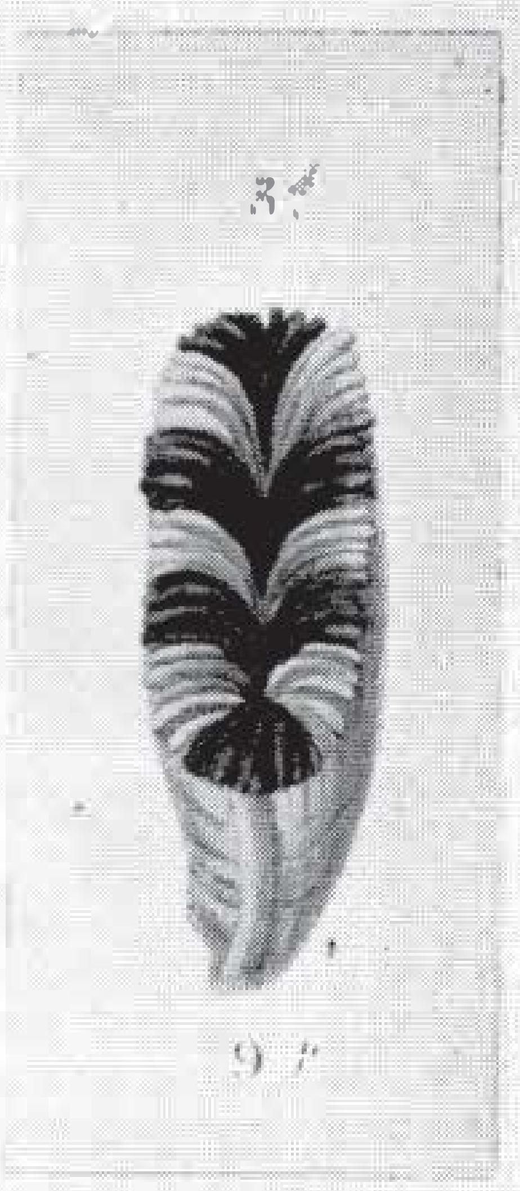


9

5 9 TUBINOLIE ROUGE. (NOUV.-ZELANDE)

10

PLATE 1

PLATE 2

(Unless otherwise noted, all specimens photographed are ones taken in N.Z.O.I. Sta. A 489, Cook Strait (41° 27′ S, 174° 50·8′ E) at a depth of 55 fm. Magnifications are approximate.)

Fig. 1. Earliest observed skeletal stage of *F. rubrum* showing the initial pad of basal plate secreted in the area proximal to the six protosepta. Notice thinning of basal plate distally. Largest diameter of specimen 2·8 mm. Magnification × 13. Photograph is taken of ultraviolet (3650 Å) generated fluorescence from the aragonite of the corallum with suitable filtration to suppress the ultraviolet radiation. The shell substrate (*Chlamys gemmulata*) does not fluoresce. The basal plate of this specimen is not visible under ordinary light.

Fig. 2. Specimen of *F. rubrum* with complete basal plate and initial stages of upward wall building. Dark areas within wall result from basal plate being removed during cleaning. Notice development of spines on basal plate along the growth rugosities of the ribs of the substrate, *Chlamys gemmulata*. Largest diameter of specimen is 3·9 mm. Magnification × 13. Specimen photographed using techniques described above.

Fig. 3. Young specimen of *F. rubrum* developed on wall of adult *F. rubrum*, showing extension of septum into columellar area to form protocolumella. Spines and lappets are developed in upper right loculus. Largest diameter of specimen is 3·6 mm. Magnification × 7. Specimen photographed by ordinary techniques.

Fig. 4, 5. Most usual corallum forms of *F. rubrum*. Note change in septal appearance in pedicel area. Magnification × 1·0.

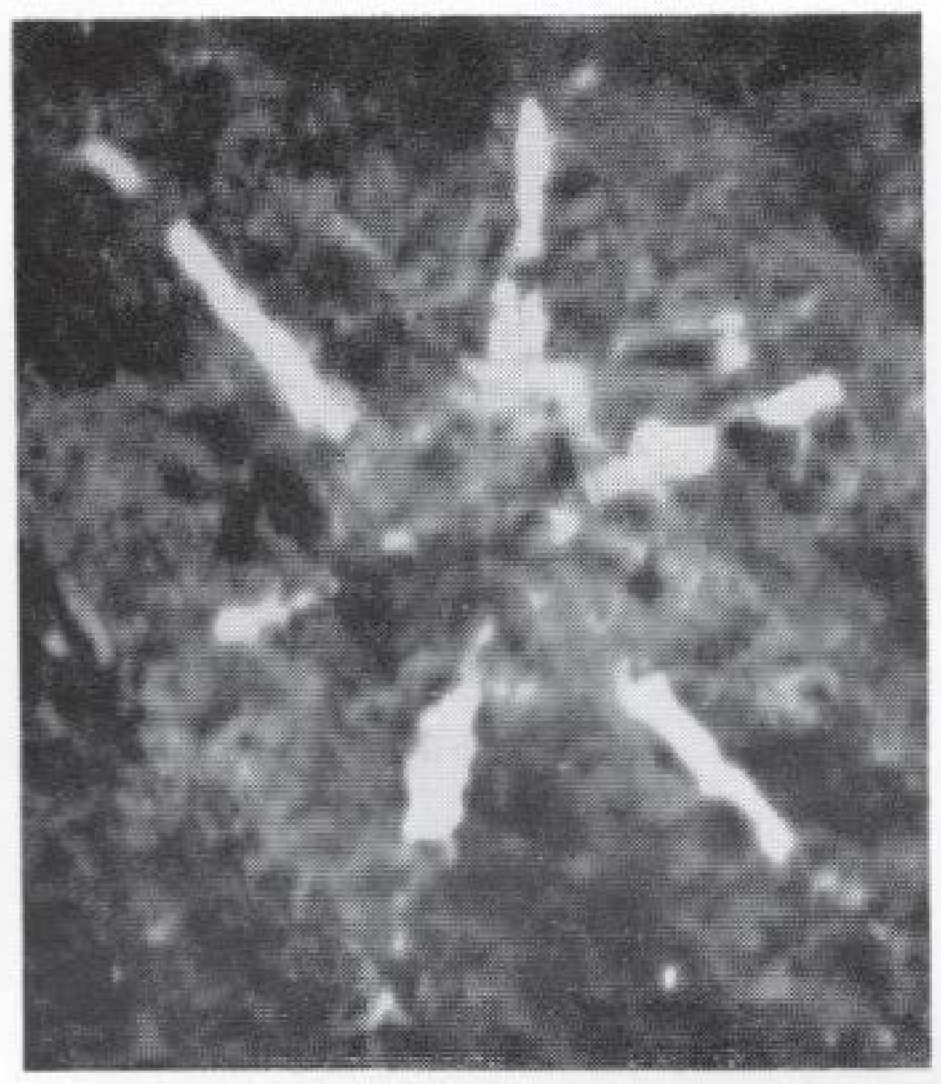
Fig. 6, 7. Specimen from Taranaki Bight showing talon development and polycentric base. Reproduced from Squires (1958, pl. 12, figures 4, 5). Magnification × 2.

Fig. 8. Tentacles of *F. rubrum* in relation to septa. Drawn from preserved specimen. Approximately × 1½.

Fig. 9. Young corallum of *F. rubrum* showing well developed prominent lappets in three loculi on left side of corallum. Long septal spines are apparent arising both from the basal plate and the wall in the position of the second cycle septa. Specimen, attached to *Chlamys gemmulata*, has a maximum diameter of 4·1 mm. Magnification × 8. Specimen photographed under ultraviolet radiation (3650 Å), visible wave lengths suppressed.

Fig. 10. Development of a columellar ring in *F. rubrum*. The initial row of spines forming proximally to the protosepta and connecting their ends later develops into a columellar ring. Abundant spines arising from the basal disc in the position of the second cycle septa are present in most loculi. One second cycle septum is inserted in lower right loculus. Specimen is on *Chlamys gemmulata* and its largest diameter is 3·4 mm. Magnification × 7. Photographic techniques as in fig. 9.

Fig. 11–14. Coralla of *F. rubrum*. Photographed under white light. 11. Corallum bent in plane at right angles to that of the photograph. Pedicel broken (during life of coral?) when taken in dredge. 12. Specimen from Taranaki Bight with cylindrical form. Contrast with fig. 4, 5, 11, 13. 13. Specimens attached to pebble together with Cheilostome Bryozoans. Observe mode of attachment, absence of talons and curvature of corallum. 14. Specimen oriented to show the conspicuous change in shape of corallum and appearance of epithecal wall at stage of addition of third-cycle septa.



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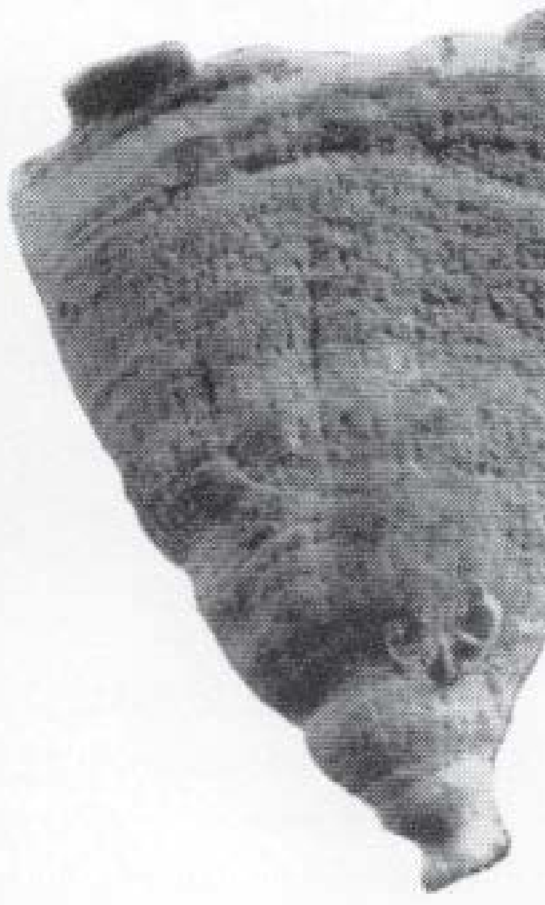

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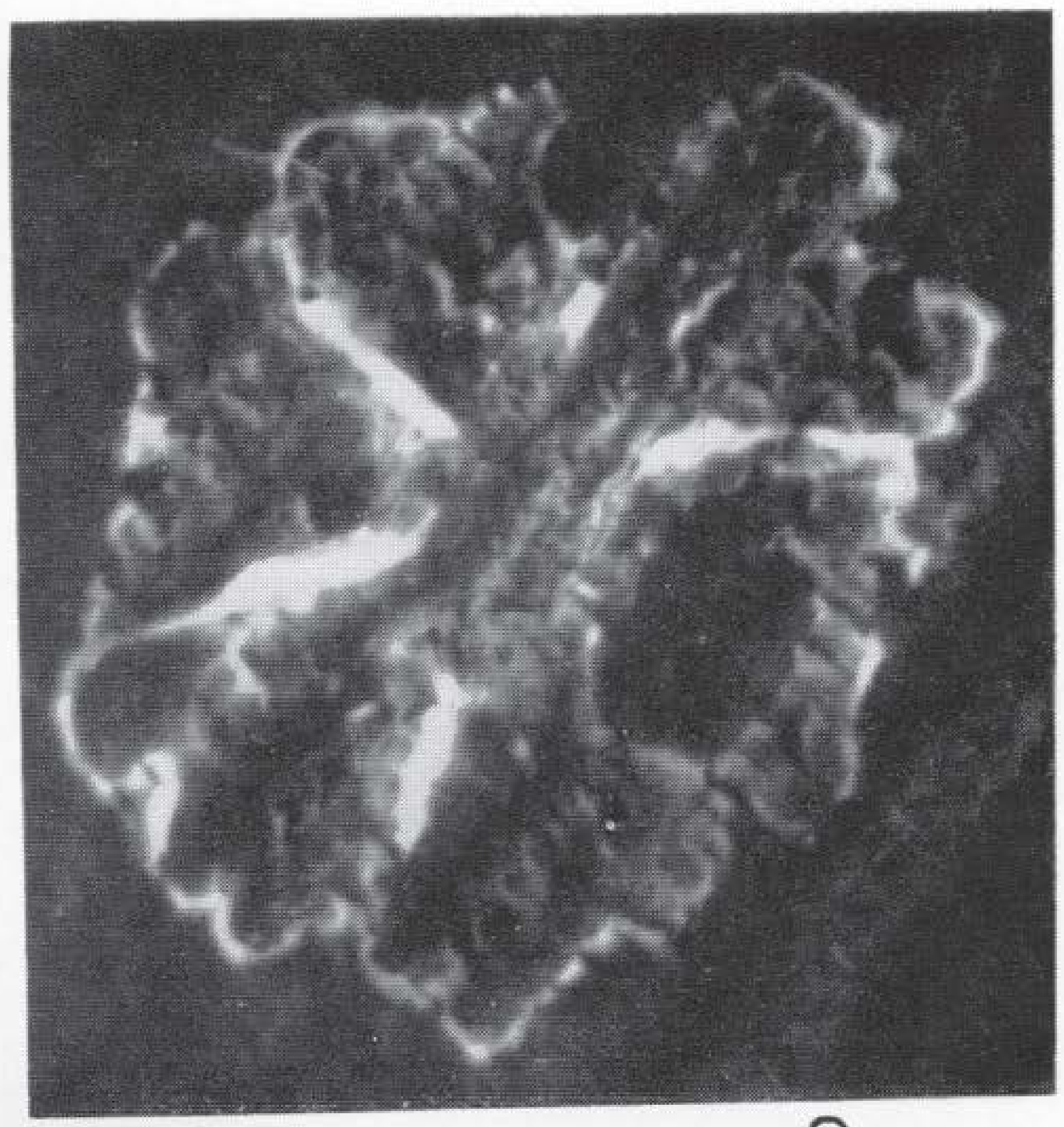

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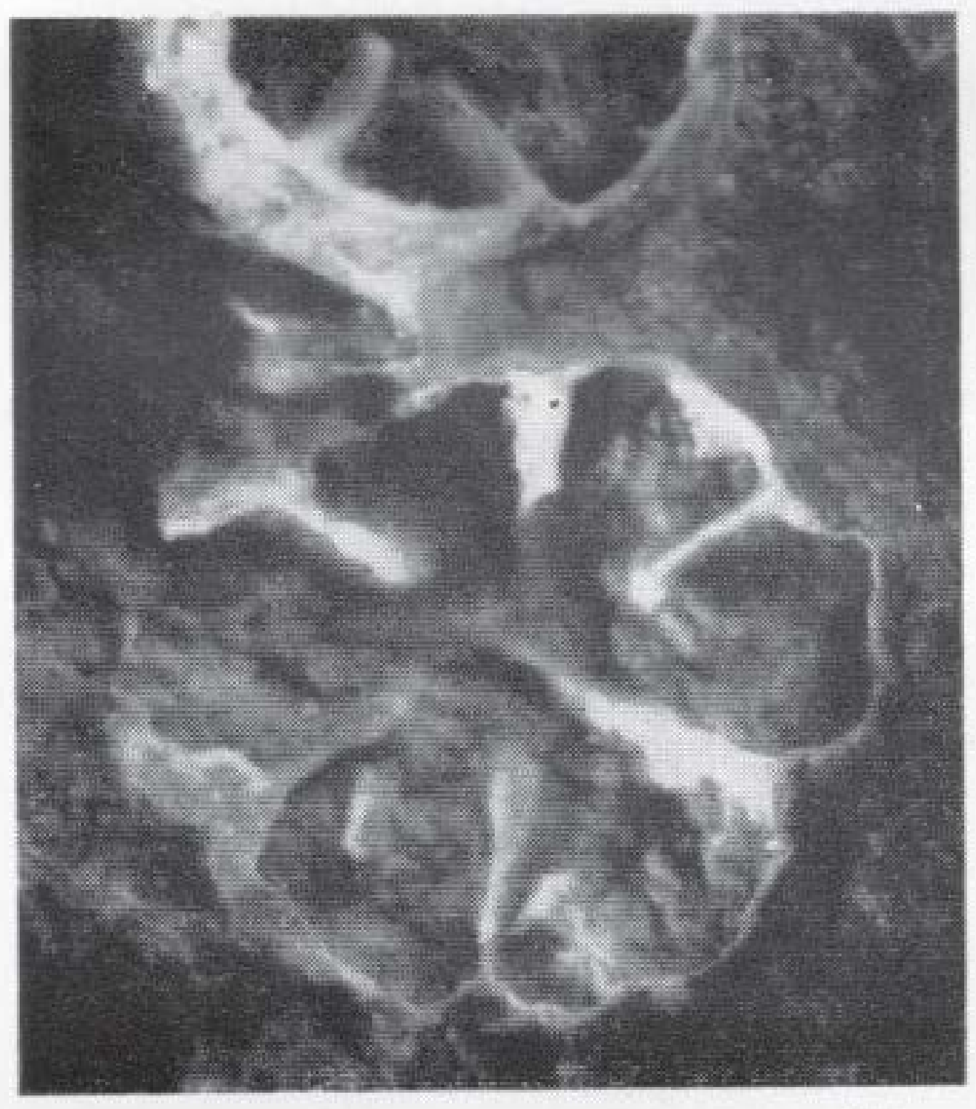

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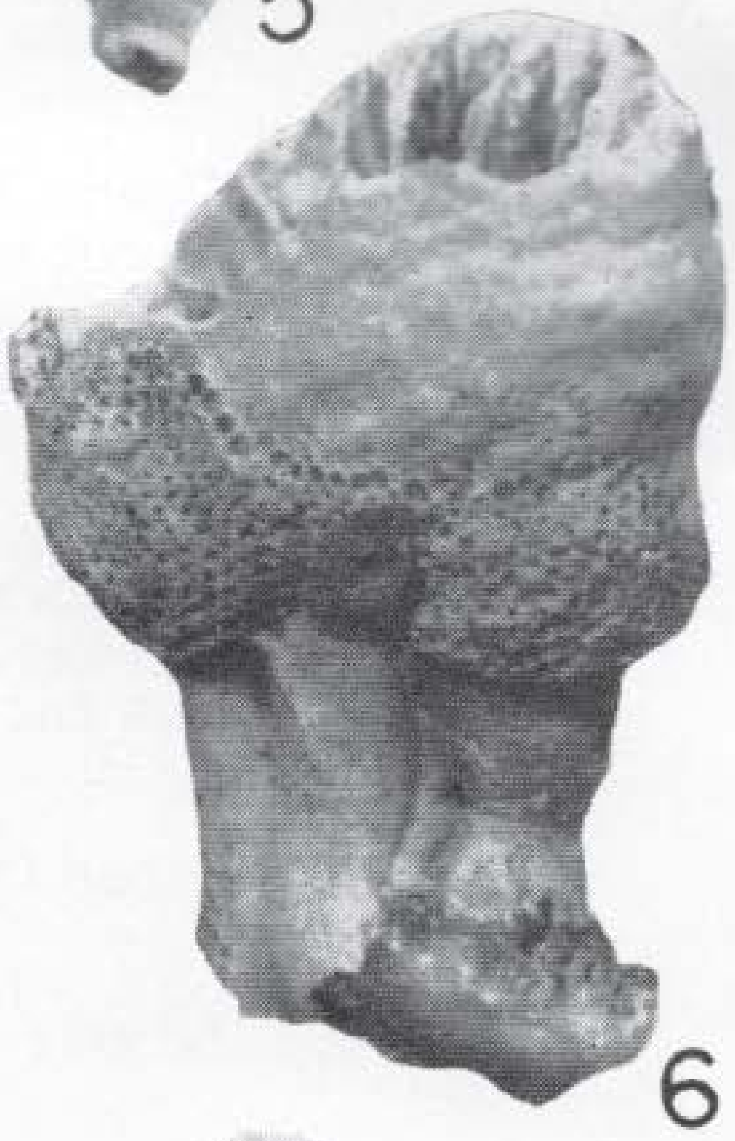

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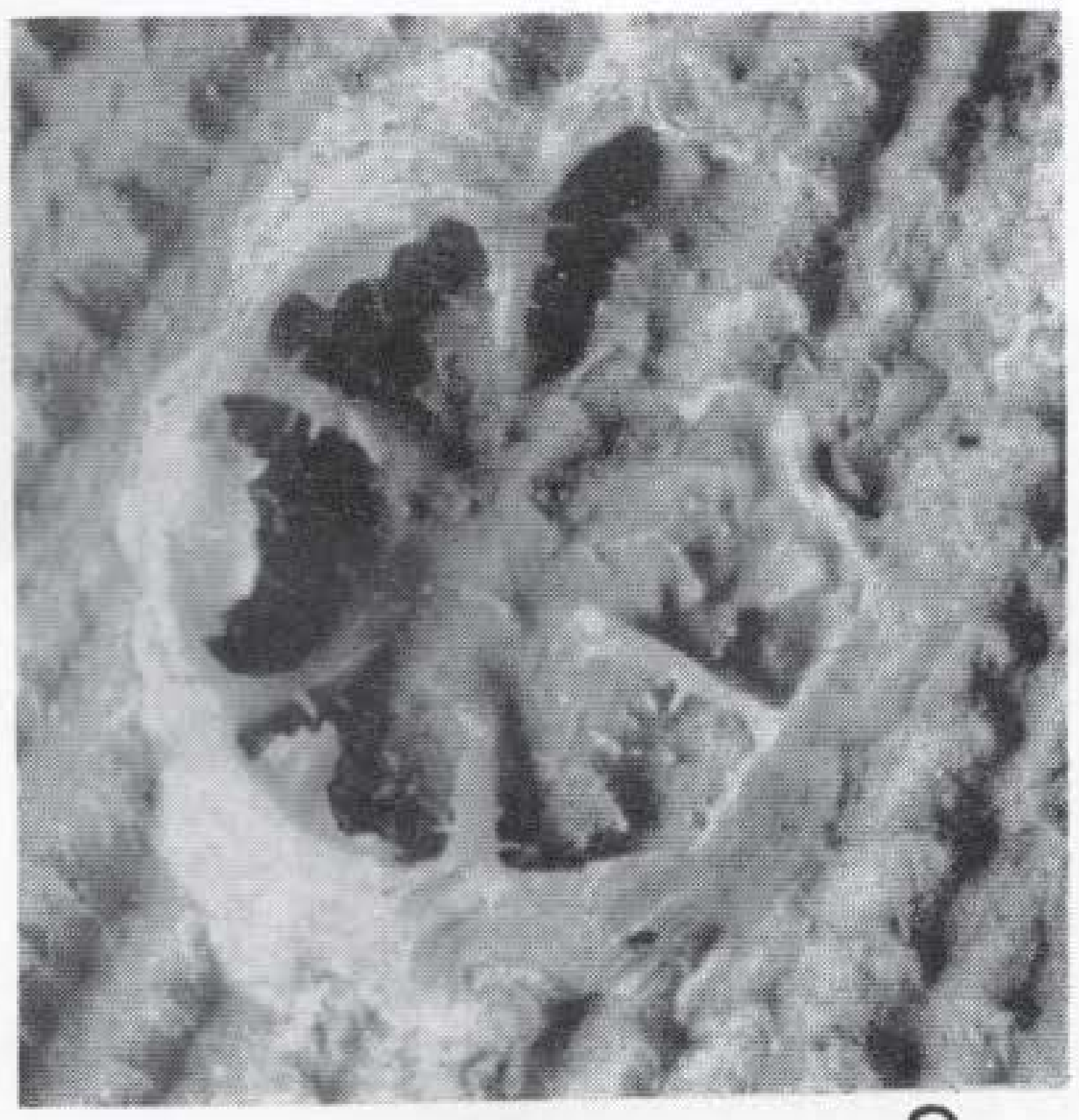

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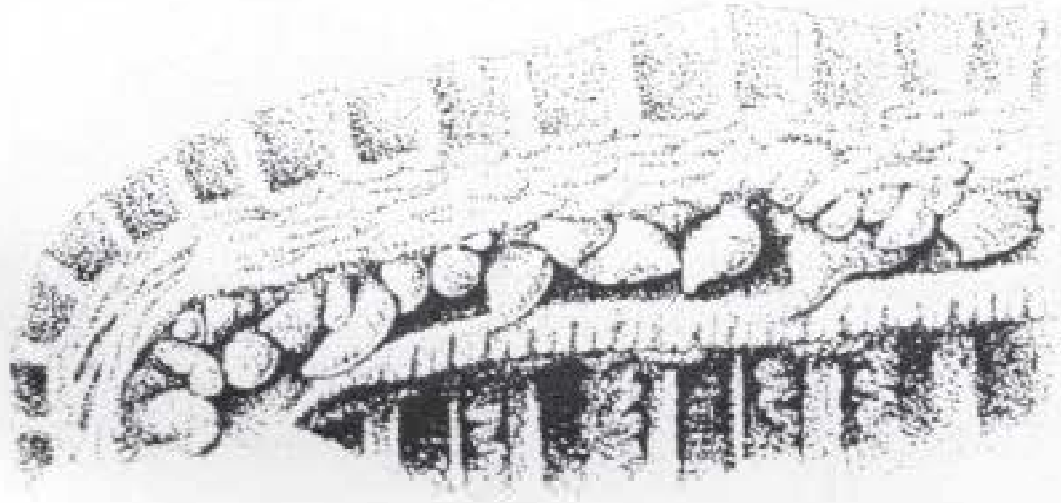

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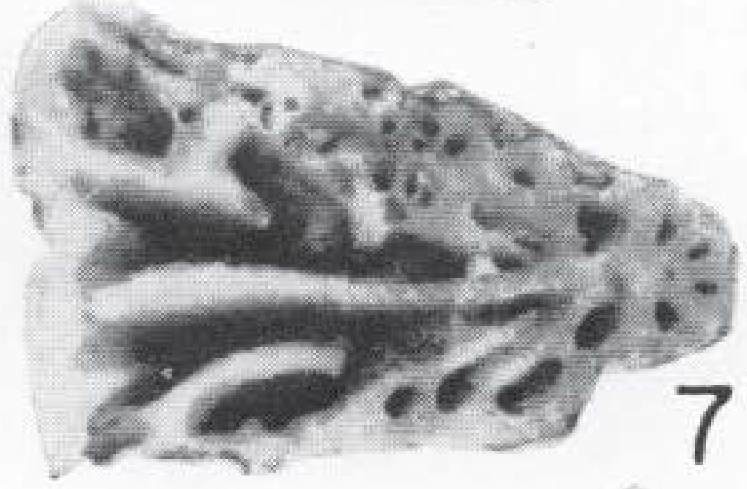

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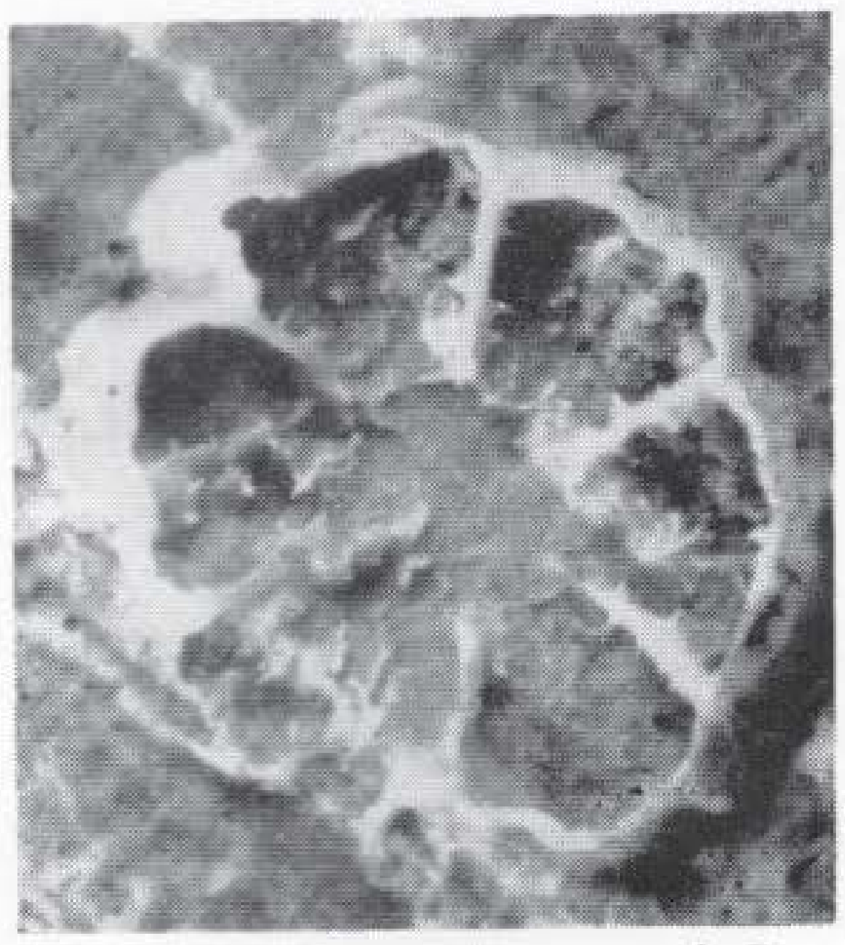

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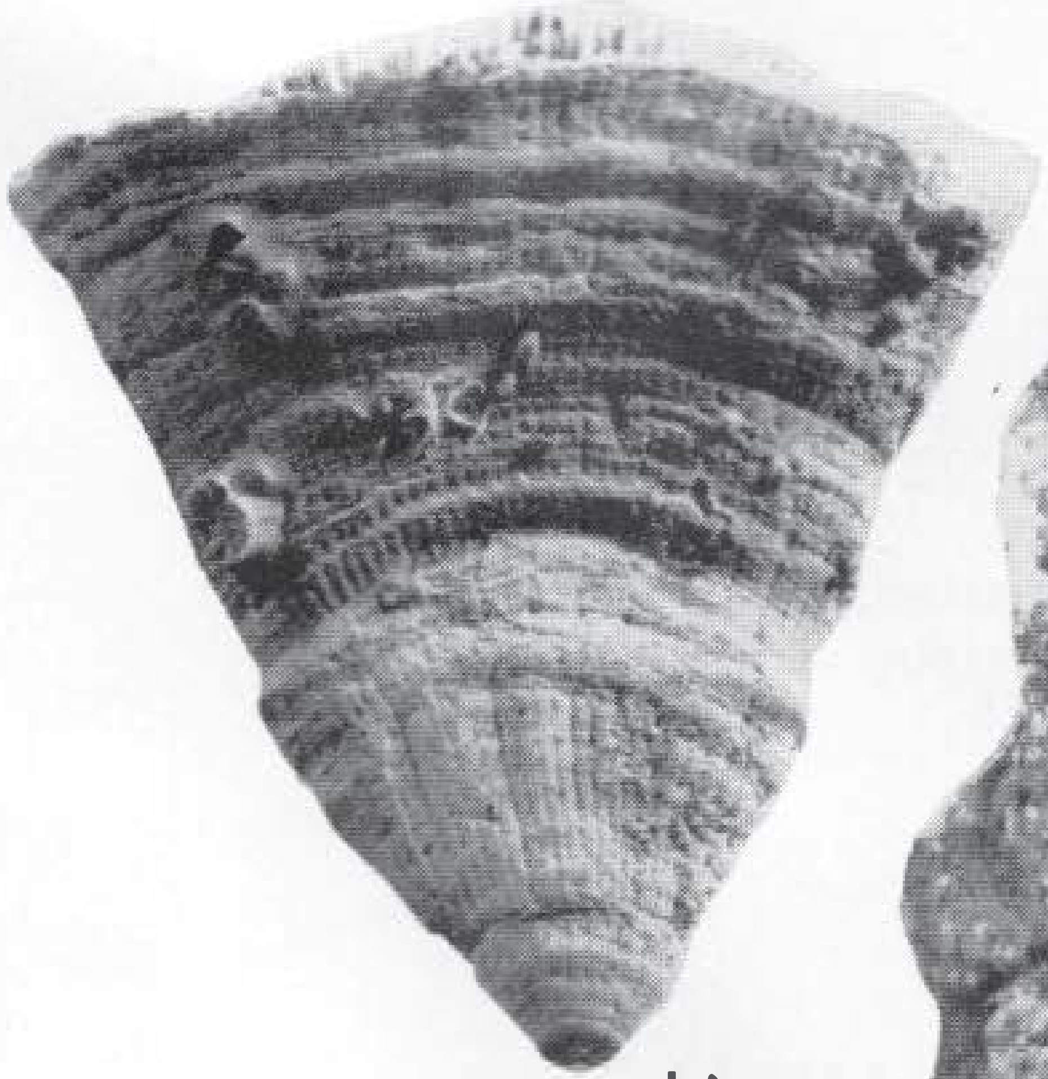

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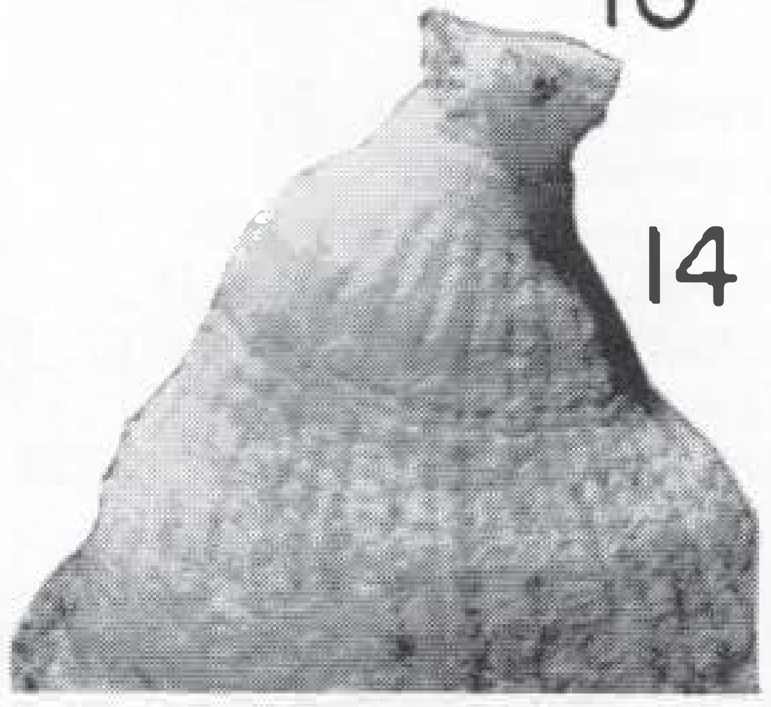

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PLATE 2

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