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Henricia pumila sp. nov.: A brooding seastar (Asteroidea) from the coastal northeastern Pacific

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Abstract

A small species of the seastar genus *Henricia* Gray, 1840 occurs along the cool temperate Pacific coast of North America from near Sitka, Alaska to just south of Ensenada, Baja California, Mexico. Its small adult size, mottled aboral colors, and benthic external brooding reproductive mode have long been noted, but it has never been formally separated from the larger, free-spawning *Henricia leviuscula* (Stimpson, 1857), with which it has been confused. Here we amplify the description of *H. leviuscula*, based on examination of the holotype and new specimens, and restrict it to only one of several similar species that co-occur in Puget Sound and vicinity. We also describe the small mottled brooder as *Henricia pumila* **sp. nov.,** characterize its distribution, and contrast its morphology with *H. leviuscula* based on the arrangement of marginal plates and the microanatomy of aboral spines.

Key words: North America, cool temperate Pacific coast, Echinodermata, Asteroidea

Introduction

Several northeastern Pacific (North American "West Coast") members of *Henricia* Gray, 1840 have long been collectively known as *H. leviuscula* (Stimpson, 1857), whose type locality is Puget Sound, Washington. The popular assignment of most shallow water West Coast *Henricia* to a single species, despite considerable apparent variation in form and color, is in contrast to the bewildering assortment of nominal species or varieties earlier proposed by echinoderm specialists. One problem is that named species or varieties were often provided only with scantly documented differences in plate numbers or shapes or body proportions. For example, H. L. Clark (1901) introduced new varieties of *Cribella* (=*Henricia*) *laeviuscula* based solely on ray shape and length relative to disc diameter.

In his compendium on Asteroidea of the North Pacific, Fisher (1911:280–295) treated *Henricia leviuscula* as a highly variable species comprising six varieties, designated A to F, and three subspecies. Most interesting to us was Fisher's characterization (1911: 282–284) of his variety F, a small brooder. He noted its varied aboral coloration of mottled hues of gray, brown, red, orange, yellow, and lavender, its small size at maturity, and its comparatively stout arms. He characterized its brooding mode of reproduction as follows: "…forming for that purpose a concavity about the mouth by arching the disk. The eggs are orange yellow and are hidden by the mother, which in spite of its bright colors, harmonizes fairly well with the coralline on the rocks. However, when brooding the eggs this species is usually found under rocks or hidden between them, in darkness." These descriptions imply that Fisher examined living specimens of his variety F, in contrast to the preserved specimens of *Henricia* that he usually examined (Fisher 1910, 1911, 1930). He described and photographed body proportions and arrangement of plates and spines, but not fine details of spine tips. This

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description of brooding was Fisher’s only note on reproductive mode for any West Coast member of *Henricia*. In particular, Fisher had no reports of the larger specimens either brooding or free-spawning. Unable to find consistent morphological distinctions, Fisher reluctantly designated the small mottled brooder as a mere variety of *H. leviuscula*.

A. E. Verrill (1914: 215–226), who also considered *H. leviuscula* to be a highly variable species, described or redescribed eight “local varieties” and one subspecies. Verrill apparently examined the holotype of *leviuscula* but, unfortunately, described and illustrated only gross morphology of spines. He reported a multitude of color patterns for *H. leviuscula* (p. 216), from which it may be inferred that his notion of *leviuscula* included the small mottled brooder and perhaps other species.

In a survey of spinulosid seastars of Japan, Hayashi (1940) discussed 18 nominal “forms” of *Henricia*, including *H. leviuscula*. He examined two specimens of what he believed to be *H. leviuscula* from Kodiak, Alaska, and concluded that the specimen tentatively identified as *H. leviuscula* by Uchida (1928) was not typical of that species and that *H. leviuscula* did not occur in Japanese waters. Hayashi's survey mentions small species of *Henricia* known to be brooders: *H. tumida* Verrill, 1914, *H. nipponica* Uchida, 1928 (= *H. tumida* Verrill, 1914, fide Djakonov, 1950; but considered valid by Hayashi, 1973), and *H. kinkasana* Hayashi, 1940. Although these appear to be distinct to us, their potential relationship to Fisher’s variety F remains to be investigated.

Djakonov (1950: 95) considered it probable that various species and forms had been confused under the name *H. leviuscula*. He noted the occurrence of two types of spines: stout with a thorny apical knob as found on typical specimens from Monterey Bay (his “variety B”, figs. 83, 84) and low with sharp but coarse glassy spines protruding on various sides as on a specimen from Nanaimo Bay (his “variety A”, figs. 79, 80). Djakonov's varieties A and B, however, appear to differ from Fisher's varieties A and B, and neither resembles the small mottled brooder.

The small mottled brooder continued to be lumped with larger slender-rayed, orange, red, or red-purple specimens as *Henricia leviuscula*, or even *Henricia sanguinolenta* (O.F. Müller, 1776) (type locality, south coast of Norway) long after it was known that the larger Pacific Coast *Henricia* were free-spawners with pelagic development. Early authors, noting the considerable variability, suggested that if the small or large *Henricia* comprised more than one species, these might be rather freely hybridizing. A transient hypothesis was that the small and large *Henricia* might be a single species that broods when small but free spawns when larger (F.-S. Chia, pers. comm. in Feder 1980; withdrawn by pers. comm. in M. Strathmann 1987).

We began this study in 1985 in hopes of finding evidence in addition to reproductive mode, body size, and mottled coloration that would support formal separation of the small brooder from *Henricia leviuscula*. We first used starch gel electrophoresis of enzymes, a method since successfully used to separate two Atlantic subgroups within the genus (Ringvold & Stien 2001). We found that the mottled brooder had a distinctive electromorph pattern at each of multiple presumed loci, exhibiting little if any variation between individuals from sites near Barkley Sound, southern Vancouver Island, British Columbia, Washington, or the central California coast. In contrast, sympatric larger specimens, initially identified as *H. leviuscula*, had diverse and confusing electromorph patterns. Manchenko (1987) similarly found considerable variation in electromorph patterns in starfish species from the Sea of Japan, including one he called *H. leviuscula*.

Examination of the external micro-morphology of putative *H. leviuscula* from the San Juan Archipelago, Washington revealed a potential explanation for our electrophoretic results: the possibility that *H.* “*leviuscula*” was actually several species, some probably unnamed, all with slender orange to reddish rays. The problem then became one of identifying and characterizing the true *H. leviuscula* as well as the small brooder. This necessitated finding a lost holotype and examining many similar slender-rayed specimens until we could confidently recognize *H. leviuscula* by its morphology. We are now able to distinguish these two species by their body shape, reproductive mode, and spine microanatomy. Here, we describe and name the small mottled brooding species and redescribe *H. leviuscula*, restricting it to only one of several similar species in the northeastern Pacific. A regional treatment of the many shallow water species of the genus, including an array of *leviuscula*-like species, will be presented separately (D. Eernisse and M. Strathmann, in prep.). These studies are also related to an ongoing phylogenetic and biogeographic analysis of near worldwide *Henricia* based on mitochondrial 16S and COI gene regions (D. Eernisse, M. Strathmann, E. Corstorphine, R. Clark, and C. Mah, in prep.).

Methods

Most of the specimens referred to in this study were collected on San Juan Island (San Juan Co., Washington, USA) from rocky intertidal areas during low tides, subtidally by SCUBA divers, or by dredging or trawling from the Friday Harbor Laboratories' R/V *Nugget* or R/V *Centennial*. Additional specimens were collected from elsewhere in the San Juan Archipelago, Washington (48°N, 123°W), from the outer coast of Vancouver Island, British Columbia, Canada, especially in the vicinity of Bamfield Marine Science Centre (48.84°N, 125.14°W), from the coast of central California (38.32°N 123.07°W to 35.15° N 120.66°W), and from cool upwelling sites in northern Baja California (31.69°N 116.68°W).

We examined specimens in our collections (DJE or MFS) alive and after preservation and drying. Ray length (R, mm from disc center to ray tip) and disc diameter (r, mm from disc center to interradial disc edge) were measured on the madreporal radius and interradius respectively; however, if the madreporal ray was noticeably short, damaged, or curled, the longest or straightest intact ray and opposing interradius were measured. This convention was followed to improve the repeatablility of our measurements, not because these particular radial/interradial measurements were noticeably different from the others. Spine micromorphology was examined at 500X magnification on a dissecting microscope.

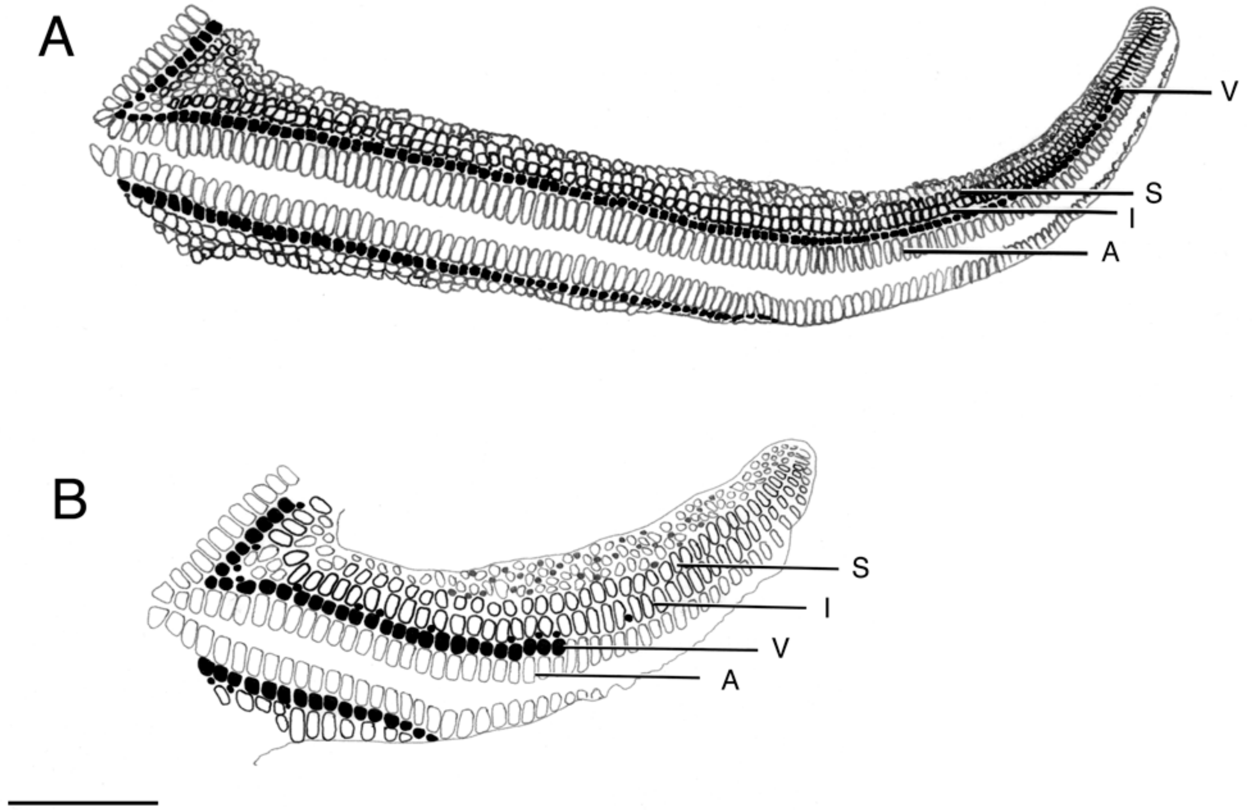

FIGURE 1. A drawing representing the plate series that flank the ambulacral groove on rays of A, *Henricia leviuscula* and B, *H. pumila* **n. sp.** Terms in parentheses are synonyms that have been used by other authors in published descriptions of species in the genus. Abbreviations: A adambulacral, V ventrolateral, shown in solid black (intermediate actinal, interactinal, actinal intermediate, peractinal, subactinal, oral intermediate), I inferomarginal (inframarginal), S superomarginal (supramarginal). Scale bar: A=1.0 cm, B=0.5 cm.

We also examined preserved type and non-type material at the Smithsonian Institution National Museum of Natural History (USNM), the California Academy of Science Invertebrate Zoology Department (CASIZ), the Natural History Museum of Los Angeles County (LACM), the Yale University Peabody Museum (YPM) and the Harvard University Museum of Comparative Zoology (MCZ).

Terms used for series of marginal plates are illustrated in Figure 1. Synonymous terms used by other authors are included in the caption. Counts of spines per pseudopaxilla (a group of spines attached to one skeletal plate) and papulae in the papular areas between pseudopaxillae were made near the base of a ray. The numbers of marginal, ventrolateral and adambulacral plates in longitudinal series on a ray were counted without removing spines, assuming there to be one group of spines per plate. Very small plates may have been hidden by the spines.

Live specimens were maintained in flowing seawater. Spawning was induced by intracoelomic injection of 10^{-4} M 1-methyladenine in distilled water, at a dosage of approximately 1 ml per 100 ml body volume (see Kanatani, 1979; Meijer & Guerrier, 1984; Strathmann, 1987).

To preserve whole specimens, some were relaxed in a solution of 1 part 7% $MgCl_2$: 4 parts seawater at room temperature, soaked 24 hours in 5–10% buffered formalin in seawater, and dried. Others were relaxed by gradual addition of 70% ethanol to seawater then preserved in 95% ethanol or were put directly into 95–100% ethanol. Specimens that had been frozen were either simply dried or soaked in buffered 10% formalin and dried.

Taxonomic account

Asteroidea de Blainville 1830

Spinulosida Perrier 1884

Echinasteridae Verrill 1870

Henricia Gray 1840

(type species *Asterias oculata* Pennant 1777 by monotypy)

Henricia leviuscula (Stimpson 1857)

Figs. 2A–E, 3A, 4A, 5A, 5C, 5E

Type: USNM 03357 (holotype)
Type Locality: Puget Sound, Washington, USA
Linckia leviuscula Stimpson, 1857: 529.
? *Cribrella leviuscula* (Stimpson), *Cribrella laeviuscula* (Stimpson), or *Henricia leviuscula* (Stimpson): Numerous authors reviewed by Fisher, 1911 and by A. Clark, 1996.
Henricia leviuscula (Stimpson 1857): in part Fisher, 1910: 570; in part Verrill, 1914: 215; in part Djakonov 1961:23, Pl. II, fig 9; in part Lambert, 1981: 100–103; 2000: 104–106.
Henricia leviuscula "var. A after Fisher": Djakonov 1950: 95, f. 79, 80
Henricia leviuscula var. B: in part Fisher 1911: 280–291, pl. 70, f. 2, pl. 111, f. 6
Henricia leviuscula var. *leviuscula*: in part Verrill 1914: 217, pl. XII–f. 5, pl. XIII, f. 1–2.
Henricia leviuscula var. *lunula*: in part Verrill 1914: 219

Type material examined: A specimen (Fig. 2A–E) originally labeled only "*Henricia leviuscula*, Id. W.K. Fisher, Ft. Steilacoom [near Tacoma, Pierce Co., Washington; 47°10.80′N 122°35.42′W], Pudget [sic] Sound, Dr. Geo. Suckley Col." matched Stimpson's brief published locality: "Found in Puget Sound, by Dr. Suckley." Our analysis revealed this specimen to be the likely holotype and it has since been labeled as such in the USNM collection.

Other material examined: more than 40 specimens in our collections from the San Juan Archipelago, including USNM 1116587 (Figs. 3A, 4A, 5C, 5E), Cattle Pt., San Juan Id., San Juan Co., Washington, intertidal, and MFS 149 (Fig. 5A), and two from Lovit Island, British Columbia. Museum specimens identified included: USNM 5991 (Baranoff Id., Alaska, 18m); USNM 3386 and 9225 (Puget Sound); USNM E4679 ("probably Alaska"); USNM E8678 (Departure Bay, British Columbia); USNM E3780 (Mouth of Strait of Juan de Fuca, 73 m); USNM E3820 (Port Townsend, Washington, 27–48 m); CASIZ 008559 (1 of 9 previously designated as vouchers for *Henricia leviuscula* by Fisher (1911:281–282, 285)); CASIZ 112955 (Anchor Pt., Kenai Peninsula, Alaska); CASIZ 180558 (San Juan Channel off Lopez Id., San Juan Co., Washington, 100–110); LACM 1959-281.3 (Monterey, California); LACM 1966-36.16 (lot of 2, off Cowichan, Sydney Channel, British Columbia 18–37 m); LACM 1966-37.19 (lot of 2, Sister's Rocks, outer Squamish Harbor, Hood Canal, Washington, intertidal); LACM 1966.39.23 (lot of 2, MacKaye Harbor, Lopez Id., Washington, intertidal); YPM 9836 (1 of 2 syntypes for *Henricia leviuscula* (Stimpson) var. *lunula* Verrill, 1914, Victoria, British Columbia, Canada, 20m).

Description: Most specimens have 5 slender rays, but 6-rayed individuals occur. Slender rays are without basal swelling and taper evenly to the ray tip. The dried holotype has 5 slender rays, not basally swollen, with R about 35 mm and r about 6.3 mm, R/r = 5.6 (Fig. 2A–E). Of 42 specimens from the San Juan Archipelago and 2 from Lovit Id., British Columbia, the largest had R = 70 mm, r = 10 mm and the smallest, R = 22 mm, r = 4.0 mm. The range of R/r was 5.0 to 8.3.

The aboral color in living specimens is distinctive bright orange, sometimes slightly red-orange (Fig. 3A), with the color characteristically continuing onto the oral surface, fading to light orange or yellow sometimes over the ventrolateral plates but most usually on only the adambulacral plates.

The aboral surface appears smoothly and regularly paved or scaled, this surface being composed of close-set pseudopaxillae with narrow intervening spaces and small recessed papular areas. In outline the pseudopaxillae are oblong or irregularly polygonal on the disc and oval, crescentic, heart-shaped, or triangular on the rays, with the concave or flat side toward the disc (Fig. 2B, 2D, 4A, 5C, 5E). The madreporite is not particularly prominent and bears single rows of spines that are like those on the pseudopaxillae.

Aboral papular areas have 1, sometimes 2, rarely 3 papulae. A regular series of single papulae occurs on the oral surface between the inferomarginal and ventrolateral plates on the disc and most of the ray length. A few single papulae may occur in an irregular series between some ventrolateral and adambulacral plates.

Aboral pseudopaxillae are composed of spines set in tissue-covered, close-packed, upright arrays of 20 to 100, but usually 25 to 55 (Fig. 5C, 5E). In living specimens the pseudopaxillae are covered by pigmented tissue through which some of the radiating glassy thorny tips of the spines might just be discerned. The aboral spines are stout with fenestrated glassy shafts, commonly 80 to 100 µm in diameter, with smooth sides. The ends of the spines have 3 to 7 heavy thorn-like points or tips (as noted by Djakonov 1961), of about equal sizes that flare in a fairly even radiating pattern that spans 100 to 190 µm (Figs. 2D, 5A, 5C, 5E). A large spine on the holotype is about 220 µm long, has a shaft about 70 µm in diameter, and ends in prominent sharp points radiating over a span up to 165 µm.

Ray sides have the lowermost dorsolateral pseudopaxillae in approximate 1:1 alignment with the superomarginal pseudopaxillae (plates) below them, but in offset alignment with the pseudopaxillae above them. Superomarginal pseudopaxillae are larger than the dorsolaterals, sometimes as much as twice the size.

Ray lower sides have three conspicuous series of pseudopaxillae: rectangular superomarginals and inferomarginals and smaller, squarish ventrolaterals. These series of pseudopaxillae are aligned in 1:1 correspondence beside the adambulacral plates for most of the ray length. The superomarginal series descends abruptly in the interradial area to lie adjacent to the inferomarginal series, enclosing a very small interradial triangle of only a few intermediate plates and, as Hayashi (1940) noted, there are no secondary ventrolaterals, singly or in series. The ventrolateral series usually extends most of the ray length, but sometimes only half. Among 21 specimens, the ratio of ventrolateral to adambulacral plates (V/A, counted from mouth to ray tip) ranged from 0.43 to 0.85 but only 2 specimens had ratios of 0.5 or lower.

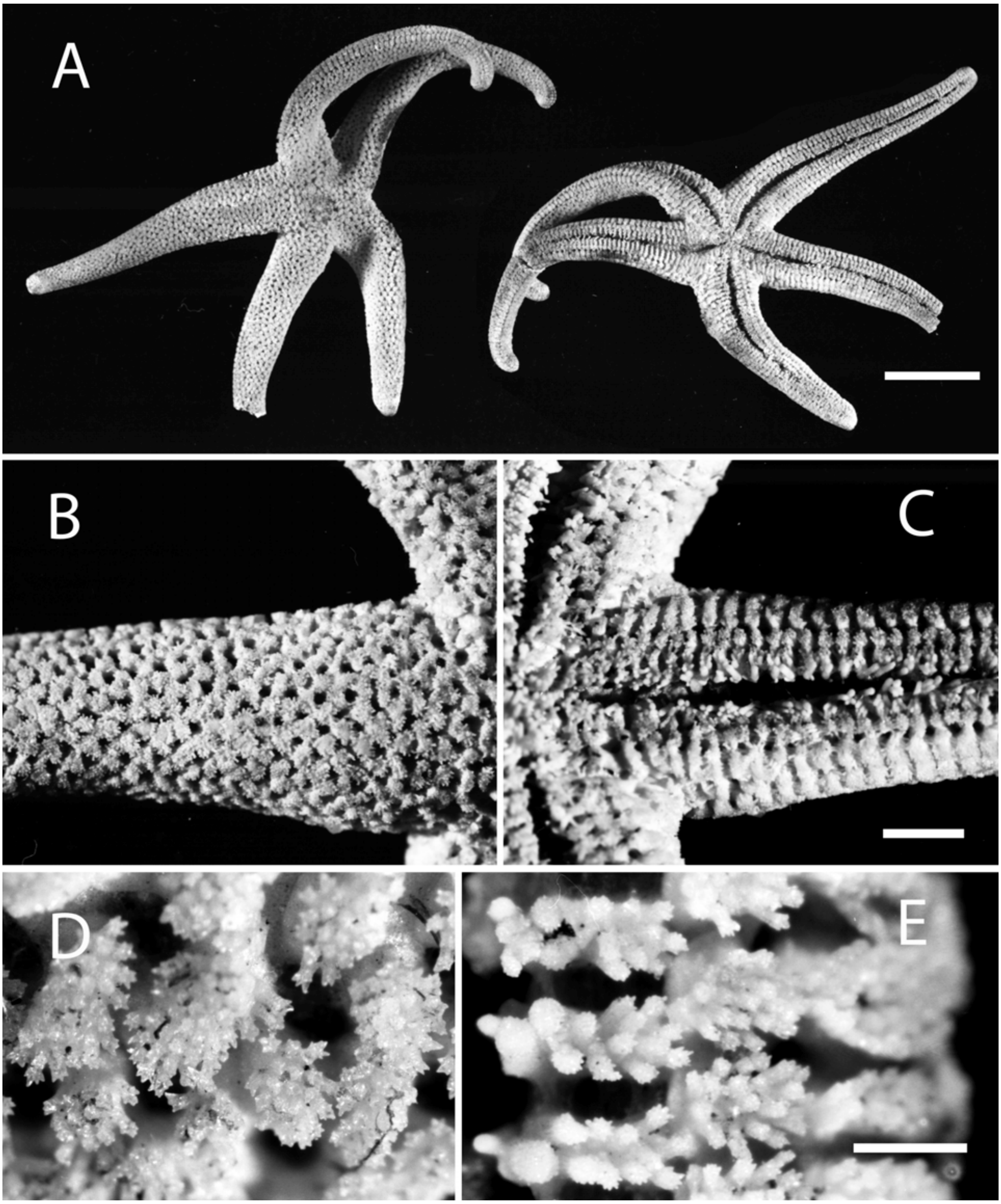

FIGURE 2. *Henricia leviuscula* holotype USNM 03357, dry. A. aboral and oral views, scale bar = 10 mm. Note slender rays and small disc. Two ray tips are broken. B–C. ray base to mid-ray, scale bar = 2 mm. B. aboral surface. Note close-set aboral pseudopaxillae and small papular areas. C. oral surface. Note 1:1 correspondence of adambulacral, ventrolateral, and, partially in view, inferomarginal plates covered with spines. D–E. ray base at higher magnification, scale bar = 0.5 mm. D. aboral pseudopaxillae. Note glassy spines with smooth-sided shafts and splayed points. E. oral view showing three sets of adambulacral, ventrolateral, and inferomarginal plates, with adambulacral furrow to the left. Adambulacral plates bear 1 deep furrow spine and 13 to 14 spines of diminishing size. Adjacent ventrolateral plates bear about 15 smaller spines. Inferomarginal plates (not in focus) are elongated and more spinous. Superomarginal plates, which lie aboral to the inferomarginals, are not in view.

Near the base of the ray, a superomarginal pseudopaxilla bears 25 to 100 spines; an inferomarginal, 32 to 100 spines; and a ventrolateral, 5 to 20 spines. The spine count varies among individuals and is not correlated with body size. Each adambulacral plate (Fig. 2C, 2E) bears 1 thin curved deep-furrow spine and 8 to 17 large, slightly curved, columnar spines in a zigzag or double row that becomes a triple or quadruple row on the edge farthest from the ambulacral furrow. The larger spines near the furrow are blunt-ended with finely spinous surfaces; those farther from the furrow are smaller and more coarsely spinous with sharp terminal points but not radiating thorns. On the holotype, the largest adambulacral spine is about 175 µm in diameter and 775 µm long.

Distribution: *H. leviuscula*, as restricted herein, has a confirmed range limited to southern Alaska (Kenai Pt.) south to Puget Sound (see Remarks). In the San Juan Archipelago it is uncommon in rocky intertidal areas but occurs more often in shallow subtidal areas. Many of the museum specimens whose identity we have confirmed are from the San Juan Archipelago, northern Puget Sound, or Vancouver Island.

Reproduction. We assume that sexes are separate. When specimens of *H. leviuscula*, or one of a number of similar co-occurring species, have been spawned in isolation, eggs have not been observed to develop. Spawned eggs have been measured at 1342 µm diameter (Strathmann *et al.*, 2002), and we confirmed that one female induced to spawn released slightly ovoid red-brown eggs 1.45 x 1.16 mm in diameter. Spawning individuals have been seen with the disc elevated to shed sperm or eggs freely into the water through aboral gonopores (Strathmann, 1987). Spawning season, like that of congeners with pelagic development, is probably early spring in the San Juan Archipelago. Development is similar to that described for other *Henricia* species (Masterman 1902, Strathmann 1987, Komatsu *et al.* 1995). Embryonic stages do not adhere to one another but float freely. Post-hatching larvae are ciliated and swim. Future reproductive observations need to be considered with respect to knowledge of multiple *H. leviuscula*-like species, but no one has ever reported feeding in any *Henricia* larva. This and the large size of their yolky eggs implies that larvae of *H. leviuscula* are lecithotrophic. However, the possibility that *Henricia* larvae might uptake dissolved organic matter has not been tested and no one has sectioned *Henricia* larvae to see if some might have an open mouth. The brachiolar larva has an anterior lobe with three brachiolar arms surrounding an adhesive disc and late in development has five groups of podia protruding on the left side. Metamorphosis begins after about 30 to 40 days; the anterior lobe is resorbed into the oral edge of the disc.

Remarks. We discovered a dried specimen in the USNM collections that matches the published record and we consider it to be the holotype. This specimen may be the one Fisher (1911: 284) wrote of as "perhaps the type; if not, it is at least a topotype." In describing a multi-species collection from Puget Sound made by N. R. Harrington from Columbia University in 1896 and 1897, H. L. Clark (1901) introduced two nominal varieties for Stimpson's *leviuscula* (as "*laeviuscula*"): *crassa* and *attenuata*. He provided only a brief diagnosis for each involving a ratio of the distance from the disc center to either the ray tip (R) or the disc edge between rays (r). R/r ranged from 2.0 to 3.5, n = 25 for *crassa* vs. R/r = 5.0, n = 1 for *attenuata*. We have been unable to locate Clark's type material at either the American Museum of Natural History (affiliated with Columbia University) or MCZ (where Clark later worked). Given the insufficient nature of Clark's characterization and the absence of known type material, we consider these nominal varieties as *nomen dubia*. Verrill's (1914) description of the color of *H. leviuscula* var. *attenuata* (Clark 1901) as "orange and orange-red above, yellow below" does not apply to *H. leviuscula* as restricted herein.

We consider Fisher's *H. leviuscula* variety B to correspond in part to *H. leviuscula* based on his statement (1911:281) that variety B is typical of the "littoral form from Puget Sound with very regular marginal plates, eight to fifteen adambulacral spinelets, and the abactinal spinelets ending in numerous sharp denticulations rather than in a solid glassy tip." He had examined "a specimen evidently labeled by Stimpson," and wrote that "the type is therefore one of the various forms of variety B, among those listed herewith." His photographs (Fisher, 1911: pl. 70, fig. b, c) are not at high enough magnification to show the form of the "sharp denticulations" of the aboral spines. Nothing in his description of variety B is incompatible with *H. leviuscula*, but his variety B may include at least one other sympatric species that has subtly different spines. We re-examined many museum specimens identified as *H. leviuscula* by Fisher and found that most lack the characteristic aboral spines exhibited by the holotype and belong instead to other species, some of which are likely undescribed. We believe that most reports of *H. leviuscula* from the North Pacific refer to other similar species. Fisher's *H. leviuscula* varieties A and C to F are probably all other species, some of which will be assessed in a regional revision of the genus (D. Eernisse and M. Strathmann, in prep.).

Verrill's (1914) eight varieties and one subspecies of *leviuscula* are mostly other species. We were able examine the only two known syntypes of *H. leviuscula* (Stimpson, 1857) var. *lunula* Verrill, 1914 and have tentatively identified one of these (YPM 9836), from Victoria, Vancouver Island, as *H. leviuscula*. We designate YPM 9836 as a paralectotype of *H. leviuscula*. We designate the other syntype (YPM 9835) as lectotype of *lunula* because this is clearly the only specimen figured and the only *lunula* “type” mentioned by Verrill. The aboral plates denuded of spines accord with his figures 2a–b (Plate 88) and the specimen is from Monterey, California, as stated by Verrill in reference to the figured specimen (p. 218); however, it is unclear whether he considered both specimens in the lot as “types” or only the figured specimen as holotype in a modern sense. Given the uncertainty, a lectotype designation is appropriate but the lectotype is not *H. leviuscula* and will be treated in a subsequent study (D. Eernisse and M. Strathmann, in prep.).

Djakonov (1950: 95) distinguished two varieties of *H. leviuscula* based on form of aboral spines. The aboral spines he described for *H. leviuscula* variety A, as “low with sharp but coarse glassy spines protruding on various sides as found in a specimen from Nanaimo Bay” (Djakonov 1950: figs. 79, 80), corresponds to the spine morphology we found on the rediscovered holotype. We have not seen any specimens studied by Djakonov but his *H. leviuscula* variety A could be *H. leviuscula*. It should be noted, however, that Djakonov's variety A is not equivalent to Fisher's variety A, which had aboral spines ending in a solid glassy tip. Djakonov's *H. leviuscula* variety B, characterized by aboral spines “stout with a thorny apical knob as found on typical specimens from Monterey Bay” (Djakonov, 1950: figs. 83, 84) is not *H. leviuscula* but another species possibly still undescribed.

Fisher (1911) reported that *leviuscula* in “typical form” (his variety B) occurred from the Aleutian Islands, Alaska, to Monterey Bay, California, and that southern specimens that were not “typical” extended to Santa Barbara Channel and San Diego, California. In contrast, Verrill (1914) considered *H. leviuscula* to be a “southern” form, noting that most of Fisher's specimens were from sites south of Sitka, Alaska. We have confirmed Fisher's identification of some *H. leviuscula* from near Sitka and Fort Wrangel (Alaska), Port Renfrew (Vancouver Island, British Columbia), Port Townsend (North Puget Sound), and Hecata (= Heceta) Bank off Oregon. Djakonov (1950, figs. 79, 80) described and illustrated his variety A from a specimen from Nanaimo, British Columbia and said that it had spines like those of the holotype.

Uchida (1928) described a single specimen of *leviuscula* from Japan, but Hayashi (1940) compared material from Japan with specimens thought to be of *leviuscula* from Kodiak, Alaska, and concluded that *leviuscula* was not present in collections from Japanese waters. Djakonov (1950) reported *leviuscula* from the Sea of Japan, but later (Djakonov 1961: 23), having decided that at least two species were known under the name, stated it difficult to define the true range, which might include Sea of Japan and near Paramushir Island of the Kurile Islands. Hayashi (1973: 11) did not list *leviuscula* among seastars from Japan. We did not find *leviuscula* in a small sample of representative species from Japan kindly made available to us by Mr. Masaki Saba and Mr. Yasuo Kano through the courtesy of Dr. Chitaro Oguro and Dr. Mieko Komatsu.

H. leviuscula is distinct from congeners described from Japanese waters (Hayashi 1940, 1973) or the North Atlantic (Heding 1935; Rasmussen1965; Madsen 1987, A. M. Clark & Downey 1992), and we have not seen any specimens of *H. leviuscula* as restricted herein from north or west of Kenai Peninsula, Alaska or south of Puget Sound, Washington. In the northern part of its range, in southeastern Alaska, it appears to be less common than its similar congeners (D. Eernisse and M. Strathmann, in prep.) and it is likely endemic to northeastern Pacific cool temperate coastal areas (northern Oregonian province).

***Henricia pumila*, n. sp.**

Figs. 1B, 3B–D, 4B–C, 5B, 5D, 5F–G

Type Material: Holotype USNM 1116585; paratypes USNM 1116586; CASIZ 180559 and 180560; LACM 1987-519.001 and 2005-065.001; MFS 109

Type Locality: Mar Vista Resort, San Juan Island, Washington, USA (48°28.595′N 123°04.015′W), rocky intertidal under rock in tidepool

?*Cribrella laeviuscula* var. *crassa* H.L. Clark 1901:328
Henricia leviuscula variety F, in part, Fisher 1911 (see also Feder, 1980; Lambert, 1981; Mah, 2007)
Henricia leviuscula (*non* Stimpson, 1857); in part, Hopkins, 1967: 19–23, 65–68

Other material examined: More than 100 specimens in our collections from the San Juan Archipelago, San Juan Co., Washington, plus other specimens from southern Vancouver Island, British Columbia, Canada, intertidal; Bodega Head, Sonoma Co., California, intertidal; Franklin Pt., San Mateo Co., California, intertidal; Monterey Breakwater, Monterey Co., California, approx. 12–15 m, including one brooding female; Shelter Cove, between Shell Beach and Pismo Beach, San Luis Obispo Co., California, intertidal; Arbolitos, south of Punta Banda, Baja California, Mexico, intertidal. Museum specimens identified included: USNM 1083883 (3 in lot), Carmel, Monterey Co., California; USNM E3831 (2 in lot), Monterey Bay, California; USNM E3832 (2 in lot), Strait of Juan de Fuca, Washington; USNM E21533, San Nicolas Id., California; USNM 1083885 (3 in lot), Puget Sound, Washington; CASIZ 008558 Crescent City, California (1 specimen in alcohol, likely “variety F” voucher for Fisher, 1911:285); LACM 1959-281.12 (1 specimen), Monterey Co., California, intertidal, 36°32’N 121°56’W; LACM 1928-3.1, Pacific Grove, California, intertidal. We have additionally examined images of seastars from the vicinity of Sitka, Alaska (Fig. 3C) and from Cape Arago, Oregon (Fig. 3D) that appear to be the same species.

Diagnosis. Small in size; rays stout and short (R/r less than 5), aboral pseudopaxillae well-spaced, bearing up to 50 short spines with fenestrated, crystalline, smooth-sided shafts tipped by up to 10 heavy sharp points that do not noticeably splay. Aboral color in life usually a mottled pattern of ochre, brown, gray, rust-red, or yellow; oral color yellow to cream. Gonopores orally-directed, eggs non-buoyant, development benthic and brooded.

Description. Holotype (Figs. 3B, 4B, 5D, 5F), collected by RRS and MFS on March 30, 2005, is a medium-sized specimen, in life R = 19.7 mm, r = 6.4 mm. Madreporal ray 6.8 mm wide at base. Living aboral colors are ochre mottled with red-brown spots on every ray, orange-red around the anus extending toward one interradius, and orange at the ray tips (Figs. 3B). Madreporite cream yellow. Oral color orange yellow. A large aboral pseudopaxilla with 25 spines (Fig. 4B, 5D, 5F).

Most specimens have 5 rays; 4- or 6-rayed individuals are rare. The rays taper rather evenly from base to tip but are short and stout. Among 34 specimens from the San Juan Archipelago (the largest having R = 29.4 mm and r = 6.3 mm and the smallest having R = 4.1 mm and r = 1.4 mm), R/r varied from 1.8 to 4.7, average 3.0. Aboral color usually mottled, the mix may include yellow, ochre, brown, rust-red and gray, all colors not always present on each individual (southern specimens show a greater range of mottling); oral color cream to orange yellow. Madreporite distinct; madreporal spines grouped at the periphery and in single rows across the center and the same size as the aboral pseudopaxillar spines. Aboral pseudopaxillae well-spaced and separated by recessed tissue and papular areas containing 1 to 4 papulae, the maximum number increasing with body size. Aboral pseudopaxillae oval or irregularly oblong on the disc and oval to crescentic on the rays consisting of tissue-covered spines in groups of 2 to 50, usually 12 to 45, the number increasing with body size.

Aboral spines are short and stout and terminate in multiple short sharp points that do not markedly splay and so are directed more or less distally (Figs. 5B, 5D, 5F), which can be obscured by tissue in living or air-dried (Fig. 5G) specimens. On the rays, two marginal and one ventrolateral series of pseudopaxillae form regular and obvious rows flanking the ambulacral plates that edge the ambulacral furrow. Near the ray base, a small triangle of interradial pseudopaxillae is enclosed between the superomarginal series, as it descends from the aboral disc to lie along the ray side, and the inferomarginal series. Both the supero- and inferomarginal pseudopaxillae are slightly larger than the aboral pseudopaxillae and extend to the ray tip in 1:1 correspondence with the ambulacral plates. The ventrolateral pseudopaxillae are small and this series extends half to three-fourths of the length of the ray (Fig. 1B, 4C). Among specimens with R ranging from 9.0 to 29.4 mm, the ratio of ventrolateral to adambulacral pseudopaxillae (V/A, counted from mouth to ray tip) ranged from 0.34 to 0.79, averaging 0.62 (N = 53; holotype V/A = 0.74).

A regular series of single papulae occurs between the inferomarginal and ventrolateral pseudopaxillae and single papulae between some ventrolateral and adambulacral pseudopaxillae.

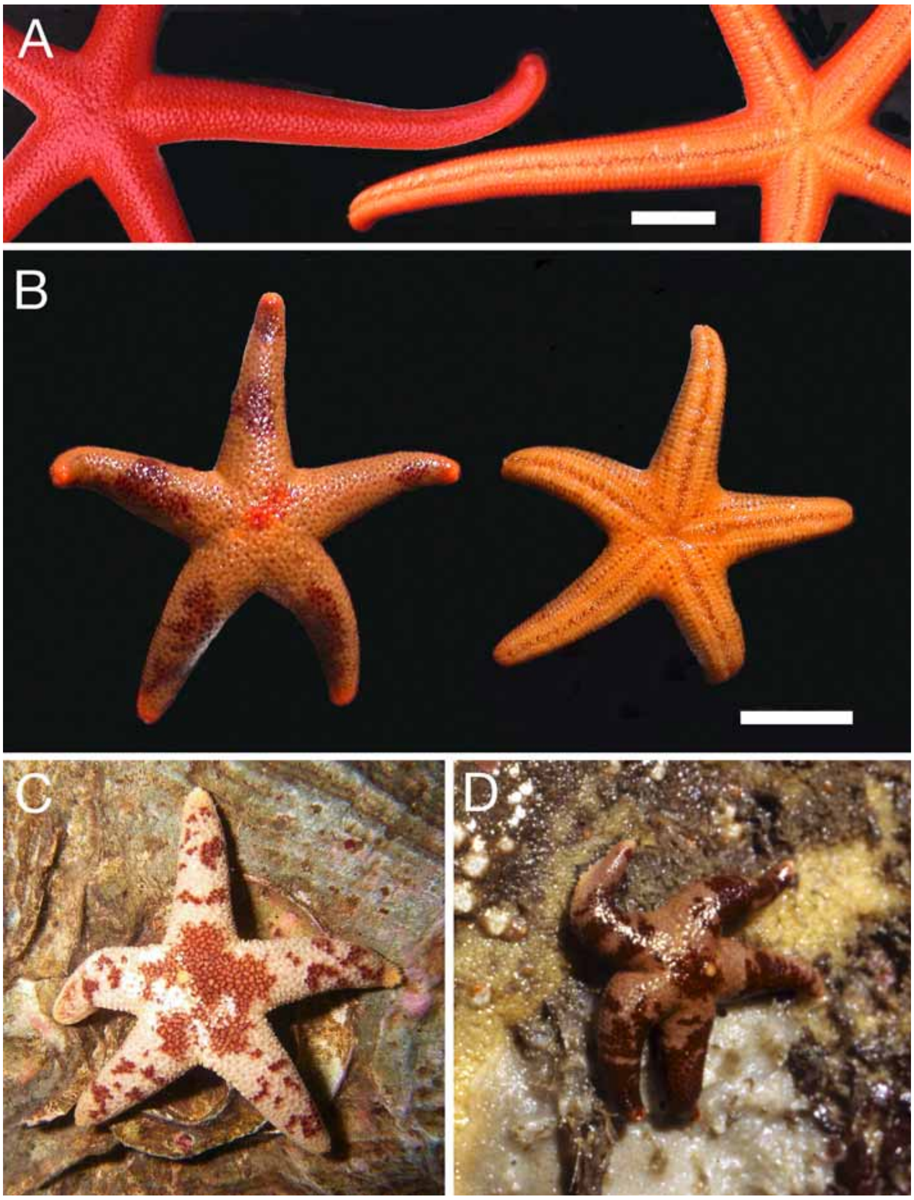

FIGURE 3. Living coloration. A. *Henricia leviuscula* voucher USNM 1116587. B. *Henricia pumila* **n. sp.** holotype USNM1116585. A whole seastar, aboral and oral views, scale bar = 1 cm. Note the small size, short rays in relation to disc diameter. B–C. ray and disc, scale bar = 1 cm. B. aboral and oral views. On aboral surface note small, crescentic pseudopaxillae and relatively larger papular areas. On oral surface note elongated adambulacral plates with few spines, ventrolateral plates extending only four-fifths the ray length, and elongated inferomarginal and superomarginal plates (the latter not entirely in view). C. Color in field for likely *H. pumila* from near Sitka, Alaska (image by A. Baldwin). D. Color in field for likely *H. pumila* from Cape Arago, Oregon (image by J. Goddard).

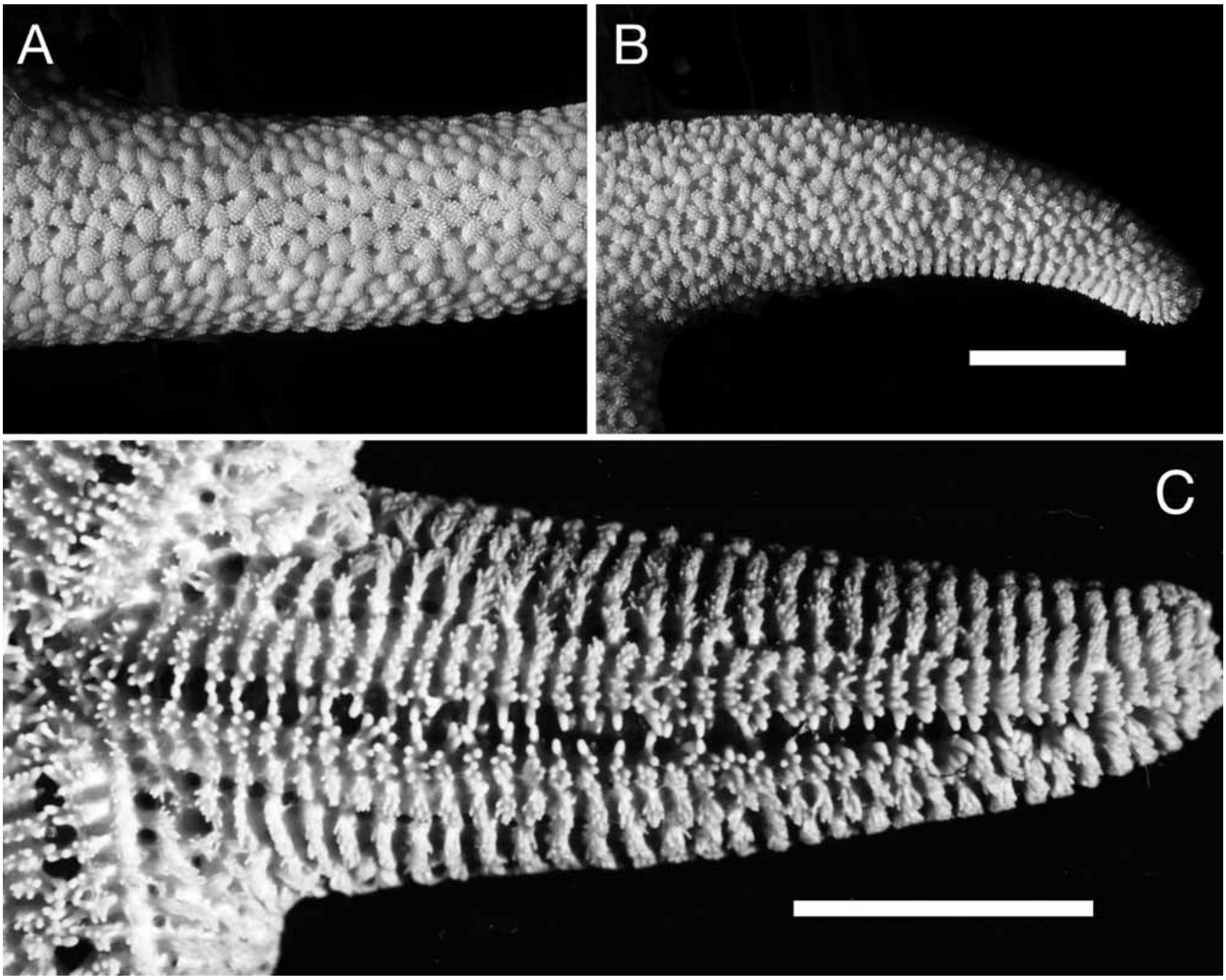

FIGURE 4. A–B. Detail of aboral surface of single ray. A. *Henricia leviuscula* voucher USNM 1116587 (see also Figs. 3A, 5C, 5E). B. *H. pumila* **n. sp.** holotype. C. Oral surface of single ray, *H. pumila* **n. sp.** USNM 1116586 paratype. Note the ventrolateral series of plates/spines extends unusually far in this individual (contrast with Fig. 1B). A–B same scale bar = 4 mm. C scale bar = 4 mm. Images A–B by A. Draeger.

Near the base of the ray, superomarginal pseudopaxillae have 12–37 spines each; inferomarginals, 10–32; and ventrolaterals, 5–20. Number of spines per pseudopaxilla generally increases with body size. Each adambulacral plate bears one thin, curved deep-furrow spine and 6–14, usually no more than 10, large, slightly curved, columnar spines in one row that becomes double then triple farthest from the ambulacral furrow. The large spines nearest the furrow are blunt-ended with finely spinous surfaces, the tips sometimes slightly flattened but not spatulate; those farther from the furrow are smaller and more coarsely spinous with sharp terminal points but not radiating thorns. On the holotype, the largest adambulacral spine is about 500 µm long and the points at the tip span 160–200 µm.

Distribution. *H. pumila* is the only small, brooding species of this genus presently known in Puget Sound and the San Juan Archipelago, Washington. It seems to be a widespread Pacific Coast shallow-water coastal species. In the north, it occurs in southern British Columbia, Canada and probably ranges further north to Sitka, Alaska, USA. The southern-most record is from areas of cold-water upwelling at Arbolitos, south of Punta Banda, Baja California, Mexico, but the species appears to skip over southern California, with the next-most southern record near Pismo Beach, California, north of Pt. Conception. Despite the lack of records from southern California, it might be present in the Channel Islands or in unexplored subtidal areas.

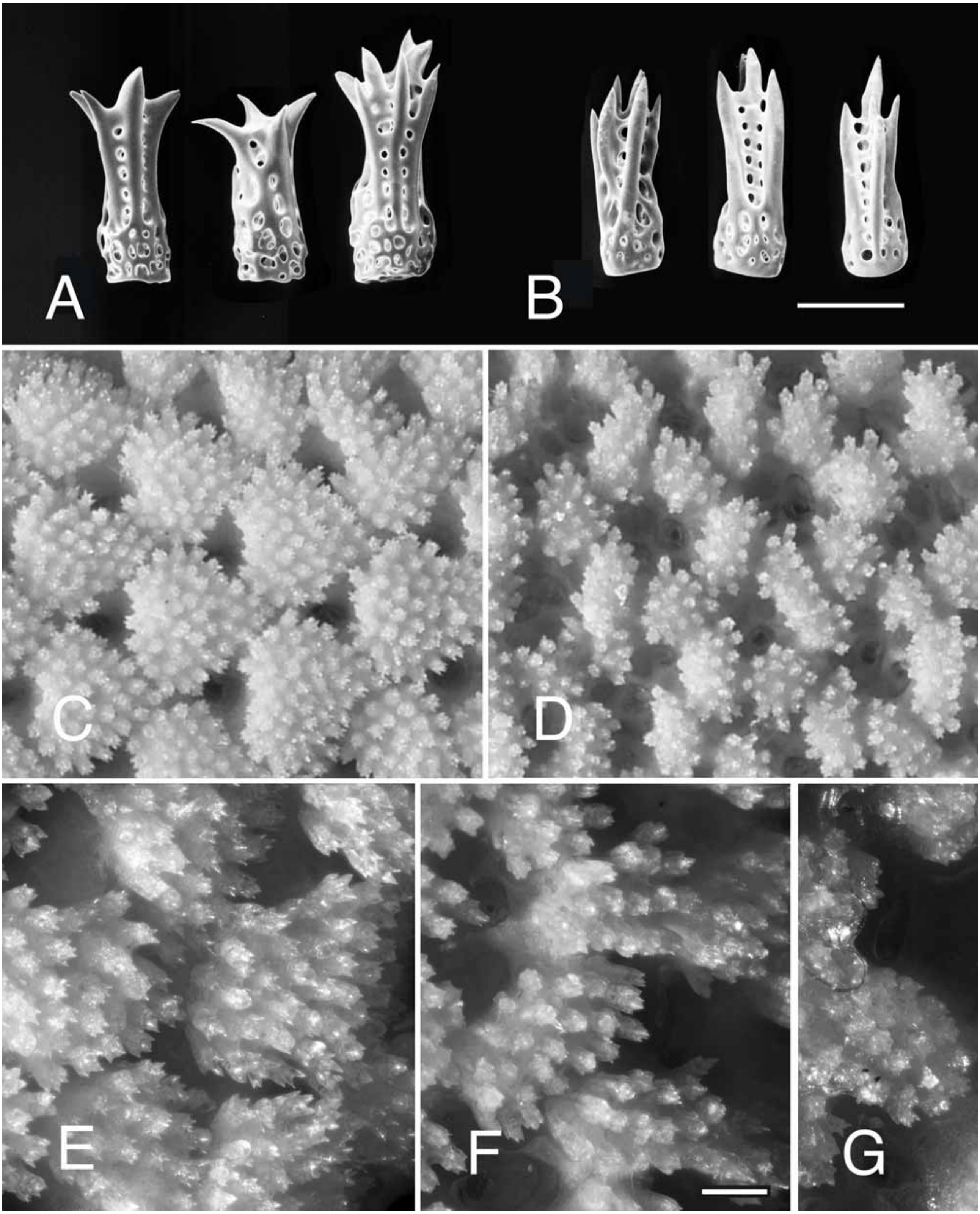

FIGURE 5. A–B SEM images of aboral spines, scale bar = 100µm. A. *Henricia leviuscula* (MFS 149) spines with fenestrated smooth-sided shafts tipped with splayed sharp points. B. *Henricia pumila*, **n. sp.** (MFS 109 paratype) spines with fenestrated smooth-sided shafts tipped with sharp points that do not splay. C–G close-ups of aboral pseudopaxillae. C, E. *H. leviuscula* USNM 1116587. D,F. *H. pumila* **n. sp.** holotype. G. *H. pumila* **n. sp.** USNM 1116586 paratype, fixed in formalin and air-dried. Note tissue obscuring spine tips.

Reproduction. We have assumed sexes are separate but have not dissected gonads to thoroughly search for evidence of hermaphroditic tissues, as is known for some small brooding marine invertebrates (e.g., Strathmann *et al.*, 1984; Eernisse, 1988; Colgan *et al.*, 2005; Keever and Hart, 2008). Eggs are shed through gonopores on the oral side of the disc edge between rays (Chia, 1966; Hopkins, 1967), in contrast to their aboral position in *H. leviuscula* and other free-spawning species. Eggs about 1144 µm diameter (Strathmann *et al.*, 2002) are neither buoyant nor sticky when shed and are held beneath the maternal body with the rays spiraled, pinwheel fashion, around a slightly elevated disc (R. Strathmann, unpubl. observ.). Embyos are brooded under the disc and emerge as crawl-away juveniles. Brooding in rocky low intertidal areas of the San Juan Archipelago and central California has been seen in January to April. The Atlantic deep-water congener, *Henricia lisa*, has recently been shown to be a facultative brooder (Mercier and Hamel, 2008) and, although the mode of brooding differs, the same possibility exists for *H. pumila* and other asteroid species known to brood.

Etymology. From the Latin for dwarf, the term used by Fisher (1911) for the small adult body size of this species.

Remarks. It is possible that this species is the same as Hubert Lyman Clark's (1901) stout-rayed variety *Cribrella* (=*Henricia*) *laeviuscula* [sic] variety *crassa* from Puget Sound. Clark was an affiliate of Olivet College, Olivet, MI, about the time he described this variety by only its body size and ray shape. The museum at Olivet College was unfortunately destroyed by fire in 1968, and most of the records were lost (Marie Davis to Robert Woollacott, pers. comm.). We have not found types for Clark's nominal variety in museums where it seemed plausible that he might have deposited material, including the Museum of Comparative Zoology at Harvard University (where Clark was later curator of echinoderms from 1910 to 1946) or the American Museum of Natural History (Clark reported that the specimens were collected in Puget Sound by a group from Columbia University, and Columbia's museum later became part of the AMNH collections). A partially dissected dried specimen was found at Harvard's MCZ; its only label is clearly not the original because it reads "*Henricia laeviuscula crassa* (Clark) Locality: Puget Sound, Washington" (MCZ 1046). The morphology of this specimen corresponds to *H. pumila* but the entries for it in the accession catalogue and a 1930s list of specimens do not give collection information or an accession date. Given the brevity of the description and the lack of verifiable type material, we consider Clark's varietal name, *crassa*, to be a *nomen dubium*, as similarly concluded by Fisher (1911, 1930) and Verrill (1914).

Fisher's (1911) specimens of the small form that he called *H. leviuscula* variety F were collected from the vicinities of Monterey, San Francisco, and Crescent City in California and the Straits of [Juan de] Fuca and Puget Sound in Washington. Although Fisher knew some of these to be brooders, and described the brooding posture as arched, his specimens (see also Kozloff, 1996; Mah, 2007) may have included more than the one species we describe here as *H. pumila*.

There is at least one other at least partly co-occurring, and probably undescribed, small-bodied species from British Columbia south to northern Baja California. Yet another species is usually small and is so far known from the subtidal of central and southern California (D. J. Eernisse and M. Strathmann, in prep.). Both of these species have finer and more numerous spines per plate. Nothing is yet known of their life history traits so the possibility remains that one or both might be brooders. Other *Henricia* species are known to be brooders but differ in their distribution and morphology. *H. tumida* Verrill 1909 grows larger and has broader, thicker arms and is reported from the Aleutians Islands, Alaska, and the Bering Sea. It was discussed as *H. sanguinolenta eschrichtii* or *H. tumida* by Fisher (1911, 1930), and as *H. tumida* or *H. tumida borealis*, or possibly as *H. arctica,* by Verrill (1909, 1914). Djakonov (1950: 85–86) later described and illustrated specimens of *H. tumida, H. tumida borealis,* and a similar smaller species, *H. arctica*, from the Sea of Okhotsk and the Bering Sea. He reported that *H. arctica* is also found in the Litke Strait and off Cape Lisburne, Alaska. It is not known if *H. arctica* is a brooding species. Small brooding species have been reported from Japan, and the development of one, *H. nipponica*, has been described (Komatsu & Tayayama 1980). We have not studied *H. nipponica* but believe it unlikely to be the same as *H. pumila* because nothing resembling *H. pumila* is yet known from the intervening Aleutian Islands. We have seen little genetic evidence of marine species with such a disjunct eastern and western Pacific distribution. Thus, we speculate that any brooding *Henricia* in the northwestern Pacific might be closely related to, but not conspecific with, *H. pumila*. An extension of the study of small brooding species of *Henricia* to the far northern and northwestern Pacific is still needed.

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