1-1-1978

A Revision of the Comatulid Genus Comactinia A. H. Clark (Crinoidea: Echinodermata)

Charles G. Messing
University of Miami, messingc@nova.edu

BULLETIN OF MARINE SCIENCE, 28(1): 49–80, 1978

BIOLOGICAL RESULTS OF THE UNIVERSITY OF MIAMI DEEP-SEA EXPEDITIONS. 128

A REVISION OF THE COMATULID GENUS *COMACTINIA* A. H. CLARK (CRINOIDEA: ECHINODERMATA)

Charles Garrett Messing

ABSTRACT

The formerly monotypic genus *Comactinia* is found to comprise two valid species. One of these is further divided into two subspecies. The variability of the genus is examined and illustrated. A discussion of ecology, affinities, and zoogeography is included.

Comactinia is a genus of Comasteridae widespread in the tropical and northern subtropical western Atlantic at shallow to moderate depths. When A. H. Clark erected the genus (1909a), he designated *Alecto echinoptera* Müller (1841) as the type-species. Shortly thereafter, he referred to *Comactinia echinoptera* and *C. meridionalis* without specific diagnoses (1909b: 149, 150). *Comactinia meridionalis* was first mentioned as *Comatula* sp. by A. Agassiz (1864), and was briefly discussed and figured by E. C. and A. Agassiz (1865) under the names *Comatula* sp. and *Alecto meridionalis* (an ms name given it by L. Agassiz), but was first described by Pourtalès (1869) as *Antedon meridionalis*.

Carpenter (1879, 1881, 1888) successively transferred Müller's and Agassiz' species to the genera *Comatula* and *Actinometra* (the latter corresponding to the *Comasteridae* of current usage) but never diagnosed them satisfactorily. He maintained them as distinct species though he suggested that they might prove identical. Hartlaub (1912), following Carpenter's scheme of classification, considered *echinoptera* and *meridionalis* as distinct varieties of *Actinometra echinoptera*, in which he included what are currently recognized as two subfamilies and several genera of western Atlantic comatulids. His *A. e.* var. *echinoptera* included only Müller's type-specimen.

A. H. Clark continued to consider *C. echinoptera* and *C. meridionalis* as distinct species in several publications following those mentioned above, including parts one and two of his monograph (1915, 1921a, b), but he never diagnosed them. In 1931, however, he synonymized both under *C. echinoptera* and commented: "In the bewildering diversity of arm structure, the single species of this genus exceeds all other crinoids" (p. 375).

During a systematic and distributional study of the comatulids collected by the University of Miami's R/V GERDA in the Straits of Florida and adjacent waters (Messing, 1975), I examined over 100 specimens of *Comactinia* and consider that two valid species exist. One of these corresponds to Müller's *Alecto echinoptera* and the other approaches Agassiz' *Alecto meridionalis*. The GERDA material differs in certain respects from the type series of *meridionalis* but not enough to warrant separate status, though future studies may alter this. Several lots of GERDA material are referrable to *Actinometra echinoptera* var. *valida* Hartlaub. A. H. Clark (1931) treated this as an infrasubspecific variety of *C. echinoptera*. Morphological and distributional evidence has led me, however, to consider it a subspecies of *C. meridionalis*. The name *valida* is preoccupied in the genus *Actinometra* and the taxon is here renamed. Additional specimens included in this study were collected by the R/V EASTWARD of Duke University, by scientists from Texas A&M University, and by several researchers using SCUBA.

I have also had the opportunity to examine the extensive collections of *Comactinia* at the National Museum of Natural History and Harvard's Museum of Comparative Zoology. Except for the type series, I have not included the specimens in these collections in the detailed descriptions in this paper. I merely ascertained to which taxon they belonged and noted any peculiar variations. Again, except for the type series, detailed collection data accompany only new records or records for which these data were heretofore unpublished or generally unavailable. Collection data for all other specimens examined by me may be found in A. H. Clark (1931).

My synonymies include only the major references to the taxa and important nomenclatural changes. Since some authors did not adequately define their concepts of the two species, it has in certain cases been impossible to determine whether or not an author's usage of the name *meridionalis* actually included specimens of *echinoptera*, or vice versa. Such entries are indicated in the synonymies by "(part?)." A complete synonymy is found in A. H. Clark (1931), the most thorough treatment of the genus to date.

Several innovations in terminology are introduced in this paper. DH indicates the ratio of the basal diameter (D) to the height (H) of the centrodorsal. Cirrus LW is the ratio of the median length (L) to the proximal width (W, measured dorsoventrally) of a cirrus segment. WL is the ratio of the greatest width (W) to the median length (L) of a radial (visible portion), division series ossicle or brachial. LW and WL are employed to indicate the proportions of ossicles and their variability. By using both ratios as indicated, rather than one exclusively, the resultant figures are almost always greater than 1.0 and easier to interpret. I have included the WL ratio for a large number of division series and arm ossicles chiefly as an indication of variability. Though not of primary systematic value, this ratio may be of use in future comparisons of so-called "corresponding" Caribbean and Indo-West Pacific genera and species.

LD is the length from the centrodorsal margin to Br_{3+4} (L) measured midradially, divided by the centrodorsal diameter (D). Since the placement of the second syzygy varies in *Comactinia*, this ratio is of greater use than the 1:br of A. M. Clark (1970) as a supplementary diagnostic character. A. H. Clark (1915), A. M. Clark (1970) and Messing (1975) gave thorough accounts of comatulid terminology.

All meristics and morphometrics are included within the text of the species descriptions. The tables illustrate variations with growth for a number of important systematic characters. The tabular arrangement of data generally follows that of A. M. Clark (1970, 1972). Under "Arm Length" on the tables, the figures represent the longest arm retained. Detached arm fragments are included in the figures only when the owner can be reliably inferred (e.g., one specimen in a lot).

In the text, the following abbreviations are used: G (R/V GERDA stations), J-SE (Johnson-Smithsonian Expedition, stations made from the yacht CAROLINE), MCZ (Museum of Comparative Zoology at Harvard, catalogue numbers), UIB-AE (University of Iowa Barbados-Antigua Expedition, 1918), UIBE (University of Iowa Bahamas Expedition, 1918), USNM (United States National Museum, now the National Museum of Natural History, Washington, D.C., catalogue numbers).

In the distributional sections, the possible depth range extends from the shallowest point of the shallowest station to the deepest point of the deepest station, and the confirmed range extends from the deepest point of the shallowest station to the shallowest point of the deepest station. While the specimen *may* have been collected within the former range, it *must* have been collected within the latter.

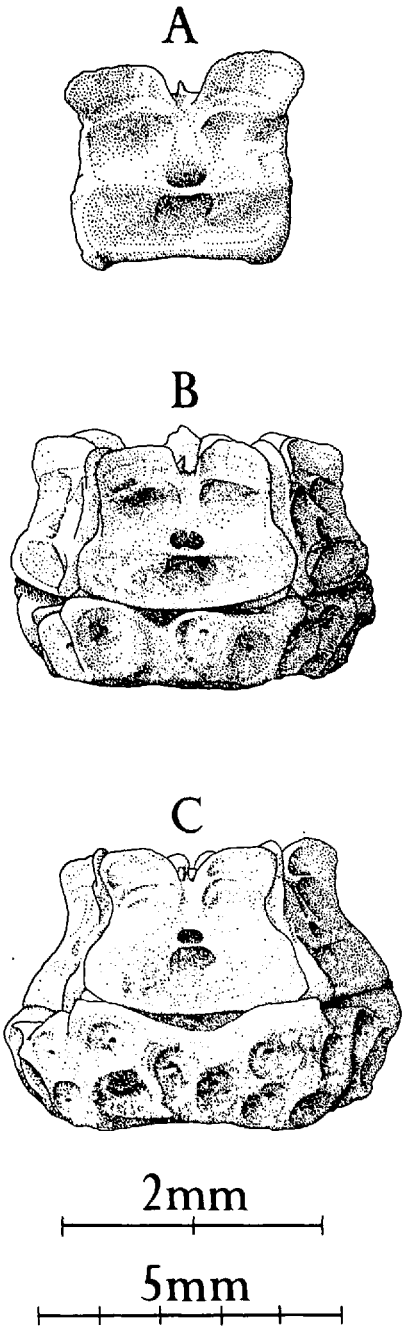


Figure 1. A. *Comactinia echinoptera* (Müller); radial face, G-956. B. *Comactinia meridionalis meridionalis* (L. Agassiz); centrodorsal and radial pentagon in lateral view, G-392. C. *Comactinia meridionalis hartlaubi* nomen novum; centrodorsal and radial pentagon in lateral view, G-698. Scales: A, B—2 mm; C—5 mm.

Genus *Comactinia* A. H. Clark

Comactinia A. H. Clark, 1909a: 498; 1915: 117, 238, 240, 266, 268, 296, 298, 335, 336, 339; 1921a: 176, 211, 312, 557, 587, 606, 618, 744; 1931: 37, 39, 82, 293, 294, 295, 339, 374–375.—Tommasi, 1965: 6.

Diagnosis.—Centrodorsal discoidal, large and thick to small and thin; radials exposed or hidden; arms ten; anterior arms longer; division series and arm bases separated or closely apposed; IBr_1 and Br_1 united laterally (Br_1 only interiorly), only proximally in small specimens; division series ossicles and first brachial pair both united by synarthry; cirri usually XV–XXV, 9–12 (extremes: X–XXXIX, 8–17), strong, as broad distally as basally or broader distally; LW of longest cirral 1.3 to 2.2; opposing spine present; dorsal processes on preceding cirrals generally absent though a weak spine or tubercle sometimes developed on one or two cirrals preceding penultimate; proximal pinnulars of oral pinnules squarish, triangular or rhombic (the last giving the pinnule a strongly serrate profile), rarely smooth, each usually provided with a distal rim of spines or bearing a high, rounded carina; comb present on P_1, almost always present on P_2, sometimes on P_3 and P_4. (Amended from A. H. Clark, 1931: 375.)

Geographic distribution.—Western Atlantic from Cape Lookout, North Carolina, south to Isla de los Alcatraces off São Paulo, Brazil, and throughout the Caribbean Sea and Gulf of Mexico wherever suitable habitats occur.

Bathymetric distribution.—Possible: shore line to 549 m. Confirmed: 3 to 508 m. Infrequently taken below 300 m.

Type-species.—*Alecto echinoptera* J. Müller, 1841, by original designation: A. H. Clark, 1909a: 498.

Affinities.—The genus *Comactinia* is similar to the Indo-Pacific genus *Comatula* (A. H. Clark, 1911a, b; 1912a, b; 1914a, b; 1931). Current diagnostic characters are not entirely satisfactory and future compara-

tive studies may reveal the two to be congeneric. Both genera exhibit typical comasterid evolutionary trends (e.g., loss of posterior arm ambulacra; diminishing size of centrodorsal; reduction in number and eventual loss of cirri; concentration of gonads on posterior arms) but these are carried much further in *Comatula*. *Comactinia* always possesses cirri and I have not seen any specimen lacking posterior arm ambulacra though David Meyer (pers. comm.) has observed the latter character in specimens from the southern Caribbean.

KEY TO THE SPECIES OF *Comactinia*

1a. Cirri narrow and cylindrical proximally, broader and laterally compressed distally; comb generally present on P_1 to P_4; middle comb teeth trapezoidal or quadrate, often terminally notched; high, round carinae usually present on some proximal pinnulars of oral pinnules; distal dorsal edge of brachials totally lacking spines; color reddish, purple or pale pink ..... *Comactinia echinoptera* (Müller)

1b. Cirri little, if at all, broader distally than proximally; comb present on P_1 and P_2, sometimes on P_3 and P_4; teeth round or triangular, weak or strong; carinae absent; proximal pinnulars of proximal pinnules with weak rim of spines which may be produced laterally as a spinose flange; proximal pinnulars sometimes rhombic giving pinnule a strongly serrate profile; distal dorsal edge of brachials spinose; color white, yellow, tan or brown (sometimes stained purple by sponges) ..... *Comactinia meridionalis* (L. Agassiz)

Comactinia echinoptera (Müller)
Figures 1A, 2, 3, 4; Table 1.

Comatula echinoptera Müller, 1840: 93.—Carpenter, 1879: 27, 28.

Alecto echinoptera: Müller, 1841: 143.—A. H. Clark, 1909a: 498.

Antedon meridionalis: Pourtalès, 1869: 355 (part).—Carpenter, 1881: 156 (part).

Actinometra echinoptera: Carpenter, 1881: 156.—Hartlaub, 1912: 280, 281, 413, 415–471; pls. 16, 17, 18 (part).

Actinometra braziliensis Carpenter, 1888: 302; pl. 4, fig. 4a-c.

Comactinia echinoptera: A. H. Clark, 1909b: 149, 150 (part?); 1915: 29, 31, 32, 46, 129, 249, 281, 291, 298, 325, 355 (part); 1921a: 14, 15, 16, 71, 219, 255, 323, 341, 662, 664, 665, 666, 672, 681 (part?); 1931: 128, 133, 231, 277, 280, 301, 351, 359, 375–400, 692; pls. 42–44 (part).—Tommasi, 1963: 98–100 (part?); 1965: 6, 7, 8, 14; figs. 12–18 (part).—Meyer, 1973a: 253–255.—Macurda, 1975: 6, 8, 12, 14, 16, 17.

Comactinia meridionalis: A. H. Clark, 1909b: 150 (part?); 1915: 34, 46, 315, 317, 321, 326 (part?); 1921a: 16, 220, 222, 225, 233, 280, 291, 312, 341, 370, 374, 509–510, 513, 514–517, 518, 520, 549, 555, 577–586, 588–590, 596, 662, 663, 665, 666, 668, 672, 681, 706, 725; pl. 1, figs. 963–964 (part); 1921b: 9–11, 25–28 (part); 1931: 50, 136, 277, 283, 378 (part).

Actinometra echinoptera variety *echinoptera*: Hartlaub, 1912: 416, 418, 424–426.

Actinometra echinoptera variety *meridionalis*: Hartlaub, 1912: 416, 417, 418, 426–430; pl. 16, figs. 1–5, 10–12 (part).

Comactinia echinoptera variety *meridionalis*: Tommasi, 1963: 99 (part?).

Comactinia echinoptera variety *valida*: Meyer, 1973b: 118–120.—Macurda, 1973: 17, 18, 20, 21. [not *Comactinia echinoptera* variety *valida* (Hartlaub)].

Material examined.—HOLOTYPE: Berlin Museum cat. no. 1047, locality unknown. SOUTH CAROLINA: A. S. Merrill, coll., Racoon Key, S.C., 46 m, 3 July 1963, Porter Kier, donor; 1 specimen, USNM E-9805. SOUTHEASTERN FLORIDA: G-412, 27°36'N, 79°59'W, 37 m, 3 m try net, 22 September 1964; 1.—G-423, 26°07.5' N, 80°05'W, 46–55 m, 3 m try net, 22 September 1964; 2.—G-582, 24°31'N, 81°23'W, 92 m, triangular dredge, 14 April 1965; 1.—G-600, 25°02.5' N, 80°18.8'W, 71–73 m, triangular dredge, 15 April 1965; 3.—W. Goldberg, coll., 1 to 1¼ miles off Boca Raton Inlet, 45 m, SCUBA, 5 December 1969; 2.—BIBB coll.; 2, MCZ 433.—4½ miles SE of Carysfort Light, 168–183 m; 5, MCZ 1107.—1, MCZ 80. BAHAMAS: M. P. Wennekens, coll., Tongue of the Ocean east of Green Cay, 270 m (?), dredge, 29 July 1958; 1.—D. B. Macurda, Jr., coll., 340° NW of Golding Cay, Andros I., 24° 15.5'N, 77°37.25'W, 12–15 m, SCUBA, September 1973; 3. TURKS AND CAICOS ISLANDS: D. B. Macurda, Jr., coll., 21°50.05'N, 72°20.05'W, 15–27 m, SCUBA, September 1973; 1. NORTHERN CUBA: UIBE, dredging sta. 9, off Havana; 1, USNM E-5289.—UIBE, dredging sta. 13; 1, MCZ 743.—ALBATROSS coll.; detached arm, USNM 34542; 1, USNM 34618; 2, USNM 34832; 1, USNM 34917. SOUTHEASTERN GULF OF MEXICO(?): BACHE sta. 35S; arm fragment, MCZ 432—see A. H. Clark, 1931: 394. YUCATAN CHANNEL: G-956, 20°50'N, 86°30'W, 46–183 m, 3 m try net, 29 January 1968; 5. ANTILLEAN ARC: J-SE, CAROLINE sta. 45, 18°13'10"N, 67° 25'30" W, 37–73 m, tangle, 13 February 1933; 1, USNM E-5248.—UIB-AE, dredging sta. 96, Shoal Bank about 3 miles W of Needham Point, Barbados, 37–73 m, sponge bottom, June(?) 1918; 3, USNM E-4251; 1, USNM E-4252. TRINIDAD: E. Deichmann, legacy, Maguerepe, outside bay, July 1937; 8, MCZ 1103.—Between Maguerepe and Cerozal Point; 15, MCZ 968. CAPE FRIO, BRAZIL: HASSLER coll.; 24, USNM 34623; 14, USNM 35630; 6, MCZ 31; 26, MCZ 199; 42, MCZ 443.

Diagnosis.—Centrodorsal small and thin; radials well exposed; radial articular faces broadest across muscular fossae; cirri narrow and cylindrical proximally, broader and laterally compressed distally; LW of longest cirral usually 1.7 to 2.0; combs generally present on P_1 to P_4, strong; comb teeth contiguous or only slightly separated; middle comb teeth trapezoidal or quadrate, often terminally notched; proximal and distal teeth narrower; high rounded carinae, similar to those of *Leptonemaster venustus*, present on some proximal pinnulars of oral pinnules; number of pinnulars and pinnules possessing carinae variable; carinae rarely absent; distal dorsal margin of proximal and middle brachials slightly raised but totally lacking spines; disk inflated and scattered with small, elongate nodules giving disk a papillose appearance; arms reddish when alive; ossicles retain purplish color when preserved and even when dissociated.

Description.—Centrodorsal small, flat, thin and discoidal or pentagonal, 1.3 to 2.9 mm across; DH 3.0 to 6.0. Cirrus sockets arranged in single, rarely partly double, irregular, marginal row. Polar area usually flat and smooth, sometimes with small, weak central convexity or weak, radiating interradial ridges developed only near polar area margin.

Cirri XV–XXII, usually 10–12 (extremes: 9–13), 5 to 10 mm long, slender and cylindrical proximally, broader and laterally compressed distally; fourth and/or fifth (rarely, third and fourth) cirral longest; LW usually 1.7 to 2.0 (extremes: 1.5 to 2.2); subsequent cirrals decreasing in length; distal cirrals squarish; penultimate cirral squarish or longer than broad; opposing spine short, conical, erect and subterminal; weak spine or tubercle absent from all preceding cirrals; terminal claw curved, as long as or longer than penultimate cirral.

Basal rays hidden. Radials always visible; radial articular faces broadest across muscular fossae; interarticular and dorsal ligament fossae equally broad.

Division series usually dorsally rounded, infrequently flattened, rarely closely apposed; arm bases and division series often with weak synarthrial swellings. IBr_1 short, united at least proximally, oblong, usually broader distally than proximally and often slightly inflated laterally; WL 3.0 to 4.0. IBr_2 triangular, laterally free; WL 1.9 to 2.7.

Arms 30 to 165 mm long, slightly broader in middle than at base; greatest width reached proximally by about Br_{15}. In complete specimens, posterior arms usually less than half length of anterior arms. Alternating articular tubercles strongly or weakly developed on proximal brachials or entirely lacking. Distal dorsal rim of all brachials lacking spines, and concave, thickened and slightly raised from between Br_6 and Br_8 to between Br_{25} and Br_{40} but not overlapping; this character subsequently weakening, absent from distal brachials. Br_1 oblong, united interiorly, sometimes slightly longer exteriorly; WL 2.1 to 3.3. Br_2 oblong to almost triangular (longer exteriorly), laterally free; WL 2.2 to 4.0. Br_{3+4} oblong, sometimes slightly longer interiorly, 0.8 to 2.3 mm across; WL 1.2 to 3.5. Br_5 oblong or wedge-shaped; WL 1.6 to 3.5. Next few brachials increasingly wedge-shaped, becoming triangular between Br_7 and Br_9. Subsequent brachials in proximal half of posterior arms and proximal third of anterior arms short, triangular and of uniform width, appearing wider than arm bases often only because of their thickened distal edges; distal brachials wedge-shaped, becoming elongate near arm tip; in small specimens, brachials becoming wedge-shaped between Br_{20} and Br_{35}. LD 1.5 to 2.0.

Syzygies at Br_{3+4}, Br_{11+12} (rarely, Br_{10+11} or Br_{12+13}; in one specimen, ray C bearing one arm with Br_{13+14} and the other arm with Br_{14+15}); subsequent intersyzygial interval usually four (extremes: two to seven).

P_1 6 to 12.5 mm long with 24 to 40 pinnulars; proximal pinnulars short; middle pinnulars squarish; distal pinnulars longer than broad but appearing short due to presence of high comb teeth. Dorsal side of second to

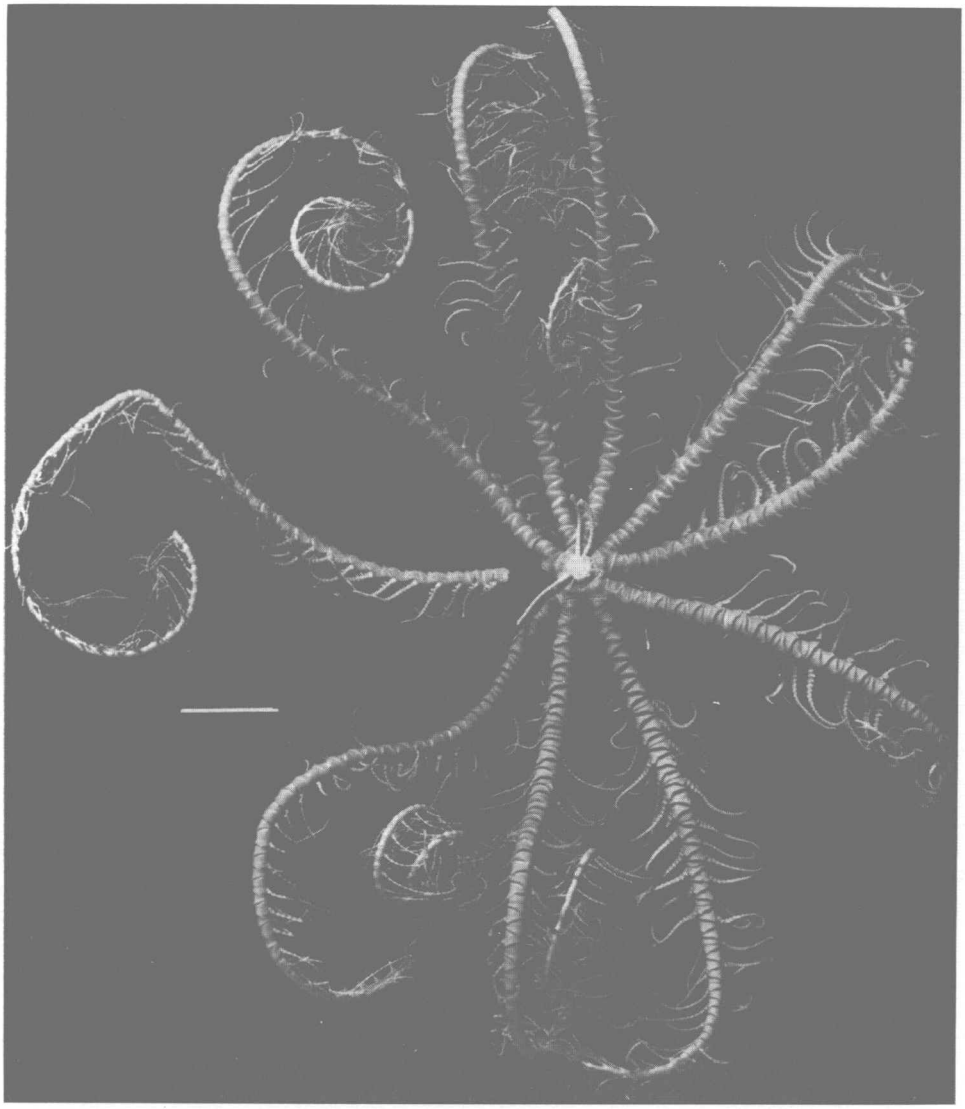


Figure 2. *Comactinia echinoptera* (Müller). Specimen collected by D. B. Macurda, Jr., Turks and Caicos Islands. Scale: 1 cm.

third, fourth or fifth (rarely, sixth or seventh) pinnulars produced as high rounded carinae which are often similar to but more variable than those of *Leptonemaster venustus*, rarely reduced in size or altogether absent. Comb of four to nine teeth short and strong; first and last teeth narrow (and sometimes shorter); intervening teeth broad, trapezoidal (sometimes terminally rounded) or quadrate and often terminally notched.

P_2 one-third to little more than one-half length of P_1, 2 to 8.5 mm long with nine to 28 pinnulars and comb of three to eight teeth; carinae sometimes present on second and third (sometimes to fourth or fifth) pinnulars. P_3 2 to 6 mm long, of nine to 18

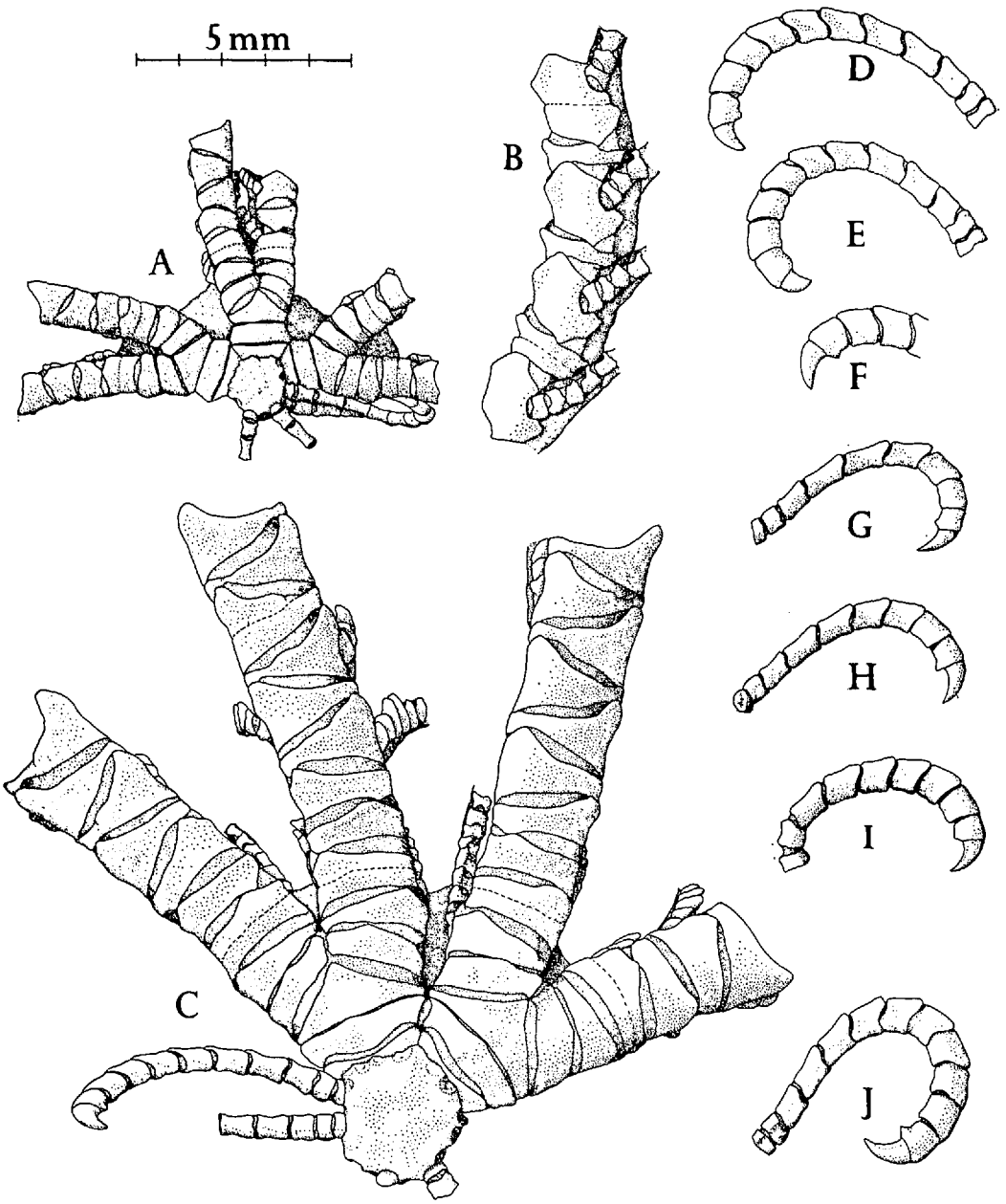


Figure 3. *Comactinia echinoptera* (Müller). A. Centrodorsal, cirrus and proximal part of three rays in dorsal view, G-600. B. Nine middle brachials in lateral view, Green Cay, Bahamas. C. Centrodorsal, cirrus and proximal part of two rays in dorsal view, Turks and Caicos Islands. D–F. Cirri of holotype. G. Cirrus, G-956. H. Cirrus, another specimen from G-956. I. Cirrus, Andros Island. J. Cirrus, Turks and Caicos Islands.

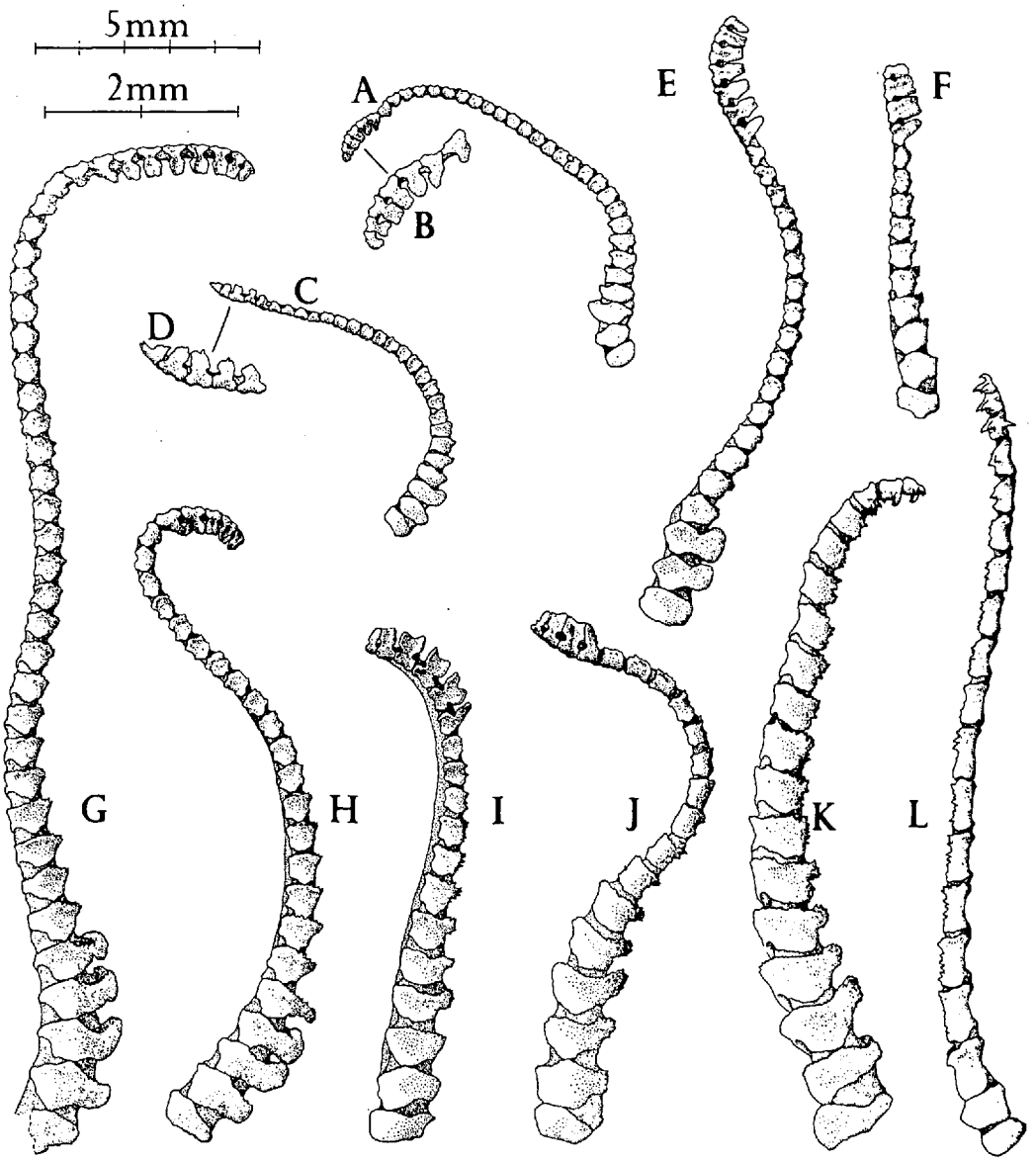


Figure 4. *Comactinia echinoptera* (Müller) pinnules. A. P_a of holotype. B. Comb of same, enlarged. C. P_2 of holotype. D. Comb of same, enlarged. E. P_a, Boca Raton, Florida. F. P_b same specimen and arm. G. P_1, Turks and Caicos Islands. H. P_2, same specimen and arm. I. P_3, same. J. P_4, same. K. P_5, same. L. P_{distal}, same. Scales: A, C, E–L—5 mm. B, D—2 mm.

pinnulars, usually the shortest pinnule although sometimes as long as P_2, only rarely carinate; comb higher than on P_1 or P_2, of two to eight teeth; middle teeth broader and more deeply notched. P_4 the last comb-bearing pinnule, up to 7 mm long with 20 pinnulars and five comb teeth; comb similar to that on P_3. Subsequent pinnules increasing to distal maximum of 11 mm with over 20 pinnulars; middle pinnules stout with

squarish middle and distal pinnulars and rarely bearing reduced carinae on some proximal pinnulars; distal pinnules slender, with elongate pinnulars (excepting short basal two). Gonads first appearing on P_2, P_3 or P_4 and continuing to between P_{11} and P_{20}. More pinnules bearing gonads on posterior arms than on anterior arms.

Disk inflated, with small, conical, elongate or irregular nodules quite evenly spaced, projecting from tissue and appearing as papillae to the unaided eye; nodules rarely absent or restricted to anal cone or disk ambulacra. Mouth marginal, interradial; anal cone central.

Color.—In living specimens, centrodorsal and cirri white; radials, division series and arms reddish flecked with yellow; pinnules yellow. In preserved material, radials, division series and arms ranging from deep pink to very pale lavender; pinnules, ambulacra and disk tan or white. Ossicles retain lavender color in dissociated specimens.

Holotype.—Locality unknown but probably West Indies; collected by Captain Wendt; Museum für Naturkunde, Berlin, cat. no. 1047.

The holotype is larger and stouter than any of the GERDA specimens. The centrodorsal is 3.0 mm across with DH 3.5. The cirri are XXV (plus a few very small, regenerating cirri), 11–12 (almost all are 12), up to 9.5 mm long. The fourth through sixth cirrals are longest, with LW 1.5 to 1.7.

The IBr_2 are closely apposed. Br_{3+4} is 2.3 to 2.4 mm across with WL 3.0. LD is 1.4. The short, triangular, middle brachials have WL 2.9 to 4.6. The longest anterior arms were probably 140 to 150 mm long; all are broken but fragments composing an entire arm remain; the longest fragment is 85 mm. The short posterior arms may have been 50 mm long when intact.

P_1 is about 12 mm long, composed of 34 to 36 pinnulars with five to seven comb teeth. Dorsal carinae are moderately developed on the third pinnular and weakly developed, if present at all, on the fourth. P_n is about 11 mm long. P_2 is 6 to 10 mm long, of 26 to 28 pinnulars with four to six comb teeth, and with dorsal carinae weak or absent. P_3 and P_4 are similar, 5.5 to 6 mm long, of 17 to 18 pinnulars with five comb teeth. Gonads are present on P_2 through at least P_{12}. The centrodorsal and cirri are white and the division series and arms are pale purplish red.

Ecology.—The living habits and feeding behavior were described by Meyer (1973a, b) from observations made on coral reefs off Jamaica, Colombia and Panamá and by Macurda (1973, 1975) in the Bahama Islands. These authors (except Macurda, 1975) used the name *Comactinia echinoptera* cf. var. *valida.*

This species attaches by its cirri under corals and within solution passages. It is completely cryptic during the day and extends its longer arms for feeding only at night; the disk is rarely exposed. *Comactinia echinoptera* appears to be uncommon in most areas from which it has been collected. Meyer counted 17 individuals in a 20 m^2 area at 10 m in the San Blas Islands off Panamá and suggested that a substantial population may occur at Punta Betin, Santa Marta, Colombia. In Jamaica, the Bahamas, southeastern Florida and the Lesser Antilles, however, it is met with only rarely.

Geographic distribution.—Southeastern Florida; Bahama and Turks and Caicos Islands; Arrowsmith Bank off Yucatán; throughout the lower Caribbean and south to Cape Frio, Brazil and, perhaps, to Isla de los Alcatraces off São Paulo, Brazil. One specimen is recorded from South Carolina waters.

Bathymetric distribution.—For the GERDA material and other specimens of recent collection that I have examined, the possible range is 12 to 183 m and the confirmed range is 15 to 92 m. One questionable record from 270 m exists. Most specimens from earlier expeditions fall within this range. However, several lots of material were taken by the ALBATROSS off Havana at depths up to 368 m. It must be kept in mind

Table 1. Numerical data for 11 specimens of *Comactinia echinoptera* (Müller) collected by R/V GERDA and by SCUBA

Station Number	CENTRODORSAL		CIRRI						ARMS			P_1		P_2		P_3	
	Diam. (mm)	DH*	No.	Cirrals	Max. Length (mm)	Longest Cirral	Longest Cirral Length (mm)	Longest Cirral LW†	Width Br_{3+4} (mm)	LD‡	Length (mm)	No. Pinnulars (No. Comb teeth)	Length (mm)	No. Pinnulars (No. Comb teeth)	Length (mm)	No. Pinnulars (No. Comb teeth)	Length (mm)
G-600	1.3	4.2	XV	9–10	5.5	3–4	0.7	1.8–2.2	0.8–0.9	2.0	32a§ 18p	26(4)	6	9(3)	2	9(2)	2
G-412	1.5	3.0	XXI	9–10	6	4	0.7	1.8	1.1	2.0	~30‖	24(7)	6	11(4)	2.5	10(4)	2.5
G-582	1.8	3.3	XVIII	10	7	4	0.8	1.8	1.3	1.9	30	27(4)	6.5	12(3)	3	12(3)	3
G-423	1.8	4.5	XVIII	—	—	—	—	—	1.2	1.5	—	30(7)	6.5	14(4)	3	13(4)	3
G-600	2.0	5.0	XVIII	11	5.5	4–5	0.6	1.6	1.5	1.6	40	32(4)	8.5	17(6)	4	13(3)	3.5
Boca Raton	2.1	3.9	XX	10–11	7.5	4	0.8	1.7	1.5	1.7	45	33(7)	9	16(5)	4	11(3)	3.5
G-423	2.2	4.3	XXII	12	8	4	0.8	1.7	1.5	1.7	~50	29(6)	8	13(4)	3.5	11(2)	3
G-956	2.4	4.0	XXI	10–11	7.5	4–5	0.9	1.7–2.0	1.9	1.6	35++**	31(7)	9	16(8)	4.5	16(8)	4.5
G-956	2.5	4.0	XVII	10–11	7.5	4	0.9	2.0	2.2	1.6	—	32(6)	10	19(5)	5	15(4)	5
Andros	2.8	4.0	XX	10–12	8.5	4–5	0.9	1.7–2.0	2.3	1.5	165a 65p	35(6)	10	18(5)	4.5	15(6)	4
Providenciales	2.8	6.0	XX	11–13	10	4	0.9	1.5	2.3	1.5	135a 50p	40(8)	12.5	28(5)	8.5	18(6)	6

* Diameter (D) divided by height (H) of centrodorsal.
† Length (L) divided by width (W) of longest cirral.
‡ Length from edge of centrodorsal to Br_{3+4} measured midradially (L) divided by centrodorsal diameter (D).
§ a = anterior arm; p = posterior arm.
‖ The approximation sign (~) indicates that only a small portion of the arm near the tip is broken off.
**The double plus sign (++) indicates that probably less than half of the arm remains.

that the sea floor in this area is rugged and slopes steeply and that only one sounding was made at each station. Although problems certainly still exist in pinpointing the depth of collection, continuous depth recorders such as used aboard the GERDA give a better idea of the (range of) depth of collection.

Remarks.—Several important systematic characters are given in Table 1 for a number of specimens collected by the GERDA and by SCUBA. Most of the material in the USNM and MCZ collections agree with these.

All of the specimens from Cape Frio, Brazil (USNM 34623, 35630; MCZ 31, 199, 443) are very small, slender and most lack pinnular carinae. They resemble the small *C. m. meridionalis* taken in shallow water off Yucatán by the ALBATROSS (USNM 34611). Other specimens with carinae reduced or absent come from off Yucatán (G-956), Barbados (USNM E-4252) and Trinidad (MCZ 1103). The last mentioned lot includes specimens with distal brachial margins somewhat spinose and a small specimen with the centrodorsal about 1.0 mm across and cirri XI, 8–9. Some other very small specimens from Trinidad (MCZ 968) with centrodorsal diameters of 0.8 mm lack the third and fourth pinnule pairs and retain interbrachial plates on the aboral surface of the disk.

Comactinia echinoptera was collected with *C. m. meridionalis* at one of the five GERDA stations and at six of the 16 stations represented by material at the USNM and MCZ. These co-occurrences are limited to southeastern Florida and off Havana. The two are definitely sympatric off Panamá (Meyer, 1973b). At ALBATROSS sta. 2326 off Havana (USNM 34542) an isolated arm probably belonging to *C. echinoptera* was collected with both subspecies of *C. meridionalis*. None of the stations immediately preceding included any *C. echinoptera*.

In the southern Caribbean, this comatulid has been collected as shallow as 3 m.

Discussion.—*Comactinia echinoptera* is unquestionably distinct from *C. meridionalis*. I have discovered no intermediates and the two species are sympatric in some areas (see above).

The species is somewhat variable, ranging from small and slender to large and quite robust but the basic, diagnostic characters are always retained and the extreme variability of *C. meridionalis* is not encountered. The absence of pinnular carinae in some specimens does not constitute a true intergradation with *C. meridionalis*. The variability of this character in *C. echinoptera* and in other comasterids, including *Leptonemaster venustus* and *Nemaster rubiginosa*, indicates that its occasional absence represents no fundamental difference.

Comactinia meridionalis (L. Agassiz)

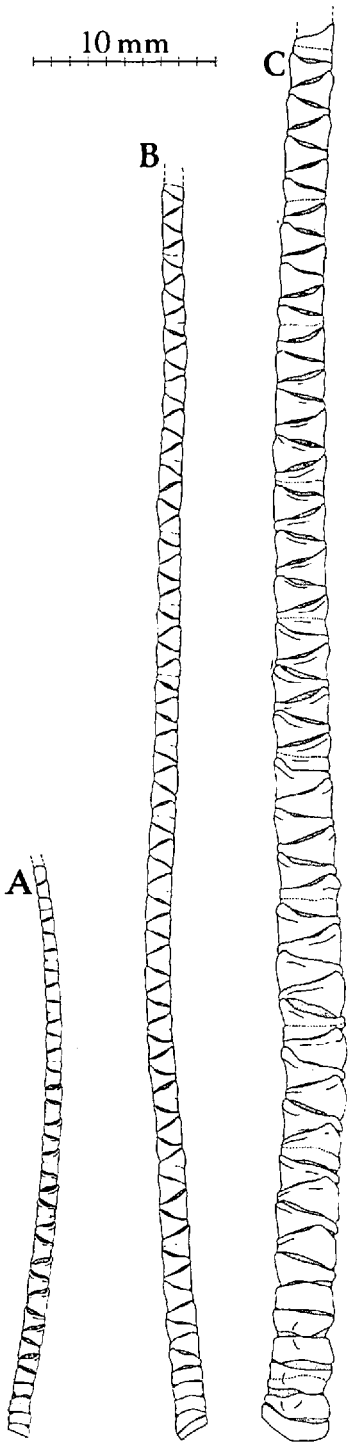
Alecto meridionalis L. Agassiz *in* E. C. and A. Agassiz, 1865: 121, 122, 153, 154[1].

Despite the division of *Comactinia* into two species, much of the variation recorded by A. H. Clark (1931) for the then monotypic genus is characteristic of *C. meridionalis* alone. The bulk of earlier collections, particularly those of the BLAKE and ALBATROSS, consists of *C. meridionalis*. This is consistent with the almost exclusive occurrence of *C. echinoptera* on coral reefs—communities not sampled by trawling or dredging—and with the wide depth distribution of *C. meridionalis*.

From the specimens at my disposal, I have found three general morphological forms of the species. These agree with A. H. Clark's comment that "As a general rule, the size increases proportionately with the depth, the smallest examples being those taken along the shores and the largest those from about 200 meters or over (1931: 379).

The first is known primarily from shallow water off South Carolina where Louis Agas-

[1] The original citation is "*Alecto meridionalis* Ag." In this book, many of the species are ascribed either to "Ag." or "A. Ag." Investigation of several names attributed to "Ag." revealed that they were described by Louis Agassiz in other works (e.g., the medusae *Tima formosa* and *Zygodactyla groenlandica*). It is, therefore, certain that the elder Agassiz is the author of this name.



siz collected the type-series and off Panamá where Meyer (1973b) studied its ecology and feeding behavior. This form is small; arm length usually does not exceed 45–50 mm. The cirri are numerous, long in relation to centrodorsal diameter and are usually of more than ten cirrals each. They are more slender and their longest cirrals are more elongate than in specimens from deeper water. A relatively strong comb is present on P_1 through P_3. In the Panamanian specimens, the centrodorsal is smaller than in specimens from elsewhere, the radials are exposed and the division series are well separated.

The character of the cirri and small size of this form appear to be adaptations to the shallow, high physical energy environments in which they live. Off Panamá, the comatulids live exposed at least as shallow as 3 m, and off South Carolina they occur at least as shallow as 11 m. The numerous cirri probably provide better anchorage than would fewer shorter cirri and the shorter arms are less likely to break. This form appears to be stunted.

The second form dominates the collections. The GERDA material occurs roughly between 50 and 200 m. The cirri are most often composed of 9–11 cirrals; the animals are larger and have longer arms; combs are present on P_1 and P_2. I have not separated this form from the shallow water form because the differences appear chiefly to be the result of environmental stresses. The morphological type that dominates the GERDA collections is not exposed to the high levels of physical energy characteristic of shallow water and, as a result, it need not anchor as securely and it can grow longer, more slender arms. In addition, a number of intermediate specimens exist.

The third form is bathymetrically allo-

←

Figure 5. *Comactinia meridionalis* (L. Agassiz) arms. A. *C. m. meridionalis*, shallow water form, Panamá. B. *C. m. meridionalis*, deeper water form, G-392. C. *C. m. hartlaubi*, G-1329.

patric, occurring in deeper water than the previous forms. It is much larger and more robust, with longer and irregular intersyzygial intervals. The cirri are longer, heavier, with more, but shorter cirrals than the previous form. The proximal pinnules differ considerably from those of the previous forms and P_1 through P_3 or P_4 bear weak combs. Although some intergradation with the previous form occurs, I consider this to be a valid subspecies (see discussion below).

Comactinia meridionalis meridionalis L. Agassiz

Figures 1B, 5A–B, 6A–G, 7–10; Table 2.

Alecto meridionalis L. Agassiz *in* E. C. and A. Agassiz, 1865: 121, 122, 153, 154.

Antedon meridionalis: Pourtalès, 1869: 355 (part); 1878: 214 (part?).—Carpenter, 1879: 20 (part); 1881: 156 (part).

Comatula meridionalis: Carpenter, 1879: 20, 27, 28 (part).

Actinometra meridionalis: Carpenter, 1881: 155, 156–157, 161, 162, 164 (part); 1888: 301–302; pl. 4, fig. 4a–c; pl. 56, figs. 1–2 (part).

Actinometra echinoptera: Hartlaub, 1912: 280, 281, 413, 415–471; pls. 16, 17, 18 (part).

Comactinia echinoptera: A. H. Clark, 1909b: 149, 150 (part?); 1915: 29, 31, 32, 46, 129, 249, 281, 291, 298, 325, 355 (part); 1921a: 14, 15, 16, 71, 219, 255, 323, 341, 662, 664, 665, 666, 672, 681 (part?); 1931: 128, 133, 231, 277, 280, 301, 351, 359, 375–400, 692; pl. 42, figs. 125–128; pl. 43, figs. 129–130; pl. 44, figs. 131–135 (part).—Tommasi, 1963: 98–100 (part?); 1965: 6, 7, 8, 14; figs. 12–18 (part?).

Comactinia meridionalis: A. H. Clark, 1909b: 150 (part?); 1915: 34, 46, 315, 317, 321, 326; pl. 4, fig. 548 (part); 1921a: 16, 220, 222, 225, 233, 280, 291, 312, 341, 370, 374, 509–510, 513, 514–517, 518, 520, 549, 555, 577–586, 588–590, 596, 662, 663, 665, 666, 668, 672, 681, 706, 725; pl. 1, figs. 963–964 (part); 1921b: 9–11, 25–28 (part); 1931: 50, 136, 277, 283, 378 (part).

Actinometra echinoptera variety *meridionalis*: Hartlaub, 1912: 416, 417, 418, 426–430; pl. 16, figs. 1–5, 10–12 (part).

Comactinia echinoptera variety *meridionalis*: Tommasi, 1963: 99 (part?).—Meyer, 1973b. 118–120.

Material examined.—LECTOTYPE: L. Agassiz, Charleston, South Carolina; larger of two specimens, MCZ 33. PARALECTOTYPES: L. Agassiz, Charleston, South Carolina; 2, MCZ 32; 1, MCZ 33; several pentacrinoids, MCZ 34; 2, MCZ 446. OFF CAPE LOOKOUT, NORTH CAROLINA: EASTWARD sta. 4943, 34°07.5'N, 76°14.5' W, 75 m; 1, Duke University Marine Laboratory cat. no. 2680.—EASTWARD sta. 7702, 33°12'N, 77° 24'W, 60 m, 27 July 1967; 2, Duke University Marine Laboratory cat. no. 1854.—EASTWARD sta. 17013, 34°07'N, 76°12.3'W, 82 m, 16 May 1971; 1.—FISH HAWK coll.; 4, USNM 34641. SOUTH CAROLINA: R. E. Earll, coll.; 1, USNM 3803. SOUTHEASTERN FLORIDA: G-600, 25° 02.5'N, 80°18.8'W, 73 m, triangular dredge, 15 April 1965; 3.—4 miles NE of Elbow, Key Largo; 1, MCZ 1105.—Between Carysfort and Molasses Reefs, Key Largo, 92–214 m; 8, MCZ 1106.—4.5 miles SE of Carysfort Light, Key Largo, 168–183 m; 1, MCZ 1107.—Off Carysfort Light, Key Largo, 137–183 m; 3, MCZ 1108.—Off Carysfort Light, Key Largo, 121–198 m; 3, MCZ 1109.—Probably U.S. Coast Survey, BIBB coll., French Reef,

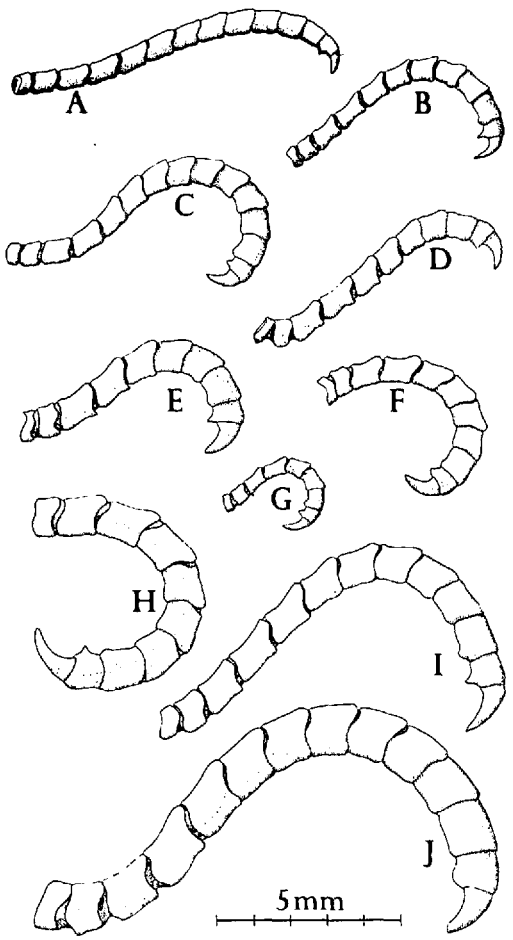


Figure 6. *Comactinia meridionalis* (L. Agassiz) cirri. A. *C. m. meridionalis*, shallow water form, lectotype. B. Same, Panamá. C. Same, Nicaragua. D. Deeper water form, G-713. E. Same, G-392. F. Same, another specimen from G-392. G. Same, a third specimen from G-392. H. *C. m. hartlaubi*, G-493. I. Same, G-725. J. Same, G-510.

81 m; 3, MCZ 120.—U.S. Coast Survey; 2, MCZ 79.—BIBB coll.; 9, USNM 34624 (labelled CORWIN coll., 1869, though that vessel operated in 1867); 4, MCZ 115; 10, MCZ 200; 7, MCZ 294; 2, MCZ 417; 29, MCZ 433.—1, MCZ 80; 1, MCZ 81; 1, MCZ 413 ("undoubtedly Southern Florida" according to A. H. Clark, 1931: 389); 1, MCZ 452. SOUTHEASTERN GULF OF MEXICO: G-562, 24°32'N, 83°20'W, 71 m, 3 m try net, 12 April 1965; 1.—G-564, end of tow 24°32'N, 83° 15'W, 68–69 m, 3 m try net, 12 April 1965; 11.—1, USNM 34825; 2, MCZ 431; 1, MCZ 447. BAHAMAS: G-391, no locality, previous station 27° 19'N, 79°11.5'W, 46–91 m, screen dredge, 19 September 1964; 1.—G-392, 27°21'N, 79°11'W, 125–137 m, screen dredge, 19 September 1964; 34.—G-393, 27°21.5'N, 79°11'W, 165 m, screen dredge, 19 September 1964; 1.—G-636, 26°04'N, 79°13'W, 46–128 m, triangular dredge, 30 June 1965; 1.—G-713, 25°58.6'N, 79°15.4'W, 190–201 m, 3 m try net, 2 August 1965; 8.—G-724, 26°00'N, 78°48'W, 101–134 m, triangular dredge, 3 August 1965; 6.—G-1246, 23°57.7'N, 80°28.6'W, 65 m, SCUBA, 11 March 1970; 1. NORTHERN CUBA: UIBE; 4, USNM E-4499; 3, USNM E-9472; 1, MCZ 743; 1, MCZ 745.—ALBATROSS coll.; 1, USNM 16903; 1, USNM 16908; 1 + fragments, USNM 16909; 2, USNM 21708; 5, USNM 34542; 3, USNM 34543; 3, USNM 34549; 2, USNM 34551; 36, USNM 34610 (labelled sta. 2334, off western Cuba, but that station was made off Havana according to A. H. Clark, 1931: 390); 1, USNM 34638; 4, USNM 34642; 2, USNM 34817; 1, USNM 34819; 2, USNM 34824; 3, USNM 34827; 5, USNM 34832; 9, USNM 34917 (plus one *Leptonemaster venustus*); 4, USNM 35885; 3, USNM 36145. OFF YUCATAN: ALBATROSS coll.; 28, USNM 34611; several pentacrinoids, USNM 34612; 1 + several pentacrinoids, USNM 36223.—BLAKE coll.; 1, MCZ 213. ANTILLEAN ARC: J-SE, CAROLINE sta. 17, 18°30'00"N, 66°10'30"W, 84–165 m, 6 ft trawl, 3 February 1933; 1, USNM E-5233; 1, USNM E-5247; 2, USNM E-5249; 1, USNM E-5250.—J-SE, CAROLINE sta. 26, 18°30'20"N, 66° 22'05"W, 60–73 m, 3 ft dredge, 7 February 1933; 21, USNM E-5234.—J-SE, CAROLINE sta. 104, 18° 30'40"N, 66°13'20"W, 146–220 m, Chesapeake Bay oyster dredge, 8 March 1933; 3, USNM E-5232.—UIB-AE, dredging sta. 11, 1¼ miles due W from white lighthouse at Needham Point, Barbados, 123–128 m, stony bottom, 17 May 1918; 4, USNM E-4259.—UIB-AE, dredging sta. 14, no data, probably Barbados, ca. 17–18 May 1918; 1, USNM E-4261.—UIB-AE, dredging sta. 51, WNW of Lazaretto, Barbados, NNW of Pelican Id., 60 m, rocky bottom, dredge, 27 May 1918; 1, USNM E-4253; 1, USNM E-4257.—UIB-AE, dredging sta. 67, W by N of Telegraph sta., Barbados, ½ mile or more offshore, about edge of dropoff, 91–128 m, rocky bottom, tangles, 1 June 1918; 2, USNM E-4254; 3, USNM E-4255.—UIB-AE, dredging sta. 78, Barbados Cable sta., ES by E, Paynes Bay Church NE, ¾ mile offshore, 134–137 m, bottom alternate sand and rocks, 3-5(?) June 1918; 1, USNM E-4256.—UIB-AE, dredging sta. 85, no data, probably Barbados, ca. 6 June 1918; 1, USNM E-4258.—BLAKE sta. 203; 7, MCZ 784; 1, MCZ 786.—Probably BLAKE sta. 155; 2, MCZ 787.—BLAKE coll.; 3, MCZ 216; 8, MCZ 218; 2, MCZ 219; 1, MCZ 226; 11, MCZ 411; 3, MCZ 412; 1, MCZ 415; 1, MCZ 416; 3, MCZ 435; 1, MCZ 436; 6, MCZ 437 (plus one *Leptonemaster venustus*); 2, MCZ 438; 1, MCZ 439; 1, MCZ 440; 3, MCZ 441; 1 + fragments, MCZ 442; 1, MCZ 453; 4, MCZ 454; 1, MCZ 473; 1, MCZ 486 (very tiny, identity questionable); 1, MCZ 495.—INVESTIGATOR; 1, MCZ 456. CENTRAL AMERICA: J. Garcia, coll., 12°47'N, 83°29'W, 14 m, 7 August 1974; 1.—D. B. Macurda, Jr. and D. L. Meyer, coll., 9°24' 18"N, 79°51'53"W, 11–21 m, SCUBA, 26 February 1972; 3. BRAZIL(?): Rio de Janeiro (?); 1, MCZ 276. LOCALITY UNKNOWN: University of Iowa, label lost; 4, USNM E-4384.—Both probably BLAKE coll.; 3, MCZ 222; 1, MCZ 451 (specimens of both lots very small, similar to material collected by the BLAKE in the Lesser Antilles).

Diagnosis.—Radials hidden, just visible in interradial angles or well exposed; cirri up to 11 mm long, of uniform width or slightly broader distally; penultimate cirral usually broader than long; LW of longest cirral usually 1.5 to 1.7; division series infrequently closely apposed; intersyzygial interval usually three; P_1, P_2 and sometimes P_3 comb-bearing; comb teeth round or triangular, short or tall; proximal pinnulars (excepting basal one or two) of proximal and middle pinnules as far as P_{20} with weak rim of spines which may be produced laterally into a spinose flange; pinnular carinae absent; disk naked or bearing nodules.

Description.—Centrodorsal discoidal or pentagonal, comparatively larger than in individuals of *C. echinoptera* (Müller) having arms of similar length and strength; 1.2 to 3.7 mm across; DH 2.9 to 5.2. Cirri arranged in single or, rarely, partly double, irregular marginal row. Polar area usually smooth and flat, sometimes slightly depressed centrally with traces of radiating, interradial (often paired) lines or very weak ridges; one specimen bearing very weak papillae in center of polar area.

Cirri X–XXX, 8–17 (usually 9–12), 5 to 11 mm, slightly compressed distally, of constant width or, rarely, slightly broader distally; third and/or fourth (rarely, fifth) cirral longest; LW 1.3 to 2.2 (usually 1.5 to 1.7; often 2.0 in shallow water form); subsequent cirrals decreasing in length; third

Figure 7. *Comactinia meridionalis meridionalis* (L. Agassiz). Deeper water form. A. G-564. B. G-392. Scale: 1 cm.

through antepenultimate cirrals of subequal length in larger individuals; penultimate cirral usually broader than long; opposing spine short, erect, conical and subterminal; low dorsal subterminal tubercle often present on antepenultimate cirral; terminal claw longer than preceding cirral.

Basal rays hidden, barely visible or appearing as prominent tubercles in interradial angles. Radials just visible in interradial angles or well exposed, rarely hidden. Radial articular face broadest across dorsal ligament fossa; muscular fossae and interarticular ligament fossae equally broad.

Division series smoothly rounded dorsally and infrequently closely apposed; synarthrial tubercles absent. IBr_1 short, united laterally (only proximally in small specimens), usually broader distally than proximally, sometimes slightly inflated laterally, WL 3.0 to 4.0 (rarely to 4.8). IBr_2 triangular, usually separated laterally, infrequently pentagonal with short lateral edges; WL 1.8 to 2.8.

Arms 20 to 95 mm long, usually slightly broader in middle than at base; greatest width reached proximally between Br_{10} and Br_{20}; in complete specimens, anterior arms

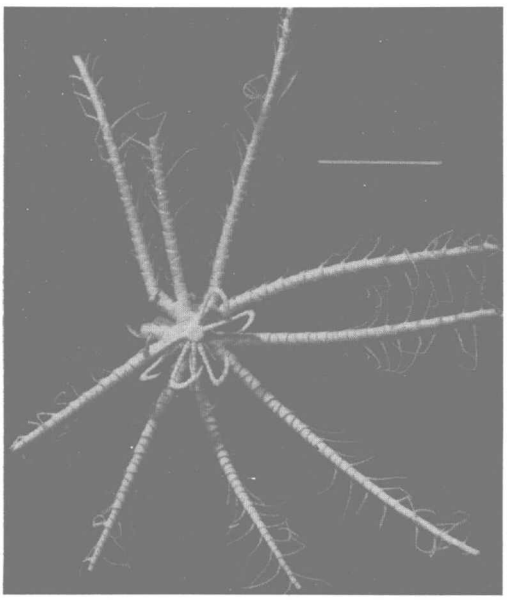


Figure 8. *Comactinia meridionalis meridionalis* (L. Agassiz). Shallow water form. Specimen collected by Macurda and Meyer, Panamá. Scale: 1 cm.

more or less than twice length of posterior arms; weak alternating articular tubercles sometimes developed on proximal brachials; distal, dorsal edge of brachials from between Br_5 and Br_7 to between Br_{20} and Br_{30} raised, sometimes everted, finely or coarsely spined but not overlapping succeeding brachial; this character limited to several proximal brachials in some specimens or extending in weakened form almost to arm tip in others. Br_1 short, oblong or slightly longer exteriorly, united interiorly (at least proximally); WL 2.4 to 3.7. Br_2 oblong to strongly wedge-shaped, laterally free; WL 2.2 to 3.7. Br_{3+4} oblong, slightly longer than Br_2, 0.9 to 2.5 mm across; WL 1.4 to 3.2. Br_5 and Br_6 oblong, less often wedge-shaped; WL 1.7 to 3.5. Next several brachials increasingly wedge-shaped, becoming triangular between Br_8 and Br_{11} and wedge-shaped again anywhere between Br_{17} and Br_{50}; WL 1.5 to 3.0. Triangular brachials extending almost to arm tip in some large specimens, absent in some small individuals; distal brachials less strongly wedge-shaped, usually elongate near arm tip; strongly raised and everted distal, dorsal rims of middle brachials typically found on very small specimens (though never as strongly as in *Neocomatella alata*) or on individuals with particularly short, triangular middle brachials.

Syzygies at B_{3+4} and Br_{11+12} (infrequently from Br_{8+9} to Br_{13+14}); subsequent intersyzygial interval three (less often four and, rarely, two, five or six).

P_1 slender, 4.5 to 13.5 mm long, composed of 23 to 40 pinnulars; proximal pinnulars short and squarish or triangular; middle pinnulars squarish; distal pinnulars longer than broad; comb of three to 11 rounded or triangular, weak or strong, well-separated teeth. P_2 2.0 to 9.0 mm long, from less than half to ⅘ as long as P_1, composed of 11 to 28 pinnulars with three to 12 comb teeth similar to those of P_1. P_b sometimes lacking a comb. P_3 2.0 to 6.0 mm long, of up to 17 pinnulars; proximal and middle pinnulars squarish or triangular; distal pinnulars longer than broad; when present, comb of 3 to 10 teeth. Either P_2 or P_3 shortest pinnule. Subsequent pinnules increasing in length to distal maximum of 13.5 mm with 24 pinnulars. Proximal pinnulars (excepting basal one or two) of as many as the proximal 20 pairs of pinnules infrequently produced laterally (on one or both sides) into a spinose flange or rim rarely as strong as that found in the deeper water subspecies (see below); this character often reduced to a weak rim of spines present only on P_1 to P_3 or P_4. Middle pinnules stout with squarish proximal and middle pinnulars; distal pinnules slender with elongate pinnules (excepting short basal two).

Gonads on P_3 to between P_7 and P_{16}; in one individual, gonads absent from ray B, weakly developed on ray A and most strongly developed on ray D. Intrinsic calcareous debris and sometimes small, fenestrated plates lining pinnule ambulacra.

Disk naked, sometimes with sparse, small

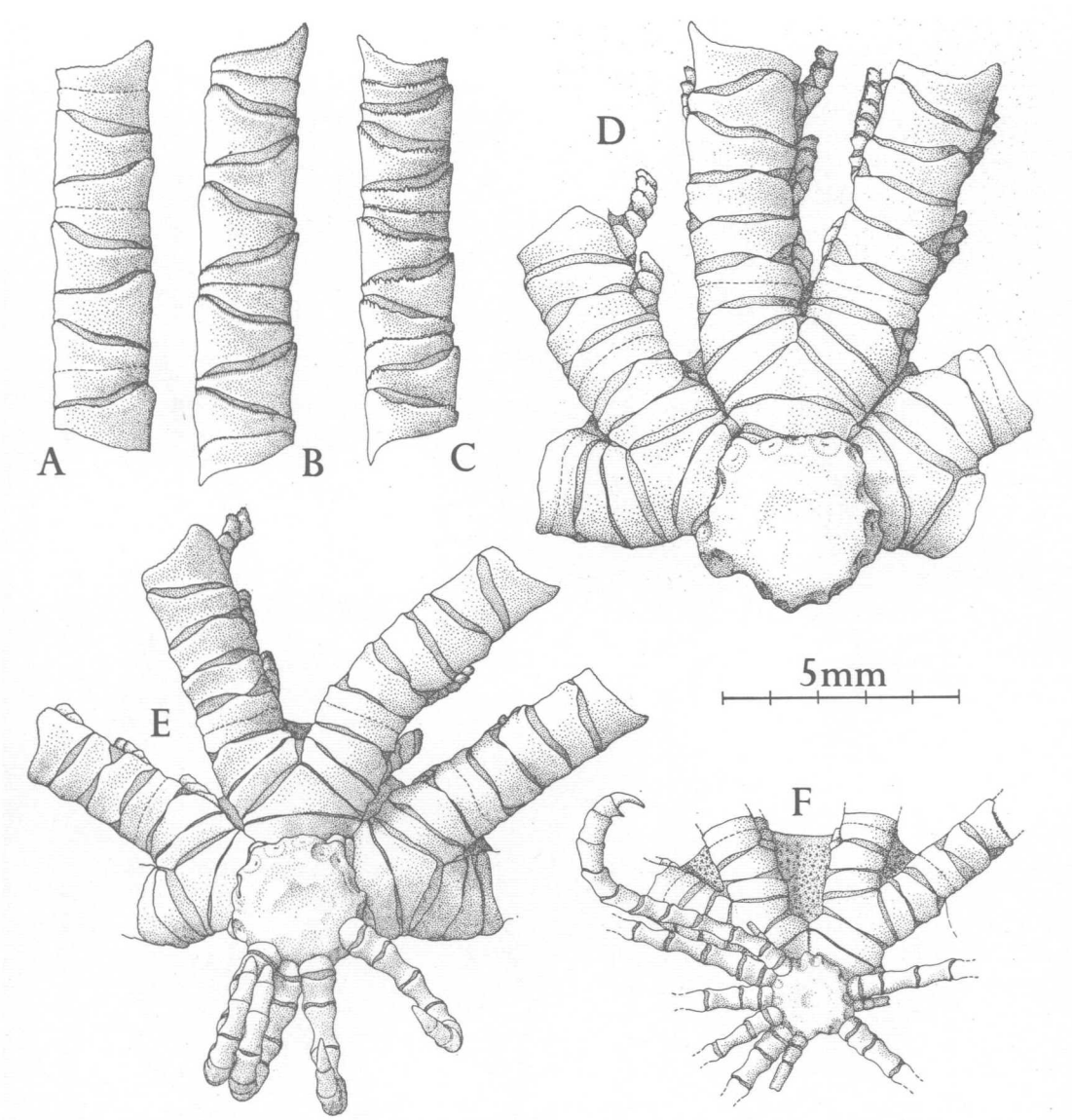


Figure 9. *Comactinia meridionalis meridionalis* (L. Agassiz). A–E. Deeper water form. A. Middle brachials, dorsal view, G-562. B. Same, G-724. C. Same, EASTWARD-4943. D. Centrodorsal and proximal part of three rays in dorsal view, G-724. E. Centrodorsal, cirri and proximal part of three rays in dorsal view, G-392. F. Shallow water form; centrodorsal, cirri and proximal part of two rays in dorsal view, Panamá.

nodules and rarely crowded with large, irregular nodules. Mouth marginal.

Color.—In alcohol, white, pale or dark brown, or white with a brown longitudinal band on the arms. Purple specimens of *C. m. meridionalis* do not retain their color when dissociated with sodium hypochlorite solution (unlike *C. echinoptera*); this color derives from sponges with which the comatulid associates (at least as a vestige of

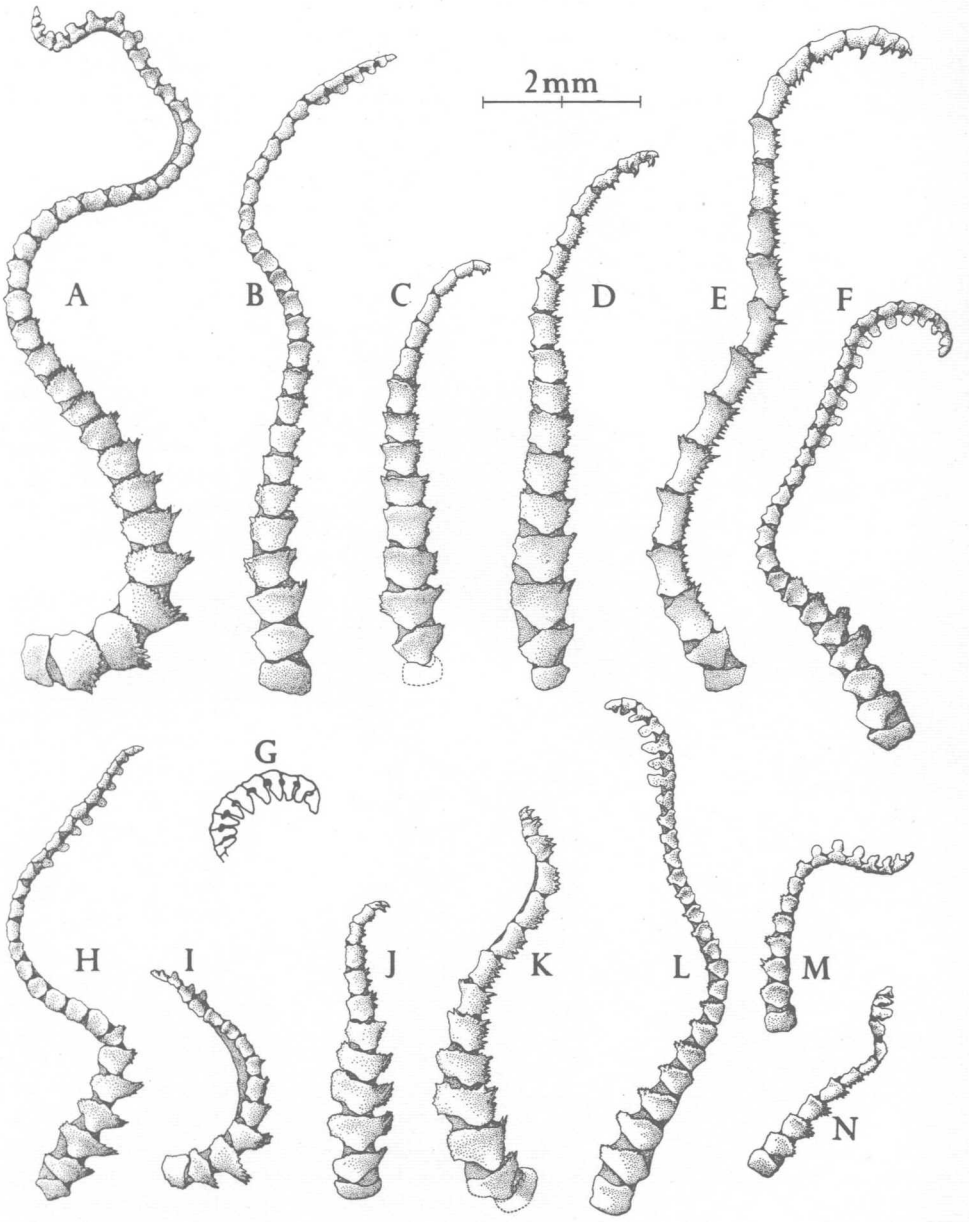


Figure 10. *Comactinia meridionalis meridionalis* (L. Agassiz) pinnules. A. P_1, G-562. B. P_2, same specimen and arm. C. P_3, same. D. P_4, same. E. P_{distal}, same. F. P_2, G-724. G. Comb on P_3 of lectotype. H. P_a, G-713. I. P_b, same specimen and arm. J. P_c, same. K. P_n, same. L. P_1, shallow water form, Panamá. M. P_2, same specimen and arm. N. P_3, same.

collection). A. H. Clark (1921a: 706) described additional color patterns most of which probably refer to *C. echinoptera*.[2]

Holotype.—None designated. Six specimens and several pentacrinoids labelled as type or cotype (MCZ cat. nos. 32, 33, 34, 446) collected by Louis Agassiz in shallow water off Charleston, South Carolina, comprise the syntype series. Of these, I have designated the largest and best preserved specimen of MCZ 33 as lectotype. The other specimens, as listed under "*Material examined*," are paralectotypes.

The centrodorsal of the lectotype is round, 3.0 mm across, with DH 4.0. The cirri are XXX, 13–15, about 10 mm long and slightly broader distally. The third, fourth, and sometimes fifth cirrals are longest, with WL 1.4–1.5. The radials are visible only in the interradial angles. The IBr_1 are united, with WL 3.6. The IBr_2 are triangular and separated, with WL about 2.0. The Br_{3+4} are 2.0–2.2 mm across with WL 2.3. LD is 1.3. The brachials become triangular by Br_8 or Br_9. Middle brachials are short and triangular, with WL 2.8. The brachials beyond the proximal few have raised and finely spinose distal edges that are moderately everted on some arms. The arms are broadest between Br_{10} and Br_{20}. The longest remaining arm fragment is 32 mm. Combs of strong, triangular teeth are present on P_1 through P_3.

Ecology.—Meyer (1973b) discussed the habits and feeding behavior of a *Comactinia* from off Panamá which he provisionally referred to *C. echinoptera* variety *meridionalis*. I have examined a small number of specimens of this form and have found that it belongs to *C. m. meridionalis*. In certain characters, this form approaches the type specimens more closely than do the GERDA specimens.

The Panamanian *C. m. meridionalis* attaches by the cirri within rock crevices or to the undersides of corals and extends the arms for feeding. Unlike *C. echinoptera*, this species is frequently entirely exposed and feeds day and night. Both species live close to the main reef substrate and the arms of both create vertical filtration fans normal to the direction of wave oscillation. The ambulacra face into and away from the surge, but since the direction of water movement constantly reverses, neither the pinnules nor the arms need to twist to maintain proper orientation.

Meyer observed *C. m. meridionalis* to occasionally change its pinnule orientation from the typical monoplanar to the biplanar or radial posture characteristic of *Nemaster*. At Galeta Point, Canal Zone, he found this comatulid to reach "the highest population density of any shallow water Caribbean crinoid observed so far" (1973b: 119). He recorded densities up to 20/m² in 8 to 10 m of water.

Comactinia m. meridionalis occurs in considerably deeper water in the Straits of Florida but I expect its habits differ little. Since there is no surge at the depths at which the GERDA trawled it, the arm and pinnule ambulacra may orient in only one direction.

Geographic distribution.—Gulf of Mexico; southeastern United States from Cape Lookout, North Carolina to the Florida Keys; Bahama Islands; throughout the Caribbean from Yucatán and Cuba to Surinam (possibly extending southward to São Paulo, Brazil, but material previously collected there must be reexamined).

Bathymetric distribution.—Possible: 3–508 m. For the GERDA collections, the possible and confirmed ranges are 46–201 m and 69–190 m, respectively. A single juvenile speci-

[2] Since this was written, I have received from Judith Land of the University of Texas at Austin, a specimen of *C. m. meridionalis* collected during a dive aboard the submersible NEKTON-BETA in the Tongue-of-the-Ocean, Bahamas, and described as bright yellow in life. Land also observed a "yellow comatulid" and a "creamish comatulid with maroon pinnules" at 134 m during this program. These correspond well with A. H. Clark's first three color patterns for *C. meridionalis* (he listed none for *C. echinoptera*): "a) Light yellow," "b) Dark yellow" and "c) Arms light yellow, the pinnules deep carmine, usually tipped with yellow." The remainder of the color patterns listed by Clark for this species appear to refer to *C. echinoptera* with the possible exceptions of "e) Rich carmine" and "h) Bright purple, the pinnules brighter purple" which may refer to *C. meridionalis* stained by sponges. Clark also attributed a yellow color to some specimens of *Leptonemaster venustus*.

men was collected on an antipatharian in about 65 m (G-1246). In the lower Caribbean, the extensive collections made by the R/V PILLSBURY include few records from depths greater than 100 m. The greater depths recorded for this species by the BLAKE in the Lesser Antilles reflect the same problems discussed for the ALBATROSS collections made off northern Cuba (see bathymetric distribution under *C. echinoptera*).

The depth records for the material from the GERDA and BIBB stations along the continental side of the Straits of Florida and the material collected off the Carolinas are significantly shallower than the records for the GERDA material from the Bahama side of the Straits and the ALBATROSS and University of Iowa Bahamas Expedition specimens collected off Havana (but see above). This suggests that the bathymetric distribution is temperature controlled, conforming to the steep isothermal tilting across the Straits caused by the Florida Current. I have, however, examined four lots of specimens (MCZ 1106–1109) collected by an unknown source off Key Largo at depths typical of collections made along the insular margin of the Straits.

Remarks.—In the paralectotype series, the smaller MCZ 232 specimen has a centrodorsal diameter of 2.5 mm and stout, robust arms at least 35 mm long. The cirri are XX, 14, up to 9.5 mm long. The fourth and fifth cirrals are longest, with LW 2.0. The brachials are short and everted. P_1 is about 9 mm long, composed of 35 segments including nine high comb teeth. P_2 is about 5 mm, of 22 segments with eight teeth. P_3 is about 4 mm, of 17 segments with five teeth. The intersyzygial interval is three. The larger specimen has the centrodorsal 3.2 mm across with XXVII cirri but none remain attached. No complete pinnules remain and the longest arm is complete only to Br_{15}. Both specimens have an arm width at Br_{3+4} of 1.8 mm.

The paralectotype MCZ 33 has the centrodorsal 1.5 mm across and cirri XXIII, 10–11, up to 5.7 mm long. The fourth and fifth cirrals are longest, with LW 1.7. The radials are exposed. P_1 is 7 mm long, composed of 29 pinnulars including ten high, round comb teeth. The longest remaining attached arm is 18 mm.

The two paralectotypes MCZ 446 have cirri XXIII–XXVI, 10–13. Combs are present on P_1 through P_3 but are sometimes lacking on P_c. The entire type series are characteristic, shallow water forms.

The specimen collected off Nicaragua by J. Garcia is 3.5 mm across the centrodorsal with cirri XXVIII, 13–17, up to 11 mm long. The fourth or fifth cirrals are longest with LW 1.4, shorter than in the type series specimens. The brachials beyond Br_6 are coarsely spinose and the arms are about 30 mm.

The shallow water Panamanian specimens differ somewhat. Although arm lengths are 30–40 mm, similar to those of the preceding specimens, the centrodorsals are smaller (1.7–1.8 mm across) and the cirri are fewer (XV–XVIII) though of similar length and number of cirrals (7 to 9 mm long, 11–13). The fourth or fifth cirrals are longest with LW 1.5–1.8. The radials are exposed; the division series are separated and the arms are slender (width at Br_{3+4} only 1.1–1.2 mm). One specimen bears gonads on P_2 to P_7 or P_8.

Except for the type-series, very little characteristic shallow water material exists in the USNM and MCZ collections. A specimen collected off western Florida (USNM 34825) has the centrodorsal 3 mm across, cirri XX, 11–13, slender, 14 mm long, with strong combs on P_1–P_3. The longest remaining arm attached is 70 mm and there is a detached fragment 160 mm long. Also from western Florida, the larger specimen of MCZ 431 has tall, well-developed comb teeth on P_1–P_3 but has robust arms 100 mm long. The smaller specimen has cirri of 12 segments.

USNM 3803 collected off South Carolina has cirri XXVIII, 12–13, arms about 50 mm but, unlike the type material, lacks a comb on P_3 on some arms.

The 28 specimens of USNM 34611, col-

lected off Yucatán, are all small and slender. The largest specimen has the centrodorsal 2.3 mm across and cirri up to 8 mm long. Another specimen with a centrodorsal diameter of about 1 mm has cirri XIX, 11–13, up to 8.5 mm long; the fourth cirral is longest, with LW 1.5–1.8. The specimen with the most cirri bears XXVII, 15. All have small centrodorsals, radials exposed, IBr_1 separated, no triangular brachials and arms no longer than about 30 mm. The combs on P_1–P_3 are composed of tall, broad teeth sometimes approaching those of *C. echinoptera*. Some specimens bear pentacrinoid stalks on some of their cirri. These specimens plus USNM 16909 (1 specimen + fragments), 34607 (1 specimen), 34612 (several pentacrinoids) and 36233 (1 specimen + pentacrinoids) represent the material from which Frank Springer (1920) drew his description of the development of *C. meridionalis*.

Several important characters for a number of specimens collected by the GERDA are given in Table 2. These represent the deeper water form of *C. m. meridionalis* and are similar to the majority of USNM and MCZ material. Some individuals collected off Puerto Rico (USNM E-5249) and in the Lesser Antilles (MCZ 222, 786, 787), however, have P_2 very short and combless.

Another specimen from the Lesser Antilles (USNM E-4254) has a pair of dark, longitudinal arm bands, one on either side of the median line.

A single individual collected off French Reef, Florida (MCZ 200) has one ray with a IIBr2 series and Br_{1+2} on the interior arm.

Material intermediate between *C. m. meridionalis* and *C. m. hartlaubi* will be discussed separately below. However, there are a number of specimens that I have placed in the first subspecies but that approach *hartlaubi* in some respects, as follows.

USNM 34817: The larger specimen is robust, with the centrodorsal 3.2 mm across, cirri XIX, 11–12, the longest cirral with LW 1.7, division series and arm bases apposed, LD 1.1, intersyzygial interval 3–4, comb present on P_3 but dorsal pinnular projections only moderately developed. It appears generally closer to *C. m. meridionalis*. The other specimen in this lot is definitely *C. m. meridionalis*.

USNM 34827: All three specimens approach *hartlaubi* in some fashion. One has cirri XVI, 9–10, division series apposed, brachials short with everted, coarsely spinose, distal edges, intersyzygial interval 3–5, pinnules with spinose projections but unlike those characteristic of *hartlaubi*. Another has cirri XVI, 11–12, with LW of the longest cirral 1.4.

USNM E-4499: Of the four robust specimens of *C. m. meridionalis*, one has division series short and approaching those of *hartlaubi*.

USNM 34610: Of the 36 specimens, one is large and robust with comb present or absent on P_3, intersyzygial interval mostly 4 (with some 5) and LD 1.0.

USNM 16908: Specimen broken. Short division series approach those of *hartlaubi* but P_3 lacks a comb and the intersyzygial interval is 3.

USNM 34542: One specimen approaches *hartlaubi* neither in size nor robustness yet has an intersyzygial interval of 7–8.

MCZ 412: The largest of three *C. m. meridionalis* has the brachials short and everted, pinnules dorsally produced and intersyzygial interval 4–5 but the division series are separated beyond IBr_1 and the cirri have only nine segments.

MCZ 442: Small specimen with intersyzygial interval 3–4, comb on P_1–P_3 but pinnules typical of *C. m. meridionalis*, and division series wall-sided and apposed.

The USNM and MCZ collections contain material identified by me as *C. m. meridionalis* from about 65 station localities. *Comactinia echinoptera* was also collected at five of these stations, *C. meridionalis hartlaubi* at two stations, a specimen intermediate between *C. m. meridionalis* and *C. m. hart-*

Table 2. Numerical data for 18 specimens of *Comactinia meridionalis meridionalis* (L. Agassiz) (deeper water form) collected by R/V GERDA

Station Number	CENTRODORSAL		CIRRI						ARMS			P_1		P_2		P_3	
	Diam. (mm)	DH	No.	Cirrals	Max. Length (mm)	Longest Cirral	Longest Cirral Length (mm)	Longest Cirral LW	Width Br_{3+4} (mm)	LD	Length (mm)	No. Pinnulars (No. Comb teeth)	Length (mm)	No. Pinnulars (No. Comb teeth)	Length (mm)	No. Pinnulars (No. Comb teeth)	Length (mm)
G-724	1.5	2.9	X	8–9	5	3	0.8	1.7	1.0	1.4	35+*	26(8)	6	13(6)	2	12(none)	2.5
G-1246	1.6	4.1	XVII	9–10	6	3–4	0.8	2.0	0.9	1.5	15+	23(8)	4.5	15(4)	3	—	—
G-392	1.8	4.0	XIII	8–10	6	4	0.7	1.5	1.2	1.3	40	26(11)	6.5	16(7)	4	11(none)	2.5
G-393	1.9	3.6	XIV	9–10	5.5	3–4	0.8	1.7	1.2	1.3	20+	26(8)	6	11(3)	2	10(none)	2
G-392	2.3	3.8	XV	9–10	6	3	0.9	1.5	1.2	1.0	40	27(8)	6.5	17(7)	3.5	11(none)	3
G-636	2.4	3.9	XV	10–11	6.5	3	0.8	1.6	1.5	1.4	50	30(8)	7.5	20(none)	4.5	13(none)	3.5
G-600	2.5	5.0	XV	11	8	3–4	0.9	1.4	1.4–1.5	1.1	40+	25(3)	8	23(7)	6	12(none)	4
G-392	2.9	3.8	XV	9–10	7	3–4	0.9	1.5	1.7	1.0	70	29(10)	8	21(9)	5	13(none)	3.5
G-564	2.9	3.8	XX	10–11	9	4	1.1	1.6	2.0	1.3	70a 55p	28(8)	10	24(7)	8	16(none)	6.5
G-564	3.1	5.0	XVII	10–12	9.5	3	1.2	1.7	1.8–2.0	1.4	50+	31(8)	11	21(7)	7	15(none)	5.5
G-713	3.1	5.0	XVIII	10–11	8	4	1.0	1.6	1.8	1.2	40+	33(8)	9.5	20(7)	5	12(none)	3.5
G-392	3.2	4.0	XIX	9–11	8	3	1.0	1.3	2.0	1.3	55	33(8)	11	23(8)	6.5	16(none)	5
G-392	3.2	5.2	XV	10	7.5	3	0.9	1.4	1.7	1.0	70	31(11)	8.5	16(7)	3.5	14(none)	4
G-564	3.2	3.5	XVIII	11–12	9	4	1.0	1.6	1.8	1.2	95	34(10)	11	26(7)	7.5	15(none)	5.5
G-391	3.5	4.6	XIV	—	—	—	—	—	2.3	1.3	50+	40(7)	13.5	—	—	17(none)	5.5
G-562	3.5	4.6	XVIII	11–12	9	3	1.1	1.6	2.0	1.3	80+a 45p	36(9)	12.5	28(6)	9	15(none)	6
G-724	3.7	4.0	XVI	10–11	8	4	1.0	1.3	2.5	0.9	85	33(10)	9 (P_a)	19(6)	5 (P_b)	16(none)	5.5(P_c)
G-724	3.7	4.0	XIX	—	—	—	—	—	2.2	0.9	70+	31(7)	9.5	23(9)	6	16(none)	5.0

* A plus sign (+) indicates that more than half of the arm remains attached but that some substantial length has been lost.

laubi at another. The co-occurrences of *C. m. meridionalis* with *C. meridionalis hartlaubi*, specimens intermediate between the two and specimens of *C. m. meridionalis* that at all approach *hartlaubi* in any character are limited to waters off northern Cuba and the Lesser Antilles. GERDA never collected both subspecies in the same haul nor any specimens intermediate between the two (with the possible exception of a small, slender individual from G-493—see "*Remarks*" for following subspecies).

Comactinia meridionalis hartlaubi
new name

Figures 1C, 5C, 6H–J, 11–13; Table 3

Antedon meridionalis: Pourtalès, 1878: 214 (part?).

Actinometra echinoptera variety *valida* Hartlaub, 1912: 416, 417, 418, 430–431; pl. 16, figs. 7, 8; pl. 17, fig. 10 (not *Actinometra valida* Carpenter, 1888).

Actinometra echinoptera variety *meridionalis-valida* Hartlaub, 1912: 416, 417, 418, 432; pl. 16, fig. 13; pl. 17, fig. 3 (part).

Comactinia echinoptera: A. H. Clark, 1921b: 9–11.—1931: 375–400 (pl. 42, fig. 127 and pl. 43, fig. 129 show specimens of this subspecies) (part).

Comactinia meridionalis: A. H. Clark, 1921b: 9–11, 25–28 (part).

Material examined.—LECTOTYPE: BLAKE sta. 157, Montserrat, 220 m; 1, MCZ 498. PARALECTOTYPES: BLAKE sta. 277, Barbados, 194 m; 2, MCZ 225; 4, MCZ 501. BAHAMAS: G-493, 26°32'N, 78°55'W, 183–549 m, 3 m try net, 3 February 1965; 16.—G-510, 26°07.5'N, 79°09'W, 293–329 m, 3 m try net, 2 March 1965; 1.—G-526, 26°28'N, 78°40'W, 278–329 m, 3 m try net, 3 March 1965; 1.—G-692, 26°35'N, 78°25.4'W, 329–421 m, 3 m try net, 21 July 1965; 1.—G-693, 26°34'N, 78°25.5'W, 275–293 m, 3 m try net, 21 July 1965; 1.—G-698, 26°28'N, 78°41.5'W, 165–329 m, 3 m try net, 22 July 1965; 2.—G-725, 26°00.8'N, 79°09.8'W, 143–210 m, triangular dredge, 3 August 1965; 16.—G-1329, 25°50'N, 78°22'W, 236–265 m, 3 m try net, 11 December 1971; 1 + fragments. NORTHERN CUBA: ALBATROSS coll.; 1, USNM 14698; 2, USNM 34537; 3, USNM 34538; 1, USNM 34539; 2, USNM 34540; 2, USNM 34541; 1, USNM 34542; 2, USNM 34543; 1, USNM 34544; 2, USNM 34545; 2, USNM 34546; 2, USNM 34547; 1, USNM 34548; 1, USNM 34549; 3, USNM 34552; 5, USNM 34589; 2, USNM 34590; 3, USNM 34621; 1, USNM 34637; 3, USNM 34642; 1, USNM 34826; 1, USNM 34828; 2, USNM 34889; 1, USNM 36268.—UIBE coll.; 1, USNM E-4502; 11, USNM E-9468; 1, MCZ 731; 3, MCZ 751. GULF OF MEXICO: Texas A&M 71-A-2, sta. 60, 28°03'N, 92°48'W, 90 m, 20 ft trawl, 17 May 1971; 1.—Texas A&M 71-A-10, sta. 43, 21°56'N, 97°21'W, 58 m, 20 ft trawl, 23 September 1971, 7. YUCATAN(?): 2, MCZ 502. ANTILLEAN ARC: FISH HAWK coll.; 4, USNM 21464.—BLAKE coll.; 1, MCZ 224; 2, MCZ 409; 2, MCZ 458; 1, MCZ 500.

Diagnosis.—Large and robust; centrodorsal 6 mm across in large individuals; cirri most frequently XX–XXX, 11–14, crowded, as broad distally as proximally, up to 18 mm long; LW of longest cirral usually 1.3 to 1.5; division series and arm bases usually in close lateral apposition; intersyzygial interval usually irregular, most often three to seven; proximal pinnulars of oral pinnules short and rhombic or triangular, imparting strongly serrate profile to pinnules; dorsal corner of these pinnulars sometimes strongly projecting and spinose; comb teeth rounded, separated and usually very weak; P_3 always and P_4 sometimes bearing comb; white (sometimes stained purple by sponge).

Description.—Centrodorsal large, discoidal, 4.0 to 6.6 mm across; DH 3.3 to 5.0. Cirri arranged in single or partly double (rarely, partly triple), crowded, irregular marginal row. Several small, newly developing cirri often present. Polar area flat and smooth, occasionally with weak interradial ridges or paired lines radiating from flat, raised or depressed central area; polar area rarely slightly convex, pitted or covered with traces or obsolete cirrus sockets.

Cirri large and strong, usually XX–XXX, 11–14 (extremes: XIV–XXXIX, 9–15), up to 18 mm long, as broad distally as proximally, sometimes slightly broader and somewhat laterally compressed distally. Fourth cirral (rarely, third) longest; LW 1.3 to 1.6 (usually only to 1.5; in a small specimen, LW reaches 1.9). Following cirrals decreasing very gradually in length; distal cirrals as long as broad or slightly longer; penultimate cirral squarish; opposing spine small, conical, erect, sometimes reduced; terminal claw curved and longer than preceding cirral; occasionally a weak dorsal tubercle developed on antepenultimate cirral.

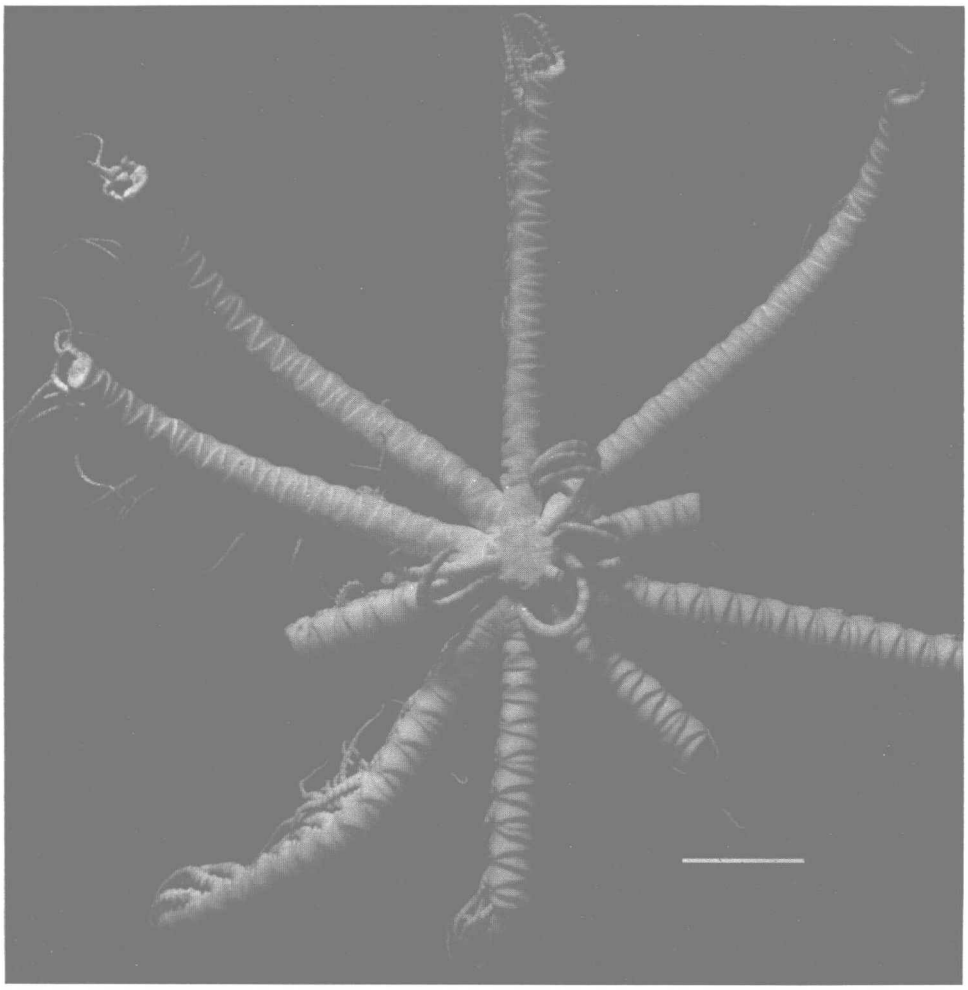


Figure 11. *Comactinia meridionalis hartlaubi* new name. G-693. Scale: 1 cm.

Basal rays hidden or visible as tubercles bridging deep but very narrow subradial clefts which often are absent.

Radials visible only in interradial angles or, less often, hidden by centrodorsal; in some small individuals, entire distal edge of radials just visible; radial articular face narrowest across interarticular ligament fossae; dorsal ligament fossa slightly wider than muscular fossae.

Division series short, closely apposed, often wall-sided and dorsally flattened; close apposition often extending to Br_1 exteriorly and to Br_{3+4} interiorly; in smaller and less robust individuals, division series ossicles and arm bases dorsally rounded and slightly separated. IBr_1 very short, oblong, laterally united, partly (rarely, completely) hidden by centrodorsal, occasionally slightly inflated laterally; WL 3.2 to 5.0; in a single specimen, IBr_1 bearing a small, median tubercle. IBr_2 triangular; WL 2.0 to 2.3.

Arms 50 to 170 mm long, robust, broadening slightly from the base to about Br_{10} before tapering beyond about Br_{20} or tapering directly from base. Posterior arms about half as long as anterior arms; all arms of similar width and appearance proximally.

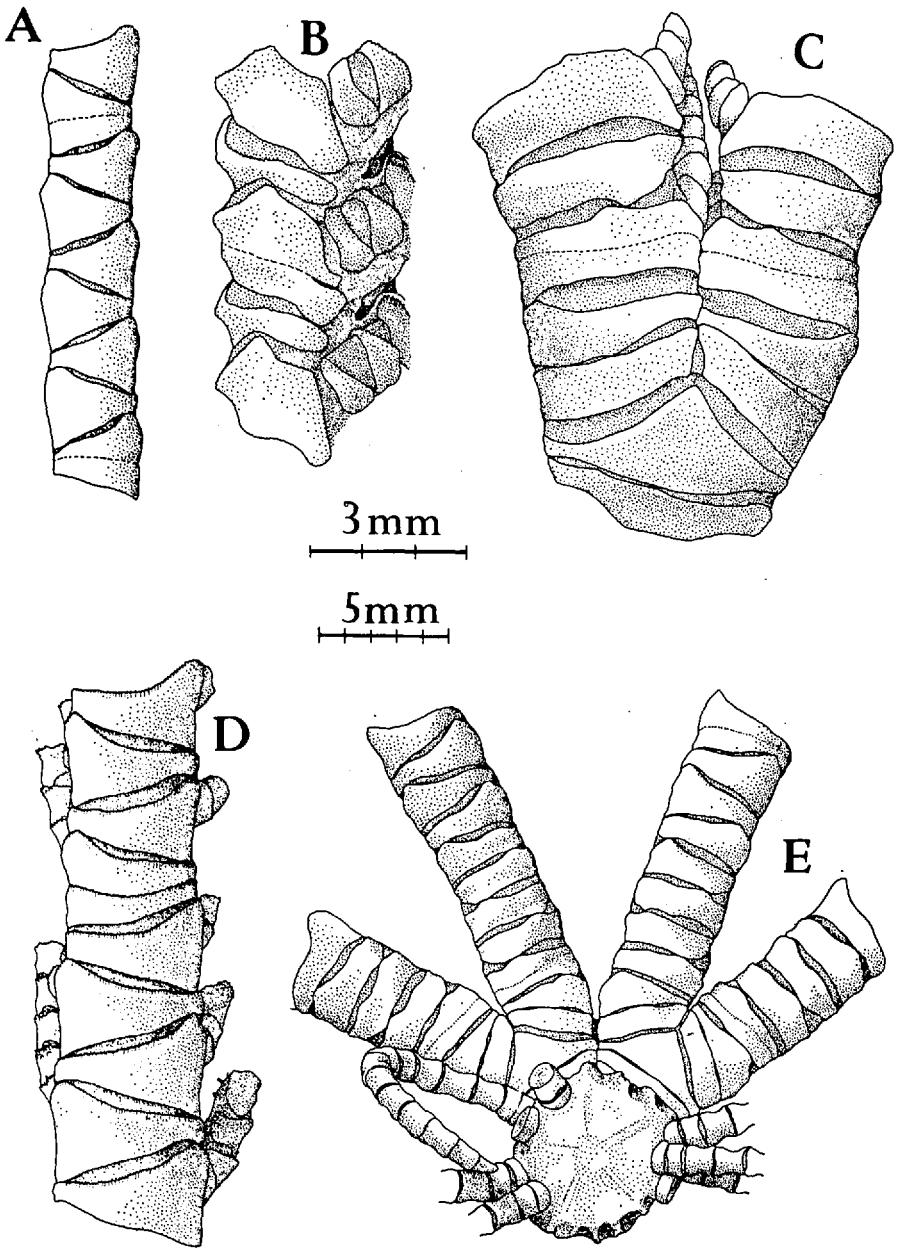


Figure 12. *Comactinia meridionalis hartlaubi* new name. A. Distal brachials in dorsal view, G-725. B. Proximal brachials in lateral view, G-698. C. Proximal part of one postradial series showing close interior apposition of brachials, G-526. D. Middle brachials in dorsal view, G-725. E. Centrodorsal, cirrus and proximal part of two rays in dorsal view, G-693. Scales: A–D—3 mm; E—5 mm.

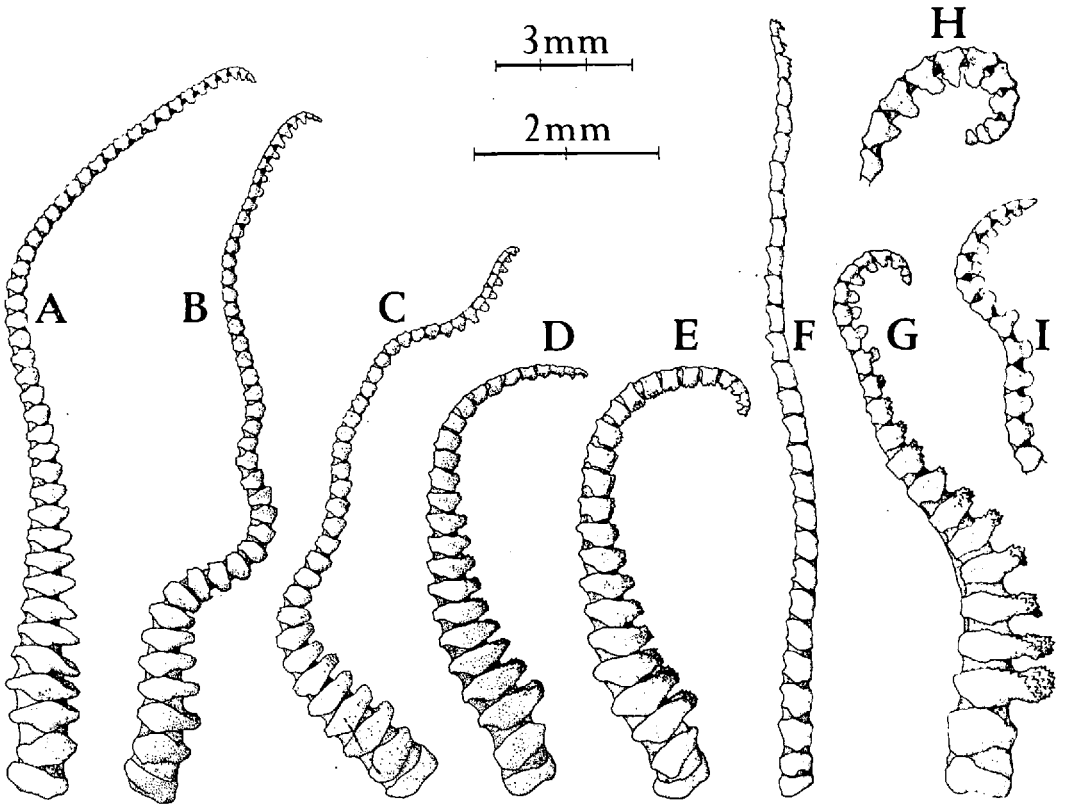


Figure 13. *Comactinia meridionalis hartlaubi* new name, pinnules. A. P_a, G-693. B. P_b, same specimen and arm. C. P_c, same. D. P_d, same. E. P_e, same. F. P_{distal}, same. G. P_3 bearing strong, spinose, dorsal projections, G-493. H. Comb on P_4, G-510. I. Comb on P_1, G-493. Scales: A–F—3 mm; G–I—2 mm.

Br_1 short, slightly wedge-shaped or oblong, united interiorly; WL 3.0 to 4.2. Br_2 short, almost triangular, longer exteriorly, usually flattened and apposed interiorly; WL 3.0 to 3.8 (2.6 in a small specimen). Br_{3+4} oblong, only slightly longer than either Br_1 or Br_2, dorsally rounded, apposed or separated interiorly, 1.5 to 4.0 mm across; WL 2.4 to 3.6; the syzygial articulation often sinuous. Br_5 to Br_7 short and oblong; WL 2.4 to 3.6. Brachials triangular by Br_9 or Br_{10}, remaining uniformly triangular far out on arm; WL 1.6 to 2.7; brachials near arm tip wedge-shaped or elongate. Proximal and middle brachials with distal edges raised and finely spinose; dorsal surface of arms smooth beyond Br_{30} or Br_{40}. Proximal brachials usually possessing well-developed alternating articular tubercles. In small specimens, only a few proximal brachials (about Br_{10} to Br_{15}) triangular—the rest wedge-shaped—and the middle brachials sometimes with distal edges strongly everted. One specimen (G-493) possessing 11 arms; single IIBr2 series present.

Syzygies at Br_{3+4} (rarely, Br_{4+5}), almost always at Br_{11+12} or Br_{12+13} (extremes: Br_{10+11} to Br_{16+17}); subsequent intersyzygial interval irregular, usually three to seven (extremes: two to 15). One specimen bearing Br_{1+2}, Br_{8+9} and Br_{15+16} on one arm; in another individual, Br_{10+11} the first syzygy on one arm; Br_{1+2} present on both arms arising from IIBr series of 11-armed specimen.

P_1 up to 23 mm long with as many as 52

pinnulars; comb short, composed of five to 12 rounded, separated, usually weak teeth. P_2 similar to P_1 but shorter, up to 20 mm long with 48 pinnulars and usually with one or two more comb teeth. P_3 similar to P_2 but occasionally much shorter. P_4 usually shortest; comb present or absent. Subsequent pinnules increasing in length to distal maximum of 23 mm with 34 pinnulars (distal pinnules usually slightly shorter than P_1).

Proximal pinnulars (excepting basal two) of oral and some middle pinnules triangular or rhombic, projecting dorsally and giving pinnules strongly serrate profile; dorsal projections sometimes very strong and spinose, strongest on pinnules immediately following orals and weakening beyond about P_{15}. Most pinnulars on oral pinnules short; distal pinnulars longer than broad but appearing short due to presence of comb teeth; pinnulars longer than broad in distal third of P_6 and distal half of P_{10}. Distal pinnules smooth, slenderer than middle pinnules and with all pinnulars except basal two or three longer than broad; distal pinnulars of these pinnules sometimes extremely elongated. Comb teeth occasionally as high as width of pinnulars bearing them, thin and fragile, rarely parabolic or very short and truncated; in some small individuals, combs better developed and, on P_2, sometimes occupying entire distal half of pinnule.

Mouth marginal and interradial (in right anterior interradius—interradius A–B); anal cone central; disk usually bearing sparsely scattered nodules; infrequently, nodules densely covering anal cone and interambulacral area.

Color.—White or very pale tan; stained purple when preserved with certain sponges; whether the comatulids and sponges occur together in life is unknown.

Holotype.—None formally designated. Hartlaub (1912:431) wrote; "Am ausgeprägtesten zeigen die Charaktere der Varietät zwei Exemplare von Dominica oder Guadeloupe M.C.Z. 409, vier von Barbados, 106 fms. BLAKE 277, M.C.Z. 225, 501, zwei mit verlorener Etiquette, wahrscheinlich von 23°52′N. und 88°W. oder 25°N. und 84°W M.C.Z. 502?, und ein Exemplar von Montserrat 120 Faden BLAKE 157, M.C.Z. 498." I have designated the last named specimen as lectotype.

Ecology.—Though larger, this subspecies probably lives much like the preceding: clinging to a hard substrate with the arms extended and the pinnules arranged in a monoplanar orientation. Plate 43, fig. 129 of A. H. Clark (1931) illustrates a typical specimen of *hartlaubi* attached to a small piece of rock.

Geographic distribution.—Gulf of Mexico; Bahamas; Antillean Arc from the north coast of Cuba to Carriacou and Barbados; Caribbean coast of Colombia; Surinam.

Bathymetric distribution.—Possible: 58 to 549 m. Confirmed: 58 to 373 m. For the GERDA collection the possible range is 143 to 549 m and the confirmed range is 210 to 329 m. The few shallow records of this subspecies come from the Gulf of Mexico and the southern Caribbean (see discussion below).

Derivation of name.—Hartlaub (1912) established the name *Actinometra echinoptera* variety *valida* for this robust comatulid. According to Article 45-d-i and 45-e-i of the International Code of Zoological Nomenclature (1964:45), the original status of this name is subspecific rather than infrasubspecific. According to Article 46, then, *Actinometra echinoptera* variety *valida* Hartlaub (1912) is a junior homonym of *Actinometra valida* (Carpenter (1888) [= *Comanthus timorensis* (Müller, 1841)] and, therefore, must be renamed. I have here established the new name *Comactinia meridionalis hartlaubi* for Clemens Hartlaub who first recognized it as a distinct form; *hartlaubi* is masculine. The new combination, with *meridionalis* rather than with *echinoptera*, more clearly demonstrates the

Table 3. Numerical data for 12 specimens of *Comactinia meridionalis hartlaubi* new name collected by R/V GERDA

Station Number	CENTRODORSAL		CIRRI						ARMS			P_1		P_2		P_3	
	Diam. (mm)	DH	No.	Cirrals	Max. Length (mm)	Longest Cirral	Longest Cirral Length (mm)	Longest Cirral LW	Width Br_{3+4} (mm)	LD	Length (mm)	No. Pinnulars (No. Comb teeth)	Length (mm)	No. Pinnulars (No. Comb teeth)	Length (mm)	No. Pinnulars (No. Comb teeth)	Length (mm)
G-725	2.3	3.3	XXII	9–10	8.5	3–4	1.2	1.9	1.5	1.3	30+	28(10)	7.5	22(12)	5	13(none)	4
G-698	4.3	4.0	XVIII	11	—	—	—	—	2.5	1.0	50	33(7)	11.5	—	—	—	—
G-493	4.9	4.0	XXV	11–12	10.5	4	1.2	1.3	3.1	1.2	75+	40(5)	15	31(7)	10	28(6)	10
G-493	5.1	4.7	XIX	12–13	14.5	4	1.4	1.5	2.7	0.8	125+	37(9)	13	32(10)	11	21(7)	6.5
G-493	5.4	4.4	XXV	11–12	11	3	1.4	1.5	2.9	0.9	170	—	—	—	—	23(11)	14
G-493	5.4	3.9	XXII	9–13	13	4	1.4	1.5	2.8	0.8	80+	40(6)	16	33(9)	12.5	26(7)	9
G-725	5.4	4.4	XXX	12–14	17	4	1.7	1.6	3.0	0.9	—	—	—	—	—	—	—
G-692	5.8	4.8	XXV	12–15	16	4	1.4	1.5	3.2	0.8	90+	32(6)	14.5	29(11)	11.5	31(14)	11
G-725	6.2	5.0	XXVI	12–14	13.5	4	1.4	1.5	2.9	0.9	80+	—	—	—	—	—	—
G-526	6.5	4.2	XXVIII	13–14	15	4	1.5	1.4	3.1	0.8	70++	37(8)	14	31(10)	10	28(9)	9
G-693	6.6	4.3	XXVII	14–15	14.5	4	1.5	1.4	3.5	0.7	170	45(8)	18.5(P_a)	44(8)	16.5(P_b)	38(9)	14.5(P_c)
G-510	6.6	3.3	XXXIX	11–14	18	4	1.6	1.3	4.0	0.8	70++	42(9)	18	—	—	31(8)	13

relationship of this form to the other members of the genus.

Remarks.—In Table 3, several important characters are listed for a number of GERDA specimens. The USNM and MCZ material chiefly agrees with these. Some deviations from the typical form of this subspecies are as follows.

The intersyzygial intervals (following the second syzygy) of a few specimens from G-493 and G-725 are chiefly three and four with longer intervals infrequent. These specimens are in the minority at both stations. One very small, slender specimen from G-493 with cirri XVI, 10–11, has the intersyzygial interval 5–10.

A number of specimens (the smallest from USNM 34537 and 34538, one from USNM 34543, MCZ 410 and MCZ 458) have intersyzygial intervals of 3–4, 4, or 4–5. The USNM specimens were collected off Havana and the MCZ specimens off Barbados.

The smallest USNM 21464 specimen (centrodorsal diam 3.2 mm) has division series apposed and wall-sided and long irregular intersyzygial intervals (4–7), but has cirri XVII, 10.

One of the two USNM 34540 specimens lacks a comb on P_3 on at least most of its arms.

The USNM and MCZ collections contain material identified by me as *C. meridionalis hartlaubi* from about 30 station localities. *Comactinia meridionalis meridionalis* was also taken at three of these stations (although the *C. m. meridionalis* at one of these stations approach *hartlaubi* in some respects—see below), specimens intermediate between the two subspecies were also taken at three stations and both *C. m. meridionalis* and an intermediate individual were also taken at one. Again, the two subspecies and the intermediate individuals occur together only off Havana and the southern Lesser Antilles.

Comactinia meridionalis MATERIAL INTERMEDIATE BETWEEN THE TWO NOMINATE SUBSPECIES OR

INDETERMINATE. NORTHERN CUBA: ALBATROSS coll.; 1, USNM 34549; 1, USNM 34588; 2, USNM 34589; 3, USNM 34590; 1, USNM 34638; 1, USNM 34642; 1, USNM 36267. OFF YUCATAN: BLAKE coll.; arm fragments, MCZ 434. LESSER ANTILLES: FISH HAWK coll.; arms, USNM 21465, 21466.—BLAKE and HASSLER colls.; 1, MCZ 224; 1, MCZ 410; 3, MCZ 455; 1, MCZ 457; arms, MCZ 499.—Prob. BLAKE coll. but no locality; 1, MCZ 414. "HONG KONG": 1, MCZ 445—see A. H. Clark, 1931:394.

Remarks.—USNM 34549: The smaller of two specimens approaches *C. m. hartlaubi* in having the intersyzygial interval 4–5 and combs on P_1–P_3 (although not on P_c), but the cirri are typical of the deeper water form of *C. m. meridionalis.*

USNM 34588: This is probably a small *C. m. hartlaubi.* The division series are apposed and wall-sided; brachials short and distally everted; cirri XVII, strong, of at least 11 cirrals, with longest having LW 1.1–1.2; centrodorsal diam 3.1 mm.

USNM 34589: Of the total of seven specimens in this lot, five are *C. m. hartlaubi.* The remaining two are smaller and broken. One of these is probably *hartlaubi* but is too fragmented to determine with certainty. The other is 3.5 mm across the centrodorsal with an intersyzygial interval of 3–4; perhaps a robust *C. m. meridionalis.*

USNM 34590: Three of the five specimens have centrodorsals 3.2–3.3 mm across; cirri XVII–XX, 11–12, up to about 7 mm long with LW of the longest cirral 1.7, division series and arm bases apposed, LD 1.1, intersyzygial interval 3–4; dorsal pinnular projections present but not typical of *hartlaubi*; comb present or absent on P_3. These specimens appear closer to *C. m. meridionalis.* The other two specimens in this lot are *hartlaubi.*

USNM 34638: One specimen generally intermediate between the two subspecies. The other specimen in this lot is a robust *C. m. meridionalis.*

USNM 34642: An intermediate specimen lacking cirri, with arms broken but with intersyzygial interval 3. This is the only lot (and station—ALBATROSS 2159) in which an intermediate and both subspecies are all found together.

USNM 36267: Centrodorsal and radial pentagon only and in poor condition. Probably *C. meridionalis.*

USNM 21465: Arms only; identification uncertain.

USNM 21466: Arms only, with dorsal stripe. Perhaps *C. m. meridionalis.*

MCZ 434: Arm fragments with intersyzygial interval 4–5. Probably *C. meridionalis.*

MCZ 224: One specimen intermediate; robust but with division series slightly separated; comb present or absent on P_3; pinnules strongly produced dorsally; cirri of 10–11 cirrals; intersyzygial interval 3–4. The other specimen is *C. m. hartlaubi.*

MCZ 410: Probably *C. m. hartlaubi* but badly broken, single remaining cirrus of 10 cirrals and intersyzygial interval 4.

MCZ 455: Three specimens all intermediate. All robust and moderately large; comb present on P_3 and pinnules typical of *hartlaubi*, but with division series slightly separated. Intersyzygial interval 3–4 on one, 4–6 on another.

MCZ 457: Specimen badly broken, small but robust; could belong to either subspecies.

MCZ 499: Unidentifiable arm fragments.

MCZ 414: Very small specimen; centrodorsal about 0.6 mm across, cirri XII, 10–11, about 3 mm long, arms about 8 mm long. Probably *C. m. meridionalis.*

MCZ 445: Small specimen; only centrodorsal, division series and arm bases remain. No complete cirri or pinnules. Identity uncertain.

Of the nine stations at which intermediate specimens were collected, four also included *C. m. hartlaubi*, one also included *C. m. meridionalis* and one also included both subspecies. The specimens from two other stations of these nine are probably *hartlaubi* although they differ somewhat from the characteristic form of this subspecies.

Discussion.—Comactinia meridionalis is polytypic. The Caribbean and Carolinian

populations of the shallow water form are isolated from each other. Though specimens from these two areas usually differ in certain characters (see *C. m. meridionalis* "*Remarks*" but note Nicaragua specimen), it is not known whether they represent distinct genotypes, differing from each other and from the deeper water form, or phenotypes responding to particular environments and genetically continuous with the common deeper water *C. m. meridionalis* which occurs throughout the region. Since most of the distinguishing characteristics of the shallow water form appear to be the result of environmental stresses, I have not separated it from the deeper water *C. m. meridionalis*.

The magnitude and nature of the morphological differences separating the deep-water *C. m. meridionalis* from *C. m. hartlaubi* are similar to those separating the shallow- from the deep-water form of *C. m. meridionalis*. On this basis, *hartlaubi* does not merit subspecific status. However, the differences that distinguish *hartlaubi* are not obviously related to environmental demands. Combining this with distribution, *hartlaubi* does merit subspecific status. In the Straits of Florida, *C. m. meridionalis* rarely occurs as deep as 200 m while *C. m. hartlaubi* rarely occurs as shallow as this (GERDA records). Specimens of *hartlaubi* collected by the R/V PILLSBURY in the southern Caribbean have a considerably shallower depth range than the GERDA material (possible: 92–348 m, confirmed: 99–174 m). However, only two of the 12 PILLSBURY records are definitely from less than 100 m, indicating that *C. m. hartlaubi* occurs significantly deeper than *C. m. meridionalis* here as well. (A third record, from very shallow water, is questionable.) The two subspecies were collected together at one PILLSBURY station with a narrow depth range (P-403) but a large number of *C. m. meridionalis* were collected at the previous station. Specimens are commonly caught in the belly of the trawl and are only recovered on subsequent stations. Of the approximately 125 stations from which I have examined material of *C. meridionalis*, both subspecies and/or intermediates occur at less than 10%. These two subspecies, then, are essentially bathymetrically allopatric. Further, *C. m. meridionalis* occurs on both sides of the Straits of Florida while *C. m. hartlaubi* is restricted to Bahamian and Cuban slopes.

Comactinia meridionalis hartlaubi is not the only comatulid that occurs in shallower water in the southern Caribbean than in the Straits of Florida. *Leptonemaster venustus* and *Hypalometra defecta* both occur primarily shallower than 100 m in the southern Caribbean and deeper than this in the Straits. In addition, *Neocomatella pulchella*, which occurs chiefly between 200 and 400 m in the Straits, has been collected in 10 m off Panamá (Meyer, 1973b).

It does remain possible that these two subspecies are merely ecological variants. A comparison of the smallest specimen in Table 3 with a specimen of similar centrodorsal width in Table 2 illustrates that small individuals may not be as readily referrable to subspecies as large ones (although the tables do not shown such characters as arm base apposition and pinnule ornamentation). Also, the shallow ocurrence of *C. m. hartlaubi* in the western Gulf of Mexico suggests that colder temperatures could be at least in part responsible for the development of this subspecies. Nevertheless, the distinctive morphology of *C. m. hartlaubi* is certainly not as obviously related to environmental factors as the shallow water *C. m. meridionalis*. In any case, the determination of the true status of all of the forms of *C. meridionalis* requires developmental and genetic studies.

ACKNOWLEDGMENTS

I thank the following people for their assistance in connection with this paper. Drs. F. M. Bayer and G. L. Voss made the GERDA material available to me and, with Drs. L. P. Thomas and D. R. Moore, supervised my thesis work on the GERDA comatulids. Dr. D. Pawson (National Museum of Natural History, Washington, D.C.) and Dr. H. Levi (Museum of Comparative Zoology, Harvard) provided access to the collections at their respec-

tive institutions. R. DuBois and R. Defenbaugh (Texas A&M University), involved in research on the echinoderms of the western Gulf of Mexico, generously provided specimens from their collections. Dr. W. Kirby-Smith (Duke University) loaned specimens from the EASTWARD collections. Drs. D. B. Macurda, Jr. (University of Michigan) and D. L. Meyer (University of Cincinnati) provided specimens from Panamá and the Bahamas and fueled a lively and greatly appreciated correspondence. Miss A. M. Clark (British Museum, Natural History) critically read my thesis, which contained some of this work. I was supported for 3 years by a National Science Foundation research traineeship during which period much of this work was completed. This is a contribution from the Rosenstiel School of Marine and Atmospheric Science, University of Miami.

LITERATURE CITED

Agassiz, A. 1864. Contrib. Nat. Hist. U.S., 5: 79. (Cited from A. H. Clark, 1931: 376.)

Agassiz, E. C., and A. Agassiz. 1865. Seaside studies in natural history. Marine animals of Massachusetts Bay. Radiates. Ticknor and Fields, Boston. viii + 155 pp.

Carpenter, P. H. 1879. On the genus *Actinometra* Müll., with a morphological account of a new species (*A.*) *polymorpha* from the Philippine Islands.—Part 1. Trans. Linn. Soc. Lond., (2) 2: 1–222; 8 pls.

———. 1881. Reports on the results of dredging under the supervision of Alexander Agassiz, in the Gulf of Mexico (1877–78), in the Caribbean Sea (1878–79), and the east coast of the United States (1880), by the U.S.C.S. Str. "Blake," Lieut.-Commander C. D. Sigsbee, U.S.N., and Commander J. R. Bartlett, U.S.N. Commanding. XVI. Preliminary Report on the Comatulae. Bull. Mus. Comp. Zool., Harvard 9: 151–169; 1 pl.

———. 1888. Report upon the Crinoidea collected during the voyage of H.M.S. Challenger during the years 1873–1876. Part II.—The Comatulae. Report on the scientific results of the voyage of H.M.S. Challenger 1873–1876, 26: ix (+1) + 399 (+5); 70 pls. (Chall. Rep. Zool. Pt. 60.)

Clark, A. H. 1909a. Revision of the crinoid family Comasteridae, with descriptions of new genera and species. Proc. U.S. Nat. Mus. 36(1685): 493–507.

———. 1909b. On a collection of crinoids from the Copenhagen Museum. Vidensk. Medd. fra den naturhist. Forening i København. 1909: 115–194.

———. 1911a. The recent crinoids of the coasts of Africa. Proc. U.S. Nat. Mus. 40(1808): 1–51.

———. 1911b. "Thetis" scientific results. The recent crinoids of Australia. Mem. Austral. Mus. 1911: 705–804.

———. 1912a. The crinoids of the Museum fuer Naturkunde, Berlin. Proc. U.S. Nat. Mus. 43(1937): 381–410.

———. 1912b. The crinoids of the Indian Ocean. Echinoderms of the Indian Museum, Pt. 7, Crinoidea. iii + 325 pp; 61 text figs.

———. 1914a. Internationale Revue der gesamten Hydrobiologie und Hydrographie, 1914: 4 et seq. (Cited from A. H. Clark, 1931: 374.)

———. 1914b. Beitrage zur Kenntnis der Meeresfauna Westafrikas, Echinod. II, Crinoidea: 309. (Cited from A. H. Clark, 1931: 374.)

———. 1915. A monograph of the existing crinoids, 1(1). Bull. U.S. Nat. Mus. (82): vi + 406 pp; 17 pls.

——— 1921a. A monograph of the existing crinoids, 1(2). Bull. U.S. Nat. Mus. (82): xxv + 795 pp; 57 pls.

———. 1921b. Report on the crinoids collected by the Barbados-Antigua Expedition from the University of Iowa in 1918. Univ. Iowa Stud. Nat. Hist. 9: 3–28.

———. 1931. A monograph on the existing crinoids, 1(3). Bull. U.S. Nat. Mus. (82). vii + 816 pp; 86 pls.

Clark, A. M. 1970. Marine invertebrates of Scandinavia, 3. Echinodermata Crinoidea. Universitets forlaget, Oslo. 55 pp.

———. 1972. Some crinoids from the Indian Ocean. Bull. Brit. Mus. (Nat. Hist.), Zool. 24: 75–156.

Hartlaub, C. 1912. Reports on the results of dredging . . . by the U.S. Coast Survey Steamer "Blake" . . . XLV. Die Comatuliden. Mem. Mus. Comp. Zool., Harvard 27: 275–491; 8 pls.

International Code of Zoological Nomenclature adopted by the XV International Congress of Zoology 1964. xx + 176 pp.

Macurda, D. B., Jr., 1973. Ecology of comatulid crinoids at Grand Bahama Island. Hydrolab Jour. 2: 9–24.

———. 1975. The bathymetry and zoogeography of shallow-water crinoids in the Bahama Islands. Hydro-lab Jour. 3: 5–24.

Messing, C. G. 1975. The systematics and distribution of the Crinoidea Comatulida (exclusive of the Macrophreatina) collected by the R/V GERDA in the Straits of Florida and adjacent waters. Master's thesis, University of Miami, Coral Gables, Florida. x + 285 pp (+1).

Meyer, D. L. 1973a. Coral Reef Project—Papers in memory of Dr. Thomas F. Goreau. 10. Distribution and living habits of comatulid

crinoids near Discovery Bay, Jamaica. Bull. Mar. Sci. 23: 244–259.

———. 1973b. Feeding behavior and ecology of shallow water unstalked crinoids (Echinodermata) in the Caribbean Sea. Mar. Biol. (Berlin) 22: 105–129.

Müller, J. 1840. Monatsber. d. k. preuss. Akad. d. Wiss., p. 93. (Cited from A. H. Clark, 1931: 374.)

———. 1841. Ueber die Gattung und Arten der Comatulen. Archiv. fuer Naturgeschichte (Berlin) 7: 139–148.

Pourtalès, L. F. de. 1869. List of the crinoids obtained on the coasts of Florida and Cuba, by the U.S. Coast Survey Expeditions in 1867, 1868, 1869. Bull. Mus. Comp. Zool., Harvard 1: 355–358.

———. 1878. Report on the dredging operations of the U.S. Coast Survey Steamer "Blake." Crinoids and Corals (including: Description of a young *Holopus*). Bull. Mus. Comp. Zool., Harvard 5: 213–216; pl. 2.

Springer, F. 1920. The Crinoidea Flexibilia. 1 (text): vi + 486 pp., 2 pls.; 158 pp., 79 pls. Smithsonian Institution.

Tommasi, L. R. 1963. Notas sobre algunas crinoideos del Brasil. Neotropica 9: 95–102.

———. 1965. Lista dos crinoides recentes do Brasil. Contrcoes Inst. oceanogr. Univ. S. Paulo, ser. Ocean. biol. 9: 1–33.

DATE ACCEPTED: January 31, 1977.

ADDRESS: *Rosenstiel School of Marine and Atmospheric Science, 4600 Rickenbacker Causeway, Miami, Florida 33149.*