RECLASSIFICATION AND REDESCRIPTION OF THE COMATULID COMATONIA CRISTATA (HARTLAUB) (ECHINODERMATA: CRINOIDEA)

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Abstract.—Comatonia cristata (Hartlaub) is redescribed and illustrated on the basis of new and existing material. Well-developed pinnular combs, the only character relating this species to the Comasteridae, are modifications of rudimentary combs found in heliometrine antedonids. Comatonia agrees with all diagnostic characteristics of, and is here transferred to, the family Antedonidae, approaching most closely the heliometrine Anthometra adriani (Bell). Cirrus morphology may be convergent with sympatric Coccometra hagenii (Pourtales).

The comatulid genus Comatonia A. H. Clark contains a single species, C. cristata (Hartlaub), found primarily at moderate depths off the southeastern United States. A. H. Clark (1916, 1921, 1931) included it in the family Comasteridae (suborder Comasteracea) entirely on the basis of the well-developed combs on the first pair of oral pinnules. Such combs, the teeth of which are flat, usually triangular or spade-shaped expansions of the aboral surface of distal pinnule segments, are diagnostic of this family. In all other respects, however, Comatonia belongs in the family Antedonidae (suborder Antedonacea). Although Gislén (1924) proposed that the species be referred to this family, he was not followed by later authors (Clark, 1931; Messing, 1975; Rasmussen, 1978) with the exception of Meyer (1972). In the course of revising the extant crinoids of the tropical western Atlantic, I have discovered that the comb teeth of Comatonia appear to be modifications of comb rudiments found in some antedonid genera; they are convergent with rather than homologous to comasterid comb teeth. No reason remains for retaining this comatulid within the Comasteridae. Its placement within the Antedonidae is discussed below.

In addition, new material, collected primarily by the University of Miami's R/V Gerda, together with a re-examination of existing collections, has revealed several previously unrecorded variations. I have, therefore, redescribed and illustrated the species as follows. The tabular arrangement of data follows that of A. M. Clark (1970) and Messing (1978). USNM, UMML and MCZ refer to National Museum of Natural History, University of Miami Marine Laboratory (Rosenstiel School of Marine & Atmospheric Science) and Museum of Comparative Zoology (Harvard University) catalogs, respectively.
Genus *Comatonia* A. H. Clark (1916)

**Diagnosis.**—Radials 5; arms 10, aborally rounded; cirri slender and numerous, up to 20 mm with 23 cirrals and lacking aboral processes; comb on P₁ and Pₐ, rarely absent, rarely present on P₃, occupying all but proximal third of pinnule and composed of large, round teeth; one or more proximal pinnulars of P₁ sometimes longer than wide; Br₅–Br₈ (sometimes Br₃–Br₁₄) each with spinose, median, aboral knob or ridge; division series lacking spines. (Modified from A. H. Clark, 1931:289.) Type-species: *Actinometra cristata* (Carpenter MS.) Hartlaub, 1912, by original designation and monotypy (A. H. Clark, 1916:115).

*Comatonia cristata* (Hartlaub)

Figs. 1–3, 4b, c, h, i, 5a–g

*Antedon* sp. Carpenter, 1881:155.

*Actinometra cristata* (Carpenter MS.) Hartlaub, 1912:280, 413, 473–475; pl. 10, figs. 1–5; pl. 15, figs. 10–11.


**Description.**—Centrodorsal hemispherical or low, rounded conical, 1.3–4.4 mm across; DH 1.3–1.8 (Figs. 1a, d, e). Cirrus sockets crowded, arranged in spiral whorls overlain by irregular columns of 3–6 sockets and almost completely covering centrodorsal. Aboral pole small, not more than 0.4 × basal diameter of centrodorsal, flat or convex, almost smooth to strongly papillose, rarely depressed and ringed with papillae; when present, papillae arising, one each, from obsolete, apical sockets. Centrodorsal margin midradially concave; interradial projections rounded or triangular; central cavity broad and deep, with prominent oral lip and slightly more than half basal diameter of centrodorsal; interior, lateral walls of cavity bearing narrow, interradial buttresses; oral opening pentagonal or irregularly scalloped (Fig. 2j).

Cirri (Figs. 2a–g) slender, about L-C, 12–23, up to 20 mm long, laterally compressed distally. Apical cirri shorter, weaker and composed of fewer cirrals than peripheral cirri. First cirral short; second squarish; third with LW almost 2.0; third to sixth (usually fifth) longest, with LW 2.3–4.0; following cirrals decreasing in length but remaining longer than wide; antepenultimate squarish; all but basal few cirrals somewhat expanded distally: aboral spines or carinae absent; opposing spine directed obliquely distally; terminal claw curved and slightly shorter than penultimate cirral.

Rosette at or just below aboral surface of radial pentagon, bearing large, orally curved, flaring, radial processes and short, triangular, interradial pro-
Fig. 1. *Comatonia cristata*: a, Radial side view of a specimen (USNM E17863) showing centrodorsal, bases of five cirri and proximal part of three rays (partly shaded); b, Radial articular facet (USNM E19971) showing calcareous deposit bridging high, intermuscular walls; c, Another radial facet from same specimen; d, Interradial side view of centrodorsal (USNM E19971); e, Same (USNM E19188); f, Proximal part of single postradial series (IBr₁ to Br₃), aboral view (USNM E19971); g, Oral view of rosette (USNM E19188); h, Same, radial side view. Scale: a–f = 2 mm; g–h = 1 mm.
Fig. 2. *Comatonia cristata*: a, Peripheral cirrus (USNM E19971); b, Apical cirrus, same specimen; c, Peripheral cirrus (USNM E19177); d, Cirrus of small specimen (USNM E19971); e, Peripheral cirrus (USNM E17863); f, Apical cirrus, same specimen; g, Apical cirrus, same specimen as c; h, Proximal brachials (Br₃–Br₈), lateral view, showing bases of P₂, P₃, P₄ and spinose, aboral knobs on Br₅–Br₈ (USNM E19177); i, Radial side view of small specimen (USNM E19971) showing centrodorsal, bases of several cirri and proximal part of 3 rays; j, Centrodorsal, oral view, with lip cut away at left to show actual extent of central cavity (USNM E19188). Scale: a–g = 4 mm; h–j = 2 mm.
cesses (Figs. 1g, h). Basal rays absent; possible vestiges in one specimen fused to centrodorsal (Fig. 2j).

Radials visible only interradially or as extremely narrow band (Fig. 1a). Articular facet slightly longer along oral-aboral axis than wide, deeply excavated and not parallel to oral-aboral axis of specimen; muscular fossae about twice height of interarticular ligament fossae, thin and laminar, flat or overhanging orally, separated by low, narrow ridge. In a single specimen (USNM E19971, Figs. 1b, c), a pair of thin, irregular septa project distally (along the longitudinal axis of the ray) from the margins of the intermuscular ridge to the level of the central canal opening; these vary among the facets and, at one point on one facet, fuse together, creating the illusion of a double central canal (Fig. 1b).

Division series (Figs. 1a, f) separated. IB_r, very short, usually with median tubercle and concave distally. Primaxil (IB_{r3}) rhombic or triangular, round and swollen proximally, forming, with median tubercle of IB_{r1}, prominent synarthrial swelling; distal half flat, narrow and acute; WL 1.2–1.3.

Arms increasing slightly in width from base to Br_{5–6} before tapering; longest attached fragment 40 mm; estimated original length up to 70 mm. Br_{1} very short, longer exteriorly, united interiorly over primaxil, deeply incised distally by prominent, usually swollen, proximal synarthrial projection of large, irregularly quadrate Br_{2} (Figs. 1a, f). Br_{3–4} oblong, up to 2.1 mm across; WL 1.2–1.7. Br_{5} to Br_{8} oblong or slightly trapezoidal, rarely bearing prominent, alternating articular swellings; WL 1.7–2.5. Br_{9–10} oblong; following brachials trapezoidal, becoming triangular between Br_{12} and about Br_{15}; WL 1.3–2.0.

Spinose, median, aboral knob or longitudinal ridge present on Br_{5–8}, sometimes present but weak as far as Br_{14}, disappearing abruptly thereafter or incorporating into finely crenulate distal margin of brachials, usually absent from syzygial pairs but sometimes present on Br_{4} (Fig. 2h). In smallest individual (Fig. 2i), synarthrial swellings reduced, brachials elongated after Br_{15} and never triangular.

Syzygies at Br_{3+4}, Br_{9+10}, usually Br_{14+15} (sometimes Br_{15+16}); subsequent interval three or, rarely, four.

P_{1} (Figs. 3c, j) flagelliform, up to 14 mm with as many as 52 pinnulars; all

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Fig. 3. Comatonia cristata: a, P_{a} lacking comb (USNM E19971); b, P_{a}, same specimen and arm; c, P_{1} (USNM E19188); d, P_{2}, same specimen and arm; e, P_{a} with comb developed on both sides of pinnule: arrow denotes pinnular with comb tooth similar to that of Anthometra adriani (USNM E19971); f, P_{a} (USNM E19177); g, P_{a}, same specimen and arm; h, P_{a}, same; i, P_{a}, same; j, P_{1}, small specimen (USNM E19971); k, P_{a} with rudimentary comb (USNM E17863).

Scale: 2 mm.
but proximal 8–12 pinnulars each bearing a flat, round, somewhat distally-directed comb tooth at least as high as width of pinnular bearing it and sometimes 2–3× higher; proximal 3–6 pinnulars short and rhombic; subsequent pinnulars squarish to twice as long as wide but appearing short due to relative height of comb teeth; teeth rarely developed on both sides of pinnular (Fig. 3e). P₂ (Fig. 3d) basally stouter than P₁, up to 10 mm with 18 pinnulars but often only half length of P₁; proximal 2 pinnulars short; third squarish; following of about equal length (except near tip) but with LW increasing from about 1.3 to 4.0 as pinnule tapers; all except basal 2 with finely spinose, expanded, distal margins or with 1 or 2 stout, distal, aboral spines. P₂ occasionally bearing a comb similar to that of P₁ but with fewer, less well-developed teeth or with relatively few, low, distal teeth on pinnulars similar to those of combless P₂ (Fig. 3k). Following pinnules similar to combless P₂ but with second segment becoming abruptly tapered. P₃ slightly longer or shorter than P₂, of about 11 segments. P₄ up to 10 mm with 18 pinnulars. Genital pinnules (Fig. 3i) stouter than distal pinnules. Longest intact distal pinnules incomplete, at least 10 mm with at least 19 segments. P₁₃ 6.5 mm with 15 pinnulars on arm of specimen bearing P₄ of 5.5 mm with 11 segments. Interior pinnules similar to exterior ones (Figs. 3a, b, e–i). Single P₄ lacking comb and resembling subsequent pinnules though shorter and composed of fewer segments than succeeding P₅ (Figs. 3a, b).

Gonads borne on third through sixth to eighth pinnulars from P₄–P₅ (rarely, P₂ or P₃ and, perhaps in one specimen, P₁) to at least P₁₃. Pinnule ambulacra lined with fine, unbranched rods sometimes slightly expanded and perforated at one end.

Tegmen naked; mouth central or subcentral; anus submarginal; a few, small dark saccules present on pinnule ambulacra in two specimens (USNM E548, 34634).

Color.—In life, yellow. In alcohol, white or pale brown, sometimes with dark brown ambulacra, gonads, and tegmen.

Biology.—A. C. Neumann and J. C. Lang, during a DSRV Alvin dive, collected a single individual in 580 m clinging to a fragment of the branching, ahermatypic coral Lophelia prolifera (Pallas) and in association with large numbers of the small comasterid Comatilia iridometriformis A. H. Clark which is usually found on this coral (Messing, unpublished). Most specimens have been collected with the Pourtales Terrace south of the Florida Keys apparently on hard, sediment-free substrates and usually in association with large numbers of the antedonid Coccometra hagenii (Pourtales).

Material examined.—NORTH CAROLINA: Fish Hawk sta. 7302 (USNM 34634, 1 specimen). POURTALES TERRACE (SOUTH OF THE FLORIDA KEYS): Gerda sta. 220 (UMML 44-169, 1), Gerda sta. 589 (USNM E19178, 1), Gerda sta. 840 (USNM E19180, 1), Gerda sta. 865
(USNM E19177, 1), Gerda sta. 977 [USNM E17863, 1; UMML 44-174, 2 (1 sent to D. B. Macurda, Jr.)], Gerda sta. 978 (USNM E19188, 1 dissociated), Gerda sta. 1102 (USNM E19971, 4, 1 dissociated), Fish Hawk sta. 7298 (USNM 34628, 1), Univ. Iowa Bahama Exped. 1893, sta. 48 (USNM E4290, 1 dissociated, not Univ. Iowa Barbados-Antigua Exped. as labelled; MCZ 747, 1), Eolis, J. B. Henderson coll. (USNM E548, 1), No expedition data (MCZ 800, 2; removed from MCZ 755). BAHAMAS: Alvin dive 761 (USNM E19181, 1). YUCATAN CHANNEL: Gerda sta. 885 (USNM E19179, 1).

Type.—Carpenter (1881) mentioned a new species of Antedon undoubtedly referable to Comatonia cristata as occurring with Antedon hagenii (= Coccometra hagenii) in the Straits of Florida. Hartlaub (1912) described in detail a single specimen accompanied by the label "Com. 101, Stn. —'' and suggested that it possibly came from the Challenger rather than from the Blake collection. At the end of his description (p. 475), he gave the locality as unknown.

A. H. Clark re-examined the specimen and reinterpreted the label as reading "Corw. Po. 1, Stn. —'' which he identified as Corwin station 1P (5 mi. SSW of Sand Key, Florida, 164–183 m, 17 May 1867) (1931:292). He also wrote that Hartlaub had "a single specimen of this species without a locality label," a lapse resulting from Hartlaub’s listing of the locality as unknown the CORWIN specimen, according to Clark, is in the MCZ (cat. no. 7), but I have not seen it.

Distribution.—Cape Lookout, North Carolina; Straits of Florida; Yucatán Channel. All but 3 specimens were collected on the Pourtalès Terrace south of the Florida Keys. Possible depth range: 14–580 m. Confirmed depth range: 14–580 m. For material collected on the Pourtalès Terrace, the ranges are 146–411 and 152–306 m, respectively. The Cape Lookout specimen was taken in 14 m and the specimen from Arrowsmith Bank, Yucatán Channel in 419–434 m. (Emended from Meyer et al., 1978:417.)

The specimen collected by Alvin in 580 m represents the only record from the insular margin of the Straits. Its greater depth relative to continental margin records parallels records for its frequent associate, Coccometra hagenii. The latter occurs primarily between 150 and 250 m on the Pourtalès Terrace (locality data for the 2 records in excess of 300 m here fall in less than 250 m on recent bathymetric charts) and as deep as 442 m off Cuba. Two records from the Blake Plateau are still deeper (805 and 1046 m) and one of these includes Lophelia.

Discussion.—A. H. Clark (1921, 1931) considered Comatonia, Comatilia and Comatulides as "primitive generalized" (1921:619) members of the family Comasteridae. He included Comatonia in the subfamily Capillasterinace because of its supposed resemblance to the small, 10-armed, monotypic genera Comatilia and Microcomatula and despite the absence of diagnostic,
aboral, cirral processes. *Comatonia* and *Comatilia* both occasionally bear saccules along their ambulacra but the resemblance ends here. *Comatilia* appears to be paedomorphic; its "generalized" appearance (e.g., 10 arms, central mouth) along with other characteristics (e.g., large radials, deficient pinnulation, elongated cirrals and brachials) are the result, I believe, of accelerated sexual maturation and persistent juvenile morphology (progenesis sensu Gould, 1977) (Messing, unpublished). *Microcomatula mortenseni* A. H. Clark is known from a single, incompletely described specimen. Although discussion of its affinities must await re-examination of the type, the published description (A. H. Clark, 1931) also agrees with specimens of the comb-bearing antedonid *Ctenantedon kinziei* Meyer in some respects.

*Comatonia* agrees with the suborder Antedonacea and family Antedoniidae in all diagnostic characters (Clark and Clark, 1967; Rasmussen, 1978). It also exhibits non-diagnostic traits, including its cirrus arrangement and morphology and prominent synarthrial swellings (Gislen, 1924:229, footnote), found in many antedonids but unknown in the Comasteridae. Its typically antedonid centrodorsal, almost covered with cirrus sockets, occurs in the Comasteridae only in *Microcomatula* which, as mentioned above, also may not belong in this family. Meyer (1972) noted that its radial articular facets and large centrodorsal cavity are characteristically macrophreatine (antedonacean) and agreed with Gislen that its affinities lay with this suborder rather than with the comasterids.

Following Gislen (1924:229, footnote), I believe *Comatonia* most closely approaches the antedonid subfamily Heliometrinae. Although the antedonid subfamilies are not uniformly well-defined, I here follow Clark and Clark's (1967) treatment. Some heliometrine species bear rudimentary or moderately developed combs on their oral pinnules, although these are never nearly as developed as in *Comatonia* and are weaker than in most comasterids. In the latter, comb tooth rudiments usually develop from the middle of the aboral side of the pinnular. In *Comatonia* and the heliometrines *Anthometra* and *Florometra*, the comb teeth develop as modifications of the spinose, distal, aboral margin of pinnulars proximal to the comb. As the teeth increase in size on more distal pinnulars, they expand proximally, occupying more and more of the aboral surface of the pinnular. In *Comatonia*, this derivation is most obvious in small specimens and on comb-bearing P₂ (Figs. 3f, j, k). It is obscured in larger specimens in which pinnulars proximal to the comb lack spinose, distal margins. Figures 4 and 5 show the close resemblance of rudimentary comb teeth and pinnular articular facets in *Comatonia* and the heliometrine *Anthometra adriani* (Bell) as well as the strong distinction between these characters in these two species and corresponding structures in the comasterid *Neocomatella alata* (Pourtales). The arrow in Fig. 3e indicates an apparently regenerating, comb tooth-bearing pinnular in *Comatonia* that is similar to fully developed teeth in *Anthometra adriani*.
Table 1.—Numerical data for 9 specimens of *Comatula cristata* (Hartlaub) collected by R.V. *Gorda*. Arms too broken to estimate total length. "DH = ratio of basal diameter to height of centrodorsal. "Longest cirral L.W. = ratio of greatest length to proximal width. "Arm L.W. = ratio of arm width at B3=4 to length from distal edge of radial to B3=4 measured midradially.

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In the heliometrine genus *Florometra*, comb teeth normally do not develop beyond the rudimentary, distal, spinose stage.*

* A. M. Clark (personal communication) has brought to my attention the fact that another antedonid, *Annametra occidentalis* (A. H. Clark) (subfamily Antedoninae), may also bear
Fig. 5. a–g, Comatonia cristata: a, Distal pinnular with well developed comb tooth, abambulacral view; b–c, Same, ambulacral view, stereo pair; d, Middle pinnular with moderately developed comb tooth, ambulacral view; e–f, Middle pinnular (more proximal than d, with less well developed comb tooth), ambulacral view, stereo pair; g, Same, abambulacral view; h, Anthometra adriani (Bell), distal pinnular with well developed comb tooth, ambulacral view; i, Neocomatella alata (Pourtales), same, obliquely ambulacral view. Scales: 0.1 mm.

It appears from Figure 6 in Clark and Clark (1967:95) that these teeth are also derived from the distal aboral pinnular margin as discussed above. I have not yet examined specimens of this species.
Within the Heliometrinae as currently construed, Comatonia appears most similar to Anthometra adriani. Both bear a median, aboral knob or ridge on the proximal brachials, although these are more prominent and occur on more brachials in Anthometra. Both have only the first pair of pinnules modified (rarely, \( P_2 \) in Comatonia). The radial articular facets of the two species, and of another heliometrine, Solanometra antarctica (Carpenter), are also closely similar. The paired, irregular “septa” projecting distally (along the longitudinal axis of the ray) from the sides of the intermuscular ridge in one specimen of Comatonia vary among the facets, appear to represent a secondary deposition of stereom and do not alter the basic architecture of the facet.

The relatively short, slender cirri of Comatonia differ from those of other heliometrine species although they do resemble those of juvenile Anthometra (centrodorsal diameter 1.5 mm). They are also similar, however, to cirri of the thysanometrine antedonid Coccometra hagenii. Comatonia and Coccometra hagenii have almost identical, restricted ranges: from the Mexican side of the Yucatán Channel to Cape Lookout, North Carolina. They occur sympatrically and in the greatest abundance on the Pourtales Terrace (Clark and Clark, 1967; Messing, 1975; Meyer et al., 1978). The terrace is largely sediment-free, is subject to strong currents, exhibits some karst-like topography (Jordan, 1954; Jordan et al., 1964; Gorsline and Milligan, 1963) and apparently represents a distinctive, if not unique, environment in the tropical western Atlantic Ocean. That Comatonia and Coccometra hagenii are virtually the only crinoids ever collected here despite intensive dredging suggests that their cirrus morphology may be adaptively convergent.*

Comatonia conforms least to the Heliometrinae in terms of distribution. It occurs tropically and subtropically at moderate depths, whereas the remaining genera are found in polar, subpolar and cold, eastern Pacific waters. It is morphologically distinct enough, however, to suggest that it diverged from heliometrine stock before they became exclusively cold-water forms. The Bathymetrinae, allied to the Heliometrinae through Anthometra according to A. H. Clark (Clark and Clark, 1967), is a primarily deep and cold-water subfamily that includes species that enter warmer water, e.g., Trichometra cubensis (Pourtales). Despite the relatively low latitudes at which it occurs, steep isothermal tilting across the Straits of Florida and Yucatán Channel indicates that Comatonia most likely occurs in water of less than 10°C.

Acknowledgments

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* Despite these similarities, they do not appear to be closely related. In C. hagenii, the low hemispheric centrodorsal has a broad, smooth aboral pole; the cirri, though similar to those of Comatonia, are more delicate and are lost far more often; the arms, usually broken near the base in Comatonia, are far more often preserved in C. hagenii. Although PI in both species is composed of many short pinnulars which may also be adaptively convergent, in C. hagenii, as in other thysanometrine species, the corners of the pinnulars are cut away giving the pinnule a distinctively beaded appearance.
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