

SACCOGLOSSUS HORSTI SP.N., AN ENTEROPNEUST OCCURRING IN THE SOLENT

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(Text-figs. 1-8)

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INTRODUCTION

The species described in this paper was found at Lymington by one of the authors (C.B.G.) in the summer of 1940. It differs from the three species of this genus that have been described from the British coasts and from *Saccoglossus kowalevskyi* Agassiz, the American species, which Caullery & Mesnil (1916) claimed to have found on the French coast of the English Channel at St Martin, near Cap de la Hague. Its characters, though distinctive, are such as might lead to confusion with *S. kowalevskyi*. It seems possible, therefore, that the record from the coast of France may refer to this and not to the American species. Since St Martin is directly opposite Lymington and only some 75 miles distant, this explanation appears more probable than that the French record really refers to the American species, especially when it is remembered that, so far as is known (van der Horst, 1927-39), all other species of *Saccoglossus* have very restricted distributions. Doubtless the local character of the species of this genus, and indeed of the other members of the Harrimanidae, is associated with their direct development and it contrasts sharply with the wide distribution of several members of the Ptychoderidae, in which a free-swimming stage in development, the *Tornaria* larva, provides for dispersal.

The specific name is chosen in recognition of Prof C.J. van der Horst's many contributions to the subject and in particular his exhaustive account of the Enteropneusta in Bronn's *Klassen und Ordnungen des Tier-Reichs*.

ENVIRONMENT

S. horsti occurs on the Hampshire coast, near the mouth of the Lymington River which runs into the western end of the Solent. The species extends about half a mile both east and west of the mouth of the river, but does not go up the estuary, where the mud soon becomes foul and black below the surface. It occurs in the deep grey mud (see Appendix for analysis), which is of the most glutinous type, from just above low-water mark spring tides to a short way above low-water mark neap tides. The animals live about 4-8 in. below the surface in rather diffuse burrows and no 'casts' could be distinguished at the surface. They occur also higher up the shore at about half-tide mark in the chunks of dead rhizomes of *Spartina Townshendii* Groves which are scattered on the surface of the soft mud, having broken away from the edge of the *Spartina* flats which fringe the Solent. Their burrows in this situation are in the under surfaces of those chunks of rhizomes which are not deeply embedded in the mud. Such pieces lie in pools of water and so the animals below them are never completely uncovered at low tide. The proboscis was found protruding from the mouth of the burrow when the chunk was lifted, while the tail went vertically upwards into the mass of dead roots. They do not occur in those masses so deeply embedded in the mud as to have their under surfaces foul and black, nor in the mud itself at this level.

The environment of *S. horsti* thus is strikingly different from that of *S. cambrensis*, Brambell & Cole (1939a), which occurs in Wales in relatively clean sand and fine shell gravel and is absent from adjoining stretches of mud flats. Moreover at Hurst Castle, 4 miles to the west of the Lymington River, there are flats uncovered at low-water spring tides, grading from quite clean to distinctly muddy sand, in which *S. horsti* could not be found. It was observed in the laboratory that when living specimens of *S. horsti* were put in a dish over mud they soon burrowed down, while over sand they lay on the surface and made no attempt to burrow but formed loose tubes of sand grains and mucus in which, however, they seemed to live quite happily. It appears, therefore, that *S. horsti* is essentially a mud-living species whereas *S. cambrensis* is sand-living.

S. horsti occurs in association with the amphipod, *Corophium volutator* (Pallas). It is very common in the mud and more numerous than all the annelids put together; in a good patch there may be half a dozen specimens in a trowelfull of mud.

MATERIAL AND TECHNIQUE

S. horsti is fragile and liable to fragment when handled, yet it is more robust and fragments less readily than *S. cambrensis*. Moreover, it is much more amenable to narcotization and fixation. Although each of the authors is well acquainted with either one or other of these two species neither has had an

opportunity of examining both in the living condition. Therefore these conclusions are based on comparison of preserved specimens and of notes on the preservation. The specimens show in a striking manner that much more perfect examples can be obtained of *S. horsti* than of *S. cambrensis* and that they can be narcotized and preserved in a much more expanded state. Commercial specimens of *S. kowalevskyi* indicate that probably this species is still more readily preserved intact and in a flaccid condition. It may be significant

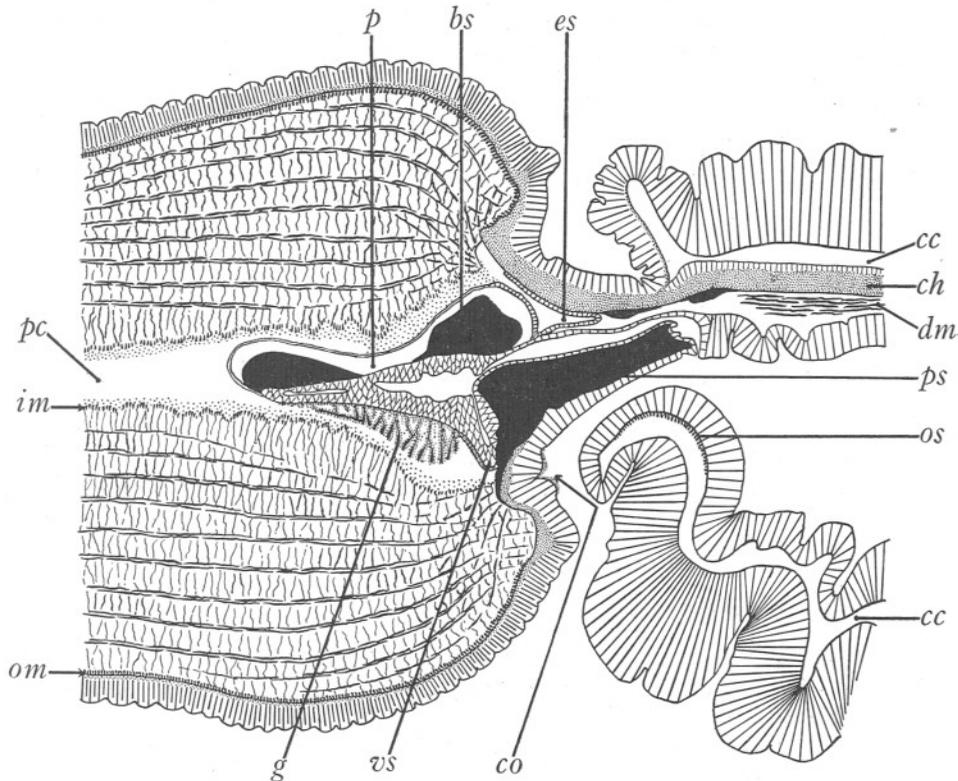


Fig. 1. Longitudinal sagittal section of the base of the proboscis. $\times 37$. *bs.* blood sinus; *cc.* coelomic cavity of collar; *ch.* nerve cord of collar; *co.* preoral ciliary organ; *dm.* longitudinal muscle fibres of trunk in periaemal cavity; *es.* end-sac; *g.* glomerulus; *im.* inner circular muscle fibres of proboscis; *om.* outer circular muscle fibres of proboscis; *os.* oral sphincter; *p.* pericardium; *pc.* coelomic cavity of proboscis; *ps.* body of proboscis skeleton; *vs.* ventral diverticulum of stomochord.

that these differences are associated with differences in the epidermis and in the development of the musculature, which in turn may be related to the nature of the substratum in which the animal lives.

Narcotization was effected readily both by the menthol and by the gradual alcoholization methods, provided the animals were treated soon after collection. Specimens kept in the laboratory for some hours, though apparently

healthy, responded to narcotization by copious secretion of mucus and by autolysis. Specimens, both narcotized and without narcotization, were fixed either in formalin or in Bouin's fluid. Thus both expanded and contracted examples were available for comparison. Both fixatives gave excellent results. Serial sections were cut at a thickness of 10μ and were stained with Ehrlich's haematoxylin and either eosin or Tischutkin's orange G-erythrosin. The

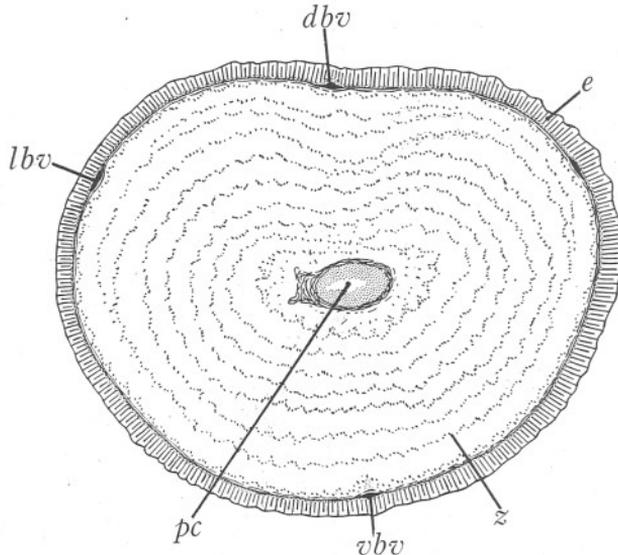


Fig. 2. Transverse section of contracted proboscis. $\times 24$. *dbv*. dorsal blood vessel; *e*. epidermis; *lbv*. lateral blood vessel; *pc*. proboscis coelom; *vbv*. ventral blood vessel; *z*. concentric zone of longitudinal muscle fibres.

latter stain was suggested to us by Dr N.B. Eales and has proved to be especially useful for the definition it imparts to epidermal basement membranes and blood sinuses.

SPECIFIC CHARACTERS

Externals

The total length of one complete specimen, but not a large one, was 20.5 cm. when narcotized. Another specimen, which was a very large one but was incomplete posteriorly, was 31.5 cm. long and it is estimated that it must have exceeded 35 cm. in length when complete. The partly contracted proboscis of large living specimens measured 1.3–1.8 cm. long and 4–5 mm. in diameter at the thickest part near the base. The proboscis of narcotized specimens, in which it appeared to be fully extended, was 2.8–3.2 cm. long. The collar in large narcotized specimens was 4.5–5.5 mm. long in the dorsal middle line and 3.0–4.0 mm. long ventrally; it was 3.5–4.0 mm. in diameter

anteriorly and 4.0-4.5 mm. in diameter posteriorly. Thus this species is slightly larger than *S. cambrensis*.

There is a very distinct dorsal groove reaching from the base to the tip of the proboscis. It is sufficiently marked posteriorly to render the base of the proboscis almost heart-shaped when viewed from above. There is also quite a distinct ventral groove reaching almost to the tip of the proboscis in the living animal. It is not apparent in material fixed with the proboscis contracted, but is distinguishable in specimens which were narcotized and in which the

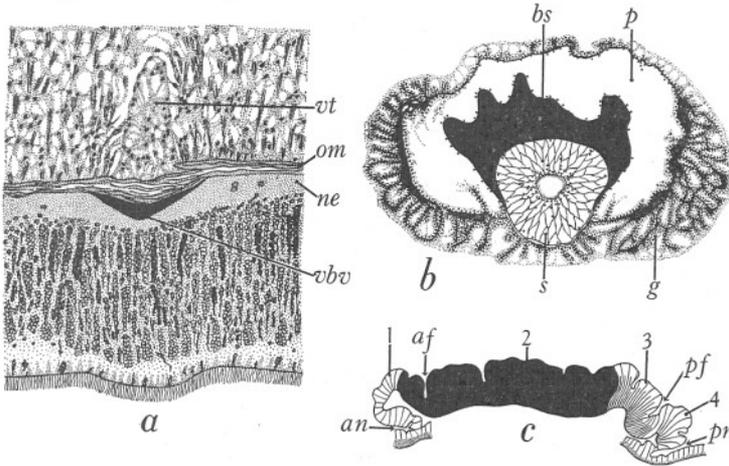


Fig. 3. *a*. Transverse section of ventral region of contracted proboscis shown in Fig. 2. $\times 150$. *b*. Transverse section of the proboscis organs. $\times 60$. *c*. Dorsal longitudinal sagittal section of the epidermis of the collar. The epidermal zones are numbered 1 to 4 from anterior to posterior. $\times 17$. *af*. anterior furrow; *an*. anterior neuropore; *ne*. nerve fibre layer of epidermis; *pf*. posterior furrow; *pn*. posterior neuropore; *s*. stomochord; *vt*. ventral longitudinal tract overlying the ventral blood vessel; other guide letters as in previous figures.

proboscis was preserved in an expanded condition. A preoral ciliary organ, similar to that of *S. cambrensis* (Brambell & Cole, 1939*b*), but less apparent in the living animal, since its coloration is not distinctive, is present on the base of the proboscis.

The anterior border of the collar is slightly thickened and the posterior quarter is more definitely so. Posteriorly the margin of the collar overhangs the first two or three gill pores, forming a slight operculum.

The ventral muscle bands of the trunk project in the branchial and genital regions as a conspicuous rounded keel (Figs. 7, 8*b*). When the animal contracts this keel shortens more than the dorsal pharyngeal region. Consequently the muscular keel becomes more or less straight while the dorsal region coils sinuously around it. The gonads begin about 1 mm. behind the collar and extend a considerable distance behind the branchial region, overlapping the beginning of the hepatic region. They attain their greatest development at the anterior extremity of the oesophageal region, where they form

rounded projecting ridges on each side of the body (Fig. 7). The genital ridges and the muscle bands, though projecting distinctly, are never so pronounced as those of *S. kowalevskyi* (Spengel, 1893). The number of branchial pores varies from specimen to specimen, as is the rule in allied species. The number of gill slits in three adult specimens in which they were counted were 104 pairs, 115 pairs and, in one large specimen in which the series was not quite complete, 137 pairs. Thus they are more numerous than in any other known species of the genus.

The animal has two clearly distinguishable colour forms occurring in approximately equal numbers and intermixed in the same environment. The paler form has a yellowish white proboscis with a brown base and a rust-brown collar tinged with orange with a white ring round the posterior margin. The darker form has a salmon-pink proboscis with a brown base and with a brick-red collar with a white ring round its posterior margin. The colour of the trunk is the same in either variety. The branchial region is a rather transparent grey tinged with salmon-pink and there is no deep red patch such as is found in *S. cambrensis* just behind the collar on each side of the body. The pink gonads show through the body wall; in some specimens their colour is pronounced. The trunk immediately behind the branchial region is a rich dark brown and thereafter it gradually pales towards the posterior extremity, which is fawn. The whole of the trunk is sprinkled with numerous small raised spots that are paler in colour than their background. No carmine spots, like those in *S. cambrensis*, were observed. Throughout the trunk the dorsal nerve cord is sharply defined with a pale margin on each side.

Proboscis

The nerve-fibre layer of the epidermis is well developed throughout the proboscis, but is thickened over the basal region (Fig. 1), where the epidermis is less glandular and more strongly ciliated than elsewhere. A preoral ciliary organ, so similar to that described in detail in *S. cambrensis* that it does not merit separate description (Brambell & Cole, 1939*b*), is present. The dorsal groove of the proboscis is more pronounced than in *S. cambrensis* or *S. kowalevskyi* and the nerve-fibre layer beneath it is thickened, forming a longitudinal tract lying between the groove and the dorsal subneural blood vessel. The ventral longitudinal groove is apparent in transverse sections of the extended proboscis, but is not accompanied by any thickening of the nerve-fibre layer, which tends rather to be reduced in thickness where it overlies the ventral longitudinal blood vessel (Fig. 3*a*). The circular muscle layer is fairly well developed and is as thick as, or slightly thicker than, the nerve-fibre layer. It is not thickened in the form of a sphincter at the end of the proboscis. The longitudinal muscles are arranged in nine or more concentric rings (Fig. 2) which are apparent even at the centre, though more clearly seen at the periphery. This complete concentric arrangement of the longitudinal musculature resembles that of *S. kowalevskyi*, although it is not so clearly defined as in

that species, rather than that of *S. cambrensis*, and it distinguishes the species from the two remaining British species, *S. ruber*, Tattersall (1905) and *S. serpentinus*, Assheton (1908). The cavity of the proboscis is narrow, having a diameter at the narrowest part in the anterior half of the contracted proboscis of about one-tenth that of the whole organ. It is nearly filled with rounded coelomic cells, with very vacuolated cytoplasm and relatively small nuclei, which are either attached to its wall or floating freely in it. A thin layer of

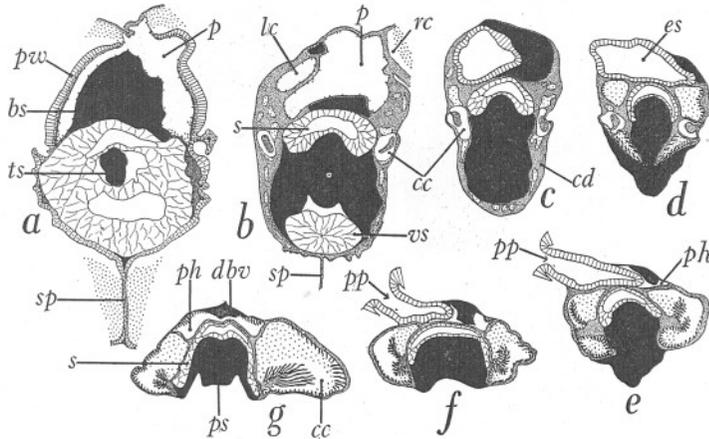


Fig. 4. Series of seven transverse sections at intervals of 100μ through the neck of the proboscis, showing the relations of the coelomic cavities, blood vessels, etc., and the shape of the body of the proboscis skeleton. Blood vessels and skeleton shown in solid black. The crura of the skeleton diverge within 50μ of the last section depicted in *g*. $\times 45$. *cc*, extension of coelomic cavity of collar; *cd*, chondroid tissues; *lc*, left dorsal pouch of proboscis coelom; *ph*, periaermal cavity; *pp*, proboscis pore; *pw*, pericardial wall, very thick in this region; *rc*, right dorsal pouch of proboscis coelom; *sp*, ventral septum of proboscis; *ts*, tip of proboscis skeleton; other guide letters as in previous figures.

circular muscle fibres bounds the cavity (Figs. 1 and 2), which is not enlarged at the anterior end. Within the outer circular muscle layer and overlying the ventral blood vessel the stromal tissue is slightly differentiated to form a longitudinal tract, conical in cross-section (Fig. 3*a*), which can be distinguished only in well-preserved material. This tract appears to be free from longitudinal muscle fibres. Posteriorly it is continuous with the ventral extremity of the ventral septum through which the ventral blood vessel runs. Its function is obscure, but its structure and position are suggestive of some sort of neuromotor organ. The ventral septum is very short (Figs. 4*a* and *b*), extending only about 100μ in front of the caudal ends of the shallow ventral coelomic sacs. The left dorsal coelomic sac is connected to the wide median end sac, from which the proboscis pore opens to the exterior on the left side of the neck of the proboscis (Fig. 4). The stomochord is straight with a wide and continuous lumen throughout (Fig. 1). It is provided with a single ventral diverticulum. The walls of that region which lies above the proboscis skeleton

are very thin (Fig. 4). Thus the stomochord is similar in shape to that of *S. kowalevskyi* and differs from that of *S. cambrensis*, in the absence of an S-shaped bend, in being shorter and stouter and in having thinner walls posteriorly. This character alone readily distinguishes the species from *S. cambrensis*. The large pericardium extends more than half-way round the stomochord (Fig. 3*b*). The glomerulus is continued around the stomochord

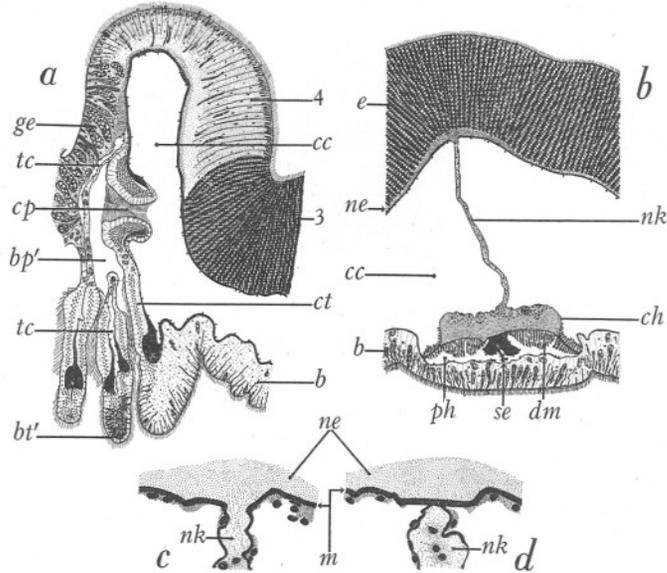


Fig. 5. *a*. Longitudinal section through the region of the collar pore. $\times 60$. *b*. Transverse section through the dorsal region of the collar. $\times 45$. *c* and *d*. Two transverse sections 30μ apart through the junction of the neural keel with the epidermis, showing an interruption in the epidermal basement membrane (*m*) in *c* and its continuity in *d*. $\times 325$. *b*. epithelium of buccal cavity; *bp'*. first branchial pouch; *bt'*. first tongue; *cp*. collar pore; *ct*. collar-trunk septum; *ge*. branchial epidermis; *nk*. neural keel; *se*. septum between periahaemal cavities; *tc*. trunk coelom; other guide letters as in previous figures.

ventrally and the right and left halves extend considerably more than half-way towards the mid-dorsal line of the pericardium, though there is no dorsal glomerulus. The form of the body of the proboscis skeleton (Figs. 1 and 4) is similar to that of *S. cambrensis* and the crura embrace between one-half and two-thirds of the circumference of the buccal cavity, though they only extend backwards between one-quarter and one-third of the length of the collar from its anterior margin. No hard concretion, like that described in *S. cambrensis*, was found in the core of the proboscis skeleton of any specimen.

Collar

There are four epidermal zones in the collar (Fig. 3*c*). The first forms the anterior margin of the collar and is composed mainly of ciliated cells; the

second, in which basophil glandular cells are predominant and the epidermis is thickest, extends over the anterior two-thirds of the surface; the third does not stain so densely basophil as the second, but glandular elements are numerous in it and the epidermis is almost as thick; the fourth, which is composed mainly of ciliated cells with relatively few glandular elements, forms the posterior margin. The first, second and fourth zones evidently correspond to the first, second and fifth zones of the collar respectively in *S. cambrensis*, while the third zone probably represents both the third and fourth zones of the Welsh species. The number of epidermal folds in the collar varies according to the state of contraction, but one deep fold in the second zone near the anterior margin and another between the third and fourth zones appear to be constant and are responsible for the appearance of rims around the anterior and posterior margins.

The right and left coelomic cavities of the collar are separate from each other. The ventral mesentery is complete. Dorsally the coelomic cavities are separated by the nerve cord, joined throughout its length to the epidermis by a pronounced keel, by the perihæmal cavities, the stomochord and the proboscis skeleton. Anterior prolongations of the collar cavities extend throughout the neck of the proboscis, reaching almost to the level of the anterior extremity of the proboscis skeleton (Fig. 4). The epithelium of the collar pores is thick and the nuclei of the cells are arranged in many rows (Fig. 5a). The two perihæmal cavities in the collar are completely separated from each other posteriorly by the septum, in which the dorsal subneural blood vessel runs (Fig. 5b). They join at the level of the posterior extremities of the crura of the proboscis skeleton and the dorsal subneural blood vessel in front of this point runs in the dorsal wall of the single perihæmal cavity, between it and the nerve cord (Fig. 4). This median perihæmal cavity extends into the neck of the proboscis as far as the proboscis pore (Fig. 4e). The anterior extensions of the dorsal longitudinal muscles of the trunk extend throughout the length of the perihæmal cavities. The collar-trunk septum is deflected forwards on each side of the buccal cavity ventro-laterally, as in *S. cambrensis* and *S. kowalevskyi*, forming triangular diverticulae of the trunk cavities which taper anteriorly and end a short distance behind the extremities of the crura of the proboscis skeleton. Prolongations of the ventral longitudinal muscle bands of the trunk extend throughout the length of these cavities, the fibres being attached anteriorly to the posterior surface of the septum. These muscles, together with the longitudinal muscle fibres of the collar which are attached to the anterior wall of the septum and to the crura of the proboscis skeleton, form presumably the retractor mechanism of the collar and of the neck of the proboscis.

The nerve cord is solid throughout its length, the anterior and posterior neuropores, if the shallow depressions which represent them justify the name, ending blindly. The neural crest or keel, connecting the nerve cord with the epidermis throughout its length, is well developed (Fig. 5b). The tissues of this

keel are in direct continuity with the nerve-fibre layer of the epidermis at several separate points throughout the length of the collar, but in the intervening regions they are separated by the basement membrane of the epidermis (Fig. 5*c* and *d*). The points of continuity are in the nature of perforations in the basement membrane, perhaps 10μ in diameter, and are not associated with any local thickening of the keel. This is similar to the condition in *S. kowalevskyi* and is intermediate between that in some species, such as *S. cambrensis*, in which there is no continuity between the keel and epidermis, the continuous basement membrane intervening, and that in others, such as *S. inhacensis*, Kapelus (1936), and *S. pusillus* (Ritter) (van der Horst, 1930), in which the tissues of the keel are in uninterrupted continuity with the epidermis.

Circular muscle fibres in the collar cavities around the mouth form an oral sphincter (Fig. 1). The buccal cavity has no dorsal diverticulum, such as is found in *S. gurneyi* (Robinson, 1927) and *S. otagoensis* (Benham) (van der Horst, 1930).

Trunk

The epidermis of the branchial region surrounding the gill pores is characteristic (Fig. 8*a*). It is strongly ciliated and is packed with long narrow glandular elements, filled with homogeneous secretion which stains intensely with eosin. Consequently this epithelium can be distinguished in sections, even with the naked eye, by its eosinophilia. Scattered among the eosinophil elements are a few basophil goblet cells, oval or pear-shaped in form with vacuolated cytoplasm. These are more numerous where the branchial epidermis joins that of the collar. The branchial epidermis thus differs widely from that of *S. cambrensis*, in which the dominant glandular elements are mucous-secreting goblet cells which appear vacuolated and partly disorganized with little affinity for stains, since large numbers of them discharge their secretions before fixation. The epidermis of the trunk behind the branchial region is thinner and is composed mainly of ciliated cells with relatively few glandular elements, except for numerous scattered patches of thicker, more glandular, epithelium.

The dorsal nerve cord is clearly defined in the branchial region, but there is no definite dorsal groove in any part of the trunk. The ventral nerve cord, which is much the larger, lies above a shallow ventral groove that extends throughout the branchial region, and gradually fades out in the oesophageal region. Otherwise the epidermal nerve-fibre layer is fairly well developed throughout the branchial region, but is very thin behind it.

The ventral longitudinal muscles of the trunk are well developed and the dorsal longitudinal muscles form two much smaller bundles extending throughout the branchial region (Fig. 6).

The dorsal blood vessel runs in the dorsal mesentery of the gut, which is continuous throughout the trunk. Anteriorly the epidermal basal membrane of the ventral nerve cord is in contact with the wall of the pharynx in the

mid-ventral line, there being no ventral mesentery in this region in consequence (Fig. 6). Throughout the remainder of the trunk there is a continuous ventral mesentery, containing the ventral blood vessel (Figs. 7, 8*b*,

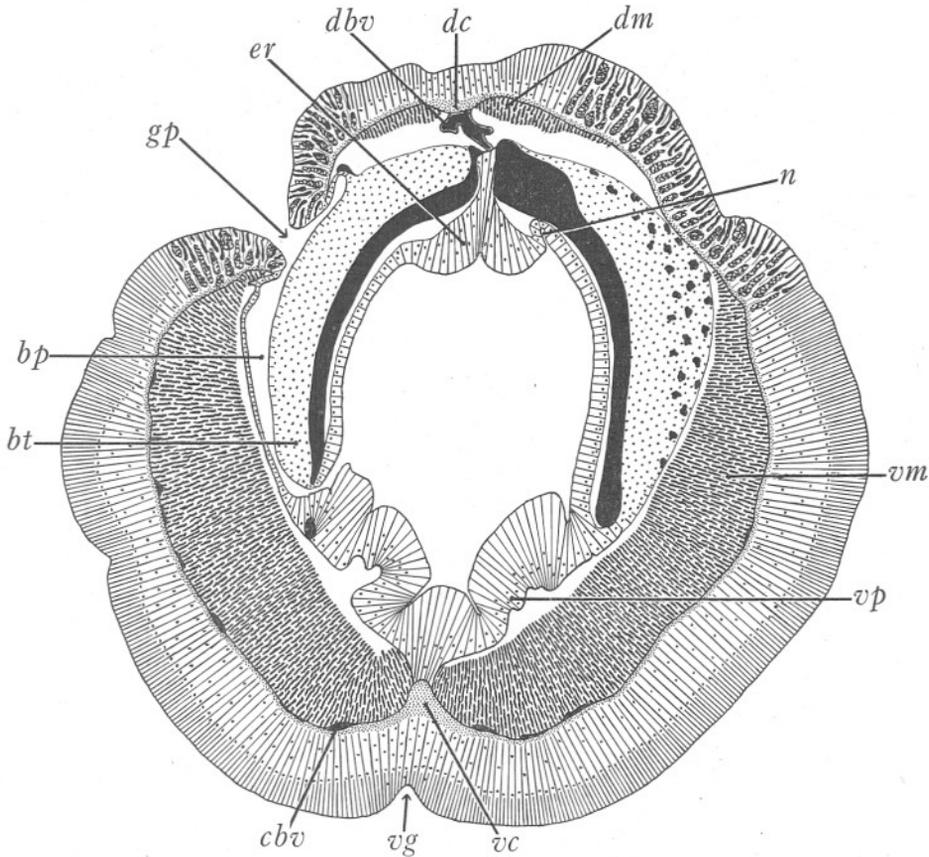


Fig. 6. Transverse section through the anterior part of the branchial region, passing through a branchial pore and tongue on the left and a septum on the right. $\times 46$. *bp*. branchial pouch; *bt*. tongue; *cbv*. circular blood vessel; *dbv*. dorsal blood vessel; *dc*. dorsal nerve cord; *dm*. dorsal longitudinal muscle band of trunk; *er*. epibranchial ridge; *gp*. branchial pore; *n*. niche or recess between septum and epibranchial ridge; *vc*. ventral nerve cord; *vg*. ventral groove; *vm*. ventral longitudinal muscle band of trunk; *vp*. ventral non-branchial region of pharynx. Skeletal rods and blood vessels shown in solid black.

8*c* and 8*d*). Thus the two trunk cavities do not appear to communicate at any point.

The gill slits embrace the dorsal two-thirds of the pharynx (Fig. 6). At the posterior extremity of the series the last few gill slits decrease progressively in size but tongues are present even in the last and smallest. Concretions such as those described in *S. cambrensis* are not found in the skeletal bars of this

species. The tongues are broader and project farther into the lumen of the pharynx than do the septa (Fig. 8a). The ciliated epithelium covering the

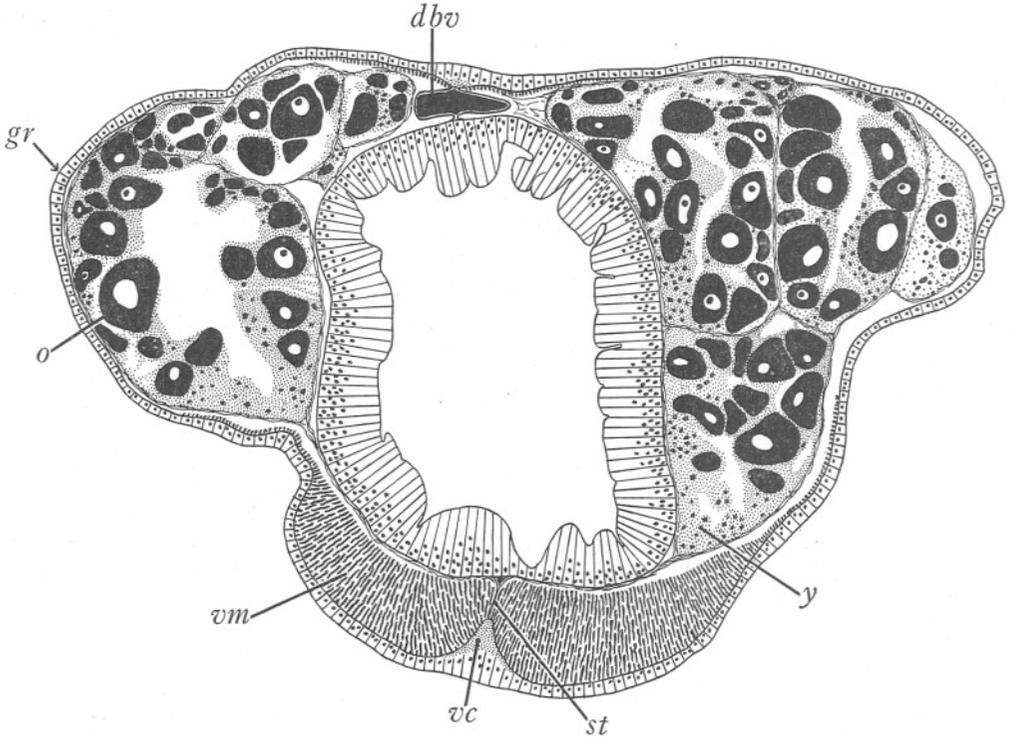


Fig. 7. Transverse section through the first region of the oesophagus showing the maximum development of the genital ridges. $\times 46$. *gr.* genital ridge; *o.* oocyte in ovary; *st.* ventral septum of trunk; *y.* yolk-cells in ovary; other guide letters as in previous figures.

inner surface of the tongues and septa is similar, except that that on the tongues is thicker and contains many basophil glandular elements while that on the septa contains few. A thick epithelium, with long cilia and regularly arranged nuclei but devoid of glandular elements, covers the sides of both the tongues and septa. The epithelium lining the gill chambers and covering the outer surfaces of the tongues is not ciliated and the nuclei are not regularly arranged. Numerous large stellate pigment cells are scattered throughout this epithelium, except where it covers the tongues. The epibranchial ridge is grooved longitudinally in the mid-dorsal line and hence appears bilobed in transverse sections (Fig. 6). It differs in this respect from the epibranchial ridges in both *S. cambrensis* and *S. kowalevskyi*. The epithelium on the inner surfaces of the septa at their dorsal extremities, where they join the epibranchial ridge, is reduced in thickness, thus forming a niche

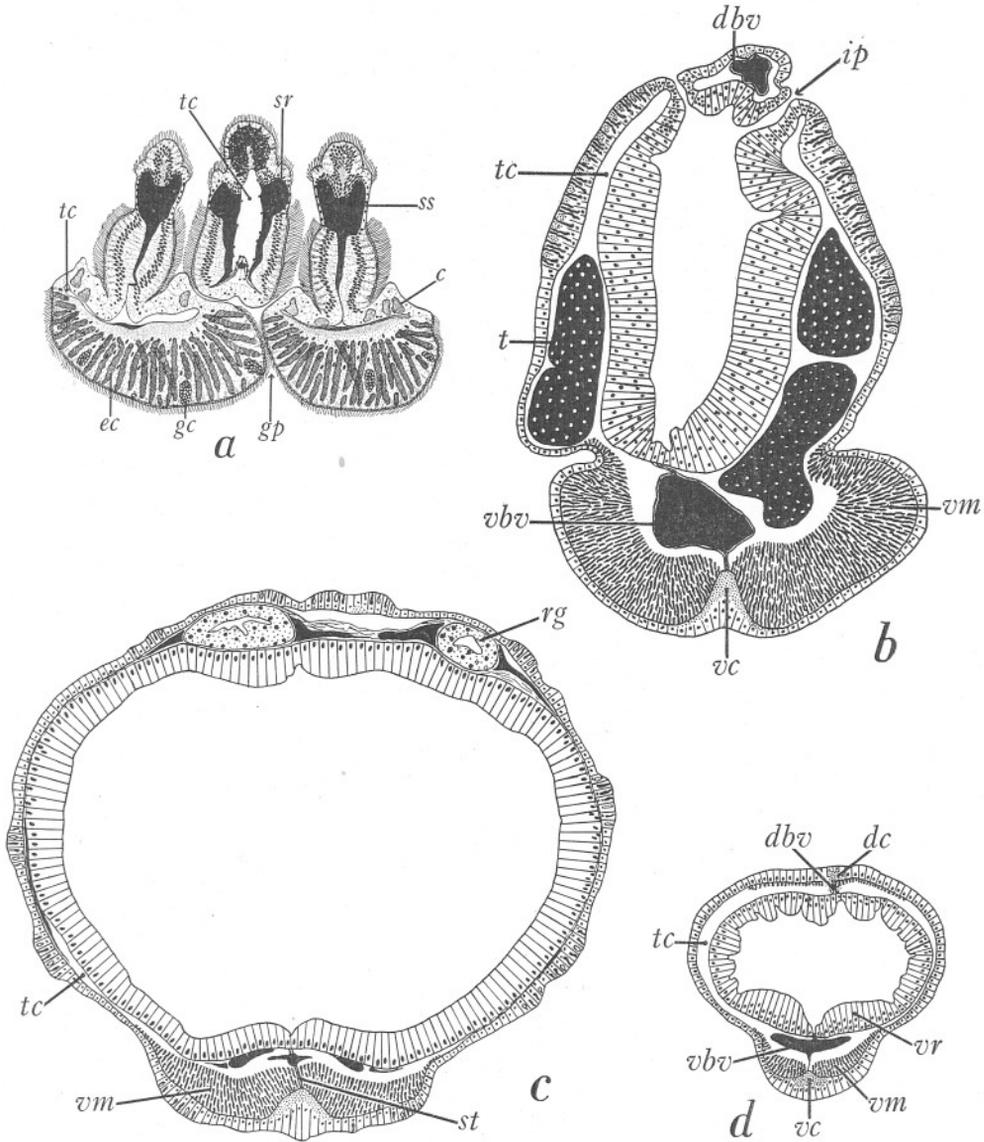


Fig. 8. *a*. Longitudinal horizontal section through two branchial septa, a tongue and a branchial pore. The character of the branchial epidermis is shown. $\times 127$. *b*. Transverse section through the beginning of the second region of the oesophagus showing intestinal pores. $\times 46$. *c*. Transverse section through the hepatic region. $\times 46$. *d*. Transverse section through the intestinal region. $\times 46$. *c*. pigment cell; *ec*. eosinophil glandular cell of epidermis; *gc*. goblet-cell; *ip*. intestinal pore; *rg*. rudimentary gonad; *sr*. skeletal rod in tongue; *ss*. skeletal rod in septum; *t*. testis; *vr*. ventrolateral ridge of intestinal epithelium; other guide letters as in previous figures.

or recess on each. No such recesses are found on the dorsal ends of the tongues. The epithelium of both the epibranchial ridge and the ventral non-branchial part of the pharynx resembles that of the buccal cavity. It is thick, strongly ciliated and contains a number of basophil glandular elements.

The oesophagus is relatively short, though, owing to contraction, its length could not be measured with precision. It is divided into three distinct regions. The epithelium lining the first (Fig. 7) resembles that of the ventral non-branchial part of the pharynx, but the glandular elements are rather more numerous and are regularly arranged, the oval bodies of the cells occupying the central zone of the epithelium and not extending into the basal zone, while their narrow necks traverse the peripheral zone to reach the surface. The second region has much thicker walls. A transverse section through the middle of this region reveals a cruciform lumen. The thickest epithelium lines the dorsal arm of the lumen. It is full of basophil glandular elements. The epithelium of the horizontal arms of the lumen is much thinner and is sharply differentiated from the rest by its lack of chromophilia. The epithelium of the ventral arm is very thick, though not so thick as that of the dorsal arm, and it stains still more densely with haematoxylin. The horizontal arms of the lumen constitute two lateral longitudinal grooves in the wall which begin dorsally and slope backwards and downwards. The intestinal pores open into these grooves at their anterior and dorsal extremities (Fig. 8*b*). The epithelium lining these pores is similar to that lining the grooves into which they open internally. The number of pores varies from 4 to 8 in different specimens and indeed on the two sides of the same specimen. The numbers observed were 4+5, 5+5, 5+7 and 7+8. No rudimentary pores such as those described in *S. cambrensis* were observed. The third region of the oesophagus is lined by thinner epithelium, less crowded with glandular elements and distinguished by the oval nuclei being confined to the basal regions of the columnar cells.

The epithelium of the posterior part of the oesophagus grades into that of the long hepatic region, where it is somewhat thicker but otherwise very similar, without any sharply defined transition. The hepatic region of the gut (Fig. 8*c*) of this species is remarkable for the total absence of any trace of sacculation of its walls. The lumen is expanded and the gut nearly fills the trunk cavities, its outer surface being almost in contact with the body wall laterally and only separated from it by the gonads dorsally and the muscle bands ventrally.

The intestine is also expanded and has a wide lumen (Fig. 8*d*). The coelomic cavities in both the hepatic and intestinal regions are much narrower than in *S. cambrensis*. The epithelium of the intestine is somewhat thinner than that of the hepatic region, but is thickened ventrally to form two broad convex ridges, one on each side of a mid-ventral groove. The anal region was missing from all the specimens sectioned.

The gonads, both ovaries and testes, are simple unlobed sacs. The more posterior gonads of the series are rudimentary and do not display active gametogenesis. The genital ducts are extremely short, so that the gonads open almost directly at the genital pores. The ovaries (Fig. 7) contain yolk cells and the oocytes were observed to attain a size of 0.23 mm. long by 0.17 mm. broad. Thus, assuming that some of the specimens were mature, the oocytes are considerably smaller than those of *S. cambrensis* and the number present in a single ovary is correspondingly greater.

COMPARISON WITH OTHER SPECIES

S. horsti is a well-defined species. It is readily distinguishable from *S. ruber* and *S. serpentinus*, though neither has been described in detail, both by the large number of gill slits and by the concentric arrangement of the musculature of the proboscis. It resembles more closely both *S. cambrensis* and *S. kowalevskyi* and appears to occupy a systematic position intermediate between them, though probably more closely allied to the latter than to the former species. It differs from *S. cambrensis* in coloration, habitat and size; in the more complete concentric arrangement of the longitudinal musculature of the proboscis; the presence of a ventral groove on the proboscis; the straight stomochord; the presence of only four epidermal zones in the collar; the shorter crura of the proboscis skeleton; the slight operculum; the continuity at intervals between the tissues of the neural keel and the nerve-fibre layer of the epidermis; the larger number of gill slits; the projecting ventral muscle bands of the trunk; the genital ridges and extreme anterior extension of the gonads; the form of the epibranchial ridge; the number of intestinal pores. It differs from *S. kowalevskyi* in the presence of dorsal and ventral grooves on the proboscis; the complete separation of the collar cavities; the shorter crura of the proboscis skeleton; the larger number of gill slits; the fact that the tongues project further into the lumen of the pharynx than do the septa; the form of the epibranchial ridge; the less projecting ridges formed by the ventral muscle bands and the gonads.

The structural similarity of *S. horsti* and *S. kowalevskyi* raises the problem of whether Caullery & Mesnil's (1916) record from the coast of France should be ascribed to the British or American species. They had only one fragmentary specimen, which included part of the proboscis, the collar and the anterior part of the branchial region. It was found in very fine and compact grey sand at low-water mark of spring tides. The collar was 3 mm. in diameter and 4-5 mm. long with a marked posterior thickening. There were numerous gill pores which were not covered by lateral folds of the trunk. The proboscis was rosy white in colour and the predominant colour of the rest of the body was orange-salmon. They stated that this coloration was closely similar to that in Spengel's (1893) figure of *S. kowalevskyi*, though not so bright. The musculature of the proboscis was well developed and concentrically arranged.

A single proboscis pore was present on the left side. The proboscis skeleton was similar to that described by Spengel in *S. kowalevskyi*. The periaermal spaces were fused anteriorly and the muscles in them were much less developed than those figured by Spengel. The branchial epithelium was of the same type as *S. kowalevskyi* and the ectoderm of the collar was very thick with an enormous development of mucus glands. This description is applicable equally to either species, except for the poor development of the muscles in the periaermal cavities, which conforms with neither. The size, coloration and musculature of the proboscis serve to distinguish it from the other British species, *S. ruber*, *S. serpentinus* and *S. cambrensis*. Thus, while the characters permit of assigning the specimen to either *S. horsti* or *S. kowalevskyi* they do not allow of distinguishing to which it belongs. The geographical evidence points strongly to *S. horsti*, which occurs within 75 miles, whereas all other records of *S. kowalevskyi* are from the other side of the Atlantic Ocean. On this assumption *S. kowalevskyi* falls into line with all other members of the genus in being confined in its distribution.

The known species of the genus *Saccoglossus* now number fourteen. The characters of these, excepting *S. cambrensis* and *S. horsti*, are admirably summarized and a full bibliography of the original literature is provided by van der Horst (1927-39). Nevertheless it may be convenient to include herein a very brief summary in English of the more important and distinctive characters of the species other than that now described.

S. sulcatus (Spengel), from Japan. Deep dorsal sulcus on proboscis rendering it half-moon shaped in cross-section. Collar as broad as long. There appear to be only 10-11 pairs of gill pores. Other characters unknown.

S. otagoensis (Benham), from New Zealand. Deep dorsal groove on proboscis but not so pronounced as in last-named species. Collar as broad as long. 10-15 pairs of gill pores. Longitudinal muscle fibres of proboscis in concentric rings. Dorsal diverticulum of buccal cavity present. Dorsal and ventral mesenteries of collar absent. Gonads extending anteriorly to level of 4th gill pore. Ventral septum of proboscis short. One pair of intestinal pores.

S. pygmaeus Hinrichs and Jacobi, 1938, from Heligoland. Proboscis without pronounced dorsal groove. Collar broader than long. 9-22 pairs of gill pores. Longitudinal muscle fibres of proboscis not in concentric rings. No dorsal diverticulum of buccal cavity. Dorsal and ventral mesenteries of collar complete. Gonads begin at posterior extremity of branchial region. Ventral septum of proboscis very short. One pair of intestinal pores. Very small form, about 3 cm. long.

S. gurneyi (Robinson), from Suez. Collar nearly twice as broad as long. 40-60 pairs of gill pores. Ventral septum of proboscis very long, extending beyond tip of stomochord. Dorsal diverticulum of buccal cavity present. Median proboscis pore. Gonads beginning immediately behind collar. Dorsal and ventral mesenteries of collar complete throughout 4/5ths of length of collar.

S. caraibicus (van der Horst), from West Indies. Collar longer than broad. More than 50 pairs of gill pores. Ventral septum of proboscis long, extending to tip of stomochord. No dorsal diverticulum of buccal cavity. Median proboscis pore. Gonads beginning behind 4th gill pore. Dorsal and ventral mesenteries of collar complete. Perihaemal cavities separate throughout length and not extending into proboscis stalk. Dorsal glomerulus present.

S. bournei (Menon), from Madras. Collar broader than long. More than 62 pairs of gill pores. Ventral septum of proboscis very long, extending in front of tip of stomochord. No dorsal diverticulum of buccal cavity. Gonads beginning immediately behind collar. Dorsal mesentery of collar complete, ventral lacking in anterior half. Very deep anterior neuropore.

S. pusillus (Ritter), from California. Both gonads and ventral longitudinal muscle bands form projecting ridges on trunk. 60 pairs of gill pores. Longitudinal muscle fibres of proboscis in concentric rings. Ventral septum of proboscis short. Ventral mesentery of collar complete. Gonads beginning behind 12th-17th gill pore. One pair of intestinal pores.

S. mereschkowskii (Nic. Wagner), from Northern and Eastern Russia. Both gonads and ventral longitudinal muscle bands form projecting ridges on trunk. 50 pairs of gill pores. Longitudinal muscle fibres of proboscis in concentric rings. Ventral septum of proboscis short. Dorsal mesentery of collar complete, ventral incomplete anteriorly. Gonads beginning in middle of branchial region. Epidermis of collar very thick (0.5 mm.). Seven pairs of intestinal pores.

S. inhacensis Kapelus, 1936, from S. Africa. Both gonads and ventral longitudinal muscle bands form projecting ridges on trunk. 82 or more pairs of gill pores. Longitudinal muscle fibres of proboscis not in concentric rings. Ventral septum of proboscis short. Ventral mesentery of collar complete. Gonads beginning at level of 4th gill pore. Four pairs of intestinal pores, the first with several internal openings each.

S. kowalevskyi (A. Agassiz), from Atlantic coast of U.S.A. Both gonads and ventral longitudinal muscle bands form projecting ridges on trunk. 100 pairs of gill pores. Longitudinal muscle fibres of proboscis in concentric rings. Ventral septum of proboscis short. Dorsal and ventral mesenteries of collar incomplete. Gonads beginning within $\frac{1}{2}$ mm. of collar. 4 to 6 pairs of intestinal pores.

S. cambrensis Brambell and Cole, 1939, from Wales. Trunk circular in cross-section, without genital or muscular ridges. 60-90 pairs of gill pores. Longitudinal muscle fibres of proboscis in concentric rings. Ventral septum of proboscis short. Dorsal and ventral mesenteries of collar complete. Gonads beginning in middle of branchial region. S-shaped bend on stomochord in front of ventral diverticulum. 8-12 pairs of intestinal pores, the first 3-5 pairs being rudimentary.

S. ruber (Tattersall), from Ireland. Trunk circular in cross-section, without genital or muscular ridges. 56-64 pairs of gill pores. Longitudinal muscle fibres of proboscis not in concentric rings. S-shaped bend on stomochord in

front of ventral diverticulum. Ventral septum of proboscis short. Wide proboscis coelom.

S. serpentinus (Assheton), from Scotland. Trunk circular in cross-section, without genital or muscular ridges. 60 pairs of gill pores. Longitudinal muscle fibres of proboscis not in concentric rings. Narrow proboscis coelom. Very elongated form, proboscis at least 25 mm. long.

SUMMARY

1. *S. horsti* occurs on the Hampshire coast of the Solent near the mouth of the Lymington River, in glutinous grey mud associated with *Corophium volutator*.

2. The species is distinguished by the following characters: coloration; dorsal and ventral grooves present on the proboscis throughout its length; collar forming a slight operculum posteriorly; ventral muscle bands of the trunk forming projecting ridges; rounded genital ridges present, the gonads beginning within 1 mm. of the collar; 100-140 pairs of gill slits; longitudinal muscle fibres of the proboscis arranged in nine or more concentric rings; ventral septum of the proboscis short; stomochord straight, with ventral diverticulum and wide lumen throughout; no dorsal glomerulus present; single proboscis pore on the left side; proboscis skeleton embracing half to two-thirds of the circumference of the buccal cavity and extending one-fourth to one-third of the length of the collar; four epidermal zones present in the collar; collar cavities completely separated; anterior extensions of the collar cavities extending into the neck of the proboscis; periaemal cavities separate posteriorly but confluent in front of the level of the tips of the crura, and extending into the neck of the proboscis as far as the proboscis pore; neural keel well developed and in continuity with the epidermal nerve layer at intervals; no dorsal diverticulum of the buccal cavity; branchial epidermis characterized by the predominant intensely eosinophil glandular elements; tongues broader and projecting further into the lumen of the pharynx than the septa; epibranchial ridge formed by two convex ridges bounding a median groove; oesophagus divided into three regions; 4-8 intestinal pores; hepatic region of gut not sacculated and with an expanded lumen; gonads not lobed; oocytes attain a size of 0.23×0.17 mm.; yolk cells present in the ovaries.

3. The probable identity of the specimen of *Saccoglossus* from the French coast of the English Channel, recorded by Caullery & Mesnil (1916) as *S. kowalevskyi*, with this species is discussed.

APPENDIX

Analysis of sample of mud, in which *S. horsti* occurs, for which we are indebted to Prof. G. W. Robinson:

Coarse sand (particles 2.0-0.2 mm. in diameter)	0.0
Fine sand (particles 0.2-0.02 mm. in diameter)	39.0
Silt (particles 0.02-0.002 mm. in diameter)	19.7
Clay (particles less than 0.002 mm. in diameter)	30.1
Moisture in air-dry sample	3.2
Calcium carbonate	1.6
Organic carbon	2.5

The sample was oven dried at 105° C. before analysis. Comparison with the analyses of sand in which *S. cambrensis* occurs (Brambell & Cole, 1939a) shows that this sample contains a much higher proportion of silt and clay and that the organic content is considerably greater.

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