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CONTRIBUTIONS TO THE NOMENCLATURE, SYSTEMATICS, AND MORPHOLOGY OF THE OCTOCORALLIA

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This paper records certain information resulting from work done toward preparation of the chapter on Octocorallia for the "Treatise of Invertebrate Paleontology." Regrettably, it must include material of very diverse nature—nomenclature, systematics, morphology, phylogeny, and paleontology. Likewise regrettably, the diagnoses of new taxonomic units must for the present be of a brief and preliminary nature. It is hoped that each may be suitably expanded in future treatments.

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Order ALCYONACEA Lamouroux, 1816

Family Alcyoniidae Lamouroux, 1812

Genus *Sphaerella* Gray, 1869

Lobularia Ehrenberg, 1834, p. 281; Tixier-Durivault, 1948, p. 1; not Lamarck 1816, p. 412.

Sphaerella Gray, 1869, p. 122. (Type species: *Alcyonium tuberculosum* Quoy and Gaimard = *Lobularia tuberculosum* (Quoy and Gaimard) Tixier-Durivault, 1948, by monotypy.)

Microspicularia Macfadyen, 1936, p. 28. (Type species: *Alcyonium pachyclados* Klunzinger, by original designation.)

I am in agreement with Utinomi (1953) and Macfadyen (1936) that the name *Lobularia* Lamarck cannot be used for the Indo-Pacific genus of Alcyoniidae to which it is usually applied. Macfadyen's replacement was scarcely necessary, however, because earlier names were available. J. E. Gray, in 1869, established the genus *Sphaerella* for a single species, *Alcyonium tuberculosum* Quoy and Gaimard, from Tonga. Tixier-Durivault (1948) redescribed Quoy and Gaimard's type specimen and made it clear that *A. tuberculosum* is a *Lobularia* sensu Ehrenberg, thus defining Gray's genus. Inasmuch as the name *Sphaerella* has some 67 years' priority over *Microspicularia*, I advocate its use. Since none of the original three species of *Lobularia* Lamarck, 1816, belongs to *Lobularia* sensu Tixier-Durivault and other authors, that name is absolutely inadmissible regardless of which of the three species is taken as its genotype.

Order GORGONACEA Lamouroux, 1816

Suborder SCLERAXONIA Studer, 1887

Family ANTHOTHELIDAE Broch, 1916

Subfamily Spongiodermatinae Aurivillius, 1931

Tripalea, new genus

Suberia Studer, 1878, p. 666 (part).

The valid type designation for Studer's genus *Suberia* seems to be that of Nutting, 1911 (p. 13), selecting *Suberia köllikeri*, a species shown by Kükenthal to be a *Semperina*. *Suberia* is thus a subjective junior synonym of *Semperina*, and *Suberia clavaria* Studer (which is not congeneric) is left without a genus. For this species I therefore establish the genus *Tripalea*, which may be briefly diagnosed as follows:

Monomorphic Scleraxonia with the medullar zone perforated throughout by gastrodermal solenia; a single ring of wide boundary canals separating medulla from cortex. Cortex with two distinct layers, the inner and thicker one very open and spongy with the walls of its spacious lacunae containing few spicules; the outer and thinner layer compact, densely packed with spicules different from those of the inner layer, extending into the inner cortex as an investment of the gastric cavities, which continues as a sheath around the major gastrodermal canals.

TYPE SPECIES: *Suberia clavaria* Studer, 1878 = *Tripalea clavaria*, new combination. Colonies simple, clavate, arising from an encrusting base. The spicules of the thin outer cortex are short capstans; of the lacunar walls of the inner layer, longer spindles with simple, conical processes or complex tubercles; of the medulla, irregular rods often with forked ends.

DISTRIBUTION: Eastern coast of South America.

Family CORALLIIDAE Lamouroux, 1812

Genus *Corallium* Cuvier, 1798

The *E. W. Scripps*, research vessel of the Scripps Institution of Oceanography, on a recent cruise obtained specimens of two species of precious corals from deep water off Guadalupe Island. These specimens, which were kindly submitted by Robert H. Parker of Scripps Institution, represent the first find of the genus *Corallium* in North American waters.

***Corallium imperiale*, new species**

PLATE 2,*c*–*h*

DESCRIPTION: Colony large, spread in one plane, abundantly branched in a subpinnate fashion. Main branches practically circular in cross section, about 5 mm. in diameter; end twigs slender, about 1.5 mm. in diameter; axis very weakly and obscurely striated. Autozooids restricted to one face of the colony, their calyces tall, cylindrical, 8-ribbed; the tentacles are fully retractile, but in preservation may remain exsert. The calyces are about 2.5 mm. tall, up to 3 mm. if the tentacles are not fully retracted, and 1.5 mm. in diameter. Siphonozooids forming small, irregular verrucae between the autozooids. On the naked back face of the colony the surface of the coenenchyme shows a predominantly longitudinal and parallel system of narrow ridges, here and there with cross-connections or densely anastomosing, that marks the presence of the coenenchymal solenial network.

Spiculation consists predominantly of 8-radiates and double clubs in the general coenenchyme and calyces, and irregularly spinous rods in the tentacles. The so-called double clubs or opera-glasses (pl. 2,*d*), actually asymmetrical derivatives of the 8-radiate capstan, are very abundant; they average 0.05–0.06 mm. in length. The 8-radiates of typical form (pl. 2,*e*) attain a length of 0.08–0.09 mm., and occasional atypical examples (pl. 2,*g*) may reach 0.1 mm. Crosses (pl. 2,*f*) are not uncommon. In the distal part of the calyces a few rods (pl. 2,*h*) 0.10–0.11 mm. in length may be found, and this type of spicule is the predominant one in the tentacles. Small 8-radiate capstans also occur in the tentacles, where the spicules are irregularly packed, extending as points into the bases of the pinnules.

In color the colony is a rich pink (approximately "vinaceous pink" of Ridgway), coenenchyme and axis being colored alike.

Holotype: USNM 50110. Southwest of Guadalupe Island, lat. 27°23′ N., long. 119°19′ W., 1,000–2,000 meters, Scripps Institution Pelagic Area Studies Cruise, Apr. 24, 1954.

Remarks: *Corallium imperiale* seems to be closely allied to *C. bōshūense* Kishinouye and *C. sulcatum* Kishinouye, from Japan, but differs from both in the absence of massive, irregular sclerites and the predominance of double clubs rather than 8-radiates. *Corallium imperiale* differs further from *C. sulcatum* in its less profuse branching and more prominent autozooids (pl. 2,*c*), and from *C. bōshūense* in its lack of compression of the branches and its rich pink color.

Corallium ducale, new species

Plate 1

Description: Colony spread in one plane, openly branched laterally and dichotomously. Branches round or slightly compressed at right angles to the plane of branching, the largest nearly 10 mm. in diameter. The terminal twigs are 1.5–2.0 mm. in diameter. Axis faintly striated; in the terminal portions it shows low surface irregularities and is distinctly granulated. The autozooids are restricted to one face of the colony, their calyces short cylindrical or blunt conical, distinctly 8-ribbed (pl. 1,*n*); the tentacles are fully retractile and none remain exsert in preservation. The calyces are 1.5 mm. or less in height, and up to 2.0 mm. in diameter at the base, more or less tapering apically. The siphonozooids form small, hemispherical or irregular calyces near the autozooids. The coenenchyme of the back face of the colony is wrinkled by an anastomosing reticulum of narrow ridges marking the presence of the solenial system, and there are sinuous grooves on the coenenchyme between the autozooids.

The spiculation consists of abundant double clubs (pl. 1,*a*) derived from radiate forms by asymmetrical development of two radii, measuring 0.060–0.085 mm. in length; 6-, 7-, and 8-radiates (pl. 1,*b–d*) up to 0.1 mm. in length, some of which may show a considerable subdivision of the radii or are otherwise misshapen (pl. 1,*e–g*); crosses (pl. 1,*h*); massive, irregular bodies (pl. 1,*i–k*); slender, spinous rods (pl. 1,*l*) in the pharyngeal region and oral disk; and abundant stouter rods (pl. 1,*m*) in the tentacles.

In color the colony is a dark pink, tending more toward red than does the color of *C. imperiale;* in alcohol, the axis is of a richer and deeper color than the rind.

Holotype: USNM 50111. Southwest of Guadalupe Island, lat. 27°23′ N., long. 119°19′ W., 1,000–2,000 meters, Scripps Institution Pelagic Area Studies Cruise, Apr. 24, 1954.

REMARKS: The massive, irregular sclerites of *Corallium ducale* resemble those of *C. bōshūense* and *C. sulcatum* from Japan. From both of those species *C. ducale* differs widely in its open, lateral-dichotomous plan of ramification, lower autozooid calyces, and presence of both 6- and 7-radiates as well as the usual 8-radiate forms.

Family PARISIDIDAE Aurivillius, 1931

It is quite clear from the descriptions of fossil Isididae that the species involved are usually not attributable to *Isis* in a strict sense nor even, in many cases, to the family Isididae. Some of the fossil species referred to *Isis* seem to belong rather to the Parisididae (suborder Scleraxonia), which are characterized by strong radial ridges on the ends of the internodes. Thin sections of the fossils have been neither illustrated nor described, and until such sections are studied it cannot definitively be stated that these species are unquestionably scleraxonians. Every available clue indicates that they are, however, and I therefore reassign those species which have been sufficiently well illustrated to warrant the change.

Parisis danae (P. M. Duncan)

Isis Danae Duncan, 1880, p. 108, pl. 28, figs. 1–3.

Radial ridges on ends of the internodes increasing in number by intercalation rather than by dichotomy. Ramification from distal ends of internodes. A large species; axis up to 1.2 inches in diameter.

The intercalary increase of the radial lamellae may indicate a genus distinct from *Parisis*.

HORIZON AND LOCALITY: Gáj series (Miocene): Naigh-Nai Valley; 5 miles northwest of Tong; Tandra Ráhim Khan (Sind).

Parisis compressa (P. M. Duncan)

Isis compressa Duncan, 1880, p. 109, pl. 28, figs. 4, 5.

Radial ridges on ends of internodes increasing in number by dichotomy. Branches large, laterally coalescent.

HORIZON AND LOCALITY: Gáj series (Miocene): Tandra Ráhim Khán (Sind).

Parisis sp.

Isis sp. 1, Duncan, 1880, p. 109, pl. 28, figs. 8–9.

The illustrations of this fossil given by Duncan distinctly recall the Recent *Parisis fruticosa* Verrill, but identity of the fossil with the modern species must be verified by further study of specimens.

HORIZON AND LOCALITY: Gáj series (Miocene): Naigh-Nai Valley, southwest of Sehwán (Sind).

***Parisis ?brevis* (D'Achiardi)**

?*Isis brevis* D'Achiardi, 1868, p. 75, pl. 1, figs. 1a, 1b.
Isis brevis Reuss, 1869, p. 292, pl. 28, figs. 14–16.

Reuss' specimens are clearly referable to *Parisis*, and his figures correspond very closely with *P. fruticosa* Verrill. The identity of Reuss' material with D'Achiardi's is still open to question.

HORIZON AND LOCALITY: Terebratulinenschichten von San Martino (Reuss); Sassello (Miocene); Castelgomberto (Oligocene) (D'Achiardi); all Italy.

Suborder HOLAXONIA Studer, 1887

Family PLEXAURIDAE Gray, 1859

Genus *Eunicea* Lamouroux, 1816

Because doubtful species are excluded from consideration in the subsequent designation of generic types, the usually accepted type species of *Eunicea* (*Gorgonia succinea* Pallas, 1766; designated by Kükenthal, 1917, p. 335) is ruled out. Lamouroux himself considered *Eunicea succinea* "une espèce douteuse." Inasmuch as no other type designation appears to have been made, I here select *Eunicea mammosa* Lamouroux, 1816, as genolectotype of *Eunicea* Lamouroux, 1816.

Rumphella, new genus

PLATE 2,*a*,*b*

Plexaurids with moderately thick branches often terminally clavate, calyces low or absent, anthocodiae armed with a crown and points. Base of axis secondarily enlarged to form a dense calcareous mass, especially in old specimens. Cortical spicules in the form of spindles and clubs; the clubs are symmetrical wart-clubs only, derived from capstans. There are no long rods as in *Hicksonella* Nutting; no thorny clubs as in *Psammogorgia* Verrill; no large spheroids as in *Euplexaura* Verrill; no foliate clubs and torches as in *Plexaura* Lamouroux. Spicules of the inner cortex never purple or lavendar.

TYPE SPECIES: *Plexaura aggregata* Nutting, 1910a=*Rumphella aggregata*, new combination (pl. 2,*a*,*b*). Syntype, USNM 43461, Flores Sea and environs, station data illegible (*Siboga* Exped.).

REMARKS: Also referable to *Rumphella* are *Gorgonia antipathes* variety β, Esper, 1792 (including also *Plexaura antipathes* Klunzinger, 1877 and *Euplexaura antipathes* Hiles, 1899) and *Gorgonia suffruticosa* Dana, 1846. Esper's, Klunzinger's, and Hiles' specimens seem to represent a single species in all probability identical with the *Corallium nigrum* of Rumphius and the *Gorgonia antipathes* of Linnaeus.

Esper's typical *G. antipathes*, which had purple spicules in the inner cortex, is the West Indian species that Houttuyn, P. L. S. Müller, and Esper himself had called *Gorgonia porosa*.

IFALUKELLIDAE, new family

Holaxonia in which the axis is strongly calcified, its core not chambered; calcareous material not oriented in a radial pattern; concentric layers nearly smooth. Spicules in the form of minute calcareous corpuscles, oval or elongate, usually with a median constriction, their sculpture irregularly granular; length 0.025–0.07 mm.

Ifalukella, new genus

Colonies low, arborescent, finely branched in an irregular, lateral pattern. Axis calcareous, brittle, spirally ridged, arising from a massive calcareous base onto which the ridges extend as high crests with lobed or strongly laciniated edges that may produce small twigs, some of which may develop into full-sized colonies. Coenenchyme thin; polyps unarmed. Spicules very small, up to 0.035 mm. in length, of characteristic outline.

TYPE SPECIES: *Ifalukella yanii*, new species.

Ifalukella yanii, new species

PLATE 3,*a–c*

DESCRIPTION: Scrubby little colonies reaching a height of 15 cm. but averaging only 8–10 cm. Terminal branchlets up to 10 mm. in length, very slender, 0.25–0.30 mm. in diameter, acutely pointed (the apex of the twig shown in plate 3,*a* is atypical). Polyps small, fully retractile into low verrucae about 0.1 mm. in height, arranged in loose, irregular spiral rows. Coenenchyme thin; endoderm packed with zooxanthellae. Spicules in the form of oval rods and disks up to 0.035 mm. in length, very scarce (pl. 3,*b*).

HOLOTYPE: USNM 50142. Ifaluk Atoll, central Caroline Islands: seaward reef beyond breaker-line in 15–20 feet of water. Collected Oct. 8, 1953, by Yaniseiman, schoolteacher of Ifaluk, able interpreter and aide to the Ifaluk Atoll Survey team of the Pacific Science Board.

REMARKS: The genus *Ifalukella* is apparently related to *Plumigorgia* Nutting, which differs in its regular, pinnate plan of branching and (in all specimens seen thus far) weaker development of the base of attachment. Nutting placed his genus in the family Gorgonellidae (now Ellisellidae) and was followed by Stiasny, 1940. *Plumigorgia*, like *Ifalukella*, shows no trace of the radial orientation of axis calcification which is characteristic of the Ellisellidae, and can hardly be assigned to that family. Because of this fact, as well as the similarity of their spicules, it is clear that *Plumigorgia* should be reassigned to the Ifalukellidae.

Genus *Plumigorgia* Nutting, 1910

Plumigorgia hydroides Nutting

PLATE 3,*f*,*g*

Plumigorgia hydroides Nutting, 1910b, p. 32, pl. 9, figs. 3, 3a, pl. 11, fig. 4 (Pearl Bank, Sulu Archipelago; Biaru Island, northern Celebes).—Stiasny, 1940, p. 248, fig. 0, pl. 11, figs. 22, 23 (Binongko, Toekang Besi Islands).

In this species the calyces are biserial along the branches and twigs (pl. 3,*f*). The photographs published by Nutting and by Stiasny give a good idea of the general appearance of the colonies. The spicules are rather thin and scale-like, and their median constriction is slight (pl. 3,*g*).

The U. S. Fish Commission steamer *Albatross* dredged typical specimens at Station 5321, off Ibugos Island in the China Sea, in 26 fathoms, Nov. 9, 1908.

Plumigorgia wellsi, new species

Plate 3,*d*,*e*

DESCRIPTION: Colony about 22 cm. in height, flexible, regularly pinnately branched. Terminal twigs slender, about 0.5 mm. in diameter. Polyps on all sides, retractile within low verrucae. The spicules are characteristically small, strongly constricted rodlets (pl. 3,*e*) measuring 0.045–0.065 mm. in length; some are so constricted as to suggest a pair of tangent disks. Spicules of the verrucae sometimes in eight interseptal bands, sometimes not clearly so. Tentacles unarmed. On the branchlets there are small areas free of spicules, suggesting the presence of siphonozooids, but histological confirmation of these structures has not yet been made.

HOLOTYPE: USNM 49798. Arno Atoll, Marshall Islands, from coral knoll in southeast corner of lagoon, 10–18 fathoms. Collected July 31, 1950, by John W. Wells, Arno Atoll Survey team, Pacific Science Board.

REMARKS: *Plumigorgia wellsi* is a species larger and stouter than *P. hydroides*, from which it differs further in the general distribution of autozooids and in the shape of its spicules.

Family ELLISELLIDAE Gray, 1859

=Elliselladae Gray; Gorgonellidae Auctt.

NOMENCLATURE: The nomenclature of the genera usually called *Gorgonella* Valenciennes and *Scirpearia* Cuvier is rather tangled. The type species of the former appears to be *Gorgonia sarmentosa* Esper (Nutting, 1910b, p. 7; Verrill, 1912, p. 390; also it is clear that Gray in 1859 considered this species to be the type, but he did not clearly designate), which is a gorgoniid and not a gorgonellid in the usual sense. The name *Gorgonella* therefore is not available for the genus to which it is usually applied, and the next available name must be employed. This is *Verrucella* Milne Edwards and Haime, 1857 (type species: *Gorgonia flexuosa* Lamarck, 1816=*Gorgonia umbraculum* Ellis and Solander, 1786=*Verrucella umbraculum*, here designated).

Scirpearia has long been a subject of debate and should almost certainly apply to a pennatulid rather than to a gorgonacean. It probably will never be known exactly what *Scirpearia* Cuvier is. The first subsequent generic name available for a member of this genus as commonly defined is *Ellisella* Gray, 1858 (type species: *Gorgonia elongata* Pallas, 1766=*Ellisella elongata;* by subsequent designation, Nutting, 1910b, p. 31). The family name established by Gray will replace the nominal family Gorgonellidae Valenciennes.

Structure of the colonial axis: In 1865 A. von Kölliker described certain structural features of gorgonacean axes that seem worthy of closer study. He noted that the axis of gorgonellids (now ellisellids), with the exception of *Junceella*, showed a distinct radial pattern in cross section. The thin sections prepared in the course of the present study confirm Kölliker's observations and demonstrate the occurrence of the radial pattern of calcification in *Junceella* also, thus making it universally characteristic of the family Ellisellidae. Moreover, it was observed that the axis structure of this family is similar to that of the Isididae, which is also radial, but distinctly different from that of the Chrysogorgiidae, Primnoidae, and Ifalukellidae, which are never so. Thus, in respect to axial structure, the former two families have more in common with the pennatulids than with other gorgonacean families.

When transverse, longitudinal, and tangential thin sections are examined by polarized light it can be seen that although the calcareous units (sclerodermites) of the axis are built up in layers concentric with the axis core, they are arranged in a distinctly radial fashion and grouped in irregular, interlocking rays or sectors whose component calcareous fibers are of different optical orientation. Representatives of all genera were examined and found to have similar structure. The so-called chrysogorgiid genus *Riisea*, which has spicules like those of the ellisellid genus *Nicella*, was examined and found to have axis structure (pl. 5,*a*,*b*) like *Nicella* and unlike Chrysogorgiidae (pl. 4,*c*,*d*). *Riisea* is thus to be reckoned among the Ellisellidae where Kölliker placed it, close to *Nicella*, and not among the Chrysogorgiidae where Wright and Studer, Versluys, and all subsequent modern authors have arranged it.

The radial orientation of the calcareous material in the ellisellid axis differs markedly from the situation seen in the families Primnoidae and Chrysogorgiidae, in which the calcareous material permeates imbricating, concentric lamellae and there is no evidence of radial arrangement. The accompanying photomicrographs of axis thin sections permit comparison of calcification as seen in Ellisellidae (pl. 5) with that of Chrysogorgiidae (pl. 4,*c*,*d*) and Primnoidae (pl. 4,*e*,*f*).

Family Isididae Lamouroux, 1812

Structure of the colonial axis: Although the axes of Isididae differ widely from those of Ellisellidae in their articulation of alternating horny and calcareous segments, they are similar in having the calcareous material radially oriented.

In *Isis hippuris* Linnaeus, the calcareous fibers are united into bundles, much like the sclerodermites of stony corals, radiating outward from the central core (pl. 6,*a*,*b*). The fibers diverge outward from the center of the sclerodermites (pl. 6,*c*,*d*) in much the same way the fibers of the coenenchymal spicules diverge outward from the spicule core, and I suggest that the sclerodermites of *Isis* are actually highly modified spicules. This suggestion is corroborated by a comparison of the axis of *Isis* with that of *Parisis*, an undisputed scleraxonian with spicules in the horny nodes. In that genus we see similar but shorter sclerodermites radiating out from the axis core; the secondary thickening consists of sclerodermites oriented longitudinally (pl. 4,*b*) and continuous with the spicules imbedded in the horny nodes (pl. 4,*a*).

In the translucent, glassy axis of *Primnoisis* (pl. 6,*e*) the radial sclerodermites extend from the axis core to its surface as more or less regular prismatic rays, just as in the Ellisellidae. In *Acanella* and *Keratoisis* the orientation of calcareous elements is clearly radial but individual sclerodermites are obscured.

Order PENNATULACEA Verrill, 1865

Structure of the colonial axis: Since nothing of pennatulids but the axial rod is ordinarily fossilized, intrinsic features of these structures must be sought for generic separation of fossil material. External form and sculpture are too variable to be of use, so internal structure and system of calcification is the last resort. Thin sections of the axis show that its pattern of calcification (pl. 7) is strongly suggestive of the Ellisellidae (as Kölliker pointed out) and Isididae: Longer or shorter, continuous or interrupted prismatic or irregularly columnar sclerodermites radiate outward from a distinct core composed of granular calcareous material intermixed with abundant organic matter. Samplings were made of genera in various pennatulacean families and were found all to agree in basic pattern. Differences in detail were noted among the various families and genera, indicating that it may someday be possible to place any pennatulid axis in its proper genus without recourse to gross colonial morphology.

The genus *Stylatula* shows very long columns of irregular circumference radiating virtually without interruption from the core of the axis to its outer surface (pl. 7, *a–c*, *e*). The fibers of the sclerodermites converge instead of diverging as they do in the Isididae. A system of minute radial tubules extending from core to surface (the "uncalcified radial strands" of Kölliker) can be distinguished (pl. 8,*a*). Although these tubules seem to have contained organic matter, I do not believe they are uncalcified strands, but actually canaliculae, a clue to the function of which may be found in a statement by Marshall and Marshall (1882, p. 5). In their discussion of the axis of *Funiculina* these authors say: "As the stem grows in thickness by the addition of successive lamellae on its exterior, and as the proportions between the hard outer rind and the soft core are much the same in both young and old specimens, it is clear that the process of deposition of calcareous lamellae on the outside must be accompanied by absorption of the calcareous matter previously deposited in the more central portion." For such a process to take place, communication from the core to the outside would be necessary, and in the system of tubules we may have that means of communication. The organic material that they contain may be the remains of scleroclastic cells which would probably be necessary for removal of calcareous material from the core of the axis.

Four species of *Stylatula* (including *S. elongata,* the type species) from widely separated localities were found to have practically identical structure.

The closely related genus *Virgularia,* on the other hand, has the sclerodermites short and much interrupted (pl. 7,*f*). In other genera, the radial units resemble more closely those of ellisellids, or show various modifications.

In an effort to determine the systematic position of *Graphularia,* a section was examined and found to conform in most respects with the structure of *Stylatula.* The core (blackened perhaps by carbonization of the organic matter) is wider in proportion to the cortical zone, and the radial columns are shorter and thicker (pl. 7,*d*). The tubules seen in Recent *Stylatula* are present also in *Graphularia,* and contain a black material that may be carbonized organic substances. It is evident that *Graphularia* is very close to *Stylatula* and should be removed from the Pennatulidae, in which the axis structure is clearly different in detail.

When the axis structure of all modern pennatulids has been studied, it may be possible to reinterpret the fossil genera and to assign them to their proper positions in the biological system.

SUMMARY OF AXIS STRUCTURES

Among the gorgonians with calcified axes, the calcareous material is oriented in two different ways. In the families Chrysogorgiidae, Ifalukellidae, and Primnoidae it permeates the scale-like or lamellar horny sclerodermites, which are concentrically deposited and tightly imbricated in each layer. No trace of radial orientation can be seen either in transverse or in longitudinal sections. In the Ellisellidae (pl. 8,*b*) and Isididae, the former with a continuous and the latter with an articulated axis, the calcareous fibers are radially oriented and grouped to form sclerodermites more or less suggestive of those seen in the massive coralla of the Scleractinia. The sclerodermites forming the calcareous axis internodes of the scleraxonian *Parisis* (pl. 8,*e*) are radially arranged immediately adjacent to the axis core and assume a longitudinal direction (but still in radial rows corresponding to the surface grooves) in the secondary thickening of the axis. They are continuous with the spicules of the horny nodes and are nothing more than modified spicules. The axis of *Isis* (pl. 8,*c–d*) differs only in the predominantly radial arrangement of sclerodermites, which are not essentially different from those of *Parisis*, and in the absence of spicules from the horny nodes. The axis structure of the Pennatulacea corresponds very closely with that of the Ellisellidae and Isididae.

In those forms with radial orientation of the calcareous fibers the axis substance is concentrically stratified and it therefore is apparently deposited by the cells of a continuous tissue, the axis epithelium, just as it is in other gorgonaceans. It seems necessary to suppose that groups of adjacent axoblasts in the axis epithelium are functioning as units for longer or shorter periods, depositing the radially oriented sclerodermites. The relationship of the horny material to the calcareous substance has yet to be thoroughly investigated, but it appears that any scleroblast has the ability to produce both substances.

PHYLOGENETIC IMPLICATIONS

Assuming that the sclerodermites of the Isididae are structurally the same as those of the Parisididae, and from all indications such is indeed the case, the articulate Holaxonia and Scleraxonia are phylogenetically close rather than far separated as end-points of different lines of evolution. The isidids could have arisen from articulate scleraxonians by elimination of the spicules from the horny axis segments. Extending this theory, it is possible that the ellisellids arose from ancestral isidids by elimination of the horny nodes. That such an evolutionary trend actually existed is intimated by *Moltkia*, an articulated form (Isididae? I have not examined its axis structure) from the Danian formations of northern Europe, in which the horny nodes are overgrown by the calcareous internodes and the axis articulation is consequently obliterated.

The phylogenetic significance of the similarity of axis structure of the Pennatulacea and the ellisellid gorgonians remains to be determined. It seems to speak as strongly for the origin of the Pennatulacea from gorgonacean ancestors as other features do for its descent from alcyonacean stock. However, the Pennatulacea seems to be a very old group, antedating any known Gorgonacea.

References

D'Achiardi, Antonio

1868. Studio compartivo fra i coralli dei terreni terziari del Piemonte e dell' Alpi Venete. Ann. Univ. Toscane, vol. 10; pp. 73–144, pls. 1, 2.

Duncan, P. Martin

1880. A monograph of the fossil corals and Alcyonaria of Sind. Mem. Geol. Surv. India, Palaeontologia Indica, ser. 14, vol. 1, No. 1, pp. 1–110, pls. 1–28.

Ehrenberg, Christian Gottfried

1834. Beiträge zur physiologischen Kenntniss der Corallenthiere im Allgemeinen, und besonders des rothen Meeres, nebst einem Versuche zur physiologischen Systematik derselben. Abhandl. königl. [preussischen] Akad. Wiss. Berlin (1832), Theil 1, pp. 225–380.

Gray, John Edward

1869. Notes on the fleshy alcyonoid corals (*Alcyonium*, Linn., or *Zoophytaria carnosa*). Ann. Mag. Nat. Hist., ser. 4, vol. 3, pp. 117–131.

Kölliker, Albert

1865. Icones histiologicae oder Atlas der vergleichenden Gewebelehre. II. Der feinere Bau der höheren Thiere. Erstes Heft. Die Bindesubstanz der Coelenteraten, pp. 87–181, figs. 16–28; figs. A–B; pls. 10–19.

Kükenthal, Willy

1917. System und Stammesgeschichte der Plexauridae. Zool. Anz., vol. 48, No. 11, pp. 330–336.

Lamarck, J. B. P. A.

1816. Histoire naturelle des animaux sans vertèbres, vol. 2, iv+568 pp.

Lamouroux, J. V. F.

1816. Histoire des polypiers coralligènes flexibles, vulgairement nommés zoophytes, lxxxiv+560, pls. 1–19.

Macfadyen, Laura M. I.

1936. Alcyonaria (Stolonifera, Alcyonacea, Telestacea and Gorgonacea). Great Barrier Reef Expedition Sci. Rep., vol. 5, No. 2, pp. 19–72, figs. 1–11, pls. 1–5.

Marshall, A. Milnes, and Marshall, William P.
1882. Report on the Pennatulida collected in the Oban dredging excursion of the Birmingham Natural History and Microscopical Society, July 1881, pp. 1–77[81], pls. 1–4.

Nutting, Charles Cleveland
1910a. The Gorgonacea of the *Siboga* Expedition. IV. The Plexauridae. *Siboga* Exped. Monogr. 13b [1], pp. 1–20, pls. 1–4.
1910b. Ibid. VI. The Gorgonellidae. *Siboga* Exped. Monogr. 13b [3], 1–39, pls. 1–11.
1911. Ibid. VIII. The Scleraxonia. *Siboga* Exped. Monogr. 13b [5], 1–62, pls. 1–12.

Reuss, A. E.
1869. Paläontologische Studien über die älteren Tertiärschichten der Alpen. II. Die fossilen Anthozoen und Bryozoen der Schichtengruppe von Crosara. Denkschr. kaiserl. Akad. Wiss. Wien, math.-naturw. Classe, vol. 29, pp. 215–298, pls. 17–36.

Stiasny, Gustav
1940. Die Gorgonarien-Sammlung der *Snellius*-Expedition. Temminckia, vol. 5, pp. 191–256, figs. a–o, pls. 6–14.

Studer, Théophile
1878. Uebersicht der Anthozoa Alcyonaria, welche während der Reise S. M. S. *Gazelle* um die Erde gesammelt wurden. Monatsb. preuss. Akad. Wiss. Berlin, Sept.–Oct. 1878, pp. 632–688, pls. 1–5.

Tixier-Durivault, Andrée
1948. Revision de la famille des Alcyoniidae. Mém. Mus. Hist. Nat. Paris, new ser., vol. 23, No. 1, pp. 1–255, figs. 1–248.

Utinomi, Huzio
1953. Alcyonaria. Invertebrate fauna of the intertidal zone of the Tokara Islands, VI. Publ. Seto Marine Biol. Lab. vol. 3, No. 2, pp. 149–160, figs. 1–5, pl. 8.

Verrill, Addison Emery
1912. The gorgonians of the Brazilian coast. Journ. Acad. Nat. Sci. Philadelphia, ser. 2, vol. 15, pp. 373–404, pls. 29–35.

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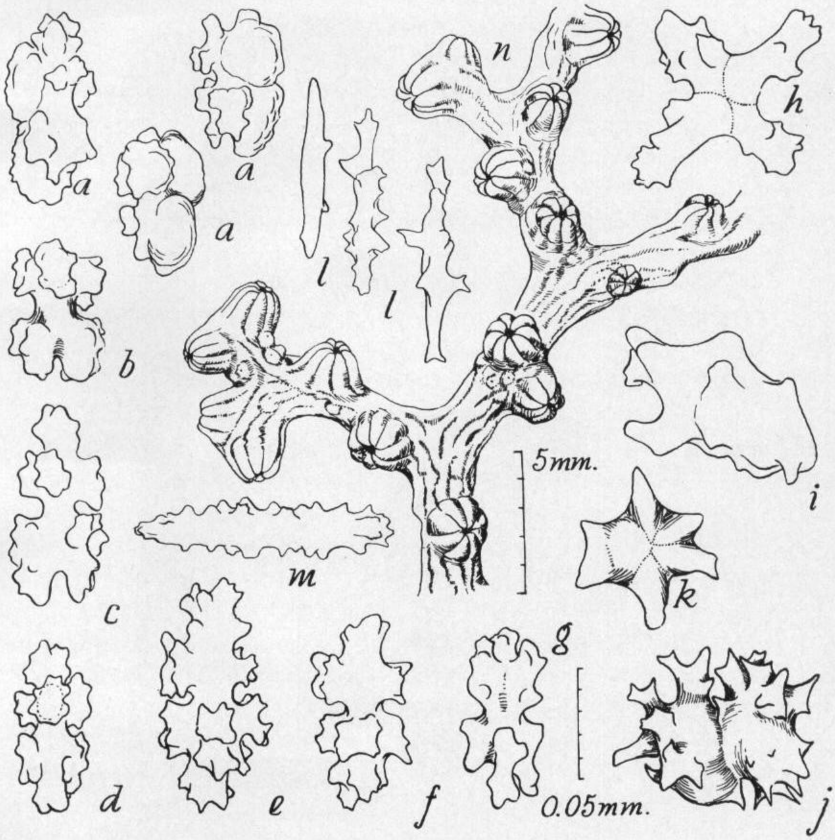
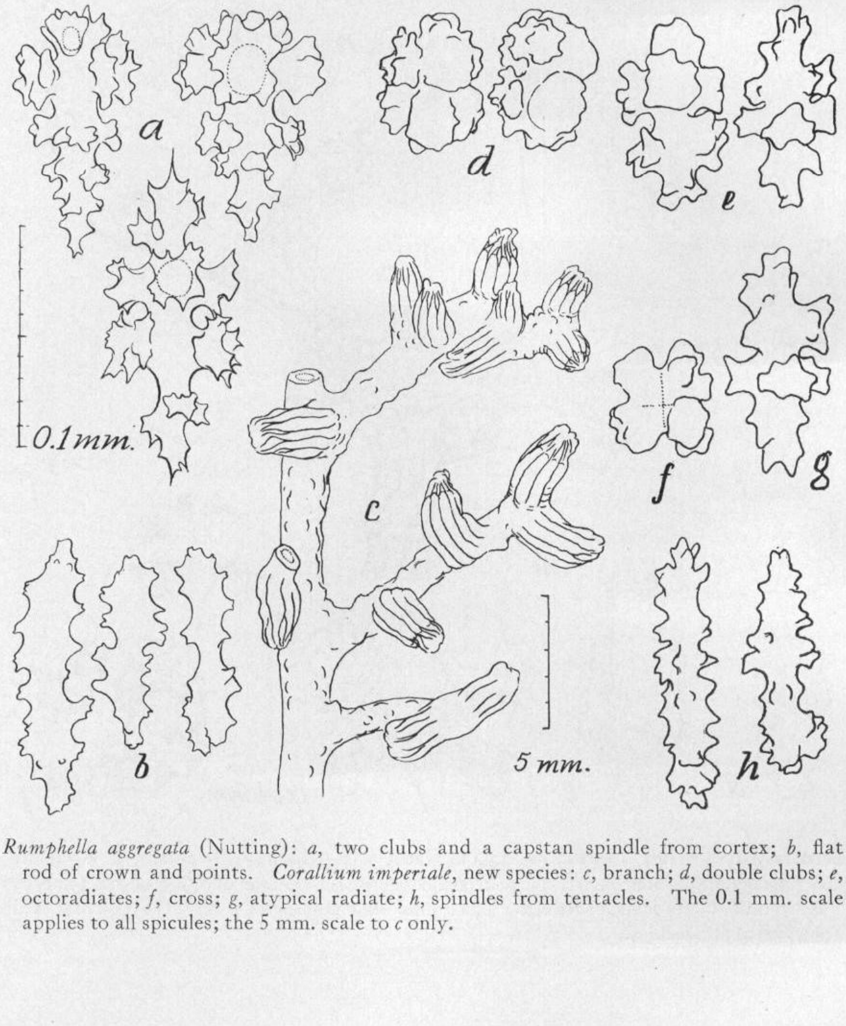
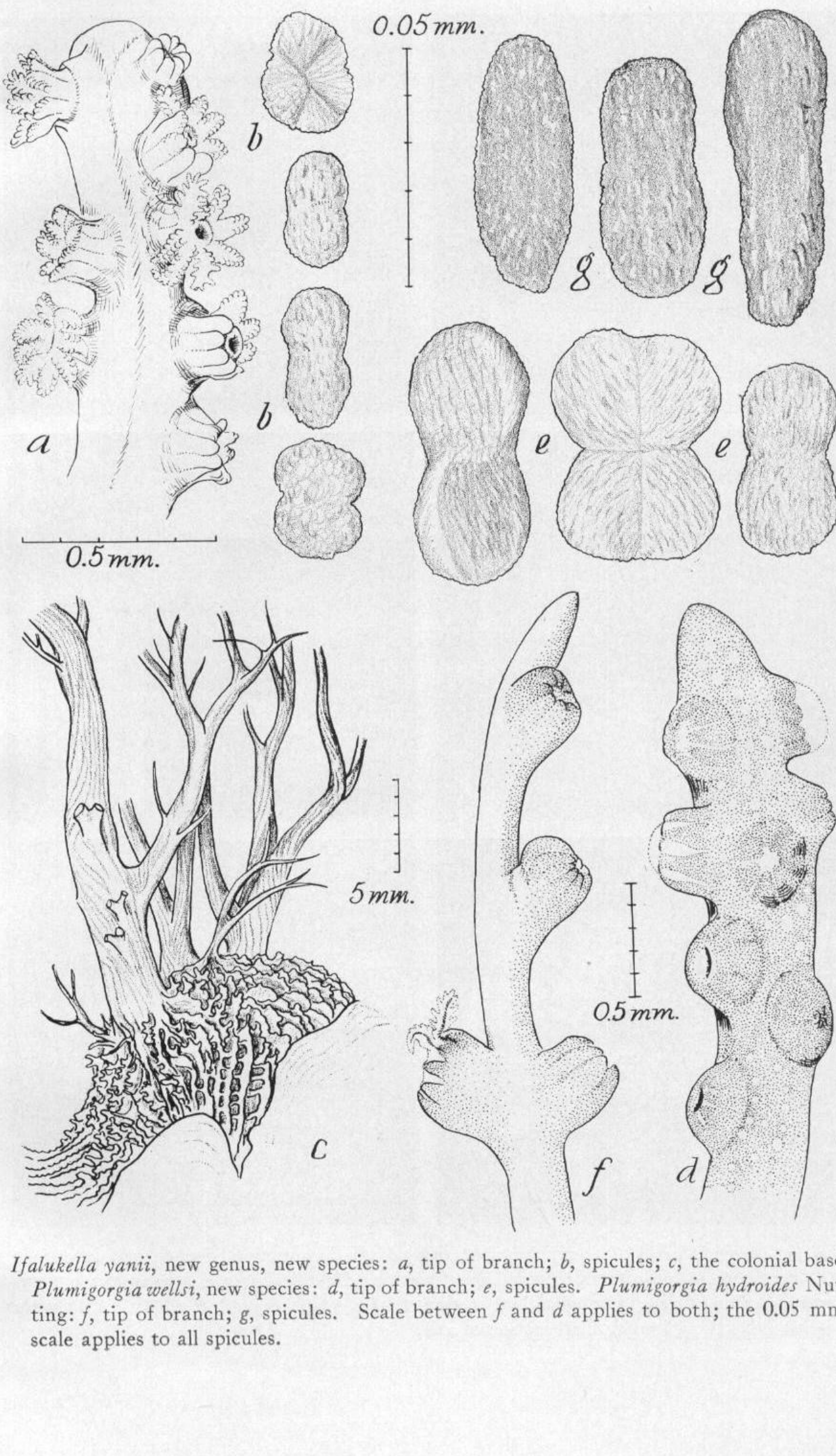
PLATES 1–8



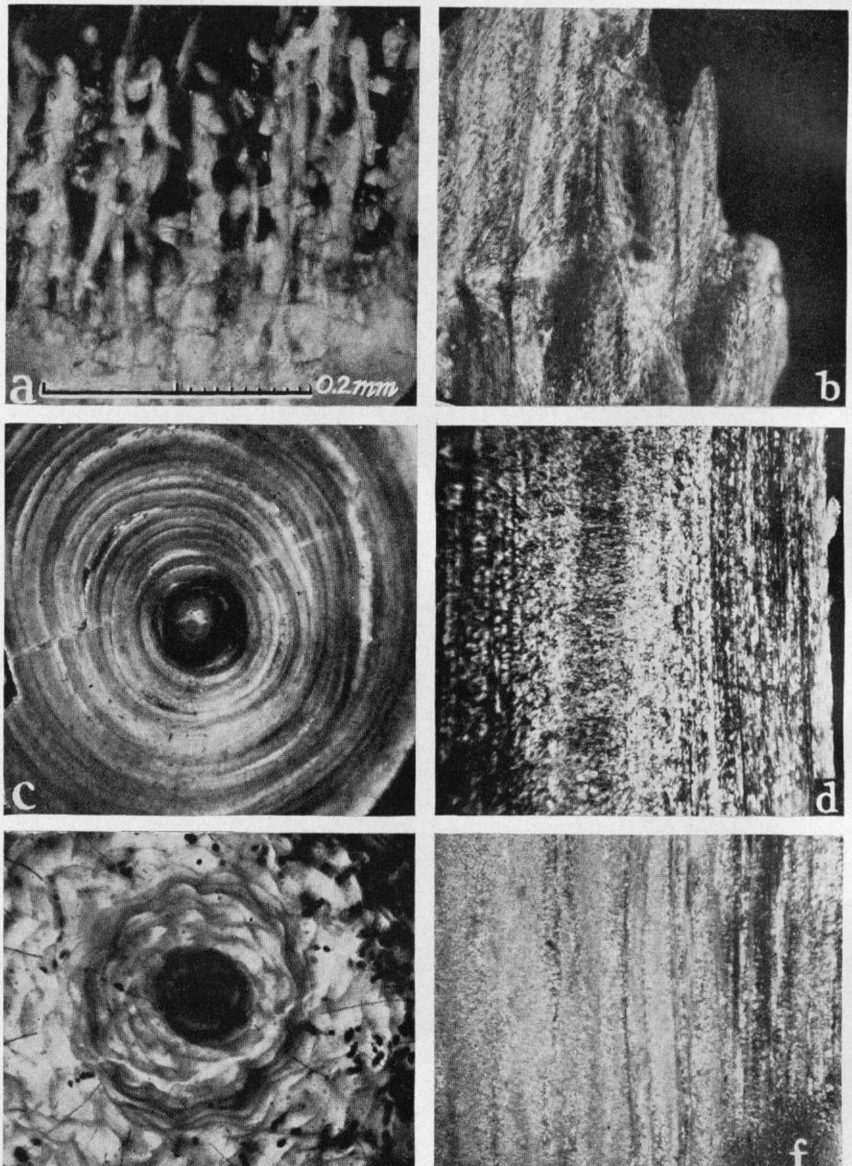
Corallium ducale, new species: *a*, double clubs; *b*, 6-radiate; *c*, 7-radiate; *d*, 8-radiate; *e–g*, irregular radiates; *h*, cross; *i–k*, irregular sclerites; *l*, spindles of oral disk and pharynx; *m*, spindle of tentacles; *n*, branch. The 5 mm. scale applies to *n* only; the 0.05 mm. scale applies to all spicules.



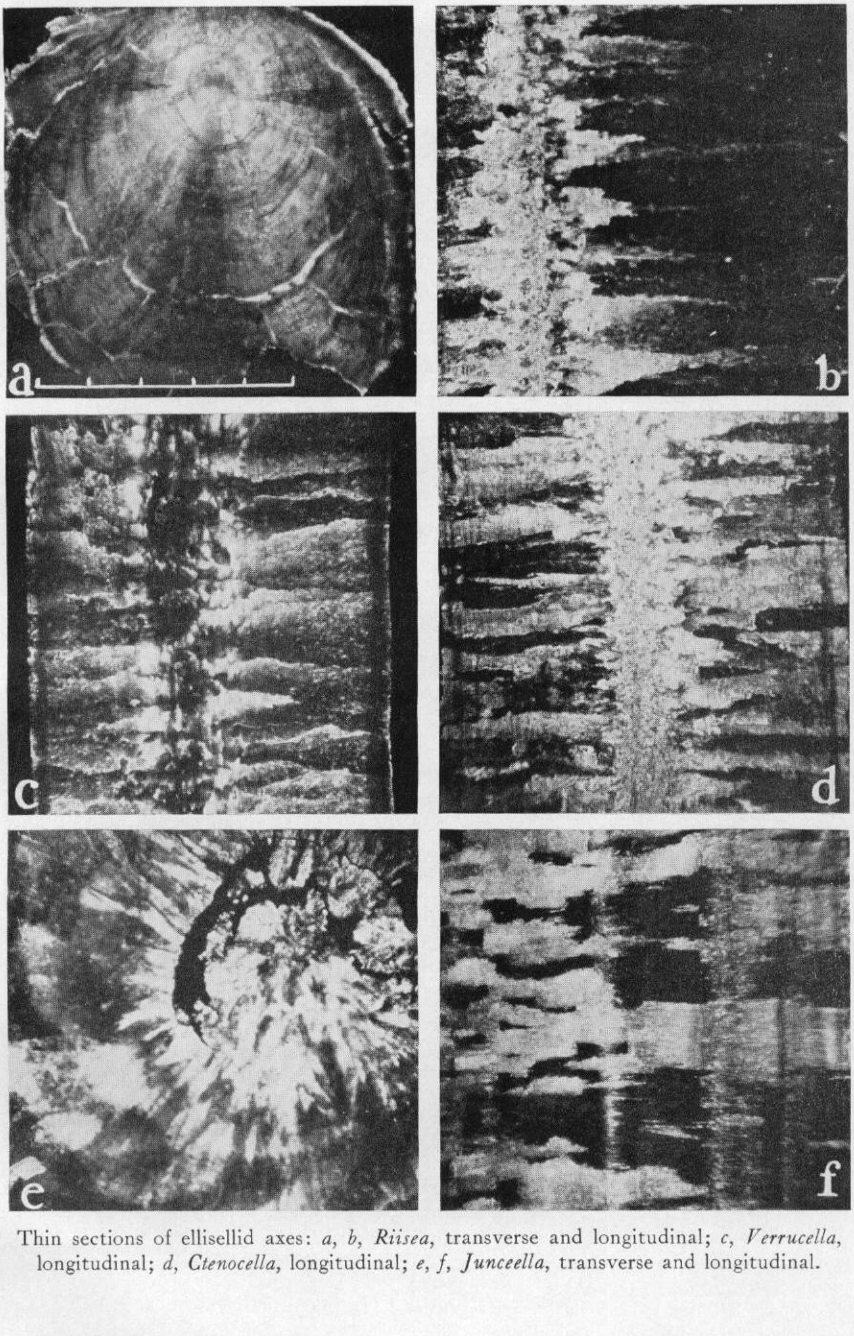
Rumphella aggregata (Nutting): *a*, two clubs and a capstan spindle from cortex; *b*, flat rod of crown and points. *Corallium imperiale*, new species: *c*, branch; *d*, double clubs; *e*, octoradiates; *f*, cross; *g*, atypical radiate; *h*, spindles from tentacles. The 0.1 mm. scale applies to all spicules; the 5 mm. scale to *c* only.



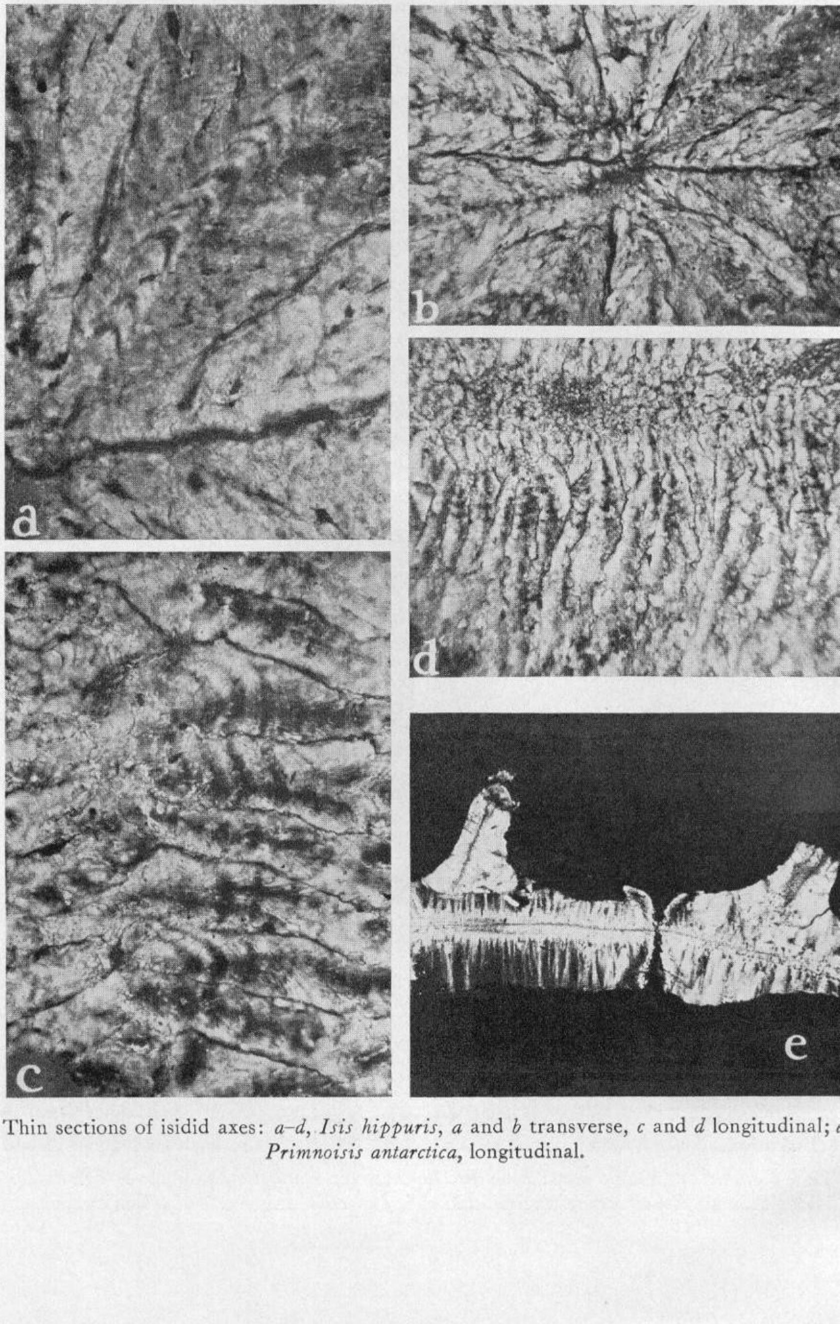
Ifalukella yanii, new genus, new species: *a*, tip of branch; *b*, spicules; *c*, the colonial base. *Plumigorgia wellsi*, new species: *d*, tip of branch; *e*, spicules. *Plumigorgia hydroides* Nutting: *f*, tip of branch; *g*, spicules. Scale between *f* and *d* applies to both; the 0.05 mm. scale applies to all spicules.



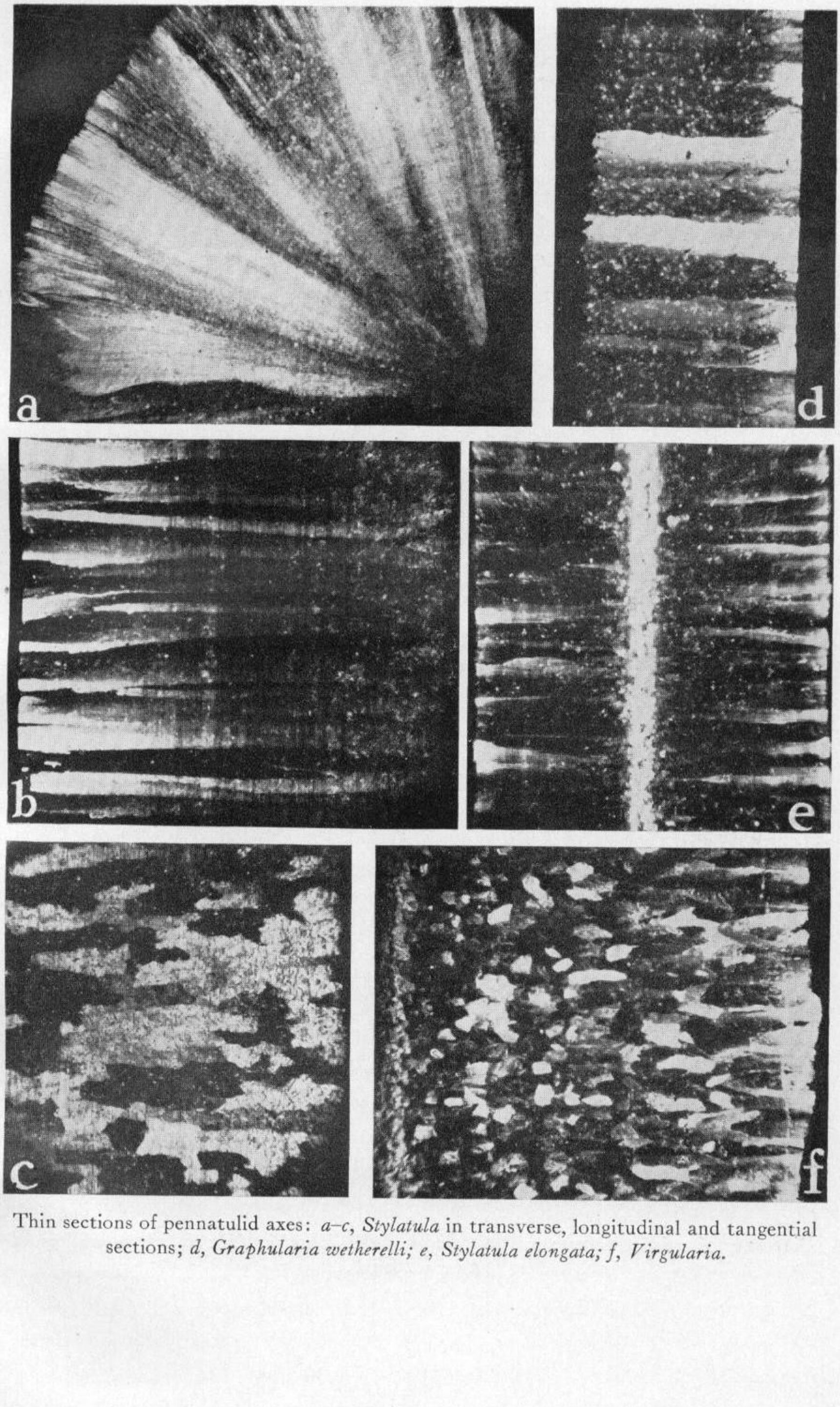
Parisis fruticosa Verrill: *a*, longitudinal section of axis at junction of node and internode; *b*, sclerodermites of internode, longitudinal section. *Metallogorgia melanotrichos*: *c*, transverse section of axis; *d*, longitudinal section of axis. *Caligorgia kinoshitae*: *e*, transverse section of axis; *f*, longitudinal section of axis.



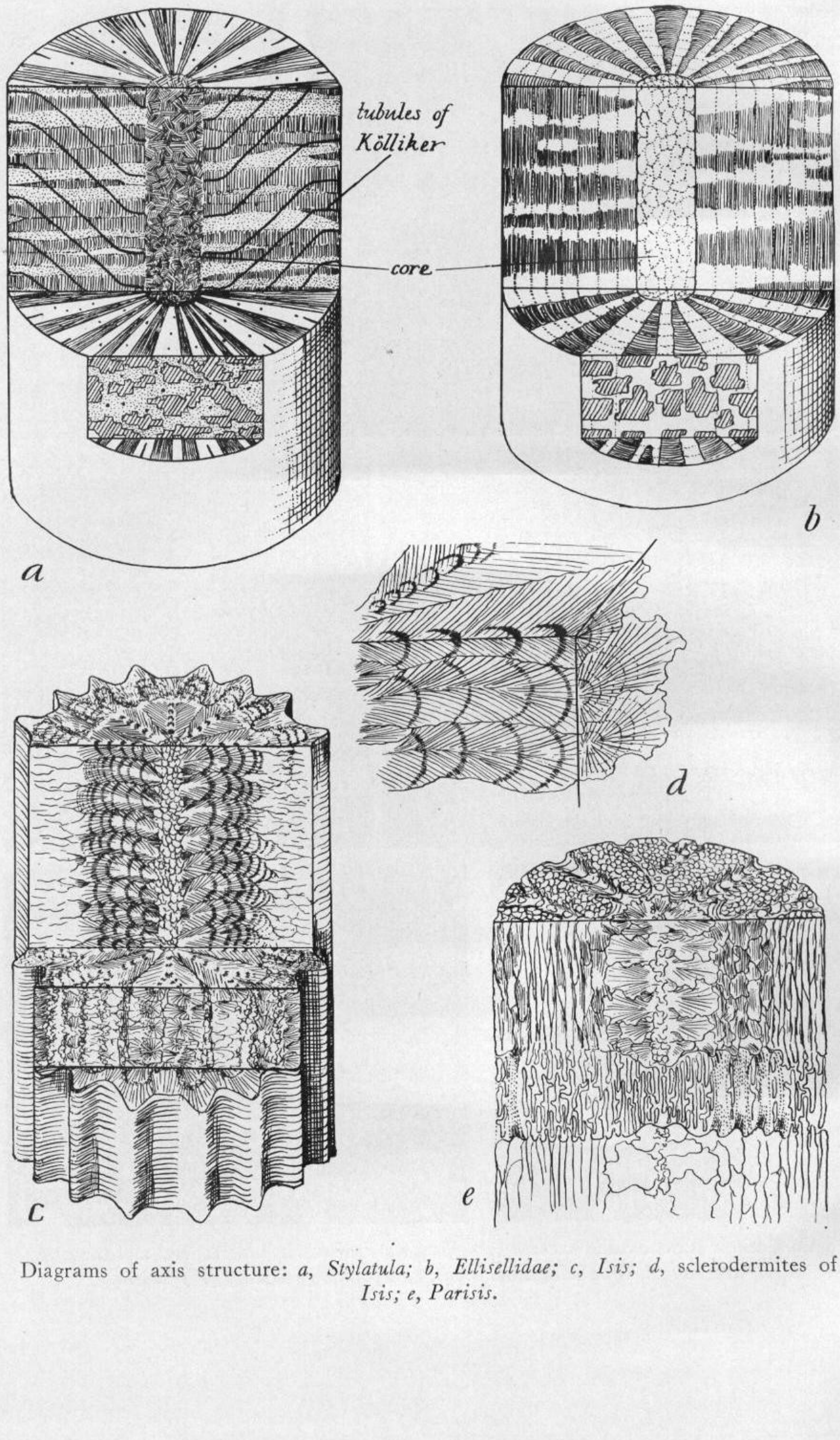
Thin sections of ellisellid axes: *a, b, Riisea*, transverse and longitudinal; *c, Verrucella*, longitudinal; *d, Ctenocella*, longitudinal; *e, f, Junceella*, transverse and longitudinal.



Thin sections of isidid axes: *a–d*, *Isis hippuris*, *a* and *b* transverse, *c* and *d* longitudinal; *e*, *Primnoisis antarctica*, longitudinal.



Thin sections of pennatulid axes: *a–c*, *Stylatula* in transverse, longitudinal and tangential sections; *d*, *Graphularia wetherelli*; *e*, *Stylatula elongata*; *f*, *Virgularia*.



Diagrams of axis structure: *a*, *Stylatula;* *b*, *Ellisellidae;* *c*, *Isis;* *d*, sclerodermites of *Isis;* *e*, *Parisis.*