Observations on the Branchial Crown of the Serpulidae (Annelida, Polychaeta)

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CONTENTS

INTRODUCTION

DURING investigations on the blood systems of serpulids (Hanson, 1949) observations were made on the internal anatomy of the branchial crown. Previous accounts were found to be incomplete and in some respects inaccurate; so I decided to publish some of my observations. Thomas (1940) has given the most recent general description of the crown of a serpulid, *Pomatoceros*. Pruvot (1885) and Johansson (1927) showed, by studies on its innervation, that the crown of the Serpulimorpha represents the two prostomial palps of other polychaetes. It consists of filaments bearing pinnules, of the so-called 'palps', and, in most serpulids, of an operculum borne on a peduncle. It is generally recognized that the operculum and peduncle represent a modified filament (Zeleny, 1905; Segrove, 1941).

The following species were used: *Serpula vermicularis* L., *Hydroides norvegica* (Gunnerus), *Vermiliopsis infundibulum* (Philippi), *Pomatoceros triqueter* L., *Salmacina incrustans* Claparède, *Protula intestinum* (Lamarck), *Spirorbis corrugatus* (Montagu), and *S. militaris* (Claparède). *Pomatoceros* was obtained from Plymouth. The other species were studied at Naples. Most of the observations were made on sectioned specimens. The fixing solutions and staining methods I used are listed in my account of the blood system in the Serpulimorpha (Hanson, 1949).

OBSERVATIONS

Muscles

The muscles of the filaments (Text-fig. 1), pinnules (Text-fig. 6), 'palps

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(Text-fig. 7), and opercular peduncle (Text-fig. 2) of *Pomatoceros* are all longitudinal.

In each *filament* are the following muscles:

(*a*) Two external branchial muscles (Thomas, 1940) situated in the two corners of the abfrontal side of the filament. Near to them are the two external branchial nerves.

(*b*) Two internal branchial muscles (Thomas) situated on the frontal side of the filament. The fibres of these muscles are grouped round the internal branchial nerve. Most of them lie on each side of the nerve, but some are abfrontal to it.
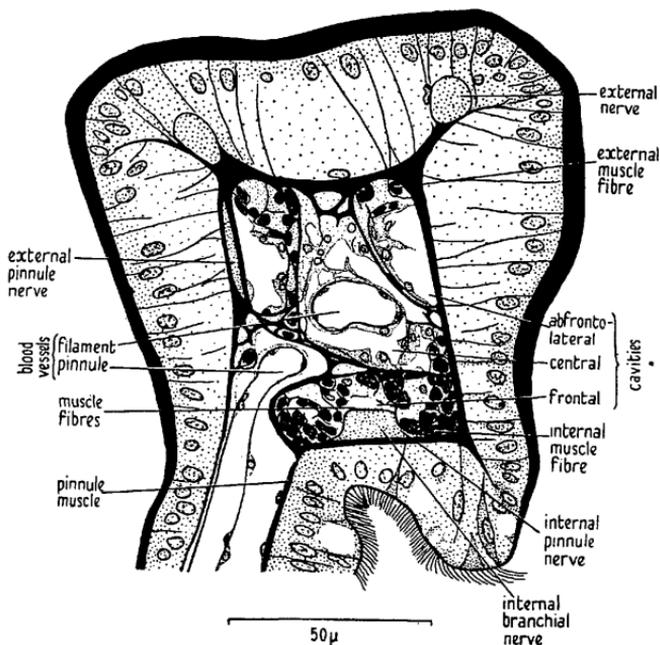
(*c*) A single layer of small muscle-fibres situated on the abfrontal surface of the internal branchial nerve. They are not present on the external branchial nerves or on any other nerves except the internal peduncular nerve.

The *peduncle* (Text-fig. 2) is triangular in cross-section, and contains a single group of muscle-fibres situated in the apical angle (frontal) and along the two sides. The fibres do not enter the operculum, but terminate at the top of the peduncle. Here they are attached to the basement membrane of the epidermis which roofs the peduncle, except for a small aperture through which the blood-vessel and its surrounding connective tissue and the three opercular nerves enter the operculum. McIntosh (1922–3) stated that the muscles of the peduncle are 'chiefly transverse', and concluded: 'The thrusting out of the operculum—if such happens—is thus voluntary, the withdrawal and retention more or less involuntary.' I have found that the peduncular muscle, like the branchial muscles, consists of longitudinal fibres, the contraction of which will draw the operculum towards the centre of the crown when the animal withdraws into its tube. When the crown is expanded the peduncle is sometimes held out nearly at right angles to the long axis of the body.

Each *pinnule* (Text-fig. 6) and *'palp'* (Text-fig. 7) has only a few muscle-fibres, situated just inside the basement membrane of the frontal epidermis.

A pair of internal and a pair of external branchial muscles are present in each filament of *Serpula* (Text-fig. 3), *Hydroides*, *Vermiliopsis*, *Salmacina*, and *Spirorbis militaris*. As in *Pomatoceros*, the external branchial muscles are less well developed than the internal branchial muscles, but they are more reduced in these serpulids than in *Pomatoceros*. In *Protula* and *Spirorbis corrugatus* external branchial muscles could not be found, but internal branchial muscles are present. In their internal structure the peduncles of both functional and reserve opercula of *Serpula* and *Hydroides* are very similar to filaments; the internal and external peduncular muscles have the same appearance as their counterparts in the filaments. The arrangement of the muscles in the pinnules and 'palps' of *Serpula*, *Hydroides*, and *Vermiliopsis*, and in the pinnules of *Protula* and *Spirorbis militaris* is the same as in *Pomatoceros*. Muscle-fibres on the abfrontal surface of the internal branchial nerve have been found in the following serpulids besides *Pomatoceros*: *Serpula*, *Hydroides*, *Vermiliopsis*, *Protula*, and *Spirorbis militaris*. Their function is not known. Comparable

muscles of unknown function occur on the dorsal surface of the ventral nerve cord of *Nereis* and other errant polychaetes (Prenant, 1929), and on the lateral nerves of pelagic nemerteans (Coe, 1926). Probably other cases exist.

TEXT-FIG. 1. Transverse section through filament of *Pomatoceros triqueter*, and longitudinal section through base of one pinnule.
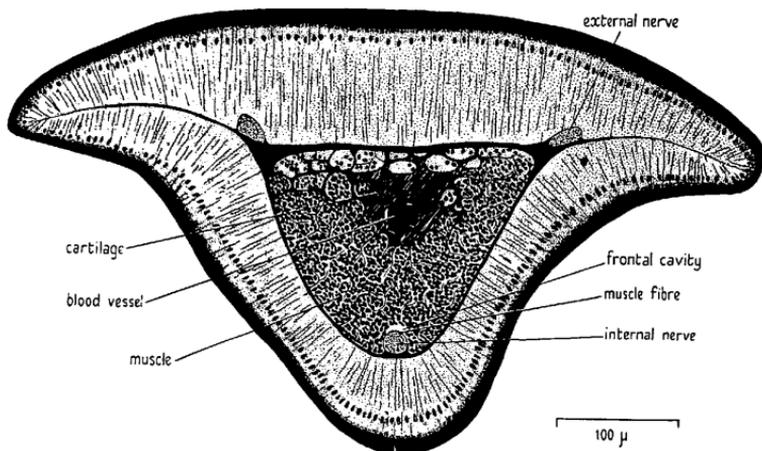
Nerves

In the *peduncle* and each *filament* of *Pomatoceros* there are three nerves (Thomas, 1940). Two are situated in the abfrontal corners (the external peduncular and external branchial nerves) and the third on the frontal face (internal peduncular and internal branchial nerves). The abfrontal nerves lie outside the basement membrane of the epidermis. The frontal nerve lies just inside the basement membrane. On its abfrontal surface is a layer of small muscle-fibres (see above) and a small well-defined canal, part of the system of cavities in the crown (p. 229). No muscles or canals accompany the abfrontal nerves.

All three branchial nerves send branches into the *pinnules*. The branches of the internal and external branchial nerves are respectively the frontal and abfrontal nerves of the pinnules (Text-figs. 1 and 6). The nerves of the

pinnules lie outside the basement membrane of the epidermis. Thomas found the frontal pinnule nerves, but has stated that abfrontal nerves are absent.

At the top of the *peduncle* the muscles and canal accompanying the internal peduncular nerve terminate, and the two external peduncular nerves come to lie just inside the basement membrane of the epidermis. Each of the three nerves now gives off two small branches which I have been able to trace for a short distance only. The three nerves enter the operculum through the

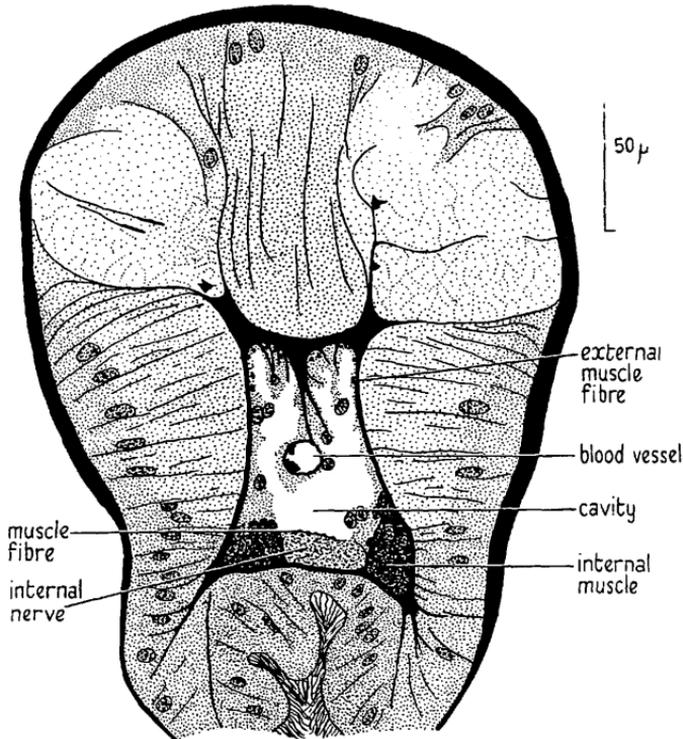TEXT-FIG. 2. Transverse section through opercular peduncle of *Pomatoceros triqueter.*

small gap by which the inside of the operculum communicates with the inside of the peduncle. Within the operculum all three nerves pass to the outside of the basement membrane. They give off many small branches, and can be traced as far as the rim round the top of the operculum.

The internal and external branchial nerves of the following serpulids are like those of *Pomatoceros*: *Hydroides, Vermiliopsis, Protula, Salmacina, Spirorbis corrugatus,* and *S. militaris.* No external branchial nerves could be found in *Serpula.* All my material was stained with 'Azan', however; different histological methods might reveal them, although they are distinct in Azan-stained sections of other serpulids. The internal and external peduncular nerves of *Hydroides* are like the corresponding nerves in the filaments. Both internal and external pinnule nerves have been found in *Hydroides*; internal pinnule nerves are present in *Vermiliopsis, Protula,* and *Spirorbis militaris,* but external pinnule nerves could not be found. Meyer (1888) was unable to find external pinnule nerves in *Eupomatus lunuliferus* (= *Hydroides lunulifera*) or *Psygmobranchus protensus* (= *Protula tubularia*), but Faulkner (1930) saw them in *Filograna implexa.*

The functional significance of the double nerve-supply to the serpulid crown is not known.

Skeleton

The internal skeleton of the *filament* of *Pomatoceros* consists of fibres enmeshing the muscle-fibres of the internal and external branchial muscles,
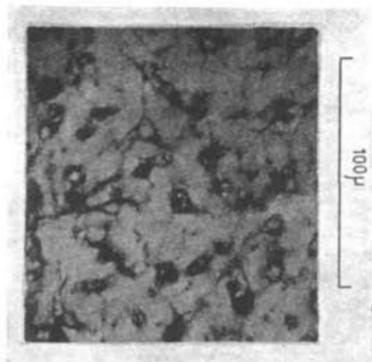

Text-fig. 3. Transverse section through filament of *Serpula vermicularis*.

and of sheets, namely, the basement membrane of the epidermis and the skeletal coat of the blood-vessel wall (Hanson, 1949). Both the fibres and the sheets give the staining reactions of collagen. The fibres, and the basement membrane of the epidermis, but not the skeletal coat of the vessel wall, enclose reticular fibres. No elastic fibres are present.

In the *peduncle*, as in the filaments, the muscle-fibres are enmeshed by connective tissue-fibres. On the abfrontal surface of the peduncular muscle these fibres pass into the ground substance of a cartilage-like tissue which

occupies the abfrontal part of the peduncle and fills the operculum, except for the space taken by the spiral opercular blood-vessel (Hanson, 1949). The ground substance gives the staining reactions of collagen, and is penetrated by reticular fibres and by a network of cytoplasm containing nuclei (Text-fig. 4). Ewer and Hanson (1945) have found that the ground substance reacts negatively to mucicarmine, thionin, resorcin-fuchsin, orcein, and safranin, all of which stain the ground substance (mucoprotein) of mammalian cartilage in a characteristic ('positive') manner. The cartilage-like tissue of *Pomatoceros* is very similar to the 'perichondrial' part of the branchial skeleton

TEXT-FIG. 4. Photomicrograph of section through 'cartilage' in operculum of *Pomatoceros triqueter*. Flemming. Iron haematoxylin.

of *Sabella pavonina*, as described by Nicol (1930). Ewer and Hanson have found that the 'perichondrium' of *S. spallanzanii* reacts negatively to muco-protein stains, but that the thick walls of the large vacuolated cells which make up the axial part of the skeleton are coloured by these stains in the same manner as mammalian cartilage (and sabellid mucous cells); they presumably contain a mucoprotein. Some similar results were obtained by Nowikoff (1912).

In the *pinnule* and '*palp*' of *Pomatoceros* and other serpulids, the internal skeleton is represented only by the basement membrane of the epidermis and the skeletal coat of the vessel wall.

In the filaments of serpulids other than *Pomatoceros*, external branchial muscles either appear to be absent or are represented only by a few fibres lying near the basement membrane of the abfrontal epidermis (Text-fig. 3). There are no connective tissue-fibres enmeshing these muscle-fibres. The skeleton associated with the internal branchial muscles is as well developed as in *Pomatoceros*. In *Hydroides*, a single stout fibrous sheet stretches from the skeletal coat of the blood-vessel wall to the medial line of the basement membrane of the abfrontal epidermis (figured by McIntosh, 1926). *Serpula*

(Text-fig. 3) and *Protula* are similar. In *Vermiliopsis* the vessel is anchored by several such fibrous sheets. In *Salmacina, Spirorbis militaris,* and *S. corrugatus* the vessel lies on the basement membrane of the abfrontal epidermis. In *Pomatoceros* the vessel lies in the centre of the filament, and fine fibres anchor it mainly to the skeleton around the external and internal branchial muscles.

The branchial skeleton of *Sabella* consists of large, vacuolated thick-walled cells surrounded by a cartilage-like sheath (Nicol, 1930). I have seen a similar skeleton in *Potamilla* sp. and *Dasychone lucullana* Delle Chiaje. No serpulid has yet been found to possess a skeleton like this. Large vacuolated cells with strong walls are commonly found in the *epidermis* of the serpulid crown, e.g. in *Filograna implexa* (Faulkner, 1930) and *Protula* (= *Salmacina*) *dysteri* (Huxley, 1855). In *Pomatoceros* their walls are not as thick as those of the axial part of the sabellid skeleton, and do not give the same staining reactions.
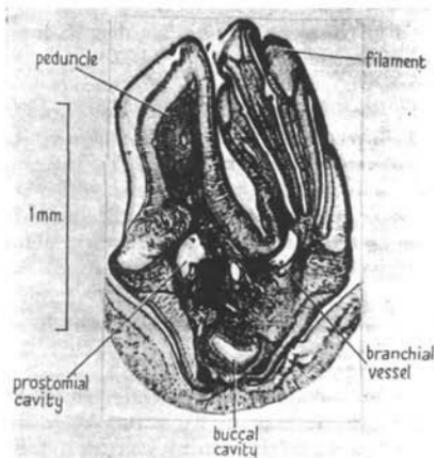
The internal skeleton in the peduncles of the functional and reserve opercula of *Serpula* and *Hydroides* is very similar to that in their filaments. 'Cartilage', of the same type as in *Pomatoceros*, is confined to the opercula which it fills, except for the spaces taken by the branched blood-vessels. The 'cartilage' in the reserve opercula has a much denser cell population than in the functional opercula. The 'cartilage' of *Serpula* and *Hydroides* was described by Örley (1884) and Zeleny (1905), respectively.

Cavities

The cavities in the prostomium and peristomium of *Pomatoceros* have processes extending into the base of the crown, where they end blindly. I have found that they are not, as previously stated (McIntosh, 1918; Thomas, 1940), continuous with the cavities in the filaments. The nature of all these cavities is obscure. 'It is difficult to determine whether the cavity in this region, which represents the head and collar segment, is of blastocoelic or coelomic origin . . .' (Segrove, 1941). Observations now to be reported have been made on the arrangement of the cavities in the peristomium, prostomium, and base of crown of *Pomatoceros*, and in the filaments, pinnules, 'palps', and peduncle of *Pomatoceros* and other serpulids.

The posterior septum of the cavity of the peristomium of *Pomatoceros* joins the alimentary canal at the junction between the oesophagus and the stomach. The main part of the peristomial cavity extends forwards as far as the level of the cerebral ganglia, and two processes from it accompany the two branchial blood-vessels to the base of the crown. I have found that the ventral mesentery extends throughout the peristomium as far as its front wall, and does not end behind the peristomium as stated by Thomas (1940). The peristomial part of the dorsal mesentery extends forwards only as far as the level of the transverse canal joining the two thoracic nephridia. Here the tissue of the dorsal mesentery becomes detached both from the roof of the peristomial cavity and from the wall of the oesophagus, and becomes a sheath around the dorsal blood-vessel. Posteriorly, the peristomial cavity consists of two halves,

right and left, separated by the dorsal and ventral mesenteries. Anteriorly it is irregularly subdivided by the ventral mesentery and by strands of tissue stretching from the body-wall to the wall of the oesophagus. The ciliated funnels of the two thoracic nephridia open laterally into the peristomial cavity in this anterior region. If, as Meyer's work on *Protula tubularia* (Meyer, 1888) seems to indicate, these ciliated funnels are coelomoducts, the fact that they open into the peristomial cavity suggests that this cavity is

TEXT-FIG. 5. Photomicrograph of obliquely transverse section through base
of crown of *Pomatoceros triqueter*.

coelomic, and the presence of dorsal and ventral mesenteries strengthens this supposition.

The cavity of the prostomium is confined to the dorsal part of the animal; it extends posteriorly for a short distance behind the cerebral ganglia, and anteriorly into the base of the crown. It is separated into two halves, right and left, by a septum enclosing the common median duct of the nephridia.

The base of each branchial blood-vessel lies in a process of the peristomial cavity, passing forwards between the dorsal and ventral roots of the circum-oesophageal nerve commissures, and ending blindly before the branchial vessel gives off the first of the filament vessels. Also accompanying each branchial vessel is one-half of the cavity of the prostomium (Text-fig. 5); it extends round the base of the crown and ends blindly where the branchial vessel enters the most ventral filament. The cavities of the prostomium and peristomium do not communicate with each other. On the left side each sends a blind-ending branch into the base of the peduncle; they accompany the

opercular blood-vessel, which is a branch of the left branchial vessel. The peristomial and prostomial cavities have no connexion with the cavities in the filaments.

McIntosh (1918) noticed cavities in the filaments of *Pomatoceros*, and thought it probable that they communicate with the 'coelomic' space around the branchial vessel, although he was not able to find the communication. He did not describe the derivation of this 'coelomic' space, but from his figures it is clear that he was referring to the anterior part of the prostomial cavity. Thomas (1940) has stated that the 'coelom' of the peristomium 'sends a pair of extensions passing between the dorsal and ventral roots of the oesophageal connectives giving branches into the filaments . . . '. Her figure of a transverse section through one of the filaments (Fig. 8) suggests that she has mistaken as a coelomic channel the space which usually appears in fixed specimens between the wall of the vessel and the mass of coagulated blood lying in its centre. It may be concluded that she has not demonstrated any extension of the peristomial cavity into the filaments. Meyer (1888) thought that the 'secundäre Leibeshöhle des Kopfmundsegmentes' of *Hydroides lunulifera* and *Protula tubularia* is continuous with the channel surrounding the vessel in the centre of each filament. Faulkner (1930) has stated that in *Filograna implexa* the prostomial cavity sends a process on each side into the base of the crown, with branches into each of the filaments.

Each *pinnule* and '*palp*' of *Pomatoceros* contains a large central cavity lined by a thin epithelium lying on the basement membrane of the epidermis. In the frontal part of the lining are situated the longitudinal muscles; fused to the abfrontal lining is the blood-vessel.

The cavities of the pinnules are branches of the central cavities of the *filaments* (Text-fig. 1). Each filament contains four cavities, which extend without interruption along the whole of its length.

(*a*) A central channel surrounding the blood-vessel.

(*b*, *c*) A pair of abfronto-lateral channels situated between the lateral epidermis and the external branchial muscles. These are probably the 'coelomic' cavities of McIntosh (1918).
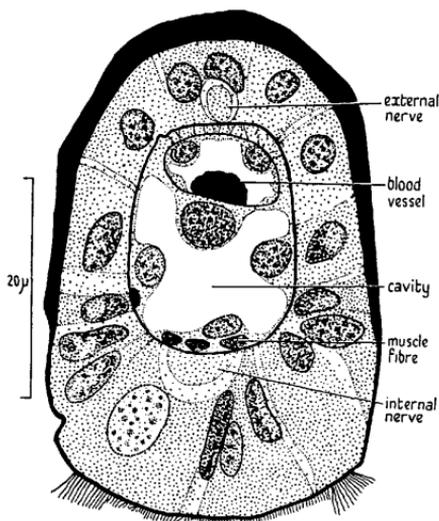
(*d*) A small channel situated on the abfrontal face of the internal branchial nerve, and separated from the central cavity by some of the fibres of the internal branchial muscles and their surrounding connective tissue.

The *operculum* contains no cavities. The first three cavities of the filaments are not represented in the *peduncle*, but the internal peduncular nerve is accompanied by a small channel like that of the internal branchial nerve (Text-fig. 2).

In the following serpulids the pinnule cavity is like that of *Pomatoceros*, but in the filaments there is only a single cavity, which is large and occupies most of the interior: *Serpula* (Text-fig. 3), *Hydroides*, *Vermiliopsis*, *Protula*, and *Spirorbis militaris*. The cavities in the peduncles of the functional and reserve opercula of *Serpula* and *Hydroides* are like filament cavities.

The 'palps'

The so-called 'palps' of *Pomatoceros* are two short processes situated between the dorsal lip and the most dorsal filaments of the two halves of the crown. Studies on the feeding method (Johansson, 1927; Thomas, 1940) have shown that the 'palps' are concerned with the rejection of unwanted particles. Except in a few minor points, the structure of a 'palp' of *Pomatoceros* is identical with that of a pinnule.
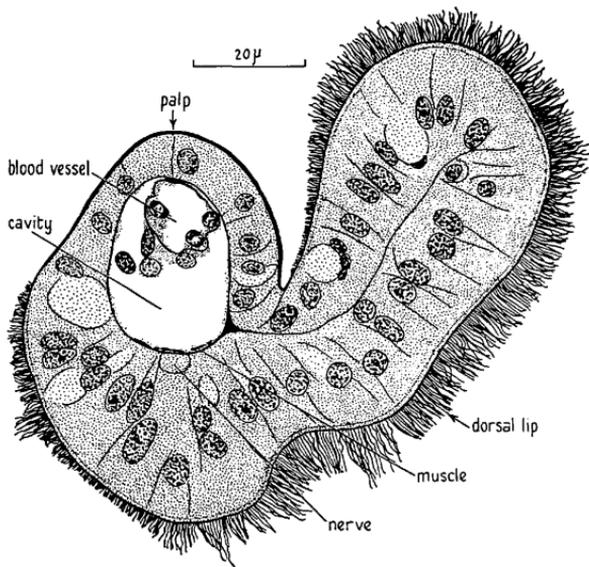

TEXT-FIG. 6. Transverse section through pinnule of *Pomatoceros triqueter*.

At its base the 'palp' is fused both with the adjacent filament and with the dorsal lip. A short distance from the base it becomes detached from the filament, but remains attached to the lip, from which it becomes free only at its tip. The lip consists of two epithelia, whose basement membranes are fused except where blood-vessels and nerves are situated between them. As Thomas has shown, these nerves arise from a branch of the internal branchial nerve of the most dorsal filament of each side. The lip vessels have no connexion with the 'palp' vessels, and are supplied with blood from the circum-oesophageal vessels (Hanson, 1949).

The epidermis of the 'palp' (Text-fig. 7) rests on a basement membrane inside which is the central cavity, lined by a thin epithelium as in a pinnule. The disposition of the muscles and blood-vessel of the 'palp' is the same as in a pinnule. The vessel is a branch of the vessel of the adjacent filament. As Thomas has shown, the internal branchial nerve of this filament gives off a

branch which innervates both the 'palp' and the dorsal lip. In the 'palp' the nerve is situated at the base of the frontal epidermis; it corresponds to the internal pinnule nerve. I have been unable to find an abfrontal nerve in the 'palp', although one is present in the pinnule.

The very close structural resemblance between 'palp' and pinnule suggests that the 'palp' may be a modified pinnule (compare Text-figs. 6 and 7). This

TEXT-FIG. 7. Transverse section through 'palp' and accompanying part of dorsal lip of *Pomatoceros triqueter*.

is supported by the fact that its blood-vessel and nerve are branches of those of the adjacent (most dorsal) filament. Moreover, the arrangement of pinnules at the base of this dorsal filament is atypical. In other filaments the pinnules are arranged in pairs from the base to the tip. In each of the most dorsal filaments there are two unpaired pinnules situated below the most basal paired pinnules, and both arise from the side adjacent to the 'palp'. Segrove (1941) has noticed that, at an early stage in development, the basal pinnule of the most dorsal filament 'is unpaired and arises on the median side of the filament'.

Segrove's account of the early development of the branchial crown, however, does not lend any support to the view that the 'palp' is a modified pinnule. He has found that the crown first appears as six primary branchial processes, three on each side of the head. The most dorsal pair develops into the 'palps',

and the others into filaments, except one on the left side which becomes the operculum and its peduncle. At first, the ciliation of the primary branchial processes is like that of adult pinnules. The 'palps' retain this type of ciliation, do not grow as rapidly as the other processes, and do not develop pinnules. The other processes acquire the ciliation of filaments when their pinnules develop. This account of the external appearance of the developing crown suggests that the 'palps' represent filaments which have retained their juvenile ciliation. However, it is possible that they are precociously developed pinnules belonging to the adjacent filaments. It is clear that information about the internal anatomy of the crown of very young specimens is needed to elucidate the morphological nature of the 'palps'. The development of the 'palps' of the sabellid *Branchiomma* (Wilson, 1936) is similar to that of *Pomatoceros*.

The 'palps' of *Serpula*, *Hydroides*, and *Vermiliopsis* are like pinnules in structure, and their blood-vessels are branches of the vessels supplying the most dorsal filaments in the crown.

Summary

1. This paper records various observations supplementing, and in some cases correcting previous accounts of the internal structure of the branchial crown in *Pomatoceros triqueter*, *Serpula vermicularis*, *Hydroides norvegica*, *Vermiliopsis infundibulum*, *Salmacina incrustans*, *Protula intestinum*, *Spirorbis corrugatus*, and *Spirorbis militaris*.

2. The muscles in the opercular peduncle of *Pomatoceros* are longitudinal.

3. A single layer of small longitudinal muscle-fibres, of unknown function, has been found on the abfrontal face of the internal branchial and internal peduncular nerves of most of these serpulids.

4. External branchial muscles are well developed in *Pomatoceros*, reduced in *Serpula*, *Hydroides*, *Vermiliopsis*, and *Spirorbis militaris*, and apparently absent in *Protula* and *Spirorbis corrugatus*.

5. The pinnules of *Pomatoceros* and *Hydroides*, like filaments and opercular peduncles, have a double innervation.

6. The internal skeleton of the serpulid crown consists of sheets and strands of connective tissue-fibres and, in the opercula, of a cartilage-like tissue with a ground substance giving the staining reactions of collagen. The serpulid branchial skeleton is compared with that of sabellids, and the chemical nature of these skeletons is discussed.

7. Extensions of the prostomial and peristomial cavities accompany the branchial blood-vessels into the base of the crown, but have no connexion with the cavities in the branches of the crown. The arrangement of the latter

is described. The nature of all these cavities, whether coelomic or blastocoelic, is obscure.

8. The 'palps' of *Pomatoceros, Serpula, Hydroides,* and *Vermiliopsis* closely resemble pinnules. The blood-vessel and nerve of the 'palp' of *Pomatoceros* are branches of those in the adjacent filament. It is suggested that the serpulid 'palp' is a modified pinnule.

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