

Cheilostome Bryozoa of Late Eocene Age From Eua, Tonga

GEOLOGICAL SURVEY PROFESSIONAL PAPER 640-E



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By ALAN H. CHEETHAM

LATE EOCENE FOSSILS FROM EUA, TONGA

GEOLOGICAL SURVEY PROFESSIONAL PAPER 640-E

*Mixed assemblage of shallow- and deep-sea species
from offreef tuffaceous limestone*



UNITED STATES DEPARTMENT OF THE INTERIOR

ROGERS C. B. MORTON, *Secretary*

GEOLOGICAL SURVEY

W. A. Radlinski, *Acting Director*

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LATE EOCENE FOSSILS FROM EUA, TONGA—FOREWORD

One of the most widespread units of the Cenozoic section in the islands of the open Pacific is a series of limestones assigned to the upper Eocene (Tertiary *b*). Such limestones, containing diagnostic larger Foraminifera, have been reported in many parts of an area spreading 4,000 miles across the tropical Pacific (fig. 1), from Palau and the Mariana Islands on the northwest through the Marshall Islands (Eniwetok) to Fiji and Tonga on the southeast (Whipple, in Hoffmeister, 1932, p. 79–86; Asano, 1939; Cole, 1950, 1957a, 1957b, 1960). In almost all the islands the limestones are dense and crystalline. Foraminifera and algae are abundant locally, but in most places fossils cannot be extracted and must therefore be studied in random thin sections. On the little island of Eua, Tonga, a locality was recently found where the Eocene limestone is tuffaceous, considerably weathered, and richly fossiliferous. Abundant fossils that represent a dozen organic groups were found. Such abundance and diversity signaled the find as a remarkable one that would add greatly to our knowledge of life in the western Pacific during the Eocene.

The island of Eua measures only 12 by 5 miles but it rises 1,000 feet above sea level. It occupies an interesting position tectonically, as its steep eastern side faces the Tonga Trench. In addition, Eua is the oldest island in the Tonga group that has a plutonic core (Guest, 1959) and a series of associated volcanic rocks, which are partly blanketed by thick limestones of late Eocene age. Younger volcanic rocks and sediments of late Tertiary age are also present (Hoffmeister, 1932).

This series of reports is concerned with one facies of the upper Eocene limestone. After the limestone series was deposited, Eua was uplifted periodically and a sequence of six terraces was cut in the limestones on the windward (eastern) side. Hoffmeister was the first to recognize the Eocene age of the main limestone of the terraces, three of which have veneers of Pliocene reef corals. He made a planetable map of the terraced eastern ridge and recorded the average altitudes of the terraces as 100, 200, 340, 400, 550, and 760 feet. The east-facing “rocky backbone” of Eua thus looks in profile like a giant staircase facing the Tonga Trench. The Eocene limestone may once have covered all of Eua

but is now largely limited to the eastern ridge (Hoffmeister, 1932; the Eocene Foraminifera were described by Whipple in this same report, p. 79–86).

The fossils described in this series of reports were obtained from an outcrop on the 400-foot terrace about a quarter of a mile north of Vaingana (fig. 2). At this locality, the limestone lies close to the underlying volcanic rock and is tuffaceous and partly weathered; almost everywhere else on Eua the limestone is pure, hard, and crystalline.

In 1943, Harold T. Stearns, then of the U.S. Geological Survey, also served as a consultant to the Armed Forces at Pacific bases and made a brief visit to Eua. He collected a sample that contained half a dozen fossil brachiopods from the 400-foot terrace on the eastern side of the island. Stearns recorded the locality as: “Tele-a-hiva at elevation of 400 feet about $\frac{1}{2}$ mile north of army lookout tower, at the second stream north of Vaigana [sic].” The brachiopods were examined by G. A. Cooper of the U.S. National Museum. Some years later when I was studying other island fossils collected by Stearns, Cooper showed me the brachiopods and expressed a desire for additional specimens so that he could continue his study of their internal structures.

In 1966, I learned that Yoshio Kondo of the Berrice P. Bishop Museum in Honolulu intended to visit Eua in connection with his studies of living Pacific island land snails (under National Science Foundation grant GB-3974). I sent Stearns’ locality data and marked copy of Hoffmeister’s Eua map to Kondo, and I informed Stearns of the plan to collect additional material.

Late in August 1967, Kondo reached Eua and, aided by a Tongan guide, Tomiki, and an interpreter, Mosese Ve’a, spent 2 days searching for the fossil locality. The lookout tower mentioned by Stearns no longer exists and Kondo found that Tele-a-hiva translates to “Nine Gulches.” Traveling northward from “Vaigana” (Otu Vaingana) through heavy brush on exceedingly rugged karst topography for about 1,000 feet, he reached the first of the gulches. There he found a soft fossiliferous layer between two harder limestones and collected a

40-pound sample of the material. This gulch locality is probably not the exact spot visited by Stearns. The two collections have minor differences in nature of preservation, but they obviously came from the same formation.

In 1969 Wilfred Bryan of the Carnegie Institution of Washington collected additional material from the locality sampled by Kondo. Bryan's material was taken from soft calcareous tuffs 2-3 feet in thickness that dipped 30°-40° E. These calcareous tuffs were

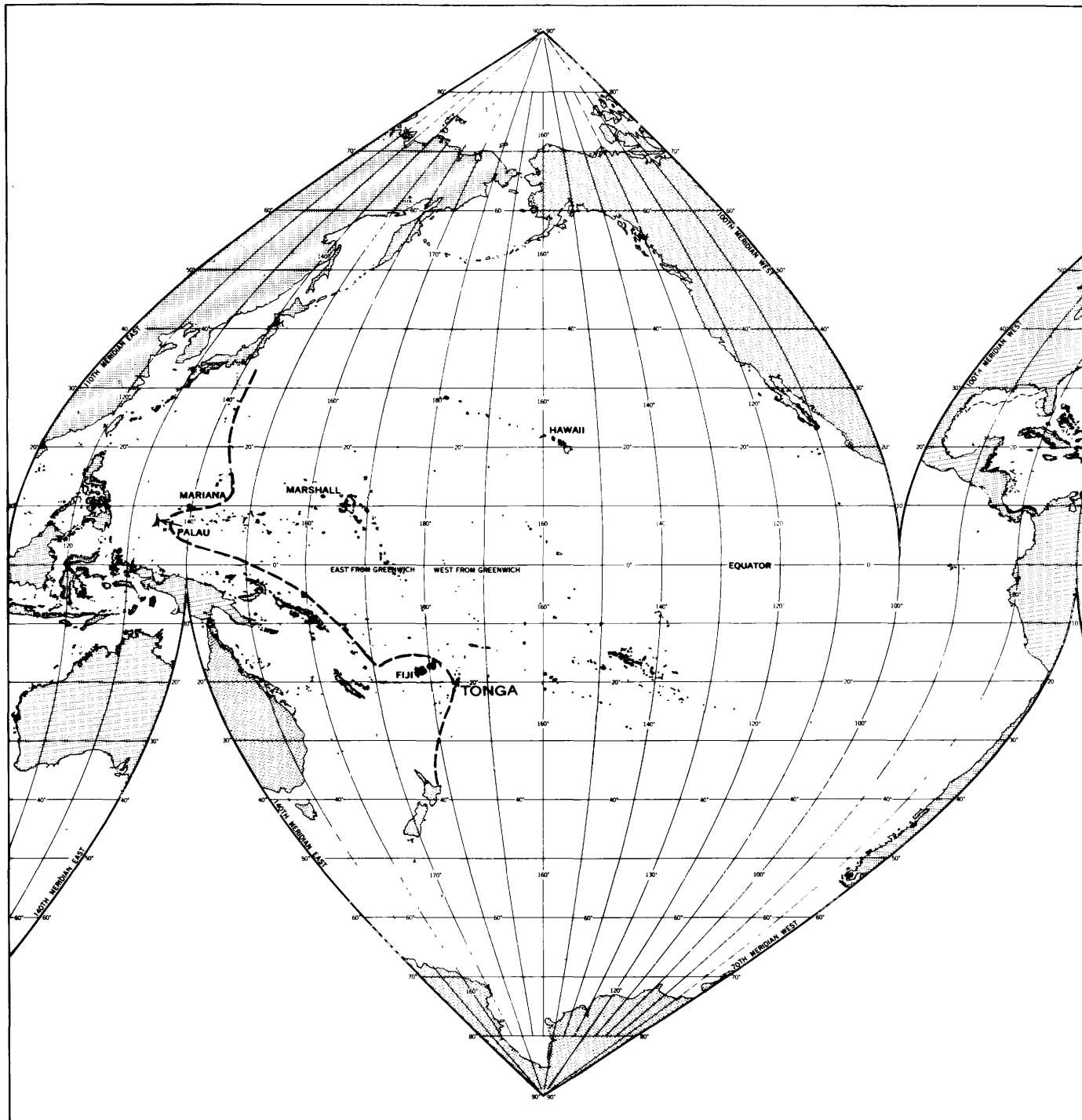


FIGURE 1.—Location of Tonga and other island groups in the southwest Pacific where upper Eocene limestone has been identified. Dashed line marks structural boundary of the Pacific Basin (andesite line). Islands shown include the surrounding reefs.

directly underlain by several feet of harder fossiliferous material that, in turn, lay above agglomerate with truncated dikes. The horizon sampled was at an altitude of about 355 feet in a gully notched into the 400-foot terrace.

The exact extent of the richly fossiliferous bed is not known. In 1926, when Hoffmeister made his

map of the terraces, he did not come upon this facies, and in 1928 when I spent 2 weeks on Eua with Hoffmeister, reviewing his mapping, no exposures of this zone were seen although we visited Vaingana. Additional fieldwork in the area of the rugged "Nine Gulches" would be worthwhile.

William Melson of the Smithsonian Institution examined hand specimens and thin sections of the tuffaceous limestone and noted that the volcanic constituents are highly altered, making it difficult to determine their original nature. The rock is composed of 50 percent or more of volcanoclastic debris, much of which has been replaced by calcite. The predominant volcanic fragments are of porphyritic pumiceous glassy material; most of the phenocrysts are plagioclase, now largely replaced by calcite. The original groundmass of pumiceous glass is now devitrified and dark brown. Fragments of tuff are rare. There appears to be a large and varied assemblage of secondary minerals. The volcanic fragments are mainly porphyritic andesitic rocks, or possibly plagioclase-bearing dacites. The presence of abundant fossils suggests that the volcanic material has been reworked.

The soft tuffaceous limestones collected on Eua were treated with a wetting agent and penetrant in the laboratory. The material broke down easily, revealing a variety of fossil remains: Foraminifera, discoasters, corals, hydrozoans, brachiopods, bryozoans, annelids, crinoids, echinoids, ostracodes, barnacles, decapod crustaceans, mollusks, shark teeth, otoliths, and spores and other plant microfossils.

W. Storrs Cole has described the larger Foraminifera; these fossils suggest to him a depth of deposition of about 200 feet, but other groups—notably the smaller Foraminifera, the corals, brachiopods, bryozoans, mollusks, ostracodes, and barnacles—point to a considerably greater depth of deposition.

Material representing a total of 17 organic groups was distributed to paleontologists for study and report. Seven of these collections were small or were made up of incomplete specimens leading only to summary reports, but the others, except for the larger Foraminifera, contained much new material. The brachiopod, bryozoan, ostracode, barnacle, and mollusk collections contained the first identifiable Eocene species from the islands of the open Pacific, an area extending 4,000 miles from Palau to Tonga.

HARRY S. LADD

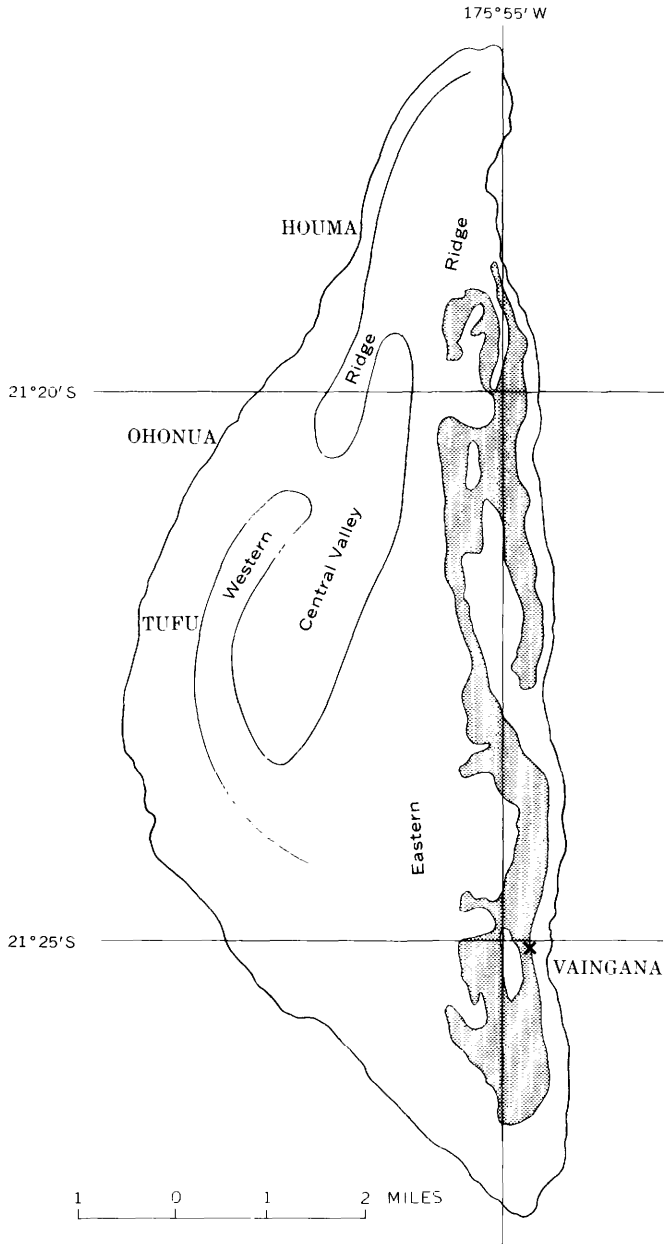


FIGURE 2.—Map of Eua, Tonga, showing the location of the recently discovered fossil outcrop (X) and the main mass of Eocene limestone (patterned area) on the east side of the island, as mapped by Hoffmeister (1932).



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CHEILOSTOME BRYOZOA OF LATE EOCENE AGE FROM EUA, TONGA

By ALAN H. CHEETHAM¹

ABSTRACT

An assemblage of cheilostome Bryozoa from upper Eocene (Tertiary *b*) beds on Eua, Tonga, appears to be a mixture of five autochthonous and 13 allochthonous species. The autochthonous element, which makes up about 85 percent of the specimens in the assemblage, includes the first known fossil cryophilic deep-sea cheilostomes. It can be inferred that these species have lived in water cooler than 13°C at a depth that in the tropics or subtropics exceeded 200 meters. The much rarer but more diversified allochthonous element includes some thermophilic taxa that probably lived at depths less than 100 meters in water having an average temperature of not much less than 20°C in the coolest months. At least some of the allochthonous species grew attached to nonbuoyant substrates and therefore must have been transported to the burial site from a shallow-bottom habitat.

In contrast to the allochthonous species, which show a variety of colony forms, all the inferred deep-water species had nonfenestrate, rigidly erect, subcylindrical to compressed, branched colonies probably attached to the substrate by encrusting bases. Outer skeletal walls probably thickened throughout life; this accretion allowed proximal trunks and branches to thicken greatly and suggests that the colonies grew up from the substrate to filter food from the water, much as do shelf species having similar colonies.

Seven new species, four autochthonous and three allochthonous, are described. Additional allochthonous material seems identifiable with five species known from deposits of middle Eocene to early Miocene age in Australia or India. The remaining material, apparently belonging to six genera, is inadequate for assignment to species.

INTRODUCTION

An assemblage of 18 species of cheilostomes from upper Eocene (Tertiary *b*) beds on Eua, Tonga, includes the first known fossil deep-sea Bryozoa. The five species inferred to be part of this deep-water faunal element belong to four ascophoran genera, and four of the species are morphologically closely comparable to congeneric Holocene deep-sea species. A significant evolutionary history in the deep sea thus probably preceded the entombment of deep-water cheilostomes in sediments now cropping out

in Tonga. The species in this faunal element all had nonfenestrate, rigidly erect, subcylindrical to slightly flattened, branched colonies, in which calcareous accretion seemingly continued throughout life to thicken markedly the more proximal branches. If similar heavily calcified zoaria characterize deep-water species generally, then other deep-water assemblages may be preserved in Tertiary deposits.

In addition to the deep-water element, 13 species occurring less commonly in the assemblage are inferred to have been transported to the site of burial from a shallow-bottom, tropical or subtropical habitat, probably not on a reef. These species belong to genera that are common in Tertiary deposits in the Australia-New Zealand region, and some of the genera have virtually circumtropical distributions. Tongan specimens are identifiable with the following four Australian Tertiary species: *Cellaria cucullata* MacGillivray, from the upper Eocene Glenaulin Clay and Cape Otway beds of Brown (1958); and *Canda fossilis* Waters, *Menipea innocua* Waters, and *Tubitrabecularia clypeata* (Waters), from the lower Miocene Balcombian Stage. Tongan material also seems identifiable with *Tetraplaria turgida* Tewari and Srivastava, a species described from the middle Eocene Kirthar Stage of India.

Specimens of both shallow- and deep-water species are poorly preserved; a few inferred shallow-water specimens show abrasion. The material is from two samples collected from approximately the same outcrop about one-quarter mile north of Vaingana, Eua, Tonga (see "Foreword" and fig. 2), at 400 feet altitude. The samples are listed separately in table 1 (sample 1, station 24686, collected by Y. Kondo, 1967; sample 2, station 24745, collected by Wilfred Bryan, 1969); the differences between them appear to be within the expected sampling error. The material has been dated by Cole (1970) as late Eocene, and by Todd (1970) as from the *Globigerina gortanii* planktonic foraminiferal zone.

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A less abundant assemblage of cyclostome Bryozoa in the same samples has not been studied.

I am indebted to Harry S. Ladd for the specimens on which this study is based and for comments on the manuscript; to Richard S. Boardman and Joseph E. Hazel for critical reviews of the manuscript; and to JoAnn Sanner and Lorenzo Ford for valuable technical assistance.

PALEOENVIRONMENTS

In the absence of living species in this assemblage, the conditions under which it lived and was buried can be inferred only from the geographic and bathymetric ranges of living congeneric species. All the Tongan Eocene species but one, *Tubitrabecularia clypeata*, have living congeners.

The geographic and bathymetric ranges of genera

can, of course, be equal to those of each included species, but in general they are appreciably greater. It is not surprising, therefore, that nine of the 15 genera represented, or probably represented, in the Tongan Eocene assemblage include living species whose composite ranges extend more than 45° latitudinally from the equator and from shallow depths to 200 meters or more, with shallow occurrences at both low and middle latitudes. These eurythermal, eurybathic genera—*Beania*, *Cellaria*, *Chiastosella*, *Figularia*, *Menipea*, *Patsyella*, *Reteporellina*, *Schizoporella*, and *Spiroporina*—account for more than half the species and about 60 percent of the specimens in the assemblage (table 1). The Tongan species of two of these genera, however, are morphologically closely similar to living species having much more restricted ranges, as discussed below.

TABLE 1.—Specimen abundance, other properties of cheilostome bryozoan species in two samples from upper Eocene beds on Eua, Tonga

[Estimated temperature tolerances are based on depth-latitude distribution of morphologically similar living species]

Species	Number of samples		Temperature tolerance	Inferred growth form
	Sample 1	Sample 2		
<i>Spiroporina kondoi</i> , n. sp.	74	10	Cryophilic	Vinculariiform
<i>Bifaxaria diaphyota</i> , n. sp.	31	19	do	Do.
<i>Reteporellina?</i> sp.	12	7	Eurythermal	Eschariiform
<i>Bifaxaria bryani</i> , n. sp.	2	4	Cryophilic	Vinculariiform
<i>Tubitrabecularia clypeata</i> (Waters)	5	0	Eurythermal	Do.
<i>Tetraplaria simata</i> , n. sp.	3	2	Thermophilic	Cellariiform
<i>Spiroporina deliqua</i> , n. sp.	5	0	do	Vinculariiform
<i>Tessaradoma bifax</i> , n. sp.	3	1	Cryophilic	Do.
<i>Canda fossilis</i> Waters	0	4	Thermophilic	Reteporiiform
<i>Tetraplaria</i> cf. <i>T. turgida</i> Tewari and Srivastava	0	3	do	Cellariiform
<i>Schizoporella</i> aff. <i>S. macgillivrayi</i> Canu and Bassler	2	0	Eurythermal	Vinculariiform
<i>Beania diademata</i> , n. sp.	0	1	Thermophilic	Petrariiform
<i>Cellaria cucullata</i> MacGillivray	1	0	Eurythermal	Cellariiform
<i>Chiastosella?</i> sp.	0	1	do	Membraniporiiform
<i>Figularia?</i> sp.	0	1	do	Vinculariiform
<i>Menipea innocua</i> Waters	0	1	do	Eschariiform
<i>Patsyella?</i> sp.	1	0	do	Vinculariiform
<i>Tripurula</i> aff. <i>T. biarmata</i> (Waters)	0	1	Thermophilic	Membraniporiiform

Five of the genera represented in the Tongan assemblage have Holocene depth-latitude distributions suggesting stenothermal tolerances. The known occurrences of *Canda* (see Harmer, 1926), *Tetraplaria* (see below), and *Tripurula* (see Cook, 1967) are consistent with a thermophilic restriction to shallow-water, tropical or subtropical habitats. On the other hand, *Bifaxaria* seems to be cryophilic, occurring chiefly, perhaps exclusively as discussed below, at bathyal and abyssal depths. *Tessaradoma* appears to be unique among the genera in this assemblage in being cryophilic with extremely broad latitudinal and bathymetric ranges.

A paleoenvironmental interpretation of the Tongan assemblage thus depends upon the seemingly

anomalous association of the cryophilic genera *Bifaxaria* and *Tessaradoma* with thermophilic genera exemplified by *Tetraplaria*. The importance of the Holocene distributions of these genera and the expectation that their Eocene distributions conformed to the same thermal control necessitate more detailed discussion than is available in previous literature.

DISTRIBUTION OF TETRAPLARIA

The living species of *Tetraplaria* are distributed nearly circumtropically (fig. 3). The only tropical region in which the genus has not been found is the West African province, the cheilostome fauna of which has been extensively studied (see Cook, 1968).

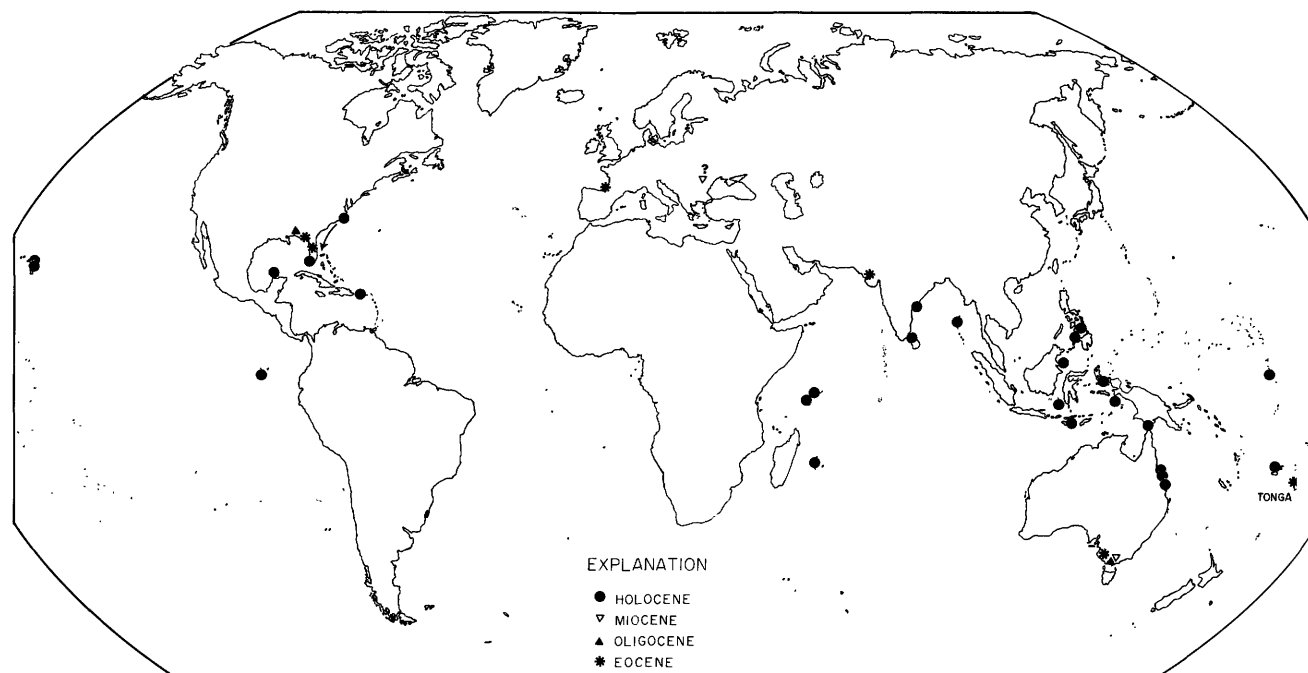


FIGURE 3.—Geographic and stratigraphic distribution of *Tetraplaria*. Sources of data are Brown (1958), Canu and Bassler (1920, 1928b, 1929), Cheetham (1959; 1963), Ghiurca (1966), Harmer (1957), Haswell (1880), Kirchenpauer (1869), Kirkpatrick (1888), Labracherie (1968), MacGillivray (1895), Maplestone (1900, 1909), Maturó (1968), Osburn (1914, 1940, 1952), Robertson (1921), Tenison-Woods (1879), Tewari and Srivastava (1967), Thornely (1905, 1907), Waters (1881, 1883), and the following addi-

tional specimens in the collections of the National Museum of Natural History, Smithsonian Institution: *Tetraplaria* sp. (Oligocene, Marianna Limestone, St. Stephens quarry, Ala.); *T. tuberculata* (upper Eocene, Crystal River Limestone of Cheetham (1963), Sepulga River bridge, Brooklyn, Ala.); *T. australis* (Oligocene, Janjukian Stage, Bird Rock, Torquay near Geelong, Victoria, Australia); *T. australis* (lower Miocene, Balcombian Stage, Altona Bay Coal Shaft, Port Phillips, Victoria, Australia).

The most widely distributed species is the Indo-Pacific *T. ventricosa* (Haswell), known under four names (Harmer, 1957), from the Amirante Islands and Seychelles (long 53°30' E.) eastward to the Fiji Islands (long 178°45' E.). All the known occurrences of *T. ventricosa* lie between latitudes 17° N. and 20° S. Three more names (*Pollaploecium gilbertensis* Maplestone; *P. brevis* Canu and Bassler; and *Tetraplaria veleroae* Osburn) probably refer to a second species distributed from the Gilbert Islands (long 174° E.) eastward to the Galapagos (long 90°30' W.) and from just south of the equator to about latitude 20° N. Two other species have contrastingly restricted distributions; the Atlantic *T. dichotoma* (Osburn) occurs only north of the equator (lat 17°55'–24°45' N.), whereas the Australian *T. immersa* (Haswell) is known only from the south (lat 9°55'–21°39' S.).

The thermal significance of the present latitudinal range of *Tetraplaria* is not known directly because bottom-temperature data are available for only one of the stations at which it occurs (26° C in April 1902, at 36–38 m, Albatross sta. D. 4168, Hawaii). All the modern occurrences are in areas where the

surface waters average 20° C or more during the coolest month of the year. The Atlantic and Indian Ocean occurrences are all in shallow water, 11–18 m and 7–31 m, respectively. Bottom-water temperatures at these depths are no doubt only slightly cooler than surface water temperature. The Pacific occurrences, however, are less restricted in depth, five reported at more than 50 m and three of these at more than 100 m.

Two of the records at more than 100 m, one in the Philippines (104 m; Canu and Bassler, 1929) and one in the Galapagos (110 m; Osburn, 1952), appear not to be extreme if compared with the shallower occurrences, but the third, between 147 and 183 m in the Galapagos (Osburn, 1952), may be outside the living range of the genus. The jointed colonies of *Tetraplaria* readily disintegrate to form small, subcylindrical internodes that could be transported easily down submarine slopes. Encrusting attachment bases of colonies, which probably are more difficult to transport, have been described for only two occurrences, one at 110 m in the Galapagos (Osburn, 1952) and the other at 13 m in Indonesia (Harmer, 1957).

Because of the great morphological differences between zooecia making up the encrusting bases and zooecia in the erect parts of the colony, these bases may have been overlooked for some occurrences of the genus; it is unlikely, however, that this possibility would explain the depth difference in the two Galapagos occurrences, both reported by Osburn (1952).

The 20° C or warmer survival range suggested by the depth-latitude distribution of the living species can be applied to fossil species of *Tetraplaria* only in the absence of morphological and distributional evidence indicating evolutionary changes in temperature tolerance. The nearest known counterpart in distribution and morphology to the widespread Holocene Indo-Pacific species *T. ventricosa* is *T. turgida* Te-wari and Srivastava, from the middle Eocene of India, which may be represented in the Tongan material. Other fossil species, however, give the genus an appreciably broader Eocene latitudinal range (43° 29' N.–38° S.) than it now has. Aside from *T. simata*, n. sp., in the Tongan Eocene, these species form two morphologically and distributionally distinct groups, one in the Eocene-Miocene of Australia (*T. australis* Tension-Woods, *T. pedunculata* (MacGillivray)) and the other in the Eocene-Oligocene of the Atlantic and Gulf Coastal Plains (*T. obesa* Cheetham, *T. petila* Cheetham, *T. tuberculata* Canu and Bassler). The occurrence of a species apparently intermediate between the Australian and American groups in the Eocene of southwestern France (*T. sp.* Labracherie, 1968) may record a Tethyan dispersal route between the two areas. The living American *T. dichotoma*, however, appears morphologically more closely related to *T. turgida* than to the American Eocene species. Thus it may represent a relict outlier of a once-continuous Indo-Pacific-western Atlantic relative of the two Indo-Pacific species. It seems unlikely, therefore, that the thermal significance of *T. turgida* was much different from that of living species of *Tetraplaria*, and the broader latitudinal distribution of the genus in the Eocene may be related to the generally broader tropical climatic belt of that time (see summary in Schwarzbach, 1963, p. 178–180).

DISTRIBUTION OF *BIFAXARIA*

The 14 nominal species of *Bifaxaria* as constituted here (see discussion p. E11) are only slightly less limited latitudinally than *Tetraplaria* (fig. 4). In the Atlantic five species occur between 38° 25' N. and 9° 05' S.; in the Pacific ten species are distributed from 38° 09' N. to 8° 18' S. Only one species, *B. submucronata* Busk, apparently is common to the two oceans (see Harmer, 1957; Hastings, 1966).

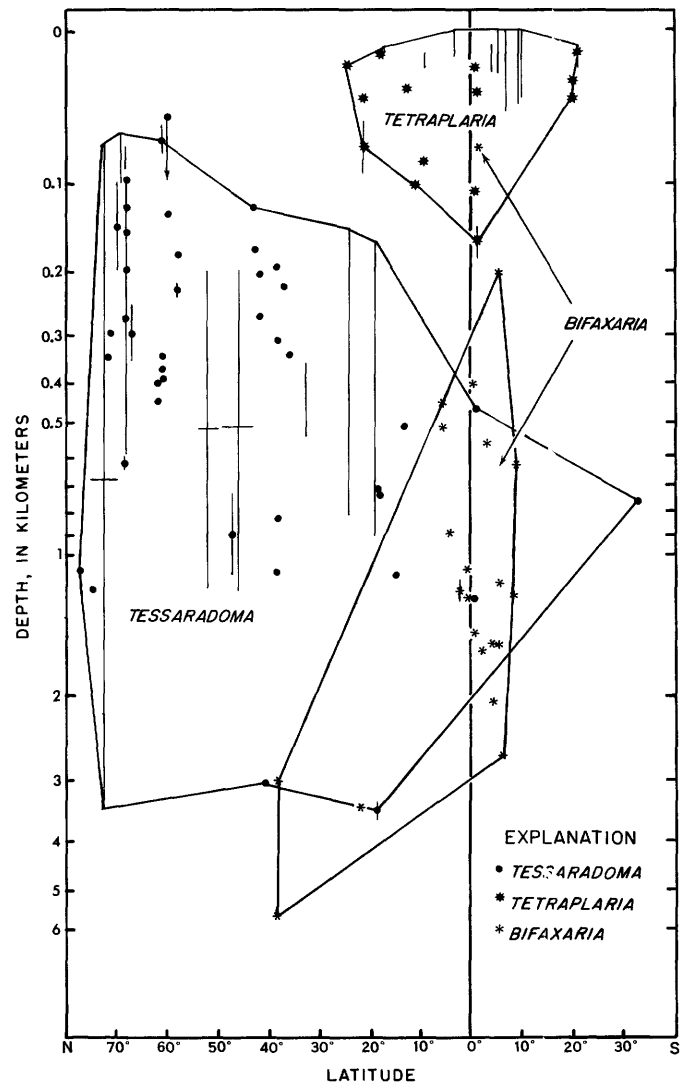


FIGURE 4.—Depth-latitude distribution of living species of three genera of cheilostome Bryozoa represented in upper Eocene beds on Eua, Tonga. Dots indicate single occurrences with specific depth-latitude data recorded; lines with median dots indicate single occurrences with only a range of depth or latitude recorded; lines alone indicate composite of occurrences with specific depth-latitude data recorded. The depth and latitude limits of each genus are shown by a polygon enclosing dots. Exclusion of the shallow-water occurrence of *Bifaxaria* is explained in the text. Sources of data for *Tetraplaria* and *Tessaradoma* are the same as in figures 3 and 5; data for *Bifaxaria* are from Busk (1884), Canu and Bassler (1930), Harmer (1957), Hastings (1966), and Pourtalés (1874).

Bifaxaria is distinctly a deep-water genus, having only four of 23 reported occurrences at depths less than 500 m. It occurs as deep as 3,477 m in the Atlantic and 5,719 m in the Pacific. Not all of the reported occurrences are at depths greater than 200 m,

however, as suggested by Harmer (1957, p. 860; his *Bifaxaria* and *Sclerodomus*, see p. E11). *Diplonotus costulatum* Canu and Bassler is, as recognized by Harmer (1957), a bifaxariid, indeed a member of *Bifaxaria* as here constituted; it was reported from two stations in the Galapagos at 72 and 1,252 m by Canu and Bassler (1930). The deeper occurrence (Albatross sta. D. 3408) is represented by five large and four small pieces of colonies (paratypes, USNM 8503) retaining their covering membranes; these specimens were found with only two other cheilostome species, neither of which has been reported from other stations. Three small pieces, apparently broken from a single fragment (holotype, USNM 8502), all devoid of covering membranes, record the shallower occurrence (Albatross sta. D. 2813); 30 additional species, either well-known shallow-water species or species each represented by several specimens, were reported from this station. Additional bulk material from the 72-m sample failed to yield specimens of *B. costulata*. It is thus possible that the reported presence of this species at 72 m represents an accidental occurrence outside the living range of the genus, brought about, for example, by its transporta-

tion on or in a nektonic organism.

The only direct indication of the thermal tolerance of *Bifaxaria* is the 4° C bottom temperature reported for the 1,252-m occurrence in the Galapagos (Albatross sta. D. 3408); the presence of covering membranes may indicate that the specimens were alive when collected. Occurrences deeper than 2000 m in both the Atlantic and Pacific could correspond to bottom temperatures of about 2° C. By interpolation, the occurrences between 200 and 500 m, all in the Philippine-Indonesian region, could be as warm as 15° C and are probably no colder than 10° C. Thus, if the shallow-water Galapagos occurrence is ignored, the survival range for *Bifaxaria* appears to be between about 2° C and a few degrees less than 15° C.

If this temperature range is indeed the controlling factor for the depth of occurrence of *Bifaxaria* within its limited latitudinal distribution, it still does not explain the apparent absence of the genus from high latitudes, where it might be expected to occur in both shallow and deep water, or from the Indian Ocean. Other abiotic factors, geographic barriers, competition with other species, or a combination of factors,

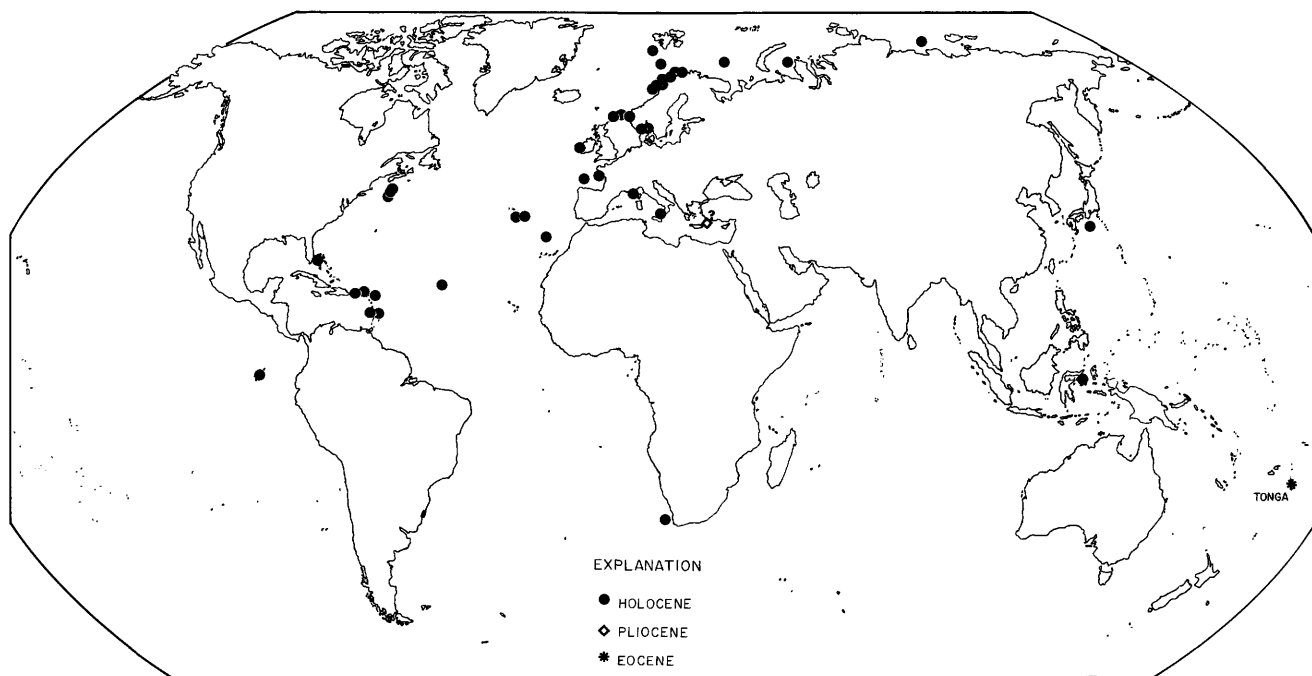


FIGURE 5.—Geographic and stratigraphic distribution of *Tesaradoma*. Sources of data are Burdon-Jones and Tambs-Lyche (1960), Busk (1881, 1884), Calvet (1931), Canu and Bassler (1928a, 1930), LeDanois (1948), O'Donoghue (1924), Gautier (1962), Harmer (1957), Hincks (1880), Jullien and Calvet (1903), Kluge (1962), Lagaaij and Gautier (1965), Manzoni (1877), Nordgaard (1900, 1905, 1918, 1927), Norman (1894, 1909), Osburn (1940), Ryland

(1963), Sars (1851, 1862), Silén (1935), Smitt (1868, 1873), and the following additional specimens in the collections of the National Museum of Natural History, Smithsonian Institution: *T. boreale* (Holocene, Albatross sta. D.2062, 42°17' N., 66°37' W., 275 m; Albatross sta. D.2573, 40°34' N., 66°09' W., 3181 m; Albatross sta. D.2071, 41°56' N., 65°49' W., 207 m; Caroline sta. 102, 18°51' N., 64°33' W., 164–915 m).

might limit the geographic extent of *Bifaxaria* to only a part of the area within which it would encounter favorable temperatures.

DISTRIBUTION OF *TESSARADOMA*

The distribution of the three known living species of *Tessaradoma* (figs. 4, 5) is consistent with a similar temperature range to that inferred for *Bifaxaria*, from about 2° C to about 13° C. *Tessaradoma*, however, has a total depth range of 70 to 3,700 m and a latitudinal range of 77°05' N. to 33°32' S.

The greatest number of reports of this genus refer to the Arctic and Atlantic species *T. boreale* (Busk), whose latitudinal and depth ranges coincide with those of the genus. The two Pacific species, *T. bipatens* Harmer and *T. striatum* (Canu and Bassler), are known only from lat 30°45' N. to 0°12' N. and from depths of 469 to 1,252 m.

In the Arctic and Norwegian regions, *Tessaradoma* occurs virtually throughout the whole range of depth. Equatorward, the deepest records remain about the same, 3,500 m, but the shallowest occurrences show a gradual submergence from 70 m at lat 65°–75° N. to 120 m at lat 45° N. to 150–160 m at lat 20°–25° N. to 450–500 m at lat 0°–10° N. The relation of the southern hemisphere outlier to this trend is not apparent.

The equatorward submergence of *Tessaradoma* in the North Atlantic is consistent with a cryophilic stenothermy having an upper limit for survival of about 12° C. This limit must be slightly higher, however, for the genus occurs in the Mediterranean where bottom temperatures are never below about 13° C, even at great depth (Furnestin, 1960).

Fossil occurrences of *Tessaradoma* have been reported from the Eocene of North Carolina and Alabama (Canu and Bassler, 1920), from the Miocene of Australia (MacGillivray, 1895), and from the Pliocene of Rhodes (Manzoni, 1877). The American species are not *Tessaradoma* but probably are referable to *Semihawswellia*; the Australian species belongs to *Tubiporella*; and the Rhodian species has not been found in subsequent study of the Pliocene fauna of that island (Pergens, 1887).

TONGAN CHEILOSTOME FAUNAL ELEMENTS

Association of *Bifaxaria* and *Tessaradoma* with *Tetraplaria*, *Canda*, and *Tripurula* almost certainly indicates that the Tongan Eocene assemblage is a mixture of autochthonous and allochthonous elements. The habitats of these groups of species were tropical or subtropical but were separated bathymetrically by at least 85 m (fig. 4) and very probably by more than 150 m, if the following assumptions are correct: (1) that the five apparently stenother-

mal genera had approximately the same thermal requirements and bathymetric distributions in Eocene time as at present; and (2) either that *Tessaradoma* had the same gradient of submergence approaching the equator from the south in the Eocene as it does approaching the equator from the north at present, or that its present minimum depth at the equator characterized a broader latitudinal belt within a more widespread Eocene tropics. If, in addition, the extreme bathymetric occurrences of Holocene species of *Tetraplaria* and *Bifaxaria* are accidental and outside the living ranges of Holocene species of the two genera, this reinforces interpretation of bathymetric disjunction of the Tongan faunas.

The autochthonous element is assumed to include all of the species represented in the assemblage by significant numbers of specimens plus any others inferred to have the same thermal significance. Each of the first three species listed in table 1 is represented by at least three times as many specimens as are any of the other species. The three abundant species plus two others having the same thermal significance make up almost 85 percent of the specimens in the assemblage.

Of the well-represented species, one is a *Bifaxaria*, and the other two apparently belong to eurythermal genera, *Spiroporina* and *Reteporellina*. This species of *Spiroporina* is morphologically comparable to an apparently cryophilic living species, *S. brevitubulata* Harmer, which occurs in the Philippine-Indonesian region at depths of 204 to 1,633 m (Harmer, 1957). *Bifaxaria diaphyota* and *Spiroporina kondoi* then indicate the cool- and deep-water character of the autochthonous element, and two other cryophilic species can be inferred to be part of this element, even though they are represented by far fewer specimens (table 1); these species belong to *Bifaxaria* and *Tessaradoma*. The autochthonous group of species, then, lived at a depth of probably more than 200 m and perhaps more than 1,000 m.

The allochthonous faunal element, as interpreted here, includes those species except *Tessaradoma bifax* which occur in minor frequencies (1-5; table 1) in the assemblage. These 13 species make up slightly more than 15 percent of the specimens.

Six species are inferred to have been thermophilic and restricted to shallow water, probably less than 100 m deep. These include two species of *Tetraplaria*, a *Canda*, a *Tripurula*, and apparently thermophilic species of the eurythermal genera *Spiroporina* and *Beania*. The species of *Spiroporina* is comparable morphologically to *S. longicollis* (Canu and Bassler), which occurs in the Philippine-Indonesian region at

depths no greater than 73 m (Harmer, 1957). The Tongan species of *Beania* has its nearest living counterpart in the Indonesian *B. asymmetrica* Harmer, known from depths no greater than 40 m (Harmer, 1926). Six of the remaining species belong probably to eurythermal genera, and none of them is closely comparable with stenothermal living species. They are included tentatively in the allochthonous element because of their low frequencies of occurrence and the lack of evidence that they were restricted to cool water. The last species, *Tubitrabecularia clypeata*, is assigned to the allochthonous element even more tentatively, for the genus *Tubitrabecularia* is extinct. The probably closely related, living genus *Siphonicytara* is known from depths of 469 to 1,901 m in Indonesia (Harmer, 1957), but species of *Tubitrabecularia* occur in the Australian Tertiary with distinctly shallow-water genera.

The autochthonous element includes only typically benthic species, as indicated by growth forms that require attachment to a firm substrate. The allochthonous fauna, on the other hand, could have been benthic, and therefore transported laterally as well as vertically to a deeper burial site, or epiplanktonic, and therefore moved essentially only vertically to the sea floor. This faunal element includes a variety of growth forms, some of which, as in *Beania diademata*, both species of *Tetraplaria*, and *Cellaria cucullata*, are adapted to movable substrates including floating objects. If they consistently followed this mode of life, however, these species could have highly eurybathic distributions. Furthermore, Tongan specimens of *Triporula* and *Chiastosella*(?) are clearly adherent to nonbuoyant substrates. Thus, part if not all of the allochthonous group of species was probably transported to the site of burial from a shallower bottom habitat.

Some, but by no means all, of the Holocene occurrences of *Canda*, *Tetraplaria*, and *Triporula* have been reported to be on coral, coral sand, or *Lithothamnium* associated with reefs. Other cheilostome genera commonly associated with Holocene reefs include *Celleporaria*, *Nellia*, *Poricellaria*, *Steganoporella*, and *Thalamoporella*, all known to occur in rocks of Eocene age in Europe and North America, as well as several genera not known from the Eocene. All of these genera have been reported from numerous Holocene localities in the Indo-Pacific. The likelihood of a reefal origin for the allochthonous Tongan element thus is not strong.

Four species considered to belong to the allochthonous, shallow-water Tongan faunal element—*Beania diademata*, *Canda fossilis*, *Menipea innocua*, and *Cellaria cucullata*—are members of families (Bicellariellidae, Scrupocellariidae, and Cellariidae) regarded as characteristic of the deep sea (Schopf, 1969, p. 470). Each family, however, includes one genus or more that occurs eury- or stenobathically in shallow water.

MORPHOLOGY OF DEEP-WATER SPECIES

In contrast to the wide variety of colony forms displayed by the allochthonous component of the Tongan Eocene assemblage, the inferred deep-water species appear to have had more uniform colonies and therefore to represent more restricted adaptations (table 1). They belong to three ascophoran families, Bifaxariidae, Spiroporinidae, and Sertellidae. There is no positive evidence that anascans were represented in the autochthonous faunal element, and the least calcified forms, *Beania diademata* and *Canda fossilis*, were apparently distinctly shallow-water allochthones in this assemblage. All the Tongan deep-water species have zoecial frontal shields susceptible of continued calcareous accretion throughout ontogeny. This property characterizes ascophorans having both known modes of frontal shield development (see Boardman and Cheetham, 1969, p. 222).

The growth forms of colonies of these deep-water species are not observable directly because all specimens are small zoarial fragments, the largest being less than a centimeter long. Some of these fragments preserve stubs of distalward branches, and from these and from changes in morphology associated with ontogenetic thickening of zoecial frontal shields, the form and size of colonies can be estimated. Within each zoarial fragment, frontal shields of proximal zoecia are slightly thicker than those of distal zoecia; other morphologic features, such as frontal pores, avicularia, and secondary orifices, may show correlated ontogenetic differences. In the three species having zoecia arranged biserially back to back (*Bifaxaria bryani*, *B. diaphyota*, and *Tessaradoma bifax*), the frontal shields of the two series of zoecia meet on the lateral surfaces of the branches, and zoecia placed more proximally on a fragment are slightly wider, viewed frontally, than those distal to them (see pl. 3, figs. 1, 2; pl. 4, figs. 4, 5; pl. 5, figs. 4, 5). *B. diaphyota* is sufficiently abundant that zoarial fragments having zoecia of differing widths form a series with overlapping ranges. Even though the differences within a fragment are barely perceptible, the mean widths in all fragments having zoecia with thicker frontal shields are significantly greater than all those having thinner shields (see measurements, p. E13). A colony of *B. diaphyota* may

have consisted of many such fragments arranged in a distalward branching form, with the base diameter of the stem almost twice as thick as the diameter of the branches near their growing tips. By analogy, it can be inferred that the two rarer biserial species had the same general growth form.

In *Spiroporina kondoi*, the zooecia are in four series opening radially around the branch. Distalward branching and ontogenetic zooecial changes suggest that otherwise the colonies were similar to the biserial ones. In *Reteporellina?* sp., the two- to four-serially arranged zooecia all open on one zoarial surface. On the opposite sides of the fragments, extrazooecial calcareous material appears to follow the same ontogenetic gradient of thickening as do the zooecial frontal shields.

All these deep-water species appear to have had rigidly erect, nonfenestrate colonies with subcylindrical or slightly compressed branches (vinculariform and eschariform; table 1) in which outer skeletal walls continuously thickened throughout life. The proximal ends of these colonies seem missing in the material at hand, but, in the absence of skeletal evidence of attachments for noncalcified rootlets or tendrils, it is assumed that colonies were attached directly to the substrate by small encrusting bases, as shown in the living deep-sea species *Tessaradoma striatum* by Canu and Bassler (1930, pl. 10, fig. 1). This morphology is similar to that of shelf cheilostomes having vinculariform and eschariform colonies, and it appears to represent a similar adaptation for growth approximately perpendicular to the substrate, increasing exposure to the water column. This mode of growth seems advantageous in filter feeding.

A survey of living faunas has suggested that deep-sea cheilostomes are generally characterized by bushlike commonly lightly calcified colonies attached to the substrate by noncalcified rootlets and tendrils which may hold them in a prostrate rather than an erect position (Schopf, 1968, p. 154; 1969, p. 470). This morphology was thought to be an adaptation for growth on the finely particulate substrates in the deep sea and possibly for detritus-feeding from the fine sediment (Schopf, 1969, p. 469-471). This characterization was based on genera in the anascan families Farciminariidae, Scrupocellariidae, Biculariellidae, and Cellariidae (especially the genus *Euginoma*) and in one ascophoran family, the Bifaxariidae. The heavily calcified colonies of all the Tongan Eocene species inferred to live in deep water suggest that deep-sea cheilostomes may have adaptations comparable with those of shallow-water forms, and similar bifaxariids, spiroporinids, and

sertellids are, of course, known in the living faunas (see Harmer, 1957).

SYSTEMATIC PALEONTOLOGY

Suborder ANASCA Levinsen, 1909
Family CHAPERIIDAE Jullien, 1888
Genus PATSYELLA Brown, 1948 (?)

Patsyella? sp.

Plate 1, figure 3

A single zoarial fragment from sample 1 may belong to *Patsyella*, a genus known from Oligocene to Holocene in New Zealand (Brown, 1952, p. 118, 122).

The colony was apparently erect, the zooecia arranged in four alternating series, one on each face. There is no evidence of branching.

The zooecia are quadrate, their distal margins convexly rounded, their proximal margins concavely rounded. Deep grooves separate laterally adjacent zooecia. The narrow, smooth, rounded mural rim lies at the interzooecial boundaries, without intervening gymnocyst. The concave, imperforate, finely tuberculate cryptocyst slopes gently away from the proximal and lateral mural rim to the broadly ovate opesia which occupies the distal half of the frontal surface of the zooecium. On some zooecia, a pair of ill-defined ridges diverge proximally from the lateral mural rim and extend to the proximal end of the cryptocyst.

The opesia is bordered on its proximal and lateral margins by a narrow, smooth rim turned slightly under. Below the opesia, an occlusor-lamina runs from the distal wall to each lateral wall, forming small distolateral pouches opening frontally. The occlusor-laminae are more strongly developed in this specimen than is typical of *Patsyella*, though their development is considerably less than in *Chaperia*.

Entozooecial ovicells are present on several zooecia placed around the zoarial fragment without apparent pattern. The ovicell is immersed in the distal zooecium, just visible frontally as a small swelling on the cryptocyst. The opesiae of the ovicelled zooecia are slightly larger than those of nonovicelled zooecia.

Oral spines and avicularia are not present on the specimen.

Family CELLARIIDAE Hincks, 1880
Genus CELLARIA Ellis and Solander, 1786

Cellaria cucullata MacGillivray

Plate 1, figure 4

Cellaria cucullata MacGillivray, 1895, Royal Soc. Victoria Trans., v. 4, p. 31, pl. 22, fig. 15.

Brown, 1958, Geol. Survey Victoria Mem., no. 20, p. 47, figs. 20, 21.

A single internode fragment from sample 1 belongs to *Cellaria cucullata*. The preserved distal end of the internode shows three large, subcircular openings alternating with three small, triangular ones; the proximal end is broken. The uniformly hexagonal zooecia are arranged in six alternating series, in three of which, corresponding to the smaller distal openings, the zooecia terminate with the internode. The rounded-quadrangle opesia lies at about zooecial midlength, lacks denticles, and is surrounded by a narrow, slightly raised rim from which the cryptocyst falls away more steeply distally to form, in some zooecia, the ovate hollow characteristic of the species (Brown, 1958, p. 47). Ovicells and avicularia were not found.

C. cucullata has been reported from beds of late Eocene age in Victoria, Australia.

Family BICELLARIELLIDAE Levinsen, 1909
Genus BEANIA Johnston, 1840

Beania diademata, n. sp.

Plate 2, figure 3

Zoarium unilaminar, apparently loosely encrusting, multiserial, with small, ovate fenestrae, visible only in basal view, between zooecia. Connecting tubes stout, joining each zooecium to six neighbors.

Zooecia very heavily calcified for genus, cucullate; proximal portion short, stout, forming part of proximal connecting tube; distal portion raised obliquely to overhang, but not rest upon, succeeding zooecium, hiding its proximal end from frontal view. Mural rim thick, rounded, finely tuberculate, slightly constricted in oral region, more constricted on one side which supports a large protuberant tubular collar probably marking attachment of avicularium. Spine bases distributed in four series: (1) bases of seven to nine small closely spaced spines placed along each lateral mural rim, proximal to oral constriction, paired bilaterally except for most distal spine base opposite apparent avicularium base, all projecting frontally; (2) bases of two small oral spines placed bilaterally on distolateral mural rim, projecting frontally; (3) bases of nine small spines placed in a symmetrical distolateral crown, one spine base occupying a medial position, around distal third of zooecium, just outside the spine bases on mural rim and more widely spaced, projecting distofrontally and frontolaterally; and (4) bases of five to eight larger spines irregularly distributed over basal surface. Opesia elongate, elliptical, occupying almost all of zooecial surface in frontal view.

Ovicells not observed.

Zooecial dimensions (in $\text{dk}\mu$) measured in frontal

view on holotype are as follows (mean and standard deviation given to two decimal places for purposes of calculation only):

Dimension	Number measured	Mean	Standard deviation	Observed range
Length of zooecium.....	7	61.68	4.46	55-68
Width of zooecium.....	7	40.68	1.73	38-43
Length of opesia	7	51.60	3.14	48-57
Width of opesia	7	29.28	1.14	27-30

Holotype, USNM 169234, sample 2. Upper Eocene, about one-quarter mile north of Vaingana, Eua, Tonga, at altitude 400 feet.

Beania diademata resembles the living species *B. asymmetrica* Harmer, 1957, in the placement of its (probable) avicularium and in the size of its zoarial fenestrae, the connection of its zooecia by six tubes, and the distribution of its basal spines. *B. asymmetrica* has no spines on the mural rim or in a distolateral crown, however. The number of spines on the frontal side of the zooecium in *B. diademata* is similar to that in the living species *B. hirtissima* (Heller, 1867), but the spines are distributed differently. Thus *B. diademata*, though represented by the single specimen, is highly distinctive.

Two fossil occurrences of *Beania* have been reported previously. MacGillivray (1895, p. 27) identified a poorly preserved early Miocene specimen from Australia, having only its basal surface observable, with *B. spinigera* (MacGillivray, 1880), a living Australian species, from which *B. diademata* differs in its smaller fenestrae and more numerous, differently distributed spines. The second fossil species, *B. bermudezi* Lagaaij (1968, p. 349, pl. 11, figs. 11-14), described from middle and upper Eocene beds in Cuba, differs from *B. diademata* in having only four connecting tubes for each zooecium, differently arranged spines, and ovicells.

Family SCRUPOCELLARIIDAE Levinsen, 1909
Genus CANDA Lamouroux, 1816

Canda fossilis Waters

Plate 1, figures 1, 2

Canda fossilis Waters, 1881, Geol. Soc. London Quart. Jour., v. 37, p. 322, pl. 16, figs. 51, 52.

Waters, 1882, Geol. Soc. London Quart. Jour., v. 38, p. 261.

Waters, 1883, Geol. Soc. London Quart. Jour., v. 39, p. 433.

MacGillivray, 1895, Royal Soc. Victoria Trans., v. 4, p. 25, pl. 3, figs. 12-14.

Brown, 1958, Geol. Survey Victoria Mem., no. 20, p. 50.

Four zoarial fragments, all from sample 2, belong to *Canda fossilis*, described from lower Miocene beds (Balcombian Stage), in Victoria, Australia.

The growth form of these colonies apparently was unjointed, for one of them (pl. 1, fig. 2) exhibits a

dichotomy with the zooecia continuously calcified from stem to both branches. The arrangement of zooecia in these biserial specimens is typical of *Canda* (see Harmer, 1926, p. 385) and conforms at the dichotomy to Harmer's (1923, p. 328) type 17 bifurcation. The inner zooecia at the proximal ends of the branches (denoted F and G by Harmer) meet in their proximal segments above the axillary zooecium (denoted E). Both zooecia F and G are provided with basal vibracula, as in living species of *Canda*.

The zooecia are slightly curved outward in frontal view; have a pair of symmetrically placed, small distal spine bases; and support a prominent scutum attachment just distal to the middle of their inner margin. The scutum attachment seems to correspond to the structure in the Australian specimens interpreted by Waters (1881, p. 322) as an avicularium or spine and by MacGillivray (1895, p. 26) as a sessile avicularium; it lies distinctly on the inner frontal surface of the zooecium, rather than on the lateral slope that forms the keel of the branch and on which avicularia commonly occur in living species of *Canda* (see Harmer, 1926, p. 384). The zooecial opesia is V-shaped as is characteristic of *C. fossilis*. In basal view, a markedly zigzag suture separates the zooecia.

Frontal avicularia occur only on the branched specimen on zooecia considerably proximal to the bifurcation, rather than at the bifurcation as is typical of some species of *Canda* (see Harmer, 1926, p. 384). The avicularia lie on the inner margins of the zooecia, just proximal to the scutum attachment. Their rostra, though broken, appear to be directed laterally toward the opesiae of adjacent zooecia.

The vibracula lie on the interzooecial sutures on the basal sides of the branches; their articular ends are just visible in frontal view. The rostral channels curve around prominent rootlet foramina.

Ovicells were not found in the Tongan material.

Genus *MENIPEA* Lamouroux, 1812

Menipea innocua Waters

Plate 2, figure 2

Menipea innocua Waters, 1882, Geol. Soc. London Quart. Jour. v. 38, p. 261, pl. 9, fig. 24.

A single zoarial fragment from sample 2 seems identifiable with *Menipea innocua* described from the lower Miocene (Balcombian Stage) of Victoria, Australia.

The colony apparently was not jointed, but dichotomously branched. The zooecia are in biserial, alternating rows. Their arrangement at the bifurca-

tions appears to be consistent with Harmer's (1923, p. 328) type 17, with the inner zooecia of the branches meeting over the axillary zooecium. The outlines of zooecia of all rows are visible on the otherwise smooth basal surface of the fragment. The arrangement of zooecia, especially as shown on the basal surface, differs markedly from that in the Australian Miocene species *M. elongata* (Canu and Bassler, 1935, p. 14, pl. 3, figs. 6, 7) in which the morphology of the zooecia is similar, and similar to that in the living Philippines species *M. crassa* (Canu and Bassler, 1929, p. 221, pl. 10, figs. 10-13).

The zooecia of the Tongan specimen differ from those of *M. crassa* in having more sharply raised mural rims enclosing more steeply plunging cryptocysts. The elongate gymnocysts of about half the zooecia support, just proximal to their mural rims, adventitious avicularia with pointed rostra directed laterally toward the outer margins of the zooecia. The avicularia are longer than those of *M. crassa* and, on the proximal sides of their chambers, are each provided with a foramen, possibly for attachment of a rootlet. The form and distribution of the adventitious avicularia differ from those in two Australian Eocene-Oligocene species, *M. retrorsa* and *M. biaviculata*, described by Maplestone (1900, p. 164, 165, pl. 17, figs. 8, 10).

Family CRIBRILINIDAE Hincks, 1880
Genus FIGULARIA Jullien, 1886 (?)

Figularia? sp.

Plate 2, figure 1

One zoarial fragment, from sample 2, may belong to *Figularia*. It is similar in its apparent growth form and zooecial morphology to *F. kenleyi* Brown (1958), p. 53, fig. 31), a species described from the upper Eocene of Victoria, Australia, but differs from all known species of *Figularia* in its ovicells and avicularia.

The colony was apparently erect, with the zooecia arranged in four alternating series, one on each face. There is no evidence of branching.

The elongate-claviform zooecia have long, smooth proximal gymnocysts, extending as much as one-third the zooecial length and continuing as narrow strips along the lateral margins nearly to the distal end. Around the inner margins of the proximal and lateral gymnocyst are distributed 20 to 23 bases of costae or spines. On one zooecium at least the proximal two pairs of bases apparently were parts of costae, for the most proximal pair reaches the midline where their inner ends are fused, and the next pair approaches the midline with their inner ends

fused to those of the proximal pair. A single slitlike lacuna is left between adjacent costae. The frontal surfaces of the costae are smooth and imperforate. The distal pair of bases on the nonovicelled zooecia are larger and have larger lumina than the more proximal bases and thus may be parts of oral spines rather than costae. *F. kenleyi* has similar frontal structure, but has fewer costae and no oral spines.

Just proximal to the remnants of its costal shield, each zooecium has an adventitious avicularium placed laterally on the proximal gymnocyst. The mandibular palate is elevated and inclined distolaterally, and the rostrum is directed medially, frontally, and slightly distally. Pivotal structures were not observed. Avicularia are lacking in *F. kenleyi*.

Broken ovicells are present on two zooecia. Unlike those of *F. kenleyi*, the ovicells are entozoecial, immersed in the distal zooecia, and visible frontally only as small swellings in their proximal gymnocysts. The larger pair of spine (?) bases is lacking on the ovicelled zooecia.

Suborder ASCOPHORA Levinsen, 1909
Family EXECHONELLIDAE Harmer, 1957
Genus TRIPORULA Canu and Bassler, 1927

Tripoporula aff. *T. biarmata* (Waters)

Plate 2, figure 4

One poorly preserved zoarial fragment, encrusting a worn piece of decapod crustacean from sample 2, belongs to *Tripoporula*. Like *T. biarmata* (Waters, 1882, p. 268, pl. 8, fig. 18), a species living in Australian waters and occurring as fossils in beds of early Miocene age in Australia and in beds of Oligocene-Pliocene age in New Zealand (Brown, 1952, p. 358), this specimen displays numerous small frontal pores and small, paired lateral-oral avicularia in addition to a median distal avicularium. The lateral-oral avicularia, however, are directed medially, rather than distally as in *T. biarmata* and most other species of this genus, and their rostra commonly meet on the proximal lip of the orifice. Also, the zooecia of the Tongan specimen are less than half as large as those of *T. biarmata* (see Brown, 1952, p. 357; Cook, 1967, p. 341). *T. verrucosa* (Canu and Bassler, 1920), a Paleocene species from Georgia, has small zooecia, but its lateral-oral avicularia are placed more distally relative to the orifice than in the Tongan specimen and are directed distally.

The frontal pores of the Tongan specimen appear not to be stellate, but their original shape may not be preserved. Each pore, even in zooecia apparently near the growing margin of the colony, is surrounded by a distinct tubular collar. The three avicularia on

each zooecium are in series with the outer row of pores, and, on zooecia apparently at the growing margin, this row of pores lies frontally away from the dietellae from which they are separated by an interval of vertical wall, as noted by Cook (1967, p. 342) in living species of *Tripoporula*.

Family BIFAXARIIDAE Busk, 1884

Harmer (1957, p. 859) considered this family and the family Sclerodomidae Levinsen, 1909, synonymous; so he combined them under the name Bifaxariidae. As discussed below, Harmer's (1957, p. 866) concept of *Sclerodomus* Levinsen, 1909, appears to be inconsistent with the characters of its type species, *Bifaxaria denticulata* Busk, 1884, which is morphologically unlike the other species included by Busk in *Bifaxaria*, and those included in *Urceolipora* MacGillivray, 1881. Also unlike bifaxariids, *Sclerodomus* sensu stricto and other genera, such as *Cellarinella* Waters, 1904, that have been assigned to the Sclerodomidae, have distributions including the Antarctic and subantarctic regions. Bifaxariids and sclerodomids should probably be maintained as separate families.

Genus BIFAXARIA Busk, 1884

The Tongan specimens described below as *Bifaxaria bryani*, n. sp., and *B. diaphyota*, n. sp., appear to be the first known fossil bifaxariids, and their affinities seem to be with the living species *B. corrugata* Busk, 1884, and *B. papillata* Busk, 1884. Both these living species were referred by Harmer (1957, p. 867-868) to *Sclerodomus*, but there are reasons, some of which were mentioned by Hastings (1966, p. 59), to question this assignment.

As constituted by Busk (1884, p. 79), *Bifaxaria* included a heterogeneous assemblage of eight species; the heterogeneity was recognized by Waters (1888, p. 15) and Levinsen (1909, p. 302-304), who established *Sclerodomus* for *B. denticulata*, the only species included in *Bifaxaria* having more than two series of zooids, sinuate secondary orifices, and median suboral avicularia equipped with complete cross-bars. Harmer (1957, p. 861, 866) considered all the originally included species in which the colonies are not jointed, except *B. abyssicola* Busk, 1884, to belong in *Sclerodomus*. He implied that the development of secondary avicularia covering earlier frontal structures also distinguishes *Sclerodomus* from *Bifaxaria*, but in *B. corrugata* secondary avicularia are lacking (Hastings, 1966, p. 60); the specimen on which Busk (1884, p. 80) noted their presence belongs to *B. papillata* (Hastings, 1966, p. 59). The

concept of *Sclerodomus* proposed by Harmer thus is too broad and probably should not include the biserial species. If the nonjointed species here considered to belong to *Bifaxaria* were separated generically from the jointed ones, a new genus would be required for them.

In both the Tongan species described below, the bases of the branches, where they join the colony stem, consist of two zooecia in opposition, back to back. This arrangement appears not to differ from that in the bipartite bases rami shown by jointed species of *Bifaxaria* (Harmer, 1957, p. 861) and suggests that there is little structural difference between the jointed and the unjointed biserial bifaxariids.

Bifaxaria bryani, n. sp.

Plate 4, figures 4, 5

Zoarium rigidly erect, apparently not anastomosing, pinnately branched; branches given off singly, their distribution suggesting arrangement in alternating pairs from main stem. Stem and branches subcylindrical, consisting of two alternating series of zooids arranged back to back; at base of branch, first pair of zooecia oppose rather than alternate. Branches arise from frontal sides of stem zooecia, all zooecia thus open in plane of branching. Zoarial fragments apparently from proximal parts of colonies have diameters almost twice those apparently from distal parts. Basal attachments not found.

Zooecia with transversely hexagonal frontal surfaces, lateral portions of which wrap around lateral surfaces of branch so that in lateral view, adjacent zooecia are separated by narrow, slightly raised, markedly zigzag ridge. Viewed frontally, zooecia appear rounded rectangular, their width about five-sixths length in distal fragments and as much as $1\frac{1}{2}$ times length in proximal fragments. Frontal shield inflated, smooth except for narrow, discontinuous, irregularly sinuous, slightly raised submedian ridge, on each side of which are six to eight approximately aligned longitudinal rows of oval to slitlike pores; on distal zooecia, frontal shields are thinner with submedian ridge more regularly positioned than on proximal zooecia. Secondary orifice terminal on frontal surface, slightly wider than long, rounded trapezoidal with the longest side distal; distal margin broadly arcuate; proximal margin almost straight-sided laterally, strongly indented medially by a prominent, pointed mucro which usually continues the frontal submedian ridge. Secondary orifices of presumed ovicelled zooecia not apparently different from those of nonovicelled zooecia.

Avicularia adventitious, of two positions: lateral-oral and lateral. Lateral-oral avicularia small, paired, paralleling margins of secondary orifice, with rostra directed distolaterally. Lateral avicularia larger, single or paired, rarely occurring in greater numbers on zooecia at base of branch or distal to ovicell, lacking on distal zooecia except at points of branching; placed on lateral portions of zoecial frontal shield, near zigzag interzoecial boundary, commonly in an irregularly longitudinal line; rostra oriented distally, proximally, laterally, or medially, but rarely obliquely. Rostra of both lateral and lateral-oral avicularia broadly spatulate; pivotal condyles are broad, rounded knobs at about midlength on palatal surface.

Ovicells, if present, completely immersed in distal zooecia, apparent externally only as swellings in their frontal shields.

Zoecial dimensions (in $\text{dk}\mu$) measured in frontal view on six zoarial fragments (holotype and five paratypes) are summarized as follows (mean and standard deviation given to two decimal places for purposes of calculation only):

Dimension	Number measured	Mean	Standard deviation	Observed range
Length of zooecium:				
Distal zooecia	5	66.19	3.50	61-71
Proximal zooecia	13	71.27	9.59	57-91
Width of zooecium:				
Distal zooecia	5	56.78	1.56	55-59
Proximal zooecia	13	99.90	14.71	77-122
Length of orifice (secondary)	10	18.10	1.81	14-21
Width of orifice (secondary)	10	20.10	2.61	17-25
Length of avicularium:				
Lateral-oral	18	10.41	1.80	7-15
Lateral	16	16.38	4.04	8-22

Tested by Student's *t*, the difference in mean lengths of distal and proximal zooecia is not significant (0.05 level), and the difference in mean widths of distal and proximal zooecia is highly significant (0.01 level). The difference in mean lengths of lateral-oral and lateral avicularia is also highly significant.

Holotype, USNM 169241, paratype, USNM 169242, and 2 paratypes, USNM 169243, sample 2. Two paratypes, USNM 169244, sample 1. Upper Eocene, about one-quarter mile north of Vaingana, Eua, Tonga, at altitude 400 feet.

Bifaxaria bryani is most similar to the living species *B. corrugata* Busk, from which it differs in the frontal shield being smooth rather than longitudinally ridged between the rows of pores, the secondary orifice having a prominent mucro, and the lateral portions of the frontal shield being equipped

with avicularia in the more heavily calcified proximal zooecia. The presence of lateral avicularia in *B. bryani* links it with the living species *B. papillata* Busk, *B. gigantea* (Harmer), and *B. rugata* (Harmer) and with the Tongan Eocene *B. diaphyota*, n. sp., described below. Unlike the living species, the Tongan species appear to have the lateral avicularia no larger distal to ovicells and at the points of branching than at other locations.

As in other species of *Bifaxaria*, the zooids in the proximal parts of colonies of *B. bryani* apparently differed markedly from those in the distal parts, chiefly as the result of ontogenetic changes in the frontal shield. The most conspicuous change (compare pl. 4, figs. 4 and 5) is the increase in shield thickness, resulting in doubling the diameter of the branch. As in *B. corrugata* (see Hastings, 1966, p. 59-60), thickening took place without the development of frontal avicularia, except at the lateral extremities of the shield in *B. bryani*, so that the submedian ridge, the oral mucro, and the longitudinal rows of pores continue, for the most part, into the later ontogenetic stages with little change in form. Unlike *B. corrugata*, however, *B. bryani* shows no tendency to develop longitudinal ridges between pore rows and therefore lacks, at all stages, the corrugated appearance of the living species. The pattern of pore rows in *B. bryani* is interrupted around lateral avicularia on the more heavily calcified zooecia and on zooecia at the base of a branch; the pores around these avicularia appear to be radially arranged.

Bifaxaria diaphyota, n. sp.

Plate 3, figures 1-7

Zoarium rigidly erect, apparently not anastomosing, pinnately branched; branches given off in opposing pairs. Stem and branches subcylindrical, consisting of two alternating series of zooecia arranged back to back; at base of branch, first pair of zooecia oppose rather than alternate. Branches arise from frontal sides of stem zooecia, all zooecia thus opening in plane of branching. Zoarial fragments apparently from proximal parts of colonies have diameters up to twice as large as those from distal parts. Basal attachments not found.

Zooecia with trapezoidal frontal surfaces, the widest margin at proximal end; lateral portions wrap around lateral surfaces of branch, so that, in lateral view, adjacent zooecia are separated by deep, moderately zigzag groove. Viewed frontally, zooecia appear almost triangular, with rounded apex at distal end; zooecial width varies from subequal in

length in distal fragments to nearly twice length in proximal fragments. Frontal shield inflated, incised medially with a deep longitudinal groove, on each side of which are few scattered large pores; frontal surface finely pitted, the pits in places aligned in striate patterns; shields appear thick even on distal zooecia, thicker on proximal ones; on heavily calcified zooecia, buildup of avicularia imparts a papillose surface texture within which interzooecial boundaries become obscure. Secondary orifice terminal on frontal surface, strongly inclined distally, roughly semicircular with broadly rounded distal margin, nearly straight proximal lip slightly cleft by median frontal groove.

Avicularia adventitious, of two positions; lateral-oral and frontal. Lateral-oral avicularia (not observable on most zooecia because of poor preservation) very small, paired, placed at distolateral corners of secondary orifice, facing slightly into peristome, directed distomedially. Frontal avicularia numerous, variable in position on surface of frontal shield, tending to bilaterally symmetrical placement; distal zooecia have two or three pairs of avicularia placed laterally, near zigzag interzooecial grooves; more proximal zooecia have three to five additional pairs placed more medially, usually including a pair placed on either side of median frontal groove in vicinity of secondary orifice; heavily calcified, most proximal zooecia in material have many additional avicularia scattered over both median and lateral portions of frontal surface. Rostra narrowly to broadly spatulate, directed in apparently any direction. Pivotal condyles indistinct.

Ovicells not apparent in material studied.

Zooecial dimensions (in $\text{dk}\mu$) measured in frontal view on eight zoarial fragments (holotype and paratypes 169246-169252) are summarized as follows (mean and standard deviation given to two decimal places for purposes of calculation only):

Dimension	Number measured	Mean	Standard deviation	Observed range
Length of zooecium:				
Distal zooecia	1	(¹)	(1)	69
Intermediate zooecia	3	59.08	(1)	59-60
Proximal zooecia	25	65.35	10.70	51-97
Width of zooecium:				
Distal zooecia	2	63.84	(1)	60-67
Intermediate zooecia	3	70.84	(1)	66-78
Proximal zooecia	25	89.82	8.84	76-113
Length of orifice				
(secondary)	31	19.46	3.49	10-25
Width of orifice				
(secondary)	31	30.29	5.22	22-42
Length of avicularium:				
Lateral-oral	2	7.14	(1)	7-8
Frontal	94	10.13	1.99	7-16

¹ Not calculated.

The difference in mean lengths of proximal zooecia

and distal and intermediate zoecia is not significant (0.05 level, Student's *t* test); the mean width of proximal zoecia differs highly significantly from mean width of distal and intermediate zoecia (0.01 level, Student's *t* test).

Holotype, USNM 169245; paratypes, USNM 169246-169252; and 23 paratypes, USNM 169253; sample 1. Nineteen paratypes, NSNM 169254, sample 2. Upper Eocene, about one-quarter mile north of Vaingana, Eua, Tonga, at altitude 400 feet.

Bifaxaria diaphyota resembles one or the other of two living species, *B. papillata* Busk and *B. rugata* (Harmer), in the following characters: (1) its numerous frontal avicularia on the more proximal zoecia imparting a papillose surface texture to the colony; (2) its frontal pitting; and (3) its small lateral-oral avicularia partly hidden in the peristome. It differs from both of these species in lacking large avicularia at points of branching. The distinctive median frontal groove of *B. diaphyota* distinguishes it from all other known species of the genus.

The marked ontogenetic differences between proximal and distal zooids in *B. diaphyota* is apparently attributable to the development of frontal avicularia, unlike the ontogenetic changes noted in *B. bryani* above. This development also resulted in an approximate doubling of the diameter of branches. Frontal pores appear to have been lost in the process, but the median frontal groove and the surface pitting remained as the frontal avicularia multiplied.

Family SPIROPORINIDAE Harmer, 1957

Genus SPIROPORINA Stoliczka, 1865

The suggestion (Brown, 1958, p. 55) that the type species of the genus *Spiroporina*, *S. vertebralis* Stoliczka, 1865, is a synonym of *Eschara gracilis* Lamarck, 1816, the type species of *Porina* d'Orbigny, 1852, seems unlikely because the nature of their median frontal pores is different (see Harmer, 1957, p. 846-848, and Brown, 1952, p. 191-192). The relation between the ascus and the median frontal pore in the two species, and in the genera that they represent, appears to be distinctive, even though Harmer (1957, p. 844) expressed doubt about the significance of the difference between ascopores and spiramina. In *S. vertebralis*, the ascus opens through the sinus in the primary orifice (Harmer, 1957, pl. 56, fig. 2), although that opening is enclosed within the peristome, and the sinus is thus presumably the homologue of the ascopore in *Porina gracilis*.

Spiroporina kondoi, n. sp.

Plate 4, figures 1, 2

Zoarium rigidly erect, delicate, dichotomously branched. Stems and branches slender, subcylindrical, consisting of four to six alternating series of zoecia opening on all faces. Axes of stems and branches with longitudinal tubes.

Zoecia separated frontally by shallow, inconspicuous grooves in apparently distal zoarial fragments, absent in apparently proximal ones; in frontal view, elongate-rhombic, convexly rounded distally, concavely rounded proximally. Zoecial length about three times width. Frontal shield slightly inflated; surface covered with short longitudinal grooves each containing a small pore; pores widely spaced, arranged in quincunx, those in marginal row ordinarily larger. Peristome completely hides primary orifice; moderately long, tubular, slightly inflated on ovicelled zoecia, free for as much as one-half the distance distal to spiramen, usually perforated proximolaterally by a pair of circular, slightly enlarged pores; free edge thin, cusped in distal zoecia, thick, rounded in proximal zoecia. Secondary orifice subcircular. Spiramen slightly larger than other medial frontal pores, surrounded by tubular, commonly protuberant collar.

Avicularia adventitious, represented by as many as five minute pits of irregular form distributed around free margins of apparently broken peristomes. Pivotal structures not observed.

Ovicells completely immersed, apparent externally only as swellings in distal parts of peristomes of ovicelled zoecia.

Zoecial dimensions (in $\text{dk}\mu$) measured in frontal view on five zoarial fragments (holotype and 4 paratypes USNM 169257, 169258) are summarized as follows (mean and standard deviation given to two decimal places for purposes of calculation only):

Dimension	Number measured	Mean	Standard deviation	Observed range
Length of zoecium	34	103.89	14.39	82-132
Width of zoecium	42	42.54	3.93	34-51
Length of orifice (secondary)	45	15.14	5.73	12-22
Width of orifice (secondary)	45	15.94	5.55	13-25

Holotype, USNM 169255, and 9 paratypes, USNM 169256; sample 2. Paratype, USNM 169257, 3 paratypes, USNM 169258, and 70 paratypes, USNM 169259, sample 1. Upper Eocene, about one-quarter mile north of Vaingana, Eua, Tonga, at altitude 400 feet.

Spiroporina kondoi resembles the living species *S. brevitubulata* Harmer, 1957, in its inconspicuous frontal pores placed in slitlike grooves; in *S. brevitubulata*, however, the colony is eight-serial, and the frontal wall supports numerous avicularia. The large lateral pores commonly present on the proximal part of the peristome distinguish *S. kondoi* from all previously known species of *Spiroporina*. Superficially, *S. kondoi* resembles *Tessaradoma boreale* (Busk, 1860), a widespread living cool-water species, which, however, lacks axial tubes in its branches and has only marginal pores on its frontal shields.

Spiroporina deliqua, n. sp.

Plate 5, figures 1, 2

Zoarium rigidly erect, delicate, dichotomously branched. Stems and branches subcylindrical, consisting of transverse whorls composed of four zooecia each; zooecia opening on all four faces, those in adjacent whorls alternating in longitudinal position. Axes of stems and branches apparently without longitudinal tubes.

Zooecia without evident boundaries in frontal view, except for shallow depression separating zooecial whorls; interwhorl boundary forms V-shaped lobes directed proximally between laterally adjacent peristomes, thus marking lateral margins of zooecia. Zooecial length about three times width. Frontal shield inflated, closely and uniformly perforated with numerous small pores arranged in quincunx. Peristome completely hides primary orifice; moderately long, tubular, free more than half distance distal to spiramen on some zooecia, perforated with small pores similar to those on shield; free edge thin, slightly cusped. Secondary orifice subcircular. Spiramen much larger than other frontal pores, surrounded by prominent, tubular collar.

Avicularia adventitious, of two positions: peristomial and frontal. Peristomial avicularia represented by six or more minute pits of irregular form distributed around free margins of apparently broken peristomes. Frontal avicularia rarely present, placed just proximal to V's of interwhorl boundaries; oriented approximately longitudinally; rounded. Pivotal structures not observed.

Ovicells not found.

Zooecial dimensions (in $dk\mu$) of five zoarial fragments (holotype and paratypes) are summarized as follows (mean and standard deviation given to two decimal places for purposes of calculation only):

Dimension	Number measured	Mean	Standard deviation	Observed range
Length of zooecium	42	93.06	13.09	76-124
Width of zooecium	45	48.05	4.37	37-54
Length of orifice (secondary)	48	12.60	1.81	10-18
Width of orifice (secondary)	46	12.91	1.59	10-18

Holotype, USNM 169260, paratype, USNM 169261, and 3 paratypes, USNM 169262, sample 1. Upper Eocene, about one-quarter mile north of Vaingana, Eua, Tonga, at altitude 400 feet.

Spiroporina deliqua resembles the living species *S. longicollis* (Canu and Bassler, 1929) in its frontal perforations, long peristomes, and lack of axial tubes; it differs from that species in having fewer frontal avicularia and more slender branches with fewer zooecia per whorl. In both sets of characteristics, *S. deliqua* is similar to *Porina tubulifera* (MacGillivray, 1895), a species known from Eocene-Miocene beds in Australia (Brown, 1958, p. 55) and from Oligocene beds in New Zealand (Brown, 1952, p. 193); the resemblance appears to be superficial, however, for in *P. tubulifera* the median frontal pore is an ascopore rather than a spiramen (Brown, 1952, p. 192).

Genus TESSARADOMA Norman, 1869

Tessaradoma bifax, n. sp.

Plate 5, figures 4, 5

Zoarium apparently rigidly erect; branching not observed in fragments studied. Stems subcylindrical, consisting of two alternating series of zooecia arranged back to back. Zoarial fragments apparently from proximal parts of colonies have diameters almost twice those apparently from distal parts. Basal attachments not found.

Zooecia lack distinct frontal boundaries, even in least heavily calcified specimens found; in lateral view, roughly zigzag double line of apparently marginal pores probably limits interzooecial boundary. In frontal view, zooecial width about five-sixths length in distal fragments, nearly $1\frac{1}{2}$ times length in proximal fragments. Frontal shield inflated, thick in all fragments studied; surface covered with discontinuous, irregularly longitudinal ridges, fine on distal zooecia, coarse on proximal zooecia; lateral and proximal margins of shields on distal zooecia apparently marked by single row of pores, lacking on proximal zooecia; circumoral region slightly attenuated to form peristome. Secondary orifice subterminal on frontal shield at apex of peristome, subcircular; in distal zooecia, proximal part of

secondary orifice sinuate, the sinus almost isolated from rest of opening by a pair of proximolateral denticles in peristome; in proximal zooecia, sinus lacking. Secondary orifices of ovicelled zooecia not apparently different from those of nonovicelled zooecia.

Avicularia adventitious, a pair placed on lateral extremities of frontal shield in series with apparently marginal pores, at about mid-zooecial length; lacking on proximal zooecia. Avicularian cavity rounded, without apparent pivotal structures.

Ovicells immersed in distal zooecia, apparent only from slight enlargement of peristomes of ovicelled zooecia and swellings in frontal shields of distal zooecia.

Zooecial dimensions (in $dk\mu$) measured in frontal view on four zoarial fragments (holotype and paratypes) are summarized as follows (mean and standard deviation given to two decimal places for purposes of calculation only):

Dimension	Number measured	Mean	Standard deviation	Observed range
Length of zooecium	15	70.00	6.77	59-80
Width of zooecium:				
Distal zooecia	8	60.08	2.01	59-65
Intermediate zooecia....	4	66.57	4.17	62-72
Proximal zooecia	3	86.80	5.33	81-94
Length of orifice				
(secondary)	17	20.06	1.90	15-24
Width of orifice				
(secondary)	17	21.94	2.01	18-26
Length of avicularium ...	13	7.56	1.66	6-12

Tested by Student's *t*, the differences in mean widths of the distal, intermediate, and proximal zooecia are highly significant (0.01 level).

Holotype, USNM 169263, sample 2. Paratype, USNM 169264, and 2 paratypes, USNM 169265, sample 1. Upper Eocene, about one-quarter mile north of Vaingana, Eua, Tonga, at altitude 400 feet.

Tessaradoma bifax appears to be related to the living species *T. striatum* (Canu and Bassler, 1930), which differs from the Tongan species in having the frontal shields irregularly and coarsely grooved rather than ridged and the secondary oral sinus isolated as a spiramen in the distal zooecia and then persistent, though confluent with the orifice, in the proximal zooecia.

These two species and a third, *T. bipatens* Harmer, 1957, differ from the type species of *Tessaradoma*, *T. boreale* (Busk, 1860) in their biserial colonies and the intimate association or complete confluence of their spiramina with the secondary orifices. *T. striatum* was originally assigned by Canu and Bassler (1930, p. 31) to their genus *Diplonotos*, the type species of which (*D. costulatum* Canu and Bassler,

1930, by original designation) belongs to *Bifaxaria* as that genus is constituted above. Examination of the syntypes (USNM 8504) of *Diplonotos striatum* reveals that the primary orifice, contrary to the original description, lies at the base of a peristomial shaft that is very long in the heavily calcified parts of colonies, though the peristome is almost totally immersed in the thickened frontal shield. The sinuate opening described as a primary orifice thus is actually the secondary orifice, and, as mentioned above, this structure is isolated as a separate spiramen in distal zooecia (Canu and Bassler, 1930, pl. 10, fig. 3). With upgrowth of the peristome and surrounding frontal shield, the medial part of the bar separating the spiramen from the secondary orifice is discontinued so that the two openings are confluent in the more proximal zooecia. In *T. bipatens*, in which the peristome is less thoroughly immersed in the frontal shield, the spiramen is a tube extending up the proximal side of the peristomial collar in both distal and proximal zooecia (Harmer, 1957, p. 853), thus linking the biserial species with *T. boreale*, in which the spiramen is removed from the secondary orifice completely.

The ontogenetic changes in *T. bifax*, though not so clearly shown in this fossil material, thus appear to parallel those shown by *T. striatum* and to some extent, those shown by *T. boreale*. These changes are superficially similar to those noted above in species of *Bifaxaria* in that the diameters of stems approximately doubled by the thickening of the frontal shield. In the process, however, lateral avicularia disappeared together with the apparently marginal pores, rather than multiplying as in the species of *Bifaxaria*.

Family SIPHONICYTARIDAE Harmer, 1957

Genus TUBITRABECULARIA Canu and Bassler, 1934

Tubitrabecularia is one of the four genera the assignment of which by Bassler (1935, p. 34; 1953, p. G211) to the family Tubucellariidae Busk, 1884, was questioned by Harmer (1957, p. 824). The family Siphonicytaridae was established by Harmer (1957, p. 892) for one of the four genera, *Siphonicytara* Busk, 1884, a living deep-water genus. A distinctive feature of *Siphonicytara*, the demarcation of the ascopore area by raised ridges, is also characteristic of *Tubitrabecularia*; however, additional ridges are present in species of this genus, especially in the type species, *T. elevata* (Tenison-Woods, 1876) (see Waters, 1881, pl. 17, fig. 63). The frontal ridges of *T. elevata* greatly alter the frontal appearance of its highly calcified zooecia, making its morphologic interpretation difficult.

Tubitrabecularia clypeata (Waters)

Plate 6, figure 2

Porina clypeata Waters, 1881, Geol. Soc. London Quart. Jour., v. 37, p. 332, pl. 17, fig. 67.

Tubitrabecularia proditor Canu and Bassler, 1935, Smithsonian Misc. Colln., v. 93, p. 18, pl. 4, fig. 10.

Five poorly preserved zoarial fragments, all from sample 1, belong to *Tubitrabecularia clypeata*, which was described from lower Miocene beds (Balcombian Stage) at Mount Gambier, South Australia, and Muddy Creek, Victoria. The specimens are four- to ten-serial, those with fewer zoecial series being subcylindrical, and those with more being slightly compressed. Australian specimens, for example, USNM 85887 from Muddy Creek, range from subcylindrical to highly compressed, and the holotype of *T. proditor*, USNM 85886, shows distalward flattening from a subcylindrical proximal end, perhaps the growth form of all fully developed colonies. There is no evidence in any of the material examined that the colonies were jointed (compare, Canu and Bassler, 1935, p. 18).

The zoecia in the Tongan specimens of *T. clypeata* are elongate and divided into two subequal frontal portions; a flat proximal area terminating distally in the tubular collar surrounding the ascopore, and an inflated distal peristome which is sessile for most of its length. The ridges demarcating these areas are less distinct in the Tongan specimens than in the Australian specimens, but this difference may be a result of preservation. The ascopore collar projects obliquely proximally, so that the ascopore faces proximally. A faint ridge runs distally from the ascopore up the midline of the peristome to the secondary orifice on some Tongan specimens (plate 6, fig. 2); this feature is not constant even in the better preserved Australian specimens.

The ascopore collar, in all material examined, rises from a slight depression and is bounded on either side by a small pore which seems to be in series with the larger pores that margin the peristome and the proximal frontal area. Lateral to each of the smaller pores is an adventitious avicularium of which the pointed rostrum extends slightly distally and up the side of the peristome of the laterally adjacent zoecium. Because of the lateral pore between it and the ascopore, the avicularium appears to be part of the zoecium whose orifice it flanks rather than of the zoecium whose ascopore it is near, as was assumed by Waters (1881, p. 332, pl. 17, fig. 67).

Ovicells were not found in the Tongan specimens. Frontally swollen areas on the holotype of *T. proditor*, interpreted as ovicells by Canu and Bassler

(1935, p. 18), appear to be solid masses of thick frontal shield.

Family SERTELLIDAE Jullien, 1903
Genus RETEPORELLINA Harmer, 1933 (?)

Reteporellina? sp.

Plate 6, figures 1, 3, 4

Twelve zoarial fragments from sample 1 and seven from sample 2, all poorly preserved, have zoarial and some zoecial features indicating that they may belong to *Reteporellina*.

The growth form of these specimens of *Reteporellina?* was apparently rigidly erect, unilaminar, dichotomously branched, and without anastomoses. The branches are two- or four-serial with indistinct zoecial boundaries rarely showing one or two proximo-lateral pores. The basal sides of the branches are tuberculate and have a few irregularly transverse ridges.

Some of the badly worn peristomes have a labial pore and a rounded labial avicularium of about the same size as the pore, giving the secondary orifice a biperforate-appearing proximal lip. Evidence of oral spines or denticles is lacking. The few ovicells present are all broken, so their frontal morphology is not observable.

Besides the labial avicularia, apparently present on all zoecia, some zoecia, especially in the vicinity of ovicells, have larger avicularia placed proximolaterally on their frontal shields. The spatulate rostra of the frontal avicularia are directed laterally. Large spatulate avicularia are also present on the basal sides of some branches, placed in the axils of bifurcations with their rostra directed obliquely distalward.

In the absence of better preserved zoecial morphology, especially that of the ovicell, it is not possible to identify these specimens definitely with *Reteporellina* or to compare them with known species of that genus.

Family SCHIZOPORELLIDAE Jullien, 1883
Genus SCHIZOPORELLA Hincks, 1877

Schizoporella aff. *S. macgillivrayi* Canu and Bassler

Plate 5, figure 3

Two zoarial fragments, both from sample 1, appear related to *Schizoporella macgillivrayi* Canu and Bassler (1935, p. 29, pl. 9, fig. 5), which was described from the lower Miocene (Balcombian Stage) of Victoria, Australia. Like *S. macgillivrayi*, the Tongan specimens have transversely hexagonal zoecia separated frontally by salient ridges and have frontal shields closely perforated by small pores; these

characters are better shown in the specimen illustrated by MacGillivray (1895, pl. 11, fig. 3), which Canu and Bassler (1935, p. 29) included in *S. macgillivrayi*, than they are in the holotype (USNM 85859). The growth form of the Tongan specimens, however, is erect rather than encrusting, the orifice is more broadly sinuate, and there is little tendency for the zooecial axes to be disarranged as they are in the holotype of *S. macgillivrayi*. Avicularia are lacking on the Tongan specimens, but, contrary to the original description of *S. macgillivrayi*, they are present laterally on the frontal shields of some zooecia on the holotype; this observation accords with the suggestion of Brown (1958, p. 59) that avicularia might be present on some material from Victoria.

Genus CHIASTOSELLA Canu and Bassler, 1934 (?)

Chiastosella? sp.

Plate 4, figure 3

One zoarial fragment from sample 2, encrusting an unidentifiable piece of shell, may belong to *Chiastosella*.

One nearly complete zooecium and small parts of four others are preserved. The zooecium is rhombic and separated from the others by a distinct groove. Its frontal shield is inflated, perforated with large quincuncially arranged pores around all its margins and proximal to the orifice; the central imperforate portion is smooth. The interspaces between frontal pores tend to form radial ridges, as in *C. porosa* Canu and Bassler (1935, pl. 6, fig. 4). The orifice is semicircular distally, broadly sinuate proximally; its border is marked by a low peristome which supports four spine bases distally.

Lateral to this zooecium, the distal piece of the adjacent zooecium may have an ovicell. This structure is expressed frontally as a crescentic depression with a thick, perforate, raised ridge distal to the depression and suggests the immersed ovicells characteristic of the genus (see Brown, 1952, p. 219).

No avicularia were observed on this fragment.

In the absence of avicularia and of more definite ovicell structure, it is not possible to identify this fragment certainly as *Chiastosella* or to compare it with any known species of the genus. Species of this genus have been recorded from Australia and New Zealand, ranging from Eocene to Holocene (Brown, 1958, p. 57).

Family TETRAPLARIIDAE Harmer, 1957
Genus TETRAPLARIA Tenison-Woods, 1879

The fossil species referred to the genus *Tetrapla-*

ria, including the type species, *T. australis* Tenison-Woods, 1879, from beds of Eocene-Miocene age in Australia, show more morphologic diversity than allowed in Harmer's (1957, p. 1053) diagnosis, which apparently was based only on studies of Holocene species. Some of this variation, especially in colony form, probably should not be included in the concept of *Tetraplaria*.

Unlike *T. australis* and all the living species, some fossils have not yielded skeletal evidence of an erect-jointed colony form, that is, internodes beginning with a bipartite connecting tube proximally and ending with a pair of bipartite bases rami distally. *Celularia schreibersi* Reuss, 1848, from the upper Eocene of Italy, placed in *Tetraplaria* by Canu and Bassler (1920, p. 367) and Braga (1963, p. 39; 1965, p. 231), not only lacks these structures but also exhibits dichotomous branching within single calcified fragments (Reuss, 1848, p. 63). *Tetraplaria caudifera* Canu and Bassler, 1920, from the upper Eocene of South Carolina, and *Smittia centralis* var. *laevigata* Waters, 1881 (presumably the taxon called *Smittea laevigata* Waters in Canu and Bassler's 1920, p. 395, list of species of *Tetraplaria*), from the lower Miocene of Australia, also lack nodal structures and, additionally, have frontal pores limited to the margins of the shield, rather than dispersed uniformly over it as in all other fossil and all living species of *Tetraplaria*. These three species should probably be assigned to other genera. Examination of the syntypes of *T. caudifera* (USNM 64071) suggests that they may be conspecific with *Hippopleurifera costulata* (Canu and Bassler, 1920).

Brooding arrangements are variable in *Tetraplaria*. Hyperstomial ovicells are known in most species, including *T. australis* (see Brown, 1958, p. 58). Exceptions, in addition to the three nonjointed species mentioned above, are *T. tuberculata* Canu and Bassler, 1920, from the upper Eocene of Florida, and *T. immersa* (Haswell, 1880), a living species from Australia, which has inflated brooding zooids (Harmer, 1957, p. 1055). In *T. australis* the ovicell is deeply immersed in the distal zooecium (Brown, 1958, p. 58), whereas in all other ovicelled species it is prominent, especially so in the Florida late Eocene species *T. petila* Cheetham, 1963, and *T. obesa* Cheetham, 1963.

In three living species, *T. ventricosa* (Haswell, 1880), from the Indo-Pacific, *T. dichotoma* (Osburn, 1914) from the Gulf of Mexico and Caribbean, and *T. gilbertensis* (Maplestone, 1909), from the Gilbert Islands, Hawaii, and the Galapagos, the orifices of ovicelled zooecia are larger than those of non-ovicelled zooecia. This dimorphism has not been noted pre-

viously in fossils referred to *Tetraplaria*, but it is prominent in one of the two Tongan species, *T. simata*, n. sp.

Apart from the three apparently nonjointed species, which seem not to belong in *Tetraplaria*, avicularia are known in *T. australis*. According to Brown (1958, p. 58), specimens having avicularia are limited to the earlier populations of this species. The Tongan specimens, which are approximately coeval with the earliest populations of *T. australis*, do not have avicularia.

Tetraplaria simata, n. sp.

Plate 7, figures 1, 4, 5

Zoarium erect-jointed, consisting of quadriserial internodes of four or five alternating pairs of auto-

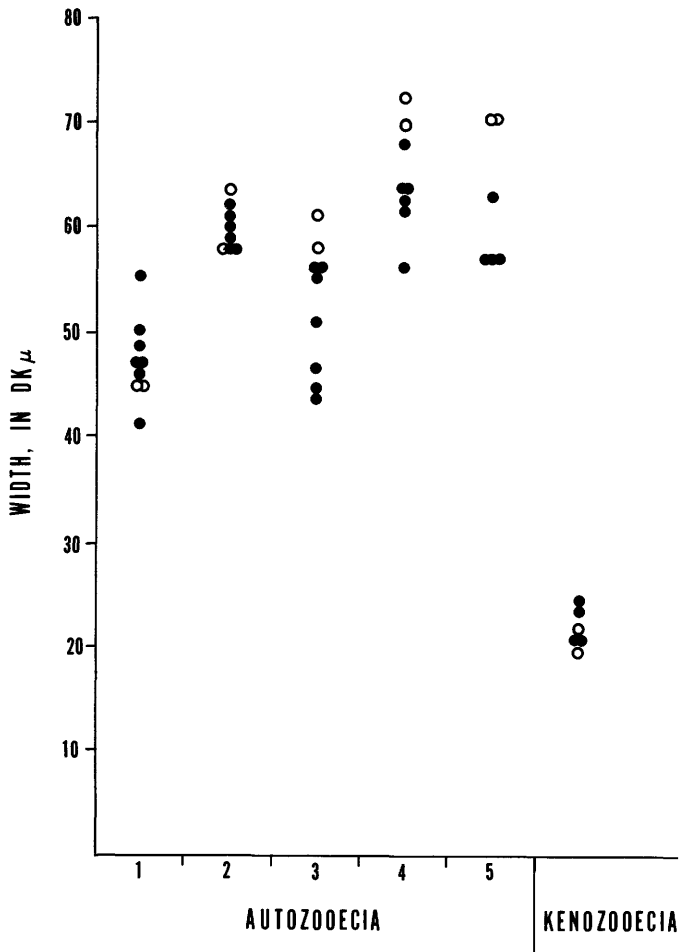


FIGURE 6.—Variations in width of successive pairs of autozoecia (1-5) and distal kenozoecia in five internodes of *Tetraplaria simata*, n. sp. Open circles, holotype (third pair of autozoecia ovicelled); closed circles, paratypes. One paratype has only four pairs of autozoecia preceding kenozoecia. A few zoecia in paratypes were not measured because of poor preservation.

zoecia and one pair of distal kenozoecia bearing bases rami; one pair of autozoecia can bear ovicells. Internodes stubby, tapered proximally, blunt distally, the proximal two-thirds to three-fourths slightly flattened in plane parallel to frontal surfaces of even-numbered pairs of zoecia; these zoecia thus are wider than the first two odd-numbered pairs (fig. 6). Proximal end of internode is an imperforate, bipartite tube, slightly flattened in same plane as internode, formed from attenuated caudal portions of first pair of zoecia. Distal end of internode is a pair of elliptical bases rami with long axes oblique to axis of internode, on small kenozoecia slightly below distal margins of last pair of autozoecia, and, in some specimens, recessed below frontal surfaces of autozoecia proximal to them. Opening of basis rami bipartite.

Autozoecia separated frontally by narrow ridges. Zoecial length decreases distally within each internode (fig. 7); first through third pairs of zoecia show marked decrease in length, fourth pair no significant change, and fifth pair, where present, slight decrease. Widths of first and third pairs of zoecia about five-sixths those of second, fourth, and (where present) fifth pairs; widths of ovicelled zoecia and of all succeeding zoecia greater than those of corresponding pairs in nonovicelled internodes (fig. 6). First pair of zoecia elongate-claviform; second pair rhombic with distal corner convexly rounded; all following pairs transversely hexagonal, rounded concavely on proximal side and convexly on distal side. Frontal shield inflated, uniformly perforate except on caudal portion of first pair; pores small, numerous, quincuncially arranged. Orifice terminal on frontal shield, very slightly inclined distally; distal portion semicircular; proximal sinus broadly rounded, apparently lacking condyles; orifices of nonovicelled zoecia about four-fifths as large as those of ovicelled zoecia. Oral spines lacking.

Kenozoecia rounded-rectangular; about one-third as large as autozoecia; distal half occupied by oblique basis rami; proximal half covered with inflated, finely perforate frontal shield.

Ovicells present on both zoecia of third pair in some internodes (seen in one internode); hyperstomial, prominent, covering proximal five-sixths of distal zoecium. Frontal cover uniformly and finely perforate, except for semicircular strip around orifice; set off from frontal shields of distal and proximal zoecia by narrow ridges.

Avicularia lacking.

Zoecial dimensions (in dkμ) measured in frontal view on five internodes (holotype and paratypes) are

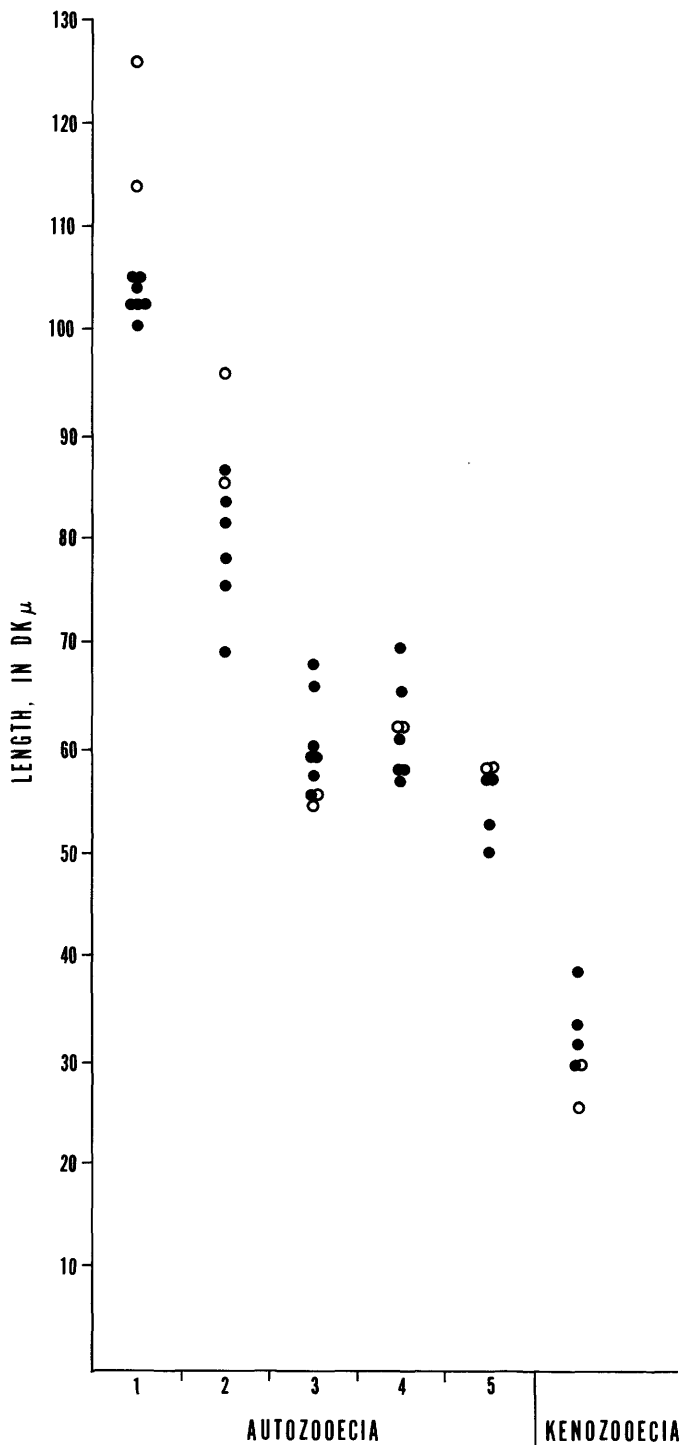


FIGURE 7.—Variations in length of successive pairs of autozoecia (1-5) and distal kenozoecia in five internodes of *Tetraptaria simata*, n. sp. Specimens and symbols as in figure 6.

summarized as follows (mean and standard deviation given to two decimal places for purposes of calculation only) :

Dimension	Number measured	Mean	Standard deviation	Observed range
Length of autozoecium :				
First pair	9	105.93	7.35	100-124
Second pair	8	80.85	7.04	69-94
Third pair	9	59.17	4.19	55-67
Fourth pair	8	62.48	5.02	56-71
Fifth pair	6	54.74	2.89	50-57
Width of autozoecium :				
First pair	9	46.67	3.57	41-55
Second pair	8	59.54	.98	58-62
Third pair	9	53.85	3.87	46-60
Fourth pair	8	64.16	4.48	56-71
Fifth pair	6	62.58	6.01	57-71
Length of zoecial orifice :				
Nonovicelled zoecia	36	15.89	.70	14-17
Ovicelled zoecia	2	18.90	.42	18-19
Width of zoecial orifice :				
Nonovicelled zoecia	36	16.50	.82	14-18
Ovicelled zoecia	2	19.74	.42	19-20
Length of ovicell	2	50.40	.00	50
Width of ovicell	2	54.60	4.20	50-59
Length of kenozoecium	6	30.94	3.83	25-38
Width of kenozoecium	6	21.14	1.49	19-24

The differences between means were tested by Student's *t* with the following results (significant = 0.05 level; highly significant = 0.01 level) :

Dimension	Means tested	Difference
Length of zoecium	First versus second pairs.	Highly significant.
	Second versus third pairs.	Do.
	Third versus fourth pairs.	Not significant.
	Fourth versus fifth pairs.	Highly significant.
Width of zoecium	First versus second vs. third pairs.	Do.
	First versus third vs. fourth pairs.	Do.
	Second versus fourth pairs.	Significant.
Length of zoecial orifice	Fourth versus fifth pairs.	Not significant.
	Nonovicelled versus ovicelled zoecia.	Highly significant.
Width of zoecial orifice	do	Do.

Holotype, USNM 169276; paratype, USNM 169277; sample 2. Paratype, USNM 169278, and 2 paratypes, USNM 169279, sample 1. Upper Eocene, about one-quarter mile north of Vaingana, Eua, Tonga, at altitude 400 feet.

Tetraptaria simata is distinguished by its slightly flattened internodes having the even-numbered pairs of autozoecia distinctly wider than the first two odd-numbered pairs; by the regular distalward decrease in lengths of the first three pairs of autozoecia in an internode; and by the combination of prominent ovicells, broadly sinuate orifices which are dimorphic in association with brooding, and ridges separating zoecia. If the limited variation in number of autozoecial pairs per internode, four or five, is significant in this small sample, this character would also differentiate *T. simata* from all other known species of the genus.

Although the widths of the first four pairs of autozoecia of *T. simata* (fig. 6) differ significantly statistically, those of the first and third pairs overlap broadly, as do those of the second, fourth, and fifth pairs. Except for the two ovicelled zoecia forming the third pair in one internode, there is almost no overlap between the two groups of autozoecial pairs.

This difference in width is correlated with the flattening of the proximal part of the internode.

The third to fifth pairs of autozoecia in the ovicelled internode are wider than their counterparts in the nonovicelled internodes (fig. 6). The greater width is apparently a direct accommodation to the size of the ovicell, as it is restricted to the ovicelled and more distal zoecia. Thus, the ovicelled internode began growth with zooids like the first pair of zooids in the nonovicelled internodes and then, beginning with the ovicelled zooids, developed a different morphology.

The successive, pronounced distalward decreases in the lengths of the first three pairs of autozoecia within each internode (fig. 7) appear to follow an astogenetic gradient. If one can assume that all of the internodes beyond the unknown encrusting base of the colony had the form of the specimens described here, the astogenetic zonation in *T. simata* is of the cyclic type described by Boardman, Cheetham, and Cook (1970, p. 300, fig. 4), with each internode comprising subsequent zones of both astogenetic change and astogenetic repetition. The number of generations of zooids within a zone of repetition in *T. simata*, however, appears drastically limited compared to other cheilostomes in which cyclic zonation has been described.

In an internode having just four pairs of autozoecia preceding the distal kenozoecia, the zone of astogenetic repetition appears to consist of the fourth pair of autozoecia, which do not differ significantly in length from the third pair, and the pair of kenozoecia, which can be considered positional polymorphs similar to zoecia making up monticules in trepostomes (Boardman and others, 1970, p. 303). Where present, a fifth pair of autozoecia would thus also be included in the zone of repetition, and their slight, but statistically significant, decrease in length from the fourth pair could be regarded either as a chance variation because of the small sample or as a further expression of positional polymorphism. That this difference may be a chance variation is suggested by the broad overlap between the fourth and fifth pairs, as compared to no overlap of the first three pairs (fig. 7).

Alternatively, the slight decrease in length of the fifth pair of autozoecia could be considered the start of a series of astogenetic changes continuing into the next internode. This interpretation seems unlikely because it would restrict the kenozoecia to zones of change and because the zone of change would include zoecia showing first a decrease in length (fifth pair of autozoecia to kenozoecia), then an increase

(kenozoecia to first pair of autozoecia in next internode), and again a decrease (first to third pairs of autozoecia).

The decreasing lengths of autozoecia in each internode reduce the distances between the distal margins of alternating pairs toward the distal end of the internode. If all pairs of zooids were the same length, the last two pairs would be half a zoecial length out of phase, and the kenozooids would have to be more than half as long as the autozooids in order to hold the bases rami beyond the ends of the last pair of autozooids. In *T. simata* the kenozoecia are less than a third as long as the longest autozoecia (fig. 7). In other species of *Tetraplaria* (see *T. cf. T. turgida* below), the autozoecia remain half a length out of phase and are followed by a relatively longer pair of kenozoecia.

Tetraplaria cf. *T. turgida* Tewari and Srivastava

Plate 7, figures 2, 3

?*Tetraplaria turgida* Tewari and Srivastava, 1967, Jour. Geol. Soc. India, v. 8, p. 26, text-fig. 2 (4, 4a).

Three specimens, all from sample 2, may belong to *Tetraplaria turgida* which was described from the middle Eocene (Kirthar Stage) of Kutch, India.

Although not shown in Tewari and Srivastava's (1967) drawings, frontal perforations seem to be implied in their description (frontals "covered by tremocysts," p. 27). All the Tongan specimens have large, prominent, evenly distributed frontal pores.

One complete internode, consisting of five pairs of autozoecia plus a distal pair of kenozoecia each bearing a bipartite basis rami, has ovicells. These are borne on both zoecia of the third pair, as are those on the specimen illustrated by Tewari and Srivastava, and as in the latter, the ovicells are prominent, rather than immersed in the distal zoecium.

Tewari and Srivastava compared this species with *T. australis* in which the ovicells are deeply immersed in the distal zoecium (Brown, 1958, p. 58). *T. australis* also has the frontal shield covered with fine tubercles between which are exceedingly small pores, which were overlooked in Tenison-Woods' (1879, p. 61) original description, and has the orifice interrupted proximally by a narrow, cleftlike sinus.

The Tongan specimens, and presumably the Indian specimens, more closely resemble another Australian species, *T. pedunculata* (MacGillivray, 1895), than they do *T. australis*. In *T. pedunculata*, the frontal shield is coarsely perforate and the ovicell (present in USNM 169283, Balcombian, Mitchell River, Bairnesdale, Victoria; not previously noted) is prominent; the oral sinus, however, is narrow, and the zoecia are separated by prominent ridges.

The internodes of the Tongan material appear to consist of variable numbers of autozoecial pairs. In addition to the five-paired complete internode, one specimen broken at both ends has six pairs, and the third, seemingly missing only a small part of the proximal zooecia and preserving the bases rami distally, shows only three pairs. In this respect, the Tongan specimens resemble living species of *Tetraplaria*, such as *T. ventricosa* (Haswell, 1880), in which Harmer (1957, p. 1054) described single colonies having the number of pairs of zooecia per internode ranging from one to ten or more.

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PLATES 1-7

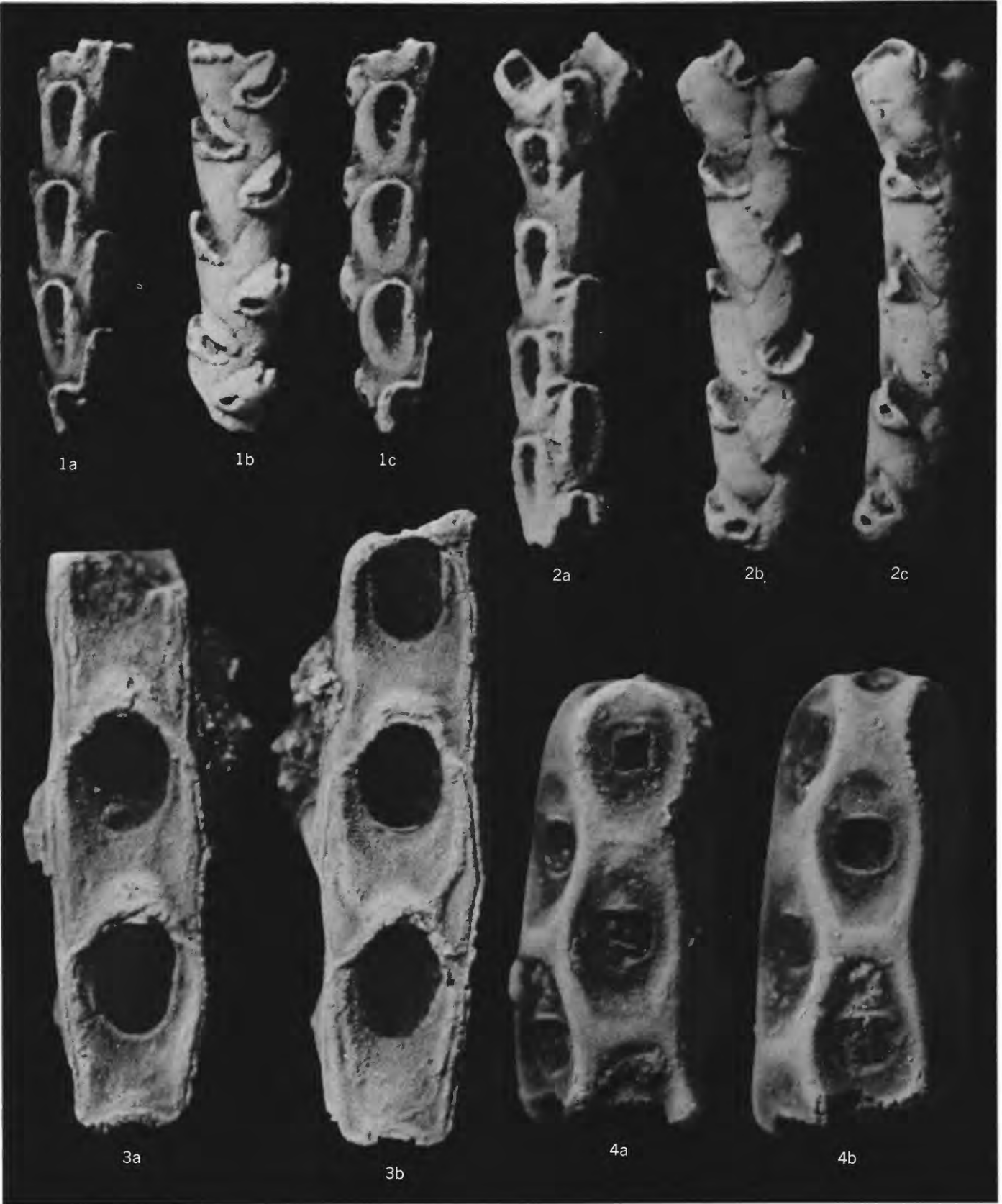
[Contact photographs of the plates in this report are available, at cost, from U.S. Geological
Survey Library, Federal Center, Denver, Colorado 80225]

PLATE 1

[All figures $\times 50$; specimens coated with ammonium chloride]

FIGURES 1, 2. *Canda fossilis* Waters (p. E9).

1. Frontal (a), basal (b), and left-frontal (c) views of unbranched zoarial fragment showing zooecia with prominent scutum attachments and vibracula with curved rostral channels and large rootlet⁺ foramina; USNM 169235, sample 2.
2. Frontal (a), basal (b), and right-lateral (c) views of dichotomous zoarial fragment; proximal zooecia have frontal avicularia; two most distal, broken zooecia are inner members of branches (Harmer's (1923) zooecia F and G), meet above axillary zoecium (zoecium E) in basal view, and have basal vibracula; vibracula lie on interzoecial suture; USNM 169236, sample 2.
3. *Patysella?* sp. (p. E8).
Frontal views of zoarial fragment, showing ovicelled (a) and nonovicelled (b) zooecia; small occlusor-laminae are visible below distolateral portions of opesia; USNM 169232, sample 1.
4. *Cellaria cucullata* MacGillivray (p. E8).
Frontal views of a zoecial series terminating at distal end of internode (a) and of one intersecting the joint (b); USNM 169233; sample 1.



CANDA, PATSYELLA?, AND CELLARIA

PLATE 2

[All figures $\times 50$; specimens coated with ammonium chloride]

FIGURE 1. *Figularia?* sp. (p. E10).

Frontal views of zoarial fragment, showing ovicelled (proximal zoecium, a) and nonovicelled (distal zoecium, a; b) zooecia; bases of spines(?) and costae (fused in right proximal zoecium shown in profile, b) and avicularia; USNM 169239, sample 2.

2. *Menipea innocua* Waters (p. E10).

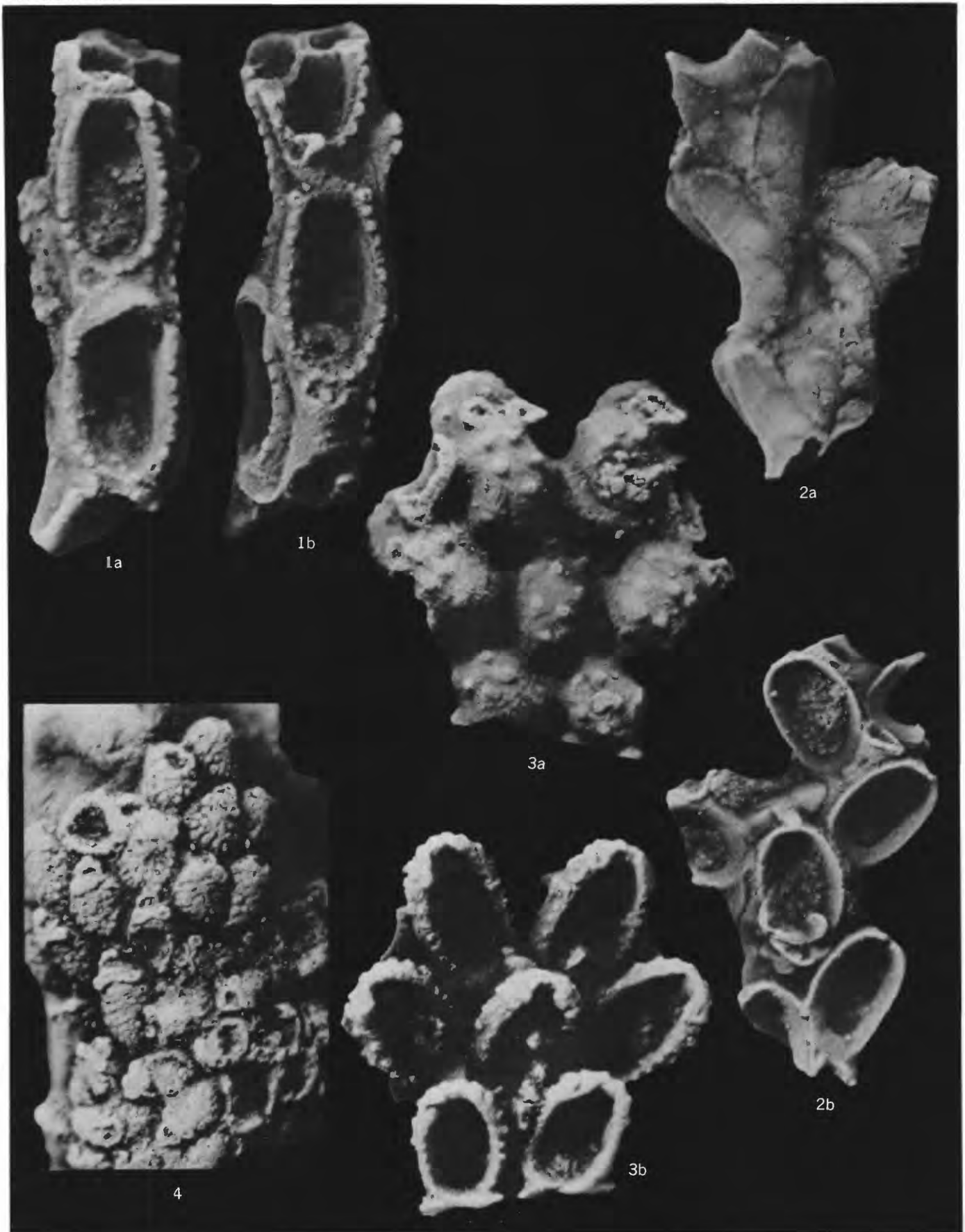
Basal (a) and frontal (b) views of branched zoarial fragment showing long, laterally directed avicularia with proximal foramina placed on gymnocysts of biserially arranged zooecia; USNM 169238, sample 2.

3. *Beania diademata*, n. sp. (p. E9).

Basal (a) and frontal (b) views of zoarial fragment; small fenestrae show only basally among six connecting tubes for each zoecium; spine bases appear on mural rims, around distolateral margins, and on basal surfaces of zooecia; larger, unilateral (probable) base of avicularium shows on each zoecium just proximal to oral end; holotype, USNM 169234; sample 2.

4. *Tripurula* aff. *T. biarmata* (Waters) (p. E11).

Frontal view of encrusting zoarium showing irregularly arranged zooecia and apparent growing margin of colony (top of view); USNM 169240, sample 2.



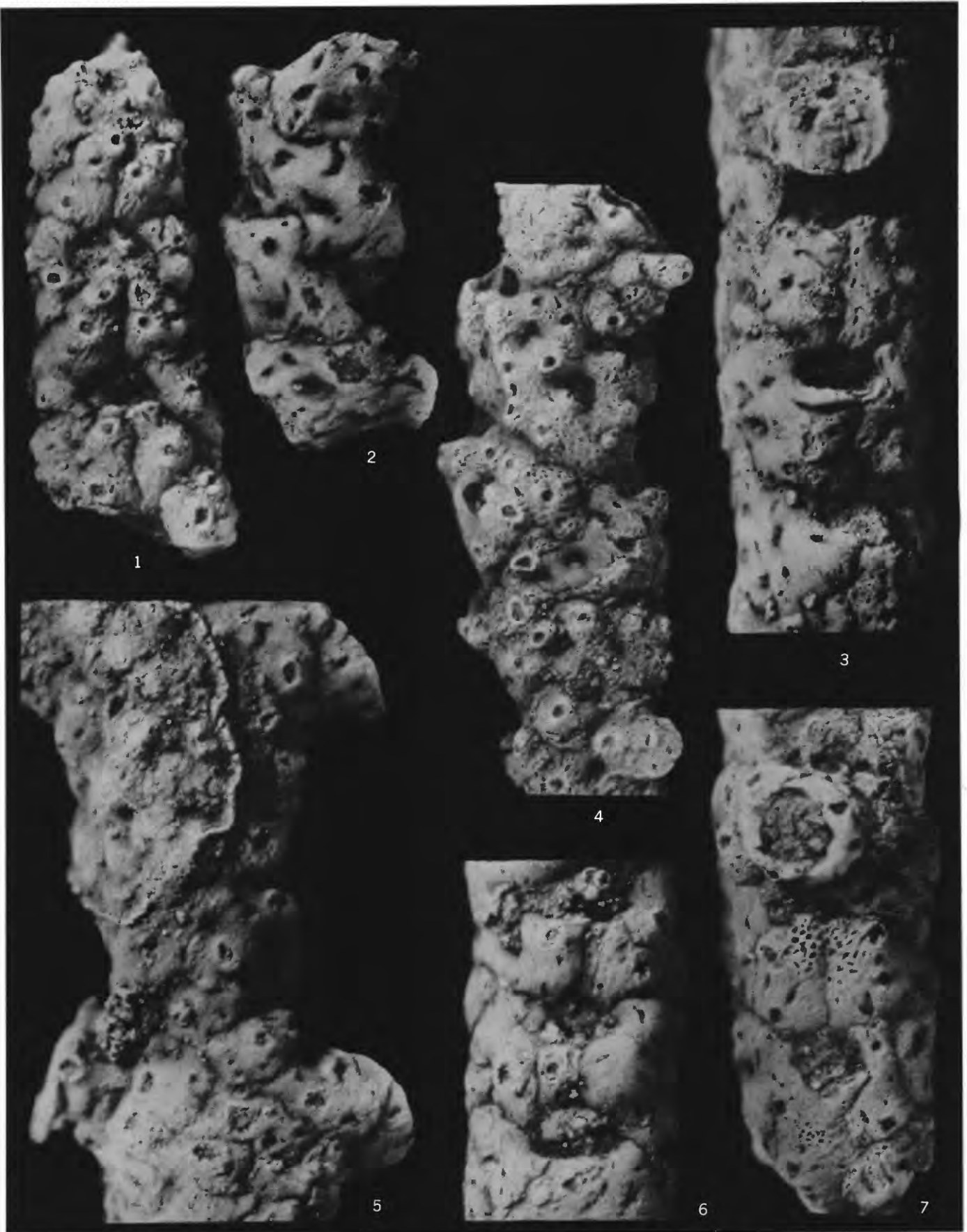
FIGULARIA?, *MENIPEA*, *BEANIA*, AND *TRIPORULA*

PLATE 3

[All figures $\times 50$; specimens coated with ammonium chloride]

FIGURES 1-7. *Bifaxaria diaphyota*, n. sp. (p. E13).

1. Frontal view of zoarial fragment apparently from intermediate part of colony, showing median frontal furrow, bilaterally disposed frontal avicularia, and surface pitting; paratype, USNM 169246; sample 1.
2. Lateral view of zoarial fragment apparently from distal part of colony, showing interzooecial groove, lateral row of avicularia, striation-like pattern of fine pits, scattered frontal pores; holotype, USNM 169245; sample 1.
3. Frontal view of zoarial fragment apparently from proximal part of colony, showing one pair of lateral-oral avicularia (in middle orifice), numerous frontal avicularia and broken base of branch; paratype USNM 169247; sample 1.
- 4, 5. Lateral views of zoarial fragments apparently from proximal parts of colonies, showing broken bases of opposing branches and extreme development of frontal avicularia; paratypes, USNM 169248, 169249; sample 1.
- 6, 7. Frontal views of zoarial fragments apparently from proximal parts of colonies, showing extreme development of frontal avicularia; paratypes, USNM 169250, 169251; sample 1.



BIFAXARIA

PLATE 4

[All figures $\times 50$; specimens coated with ammonium chloride]

FIGURES 1, 2. *Spiroporina kondoi*, n. sp. (p. E14).

1. Oblique frontal view of two zooecial series showing broken peristomes with proximolateral pores, spiramina, and frontal pores; holotype, USNM 169255, sample 1.

2. Frontal view of zoarial fragment preserving bifurcation; paratype, USNM 169257, sample 1.

3. *Chiaستosella?* sp. (p. E18).

Frontal view of encrusting zoarial fragment, showing one nearly complete zooecium and parts of four others; that on right is possibly ovicelled; USNM 169275, sample 2.

4, 5. *Bifaxaria bryani*, n. sp. (p. E12).

4. Frontal (a) and lateral (b) views of zoarial fragment apparently from distal part of colony, showing stem with broken unopposed branch, at base of which are lateral avicularia; holotype, USNM 169241, sample 2.

5. Lateral (a) and frontal (b) views of zoarial fragment apparently from proximal part of colony, showing approximately aligned lateral avicularia and swellings indicating possible ovicells; paratype, USNM 169242, sample 2.



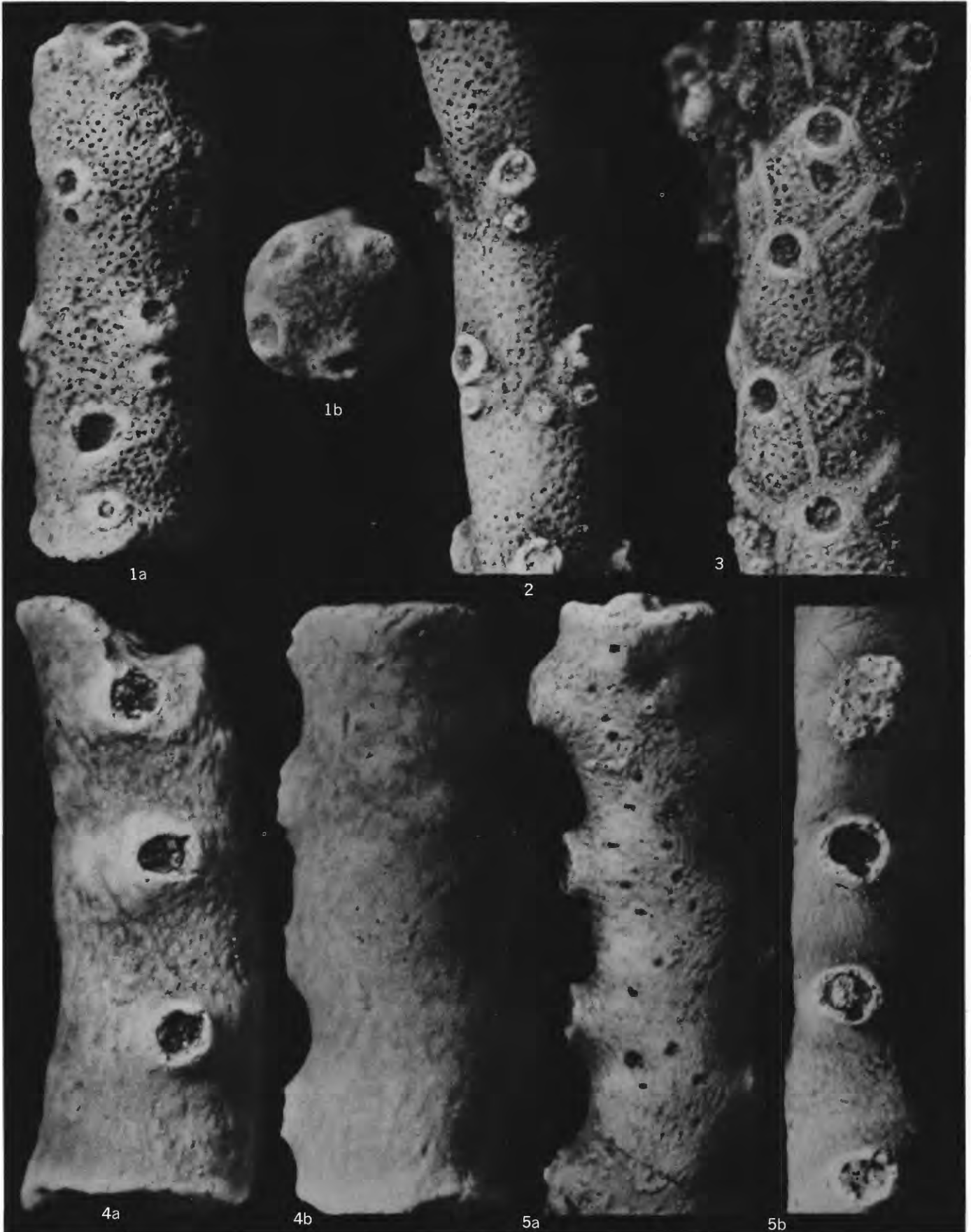
BIFAXARIA, CHIASTOSELLA?, AND SPIROPORINA

PLATE 5

[All figures $\times 50$; specimens coated with ammonium chloride]

FIGURES 1, 2. *Spiroporina deliqua*, n. sp. (p. E15).

1. Frontal (a) and distal (b) views of abraded zoarial fragment preserving growing tip; paratype, USNM 169261; sample 1.
2. Frontal view of parts of four whorls of zooecia separated by shallow grooves with V-shaped lobes directed proximally between peristomes; frontal avicularium in one proximal lobe; holotype, USNM 169260, sample 1.
3. *Schizoporella* aff. *S. macgillivrayi* Canu and Bassler (p. E17).
Frontal view of subcylindrical zoarial fragment; USNM 169273, sample 1.
- 4, 5. *Tessaradoma bifax*, n. sp. (p. E15).
 4. Frontal (a) and lateral (b) views of zoarial fragment apparently from proximal part of colony, showing nonsinuate secondary orifices and imperforate frontal surfaces; paratype, USNM 169264, sample 1.
 5. Lateral (a) and frontal (b) views of zoarial fragment apparently from distal part of colony, showing sinuate secondary orifices, apparently marginal pores, and lateral avicularia; holotype, USNM 169263, sample 2.



SPIROPORINA, SCHIZOPORELLA, AND TESSARADOMA

PLATE 6

[All figures $\times 50$; specimens coated with ammonium chloride]

FIGURES 1, 3, 4. *Reteporellina?* sp. (p. E17).

1. Frontal (a) and basal (b) views of quadriserial, ovicelled zoarial fragment, showing broken ovicells, frontal avicularia, and nearly smooth basal surface; USNM 169268, sample 1.
3. Basal view of nonovicelled, quadriserial zoarial fragment, showing two bifurcations; USNM 169269, sample 2.
4. Frontal (a) and basal (b) views of nonovicelled, biserial zoarial fragment, showing biperforate-appearing secondary orifices, tuberculate basal surface with one transverse ridge, and two basal avicularia in axils; USNM 169270, sample 2.
2. *Tubitrabecularia clypeata* (Waters) (p. E17).
Frontal view of zoarial fragments showing elongate zoecia divided at tubular ascopore collar into subequal proximal and peristomal areas; faint longitudinal ridge on peristome; and paired lateral-oral avicularia with complete crossbars; USNM 169266, sample 1.



RETEPORELLINA? AND *TUBITRABECULARIA*

PLATE 7

[All figures $\times 50$; specimens coated with ammonium chloride]

FIGURES 1, 4, 5. *Tetraplaria simata*, n. sp. (p. E19).

1. Frontal views of zoecia of first, third, and fifth pairs (a) and of second and fourth pairs (b) of complete, abraded internode; paratype, USNM 169277, sample 2.
 4. Frontal views of zoecia of first, third, and fifth pairs (a) and of second and fourth pairs (b) of complete, ovicelled internode; holotype, USNM 169276, sample 2.
 5. Frontal views of zoecia of first, third, and fifth pairs (a) and of second and fourth pairs (b) of complete internode; paratype, USNM 169278, sample 1.
- 2, 3. *Tetraplaria* cf. *T. turgida* Tewari and Srivastava (p. E21).
2. Frontal views of zoecia of second and fourth pairs (a) and of first, third, and fifth pairs (b) of complete, ovicelled internode; USNM 169280, sample 2.
 3. Frontal views of zoecia of second pair (a) and of first and third pairs (b) of nearly complete internode; USNM 169281, sample 2.



TETRAPLARIA

