7-1-2015

A Revision of the Genera of Charitometridae with Abruptly Expanded Genital Pinnules

Alois Romanowski
Nova Southeastern University, aloisromanowski@gmail.com

NOVA SOUTHEASTERN UNIVERSITY
HALMOS COLLEGE OF NATURAL SCIENCES AND
OCEANOGRAPHY

A Revision of the Genera of Charitometridae with Abruptly Expanded Genital Pinnules

By

Alois Romanowski

Submitted to the Faculty of
Nova Southeastern University Oceanographic Center
in partial fulfillment of the requirements for
the degree of Master of Science with a specialty in:

Marine Biology

Nova Southeastern University

July 2015

Thesis of
Alois R. J. Romanowski

Submitted in Partial Fulfillment of the Requirements for the Degree of

Masters of Science:

Marine Biology

Nova Southeastern University
Oceanographic Center

July 2015

Approved:

Thesis Committee

Major Professor :________________________________
Charles G. Messing, Ph.D.

Committee Member :____________________________
James D. Thomas, Ph.D.

Committee Member :____________________________
Jose V. Lopez, Ph.D.

Abstract

Feather star (Echinodermata: Crinoidea: Comatulida) family Charitometridae has not been revised since 1950. Molecular analysis, new specimens of existing species, and the discovery of a new species has revealed the need for a generic-level revision of those genera that exhibit abruptly expanded genital pinnules. A morphological study was conducted using 57 specimens representing 10 species of the Charitometridae. The genus *Poecilometra* is redescribed, and two species formerly placed in *Strotometra* have been moved to the genus based primarily on possession of pedunculate genital pinnules and a wide flange on the first pinnular of the proximal pinnules. A new species was described: *Poecilometra tibicinem* n. sp. The genus *Strotometra* is redescribed based on its cirri and laterally expanded genital pinnulars and its extant two species synonymized under *Strotometra parvipinna*. An undescribed stereomic structure was discovered on the proximal brachial articulations in the medial angles of the muscular fossae in some specimens, but its taxonomic significance remains unresolved.

Keywords: *Poecilometra tibicinem*, *Poeceilometra*, *Strotometra*, Taxonomy, Feather stars, Crinoid morphology, Crinoids

Acknowledgements

This has been a long road, and none of it would be possible without my advisor, Dr. Messing. He has kept me on that road with the patience of a bodhisattva and I cannot thank him enough for his help. Additional thanks go to my committee members, Dr. Thomas and Dr. Lopez.

Tracy Cowell, I wouldn't have finished this at all without your help, especially when it came to hell-crunch time. I love you.

I also recognize the help of many family and friends who've gotten me here. Special thanks go to: my mother, Dr. Carol Romanowski, for her unflagging support (and a few choice constructive criticisms); my father, Joseph Romanowski, for his sympathetic ear and his numerous suggestions (and don't forget the frozen foodstuffs); my older sister, Margaret Romanowski, for her help in processing my pictures (I owe you 2 lobsters!); my little sister, Jean Romanowski, for keeping me from going insane; Joshua and Maureen Appelt, my Florida uncle and aunt, for their invaluable advice; Daniel, Paola, and little Elizabeth King, for keeping me in place with well-timed reminders and Iron Maiden jokes.

I would also be remiss not to mention the NSU Oceanography Library team. Special thanks to Jaime Goldman: you're the best boss anyone could ever ask to have, and without your help and understanding I would never have completed this thesis.

Additional thanks are due to Dr. Patricia Blackwelder for her invaluable expertise and assistance with the scanning electron microscope, and for keeping me company during long stints in front of the SEM. Thanks also go to David Pawson (Smithsonian Institution), Marc Eleaume (Musée national d'Histoire naturelle, Paris) and Amy Baco-Taylor (Florida State University) for loans of specimens from their respective institutions and collections.

This research was partly funded through the Assembling the Echinoderm Tree of Life Project grant to C. G. Messing, National Science Foundation.

Contents

Table of Figures

Introduction

Crinoidea is the only extant class of Echinodermata characterized by a stalk. Members are commonly known as sea lilies and feather stars. The group is sister to the remaining four extant classes, collectively called Eleutherozoa (Smith 1984). The crinoid body consists of a cup-like central body (theca), from which five usually branched and featherlike rays arise. The rays and theca are supported by an endoskeleton of calcareous ossicles arranged chiefly in linear series and articulated via ligaments and muscles (Messing 1997, Roux et al. 2002). The digestive tract is coiled and, unlike in other extant echinoderms, both mouth and anus open on the upper surface, the latter on the tip of a tube or papilla (Jangoux 1982). All are selective suspension feeders that use fingerlike podia (tube feet) to capture zooplankton and detritus (Nichols 1960, Meyer 1982). Although they do not generate their own feeding current, they arrange their rays to take advantage of ambient flow orientation and strength (Macurda & Meyer 1974, Baumiller 2008). Many are mobile and actively seek suitable perches from which to feed (Meyer et al. 1984, Shaw & Fontaine 1990).

All extant crinoids are members of subclass Articulata, which arose from advanced cladid crinoids during the late Paleozoic and represent the only major taxon to survive the Permo-Triassic mass extinction (Simms 1993). Debate surrounds which genera should be considered basal, and a precise diagnosis remains elusive (Cohen et al. 2004, Rouse et al. 2013). However, the following features are usually attributed: cup incorporating infrabasal plates (at least in ancestral forms; mouth exposed; nerve canals enclosed within ray ossicles; muscular articulations present, and arms pinnate (modified from Hess & Messing 2011). Current taxonomy recognizes four orders. Members of Hyocrinida have a generally thin-walled theca, and a stalk cemented to the seafloor and composed of numerous similar ossicles. Most species occur at depths >700 m (Mironov & Sorokina 1998; Roux 2004; Tunnicliffe et al. 2015). In Isocrinida, the theca is reduced, and whorls of hooklike anchoring cirri arise at intervals along the stalk. They can detach from the seafloor and crawl with their arms (Baumiller et al. 1991; Birenheide & Motokawa 1994; Messing et al. 1988). Most occur at depths between 200 and 900 m (Messing et al. 1990). In Cyrtocrinida, the stalk is reduced or eliminated and the theca cements directly to hard substrates via an expanded base; they chiefly occur at depths between 300 and 1000 m (Hess & Messing 2011). Comatulida accounts for about 90% of the ~650 extant crinoid species. The majority take up a free existence as feather stars by discarding the postlarval stalk and are able to crawl and, in some cases, swim (Meyer & Macurda 1977, Shaw & Fontaine 1990). However, recent research includes in this order two formerly separate groups that retain the stalk as adults, probably via paedomorphosis: Bourgueticrinina and Guillecrinina (Rouse et al. 2013).

Crinoids are found throughout the world's oceans, except in the Baltic and Black Seas. The shallowest-living stalked species, the isocrinid *Metacrinus rotundus* Carpenter 1885, occurs in as little as 100 m off Japan, but most live in deeper-water (Roux et al. 2002). *Bathycrinus* Thomson, 1872, has been found deeper than 9,000 m, also off Japan (Mironov 2000; Oji & Kitasawa 2008). Comatulid feather stars are the only crinoids found in shallow water, some even in the lower intertidal zone (Messing 1997), but others reach depths of >5000 m (AH Clark and AM Clark 1967). The tropical Indo-West-Pacific supports the greatest crinoid richness, with the East Indian Archipelago from shallow water to ~1000 m housing about a third of all living species (Messing et al. 2000; Messing 2007).

Crinoid taxonomy remains largely based on morphology, and recent molecular analyses have revealed a need for substantial revision at all taxonomic levels (Cohen et al. 2004, Hemery et al. 2013; Rouse et al. 2013; Summers et al. 2014; Taylor et al. in press). The primary difficulty in describing a species comes from the crinoid's remarkable morphological plasticity. Because most of a crinoid body is suspension feeding apparatus, multiple environmental factors can create noticeable morphological changes within the same species (White 2000), leading to taxonomic oversplitting. A. H. Clark is responsible for establishing 310 species in a fifty-year period (e.g., AH Clark 1931, 1941, 1947, 1950, AH Clark & AM Clark 1967), often on the basis of one or a few broken specimens, sometimes juveniles (Rankin 2000). Diagnostic and descriptive terms are often either poorly defined, e.g., the "screwed" columnals of *Naumachocrinus hawaiiensis* AH Clark, 1912 (McKnight 1989) or relative, e.g., "strongly," "weakly" (AH Clark 1950).

Descriptions written during the late nineteenth and early twentieth centuries—the majority of known taxa—also suffered from imperfect understanding of what constitutes a species. Tropical western Atlantic *Crinometra brevipinna* (Pourtalés, 1868) (Comatulida: Charitometridae) has been split into four varietal types, two of which blend "insensibly" together. These four types are currently split into 19 varieties, 11 of which were treated as discrete species at some point (AH Clark 1950). Although all varieties (currently accepted as subspecies by the International Code of Zoological Nomenclature article 45.6.4) are currently placed under *C. brevipinna*, the morphological features of at least some, e.g., smooth *C. brevipinna* var. *pulchra* and heavily ornamented *C. brevipinna* var. *insculpta*, suggest that they could be distinct species.

Molecular techniques might solve such problems, but many species are known only from specimens too old to successfully sample for DNA. Among charitometrids, for example, many have not been collected since the Dutch *Siboga* (1899-1900) or US Fish Commission *Albatross* (decommissioned in 1921) expeditions. *Glyptometra macilenta* (AH Clark, 1909) is known from three specimens discovered by cable repair ships in 1929 and 1934. *Glyptometra septentrionalis* (AH Clark, 1911) owes its discovery to a private yacht owner in 1908 and another specimen found in 1915 (AH Clark 1950). Morphological analysis thus remains the only method of placing and revising such taxa.

Feather Star Morphology.---

As this study focuses on a group of deep-water feather stars currently classified within order Comatulida, this section specifically treats feather star morphology. Classification is based chiefly on the structure and arrangement of calcareous endoskeletal ossicles, which are usually visible, covered only with a thin epidermis. Small size generally requires examination of diagnostic features with a dissecting microscope. The following section on feather star morphology is adapted from Messing (2000) and Messing & Dearborn (1990). Figure 1 illustrates a generalized feather star.

Most comatulids possess five branched, feathery rays that extend from a central body. The ray bases support the disk, a visceral mass with an anus and mouth on its oral surface, called the tegmen. The rays also support the ambulacra: ciliated, open food grooves filled with extensions of the water vascular system called podia. These grooves converge on the mouth.

The ray bases rest on the centrodorsal, the largest skeletal ossicle. The centrodorsal may have many shapes, many of which may be diagnostic. The centrodorsal bears sockets for the hook-like cirri, prehensile segmented hooks used to anchor the comatulid to substrate. These sockets are may lose their cirri, becoming obsolete sockets; new cirri usually bud close to the base of the centrodorsal. The apex of the centrodorsal, the aboral pole, usually lacks cirrus sockets and may have different morphological characteristics depending on the species.

Cirri are segmented, unbranched, hook-like anchoring appendages composed of ossicles called cirrals. The last cirral forms a curved terminal claw, while the penultimate cirral possesses an opposing spine. The proximal and distal cirrals are usually short, the medial cirrals are often distinctly long.

The rays emanate from the base of the centrodorsal, starting with the five radials. They form a radial pentagon that is often hidden by the centrodorsal. Basal ossicles may be found between the radials with other interradial structures but are reduced in almost all feather stars. The brachial ossicles extend from the radials, starting with the division series, also known as the brachitaxes. The brachitaxes typically possess 2 or 4 brachials, ending with a branching ossicle called an axil, which gives rise to another pair of brachitaxes, a pair of unbranched arms, or one of each. The axis of the brachitaxes may be used to designate interior vs exterior arms, brachitaxes, or other structures; interior is closest to the axis and exterior is farthest from the axis.

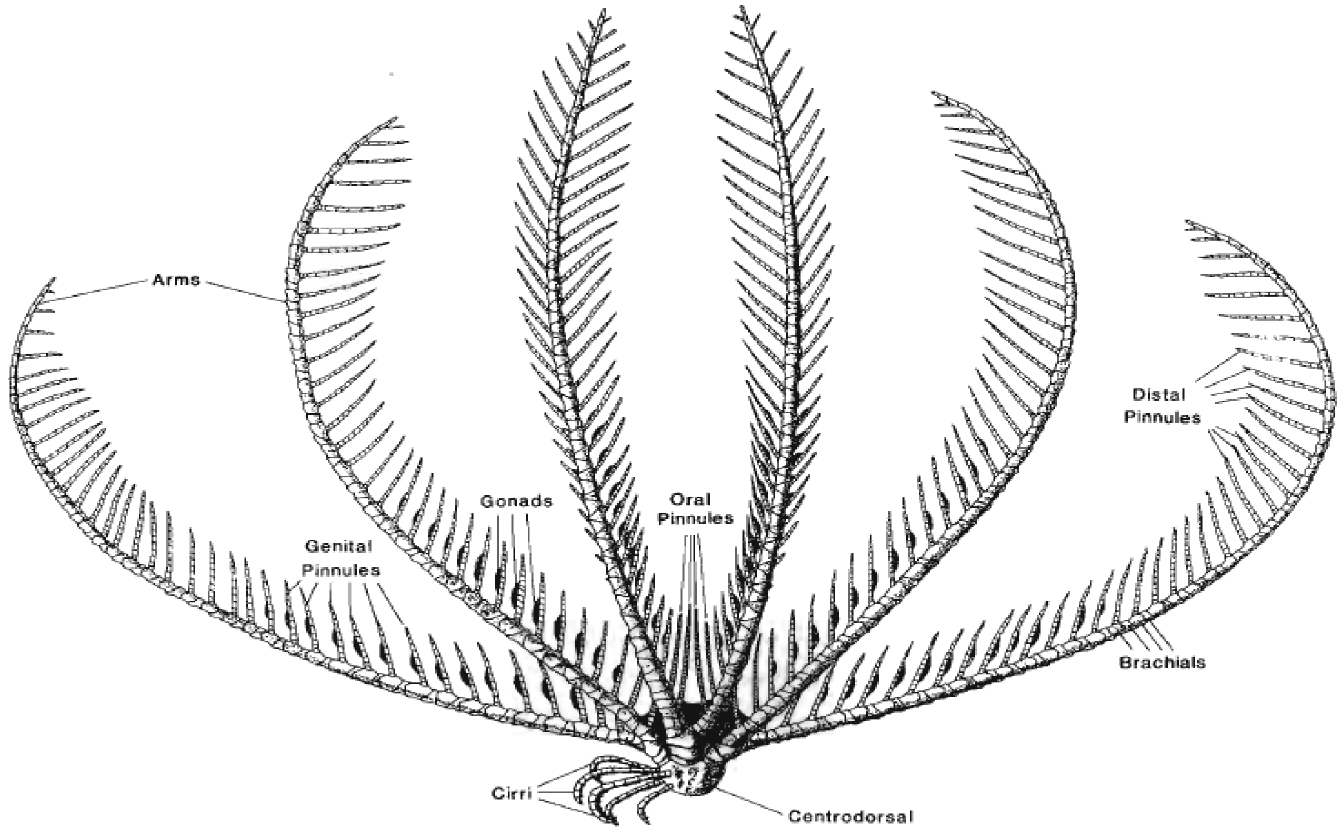

Figure 1. Lateral view of a feather star showing cirri, a centrodorsal, three rays, and pinnules (Messing and Dearborn 1990).

Most brachials are connected via muscular articulations composed of muscles and ligaments. These anchor in depressions called fossae in the articular face. Each articulation is composed of a pair of muscular fossae, a pair of interarticular ligament fossae, a transverse fulcral ridge, an axial canal, and a semicircular aboral ligament fossa. The axial canal is surrounded by a raised area called the periaxial.

Some brachials are connected by syzygies, rigid ligamentary articulations connected by interlocking ridges known as culminae. The flat areas between culminate are called crenellae. Syzygies appear externally as a perforated line and represent autotomy points. They usually appear between the third and fourth ossicles of brachitaxes and arm brachials and may be found at diagnostic intervals down the arm.

Synarthries connect the first two ossicles of a brachitaxes and the first two arm brachials, though they may be occasionally replaced by syzygies or modified into irregular cryptosynarthries. Synarthries are formed by a pair of semicircular ligaments separated by a single fulcral ridge oriented along the adambulacral/abambulacral axis of the articular face of the ossicle. The aboral surface may be swollen into a synarthrial swelling/tubercle.

The aboral ossicle surfaces, margins, or midaboral ridges of feather star brachitaxes and proximal arm brachials are often ornamented. These ornamentations may take the form of lamellae (laterally flattened plates), crenulae (small serrations), teeth, knobs, tubercles, and spines.

Pinnules are segmented, unbranched appendages that extend from alternating sides of the arm brachials. Pinnules are composed of small ossicles called pinnulars and possess smaller ambulacral grooves which feed into the main arm ambulacral groove, making them the primary food-collection site of the organism. The proximal pinnules are often modified as oral pinnules; their primary function is protecting the disc, so they may be long and flexible, robust and spiny, or may lack an ambulacral groove. Genital pinnules may be found after the oral pinnules; they bear the gonads. In most comatulids the genital pinnules are unmodified, but in the Charitometridae they are heavily modified and diagnostic of the family and some genera within the family.

Morphological Symbols and Terminology.---

Crinoid ossicles are extremely repetitive and difficult to differentiate in text. For this document, I will follow the examples set by Messing & Dearborn (1990) and Messing (2000). Figure 2 provides visual examples of crinoid taxonomic shorthand.

The number of cirri is given in roman numerals, e.g., ten cirri is represented as a X. Each cirral is given as C followed by an Arabic numeral, so the fifth cirral is C5. LW represents the ratio of the length of a cirral to its median width.

For the centrodorsal, DH is the ratio of its diameter to height.

Brachitaxes are differentiated by a Roman numeral representing its proximity to the radials followed by Br to represent the brachial. Individual brachials of a brachitaxes use br instead; the axil of a brachitaxes is referred to as ax instead of br. This is followed by an Arabic numeral representing the number of brachials in the division series, or a subscript Arabic numeral for an individual ossicle. Syzygies connect two brachials and are represented with a + sign between the two numbers representing the brachial; since these are often diagnostic, they are written out in parentheses after the total number of brachials. Therefore, an example of a second division series with four ossicles culminating in a syzygal pairing between the third brachial and an axil is given as IIBr4(3+4$_{)}$. The first brachial of this division series is written as IIbr$_1$ and the axil is written as IIax$_{(3+4)}$.

The symbols for brachials after the division series are represented by lower-case br followed by a subscript Arabic numeral to represent their number. Syzygies once again are represented with the + sign, so the 3rd and 4th brachial connected by a syzygy is written as br$_{3+4}$. Brachials and division series may also be measured in terms of LW ratios, with L representing the length (in terms of greatest length measured along the ray) and W representing the median width across the ossicle.

Pinnules are abbreviated P. Interior pinnules are indicated by lower case letters while exterior pinnules are indicated by Arabic numerals. The fifth exterior pinnule would be represented by P5, and the fifth interior pinnule is Pe.

Previously, pinnulars have not been given any abbreviations (e.g., "fifth and sixth segments"). However, because this thesis examined extensively modified pinnulars; therefore a new shorthand symbol is given in terms of the range of modified pinnulars, written in Arabic numerals connected with a hyphen in a subscript parentheses. If a pinnule's placement on the arm is unknown, it can be noted with just the parenthetical. As an example, an eighth exterior genital pinnule with an abrupt expansion between the third and sixth pinnulars is be written as P8$_{(3-6)}$. If the placement of the pinnule is unknown, it can be written simply as P$_{(3-6)}$.

The surface bearing the mouth and anus is the oral surface, while the opposite side is the aboral surface. The oral/aboral axis is used to determine ossicle direction and position: proximal directs towards the centrodorsal or structural base, while medial directs towards the middle and distal directs away. Adambulacral directs towards the surface bearing an ambulacral groove, abambulcral directs away from the ambulacrum.

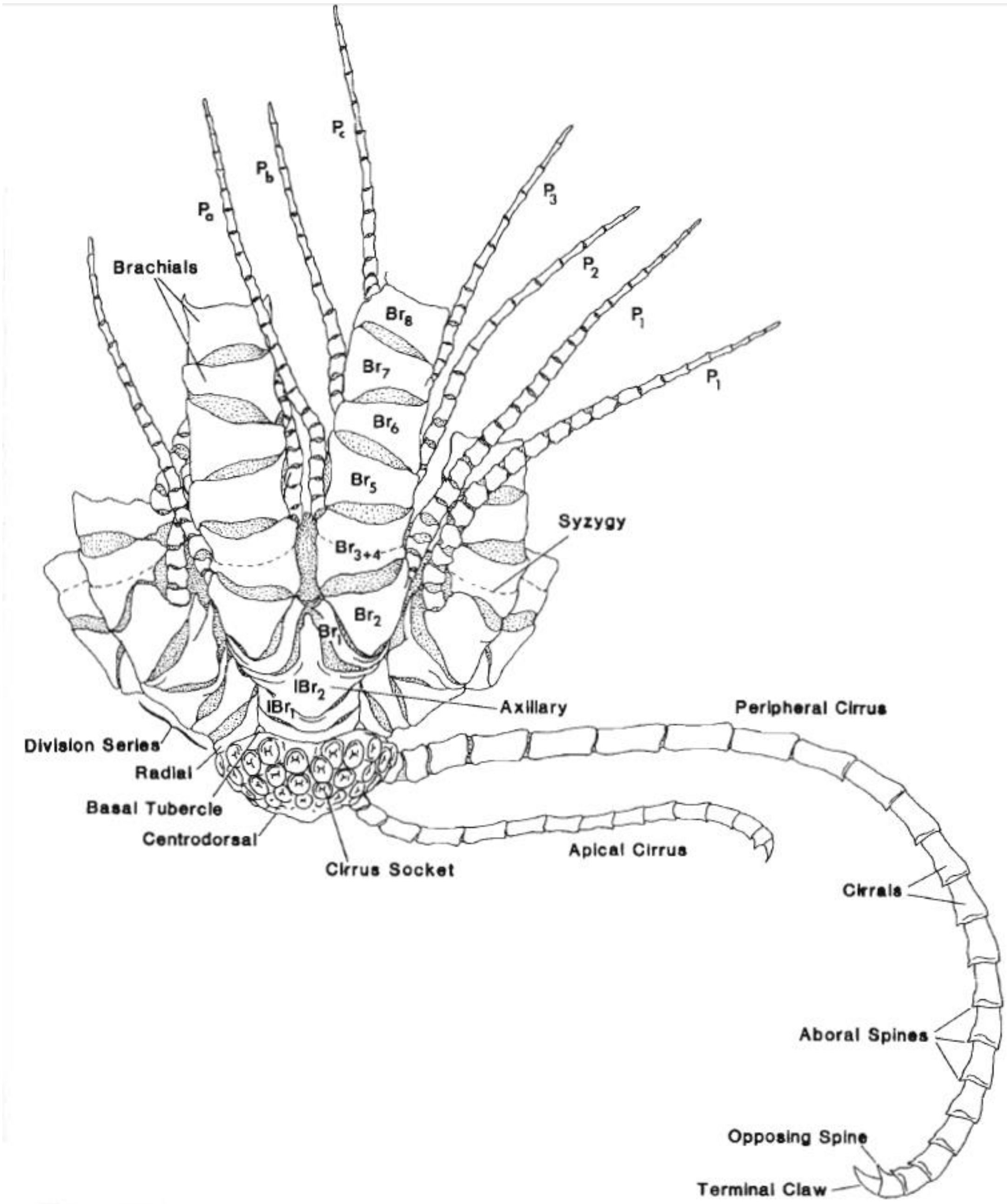

Figure 2. Lateral view of a feather star, including labeled morphological features in taxonomic shorthand (Messing and Dearborn 1990). Brachitaxes brachials are now br instead of Br; pinnules no longer feature subscript numerals or letters.

History of Family Charitometridae.---

Species eventually placed in family Charitometridae AH Clark, 1909, were first arranged by Carpenter (1888) within a hierarchy of groups within series in genus *Antedon*: Series II (ten-armed species)—*Basicurva* and *Acoela* groups; Series III (secundibrachs of two ossicles)—*Spinifera* group, and Series IV (division series 4(3+4))—*Granulifera* group. In 1905, other species later treated as Charitometridae were included in the *Brevipinna* (Minckert 1905) and *Savignyi* groups (Bell 1905). AH Clark (1907a) established two genera for species formerly placed in Carpenter's various groups: *Charitometra* AH Clark, 1907, with 19 species, and *Antedon incisa* (Carpenter, 1888), as the type species, and *Poecilometra* AH Clark, 1907, containing only the type species, *Antedon acoela* (Carpenter, 1884), and *A. scalaris* (AH Clark, 1907), both eventually placed in Charitometridae. He distinguished the genera on several morphological differences, including up to fifty arms in the former, and only ten arms with sharply expanded genital pinnules in the latter. AH Clark (1908a) first placed *Charitometra* AH Clark, 1907 in family Thalassometridae AH Clark, 1908, next grouped it with *Poecilometra* in the thalassometrid subfamily Charitometrinae with five new genera, *Glyptometra* AH Clark, 1909, *Strotometra* (AH Clark, 1907), *Crinometra* AH Clark, 1909, *Pachylometra* (AH Clark, 1909), and *Chlorometra* AH Clark, 1909, (AH Clark 1909a), and finally elevated Charitometrinae to family-level status as Charitometridae (AH Clark, 1911). This taxonomic shuffling led Hartlaub (1912) to reject the new classification and restore the included species to *Antedon* de Fréminville, 1811, following Carpenter (1888).

A. H. Clark (1916) added five more genera: *Crossometra* (AH Clark, 1909), *Perissometra* (AH Clark, 1909), and *Monachometra* AH Clark, 1916 (for species formerly in *Pachylometra* and *Glyptometra*), *Calyptometra* AH Clark, 1909 (for *Charitometra lateralis* [AH Clark, 1908]), and *Chondrometra* AH Clark, 1916 (for species formerly in *Chlorometra*). Gislén added *Diodontometra* Gislén, 1922, and proposed a full taxonomic revision of the family. He further pushed for the focus of taxonomy to move from differences in arm ornamentation and pinnule length to differences in cirri (Gislén 1922). This debate sparked a detailed look into what morphological characters were relevant and useful. After review, AH Clark concluded that many standard characters used in differentiating the genera, including arm ornamentation and the type of genital pinnules, were unimportant taxonomic characters. AH Clark subsequently condensed the twelve genera of the Charitometridae into eight, subsuming *Diodontometra* under *Chlorometra*, and subsuming *Calyptometra, Crossometra*, *Perissometra*, and *Pachylometra* under *Glyptometra* (AH Clark 1950). AH Clark's (1950) final and major revision of the family and all of its included taxa divided the genera among two informal groups based on differences in genital pinnule structure: 1) tapering from more or less broadened proximal segments to a longer delicate distal portion (*Chondrometra*, *Crinometra, Monachometra,* and *Glyptometra*), versus 2) having two to four abruptly broader segments with a shorter slender tip (*Chlorometra, Strotometra, Poecilometra,* and *Charitometra*). Within these two groups, distinguishing features at the generic level include compressed versus rounded arms, development of synarthrial tubercles, secundibrachials of two versus four ossicles, and relative lengths of oral and genital pinnules (AH Clark 1950).

The taxonomy of Charitometridae has not been altered since, except for the addition of *Monachometra kermadecensis* McKnight, 1977 and *Chondrometra crosnieri* Marshall and Rowe, 1981 and slight modifications of the familial and generic diagnoses in Hess and Messing (2011). However, the serial reassignment of many species among several genera as outlined above; the synonymy of numerous nominal species (e.g., *Diodontometra bocki* Gislen, 1922 under *Chlorometra garrettiana* [AH Clark, 1907]; *Pachylometra smithi* [AH Clark, 1908] and *Pachylometra selene* AH Clark, 1911 under *Glyptometra distincta* [Carpenter, 1888]), and the similarly fine distinctions separating species of *Glyptometra* on one hand and varieties of *Crinometra brevipinna* on the other, all reflect the still problematic state of character identification and application at both generic and specific levels. As an example, with respect to the first order distinguishing feature within the family, McKnight (1975) noted enlarged genital pinnules but often ignored them in favor of characteristics of the cirri (McKnight 1977b, 1977c, 1989). However, he did use the size of the expanded genital pinnules to distinguish between *Charitometra incisa* (Carpenter, 1888) and *C. basicurva* (Carpenter, 1888) (McKnight 1977a), while Kogo (1998) used genital pinnule structure as the first key characteristic for identifying three species of Charitometridae in Japanese waters, but did not note the expanded genital pinnules in his description of *Strotometra hepburniana* (AH Clark, 1907).

Hess & Messing (2011, p. 112-113) diagnosed the family as follows: "Centrodorsal hemispherical, conical, or truncated conical to discoidal with rounded or flattened, cirrus-free, commonly rugose or tuberculate aboral apex; some species of *Monachometra* with a dorsal star. No adoral radial pits. Cirrus sockets commonly with distinct articular tubercles and, in some genera, with marginal crenulae; sockets large, irregularly crowded or in 10 to 15 distinct columns (5 or 10 in *Chondrometra*). Cirri short and stout. Cirrals commonly fewer than 25, cylindrical or laterally compressed, without aboral spines, but sometimes carinate or with low distal tubercle. Rod-shaped basals exposed interradially or concealed. Subradial cleft commonly present. Radials concealed or narrowly exposed. Radial articular facet moderately sloping, not angularly bent. Muscle fossae high and narrow. Radial cavity narrow. Arms 10 to 33. Synarthry between brachials 1 and 2, syzygy between brachials 3 and 4, or between 1 and 2 in distal branches, and at intervals of 2 to 26 (commonly 6 to 11) distally. Arms aborally rounded or laterally compressed and carinate, commonly with rugose or tuberculate surface. First and second pinnules slender, with numerous short pinnulars. Genital pinnules may have segments broadened and covering gonad. Pinnules with distinct ambulacral covering plates."

With respect to placement of the family relative to other Comatulida, AH Clark (1908b) first grouped three genera, *Charitometra*, *Thalassometra* AH Clark, 1907 and *Tropiometra* AH Clark, 1907, in a "group" (later referred to as a suborder [AH Clark 1931]) Thalassometroida on the basis of their having small eggs and triangular pinnulars. Gislén (1924) placed Charitometridae with several other families in tribe Thalassometrida, characterized in part by cirrus sockets often sculptured; large, often narrow and high radial muscle fossae; ray bases and distal arms usually laterally flattened; arms terminating abruptly; pinnulars rectangular or triangular, and disk often plated. Within this grouping, he placed Charitometridae, Thalassometridae and Calometridae in subtribe Thalassometrida *sensu stricto*, distinguished by a lack of radial pits, and narrow synarthrial facets. AH Clark (1931) treated the group as superfamily

Tropiometrida, again characterized by triangular (prismatic), keeled pinnulars, and including Tropiometridae, an arrangement continued with little change in subsequent publications except for the additional recognition of Ptilometridae AH Clark, 1914 and Asterometridae Gislén, 1924 (AH Clark 1947, 1950). Rasmussen and Sieverts-Doreck (1978) maintained the same arrangement but renamed the group Tropiometracea and added two exclusively fossil families. Hess and Messing (2011) continued the same treatment—as Tropiometroidea (International Commission on Zoological Nomenclature [ICZN] article 29.2)(ICZN 1999)—and added one more fossil family. However, recent molecular analyses returned the superfamily as polyphyletic, with monophyletic Charitometridae sister to the five-armed Pentametrocrinidae (Rouse et al. 2013; Hemery et al. 2013).

Objectives.---

The character of the genital pinnules is a primary dividing feature within Charitometridae (see above). Examination of specimens suggests that the taxa with abruptly expanded genital pinnules followed by a short slender tip require taxonomic reevaluation. This group consists of four genera including a total of nine species: *Chlorometra* (1 species), *Charitometra* (2), *Poecilometra* (2) and *Strotometra* (4). It is unclear if the expansion of the genital pinnules is structurally similar and homologous among these genera, whether the existing genera constitute monophyletic taxa, or whether the species are currently correctly assigned. In addition, new material represents a new species collected by several French Expeditions to the southwestern Pacific. Extravagantly developed flanges on the first pinnular of the proximal pinnules suggest that this might represent a new genus. However, examination of existing material of two species of *Strotometra* has revealed rudimentary versions of such flanges, which have not been described in the literature.

This study proposes to revise the genera of the family Charitometridae with these expanded genital pinnules using morphological methods, as specimens suitable for molecular analysis are currently unavailable. Doing so will help properly define and place the new specimens.

It is also the goal of this thesis to include any new information about any of the family Charitometridae and to update species descriptions with additional features whenever possible. New specimens of existing species provided by the Muséum National d'Histoire Naturelle and Florida State University provide the opportunity to refine and update the morphological description of several species of Charitometridae.

Materials and Methods

This project examined 57 specimens of Charitometridae (Table 2); 21 were provided by the National Museum of Natural History (USNM) in Washington, D. C., 15 by the Muséum National d'Histoire Naturelle (MNHN), Paris; ten by the Copenhagen Zoological Museum (CZM); nine by Florida State University (FSU), two by the New Zealand Oceanographic Institute (NZOI), and one by Nova Southeastern University (NSU). Three specimens of *Glyptometra lateralis* (AH Clark, 1908), a specimen of *Monachometra patula* (Carpenter, 1888), and numerous specimens of *Crinometra brevipinna,* all from the group of charitometrids genera lacking abruptly expanded genital pinnules, were used for comparison of morphological characteristics.

Specimens were examined with a Wild M-5 dissecting microscope with camera lucida attachment. Photographs were taken with a Canon EOS Rebel T3 camera directed through a Leica M275 dissecting microscope. Images taken at multiple focal points were combined and rendered with Helicon Focus 6 Lite focus-stacking software and edited in a photo-editing program.

Some specimens were disassociated with full-strength commercial bleach (5% sodium hypochlorite solution) to examine brachials and pinnulars using scanning electron microscopy (SEM). Ossicles were rinsed in distilled water, dried and mounted on scanning electron microscopy stubs, sputter-coated with palladium, and examined with an ISI-DS130 scanning electron microscope operated at 10 KV. SEM pictures were taken and processed with ORION digital capture software and edited in a photo-editing program.

Table 1.—A complete list of examined specimens. [a]Species name is the name given on the jar at time of loan. [b]Lenders: Copenhagen Zoological Museum (CZM) , Florida State University (FSU), National Museum of Natural History (USNM), Musée national d'Histoire naturelle (MNHN), New Zealand Oceanographic Institute (NZOI), Nova Southeastern University (NSU). [c]In case of the depth given as a range, I have averaged the depth and rounded to the nearest 5m.

Species Name[a]	Lender[b]	Cat. no.	Year	Expedition Station	General Location	Depth (m)[c]	No. Specimens
Poecilometra acoela	CZM		1875	Challenger 214	Philippines	915	1
	FSU	2633	2011	NOAA Okeanos Explorer P4-256	Hawaii	1748	1
	FSU	2635	2011	NOAA Okeanos Explorer P4-256	Hawaii	1748	1
	FSU	2639	2011	NOAA Okeanos Explorer P4-256	Hawaii	1746	1
	FSU	2641	2011	NOAA Okeanos Explorer P4-256	Hawaii	1746	1
	FSU	2665	2011	NOAA Okeanos Explorer P4-257	Hawaii	1802	2
	USNM	E439	1875	Challenger 214	Philippines	915	1
Poecilometra scalaris	USNM	22629	1906	Albatross 4918	Japan	660	1
Strotometra priamus	CZM		1922	Danish Exp. to the Kei Isl.	Indonesia	370	2
	CZM		1922	Danish Exp. to the Kei Isl.	Indonesia	345	1
	MNHN	EcCs10304	1993	BATHUS 3 DW790	New Caledonia	700	1
	USNM	E3151	1922	Danish Exp. to the Kei Isl. St. 1	Indonesia	385	1
	USNM	E427	1899	Siboga 266	Indonesia	595	9
	MNHN	IE-2007-6012	2011	EXBODI DW3833	New Caledonia	475	1

Table 1.—Continued.

Species Name	Lender	Cat. no.	Year	Expedition Station	General Location	Depth (m)[a]	No. Specimens
Strotometra ornatissimus	MNHN	STRO81	1998	MUSORSTOM 10	Fiji	1075	1
	CZM	E2088	1899	Siboga 122	Philippines	1215	1
	NZOI	T243	1982		New Zealand	1035	2
Strotometra nsp.	MNHN	STRO57		NORFOLK 1 CP1271	New Caledonia	420	4
	MNHN	EcCh193	1985	MUSORSTOM 4 CP216	New Caledonia	500	1
	MNHN	EcCs10237	1978	VAUBAN DRO4	New Caledonia	400	3
	MNHN	IE-2007-5904	2011	EXBODI DW3784	New Caledonia	360	1
	MNHN	EcCh194	1985	MUSORSTOM 4 CP216	New Caledonia	400	1
Strotometra hepburniana	CZM		1911				1
	CZM		1898	Captain Schönau	Japan	180	1
	USNM	35692	1906	Albatross 4890	Japan	243	4
Strotometra parvipinna	CZM		1922	Danish Exp. to the Kei Isl. St. 56	Indonesia	245	3
	USNM	E3142	1922	Danish Exp. to the Kei Isl. St. 56	Indonesia	245	4
	USNM	E418	1900	Siboga 297	Indonesia	520	2
Glyptometra lateralis	FSU	2680	2011	NOAA Okeanos Explorer P4-257	Hawaii	1800	1
Monachometra patula	MNHN	IE-2007-6012	2011	EXBODI CP3833	New Caledonia	475	2
Crinometra brevipinna	NSU	CRI560	1965	W.E. Pequegnat 65-A-9-XX	Gulf of Mexico	132	1

Taxonomic section

Genus *Poecilometra* A. H. Clark, 1907a

Figures 3, 5-27; Table 1

Antedon (Part) P. H. Carpenter 1880:pl. 6, fig. 10

Poecilometra A. H. Clark 1907a:361; 1908d:245; 1908a:136; 1908c:211-212; 1909a:18; 1912b:9, 11, 25, 60, 225; 1918:172, 19.—Gislén 1928:9; 1934:18.--Hess and Messing 2011:115

Diagnosis.—Centrodorsal hemispherical or discoidal; cirrus sockets in irregular marginal rows or three rows and irregular columns; arms 10 or 20; brachitaxes and proximal brachials narrow and well separated or closely laterally apposed, gaps bridged by lateral flanges; distal border of the cirrals ƨ-shaped in lateral view; genital pinnules pedunculate, pinnulars expanded over gonad; $P_{(1)}$ of proximal pinnules with a weak to well-developed flange or flattened, curved tongue directed towards aboral side of arm.

Type species.—Antedon acoela (Carpenter, 1888).

Other included species.—*Antedon scalaris* (AH Clark, 1907)*; Strotometra ornatissimus* AH Clark, 1912*; Strotometra priamus* AH Clark, 1912*; Poecilometra tibicinem n. sp.*

Geographic distribution.—Northwestern, western, southwestern, and central Pacific Ocean.

Bathymetric distribution.—345 to 1800 m.

Remarks.—The genital pinnules are markedly pedunculate, that is, they consist of two to seven typical narrow basal pinnulars followed by three to eight abruptly expanded segments, and terminate in a series of four to ten abruptly thinner, much smaller pinnulars

(Fig. 3). Such genital pinnules are unique among charitometrids and appear to represent a synapomorphy. On this basis, *Strotometra priamus* and *Strotometra ornatissimus* are herein moved to *Poecilometra. Poecilometra tibicinem* n. sp., described below, has also similar pedunculate genital pinnules. A Maximum Likelihood analysis (combined CO1, 16S, 28S and 18S) placed this new species as sister to a clade composed of three *S. ornatissimus* terminals (Hemery 2011, Fig. 4). *Strotometra hepburniana* and *S. parvipinna*, two taxa that do not bear pedunculate genital pinnules, returned in a separate charitometrid clade as sister to *Glyptometra* sp. However, *Poecilometra acoela* and *P. scalaris* exhibit distinctively well-separated brachitaxis not present in *P. priamus, P. ornatissimus*, and *P. tibicinem* n. sp. (AH Clark 1950, and herein), though all five exhibit a lateral aboral flange on the brachitaxes and proximal ray ossicles. As a result, sequence data may place these latter three in a different sister clade, possibly requiring a new generic name, as *P. acoela* is the type species of *Poecilometra*.

Figure 3. Examples of pedunculate genital pinnules on a Hawaiian specimen of *Poecilometra acoela,* FSU-2665*.* a: reduced winglike flanges on $P_{(1)}$.

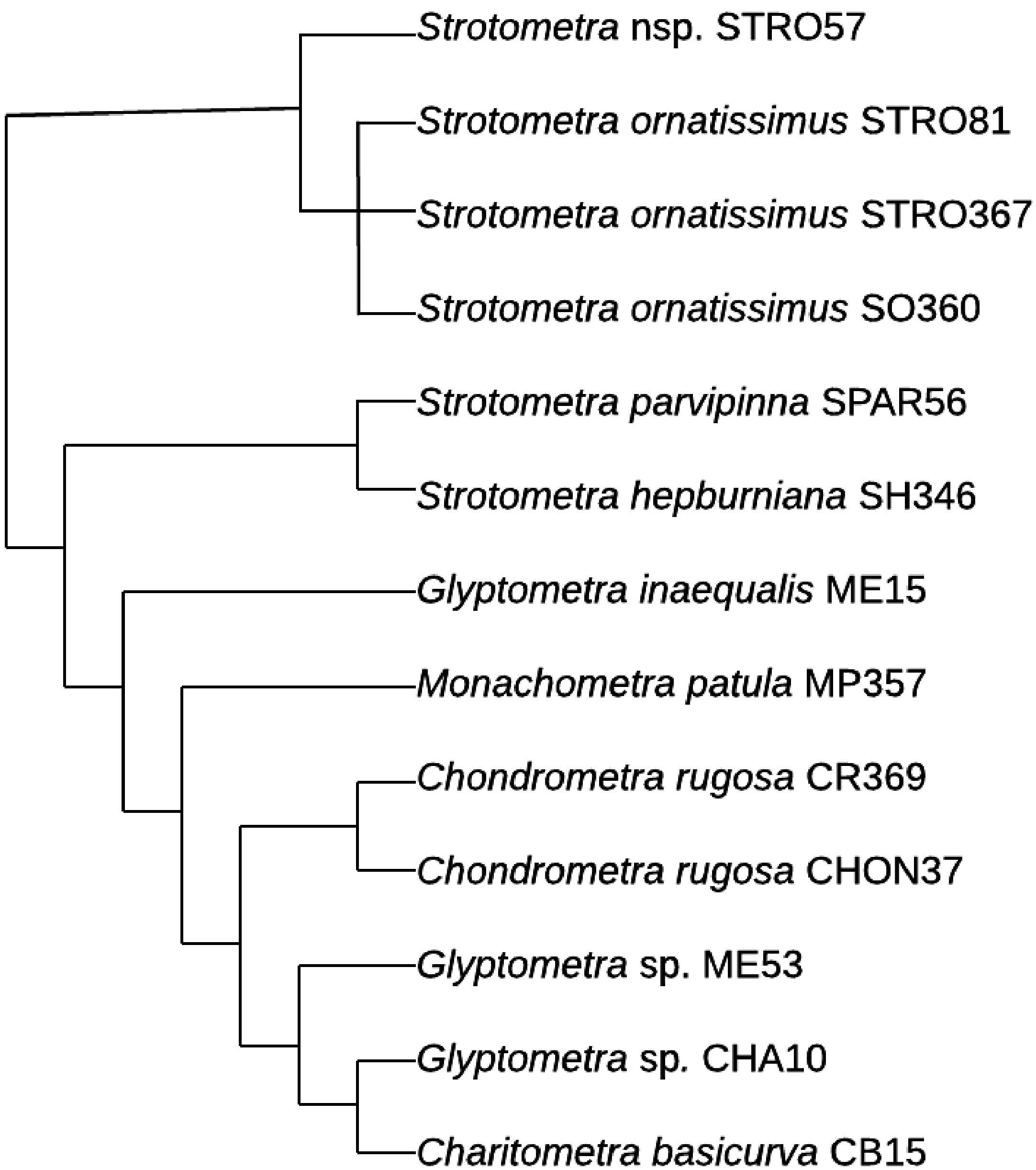

Figure 4. A simplified phylogeny of select genera of Charitometridae, adapted from Hemery (2011 Figure IV.B.9). Bootstrap values may be found in her dissertation. This phylogeny is assembled from a Maximum Likelihood analysis of four combined genes (COI, 16S, 28S and 18S).

Poecilometra acoela (P. H. Carpenter, 1884)

Figures 3, 5-6; Table 1

Antedon sp. Carpenter 1880:pl. 6, fig. 10, pl. 15, fig. 9

Antedon acoela Carpenter 1884:57, 83-84, 93, 109-110, 113, 128, pl.54, figs. 1-4, pl 55, fig. 5; 1887:391, pl. 30, fig. 3; 1888:132, pl. 2, fig. 3 a-d, pl. 16., figs 1-5.—Hartlaub 1891:113 —Shipley and MacBride 1901:269.—Minckert 1905:190.—Hamann 1907:1578, pl. 12, fig. 1 —A. H. Clark 1912b:33

Poecilometra acoela: A. H. Clark 1907:362; 1909a:18; 1912b:33, 225; 1913:50; 1918:190, 273.—Gislén 1924:280.—A. H. Clark 1950:355-359.

Material examined.— USNM E439, Challenger station 214, Meangis Islands, 4°33’N, 127°06’E, 914m, 1875; CZM (no cat. no.), Challenger station 214, Meangis Islands, 4°33’N, 127°06’E, 914m, 1875; FSU 2633, NOAA Okeanos Explorer station P4-256, Necker Ridge, 21°38’N, 167°49’W, 1748m, 2011; FSU 2635, NOAA Okeanos Explorer station P4-256, Necker Ridge, 21°38’N, 167°49’W, 1748m, 2011; FSU 2639, NOAA Okeanos Explorer station P4-256, Necker Ridge, 21°38’N, 167°49’W, 1746m, 2011; FSU 2641, NOAA Okeanos Explorer station P4-256, Necker Ridge, 21°38’N, 167°49’W, 1746m, 2011; FSU 2665, NOAA Okeanos Explorer station P4-257, Necker Ridge, 21°31’N, 167°56’W, 1802m, 2011, 2 specimens.

Holotype.—USNM E439, Challenger station 214, Meangis Islands, 4°33’N, 127°06’E, 914m, 1875.

Diagnosis.—Poecilometra with IBr and proximal brachials narrow, well separated; lateral aboral flanges almost bridge gap between adjacent rays; cirri XXV-XXX, 15-18.

Description.—Centrodorsal subconical or hemispherical, diameter 4-5mm, DH 1.0-1.5 (Fig. 5). Polar area trapezoidal or conical, often with eroded obsolete sockets. Cirri XX-XXV, 15-18, slender, to 40mm long, arranged in two irregular rows. Cirrals increasing in length from very short C1; cirrals C2 onward with proximal and distal margins weakly Ƨ-shaped in lateral view; C4-7 longest, LW 2.0; distal cirrals with LW 1.5-2.0; penultimate cirral distinctly narrower than preceding, without opposing spine; terminal claw shorter than preceding cirral (Fig. 6).

Radials completely hidden by centrodorsal. Brachitaxes and br_1 to br_4 well-separated; gaps almost bridged by lateral flanges by brachitaxes, but almost completely bridged by br_{3+4}. Ibr_1 thick, crescent-shaped, WL 2.3-2.5, with low synarthrial swelling in middle of proximal border with Iax_2; proximal border covered with projecting flange extending towards centrodorsal, leaving triangular interradial gaps that show interradial tubercule. Iax_2 diamond-shaped, WL 1.5, with low synarthrial swelling at proximal border with $1br_1$ with lateral flanges forming gaps between adjacent brachitaxes (Fig. 5).

Arms 10, longest 90-100mm. Br1 and br2 wider than long, with WL 2.0; synarthrial swelling low and rounded; lateral margins of br1 bridge interior gap; br2 with strong v-shaped proximal margin, creating interior water pore. Br_{3+4} closely laterally apposed with interior and exterior neighbors, WL 2.6-3.0 (Fig. 5). Following brachials wedge-shaped, WL 1.3-1.5. Distal brachials rectangular, WL 1.0.

Syzygy following br3+4 usually 12+13 or 13+14. Distal syzygial interval 3 to 6 (usually 4 to 5) after second syzygy.

P1 of 22-30 pinnulars, 7-8mm long. P2 of 14 pinnulars, 6-7mm long. Distal pinnules of 11-13 pinnulars, 11-12mm long. First pinnular ($P_{(1)}$) of proximal pinnules beginning on P2 or P3 much broader than following two pinnulars, approximately three times as wide, with short flange about as long as the width of the succeeding pinnular and extending towards aboral axis of arm.

Gonads beginning on P3 (and occasionally P2) extending far up arm, sometimes past P15, where they abruptly stop; genital pinnules pedunculate, 4-7mm long; two to three pinnulars after $P_{(1)}$ narrow; usually $P_{(4\text{-}7)}$ but occasionally $P_{(4\text{-}6)}$, $P_{(4\text{-}8)}$, or $P_{(5\text{-}8)}$ square and abruptly expanded; gonad enclosed by large rectangular roof plates; gonad followed by 5-6 narrower pinnulars (Fig. 3).

Disc covered with small blunt spines, diameter 8-10mm.

Geographic distribution.—Western and central Pacific.

Bathymetric distribution.—914 to 1800 m.

Remarks.—New specimens found off the Necker Ridge expand the species range to the central Pacific and expand the bathymetric distribution to 1800 meters.

These new specimens closely greatly resemble each other and usually match the previous description of the species except for small differences in measurements. Their discs are uniformly smaller (8-9mm vs the description's 10mm). AH Clark (1950) did not provide measurements of cirri and pinnule length for easy comparison with new specimens. Additionally, most specimens have broken arms, making it difficult to identify the distalmost genital pinnule.

Specimen 1 of FSU-2665 has very divergent rays; the lateral flanges of the brachitaxes and proximal brachials do not bridge over to adjacent brachials at all, including the interior angle of the arm. Specimen 2 of FSU-2665 has a greatly pronounced synarthrial swelling on the brachitaxes and greatly diverging margins, creating nearly circular pores in the interradial margin.

All Necker Ridge specimens differ from AH Clark's (1950) description in that their genital pinnules start before P4. P3 is the first genital pinnule in specimens FSU-2633, FSU-2641, and FSU-2665; P2 in specimens FSU-2635 and FSU-2639, something Clark recognized in his notes on the species but did not include in his description.

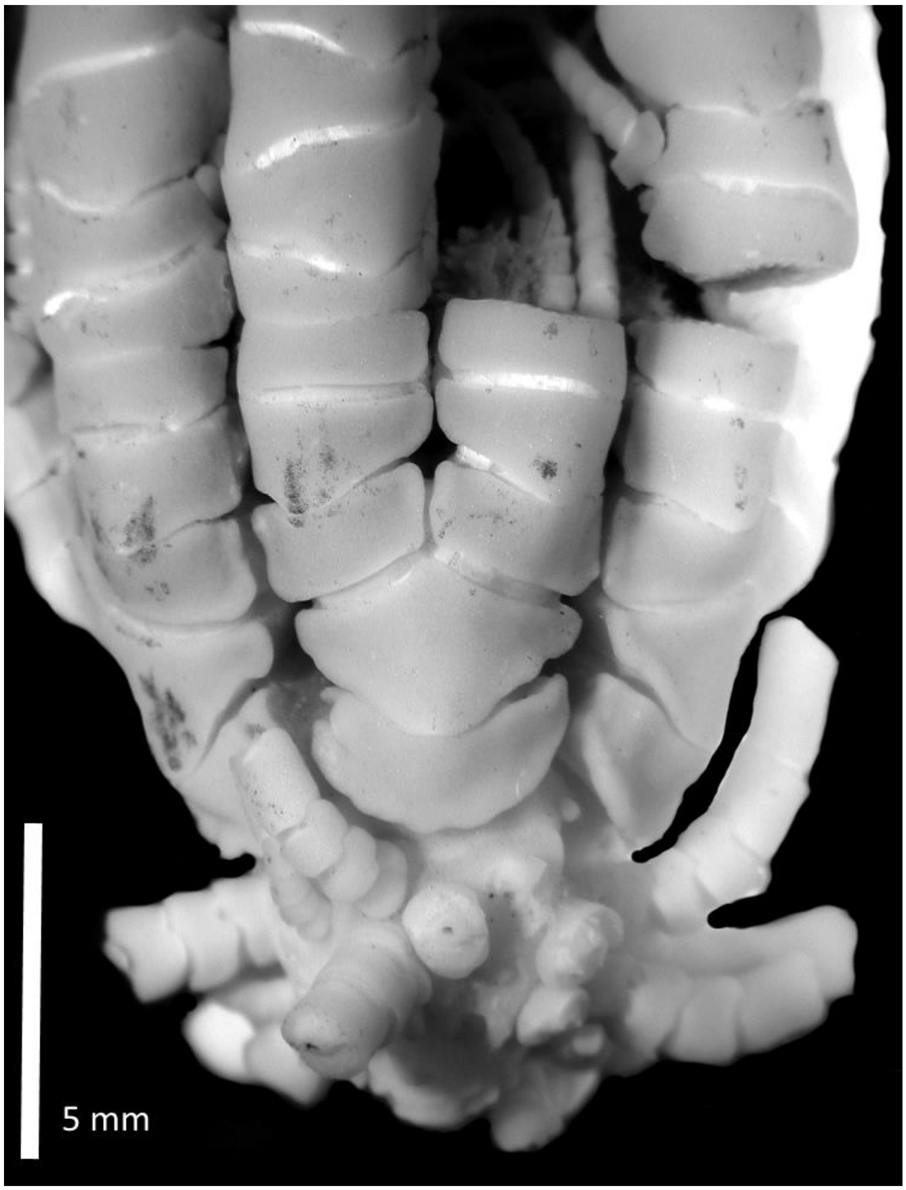

Figure 5. Centrodorsal and brachitaxes of *Poecilometra acoela*. Holotype, USNM E439.

Figure 6. A typical cirrus from a Hawaiian specimen of *Poecilometra acoela,* FSU-2665.

Poecilometra scalaris (A. H. Clark, 1907)

Figures 7-9; Table 1

Antedon scalaris A. H. Clark 1907b:141; 1908a:437, 493

Poecilometra scalaris A. H. Clark 1907a:362; 1909a:18; 1912b:225; 1913:50; 1915:215; 1918:190; 1950:359-360

Poecilometra acoela A. H. Clark 1908a:265, fig. 1, 318

Holotype.—USNM 22629, Albatross station 4918, Eastern Sea near Kagoshima Gulf, 30°22’N, 129°08’E, 660m, 1906 (photographs examined only).

Diagnosis.—*Poecilometra* with profiles of IBr series and arm smooth and continuous; ray base profiles making an angle of about 60° with the centrodorsal; cirri XX, 20, with a small opposing spine; arms 110 mm long.

Description.—Centrodorsal hemispherical, diameter 4mm, DH 2.0 (Fig. 7). Polar area rounded. Cirri XX, 20, to 20mm long, arranged in two irregular rows. Cirrals increasing in length from very short C1; cirrals with proximal and distal margins Ƨ-shaped in lateral view, the longer the cirral the more pronounced the ƨ-shaped margins; C4-6 longest, LW 2.0; distal cirrals with LW 1.5-1.75; penultimate cirral distinctly narrower than preceding, with small opposing spine; terminal claw shorter than preceding cirral (Fig. 8).

Radials completely hidden by centrodorsal. Brachitaxes and br$_1$ to br$_{3+4}$ very well-separated, bridged weakly by lateral flanges from brachitaxes, extending outward from ray base at 60° angle and with a smooth continuous profile. Ibr$_1$ thick, crescent-shaped, WL 2.5, with low synarthrial swelling in middle of proximal border with Iax$_2$; proximal border covered with projecting scalloped flange extending towards centrodorsal, leaving large interradial gaps that show interradial tubercule. Iax$_2$ rhomboid, WL 1.5-2.0, with low synarthrial swelling at proximal border with 1br$_1$ with lateral flanges (Fig. 7).

Arms 10, longest 110mm. Br1 and br2 wider than long, with WL 2.0, but with lateral flanges 2.3 to 3; synarthrial swelling low and rounded, extending to br$_{3+4}$; lateral margins of br1 extend into interior gap, but do not bridge; br2 with shallow v-shaped proximal margin. Br$_{3+4}$ parallel with interior and exterior neighbors, WL 2.0. Following brachials to br$_8$ wedge-shaped, WL 1.75-2.0. Br$_{9+10}$ rectangular, 2.5-3.0. Distal brachials starting at br$_{11}$ triangular, WL 1.0.

Syzygy following br3+4 usually 9+10 to 13+14. Distal syzygyial interval 3 to 4 after second syzygy.

P1 of 22 pinnulars, slender, 7mm long. P2 of 15 pinnulars, the first seven short and broad. Distal pinnules of 11-13 pinnulars, 11-12mm long. First pinnular (P$_{(1)}$) of proximal pinnules much broader than following two pinnulars, approximately three times as wide, with short flange about as long as the width of the succeeding pinnular, extending towards aboral axis of arm.

Gonads beginning on P3 to P9; genital pinnules pedunculate; two to three pinnulars after $P_{(1)}$ narrow; $P_{(4\text{-}8)}$ abruptly expanded, with a blunt aboral keel; gonad enclosed by large rectangular roof plates; gonad followed by 4 narrower pinnulars (Fig. 9).

Geographic distribution.—Northwestern Pacific.

Bathymetric distribution.—660 meters.

Remarks.—P. scalaris shares many similarities with *P. acoela,* including a similarly shaped brachitaxes with lateral flanges, and it can be difficult to differentiate between the two if a specimen of *P. acoela* has large interradial gaps. This species is based on only a single specimen, and given its similarities to *P. acoela,* it may be a synonym.

However, the cirri of *P. scalaris* and *P. acoela* differ: *P. scalaris* has a much more developed ƻ–shaped distal margin than *P. acoela*, and a small but developed opposing spine.

There is no information on the disc of *P. scalaris*. The flange on $P_{(1)}$ tends to be more robust than that of *P. acoela*. Pictures of the *P. scalaris* holotype were provided by C. G. Messing.

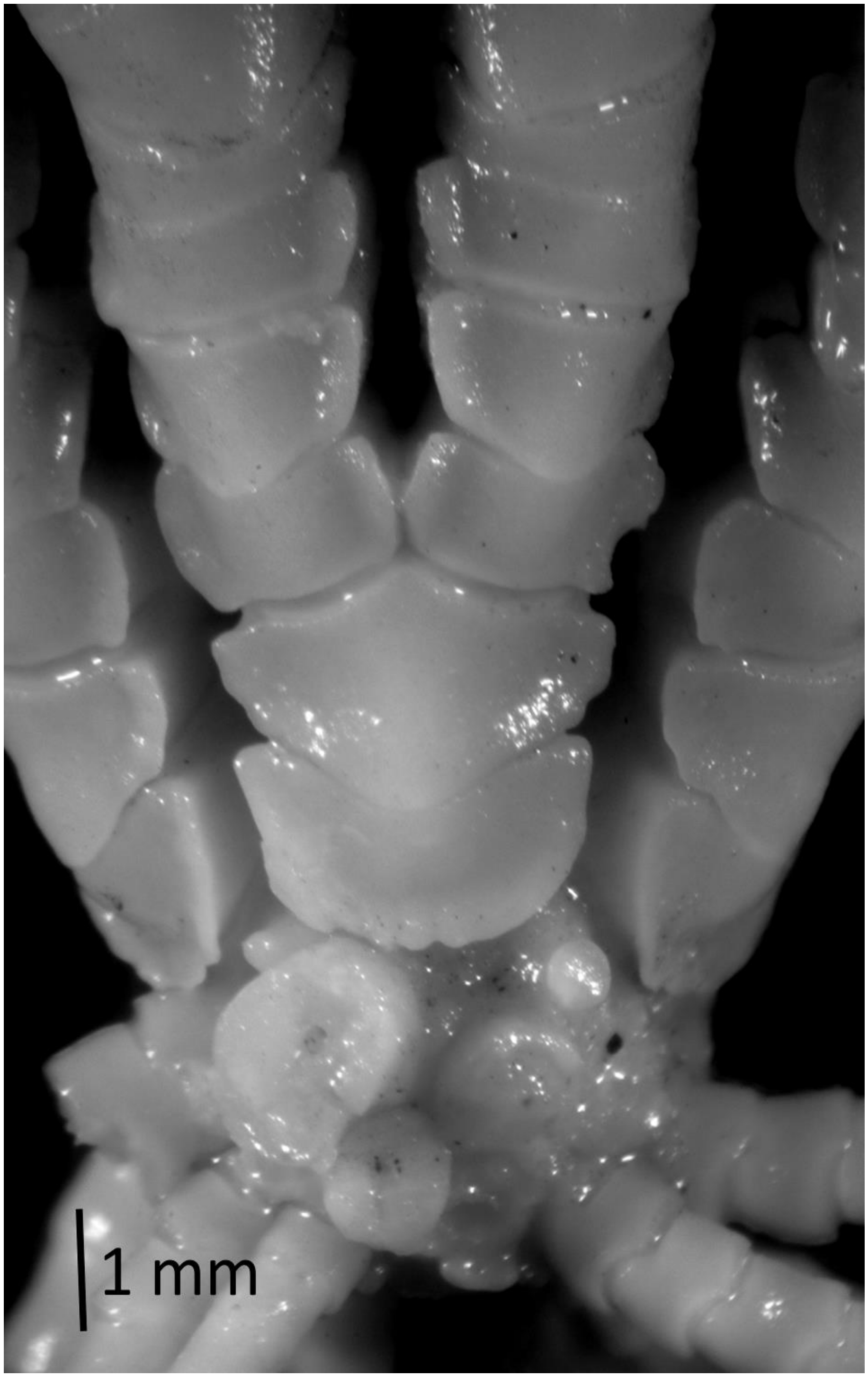

Figure 7. Centrodorsal and brachitaxes of *Poecilometra scalaris.* Holotype, USNM 2269.

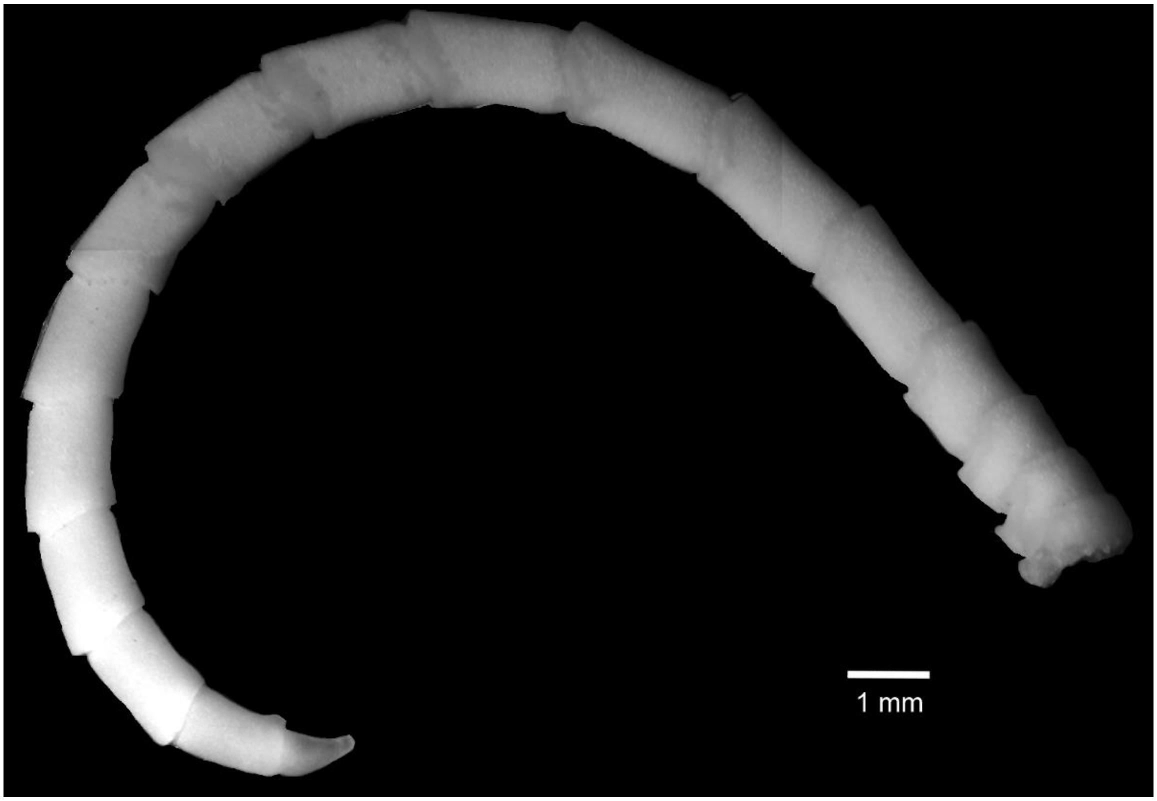

Figure 8. Cirrus of *Poecilometra scalaris.* Holotype, USNM 2269.

Figure 9. Pedunculate genital pinnules on *Poecilometra scalaris.* Holotype, USNM 2269*.* a: rudimentary winglike flanges on $P_{(1)}$.

Poecilometra ornatissimus A. H. Clark, 1912

Figures 10-12; Table 1

Strotometra ornatissimus A. H. Clark 1912a:82; 1918:pl. IX, 191-193, figs.10-11, 273, pl. 24, fig. 70; 1950:362-363, pl. 20 fig. 65.—McKnight, 1989:34.—Hess and Messing 2011:115.—Hemery 2011:179-188, figs. IV.B.1-IV.B.10

Strotometra ornatissimns A. H. Clark 1918:191

Materials examined.—CZM E2088, Albatross station 1899, Celebes Sea, 1°58'30"N, 125°00'30"E, 1035-1264m, 1906 (photographs only); NZOI T243, Kermadec Islands, 30°05'S, 178°15'E, 1035m, 1982, 2 specimens (drawings only); MNHN STRO81, MUSORSTOM 10 station CP1361, Fiji, 18°00'S, 178°53'E, 1058-1091 m, 1998.

Holotype.—CZM, Albatross station 1899, Celebes Sea, 1°58'30"N, 125°00'30"E, 1035-1264m, 1906.

Diagnosis.—Poecilometra with distal edges of br2, br4, and br5 strongly everted, forming high crest perpendicular to midaboral axis; axillaries chevron-shaped instead of triangular; C4 and C5 LW 3.0-3.3, strongly constricted centrally with expanded distal margins.

Description.—Centrodorsal low hemispherical or discoidal, diameter 2.5-3mm, DH 2.5 (Fig. 10). Polar area domelike. Cirri XXXV, 10-15, arranged in two irregular rows. Cirrals increasing in length from very short C1; C2-C10 with proximal and distal margins ƨ-shaped in lateral view, the longer the cirral the more pronounced the ƨ-shaped margins; C2 to C11 strongly constricted centrally; C4 to C5 longest, LW 3.0-3.3; distal cirrals with

LW 2.5-2.7; penultimate cirral slightly smaller than preceding, with small opposing spine; terminal claw about as long as preceding cirral (Fig. 11).

Radials visible over rim of centrodorsal or hidden by Ibr_1, visible only at interradial angles. Brachitaxes and br_{1-2} flat-sided and closely apposed laterally with lateral margins of each ossicle extended as short, straight flange. Ibr_1 rectangular or trapezoidal, WL 4.0-5.0. Iax_2 chevron-shaped or pentagonal, with short lateral diverging margins extending past articulations and with well-developed water pores, WL 3.3-3.5.

Arms 10, longest 40mm. Br_1 and br_2 with parallel proximal and distal margins, exterior margins everted or scalloped, internal margins closely apposed; wider than long, with WL 2.5; distal margin of br2 everted perpendicular to midaboral axis of arm, may be up to three times the length of the ossicle; with small rounded synarthrial swelling at articulation between br_1 and br_2. Br_{3+4} short, oblong, with br_4 possessing a similarly large crest as br_2. Crests reduce in size and beginning to lie flat against underside of arm until br_{10} to br_{12}. Middle brachials to br16 triangular, WL 1.0. Distal brachials wedge-shaped and smooth except for finely spinous distal edge; LW 1.0.

P1 of 13 pinnulars, 4.5 mm long. P2 of 12 pinnulars, 4mm long. Distal pinnules of 15-16 pinnulars, 8-10mm long. First pinnular beginning on P1 with small rounded flange as long as the width of the succeeding pinnular extending towards aboral axis of arm.

Gonads on P3 to P6-7, occasionally P1 or P2; genital pinnules distinctly pedunculate, 4 mm long; proximal 4-5 pinnulars narrow; usually $P_{(4-6)}$ or $P_{(8-12)}$ abruptly expanded with shallow dish-shaped pinnulars; gonad enclosed by many small irregular roof plates (Fig. 12); gonad followed by 6 abruptly narrower, fragile pinnulars.

Geographic distribution.—Western and southwestern Pacific Ocean.

Bathymetric distribution.—1035 to 1264 meters.

Remarks.—D. G. McKnight (1989) found two specimens off of the Kermadec Islands. Some differences between these and the holotype may result from their much more complete condition. The description above includes information from McKnight (1989), though those specimens were not examined.

Little to no information exists on the syzygies or disc of *P. ornatissimus*.

Specimen STRO81 is missing most of its arms and all of its cirri.

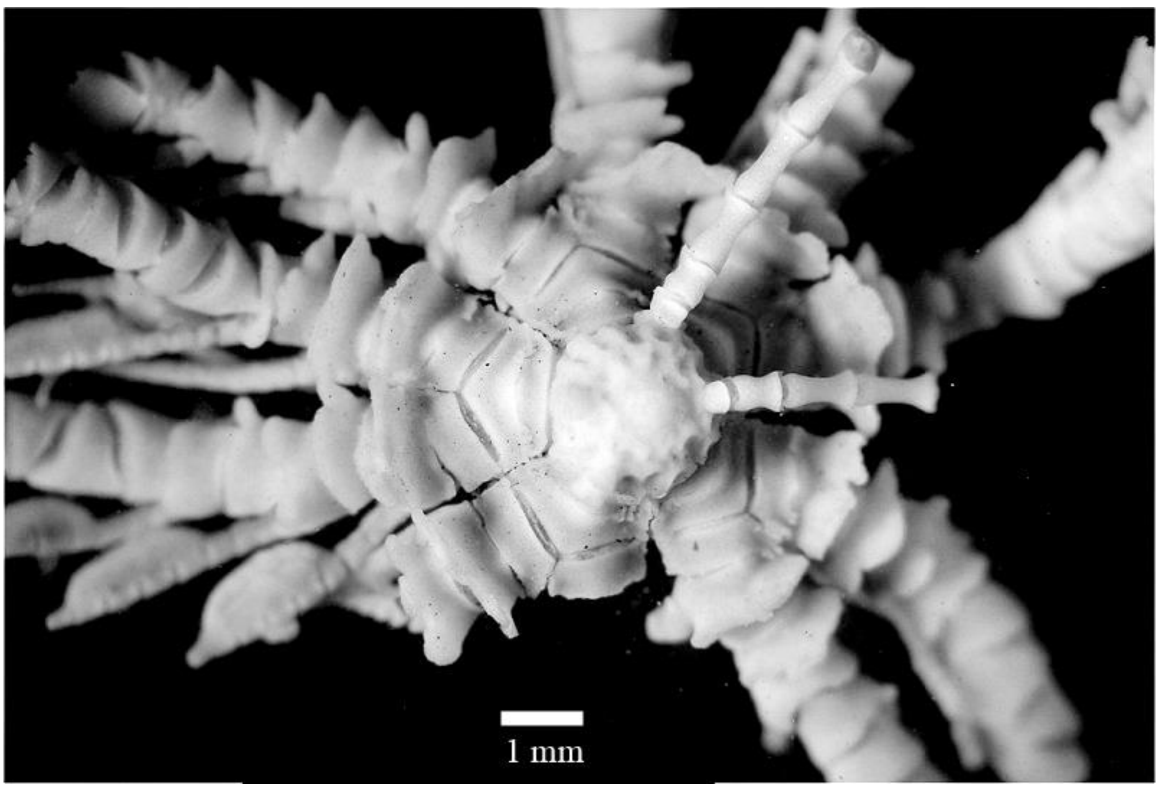

Figure 10. Centrodorsal and brachitaxes of *Poecilometra ornatissimus.* Holotype, CZM E2008.

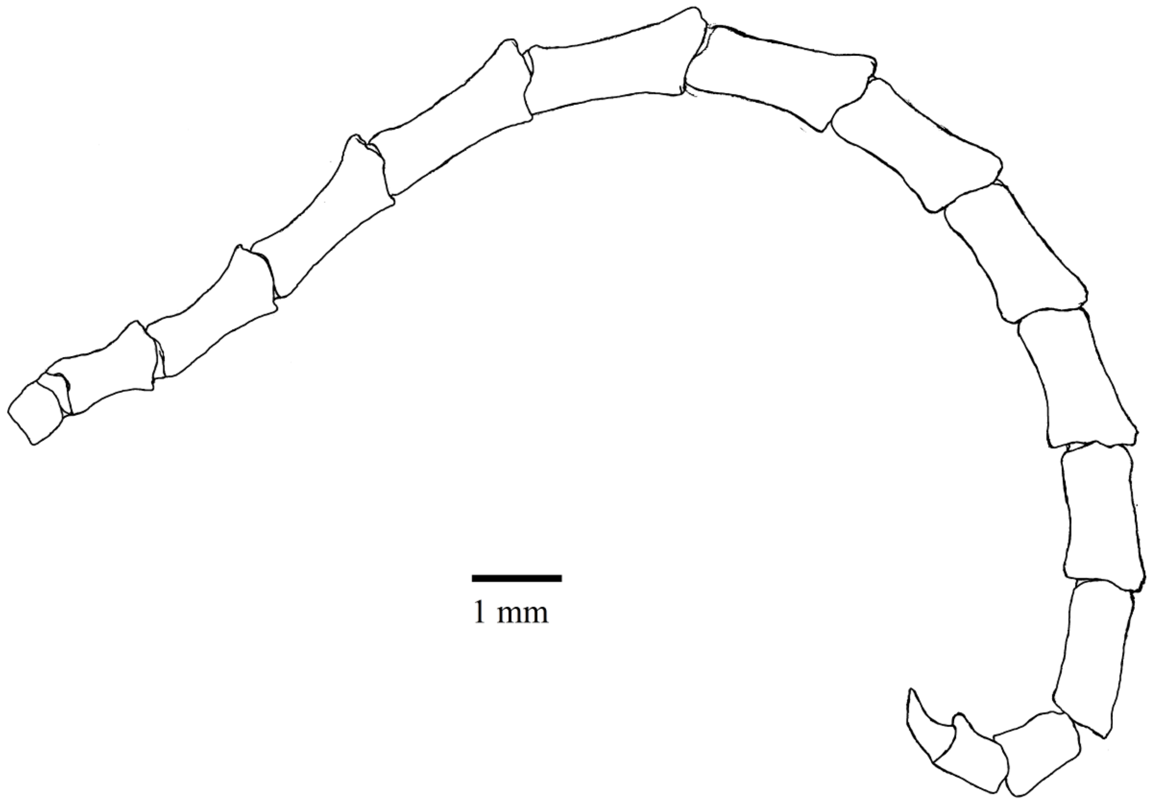

Figure 11. Cirrus of *Poecilometra ornatissimus,* NZOI T243*.* Drawing by C.G. Messing.

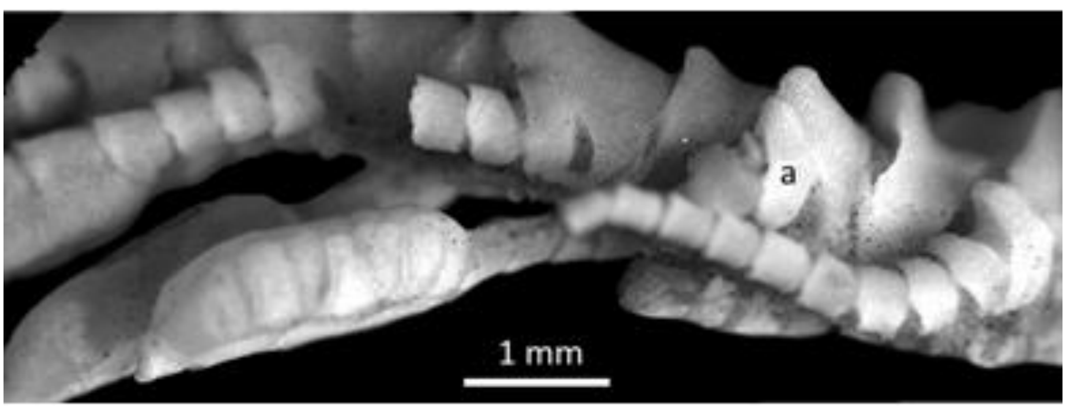

Figure 12. Pedunculate genital pinnules of *Poecilometra ornatissimus.* Holotype, CZM E2088*.* a: well-developed winglike flanges on $P_{(1)}$.

Poecilometra priamus A. H. Clark, 1912

Figures 13-16; Table 1

Stotometra priamus A. H. Clark 1912a:81; 1918:192, 194, 275, pl.4, figs. 64, 65; 1950:363-365, pl. 31, fig. 97.—Hess and Messing 2011:115

Material examined.—CZM (no cat. no.), Danish Expedition to the Kei Islands, Kei Islands, Indonesia, 5°34'S, 132°50'E, 370m, 1922, 2 specimens; CZM (no cat. no.), Danish Expedition to the Kei Islands, Kei Islands, 5°30'20"S, 132°51'E, 345m, 1922; MNHN EcCs10304, BATHUS 3 station DW790, New Caledonia, 23°49'S, 169°48'E, 685-715m, 1993, dried; MNHN IE-2007-5904, EXBODI station DW3784, New Caledonia, 22°13'S, 167°09'E, 360m, 2011; MNHN IE-2007-6012, EXBODI station CP3833, New Caledonia, 22°02'S, 167°04'E, 475m, 2011

Diagnosis.—*Poecilometra* with short, slender cirri, LW 3.0; genital pinnules markedly pedunculate, with massively expanded $P_{(5\text{-}8)}$, the pinnulars rectangular and twice as broad as preceding pinnulars; IBr_1 and arms lacking keel.

Description.—Centrodorsal discoidal, diameter 1.5-2.0mm, DH 2.0 (Fig. 13). Polar area flat, about three-quarters of centrodorsal diameter. Cirri XVII, 11-12, slender, 8 to 11mm long, arranged in irregular and closely crowded rows. Cirrals increasing in length from very short C1; middle and distal cirrals cylindrical, with proximal and distal margins strongly ƻ-shaped in lateral view; C4-5 longest, LW 3.0; middle cirrals slightly constricted centrally, with distal border overlapping oral side of succeeding cirral; distal cirrals with LW 0.41; penultimate cirral narrower than preceding, with small, terminal opposing spine; terminal claw sharp, curved, as long as penultimate cirral (Fig. 13).

Radials visible as prominent tubercles at interradial angles. Brachitaxes and br1-2 flat-sided and closely apposed laterally with lateral margins of each ossicle extended as short, slightly irregular flange with scalloped, rounded ends. Ibr_1 rectangular, WL 4:1. Iax_2 short pentagonal, WL 2.5, with low, broad or knoblike, synarthrial swelling (Fig. 14).

Arms 10, longest 40mm. Br_1 and br_2 wider than long, WL 1.5; synarthrial swelling low, rounded and elongated; all margins scalloped, closely apposed on interior; br2 with shallow V-shaped proximal margin. Br_{3+4} short, rectangular, with everted exterior marginal flange; WL 3.0. Following 6 brachials weakly wedge-shaped; distal edge prominently overlapping succeeding brachial (Fig. 15). Middle brachials triangular; LW 1.5-2.0. Distal brachials weakly wedge-shaped; LW 1.0-1.5.

Syzygy following br_{3+4} br_{10+11} to br_{13+14}, usually br_{12+13}. Distal syzygyial interval 3 to 4 after br_{15+16}.

P1 of 27-30 pinnulars, 5-6mm long. P2 of 12-18 pinnulars, 5-6mm long. Distal pinnules of 11-12 pinnulars, 5mm long. Proximal three pinnulars with reduced tongue-like flange wrapping towards aboral side of arm, the flange almost as long as the width of the succeeding pinnular, but reduced or absent in later pinnules.

Gonads on P2 to P4, ending abruptly; genital pinnules distinctly pedunculate, 4.5-6mm long; proximal 4-5 pinnulars narrow; usually $P_{(6-10)}$ but sometimes $P_{(5-7)}$ abruptly expanded; gonad enclosed by heavy large roof plates; gonad followed by 3-7 abruptly narrower, very fragile pinnulars (Fig. 16).

Geographic distribution.—Western and southwestern Pacific Ocean.

Bathymetric distribution.—245 to 700 meters.

Remarks— The new specimens extend this species' range to New Caledonia and increases the bathymetric distribution to 700 meters.

Little to no information exists on the disc of *P. priamus*; it is missing or damaged in most specimens.

IE-2007-6012 and IE-2007-5904 were labeled as *Strotometra* n.sp. and *Strotometra cf. priamus*, respectively; both appear very similar to *Poecilometra tibicinem* n. sp. due to their long $P_{(1)}$ flanges; these are unusual for *P. priamus*, as its $P_{(1)}$ is the smallest and least visible of the genus. IE-2007-5904 possesses large $P_{(1)}$ flanges to P6. These specimens are small for both species and may represent juveniles, though IE-2007-5904 possesses a large centrodorsal for the species: 3.5mm, DW 1.75. They are here tentatively placed as members of *P. priamus* due to their visible and unadorned $1br_1$, their 10 arms, and their P1 and P2 more closely resembling *P. priamus* than the new species.

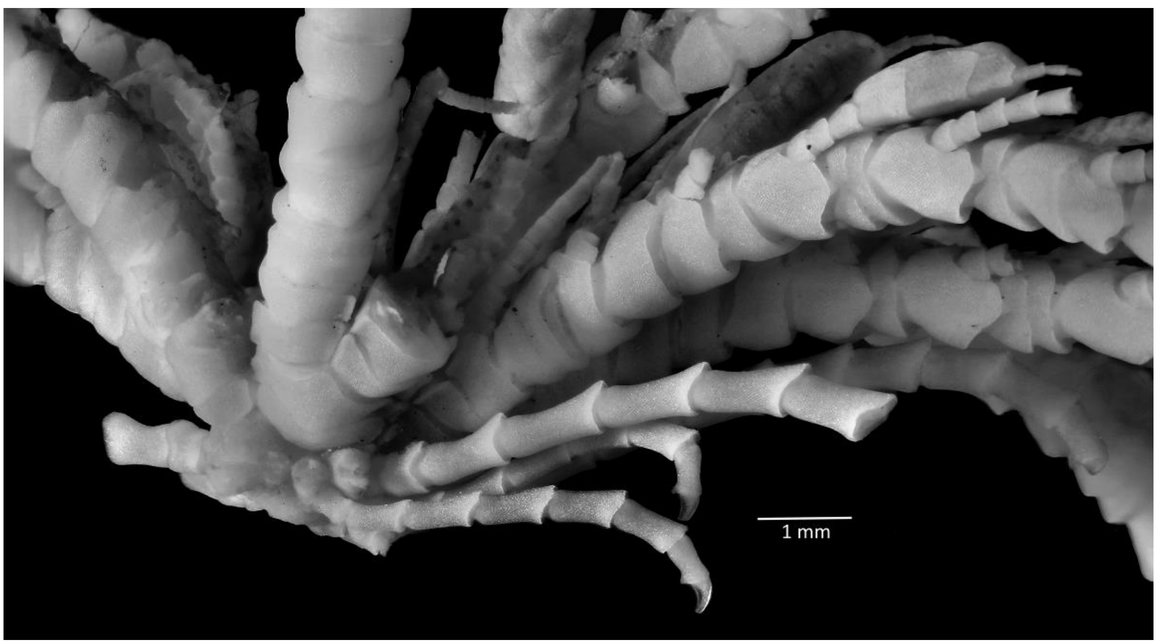

Figure 13. Centrodorsal and cirri of *Poecilometra priamus,* MNHN EcCs10304.

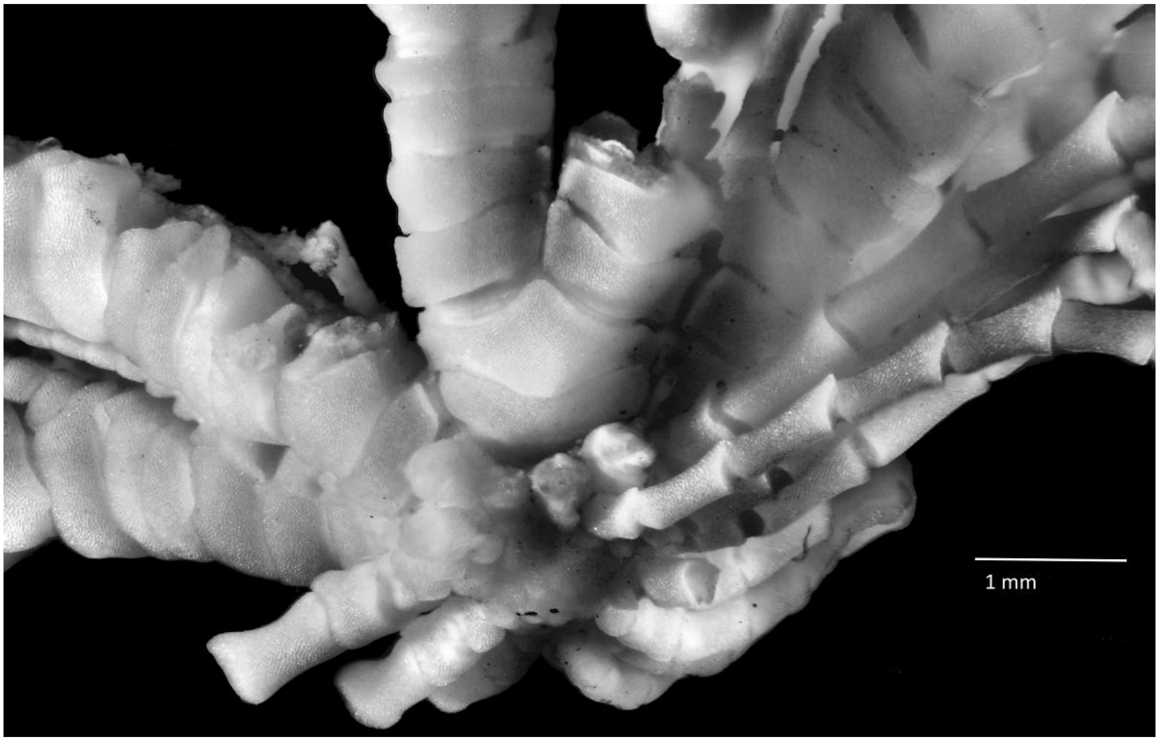

Figure 14. Centrodorsal and brachitaxes of *Poecilometra priamus,* MNHN EcCs10304.

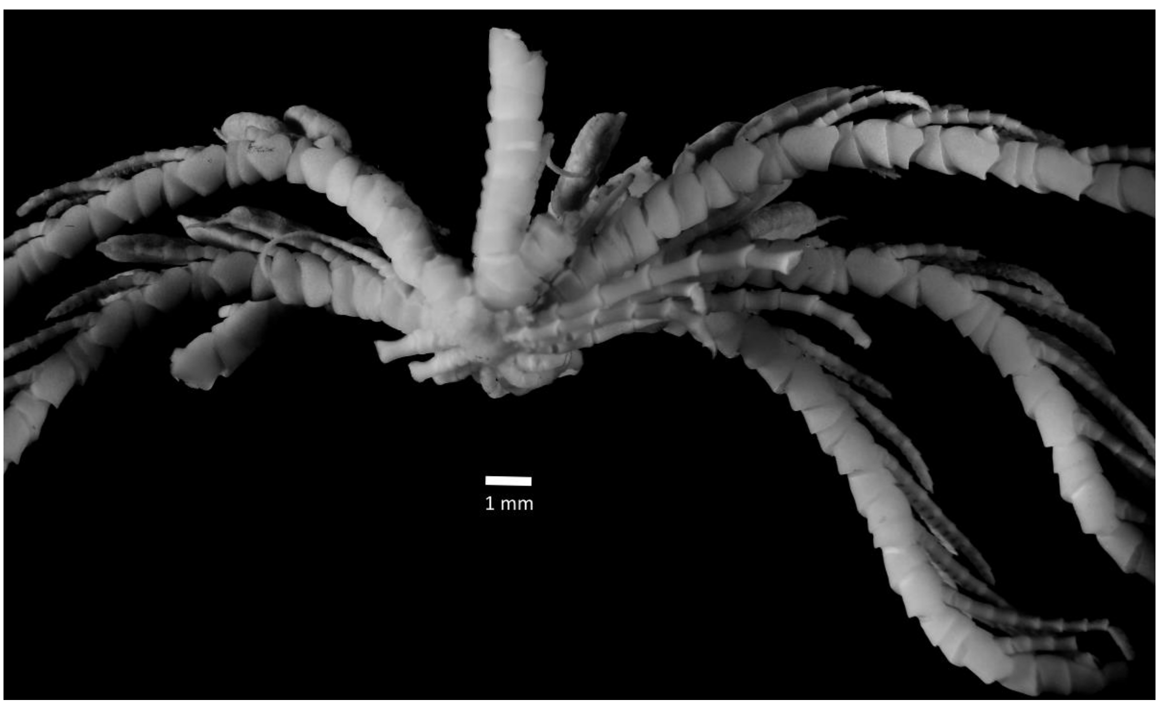

Figure 15. Lateral view of *Poecilometra priamus,* MNHN EcCs10304.

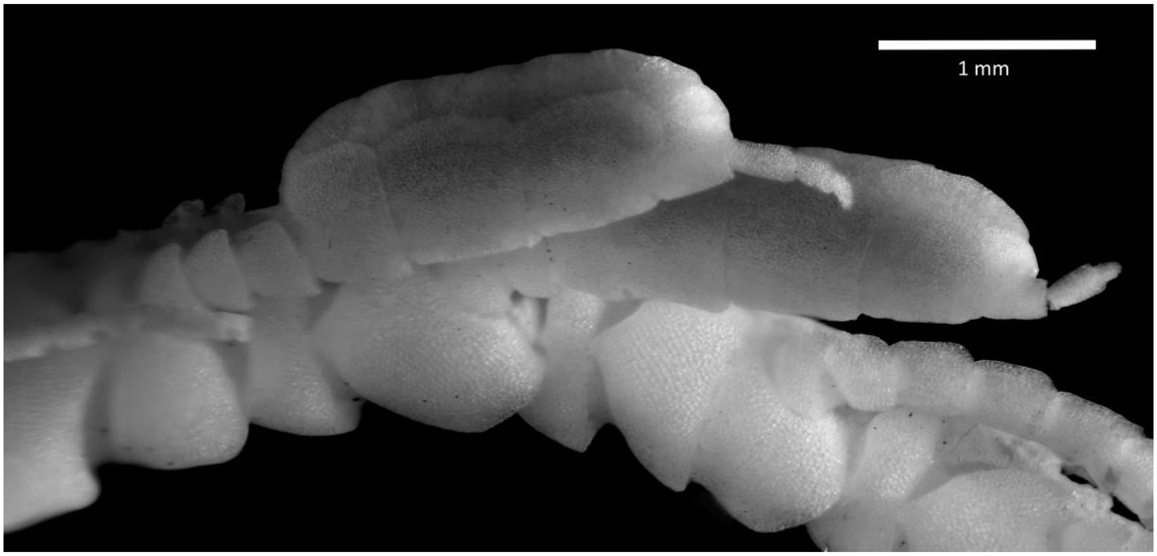

Figure 16. Genital pinnules of *Poecilometra priamus,* MNHN EcCs10304.

Poecilometra tibicinem n. sp. Romanowski and Messing

Figures 17-26; Table 1

Holotype.—MNHN EcCh 193, MUSORSTOM 4 station CP216, New Caledonia, 22°59'S, 167°22'E, 490-515m, 1985.

Other Material Examined.—MNHN STRO57, NORFOLK 1 station CP1721, New Caledonia, 23°19'S, 168°01'E, 416-443m, 2001, 4 specimens (3 heavily fragmented); MNHN EcCs10237, VAUBAN station DR04, New Caledonia, 22°17'S, 167°13'E, 400m, 1978, 3 specimens (dried); MNHN EcCh194, MUSORSTOM 4 station CP216, New Caledonia, 22°59'S, 167°22'E, 490-515m, 1985, 2 specimens.

Diagnosis.—*Poecilometra* with cirri XXX-XL, crowded in three rows and irregular columns (Fig. 17); arms 20; IBr_1 mostly hidden by centrodorsal; distolateral corners visible and covered with small nodules; first pinnular ($P_{(1)}$) of proximal pinnules with elongated, curved flange extending around to aboral surface of arm (Figs. 18, 19).

Description of the holotype.—Centrodorsal low, flattened hemispherical; diameter 3.5mm, DH 1.5 (Fig. 20). Polar area flat, about a third of centrodorsal diameter, with traces of obsolete sockets. Cirri XXXV, 12-17, slender, to 23 mm long, arranged in irregular crowded columns of 2-3 sockets. Cirrals increasing in length from very short C1; proximal cirrals cylindrical; middle and distal cirrals compressed and wider in lateral view; C3 squarish with proximal and distal margins strongly ƨ-shaped in lateral view; C5-7 longest, LW 2.2-2.5; middle and distal cirrals slightly constricted centrally, with distal border overlapping oral side of succeeding cirral; distal cirrals with LW 0.67; penultimate cirral distinctly narrower than preceding, with small, terminal opposing spine; terminal claw shorter than preceding cirral (Fig. 21).

Radials completely hidden by centrodorsal. Brachitaxes and br1-2 flat-sided and closely apposed laterally with lateral margins of each ossicle extended as short, slightly irregular flange with rounded ends. Ibr_1 mostly hidden by the centrodorsal; distolateral corners visible in interradial angles and covered with small nodules. Iax2 short hexagonal, with short lateral diverging margins, WL 2.5, with low, broad or knoblike, synarthrial swelling not reaching distal angle; proximolateral margins with few, weak, irregular knobs (Fig. 22). IIBr2 series similar to IBr2 but with ossicles proportionally longer. $IIbr_1$ short, slightly curved rectangles, with diverging lateral margins; WL 3.0; $IIax_2$ hexagonal to almost pentagonal (proximal angle gently curved); synarthrial swelling weak, elongated; WL 2.0-2.5 (Fig. 23).

Arms 20, longest 75mm. Br_1 and br_2 wider than long, with WL 2.0; synarthrial swelling low, rounded and elongated; all ossicle margins slightly raised; br_2 longer exteriorly, with shallow V-shaped proximal margin. Br_{3+4} short, rectangular, with WL 3.0. Following 5-6 brachials weakly wedge-shaped, with low knoblike alternating articular tubercles; WL 2.0. Middle brachials to br_{23} more strongly wedge-shaped to triangular, with low midaboral knob; WL 2.0-2.3. Distal brachials rectangular; WL 1.0.

Syzygy following br_{3+4} usually br_{8+9} or br_{9+10}; sometimes from br_{12+13} to br_{16+17}. Distal syzygial interval 5 to 6 after br_{16+17} (Fig. 22).

P1 of 39 pinnulars, 10-11 mm long; proximal first three pinnulars with high aboral keel (Fig. 24). P2 of 21 pinnulars, 8-9mm long; proximal first three pinnulars with diminished aboral keel. Distal pinnules of 15-16 pinnulars, 8-10mm long (Fig. 25). First pinnular beginning on P3 with long, narrow, wing- or flattened tongue-like flange wrapping around arm and sometimes almost reaching midaboral line, remaining well developed to P6 or Pg, weakening and lying flat against brachial side on following brachials, reduced to a slight flange or widened first pinnular in distal pinnules.

Gonads on P3 to P6-7, with progressively weaker expansion after P4; genital pinnules distinctly pedunculate, 7-9 mm long; proximal 4-5 pinnulars narrow; usually $P_{(6-11)}$ abruptly expanded; gonad enclosed by many small irregular roof plates (Fig. 26); gonad followed by 8-10 abruptly narrower, fragile pinnulars (Fig. 27).

Disc pebbly, diameter 10mm; mouth diameter 1mm; anal papilla cylindrical, lying flat on disc, 3mm.

Other specimens.—The remaining specimens differ from the holotype in having centrodorsals hemispheric, 3.0-3.5mm across (4.0mm in specimen 1 of EcCh194), DH 2.0-3.0 in EcCs10237. Polar area flat or concave, roughened, about half of centrodorsal diameter in EcCs10237. Cirri XXX in specimen 2 of EcCh194 and in intact specimen of

STRO57; up to 23 segments in specimen 1 EcCh194, and only to 17mm long in EcCh194; all but one small cirrus missing in complete specimen of STRO57; cirri missing in EcCs10237.

Centrodorsal of STRO57 chipped, revealing Ibr1; WL 4.0 with knoblike synarthrial swelling; proximal margin broadly U-shaped. Iax_2 with WL 2.0 in EcCh194 and STRO57; WL 2.5-3.5 in EcCs10237. IIbr1 WL 3.0-4.0 in EcCs10237.

Longest arms 63-70mm in EcCh194, 72mm in STRO57. Br_2 lacking V-shaped proximal margin, instead shallow diagonal margin in EcCh194. Br_{3+4} WL 2.0-2.5 in EcCs10237. Middle brachials triangular to br_{31} in specimen 1, br_{45} in specimen 2 in EcCh194, br_{38} in STRO57; WL 1.5-2.0 in EcCs10237. Distal brachials missing in EcCs10237.

P1 of 20 pinnulars, 8mm long in specimen 2 of EcCs10237, 36-39 pinnulars and 8-10mm long in EcCh194, 23 segments and 6mm long in STRO57; P1 missing in specimens 1 and 3 of EcCs10237. P2 of 25-30 pinnulars in EcCh194; occluded in intact specimen of STRO57; missing in EcCs10237. Distal pinnules of specimen 2 of EcCh194 11-12mm long. $P_{(1)}$ flanges greatly reduced in EcCs10237.

Gonads to P8 in specimen 2 of EcCh194; 6-8mm long in EcCh194 and STRO57; proximal three to five pinnulars narrow in STRO57, six to seven pinnulars narrow in EcCh194; three to four pinnulars (e.g. $P_{(4-7)}$ or $P_{(6-8)}$) abruptly expanded in STRO57, up to eight pinnulars (e.g. $P_{(6-14)}$ or $P_{8-16)}$) abruptly expanded in EcCh194.

Disc diameter 8mm in STRO57 and IE-2007-6012, 7-9mm in EcCh194; anal papilla 2.0-2.5mm in EcCh194 and missing in STRO57. Disc, mouth, and anal papilla dried and damaged in EcCs10237.

Geographic distribution.—Known only from New Caledonia.

Bathymetric distribution.—Known only from 400-500 m.

Etymology.—From *tibicinem*, meaning flutist in Latin, from the wing-like pinnular flanges that resemble fingers wrapping around a flute, recorder or tin whistle.

Remarks.—P. tibicinem differs from other species of *Poecilometra* in having twenty arms, the mostly hidden and nodulose Ibr1, and the long aboral $P_{(1)}$ flanges. Two young specimens thought to be the new species (IE-2007-5904 and IE-2007-6012) have tentatively been identified as *P. priamus* instead due to their visible and smooth Ibr_1.

Three specimens of STRO57 are very badly fragmented.

Smaller specimens (e.g., EcCs10237) may have smaller, less-developed winglike flanges. These flanges lie flat against the aboral side of the arm, very rarely reaching the midaboral line.

Hemery's (2011) Maximum Likelihood tree placed this species (as *Strotometra* n. sp.) close to *Poecilometra ornatissimus* (Fig. 4). Both species have similar cirrals, brachitaxes, pedunculate genital pinnules, and the aboral $P_{(1)}$ flange.

Figure 17. Centrodorsal, cirri and ray bases of *Poecilometra tibicinem* n. sp. In oblique aboral view. MNHN EcCs10237 specimen 1.

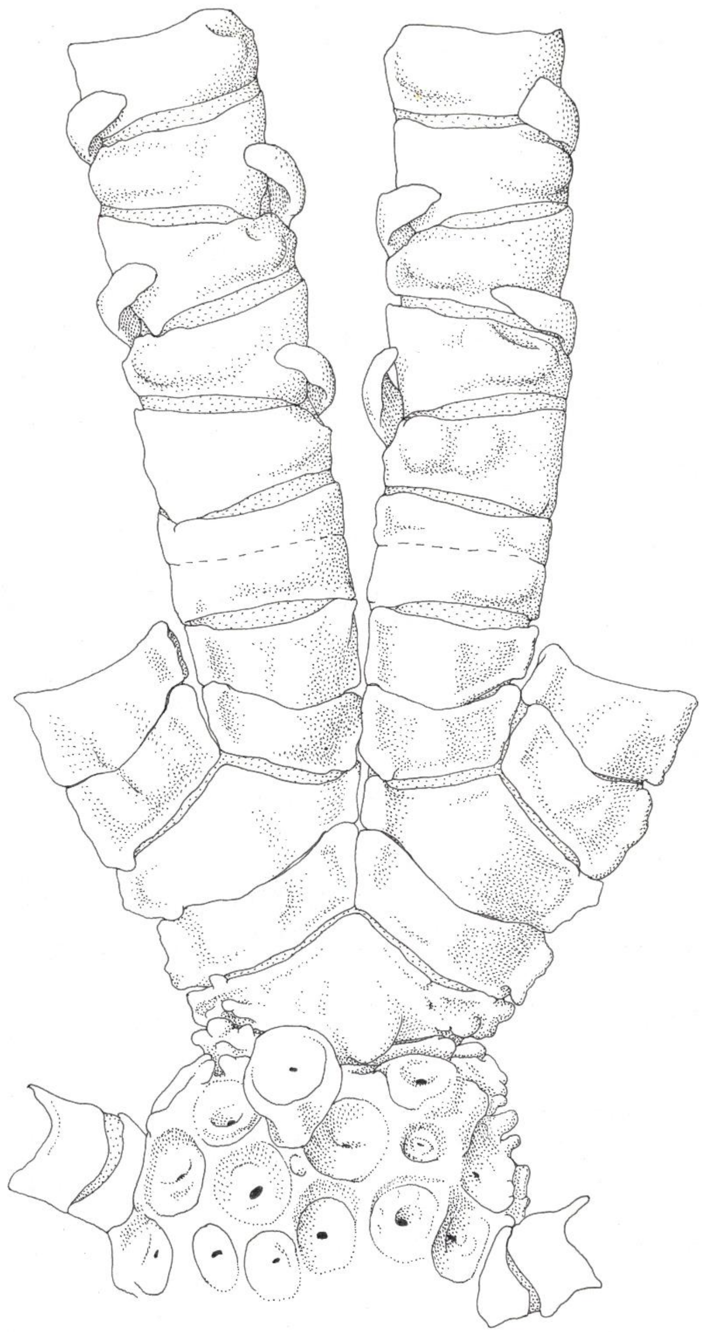

Figure 18. Portion of centrodorsal, bases of two rays, and diagnostic pinnular flanges of *Poecilometra tibicinem* n. sp., holotype MNHN EcCh193. Drawing by C.G. Messing.

Figure 19. Complete aboral side of *Poecilometra tibicinem,* holotype MNHN EcCh193.

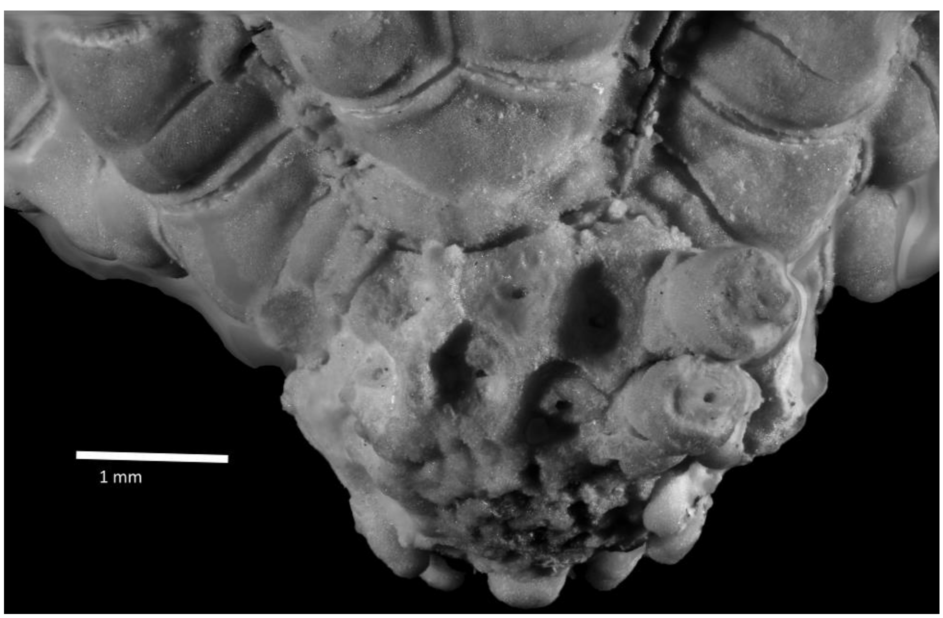

Figure 20. Centrodorsal of *Poecilometra tibicinem,* MNHN EcCs10237 specimen 2.

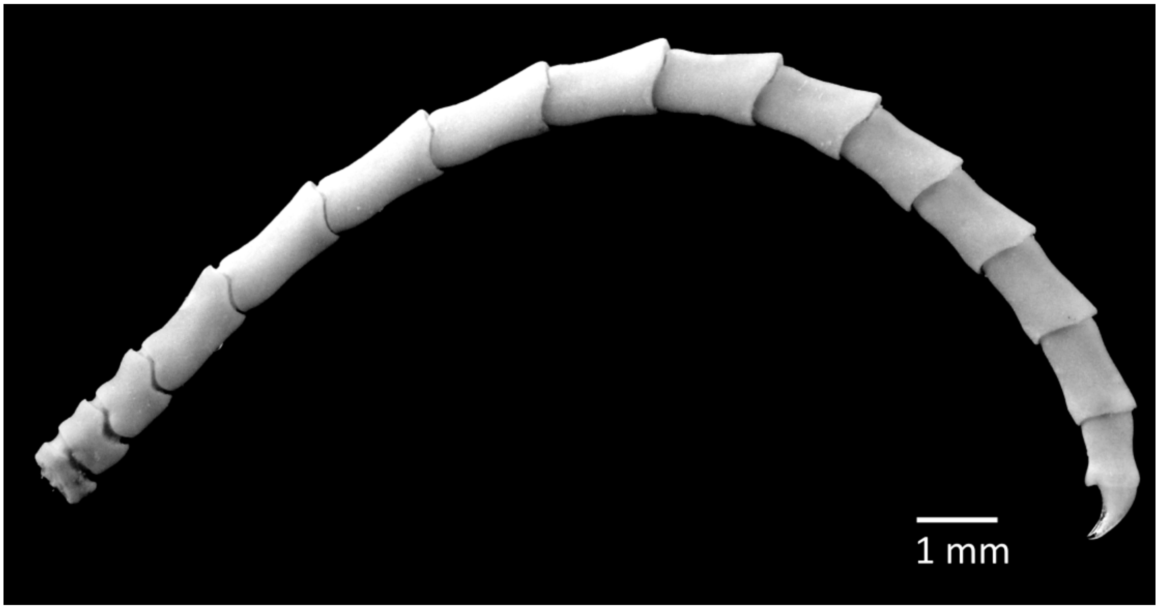

Figure 21. Cirrus of *Poecilometra tibicinem,* holotype, MNHN EcCh193.

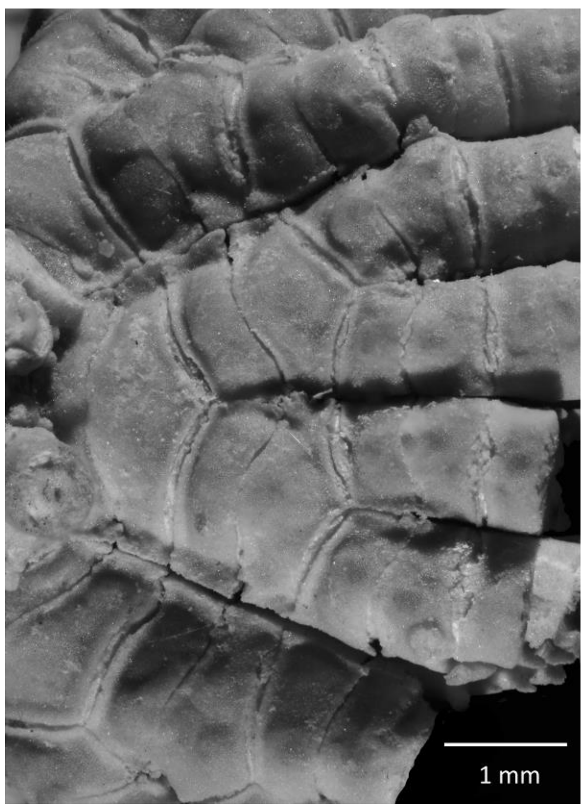

Figure 22. Brachitaxes of *Poecilometra tibicinem,* MNHN EcCs12037 specimen 1.

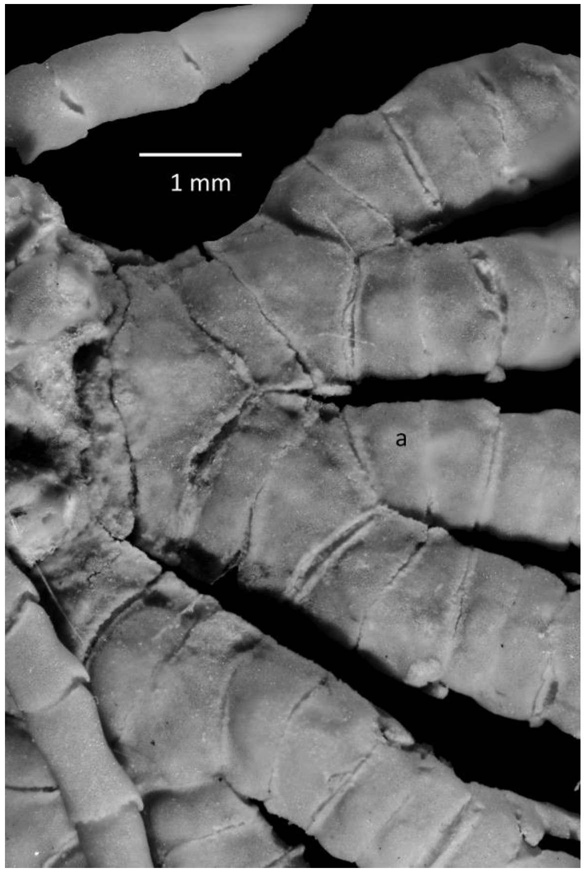

Figure 23. Brachitaxes of *Poecilometra tibicinem,* MNHN EcCs10237 specimen 3. a: swollen hump extendomg from earlier division series to the proximal brachials.

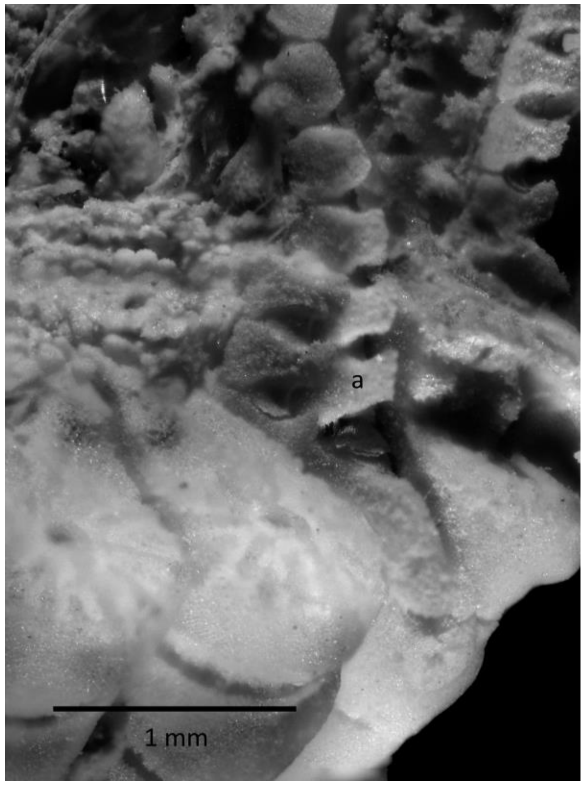

Figure 24. Aboral view of P1 of *Poecilometra tibicinem,* MNHN EcCs10237 specimen 1. a: prominent aboral keel.

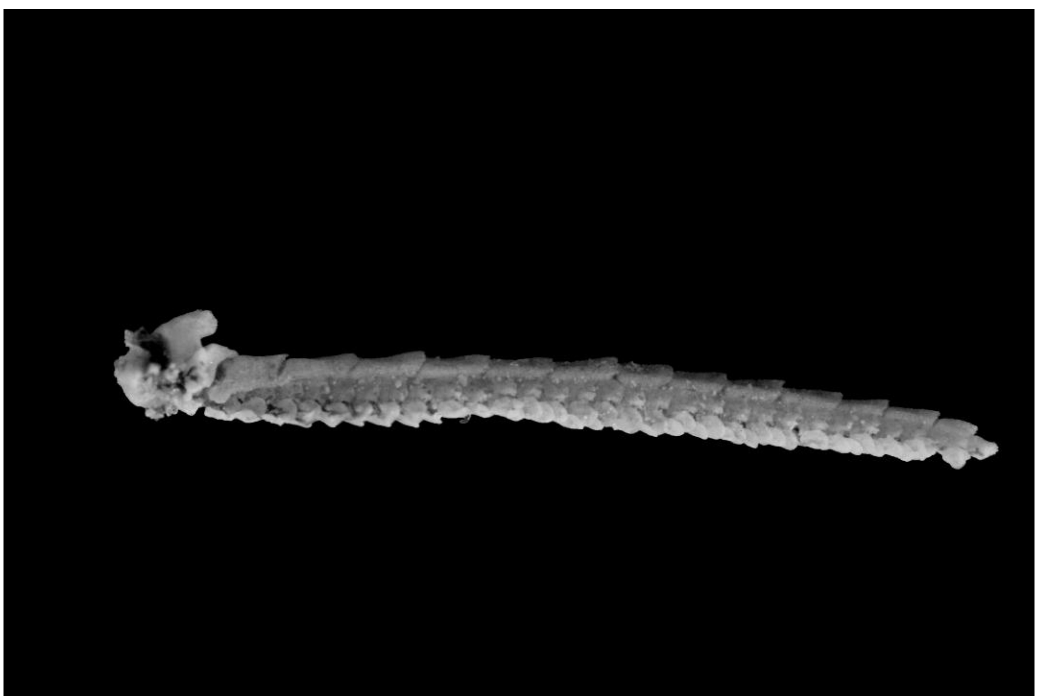

Figure 25. Distal pinnule of *Poecilometra tibicinem,* holotype, MNHN EcCh193.

Figure 26. Oral view of *Poecilometra tibicinem,* holotype, MNHN EcCh193.

Figure 27. Pedunculate genital pinnules of *Poecilometra tibicinem* holotype MNHN EcCh193. a: characteristically developed winglike flanges on $P_{(1)}$.

Genus *Strotometra* A. H. Clark, 1909

Figures 28-35; Table 1

Antedon (Part) P. H. Carpenter 1888:127

Charitometra (Part) A. H. Clark 1907a:361

Strotometra A. H. Clark 1909a:19; 1912:9, 11, 25, 60, 226; 1918:172, 191.—Gislén 1928:9; 1934:18.—A. H. Clark 1950:361.—Hess and Messing 2011:115

Type species.—Antedon hepburniana: A. H. Clark 1907b.

Other included species.— Strotometra parvipinna P. H. Carpenter, 1888.

Diagnosis.—Centrodorsal hemispherical or discoidal; cirrus sockets in irregular marginal rows; cirri short and stout, between X and XV with 10-15 segments (Fig. 28); ten arms; rays extend outward from oral-aboral axis; early genital pinnule segments expanded laterally under gonad, usually at $P_{(3-5)}$ (Fig. 29).

Geographic distribution.—Western and northwestern Pacific Ocean.

Bathymetric distribution.—185 to 520 meters.

Remarks.—*Strotometra ornatissimus* and *S. priamus* are herein moved to *Poecilometra*. Based on molecular analyses, *Strotometra parvipinna* and *S. hepburniana* do not belong in the same genus. They fall paraphyletically alongside the genera *Monachometra, Charitometra, Glyptometra,* and *Chondrometra* (Hemery 2011, Fig. 4). This corroborates A.H. Clark's (1950) remarks that *S. parvipinna* closely resembled *Glyptometra tuberosa* (Carpenter, 1888) and Gislén's (1934) observation that the arm division pattern in *S. parvipinna* is similar to that of *Monachometra fragilis* (AH Clark, 1912). *S. parvipinna* and *S. hepburniana* are also treated tentatively here as same species, as they differ only on size-related characters. Further genetic testing to compare *Strotometra* with *Poecilometra* and *Chlorometra* is recommended.

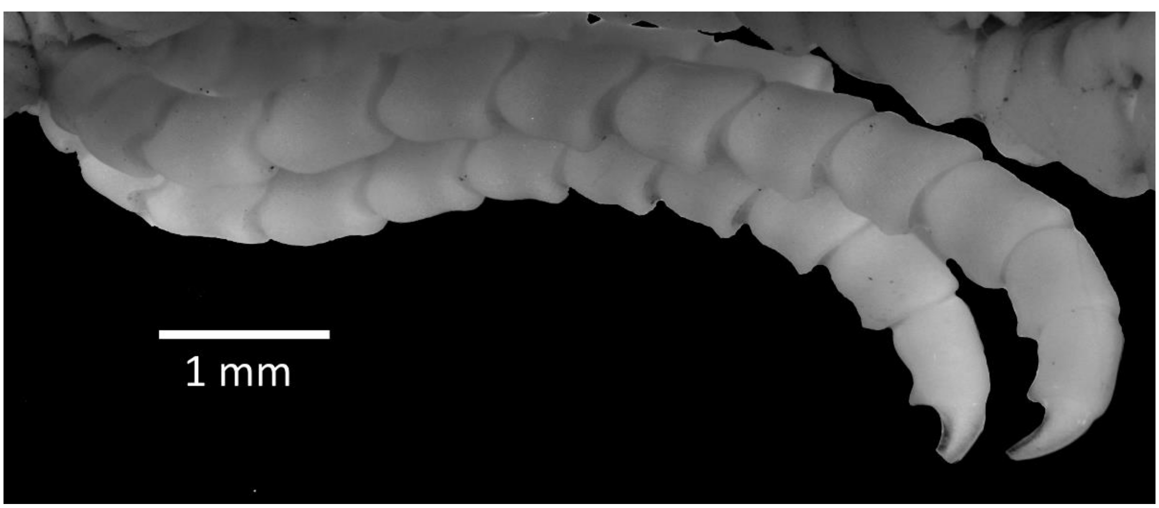

Figure 28. Short and stout cirri of *Strotometra parvipinna* CZM.

Figure 29. Expanded genital pinnules of *Strotometra hepburniana* CZM (no cat no.), here treated as a synonym of *S. parvipinna.*

Strotometra parvipinna P. H. Carpenter, 1888

Antedon parvipinna P. H. Carpenter 1888:127, pl. 15, fig. 9.—Hartlaub 1895:130.—Hamann 1907:1578.—A. H. Clark 1912b:33

Antedon hepburniana: A. H. Clark 1907b:139

Charitometra parvipinna: A. H. Clark 1907a:361

Charitometra hepburniana: A. H. Clark 1907a:361; 1908a:603

Strotometra parvipinna: A. H. Clark 1909a:20; 1912b:33, 226; 1913:50; 1918:pl. IX, 192, 194, 274-275.—Gislén 1928:9; 1934:18.—A. H. Clark 1950:365-368, 370

Strotometra hepburniana: A. H. Clark, 1909a:20; 1909b:187; 1912:226; 1913:179; 1913:50; 1915:215; 1918:192, 194, pl. IX; 1921:pl. 2, fig. 28; 1950:367-370, pl. 31 figs. 95-96, pl. 32 fig. 104.—Kogo 1968:51; 1998:115-116.—Hemery 2011:179-188, figs. IV.B.1-IV.B.10

Materials Examined.—CZM (no cat no.), Danish Expedition to the Kei Islands station 56, Kei Islands, 5°33'S, 132°51'30"E, 245m, 1922, 3 specimens; USNM 3142, Danish Expedition to the Kei Islands station 56, Kei Islands, 5°33'S, 132°51'30"E, 245m, 1922, 4 specimens; USNM E418, Siboga station 297, Lesser Sunda Islands, 10°39'S, 123°40'E, 520m, 1900, 2 specimens; CZM (no cat no.), Captain Schönau, Eastern Sea, 32°10'N, 128°20'E, 180m; CZM (no cat no.), Japan, 1911.

Holotype.— BMNH, Challenger station 192, Kei Islands, 5°49'15"S, 132°14'15"E, 256m, 1874.

Description.—Centrodorsal low hemispherical or discoidal, diameter 1.5-2.0mm, DH 3:1 (Fig. 30). Polar area flat, roughened, almost as wide as diameter (Fig. 31). Cirri X-CV, 10-15, 5-7mm, arranged in a single or partially double marginal row. Cirrals of uniform length after very short C1; following cirrals square, LW 1.0; penultimate cirral with prominent opposing spine, terminal claw as long as penultimate cirral with stout curve (Fig. 28).

Radials visible as interradial tubercules. Brachitaxes and br_{1-2} closely apposed with flat margins and a medial keel. Ibr_1 short, rectangular, WL 3.0-4.0. $1ax_2$ triangular or pentagonal, WL 2.5-3.0.

Arms 10, longest 45-60mm. Br1 and br2 with exterior margins closely apposed; wider than long, WL 1.5. Br3+4 short, rectangular, WL 2.5-3.0. Br_{5-10} rectangular, br_{11-17} wedge-shaped, both WL 2.0; distal brachials triangular, WL 1.0-1.5 (Fig. 32).

P1 of 16-22 pinnulars, 3-6mm long. P2 of 11-13 pinnulars, 3-6mm long. Distal pinnules of 11-12 pinnulars, 3.5-4mm long.

Gonads on P3 to P6; genital pinnules broad at base, tapering to a thin tip; proximal pinnulars broad, expanding gradually to very broad $P_{(3-5)}$ genital pinnulars with pronounced distal ends (Fig. 29); globose gonad followed by 5-6 smaller pinnulars narrowing to a fine tip.

Remarks.—A. H. Clark (1950) noted the many similarities between *Strotometra hepburniana* and *S. parvipinna* (Figs. 33, 34), with overall size and the pinnules the most visible differences between the two. The expanded genital pinnules of the *S. parvipinna* type specimen may exhibit distinct lateral extensions especially visible from the aboral surface, giving them an axehead-like appearance (Fig. 35). Molecular analysis by Hemery (2011) places these two as the same species (Fig. 4); it may be that *parvipinna*-type (found in Indonesia) and *hepburniana*-type (Japan) represent two very closely related subspecies. I have tentatively synonymized both as *S. parvipinna*, the senior of the two names.

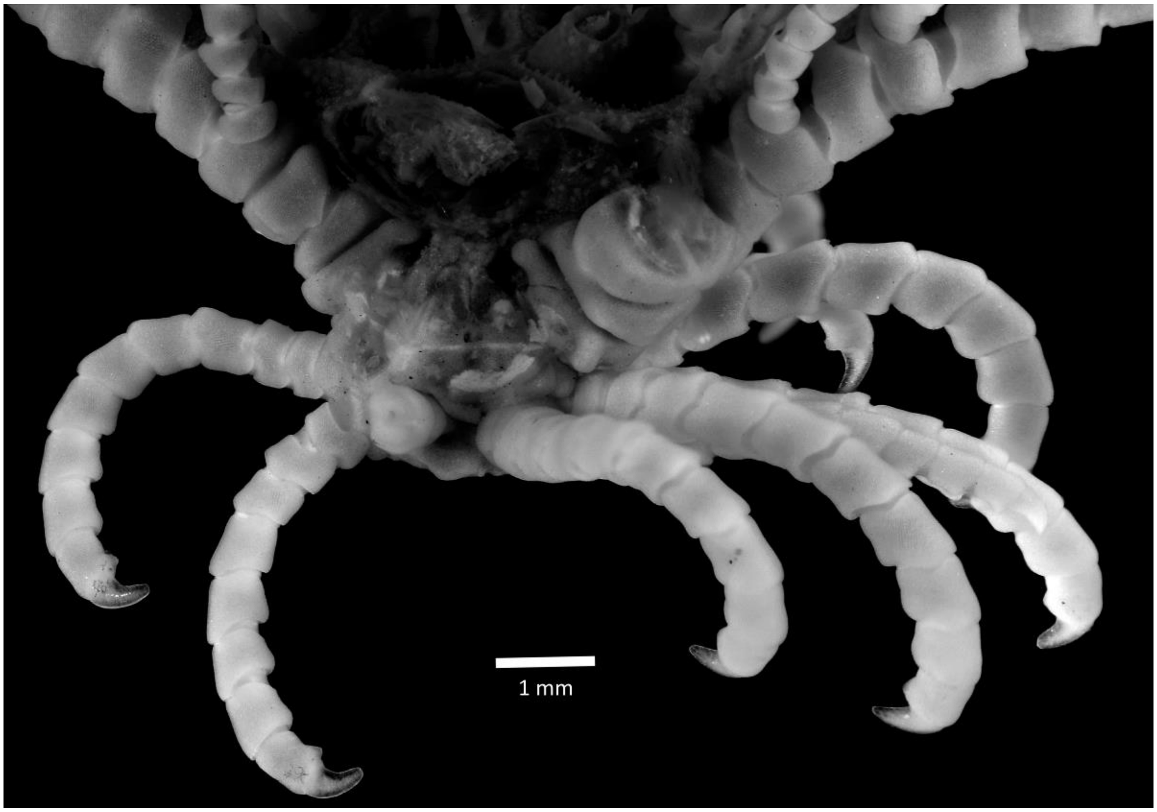

Figure 30. Centrodorsal of *Strotometra hepburniana* CZM, treated here as a synonym of *S. parvipinna*.

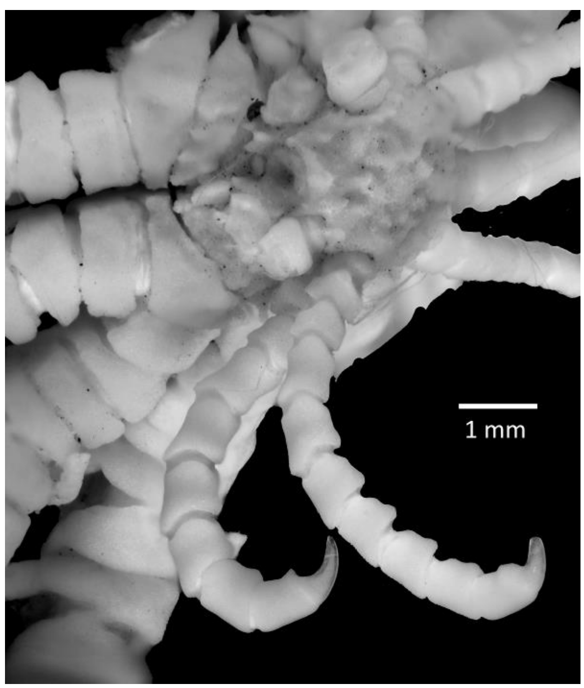

Figure 31. Centrodorsal of *Strotometra parvipinna* CZM*.*

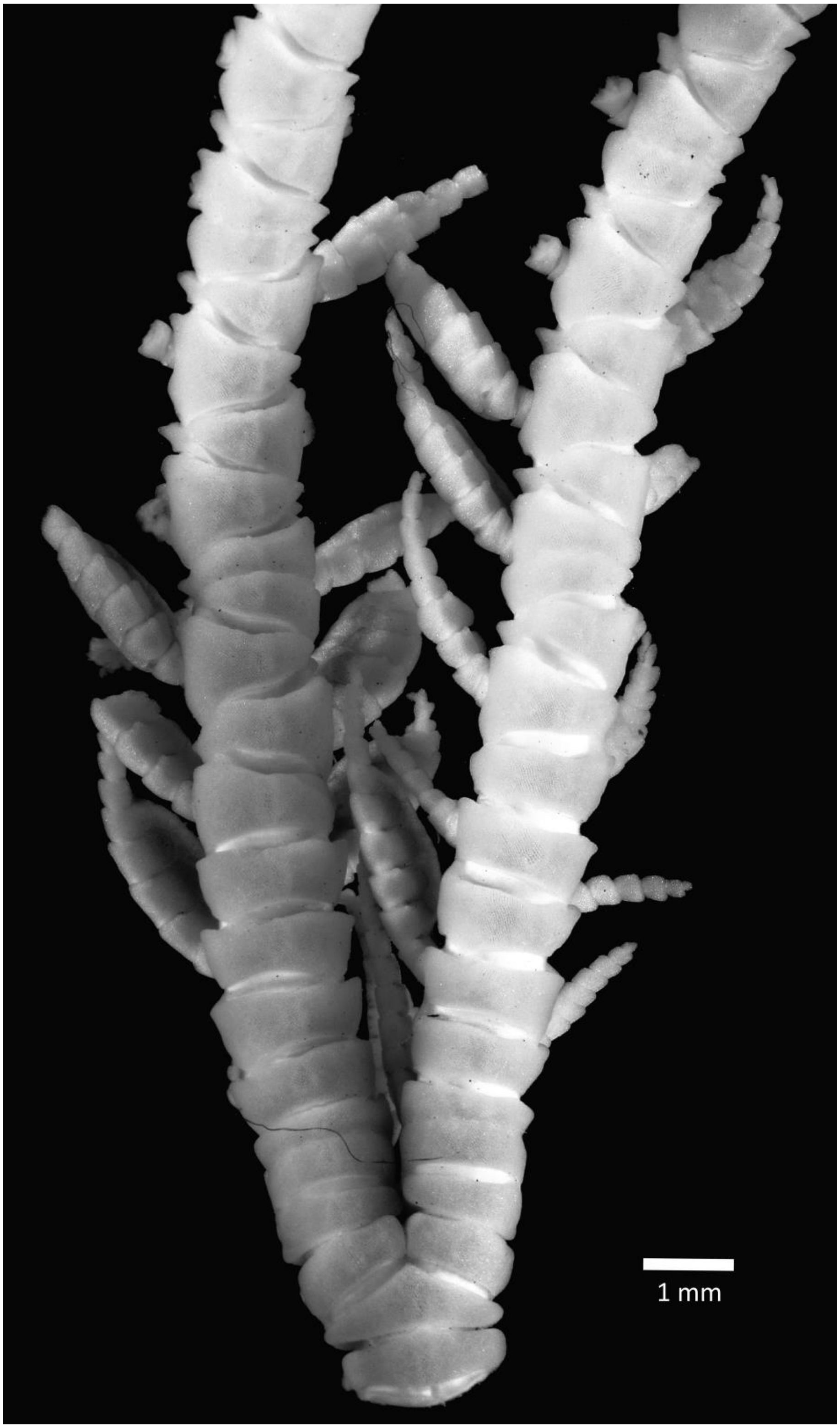

Figure 32. Ray showing division series, proximal and middle brachials, and syzygies. Specimen labeled as *Strotometra hepburniana* CZM, here treated as a synonym of *S. parvipinna.*

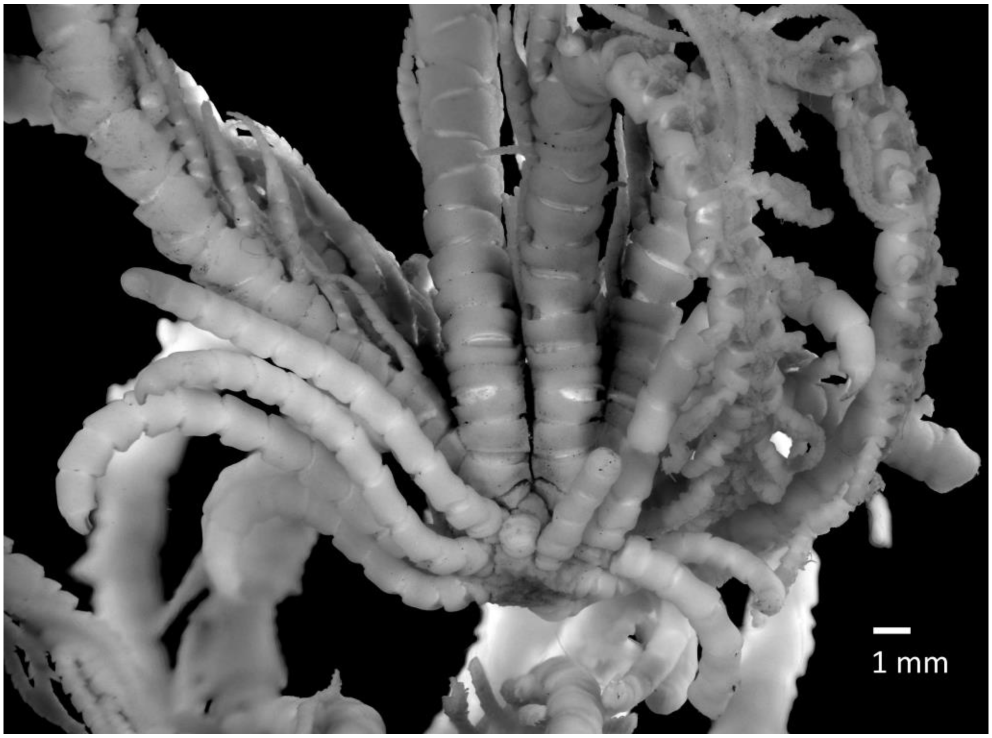

Figure 33. Full specimen of *Strotometra parvipinna* CZM for comparison with Figure 34.

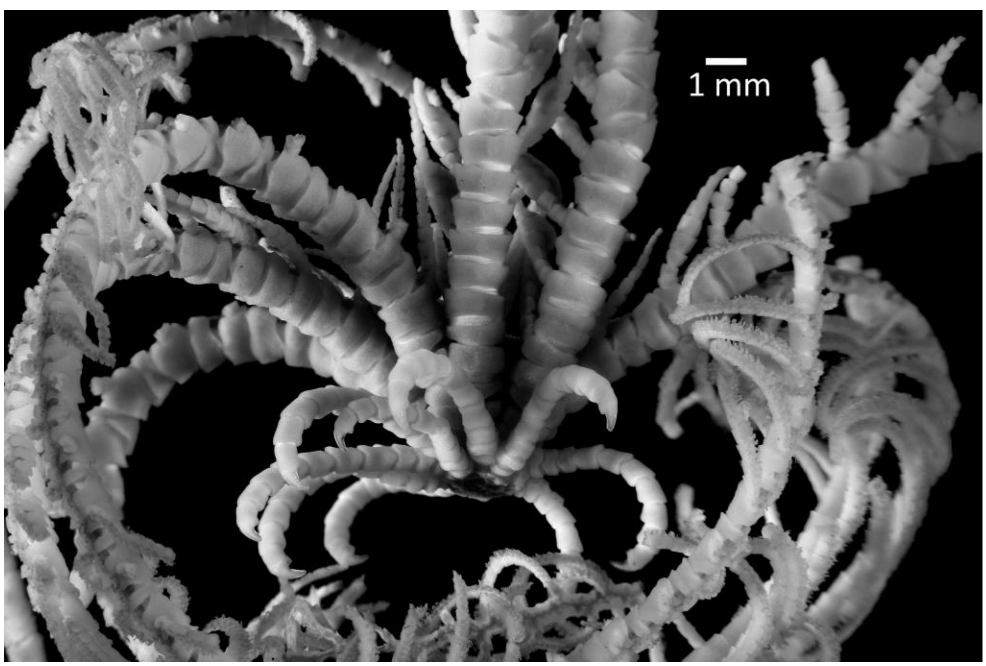

Figure 34. Full specimen of *Strotometra hepburniana* CZM, here treated as a synonym of *S. parvipinna,* for comparison with Figure 33.

Figure 35. Genital pinnules of *Strotometra parvipinna* CZM. a: axehead-like lateral extensions of pinnulars.

Other Notes

Scanning Electron Microscopy.---

Initial research with scanning electron microscopy pointed at two different types of genital pinnular cross-sections, a symmetrical V-shape (in *Poecilometra tibicinem* n. sp.), and an asymmetrical hook-like shape (in *Glyptometra lateralis*) (Fig. 36a, 36b). It was hypothesized that the symmetrical pinnular would be found in all of the genera with expanded genital pinnules and could be used as a diagnostic character, but it was found in other members of the Charitometridae. The presence of the symmetrical pinnulars in *Strotometra parvipinna* (Fig. 36c) and the molecular analysis by Hemery (2011) made it clear that the symmetrical V-shaped pinnular is an unreliable characteristic.

Preliminary SEM work on several charitometrid genera also revealed an undescribed stereomic structure on the proximal brachial articulations in the medial angles of the muscular fossae (Fig. 37). This structure occurs in varying degrees of development and distinctness in the genera with gradually tapering genital pinnules, but also in *Strotometra parvipinna* (Fig. 37b). *Poecilometra priamus (*Fig. 37c) and *Stylometra spinifera*, a member of the supposedly closely related Thalassometridae, both lack this feature. It was not possible to subject the rest of the *Poecilometra* to SEM analysis. Further research into this structure might provide a useful diagnostic characteristic for the two clades within the Charitometridae.

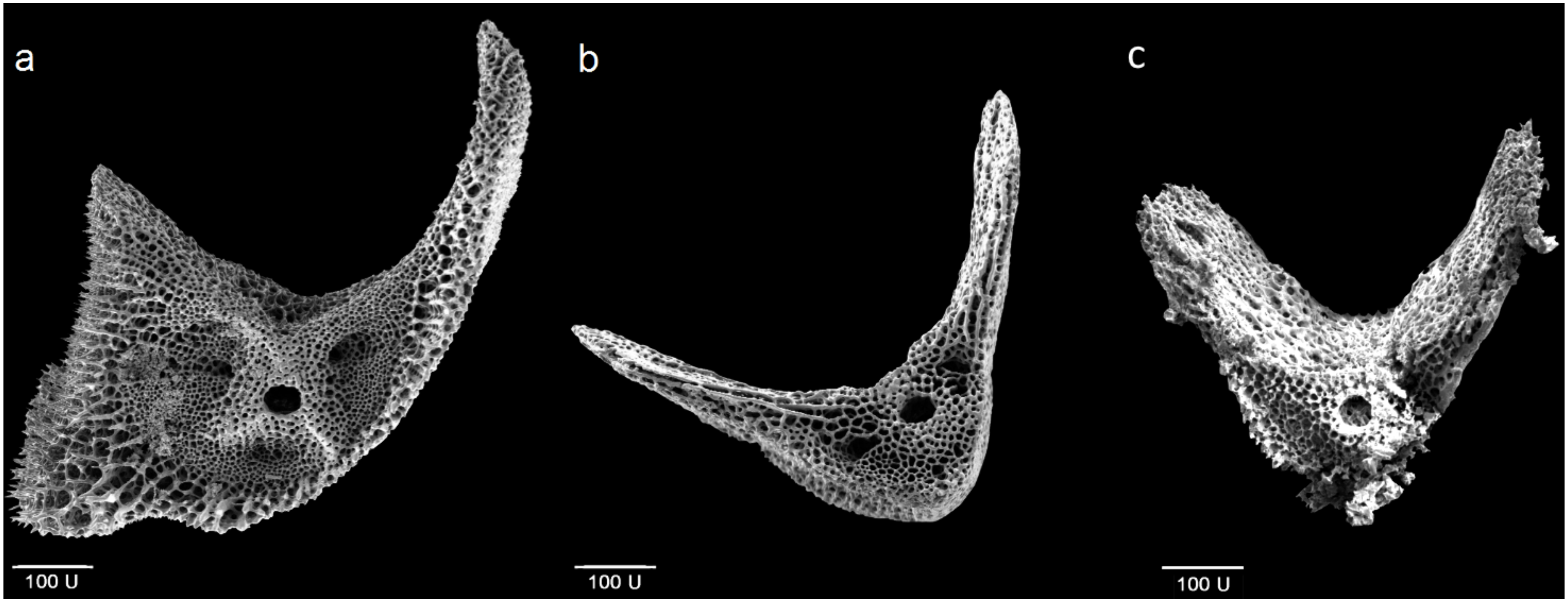

Figure 36. SEM images of Charitometridae genital-bearing pinnulars: a) Asymmetrical hook-shaped pinnular from *Glyptometra lateralis* FSU-2680; b) Symmetrical V-shaped pinnular from *Poecilometra tibicinem* holotype MNHN EcCh193; c) Symmetrical V-shaped pinnular from *Strotometra parvipinna* USNM E3142.

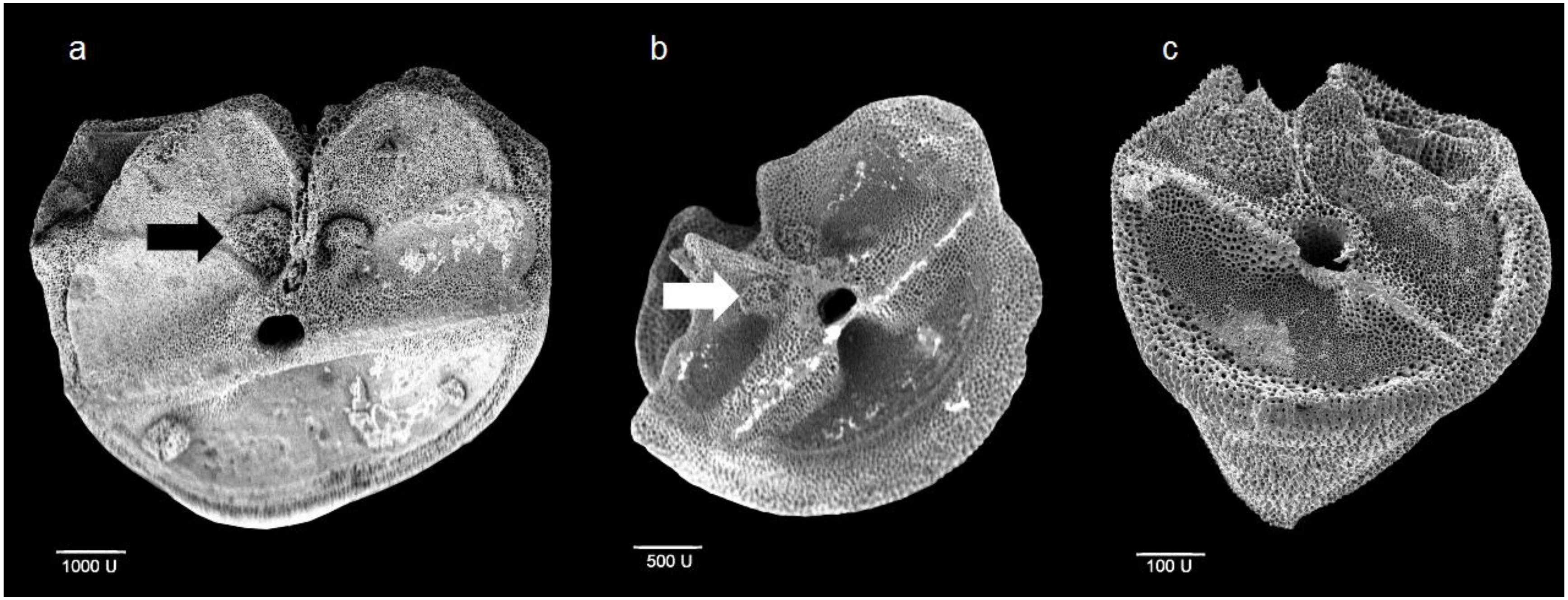

Figure 37. SEM images of brachial articulations: a) *Monachometra robusta*; b) *Strotometra parvipinna* USNM E3142; c) *Strotometra priamus* USNM E427*.* Arrows indicate new stereomic structure on muscular fossae.

Conclusion

The family Charitometridae appeared to be divisible into two components, separating genera with abruptly expanded, pedunculate genital pinnules from those with broad, tapering genital pinnules. Morphological and previously published molecular investigations were used to analyze the family and concluded the following.

Two members of genus *Strotometra* were moved to *Poecilometra* on the basis of their abruptly expanded, pedunculate genital pinnules: *Poecilometra priamus* and *P. ornatissimus.* The remaining two members of *Strotometra, S. hepburniana* and *S. parvipinna* were found to be morphologically similar, and Hemery (2011) found them to be molecularly identical (Fig. 4). They are treated as synonyms herein, as the senior *S. parvipinna*.

The diagnosis of *Poecilometra* was redefined to include the presence of pedunculate genital pinnules as well as aborally-directed flanges on $P_{(1)}$.

Poecilometra tibicinem n. sp., was named, described, and tentatively placed in *Poecilometra* on the basis of its distinctive aborally-directed, winglike flanges and its pedunculate genital pinnules. *P. tibicinem* is also unusual in having 20 arms, a trait not found in most of the genera with expanded genital pinnules. It is morphologically similar to *P. ornatissimus* and *P. priamus*, and the three may form a distinct clade within *Poecilometra*.

Morphological data in conjunction with Hemery's (2011) analysis finds that abruptly expanded genital pinnules (but not pedunculate pinnules) is a polyphyletic trait. *Strotometra parvipinna* is more closely related to *Glyptometra inaequalis* than *Poecilometra ornatissimus*, and *Charitometra basicurva* is closely related to an unknown

Glyptometra species (Fig. 4).

Future studies should focus on molecular analysis of the Charitometridae. Hemery's (2011) analysis left out three genera: *Charitometra*, *Chlorometra* and *Poecilometra*. The two differing morphological clades in *Poecilometra* may represent two separate genera, and morphological analysis would help determine if the $P_{(1)}$ flanges and pedunculate genital pinnules are monophyletic. Further studies should attempt to do a full scanning electron microscopy analysis of Charitometridae brachials to determine the usefulness of the unknown stereomic structure as a diagnostic characteristic.

Literature Cited

Baumiller, T. K., M. LaBarbera, & J. D. Woodley. 1991. Ecology and functional morphology of the isocrinid Cenocrinus asterius (Linnaeus) (Echinodermata: Crinoidea): in situ and laboratory experiments and observations. Bulletin of Marine Science 48: 731—748.

Baumiller, T. K. 2008. Crinoid ecological morphology. Annual Reviews of Earth and Planetary Sciences 36: 221—49.

Birenheide, R., & T. Motokawa. (1994). Morphological basis and mechanics of arm movement in the stalked crinoid Metacrinus rotundus (Echinodermata, Crinoida). Marine Biology 121: 273—283.

Bell, F. J. 1905. Echinoderma found off the coast of South Africa. IV. Crinoidea. Marine Investigations in South Africa 4:139—142.

Carpenter, P. H. 1880. Feather-stars, recent and fossil. Popular Science Review 4(15):193—204.

Carpenter, P. H. 1884. Report upon the Crinoidea collected during the Voyage of H.M.S. Challenger during the Years 1873-76, Report of the Scientific Results of the

Exploratory Voyage of the H.M.S. Challenger, Zoology, Part I, General morphology, with descriptions of the stalked crinoids, v. 11 (1884): 1—442 pp., text-fig. 1—21, pl. 1—62.

Carpenter, P. H. 1887. Notes on Echinoderm morphology, no. X. On the supposed presence of symbiotic algae in *Antedon rosacea*. Quarterly Journal of Microscopical Science 27:379—391.

Carpenter, P. H. 1888. Report upon the Crinoidea collected during the voyage of H.M.S. Challenger during the Years 1873-76, Report of the Scientific Results of the Exploratory Voyage of the H.M.S. Challenger, Zoology, Part II, The Comatulae, v. 26 (1888):1—400 pp., text-fig. 1—6, pl. 1—70.

Clark, A. H. 1907a. New genera of recent free crinoids. Smithsonian Miscellaneous Collection, Quarterly Issue 50(3):343—364.

Clark, A. H. 1907b. Description of new species of recent unstalked crinoids from the coast of northeastern Asia. U.S. National Museum, Proceedings 33:127—156.

Clark, A. H. 1908a. New genera of unstalked crinoids. Biological Society of Washington, Proceedings 21:125—136.

Clark, A. H. 1908b. Some Points in the Ecology of Recent Crinoids. American Naturalist

42(503):717—726.

Clark, A. H. 1908c. Description of new species of crinoids, chiefly from the collections made by U.S. Fisheries steamer "Albatross" at the Hawaiian Islands in 1902; with remarks on the classification of the Comatulida. U.S. National Museum, Proceedings 34:209—239.

Clark, A. H. 1908d. Notice of some crinoids in the collection of the Museum of Comparative Zoology. Harvard University, Museum of Comparative Zoology, Bulletin 51(8):233—248.

Clark, A. H. 1909a. A revision of the crinoid families Thalassometridae and Himerometridae. Biological Society of Washington, Proceedings 22:1—22.

Clark, A. H. 1909b. On a collection of crinoids from the Zoological Museum of Copenhagen. Vidensk. Medd, Dansk Naturhist. Foren. 61:115—195.

Clark, A. H. 1911a. The recent crinoids of Australia. Australian Museum, Memoir 4, pt. 15:705—804.

Clark, A. H. 1912a. Six new East Indian crinoids belonging to the family Charitometridae. Biological Society of Washington, Proceedings 25:77—84.

Clark, A. H. 1912b. The crinoids of the Indian Ocean. Echinoderma of the Indian Museum, pt. 7, Crinoidea. The Indian Museum, Calcutta, 325 pp.

Clark, A. H. 1913. Notes on the recent crinoids in the British Museum. Smithsonian Miscellaneous Collection 61(15):1—89.

Clark, A. H. 1915. The bathymetrical and thermal distribution of the unstalked crinoids, or comatulids, occurring on the coasts of China and Japan. Journal of the Washington Academy of Sciences 5(6):213—218.

Clark, A. H. 1916. Six new genera of unstalked crinoids belonging to the families Thalassometridae and Charitometridae. Washington Academy of Sciences, Journal 6(17):605—608.

Clark, A. H. 1918. The unstalked crinoids of the Siboga Expedition. Siboga Expedition 42b:1—300, 28 pl.

Clark, A. H. 1931. A monograph of the existing crinoids. 1. The comatulids. Part 3. Superfamily Comasterida. Bulletin of the United States National Museum 82(3):816pp., 82 pls.

Clark, A. H. 1941. A monograph of the existing crinoids. 1. The comatulids. Part 4a. Superfamily Mariametrida (except the family Colobometridae). Bulletin of the

United States National Museum 82(4a):603pp., 61 pls.

Clark, A. H. 1947. A monograph of the existing crinoids. 1. The comatulids. Part 4b. Superfamily Mariametrida (concluded- the family Colobometridae) and Superfamily Tropiometrida (except the families Thalassometridae and Charitometridae). Bulletin of the United States National Museum 82(4b):473 pp., 43 pls.

Clark, A. H. 1950. A monograph of the existing crinoids. 1. The comatulids. Part 4C. Superfamily Tropiometrida (the families Thalassometridae and Charitometridae). Bulletin of the United States National Museum 82(4c):383pp., 32 pls.

Clark, A. H., & A. M. Clark. 1967. A monograph of the existing crinoids. 1. The comatulids. Part 5. Suborders Oligophreata (concluded) and Macrophreata. Bulletin of the United States National Museum 82(5):860pp.

Cohen, B. L., N. Améziane, M. Eleaume, & B. Richer de Forges. 2004. Crinoid phylogeny: a preliminary analysis. Marine Biology 144:605—617.

Gislén, T. 1922. The crinoids from Dr. S. Bock's expedition to Japan 1914. Regiae Soc. Sci. Upsaliensis, Nova Acta, ser. 4, v. 5, no. 6:1—183, text-fig. 1—162, pl. 1, 2.

Gislén, T. 1924. Echinoderm studies. Zool. Bidrag fran Uppsala 9:1—316.

Gislén, T. 1928. Notes on some crinoids in the British Natural History Museum. K. Svenska Vetenskapsakad., Arkiv f. Zoologi 19A (32):1—15.

Gislén, T. 1934. A reconstruction problem: Analysis of fossil comatulids from North America, with a survey of all known types of comatulid arm ramifications. Lunds Universitets Årsskrift (Acta Univ. Lundensis), new series, 30(2):1—59.

Hamann, O. 1907. Dr. H. G. Bronne’s Klassen und Ordnungen des Tier-Reichs. Leipzig und Heidelberg, Leipzig, Germany, Bd. 2, Abt. 3, Bu. 5, 1602 pp.

Hartlaub, C. 1891. Beitrag zur Kenntniss der Comatuliden Fauna des Indischen Archipels. Nova Acta K. Leop. Carol. Akad. Naturforscher 58(1):1—120, pl. 1—5.

Hartlaub C. 1895. Reports on the dredging operations off the west coast of Central America to the Galapagos, to the west coast of Mexico, and to the Gulf of California, charge of Alexander Agassiz, carried on by the U.S. Fish Commission steamer "Albatross," during 1891, Lieut.-Commander Z. L. Tanner, U. S. N., commanding. Die Comatuliden. Bulletin of the Museum of Comparative Anatomy, Harvard, 27(4):129—152, pls. 1-4.

Hartlaub, C. 1912. Reports on the results of dredging under the supervision of Alexander

Agassiz in the Gulf of Mexico (1877-78), in the Caribbean Sea (1878-79), and along the Atlantic Coast of the United States (1880) by the U.S. Coast Survey Steamer "Blake". XLV. Die Comatuliden. Harvard Univ., Museum Comp. Zoology, Mem. 27(4):277—491, pl. 1—18.

Hemery, L. G. 2011. Diversite moleculaire, phylogeographie et phylogenie des Crinoides (Echinodermes) dans un environnement extreme: l'ocean Austral. PhD Dissertation. Museum national d'Histoire naturelle, Paris, 381 pp.

Hemery, L. G., M. Roux, N. Ameziane, & M. Elaume. 2013. High-resolution crinoid phyletic inter-relationships derived from molecular data. Cahiers de Biologie Marine 54:511—523.

Hess, H., & C. G. Messing. 2011. Part T: Echinodermata 2. Revised Crinoidea, Volume 3, pp.1—261 *in* P. A. Selden, ed., Treatise on Invertebrate Paleontology. University of Kansas Paleontological Institute, Lawrence, Kansas.

International Commission on Zoological Nomenclature, 1999. International Code of Zoological Nomenclature, 4th edition. International Trust for Zoological Nomenclature, London, 289 pp.

Jangoux, M. 1982. Chapter 8: Digestive systems: Crinozoa. Pp. 185—190. *in* M. Jangoux & J. M. Lawrence, Echinoderm Nutrition, First Edition. CRC Press, Rotterdam, Netherlands, 700 pp.

Kogo, I. 1998. Crinoids from Japan and its adjacent waters. Special publications from Osaka Museum of Natural History 30: 148 pp.

Macurda, D.B., Jr., & D. L. Meyer. 1974. Feeding posture of modern stalked crinoids. Nature 247(5440):394—396.

McKnight, D. G. 1975. Some echinoderms from the northern Tasman sea. NZOI Records 2(5):49—76.

McKnight, D. G. 1977a. Additions to the New Zealand crinoid fauna. NZOI Records 3(11):93—112.

McKnight, D. G. 1977b. Some crinoids from the Kermadec Islands. NZOI Records 3(13):121—128.

McKnight, D. G. 1977c. Crinoids from Norfolk Island and Wanganella Bank. NZOI Records 3(14):129—137.

McKnight, D. G. 1989. Further crinoids (Echinodermata) from off the Kermadec Islands, southwest Pacific Ocean. DMFS Reports 3(3):31—35.

Messing, C.G., M. C. RoseSmyth, S. R. Mailer, & J. E. Miller. 1988. Relocation movement in a stalked crinoid (Echinodermata). Bulletin of Marine Science 42:480—487.

Messing, C. G., A. C. Neumann, & J. C. Lang. 1990. Biozonation of deep-water lithoherms and associated hardgrounds in the northeastern Straits of Florida. Palaios 5:15—33.

Messing, C. G. 1997. Living Comatulids. pp. 3—30 *in* J. A. Waters & C. G. Maples, eds., Geobiology of Echinoderms. Paleontological Society Papers Volume 3, 355 pp.

Messing C. G., N. Améziane, & M. Eleaume. 2000. Echinodermata Crinoidea: Comatulid crinoids of the KARUBAR Expedition to Indonesia. The families Comasteridae, Asterometridae, Calometridae and Thalassometridae. Pp. 627-702. *in* Crosnier, A. (ed.), Résultats des Campagnes MUSORSTOM, vol. 21. Mémoires du Muséum national d'Histoire naturelle, 184, 813 pp.

Messing, C. G. 2007. The crinoid fauna (Echinodermata: Crinoidea) of Palau. Pacific Science 61(1):91—111.

Messing, C. G., & J. H. Dearborn. 1990. Marine flora and fauna of the northeastern United States. Echinodermata: Crinoidea. National Oceanic and Atmospheric Administration Technical Report NMFS 91, 29 pp.

Meyer, M. 1982. Chapter 2: Food and feeding mechanisms: Crinozoa. Pp. 25—41. *in* M. Jangoux & J. M. Lawrence, Echinoderm Nutrition, First Edition. CRC Press, Rotterdam, Netherlands, 700 pp.

Meyer, D.L., C. A. LaHaye, N. D. Holland, A. C. Arneson, & J. R. Strickler. 1984. Time-lapse cinematography of feather stars (Echinodermata: Crinoidea) on the Great Barrier Reef, Australia: demonstrations of posture changes, locomotion, spawning and possible predation by fish. Marine Biology 78:179—184.

Meyer, D. L., & D. B. Macurda, Jr. 1977. Adaptive radiation of the comatulid crinoids. Paleobiology 3:74—82.

Minckert, W. 1905. Das Genus *Promachocrinus*, zugleich ein Beitrag zur Faunistik der Antarktis. Zool. Anzeiger 28:490—501.

Mironov, A. N. 2000. New taxa of stalked crinoids from the suborder Bourgueticrinina (Echinodermata, Crinoidea). Zoologicheskii Zhurnal 79(6):712—728.

Mironov, A. N., & O. A. Sorokina. 1998. Sea lilies of the order Hyocrinida (Echinodermata, Crinoidea). Zoologicheskie Issledovania 2:118 pp., 13 pl.

Nichols, D. 1960. The histology and activities of the tube feet of *Antedon bifida*.

Quarterly Journal of Microscopial Science 101:105—117.

Oji, T., & K. Kitasawa. 2008. Discovery of two rare species of stalked crinoids from Okinawa Trough, southwestern Japan, and their systematic and biogeographic implications. Zoological Science 25(1):115—121.

Rankin, D. L. 2000. A taxonomic evaluation of the comatulid genus *Stephanometra* (Echinodermata: Crinoidea). Masters thesis. Nova Southeastern University, Fort Lauderdale, Florida, 136 pp.

Rankin, D. L., & C. G. Messing. 2008. A revision of the comatulid genus *Stephanometra* AH Clark with a rediagnosis of the genus *Lamprometra* AH Clark (Echinodermata: Crinoidea). Zootaxa 1888:1—35.

Rouse, G. W., L. S. Jermiin, N. G. Wilson, I., Eeckhaut, D. Lanterbecq, T. Oji, C. M. Young, T. Browning, P. Cisternas, L. E. Helgen, M. Stuckey, & C. G. Messing. 2013. Fixed, free, and fixed: The fickle phylogeny of extant Crinoidea (Echinodermata) and their Permian-Triassic origin. Molecular Phylogenetics and Evolution 66:161—181.

Roux, M., C.G. Messing, & N. Améziane. 2002. Artificial keys to the genera of living stalked crinoids (Echinodermata). Bulletin of Marine Science 70(3):799—830.

Roux, M. 2004. New hyocrinid crinoids (Echinodermata) from submersible investigations in the Pacific Ocean. Pacific Science 58(4):597-613.

Shaw, G. D., & A. R. Fontaine. 1990. The locomotion of the comatulid *Florometra serratissima* (Echinodermata:Crinoidea) and its adaptive significance. Canadian Journal of Zoology 68:942—950.

Shipley, A. E., & E. W. MacBride. 1901. Zoology: An elementary textbook. The MacMillan Company, New York City, New York, 632 pp.

Simms, M. J. 1993. Reinterpretation of thecal plate homology and phylogeny in the Class Crinoidea. Lethaia 26:303—312.

Smith, A. B. 1984. Classification of the Echinodermata. Palaeontology 27(3):431—459.

Summers, M. M., C. G. Messing, & G. W. Rouse. 2014. Phylogeny of Comatulidae (Echinodermata: Crinoidea: Comatulida): A new classification and an assessment of morphological characters for crinoid taxonomy. Molecular Phylogenetics and Evolution 80:319—339.

Taylor In Press (submitted).

Tunnicliffe et al. (submitted).

Utinomi, H., & I. Kogo. 1965. A revised catalogue of crinoids collected from Japanese waters. Proceeding of the Japanese Society of Systematic Zoology 4:46—53.

White, C. M. 2000. The initial inquiry into the phylogeny of the family Comasteridae (Echinodermata: Crinoidea) from mitochondrial DNA sequence data. Masters thesis. Nova Southeastern University, Fort Lauderdale, Florida, 86 pp.