

Contributions

from the Museum of Paleontology, University of Michigan
VOL. 34, NO. 12, PP. 158-192

JUNE 9, 2022

A REVISION OF THE FEATHER STAR GENERA *POECILOMETRA* AND *STROTOMETRA* (ECHINODERMATA: CRINOIDEA: CHARITOMETRIDAE)

BY

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Abstract — The chiefly tropical, deep-water (>100 m) feather star family Charitometridae (Echinodermata: Crinoidea: Comatulida) currently consists of 34 species in eight genera and has not been revised since 1950. Recent molecular analyses and the discovery of both new specimens of known species and a new species prompted a morphological re-examination of those genera with abruptly expanded genital pinnules. As a result, *Poecilometra* is redescribed, and now includes four species, including two formerly placed in *Strotometra*, plus *Poecilometra baumilleri* n. sp. *Poecilometra scalaris* is placed in synonymy under *P. acoela*. *Strotometra* is redescribed and *S. hepburniana* placed in synonymy under *S. parvipinna*. The diagnoses of both genera and their component species are revised.

INTRODUCTION

Charitometridae A. H. Clark, 1909a, is a family of feather stars (Order Comatulida) that currently includes 34 species in eight genera, with the majority of specimens collected at depths between 200 and 600 m. The family is restricted to the Indo-western Pacific region except for monotypic, western Atlantic *Crinometra brevipinna* (Pourtalès, 1868). Most records are tropical, with a few species extending to temperate latitudes: Sagami Bay, Japan (Gislén, 1922, 1927; A. H. Clark, 1950; Kogo, 1998; Kogo and Fujita, 2005), East London, South Africa (Gislén, 1938), Ulladulla, NSW, Australia (Rowe and Gates, 1995), northern Gulf of Mexico (Meyer et al. 1978), Rio Grande do Sul, Brazil (Tommasi, 1969), and St. Helena (Gislén, 1933). Charitometrids can be important and sometimes dominant megafauna on hard substrates (Messing

et al. 2019, and unpublished observations). The taxonomy of the family was most recently revised more than one half a century ago (A. H. Clark, 1950) and remains based exclusively on morphology. Its history is particularly convoluted and is, therefore, summarized here.

Carpenter (1888) first arranged the species eventually placed in the family in a hierarchy of groups within series in genus *Antedon* and distinguished them based on arm number (i.e., ten vs. more than ten) and number of ossicles in brachitaxes (i.e., IIBr2 versus IIBr4(3+4) (see terminology and abbreviations below). A. H. Clark (1907a) established two genera for species formerly placed in Carpenter's groups: *Charitometra* A. H. Clark, 1907a, with 19 species (type species: *Antedon incisa* Carpenter, 1888) and *Poecilometra* A. H. Clark, 1907a (type species: *Antedon acoela* Carpenter, 1884, plus *A. scalaris* A. H. Clark, 1907b). His genus-level

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diagnostic features included up to 50 arms in the former, and only ten arms with sharply expanded genital pinnules in the latter. He (A. H. Clark 1908a) first placed *Charitometra* in the family Thalassometridae A. H. Clark, 1908a. Next, A. H. Clark (1909a) grouped it with *Poecilometra* in the thalassometrid subfamily Charitometrinae A. H. Clark, 1909a, with five new genera: *Glyptometra*, *Strotometra*, *Crinometra*, *Pachylometra*, and *Chlorometra*; and finally (A. H. Clark (1911) elevated the subfamily to family-level status as Charitometridae. Hartlaub (1912), who had inherited the large U.S. Coast and Geodetic Survey Steamer *Blake* collection from the late Carpenter, felt bound to use the earlier classification and restored all the included species to *Antedon*, an arrangement not followed since.

A. H. Clark (1916) added five more genera: *Crossometra* (3 species), *Perissometra* (11), and *Monachometra* (1) for species formerly in *Pachylometra* and *Glyptometra*; *Chondrometra* (3) for species formerly in *Chlorometra*; and *Calyptometra* for *Charitometra lateralis* A. H. Clark, 1908b. A. H. Clark's (1918) detailed key to the family included 42 species (including nine nominal species and 11 varieties of *Crinometra*) in twelve genera. Genus-level characters included relative lengths of proximal versus middle and distal pinnules; brachitaxes all of two ossicles versus IIBr4(3+4), narrow and laterally well-separated versus apposed with laterally flattened ossicles, and aborally keeled or not; genital pinnules with the third and fourth pinnulars (P_{3-4}) abruptly expanded versus a slight, gradually tapered expansion; 10 versus >10 arms; distal arms laterally compressed or not; centrodorsal shape, and overall size ("large" versus "small").

In a series of papers, Gislén (1922) first added *Diodontometra* (for *D. bocki* n. sp.), which raised the number of genera to 13. Although Gislén (1927, 1933) identified ambiguities among generic diagnoses, recommended transferring several species to different genera, and proposed characters of the centrodorsal and cirri as more reliable than arm ornamentation and relative pinnule lengths in distinguishing genera, e.g., cirri stout versus slender and with versus without aboral spines (Gislén, 1928), he maintained the 13 genera (Gislén, 1934).

In the last complete revision of the family, A. H. Clark (1950) concluded that many standard characters used in differentiating the genera were unimportant. He reduced the number of genera to eight, placing *Diodontometra* under *Chlorometra*; and *Calyptometra*, *Crossometra*, *Perissometra*, and *Pachylometra* under *Glyptometra*; and 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) two to four abruptly broader pinnulars with a shorter slender tip (*Chlorometra*, *Strotometra*, *Poecilometra*, and *Charitometra*). Within these two groups, distinguishing features at the generic level included compressed versus rounded arms, development of synarthrial tubercles, IIBr series of two versus four ossicles, and relative lengths of oral and genital pinnules (A. H. Clark, 1950). Inconsistencies

remain, however. In his remarks on the family, he considered the type of genital pinnules and length of oral pinnules as "unreliable and undiagnostic" (p. 198), but a few lines later noted that the "characters presented by the genital pinnules seem to be reliable." Although he placed *Monachometra* in the first group and *Chlorometra* in the second, he noted (p. 199) that the "genital pinnules of *Chlorometra* are very little different from those of *Monachometra*, of which *Chlorometra* should perhaps be regarded as a synonym." Similarly, he used similar variations in ornamentation to distinguish species of *Glyptometra* but only varieties (accepted as subspecies; ICZN 45.6.4) of *Crinometra brevipinna*. The taxonomy of the family has not been altered since, except for the addition of *Monachometra kermadecensis* McKnight, 1977a; and *Chondrometra crosnieri* Marshall and Rowe, 1981; and slight modifications of the familial and generic diagnoses in Hess and Messing (2011). Hemery's (2011) molecular phylogeny included 13 charitometrid terminals representing five genera. Of those with multiple species-level taxa, *Chondrometra* (2 terminals) returned as monophyletic, but both *Strotometra* (5) and *Glyptometra* (2) returned as polyphyletic. However, no species were re-assigned, and no taxonomy was revised. Other additions have been new faunal records, e.g., off Japan and adjacent waters (Kogo, 1998; Kogo and Fujita, 2005), New Zealand (McKnight, 1975, 1977a,b,c, 1989a,b,c), and in the tropical western Atlantic (Meyer et al., 1978) and ecological relationships, e.g., in the tropical western Atlantic (Messing et al., 1990) and northeastern Atlantic (Bullimore et al., 2013).

Within the order Comatulida, Charitometridae was long placed with several other families in a grouping variously treated as a suborder, tribe, subtribe, or superfamily (e.g., A. H. Clark, 1908b, 1932; Gislén, 1924) based primarily on the possession of pinnules that are triangular in cross section (prismatic) with a sharp or sharply rounded aboral (dorsal in earlier literature) keel. Other characters have included well-developed ambulacral plates (except in Tropiometridae), and distalmost pinnules extending beyond the minute terminal brachials (Gislén, 1924; A. H. Clark, 1931, 1947, 1950; Rasmussen, 1978). The other families in the most recent arrangement, as superfamily Tropiometroidea (Hess and Messing, 2011), are Thalassometridae A. H. Clark, 1908a, Calometridae A. H. Clark, 1911, Tropiometridae A. H. Clark, 1908a, Ptilometridae A. H. Clark, 1914, Asterometridae Gislén, 1924, and the fossil families Conometridae Gislén, 1924, Pseudoconometridae Eagle, 2001, and Pterocomidae Rasmussen, 1978. However, recent molecular analyses returned the superfamily as polyphyletic, with monophyletic Charitometridae sister to a deep-sea clade composed of the stalked Guillecrinidae Mironov and Sorokina, 1998, and the feather star family Pentametocrinidae A. H. Clark, 1908a, (Cohen and Pisera 2016; Rouse et al. 2013; Hemery et al. 2013; Hess and Messing, 2011).

Hemery's (2011) Maximum Likelihood and Bayesian Inference analyses of 13 charitometrid terminals (combined CO1, 16S, 28S and 18S) represent the most inclusive sequence data yet available for the family. Both analyses returned two

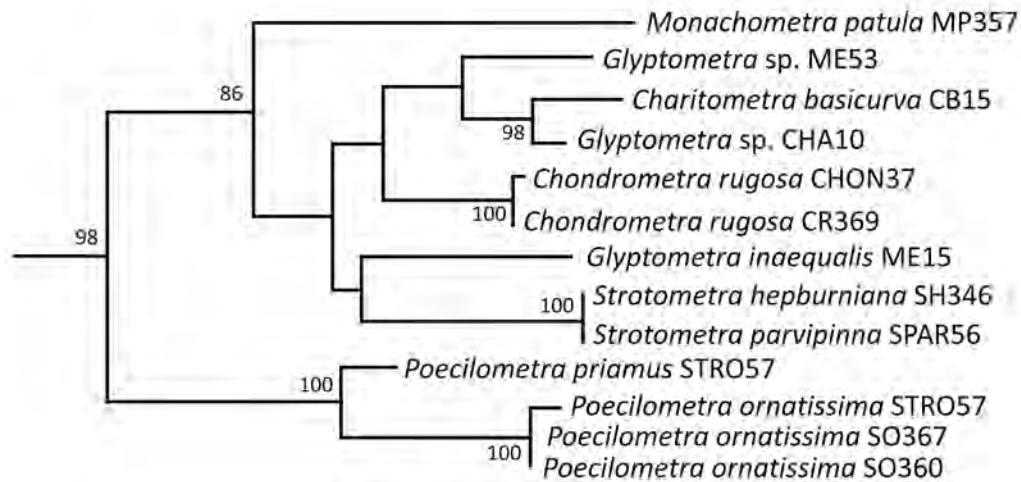


FIGURE 1 — Phylogeny of Charitometridae assembled from a Maximum Likelihood analysis of four combined genes (COI, 16S, 28S and 18S). Adapted from Hemery (2011, figure 4.B.9; bootstrap values shown on nodes are those >80%).

sister clades with the same composition. One clade returned with the same topology in both analyses: a *Poecilometra priamus* (originally identified as *Strotometra* n. sp.) sister to a clade of three *P. ornatissima* (originally a *Strotometra* sp. and two *S. ornatissimus*) terminals. The topology of the other clade differed between the two analyses. Figure 1 shows the ML results. In BI, a clade of *Strotometra hepburniana* and *S. parvipinna* returned basal to the seven remaining terminals representing five other charitometrid genera. Both analyses support the monophyly of *Poecilometra* and *Strotometra* as treated herein but returned *Glyptometra* as polyphyletic.

As noted above, A. H. Clark (1950) used the characters of the genital pinnules to divide the genera into two groups. The current work was prompted by an initial examination of several specimens, which suggested that the supposedly diagnostic expansion of the genital pinnules was not structurally similar among these genera and included specimens of an apparently new species. This paper focuses on two of the four genera and six of the nine species in A. H. Clark's (1950) second group: those supposedly with abruptly expanded genital pinnules followed by a short slender tip: *Poecilometra* (2 species) and *Strotometra* (4). Of the other two genera in that group, we point out here that *Charitometra* has genital pinnules more similar to those of A. H. Clark's other group of genera and provide evidence that monotypic *Chlorometra garrettiana* A. H. Clark, 1907b, also belongs with the first group of genera.

Terminology chiefly follows Messing and Dearborn (1990), Messing *et al.* (2000), and Hess (2011). Abbreviations are as follows: number of cirri in Roman numerals followed by the number of component segments (cirrals) in Arabic numerals (e.g., X–XV, 11–17), with individual cirrals indicated by 'C' (e.g., C5 = fifth cirral from the base). Arm branching series (brachitaxes, or division series) are numbered from the arm base (following the radial ossicle) with a Roman numeral followed by 'Br' and the number

of component ossicles by an Arabic numeral (e.g., IIIBr2 = third brachitaxis composed of two ossicles). 'br' indicates individual arm ossicles (brachials; br = plural) (e.g., IVbr2 = second ossicle of the fourth brachitaxis; br5 = fifth brachial of an undivided arm following the distalmost axil). Axils (the ossicles at which a ray branches) are indicated by 'ax' (e.g., IIIax4 = the fourth ossicle of the third brachitaxis is an axil). A plus sign (+) indicates a syzygy between two brachials (e.g., IIBr4(3+4) = second brachitaxis composed of four ossicles, with the third and fourth joined by syzygy; br9+10 = ninth and tenth brachials of an undivided arm joined by syzygy).

For ossicle proportions, LW = ratio of length to median width of a cirral or pinnular (in side view); WL = ratio of median width to midaboral length of a brachial (in aboral view) (the different ratios used in order to maintain values generally >1.0); DH = ratio of centrodorsal basal diameter to height. Pinnules are abbreviated P, with interior pinnules (those closest to the extrapolated axis of the preceding brachitaxis) indicated by lower case letters and exterior pinnules by Arabic numerals, e.g., Pe and P5 = fifth interior and exterior pinnules, respectively, counting from the most proximal. Following Messing (2020a, 2020b), individual pinnulars are indicated as Arabic subscript numerals in parentheses (e.g., P8₍₃₋₆₎ = third through sixth pinnulars of the eighth pinnule). Pinnulars of pinnules with unknown placement along the arm (e.g., detached) are noted with just the parenthetical (e.g., P(3–6), or perhaps Pgen₍₃₋₆₎ or Pmid₍₃₋₆₎, if the pinnule is recognizable as genital or arising from the middle portion of the arm, respectively). Pinnulars expanded over the gonad on genital pinnules are referred to as gonadal.

MATERIALS AND METHODS

We examined 12 specimens originally identified as *Poecilometra* (including the new species); 31 of *Strotometra*; three of *Glyptometra lateralis* (A. H. Clark, 1908c); one

of *Monachometra patula* (Carpenter, 1888); several of *Crinometra brevipinna* (Pourtalès, 1868); and photographs of type specimens belonging to *Charitometra basicurva* (Carpenter, 1888), *Charitometra incisa* (Carpenter, 1888), *Chondrometra rugosa* A. H. Clark, 1918, *Chondrometra crosnieri* Marshall and Rowe, 1981, *Chlorometra garrettiana*, *Glyptometra* spp., and *Monachometra* spp.

Specimens were examined with Wild M-5 or Leica M275 dissecting microscopes, both with camera lucida attachment. Most photographs were taken with a Canon EOS Rebel T3 camera directed through the Leica M275. Some specimens photographed in museums (e.g., Smithsonian, London, Amsterdam, Copenhagen, Leiden) were taken with equipment available at the institution. Images taken at multiple focal points were combined and rendered with Helicon Focus 7 Lite focus-stacking software and edited in a photo-editing program.

Pinnulars of some specimens were dissociated with full-strength commercial bleach (5% sodium hypochlorite solution) to examine ossicles 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 either an ISI-DS130 SEM (NSU Ocean Campus) or FEI ESEM Quanta 200 Environmental SEM (NSU School of Dentistry).

INSTITUTIONAL ABBREVIATIONS

FLMNH	—	Florida Museum of Natural History, Gainesville, Florida, U.S.A.
MNHN	—	Muséum national d'Histoire naturelle, Paris, France.
NHM	—	Natural History Museum, Cromwell Road, London, U.K.
NSU-CRI	—	Nova Southeastern University, Ocean Campus, Dania Beach, Florida, U.S.A. (Crinoid collection, Schure bldg. rm 205).
NIWA	—	National Institute of Water and Atmospheric Research, Auckland, New Zealand.
RMNH	—	Rijksmuseum van Natuurlijke Historie (formerly Amsterdam, now housed at Naturalis Biodiversity Centre, Leiden, Netherlands).
USNM	—	National Museum of Natural History, Smithsonian Institution, Washington, D.C., U.S.A. (United States National Museum)
UUZM	—	Uppsala University Museum of Evolution, Zoology section, Uppsala, Sweden.
NHMD	—	Natural History Museum Denmark.

TAXONOMIC SECTION

CHARITOMETRIDAE A. H. Clark, 1909a

Diagnosis.— Aboral apex of centrodorsal commonly rugose or tuberculate; no adoral radial pits. Cirrus sockets commonly with distinct articular tubercles and, in some genera, with marginal crenulae; sockets large, irregularly crowded or in 5, 10, or 15 distinct columns. Cirri typically of 20-30 cirrals (range 10-50); generally less than 20% of arm length, cylindrical or laterally compressed, and lacking transition segment. Cirrals usually <25 (rarely up to ~30), without aboral spines, but sometimes carinate or with low distal tubercle. Distal cirrals usually as long as wide or longer, often not much shorter than proximal cirrals. Rod-shaped basals exposed interradially or concealed. Subradial cleft commonly present. Radials concealed or narrowly exposed. Radial articular facet moderately sloping inward adorally; profile of facet straight with no angle or bend. Muscle fossae tall and narrow. Radial cavity narrow. Arms 10 to 33. IBr2 joined by synarthry; IIBr either 2 or 4(3+4); following brachitaxes 2, 2(1+2), or 4(3+4) (rarely 3(2+3) or 4 [no syzygy]); initial syzygies of undivided arms at br1+2, br3+4, or br1+2, 3+4; distal intervals between syzygies 2 to 26 (commonly 6 to 11) articulations. Arms aborally rounded or laterally compressed and carinate, often with rugose or tuberculate surface. P1, P2, and sometimes P3 (oral pinnules) more flexible and composed of more, mostly short, pinnulars than succeeding pinnules; lengths similar, or increasing or decreasing from the most proximal; number of pinnulars of oral pinnules usually decreasing from P1 onward. Pinnules triangular or rounded triangular in cross section (=prismatic), with distinct ambulacral covering plates; oral pinnules sometimes more rounded in cross section. Genital pinnules with proximal segments at least somewhat broadened, or with a few segments abruptly broadened, and covering gonad (modified from A. H. Clark, 1950; Hess and Messing, 2011).

Remarks.— Characters included in the diagnosis in Hess and Messing (2011) but omitted here, as they are widely variable and present in other feather star families as well or restricted to one genus within Charitometridae, are: centrodorsal hemispherical, conical, or truncated conical to discoidal with rounded or flattened, cirrus-free aboral apex; some species of *Monachometra* with a dorsal star.

Key to the Genera and Species of *Poecilometra* and *Strotometra*

1a. Genital pinnules with 3-5 narrow basal pinnulars following a usually wider P₍₁₎ and preceding expanded pinnulars bearing the gonad (pedunculate); expanded gonadal pinnulars symmetrical in cross-sectional view, with small articular area, especially the abambulacral ligament fossa, and long, thin lateral "wing-like" flanges; pinnulars distal to expanded gonadal pinnulars abruptly narrower; abambulacral side of P₍₁₎ of proximal pinnules with weak to well-developed

flange, or flattened, curved tongue directed aboral side of arm; arms 10–20.....*Poecilometra* (2)

1b. Genital pinnules with 1–2 narrow basal pinnulars or broadening gradually from the base and tapering gradually distal to gonad; no abambulacral projection on $P_{(1)}$; expanded gonadal pinnulars asymmetrical in cross-sectional view, with a longer, curved flange and usually shorter, thicker triangular flange, and articulation proportionally larger than in *Poecilometra*; arms 10.....*Strotometra parvipinna*

2a. Brachitaxes and br1-2 well separated with distinct gaps between adjacent ray bases, but with projecting lateral and/or proximal flanges; distal portion of genital pinnules shorter than gonad; 10 arms only.....3

2b. Brachitaxes and br1-2 laterally flattened and apposed against adjacent ossicles, often with everted lateral margins; 10 or up to 20 arms.....4

3a. Proximal and lateral aboral margins of Ibr1 with continuous curved flange overhanging radial proximally and almost bridging gap between adjacent rays laterally; cirri XX–XXV, up to 18, and ~22 mm long; longest cirrals with LW up to 2.2; distal portion of genital pinnules typically consisting of only 3–4 small, abruptly narrower pinnulars.....*Poecilometra acoela*

3b. Ibr1 with proximal margin almost straight to slightly convex, and lateral margins converging and bearing low thick lateral flange or ridge; cirri X–XVI, up to 19 cirrals, and 42 mm long; longest cirrals with LW chiefly 2.4–2.7; distal portion of genital pinnules consisting of up to 7 small, narrow pinnulars.....*Poecilometra baumilleri* n. sp.

4a. Distal edges of br2, br4, and br5 strongly everted as a high crest perpendicular to midaboral axis; 10 arms; $P_{(1)}$ of proximal pinnules with at most weak abambulacral projection.....*Poecilometra ornatissima*

4b. No strongly everted crest on distal edges of any proximal brachials; up to 20 arms; $P_{(1)}$ of proximal pinnules (sometimes excluding P1) bearing elongated, flat, abambulacral projection, sometimes weak, but often curved, tongue-like and, in larger specimens, extending around to aboral surface of arm.....*Poecilometra priamus*

Poecilometra A. H. Clark, 1907a

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

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

Revised diagnosis.—Centrodorsal hemispherical or discoidal; cirrus sockets in 1–3 irregular marginal tiers, or in 2–3 irregular columns of 1–3 sockets in each radial area; arms 10 to 20; brachitaxes and proximal brachials well separated with gaps bridged by lateral flanges, or closely laterally apposed; abambulacral side of $P_{(1)}$ of proximal pinnules with weak to well-developed flange, or flattened, curved tongue directed toward aboral side of arm; genital pinnules usually with 3–5 narrow basal pinnulars (infrequently 2–7) following

a usually wider $P_{(1)}$ and preceding abruptly expanded pinnulars bearing the gonad (pedunculate); pinnulars expanded over gonad, symmetrical in cross-sectional view, with small articular area, especially the abambulacral ligament fossa, and long, thin lateral “wing-like” flanges; pinnulars distal to gonad abruptly narrower.

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

Other included species.—*Antedon scalaris* (A. H. Clark, 1907b); *Strotometra ornatissimus* A. H. Clark, 1912b; *Strotometra priamus* A. H. Clark, 1912b; *Poecilometra baumilleri* n. sp.

Distribution.—Northwestern, western, southwestern, and central Pacific Ocean; 345 to 1800 m.

Remarks.—The genital pinnules consist of 2–7 narrow basal pinnulars followed by 3–8 abruptly expanded pinnulars, and terminate in 4–10 abruptly thinner, much smaller pinnulars, an appearance referred to here as pedunculate (see Figs. 4, 7, 12, 14, 18, 22I–L). 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 baumilleri* n. sp., described below, also has similar pedunculate genital pinnules.

In addition to the pedunculate genital pinnules, all four species placed in *Poecilometra* herein have brachitaxes and proximal arm brachials with lateral extensions referred to here as flanges, either prominent, smooth, and associated with well-separated ray bases (*P. acoela* (including *P. scalaris*, see below) and *P. baumilleri* n. sp.) or comparatively narrow, with ossicle margins often everted and irregular, and associated with laterally flattened and apposed ray bases (*P. priamus* and *P. ornatissima*) (A. H. Clark 1950, and herein). However, because Hemery’s (2011) analysis did not include either *Poecilometra* species with prominent lateral flanges and well-separated ray bases (*P. acoela*, *P. baumilleri*), additional data is needed to determine if these different ray base features warrant generic-level distinctions or not. If so, *P. priamus* and *P. ornatissima* might require a new generic name, as *acoela* is the type species of *Poecilometra*.

Poecilometra acoela (Carpenter, 1888)

Figures 2–4, 8–9, 22J, 23F

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.—Shiple and MacBride 1901: 269.—Minckert 1905: 190.—Hamann 1907: 1578, pl. 12, fig. 1.—A. H. Clark 1912a: 33, 225; 1915a: 43.

Poecilometra acoela: A. H. Clark 1907a: 362; 1909a: 18; 1912a: 33, 225; 1913a: 50; 1915a: 43, 63 (fig. 8), 367 (fig. 493); 1918: 190, 273; 1921: 49, 75, 152, 228, 230, 359, 754, 763, pl. 26, fig. 1161.—Gislén 1924: 280.—A. H. Clark 1950: 355–359.

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

Poecilometra scalaris: A. H. Clark 1907a: 362; 1909a: 18; 1912a: 225; 1913a: 50; 1915b: 215; 1918: 190; 1921: 79

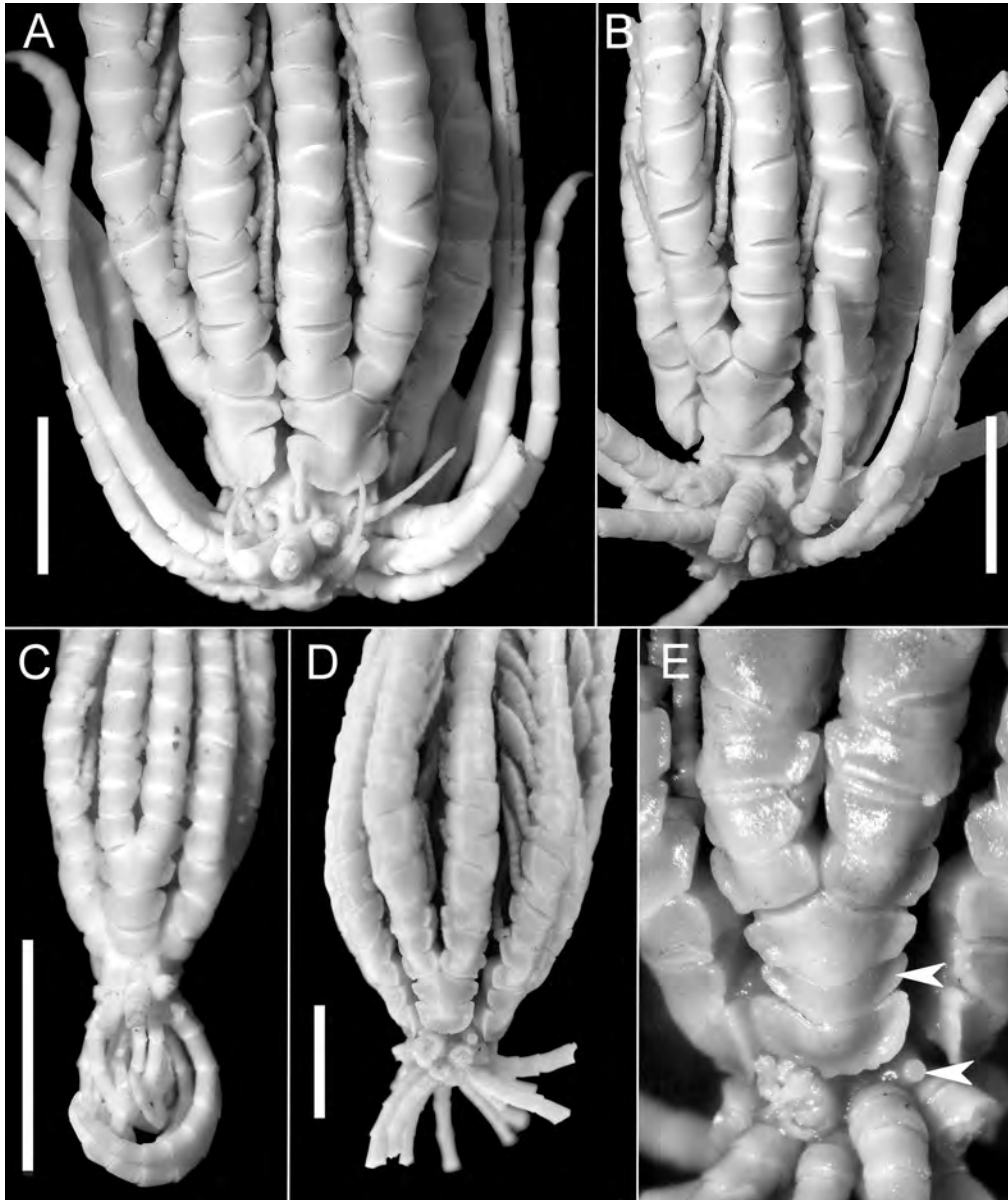


FIGURE 2 — **A–C**, *Poecilometra acoela* (Carpenter, 1884), syntypes, NHM 88.11.9.31. **A**, specimen 1, proximal portion in lateral view (composite image). **B**, specimen 2, proximal portion in lateral view. **C**, specimen 3, proximal portion. **D–E**, *Antedon scalaris* A. H. Clark, 1907b, holotype, USNM 22629. **D**, proximal portion in lateral view. **E**, close-up of a different ray showing small extra ossicle in IBr series (upper arrow) and round projection at interradiial angle of centrodorsal (lower arrow); scale bars = 5 mm (E, no scale recorded).

(figs. 118, 132), 186 (fig. 229), 221 (fig. 288), 263, 279, 286, 289 (figs. 539–542), 293, 412 (figs. 849–855), 722, 729; 1950: 359–360

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

Material examined.— INDONESIA: *Challenger* sta. 214, SW of Pulau Kakalotan, Kepulauan Talaud (=Meangis Is.), 4°33'N, 127°06'E, 914 m, bottom temp. 5.44°C, blue mud, 10 Feb 1875 (NHM 88.11.9.31 (3 of 6 specimens),

NHMD-873490 (1), *Antedon acoela* syntypes); *Siboga* sta. 122, N of the NE tip of Sulawesi, 01°58'30"N, 125°00'30"E, 1,165–1,264 m, stone, 17 Jul 1899 (USNM E439, 1). JAPAN: *Albatross* sta. 4918, East China Sea SW of Kagoshima, Japan, 30°22'N, 129°08'E, 660 m, bottom temp. 5.95 C, gray sand, foraminifera, and broken shells, 13 Aug 1906 (USNM 22629, holotype of *Antedon scalaris*).

Diagnosis.— A species of *Poecilometra* with 10 arms; IBr and proximal brachials well separated; proximal and

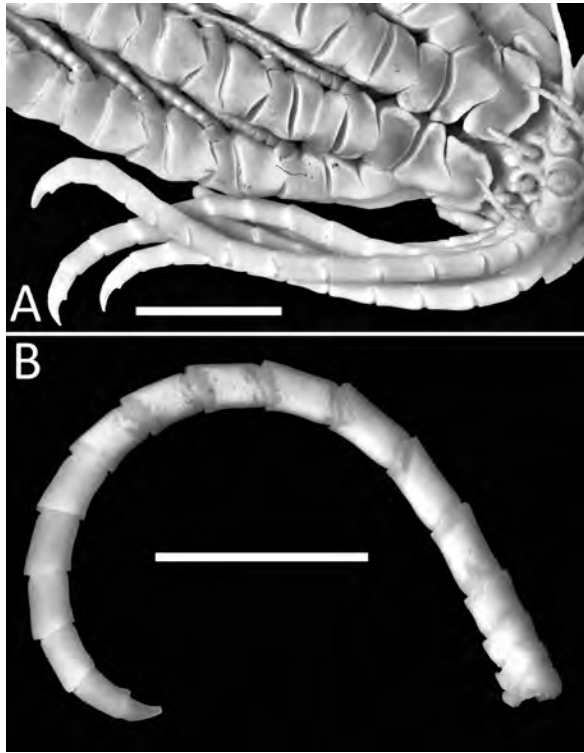


FIGURE 3 — *Poecilometra acoela* (Carpenter, 1884). **A**, syntype, NHM 88.11.9.31, specimen 1, base of one ray and cirri. **B**, *Antedon scalaris* A. H. Clark, 1907b, holotype, USNM 22629, detached cirrus; scale bar = 5 mm.

lateral aboral margins of Ibr1 with continuous curved flange overhanging radial proximally and almost bridging gap between adjacent rays laterally; flange continued but weaker on lateral ends of Iax2 and br1–2 (flanges reduced in small specimens); cirri in large specimens (centrodorsal diameter 3.5–5.0 mm) XX–XXXV, up to 18, and ~22 mm long; longest cirrals with LW up to 2.2. Distal portion of genital pinnules shorter than gonad, typically consisting of only 3–4 small, abruptly narrower pinnulars.

Description.— Centrodorsal rounded conical or hemispherical, 1.7–5.2 mm across adoral (basal) diameter; DH 1.2–1.5, with interradian ridge or knob adjacent to base, ranging from short and rounded to narrow, irregular and almost half centrodorsal height (the latter visible in Figure 2B). Aboral pole convex or dome-like, 0.3–0.4x centrodorsal diameter. Cirrus sockets in 2 columns (3 in largest specimens) per radial area of chiefly 2 or 3 (rarely 1) sockets each (Figs. 2, 3).

Cirri XX to ~XXXV, 14–18, up to at least 22 mm long (XV, 11, 6.2 mm long in small NHM 88.11.9.31 syntype with centrodorsal diameter 1.7 mm). Cirrals increasing in length from very short or squarish C1; C2 and at least following few cirrals with proximal and distal margins sinuous in lateral view; C4–6 longest, up to C6–8 in larger specimens; these

long middle cirrals with LW 1.8–2.2 (small NHM 88.11.9.31 syntype with longest cirral C3–4, LW 1.7); following cirrals becoming shorter but remaining longer than wide; cirri slightly tapering near tip; penultimate cirral distinctly narrower than those preceding; opposing spine tiny, distally-directed, rounded-conical and located at distal end of cirral; terminal claw curved, shorter or longer than preceding cirral (Figs. 2A–C, 3).

Radials hidden, or very short and almost completely hidden in larger specimens, by overhanging proximal flange of Ibr1; radial WL rarely measurable (3.6 in one specimen); some larger specimens with a small beadlike tubercle on at least some radials; another with a small low bump on either side of midaboral line (or just one) on two radials; and with WL 3.6. Radials in small NHM 88.11.9.31 syntype crescent-shaped with distal margin shallowly concave and no ornamentation; WL 1.4 (Fig. 2C).

Brachitaxes and arm bases separated laterally, but IBr2 and br1 with lateral flanges at least partly bridging gaps between adjacent rays (Figs. 2A–B, D–E, 3A). IBr2 with low, midaboral, convex synarthrial swelling; Ibr1 crescent-shaped, WL 2.4–3.4, with broad, thick, continuous flange extending outward from proximal and lateral margins, sometimes slightly sinuous or irregular laterally, and with distal margin shallow or deeply concave. Iax2 wider than Ibr1, hexagonal with short, diverging lateral flanged margins, or rhombic with flanges either restricted to lateral portions or running along entire shallow V-shaped proximal margin; WL 1.4–2.1. One IBr series of *A. scalaris* holotype with an additional, shallow V-shaped ossicle between Ibr1 and Iax2, with lateral flanges but not as wide as either other ossicle; WL 4.5 (Fig. 2E). Small NHM syntype with IBr2 smoothly rounded aborally and no synarthrial swelling; Ibr1 with weak straight flange on diverging lateral margins; distal margin very slightly concave; WL 2.0; Iax2 hexagonal with proximal margin slightly convex; lateral margins with ear-like flanges; WL 1.4 (Fig. 2C).

Arms 10, up to 110 mm (incomplete in most specimens). Br1 roughly rectangular or slightly longer exteriorly, with convex or straight lateral flanges; weaker, shorter or absent interiorly, and distal margin slightly concave; WL 2.2–2.7. Br2 roughly pentagonal, shallow V-shaped proximally, with lateral margins diverging or straight, with or without flanges; WL 1.8–1.9. Br3+4 oblong or with exterior lateral margin longer than interior; 0.8–2.0 mm across; WL 1.2–1.5; br3 with lateral flanges weak, present only interiorly in some specimens. Br5–8 or 9 wedge-shaped; WL 1.6–2.2; one or two following brachials almost rectangular. Middle brr almost triangular; WL 1.8. Distal brachials strongly wedge-shaped; distal margins slightly raised but not overlapping; WL 1.1–1.2. Small NHM syntype with br1 oblong, with convex exterior lateral flange; WL 1.7 (Fig. 2C). Br2 almost oblong but with diverging interior lateral margin and no flange; WL 1.5. Br3+4 oblong, slightly longer than wide, 0.9 mm across; WL 0.9; following few brr only slightly wedge-shaped; WL 1.1–1.3.

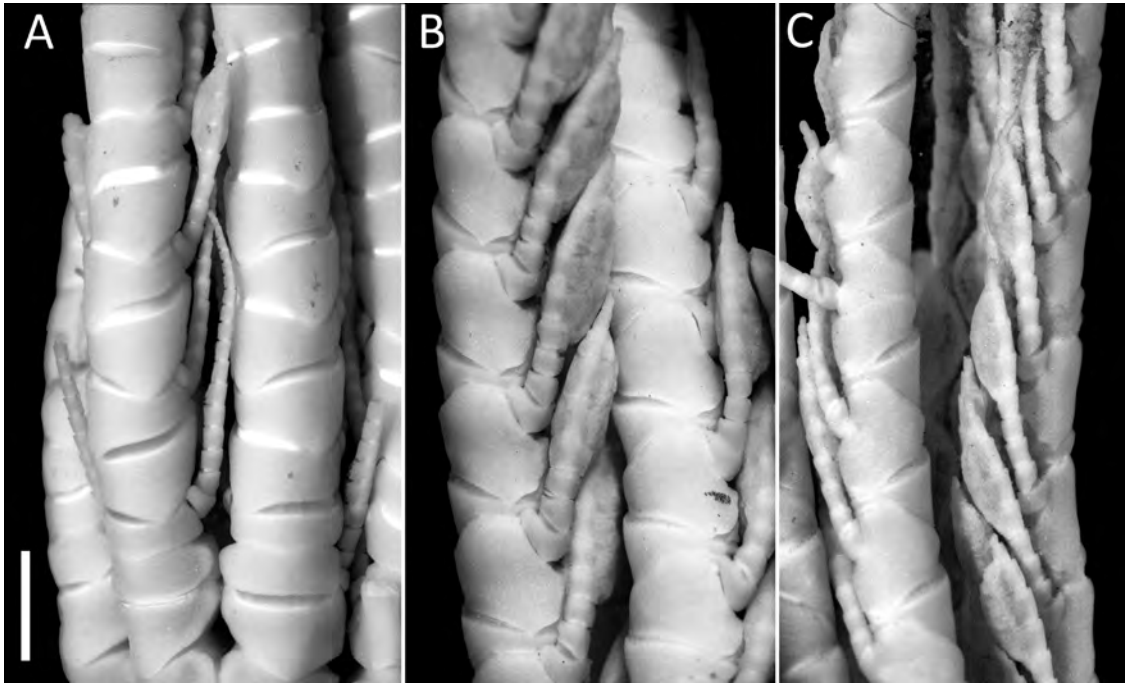


FIGURE 4 — *Poecilometra acoela* (Carpenter, 1884), syntype, NHM 88.11.9.31, specimen 2. **A**, proximal interior pinnules (center) Pa, Pb, Pc (genital). **B**, Middle genital pinnules. **C**, More distal genital pinnules; A scale bar = 2 mm; B, C = no scale recorded.

Second syzygy at br9+10 to br13+14. Distal intersyzygial interval usually 4–5 (sometimes 3–6). In small specimen (NHM 88.11.9.31), second syzygy at br13+14 to br15+16; following intersyzygial interval 7 to at least 12 (longest remaining arms broken beyond br12 to br26).

P1 of 18–24 pinnulars, up to 7.1 mm long (2.5 mm in small NHM syntype); P1₍₁₎ wider than those following, with convex or truncated abambulacral flange; following proximal pinnulars squarish; middle pinnulars slightly longer than wide; LW at most 1.3; distal pinnulars almost squarish. Pa similar but with a weak convex abambulacral keel spanning Pa₍₅₋₆₎ or (5-8). P2 shorter than P1, with fewer pinnulars; in small NHM syntype segments longer than in P1 with very slight expansion at P2₍₅₋₆₎ or (6-7). P3 first genital pinnule; genital pinnules with 9–14 pinnulars; Pgen₍₁₎ wider than those following, usually with weak to well-developed convex abambulacral flange (Fig. 4); following 2–4 pinnulars squarish or slightly longer than wide—P_(2-3 or 4) on proximal genital pinnules, P_(2-4 or 5) on middle genital pinnules; following 3–5 pinnulars, e.g., Pgen_{(4-7), (5-7), (4-8), or (6-8)}, abruptly expanded over gonad; following few distal pinnulars abruptly narrower, tapering to pinnule tip. Distal pinnules of up to 19 pinnulars, 11 mm long; Pdist₍₁₎ much wider than long and wider than following pinnulars; Pdist₍₂₎ roughly trapezoidal and narrower distally; Pdist₍₃₎ squarish; following pinnulars increasingly longer than wide except near tip; LW at most 1.7. One NHM syntype with gonads weaker on P8, absent by P10 of 10 pinnulars; longest pinnular with LW 2.0. Another smaller NHM syntype with no genital expansion; middle pinnules of 8 pinnulars, and middle pinnulars with LW to 2.6.

Disk completely covered with irregular plates bearing short and blunt rodlike spines.

Distribution.— Northern Indonesia to just south of Japan; 660–1,327 m (A. H. Clark, 1950).

Remarks.— The preceding description is based on A. H. Clark's (1950) text plus photographs of three syntypes of *Antedon acoela* (Challenger sta. 214) and the holotype of *Antedon scalaris* (taken by CGM), and direct examination of one syntype (NHMD-873490). A. H. Clark (1950) distinguished *P. acoela* from *P. scalaris* on the basis of differences in the profiles of the brachitaxes and arm bases in side view of the specimens: in *P. acoela* “the lateral profiles of the IBr series are almost parallel, those of the arm bases slightly diverging; the IBr series are constricted so that there is a sudden broadening at the first brachial” (p. 355); in *P. scalaris* “the profiles of the IBr series and arm are smooth and continuous, those of the two sides making with each other an angle of about 60°” (p. 359). However, the profiles are smooth and continuous in at least one *P. acoela* syntype (Fig. 2B), whereas the holotype of *P. scalaris* and at least one syntype of *P. acoela* both exhibit a similar gentle “broadening at the first brachial” (Fig. 2A, D). The remaining diagnostic characters listed by Clark either overlap or are minor and size-related, i.e., centrodorsal diameter 4 versus 5 mm; cirri XXV–XXX, 15–18 versus XX, 20, and arm length 100 versus 110 mm, for *P. acoela* versus *P. scalaris*, respectively. [Note: for the single known specimen of *P. scalaris*, Clark indicated 20 cirrals in the diagnosis but 15 cirrals in the description; the specimen no longer has any attached complete cirri, but a complete detached cirrus has 17 cirrals (Fig. 3B), so 20 is its

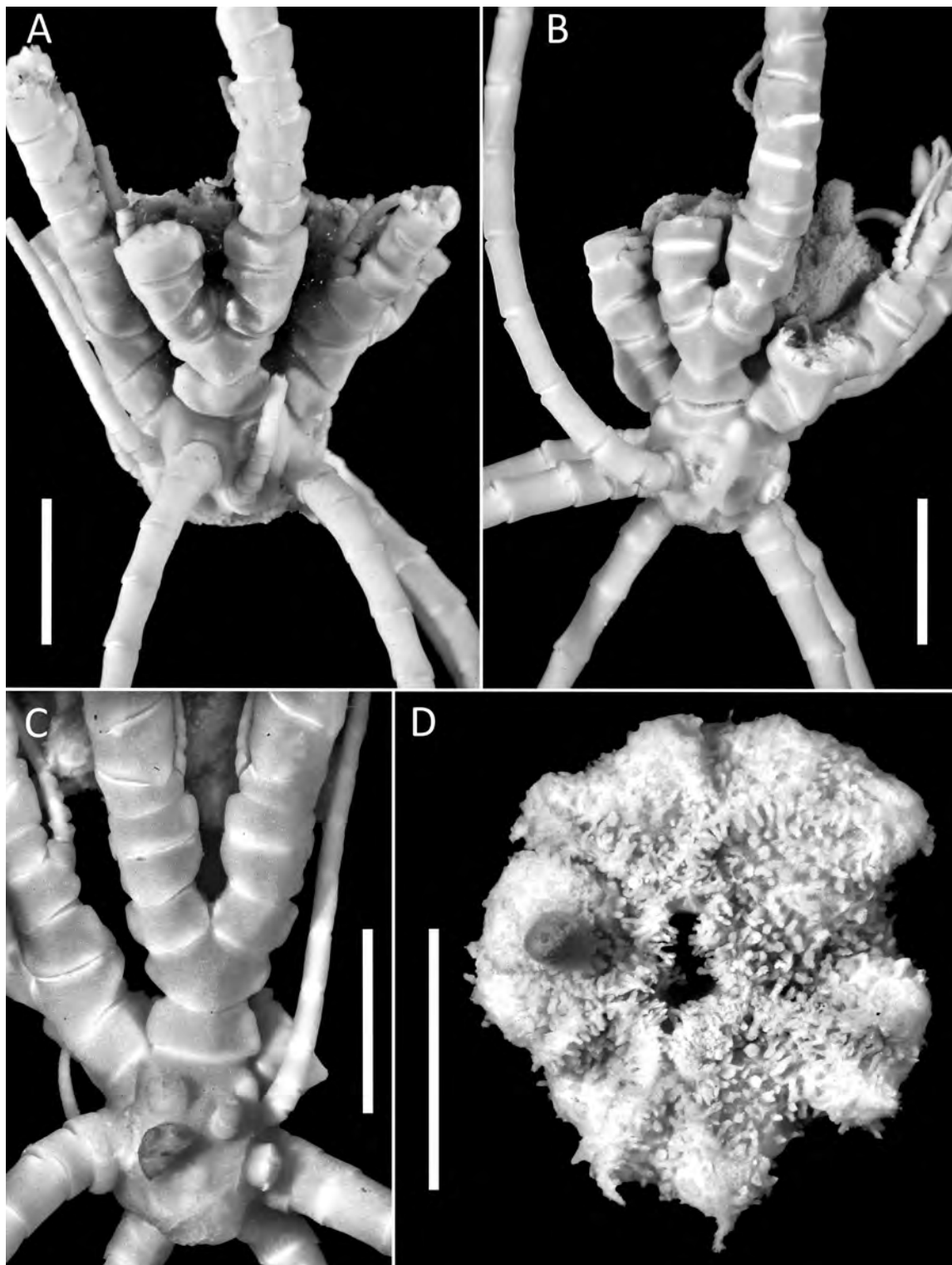


FIGURE 5 — *Poecilometra baumilleri* new species. **A-C**, centrodorsals, and bases of rays and cirri; **A**, FLMNH 21594, **B**, USNM 1660641, **C**, FLMNH 21597. **D**, detached disk, oral surface, FLMNH 21597; scale bars = 5 mm.

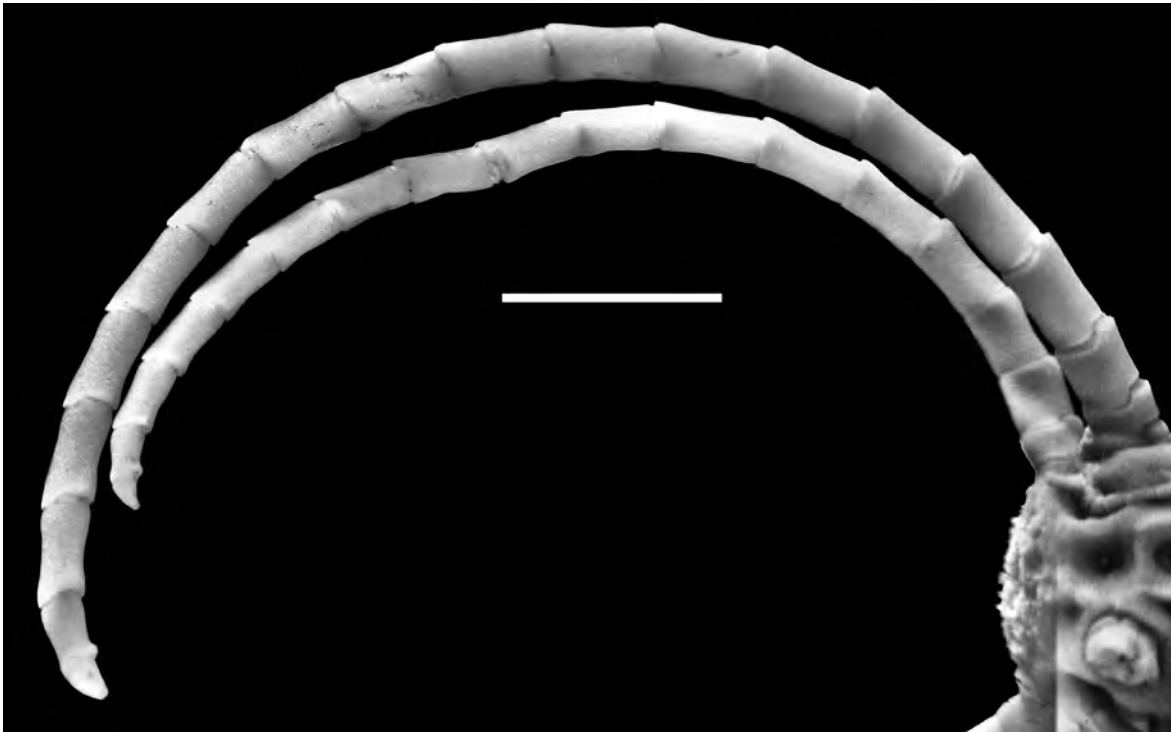


FIGURE 6 — *Poecilometra baumilleri* new species, cirri, FLMNH 21594; scale bar = 5 mm. (Composite image.)

likelier maximum number of cirrals.] We, therefore, treat *P. scalaris* as a junior synonym of *P. acoela*. The addition of *P. scalaris* extends the distribution of *P. acoela* to just south of Japan. The shallower depth record is not surprising given its considerably more northern latitude. More recent mentions of *P. scalaris* refer to no additional material (Kogo, 1998; Kogo and Fujita, 2005).

Small specimens differ from larger ones in having more widely exposed radials and proportionally more elongated proximal brachials with less developed or absent flanges (Fig. 2C).

Poecilometra baumilleri sp. nov.
Figures 5–9, 22I

Holotype.— NOAA *Okeanos Explorer* sta. P4-256, Necker Ridge, SW of Necker I., 21°38'N, 167°49'W, 14 Oct 2011, 1,746 m (FLMNH 21594, 1 specimen).

Paratypes.— NOAA *Okeanos Explorer* sta. P4-257, Necker Ridge, SW of Necker I., 21°31'N, 167°56'W, 15 Oct 2011, 1,802 m (FLMNH 21597, 1; USNM 1660641, 1).

Other material examined.— HAWAIIAN ISLANDS: NOAA *Okeanos Explorer* sta. P4-256, Necker Ridge, SW of Necker I., 21°38'N, 167°49'W, 14 Oct 2011, 1,748 m (FLMNH 21590 (1), 21592 (1)), 1,746 m (FLMNH 21593 (1)).

Diagnosis.— A species of *Poecilometra* with 10 arms; IBr and proximal brachials well separated; Ibr1 with proximal margin almost straight to slightly convex, distal margin

shallowly concave, and lateral margins converging and bearing low thick lateral flange or ridge that may be more strongly developed along one side; flange continued but weaker on lateral edges of Iax2 and br1 (sometimes to br2; flanges reduced in small specimens); cirri in large specimens (centrodorsal diameter 3.9–6.5 mm) X–XVI, up to 19 cirrals, and 42 mm long; longest cirrals with LW typically 2.4–2.7. Distal portion of genital pinnules shorter than gonad, consisting of up to 7 small, narrow pinnulars.

Description.— Centrodorsal dome-shaped, or rounded or truncated conical, and with short thick interradiar ridges adjacent to base continuous with slightly swollen proximal corners of radials; centrodorsal proportionally taller in smaller specimens (DH 1.3–1.4 with adoral diameter 3.9–4.6 mm; 1.9 with diameter 6.5 mm); adoral margin in radial area variable, from shallowly concave to deeply V-shaped. Aboral pole flat or gently convex, bearing fine papillae, irregular fine spinules, or radiating ridges; convex without ornament in smallest specimen. Cirrus sockets in two columns per radial area of 1–2 sockets each, often with one socket rudimentary and peripheral, or one obsolete and apical, so that most radial areas have at most 3 sockets; rims of at least some mature peripheral sockets slightly projecting.

Cirri X–XVI (including up to 4 rudimentary), 16–19, to 42 mm long; proximal cirrals increasing in length from base; C1–2 short; C5–6 to C7–8 longest (C7–10 in one specimen), LW chiefly 2.4–2.7 (extremes 2.0–2.9); following cirrals gradually shorter and slightly compressed but remaining longer than wide; penultimate cirral slightly tapering distally,

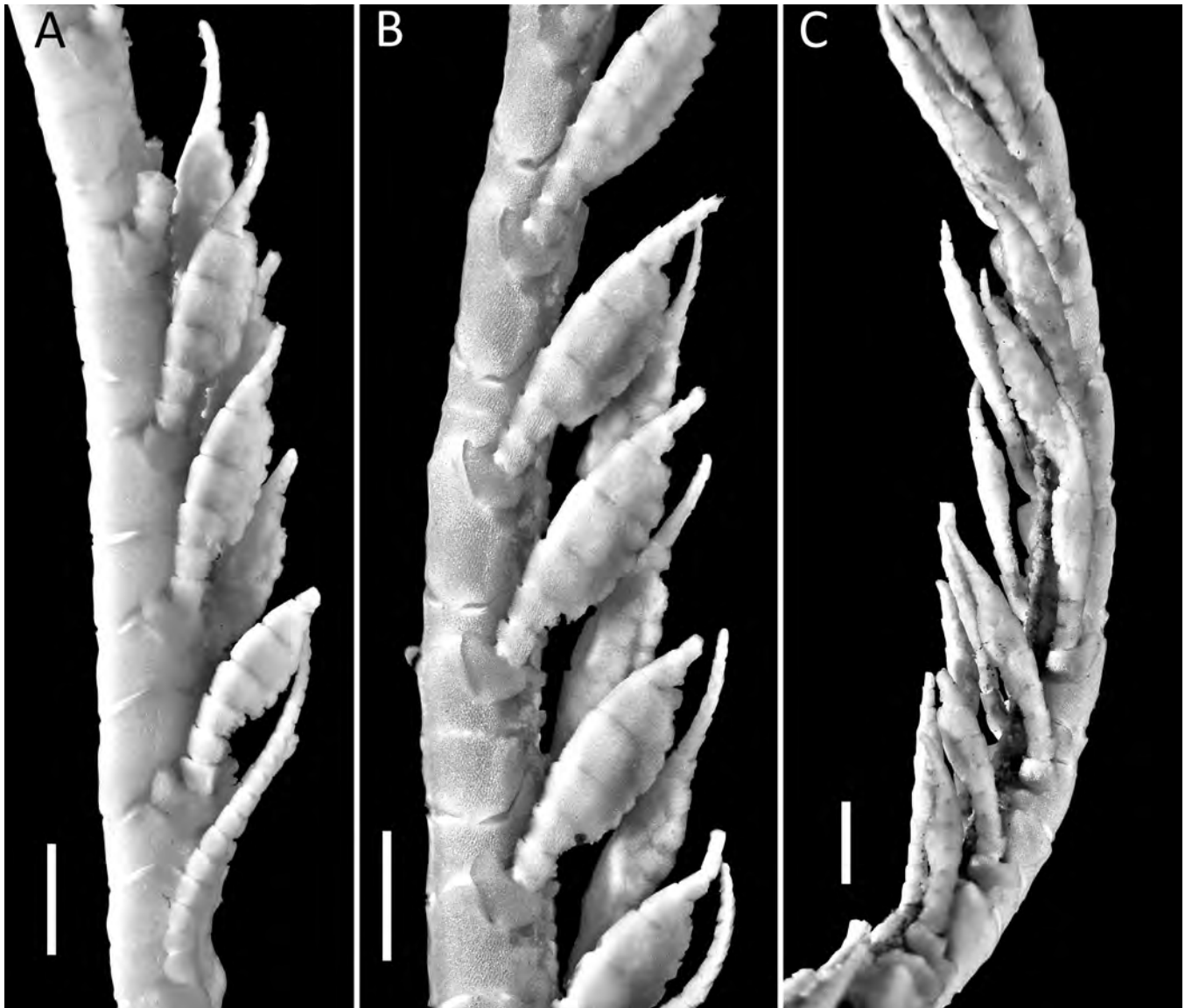


FIGURE 7 — *Poecilometra baumilleri* new species, genital pinnules. A, FLMNH 21597. B, USNM 1660641. C, FLMNH 21594, genital expansion weaker; scale bars = 2 mm.

with weak distal rounded opposing knob, LW 1.8–2.2; terminal claw shorter than preceding cirral, usually gently curved; proximal and distal margins (in lateral view) of C1–2 or 3 sinuous.

Radials hidden or visible as narrow band or small area recessed within V-shaped incision in centrodorsal margin, WL 3.3–4.9. When exposed, with proximolateral corners slightly swollen against interradial ridges of centrodorsal.

Ibr2 and brr1–2 with weak to moderately developed, broad rounded synarthrial swelling. Ibr1 narrower distally; proximal margin almost straight, slightly projecting proximally in one specimen; distal margin weakly concave or shallowly V-shaped; lateral margins converging, with low, straight or

rounded, thick flange projecting beyond ossicle margin, WL 2.2–3.4. Iax2 rhombic to hexagonal with short lateral margins, wider than Ibr1; lateral corners with small knob, weak rounded flange or irregular projection, WL 1.6–1.9; narrow distolateral margin of Ibr1 and projecting lateral margins of Iax2 create roughly rhombic gap between adjacent rays.

Arms 10, up to ~110 mm long (reconstructed from detached arm). Br1 oblong or with converging interior lateral margin; exterior lateral margin flattened with distolateral knob, or with low ridge or flange, WL 1.4–2.3. Br2 with proximal margin rounded V-shaped; interior lateral margin diverging, sometimes with distolateral knob (3 small knobs on one arm) or weak flange; exterior lateral margin flattened

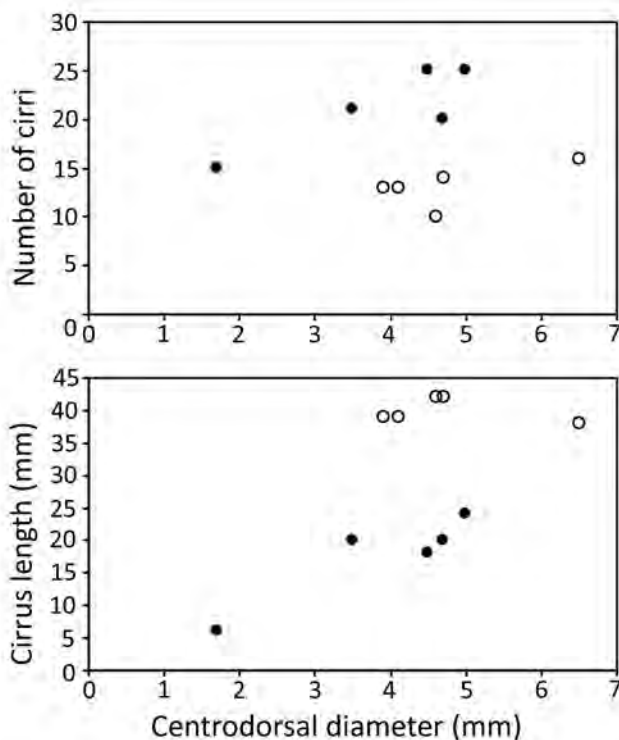


FIGURE 8 — Graph illustrating differences in cirrus number and length relative to centrodorsal diameter in *Poecilometra acoela* (solid circles) versus *Poecilometra baumilleri* new species (open circles).

or with short flange or small knob similar to that on Iax2; WL 1.1–2.0. Truncated interior distolateral corner of br1 and projecting interior lateral margin of br2 create gap between bases of arms arising from the same axil. Most arms detached following br3; most remaining attached arm fragments regenerating at br3+4. br3+4 on attached arm with WL ~1.0; br3 interior lateral margin with distolateral projection, knob, or flange—a continuation of distolateral projection of br2—also on br4 to br6 on a few arms. Following br7 increasingly wedge-shaped, but 1 or 2 ossicles from br8 to br10 oblong or almost square; subsequent br7 becoming more strongly wedge-shaped, almost triangular by br15. Middle br7 strongly wedge-shaped or almost triangular, WL 1.0–1.4, with long lateral margin up to 3.5x length of short lateral margin. Distal br7 becoming less strongly wedge-shaped, longer than wide, WL 0.6–1.0 (0.5 nearer arm tip); longer lateral margin ~2x longer than shorter lateral margin; distal margins slightly raised but smooth. Second syzygy at br8+9 to 14+15 (br22+23 on a regenerating arm); distal intersyzygial interval variable, chiefly 2–4, chiefly 4, or 5–9.

P1 of up to 28 pinnulars, 7.8 mm long; all pinnulars short, mostly shorter than wide; some middle segments squarish; P1₍₁₎ wider than those following, with abambulacral projection tongue-like and as tall as pinnular width, or weak and rounded or triangular; P1₍₂₎ wider distally; P1_(3–4) with thick adambulacral keel. P2–P4 first genital pinnule. P2 with

up to 16 pinnulars, 5.7 mm long, with weak genital expansion on 2–3 middle pinnulars (e.g., P2_(5–7) or _(6–8)), and middle and distal pinnulars longer than wide, or without genital expansion and resembling P1. Following genital pinnules of up to 14 pinnulars, to 6.9 mm long, shorter with fewer pinnulars (9–13) in most specimens; Pgen₍₁₎ with tongue-like abambulacral flange as tall as pinnular width, diminishing on more distal genital pinnules; initial pinnules with well-developed gonad (e.g., Pb, P2–3) with 4 narrow basal pinnulars and genital expansion widest on Pgen_(5–7); following genital pinnules with only 2–3 narrow basal pinnulars and genital expansion often widest on Pgen_(4–6); segments distal to gonad much narrower. Genital expansion variable (e.g., wide in fig. 7A, B; narrow in figs. 7C, 22I); expansion over gonad reduced on more distal genital pinnules and developing more gradually from proximal pinnulars. Distal pinnules of up to 17 pinnulars, to 12 mm long, tapered near tip, more strongly prismatic than proximal pinnules; Pdist₍₁₎ wider than those following, with concave distal margin and weak abambulacral projection (if any); following pinnulars longer than wide, LW 1.8–2.7, except for short, smaller distalmost 1–3 pinnulars.

Disk poorly preserved; sides apparently paved with irregular polygonal plates; plates covering oral surface bearing rounded knob or short blunt spine; disk ambulacra apparently lined with short fingerlike spines.

Distribution.— Currently only known from Necker Ridge, south of the Hawaiian Islands; 1,746–1,802 m.

Etymology.— The species is named *baumilleri* in celebration of Tomasz K. Baumiller, Ph.D., long-term Professor of Earth and Environmental Sciences and Curator of Invertebrates at the Museum of Paleontology, University of Michigan, for his many important contributions to research on both living and fossils crinoids, including evolution, ecology, functional morphology, biomechanics, and taphonomy.

Remarks.— *Poecilometra baumilleri* n. sp. differs from *P. acoela* in having 1) substantially fewer, much longer cirri at similar centrodorsal diameters (Figs. 8, 9); 2) differently shaped Ibr1, in particular with distinctly converging lateral margins and lacking a projecting proximal flange; 3) fine papillae or irregular fine spinules on the centrodorsal apex, at least in larger specimens, and 4) radials remaining more visible in similarly sized specimens. The converging lateral margins of Ibr1 and the narrowing lateral portions of Iax2 create distinct, large, more-or-less rhombic gaps, referred to by A. H. Clark (1915a, 1950) as water pores, between adjacent ray bases.

Poecilometra ornatissima A. H. Clark, 1912a
Figures 10–11

Strotometra ornatissimus A. H. Clark 1912a: 82; 1918: 192–193, figs. 10–11; 1950: 362–363, pl. 20 fig. 65.—McKnight, 1989a: 34.—Hess and Messing 2011: 115.—Hemery 2011: 179–188, figs. IV.B.1–IV.B.10.

Strotometra ornatissimns: A. H. Clark 1918: 191 (sic.).

Strotometra ornatissima: A. H. Clark, 1915a: 163, figs. 101–102; 1918: 273, pl. 24, fig. 70.

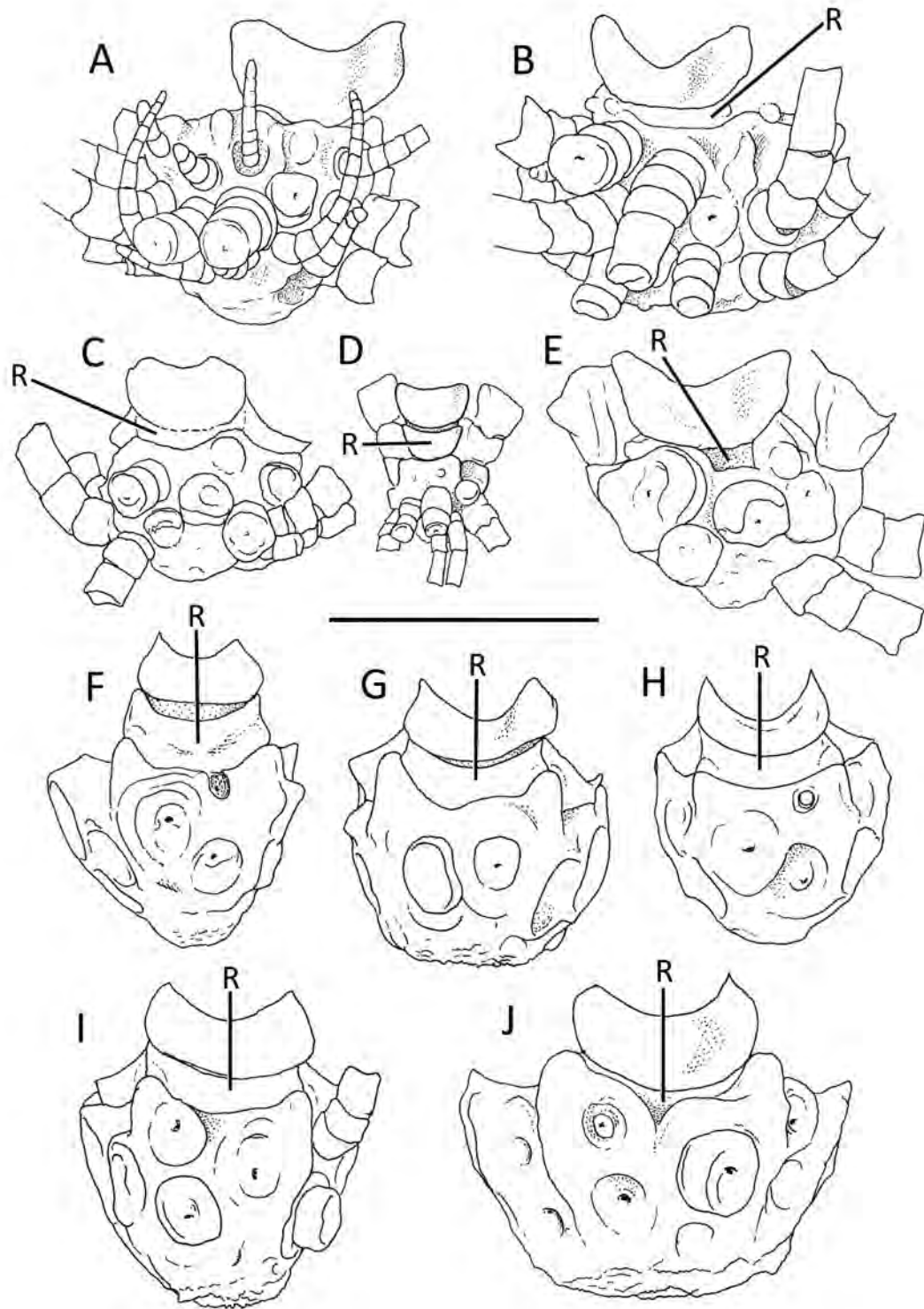


FIGURE 9 — Centrodorsal schematics illustrating numerous versus relatively few cirri in *P. acoela* versus *P. baumilleri*, respectively. A–E, *Poecilometra acoela* (Carpenter, 1884). A, NHM 88.11.9.31 spec. 1. B, NHM 88.11.9.31 spec. 2. C, NHMD-873490. D, NHM 88.11.9.31 spec. 3. E, USNM 22629 (holotype of *Antedon scalaris*). F–J, *Poecilometra baumilleri* new species. F, FLMNH 21590. G, USNM 1660641. H, FLMNH 21592. I, FLMNH 21597. J, FLMNH 21594. R = exposed surface of radial; scale bar = 5 mm.

Material examined.— INDONESIA: *Albatross* sta. 1899, Celebes Sea, 1°58'30"N, 125°00'30"E, 1035–1264 m, 1906 (NHMD E2088, holotype, photographs only); KERMADEC IS.: M/V *Tangaroa* sta. T243, 30°05'S, 178°15'E, 1035 m, 24 Mar 1982 (NIWA 115369, drawing of 1 of 2); FIJI: MUSORSTOM 10 sta. CP1361, 18°00'S, 178°53'42.6192"E, 1058–1091 m, 13 Aug 1998, sample STRO81 (MHNH-IE-2012-876, 1).

Diagnosis.— A species of *Poecilometra* with 10 arms and distal edges of br2, br4, and br5 strongly everted as a high crest perpendicular to midaboral axis; axils chevron-shaped instead of triangular; C4 or 5 to C6 with LW 2.8–3.4, with expanded distal margins.

Description.— Centrodorsal low hemispherical or discoidal, 2.4–3.0 mm across, DH 2.5. Aboral pole convex. Cirri XXII–XXXVI, 10–15, arranged in one and a partial second, or two to three, irregular marginal tiers (Fig. 10A, 11A). C1 very short; C2 LW 1.1–2.2; C3 LW 2.4–3.3; proximal cirrals strongly constricted centrally; cirrals becoming laterally compressed distally; C4 or 5 to C6 longest, LW 2.8–3.4 (Fig. 10D) (longest cirral unidentified, LW to 2.0 in McKnight (1989a)); distal ends of most cirrals except distalmost 2–3 expanded; distal cirrals with LW 2.0–2.7; distalmost 3–4 cirrals gradually slightly narrower; penultimate cirral slightly smaller than preceding, with small opposing spine and LW 1.4; terminal claw about as long as preceding cirral.

Radials narrowly visible over rim of centrodorsal or hidden by Ibr1, or visible only at interradiial angles. Ibr2 flat-sided, closely apposed laterally, and with lateral margins of each ossicle diverging and extended as short, often slightly everted and sometimes irregular or weakly scalloped flange; synarthry with weak midaboral swelling. Ibr1 with slightly convex or shallowly Λ -shaped distal margin and with diverging lateral margins, WL 3.3–3.8. Note that the illustration of this feature in the type specimen in A. H. Clark, 1915a (p. 163, Figs. 101–102), is more strongly Λ -shaped than in the photographs (Figs. 10A, C) of the same specimen herein. Iax2 pentagonal or weakly chevron-shaped, WL 2.5–2.8. Lateral thirds of Ibr1 distal margin and Iax2 proximal margin irregularly scalloped or bearing small tubercles that interlock across the articulation.

Arms 10, longest known 40 mm. Brr1–2 also closely apposed laterally, with parallel proximal and distal margins; exterior lateral margins straight; interior lateral margins diverging; lateral eversions and synarthrial swelling weaker than on Ibr2. Br1 with interior distal corner extended as triangular projection, WL 2.4–2.7. Br2 with distal margin everted and projecting aborally at right angle to midaboral axis of arm as enormous thin, roughly fan-shaped, crest or shelf, with projecting edge rounded, irregularly scalloped or divided midaborally (Figs. 10A, C); crest height up to three times br2 length; exterior proximolateral corner sometimes produced proximally over distal exterior corner of br1 and scalloped or with weak tubercles; WL ~2.6–2.7. Br3+4 short, oblong; distal margin of br4 bearing crest similar to that of 2. Distal margin crests present to brr10–12 but gradually weakening and projecting more distally, sometimes chiefly reduced to tongue-like projection on one side of distal margin. Middle

brachials to br16 triangular, with distal margins projecting distally but not overlapping succeeding brachial; WL 1.7–1.8. Distal brachials wedge-shaped, smooth, with distal margin finely spinose, LW 1.0.

$P_{(1)}$ of proximal pinnules with abambulacral projection similar to those on smaller *P. priamus* specimens. Remaining portion of P1 in holotype of +17 pinnulars, 4.8 mm long (26 pinnulars, 5 mm long in McKnight (1989a)). Remaining P2 in holotype missing narrow terminal portion distal to gonad, of ~11 remaining pinnulars, 4.6 mm long. $P_{(1)}$ with small, rounded abambulacral flange as tall as width of $P_{(2)}$ (Fig. 10B, bottom), also present on following pinnules. Gonads on P3 to P6–7, occasionally P1 or P2 (P2–P3 in McKnight (1989a)); genital pinnules distinctly pedunculate (Fig. 10E), to 4 mm long; $P_{gen(1)}$ as in P1; following 3–4 pinnulars narrow; abrupt gonadal expansion variable, of 3–4 pinnulars ($P_{gen(4-6)}$ to $(5-8)$); gonad covered by large plates; gonad followed by up to 6 abruptly narrower, fragile pinnulars. Distal pinnules of 12–16 pinnulars, 8–10 mm long; all pinnulars elongated except for short $P_{dist(1)}$, which bears distinct aboral keel.

A large specimen (MHNH-IE-2012-876) differs as follows (Fig. 11): centrodorsal 3.6 mm across, DH 1.7, with convex polar area 0.66x basal diameter and cirrus sockets in 2–3 crowded irregular tiers. Cirri LXVII, 15; C4–7 longest, LW diminishing from 3.1 to 2.4 as cirrals become slightly wider distally; distal 2–3 cirrals preceding penultimate sometimes with distal aboral end expanded; antepenultimate cirral of one cirrus with rounded distal projection similar to but weaker than opposing spine (Fig. 11C).

Distal corners of radials barely visible in interradiial angles. Ibr2 aborally smooth, not laterally flattened or apposed, and with large rhombic gap (“water pore”) between adjacent ray bases (similar gap between adjacent brr1–2; Fig. 11A). Ibr1 with lateral margins converging and bearing smooth, short lateral flange, WL 2.0. Iax2 short, rhombic, much wider than Ibr1, with portion of proximal margin extending beyond Ibr1 bearing smooth or irregular flange, WL 1.9–2.2. Longest remaining attached arm 19 mm. Br1 oblong with proximal and distal exterior corners and proximal interior corner everted, and with interior distal corner cut away, WL 2.0; one br1 with interior half of distal margin strongly everted as a broad, fan-like shelf projecting at right angle to arm axis. Br2 short, with strongly diverging lateral margins, WL 2.3. Br3+4 oblong, WL 2.0, 2.4 mm across; br4 shorter than br3. Br5 oblong or wedge-shaped, WL 2.6. Brr5–7 or 8, short, wedge-shaped, with diverging lateral margins, WL 2.1–2.5. Distal margins of brr2, 4, 5, and 6 or 7 bearing projecting crests as in other specimens, strongest on br2, chiefly divided or reduced to 2–3 thick flattened knobs on following brachials. Brachials smooth and triangular by br12. Second syzygy at br9+10 or br10+11. No pinnules intact. $P_{(1)}$ of proximal pinnules with elongated, abambulacral, tongue-like projection similar to that of large *P. priamus*. Disk covered with small, rounded plates (Fig. 5D) similar to those of *P. priamus* but with those lining disk ambulacra apparently not as elongated (Fig. 11B).

Distribution.— Celebes Sea, Indonesia, Kermadec Is., Fiji; 1,035 to 1,264 m (A. H. Clark, 1950; McKnight, 1989a).

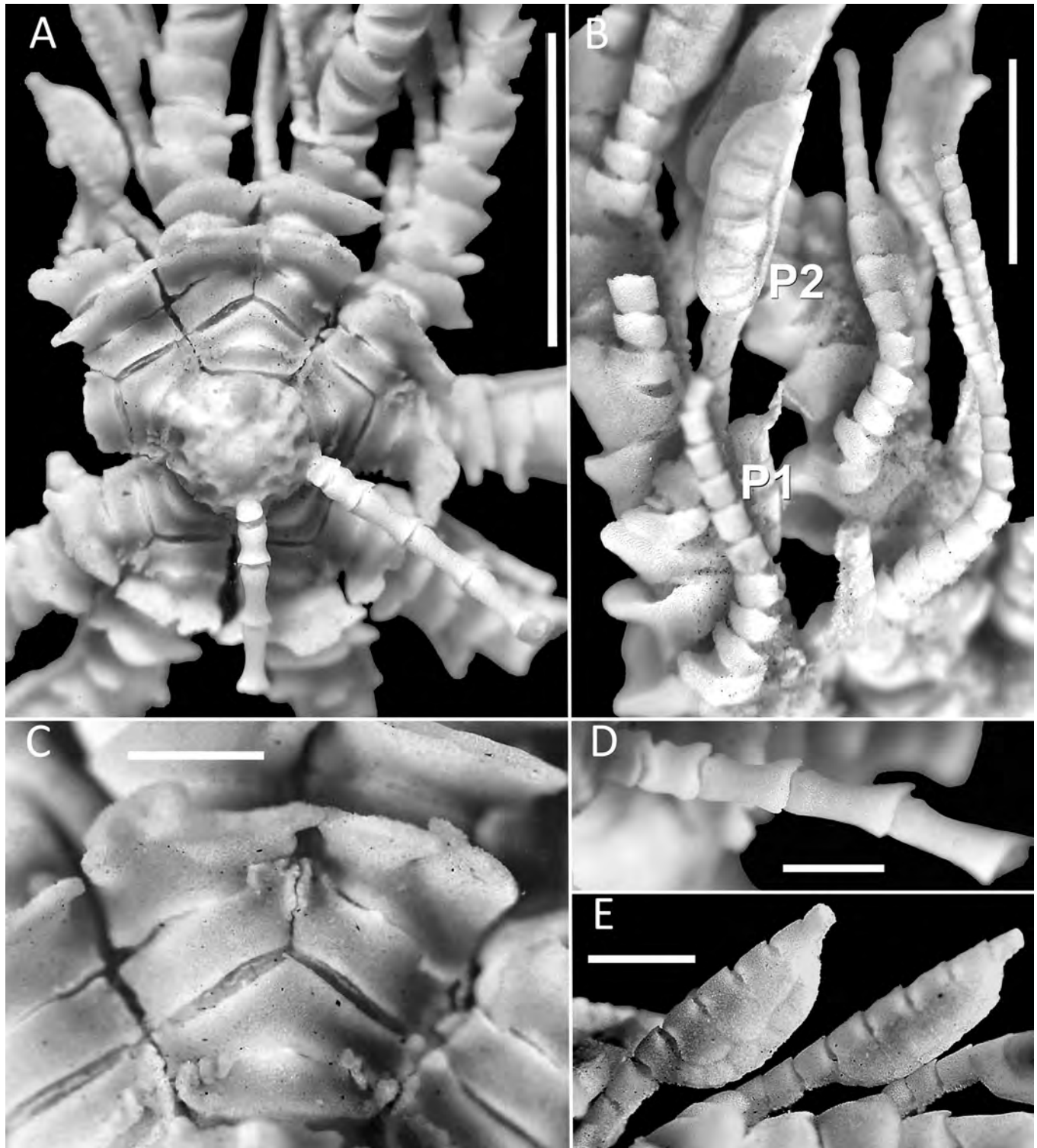


FIGURE 10 — *Poecilometra ornatissima*, holotype, RMNH ECH.2088. **A**, centrodorsal and ray bases, aboral view. **B**, proximal pinnules, lateral view. **C**, IBr2 and proximal brachials of one ray, aboral view. **D**, base of cirrus. **E**, genital pinnules, lateral view; A scale bar = 5 mm; B scale bar = 2 mm; C–E scale bars = 1 mm.

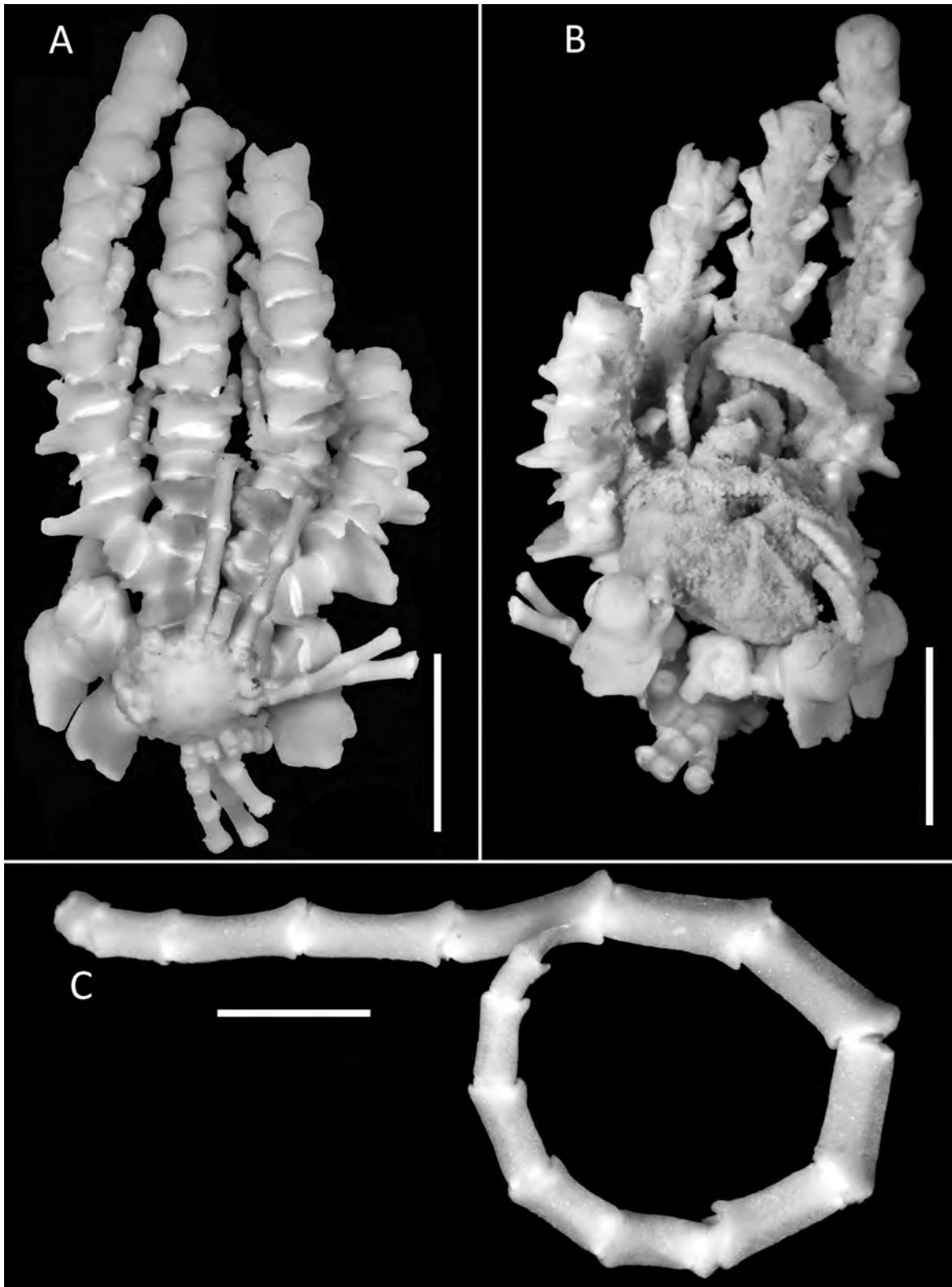


FIGURE 11 — *Poecilometra ornatissima*, MHNH-IE-2012-876. **A–B**, entire specimen. **A**, aboral view. **B**, oral view showing disk and one enlarged genital pinnule. **C**. Cirrus; **A, B** scale bars = 5 mm; **C** scale bar = 2 mm.

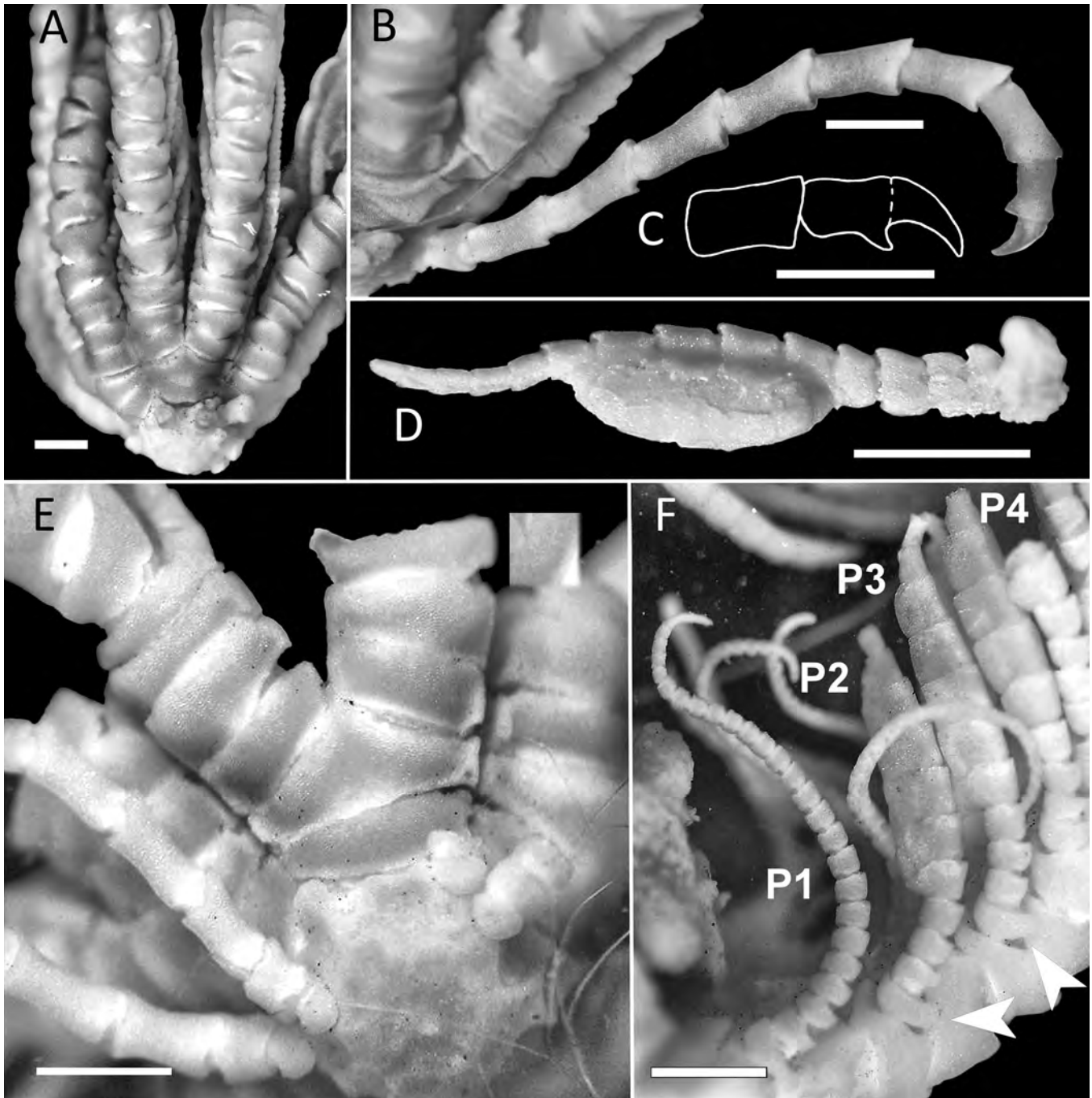


FIGURE 12 — *Poecilometra priamus*, small specimens. A–B, RMNH.ECH.1813 A, centrodorsal and proximal rays, lateral view. B, cirrus with opposing spine triangular in profile. C–F, USNM E427. C, cirrus tip opposing spine distally curved in profile. D, detached genital pinnule with tongue-like projection on $P_{(1)}$, adambulacral view. E, centrodorsal and ray base, aboral view. F, proximal pinnules with narrow genital expansions on P2–P4, lateral view; arrows indicate short, tongue-like projections on $P2_{(1)}$ and $P3_{(1)}$; scale bars = 1 mm.

Remarks.— Although A. H. Clark (1915a, 1918) repeatedly spelled the species epithet as *ornatissima*, the genus and species epithets of his (A. H. Clark 1912a) original description

(and his full description (A. H. Clark 1950)) did not agree in gender (*Strotometra* feminine; *ornatissimus* masculine). As *Poecilometra* is also feminine, the species epithet is herein

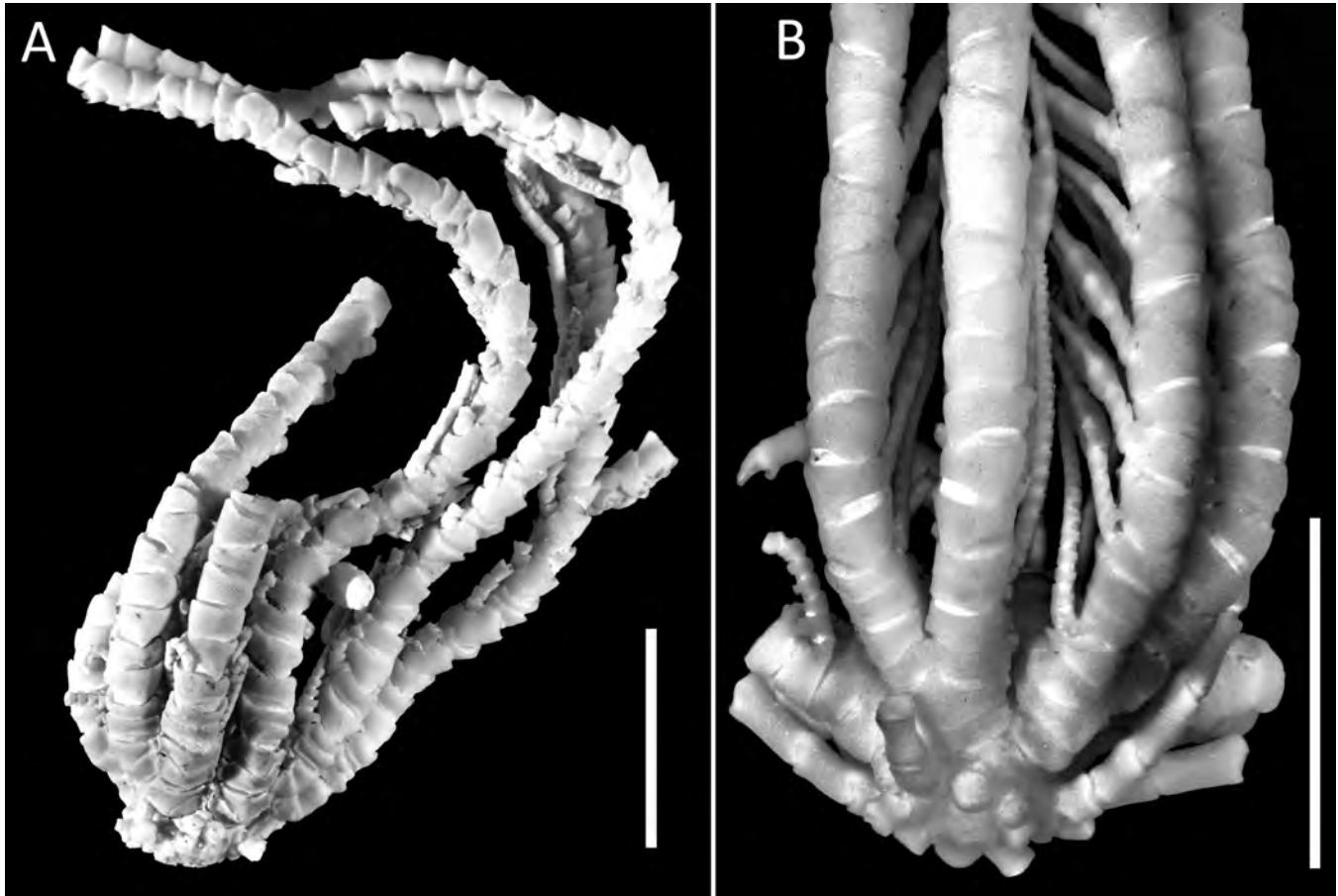


FIGURE 13 — *Poecilometra priamus*, small specimens. **A**, MNHN IE-2019-4434, entire specimen, lateral view. **B**, MNHN IE-2007-5904, centrodorsal and proximal rays, lateral view; scale bars = 5 mm.

formally modified to *ornatissima* (feminine) following Article 31.2 of the International Code of Zoological Nomenclature (ICZN, 1999).

The description above includes information from McKnight (1989a), who found two specimens off the Kermadec Islands that differed somewhat from the holotype, likely associated with their much more complete condition. Those specimens were not examined.

Poecilometra priamus (A. H. Clark, 1912a)

Figures 12–17, 22K, L, 23G

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

Material examined.— KEPULAUAN KAI (KEI IS.), INDONESIA: *Siboga* sta. 266, 05°56'30"S, 137°47'42"E, 595 m, gray mud with coral and stones; 19 Dec 1899 (USNM E427 (syntypes, 3 of 10 specimens); RMNH.ECH.1813 (syntypes, 2)); Danish Expedition to the Kei Islands, sta. 1, 5°34'S, 132°50'E, 370 m, mud, 30 Mar 1922 (NHMD-873541, 2); Danish Expedition to the Kei Islands, sta. 56,

5°30'20"S, 132°51'E, 345 m, mud, 10 May 1922 (NHMD-873492, 1). NEW CALEDONIA: *Alis* sta. DW790, BATHUS 3, 23°49'S, 169°48'E, 685–715 m, 25 Nov 1993 (MNHN IE-2019-4434, 1, dry); *Vauban* sta. DR04, VAUBAN, 22°17'S, 167°13'E, 400 m, 22 May 1978 (MNHN-IE-2012-831, 3, dry); EXBODI sta. DW3784, 22°13'12"S, 167°09'18"E, 353–365 m, 02 Sep 2011 (MNHN IE-2007-5904, 1); *Alis* sta. CP3833, EXBODI, 22°01'36.0012"S, 167°03'42.0012"E, 325–332 m, 08 Sep 2011 (MNHN IE-2007-6012, 1); *Vauban* sta. CP216, MUSORSTOM 4, 22°59'S, 167°22'E, 490–515 m, 29 Sep 1985 (MNHN IE-2019-4432, 1; MNHN IE-2019-4433, 2); *Alis* sta. CP1721, NORFOLK 1, 23°18'14.8212"S, 168°00'52.1856"E, 416–443 m, 26 Jun 2001, sample STRO57 (MNHN-IE-2012-875, 4 (3 badly fragmented)).

Diagnosis.— A species of *Poecilometra* with as many as 20 arms; IBr and br1–2 laterally flattened and apposed against adjacent ossicles, with lateral margins bearing projecting and often everted short flange; cirri in large specimens (3.4–4.6 mm across) XXVIII–LXIV, 12–17, to 23 mm long; longest cirrals with LW 2.2–2.5 (to 3.2 in small specimens); first pinnular (P(1)) of proximal several pairs of

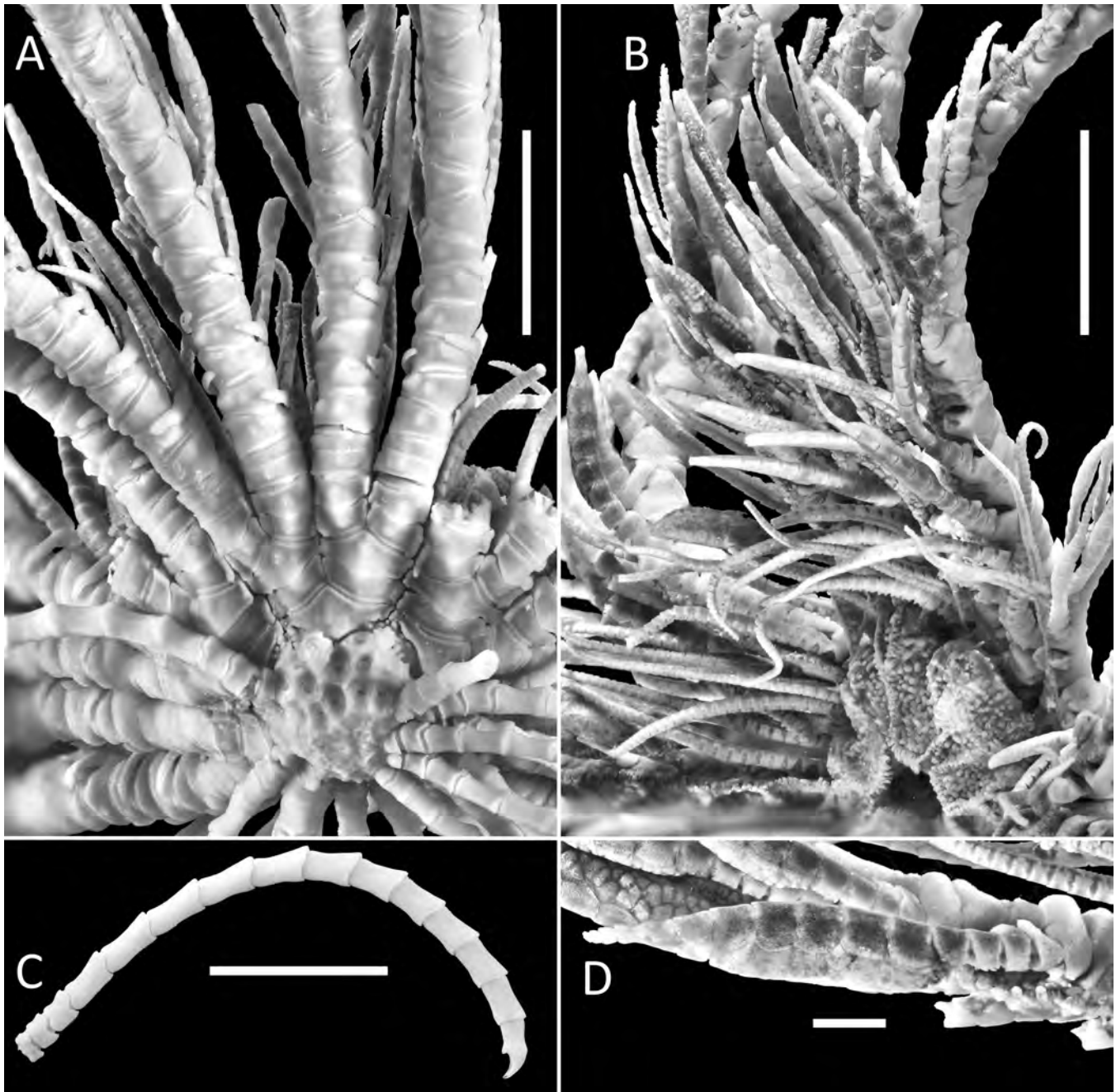


FIGURE 14 — *Poecilometra priamus*, large specimen, MNHN IE-2019-4432. **A**, centrodorsal and ray bases, aboral view. **B**, proximal pinnules and portion of disk showing pavement of nodules, lateral view. **C**, cirrus. **D**, genital pinnule, lateral view; A–C scale bars = 5 mm; D scale bar = 1 mm.

pinnules (sometimes excluding P1) bearing elongated, flat, abambulacral projection, often curved, tongue-like and, in larger specimens, extending around to aboral surface of arm. Distal portion of genital pinnules shorter than or occasionally as long as gonad, composed of up to 7 small, abruptly narrower pinnulars.

Description of smaller specimens (including syntypes).— Centrodorsal a pentagonal convex disk, shallow dome or flattened hemisphere, 1.5–2.9 mm across; DH 1.4–2.5 (Fig. 12A, 13). Interradial corners sometimes with weak irregular papillae or distinct tubercle (Fig. 12E). Aboral pole flat or convex, smooth or with irregular low papillae or traces

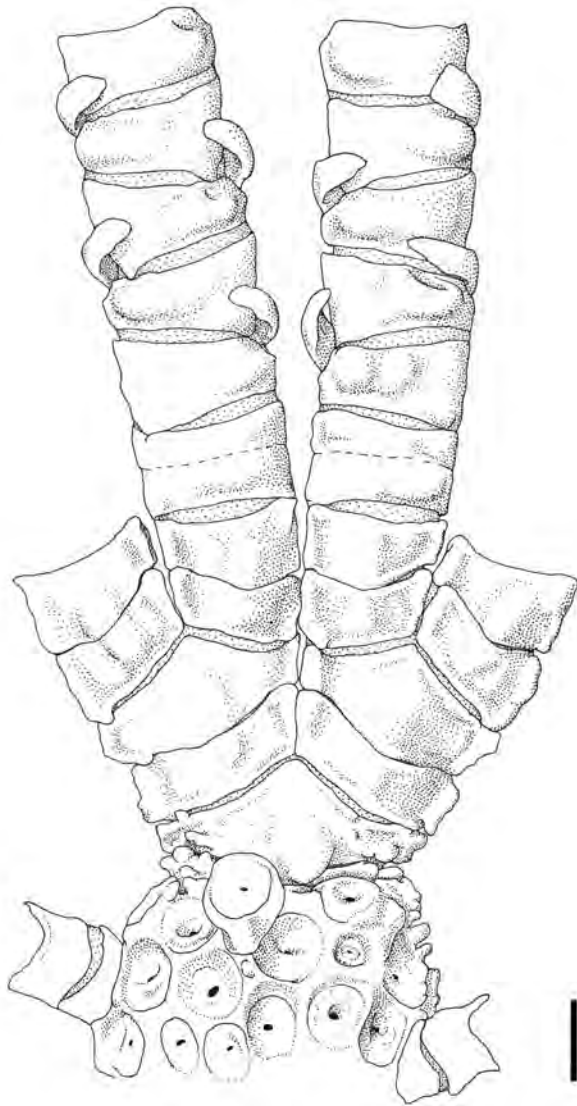


FIGURE 15 — *Poecilometra priamus*, MNHN IE-2019-4432, large specimen. Centrodorsal and base of one ray, aboral view; scale bar = 1 mm. Illustration by C. G. Messing.

of obsolete sockets, 0.5–0.75x centrodorsal diameter; one specimen with tiny apical bump; another with a small apical pit. Cirrus sockets crowded in single and partially double, irregular marginal tiers, rarely encroaching on polar area.

Cirri XI–XXII, 9–13 (possibly to ~15), 8 to ~14 mm long, slender, increasing in length from very short C1; C1 usually with weak to large aboral knob; C2 usually squarish; C4–5 (sometimes C5–6) longest, with LW 2.4–3.2; following cirrals slightly shorter, becoming compressed, wider and slightly constricted centrally with prominent distal end overlapping oral side of succeeding cirral, LW 2.5; distal cirrals with LW 2.0–2.4; antepenultimate cirral LW 1.4–2.1; penultimate cirral narrower, LW 1.5–1.8; opposing spine small, terminal, prominent, distally curved (rarely conical); terminal claw

sharp, curved, slightly shorter than or as long as penultimate cirral (Figs. 12B, C).

Radials not exposed, or visible as extremely short, shallow concave band, WL ~6.0–6.5; sometimes only articulation between radial and Ibr1 visible.

IBr2 and br1–2 flat-sided and closely apposed laterally, with lateral margins of each ossicle diverging and extended as short, often slightly irregular and slightly everted flange, sometimes with weakly scalloped edge and rounded ends (Figs. 12A, E, 13). Synarthrial swelling usually low and rounded, sometimes negligible, typically stronger on IBr2 than br1–2. Both Ibr1 and lax2 with lateral margins diverging so that axil is much wider than base of the ray. Ibr1 oblong or shallowly V-shaped, or with lateral portions of proximal and distal margins straight and midaboral portions of proximal margin gently convex and distal margin gently concave; WL chiefly 3.1–4.2 (extremes 2.6–5.0). Iax2 ranging from almost triangular or rhombic (with straight versus shallowly V-shaped proximal margin), both with very short diverging and projecting lateral margins, to distinctly pentagonal or hexagonal (straight versus convex proximal margin, respectively) with more distinct short diverging lateral margins; everted and projecting lateral margins similar to those of Ibr1 but shorter; WL chiefly 2.0–2.3 (extremes 1.8–2.6).

Arms 10–13, longest intact 40–45 mm. All proximal through middle brachials wider than long. Brr1–2 similar to IBr2 in having lateral margins apposed; lateral everted flanges continued from IBr2 but usually weaker. Br1 oblong or with exterior lateral margin longer; distal margin straight or shallowly concave to accommodate synarthrial swelling of br2; exterior lateral margin sometimes ending in rounded triangular projection; WL chiefly 2.1–2.6 (extremes 1.5–2.7). Br2 shorter than br1, almost oblong or slightly wedge-shaped with longer exterior lateral margin and with proximal margin usually convex; WL 2.0–3.0; one specimen with exterior lateral flange rounded and bifid. Br3+4 short, oblong, with lateral margins as in br1–2 or with lateral eversion weak or absent; WL 1.5–2.0. Brr5–6 (sometimes also br7) weakly to strongly wedge-shaped, wider distally, with or without weak alternating synarthrial swellings; WL 1.8–2.3 (Fig. 12A). Brr7–8 usually almost oblong; WL chiefly 1.7–2.0 (2.3 in one specimen; Fig. 13). Following brachials wedge-shaped, becoming almost triangular; middle brachials ranging from almost triangular to less strongly wedge-shaped; distal margins raised and finely spinose; WL 1.3–1.7. Triangular middle brachials with longer lateral margin to 3.5x length of shorter lateral margin. More distal brachials becoming less wedge-shaped, with finely spinose distal margins; WL 1.0–1.6; weakly wedge-shaped distal brachials with longer lateral margin often only 1.3x length of shorter lateral margin.

Second syzygy from br10+11 to br14+15; following interval 3–4.

First pinnular ($P_{(1)}$) of proximal pinnules from P1 to P4–P7 with abambulacral projection ranging from weak and triangular to well-developed, flattened, and tongue-like (rounded, truncated or irregular), usually strongest on

proximal genital pinnules on which the tip of the “tongue” may curve around to the aboral side of the arm (Figs. 14A, 15), and weakening on more distal pinnules. Although least developed on smallest specimens (Figs. 12F, 13), as indicated by the width ratio of $P1_{(1)}$ to $P1_{(2)}$, no more than about 1.5 (Fig. 17C), this projection is variably developed on similarly sized larger specimens (based on centrodorsal diameter) and is often not uniformly developed on different arms, i.e., weak or absent on one arm (Figs. 16 D, G) but well developed on another (Figs. 16E, H). Second pinnular ($P_{(2)}$) on P1 to P2 or P3 sometimes with weak abambulacral triangular projection. P1 of up to 35 pinnulars, 6 mm long (usually fewer and shorter, e.g., 17–23 segments, 4.7–5.0 mm), slender, delicate; pinnulars chiefly short; mid-distal pinnulars with LW up to 1.5. P2 sometimes not genital, 14 segments, 4.2 mm, similar to P1 but shorter, with more elongated middle pinnulars with LW to 2.25. Genital pinnules usually P2–P4 (Pa on at least one arm of one specimen with $Pa_{(8-10)}$ expanded; P3–P6 on another specimen, with expansion on P6 weaker), pedunculate and composed of distinctly narrower pinnulars preceding and following those bearing gonad; genital expansion variable, of 3–5 (rarely 6) pinnulars, e.g., $P_{(4-6 \text{ or } 7, 5-7 \text{ or } 9, 6-9, 10 \text{ or } 11)}$ (Fig. 12D; Figs. 22K vs. 22L), with broadest pinnulars ranging from 1.1x – 1.7x wider than more proximal narrower pinnular in abambulacral view; 3–7 pinnulars distal to gonad fragile, tapering to pinnule tip; initial pinnular distal to gonad no more than half width of widest genital pinnule. Genital P2 of 12–18 pinnulars, 4–6 mm. P3 similar to P2, 11–14 pinnulars, 3.75–4.5 mm long. P5 of 10 short, prismatic segments, 2.9–3.0 mm; sometimes with slight gonadal expansion on $P5_{(4-5)}$. P6 chiefly non-genital. Following pinnules gradually increasing in length. Middle pinnules of 10–12 pinnulars, 4.0–5.0 mm; most middle pinnulars of equal length, LW 1.4–1.75, becoming proportionally longer as pinnule narrows distally. Distal pinnules longer, probably reaching ~16–17 pinnulars.

Disk covered with rounded nodules.

Description of larger specimens.—Centrodorsal a flattened pentagonal hemisphere, 3.7–5.1 mm across, DH 1.6–3.1; Aboral pole usually no more than half adoral diameter of centrodorsal, flat or slightly convex, irregularly shaped, pitted or with traces of obsolete sockets, usually with apical sockets encroaching around margin. Centrodorsal margin shallowly concave radially, sometimes with a few small, rounded projections. Cirrus sockets in 2–3 crowded, irregular tiers, sometimes with each radial area having sockets arranged in a lateral column of 2–3 sockets each with midradial sockets arranged irregularly (Fig. 14A, 15).

Cirri XXXVII–XL, 12–18, 12–20 mm long (Fig. 14C). C1 short; following cirrals increasing in length; longest cirrals varying from C4–5 to C6–8, with LW chiefly 1.7–2.2 (to 2.4 on apical cirri); following cirrals decreasing gradually in length but remaining longer than wide; penultimate cirral narrower, WL 1.3; opposing spine located distally on cirral, triangular or rounded in profile, well developed (Fig. 12B, C) or small (Fig. 14C), with spine tip directed aborally (Fig. 12B) or curved distally (Fig. 12C); opposing spine on some cirri of one

specimen (MNHN IE-2019-4433) broad and scoop-shaped in distal view; terminal claw usually shorter than preceding cirral, sometimes shorter and rounded (possibly eroded); cirrals beyond basal few with expanded distal margins.

Radials either hidden by centrodorsal or just visible in interradian angles; distal margin with a few weak tubercles. IBr2, IIBr2 and brr1–2 closely apposed and laterally flat-sided; aboral surface ranging from flat through gently to strongly convex, usually with rounded midaboral synarthrial swellings; swellings weaker on IIBr2, and sometimes absent on brr1–2. Lateral margins of brachitaxes ossicles extending beyond articulations as short thick flange, slightly everted, often weakly scalloped or wrinkled, and sometimes interlocking with adjacent ossicle; proximal and distal margins of ossicles sometimes raised as weak, narrow ridge, smooth or slightly wrinkled. Interior distal corners of Iibr1 and br1 sometimes with extended triangular or rounded tip (Fig. 14A, 15). Ibr1 shallowly V-shaped, extremely short, partly to mostly hidden by centrodorsal; lateral portion of distal margin sometimes with few weak knobs. Iax2 pentagonal or hexagonal with short diverging lateral margins; WL 1.8–2.6. Iibr1 oblong or shallowly V-shaped, with diverging lateral margins, WL 2.3–3.4; Iiax2 similar to Iax2, WL 1.5–2.25.

Arms 18–20; longest intact arms ~80–100 mm. Brr1–2 flat-sided and apposed, sometimes with lateral margins weakly extended beyond articulation (Fig. 14A, 15). Br1 oblong or slightly longer exteriorly, sometimes with shallowly concave distal margin, WL 1.8–2.4. Br2 longer exteriorly, WL 1.9–2.4. Br3+4 oblong, WL 1.2–1.7; 1.2–1.66 mm across; low midaboral swelling sometimes present; br4 shorter than br3. Following few brachials weakly wedge-shaped, sometimes with low, broad swelling on alternating sides of successive brachials, WL 1.9–2.4. Brr9–10 or brr10–11 (sometimes only one) oblong, WL 2.0–2.1. Following brachials becoming triangular with weakly raised, finely spinulose distal margins, WL 1.7–2.1 (rarely to 2.4). Middle brachials strongly wedge-shaped to almost triangular, with longer lateral margin gently convex, WL 1.4–1.9 (rarely to 2.2). Brachials becoming wedge-shaped again distal to mid-arm, becoming weakly wedge-shaped distally, with longer lateral margin slightly convex and with distal margins slightly raised and weakly spinulose, WL 1.0–1.1, becoming longer than wide near arm tip.

Second syzygy widely variable, including on same specimen, from br8+9 to at least br24+25 (one specimen with 5+6 and 7+8 on separate arms); distal interval 3–6 (sometime to 9).

P1 with up to 41 short pinnulars, to 8.8 mm long, tapering from base to slender flexible tip (Fig. 14B); $P1_{(1)}$ usually with abambulacral flange or irregularly triangular projection ranging from weak to taller than width of body of pinnular, often variably developed on different arms of a specimen and infrequently absent (Fig. 16F–I); following several pinnulars with abambulacral keel; remaining pinnulars cylindrical. Abambulacral flange on following several pinnules increasingly longer, tongue-like, and in larger specimens often

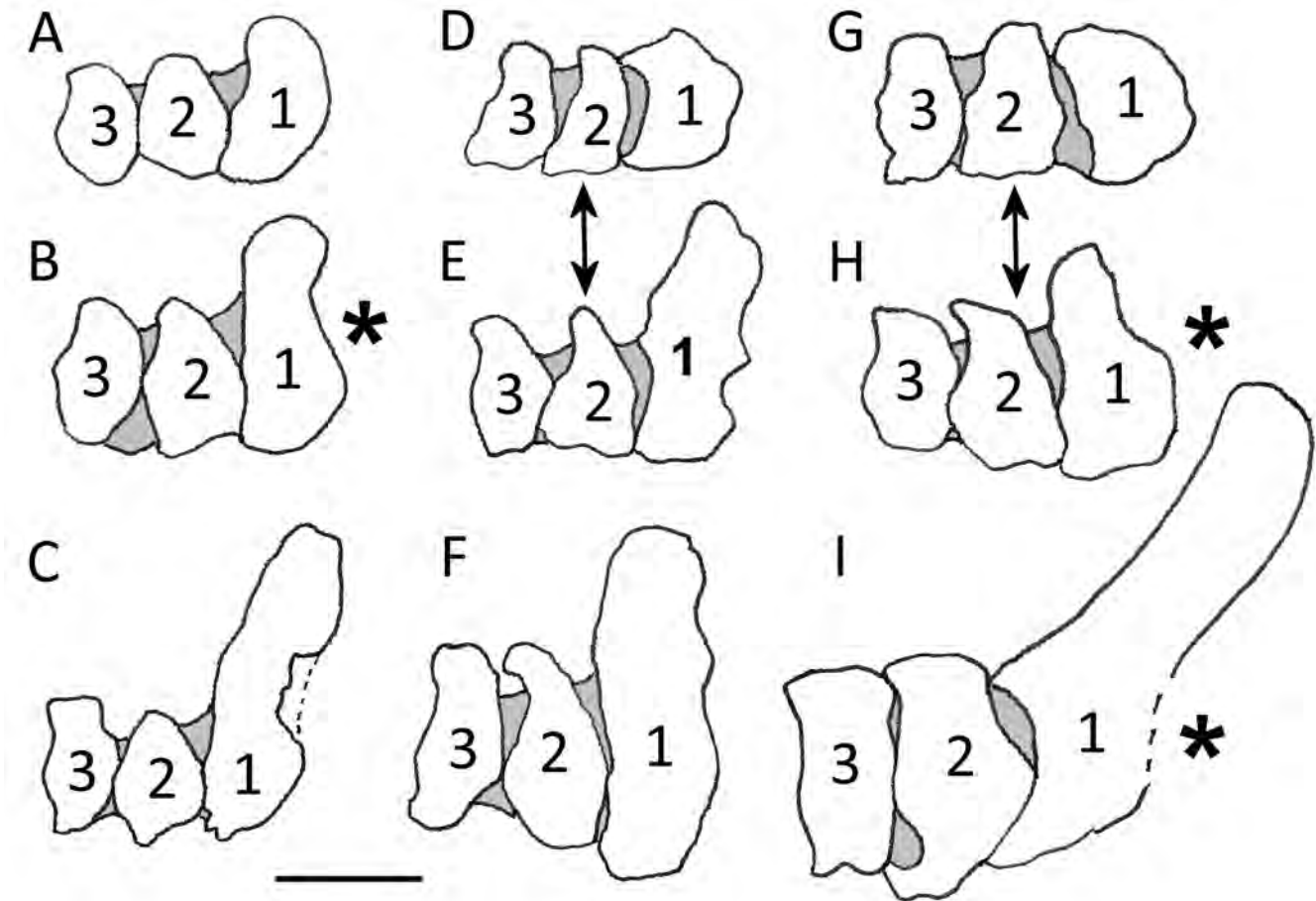


FIGURE 16 — *Poecilometra priamus*. Variations in abambulacral flange development on P1. **A**, NHMD-873492. **B**, NHMD-873541. **C**, MNHN IE-2012-831. **D–E**, MNHN IE-2007-5904, different arms. **F**, MNHN-IE-2012-875. **G–H**, MNHN-IE-2012-875 [different specimen than F], adjacent arms. **I**, MNHN IE-2019-4432, slightly oblique view. Numbers inside ossicles indicate first through third pinnulars ($P1_{(1-3)}$). Asterisks (*) indicate images that have been reversed for ease of comparison. Double-ended arrows indicate pinnules from different arms on the same specimen. Dashed line on right side of $P1_{(1)}$ in C indicates broken portion. Dashed line on right side of $P1_{(1)}$ in I indicates portion of ossicle hidden by adjacent arm; scale bar = 0.5 mm.

curving around onto aboral surface of arm (Fig. 15); becoming weaker anywhere from P5 to P12; absent on distal pinnules. Non-genital P2 similar to P1, of up to 29 pinnulars, 8.7 mm long; middle and following pinnulars longer than wide except near tip. Gonads usually on P2–P6, sometimes to P10; sometimes only 1–2 pinnules with fully developed gonads per side of arm; genital expansion ranging from narrow to broad (Figs. 14B, D). Genital P2 with narrow to well-developed gonad on $P2_{(9 \text{ or } 10 \text{ to } 15, 6-11, \text{ or } 8-14)}$, on $P2_{(4-6)}$ of smaller specimen; narrow distal portion of pinnule shorter than gonad, of up to 10 pinnulars, each longer than wide except near tip. Gonad irregularly plated. P3 of up to 22 pinnulars, to 8.4 mm long; genital expansion variable, of 4–5 pinnulars beginning anywhere from $P3_{(6)}$ to $P3_{(9)}$; up to ~7 narrow pinnulars distal to gonad. Middle and distal pinnules prismatic; middle pinnules up to 18 pinnulars, to 8.7 mm long; distal pinnules up to 17 pinnulars to 7.9 mm long; Pdistal₍₁₎ short and wide, no flange;

Pdistal₍₂₎ squarish; following pinnulars with LW 1.2–1.3.

Disk covered with numerous small, rounded nodules (Fig. 14B).

Distribution.— South of Timor I., eastern Indonesia, and New Caledonia; 245–685 (possibly 715) m (A. H. Clark, 1950 and herein).

Remarks.— Small and large specimens have been described separately above, because the larger specimens were initially thought to be a species distinct from *S. priamus* based on the enormously elongated, tongue-like projections on the first pinnular of proximal pinnules that often wrapped around to the aboral arm surface and looked like the fingers of a reed instrument player (Romanowski, 2015), and because specimens of intermediate size are lacking. However, examination of the type material of *S. priamus* (all small and ten-armed) revealed weakly developed versions of these projections in some specimens. In addition, new, small

specimens collected off New Caledonia with the distinctive large specimens resemble type specimens. A comparison of all specimens indicated that the pinnular projection is somewhat size related (i.e., least developed on smallest individuals) but may vary substantially among different arms of an individual (Figs. 16, 17C).

A. H. Clark (1912a) based his original description of *Strotometra priamus* on more than one specimen from *Siboga* sta. 266 (e.g., “centrodorsal...1.5 mm. to 2.0 mm in diameter”, p. 81), which he designated as the type locality, but he did not indicate the number of specimens. His re-description (A. H. Clark, 1950, p. 365) indicates the number and location of specimens from this sta. as “(39, U.S.N.M., E. 427; Amsterdam Mus.)”. However, USNM E427 includes 10 specimens; C.G.M. examined 2 specimens in RMNH. ECH.1813, and ZMA.ECH.CR.2089 includes 39 specimens listed as syntypes that were not examined. All are from sta. 266, indicating a total of 51 syntype specimens. Note: the original NHMD labels indicate 370 m and 345 m for the specimens from stations 1 and 56, respectively, but A. H. Clark (1950) gives the depths as 370-400 m and 245 m.

The new specimens extend this species' range to New Caledonia and increase the depth range to about 700 m.

Hemery's (2011) Maximum Likelihood tree placed a specimen identified as *Strotometra* n. sp. (MHNH-IE-2012-875, here treated as *P. priamus*) close to *Poecilometra ornatissima*. Both species have similar cirrals, brachitaxes, pedunculate genital pinnules, and an aboral P(1) flange.

Strotometra A. H. Clark, 1909a

Antedon (Part) Carpenter 1888: 127

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

Strotometra A. H. Clark 1909a: 19; 1912a: 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* Carpenter, 1888.

Diagnosis.—A genus of Charitometridae with centrodorsal hemispherical or discoidal; cirrus sockets in irregular marginal rows; cirri short and stout, X-XV, 10–15; ten arms; rays extending outward from oral-aboral axis; genital pinnules either with 1–2 narrow basal pinnulars or broadening gradually from the base; genital expansion over gonad usually at P(3–5) and tapering gradually distally; expanded pinnulars asymmetrical in cross-sectional view, with a longer, curved flange and usually shorter, thicker triangular flange, and articulation proportionally larger than in *Poecilometra*.

Distribution.—SW of Timor, eastern Indonesia (Kepulauan Kai), East China Sea, Ogasawara Is. and southern Japan; (160?) 183 to 660 m (A. H. Clark, 1950; Utinomi and Kogo 1968; Kogo, 1998; Kogo and Fujita, 2005).

Remarks.—With the transfer of *Strotometra ornatissima* and *S. priamus* to *Poecilometra* herein, *Strotometra*

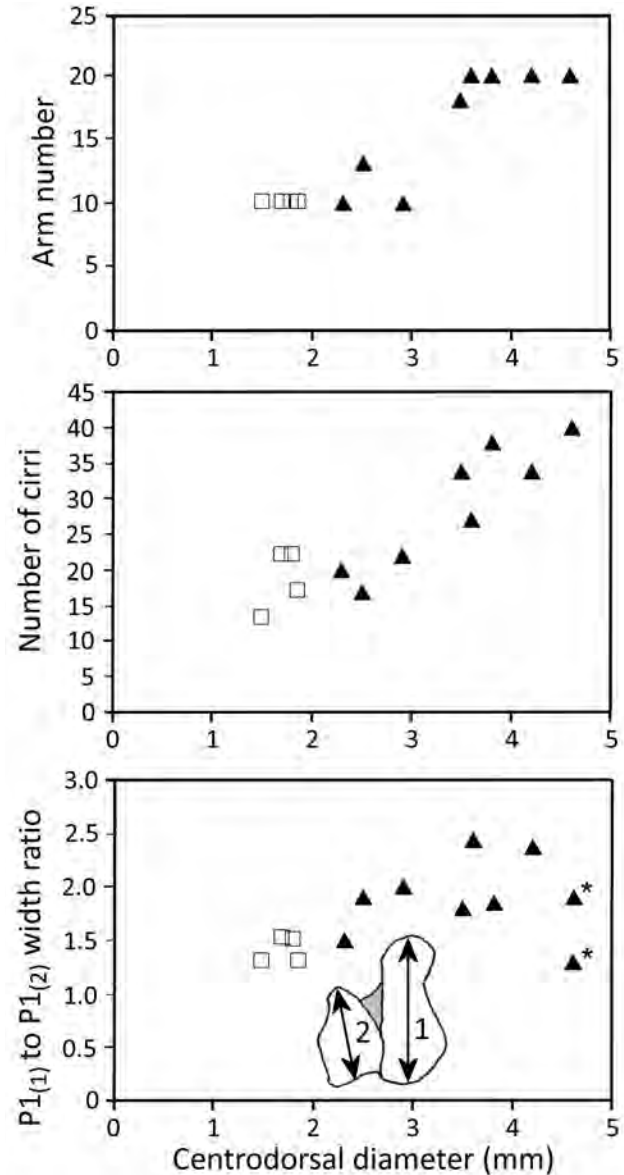


FIGURE 17 — *Poecilometra priamus*. Graphs illustrating variations in arm number, number of cirri, and width ratio of first two pinnulars ($P1_{(1)}$ to $P1_{(2)}$) relative to specimen size based on centrodorsal diameter. Double-ended arrows in bottom graph indicate width measurements of illustrated $P1_{(1)}$ and $P1_{(2)}$, giving a width ratio = 1.53. Open squares = syntypes: USNM E427, NHMD-873492, and NHMD-873541 (2). Black triangles, MNHN specimens from New Caledonia: IE-2019-4434, IE-2007-6012, IE-2007-5904, IE-2012-831 (2), IE-2012-875, IE-2019-4432, and IE-2019-4433 (2). * indicates values from two arms of one specimen.

retains only *S. parvipinna* and *S. hepburniana*. However, a combination of morphological and molecular data strongly suggest that they represent a single species, and we treat the genus as monotypic (see below).

Strotometra parvipinna (Carpenter, 1888)
 Figures 18–21, 22M–O

Antedon parvipinna Carpenter 1888: 127, pl. 15, fig. 9.—
 Hartlaub 1895: 130.—Hamann 1907: 1578.—A. H. Clark
 1912a: 33, 226.

Antedon hepburniana A. H. Clark 1907b: 139; 1912a: 33,
 226.

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

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

Strotometra parvipinna: A. H. Clark 1909a: 20; 1912a: 33,
 226; 1913a: 50; 1918: pl. 10, 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; 1912a: 33, 226; 1913a: 50; 1913b: 179; 1915b: 215;
 1918: 192, 194, pl. 9; 1921: pl. 2, fig. 28; 1950: 367–370,
 pl. 31, figs. 95–96, pl. 32 fig. 104.—Utinomi and Kogo
 1968: 51; Kogo, 1998: 111, 115–116, fig. 93.—Kogo and
 Fujita, 2005: 350.—Hemery 2011: 179–188, figs. IV.B.1–
 IV.B.10.

Holotype.—*Antedon parvipinna* Carpenter, 1888, NHM
 88.11.9.26, *Challenger* sta. 192, Kei Islands, 5°49'15"S,
 132°14'15"E, 256 m, 26 Sep 1874.

Material Examined.—INDONESIA: *Challenger* sta.
 192, Kepulauan Kai (Kei Is.), 5°49'15"S, 132°14'15"E, 256
 m, 26 Sep 1874 (NHM 88.11.9.26, holotype, photographs
 only); Danish Expedition to the Kei Islands sta. 56, 5°33'S,
 132°51'30"E, 345 m, 10 May 1922 (USNM E3142 (identified
 as *S. parvipinna*, 1 specimen, photographs only), NHMD-
 874397, 4). JAPAN: *Albatross* sta. 4890; 10 miles SW of Goto
 Is., 32°26'30"N, 128°36'30"E, 243 m, 9 Aug 1906, bottom
 temp. 11.28°C, rocky bottom (USNM 35692 (identified as *S.*
hepburniana, photographs only); Captain Schönau, Eastern
 Sea, S of Goto Is., 32°10'N, 128°20'E, 183 m [180 m in AHC
 1950], 23 Apr 1898 (NHMD-873531, 1, as *S. hepburniana*).
 "EAST ASIA" [probably East or South China Sea]: [Capt.]
 Suensson, [Danish cable-repair ship] Eastern Asia, 19 Apr
 1911 (NHMD-873536, 1, as *S. hepburniana*).

Description.—Centrodorsal discoidal or low hemispheric,
 with strongly projecting, rounded or irregularly triangular
 interradial projections visible in some specimens (identified
 as basal rays in A. H. Clark (1950)), ~2.0–3.3 mm diameter,
 DH 2.1–2.5. Interradial projections sometimes roughened
 or bearing tiny conical tubercles. Cirrus sockets crowded
 in single or partly double, irregular, marginal row(s) (apical
 aboral to basal socket in an irregularly columnar arrangement
 in one specimen). Apical pole flat or gently convex, covered
 with weak irregular sculpture (irregular tubercles, ridges)
 imparting a sponge-like appearance, rarely smooth, 0.6–0.8x
 centrodorsal diameter; one specimen with a gently convex
 center surrounded by small irregular bumps and vestiges of
 apical sockets.

Cirri short, stout, X–XVIII (chiefly XIII–XVI), 9–15
 (chiefly 11–13), up to ~12 mm long; C1 very short;

following cirrals progressively longer; C4–5 to C5–6 (rarely
 to C7) longest, LW 0.9 to 1.2 (maximum 1.6); following
 cirrals shorter, LW 0.7 to 1.0; cirrals in distal half slightly
 compressed and wider than proximal cirrals; distal few
 cirrals preceding penultimate with swollen, rounded aboral
 distal end; antepenultimate cirral sometimes narrower than
 preceding; penultimate cirral always narrower than preceding,
 LW 1.1–1.3; small opposing spine usually rounded triangular
 and distally directed, sometimes sharply conical and/or erect,
 sometimes eroded and blunt; terminal claw curved, shorter or
 longer than penultimate cirral.

Radials completely hidden by centrodorsal or cirri, visible
 only in interradian angles, or exposed as extremely short,
 gently curved bands (concave distally), with lateral margins
 sometimes swollen. IBr2 gently to moderately convex
 aborally, laterally flattened and apposed, with midaboral
 rounded synarthrial swelling or weak narrow keel; lateral
 margins sometimes projecting as thin flange or short ridge.
 Ibr1 oblong to slightly crescentic (concave distally), often
 narrowing laterally, with lateral portions of aboral surface
 bearing one or more rounded knobs or small irregular conical
 tubercles (sponge-like appearance); lateral margins sometimes
 weakly everted; WL 3.7–5.2. Iax2 usually pentagonal, often
 with proximal margin slightly V-shaped; lateral margins
 diverging or straight (rarely negligible so that axil appears
 triangular), usually slightly everted with slightly irregular
 flange, WL 1.8–3.0; lateral portions of either proximal or
 distal margins (or both) sometimes slightly everted and
 lined with fine tubercles or tiny irregular teeth; distal margin
 sometimes irregularly swollen.

Arms 10, to 75 mm long, increasing in width from base to
 br6–10; weak (usually barely noticeable), narrow midaboral
 ridge present, sometimes a low round or slightly elongated
 knob on proximal brachials, sometimes limited to proximal
 brachials, rarely absent on some or all brachials. Brr1–2
 laterally flattened and apposed; lateral margins with weak
 projecting flange, sometimes weakly everted with finely
 irregular or dentate edge. Br1 oblong or weakly wedge-
 shaped and slightly longer exteriorly, sometimes slightly
 curved (concave distally); interior distolateral corner a
 rounded or triangular projection; WL 1.9–2.6. Br2 longer
 exteriorly, WL 2.1–2.8. Br3+4 oblong; lateral margins at
 least slightly flattened (rounded in one specimen); br4 (rarely
 also br3) with thickened, flared distal margin; WL 1.4–1.9,
 1.1–1.55 mm across. Br5 oblong or with interior margin
 slightly longer; one or both lateral margins often diverging;
 distal margin thickened and flared; WL 2.0–2.8. Following
 several brachials (to br9–10) short, wedge-shaped, with
 diverging lateral margins, and distal margin thickened, flared
 and concave, much wider than visible span of succeeding
 articular ligament; WL 1.9–3.0. Following brachials
 becoming strongly wedge-shaped, then triangular, with distal
 margin not as thickened, flared and concave as more proximal
 brachials; middle brachials proportionally more elongated,
 but remaining wider than long. Brachials becoming wedge-
 shaped distally, with distal margin less thickened than on

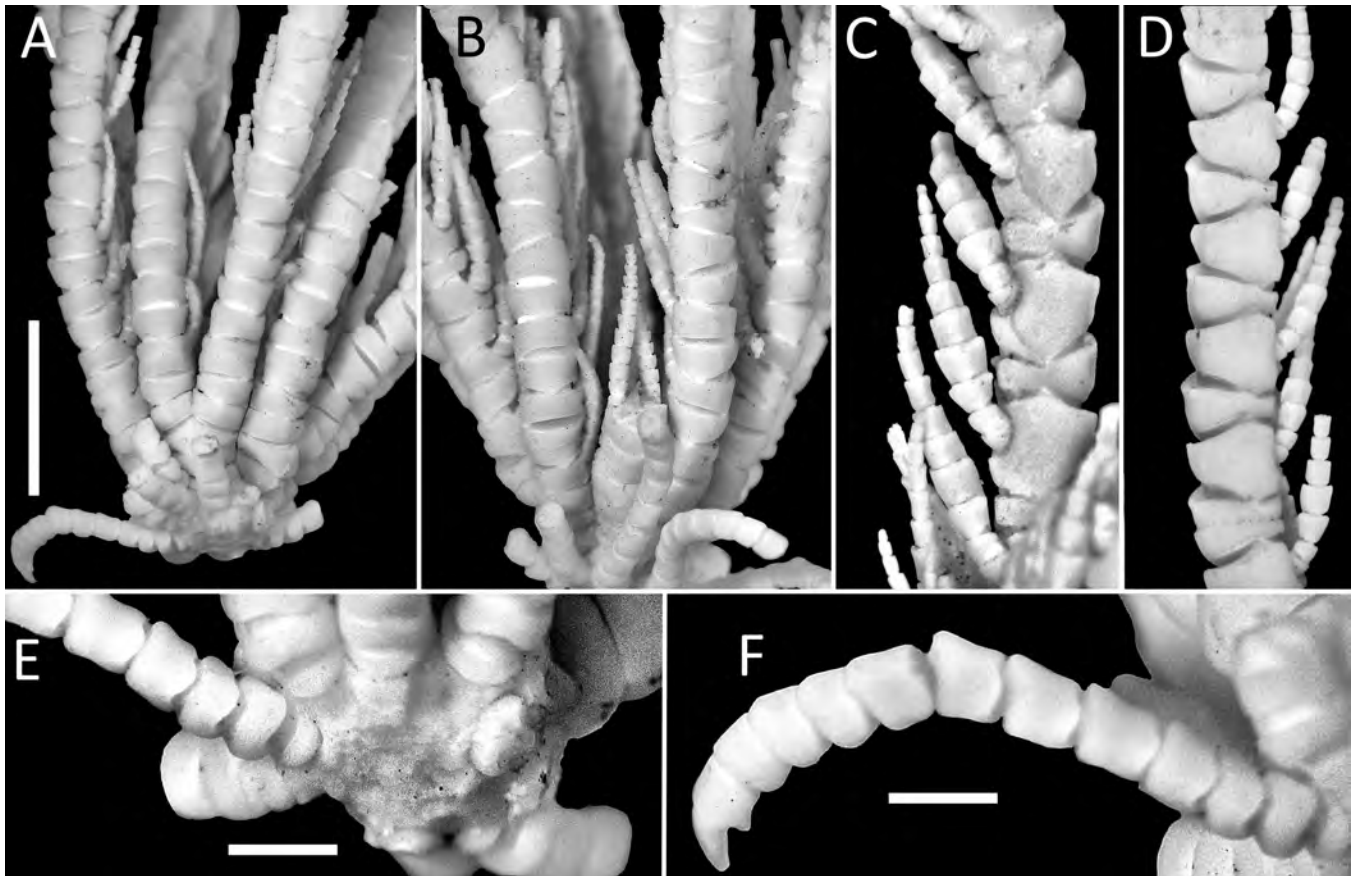


FIGURE 18 — *Strotometra parvipinna* NHM 88.11.9.26 (holotype). **A**, centrodorsal and proximal arms, lateral view. **B**, proximal arms showing proximal pinnules, lateral view. **C**, genital pinnules. **D**, middle arm. **E**, centrodorsal. **F**, cirrus. Portions of strongly out-of-focus cirri deleted in **E** and **F**; A–D scale bars = 5 mm; E–F scale bars = 1 mm

more proximal brachials; WL 1.5–1.7, and proportionally more elongated near arm tip; WL 1.0–1.3.

Syzygies at br3+4 (absent on at least 4 arms (1 on each ray) on one specimen); second widely variable, usually br13+14 to br15+16 (extremes br8+9 to br18+19); distal interval chiefly 4–9 (extremes 3–10).

P1 to 23 pinnulars, 5.0 mm long (usually shorter with fewer pinnulars, e.g., 13–17, 4.4–4.6 mm), sometimes much smaller and shorter on at least some arms; pinnulars all short, most with abambulacral margin slightly diverging and distal corner projecting; 1–3 pinnulars near tip sometimes longer than wide, LW to 1.3; ambulacral groove present; P1₍₁₎ wider than P1₍₂₎, with abambulacral projection; P1₍₂₎ short; P1₍₃₋₄₎ wider with diverging abambulacral margin; following pinnulars gradually narrower, with lateral margins becoming parallel. P2 usually non-genital, similar to P1 (sometimes shorter or longer) with up to 17 pinnulars, 4.2 mm long; P2₍₃₋₅₎ to ₍₄₋₆₎ with diverging lateral margins, expanded but not as much as on genital pinnules; following pinnulars gradually narrower; distal few pinnulars squarish or with LW to 1.2. One specimen with P2 genital, 12 pinnulars, 4.0 mm long, with P2₍₃₋₆₎ expanded over gonad; P2₍₄₎ widest, LW 0.55,

rapidly narrowing distally with 2–3 pinnulars near tip longer than wide, LW to 1.7. P3 genital or not.

P4 usually first genital pinnule, up to 13 pinnulars, 4.8 mm long; Pgen₍₁₎ wider than Pgen₍₂₎; Pgen₍₂₎ short, with diverging lateral margins; Pgen_(3 or 4) to _(5 or 6) (rarely to Pgen₍₇₎) expanded over plated gonad; expanded pinnulars either with both lateral margins diverging, or with abambulacral margin diverging with rounded triangular distal end, and adambulacral margin rounded, LW 0.5–0.8; pinnule distal to gonad gradually tapering; longer distal pinnulars with LW 1.2–1.7. Mid-abambulacral ridge on expanded gonadal pinnulars in NHMD-873531 (identified as *S. hepburniana*) with rounded distal projection so that distal margins of these pinnulars appear to have a pair of rounded distal knobs (Fig. 22O). Distalmost gonad variable, on P8 to P12, sometimes variably developed on different pinnules of a single arm. Middle (non-genital) pinnules to 14 pinnulars, 5.2 mm long; Pmid₍₃₋₄₎ weakly expanded; 1–3 pinnulars near tip with LW to 1.3. Distal pinnules to 17 pinnulars, 5.0 mm long; Pdist₍₁₎ short, Pdist₍₂₎ with LW ~1.0; following pinnulars longer than wide, to LW 1.8 near tip; distal end of abambulacral ridge pointed and slightly projecting distally.

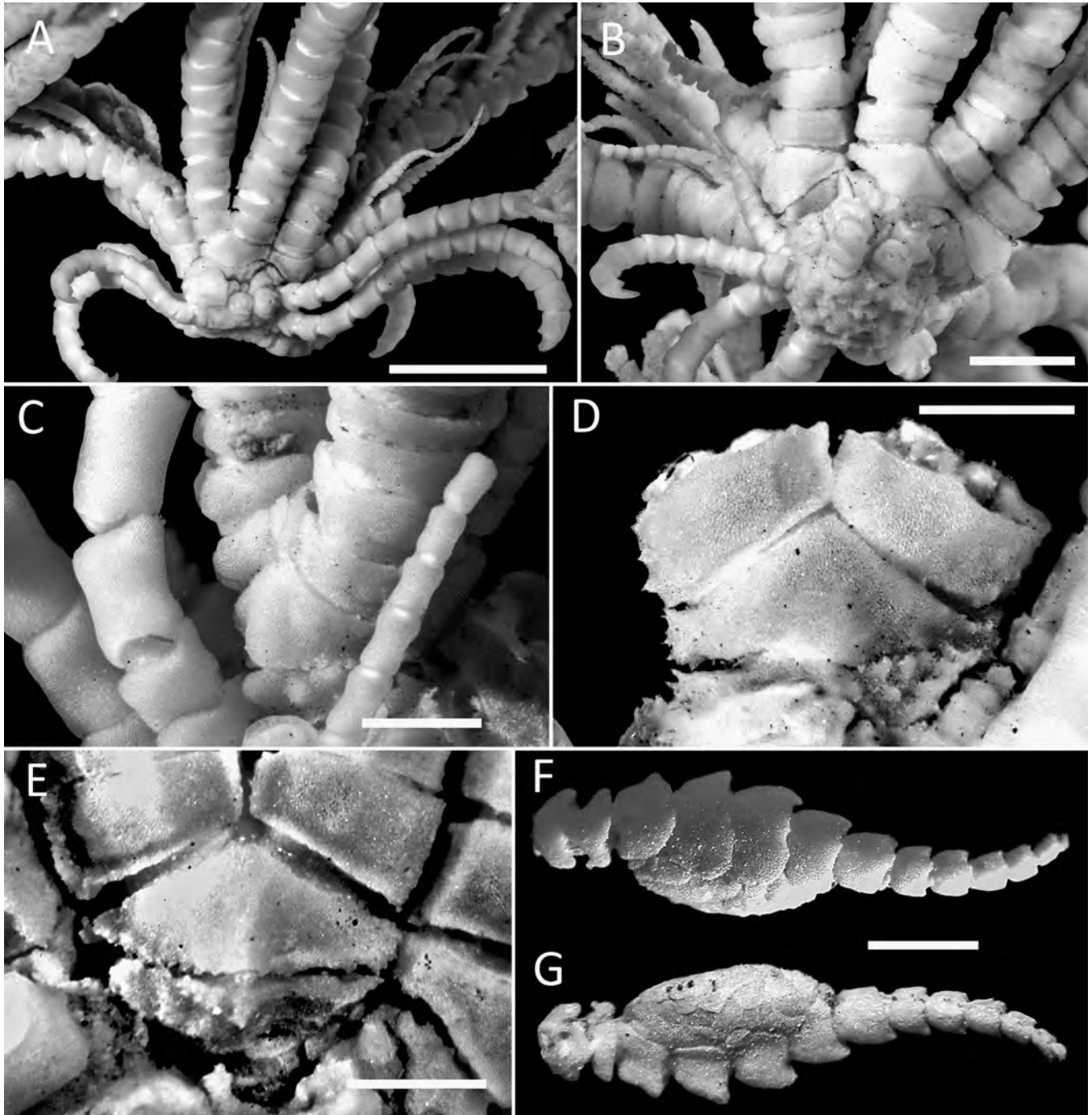


FIGURE 19 — *Strotometra parvipinna*. A–D, NHMD-874397, four specimens illustrating variations in ray base features. A, Ibr1 with weak irregular surface; Iax2 with finely irregular lateral and proximal margins. B, Ibr1 with midaboral knob and second knob to left of right-hand axil; Iax2 with weak midaboral swelling and lateral margins almost smooth. C, Ibr1 with multiple knobs; Iax2 with strong, midaboral “nose-like” synarthrial swelling. D, Ibr1 partly hidden by centrodorsal, with blunt spines on right side and short fine spines along lateral margin; Iax2 with fine spines along lateral margins (and on left-hand lateral margin of br1). E–G, USNM E3142. E, ray base with sponge-like aboral surface of Ibr1 and weakly dentate proximal margin of Iax2. F–G, genital pinnules, abambulacral (F) and adambulacral (G) views; A scale bar = 5 mm; B scale bar = 2 mm; C–D, F–G scale bars = 1 mm.

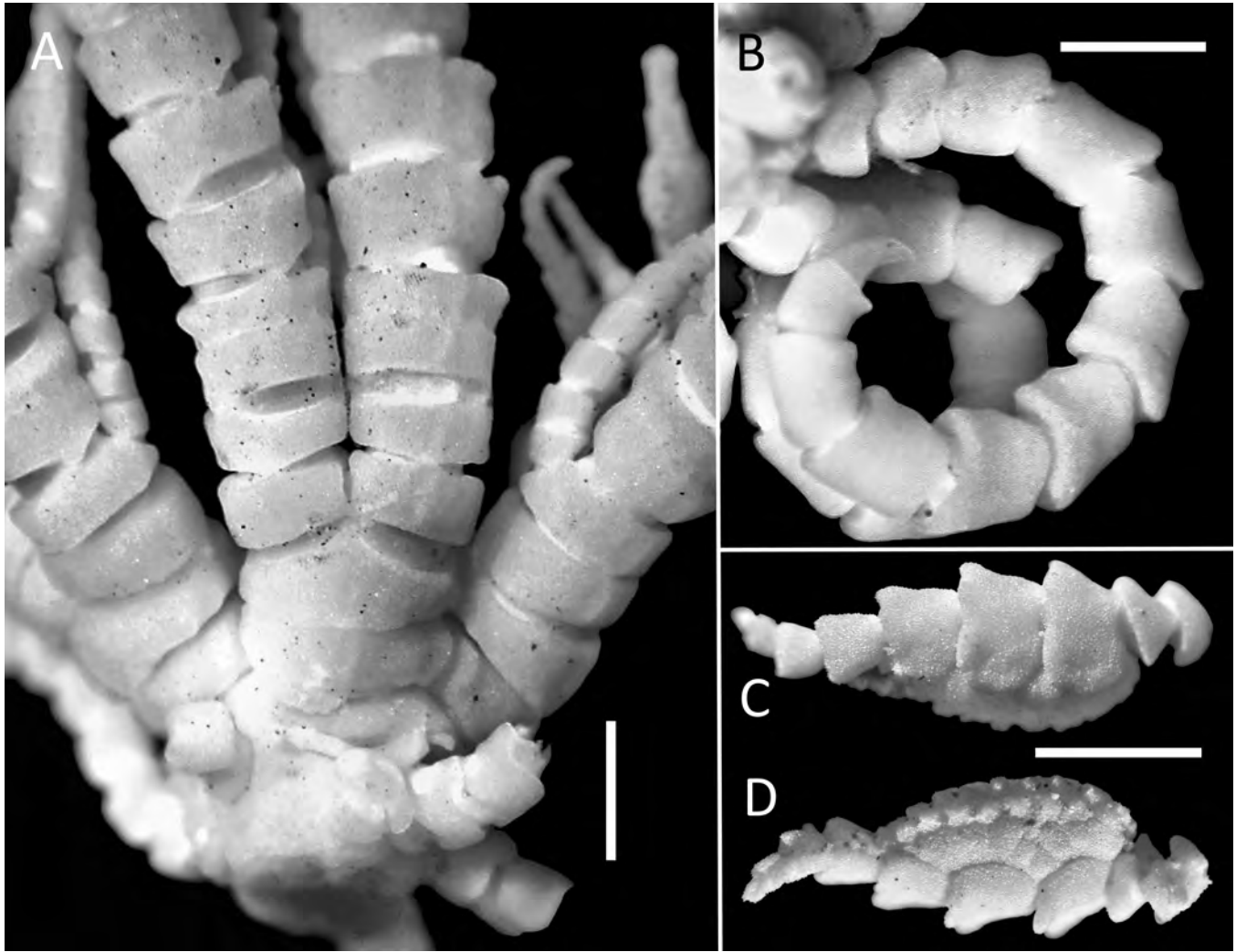


FIGURE 20 — *Strotometra hepburniana* USNM 35692. **A**, centrodorsal and ray bases. **B**, cirrus. **C–D**, detached genital pinnule. **C**, abambulacral view. **D**, oblique adambulacral view showing side and covering plates on gonad; scale bars = 1 mm.

Interambulacral areas of disk with separated or sparse small nodules, round or irregular; nodules crowded in thick band along ambulacra.

Color yellow or dull orange.

Distribution.— Same as for genus.

Remarks.— A. H. Clark (1950) distinguished *Strotometra parvipinna* from *S. hepburniana* chiefly on the basis of size-related characters, i.e., P1 with 20–22 versus 10–11 segments and 6 mm vs. 3.5 mm long, arms 60–75 mm vs. 45 mm long, and cirri with 10 vs. 11–15 cirrals, respectively. His other distinction was between the proximal pinnules: “smooth or nearly so” in *S. parvipinna* versus “with conspicuously flaring and overlapping distal ends, appearing very rough” in *S. hepburniana* (pp. 361–362). However, examination of type material and other specimens identified by A. H. Clark revealed no consistent difference in proximal pinnule

characters between the two nominal species (Figs. 18B, 19A, 20A, 21). His reference to the “flaring and overlapping distal ends” appears to apply more to the genital pinnules of *S. hepburniana* than to the proximal pinnules (Figs. 20C–D, 21B). The expansion of the genital pinnules is wider in the examined specimens of *S. hepburniana* (Figs. 20C, D, 21B) relative to *S. parvipinna* (Figs. 18C, 19F, G, 21A). However, genital pinnule expansion may vary even within an individual (see fig. 14B above center); and it is possible, though not documented in Charitometridae, that male and female genital pinnules might differ, as they do in brooding *Isometra* (Holland, 1991).

Other features also do not appear to vary consistently between the two. As examples, specimens attributed to both species have a weak midaboral ridge or keel on the brachials, although A. H. Clark (1950) did not mention it in

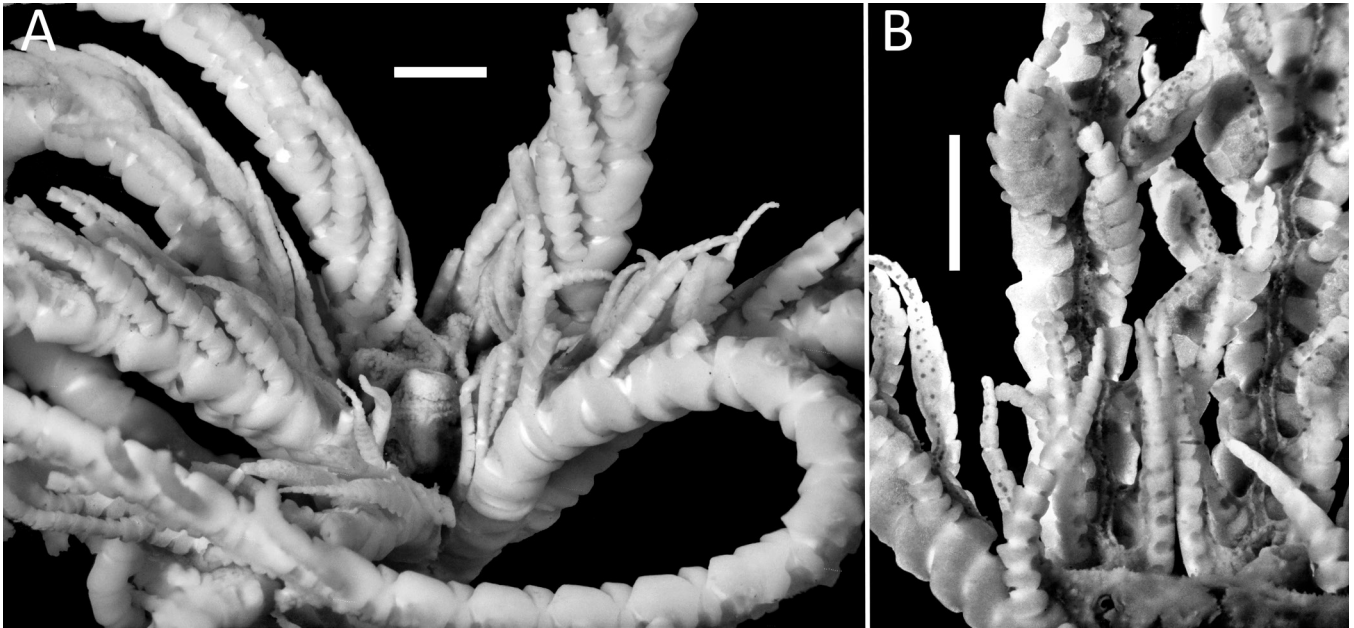


FIGURE 21 — Proximal pinnules. **A**, *Strotometra parvipinna* NHMD-874397. **B**, *Strotometra hepburniana* NHMD-873531, proximal pinnules; scale bars = 5 mm.

his description of *S. hepburniana*, and it was not recognizable in one of four *S. parvipinna* examined from NHMD-874397. The IBr2 ossicles vary from having little or no sculpture (apart from lateral flanges) along the margins in both the holotype of *S. parvipinna* (Fig. 18A) and specimens of *S. hepburniana* (e.g., Fig. 20A), to an irregularly dentate proximal margin on the Iax2 and irregularly sponge-like sculpture on the aboral surface of Ibr1 in specimens of *S. parvipinna* (Figs. 19D, E), or distinct knobs especially on Ibr1 in other *S. parvipinna* (Fig. 19B, C). Although all *S. hepburniana* specimens examined for the current paper lack any spiny or knobby ornamentation on IBr2, Kogo (1998) described new specimens identified as *S. hepburniana* from Japan as having the division series “granulated with minute tubercles” (p. 116), accompanied by an illustration showing irregular ornamentation along the lateral margins (his fig. 93a). We therefore treat *S. hepburniana* as a junior synonym of *S. parvipinna*. In addition, Hemery (2011) returned specimens identified as *S. parvipinna* and *S. hepburniana* as well-supported sister terminals (Fig. 1).

A. H. Clark identified (according to the specimen label) a small specimen (NHMD-873536) collected by Capt. Suensson in “East Asia” as *S. hepburniana* (catalogued 19 Sep 1911) but did not include it in his monograph (A. H. Clark, 1950), although he did include other NHMD-874397 specimens that he identified as *S. parvipinna* collected later (10 May 1922). The omission might have been due to the small size and immaturity of the specimen: arms 10, ~15 mm long, curled over the aboral surface, obscuring the centrodorsal, most cirri and brachitaxis. Cirri stout, of 8 short cirrals, 3.2 mm long. P1 developed on some arms, 8 short segments, ~1.5 mm long; following several pairs of pinnules not developed

or rudimentary; no genital expansion. Cirri, brachials, and pinnules similar to those of *S. parvipinna*. A. H. Clark (1913b) also noted the provenance of this specimen as “probably Korean Straits.”

Alcohol-preserved specimens attributed to both *S. parvipinna* and *S. hepburniana* have no obvious ambulacral groove on most pinnules with large gonads. Instead, the mid-ambulacral surface is a series of sacculi alternating with covering plates. However, this may be a function of preservation, although podia and a distinct groove are visible on many distal pinnules.

DISCUSSION

As noted in the introduction, A. H. Clark (1950) placed the genera of Charitometridae in 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) two to four abruptly broader pinnulars with a shorter slender tip (*Strotometra*, *Poecilometra*, *Chlorometra*, and *Charitometra*). A comparison of genital pinnules across all charitometrid genera (Fig. 22), plus the descriptions and illustrations in the taxonomic section above, and additional details discussed below, support placing *Charitometra* (Fig. 22A–B), *Chlorometra* (Fig. 22C), and *Strotometra* (Fig. 22M–O) in the first group, leaving *Poecilometra* as the only genus with genital pinnules characteristic of his second group, what we have termed “pedunculate”. Hemery’s (2011) sequence results (Fig. 1) also place *Strotometra* in the same charitometrid clade as

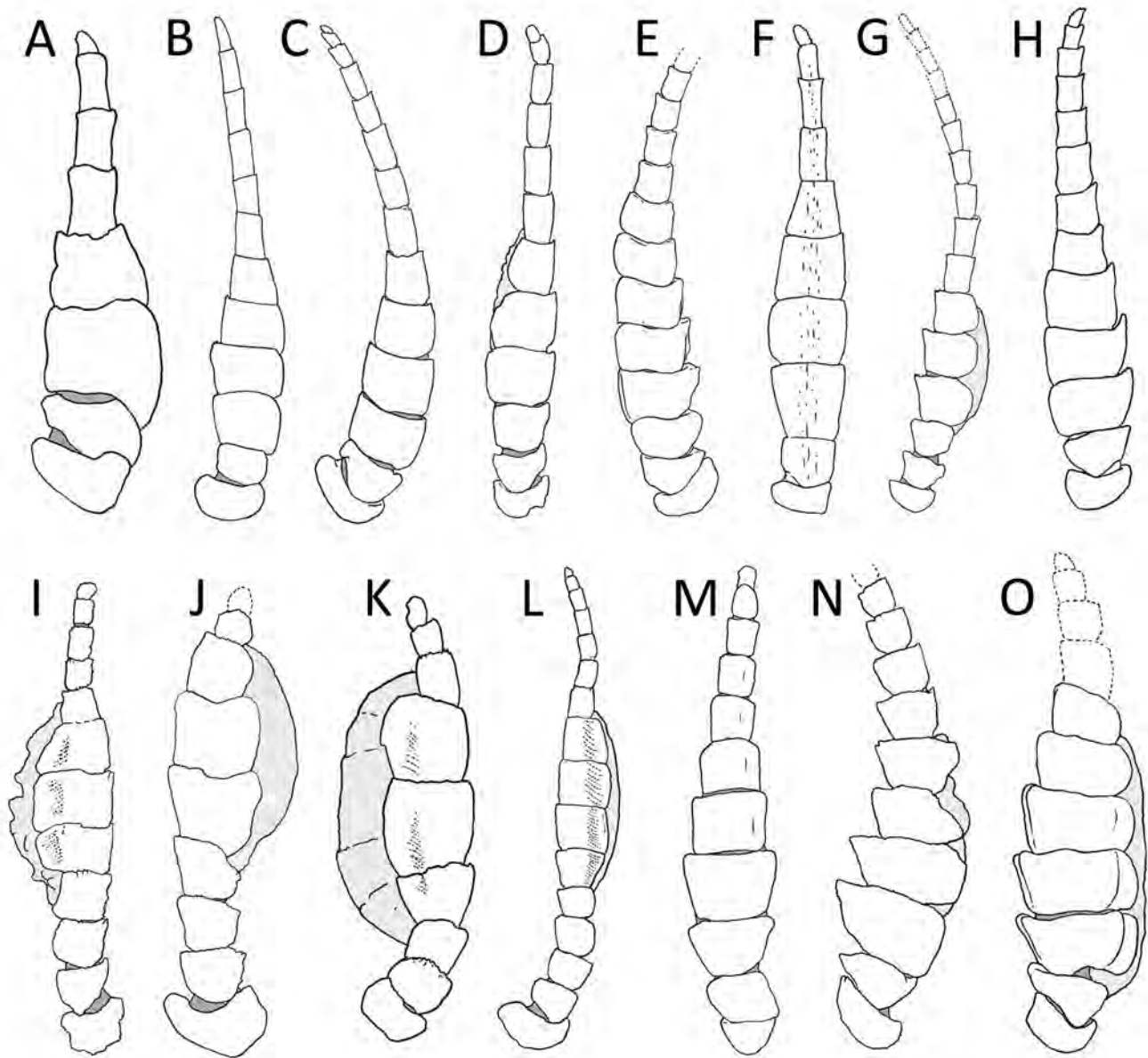


FIGURE 22 — Charitometrid genital pinnules (not to scale). **A.** *Charitometra basicurva* NHM 88.11.9.22, syntype. **B.** *Charitometra incisa*, NHM 88.11.9.23, syntype. **C.** *Chondrometra rugosa*, RMNH.ECH.2101. **D.** *Crinometra brevipinna* NSU-CRI 649. **E.** *Monachometra flexilis* NHM 88.11.9.27, cotype (distal end out of photograph). **F.** *Chlorometra garrettiana* (holotype of *Diodontometra bocki*, UUZM 254 (redrawn from Gislén, 1922, fig. 82, p. 88). **G.** *Glyptometra tuberosa*, NHM 88.11.9.25, syntype (distal four pinnulars missing, reconstructed from adjacent pinnule). **H.** *Glyptometra inaequalis* NHM 88.11.9.81, cotype. **I.** *Poecilometra baumilleri* USNM 1660641 (FLMNH 21597 spec. 2) paratype. **J.** *Poecilometra acoela* NHMD-873490 (tip reconstructed from nearby pinnule). **K.** *Poecilometra priamus* RMNH.ECH.1813, syntype. **L.** *Poecilometra priamus* USNM E427. **M.** *Strotometra parvipinna* NHM 88.11.9.26, holotype. **N.** *Strotometra parvipinna* NHMD-874397 (tip missing). **O.** *Strotometra hepburniana* NHMD-873531 (distal four pinnulars missing, reconstructed from adjacent pinnule). A–C, E–H, K, M. from photographs. D, I–J, L, N–O. from specimens.

representatives of three other group-one genera (per A. H. Clark's usage) (*Chondrometra*, Fig. 22C; *Monachometra*, Fig. 22E; *Glyptometra*, Fig. 22G), separate from a *Poecilometra* clade (although those sequences did not include either *P. acoela* or *P. baumilleri*). We have also re-assigned both

priamus and *ornatissima* to *Poecilometra* based on genital pinnule features, leaving only *parvipinna* and its synonym *hepburniana* in *Strotometra*. Synonymizing the latter two was supported by the broadly overlapping morphology revealed by our re-examination of type and other specimens.

Of the other two genera in Clark's second grouping, *Chlorometra* and *Charitometra*, the former has genital pinnules more similar to those of genera in his first group (Fig. 22F). The holotype of *Chlorometra garrettiana* A. H. Clark, 1907b (USNM 22633) is badly fragmented, and no images of its genital pinnules are available. A. H. Clark (1950, p. 221) diagnosed this monotypic genus as having genital pinnules with $P_{(3-5 \text{ or } 6)}$ "flattened and expanded with winglike borders, the portion of the pinnules beyond being abruptly narrower and shorter than the expanded portion." However, he described them (p. 223) as having the pinnulars following $P_{(1-2)}$ wider than long, and the following pinnulars longer than wide, with the two terminal pinnulars small [no mention of the expansion, but see below]. He then distinguished shorter genital pinnules as having $P_{(3-4)}$ "markedly longer and slightly broader than those following, though they are not broader than the two basal segments". He synonymized *Diodontometra bocki* Gislén, 1922, under *C. garrettiana*, and considered the latter as an immature specimen of the former. In comparing the two, he wrote: "In the genital pinnules of *garrettiana* the third and fourth segments are often abruptly larger than those following and flattened; but they are not broader than those preceding and do not have produced lateral borders as in *bocki*; this is probably an indication of immaturity..." Gislén's (1922) drawing of a *D. bocki* genital pinnule (Fig. 22F) shows similarities to those of *Glyptometra* (Fig. 22H), *Crinometra* (Fig. 22D), and some *Strotometra* (Fig. 22M), all members of the first group of genera. Despite placing *Chlorometra* in group two, A. H. Clark (1950, p. 199) also wrote: "the genital pinnules are not so abruptly and greatly swollen as they are in the other members of this [second] group and they may not be swollen at all, though the genital segments are usually enlarged. The genital pinnules of *Chlorometra* are very little different from those of *Monachometra* [group one], of which *Chlorometra* should perhaps be regarded as a synonym." His comment that "they may not be swollen at all" reflects our observation that the expansion of genital pinnules may vary substantially among arms of an individual and from small to large specimens, even at similar distances along the arms (Fig. 14B).

For the final genus in group two, A. H. Clark (1950, p. 348) diagnosed *Charitometra* as having genital pinnules with an abruptly narrower distal portion shorter than the expanded gonadal portion (group two). However, examination of type specimens reveals that, although many genital pinnules of *Charitometra basicurva* (Carpenter, 1884) have an abruptly narrower distal portion, it is often just as long as or longer than the expanded gonadal portion (Fig. 22A) and tapers rather gradually in some. Likewise, those of the type species, *Charitometra incisa* (Carpenter, 1888), have a gradually tapering distal portion that may be longer than the expanded gonadal portion (Fig. 22B). Hemery's (2011) sequence results place *Charitometra basicurva* well within the clade of genera characterized by group one genital pinnules (Fig. 1).

An initial examination of expanded gonadal pinnulars in

a selection of genera using scanning electron microscopy (SEM) supports separating *Poecilometra* (Fig. 23F–G) from representatives of all four other genera examined: *Monachometra* (Fig. 23A), *Crinometra* (Fig. 23B), *Glyptometra* (Fig. 23C), and *Strotometra* (Fig. 23D–E). Viewed in cross-section, these pinnulars in *Poecilometra* are symmetrical, with a proportionally much smaller articular area, especially the abambulacral ligament fossa, and proportionally much longer, thinner lateral "wing-like" flanges than in the other genera. They appear to be uniform across the genus; those of *P. baumilleri* (not shown) are similar in all respects to those of *P. acoela* (Fig. 23F) and *P. priamus* (Fig. 23G). Although not examined with SEM, those of *P. ornatissima* appear similar (see Figs. 10E, 11B). By contrast, those of *Monachometra*, *Glyptometra*, *Crinometra*, and *Strotometra* are asymmetrical, with one flange longer and curved, and the other shorter, thicker, and triangular and a proportionally larger articular facet with a larger ligament fossa than in *Poecilometra*. However, the "wing-like" flanges approach similar lengths in a specimen originally identified as *S. hepburniana* (here treated as a synonym of *S. parvipinna*). As a result, these flanges and articular features require additional inquiry to evaluate their potential diagnostic status, e.g., how they vary with growth along and among arms, with gonadal development, and among additional charitometrid taxa.

CONCLUSION

Family Charitometridae appears to be divisible into two groups based on both morphological and molecular sequence data: those with a series of narrow basal pinnulars followed by an abruptly expanded short series of pinnulars associated with the gonad (pedunculate) versus those with gradually tapering genital pinnules. Symmetrically versus asymmetrically expanded gonadal pinnulars may offer an additional distinction. Two species formerly placed in *Strotometra* (*priamus* and *ornatissima*) have been re-assigned to *Poecilometra* based on these genital pinnule features, although the former differs from the other members of the genus in having up to 20 rather than just 10 arms. As no consistent morphological features distinguish the remaining two *Strotometra* species (*S. hepburniana* and *S. parvipinna*), they are treated as synonyms herein, as the senior *S. parvipinna*. We re-diagnosed *Poecilometra* to include both the features of the genital pinnules as well as the aborally-directed flange on $P(1)$. *Poecilometra baumilleri* n. sp. was described and placed in *Poecilometra* on the basis of both of these features. Future studies should combine molecular analyses and morphological re-evaluation, including ontogenetic variations, of the remaining charitometrid genera. Both generic- and specific-level distinctions remain unclear in many cases, e.g., similar characters currently diagnose species of *Glyptometra* but only varieties of *Crinometra* (A. H. Clark, 1950).

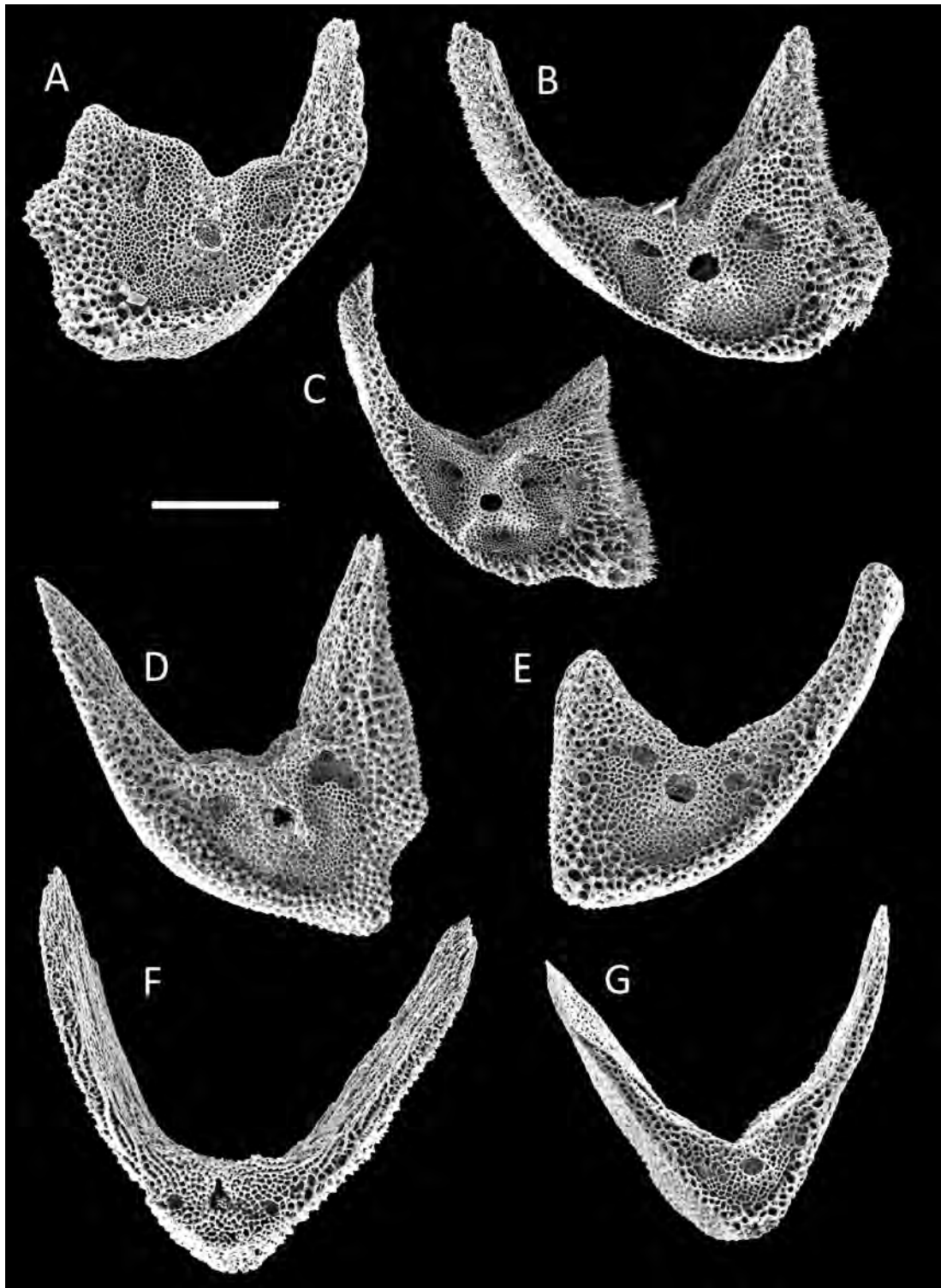


FIGURE 23 — Expanded gonadal pinnulars. **A**, *Monachometra patula* MNHN IE-2007-6012. **B**, *Crinometra brevipinna* NSU-CRI 649. **C**, *Glyptometra lateralis* FLMNH 21599. **D–E**, *Strotometra parvipinna*. **D**, NHMD-873531 (originally *S. hepburniana*). **E**, USNM E3142. **F**, *Poecilometra acoela* NHMD-873490. **G**, *Poecilometra priamus* NHMD-873492. Note that A, E and G versus B, C, D and F are from pinnules on opposite sides of arms; scale bar = 250 μ m.

ACKNOWLEDGEMENTS

The authors wish to thank David Pawson, William Keel, and William Moser (National Museum of Natural History, Smithsonian Institution); Marc Eléaume, Nadia Améziane, and Pierre Lozouet (Muséum national d'Histoire naturelle, Paris); Amy Baco-Taylor, John Slapcinsky, and Gustav Paulay (Florida State University), and Tom Schiøette (Zoologisk Museum København) for loans of specimens from their respective institutions and collections. We also wish to thank Dr. Patricia Blackwelder and Ria Achong-Bowe (NSU) for their invaluable expertise and assistance with the scanning electron microscopes. This research was partly funded through the Collaborative Research: Assembling the Echinoderm Tree of Life project (National Science Foundation, Award ID: 1036219), to one of us (CGM).

LITERATURE CITED

- BULLIMORE, R. D., N. L. FOSTER, and K. L. HOWELL. 2013. Coral-characterized benthic assemblages of the deep Northeast Atlantic: defining "Coral Gardens" to support future habitat mapping efforts. *ICES Journal of Marine Science*, 70: 511–522.
- CARPENTER, P. H. 1880. Feather-stars, recent and fossil. *Popular Science Review*, 4(15): 193–204.
- _____. 1883. On a new crinoid from the Southern Sea. *Annals and Magazine of Natural History* (5th series), 12, 143–144.
- _____. 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 Voyage of H.M.S. Challenger, Zoology, Part I, General morphology, with descriptions of the stalked crinoids, v. 11 (1884): 1–442 pp., text-figs. 1–21, pl. 1–62.
- _____. 1887. Notes on echinoderm morphology, No. X. On the supposed presence of symbiotic algae in Antedon rosacea. *Quarterly Journal of Microscopical Science* (New series), 27: 379–391, pl. XXX, fig. 3
- _____. 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 Voyage of H.M.S. Challenger, Zoology, Part II, The Comatulæ, 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.
- _____. 1907b. Description of new species of recent unstalked crinoids from the coast of northeastern Asia. *Proceedings of the United States National Museum*, 33: 127–156.
- _____. 1908a. New genera of unstalked crinoids. *Proceedings of the Biological Society of Washington*, 21: 125–136.
- _____. 1908b. Some points in the Ecology of Recent Crinoids. *American Naturalist*, 42(503): 717–726.
- _____. 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.
- _____. 1908d. Notice of some crinoids in the collection of the Museum of Comparative Zoology. *Bulletin of the Museum of Comparative Zoology, Harvard*, 51(8): 233–248.
- _____. 1909a. A revision of the crinoid families Thalassometridae and Himerometridae. *Proceedings of the Biological Society of Washington*, 22: 1–22.
- _____. 1909b. On a collection of crinoids from the Zoological Museum of Copenhagen. *Videnskabelige Meddelelser den naturhistoriske Forening i Kjøbenhavn*, 61:115–194.
- _____. 1911. The recent crinoids of Australia. *Memoir of the Australian Museum*, 4(15) :705–804.
- _____. 1912a. The crinoids of the Indian Ocean. *Echinoderma of the Indian Museum*, pt. 7, Crinoidea. *The Indian Museum, Calcutta*, 325 pp.
- _____. 1912b. Six new East Indian crinoids belonging to the family Charitometridae. *Proceedings of the Biological Society of Washington*, 25: 77–84.
- _____. 1913a. Notes on the recent crinoids in the British Museum. *Smithsonian Miscellaneous Collection*, 61(15): 1–89.
- _____. 1913b. Description of a collection of unstalked crinoids made by Captain Suenson in Eastern Asia. *Proceedings of the Biological Society of Washington*, 26: 177–182.
- _____. 1914. Une étude philosophique de la relation entre les crinoïdes actuels et la température de leur habitat. *Bulletin de l'Institut océanographique, Monaco*, 294: 1–11.
- _____. 1915a. A monograph of the existing crinoids. 1. The comatulids. Part 1. *Bulletin of the United States National Museum*, 82(1): 406 pp., 17 pls.
- _____. 1915b. 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.
- _____. 1916. Six new genera of unstalked crinoids belonging to the families Thalassometridae and Charitometridae. *Journal of the Washington Academy of Sciences*, 6(17): 605–608.
- _____. 1918. The unstalked crinoids of the Siboga Expedition. *Siboga Expedition*, 42b: 1–300, 28 pl.
- _____. 1921. A monograph of the existing crinoids. 1. The comatulids. Part 2. *Bulletin of the United States National Museum*, 82(2): 1–795, fig. 1–949, pl. 1–57.
- _____. 1931. A monograph of the existing crinoids. 1. The comatulids. Part 3. Superfamily Comasterida. *Bulletin of the United States National Museum*, 82(3): 816 pp., 82 pls.
- _____. 1932. On a collection of crinoids from the Indian Ocean and the Bay of Bengal. *Records of the Indian Museum*, 34: 551–566.

- _____. 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.
- _____. 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): 383 pp., 32 pls.
- EAGLE, M. K. 2001. New fossil crinoids (Articulata: Comatulida) from the Late Oligocene of Waitete Bay, northern Coromandel Peninsula, New Zealand. *Records of the Auckland Museum* 37: 81–92, 22 fig.
- GISLÉN, T. 1922. The crinoids from Dr. S. Bock's expedition to Japan 1914. *Nova Acta Regiae Societatis Scientiarum Upsaliensis*, (4)5(6): 1–183, text-fig. 1–162, pl. 1, 2.
- _____. 1924. Echinoderm studies. *Zoologisk Bidrag från Uppsala*, 9: 1–316.
- _____. 1927. Papers from Dr. Th. Mortensen's Pacific Expedition 1914–16. 37. Japanese crinoids. *Videnskabelige Meddelelser frå Dansk Naturhistorisk Forening i København*, 83: 1–69, fig. 1–80, pl. 1–2.
- _____. 1928. Notes on some crinoids in the British Natural History Museum. *Kungliga Svenska Vetenskapsakademiens, Arkiv för Zoologi*, 19A (32): 1–15.
- _____. 1933. Papers from Dr. Th. Mortensen's Pacific Expedition 1914–16. LXVII. A small collection of crinoids from St. Helena. *Videnskabelige Meddelelser frå Dansk Naturhistorisk Forening i København*, 93: 475–485.
- _____. 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.
- _____. 1938. Crinoids of S. Africa. *Kungliga Svenska Vetenskapsakademiens Sällskapet Lund, Handlingar*, (series 3) 17(2): 1–22, pl. 1–2.
- 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 Leopoldina (Abhandlungen der Kaiserlich Leopoldinisch-Carolinischen Deutschen Akademie der Naturforscher)* 58(1): 1–120, pl. 1–5.
- _____. 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.
- _____. 1912. XLV. Die Comatuliden. 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". *Memoirs of the Museum of Comparative Zoology*, Harvard, 27(4): 277–491, pl. 1–18.
- HEMERY, L. G. 2011. Diversité moléculaire, phylogéographie et phylogénie des Crinoïdes (Echinodermes) dans un environnement extrême : l'océan Austral. PhD Dissertation. *Museum national d'Histoire naturelle*, Paris, 381 pp.
- _____, M. ROUX, N. AMÉZIANE, and M. ELÉAUME. 2013. High-resolution crinoid phyletic inter-relationships derived from molecular data. *Cahiers de Biologie Marine*, 54: 511–523.
- HESS, H. 2011. Articulata: Introduction. In Hess, H., and C. G. Messing. Part T: Echinodermata 2. Revised Crinoidea, Volume 3, P. A. Selden (ed.), *Treatise on Invertebrate Paleontology*. University of Kansas Paleontological Institute, Lawrence, Kansas, pp. 1–22.
- _____, and C. G. MESSING. 2011. Part T: Echinodermata 2. Revised Crinoidea, Volume 3. In P. A. Selden (ed.), *Treatise on Invertebrate Paleontology*. University of Kansas Paleontological Institute, Lawrence, Kansas, pp. 1–261.
- HOLLAND, N. D. 1991. Echinoderms and Lophophorates. In Giese, A. C., Pearse, J. S. & Pearse, V. B. (eds.), *Reproduction of Marine Invertebrates*, Boxwood Press, Pacific Grove, CA, vol. 6, pp. 247–299.
- ICZN (International Commission on Zoological Nomenclature). 1999. *International Code of Zoological Nomenclature*, 4th edition. International Trust for Zoological Nomenclature, London, 289 pp. <https://www.iczn.org/the-code/the-international-code-of-zoological-nomenclature/the-code-online/>
- KOGO, I. 1998. Crinoids from Japan and its adjacent waters. *Special publications from Osaka Museum of Natural History*, 30: 1–148.
- _____, and T. FUJITA, T. 2005. Geographic distribution of crinoids (Echinodermata) in southwestern Japan. In Hasegawa, K., G. Shinohara, and M. Takeda (eds.) *Deep-Sea Fauna and Pollutants in Nansei Islands*, National Science Museum Monographs, Tokyo, no. 29, pp. 297–355.
- MARSHALL, J. I., and F. W. E. ROWE. 1981. The Crinoids of Madagascar. *Bulletin du Muséum national d'Histoire naturelle*, Paris, 4(3): 379–413.
- MCKNIGHT, D. G. 1975. Some echinoderms from the northern Tasman Sea. *NZOI Records / New Zealand Oceanographic Institute*, 2(5): 49–76.
- _____. 1977a. Some crinoids from the Kermadec Islands. *NZOI Records / New Zealand Oceanographic Institute*, 3(13): 121–128.
- _____. 1977b. Additions to the New Zealand crinoid fauna. *NZOI Records / New Zealand Oceanographic Institute*, 3(11): 93–112.

- _____. 1977c. Crinoids from Norfolk Island and Wanganella Bank. NZOI Records / New Zealand Oceanographic Institute, 3(14): 129–137.
- _____. 1989a. Further crinoids (Echinodermata) from off the Kermadec Islands, southwest Pacific Ocean. DMFS Reports (NZOI) 3(3): 31–35.
- _____. 1989b. Some echinoderm records from the tropical south-western Pacific Ocean. DMFS Reports (NZOI) 3(2): 19–30.
- _____. 1989c. Further records of Tasman Sea and Coral Sea Echinoderms. DMFS Reports (NZOI) 3(1): 3–17.
- MESSING, C. G. 2020a. A revision of the unusual feather star genus *Atopocrinus* with a description of a new species (Echinodermata: Crinoidea). *Zootaxa*, 4731(4): 471–491. <https://doi.org/10.11646/zootaxa.4731.4.2>
- _____. 2020b. Erratum: A revision of the unusual feather star genus *Atopocrinus* with a description of a new species (Echinodermata: Crinoidea). *Zootaxa*, 4772 (3): 600. <https://doi.org/10.11646/zootaxa.4772.3.11>
- _____, and J. H. DEARBORN. 1990. Marine flora and fauna of the northeastern United States. Echinodermata: Crinoidea. National Oceanic and Atmospheric Administration Technical Report, National Marine Fisheries Service 91: 1–29.
- _____, N. AMÉZIANE, and M. ELÉAUME. 2000. Echinodermata Crinoidea: Comatulid crinoids of the KARUBAR Expedition to Indonesia. The families Comasteridae, Asterometridae, Calometridae and Thalassometridae. In Crosnier, A. (ed.), *Résultats des Campagnes MUSORSTOM*, vol. 21. *Mémoires du Muséum national d'Histoire naturelle*, 184: 627–702.
- _____, A. C. NEUMANN, and J. C. LANG. 1990. Biozonation of deep-water lithohermes and associated hardgrounds in the northeastern Straits of Florida. *Palaios*, 5: 15–33.
- _____, V. J. SYVERSON, M. A. VEITCH, K. STANLEY, AND T. K. BAUMILLER. 2019. Advances in Understanding the Deep Tropical Western Atlantic Crinoid Fauna (Echinodermata). ASLO Aquatic Sciences Meeting, “Planet Water: Challenges and Successes,” San Juan, Puerto Rico, 23 Feb-2 Mar 2019. <https://www.aslo.org/wp-content/uploads/ASLO-2019-Program-Book-with-addendum.pdf>
- MEYER, D. L., C. G. MESSING, and D. B. MACURDA Jr. 1978. Biological results of the University of Miami deep-sea expeditions. 129. Zoogeography of tropical western Atlantic Crinoidea (Echinodermata). *Bulletin of Marine Science*, 28(3): 412–441.
- MINCKERT, W. 1905. Das Genus *Promachocrinus*, zugleich ein Beitrag zur Faunistik der Antarktis. *Zoologische Anzeiger*, 28: 490–501.
- NORMAN, A. M. 1865. On the genera and species of British Echinodermata. 1, Crinoidea, Ophiuroidea, Asteroidea. *Annals and Magazine of Natural History (series 3)*, 15, 98–129.
- POURTALÈS, L. F. de. 1868. Contributions to the fauna of the Gulf Stream at great depths. *Bulletin of the Museum of Comparative Zoölogy*, 1(6), 103–142.
- RASMUSSEN, H. W. 1978. Articulata. In Moore, R. C. and Teichert, C. (eds.) *Treatise on Invertebrate Paleontology*, Part T. Echinodermata 2(3). The Geological Society of America, Inc. & The University of Kansas Press. Boulder, CO & Lawrence, Kansas, pp. T813–T928, T938–T998.
- ROMANOWSKI, A. 2015. A Revision of the Genera of Charitometridae with Abruptly Expanded Genital Pinnules. M. S. Thesis, Nova Southeastern University. 87 pp. https://nsuworks.nova.edu/occ_stuetd/383/
- ROUSE, G. W., L. S. JERMIIN, N. G. WILSON, I., EECKHUAT, D. LANTERBECQ, T. OJI, C. M. YOUNG, T. BROWNING, P. CISTERNAS, L. E. HELGEN, M. STUCKEY, and 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.
- ROWE, F. E. W., and J. GATES. 1995. Echinodermata. In Wells, A. (ed.) *Zoological Catalogue of Australia*, CSIRO Australia, Melbourne, vol. 33, pp. xiii + 510.
- SHIPLEY, A. E., and E. W. MACBRIDE. 1901. *Zoology: An elementary textbook*. The MacMillan Company, New York City, New York, 632 pp.
- TOMMASI, L. R. 1969. Nova contribuição a lista dos crinóides recentes do Brasil. Contribuições avulsas do Instituto Oceanográfico, Universidade de São Paulo, sér. Oceanografía biológica. 17, 8 pp.
- UTINOMI, H. and KOGO, I. 1968. A revised catalogue of crinoids collected from Japanese waters. *Proceedings of the Japan Society of Systematic Zoology*, 4: 46–53 (In Japanese).

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Contributions from the Museum of Paleontology, University of Michigan is a medium for publication of reports based chiefly on museum collections and field research sponsored by the museum. Jennifer Bauer and William Ausich, Guest Editors;
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Print (ISSN 0097-3556), Online (ISSN 2771-2192)