

PROCEEDINGS
OF THE
CALIFORNIA ACADEMY OF SCIENCES

Vol. 48, No. 15, pp. 315-328, 7 figs., 1 table.

August 1, 1995

THE ENIGMATIC SEA PEN GENUS *GYROPHYLLUM*—
A PHYLOGENETIC REASSESSMENT AND
DESCRIPTION OF *G. SIBOGAE* FROM
TASMANIAN WATERS (COELENTERATA: OCTOCORALLIA)

By

Gary C. Williams

Department of Invertebrate Zoology, California Academy of Sciences,
Golden Gate Park, San Francisco, California 94118

Marine Biological Laboratory/
Woods Hole Oceanographic Institution
Library

AUG 07 1995

Woods Hole, MA 02543

ABSTRACT: The enigmatic sea pen, *Gyrophyllum sibogae* Hickson, 1916, is redescribed from Tasmanian material, extending the range of the species from the Malay Archipelago and Madagascar. A phylogenetic analysis of several related pennatulacean taxa attempts to resolve some problematic aspects of the literature regarding the systematics of the genus *Gyrophyllum*. Six taxa are compared in the analysis: *Pennatula inflata*, *Ptilosarcus undulatus*, *Gyrophyllum sibogae*, *Sarcoptilus grandis*, *Crassophyllum cristatum*, and *Pteroeides spinosum*. *Gyrophyllum* is shown to have characters intermediate between the Pennatulidae and Pteroeididae, thereby obviating the separation of the two families. It is therefore proposed that only one family be recognized, the Pennatulidae, comprising the six genera *Pennatula*, *Ptilosarcus*, *Gyrophyllum*, *Sarcoptilus*, *Crassophyllum*, and *Pteroeides*.

Received August 10, 1994. Accepted March 8, 1995.

INTRODUCTION

At least fifteen species in nine genera of sea pens have been recorded or are known to occur in southern Australia (Williams, in press). The recent discovery of *Gyrophyllum sibogae* off Tasmania represents a new record to the Australian fauna. Southern Australia is defined here as the continental shelf region of southern Western Australia, South Australia, Victoria, Tasmania, and southern New South Wales (i.e., the southern coastal waters extending from Perth to Sydney).

Hickson (1916) originally described *Gyrophyllum sibogae* from the Malay Archipelago and differentiated it from the type species *G. hiron-dellei* of the northern Atlantic, the only other species known for the genus. Hickson differen-

tiated the two species as follows—*G. sibogae* with two calyx teeth per polyp and larger colony size (up to 295 mm in length); and *G. hiron-dellei* without calyx teeth and smaller colony size (up to 127 mm long). In addition, he noted distributional and bathymetric differences—*G. sibogae* (Indonesia at 567 m), compared to *G. hiron-dellei* (vicinity of the Azores at 1222–2220 m).

The enigmatic nature of the genus *Gyrophyllum* has resulted in some disputation by previous authors regarding the systematics of the taxon. It is shown here that *Gyrophyllum* represents a morphological intermediate between the Pennatulidae and Pteroeididae thereby making the distinction between the two families tenuous.

MATERIALS AND METHODS

The following material was examined for this study. *Pennatula inflata* Kükenthal, 1910—SAFRM H MAD 28 KKK, Subantarctic, between Prince Edward and Marion Islands (37°55'90" E; 46°43'56" S), 225–243 m, 28 April 1987, SA *Agulhas* dredging cruise, 1 partial specimen (peduncle missing). SAFRM H3238, South Africa, northwest of Lambert's Bay (31°43.6' S; 16°13.2' E), 457 m, 9 June 1947, two specimens trawled, University of Cape Town Ecological Survey. *Ptilosarcus undulatus* (Verrill, 1865)—CASIZG 013015, Mexico, Baja California Sur, La Paz, intertidal, 22 March 1940, coll. Edward F. Ricketts, 1940 Steinbeck/Ricketts Sea of Cortez Expedition, FV *Western Flyer*, six whole specimens. *Gyrophyllum sibogae* Hickson, 1916—see "Material" section under Systematic Account below. *Sarcoptilus grandis* Gray, 1848—SAUSM H11921, South Australia, Spencer Gulf, approximately 18.5 km northwest of Point Riley (35° 53' S; 137°24' E), 25 m, 3–4 May 1989, K. Gowlett-Holmes and P. Tudorovic, FV *Angela Kaye*, two whole specimens. *Crassophyllum cristatum* Tixier-Durivault, 1961—NMNHP St. 51, Angola, off Moita Seca, 44 m, 25 October 1948, one whole specimen. *Pteroeides spinosum* (Ellis, 1764)—CASIZG 088063, France, Mediterranean Sea, Banyuls-sur-Mer, 35 m, 15 October 1992, R. J. Moci and B. David, RV *Nereis*, one whole specimen.

Abbreviations used in the text refer to the following: SAFRM (South African Museum, Cape Town), SAUSM (South Australian Museum, Adelaide), CASIZG (California Academy of Sciences, Department of Invertebrate Zoology and Geology, San Francisco), NMNHP (National Museum of Natural History, Paris). Terminology used in the present work conforms to that of Bayer, Grasshoff, and Verseveldt (1983). All figures and scanning electron micrographs are by the author.

SYSTEMATIC ACCOUNT

Gyrophyllum Studer, 1891

Gyrophyllum Studer, 1891: 94. 1901: 34. Roule, 1905: 454.

Kükenthal, 1915: 120. Hickson, 1916: 252.

?*Bathypenna* Marion, 1906: 147.

Two species of the northern Atlantic, Indo-West Pacific, and southeastern Australia.

Gyrophyllum sibogae Hickson, 1916

(Figs. 1–4, 5C)

Gyrophyllum sibogae Hickson, 1916: 253, fig. 45, pl. 3 fig. 17, pl. 8 fig. 48. Tixier-Durivault and D'Hondt, 1973: 263.

MATERIAL.—SAUSM H11844, Tasmania, 46 km west of Richardson Point (41°15' S; 144°08' E), 520 m, 20 October 1984, W. Zeidler CSIRO "Soela" Stn. 51, 7 whole and 3 partial specimens.

DESCRIPTION (Figs. 1–3, 5C).—The seven whole colonies that were examined range in length from 185–250 mm. The colonies excluding the polyp leaves are somewhat clavate, with the distal portion of the rachis distinctly wider than the rest of the colony. The rachis comprises roughly 30%–40% of the total colony length, while the peduncle makes up approximately 60%–70%. The maximum width of the rachis varies from 12–17 mm, while that of the peduncle ranges from 8–12 mm.

The number of polyp leaves per side varies from 6–10, but most colonies have 6 or 7 per side. The polyp leaves are fanlike, thick and fleshy (3–6 mm thick and 15–50 mm in breadth). The autozooids are confined to the outer margin of the leaves, where they are congested and disposed roughly in two adjacent rows.

Each polyp leaf contains 20–50 autozooids. The autozooids are 1.5–2.5 mm in diameter and protrude from a fleshy calyx-like base that usually contains two more-or-less distinct teeth or pointed lobes on opposite sides or adjacent to one another. These lobes contain relatively sparsely-set polyp leaf sclerites.

The siphonozooids are numerous but scattered (not particularly densely-set) on both sides of the polyp leaves between the autozooids and onto the faces of the leaves below the autozooids. Each siphonozooid is approximately 0.5 mm in diameter, and appears as an inconspicuous hemispherical protuberance, sparsely spiculated. The siphonozooids are scattered over the surface of the polyp leaves, are not congested or restricted in distribution, and thus do not form zones or pads.

The sclerites of the tentacles are short, blunt rods (0.10–0.24 mm in length), smooth to somewhat longitudinally grooved but not three-flanged. The sclerites of the polyp leaves, rachis and peduncle are elongated, three-flanged rods. Those from the polyp leaves are 0.28–0.48 mm long. Sclerites from the surface and interior of the rachis are 0.27–0.45 mm in length, while those

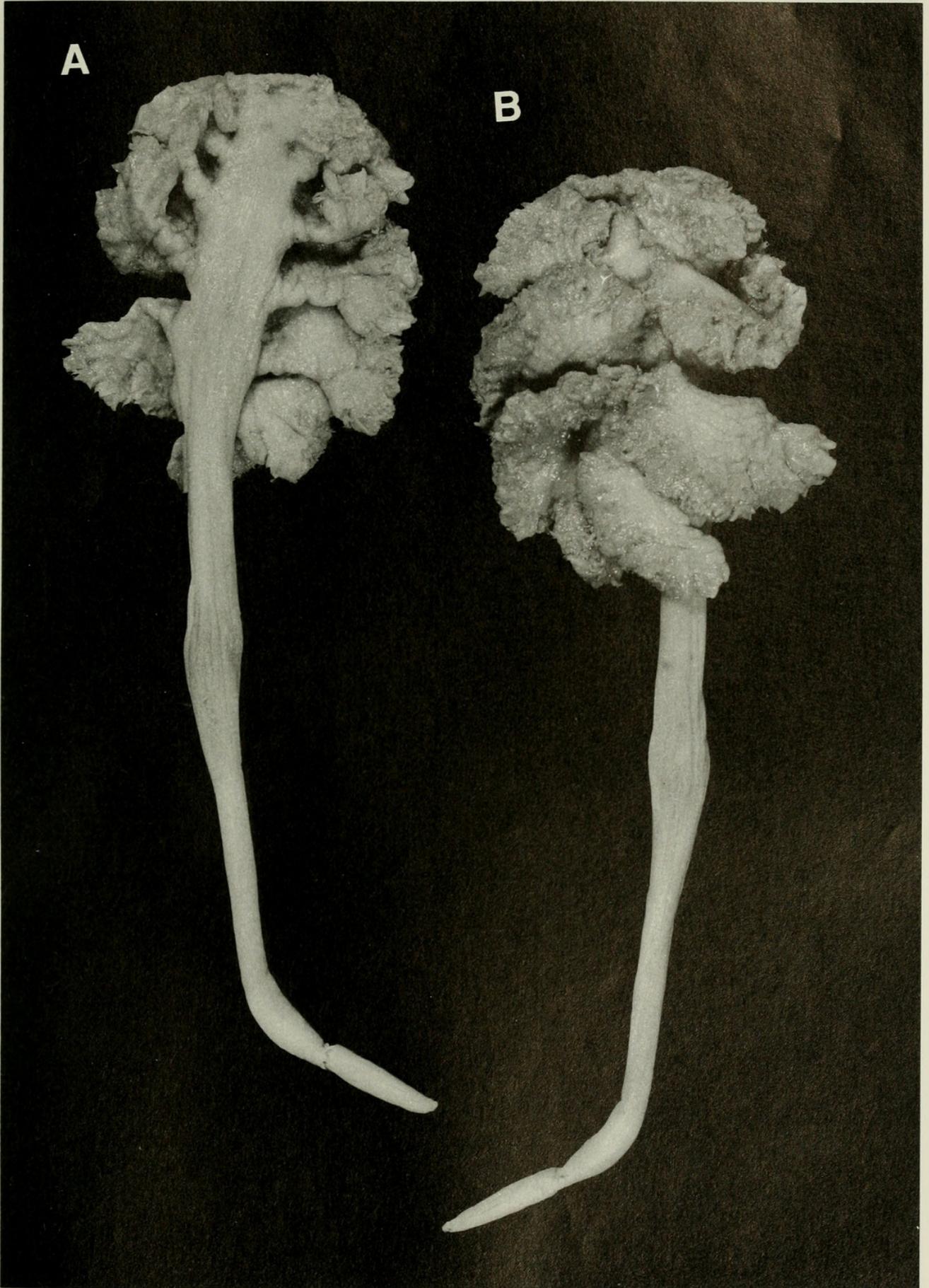


FIGURE 1. *Gyrophyllum sibogae* (SAUSM-H11844). Photographs of a single specimen, 185 mm in length. A. Dorsal view. B. Ventral view.

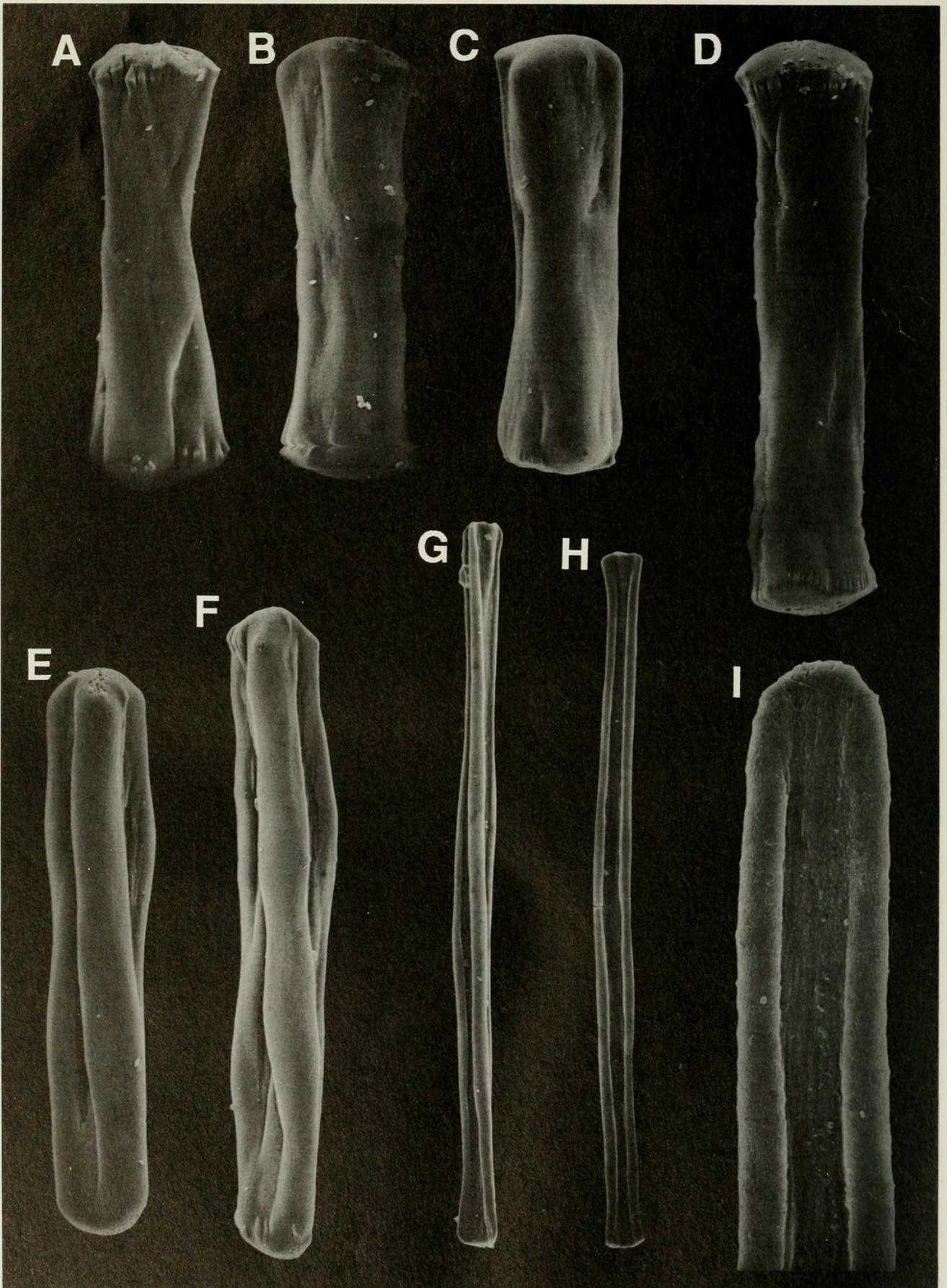


FIGURE 2. *Gyrophyllum sibogae* (SAUSM-H11844). Scanning electron micrographs of sclerites. A-F. Sclerites from the tentacles. A. 0.16 mm. B. 0.16 mm. C. 0.16 mm. D. 0.21 mm. E. 0.21 mm. F. 0.24 mm., G-I. Sclerites from the polyp leaves. G. 0.43 mm. H. 0.34 mm. I. 0.07 mm.

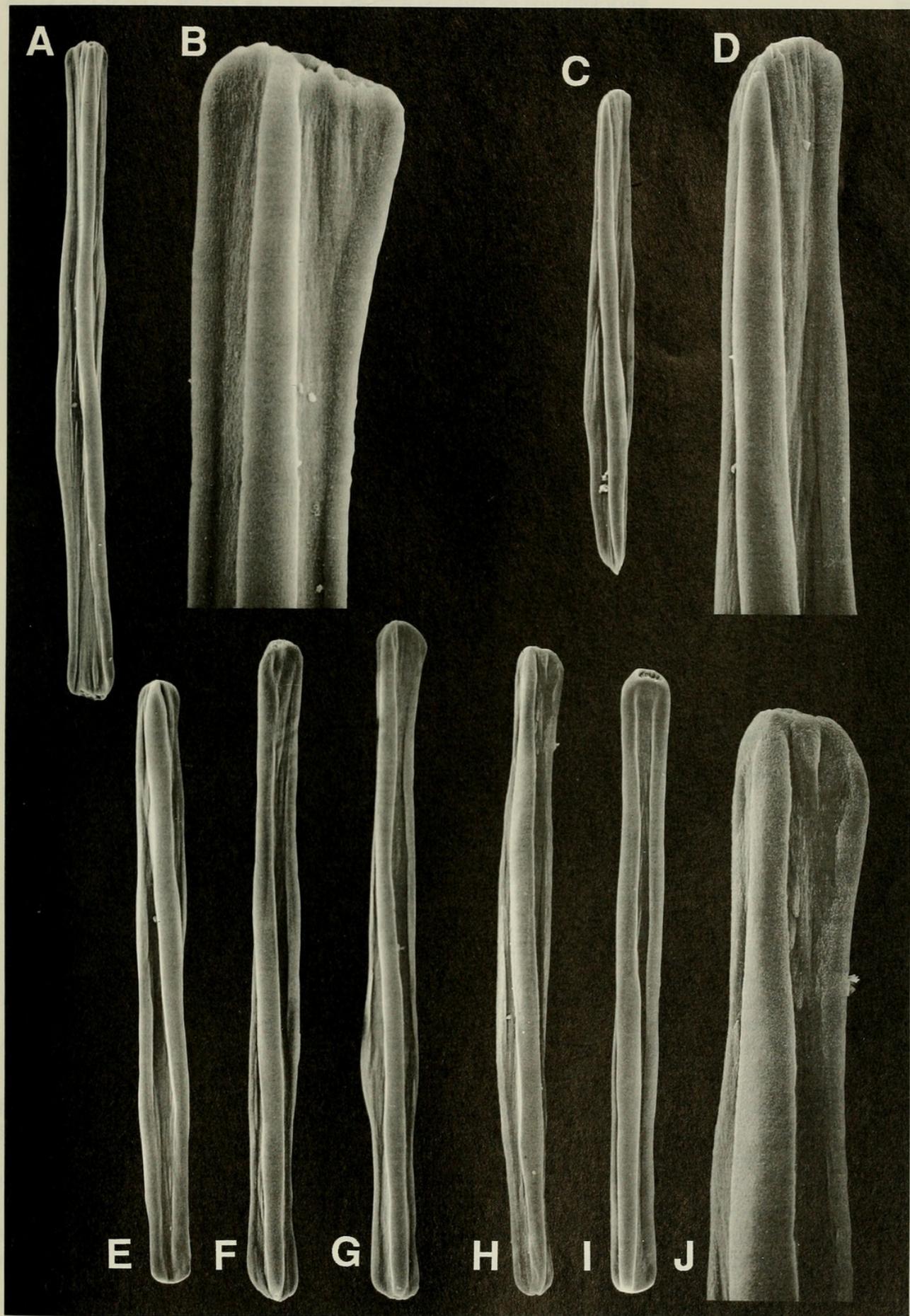
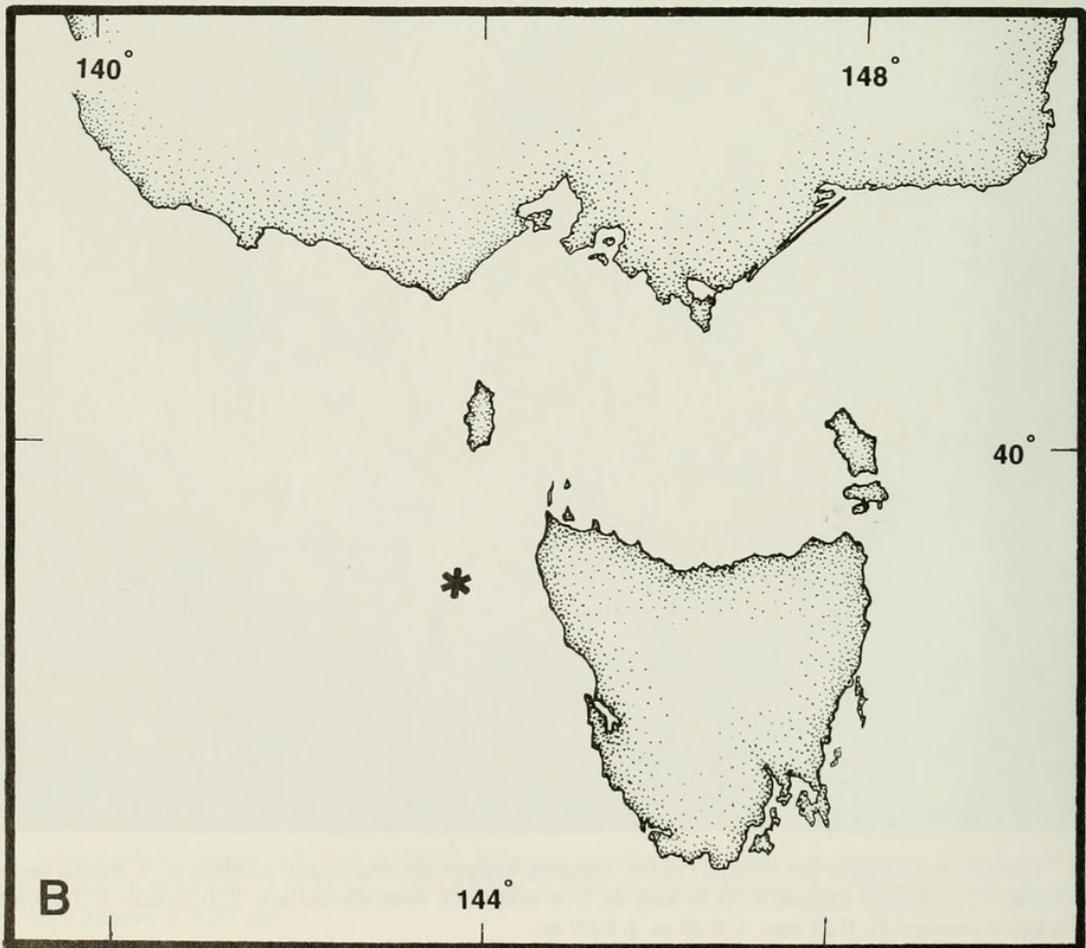
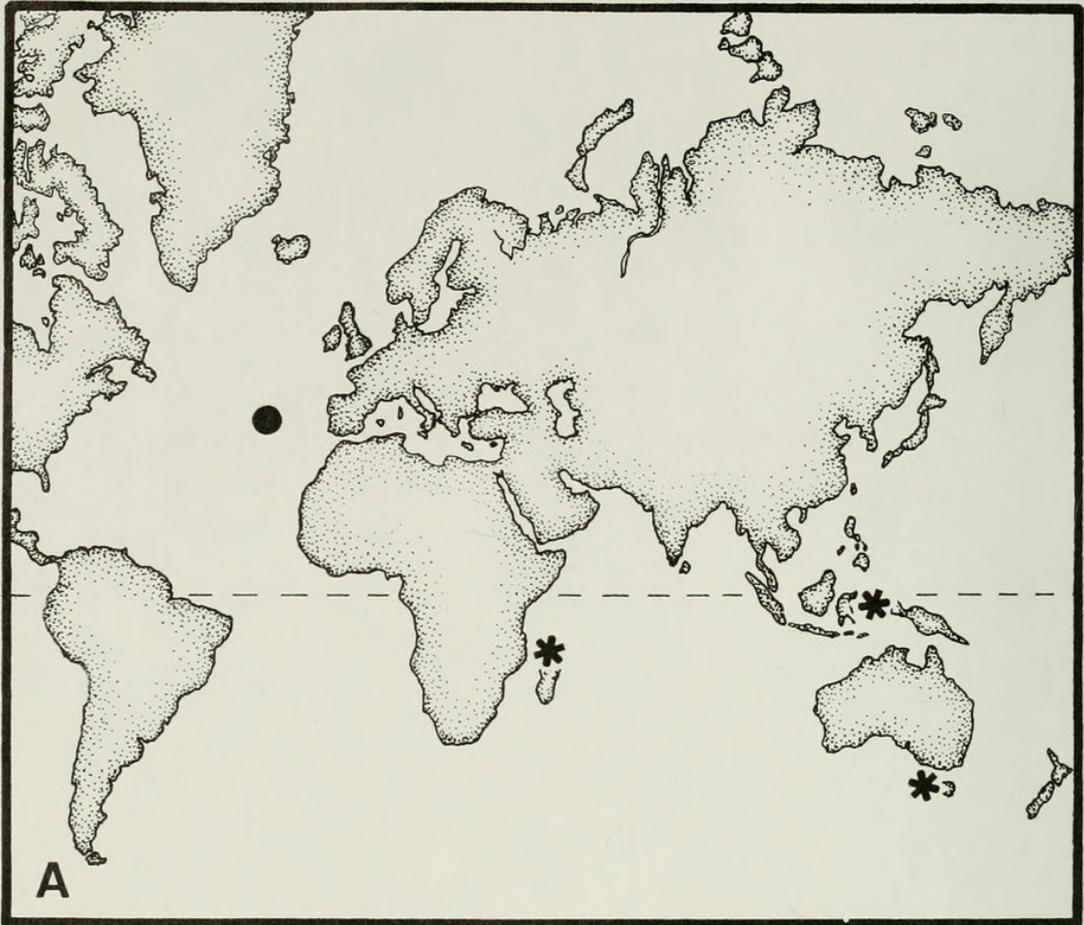


FIGURE 3. *Gyrophyllum sibogae* (SAUSM-H11844). Scanning electron micrographs of sclerites. A, B. Rachis surface. A. 0.41 mm. B. 0.07 mm. C, D. Rachis interior. C. 0.25 mm. D. 0.09 mm. E-G. Peduncle surface. E. 0.26 mm. F. 0.29 mm. G. 0.30 mm. H-J. Peduncle interior. H. 0.29 mm. I. 0.28 m. J. 0.09 m.



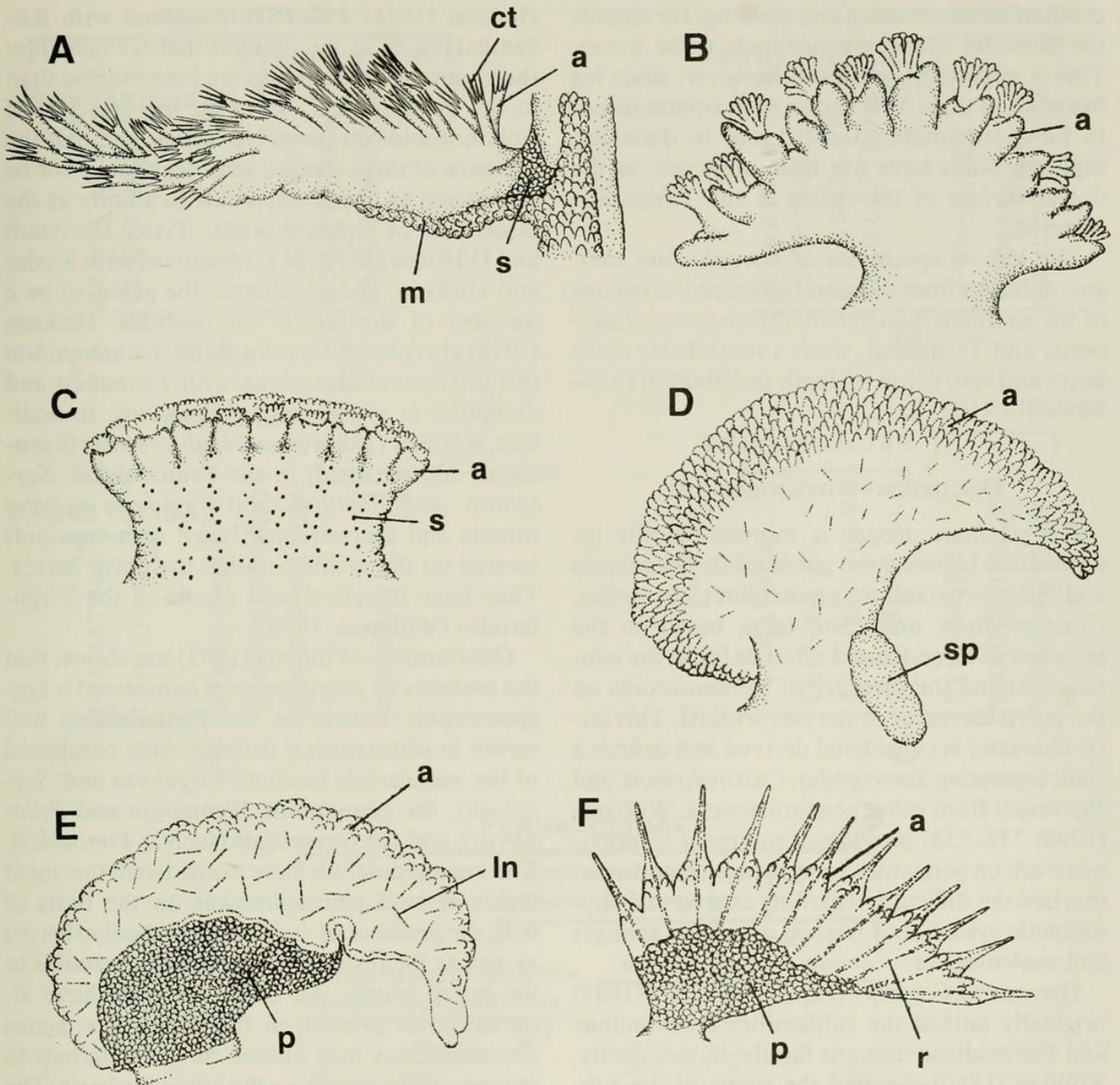


FIGURE 5. Comparison of polyp leaf morphology in six pennatulid and pteroeid taxa. A. *Pennatula inflata*, 33 mm in length. B. *Ptilosarcus undulatus*, 6 mm in length. C. *Gyrophyllum sibogae*, 35 mm in length. D. *Sarcoptilus grandis*, 31 mm in length. E. *Crassophyllum cristatum*, 32 mm in length. F. *Pteroeides spinosum*, 30 mm in length; a- autozooid, ct- spiculated calyx teeth, ln- large leaf needle, m- mesozooid, p- siphonozooid plate, r- polyp leaf ray, s- siphonozooid, sp- siphonozooid pad.

from the surface and interior of the peduncle are 0.17–0.38 mm long.

Color of the colonies varies from tan to light brown.

DISTRIBUTION (Fig. 4).—Indo-West Pacific and southeastern Australia, 520–585 m in depth: Ceram (Malay Archipelago), 567 m depth (Hick-

son, 1916); Nosy Bé (Madagascar), 580–585 m depth (Tixier-Durivault and d’Hondt, 1973); Tasmania, 520 m depth (present study).

REMARKS.—Hickson (1916: 254) reported numerous but inconspicuous siphonozooids on the dorsal surface of the rachis of the type specimen from Indonesia—these were discerned only as a

FIGURE 4. A. World map showing geographical distribution for the genus *Gyrophyllum* (● = collecting stations for *G. hirondellei*; * = collecting stations *G. sibogae*). B. Map of Tasmania showing collecting station of *Gyrophyllum sibogae* for material studied in the present paper (*).

result of thin sectioning and staining. He records the diameter of the siphonozooids to be 5 mm. This is apparently mistaken however, since his figure 48 of plate VIII shows each siphonozooid to be approximately 0.4–0.5 mm in diameter. Siphonozooids have not been observed on the dorsal surface of the rachis in the Tasmanian material.

The known specimens of *Gyrophyllum sibogae*, although from disparate geographical regions of the southern hemisphere (Madagascar, Indonesia, and Tasmania), show a remarkable similarity and restriction of depth distribution (520–585 m).

DISCUSSION—PHYLOGENETICS

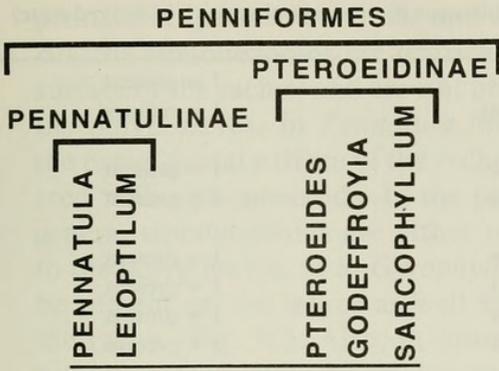
Gyrophyllum sibogae is morphologically intermediate between the pennatulids (*Pennatula* and *Ptilosarcus*) and the pteroeidids (*Sarcoptilus*, *Crassophyllum*, and *Pteroeides*), based on the presence of three-flanged sclerites (as in the pennatulids) and the presence of siphonozooids on the polyp leaves (as in the pteroeidids). This latter character is considered derived and defines a clade separating *Sarcoptilus*, *Crassophyllum*, and *Pteroeides* from other pennatulaceans. Williams (1993: 732–733) provides a summary of previous work on pennatulacean phylogeny, and summarizes the difficulty regarding analyses of phylogenetic systematics in such groups as sponges and coelenterates.

HISTORICAL CONTEXT (Fig. 6).—Kölliker (1869) originally unified the subfamilies Pennatulinae and Pteroeidinae into one family. Subsequently, Kölliker (1880) elevated the status of the subfamilies to separate families. Studer (1901: 34) placed the new genus *Gyrophyllum* in the family Pteroeididae. Kükenthal and Broch (1911: 394) stated that *Gyrophyllum* should not be placed in the Pteroeididae due to the presence of three-flanged sclerites, which are characteristic of the family Pennatulidae. Kükenthal and Broch (1911: 463) and Kükenthal (1915: 120) considered the taxon to be a systematic enigma and consequently labeled it as “*incertae sedis*” at the end of their accounts of the Pennatulacea (Williams, 1995).

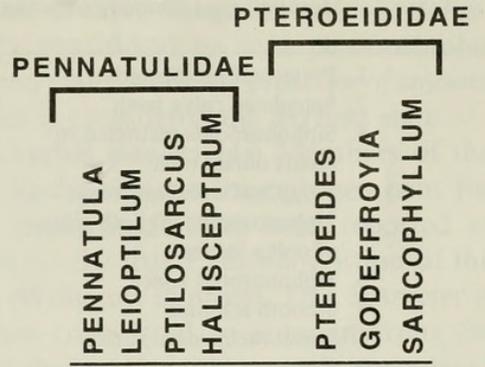
Hickson (1916: 252–253), disagreed with Kükenthal, being of the opinion that *Gyrophyllum* shows stronger affinities to the Pteroeididae than to the Pennatulidae, based on the presence of siphonozooids on the polyp leaves, and that the presence of three-flanged sclerites should not be considered as important a clue to affinity as the placement of siphonozooids. Tixier-Durivault and D’Hondt (1973: 263) concurred with Studer and Hickson, and considered the genus to be a member of the family Pteroeididae. Hickson (1916) also placed *Scytalium* and *Acanthoptilum* in the Pennatulidae along with *Pennatula* and *Leioptilus* (a synonym of *Ptilosarcus*). In addition, Kölliker (1880) placed *Halisceptrum* (a synonym of *Virgularia*) in the Pennatulidae. *Scytalium*, *Acanthoptilum*, and *Virgularia* all have minute and sparsely distributed siphonozooids located on the rachis between the polyp leaves. They have therefore been placed in the Virgulariidae (Williams, 1995).

OUTGROUP.—Williams (1993) has shown that the presence of polyp leaves is considered a synapomorphic feature in the Pennatulacea and serves to distinguish a derived clade composed of the virgulariids (such as *Virgularia* and *Scytalium*), the pennatulids (*Pennatula* and *Ptilosarcus*), and the pteroeidids (such as *Pteroeides*). The pteroeidids are here considered the most highly-derived pennatulaceans on the basis of both the presence of well-developed polyp leaves as well as the restriction of the siphonozooids to the polyp leaves. All other sea pens have siphonozooids present on the rachis. The genus *Pennatula* was here chosen as the outgroup to the pteroeidid genera on the following basis. The well-developed polyp leaves of *Pennatula* are similar to those of the pteroeidids in being large, often thick, fleshy, and opaque, as well as containing numerous autozooids in several layers within the leaves. Most often, the polyps are imbedded within the fleshy matrix composing the leaves. The virgulariids, on the other hand, have polyp leaves that are not as highly developed as the pennatulids and pteroeidids. The virgulariid polyp leaves are often small, thin, and translucent, being composed of the fused polyp

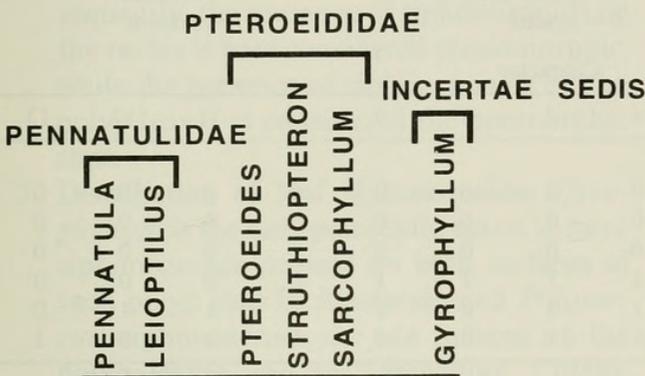
FIGURE 6. Summary of classification schemes for pennatulid and pteroeidid taxa. A. Kölliker, 1869. B. Kölliker, 1880. C. Kükenthal, 1915. D. Hickson, 1916. E. Present study with cladogram showing overlapping characters that unify the six taxa. Williams (1995) considers *Leioptilum* and *Leioptilus* as synonyms of *Ptilosarcus*, *Halisceptrum* as a synonym of *Virgularia*, *Sarcophyllum* as a synonym of *Sarcoptilus*, *Godeffroyia* and *Struthiopterion* as synonyms of *Pteroeides*.



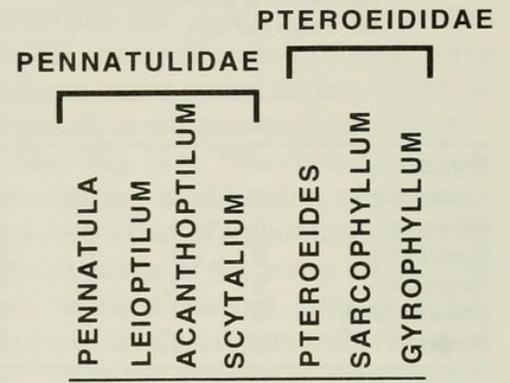
A



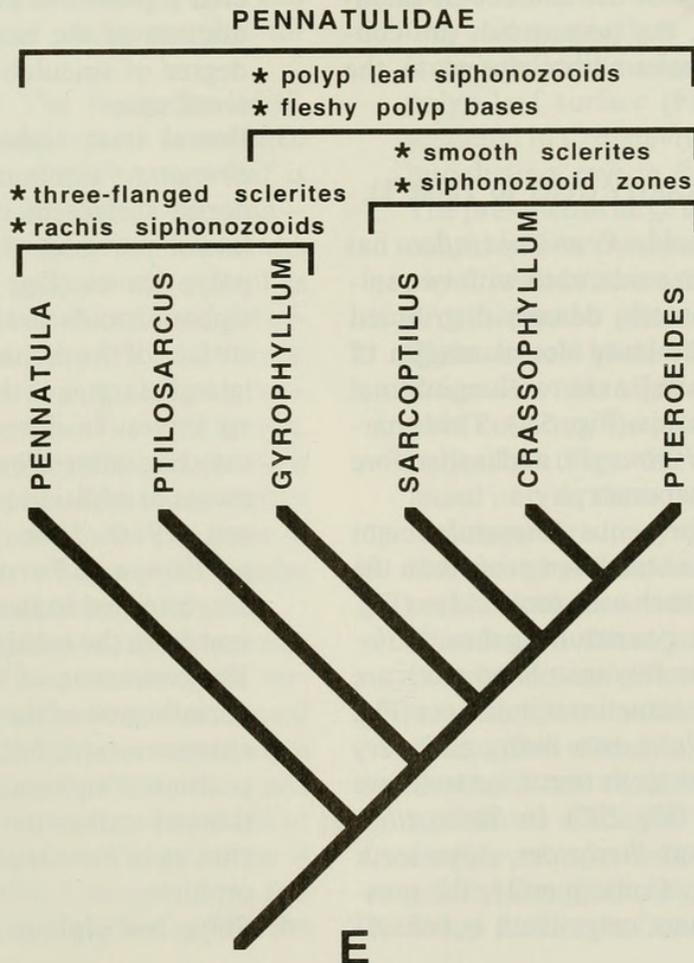
B



C



D



E

TABLE 1. Morphological diversity of pennatulid and pteroeidid pennatulaceans (0 = ancestral state, 1 = derived state).

	Character												
	1	2	3	4	5	6	7	8	9	10	11	12	13
1. Polyp leaf mesozooids													
2. Spiculated calyx teeth													
3. Siphonozooids restricted to rachis dorsal tract													
4. Polyp leaf siphonozooids													
5. Siphonozooids on both sides of polyp leaves													
6. Siphonozooid zones													
7. Smooth sclerites													
8. Distal rachis mesozooids													
9. Siphonozooid pads													
10. Large leaf needles													
11. Siphonozooid plates													
12. Rachis & peduncle sclerites													
13. Polyp leaf rays													
<i>Pennatula</i> (Outgroup)	1	0	0	0	0	0	0	0	0	0	0	0	0
<i>Ptilosarcus</i>	0	1	1	0	0	0	0	0	0	0	0	0	0
<i>Gyrophyllum</i>	0	1	0	1	1	0	0	0	0	0	0	0	0
<i>Sarcoptilus</i>	0	1	0	1	0	1	1	1	1	0	0	0	0
<i>Crassophyllum</i>	0	1	0	1	0	1	1	0	0	1	1	1	0
<i>Pteroeides</i>	0	1	0	1	0	1	1	0	0	1	1	0	1

bodies of a single layer of the autozooids themselves. Consequently, the pennatulids are considered the pennatulacean taxa closest to the pteroeidid clade.

CHARACTERS AND POLARITY (refer to Table 1).

- 1. Polyp leaf mesozooids:** *Pennatula inflata* has conspicuous mesozooids, each with two spiculated terminal teeth, densely-distributed in a row along the basal dorsal margin of each polyp leaf, as well as in two longitudinal rows along the rachis (Fig. 5A). This character is unique to *Pennatula*, and is therefore considered an autapomorphy.
- 2. Calyx teeth:** In the genus *Pennatula*, eight distinctly spiculated teeth are present on the distal portions of each autozooid calyx (Fig. 5A). In the other pennatulid genus, *Ptilosarcus*, only one or two spiculated teeth are present, which are sometimes indistinct (Fig. 5B). In *Gyrophyllum*, two fleshy and very sparsely spiculated teeth occur, or teeth are absent altogether (Fig. 5C). In *Sarcoptilus*, *Crassophyllum*, and *Pteroeides*, calyx teeth are mostly absent. Consequently, the presence of eight distinct calyx teeth is consid-

ered a plesiomorphic character, while a reduction of the number of teeth or of the degree of spiculation is considered the derived state.

- 3. Dorsal tract siphonozooids:** In species of *Pennatula*, siphonozooids are present on the dorsal surface of the rachis as well as the lateral portions of the rachis between the polyp leaves (Fig. 5A). In *Ptilosarcus*, the siphonozooids are restricted to the dorsal surface of the rachis and are absent from the lateral margins of the rachis between the polyp leaves. In *Gyrophyllum*, siphonozooids may be scattered on the dorsal surface of the rachis in addition to the polyp leaves (Hickson, 1916: 254). In *Sarcoptilus*, *Crassophyllum*, and *Pteroeides*, the siphonozooids are restricted to the polyp leaves—being absent from the rachis altogether (Figs. 5D–F). The restriction of the siphonozooids to the dorsal region of the rachis is here considered autapomorphic for *Ptilosarcus* while the disposition of siphonozooids on the lateral portions as well as the dorsal surface of the rachis, as in *Pennatula*, is considered plesiomorphic.
- 4. Polyp leaf siphonozooids:** In species of the

- pennatulid genera *Pennatula* and *Ptilosarcus*, the siphonozooids are restricted to the surface of the rachis, and are not present on the polyp leaves. In *Pennatula firmbriata*, the entire dorsal surface of the rachis is covered with siphonozooids. In the pteroeidid genera, siphonozooids are either restricted to the polyp leaves, or in *Gyrophyllum* may be present on the leaves as well as part of the rachis (Fig. 5C). Also, in other pennatulacean genera with polyp leaves such as *Virgularia*, *Scytalium*, and *Stylatula*, siphonozooids are present on the rachis. Consequently, the presence of siphonozooids on the rachis is here considered plesiomorphic, while the presence of siphonozooids on the polyp leaves is considered the apomorphic state.
5. **Distribution of leaf siphonozooids:** *Gyrophyllum* is the only pteroeidid taxon to have siphonozooids present on both surfaces of each polyp leaf. In *Pennatula* and *Ptilosarcus*, siphonozooids are not present on the polyp leaves and in *Sarcoptilus*, *Crassophyllum*, and *Pteroeides*, they are present only on the lower side of each leaf. The presence of siphonozooids on both sides of each leaf is therefore considered autapomorphic for *Gyrophyllum*.
 6. **Siphonozooid zones:** The restriction of siphonozooids to distinct regions or zones in the proximal region of each polyp leaf is found only in three pennatulacean taxa—*Sarcoptilus*, *Crassophyllum*, and *Pteroeides* (Figs. 5D–F). In the pennatulids, as well as *Gyrophyllum*, the siphonozooids are not organized into distinct zones on the leaves. The presence of siphonozooid zones is considered a synapomorphy for *Sarcoptilus*, *Crassophyllum*, and *Pteroeides*, while their absence is plesiomorphic. In *Crassophyllum* and *Pteroeides*, the zones take the form of siphonozooid plates, while in *Sarcoptilus* they are modified as siphonozooid pads.
 7. **Sclerites:** Three-flanged sclerites, composed of three longitudinal grooves along the surface of an otherwise smooth and elongated sclerite, are present in many pennatulacean taxa including *Pennatula*, *Ptilosarcus*, and *Gyrophyllum*, as well as many less-derived taxa (Figs. 2, 3). The three-flanged state is not found in *Sarcoptilus*, *Crassophyllum*, and *Pteroeides*. Regarding the pteroeidids, the presence of three-flanged sclerites is consequently considered to be a plesiomorphic character state, while the presence of smooth sclerites is considered the derived state.
 8. **Distal rachis mesozooids:** Members of the genus *Sarcoptilus* are the only sea pens for which mesozooids have been reported as present on the distal ventral portion of the rachis (Williams, in press). This character is therefore considered an autapomorphy for *Sarcoptilus*, while its absence is considered plesiomorphic.
 9. **Siphonozooid pads:** The arrangement of the siphonozooids into distinct ovoid swollen pads in the proximal region of each polyp leaf adjacent to the dorsal surface of the rachis, is unique to one pennatulacean taxon—*Sarcoptilus* (Fig. 5D). This character is considered a further modification of the zonation and restriction of siphonozooids in the proximal portions of the polyp leaves. The presence of siphonozooid pads is consequently considered autapomorphic for *Sarcoptilus*, while the absence of these pads is considered the plesiomorphic state.
 10. **Large leaf needles:** Of the eleven genera of sea pens with well-developed polyp leaves, only *Crassophyllum* and *Pteroeides* have large needle-like sclerites contained on the polyp leaf surface (Figs. 5E, F). They are scattered in *Crassophyllum* and are arranged into distinct rays in *Pteroeides* (Figs. 5E, F). The presence of large leaf needles is therefore considered a synapomorphy for *Crassophyllum* and *Pteroeides*, while their absence is considered a plesiomorphy.
 11. **Siphonozooid plates:** In *Crassophyllum* and *Pteroeides*, the siphonozooids form a flat plate covering the proximal portion of each polyp leaf (Figs. 5E, F). This character is found only in these two genera and is therefore considered a synapomorphy.
 12. **Rachis and peduncle sclerites:** In the six pennatulid and pteroeidid genera, sclerites are abundant in the rachis and peduncle of all except *Crassophyllum*, where these sclerites are very sparse or absent. The reduction in the number of rachis and peduncle sclerites is considered an autapomorphy for *Crassophyllum*, while the presence of abundant densely-set sclerites in these regions is considered the plesiomorphic state.
 13. **Polyp leaf rays:** One to several polyp leaf

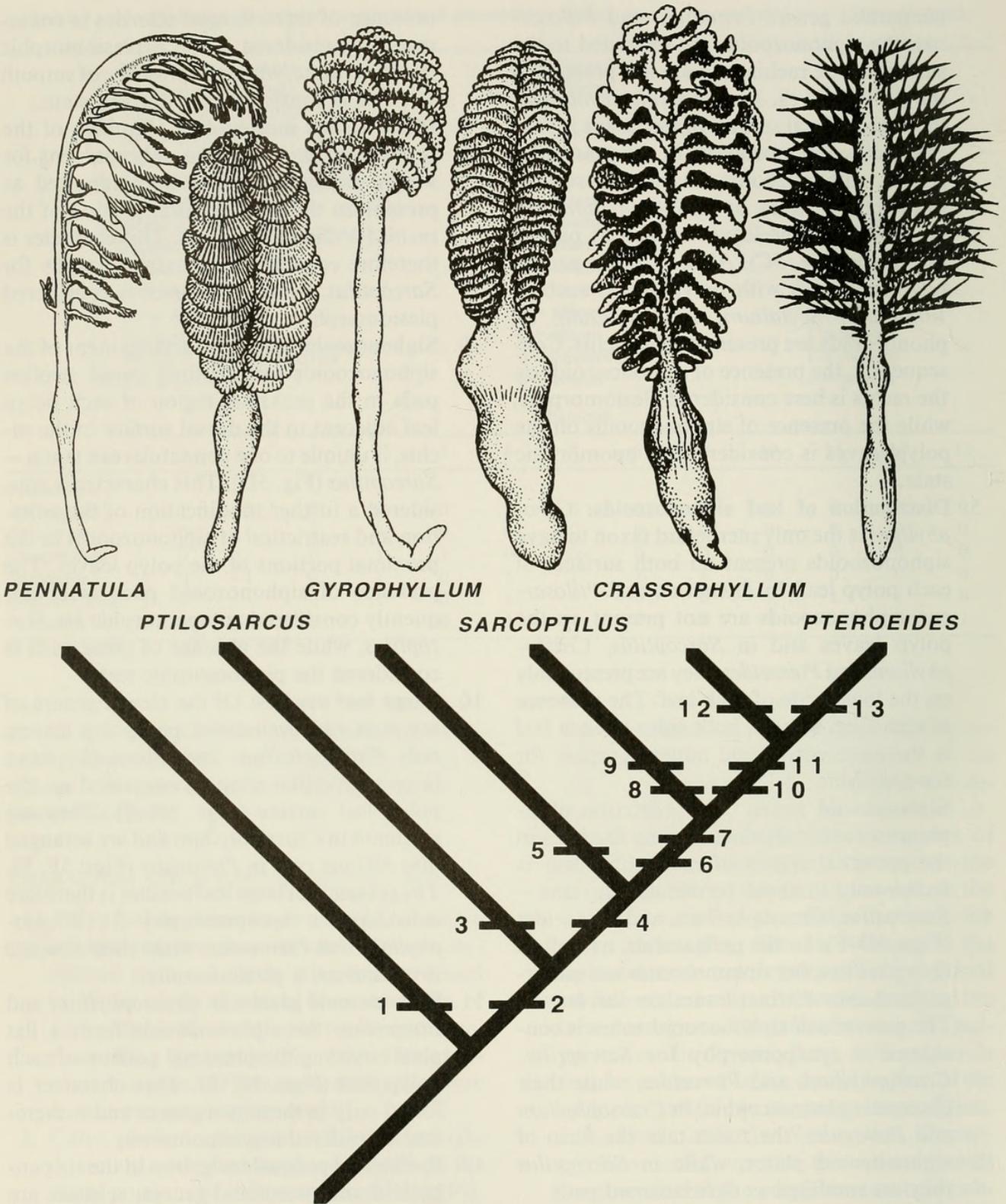


FIGURE 7. Illustrated cladogram of six pennatulid and pteroeidid taxa. Numbered synapomorphies correspond to those in Table 1 and the text (see Discussion).

rays are found in the genus *Pteroeides* and are not present in any other pennatulacean taxon (Fig 5F). These rays are composed of elongate needle-like sclerites aligned in parallel and in close proximity. They act as supporting rays to give a state of rigidity to the

leaves. The rays radiate outward from the proximal siphonozooid zone to (and often beyond) the distal margins of the polyp leaves often resulting in a spiny appearance. In *Pteroeides dofleini* Balss, 1909, a single conspicuous ray is present along the dorsal mar-

gin of each leaf, but multiple rays throughout the surface of the leaf are absent. Because of the uniqueness of this character, its presence is considered autapomorphic to *Pteroeides*, and its absence is considered the plesiomorphic state.

CONCLUSION

The cladogram in Figure 7 was produced from the character matrix in Table 1 using PAUP (Phylogenetic Analysis Using Parsimony) version 3.1. A single tree was generated with a CI (Consistency Index) of 0.923.

A detailed comparative examination of the taxa *Pennatula*, *Ptilosarcus*, *Gyrophyllum*, *Sarcoptilus*, *Crassophyllum*, and *Pteroeides*, shows that *Gyrophyllum* clearly shares characters with both families and therefore bridges the morphological gap between the two (Fig. 6E). In addition, a preliminary cladistic analysis suggests that these six genera formerly assigned to the two families Pennatulidae and Pteroeididae, can best be viewed as representing a single monophyletic group (Fig. 7), thereby making the distinction and retention of the two families, as one of only nominal significance (Williams, 1995).

As a result of the present study, there is no justification for recognizing two distinct families. I therefore consider the Pteroeididae Kölliker, 1880, to be synonymous with the Pennatulidae Ehrenberg, 1834, which has priority. The six genera listed above are here considered members of the family Pennatulidae.

The family Pennatulidae is here defined as follows: bilaterally symmetrical sea pens with large, mostly fleshy polyp leaves; autozooids in one or more rows along the margins of the polyp leaves; anthocodiae retractile into the base of the polyps, which may be fleshy or in the form of spiculated calyces with terminal teeth; mesozooids present or absent; siphonozooids are usually conspicuous and numerous in bands or longitudinal rows on the rachis or polyp leaves, or in pads or plates at the base of the polyp leaves; sclerites are three-flanged or smooth needles, rods, plates, or ovals.

ACKNOWLEDGMENTS

I am grateful to Shane Parker, late Curator of Lower Marine Invertebrates at the South Australian Museum in Adelaide, for originally suggesting the study of the southern Australian pennatulacean fauna and for kindly lending the ma-

terial used in this study. I also thank Karen Gowllett-Holmes, Wolfgang Zeidler, and Eric Matthews of the South Australian Museum for their cooperation. I thank Dr. Stephen D. Cairns (United States National Museum, Washington, D.C.) for his helpful comments regarding the manuscript.

LITERATURE CITED

- BAYER, F. M., GRASSHOFF, M., AND VERSEVELDT, J. 1983. Illustrated trilingual glossary of morphological and anatomical terms applied to Octocorallia. Leiden: E. J. Brill.
- HICKSON, S. J. 1916. The Pennatulacea of the Siboga Expedition, with a general survey of the order. Siboga Expeditie Monogr. 14 (Livr. 77): 1-265.
- KÖLLIKER, R. A. VON. 1869-72. Anatomisch-Systematische Beschreibung der Alcyonarien. I. Die Pennatuliden. Abhandlungen von der Senckenbergischen naturforschenden Gesellschaft 7: 111-2555 (1869); 487-602 (1870); 8: 85-275 (1872).
- . 1880. Report on the Pennatulida dredged by HMS *Challenger* during the years 1873-1876. Report on the Scientific Results of the Voyage of HMS *Challenger* during the years 1873-76, Zoology 1(2): 1-41.
- KÜKENTHAL, W. 1915. Pennatularia. Das Tierreich 43: 1-132. Berlin: Verlag von R. Friedländer.
- KÜKENTHAL, W. AND BROCH, H. 1911. Pennatulacea. Wissenschaftliche Ergebnisse der Deutschen Tiefsee-Expedition auf dem Dampfer 'Valdivia' 1898-1899 13 (1) Lieferung 2: 113-576.
- MARION, A. F. 1906. Étude des coelentérés atlantiques recueillis par la Commission de dragages de l'avis le "Travailleur" durant les campagnes 1880-1881. Oeuvres posthumes du A. F. Marion. Reunies par Paul Gourret. IV. Les Alcyonaires de la première expedition du Travailleur. Expedition scientifique Travailleur et Talisman: 103-151. Paris: Masson.
- ROULE, L. 1905. Notice préliminaire sur les pennatulides recueillis par le Travailleur et le Talisman, dans l'Océan Atlantique, au large du Maroc. Bulletin du Muséum national d'Histoire naturelle 11: 454-458.
- STUDER, T. 1891. Note préliminaire sur les alcyonaires provenant des campagnes du yacht "l'Hirondelle" 1886, 1887, 1888. Part 2. Alcyonacea and Pennatulacea. Mémoires de la Société zoologique de France 4: 86-95.
- . 1901. Alcyonaires provenant des campagnes de l'Hirondelle (1886-1888). Res. Camp. Sci. Monaco 20: 1-64.
- TIXIER-DURIVAUT, A. AND D'HONDT, M.-J. 1973. Nouvelles Récoltes D'Octocoralliaires a Madagascar. Tethys 5 (2-3): 251-266.
- WILLIAMS, G. C. 1993. Biotic diversity, biogeography and phylogeny of pennatulacean octocorals associated with coral reefs in the Indo-Pacific. Proceedings of the Seventh International Coral Reef Symposium, Guam, 1992, 2: 729-735.
- . 1995. Living genera of the sea pens of world seas—illustrated key and synopses (Coelenterata: Octocorallia: Pennatulacea). Zoological Journal of the Linnean Society 113: 93-140.
- . (In press). Revision of the pennatulacean genus *Sarcoptilus* (Coelenterata: Octocorallia), with descriptions of three new species from southern Australia. Records of the South Australian Museum.



Williams, Gary C. 1995. "The enigmatic sea pen genus *Gyrophyllum* — a phylogenetic reassessment and description of *G. sibogae* from Tasmanian waters (Coelenterata: Octocorallia)." *Proceedings of the California Academy of Sciences, 4th series* 48, 315–328.

View This Item Online: <https://www.biodiversitylibrary.org/item/53709>

Permalink: <https://www.biodiversitylibrary.org/partpdf/52962>

Holding Institution

MBLWHOI Library

Sponsored by

MBLWHOI Library

Copyright & Reuse

Copyright Status: In copyright. Digitized with the permission of the rights holder.

Rights Holder: California Academy of Sciences

License: <http://creativecommons.org/licenses/by-nc-sa/3.0/>

Rights: <https://biodiversitylibrary.org/permissions>

This document was created from content at the **Biodiversity Heritage Library**, the world's largest open access digital library for biodiversity literature and archives. Visit BHL at <https://www.biodiversitylibrary.org>.