

# *American Museum* **Novitates**

---

PUBLISHED BY THE AMERICAN MUSEUM OF NATURAL HISTORY  
CENTRAL PARK WEST AT 79TH STREET, NEW YORK 24, N.Y.

---

NUMBER 2046

AUGUST 11, 1961

---

## Deep Sea Corals Collected by the Lamont Geological Observatory. 2 Scotia Sea Corals<sup>1</sup>

BY DONALD F. SQUIRES

### INTRODUCTION

In the region of the Scotia Arc, the temperate and subantarctic faunas of South America come in closest geographical proximity to those of the Antarctic. Nowhere else is such a close relationship obtained, for no other land mass extends into the Southern Ocean below the temperate marine zone. Recent renewed interest in Antarctic faunas has resulted in an extensive enlargement of our knowledge of the variety and distribution of these faunas. On the other hand, faunas of the Cape Horn region are poorly known, particularly the Scleractinia.

Accordingly, when, during the fourteenth cruise of the Lamont Geological Observatory vessel R/V "Vema" in 1957-1958, 20 bottom trawls were made in the northern portion of the Scotia Sea on the Patagonian Shelf, several of which recovered corals, an opportunity was presented for a review of the coral fauna of the region and the presentation of some data on the ecology of these solitary forms. Although the collections recorded here are from the Patagonian Shelf on the northern margin of the Scotia Sea, the opportunity is taken to review the Scleractinia of the Scotia Sea, including the Scotia Arc, and Graham Land.

Dredgings in the region are few. Collections made by the "Petit-

---

<sup>1</sup> Contribution from the Lamont Geological Observatory, Columbia University, number 492.

TABLE 1  
STATION DATA FOR THE CORAL-BEARING TRAWLS OF THE FOURTEENTH CRUISE OF THE LAMONT GEOLOGICAL OBSERVATORY R/V "VEMA"

Trawl Number	Date in 1958	Position	Depth in Meters	Species and Specimens
8	February 6	50° 09' S., 65° 38' W.	106	<i>Flabellum thouarsii</i> , 3 alive
11	February 9	52° 11' S., 64° 00' W.	194	<i>Flabellum</i> sp., 1 badly worn
12	February 10	52° 32' S., 61° 15' W.	358	<i>Balanophyllia malouinensis</i> , 6 dead <i>Flabellum curvatum</i> , 15, most alive
14B	February 19	54° 23' S., 65° 35' W.	75	<i>Sphenotrochus gardineri</i> , 12 dead
16	February 20	52° 22' S., 65° 45' W.	115	Dendrophyllid coral fragments <i>Sphenotrochus gardineri</i> , 1 dead <i>Flabellum thouarsii</i> , 27 alive, 24 dead
18	February 21	52° 43' S., 62° 25' W.	305	<i>Balanophyllia malouinensis</i> , 1 dead <i>Flabellum curvatum</i> , 2 alive

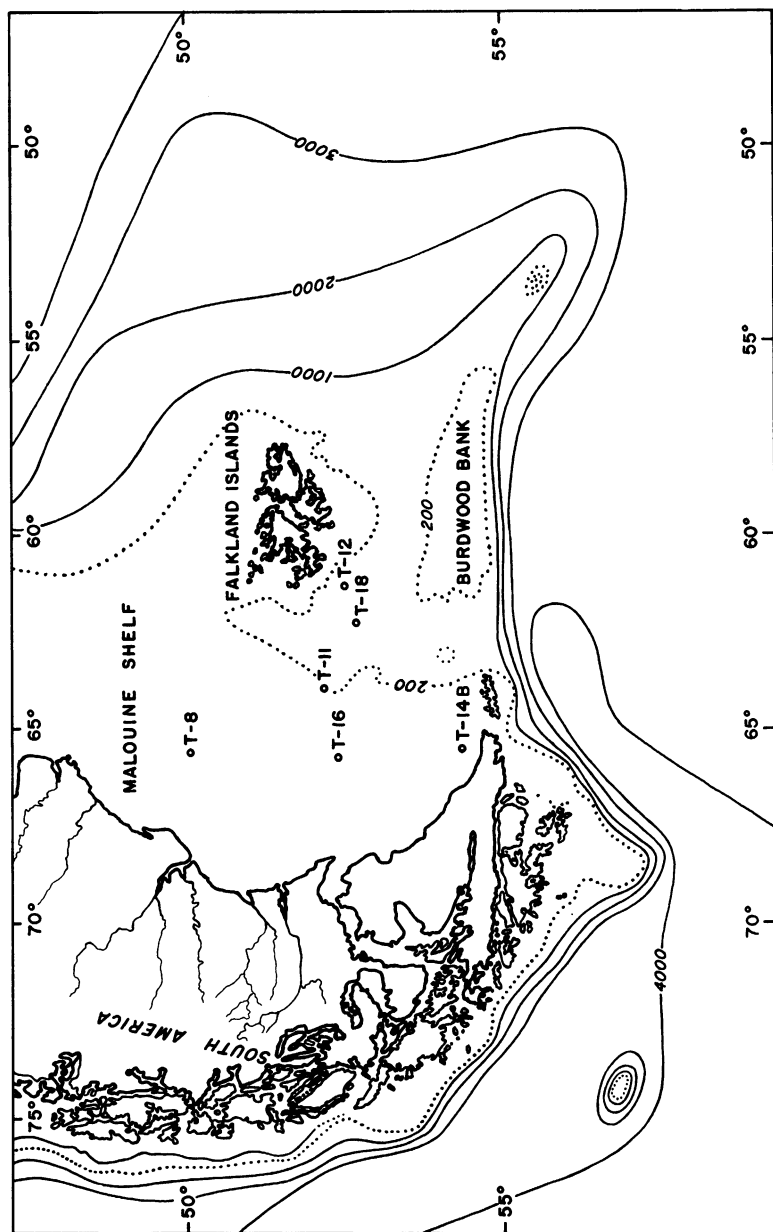


FIG. 1. Location of trawls made during the fourteenth cruise of the "Vema" on the Patagonian continental shelf, northern Scotia Sea.

Thouars" and the "Challenger" provide the only early material and were casual, not the intensive operations of the "Discovery II" and the "William Scoresby" during the period of 1926 to 1938. Corals thus obtained were described, respectively, by Milne-Edwards and Haime (1848), Moseley (1881), and Gardiner (1939a). The last-named work is the most inclusive, but it is difficult to use because the descriptions are too brief or are absent altogether, the illustrations are meager, and the species are broadly drawn.

Corals were recovered from six of the "Vema" bottom trawls, some in sufficient numbers to permit variation studies. Of particular interest is a suite of *Flabellum thouarsii* which clarifies relationships between that species, *Flabellum curvatum*, and Antarctic *Flabellum* referred to *F. thouarsii*. The distribution of the stations and a list of species recovered from each are given in table 1. Two areas were sampled by the "Vema" trawlings: the Malouine or eastern Patagonian Shelf, and the depression between it and Burdwood Bank—the Falkland Trough. Trawls containing corals from the Shelf were from depths of 75 to 115 meters (trawls 12, 18). Trawl 11 was taken on the slope between the Shelf and the Trough at a depth of 194 meters.

In the discussion that follows, the 200-meter line has been taken as the edge of the continental shelf in conformity with the usual practice (Matthews, 1934; Powell, 1951). The shelf delimited by this contour line includes the Falkland Islands (fig. 1) and represents an area greater than 185,000 square miles. Burdwood Bank, a shoal much of which is less than 50 meters deep, is separated from this shelf by the Falkland Trough which cuts into the Malouine Shelf from the east, branching north and south in the center of the shelf. Depths of 500 meters are reached in the central and eastern parts of the Trough, while a sill between 300 and 400 meters in depth separates it from deep waters to the south and west of Burdwood Bank. As indicated by Matthews (1934), the northern portion of the Malouine Bank lies mostly at depths less than 100 meters, while the southern portion is mostly 100 to 200 meters deep. Near the Falkland Islands, the 200-meter contour is close to the shore, thus the slopes to the east and south of the islands are steep to depths of 2000 meters or more. The slope of the shelf itself is gentle.

*Flabellum thouarsii* was collected alive in the northern portion of the area (trawl 8), where it occurred in considerable abundance, and again in trawl 16 which contained many specimens living and dead. *Sphenotrochus gardineri* occurred in numbers in trawl 14B, but none of the specimens was taken alive, most being badly worn. Trawl 11, on the edge of the shelf, recovered only a badly worn specimen of *Flabellum* sp. From



the Falkland Trough, trawls took numbers of *Flabellum curvatum*, both living and dead. *Balanophyllia malouinensis* also occurred there, but no living specimens were taken, most specimens being worn.

The following abbreviations and shortened forms are used:

A.M.N.H., the American Museum of Natural History, Department of Living Invertebrates

N.Z.O.I., New Zealand Oceanographic Institute

Vema 14, the fourteenth cruise of R/V "Vema"

#### ACKNOWLEDGMENTS

Dr. Robert Menzies, formerly of the Lamont Geological Observatory, made available the specimens recorded in the present paper. Mr. Peter Trurnit was in charge of the biological operations of the fourteenth cruise of the "Vema," and his part in obtaining these collections is acknowledged. For permission to include data derived from collections obtained by the New Zealand Oceanographic Institute, I am indebted to Mr. James Brodie, Director.

The photographs of corals that are reproduced here were made by Mr. G. R. Adlington. All specimens were photographed by ultraviolet-light techniques developed by Messrs. Chester Tarka and G. R. Adlington of the American Museum.

#### ECOLOGICAL NOTES

##### LARVAL SIZE AND PEDICEL DIAMETER

The pedicel diameters of *Flabellum thouarsii* collected from the Malouine Shelf range from 2.4 to 4.2 mm. (mean, 3.21 mm.;  $\sigma$ , 0.40;  $n$ , 39). These are somewhat greater than the pedicel size of *Flabellum rubrum*,<sup>1</sup> a similar and closely related species living in temperate waters and less than diameters of specimens of *Flabellum "thouarsii"* from the Ross Sea. A suite

---

<sup>1</sup> *Flabellum rubrum* (Quoy and Gaimard) is a form that lives attached to the substrate throughout much of its life. It is a common constituent of the shelf fauna of New Zealand waters and is even found intertidally there. Unfortunately, the concept of the species and its application to *Flabellum* from other areas have been corrupted through general acceptance of the usage as applied by Gardiner (1904). Gardiner has not made clear the distinctions between transverse "fission" of the upper portion of the corallum from the attached base, as described by Semper (1872) and typified by *Flabellum stokesii* Milne-Edwards and Haime (= *Flabellum aculeatum* Semper), and the simple decay of the attachment cement as in the case of *Flabellum curvatum* in which the basal plate remains a portion of the corallum. Pending the completion of a redescription of *Flabellum rubrum* (*sensu stricto*) now in process, I limit the use of *F. rubrum* in the present discussion to specimens from New Zealand waters closely conforming to the original description. Where cited in quotation marks in this paper, the name is used incorrectly.

of *Flabellum rubrum* from Cook Strait (N.Z.O.I. station A489) had pedicel diameters ranging from 2.1 to 3.7 mm. (mean, 2.75 mm.;  $\sigma$ , 0.36;  $n$ , 23), and specimens from the Ross Sea (N.Z.O.I. station A464) range from 3.4 to 6.0 mm. in diameter (mean, 3.76;  $\sigma$ , 0.77;  $n$ , 16). These relationships are shown graphically in figure 2.

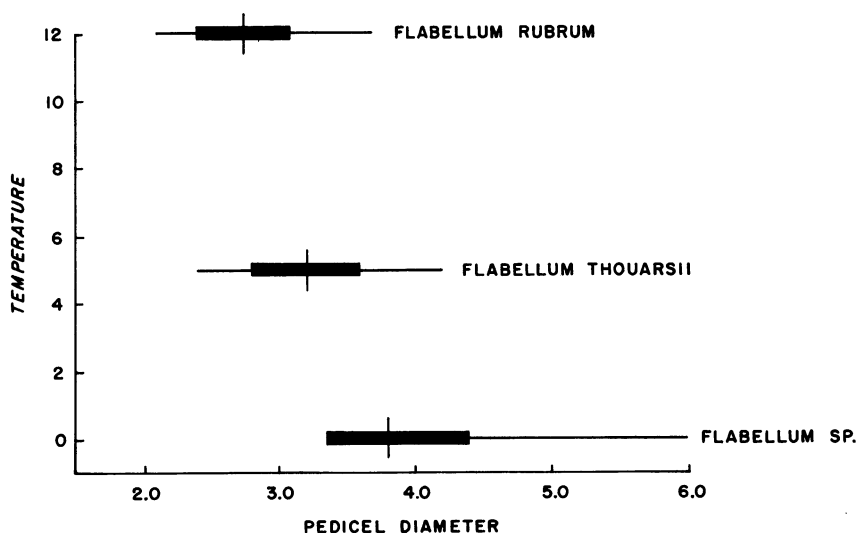


FIG. 2. Comparison of pedicel size to temperature in three species of attached *Flabellum*: *F. rubrum* from Cook Strait, New Zealand, *F. thouarsii* from the Scotia Sea, and *Flabellum* sp. (= *F. thouarsii* of authors) from the Ross Sea, Antarctica. Range of measurements is indicated by the horizontal line, the mean value by the vertical line, the length of the bar being equal to one standard deviation on each side of the mean.

The differences in initial pedicel diameter are directly related to differences in larval size. The pedicel diameter is essentially equal to the diameter of the basal plate secreted by the larva immediately after settlement on the substrate, and, when pedicel and basal plate diameters are not the same, the basal plate is larger; but the pedicel diameters, which are more easily measured and more often preserved, may be conveniently utilized for this measurement.

As a general rule, larvae become larger with decreasing temperatures. Hesse, Allee, and Schmidt (1937, p. 274) state: "Because of low temperature, fertility is reduced, and, correlated with this fact, is an increased size of egg. . . . The suppression of free-swimming larval forms is a re-

sult, especially among the benthic animals. The descendants therefore remain in the immediate vicinity of their parents; thus enormous aggregations of single species occur in many places, as is well known in arctic seas." Thorson (1950) writes that the percentage of bottom invertebrates with a non-pelagic development is even higher in Antarctic waters than in the Arctic where 95 per cent of the species develop from large, yolky eggs.

The large size of the basal disc indicates that the larvae of *Flabellum thouarsii* are large in comparison to their more temperate (thermally) relations. Can this analogy be extended to the next assumption, that such a condition indicates a short-lived larva? If so, one would expect local populations to be more unified and the effect of barriers such as Drake Strait to be enhanced as faunal boundaries.

Unfortunately, nothing is known of the reproduction of most species of cold- or deep-water corals. *Flabellum "rubrum"* is stated by Stephenson (1933, p. 222; based on Gardiner's 1904 work on the South African *Flabellum "rubrum"* [= *F. stokesii*]) to be male in its early stages, becoming hermaphroditic, and finally female. Corals are apparently exclusively viviparous. Planular larvae are extruded through the mouth of the polyp in various stages of development, and those that are most advanced are short-lived, settle rapidly, and begin secretion of the basal disc. Less well-developed larvae have a longer free life. Beyond these generalizations, based largely on hermatypic coral reproductive and larval behavior, little is known of the habits of the deep-water forms.

An abundance of individuals and paucity of species associated with boreal faunas are demonstrated in the "Vema" collections: trawl 16 contained 57 specimens of coral representing three species. Such numbers are in contrast to deep-water hauls in warmer waters where the numbers of species may be relatively large, for example, in the now famous haul of the "Siboga" expedition, station 95 in the Sulu Sea (Alcock, 1902). Here at a depth of 522 meters, 22 species of 14 genera of corals were recovered; 15 of the species were taken alive, and of the total of not more than 100 specimens, somewhat more than 50 were alive.

#### ASSOCIATION OF CORALS AND SPONGES

An association of specimens of *Flabellum curvatum* with sponges as found in trawl 12 is intriguing. Most specimens of *Flabellum* from this trawl were dead, often were badly corroded, and almost invariably possessed severely abraded pedicels; none showed a fresh basal scar. All but two specimens from the station were enclosed by a living sponge, the live corals surrounded up to the calices, and completely incorporated in the

instance of the dead specimens. Gravier (1914) also records a specimen of *Flabellum thouarsii* from the type collection bearing a label indicating that it, too, was taken from a sponge. Because some specimens were completely surrounded by the sponge, it is apparent that they were no longer in contact with the substrate. Alternative interpretations may be suggested: (1) the corals were initially living on the substrate, later becoming incorporated within and being lifted from the substrate by the growth of the sponge; or (2) the larva from which the corals grew may have settled upon the sponge and developed there. The second alternative is considered as less likely. Many sponges grow peripherally near the base and spread outward as a mat, incorporating foreign objects within their tissues, so that a coral could become completely enclosed.

#### GROWTH HABIT AND ATTACHMENT

As pointed out by Gardiner (1939b) and Vaughan and Wells (1943), there are several life positions of *Flabellum*. Most common are free forms (for example, *Flabellum pavoninum*), some of which are partially embedded in the substrate; others even lie free on the bottom. Some coralla, such as those of *Flabellum rubrum*, are attached and remain so throughout their life. Although the specimens of *Flabellum thouarsii* from trawl 16 are not invariably attached to pebbles, a sufficient number of coralla of various sizes indicate that such is the probable habit, at least in early life. Specimens having a fresh scar on the base are presumed to have been only recently removed from their attachment, most probably in the course of dredging. Although irregularities of corallum form in *Flabellum curvatum* might be attributed to exigencies of growth within a sponge, the deformation is not so great as that of Moseley's specimens. As demonstrated by Wells (1937), the overturning of an unstable corallum and subsequent differential growth are the most probable cause of such deformity.

When the relationship between the size of the object to which the corallum is attached and the height and weight of the corallum reaches certain critical proportions, the structure becomes unstable and the corallum topples. Differential growth resulting from negative geotropism will then tend to right the coral, so that the margins of the calice achieve a plane nearly parallel to the substrate. Because the polyp does not invest the corallum, the outer flanks of the corallum are vulnerable to other organisms both as a site of settlement of larvae and as an area of attack (Roger, 1944; Fage, 1937). In some instances, as in the case of the intertidal or shallow littoral occurrences of *Flabellum rubrum* from New Zealand, the polyp may secrete epithelial rootlets or talons strengthening this support, damaged either through predation or instability

(Squires, 1958). *Flabellum curvatum* shows none of these features, and, indeed, in none of the specimens examined is the basal scar fresh, even in those not associated with sponge. In all instances there is apparent chemical corrosion or deep etching, conclusively showing that there was no attachment to the substrate in the adult stage. A young specimen attached to a mature corallum indicated not only that young coralla attach, but also that the host was lying on its side.

What is the mechanism of the attachment and its subsequent failure? The attachment is obviously the result of the secretion of the basal plate on the bit of substrate selected by the larva. There is no apparent rugotropism involved in the selection, smooth pebbles being the most frequent attachment for *Flabellum thouarsii*, the attachment being maintained by a penetration of the calcium carbonate forming the basal plate into whatever minute openings may be present on the substrate. The mechanism of detachment remains obscure. Many young coralla have cheilostome Bryozoa, hydroids, or bits of sponge adhering to the base, usually closely adjacent to the basal plate. More commonly, however, the attachment is remarkably free from adhering organisms. In the adult state, the accumulation of these other organisms about the scar of attachment, as well as possible sediment accumulation about the base, possibly results in a local acidic environment causing chemical corrosion of the attachment. Mechanical abrasion is not a factor in the loosening of the basal attachment, for there is no evidence elsewhere on the corallum of attrition.

Of the 25 specimens of *Flabellum thouarsii* from trawl 16 that were taken alive, four were free and had basal attachments which were corroded or had other organisms attached to the basal scar; 12 specimens were free but possessed a clean, fresh basal scar indicative of very recent removal from the substrate; and nine specimens were still attached to pebbles. The latter group ranged in height from 4.4 to 18.5 mm. Free coralla with fresh scars ranged from 14.0 to 19.4 mm., while free coralla with old scars were 19.8 to 24.6 mm. in height. Although the absolute relationship between height and age is not known, one should be an index to the other. Thus, one may state that the basal attachment was no longer functional when the coral attained age x, or a height of about 20 mm. It is tempting, but premature, to ascribe freedom of the corallum to the attainment of a particular stage of sexual development. Histological studies may provide some evidence here.

Among coralla of *Flabellum thouarsii*, free specimens show little or no bending of the corallum indicative of growth of a cornute type. Most of the free specimens show a pronounced arching of the calicular rim, and

in the instance of specimens in which upper and lower faces can be determined (by the presence and absence of attaching organisms), the lower margin of the calice is slightly produced. In a very loose way, these features are related to size (compare figs. 15 and 17) and are presumed to be related to freedom of the corallum and subsequent differential growth. Arching of the calicular margin is probably a structural realignment permitting tentacles at the lateral edges of the oral disc to reach upward. Such structural deformation has been noted in fossil *Flabellum* by Roger (1944).

*Flabellum curvatum* is attached at least until a height of 16 mm. is attained (the largest attached specimen), but apparently becomes free soon after. Because this species is relatively larger than *F. thouarsii*, and because it becomes free at about the same size, it is possible that the free state is attained at a relatively earlier age. Adaptation to free life is more clearly demonstrated by *F. curvatum* than by *F. thouarsii*: definite tendencies towards a cornutiform shape are seen (figs. 11–13), the curvature occurring at right angles to the longer calicular axis, so that the corallum lies upon the broader faces and curves upward.

*Flabellum rubrum* from New Zealand most closely approaches *F. curvatum* in habit. In another place this will be discussed more fully and it will be shown that a fundamental difference between *F. rubrum* and *F. curvatum* and *F. thouarsii* is in the absence of epithecal talons or rootlets in the latter two. None of the specimens examined showed evidence of secondary deposition of carbonate about the basal attachment, the presence of attaching organisms, particularly cheilostome Bryozoa, indicating that the polyp remained entirely within the calice. It appears, then, that at least three behavioral types can be defined in these species with regard to attachment phenomena. Evident adaptations towards a free life observed in *F. curvatum* is evidence of a fundamental behavioral difference between it and *F. thouarsii* and *F. rubrum*.

#### SIGNIFICANCE OF SUBSTRATE IN DISTRIBUTION OF CORALS

Because the larvae of most corals require a solid, clean substrate upon which to settle, it is usual to find the basal portion of the corallum of the caryophylliid corals adhering to a pebble, a bit of shell, or, as in the turbinoliid corals, to find a grain of sand, a shell fragment, or some other similar object incorporated into the corallum. Among the corals from the Scotia Sea, at least individuals of *Flabellum* require a relatively large object upon which to settle and grow; and the character of the substrate then becomes a critical ecological factor. It is fortunate that a study of the bottom sediments of the Patagonian Shelf has been made by Mat-

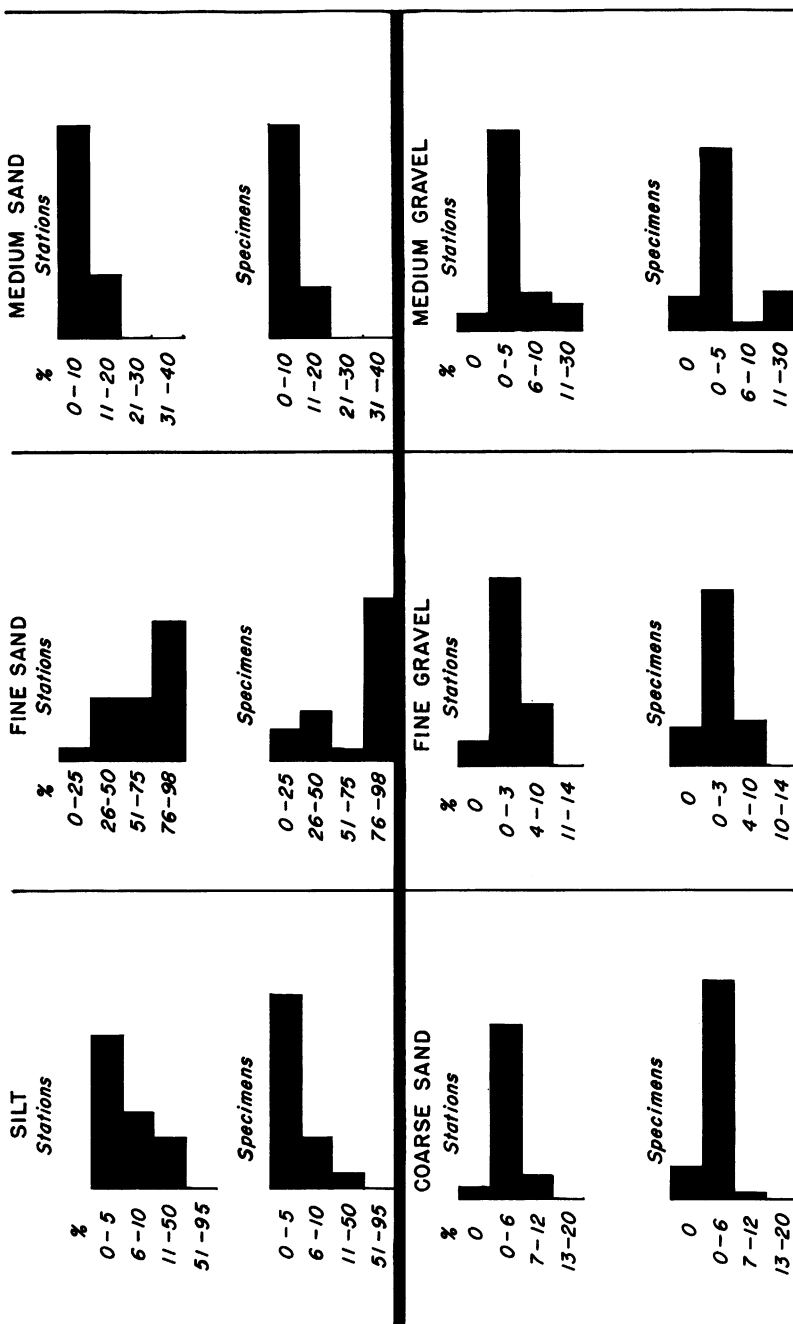
thews (1934) and that direct comparison of coral distribution and sediment type can be made.

The term "Patagonian Shelf" was defined by Matthews (1934) as the area limited by the 200-meter contour line, south of latitude 42° S., including the Malouine Shelf, the Falkland Trough, and Burdwood Bank. The entire Shelf is characterized by masses of fine sand and silt, the latter mainly in the northern and eastern portions, the former predominating to the south and west. Small areas of a coarser bottom texture are found scattered through the region but are apparently largely governed in distribution by the prevailing easterly set of the currents.

Neverson (1934) analyzed many samples from the region and considered them as being of terrigenous origin. A preponderance of quartz together with an abundance of hypersthene crystals is interpreted by Neverson as indicating a volcanic origin for much of the sediment. Foraminifera and diatoms are abundant in all samples; two stations, in the deeper portions of the Falkland Trough, were classed as diatomaceous ooze, but neither occurrence, nor the broader region from which the samples were taken, yielded corals. The absence of large rivers supplying sediment to the region suggests low sedimentation rates, and the presence of reworked Foraminifera (Macfayden, 1933) is evidence that some of the sediment formed *in situ* (Matthews, 1934; Neverson, 1934). Glauconitic sediments are present on the Burdwood Bank, and fragments of shale have been attributed to destruction *in situ* of outcroppings there.

Figure 3 shows histograms of the occurrence of *Flabellum thouarsii* and *Flabellum curvatum* according to sediment types as given by Matthews (1934). At an early stage of the study of the relationship, it became apparent that certain differences might arise between the plotting of stations at which corals occurred or the numbers of live corals taken, against sediment grade. Accordingly, two parallel sets of histograms are given, but despite some small differences between results, either method indicates the same conclusions. "William Scoresby," "Discovery II," and "Vema" collections were plotted. As it is difficult to interpret the number of specimens taken alive or dead from the data given by Gardiner (1939a), the absolute proportions of the specimen histogram may require alteration upon restudy.

The histograms show that there is a marked preference by *Flabellum* for the "fine-sand" grade and for substrates in which fine sand is a predominant constituent, while silt-grade facies are less commonly occupied by *Flabellum*. Such a result is not unexpected, for Matthews (1934, p. 187) states that fine sand is the characteristic component and occurs





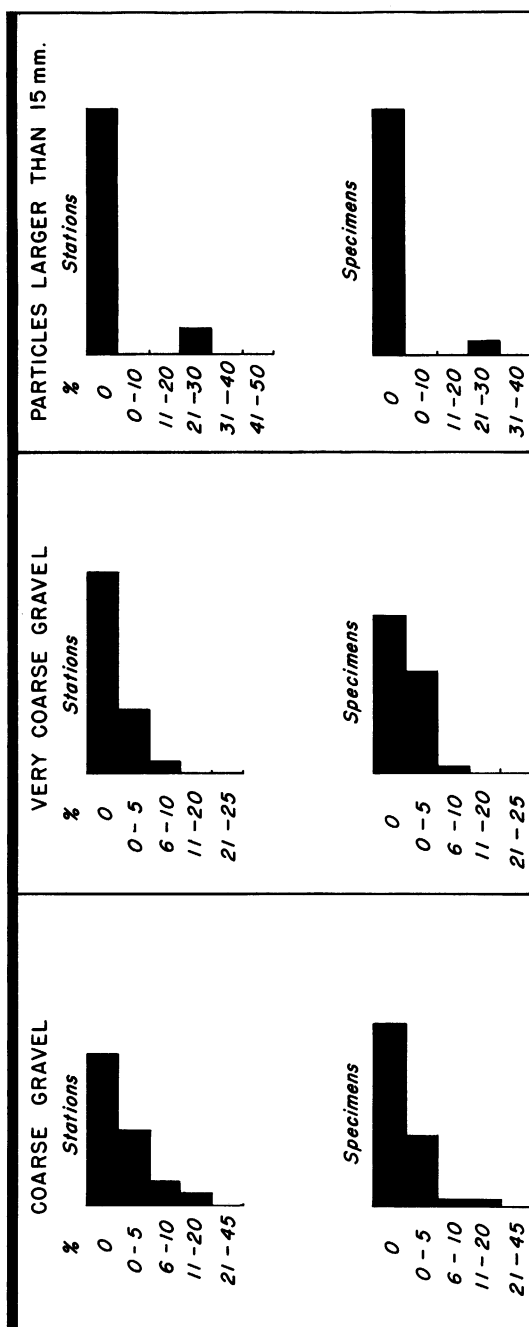


FIG. 3 (on this and opposite page). Histograms presented on this and the facing page show the relationship between sediment grade as determined by Matthew (1934) and the occurrence of *Flabellum thouratii*. "Station" histograms give the relationship between coral occurrences and constituent sediment grade expressed as percentage of the entire sample. "Specimen" histograms show the numbers of specimens as they occurred on the various sediment types. Twenty-two stations are represented, 207 specimens having been taken from them.

everywhere, forming up to 76 to 90 per cent of the deposits in more than half of the region. However, sediments on the top of Burdwood Bank which contain only 1 per cent of fine sand are notably lacking in *Flabellum*. Only on the flanks of the bank, where the percentage of fine sand increases, is the coral found. In addition, grades coarser than fine sand are limited in distribution, but no corals occur where they are a dominant element.

Besides the preference shown for fine-sand grade, there is a marked feature of the histograms of coarse sand and fine- and medium-gravel grades which requires attention. These show a small number of occurrences of *Flabellum*, and small numbers of specimens in areas where these grades are totally lacking, but that corals are decidedly prevalent where low percentages of the same grade are encountered. In contrast, areas with grades coarser than coarse gravel are not commonly inhabited, as indicated by the non-occurrence of corals where these fractions form an appreciable amount of the substrate. The large larvae of *Flabellum thouarsii* require sediment particles of some size for settlement. All specimens at hand which retain the object upon which they settled are on medium-gravel grade. Large quantities of coarser grades of sediment are apparently detrimental. Gardiner (1939a, p. 328) describes a single specimen occurring on coarse gravel as a “. . . heavy massive form.” Probably the coarser substrates are subject to the set of the easterly current and may be in motion or subject to attrition, preventing the settlement and maturation of corals.

The lack of attachment of *Flabellum curvatum* to the substrate cannot be attributed to the absence of larger particles for the larvae to settle upon, for, in all instances, at least fine gravel was present in the localities from which the specimens were collected.

The summary histograms (fig. 4) represent the distribution of corals according to a characterization of the samples as given by Matthews (1934). Figure 4A shows the distribution by grade of sediment and the striking preference of *Flabellum* for finer grades, particularly fine sand. Figure 4B represents Matthews' (1934, p. 190) grouping of sediments into the six main types “. . . as described by composition and color and to a lesser degree by their texture.” Unfortunately, mineralogical composition is not given. Aside from the anomaly in the gray sand and silt facies, no feature of significance is seen. Gray sand and silt facies are most limited in distribution, but seem to support high populations of *Flabellum*. The absence of *Flabellum* from the shell and coral-fragment facies is marked, but it is possibly the habitat of *Sphenotrochus gardineri*, for Matthews (1934, p. 190) cites the occurrence of turbinoliid corals

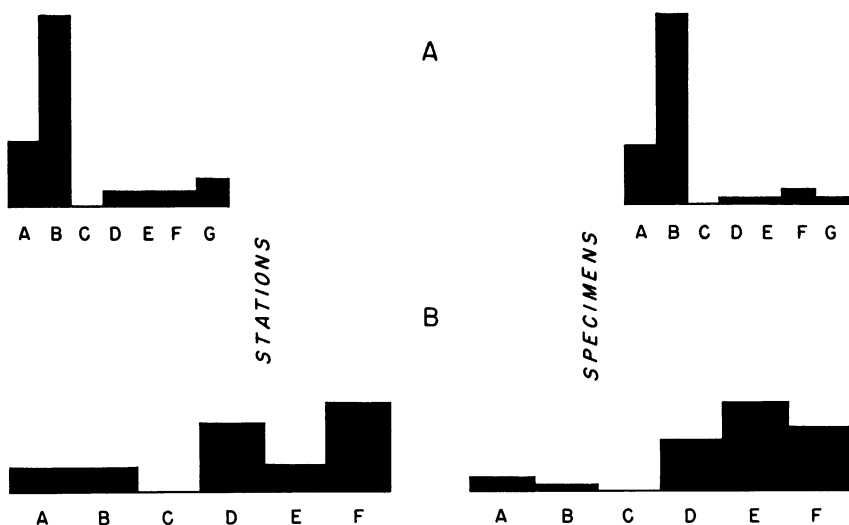


FIG. 4. Occurrence of *Flabellum* on various types of sediment as characterized by Matthew (1934). Method of plotting as in figure 3. A. A, silt; B, fine sand, C, medium sand; D, coarse sand; E, fine gravel; F, medium gravel; G, coarse gravel. B. A, shell and coral fragments; B, white or yellow sand; C, brown sand; D, grayish brown sand; E, gray sand and silt; F, green sand and silt.

there. Gardiner (1939a) records *Sphenotrochus* only from stations outside the area discussed by Matthews and apparently did not see specimens from that facies. *Flabellum curvatum* is found principally on green sands and silt and is the preponderant coral from that facies. Its occurrence is largely a reflection of the distribution of that facies in the deeper waters of the Falkland Trough.

Although samples of *Sphenotrochus* and *Balanophyllia* are too small to permit an analysis of grade preference, several general conclusions can be drawn. The specimens of *Balanophyllia* from the Patagonian Shelf occur in two morphological types, according to Gardiner (1939a, p. 335): specimens that have an expanded base, and those that are cornutiform. As would be expected, coralla having an expanded base are from stations having a medium- to coarse-gravel substrate and were attached to the substrate in the manner of *Flabellum*. Cornute specimens, on the other hand, were collected only from fine sand and silt bottoms. The only occurrence of *Sphenotrochus* for which data on sediment grade are available is a coarse bottom of a medium-gravel grade. Matthews notes that the various grades of the coral-shell fragment facies extend from fine through coarse, and the single occurrence in the medium

grade may not be significant and, indeed, must be questioned because of the absence of living specimens from the trawl.

#### BREEDING DATA

Unfortunately, so little is known of growth rates of ahermatypic corals that it is impossible to make estimates of age of specimens from their size. Immature coralla 1 to 2 mm. in height were found on specimens from Vema 14, trawl 18 (*Flabellum curvatum*), and trawl 8 (*Flabellum thouarsii*), indicating that reproduction, if seasonal, probably occurred during the previous summer months.

#### ZOOGEOGRAPHY

Wells (1958, p. 260) states: "Ten years later [than a report on the Antarctic corals], Gardiner (1939) reported on corals obtained on various cruises of the *Discovery* and *William Scoresby* (1926-1933) at a number of stations from the Patagonian Shelf southward into the Palmer Peninsula and eastward to Tristan da Cunha and Gough Island. These indicate a transitional zone between the Atlantic fauna and that of the Antarctic. A few species of the former extend into the latter, but few if any of the endemic Antarctic species are found north of 55° S."

The juxtaposition of the South Orkney Islands, the South Sandwich Islands, and South Georgia to the Patagonian Shelf indicates that the Shelf is the most probable source of, or should bear the closest relationship to, the shelf fauna of Antarctica. Wells (1958) listed the occurrences of species of coral south of latitude 35° S., and, although his table does not differentiate between shelf, slope, and basin faunas, several faunas are distinguished. The hydrology of the waters and bottom topography of the Southern Ocean are such that the Antarctic, Patagonian, South African, Australian, and New Zealand regions are not only geographically separate but are influenced by strong thermal boundaries.

Faunas of the five regions are listed below, under the respective headings, only occurrences on the shelf being given. In all cases, the 200-meter line has been taken as the boundary of the shelf.

#### SOUTH AFRICAN FAUNA (CAPE OF GOOD HOPE)

Despite the complexities to be expected in the fauna of a region that is the meeting ground between two large and distinct regions, the South African marine fauna has a characteristic assemblage of corals. Ekman (1953) called this the Warm Temperate South African Fauna in preference to the term "Cape Province." Thirty species are known from the region, 13 of which are endemic. Most of the remainder are Atlantic

forms, although Indian Ocean components are also present. The cosmopolitan species are probably too broadly drawn and may become more useful zoogeographically only after restudy. A striking characteristic of the South African fauna is the abundance and apparent diversity of the dendrophylliid corals present there, in part, at least, a tribute to the assiduous studies of van der Horst (1928, 1933, 1938). The artificiality of the species of *Caryophyllia* described by Duncan has been commented upon by others.

The species that constitute the coral fauna of the South African shelf are as follows:

*Balanophyllia annae* van der Horst  
*Balanophyllia bonae spei* van der Horst  
*Balanophyllia capensis* Verrill  
*Balanophyllia diademata* van der Horst  
*Balanophyllia italica* (Michelin)  
*Caryophyllia berteriana* Duchassaing  
*Caryophyllia clavus* Scacchi  
*Caryophyllia cyathus* Ellis and Solander  
*Caryophyllia epithecata* Duncan  
*Ceratotrochus delicatus* Marenzeller  
*Ceratotrochus johnsoni* Duncan  
*Cladocora arbuscula* Milne-Edwards and Haime  
*Dendrophyllia cladonia* van der Horst  
*Dendrophyllia cornigera* (Lamarck)  
*Dendrophyllia dilatata* van der Horst  
*Desmophyllum capense* Gardiner  
*Endopachys grayi* Milne-Edwards and Haime  
*Flabellum inconstans* Marenzeller  
*Flabellum pavoninum* Lesson  
*Flabellum rubrum* (Quoy and Gaimard)  
*Flabellum sibogae* Alcock  
*Gordineria capensis* Gardiner  
*Heterocyathus aequicostatus* Milne-Edwards and Haime  
*Madraxis scotiae* Gardiner  
*Monomyces fragilis* (Pourtalès)  
*Sphenotrochus aurantiacus* Marenzeller  
*Sphenotrochus (Eusthenotrochus) gilchristi* Gardiner  
*Stephanophyllia* sp.  
*Trochocyathus cincticulatus* Alcock  
*Trochocyathus rawsoni* Pourtalès

#### SOUTH AUSTRALIAN FAUNA

Ekman (1953) considers the South Australian province as warm temperate, more or less coinciding with the Flindersian Province. The zoogeographic relationships of the 41 species of corals of South Aus-

tralia are not with coral faunas of temperate regions, but rather, together with other groups of marine organisms, the fauna is largely unique and autochthonous. Vaughan and Wells (1943, p. 88) wrote: "The waters off the southern and southeastern coasts of Australia from the Great Australian Bight through Bass Strait to the latitude of Brisbane . . . have in depths from 18 to 915 meters, a distinctive fauna of over 50 species of which only 14 are identical with species of other faunas." Throughout the Tertiary of Australia this same degree of isolation of corals was present, for a great many of the endemic genera are autochthonous in the Tertiary of Victoria.

The species of the coral fauna of the South Australian shelf are:

- Anthemiphyllia dentata* (Alcock)
- Balanophyllia bairdiana* Moseley
- Balanophyllia dentata* Tenison-Woods
- Caryophyllia clavus* (Scacchi)
- Caryophyllia cyathus* (Ellis and Solander)
- Caryophyllia planilamellata* Dennant
- Ceratotrochus inornatus* Tenison-Woods
- Ceratotrochus recidivus* Dennant
- Ceratotrochus (Conotrochus) typus* Sequenza
- Conocyathus compressus* Tenison-Woods
- Conocyathus sulcatus* Tenison-Woods
- Conocyathus zelandiae* Duncan
- Culicia australiensis* Hoffmeister
- Culicia* (?) sp. cf. *C. ? quinaria* Tenison-Woods
- Culicia tenella* Dana
- Cyathoceras cornu* Moseley
- Deltocyathus vincentinus* Dennant
- Desmophyllum cristagalli* Milne-Edwards and Haime
- Dunocyathus parasiticus* Tenison-Woods
- Endopachys australiae* Tenison-Woods
- Flabellum affine* Milne-Edwards and Haime
- Flabellum australe* Moseley
- Flabellum japonicum* Moseley
- Flabellum pavoninum* var. *distinctum* Milne-Edwards and Haime
- Flabellum transversale* Moseley
- Fungiacyathus symmetricus* (Pourtales)
- Heteropsammia ? elliptica* Tenison-Woods
- Holcotrochus crenulatus* Dennant
- Holcotrochus scriptus* Dennant
- Idiotrochus emarciatus* (Duncan)
- Monomyces radiatus* (Dennant)
- Notophyllia etheridgei* Hoffmeister
- Paracyathus vittatus* Dennant
- Platytrichus compressus* (Tenison-Woods)
- Platytrichus (Koilotrochus) hastatus* (Dennant)

*Platytrochus victoriae* (Duncan)  
*Sphenotrochus excavatus* Tenison-Woods  
*Sphenotrochus variolaris* Tenison-Woods  
*Stephanophyllia formosissima* Moseley  
*Trematotrochus verconis* Dennant  
*Tubastrea atrata* (Dennant)

#### NEW ZEALAND FAUNA

Ekman (1953) calls attention to the critical position of New Zealand and suggests that the northern portion of the country has a temperate fauna. The corals support this contention, ably demonstrated among many groups of marine organisms (Fleming, 1951; Powell, MS). The corals of New Zealand are of mixed background and contain elements of both cooler- and warmer-water faunas, as would be expected, for, historically, marine temperatures have been subject to rather great fluctuations. During the upper Oligocene and Miocene, reef corals were present in the Auckland region, and, in Pliocene and Pleistocene time, subantarctic conditions prevailed (Squires, 1958). Wells (1958) lists only seven species of coral from New Zealand, but studies now in progress (Ralph and Squires, in preparation) indicate that the extant fauna of New Zealand totals at least 24 species, with a still greater variety to be expected. Some of the species are apparently endemic and can be related to a Tertiary ancestry, but most are of Indo-Pacific affinities, while a surprising number are indicative of close relationships with South America. Unfortunately, nothing is known of the modern coral fauna of the Subantarctic Islands of New Zealand which should demonstrate these ties more closely.

The species that constitute the coral fauna of the New Zealand Shelf are:

*Balanophyllia* sp.  
*Caryophyllia lamellifera* Moseley  
*Caryophyllia maculata* Moseley  
*Caryophyllia profunda* Moseley  
*Conocyathus zelandiae* Duncan  
*Culicia huttoni* Tenison-Woods  
*Culicia rubeola* (Quoy and Gaimard)  
*Culicia smithi* Milne-Edwards and Haime  
*Deltocyathus lens* Alcock  
*Dendrophyllia japonica* Rehberg  
*Desmophyllum cristagalli* Milne-Edwards and Haime  
*Flabellum harmeri* Gardiner  
*Flabellum pavoninum* Lesson  
*Flabellum rubrum* (Quoy and Gaimard)  
*Flabellum rugulosum* Tenison-Woods

*Gardineria* sp. Gardiner  
*Goniocorella* sp.  
*Kionotrochus suteri* Dennant  
*Oculina virgosa* Squires  
*Paracyathus* sp.  
*Sphenotrochus intermedius* Duncan  
*Stenocyathus* sp.  
? *Stephanophyllia formosissima* Moseley  
*Trochocyathus* [*Theocyathus*] sp. ?Gardiner

#### ANTARCTIC FAUNA

This fauna has been considered in detail by Wells (1958). Some revisions may be necessary as a result of studies of large suites of materials collected in the Ross Sea region by the New Zealand Oceanographic Institute, but the fauna is apparently well known. *Flabellum thouarsii*, commonly cited as an element of the Antarctic fauna, has been incorrectly identified.

The species that constitute the coral fauna of the Antarctic Shelf are:

*Caryophyllia antarctica* Marenzeller  
*Flabellum thouarsii* Milne-Edwards and Haime<sup>1</sup>  
*Flabellum antarcticum* (Gravier)  
*Gardineria antarctica* Gardiner  
*Gardineria lillei* Gardiner

#### PATAGONIAN SHELF FAUNA

Only four species are definitely recorded from the Shelf, all of which are described in the present study. An occurrence of *Astrangia* mentioned by Pax (1910) and Gravier (1914) from Magellan Strait would be of considerable interest if it could be verified, but both are citations of a previous record unknown to me.

Inasmuch as it is the Cape Horn region that we are concerned with here, it is appropriate to give the fauna recorded from the continental slope and the Falkland Trough:

*Flabellum thouarsii* Milne-Edwards and Haime  
*Sphenotrochus gardineri*, new species  
*Balanophyllia malouinensis*, new species  
*Astrangia* sp.

Moseley (1881) recorded many species from western Patagonia, including *Flabellum patagonicum*, *Desmophyllum ingens*, and *Caryophyllia clavus* var. *borealis*, all of which were taken from deep basins (300 to 700 meters)

<sup>1</sup> Incorrectly identified with this species. A new name is being proposed elsewhere.



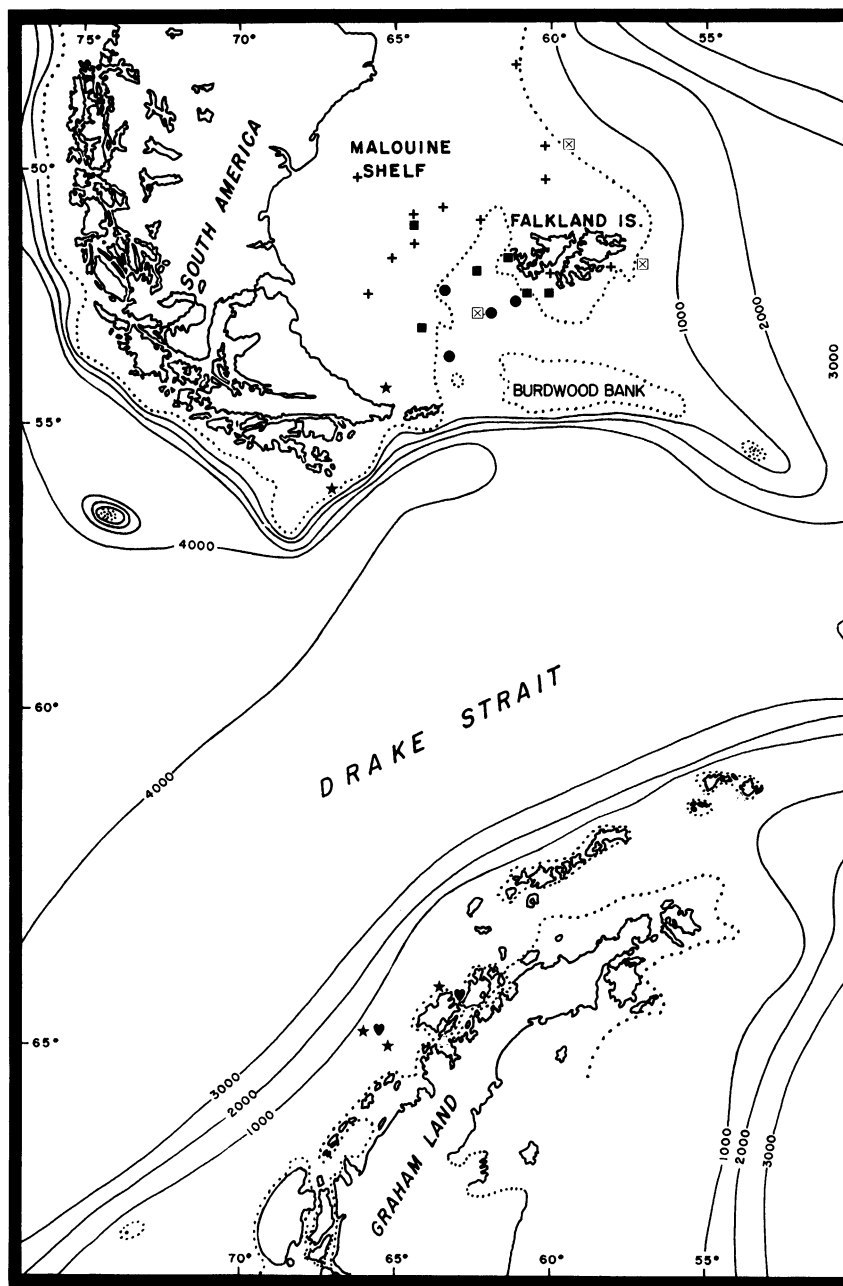
on the inshore side of the island chains of western Chile. Some of these species (*D. ingens* and *C. clavus* var. *borealis*) are found elsewhere in the Southern Ocean, but none appears on the eastern side of the Cape. From the dredgings off the Rio de la Plata, Moseley recorded *Flabellum curvatum* and *Desmophyllum cornu*, the latter also known from South Africa.

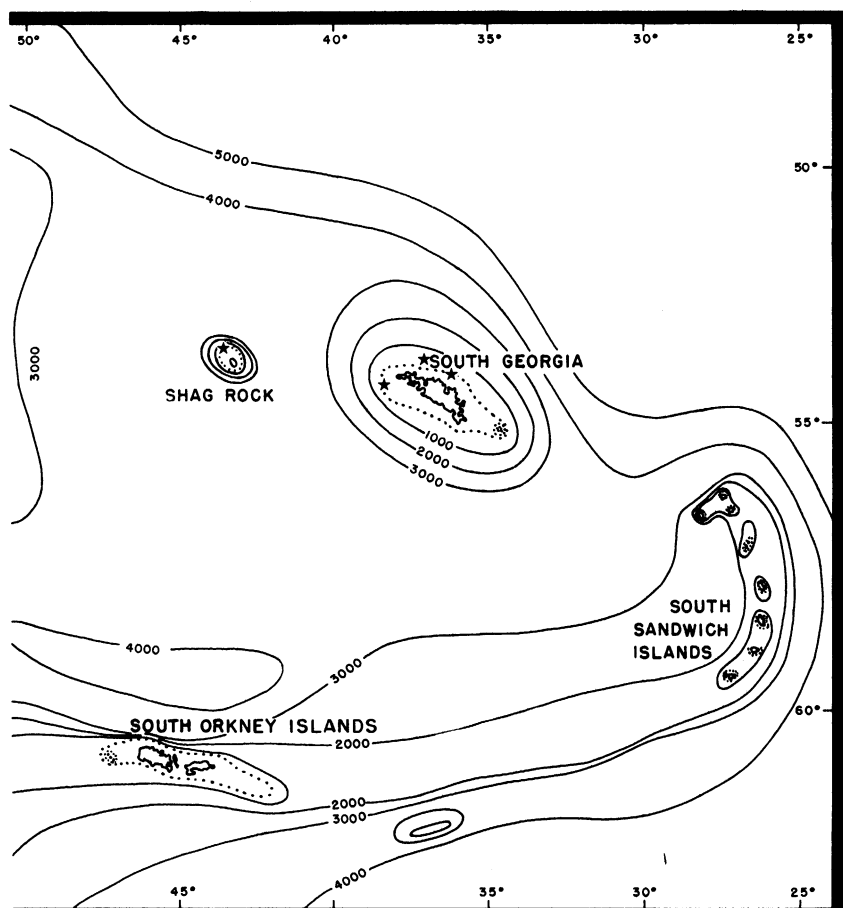
The shelf fauna of Cape Horn has little in common with that of any other region, and the slope fauna has very little apparent affinity to that of other regions, with the exception of *Dendrophyllia oahensis* (probably more closely related to the Atlantic *Dendrophyllia cornigera*) and *Cyathoceras cornu*. To the south is the Antarctic fauna; to the north is the temperate Atlantic fauna. Little is known of the position of the faunal boundaries.

The corals of the Patagonian Shelf and those of the Antarctic Shelf are closely related through the Scotia Arc faunas, which are intermediate geographically. Although not well represented in coral collections from the Southern Ocean, a few species have been recorded from this area. Gardiner (1939a) listed *Gardineria antarctica* from South Georgia, *Gardineria lillei* from Shag Rock, and *Flabellum harmeri*, *Gardineria lillei*, *G. antarctica*, *Caryophyllia mabahithi*, *C. arcuata*, and *C. cyathus* from a number of stations in the Palmer Archipelago. "Pourquoi Pas?" stations 4 and 8 in the northern Palmer Archipelago (Gravier, 1914) yielded *Flabellum antarcticum* (Gravier). Of these records *Flabellum harmeri* is probably a misidentification of *Flabellum "thouarsii"* of the Antarctic. The three species of *Caryophyllia* recorded by Gardiner from the Palmer Archipelago all occur on the slope. The broken specimens identified as *Caryophyllia arcuata* could, from the few notes given by Gardiner, be referred to *C. antarctica* which is also elongate-cornute, usually has 12 pali, and costae that are visible only on the upper portion of the corallum. *Caryophyllia cyathus* is fairly well described, but *C. mabahithi* is only mentioned. If the identification of these species is correct, then they are the only representatives of the Atlantic fauna to have penetrated to the Antarctic and are, surprisingly, absent from the Patagonian area (*C. mabahithi* is an Indian Ocean species and probably misidentified).

#### SPECIES DISTRIBUTION AND THERMAL BOUNDARIES

To discuss the coral fauna of the shelf as an entity separate from that of the slope would be an artificiality, were it not for the correspondence between thermal and bathymetric boundaries. Deacon (1937) indicates that the water on the Patagonian Shelf is well mixed from top to bottom (depths of from 150 to 200 meters) except during the summer when a warm, poorly saline, surface layer may develop. The shelf water does





- |                              |                                     |
|------------------------------|-------------------------------------|
| + <i>Flabellum thouarsii</i> | ♥ <i>Caryophyllia</i> spp.          |
| ● <i>Flabellum curvatum</i>  | ☆ <i>Sphenotrochus gardineri</i>    |
| △ <i>Flabellum</i> sp.       | ■ <i>Balanophyllia malouinensis</i> |
| ★ <i>Gardineria</i> spp.     | ⊠ <i>Desmophyllum capensis</i>      |

FIG. 5 (on this and opposite page). Distribution of Magellanian and Antarctic shelf corals. *Flabellum thouarsii*, *F. curvatum*, *Sphenotrochus gardineri*, *Balanophyllia malouinensis*, and *Desmophyllum capensis* constitute the Magellanian fauna. The remainder, with the exception of *Caryophyllia* spp. (cosmopolitan), are strictly Antarctic.

not extend south to the Antarctic Shelf but, rather, is lost at the Antarctic Convergence which is marked by a temperature change of the magnitude of  $5^{\circ}$  C. Thus on the Patagonian Shelf, in the region of the Falkland Islands, a temperature range of  $4^{\circ}$  to  $6^{\circ}$  C. may be expected, while in the Scotia Arc, at South Georgia, temperatures are of the order of  $1.5^{\circ}$  to  $-1.5^{\circ}$  C., but may be as high as  $3^{\circ}$  C. (Mackintosh, 1946). It is the sharp contrast in temperatures (and salinity) across the Antarctic Convergence which forms the southern limit for the Patagonian Shelf fauna. This together with the difficulty of larval transportation across the West Wind Drift in the region of Drake Strait creates a faunal entity—the Magellan Province. Deacon (1937, p. 51) cites eastward travel in the West Wind Drift of as much as 40 miles per day, and speeds of 0.5 knot to 1.0 knot are recorded in Drake Strait by the United States Navy Hydrographic Office (1957). Pelagic larvae from the Patagonian Shelf caught up in a current of this speed would be carried away from the Scotia Arc into more northern waters of the central South Atlantic.

To the north, the boundary between the temperate fauna of the east coast of South America and the Patagonian (Magellanian) fauna is probably in the region of contact between the Brazil and Falkland currents. The boundary is not sharp, but irregular, extending farther south along the coast (Hart, 1946), but is, in a general sense, roughly from latitude  $43^{\circ}$  S. to latitude  $49^{\circ}$  S. The temperature gradient at the boundary is approximately  $3^{\circ}$  or  $4^{\circ}$  C. The temperature of the Brazil Current ranges from  $8^{\circ}$  to  $12^{\circ}$  C. (Klaehn, 1911; Hart, 1946).

The effectiveness of the thermal boundaries in the delimiting of faunal provinces is shown in figure 5. None of the characteristic Antarctic elements is found to the north of the Antarctic Convergence, and of the subantarctic Patagonian fauna only species of *Caryophyllia* apparently are able to survive in the colder waters of the Antarctic. A similar degree of dissimilitude is noted by Powell (1951, p. 50) as a result of his studies on the more abundant and diversified molluscan fauna. He states: "One species of the characteristic Antarctic genus *Prosipho* occurs [on the East Patagonian Continental Shelf], but otherwise, Antarctic forms are almost wholly absent."

Corals of the northern region of the Scotia Arc, particularly Shag Rock and South Georgia, should be more closely related to Antarctic faunas, as the convergence lies to the north and west of Shag Rock, placing both regions in the same thermal regime, and because they are geographically closely linked through the islands of the Arc. Among the corals, this close relationship is demonstrated by the presence of *Gardineria lillei* at Shag Rock and of both *G. lillei* and *G. antarctica* at South

Georgia (Gardiner, 1939a), both species being of Antarctic affinities. Earland (1934) indicated that South Georgia is an isolated area which has developed or preserved species of Foraminifera confined to the island, and Powell (1951, p. 57) shows that there is little relationship between the fauna of the Falkland Islands and that of South Georgia, but that the latter have many similarities with the Kerguelen and Ross Sea faunas. Although Earland (1934) and Powell (1951) found sufficient evidence for subdividing the region extending from the South Sandwich Islands to the Bellinghausen Sea into several biogeographical units, no such division is apparent in the small coral faunas.

#### SOUTHERN HIGH LATITUDE FAUNAL PROVINCES

A full discussion of the previous nomenclature of the Southern Ocean biogeographical units is given by Powell (1951). Four units were described: (1) Magellan, including Patagonia from south of Chiloe Island (west coast) and Cape Blanco (east coast) to and including Burdwood Bank and the Falkland Islands; (2) Georgian, including South Georgia and Shag Rock; (3) Kerguelenian, including Kerguelen, Heard, the Crozets, Marion, and Prince Edward Islands; and (4) Antipodean, including the Subantarctic Islands of New Zealand. Powell concludes that the bulk of the Southern Ocean, high-latitude forms could have been derived from the Americas, dispersing by means of the various cross and radial submarine ridges of the Southern Pacific. Further, he considers that the molluscan faunas of these regions show no evidence of being of great antiquity.

These conclusions are essentially those that must be drawn from the more limited evidence of the coral faunas, although the Georgian Province cannot be distinguished from the Antarctic Province, and the Antipodean Province is totally unknown as yet as far as its scleractinian components are concerned. The Kerguelenian fauna does contain a number of distinct species, most of which are in need of restudy, and is particularly characterized by *Caryophyllia profunda*. Although the Tertiary fossil record in the Kerguelenian Province is not helpful, it is possible to recognize in the later Tertiary (upper Miocene to Pliocene) sediments of New Zealand the influx of a fauna which bears a very close relationship to the modern Kerguelenian with South American additives.<sup>1</sup> Despite the fact that the deeper shelf coral fauna of southern New Zealand and the Sub-

---

<sup>1</sup> Squires (1958) did not recognize an influx of cooler water elements which might be characteristic of southern invasion. Recently collected materials, particularly those from deeper water facies of the North Island, New Zealand, strongly support the concept of additions to the fauna as well as the depletion of earlier faunas as recorded there.

antarctic Islands is virtually unknown, it is probable that investigation of these regions will demonstrate a fauna having close relationships with, if not identical to, the Kerguelenian.

Although well represented in trawls and dredgings from Patagonia, Antarctica, and New Zealand, corals of the *Flabellum rubrum* group (*F. thouarsii*, *F. rubrum*, *F. antarcticum*) are not always present in the fossil record. *Flabellum rubrum* (*sensu stricto*) in New Zealand is well represented in Pliocene and Pleistocene sediments. In raised moraines in the Ross Sector, Antarctica, *Flabellum* is not represented, although *Gardineria* is present (I. G. Speden, personal communication). No record of the species from South America is known to me. The history of the migrations of this characteristically Southern Ocean faunal element will undoubtedly aid in our coming to sounder biogeographical conclusions.

## SYSTEMATICS

### FAMILY CARYOPHYLLIIDAE

#### GENUS *SPHENOTROCHUS* MILNE-EDWARDS AND HAIME

#### *Sphenotrochus gardineri*, new species

Figures 6-8

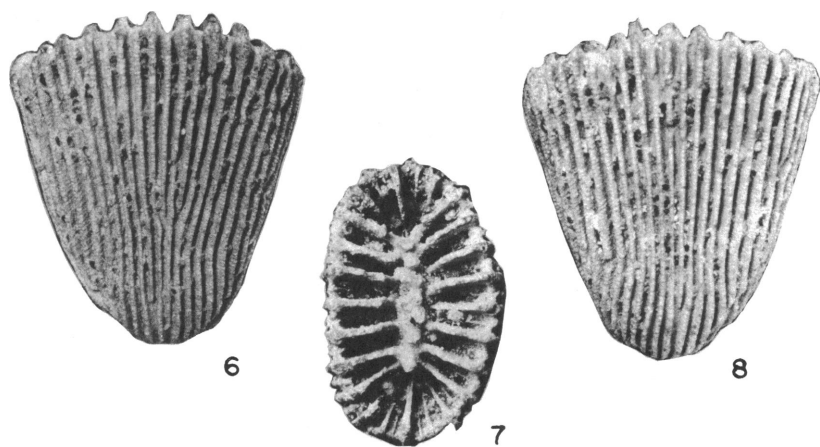
*Sphenotrochus intermedius* (Münster) [*sic*] GARDINER, 1939, in *Discovery reports*, vol. 18, p. 333 (part).

**HOLOTYPE:** A.M.N.H. No. 3367; Vema 14, trawl 14B, latitude 54° 23' S., longitude 62° 25' W.; depth, 75 meters; northern Scotia Sea on Malouine Shelf; collected by Peter Trurnit, Lamont Geological Observatory R/V "Vema," February 19, 1958.

**MATERIALS:** Twelve specimens, all dead, some badly worn, from trawl 14B. One additional specimen from trawl 16 (see table 1 for locality data).

**DESCRIPTION:** Corallum compressed, with flat to slightly concave sides. Profile evenly rounded, base not sharp. Costae on the lateral faces extending more or less evenly and directly to the base, or to the point of intersection with the lateral edges where they curve gently outward to meet the end costae. Branching of costae on lateral faces rare, occurring only high on the corallum. End costae straight, unbranched, and extending to the base. Costae granular, composed of a single row, alternating rows, or multiple rows of granules according to their width. Width of costal interspaces about twice that of the costae and in rough correspondence to costal order. Septa arranged in four complete cycles, with portions of fifth cycle usually present. Septa of the first three cycles of about the same size and meeting at the columella. Fourth- and fifth-

cycle septa short and thin. Columella relatively solid but not lamellar, having five to eight discrete, trabecular knobs projecting at the surface. Septa having smooth margins and laterally bearing coarse granules arranged in nearly vertical rows. In profile the septa may be very coarsely dentate, often having a prominent lobe before septa of the first three cycles.



FIGS. 6-8. *Sphenotrochus gardineri*, new species, holotype, A.M.N.H. No. 3367, Vema 14, trawl 14B. 6. Side, showing branching of costae in center of corallum face. 7. Calice, showing trabecular prominences on columella. 8. Corallum face opposite that shown in figure 6. Costae are unbranched on this face. All  $\times 5$ .

DISCUSSION: Modern species of *Sphenotrochus* are readily divisible into two morphological groups on the character of the upper surface of the columella: those in which the upper surface appears to be lamellar, and those in which the upper surface is trabecular. Among the former are *Sphenotrochus intermedius* Duncan (Münster), *S. aurantiacus* Marenzeller, *S. auritus* Pourtalès, and *S. excavatus* Tenison-Woods. Species in which the upper columellar surface is trabecular include *Sphenotrochus rubescens* (Moseley), an undescribed species from New Zealand, and the present species.

*Sphenotrochus rubescens* (Moseley) (1881, p. 157, pl. 6, figs. 8, 8a) was described from the Kei Islands and is readily distinguished from the present species by its fewer columellar processes and in having smooth aliform extensions of the lateral costae. *Sphenotrochus gardineri* has an expanded base, but no aliform processes are developed.

Gardiner on two occasions (*in* Gardiner and Waugh, 1938; 1939a, p. 333) recorded *Sphenotrochus intermedius* (Münster) from deep-water dredgings. The first record included specimens from the North Atlantic and were probably correctly assigned. The latter occurrence, in dredgings of "Discovery II," included specimens from Cape Horn and New Zealand. The genus had not been previously recorded from either area, but recently I have seen specimens from both. An as yet undescribed species

TABLE 2  
MEASUREMENTS (IN MILLIMETERS) OF *Sphenotrochus gardineri*, NEW SPECIES

Specimen	Number of Septa	Height of Corallum	Diameters of Corallum	Columella Length	Number of Columellar Processes	Condition of Specimen
Trawl 14B						
1 (holotype)	52	7.7	$6.9 \times 4.1$	3.3	7	Dead
2	52	9.1	$8.0 \times 4.8$	—	—	Dead
3	43	8.9	$6.9 \times 4.3$	3.0	7	Dead
4	51	7.6	$7.5 \times 4.9$	3.1	5	Worn
5	48	—	— —	3.5	7	Worn
6	44	—	— —	—	—	Worn
7	45	5.2	$4.5 \times 2.6$	2.4	7	Dead
8	43	—	— —	—	—	Worn
Trawl 16						
1	51	8.4	$8.1 \times 5.1$	4.3	8	Dead

from New Zealand is much closer in appearance to *S. intermedius* Duncan than are the specimens from Cape Horn. Although it is impossible to determine from his description alone which of the two groups of specimens he discusses, the all too brief remarks could be applied to either, judging from the specimens I have seen. The specimens from "Discovery II" station 934 (north of New Zealand) are larger than those from "Discovery II" station 388 (Scotia Sea), which correspond in size rather closely to *S. gardineri*. Gardiner's remark that the columella is trabecular clearly places both suites of specimens with *S. rubescens* and other species having this type of columella, while the usually unbranched costae on the lateral faces and unbranched end costae of the Cape Horn form suggest a relationship with *S. gardineri*.

The species from New Zealand is pointed basally, corresponding in this respect to *Sphenotrochus intermedius*. *Sphenotrochus gardineri* differs from *Sphenotrochus intermedius* Duncan in the presence of trabecular knobs on the summit of the columella, the presence of septa of the fourth and fifth



TABLE 3  
COMPARISONS OF SEVERAL SPECIES OF *Flabellum*

	<i>Flabellum thoursii</i>	<i>Flabellum curvatum</i>	<i>Flabellum</i> sp. <sup>a</sup>	<i>Flabellum rubrum</i>
Size	Small to medium	Medium to large	Large	Medium
Height	Short	Tall	Tall	Medium
Regularity of shape	Regular	Irregular	Regular	Regular
Pedicle diameter	Large	Medium	Very large	Medium
Maximum diameter calice/ minimum diameter calice	About 1.5	Less than 1.5	1.5-2.0	1.5-2.0
Septal granulation	Coarse, short	Fine, spinose	Fine, spinose	Medium to coarse, granular
Septal ridges	Coarse	Fine	Fine	Fine
Leading edge of septum	Slightly thickened	Thin	Thin	Thickened
Straightness of leading edge	Wavy at depth	Nearly straight	Usually straight	Straight
Septal notch	Present only in immature specimens	Present, deep	Absent or slightly developed	Not present
Dentation of notch	Very fine	Fine to coarse	—	—
Edge of calice	Arched	Nearly planar	Planar	Planar
Habit	Attached	Free in maturity	Attached	Attached
Distribution	Patagonian Shelf	Patagonian Shelf	Antarctica	New Zealand
Depth range	Shallow shelf to 200 m.	Deep shelf and slope, 150 to 1500 m.	Shelf and slope	Shelf

<sup>a</sup> The Antarctic species usually referred to *Flabellum thoursii* Milne-Edwards and Haime.

cycle in the calice, and in the lesser degree of the branching of the costae on the lateral faces.

The measurements of the specimens are given in table 2.

# FAMILY FLABELLIDAE

## GENUS *FLABELLUM* LESSON

Five species of *Flabellum* have been recorded from the Southern Ocean, two of them from the Scotia Sea. *Flabellum thouarsii* and *Flabellum curvatum*

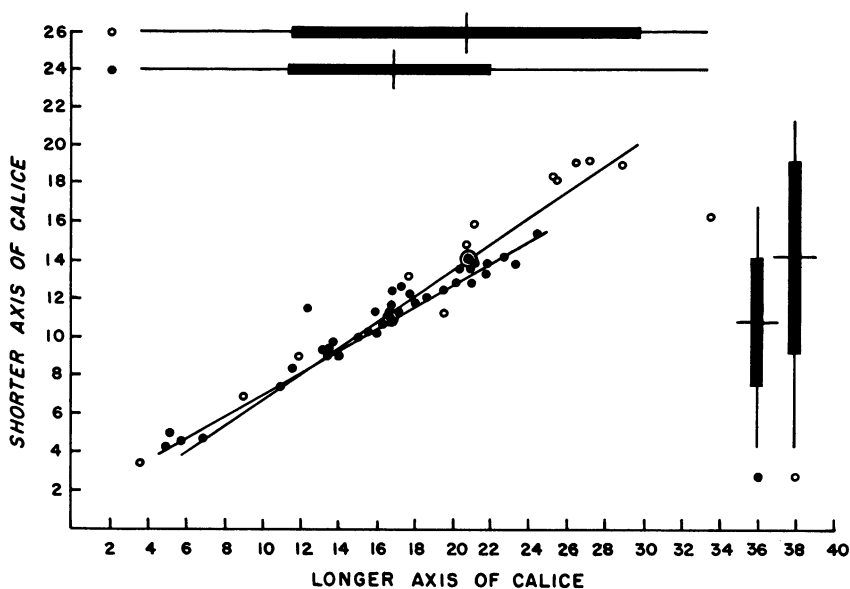


FIG. 9. Relationships between axes of calice in *Flabellum thouarsii* (solid circles) and *F. curvatum* (open circles). Reduced major axes plotted for respective species. Significance of the difference in slopes is at the 5 per cent level. Bars at top of graph give range, mean, and one standard deviation on each side of mean for longer axis of calice. Bars on right side of graph give similar data for shorter axis of calice.

are considered in greater detail below. *Flabellum patagonicum* Moseley was described from deep basins on the western side of Patagonia, and *Flabellum antarcticum* is an Antarctic form not found in the northern waters.

*Flabellum thouarsii* and *Flabellum curvatum* have been treated as synonyms and as separate identities by various authors. Wells (1958, p. 268) concluded: "The range of variation in *F. curvatum* was well illustrated by

Gardiner and clearly indicates that the species includes the earlier named *F. thouarsi* [sic] and probably some other southern species of the *F. rubrum* group with at least four complete cycles of septa plus most of the fifth." It is not apparent from Gardiner's (1939a) discussion whether or not he was aware of Milne-Edwards and Haime's species *F. thouarsii*, and he certainly did not consider it in relation to the specimens at hand, despite the fact that they could have been considered as topotypes.

An examination of the materials collected by the "Vema" leads to the

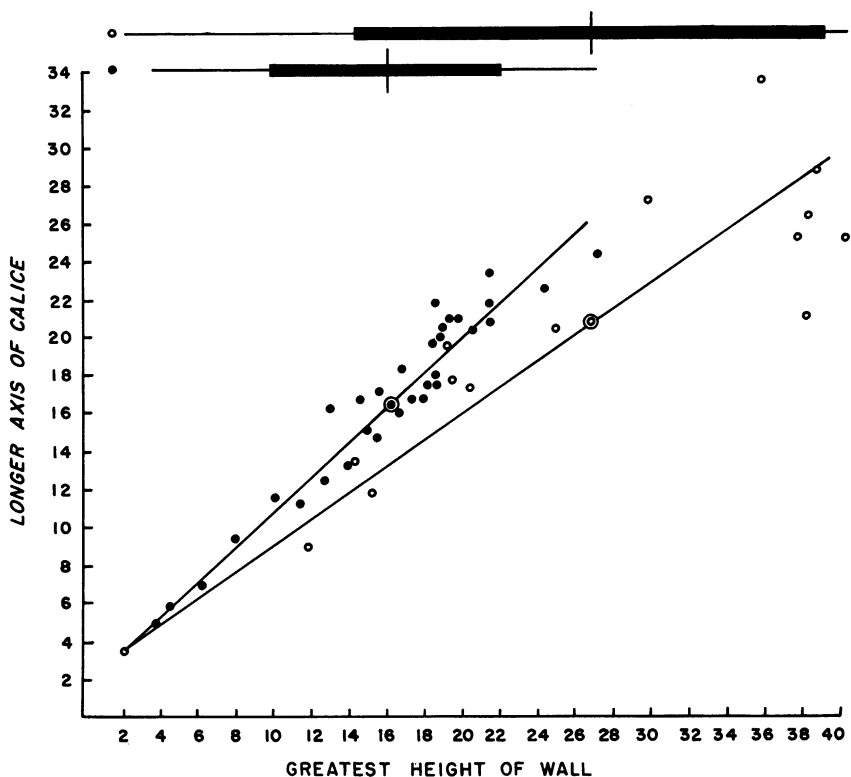


FIG. 10. Relationships between longer axis of calice and greatest height of wall in *Flabellum thouarsii* (solid circles) and *F. curvatum* (open circles). Reduced major axes are plotted for respective species. Differences between slope and position of lines are not significant. Bars at top of graph give range, mean, and one standard deviation on each side of mean for the greatest height of wall.

conclusion that two rather clearly separable groups are present (see figs. 11–19). However, the more extensive series examined by Gardiner must

be considered, and, although his systematics are very broadly drawn, his judgment concerning variation should be accurate. Unfortunately, of the characters here deemed important, little mention is made. Gardiner (1939a) states that some specimens were attached, but that the corallum becomes free. The calicular ratio as stated is not distinctive, and unfortunately the citation of only one measurement of the specimens makes size comparisons difficult. Although it is stated that a septal notch is present, it is not clear whether it is invariable or not, or how large it is. Most of the specimens figured are, on the basis of corallum form, probably *F. thouarsii*, a conclusion agreeing with their affinities as judged by distribution.

Differences between several of the species of *Flabellum* that are attached through their life, and *Flabellum curvatum*, are shown in table 3. The relationship between *Flabellum thouarsii* and the species referred to by that name from the Antarctic is quite clear; they are distinct. *Flabellum rubrum* from New Zealand is also included in the comparative chart (table 3).

*Flabellum thouarsii* Milne-Edwards and Haime, 1848

Figures 14–19, 21, 23

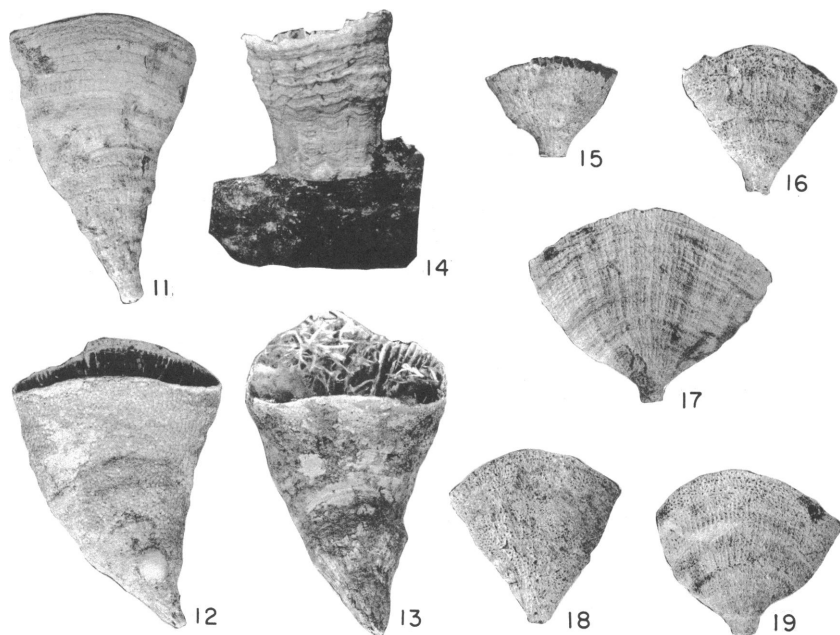
*Flabellum thouarsii* MILNE-EDWARDS AND HAIME, 1848, Ann. Sci. Nat., Paris, ser. 3, vol. 9, p. 265, pl. 8, fig. 5.

? *Flabellum thouarsii*, STUDER, 1877, Monatsber. K. Akad. Wiss. Berlin, p. 630.

*Flabellum curvatum* Moseley, GARDINER, 1939, in Discovery reports, vol. 18, p. 327 (part).

Milne-Edwards and Haime make the distinction between this and other species of *Flabellum* principally on the size of the pedicel. They give the angle formed by the lateral edges as about 70 degrees, but in the specimens before me the growth of the corallum is such that measurement of an angle on a consistent pattern is problematical. Of particular interest is their statement that the two axes of the calice are in approximately the same plane. The illustration of the species, although showing some of the later growth lines as being horizontal (while earlier ones are distinctly curved), has the appearance of a highly arched calicular margin. No mention is made of the presence of a notch in the septa adjacent to the wall, and the illustration shows the septa leaving the wall nearly horizontally.

A majority of the specimens at hand have a distinctly arched calice. The growth lines on the upper corallum are arched, becoming less so downward. Many of the larger specimens, particularly those that have the largest lateral angle, show a rapid expansion in the longer diameter of the calice abruptly above the pedicel. A character of some significance is the presence of a notch or a depression in the edge of the septa



FIGS. 11–13. *Flabellum curvatum* Moseley, A.M.N.H. No. 3371, Vema 14, trawl 12. 11. Specimen enclosed in sponge, only slightly irregular in shape. Pedicel slightly corroded. 12. Cornute specimen taken alive. Corallum bent in two planes. Photographed from upper side as evinced by attached bryozoans; pedicel badly worn. 13. Specimen completely buried in sponge. Basal portion of corallum badly corroded. Corallum strongly cornute. All  $\times 1$ .

FIGS. 14–19. *Flabellum thoursii* Milne-Edwards and Haime, A.M.N.H. No. 3371, Vema 14, trawl 16. 14. Specimen in cylindrical stage (first year ?) taken alive, attached to pebble. Thirty-six septa present in corallum. 15. Small specimen with fresh basal scar. Note abrupt change in shape following cylindrical “pedicel” stage. 16. Dead, but unworn, specimen with a fresh basal scar. Profile not so abrupt as in figure 15. 17. Mature specimen taken alive. Basal scar quite fresh, indicating recent detachment. Opposite face covered with cheilostome Bryozoa. 18. Dead and worn specimen with flattened conical profile. 19. Dead and slightly worn specimen with irregular form. Pedicel somewhat corroded. Figure 14,  $\times 10$ ; figures 15–19,  $\times 1$ .

adjacent to the wall. This is generally present in younger specimens, becoming less apparent in larger ones. Septal granulation is quite coarse and dense, the granules being aligned parallel to the leading edge of the septum which itself may be slightly thickened. Just above the columella, the major septa become somewhat irregular and wavy. Specimens preserved in formalin had a scarlet peristome, and the tentacles were a dark



FIG. 20. *Flabellum curvatum* Moseley, A.M.N.H. No. 3369, mature specimen 41.3 mm. in height, Vema 14, trawl 12. Note concavity in upper profile of septa with small denticles. Proximal edge of septum thin, somewhat sinuous.  $\times 20$ .



FIG. 21. *Flabellum thouarsii* Milne-Edwards and Haime, A.M.N.H. No. 3371, mature specimen 29.2 mm. in height, Vema 14, trawl 16. Compare thinner, more coarsely granulate septa with those in figure 20. Note slight concavity on upper septal margin.  $\times 20$ .



FIG. 22. *Flabellum curvatum* Moseley, same specimen as that shown in figure 20, with sponge spicules only partially cleaned away. Compare septal granulation and coarseness with those in figure 23.





FIG. 23. *Flabellum thouarsii* Milne-Edwards and Haime, A.M.N.H. No. 3372, mature specimen 33.7 mm. in height, Vema 14, trawl 8. Upper edges of septa broken back. Note density of granulation and proximal sinuosity of septa.  $\times 20$ .

purple-red when retracted. Similar coloration was observed by Gardiner.

The differences between *Flabellum thouarsii* and *F. curvatum* are given in the discussion of the latter species. Generally included with *Flabellum thouarsii* (see Wells, 1958) are species of *Flabellum* from the Antarctic, exclusive of *F. antarcticum* Marenzeller. This misinterpretation of *F. thouarsii* is to be rectified in a forthcoming report on the corals from the Ross Sea. The principal differences between that species and *Flabellum thouarsii* (*sensu stricto*) consist of the larger size of the Antarctic form, its even, flat uncurved calice, the absence of a septal notch, a larger pedicel, and coarser septal ornamentation.

As defined here, *Flabellum thouarsii* is a common constituent of the upper portions of the Malouine Shelf, particularly in depths of less than 150 meters. In its restricted sense, the species is not known beyond the Patagonian Shelf.

*Flabellum curvatum* Moseley, 1881

Figures 11–13, 20, 22

*Flabellum curvatum* MOSELEY, 1881, in Report on the scientific results of the voyage of H.M.S. Challenger during the years 1873–76, Zoology, vol. 2, pt. 7, p. 174, pl. 6, figs. 3a–3d. GARDINER, 1939, in Discovery reports, vol. 18, p. 327, pl. 20, figs. 1, 2 (part).

Moseley stressed the great curvature of the corallum which was extreme in his specimens. None of the materials I have seen, nor those remarked upon by Gardiner (1939a), is so distorted. As indicated by Moseley, the angle formed by the lateral edges is nearly 50 degrees, and the upper edge of the calice is nearly horizontal or only slightly arched. Septa are notched close to the wall in Moseley's figures, and the light ornamentation of the septa is also suggested.

The specimens from the "Vema" collections placed in this species are tall, large coralla broadly open at the calice and having a distinct calicular rim above the septa. This initial concavity or notch in the profile of the septa is, in most specimens, marked by the presence of a number of very fine denticles. Laterally and proximally the septa are finely dentate and bear few raised lines. In these morphological characteristics *Flabellum curvatum* differs from *F. thouarsii*. Of considerable importance is the difference in habit. *Flabellum curvatum* is free in the ephebic stage, while *F. thouarsii* remains attached. The Antarctic species differs from *F. curvatum* in its greater size, the usually greater angle that is developed between the lateral edges, and in the less well-developed notch in the septa.

*Flabellum curvatum* is known only from the Falkland Trough, where it

occurs in depths of 150 to 200 meters, and from its type locality off the Rio de la Plata in 1160 meters. The increasing depth of its occurrence to the north is related to the temperature gradient.

FAMILY DENDROPHYLLIIDAE

***Balanophyllia malouinensis*, new species**

Figures 24–26

*Balanophyllia cornu* (Moseley), GARDINER, 1939, in *Discovery reports*, vol. 18, p. 335 (part).

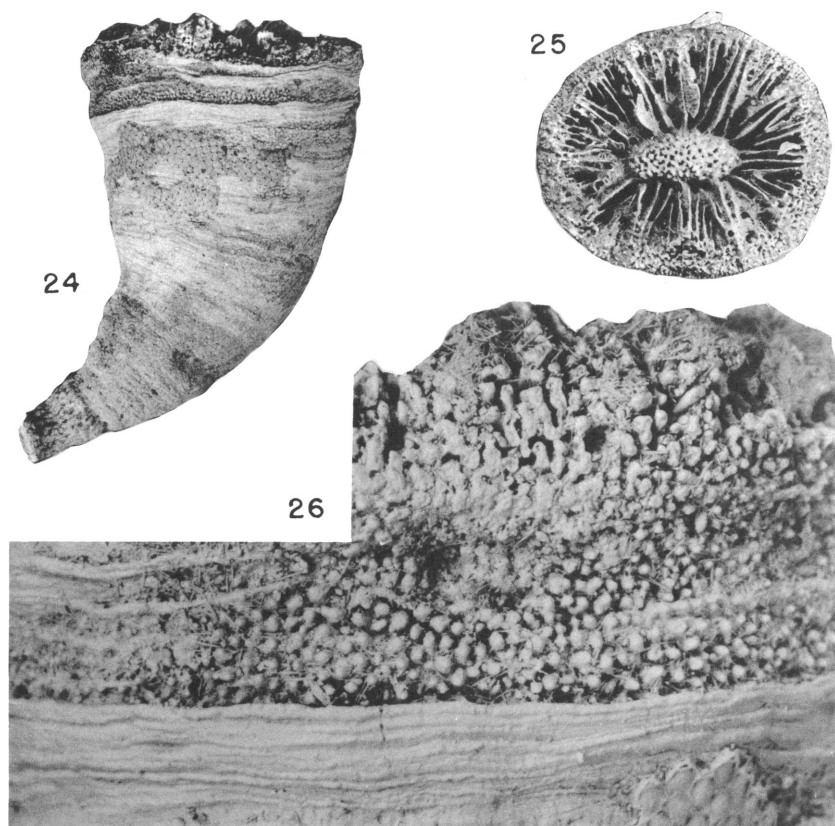
HOLOTYPE: A.M.N.H. No. 3368; Vema 14, trawl 12, latitude 52° 32' S., longitude 61° 15' W.; depth, 358 meters; northern Scotia Sea, in Falkland Trench; collected by Peter Trurnit, Lamont Geological Observatory R/V "Vema," February 10, 1958.

MATERIALS: Six specimens, all dead and most badly worn, from trawl 12.

DESCRIPTION: Corallum large, cornute, often with heavy epitheca surrounding a porous wall. Epitheca extending nearly to the calicular lip in some specimens. Wall not costate, but appearing as a series of sharply pointed granules with no particular orientation. Wall thick, up to 1.5 mm. at the upper edge. Basal pedicel large and bearing a flat attachment area. Some specimens are cornute and have an abraded pedicel, indicating that they were free, while others were attached by an expanded base. Septa exsert, numbering about 68, arranged in four complete cycles, with portions of the fifth cycle present in most systems. Septa of the first two cycles lightly granulate laterally, and entire except near the wall where they may be dentate. Septa of the third and higher cycles more highly dentate, and may be fenestrated or deeply notched. Columella high, large, and papillose.

The holotype, and only measurable specimen, is 28.2 mm. in height and has calicular diameters of 19.2 by 16.8 mm. The columella is 7.3 mm. in length and 3.1 mm. in width.

Gardiner (1939a, p. 335) discusses specimens of a balanophylliid coral from the Falkland Islands and Graham Land region which he assigns to *Balanophyllia cornu* (Moseley [*sic*]). This species, originally described from the Kei Islands, was based on specimens not having an external epitheca and with a wide encrusting base. Gardiner (1939a) indicates that his specimens from Cape Horn have an epitheca, and "Some would be described as of the *Thecopsammia facies*." He notes also that the costae are not well marked and that the corallum is not so firm as that of *Balanophyllia cornu*.



FIGS. 24–26. *Balanophyllia malouinensis*, new species, holotype, A.M.N.H. No. 3368, Vema 14, trawl 12. 24. Corallum. Note thick epitheca, corroded pedicel.  $\times 2$ . 25. Calice.  $\times 2$ . 26. Wall details. Note non-alignment of costal prominences.  $\times 10$ .

Four genera of modern dendrophylliid corals may possess an epitheca: *Balanophyllia*, *Trochopsammia*, *Bathypsammia*, and *Thecopsammia*. *Trochopsammia* is unique in having greatly thickened septa and costae; *Bathypsammia* and *Thecopsammia* are differentiated by the condition of the septa in their younger stages, but both have the normal arrangement of septa in later stages of development. *Balanophyllia*, then, is the only genus in which the epitheca and Pourtalès' plan of septal arrangement in the adult stages are associated. Marenzeller (1906) and van der Horst (1922, p. 61) are unanimous in stating that the presence or absence of an epitheca in *Balanophyllia* is variable and not significant for systematic purposes. If adaptational, its function is yet not understood.



FIG. 27. Silt bottom with polyps about 5 inches in diameter, believed to be *Flabellum thouarsii*, in lower left and center. Bottom edge of photograph represents about 3 feet. The absence of shadows about polyps suggests they are partially immersed in substrate. Compare with figure 30. Photograph by Maurice Ewing, with Lamont Multiple Exposure Camera. Vema 14, station 12, latitude  $43^{\circ} 05' S.$ , longitude  $61^{\circ} 42' W.$ ; depth, 77 meters.



FIG. 28. Coarse gravel bottom south of Falkland Islands. Although *Balanophyllia* was found on this substrate, no unquestioned corals are seen in the photograph. Bottom edge of photograph represents about 3 feet. Photograph by Maurice Ewing, with Lamont Multiple Exposure Camera. Vema 14, station 24, latitude  $52^{\circ} 49' S.$ , longitude  $59^{\circ} 02' W.$ ; depth, 106 meters.

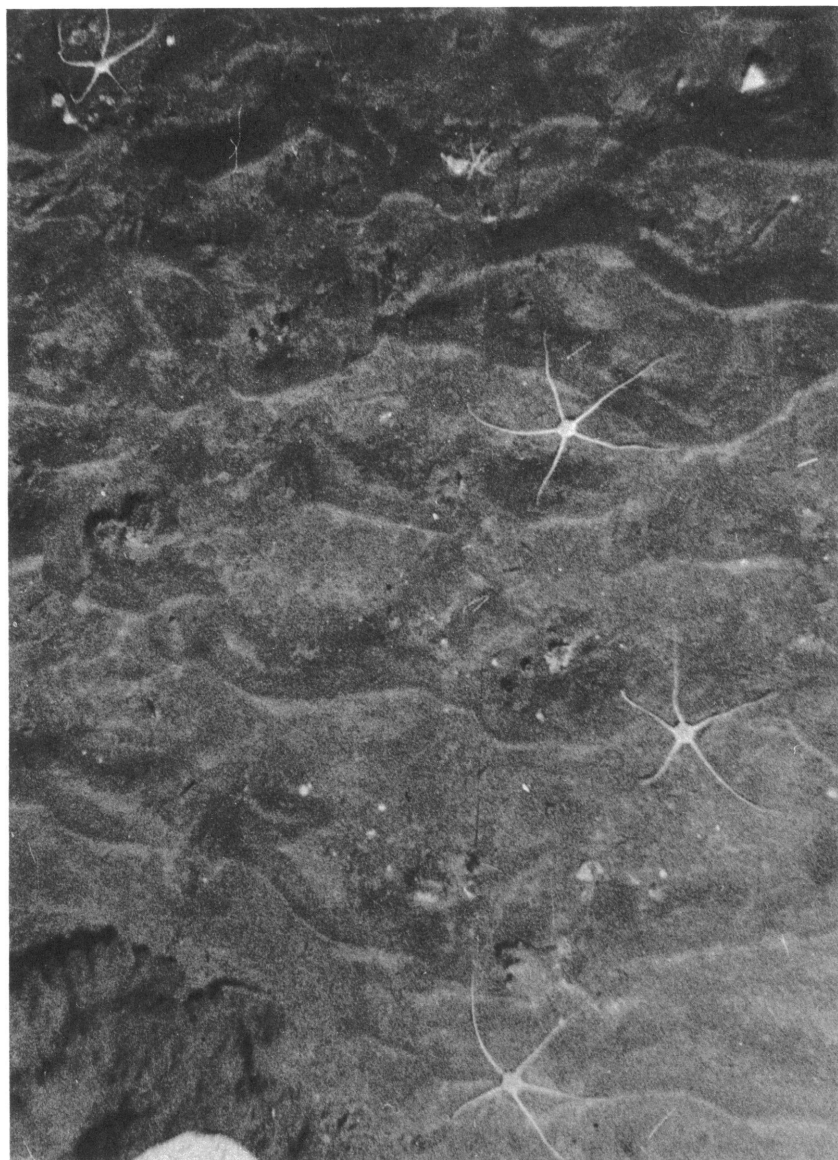


FIG. 29. Silt bottom with presumed Scleractinia. *Upper right*: A free corallum with polyp. *Left middle ground and center foreground*: Upright polyps. Bottom edge of photograph represents about 3 feet. Photograph by Maurice Ewing, with Lamont Multiple Exposure Camera. Vema 14, station 22, latitude 52° 22' S., longitude 65° 43' W.; depth, 117 meters.





FIG. 30. Silt bottom in Falkland Trough with presumed *Flabellum curvatum*. *Left foreground*: Free coralla lying on their side. *Middle ground*: Upright coralla. Photograph by Maurice Ewing, with Lamont Multiple Exposure Camera. Vema 14, station 17, latitude 52° 41' S., longitude 61° 11' W.; depth, 364 meters.





FIG. 31. Silt bottom in Falkland Trough, in approximately the position of figure 30. Note different color patterns of polyps in center of photograph. Upright bushy organisms not identified. Data for this photograph are the same as for figure 30.

*Balanophyllia malouinensis* is distinguished from *B. cornu* Moseley by the absence of costae, well defined or otherwise.

### LITERATURE CITED

ALCOCK, A.

1902. Report on the deep-sea Madreporaria of the Siboga Expedition. *In* Siboga-Expeditie Vitkomsten op Zoologisch, Botanisch, Oceanographisch en Geologisch gebied verzameld in Nederlandsch Oost-Indië 1899-1900. Leiden, Monogr. 16a, 53 pp., 5 pls.

DEACON, G. E. R.

1937. The hydrology of the Southern Ocean. *In* Discovery reports. Cambridge, vol. 15, pp. 3-124, pls. 1-44.

EARLAND, A.

1934. Foraminifera. Part III. The Falkland sector of the Antarctic (excluding South Georgia). *In* Discovery reports. Cambridge, vol. 10, pp. 1-208, pls. 1-10.

EKMEN, SVEN

1953. Zoogeography of the sea. London, xiv + 417 pp., figs.

FAGE, L.

1937. Sur l'association d'une annélide polychète *Lumbriconereis flabellicola* n. sp. et d'un madrépore *Flabellum pavoninum distinctum* E. & H. *Compte Rendu Congr. Internl. Zool. XII*, Lisbon, pp. 941-945, 2 figs.

FLEMING, C. A.

1951. Some post-Miocene changes in New Zealand environments. *New Zealand Sci. Rev.*, no. 9, pp. 166-171.

GARDINER, J. S.

1904. South African corals of the genus *Flabellum*, with an account of their anatomy and development. *Marine Invest. South Africa*, vol. 2, pp. 116-154, pls. 1-4.
- 1939a. Madreporarian corals, with an account of variation in *Caryophyllia*. *In* Discovery reports. Cambridge, vol. 18, pp. 323-338, pls. 20, 21.
- 1939b. The ecology of solitary corals. *In* Scientific reports of the John Murray Expedition, 1933-34, British Museum (Natural History). London, vol. 6, pp. 243-250.

GARDINER, J. S., AND P. WAUGH

1938. The flabellid and turbinolid corals. *In* Scientific reports of the John Murray Expedition 1933-34, British Museum (Natural History). London, vol. 5, no. 7, pp. 167-202, pls. 1-7.

GRAVIER, C.

1914. Madréporaires. *In* Deuxieme Expedition Antarctique Française, 1908-1910. Paris, vol. 5, pp. 119-133, 1 pl.

HART, T. J.

1946. Report on trawling surveys on the Patagonian continental shelf. *In* Discovery reports. Cambridge, vol. 23, pp. 226-408, pl. 16.

HESSE, R., W. ALLEE, AND K. P. SCHMIDT

1937. Ecological animal geography. New York, John Wiley and Sons, 597 pp.

HORST, C. J. VAN DER

1922. Madreporaria of the Siboga-Expedition. *In* Siboga-Expeditie Vitkomsten

op Zoologisch, Botanisch, Oceanographisch en Geologisch gebied verzameld in Nederlandsch Oost-Indië 1899–1900. Leiden, Monogr. 16c, pp. 99–127, pls. 7, 8.

1928. Eupsammid corals from South Africa. Union of South Africa Fish and Marine Biol. Surv. Rept., for 1925–1927, no. 5, pp. 1–7, pls. 1, 2.

1933. *Balanophyllia annae*, a new species of coral from the Cape seas. Ann. Mag. Nat. Hist., ser. 10, vol. 12, pp. 156–158, pl. 7.

1938. *Balanophyllias* from the Cape of Good Hope. *Ibid.*, ser. 11, vol. 2, pp. 139–145, pls. 5–6.

KLAHEHN, J.

1911. Über die Meeresströmungen zwischen Kap Horn und der La Plata-Mündung. Ann. Hydrog. Maritimen Met., vol. 39, pp. 647–665.

MACFAYDEN, W. A.

1933. Fossil Foraminifera from the Burdwood Bank and their geological significance. In Discovery reports. Cambridge, vol. 7, pp. 1–16.

MACKINTOSH, N. A.

1946. The Antarctic Convergence and the distribution of surface temperatures in Antarctic waters. In Discovery reports. Cambridge, vol. 23, pp. 179–212, pls. 1–14.

MARENZELLER, E. VON

1906. Riffkorallen des Rofen Meeres. Number 26 of Zoologische Ergebnisse, Expedition S.M. Schiff "Pola" in das Rote Meer, Nördliche und Südliche Hälfte, 1895/96–1897/98. Denkschr. Akad. Wiss., Vienna, Math.-Nat. Kl., vol. 80, Ber. Komm. für Ozeanogr. Forsch., pp. 27–97, pls. 1–29.

MATTHEWS, L. H.

1934. The marine deposits of the Patagonian continental shelf. In Discovery reports. Cambridge, vol. 9, pp. 177–206, pls. 2–14.

MILNE-EDWARDS, H., AND J. HAIME

1848. Recherches sur les polypiers. Deuxieme mémoire. Monographie des turbinolides. Ann. Sci. Nat., Paris, ser. 3, vol. 9, pp. 211–344, pls. 7–10.

MOSELEY, H. N.

1881. Report on certain hydroid alcyonarian and madreporarian corals procured during the voyage of H.M.S. "Challenger." In Report on the scientific results of the voyage of H.M.S. "Challenger" during the years 1873–76. London, Zoology, vol. 2, pp. 1–248, pls. 1–16.

NEVERSON, E.

1934. The sea floor deposits. I. General characters and distribution. In Discovery reports. Cambridge, vol. 9, pp. 297–349, pls. 17–22.

PAX, F.

1910. Die Steinkorallen der Deutschen Südpolar-Expedition 1901–1903. In Drygalski, Erich von (ed.), Deutsche Südpolar-Expedition 1901–1903. Berlin, vol. 12, Zoologie, vol. 4, pt. 1, pp. 63–76, pls. 11–12.

POWELL, A. W. B.

1951. Antarctic and Subantarctic Mollusca: Pelecypoda and Gastropoda. In Discovery reports. Cambridge, vol. 26, pp. 49–196, pls. 5–10.

[MS.] New Zealand biotic provinces. Abstract of Memorandum O.R. 87, New Zealand Committee on Oceanography. Cyclostyled in 1954, not published.

## ROGER, J.

1944. Essai d'interpretation d'une form curieuse de *Flabellum* du Pliocene ancien de Dar Bel Harmi (Maroc). Bull. Mus. Natl. d'Hist. Nat., Paris, vol. 16, pp. 245-254, pls. 1, 2.

## SEMPER, C.

1872. Ueber Generations-wechsel bei Steinkorallen und über das M. Edwards'sche Wachsthums-gesetz der Polypche. Zeitschr. Wiss. Zool., vol. 22, pp. 235-277, pls. 16-21.

## SQUIRES, D. F.

1958. The Cretaceous and Tertiary corals of New Zealand. New Zealand Geol. Surv. Paleont. Bull., no. 29, 107 pp., 16 pls.

## STEPHENSON, T. A.

1933. The gonads of corals. In Marshall, S. M., and T. A. Stephenson, The breeding of reef animals. Part I. The corals. In Scientific reports, Great Barrier Reef expedition 1928-1929, British Museum (Natural History). London, vol. 3, no. 8, pp. 220-235.

## THORSON, G.

1950. Reproductive and larval ecology of marine bottom invertebrates. Biol. Rev., vol. 25, pp. 1-45.

## UNITED STATES NAVY HYDROGRAPHIC OFFICE

1957. Oceanographic atlas of the polar seas. Part I. Antarctic. Publication no. 705, 70 pp., charts.

## VAUGHAN, T. W., AND J. W. WELLS

1943. Revision of the suborders, families, and genera of the Scleractinia. Spec. Paper Geol. Soc. Amer., no. 44, pp. 1-363, pls. 1-51.

## WELLS, J. W.

1937. Individual variation in the rugose coral species *Heliophyllum halli* E. & H. Palaeont. Amer., vol. 2, pp. 5-22, pl. 1.
1958. Scleractinian corals. In Reports B.A.N.Z. Antarctic Research Expedition 1929-1931. Adelaide, series B (Zoology and Botany), vol. 6, pt. 11, pp. 257-275, pls. 1, 2.