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Account of *Ophionereis diabloensis*, a new species of brittle star, and of *O. amphilogus*, with information on their brooding reproduction and distribution (Echinodermata: Ophiuroidea: Ophionereididae)

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Abstract.—The present report on *Ophionereis diabloensis,* new species, and *Ophionereis* (= *Ophiodesmus*) *amphilogus,* doubles the number of *Ophionereis* species known from California waters and the number of brooding species known in the genus *Ophionereis. Ophionereis diabloensis* reaches at least 6 mm in disk diameter, with arms 17 mm in length. It is similar in appearance to *O. amphilogus* but for its more irregularly arranged and exposed disk scales, more robust arms and thick, truncate arm spines, larger accessory dorsal arm plates, and distinctively shaped oral shields. The description of *O. diabloensis* is based on material from Diablo Cove, California, the only locality where the species is presently found. Evidence is presented, however, that individuals of *O. diabloensis,* mistakenly identified as *Ophionereis eurybrachiplax,* formerly occurred at Pacific Grove, California. *Ophionereis amphilogus* is reported from the Baja California coast and from the California Channel Islands, extending the known range of the species by approximately 800 km. Most specimens of *O. amphilogus,* and many of *O. diabloensis* were brooding embryos. Individuals of *O. diabloensis* contained up to 8 embryos, at different stages of development and had no more than one embryo per bursa. The largest embryos, 1.4 mm disk diameter, with approximately 15 arm joints, were similar in size to the smallest free-living individuals collected in the field. Both species are slow moving. *Ophionereis diabloensis* lives in algal turf in the intertidal zone, and may be locally abundant, with a population density estimated at 20/m^2. *Ophionereis amphilogus* is found subtidally in kelp holdfasts. That two of the four Californian species of *Ophionereis* have been overlooked and are so little known, is illustrative of the general lack of study and of rigorous, systematic surveys of Eastern Pacific echinoderms.

In 1996, while attempting to determine the geographic range of *Amphiodia akosmos* Hendler & Bundrick, 2001, I sought access to the coastline adjacent to Diablo Canyon Power Plant, a nuclear generating station midway between Los Angeles and San Francisco. Eventually I was permitted to examine specimens of several ophiuroids that had been collected from the buffer zone around the plant, and found among them a small *Ophionereis* species that is a subject of the present report. In the following years, I collected similar specimens at the site and acquired additional material from biologists at the power plant. They represent an undescribed species which, although distinctive, strongly resembles *Ophiodesmus amphilogus* Ziesenhenne, 1940.

Prior to the present study, the only specimens of *O. amphilogus* that had been reported were the three dredged in 1934, at Cedros Island, off the western coast of Baja California, Mexico. Ziesenhenne (1940) assigned them to a new genus, *Ophiodesmus,* believing that they resembled both *Ophionereis* (Ophionereididae) and *Ophiactis* (Ophiactidae) species. He formed the name *Ophiodesmus* by combining the Greek for "serpent" (*ophis*) used in both generic names with the Greek for "bond" (*desmos*), intending to reflect a linkage between the two families, and chose the epithet *amphilogus* apropos of the "doubtful position" of the species. However, he placed it in the family Ophiochitonidae, to which *Ophionereis* was at that time assigned.

My initial impression that the specimens from Diablo Cove were of an *Ophionereis* species was confirmed by A. M. Clark's (1953) review of the genus. She considered, but rejected, inclusion of *O. amphilogus* in a possible "subgenus *Ophiodesmus*" with several other ophionereidid species that retain seemingly juvenile features in the adult growth stage. A. M. Clark (1953) disregarded *Ophiodesmus degeneri* A. H. Clark, 1949, the only other described species of the genus, and A. M. Clark & Rowe (1971) simply treated it as a species of *Ophionereis* without reference to its original generic name. It seems clear that nominal *Ophiodesmus* species lack features distinguishing them from *Ophionereis* species. Therefore, A. M. Clark's decision to merge *Ophiodesmus* with *Ophionereis* is adopted here.

Consideration of the type specimens of *O. amphilogus* coupled with study of individuals from the Channel Islands, confirmed that the species occurs in California waters and is not restricted to the Mexican type locality. Furthermore, examination of individuals of *O. amphilogus* and the new *Ophionereis* species described herein confirm that both brood their young. Those matters are covered below, along with a consideration of the range of the species and unpublished records that suggest that, at least in the past, the new species occurred on the Monterey Peninsula.

Materials and Methods

In this publication, the customary methodology and terminology used for ophiuroids are employed (Hendler et al. 1995). The diameter of the disk (dd), a standard indicator of body size, was measured from the outer edge of the radial shields to the opposite edge of the disk. The length of the arm (AL) was measured for the longest arm of an individual, from the edge of the disk to the arm tip.

Observations and measurements were made with a stereomicroscope, using a calibrated ocular micrometer. Scanning electron microscopic (SEM) examination was made using a Cambridge Stereoscan 360. Specimens were treated briefly with dilute sodium hypochlorite solution (bleach) to remove soft tissue, washed in water and ethanol, dried, sputter-coated with gold, and viewed at 10 KV.

Specimens were surveyed for evidence of embryos by examining their open bursal slits, without dissection. The estimated incidence of brooding based on superficial inspection is conservative, because in many cases the contents of the bursae were not visible. All specimens studied, except as noted below, are deposited in the echinoderm collection of the Natural History Museum of Los Angeles County (LACM).

Individuals of the new species, *O. diabloensis,* were collected in the vicinity of Diablo Cove, California (Fig. 1). Many specimens were obtained in the course of a multi-year, algal-faunal association study, and were extracted from 0.01 m^2 patches of *Gastroclonium subarticulatum* (Turner) Kützing that were scraped from rock substrate exposed at low tide, then bagged in the field and preserved in 70% ethanol within several hours (J. Tupen, pers. comm.). Others were collected from *Centroceras clavulatum* (C. A. Agardh) Montagne and similarly preserved, and a few specimens were extracted from a mixture of various algae and anesthetized in isotonic $MgCl_2$ before preservation.

Individuals of *O. amphilogus* that were collected in the vicinity of Catalina Island were removed from the holdfasts of *Macrocystis pyrifera* (Linnaeus) C. A. Agardh, and *Eisenia arborea* Areschoug. Using scuba, the subtidal holdfasts were pried from the substrate with hammer and crowbar after removing the stipe, and sealed in plastic bags. Animals removed from the holdfasts in the lab were preserved in 5% formalin (Sherlock 1995). Individuals of *O. amphilogus* from Santa Barbara and San Nicolas islands were anesthetized and preserved in ethanol, following removal from *M. pyrifera* holdfasts that had been collected subtidally using scuba. Collecting data are lacking for the single specimen from Bahía Tortugas, Mexico, save that it was associated with an algal holdfast (Fig. 1).

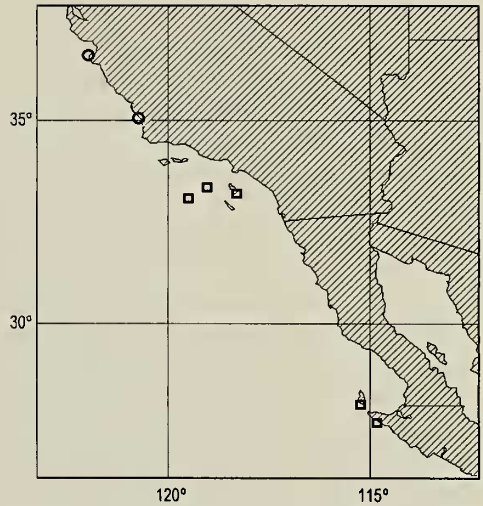

Fig. 1. Chart of Baja California, Mexico and the California coast showing the distribution of *Ophionereis diabloensis* n. sp. (circles) and *Ophionereis amphilogus* (squares). *Ophionereis diabloensis* is found intertidally at Diablo Cove, California (35°12.53′N, 120°51.36′W) and, early in the last century, probably occurred in the intertidal at Pacific Grove, California (36°37.7′N, 121°56.20′W). *Ophionereis amphilogus* is known from Cedros Island, Mexico (28°80.4′N, 115°10.21′W, 18–27 m), Bahía Tortugas, Mexico (27°41′N, 114°53′W, depth unknown), Santa Catalina Island, California (33°28.0′N, 118°29.0′W, 5–10 m), San Nicolas Island, California (33°15.736′N, 119°27.719′W, 11.3 m), and Santa Barbara Island, California (33°29.210′N, 119°01.657′W, 14.0 m).

Systematic Account

Family Ophionereididae Ljungman, 1867
Genus *Ophionereis* Lütken, 1859

Ophionereis diabloensis, new species
Figs. 2A–C, 3A–D, 4, 5A, B, 6A–C

[?] *Ophionereis* species.—May, 1924, 299–300, fig. 16.
Ophionereis eurybrachiplax [not H. L. Clark, 1911].—Weesner, 1954: 290–291 [in part?].—Sutton, 1975: 630, 633 [in part?].

Material examined.—Unless otherwise stated all specimens are preserved in alcohol, and were collected by J. Tupen and M. Behrens at approximately 0 to +1 ft MLLW in the intertidal, on the southern shore of Diablo Cove (35°12′32″N, 120°51′22″W), which is about 12 km NW of Point San Luis, California. Series of stations listed below are followed by collecting date.

Holotype.—Off Diablo Canyon., California: LACM 1999-29.20, (1 spec., dry), Coll: M. Behrens & R. Moran, 35°12′44″N, 120°51′28″W, 5 Oct 1999.

Paratypes.—Off Diablo Canyon., California; LACM 1992-195.1, (1 spec.), Sta. AFAS 33752; LACM 1992-196.1, (3), Sta. AFAS 33753; LACM 1992-197.1, (3), Sta. AFAS 33755; LACM 1992-198.1, (1), Sta. AFAS 33758, 12 Nov 1992; LACM 1992-208.2, (2), Sta. AFAS 33654, 31 Jul 1992; LACM 1993-176.1, (1), Sta. AFAS 33956, 7 May 1993; LACM 1993-178.1, (1), Sta. AFAS 34053; LACM 1993-179.1, (1), Sta. AFAS 34054; LACM 1993-180.1, (4), Sta. AFAS 34058, 18 Aug 1993; LACM 1993-181.1, (1), Sta. AFAS 34155, 12 Nov 1993; LACM 1993-182.1, (2), Sta. AFAS 34157, 12 Nov 1993; LACM 1993-183.1, (4), Sta. AFAS 34158; LACM 1993-184.1, (5), Sta. AFAS 34154, 12 Nov 1993; LACM 1994-146.1, (1), Sta. AFAS 34253; LACM 1994-147.1, (1), Sta. AFAS 34254, 10 Feb 1994; LACM 1994-148.1, (2), Sta. AFAS 34354, 27 May 1994; LACM 1994-149.1, (7), Sta. AFAS 34251, 10 Feb 1994; LACM 1994-158.2, (1), Sta. AFAS 34553; LACM 1994-160.1, (1), Sta. AFAS 34551, 15 Nov 1994; LACM 1994-161.1, (1), Sta. AFAS 34557, 15 Nov 1994; LACM 1995-166.1, (3), Sta. AFAS 34651; LACM 1995-167.1, (1), Sta. AFAS 34652, 25 Feb 1995; LACM 1995-168.1, (5), Sta. AFAS 34656, 25 Feb 1995; LACM 1995-169.1, (4), Sta. AFAS 34657, 25 Feb 1995; LACM 1995-169.3, (1), Sta. AFAS 34657, 25 Feb 1995; LACM 1995-169.4, (1), Sta. AFAS 34657, 25 Feb 1995; LACM 1995-170.1, (6), Sta. AFAS 34658, 25 Feb 1995; LACM 1997-41.14, (3), Sta. GH site 1, Coll: G. Hendler et al., −1 ft MLLW, 22 Jun 1997; LACM 1999-29.1, (1); LACM 1999-29.2, (4); LACM 1999-29.3, (13); LACM 1999-29.4, (1); LACM 1999-29.5, (1); LACM 1999-29.6, (1); LACM 1999-29.7, (11); LACM 1999-29.8, (5); LACM 1999-29.9, (6); LACM 1999-29.11, (3); LACM 1999-29.12, (1, dry), LACM 1999-29.14, (1); LACM 1999-29.15, (1); LACM 1999-29.16, (1); LACM 1999-29.17, (1); LACM 1999-29.18, (1); LACM 1999-29.19, (1); Coll: M. Behrens & R. Moran, 35°12′44″N, 120°51′28″W, 5 Oct 1999; LACM 1993-177.1, (1), Sta. AFAS 34013, Field's Cove, 35°12′56″N, 120°51′30″W, 18 Aug 1993; LACM 1997-42.10, (2), Sta. GH site 2, Coll: G. Hendler et al., Field's Cove, 35°12′56″N, 120°51′30″W, −1 ft MLLW, 22 Jun 1997.

In addition, the following specimens of *Ophionereis amphilogus*:

Type material.—Cedros Is., Mexico: LACM 1934-161.014, holotype (1 spec., dry), LACM 1934-161.013, paratype (2, dry). All types from R/V *Velero III,* Sta. 287-34, 28°4.80′N, 115°21.10′W, 18–27 m, 10 Mar 1934.

Non-type material.—Bahía Tortugas, Baja California, Mexico: SIO E1934, (1), Stipe holdfast #33, ca. 27°41′N, 114°53′W, 20 Nov 1959. Santa Catalina Is., California: LACM 1993-125.2, (2), Sta. RS 93-8, Coll: R. Sherlock, Empire Landing, NW of Long Pt., 5–7 m, 18 Aug 1993; LACM 1993-117.2, (1), Sta. RS 93-3, Coll: R. Sherlock, Guano Rock, SE of Long Pt., 7–8 m, 3 Jul 1993; LACM 1993-116.2, (1), Sta. RS 93-5, Coll: R. Sherlock, Italian Gardens II, NW of Long Pt., 6–10 m, 30 Jun 1993; LACM 1993-121.2, (2), Sta. RS 93-5, Coll: R. Sherlock, Italian Gardens II, NW of Long Pt., 5–7 m, 19 Aug 1993. San Nicolas Is., California: LACM 1999-88.1, (1), Sta. CI-99-4, Coll: G. Hendler et al., NE side of island near navigational light, 11.2 m, 33°15.736′N, 119°27.719′W, 11 Sep 1999. Santa Barbara Is., California: LACM 1999-87.1, (1); LACM 1999-87.2 (1); Sta. CI-99-2, Coll: G. Hendler et al., Arch Point, 14.0 m, 33°29.210′N, 119°01.657′W, 10 Sep 1999.

Diagnosis.—Small, brooding species with arm length:disk diameter ratio less than 4. Disk scale-covered, lacking primary rosette. Disk scales conspicuous, rounded, some completely exposed, others partially surrounded by small imbricating scales. Large, exposed, dorsal interradial disk scales wider than long, irregularly arranged; medial series of scales neither narrow nor compacted. Radial shields small; distance between paired shields slightly more than their length. Three to four oral papillae and one tentacle scale on each side of jaw. Dorsal arm plates subhexagonal, overlapping. Largest arm plates and spines on fourth to sixth joint beyond disk edge, beyond which arms taper considerably. One pair of conspicuous accessory dorsal arm plates flanking each dorsal arm plate on proximal three-quarters of arm; approximately one-sixth to one-fifth size of dorsal arm plate on basal joints. Ventral arms plates suboctagonal, with deep medial constriction, conspicuously expanded distal lobe; width of plate generally exceeding length, even at midpoint of arm. Lateral arm plates constricted proximally, with prominent, flaring spine ridge. Three thick, somewhat compressed arm spines, with truncate distal tips; dorsal spines near disk longest, largest. Tentacle scales single, large, ovoid, length equaling one-half that of associated ventral arm plate. In life, irregular, radial patches or swirls of brown, greenish brown, pale green, and cream on disk; bands of similar colors on arms; ventral interradii lack patches of dark pigmentation immediately distal to oral shield.

Description.—Disk diameter range 1.3–5.8 mm (holotype 5.1 mm); Arm length range 2.5–16.9 mm (holotype 14.2 mm); AL:dd ratio range 1.4–3.5 (holotype 2.8). Disk nearly circular, slightly inflated; arms gradually tapering beyond fourth joint.

Disk covered by numerous, conspicuous, rounded, unequal imbricating scales (Figs. 2B, 3A, 4). Larger scales separated to varying degrees by irregularly arranged smaller scales; some large scales free of overlapping scales. Large, exposed dorsal interradial disk scales wider than long, irregularly arranged; medial series not crowded, compacted. Rosette of primary plates lacking.

Radial shields small, approximately twice as long as wide; length approximately one-ninth of disk diameter; central area slightly raised, ovoid in outline. Pairs of shields separated by slightly more than their length, surrounded by scales of varied sizes.

Jaws protruding slightly beyond adoral shield. Three to four oral papillae on each side of jaw, close-set, somewhat dorso-ventrally compressed (Fig. 2C). Outermost papilla largest, broadest, flattest, with free margin broadly rounded; inner three papillae narrow, longer than broad, bluntly pointed. Rarely, unpaired oral papilla at tip of jaw. Tentacle scale of second oral tentacle with bevelled apical edge; arising from adoral shield, distal to outermost oral papilla. Tentacle scale of first oral tentacle set high on jaw in oral slit, rudimentary in specimens approximately 2 mm dd, fully developed in most specimens ≥3 mm dd. Teeth four in number, broad, of equal length, wedge-shaped in sagittal section, apex convex or notched, surface of cutting edge composed of imperforate stereom.

Oral shields quadrangular, approximately as long as broad, inner edges longer than outer edges; inner apex of the shield truncate (Figs. 2C, 3B). Adoral shields triangular, widest distally, narrowing proximally, somewhat separated; radial edge slightly concave; radial corner rounded, lobate, partially overlapping first ventral arm plate.

Ventral interradii covered with unequal imbricating scales; medial scales largest, those beside genital slit smaller, more closely crowded (Fig. 2C). Genital slit short, equal in length to two arm segments. Rarely 1–2 granules (genital papillae) on genital slit edge.

Arms considerably tapering, wider than high in cross section, dorsal and ventral surfaces somewhat convex; widest portion with longest arm spines and largest plates includes fourth to sixth joints beyond edge of disk, terminal joints dorso-ventrally compressed (Figs. 2, 5A, B). Arm plates granular due to shape of microscopic, protruding, expanded peripheral trabeculae of stereom; dorsal arm plates somewhat less granulose than lateral and ventral plates.

Dorsal arm plates subhexagonal, with medial section widest, distal edge convex (Figs. 2B, 3C). First two plates smaller than succeeding plates, wider than long, with convex distal margin. Basal plates slightly wider than long; distal plates subtriangular, with rounded distal edge, length equal to width. Plates overlapping at base of arm, separated by lateral arm plates on outer one-fifth of arm.

Lateral arm plates wider than long, constricted proximally, with prominent, protruding spine ridge, (Figs. 2B, C, 3C, D). Arm spines three in number on each plate, subequal, thick, broad, proximo-distally compressed, with truncate distal tip; uppermost spine heaviest. Spines approximately as long as basal arm segments, gradually diminishing in relative length distally, approximately one-third the length of a segment near the arm tip.

Accessory dorsal arm plates conspicuous, subtriangular, approximately one-half length and one-sixth to one-fifth size of exposed portion of dorsal arm plate on proximal joints, diminishing in size toward tip of arm (Figs. 2B, 3C). In small specimens, only one basal arm joint bears accessory arm plates; in large specimens, up to 30

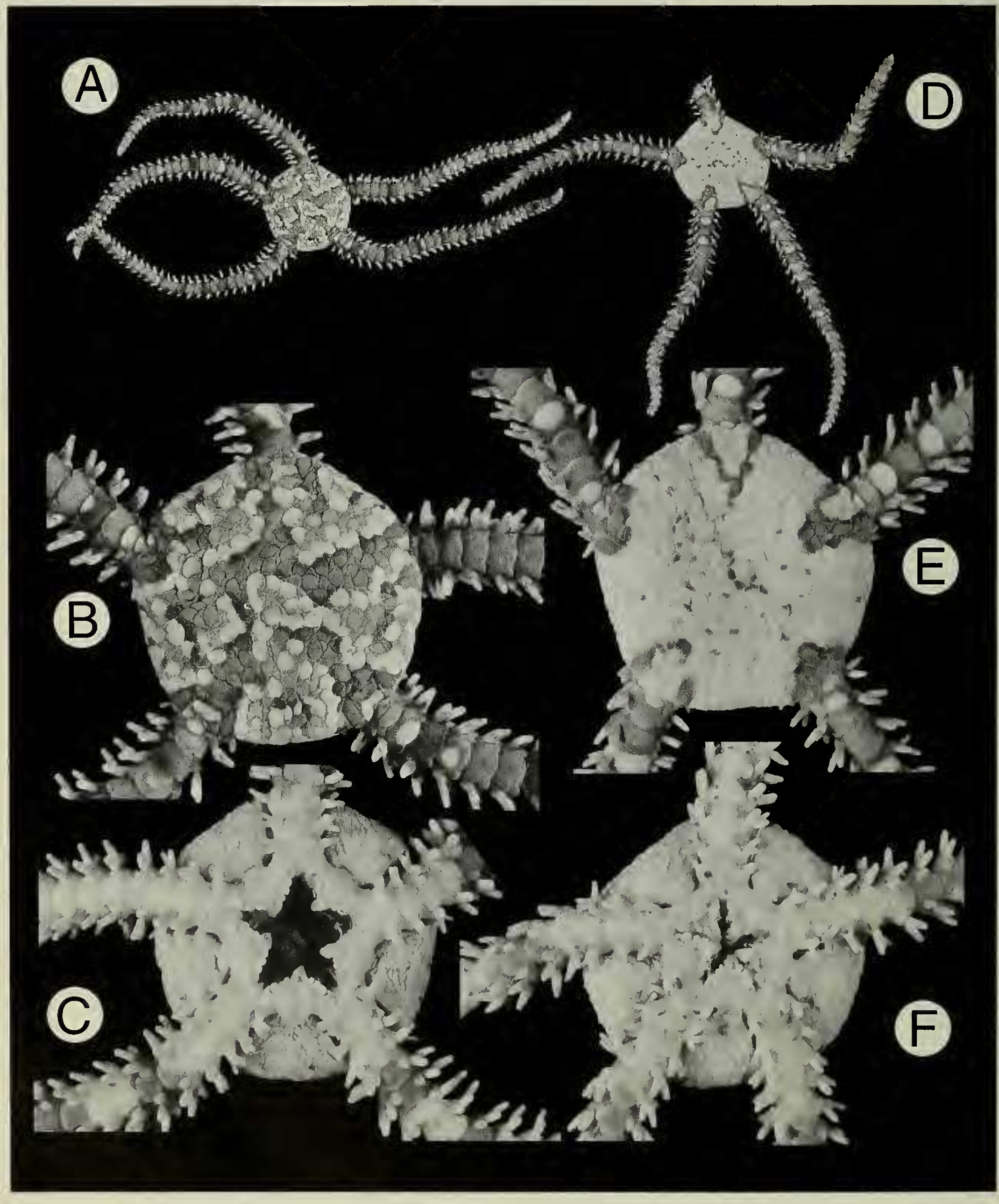

Fig. 2. *Ophionereis diabloensis,* new species and *Ophionereis amphilogus.* A–C, *Ophionereis diabloensis,* 5.1 mm dd, holotype, LACM 1999-29.20: A, entire specimen in dorsal view; B, detail of disk, dorsal view; C, detail of disk, ventral view. D–F, *Ophionereis amphilogus,* 4.4 mm dd, holotype, LACM 1934-161.14: D, entire specimen in dorsal view; E, detail of disk, dorsal view; F, detail of disk, ventral view.

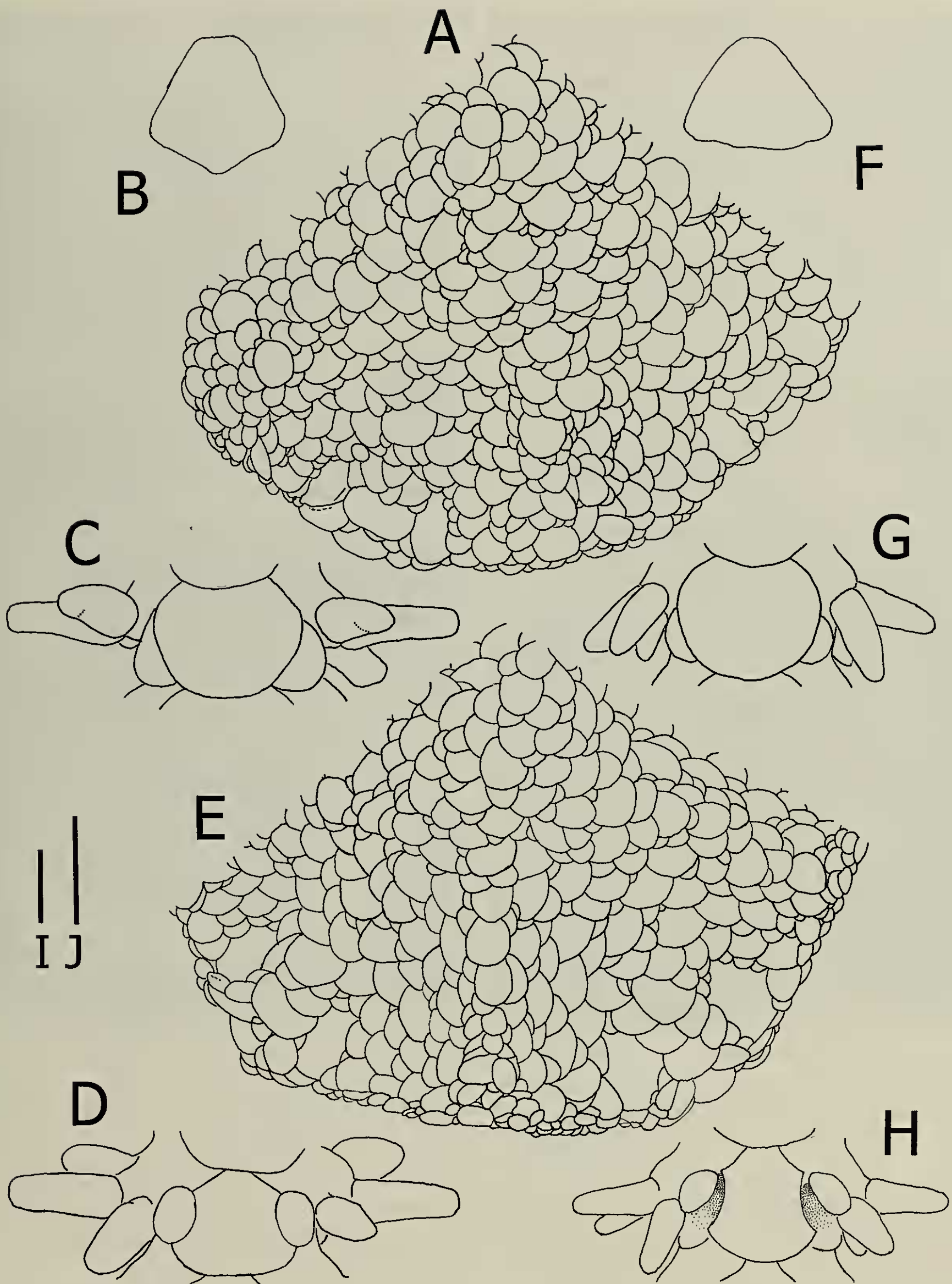

Fig. 3. *Ophionereis diabloensis,* new species and *Ophionereis amphilogus.* A–D, *Ophionereis diabloensis,* 5.23 mm dd, LACM 1999-29.19: A, Dorsal view of a portion of the disk including two pairs of radial shields, showing the size and pattern of the scales; B, oral shield with truncate apex; C, fifth arm joint from the edge of the disk in dorsal view showing the shapes of the dorsal arm plate, relatively large accessory dorsal arm plate, and truncate arm spines D, fifth arm joint in ventral view showing the shape of the ventral arm plates. E–H, *Ophionereis amphilogus,* 5.43 mm dd, LACM 1999-87.2: E, Dorsal view of a portion of the disk including two pairs of radial shields, showing the size and pattern of the scales; F, oral shield with rounded apex; G, fifth arm joint from the edge of the disk in dorsal view showing the shapes of the dorsal arm plate, small accessory dorsal arm plates, and arm spines with bluntly rounded tips; H, fifth arm joint in ventral view showing the shape of the ventral arm plate. Scale: I, 0.5 mm for A, E; J, 0.5 mm for B–D, F–H.

joints (proximal three-quarters of arm) bear accessory plates.

Tentacle scales ovoid, longer than wide, length one-half that of ventral arm plate, seated in depression below tentacle pore, proximal end hinged to lateral arm plate (Fig. 3D).

First ventral arm plate small, longer than broad, distal margin convex, proximal end within oral slit. Plates at base of arm large, suboctagonal, longer than wide; proximal end narrow, lateral margins deeply concave, distal margin conspicuously flared, with edge straight to broadly convex (Figs. 2C, 3D). Width of plate generally exceeds length at midpoint of arm. Plates pentagonal on distal joints, triangular at tip of arm. Plates in contact basally, separated by side arm plates on outer one-fifth of arm.

Terminal arm plate slightly longer than wide, equally long and wide in some large individuals; base of plate inflated, apex bluntly rounded or truncate.

Tube feet in living individuals smooth, translucent, with long, somewhat expanded tip. Individuals are slow moving; locomotion involves use of tube feet in addition to arm flexure.

Color.—Pigmentation and color pattern generally increase in intensity and complexity with increasing body size (Figs. 4, 5A, B). In alcohol, small individuals, including large embryos, predominantly cream colored, with small dark brown patches on disk and widely-spaced brown bands on arms. Disk of small individuals predominantly cream colored with small, irregular, dark brown to greenish brown blotches, and some intervening pale green pigmentation; arms cream colored with widely-spaced brown and green bands. Disk of moderate-sized individuals with large, irregular, interconnected, radiating patches and swirls of brown and greenish brown, discontinuously bordered with dark brown spots, and with patches of pale green in intervening cream colored region; arms pale green, with narrow, dark brown band every few segments, and with portions of green and brown bands incorporating small patches of cream pigmentation. Disks of large individuals predominantly brown and greenish brown, irregularly marked with dark brown and cream, radiating pigmentation pattern indistinct; arms greenish brown, with patches of cream color and dark brown bands at intervals of several joints. Ventral surface of all individuals predominantly cream colored, with darkly pigmented arm joints banded; largest individuals sometimes having very small splotches of brown in ventral interradii. Large patches of dark pigmentation typical of many *Ophionereis* species, lacking distal to oral shields. Some arm spines of moderate- and large-sized individuals banded with greenish or brown. In alcohol greenish brown pigmentation turns to green, green pigmentation fades; color loss more dramatic in dried specimens, greens and browns fading to shades of gray.

Variation.—The features of moderately large and large specimens ($\geq$3.5 mm dd) of *O. diabloensis* are consistent (Table 1). Smaller individuals, however, do not exhibit the diagnostic oral shield shape, arm spine shape, arrangement and shape of the disk scales, and color pattern.

Notably, rare individuals have one or two granules beside several genital slits, which are presumably homologous with genital papillae. Thus, the presence of genital papillae is an inconsistent character for the species. The variable degree with which genital papillae are expressed in *O. diabloensis* confounds a clear-cut distinction among *Ophionereis* species based on the presence or absence of genital papillae. However, the species falls in the group of species with "genital papillae absent" (sensu A. M. Clark 1953).

Comparisons.—The virtual absence of genital papillae and the lack of an interradial patch of dark pigmentation just distal to the oral shield set *O. diabloensis* apart from two much larger Californian congeners, *Ophionereis eurybrachiplax* H. L. Clark, 1911 and *Ophionereis annulata* (Le Conte, 1851). *Ophionereis eurybrachiplax*

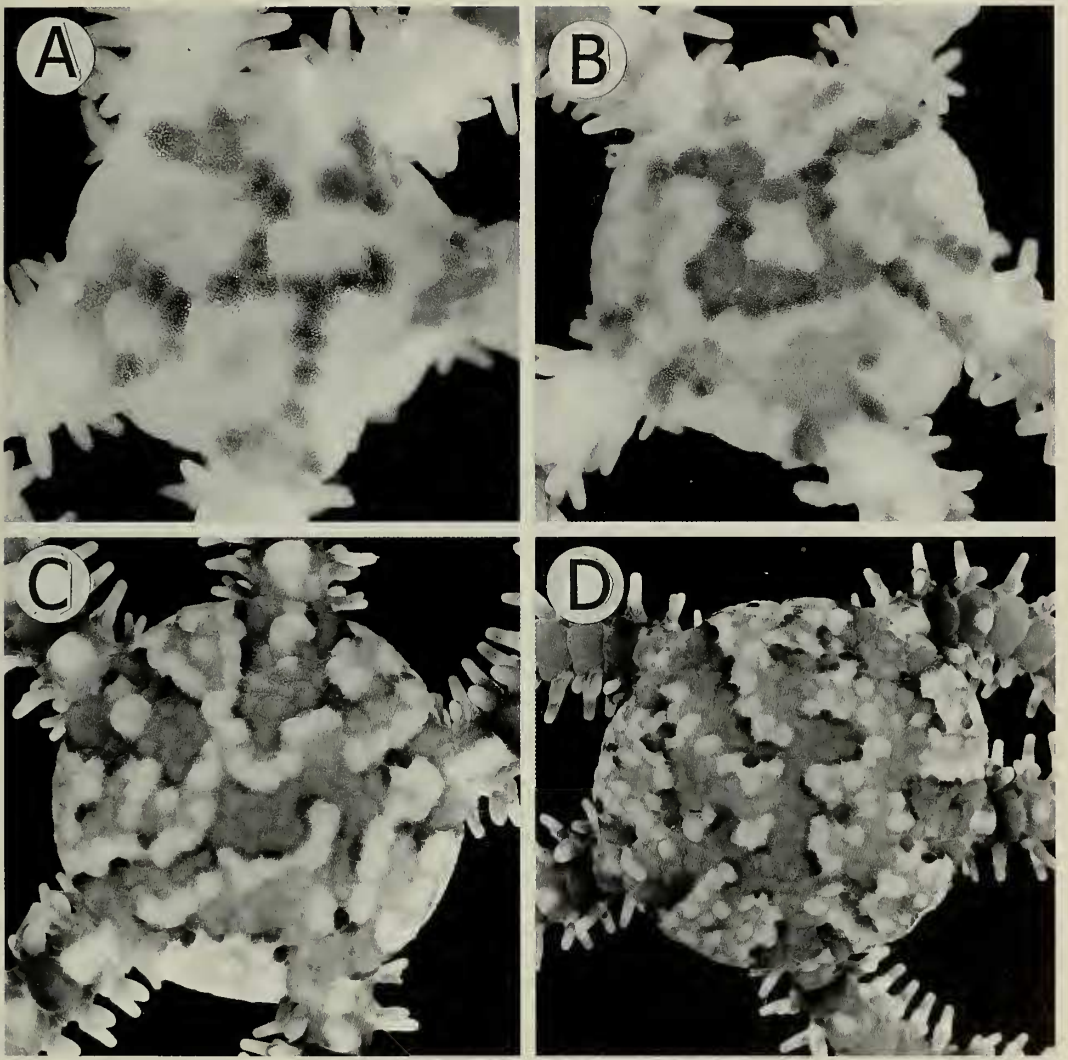

Fig. 4. *Ophionereis diabloensis,* new species. Detail of the disks of four specimens showing growth-related changes in pigmentation pattern, and development of discontinuous dark brown pigmentation separating regions of greenish-brown and cream coloration. A. 1.47 mm dd, LACM 1995-169.4; B, 2.07 mm dd, LACM 1995-169.3; C, 4.08 mm dd, LACM 1999-029.18; D, 5.56 mm dd, 1999-029.16.

is further distinguished by having four basal arm spines and dorsal arm plates that are at least twice wider than long. *Ophionereis annulata* differs in the exaggerated length of its middle arm spine, and in its accessory dorsal arm plates that are equal in length to the dorsal arm plates.

Ophionereis diabloensis and *O. amphilogus* fall into a small group of congeners characterized by A. M. Clark (1953) as retaining seemingly juvenile features in the adult growth stage. It includes *O. sexradia* Mortensen, 1936, *O. vivipara* Mortensen, 1933, *O. olivacea* H. L. Clark, 1901a, *O. novaezelandiae* Mortensen, 1936, and *O. dolabriformis* John & A. M. Clark, 1954, which are distinguished from one another in her key to the species of *Ophionereis* (A. M. Clark 1953).

The only species with which *O. diabloensis* might be confused is *O. amphilogus,* and the differences between moderate-

Table 1.—Characteristics of individuals of *Ophionereis diabloensis* n. sp. and *Ophionereis amphilogus* equal or greater than 3.5 mm dd.

Structure	*O. diabloensis*	*O. amphilogus*
Dorsal interradial disk scales	Mid-interradial scales wider than long, irregularly arranged, not crowded. Some conspicuous scales completely exposed	Mid-interradial scales longer than wide, crowded into narrow columns. Few if any scales completely exposed
Oral shield	Truncate proximal tip	Bluntly pointed proximal tip
Arm shape	Arms robust, taper dramatically; largest dorsal arm plates and arm spines on fourth to sixth joint	Arms slender, gradually tapering from disk, although first 2 dorsal arm plates reduced in size
Accessory dorsal arm plate on basal joints	Approx. $\frac{1}{6}$–$\frac{1}{5}$ size of dorsal arm plate; overlapping and covering constriction at proximal end of arm joint	Approx. $\frac{1}{10}$ size of dorsal arm plate, not obscuring constriction at proximal end of arm joint
Ventral arm plates	At mid-arm $W \geq L$; distal portion of plate appears much wider than proximal portion	At mid arm $W \leq L$; distal portion of plate appears slightly wider than proximal portion
Arm spine shape	At base of arm thick, robust; at midpoint of arm truncate	At base of arm compressed; at midpoint of arm bluntly rounded
Expanded peripheral trabeculae on dorsal and lateral arm plates	Relatively large and evident at low magnification	Relatively small and inconspicuous
Coloration	Green and green-brown pigmentation prominent; Arms greenish brown, irregularly-banded with dark brown and small, irregular cream-colored spots; Disk greenish brown with cream-colored patches separated or associated with discontinuous series of dark brown scales	Greenish pigmentation may be insignificant; Arms brown or greenish, irregularly-banded with dark brown and small, irregular cream-colored spots; Disk irregularly variegated with brown and cream, sometimes predominantly cream-colored

ly large and large individuals of the two species are summarized in Table 1 and shown in Figs. 2, 3, and 5. Small individuals of the two species can be separated by the more robust development of the arms and arm spines of *O. diabloensis* that is evident in specimens compared side by side (Fig. 5).

Etymology.—The specific name refers to the type locality of the species at Diablo Cove, near the Diablo Canyon Nuclear Power Plant, Diablo Canyon, San Luis Obispo County, California.

Discussion

Habitat.—*Ophionereis amphilogus* occurs subtidally and in association with large kelp plants. Individuals have been dredged from "from rock along the margins of a kelp bed" at 18–27 m depth, off Cedros Island, Mexico (Fraser 1943:65, habitat illustrated in pl. 32, figs. 70–71), removed from a "stipe holdfast" at Bahía Tortugas, on the Baja California mainland, and collected from *Macrocystis pyrifera* and *Eisenia arborea* holdfasts at 4.6–14.0 m depth off Santa Cruz, San Nicolas, and Santa Barbara islands in southern California.

In contrast, *Ophionereis diabloensis* has been found associated with algal turf in the intertidal zone. At Diablo Cove and environs *O. diabloensis* was collected intertidally, on a gradually-sloping rocky shelf dissected by fissures and tide pools, densely covered with algae, masses of *Phragmatopoma californica* (Fewkes, 1889), sponge, and other sessile fauna. Echinoderms in the habitat included *Asterina miniata* (Brandt, 1835), *Henricia* cf. *leviuscula* (Stimpson, 1857), *Leptasterias pusilla* (Fisher, 1930), *Pisaster ochraceus* (Brandt, 1835), *Pycnopodia helianthoides* (Brandt, 1835), *Lytechinus anamesus* H. L. Clark, 1912, *Strongylocentrotus purpuratus* (Stimpson, 1857),

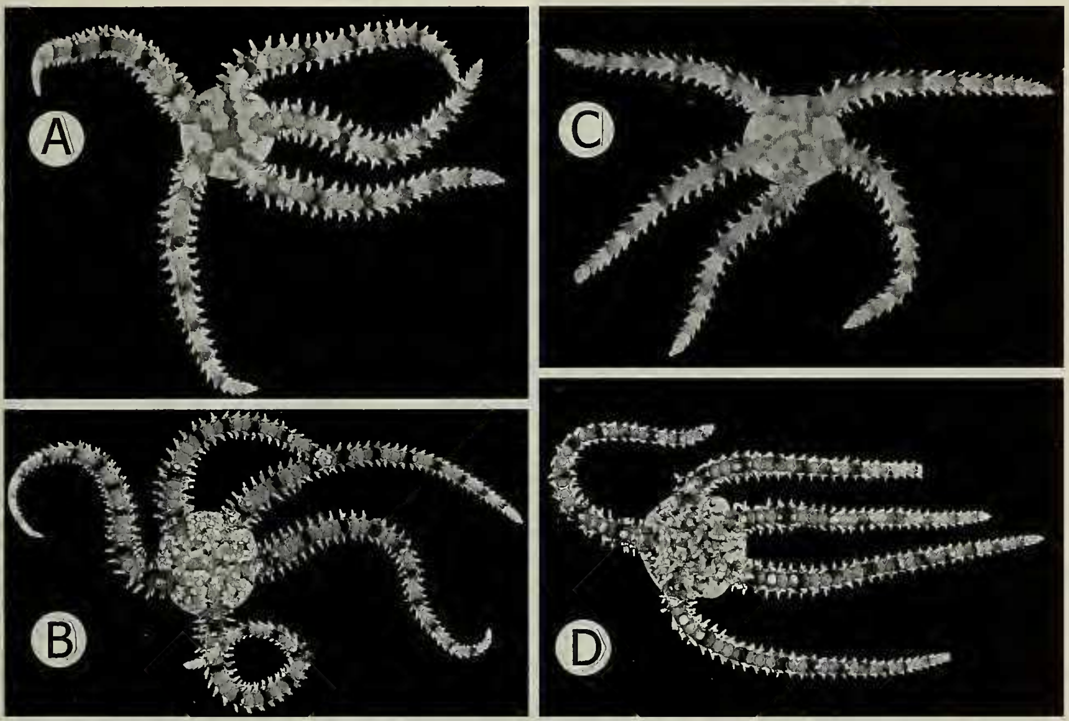

Fig. 5. *Ophionereis diabloensis,* new species and *Ophionereis amphilogus*: small and large individuals in dorsal view, showing that the former species consistently has more robust arm and spine morphology. A–B, *Ophionereis diabloensis*: A, 3.02 mm dd, LACM 1999-29.15; B, 5.23 mm dd, LACM 1999-29.2. C–D *Ophionereis amphilogus*: C, 2.88 mm dd, LACM 1999-88.1; D, 5.43 mm dd, LACM 1999-87.2.

Leptosynapta sp., *Pachythyone rubra* (H. L. Clark, 1901b), *Ophioplocus esmarki* Lyman, 1874, *Ophiothrix spiculata* Le Conte, 1851, *Ophiopteris papillosa* (Lyman, 1875), *Amphiodia occidentalis* (Lyman, 1860), *Ophiactis simplex* (Le Conte, 1851), and *Amphipholis squamata* (Delle Chiaje, 1828).

At Diablo Cove, *O. amphilogus* was found in quantitative algal samples of *Gastroclonium subarticulatum,* which tends to form large, pure stands at the 0 to +1 ft MLLW tide level. None were found in equivalent samples of *Endocladia muricata* (Postels & Ruprecht) J. G. Agardh at the +3 ft tide level. Individuals were abundant in non-quantitative samples of *Centroceras clavulatum* which tends to form pure stands found at +1 to 2 ft MLLW. In the course of a survey for *O. diabloensis* during a −1.1 ft low tide, individuals were found in mixed samples of unidentified algae, but were not seen in tide pools, under rocks, or in gravel. Although these results might indicate that *O. diabloensis* avoids *E. muricata,* its abundance in algae in the lower portion of the intertidal suggests that it is restricted to the low intertidal and might perhaps occur subtidally. During the −1.1 ft low tide, a spot survey at three stations yielded three specimens of *O. amphilogus* at one site in southern Diablo Cove that was predominantly covered by *G. subarticulatum,* and yielded two specimens in Field's Cove, approximately 1 km to the north, in *G. subarticulatum* and *Gelidium coulteri* Harvey, collected from deep channels in the rocky intertidal. In contrast, among the 65 individuals of *O. amphilogus* collected in quantitative samples from Diablo Cove and environs, only one was in a sample taken at Field's Cove and the remainder were in

24 samples from the southern coast of Diablo Cove.

The seemingly greater incidence of the species evidenced in the quantitative samples at Diablo Cove, as opposed to Field's Cove, may be an artifact of the quantitative sampling program. However, differences in the physical characteristics of the two coves might come into play. Diablo Cove receives the effluent cooling water from the Diablo Canyon Nuclear Power Plant, at a rate of 2.5 billion gallons per day of seawater heated to about 11°C above the ambient seawater temperature. Normal seawater temperatures in the area range from 9–15°C, whereas the mean intertidal temperatures in Diablo Cove are 3–5°C higher than ambient and only 1–2° higher at Field's Cove, which is less in the path of the discharge plume (Tenera 1997).

On at least two occasions in the late summer of 1999, during low tides at 0200–0400 hrs, exposed individuals of *O. amphilogus* were seen at the +1 ft tidal level, clinging to algae in beds of *Centroceras clavulatum* and *Polysiphonia* spp. (J. Tupen, pers. comm). The presence of large individuals on top of algal mats at that time may reflect a nocturnal behavior pattern, or a behavior elicited by low tides. The density of the exposed *O. amphilogus* population was estimated at 20/m^2, and in nearby tide pools fewer numbers of *Ophiothrix spiculata* (2–3/m^2) and *Amphiodia occidentalis* (0.25/m^2) were seen (J. Tupen, pers. comm.). At that time, individuals of *O. amphilogus* collected from a *Centroceras* bed proved to be significantly larger ($\bar{X}$ = 2.37 mm, *SD* = 0.92, n = 65, range = 1.31–4.82) than those extracted from pooled quantitative samples of *G. coulteri* ($\bar{X}$ = 4.38 mm, *SD* = 0.86, n = 54, range = 1.81–5.76) that had been collected at various times somewhat lower in the intertidal (two-tailed Student's t test, $t = -11.9532$, $P < 0.001$). The contrast in the size range of specimens from the two substrates suggests that *Gastroclonium* serves as a nursery habitat for smaller individuals, and/or that larger specimens have a preference for *Centroceras* or its slightly higher location in the intertidal, but it might also reflect a sampling artifact due to bias in the single sample of the latter alga.

Reproduction and development.—*Ophionereis amphilogus* is grouped with species that are "not viviparous (so far as is known)" in A. M. Clark's (1953:70) key to the species of *Ophionereis*. However, in the present study the species was found to brood its young, as was *O. diabloensis* (Fig. 6). This finding raises the number of known brooding *Ophionereis* species to four, *O. vivipara* and *O. olivacea,* both small tropical species, having been found to bear live young (Mortensen 1933, Hendler & Littman 1986, Byrne 1991, Hendler 1991).

Extremely small gonads were observed in three of the five individuals of *O. diabloensis* that were dissected. No more than two gonads were seen in an individual. Two appeared to be ovaries; the sex of the others was indeterminable in the alcohol preserved tissue viewed with a stereomicroscope. Because of the limited amount of material available, additional dissections were not conducted and the characteristics of the gonads, gametes, and mode of sexuality of the species are unknown.

Among the specimens inspected externally and the few that were dissected, at least 16 (13%) of the 124 specimens of the *O. diabloensis* specimens were brooding embryos, and at least 7 (54%) of the 13 specimens of *O. amphilogus* were brooding. The estimated incidence of brooding is conservative, based primarily on specimens that had the arms of advanced embryos protruding from their bursal slits (Fig. 6B). Three specimens of *O. diabloensis* were selected at random from among the larger individuals collected on 5 Nov 1999. Brooded embryos were found in all three, suggesting that the incidence of brooding was underestimated by external examination.

The individuals of *O. amphilogus* examined were 2.0–4.8 mm dd, and brooding individuals were 2.1–3.9 mm dd. The *O.*

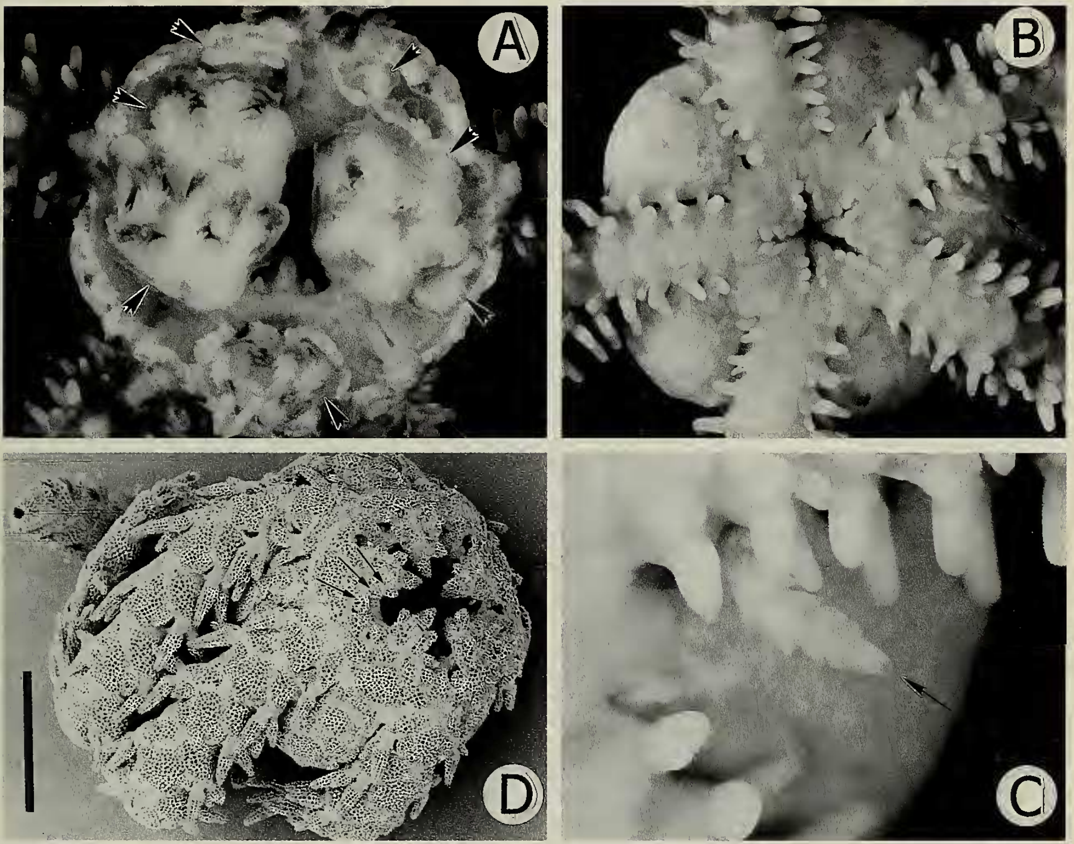

Fig. 6. *Ophionereis diabloensis,* new species and *Ophionereis amphilogus*: brooding individuals and embryos. A–C, *Ophionereis diabloensis*: A, Individual, 5.03 mm dd, LACM 1999-29.14, with dorsal wall of the disk removed to reveal 7 embryos (arrowheads) each in a separate bursa. B, Individual, 5.09 mm dd, LACM 1999-29.17, with arm of brooded embryo protruding from a bursal slit (arrow); C, detail of the arm of the brooded embryo (arrow). D, *Ophionereis amphilogus* embryo removed from the bursa of an adult (LACM 1993-116.2) from Santa Catalina Island, SEM image showing developing oral papillae (arrows); scale, 0.5 mm.

diabloensis examined were 1.3–5.8 mm dd, and the brooding individuals were 3.2–5.4 mm dd. Limited evidence suggests that both species brood embryos throughout the year. Brooding individuals of *O. diabloensis* were found in February (3 of 30 specimens), June (2 of 5), October (8 of 54), November (3 of 23), although not in May (0 of 3), July (0 of 2), or August (0 of 7). Without dissection, brooding *O. amphilogus* were identified in material collected from Cedros Island in March (2 of 3), from nearby Bahía Tortugas in November (1 of 1), and from Catalina Island in June (1 of 1) and August (2 of 4), although not in July (1 of 1). The three individuals from the northern Channel Islands collected in September did not appear to be brooding.

Three specimens of *O. diabloensis* from a sample taken in Diablo Cove in November, which were selected at random from among individuals greater than 4 mm dd, were dissected by opening their ventral interradii. The incomplete dissection did not give an unobstructed view of the contents of all the bursae, but one individual had at least 2 embryos, one had 3, and the third had 5. No more than one embryo was seen in each bursa. One small individual in the same sample, 3.08 mm dd, which was examined by removing the entire dorsal wall of the disk and the stomach, lacked embryos and had two gonads attached to the genital scales in one interradius, both 0.24 mm in diameter, and based on stereomicroscope examination were of indeterminate sex.

A brooding individual of *O. diabloensis* (5.0 mm dd) from the same collection was dissected by removing the disk wall (Fig. 6A). It contained 7 embryos with disk diameters of 0.19, 0.48, 0.58, 0.96, 1.28, 1.31, and 1.41 mm. The smallest had 1–2 arm joints, and the 1.28 mm dd embryo had approximately 15 arm joints. The largest four embryos had dark bands on the arms and flecks of dark pigment on the disk; the smallest embryos were entirely white. The smallest individuals found in the field were 1.3 mm dd. Although there is a possibility that they emerged prematurely from adults held under adverse conditions, the size and advanced developmental state of the embryos indicates that they are capable, or nearly capable, of living independently.

A 3.6 mm dd specimen collected on 22 June 1997 was dissected in a similar manner, and found to contain embryos with disk diameters of 0.24, 0.27, 0.27, 0.32, 0.83, and 0.93 mm. The 3 smallest had only a terminal arm plate, and the 3 largest had 1, 8, and 9 arm joints respectively. The embryos at a point of development with only the terminal arm plate and no discernible arm joints, appeared as a heavily calcified star surmounted by a bubble of thin tissue in which small multi-radiate ossicles were embedded. In two bursae there were early embryonic stages only 0.14 and 0.18 mm in diameter. Both were composed of a thin, transparent sphere of tissue, at one pole of which were relatively heavily calcified plates; multi-radiate ossicles were embedded elsewhere on the wall of the sphere within which was a small mass of opaque tissue.

It is difficult to compare the mode of development in the embryos of *O. diabloensis* with that in *O. vivipara,* which is reportedly "of the type where the nuclei lie scattered irregularly all through the yolk" (Mortensen 1933:192). The embryos seem to differ from those of *O. olivacea* as well, which has large yolky eggs and embryos with a "modified vitellaria" stage (Byrne 1991). Although the embryos of *O. diabloensis* are not noticeably yolky, they are similar in structure to the yolky embryos brooded by *Amphiura belgicae* Koehler, 1901 and *Amphiura stimpsonii* Lütken, 1859 which are probably meroblastic (Mortensen 1921, 1936).

The presence of embryos of various sizes in *O. diabloensis* collected in the winter and summer, suggests that embryos may be produced throughout the year and that spawning occurred and new embryos began to develop before the previous cohort was released. Individuals of *O. vivipara* also brood young in various stages of development "a few at a time," a situation interpreted as indicating that "breeding goes on without interruption" (Mortensen 1933: 192). These characteristics and those of *O. diabloensis,* contrast sharply with those in *O. olivacea.* Reproduction in the latter species is seasonal, and individual females brood as many as 165 embryos at the same stage of development, releasing young with only two to three arm joints (Byrne 1991).

In *O. diabloensis,* no more than one embryo was found in each bursa of a brooding individual (Fig. 6A). The advanced embryos held their arms beside their disk or flexed dorsally, such that the mouth and proximal tube feet of the embryo were pressed against the wall of the bursa. The position may be typical of brooded ophiuroid embryos, and may facilitate the uptake of nutrients from the bursal wall (Walker & Lesser 1989, Byrne 1994, Hendler & Tran 2001, Hendler & Bundrick 2001).

An embryo removed from a 3.7 mm dd specimen of *O. amphilogus* from Catalina Island, was 0.80 mm dd with 1.6 mm long arms consisting of 13 joints, and had the greenish brown pigmentation expressed in large embryos. The embryo had 3–4 oral papillae on each side of the jaw, but lacked a tentacle scale of the outer oral tentacle.

The largest oral papilla was associated with the adoral shield and the most proximal oral papillae were relatively larger than those on the side of the jaw. The arrangement of the oral papillae in *O. amphilogus,* and Mortensen's (1921) observations on *Ophionereis squamulosa* Koehler, 1914, indicate that the distal oral papilla in *Ophionereis* species is homologous to the adoral shield spine, and the proximal papillae represent homologues of buccal scale and/or infradental papilla as suggested by Hendler (1998).

Distribution.–Following the discovery of *O. diabloensis* at Diablo Cove, near the Diablo Canyon Power Plant, it seemed possible that the population of the species was anomalous, having become established in a restricted body of water that was buffered from local temperature fluctuations by the outflow of the nuclear generator. Unfortunately, benthic collections that were made prior to the establishment of the generating station have either been discarded or are unavailable for scientific study, and so the history of the Diablo Cove population is moot (J. Tupen, pers. comm).

Several references in the literature to *Ophionereis* from the central California coast point to occurrences of *O. diabloensis* approximately 200 km to the north of Diablo Cove, as many as 63 years before the plant went into operation. In 1921, at Pacific Grove, May (1924:264) found "one young *Ophionereis* under a rock, on sandy bottom, at low tide," whose size (3 mm dd, 8 mm AL) and appearance accord well with *O. amphilogus,* particularly its color, "Aboral side of disk and arms mottled irregularly with light olive, white, and blackish brown . . . interbrachial spaces pinkish; arms white, with cross bands of dark gray irregularly covering one to three plates, and spaced every one to three plates."

Twenty-seven years later, likewise in Pacific Grove, three specimens were collected "on the side of a rock under *Pelvetia*" in the Point Pinos intertidal that, with reservations, were identified as "*Ophionereis eurybrachyplax*" [sic] (quotes from unpublished manuscript by Ephraim Friedman, entitled "The intertidal ophiuroids of Monterey Bay. Zoology S112, July 1948," which is housed in the Cadet Hand Library, Bodega Bay Marine Laboratory, Bodega Bay, California). They were similar in size (4 mm dd, 12 mm AL) to *O. diabloensis.* Their coloration was like the latter species, "The disk has white, light green, dark green, and brown scales giving it a mottled appearance. The arms are green with dark green and brown stripes every 5 or 6 segments" (Friedman manuscript). Fortunately, Freidman photographed his specimens of "*Ophionereis eurybrachiplax,*" and although the illustrations in his report provide limited detail, the distinctive body shape, robust arms and arm spines, and color pattern all resemble *O. diabloensis.*

The second and third editions of "Light's Manual" (Weesner 1954, Sutton 1975) reported *O. eurybrachiplax* from the intertidal of the central California coast, but the basis for the citations is unclear. The key characters and brief descriptions provided in both editions could apply to *O. amphilogus* or *O. annulata* as well as *O. eurybrachiplax.* However, *O. annulata* does not occur north of the Channel Islands in southern California, and *O. eurybrachiplax* is restricted to moderately deep water (53–145 m) (Ziesenhenne 1937; Hendler, prev. unpub.). The specimens or data that were the source for the citation in the second edition are unknown (Weesner, pers. comm.). Furthermore, the specimens that were reported by May and Freidman are lost; some of the material that they collected was transferred from Hopkins Marine Station to the California Academy of Sciences, but not their specimens of *Ophionereis* (Hendler, pers. obs.).

The range of *O. amphilogus* had been reported to extend from Cedros Island to the northern Channel Islands and from 18–183 m depth, based primarily on museum records at LACM and SIO (Maluf 1988). However, evaluation of the museum specimens revealed that all but the types had been misidentified. Thus, prior to the present study the only correct distribution record for the species was the type locality at Cedros Island. A second Mexican locality was established in this study based on a specimen in the SIO collection collected in 1959, from Bahía Tortugas on the Baja California mainland. Furthermore, the known range of the species was extended to Santa Catalina, San Nicolas, and Santa Barbara islands based on more recently collected specimens in the LACM collection. Thus, the range of *O. amphilogus* extends at least 800 km, from Baja California, Mexico almost to Pt. Conception, California (Fig. 1). Within that range only 13 individuals have been found since 1934. Moreover, only nine specimens have been collected in the Channel Islands, although the islands have been monitored and repeatedly sampled since the 1930's by a variety of academic, environmental and governmental programs and agencies.

Ophionereis diabloensis was found at Pacific Grove in 1921 and 1948, but evidently was never seen by Ricketts (Ricketts et al. 1985), whose work in Pacific Grove during that time laid the foundation for West Coast intertidal ecology (Fig. 1). The species has not since been reported by the many individuals and organizations that have investigated the coast of Monterey Bay and environs. It was undetected during intertidal surveys at Pacific Grove carried out in the 1930's and 1990's, which have purportedly demonstrated range-related shifts in intertidal organisms attributable to long-term climate change. In the latter study, as in most long-term, marine monitoring programs, only those "species that could be readily enumerated with the unaided eye" were tallied (Sagarin et al. 1999: 468), a methodology in which most benthic species are overlooked and accurate taxonomic identification is compromised.

The lack of information regarding *O. amphilogus* and *O. diabloensis* reflects the regrettable lack of research on the natural history of most Eastern Pacific echinoderms. Even their distributions are poorly understood because of the emphasis on expediency in many ecological surveys. The situation might have been different if consistent efforts had been made to explore and collect systematically, and to voucher specimens from the myriad surveys of marine organisms that have been made on the Pacific coasts of Central and North America. However, the important archival role of natural history museums has rarely been effectively developed or supported. As a consequence, we still know all too little about the Eastern Pacific marine fauna.

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