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A NEW WEST AMERICAN MIOCENE SPECIES OF THE MODERN AUSTRALIAN OPHIUROID *OPHIOCROSSOTA*

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ABSTRACT—*Ophiocrossota oweni*, a new species of ophiuroid, is described from the Olcese Sand and the Branch Canyon Formation, both Middle Miocene of California. Two other species belonging to the genus have been described, one from Upper Eocene rocks of Oregon (*O. baconi*) and a modern species from Australia (*O. multispina*). *O. oweni* lived either scattered or in dense mat-like groups. Tenuous evidence suggests very slow species succession and that the divergence of the lineage leading to *O. multispina* from the North American lineage took place no later than the time of *O. baconi*.

INTRODUCTION

THE only extant species of the distinctive ophiuroid genus *Ophiocrossota*, *O. multispina* (Ljungman), 1867 has reported (Clark, 1928, p. 452, under the name *O. heteracantha*) as common in St. Vincent and Spencer gulfs on the coast of South Australia. Blake and Allison (1970) described an Eocene species (*O. baconi*) from Oregon. Three specimens of a distinctive new species, herein named *O. oweni*, were discovered by Mr. David Owen in the Miocene Olcese Sand near Bakersfield, California. Other specimens assignable to *O. oweni* have been collected by U. S. Geological Survey geologists from the Branch Canyon Formation near Cuyama Ranch, California. Because of poor preservation, the latter specimens could not be adequately assessed and were discussed under the name *O. baconi* (?) by Blake and Allison (1970). Discovery of this new material suggests that *Ophiocrossota* may have been relatively common in western North America during mid-Cenozoic times.

I am indebted to Mr. David Owen who discovered the Olcese fossils and donated them to the Los Angeles County Museum, and to Dr. Edward C. Wilson who made these specimens available to me. I am also grateful to Dr. J. Wyatt Durham and Mr. Joseph H. Peck of the Museum of Paleontology of the University of California for the loan of several specimens of *O. baconi* and the Branch Canyon material, and to Ms. Maureen E. Downey (Nat. Mus. Nat. Hist.) and Dr. Dennis R. Kolata (Univ. Illinois) for numerous useful comments. The fossils are deposited in the Invertebrate Paleontology Collections of the Los Angeles County Museum (LACMIP) and the University of California Museum of Paleontology (UCMP).

Ophiuroid skeletal terminology is not fully settled. Usage here follows Fell (1960), Spencer and Wright (1966) and Schoener (1969).

OCCURRENCE OF *OPHIOCROSSOTA OWENI*

All known specimens of *O. baconi*, and the *O. oweni* specimens from the Olcese Sand occur singly or in small groups, whereas the specimens from the Branch Canyon Formation occur concentrated in great numbers, forming most of the material of a block approximately 300 mm long, 100 mm wide at the widest point, and 50 mm thick (partially illustrated in Blake and Allison, 1970, pl. 132, fig. 8). More than ten individuals appear to occur superimposed in one vertical section through the block. These fossils were preserved largely intact with the plane of their discs parallel to the bedding planes. Many arms and spines are still in place but some arms have been broken from their discs. Many individuals are inverted. Environmental interpretations must be based on this single block; information on the geological setting of the specimen, including identification of its upper surface, is unavailable.

There would appear to be three possible explanations for the high density of individuals. Either the ophiuroids were concentrated by physical processes, such as a storm, or they were buried where they lived. In the latter case, the fossils may have accumulated either over an extended interval in which only the surface individuals were alive at any one time, or a brief interval, in which all the individuals were alive at once. The last hypothesis is preferred, largely because of the existence of modern analogs. Vevers (1952) described dense, mat-like populations of

Ophiothrix fragilis Abildgaard occurring in a band ". . . at least 2 miles in length and ½ mile in breadth" off the coast of England. Vevers estimated at least 340 individuals per square meter, counting only those discs visible in the surface layer. He considered the population to be long-lasting as he found it on three occasions during 1950–51 and because a similar concentration was reported in the same area during 1899. The permanent nature of the mats suggested to Vevers that the ophiuroids depend for food upon materials suspended in the tidal streams which occur in the area. The Branch Canyon Formation suite, originally a mat of living ophiuroids, is inferred to have been buried by a layer of sediment too thick for the ophiuroids to escape, and, because the ophiuroids were not subsequently disrupted, too thick to permit the establishment of burrowing organisms. Of 14 measurable specimens, some partially distorted in preservation, 13 range in disc diameter between 11 mm and 14 mm; one specimen has a diameter of 7 mm. Buchanan (1964) described a living population of the ophiuroid *Amphiura chiajei* Forbes in which measurements of size produced a single normal distribution curve; the population was believed to be derived from one settlement. Sampling over a five year period revealed introduction of no new individuals. The fossils might represent a similar long standing population in which recruitment was infrequent.

Physical disruption of a living community and subsequent concentration might be possible if the living ophiuroids were moved and redeposited relatively quickly. This interpretation is not preferred, in part because of the generally good condition of the ophiuroids, and in part because the discs are not jumbled, but rather they are oriented essentially parallel to the bedding planes. The inverted orientation of many of the fossil individuals need not require mechanical disruption of living communities because modern ophiuroids have been reported living with the disc inverted (Fell, 1961).

Slow accumulation of ophiuroids appears least likely. The limestone block is constructed predominantly of ophiuroids and contains only scattered small stringers of sand-size grains; organic materials appear to be limited or lacking. The bottom therefore seems to have been well oxygenated with currents sufficient to preclude accumulation of fine-grained materials. Schäfer (1972) notes that ophiuroid arms will begin to decay and fall apart fifteen hours after death. It therefore seems highly unlikely that many layers of dead ophiuroids, only partially separated by thin stringers of sand, would remain intact for any significant period.

EVOLUTION

The summary time-scale chart of Harland et al. (1964, p. 260) shows an interval of 18 to 33 million years between the times of the two fossil species, using dates of about 12 million years and 18–19 million years for the bases of the Upper and Middle Miocene, respectively, and dates of 37–38 million years and about 45 million years for the bases of the Oligocene and Upper Eocene, respectively.

The two fossil species are morphologically quite similar with only the first ventral arm ossicle differing significantly in basic shape. Because of these similarities, *O. baconi* almost certainly is on or extremely close to the lineage leading to *O. oweni*. *O. baconi* is here treated as a direct ancestor of *O. oweni*.

Differences between *O. baconi* and *O. oweni* are clearly adequate for recognition of two species; it is difficult, however, to picture a third morphologically distinctive species interposed between these two unless rates of change for the individual characters were not constant. For example, if the features of the arm were changing while those of the disc temporarily remained constant, an intermediate might have existed. Barring this possibility, it appears likely that only two successive species existed in this *Ophiocrossota* lineage, thus suggesting a relatively slow rate of species succession; the minimum survival for at least one species was 9 to 16 million years. Duration of at least one species could have been greater if the known occurrences do not represent the oldest *O. baconi* or the youngest *O. oweni*, or if the 18 to 33 million year interval separating the two species was not equally divided between them. Even if species concepts other than those on which the above discussion is based are preferred, it remains true that limited morphological change occurred through a long period of time.

Estimates of rates of morphological evolution and species duration in macroinvertebrates are somewhat limited. Schuchert (1915, p. 107) noted that skeletal changes took place relatively slowly in Paleozoic starfishes. Nicol (1953) estimated ranges of from less than one to more than 15 million years, and an average of 6.5 million years, for duration of 20 species of bivalves from the Atlantic Coastal

Plain. Teichert (1956) suggests 12 million years for the time required for complete renewal of a marine molluscan fauna in a given area. Zeuner (1958) suggests about 30 million years is the maximum period through which any modern animal species has persisted. The species of the *O. baconi-O. oweni* lineage thus appear to be relatively enduring but not uniquely so.

No attempt is made here to quantify morphological rates of change (*sensu* Haldane, 1949, for example) because available information is inadequate from a number of standpoints. The number of years separating the populations is only very broadly known, there is no evidence whether the changes were gradational through time or took place relatively rapidly during some period or periods between the times of the known fossils, and it is not known if the very small samples available are representative of the parent populations.

In a number of features, *O. baconi* is closer to the modern *O. multispina* than is *O. oweni*, although *O. baconi* is the older of the two known fossil species. For example, the development of the triangular ossicle of the dorsal surface, the dorsal arm ossicles, the outline of the interradially situated oral shields, the outline and convexity of the first ventral arm ossicles and the convexity of subsequent ventral arm ossicles are all more similar between *O. baconi* and *O. multispina* than between *O. oweni* and *O. multispina*. *O. oweni* therefore appears to be on a lineage morphologically trending away from that followed by the lineage leading to the extant species. Although evidence is certainly tenuous, it would appear likely, if *O. oweni* represents the primary direction of morphological adaptation in North American mid-Tertiary species of *Ophiocrossota*, that the divergence between the North American and Australian lineages, and the migration that linked them, took place no later than the Late Eocene time of *O. baconi*.

The morphological similarities between *O. baconi* and *O. multispina* do not mean that *O. baconi* was directly ancestral to *O. multispina*, thereby implying migration from North America to Australia. The two species could have had a common ancestor in North America, in Australia, or in some third area.

SYSTEMATIC PALEONTOLOGY

Order Ophiurida
Family Ophiuridae
Genus Ophiocrossota Clark, 1928

Ophiocrossota oweni n. sp.

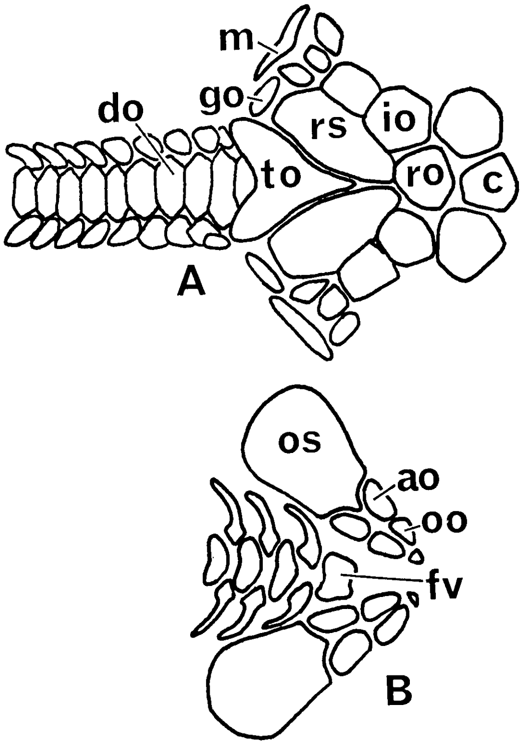
Pl. 1, figs. 1–8; Text-fig. 1A-B

Ophiocrossota baconi (?) Blake and Allison, 1970, p. 927, Pl. 132, figs. 7, 8.

Description.—Moderate sized ophiuroids with disc formed of large, closely spaced ossicles; arms massive, angular in outline, and rapidly tapering.

Aboral surface of disc formed by a pavement of about 41 large granulose ossicles. A small polygonal centrale is surrounded by a ring of five polygonal radials, which are larger than the centrale. The radial shields are overlapped by the radial ring; the shields are large, elongate, widest medially, and are overlapped abradially by the interradials. Members of a radial pair abut one another along their proximal adradial margins and are separated distally by a large triangular ossicle; their adradial margin is developed in a serrated ridge-and-groove pattern. The distal margin of the large triangular ossicle is deeply recurved and the lateral margins are sinuously curved proximally where they contact the radials but straight distally where they abut the genital ossicles; the lateral margins of the triangular ossicles are developed in a serrated ridge-and-groove pattern. Interradial areas are covered primarily by two large polygonal interradials; the proximal interradial (second interradial of Schoener, 1969) is wider than long and asymmetrically hexagonal, the widest point occurring proximally; the distal interradial (first interradial of Schoener, *ibid*) is elongate, distally tapering and smaller and narrower than the second interradial; probably three small ossicles are present along the distal margin of the first interradial. The first dorsal arm ossicle is reduced and partially overlapped by the triangular ossicles of the disc; subsequent dorsal arm ossicles are short, wide, approximately hexagonal, becoming proportionately narrower distally but remaining in contact along longitudinal margins for at least the first 14 ossicles; the proximal dorsal arm ossicles bear a row of about four small spinelet (?) bases along their proximal margins.

The oral interradial areas are largely covered by oral shields; these ossicles are elongate and broadly rounded distally, their straight sides taper gently toward the mouth, and the proximal margin is produced into a medial point separating two concave sides, which contact the adoral ossicles. The adoral ossicles are elongate, broadly in contact along their adradial margins. The oral ossicles are inflated, prominent;



TEXT-FIG. 1—Diagram of A. dorsal and B. ventral surfaces of *O. oweni*, n. sp., showing approximate ossicle shapes and arrangement, and ossicle terminology. ao, adoral ossicle; c, centrale; do, dorsal arm ossicle; fv, first ventral arm ossicle; go, genital ossicle; io, interradial ossicle; m, marginal ossicle; oo, oral ossicle; os, oral shield; ro, radial ossicle; rs, radial shield; to, triangular radial ossicle.

the dental ossicles trapezoidal in oral view. The dental ossicle appears to bear a double column of large, pointed teeth along the proximal margin; the abradial margin of each tooth is convex, the adradial margin gently curved; on their lateral sides, the dental ossicles bear a single oral papilla which is similar to but smaller than the teeth; the oral ossicles bear a row of about four papillae, the first two of which are similar to, but smaller than, the first (dental ossicle) papilla, the last two are slightly larger and paddle-shaped. The first ventral arm ossicles are large, approximately rectangular in outline, somewhat wider than long and tapering slightly proximally; they are saddle-shaped, curved aborally along the proximal and distal margins and curved orally along the lateral margins. Subsequent ventral arm ossicles are arrow-shaped and concave, the point of the arrow being directed proximally and the wings of the arrow directed slightly orally; proximal ventral arm ossicles are wide and short, becoming more nearly equidimensional distally through at least the twelfth ossicle. Margins of all ossicles are rounded; successive ossicles are not in contact with one another. Laterals are high, short, shield-shaped and inflated near their oral adradial margins. They bear several prominent spine bases along the adoral part of the distal margin and a row of fine spines on very weakly developed bases aboral to the prominent bases on the distal margin; at least one flat, broad, slightly attenuated tentacle scale protects each large tentacle pore; the scale is attached to the massive adradial section of the lateral.

The lateral interradial area is dominated by apparently wide, low marginal ossicles which are overlapped along their oral margins by a pair of small ossicles; these are in turn overlapped by the radial margin of the aborally-curved oral shields. A single large genital ossicle is present on each side of the marginals; the genitals are overlapped abradially by the marginals, and, on their abradial margins, bear a row of spines; at least the aboral part of the adradial margin bears the serrated ridge-and-grove pattern similar to that developed on the radials and triangular ossicles. The aboral margin of the genital ossicles are broadly curved except for a distinct notch near the adradial margin.

Disc diameter of holotype, 15 mm, arm diameter near base, 3½ mm; disc diameter of paratype LACMIP 4891, 13 mm, arm diameter at base, 3½ mm; disc diameter of paratype LACMIP 4892, 12 mm, arm diameter at base, 4 mm; disc diameter paratype UCMP 10595, 12 mm, arm diameter at base, 4 mm, arm length, approx. 34 mm.

Material.—Three specimens in which the disc and proximal portions of the arms have been preserved; and four arm fragments, all LACM specimens. Although many details are unusually well preserved, all specimens have suffered some ossicle disruption. Holotype, LACMIP type number 4890, from LACMIP locality number 3991; paratypes, LACMIP type numbers 4891–4896, all from LACMIP locality number 463. A single block of ophiuroid limestone, UCMP locality number D-960, containing a large number of individuals. Specimens are jumbled but largely intact; recrystallization has obscured many details. UCMP numbered paratypes 10595–10598 and 14137–14140.

Remarks.—*O. oweni* is similar to *O. baconi* in ossicle number and distribution but differs in the shape of many ossicles. Differences be-

TABLE 1—Comparisons between *Ophiocrossota oweni* and *Ophiocrossota baconi.*

	O. oweni	*O. baconi*
Aboral surface		
shape of the radials	slightly elongate, distal-lateral sides longer than other sides	approximately regular hexagons
triangular ossicles	relatively large ossicles, distal margin with deep reentrant, proximal ⅔ of lateral margins concave, distal ⅓ straight	relatively small ossicles, distal side with shallow reentrant, lateral margins straight or slightly concave
radial pair	distal lateral margins curved (corresponds to margins of triangular ossicles)	distal lateral margins straight (corresponds to margins of triangular ossicles)
second (proximal) interradial ossicles	polygonal, wider than long	polygonal, longer than wide
dorsal arm ossicles	first dorsal arm ossicle is reduced and partially covered by triangular ossicle; subsequent ossicles wider than long, hexagonal, becoming proportionately narrower distally but retaining the basic shape and remaining in successive contact through at least the first 15 ossicles	first dorsal arm ossicles largest of the series; subsequent ossicles wider than long, hexagonal but rapidly becoming narrow, triangular, and disjunct from one another
oral surface		
oral shield	ossicles taper gently toward mouth	ossicles essentially parallel-sided
ventral arm ossicles	first ventral arm ossicle approximately rectangular, saddle-shaped, subsequent ossicles gently concave	first ventral arm ossicle triangular with medial ridge; triangular apex and ridge directed toward mouth region; subsequent ossicles gently arched
Lateral margin of the disc		
marginal	marginal probably wider than high	marginal approximately square

tween the two species are summarized in Table 1.

The Branch Canyon specimens questionably assigned to *O. baconi* by Blake and Allison (1970) bear the critical characters of *O. oweni* and are here assigned to and considered a part of the hypodigm of this new species. In the Branch Canyon fossils, the aboral triangular ossicles, the dorsal arm ossicles, the oral shields and the ventral arm ossicles all display the critical features of *O. oweni,* although the aboral triangular ossicles tend to be less distinctly concave and proportionately smaller in the Branch Canyon fossils.

LOCALITIES

LACMIP locality 463; 750 ft. S, 70 ft. E of NW corner sec. 33, T.28S., R.29E. Rio Bravo Ranch quadrangle, California; 7½ min., ed. 1954. Upper part of Olcese Sand, Middle Miocene. Addicott (1970) provides the geologic setting for the Olcese Sand in the Bakersfield area; LACMIP 463 is among the localities Addicott discusses.

LACMIP locality 3991; NW SW NW sec. 28, T.28S., R29E. near head of wash east of Round Mountain Road and approximately ¾ mile north of LACMIP locality 463. Rio Bravo Ranch quadrangle, California; 7½ min.; ed. 1954. Olcese Sand, Middle Miocene.

UCMP locality D-960; Castro Canyon east of Cuyama Ranch, California; upper Branch Canyon Formation, Middle Miocene.

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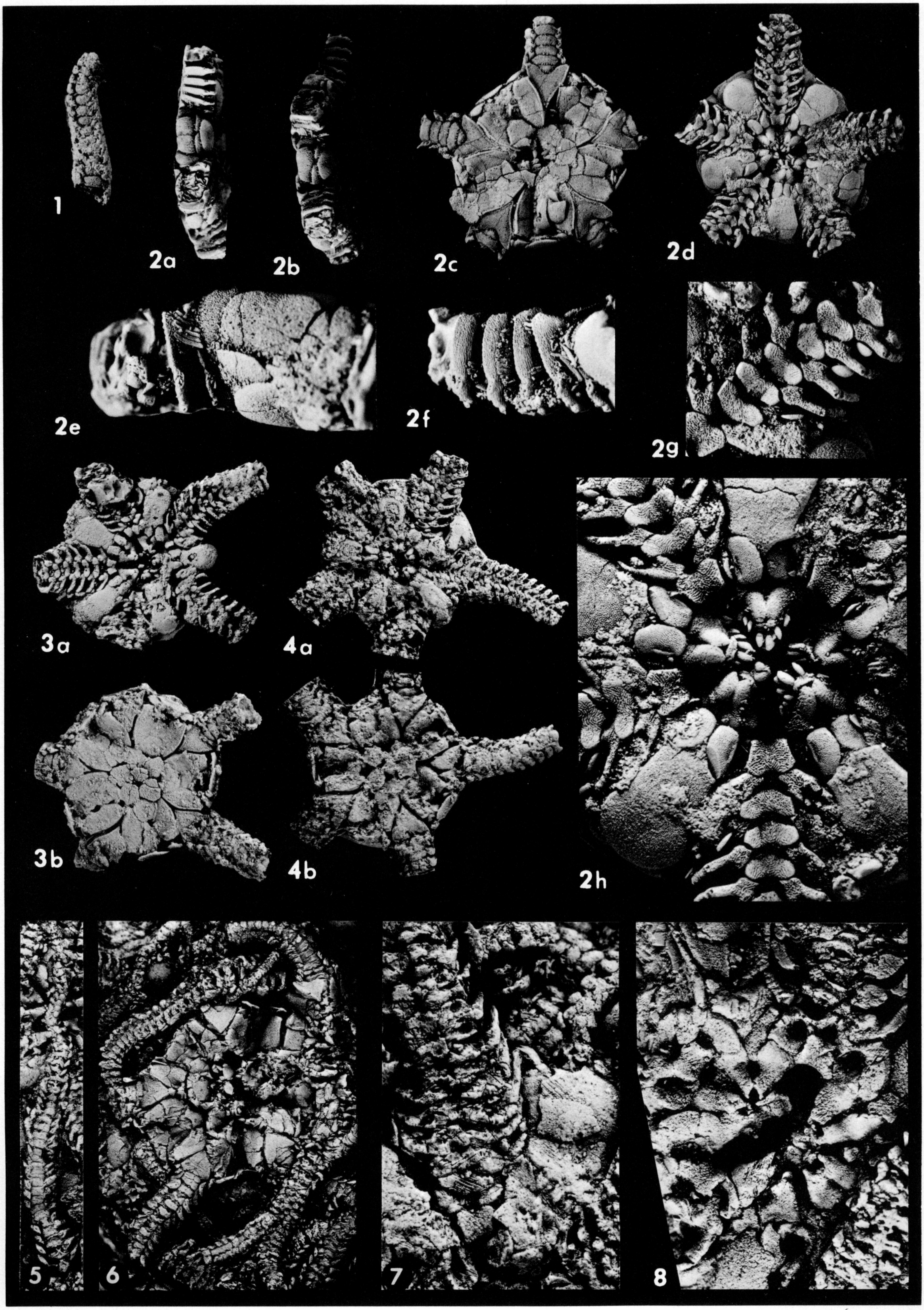
EXPLANATION OF PLATE 1

FIGS. *1–8*—*Ophiocrossota oweni*, n. sp.; *1*, LACMIP paratype 4893, dorsal view of arm fragment, ×2. *2a–h*, LACMIP holotype 4890; *2a*, *2b*, views of two interradial areas, ×2; *2c*, dorsal view, ×2; *2d*, ventral view, ×2; *2e*, lateral view of interradial area showing spinelets on genital ossicle, ×6; *2f*, lateral view of arm showing spinelets on lateral, ×6; *2g*, ventral view showing tentacle scales between laterals, ×6; *2h*, ventral view of central portion of disc, showing distribution of oral papillae, teeth, and the saddle-shaped first ventral arm ossicle, ×6. *3a–b*, LACMIP paratype 4891, ventral view and dorsal view, ×2. *4a–b*, LACMIP paratype 4892, ventral and dorsal view, ×2. *5*, UCMP paratype 14137, dorsal view of arm, ×2. *6*, UCMP paratype 14138, dorsal view of disc and arms, ×2. *7*, UCMP paratype 14139 showing oral shield and first ventral arm ossicle, × 6. *8*, UCMP paratype 14140 showing oral region and shape of first ventral arm ossicle, ×6.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2a
2b
2c
2d
2e
2f
2g
3a
4a
2h
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4b
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