Article

A revision of the genus *Saccoglossus* (Hemichordata: Enteropneusta: Harrimaniidae) with taxonomic descriptions of five new species from the Eastern Pacific

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Abstract

Here we describe five new North Eastern Pacific species of acorn worms in the genus *Saccoglossus* (*S. porochordus*, *S. rhabdorhyncus*, *S. shumaginensis*, *S. sonorensis*, and *S. palmeri*) on the basis of morphology. Notes on the habit and localization of each species are provided. A summary table lists the morphological characters defining the five new species and ten previously described ones in the genus *Saccoglossus*. Observation on the biogeography of Enteropneusta suggests that it is an ancient and declining group.

Key words: Enteropneusta, acorn worms, Harrimaniidae, new species, zoogeography

Introduction

Saccoglossus is the most speciose enteropneust genus, even after Deland et al. (2010) transferred five species of *Saccoglossus* to other genera. It contains 18 species worldwide including two (*S. pusillus*, *S. bromophenolosus*) from the Eastern Pacific. It may be more speciose than some ptychoderids because it does not have a pelagic larva and thus a low dispersal distance, increasing opportunity for speciation. It's richness with respect to other harrimaniids, also direct developers, is more difficult to explain but may be due to its unusually long proboscis allowing it great success in surface deposit feeding. Whatever the explanation for the speciosity of the genera, the outcome is that they are well know from several locations along the Eastern Pacific shorelines.

Saccoglossus is the most common genus of acorn worms occurring in the Eastern Pacific. It has been collected from Barkley Sound, BC, Coos Bay, OR, San Pedro, San Diego, La Jolla, Anaheim, and Newport Bay, CA, Ensenada, Mexico (*S. pusillus*) and Willapa Bay, WA (*S. bromophenolosus*) but more often than not the species has remained unknown.

Here we present 5 new species based on specimens from the collections of Ritter and Bullock, deposited at the Smithsonian Museum (US Natural History Museum, Washington). The *S. shumaginensis* specimens were taken by W.E. Ritter on the Harriman Alaska expedition of 1899 and the others have been collected by T.H. Bullock, G.E. MacGinitie and J. McNab between 1938 and 1971.

The species descriptions are accompanied by photographic illustrations and discussions of zoogeography, species characters and relationships. A table listing the characteristic features of each species of the genus should be a useful tool for species identification. It is hoped that these contributions will make the work useful to non-specialists.

Material and methods

The specimens used in this study are part of T. H. Bullock's enteropneust slides collection deposited at the Smithsonian Institution National Museum of Natural History, Washington, DC. Most of the material in this collection has been fixed in Bouin's solution, while some of it was fixed in formol-acetic-alcohol and all the material has been 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 or an Olympus SZX16 stereomicroscope for lower magnifications.

Diagnoses of the Harrimaniidae and the genera *Saccoglossus*

Class Enteropneusta Gegenbaur, 1870

Family Harrimaniidae Spengel, 1901

Balanoglossidae: Willey, 1899

Harrimaniidae: van der Horst, 1935

Diagnosis. Enteropneusta characterized by the absence of circular muscle fibers in the trunk. In those cases where the development has been studied, the typical tornaria larva is absent and the 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 the stomochord, absence of hepatic caeca in the trunk and absence of synapticulae joining the primary and secondary gill bars (for a drawing of a generalized enteropneust, see Fig. 1 from Cameron, 2005). The dorsal nerve roots in the collar mesentery and the intestinal pores may be present or absent. The skeletal cornua extend at least to the middle of the collar (Deland et al. 2010).

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. 2 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, 1895), *S. pusillus* (Ritter, 1902, 1929), *S. ruber* Tattersall, 1905, and *S. sulcatus* (Spengel, 1893). *S. cambrensis* (Brambell, Rogers and Goodhart, 1939), *S. serpentinus* (Assheton, 1908) and *S. ruber* (Tattersall, 1905) are synonymous species from the United Kingdom (Burdon-Jones, 1960) and so *S. ruber* takes precedence. *S. ruber* characteristics found in this article, including Table 1, are taken from the more

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comprehensive taxonomic treatment of Brambell, Rogers and Goodhart (1939). Five new species collected from the Eastern Pacific are described below.

New species descriptions

Saccoglossus porochordus **n. sp.**
(Figs 1A, B; 2A–F)

Material examined. Several (18) specimens have been collected from intertidal mud flat in Newport Bay, California, (33° 35' N, 117° 53' W) by Professor G.E. MacGinitie of the Corona del Mar Marine Laboratory of the California Institute of Technology. *Holotype:* Accession no. NMNH 58897, Smithsonian Institution. *Paratypes:* Accession nos. 58899, 58916, 58917 and 58918.

External features (Figure 1 A, B)**:** The proboscis is 7 mm long and 4 mm broad, round in cross section but with a distinct middorsal longitudinal groove. The collar is 4 mm long and 3.5 mm broad. The genital ridges commence about 8 mm behind the collar. Ventral muscular ridges are absent from the trunk.

Internal features (Figure 2)**:** There is a fairly conspicuous circular muscle fiber layer in the proboscis, which is four to five fibers in thickness. The nerve fiber layer is thickened middorsally. The proboscis epidermis is about 200 μm thick. The longitudinal muscle fibers are arranged in 8 to 10 concentric rings. The proboscis cavity extends almost to the tip of the proboscis as a narrow lumen lined by connective tissue cells and circular fibers. The dorsal groove of the proboscis is lined by a glandular epithelium (Fig. 2A). The right and left halves of the glomerulus are confluent over the tip of the stomochord at the cardiac vesicle, and also meet along the midventral line. The stomochordal lumen extends nearly to its tip. There is a single midventral caecum in the stomochord lumen. Anterior to the midventral caecum, the stomochord has a deep dorsal pit descending into its dorsal wall. The ventral and dorsal septa are absent. The proboscis skeleton has an anterior marginal middorsal spine projecting forward into the stomochordal tissue (Fig. 2B). The keel of the skeleton may or may not be sharp but is deep, and short in the antero-posterior direction. The left proboscis canal is rather long, in the form of a narrow tube. At about the level of the skeletal plate, the left proboscis canal tends to occupy a middorsal position. Only the left proboscis pore is present (Fig. 2C).

The perihaemal cavities extend into the peduncle, stopping short of the proboscis pore by about 180 μm; they are confluent anteriorly (Fig. 2C). There is no neuropore on either ends of the collar. Both the dorsal and ventral collar mesenteries are complete. The collar epidermis is about 500 μm thick. The neural crest on the collar nerve cord appears at about the middle of the collar (Fig. 2D and inset). The septum separating the perihaemal cavities also extends anteriorly up to this level. At its commencement the neural crest is low and does not reach the basal membrane of the epidermis dorsally. But a little distance posteriorly it comes in direct communication with the epidermal nerve layer through a break in the basal membrane of the epidermis. The skeletal cornua reach almost to the posterior margin of the collar. They are confined to the dorsolateral aspect of the buccal cavity throughout (Fig. 2D). Peribuccal cavities extend only a short distance into the collar as triangular spaces on either side of the collar lumen. The collar canals are almost vertical in their disposition (Fig. 2E, F). At the posterior end of the collar there is sometimes a middorsal narrow, deep groove entirely lined by mucus secreting cells, which appear stainless in section (Fig. 2G).

The branchial part of the pharynx is equal to or slightly larger than the ventral part. The tongues and septa are all in one plane. The nuclei in the ciliated branchial epithelium are disposed in several strata. Gonads, which are not lobed, appear about 1 or 1.5 mm behind the collar. The gonadal pores appear to be opposite and parallel to the branchial pores and they do not alternate. Ventral longitudinal muscle fibers of the trunk, though heavily developed, do not form ventral longitudinal ridges (Fig. 2H).

Remarks. The nearest relationships of the form under consideration are with *S. rhabdorhynchus*, *S. horsti* and *S. otagoensis*, which it resembles in several characters such as the narrow proboscis coelom, several strata of nuclei in the ciliated branchial epithelium, unlobed gonads and the extent of the skeletal cornua in the collar. But in the possession of a dorsal pit on the stomochord and in the appearance of the genital ridges
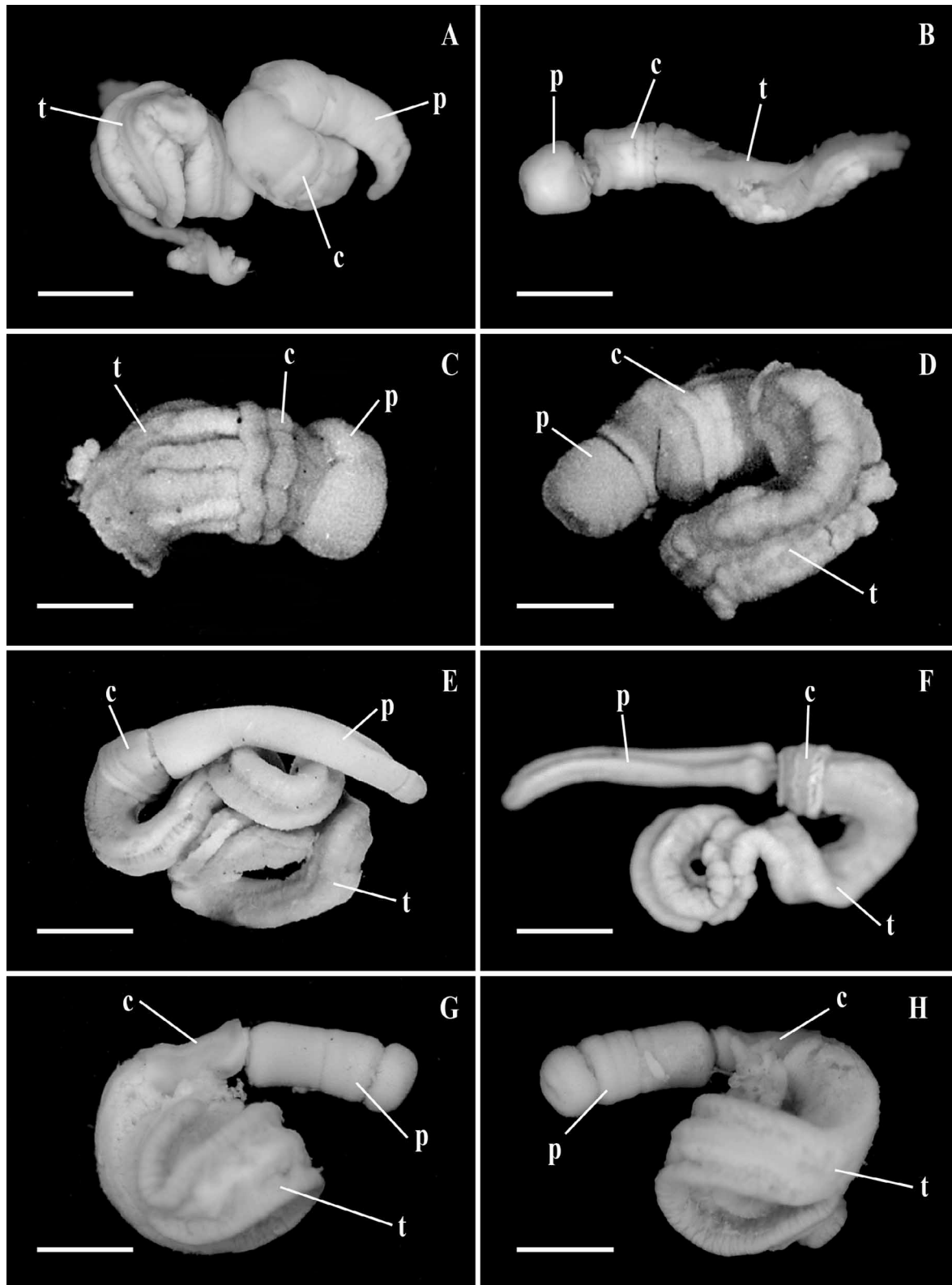
FIGURE 1. Photographs of fixed specimens from the NMNH (Smithsonian). With the exception of A and F, all of the specimens have lost the anterior end of the proboscis. A, Photograph of a coiled specimen of *Saccoglossus porochordus* **n. sp**. showing the proboscis and dorsal side. B, Photograph of the ventral side of *S. porochordus* **n. sp.** C, Photograph of the dorsal side of *S. rhabdorhynchus* **n. sp.** D, Photograph of the lateral side of *S. rhabdorhynchus* **n. sp.** E, Photograph of the right side of *S. shumaginensis* **n. sp.** F, Photograph of the left side of *S. shumaginensis* **n. sp.** G, Photograph of the right side of *S. sonorensis* **n. sp.** H, Photograph of the left side of *S. sonorensis* **n. sp.** c, collar; p, proboscis; t, trunk. Scale bars = 5 mm.
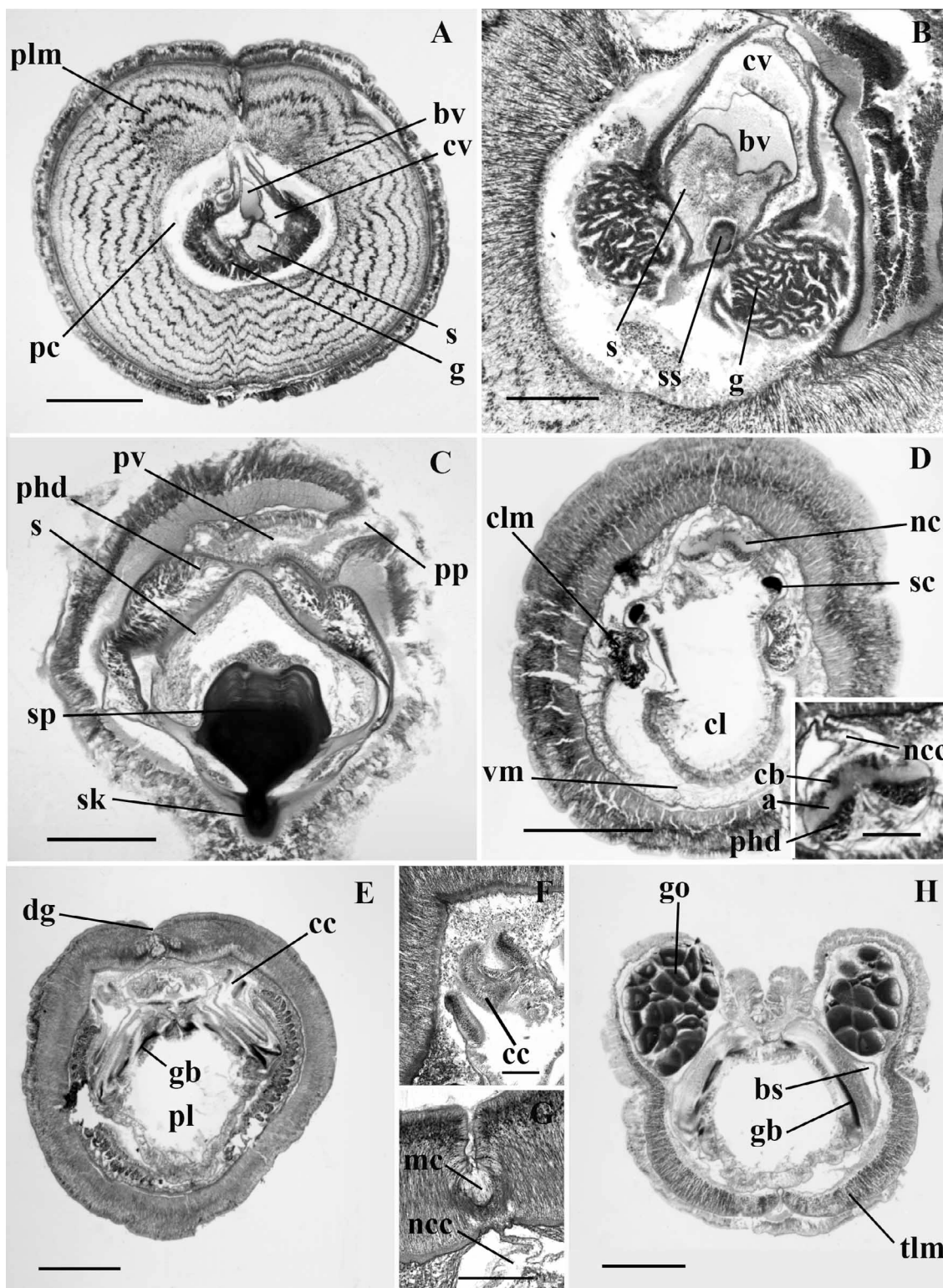
FIGURE 2. Light micrographs of transverse sections of *Saccoglossus porochordus* **n. sp.**: A, Proboscis with heart-kidney complex. B, Heart-kidney complex. C, Proboscis neck. D, Anterior region of the collar. Inset: Dorsal collar nerve cord and crest. E, Posterior region of the collar. F, Collar canal. G, Dorsal groove of the collar. H, Anterior pharyngeal region of the trunk. a, axons; bs, branchial sac; bv, blood vessel; cb, cell bodies; cc, collar canal; cl, collar lumen; clm, collar longitudinal muscles; cv, cardiac vesicle; dg, dorsal groove; g, glomerulus; gb, gill bar; go, gonad; mc, mucous cells; nc, nerve cord; ncc, nerve cord crest; pc, proboscis coelom; phd, periheamal diverticulum; pl, pharynx lumen; plm, proboscis longitudinal muscles; pp, proboscis pore; pv, proboscis vesicle; s, stomochord; sc, skeletal cornua; sk, skeletal keel; sp, skeletal plate; ss, skeletal spine; tlm, trunk longitudinal muscles; vm, ventral mesentery. Scale bars A, D and F = 750 µm; B and C = 300 µm; D inset and E inset = 200 µm.

rather far from the collar (8 mm) the present species differs from all other species of the genus. Among the *Saccoglossus* species occurring in the Eastern Pacific region, it resembles in a few characters *S. pusillus* (complete dorsal and ventral mesenteries in the collar; extent of the skeletal cornua in the collar), besides being closely related to *S. rhabdorhynchus* (Table 1). In view of these considerations it is necessary to recognize it as a new species.

Etymology. The trivial name is derived from the fact that the stomochord bears a pit on the dorsal side.

Saccoglossus rhabdorhynchus **n. sp.**
(Figs 1C,D; 3A–F)

Material examined. Six specimens were dredged in 1939 from a depth of 36 meters on rocky bottom off Half Moon Bay, California, (37° 12' N, 122° 30' W). The specimens were found in the surface debris on hard shale rock. *Holotype:* Accession no. NMNH 1132795. *Paratype:* Accession no. NMNH 1132796.

External features (Figure 1 C, D)**:** The total length is about 20 to 30 mm; the length of the proboscis is 2.5 mm, and the collar is 1.5 mm, after fixation. The collar is broader than long with two posterior annular thickenings. The posterior end of the collar is broader than the anterior. The length of the branchial region is about 4 mm. Openings of the branchial sacs are externally visible. The proboscis has a shallow middorsal longitudinal groove. The genital ridges are in the form of knob-like elevations on either side of the gill pores, extending posteriorly beyond the branchial region. The color in life is bright red.

Internal features (Figure 3)**:** The nerve fiber layer of the proboscis is thickened middorsally along the shallow middorsal groove. The circular muscle fiber layer is quite conspicuous, being 4 or 5 fibers in thickness. Longitudinal muscle fibers are arranged concentrically, forming 8 or 9 rings. The proboscis cavity is narrow, extending nearly to the tip of the proboscis, completely filled anterior to the proboscis complex with irregular, granulated cells (connective tissue elements) limited all around by a layer of circular fibers. There is no dorsal septum and the ventral one extends only up to the ventral blind lumen of the stomochord (Fig 3A). Only the left dorsal coelomic cavity is in communication with the median proboscis canal, which opens to the exterior by a left proboscis pore. The lumen of the stomochord is continuous extending nearly to the tip. The anterior part of the stomochord is slightly bent dorsal wards and this part shows only lacunae. The ventro lateral caeca of the stomochord lumen are united with one another and wide open to the primary lumen (Fig. 3B). The cardiac vesicle extends ventrally over the sides of the stomochord. The glomerulus is present on the lateral sides of the stomochord and the halves are united anteriorly in front of the cardiac vesicle and the stomochord. The anterior face of the skeleton is projecting forward into a spine or obtuse projection (Fig. 3B). The keel of the skeleton is quite distinct and deep anteriorly (Fig. 3C); its cornua extend nearly to the posterior margin of the collar (Fig. 3D).

Both dorsal and ventral mesenteries of the collar are incomplete, being confined to the posterior third or fourth of the collar. The collar canals are short and vertically oriented, the walls being thick, with nuclei arranged in many strata (Fig. 3E). The perihaemal cavities extend up to the proboscis pore, separate from one another throughout. Peribuccal cavities are not distinguishable. The collar nerve cord is almost solid with only a few lacunae. It is continuous at both ends with epidermal invaginations (Fig. 3E). No dorsal nerve roots are present. The stomochord opens into the buccal cavity in the anterior part of the collar. There is an invagination of the trunk gut in the posterior part of the collar that fuses posteriorly with the collar gut.

The ventral part of the pharynx is about a third of the total. The ciliated epithelium of the gill septa is thick with the nuclei in many strata. The ventral longitudinal musculature is heavily formed (Fig. 3F). Gonads do not alternate with gill openings; only the lateral gonads are present.

Remarks. *S. rhabdorhynchus* is, as may be seen from the above description, similar to *S. otagoensis* in several characters, such as the extent of the skeletal cornua, the absence of the dorsal crest on the collar nerve cord, the absence of the ventral mesentery in the anterior part of the collar, the absence of lobed gonads, the origin of the genital ridges close to the collar and the arrangement in several strata of the nuclei in the ciliated branchial epithelium. One or more of these features are shared by certain other species of *Saccoglossus*, such
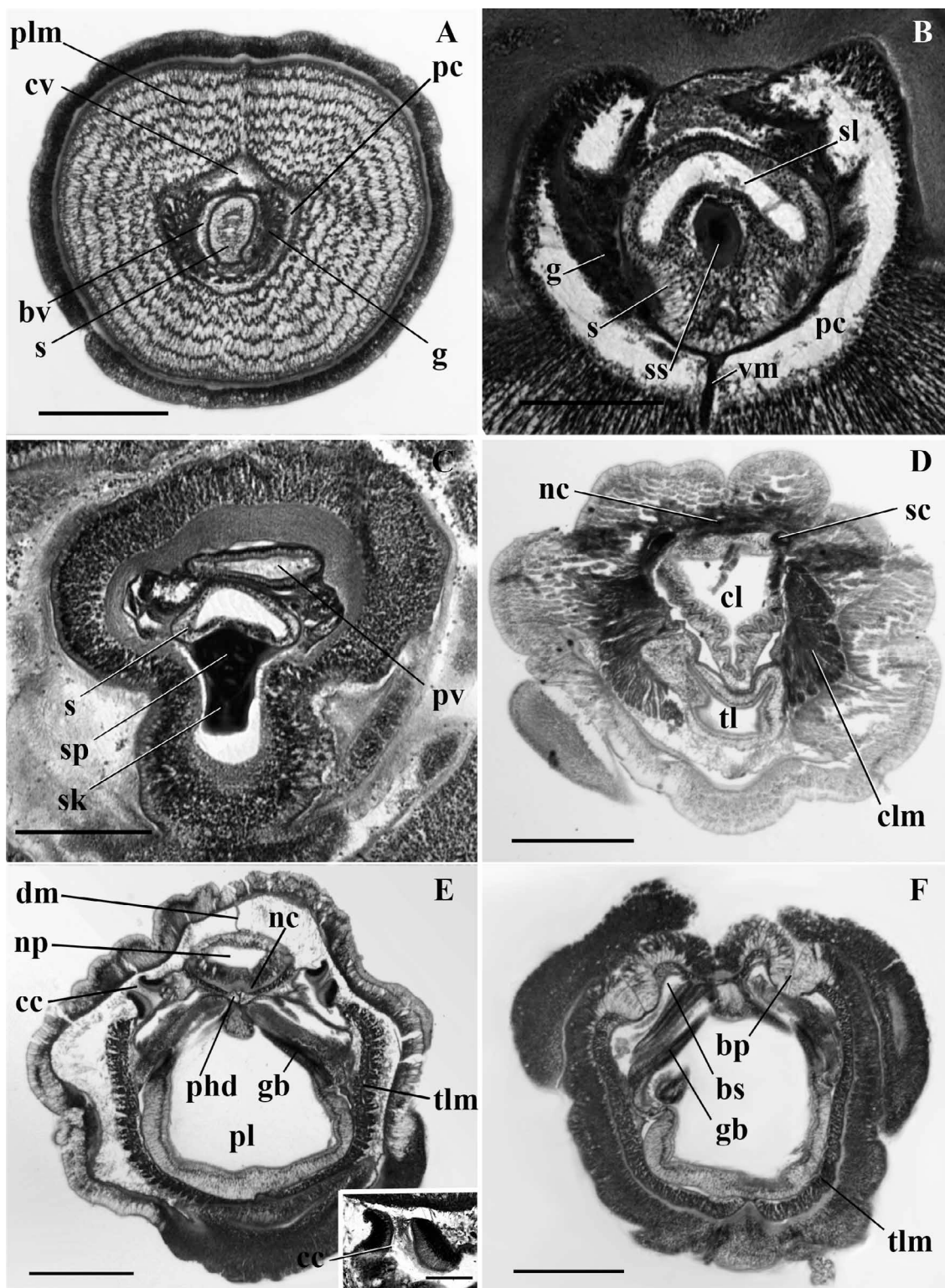
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FIGURE 3. Light micrographs of transverse sections of *Saccoglossus rhabdorhynchus* **n. sp.**: A, Proboscis with heart-kidney complex. B, Proboscis neck showing the spine of the proboscis skeleton. C, Proboscis neck showing the proboscis vesicle. D, Anterior region of the collar. E, Posterior region of the collar. Inset: Collar canal. F, Anterior pharyngeal region of the trunk. bp, branchial pore; bs, branchial sac; bv, blood vessel; cc, collar canal; cl, collar lumen; clm, collar longitudinal muscles; cv, cardiac vesicle; dm, dorsal mesentery; g, glomerulus; gb, gill bar; nc, nerve cord; pc, proboscis coelom; np, neuropore; phd, periheamal diverticulum; pl, pharynx lumen; plm, proboscis longitudinal muscles; pv, proboscis vesicle; s, stomochord; sc, skeletal cornua; sk, skeletal keel; sl, stomochord lumen; sp, skeletal plate; ss, skeletal spine; tl, trunk lumen; tlm, trunk longitudinal muscles; vm, ventral mesentery. Scale bars A, B, C, D, E, F = 500 μm; E inset = 100 μm.

as, *S. horsti, S. shumaginensis, S. mereschkowskii, S. pusillus, S. kowalevskii*, and *S. ruber*. While *S. pusillus* and *S. ruber* have only one character each in common with the species under consideration, *S. horsti* on the other hand is next only to *S. otagoensis* in its resemblance to the new species. Thus, they both have well developed ventral muscular ridges in the trunk; in both the genital ridges start near the collar; in both the gonads are not lobed; and finally in both the nuclei of the ciliated branchial epithelium are in several strata (Table 1).

Although *S. rhabdorhynchus* more or less resembles certain other species of *Saccoglossus*, it exhibits some features that are shared by no other species of the genus. The complete filling up of the proboscis coelom by irregular granulated cells, the possession of a dorsal glomerulus and the complete separation of the perihaemal cavities through their entire length are characteristic of this species of *Saccoglossus*. The type of substratum from which this species was collected, hard shale rock, is also rather unexpected. *Saxipendium coronatum* lives upon rock (Woodwick & Sensenbaugh, 1985) but this type of habitat has no parallel among the known species of *Saccoglossus* and is to be considered a unique feature of this species, unless in fact the debris on the shale amounts to a considerable layer of muddy sand.

Etymology. The trivial name of this species is derived from the fact that the proboscis coelom is solidly filled with granulated cells unlike that in all other known species of the genus.

Saccoglossus shumaginensis **n. sp.**
(Figs. 1E,F; 4A-F)

Material examined. Nineteen specimens were collected by Ritter from the sand flat at the northwestern extremity of Popoff Island, in the Shumagin group in Alaska, immediately opposite to the small rocky Range Island (55° 19' N, 160° 24' W). *Holotype:* Accession no. 1132797. *Paratype:* NMNH 1132798. The following is an extract from Ritter's manuscript: "I was able to get it only at extreme low tide and then not in abundance. Vigorous digging on three successive mornings yielded nineteen specimens. It seems to occur only in sand containing much decaying organic matter, for I found it only in places where the eelgrass had filled the sand with roots and where, consequently, the sand was black with products of organic decay ...There is an absence of the spirally coiled cast of sand on the surface... It is usually found at a depth of eight or ten inches. It has very little of the usual enteropneust odor."

External features (Figure 1 E, F)**:** The total length is about 55 mm; the proboscis is 11 to 18 mm long or five times the length of the collar. The proboscis has a middorsal groove. The collar is somewhat broader than long, the posterior end being especially broader than the anterior. The branchial region is more or less three times the length of the collar. The genital ridges are present and start immediately behind the collar. The ventral muscular ridges of the trunk are quite prominent. There are about 30 to 40 gill pores.

The proboscis is vermillion red, slightly more intense at the tip. The collar, pharynx and abdomen are purplish red with a tinge of green, the anterior parts being somewhat darker. Behind the pharyngeal region, the body gradually shades into a greenish tint in which there is very little red.

Internal features (Figure 4)**:** The layer of circular muscle fibers in the proboscis is delicate and scarcely as thick as the nerve fiber layer, which is thickened along the dorsal midline in the posterior half of the organ. Longitudinal fibers are arranged in about eight concentric rings. The proboscis coelom extends almost to the tip of the organ (Fig. 4A). Its anterior portion is filled with connective tissue and surrounded by a thick layer of circular fibers. It becomes very broad in the posterior half of the proboscis (Fig. 4B). There is single left proboscis pore communicating by a conspicuous proboscis vesicle. The stomochord has a distinct lumen but the single ventral caecum is not prominent. The cardiac vesicle is normally formed (Fig. 4B). The glomerulus completely surrounds the proboscis complex in its anterior half, but does not cover the cardiac vesicle dorsally in the posterior half of the complex, it is projecting over the anterior tip of the stomochord. There is a dorsal mesentery in the posterior half of the proboscis, but the ventral septum is little developed or absent. The skeletal keel is not sharp and extends only on a short distance before the proboscis pore (Fig. 4C).
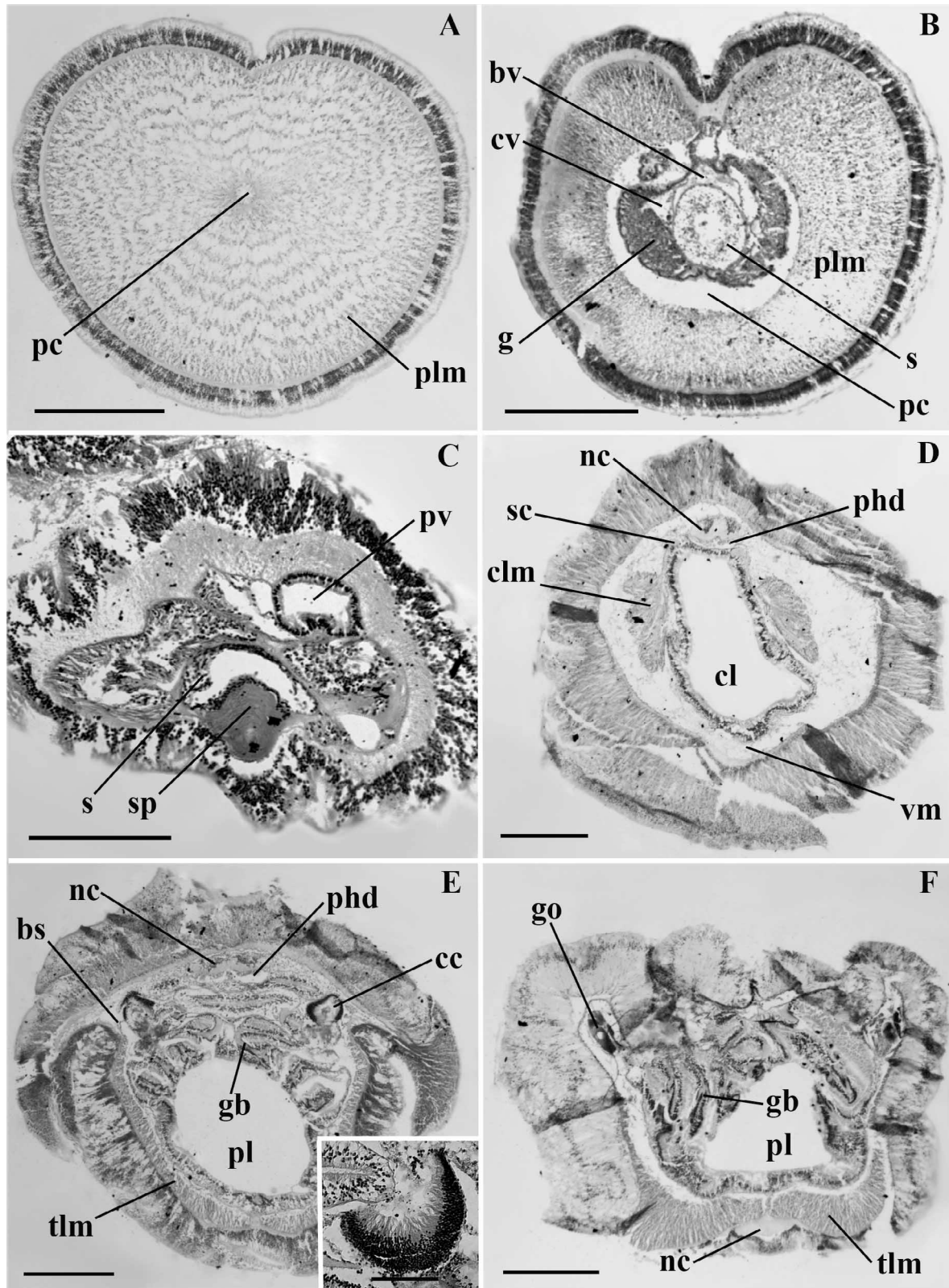
FIGURE 4. Light micrographs of transverse sections of *Saccoglossus shumaginensis* **n. sp.**: A, Proboscis. B, Proboscis with heart-kidney complex. C, Proboscis neck. D, Anterior region of the collar. E, Posterior region of the collar. Inset: Collar canal. F, Anterior pharyngeal region of the trunk. bs, branchial sac; bv, blood vessel; cc, collar canal; cl, collar lumen; clm, collar longitudinal muscles; cv, cardiac vesicle; g, glomerulus; gb, gill bar; go, gonad; nc, nerve cord; pc, proboscis coelom; phd, periheamal diverticulum; pl, pharynx lumen; plm, proboscis longitudinal muscles; pv, proboscis vesicle; s, stomochord; sc, skeletal cornua; sp, skeletal plate; tlm, trunk longitudinal muscles; vm, ventral mesentery. Scale bars A, B, D, E, F = 500 µm; C = 200 µm; E inset = 100 µm.

Neither dorsal nerve crest nor dorsal nerve roots are present in the collar (Fig. 4D), but the collar nerve cord may be in contact middorsally with the basement membrane of the epidermis. There is no neuropore. The ventral mesentery is present. The perihaemal cavities are connected anteriorly. Peribuccal cavities are present (Fig. 4D). The skeletal cornua reach back somewhat behind the middle of the collar. At their posterior ends they bend abruptly ventral-wards. The ventral longitudinal musculature is poorly developed.

The branchial part of the pharynx is equal or slightly larger than the ventral part (Fig. 4E). The nuclei in the ciliated branchial epithelium may be arranged in one or few strata. There are six to seven pairs of intestinal pores. The gonads begin a little behind the tenth gill pore. The testes are lobed. The ventral longitudinal musculature is heavily developed forming a ridge on the external surface of the trunk (Fig. 4F).

Remarks. From the description of *S. shumaginensis* given above, it is evident that it resembles in a number of characters *S. mereschkowskii* and *S. otagoensis*. But both these species differ from *S. shumaginensis* in not possessing the peribuccal cavities, having several strata of nuclei in the ciliated branchial epithelium and in lacking a well developed epitheloid lining for the proboscis cavity. Furthermore, the presence of several pairs of intestinal pores and the lobed gonads in the species under consideration are additional differences with *S. otagoensis*. Likewise *S. mereschkowskii* does not have a dorsal knee (or sigmoid bend) in the stomochord, unlike the present species.

The present species resembles in one or more characters certain other species of *Saccoglossus*. Thus in the possession of a single ventral stomochordal diverticulum (caecum) and several pairs of intestinal pores, both *S. ruber* and *S. horsti* resemble the present form. Further in *S. horsti*, as in the new species, the peribuccal cavities are present and the genital ridges start close to the collar. *S. shumaginensis* resembles *S. kowalevskii* in the possession of the peribuccal cavities and the several pairs of intestinal pores as also in the arrangement of the nuclei of the ciliated branchial epithelium in a single or a few strata. The most common species of the west coast of North America, namely *S. pusillus*, is easily distinguishable from the present form even from the external coloration. Only in the single ventral stomochordal caecum and the lobed testes do these two species resemble each other.

The brilliant coloration, the peculiar shape of the collar and the well defined epitheloid lining of the proboscis cavity are the most striking features of this species.

The above description is based on the manuscript of Ritter and expanded in certain details by our own observations on sections of the material collected by him. At the time he wrote the description only four or five species under this genus were known. In view of the several new species discovered in recent times, the discussion above is entirely new.

Etymology. The trivial name is derived from the Shumagin Islands.

Saccoglossus sonorensis **n. sp.**
(Figs 1G, H; 5A–G)

Material examined. A single specimen in good condition which will be the type (T.H.B. accession no. 409) was collected from Cholla Bay, near Puerto Penasco, Sonora, Mexico (31° 17' N, 113° 35 W) in the Gulf of California, by T.H.B. in January, 1949, in slightly muddy sand. Three more anterior fragments were taken in January, 1957, at the same place and a dozen more in 1971. When an area with typical castings every few meters was found, nearly every casting yielding at least a tail fragment the habit similar to that of *S. pusillus, S. kowalevskii, S. bromophenolosus* and perhaps typical for the genus. *Holotype:* Accession no. NMNH 1132799. *Paratype:* Accession no. NMNH 1132800.

External features (Figure 1 G, H)**:** The total length is commonly 120-150 mm or more, the proboscis is 25 mm long, the collar is 2-4 mm. The proboscis is 2-3 mm wide and yellow orange; the collar is only slightly wider and a little deeper orange. Genital ridges are not conspicuous but the gonads commence immediately behind the collar. Ventral muscular ridges in the trunk are not present.

Internal features (Figure 5)**:** The proboscis nerve fiber layer is rather thin, but shows a slight middorsal thickening. The circular muscle fiber layer is only about 4 fibers thick. Longitudinal muscle fibers are

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arranged in 5 to 6 concentric rings (Fig. 5A). The proboscis lumen extends as a narrow round space almost to the tip of the proboscis, the anterior most part being occupied by connective tissue cells. It is lined by a layer of amoeboid cells in turn surrounded by a thin layer of circular fibers (Fig. 5A inset). The glomerulus extends anteriorly a little over the tip of the stomochord. The tip of the cardiac vesicle, which extends slightly beyond the stomochord, is surrounded on all sides by the glomerulus. The lumen of the stomochord extends to its tip only in the form of small irregular spaces, which are not continuous with each other. There is a dorsal glomerulus. The glomerulus covers even the ventral side of the stomochord, appearing in cross section as four or five finger-like processes hanging down from the ventral side of the stomochord. The cardiac vesicle is rather large and surrounds the stomochord on all sides except ventrally. But the lumen of the cardiac vesicle is quite filled with connective tissue, excepting the middorsal part (Fig. 5A). The stomochord lumen has two ventro lateral caeca, equally well developed and continuous with the primary central lumen (Fig. 5B). Posterior to these ventro lateral caeca, that is in the neck region, the wall of the stomochord becomes thinner and the stomochord now has a spacious and clear lumen. The end plate of the proboscis skeleton has a conspicuous middorsal spine which projects into the ventral caeca of the stomochord (Fig. 5C). The proboscis skeleton has a distinct and deep keel over a short length in its anterior part (Fig. 5C), but the keel is absent posterior to this, although the skeletal body is normal; the length of the keel antero-posteriorly is about 200 µm. Only the right proboscis canal is present (Fig. 5C), occupying a median dorsal position posterior to the cardiac vesicle, and opening by a right proboscis pore. The dorsal and ventral septa are absent.

The collar epithelium is about 700 µm in thickness. There are no neuropores. The perihaemal cavities extend up to a few microns anterior to the proboscis pore. They are confluent at their anterior end. The collar nerve cord has neither a lumen nor any lacunae (Fig. 5D). There are three dorsal roots arising from the collar nerve cord and entering the dorsal epidermal nerve layer. A dorsal mesentery is absent and the ventral one is confined to the posterior half of the collar. The skeletal cornua extend nearly to the posterior end of the collar, but just before their posterior extremity they take a sharp turn ventral wards from their dorsolateral position. The peribuccal diverticula are absent. The collar canals are vertically oriented (Fig. 5E, and inset). Their walls are not thick but the nuclei are arranged in several strata.

The openings of the branchial sacs on either side are in pairs, that is the left and the right pore are opposite to each other and not alternating. These openings are at the bottom of a deep and narrow groove along the sublateral line on either side of the middorsal line (Fig. 5F). The gonads commence immediately behind the collar. They are simple, unlobed sacs which open individually onto the lateral (outer) wall of the sublateral groove. The gonads open along with the gill pouches and do not alternate with the latter. The branchial part is twice as large as the ventral part. The ventral and lateral aspects of the trunk coelom are filled with longitudinal muscle fibers but no ventro-lateral ridges are formed (Fig. 5F).

Remarks. *S. sonorensis* does not resemble any known species of the genus in more than one or two of the usual specific characters. The only exception to this statement is *S. otagoensis*, which resembles the present species in the absence of the ventral muscular ridges in the trunk, the absence of the dorsal mesentery in the collar, the absence of the dorsal crest on the collar nerve cord and in the posterior extent of the skeletal cornua in the collar but differs in a number features such as the number of concentric muscle fiber rings in the proboscis, the external color, the side of the proboscis pore and the presence of a dorsal glomerulus.

Among the species of *Saccoglossus* commonly occurring on the west coast of America. *S. pusillus* resembles the present species only in the large branchial pharynx and in the posterior extent of the cornua. Other species of the genus like *S. porochordus, S. rubur, S. kowalevskii, S. shumaginensis* and *S. rhabdorhynchus* have at the most only one character each in common with the form consideration. Thus the specimen described above does not resemble any known species sufficiently well to warrant its inclusion in that species and hence a new species has been created to receive it. In the possession of only the right proboscis pore, it appears to be unique, but this character needs confirmation from several more specimens before it could be accepted as of specific value.

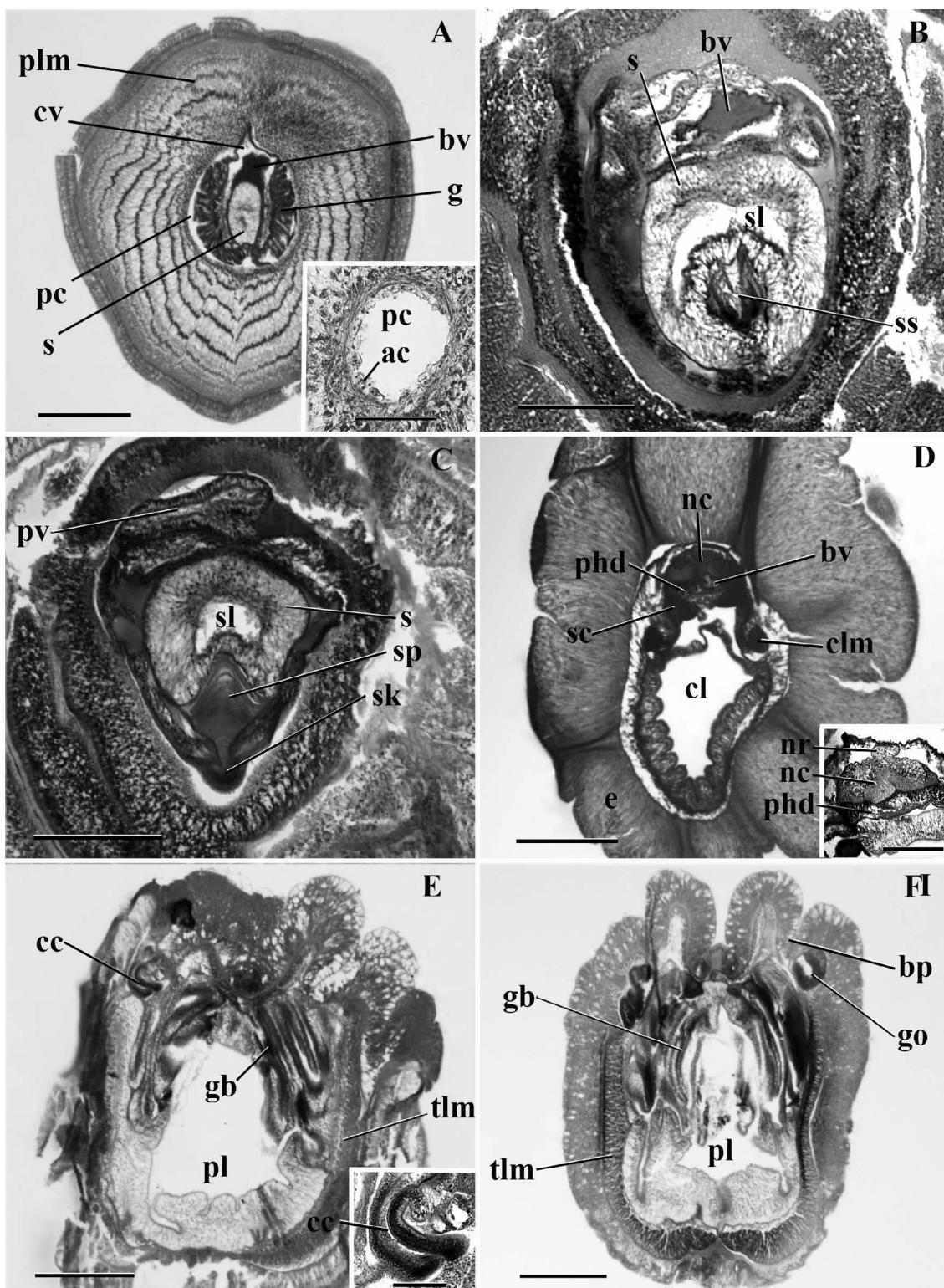**Etymology.** The species is named after the Mexican state of Sonora.

FIGURE 5. Light micrographs of transverse sections of *Saccoglossus sonorensis* **n. sp.**: A, Proboscis with heart-kidney complex. Inset: Anterior region of the proboscis coelom. B, Proboscis neck showing the skeletal spine of the proboscis skeleton. C, Proboscis neck showing the proboscis vesicle. D, Anterior region of the collar. Inset: Collar nerve cord showing a nerve root. E, Posterior region of the collar. Inset: Collar canal. F, Anterior pharyngeal region of the trunk. ac, amoeboid cells; bp, branchial pore; 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; nc, nerve cord; nr, nerve root; pc, proboscis coelom; phd, periheamal diverticulum; pl, pharynx lumen; plm, proboscis longitudinal muscles; pv, proboscis vesicle; s, stomochord; sc, skeletal cornua; sk, skeletal keel; sl, stomochord lumen; sp, skeletal plate; ss, skeletal spine; tlm, trunk longitudinal muscles. Scale bars A, E, F, G = 500 µm; B and F inset = 100 µm; C, D, E inset = 200 µm.

TABLE 1. Comparison of external and internal characters of the species of the genus *Saccoglossus*. Characters from previously described species were obtained from the literature.

Question marks indicate unknown character states. Three species are not included in this table: *S. sulcatus* (Spengel, 1893) – only a figure available (no description), *S. hwangtauensis* (Tchang and Koo, 1935) (unable to locate the paper), *S. madrasensis* (Rao, 1957) (exists only as a conference abstract – there are no figures). *S. cambrensis*, *S. serpentinus* (Assheton, 1908) and *S. ruber* are synonymous species from the United Kingdom (Burdon-Jones, 1960). There is little information available from the single specimen of *S. ruber* (Tattersall, 1905) and so we used *S. cambrensis* (Brambell, Rogers and Goodhart, 1939) for our table.

Species characteristics were compiled from the following references: 1. Thomas, 1956; 2. Thomas, 1968; 3. King, Giray & Kornfield, 1994; 4. Brambell & Goodhart, 1941; 5. Kapelin, 1936; 6 & 7. Horst, 1939; 8. Benham, 1895; 9. Ritter, 1902, 1929; and 10. Brambell, Rogers & Cole, 1939; *New species.

	Saccoglossus apatensis[1]	Saccoglossus aulakoeis[2]	Saccoglossus bromophenolosus[3]
Proboscis shape	tapered, long	long pear-shaped	long pointed
Proboscis length: width	longer	longer	longer
Proboscis longitudinal musculature	9-11 rings	9-10 rings	6-7 rings
Proboscis coelom	start at the tip of proboscis	?	?
Proboscis groove	dorsal	dorsal	dorsal
Proboscis pores	left	left	one
Collar length: width	as long as broad	longer than broad	longer than broad
Collar shape	annular groove at posterior end	2 posterior elevated bands separated by a groove	anterior and posterior rings
Neuropore	?	?	?
Nerve crest	?	?	?
Extent of periheamal diverticula	?	?	?
Peribuccal cavities	?	?	?
Skeleton shape	middorsal ridge	rounded tip	?
Extent of cornua	1/2 collar	1/2 collar	?
Presence and extent of parabuccal ridges	?	?	?
Presence and shape of collar canals	?	?	?
Proboscis septa	?	dorsal, ventral	?
Collar septa	?	dorsal, ventral	?
Trunk septa	?	?	?
Size of branchial pharynx: digestive	equal	?	?
Rows of gonads	lateral	lateral	lateral
Genital ridges	yes	yes	?
Number of gill pores	30-45 pairs	12-25 pairs	60-110 pairs
Gonads start	middle of gill region	behind collar	end of gill region
Number of esophageal pores	6-8 pairs	2-5 pairs	4-8 pairs
Ventral muscular ridge	Yes	?	?

TABLE 1. (continued)

	Saccoglossus horsti[4]	Saccoglossus inhacensis[5]	Saccoglossus kowalevskii[6]
Proboscis shape	?	tapered anteriorly	?
Proboscis length: width	longer	longer	longer
Proboscis longitudinal musculature	over 9 rings	rings present but not well defined	4-5 rings
Proboscis coelom	filled with coelomic cells	filled with granulated cells	anterior filled with cells
Proboscis groove	dorsal, ventral	?	dorsal
Proboscis pores	left	left	left
Collar length: width	longer than broad	longer than broad	equal
Collar shape	anterior and posterior thickened	posterior ring	?
Neuropore	?	anterior	?
Nerve crest	?	yes	yes
Extent of periheamal diverticula	to neck	to neck, connected anteriorly	to proboscis pore, connected anteriorly
Peribuccal cavities	?	?	yes
Skeleton shape	?	anterior median projection, rounded keel, middorsal ridge	plate flat, body narrow, keel blunt
Extent of cornua	1/2 collar	2/3 collar	1/2 collar
Presence and extent of parabuccal ridges	?	yes	?
Presence and shape of collar canals	?	horizontal, horseshoe shaped	with dorsal ridge
Proboscis septa	ventral	ventral	dorsal
Collar septa	dorsal, ventral	ventral	dorsal, ventral
Trunk septa	?	dorsal, ventral	?
Size of branchial pharynx: digestive	?	equal	branchial larger
Rows of gonads	lateral	lateral	lateral
Genital ridges	yes	yes	yes
Number of gill pores	100-137 pairs	about 100 pairs	about 100 pairs
Gonads start	1mm after collar	1 mm after collar	few mm behind collar
Number of esophageal pores	4-8 pairs	4-6 pairs	4-6 pairs
Ventral muscular ridge	yes	yes	yes

TABLE 1. (continued)

	Saccoglossus mereschkowskii[7]	Saccoglossus otagoensis[8]	Saccoglossus pusillus[9]
Proboscis shape	?		cylindrical, rounded at tip
Proboscis length: width	?	longer	longer
Proboscis longitudinal musculature	7-10 rings	3-4 rings	6-10 rings
Proboscis coelom	?	almost to tip of proboscis	almost to tip of proboscis, empty
Proboscis groove	dorsal	dorsal	dorsal
Proboscis pores	left	left	left
Collar length: width	equal	equal	longer than broad
Collar shape	?	2 circular grooves	posterior rim
Neuropore	?	maybe posterior	?
Nerve crest	yes	no	yes
Extent of periheamal diverticula	to proboscis pore, connected anteriorly	to proboscis pore, connected anteriorly	to stomochord opening, connected anteriorly
Peribuccal cavities	no	no	no
Skeleton shape	plate with dorso-median spine	long projecting spine, small keel	small plate and keel
Extent of cornua	?	posterior collar	posterior collar
Presence and extent of parabuccal ridges	?	yes	?
Presence and shape of collar canals	with dorsal fold	oblique, no fold	present
Proboscis septa	ventral	ventral	ventral
Collar septa	dorsal, ventral	no	dorsal, ventral
Trunk septa	?	dorsal, ventral	dorsal, ventral
Size of branchial pharynx: digestive	branchial larger	equal	branchial larger
Rows of gonads	lateral	lateral	lateral
Genital ridges	yes only in females	yes	yes
Number of gill pores	up to 50 pairs	about 10 pairs	about 60 pairs
Gonads start	behind collar	behind collar	not reaching collar
Number of esophageal pores	?	1 pair	1 pair
Ventral muscular ridge	?	no	yes

TABLE 1. (continued)

	Saccoglossus ruber (cambrensis)[10]	Saccoglossus porochordus*	Saccoglossus sonorensis*
Proboscis shape	?	round in cross section	elongate
Proboscis length: width	longer	longer	longer
Proboscis longitudinal musculature	4-6 rings	8-10 rings	5-6 rings
Proboscis coelom	almost to tip of proboscis	almost to tip of proboscis, lined by connective tissue	to tip of proboscis, anterior filled with connective tissue
Proboscis groove	dorsal	dorsal	dorsal
Proboscis pores	left	left	right
Collar length: width	longer than broad	slightly longer than broad	slightly broader than long
Collar shape	anterior and posterior thickened, posterior groove	posterior ring	?
Neuropore	anterior	no	no
Nerve crest	yes	yes	no
Extent of periheamal diverticula	into neck, connected anteriorly	into neck, connected anteriorly	anterior to proboscis pore, connected anteriorly
Peribuccal cavities	no	yes	no
Skeleton shape	plate cup shaped, large keel	middorsal spine, deep keel	middorsal spine, deep keel
Extent of cornua	1/2 collar	posterior collar	posterior collar
Presence and extent of parabuccal ridges	no	no	no
Presence and shape of collar canals	horizontal, thick	vertical	vertical
Proboscis septa	ventral	no	ventral
Collar septa	dorsal, ventral	dorsal, ventral	ventral
Trunk septa	dorsal, ventral	no	no
Size of branchial pharynx: digestive	branchial larger	equal or branchial slightly larger	branchial twice larger
Rows of gonads	lateral	lateral	lateral
Genital ridges	no	yes	no
Number of gill pores	60-90 pairs	?	?
Gonads start	mid branchial region	1-1.5 mm behind collar	behind collar
Number of esophageal pores	8-12 pairs	?	?
Ventral muscular ridge	no	no	no

TABLE 1. (continued)

	Saccoglossus shumaginensis*	Saccoglossus rhabdorhynchus*	Saccoglossus palmeri*
Proboscis shape	elongate	?	long and conical
Proboscis length: width	longer	longer	longer
Proboscis longitudinal musculature	8 rings	8-9 rings	6 rings
Proboscis coelom	to tip of proboscis, anterior filled with connective tissue	almost to tip of proboscis, anterior filled with connective tissue	almost to tip of proboscis
Proboscis groove	dorsal	dorsal	dorsal
Proboscis pores	left	left	left
Collar length: width	broader than long	broader than long	?
Collar shape	two posterior rings	two posterior annular thickenings	?
Neuropore	no	anterior and posterior	anterior maybe present
Nerve crest	no	no	?
Extent of periheamal diverticula	into neck, connected anteriorly	to proboscis pore, seperate	?
Peribuccal cavities	yes	no	present
Skeleton shape	keel not sharp	middorsal spine	keel obtuse and short
Extent of cornua	behind middle of collar	posterior collar	?
Presence and extent of parabuccal ridges	no	no	no
Presence and shape of collar canals	horizontal	vertical	?
Proboscis septa	dorsal	ventral	dorsal, ventral
Collar septa	ventral	dorsal, ventral	dorsal
Trunk septa	no	dorsal	?
Size of branchial pharynx: digestive	equal or branchial slightly larger	branchial larger	branchial equal or larger
Rows of gonads	lateral	lateral	lateral
Genital ridges	yes	yes	?
Number of gill pores	30-40	?	?
Gonads start	behind tenth gill pore	behind collar	?
Number of esophageal pores	6-7	?	?
Ventral muscular ridge	yes	no	?

Saccoglossus palmeri **n. sp.**
(Fig 6A–E)

Material examined. One specimen (anterior end through branchial region) was dredged at a depth of 250 m offshore NNW of Coos Bay entrance, OR (43° 21' N, 124° 21 W) by J. McNab on August 6th 1958. Two fragments have also been dredged at a depth of 25 meters on July 30th 1958. *Holotype:* Accession no. NMNH 1132801.
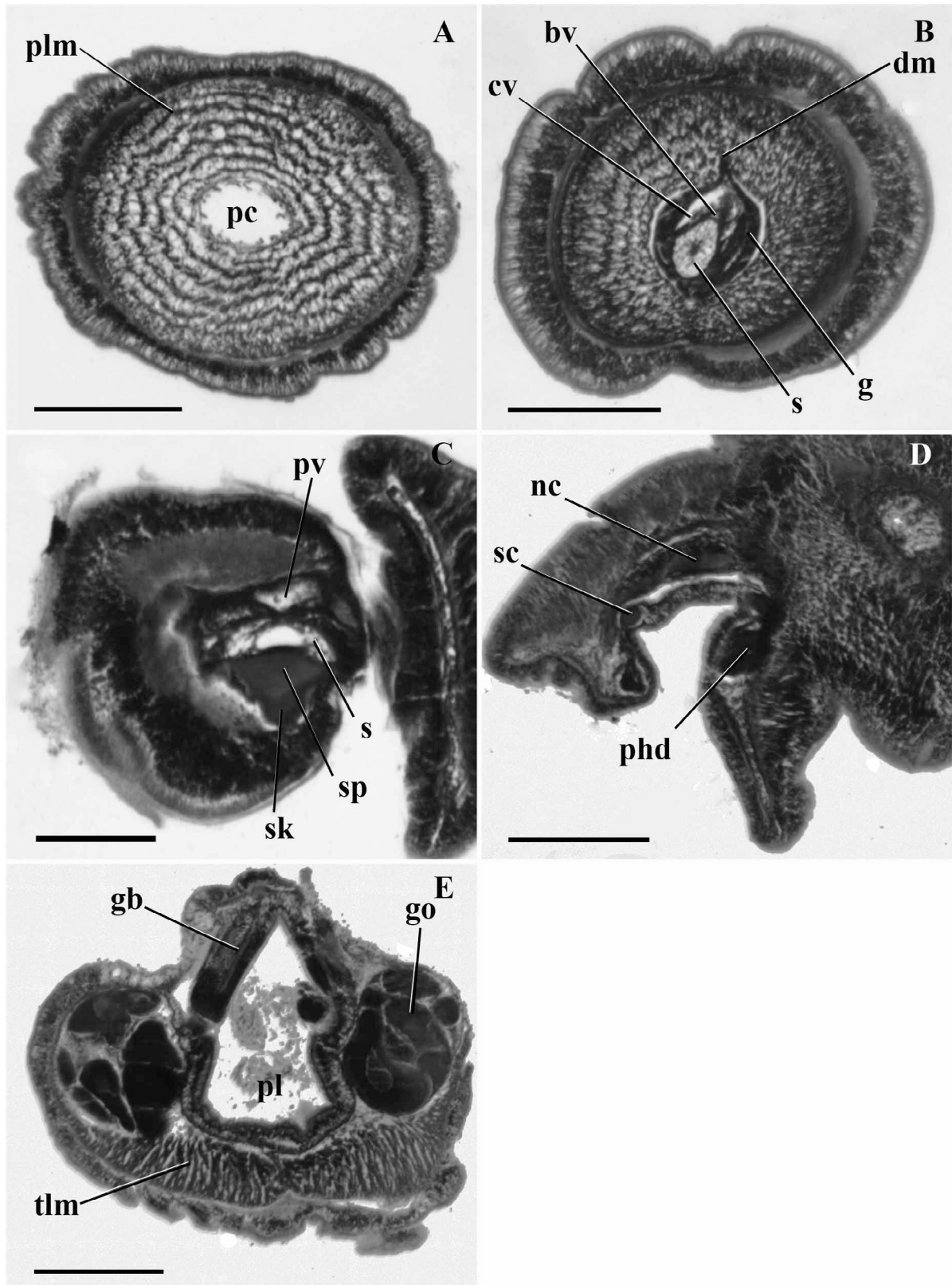
FIGURE 6. Light micrographs of transverse sections of *Saccoglossus palmeri* **n. sp.**: A, Anterior region of the proboscis. B, Proboscis with heart-kidney complex. C, Proboscis neck. D, Anterior region of the collar. E, Anterior pharyngeal region of the trunk. bv, blood vessel; cv, cardiac vesicle; dm, dorsal mesentery; g, glomerulus; gb, gill bar; go, gonad; nc, nerve cord; pc, proboscis coelom; phd, periheamal diverticulum; pl, pharynx lumen; plm, proboscis longitudinal muscles; pv, proboscis vesicle; s, stomochord; sc, skeletal cornua; sk, skeletal keel; sp, skeletal plate; tlm, trunk longitudinal muscles. Scale bars A, B, D, E = 250 μm; C = 150 μm.

External features: The proboscis is long and conical with a small groove in the posterior third of its length. The total length is estimated to be 1 cm. The length of the proboscis is 3 mm and the collar is 0.5 mm. In live material, the proboscis is white and the collar and trunk are salmon pink.

Internal features (Figure 6)**:** The nerve fiber layer of the proboscis does not show any thickening along the dorsal midline. The proboscis coelom almost extends to the tip of the organ as a narrow cavity closely surrounding the proboscis complex (Fig. 6A). The ventral and dorsal septa are present and start in the posterior half of the proboscis. They are both continuous throughout the length of the organ. The circular muscle fiber layer is thinner than the nerve fiber layer. The longitudinal muscle fibers are arranged in about 6 concentric rings (Fig. 6B). The glomerulus extends over the tip of the stomochord and surrounds the entire proboscis complex. The cardiac vesicle is well developed and extends to the tip of stomochord. Its anterior half is filled with connective tissue. The stomochord has thick walls and a narrow lumen throughout its length. Its lumen presents a large ventral diverticulum, which is twice as big as the primary lumen and join each other at the beginning of the skeleton plate. The skeletal plate starts on the ventral side of the stomochord and the keel is obtuse and short. The two coelomic cavities in the neck are present and there is also one conspicuous left vesicle leading to the exterior by a left proboscis pore (Fig. 6C).

Very few characters could be determined from the collar (Fig. 6D) and trunk (Fig. 6E) due to distortions in the sections. Only the few characters described below could be assessed. The dorsal mesentery of the collar is present, but it has been impossible to determine its extent, as for the presence and extent of the ventral one. An anterior neuropore may be present.

The branchial portion of the pharynx is equal in size to the ventral portion or slightly larger. There is a pair of dorso-lateral gonads, which are not lobed. The ventro-lateral longitudinal muscles of the trunk are well developed (Fig. 6E).

Etymology. We dedicate the name of this animal to Professor A. Richard Palmer, University of Alberta, who has greatly contributed to our understanding of the comparative morphology and development of Pacific Coast invertebrates.

Discussion

Four harrimaniids previously assigned to the genus *Saccoglossus* have been reassigned to the genus *Mesoglossus* including *M. bournei*, *M. caraibicus*, *M. gurneyi* and *M. pygmaeus*, and *Saccoglossus borealis* has been reassigned to the genus *Harrimania* (Deland et al., 2010). The genus *Saccoglossus* as revised now includes the following species: *S. apatensis* (Thomas, 1956), *S. aulakoeis* (Thomas, 1968), *S. bromophenolosus* (King, Giray & Kornfield, 1994), *S. horsti* (Brambell & Goodhart, 1941), *S. hwangtauensis* (Tchang & Koo, 1935), *S. inhacensis* (Kapelus, 1936), *S. kowalevskii* (Agassiz, 1873), *S. madrasensis* (Rao, 1957), *S. mereschkowskii* (Wagner, 1885), *S. otagoensis* (Benham, 1895), *S. pusillus* (Ritter, 1902, 1929), *S. ruber* (Tattersall, 1905), *S. sulcatus* (Spengel, 1893). Adding to the Eastern Pacific congenerics (*S. pusillus* and *S. bromophenolosus*) are five new including *S. porochordus*, *S. shumaginensis*, *S. sonorensis*, *S. rhabdorhynchus* and *S. palmeri*.

With 21 of 89 species, about 1/4 of all enteropneusts, now known off the west coast of North America, three from deep water (*Torquarator bullocki* Holland et al. 2005; *Tergivelum baldwinae* Holland et al. 2009; *Saxipendium coronatum* Woodwick & Sensenbaugh, 1985) and the remainder from shallow waters, it appears that this coast is unaccountably rich. However, from our own experience, it seems unsafe to assume that the real enteropneust fauna is known for other coasts, even of relatively well-worked continents. The reasons for this are several: i) Many enteropneusts treated here turned up in already familiar areas that had been combed for decades by competent zoologists. ii) These animals are less conspicuous than other invertebrates, typically infaunal and always soft and fragile, that, unless abundant or large in size, they are readily overlooked. iii) Most species are rare and on most coasts only the abundant species are known. iv) Sustained search over many years by individuals especially conscious of enteropneusts certainly accounts for a good proportion of the species here reported, since we have noted large fluctuations in the availability of certain forms at the same site in successive years as well as variations in population densities between seasons. Sometimes for

more than five years we have seen not a single specimen of a once common form. This cannot be taken immediately as meaning they are "collected out" or "polluted out." We have equally dramatic years when a formerly barren site yields well. v) Possibly the intertidal, upon which we inordinately depend, is fringe area for many subtidal species, therefore particularly inconsistent in its standing crop. This may be particularly pertinent to *Saccoglossus* species because they are surface deposit feeders and thus particularly sensitive to wave action. vi) Patchiness of colonies of enteropneusts in large mud flats is often so combined with sparseness that a resident population could be overlooked time and again.

We believe that most of the species have yet to be found, possibly even within the area here treated. Besides the factors just cited, the following additional reasons apply to this conclusion. (a) Reports of finds are increasing, including localities not previously reported to have enteropneusts. (b) The greater part of the coast has hardly been combed at all, let alone by enteropneust conscious zoologists. This includes the coasts of Alaska, British Columbia, Mexico, Central and South America. Few specimens have ever been taken, to our knowledge, from the west coast of South America, one before 1893, one in 1935 and several is 2006. Nothing has come to our attention from Alaska since Ritter's rich haul 111 years ago. (c) Tornaria larvae have not been studied in most of this area. (d) New methods of sampling small, delicate infauna of both muddy and rubble sea bottom, even if only useful to a few tens of meters of depth could open up what must be the richest zone, presently barely represented in our lists.

With the severe limitations of our knowledge, suggested by these considerations in mind, we may attempt some zoogeographical conclusions. These can hardly be of the usual type since most species are known from a single locality and of those known from more than one, the localities are likely to be within one or two hundred kilometers. Very few species, and only one, *Ptychodera flava* in the eastern Pacific are known from enough localities over sufficient extent to speak of an area or range of distribution. *P. flava* is virtually pantropical IndoPacific having seen specimens from Sydney, Guam, Hawaii and the Galapagos as well as from Mauritius.

Several species have widely discontinuous though still stenotopic distributions. *Stereobalanus canadensis* is known from eastern Canada and New England and from southern California (Deland et al. 2010). *Saccoglossus bromophenolosus* occurs in the states of Maine and Washington (King et al. 1994, Smith et al. 2003). *Balanoglossus occidentalis* (a manuscript species) from a few sites in southern California and Puget Sound, Washington is unknown in the 2200 km between. These instances recall others in the group: *Balanoglossus carnosus* from Japan, the Great Barrier Reef and the Maldives; *Glossobalanus minutus* from the Mediterranean and Rio de Janeiro; *Saccoglossus kowalevskii* from New England and the English Channel; *Harrimania kupferi* from the North Sea and western Greenland (van der Horst, 1939); *G. elongatus* from Madras, India and Naples (Rao, 1957).

Each of these cases could represent the relict populations of a formerly wide spread species if indeed it is absent from the intervening, often poorly known waters. Alternately, in some instances the two populations may be polyphyletic and derived by parallelism from a common antecedent once wide spread, or even by convergence from separate antecedent species. This is not asking too much of evolution because (1) the species are defined and distinguished from each other by a very modest number of features and (2) many of the features are simply in one or the other of two opposing conditions, like alleles. Therefore a small number of simultaneous mutations, like those whose permutations and recombination's largely account for the species differences, would suffice. This would mean that further study and the use of more characters, especially molecular characters (Cameron et al., 2000; Smith et al., 2003) should reveal differences between the populations at the specific level. How that level is to be recognized, as opposed to subspecific differences we will not try to discuss! We simply know too little about the individual variation, the population norms, the value of characters and the detailed structure and chemistry of animals to decide which possibility, conspecific disjunct populations or polyphyletic twin species, may apply to *Saccoglossus pusillus* or *Stereobalanus canadensis*. It is easier to assume the former of *Balanoglossus occidentalis* because it likely has a tornaria larva.

The significance of the punctate or one-locality distribution of most species deserves attention. Setting aside the 12 species known from single individual or single lots (including *Stereobalanus canadensis* found

also in the Atlantic, and *S. willeyi*, *Saccoglossus shumaginensis*, *S. rhabdorhynchus*, *S. palmeri*, *S. porchordus*, *Horstia kincaidi*, *Mesoglossus macginitiei*, *Ritteria ambigua*, *Glossobalanus berkeleyi* and *G. barnharti*) as indicative only of rarity, four of our species have been taken repeatedly but only from a limited area, not more than 250 km in extent (*Harrimania maculosa*, *Harrimania planktophilus*, *Mesoglossus intermedius* and the disjunct *Balanoglossus occidentalis*) and two species repeatedly but only from a single locality, that is from spots within one to 5 km (*S. sonorensis, Glossobalanus hartmani*). Rarity is not an adequate explanation in these distributions. Lack of systematic search in contiguous habitats may play some role. The lack of suitable habitats may also, if for example shallow water weed flats are required. But in the main there is no satisfactory way of accounting for the extremely stenotopic ranges.

We may consider *Saccoglossus pusillus* that is abundant subtidally in Barkely Sound, B.C., south in Cape Arago, Oregon and is in some years an abundant form in the bays of northern California. The next likely mud flats, at Morro Bay, Santa Barbara, Mugu Lagoon and Ballona Creek have proven negative over many years. San Pedro, once hospitable to this form, has not often been searched since its industrialization. The worm reappears again in Anaheim and south to Ensenada. Its northern limit may well be an artifact of inadequate search in the subtidal for the central B.C. coast has precious few beaches, and its southern limits may be due to few suitable bays below Punta Banda. This then is a common species with an apparent latitudinal range along the coast more than any other *Saccoglossus* in the range.

Saccoglossus bromophenolosus is a common species known from two muddy localities, Willapa Bay and Padilla Bay on the coast of Washington. We do not know of any considerable effort to look for it in other suitable bays. However it is probably significant that it has not turned up in Puget Sound or Vancouver Island where at least four other species have been taken or in the well worked bays of central California like Bodega and Tomales Bays. We may therefore consider this species as another highly local one. It's broad range off the East Coast (King et al., 1995) and narrow range off the West suggest that it may have been introduced, perhaps along with the sympatric Japanese oyster *Crassostrea gigas*, itself moved between the East and West coasts for aquaculture (Kincaid, 1968).

S. sonorensis is apparently similar though the collecting effort in other parts of the Gulf of California has not been great. It is not trivial, however; Glossell, Ricketts and Cameron have turned up several enteropneusts of other species and other collectors have repeatedly sampled many stations. Therefore this is probably not a wide spread species.

A first order interpretation of such stenotopic distributions is that they are relics of once wider ranging species. We reject on the available evidence the hypothesis that all these species are very young. This type of distribution, together with the fact of widely scattered species of single genera, and the prevalent patchiness manifested by the large number of seemingly suitable localities lacking any enteropneust, between the sites where they occur, suggests an ancient and declining group.

Acknowledgements

References

Agassiz, A. (1873) The History of *Balanoglossus* and tornaria. *Memoirs of the American Academy of Arts and Sciences, New Series,* 9, 421–436.

Benham, W.B. (1895) *Balanoglossus otagoensis*, n. sp. *Proceedings of the Linnean Society of New South Wales*, 42, 497–504, pl. 45.

Brambell, F.W.R. & Goodhart, C.B. (1941) *Saccoglossus horsti* sp.n., an enteropneust occurring in the Solent. *Journal of*

the Marine Biological Association of the United Kingdom, 25, 283–301.

Brambell, F.W.R., Rogers, W. & Cole, A.J. (1939) *Saccoglossus cambrensis* sp. n., an enteropneust ocuring in Whales. *Proceedings of the Zoological Society of London, B,* 109, 211–236.

Burdon-Jones, C. & Patil, A.M. (1960) A revision of the genus *Saccoglossus* (Enteropneusta) in British waters. *Proceedings of the Zoological Society of London*, 134, 635–645.

Cameron, C.B. (2005) A phylogeny of the hemichordates based on morphological characters. *Canadian Journal of Zoology*, 83, 196–215.

Cameron, C.B., Swalla, B.J. & Garey, J.R. (2000) Evolution of the chordate body plan: New insights from phylogenetic analysis of deuterostome phyla. *Proceedings of the National Academy of Sciences (USA)* 97(9), 4469–4474.

Deland, C., Cameron, C.B., Rao, K.P., Ritter, W.E. & Bullock, T.H. (2010) A taxonomic revision of the family Harrimaniidae (Hemichordata: Enteropneusta) with descriptions of seven species from the Eastern Pacific. *Zootaxa*, 2408, 1–30.

Holland, N.D., Jones, W.J., Ellena, J., Ruhl, H.A. & Smith, Jr K.L. (2009) A new deep-sea species of epibenthic acorn worm (Hemichordata, Enteropneusta). *Zoosystema,* 31(2), 333–346.

Holland, N.D., Clague, D.A., Gordon, D.P., Gebruk, A., Pawson, D.L. & Vecchione, M. (2005) Lophenteropneust hypothesis refuted by collection and photos of new deep-sea hemichordates. *Nature*, 434(7031), 374–376.

Horst, C.J. van der (1939) Hemichordata. *In*: Bronn, H.G. (ed.) *Klassen und Ordnungen des Tierreichs wissenschaftlich dargestellt in Wort und Bild*. Leipzig, Akademische Verlagsgesellschaft. Vol. 4 (4), Buch 2, Tiel 2. 737 p.

Kapelus, F.F. (1936) The anatomy of the enteropneust *Saccoglossus inhacensis* sp. n. *Annals of the Natal Museum*, 8, 47–94.

King, G.M., Giray, C. & Kornfield, I. (1994) A new hemichordate, *Saccoglossus bromophenolosus* (Hemichordata: Enteropneusta: Harrimaniidae), from North America. *Proceedings of the Biological Society of Washington,* 107, 383–390.

Kincaid, T. (1968) The ecology of Willapa Bay, Washington, in relation to the oyster industry. *University of Washington Press*, Seattle.

Rao, K.P. (1957) Two species of Enteropneusta from off the coast of Madras. *Proceedings of the Indian Science Congress,* 42, 301.

Ritter, W.E. (1902) The movements of the Enteropneusta and the mechanism by which they are accomplished. *Biological Bulletin*, 3, 255–261.

Ritter, W.E. (1929) A Monograph of the Enteropneusta of Pacific North America. *Dolichoglossus pusillus* n.sp. *Videnskabelige Meddelelser Dansk Naturhistorisk Forening*, 87, 154–195.

Schimkewitsch, W.M. (1892) *Über die Beziehungen zwischen den Enteropneusta und Acrania*: St. Petersburg.

Smith, S.E., Douglas, R., Burke de Silva, K. & Swalla, B.J. (2003) Morphological and molecular identification of *Saccoglossus* species (Hemichordata: Harrimaniidae) in the Pacific Northwest. *Canadian Journal of Zoology*, 81, 131–141.

Spengel, J.W. (1893) *Fauna und Flora des Golfes von Neapel und der angrenzenden Meeres-Abschnitte*. Berlin, Friedländer. Herausgegeben von der Zoologischen Station zu Neapel. monograph 18, 757 p.

Spengel, J.W. (1901) Die Benennung der Enteropneusten-Gattungen. *Zoologische Jahrbücher, Abteilung fuer Systematik Oekologie und Geographie der Tiere*, 15, 209–218.

Tattersall, W.M. (1905) Enteropneusta from west coast of Ireland. *Annual Report of Fisheries, Ireland Scientific Investigations*, 1902, 213–214.

Tchang, S. & Koo, G. (1935) Two enteropneusts in Jiaozhou Bay. *Publication of the Beijing Institute of Zoology,* 13, 1–12.

Thomas, I.M. (1956) *Saccoglossus apantesis*, a new species of enteropneust from South Australia. *Transactions of the Royal Society of South Australia*, 79, 167–176.

Thomas, I.M. (1968) Two species of *Saccoglossus* (Enteropneusta) from South Australia. *Transactions of the Royal Society of South Australia*, 92, 73–84.

Wagner, N. (1885) Die Wirbellosen des Weissen Meeres. *Zoologische Forschungen an der Küste des Solowetzkischen Meerbusens in den Sommermonaten der Jahre 1877, 1878, 1879 und 1882*, Leipzig, Engelmann, 167.

Willey, A. (1899) Remarks on some recent work on the Protochordata, with a condensed account of some fresh observations on the Enteropneusta. *Quarterly Journal of Microscopical Science*, 42, 223–244.

Woodwick, K.H. & Sensenbaugh, T. (1985) *Saxipendium coronatum*, new genus, new species (Hemichordata: Enteropneusta): the unusual spaghetti worms of the Galapagos Rift hydrothermal vents. *Proceedings of the Biological Society of Washington*, 98, 351–365.