

NEW ZEALAND
DEPARTMENT OF SCIENTIFIC AND INDUSTRIAL RESEARCH

BULLETIN 139 (6)

**Biological Results of
The Chatham Islands 1954 Expedition**

PART 6

Scleractinia BY DONALD F. SQUIRES

New Zealand Oceanographic Institute
Memoir No. 29

1964

This publication is the sixth part of the Department of Scientific and Industrial Research Bulletin 139, which records the Biological Results of the Chatham Islands 1954 Expedition. Parts already published are:

- Part 1. Crustacea, by R. K. Dell, N. S. Jones, and J. C. Yaldwyn.
- Part 2. Archibenthal and Littoral Echinoderms, by H. Barraclough Fell.
- Part 3. Polychaeta Errantia, by G. A. Knox.
- Part 4. Marine Mollusca, by R. K. Dell; Sipunculoidea, by S. J. Edmonds.
- Part 5. Porifera: Demospongiae, by Patricia R. Bergquist;
Porifera: Keratosa, by Patricia R. Bergquist;
Crustacea Isopoda: Bopyridae, by R. B. Pike;
Crustacea Isopoda: Serolidae, by D. E. Hurley;
Hydroida, by Patricia M. Ralph.

Additional parts are in preparation. A "General Account" of the Expedition was published as N.Z. Department of Scientific and Industrial Research Bulletin No. 122 (1957).

BIOLOGICAL RESULTS OF
THE CHATHAM ISLANDS 1954 EXPEDITION
PART 6—SCLERACTINIA



Photograph: G. A. Knox.

The *Serolis bromleyana* – *Spatangus multispinus* community on the sorting screen. Aberrant growth form of *Flabellum knoxi* is in the lower left (see also plate 1, figs. 4–6). The abundant tubes are those of *Hyalinoecia tubicola*, the large starfish is *Zoroaster spinulosus*, the echinoids *Parameretia multituberculata*.

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FOREWORD

The Chatham Islands 1954 Expedition was organised and led by Prof. G. A. Knox of the Zoology Department of Canterbury University. The expedition was planned to explore the distribution of benthic and pelagic animals between the New Zealand coast and the Chatham Islands over the Chatham Rise, and to investigate the faunal affinities of the Chathams group, which lies in the Sub-tropical Convergence zone.

A substantial grant towards the cost of the expedition was made by the Council for Scientific and Industrial Research on the recommendation of the N.Z. Oceanographic Committee: further financial support was given by Canterbury University, Canterbury Museum, Dominion Museum and Canterbury and Southland Branches of the Royal Society of New Zealand. The expedition was carried out from the m.v. *Alert* under the command of her owner and master, Mr A. J. Black.

The scientific staff was drawn from the following organisations: Canterbury Museum (R. R. Forster); Canterbury University (G. A. Knox, E. W. Dawson, J. R. MacIntyre); Dominion Museum (R. K. Dell, J. M. Moreland); N.Z. Oceanographic Institute (D. M. Garner); Otago University (D. Marshall); Portobello Marine Biological Station (E. J. Batham); Victoria University of Wellington (J. C. Yaldwyn).

Prof. G. A. Knox has been responsible for organisation of the sorting and allocation of material. Type material from the expedition is deposited at Canterbury Museum. Preliminary editing of the manuscript has been carried out by Mrs P. M. Cullen. Miss G. L. Smith (Information Service, D.S.I.R.) has been responsible for final editing.

Further results of the expedition will be published in this series as the examinations of other animal groups are completed.

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

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The Scleractinia Collected by the Chatham Islands 1954 Expedition

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Abstract

Three previously described species of stony corals were collected by the Chatham Islands 1954 Expedition. The occurrences of these are given. Growth forms of *Flabellum knoxi* are described in particular relation to the living position of this coral. Living position of other *Flabellum* is discussed and evidence contributing towards identification of the living position is presented. Adaptive growth resulting from living positions is considered as reflected in the form of the corallum. Developmental patterns of abnormal coralla are described in relation to the external causal stimuli.

INTRODUCTION

Three species of corals were collected by the Chatham Islands 1954 Expedition, but only one was taken in large numbers of specimens. The coral fauna of both the Chatham Islands and New Zealand are at present inadequately known and the comparison of the coral faunas of these two areas is not enlightening. Of the three species collected, one, *Caryophyllia profunda*, is typical of the Southern Ocean faunas; a second, *Goniocorella dumosa*, is distributed throughout the western Indo-Pacific from Japan to New Zealand; and the last, *Flabellum knoxi*, the best represented species in the Chatham Islands collections, is known only from the Chatham Rise.

Corals were taken at only five stations, or 8 per cent of the 60 stations occupied by the Chatham Islands 1954 Expedition. If shore collections are eliminated from consideration, random sampling by dredging indicates the presence of coral in only 11 per cent of the stations, suggesting a general scarcity of coral in the vicinity of the Chatham Islands. Fig. 1 shows that the number of collections falls off rapidly with increasing depth. Faunas

living in waters less than 100 fathoms deep were sampled with some frequency, but corals were absent. If only dredgings in water greater than 100 fathoms in depth are considered corals were present in nearly 24 per cent of the trials, a much more substantial figure. Available hydrological data (Garner, 1957; Burling, 1961) do not immediately reveal an explanation for this distribution: Along the Chatham Rise there is a marked change in thermal gradient at about 100 fathoms. If this change marks the presence of subantarctic waters at this depth there may be cause for the absence of many of the more temperate water corals of northern New Zealand.

Only eight of the occupied stations were over mud substrates. From four of these *F. knoxi* was collected. Two of the remaining four stations were from considerably shallower depths (120–155 as opposed to 220–290 fathoms), and a third is recorded as a muddy sand rather than a true mud. The occurrence of *F. knoxi* on the Chatham Rise may well be governed by the distribution of mud substrates.

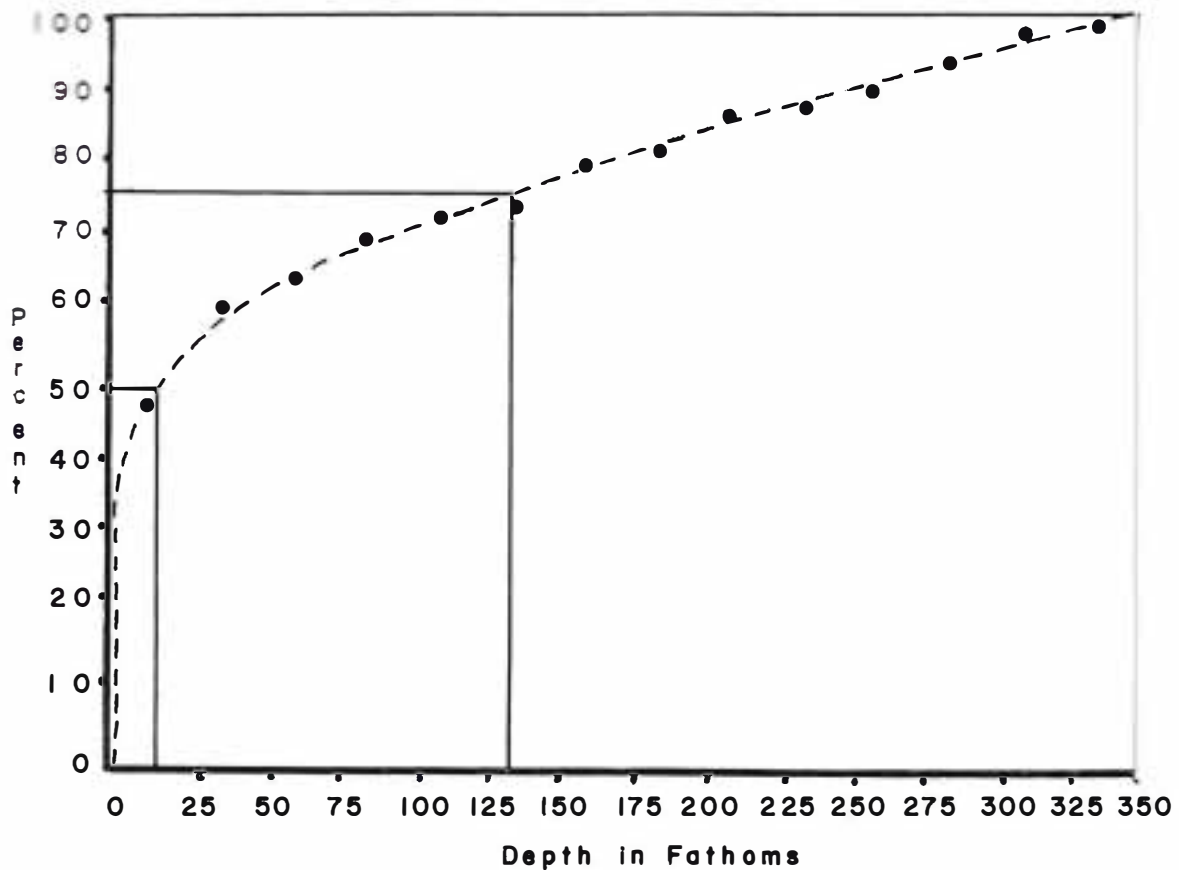


FIG. 1: Cumulative frequency curve of collecting stations of the Chatham Islands 1954 Expedition as a function of depth. The 50 and 75 percentiles are indicated.

Hurley (1961) has suggested the term *Serolis bromleyana* - *Spatangus multispinus* community for the abyssal benthic association found in many samples from the Chatham Islands - New Zealand area. This community, sampled at stations 6, 7, 41, 51, 52, 53, 58, and 59 of the Chatham Islands 1954 Expedition, also contains *Ophiuroglypha irrotata* (an echinoid), *Campylonotus rathburnae* (a decapod), *Hyalinoecia tubicola* (a polychaete), and the Mollusca *Nassarius ephamilus*, *Micantapex parengonius*, *Neilo australis*, *Falsilunatia powelli*,

Fusitron landonensis, *Fax alertae*, and *Coluzea mariae*. *Flabellum knoxi* is another constituent of this fauna (frontispiece), being found in four of the eight stations sampling the association. Although a noteworthy member of the community on the Chatham Rise, *F. knoxi* is not present in the known occurrence of the *Serolis bromleyana* - *Spatangus multispinus* community in New Zealand waters, for it has not been recorded and could scarcely have been overlooked.

LIST OF SPECIES

All of the species collected by the Chatham Islands 1954 Expedition have been previously described. All have been refigured photographically (Ralph and Squires, 1962) and accordingly are not treated here in detail. The type of *Flabellum knoxi*, and figured specimens of this species, as well as representatives of the other species are deposited at the Canterbury Museum, Christchurch.

Order **SCLERACTINIA** Bourne, 1900
Suborder **CARYOPHYLLIINA** Vaughan and Wells, 1943
Family **CARYOPHYLLIIDAE** Gray, 1847
Subfamily **CARYOPHYLLIINAE** Gray, 1847

Caryophyllia profunda Moseley, 1881
Subfamily **PARASMILIINAE** Vaughan and Wells, 1943
Goniocorella dumosa (Alcock), 1902
Family **FLABELLIDAE** Bourne, 1905
Flabellum knoxi Ralph and Squires, 1962

SYSTEMATIC ACCOUNT

Family **CARYOPHYLLIIDAE** Gray, 1847
Subfamily **CARYOPHYLLIINAE** Gray, 1847
Genus **Caryophyllia** Lamarck, 1801

Caryophyllia profunda Moseley, 1881

Caryophyllia profunda Moseley, 1881, p. 138, pl. 1, figs. 6, 6a, 6b. Ralph and Squires, 1962, p. 6, pl. 1, figs. 8–11.

Fragments and immature specimens belonging to this species were collected. The species is distributed through the Southern Ocean and around New Zealand, where it is apparently a member of the cold water fauna.

Material examined

Chatham Islands 1954 Expedition: Sta. 34.
Immature specimens and fragments of coralla.

Subfamily **PARASMILIINAE** Vaughan and Wells, 1943

Genus **Goniocorella** Yabe and Eguchi, 1932

Goniocorella dumosa (Alcock), 1902

Pourtalesmilia dumosa Alcock, 1902, p. 36, pl. 5, figs. 33–33a.

Goniocorella dumosa (Alcock), Yabe and Eguchi, 1932, p. 389; Squires, 1960, p. 197, pl. 33, figs. 1–4; Ralph and Squires, 1962, p. 11, pl. 4, fig. 1.

A few fragments of coralla of this species were obtained. It is possible that from somewhat shallower depths greater quantities of this colonial form could be obtained, for it is usually present in large masses of dead and living coralla.

Material examined

Chatham Islands 1954 Expedition: Sta. 34.
Fragments of coralla.

Family **FLABELLIDAE** Bourne, 1905

Genus **Flabellum** Lesson, 1831

Flabellum knoxi Ralph and Squires, 1962, pl. 1, figs. 4–6; pl. 2, fig. 7; pl. 3, figs. 3–5; pl. 4, figs. 1–4.

Flabellum knoxi Ralph and Squires, 1962, p. 14, pl. 7, figs. 1, 2.

The species has been adequately described in the original citation. Numbers of these large and handsome corals were taken in several trawls on the Chatham Rise where it is apparently common on mud bottoms at depths of 400–500 m. Of particular interest is the observed variation in form of corallum reflecting the attitude of the coral in life and having implications towards the interpretation of growth habit of many solitary Scleractinia.

Several specimens were unusual in form, one face of the corallum being concave, the other remaining flat or nearly so. The lateral edges of the corallum, instead of extending along a nearly straight line, were curved backward about the pedicel. Similar growths have been described from occurrences among fossil corals by Roger (1944) and other authors, and have been interpreted by Roger as resulting from differential growth stimulated by the falling over of the corallum. Similar growth forms described from middle Tertiary

horizons in Patagonia and Chile by Philippi (1887) as the genus *Lithomyces* were later reviewed by Frenguelli (1942). For ecological and systematic considerations, the correct interpretation of the unusual growth forms is important. Although the fossil forms and their systematics will not be dealt with here, and will be the subject of a longer discussion elsewhere, this opportunity will be

utilised to consider growth habit in some *Flabellum*, enlarging upon views expressed earlier (Squires, 1961).

Materials examined

Chatham Islands 1954 Expedition: Sta. 6, one specimen taken alive; Sta. 7, nine specimens taken alive; Sta. 52, six specimens taken alive; Sta. 59, one specimen taken alive.

TABLE 1—STATION DATA FOR THOSE DREDGINGS CONTAINING SCLERACTINIA (Data after Knox, 1957)

Stations	6	7	34	52	59
Latitude	43° 40' S	43° 42' S	44° 04' S	44° 04' S	43° 38' S
Longitude	179° 28' E	179° 55' E	175° 23·5' W	178° 04' W	177° 19' E
Area	Chatham Rise	Chatham Rise	E of 44' S	Chatham Rise	Chatham Rise
Depth	403 m	512 m	238 m	476 m	531 m
Substrate	Fine grey sandy mud	Fine grey sandy mud	Fine sandy gravel	Fine green sandy mud	Fine green sandy mud
Bottom temperature			51·9°F	43·5°F	45·5°F
Bottom salinity			35·00%	34·97%	34·48%
Species taken	<i>F. knoxi</i>	<i>F. knoxi</i>	<i>C. profunda</i> <i>G. dumosa</i>	<i>F. knoxi</i>	<i>F. knoxi</i>

LIVING POSITION OF *Flabellum*

GENERAL CONSIDERATIONS

The normal life position and body orientation of many free-living solitary corals found below the depths attainable by diving is unknown. Attached forms of coral can be collected by a variety of means, many of which will indicate the position of the surface of attachment and therefore, the position and orientation of the coral. For deeper-water free-living species, the only promising methods of determining life position are remote visual aids, particularly bottom photography. Unfortunately corals are not sufficiently common to provide anything except chance photographic coverage of a relatively few of these deeper water species, and much important information about their habits remains unknown. As a result, many of the oft-quoted statements concerning the position in life are based upon deductive arguments. Gardiner (1939, p. 247) wrote:

“Freedom [of the corallum], when not genetical, is often a matter of weight; the cone tumbles and from it a bent horn may be produced by further growth, the mouth bending away from the ground, the whole calicle comfortably rocking if there are any slight currents.”

Gardiner clearly indicates the probable development of a cornute corallum from the accidental release of a lightly attached coral. Also implied is a preferred position for the polyp with the oral surface oriented upward, away from the substrate.

Wells (1937, p. 16, footnote) suggested that negatively geotrophic growth might be a primary factor in coral development and in the determination of form. Vaughan and Wells (1943, p. 62) stated with direct reference to the flabellids:

“In all sessile and free-lying anthozoans the oral disc is directed upwards and away from the bottom (towards the source of food), and it may be presumed that the free living flabellids and conical turbinolians are no exception to this rule. The flabellids may rest upright in the mud with the sharp base pushed deeper into the mud as the coral increases in size . . .”

Important in this statement is the suggestion that free-living flabellids are upright forms, the corallum erect on the sediment surface, stabilised by those portions of the corallum which have penetrated into the substrate.

Much of the confusion regarding form response to environment, or so called “plasticity” of shape of the corals has arisen from over-generalisation of data, particularly in the instance of life position. From a consideration of only a few types of coral for which such information is available, variation of coralla with respect to ecology must be carefully considered in the instance of the solitary corals. Colonial forms will have much more latitude in the development of the colony for each newly budded polyp will define, even within a small limit, the shape of the next stages of growth. Such

small alterations compounded through thousands of minor adjustments can result in striking morphological response of the colony to the environment.

Within the positional potential of corals such as *Flabellum* are several methods of life while fixed to the substrate and several ways of free life. Among the types of species of this genus which remain attached to the substrate throughout their lives are *F. rubrum*, *F. thoursii*, and *F. impensum*, all of which may add calcium carbonate structures at various times in their life to strengthen the attachment of the corallum to the substrate much in the manner of *Monomyces* (Squires, 1961, 1963). Basic form of the skeleton in these species is regular and is rather consistently reproduced. Exceptions in corallum form are readily attributable to abnormalities of growth pattern induced by crowding, or eccentricities in the shape of the substrate. Another species of the genus, *Flabellum curvatum*, begins life attached to the substrate, but only lightly so, and eventually becomes free, the corallum lying on its side on the substrate. There is no doubt that the corals are successful and continue to thrive in this way of life (Squires, 1962, fig. 1). Subsequent growth of the corallum of these corals is often irregular, or the corallum form approaches the cornute. The mechanics of this growth are probably identical with those postulated for *Caryophyllia* (Wells, 1937).

Ways of becoming free are perhaps more striking because of their dynamism, for it is assumed that all flabellids begin life attached to some bit of substrate and are therefore, at least initially, attached. The most dramatic method is perhaps that of the *Flabellum stokesii* group, including a multitude of forms apparently strobilising from an attached trophozoid, the anthocyathus being free. The trophozoid stage of this species is similar in form to, and has been confused with, *F. rubrum*. More commonly, however, freedom is attained by the simple procedure of incorporation.

In the instance of *F. curvatum*, the larval stage attaches to a bit of substrate that is too small to afford the increasingly larger polyp with indefinite stability. At some stage in the growth of the coral, the centre of gravity is raised sufficiently high from the surface of the substrate so that stability given the unit by the weight of the attached substrate and such penetration of the substrate by the corallum as may have occurred, is insufficient to maintain the upright position of the coral. Other species initiate corallum development in the same fashion as *F. curvatum*, but stability and an upright position are maintained throughout the life of the coral, as, for example, in *F. pavoninum*

and *F. knoxi*. The larvae of these species settle on some very fine bit of substrate such as a grain of sand or a minute shell fragment and begin secretion of the skeleton. The original attachment, because of its minute size, is rapidly incorporated into the skeleton of the coral and is no longer of any significance in imparting stability. Erectness of the corallum is achieved and maintained, however, by the sinking of the pedicel into the substrate as the corallum grows. These corals are generally found in areas of soft bottom sediments (which allow easy penetration by the corallum) and presumably are also living where there is low current activity, for the centre of gravity of the polyp-corallum system remains fairly high. The corallum of these species may have crests or flutings developed along the lateral edges which have, in the past, been thought to represent stabilising structures. Evidence to be presented here suggests that they are not adaptations for this way of life, but are, in all probability, only excess of calcium carbonate secreted by the tissues where they are crowded in the angular extremities of the corallum.

The developmental histories of *F. curvatum* and *F. pavoninum* are then quite similar, both having early stages attached to a small portion of substrate which does not afford stability for the adult. In the case of *F. curvatum*, attachment to small particles of substrate does not seem to be preferred, but rather is dictated by the absence of larger materials upon which the larvae can settle. This point will be enlarged upon in another place, but suffice to suggest here that as a derivative (?) of *F. thoursii*, a securely attached form, *F. curvatum* is adjusting to a new ecological condition and is able to survive without remaining in an upright position. The contorted and curved coralla of this species, which sometimes approach the cornute, suggest that the polyp is oriented negatively with respect to the substrate and attempts to reorient itself. *F. pavoninum*, on the other hand, has a long evolutionary history, and represents adaptation for life on substrates of fine material. I have not seen a specimen of this species group attached to a large object, despite the fact that many collections have been made from substrates which potentially could furnish such material.

There are species among the *F. pavoninum* species group, which apparently live in a horizontal, or prone, position with the major plane of symmetry of the coral more or less horizontal. The small amount of corallum deformation in this group, induced by life in this position, suggests that it is normal for the species. It would be expected that strong geotrophic reactions would be found among those corals which live attached (particularly those

living below the depth at which phototropisms are effective as orienting devices), while free-living corals would show less reactivity to these stimuli.

DEFINITION OF TERMS

For those species of *Flabellum* in which the two sides of the corallum have become elongate and which tend to meet in an acute angle, a system of nomenclature for the corallum has grown up which requires some modification for the present discussion. Meanings of most of these terms are evident from fig. 2. Two additional terms are defined as:

REFLEXED CORALLUM—a corallum with asymmetrical lateral faces, the more concave of which is bent more-or-less sharply near the upper edge so as to become more strongly concave. Such an increase in concavity may be gradual, with a curvature progressively increasing in intensity, or it may be sudden and marked by a pronounced geniculation. Reflexure results in asymmetry of the corallum of a greater or lesser extent. It is measurable either through assessment of the concavity of the face, or by the amount of shortening of the "straight-line" height of the reflexed face.

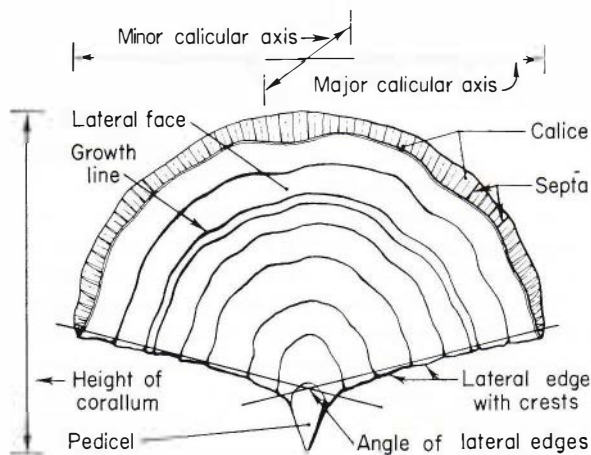


FIG. 2: Diagrammatic representation of a corallum of the *Flabellum pavoninum* type. Significant morphological features are indicated. In particular, note the method by which the angle of the lateral edges is measured.

RECURVED CORALLUM—A corallum more-or-less symmetrically developed, but in which the angle formed by the lateral edges exceeds 180° . A recurved corallum is generally also reflexed. Although recurvature of the lateral edges begins as a continuation of the lateral edges as straight terminations of the lateral faces, it may culminate in highly curved lateral edges as the upper margin of the lateral face is constructed in an upward and lateral direction with greater rapidity. In its final

form, recurvature results in the pedicel being enclosed in a fornix formed by the lateral edges.

UPRIGHT—A corallum position in which the axial plane of symmetry is essentially vertical. The oral surface of the polyp is more or less horizontal and faces upward. Such an orientation presumes that stability is achieved through attachment of the corallum to substrate objects or by penetration of portions of the corallum into the substrate. Such an orientation is presumably a response to a negative geotropism or such other orienting tropisms as may be effective.

PRONE—A corallum position in which the axial plane of symmetry is essentially horizontal. Stability of the corallum results from a lowered centre of gravity of the corallum polyp unit, or from assumption of a hydrodynamically less resistant position, or from both. Orientation of the polyp with respect to the substrate is not determined by position or growth, although subsequent secretions may demonstrate negative geotrophic responses.

DETERMINATION OF LIVING POSITION

It is possible to test hypotheses concerning the life position of some *Flabellum* for the skeletal wall of these corals is formed of an epitheca. This surface, relatively smooth, is formed during the upward (relative to direction of growth) withdrawal of the calcium carbonate secreting edge-zone of the polyp, and is, as a result, exposed for the settlement of the larvae of benthic organisms. Exceptions are noted in a number of species, as, for example, *F. deludens*, in which the epitheca remains as a glistening surface, untouched by foreign objects. These striking cases need further study to determine the nature of the wall and the possible presence of antibiotic substances inhibiting the settlement of larvae.

The *Flabellum* dealt with in this study usually have benthic organisms attached to one, or both, of the planar lateral faces. By examination of these organisms, the orientation of the corallum can often be derived, for if one face bears epifauna, and the other shows traces of burrowing organisms, or is clean, it is a reasonable supposition that the first-mentioned face was upwardly oriented and not immersed in, or close to, the substrate. Similarly, the presence of live epifauna on both faces of the corallum indicates an upright position or the erect orientation. Both premises require evidence from a coral collected while still living for the determination of orientation; coralla without polyps cannot be utilised, nor can fossils be used for this type of determination.

The possible selective preference for one or the other face of an erect coral by settling larvae of epifauna, because of directive ecological factors, was not considered as important. The depth from which the samples were taken eliminates many factors and the effects of those which may be operative, particularly current action, are believed to be randomly distributed through both samples so that no bias is introduced. Within the limits imposed by dangers of circular reasoning, the possibility of preferential settling of epifauna may be tested by consideration of corallum shape. When such a test is imposed, no preference is seen in the samples. The possibility of prone specimens being oriented with respect to a bottom current, particularly in view of the possible locomotive powers of the polyp in such an orientation, was considered. No means of testing such a hypothesis aside from photographic observation was devised. *F. curvatum*, a prone form, was photographed in numbers on the Falkland Trough (Squires, 1961, fig. 30) and the coralla show no orientation. How broadly this observation may be applied remains to be seen.

The collections of the Smithsonian Institution contain several large collections of *F. pavoninum*¹ from the Philippine and Hawaiian Islands. These collections were examined with respect to the life orientation of the corals, the results of this examination being tabulated in table 2.

In the construction of tables 2 and 3 it was found that evidence of a prone position for the corallum was more easily obtained than that for an erect position, particularly as the nature of the latter evidence is essentially negative. Only corals collected while alive were considered. Organisms found attached to the lateral faces were examined with particular attention to their ecologies. Presence of holdfasts or colonies of such organisms as stylasterine corals, alcyonaria, erect sponges, barnacles, or cheilostome Bryozoa on a lateral face was taken to indicate that the face was directed away from the sediment and that it was not immersed in the sediment. If, at the same time, the other face lacked evidence of such holdfasts, or had evidence of burrowing or boring animals, aggluti-

¹*Flabellum pavoninum* is utilised here in the sense of Vaughan (1907) as this is perhaps the latest attempt at a taxonomy in this group, but it is clearly apparent that in addition to the many varieties recognised by Vaughan (many of which should be considered as valid species) there are at least three undescribed Indo-Pacific species which are included in the group *F. pavoninum typicus*, based upon differences in characters of the septa, the mode of insertion of the septa, and the biology of the corals. The specimens considered here are representative of only one of these presumed species.

TABLE 2—DATA FOR DETERMINATION OF LIFE POSITION IN POPULATIONS OF *Flabellum pavoninum* FROM THE PHILIPPINE ISLANDS AND *Flabellum paripavoninum* FROM THE HAWAIIAN ISLANDS¹

	Number of Specimens	Percentage of Total Sample
<i>Flabellum paripavoninum</i>		
Number of specimens examined . .	45	100
Epifauna on both sides of corallum . .	41	91
Epifauna on one side of corallum	4	9
Epifauna absent from corallum	0	0
<i>Flabellum pavoninum</i>		
Number of specimens examined . .	53	100
Epifauna on both sides of corallum . .	4	7.5
Epifauna on one side of corallum	23	43.4
Epifauna absent from corallum, or evidence equivocal	26	49.1

¹Specimens of *F. pavoninum* were from the following *Albatross* Expedition 1907–10 stations: D 5116, D 5117, D 5118, D 5273, D 5280, D 5281, D 5392, D 5393, D 5412, D 5505, D 5523, D 5590. All stations are in the Philippine Islands. Full station data are given in Anonymous (1910). Specimens of *F. paripavoninum* were taken from *Albatross* Expedition 1901–2 Station D 4080. This station, off Puniawa Point, north coast of Maui Island, was made in 178–202 fathoms, on a grey foraminiferous sand bottom.

nated worm tubes or other similar objects, it was taken that this face was against the sediment or on the sediment-water interface. The corallum was then considered to have been prone.

Often, however, the evidence was not clear cut and these coralla were placed in the category of "unknown orientation." When evidence of epifaunal growths and holdfasts was found on both faces, and such growths were absent from the pedicel and lateral edge regions of the corallum, it was assumed that the corallum was oriented in an upright fashion. In all of these arguments it is a presupposition that the polyp is never immersed below the sediment-water interface. This assumption is probably valid, for there is evidence among some upright coralla, of the upward retreat of the polyp along a line representing successive levels of sediment accumulation. At the present time there is no evidence of any coral inhabiting the substrate although a semi-burrowing mode of life has been postulated for several of the turbinolid corals (Vaughan and Wells, 1943, p. 62).

Although only slightly more than half of the specimens examined could be oriented with certainty, the greater number of those which could be were found to have been prone during life (table 3).

TABLE 3—LIFE POSITION OF *Flabellum pavoninum*¹

	Number of Specimens	Percentage of Total Sample
Number of specimens examined ..	53	100
Specimens living in prone position	23	43.4
Specimens living in upright position	4	7.5
Specimens for which orientation could not be determined ..	26	49.1
Number of specimens for which orientation was established	27	100
Specimens in prone position	23	85.2
Specimens in erect position	4	14.8

¹Sample data given in table 2.

TABLE 4—FORM OF CORALLUM IN RELATION TO LIFE POSITION OF *Flabellum pavoninum*¹

	Number of Specimens	Percentage of Sample
Prone coralla ..	23	100
Upper face concave	19	82.6
Upper face convex	1	4.3
Upper face flat	3	13.1
Lower face concave	12	52.2
Lower face convex	1	4.3
Lower face flat	10	43.5
Specimens with concave upper face ..	19	100
Specimens with recurved upper face	2	10.5
Specimens with non-recurved upper face	17	89.5
Number of specimens examined ..	53	100
Specimens with plano-concave faces	19	35.8
Specimens with concavo-concave faces	23	43.4
Specimens with bi-planar faces ..	6	11.3
Specimens with concavo-convex faces	4	7.6
Specimens with plano-convex faces	1	1.9

¹Data for specimens examined given in table 2.

All but two specimens showing evidence of the prone position were taken from mud bottoms, the exceptions being from sand substrates. Correlation between substrate and attitude is apparently low, for upright specimens were present in collections from both types of substrate.

Of interest is the morphological expression of the prone habit of the corallum. Should the polyp endeavour to right itself through the process of differential growth, the resulting corallum should be cornutiform. However, the two lateral faces of *F. pavoninum* are usually concave (table 4), the degree of concavity approximating a logarithmic function. The earliest formed portion of the wall is nearly plane, but the curvature of the wall increases proportionately more than height, so that near the upper margin of the corallum the wall is bent sharply, but smoothly, outward. Expressed differently, increase in polyp width as measured along the minor axis of the corallum increases proportionately faster than corallum height. Variation noticed

in the conformation of the lateral faces is largely the result of external influences. Repair of a broken corallum generally is evidenced by that injured face being, at least in the region of the injury, convex outward.

As seen in table 3, over 80 per cent of the specimens examined have at least one concave lateral face, nearly half of those examined having both faces concave. Among those specimens known to be lying on one side, 52 per cent had a concave lower face and less than 5 per cent had a convex lower face. The upper face of the corallum in these prone specimens was in nearly 83 per cent of the instances concave. There is then an asymmetry in the lateral profile of the corallum, the upper face tending to become more concave, and the lower face tending to become less concave, perhaps with a more pronounced tendency to be flat. Such asymmetry is not sufficient, even if continued indefinitely (an impossibility, for the resulting corallum would house a polyp whose dimensions would be astronomical after a very short increase in height), to produce a cornute corallum, for in this form both faces must be curved upward, the upper being concave, the lower convex.

Another morphological expression of the prone position of the corallum which might be anticipated is the reflexure of the upper face. As discussed later in this study, the reflexure of the upper face is considered to be a normal part of the righting behaviour of a disoriented polyp. Reflexure was observed in only two specimens of the 53 examined. In respect to that portion of the sample in which the upper face was concave, these specimens represent only 10 per cent of the sample. Both of these specimens are also recurved.

The significance of lateral edge angle variation in the systematics or ecology of *Flabellum* has not been satisfactorily determined. Vaughan (1907) utilised the character in defining the different varieties recognised. Ralph and Squires (1962) independently concluded that lateral edge angle was not of systematic value for *F. rubrum* and found that variation in this character could not be correlated with several ecological variables considered. There is no particular correlation between the angle formed by the lateral edges and the position in life of the coral in the instance of *F. pavoninum* as shown in table 5. Prone coralla are found having a variety of lateral edge angles, but show a bias towards a value of 180°, a factor more probably genetic than ecologic. Variation in the lateral edge angle is approximately that of *F. paripavoninum* as measured in a single population from the Hawaiian Islands (fig. 3). This latter species is an upright form, none of the 51 specimens

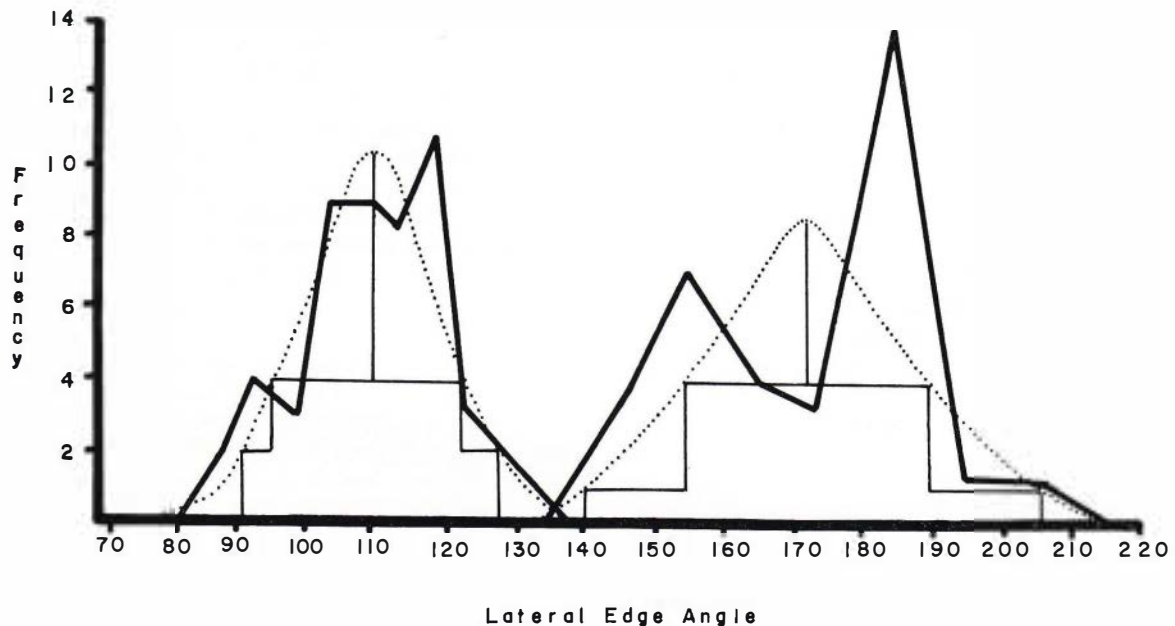


FIG. 3: Comparative curves of the distribution of the lateral edge angle as measured in two populations. Curve on the left is for *Flabellum paripavoninum* from the Hawaiian Islands. Collection data are given in table 2 and statistical parameters in table 5. The right-hand curve is for *Flabellum pavoninum* from the Philippine Islands. Sample data are given in table 2 and statistical parameters in table 5. The lightly drawn curve is a fitted normal distribution for these data for each curve. The two rectangular areas within each curve represent the first and second standard deviations and the position of the mean for each distribution.

examined showing any evidence of having been in a prone position. Coefficients of variation for the two populations are both 9.35 (table 6). The distributions shown graphically in fig. 3 represent the lateral edge angle distribution in the population of *F. paripavoninum* which closely approaches a normal distribution although slightly skewed to the left ($\alpha_3 = -0.168$). For the population of prone *F. pavoninum*, the sample distribution also shows skewness ($\alpha_3 = -0.198$), a definite bias towards a measurement of 180° . Both curves derived from the sample populations are platykurtic (table 6). In this instance, the assumption that lateral edge angle variation is normally distributed, and is essentially genetically controlled, seems to be warranted.

It may be concluded that cornutiform coralla are not the inevitable result of the continued

growth of a coral in a prone position. Such a conclusion could be reached with less arduous efforts than those used in the reasoning here. What is of significance is the recognition of at least one species of *Flabellum* in which the prone position is apparently normal, and in which reaction to this position in the form of differential growth is minimal. Further, this "species" shows adaptation to life in the prone position in the enlargement of the oral area of the polyp as reflected in the increased calicular length represented by the recurvature of the corallum. Distortions of the "normal" symmetrical growth pattern which have been described are of small magnitude and indicate either a tolerance to the prone position, amounting to adaptation, or total inability of the polyp to rectify an accidentally assumed position.

TABLE 5—RELATIONSHIP BETWEEN POSITION IN LIFE OF *Flabellum pavoninum* AND THE LATERAL EDGE ANGLE¹

	180°+	180°	170°	160°	150°	140°	130°	Totals
Specimen prone	3	9	2	5	1	2	22	
Specimen upright	2	2	1	1	3	2	22	
Position not known	3	25	1	3	6	4	46	

¹Data from specimens in samples described in table 2.

TABLE 6—STATISTICAL PARAMETERS FOR TWO POPULATIONS IN WHICH LATERAL EDGE ANGLE WAS STUDIED¹

	<i>Flabellum paripavoninum</i>	<i>Flabellum pavoninum</i>
Sample size (n)	52	32
Range	87°–134°	145°–200°
Median	109·5°	174°
Mean	109·75°	171·69°
Standard deviation (σ)	10·26	16·05
Coefficient of variation (V)	9·35	9·35
Skewness (α_3)	–0·168	–0·198
Kurtosis (α_4)	2·6	1·9

¹Data for samples given in table 2.

FORMATION OF THE RECURVED CORALLUM

In *F. pavoninum* the two lateral faces join in such a way that an acute angle is formed with very little rounding of the narrow ends of the calice. This condition contrasts with another group of *Flabellum* (cf. *F. pavoninum* var. *latum* of Vaughan, 1907) in which the lateral faces of the corallum join along a smoothly rounded juncture. The acute lateral edge is particularly characterised by the development of irregular deposits of epitheca which have been called crests or flanges and which in the past have been interpreted as stabilising structures aiding in the upright support of a broadly explanate corallum. These crests are absent in the type of corallum with rounded lateral edges.

The interpretation of the function of the crests may now be questioned, for the presence of crests on specimens determined to have lived in a prone position suggests a non-adaptive nature of the structure. Presence of flanges on coralla which are recurved is clear evidence that they were non-functional, at least in these instances. A more probable interpretation is that the narrow angle formed by the lateral edges causes some constriction in the polyp with the result that the crowded tissues deposit "excess" of epitheca during the retracted stage. There are instances among the coralla studied of the acuity of the lateral face juncture decreasing until a rounded edge is formed, and at this point the crests have diminished in size and are no longer present. It must be remembered that, when extended, the polyp rises high above the corallum and that in the extended position there is considerable freedom of the polyp with relation to the corallum.

The formation of the recurved corallum can result only from the phenomena of induced lateral growth of the polyp along the lateral margins of the corallum as well as along its upper edges, i.e., holoperipheral growth (equal growth rates along all portions of the calice periphery). The longer dimension of the corallum, measured along the curved calicular margin, lengthens relative to

height either in response to growth stimulated by the position of the corallum, or in the case of prone coralla, as a normal variation of the growth pattern. The medial portions of coralla of the *F. pavoninum* type enlarge more rapidly than the lateral portions. In some species the differential growth may be extreme, as, for example, in *F. circulare* (Squires, 1958, pl. 12, fig. 12). Elongation of the lateral portions of the corallum results from equal growth rates along the perimeter of the calice, but the conical enlargement of the corallum is decreased as the angle of the lateral edges reaches 180° and extends no more. Holoperipheral growth, on the other hand, in which all portions of the margin are growing at the same rate, results in continual enlargement of the conical corallum and is, in the end, expressed by lateral edge angles in excess of 180°, except in the instances where conical increase in size is achieved by the polyp through the upward arch-like growth of the columella, which extends the effective basal diameter of the corallum greatly. It is interesting to note that this type of growth occurs in Vaughan's *F. pavoninum* var. *latum* which has rounded junctures of the lateral faces.

Recurvature is an expression of allometric, genetic, growth rates and is variously influenced internally and externally by ecological (chiefly positional) factors. Recurvature may be the result of a normal pattern of growth or may represent a reaction on the part of the polyp to an abnormal situation with consequent disruption of normal growth routine.

Recognition of various types of recurvature is as important in interpreting recurvature as recognition of that condition is in systematic and ecological work. Coralla having recurved, but straight, lateral edges (pl. 3, fig. 1) can only be interpreted as resulting from normal variation occurring among coralla which have a normal prone living position. Normal variation of specimens having an edge angle of about 180° might be expected to produce angles in excess of this value, particularly among prone forms. These types could be readily distinguished by their straight lateral edges, for the angle in excess of 180° would be genetically determined and the corallum would be formed from the earliest growth stages with this angle.

On the other hand, recurvature induced by accidental assumption of the prone position will result in abnormal recurvature in which the lateral edge is not straight. In the expanded state as the polyp curves upward and outward from the corallum, secretion will be directed in a new manner along the upper edge of the calice, and the polyp will be able to expand at the juncture of the

lateral faces as this point will no longer be against the substrate. Thus, in holoperipheral growth, the lateral edges will grow as will the calicular margins. The induced growth of the lateral edge will cause continual enlargement of the corallum at this point, resulting in a curved lateral edge, rather than a straight one.

RECURVATURE AND REFLEXURE IN THE CORALLUM OF *Flabellum knoxi*

Seventeen specimens of *F. knoxi* were collected by the Chatham Rise 1954 Expedition, two of which show extreme recurvature, greater than any yet discussed. One specimen is of an intermediate type morphologically between the recurved and reflexed specimens and the more normal growth forms. The angle formed by the lateral edges of the corallum of *F. knoxi* is usually between 170° and 180°, and the lateral edges are rounded, not sharp. Crests are absent from the lateral edges. The two lateral faces are slightly concave and show no evidence of asymmetrical growth. In short, there is every evidence from the general morphological form that this is a species which lives erect and upright with the pedicel embedded in the substrate.

All of the asymmetrical specimens show evidence of having been broken off just above the pedicel early in their development and of the corallum having been greatly regenerated. The relationship between this injury and deformity of the corallum is of great importance for it can be demonstrated that deformation of the corallum of these forms began at the time of the regenerated growth. This is in contrast to the prone *F. pavoninum* discussed above in which deformed growth and regeneration are discrete and independent factors. Predation on *F. paripavoninum* was not as marked as in the latter species, but it is apparent from observation of almost all species of *Flabellum* that corallum breakage is not uncommon. The cause of the breakage is believed to be the result of crushing of the corallum by bottom feeding fish.

The pedicel of the least deformed of the deformed *F. knoxi* has been broken off, and the injury healed (pl. 4, fig. 3; pl. 3, figs. 3-5). The corallum was broken back to a height of 15 mm and apparently split longitudinally, although this injury was also healed. From this point, growth was asymmetrical the lower face becoming curved and convex, while the upper face became concave. No reflexure or recurvature is present. At least half a dozen other injuries can be seen recorded in the corallum, all of which were healed. It is postulated that at the time of the initial injury the corallum of this coral was larger than the 15 mm indicated.

A second specimen, a complete one (pl. 4, fig. 4; pl. 1, figs. 4-6) shows deformity commencing at a height of about 14 mm with differential growth increasing with height. There is only slight evidence of injury at this early stage although there are three healed scars elsewhere on the corallum. For a height of 20 mm the angle formed by the lateral edges remained at approximately 180°, although through this same growth the upper face was markedly concave and the lower convex. Through a height of 34 mm the lateral edges grew at the compound angle of about 250°, the departure from the 180° orientation being sharp, and the growth at the new angle being almost straight. At a height of 40 mm, the lateral edges extend straight back and are nearly parallel. Finally, at a height of 75 mm, the upper face of the corallum is geniculated and grows vertically. This portion of the corallum was badly damaged during collection. Of considerable interest is the narrowness of the calicular opening through most of this growth. At the geniculation, a height of 70 mm, the calice is only 33.5 mm in minor diameter. This contrasts with a corallum minor diameter of 51.0 mm at the same height in a normal specimen, and 65 mm in the specimen described above at the same height.

The third deformed specimen was badly broken during collection. It shows strong evidence of having been broken back during life to a height of 14 mm, the upper edge of the corallum being quite ragged at that point. From that height onward, growth was asymmetrical, but the recurvature of the corallum around the pedicel is much sharper and is more or less in the form of a continuous curve rather than a series of discrete linear developments. The end of the growth series is again, a state where the uppermost portions of the lateral edges are growing parallel, but in a reversed direction. The corallum of this form is somewhat more open, having a minor diameter of 39 mm at the base of the geniculation. The sharp undulations in the upper face become almost angular (pl. 2, fig. 7).

The incidence of highly recurved and reflexed coralla among *F. knoxi* indicates that for species in which the normal position of the corallum is upright, there may be overturn, and that the resultant growth stimulus may be reflected by a deformation in the growth gradients of the corallum. As such stimuli may be of variable intensity and effect, it is possible that the resulting forms would be of a complete series from the moderately deformed to the complexly contorted corallum. Slow overturn with resulting low intensity stimulus can be contrasted with rapid or catastrophic

overturn with sudden stimulus. The age at which overturn occurs would similarly be a factor in determining final form.

In the instance of *F. knoxi* the stimulus for two specimens was severe, while in the third it was only moderate. The mechanism for the overturn seems to be a form of predation. For two of the specimens there is good evidence of corallum breakage before the recurrence of growth in the new directions.

Reconstruction of the events of the two severely deformed coralla begins with normal growth of the corallum to an unknown size, probably considerably in excess of that indicated by the broken stub of the corallum. After the corallum was displaced, broken, and the polyp damaged, the polyp regenerated tissues and commenced secretion of new corallum in response to the new orientation. Because of the disparity in lengths of the calicular axis, the polyp was unable simply to grow in a new direction, but rather extended itself upward all along the margins of the calice, the tentacular ring and oral surface at the lateral portions of the corallum probably extending both upward and backward (relative to the pedicel growth direction) in the attempt to regain the upward orientation. This display of the polyp around all edges of the upper face of the corallum resulted in the secretion of carbonate along the entire calicular margin and in growth of the corallum holoperipherally, leading to recurvature. As recurvature began, the stress was not alleviated, for the polyp was still forced to reach over and around the upper margin of the corallum. The curve of the corallum edge as it recurves about the pedicel resulted in irregularities in the smoothness of the curve developing from differential growth rates respective to time. The diameter of the lacuna formed about the pedicel is dependent upon the time at which new growth commences.

Reflexure of the corallum was apparently a different matter. It would seem that the simplest growth pattern leading to a righting of the corallum would be upward, vertical growth, resulting in a sharp geniculation of the corallum. Rather, the increase in width of the polyp along the minor axis of the corallum continued at about the same general rate as that of normal corals. The stimulus acting upon the coral was directed at the upper half of the tentacular ring, for the lower half was only at a somewhat lessened advantage in the fallen over position. There was no apparent growth change on the lower face, which remained flat. The polyp was apparently unable to adjust to this new position by widening of the oral disc, and was constrained by the normal genetically controlled growth ratios.

RECURVATURE AND REFLEXURE AMONG FOSSIL *Flabellum*

Among the literature on recurvature and reflexure in fossil *Flabellum* there are only two significant papers. Frenguelli (1942) in a very important paper, generally overlooked, has treated the Patagonian forms, and Roger (1944) has dealt with occurrences in Algeria in some detail. Additional evidence is available from the fossils from the New Zealand Tertiary which has considerable bearing on the subject and which will be dealt with in another study.

The mechanism of recurvature and reflexure is discussed by Roger (1944) and it is of interest to review his work and compare the results of his study with the conclusions reached here. Roger discovered two complete, five corroded, and numerous fragments of coralla of an extremely contorted form of *Flabellum* in the lower Pliocene sediments of Morocco. These were associated with normal growth forms of *F. avicula*, with which Roger aligned the contorted forms. These are considered the gerontic results of exaggerated growth resulting from the falling over of the corallum of *F. avicula* and the stresses on the polyp induced by this accident. Roger (1944) noted the deficiencies in this argument: (1) the much greater size and complexity of the abnormal forms; (2) the absence of intermediate individuals in the fauna; and (3) absence of similar developments in the modern fauna. To these should be added the absence of solid evidence of the upright live position of *F. avicula*.

A comparison of the "gerontic" *Flabellum* with *F. avicula* would need to be more penetrating than that of Roger to enable a conclusive answer to the systematic relationships between the two. If it can be demonstrated that the two forms are identical, then there is no question but that the growth represents an adaptation of the corallum to the exigencies of life. In this same respect, the absence of intermediate forms seems indicative of genetic rather than environmental control, for although the forms described by Roger are undoubtedly end products, lesser degrees of development should result unless all individuals fall over at the same size and hence age, a not impossible occurrence. An answer, of course, to Roger's final argument (3), is the present description of fallen-over forms from modern seas.

Rogers affirmative argument for the "gerontic" forms being a development of abnormal growth stimulation is weakened by comparison with modern forms such as *Caryophyllia*. Generalised

plasticity of form based upon a few incompletely studied types has led to unfortunate results in the systematics of the Scleractinia. It has been shown in this study that there are several growth habits

among the *Flabellum*, and that although adaptational growth from abnormal living position may appear as "morphological plasticity", such variability is not general in its application.

SUMMARY

Flabellum knoxi has been observed predominantly in its normal growth form. Three individuals departing from this type have been described in detail and the causation of the abnormal growth considered. Comparisons have been made to other *Flabellum* both living and fossil. It has been shown that:

1. Life position among *Flabellum* is quite variable, some forms preferring an upright position, others apparently living on their side.

2. For many species, life position can be determined from inspection of the corallum alone.

3. Plasticity in growth must be limited in application to individual species and the exigencies under which they have developed.

4. Stimulated differential growth from falling over occurs only among those *Flabellum* which

habitually live upright, those types living with the corallum horizontally directed show only random variation in the directions of the reactionary growth.

5. Upright living types, upon overturn, begin corallum growth reflecting attempts at the righting of the upper half of the polyp relative to the surface of the substrate.

6. The upper portion of such coralla are deformed while the lower portion remains relatively normal in configuration.

7. Deformation of coralla through differential growth externally stimulated will yield a variety of types of graded complexity indicating varying degrees and types of stimulation.

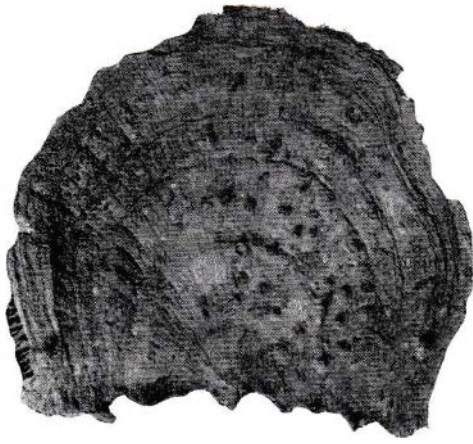
8. Deformation of growth in *Flabellum knoxi* is stimulated by overturn of the corallum after injury possibly by predation.

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PLATE 1

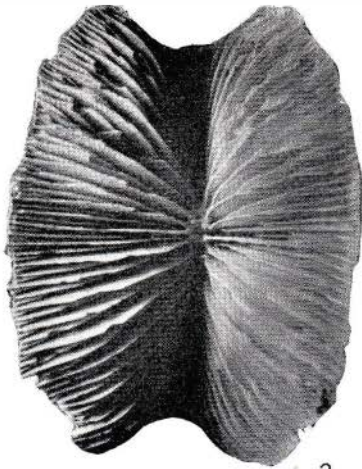
- 1, 2 *Flabellum pavoninum*. Approximately $\times 1$. U.S. National Museum 45483, Philippine Islands, *Albatross* Station D5273. 1. The obverse lateral face of a prone corallum. The specimen is slightly recurved and reflexed. Note the basal attachments of various organisms on this face and the slight asymmetry of the calice. 2. The corallum seen from the anterior. The reverse face of this corallum is shown on Pl. 3, Fig. 1.
- 3 *Flabellum pavoninum*. Approximately $\times 1$. U.S. National Museum 45484, Philippine Islands, *Albatross* Station D5273. The obverse face of a prone specimen. Note holdfasts on upper margin of the lateral face.
- 4–6 *Flabellum knoxi*. Approximately $\times 0.75$. Chatham Islands 1954 Expedition, Station 6. The most recurved and reflexed specimen taken. Also figured in Frontispiece. 4. The reverse or basal face. 5. Calice seen from the anterior with the reflexed face up, the basal face down. 6. The obverse or reflexed face showing the corallum as it would appear in the life position.



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4



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PLATE 2

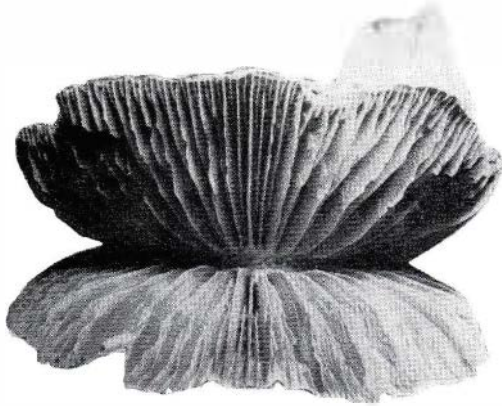
- 1, 2 *Flabellum pavonium*. Approximately $\times 1$. U.S. National Museum 45485, Philippine Islands, *Albatross* Station D5392. 1. The obverse side of a prone corallum having a heavy epifaunal growth. The corallum is slightly reflexed and recurved. 2. The same corallum seen from the anterior. The reverse face of this corallum is figured on Pl. 3, Fig. 2.
- 3–6 *Flabellum pavoninum*. Approximately $\times 1$. U.S. National Museum 20707, Hawaiian Islands. Station unknown. This is the “typical” *F. pavoninum* of Vaughan (1907). This specimen is No. 10 of Vaughan (1907), table 1, p. 53. 3, 4. The two lateral faces of the corallum showing borings and etching of the surface. 5. The basal portion of the corallum. Note slight arching, due perhaps to righting activity of an overturned erect form. 6. Calicular view of this corallum.
- 7 *Flabellum knoxi*. Approximately $\times 0.75$. Chatham Islands 1954 Expedition, Station 52. A small reflexed and recurved corallum showing the obverse face. Notice the sharp folds commencing immediately above the point of regeneration and related to the development of reflexure.



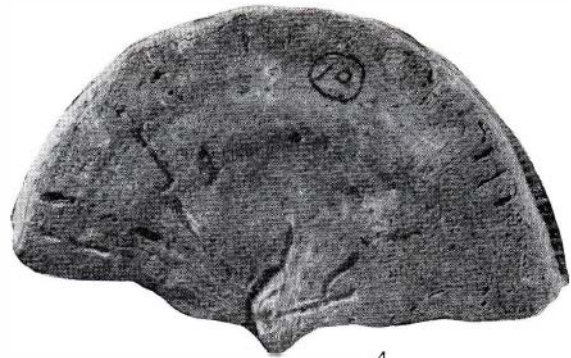
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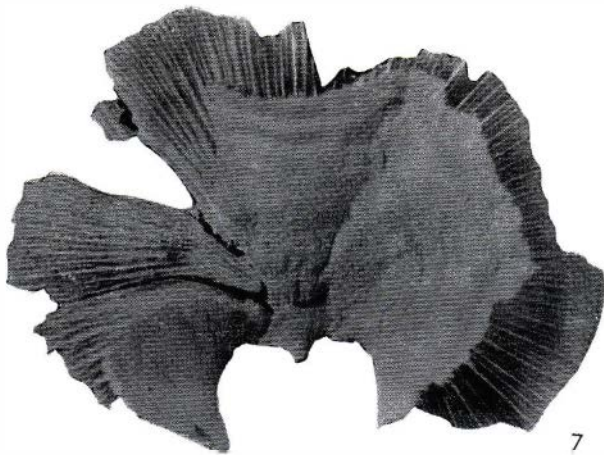
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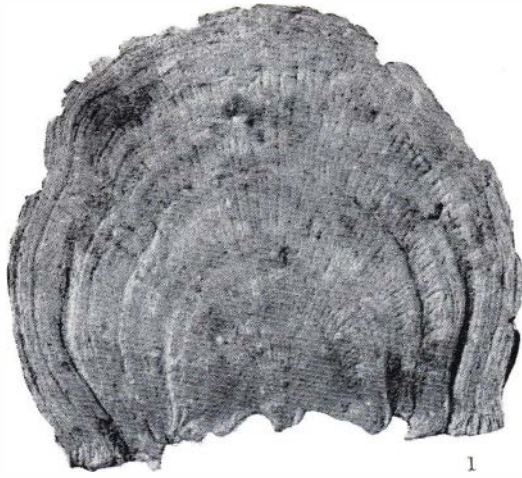
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PLATE 3

- 1 *Flabellum pavoninum*. Approximately $\times 1$. The reverse face of the specimen figured on Pl. 1, Fig. 1, 2.
- 2 *Flabellum pavoninum*. Approximately $\times 1$. The reverse face of the specimen figured on Pl. 2, Fig. 1, 2.
- 3-5 *Flabellum knoxi*. Approximately $\times 0.75$. Chatham Islands 1954 Expedition, Station 7. This specimen is severely bent but is neither reflexed or recurved. See description in text. 3. The reverse face of the corallum. Note the number of regeneration scars. 4. The obverse face of the corallum. 5. The calice.



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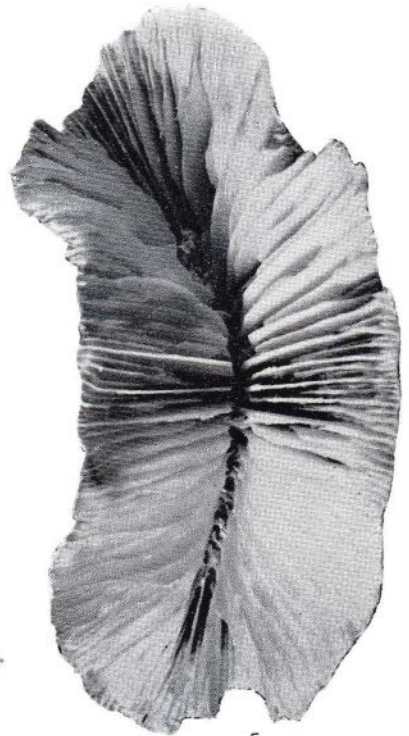
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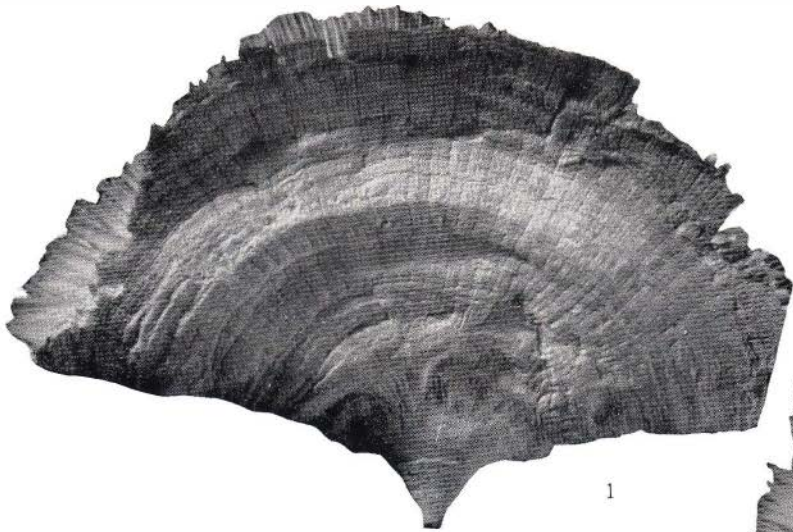
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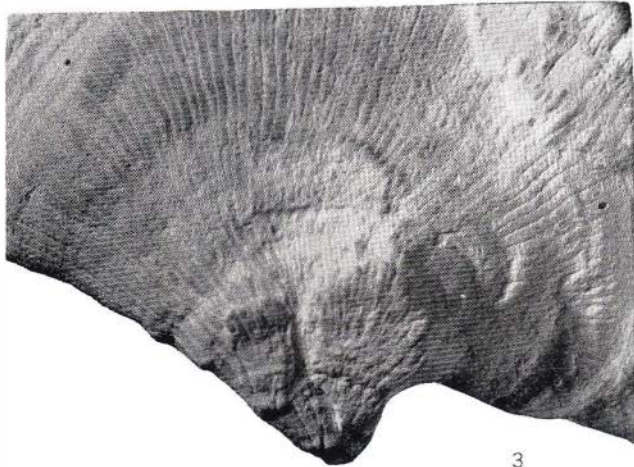
5

PLATE 4

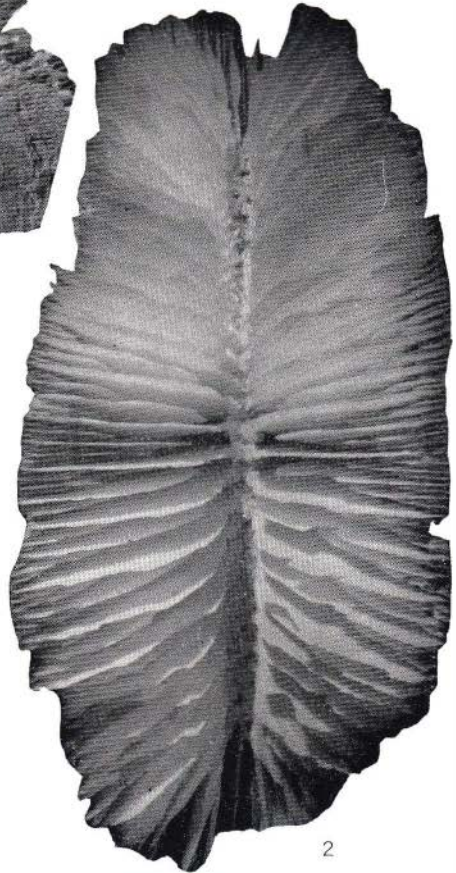
- 1, 2 *Flabellum knoxi*. Approximately $\times 1$. Chatham Islands 1954 Expedition, Station 52. The holotype, also figured in Ralph and Squires (1962, Pl. 7, Figs. 1, 2.). Note regeneration of corallum, which is essentially undistorted in growth form. Photo by M. King.
- 3 *Flabellum knoxi*. Approximately $\times 2$. Specimen figured on Pl. 3, Figs. 3–5. The stump of the pedicel and the area of regeneration. Notice the worn condition of the pedicel and the absence of the original scar of attachment.
- 4 *Flabellum knoxi*. Approximately $\times 2$. This specimen is figured on Pl. 1, Figs. 4–6. The pedicel from the reverse side showing the area of regeneration after decapitation of the corallum. Above the first area of regeneration are several other scars.



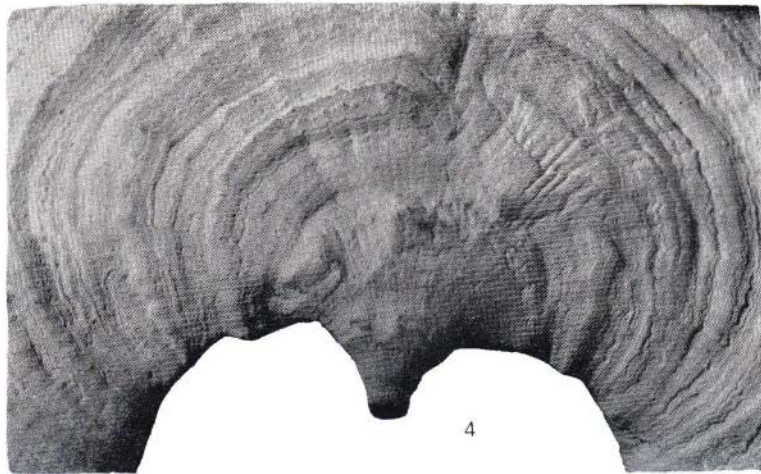
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3



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