Three new species of Comasteridae (Echinodermata, Crinoidea) from the tropical western Pacific

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ABSTRACT
Three new species of unstalked crinoids (Echinodermata, Crinoidea) belonging to the comasterid genera *Comactinia* A. H. Clark, 1909, *Capillaster* A. H. Clark, 1909 and *Cenolia* A. H. Clark, 1916 from depths of 73-310 m, are described. *Comactinia titan* n. sp., from the Philippines and New Caledonia, which bears thicker arms than any other comasterid, is the first representative of its genus recorded outside the tropical western Atlantic. *Capillaster squarrosus* n. sp., from Vanuatu, resembles *C. multiradiatus* (Linnaeus, 1758) but has uniquely modified arms. *Cenolia amezianeae* n. sp., from southern New Caledonia and Vanuatu, resembles its congeners but bears combs on pinnules as far as P_{19} (rather than just to P_4 as in other *Cenolia*), which requires an emendation of the generic diagnosis.

KEY WORDS
Echinodermata,
Crinoidea,
Comatulida,
Comasteridae,
Indo-Pacific,
new species.

RÉSUMÉ
Trois nouvelles espèces de Comasteridae (Echinodermata, Crinoidea) du Pacifique occidental tropical.
Trois espèces nouvelles de crinoïdes non pédonculés (Echinodermata, Crinoidea) attribuées aux trois genres *Comactinia* A. H. Clark, 1909, *Capillaster* A. H. Clark, 1909 et *Cenolia* A. H. Clark, 1916 de la famille des Comasteridae, sont décrites. Ces trois espèces ont été récoltées à des profondeurs allant de 73 à 310 m. *Comactinia titan* n. sp., des Philippines et de Nouvelle-Calédonie, est le premier représentant de son genre signalé en dehors de l'Atlantique tropical occidental et possède les bras les plus larges de tous les Comasteridae. *Capillaster squarrosus* n. sp., du Vanuatu, ressemble à *C. multiradiatus* (Linnaeus, 1758) mais présente des modifications originales des caractères des bras. *Cenolia amezianeae* n. sp., du sud de la Nouvelle-Calédonie et du Vanuatu, porte un peigne sur les pinnules jusqu'à la P_{19} contrairement aux autres espèces du genre qui ne portent un peigne que jusqu'à la P_4. Ces observations entraînent une modification de la diagnose du genre *Cenolia*.

MOTS CLÉS
Echinodermata,
Crinoidea,
Comatulida,
Comasteridae,
Indo-Pacifique,
nouvelles espèces.

INTRODUCTION

Members of the Comasteridae A. H. Clark, 1908, a taxon of unstalked crinoids (comatulids, or feather stars), typically account for at least half the crinoid species found in shallow-water (< 50 m) surveys in the tropical western Pacific Ocean (Meyer & Macurda 1980; Messing 1994, 1998). With increasing depth, however, comasterid richness declines both absolutely and relatively as other families (i.e., Antedonidae Norman, 1865; Thalassometridae A. H. Clark, 1908; Charitometridae A. H. Clark, 1909; Colobometridae A. H. Clark, 1909; Calometridae A. H. Clark, 1911, and Asterometridae Gislén, 1924) become more abundant and diverse. Of the 107 comatulid species recorded from the East Indian Archipelago (Indonesia, Malaysia, Papua New Guinea and the Philippines) in 100-1000 m, only 12 are comasterids (Messing *et al.* 2000; Messing 2001). This paper adds three new comasterids to this deeper fauna, all collected during expeditions to the western Pacific mounted by IRD (Institut de Recherche pour le Développement, Paris; formerly ORSTOM, Office de Recherche scientifique et technique d'Outre-Mer). Several other papers based on these collections have contributed importantly to our understanding of this crinoid fauna (Roux 1981; Améziane-Cominardi *et al.* 1990; Bourseau *et al.* 1991; Améziane 1997; Messing *et al.* 2000), but this is the first one to describe new members of the Comasteridae. A recent detailed treatment of comasterid morphology can be found in Messing (2001). For authorship citations of previously described taxa, please consult A. H. Clark (1931), Rasmussen & Sieverts-Doreck (1978), Hoggett & Rowe (1986) and Rowe *et al.* (1986).

ABBREVIATIONS

Br	division series (or brachitaxis): a series of ossicles following a radial ossicle or branching point (axil) and including the next axil; a preceding Roman numeral indicates the location beginning with the most proximal (IBr); a following Arabic numeral indicates the number of ossicles in the series (e.g., IBr2);
br (plural: brr)	individual ossicle of a division series or undivided arm. An Arabic subscript indicates location in a sequence (e.g., $IIbr_2$: the second ossicle of the second brachitaxis; br_6: the sixth ossicle of an undivided arm [following the distalmost axil]);
c	cirral (cirrus segment), numbered from the base (i.e., c1);
D/H	diameter to height ratio of the centrodorsal;
L/W, W/L	length-to-width and width-to-length ratios of ossicles, measured midaborally;
P	pinnule; the short segmented side branches of the arms; an Arabic or letter subscript indicates a specific pinnule beginning with the most proximal (e.g., P_1, P_a) along the exterior or interior side of the arm, respectively; a Roman subscript indicates a pinnule on a brachitaxis (e.g., P_{II} on the second brachitaxis);
+	indicates a syzygial articulation (e.g., IIBr4(3+4): a second brachitaxis of four ossicles with the third and fourth joined by syzygy; br_{3+4}: the third and fourth ossicles of an undivided arm joined by syzygy);
AM	Australian Museum, Sydney;
CRI	Oceanographic Center, Nova Southeastern University, Dania Beach, Florida, Comatulid crinoid catalogue;
MNHN EcCs	Muséum national d'Histoire naturelle, Paris; Echinoderm, Comatulid crinoid catalogue, dry specimens;
MNHN EcCh	Muséum national d'Histoire naturelle, Paris; Echinoderm, Comatulid crinoid catalogue, specimens preserved in alcohol;
USNM	National Museum of Natural History, Smithsonian Institution, Washington DC.

SYSTEMATICS

Family COMASTERIDAE A. H. Clark, 1908
Genus *Comactinia* A. H. Clark, 1909

Comactinia titan n. sp.
(Fig. 1)

HOLOTYPE. — **Philippines.** MUSORSTOM 3, stn CP121, 12°08'S, 121°17'E, 73-84 m, 3.VI.1985 (MNHN EcCh 186).

PARATYPES. — **Philippines.** MUSORSTOM 3 (no data) (MNHN EcCh 185).
New Caledonia. SMIB 5, stn DW100, 23°23.9'S, 168°05.4'E, 80-120 m, 14.IX.1989 (MNHN EcCs 10234).

ETYMOLOGY. — From the Greek *titan*, one of a family of mythological giants that ruled the earth until overthrown by the Olympian gods; now, more broadly, one of gigantic size or power, a reference to the great thickness of the arms of this species relative to those of other comatulids.

DISTRIBUTION. — Known only from the Philippines and New Caledonia in 73-84 m (possibly to 120 m). The specimen lacking data was found in a jar with a label for RV *Coriolis* stn 116. However, the depth at this station was 804-812 m and the accompanying specimens included *Asterometra longicirra* (Carpenter, 1888), typical of 200-300 m, and *Comatella nigra* (Carpenter, 1888), characteristic of < 50 m. The correct label is thus considered lost. RV *Coriolis* occupied all 54 MUSORSTOM 3 stations in the vicinity of Mindoro Island.

DIAGNOSIS. — A species of *Comactinia* reaching extremely large size, with proximal arms bearing strong alternating articular tubercles and reaching a diameter of 5 mm; cirri up to XXXVI in number, up to 31.4 mm in length with 22 segments; proximal segments of proximal pinnules smooth and cylindrical or rounded rhombic; combs tapering to a point, present to P_5 in large specimens.

DESCRIPTION

Centrodorsal discoidal, up to 10.0 mm across; polar area flat or slightly concave, smooth, up to 7.6 mm across. Polar area of small specimen with crescentic traces of obsolete sockets.

Cirri of large specimens XXVII-XXXVI (up to X regenerating), 16-22, maximum length 31.4 mm, in crowded single and partly double marginal row. Proximal cirrals cylindrical; c1 short; following segments increasing in length to c5-7; L/W of longest cirral 1.0; following cirrals gradually shorter and slightly compressed with L/W becoming 0.8, sometimes wider than proximal cirrals. Distal 2-3 cirrals preceding penultimate slightly narrower and more elongated, L/W 1.0-1.1; antepenultimate distally polished; penultimate cirral smaller than preceding, L/W 0.9-1.1, with erect conical opposing spine; claw curved, longer than penultimate cirral. Small specimen with cirri XXII, 14-15, up to 13.2 mm long; c4 longest, L/W 1.4; antepenultimate cirral with a weak aboral tubercle.

Radials visible in interradial angles or completely hidden by centrodorsal. Single tip of basal ray possibly visible under edge of centrodorsal in one interradius of one specimen. IBr2 short, apposed laterally and flattened aborally, joined by close synarthry (possibly cryptosynarthry). Ibr_1 oblong with diverging lateral margins, partly hidden by centrodorsal in the two large specimens; W/L *c.* 5.0 in small specimen. Ibr_2 (axil) pentagonal with short diverging lateral margins, or triangular; W/L 1.9-3.0. Lateral aboral margins of brachitaxes ossicles and exterior lateral margins of proximal few arm ossicles thickened and covered with superficial pale reticulated stereom. Articulations between brachitaxes ossicles and proximal brachials also sometimes covered with pale yellowish tissue that obscures articulations.

Arms 10; anterior arms longer; small specimen with anterior ray length 145 mm and posterior 65 mm. Large paratype with posterior ray length 137 mm; anterior rays broken at 140 mm. Arms of holotype broken at 110 mm or less; longest arm fragment tapering rapidly near broken tip as in posterior arms of small specimen. An apparently anterior arm (remaining ray length 100 mm) is 2.5 mm across at its broken tip. A comparison with the small specimen suggests that the holotype's intact anterior ray length may have reached 300 mm.

Arm ossicles (except brr_{1-2} and slender distalmost ossicles) with convex lateral margins; middle brachials with thickened distal margins, the combination making each ossicle appear swollen. Brachials from brr_{2-5} to brr_{9-13} (br_2 to brr_{5-7} in small specimen) with well developed alternating articular swellings. br_1 oblong (slightly longer exteriorly in small specimen), united interiorly; W/L 3.0-4.4. br_2 longer exteriorly and with P_1 articulation clearly visible in aboral view; W/L 2.6-3.1. Exterior lateral margins of both br_1 and br_2 thickened, apposed and flattened against ossicles of adjacent rays; midaboral surface of brr_{1-2} with low synarthrial swelling. br_{3+4} short, oblong; syzygial articulation usually sinusoidal; W/L 2.3-

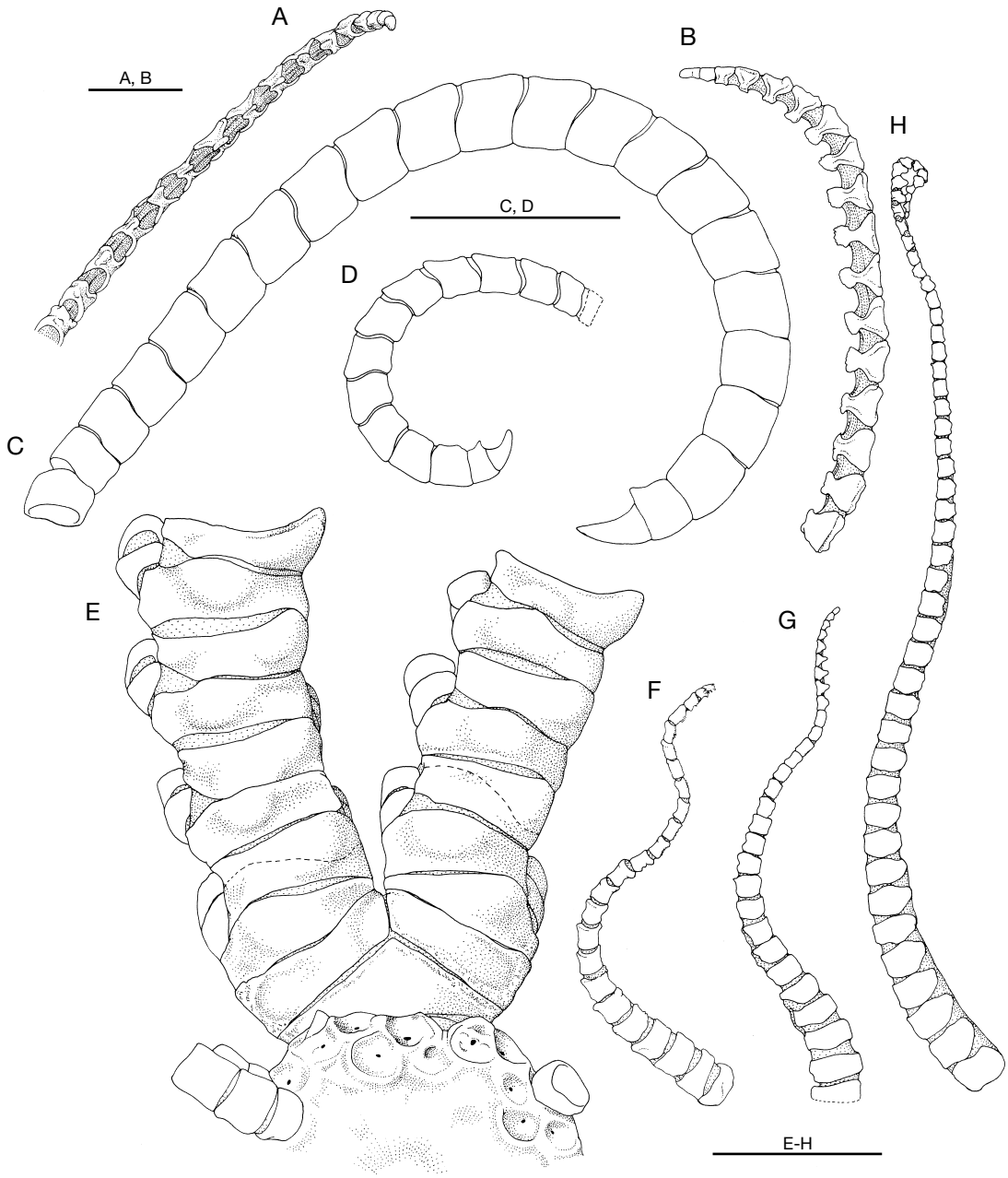

FIG. 1. — *Comactinia titan* n. sp.; **A**, **B**, P_1 pinnule comb in aboral (**A**) and lateral (**B**) views (MNHN EcCh 185); **C**, cirrus (MNHN EcCh 186); **D**, cirrus (MNHN EcCs 10234); **E**, portion of centrodorsal and base of one ray (with abnormal br_{4+5} on right arm) (MNHN EcCh 186); **F**-**H**, pinnules (MNHN EcCh 186); **F**, P_{14}; **G**, P_5; **H**, P_1. Scale bars: A, B, 1 mm; C-H, 5 mm.

3.0; diameter 2.5-4.0 mm. One to several following brachials short, oblong; W/L 2.8-3.8. Following few brachials cuneate, becoming triangular with smooth, thickened distal margins concave in aboral view (with fine short tooth-like spines in the small specimen). Middle brachials short, triangular, with distal margins as in preceding brachials; W/L 2.8-4.1. Some arms of larger specimens distinctly wider in middle than at base, up to 5.0 mm across. Brachials becoming cuneate distally, proportionally not as short as middle brachials; lateral margins not as convex; distal margins neither concave nor thickened; W/L 1.5-2.5.

First syzygy at br_{3+4} (br_{4+5} on one arm of large paratype); second chiefly at br_{11+12}, but varying from br_{8+9} to br_{24+25}. Following interval widely variable with no uniform pattern; chiefly 4-5 (rarely 3, 7 or 8) in small specimen. In the holotype, second syzygies between br_{8+9} and br_{12+13} chiefly followed by two to five intervals of 4-7 muscular articulations each, with intervals of chiefly 8-9 thereafter. In the large paratype, two to three intervals following second syzygies at br_{10+11} or br_{11+12} consist of four or five articulations and intervals of 6-10 thereafter. Intervals following a second syzygy at br_{23+24} or br_{24+25} are chiefly 11-12; arm with br_{4+5} followed by intervals of 17, 17, 8 and 12 muscular articulations.

Proximal pinnules decreasing in length from P_1 to P_4 or P_5, robust proximally, slender and flagellate distally. P_1 of up to 52 segments, 33.4 mm long, with up to 13 low, separated, nonconfluent teeth with flat or rounded apical profiles; fully developed teeth often slightly displaced toward one lateral margin; two or three distal pinnulars with diminishing teeth, tapering to a terminal pinnular that lacks a tooth. Proximal pinnulars cylindrical (rounded rhombic in the small specimen), wider than long; middle segments cylindrical and about as long as wide; distal segments preceding comb slightly constricted with L/W 1.5-1.7. Large specimens with all segments smooth. P_1 of small specimen with 32 segments and six teeth, 16.1 mm long, with numerous very short spines on lateral margins of pinnulars facing arm tip.

P_2 similar to P_1, up to 51 segments, 32.4 mm long, with up to 16 teeth; the longest segments preceding the comb shorter than in P_1, L/W 1.2. P_2 distinctly shorter than P_1 in small specimen. P_3 similar to P_2 but not quite as wide across the base, 44 segments, 26.9 mm, 15 teeth; proximal teeth short and flat-topped; more distal teeth rounded and proportionally taller than on preceding pinnules; distal three pinnulars tapering to point. P_3 on small specimen much shorter and less robust than P_2, 18 segments, 8.4 mm, six teeth (the first rudimentary). P_4 up to 36 segments, 21.5 mm, with 13 teeth (not including two rudimentary initial teeth); small specimen with P_4 of 12 segments, 6.8 mm long, no comb and with distal pinnulars compressed and longer than wide. P_5 with or without comb in large specimens; comb-bearing P_5 of up to 28 segments, 16.5 mm, with eight teeth (including tapering final three pinnulars); P_5 without comb of up to 23 segments, 16.5 mm; proximal pinnulars short and cylindrical as in preceding pinnules; middle segments squarish; distal segments longer than wide, compressed and with fine spines on lateral margin facing arm tip.

Middle pinnules longer than those immediately following oral pinnules, of up to 33 segments, 20.3 mm; basal few pinnulars short, following segments squarish with distal adambulacral margins thickened; distal segments slender and elongated, L/W to 2.4. Distal pinnules more slender than middle pinnules, up to 26 segments, 16.1 mm; pinnulars beyond basal few longer than wide; distal pinnulars in small specimen with L/W up to 3.0.

Mouth marginal; anus central; tegmen naked.

Color of rays (preserved) tan or pinkish tan with short bands of darker faded purple. Cirri and pinnules tan. One large specimen with distal cirrals dark brown; the other with the proximal parts of the rays faded purple. The small specimen is faded pink.

Discussion

At a maximum diameter of 5 mm, *C. titan* n. sp. has thicker, more massive arms than any other comasterid. The arms actually appear wider

because the distance from the left side of one brachial to the right side of the succeeding brachial is slightly greater than the diameter of each brachial. The species is placed in *Comactinia* because it shares with the other two members of the genus – *C. meridionalis* (Agassiz, 1865) and *C. echinoptera* (Müller, 1841) – the following diagnostic features: 10 arms; IBr2 series joined by synarthry; first brachial syzygy at br_{3+4}; mouth excentric, and oral pinnule combs consisting of nonconfluent, often off-center, single teeth flattened along the pinnule axis. *C. titan* n. sp. also shares with *C. meridionalis* terminal oral pinnulars that taper to a point, and short cirrals of similar length, almost completely lacking any aboral ornamentation. The small specimen of *C. titan* n. sp. shares with some specimens of *C. echinoptera* a weak, rudimentary aboral spine on the antepenultimate cirral (Messing 1978; Messing & Dearborn 1990). Apart from its longer cirri with more numerous segments and strongly developed alternating articular tubercles, both of which may derive simply from its much greater size, *C. titan* n. sp. differs from the other two in having the proximal segments of the oral pinnules smooth and cylindrical or rounded rhombic. In *C. meridionalis*, these ossicles are spinose, rhombic and sometimes strongly projecting; in *C. echinoptera*, the basal pinnulars of the oral pinnules bear rounded keels.

With the addition of *C. titan* n. sp., *Comactinia* becomes the only comasterid genus known from the tropical western regions of both Atlantic and Pacific oceans. *Antedon* de Freminville, 1811 (family Antedonidae Norman, 1865) is the only other comatulid genus known from shelf depths in both regions, but it is far more widespread, also occurring in European and West African waters. The possibility exists that *C. titan* n. sp. is convergent rather than congeneric with the two Atlantic species, especially given the relatively generalized features of the genus (i.e., 10 arms, excentric mouth, IBr2 with a synarthry, and first syzygy at br_{3+4}). However, *C. titan* n. sp. exhibits no characteristics that place it outside the genus as currently construed.

Genus *Capillaster* A. H. Clark, 1909

Capillaster squarrosus n. sp.
(Fig. 2)

HOLOTYPE. — **Vanuatu.** MUSORSTOM 8, stn DW1071, 15°37'S, 167°16'E, 180-191 m, 4.X.1994 (MNHN EcCh 189).

PARATYPES. — **Vanuatu.** MUSORSTOM 8, stn DW1021, 17°43'S, 168°37'E, 124-130 m, 28.IX.1994 (MNHN EcCh 188); stn DW1086, 15°37'S, 167°16'E, 182-215 m, 5.X.1994 (MNHN EcCh 187); stn DW1071, 15°37'S, 167°16'E, 180-191 m, 4.X.1994 (MNHN EcCh 190).

ETYMOLOGY. — From the Latin *squarrosus* meaning "rough with stiff scales" (Brown 1956), a reference to the scaly roughened appearance in naked-eye view of arm ossicles from brr_{6-10} to brr_{20-25}.

DISTRIBUTION. — Known only from Vanuatu in 130 to about 180 m (possibly 215 m). Two specimens identified as *Capillaster multiradiatus* (Linnaeus, 1758) by A. H. Clark (1931) from the Kei Islands, Indonesia, in 20-85 m, may represent this species (see below).

DIAGNOSIS. — A small species of *Capillaster* (ray length up to *c.* 100 mm) with up to 20 arms; cirri with up to 30 segments, 21.0 mm long; brachials brr_{6-10} through brr_{20-25} triangular, distinctly wider than those preceding, swollen and with strongly thickened spinose distal margins, so that the proximal half of the arm appears distinctly roughened, scaly and up to 1.5 times wider than the arm base in naked-eye view; pinnule combs present to about P_{16-19}.

DESCRIPTION

Centrodorsal discoidal, often with sloping sides, 4.0-5.4 mm across; D/H 3.4-4.0. Polar area faintly depressed or convex; larger specimens with five faint interradial swellings radiating from around a shallow central depression.

Cirri XX-XXVIII, 23-30, up to 21.0 mm, in single or partly double crowded marginal row. Larger specimens have fewer cirri; c1 short; following cirrals increasing in length to c5; c4 with L/W 0.8-1.1; c5 longest, transitional, with oral margin slightly concave and with slightly raised dentate distal aboral margin, L/W 1.3-1.8. Following cirrals polished, becoming shorter, compressed, squarish by c9, shorter than wide thereafter with L/W 0.8-0.9. Cirrus slightly tapered distally; distal 2-3 cirrals preceding claw

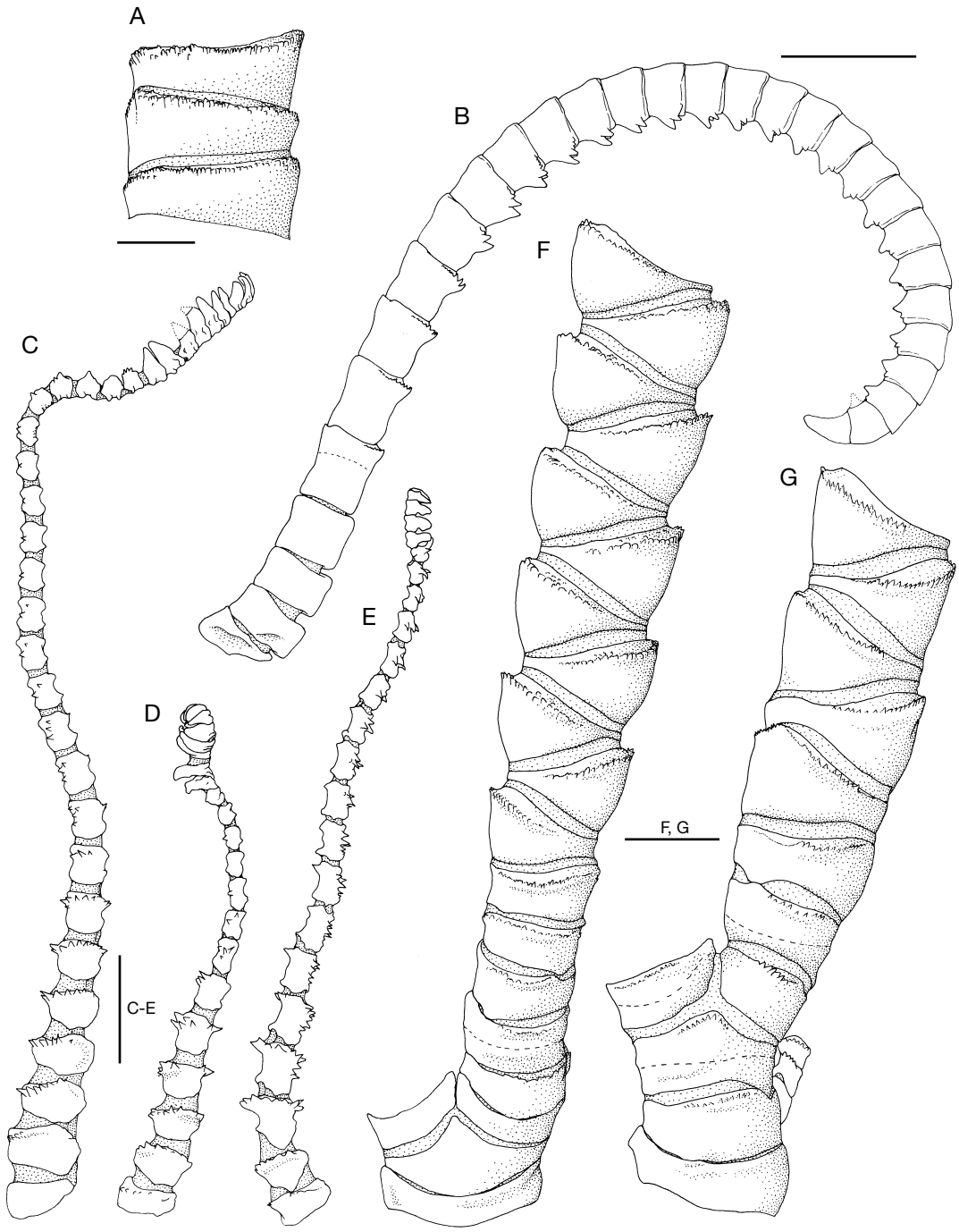

FIG. 2. — **A**, *Capillaster multiradiatus* (Linnaeus, 1758), brr_{9-11}, 09°45'N, 118°42'E, 18 m, 17.IV.1995, Messing coll. (CRI-014); **B**-**G**, *Capillaster squarrosus* n. sp.; **B**, cirrus (MNHN EcCh 189); **C**, P_{II} (MNHN EcCh 187); **D**, P_2, same; **E**, P_{19} (MNHN EcCh 189); **F**, IBr2 and proximal part of one arm (MNHN EcCh 188); **G**, IIBr4(3+4) plus proximal part of normal arm (right) with br_{2+3}, and abnormal arm base with br_{1+2} (left) (MNHN EcCh 189). Scale bars: A, C-E, 1 mm; B, F, G, 2 mm.

sometimes with L/W 1.0. Raised, dentate aboral distal margin of c5-6 becoming strong curved midaboral spine flanked by one to three pairs of smaller spines by c7-9; flanking spines usually reduced to single pair on distal cirrals, but sometimes disappearing beyond about c20; strong midaboral spine becoming erect on distal cirrals. Opposing spine erect and sharp; penultimate cirral squarish, smaller than preceding cirrals, without flanking spines; claw longer than penultimate cirral.
Distal margin of radials just visible beyond centrodorsal margin, more visible in interradial angles; distal margin concave, slightly concave in smaller specimens. Brachitaxes aborally convex, with or without weak midaboral synarthrial swellings. Ibr_1 short, oblong or shallow U-shaped in aboral view, united and sometimes slightly inflated laterally, with slightly diverging lateral margins; W/L 4.0-5.6 (MNHN EcCh 190 with lateral margins united only proximally and converging distolaterally; W/L 3.9). Ibr_2 (axil) almost triangular (lateral margins extremely short), apposed or separated laterally; W/L 1.8-2.4. IIBr series chiefly 4(3+4); $IIbr_1$ short, oblong, united interiorly, sometimes with a few small midaboral spines; $IIbr_2$ cuneate or almost triangular, longer exteriorly, with a strongly thickened and finely spinose aboral distal margin, and with W/L 2.3-3.1. $IIbr_{3+4}$ pentagonal, the distal angle thickened and finely spinose; W/L 1.8-1.9. MNHN EcCh 188 bearing two IIBr2 on one ray, resembling IBr2 but smaller; MNHN EcCh 189 with 7 IIBr4(3+4) and 3 IIBr3(2+3).
Arms 12-20; ray length 85-102 mm. Some arms sometimes distinctly broader at the base than others. Distal aboral margins of brachials thickened and finely spinose. On arms arising from IBr series, br_1 and br_2 both longer exteriorly; br_1 united interiorly, with W/L 2.9-3.2; br_2 longer than br_1, with W/L 2.5; br_{3+4} oblong, W/L 2.2-2.5 and 2.1-2.5 mm across. On arms arising from IIBr series, br_1 oblong or cuneate, united interiorly, with W/L 1.4-1.9; br_{2+3} oblong, with W/L 1.7-2.1 and 1.8-2.4 mm across. br_4 and br_5 usually oblong and no wider than br_{2+3}, sometimes slightly cuneate and wider; W/L 2.0-2.6. Following brachials cuneate, becoming distinctly wider, swollen and almost triangular with strongly thickened, spinose distal margins and distinctly darker articulations by brr_{6-10}; W/L 2.3-2.6. Widest brachials 1.2-1.3 times diameter of arm base, but up to 1.5 times when measured across the combined width of two successive brachials. Brachials gradually diminishing in width beyond about br_{20}, reduced to same diameter as arm base by about brr_{25-28}; the combination of swollen brachials and dark narrow articulations giving the proximal half of the arm a distinctly roughened, scaly appearance in naked-eye view. Following middle brachials smaller, narrower, less swollen, not as strongly cuneate, with weaker distal thickening; W/L 2.2-2.6. Distal brachials short, weakly cuneate; distal margins finely spinose but only slightly thickened; W/L 1.5-2.1. Brachials near arm tip almost oblong or squarish.
Syzygies on arms arising from IBr series at br_{3+4}, br_{11+12} to br_{14+15}, and at intervals of 4-6 muscular articulations thereafter. On arms arising from IIBr series, syzygies at br_{2+3}, br_{10+11} to br_{20+21}, and at intervals of 5-8 (rarely 9) thereafter. Some arms tend to have two longer intervals (7-9) following the second syzygy and shorter intervals (5-6) thereafter.
P_{II} of up to 33 segments, 14.2 mm, with nine tall triangular teeth. Proximal several pinnulars wider than long with expanded, spinose distal rims; middle segments with L/W 1.8-1.9, only slightly shorter than proximal pinnulars, but much narrower and centrally constricted, with distal spines disappearing by mid-pinnule and only a single strong, conical, lateral spine remaining on distal segments preceding comb. Several pinnulars just preceding comb shorter and wider, with L/W 1.6. P_1 sometimes similar to P_{II}, of up to 34 segments, 11 teeth, 11.8 mm long; sometimes slenderer and much shorter, with proximal pinnulars as long as wide by the fourth segment and middle segments with L/W 2.0-2.1. P_2 of up to 30 segments, 13 teeth, 6.6 mm. Following several pinnules similarly short but with more elongated middle segments. P_7 up to 22 segments, nine teeth, 6.1 mm; following pinnules gradually becoming longer. Combs present to about P_{16-19}.

Middle pinnules of up to 24 segments, nine teeth, 7.3 mm; proximal few pinnulars (sometimes excepting the short first) with expanded, spinose distal rims; middle pinnulars with cluster of spines on side facing arm tip, L/W 1.8; pinnulars preceding comb with two or three strong lateral spines arranged in a transverse row. Distal pinnules slender, up to 22 segments, 7.4 mm; pinnulars beyond basal two longer than wide, centrally constricted and with one or a few lateral spines, L/W 2.4-2.7.

Disk naked, anus central, mouth excentric. Anal cone and surrounding interambulacral area with small, scattered papillae in one specimen.

DISCUSSION

Hoggett & Rowe (1986) include seven species in *Capillaster*. *C. macrobrachius* (Hartlaub, 1890) bears a small stellate centrodorsal lacking cirri, and *C. asterias* A. H. Clark, 1931 bears a few cirri composed of elongated segments that taper to a fine tip. The remaining species have more than 10 cirri with distal cirrals shorter than proximal cirrals. Of these, *C. sentosus* (Carpenter, 1888) and *C. gracilicirrus* A. H. Clark, 1912 bear more than 40 (often more than 60) arms, while the remaining three (*C. mariae* (A. H. Clark, 1907), *C. multiradiatus* (Linnaeus, 1758) and *C. tenuicirrus* A. H. Clark, 1912) rarely have more than 30. *C. mariae* differs from *C. multiradiatus* in having perfectly smooth brachitaxes (division series) and a mottled disk lacking any calcareous nodules. However, the distinctions among several of these species remain unclear. A. H. Clark (1931) mentions five specimens of *C. multiradiatus* (out of 214) with 40-43 arms and seven specimens of *C. sentosus* (out of 32) with fewer than 37 arms. Although cirri are typically ≤ 25 mm long with ≤ 25 segments in the former and greater than this in the latter, he also refers to individuals of *C. multiradiatus* with cirri of up to 27 segments or up to 30 mm long. No other features are known to distinguish the two. *C. gracilicirrus* differs from *C. sentosus*, and *C. tenuicirrus* differs from *C. multiradiatus*, only in having distal cirrals slightly longer than broad rather than broader than long. However, A. H. Clark (1931) placed the type of *C. borneensis* (Grube, 1875) as a synonym of *C. multiradiatus* rather than *C. tenuicirrus* despite its having cirrals longer than broad from the fifth onward.

Capillaster squarrosus n. sp. most closely resembles *C. multiradiatus* but differs consistently as follows. *C. squarrosus* n. sp. has a distinctive series of swollen triangular proximal brachials (Fig. 2F, G) whereas the same ossicles in *C. multiradiatus* are short and resemble the following brachials (Fig. 2A). The cirri in *C. squarrosus* n. sp. consist of more cirrals at a shorter length than in *C. multiradiatus*. Finally, pinnule combs occur as far as $P_{4\text{-}10}$ (rarely P_{15}) in *C. multiradiatus* and as far as $P_{16\text{-}19}$ in *C. squarrosus* n. sp. Two specimens briefly described by A. H. Clark (1931: 188, 189; probably in the Zoologisk Museum, Copenhagen, but Clark listed no catalogue numbers) as *C. multiradiatus* may represent *C. squarrosus* n. sp., although both were collected in shallower water than the specimens described above. One (Danish Kei Islands Expedition, stn 40, 25.IV.1922, 25 m, T. Mortensen coll.) has 19 "unusually stout" arms that "increase in width to about the twentieth brachial, where they are twice as broad as at the base"; cirri of 29-30 segments, 22 mm long, and pinnule combs present to near the arm tips, though "becoming more and more reduced". The other (stn 53, 8.V.1922, 85 m) has 15 arms (140 mm; longer than in *C. squarrosus* n. sp.), and cirri of 31-32 segments, 25-30 mm long. Its largest cirri are similar to those of several *C. sentosus* examined, but the latter have many more arms (33-80). Likewise, a specimen of *C. sentosus* with cirri similar to those of *C. squarrosus* n. sp. also has many more arms (60).

Genus *Cenolia* A. H. Clark, 1916

TYPE SPECIES. — *Comatula trichoptera* Müller, 1846.

DIAGNOSIS. — A genus of Comasteridae with IBr2 joined by synarthry; first brachial syzygy at br_{3+4} on all arms; brachitaxes beyond IBr usually 4(3+4), any series of two ossicles occurring irregularly; P_1 on br_2; pinnule combs usually present as far as P_4, sometimes to P_{19}, consisting of pairs of straight teeth of more or less

equal size, each confluent with the pinnular margin; teeth of a pair sometimes joined to form a transverse bar; aboral surface of disk not heavily plated; mouth excentric (emended from Rowe *et al.* 1986).

REMARKS

Cenolia amezianeae n. sp., described below, differs from all species previously assigned to *Cenolia* in having combs present on pinnules distal to P_4. Instead, combs occur to between P_8 and P_{19}, although one or two more proximal pinnules sometimes lack one. It also differs in having usually rod-shaped calcareous nodules on the disk and proximal arm ambulacra, although tegminal deposits vary within the genus, and these may be similar to the small spines reported around the anal cone in *C. tasmaniae* (A. H. Clark, 1918). *C. amezianeae* n. sp. shares with the other five members of the genus all other diagnostic features.

Cenolia amezianeae n. sp.
(Fig. 3)

HOLOTYPE. — **South New Caledonia.** CHALCAL 2, stn CH05, 24°44'S, 168°08'E, 223 m, 27.X.1986 (MNHN EcCh 191).

PARATYPES. — **South New Caledonia.** CHALCAL 2, stn CH05, 24°44'S, 168°08'E, 223 m, 27.X.1986 (MNHN EcCh 192, 1).
Vanuatu. MUSORSTOM 8, stn CP970, 20°19'S, 169°53'E, 252-310 m, 21.IX.1994 (MNHN EcCs 10235); stn CP1018, 17°53'S, 168°25'E, 300-301 m, 27.IX.1994 (MNHN EcCs 10236, 1).

ETYMOLOGY. — Named for Nadia Améziane, Curator of Echinoderms at the Muséum national d'Histoire naturelle, Paris, who has contributed substantially to our understanding of crinoid systematics and through whose good offices this collection was made available for study.

DISTRIBUTION. — Known only from off southern New Caledonia and Vanuatu in 223 to 300 m. *C. amezianeae* n. sp. occurs in more tropical waters than other *Cenolia*, but the gap between its southernmost record and the northernmost previous records is only a few degrees of latitude. Rowe & Gates (1995) recorded *Cenolia spanoschistum* (H. L. Clark, 1916) and *C. glebosus* Rowe, Hoggett, Birtles & Vail, 1986, from southern Queensland; McKnight (1977) recorded *C. trichoptera* (Müller, 1846) (probably *C. spanoschistum* according to Rowe *et al.* 1986) from Norfolk Island in 310 m.

DIAGNOSIS. — A species of *Cenolia* with stout cirri of up to 17 short segments; distal cirrals each bearing a transverse aboral ridge; up to 20 arms; pinnule combs occurring as far as P_8 to P_{19}, though one or two more proximal pinnules may lack a comb, and with numerous chiefly rod-shaped calcareous nodules on anal interambulacral area, along ambulacra of proximal arms and, sparsely, along genital pinnule ambulacra.

DESCRIPTION

Centrodorsal discoidal, usually with small, triangular, orally-directed interradial processes, 7.9-10.3 mm across; D/H 3.4-4.1. Polar area with faint interradial swellings radiating from around shallow central depression. Apical margins of cirrus sockets project above polar area in one specimen.

Cirri XXXII-XLI, 14-17, up to 15.6 mm long, in crowded double marginal row. c1 short; following segments increasing in length to c5-6, which have L/W 1.1-1.4; following segments progressively shorter, becoming as wide as long by c7-8 and shorter thereafter. c6-7 with distal aboral margin thickened, appearing rounded triangular in lateral view, increasing slightly in strength and moving to middle of segment in side view on distal cirrals, becoming a sharp, transverse ridge on 1-2 cirrals preceding penultimate on some cirri. Penultimate cirral smaller than preceding; opposing spine weak or distinct, conical or rounded, occasionally transversely chisel-shaped. Claw longer than preceding segment; tip bluntly rounded.

Radials completely hidden by centrodorsal or just visible in interradial angles. IBr2 short, aborally flattened; Ibr_1 very short, oblong, united laterally, partly hidden by centrodorsal; Ibr_2 (axil) triangular or with very short diverging lateral margins, apposed or just separated laterally, with W/L 2.2-2.3. IIBr4(3+4) present on at least some rays of all specimens (one IIBr2 on MNHN EcCh 192). $IIbr_1$ short, oblong, united interiorly; W/L 3.3-3.4. $IIbr_2$ triangular (longer exteriorly), with a strong, distolateral, alternating articular tubercle; W/L 3.0-3.9. $IIbr_{3+4}$ pentagonal with slightly diverging lateral margins and W/L 1.5-1.75; each ossicle with a distinct transverse groove across the aboral surface. Specimen MNHN EcCs 10235

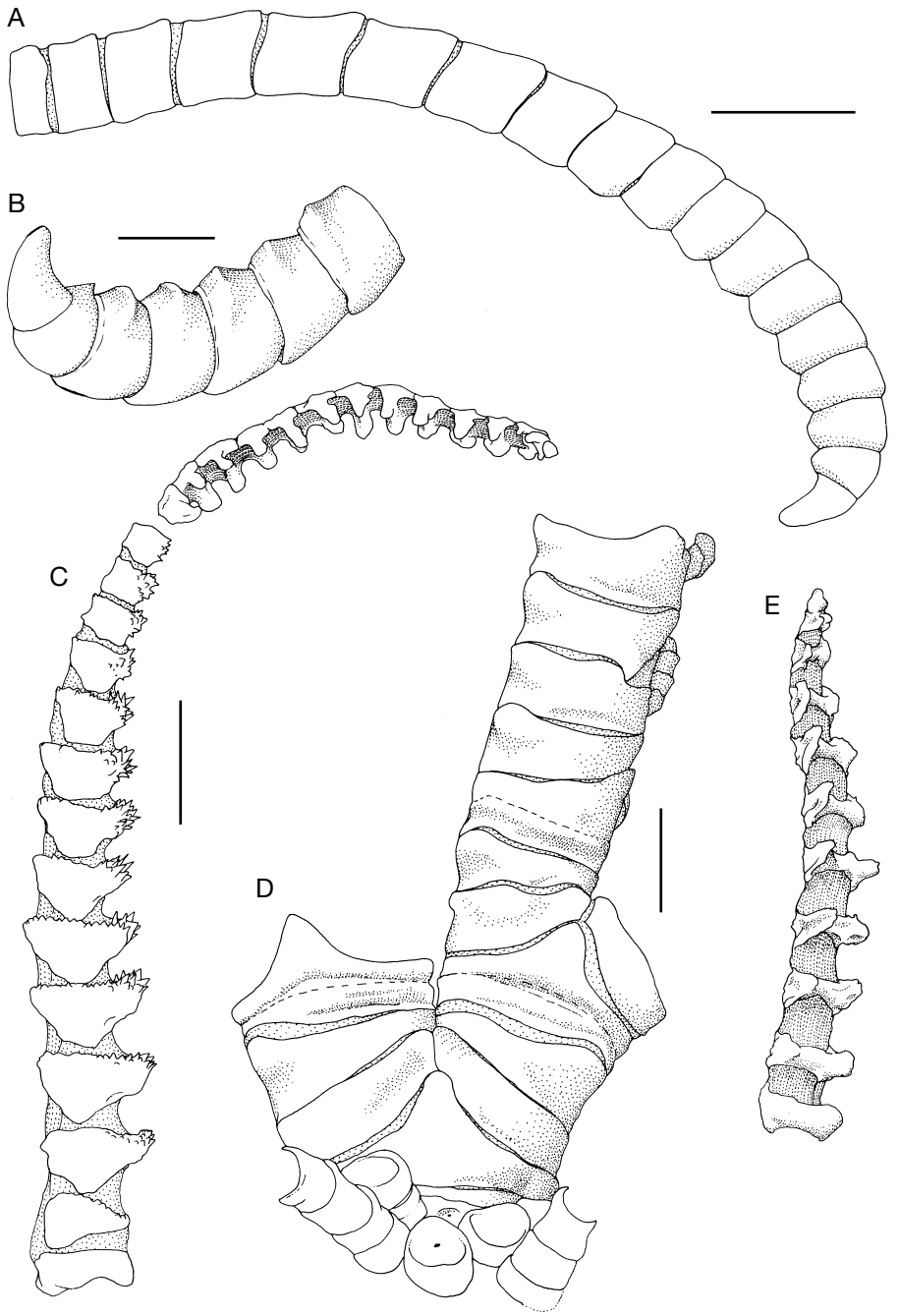

FIG. 3. — *Cenolia amezianeae* n. sp.; **A**, cirrus (MNHN EcCh 192); **B**, cirrus tip showing transverse aboral ridges (MNHN EcCs 10236); **C**, P_{14} (comb detached and viewed obliquely to show paired teeth) (MNHN EcCh 191); **D**, centrodorsal margin with bases of cirri and base of one ray with proximal part of one arm (MNHN EcCh 191); **E**, P_h pinnule comb, oblique aboral view (MNHN EcCs 10235). Scale bars: A, D, 2 mm; B, C, E, 1 mm.

bearing six rays: four rays normal; two remaining rays with short IBr2 crowded together and with adjacent margins closely united and irregular.
Arms 14-20, mostly broken. (Arm numbers in specimens with rays broken at their bases are estimated by comparing the diameters of terminal remaining ossicles with those of $IIbr_2$ and br_2). Specimen MNHN EcCh 192 with an almost intact posterior arm (ray length 85 mm); its longest anterior ray broken at 98 mm. Proximal several brachials with strong, rounded, alternating articular swellings. br_1 oblong or weakly cuneate and longer exteriorly, interiorly united proximally (adjacent interior distolateral margins diverging from each other so that br_2 are separated interiorly), with W/L 2.3-2.7; br_2 longer exteriorly, with W/L 3.0-3.7; br_{3+4} oblong, with W/L 2.0-2.5 and diameter 1.9-2.6 mm (on arms arising from IBr2, W/L 3.2; diameter 2.8-3.1 mm); br_3 with a shallow groove running transversely across the aboral surface; brr_{5-6} oblong, with W/L 2.3-2.8. Following brachials becoming strongly cuneate, slightly wider than arm base, and almost triangular by br_9, with W/L 2.7; brachials brr_{8-10} and following with thickened distal aboral margins. Middle brachials triangular with strongly thickened and very finely spinulose distal aboral margins; W/L 2.3-2.7. Distal brachials triangular or strongly cuneate with distal aboral margins finely spinose; thickening of distal aboral margins reduced beyond mid-arm and disappearing distally.
First arm syzygy at br_{3+4}; second chiefly from br_{11+12} to br_{14+15} (rarely br_{7+8} to br_{17+18}); following interval chiefly 4-6 muscular articulations (rarely 3, 7, 9).
P_{II} of up to 52 segments, 17.8 mm long, with 7-10 comb teeth; all pinnulars rhombic and wider than long; proximal two teeth developed as transverse filled arches (the transverse bars of Rowe *et al.* 1986); following teeth erect, confluent, separated and paired; distal three pinnulars diminishing to a blunt tip. P_1 of up to 50 segments, 17.6 mm, with 10-12 teeth; comb as in P_{II} but with up to 4 proximal transversely oriented teeth and up to 4 terminal pinnulars tapering to a point. Several comb-bearing pinnulars in a row sometimes having the teeth on one side weaker than on the other; a single confluent tooth rarely developed on the opposite face of a pinnular bearing a normal pair, producing a bipectinate profile (these two features occurring on any oral pinnule).
P_2 of up to 34 segments, 10.3 mm, 14 teeth; comb-bearing pinnulars on this and succeeding pinnules flat and transversely broadened so that the teeth of a pair are widely separated and sometimes connected by a low narrow ridge. P_3 the shortest pinnule, bearing a gonad, of up to 26 segments, 7.8 mm, 12-15 teeth; third to sixth or seventh pinnulars of this and following pinnules strongly projecting laterally, giving proximal pinnule a strongly serrate profile on the side facing the arm tip. P_4 of up to 28 segments, 10.0 mm, 17 teeth. Following pinnules similar; combs present to between P_{14} and P_{19} (only to P_8 or P_9 in MNHN EcCs 10236), but one or two more proximal pinnules sometimes without comb. Middle pinnules of up to 30 segments, 8.8-11.5 mm, 13-14 teeth. Distal pinnules slender; proximal and middle segments with distal spinose rim; no strong lateral projections; pinnulars following the third longer than wide, with L/W up to 1.6.
Anus central; mouth marginal; numerous chiefly rod-shaped calcareous nodules on large inflated anal interambulacral area, along ambulacra of proximal arms and with a few along ambulacra of genital pinnules. Nodules also round, irregular, club-shaped or slender conical, and sometimes concentrated on anal tube.

DISCUSSION

Cenolia amezianeae n. sp. shares with *C. spanoschistum* transverse aboral ridges (or bars, Rowe *et al.* 1986) on the distal cirrals and no more than 20 arms. However, *C. spanoschistum* is apparently a smaller, less robust species with a centrodorsal reaching only 5 mm across (A. H. Clark 1931). Specimens with centrodorsals 3-4 mm across (AM J11075, TAS 212) have mature gonads, 20 arms, ray length 40-70 mm, and longest cirral (c4) with L/W up to 3.0. Unlike *C. amezianeae* n. sp., the brachitaxes in *C. spanoschistum* (and its synonym *C. novaezelandiae* (A. H. Clark, 1918)) are smooth and lack both alternating articular tubercles and transverse grooves.

The holotype of *Cenolia benhami* (A. H. Clark, 1916) (USNM 38684) has a large centrodorsal (9.5 mm across) similar to that of *C. amezianeae* n. sp., but has LXVII cirri up to 23 mm long with 24-27 segments. Although it has more arms (28) than *C. amezianeae* n. sp., the ossicles of the brachitaxes are proportionally more elongated (a feature expected of smaller specimens); W/L of $IIbr_{3+4}$ is 1.4 in *C. benhami* and 1.8 in *C. amezianeae* n. sp. Brachitaxes ossicles are smoothly rounded as in *C. spanoschistum*. Also unlike *C. amezianeae* n. sp., the distal cirrals in *C. benhami* bear a curved transverse aboral ridge (that may appear weakly forked in aboral view) or tubercle. The opposing spine is conical or weak.

Cenolia tasmaniae (A. H. Clark, 1918) differs from *C. amezianeae* n. sp. in having more arms (up to 37) at a smaller size; distal cirrals with a small pointed aboral tubercle or rounded hump; brachitaxes without alternating articular tubercles or transverse grooves, and combs only to P_2 or P_3. A. H. Clark (1931) refers to brachitaxes ossicles as everted and finely spinous in *C. tasmaniae*. Rowe *et al.* (1986) note that small spines (perhaps similar to the rods in *C. amezianeae* n. sp.?) usually occur around the anal cone. However, AM J14791, a specimen of *C. tasmaniae* similar in size to the holotype of that species (centrodorsal diameter 4.0 mm; cirrus length 9.0 mm), has smooth brachitaxes and a naked disk.

Cenolia trichoptera and *C. glebosus* both bear up to 40 arms. The former has combs as far as P_3 with 6-27 teeth consisting chiefly of filled arches (= transverse bars; see Messing 2001: fig. 5d), sometimes with some distal paired teeth. A large sexually mature specimen (AM J14408; centrodorsal diameter 7.1 mm; cirrus length 13.0 mm; 36 arms; ray length 125 mm) has smooth brachitaxes with weak alternating articular tubercles on the exterior sides of the IIBr series and on the articulation between br_2 and br_3. The comb-bearing pinnulars are not as wide and the projections on the proximal pinnulars are not as strong as in *C. amezianeae* n. sp. *C. glebosus* differs from all other *Cenolia* in having hemispherical or globular reticulate calcareous nodules on the disk.

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