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A Taxonomic Evaluation of the Comatulid Genus Stephanometra (Echinodermata:Crinoidea)

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A TAXONOMIC EVALUATION

OF THE COMATULID GENUS *STEPHANOMETRA*

(ECHINODERMATA:CRINOIDEA)

BY

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A Thesis

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ABSTRACT

Several genera in the comatulid family Mariametridae are currently ambiguously distinguished on the basis of variations in length and robustness of oral pinnules. Previous descriptions have suggested that at least the genera *Stephanometra* and *Lamprometra* are imperfectly distinguishable. A detailed re-examination of morphology coupled with principal component analyses of morphometric data and cladistic analyses provide support for a monophyletic *Stephanometra* distinct from *Lamprometra.* A preliminary morphological analysis suggests that *Dichrometra* and *Liparometra* should be synonymized with *Lamprometra.* The six currently recognized species of *Stephanometra* uniquely share at least one pair of oral pinnules characterized by enlarged size, reduced ambulacral groove and flat, almost featureless articular facets that together produce a large, stiff, spinelike pinnule. Additional features distinguishing *Lamprometra* from *Stephanometra* include oral pinnular proportions, distribution of cirri and the nature of the adambulacral margin along the brachitaxes and arm bases.

Within *Stephanometra,* two groups of species are currently recognized. Those of the first group, *S. echinus* and *S. tenuipinna,* have long sharp aboral spines on distal cirrals and a spinelike first pinnule. Those in the second group, *S. spinipinna, S. indica, S. spicata* and *S. oxyacantha,* lack aboral cirral spines and are differentiated by oral pinnule features. The latter three have a slender, flexible first pinnule and are distinguished by the number of enlarged spinelike pinnules that follow. In *S. spinipinna,* the first pinnule is also spinelike. Twenty percent of the specimens examined in the *indica-spicata-oxyacantha* series are intermediates that cannot be satisfactorily assigned to species based on current diagnoses. Cladistic analyses suggest that these three form a continuum and should be synonymized (under *S. indica*), that *S. spinipinna*

should be assigned to *S. indica,* and that *S. echinus* and *S. tenuipinna* are synonymous (with *S. tenuipinna* the senior name). Likewise principal component analysis illustrates distinct groupings for these two species.

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TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

INTRODUCTION

The class Crinoidea is widely recognized as the basal group of living echinoderms and includes the stalked sea lilies and the unstalked feather stars. As in most echinoderms, crinoids are composed mainly of calcareous ossicles that form an endoskeleton. A thin layer of epidermal tissue covers the majority of these ossicles. Ossicles contribute greatly to crinoid morphology and are, therefore, important in taxonomy. The crinoid body consists of two distinct regions, the stalk and the crown. Skeletal components called columnals compose the stalk. The crown consists of the calyx and the rays. The calyx typically consists of two coupled circlets of ossicles that support the animal's visceral mass. The oral surface of the visceral mass contains the mouth and the anus. The mouth is typically central, while the anus is located to one side on the apex of a small tube (Messing and Dearborn, 1990).

Eighty-five percent of the ≈600 nominal extant crinoid species are feather-stars, or comatulids (Infraorder Comatulidina) (Simms, 1988). Comatulids differ somewhat from the basic crinoid design. While sea lilies retain a stalk throughout their lives, comatulids only possess a stalk as postlarvae. They take up a free existence as juveniles when their stalks are discarded. Although several groups of fossil crinoids also discarded their stalks, the comatulids are the only ones still extant. Present in abundance since the Lower Jurassic, they now comprise 17 families with 138 genera and 530 species (Rasmussen, 1978). In a series of papers spanning 1907 to 1950, A. H. Clark established 310 of the nominal species.

Comatulids occur in all seas with the exception of the Baltic and Black. They inhabit the shallower subtidal zone down to depths of 5300 m, with most species occurring at shelf depths. The region of greatest diversity occurs in the tropical Indo-West Pacific (Messing, 1975). Shallow waters (<50 m) of the Indo-Malayan/Philippine region of the tropical Pacific support about 100 nominal species (Messing, 1994).

Characterization of comatulid species is frequently based on incomplete species descriptions in which clear and precise lines of division often do not exist (A. H. Clark, 1941). Messing (unpublished) estimates that 40% of nominal comatulid species are described from five or fewer specimens that are often in poor condition. Currently, taxonomy is based on morphological features many of which vary ecophenotypically, geographically, and bathymetrically as well as ontogenetically, confusing species descriptions (Messing, 1994). The ability to accurately identify crinoid species is important for several reasons. First, crinoids are abundant and important in the fossil record and include critical indicator species due to their small stratigraphic ranges and large numbers. Analyses of living assemblages provide important clues for the determination of fossil species (Messing, unpublished). Second, ecology of comatulids is poorly understood due to imprecise species descriptions. Finally, recent findings suggest that compounds produced by comatulids may be useful in the medical field (D. Newman, personal communication with Messing, Feb., 1995). Therefore, the benefits of accurate species identification extend beyond simple phylogenetic relationships into ecosystems, fossil records and medical science.

This research critically re-evaluates the comatulid genus, *Stephanometra* A. H. Clark, and its relationship to other members of the family. Species of *Stephanometra* are abundant and widespread in the Pacific from northern Australia to the Philippines and from Polynesia to east Africa. Current species descriptions are muddled and in need of clarification. Some question also exists about the relation of *Stephanometra* to other members of its family, the Mariametridae. This research will precisely define the morphological features used in taxonomy and to correct inaccurately identified specimens in the literature.

COMATULID MORPHOLOGY

Although comatulids discard their stalk when young, they retain the topmost stalk segment, known as the centrodorsal (Figs. 1 & 2). Hooklike, segmented cirri, composed of ossicles called cirrals, arise in rows, whorls or columns from the centrodorsal and serve to anchor the comatulid (Figs. 1 & 2). Distal cirrus segments may bear aboral spines or ridges; the penultimate cirral may bear an opposing spine, and the terminal segment is usually modified as a claw. The cirri are important characteristics in taxonomy as well as in determination of habitat. Long, prehensile cirri composed of short segments are readily suitable for attachment to gorgonaceans, whereas short, thick cirri are useful for attachment to uneven surfaces of corals, sponges and rocks (Messing, 1975). In species descriptions, the number of cirri is given in Roman numerals, and the number of component segments in Arabic numerals; individual cirrus segments (cirrals) are designated by a "C" followed by an Arabic subscript counting from the base of the cirrus.

Comatulids lack a true calyx structure. The oral surface of the tegmen, or disk, contains both the anus and mouth. The anus is located at the apex of a small tube and is usually displaced to one side, while the mouth is centrally located. The first circlet of ossicles (basals) are reduced and are only visible by dissection. The second circlet, the radial ossicles, form a pentagon that sits on top of and may be concealed by the centrodorsal. Subsequent ossicles (brachials) extend distally and compose the rays (Fig. 2). Brachitaxes are series of two to four brachials terminating in an axil at which the rays branch. Axils may give rise to two unbranched arms, two brachitaxes or one of each. The pattern of ray division is often critical to family- or genus-level taxonomy. Brachitaxes are indicated by Roman numerals beginning with the most proximal, followed by "Br" and the number of component ossicles. Subscripts following "br" indicate specific ossicles. Thus, IIBr2 indicates the second brachitaxis (secundibrach series) composed of two ossicles, whereas $IIIbr_4$ refers to the fourth ossicle of the third brachitaxis (tertibrach series). Brachial ossicles of the free, undivided arms beyond the last axil are indicated by "br" followed by a subscript number (e.g., br_1) (Messing and Dearborn, 1990).

Pinnules, the segmented appendages arranged in alternating series on either side of the arm, are used primarily in food collection (Figs. 1 & 2). However, the first one to several pairs, or oral pinnules (Fig. 2), are often modified for protection of the disk. The length and characteristics of oral pinnules are important in determining generic and familial affinities. Oral pinnules are succeeded by several pairs of genital pinnules which bear the gonads. Genital pinnules typically resemble the following pinnules although they are often shorter. Pinnules are indicated, beginning at the arm base, by subscript numbers for those along the outer side, and letters for those along the inner side of the arm. The inner side of an arm is the side closer to the extrapolated median axis of the preceding axil.

Arm articulations in crinoids generally consist of muscular articulations which contain both muscles and ligaments that provide flexibility and movement. Exclusively ligamentary articulations are also present but provide little flexibility. Two major types of ligamentary articulations appear in comatulids: syzygies and synarthries. A syzygy appears externally as a perforated line and represents an autotomy fracture point (Fig. 2). The perforated appearance is created by radiating ridges of the two faces which are in apposition to one another. Syzygial pairs may be located at regular or irregular intervals and are indicated by a "+" sign connecting the brachial ossicles joined by the syzygy (e.g., br_{9+10}) (Rasmussen, 1978).

Synarthries permit side to side movement by means of a pair of semicircular ligaments separated by a vertically oriented fulcral ridge. In comatulids, synarthries are usually limited to the first joint in a brachitaxes of four ossicles or to the single joint of a brachitaxes composed of two ossicles. Synarthries also occur between the first two arm brachials although they may be replaced here and elsewhere by syzygies (Rasmussen, 1978).

Comatulids are selective suspension feeders, dependent on currents for delivery of food. They modify the posture of both their arms and pinnules to take maximum advantage of the currents. Food consists of protozoans, phytoplankton, crustaceans, molluscs, sediment grains and detritus (Gislén, 1924; Meyer, 1982). Eighty to ninety percent of the particles ingested are <400 μm in length (Liddell, 1982). Transfer of food to the mouth is accomplished via the ambulacral grooves and accompanying tube feet located on the oral surface of the tegmen, arms and pinnules. Tube feet are arranged in groups of three. One long tube foot assists in the capture of food particles while cilia are responsible for transfer of food down the ambulacral groove (Liddell, 1982). Width of the ambulacral groove, length and spacing of the tube feet, number of arms and feeding posture all influence the size of particles ingested (Meyer, 1982).

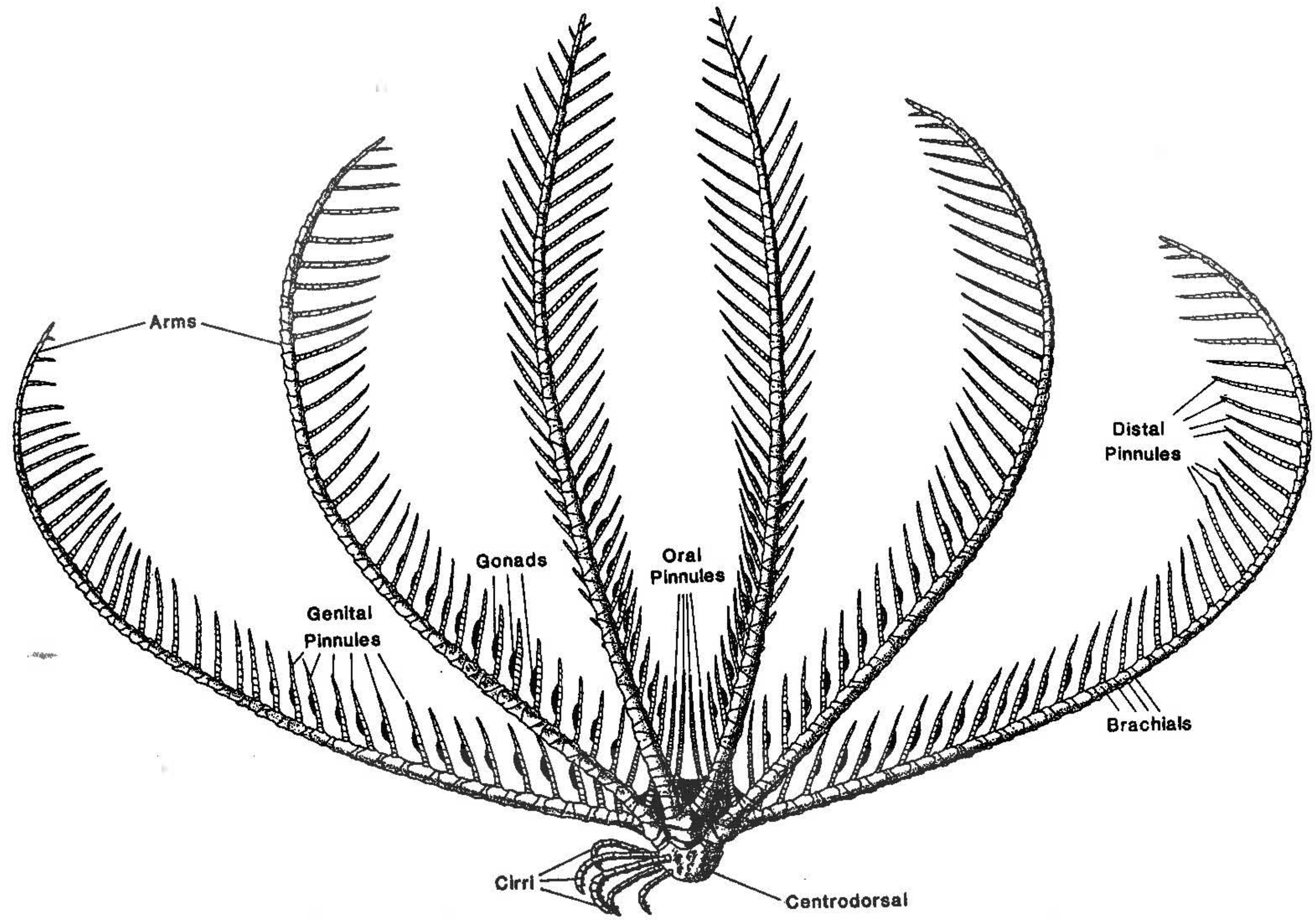


Figure 1. Lateral view of a comatulid, showing centrodorsal, cirri and three rays (Messing and Dearborn, 1990).

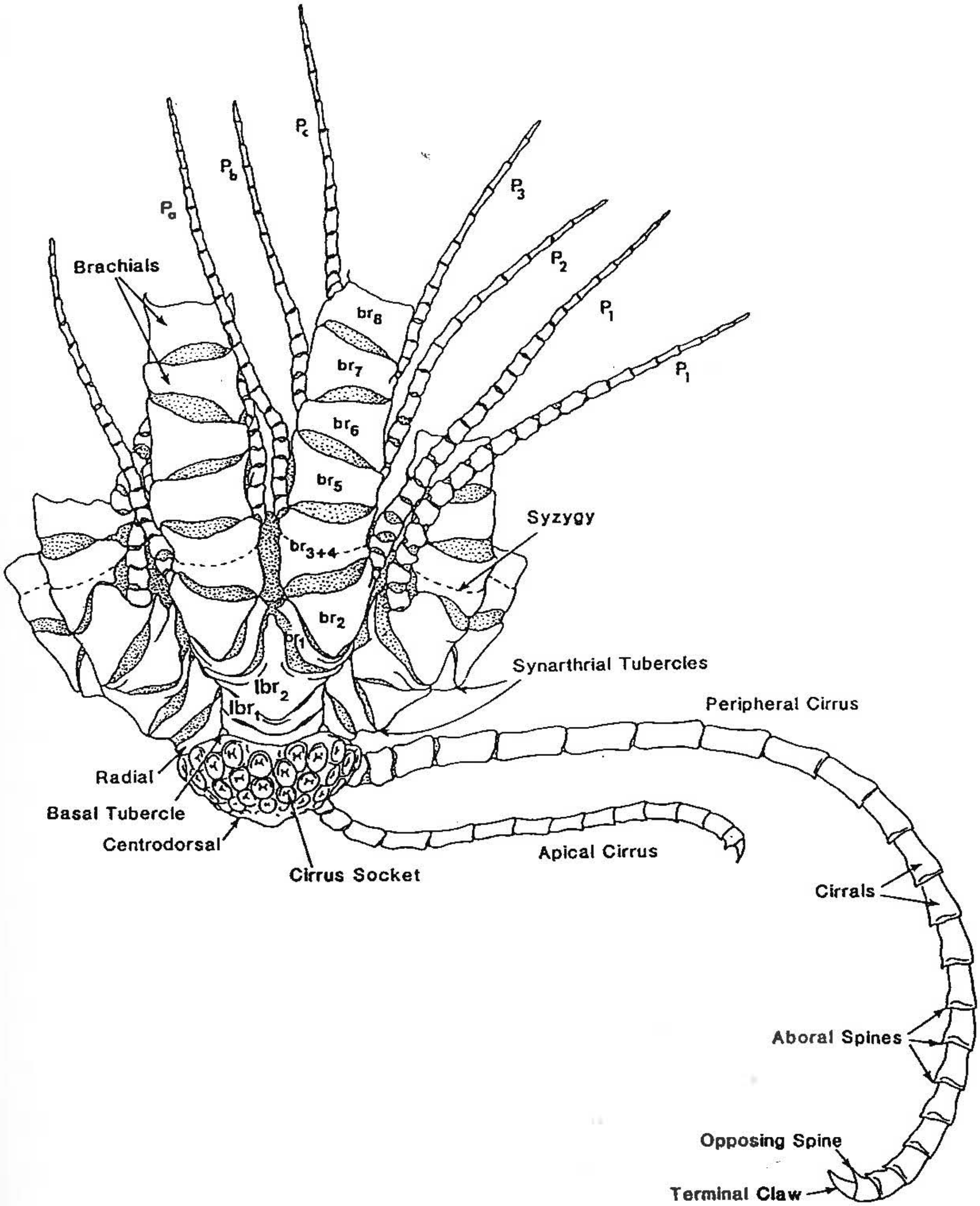


Figure 2. Lateral view of a comatulid, illustrating centrodorsal, cirri and rays. (Messing, 1997)

HISTORY OF THE GENUS *STEPHANOMETRA* AND THE FAMILY MARIAMETRIDAE

The genus *Stephanometra* is currently placed in the family Mariametridae and comprises six species (A. H. Clark, 1941): *S. echinus* (A. H. Clark, 1908a), *S. tenuipinna* (Hartlaub, 1890), *S. spinipinna* (Hartlaub, 1890), *S. oxyacantha* (Hartlaub, 1890), *S. spicata* (Carpenter, 1881) and *S. indica* (Smith, 1876). Clark recognizes 2 subspecies of *S. indica*: *S. indica indica* and *S. indica protectus* (A. H. Clark, 1941).[1]

Both the genus *Stephanometra* and family Mariametridae have fairly convoluted histories that deserve some mention here, especially since the validity of some generic boundaries in the family has recently been brought into question (A. M. Clark, 1972). The family Mariametridae endured some thirty years of modification before arriving at its current standing. In 1874, Lütken (unpublished manuscript, in Carpenter, 1879) described and placed the first species now included in *Stephanometra* in the genus *Antedon*, which, at that time, included most comatulid species. At the time, characteristics of *Antedon* included long, slender, flexible pinnules, with the oral pinnules longer than their successors, and a central or subcentral mouth with the anus off to one side (Carpenter, 1888). During the 1880's, Carpenter revised *Antedon*, placing one or more groups of species into four separate series. Members of the *"Palmata"* group (Carpenter's usage) were differentiated from other groups in having stiff and spinelike P_2 and P_3, which were always longer than P_1. The *"Palmata"* group comprised 23 species including *A. indica, A. protectus, A. spicata* and *A. palmata*. The first three

[1]When referring to the original authors' usage, their (incorrect) spelling of "*protectus*" is used. When referring to the current usage, the correct spelling of "*protecta*" is used.

are now placed in *Stephanometra* and the last in the closely related *Lamprometra (*A. H. Clark, 1913a). In 1907, Clark described a new genus, *Himerometra*, in which he placed the members of both the "*Palmata* " group and another, the "*Savignyii*" group (Carpenter's usage; ten species with ray bases not laterally flattened). In 1908, Clark assigned *Himerometra* and three other new genera, *Pontiometra, Cyllometra* and *Oligometra,* to a new family, Himerometridae. Characteristics of the Himerometridae included oral pinnules sometimes stiffer and stouter than other pinnules, but not notably defined; one or more oral pinnules elongated; proximal joints of lower pinnules with thin, elongated processes; short cirri, and ten or more arms (A. H. Clark, 1908b).

In 1909, Clark expanded the himerometrids to accommodate seven new genera, one of which was *Stephanometra* (A. H. Clark, 1909a). Distinguishing characteristics of *Stephanometra* included lateral processes on brachitaxis ossicles and one or more stiff and spinelike oral pinnules (A. H. Clark, 1909a). The genus included nine species: *S. acuta* (A. H. Clark, 1909a), *S. echinus, S. indica, S. monacantha* (Hartlaub, 1890), *S. oxyacantha, S. spicata, S. spinipinna, S. tenuipinna* and *S. tuberculata* (Carpenter, 1888). Three of these, *S. acuta* (A. H. Clark, 1900a), *S. monacantha* and *S. tuberculata,* were subsequently synonymized under *S. indica protectus, S. indica indica* and *S. spicata,* respectively (A. H. Clark, 1909a). Later the same year, Clark (1909b) erected a new family, Pontiometridae, which included species with greatly elongated and slender oral pinnules. The Pontiometridae included three subfamilies: Himerometrinae, Stephanometrinae and Mariametrinae. He distinguished the Himerometrinae by short brachials and a IIBr series composed of four ossicles, whereas both the Mariametrinae and Stephanometrinae had cuneate (wedge-shaped) brachials and brachitaxes composed of two ossicles. Members of the Mariametrinae lacked lateral processes on their brachitaxis ossicles and had enlarged but flagellate proximal pinnules. Members of Stephanometrinae possessed lateral processes and included species in the genera *Oxymetra* and *Stephanometra.*

In 1911a, A. H. Clark elevated each of the three subfamilies to family level. The proximal pinnules of the Mariametridae and Himerometridae were unmodified and similar in length, whereas the proximal pinnules of Stephanometridae were distinguished by varying length and stiffness.

A. H. Clark (1912a) transferred *Oxymetra* to the family Mariametridae, leaving the family Stephanometridae monogeneric. In 1913a, he revised the Mariametridae to include those species that possessed more than ten arms, brachitaxes composed of two ossicles, cirri with a median aboral process, and flagellate enlarged proximal pinnules. Genera of this revised family included *Pontiometra, Oxymetra, Selenemetra* (now a synonym of *Oxymetra*), *Mariametra* and *Dichrometra.*

In 1924, Gislén described the superfamily Mariametrida as having a central mouth, ten or more arms, a flat radial articular face, discoidal centrodorsal, the first two ossicles of the IIBr united by a synarthry, oral pinnules carinate, distal pinnules not carinate, well developed cirri, aboral side of cirrals rounded or carinate with or without aboral spines, and cirrus sockets rarely in more than two alternating whorls.

In 1941, A. H. Clark eliminated the family Stephanometridae, removing its single genus, *Stephanometra*, to the family Mariametridae. He distinguished the Mariametridae by a steep radial articular face, IIBr series composed of two ossicles, and distal cirrals aborally carinate or bearing aboral spines. The seven included genera were: *Oxymetra, Pelometra, Liparometra, Lamprometra, Dichrometra, Mariametra* and *Stephanometra.*

He characterized the genus *Stephanometra* as having: 1) cirri of fewer than 40 segments, 2) stiffened oral pinnules, and 3) brachitaxis ossicles well separated with lateral processes.

Depending on the species, one or more of the oral pinnules might be prominently stiff and spinelike (A. H. Clark, 1941).

Currently, the main diagnostic features for species in the genus are the number of stiff oral pinnules and the presence or absence of aboral cirral spines (A. H. Clark, 1941; Gislén, 1940; A. M. Clark, 1972), although A. H. Clark (1941) claims that pinnules stiffen with age. Confusion arises because in some specimens, different rays bear numbers of stiffened pinnules characteristic of different species. If pinnules do indeed stiffen with age, certain species of *Stephanometra* may represent a growth series. This research will also examine other diagnostic features to provide further taxonomic clarification.

The genus currently comprises six species divisible into two groups. Those in the first group, *S. echinus* and *S. tenuipinna,* have long, sharp aboral spines on their distal cirrals, and a stiff and spinelike P_1. The four species that constitute the second group, *S. spinipinna, S. oxyacantha, S. spicata,* and *S. indica*; lack aboral spines on the cirri and are differentiated by features of the oral pinnules (A. H. Clark, 1941). All members are characterized by a stiff and spinelike P_2. *S. spinipinna,* apart from the rest, has P_1 stiff and spinelike and shorter than P_2. The latter three species have a slender flexible P_1 and are primarily characterized by the number of enlarged oral pinnules that follow. The second to fourth or fifth pinnules are spinelike in *S. oxyacantha.* The second and third are spinelike in *S. spicata,* and only the second is spinelike and stiffened in *S. indica.*

A. H. Clark (1941) treated *S. protectus* as a subspecies of *S. indica,* the only distinction between the two being the length and shape of P_2. P_2 of *S. indica indica* consists of 16-20 pinnulars and tapers to a fine point. P_2 of *S. indica protectus* consists of 9-16 pinnulars and is sharply pointed.

A. M. Clark (1972) noted vague areas regarding A. H. Clark's account of the genera *Stephanometra* and *Lamprometra*. According to her, pinnule descriptions of *S. indica indica* and *S. indica protecta* closely parallel that of *L. palmata*, suggesting that the two genera might not be properly recognized as distinct.

OBJECTIVES

This research examines the taxonomic status and interrelationships of the six species in the genus *Stephanometra*. Special attention is given to the *S. indica*–*S. spicata*–*S. oxyacantha* series, which, based on existing descriptions, may represent a growth series. The status of *S. echinus* and *S. tenuipinna* is investigated in light of A. H. Clark's (1941) suggestion that *S. tenuipinna* may be the juvenile of *S. echinus*. The obscure line between *S. indica indica* and *S. indica protecta* is clarified. Finally, this project emends the generic diagnosis by reexamining old characters and exploring new ones, especially with respect to distinguishing *Stephanometra* from the morphologically similar genus *Lamprometra*.

MATERIALS AND METHODS

This research employed a total of 203 preserved specimens collected from the Republic of the Marshall Islands, Kiribati (Gilbert Islands), Micronesia, Fiji, Australia, Louisiades Archipelago, Papua New Guinea, Indonesia, Malaysia, Thailand, South China Sea, Philippines, Andaman Sea, Maldives, Seychelles and Mauritius. Ninety-three of these specimens are in the Nova Southeastern University Oceanographic Center (NSUOC) collection were collected by C. G. Messing, D. L. Rankin, P. Colin, C. Arneson, L. Harris and L. Sharron; one specimen is on loan from Gustav Paulay; four are Coral Reef Research Foundation (CRRF) specimens; 60 are from the United States National Museum (USNM, now the National Museum of Natural History, Washington, D.C.); nine are from the British Museum of Natural History (BMNH), and

36 are on loan from the Institut Royal des Sciences Naturelles de Belgique (IRSCB) collected by M. C. Lahaye at Papua New Guinea.

The majority of specimens were collected via SCUBA. Exceptions are older dredged specimens in the BMNH and USNM, or specimens for which the date and/or collection method is unknown. Approximately 115 of the specimens collected by C. G. Messing and M. C. Lahaye, and about 20 specimens on loan from the Smithsonian, were collected within 20-25 m of the surface; 13 were collected as deep as 41 m. Four specimens collected by the Challenger expedition were reported from 411 m. However, these depths are probably inaccurate since these specimens were most likely taken during shore collection (A. H. Clark, 1941).

Specimens collected by C. G. Messing and D. L. Rankin were fixed in 90-95% ethanol and transferred to 70% ethanol for storage. The IRSCB collection consist mostly of dry specimens; all other specimens were preserved in ethanol.

Measurements and illustrations were made by means of a Wild M-5 binocular dissecting microscope with camera lucida attachment. Measurements were calculated by dividing image size by magnification to obtain the actual length. Centrodorsal, aboral pole and brachial measurements were rounded to the nearest 0.5 mm, cirrus length was rounded to the nearest 1.0 mm and ray length to the nearest 5.0 mm.

Measured skeletal components include: centrodorsal height (H) and basal diameter (D), aboral pole diameter (P), cirrus length, ray length, length and width of Ibr_1 (both measurements taken from center of ossicle) and Ibr_2 (length taken down center, width taken from outermost corner to outermost corner), width of br_{10}, length of the 6^{th} pinnular on P_2, and length of oral pinnules P_1-P_5. D/H indicates the ration of centrodorsal basal diameter to height; D/P indicates the ratio of the centrodorsal basal diameter to aboral pole diameter; W/L indicates the width (W) to length (L) ratio of individual ossicles or pinnulars. Measured pinnules and brachials were taken from exterior rays only. Only the largest cirrus from each specimen was measured. Curved structures were traced with the camera lucida and measured by running a wax string along the traced image and straightening the string along a metric ruler. Ray length was determined by placing a wax string along an outer arm from the radial to the distal tip of the arm.

Other described components include: shape of aboral pole and centrodorsal, development of synarthrial tubercles, appearance of radials, appearance and fusion versus lateral separation of Ibr_1, appearance of Ibr_2, shape of outer margin of primibrach series, features of lateral adambulacral margin of $IIbr_1$ (chosen because of its long, distinctive margin), number of rows of cirri, number of cirri, number of cirrals, arm number, location of IIIBr, location of syzygies on exterior rays, ambulacral groove and articular facet development on oral pinnules, number of pinnulars, and description of oral pinnules.

Selected specimens were dissociated in full strength commercial bleach (5% sodium hypochlorite solution) for examination of articular facets and other skeletal features using both light and scanning electron microscopy (SEM). Ossicles were dried and mounted on SEM stubs with double-sided adhesive tape. Samples were coated with palladium and examined in an ISIDS130 SEM operated at 20 KV.

Principal component analyses (PCA) were performed using SYSTAT 8.0. PCA is a method that reduces multidimensional, multivariate data to fewer components. It does so by identifying those variables that are highly correlated and combining them into fewer components. PCA is effective in determining the correlation of variables and was used to verify and support visual examination of morphological features (Kachigan, 1991). Data were standardized to ensure that all variables were weighed equally (Sharma, 1996). Varimax rotation was used to improve the interpretability of the components (factors). Varimax rotation minimizes the complexity of components by maximizing the variance of loading on each component (Tabachnick and Fidell, 1996). Scree tests were used to determine the number of components retained (Appendices 1, 3 & 4). Components scores, scores the variables would have received on each of the components had the variables been measured directly, were saved and used to plot the components. The advantage of using these scores is that the new variables are not correlated; therefore, the problem of multicolinearity is avoided (Sharma, 1996).

Phylogenetic relationships of *Stephanometra* and *Lamprometra* were evaluated with PAUP* 4.0b4 (Swofford, 1993) and MacClade 3.0 (Maddison and Maddison, 1992). A total of 7 species in two genera were analyzed: *Stephanometra echinus, S. tenuipinna, S. spinipinna, S. oxyacantha, S. spicata, S. indica* and *Lamprometra palmata* (treated as the outgroup).

Characters and character states are listed below. Asterisks indicate continuous gap-weighted characters: and a superscript 'o' indicates ordered characters. Characters were ordered if the relationship between the character states was known.

Characters and Character States used in the Phylogenetic Analysis

1. Centrodorsal diameter (mm) / aboral pole diameter (mm).*
2. Centrodorsal diameter (mm) / height (mm).*
3. Centrodorsal: 0) dome shaped with sloping sides; 1) flat-topped with sides slightly sloping or vertical.
4. Cirrus length (mm)/ number of segments.*
5. Arm number*
6. Arm radius (mm).*
7. P_1 number of segments / length (mm).*
8. P_2 number of segments / length (mm).*
9. P_3 number of segments / length (mm).*
10. P_4 number of segments / length (mm).*
11. P_5 number of segments / length (mm).*.
12. [Pinnular 6 (of P_2) length (mm) / length P_2 (mm)] X 100. *

13. Aboral pole: 0) cirri encroaching on pole; 1) cirri restricted to lateral margins of the centrodorsal. O Characteristically, cirri encroaches the aboral pole in juvenile specimens; whereas, in more mature specimens the cirri are restricted to the margins of the centrodorsal.

14. Lateral margin of Ibr_1 in aboral view: 0) parallel; 1) converging; 2) diverging.

15. Lateral adambulacral margin of brachitaxis ossicles: 0) curved; 1) parallel; 2) oblique.

16. Crenulated exterior margins of brachitaxis ossicles: 0) absent; 1) present.

17. Adambulacral margin scallops: 0) absent; 1) weak; 2) strong.

18. Aboral view of axil scallop: 0) absent; 1) extends entire length of axil; 2) proximal.

19. Aboral view of $IIbr_1$ scallop: 0) absent; 1) extends entire length of $IIbr_1$; 2) proximal.

20. Lateral profile of ray bases: 0) rounded; 1) flat sided.

21. Aboral cirrus ornamentation: 0) strong spines; 1) carinate; 2) swollen processes with triangular spine; 3) no spines.

22. Aboral carination of oral pinnules: 0) absent; 1) present.

23. Terminal oral pinnular: 0) flagellate; 1) conical.

24. Pinnular 6 of P_2 L/W Ratio: 0) <1.5; 1) >1.5.

25. Articular facets: 0) articulated; 1) flat. O The presence of flattened articular facets is unique to species of *Stephanometra*.

26. Development of triangular fossae on articular facets: 0) absent; 1) present

27. Process on distal ends of pinnulars: 0) present; 1) absent. O Distal processes are common in comatulids: whereas absence of these processes is exclusive to species of *Stephanometra*.

28. Number of stiff and spinelike pinnules: 0) none; 1) one; 2) two; 3) three; 4) four; 5) five. O Stiff pinnules are unique to species of *Stephanometra* within the family and rare outside it.

29. Number of rows of cirri: 0) one; 1) one-two; 2) two; 3) two-three; 4) three; 5) three-four.

30. Ibr_1: 0) free; 1) partly united with adjacent Ibr_1; 2) united with adjacent Ibr_1.

31. Stiff and spinelike P_1: 0) absent; 1) present.

32. Synarthrial tubercles: 0) weak; 1) moderate; 2) well developed; 3) rugose.

Controversy exists as to whether quantitative characters should be employed in cladistic analysis. Such characters have not been considered suitable for cladistic analysis because no justifiable basis exists for recognizing discrete states among them; they are often viewed as "not cladistic" (Pimental and Riggins, 1987). Thiele (1993), however, demonstrated that morphometric data are just as informative of cladistic patterns as qualitative data and should not be excluded from consideration in cladistic analysis. Gap weighting, a method for coding morphometric data, retains information on rank order of character states and sizes of gaps between states. All differences between states are accepted as informative (Thiele, 1993). A modified version of gap weighting was applied to morphometric data here according to the following formula:

$$x_s = [(x_i - x_{min})/(x_{max} - x_{min})] * n \qquad (1)$$

where x_s is the standardized value; x_i is the value of the morphometric character for an individual specimen; x_{min} is the minimum value of the morphometric character of all individuals included in the species and x_{max} is the maximum value of the morphometric character for all individuals included in the species.

Each specimen was treated as a taxon; therefore, x_i refers to the data for the individual specimen (not the mean, median or mode). Data was analyzed using both MacClade and PAUP*. The maximum number of ordered states allowed for MacClade is 26 and for PAUP 32; thus, n was given the value 25. Gap weighted data was rounded to the nearest integer and entered into MacClade along with the qualitative data.

Trees were constructed using PAUP*4.0*b*4 on a Power Macintosh G3 computer. Since there were 177 "taxa" and only 32 characters, the number of taxa had to be reduced (Brian Crother, per. comm. May 2000). Representative specimens were chosen randomly by number from pools of identified specimens by Chris White, a colleague unfamiliar with the species in question. A minimum of two specimens from each "species" and intermediate specimen groupings ("*indica/spicata*" and "*spicata/oxyacantha*") were chosen. Branch and bound searches with bootstrap analysis using maximum parsimony criteria were performed to provide statistical support for the resulting tree nodes. Tree length (TL), consistency index (CI), retention index (RI) and rescaled consistency index (RCI) were calculated from the resulting topology.

SYSTEMATIC PART

Family Mariametridae A. H. Clark, 1911

Mariametridae A. H. Clark, 1911b:649; 1941:391-396.—Utinomi and Kogo, 1965:273-276, fig. 7.—A. M. Clark, 1972:95-97.—Zmarzly, 1985: 352-353.— Chen *et al.*, 1988:78, figs. 20, 21.— Stevens, 1989:4-20-4-23. — Kogo, 1998:61-70, figs. 49-56.

Genus *Stephanometra* A.H. Clark, 1909

Antedon (part) Lütken, 1874:190 (in Carpenter, 1879).

Comatula (part) Smith, 1876:406.

Himerometra (part) A. H. Clark, 1907:356.

Dichrometra (part) A. H. Clark, 1909a:13.

Stephanometra A. H. Clark, 1909a:9; 1909b:176; 1911c:185; 1912b:269; 1912c:35; 1912d:145; 1912e:401; 1912f:11,13, 57, 132; 1941:407-409. — Gislén, 1924:59, 64, 66, 89, 99, 100, 235. — Zmarzly, 1985:352-353. — Chen *et al.*, 1988:78.— Kogo, 1998:61-63.

Lamprometra (part) H. L. Clark, 1915b:104. —A. H. Clark 1941:472-475. — Utinomi and Kogo, 1965:274-276.— Zmarzly, 1985:352.— Chen *et al.*, 1988:78. —Kogo, 1998:61-63, 65-67.

Diagnosis.—A genus of Mariametridae having the centrodorsal convex discoidal with gently sloping sides; cirrus sockets encroaching on aboral pole; brachitaxes well-separated; brachitaxis ossicles bearing rounded adambulacral processes that may be parallel or oblique to the longitudinal axis of the ossicle and producing characteristically scalloped lateral or knobbed margins; fewer than 40 cirrals; distal cirrals with prominent aboral spine or slight aboral carination; one or more pairs of oral pinnules with reduced ambulacral groove, flat articular facets, conical tip, and with most pinnulars 1.5-4.0 times longer than broad.

Geographic distribution.—Recorded from Tanzania in the west to the Republic of the Marshall Islands and Fiji in the east, including tropical Australia as far south as the Capricorn Channel of Queensland, and from the Red Sea to Madras, India, east to Taiwan and as far north as Japan.

Bathymetric range.—Littoral to 62 meters.

Remarks.— A. H. Clark (1941: 407) distinguished *Stephanometra* from other members of the family Mariametridae chiefly on the basis of "one or more of the oral pinnules enlarged, greatly stiffened, sharp pointed, and spinelike . . ." His diagnosis of the most closely similar genus, *Lamprometra*, refers to the longest, stoutest pinnule (P_2) as ranging from very stout to slender. Unfortunately, his species descriptions include substantial overlap between the two. He refers to P_2 of *S. indica* in comparison with other members of S*tephanometra* as "somewhat less enlarged and stiffened, usually more or less strongly recurved distally becoming slender and delicate, though not flagellate" (1941:409). P_2 of *Lamprometra palmata palmata*, "though tapering . . . may be straight and almost spinelike." As a result, A. M. Clark (1972) found it difficult to distinguish *Lamprometra palmata* from *Stephanometra indica* and thought that the two genera tended to intergrade. She noted that a specimen from Muhlos, Maldives, appeared twice in the monograph (A. H. Clark, 1941), first as *S. indica* (p. 453) and later as *L. palmata* (p. 502). A. M. Clark's illustration of P_2 of the Muhlos specimen her Fig. 10e and P_2 of the holotype *S. indica* her Fig. 10g were meant to provide a comparison of the flagellate versus spinelike forms. P_2 of the Muhlos specimen, composed of elongated pinnulars and tapering to a fine point, was illustrated as *L. palmata palmata*. I disagree with A. M. Clark and regard this specimen to be a much smaller specimen of *S. indica* than the holotype, which bears the third largest P_2 in the current study (see pp. 66, Fig. 28). Figure 3 accurately illustrates the difference between "stiff and spinelike" (Figs. 3a-d) and "flagellate" (Figs. 3e-g).

A. M. Clark (1972), after noting the unreliability of the pinnules as a consistent character, suggested that the shape of the lateral adambulacral margins of division series ossicles may be the defining characteristic of the genus *Stephanometra*. Lateral margins of *Lamprometra* tend to be smooth in comparison with the broad, scalloped lateral processes of *Stephanometra*. A. H. Clark (1941:407) described brachitaxes of *Stephanometra* as well separated, with component ossicles bearing rounded ventrolateral (adambulacral) extensions. In comparison, he described those of *Lamprometra* as typically in close lateral contact, having component ossicles with flattened sides; rarely are the ossicles just in contact and the sides slightly or not at all flattened. Lateral adambulacral margins in *Lamprometra* bear a straight continuous edge and are blunter than those in *Stephanometra*. In the latter, the margins are flanged and rounded off at each end, producing a scalloped appearance (A. M. Clark, 1972). However, she also noted specimens in which the lateral adambulacral margins were slightly scalloped, as in *Stephanometra*, while P_2 had a flagellate tip, as in *Lamprometra*.

The current study reveals that, while specimens of both genera may bear robust, straight oral pinnules, several additional features consistently distinguish the two. In *Stephanometra*, the enlarged oral pinnules bear a reduced ambulacral groove and are composed of pinnulars that are chiefly 2-3 times longer than wide. The articulations between these segments consist of flattened, often almost smooth, facets joined by reduced tissue (Figs. 4a & b). Scallop-like processes along the lateral adambulacral margins of the brachitaxes are oriented obliquely and may produce elongated knobs on the proximal lateral portion of the axils. In addition, the centrodorsal is convex with sloping sides and the aboral pole is reduced by encroachment of the apical cirrus sockets. Reduced articular facets contribute to both the styliform appearance and stiffness of oral pinnules; however, A. H. Clark (1941:44) did not include this feature in his generic diagnosis.

By contrast, the pinnulars of the robust and occasionally spinelike P_2 in *Lamprometra* are barely longer than wide and always bear typical, well-developed ambulacral grooves and articular facets (Figs. 5a & b). The lateral adambulacral margins of the brachitaxis ossicles lack scalloped processes and range from strongly flattened against each other to separated. The centrodorsal bears a broad aboral pole with cirrus sockets restricted to its lateral margins.

Characters for *Stephanometra* thus include: P_2 of 8 to 18 pinnulars, L/W of middle pinnulars 1.5-4.0; at least P_2 with reduced articular facets, reduced tissue between pinnulars, and a conical tip (Fig. 6), together producing a large, stiff spinelike pinnule; centrodorsal discoidal or dome-shaped; polar area with encroaching cirrus sockets; lateral margins of brachitaxis ossicles straight, weakly swollen or with well-rounded lateral processes or oriented obliquely oriented and restricted to the proximal portion of the ossicle as elongated knobs; those on $IIbr_1$ obliquely oriented and spanning the entire length of the ossicle.

In contrast, *Lamprometra* has P_2 of 12-37 pinnulars, L/W of middle pinnulars 1.0-1.5, rarely longer; oral pinnules with normally developed articular facets and tissue between pinnulars, and a flagellate tip embellished with small spines, together lending a tapering, flagellate appearance; centrodorsal thin and discoidal with a flat aboral pole surrounded on outer margins by cirri; lateral adambulacral margins either flat sided, apposed and weakly thickened laterally, or neither flat sided, apposed nor laterally thickened (scalloped processes absent).

A plot of aboral pole diameter against centrodorsal diameter for *Stephanometra* and *Lamprometra* indicates that for a given aboral pole diameter, the centrodorsal diameter in

L. palmata specimens is wider (Fig. 7). There is a sight overlap among several of the juvenile specimens; however, the two genera otherwise fall out in separate clouds. Diameters of the centrodorsal and aboral pole were selected for graphing because they vary with growth and size. Plots of the length of pinnular 6 of P_2 against several growth-related characters (Figs. 8-10) show two genera as distinctly separate clouds with very little overlap among the juvenile specimens. Length of pinnular 6 was selected because it consistently distinguishes the two genera. Of the two species of *Stephanometra* recognized herein, *S. tenuipinna* forms a continuum with *S. indica*, reflecting the close relationship of these species. In addition, of the plots of principal component scores (Figs. 11-13) for *S. tenuipinna*, *S. indica*, and *Lamprometra palmata*, that of component 1 versus component 3 (Fig. 12) in particular, illustrates distinct groupings for the two genera with *S. tenuipinna* and *S. indica* forming a continuum, in agreement with the qualitative morphologic data. Component loadings exceeding 0.50 were interpreted as follows: component one represents a size factor including variables such as cirrus length, arm radius, length of Ibr_1, and the length of P_1-P_5, component two designates shape-related data including aboral pole diameter and arm number, component three loads high on length of the 6^{th} pinnular from P_2 and is therefore considered a pinnular shape factor (Appendix 1).

A. M. Clark (1972) concluded that *Stephanometra* should be included in synonymy with *Lamprometra, Liparometra* and *Dichrometra* because it tends to integrate with *L. palmata*. However, a detailed re-examination of morphologic features as well as cladistic analyses (Fig. 14) support a monophyletic *Stephanometra* distinct from *Lamprometra*. A branch and bound search with bootstrap analysis (250 replicates) using maximum parsimony, all characters weighted equally, resulted in one most parsimonious tree with TL = 175, CI = 0.621, RI = 0.177, and RCI = 0.088. The relationship of *Dichrometra* and *Liparometra to Lamprometra* will be discussed under the latter genus.

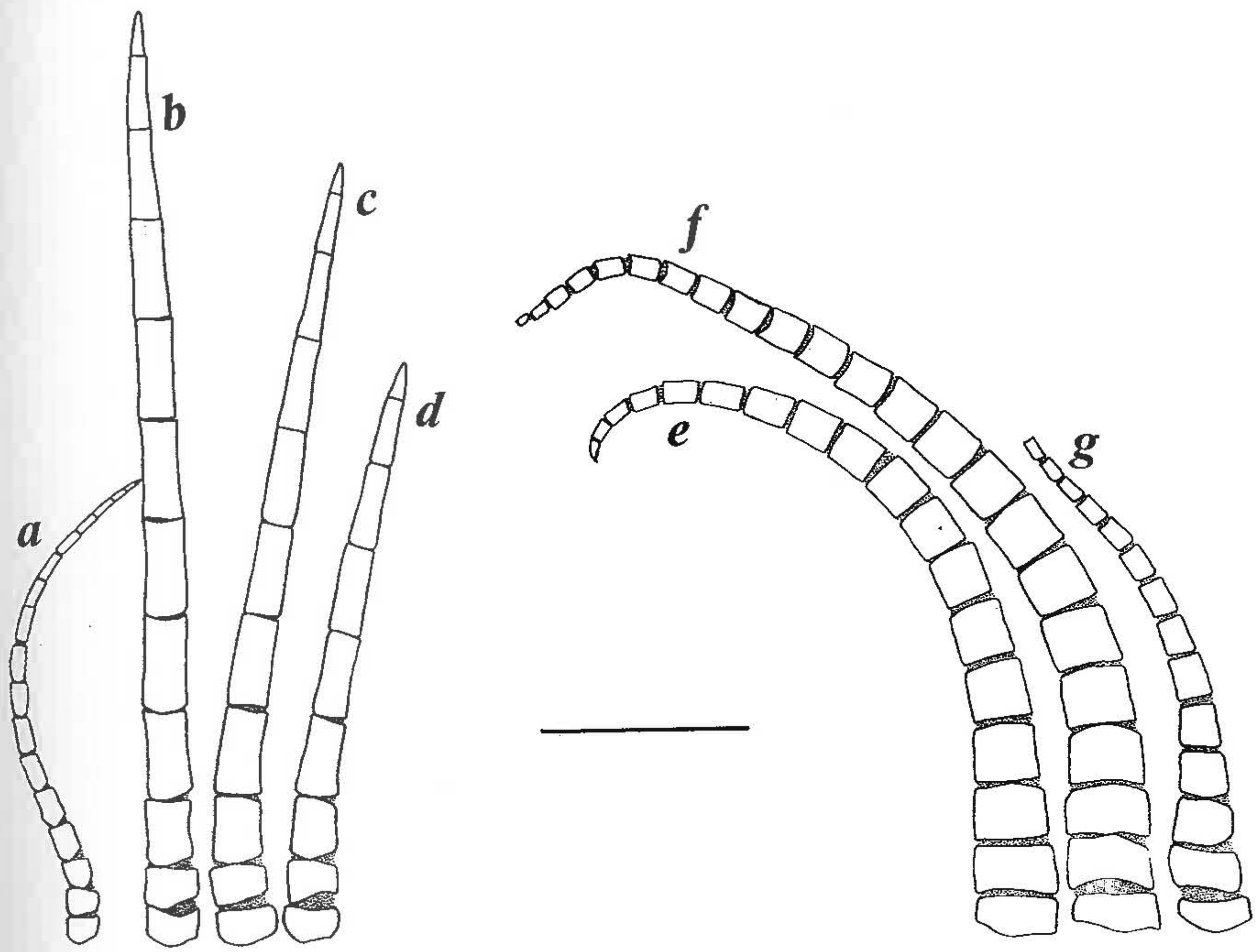


Figure 3. *Stephanometra* versus *Lamprometra*. Figs. a-d: *Stephanometra* with P_2- P_4 stiff and spinelike. a. P_1, IRSCB 232. b. P_2, same. c. P_3, same. d. P_4, same. Figs. e-g: *Lamprometra* with flagellate pinnules. e. P_1, IRSCB 326. f. P_2, same. g. P_3, same. Scale: 2mm.

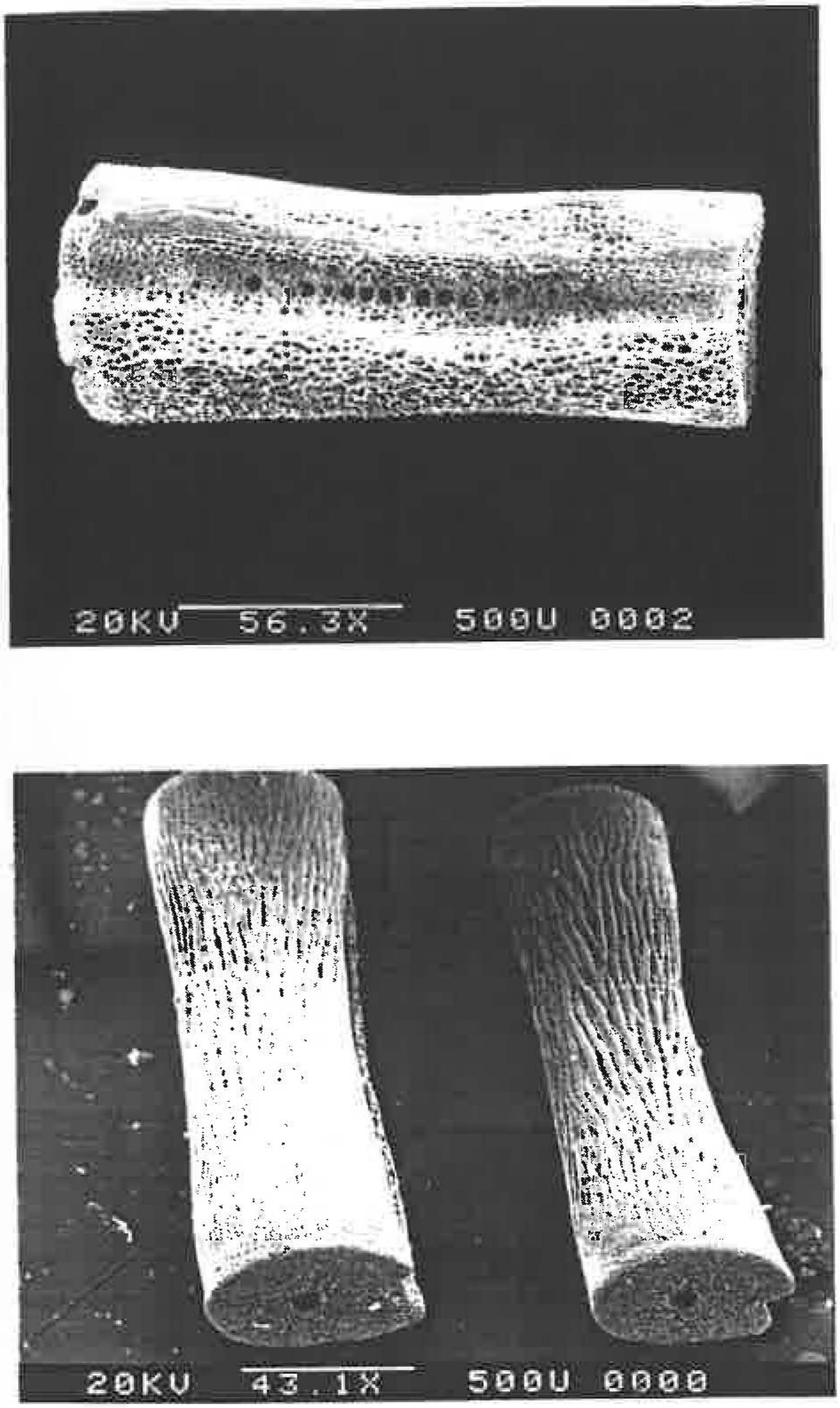
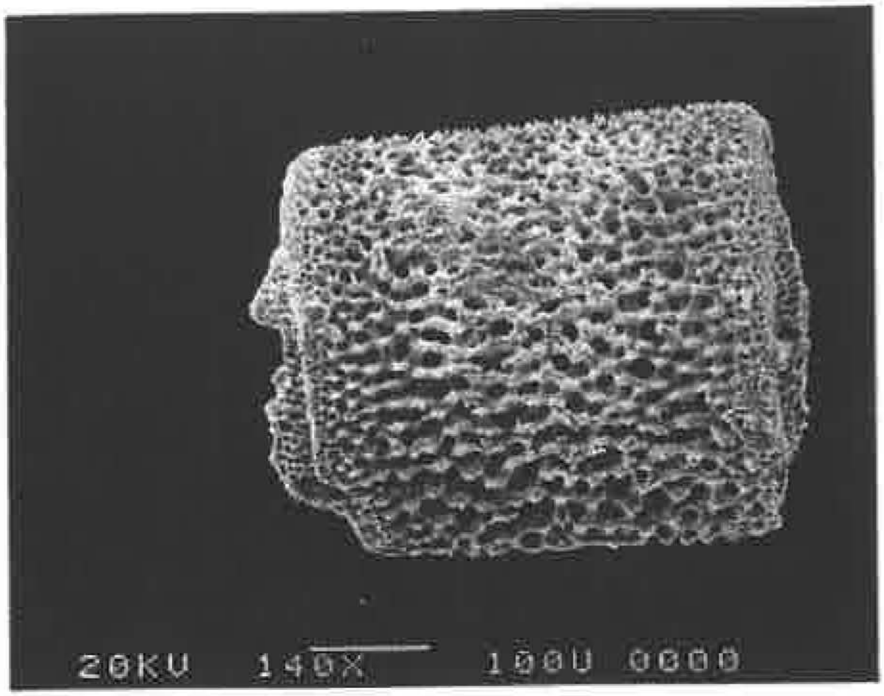


Figure 4. *Stephanometra indica*. Flat articular facets of pinnulars typical of enlarged oral pinnules. Scale: 500μm (1/2 mm).



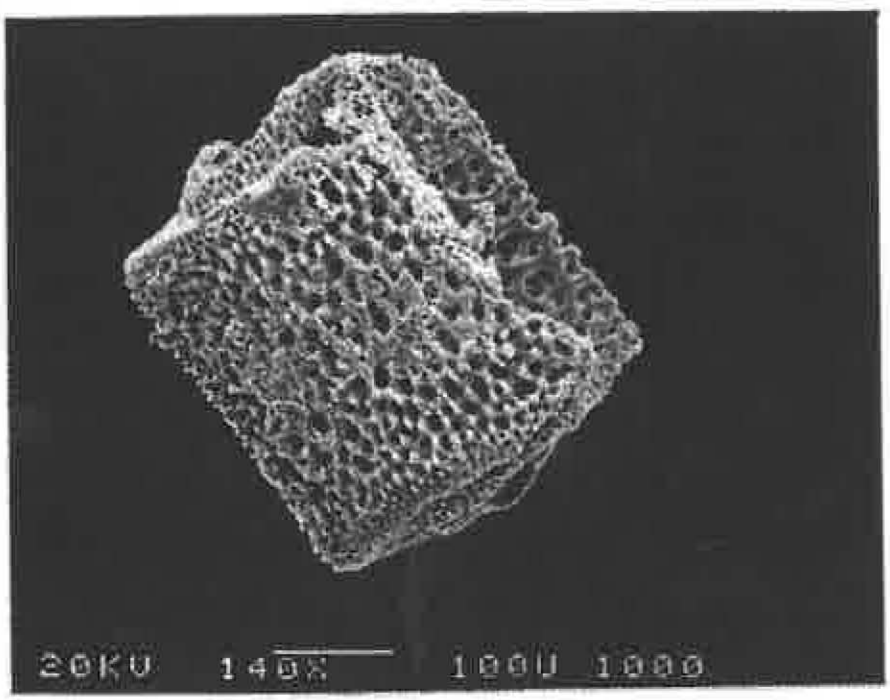


Figure 5. *Lamprometra palmata.* Developed articular facets of pinnulars from P_2. Scale: 100µm (1/10 mm).

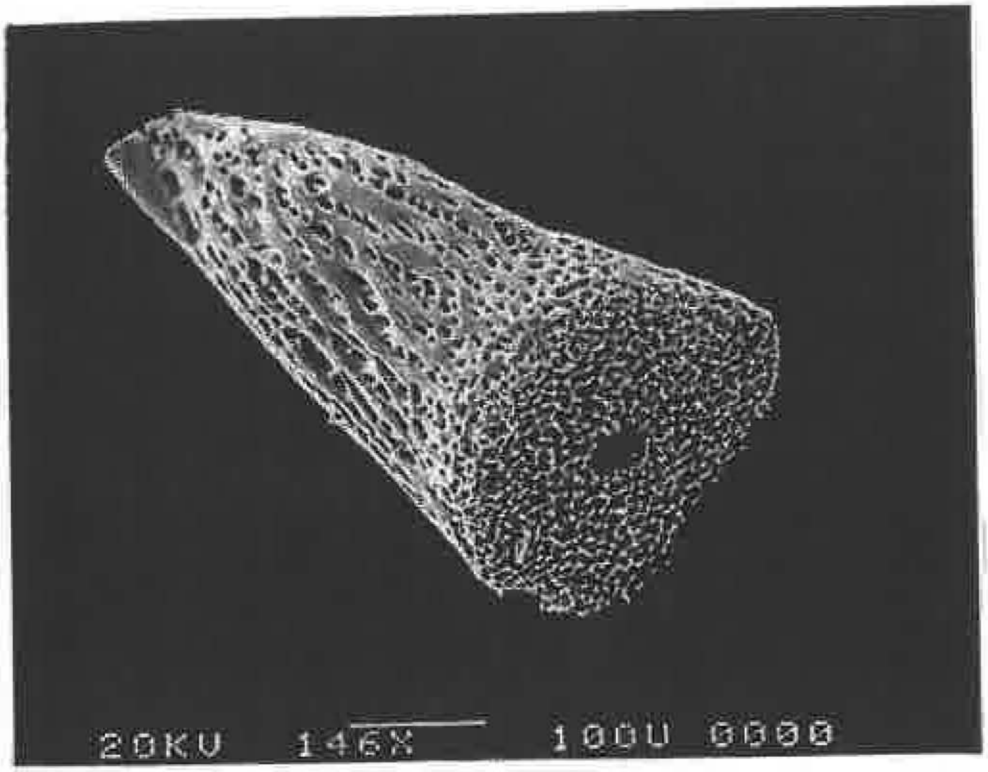


Figure 6. *Stephanometra indica.* Conical terminal pinnular typical of enlarged oral pinnules. Scale: 100µm (1/10 mm).

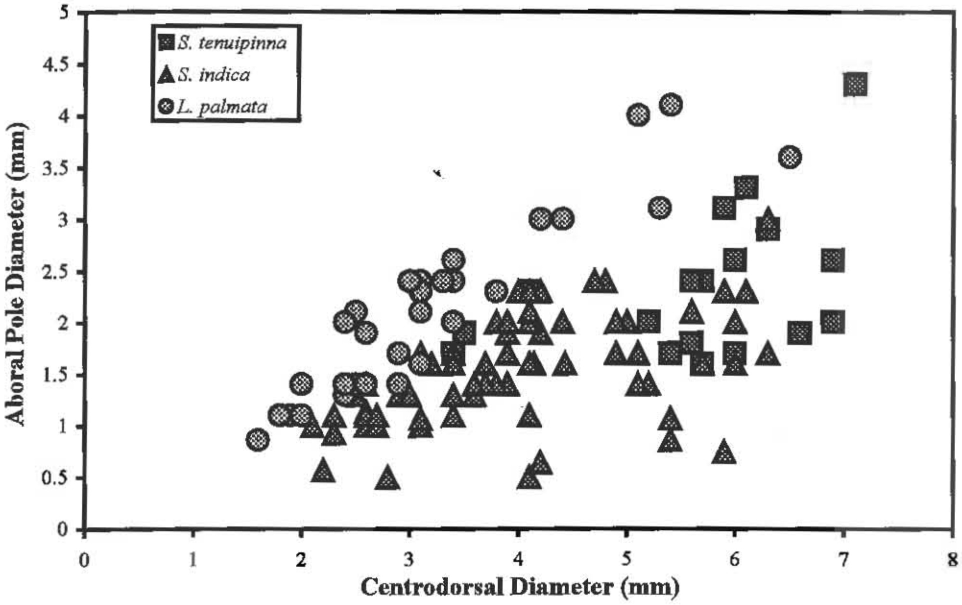


Figure 7. Plot of aboral pole diameter against centrodorsal diameter for *S. tenuipinna* (including "*echinus*" specimens), *S. indica* (including "*oxyacantha*", "*spicata*" and intermediate specimens) and *Lamprometra palmata*.

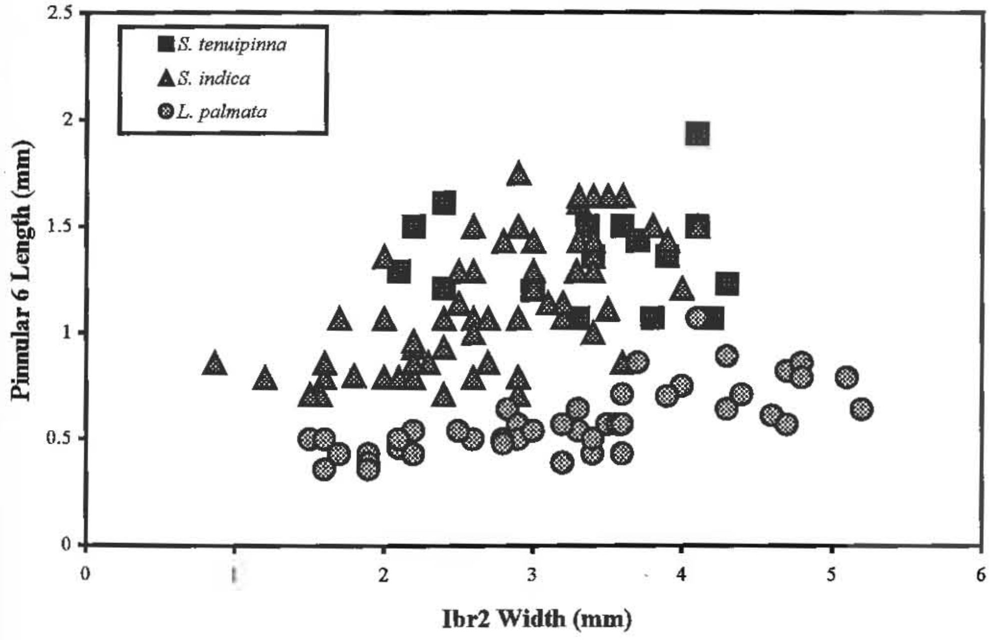


Figure 8. Plot of length of pinnular 6 from P_2 against width of Ibr_2 for *S. tenuipinna* (including "*echinus*" specimens), *S. indica* (including "*oxyacantha*", "*spicata*" and intermediate specimens) and *Lamprometra palmata*.

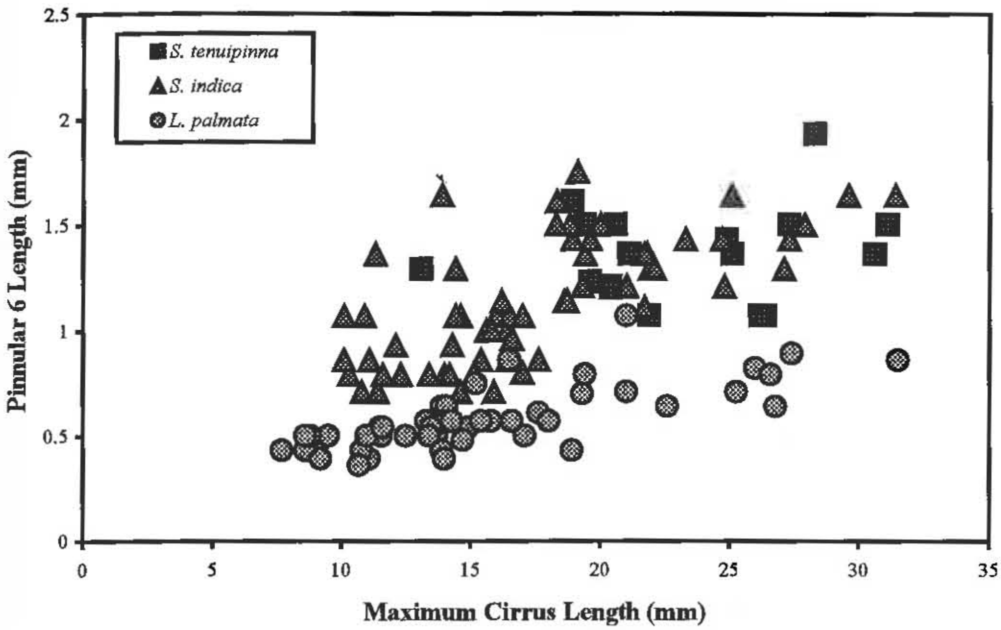


Figure 9. Plot of length of pinnular 6 from P_2 against maximum cirrus length for *S. tenuipinna* (includes *S. "echinus"* specimens), *S. indica* (includes *S. "oxyacantha"*, *S. "spicata"* and intermediate specimens) and *Lamprometra palmata*.

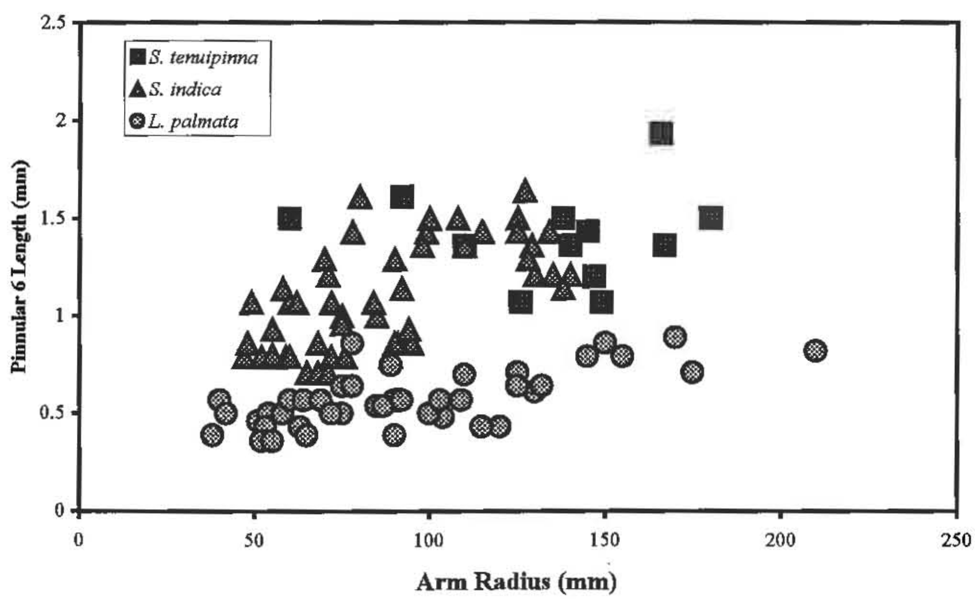


Figure 10. Plot of length of pinnular 6 from P_2 against arm radius for *S. tenuipinna* (including *"echinus"* specimens), *S. indica* (including *"oxyacantha"*, *"spicata"* and intermediate specimens) and *Lamprometra palmata*.

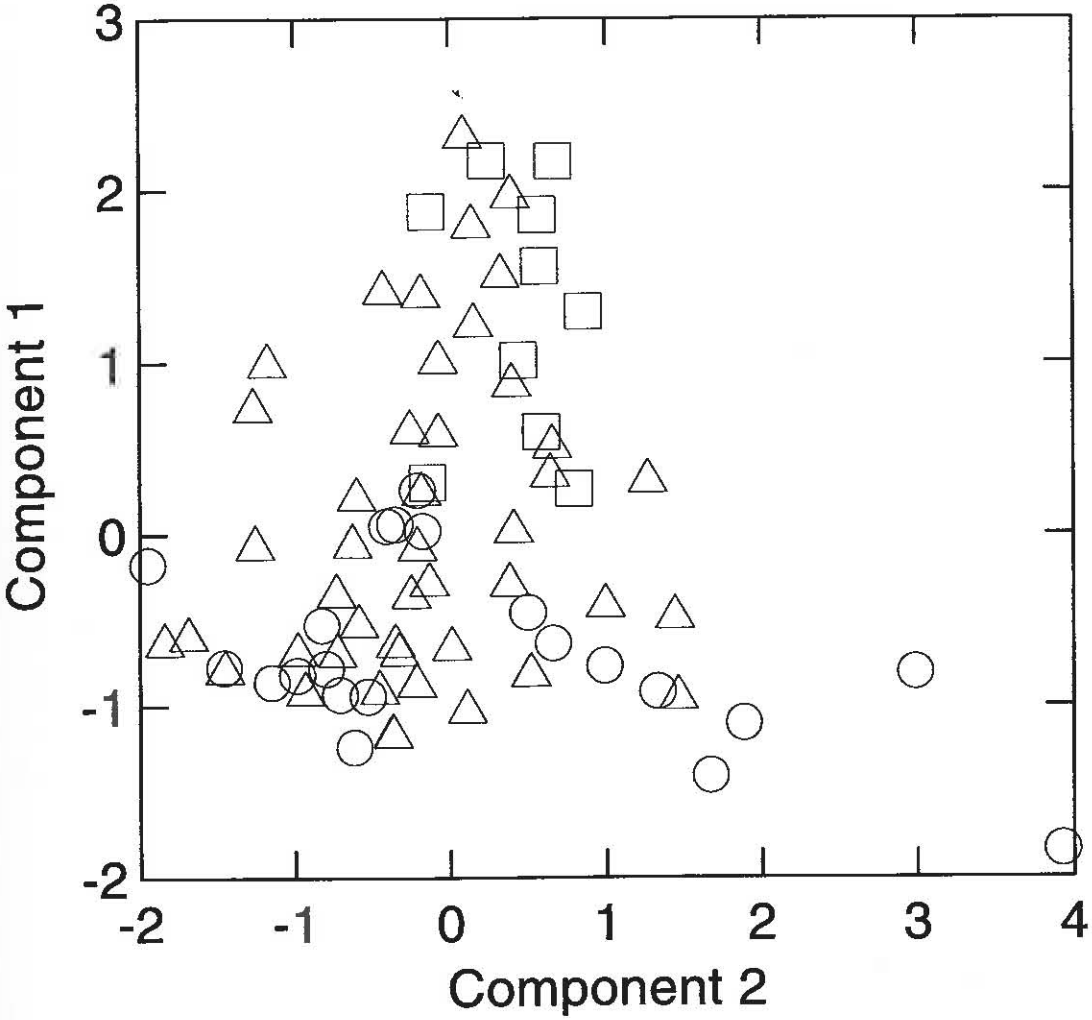


Figure 11. Graph of component scores from Component 1 against Component 2 in principal component analysis for *S. tenuipinna* (□) (including *S. "echinus"*), *S. indica* (Δ) (including *S. "spicata"*, *S. "oxyacantha"*, *S. "spinipinna"* and intermediate specimens) and *L. palmata* (O).

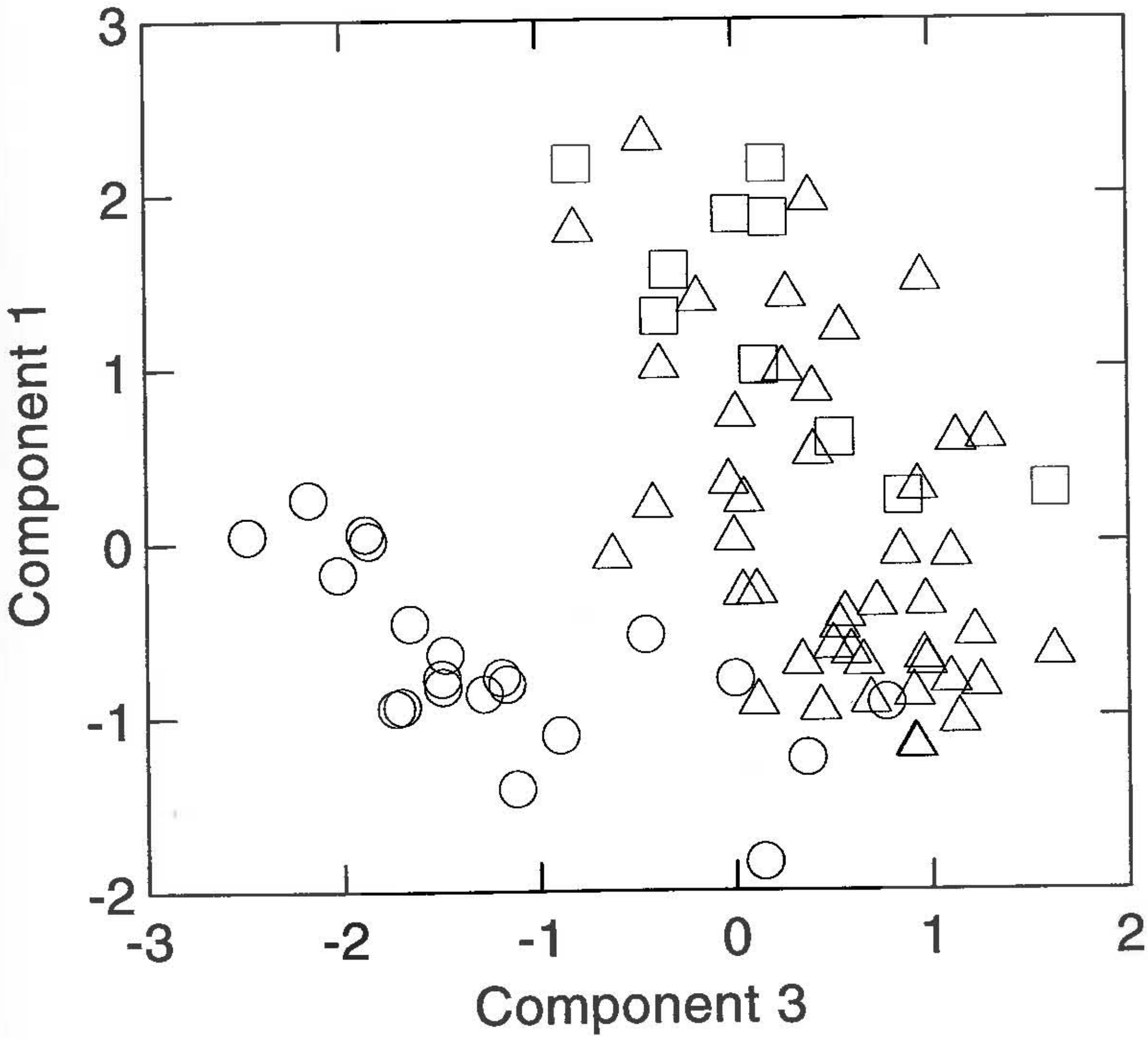


Figure 12. Graph of component scores from Component 1 against Component 3 in principal component analysis for *S. tenuipinna* (□) (including *S.* "*echinus*"), *S. indica* (Δ) (including *S.* "*spicata*", *S.* "*oxyacantha*", *S.* "*spinipinna*" and intermediate specimens) and *L. palmata* (O).

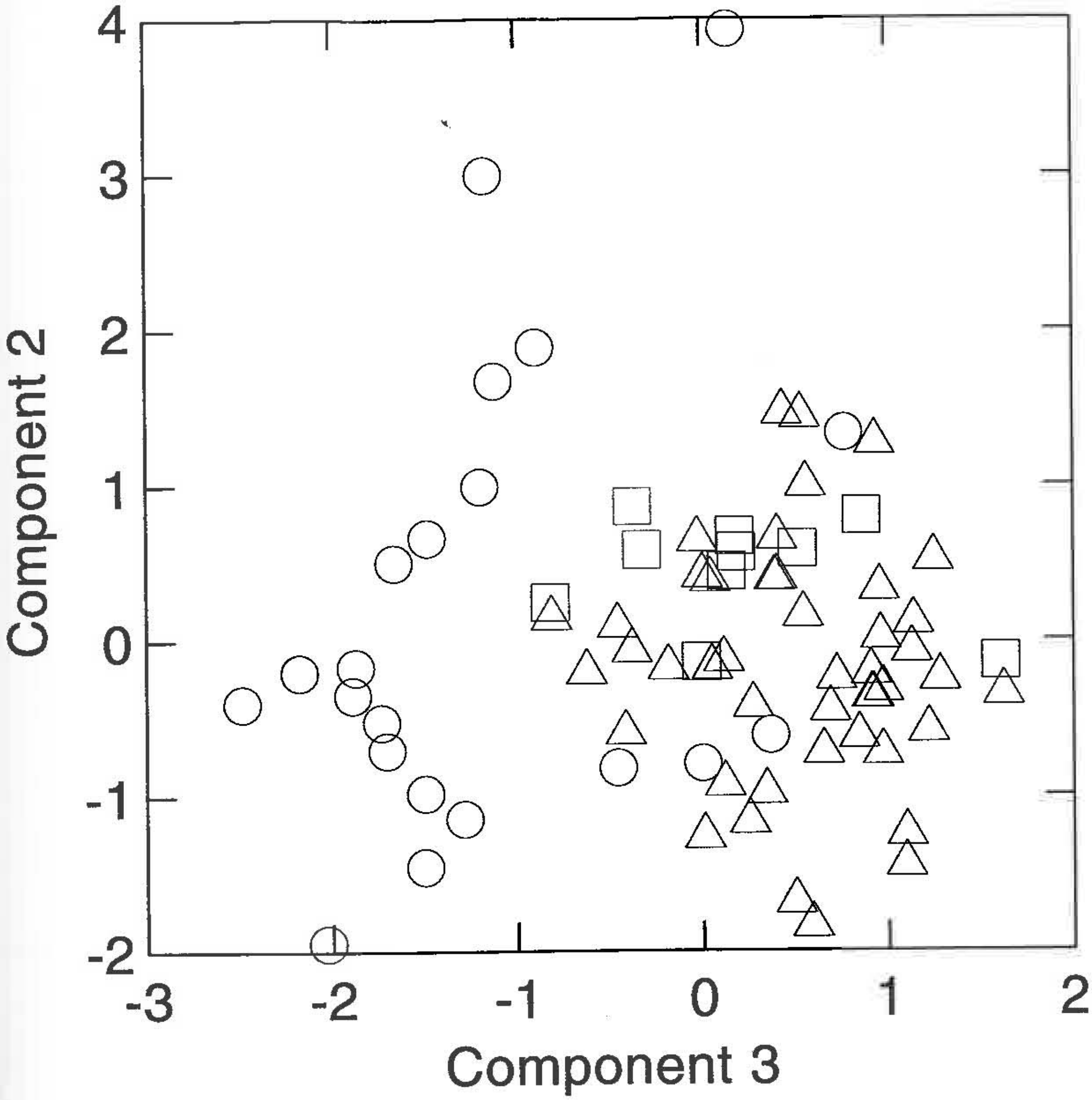


Figure 13. Graph of component scores from Component 2 against Component 3 in principal component analysis for *S. tenuipinna* (□) (including *S.* "*echinus*"), *S. indica* (Δ) (including *S.* "*spicata*", *S.* "*oxyacantha*", *S.* "*spinipinna*" and intermediate specimens) and *L. palmata* (O).

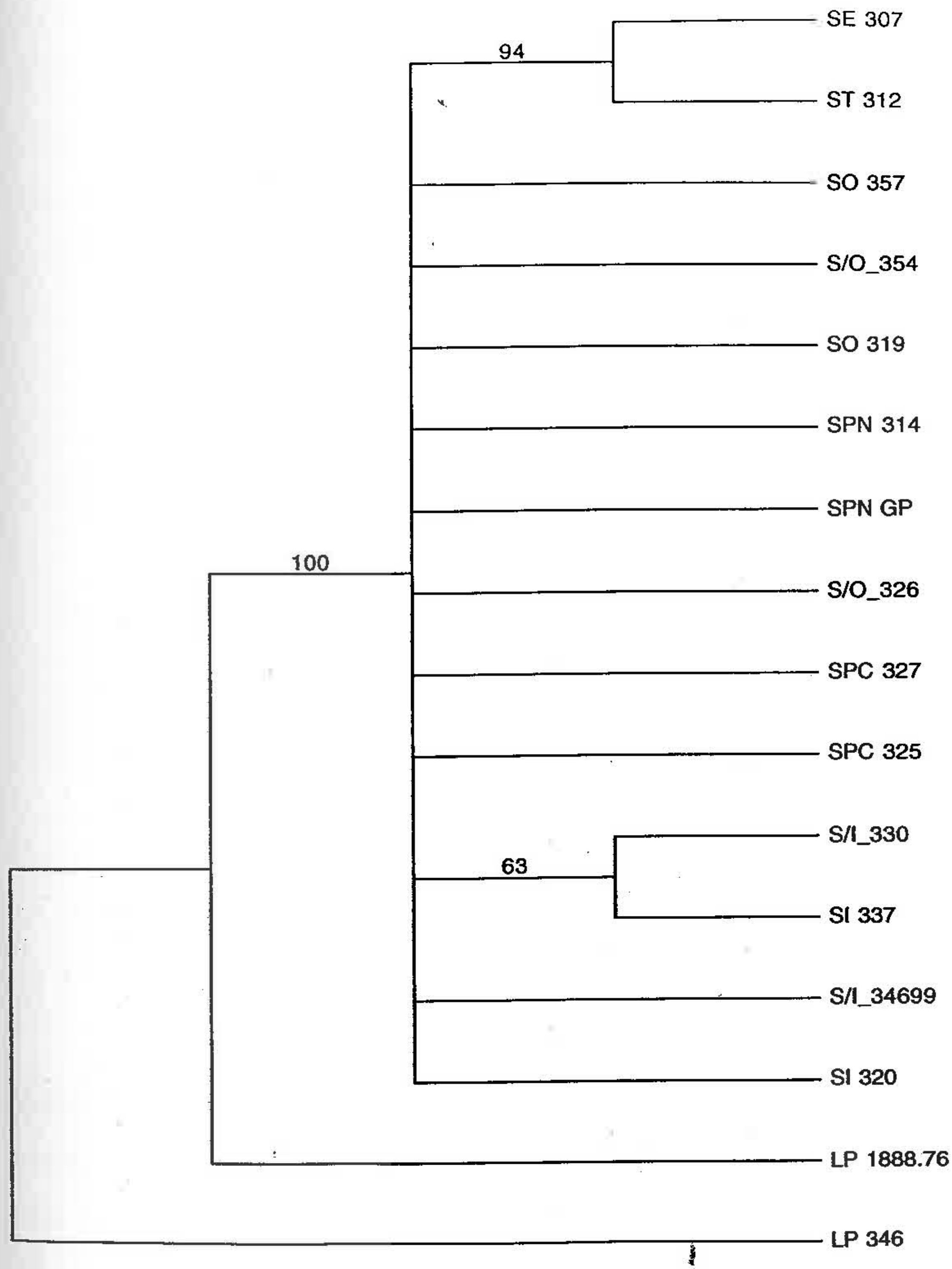


Figure 14. Fifty percent majority rule tree with bootstrap analysis for *Stephanometra* and *Lamprometra*. Tables 1 and 2 provide a key to the terminal names.

Stephanometra tenuipinna **Hartlaub, 1890**

Figures 15-22; Table 1.

Antedon tenuipinna Hartlaub, 1890:178; 1891:54, 58, 113, pl. 3, figs. 28, 30, 34.—A. H. Clark, 1912e:383; 1912f:37.

Himerometra tenuipinna: A. H. Clark, 1907:356; 1908a:219.

Himerometra echinus A. H. Clark, 1908a:218.

Stephanometra coronata A. H. Clark, 1909c:639; 1911d:541; 1912a:19; 1912d:133, figs. 13 a, b:133; 1918:93; 1941:412.

Stephanometra echinus: A. H. Clark, 1909a:10; 1912a:19; 1912f:132; 1918: 94, 271; 1921a, pl. 15, fig. 52; 1941: 409-413, pl. 45, figs. 205-207, pl. 46, figs. 210, 211, pl. 47, figs. 212-216—Gislén, 1936:4, 5, 11, figs. 2, 2a. —A. M. Clark and Rowe, 1971:24.—Meyer and Macurda,1980:85-86, figs. 5e, 7b.—Stevens, 1989:4-28.—Messing, 1994:239; 1998:189, 191.

Stephanometra tenuipinna: A. H. Clark, 1909a:10; 1909c:639; 1909d:170, 193; 1912e:383, 397; 1912f:37, 135; 1918:93; 1941:413-415, pl. 45, figs. 208, 209. —H. L. Clark, 1915a:93.—A. M. Clark and Rowe, 1971:24.—Messing, 1998:189, 191.

Stephanometra tenuispina: Gislén, 1934:20.

Material examined.—MALDIVE ISLANDS: NSUOC 629-632 (5 specimens), Jewellers' Is., Nilandu Atoll, E of Madali I., 02°52'6"N, 72°50'8"E, 4.5-12 m, 21 Jan 1999, D. L. Rankin, coll.; CRRF M48 (1), S Male Atoll Lagoon Reef, 20 m, 29 Sep 1997. PHILIPPINES: NSUOC 305 & 306 (2), Jesse Beasley Reef, Sulu Sea, 09°01'N, 119°48'E, 3-9 m, 19 Apr 1995, C. G. Messing, coll.; NSUOC 310 & 312 (2), S end of Green Is., Palawan, 10°15'N,119°30'E, 23 Apr 1995, C.

G. Messing & C. Arneson, colls.; NSUOC 308 (1), Sulu Sea S Tubbataha Reef (W end), 09°49'N, 119°52'E, 21 m max., 21 Apr 1995, C. G. Messing, coll.; USNM E35256 (1), R/V *Albatross*, Sta. 5174, Sulu Sea, Jolo I., Candea Point, 06°03'45"N, 120°57'00"E, 5 Mar 1908; CHUUK ATOLL, MICRONESIA: NSUOC 309 (1), N side of NE Pass., S of Quoi I., 07°31'38"N, 151°58'05"E, 9-19 m, 11 June 1993, P. Colin, coll. MALAYSIA: NSUOC 256 (1), Sabah, Borneo, Sipadan I., 04°07'N, 118°38'N, 11 m, 23 Apr 1997, C. G. Messing, coll.; NSUOC 302 (1), Mabul Wall, E side of Mabul I., 04°15'N, 118°38'E, 8 m, 22 Apr 1997, C. G. Messing, coll.; NSUOC 304 (1), Dive Center, Mabul I., 04°15'N, 118°38'E, 6 m, 24 Apr 1997, C. G. Messing coll. PAPUA NEW GUINEA: NSUOC 303 (1), Barracuda Rock, off Pig I., Madang, 05°10'20"N, 145°51'53"E, 11 m, 18 July 1991, C. G. Messing, coll.; NSUOC 307 & 311 (2), Outside Pig I., Madang, 05°10'20"N, 145°51'53"E, 11-14 m, 16-18 July 1991, C. G. Messing coll; IRSCB 338 (1), Platier I., Hansa Bay (NE), 20 m, 16 July 1989, M. C. Lahaye, coll.; IRSCB 379 (1), Pointe 0, Laing I., Hansa Bay, 25 m, 22 July 1989, M. C. Lahaye, coll.; IRSCB 398 (1), Mandy Passage, near Hansa Bay, 36 m, 23 July 1989, M. C. Lahaye, coll.

Diagnosis.—A species of *Stephanometra* with lateral margins of brachitaxis ossicles weakly swollen or with well-rounded lateral processes oriented perpendicular to ray axis; cirri bearing prominent aboral spines. P_1-P_4 and sometimes P_5 composed of elongated pinnulars, L/W 1.5-3.5, with reduced ambulacral groove and conical terminal segment. Proximal and distal pinnular facets with elongated triangular fossae on either side of the ambulacral groove.

Description.—Centrodorsal discoidal or dome-shaped (Fig. 15g-l), 3.4-7.1 mm across, 0.9-2.4 mm high; D/H 2.2-4.7. Cirri arranged in two to three alternating marginal rows. Polar area small, irregular in shape, slightly concave or flat with encroaching cirri, 1.0-4.3 mm across; D/P 1.7-3.6.

Cirri XIX-XXXVIII, 23-36, 13-31 mm; C_{8-10} longest, L/W 1.0-1.5. C_1-C_3 short; C_4-C_8 longer than broad; C_9-C_{14} and following cirrals compressed, each bearing a sharp distally directed aboral spine (Figs. 16c-h). Terminal claw longer than penultimate segment and curved. Specimens from the Jewellers' Islands with spines restricted to the distalmost one or two cirrals (Figs. 16a & b).

Basal ossicles not visible externally; radials projecting slightly beyond the edge of the centrodorsal or visible in the interradial angles. IIIBr developed only externally or both internally and externally on the same specimen. Ibr_1 oblong, with converging lateral margins, usually free laterally but may be united proximally (Figs. 15a-f); 0.7-1.5 mm long, 1.4-3.7 mm wide; W/L 2.0-3.5, rarely less. Ibr_2 (axil), with diverging lateral margins 1.6-2.4 mm long, 2.1-4.2 mm wide; W/L 1.5-2.0, rarely less than 1.5. Brachitaxis ossicles well separated, 1.5-2.7 mm apart (measured between adjacent Ibr_1 ossicles). Ibr_2 and $IIbr_1$ bear weak (Figs. 15a & b) to strong, rounded, lateral adambulacral swellings (Figs. 15c-f). Weak adambulacral processes may be obliquely-oriented and restricted to the proximal corners of Ibr_2 and $IIbr_1$ (Figs. 15a & b), while strong processes run the entire length of Ibr_2, $IIbr_1$ and $IIbr_2$ (Figs. 15c-f). Synarthrial tubercles weakly to well-developed. Arms 22-33; rays 60-185 mm long. Rays most commonly with six arms each, less frequently with 2, 4, 5, 7 or 8. br_1 through br_8-br_{10} oblong, about twice as broad as long. Subsequent brachials cuneate. br_{10} 1.1-2.1 mm wide, 0.4-1.1 mm long, with W/L 1.7-2.8.

Syzygies at br_{3+4}, br_{21+22} (infrequently between br_{8+9}, br_{9+10}, br_{13+14}, or br_{28+29}). Subsequent intersyzygial intervals 7-11 (less often from 2-6 or 15-18).

P_1 through P_3 or P_4 and sometimes P_5, stiff and spinelike, composed of cylindrical segments with ambulacral groove and tube feet reduced. Pinnules on outer arms generally longer and thicker than those on inner arms. The first two pinnulars slightly broader than long, the third and sometimes fourth slightly longer than broad, the fourth and following with L/W 1.5-3.5, and the terminal pinnular a conical spike (Figs. 17a-u). The proximal three to five pinnulars laterally compressed. P_1 8.1-17.3 mm, of 10-15, rarely 18, pinnulars; usually slightly slenderer and shorter than P_2; rarely the largest pinnule (Figs. 17a, f, l & q).

P_2 the longest, thickest pinnule, 10.7-19.7 mm long, of 9-14 pinnulars; pinnular 6 with L/W 1.4-3.6 (Figs. 17b, g, m & r). P_3 4.5-13.7 mm long, of 7-12 pinnulars; sometimes as thick as P_2 but always shorter; often as thick as P_1 but slightly longer or shorter (Figs. 17c, h, n & s). P_4 5.3-10.5 mm long, of 7-11 pinnulars; similar to P_3 or small, weak and flexible like the following pinnules (Figs. 17d, i, o & t). P_5 either resembling P_4 or the following, 3.3-7.6 mm long with 7-10 pinnulars (Figs. 17j, p & u). P_6 and the following pinnules small, weak and flexible with a well-developed ambulacral groove (Figs. 17k). Subsequent pinnules gradually increasing in length. P_{distal} 10.4 mm with about 22 pinnulars; the first pinnular broader than long, the second longer than broad, and subsequent pinnulars longer than broad; the terminal segment elongated and covered with small spines (Fig. 17e).

Color patterns.— 1) rays white with red tips; 2) rays red proximally, white distally with or without red arm tips; 3) brachitaxes dark rose with abundant pale dots; 4) brachitaxes and proximal arms gray, distal arms deep purple; 5) brachitaxes rich pinkish-red with orange blotches; 6) brachitaxes orange scattered with pink and white areas; middle of arm dark orange-brown with numerous white or tan bands; 7) brachitaxes reddish with orange blotches; arms reddish purple and white banded with orange blotches; 8) rays irregularly banded red, brown and white; 9) brachitaxes orange with brown speckles; 10) brachitaxes speckled pink and white; 11) brachitaxes rusty orange and white speckled; 12) rays orange/maroon and cream; 13) arms orange and cream banded; 14) brachitaxes purple/maroon and white speckled.

A. H. Clark (1921b) mentioned the following additional colors: 1) brachitaxes and arms solid dark purple, and 2) rays alternating silver and bright red, tips of enlarged pinnules orange. Previously published records of color (A. H. Clark, 1921b; Meyer and Macurda, 1980; and Stevens, 1989) may be based on incorrectly identified species.

Geographic distribution.—From India and the Maldives to Chuuk Atoll, Micronesia, and from Queensland, Australia, to Cochin, China, and the Philippines. Previously published records of distribution (A. H. Clark, 1921b; Meyer and Macurda, 1980; and Stevens, 1989) may be based on incorrectly identified species.

Bathymetric range.—Shoreline down to 48 m; reef dwellers.

Remarks.— A. H. Clark diagnosed *S. echinus* as having 30-40 arms 110-170 mm long, cirri with 25-37 cirrals, and P_1-P_4 stiff and spinelike, while *S. tenuipinna* had 16-24 arms 60-70 mm long, with 20 cirrals and P_1-P_3 stiff and spinelike. In fact, A. H. Clark suggested the possibility that *S. echinus* might prove to be a full-sized *S. tenuipinna*. Table 1 and figures 18-21 suggest that *S. tenuipinna* is simply a smaller growth stage of *S. echinus*. Cladistic analysis (Fig. 20), indicates a monophyletic *S. tenuipinna*, with small specimens formerly separated as *S. tenuipinna* submerged among the *S. "echinus"* specimens. A branch and bound search with bootstrap analysis of 250 replicates using maximum parsimony and all characters weighted equally resulted in one most parsimonious tree with TL = 142, CI = 0.641, RI = 0.227, and RCI = 0.146. *S. echinus* is thus synonymized under the senior name *S. tenuipinna*. Messing (1998) proposed that *Comatella maculata* and *C. stelligera* represent another growth series and are conspecific on similar grounds. *S. echinus* and *S. tenuipinna* specimens in the current study closely resemble the holotype specimen of *Stephanometra coronata* (USNM E35242) from India (Fig. 23, illustration courtesy of C. G. Messing), which is retained within the synonomy of *S. tenuipinna*.

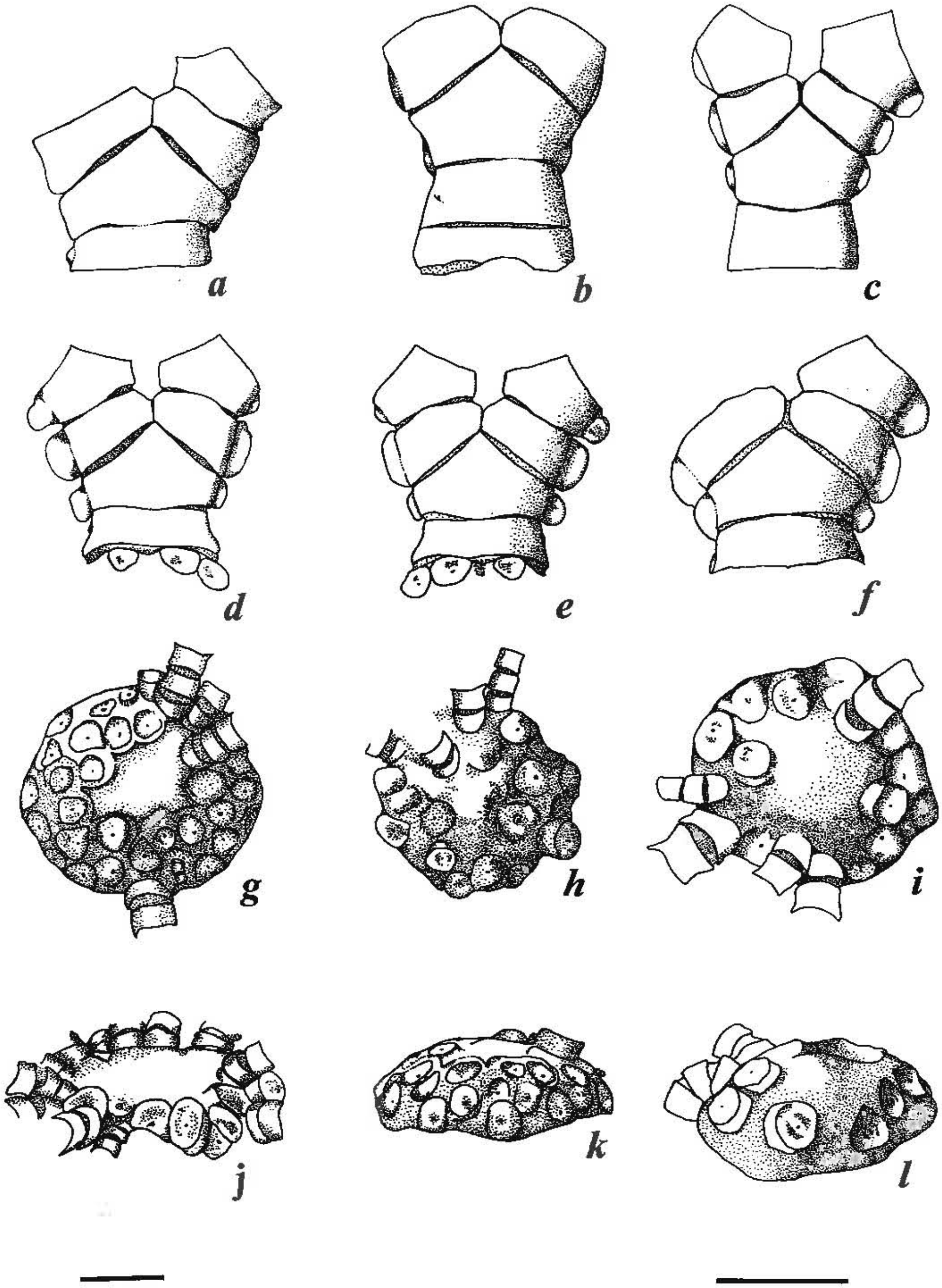


Figure 15. *Stephanometra tenuipinna*. Figs. a-f: lateral adambulacral margins of brachitaxes ossicles, in aboral view. a. IBr2, IIBr2 & br_1, NSUOC 309. b. Radial, IBr2 & br_1, NSUOC 312. c. IBr2 & IIBr2, USNM E35256. d. IBr2 & IIBr2, NSUOC 256. e. IBr2 & IIBr2, IRSCB 398. f. IBr2, IIBr2 & br_1, IRSCB 338. Figs. g-i: centrodorsal in aboral view. g. NSUOC 256. h. NSUOC 310. i. NSUOC 312. Figs. j-l: centrodorsal in lateral view. j. NSUOC 311. k. NSUOC 256. l. NSUOC 312. Scale (left): g, h, & k, 3 mm; Scale (right): a-f, i, j & l, 2 mm.

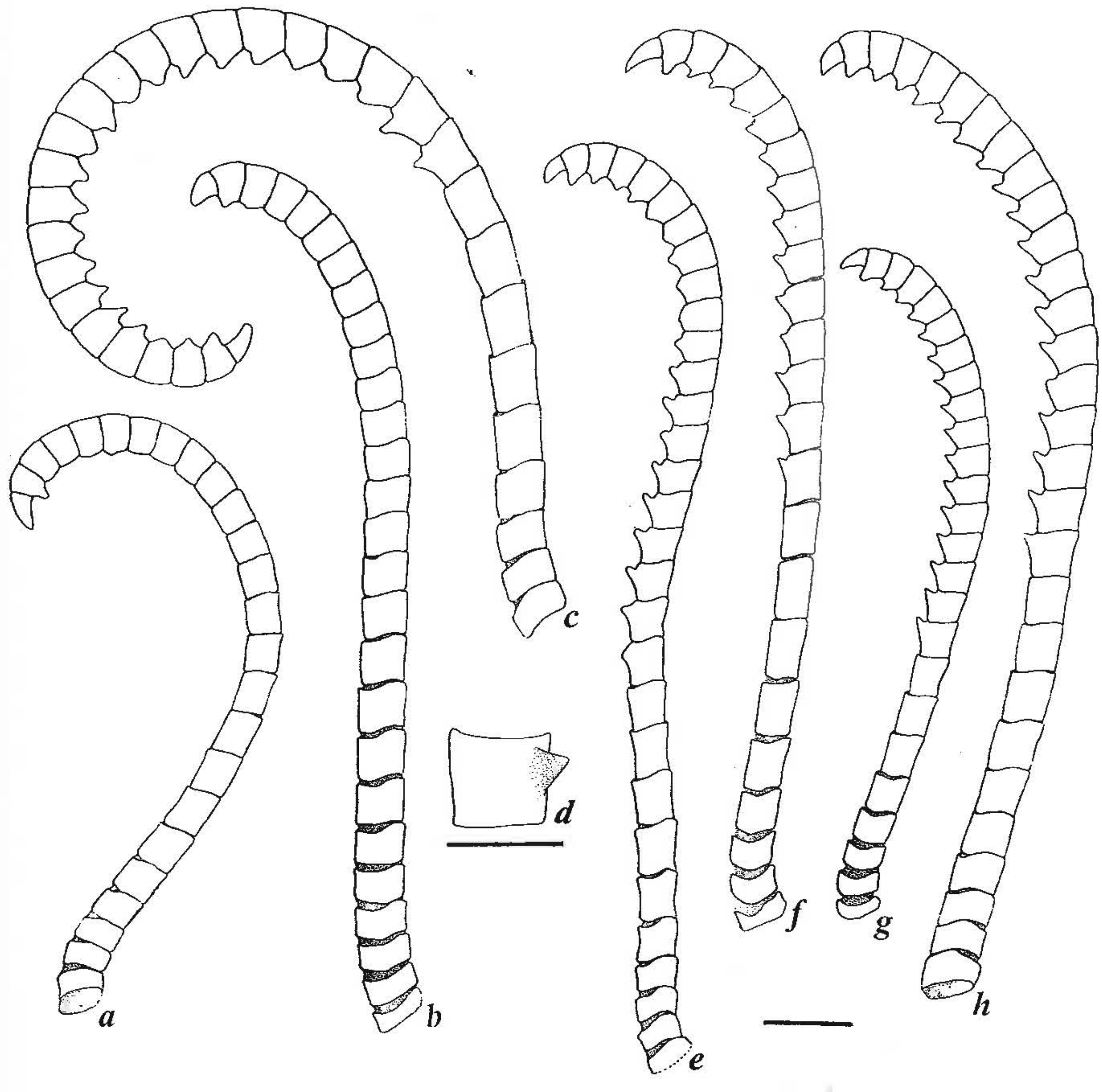


Figure 16. *Stephanometra tenuipinna.* a. Cirrus, NSUOC 628. b. Cirrus, NSUOC 629. c. Cirrus, NSUOC 305. d. Distal cirral, NSUOC 305. e. Cirrus, NSUOC 312. f. Cirrus, NSUOC 311. g. Cirrus, NSUOC 256. h. Cirrus, NSUOC 305. Scale (upper): d, 1 mm; scale (lower right): a-c, e-h, 2 mm.

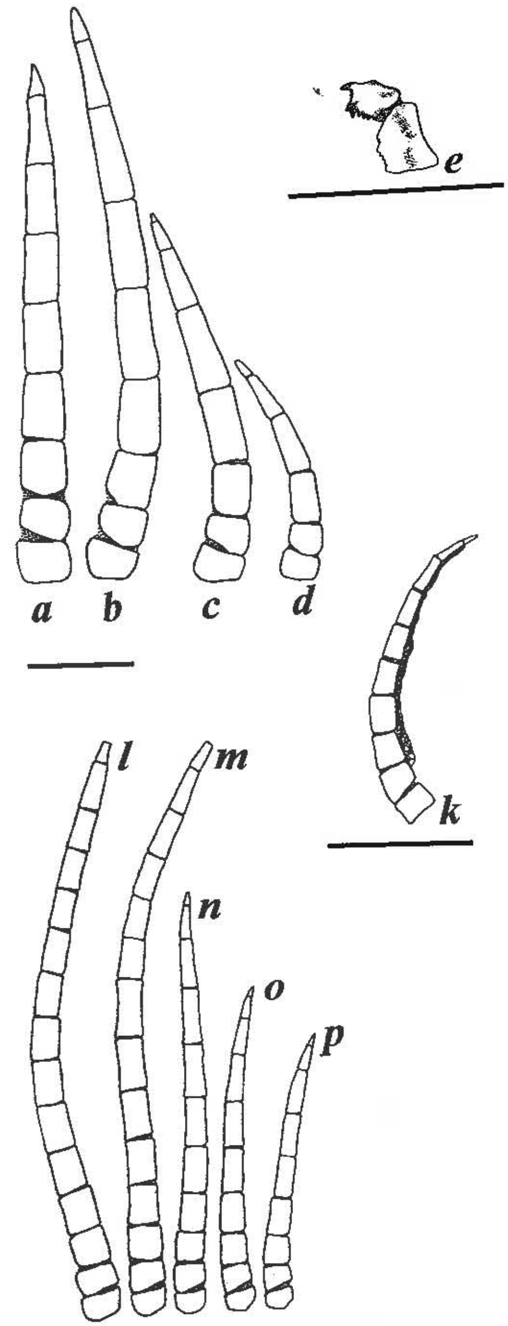


Figure 17. *Stephanometra tenuipinna*. Pinnules. a. P_1, NSUOC 312. b. P_2, same. c. P_3, same. d. P_4, same. e. Terminal pinnulars of distal pinnules, NSUOC 77. f. P_1, same. g. P_2, same. h. P_3, same. i. P_4, same. j. P_5, same. k. Distal pinnule, same. l. P_1, NSUOC 628. m. P_2, same. n. P_3, same. o. P_4, same. p. P_5, same. q. P_1, NSUOC 308. r. P_2, same. s. P_3, same. t. P_4, same. u. P_5, same. Scale (upper): a-i, l-u, 2 mm; scale (center): j, 2 mm; scale (lower): k, 1 mm.

Table 1. Meristic and morphometric data for *S. tenuipinna* and *S. "echinus"*

	CENTRODORSAL			ABORAL POLE	CIRRI			ARMS		BRACHITAXES						br_{10}	P_1		P_2		P_3		P_4		P_5	
Specimen #	D (mm)	Height (mm)	D/H	Diameter (mm)	Cirri #	# Cirrals	Cirrus L (mm)	Arm #	Ray L (mm)	Ibr_1 L (mm)	Ibr_1 W (mm)	Ibr_1 W/L	Ibr_2 L (mm)	Ibr_2 W (mm)	Ibr_2 W/L	W (mm)	# Plrs.	L (mm)	# Plrs.	L (mm)	# Plrs.	L (mm)	# Plrs.	L (mm)	# Plrs.	L (mm)
S. tenuipinna																										
NSUOC 312	3.5	0.9	3.9	1.4	19	26	19.4	22	60	1.1	1.4	1.3	1.6	2.2	3.1	1.3	10	10.8	9	10.9	7	6.6	7	5.5	6	5.0
USNM E35256	3.4	1.1	3.1	1.0	24	23	13.1	--	—	0.7	1.4	2.0	1.6	2.1	3.1	--	12	9.9	—	--	10	4.5	8	4.3	--	--
S. "echinus"																										
NSUOC 305	6.6	1.6	4.1	1.9	32	31	28.3	28	170	1.1	3.7	3.5	2.1	4.1	2.4	1.9	12	17.3	12	19.7	8	10.4	7	7.8	8	5.6
NSUOC 306	5.2	1.3	4.0	2.0	26	34	27.3	26	140	1.4	3.0	2.1	2.0	3.6	2.5	1.6	12	10.1	12	12.6	8	6.4	9	5.3	8	3.3
NSUOC 310	6.9	1.9	3.6	2.6	30	30	25.1	29	140	1.1	3.1	2.8	2.0	3.9	2.5	1.9	12	11.1	12	13.1	11	11.4	7	10.5	7	7.3
NSUOC 303	4.1	1.9	2.2	2.3	22	28	20.4	26	—	0.7	2.2	3.1	1.6	2.4	3.1	1.2	10	9.1	10	12.1	8	6.7	6	4.8	7	3.7
NSUOC 311	6.1	1.3	4.7	3.3	35	30	21.9	25	--	1.5	3.3	2.2	2.3	4.2	2.2	1.7	13	12.4	14	16.4	11	13.1	9	6.8	9	6.9
NSUOC 307	5.4	1.6	3.4	1.7	33	32	21.1	29	110	1.0	2.9	2.9	2.3	3.4	2.2	1.3	12	9.6	12	11.6	9	7.1	8	5.4	8	4.4
NSUOC 308	6.0	1.7	3.5	2.6	30	29	30.6	27	170	1.3	3.1	2.4	2.1	3.9	2.3	2.1	15	16.7	14	18.0	12	13.4	9	9.0	9	7.1
NSUOC 309	6.0	1.9	3.2	1.7	32	36	26.4	29	130	1.1	2.9	2.6	2.2	3.3	2.3	1.7	15	12.5	13	12.5	10	9.1	8	7.0	8	5
IRSCB 398	5.9	1.7	3.5	3.1	33	30	20.6	32	--	1.0	2.7	2.7	1.8	3.4	2.8	1.3	12	8.1	11	11.1	8	6.7	7	6.1	--	--
IRSCB 379	7.1	1.7	4.2	4.3	38	29	19.6	30	—	1.3	3.6	2.8	2.0	4.3	2.5	1.4	12	9.8	12	11.1	12	11.1	9	7.3	9	6.4
IRSCB 338	6.3	1.6	3.9	2.9	30	33	26.2	30	150	1.4	3.3	2.4	2.1	3.8	2.3	1.6	15	11.6	12	12.7	12	11.1	11	9.1	10	7.6
NSUOC 256	6.9	2.3	3.0	2.0	32	32	31.1	31	180	1.4	3.9	2.8	2.6	4.1	1.9	2.0	12	16.1	12	14.6	10	11.2	8	8.7	8	8.0
NSUOC 302	5.6	1.7	3.3	1.8	25	28	18.9	26	90	0.9	1.9	2.1	1.8	2.4	2.8	1.1	11	9.6	11	10.7	9	7.6	7	6.1	7	4.3
NSUOC 304	5.7	2.0	2.9	1.6	22	30	24.9	30	145	1.1	3.3	3.0	2.1	3.7	2.4	1.9	14	12.8	12	14.1	11	12.0	10	7.9	9	6.3
CRRF M48	--	2.0	—	--	--	25	20.4	--	145	1.1	2.4	2.2	2.1	3.0	2.3	1.7	14	14.3	—	--	12	13.7	8	6.9	8	—
NSUOC 629	6.0	2.3	2.6	2.6	34	28	24.4	—	185	1.3	3.3	2.5	2.4	4.1	2.1	1.9	18	15.9	15	16.3	11	9.7	9	7.1	10	6.4
NSUOC 630	6.0	1.6	3.8	2.4	28	26	20.7	27	160	1.1	3.1	2.7	2.3	3.7	2.2	1.4	15	13.0	12	12.4	10	9.1	7	4.9	7	4.7
NSUOC 632	5.7	2.4	2.4	2.4	31	29	24.4	29	180	1.0	3.1	3.1	2.3	4.0	2.2	1.6	14	12.3	--	—	12	10.3	9	6.7	8	5.0
NSUOC 631	5.7	2.0	2.9	2.4	30	29	23.9	33	160	1.3	2.9	2.2	2.3	3.7	2.2	1.7	15	12.9	12	11.3	11	10.7	10	7.7	--	—
NSUOC 628	5.6	1.3	4.3	1.9	28	27	21.3	27	155	1.4	2.9	2.1	2.0	3.7	2.5	1.6	15	14.3	12	10.0	9	8.1	6	4.4	—	—

NSUOC designates Nova Southeastern University-Oceanographic Center.
CRRF designates Coral Reef Research Foundation.
USNM designates United States National Museum (now the National Museum of Natural History).
D indicates the diameter.
D/H indicates diameter (D) divided by height (H), of centrodorsal.
L indicates the length of cirrus, brachitaxes ossicles, rays or pinnules.
W indicates the width of brachitaxes ossicles, or br_{10}.
W/L indicates the width (W) divided by the length (L), of brachitaxes ossicles.
Plrs. indicates pinnulars

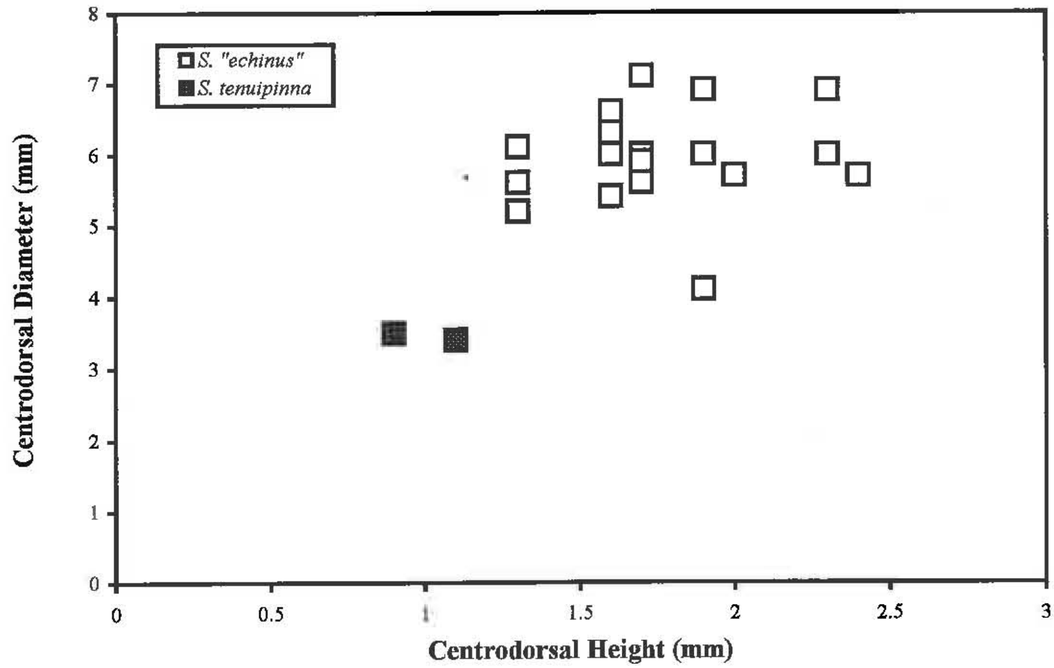


Figure 18. Plot of centrodorsal diameter against height for *S*. "*echinus*" and *S. tenuipinna.*

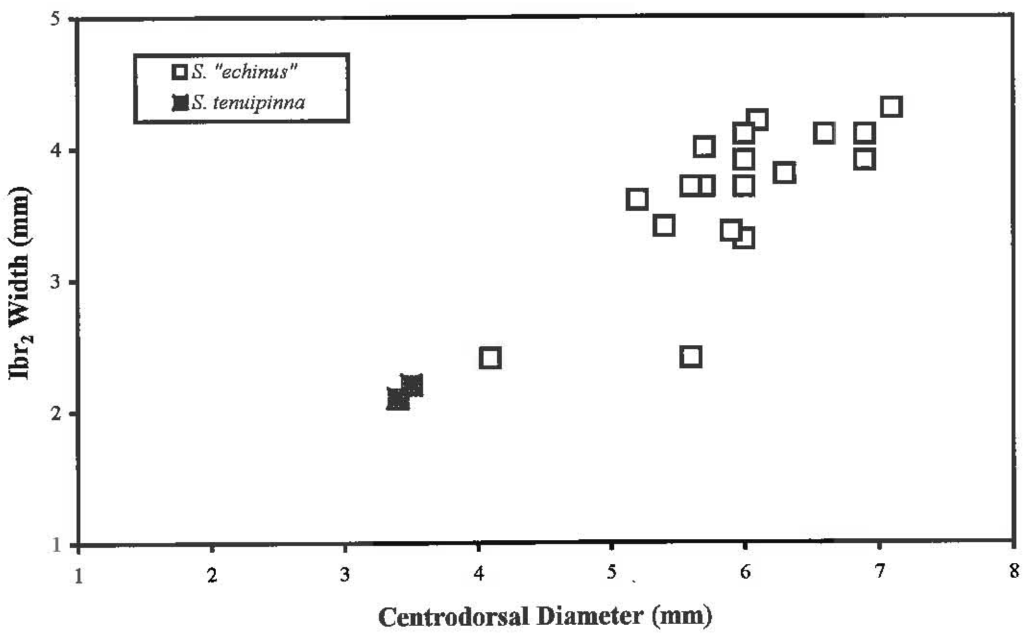


Figure 19. Plot of Ibr_2 width against centrodorsal diameter for *S*. "*echinus*" and *S. tenuipinna.*

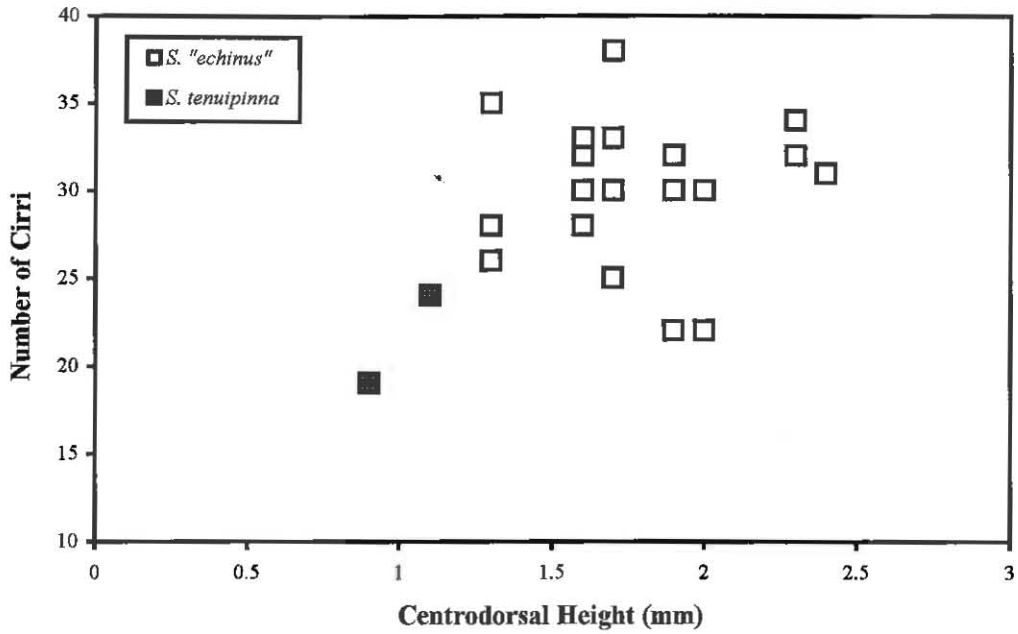


Figure 20. Plot of number of cirri against centrodorsal height for *S. "echinus"* and *S. tenuipinna.*

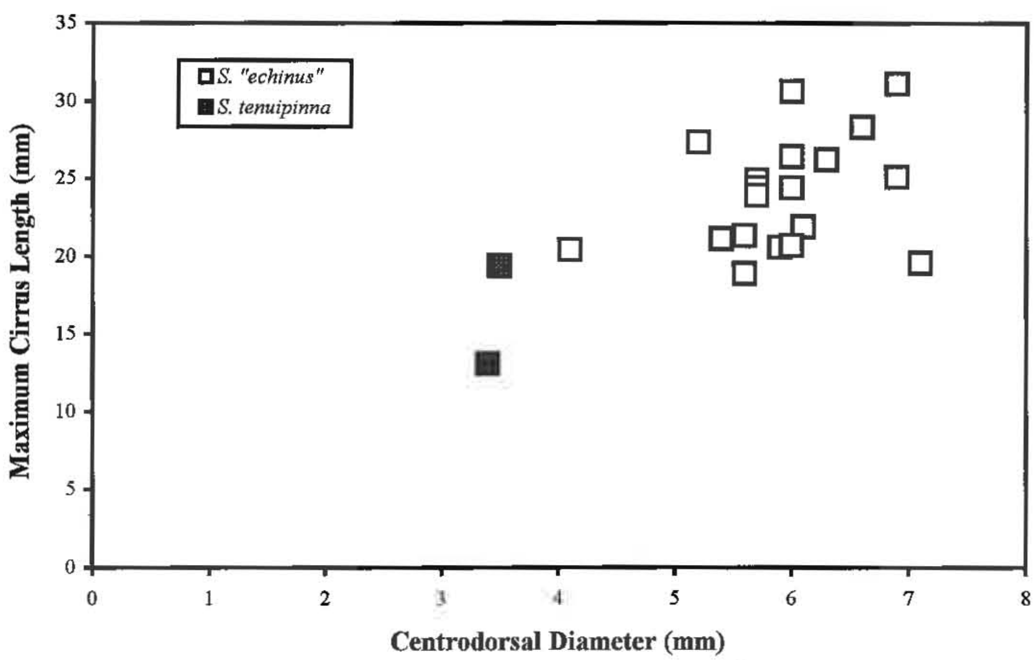


Figure 21. Plot of maximum cirrus length against centrodorsal diameter for *S. "echinus"* and *S. tenuipinna.*

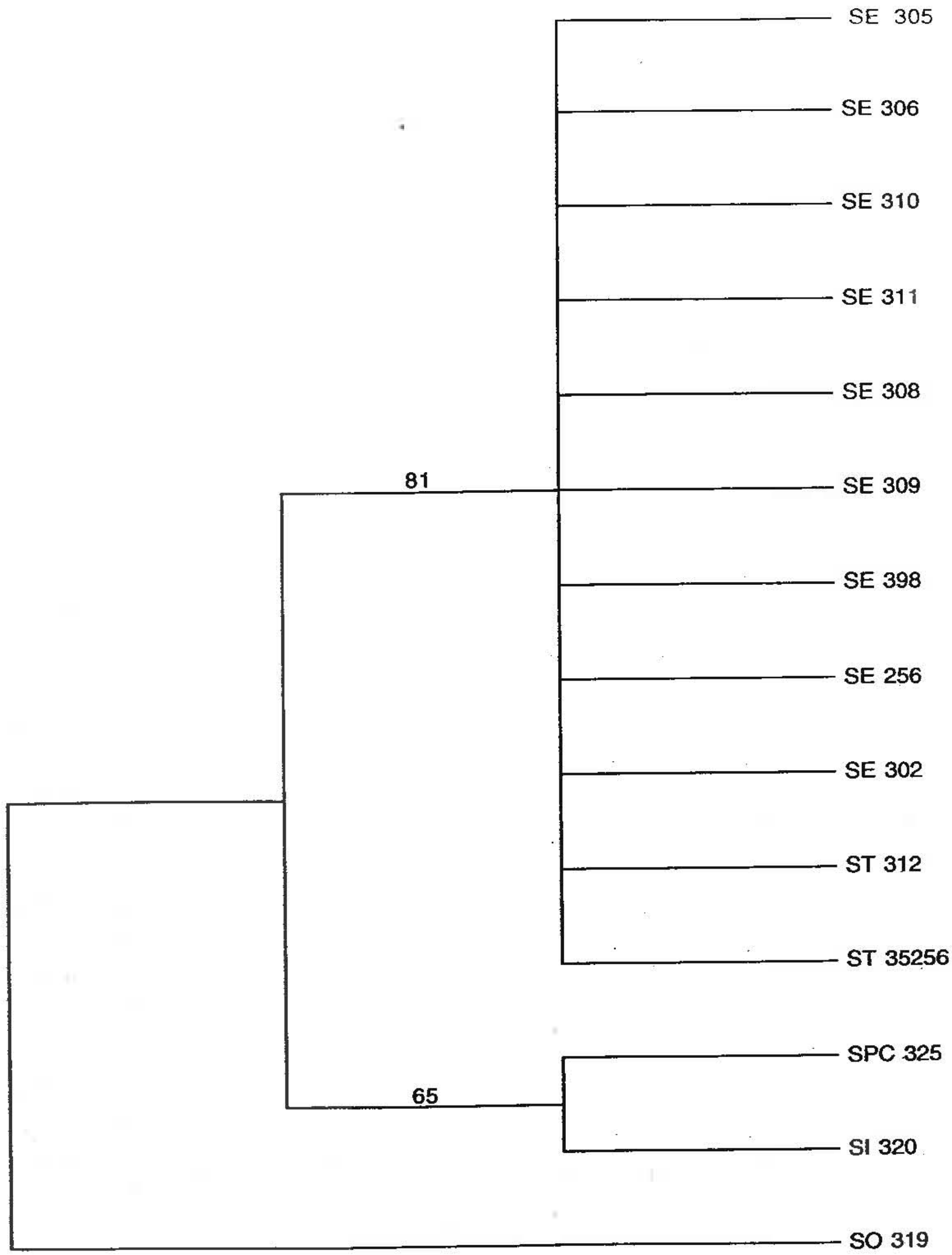


Figure 22. Fifty percent majority rule tree with bootstrap analysis for *Stephanometra* "*echinus*" and *S. tenuipinna*. Tables 1 and 2 provide a key to the terminal names.

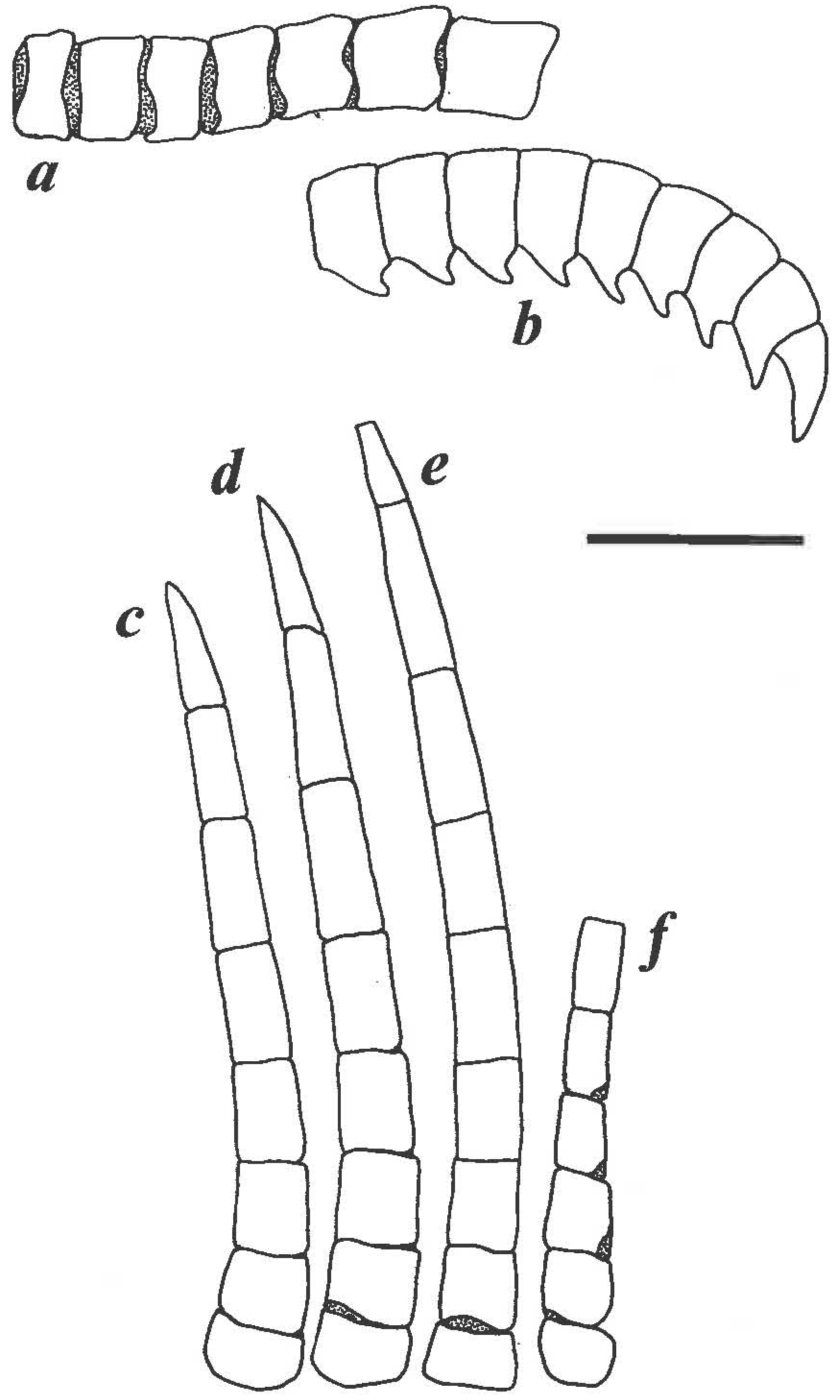


Figure 23. Holotype specimen of *Stephanometra coronata* A. H. Clark (USNM E35242) a. Base of cirrus. b. Tip of cirrus. c-f. Pinnules from interior arm. c. P_1. d. P_2. e. P_3. f. P_4. Scale: 2 mm.

Stephanometra indica Smith, 1876

Figures 24-55; Table 2.

Comatula indica Smith, 1876:406; 1879:564, pl. 51, figs. 3, 3b [not 3a].

Antedon protectus Lütken, 1874:190 (*nomen nudum*, in Carpenter, 1879, p. 18-19). —Carpenter, 1879:19.

Antedon spicata Carpenter, 1881:190; 1888:225.— Bell, 1882:533; 1884, 885:497.— Hartlaub, 1891:38, 58.—A. H. Clark,1912g:81; 1912f:35, 36, 41, 136.

Antedon indica: Carpenter, 1882:746; 1888:35, 54, 210, 225, 232, 233, 366, 379; 1889:310, 311.— A. H. Clark, 1912f:34, 39, 40.

Antedon oxyacantha Hartlaub, 1890:178; 1891:6, 11, 15, 39, 55, 58, 113, pl. 3, figs. 35, 37.—A. H. Clark, 1912a:2; 1912f:37.

Antedon monacantha Hartlaub, 1890:179.

Antedon spinipinna Hartlaub, 1890:179; 1891:11, 39, 58, 61, 113, pl. 4, figs. 42, 44.—A. H. Clark, 1912f:37.

Antedon tuberculata Hartlaub, 1891:38, 58, 59.—A. H. Clark, 1912e:385; 1912f:35, 39.

Antedon? spicata: Bell, 1894:396.—A. H. Clark, 1912f:38.

Himerometra monocantha: A. H. Clark, 1907:356 (part).

Stephanometra spicata: A. H. Clark, 1909a:10; 1911c:176, 183; 1912g:84; 1912f:35, 36, 132; 1918:94, 95, 272, pl. 7; 1936b:87, 88, 100, 104; 1941, 424-436, pl. 49, figs. 223, 224; pl. 91, fig. 447.— Gislén, 1936:3, 4, 5, 11. —A. M. Clark and Rowe, 1971:24.—A. M. Clark, 1972:108.— Chen *et al.*, 1988:78, fig, 20. — Stevens, 1989:4-23, 4-28, 5-8, fig. 5.3.— Messing, 1998:189, 191.—Kogo, 1998:61-63, fig. 49.

Stephanometra tuberculata: A. H. Clark, 1909a:10; 1912a:20; 1912e:385, 396; 1912f:35, 38, 39, 133; 1913b:28.—Hartmeyer, 1916:235.

Stephanometra monacantha: A. H. Clark, 1909a:10 (part); 1912a:21.—H. L. Clark, 1921:22; 1946:46.

Stephanometra marginata A. H. Clark, 1909d:169, 170; 1912a:19, 20; 1912e:385, 396; 1912f:34, 40, 41, 135.

Stephanometra indica: A. H. Clark, 1911e:6, 8 , 13, 26; 1913b:29; 1918: 94, 97; 1936b:88, 104.— Gislén, 1934:20.—A. M. Clark and Rowe, 1971:23, fig. 8c —A. M. Clark, 1972:107-108, fig. 10 (f-h).— Meyer and Macurda, 1980:86-87. — Zmarzly, 1985:352-353.— Stevens, 1989:4-2, 4-22, pls. 8a, 8b, 5-8, fig. 5.3. — Messing, 1994:239; 1998:189 & 191.

Stephanometra oxyacantha: A. H. Clark, 1911c:183; 1912a:2, 19; 1912f:37, 132; 1912g:82; 1918:94, 272, 276; 1936a: 302; 1941:418-423, pl. 47, fig. 217, pl. 48, figs. 218-221.—Gislén, 1934:25. —A. M. Clark and Rowe, 1971:24.— Meyer and Macurda, 1980:87-88, fig. 7c.— Stevens, 1989: 4-22, 4-23, pl. 8c, fig. 5.3. — Messing, 1998:189,191.

Stephanometra spinipinna: A. H. Clark, 1912f:37, 132; 1918:95; 1941:415-418. — Gislén, 1934:20.—A. M. Clark and Rowe, 1971:24.— Stevens, 1989:4-28. — Messing, 1998:189.

Stephanometra stypacantha H. L. Clark, 1915b:103.

Stephanometra indica protectus: A. H. Clark, 1941:443-439, pl. 49, fig. 222, pl. 50, figs. 225-230, pl. 51, figs. 231, 232.

Stephanometra indica indica: A. H. Clark, 1936b:88, 100; 1941:436-443, pl. 51, fig. 233, 234, pl. 91, figs. 449, 450.

Stephanometra indica protecta: A. M. Clark, 1975:401.

Holotype. —BMNH 76.5.5.24, holotype specimen (1 specimen), Mauritius, Rodriguez I., Henry Slater, coll., no additional data.

Other material examined. — RED SEA: USNM E34613 (1), Gulf of Aqaba, D. L. Meyer coll., no additional data. SRI LANKA: USNM E35079 (1), off NE Corner, 08°51'30" N, 081°11'52"E, 51 m, no additional data. MAURITIUS: USNM E34699 (1), D. L. Meyer coll., no additional data. SEYCHELLES: USNM E34960 (2), June 1975, D. L. Meyer, coll. MALDIVE ISLANDS: BMNH 1902.3.31.21 (1), Hulule, Male I, S. Gardiner, coll.; NSUOC 633 (1), Jewellers' Is., Nilandu Atoll (E of Madali I.), 02°52'6"N, 72°50'8"E, 4.5 m-12 m, 21 Jan 1999, D. L. Rankin, coll. COCOS ISLANDS: USNM E11712 (1), 1941, Gibson-Hill, CA, coll., no additional data. INDONESIA: USNM E35050 (2), Banda Is., NW coast of Banda Besar, 2-3 m, 31 Jan 1975, D. L. Meyer, coll.; Greater Sunda Islands, USNM E469 (2), Java I., R/V *Siboga,* Sta. N/A, Mar 1899; Ceram, USNM E34838 (2), Ceram Sea, E coast of Marsegoe I., 02°59'48"S, 128°03'E, 0-15.2 m, D. L. Meyer, coll.; Moluccas, USNM E35376 (1), Tapalol Is., Biga Bay, 02°01'30"S, 130°19'18"E, 24 Jan 1975, R/V *Rumphius II,* coll. SINGAPORE: USNM E34854 (4+) & USNM E34549 (3), D. L. Meyer, coll., no additional data. MALAYSIA: NSUOC 313 (1), Sabah, Borneo, Dive Center, Mabul I., 04°15'N, 118°38'E, 7 m, 24 Apr 1997, C. G. Messing coll.; NSUOC 315 (1), Mabul Wall, E side of Mabul I., 04°15'N, 118°38'E, 11 m, 22 Apr 1997, C. G. Messing, coll.; NSUOC 258, 322 & 323 (3), E side of Mabul I., 04°5'N, 118°38'E, 9-11 m, 21 Apr 1997, C. G. Messing, coll.; USNM E34546 (5), D. L. Meyer, coll., no additional data.; USNM E34548 (3+), D. L. Meyer, coll., no additional data. PHILIPPINES: USNM E5269 (2), Tawi-Tawi Islands, Bongo Island, 27 m, 9 Sep 1929, R/V *Willebrord Snellius* Expedition, coll.; NSUOC 314, 316 & 348a-d (6), Sulu Sea, N Tubbataha

Reef, 09°49'N, 119°52'E, 8-21 m, 20-21 Apr 1995, C. G. Messing & L. Sharron, colls.; NSUOC 331, 334, 336 & 337 (4), S Tubbataha Reef (W end), 09°49'N, 119°52'E, 20-30 m, 21 Apr 1995, C. G. Messing, coll.; USNM E35221 (1), Sulade I., R/V *Albatross*, Sta. 5147, 05°41'40"N, 120°47'10"E, 38 m, 16 Feb 1908; NSUOC 318 (1), Pasig Reef, off Constance Shoal, 09°55'N, 119°30'E, 11-12 m, 23 Apr 1995, C. G. Messing, coll.; NSUOC 328 (1), Honda Bay, Palawan, 10°50'N, 118°45'E, 21 m, 21 Apr 1995, C. G. Messing, coll.; NSUOC 330, 342 & 343 (3), Jesse Beasley Reef, 09°01'N, 119°48'E, 4-8 m, 19 Apr 1995, C. G. Messing, coll.; USNM E35262 (1), Luzon I., R/V *Albatross* Sta. 5109, 14°03'45"N, 120°16'30"E, 18-22 m, 15 Jan 1908. SOUTH CHINA SEA: BMNH 1892.8.22.28 (1), Macclesfield Bank, 24 m, British Admiralty, coll. CHUUK ATOLL, MICRONESIA: NSUOC 324 (1), SE of Scheiben I., NW of Weno I., 9.1 m, 10 June 1993, C. G. Messing, coll.; NSUOC 333, 335, 338 & 339 (4), N side of NE Pass, S of Quoi I., 07°31'38"N, 151°58'05"E, 9-11 m, 8-11 June 1993, C. G. Messing, coll.; NSUOC 340, 341 & 349 (3), Fringing reef, E side of Yanagi I., (between Weno & Dublon Isl.) 07°25'N, 151°50'E, 14-18 m, 13 June 1993, C. G. Messing, coll. KIRIBATI: USNM E18323 (1), Gilbert Islands, Onotoa Atoll, P.E. Cloud, coll., no additional data. PAPUA NEW GUINEA: NSUOC 317, 321, 325 & 329 (4), Jais Aben Reef, N side of Nagada Harbor, Madang, 05°09'29"S, 145°49'21"E, 3-4 m, 2 June 1992, C. G. Messing, coll.; NSUOC 320 & 332 (2), Padoz Reef, Madang, 05°09'S, 145°50'E, <18.5 m, 5 July 1991, C. G. Messing, coll.; Barrier I. outside Magic Pass, Madang, 6-8 m, 9 July 1991, L. Harris, coll., NSUOC 326 (1); NSUOC 327 (1), Barrier I. Outside Wongat I., Madang, 05°08'09"S, 145°50'51"E, 3-4.5 m, 11 June 1991, C. G. Messing, coll.; IRSCB 320 (1), Hansa Bay, M. C. Lahaye, coll., no additional data.; IRSCB 43, 69, 70 & 73 (4), Epave (Sisimangun), 5-18 m, 20-23 June 1989, M. C. Lahaye, coll.; IRSCB 241 (1), Epave, 36 m, 7 July 1989, M. C. Lahaye, coll.; IRSCB 269, 276 & 284 (2), Pointe Sud (Laing I., Hansa Bay), 12 m, 10 July 1989, M. C. Lahaye, coll.; IRSCB 374 & 380 (2), Pointe O (Laing I., Hansa Bay), 25 m, 22 July 1989, M. C. Lahaye, coll.;

IRSCB 354 & 357 (2), Pointe Nord (Laing I., Hansa Bay), 23 m, 19 July 1989, M. C. Lahaye, coll.; IRSCB 135 (1), Laing I., Hansa Bay, Station 13, 26 m, 26 June 1989, M. C. Lahaye, coll.; IRSCB 230 & 232 (2), Autour de l' Ile (Laing I., Hansa Bay), 0-5 m, 6 July 1989, M. C. Lahaye, coll.; IRSCB 298 (2), Hansa Point, Hansa Bay, 36 m, 12 July 1989, M. C. Lahaye coll.; IRSCB 316 (1), Laing I., Hansa Bay , H1-2/12 (S/O), 26 m, 15 July 1989, M. C. Lahaye, coll.; IRSCB 316 (1), Laing I., Hansa Bay, 26 m, 15 July 1989, M. C. Lahaye, coll.; IRSCB 248 (1), Platier, 12 m, 9 July 1989, M. C. Lahaye, coll.; IRSCB 422 (1), Mandy Passage, (Near Hansa Bay), 41 m, 24 July 1989, M. C. Lahaye, coll. LOUISIADES ARCHIPELAGO: (1) Panaete I. of Deboyne Group, 10°40'11"S, 152°21'08"E, 10 m, 31 May 1998, Gustav Paulay, coll. AUSTRALIA: USNM E34738 (1), Heron I., D. L. Meyer, coll., no additional data. FIJI: USNM E34572 (2), 1976, D. L. Meyer, coll., no additional data; USNM E34793 (5), Suva Point, 12 Apr 1975, D. L. Meyer, coll. NO LOCALITY DATA: CRRF 1656K (1), no additional data.

Diagnosis.—A species of *Stephanometra* with brachitaxis ossicles weakly swollen laterally or with thick rounded ridge-like extensions oriented obliquely to longitudinal axis of the ray; cirri bearing midaboral carination which may develop into a small spine; P_1 slender, tapering delicately to a conical tip; P_2 alone or P_2 and following one to three pinnules composed of elongated pinnulars with reduced ambulacral groove, a conical terminal segment, and flattened articulations lacking triangular fossae.

Description.— Centrodorsal discoidal or dome-shaped, 2.1-6.3 mm across (Figs. 24a-g), 0.7-2.4 mm high; D/H 2.0-4.0. Cirri arranged in two to four alternating marginal rows. Polar area concave, irregular in shape, with encroaching cirri, 0.7-3.1 mm across (Figs. 24a-g); D/P 1.7-3.9.

Cirri XIII-LI, 15-30 cirrals, 10-31 mm long. C_1-C_3 short; C_4-C_9 or C_{11} longer than broad; $C_{7\text{-}9}$ longest, L/W 1.0-1.9; C_{10}-C_{12} through the penultimate cirral compressed and each bearing a raised keel that begins proximally or distally on the cirral. Carination may be weak or produce a spine (Figs. 25a-g). Penultimate segment bearing a sharp, aboral spine. Terminal claw longer than the penultimate segment.

Basal ossicles not visible externally; radials projecting slightly beyond edge of the centrodorsal or not visible at all. Brachitaxis ossicles well separated, 0.4-2.0 mm apart (measured between adjacent Ibr_1 ossicles). Ibr_1 oblong 0.4-1.2 mm long, 1.0-3.1 mm wide; W/L 2.0-5.0, rarely less than 2.0; with parallel or converging lateral margins, usually free laterally but sometimes united proximally. Ibr_2 (axil) with diverging lateral margins, 0.9-2.9 mm long, 1.5-4.1 mm wide; W/L 1.7-3.7, rarely less than 1.7. Ibr_2 bearing a weak (Figs. 26a-c) to strongly developed (Figs. 26d-h) oblique (relative to ray axis) lateral extension restricted to the proximal portions of the ossicles, resulting in an elongated knob (Figs. 26d-h). IIBr series similar to IBr. $IIbr_1$ bearing a weak (Figs. 26a-c) to strongly developed (Figs. 26d-h) oblique extension that extends the entire length of the ossicle margin; $IIbr_2$ (axils) with short knobs restricted to proximal portion of the ossicle (Figs. 26d-h). IIIBr developed externally and, rarely, internally; IVBr, when present, developed externally. Synarthrial tubercles weakly to well developed.

Arms 11-33; rays 50-160 mm long. Rays most commonly with 3-6 arms each, less frequently with 2 or 7 arms each. br_1 through br_6 –br_8 oblong; subsequent brachials cuneate; br_{10} 0.5-1.9 mm wide, 0.4-1.1 mm long; W/L 0.7-3.6.

Syzygies at br_{3+4}, br_{9+10}, br_{16+17} and br_{19+20}, less frequently between br_{5+6}, br_{11+12}, and br_{25+26}. Distal syzygial intervals 4 to 8, less often 3, 9 or 10.

Pinnules on outer arms generally longer and thicker than pinnules on inner arms. P_1 3.6-14.1 mm long, of 10-27 pinnulars, slender, composed of elongated segments tapering delicately to a conical tip (Figs. 27 a, e, i, m, p, s & w). The first few proximal pinnulars laterally compressed; subsequent pinnulars cylindrical. First and second pinnulars oblong, third slightly longer than broad; the fourth and following with L/W 2.0-4.0, and the terminal pinnular a conical spike. P_2 alone, or P_2 through P_3, P_4 or P_5, robust, stiff and spinelike (Figs. 27a-a'), much larger than subsequent pinnules, composed of elongated cylindrical segments with both ambulacral groove and tube feet reduced. Specimens with P_1 and P_2 enlarged, formerly distinguished as *S. spinipinnna* (Figs. 27i-l). Specimens with P_2 through P_4 or P_5 enlarged, formerly distinguished as *S. oxyacantha* (Figs. 27s-a'); those with P_2 and P_3 enlarged, as *S. spicata* (Figs. 27e-h), and those with P_2 alone enlarged, as *S. indica* (Figs. 27 a-d, & m-r). P_2 5.4-20.0 mm long, 8-18 pinnulars; pinnular 6 L/W 1.5-4.0 (Figs. 27 b, f, j, n, q, t & x). In smaller specimens, P_3-P_5 tending to be small, weak and flexible with a well-developed ambulacral groove and resembling the following pinnules; P_3 2.1-6.0 mm long, 7-14 pinnulars (Figs. 27 c, g, k, o, r, u & y); P_4 2.0-4.8 mm long, 7-14 pinnulars (Figs. 27 d, h, l, v & z), and P_5 2.4-5.7 mm, 10-14 pinnulars (Fig. 27a'). Subsequent pinnules gradually increasing in length. P_{distal} 7.2 mm with 18 pinnulars; the terminal pinnulars elongated and covered with small spines (Fig. 27a"). In larger specimens, robust P_3 3.4-15.0 mm, 7-14 pinnulars; P_4 2.3-10.2 mm, 9-14 pinnulars; P_5 2.4-9.4 mm, 8-14 pinnulars (Figs. 27 s-a'). Subsequent pinnules gradually increasing in length. P_{distal} 6.3- 9.4 mm long, 18-23 pinnulars; the terminal pinnular elongated and covered with small spines.

Color patterns.— Wide variations in color exist for *S. indica.* The following color patterns are recorded in the current collection except where noted. Concentric banding on the rays is the most consistent pattern for this species. Banding is expressed in white, tan, brown, gray, pink, orange and in various combinations of these colors. Some specimens are entirely dark purple, maroon or purplish, sometimes with darker articulations between brachials. Others are chiefly yellow, orange or purple proximally, with purple, brown or black articulations. A speckled pattern, chiefly purple with tiny pale spots, was observed for a few specimens. A.H. Clark (1921b), Stevens (1989) and the present study noted silver, yellow or orange pinnule tips for some specimens. Previously published records of color (A. H. Clark, 1921b; Meyer and Macurda, 1980; Zmarzly, 1985 and Stevens, 1989) may be based on incorrectly identified species.

Meyer and Macurda (1980) reported great variation in color for their small number of specimens and noted that color patterns of *S. indica* differed significantly from those of *S. echinus* and *S. oxyacantha*. *S. indica* specimens expressed banding in reddish brown, purple and yellow, or a white variegated pattern. Some specimens were entirely dark reddish purple, while others were solid pink or lavender with a white section midway along the arms and pinnules. Color patterns of previously recognized species (*S. indica*, *S. spicata* and *S. oxyacantha*) overlap with each other in the current study.

Geographic distribution.—From Tanzania and Madagascar in the west to Guam and the Tonga Islands in the east, including tropical Australia as far south as the Capricorn Channel of Queensland, and as far north as the Red Sea and Okinawa, Japan. Previously published records of distribution, possibly as far east as Kwajalein (A. H. Clark, 1921b; Meyer and Macurda, 1980; Zmarzly, 1985 and Stevens, 1989) may be based on incorrectly identified species.

Bathymetric range.— Shoreline possibly down to 73 m (A. H. Clark, 1941); most collected from 30 m or less.

Remarks.—Members of the second group of *Stephanometra*— *S. spinipinna*, *S. indica*, *S. spicata* and *S. oxyacantha*— lack the strong aboral spines on the cirri and have been differentiated by features of the oral pinnules (A. H. Clark, 1941). All members of this group have a stiff and spinelike P_2. As noted in the diagnosis and descriptions above, such pinnules are more accurately characterized as having flattened articular facets (see pp. 25, Fig. 4) and reduced ambulacral grooves.

The latter three species of the above group have a flexible and slender P_1 and have been characterized according to the number of enlarged oral pinnules that follow (A. H. Clark 1941). Numerous authors have commented on the taxonomic status of these three species. Although he maintained them as separate taxa, A. H. Clark (1941:408) wrote that there is no "hard and fast line of division between these forms." He suggested that pinnules stiffen with age and that the *S. indica-S. spicata-S. oxyacantha* series may, therefore, represent a growth series. A. H. Clark described *S. oxyacantha* as having P_2-P_4 or P_5 enlarged, stiffened and spinelike; succeeding pinnules reduced in length and stiffness; 24-32 arms, 110-150 mm long. *S. spicata* was characterized as having a stiff and spinelike P_2 and P_3, with succeeding pinnules decreasing in length and stiffness; 14-33 arms, 70-120 mm long. *S. indica* had P_2 enlarged and stiffened; P_3 and following pinnules small and weak; 18-30 arms, 65-153 mm long. Similarly, Gislén (1940) thought immature specimens bore fewer cirri, had weakly developed lateral adambulacral margins on brachitaxes, and developed traces of basal stiffening in P_3. Gislén suggested that *S. protectus*, treated by A. H. Clark as separate from *S. indica*, might prove to be a juvenile *S. spicata*. Meyer and Macurda (1980) found that specimens with P_2 alone stiff and spinelike were smaller, with maximum radius 80 mm, than those with more stiff pinnules. They considered these specimens to be juveniles. Stevens (1989) suggested that these three species represent points along continua of size, arm number, form of proximal pinnules, nocturnalism and depth, and could be considered a monospecific complex. On the other hand, he claimed that the three species exhibited unique color patterns and should be kept distinct and, that overlap between characters was small. However, Stevens' study concentrated on a minute region of the geographic range of these species and measured only two characters, arm radius and cirrus length. Results of the current study indicate that a great deal of overlap occurs between these two characters for the *indica-spicata-oxyacantha* series (Fig. 29).

An apparent size continuum for the *indica-spicata-oxyacantha* series is based on several morphological characters. Radius lengths for *indica* specimens in this study range from 50 to 140 mm, with an average of 77 mm; *spicata* ranges from 50 to 160 mm, with an average of 114 mm; and *oxyacantha* ranges from 55 to 150 mm, with an average of 109 mm. This study contained one large *indica* (NSUOC 335) that approached the size of *oxyacantha* specimens with the exception of arm number, while there were no small *oxyacantha* specimens. The holotype, *Comatula indica* (BMNH 76.5.5.24), another large *S. indica*, has the third largest P_2 in the current study (Fig. 28 c). Plots of maximum cirrus length against arm radius (Fig. 29) and number of cirri against arm radius (Fig. 30) show that *indica-spicata-oxyacantha* overlap but *oxyacantha* generally falls out as the largest, while *spicata* is in the middle and *indica* falls out the lowest.

Approximately 20% of specimens referable to the *indica-spicata-oxyacantha* series in the current study are intermediates and cannot be satisfactorily assigned to species based on current diagnoses. Two types occur in this study: specimens bearing arms characteristic of both *S. indica* and *S. spicata* (Figs. 31a-e) and those with arms typical of both *S. spicata* and *S. oxyacantha* (Figs. 31f-k). Intermediates constitute 13% and 18% of all *spicata* and *oxyacantha* specimens and *indica* and *spicata* specimens combined, respectively. Figures 29, 30, and 32-38 illustrate that intermediate specimens are scattered throughout the range of the *indica-spicata-oxyacantha* series.

The strongest development of lateral adambulacral margins occurs in *S. oxyacantha*, while both *S. indica* and *S. spicata* margins range from weak to strong (Appendix 2). Traces of basal stiffening in oral pinnulars were observed in specimens of *spicata* and *indica*, which may suggest that pinnules stiffen with age. However, regenerating arms were indicative of existing arms. For example, specimens of *S. oxyacantha* regenerate *S. oxyacantha* arms, not *S. indica* arms.

Results of this study indicate that several characters vary with size, as follows: pinnular length, centrodorsal diameter and height, aboral pole diameter, number and length of cirri, width of Ibr_2, arm radius and development of lateral adambulacral margins. These characters were selected for graphing because they increase with overall specimen size, thus spanning the observed ranges of variation. It is assumed that such size increases reflect growth, but this remains uncertain. For example, Messing (1994) reports that specimens of several comasterid species tended to have shorter more numerous arms in high energy habitats. No clear distinction exists between features that increase with size. *S. oxyacantha* tends to be larger but there is too much overlap to distinguish the species. Therefore, the plots suggest that *S. indica, S. spicata,* and *S. oxyacantha* represent a continuum.

Principal component scores (Figs. 39-41) for *S. indica, S. spicata, S. oxyacantha, S. spinipinna* and intermediate specimens also illustrate overlap between these species. Component loadings exceeding 0.6 were interpreted as follows: component one represents size-related variables including cirrus length, arm radius, length of P_1–P_5, and the length of the 6^{th} pinnular from P_2, component two loads high on aboral pole diameter, centrodorsal diameter number of cirri and number of arms, while component three loads high on the length of Ibr_2 and is therefore considered the Ibr_2 size factor (Appendix 3). *S. oxyacantha* tends to separate somewhat but there is still apparent overlap among the species.

Furthermore, cladistic analysis (Fig. 43) suggests that *S. indica, S. spicata,* and *S. oxyacantha* are synonymous and should be synonomized under the senior name, *S. indica*. Intermediate specimens are scattered thoughout the clade. A branch and bound search with bootstrap analysis of 2500 replicates using maximum parsimony and all characters weighted equally resulted in one most parsimonious tree with TL = 134, CI = 0.634, RI = 0.058, and RCI = 0.037. Morphological and meristic data of important growth-related characters for *S. spinipinna, S. indica, S. spicata, S. oxyacantha* and intermediate specimens are provided in Table 2.

S. spinipinna, unlike the others, displays a stiff and spinelike P_1, which is, however, not enlarged like the following pinnules. Hartlaub, cited in A. H. Clark, 1941:418, distinguished

Antedon spinipinna as a new species even though the type specimen was not sexually mature, noting that it was a "slenderly built form" with P_1 intermediate in character between "*S. tenuipinna* on the one hand and *S. spicata* and *S. oxyacantha* on the other."

A. H. Clark's (1941) description of *S. spinipinna* is taken directly from Hartlaub's (1890:179) description of the type specimen from Amboina: 12 arms, 35 mm long; P_1 stiff and styliform with 12-14 elongated pinnulars. Yet, comments about four of five specimens that follow this description (A. H. Clark, 1941:416) contradict it: 14-31 arms, 70-150 mm long; P_1 ranging from slender and stiff to somewhat stiffened but not spinelike. An illustration (Fig. 42, courtesy of C. G. Messing, USNM E8969) of A. H. Clark's (1941) Kei Islands specimen shows a P_1 as stiff as P_2, in contrast to his description of a slender P_1 and stouter P_2 (Figs. 42 d & f). This P_1 approaches that of *S. tenuipinna* although the cirri described in the monograph are typical of *S. spinipinna.*

Stevens (1989) noted specimens of *S. indica* in which P_1 appears partially stiffened on one or more arms. A slender yet stiffened P_1 also occurs in some specimens attributable to all "species" of the second group in the current study (Figs. 27a, e, i, m, p, s & w). These pinnules orient toward the mouth and cover the disk, which contributes to a stiffened appearance. Dissociation of pinnules confirms that articulations in "stiffer" P_1 are identical to those of "slender, flexible" P_1 typical of *S. indica, S. spicata* and *S. oxyacantha.* Variations in this character may at least partly result from preservational differences.

In addition, although A. H. Clark (1941:408) describes *S. spinipinna* as easily recognized when typically developed, he acknowledged that P_1 varies and suggests "possible intergradation between *S. spinipinna* on the one hand and *S. spicata* and *S. oxyacantha* on the other." Similarly, the centrodorsal, cirri, and lateral adambulacral margins entirely resemble those of the members of the second group of species. Figures 44-49 indicate that *S. spinipinna* falls well within the *indica* series. Thus, no noteworthy distinction exists between *S. spinipinna* and *S. indica,* *S. spicata* and *S. oxyacantha*. Cladistic analysis (Fig. 43) also suggests that *S. spinipinna* should be assigned to synonymy under *S. indica* as it is scattered though out the clade.

A. H. Clark (1941) treated *S. indica protectus* as a subspecies of *S. indica*, the only distinction being the length and shape of P_2 (A. H. Clark, 1941). P_2 of *S. indica indica* consisted of 16-20 segments, tapering to a fine point, whereas P_2 of *S. indica protectus* consisted of 9-16 segments and terminated in a sharp point. Although A. H. Clark wrote that when "typically developed", these two species are very different, he noted that some specimens possessed P_2 intermediate in character between *S. indica protectus* and *S. indica indica*. Eight percent of specimens examined in this study possess a P_2 that resembles A. H. Clark's description of *S. indica protecta*. The range of these two taxa is practically co-extensive, which serves to undermine the subspecific ranking (A. M. Clark, 1972). The current study, in agreement with A. M. Clark, concludes that the subspecific ranking should not be recognized and *S. indica protecta* should be relegated to synonymy under *S. indica*.

Figures 50-53 illustrate that *S. tenuipinna* forms a distinctly separate cluster from other members of *Stephanometra*. Ibr_2 width, centrodorsal diameter, number of cirri and arm radius were selected for graphing because all increase with size and growth. Length of pinnular 6 of P_1 was selected because pinnulars from P_1 of *S. tenuipinna* are elongated in comparison with those of the other species of *Stephanometa*, in which pinnulars are not as elongated. Other characters that distinguish *S. tenuipinna* from *S. indica* are descriptive.

Principal component scores (Fig. 54) for *S. tenuipinna* and *S. indica* illustrate distinct groupings for the two species with a slight overlap. Component loadings of 0.60 and above were interpreted as follows: component one represents size-related variables including cirrus length, length of Ibr_2, length of br_{10}, arm radius, and the length of both P_1 and P_4, while component two designates a cirrus and arm shape factor with the highest loadings on the number of cirri and number of arms (Appendix 4).

Cladistic analysis (see pp. 33, Fig. 14) of *Stephanometra* species indicates that relative to *S. tenuipinna*, the *S. indica* specimens (including intermediate specimens) are paraphyletic.

A. H. Clark (1941) indicates that the IIIBr series is more frequently internal than external IIIBr series in species of *Stephanometra.* Specimens in this study contradict Clark's arrangement in having IIIBr located either externally, or internally and externally on the same specimen.

Meyer and Macurda (1980) claimed that cirri of *S. indica* were "distinctly different" from those of *S. oxyacantha* and resemble an illustration by A. H. Clark (1915:287, Fig. 340). However, they do not define "distinctly different". Cirri from specimens in the current study (including *indica, spicata, oxyacantha* and intermediate specimens) resemble Clark's illustration and do not differ except in size-related features. Similar attributes include: the slight overlap between the distal portion of one cirral and the proximal portion of the next; carination developing in the distal portion of distal cirrals, and cirrals slightly longer than broad.
Diagnostic characters for *S. indica* are limited to the description of lateral adambulacral margins, flat pinnular articular faces without triangular fossae and the number of enlarged oral pinnules. The high percentage of intermediate specimens in the current study indicates that previously defined diagnostic characters are inadequate and supports the synonomy of *indica-spicata-oxyacantha.* Growth related characters for all four "species" in this group overlap greatly. Comparison of color patterns for these "species" within the current study and against those reported in previous studies (A. H. Clark, 1921b, Meyer and Macurda, 1980, Zmarzly, 1985 and Stevens, 1989) also show tremendous overlap, providing further support for synonomizing *S. spicata, S. oxyacantha* and *S. spinipinna* under *S. indica.*

Note.—An illustration of the holotype of *Comatula indica* Smith (BMNH 76.5.5.24), is provided in Fig. 28, courtesy of C. G. Messing. Lateral margins of brachitaxes of this specimen (Fig. 28b) bear thick, obliquely oriented, rounded ridge-like extensions and axils with short, elongate knobs.

The illustration of a cirrus does not resemble a *Stephanometra* cirrus (Fig. 28a). However, Smith noted that he was not absolutely certain whether the cirri in the bottle containing this specimen were actually from this specimen (A. H. Clark, 1941:439).

An illustration of the type specimen *Antedon tuberculata* (BMHN 1888.11.9.75), courtesy of C. G. Messing, is provided in Figure 55. It is treated as a synonym of *S. indica.*

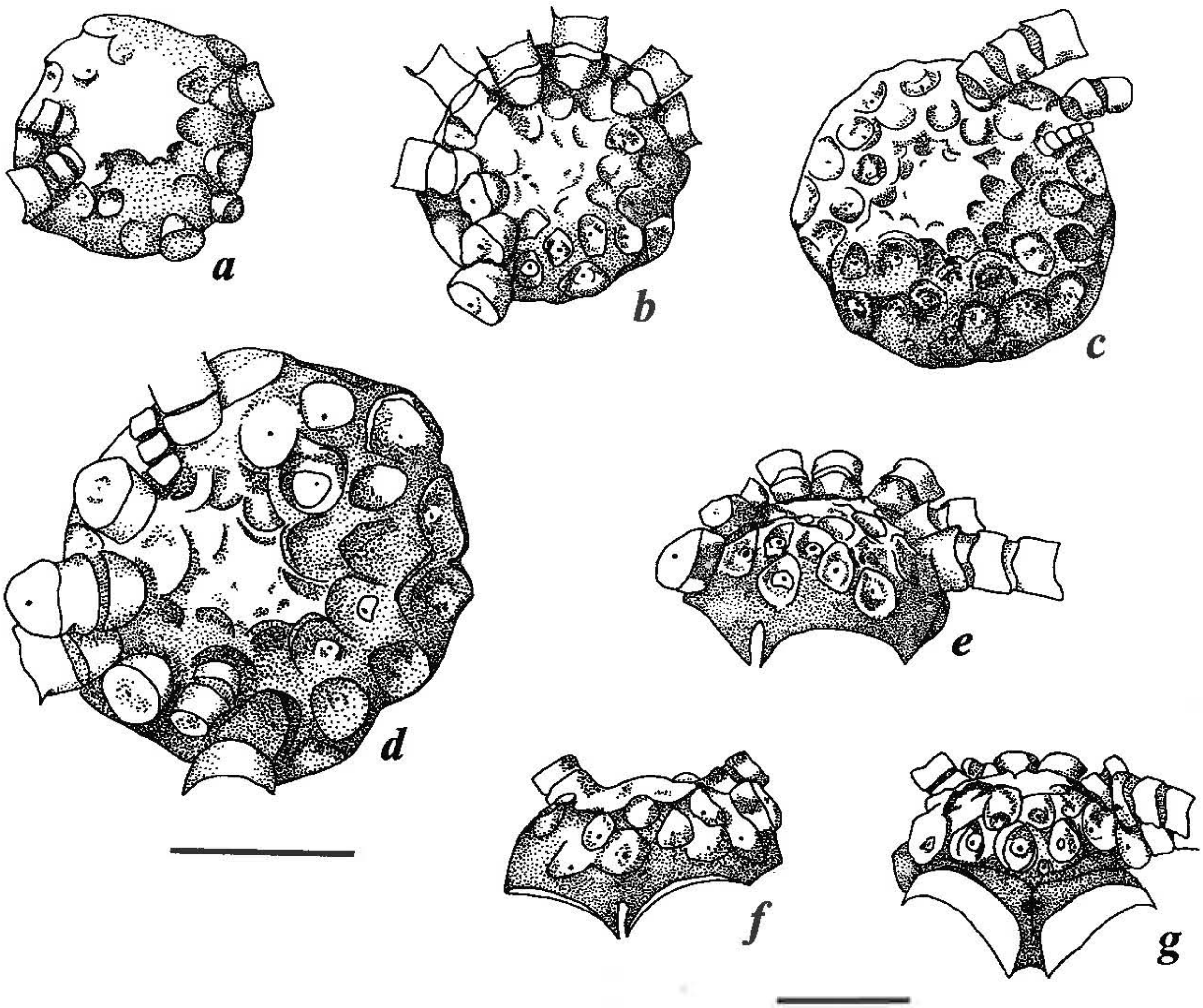


Figure 24. *Stephanometra indica*. Figs. a-d: Centrodorsal in aboral view. a. NSUOC 313. b. NSUOC 340. c. NSUOC 325. d. IRSCB 374. Figs. e-g: centrodorsal in lateral view. e. IRSCB 422. f. NSUOC 313. g. USNM E5269. Scale (left): b-d, & e, 2 mm; scale (right): a, f & g, 2 mm.

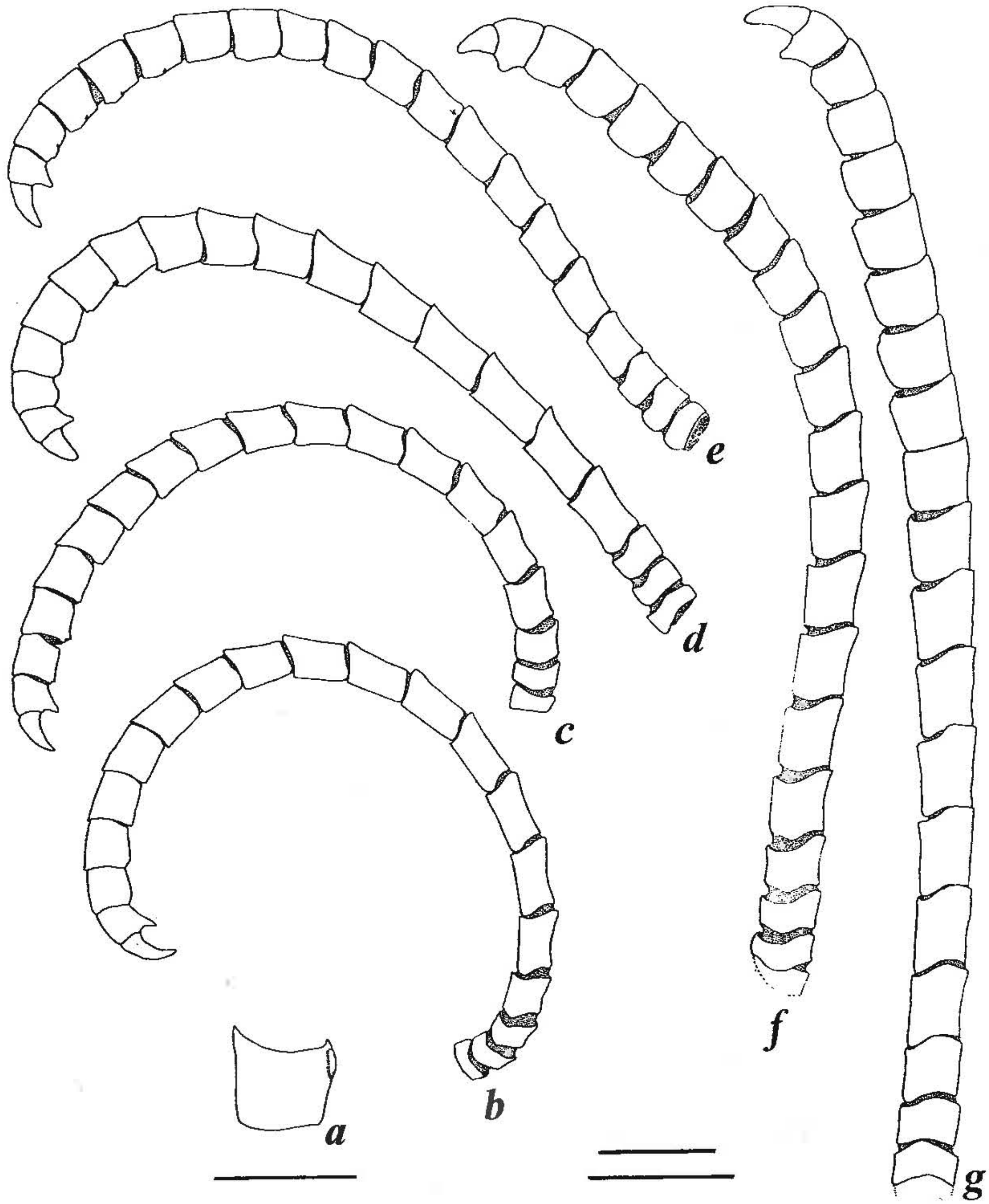


Figure 25. *Stephanometra indica*. a. Distal cirral, NSUOC 337. b. Cirrus, IRSCB 354. c. Cirrus, NSUOC 348. d. Cirrus, NSUOC 333. e. Cirrus, NSUOC 337. f. Cirrus, NSUOC 324. g. Cirrus, Gustav Paulay specimen. Scale (left): a,1 mm; scale (right, upper): b-e, 2 mm; scale right (lower): f & g, 2 mm.

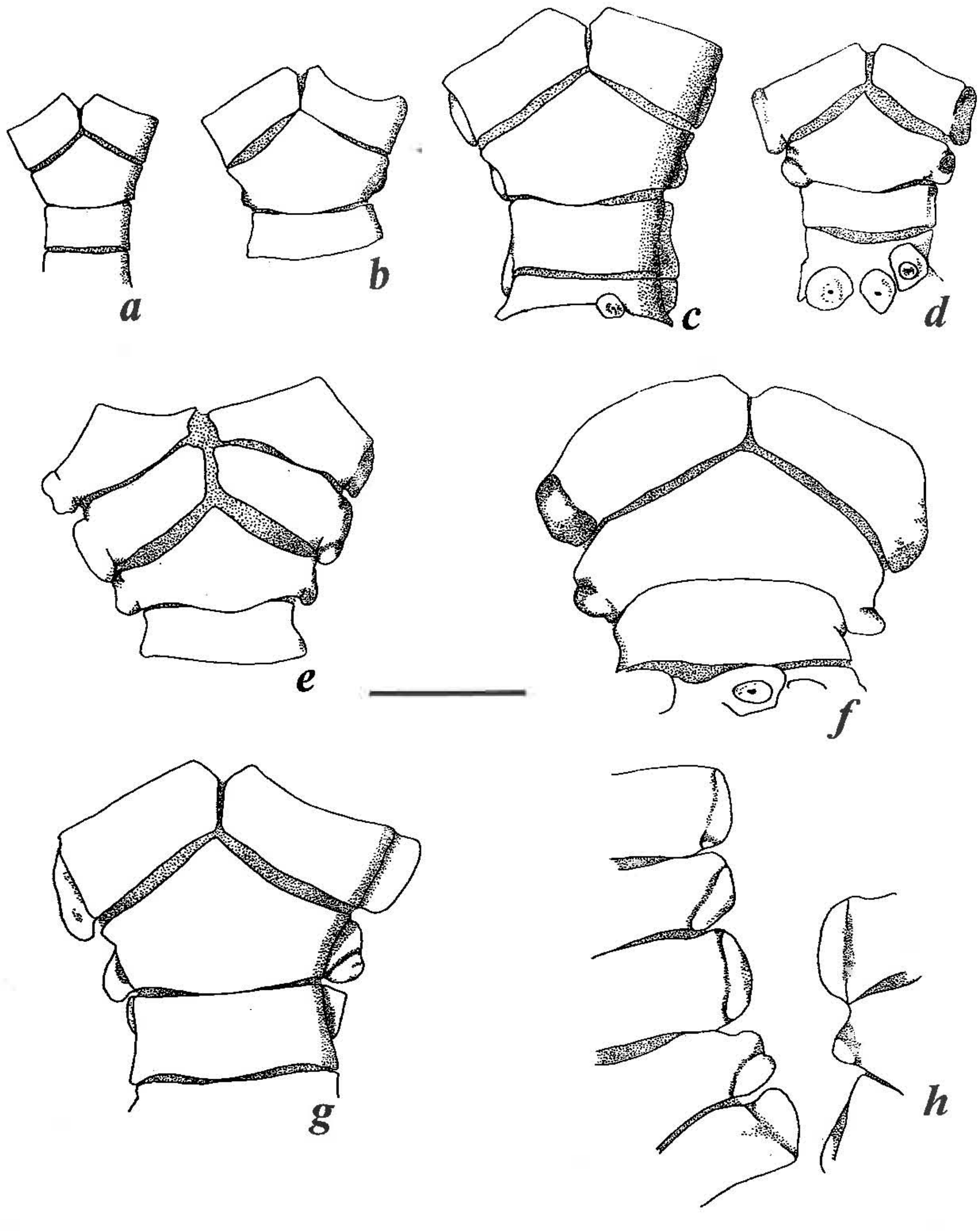


Figure 26. *Stephanometra indica*. Lateral adambulacral margins of brachitaxes ossicles, in aboral view. a. IBr2 & $IIbr_1$, NSUOC 323. b. IBr2 & $IIbr_1$, NSUOC 337. c. Radial, IBr2 & $IIbr_1$, NSUOC 313. d. Radial, IBr2 & $IIbr_1$, IRSCB 422. e. IBr2 & IIBr2, NSUOC 324. f. IBr2 & $IIbr_1$, NSUOC 316. g. IBr2 & $IIbr_1$, IRSCB 276. h. Adjacent lateral adambulacral margins of brachitaxes ossicles, IRSCB 276. Scale: 2 mm.

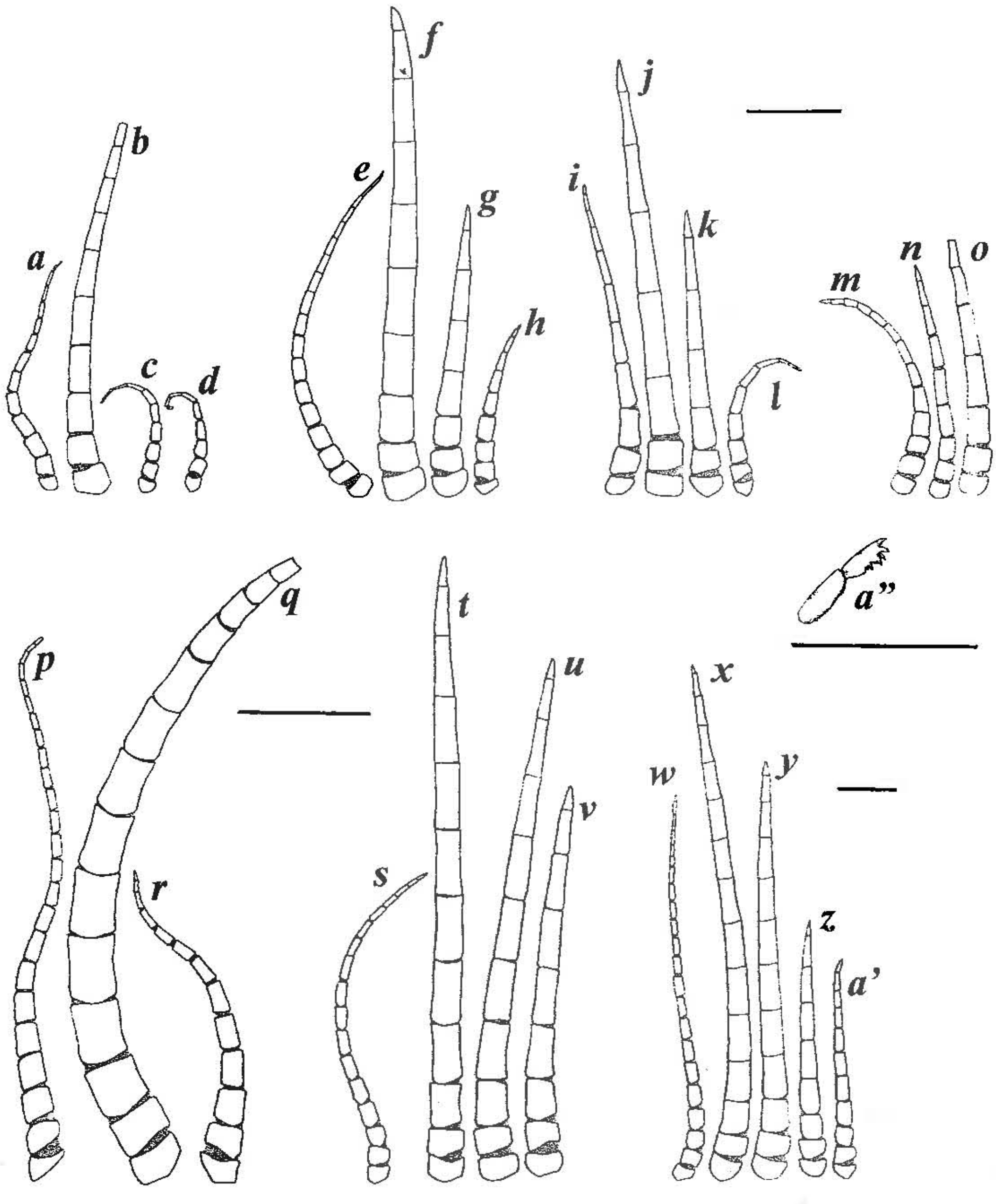


Figure 27. *Stephanometra indica*. Pinnules. a. P_1, NSUOC 348a. b. P_2, same. c. P_3, same. d. P_4, same. e. P_1, NSUOC 325. f. P_2, same. g. P_3, same. h. P_4, same. i. P_1, Gustav Paulay specimen. j. P_2, same. k. P_3, same. l. P_4, same. m. P_1, NSUOC 333. n. P_2, same. o. P_3, same. p. P_1, NSUOC 335. q. P_2, same. r. P_3, same. s. P_1, IRSCB 232. t. P_2, same. u. P_3, same. v. P_4, same. w. P_1, NSUOC 314. x. P_2, same. y. P_3, same. z. P_4, same. a’. P_5, same. a” Terminal pinnulars of distal pinnules, same. Scale (upper right): a-o, 2mm; scale (lower left): p-v, 2 mm; scale (center): a”, 1 mm; scale (lower right): w-a’, 2 mm.

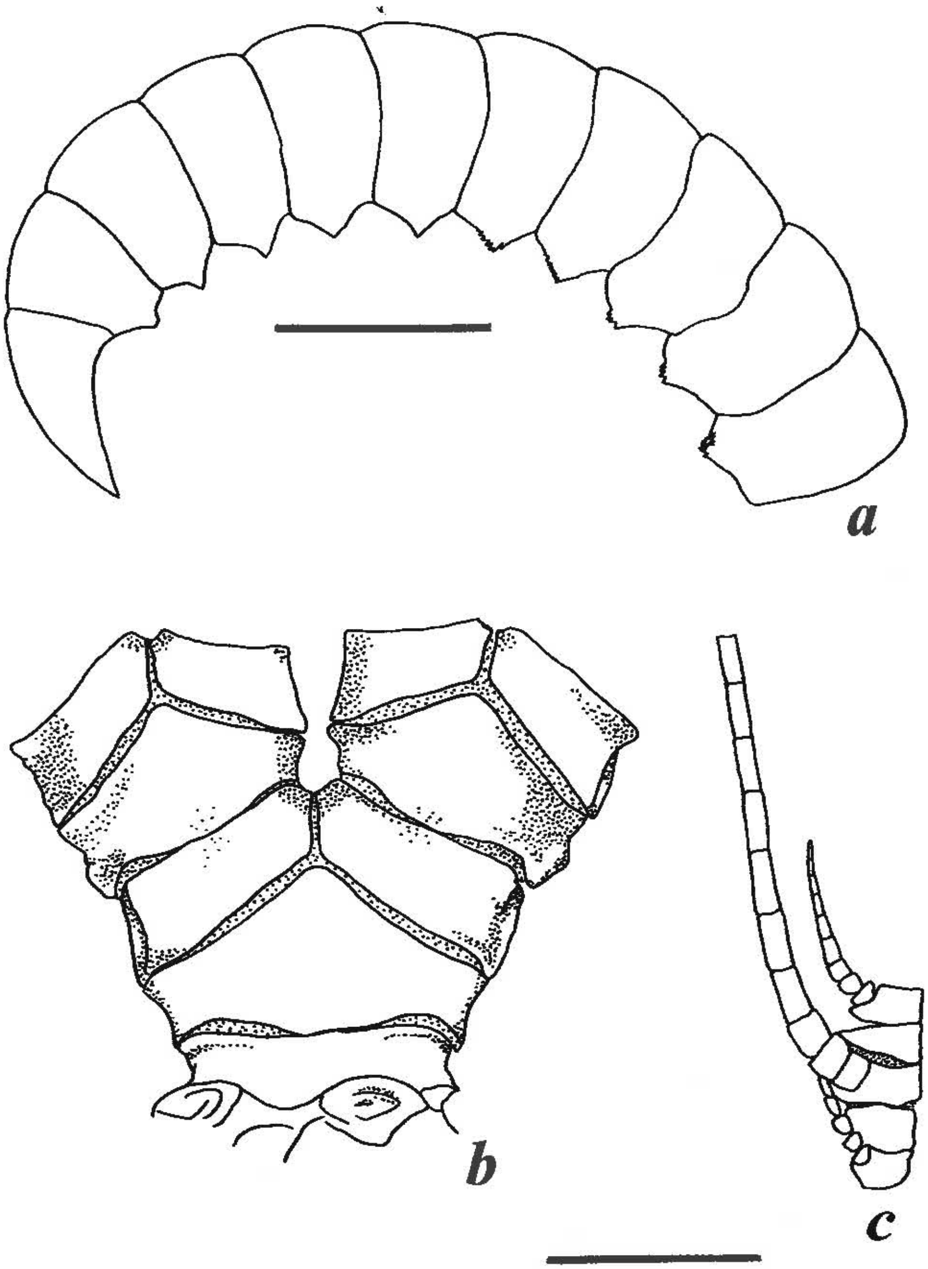


Figure 28. Holotype specimen of *Comatula indica* Smith (BMNH 76.5.5.24). a. Tip of cirrus (probably not from holotype). b. Lateral adambulacral margins of brachitaxis ossicles, in aboral view. c. P_1-P_3. Scale (upper): a, 1 mm; scale (lower): b & c, 2 mm.

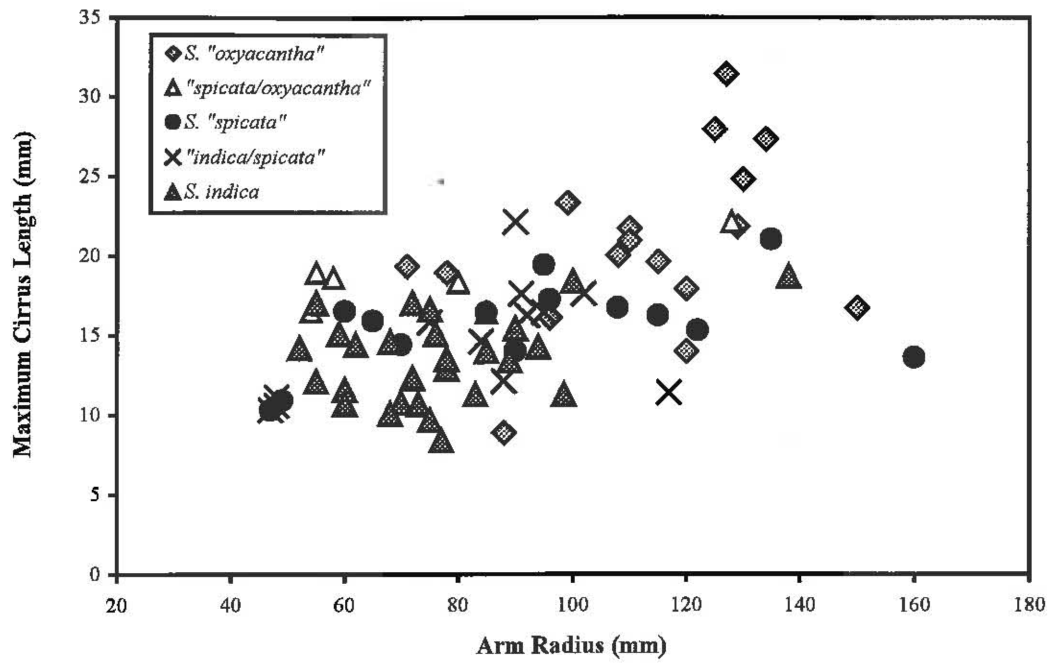


Figure 29. Plot of maximum cirrus length against arm radius for *S. indica*, *S. "spicata"*, *S. "oxyacantha"* and intermediate specimens.

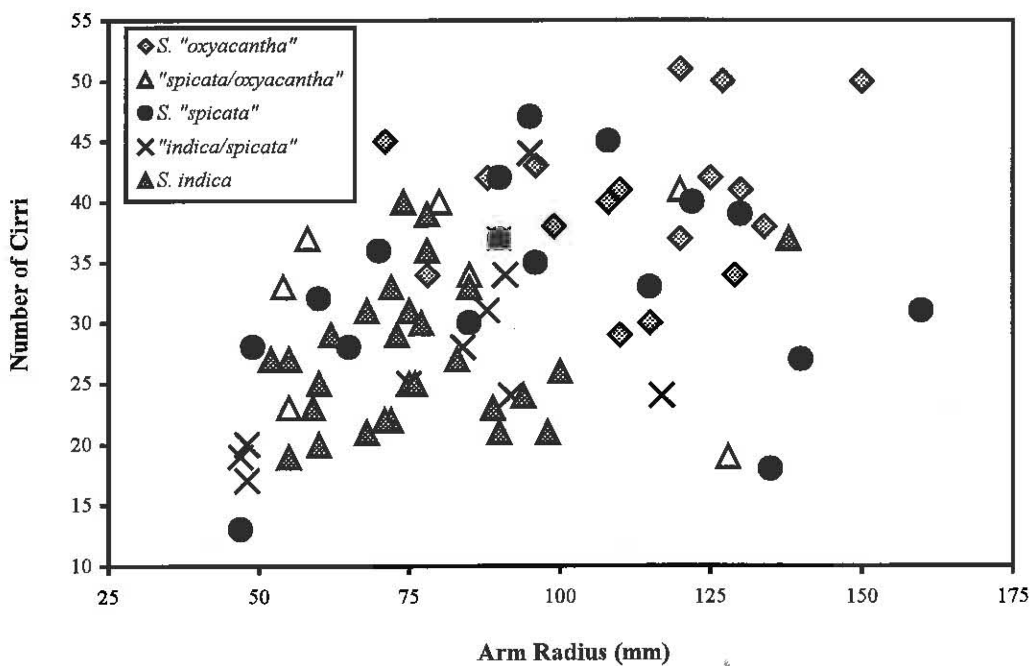


Figure 30. Plot of number of cirri against arm radius for *S. indica*, *S. "spicata"*, *S. "oxyacantha"* and intermediate specimens.

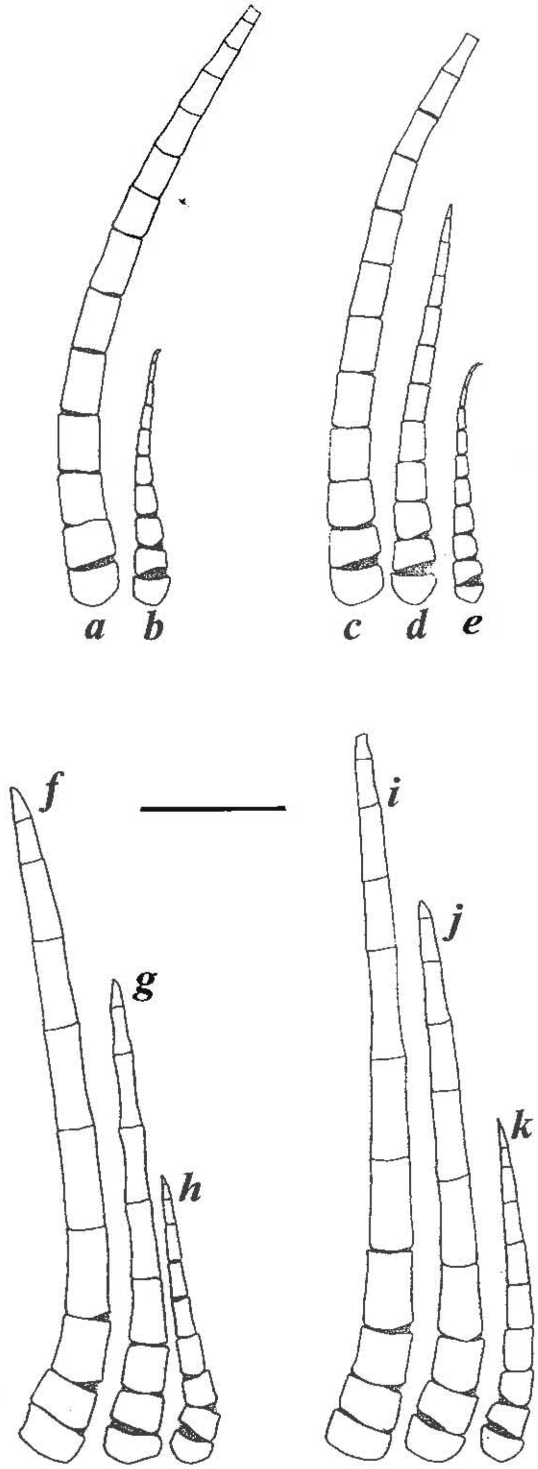


Figure 31. *Stephanometra indica.* Figs. a-e: intermediate pinnules of "*indica/spicata*" specimen, NSUOC 330. a-b "*indica*" pinnules. a. P_2. b. P_3. Figs. c-e: "*spicata*" pinnules. c. P_2. d. P_3. e. P_4. f-k Intermediate pinnules of "*spicata/oxyacantha*". Figs. f-h: "*spicata*" pinnules. f. P_2. g. P_3. h. P_4. Figs. i-k: "*oxyacantha*" pinnules. i. P_2. j. P_3. k. P_4. Scale: 2 mm.

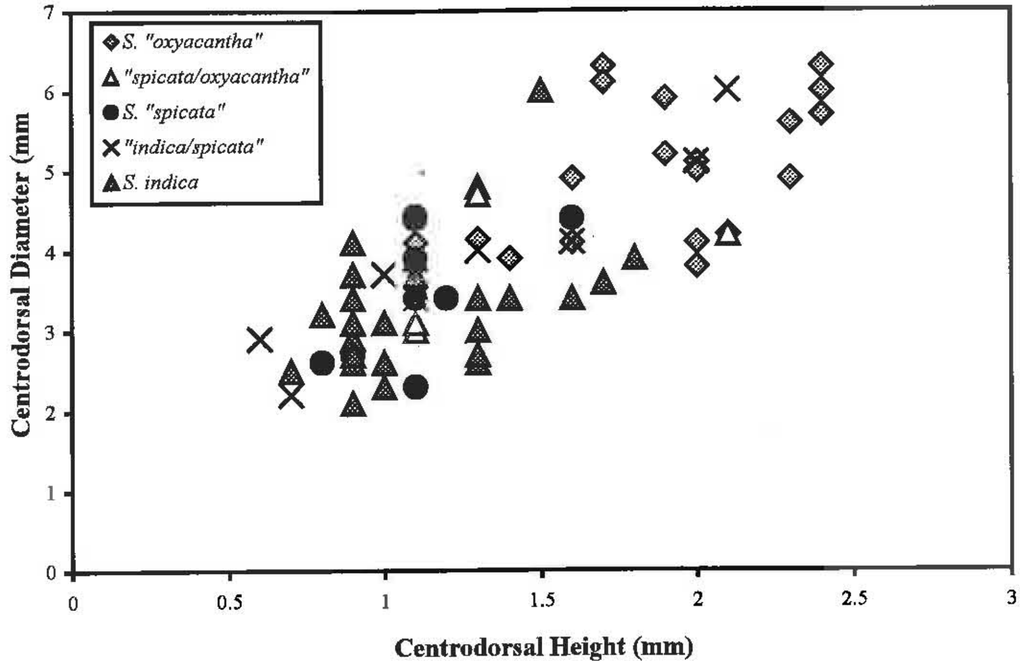


Figure 32. Plot of centrodorsal diameter against height for *S. indica*, *S. "spicata"*, *S. "oxyacantha"* and intermediate specimens.

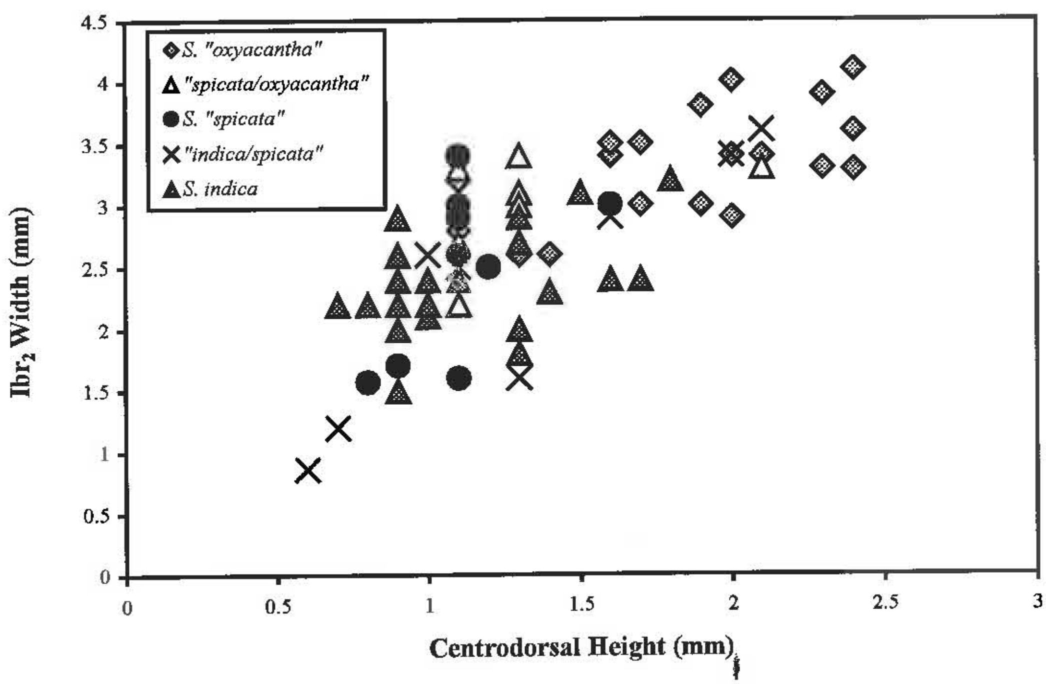


Figure 33. Plot of Ibr_2 width against centrodorsal height for *S. indica*, *S. "spicata"*, *S. "oxyacantha"* and intermediate specimens.

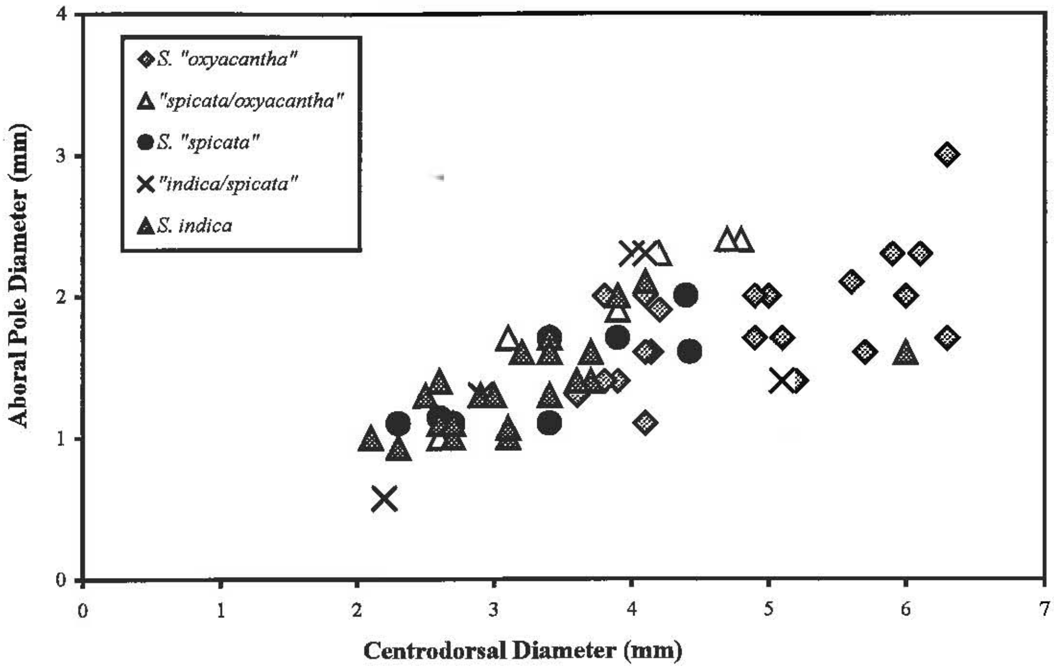


Figure 34. Plot of aboral pole diameter against centrodorsal diameter for *S. indica*, *S. "spicata"*, *S. "oxyacantha"* and intermediate specimens.

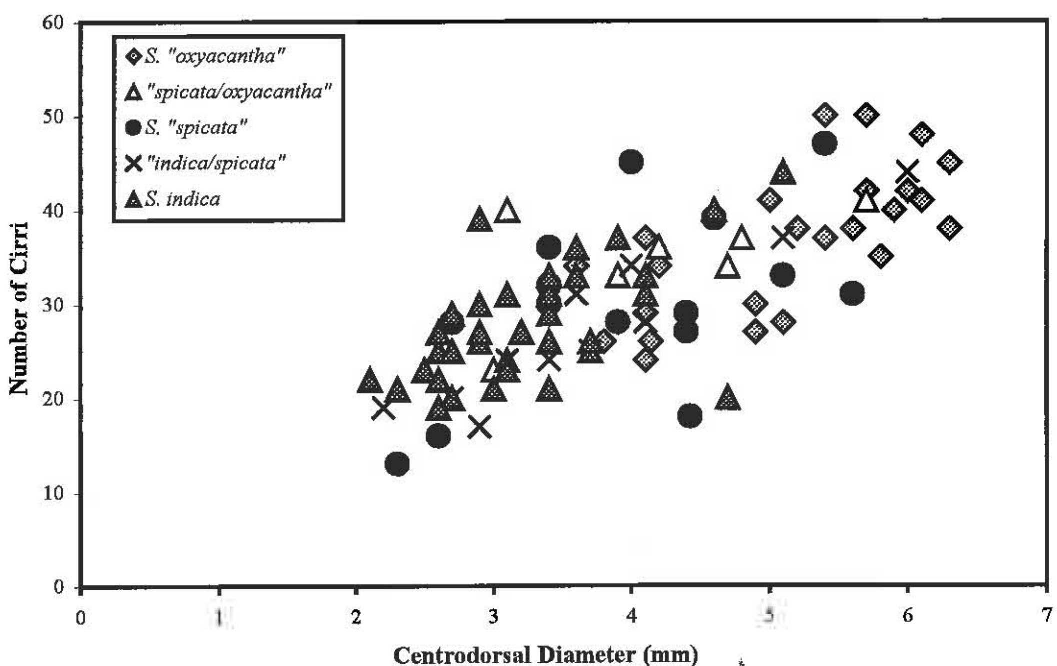


Figure 35. Plot of number of cirri against centrodorsal diameter for *S. indica*, *S. "spicata"*, *S. "oxyacantha"* and intermediate specimens.

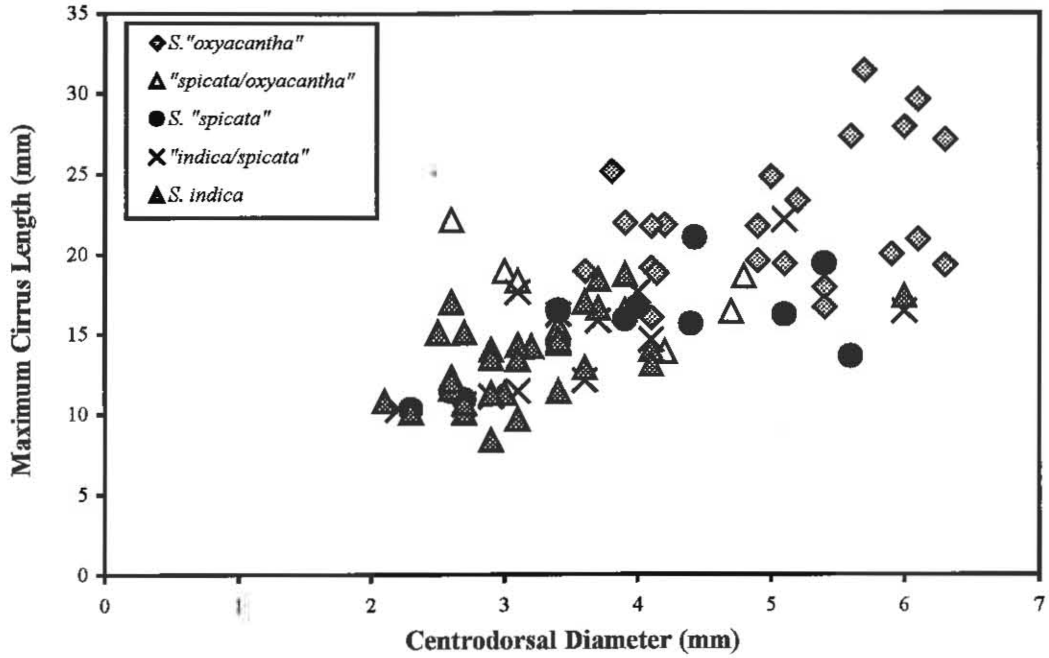


Figure 36. Plot of maximum cirrus length against centrodorsal diameter for *S. indica*, *S. "spicata"*, *S. "oxyacantha"* and intermediate specimens.

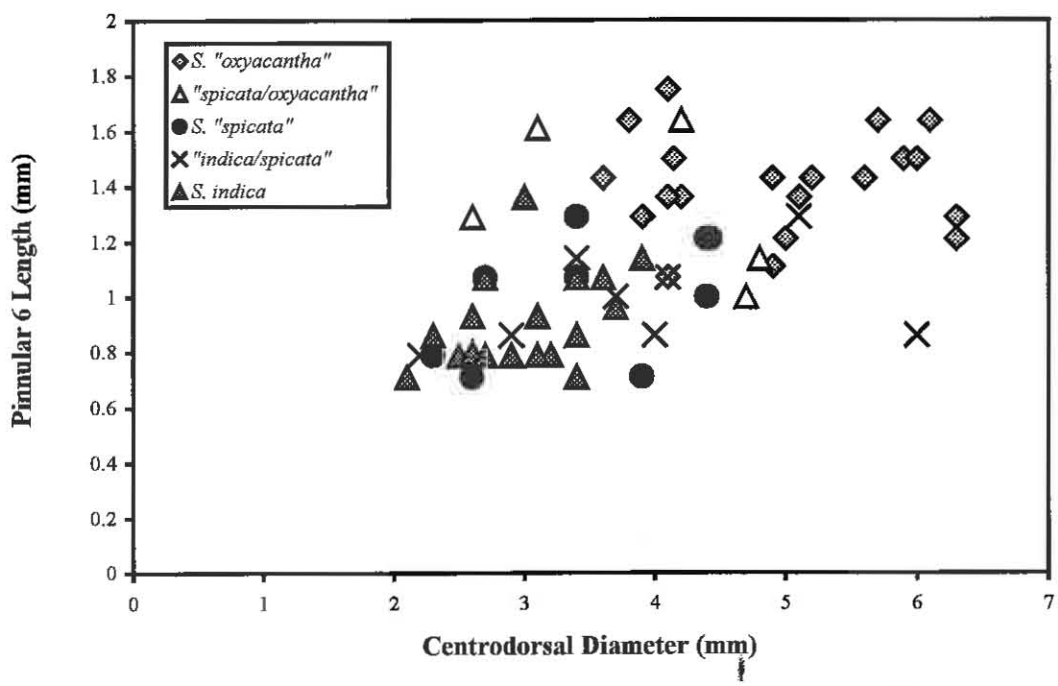


Figure 37. Plot of length of pinnular 6 from P_2 against centrodorsal diameter for S. indica, *S. "spicata"*, *S. "oxyacantha"* and intermediate specimens.

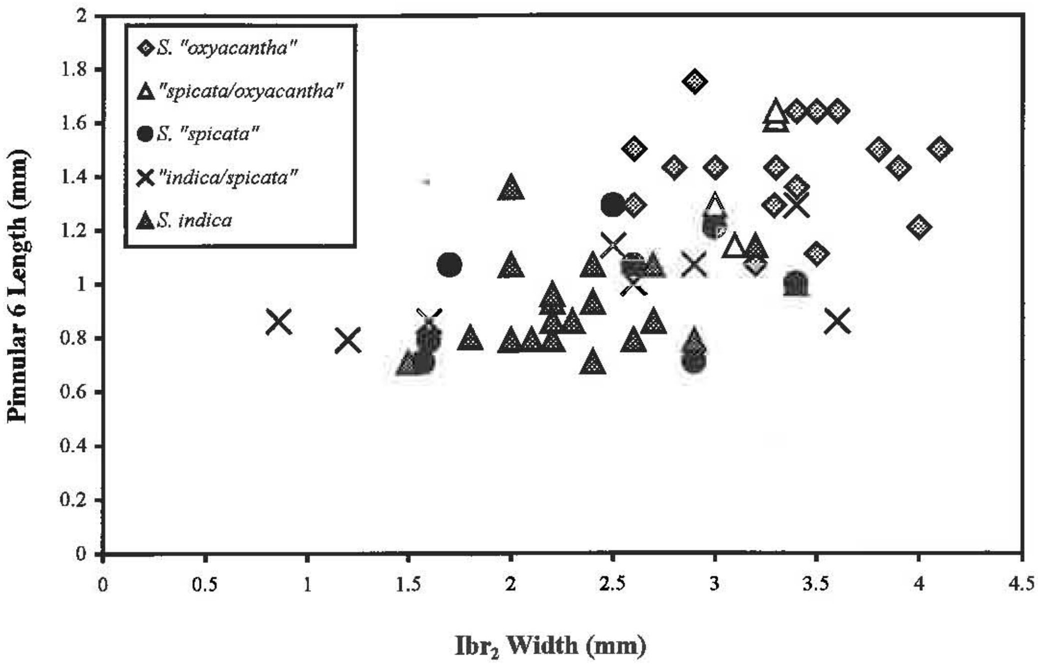


Figure 38. Plot of length of pinnular 6 from P_2 against Ibr_2 width for *S. indica*, *S. "spicata"*, *S. "oxyacantha"*, and intermediate specimens.

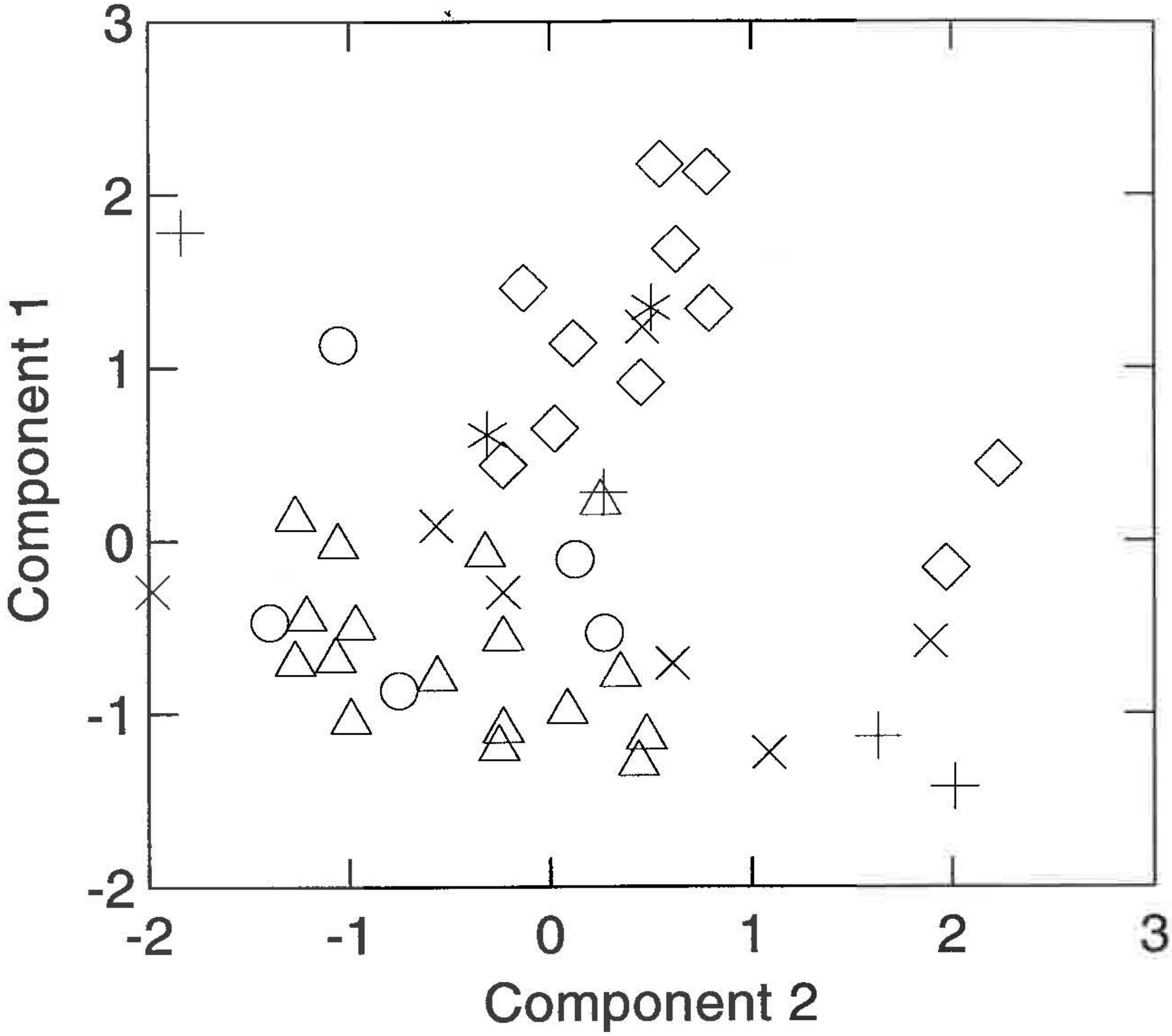


Figure 39. Graph of component scores from Component 1 vs. Component 2 in principal component analysis for *S. indica* (△), *S.* "*spicata*"(O), *S.* "*oxyacantha*"(◇), *S.* "*spinipinna*" (∗), and intermediate specimens, "*indica/spicata*" (×) and "*spicata/oxyacantha*" (+).

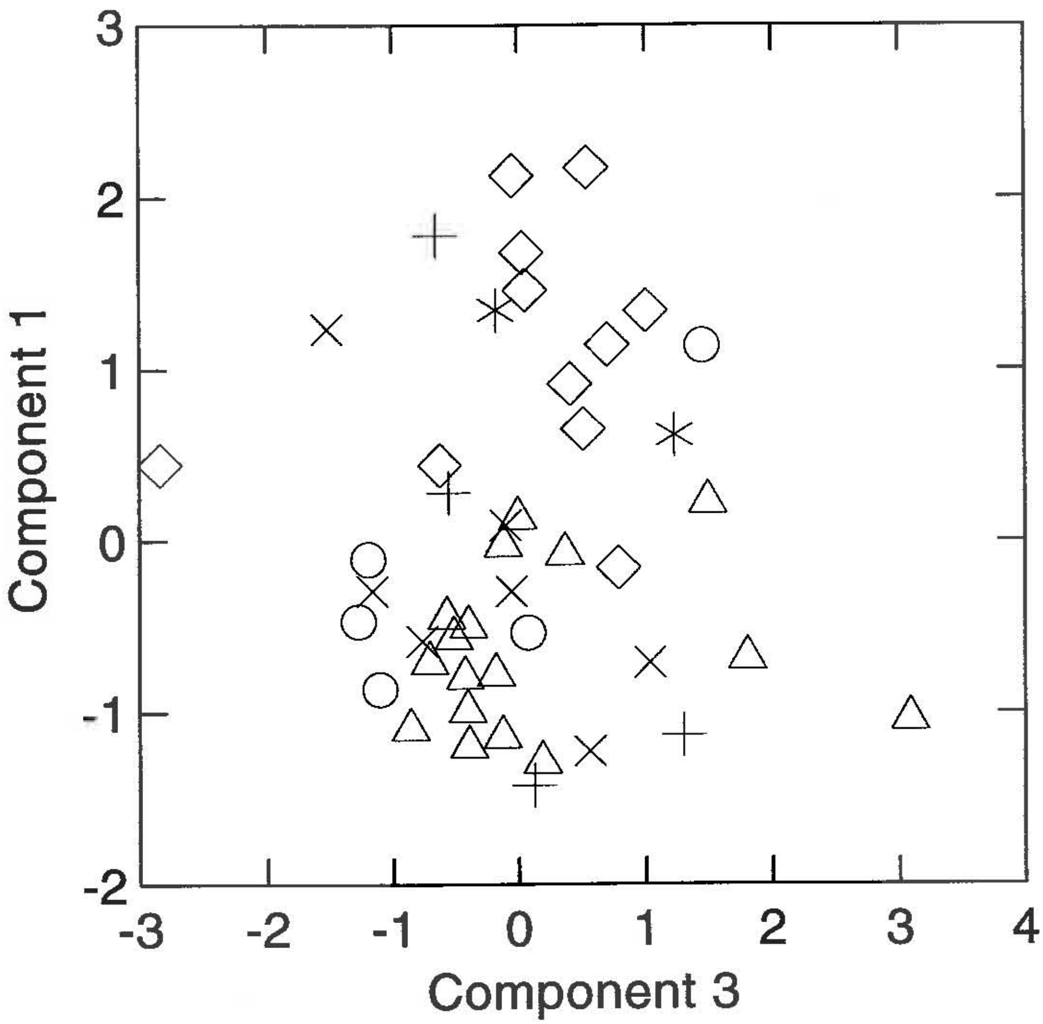


Figure 40. Graph of component scores from Component 1 vs. Component 3 in principal component analysis for *S. indica* (△), *S. "spicata"*(O), *S. "oxyacantha"*(◇), *S. "spinipinna"* (∗), and intermediate specimens, "*indica/spicata*" (×) and "*spicata/oxyacantha*" (+).

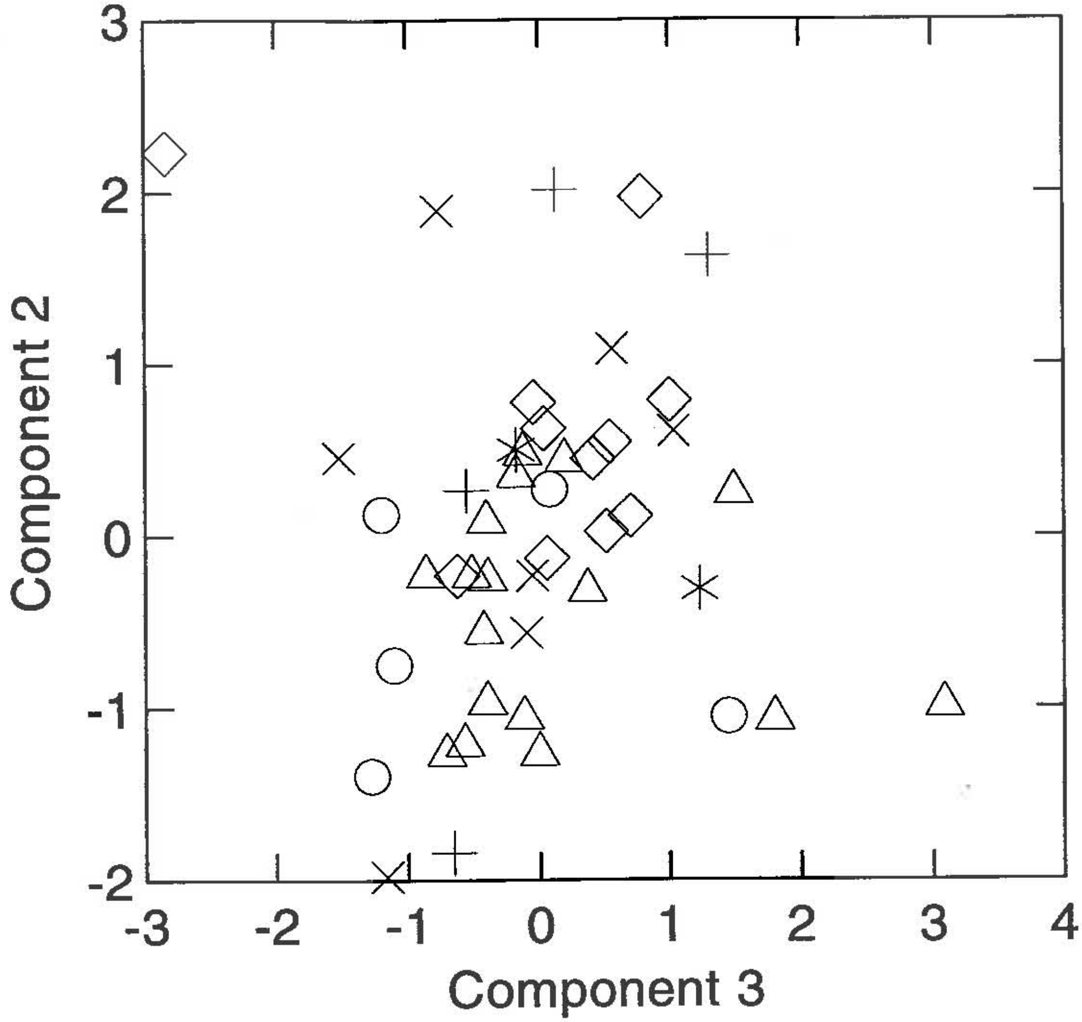


Figure 41. Graph of component scores from Component 2 vs. Component 3 in principal component analysis for *S. indica* (△), *S.* "*spicata*"(O), *S.* "*oxyacantha*"(◇), *S.* "*spinipinna*" (∗), and intermediate specimens, "*indica/spicata*" (×) and "*spicata/oxyacantha*" (+).

Table 2. Meristic and morphometric data for *S. indica*, *S.* "*spicata*", *S.* "*oxyacantha*", *S.* "*spinipinna*" and intermediate specimens.

	CENTRODORSAL			ABORAL POLE	CIRRI			ARMS		BRACHITAXES						br_{10}	P_1		P_2		P_3		P_4		P_5	
										Ibr_1			Ibr_2													
Specimen #	D (mm)	Height (mm)	D/H	Diameter (mm)	Cirri #	# Cirrals	Cirrus L (mm)	Arm #	Ray L (mm)	L (mm)	W (mm)	W/L	L (mm)	W (mm)	W/L	W (mm)	# Plrs.	L (mm)	# Plrs.	L (mm)	# Plrs.	L (mm)	# Plrs.	L (mm)	# Plrs.	L (mm)
S. indica																										
IRSCB 320	3.4	1.3	2.6	1.6	29	20	14.4	20	60	0.8	2.0	2.5	1.3	2.7	2.1	1.4	14	4.5	13	8.6	9	2.5	11	3.2	10	3.6
IRSCB 422	2.5	0.7	3.6	1.3	23	19	15.1	20	60	0.6	1.8	3.0	1.2	2.2	1.8	1.1	16	4.9	12	7.9	10	2.9	9	2.4	10	2.4
IRSCB 284	2.9	0.9	3.2	1.3	26	17	14.0	20	--	0.6	1.6	2.7	1.3	2.0	1.5	1.1	14	4.5	12	9.9	10	3.6	7	2.2	12	3.5
NSUOC 342	3.4	1.3	2.6	1.7	21	21	15.4	18	90	0.9	2.2	2.4	1.4	2.7	1.9	1.4	19	8.5	14	9.5	11	5.1	14	4.3	12	4.3
NSUOC 348a	2.6	0.9	2.9	1.1	22	18	12.3	20	70	0.6	1.6	2.7	1.2	2.2	1.8	1.1	16	5	15	8.4	9	2.9	9	2.9	11	2.9
NSUOC 348b	2.6	1.0	2.6	1.4	25	19	11.6	20	60	0.6	1.6	2.7	1.0	2.1	2.1	0.8	14	3.9	11	6.4	9	2.2	10	2.0	12	2.9
NSUOC 348c	3.4	0.9	3.8	1.7	31	21	14.6	18	70	0.6	1.8	3.0	1.4	2.4	1.7	1.2	14	4.1	11	6.2	8	2.3	9	2.1	14	3.8
NSUOC 348d	2.6	0.9	2.9	1.4	27	18	12.1	18	55	0.6	1.5	2.5	1.2	2.2	1.8	1.0	11	3.6	9	5.6	10	2.3	10	2.5	11	2.4
NSUOC 331	2.1	0.9	2.3	1.0	22	17	10.8	11	70	0.6	1.1	1.8	1.2	1.5	1.3	0.5	10	4.1	8	5.7	7	2.6	8	2.6	11	3.0
NSUOC 334	3.0	1.3	2.3	1.3	21	16	11.3	13	100	0.6	1.5	2.5	1.4	2.0	1.4	1.1	15	5.6	8	8.1	10	4.1	11	4.0	12	4.0
NSUOC 349	3.2	0.8	4.0	1.6	27	19	14.2	20	50	0.6	1.8	3.0	1.3	2.2	1.7	1.0	13	5.3	11	7.1	9	5.7	8	2.5	10	2.9
NSUOC 340	3.1	1.0	3.1	1.0	24	18	14.3	18	90	0.6	1.8	3.0	1.4	2.4	1.7	1.1	17	7.2	12	9.3	9	3.6	8	2.9	12	3.2
NSUOC 333	2.7	0.9	3.0	1.0	20	15	10.1	14	--	0.5	1.5	3.0	1.0	2.0	2.0	0.8	10	3.7	9	5.5	8	3.4	7	2.0	10	2.1
NSUOC 335	3.9	1.8	2.2	2.0	37	23	18.7	29	140	0.9	2.4	2.7	1.9	3.2	1.7	1.7	22	9.4	15	13.1	14	6.0	10	4.7	14	5.7
NSUOC 339	2.6	1.3	2.0	1.4	19	17	17.0	19	55	0.6	1.5	2.5	1.0	1.8	1.8	0.5	11	3.6	--	--	8	2.1	10	2.3	10	2.0
NSUOC 332	3.7	0.9	4.1	1.4	25	21	16.6	19	75	0.5	2.0	4.0	1.2	2.2	1.8	1.1	14	4.9	10	7.9	9	3.3	11	3.2	10	3.1
NSUOC 337	3.1	0.9	3.4	1.1	23	20	13.4	17	90	0.7	1.6	2.3	2.2	2.6	1.2	1.2	16	5.9	10	6.4	10	3.6	10	3.3	11	3.1
NSUOC 336	2.7	1.3	2.1	1.1	25	20	15.1	15	80	0.5	1.7	3.4	2.9	2.9	1.0	1.1	15	5.3	11	7.1	10	2.9	10	3.4	12	3.4
BMNH 76.5.5.24	5.1	--	--	--	44	--	--	--	--	0.5	2.2	4.4	1.5	2.9	1.9	--	18	8.0	18	16.5	11	4.0	--	--	--	--
USNM E34960a	3.4	1.4	2.4	1.3	26	--	--	29	--	0.7	1.9	2.7	1.4	2.3	1.6	1.3	16	5.0	13	7.7	8	2.0	11	3.6	11	2.7
USNM E34960b	3.6	1.7	2.1	1.4	33	20	17.0	--	70	0.5	2.1	4.2	1.4	2.4	1.7	1.1	12	5.0	13	5.4	7	2.1	7	2.1	11	1.3
USNM E35050a	2.3	1.0	2.3	0.9	21	15	10.1	15	70	0.4	1.9	4.8	1.1	2.2	2.0	1.2	16	5.3	11	7.5	10	2.0	9	2.1	11	3.4
USNM E35050b	4.1	0.9	4.6	2.1	33	22	14.0	20	85	0.8	2.1	2.6	1.4	2.9	2.1	1.4	19	6.3	14	9.4	10	3.6	11	3.2	12	3.7
NSUOC 633	3.7	1.1	3.4	1.6	26	22	18.4	--	100	0.8	1.6	2.0	1.6	2.4	1.5	1.3	18	5.9	13	10.7	10	2.9	10	3.0	11	3.8
BMNH 1902.3.13.21	6.0	1.5	4.0	3.1	--	21	17.4	30	--	0.7	2.4	3.4	1.7	3.1	1.8	1.6	19	7.8	--	--	10	2.9	12	3.7	--	--
BMNH 1892.8.22.28	3.4	1.6	2.1	1.0	33	18	11.4	20	--	0.6	2.1	3.7	1.4	2.4	1.7	1.3	20	--	13	--	13	--	--	--	--	--
USNM E34738	4.6	--	--	--	40	16	--	18	70	0.8	2.1	2.6	1.1	2.9	2.6	--	20	6.0	13	10.5	13	5.4	14	4.8	--	--
USNM E34793	2.9	--	--	--	27	20	11.3	--	80	0.6	1.5	2.5	1.2	2.1	1.8	--	14	4.3	13	7.3	9	2.3	10	2.6	--	--
USNM E34793b	2.7	--	--	--	29	18	10.7	18	70	0.6	1.6	2.7	1.4	2.1	1.5	--	16	4.4	11	6.6	9	2.6	10	3.2	--	--
USNM E34793c	3.1	--	--	--	31	19	9.7	19	75	0.6	1.7	2.8	1.4	2.4	1.7	--	17	5.6	12	5.9	10	3.3	12	3.2	--	--
USNM E34793d	2.9	--	--	--	30	16	8.4	20	80	0.6	1.6	2.7	1.2	2.2	1.8	--	14	4.9	12	6.4	9	2.4	9	2.0	--	--
USNM E34793e	3.6	--	--	--	36	20	12.9	20	80	0.7	1.9	2.7	1.3	2.3	1.8	--	13	3.4	11	6.2	9	3.6	12	3.6	--	--
USNM E18323b	2.9	--	--	--	39	23	13.5	30	80	0.5	2.5	5.0	1.5	2.4	1.6	--	23	8.2	11	8.2	12	4.5	13	4.1	--	--
USNM E11712	4.1	--	--	--	31	20	13.1	20	--	0.7	2.0	2.9	1.2	2.7	2.3	--	16	4.0	12	8.2	10	3.0	10	2.4	--	--
USNM E35262	4.7	--	--	--	20	17	--	--	60	0.4	1.5	3.8	1.1	2.8	2.5	--	19	5.7	--	--	11	3.1	--	--	--	--

Table 2. ***Stephanometra*** **spp. continued.**

	CENTRODORSAL			ABORAL POLE	CIRRI			ARMS		BRACHITAXES						br_{10}	P_1		P_2		P_3		P_4		P_5	
										Ibr_1			Ibr_2													
Specimen #	D (mm)	Height (mm)	D/H	Diameter (mm)	Cirri #	# Cirrals	Cirrus L (mm)	Arm #	Ray L (mm)	L (mm)	W (mm)	W/L	L (mm)	W (mm)	W/L	W (mm)	# Plrs.	L (mm)	# Plrs.	L (mm)	# Plrs.	L (mm)	# Plrs.	L (mm)	# Plrs.	L (mm)
"indica/spicata"	--	--	--																							
NSUOC 330	4.0	1.3	3.1	2.3	34	22	17.6	19	90	0.8	1.6	1.9	1.4	2.8	2.0	1.2	15	5.6	12	8.1	9	3.1	12	3.1	12	3.7
NSUOC 338	4.1	1.6	2.6	2.3	28	19	14.6	20	80	0.4	2.3	5.3	1.7	2.9	1.7	1.4	17	8.4	14	10.4	12	5.9	10	4.0	12	3.7
CRRF 1656K	5.1	2.0	2.6	1.4	37	22	22.1	25	90	0.8	2.7	3.3	1.0	3.4	3.4	1.6	23	11.6	14	15.0	13	10.9	11	5.3	14	5.2
NSUOC 322	2.2	0.7	3.1	0.6	19	17	10.3	12	50	0.4	1.1	2.6	1.1	1.2	1.1	0.9	14	5.3	9	6.1	8	3.4	10	2.2	10	2.9
IRSCB 248	2.9	0.6	4.8	1.3	17	18	11.1	13	50	0.6	1.4	2.2	1.2	1.7	1.4	0.7	--	--	12	9.1	7	4.3	7	2.8	9	2.8
USNM E35079	2.7	--	--	--	20	21	10.6	20	50	0.7	1.5	2.1	1.1	1.5	1.4	--	16	4.5	14	7.1	10	2.7	12	2.5	--	--
USNM E34548	3.6	--	--	--	31	19	12.1	20	90	0.6	1.4	2.3	1.4	2.1	1.5	--	16	5.5	11	7.1	10	1.9	--	--	--	--
USNM E34613	3.1	--	--	--	24	19	11.4	20	120	1.0	1.9	1.9	1.6	2.5	1.6	--	22	8.9	14	9.7	14	6.4	15	4.6	--	--
USNM E35221	3.1	--	--	--	--	23	17.6	21	100	1.1	2.6	2.4	2.0	3.1	1.6	--	18	9.3	17	14.3	18	10.4	13	5.7	--	--
NSUOC 343	3.7	1.0	3.7	1.6	25	21	15.8	21	75	0.6	2.0	3.3	1.4	2.6	1.9	1.2	18	7.2	13	10.4	12	5.0	11	4.2	12	3.6
NSUOC 341	3.4	1.1	3.1	1.6	24	19	16.2	17	90	0.6	1.8	3.0	1.3	2.5	1.9	1.3	15	7.1	14	10.9	11	4.9	10	3.5	13	4.2
USNM E34699	6.0	2.1	2.9	1.6	44	23	16.4	30	95	0.9	2.8	3.1	1.4	3.6	2.6	0.9	20	8.4	17	15.5	11	3.5	12	3.0	13	5.2
S. "spicata"																										
NSUOC 327	3.4	1.1	3.1	1.7	32	22	16.5	28	60	0.7	2.2	3.1	1.3	2.6	2.0	1.1	21	9.1	11	10.6	--	--	10	4.3	12	3.2
NSUOC 325	3.4	1.2	2.8	1.1	36	18	14.4	19	70	0.6	2.9	4.8	1.3	2.5	1.9	1.1	17	7.2	11	10.1	10	7.4	9	3.4	10	2.4
NSUOC 324	3.9	1.1	3.5	1.7	28	19	15.9	20	65	0.7	2.2	3.1	1.4	2.9	2.1	1.4	17	7.0	16	8.9	11	8.1	10	3.9	12	4.4
IRSCB 241	2.7	0.9	3.0	1.1	28	19	10.9	14	50	0.4	1.3	3.3	1.1	1.7	1.5	0.8	13	4.4	8	6.0	9	3.6	10	2.3	10	2.3
IRSCB 316	4.4	1.1	4.0	2.0	29	23	15.6	21	--	1.1	2.7	2.5	1.8	3.4	1.9	1.5	17	8.3	15	10.4	13	8.4	13	6.4	13	5.8
NSUOC 329	2.3	1.1	2.1	1.1	13	17	10.3	12	50	0.5	1.3	2.6	0.9	1.6	1.7	0.6	15	5.1	10	7.1	8	3.4	9	3.0	10	3.0
NSUOC 323	2.6	0.8	3.3	1.1	16	19	11.4	13	--	0.6	1.0	1.6	1.0	1.6	1.6	0.9	21	6.1	12	7.9	12	9.9	9	2.6	8	2.6
USNM E5269	4.4	1.6	2.8	2.0	27	--	--	20	140	1.0	2.5	2.5	1.8	3.0	1.7	1.4	16	7.9	15	14.0	13	10.4	13	6.7	13	6.0
USNM E5269	4.4	1.1	4.0	1.6	18	24	21.0	--	135	1.1	2.3	2.0	1.9	3.0	1.6	1.9	23	9.1	15	14.4	13	10.1	11	5.6	12	4.9
USNM E34549	4.6	--	--	--	39	21	--	27	130	1.1	2.1	1.9	1.8	3.2	1.8	--	27	7.1	16	13.6	12	6.6	13	4.3	--	--
USNM E34549b	4.0	--	--	--	45	21	16.7	29	110	0.8	2.9	3.6	1.5	3.4	2.3	--	21	11.4	15	14.3	11	7.9	12	4.7	--	--
USNM E34549c	5.6	--	--	--	31	21	13.6	29	160	1.1	2.5	2.3	1.8	3.4	1.9	--	21	7.4	17	14.6	13	8.6	12	4.6	--	--
USNM E34546	5.1	--	--	--	33	24	16.2	25	115	1.0	2.6	2.6	1.3	3.4	2.6	--	21	10.0	12	9.0	9	5.0	10	3.4	--	--
USNM E34546b	--	--	--	--	37	20	14.0	25	90	0.8	2.2	2.8	1.4	2.9	2.1	--	21	7.5	13	10.8	9	6.4	8	3.6	--	--
USNM E34546c	--	--	--	--	35	22	17.2	27	100	1.0	2.9	2.9	2.1	3.5	1.7	--	19	8.4	11	8.1	9	6.5	9	3.4	10	3.6
USNM E34572	--	--	--	--	42	24	--	32	90	0.8	2.1	2.6	1.5	2.6	1.7	--	17	5.5	14	11.6	10	7.6	9	3.2	--	--
USNM E34572b	3.4	--	--	--	30	22	16.4	30	85	0.8	2.6	3.3	1.6	3.2	2.0	--	19	7.6	11	7.3	9	6.9	9	3.6	--	--
USNM E34572c	5.4	--	--	--	47	24	19.4	30	95	0.7	2.9	4.1	1.6	3.2	2.0	--	22	8.6	12	9.6	11	7.5	10	3.7	--	--
USNM E35361	--	--	--	--	40	19	15.3	30	120	0.7	2.4	3.4	1.9	3.5	1.8	--	24	11.6	14	11.1	13	10.3	11	5.2	10	2.9
"spicata/oxyacantha"																										
IRSCB 354	4.8	1.3	3.7	2.4	37	25	18.6	30	60	0.8	2.4	3.0	1.4	3.1	2.2	1.5	12	5.4	11	8.5	8	6.1	7	3.0	9	2.3
IRSCB 316	3.0	1.1	2.7	1.0	23	22	18.9	18	55	0.8	1.7	2.1	1.2	2.2	1.8	0.9	18	5.9	11	9.4	10	8.9	11	6.1	9	3.1
NSUOC 328	2.6	1.3	2.0	1.0	19	24	22.1	26	130	0.8	2.2	2.8	1.1	3.0	2.7	1.4	21	9.8	13	13.8	10	9.9	9	5.9	10	3.8
NSUOC 326	3.9	1.1	3.5	1.9	33	21	16.5	30	55	0.7	2.1	3.0	1.2	2.7	2.3	1.1	20	8.2	11	11.1	9	8.1	10	5.0	10	3.6
IRSCB 298a	3.1	1.1	2.8	1.7	40	21	18.3	28	80	0.6	2.4	4.2	1.4	3.3	2.4	1.4	16	7.1	13	14.1	10	8.9	9	4.9	10	4.0
USNM E35376	4.7	1.3	3.6	2.4	34	21	16.4	22	85	0.9	2.6	2.9	2.0	3.4	1.7	1.21	19	7.8	15	10.4	10	8.4	9	4.3	9	2.3
USNM E34854	5.7	--	--	--	41	24	--	30	120	0.9	2.9	3.2	1.6	3.3	2.1		22	8.9	15	14.3	13	12.7	11	8.1	12	5.1
IRSCB 298b	4.2	2.1	2.0	2.3	36	19	13.9	30	--	0.8	2.6	3.3	1.3	3.3	2.5	1.6	20	8.3	12	12.1	10	8.4	9	3.9	10	3.9

Table 2. ***Stephanometra*** **spp. continued.**

	CENTRODORSAL			ABORAL POLE	CIRRI			ARMS		BRACHITAXES						br_{10}	P_1		P_2		P_3		P_4		P_5	
Specimen #	D (mm)	Height (mm)	D/H	Diameter (mm)	Cirri #	# Cirrals	Cirrus L (mm)	Arm #	Ray L (mm)	Ibr_1 L (mm)	Ibr_1 W (mm)	Ibr_1 W/L	Ibr_2 L (mm)	Ibr_2 W (mm)	Ibr_2 W/L	W (mm)	# Plrs.	L (mm)	# Plrs.	L (mm)	# Plrs.	L (mm)	# Plrs.	L (mm)	# Plrs.	L (mm)
S. "oxyacantha"																										
NSUOC 317	4.2	2.1	2.0	1.9	34	23	21.8	30	130	0.9	2.9	3.2	1.7	3.4	2.0	1.4	21	9.7	12	14.1	9	10.7	9	7.4	8	4.0
NSUOC 320	4.1	1.1	3.7	2.0	24	22	16.0	20	--	0.6	2.1	3.3	1.8	3.2	1.8	1.4	11	5.2	10	9.1	9	6.0	8	5.5	10	3.9
NSUOC 321	5.9	1.9	3.1	2.3	40	22	20.0	30	110	1.2	2.9	2.4	1.9	3.8	2.0	1.4	17	7.7	12	10.6	11	9.2	9	6.1	10	5.1
NSUOC 316	5.6	2.3	2.4	2.1	38	25	27.3	28	135	1.1	2.9	2.6	2.0	3.9	2.0	1.5	21	11.6	11	12.9	11	12.9	12	10.1	10	6.9
NSUOC 318	5.2	1.9	2.7	1.4	38	25	23.3	31	100	0.9	2.6	2.9	1.8	3.0	1.7	1.7	23	10.3	11	12.4	11	10.7	11	10.0	11	6.9
IRSCB 108	5.7	2.4	2.4	1.6	50	28	31.4	29	130	1.0	3.2	3.2	1.9	3.6	1.9	1.9	23	12.7	14	17.2	11	12.5	10	9.7	10	7.1
IRSCB 73	6.3	1.7	3.7	1.7	45	22	19.3	29	70	1.4	3.0	2.1	0.7	3.0	4.2	1.2	17	8.1	12	14.1	9	9.1	11	6.4	11	5.1
IRSCB 230	3.6	1.1	3.3	1.3	34	21	18.9	28	80	0.9	2.1	2.3	1.4	2.8	2.0	1.4	17	6.8	12	10.9	9	8.8	8	5.2	10	4.0
IRSCB 135	5.1	2.0	2.6	1.7	38	21	19.4	28	--	1.1	2.8	2.5	1.6	3.4	2.1	1.6	20	9.9	13	13.7	11	10.9	10	7.6	10	6.7
IRSCB 357	4.1	2.0	2.1	1.1	37	22	19.1	20	--	0.9	2.4	2.7	1.6	2.9	1.8	1.5	20	9.0	12	13.1	10	9.9	9	4.9	11	3.4
IRSCB 232	3.9	1.4	2.8	1.4	38	21	21.9	25	--	0.8	2.1	2.6	1.2	2.6	2.2	1.3	22	10.2	13	14.3	11	11.6	11	9.8	9	6.4
IRSCB 269	4.1	1.3	3.2	1.6	26	22	18.8	26	--	0.8	2.1	2.6	1.2	2.6	2.2	1.1	19	9.0	13	12.8	10	9.3	10	5.7	10	4.1
IRSCB 276	3.8	2.0	1.9	1.4	36	24	25.1	20	--	1.1	2.7	2.5	1.8	3.4	1.9	1.8	16	7.6	13	14.1	11	12.9	10	9.4	11	6.1
IRSCB 69	6.1	1.7	3.6	2.3	48	28	29.6	30	--	0.8	2.7	3.4	1.7	3.5	2.1	1.6	17	8.3	12	12.8	10	9.4	11	8.4	12	5.9
IRSCB 70	6.3	2.4	2.6	3.0	38	26	27.1	33	--	0.5	3	6.0	1.9	3.3	1.7	1.6	22	10.7	14	15.1	11	9.9	12	9.1	13	6.4
NSUOC 319	5.0	2.0	2.5	2.0	41	25	24.8	26	130	1.0	3	3.0	1.6	4.0	2.5	1.7	27	12.7	18	20.0	14	14.1	12	7.8	11	7.8
IRSCB 374	4.1	1.6	2.6	1.6	29	23	21.7	25	110	0.9	2.6	2.9	1.6	3.4	2.1	1.6	20	7.9	11	7.9	9	7.9	8	6.7	9	5.0
IRSCB 380	4.9	1.6	3.1	1.7	27	24	21.7	23	--	0.6	2.6	4.3	1.6	3.5	2.2	1.4	21	8.3	13	9.9	12	8.3	9	6.0	9	4.0
NSUOC 315	4.9	2.3	2.1	1.7	30	30	19.6	22	115	1.2	2.4	2.0	1.9	3.3	1.7	1.6	20	9.9	13	13.9	11	11.6	10	7.7	11	4.8
NSUOC 258	6.0	2.4	2.5	2.0	42	26	27.9	30	125	1.1	2.7	2.5	1.9	4.1	2.2	1.9	22	14.1	15	17.7	13	15.0	12	9.9	11	9.4
USNM E34738	--	--	--	--	43	23	16.1	30	95	1.1	2.9	2.6	2.1	3.8	1.8	--	18	8.0	--	--	8	5.9	8	5.9	10	2.7
USNM E34838	5.4	--	--	--	37	25	17.9	25	120	0.6	2.6	4.3	1.9	3.5	1.8	--	22	11.3	14	14.6	13	13.2	11	9.6	10	7.6
USNM E34838b	5.7	--	--	--	42	25	--	30	90	0.7	2.5	3.6	1.4	3.2	2.3	--	20	9.7	14	13.9	11	8.1	10	4.6	12	4.3
USNM E469a	--	--	--	--	51	22	14.0	--	120	0.9	2.9	3.2	1.6	3.9	2.4	--	21	11.0	13	13.2	11	10.9	10	6.9	10	4.5
USNM E469b	5.8	--	--	--	35	21	--	28	--	1.1	2.5	2.3	2	3.7	1.9	--	18	9.3	13	13.1	11	11.4	11	7.1	11	4.6
USNM E34546	5.4	--	--	--	50	22	16.7	30	150	0.9	3.1	3.4	2.1	3.8	1.8	--	17	5.6	15	8.6	12	7.4	12	6.5	--	--
USNM E34546b	6.1	--	--	--	41	26	20.9	29	110	1.0	2.9	2.9	1.7	3.7	2.2	--	24	10.3	16	13.1	13	10.4	--	--	--	--
S. "spinipinna"																										
NSUOC 313	3.8	1.9	2.0	2.0	24	21	18.3	23	100	0.9	2.1	2.3	2	2.9	1.5	1.4	22	10.7	11	12.4	11	7.6	12	5.4	13	5.1
NSUOC 314	4.9	2.0	2.5	2.0	38	25	24.7	30	125	1.1	2.6	2.4	1.4	3.4	2.4	1.6	20	10.1	13	14.2	10	9.5	12	10.2	9	6.6
gustav	2.4	1.1	2.2	0.7	26	19	11.6	15	50	0.6	1.3	2.3	1	1.7	1.7	0.8	10	4.6	8	6.4	7	3.9	9	2.7	11	3.3

NSUOC designates Nova Southeastern University-Oceanographic Center.
CRRF designates Coral Reef Research Foundation.
USNM designates United States National Museum (now the National Museum of Natural History).
BMNH designates the British Museum of Natural History.
D indicates the diameter.
D/H indicates diameter (D) divided by height (H), of centrodorsal.
L indicates the length of cirrus, brachitaxes ossicles, rays or pinnules.
W indicates the width of brachitaxes ossicles, or br_{10}.
W/L indicates the width (W) divided by the length (L), of brachitaxes ossicles.
Plrs. indicates pinnulars

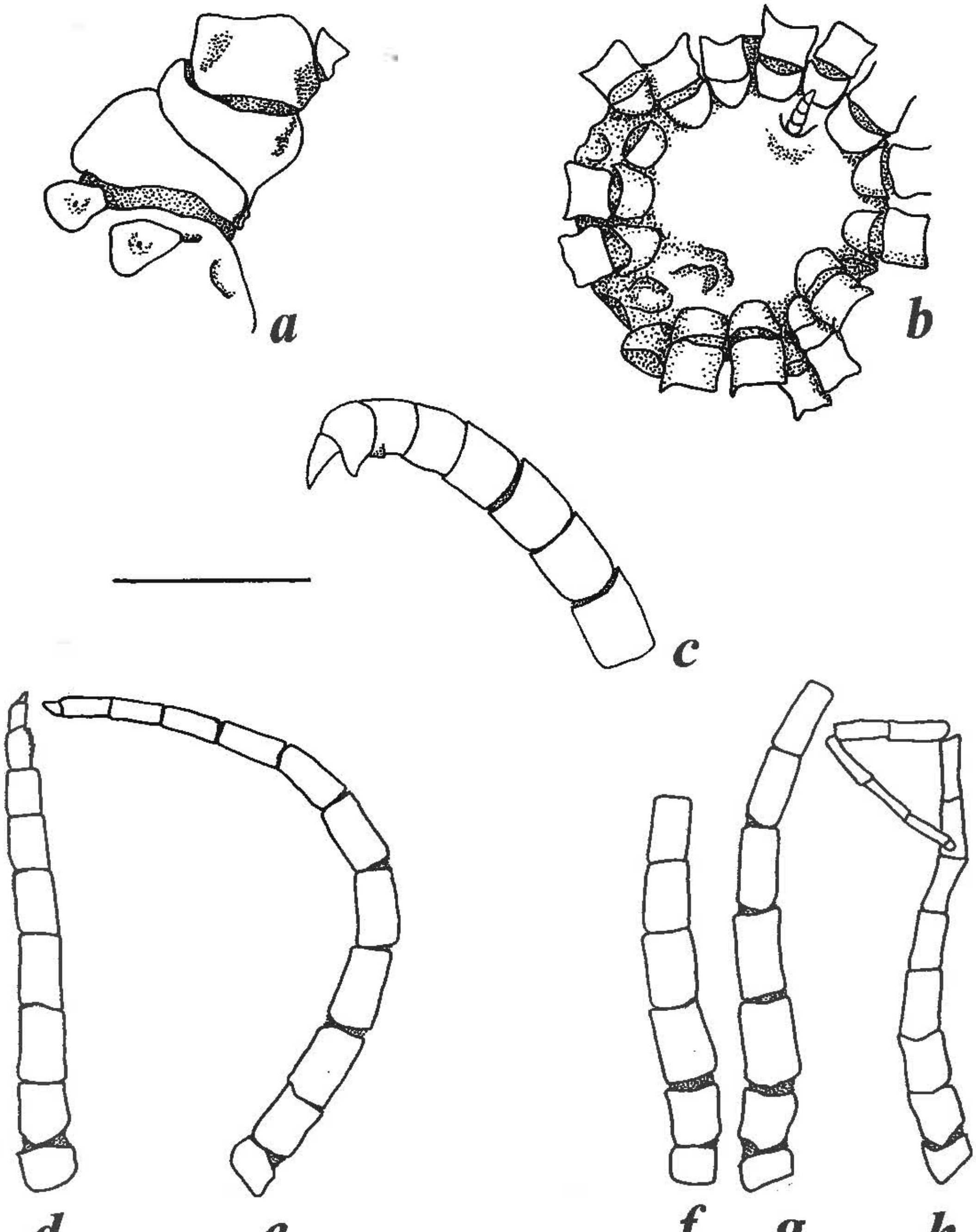


Figure 42. *Stephanometra indica*. USNM 8969. a. Lateral adambulacral margins of brachitaxis ossicles. b. Centrodorsal, in aboral view. c. Tip of cirrus. d. P_1. e. P_2. f. P_1 of another arm. g. P_2. h. P_3. Scale: 2 mm.

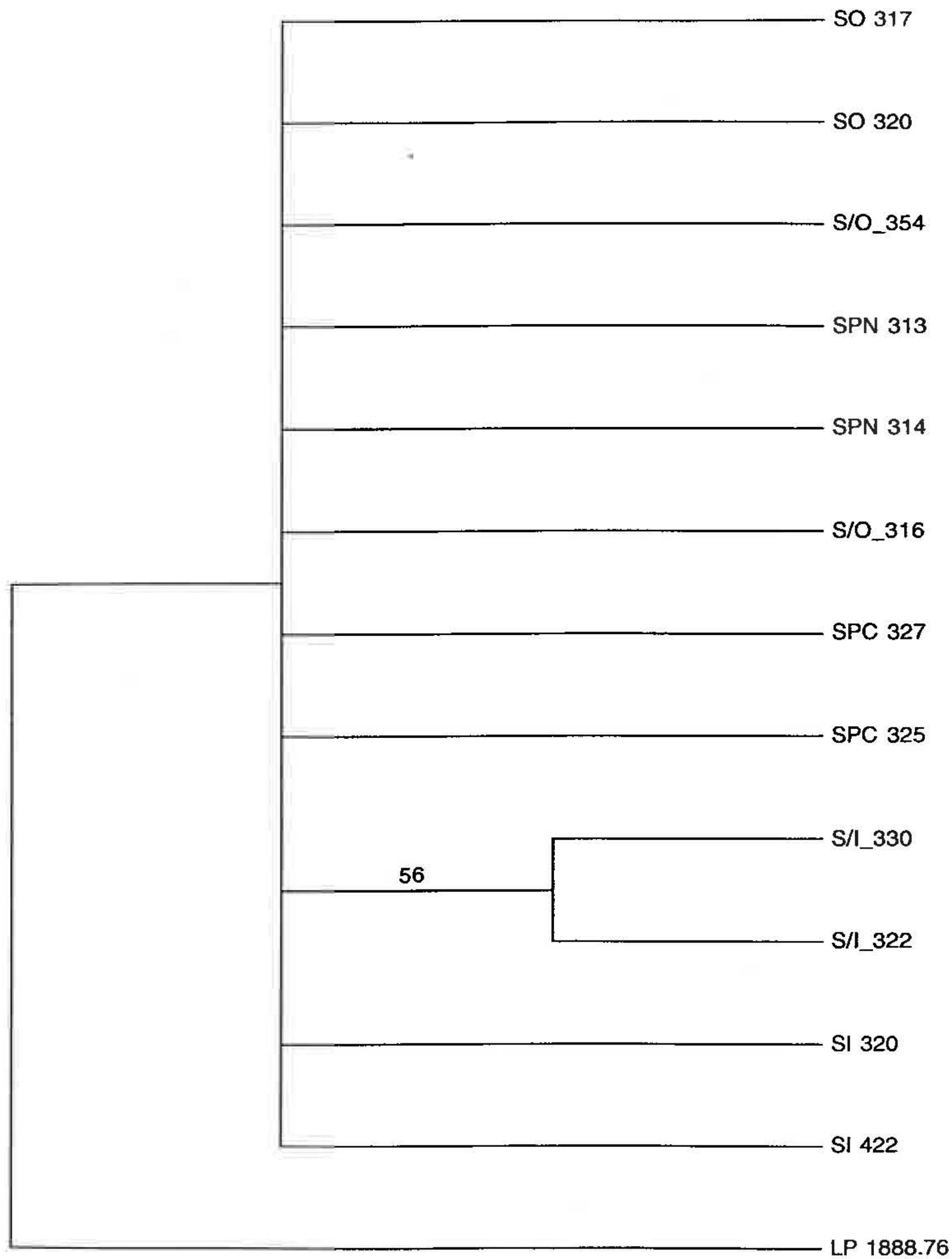


Figure 43. Fifty percent majority rule tree with bootstrap analysis for *Stephanometra indica, S. "spicata", S. "oxyacantha", S. "spinipinna"* and intermediate specimens. Tables 2 and 3 provide a key to the terminal names.

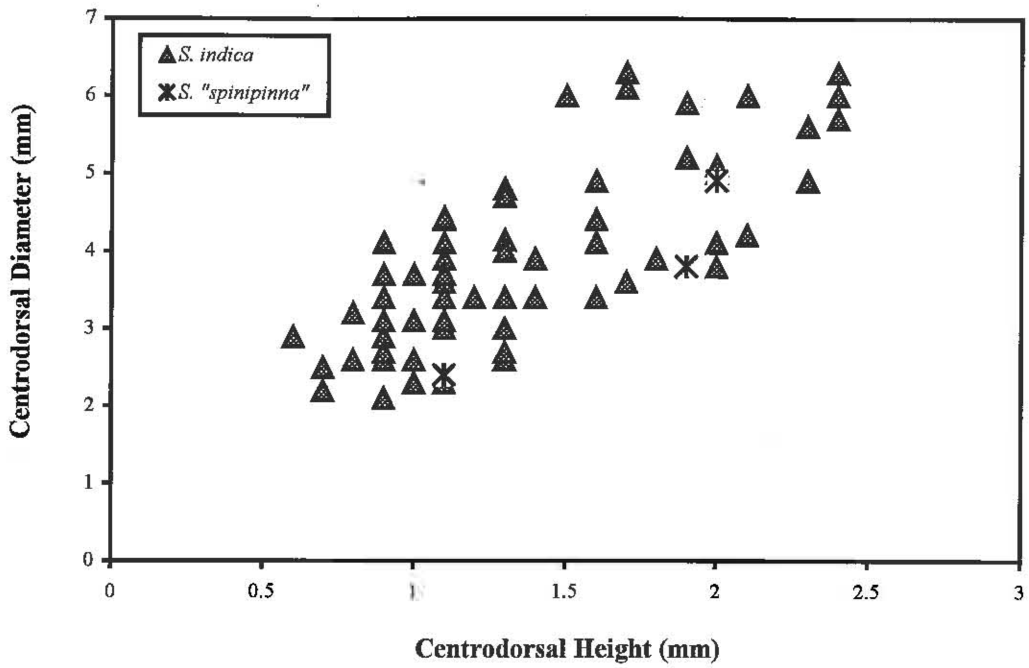


Figure 44. Plot of centrodorsal diameter against height for *S. indica* (including "*spicata*", "*oxyacantha*" and intermediate specimens) versus *S.* "*spinipinna*".

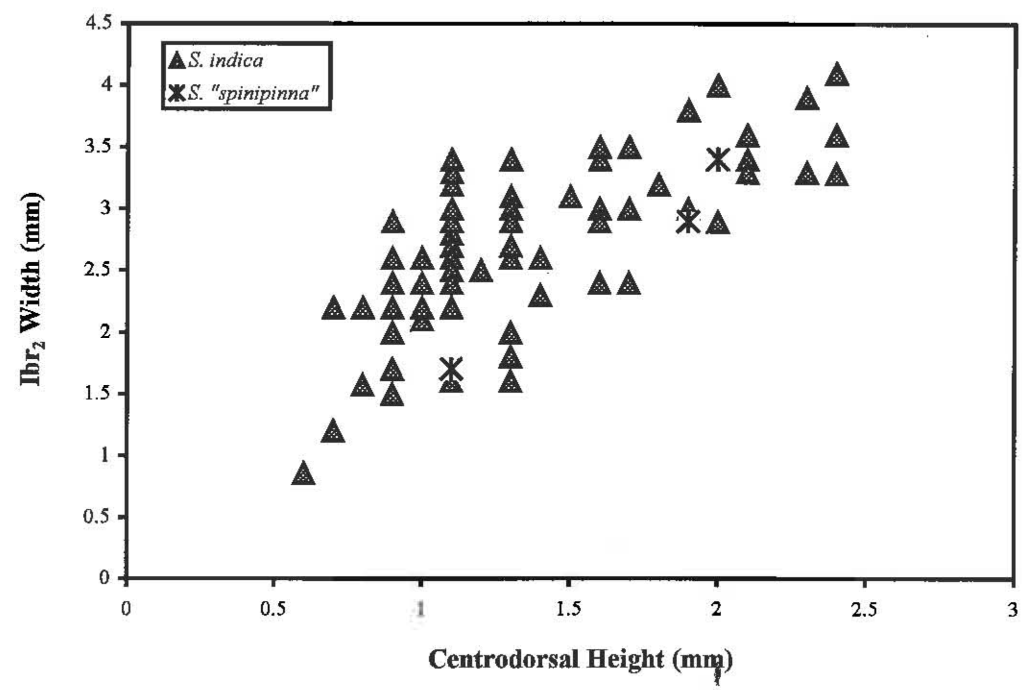


Figure 45. Plot of Ibr$_2$ width against centrodorsal height for *S. indica* (including "*spicata*", "*oxyacantha*" and intermediate specimens) versus *S.* "*spinipinna*".

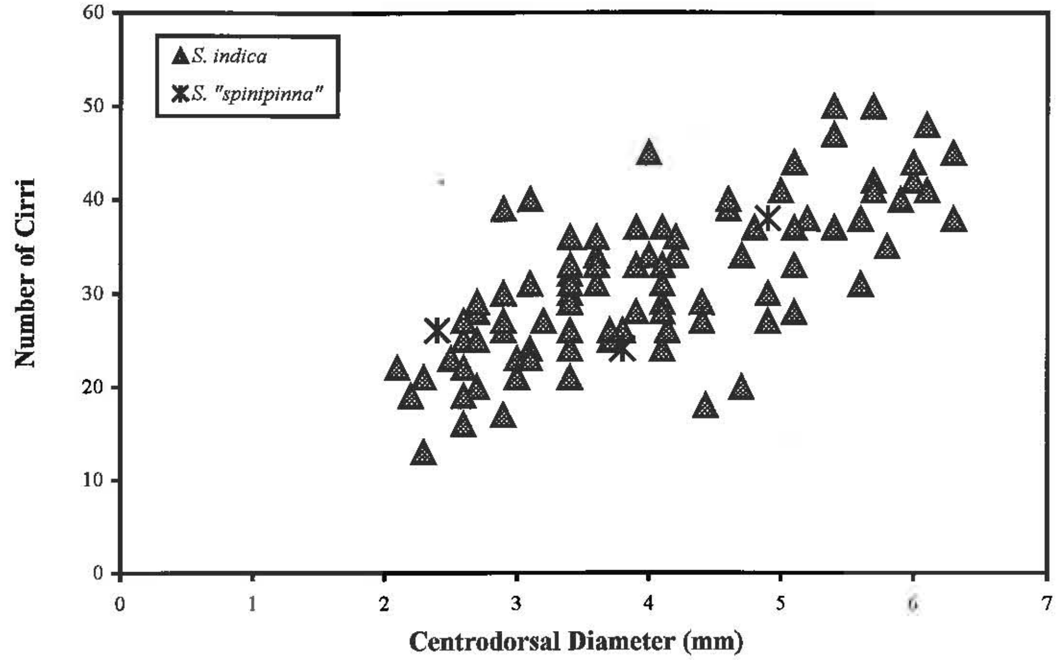


Figure 46. Plot of number of cirri against centrodorsal diameter for *S*. "*indica*" (including "*spicata*", "*oxyacantha*" and intermediate specimens) versus *S.* "*spinipinna*".

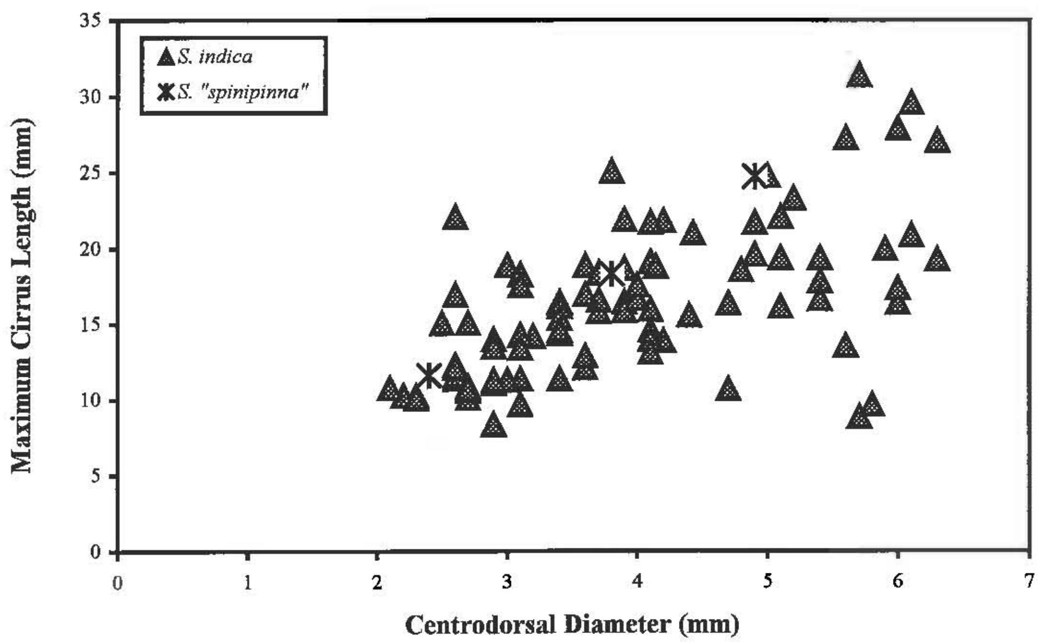


Figure 47. Plot of maximum cirrus length against centrodorsal diameter for *S. indica* (including "*spicata*", "*oxyacantha*" and intermediate specimens) versus *S.* "*spinipinna*".

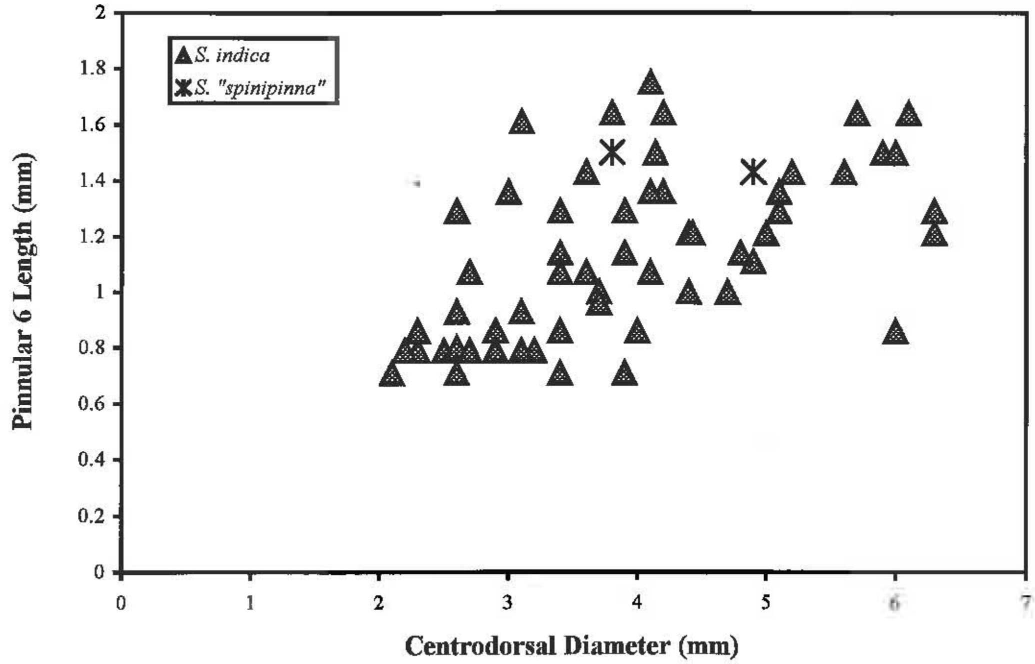


Figure 48. Plot of length of pinnular 6 from P_2 against centrodorsal diameter for *S. indica* (including *"spicata"*, *"oxyacantha"* and intermediate specimens versus *S. "spinipinna"*.

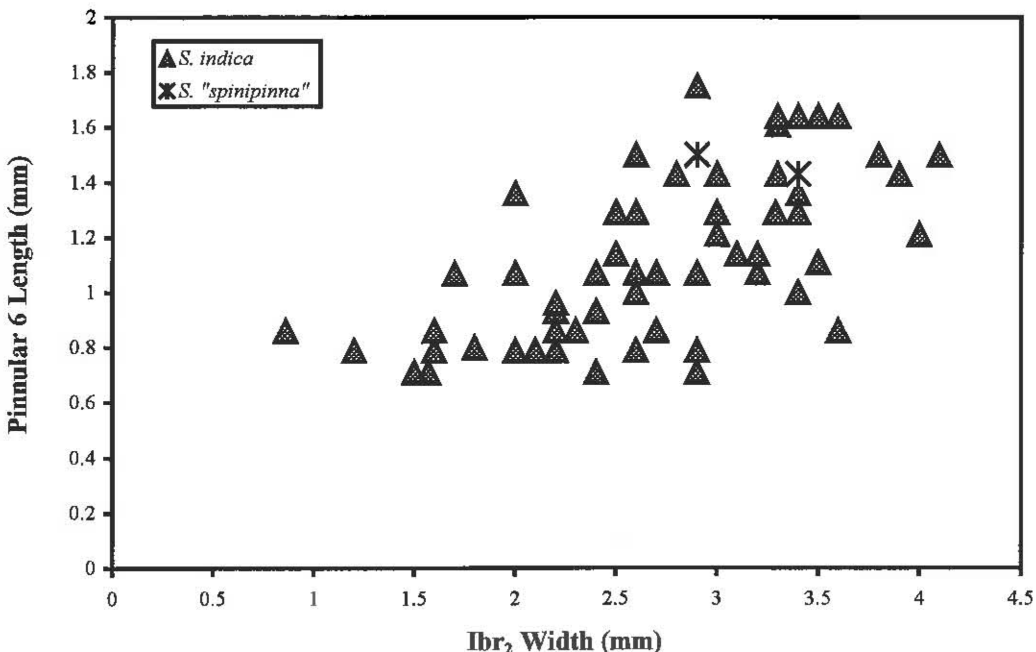


Figure 49. Plot of length of pinnular 6 from P_2 against Ibr_2 width for *S. indica* (including *"spicata"*, *"oxyacantha"* and intermediate specimens) versus *S. "spinipinna"*.

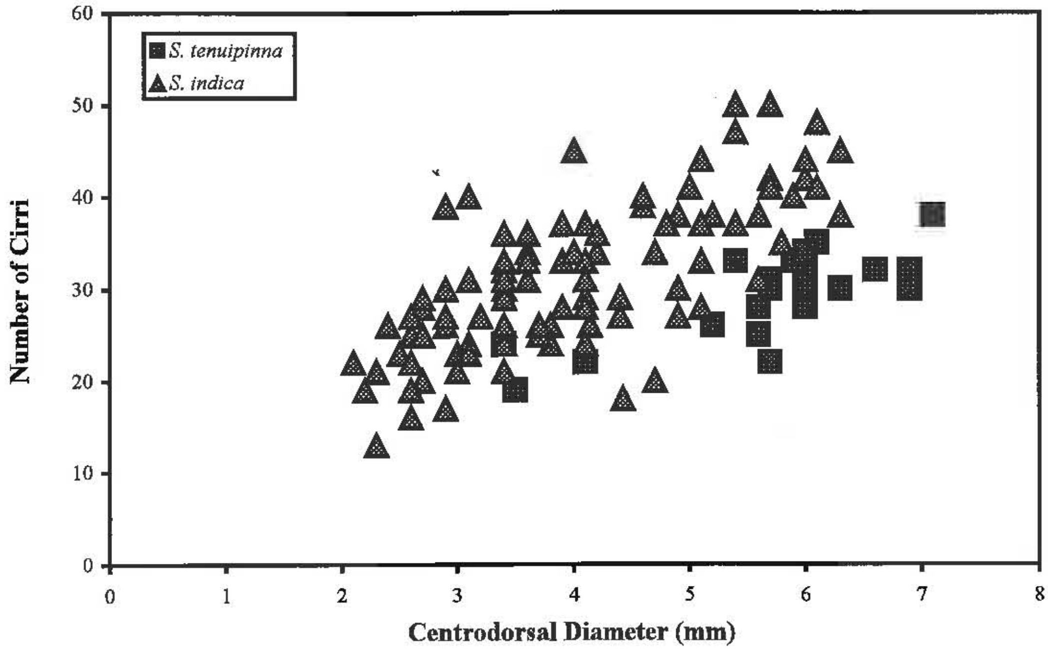


Figure 50. Plot of number of cirri against centrodorsal diameter for *S. tenuipinna* (including *S. "echinus"*) versus *S. indica* (including *S. "spicata"*, *S. "oxyacantha"* and intermediate specimens).

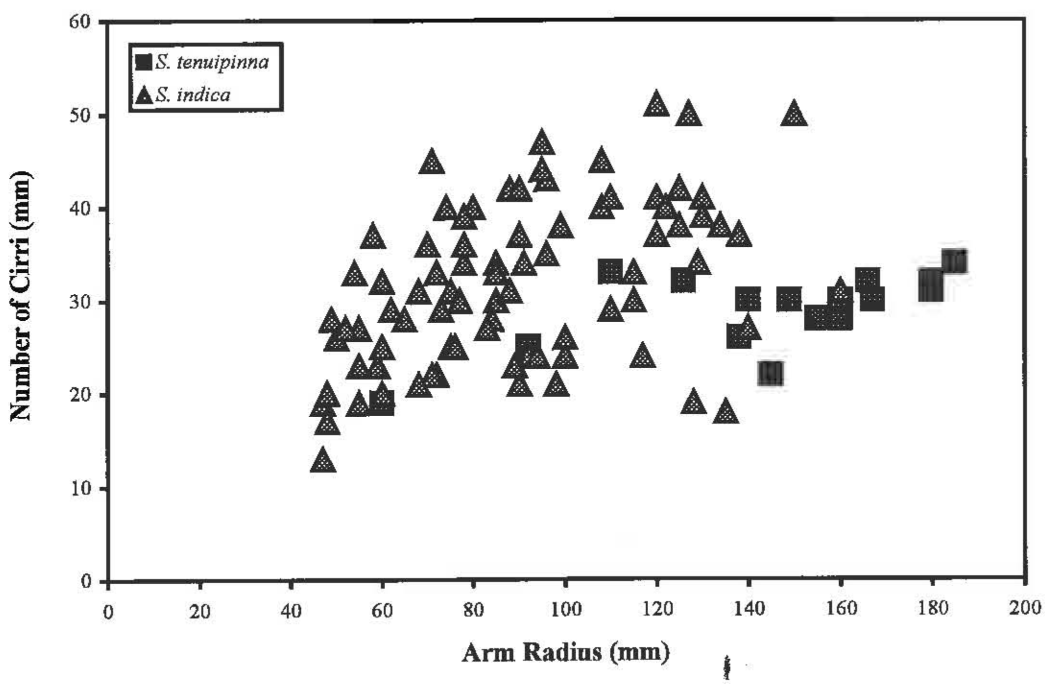


Figure 51. Plot of number of cirri against arm radius for *S. tenuipinna* (including *S. "echinus"*) versus *S. indica* (including *S. "spicata"*, *S. "oxyacantha"* and intermediate specimens).

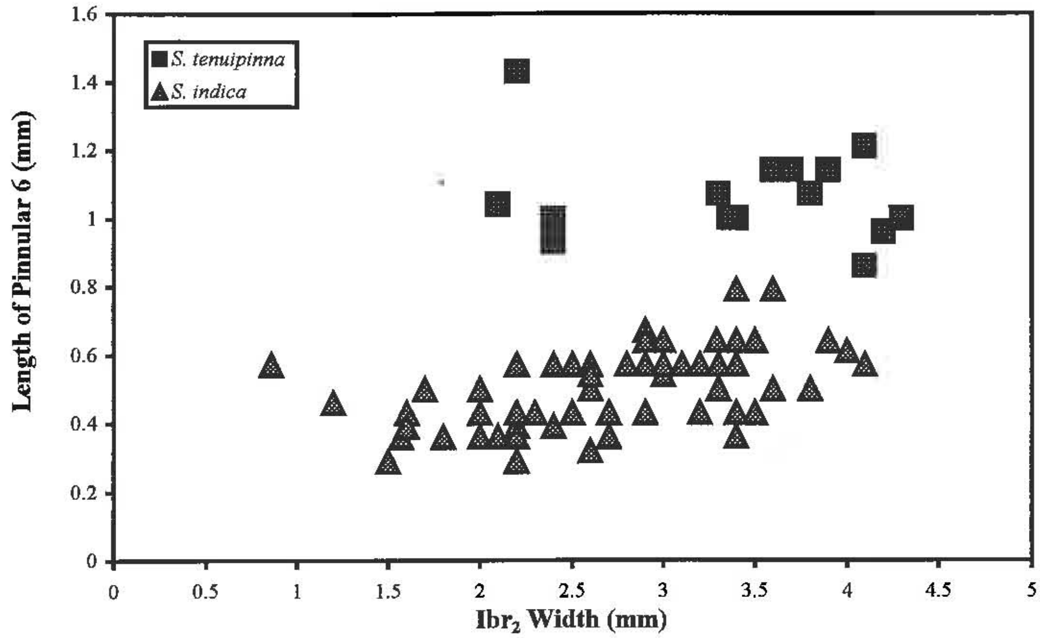


Figure 52. Plot of length of pinnular 6 from P_1 against Ibr_2 width for *S. tenuipinna* (including *S. "echinus"*) versus *S. indica* (including *S. "spicata"*, *S. "oxyacantha"* and intermediate specimens).

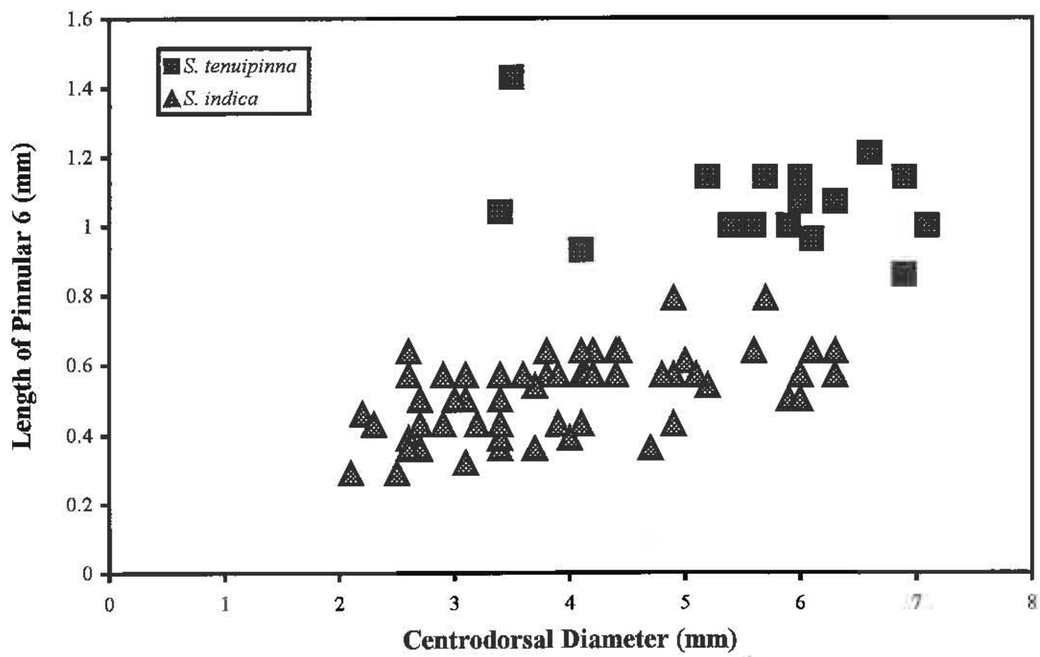


Figure 53. Plot of length of pinnular 6 from P_1 against centrodorsal diameter for *S. tenuipinna* (including *S. "echinus"*) versus *S. indica* (including *S. "spicata"*, *S. "oxyacantha"* and intermediate specimens).

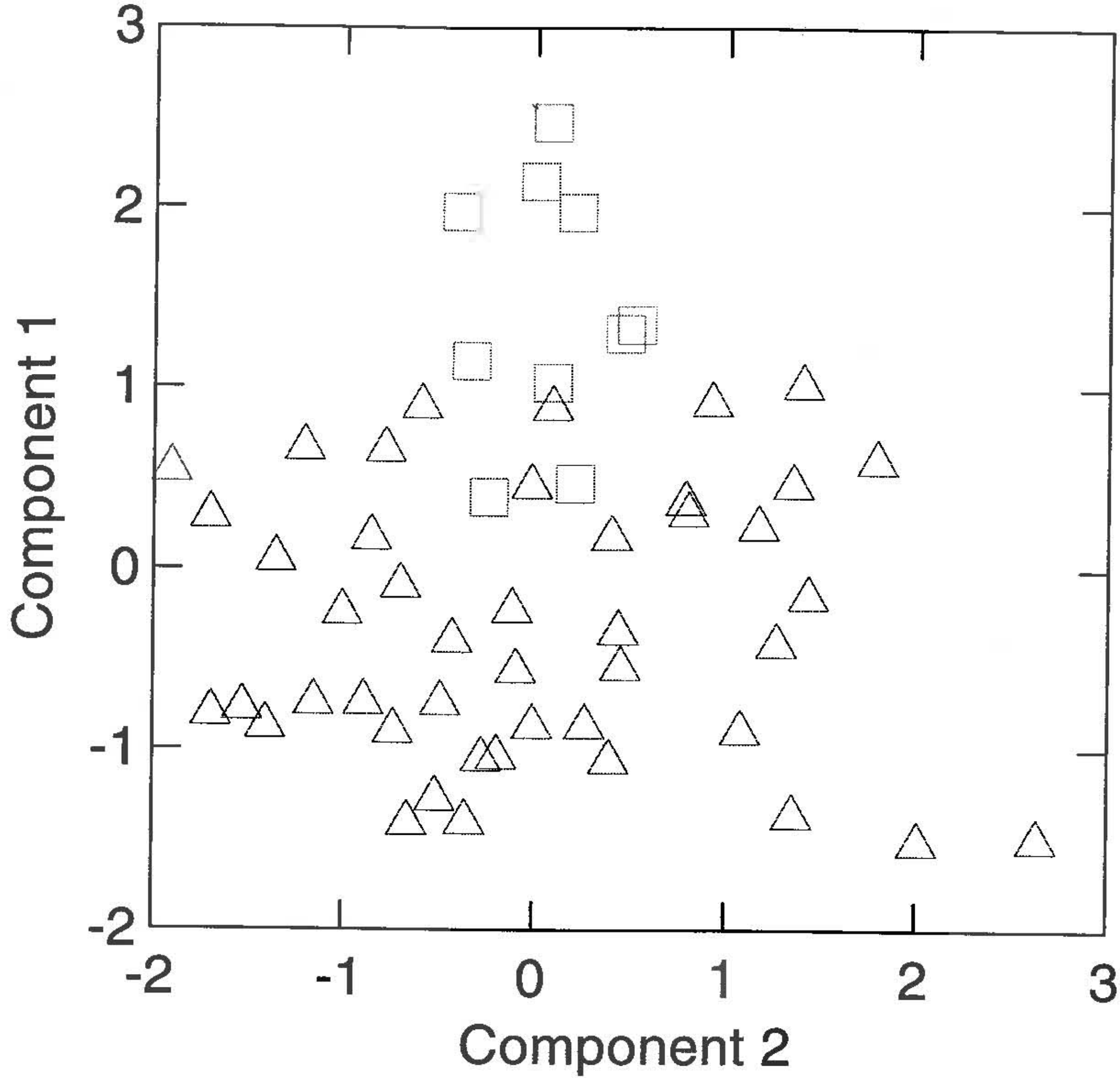


Figure 54. Graph of component scores from Component 1 vs. Component 2 in principal component analysis for *S. tenuipinna* (□) (including *S.* "*echinus*") and *S. indica* (Δ) (including *S.* "*spicata*", *S.* "*oxyacantha*", *S.* "*spinipinna*" and intermediate specimens).

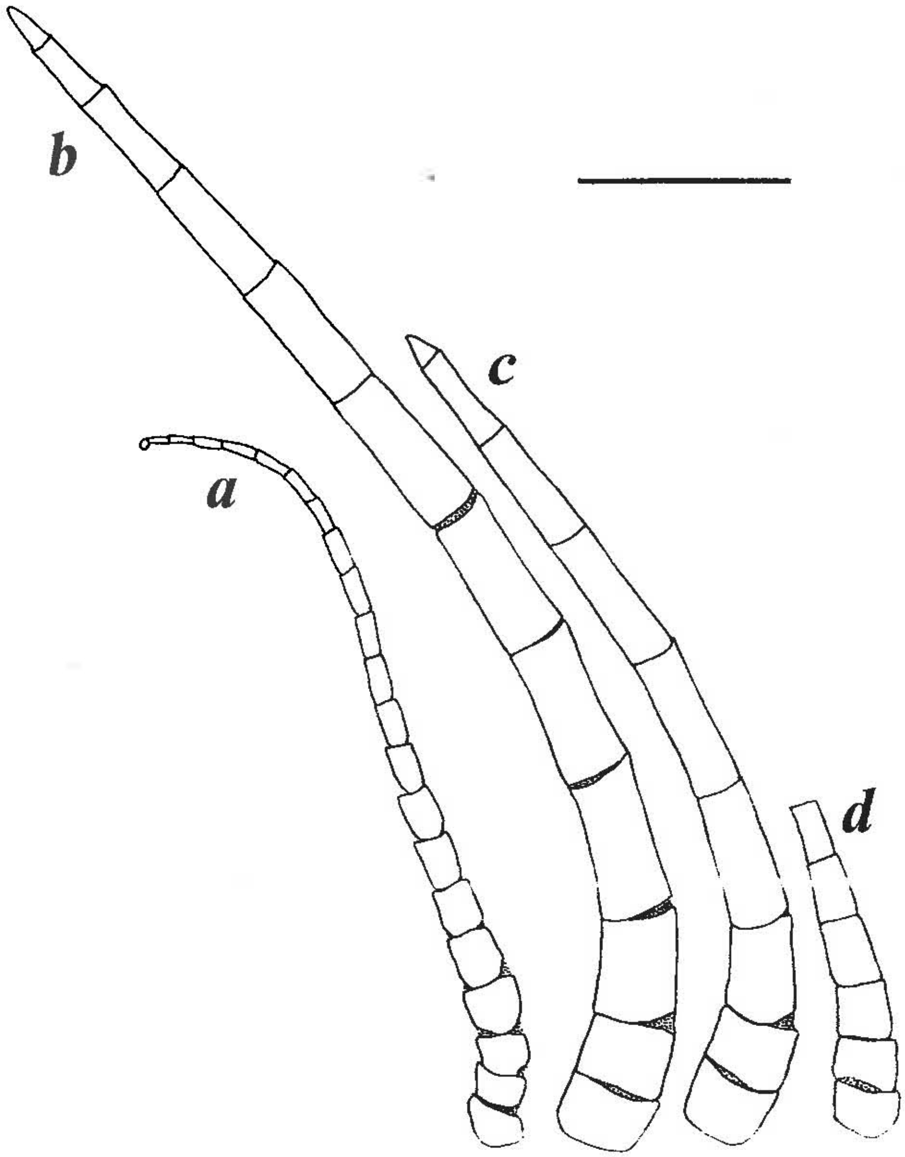


Figure 55. *Antedon tuberculata* Hartlaub (BMNH 1888.11.9.75) a. P_1. b. P_2. c. P_3. d. P_4. Scale: 2 mm.

Genus *Lamprometra* A. H. Clark, 1913

Comatula (part) Leuckart, 1833:387.

Alecto (part) Müller, 1841:185.

Comatula (*Alecto*) (part): Müller, 1847:261.

Antedon (part) Lütken, 1874:190 (in Carpenter, 1879).

Actinometra (part) Carpenter, 1888:60.

Himerometra (part) A. H. Clark, 1907:356.

Dichrometra (part) A. H. Clark, 1909a:13.

Lamprometra A. H. Clark, 1913a:142-143; 1918:98, 100.— Gislén, 1922:76; 1924:150, 1934:47. —A. H. Clark, 1941:472-537.— Utinomi and Kogo, 1965:274-276; —A. M. Clark and Rowe, 1971.—A. M. Clark, 1972 — Zmarzly, 1985:352.— Chen *et al.*, 1988:78. — Kogo, 1998:61-63, 65-67.

Diagnosis.— A genus of Mariametridae with centrodorsal thin, flat, discoidal; radials partially or completely concealed by centrodorsal; cirrus sockets restricted to centrodorsal margin, not encroaching on broad aboral pole; brachitaxes separated or in close lateral apposition; brachitaxis ossicles thickened laterally, producing characteristically apposed margins, or weakly thickened with margins not apposed; cirri composed of <35 cirrals; distal cirrals smooth or bearing aboral carination resulting in a triangular spine; P_2 enlarged, with reduced ambulacral groove and a finely flagellate tip; pinnulars barely longer than broad; articular facets normally developed.

Lamprometra palmata Müller, 1841

Figures 56-68; Table 3.

Alecto palmata Müller, 1841:185.

Comatula (Alecto) palmata: Müller, 1847:261.—Lütken, 1874:190 (in Carpenter, 1879).

Antedon protectus Lütken, 1874:190 (part) (in Carpenter, 1879). —A. H. Clark, 1913b:31.

Antedon palmata: Carpenter, 1879:23 (part), 29 (part), 45; 1882:733; 1888:35 (part), 44 (part), 54 (part), 55 (part), 208 (part), 213 (part), 366 (part), 379. —Bell, 1882:533, 534; 1888:384, 387.—Hartlaub, 1891:51-52, 113. —A. H. Clark, 1912e:385; 1912c:34, 37, 40, 41; 1913b:85.

Antedon protecta Carpenter, 1881:192; 1882:746; 1888:53, 54, 91, 225, 234, 237, 366, 379; 1889:312.—Hartlaub, 1890:170, 180; 1891:65.

Antedon gyges Bell, 1884:160-161, pl. 12, fig. b.—Carpenter, 1888:49-50, 55, 224-225, 366, 379.—Hartlaub, 1891:40.—A. H. Clark, 1911a:714, 716; 1912f:31, 34.—H. L. Clark, 1921:6.

Antedon conjungens Carpenter, 1888:233, pl. 1, fig. 1;1889:305, 311, pl. 27. —Bell, 1888:389.—A. H. Clark, 1941:482-483.

Antedon klunzingeri Hartlaub, 1890:175; 1891:46, pl. 2, figs. 22, 25; 1912:152. —A. H. Clark, 1911e:4; 1912e:399; 1912f:37; 1929:641.

Antedon protectus: A. H. Clark, 1908d:489.

Lamprometra protectus: A. H. Clark, 1913b:31, 179; 1918:100, pl. 8, pl. 27, figs. 99, 100; 1932:551.—Gislén, 1922:75; 1936:2, 4, 12, 14.

Lamprometra brachypecha H. L. Clark, 1915b:104; 1921:8, 22:192 f., pl. 2, fig. 1, pl. 22, figs. 1, 2.—A. H. Clark, 1918:100;1941:489-90.

Lamprometra protecta: H. L. Clark, 1921:23, 192; vol. 3.—A. H. Clark, 1929:641.

Lamprometra gyges: A. H. Clark, 1913a:144; 1918:100; 1929:641.—H. L. Clark, 1921:23, pl. 1, fig. 4, pl. 21, figs. 4, 5, pl. 22, fig. 3; 1932:201-202; 1938:35-36; 1946:47. —Gislén, 1934:25.

Lamprometra klunzingeri A. H. Clark, 1913a:144; 1929:641; 1932:551, 558; 1936:89, 100, 104.

Lamprometra palmata: A. H. Clark, 1929:641; 1934:11; 1936b:100. 103.— Gislén, 1936:2, 4-5,12,14.— H. L. Clark, 1946:47.—A. M. Clark, 1975:402.—A. M. Clark and Rowe, 1971:23, fig. 8b.—Meyer and Macurda, 1980: 84-85, figs. 5c, 5d, 7a.— Zmarzly, 1985:352.— Chen *et al.*, 1988:78, fig. 21.— Stevens, 1989:4-20, 4-21, pl. 7a, 4-28, 6-14, figs. 6.10-6.13, 6-20, fig. 6.8.— Messing, 1994:238-239; 1998:189, 190. —Kogo, 1998:65-67, fig. 53.

Stephanometra oxyacantha: A. H. Clark, 1941:421(one misidentified specimen).

Lamprometra palmata palmata: A. H. Clark, 1941:474-517, pl. 53, figs. 243-246, pl. 54, figs. 248-252, pl. 55, figs., 257.—A. M. Clark, 1972:104-105, fig. 10 (a-e).

Lamprometra palmata gyges: A. H. Clark, 1941:517-526, figs. 253-255.

Lamprometra parmata parmata Utinomi and Kogo, 1965:274-276, fig. 7.

Stephanometra spicata: Kogo, 1998:61-63, fig. 49.

Material examined. —RED SEA: USNM E35224 (1 specimen), Misharif I., Khor Dongola, no additional data; USNM E35769 (1), Gulf of Suez, Um el Jerman, R. Hartmeyer, coll., no additional data. THAILAND: USNM E11630 (1), Andaman Sea, W. of Phuket, 07°34'N, 98°00'E, 77 m, 21 Mar 1963. SINGAPORE: USNM E34853 (1), D.L Meyer, coll., no additional data. INDONESIA: USNM E389 (1), Ramah-Kuda Bay, R/V *Siboga*, Sta. 279, 36 m, 11-13 Dec 1899; USNM E405 (1), Greater Sunda Is., Kabaena I., R/V *Siboga*, Sta. 209, 22 m, 23 Sep 1899; USNM E35050 (1), Banda Sea, S end of Banda I., 2-3 m, 31 Jan 1975, D.L Meyer, coll.; USNM E35370 (1), Ceram Sea, NW end Seleman Bay, 02°53'50"S, 129°05'15"E, R/V *Rumphius II*, Sta. SEL-2, 20 Jan 1975; USNM E36145 (2), Halmahera Is., Weda Bay, 00°50'00"N, 127°34'00"E, 1.5-6 m., 14 July 1979, G. Hendler, coll. MALAYSIA: NSUOC 360, 361, 363 & 366 (4), Sabah, Borneo, Dive Center Mabul I., 04°15'N, 118°38'E, 12 m, 24 Apr 1997, C. G. Messing coll.; NSUOC 260, 354, 357, 359, 362 & 365 (6), Mabul Wall, E side of Mabul I., 04°15'N, 118°38'E, 10-21 m, 22-26 Apr 1997, C. G. Messing, coll. PHILIPPINES: NSUOC 347 (1), Sulu Sea, S Tubbataha Reef (W end), 09°49'N, 119°52'E, 21 m max., Apr 1995, C. G. Messing, coll; NSUOC 345 (1), Fondeado Reef, 24 Apr 1995, C. G. Messing, coll.; USNM E35252 (2), R/V *Albatross*, Sta. ?, no additional data; Zebu (Cebu) Reef: BMNH 1888.11.9.76 (2), R/V *Challenger*, no additional data. CHUUK ATOLL, MICRONESIA: NSUOC 368 (1), Wreck of Fujikawa Maru, between Dublon and Uman Is., 07°20'N, 151°53'E, 9.1-12.1 m, 14 June 1993, C. G. Messing, coll. REPUBLIC OF THE MARSHALL ISLANDS: USNM E35248 (1), Ebon I., 14 Apr 1877, Rev. B. G. Snow, coll., no additional data. PAPUA NEW GUINEA: NSUOC 358 (1), Barrier I. Outside Magic Pass, Madang, 6-8 m, 9 July 1991, L. Harris, coll.; NSUOC 353 (1), Barracuda Rock, off Pig I., Madang, 05°10'20"N, 145°51'53"E, 6 m, 8 July 1991, C. G. Messing, coll.; NSUOC 351 (1), Outside Pig I., Madang, 05°10'20"N, 145°51'53"E, 11 m, 16 July 1991, C. G. Messing, coll.; NSUOC 344 & 346 (2), Jais Aben Reef, N side of Nagada Harbor, Madang, 05°09'29"S, 145°49'21"E, 3-4 m, 2 June 1992, C. G. Messing, coll.; NSUOC 352 (1), Barrier I. Outside Wongat I., Madang, 05°08'09"S, 145°50'51"E, 3 m, 11 July 1991, C. G. Messing, coll.; NSUOC 356 (1), Banana Rock, off Christensen Research Institute, Madang, 05°9'29"S, 145°49'21"E, 6 m, 6 July 1991, L. Harris, coll.; IRSCB 384 & 382 (2), Hansa Bay, Laing I., (Pointe 0), 25 m, 22 July 1989, M. C. Lahaye, coll.; IRSCB 417, 410, & 403 (3), Platier, Hansa Bay, 20 m, 23 July 1989, M. C. Lahaye, coll.; IRSCB 326 (1), Platier (NE), 20 m, 16 July 1989, M. C. Lahaye, coll.; IRSCB 104 & 105 (2), Hansa Bay, Laing I., Sta. 13, 5 m, 24 June 1989, M. C. Lahaye, coll.; IRSCB 240 (1), Hansa Bay, Epave (Sisimangun), 6 m, 7 July 1989, M. C. Lahaye, coll; IRSCB 421 (1), Mandy Passage (Near Hansa Bay), 41 m, 24 July 1989, M. C. Lahaye, coll. AUSTRALIA: USNM E34827 (3), Lizard I., 1975, D. L. Meyer, coll., no additional data; USNM E34738 (1), Heron I., D. L. Meyer, coll., no additional data; USNM E35261 (1), Port Denison, Queensland, no additional data. FIJI: USNM E34799 (1), Makuluva I., 18°11'36"S, 178°31'16"E, 27 Apr 1975, D. L. Meyer & B. Carlson, coll.; BMNH 1888.11.9.77 (1) & 1888.11.9.78 (3), R/V *Challenger* Sta. 174, Kandavu, 19°06'S, 178°18'E, 411 m, 3 Aug 1874. NO LOCALITY DATA: CRRF 1151L (1), no additional data.

Description.— Centrodorsal thin, discoidal; cirrus sockets restricted to outer margin of aboral pole (Figs. 56e-g); 1.6-6.4 mm across, 0.6-1.6 mm high, rarely to 1.9; D/H 2.6-5.7. Cirri arranged in one to two, sometimes three alternating marginal rows. Polar area flat, bare, rarely convex; 0.86-4.6 mm across; D/P 1.2-2.3.

Cirri XVI-XLIV, 16-32, 9.0-21.0 mm long; C_1-C_3 short; C_4 –C_6 slightly longer than broad; subsequent cirrals slightly broader than long; $C_{6\text{-}8}$ longest, L/W 0.9-1.6; C_7-C_{18} and following developing sharp aboral carination, becoming a low, swollen, triangular spine sometimes worn into a low carination. Penultimate segment bearing a sharp spine; terminal claw longer than penultimate and curved (Figs. 57a-c).

Basal ossicles not visible externally; radials visible at interradial angles or not visible at all. Brachitaxis ossicles ranging from strongly flattened against each other to separated. Ibr_1 commonly with diverging outer margins although sometimes with converging or parallel/converging margins, usually united proximally, rarely free laterally, 0.4-1.1 mm long, 1.3-3.7 mm wide; W/L 2.1-5.8. Ibr_2 with diverging lateral margins, 0.6-2.0 mm long, 1.5-4.1 mm wide; W/L 1.6-5.6. Lateral adambulacral margins of brachitaxis ossicles flattened, apposed, and weakly thickened (Figs. 56a-c), sometimes crenulated (Fig. 56d) and often interlocking or smoothly rounded, neither apposed nor laterally thickened, with weak lateral adambulacral expansions. IIIBr developed externally only or externally and internally; IVBr, when present, developed both externally and internally. Synarthrial tubercles weak to well developed.

Arms 12-44, 40-110 mm long; rays most commonly with two to four or six arms each, less frequently with five, seven, eight or nine. br_1-br_6 or br_7 oblong; subsequent brachials cuneate. br_{10} 0.68-1.8 mm wide, 0.3-0.9 mm long, W/L 1.2-3.2.

Syzygies at br_{3+4}, between br_{14+15} and br_{16+17}, less frequently between br_{9+10} and br_{17+18}, and rarely between br_{12+13}, br_{19+20} or br_{20+21}. Distal syzygial intervals seven to 11, less often six or 12 brachials.

Pinnules on outer arms generally longer than those on inner arms. P_1 through P_3 composed of pinnulars barely longer than broad, tapering gradually to a slender tip, the terminal pinnular bearing numerous minute spines (Fig. 58d). The first three proximal pinnulars oblong, laterally compressed, typically bearing a moderate to strong aboral carination that may be completely reduced, especially on P_2 (Fig. 58e). Subsequent pinnulars slightly longer than broad; L/W 1.0-1.5.

P_1 3.0-11.2 mm, of 10-32 pinnulars, slender, shorter than P_2, frequently slenderer and shorter than P_3 (Figs. 58 a, f, i & l). P_2 the longest, thickest pinnule, 4.3-17.4 mm long, 12-37 pinnulars; pinnular 6 with L/W 0.9-1.5, rarely greater (Figs. 58 b, g, j & m). P_3 2.1-9.1 mm, 9-20 pinnulars, usually resembling P_1, occasionally slightly slenderer or thicker than P_1, sometimes small weak and flexible, with a well-developed ambulacral groove as in the following pinnules (Figs. 58 c, h, k & n). P_4 1.7-5.9 mm, with 9-17 pinnulars. The following pinnules small, weak and flexible with a well-developed ambulacral groove. P_5 1.3-4.7 mm. Subsequent pinnules gradually increasing in length. P_{distal} 7.2 mm, 18 pinnulars; the first pinnular broader than long, the second as long as broad; distal pinnulars barely longer than broad; the terminal segment elongated and covered with small spines.

Table 3 provides morphological and meristic data for *Lamprometra, Dichrometra, Liparometra* and intermediate specimens used in the current study.

Color patterns.—Concentric banding on the arms formed by alternating colors on the arms in bands of 4-15 brachials each is characteristic of this species. Ray banding may be expressed in various shades of white, cream or tan, which alternate with dark brown, red-brown, rusty orange, pink or green. One specimen was banded purple and rusty orange. Specimens with rusty orange or green coloration were frequently observed with white division series having rusty orange or green blotches, respectively.

The following additional color patterns may be based on incorrectly identified specimens.

Stevens (1989:4-20) observed banding patterns expressed in red and white, "...pink/gray, purple, light yellow or light brown...". Typically, colors of the proximal portion of the arms are inconspicuous while the distal portion tends to be "bright and striking". He suggested that this coloration provides camouflage when the arms are curled in.

Zmarzly (1985) recorded one additional color pattern: dark purple to brown; cirri cream with purple articulations.

Meyer and Macurda (1980) recorded that most individuals have a characteristic banded green and white chevron pattern. Pinnules are white in the white sections and green, or green and white banded, in the green sections. H. L. Clark (1915b:104) referred specimens with this color pattern to *L. brachypecha.*

A. H. Clark (1921b) noted additional colors for *L. protectus,* which he though was the same as *L. palmata*: 1) ray bases white; distally rays rich brown with a white broad band;

pinnules tips yellowish or rusty; cirri cream and brown; 2) rays banded light yellow and bright orange/yellow; cirri dull violet/red; and 3) rays purplish brown, with pinnules chocolate and white. He also described variations on the green morph similar to that of Meyer and Macurda (1980): 1) bright green variegated with brown and white; pinnules with yellow tips, and 2) arm bases white with small green spots.

Geographic distribution.—Reported from the Red Sea and Mauritius in the west to Tonga and Hawaii in the east, including tropical Australia, and as far north as southern Japan (Utinomi and Kogo, 1965; Kogo, 1998). Previously published geographic distributions may be based on incorrectly identified species.

Bathymetric range.— Littoral down to 35 meters, with the exception of 5 specimens. USNM E11630 was collected in 77 m. Four *Challenger* specimens (BMNH 1888.11.9.78) recorded from 411 m were probably taken during shore collecting and not from this depth (A. H. Clark, 1941).

Remarks.—A. H. Clark (1941) distinguished *Lamprometra* from other members of the Mariametridae by its P_2 markedly stouter and longer than other proximal pinnules, never stiff and spinelike, though exceedingly variable in character. The revised diagnosis includes several features noted by prior authors but not included as generic characteristics: flat, broad cirrus-free aboral pole; P_2 tapering to a delicate flagellate tip and composed of pinnulars that are not especially elongated; division series ossicles ranging from sharply though slightly flattened laterally to not at all flattened laterally, and occasionally with crenulated exterior margins.

Diagnostic characters not previously noted include: normally developed oral pinnular facets (see pp. 26, Fig. 5), terminal pinnulars bearing spines, and reduced ambulacral groove on P_1, P_2 and sometimes P_3.

According to A. H. Clark (1941), *L. palmata* is the most variable comatulid species known and rarely are any two specimens similar. Yet, he writes that it is "always easily distinguished from all other comatulids" (1941:473). According to him, the length and stoutness of P_2, when "typically developed", make *L. palmata* easy to recognize. A. H. Clark attributed this variability to the diverse conditions in the littoral habitat.

The genus *Lamprometra*, as diagnosed by A. H. Clark (1941), includes two species: *L. klunzingeri* and *L. palmata,* and sixteen subspecies of *L. palmata* (A. H. Clark, 1941). Specimens of *L. klunzingeri* are distinguished by their slender proximal pinnules with basal pinnulars that bear a slight carination or none at all; P_3 is always longer than P_1. He refers to *L. klunzingeri* as the western form of *L. palmata* because it is restricted to the Red Sea south to Oman and possibly Tanzania.

L. palmata on the other hand bears a strong carination on the basal pinnulars of the oral pinnules; P_2 and sometimes P_3 are stouter than the others. This species ranges from Baluchistan to Hong Kong south to Australia, including the Marshall Islands, and east to Hawaii. A. H. Clark used the term subspecies loosely. He distinguished his sixteen subspecies of *L. palmata* by length of proximal pinnules, variations in apposition of brachitaxis ossicles, and degree of cirrus carination. A. H. Clark (1941) diagnosed *L. palmata gyges* as having brachitaxis ossicles in close lateral contact, more than 30 cirrals, P_1 slightly smaller than P_2, and flattened lateral adambulacral margins, but noted intermediates between this and *L. palmata palmata.* Only one specimen examined in the current study possesses more than 30 cirrals. However, its brachitaxis ossicles are not in close lateral contact and the lateral edges of its adambulacral margins are not flat-sided. A. H. Clark's (1941) key for *gyges* states that P_1 is "not much smaller than P_2"; P_1 12 mm and P_2 18 mm, whereas *L. palmata palmata* possesses P_1 10-12 mm and P_2 9-15 mm. Thus, P_1 is not much smaller in either *gyges* and *palmata*.

A. M. Clark and Rowe (1971) divided the genus *Lamprometra* into three taxa based solely on the form of P_2. A stout P_2 characterized *L. palmata palmata*; a stout P_2 with basal carination distinguished *L. palmata gyges,* and a slender P_2 with slight basal keel diagnosed *L. klunzingeri.* However, A. M. Clark (1972) examined four specimens from the Red Sea in the British Museum collection, all with basal keels as strong as those on *L. p. gyges* from Australia. Thus, these specimens negated one of A. H. Clark's primary characters. P_3 of one specimen resembled P_2 in both length and thickness, while P_3 in the other three specimens was noticeably smaller than P_2.

Specimens in the current study display similar discrepancies. In a specimen from the Red Sea (USNM E35224), P_3 is much reduced and resembles the succeeding pinnules, and its basal pinnulars are carinate. It is thus intermediate between *L. klunzingeri* and *L. palmata.* Five of fifty-two specimens measured in this study have P_3 longer than P_1 and would, according to A. H. Clark (1941), be considered *L. klunzingeri.* However, all five exhibit basally carinate oral pinnules and none are from the Red Sea or western Indian Ocean. Specimen USNM E35769 from the Red Sea, identified by A. H. Clark as *L. klunzingeri*, possesses proximal pinnules with carinate basal segments, and P_1 (10.7 mm) longer than P_3 (6.8 mm), again contradicting two of his primary characters. A specimen from Malaysia (USNM E34717) labeled *L. klunzingeri* exhibits basal carination, P_3 15 mm of 30 pinnulars, and P_2 10 mm with 26 pinnulars. This specimen is regarded herein as *Dichrometra.*

In the current study, P_1 ranged from shorter than to 5.3 mm longer than P_2. However, in a green morph (*L. "brachypecha"*), P_2 measured 8.6 mm longer than P_1. Stevens (1989) concluded that the form of P_2 in *L. palmata* varied at a single locality. The current study examined specimens from a wide geographic distribution and also found tremendous variation in the form of P_2.

Carpenter (1882) noted that flat adambulacral margins could not be considered a reliable character due to their extreme variability. Similarly, adambulacral margins in the current study range from strongly flattened against each other (apposed) to separated. Figures 59-62 plot several characters that increase with growth and size for *Lamprometra* specimens with apposed and separated ambulacral margins. The nature of the lateral adambulacral margin was selected to illustrate the variability of this character within the genus. The plots indicate that the adambulacral margin is a variable character within *Lamprometra* since both types of margins form a solid continuum. Specimens with separated margins tended to fall out slightly smaller than specimens with flattened margins, perhaps implying that apposition and flattening of the margin is growth related.

This study examined three specimens identified by A. H. Clark (1941) as *L. p. gyges*. These exhibit 21-25 cirrals, lateral adambulacral margins not flat-sided, P_1 measuring 3.6-8.7 mm, and P_2 4.3-9.6 mm. These specimens do not represent *L. palmata gyges* and were considered *L. palmata* specimens for the current study.

The results of this study indicate that basal carination of pinnulars, closeness of lateral adambulacral margins, and number of cirrals are extremely variable characters. Often, specimens could not be satisfactorily assigned to a species or subspecies based on these diagnostic features. This study is in agreement with A. M. Clark (1975) who doubts that it is worthwhile recognizing subspecific distinctions and is not sure that *L. klunzingeri* " can be properly distinguished from *L. palmata*, the form of P_2...being extremely variable..."

Six specimens in this study are considered to be *L. palmata* form *brachypecha*. The type specimen (A. H. Clark, 1941) bears a large, thick flat centrodorsal, 5 mm in diameter; a bare aboral pole about 2.5 mm across; distal cirri laterally compressed with an inconspicuous, low longitudinal ridge; all cirrals broader than long and no lateral adambulacral processes on the brachitaxes. P_1 is 10-12 mm long with 23-24 pinnulars; P_2 13-14 mm, 25 pinnulars; P_3 is very small. All pinnules are more or less cylindrical and composed of perfectly smooth segments.

The color of this specimen is bright green, variegated with brown and white, with a broad band of white on the arms, and yellow-tipped distal pinnules. The holotype was described as a form with slender oral pinnules. A. H. Clark (1941) distinguished *brachypecha* from other subspecies by its short arms composed of approximately 100 brachials.

H. L. Clark (1915b:104) observed that, when undisturbed, the arms covered the oral surface of the animal and it resembled a tuft of green seaweed. When touched, the arms immediately extended in a flat fan and a broad white band flashed into view. "The immediate effect was obliterative and one's first thought was that the animal had vanished."

L. palmata form *brachypecha* specimens were singled out on the basis of their color and extremely thick, enlarged P_2 (Fig. 63b). Centrodorsal and division series ossicles are white or cream mottled with green spots (Fig. 63e & f); distally the arms are banded dark green. P_2 is enlarged with average pinnule widths of 0.70 mm (the largest 1.14 mm) (Fig. 63b). In comparison, the average widths for *L. palmata* specimens are 0.45 mm. Plate 53, fig. 246 in A. H. Clark (1941), referred to as *L. palmata palmata,* illustrates an example of the green morph with the characteristically enlarged P_2.

Centrodorsal and aboral pole diameter, width of Ibr_2, the number of cirri and maximum cirrus length, and arm radius were selected for graphing because they increase with growth and size. Length of pinnular 6 of P_2 was selected for graphing because it is one of the few meristic characters that tends to differentiate *L. palmata* from *L. palmata* form *brachypecha.* Plots of morphological characters that vary with growth and size (Figs. 64-68) illustrate that *L. palmata* form *brachypecha* falls well within *L. palmata.* However, plots of growth characters against length of pinnular 6 of P_2 (Figs. 67 & 68) indicate that at least larger specimens of *L. palmata* form *brachypecha* fall outside of the *L. palmata* character space. If a substantial number of additional specimens consistently maintain such distinctions of color and pinnule morphology, *L. palmata* form *brachypecha* may be justifiably treated as a distinct species.

Results of the current study indicate that the only character distinguishing *Lamprometra*, *Liparometra*, and *Dichrometra* is the length of P_2 in relation to P_3. P_3 in *Lamprometra* is always shorter than P_2; it is longer in *Dichrometra* than P_2, and the two are equally long in *Liparometra.* Lateral adambulacral margins, pinnular shape, cirrus form and centrodorsal shape are all similar in the three genera. In addition, intermediate specimens of *Lamprometra/Liparometra* and *Liparometra/Dichrometra* were encountered in the current study. Specimens USNM E34827 and NSUOC 407, were considered intermediate between *Lamprometra* and *Liparometra* since P_2 was longer and thicker than P_3 on some exterior arms and equal to P_3 on others. P_2 in specimens NSUOC 403 and IRSCB 69 was equal to P_3 in length and thickness on some arms and smaller on others, thus rendering them intermediate between *Liparometra* and *Dichrometra.* There was no indication of regeneration among these intermediate specimens. This study is in agreement with Gislén (1922:76) who concluded that *Lamprometra, Liparometra* and *Dichrometra,* being based solely on the relation between the length of P_1, P_2, and P_3, are very closely related to each other. In addition, figures 69-72 illustrate that *Lamprometra* tends to fall out smaller than *Liparometra* and *Dichrometra* specimens, suggesting that these three genera may eventually prove to be synonymous.

Note: Material examined for intermediate specimens, *Liparometra* species and *Dichrometra* species is listed in Appendix 5.

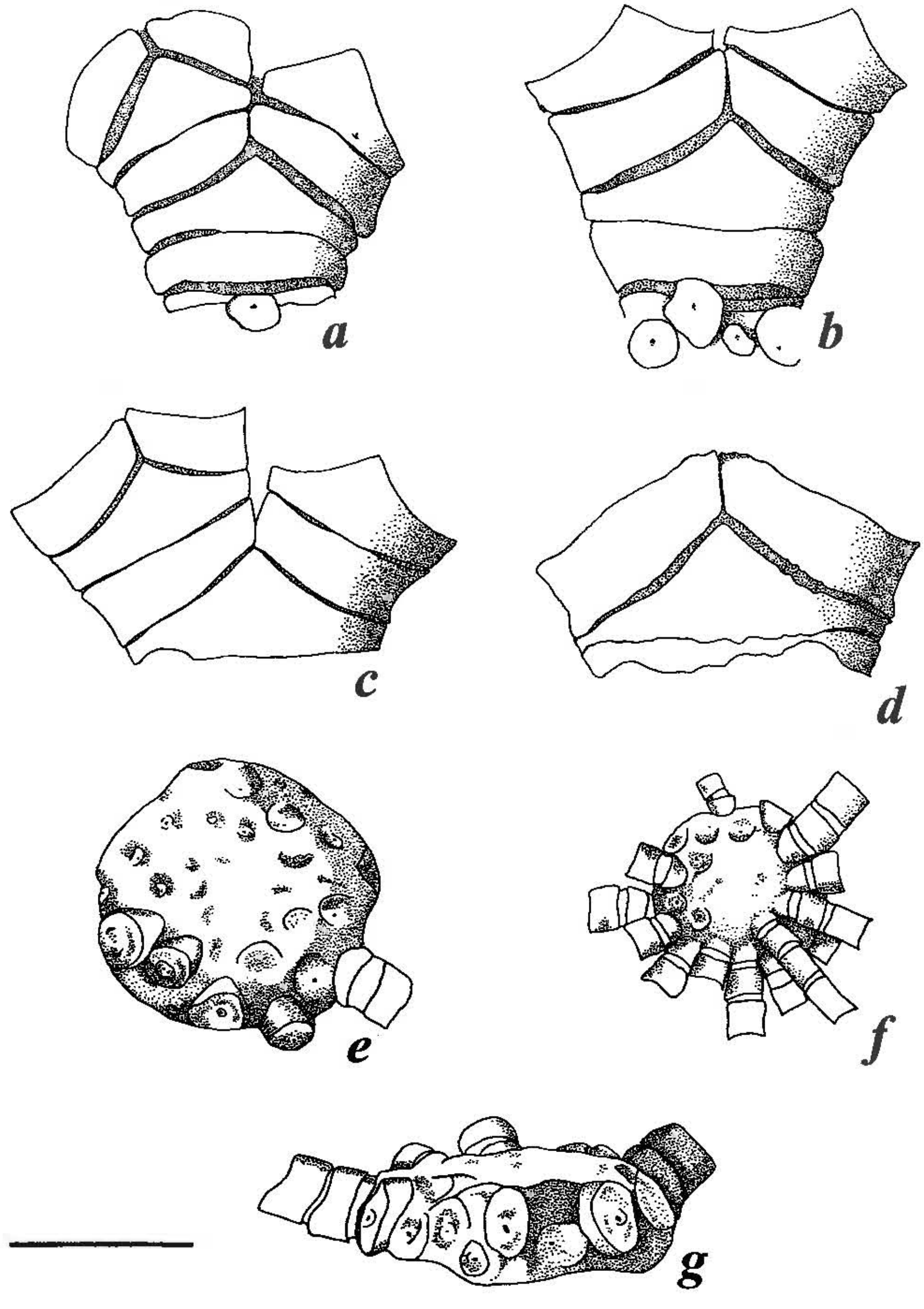


Figure 56. *Lamprometra palmata*. Figs. a-d: lateral adambulacral margins of brachitaxes ossicles, in aboral view. a. IRSCB 382. b. NSUOC 366. c NSUOC 353. d NSUOC 358. Figs. e-f: centrodorsal, in aboral view. e. CRRF 1151L. f. NSUOC 357. g. Centrodorsal in lateral view, NSUOC 351. Scale: 2 mm.

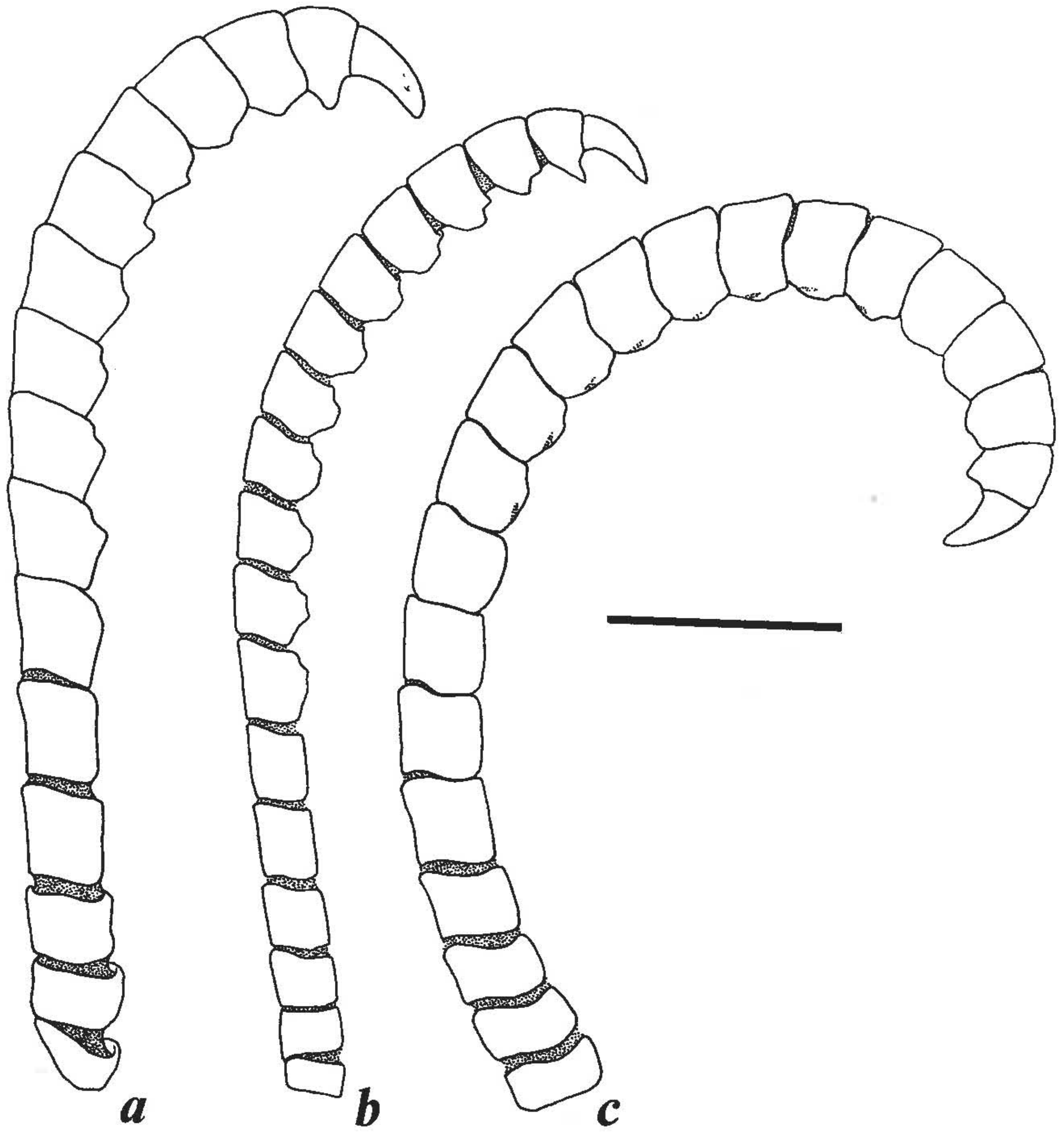


Figure 57. *Lamprometra palmata*. a. Cirrus, IRSCB 104. b. Cirrus, NSUOC 356. c. Cirrus, NSUOC 345. Scale: 2 mm.

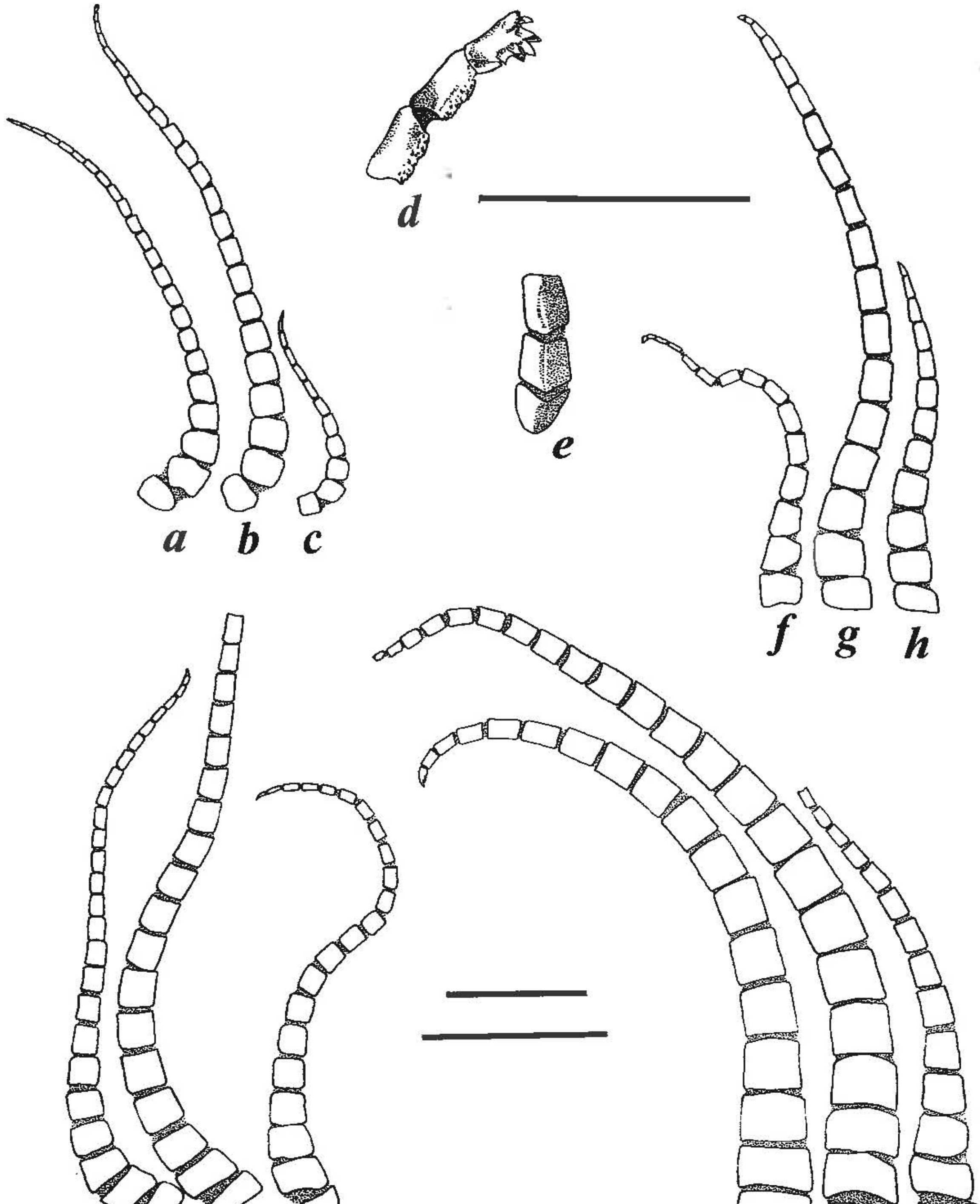


Figure 58. *Lamprometra palmata*. Pinnules. a. P_1, NSUOC 345. b. P_2, same. c. P_3, same. d. Distal pinnulars of P_2, same. e. Proximal pinnulars of P_2, NSUOC 326. f. P_1, NSUOC 360. g. P_2, same. h. P_3, same. i. P_1, NSUOC 368. j. P_2, same. k. P_3, same. l. P_1, IRSCB 326. m. P_2, same. n. P_3, same. Scale (upper): d & e, 1 mm; scale (center): a-c, f-h, 2 mm; scale (lower): i-n, 2 mm.

Table 3. Meristic and morphometric data for *Lamprometra palmata, Dichrometra* spp., *Liparometra* spp., and intermediate specimens.

	CENTRODORSAL			ABORAL POLE	CIRRI			ARMS		BRACHITAXES						br_{10}	P_1		P_2		P_3		P_4		P_5	
Specimen	D	Height	D/H	Diameter	Cirri	# Cirrals	Cirrus L	Arm	Ray L	Ibr_1			Ibr_2				#		#		#		#		#	
#	(mm)	(mm)		(mm)	#		(mm)	#	(mm)	L (mm)	W (mm)	W/L	L (mm)	W (mm)	W/L	W (mm)	Plrs.	L (mm)	Plrs.	L (mm)	Plrs.	L (mm)	Plrs.	L (mm)	Plrs.	L (mm)
L. palmata																										
IRSCB 326	2.5	0.9	2.8	2.1	22	25	15.8	21	40	0.5	2.6	5.2	0.9	2.9	3.2	1.6	18	6.4	22	9.4	19	9.1	14	5.9	12	3.4
IRSCB 421	2.0	0.7	2.9	1.4	25	17	9.1	18	50	0.4	1.7	4.3	0.6	2.1	3.5	1.0	15	4.3	12	4.4	12	3.6	11	2.9	10	2.5
IRSCB 403	1.9	0.7	2.7	1.1	23	17	8.6	19	--	0.4	1.4	3.5	0.7	1.7	2.4	0.9	10	3.4	12	4.6	10	2.9	10	2.4	9	2.1
IRSCB105	2.0	0.7	2.9	1.1	24	17	7.7	12	65	0.4	1.6	4.0	0.8	1.9	2.4	0.7	10	2.2	14	5.1	10	2.9	10	2.8	12	2.7
NSUOC 353	4.4	1.3	3.4	3.0	32	20	13.9	27	75	0.2	2.4	11.4	1.2	2.8	2.4	1.4	18	7.0	19	10.3	11	2.4	10	2.2	9	2.1
IRSCB 104	2.0	0.6	3.3	1.1	20	19	9.5	13	55	0.5	1.2	2.4	0.7	1.5	2.1	0.9	13	3.0	13	4.4	10	2.7	10	2.4	10	2.7
NSUOC 358	5.1	0.9	5.7	4.0	39	25	13.9	27	60	0.4	3.1	7.2	1.4	3.5	2.5	1.4	20	7.4	--	--	11	2.6	11	3.4	13	4.2
NSUOC 352	2.6	0.7	3.7	1.4	27	18	9.2	--	40	0.4	1.6	4.0	0.9	1.9	2.0	1.0	14	4.1	14	5.0	10	2.9	--	--	8	1.6
CRRF 1151L	2.9	1.1	2.6	1.4	17	23	13.7	20	--	0.6	2.1	3.5	1.1	2.6	2.4	0.8	30	8.0	--	--	16	4.1	13	3.3	12	2.5
NSUOC 356	3.1	1.1	2.8	2.4	30	23	13.3	31	65	0.6	2.6	4.3	1.0	2.9	2.9	1.4	16	5.6	--	--	13	5.1	11	2.5	12	3.9
NSUOC 351	3.1	0.9	3.4	2.3	20	23	11.6	25	--	0.4	2.4	6.0	1.0	2.8	2.8	1.3	11	3.3	--	--	12	3.4	11	3.1	10	2.7
NSUOC 345	2.4	0.6	4.0	1.3	19	18	11.1	20	65	0.6	1.6	2.7	1.1	1.9	1.7	0.7	23	5.6	19	6.2	14	3.0	10	2.1	10	1.9
NSUOC 347	5.4	1.3	4.2	4.1	44	23	19.3	34	110	0.7	3.0	4.2	1.7	3.9	2.3	1.7	27	11.2	28	15.1	18	6.1	12	3.6	12	4.3
IRSCB 410	3.4	1.0	3.4	2.4	31	23	16.6	24	70	0.7	2.6	3.7	1.1	2.9	2.6	1.4	18	5.9	15	6.5	16	5.6	12	3.6	12	3.7
IRSCB 417	4.2	1.4	3.0	3.0	43	22	14.9	29	--	0.6	3.0	5.3	1.2	3.3	2.7	1.4	23	7.4	16	8.5	18	6.7	14	5.1	12	4.0
IRSCB 384	2.5	0.6	4.2	1.4	16	20	11.5	14	--	0.6	1.0	1.7	0.9	2.2	2.6	0.9	12	3.7	12	5.6	11	3.4	9	2.3	8	1.3
IRSCB 382	2.4	0.7	3.4	2.0	16	21	10.8	19	55	0.6	1.7	3.0	0.7	2.2	3.1	0.9	13	3.5	16	5.9	11	3.1	10	2.6	10	2.9
NSUOC 360	2.6	0.7	3.7	1.4	17	21	11.0	19	70	0.5	1.8	3.6	0.9	2.1	2.3	1.0	15	6.8	18	7.4	12	3.7	11	3.1	10	2.6
NSUOC 361	3.3	0.9	3.7	2.4	26	22	14.1	16	90	0.5	2.5	5.0	1.2	2.9	2.4	1.4	19	6.0	20	9.4	17	6.9	14	5.4	14	4.9
NSUOC 365	1.8	0.6	3.0	1.1	18	16	--	17	50	0.6	1.3	2.3	0.8	1.6	2.1	0.7	18	4.3	15	5.1	14	4.1	9	2.4	10	2.3
NSUOC 362	2.4	0.9	2.7	1.4	17	21	10.7	15	55	0.6	1.8	3.2	0.9	1.9	2.0	0.7	15	4.4	13	4.3	10	2.9	10	2.4	11	2.8
NSUOC 359	2.6	1.0	2.6	1.9	25	22	13.5	20	85	0.5	2.4	4.8	1.4	2.5	1.8	1.6	21	7.1	26	11.6	19	5.5	15	4.9	13	4.2
NSUOC 357	1.6	0.6	2.7	0.9	16	17	8.6	12	40	0.5	1.3	2.6	0.8	1.6	2.0	1.4	13	3.5	13	7.7	12	4.2	11	3.1	10	3.0
NSUOC 366	3.0	1.1	2.7	2.4	23	23	13.4	29	70	0.5	2.5	5.0	1.2	2.9	2.4	1.4	20	6.6	24	9.7	17	6.1	14	4.3	14	3.8
NSUOC 363	3.4	1.1	3.1	2.0	26	21	11.6	22	90	0.7	2.4	3.4	1.0	3.0	3.0	1.6	24	8.5	29	13.5	17	7.0	15	5.2	15	4.4
NSUOC 368	3.4	1.1	3.1	2.6	29	23	14.7	28	105	0.6	2.6	4.3	1.0	2.8	2.8	1.4	29	8.9	21	6.6	19	2.8	17	2.1	17	4.1
USNM E34827	2.9	--	--	1.7	23	19	11.3	--	60	0.5	1.9	3.8	1.0	2.5	2.5	--	15	5.1	17	8.9	9	--	10	2.9	--	--
USNM E34827b	3.1	--	--	1.6	22	20	11.1	20	60	0.6	2.2	3.7	1.0	2.6	2.6	--	20	6.6	21	9.1	12	4.2	12	3.9	--	--
USNM E34738	4.0	--	--	--	43	28	17.7	30	115	0.6	2.5	4.2	1.3	3.2	2.5	--	--	--	20	8.6	20	7.4	16	4.5	--	--
USNM E35053	5.2	--	--	--	33	25	8.5	38	80	0.5	2.0	4.0	1.2	2.5	2.1	--	22	5.6	--	--	15	4.3	12	1.7	11	2.3
USNM E34853	4.6	--	--	--	30	23	13.6	42	70	0.5	2.9	5.8	1.4	3.0	2.1	--	32	10.7	30	15.7	16	4.5	12	2.5	--	--
USNM E36145	4.3	--	--	--	30	26	13.4	34	75	0.6	2.8	4.7	1.4	3.0	2.1	--	21	4.3	19	8.6	18	3.1	12	1.0	--	--
USNM E36145b	5.0	--	--	--	30	9	--	35	75	0.4	2.1	4.9	1.3	2.6	2.0	--	--	--	--	--	--	--	--	--	--	--
USNM E35252	2.1	--	--	--	19	20	7.8	19	50	0.5	1.2	2.4	0.8	1.6	2.0	--	23	6.6	--	--	14	4.8	13	3.9	--	--
USNM E35252b	3.5	--	--	--	28	24	14.0	29	85	0.4	2.4	6.0	1.2	2.9	2.4	--	25	8.9	22	10.9	15	4.6	--	--	--	--
USNM E11630	4.4	--	--	--	--	32	26.0	40	50	0.6	2.9	4.8	1.5	3.4	2.3	--	23	8.2	15	8.2	12	5.4	--	--	--	--
USNM E35224	5.7	--	--	--	34	--	--	--	65	0.6	2.8	4.7	1.4	3.2	2.3	--	15	5.9	24	8.9	15	4.8	14	4.0	--	--
USNM E35769	4.3	--	--	--	29	25	16.4	30	85	0.7	3.0	4.3	1.1	3.1	2.8	--	29	10.7	23	9.6	19	6.8	17	5.4	--	--
USNM E34799	4.2	--	--	--	38	24	12.9	37	50	0.2	2.1	10.5	1.1	2.3	2.1	--	18	6.0	20	8.9	10	2.1	--	--	--	--
USNM E389	--	--	--	--	--	--	--	39	60	0.5	2.9	5.8	1.4	3.1	2.2	--	--	--	--	--	--	--	--	--	--	--
USNM E35248	3.5	--	--	--	32	21	12.6	30	70	0.4	2.4	6.0	0.7	2.6	3.7	--	17	5.3	20	9.3	16	6.4	10	4.3	--	--
USNM E405	3.5	--	--	--	22	22	9.4	21	85	0.4	2.1	5.3	1.1	2.2	2.0	--	16	3.6	13	4.3	13	4.3	--	--	--	--
USNM E35261	3.7	--	--	--	26	25	15.4	38	70	0.7	1.8	2.6	1.3	2.5	1.9	--	27	8.7	27	9.6	12	3.9	--	--	--	--
BMNH 1888.11.9.76.A	4.6	1.2	3.8	2.4	28	28	19.2	40	80	0.7	2.9	4.1	1.6	3.1	1.9	1.6	23	6.1	--	--	--	--	12	3.6	10	3.3
BMNH 1888.11.9.76.B	5.0	0.9	5.8	2.9	28	25	16.0	41	80	1.0	3.4	3.4	1.6	3.7	2.3	1.4	--	--	--	--	21	8.0	--	--	--	--
BMNH 1888.11.9.78.A	6.4	1.1	5.6	4.6	51	--	--	36	--	0.3	3.7	12.8	1.1	4.1	3.6	1.4	--	--	20	8.3	20	7.7	13	4.0	14	4.7
BMNH 1888.11.9.78.B	5.4	1.4	3.9	2.9	54	--	--	--	--	--	--	--	--	--	--	1.4	26	10.1	--	--	--	--	--	--	13	3.6
BMNH 1888.11.9.78.C	4.3	1.4	3.1	2.4	52	25	14.7	44	--	--	--	--	--	--	--	1.3	--	--	--	--	--	--	--	--	--	--
BMNH 1888.11.9.77	5.0	1.6	3.1	3.0	52	27	13.6	28	--	0.4	2.4	5.6	1.0	2.9	2.9	1.6	18	5.9	20	5.5	17	6.2	12	4.2	--	--

Table 3. ***Lamprometra*** **spp. continued.**

Specimen #	CENTRODORSAL D (mm)	CENTRODORSAL Height (mm)	CENTRODORSAL D/H	ABORAL POLE Diameter (mm)	CIRRI Cirri #	CIRRI # Cirrals	CIRRI Cirrus L (mm)	ARMS Arm #	ARMS Ray L (mm)	BRACHITAXES IBr1 L (mm)	BRACHITAXES IBr1 W (mm)	BRACHITAXES IBr1 W/L	BRACHITAXES IBr2 L (mm)	BRACHITAXES IBr2 W (mm)	BRACHITAXES IBr2 W/L	br_{10} W (mm)	P_1 # Plrs.	P_1 L (mm)	P_2 # Plrs.	P_2 L (mm)	P_3 # Plrs.	P_3 L (mm)	P_4 # Plrs.	P_4 L (mm)	P_5 # Plrs.	P_5 L (mm)
L. palmata f. *brachypecha*																										
IRSCB 240	5.9	1.1	5.4	4.3	42	27	15.2	40	90	0.6	3.6	6.3	1.8	4.0	2.2	1.5	15	7.1	24	12.1	12	4.0	11	3.3	11	3.6
NSUOC 346	5.4	1.3	4.2	3.6	34	26	21.0	33	--	0.9	3.7	4.3	1.7	4.1	2.4	1.8	32	8.8	37	17.4	20	6.1	16	5.0	16	5.1
NSUOC 354	4.1	1.0	4.1	2.9	27	24	17.1	35	75	0.7	2.4	3.4	1.2	2.9	2.4	1.3	25	10.2	24	7.9	15	4.4	13	4.4	12	3.7
NSUOC 260	4.2	0.9	4.7	2.9	25	22	14.1	38	80	0.6	2.9	4.8	1.4	3.3	2.4	1.2	23	8.3	22	11.4	13	3.9	10	2.4	12	3.4
USNM E35370	5.4	1.3	4.2	3.4	30	26	16.5	40	80	0.6	3.1	4.9	1.6	3.7	2.3	1.3	26	8.3	--	--	19	4.1	13	3.1	13	2.6
NSUOC 344	2.8	0.6	4.7	1.9	16	17	8.8	16	60	0.6	1.8	3.2	0.9	2.1	2.3	1.0	22	10.4	23	12.9	15	5.5	11	3.1	12	2.6
Intermediate specimens																										
NSUOC 403	6.3	2.3	2.7	--	55	25	17.6	22	130	1.2	3.9	3.3	2.1	4.6	2.2	1.4	23	6.7	24	10.4	21	9.0	24	4.6	13	5.3
USNM E34827c	3.8			2.3	25	22	13.9	26	65	0.4	2.5	6.9	1.1	3.0	2.7	--	--	--	--	--	12	3.9	--	--	--	--
NSUOC 407	6.0	1.9	3.2	2.6	44	28	26.0	38	210	1.0	3.7	3.7	2.1	4.7	2.2	1.9	30	10.1	38	21.6	25	11.7	18	5.1	18	6.9
IRSCB 414	5.6	2.1	2.7	2.4	39	26	15.4	29	110	0.7	3.2	4.6	1.7	3.6	2.1	1.6	17	5.1	13	6.5	19	8.5	17	6.6	12	5.0
Dichrometra **spp.**																										
NSUOC 424	4.4	1.6	2.8	3.1	26	28	18.0	--	90	0.9	3.0	3.5	1.4	3.6	2.6	1.5	22	8.6	24	9.9	25	10.2	15	5.4	14	4.0
NSUOC 367	5.2	1.1	4.7	2.4	34	26	21.0	38	125	1.3	3.4	2.6	1.4	4.4	3.1	2.0	28	9.7	26	13.5	25	14.2	15	6.9	15	5.9
NSUOC 263	6.9	1.8	3.8	4.0	37	33	31.5	33	150	0.9	4.3	4.8	2.0	4.8	2.4	2.0	27	11.1	22	13.3		14.1	19	9.4	19	7.9
NSUOC 412	5.9	1.8	3.3	3.1	43	30	18.9	23	120	0.7	3.1	4.4	1.4	3.6	2.6	1.6	26	7.1	22	9.2	--	--	21	9.0	17	6.7
NSUOC 410	7.3	2.1	3.5	3.3	36	31	26.6	35	155	0.9	4.4	4.9	2.0	5.1	2.6	1.7	26	9.7	24	13.6	27	15.4	17	7.1	15	6.1
NSUOC 402	7.4	2.0	3.7	3.6	53	31	26.8	37	125	0.4	5.0	13.9	1.8	5.2	2.9	1.7	28	7.1	31	15.7	--	--	18	7.0	15	6.0
USNM E34717	4.7	--	--	--	42	28	--	39	140	0.7	3.6	5.1	1.8	4.1	2.3	--	26	8.2	26	10.4	30	15.0	22	8.2	--	--
NSUOC 364	4.3	1.3	3.3	2.7	31	21	13.9	20	115	0.6	3.1	5.2	1.4	3.4	2.4	1.8	26	8.8	25	9.6	26	11.1	17	5.9	15	4.4
Liparometra **spp.**																										
NSUOC 406a	6.3	1.7	3.7	2.7	45	30	27.4	36	170	0.9	3.6	4.0	0.9	4.3	4.6	1.7	35	12.0	35	16.4	32	15.1	18	6.6	17	6.3
NSUOC 406b	4.6	2.3	2.0	3.0	32	29	25.3	39	175	0.8	3.4	4.3	1.6	3.6	2.3	1.4	34	13.1	32	17.9	28	14.1	18	7.6	17	7.0
NSUOC 355	4.4	1.1	4.0	3.1	35	21	12.5	25	100	0.4	2.9	6.7	1.1	3.4	3.0	1.4	21	7.8	22	9.3	17	7.7	14	5.0	13	4.0
NSUOC 405	6.5	2.3	2.8	3.6	47	28	18.0	39	--	0.6	4.0	7.0	2.4	4.7	2.0	1.7	18	5.7	26	10.7	20	8.0	15	6.1	12	4.6
NSUOC 254	3.1	1.4	2.2	2.1	30	26	14.3	20	100	0.8	2.8	3.5	1.3	3.2	2.5	1.6	25	8.1	30	13.0	24	11.0	17	5.9	14	4.6
NSUOC 404	5.4	1.6	3.4	2.4	36	28	22.6	31	130	0.9	3.5	3.8	1.5	4.3	2.9	1.7	23	7.0	28	13.9	23	9.6	17	6.0	13	4.9
NSUOC 350	5.3	1.6	3.3	3.1	57	25	19.4	40	145	0.9	4.3	4.8	1.8	4.8	2.7	1.7	27	10.6	30	15.9	27	14.1	16	6.0	15	5.4
NSUOC 401	4.6	1.3	3.5	2.0	30	24	14.0	25	90	0.8	2.7	3.4	1.6	3.2	2.0	1.2	18	4.9	21	6.6	--	--	15	4.9	11	3.2

NSUOC designates Nova Southeastern University-Oceanographic Center.
CRRF designates Coral Reef Research Foundation.
USNM designates United States National Museum (now the National Museum of Natural History).
BMNH designates the British Museum of Natural History.
D Indicates the diameter.
D/H indicates diameter (D) divided by height (H), of centrodorsal.
L Indicates the length of cirrus, brachitaxes ossicles, rays or pinnules.
W indicates the width of brachitaxes ossicles, or br_{10}.
W/L Indicates the width (W) divided by the length (L), of brachitaxes ossicles.
Plrs. Indicates pinnulars

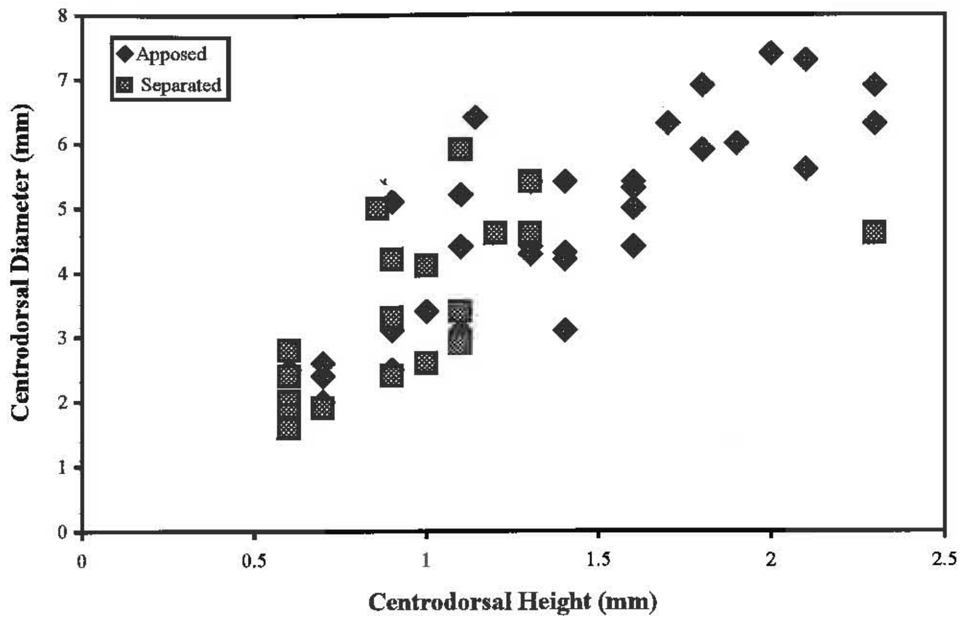


Figure 59. *Lamprometra palmata*. Plot of centrodorsal diameter against height for specimens with apposed lateral adambulacral margins and separated margins.

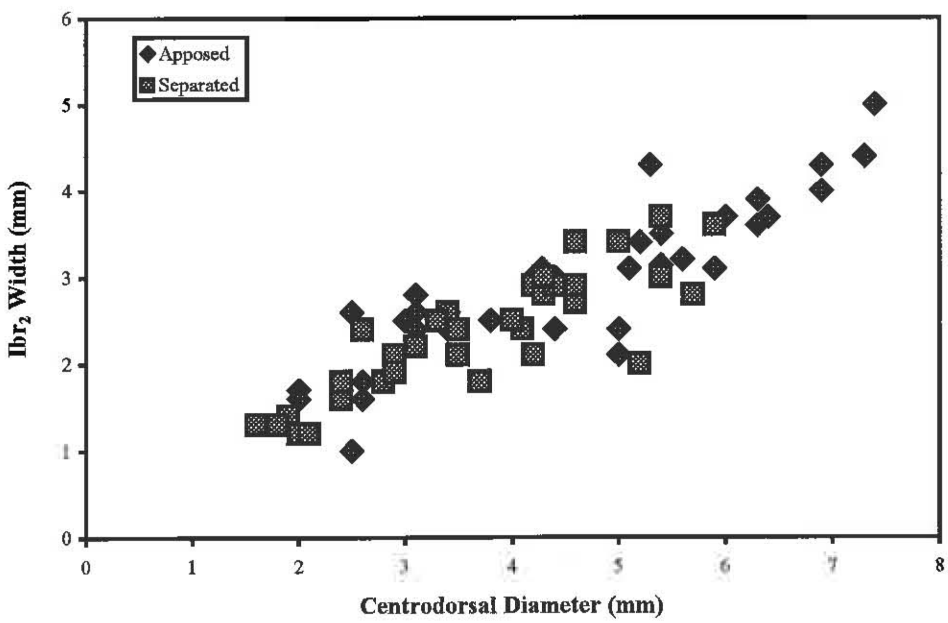


Figure 58. *Lamprometra palmata*. Plot of Ibr_2 width against centrodorsal diameter for specimens with apposed lateral adambulacral margins and separated margins.

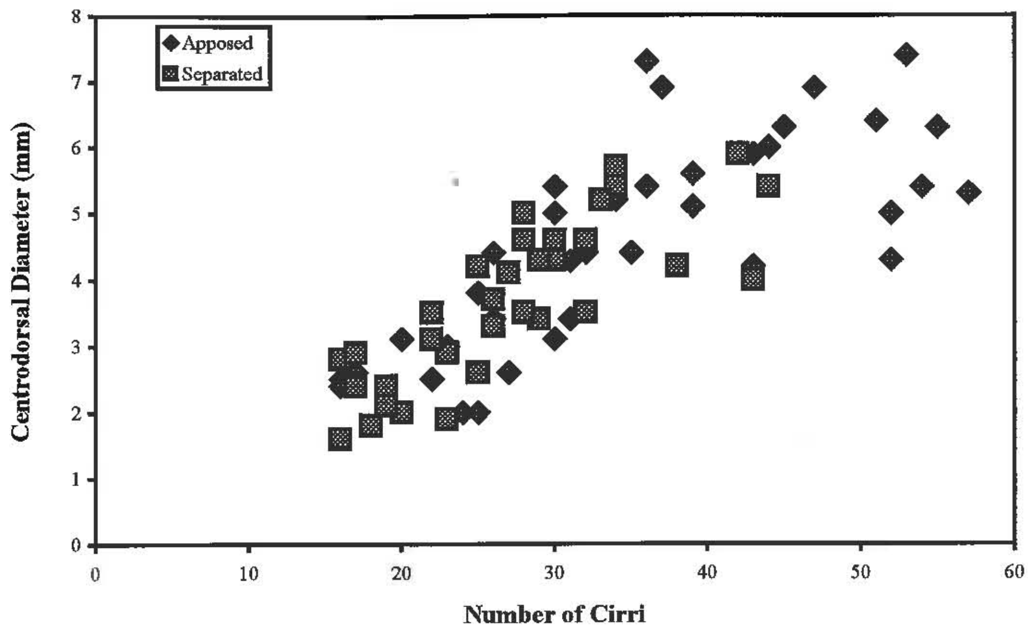


Figure 61. *Lamprometra palmata*. Plot of centrodorsal diameter against number of cirri for specimens with apposed lateral adambulacral margins and separated margins.

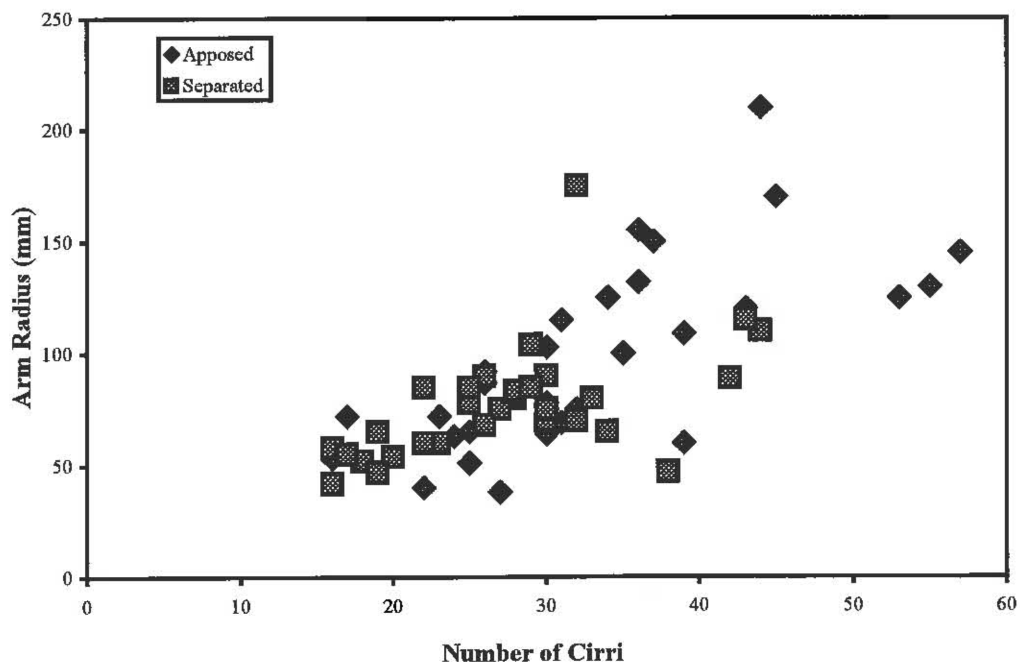


Figure 62. *Lamprometra palmata*. Plot of arm radius against number of cirri diameter for specimens with apposed lateral adambulacral margins and separated margins.

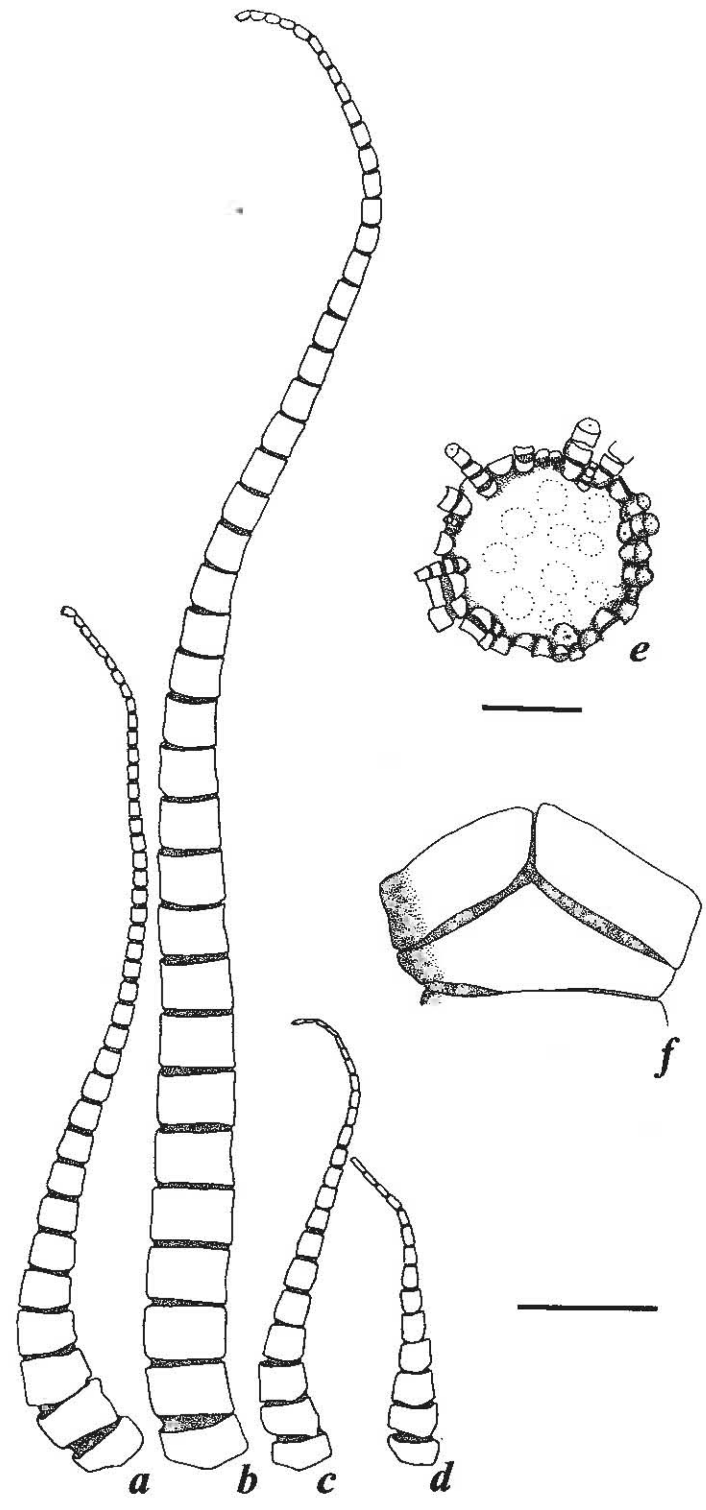


Figure 63. *Lamprometra palmata* form *brachypecha*. Figs. a-d & f from specimen NSUOC 346. a. P_1. b. P_2. c. P_3. d. P_4. e. Centrodorsal, in aboral view, IRSCB 240. f. Lateral adambulacral margins of brachitaxis ossicles. Scale (upper): 3 mm; scale (lower): 2 mm.

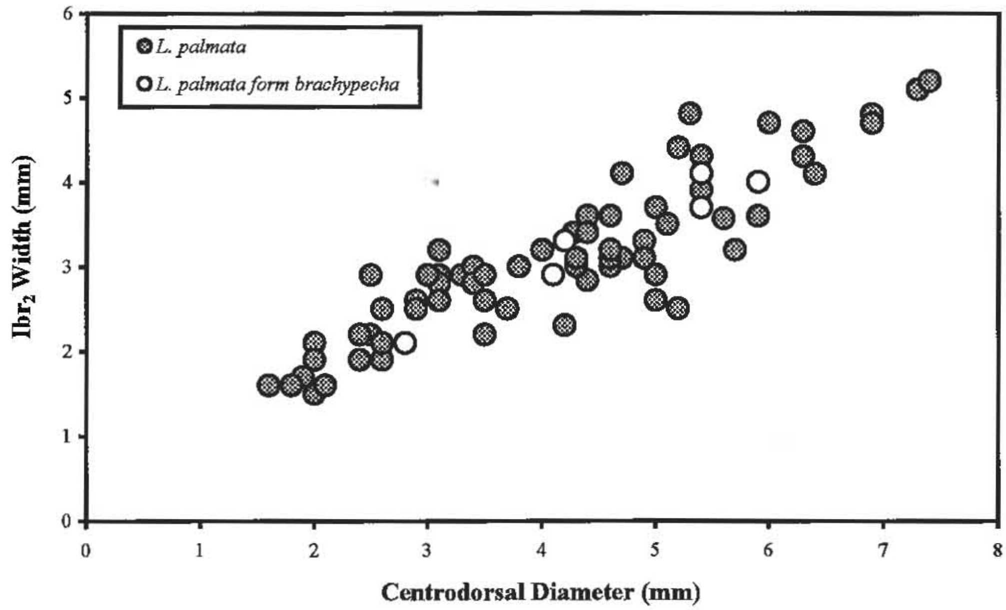


Figure 64. Plot of Ibr_2 width against centrodorsal diameter for *Lamprometra palmata* and *L. palmata* form *brachypecha*.

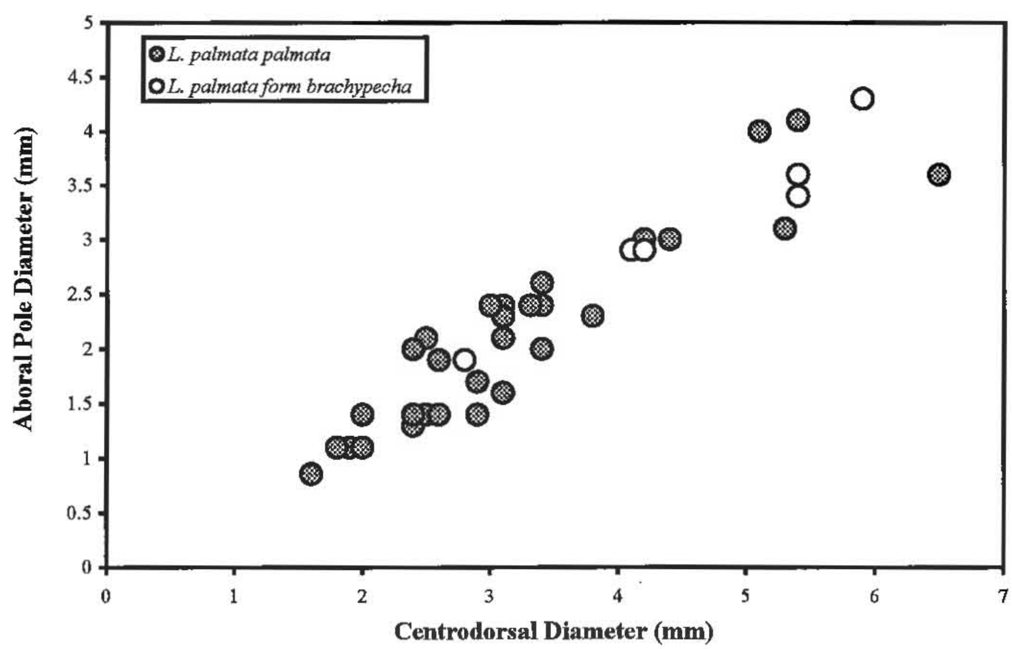


Figure 65. Plot of aboral pole diameter against centrodorsal diameter for *Lamprometra palmata* and *L. palmata* form *brachypecha*.

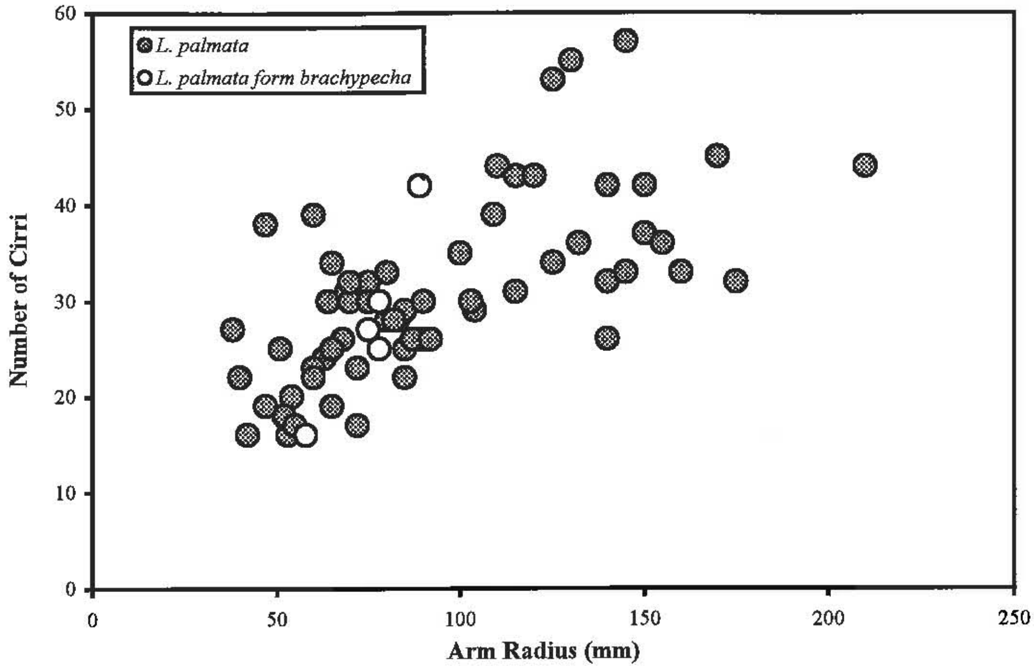


Figure 66. Plot of number of cirri against arm radius for *Lamprometra palmata* and *L. palmata* form *brachypecha* .

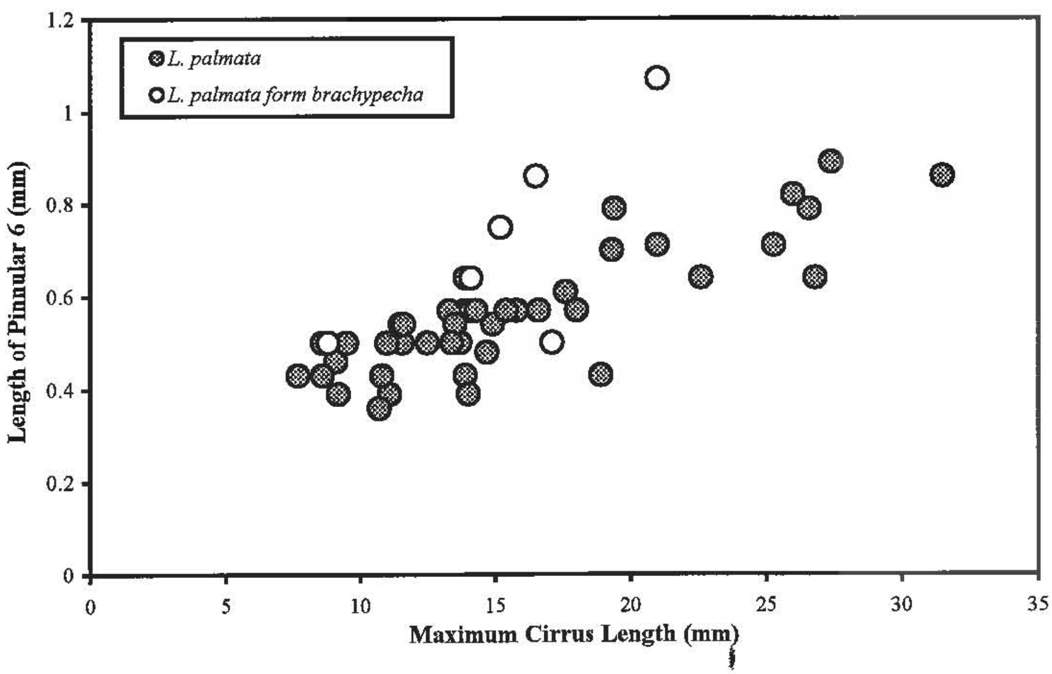


Figure 67. Plot of length of pinnular 6 from P_2 against maximum cirrus length for *Lamprometra palmata* and *L. palmata* form *brachypecha.*

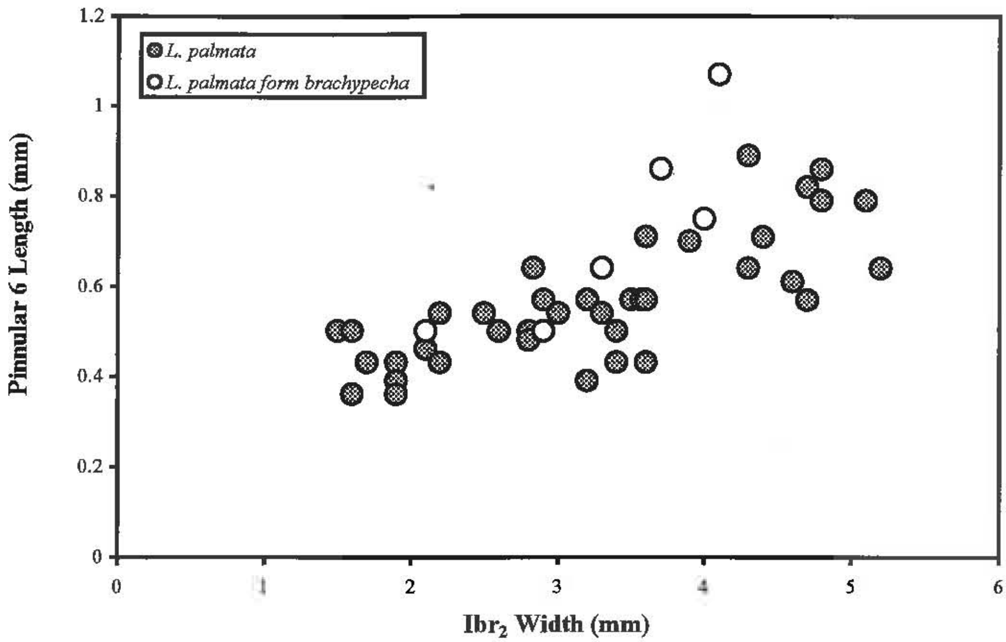


Figure 68. Plot of pinnular 6 from P_2 against Ibr_2 width for *Lamprometra palmata* and *L. palmata* form *brachypecha*.

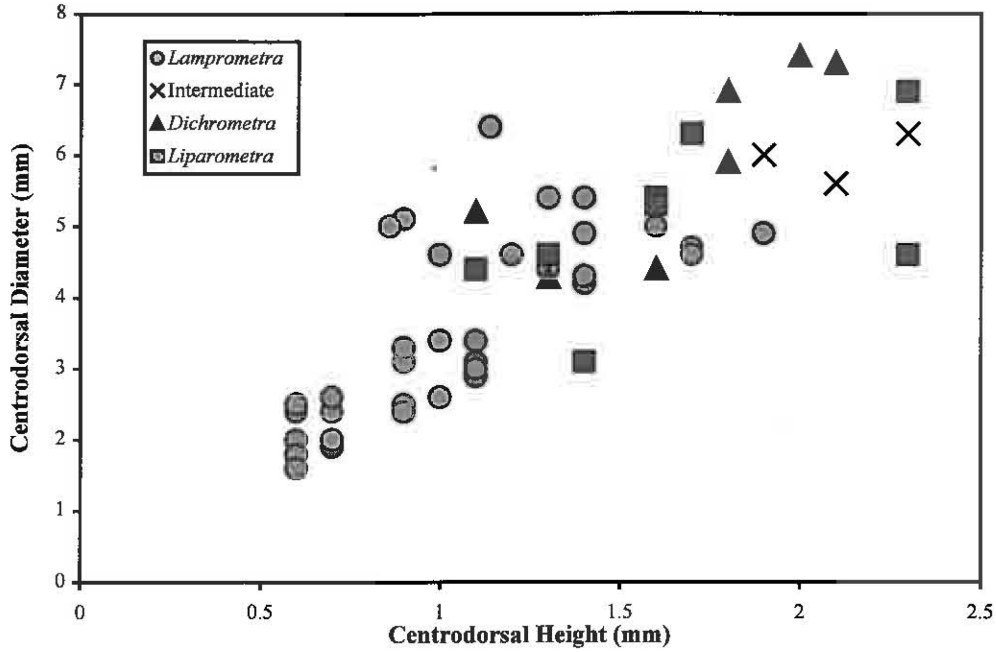


Figure 69. Plot of centrodorsal diameter against height for *Lamprometra palmata, Dichrometra* spp., *Liparometra* spp. and intermediate specimens.

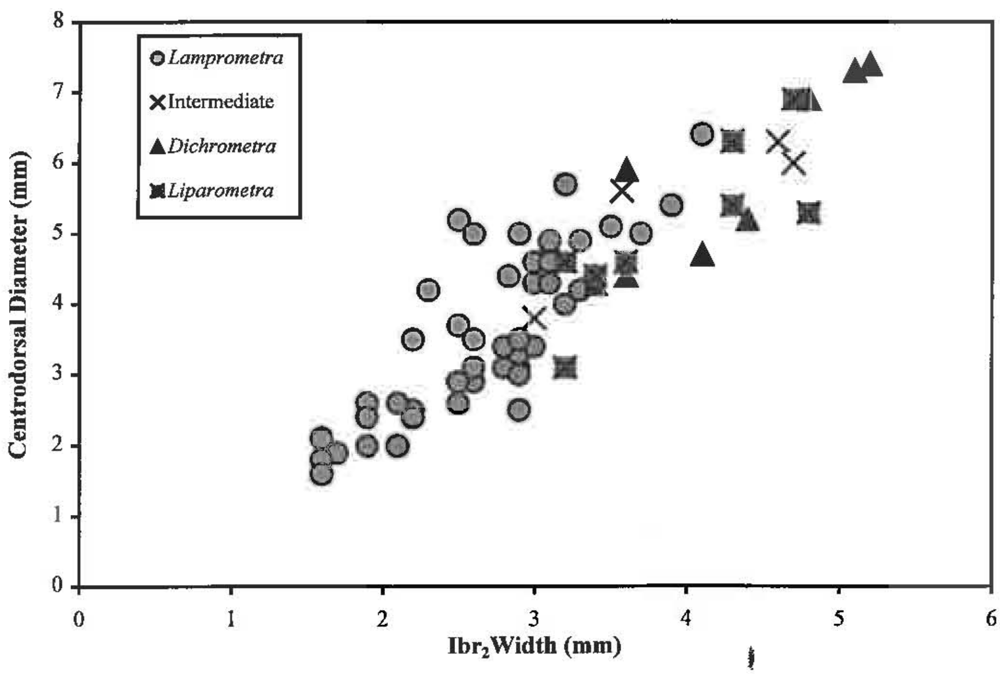


Figure 70. Plot of centrodorsal diameter against Ibr_2 width for *Lamprometra palmata, Dichrometra* spp., *Liparometra* spp. and intermediate specimens.

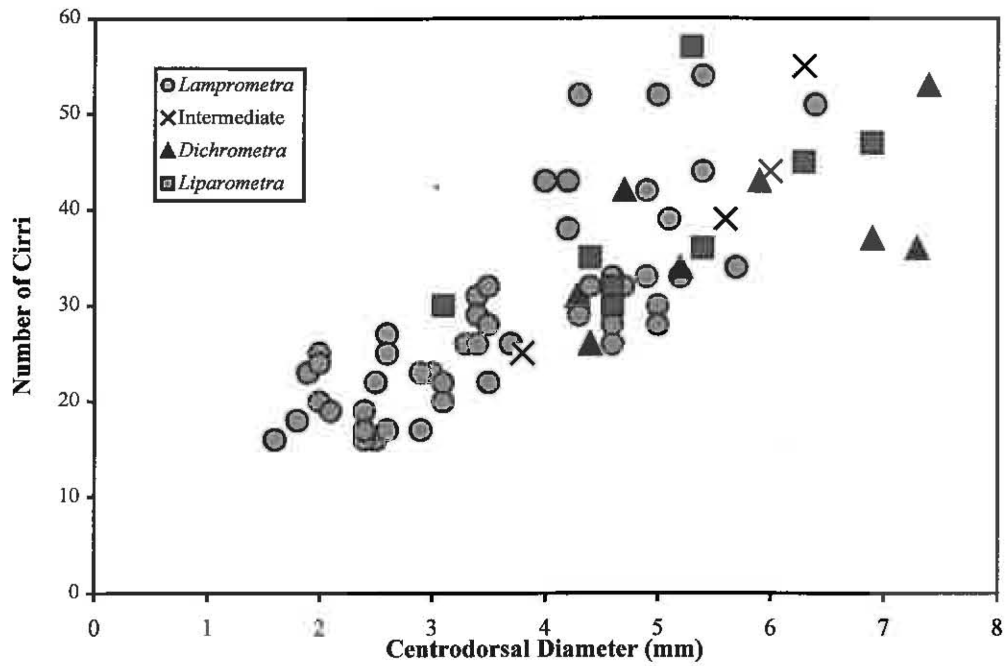


Figure 71. Plot of number of cirri against centrodorsal diameter for *Lamprometra palmata*, *Dichrometra* spp., *Liparometra* spp. and intermediate specimens.

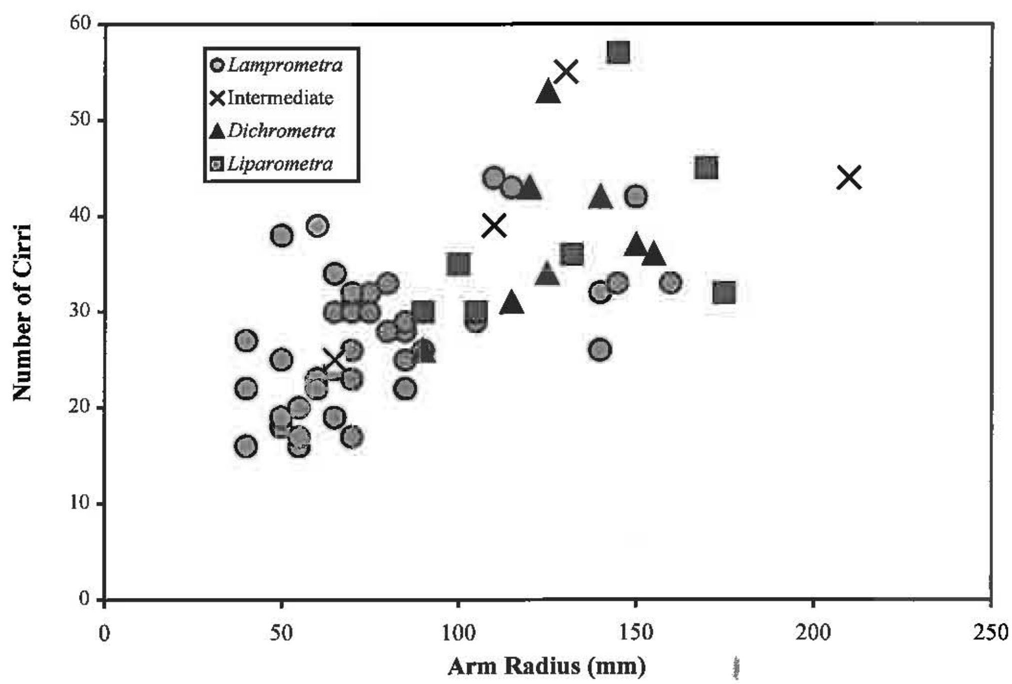


Figure 72. Plot of number of cirri against arm radius for *Lamprometra palmata, Dichrometra* spp., *Liparometra* spp. and intermediate specimens.

Incorrectly identified specimens.—The following specimens have been incorrectly identified as species of *Stephanometra* in the literature and are correctly identified as *Lamprometra palmata.* *S. oxyacantha* collected by the *Willebrord Snellius* (A. H. Clark, 1941:421) with P_1 23 mm long, of 39 pinnulars, and P_2 30 mm, with 23 pinnulars. The number of pinnulars and length of the pinnule indicate that this specimen is *L. palmata.* *S. oxyacantha,* pl. 47, Fig. 217(A. H. Clark, 1941), with a flat aboral pole and bearing carinate oral pinnules, composed of short pinnulars. *S. spicata* from the Red Sea (A. H. Clark, 1941:432), with P_2 of 17 pinnulars, "slender and delicate distally instead of stout and spinelike as usual." *S. indica indica* from the Gulf of Aqaba (A. H. Clark, 1941:438) with P_2 7 mm, of 14-16 pinnulars, slender and delicate terminally. *S. indica indica* from the Torres Strait (A. H. Clark, 1941:440) with a slender P_2 composed of 20 pinnulars of which the fourth and fifth are not elongate. *S. indica,* A. H. Clark (1941) pl. 51, in Figs. 233 & 234, with P_2 flexible and composed of short pinnulars.

Carpenter (1888:230) noted that large pinnules of *Antedon marginata* (=*S. indica protectus* according to A. H. Clark, 1941) are composed of short, uniform segments. Such short pinnulars are characteristic of *Lamprometra* not *Stephanometra.* In his key to the species, Carpenter again confused *Antedon marginata* (=*S. indica protectus*) with *Antedon conjungens* (=*L. palmata,* according to A. H. Clark). He placed both *A. marginata* (=*S. indica protectus*) and *A. conjungens* (=*L. palmata*) in the *Palmata* group in which P_2 had 25 pinnulars, none of which were elongated, while *tuberculata* (=*S. spicata*), *spicata* (=*S. spicata*) and *indica* (=*S. indica*), all with a stiff and styliform P_2 of 12-18 elongated pinnulars, were placed in a separate group.

The following specimens have been incorrectly identified as *Lamprometra* species or *Liparometra* species and are correctly identified as species of *Stephanometra.* Hartlaub (1891:113) noted five *L. palmata* specimens from Amboina that had a slender P_1 composed of 16-20 elongated pinnulars and P_2 10-12 mm long with 12-20 pinnulars mostly longer than broad.

The length of the pinnules, number of pinnulars and description of the pinnulars are all characteristic of *S. indica.*

Gislén (1922:74) described a small delicate form of *Liparometra grandis* from Bock's Station 47 with P_2 5 mm in length with 13 pinnulars, L/W 3.0, and P_3 3 mm long with 10 pinnulars. According to A.H. Clark (1941), *L. grandis* closely resembles *Lamprometra,* the only difference between the two being that P_2 equals P_3 in length in *Liparometera.* Gislén commented that relationships between pinnule length are a function of growth and that this specimen might be better referred to as a juvenile *L. palmata.* Characters of this specimen indicate that it is neither *Liparometra* or *Lamprometra*, but *Stephanometra indica.*

The aboral view illustration of *Lamprometra palmata* (Chen *et al.*, 1988:83, Fig. 21) with developed tabs and centrodorsal with encroaching cirri is characteristic of the genus *Stephanometra.* The flexible P_1, composed of short segments, is similar to that of *L. palmata.* P_2, however, composed of pinnulars in which distal ends bear spikes, is not characteristic of any member of the Mariametridae. The cirrus illustration with extremely uniform cirrals does not resemble that of either *Stephanometra* or *Lamprometra.* In addition, their key to the species (Chen *et al.* 1988, p. 75) describes *Lamprometra* as having flexible oral pinnules, which contradicts their systematic account in which P_2 is "stiff".

Finally, Kogo's (1998:62, Fig. 49) illustration and description of the centrodorsal and division series of *S. spicata* favor *Stephanometra.* However, both the pinnule illustration and description are characteristic of *Lamprometra palmata* with its flexible pinnules, pinnulars barely longer than broad and P_2 composed of more than twenty-three pinnulars.

CONCLUSION

The genus *Stephanometra* is a widespread and abundant component of Indo-Pacific reef communities. A generic revision was undertaken because current species descriptions are muddled and in need of clarification, and the relationship of *Stephanometra* to other members of its family is also unclear. This project concluded the following.

The genus *Stephanometra* is re-diagnosed as follows: Mariametridae with centrodorsal convex discoidal with gently sloping sides; cirrus sockets encroaching on aboral pole; brachitaxes well-separated; brachitaxis ossicles bearing rounded adambulacral processes parallel or oblique to the longitudinal axis of the ossicle and producing characteristically scalloped lateral or knobbed margins; less than 40 cirrals; distal cirrals with prominent aboral spine or slight aboral carination; one or more pairs of oral pinnules with reduced ambulacral groove, flat articular facets, conical tip, and with most pinnulars 2-3 times longer than broad.

Direct morphological examination, principal component analyses and cladistic analyses all reduce the number of recognized species in *Stephanometra* from six to two. *S. echinus* is a synonym of *S. tenuipinna*. *S. spinipinna*, *S. spicata* and *S. oxyacantha* are treated as synonyms of *S. indica*.

S. tenuipinna and *S. indica* are distinguished on the basis of several characters. Characters of *S. tenuipinna* include: prominent distally directed aboral cirrus spines; P_1 to P_3, P_4 or P_5 robust, stiff and spinelike; proximal and distal pinnule facets with elongated triangular fossae; lateral margin of brachitaxis ossicles weakly swollen laterally or with well-rounded lateral processes. In contrast, characters of *S. indica* include: distal cirrals with weak to strong midaboral carination; P_1 flexible and slender; P_2 alone, or P_2 through P_3, P_4 or P_5, robust, stiff and spinelike, much larger than subsequent pinnules; pinnulars with flattened articular facets lacking triangular fossae; lateral margin of brachitaxis ossicles weakly swollen laterally or with thick rounded ridge-like extensions oriented obliquely to the longitudinal axis of the ray.

S. tenuipinna is typically banded concentrically in combinations of white or cream with rose, orange or reddish purple. In addition to the concentric banding, many specimens bear blotchy combinations of red, pink or orange with white dots on the centrodorsal, cirri and division series ossicles. *S. indica* specimens do not exhibit this blotchy coloration, but maintain the concentric banding. Banding is formed by alternating colors on arms and is expressed in white, tan, brown, gray, pink, orange or a combination of these colors. Concentric banding is also characteristic of *L. palmata* although, colors for this species include white, tan, dark brown, red/brown, green and pink.

Lamprometra is maintained as distinct from *Stephanometra* and is re-diagnosed as follows: Mariametridae with centrodorsal thin, flat, discoidal; radials partially or completely concealed by centrodorsal; cirrus sockets restricted to centrodorsal margin, not encroaching on broad aboral pole; brachitaxes separated or in close lateral apposition; brachitaxis ossicles thickened laterally, producing characteristically apposed margins, or weakly thickened with margins not apposed; cirri composed of <35 cirrals, distal cirrals smooth or bearing aboral carination developing into a triangular spine; P_2 and P_b enlarged, with reduced ambulacral groove and a finely flagellate tip; pinnulars barely longer than broad; articular facets normally developed.

L. klunzingeri is considered a junior synonym of *L. palmata*. *L. palmata gyges* is an infrasubspecific variation of *L. palmata*. A small number of specimens of *L. palmata* form *brachypecha* suggest that it may be a distinct taxon.

Morphologic and meristic data indicate that *Lamprometra*, *Liparometra*, and *Dichrometra*, which are based solely on the relation among the lengths of P_1, P_2, and P_3, are very closely related to each other and possibly synonymous.

Results presented in this study provide a stepping stone for future research. Future studies should concentrate on molecular systematics. Additional studies will lend greater support to the relationships within the mariametrids.

GLOSSARY

Adapted from Messing and Dearborn, 1990.

Aboral. Away from or opposite to surface bearing mouth or ambulacrum.

Adambulacral. Toward, ambulacrum-bearing surface of ray, arm or pinnule.

Ambulacral groove. Furrow in oral surface of tegmen, arms and pinnules lined with tracts of cilia and serving to convey food to mouth.

Ambulacrum. Simple or branched, elongated area on oral surface of body, extending radially from mouth onto tegmen, arms and pinnules, overlying radial water vascular canal and consisting of groove, marginal lappets and podia.

Arm. Unbranched, linear series of ossicles arising from radial ossicle of an unbranched ray, or from distal most axillary of a branched ray.

Articular face (or facet). Usually sculptured surface of an ossicle serving as attachment site for ligaments, or ligaments and muscles, that join successive ossicles in a series.

Articulation (=Joint). Flexible to nearly immovable union of successive ossicles in a series.

Axillary (=Axil). Brachial bearing two distal articulations and representing the branching point of a ray.

Basal. Any of five interradial plates forming a circlet aboral to the radial circlet.

Brachial. Ossicle of an arm or brachitaxis.

Brachitaxis. Series of ossicles following a radial or axillary to and including the next axillary; series of ossicles between branches on a ray.

Calyx. Cuplike central skeleton consisting (in Recent species) of basal and radial circlets; reduced in comatulids.

Centrodorsal. Modified uppermost stalk ossicle attached to aboral surface of comatulids, retained after loss of larval stalk and commonly bearing cirri.

Cirral. Cirrus ossicle.

Cirrus (pl., *cirri*). Unbranched, usually hooklike, segmented appendage arising from stalk or centrodorsal.

Cirrus socket. Articular face on centrodorsal for attachment of cirrus.

Disk. Visceral mass that rests on the radial circlet and arm bases; sometimes its oral surface only (see *tegmen*).

Distal. Referring to a direction or position away from the aboral/oral axis, that is, toward tips of rays, arms and pinnules.

Distal pinnule. Pinnules distal to genital and oral pinnules.

Fossae. A depression or concavity on an articular facet in which muscles or ligaments are anchored.

Genital pinnule. Gamete-bearing pinnules; usually distal to one or several pairs of modified oral pinnules.

Interradial. Oriented between rays, that is, between structures associated with radial water vascular canals.

Ligamentary articulation. Joints bearing only ligaments, lacking muscle fibers; examples include synarthry and syzygy.

Muscular articulation. Joint bearing both muscle fibers and ligaments; opposed articular faces usually characterized by a semicircular aboral ligament fossae, transverse fulcral ridge, axial canal, paired interarticular ligament fossae and paired muscular fields. In comatulids, the great majority of arm articulations.

Oral (adj.). Toward or on the mouth-bearing surface.

Oral pinnule. Any proximal pinnule differentiated from more distal pinnules in structure, function, or both.

Ossicle. Any single calcareous segment of crinoid skeleton (e.g., cirral, basal, radial, brachial, pinnular).

Pinnular. A pinnule ossicle.

Pinnule. Unbranched, segmented appendage usually arising from alternate sides of successive brachials (except axillaries and proximal ossicle of pair joined by syzygy).

Podia (sing., *podium*). Tube feet; fine, fingerlike, external projections of the water vascular system that line ambulacral grooves and serve in food capture and respiration.

Proximal. Referring to direction or position toward aboral/oral axis, that is, toward base of ray, arm or pinnule.

Radial (n.). Most proximal ossicle of a ray, associated with any one of five radial water vascular canals that arise from the circumoral ring canal. (adj.) Associated or oriented with a ray.

Radial circlet (=Radial pentagon). Ring of five radials.

Ray. Radial ossicle together with all structures arising from it.

Synarthrial swelling (or tubercle). Rounded or inflated thickening of aboral surface of ossicles joined by synarthry.

Synarthry. Ligamentary articulation in which opposed articular faces bear an aboral/oral-oriented fulcral ridge separating two lateral fossae for attachment of ligament bundles; permits limited side-to-side movement of joint.

Syzygial pair. Two ossicles joined by syzygy; the proximal ossicle lacks a pinnule.

Syzygy. Rigid ligamentary articulation in which ridges radiating from center of one articular face are apposed to corresponding ridges on the other face; visible externally as a perforated line; serves as breakage point for autotomy.

Tegmen. Oral surface of visceral mass bearing mouth, anus and trunks of ambulacra proximal to free portions of rays.

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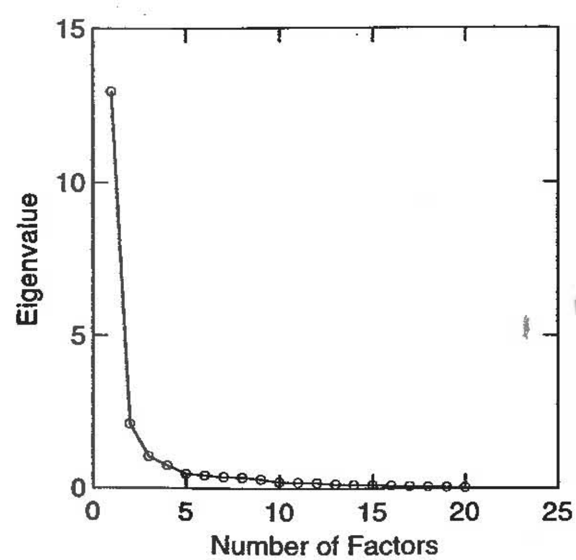
Appendix 1.

Component loadings for principal component analysis of morphometric data of *S. tenuipinna* (including *S. "echinus"*), *S. indica* (including *S. "spicata"*, *S. "oxyacantha"* *S. "spinipinna"* and intermediate specimens) and *Lamprometra palmata*.

Variable	Component 1	Component 2	Component 3
Cirrus length	0.9	0.4	0.2
Centrodorsal height	0.8	0.4	0.2
Aboral pole diameter	0.0	0.9	-0.3
Centrodorsal diameter	0.6	0.7	0.2
Length of Ibr_1	0.8	0.3	0.2
Width of Ibr_1	0.6	0.7	-0.1
Length of Ibr_2	0.5	0.4	0.4
Width of Ibr_2	0.6	0.7	0.0
Width of br_{10}	0.7	0.4	-0.2
Length of br_{10}	0.7	0.3	0.4
Number of cirri	0.4	0.7	0.1
Number of arms	0.4	0.8	0.0
Arm radius	0.8	0.4	0.1
P_1 length	0.8	0.4	0.0
P_2 length	0.8	0.4	-0.0
P_3 length	0.9	0.2	-0.1
P_4 length	0.9	0.2	0.0
P_5 length	0.9	0.2	-0.0
Length of pinnular 6 of P_2	0.7	0.2	0.5
Variance explained by rotated components	9.6	4.8	1.6
Percent of total variance explained	48.1	24.2	8.2

Scree Plot



Appendix 2. *Stephanometra* spp. Description of lateral adambulacral margins for *S. "echinus", S. tenuipinna, S. "oxyacantha", S. "spicata" ,S. "spinipinna", S. indica* and intermediate specimens.

	Axil (Ibr_2)			$IIbr_1$		
	strong/weak	**parallel/ oblique**	**proximal/ entire**	**strong/weak**	**parallel/ oblique**	**proximal/ entire**
S. "echinus"						
NSUOC 305	weak	parallel	entire	weak	parallel	entire
NSUOC 306	weak	parallel	entire	weak	parallel	entire
NSUOC 310	weak	parallel	entire	weak	parallel	entire
NSUOC 303	weak	parallel	entire	weak	parallel	entire
NSUOC 311	strong	parallel	entire	strong	parallel	entire
NSUOC 307	weak	parallel	entire	weak	parallel	entire
NSUOC 308	weak	parallel	entire	weak	parallel	entire
NSUOC 309	weak	parallel	entire	weak	parallel	entire
IRSCB 398	strong	parallel	entire	strong	parallel	entire
IRSCB 379	weak	parallel	entire	weak	parallel	entire
IRSCB 338	weak	parallel	entire	weak	parallel	entire
NSUOC 256	weak	parallel	entire	weak	parallel	entire
NSUOC 302	weak	parallel	entire	weak	parallel	entire
NSUOC 304	weak	parallel	entire	weak	parallel	entire
NSUOC 629	weak	parallel	entire	weak	parallel	entire
NSUOC 630	weak	parallel	entire	weak	parallel	entire
NSUOC 632	weak	parallel	entire	weak	parallel	entire
NSUOC 631	weak	parallel	entire	weak	parallel	entire
NSUOC 628	weak	parallel	entire	weak	parallel	entire
CRRF M48	weak	parallel	entire	weak	parallel	entire
S. tenuipinna						
NSUOC 312	weak	parallel	entire	weak	parallel	entire
USNM E35256	strong	parallel	entire	strong	parallel	entire
S. "oxyacantha"						
NSUOC 317	strong	oblique	proximal	strong	oblique	entire
NSUOC 320	strong	oblique	proximal	strong	oblique	entire
NSUOC 321	strong	oblique	proximal	strong	oblique	entire
NSUOC 316	strong	oblique	proximal	strong	oblique	entire
NSUOC 318	strong	oblique	proximal	strong	oblique	entire
IRSCB 43	strong	oblique	proximal	strong	oblique	entire
IRSCB 73	strong	oblique	proximal	strong	oblique	entire
IRSCB 230	strong	oblique	proximal	strong	oblique	entire
IRSCB 135	strong	oblique	proximal	strong	oblique	entire
IRSCB357	strong	oblique	proximal	strong	oblique	entire
IRSCB 232	strong	oblique	proximal	strong	oblique	entire
IRSCB 269	strong	oblique	proximal	strong	oblique	entire
IRSCB 276	strong	oblique	proximal	strong	oblique	entire
IRSCB 69	strong	oblique	proximal	strong	oblique	entire
IRSCB 70	strong	oblique	proximal	strong	oblique	entire
NSUOC 319	strong	oblique	proximal	strong	oblique	entire
IRSCB 374	strong	oblique	proximal	strong	oblique	entire
IRSCB 380	strong	oblique	proximal	strong	oblique	entire
NSUOC 315	strong	oblique	proximal	strong	oblique	entire
NSUOC 258	strong	oblique	proximal	strong	oblique	entire

Appendix 2. Continued.

	Axil (Ibr_2)			$IIbr_1$		
	strong/weak	**parallel/ oblique**	**proximal/ entire**	**strong/weak**	**parallel/ oblique**	**proximal/ entire**
S. "spinipinna"						
NSUOC 313	weak	oblique	proximal	weak	oblique	entire
NSUOC 314	strong	oblique	proximal	strong	oblique	entire
Gustav Paulay sp.	weak	oblique	proximal	weak	oblique	entire
"spicata/ oxyacantha"						
IRSCB 354	strong	oblique	proximal	strong	oblique	entire
IRSCB 316	very weak	oblique	proximal-slight	very weak	oblique	none visible
NSUOC 328	weak	oblique	proximal	weak	oblique	entire
NSUOC 326	weak	oblique	proximal	weak	oblique	entire
IRSCB 298a	strong	oblique	proximal	strong	oblique	entire
USNM E35376	strong	oblique	proximal	strong	oblique	entire
IRSCB 298b	strong	oblique	proximal	strong	oblique	entire
S. "spicata"						
NSUOC 327	strong	oblique	proximal	strong	oblique	entire
NSUOC 325	weak	oblique	proximal	weak	oblique	entire
NSUOC 324	strong	oblique	proximal	strong	oblique	entire
IRSCB 241	strong	oblique	proximal	strong	oblique	entire
IRSCB 316	strong	oblique	proximal	strong	oblique	entire
NSUOC 329	very weak	oblique	proximal	very weak	oblique	entire
NSUOC 323	very weak	oblique	proximal-slight	very weak	oblique	none visible
USNM E5269	weak	oblique	proximal	weak	oblique	entire
USNM E5269	strong	oblique	proximal	strong	oblique	entire
"indica/spicata"						
NSUOC 330	weak	oblique	proximal	weak	oblique	entire
NSUOC 338	strong	oblique	proximal	strong	oblique	entire
CRRF 1656K	strong	oblique	proximal	strong	oblique	entire
NSUOC 322	very weak	oblique	proximal-slight	very weak	oblique	none visible
IRSCB 248	strong	oblique	proximal	strong	oblique	entire
NSUOC 343	strong	oblique	proximal	strong	oblique	entire
NSUOC 341	strong	oblique	proximal	strong	oblique	entire
USNM E35079	strong	oblique	proximal	strong	oblique	entire
S. indica						
IRSCB 320	strong	oblique	proximal	strong	oblique	entire
IRSCB 422	strong	oblique	proximal	strong	oblique	entire
IRSCB 284	strong	oblique	proximal	strong	oblique	entire
NSUOC 342	strong	oblique	proximal	strong	oblique	entire
NSUOC 348a	weak	oblique	proximal	weak	oblique	entire
NSUOC 348b	weak	oblique	proximal	weak	oblique	entire
NSUOC 348c	weak	oblique	proximal	weak	oblique	entire
NSUOC 348d	weak	oblique	proximal	strong	oblique	entire
NSUOC 331	very weak	oblique	proximal-slight	very weak	oblique	none visible
NSUOC 334	weak	oblique	proximal	weak	slight	entire
NSUOC 349	weak	oblique	proximal	weak	oblique	entire
NSUOC 340	strong	oblique	proximal	strong	oblique	entire
NSUOC 333	strong	oblique	proximal	strong	oblique	entire
NSUOC 335	weak	oblique	proximal	weak	oblique	entire
NSUOC 339	strong	oblique	proximal	strong	oblique	entire
NSUOC 332	strong	oblique	proximal	strong	oblique	entire
NSUOC 337	weak	oblique	proximal	weak	oblique	entire

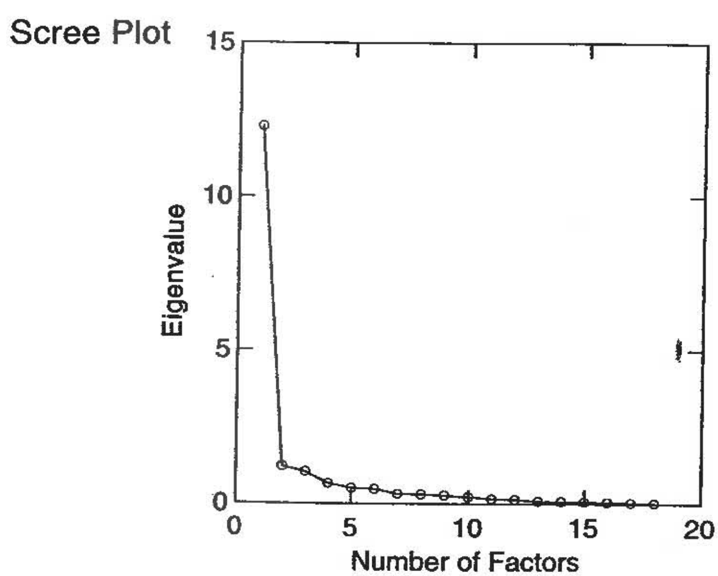
Appendix 2. Continued.

	Axil (Ibr_2)			$IIbr_1$		
S. indica	strong/weak	parallel/ oblique	proximal/ entire	strong/weak	parallel/ oblique	proximal/ entire
NSUOC331	very weak	oblique	proximal-slight	very weak	oblique	none visible
NSUOC334	weak	oblique	proximal	weak	slight	entire
NSUOC349	weak	oblique	proximal	weak	oblique	entire
NSUOC340	strong	oblique	proximal	strong	oblique	entire
NSUOC333	strong	oblique	proximal	strong	oblique	entire
NSUOC335	weak	oblique	proximal	weak	oblique	entire
NSUOC339	strong	oblique	proximal	strong	oblique	entire
NSUOC332	strong	oblique	proximal	strong	oblique	entire
NSUOC337	weak	oblique	proximal	weak	oblique	entire
NSUOC336	weak	oblique	entire	weak	oblique	entire
USNM E34960a	weak	oblique	proximal	weak	oblique	entire
USNM E34960b	very weak	oblique	entire	very weak	oblique	none visible
USNM E35050a	weak	oblique	proximal	weak	oblique	entire
USNM E35050b	strong	parallel	entire	strong	parallel	entire
NSUOC633	very weak	oblique	entire	very weak	oblique	entire

Appendix 3.

Component loadings for principal component analysis of morphometric data of *S. indica*, *S. spicata*, *S. oxyacantha*, *S. spinipinna* and intermediate specimens.

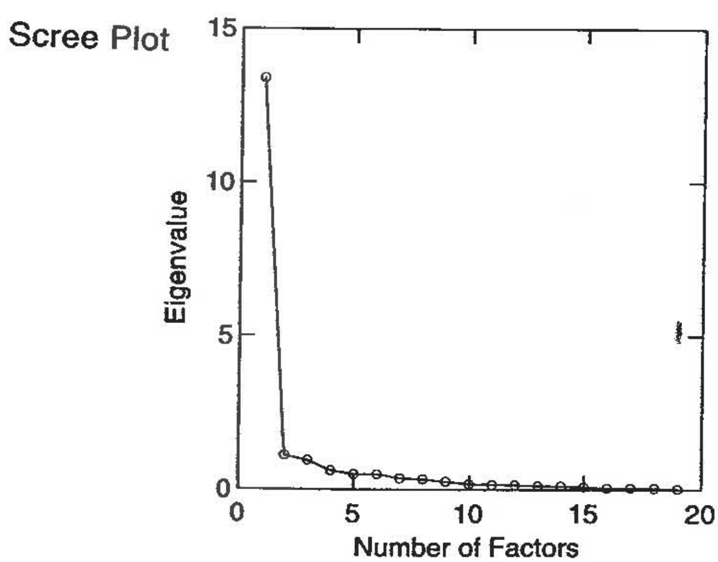
Variable	Component 1	Component 2	Component 3
Cirrus length	0.8	0.5	0.2
Centrodorsal height	0.7	0.5	0.2
Aboral pole diameter	0.1	0.8	0.4
Centrodorsal diameter	0.5	0.8	0.1
Length of Ibr_1	0.6	0.6	0.1
Width of Ibr_1	0.6	0.7	0.1
Length of Ibr_2	0.2	0.1	0.9
Width of Ibr_2	0.6	0.7	0.4
Width of br_{10}	0.7	0.3	0.4
Length of br_{10}	0.6	0.4	0.4
Number of cirri	0.4	0.8	0.1
Number of arms	0.4	0.9	0.1
Arm radius	0.8	0.2	-0.1
P_1 length	0.9	0.3	0.2
P_2 length	0.8	0.4	0.0
P_3 length	0.9	0.4	0.1
P_4 length	0.9	0.3	0.2
P_5 length	0.8	0.3	0.2
Length of pinnular 6 of P_2	0.8	0.3	0.1
Variance explained by rotated components	8.3	4.6	1.7
Percent of total variance explained	46.0	25.5	9.3



Appendix 4.

Component loadings for principal component analysis of morphometric data of *S. tenuipinna* (including *S. "echinus"*) and *S. indica* (including *S. "spicata"*, *S. "oxyacantha"* *S. "spinipinna"* and intermediate specimens)

Variable	**Component 1**	**Component 2**
Cirrus length	0.8	0.6
Centrodorsal height	0.6	0.7
Aboral pole diameter	0.4	0.5
Centrodorsal diameter	0.6	0.7
Length of Ibr_1	0.7	0.5
Width of Ibr_1	0.6	0.7
Length of Ibr_2	0.8	0.0
Width of Ibr_2	0.7	0.7
Width of br_{10}	0.8	0.5
Length of br_{10}	0.5	0.4
Number of cirri	0.0	0.9
Number of arms	0.5	0.8
Arm radius	0.9	0.3
P_1 length	0.8	0.4
P_2 length	0.6	0.6
P_3 length	0.7	0.7
P_4 length	0.8	0.5
P_5 length	0.7	0.5
Length of pinnular 6 of P_2	0.6	0.4
Variance explained by rotated components	8.1	6.3
Percent of total variance explained	42.8	33.4



Appendix 5.

Intermediate specimens. *Lamprometra/Liparometra* and *Liparometra/Dichrometra*

Material examined.— CHUUK ATOLL, MICRONESIA: NSUOC 407 (1), Fringing reef, E side of Yanagi I., (between Weno & Dublon Isl.) 07°25'N, 151°50'E, 3 m, 13 June 1993, C. G. Messing, coll. PAPUA NEW GUINEA: NSUOC 403 (1), Outside Pig I., Madang, 05°10'20"N, 145°51'53"E , 10.6 m, 16 July 1991, C. G. Messing coll; IRSCB 414 (1), Platier, 20 m, 20 July 1989, M. C. Lahaye, coll. AUSTRALIA: USNM E34827 (5+), Heron I., 1975, D. L. Meyer, coll., no additional data.

Dichrometra spp. specimens.

Material examined.— MALAYSIA: USNM E34717 (5+), 1976, D. L. Meyer, coll., no additional data; NSUOC 367 (1), Sabah, Borneo, Dive Center, Mabul I., 04°15'N, 118°38'E, 12 m, 24 Apr 1997, C. G. Messing coll.; NSUOC 364 (1) Mabul Wall, E side of Mabul I., 04°15'N, 118°38'E, 12 m, 22 Apr 1997, C. G. Messing, coll.; NSUOC 424, (1), Channel, E side of Mabul I., 04°5'N, 118°38'E, 26 m, 25 Apr 1997, C. G. Messing, coll.; NSUOC 263, (1), Barracuda Point, Sipadan, Sabah, Borneo, 04°07'N, 118°38'N, 28 m, 23 Apr 1997, C. G. Messing, coll. PHILIPPINES: NSUOC 410 (1), Sulu Sea (W end), N Tubbataha Reef, 09°49'N, 119°52'E, 9 m, 20 Apr 1995, C. G. Messing coll. PAPUA NEW GUINEA: NSUOC 412 (1), Jais Aben Reef, N side of Nagada Harbor, Madang, 05°09'29"S, 145°49'21"E, 5-8 m, 12 June 1992, C. G. Messing, coll.; NSUOC 402 (1), Outside Pig I., Madang, 05°10'20"N, 145°51'53"E , 16 July 1991, C. G. Messing coll.

Appendix 7. Continued.

Liparometra spp. specimens.

Material examined.— PHILIPPINES: NSUOC 355 (1), Sulu Sea (W end), N Tubbataha Reef, 09°49'N, 119°52'E, 9 m, 20 Apr 1995, C. G. Messing coll. CHUUK ATOLL, MICRONESIA: NSUOC 406 (2), Wreck of Fujikawa Maru, between Dublon and Uman Is., 07°20'N, 151°53'E, 10-20 m, 14 June 1993, C. G. Messing, coll. NSUOC 350 (1), N side of NE Pass., S of Quoi I., 07°31'38"N, 151°58'05"E, 9-12 m, 11 June 1993, P. Colin, coll. MALAYSIA: NSUOC 254 (1), Sabah, Borneo, Dive Center, Mabul I., 04°15'N, 118°38'E, 12 m, 24 Apr 1997, C. G. Messing coll. PAPUA NEW GUINEA: NSUOC 405 (1), Barrier I. Outside Magic Pass, Madang, 7.6 m, 16 July 1991, C. G Messing, coll.; NSUOC 404 (1), Jais Aben Reef, N side of Nagada Harbor, Madang, 05°09'29"S, 145°49'21"E, 3-4 m, 2 June 1992, C. G. Messing, coll.; NSUOC 401 (1), Padoz Reef, Madang, 05°09'S, 145°50'E, 8 m, 24 July 1991, C. G. Messing, coll.