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Author(s): Nicholas D. Holland, Karen J. Osborn, and Linda A. Kuhnz

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A new deep-sea species of harrimaniid enteropneust (Hemichordata)

Nicholas D. Holland*, Karen J. Osborn, and Linda A. Kuhnz

(NDH) Marine Biology Research Division, Scripps Institution of Oceanography, University of California at San Diego, La Jolla, California 92093, U.S.A., e-mail: nholland@ucsd.edu;
(KJO) Department of Invertebrate Zoology, Smithsonian Institution, National Museum of Natural History, Washington, D.C. 20013-7012, U.S.A.;

(LAK) Monterey Bay Aquarium Research Institute, Moss Landing, California 95039, U.S.A.

Abstract.—Ninety-two individuals of a deep-sea harrimaniid enteropneust were imaged between 1675 m and 3225 m off the California coast. Of these, about three-fourths were positioned with their posterior regions buried in sediment or hidden by rocks, and the rest were completely exposed on the substratum. When visible, the posterior end of each worm was typically associated with a dense tangle of fecal strands. One specimen was captured and is described here as the holotype of *Saxipendium implicatum*. In life, it was 22 cm long, and the color of its dome-shaped proboscis, narrow collar, and anterior trunk was medium orange. No wing-like folds of the body wall protruded anywhere along the length of the worm. The proboscis complex included a stomochord and glomeruli, but neither a heart nor a pericardial cavity could be detected. Most of the dorsal collar nerve runs along an open invagination in the dorsal midline of the collar and is only roofed over very briefly at the posterior extremity of the collar. Another unusual feature is the exaggerated posterior extension of the horns of the proboscis skeleton, which projected into the anterior extremity of the trunk. The trunk commenced anteriorly with a pharyngeal/esophageal region that included a tract of ovaries on either side of the dorsal midline. The ripest ovaries contained a single oocyte approximately 700 μm in diameter (presumably this species is gonochoric, although no males have yet been collected). The gill skeleton lacked synapticles. More posteriorly, the trunk housed a long, darkly pigmented hepatic intestine without sacculations and a short, lightly pigmented post-hepatic intestine. The geographic range of *S. implicatum* appears to be restricted to the Davidson, Guide, and Taney Seamounts region in the eastern Pacific offshore of Central California.

Keywords: collar nerve cord, Enteropneusta, Harrimaniidae, proboscis skeleton, seamount fauna

Enteropneust hemichordates, commonly called acorn worms, at present comprise roughly 100 described species. Through the end of the twentieth century, almost all of these had been collected from relatively shallow depths, with only the following three exceptions: *Glandiceps abyssicola*

Spengel, 1893 (family Spengelidae) from 4570 m, *Glossobalanus tuscarorae* Belichov, 1971 (family Ptychoderidae) from 8100 m, and *Saxipendium coronatum* Woodwick & Sensenbaugh, 1985 (family Harrimaniidae) from 2478 m. During the last few years, however, it has become clear that deep-living enteropneusts are considerably more common than previ-

* Corresponding author.

ously thought. This was emphasized by Holland et al. (2005), who established a fourth enteropneust family, the Torquaratoridae, which is evidently limited to the deep sea (Osborn et al. 2012). The following six torquaratorids have been described: *Torquarator bullocki* Holland et al., 2005; *Tergivelum baldwinae* Holland et al., 2009; *Allapasus aurantiacus* Holland et al., 2012; *Allapasus isidis* Holland in Priede et al. (2012); *Tergivelum cinnabarinum* Holland in Priede et al. (2012); and *Yoda purpurata* Holland in Priede et al. (2012). Moreover, additional deep-living members of this family have been collected and are awaiting description. These developments have contributed to an awakened interest in enteropneust systematics and ecology (Smith et al. 2005, Cannon et al. 2009, Cameron et al. 2010, Deland et al. 2010, Anderson et al. 2011, Osborn et al. 2012).

The present paper concerns a second deep-sea acorn worm in the family Harrimaniidae—the first, as already mentioned, is *Saxipendium coronatum*, which was collected by submersible near hydrothermal vents along the Galapagos Rift. The second deep-living harrimaniid was collected by a remotely operated vehicle (ROV) off the California coast and was shown to be closely related to *S. coronatum* by Bayesian- and parsimony-based phylogenetic analysis of rDNA sequences by Osborn et al. (2012), who designated it “*Saxipendium* sp. 1.” Here we describe and name this deep-sea harrimaniid as a new species.

Materials and Methods

The enteropneusts were observed and collected by the ROVs *Tiburón* and *Doc Ricketts* of the Monterey Bay Aquarium Research Institute (MBARI). Ninety-two specimens were imaged by video recording in the deep sea off the central California coast at Guide Seamount, Davidson Seamount, and Taney Seamounts A and C (Fig. 1). The observations, which were

made between March 2000 and August 2010, were opportunistic in the sense that the primary objective of the dives was to study geology, not acorn worms. The worms appeared in segments of video-recordings, each lasting from a few seconds to a few minutes. Densities were measured when quantitative information was available, either from video transects used to assess biological communities (1 m wide field of view for a known distance) or from counts within quadrats using still images. The spatial scale for both approaches was indicated by paired, calibrated lasers mounted on the ROV camera.

In addition, a single specimen, the holotype, was imaged and then collected in its entirety by suction sampler on 11 August 2010. By the time the worm reached the surface, the fragile body had broken into four pieces. A small tissue sample was fixed in chilled 95% ethanol for molecular sequencing, and the remainder of the worm was fixed in 10% formalin-sea water for histological examination. DNA extraction from the ethanol-fixed material, sequencing, and phylogenetic analysis were performed according to Osborn et al. (2012). For morphological study, selected body regions were embedded in paraplast, cut 15 μm thick, and stained with 0.1% aqueous azure A.

Results and Taxonomic Remarks

Phylum Hemichordata Bateson, 1885
 Class Enteropneusta Gegenbaur, 1870
 Family Harrimaniidae Spengel, 1901
 Genus *Saxipendium* Woodwick & Sensenbaugh, 1985

Type species.—*Saxipendium coronatum* Woodwick & Sensenbaugh, 1985

Saxipendium implicatum, new species
 Figs. 2–4

Saxipendium sp. 1 Osborn et al., 2012.

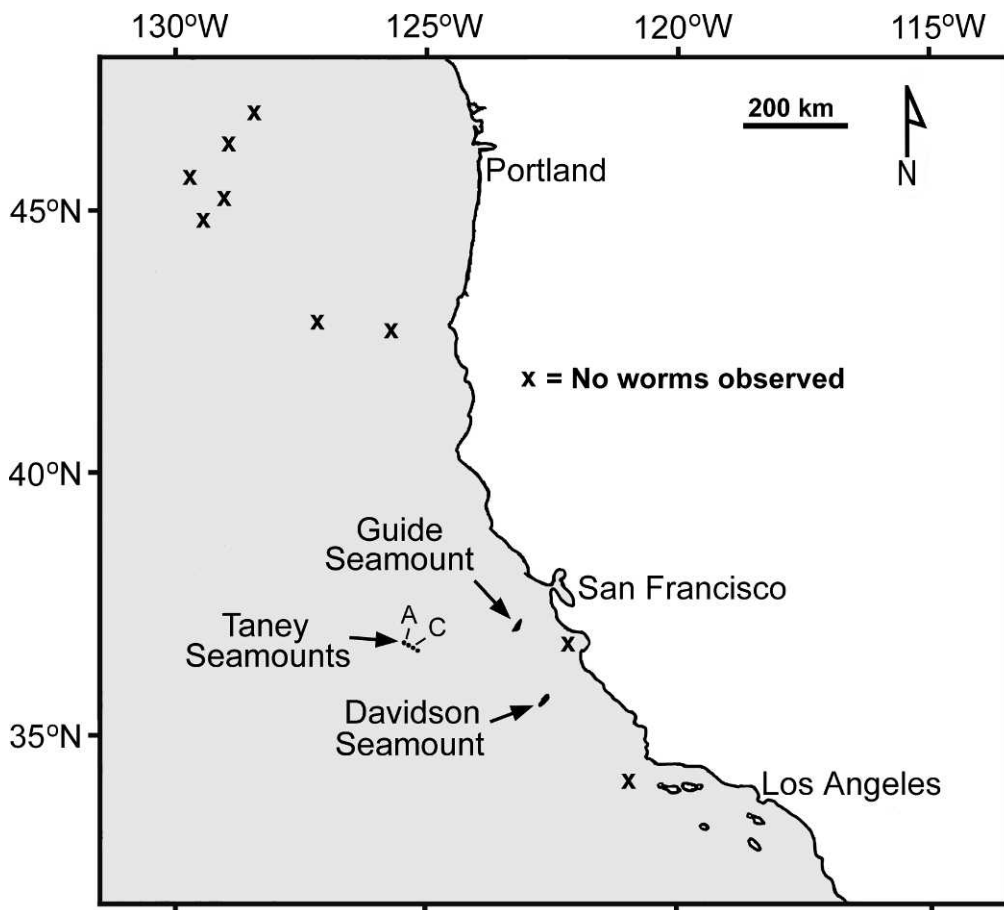


Fig. 1. Specimens of *Saxipendium implicatum* were imaged/collected on dives between 1675 m and 3225 m at the three arrowed locations (Guide Seamount; Taney Seamounts A and C, and Davidson Seamount). At sites marked "x" no worms were observed during dives to comparable habitats and depths.

Type material.—Holotype: ROV *Doc Rickets* dive 176 (36°51'N, 125°33'W), 3034 m, 11 Aug 2010, D. A. Clague. Formalin-fixed female prepared as serial cross-sections. Histological preparations and unsectioned regions of the holotype are deposited in the Scripps Institution of Oceanography Benthic Invertebrate Collection as SIO-BIC-H25. No paratypes collected, but video images of 91 uncollected specimens are available for study (MBARI video archives).

Diagnosis.—Differing from *Saxipendium coronatum* in the following respects: 1) length-to-width ratio of proboscis significantly smaller; 2) color of anterior body

regions medium orange (instead of yellow-white); 3) dorsal collar nerve incompletely invaginated (instead of completely invaginated as a tubular collar cord).

Etymology.—From the Latin *implicatum* or "entangled," referring to the contorted fecal strand generally accumulated around the posterior of the living worm.

Description, external.—The living holotype, as measured from deep-sea video images, was approximately 22 cm long (Fig. 2a). In addition, four of the uncollected worms (identified here by dive number) that were visible in their entirety and favorably oriented had body lengths

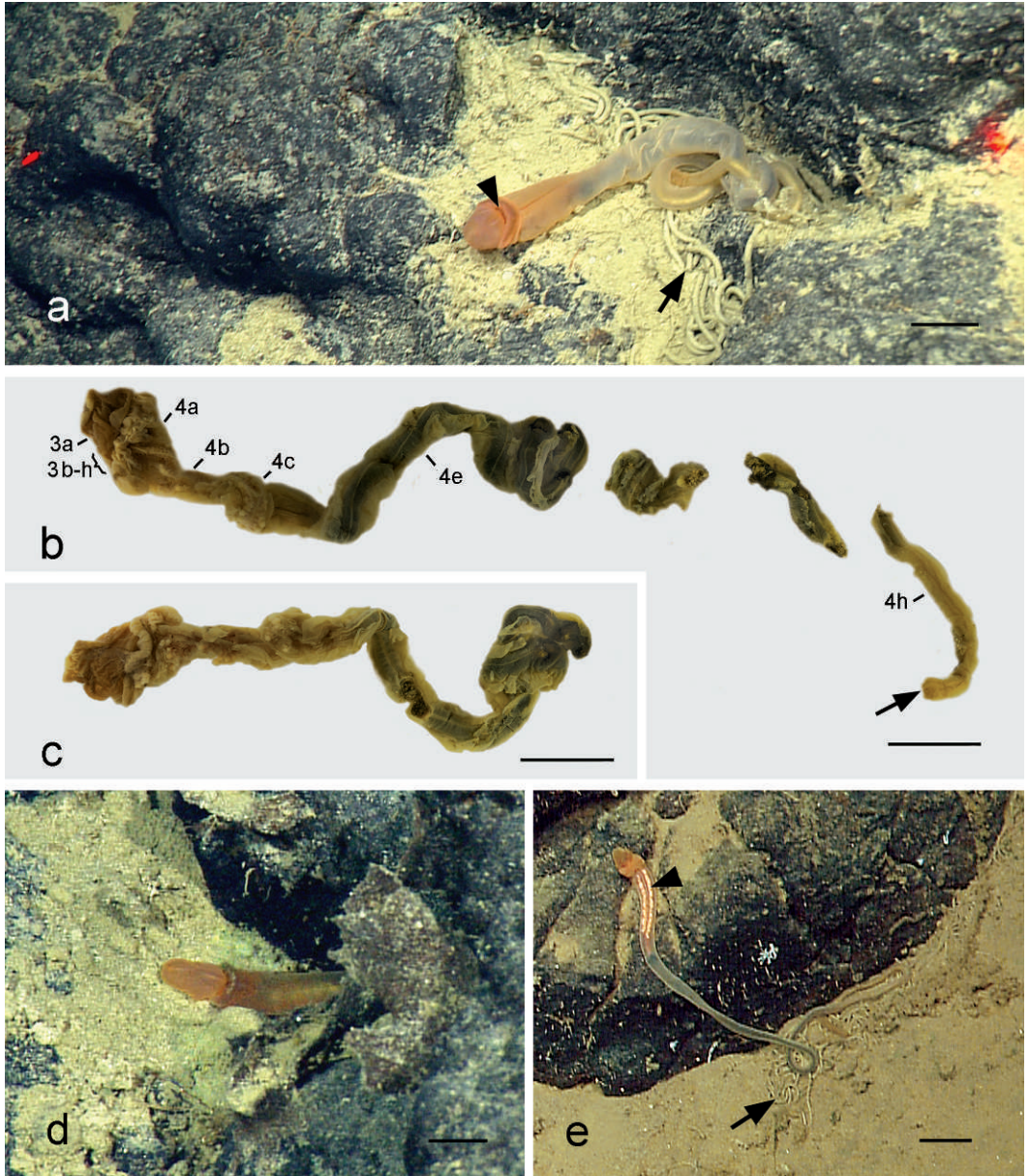


Fig. 2. *Saxipendium implicatum*. a, living holotype at 3034 m with anterior end twisted ventral side up, showing mouth (arrowhead); worm's tangled fecal strand indicated by arrow; red laser marks 29 cm apart. b, fixed holotype: major portion (anterior toward left) with proboscis and collar in dorsal view; also shown are three small posterior fragments; anus arrowed; levels of cross sections in Figs. 3 and 4 indicated. c, fixed holotype: major portion with proboscis and collar in ventral view. d, living worm at 2506 m (dive D177) but not subsequently collected; anterior end in approximately dorsal view; most of trunk hidden beneath rock overhang. e, living worm at 2973 m (dive T1074), but not subsequently collected; arrow indicates tangled fecal strand and arrowhead indicates gonads running along dorsal side of pharyngeal/esophageal portion of trunk. Scales a, d = 2 cm; b, c = 1 cm; e = 3 cm.

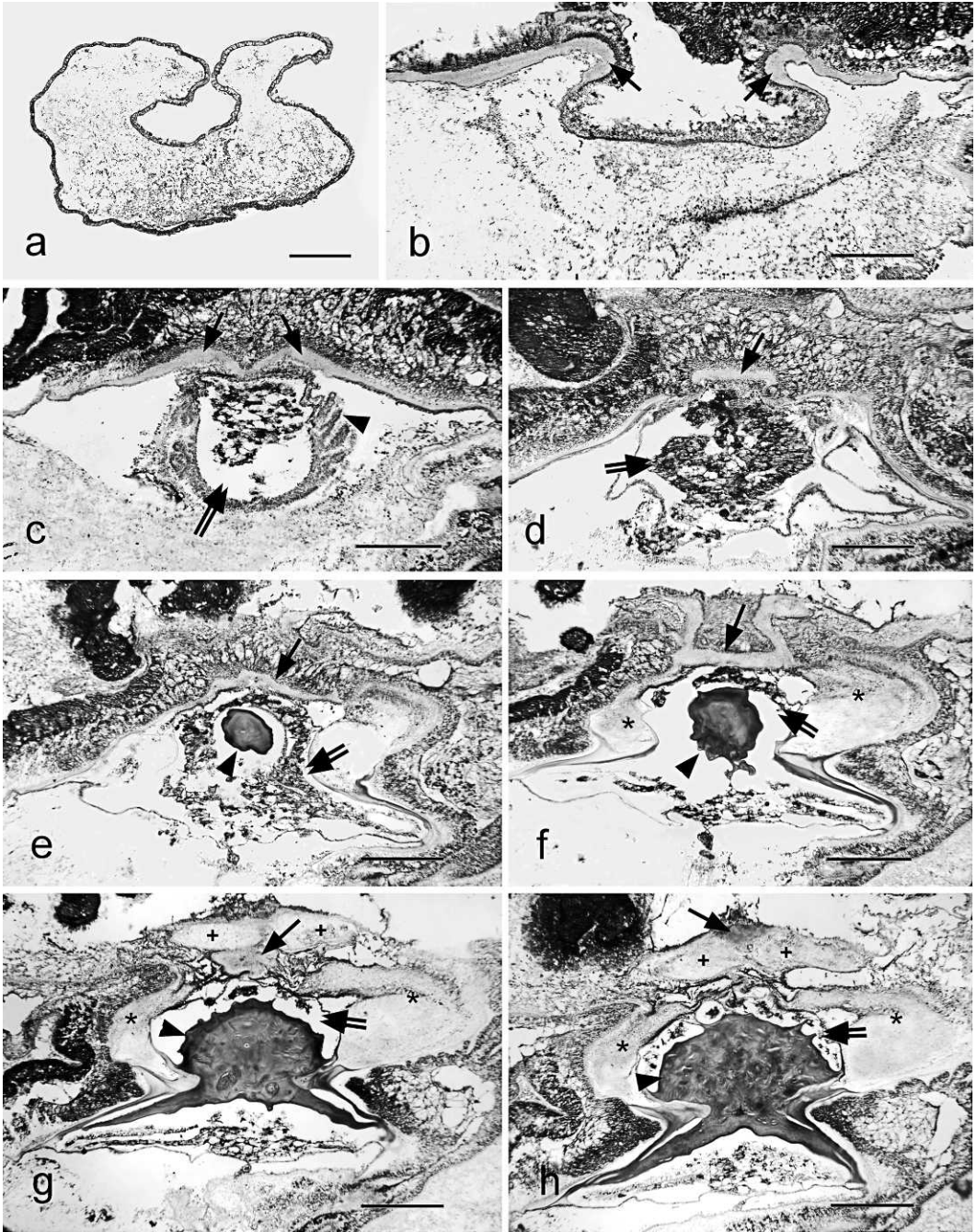


Fig. 3. *Saxipendium implicatum*. All cross sections with dorsal toward top. a, proboscis with dorsomedial groove (through level 3a in Fig. 2b). b-h, proboscis stalk and collar at successively more posterior levels in interval 3b-h in Fig. 2b. b, arrows indicate proboscis nerves on either side of dorsal midline of proboscis stalk. c, proboscis nerves (arrowed) merging mid dorsally; twin arrows indicate stomochord bearing glomeruli laterally (arrowhead). d, non-invaginated dorsal collar nerve (single arrow); stomochord (twin arrows) no longer associated with glomeruli. e, non-invaginated collar nerve (single arrow); stomochord (twin arrows); rostrum of proboscis skeleton (arrowhead). f, incompletely invaginated collar nerve cord (single arrow);

of 23 cm (D174), 26 cm (D174), 26 cm (T1074), and 35 cm (D174). In life, the color of the proboscis, collar, and the pharyngeal/esophageal region of the trunk was medium orange; more posteriorly, the intestinal region of the trunk was beige, with a slightly black tint for much of its length due to the darkly pigmented endoderm cells of the long hepatic intestine. After collection and fixation, the holotype had shrunk to a length of about 15 cm and had broken into one long anterior part and three shorter posterior portions. In general, the fixed holotype (Fig. 2b, c) was considerably wrinkled and distorted at the gross anatomical level, especially at the anterior end. As a result, nothing definitive could be said about the presence or absence of some structures. Even so, the results at the histological level permit the unequivocal description of the worm as a new species in the genus *Saxipendium*.

The proboscis was dome-shaped (1.3 cm long by 1.2 cm wide) in the living holotype but slightly extended (into a pear shape) in some of the specimens that were imaged but not collected (Fig. 2d). The length-to-width ratio of the living proboscis of *Saxipendium implicatum* ($\bar{X} = 1.15$, $SD = \pm 0.12$, $n = 8$) was significantly smaller than that of the arrow-shaped proboscis of *S. coronatum* ($\bar{X} = 1.89$, $SD = \pm 0.21$, $n = 8$); t -test, $p < 0.0001$. In the living holotype of *S. implicatum*, the collar was 1.4 cm wide by 0.6 cm long (as seen from the ventral side). No well-defined folds of body wall (for instance like the genital wings of ptychoderids) protruded anywhere along the length of the trunk. Tracts of gonads, visible through the body wall of

relatively ripe specimens, ran on either side of the dorsal midline of the pharyngeal/esophageal region of the trunk (Fig. 2e). When the worms were entirely exposed on the sea floor, the posterior end was typically seen resting on a tangled mass of the animal's own fecal strand. The 2-mm diameter strand was round in cross-section and about the same color as the surrounding sediment (Fig. 2a, e).

Description, internal.—The proboscis (Fig. 3a), which is grooved mid-dorsally, is covered with an epidermis, including relatively few mucus cells. Internally there is a sparse meshwork of widely scattered connective tissue and muscle cells with no clearly defined coelomic space. The fixed holotype was so wrinkled that it was not possible to be sure whether proboscis coelomopores or a preoral ciliary organ were present. In the proboscis stalk, the general intraepidermal nervous system is thickened into two proboscis nerves (Fig. 3b, arrows), one on either side of the dorsal midline.

The collar epidermis includes abundant mucus cells (Fig. 3b, top right; c, top). During histological processing, the mucus swelled excessively, disrupting the epidermis and making it impossible to determine whether collar coelomopores were present. The striking predominance of mucus cells in the collar epidermis contrasts with their sparse distribution in the epidermis of the proboscis and trunk. Sections near the anterior end of the collar show the proboscis nerves (Fig. 3c, single arrows) merging to form the dorsal collar nerve. Sections at this level also show the anterior extremity of the stomochord (Fig. 3c, twin

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stomochord (twin arrows); rostrum of proboscis skeleton (arrowhead); muscles associated with proboscis skeleton indicated by asterisks. g, invaginated collar nerve (single arrow) running beneath dorsal collar muscles (indicated by plus signs); proboscis skeleton body (arrowhead) becoming pitted dorsally and dividing stomochord (twin arrows) into subsections; muscles associated with proboscis skeleton indicated by asterisks. h, collar nerve (single arrow) now running above dorsal collar muscles (indicated by plus signs); body of proboscis skeleton (arrowhead) distinctly crown shaped with crown spikes dividing stomochord (twin arrows) into subsections; muscles associated with proboscis skeleton indicated by asterisks. Scales a = 1 mm; b–h = 500 μ m.

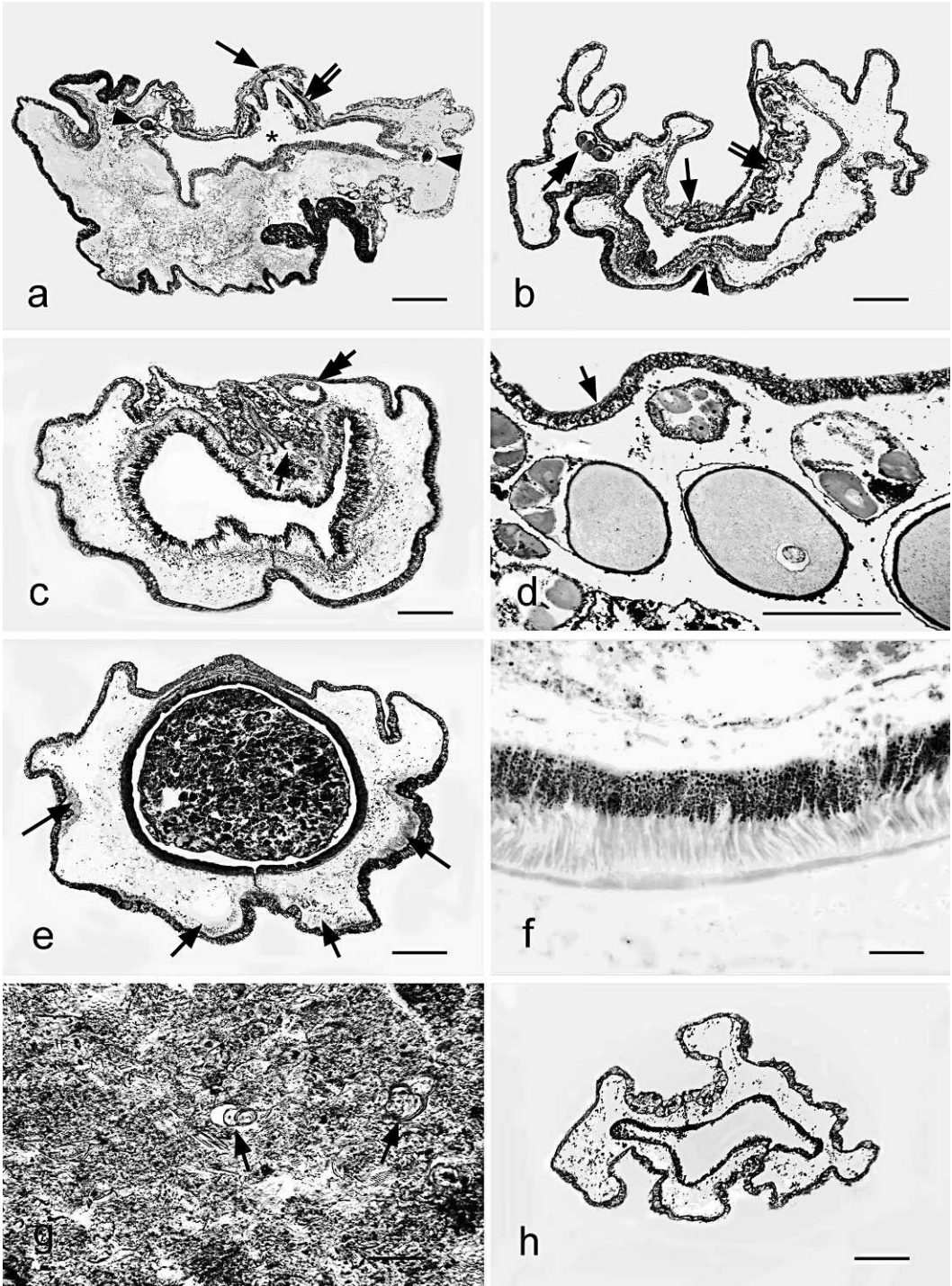


Fig. 4. *Saxipendium implicatum*. a, cross section through level 4a in Fig. 2b, at transition from collar (bottom) to pharyngeal region of trunk (top); posterior horns of proboscis skeleton (arrowheads) on either side of pharynx (asterisk); gill slits indicated by twin arrows; dorsal nerve cord of trunk indicated by single arrow. b, cross section through level 4b in Fig. 2b, showing pharyngeal region of trunk with dorsal nerve cord

arrows), the endodermal cells of which are poorly fixed and disrupted. Glomeruli (Fig. 3c, arrowhead) are associated with the anterior end of the stomochord, but neither a heart nor a pericardial cavity could be found. More posteriorly, the stomochord (Fig. 3d, twin arrows) is no longer associated with glomeruli, and the rostrum of the proboscis skeleton (Fig. 3e, arrowhead) projects into the substance of the stomochord (as diagrammed for *Saccoglossus mereschkowskii* by Ezhova & Malakhov 2009). About midway between the anterior and posterior limits of the collar, large muscles appear (marked by asterisks in Fig. 3f) that run posteriorly to insert on the proboscis skeleton.

Along most of its length, the dorsal collar nerve (Fig. 3f, single arrow) is incompletely invaginated from the worm's surface. The invagination is only closed over for a few hundred micrometers at the extreme posterior extremity of the collar (Fig. 3g). In *Saxipendium implicatum*, the collar nerve is not underlain by periaemal coeloms. Posterior to the incomplete invagination, the solid collar nerve (Fig. 3g, single arrow) runs beneath a bilateral pair of muscles and then ascends to the surface of the body (Fig. 3h, single arrow). At this level, the dorsal side of the main part of the proboscis skeleton, as seen in cross-section (Fig. 3h, arrowhead), is shaped like a crown with projecting spikes (Fig. 3h, twin arrows) that divide the stomochord into subsections. This coronate shape of the proboscis skeleton is a peculiarity shared

by *S. coronatum* and *S. implicatum* and helps justify their inclusion in the same genus in spite of the incompletely invaginated dorsal collar nerve of the latter.

Figure 4a shows the junction of the collar (toward bottom) with the pharyngeal region of the trunk (toward top). The posterior horns of the proboscis skeleton (Fig. 4a, arrowheads) are still present on either side of the pharynx (this is unusual because, in most enteropneusts, these horns do not extend beyond the posterior limit of the collar). The pharyngeal lumen is not divided into a dorsal respiratory and a ventral digestive region. The pharynx communicates with the exterior via gill slits (Fig. 4a, b, twin arrows); although these were badly distorted in the holotype, synapticles were definitely not present. Dorsal and ventral nerve cords (indicated by the arrow and arrowhead, respectively, in Fig. 4b) run along the entire length of the trunk from the pharyngeal region posteriorly to the anus.

In the esophageal region of the trunk (level 4c in Fig. 2b), the endodermal lining is relatively thick and contains moderately abundant mucus cells (such cells are only sparsely distributed in the endoderm of the other gut regions). The esophageal lumen communicates with the exterior via esophageal canals (poorly developed gill slits) (Fig. 4c, single arrow).

As shown in Fig. 2e, gonads run dorsolaterally along the pharyngeal and esophageal region of the trunk just beneath the epidermis. In *Saxipendium im-*

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(single arrow); ventral nerve cord (arrowhead); gill pores (twin arrows); and ovary (tandem arrow). c, cross section through level 4c in Fig. 2b, showing esophagus (with relatively thick endoderm) and an ovary (tandem arrow); single arrow indicates a possible esophageal pore. d, detail of ovaries underlying the dorsolateral epidermis (single arrow) of the esophageal region of the trunk. e, cross section through level 4e in Fig. 2b, showing hepatic region of intestine; intestinal lumen packed with gut contents; single arrows indicate subepidermal longitudinal muscles. f, unstained cross section (bright field) of hepatic region of intestine (gut lumen toward top) showing dark brown pigment granules in apical half of endodermal cells. g, unstained gut contents of hepatic region of intestine (phase contrast); probable foraminifera indicated by single arrows. h, cross section through level 4h in Fig. 2b showing post-hepatic region of intestine. Scales a–e, h = 500 μm ; f, g = 50 μm .

plicatum, in comparison to *S. coronatum*, anterior-posterior extent of the gonadal region along the trunk is shorter; in the latter species, gonads can be found along much of the length of the trunk (C. M. Young, pers. comm.). The conspicuously extended gonad region in *S. coronatum* likely reflects the abundance and high quality of food at hydrothermal vents as compared to seamounts. Presumably *S. implicatum* is gonochoric, although male specimens have yet to be collected. The holotype is a female with numerous ovaries (Fig. 4b, c). Each ovary that is less mature contains several small oocytes and non-germinal cells with granular contents. In more mature ovaries (Fig. 4d), a single large oocyte is present without any detectable non-germinal cells. The diameter of the largest oocytes is approximately 700 μm .

Posterior to the esophagus commences the intestine, which comprises a very long hepatic region and a short posthepatic region. This region of trunk is characterized by small bundles of parallel muscles running in an anterior/posterior direction just beneath the epidermis (Fig. 4e, single arrows). Most of the trunk tissue between the epidermis and endoderm comprises a very sparse network of fibrous connective tissue and muscle cells scattered in a relatively voluminous extracellular space. The paucity of mesodermal cells along most of the trunk gives the body of the living worm a rather flabby appearance (Fig. 2a).

The intestinal endoderm has neither small-scale plicae nor large-scale sacculations. Along the length of the hepatic intestine, dark brown cytoplasmic granules

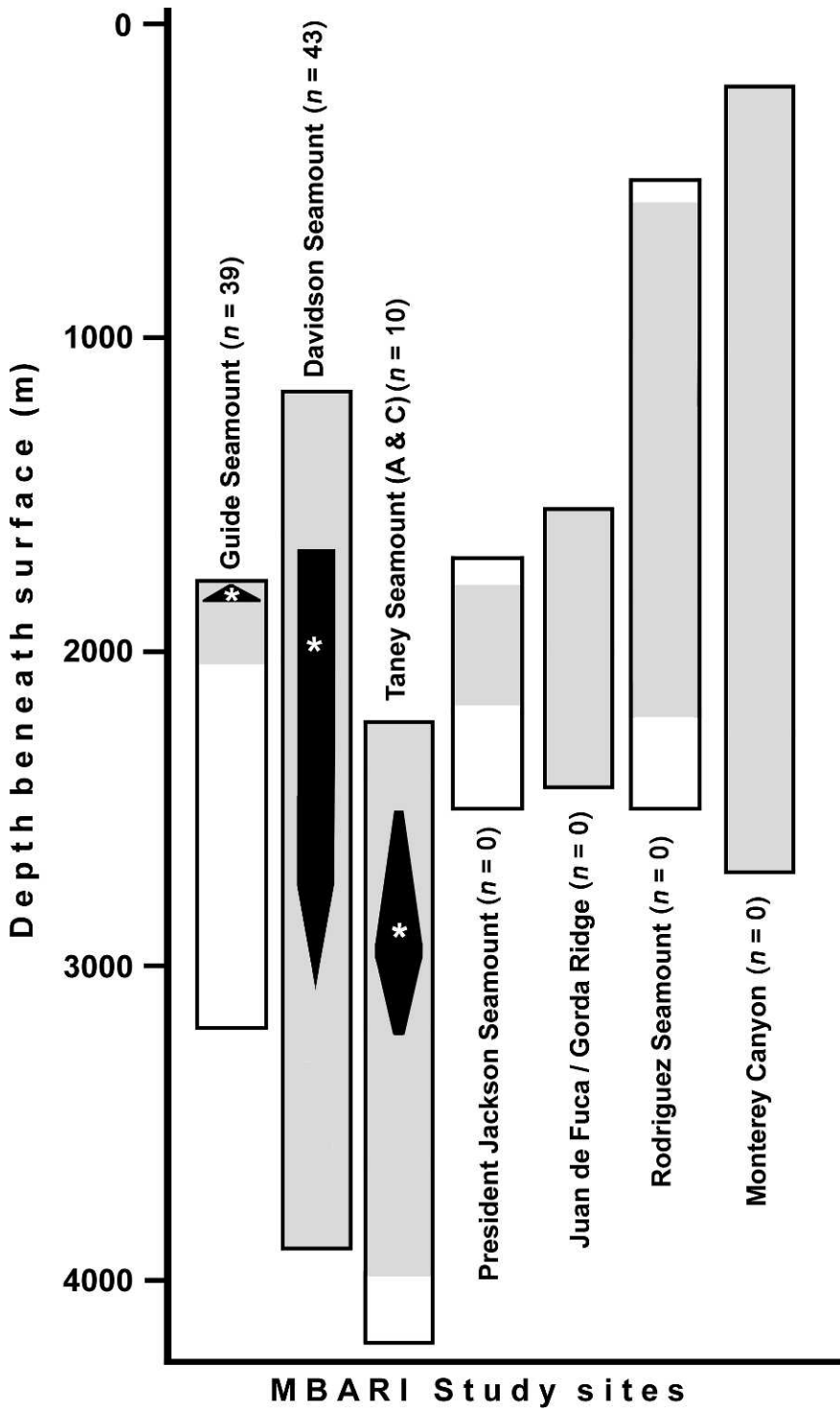
fill the apical half of most of the endodermal cells (Fig. 4f) and impart a darkish color to the gut, which is visible through the outer body wall. The contents of the lumen of the hepatic intestine (Fig. 4g) are mostly unidentifiable, except for occasional skeletal pieces of sponges, echinoderms, diatoms, and foraminiferans; mineralized sediment grains are almost absent. The transition between the hepatic and post-hepatic intestine is distinct because the latter (Fig. 4h), lacking pigmented granules in the endodermal cells, is not darkly tinged in unstained preparations.

Ecology.—Specimens of *Saxipendium implicatum* were observed on Davidson (35°43'N, 122°43'W), Guide (37°01'N, 123°20'W) and Taney (A and C) (36°45'N, 125°20'W) Seamounts off the central California coast (Fig. 1) between 1675 and 3225 m (Fig. 5). The geographic distribution of *S. implicatum* may be restricted to these three seamount areas, since no individuals were found to the northwest (Juan de Fuca/Gorda Ridge and President Jackson Seamount areas), to the northeast (Monterey Canyon), or to the south (Rodriguez Seamount) in similar habitats (Fig. 5). The density of individual worms was highest on Davidson Seamount (locally up to 5/m²), intermediate at Guide Seamount (0.17/m²), and lowest on Taney Seamounts (0.001/m²).

For the imaged worms as a whole, 58 were associated with sediments that had collected in isolated depressions on the surface of ancient lava, and 34 were on mud or among sedimentary rock outcrops. Twenty-one of the worms observed in situ were fully exposed on the sea floor, whereas the other 71 showed only their

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Fig. 5. Bathymetric distribution of *Saxipendium implicatum* off the Central California coast at seven MBARI study sites where the habitat was lava with ponded sediments or sedimentary rock outcrops. The bars indicate the depths at the summit (top) and base (bottom) topography at each feature; grey areas indicate depths explored by MBARI ROVs (note that effort was not equal over all explored depths). At each study site, the relative distribution of specimens of *S. implicatum* is indicated by the width of the black spindles. Asterisks indicate the mean depth of occurrence and *n* = the number of specimens.



anterior ends, which protruded out of soft substratum or from behind rock outcrops. A better estimate of the proportion of infaunal versus epibenthic individuals was not possible because no completely buried worms (which presumably were present) were counted, and partly buried individuals were more likely to have been missed than fully exposed ones.

Discussion

Morphologically, *Saxipendium implicatum* has two unusual features. First, the dorsal nerve cord runs for most of its length along the bottom of a shallow invagination that remains open on the mid-dorsal side of the collar. The nerve is only briefly covered by a narrow bridge of muscles and epidermis at the extreme posterior extremity of the collar. Thus the adult anatomy of the dorsal collar nerve for most of its length resembles an early developmental stage of collar cord formation in enteropneusts generally, as illustrated by Kaul & Stach (2010). For adult acorn worms, only *Saccoglossus pusillus* Ritter, 1902 has been reported to have an entirely uninvginated collar nerve (Horst 1939, p. 357). We were surprised to find a largely uninvginated dorsal collar nerve in *Saxipendium implicatum*, because the congeneric *S. coronatum* exhibits no such peculiarity (Woodwick & Sensenbaugh 1985). The second unexpected feature of *S. implicatum* is the extension of the horns of the proboscis skeleton posteriorly into the most anterior region of the trunk. Although harrimaniids in general have proportionally longer posterior horns than other enteropneusts (Ezhova & Malakhov 2009), *S. implicatum* is the first species in which the horns have been found to penetrate into the anterior extremity of the trunk.

While the worms were under observation from the ROVs (at most for only a

few minutes), no body movements were detected. This is not surprising, given the relatively slight development of the trunk musculature of *Saxipendium implicatum* as compared to that of shallow-living enteropneusts (Horst 1939). This species appears poorly equipped for swimming by muscular undulation after the fashion of the shallow-living *Glandiceps hacksi* (Urata et al., 2012), although passive drifting about the bottom, which characterizes many torquaratorids, while unlikely, cannot be ruled out from existing data. When entire specimens of *S. implicatum* were visible on the sea floor, they were typically associated with tangled strands of their own feces (Fig. 2a, e). The density of the fecal tangle indicates that a given worm spends long periods of time continuously deposit feeding in almost the same spot (although an alternative explanation is that the worms might emerge periodically onto the sea floor to release their feces). An extended period of feeding in a small area would suggest that the worms are browsing on energy-rich sediments and only infrequently need to seek new foraging sites.

The present study of *Saxipendium implicatum* brings the number of described deep-sea harrimaniids to two, as compared to 42 described from shallow water. Similar patterns are seen for the ptychoderids (one deep-sea and 44 shallow water representatives) and spengelids (one deep-sea and 18 shallow water representatives). By contrast, in the family Torquaratoridae, all six described species and several collected but still undescribed species are from the deep sea. These patterns indicate that, following the evolutionary origin of enteropneusts in shallow water, there was only sporadic migration of the harrimaniids, ptychoderids, and spengelids to great depths. In contrast, the torquaratorids entered the deep sea and subsequently diversified there (Osborn et al. 2012).

Acknowledgments

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