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 A. H. Clark. 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 (Pouralès, 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, 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et al. 2019, and unpublished observations).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: Crossoometra (3 species), Perissometra (11), and Monachometra (1) for species formerly in Pachylometra and Glyptometra; Chondrometra (3) for species formerly in Chlorometra; and Calypometra for Charitometra lateralis A. H. Clark, 1908b. A. H. Clark’s (1918) detailed key to the family included 42 species (including 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 IIIbr4(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 (P3,4) abruptly expanded versus a slight, gradually tapered expansion; 10 versus >10 arms; distal arms laterally compressed versus not; centroidal shape, and overall size (“large” versus “small”).

In a series of papers, Gislén (1922) first added Diodontometra (for D. bocci 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 centroidal 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 Calypometra, Crossoometra, 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 or 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, IIIbr 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 kermacendeensis McKnight, 1977a; and Chondrometra crozieri 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 chariotetrid 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, Ptillometridae A. H. Clark, 1914, Asterometridae Gislén, 1924, and the fossil families Conometridae Gislén, 1924, Pseudoconometridae Eagle, 2001, and Pterocometridae Rasmussen, 1978. However, recent molecular analyses returned the superfamily as polyphyletic, with monophyletic Charitometridae sister to a deep-sea clade composed of the stalked Guillericrinidae Mironov and Sorokina, 1998, and the feather star family Pentametrocrinidae 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 chariotetrid terminals (combined CO1, 16S, 28S and 18S) represent the most inclusive sequence data yet available for the family. Both analyses returned two
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; brr = 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., IIax4 = 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, Pmid, 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 brevipina (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.

Pinnulas 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).
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 tubercules 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. Cirri usually <25 (rarely up to ~30), without aboral spines, but sometimes carinate or with low distal tubercle. Distal cirri usually as long as wide or longer, often not much shorter than proximal cirri. 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; II Br 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, pinnulas than succeeding pinnules; lengths similar, or increasing or decreasing from the most proximal; number of pinnulas 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 Stirotometa

1a. Genital pinnules with 3–5 narrow basal pinnulas following a usually wider P(1) and preceding expanded pinnulas bearing the gonad (pedunculate); expanded gonadal pinnulas symmetrical in cross-sectional view, with small articular area, especially the abambulacral ligament fossa, and long, thin lateral “wing-like” flanges; pinnulas distal to expanded gonadal pinnulas 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 brr1-2 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 brr1-2 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; cirr X–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; cirr 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 ornatisima

4b. No strongly everted crest on distal edges of any proximal brachial; 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

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 ornatisima 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 charitomorphids and appear to represent a synapomorphy. On this basis, Strotometra priamus and Strotometra ornatisima 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 oscule margins often everted and irregular, and associated with laterally flattened and apposed ray bases (P. priamus and P. ornatisima) (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. ornatisima 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, 55, figs. 5; 1887: 391, pl. 30, fig. 3; 1888: 132, pl. 2, fig. 3 a-d, pl. 16., figs 1–5.—Hartlaub 1891: 113.—Shipley and MacBride 1901: 269.—Minckert 1905: 190.—Hamann 1907: 1578, pl. 12, fig. 1.—A. H. Clark 1912a: 33, 225; 1915a: 43.


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
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 brr1–2 (flanges reduced in small specimens); c irr i 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 interradial 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 4.5 (Fig. 2). Small NHM syntype with IBr2 smoothly rounded aborally and no synarthrial swelling; Ibr1 with weak straight flange on diverging lateral flanged 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). B1 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.
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(6) 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 60º” (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.
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 pinnulas.

**Description.**—Centrodorsal dome-shaped, or rounded or truncated conical, and with short thick interradial 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,
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 7 — Poecilometra baumilleri new species, genital pinnules. A, FLMNH 21597. B, USNM 1660641. C, FLMNH 21594, genital expansion weaker; scale bars = 2 mm.
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 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 brr increasingly wedge-shaped, but 1 or 2 ossicles from br8 to br10 oblong or almost square; subsequent brr becoming more strongly wedge-shaped, almost triangular by br15. Middle brr 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 brr 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 (6–7)), 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(14–6); 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 1918: 191 (sic.).

**Strotometra ornatissima**: A. H. Clark, 1915a: 163, figs. 101–102; 1918: 273, pl. 24, fig. 70.
**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′0″S, 178°53′42.6192″E, 1058–1091 m, 13 Aug 1998, sample STRO81 (MNHIE-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; axis 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 unidentifed, 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 Ib1, or visible only at interradial 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. Ib1 with slightly convex or shallowly A-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 Ʌ-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. Br1–2 also closely apposed laterally, with parallel proximal and distal margins; exterior lateral margins straight; interior lateral margins diverging; lateral eversion 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 spino, WL 1.0.

P(1) of proximal pinnules with ambabacular 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. P1(1), with small, rounded ambabacular flange as tall as width of P1(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; Pgen's, as in P1; following 3–4 pinnulars narrow; abrupt gonadal expansion variable, of 3–4 pinnulars (Pgen to (5.4) to (5.8)); gonad covered by large plates; gonad followed by up to 6 abruptly narrower, fragile pinnules. Distal pinnules of 12–16 pinnulars, 8–10 mm long; all pinnules elongated except for short Pdist, which bears distinct aboral keel.

A large specimen (MNHIE-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 interradial angles. Ib2 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). Ib1 with lateral margins converging and bearing smooth, short lateral flange, WL 2.0. Iax2 short, rhombic, much wider than Ib1, with portion of proximal margin extending beyond Ib1 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. Br5–7 or 8, short, wedge-shaped, with diverging lateral margins, WL 2.1–2.5. Distal margins of br2, 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, ambabacular, 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.
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...
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 (NHMN 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

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pinnules (sometimes excluding P1) bearing elongated, flat, abambular 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 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.
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 brr1–2 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 brr1–2. Both Ibr1 and Iax2 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. Br1–2 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. Br5–6 (sometimes also br7) weakly to strongly wedge-shaped, wider distally, with or without weak alternating synarthrial swellings; WL 1.8–2.3 (Fig. 12A). Br7–8 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 (i) ) 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 (P₉₁), 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 Pa₈₉–₁₀ 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., P₄₋₅₋₆₋₇₋₅₋₅₋₆₋₅₋₆₋₅ (Fig. 12D; Figs. 22K vs. 22L), with broadest pinnules 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 P₅₋₆₋₇₋₅₋₆ (rarely 6) pinnulars 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 cirri increasing in length; longest cirri varying from C₄–5 to C₆–8, with LW chiefly 1.7–2.2 (to 2.4 on apical cirri); following cirri 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 interradial 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 IBr₂, and sometimes absent on brr1–2. Lateral margins of brachiataxes 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 Ibr1 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. Ibr₁ oblong or shallowly V-shaped, with diverging lateral margins, WL 2.3–3.4; Iax₂ similar to Iax₁, 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
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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 or 10, or 11, or 15, or 14–15, on P2(9–10) 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(6–11) to P3(9–10), 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(i) short and wide, no flange; Pdistal(ii) 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


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; cirri 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 pinnules 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 ornatissimus* and *S. priamus* to *Poecilometra* herein, *Strotometra* 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.

**Chartiometra parvipinna**: A. H. Clark 1907a: 361.

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


**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.] Suenson, [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.

Cirr 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 interradial angles, or exposed as extremely short, gently curved bands (concave distally), with lateral margins sometimes swollen. IB2 gently to moderately convex aborally, laterally flattened and apposed, with midaboral rounded synathral swelling or weak narrow keel; lateral margins sometimes projecting as thin flange or short ridge. IB1 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 (spunge-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. Br1–2 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...
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; P1(3–4) to P1(6) with diverging lateral margins, expanded but not as much as on genital pinnules; following pinnules 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(3) short, with diverging lateral margins; Pgen(4–6) to Pgen(n) (rarely to Pgen(n)) expanded over plated gonad; expanded pinnules 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 pinnules 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 pinnules appear to have a pair of rounded distal knobs (Fig. 22O). Distalmost gonad variable, on P8 to P12, sometimes gradually 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 pinnules near tip with LW to 1.3. Distal pinnules to 17 proximal, 5.0 mm long; Pdist(1) short, Pdist(2) with LW ~1.0; following pinnules 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.
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...
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
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 borders, the portion of the pinnules beyond being abruptly narrower and shorter than the expanded portion. He then distinguished shorter genital pinnules as having $P_{(3-4)}$ “markedly longer and slightly 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), *Charitometra* (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 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 pinnules 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 ambulacral 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).
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