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A taxonomic revision of the family Harrimaniidae (Hemichordata: Enteropneusta) with descriptions of seven species from the Eastern Pacific

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Abstract

The family Harrimaniidae (Hemichordata: Enteropneusta) is revised on the basis of morphological characters. The number of harrimaniid genera is increased to nine by the addition of *Horstia* **n. gen.**, *Mesoglossus* **n. gen.**, *Ritteria* **n. gen.** and *Saxipendium*, a genus previously assigned to the monospecific family Saxipendiidae. The number of species is increased to 34, resulting from the description of five new species from the eastern Pacific — *Horstia kincaidi*, *Mesoglossus intermedius*, *M. macginitiei*, *Protoglossus mackiei* and *Ritteria ambigua*. A description is supplied for a sixth harrimaniid species, *Stereobalanus willeyi* Ritter & Davis, 1904, which previously had the status of a *nomen nudum*. Four harrimaniids previously assigned to the genus *Saccoglossus* are transfered to the genus *Mesoglossus* — *M. bournei*, *M. caraibicus*, *M. gurneyi* and *M. pygmaeus*, while *Saccoglossus borealis* is reassigned to the genus *Harrimania*. Notes on habitat and zoogeography are included for the seven foregoing species and a table of diagnostic characters for existing and new species and a dichotomous key to the enteropneust families and harrimaniid genera are provided. Finally, a phylogenetic hypothesis concerning the Harrimaniidae is postulated, with discussion on the evolution of the group.

Key words: Enteropneusta, acorn worms, Harrimaniidae, new genera, new species, *Saxipendium*, *Xenopleura*, zoogeography, dichotomous key, phylogeny

Introduction

The family Harrimaniidae is one of five families of Enteropneusta. Of the 79 enteropneust species known to date, 28 are classified in this family, which consists at the time of writing of the following five genera — *Harrimania*, *Protoglossus*, *Saccoglossus*, *Stereobalanus* and *Xenopleura*. Members of this family include common and widely distributed North American species such as *Saccoglossus kowalevskii* (Agassiz, 1873) and *S. pusillus* (Ritter, 1902). Found at all latitudes, from the intertidal zone to the deep sea, enteropneusts inhabit sand or mud, occasionally under rocks or among seaweed holdfasts. Typical habitats are clean coral-sand flats exposed at low tides and black mud under clean sea water. Some species may be located by a coiled casting of sand thrown up in a cone at one end of the burrow. But most species are encountered only by chance digging in the right place.

Our work is based in part on an unpublished manuscript and specimen collections initiated a century ago by William E. Ritter and later continued by Theodore H. Bullock and Kandula P. Rao. Our present study incorporates a part of this unpublished material to revise and update the family Harrimaniidae, to which we add five new species and three new genera. In addition, a description is provided for *Stereobalanus willeyi*, heretofore a nomen nudum. Moreover, an expanded description is provided for *Saxipendium coronatum*

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(Woodwick & Sensenbaugh, 1985) and these findings coupled with recent molecular phylogenetic results (Cannon *et al*., 2009) indicate that the monospecific genus *Saxipendium* should be transferred to the Harrimaniidae. From the older unpublished material plus our own contributions, we synthesize a new generic classification within the family.

Our morphological descriptions of harrimaniid genera and species is incorporated into a dichotomous key as well as a table listing the characteristic features of each species in the family. It is hoped that our textural material along with the photographic plates and generic relationships will make the work more accessible to non-specialists.

The specimen collection

As an outgrowth of his extensive studies on tunicates, Ritter took up the subject of the Enteropneusta in the last decade of the nineteenth century and published several accounts dealing with natural history, embryology and taxonomy (Ritter, 1900, 1902, 1908, Ritter & Davis, 1904). Over a period of years he accumulated a considerable body of material representing seven new species from the west coast of the United States and Alaska. He obtained many of his specimens during the Harriman Alaska Expedition of 1899, the results of which appeared in the 13-volume series edited by C. Hart Merriam and jointly published by Doubleday, Page & Company in New York and the Smithsonian Institution in Washington, DC (1901–1914). Spengel's (1893) summary of world Enteropneusta had listed no species from the Pacific coast so that Ritter, with a proportionately large new fauna relative to the 40 or so species known for the entire group at that time, projected a monograph for which he drafted descriptions and figures of all the west coast forms. Descriptions of two of the species were later published separately (Ritter, 1900; Ritter & Davis, 1904), but the full monograph was never completed.

Shortly before he died in 1944, Professor Ritter gave his enteropneust slides and manuscript to Theodore H. Bullock, who had recently finished a doctoral dissertation on the neuroanatomy of the group (Bullock, 1940, 1944, 1945). Bullock subsequently undertook to update and complete the paper with the aid of Kandula Pampapathi Rao who had previously studied the group extensively (Rao, 1952–1955, 1957, 1962). They then found new material in the Albatross collection through the kindness of C. A. Kofoid and S. F. Light, both of the Department of Zoology, University of California, Berkeley, and in the collections at the Scripps Institution of Oceanography Ritter through the courtesy of Percy Barnhart. In the ensuing years, Bullock found a number of additional new eastern Pacific species, as well as receiving valuable specimens from numerous other colleagues.

C. Burdon-Jones inherited the task of completing the monograph in the early 1970s but was not able to make any significant contribution to the work. In 2003 Bullock, then well into his retirement years, urged that Burdon-Jones, older and in poor health, return what material he had to California so that the whole collection could be deposited at the Smithsonian Museum in Washington. Feeling a deep obligation to see the monograph complete, Bullock then contacted Cameron, who had developed a graduate thesis on the group, including the description of a new species (Cameron, 2002) to complete the work. Following the death of Bullock in 2005, Cameron decided that it would be most practical to publish the new material as several smaller papers instead of as a comprehensive monograph.

Diagnostic morphological characters

Species (and even genera and families) of Enteropneusta are defined polythetically, i.e. on the basis of unique combinations of morphological and anatomical features including the presence or absence of soft parts as traced in serial sections. There are few consistent individual characters that are solely diagnostic and these have been established only to a limited degree based on examination of many individuals of abundant species. Even less is known of variation resulting from seasonal, ontogenetic and local environmental factors and the

like. In general, only single or very few specimens are examined for all relevant characters, both because of the rarity of finds and because of the formidable labor of serial sectioning and interpreting sizeable, sandy, coiled worms. Paucity of hard parts and distortion of soft parts in fixation add to the problems.

The net result is almost certain to be that some of the characters used are not good species characters and we may not place undue weight on the validity of the taxa named. Nevertheless, conventional characters have a certain modicum of reliability, judging from the few species repeatedly examined, and are sanctified by usage. Until better characters (e.g. molecular and biochemical) are validated, we must deal with the conventional ones.

We have faced the same dilemma as previous authors, namely whether to risk confusion by ignoring morphological differences that have not been well shown to be significant or to risk confusion by paying attention to them, in short whether to lump or to split. Our decision, after some years of dealing with this group in various respects, is that the lesser evil is to split. Especially when such a high percentage of the published species are represented by unique specimens or part of a specimen, errors uncovered in the future will be easier to correct by throwing names into synonymy than the reverse. This has already happened in the widespread and abundant species of *Ptychodera*, of which only two are now recognized. We have been particularly conscious of the possibility that this may be called for in multispecific genera like *Saccoglossus* and *Mesoglossus*.

In the present state of understanding there is no justification for collapsing harrimaniid species into synonymy, even with the substantial number of sectioned specimens we were able to examine. The resulting bulk of material and number of species at hand is quite likely to be considerably in excess of any assembly of material that has been available to any previous author. This certainly does not mean that we have achieved greater insight into evaluation of characters or regard our taxa as more likely to last; it does correlate with hesitancy and careful consideration prior to erecting new taxa such as we do in this paper.

Material and methods

The specimens used in this study are part of T. H. Bullock's enteropneust slide collection deposited at the National Museum of Natural History, Smithsonian Institution, Washington, DC. Most of the material in this collection fixed in Bouin's solution, with some of it fixed in formol-acetic-alcohol, and all the material was archived by transfer to 80% alcohol with 10% glycerin. Sections were cut either in paraffin or in low-viscosity nitrocellulose and mounted on glass slides. Heidenhain's iron alum haematoxylin, Masson's trichrome or Mallory's triple stain were used for staining the sections. Specimens were viewed and photographed with a Q Imaging Retiga-2000R digital camera mounted on an Olympus BX51 compound microscope and on an Olympus SZX16 stereomicroscope for lower magnifications. Being soft and fragile, acorn worms collected in nature are usually taken as pieces. These are nevertheless valuable. Whatever enteropneust material is collected should be carried back to the laboratory in separate containers since the chances of their suffering damage, if mixed with shells or hard-skinned marine organisms, is very great. They should be preserved soon after collection. Good preservation is most desirable as all serious study depends upon serial sectioning and histologic staining. It is quite desirable to leave them in a tray of clean sea water for a few hours to allow evacuation of sediment grains from the gut; frequent removal of sediment and the mucous sheath with entrapped particles may avoid reingestion. Fixation without coiling is aided if each worm is lifted into the air by a thin rod rod (e.g. a matchstick) under the middle of the specimen and killed by dropping fixative solution over it for a few minutes. It may then be lowered into the fixative. A general histologic fixative such as Bouin's, Heidenhain's Susa fluid, formol-acetic-alcohol or 10% formalin is satisfactory. Changing the fluid twice in the first 24 hours and again after several days is highly desirable. Collection labels should give not only details of geographic locality, date of collecting and name and address of collector, but also the nature of the substratum, color of the body parts in life and method of preservation. A sketch or photograph with measurements in life showing length and diameter of different regions, is helpful.

Diagnoses of the Harrimaniidae and its genera

Class Enteropneusta Gegenbaur, 1870

Family Harrimaniidae Spengel, 1901

Balanoglossidae: Willey, 1899

Harrimaniidae: van der Horst, 1935

Diagnosis. Enteropneusta characterized by absence of circular muscle fibers in trunk. In those cases where development has been studied, the typical tornaria larva is absent and development is direct. In addition to these two unique features may be added the following characters: absence of lateral septa, absence of vermiform process of stomochord, absence of hepatic caeca in trunk and of synapticulae joining primary and secondary gill bars (for drawing of generalized enteropneust see Fig. 1 from Cameron, 2005). Dorsal nerve roots in collar mesentery and intestinal pores may be present or absent. Skeletal cornua extend at least to middle of collar.

Remarks. Of the five known genera included in this family — *Harrimania*, *Saccoglossus*, *Protoglossus*, *Stereobalanus* and *Xenopleura*, the first two occur in the Eastern Pacific. In addition, as a result of the present work, *Protoglossus* and *Stereobalanus* can now be added to this list, along with the three new genera described here (*Ritteria*, *Horstia* and *Mesoglossus*) and *Saxipendium*, which is transferred to the Harrimanidae.

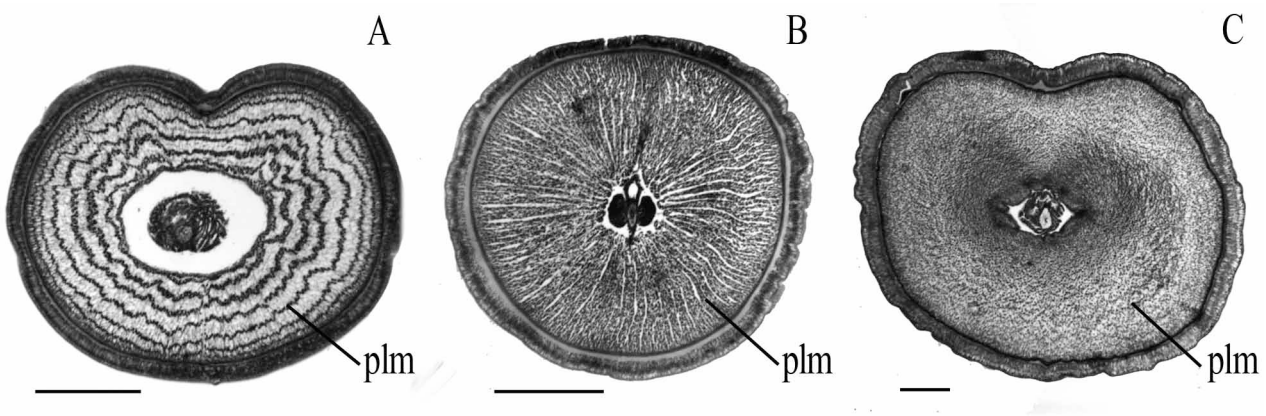

FIGURE 1. Light micrographs of transverse sections of the proboscis of: A, *Saccoglosus pusillus,* showing the arrangement of the proboscis longitudinal musculature in concentric rings. B, *Protoglossus mackiei* n. sp., showing the arrangement of the proboscis longitudinal musculature in radial plates. C, *Mesoglossus macginitiei* **n. gen.** et n. sp., showing the diffuse arrangement of the proboscis longitudinal musculature. Abbreviations: plm, proboscis longitudinal muscles. Scale bars = 500 μm.

Genus *Saccoglossus* Schimkewitsch, 1892

Dolichoglossus: Spengel, 1893
Type species. *Saccoglossus kowalevskii* (Agassiz, 1873)

Diagnosis. Proboscis usually long; middorsal longitudinal groove may be present. Collar usually very short compared to proboscis. Dorsal interbranchial genital ridges and dorsal gonads absent but lateral extrabranchial genital ridges may be present. Intestinal pores often present. Perihaemal cavities always present. Peribuccal cavities usually present, but not always. Genus most importantly characterized by arrangement of longitudinal muscle fibers of proboscis in several concentric rings (Fig. 1 A). Many species

favor quiet muddy-sandy flats not too far from the mouth of a bay, living in 'permanent' tubes and throwing up low conical mounds of quasi-spiral castings from the anus.

Remarks. The genus as revised above would now include the following species: *S. apatensis* Thomas, 1956; *S. aulakoeis* Thomas, 1968; *S. bromophenolosus* King, Giray & Kornfield, 1994; *S. horsti* Brambell & Goodhart, 1941; *S. hwangtauensis* (Si & Kwang-Chung, 1935), *S. inhacensis* (Kapelin, 1936), *S. kowalevskii* (Agassiz, 1873), *S. madrasensis* Rao, 1957, *S. mereschkowskii* (Wagner, 1885), *S. otagoensis* (Benham, 1899), *S. pusillus* (Ritter, 1902), *S. ruber* Tattersall, 1905, *S. sulcatus* (Spengel, 1893) and five new species collected from the Eastern Pacific that will be described in a forthcoming article on the genus.

Genus *Harrimania* Ritter, 1900

Type species. *Harrimania maculosa* Ritter, 1900

Diagnosis. Proboscis conical, a little longer than broad; collar broader than long. Longitudinal muscles of proboscis arranged in radial plates (Fig. 1 B). Genus often characterized by two proboscis pores. Intestinal pores and peribuccal cavities absent. Cornua very long, extending into trunk in *H. maculosa* Ritter, 1900 and *H. planktophilus* Cameron, 2002, also forming parabuccal ridges on either side of buccal cavity in collar. Both dorsal and lateral gonads can be present, occurring as simple sacs arranged in long rows. Dorsal gonads, when present, confined to branchial region.

Remarks. Three species from this genus are currently described, two of which are from the Eastern Pacific region, *H. maculosa* and *H. planktophilus*. Based on the diagnosis given above, we should now reassign *Saccoglossus borealis* Okuda & Yamada, 1955 to this genus because of its great resemblance to *H. planktophilus* in having a radial proboscis musculature, a broad collar, a left proboscis pore, lateral gonads, parabuccal ridges and the absence of peribuccal cavities.

Genus *Stereobalanus* Spengel, 1901

Balanoglossus: Spengel, 1893
Type species. *Stereobalanus canadensis* (Spengel, 1893)

Diagnosis. Genus characterized by broad dorsolateral and ventrolateral genital ridges, with broad gill openings between; gill tongues externally visible. Longitudinal musculature of proboscis arranged in radial plates. Abdominal pores present or absent. Perihaemal cavities present but peribuccal coelomic cavities absent. Two proboscis pores present but greatly reduced. Contrary to the report of Spengel (1893), collar ducts are present in this genus (Reinhard, 1942).

Remarks. Two species, *S. canadensis* and *S. willeyi* Ritter & Davis, 1904 are included in this genus and both are represented on the west coast of North America.

Genus *Xenopleura* Gilchrist, 1925

Type species. *Xenopleura vivipara* Gilchrist, 1925

Diagnosis. Genus characterized by medullary folds in trunk extending posteriorly on dorsal side into low pleurae. Proboscis not elongate, its longitudinal muscles scattered (Fig. 1 C). Stomochord lacking vermiform process and continuous through buccal cavity as two dorsolateral folds. A single proboscis pore. Posterior margin of collar fused with trunk and no nerve roots present in collar nerve cord. Branchial skeleton lacks synapticula, internal hepatic caeca present in trunk.

Remarks. This genus, described from only one specimen, could be viviparous.

Genus *Protoglossus* van der Horst, 1935

Balanocephalus Caullery & Mesnil, 1900
Protobalanus Caullery & Mesnil, 1904
Type species. *Protoglossus koehleri* (Caullery & Mesnil, 1900)

Diagnosis. Genus characterized by short conical proboscis with deep posterior dorsal groove and conspicuous horseshoe-shaped pre-oral ciliary organ. Longitudinal musculature of proboscis radial, its paired dorsal gonads not prominent. *Protoglossus* considered to have simplest arrangement of enteropneust body cavities in lacking peribuccal cavities and having rudimentary or no perihaemal cavities (Burdon-Jones, 1956). Left proboscis pore present, along with dorsal and ventral mesenteries in proboscis and collar. Cornua of skeleton extending to posterior margin of collar, forming parabuccal ridges on each side of buccal cavity.

Genus *Saxipendium* Woodwick & Sensenbaugh, 1985

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

Diagnosis. Longitudinal proboscis muscles diffuse. Proboscis skeleton coronate (crown-shaped) in cross section, keel absent, cornua long and recurved. Collar canals with pores opening to the outside of body. Dorsolateral genital ridges with gonopores externally visible; testicular antra possibly present.

Remarks. Previously assigned to its own family (Saxipendiidae), *Saxipendium* is here transferred to the Harrimaniidae. Although distinguished from other harrimaniid genera by the above combination of features, it otherwise possesses the general characters of the family.

Genus *Mesoglossus* n. gen.

Type species. *Saccoglossus bournei* Menon, 1904

Diagnosis. Proboscis about twice as long as wide, with no conspicuous dorsal groove; its longitudinal musculature arranged diffusely, not in concentric rings or radial bundles. Proboscis pore is present usually on left side. Perihaemal cavities usually present. Collar canals present. A ventral mesentery present in proboscis, with both dorsal and ventral mesenteries present in collar. Dorsal gonads absent; only lateral gonads present. Peribuccal spaces present or absent.

Remarks. It is evident from the above characters that the closest relations of *Mesoglossus bournei* **n. comb.** are three other species previously assigned to the genus *Saccoglossus* but here transferred to *Mesoglossus* — *M. caraibicus* (van der Horst, 1924) **n. comb.**, *M. gurneyi* (Robinson, 1927) **n. comb.** and *M. pygmaeus* (Hinrichs & Jacobi, 1938) **n. comb.**. Although these four species and *M. intermedius* resemble species of *Saccoglossus* a great deal, they are distinguished from the latter by the fact that the longitudinal muscle fibers of the proboscis are uniformly distributed without being arranged into concentric rings as in *Saccoglossus* (or into radial groups as in *Harrimania* and *Stereobalanus*). *Mesoglossus* is too distinct to be confused with *Stereobalanus*. Hence all of the forms that have previously been put under *Saccoglossus* but which exhibit no regular arrangement of the proboscis longitudinal muscle fibers into concentric rings are here transferred to the genus *Mesoglossus*, with *M. bournei* as the type species.

The diagnosis given above is primarily based on Ritter's account in his manuscript (written ca. 1900) plus a re-examination of his histological slides and of material collected by others. At the beginning of the twentieth century, no *Saccoglossus* species had been described with a diffuse distribution of longitudinal fibers in the proboscis, except for Benham's description of *S. otagoensis* (Benham, 1899). But it is now known that in *S. otagoensis* the longitudinal muscle fibers in the proboscis are actually arranged in three or four concentric rings (van der Horst, 1935). Thus *S. otagoensis* cannot be considered as belonging to *Mesoglossus*,

which means that *M. bournei* is the earliest described species under the genus and should be considered as its type species.

Genus *Ritteria* n. gen.

Type species. *Ritteria ambigua* **n. sp.**

Diagnosis. Proboscis short, the longitudinal muscles dispersed diffusely, not concentrically or radially. A single, left proboscis pore. Proboscis neck severely reduced, the stomochord lumen broken into lacunae. Collar with neither dorsal nor ventral septum and no peribuccal cavities. Dorsal gonads present, the lateral gonads forming two pairs of genital ridges with branchial pores recessed in the groove between them.

Remarks. The genus is monotypic for *R. ambigua* n. sp., which is fully described in the section on new species descriptions, below. The genus is named in honor of the late Professor W. E. Ritter, without whose interest and initiative our knowledge of the Enteropneusta would be very much poorer. He never saw the material on which this name is based.

Genus *Horstia* n. gen.

Type species. *Horstia kincaidi* **n. sp.**

Diagnosis. Proboscis very short and round, hardly as long as broad. Longitudinal muscles arranged in radial plates. Proboscis pore present on right or left. Anterior neuropore present, and collar nerve cord with large lacunae. Peribuccal cavities absent. Gonads conspicuous as modules projecting prominently from surface, not forming ridges. Trunk cross section regular and nearly circular, with gill pores unusually prominent, even elevated slightly above general surface. No dorsal gonads.

Remarks. *Horstia* is monotypic and named for the late C. J. van der Horst of the University of Witwatersrand. It differs in at least three or four characters from the nearest genera (*Mesoglossus*, *Saccoglossus*, *Harrimania* and *Ritteria*). *Horstia* is provisionally defined by the foregoing selection of characters of its sole species *H. kincaidi*, which would otherwise have to be forced into one of these other genera, doing violence to what we believe are defining generic features. Further discoveries may reveal some further characters of generic rank in the species description in the section below.

New species descriptions

***Stereobalanus willeyi* n. sp.**
(Fig. 2D, E, I, J; Fig. 3)

Stereobalanus willeyi Ritter & Davis, 1904 *nom. nud.*

Material examined. Three anterior fragments were found by Ritter ca. 1900 after dredging in extremely soft sandy mud at about 80 m depth in San Pedro Channel off the coast near Newport, Orange County, California. *Holotype:* Accession no. NMNH 71441, Smithsonian Institution. *Paratype:* NMNH 1132794.

External features. (Fig. 2 D, E, I, J). Proboscis conical, cylindrical in section, ca. 1 cm long. Collar less than half length of proboscis and rather broader than long, with expanded rim at anterior edge. Four genital ridges distinct, column-like, confined to branchial region. Branchio-genital region slightly longer than proboscis. A prominent ventral keel seen in abdominal region. Proboscis is cream-colored; collar similar but somewhat lighter. Gonads in female bright yellow. Pharyngeal region, excepting gonads, almost same color as collar; abdomen nearly black; gills as seen from dorsal side, when gonads pressed aside, appearing black.

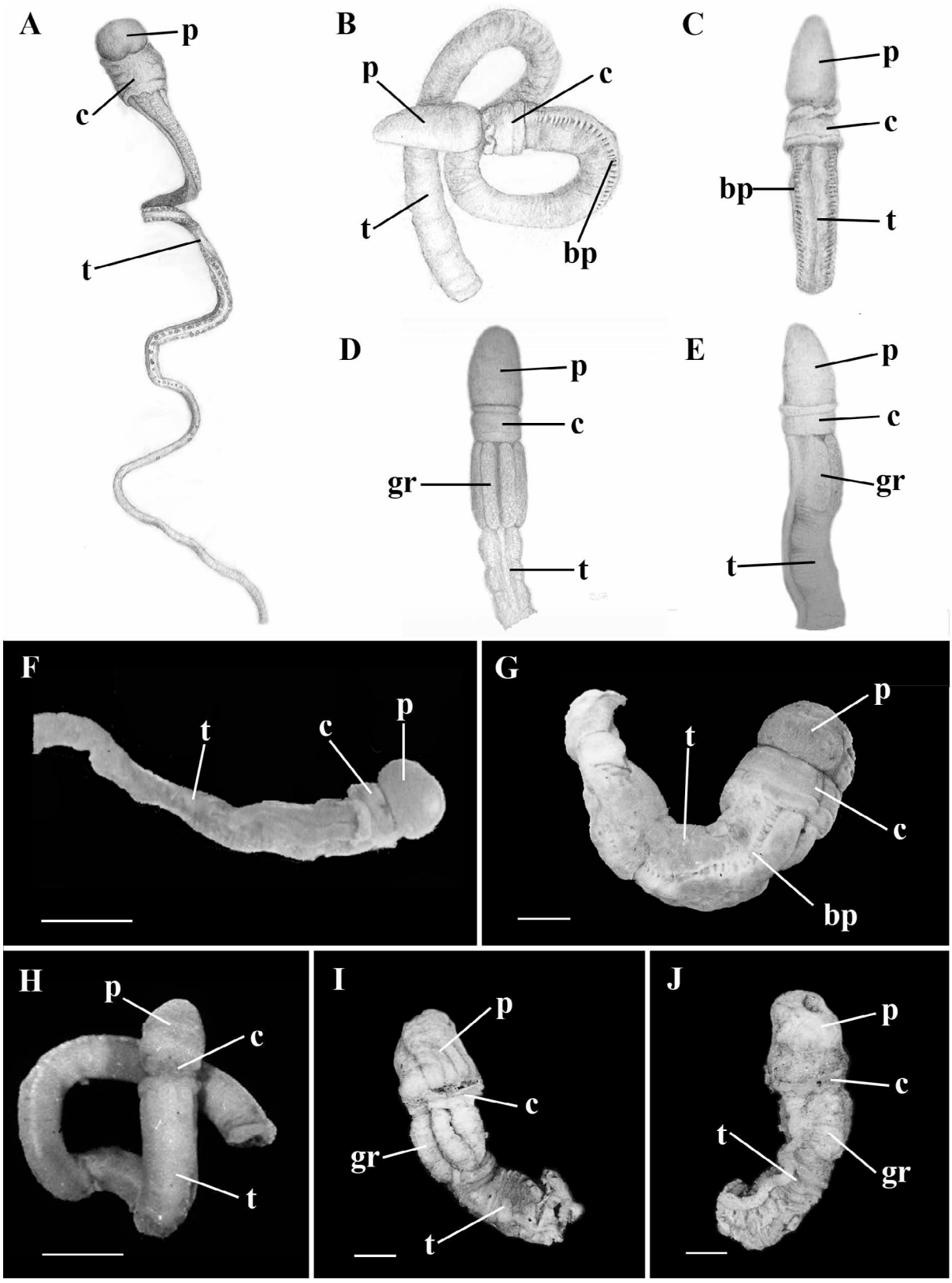

FIGURE 2. Drawings of live animals and photographs of fixed specimens of the family Harrimaniidae. A, Drawing of the dorsal side of *Horstia kincaidi* **n. gen. et n. sp.** B, Drawing of the lateral side of *Mesoglossus intermedius* **n. gen. et n. sp.** C, Drawing of the dorsal side of *Mesoglossus intermedius*. D, Drawing of the dorsal side of *Stereobalanus willeyi* **n. sp.** E, Drawing of the lateral side of *Stereobalanus willeyi*. F, Photograph of the dorsal side of *Horstia kincaidi*. G, Photograph of the lateral side of *Ritteria ambigua* **n. gen. et n. sp.** H, Photograph of the dorsal side of *Mesoglossus intermedius*. I, Photograph of the dorsal side of *Stereobalanus willeyi*. J, Photograph of the lateral side of *Stereobalanus willey*. Abbreviations: bp, branchial pore; c, collar; gr, genital ridge; p, proboscis; t, trunk. Scale bars = 2 mm

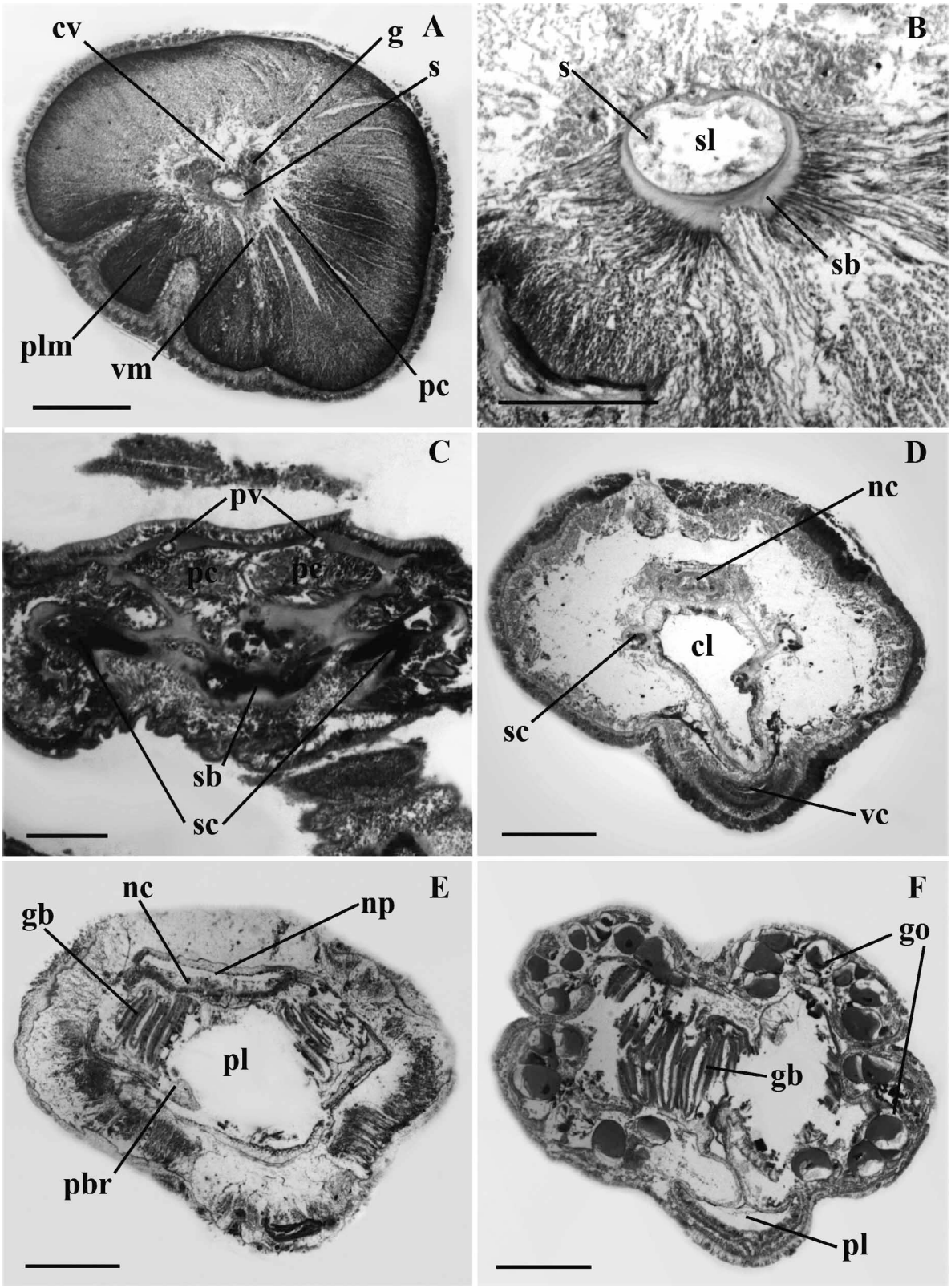

FIGURE 3. Light micrographs of transverse sections of *Stereobalanus willeyi* **n. sp.**: A, Proboscis with heart–kidney complex. B, Posterior part of the proboscis showing the skeleton. C, Proboscis neck. D, Anterior region of the collar. E, Anterior pharyngeal region of the trunk. F, Genital region of the trunk. Abbreviations: cl, collar lumen; cv, cardiac vesicle; g, glomerulus; gb, gill bar; go, gonad; nc, nerve cord; np, neuropore; pbr, parabranchial ridge; pc, proboscis coelom; pl, pharynx lumen; plm, proboscis longitudinal muscles; pv, proboscis vesicle; s, stomochord; sb, skeletal body; sc, skeletal cornua; sl, stomochord lumen; vc, ventral caecum; vm, ventral mesentery. Scale bars: A, D, E, F = 1000 μm; B = 500 μm; (C) = 750 μm.

Internal features. (Fig. 3). Circular muscle layer of proboscis well developed, somewhat thicker than nerve-fiber layer of ectoderm. Longitudinal muscle fibers in well-defined radial plates (Fig. 3A), particularly toward base of proboscis. Stomochord in form of tube without ventral caecum, with thick and even wall (Fig. 3B). Stomochordal neck completely obliterated; stomochordal sheath extremely thick. Glomerulus very limited in development and much scattered, arising as two irregular masses from dorsal side of stomochordal sheath (Fig. 3A). Proboscis cavity obliterated by musculature and glomerulus posteriorly. Cardiac vesicle rudimentary, lacking bifid tip. Proboscis vesicles with canals and pores, one on each side, reduced to mere trace; some communication between proboscis coelom and proboscis pore apparent through vesicles and canals, these all rudimentary. Proboscis skeleton also much reduced, with no keel and a small piece that is bluntly rounded anteriorly, continuing posteriorly into cornua (Fig. 3C, D); cornua arising from posterolateral margins of skeletal body, hence widely separated from each other from their start, extending to posterior margin of collar.

Dorsal nerve cord of collar without any dorsal roots. Lumen of cord distinct in about its posterior third but not so in remainder of length. Collar canals and pores absent. Peribuccal coelom not present. Perihaemal cavities conspicuous, extending into neck. Caecum large, posteriorly directed, given off from ventral side of buccal cavity in collar region. This beginning anteriorly a short distance behind mouth as a broad deep trough that becomes more and more set off by attenuation of lateral walls of buccal cavity above it, until finally the walls close together, producing a well-defined ventral caecum in middle region of collar (Fig. 3D); walls of caecum practically of same histological structure as buccal epithelium immediately adjacent to it.

About 70 branchial apertures on each side and no synapticulae. Parabranchial ridges prominent (Fig. 3E). Branchial openings large, exposing gill-tongues to view. Ova rather large, ca. 0.5 mm diameter. A pair of lateral and pair of dorsal genital ridges starting immediately behind collar. A single pair of intestinal pores in abdominal region.

Remarks. *Stereobalanus willeyi* is clearly more closely related to *S. canadensis* (Spengel, 1893) than to any other known species. It is sharply distinguished from *S. canadensis* by its color, the possession of a much larger number of branchial pores, the shape of the proboscis skeleton, the complete absence of the collar canals and pores, the caecum on the ventral side of the buccal cavity and the possession of intestinal pores.

In his manuscript account, Ritter said this of the derivation of the specific name: "I take great pleasure in dedicating this interesting form to Dr. Arthur Willey in whose extensive contributions to the Zoology of the South Pacific, the Enteropneusta had a liberal share."

The above description of *S. willeyi* is based mainly on the manuscript of Ritter. Ritter and Davis (1904) listed this species by name as one whose description was forthcoming, mentioning that it has two proboscis pores and could not be the parent of a tornaria larva they were studying. This being inadequate as an indication, the species cannot be regarded as having heretofore been published. The living authors of the present paper have examined the sections critically and have made a few changes in the description given by Ritter. The references to this name given in the synonymy clearly refer to the same specimens although no adequate indication is provided with which the species could be recognized.

The defining characters of *Stereobalanus willeyi* are listed below:

A. Proboscis conical, longer than broad.
B. No proboscis groove.
C. Longitudinal musculature of the proboscis is in radial plates.
D. Two minute proboscis pores on either sides of the dorsal midline.
E. Proboscis skeleton has no keel.
F. Posterior neuropore.
G. No peribuccal diverticula in the collar.
H. No collar canals.
I. 4 columnar genital ridges confined to the gill region.
J. 1 pair of esophageal pores.

***Protoglossus mackiei* n. sp.**
(Fig. 1B; 4A–F)

Material examined. Three complete specimens were collected by Theodore H. Bullock at Moss Beach, San Mateo, California (37°52' N, 122°52' W) on 22 May 1939. *Holotype:* Accession no. NMNH 71493 and the paratype is USNM 1132792, Smithsonian Institution. Smithsonian Institution. Individuals have been found under rocks resting in coarse sand and are not in tubes or holes.

External features. Shape of proboscis of preserved specimens conical, not short or round. Collar broader than long, with ruffled anterior border and dark central area. Length of preserved specimens 25 mm, width ca. 2 mm. Collar yellow, proboscis and trunk white, in living material.

Internal features. Nerve-fiber layer of proboscis thickened middorsally (Fig. 4A). Proboscis coelom extending to tip of organ as narrow cavity closely surrounding proboscis complex. Ventral and dorsal septa present, starting in proboscis complex; both continuous throughout length of organ. Circular-muscle-fiber layer thinner than nerve-fiber layer. Longitudinal muscle fibers arranged in radial plates, but not as well defined as in *Horstia*. Glomerulus small, extending over tip of stomochord as two small lateral wing-shaped projections (Fig. 4A and inset). Cardiac vesicle well developed, covering only dorsal side of stomochord (Fig. 4A and inset). Stomochord with thick walls and continuous narrow lumen that gives off single small ventral diverticulum anterior to pore where skeletal plate is forming. Proboscis with deep dorsal groove posteriorly. Skeleton with well-developed acute keel (Fig. 4B, C). Two coelomic cavities in neck; a conspicuous left vesicle leading to exterior by left proboscis pore (Fig. 4B).

Dorsal and ventral mesenteries of collar both complete. Perihaemal diverticula starting at level of proboscis pore, separate throughout their length (Fig. 4C). Peribuccal coeloms absent. Skeletal cornua extending to posterior margin of collar, confined to dorsolateral aspect (Fig. 4D). Cornua projecting into lateral walls of buccal cavity, forming two dorsolateral evaginations (parabuccal ridges) along their length. Collar canals well developed and horizontal (Fig. 4E and inset). Two lacunae often present in dorsal nerve cord (Fig. 4D inset), one on each side, these not continuous throughout whole length of cord. A small anterior neuropore present (Fig. 4C); posterior one present or lacking. Collar longitudinal muscles well developed, present as two irregular masses on each side of collar lumen (Fig. 4D,E).

Branchial portion of pharynx equal in size to ventral portion or slightly larger (Fig. 4F). Pair of dorsolateral gonads present, not prominent on surface of body. Well-developed branchial sacs opening by dorsolateral pores. Presence of intestinal pores not determined. Ventrolateral longitudinal muscles of trunk well developed but not forming ridges.

Remarks. We dedicate this animal to Professor George O. Mackie, University of Victoria, who extensively contributed to our understanding of the form and function of invertebrates of the Pacific Coast of North America.

The defining characters of *Protoglossus mackiei* are listed below:

A. Proboscis is conical with a deep posterior dorsal groove.
B. Longitudinal musculature of the proboscis is in radiating plates.
C. Dorsal and ventral mesenteries are present in the proboscis and collar but the ventral mesentery is absent in the trunk.
D. Perihaemal diverticula are present and start in the neck.
E. Peribuccal diverticula are absent.
F. There is an anterior neuropore.
G. There are parabuccal ridges in the collar on either side of the buccal cavity.
H. Collar canals are well developed and horizontal.
I. The two rows of lateral gonads do not form ridges.

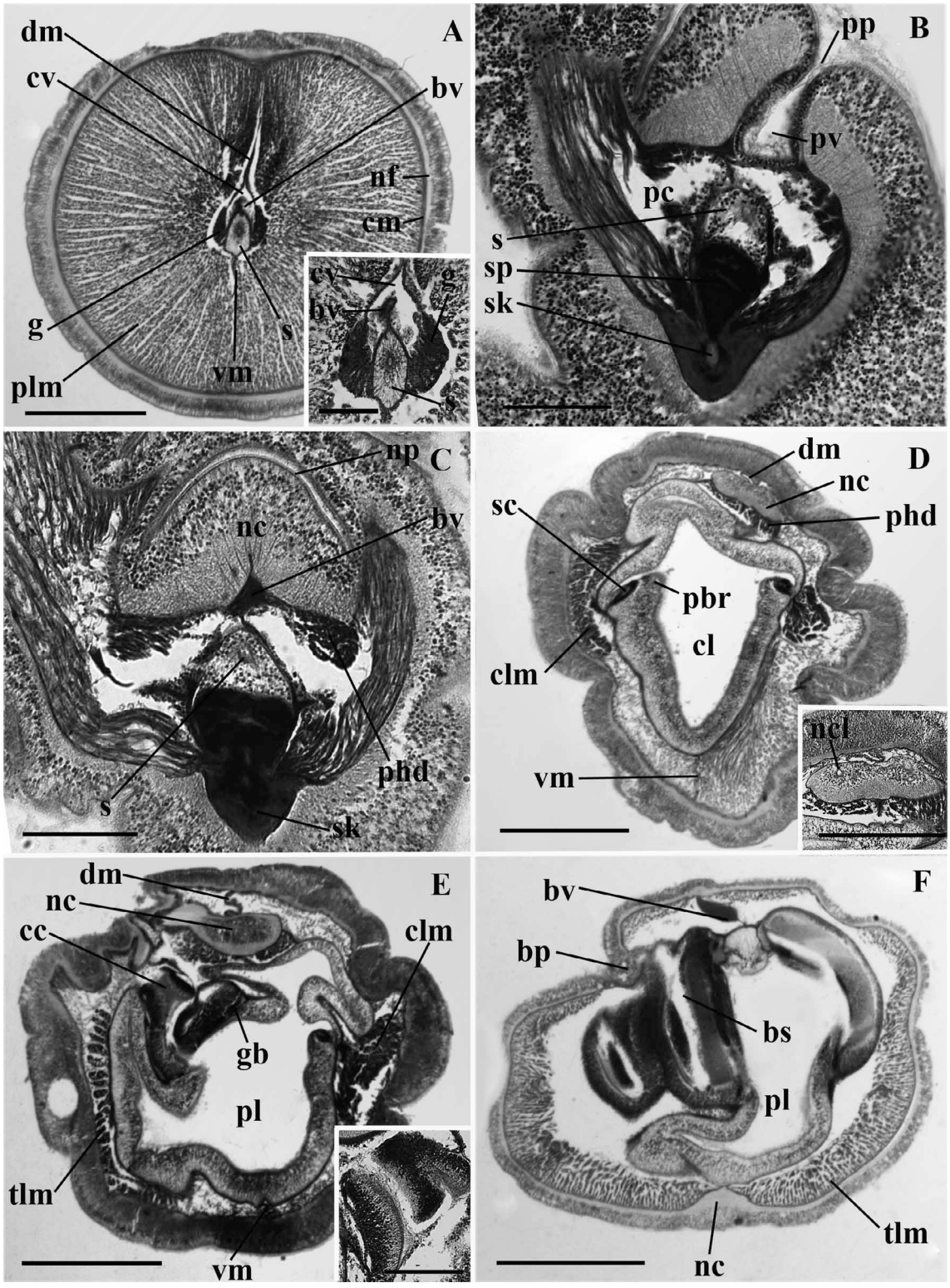

FIGURE 4. Light micrographs of transverse sections of *Protoglossus mackiei* **n. sp.**: A, Proboscis with heart–kidney complex. Inset: Proboscis complex. B, Proboscis neck. C, Proboscis neck showing the neuropore. D, Collar. Inset: Collar nerve cord. E, Anterior pharyngeal region of the trunk. Inset: Collar canal. F, Pharyngeal region of the trunk. Abbreviations: bp, branchial pore; bs, branchial sac; bv, blood vessel; cc, collar canal; clm, collar longitudinal muscles; cm, circular muscle layer; cv, cardiac vesicle; dm, dorsal mesentery; g, glomerulus; gb, gill bar; nc, nerve cord; ncl, nerve cord lacunae; nf, nerve fiber layer; np, neuropore; pbr, parabuccal ridge; pc, proboscis coelom; pl, pharynx lumen; plm, proboscis longitudinal muscles; phd, perihaemal diverticulum; pp, proboscis pore; pv, proboscis vesicle; s, stomochord, sc, skeletal cornua; sk, skeletal keel; sp, skeletal plate; tlm, trunk longitudinal muscles; vm, ventral mesentery. Scale bars: A, E, G, I = 500 μm; B, C, D, H = 100 μm; F = 300 μm.

***Saxipendium coronatum* Woodwick & Sesenbaugh, 1985**
(Fig. 5A–H)

Material examined. Eleven specimens were collected by the deep diving submersible *Alvin* in 1979 near "Rose Garden" geothermal vent, Galapagos Rift (00°47.9' N, 86°13.5' W), 2478 m depth. The holotype is NMNH 97395 and paratypes are 97396–8. Individuals were loosely attached to the rocks located at the periphery of the vent area.

External features. Proboscis arrow shaped, longer than broad, with longitudinal dorsal groove. Collar very short with elevated ring at its posterior end. Trunk slightly flattened dorsoventrally, presenting a median longitudinal groove. Dorsolateral genital ridges present on each side of body, the gonopores externally visible. Preserved specimens 25 mm long, about 2 mm thick. Color yellow-white in live material, collar darker than rest of the body and collar ring paler. Holotype measurements: overall length 215 mm, proboscis 11.0 mm, collar 3.0 mm, trunk 201 mm.

Internal features. Nerve-fiber layer of proboscis thickened dorsally (Fig. 5A). Proboscis coelom occupying posterior third of proboscis. Ventral septum present in posterior part of organ but dorsal septum formed by the large cardiac vesicle that is in contact with dorsal wall of proboscis (Fig. 5 A). Circular-muscle-fiber layer half thickness of nerve-fiber layer. Longitudinal muscle fibers diffuse. Glomerulus extending over tip of stomochord but poorly developed (Fig. 5A). Stomochord with thick walls and large central lumen, expanding ventrolaterally in neck region to form two horns, each with own lumen (Fig. 5B). Neck with two coelomic cavities, left vesicle leads to exterior by left proboscis pore (Fig. 5B). Skeletal body starts in neck, forming crown-shaped plate with spikes dividing stomochord into subsections (Fig. 5C). Skeleton with no keel. Proboscis with dorsal groove that is more conspicuous in preserved specimens.

Only dorsal mesentery of collar present. Anterior neuropore forming at level where dorsal part of collar fuses with neck (Fig. 5C). Perihaemal diverticula start at level of cornua, fused in some specimens (Fig. 5D). Peribuccal diverticula absent. Skeletal cornua extending to near end of collar (Fig. 5D,E), bending ventrally around gut then bending back anteriorly for a short portion (Fig. 5G). Collar longitudinal muscles well developed, present as masses on each side of collar lumen (Fig. 5C–E,G). Collar canals unique in connecting coelom to outside through pores located dorsomedially (Fig. 5E,F). As in other species, collar canals also connect to first gill pouch (Fig. 5G).

Branchial portion of pharynx equal in size to ventral portion or slightly smaller (Fig. 5H). Dorsal and ventral mesenteries present. Two rows of dorsolateral gonads forming external ridges; gonads connecting to exterior with externally visible gonopores situated on top of genital ridges (Fig. 5H). Branchial sacs opening by dorsolateral pores recessed between genital ridges and elevated median line of trunk (Fig. 5H). Type specimen had 54 branchial pores and 40 oesophageal pores. Ventrolateral longitudinal muscles of trunk poorly developed.

Remarks. Woodwick & Sesenbaugh (1985) mentioned the presence of an antrum, a special chamber connecting the testis and the gonopore, and thought it to be a distinctive feature of this species. There is now doubt concerning the uniqueness of this character because new observations showed that, in a single specimen, not all the gonads present this feature. Further, so little information is available on the gonads of other species that we cannot certify its absence from other taxa.

The defining characters of *Saxipendium coronatum* are listed below:

A. Proboscis is arrow shaped with a posterior dorsal groove.
B. Longitudinal musculature of the proboscis is diffuse.
C. Proboscis skeleton is coronate, without a visible keel.
D. Skeletal cornua are recurved.
E. Dorsal and ventral mesenteries are present in the trunk, but only the ventral one is present in the proboscis and the dorsal one in the collar.
F. Cardiac vesicle is in contact with the dorsal wall of the proboscis.
G. Perihaemal diverticula are present and start at the level of the skeletal cornua.

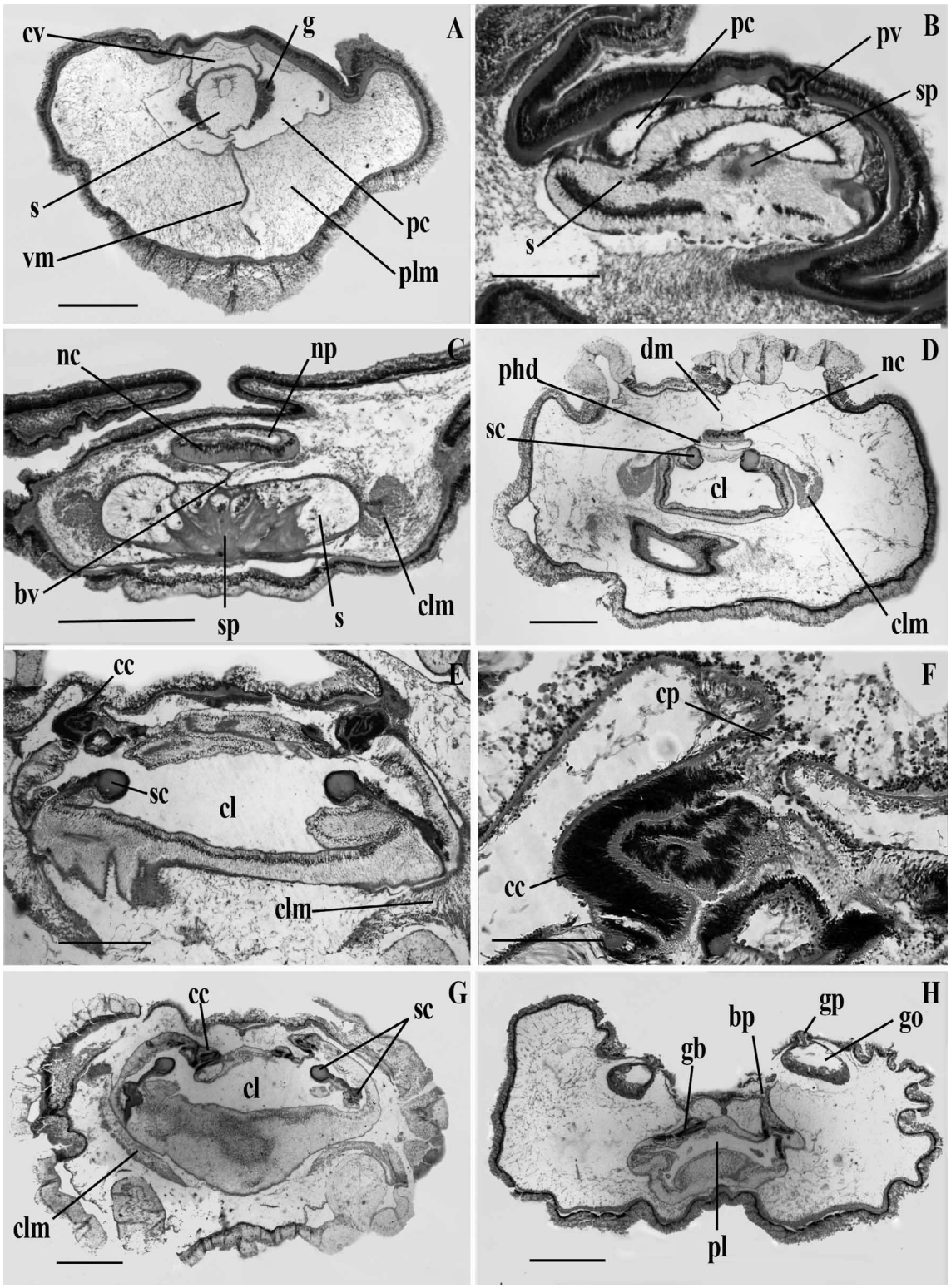

FIGURE 5. Light micrographs of transverse sections of *Saxipendium coronatum*: A, Proboscis with heart–kidney complex. B, Anterior region of the proboscis neck. C, Posterior region of the proboscis neck showing the neuropore and skeleton plate. D, Anterior region of the collar. E, Posterior region of the collar showing the collar pores. F, Collar canal and pore. G, Posterior region of the collar showing the curved skeletal cornua. H, Anterior region of the trunk. Abbreviations: bp, branchial pore; bv, blood vessel; cc, collar canal; cl, collar lumen; clm, collar longitudinal muscles; cp, collar pore; cv, cardiac vesicle; dm, dorsal mesentery; g, glomerulus; gb, gill bar; go, gonad; gp, gonopore; nc, nerve cord; np, neuropore; pc, proboscis coelom; phd, perihaemal diverticulum; pl, pharynx lumen; plm, proboscis longitudinal muscles; pv, proboscis vesicle; s, stomochord; sc, skeletal cornua; sp, skeletal plate; vm, ventral mesentery. Scale bars: A, C, D, G, H = 1000 μm; B, E = 500 μm; F = 200 μm.

H. Peribuccal diverticula are absent.
I. An anterior neuropore.
J. Collar canals open into the first branchial sac and also to the exterior via collar pores.
K. Gonads form two dorsolateral ridges and the gonopores are externally visible.

***Mesoglossus intermedius* n. gen. et n. sp.**
(Figs 2B,C,H; 6A–F)

Material examined. A single good specimen and two posterior fragments were taken from a kelp holdfast in Shelter Cover, Humbolt County, California (37°60' N, 122°51' W) in 1893 and 1894 by S. J. Holmes; the specimen with the anterior end (NMNH accession no. 71492) is here designated the primary type. For decades, northern California was entirely barren of further enteropneust finds while southern California yielded a good many. About 40 years later, enteropneusts began to turn up near Moss Beach, San Mateo County and in 1939, with an interested student making frequent trips, more than 20 were found in a few weeks (Bullock accession nos. 145, 203). They occurred typically on the under surface of sizeable rocks resting in coarse shelly sand on the protected outer coast, at zero tide level, not in noticeable burrows.

External features (Fig. 2B,C,H)**.** Relaxed living specimens 25 mm long, extending to 75 mm when crawling. Proboscis about 2 mm long when relaxed, or only about twice its thickness, conical with no trace of middorsal groove; length of collar about 1–1.5 mm or two-thirds of its thickness, its surface divided into three regions. Pharynx less than twice length of proboscis. About 25 long elliptical branchial orifices occurring on either side, situated dorsolaterally. Gonads invisible in surface view; extrabranchial only. No external liver lobes visible. No projecting ventral muscle bands seen, body presenting almost perfectly circular outline in transverse section in all regions. Color in life light yellow, proboscis somewhat darker.

Internal features. Circular-muscle-fiber layer in proboscis very thin. Longitudinal muscle fibers scattered uniformly in proboscis cavity, not arranged either in concentric rings or in radial bundles (Fig. 6A). Right and left halves of glomerulus joining anteriorly over tip of stomochord; glomerulus rather small and limited, closely enveloped by proboscis musculature (Fig. 6A). Cardiac vesicle rather small (Fig. 6A). Stomochord with thick walls in anterior part and narrow lumen (Fig. 6A). Ventral caecum single, distinct, best seen in sagittal sections. Skeleton with normally developed acute keel (Fig. 6B,C). Well-developed ventral septum present in base of proboscis, extending nearly to tip of stomochord. No dorsal septum. Well-developed left proboscis vesicle opening via left proboscis pore (Fig. 6B).

Dorsal and ventral mesenteries of collar both complete (Fig. 6D). Collar musculature delicate. No central lumen or any lacunae in collar nerve cord; nerve cord lacking dorsal crest; no dorsal roots. No epidermal pockets or neuropores in anterior or posterior face of collar. Perihaemal diverticula extending anteriorly only up to commencement of skeletal cornua (Fig. 6D). No peribuccal cavities. Collar canals comprising short vertical tubes opening along with first pair of gill pores (Fig. 6E and inset). Skeletal cornua reaching to posterior margin of collar.

Branchial part of pharynx half total cross section (Fig. 6F). Branchiae with individual pouches, each opening to exterior by pore dorsolaterally. Pores of left and right sides alternating normally, a few here and there paired or opposite. Ciliated branchial epithelium thick with nuclei in several strata. Gonads starting about 2 mm behind collar.

Remarks. The defining characters of *Mesoglossus intermedius* are listed below:

A. Proboscis is conical and longer than broad.
B. Longitudinal musculature of the proboscis is scattered.
C. No proboscis groove.
D. Collar has a ruffled anterior edge and a posterior ring.
E. Left proboscis pore.
F. Cornua extend to the posterior edge of the collar.
G. Ventral proboscis septa.

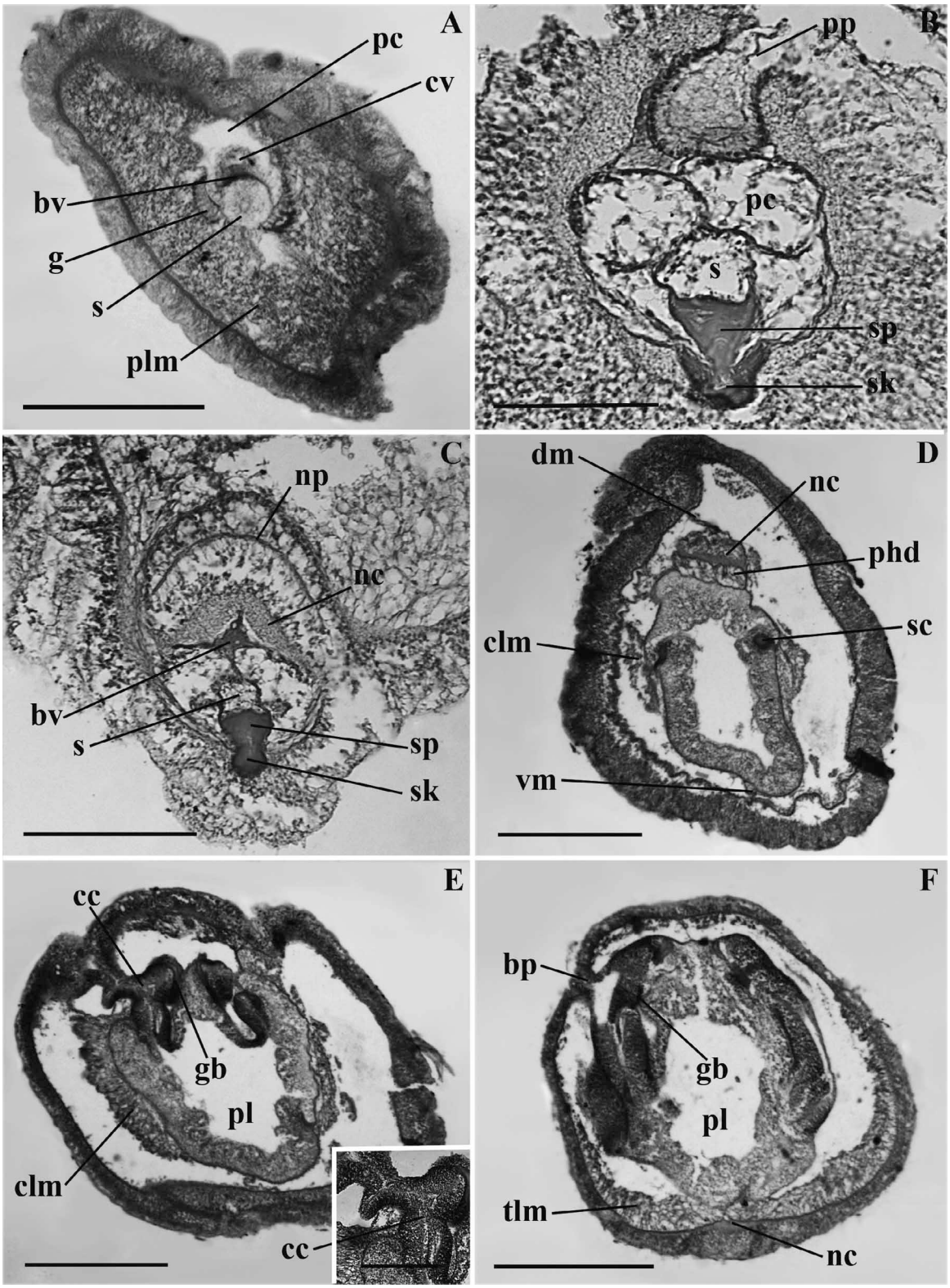

FIGURE 6. Light micrographs of transverse sections of *Mesoglossus intermedius* **n. gen. et n. sp.**: A, Proboscis with heart–kidney complex. B, Proboscis neck. C, Proboscis neck showing the neuropore. D, Collar. E, Posterior region of the collar, (inset) collar canal. F, Anterior pharyngeal region of the trunk. Abbreviations: bp, branchial pore; bv, blood vessel; cc, collar canal; clm, collar longitudinal muscles; cv, cardiac vesicle; dm, dorsal mesentery; g, glomerulus; gb, gill bar; nc, nerve cord; np, neuropore; pc; proboscis coelom; phd, perihaemal diverticulum; pl, pharynx lumen; plm, proboscis longitudinal muscles; pp, proboscis pore; s, stomochord; sc, skeletal cornua; sk, skeletal keel; sp, skeletal plate; tlm, trunk longitudinal muscles; vm, ventral mesentery. Scale bars: A, D, E, G = 500 μm; B = 100 μm; C, F = 200 μm.

H. Dorsal and ventral collar septa.
I. Short vertical collar canals.
J. The two dorsolateral rows of gonads start 2 mm behind the collar and do not form ridges.

***Mesoglossus macginitiei* n. sp.**
(Figs 1C; 7A–F)

Material examined. A single specimen was collected by Professor G. E. MacGinitie in September 1938, from the intertidal zone in Newport Bay, California (33°35' N, 117°53' W) in sandy mud. The type specimen bears accession no. NMNH 58891 and the paratype is USNM 1132791.

External features. Little is known about external features of this form. Genital ridges are present as well as ventral muscular ridges in trunk.

Internal features. Nerve-fiber layer in proboscis thickened middorsally. Circular-muscle-fiber layer quite well formed, 5 or 6 fibers in thickness. Proboscis coelom not extending to tip of proboscis. Longitudinal muscle fibers scattered irregularly in proboscis (Fig. 7A), not being arranged into either concentric rings or radial groups. Paired dorsolateral blood vessels occurring under proboscis epithelia. Glomerulus continuous anteriorly over tip of stomochord and covering its dorsal side posteriorly. Cardiac vesicle stopping short of stomochord anteriorly. About its middle region, cardiac vesicle covering stomochord laterally also (Fig. 7A). Lumen of stomochord not extending to tip; in tip a few narrow lacunae represent cavity. Ventrolateral blind pouches of stomochord lumen well developed, opening individually into primary lumen. Ventral septum of proboscis extending up to anterior margin of ventrolateral blind pouches of stomochord. Proboscis coelom lined by conspicuous amoeboid cells (Fig. 7B), opening out by single left proboscis pore. Proboscis vesicle middorsal (Fig. 7C). Body of proboscis skeleton with obtuse middorsal ridge (Fig. 7C). Keel almost absent in anterior part of skeleton but distinct and deep in posterior part.

Dorsal and ventral mesenteries of collar both complete (Fig. 7 D,E). Collar nerve cord lacking continuous lumen but lacunae present here and there. Neuropore anterior. Perihaemal diverticula extending to level of proboscis vesicle and confluent anteriorly. Nerve cord with dorsal crest (Fig. 7E and inset). Skeletal cornua extending nearly two-thirds length of collar, stopping short of posterior end of collar by about 2 mm. Peribuccal cavities present in form of triangular extensions, with longitudinal muscle fibers (Fig. 7F). Collar canals horizontally situated, opening into first pair of branchial sacs (Fig. 7F,G and inset).

Branchial part of pharynx larger than ventral part (Fig. 7G). Branchial tongue bars not projecting into pharyngeal cavity beyond primary gill bars. Nuclei of ciliated branchial epithelium lying in several strata. No dorsal or ventral septa in trunk.

Remarks. *Mesoglossus macginitiei* can be easily distinguished from *M. intermedius* by the presence in the former of the genital and ventral muscular ridges in the trunk, the ventrolateral blind pouches of the stomochord, dorsal glomerulus, less pronounced skeletal keel, median proboscis vesicle, peribuccal diverticula and neural crest. Of the other *Mesoglossus* species, the present form resembles *M. caraibicus* in having two stomochordal diverticula and a dorsal glomerulus.

We take pleasure in naming the new species after one of the historically foremost marine ecologists and naturalists of the Pacific west coast, Professor G. E. MacGinitie, long-time Director of the Corona del Mar Laboratory of the California Institute of Technology. Professor MacGinitie collected and presented this material.

The defining characters of *Mesoglossus macginitiei* are listed below:

A. Longitudinal musculature of the proboscis is scattered.
B. Left proboscis pore.
C. Proboscis skeleton bears a dorsal ridge.
D. Anterior and posterior neuropores.
E. Collar nerve cord with nerve crest.
F. Peribuccal diverticula present in the collar.

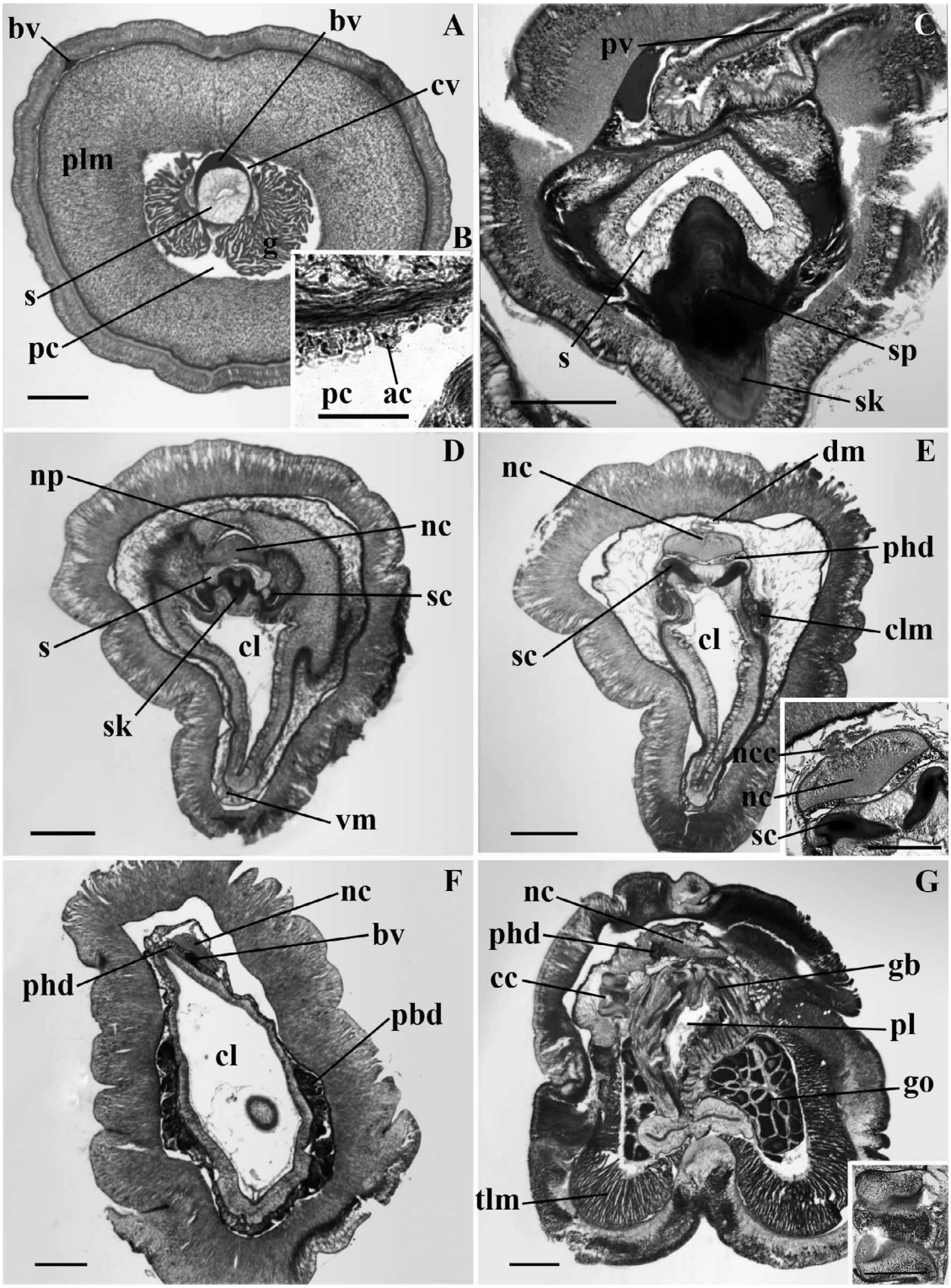

FIGURE 7. Light micrographs of transverse sections of *Mesoglossus macginitiei* **n. gen. et n. sp.**: A, Proboscis with heart–kidney complex. B, Proboscis coelomic cavity showing amoeboid-like cells. C, Proboscis neck. D, Anterior region of the collar showing the neuropore. E, Anterior region of the collar showing the dorsal nerve-cord crest. Inset: Dorsal nerve cord crest. F, Posterior region of the collar showing the peribuccal diverticula. G, Anterior pharyngeal region of the trunk. Inset: Collar canal. Abbreviations: ac, amoeboid-like cells; bv, blood vessel; cc, collar canal; cl, collar lumen; clm, collar longitudinal muscles; cv, cardiac vesicle; dm, dorsal mesentery; g, glomerulus; gb, gill bar; go, gonad; nc, nerve cord; ncc, nerve cord crest; np, neuropore; pbd, peribuccal diverticula; pc, proboscis coelom; phd, perihaemal diverticulum; pl, pharynx lumen; plm, proboscis longitudinal muscles; proboscis vesicle; s, stomochord; sc, skeletal cornua; sk, skeletal keel; sp, skeletal plate; tlm, trunk longitudinal muscles; vm, ventral mesentery. Scale bars: A, D, G, H = 500 μm; B = 50 μm; C, I = 200 μm; F = 300 μm.

G. Skeleton cornua extend to 2/3 of the collar.
H. Ventral septa in the proboscis, dorsal and ventral in the collar, and none in the trunk.
I. Two rows of dorsolateral genital ridges starting immediately behind the collar.

***Ritteria ambigua* n. gen. et n. sp.**
(Figs 2G; 8A–G)

Material examined. A single anterior fragment was collected by Dr W. K. Fisher at Station 4508 of the Albatross expedition, off Point Pinos, California (36°38' N, 121°56' W), on May 20, 1904 in soft green mud at a depth of 600 to 700 meters. This specimen, accession no. NMNH 58885, is here designated holotype and 1132793 is the paratype.

External features (Fig. 2G). Total length unknown; in preserved material from a single specimen proboscis is short, being ca. 3 mm long and 4 mm wide, collar extremely short and broad, being ca. 2 mm long dorsally, 2.7 mm ventrally and ca. 4.5 mm wide Branchial region between 10–15 mm long. Collar with expanded rim at posterior edge. Two pairs of genital ridges present on dorsolateral sides, commencing immediately behind collar, with gill pores situated along lateral grooves formed by these ridges. A small ventral muscular ridge present, hepatic lobes absent. In living material proboscis is coral red, collar is deep vermilion to poppy red, posterior margin of collar and trunk are bright orange.

Internal features. Circular-muscle-fiber layer of proboscis thinner than nerve-fiber layer, amounting to only 3 or 4 fibers in thickness. Nerve-fiber layer thickened along middorsal groove into cord-like structure (Fig. 8A). Longitudinal muscle fibers not split into radial bundles or grouped into circular rings but uniformly scattered (Fig. 8A). Proboscis coelomic cavity commencing along with anterior tip of proboscis complex. Stomochord large and conspicuous with broad lumen at tip and no lumen through middle region. Ventrolateral diverticula of lumen fused, while the lumen in neck is broken and frequently obliterated. Walls of stomochord in this region laminated by strand-like extensions from body of skeleton (Fig. 8A) and here appears broken down into several bits by these strands (Fig. 8F). These extensions of collagenous material give skeletal plate a distinctive coronate form that closely resembles that of *Saxipendium coronatum*. Just before joining buccal epithelium, central part of neck of stomochord acquires distinct lumen. Ventral proboscis septum runs along midventral line of stomochord, stopping short of its tip, dorsal septum absent. Proboscis skeleton quite massive, with large broad keel and wide plate (Fig. 8F). Normally formed left proboscis pore present, opening into anterior neuropore by a left vesicle (Fig. 8F).

Collar lacking dorsal and ventral septa. A single dorsal root emerging from collar nerve cord in posterior third of collar (Fig. 8H). Perihaemal diverticula (Fig. 8C,H) confined to collar, extending only up to level of opening of stomochord into buccal cavity. Collar longitudinal muscles well developed, forming triangular bundles on each side of collar lumen (Fig. 8C). No peribuccal diverticula. Collar canals short, horizontal, with dorsal infolding as in Ptychoderidae (Fig. 8D,G). Skeletal cornua extending to posterior extremity of collar but confined to dorsolateral aspect throughout (Fig. 8C,D). Ventral longitudinal muscles poorly developed, not forming bundles or ridges.

Branchial portion of pharynx equal in size to ventral portion. Gonads arranged in two pairs of dorsolateral ridges (Fig. 8E) but not forming wings. Branchial openings in form of pores arranged along groove formed between the two genital ridges on either side. Consequently, unlike in *Stereobalanus*, branchial basket not visible from outside. Instead, branchial sacs (Fig. 8E) opening out by branchial pores situated dorsolaterally. Ventral longitudinal musculature forming a small ridge on ventral surface of trunk. Presence of intestinal pores not determinable.

Remarks. From the above description it can be seen that this species does not fit into any of the other genera of the family. In the possession of dorsal gonads it resembles *Harrimania* and *Stereobalanus*, but these genera are characterized by proboscis muscles arranged in radial plates. *Stereobalanus* shares not only the dorsal and lateral gonads but also the apparent degeneration of the neck region of the stomochord. Among other features, the well-developed proboscis pore, and collar canals are enough to distinguish *Ritteria* from *Stereobalanus*. The differences from other genera are even more numerous.

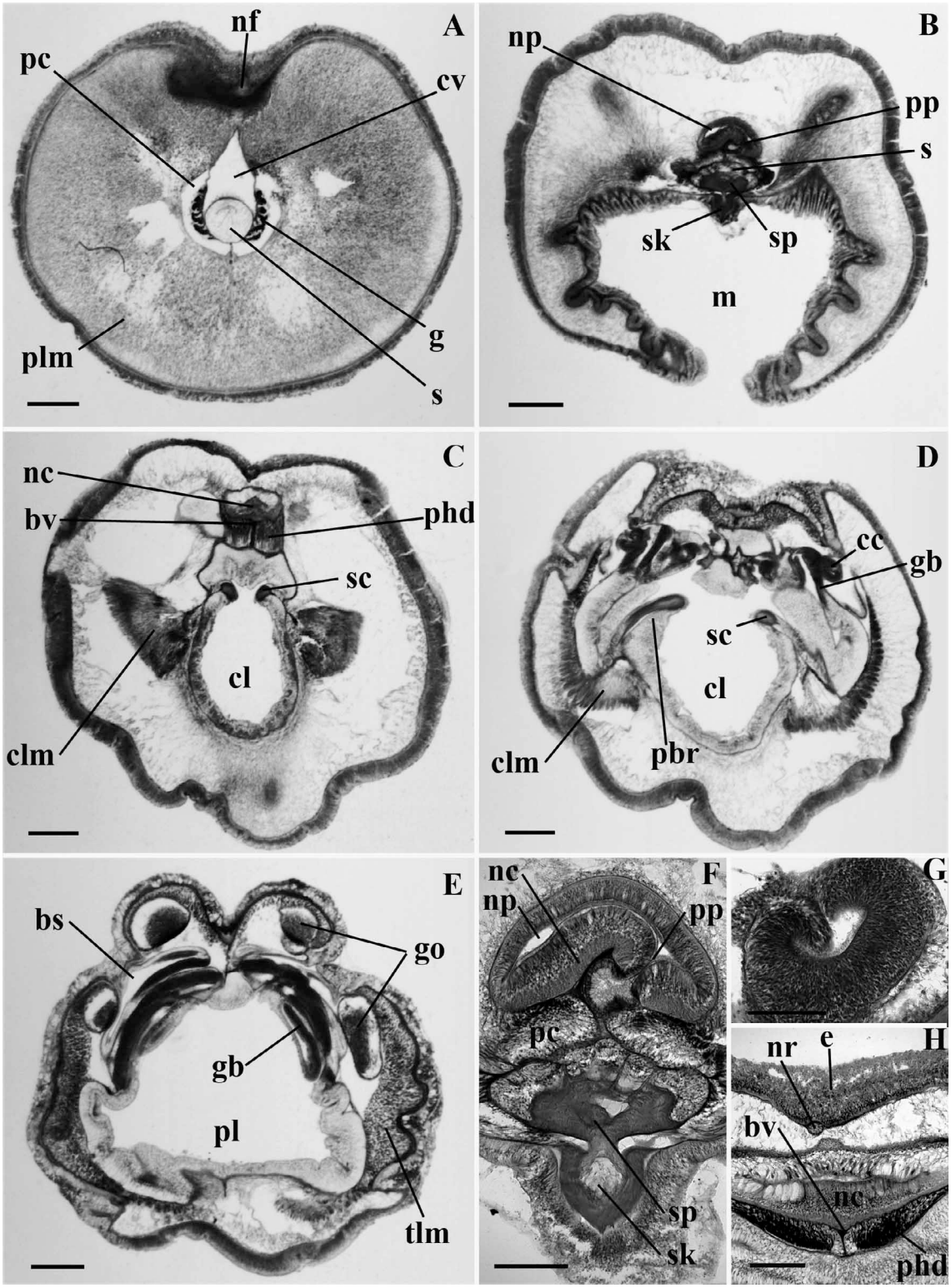

FIGURE 8. Light micrographs of transverse sections of *Ritteria ambigua*: A, Proboscis with heart-kidney complex. B, Junction of the proboscis and collar. C, Anterior region of the collar. D, Anterior pharyngeal region of the trunk. E, Genital region of the trunk. F, Proboscis skeleton, neuropore and proboscis pore. G, Collar canal. H, Collar nerve cord showing the nerve root. Abbreviations: bs, branchial sac; bv; blood vessel; cc, collar canal; cl, collar lumen; clm, collar longitudinal muscles; cv, cardiac vesicle; e, epithelia; g, glomerulus; gb, gill bar; go, gonad; m, mouth; nc, nerve cord; nf, nerve fiber layer; np, neuropore; nr, nerve root; pbr, parabuccal ridge; pc, proboscis coelom; phd, perihaemal diverticulum; plm, proboscis longitudinal muscles; pp, proboscis pore; s, stomochord; sc, skeletal cornua; sk, skeletal keel; sp, skeletal plate; tlm, trunk longitudinal muscles. Scale bars: A, B, C, D, E = 500 μm; F, G, H = 200 μm.

The resemblances of *Ritteria* to other enteropneusts are rather varied, but, as usual in this group, cannot all signify close relationship. The similarities between *Ritteria* and *Harrimania*, and between *Ritteria* and *Stereobalanus*, are respectively suggestive of a common trend toward the degeneration of several organs while increasing the emphasis on gonads. Although not conforming to the familial characters, *Ritteria* even resembles the Ptychoderidae in the relatively spacious cardiac vesicle and the extent of the ventral septum of the proboscis.

While not putting undue weight on these similarities, by no means unique in this group, we find the situation suggestive of the trivial name *ambigua*.

The defining characters of *Ritteria ambigua* are listed below:

A. Short proboscis and collar.
B. Longitudinal musculature of the proboscis is uniformly scattered.
C. Proboscis skeleton plate is coronate with extensions of collagen through the stomochord walls.
D. Only the ventral mesentery of the proboscis is present (no mesentery in the collar and trunk).
E. Left proboscis pore opening into an anterior neuropore.
F. Degeneration of the proboscis neck.
G. Presence of a nerve root in the collar nerve cord.
H. Well-developed horizontal collar canals with a dorsal infolding.
I. Two pairs of dorsolateral genital ridges starting immediately behind the collar.

***Horstia kincaidi* n. gen. et n. sp.**
(Figs 2A,F; 9A–F)

Material examined. In 1899 Professor Trevor Kincaid collected a dozen specimens on Whidbey Island in Puget Sound, Washington (47°59' N, 122°26' W). The species has not been found again. We have both old Ritter sections and more recent ones made by Bullock of nine of the specimens. Considering the faded condition of the former it seems best to designate one of the latter, accession no. USNM 71439 as the holotype; 58879 becomes the paratype.

External features (Fig. 2A,F)**.** Total length 30–40 mm. Proboscis 2 mm long, as short as wide, collar 1.5–2 mm long with irregular surface markings. Branchial region 6 mm long, tapering to 1.0–1.5 mm wide, exceptionally narrow, postbranchial trunk even more attenuated. Genital wings and hepatic lobes lacking. Branchial orifices conspicuous, their arrangement distinctive, with left and right rows close together on elevated ridge bounded laterally by groove. Gonads also conspicuous as long series of protruding nodules.

Color in life reported by Kincaid as brown. Proboscis uniform creamy white in material preserved by Perenyi's fixative, collar and anterior portion of thorax only slightly darker; remainder of animal (most of it) greenish brown with gonads yellowish white.

Internal features. Longitudinal muscle fibers of proboscis arranged in well-defined wedge-shaped radial plates (Fig. 9A). No conspicuous thickening of nerve-fiber layer in proboscis or any apparent dorsal longitudinal groove. Proboscis coelom extending to tip of organ. Glomerulus poorly developed (Fig. 9A), limited to two small bilateral masses (usually well defined in other species), standing out like wings. Pericardial sac quite spacious, covering dorsal and lateral sides of stomochord. Blood vessel also spacious, almost entirely filling inside of pericardial sac (Fig. 9A). Ventral and dorsal mesenteries present in proboscis to tip of proboscis complex (Fig. 9A).

Proboscis portion of stomochord large, simple, its cavity clearly defined, with slight posteriorly directed ventral blind lumen. A single proboscis pore present, on right or left. In one case, coelomic spaces, canals, and terminal vesicles were so nearly symmetrical apart from the single pore, that Ritter predicted individuals will be found with both pores.

Peribuccal diverticula absent. Perihaemal spaces extending forward of proboscis pore; cornua of proboscis skeleton extending nearly back to posterior edge of collar and notable for steepness and extent of their ventral projection, from their very origin, approaching transverse plane and nearly reaching ventral side

of buccal cavity. Keel deep and narrow; almost no chondroid tissue developed in connection with body of skeleton (Fig. 9B).

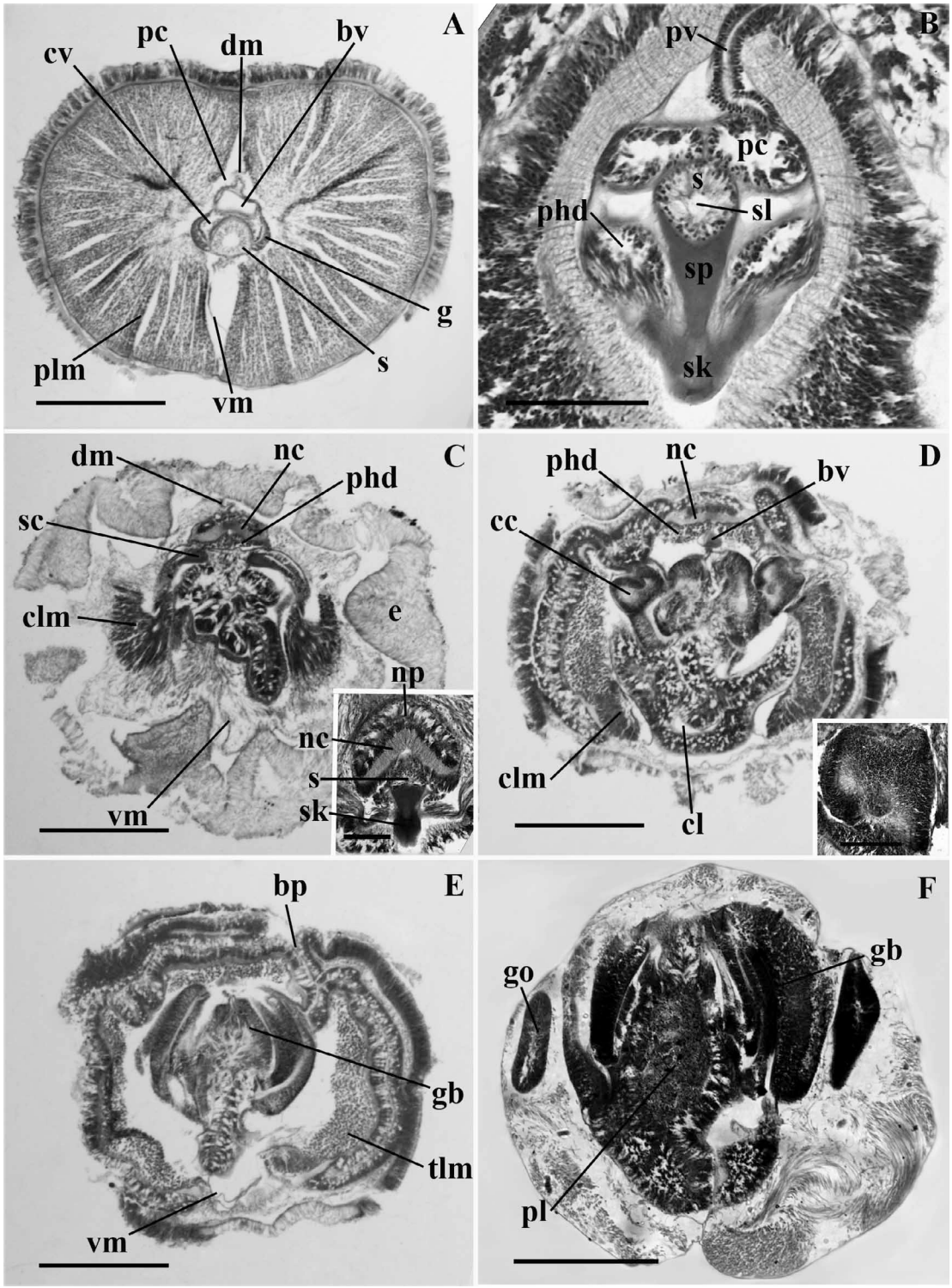

FIGURE 9. Light micrographs of transverse sections of *Horstia kincaidi* **n. gen. et n. sp.**: A, Proboscis with heart-kidney complex. B, Proboscis neck. C, Collar. Inset: Collar nerve cord and stomochord. D, Anterior pharyngeal region of the trunk. Inset: Collar canal. E, Pharyngeal region of the trunk. F, Genital region of the trunk. Abbreviations: bp, branchial pore; bv, blood vessel; cc, collar canal; cl, collar lumen; clm, collar longitudinal muscles; cv, cardiac vesicle; dm, dorsal mesentery; g, glomerulus; gb, gill bar; go, gonad; nc, nerve cord; np, neuropore; pc, proboscis coelom; phd, perihaemal diverticulum; pl, pharynx lumen; plm, proboscis longitudinal muscles; pv, proboscis vesicle; s, stomochord; sc, skeletal plate; sk, skeletal keel; sl, stomochord lumen; sp, skeletal plate; tlm, trunk longitudinal muscles; vm, ventral mesentery. Scale bars: A, C, E, G = 500 μm; B = 200 μm; D, F = 100 μm; H = 300 μm.

Stomochord continuous through neck, though narrow. Collar nerve cord with very large lacunae scattered throughout its length. A small anterior neuropore; dorsal wall of cord thicker than ventral for some distance behind neuropore (Fig. 9C inset). No dorsal crest or dorsal roots but dorsal mesentery well developed through collar (Fig. 9C). Collar canals large, vertically orientated (Fig. 9D and inset). Collar longitudinal muscles well developed, forming wing-shaped bundles on either side of collar lumen (Fig. 9D).

Ventral portion of pharynx about a third of size of branchial portion. Branchial pores on each side numbering about 30. Gonads beginning somewhat posterior to middle of branchial region (Fig. 9F). Individual gonads well separated from each other, standing out prominently from surface of body. Intestinal pores and hepatic caeca absent.

Remarks. We here carry out Ritter's intention to name the species for Professor Trevor Kincaid, long deceased of the University of Washington and a pioneer northwestern naturalist.

The defining characters of *Horstia kincaidi* are listed below:

A. Body very tapered, proboscis round.
B. Short proboscis and collar.
C. Longitudinal musculature of the proboscis in radial plates.
D. Deep and narrow skeletal keel with the cornua steeply bent ventralwards at their posterior end.
E. The dorsal and ventral mesenteries are present in the proboscis and collar.
F. Left or right proboscis pore.
G. Anterior neuropore.
H. Large vertical collar canals.
I. Two rows of lateral gonads forming small protuberances starting in the middle of the branchial region (no genital ridges or wings).
J. Gonopores on an elevated ridge.

Discussion

The present study has provided us the opportunity to evaluate the characters used to distinguish the species, even though such characters are probably of quite unequal reliability. The generic characters (see generic diagnoses and key to the genera) are sometimes used in defining species and are most likely to be stable, independent of environmental influence, season, age and individual variation. It is probably the same for a number of the common trivial characters such as the extent of dorsal and ventral mesenteries, the position of the gonads, the extent of the perihaemal and peribuccal diverticula, the cross-sectional shape of the collar canals, the presence of parabuccal ridges and the development of the skeleton body and cornua. The shape and arrangement of the proboscis complex, including the stomochord, cardiac vesicle, glomerulus and blood vessel are particularly good characters that seem to be stable and reliable. These have been consistent in the few species of which many individuals have been sectioned.

There remain many characters that are believed to be diagnostic of species but are less validated and difficult to assess. These include the extent of a proboscis groove, the number of muscle rings in the proboscis (*Saccoglossus*), the thickness of the proboscis circular-muscle-fiber layer with respect to the nerve-fiber layer, the opening of neuropore(s), the number and extent of collar nerve-cord lacunae and the presence of esophageal pores. It is generally agreed that these have a degree of reliability and hence we have leaned on them in part in the species accounts above. But the point to be stressed here is that this is a tentative and subjective judgment, and that the least confusion in the long run will be caused by erring on the side of recognizing too many taxa. While we do not place undue weight therefore on the validity of each species and genus, we feel that they should not be lumped without a new and more serious study of the diagnostic characters. Therefore our principal hopes for future validation, correction and improvement in the taxonomy of the harrimanid enteropneusts are validity tests of the present characters and the development of new characters. Because of the low number of unique features, the addition of one character, shared with some other taxa but not others, could greatly increase the discrimination and definition of each taxon.

Zoogeography

No general observations can, at this point, be made about the zoogeography of harrimaniid worms. *Harrimania planktophilus* (Cameron 2002), *Protoglossus mackiei*, *Stereobalanus willeyi*, *Horstia kincaidi*, *Mesoglossus macginitiei* and *Ritteria ambigua* are known from single individuals or single lots (Fig. 10). This may be due to a lack of sampling, especially in the subtidal.

Harrimania maculosa is known from Prince William Sound and Kodiak Island, Alaska (Ritter, 1900), and from Providence Bay in eastern Siberia, points 2200 km apart (Fig. 10). Here, the lack of effort in searching prevents a meaningful conclusion as to whether the distribution is disjunct and punctate or really a sizeable zoogeographical area of essentially continuous occurrence.

Mesoglossus intermedius is known from points on the central California coast about 200 km apart but not at many seemingly suitable sites in between (Fig. 10). This may be due to the paucity of visits. Its absence from the rocky, protected outer coast farther north may likewise be due to inadequate searching for the species. But its absence from the well-worked coast of southern California is probably real.

Stereobalanus canadensis has a discontinuous distribution that spans two oceans, occurring in the Lower Estuary and Gulf of St. Lawrence, Québec (Brunel et al. 1998), including the type-locality east of Prince Edward Island (Spengel 1893, 1901), New England (Reinhard 1942) and in Southern California (Fig. 10). A possible interpretation of such a distribution could be that *Stereobalanus canadensis* populations are relicts of a once wider-ranging species.

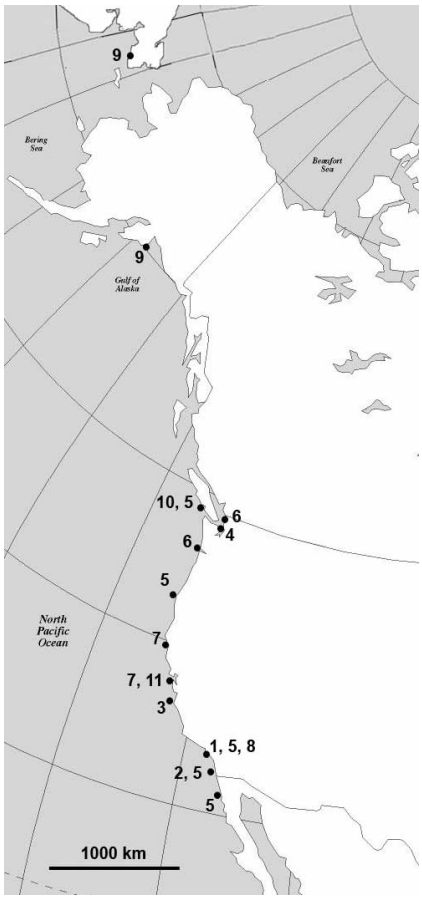

FIGURE 10. A map of the geographic distribution of harrimaniid enteropneusts on the west coast of North America: 1, *Stereobalanus willeyi* **n. sp.** Newport Bay, CA. 2, *Stereobalanus canadensis* San Diego, CA (also found in the Lower Estuary and Gulf of St. Lawrence, including east of Prince Edward Island; New England). 3, *Ritteria ambigua* **n. gen. et n. sp.** Monterey, CA. 4, *Horstia kincaidi* **n. gen. et n. sp.** Whidbey Island, WA. 5, *Saccoglossus pusillus* Barkley Sound, BC; Cape Arago, OR; San Pedro, San Diego, La Jolla, Anaheim, Newport Bay, CA; Ensenada, Mexico. 6, *Saccoglossus bromophenolosus* Padilla Bay, Willapa Bay, WA. 7, *Mesoglossus intermedius* **n. gen. et n. sp.** Shelter Cove, Moss Beach, CA. 8, *Mesoglossus macginitiei* **n. sp.** Newport Bay, CA. 9, *Harrimania maculosa* Prince William Sound, Kodiak, AK; Providence Bay, Siberia. 10, *Harrimania planktophilus* Barkley Sound, BC. 11, *Protoglossus mackiei* **n. sp.** Moss Beach, CA.

TABLE 1. Comparison of external and internal characters of the species of the family Harrimaniidae, excluding members of the genus *Saccoglossus* (to be discussed in a subsequent paper). Characters from previously described species were either obtained from the literature, or, in the case of *Harrimania maculosa* and *Saxipendium coronatum*, from the literature and the holotypes. Question marks indicate when a character state is unknown.

	Harrimania planktophilus [1]	***Harrimania maculosa*** [2]	***Harrimania kupfferi*** [3]	***Harrimania borealis*** [4]	***Protoglossus graveolens*** [5]	***Protoglossus koehleri*** [6]	***Protoglossus mackiei*** *	***Horstia kincaidi*** *	***Ritteria ambigua*** *
Distinctive characteristics								Body very tapered	No neck
Proboscis shape	Conical	Depressed, Conical	Conical	?	Pointed	Pointed	Conical	Rounded	Short, rounded
Proboscis length: width	Longer than broad	As long as broad	Longer than broad	?	Longer than broad	Longer than broad	Longer than broad	As long as broad	Little longer than broad
Proboscis longitudinal musculature	Radial	Radial	Radial	Radial	Radial	Radial	Radial	Radial	Diffuse
Proboscis coelom	Starts at the tip of proboscis	Anterior filled with connective tissue	Anterior filled with connective tissue	?	Filled with connective tissue	Starts at the tip of proboscis	Starts at the tip of proboscis	Starts at the tip of proboscis	Starts at proboscis complex
Proboscis groove	Dorsal	Dorsal	?	No	Deep dorsal	Deep dorsal	Deep dorsal	Dorsal	Dorsal
Proboscis pores	Left or both	Both	Both	Left	Left	Left	Left	Left or right	Left
Collar length: width	Broader than long	Broader than long	Broader than long	Broader than long	Broader than long	As long as broad	Broader than long	As long as broad	Broader than long
Collar shape	Posterior ruffled	Anterior ruffled	Deep posterior ring	Anterior frilled, posterior raised band	Deep posterior ring, anterior ruffled	Deep posterior ring, anterior ruffled	Anterior ruffled	Posterior ruffled	Posterior expanded rim
Neuropore	Posterior, (anterior)	(Anterior)	Anterior	?	?	Anterior, posterior	Anterior (posterior)	Anterior	Anterior
Nerve crest	?	No	No	No	?	?	No	No	No
Extent of periheamal diverticula	Seperate, in collar only	Seperate, in neck	Seperate, in collar only	Confluent anteriorly	2/3 of collar	To posterior limit of cornua	In neck	In neck	Seperate, in collar only
Peripharyngeal diverticula	No	No	No	No	?	Rudimentary	No	No	No
Skeleton shape	?	?	Funnel shaped plate	?	Plate forms 2 skewed funnels	No well developed keel, concave plate	Well developed keel	Deep and narrow keel	Coronate body
Extent of cornua	Pharynx	Pharynx	Posterior collar	?	Posterior collar	Posterior collar	Posterior collar	Posterior collar	Posterior collar
Presence and extent of parabuccal ridges	Anterior collar	Esophagus	?	Yes	Posterior collar	Posterior collar	Posterior collar	Anterior collar	Anterior collar
Presence and shape of collar canals	?	Short, horizontal	Dorsal fold	Yes	Yes	Yes	Horizontal	Large and vertical	Infolded, horizontal
Proboscis septa	Dorsal, ventral	Not complete	Dorsal, ventral	Ventral	Dorsal, ventral	Dorsal, ventral	Dorsal, ventral	Dorsal, ventral	Ventral
Collar septa	Dorsal, ventral	No	No	Dorsal, ventral	Dorsal, ventral	Dorsal, ventral	Dorsal, ventral	Dorsal, ventral	No
Trunk septa	?	No	Dorsal, ventral	Dorsal, ventral	Dorsal, ventral	Dorsal, ventral	Dorsal	Ventral	Dorsal
Size of branchial pharynx: digestive	Branchial bigger	?	Digestive bigger	?	?	Equal	Equal	Branchial bigger	Equal
Rows of gonads	Lateral	Lateral, dorsal	Lateral, dorsal	Lateral	Lateral	Lateral	Lateral	Lateral	Lateral, dorsal
Genital ridges	Irregular	No	Yes	No	?	Yes	No	No	Yes
Number of gill pores	Up to 54 pairs	40 pairs	40 pairs	30+ pairs	60-143 pairs	14-30 pairs	?	30	?
Gonads start	Posterior pharynx	Behind collar	Anterior gill region	Behind collar	In gill region	Posterior half of collar	?	Posterior half of gill region	Behind collar
Number of esophageal pores	?	?	?	?	0	0	?	0	?
Ventral muscular ridge	Yes	?	?	?	?	?	?	?	Yes

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TABLE 1. (continued)

	Mesoglossus macginitiei *	*Mesoglossus intermedius* *	*Mesoglossus bournei* [7]	*Mesoglossus caraibicus* [8]	*Mesoglossus gurneyi* [9]	*Mesoglossus pygmaeus* [10]	*Stereobalanus willeyi* *	*Stereobalanus canadensis* [11]	*Xenopleura vivipara* [12]	*Saxipendium coronatum* [13]
Distinctive characteristics				Gill pores not visible externally			4 columnar gonad ridges in branchial region	4 columnar gonad ridges in branchial region	Medullary folds, internal hepatic caeca	
Proboscis shape	?	Conical	Flattened	Flattened, conical	Flattened	?	Conical	Flattened	Rounded	Arrow shaped
Proboscis length: width	?	Longer than broad	Longer than broad	Longer than broad	Longer than broad	Longer than broad	Longer than broad	Broader than long	?	Longer than broad
Proboscis longitudinal musculature	Diffuse	Diffuse	Not concentric	Not concentric	Diffuse	Diffuse	Radial	Radial	?	Diffuse
Proboscis coelom	Starts at proboscis complex	Starts at proboscis complex	Starts at the tip of proboscis	Starts at the tip of proboscis	?	Starts at the tip of proboscis	Obliterated by tissue	?	Filled with connective tissue	In posterior third of proboscis
Proboscis groove	?	No	Dorsal and ventral on preserved specimens	?	Dorsal and ventral may be present	Fine dorsal	No	?	?	Dorsal
Proboscis pores	Left	Left	Left	Median	Median	Left	Both	Both	Left	Left
Collar length: width	?	Broader than long	Broader than long	As long as broad	Broader than long	Broader than long	Broader than long	Broader than long	?	Broader than long
Collar shape	?	Anterior ruffled, posterior ring	3 rings	?	?	?	Anterior expanded rim	Flattened	?	Posterior ring
Neuropore	Anterior, posterior	(Anterior)	Anterior	No	Anterior	?	Posterior	?	Anterior, posterior	Anterior, posterior
Nerve crest	Yes	No	?	No	No	No	No	?	?	No
Extent of periheamal diverticula	Confluent anteriorly, in neck	In collar only	?	Do not reach anterior collar	?	Posterior collar	In neck	In neck	?	In neck
Peripharyngeal diverticula	Yes	No	No	Yes	?	Yes	No	No	?	No
Skeleton shape	Mid-dorsal ridge	Well developed keel	?	Body bears a spine	?	?	No keel	Plate flat, broad blunt keel	?	Plate coronate, no keel, cornua recurved
Extent of cornua	2/3 collar	Posterior collar	Posterior collar	Mid-collar	Not to anterior collar	Posterior collar	Posterior collar	Posterior collar	?	Posterior collar
Presence and extent of parabuccal ridges	No	No	Posterior collar	?	Posterior collar	?	No	?	Trunk	No
Presence and shape of collar canals	Short, vertical	Short, vertical	?	Dorsal fold	?	Oval, no fold	No	No	Elongate	with collar pores
Proboscis septa	Ventral	Ventral	Ventral	Ventral	?	Ventral	Ventral	Ventral	Dorsal, ventral	Pericardiac vesicle in contact with dorsal wall, ventral
Collar septa	Dorsal, ventral	Dorsal, ventral	Dorsal, ventral	Dorsal, ventral	Dorsal, ventral	Dorsal, ventral	?	Ventral	?	Dorsal
Trunk septa	no	?	?	?	?	?	?	Dorsal, ventral	?	Dorsal, ventral
Size of branchial pharynx: digestive	Branchial bigger	Equal	Branchial bigger	Branchial bigger	?	?	Branchial bigger	Equal	?	Branchial bigger
Rows of gonads	Lateral	Lateral	?	?	?	?	Lateral, dorsal	Lateral, dorsal	?	Lateral
Genital ridges	Yes	No	No	?	No	?	Yes	Yes	No	Yes
Number of gill pores	?	25 pairs	?	50 pairs	?	9-22 pairs	70 pairs	?	4 pairs	54 pairs
Gonads start	Behind collar	2mm behind collar	Behind collar	?	?	Behind gill region	In gill region	In gill region	Behind collar	Behind collar
Number of esophageal pores	?	?	?	?	0	1 pair	1 pair	?	1 pair	40 pairs
Ventral muscular ridge	Yes	No	No	?	?	No	Yes	?	?	No

* New species; 1. Cameron, 2002; 2. Ritter, 1900; 3. von Willemoes-Suhm, 1871 and van der Horst, 1939; 4. Okuda & Yamada, 1955; 5. King, Giray & Kornfield, 1994; 6. Caullery & Mesnil, 1900, 1904; 7. Menon, 1904; 8. van der Horst, 1924; 9. Robinson, 1927 and van der Horst, 1939; 10. Hinrichs and Jacobi, 1938; 11. Spengel, 1893; 12. Gilchrist, 1925; 13. Woodwick & Sesenbaugh, 1985

Phylogeny

A phylogenetic hypothesis for the harrimaniid worms was constructed using the 18S rDNA gene tree (Cannon et al. 2009) as a backbone, to which we added the new genera *Horstia*, *Ritteria* and *Mesoglossus* using morphological characters (Fig. 11). Our tree shows that the proboscis musculature is a good character to define the different groups within the family. Using *Ptychodera* as an outgroup, this phylogeny suggests that the radial arrangement of proboscis muscle fibers may be ancestral to the family and that this type of arrangement would have been subsequently lost in *Ritteria*, *Saxipendium*, *Mesoglossus* and *Saccoglossus* (Fig. 11-J) and replaced by diffuse or concentrically arranged muscle fibers.

Our data suggest that *Saxipendium* is a close relative of *Ritteria*, another deep-sea genus that has been found at a depth of 700 meters off the coast of California. These species display a diffuse proboscis musculature and have a coronate proboscis skeleton (Fig. 11-L), a synapomorphy of the group. *Mesoglossus* is more closely related to *Saxipendium* and *Ritteria* than it is to *Saccoglossus*, the genus to which four *Mesoglossus* species were previously assigned. *Horstia* is a sister genus to *Protoglossus* and *Harrimania*; all three genera have a radial arrangement of proboscis musculature and ventral and dorsal proboscis mesentery. The hypothesis that *Protoglossus* may be basal among the Enteropneusta based on its simple arrangement of body cavities (Burdon-Jones 1956) is refuted here because all three species have perihaemal diverticula and *P. koehleri* has rudimentary peripharyngeal diverticula (Table 2). Furthermore, the 18S rDNA gene tree (Cannon et al. 2009) and our morphological analysis place *Protoglossus* as sister group to *Harrimania* based on the synapomorphy of parabuccal ridges (Fig. 11–F), which were once thought in *Harrimania maculosa* to be an oesophageal notochord (Ritter, 1900). The basal harrimaniid genus *Sterobalanus* has extensive gonadal ridges. They are not as extensive as the gonadal wings that characterize the family Ptychoderidae but the reduction of this feature supports the supposition that harrimaniid worm evolution has generally been characterized by a loss of morphological complexity.

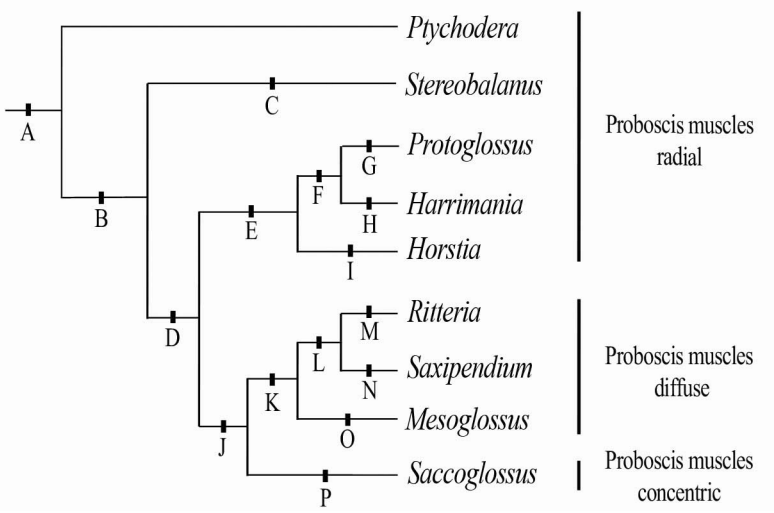

FIGURE 11. A phylogenetic hypothesis for the family Harrimaniidae that was constructed using the tree of Cannon et al. (2009) as a backbone, to which were added the new genera *Horstia*, *Ritteria* and *Mesoglossus*. A, Proboscis longitudinal musculature in radial bundles. B, Direct development, absence of branchial synapticules, hepatic caeca, genital wings, trunk lateral septa, parabranchial ridges and circular muscles in the trunk. C, Four tubular genital ridges restricted to the branchial region, reduced proboscis canals and pores. D, No individual character is known to be unique to this group. E, Dorsal and ventral proboscis septa. F, Parabuccal ridges. G, Prominent dorsal proboscis groove, proboscis short and conical, anterior edge of the collar is ruffled, anterior and posterior neuropores, parabuccal ridges extend to the posterior part of the collar, dorsal and ventral septa in the proboscis and collar. H, Collar broader than long, no peribuccal diverticula, proboscis conical, a little longer than broad. I, No genital ridges, gill pores on an elevated ridge, proboscis round and as long as broad, trunk very narrow. J, Loss of radial proboscis longitudinal musculature. K, Proboscis longitudinal musculature is diffuse. L, Live in deep sea, coronate proboscis skeleton. M, Absence of proboscis neck, two pairs of genital ridges, proboscis round, proboscis and collar broader than long, proboscis pore opens into the neuropore. N, Collar pores, cardiac vesicle attached to dorsal the wall of the proboscis, externally visible gonopores, gill pores not visible externally. O, Proboscis at least twice as long as broad, diffuse proboscis longitudinal musculature. P, Proboscis at least twice as long as broad, proboscis longitudinal musculature in concentric rings.

TABLE 2. A dichotomous key to the enteropneust families Harrimaniidae, Spengeliidae, Ptychoderidae and Torquaratoridae and to the genera of family Harrimaniidae.

1 Proboscis short, ovate; collar shorter than broad, hepatic caeca present in some genera; proboscis muscle includes thick layer of circular muscle encompassing homogenously arranged longitudinal fibers; stomochord with a vermiform process; pericardium and glomerulus with paired anterior diverticula more or less developed; chondroid tissue well developed; eggs small. .....family Spengeliidae

- Stomochord with no vermiform process; pericardium simple; ventral part of pharynx large and sometimes more or less separated from the branchial part 2
2 Proboscis short, hepatic caeca, genital wings 3
- Proboscis short or elongate, round or conical; collar peribuccal cavities absent, nerve-roots rarely present; skeletal cornua extending at least to middle of collar; trunk lacks circular muscles, lateral septa, parabranchial ridges, synapticles, and hepatic caeca; development direct, eggs large ..... 4, family Harrimaniidae
3 Proboscis short, conical; collar as long as broad with nerve roots; trunk external regionation pronounced; ventral part of pharynx large and sometimes more or less separated from branchial part by parabranchial ridges; genital wings extend into esophageal region; hepatic caeca ear-shaped; proboscis muscle in radial pattern of bands; gill bars short, curved, with synapticules; parabranchial ridges present; longitudinal ciliated intestinal grooves; eggs small, development indirect via tornaria larva. ..... family Ptychoderidae
- Proboscis short, dome shaped; collar very broad with midventral slit; short skeletal cornua; hepatic caeca; genital wings, gill bars without synapticules; eggs large ..... family Torquaratoridae
4 Proboscis longitudinal musculature in radial plates 5
- Proboscis longitudinal musculature not in radial plate 8
5 Four tubular genital ridges restricted to branchial region, proboscis canals and pores reduced or absent ..... *Stereobalanus*
- Gonads extending at least to oesophageal region, proboscis canals and pores well developed 6
6 Proboscis conical, parabuccal ridges 7
- Proboscis round, trunk very narrow, gill pores on an elevated ridge ..... *Horstia*
7 Proboscis with deep posterior dorsal groove, anterior edge of the collar is ruffled, anterior and posterior neuropores, parabuccal ridges extend to the posterior part of the collar, dorsal and ventral septa in the proboscis and collar ..... *Protoglossus*
- Proboscis a little longer than broad, no peribuccal diverticula, sometimes four rows of gonads and two proboscis pores, cornua may extend into the trunk ..... *Harrimania*
8 Proboscis at least twice its width with middorsal longitudinal groove and muscles arranged in several concentric rings ..... *Saccoglossus*
- Proboscis longitudinal musculature arranged diffusely. 9
9 Dorsal trunk with medullary folds; viviparous ..... *Xenopleura*
- No medullary folds; oviparous 10
10 Proboscis skeleton plate coronate 11
- Prooscis plate not coronate, proboscis twice its width, no conspicuous dorsal groove ..... *Mesoglossus*
11 Proboscis neck, proboscis skeleton without a keel, two genital ridges, collar canals with pores leading directly to the exterior of the body, cardiac vesicle attached to dorsal the wall of the proboscis, externally visible gonopores, gill pores not visible externally. ..... *Saxipendium*
- No proboscis neck, proboscis skeleton with keel, collar broader than long, proboscis pore opens into the neuropore, four genital ridges ..... *Ritteria*

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