PROCEEDINGS
OF THE
CALIFORNIA ACADEMY OF SCIENCES

Vol. 49, No. 12, pp. 423–437, 10 figs. April 29, 1997

A NEW GENUS AND SPECIES OF NEPHTHEID SOFT CORAL (OCTOCORALLIA: ALCYONACEA) FROM THE WESTERN PACIFIC OCEAN, AND A DISCUSSION OF CONVERGENCE WITH SEVERAL DEEP-SEA BENTHIC ORGANISMS

By

Gary C. Williams
Department of Invertebrate Zoology, California Academy of Sciences
San Francisco, California 94118.

A remarkable new genus and species of soft coral, recently discovered by SCUBA, is described from Okinawa. The new taxon is assignable to the family Nephtheidae on the basis of having a distinct stalk, multiply-branched polyparium, monomorphic polyps without calyces, and densely-spiculated stalk, and it shows some resemblances to species of two nephtheid genera—*Umbellulifera* and *Coronephthya*. It differs from all previously described nephtheid taxa by the presence of a very slender and elongate stalk together with a relatively small and sparsely branched divaricate polyparium in which the primary branches share a common point of origin, relatively few polyps sparsely distributed and not grouped into catkins, and the dense occurrence of only spindles and needles in the stalk. The unusual growth form appears to show convergence with deep-sea pennatulacean octocorals of the genus *Umbellula*, as well as species of the bryozoan genus *Kinetoskias* and the crinoid genus *Bathycrinus*.

Received June 14, 1996. Accepted August 29, 1996.

Several specimens of a newly discovered soft coral, representing a new genus and species, have recently been collected by biologist Robert Bolland at approximately 60 meters in depth off Okinawa, Ryukyu Islands, Japan. The new taxon exhibits a convergence in general growth form to species of the pennatulacean genus *Umbellula* (Cuvier, 1798), the bryozoan genus *Kinetoskias* Danielssen, 1868, and the crinoid genus *Bathycrinus* Thomson, 1872. The new soft coral is here allocated to the family Nephtheidae and shows some similarities to the nephtheid genera *Umbellulifera* Thomson and Dean, 1936, and *Coronephthya* Utinomi, 1966.

Imahara (1991) reported on the Octocorallia of the Ryukyu Islands, which included 47 species.

SYSTEMATIC ACCOUNT

Family **Nephtheidae** Gray, 1862

Mostly bushy or arborescent soft corals, upright, with a distinct stalk. Polyparium usually multiply-branched. Polyps monomorphic, well spaced or more often arranged in clusters or catkins, along the surface of branches and/or at the tips of ultimate branches. Sclerites are often densely distributed, mainly spindles, clubs, and radiates. A family of approximately eighteen genera of worldwide distribution; currently in need of revision.

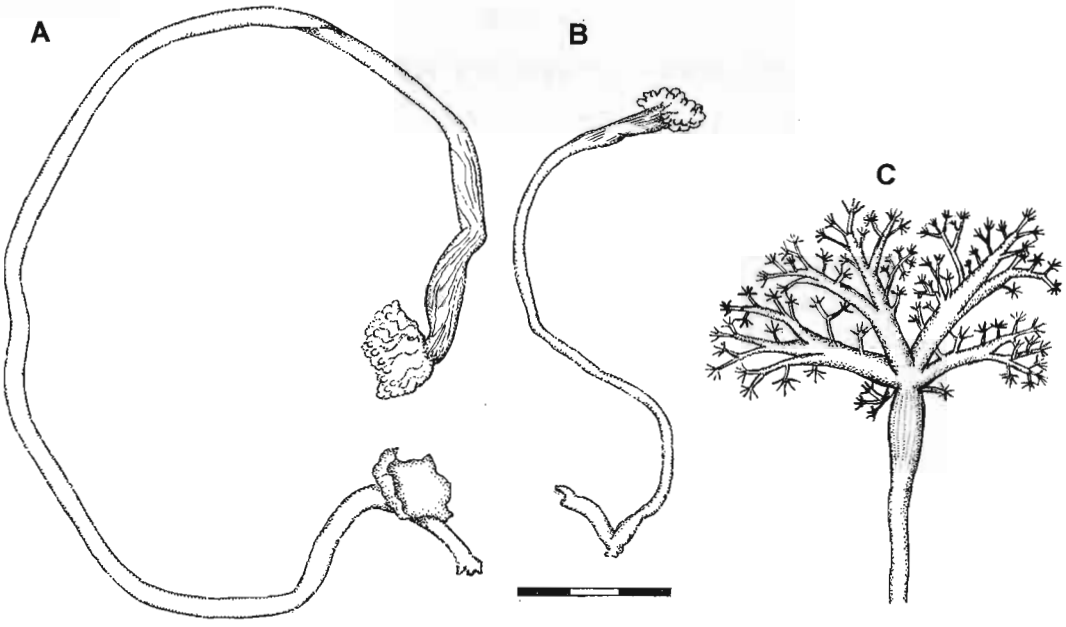


FIGURE 1. *Pacifiphyton bollandi* gen. and sp. nov. A. Holotype. B. Paratype (*CASIZ* #106206). C. Branching pattern of a fully extended polyparium from specimen photographed at 54.8 m depth by R. F. Bolland. Scale bar for A, B, and C = 30 mm.

Genus **Pacifiphyton** gen. nov.

DIAGNOSIS. — Soft corals with divaricate polyparium arising from elongated stalk. Several primary branches arise from a common point of origin, each with only few secondary and tertiary branches. Polyps monomorphic, sparsely distributed on branches of polyparium, without calyces, but with weak and variable armature of sclerites, sometimes approaching weakly constructed crown and points. Stalk densely spiculated with more or less longitudinally disposed spindles. Sclerites of stalk, polyparium, and polyp walls are spindles with highly variable tuberculation.

TYPE SPECIES. — *Pacifiphtyon bollandi* sp. nov.

ETYMOLOGY. — The new generic name is derived from 'Pacific' (Pacific Ocean) and the Greek 'phyton' (a creature, either plant or animal).

Pacifiphyton bollandi sp. nov.
Figs. 1–10

Nephtheid sp. (Slender-Stalked Soft Coral): Gosliner, Behrens, and Williams, 1996:44, pl. 113.

HOLOTYPE. — *CASIZ #106205*; RFB #3357-B; one whole specimen; collected by Robert Bolland; 12 February 1995; Seragaki, Okinawa, Japan; 68.6 m in depth.

PARATYPES. — *CASIZ #106206*; one whole specimen; same data as holotype. *CASIZ #106207*; four specimens in several pieces, attached to coral rubble; same data as holotype.

OTHER MATERIAL EXAMINED. — *CASIZ #106208*; RFB #3406-D; two specimens in three pieces; collected by Robert Bolland; 6 May 1995; Seragaki, Okinawa, Japan; 62.5 m in depth. *CASIZ #106209*; RFB #3426-H; three specimens in four pieces, attached to coral rubble; collected by Robert Bolland; 28 May 1995; Seragaki, Okinawa, Japan; 62.5 m in depth. *CASIZ #102890*; RFB #3331-A; one partial specimen; collected by Robert Bolland; 10 December 1994; Seragaki, Okinawa, Japan; 57.9 m in depth. *CASIZ #102891*; RFB #3330-B; two specimens in three pieces; collected by Robert Bolland; 9 December 1994; Seragaki, Okinawa, Japan; 57.9 m in depth. *CASIZ #102892*; RFB #3332; one whole specimen attached to coral rubble; collected by Robert Bolland; 11 December 1994; Seragaki, Okinawa, Japan; 62.5 m in depth. *CASIZ #102893*; RFB #3336; two whole specimens attached to coral rubble; collected by Robert Bolland; 18 December 1994; Seragaki, Okinawa, Japan; 57.9 m in depth. *CASIZ #102894*; RFB

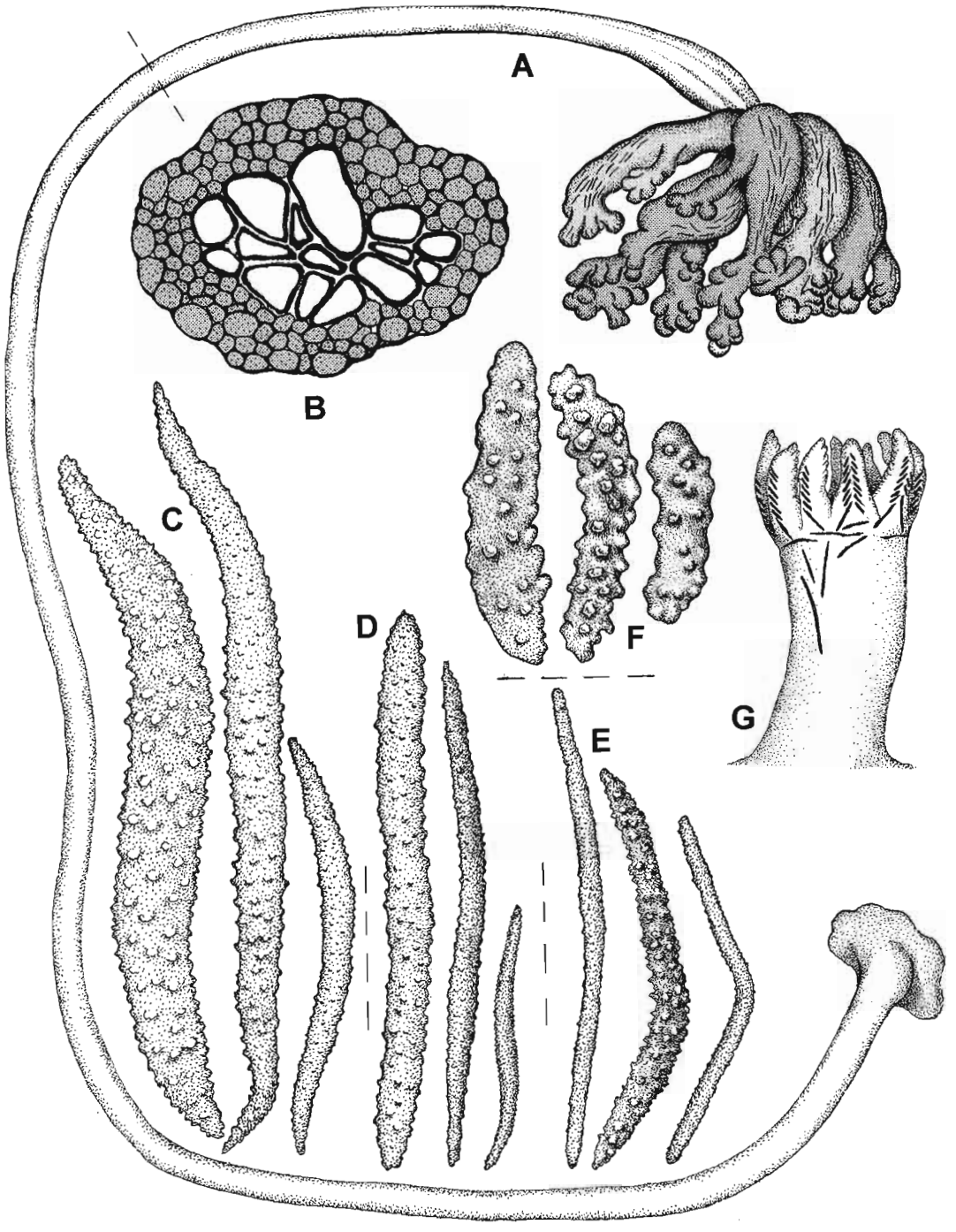


FIGURE 2. *Pacifiphyton bollandi* gen. and sp. nov. General morphology of preserved specimen *CASIZ #102894*. A. Entire specimen; total length = 305 mm. B. Transverse section at level of dashed line in A, showing central canals surrounded by densely-set sclerites; diameter of section = 3 mm. C. Sclerites from the stalk; left, 2.2 mm, center 1.65 mm, right 0.9 mm. D. Sclerites from the branches of the polyparium; left 3.5 mm, center 2.5 mm, right 1.3 mm. E. Sclerites of the polyp body wall; left 1.01 mm, center 0.57 mm, right 0.50 mm. F. Tentacle sclerites; left 0.18 mm, center 0.16 mm, right 0.11 mm. G. A single polyp, 3.2 mm in height, showing arrangement of polyp sclerites.

#3326, one specimen in two pieces; collected by Robert Bolland, 29 November 1994; Seragaki, Okinawa, Japan; 59.4 m in depth. *CASIZ #102895*; RFB #3326, two specimens in five pieces; collected by Robert Bolland; 27 November 1994; Seragaki, Okinawa, Japan; 59.4 m in depth.

In addition, twenty-nine color transparencies taken by Dr. Bolland of living specimens are cataloged in the CASIZG photo collection. Of these, ten are in situ photographs.

DIAGNOSIS. — Stalk slender and elongated. Polyparium divaricate with several primary branches emanating from a common point of origin, which is represented by the distal terminus of the stalk. Secondary and tertiary branching sparse. Polyp calyces absent. Polyps sparsely distributed on branches of polyparium, not forming catkins. Individual polyps with weakly developed armature, sometimes approaching crown and points; supporting bundles absent. Sclerites of tentacles rod-like, arranged *en chevron* along longitudinal axis of each tentacle. Branches of polyparium with or without needle-like spindles. Stalk densely spiculated with more or less longitudinally disposed needles in the swollen distal portion, and randomly disposed robust spindles in the rest of the stalk. Sclerites are tuberculate spindles throughout, some of which are needle-like.

DESCRIPTION OF THE HOLOTYPE (Figs. 1A, 4E, 6, 9).—*Stalk:* The stalk of the holotype is 306 mm in length. The spreading holdfast is ovoid in shape, 15 mm at its widest and 22 mm at its longest. The stalk varies in width from 3–4 mm (throughout most of its length) to 6–8 mm in the swollen portion just below the polyparium (Fig. 1A). The swollen portion is approximately 35 mm in length. In preservation, the entire stalk is relatively stiff and brittle.

Polyparium: The contracted polyparium is 15 mm in length by 20 mm in width, and consists of a divaricately branched arrangement at the distal end of the long, narrow stalk. The polyparium is comprised of five main branches radiating outward from the center. The main branches ramify distally to form two or three secondary branches.

Polyps: The polyps are contractile but not retractile. Calyces are absent. The polyps do not form distinct groups, clusters or catkins, but are sparsely and individually disposed on the branches. Polyps are more densely distributed in the distal portions of the polyparium and are absent from the proximal portions.

Sclerites: The sclerites from the proximal and middle portions of the stalk are predominantly robust spindles, mostly 1–2 mm in length and up to 0.3 mm in width (Fig. 6A–K), which are for the most part not disposed parallel to the axis of the stalk but are rather arranged at all angles. In contrast to this, the sclerites from the swollen distal-most region of the stalk are elongate needles, mostly 2–3.5 mm in length by 0.1 mm in width (Fig. 6L). These are arranged parallel to the axis of the stalk. Many of these needles are very narrow and sinuous with gradually tapering ends.

Sclerites of the branches of the polyparium in the holotype are apparently absent altogether.

The sclerites of the polyps are of two kinds: needles and spindles of the body wall, and rods of the tentacles. Sclerites that are mostly needle-like spindles form a relatively weak crown and points in a majority of the polyps. In addition, one or more needle-like spindles may be longitudinally disposed on the polyp wall (Fig. 4E).

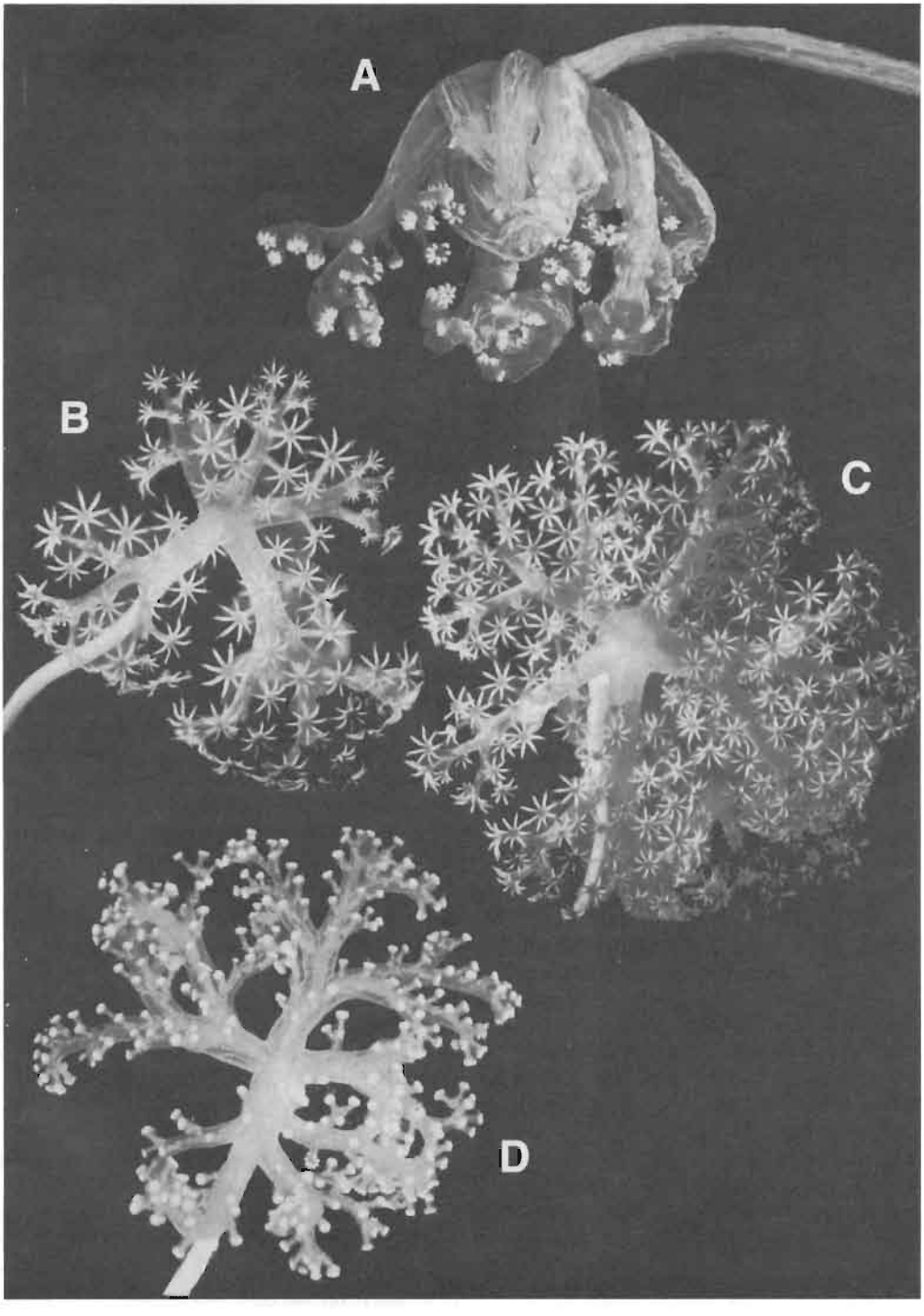
The outer surface of the tentacles is densely spiculated. The sclerites are arranged *en chevron* along most of the length of the tentacles. These sclerites are relatively robust rods with somewhat coarse tuberculation (Fig. 9A–H). They vary in length from 0.05 to 0.18 mm.

Color: The preserved holotype is cream to light tan in color, while the contracted polyps are white due to the white sclerites of the tentacles.

PHENOTYPIC VARIABILITY. — The twenty wet-preserved specimens examined range in

→

FIGURE 3. *Pacifiphyton bollandi* gen. and sp. nov. Photographs of living specimens by R. F. Bolland. A. Contracted polyparium of *CASIZ #102895*, photograph taken in aquarium; maximum dimension of polyparium shown is 44 mm. B. Photograph of a specimen with expanded polyparium and polyps taken in situ at 59 m in depth. C. Expanded polyps and polyparium of another specimen photographed in situ at 59 m in depth. D. Polyparium of a specimen with contracted polyps photographed in aquarium; maximum diameter of polyparium = 66 mm.


A
B
C
D

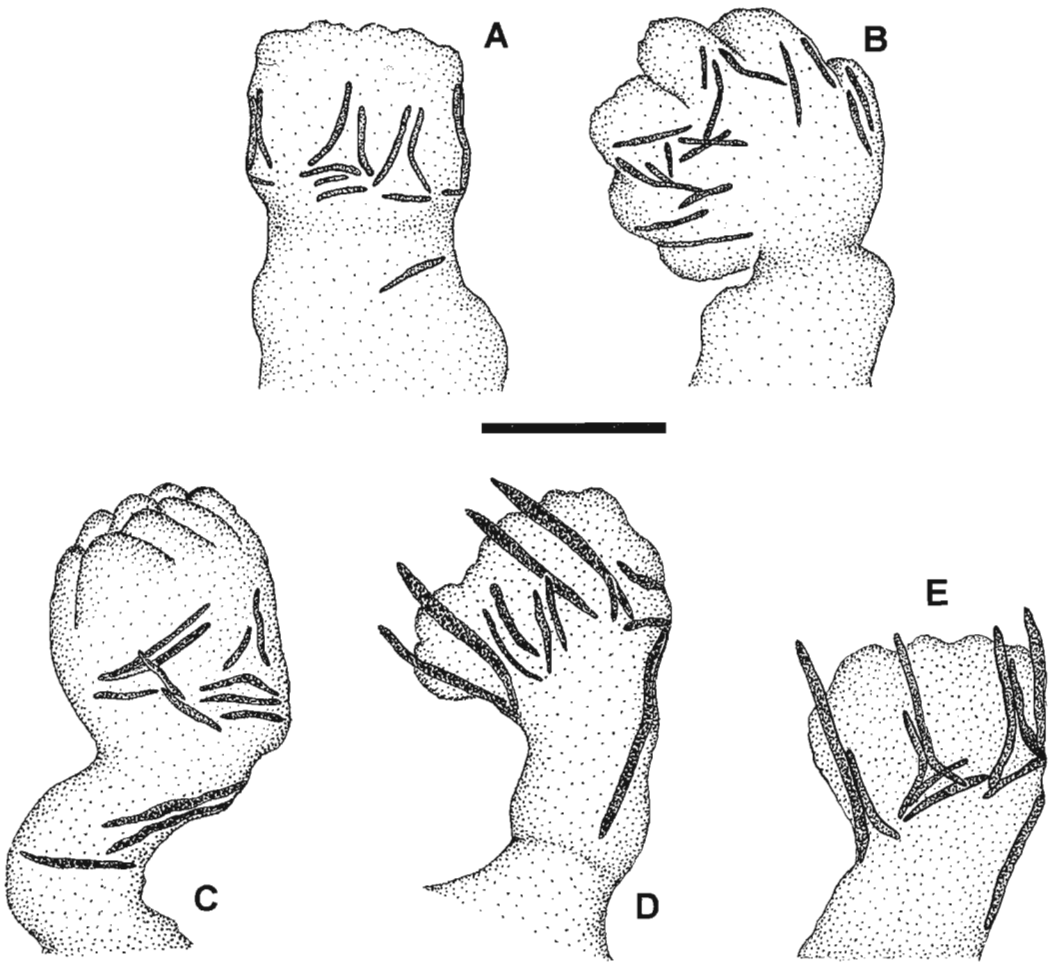


FIGURE 4. *Pacifiphyton bollandi* gen. and sp. nov. Variation in polyp armature. A. Polyp with weak crown and points arrangement. B. Polyp with scattered arrangement of sclerites at the bases of the tentacles. C. Polyp with sparse more-or-less transverse arrangement of sclerites in the polyp wall. D. Polyp with elongated needles protruding from the apex. E. Polyp from the holotype with weak crown and points. Scale bar = 1 mm.

length from 65–321 mm. The holotype is 321 mm long (Fig. 1A), and paratype (*CASIZ #106206*) 142 mm long (Fig. 1B). In both the holotype and this paratype, as well as in some of the other specimens, the holdfasts are attached to hard coral rubble.

The interior of the stalk consists of seven to fifteen large, hollow canals surrounded by an outer region of densely-set sclerites (Fig. 2B). This spiculiferous outer portion varies in thickness and in the number of layers of sclerites, depending on the portion of the stalk from which transverse sections are made. Sclerites are for the most part absent from the canal walls of the interior of the stalk, or if present, they are only very sparsely distributed.

The distal-most portion of the stalk is relatively swollen compared to the rest of the stalk (Figs. 1C, 2A, 5). The surface of this inflated portion is relatively densely-set with longitudinally disposed sclerites, which are spindles, mostly needle-like, varying from 1.5 to 4.0 mm in length (Fig. 5B, 6L). The surface of the rest of the stalk is also densely-set with spindles, but these are usually more robust than those of the distal inflated portion of the stalk, and vary in

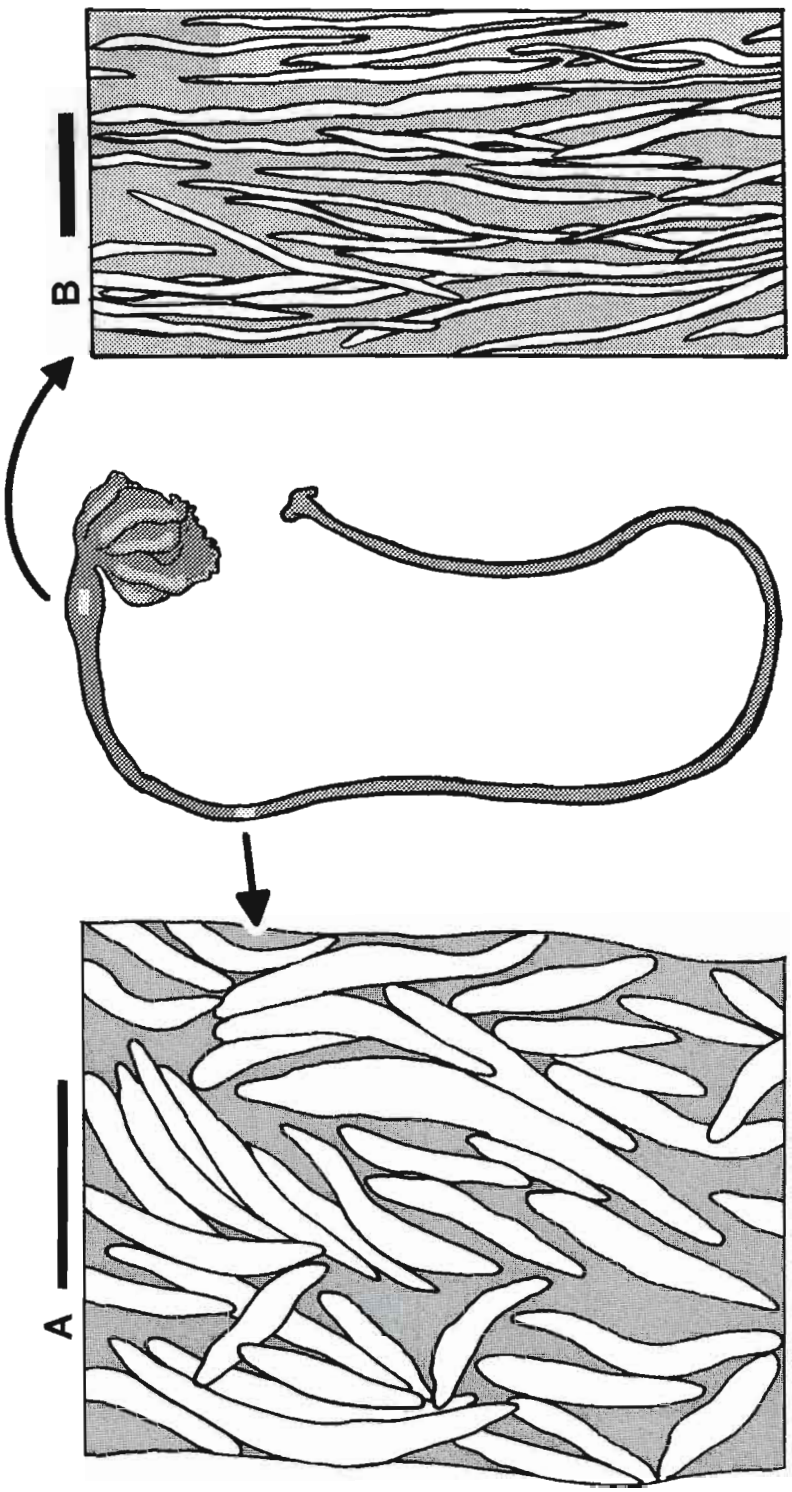


FIGURE 5. *Pacifiphyton bollandi* gen. and sp. nov. Arrangement of sclerites in the surface of the stalk from a 300 mm long specimen. A. Middle of stalk. B. Distal swollen portion of stalk. Scale bars = 1 mm.

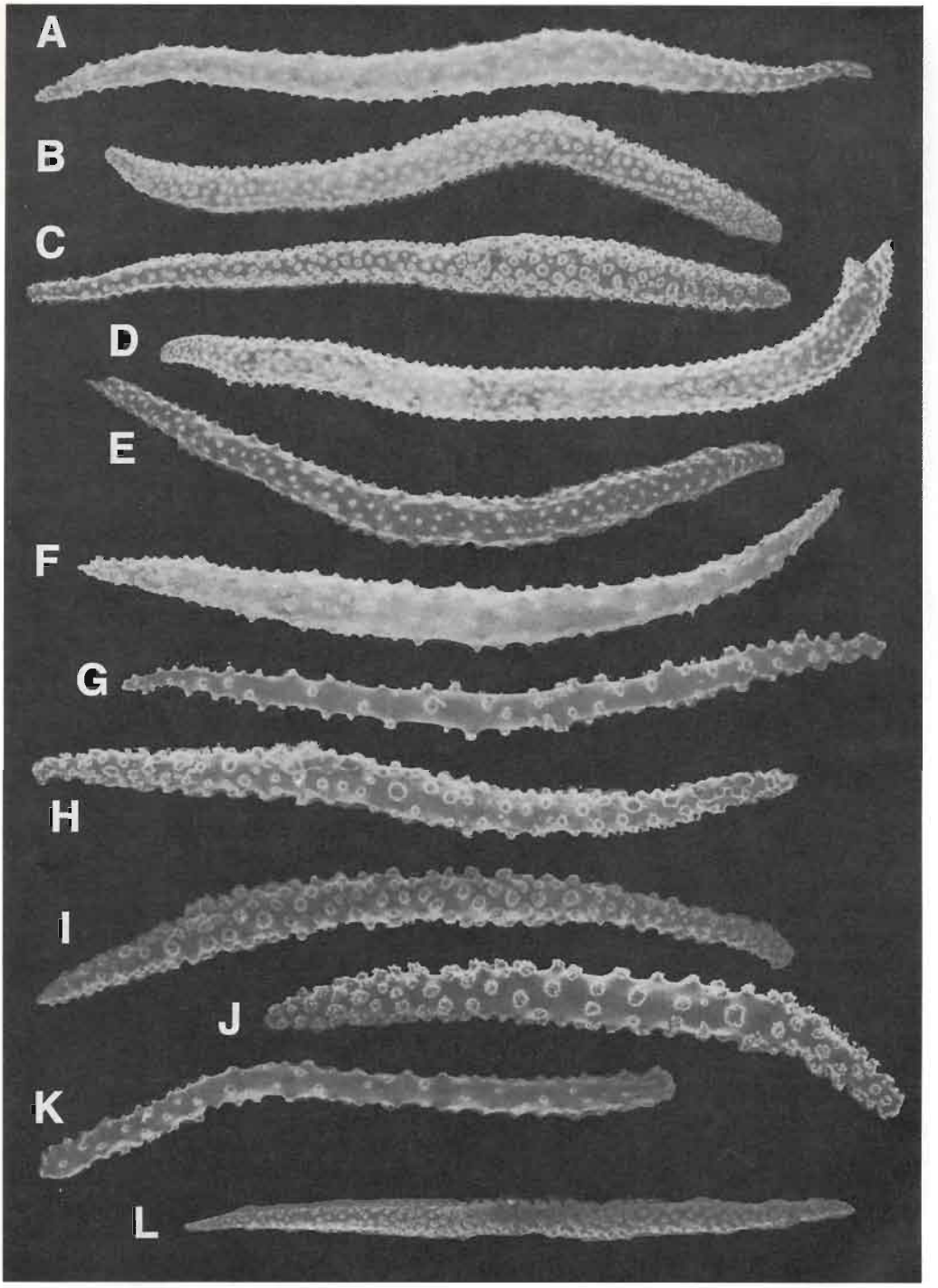


FIGURE 6. *Pacifiphyton bollandi* gen. and sp. nov. Scanning electron micrographs of stalk sclerites from the holotype. A. 1.8 mm. B. 2.1 mm. C. 2.3 mm. D. 2.3 mm. E. 1.5 mm. F. 1.0 mm. G. 0.8 mm. H. 0.9 mm. I. 1.6 mm. J. 0.6 mm. K. 0.6 mm. L. 2.6 mm.

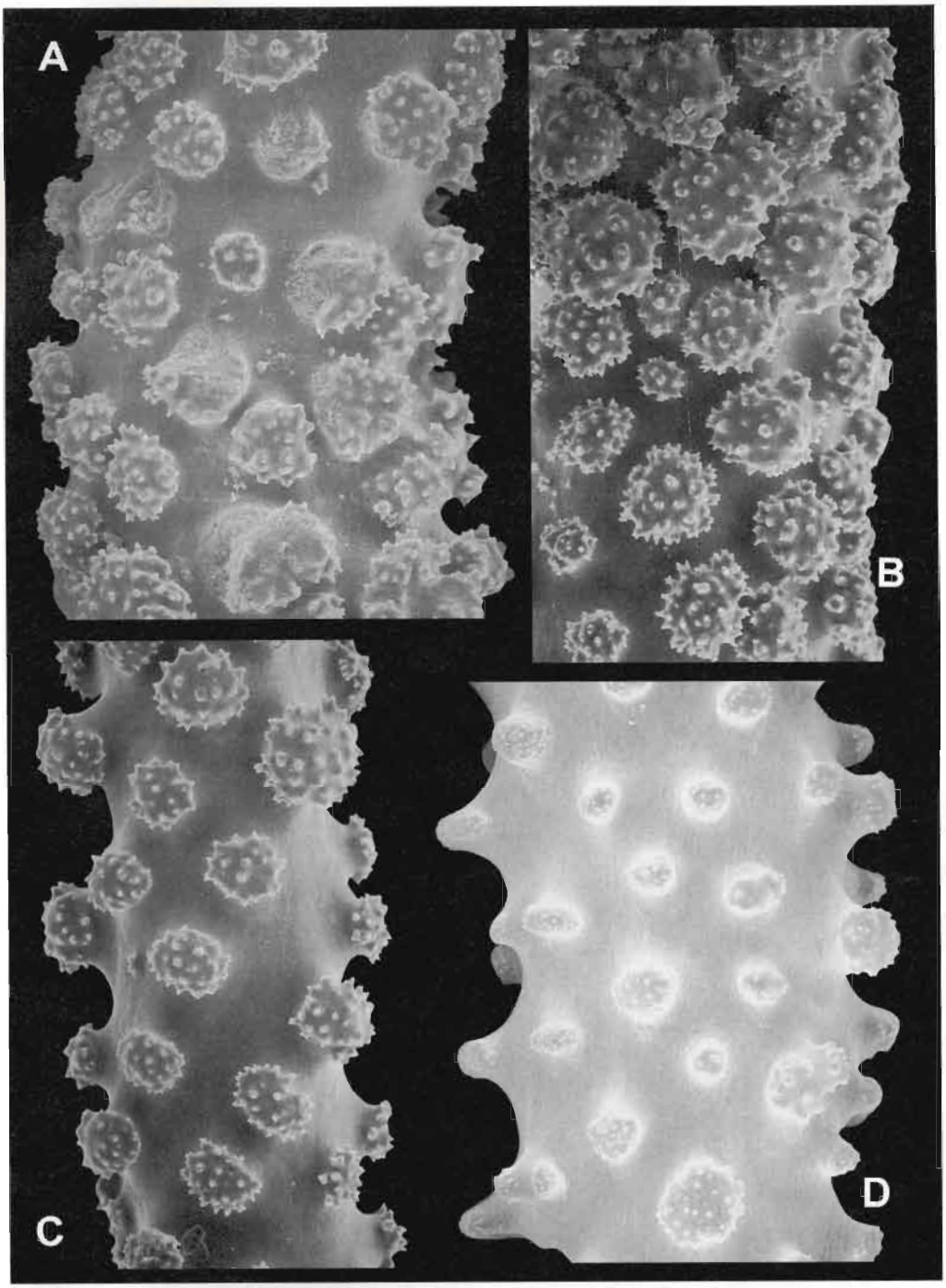


FIGURE 7. *Pacifiphyton bollandi* gen. and sp. nov. Scanning electron micrographs showing details of stalk sclerites. A. Length of portion shown = 0.19 mm. B. Length of portion shown = 0.21 mm. C. Length of portion shown = 0.26 mm. D. Length of portion shown = 0.24 mm.

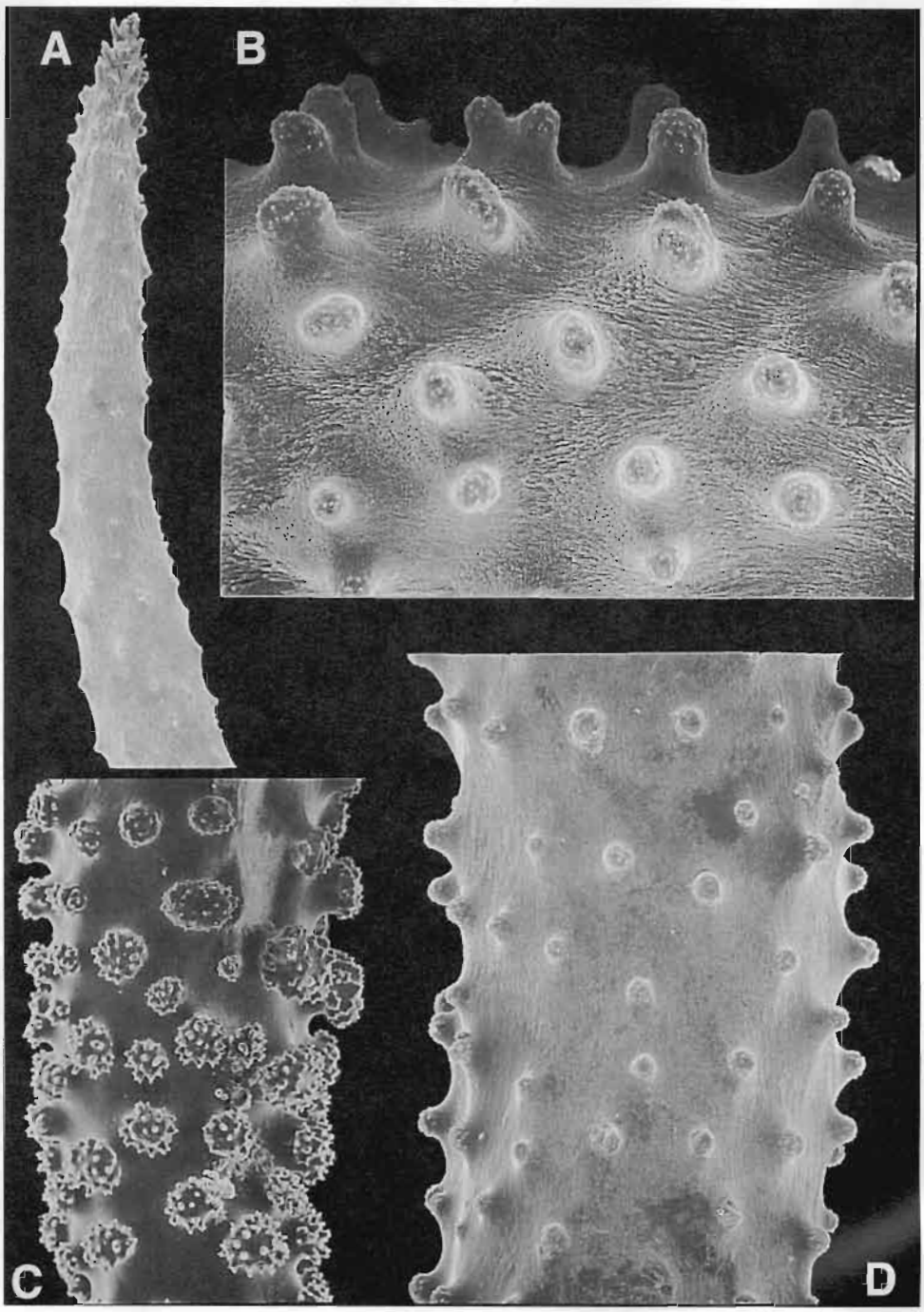


FIGURE 8. *Pacifiphyton bollandi* gen. and sp. nov. Scanning electron micrographs showing tubercle variation of stalk sclerites. A. Length of portion shown = 0.38 mm. B. Length of portion shown = 0.21 mm. C. Length of portion shown = 0.26 mm. D. Length of portion shown = 0.24 mm.

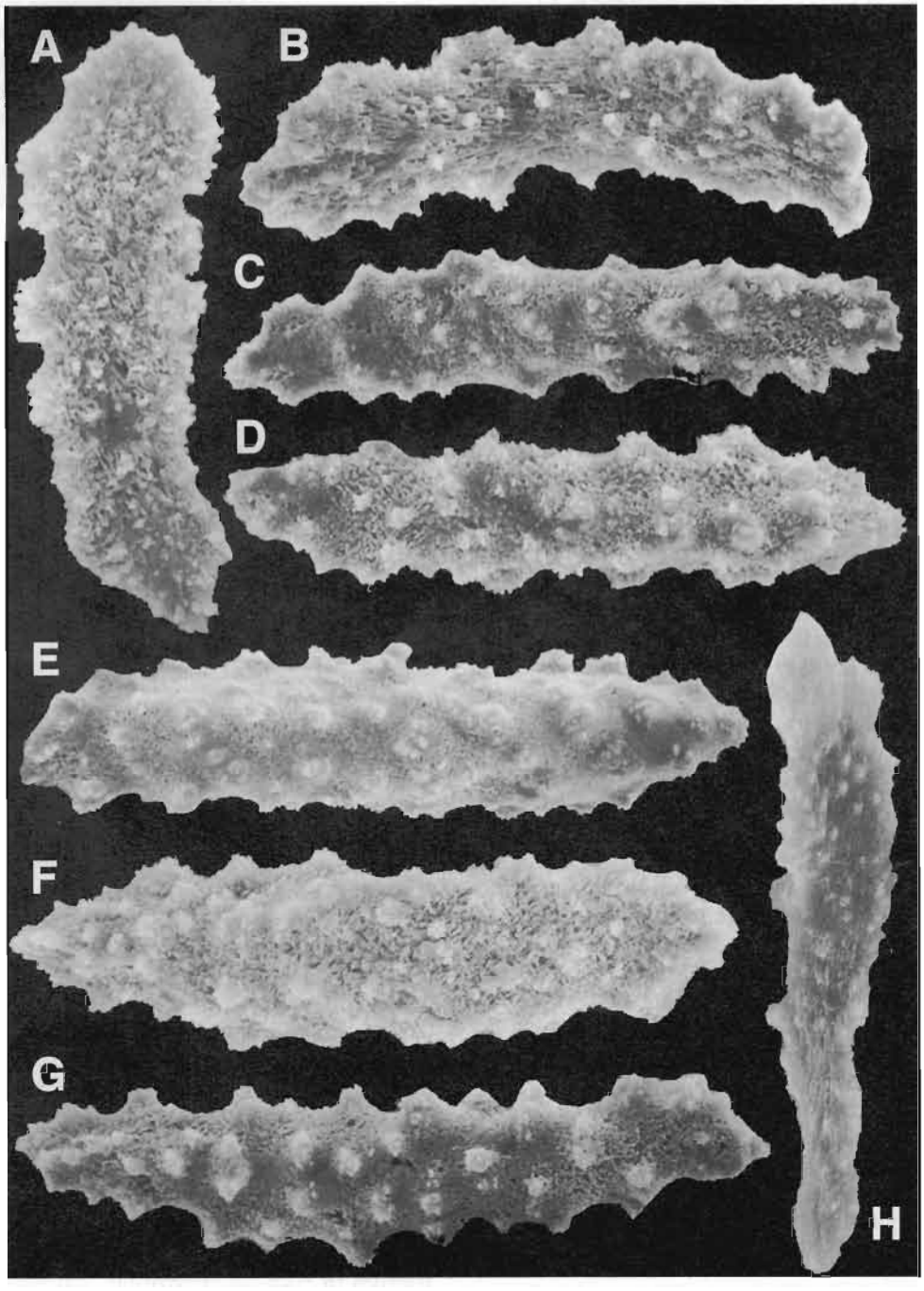


FIGURE 9. *Pacifiphyton bollandi* gen. and sp. nov. Scanning electron micrographs of tentacle sclerites from the holotype. A. 0.063 mm. B. 0.064 mm. C. 0.105 mm. D. 0.104 mm. E. 0.161 mm. F. 0.112 mm. G. 0.116 mm. H. 0.051 mm.

length from 0.6 to 2.5 mm in length (Fig. 6A–K). Many of these spindles are arranged more or less longitudinally, but many are disposed obliquely to the longitudinal axis of the stalk, at various angles. Some of these sclerites appear to be clumped together (Fig. 5A).

The tubercles of the stalk sclerites show considerable variability regarding degree of ornamentation. These may vary from simple, relatively smooth protuberances to coarsely spiny spheroid structures (Figs. 7, 8).

The polyparium may have four or five main branches emanating from the center, which represents the point of insertion of the naked stalk. The distal half of each main branch further ramifies into two to four secondary branches (Figs. 1C, 3B–D). Two or three polyps may arise from the short tertiary branches (Figs. 1C, 3D). Polyps are sparsely distributed and arise singly along the secondary and tertiary branches. Some polyps may be scattered upon the main branches as well. The tertiary branches do not form conspicuous catkins, as the polyps are nowhere distinctly clustered or grouped together. A single main branch together with its associated secondary and tertiary branches may contain 9 to approximately 90 polyps (Fig. 1C, 3).

Spiculation of the divaricate polyparium is highly variable. The polyparium, excluding the polyps, may be totally devoid of sclerites (as in the holotype), or the main branches and secondary branches may be sparsely to relatively densely spiculated with needle-like spindles. These sclerites are mostly long, narrow and sinuous and range in length from approximately 1.0 to at least 3.5 mm. They resemble sclerites from the swollen distal-most portion of the stalk that immediately subtends the polyparium. In life, most of these sclerites are aligned more-or-less parallel to the longitudinal axes of the branches, but in preserved and contracted material, they seem to be scattered about near the surface of the branches with no particular orientation or alignment (Figs. 2A, D; 3A).

The arrangement of sclerites in the polyps varies considerably, including the degree of development of the crown and points (Figs. 2G, 4A–E).

In life, the stalk is tan, light rose, or flesh colored, while the branches of the polyparium vary from colorless to light orange or yellow, sometimes with a bright green or yellow-green iridescence. The polyp walls are colorless, while the pharynxes and mesenterial filaments are apricot orange and the tentacles are white (due to the presence of densely-set sclerites) (Gosliner, Behrens, and Williams, 1996:44, pl. 113). Specimens preserved in ethanol are uniformly cream colored.

ETYMOLOGY. — This species is named for its discoverer, Dr. Robert Bolland, University of Maryland biologist.

DISTRIBUTION. — The new taxon is at present known only from the type locality—Seragaki, Okinawa, Ryukyu Islands, Japan, western Pacific; 58–69 m in depth.

DISCUSSION

COMPARISON WITH OTHER TAXA.— *Pacifiphyton bollandi* gen. and sp. nov. exhibits superficial resemblances to two nephtheid genera: *Umbellulifera* Thomson and Dean, 1936 and *Coronephthya* Utinomi, 1966. The three taxa all have congested polyparies atop elongate stalks. However, the new taxon is easily distinguished from species of these genera.

Both *Pacifiphyton* and *Umbellulifera* have long narrow stalks terminated with a branched polyparium. However, in *Umbellulifera*, the stalk contains many small six-radiate capstans, mostly less than 0.2 mm in length, and the polyps are numerous and densely distributed on a copiously branched umbellate polyparium. In addition, the armature of the polyps include a weak to well-developed supporting bundle and eight well-developed points of chevroned sclerites, but no transverse collaret or crown formation is present. In contrast, *Pacifiphyton* contains only robust spindles or elongate needles in the stalk, 0.6–4.0 mm in length, and the polyps are relatively sparsely distributed on the sparsely branched divaricate polyparium. The points of the polyps are often only weakly developed (if at all) and some polyps have crowns or transverse collarets below the points as well.

Both *Pacifiphyton bollandi* and *Coronephthya macrospiculata* (Thomson and MacKinnon, 1910) have similar sclerites of mostly robust spindles in both the polyparium and the stalk. However, in *Coronephthya*, the polyparium is unbranched, as the large polyps emanate directly from the conical distal tip of the stalk. In addition, each polyp is subtended by a conspicuous sup-

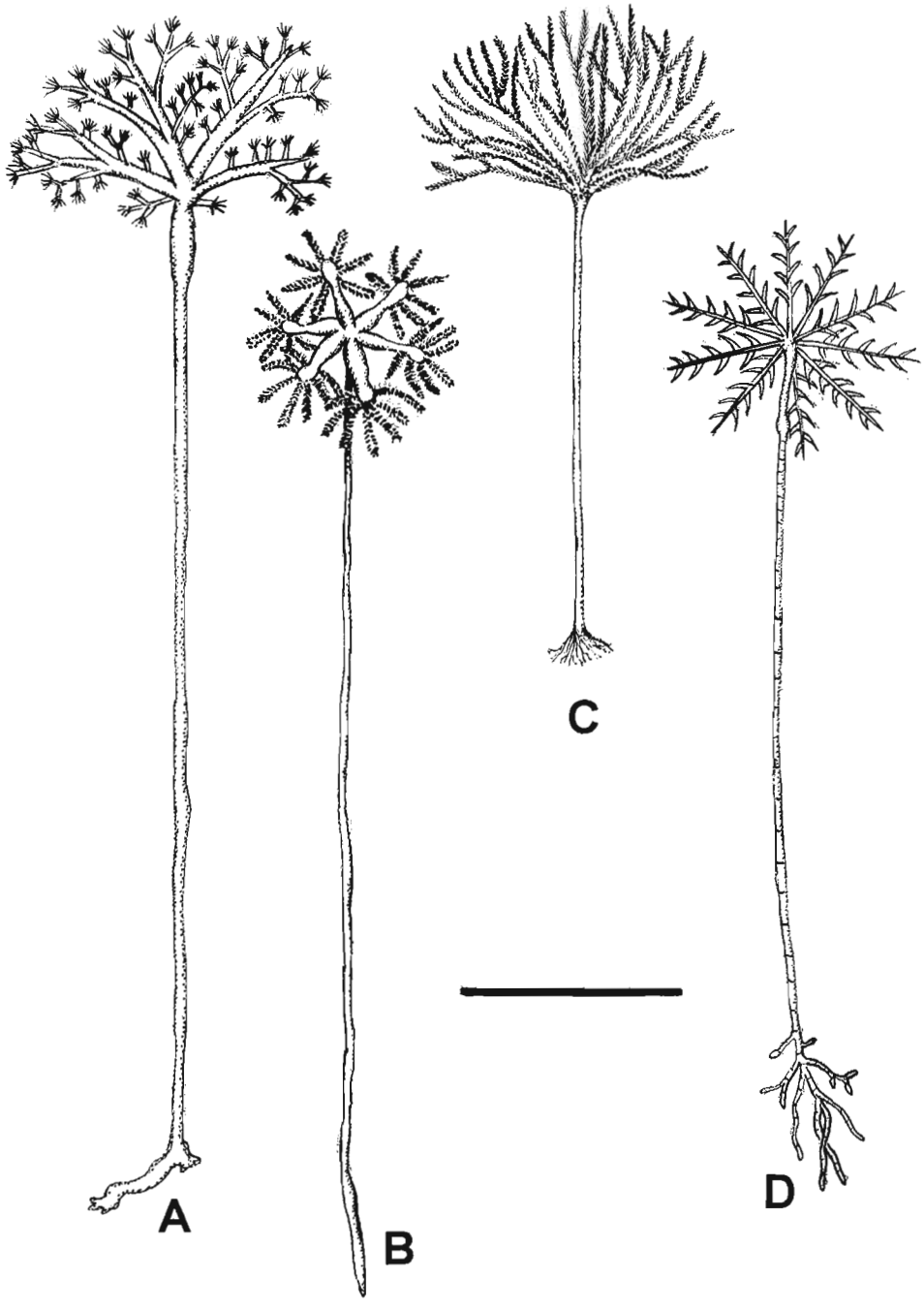


FIGURE 10. Convergence of body form in four deeper-water benthic organisms. A. The soft coral *Pacifiphyton bollandi* gen. and sp. nov. B. The pennatulacean *Umbellula* sp. (adapted from Heezen and Hollister, 1971:41, fig. 2.21). C. The bryozoan *Kinetoskias cyathus* (adapted from Marshall, 1979:168, fig. 68). D. The crinoid *Bathycrinus gracilis* (adapted from Gage and Tyler, 1991:104, fig. 4.45). Scale bar = 30 mm.

porting bundle of large spindles (Utinomi, 1966: 212, fig. 3; 215). On the other hand, in *Pacifiphyton*, the polyparium is multiply-branched and divaricate, and the polyps do not have supporting bundles of sclerites.

Chironephthya dipsacea Wright and Studer, 1889 (p. 231; pl. 37, fig. 1) also shows some resemblance to the new taxon, but as in other members of the soft coral family Nidaliidae, has permanent, strongly spiculated calyces into which the polyps retract. Calyces are absent in *Pacifiphyton bollandi*.

STALK MECHANICS.—A remarkable character of the new taxon is the differential appearance and form of spiculation between the swollen distal portion of the stalk and the rest of the stalk (Fig. 5). The swollen portion contains slender needles aligned parallel to the axis of the stalk. Between this distal portion and the basal region, the sclerites are mostly robust spindles and are more or less longitudinally disposed but many are also aligned at oblique angles. In the basal region of the stalk, many sclerites have an alignment approaching perpendicular to the longitudinal axis.

This differentiation of sclerite alignment and composition throughout the length of the stalk no doubt results in maximum rigidity toward the base and maximum flexibility just below the polypary. This morphological differentiation perhaps reflects the amount of movement the various portions of the stalk receive in strong bottom currents. The flexible and inflatable distal portion may act as a swivel and may be capable of at least some amount of back and forth rotation, giving the expanded polyparium maximum flexibility in strong currents.

Conceivably, this capability would keep the inflated polypary aligned to slight or marked changes in direction of the bottom current, somewhat like the pivoting of a wind vane with changing wind direction.

CONVERGENCE. — *Pacifiphyton* is remarkable in the similarity of its palm-like growth form to several unrelated deep-sea benthic animals (Fig. 10). They are all similar in having a congested, divaricate (Fig. 10A, C, D) or umbellate (Fig. 10B) feeding assemblage at the end of a very long and narrow stalk. These taxa include species of the pennatulacean octocoral genus *Umbellula* (see Williams, 1995:116, fig. 4E), the bryozoan genus *Kinetoskias*, and the crinoid echinoderm genus *Bathycrinus*. The resemblance between *Umbellula* and stalked crinoids has been noted by several authors including Gage and Tyler (1991:99). Marshall (1979:183) stated, " *Umbellula* is one of the classic animal types of the deep-sea floor, and so are the stalked sea-lilies (crinoids), both converging in their palm-like forms — forms that look well designed for passive suspension feeding. Bent over by currents, they look like palms in a breeze. . . ."

The often large and long-stalked suspension feeders, such as the four above-mentioned taxa, are rheophiles (current-lovers) and are most abundant in areas with prevailing currents as opposed to quieter regions of the sea floor (Marshall, 1979:295). The palm-like growth form is presumably advantageous to maximize feeding efficiency in similar benthic habitats.

Cowen (1981:332) described the mechanics of food gathering in stalked crinoids and described a resemblance to the ideal layout for harvesting roads on a banana plantation. In the stalked crinoids, food is harvested in an evenly distributed micro-particulate resource area, and is delivered to a central processing point (thus the analogy to a banana plantation). The harvested food material is transferred down the pinnules, and via the arms to the central mouth along a series of ciliated food grooves. In *Umbellula*, *Kinetoskias*, and *Pacifiphyton*, because of the modular nature of these organisms, harvesting and processing takes place on numerous distinct sites throughout the feeding structure and food is not delivered to a single central location for processing.

In stalked crinoids such as *Bathycrinus* and *Rhizocrinus*, the arms and stalk typically form a parabolic filtration fan with the stem tilted downstream in the bottom current (Gage and Tyler, 1991:105). Five, ten, or more arms radiate outward from a central mouth region. Each arm has numerous articulated pinnules. Both the pinnules and arms have a central ciliated groove. Each pinnule has several tube feet, which capture suspended particles and bring them into the central groove. In these crinoids, the entire body structure represents a single individual with a central mouth.

In contrast to this, *Pacifiphyton*, *Umbellula*, and *Kinetoskias* are modular organisms with many individual zooids or polyps, each with a separate mouth, and each similar in size and appearance. Modularity in a variety of benthic

organisms has been discussed by Hughes (1983). In *Umbellula* large tubular polyps radiate from a central point. Each polyp has eight tentacles with many pinnules in two longitudinal rows. The pinnules capture suspended food particles, then each tentacle is subsequently brought over the mouth of the respective polyp, where the food material is removed by the mouth and transferred to the pharynx. In *Pacifiphyton*, many small polyps are evenly distributed on the branches of the polyparium (Fig. 1C). In shallower habitats such as that of *Pacifiphyton*, micropredation is probably a more important source of nutrition than is suspension feeding. In *Kinetoskias*, each of the numerous minute zooids arranged along the branches of the bushy distal region of the colony gathers food with a circular tentaculated feeding structure (the lophophore).

All of these unrelated palm-like organisms inhabit unconsolidated soft ooze or mud deposits (*Umbellula*, *Bathycrinus*, and *Kinetoskias*), or areas of sand and coral/stone rubble (*Pacifiphyton*). Many stalked sea lilies such as *Bathycrinus* and *Rhizocrinus* have root-like projections at the base of the stalk (known as terminal rootlets) that root the animal in the substratum (Fig. 10D). In *Kinetoskias*, colonies are rooted into the substratum by rhizoids at the base of a long stem formed by the fusion of reduced and modified individuals known as kenozooids (Fig. 10C) (Marshall, 1979:169). *Pacifiphyton* has a holdfast which may adhere to one or several fragments of stone or coral rubble (Fig. 1B, 10A). *Umbellula* has a long muscular peduncle, which penetrates into the soft sediment (Fig. 10B).

ACKNOWLEDGMENTS

I thank Dr. Robert Bolland (University of Maryland), diligent collector and careful observer of Okinawan marine life, for bringing his discoveries to my attention.

I am grateful to Dr. Frederick Bayer (National Museum of Natural History, Washington, D. C.), Dr. Phil Alderslade (Museum and Art Gallery of the Northern Territory, Darwin, Australia), and Leen van Ofwegen (Nationaal Natuurhistorisch Museum, Leiden, The Netherlands) for their insights concerning various aspects of nephtheid systematics, and to Dr. Rich Mooi (California Academy of Sciences) for discussions regarding crinoid feeding mechanisms.

LITERATURE CITED

COWEN, R. 1981. Crinoid arms and banana plantations: an economic harvesting analogy. Paleobiology 7(3):332–343.

GAGE, J. D. AND TYLER, P. A. 1991. Deep-sea biology — a natural history of organisms at the deep-sea floor. Cambridge University Press. 504 pp.

GOSLINER, T. M., BEHRENS, D. W., AND WILLIAMS, G. C. 1996. Coral reef animals of the Indo-Pacific. Sea Challengers, Monterey. 314 pp.

HEEZEN, B. C. AND HOLLISTER, C. D. 1971. The face of the deep. Oxford University Press, New York. 659 pp.

HUGHES, R. N. 1983. Evolutionary ecology of colonial reef-organisms, with particular reference to corals. Biological Journal of the Linnean Society 20(1):39–58.

IMAHARA, Y. 1991. Report on the Octocorallia from the Ryukyu Islands of Japan. Bulletin of the Institute of Oceanic Research and Development, Tokai University 11/12:59–94.

MARSHALL, N. B. 1979. Developments in deep-sea biology. Blandford Press, Poole, Dorset. 566 pp.

THOMSON, J. A. AND MACKINNON, D. L. 1910. Alcyonarians collected on the Percy Sladen Trust Expedition by Mr. J. Stanley Gardiner. Part 2, the Stolonifera, Alcyonacea, Pseudaxonia, and Stelechotokea. Transactions of the Linnean Society of London (2)13(2):165–211.

UTINOMI, H. 1966. A revision of the nomenclature of the family Nephtheidae (Octocorallia: Alcyonacea). III. A new genus *Coronephthya* for a unique octocoral previously assigned to the genera *Dendronephthya* or *Stereonephthya*. Publications of the Seto Marine Biological Laboratory 14(3):207–218.

WILLIAMS, G. C. 1995. Living genera of sea pens (Coelenterata: Octocorallia: Pennatulacea): illustrated key and synopses. Zoological Journal of the Linnean Society 113:93–140.

WRIGHT, E. P. AND STUDER, T. 1889. Report on the Alcyonaria collected by H. M. S. Challenger during the years 1873–1876. Report on the scientific results of the exploring voyage of H. M. S. Challenger 1873–76. Zoology 31(1):1–314.

Golden Gate Park
San Francisco, California 94118