



Article

urn:lsid:zoobank.org:pub:A2CD9F16-65B7-4073-80A5-26EE2152C87A

Spengelidae (Hemichordata: Enteropneusta) from the Eastern Pacific including a new species, *Schizocardium californicum*, from California

C.B. CAMERON¹ & M. PEREZ¹

Sciences biologiques, Université de Montréal, C.P. 6128, Succ. Centre-ville,
Montreal, QC, H3C 3J7, Canada, e-mail: c.cameron@umontreal.ca

Abstract

Twenty one enteropneusts have been described from the west coast of North America, but those reports include no Spengelidae. Here we describe two species of acorn worms in the genus *Schizocardium* (*S. californicum* and *S. peruvianum*) on the basis of morphology. The former represent the first spengelid worm described from North American waters. The latter is a previously described species, and here we expand on its morphological description and extend its geographic range north from Peru to California. Notes on the habit and localization of each species, as well as a dichotomous key to the genera of the family Spengelidae are provided. Based on morphology, spengelids appears to represent an intermediate between the enteropneust families Harrimaniidae and Ptychoderidae, and *Schizocardium* is sister taxon to the ptychoderids. The disjunct and widely distributed populations of *S. peruvianum* and *S. brasiliense*, with populations in South American and North America, but none between, could represent the relict populations of formerly wide spread species, or the two extremes of ranges.

Key words: Enteropneusta, acorn worm, Spengelidae, California, dichotomous key

Introduction

Recent years have seen renewed excitement in hemichordate systematics as one family, the Saxipendidae, was absorbed into the Harrimaniidae (Deland *et al.* 2010, Cameron *et al.* 2010), and a new family, the Torquaratoridae, has emerged from specimens collected and photos taken in the deep sea (Holland *et al.* 2005, Osborn *et al.* 2011). Of the remaining two families, the Ptychoderidae, and the Spengelidae, the latter is the least known. The family Spengelidae includes 4 genera— *Spengelia*, *Glandiceps*, *Willeyia* and *Schizocardium* and 18 species. Members of the family are distributed globally, but are uncommon; none are described from North American waters.

Here we report on two species of *Schizocardium* from the coast of California. These are based on specimens from the collections of W.E. Ritter and T.H. Bullock, deposited at the Smithsonian Museum (US Natural History Museum, Washington). The *S. californiensis* specimens were taken by Bullock in 1952 and 1953. We also elaborate on the taxonomic description of *S. peruvianum*, for its original description was of an incomplete specimen (Spengel, 1893) and we also expand its known range from Peru, north to California.

Our efforts to revise the alpha taxonomy of the Enteropneusta and expand on the known species from North America has, at least with the Harrimaniidae, shed some light on the phylogenetic relationships within the family (Deland *et al.* 2010) and on the zoogeography and evolution of acorn worms in general (Cameron *et al.* 2010). In an attempt to repeat this exercise, this time with the family Spengelidae, we discovered only one new species in the Bullock collection, the first from North American waters, to add to the group. Consequently, with only the material in hand, any rigorous revision of the spengelids is not possible, and only a few general remarks can be made on the zoogeography of the group.

The objectives of this study are then to i) describe a new species of *Schizocardium californicum* from the coast of California, ii) and expand on the taxonomic description of *Schizocardium peruvianum* (Spengel, 1893), originally taken from Independence Bay, Pisco, Peru.

Material and methods

Sectioned specimens of *Schizocardium californicum* and *Schizocardium peruvianum* 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 is 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.

Additional specimens of *Schizocardium peruvianum* were collected at Independence Bay, Pisco, Peru in 34 meters depth, in January 2006 by Giannina Passuni (Universidad Nacional Mayor de San Marcos). One specimen was photographed live (Fig. 1). Two specimens were fixed and stored in Bouin's fixative, and two specimens were fixed and stored in alcohol. One of the Bouin's specimens was progressively dehydrated and embedded in wax, sectioned and mounted on glass slides. Sections were cut at 10 μm with a microtome and transferred to glass slides, rehydrated and stained in Masson's trichrome stain. Sections of 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. Two of the whole specimens, one in Bouin's and one in 90% ethanol, have been deposited in the NMNH (Smithsonian). Catalogue no.: USNM 1177534 [IZ].

The morphology of the five sectioned worms, four from the Bullock collection and one from Giannina Passuni, were compared and contrasted to establish the character distributions among the new and existing species. One species, *S. californicum* is created and the description of another, *Schizocardium puruviense*, is elaborated from its original description (Spengel, 1893) so that it could be distinguished from *S. californicum* and from the third *Schizocardium* species known to science, *S. brasiliense*.



FIGURE 1. A photograph of a living specimen of *Schizocardium peruvianum* from Independence Bay, Pisco, Peru taken by Giannina Passuni. Scale bar = 1 cm.

Diagnoses of the Spengelidae and its genera

Class Enteropneusta Gegenbaur, 1870

Family Spengelidae Willey 1899

(Glandicipitidae Spengel 1901)

Diagnosis. The family is characterized by the occurrence in all its members, of an anterior vermiform process of the stomochord and a circular muscle fibre layer inside the longitudinal muscle fibre layer in the trunk. The skeletal cornua usually extend over the whole length of collar. Dorsal nerve roots arising from the collar nerve cord are rare. The lateral septum is absent. Hepatic caeca and synaptacula may or may not be present. In those cases where the development has been studied, the life history has a typical tornaria larva.

Remarks. Of the four known genera included in this family—*Schizocardium*, *Willeyia*, *Glandiceps* and *Spengelia*, only one species, in the genus *Schizocardium*, occur in the Eastern Pacific. In addition, as a result of the present work, a second *Schizocardium* can now be added to this list.

Genus *Schizocardium* Spengel, 1893

Type species. *Schizocardium brasiliense* (Spengel, 1893)

Diagnosis. The stomochord bifurcates anteriorly and extends into the proboscis coelom as paired lateral diverticula. The cardiac vesicle extends anteriorly as a pair of long tubes and is surrounded by a paired glomerulus. The ventral septum of the proboscis extends to the tip of this process. Peribuccal cavities extend forward from the trunk coelom. The collar is broader than long. The genus is distinguished by the fact that the gills are large and comprise virtually the whole wall of the pharynx in transverse section. As a consequence of this, the midventral digestive pharynx is only a narrow hypobranchial strip. There is a well-developed mushroom-shaped dorsal epibranchial ridge that projects into the pharynx lumen that has several distinct zones of cells (see Ruppert *et al.* 1999). Peripharyngeal cavities are present in the pharynx tongue bars. Collagenous synaptacula provide a bridge between primary and secondary (tongue) gill bars. Only lateral gonads occur. The lateral genital ridges may be conspicuous posterior to the branchial region. The hepatic caeca are present as two discrete rows of sacs. Anterior and posterior intestinal pores are present.

Remarks. Of the two species hitherto known, *S. peruvianum* (Spengel, 1893) is from the area under consideration. In addition we have encountered a new species, *S. californicum*, which is described below. *S. peruvianum* has not been fully described by Spengel, since he did not have adequate material. We have obtained nearly complete specimens and hence the description given below is more detailed than that of Spengel. The genus as revised above would now include the following species: *S. peruvianum* (Spengel, 1893), *S. brasiliense* (Spengel, 1893) and *S. californicum*, n.sp.

Schizocardium peruvianum Spengel, 1893

(Figs. 1, 2A–G)

Material examined. The description given below is based on two anterior fragments, one collected from Pisco, Peru by Waldo Schmitt of the U.S. National Museum in 1935 and the other from Point Mugu, California by Theodore H. Bullock of the Scripps Institution, University of California, in 1947. The latter is the paratype. Additional specimens from Independence Bay, Pisco, Peru were collected and photographed by Giannina Passuni in 2006 (Fig. 1). We serially sectioned one of Passuni's specimens to compare with the specimens of Waldo and Bullock, and found no significant differences with the Waldo specimen. This description supplements the account given by Spengel (1893). Spengel's single specimen came from Pisco, Peru (Lat. 13°45' S, Long. 76°20' W), Schmitt and Passuni's from Independence Bay, Pisco, Peru in 40 m and 35 m depth in 1935 and 2006; T.H.B.'s from Mugu Lagoon, California, (Lat. 34°7' N, Long. 119°6' W) in 1947. At Mugu it was in mud exposed at low tide, with *Macoma*, *Polinices*, *Amphitrite*, *Bulla* and *Dendraster*. Paratype (Bullock's specimen 540-1.1 to 540-1.127). Catalogue no. NMNH: USNM 1177534 [IZ].

External features. This is a rather large species. Our incomplete Mugu specimen (T.H.B. accession no. 382) measured in life 285 mm through the anterior abdominal region. The proboscis is 15 mm long and 10 mm wide at the widest point; the collar 5 mm long and 7 mm wide; the branchial region 72 mm; the genital region overlapping with the branchial and beginning 3 mm behind the collar extends for at least 165 mm; the hepatic region begins 152 mm behind the collar and extends 45 mm. The proboscis is sharply pointed and has prominent middorsal and midventral grooves when relaxed. The genital folds are thick and stubby. T.H. Bullock observed this specimen shed sperm in thick milky streams from many places along the genital region (March 22, 1947).

The colour is notable (Fig. 1). The proboscis is reddish orange, not pale but rather dark; the collar is the same but darker—almost blood red; the trunk is the same but no darker than the proboscis except the hepatic caeca which are brown and the genital wings which are red where the skin is not too thin, yellow-orange where the gonads show through in patchy pseudosegmental folds. The terminal abdomen is pale yellow brown except for a midventral strip of bright orange.

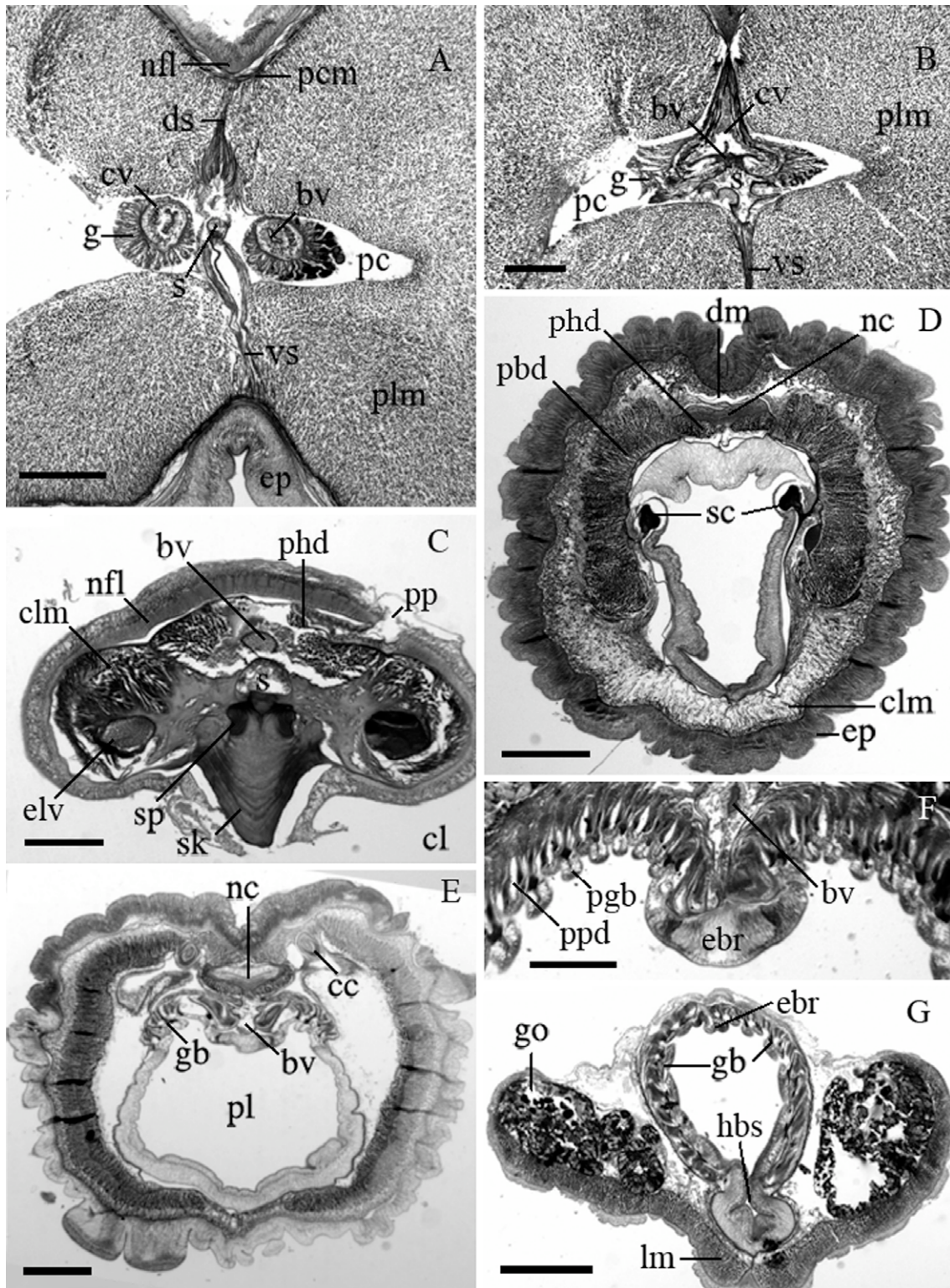


FIGURE 2. Light micrographs of transverse sections of *Schizocardium peruvianum* (A) Tubular extensions of the proboscis heart-kidney complex. (B) Proboscis showing the heart-kidney complex. (C) Proboscis neck in the anterior region of the collar. (D) Collar showing skeletal cornua. (E) Anterior region of the trunk showing collar canals. (F) Mid-dorsal part of the pharyngeal region of the trunk. (G) Anterior genital region of the trunk. **bv**, blood vessel **cc**, collar canal; **cl**, collar lumen; **clm**, collar longitudinal muscles; **cv**, cardiac vesicle; **dm**, dorsal mesentery; **ds**, dorsal septum; **en**, endostyle; **ep**, epidermis; **g**, glomerulus; **gb**, gill bar; **go**, gonad; **hbs**, hypobranchial strip; **nc**, nerve cord; **nfl**, nerve fiber layer; **pbd**, peribuccal diverticula (of the trunk coelom); **pc**, proboscis coelom; **pcm**, proboscis circular muscles; **pgb**, primary gill bar; **phd**, periaemal diverticula (of the collar coelom); **ppd**, peripharyngeal diverticula (of the secondary gill bar); **pl**, pharynx lumen; **plm**, proboscis longitudinal muscles; **s**, stomochord; **sc**, skeletal cornua; **sk**, skeletal keel; **sp**, skeletal plate; **tlm**, trunk longitudinal muscles; **vs**, ventral septum. Scale bars: (A,B and F) = 500 μm ; (C) = 300 μm ; (E) = 1500 μm ; (D and G) = 1000 μm .

Internal features. The proboscis epidermis is rather thick being about 200 to 300 μm . The nerve fiber layer may be thickened middorsally especially in the posterior region. The circular muscle fiber layer is conspicuous, comprising several layers of muscle fibers. The longitudinal musculature is also well developed in the proboscis. There is a strong dorsoventral muscle plate (Fig. 2A). The vermiform process of the stomochord is rather long, extending anteriorly just into the anterior one-third of the proboscis. The ventral septum reaches anteriorly to the tip of the vermiform process, but posteriorly it does not extend to the posterior wall of the ventral coelom. The pair of tubular extensions of the cardiac vesicle extend anteriorly a little beyond the stomochord proper, but not to the same extent as the vermiform process. Anteriorly each half of the glomerulus surrounds the tubular extension of the cardiac vesicle of its side (Fig. 2B). The glomerulus of the right and left side may or may not be continuous anteriorly. The two tubular extensions of the cardiac vesicle may be connected and continuous anteriorly at their tip (Passuni's Peru specimen) or they may be completely separate (Spengel's specimen and the Mugu specimen). Stomochord may have a continuous and spacious lumen (Spengel's specimen and Mugu specimen) or the lumen may be broken up at the tip of the stomochord and in the neck (Fig. 2B–C). Only a left proboscis coelomic canal opens by a left proboscis pore (Fig. 2C). The cardiac vesicle is quite roomy. The proboscis skeleton has a pronounced keel that may be sharp and deep (Spengel and Passuni specimens) or it may be large, conspicuously broad as well as deep (Mugu specimen). The end plate of the skeleton may be flat (Mugu specimen) or it may bear an anteriorly directed obtuse protuberance middorsally (Peru).

Both the dorsal and ventral mesenteries of the collar may be complete or one of the two may not reach fully to the anterior margin of the collar. The perihæmal cavities extend up to the proboscis canal in the peduncle and are confluent at their anterior ends (Fig. 2D). An anterior neuropore is present in the face of the collar. The collar nerve cord has no lumen or lacunae. The skeletal cornua extend over nearly four-fifths of the collar length. A posterior neuropore is present in the specimen from Peru, but in the material from Mugu, the 'neural tube' appears to continue for over 3 mm into the anterior part of the trunk region, immediately posterior to the collar. It is not clear whether this is due to the accidental fusion of the epithelia in the middorsal region resulting from maceration and poor preservation or whether it is real and anatomical. The collar canals and pores are as described by Spengel (1893), with a deep dorsal fold appearing like a large tongue (Fig 2E). Peribuccal cavities are present but confined to the posterior quarter of the collar.

The pharynx shows a morphology characteristic of the genus. There is a well developed epibranchial ridge (Fig. 2F), a possible homologue with the chordate endostyle (Ruppert et al, 1999) and the ventral pharynx is reduced to a narrow hypobranchial slit (Fig. G). Each gill has about 30 synapticula.

Remarks. *S. peruvianum* is anatomically very similar to *S. brasiliense*. The major anatomical differences between the two species occur with regard to the stomochord and the proboscis skeleton. In the former species the skeleton is conspicuous with a great keel while in the latter it is short with small body and broad, blunt keel. Likewise in the former species the neck of the stomochord is flat and continuous whereas in *S. brasiliense*, the stomochordal neck is narrow and much reduced and may sometimes be broken up. The other feature of difference is the absence of an anterior neuropore in *S. brasiliense*.

Externally these two species differ in a few features like the difference in the shape of the collar. As has been pointed out in the description of the species, there are a few differences between the Peru and the Mugu specimens. These differences are not sufficiently great to create a new species. Examination of more specimens from these two localities may change this position.

***Schizocardium californicum* n. sp.**

(Fig. 3 A–J)

Material examined. One specimen was found by T.H. Bullock in 1952 and one in 1953 at Newport Bay, California, (Lat. 33°37'N, Long. 117°53'W) in mud exposed at low tide. The type specimen is T.H.B. accession no. 422. (slides 422-1.1 to 422-1.97). USMNH catalogue number: 177533 [IZ].

Internal features. The proboscis is 7 or 8 mm long and 4 to 5 mm broad; with a sharply pointed and drawn out tip and a middorsal longitudinal groove, especially marked in the posterior half. The collar is 3 mm long and 4.5 mm broad. The trunk was 4 mm broad immediately behind the collar. All the measurements were taken from the living specimen. The proboscis is dark brownish red, the collar bright reddish with a brown tinge; the trunk has a brownish pigmentation in longitudinal hazy bands over a yellowish brown background.

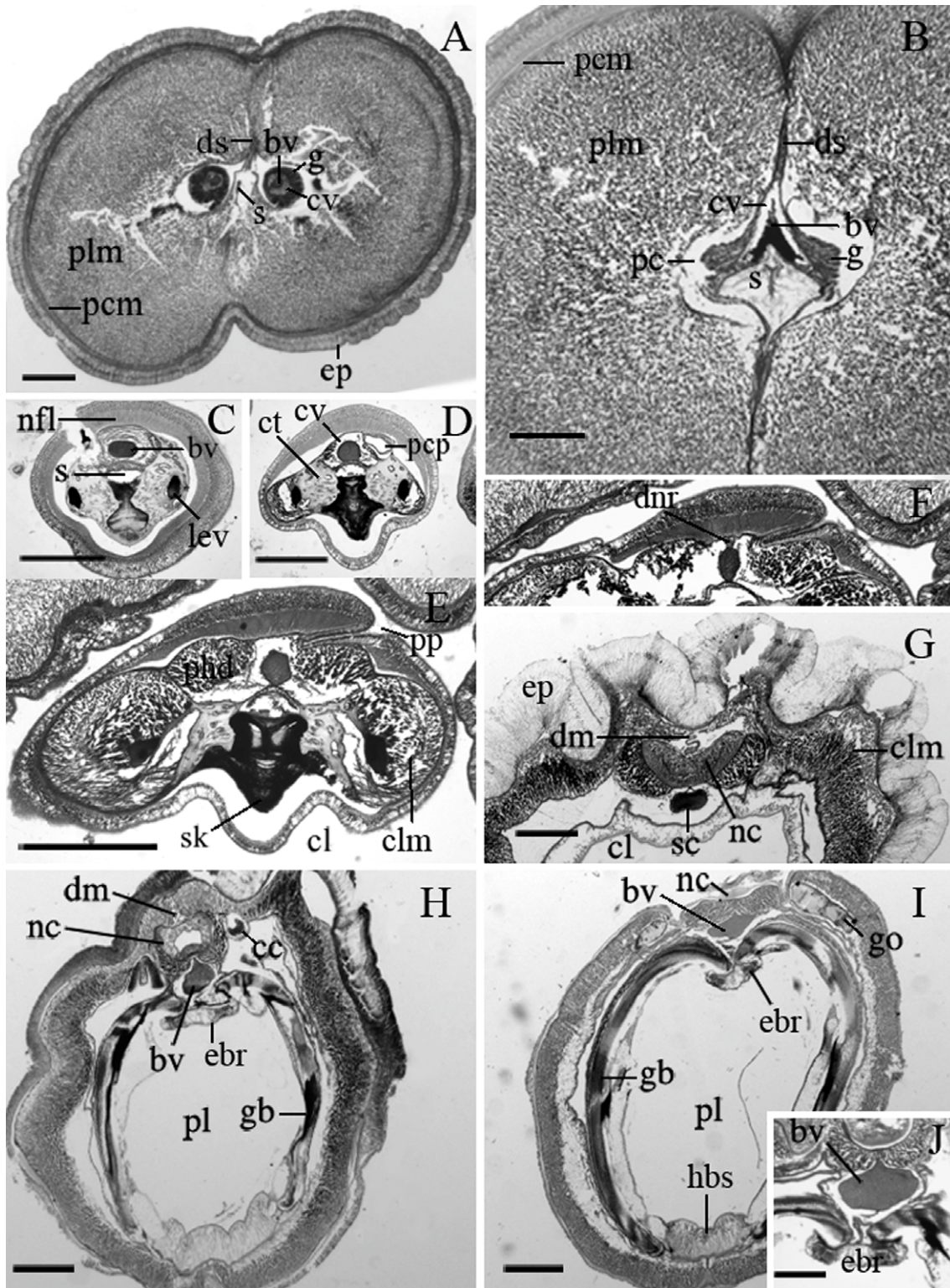


FIGURE 3. Light micrographs of transverse sections of *Schizocardium californicum*. (A) Proboscis with tubular extensions of the heart-kidney complex. (B) Proboscis heart-kidney complex. (C) Proboscis neck in the anterior region of the collar, (inset) more anterior region showing the proboscis canal. (D) Collar showing skeletal cornua. (E) Anterior region of the trunk showing collar canals. (F) Anterior genital region of the trunk. (G) Mid-dorsal part of the pharyngeal region of the trunk. **bv**, blood vessel; **cc**, collar canal; **cl**, collar lumen; **clm**, collar longitudinal muscles; **ct**, condroid tissue; **cv**, cardiac vesicle; **dep**, dorsal epidermal pocket; **dm**, dorsal mesentery; **ds**, dorsal septum; **ebr**, epibranchial ridge; **ep**, epidermis; **g**, glomerulus; **gb**, gill bar; **go**, gonad; **hbs**, hypobranchial strip; **lev**, lateral efferent vessel; **nc**, nerve cord; **nfl**, nerve fiber layer; **pc**, proboscis coelom; **pcm**, proboscis circular muscles; **pcp**, proboscis canal of the peduncle; **phd**, periaemal diverticula; **pl**, pharynx lumen; **plm**, proboscis longitudinal muscles; **s**, stomochord; **sc**, skeletal cornua; **sk**, skeletal keel; **sp**, skeletal plate; **tlm**, trunk longitudinal muscles. Scale bars: (A, C (inset) and F) = 500 μm ; (B and G) = 300 μm ; (C, D and E) = 1000 μm .

The proboscis epidermis is quite thick. Most of the nuclei of the epidermal epithelium are arranged in a single central stratum. The circular fiber layer is well developed and is 10 to 13 fibers in thickness. The nerve fiber layer is thickened middorsally, especially in the posterior part of the proboscis. The central part of the proboscis coelom is lined by connective tissue elements in the form of an epithelium and is divided into a right and a left half by a sagittal muscle plate, which is not complete throughout and the right and left tubular spaces intercommunicate here and there. The vermiform process extends forwards almost into the anterior fifth of the proboscis. The anterior part of the stomochord is spade or diamond shaped in transverse section and has a narrow slit-like lumen. The two ventrolateral blind pouches of the stomochord are spacious and well developed and are in broad communication with the central primary lumen that is here relatively wide (Fig. 3A). The neck of the stomochord is flat and broad with a narrow flattened lumen in its anterior half, while the posterior half is relatively more developed in the dorsoventral direction due to the widening of the lumen in this direction. The stomochord opens into the buccal cavity at about 1 mm from the anterior margin of the collar. The ventral septum of the proboscis extends anteriorly only half way along the vermiform process and does not reach its tip, while posteriorly it does not reach up to the posterior wall of the ventral coelom of the proboscis. The dorsal proboscis septum extends anteriorly to about the tip of the stomochord proper dividing the dorsal part of the proboscis coelom into a right and left half. Posteriorly at about the level of the ventro lateral blind pouches of the stomochord the dorsal septum stops where the cardiac vesicle reaches middorsally up to the basement membrane of the epidermis thus serving to divide the proboscis coelom into a dorsal right and dorsal left half. Only the left dorsal coelom continues into a functional left proboscis canal, which opens out by a left proboscis pore (Fig. 3F). The right and left tubular anterior extensions of the cardiac vesicle, which are surrounded by the right and left halves of the glomerulus respectively, reach anteriorly only over the posterior third of the vermiform process. The glomerulus and the tubular extension of the cardiac vesicle are confluent at their anterior tips. The cardiac vesicle has a very spacious lumen without much connective tissue inside. It never covers the stomochord laterally. But just behind the level of the ventro lateral blind pouches of the stomochord (that is, in the anterior part of the neck) the cardiac vesicle surrounds the central blood space on all sides, extending even on its ventral side, that is, between the blood space and the dorsal side of the stomochord (Fig. 3C–D). The end plate of the skeleton is concave and bears a short and sharp anteriorly projecting middorsal spine. This spine pushes anteriorly the wall of the ventro lateral blind pouches of the stomochord. The skeletal body is relatively small, while the keel is broad and deep with an obtuse ventral edge and broad lateral wings (Fig. 3C–E).

Immediately behind the proboscis pore a dorsal root-like extension from the middorsal thickened part of the nerve fiber layer enters the proboscis coelom, transversing the basement membrane. It enters the coelomic epithelium covering the middorsal part of the dorsal blood vessel (Fig. 3F). In its general appearance it resembles closely similar roots found in the collar of other enteropneusts. But, whereas in the collar the root connects the nerve fiber layer of the epidermis with the collar nerve cord (which is derived from the same source), here it comprises a supply of a bundle of nerve fibers from the middorsal epidermal nerve fiber layer of the peduncle, to the coelomic epithelium and the organs lying nearby.

Both the dorsal and the ventral mesenteries of the collar are complete anteriorly (Fig. 3G). The perihæmal diverticula extend anteriorly to the level of the proboscis coelomic canal, and are confluent anteriorly. A dorsal epidermal pocket in the anterior face of the collar is present. The collar epidermis is thick, especially ventrally and laterally. The collar nerve has neither a lumen nor any lacunae (Fig. 3G). The skeletal cornua extend posteriorly a little over half the length of the collar. The peribuccal cavities extend anteriorly in to the collar nearly up to the opening of the stomochord into the buccal cavity. The collar canals have a thick ventral wall, with nuclei arranged in several layers, while the dorsal wall is deeply infolded forming an epibranchial ridge so characteristic of the genus. Each collar canal opens into the anterior extremity of the first gill pouch. A deep and distinct posterior neuropore is present (Fig. 3H).

The pharynx is typical of the genus *Schizocardium* where the gills comprise virtually the whole wall of the pharynx in transverse section and the midventral digestive pharynx is only a narrow hypobranchial strip (Fig. 3I–J). There may be from ten to twenty synapticulae connecting the neighbouring gill bars. Gonads appear about 3 mm behind the collar and they open lateral to the gill openings. The gonadal openings alternate with the gill openings, on both the sides. The gill openings of opposite sides appear to be paired.

Discussion: In several characters, the present species differs from the two known species of the genus. Thus in the greater extent of the vermiform process of the stomochord, the short extent of the ventral septum, the

uniqueness of the disposition of the cardiac vesicle, the occurrence of a pair of spacious ventro-lateral blind pouches of the stomochord, the occurrence of a dorsal nerve 'root' in the proboscis, the short posterior extend of the skeletal cornua in the collar, the great anterior extend of the peripharyngeal cavities and the smaller number of synaptacula, the present form is distinct from the already known species of *Schizocardium* and hence is here described as a new species.

Remarks: The two previously described species of the genus have derived their names from their geographic origins. Following this practice, we name the present form after the state of California.

Discussion

With the addition of *Schizocardium californicum* to the family roster, there are 19 species described. A dichotomous key to the enteropneust families Harrimaniidae, Spengelidae, Ptychoderidae and Torquaratoridae and to the genera of family Harrimaniidae is provided in Deland *et al.* (2010). Here we provide a key to the genera of the family Spengelidae, and hope that it provides useful, even to non-specialists (Table 1).

TABLE 1. A dichotomous key to the genera of family Spengelidae.

- | | | |
|----|--|----------------------|
| 1. | Vermiform process very long; pericardial auricles very long; gill slits so long as almost meet in mid-ventral line-thus no separation into dorsal branchial and ventral digestive portion of pharynx; synaptaculae present; no dorsal gonads in branchial region; liver saccules well formed | <i>Schizocardium</i> |
| - | Liver sacs absent; ventral part of pharynx well developed; pericardial diverticula short | 2 |
| 2. | Synapticles present; nerve roots present or absent; genital region with dermal pits | <i>Spengelia</i> |
| - | Synapticles and nerve roots absent | 3 |
| 3. | Peribuccal spaces; collar longer than broad; dorsal gonads absent | <i>Willeyia</i> |
| - | Without peribuccal spaces | <i>Glandiceps</i> |

Zoogeography

Very few general observations can, at this point, be made about the zoogeography of spengelid worms. Most of the species have a very limited range, and some are known from single individuals or single lots. *Glandiceps talaboti* (Marion 1876) is unusual in that it has been taken from several locations, primarily from the Mediterranean Sea (Naples, Marseille, Cape Falcon and Cape Tenes, Algeria) but also from the west coast of Morocco.

Spengelids have a curious distribution; they are found exclusively in tropic and sub-tropic waters. Only 5 species are found outside the latitudinal boundaries of the Tropic of Cancer and the Tropic of Capricorn, and none are known from wholly temperate regions. *Glandiceps talaboti* are taken from the Mediterranean; *G. hacksi* and *G. eximius* are taken from the south of Japan (Horste, 1939); and *G. qingdaoensis* from the East China Sea (Jianmei, 2005). *Schizocardium brasiliense* has been taken from Debidue Creek, near North Inlet, South Carolina (Ruppert *et al.*, 2009) and *S. puruvianum* and *S. californicum* from California. The familial distribution is in sharp contrast to the 36 known species of acorn worm the family Harimaniidae, that are with seven exceptions (*Saccoglossus caraibicus* from Curaçao; *S. otagoensis* from New Zealand; *S. apantesis* and *S. aulakoeis* from South Australia; *S. bournei* from Madras; *S. inhacensi* and *Xenopleura vivipera* from South Africa), found exclusively north of the Tropic of Capricorn. The uneven and northern distribution of harrimaniid populations is most probably due to sampling effort, rather than anything of real biological meaning. Most species discoveries have been made in Europe, Britain and North America. By contrast, the extended effort and historical bias of searching northern latitudes has provided no spengelids from the Atlantic coast of Europe, or, with the exception of *Schizocardium*, from the coasts of North America. The only meaningful conclusion to this distribution is that spengelids are a warm water group. An explanation for this observation we cannot hope to submit!

Schizocardium peruviane and *S. brasiliense* have the greatest, though disjunct, ranges of any member of the family. *S. brasiliense* is known from Rio de Janeiro, Brazil and from Debidue Creek, near North Inlet, South Carolina (Ruppert *et al.* 2009). *S. peruvianum* is known from Independence Bay, Peru and from Point Mugu, California. These ranges span over 50 degrees of latitude and populations are unknown in the more than 5550 km between. Putative specimens of *Schizocardium sp.* have been collected at Morro Bay, San Luis Obispo, California

(Bridges & Woodwick 1994, Franzen 2001), and in the deep waters of the San Pedro Basin, the Santa Maria Basin, and the Western Santa Barbara Channel (Woodwick 1955, 1996). Additional putative *Schizocardium* sp. specimens have been collected from Corpus Cristi Bay, Texas (Flint & Kalke 1986). If these identifications are true, the species ranges remain exceptionally wide and discontinuous, but in the absence of anatomical descriptions, there is no way to confirm these diagnoses. The California specimens, collected by Keith Woodwick, having worked extensively with the group, seem very probable. The Texas species, later collected and sectioned by Cameron, is not a member of the genus *Schizocardium*.

The disjunct and widely distributed populations of *Schizocardium* could represent the relict populations of a formerly wide spread species if indeed they are absent from the intervening, often poorly known waters. Alternately, they could represent the two extremes of the ranges. This is believable as members of the genus likely form a tornaria larva, capable of long periods in the plankton. *Ptychodera flava*, also with a tornaria, is virtually pantropical IndoPacific having seen specimens from Sydney, Guam, Hawaii, the Galapagos and from Mauritius. These instances recall others in the group with tornaria and with widely discontinuous though still stenotopic distributions: *Balanoglossus carnosus* from Japan, the Great Barrier Reef and the Maldives; *Glossobalanus minutus* from the Mediterranean and Rio de Janeiro.

Phylogeny

Spengelids occupy a middle position in hypothesis of enteropneust phylogenetics, exhibiting a combination of both ptychoderid (including the familiar *Balanoglossus*) and harrimaniid (including *Saccoglossus*) features. Similar to harrimaniids, spengelids do not possess gonadal wings with lateral trunk septa and, except for the genus *Schizocardium* Spengel, 1893, also lack liver sacs. The two most familiar genera *Spengelia* Willey, 1898 and *Schizocardium* have synapticles bridging the primary and secondary gill bars and coelomic peribuccal diverticula (like ptychoderids), but the genus *Glandiceps* Spengel, 1893 has neither. The genus *Willeyia* Punnett, 1903 has peribuccal diverticula but lacks synapticles. This mélange of characters results in two contradictory and rickety phylogenetic trees (analysis not shown): Spengelids are either i) a monophyletic family and sister to group to the ptychoderids, or ii) the genera are distributed in a step-wise fashion with harrimaniids in the basal position, and with ptychoderids derived within the spengelid clade (i.e., spengelid paraphyly). In either scenario, *Schizocardium* is the sister taxon to the Ptychoderidae.

Acknowledgments

We would like to acknowledge the valuable contributions of Waldo Schmitt of the U.S. National Museum, Theodore H. Bullock of the Scripps Institution, University of California and Giannina Passuni of the Laboratorio de Ecología Marina, Universidad Nacional Mayor de San Marcos in specimen collection.

References

- An, J. & Li, X. (2005) First record of the family Spengeliidae (Hemichordata: Enteropneusta) from Chinese waters, with description of a new species. *Journal of Natural History*, 39, 1995–2004.
- Bridges, T.S. & Woodwick, K.H. (1994) Comparative morphology and function of hepatic caeca in four enteropneusts. *Acta Zoologica (Stockholm)*, 75, 371–378.
- Cameron, C.B. (2005) A phylogeny of the hemichordates based on morphological characters. *Canadian Journal of Zoology*, 83(1), 196–215.
- Cameron, C.B., Deland, C. & Bullock, T.H. (2010) A taxonomic revision of the genus *Saccoglossus* (Hemichordata: Enteropneusta) with descriptions of five new species from the Eastern Pacific. *Zootaxa* 2483, 1–22.
- Deland, C., Cameron, C.B., Bullock, T.H., Rao, K.P. & Ritter, W.E. (2010) A taxonomic revision of the family Harrimaniidae (Hemichordata: Enteropneusta) with descriptions of seven species from the Eastern Pacific. *Zootaxa*, 2408, 1–30.
- Flint, R.W. & Kalke, R.D. (1986) Biological enhancement of estuarine benthic community structure. *Marine Ecology Progress Series*, 31, 23–33.
- Franzen, A. (2001) Sperm ultrastructure in the enteropneust *Schizocardium* sp (Hemichordata, Enteropneusta) and possible

- phylogenetic implications. *Invertebrate Reproduction and Development*, 39, 37–43.
- 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 pp.
- Marion, A.F. (1886) Etudes zoologiques sur deux especes d'Enteropneustes (*Balanoglossus hacksi* et *Balanoglossus talaboti*). *Archives de Zoologie Experimental et Generale Series 2*, 4, 305–326.
- Osborn, K.J., Kuhnz, L.A., Priede, I.G., Urata, M., Gebruk, A.V. & Holland, N.D. (2011) Diversification of acorn worms (Hemichordata, Enteropneusta) revealed in the deep sea. *Proceedings of the Royal Society of London B*, 279, 1646–1654.
- Ruppert, E.E., Cameron, C.B. & Frick, J.E. (1999) Endostyle-like features of the dorsal epibranchial ridge of an enteropneust and the hypothesis of dorsal-ventral axis inversion in chordates. *Invertebrate Biology*, 118(2), 202–212.
- Spengel, J.W. (1893) Fauna und Flora des Golfes von Neapel und der angrenzenden Meeres-Abschnitte. Berlin: Friedländer, pp. 1–757.
- Woodwick, K.H. (1955) A list of Enteropneusta identified from samples of the benthos from San Pedro Basin, California. In: Hartman, O. (Ed.) *Quantitative survey of the benthos of San Pedro Basin, Southern California*. Allan Hancock Pacific Expeditions. Vol. 19. University of Southern California Press, Los Angeles, California, 166–167.
- Woodwick, K.H. (1996) Hemichordata: Enteropneusta. In: Blake J.A., Scott, P.H. & Lissner, A. (eds.) *Taxonomic Atlas of the Benthic Fauna of the Santa Maria Basin and the Western Santa Barbara Channel*. Santa Barbara, California: Santa Barbara Museum of Natural History, pp. 251–259.