



Actinometra blakei Hartlaub, 1912: resurrected and re-assigned

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Abstract

Actinometra blakei, originally described from a single specimen, was subsequently placed in synonymy, and has not been mentioned in print since 1931. This re-description was prompted by the collection of three new specimens that fit the original description. The species is assigned to *Hanshessaster* new genus, after eminent crinoid researcher Hans Hess, because *Actinometra* is a junior synonym of *Comatula* de Lamarck, 1816, to which *A. blakei* does not conform. The species cannot be assigned to any other accepted genus. The pinnule combs are similar to those of several Indo-western Pacific taxa but were previously unknown in any western Atlantic crinoid.

Keywords Crinoidea · Comatulidae · *Hanshessaster* · Taxonomy · Western Atlantic Ocean

Introduction

In his report on the feather stars collected by H.M.S. *Challenger*, Carpenter (1888, p. 301) mentioned “*Actinometra blakei*, an MS. Species of my own,” which he intended to describe and illustrate in his planned report on the specimens collected by the US Coast and Geodetic Steamer *Blake*. von Graff (1883) had previously published the name, without description but attributed to Carpenter, as the host of two myzostome worms: *Myzostoma areolatum* and *M. vastum* (both von Graff 1883), the former from *Blake* sta. 172 off Guadeloupe, and the latter from sta. 39 off Yucatán (and possibly sta. 23 off NW Cuba). However, Carpenter died in 1891 before completing the work, and the *Blake* collection was sent to Clemens Hartlaub, who described the species using Carpenter’s MS name (Hartlaub 1912). He wrote that he received no specimen labeled *A. blakei* but noted that it might have been included among specimens identified only as *Actinometra*. Hartlaub decided that a specimen collected at *Blake* sta. 171, also off Guadeloupe, and provisionally named by him *Actinometra*

echinoptera var. *multicirra*, differed enough from other varieties of *A. echinoptera* (today several species in multiple genera) to be treated as a separate species. He noted that he thought this specimen (and other similar, but unspecified, examples from Guadeloupe) was what Carpenter planned to describe as *A. blakei* (“*Immerhin glaube ich, dass Carpenter dies und ihm ähnliche Exemplare von Guadeloupe unter dem Namen Act. blakei zu beschreiben gedachte.*”) (Hartlaub 1912, p. 472). Although he described *A. blakei* as new, he listed Carpenter’s usage (as ?*Actinometra blakei* Carpenter MS) in his synonymy (p. 471). The *Blake* collection was later returned to Harvard’s Museum of Comparative Zoology, where it remains.

Clark (1915a p. 46) correctly listed Carpenter’s (1888) *A. blakei* as a nomen nudum, but indicated only “(?)” for its identity as he understood it. Subsequently, however, Clark (1931) treated both *A. blakei* Hartlaub, 1912, and *A. echinoptera* var. *multicirra* Hartlaub, 1912, from station 171 as junior synonyms of *Nemaster iowensis* (Springer 1902) [itself now a junior synonym of *Davidaster rubiginosus* (de Pourtalès 1869)]. He treated *A. blakei* Carpenter, 1888, from station 172 as *Comactinia echinoptera* (Müller 1840). This latter specimen, which is more likely *Comactinia meridionalis* (L. Agassiz, in Agassiz and Agassiz, 1865) based on its collection depth (113 m) (see Messing 1978), has apparently been lost; the *Blake* collection at Harvard includes no crinoids from station 172.

The cirri of *A. blakei*, described as very thin (“*sehr dünner*”, Hartlaub 1912, p. 472) with several proximal cirrals apparently almost four times longer than wide (his

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plate 13, Fig. 9), differ from those of any species in *Nemaster*, *Davidaster*, or *Comactinia*. In the former, the longest cirrals are about as long as wide; in the latter two, they at most slightly exceed twice as long as wide (Clark 1931; Meyer 1973). This paper describes the holotype of *A. blakei* in greater detail than in Hartlaub (1912) and includes descriptions of three additional specimens collected using the *Johnson Sea-Link II* submersible. The species is assigned to a new genus, *Hanshessaster* n. gen., because *Actinometra* is a junior synonym of *Comatula* de Lamarck, 1816, to which *A. blakei* does not conform, nor does it conform to any other accepted genus. The species bears distally tapering pinnule combs composed of non-confluent, knob-like teeth similar to those of species belonging to the Indo-western Pacific genera *Anneissia* Summers et al., 2014, and *Clarkcomanthus* Rowe et al., 1986, but previously unknown in any western Atlantic crinoid. Unlike ten-armed *A. blakei*, all species in those two genera develop more than ten arms, and usually more than 20.

Terminology follows Messing (2001) and Hess (2011). Abbreviations: IB_r2—first two ossicles of a ray following the radial ossicle (primibrachial series); IB_r1—first ossicle of the primibrachial series; Iax2 (primibrachial 2)—second ossicle, an axil at which the ray divides; br—brachial ossicle, numbered from the first following the axil; C—cirrus segment (cirral), numbered from the base; LW—length-to-width ratio of a cirrus or pinnule ossicle, with length measured along the long axis; WL—width-to-length ratio of a brachial, with length measured along the arm axis; P—pinnule (arm side branch), numbered or lettered from the most proximal along the exterior and interior side of an arm, respectively (e.g., P₂ is the second exterior pinnule; Pa is the first interior pinnule); MCZ—Museum of Comparative Zoology, Harvard University, Cambridge, MA; USNM (United States National Museum)—Department of Invertebrate Zoology, National Museum of Natural History, Smithsonian Institution, Washington, DC; ZMC—Zoologisk Museum, Copenhagen, Denmark. A + sign indicates a syzygy, an articulation between two brachials that appears externally as a perforated line (e.g., br3+4 represents the third and fourth brachials joined by syzygy).

Taxonomic section

Family Comatulidae Fleming 1828

Hanshessaster new genus

Included species *Actinometra blakei* Hartlaub 1912.

Diagnosis A genus of Comatulidae with ten arms only; centrodorsal discoidal with sockets crowded around margin in 2–3 irregular ranks. Cirri with LW of longest cirrals

(C4–5) > 3.0. Middle and distal cirrals with small distal aboral spine; opposing spine compressed, rounded triangular. Pinnule combs composed of ~9–11 knoblike, non-confluent teeth, flattened across the pinnular, arising gradually and diminishing as pinnule tapers toward tip; distal several teeth offset to one side of pinnular. Articulations between middle pinnulars on middle and distal pinnules bearing greatly enlarged muscle fossae that resemble cartoon mouse ears. Mouth central; anal papilla marginal.

Etymology The genus is named in honor of the late, eminent crinoid researcher and paleontologist, Hans Hess of Basel, Switzerland, plus the Latin *aster*, meaning ‘star’, following usage for other confamilials, i.e., *Comaster*, *Davidaster*, and *Nemaster* (Clark 1931; Brown 1954).

Distribution Bahama Islands and Lesser Antilles, at depths of 385–694 m.

Remarks The elongated cirrals, compressed opposing spine, and central mouth distinguish *Hanshessaster* from the other genera of Comatulidae (formerly Comasteridae) that include species with nonconfluent knoblike comb teeth—*Anneissia* Summers et al. (2014) and *Clarkcomanthus* Rowe et al. (1986)—both of which are restricted to the Indo-western Pacific region.

Hoggett and Rowe (1986) and Rowe et al. (1986) first identified details of comb tooth structure as important characters diagnosing genera of Comatulidae. They distinguished *Oxycomanthus* species as uniquely having nonconfluent knoblike comb teeth. Summers et al. (2014) discovered that species with such comb teeth returned in two separate clades, which required recognition of a new genus, because the type species of *Oxycomanthus*, *Comanthus* (*Vania*) *parvicirra* β *comanthipinna* Gislén 1922, fell within *Clarkcomanthus*, leaving several former *Oxycomanthus* species without a named genus. They named the new genus *Anneissia*. *Clarkcomanthus* now includes species with a variety of comb features, including those with confluent (e.g., *Cl. luteofuscum* (Clark 1915b) and non-confluent teeth (e.g., *Cl. mirus* Rowe et al. 1986). All *Anneissia* species [e.g., *A. bennetti* (Müller 1841), *A. japonica* (Müller 1841)] bear combs composed of non-confluent knoblike teeth. Two of three species currently placed in *Comactinia* Clark 1909a (western Atlantic *C. meridionalis* and western Pacific *C. titan* Messing 2003) also have nonconfluent comb teeth, but these differ from the knoblike teeth of *Hanshessaster*, *Anneissia* and *Clarkcomanthus* species in being thin, flattened along the axis of the pinnule, and often off-center. The enlarged muscle fossae on the articulations between middle pinnulars on middle and distal pinnules are absent in other western Atlantic Comatulidae examined (*Comactinia*,

Comissia, *Comatilia*, *Neocomatella*) and have not been described in any other genus in the family.

Hanshessaster blakei (Hartlaub 1912)

Actinometra blakei (not of Carpenter 1888) Hartlaub 1912:280, 413, 471–473, pl. 13, Fig. 9.

Nemaster iowensis (Springer 1902) (part) Clark 1931:219.

Diagnosis Same as for genus.

Material examined MCZ 611 (holotype), *Blake* sta. 171, off Guadeloupe I., 15°58'20"N, 61°43'12"W, 22 Jan 1879, 335 m; USNM 1490791, *Johnson Sea-Link II* dive 3687, Northwest Providence Channel, Bahamas, 26°25.448'N, 77°51.661'W, 694 m, 24 Jul 2009; USNM 1470611 (dry), *Johnson Sea-Link II* dive 1727, off Six Men's Bay, Barbados, 13°14.60'N, 59°44.32'W, 15 Apr 1989, 568 m; USNM 1470011, *Johnson Sea-Link II* dive 1728, 13°14.94'N, 59°43.5'W, off Maycock Bay Pier, Barbados, 15 Apr 1989, 518 m.

Description of the holotype (Figs. 1, 2, 4a, 5a) Centrodorsal discoidal, ~4.3 mm across, ~1.2 mm thick, with sloping sides; thickened interradially slightly or as rounded triangular projections; separated from radials midradially by deep slit-like subradial pits. Polar area ~0.75 width of centrodorsal, flat with small, low central convexity; surface crowded with small rounded pockmarks (except on central convexity) (Fig. 1b).

Cirri ~LXIII, 15–17 (Fig. 4a); sockets crowded in 2–3 irregular ranks around centrodorsal margin (Figs. 1a, 2a). Only bases of most cirri, composed chiefly of C1–2, remain attached to centrodorsal (Fig. 1b). C1 short, wider than long. C2 with adoral margin slightly concave; LW ~1.0. Single attached C3 with both aboral and adoral margins concave; LW 2.2. Large detached cirrus of 15 cirrals; basalmost cirral with LW 2.3 (treated here as C3, as it is almost identical to C3 of attached marginal cirrus stump); C4–5 increasing in length with adoral and aboral margins slightly concave; C5 LW 3.1; C6 and following cirrals decreasing in length, becoming wider and more compressed distally, with straight aboral margins and with small, rounded triangular, distal aboral spine. C6 LW 2.6; C10 LW 1.5; C15 (antepenultimate) LW 1.1; C16 (penultimate) LW 1.0; opposing spine larger than those preceding, compressed, rounded triangular; terminal claw curved, broken. Smaller complete detached cirrus of 15 cirrals similar to those of larger detached cirrus; C1 LW 0.4; C2 LW 1.2; C4 longest, LW 2.9; following cirrals decreasing in length; first aboral spine on C6; C13 (antepenultimate) LW 1.1; terminal claw slightly longer than preceding cirral.

Interradial projections of centrodorsal abut against small, triangular or poorly defined ends of narrow basals, which together bridge subradial pits to either side (Fig. 1a).

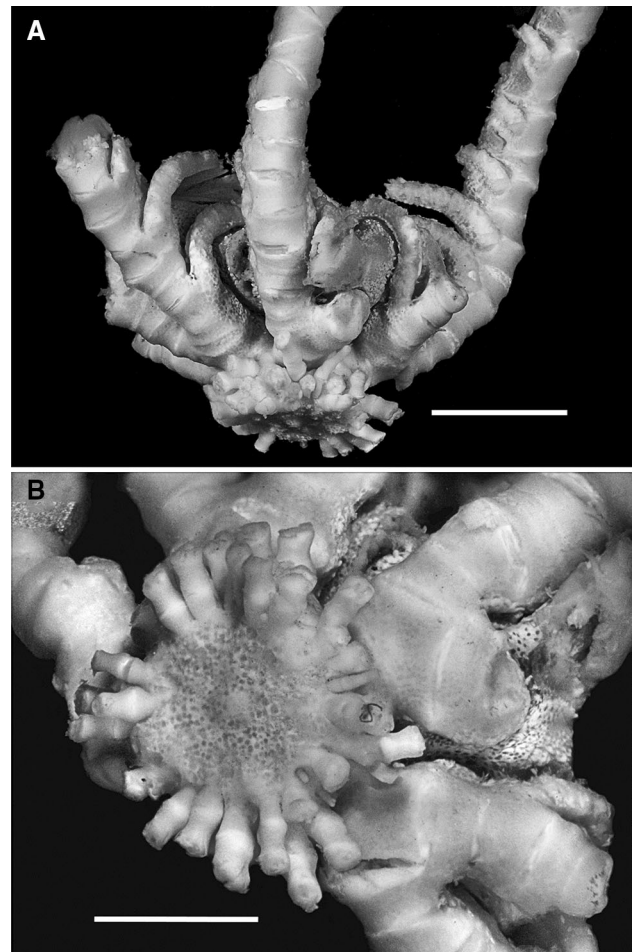


Fig. 1 *Hanshessaster blakei* (Hartlaub 1912), holotype, MCZ 611. **a** Lateral view; all cirri broken distal to bases; all proximal pinnules broken. **b** Aboral view of centrodorsal, cirrus bases, and ray bases. Scale bars: **a**—5 mm; **b**—3 mm

Aboral surface of radials barely visible midradially (chiefly hidden by bases of cirri), visible interradially adoral to basals; lateral margins of adjacent radials visible as narrow strip separating adjacent primibrachial series. Articular facet of one radial ossicle exposed but partly hidden by broken aboral portion of attached Ibr1 (Fig. 2); height ~1.25 times greater than width; broadest across fulcral ridge and narrowing adorally. Each muscle fossa ~1.5 times as high as wide, narrowing adorally, separated by narrow groove.

All but three arms broken at or near bases (Figs. 1a, 2a); longest attached arms to br8, br14 and br18. Two broken arm bases regenerating distal to br3+4, with only br4 and br4–5 remaining. Ibr1 extremely short, shallow V-shaped, slightly longer laterally than midradially; WL 7.5; lateral margins converging. Iax2 broadly rhombic (almost pentagonal), 1.3 times wider than Ibr1; lateral angles sharply acute; proximal angle shallow, rounded, ~140°; distal angle narrow, ~70°–90°. br1 almost rectangular, slightly

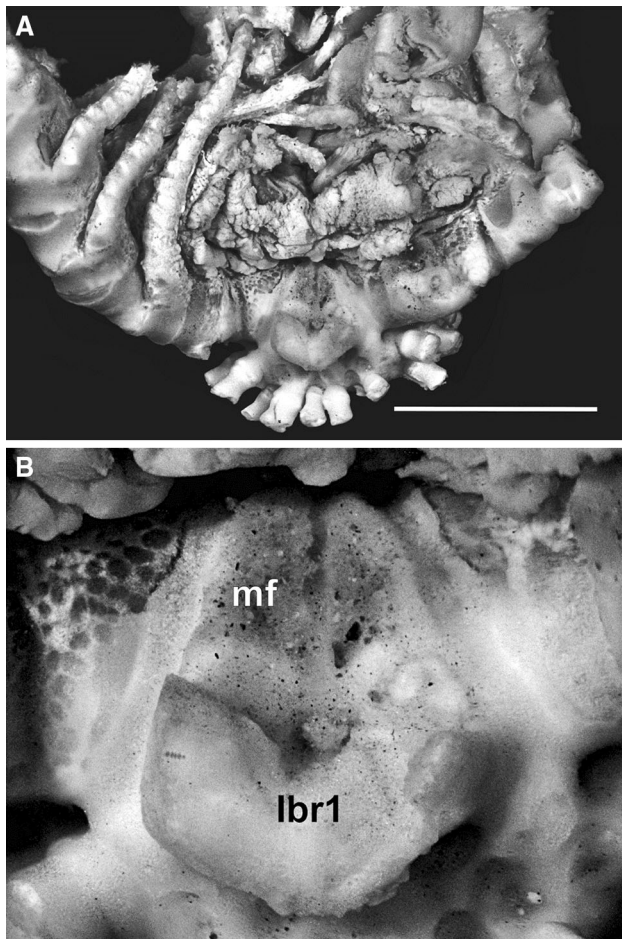


Fig. 2 *Hanshessaster blakei* (Hartlaub 1912), holotype, MCZ 611. **a** Lateral view showing partly exposed radial articular facet (below center) and proximal portions of P1, P2, and P3 (at left). **b** Enlargement of radial articular facet in **a**. *mf* Muscle fossa, *lbr1* broken but still attached aboral half of first primibrachial ossicle. Scale bar: 5 mm

longer exteriorly, WL 2.5; adjacent pairs attached for most of their interior lateral length distal to axil. br2 trapezoidal, longer exteriorly, with diverging lateral margins, 1.2 times wider than br1; WL 2.0. Interior diverging margin of br2 and weakly truncated distal interior corner of br1 together create small “water pore” between bases of adjacent arms on a ray. br3+4 roughly rectangular, 2.25 mm across; WL 1.5; interior margin slightly convex; exterior margin slightly concave. br5–7 roughly rectangular; WL 2.0. Following brachials increasingly wedge-shaped, becoming almost triangular by br10–12; WL 1.8–1.9. Weak alternating articular tubercle on articulations from br4–5 to br8–9 or br9–10. Middle brachials triangular; WL 1.8. Proximal brachials on narrower distal arm fragment wedge-shaped with WL 1.5; more distal brachials narrower but of similar length and less strongly wedge-shaped; WL 1.3–1.4. Distal brachials on distalmost remaining narrowest

arm fragment longer than wide, weakly wedge-shaped, and weakly expanded distally and proximally; WL 0.7–0.9.

One attached arm with syzygies at br3+4, 13+14, 18+19; two others with br3+4 only (distalmost remaining brachials br8 and br14). Syzygies following br3+4 on three detached arm fragments at br14+15 (2) or br15+16, and br20+21 (2), strongly wedge-shaped; WL 1.3–1.4. One fragment with fourth syzygy at br27+28, parallelogram-shaped; WL 1.1. Intersyzygial interval on mid-arm fragments chiefly 5–6 (possibly to 10); 3–6 on distal arm fragment, and with two successive syzygial pairs.

All pinnules broken (Figs. 1a, 2a, 5a). Remaining proximal pinnules mostly enveloped in tissue, so details of structure and proportions difficult to assess. Longest attached P1 incomplete, 18 pinnulars, no comb teeth; all remaining pinnulars of approximately equal length but decreasing in width beyond proximal 3–4 pinnulars; proximal pinnulars short, roughly rhombic; WL 1.7–1.5; following pinnulars with adambulacral corners truncated, becoming as long as wide or slightly longer; WL 1.0–0.9. P2 and 3 similar but progressively slightly more slender, with fewer pinnulars remaining attached. One attached incomplete P4 of ~11 pinnulars with weakly developed gonad extending from fifth to ninth pinnular; proximal 4–5 pinnulars shorter than wide or squarish, possibly becoming longer than wide by about seventh pinnular. Five detached distal oral pinnule fragments remain with combs consisting of 9–11 knoblike, nonconfluent teeth, arising gradually and weakening distally as pinnule tapers toward tip (Fig. 5a); one fragment possibly with small terminal pinnular lacking tooth. Distal several teeth offset to one side of pinnular. Remaining incomplete pinnules on distal arm fragments of up to ~17 pinnulars; proximal 2–3 pinnulars short; following pinnulars becoming longer than wide; LW to 2.5 distally. Gonads possibly to at least P14.

Disk damaged and mostly obscured by oral pinnules. Remnant of large anal papilla appears to be marginal.

Other material USNM 1490791 (Figs. 3, 4b, 5b–d, 7) Centrodorsal rounded pentagonal, 3.4 mm across, 1.0 mm thick, with no central aboral convexity; sockets in 1–2 irregular marginal ranks, and pockmarks proportionally larger than in holotype and restricted to center of aboral pole (Fig. 3a). Cirri XXVI, 16–18, to 16 mm long (Fig. 4b). C1 short, LW 0.4. C2 LW 0.9. C3–4 elongated, with aboral and adoral margins gently concave; C3 LW 2.7–2.9; C4 longest, to 1.7 mm long, LW 3.6–4.0. Following cirrals gradually decreasing in length, becoming wider and more compressed distally, with straight aboral margin, transparent distal margin, and small distal aboral spine. C5 LW 3.4–3.6. C10 LW 1.6–1.7. Antepenultimate (C15 or 16) LW 1.0. Penultimate cirral narrower than those preceding, slightly shorter than wide; opposing spine

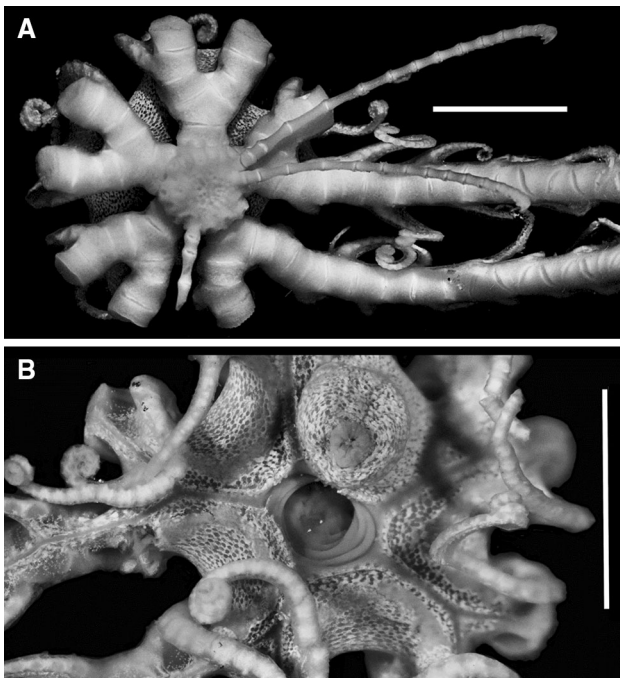


Fig. 3 *Hanshessaster blakei* (Hartlaub 1912), USNM 1490791. **a** Aboral view. **b** Oral view of disk. Scale bars: 5 mm

triangular, larger than those preceding. Terminal claw gently curved, slightly longer than penultimate cirral.

Ends of basals triangular or irregularly rhombic, visible in interradian angles. Lateral margins of adjacent radials forming a narrow triangle adoral to basals and separating adjacent primibrachial ossicles. Ray bases well separated (Fig. 3a). Ray length of two adjacent anterior arms (both broken at midarm) 70 mm. Ray length of two arms detached at br3+4 85 mm (length from ray base to br3 plus detached arm length). lbr1 almost rectangular, with lateral margins converging distally; proximal margin slightly convex and partly hidden by centrodorsal; WL 2.6. lax2 pentagonal, wider than lbr1, with short lateral margins diverging distally, proximal margin virtually straight and distal angle 80° – 90° ; WL 1.75. br1 almost rectangular, with exterior lateral margin slightly longer than interior, and interior-distal corner cut away so that brr2 are well separated interiorly; WL 2.0. br2 slightly wedge-shaped with exterior lateral margin slightly longer than interior; WL 1.9. br3+4 longer exteriorly, slightly constricted across articulation or not; 0.9 mm across; WL 1.2. Articulation at br2–3 with low exterior articular tubercle. brr5–8 roughly rectangular, with negligible alternating articular tubercles; WL 1.2–1.3. br9 slightly wedge-shaped, WL 1.7; following brachials becoming almost triangular by br11, WL 1.5. Following brachials almost triangular; longer lateral margin straight or slightly convex; articular margins slightly expanded; WL 1.1. Brachials becoming less strongly wedge-shaped and more constricted with more

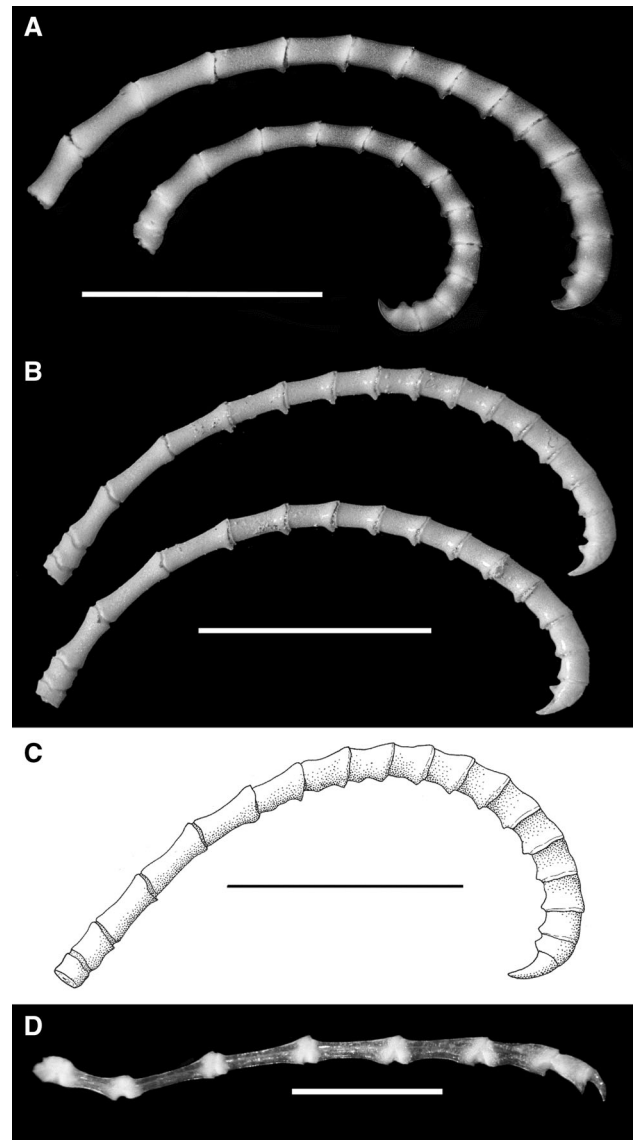


Fig. 4 Cirri. **a**, **b** *Hanshessaster blakei* (Hartlaub 1912). **a** Holotype, MCZ 611. **b** USNM 1490791. **c** *Comissia venustus* (Clark 1909a) USNM E18941 [Modified from Messing (1975)]. **d** *Microcomatula mortenseni* Clark 1931, holotype, ZMC CRI-27. Scale bars: **a**–**c**—5 mm; **d**—1 mm

expanded ends by mid arm; WL 1.0. Beyond mid arm, brachials becoming elongated and less wedge-shaped with strongly expanded ends, and more than twice as long as wide near arm tip. Syzygies at br3+4, 14+15 (one 15+16), and following at intervals chiefly of 3 or 4, occasionally 5, muscular articulations; intervals rarely longer (to ten articulations).

Pinnules enveloped in thick semi-transparent tissue, often obscuring pinnular form, articulations, and ornamentation. Pinnule tissue invested with two types of calcareous deposits: (1) rounded and irregular nodules ~ 30 – $60\ \mu\text{m}$ in longest dimension, best developed in

proximal portions of proximal and middle pinnules, arranged parallel to pinnulars and in irregular Y-shaped patterns (Fig. 6a, b), and (2) small rods $\sim 50\text{--}60\ \mu\text{m}$ long, arranged in irregular lines more-or-less perpendicular to pinnular long axes (Fig. 6c), and in crowded overlapping row within primary podia, the latter best developed on distal pinnules (Fig. 6d).

Terminal combs on first two pairs of oral pinnules tightly coiled, so that number of teeth usually cannot be counted accurately (Figs. 3, 5b). Pinnules diminishing in robustness and length from P1 through P3. Combs on P1–P3 and Pa–Pb. P1 $\sim 11\text{ mm}$ long, of ~ 32 pinnulars (Fig. 5a); first pinnular short; second pinnular largest, LW ~ 0.9 ; third and fourth pinnulars wider than long; following pinnulars squarish, becoming slightly shorter and with slightly expanded ends, with LW reaching 1.2 beyond midpinnule; third to about eleventh pinnulars with one or more spines on side facing arm tip; comb of ~ 10 erect, knoblike, nonconfluent teeth (Fig. 7a, b) diminishing in size toward pinnule tip; distalmost pinnular lacking tooth. P2 shorter than P1 (length not certain), of ~ 23 pinnulars, all short; middle pinnulars with expanded ends, with LW to 1.7; proximal few pinnulars beyond first with narrow, distally-curved subdistal spine; comb of ~ 9 teeth similar to those of P1. P3 4.7 mm long, of 18 pinnulars, abruptly

narrower following basal two pinnulars (Fig. 5c); middle pinnulars with LW to 3.0; comb of 4 weak teeth diminishing in size distally, plus small terminal pinnular lacking tooth. P4 4.0 mm long, of 15 pinnulars; first two pinnulars short; middle pinnulars with LW to ~ 5.0 . Following pinnules increasing in length; P5 and following pinnules to beyond mid-arm with tissue along middle of pinnule (from third to seventh pinnulars at most) swollen and resembling gonad in outline, but with no visible gonadal tissue. Middle pinnule 9 mm long, of 22 pinnulars; first pinnular short, second squarish; following pinnulars increasingly slender with expanded ends; middle pinnulars longest; distalmost 2–3 pinnulars short, tiny; LW of long distal pinnulars to 8.0; second and following pinnulars with long curved subdistal spine (Fig. 7c, d); spine replaced by row of fine erect, abambulacral spines on distal few pinnulars; articular facets of at least middle pinnulars with small central knob, large lumen, and pair of large thin muscle fossae resembling cartoon mouse ears (Fig. 7c, d). Distal pinnules similar but more slender, to 13 mm long, of up to 25 pinnulars; second pinnular longer than wide (Fig. 5d). Articular facets as on middle pinnules.

Mouth central; adjacent anal papilla large, almost filling anal interambulacral area (Fig. 3b). Aboral and adoral surfaces of visceral mass (disk) and anal papilla opaque white but densely covered with small, darker, apparently pigment-free oval, round, or irregular “freckles” (Fig. 3; also visible on the sides of the ray bases in the holotype, Fig. 2). In interambulacral areas toward margin of oral surface, freckles arranged in successive curved rows roughly parallel to ambulacral groove margins—appearing like strings of oval beads. Each interambulacrum with curved band of semitransparent tissue overlying and partly obscuring “freckled” epidermis, arranged parallel to outer margin of ambulacra on disk.

Other material USNM 1470011 (dry) Centrodorsal 3.9 mm across. Cirri XXXII, 15–19, to 16.4 mm long, in 2–3 crowded irregular ranks around centrodorsal margin. C5 most elongated; LW 2.9–3.4. First aboral spine on C6–7. Rays with dried epidermis thick, obscuring articulations and ossicle borders.

Visible aboral surface of radials extremely short, shallow U-shaped, separating adjacent IBr2. IBr2 with weak central synarthrial tubercle. Ibr1 short, with converging lateral margins; WL 3.2. Iax2 almost triangular with weak proximal angle and 1.2 times wider than Ibr1; WL 2.3. Most arms broken near base; one apparently regenerating arm retained to br30. br1–2 with weak synarthrial tubercle. br1 almost rectangular; WL 2.3. br2 wedge-shaped, longer exteriorly; WL 2.5. br3+4 slightly longer exteriorly, 2.0–2.1 mm across; WL 1.3. Proximal brachials from br2 to at least br12 with well-developed alternating articular

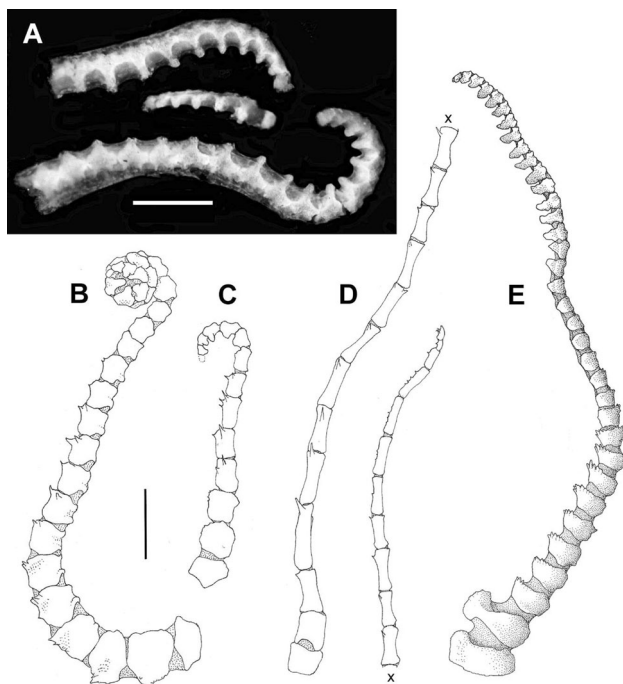


Fig. 5 Pinnules. **a–d** *Hanshessaster blakei* (Hartlaub 1912). **a** Holotype MCZ 611, detached oral pinnule combs. **b–d** USNM 1490791. **b** P1. **c** P3 (detached arm). **d** Pdistal (detached arm; figure divided at x). **e** *Comissia venustus* (Clark 1909a) USNM E17812 or E18937 (same station, Gerda-725), Pa [Modified from Messing (1975)]. Scale bars: 1 mm

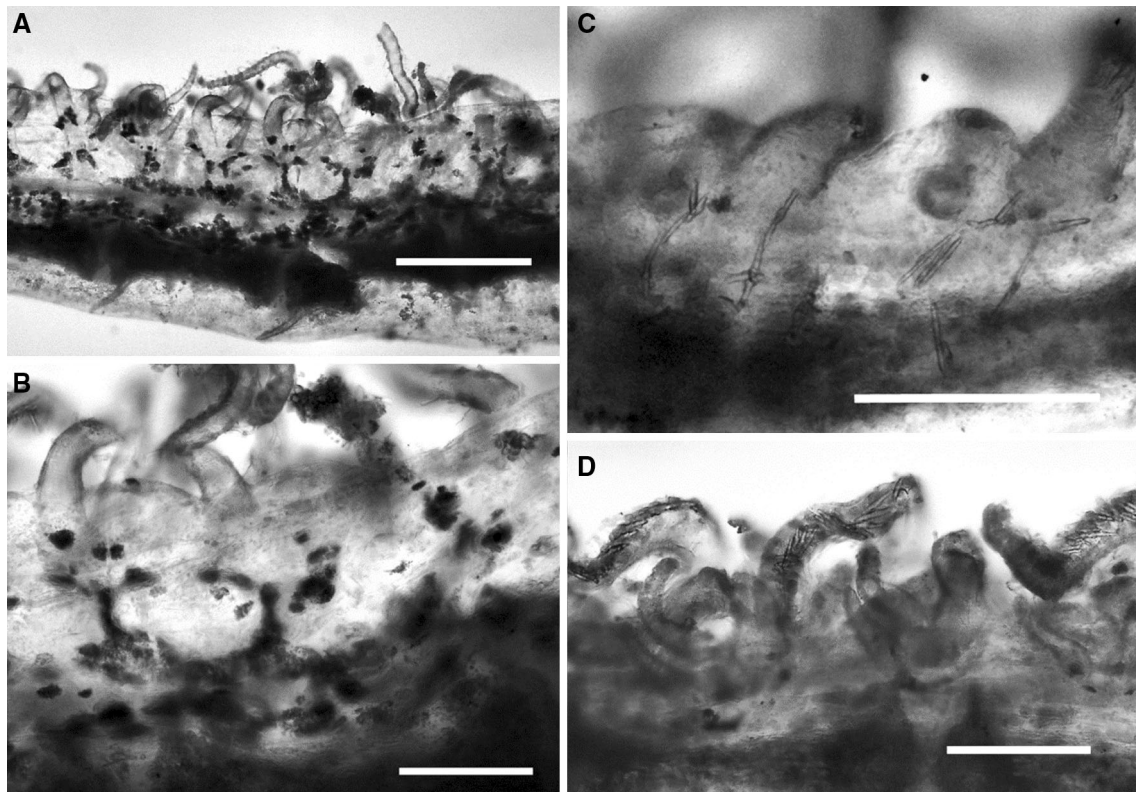


Fig. 6 *Hanshessaster blakei* (Hartlaub 1912), USNM 1490791, pinnule deposits. **a** Middle of middle pinnule showing irregular and rounded calcareous deposits. **b** Similar to **a**, enlarged; same middle

pinnule. **c** Lines of small rods along middle pinnulars of middle pinnule. **d** Crowded rows of small rods in primary podia of distal pinnule. Scale bars: **a**—500 μ m; **b–d**—200 μ m

tubercles. br5–8 roughly rectangular; following brachials progressively more wedge-shaped, almost triangular by about br12–13 with WL \sim 1.6. Second syzygy br14+15; following interval ?4–9.

All pinnules broken. Combs on terminal portions of detached oral pinnules of up to 16 nonconfluent teeth; distal 4–5 teeth diminishing in size as pinnule tapers to tip; terminal small pinnular apparently lacking tooth. Identification of at least 35 detached pinnule combs including terminal pinnular indicates that combed pinnules extend to at least P2.

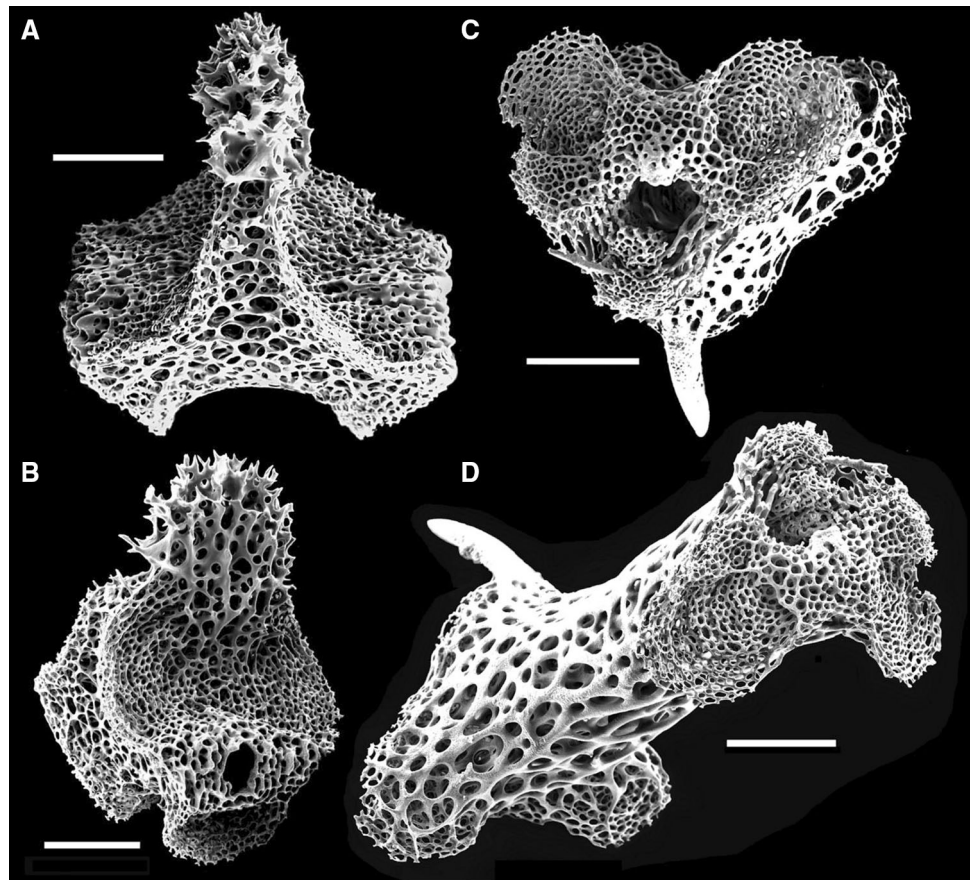
Other material USNM 1470611 Centrodorsal rounded pentagonal, 4.0 mm across. Cirri \sim XLVII, 14–17, to 16.6 mm long, in 2–3 crowded irregular marginal ranks. C5, C6 or C7 longest; C5 or C6 most elongated; LW 2.7–3.3. First aboral spine on C6–9.

Rays with thick epidermis often obscuring articulations. Radials almost completely hidden by centrodorsal and bases of cirri; corners of adjacent radials visible as small triangles in interradian angles. IBr2 with negligible synarthral tubercle. Ibr1 short, roughly rectangular; proximolateral corners of adjacent Ibr1 just separated; WL \sim 3.7. Iax2 pentagonal with short diverging lateral margins and almost straight proximal margin; WL 2.1. One almost

complete arm remaining attached; length \sim 10.0 cm. br1 roughly rectangular, slightly longer exteriorly; WL \sim 2.4. br2 strongly wedge-shaped, longer exteriorly, WL 1.9. br3+4 rectangular or longer interiorly, 1.7 mm across; WL 1.5. Alternating articular tubercles on proximal brachials weak to absent. Brr5–8 rectangular; WL 1.8. Following brachials progressively more wedge-shaped, almost triangular by br11; WL 2.2. Middle brachials wedge-shaped, with WL 1.8, becoming proportionately longer and more slender distally; WL 1.3. Distal brachials slender, weakly wedge-shaped and longer than wide; WL 0.6. Second syzygy br14+15 or 15+16; following interval 5–6 on one arm, 3–5 on two others (with one interval of 8).

Proximal pinnules mostly broken, diminishing in length from P1 to at least P3. P1 of 29 short pinnulars, 12.5 mm long. Proximal several pinnulars rhombic; comb composed of \sim 12 nonconfluent weak knoblike teeth; first tooth on 15th pinnular; distal few pinnulars tapering to pinnule tip, each with tooth reduced or absent. P3 of \sim 22 short pinnulars, 6.6 mm long. Middle pinnulars squarish; comb of \sim 5 teeth; distalmost few pinnulars tapering to tip; distalmost 1–2 pinnulars with tooth reduced or absent. Middle pinnules mostly broken; intact pinnule to 11 mm long, of 21 pinnulars, more slender than proximal pinnules.

Fig. 7 *Hanshessaster blakei* (Hartlaub 1912), USNM 1490791, scanning electron micrographs of pinnulars. **a**, **b** Comb-tooth-bearing pinnulars of detached distal portion of proximal pinnule. **a** Side view. **b** View of articular facet. **c**–**d** Middle pinnular of middle pinnule of detached arm fragment. **c** View of proximal articular facet; ambulacral surface at top. **d** Oblique view of same, ambulacral surface facing down; proximal facet at right. Scale bars: 100 μ m



Proximal three pinnulars short; following pinnulars becoming elongated and slender with expanded ends; middle pinnulars WL 3.8; distal pinnulars WL to 6.2; distalmost few pinnulars shorter as pinnule tapers to tip. Distal pinnules to 15 mm long, of 23–24 pinnulars; similar to middle pinnules but more slender. Proximal two pinnulars short; middle pinnulars with strong distal abambulacral spine. Most pinnulars in distal third of pinnule with 1–2 mid-abambulacral spines.

Disk epidermis similar to that of USNM 1490791 but with each curved band of tissue flanking ambulacral crowded with tiny apparent hydropores not visible in USNM 1490791. Ambulacra on disk bordered with uniformly-spaced, short knob-like podia.

Remarks The holotype (MCZ 611) is currently identified in the online Museum of Comparative Zoology collection database as *Davidaster rubiginosus* (de Pourtalès 1869) (<https://mczbase.mcz.harvard.edu/guid/MCZ:IZ:CRI-611>), with previous identifications as *Nemaster iowensis* (currently a junior synonym of *D. rubiginosus*), and *Actinometra blakei*. The database entry includes the following

remarks: “[*Actinometra blakei*, Hartlaub (which is written on the internal label, but not the original label) was given the designation of nomen nudum [sic] in 1915 by Austin Hobart Clark in “A Monograph of Existing Crinoids”. In Bulletin of the MCZ, 1883, v. 11, no. 7 von Graff refers to *Actinometra blakei*, Carpenter, 1888 as a Manuscript Type, unsure whether it is indeed the MS type, P[enny] B[enson] 19 May 2011]” (additions in interior square brackets mine). The hand-written catalogue identifies the specimen as *Actinometra blakei* “Adult Holotype” but notes a corrected identification as *N. iowensis*. The jar includes a fragment of an arm and detached pinnule fragments of a stalked crinoid (most likely either *Endoxocrinus* sp. or *Neocrinus* sp.), and a short arm fragment and oral pinnule comb of a different featherstar (both possibly *Neocomatella* sp.). Other small fragments also may not belong to *H. blakei*.

Hanshessaster blakei differs from other ten-armed tropical western Atlantic Comatulidae in the form of its cirri and pinnules, and in most cases placement of the second syzygy. *Comissia venustus* (Clark 1909a) (formerly

Leptonemaster venustus, see Hoggett and Rowe 1986), has the most similar cirri, of usually 12–14 cirrals (extremes 10–16), the longest with LW to 3.0, and with a small, pointed, subterminal, aboral spine on C4–C6 and following cirrals, but with a weak opposing spine (Fig. 4c). It differs from *H. blakei* in having combs on P1–P3 (and Pa–Pc) occupying the distal third to fourth of P1, as much as the distal two-thirds of P3, and composed of up to 20 incurved, triangular or spade-shaped teeth, confluent with the outer side of the pinnular (Fig. 5e). The basal two pinnulars of P1 and P2 (and sometimes P3) each bear a high, rounded carina on the side facing the arm tip (Fig. 5e), and the mouth and anal papilla are both subcentral (Clark 1931; Messing 1975). The two western Atlantic species of *Comactinia* (*C. echinoptera* and *C. meridionalis*) differ from *H. blakei* in having stouter cirri with LW at most 2.2 and no aboral spines (or a low aboral tubercle on the penultimate cirral in *C. meridionalis*); distinctly different pinnule combs, and a marginal mouth (Messing 1978, 2001; Messing and Dearborn 1990). Juvenile *Neocomatella* Clark 1909b, species with ten arms approach *H. blakei* in having the longest cirral with LW 3.0 and distal cirrals each with a pointed aboral spine. However, the comb teeth are tall, curved, triangular, and confluent with the outer side of the pinnular (Hoggett and Rowe, 1986; personal observation). In all of these taxa, the second syzygy is most often at br11+12, although it may occur more proximally or distally. *Comatilia iridometrifformis* Clark 1909c, is a tiny (arm length to ~30 mm) paedomorphic species with well separated primibrachial series, delicate cirri usually of 9–10 cirrals (rarely to 14) with cirral LW to 5.0; it lacks two to three pairs of pinnules following the proximal comb-bearing pinnules (Messing 1984, 2001; Messing and Dearborn 1990). *Microcomatula mortenseni* Clark 1931, known from one small specimen (arm length 12 mm), has its centrodorsal covered with delicate cirri of 9–10 segments, with LW to ~7.0 (Fig. 4d), and pinnule combs of three large curved triangular teeth (Clark 1931 and personal observations). It bears slender, elongated pinnulars on the middle and distal pinnules, but their articulations have not been examined.

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