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THE BLOOD VASCULAR SYSTEM OF THE GILLS OF *PHOLAS DACTYLUS* L. (MOLLUSCA, BIVALVIA, EULAMELLIBRANCHIA)

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[Plates 1–5]

CONTENTS

Scanning electron microscopical studies of acrylic corrosion casts of the blood vascular system of the gills of *Pholas dactylus* and of critical-point dried preparations of whole gills, supplemented by histological preparations and observations on whole animals, show that the blood vascular system has two interconnecting pathways, one frontal and one abfrontal, both of which arise and terminate in the primary vessels of the gills.

In the abfrontal pathway both afferent and efferent primary vessels give rise to secondary vessels at right angles to them. There is no regular alternation of afferent and efferent secondary vessels and both occur in the ascending and descending lamellae. Tertiary vessels, circumferential to the interlamellar spaces, link the secondary vessels. In the filamentary frontal pathway blood is conveyed to or from the primary vessels via perforations in their ventral walls which open into labyrinthic blood spaces; the filamentary frontal channels of descending lamellae empty into these spaces whereas those of ascending lamellae are filled from the spaces.

The two systems are joined by many short, D-shaped spaces within the filaments, which connect the filamentary frontal channels to the circumferential, tertiary vessels.

Movement of blood in the gills is more oscillatory than unidirectional. Factors that might affect the flow of blood in the two systems and in different parts of the gills are considered.

1. Introduction

During the course of work by one of us (Thorne 1983; Knight (= Thorne) 1984) on the uptake of dissolved organic matter by the gills of *Pholas dactylus* L., the common piddock, the question arose as to the precise nature of the blood vascular system within the gills. Although the gills of lamellibranch bivalves have been studied over many decades (Kellogg 1892; Pelseneer 1906; Orton 1913; Kellogg 1915; Atkins 1936, 1937*a*, *b*, 1938*a*, *b*; Yonge 1947; Franc 1960; Owen 1978), no definitive statements are made about the circulation of blood in them. Other authors, who included *P. dactylus* in their studies (Foli 1791; Deshayes 1844–48; Posner 1875; Ridewood 1903; Purchon 1955), did not give a sufficiently detailed account of its gills to form the basis of an understanding of the circulation of blood within them.

Light microscopy and scanning electron microscopy have been used to study various preparations of the gills, both living and dead. Acrylic corrosion casts of the blood vascular system have been especially useful in elucidating details. The ease of access to the posterior parts of the gills of *P. dactylus* makes this animal particularly suited to the type of investigation reported here, but there is no reason to suppose that our findings do not apply to the structurally similar anterior parts of the gills nor, indeed, to the gills of other eulamellibranchs.

We present here an account of the blood vascular system of the gills of *Pholas dactylus* and consider certain factors that might affect the passage and direction of flow of blood within various parts of the gills.

2. Materials and methods

2.1. *Source and maintenance of animals*

Specimens of *Pholas dactylus* were obtained from burrows close to low water spring tides and were kept in frequently changed seawater collected from beyond the breakwater at Plymouth, Devon.

2.2. *Preparation for injection*

Animals were relaxed in 0.37 M $MgCl_2$ and removed from their shells. A mid-ventral incision was made through the wall of the inhalant siphon from its posterior opening to the foot, and a corresponding mid-dorsal incision through the wall of the exhalant siphon from its posterior opening to a point just posterior to the anal papilla. The cut edges were pinned to a frame immersed in seawater so that the gills were freely suspended and could be viewed by both reflected and transmitted light.

2.3. *Injections*

Injections were made with 2 ml plastics syringes (polystyrene for the coloured aqueous liquids and polyethene for the methylmethacrylate). In place of a needle a slightly tapering glass tube (cut from the end of a Pasteur pipette) was passed from the inside of the barrel of the syringe through the outlet hole in which it became wedged. A 90° bend was made in the emergent part of the tube, which was then pulled in a flame into a fine tube and cut at its narrowest point (o.d. 0.1–0.2 mm) to form the injection needle.

Aqueous injections were 1% (by mass) solutions in seawater of the food colours, Certicol chocolate brown HTS and FD & C blue (Williams Ltd, Hounslow, Middlesex, U.K.).

2.4. *Production of acrylic casts*

Polymethylmethacrylate casts were made by a modification of the method devised by Lametschwandtner *et al.* (1976). The methylmethacrylate was coloured with 0.1 % (by mass) Foscolor Fluorescent Red Drycolor (Foscolor Ltd, Wigan, U.K.) by warming in a sealed container. To 4 ml of this solution was added 80 mg dibenzoyl peroxide (catalyst), which was dissolved by warming; the solution was then heated at 82–86 °C for 5 min. To the cooled solution was added 0.09 ml *N*,*N*-dimethylaniline (accelerator) and 0.4 ml di-*n*-butyl phthalate (plasticizer).

The partly polymerized mixture was injected into one or more of the primary vessels of the gills. Polymerization of the injected material was completed while the whole preparation remained immersed in seawater at about 40 °C for several hours, following which the animal was removed from the frame and the tissues dissolved in warm 15 % (by mass) aqueous NaOH. The corrosion cast was washed once in the caustic solution and several times in water before being dried in air. Some of the casts were dissected to reveal details that were not immediately apparent.

2.5. *Histological techniques*

To relate the structures seen in the casts with their positions in the whole gill one of the animals in which only part of a gill had been injected was treated as follows. The methylmethacrylate was allowed to polymerize completely, after which the gills were fixed in an aqueous solution of glutaraldehyde made by adding 20 ml of a 25 % (by mass) solution of glutaraldehyde to 80 ml of Sørensen's phosphate–sucrose buffer, pH 7.5, 695 mosmol l^{-1}. Pieces of gill were removed and embedded in Spurr resin. During this process the treatment with propylene oxide dissolved the polymethylmethacrylate, leaving voids in the tissues that later became filled with the resin. Thick sections (1–2 μm) of both injected and uninjected parts of the gill were stained in a solution containing 1g toluidine blue and 1g borax in 100 ml water, and mounted in 50 % (by volume) aqueous glycerol.

Some material, fixed as above, was embedded in wax, sectioned at 10 μm and stained with Mallory's trichrome stain.

2.6. *Scanning electron microscopy*

For the examination of surface structures gills were fixed in glutaraldehyde and Sørensen's buffer and post-fixed overnight in 1 % (by mass) aqueous osmium tetroxide at 4 °C. They were dehydrated in ethanol, transferred to acetone and dried in a critical-point drier.

Both corrosion casts and critical-point dried preparations were sputter-coated with 12 nm of gold and examined by using a Jeol T20 scanning electron microscope.

2.7. *Gross morphology*

The gross morphology was studied on living gills and those fixed (while attached to the animal) in a solution made from 100 ml of 25 % (by mass) aqueous glutaraldehyde and 900 ml seawater. Sections of the gills about 1 mm thick were cut by hand with a razor blade and examined under a stereomicroscope.

3. Results

3.1. *The validity of corrosion casts*

The pattern of interconnecting blood channels, spaces and vessels revealed by the casts is identical in the 20 casts made from different animals. That the polymer penetrated into parts of the gills normally filled by blood is confirmed by a comparison of thick resin sections of filaments that had been penetrated by the polymer and those that had not (figures 24 and 25*). The sections show haemocytes in the uninjected filaments in the places occupied by polymethylmethacrylate in the injected filaments.

3.2. *Gross anatomy of the gills*

Pholas dactylus differs from most other bivalves in that its gills extend posteriorly towards the siphonal apertures (figure 1). Details of the structure of the posterior parts of the gills are shown in figure 2.

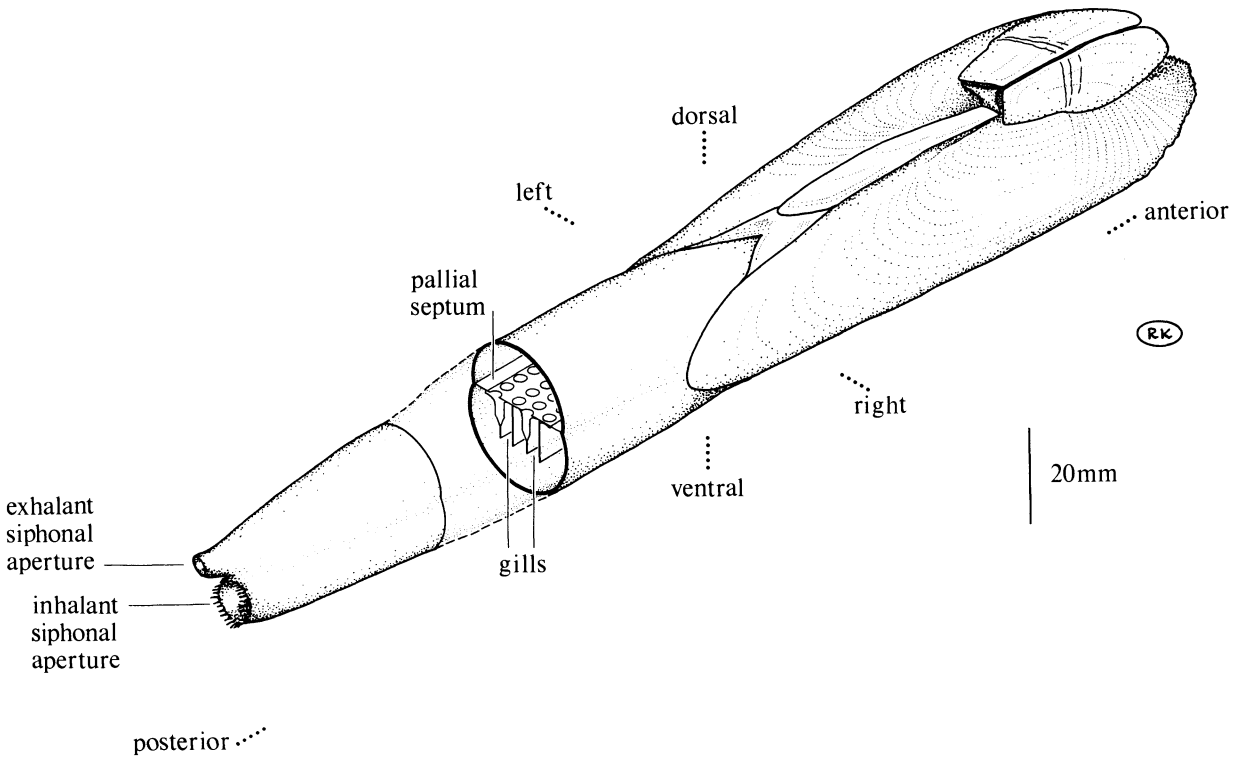


FIGURE 1. Diagrammatic isometric projection of *Pholas dactylus* to show the position of the gills in relation to the siphons in an extended animal.

The nomenclature used in this paper for gross features of the gill is also shown in figure 2. We reintroduce from Poli (1791) the word 'sacculus' equivalent to the vernacular 'water tube' and use 'demisacculus' for the distal regions of the sacculi. We use the term 'shoulder' to refer to the particular arrangement of an ascending lamella of an outer demibranch of a gill of *P. dactylus* close to its junction with the suspensory membrane.

* Figures 3–5 appear on plate 1, figures 6–7 on plate 2, figures 10–14 on plate 3, figures 17–21 on plate 4 and figures 22–25 on plate 5.

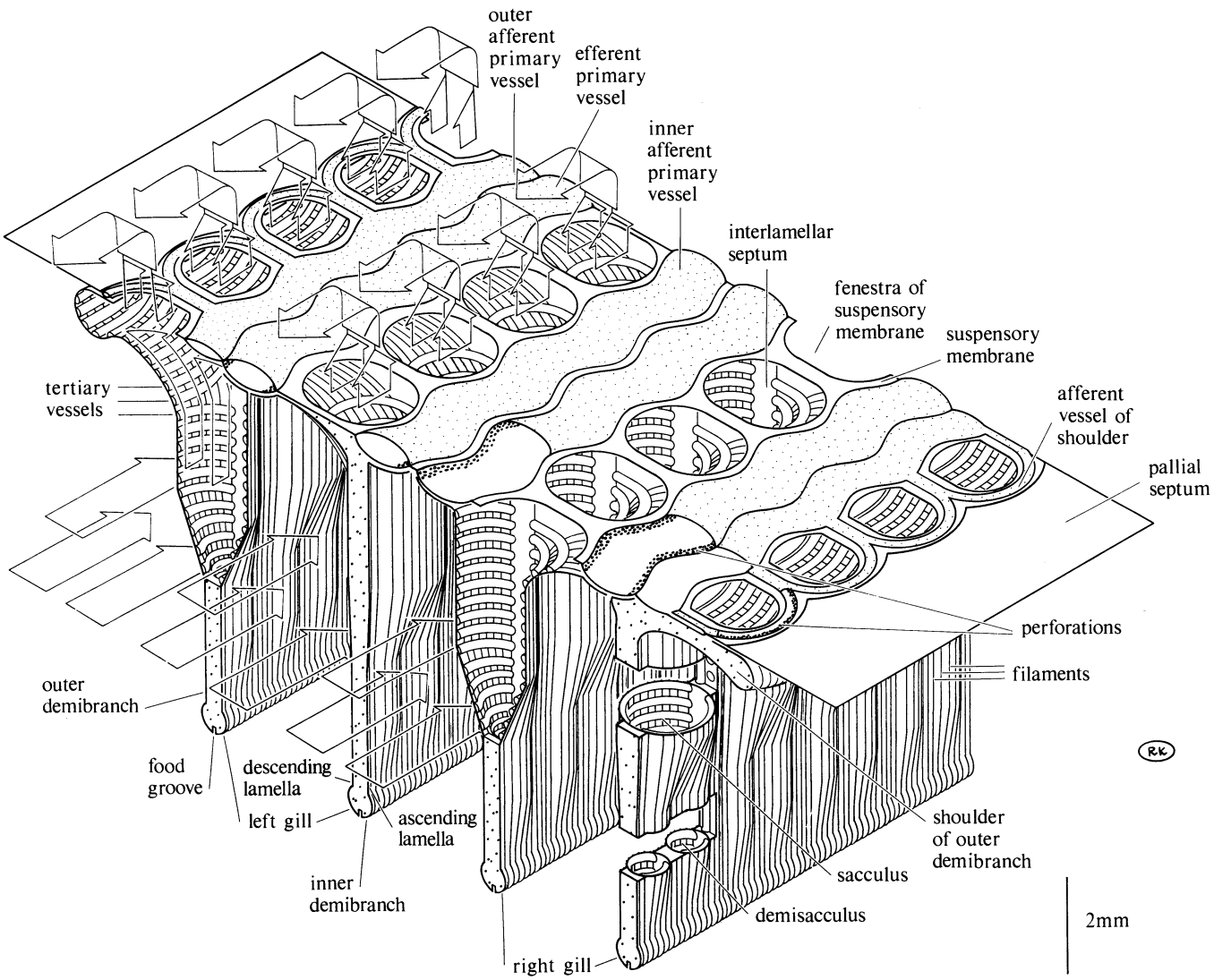


FIGURE 2. Diagrammatic isometric projection of a section of the gills (see figure 1 for location). The open arrows show the path of water from the inhalant siphon passing between the demibranchs and, after entering the sacculi through the ostia of the lamellae, issuing from the fenestrae of the suspensory membrane and being directed towards the exhalant siphon.

3.3. *Primary vessels*

Each of the two gills of *P. dactylus* has three primary blood vessels, two afferent and one efferent (figure 2). The vessels that deliver blood to the inner demibranchs of the right and left gills lie, in the posterior part of the gills, close to each other between the gills and drain the anterior visceral sinus. In the posterior parts of the gills anastomoses occur between the right and left vessels. The efferent primary vessel of each gill lies proximal to the junction between inner and outer demibranchs, while adjacent and distal to it lies the outer afferent primary vessel, which drains the posterior visceral sinus.

Also having the status of a primary vessel is the afferent vessel of the shoulder (figures 2, 6, 7 and 9), which is an extension of the outer afferent primary vessel to which it is joined between each pair of adjacent fenestrae.

Perforations are present in the ventral walls of certain primary vessels (figures 2, 3, 7, 9 and 19) immediately dorsal to the proximal terminations of filaments. Thus the ventral wall of the inner afferent primary vessel is perforated medially corresponding to the termination of the filaments of the ascending lamella of the inner demibranch. The ventral wall of the efferent primary vessel is perforated both medially and laterally (figures 2 and 7) corresponding to the terminations of the filaments of the descending lamellae of, respectively, the inner and outer demibranchs. The ventral wall of the outer afferent primary vessel is imperforate (figure 7) and no filaments terminate immediately ventral to this vessel, but the ventral wall of the afferent vessel of the shoulder is perforated corresponding to the terminations of the filaments on it (figures 2, 9 and 19). The perforations allow the passage of blood between the primary vessels and the filamentary frontal channels via the labyrinthic blood spaces (see § 3.7 below).

3.4. *Secondary vessels*

Secondary vessels are joined at right angles and in various planes to the primary vessels: some of the secondary vessels are in the plane of the suspensory membrane of the gill, whereas others travel at right angles to the plane of the suspensory membrane in the lamellae or in the interlamellar septa. All four lamellae of a gill are associated with secondary vessels deriving both from afferent and efferent primary vessels.

3.5. *Tertiary vessels*

Adjacent secondary vessels are united at regular and frequent intervals throughout their length by a system of tertiary vessels (figures 2, 6 and 8) that run at right angles to them on the inner surfaces of the sacculi. In figure 23 one tertiary vessel is shown bridging five filaments. Details of the connections between the tertiary vessels and the blood channels of the filaments are shown in figure 15 and explained below.

3.6. *Blood channels in the gill filaments*

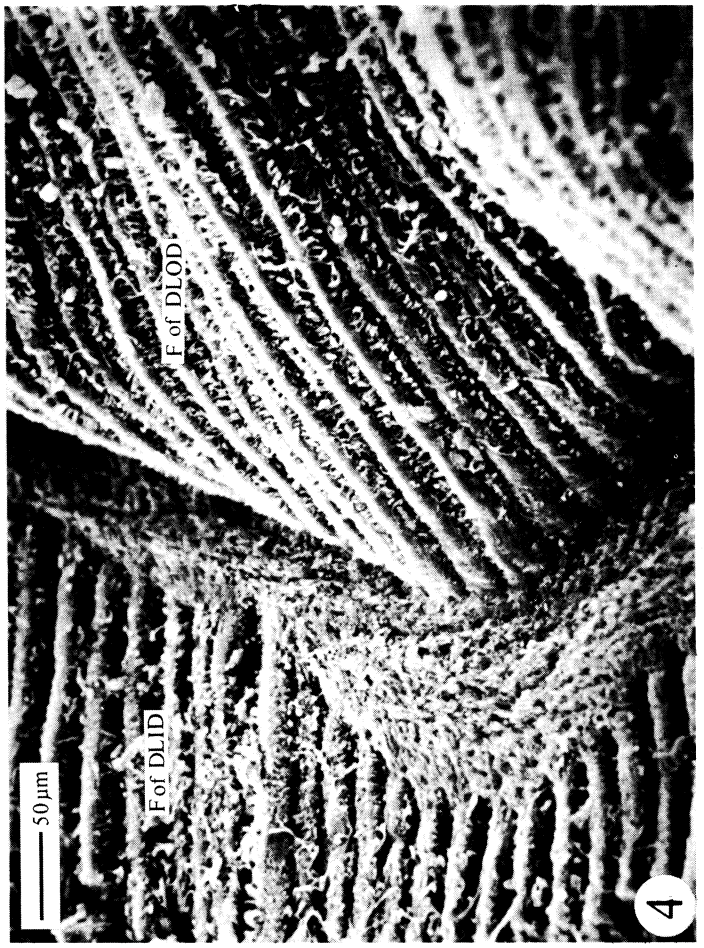
Each filament contains two types of blood channel, filamentary frontal channels and D-shaped channels (dees). The former are as long as the filaments. The straight part of each dee bridges the space between adjacent tertiary vessels, and the convex side is joined to the filamentary frontal channel (figures 11, 13, 14, 15 and 22). Each pair of adjacent tertiary vessels is joined thus by as many filamentary dees as there are filaments crossing them and, through the intermediacy of the dees, the tertiary vessels are joined to the filamentary frontal channels.

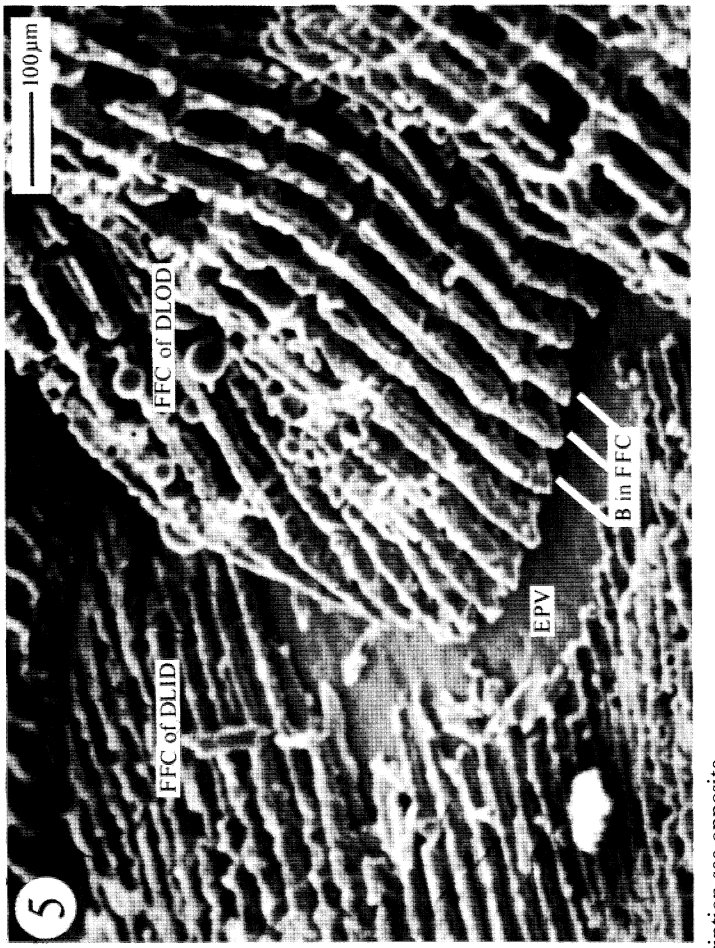
Description of plate 1

Figure 3. SEM. Critical-point dried preparation. Dorsal aspect of parts of the inner demibranchs of both gills. Most of the dorsal wall of the left inner afferent primary vessel has been removed, as have parts of both walls of the right inner afferent primary vessel.

Figure 4. SEM. Critical-point dried preparation. Ventral aspect of the frontal surfaces of the descending lamellae of the inner and outer demibranchs where the filaments terminate on the ventral surface of the efferent primary vessel.

Figure 5. SEM. Corrosion cast corresponding to figure 4.





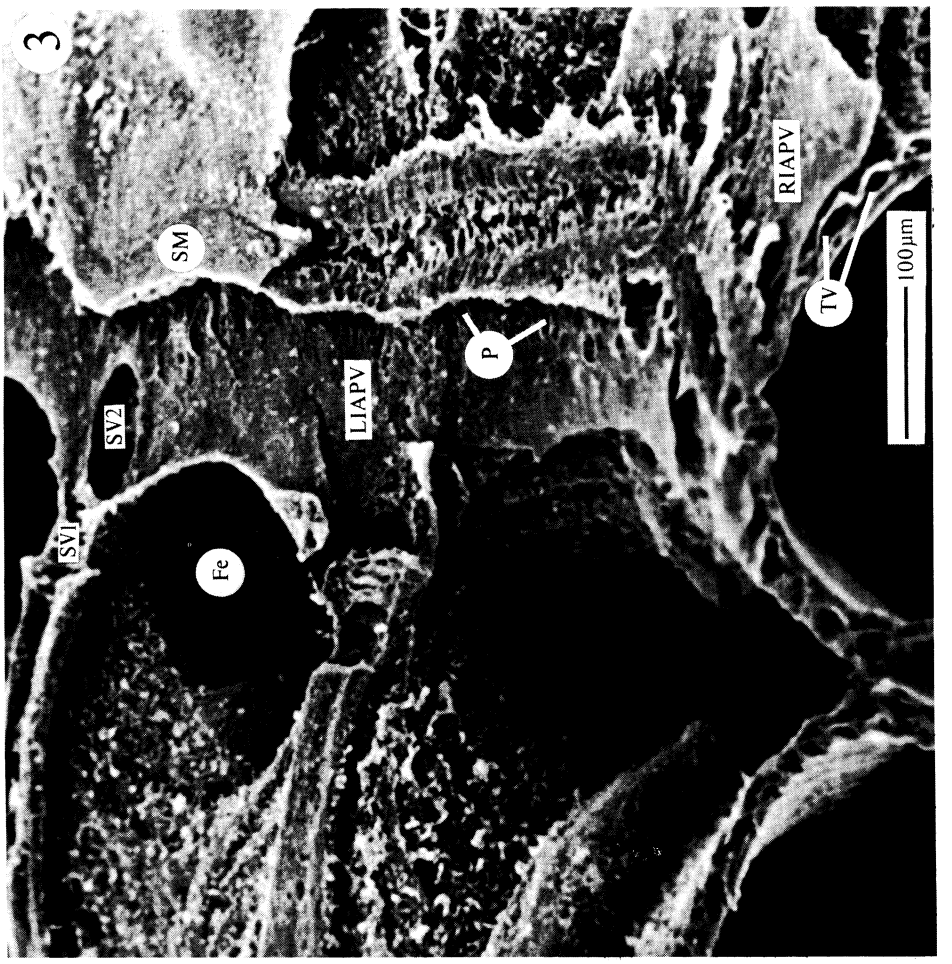


FIGURE 3–5. For description see opposite.

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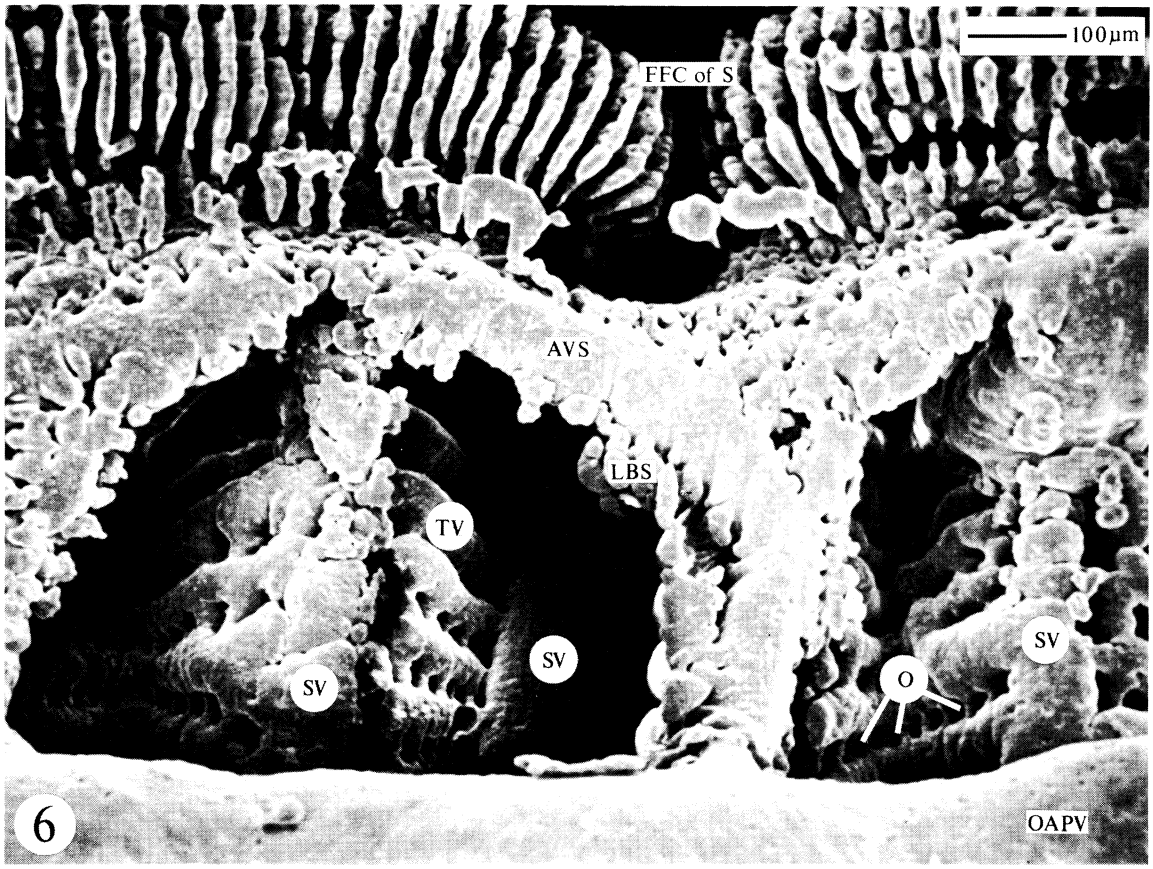
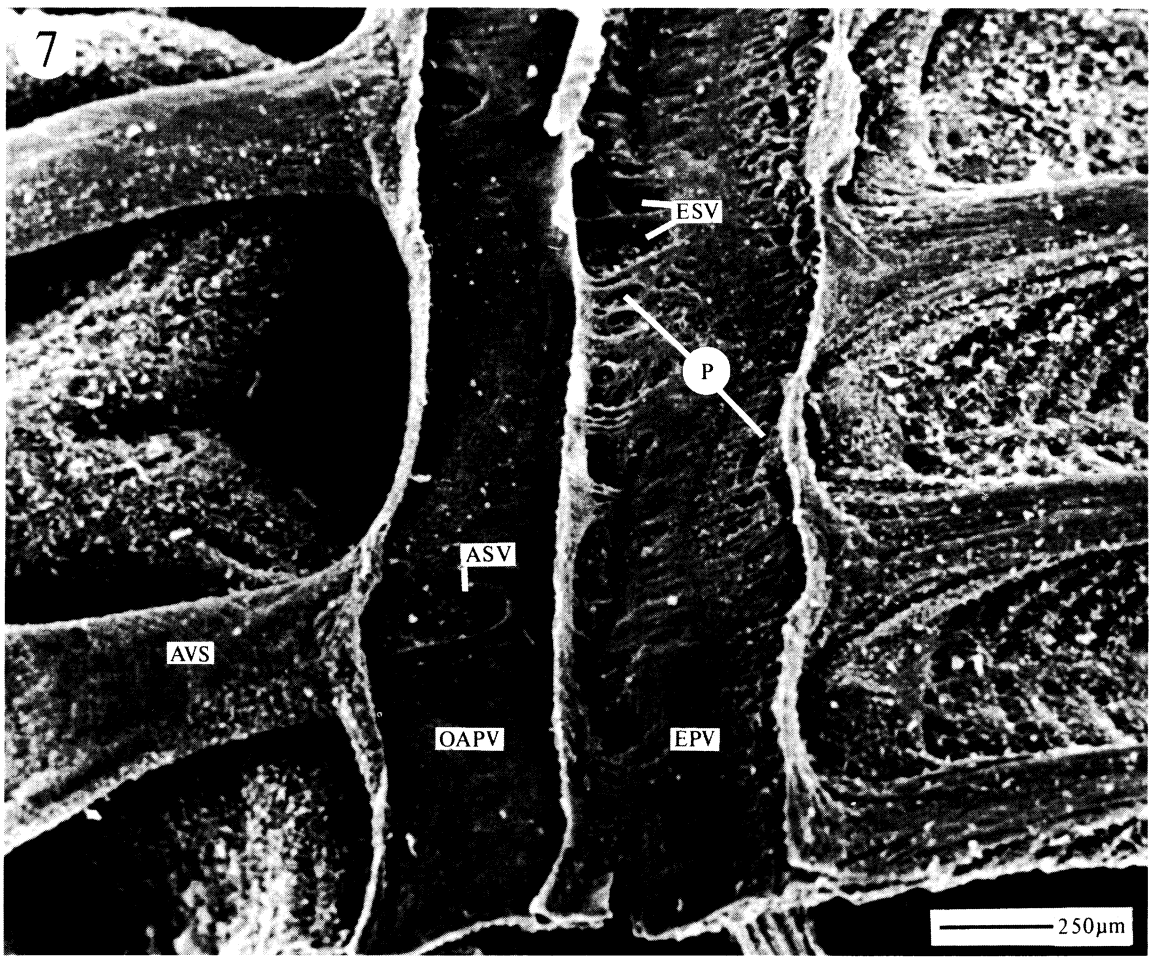


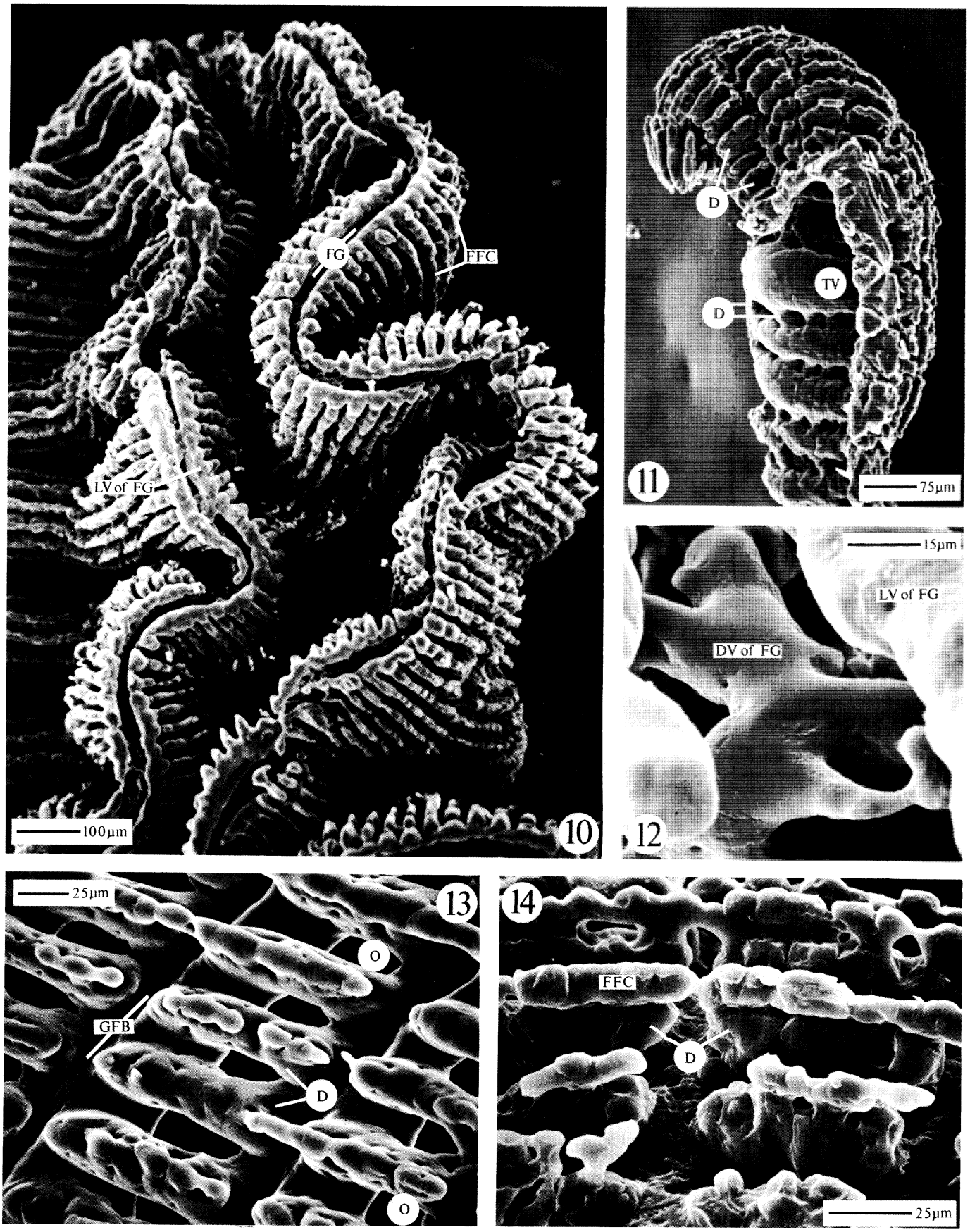


FIGURES 6 AND 7. For description see opposite.

Description of plate 2

Figure 6. SEM. Corrosion cast. Both the frontal and abfrontal aspects of the shoulder of the outer demibranch are shown. Two branches that arise from the outer afferent primary vessel and encircle the outer fenestrae are seen with their associated blood spaces. The way in which the sacculus of the shoulder is partly divided by a crest of the lamella on which is positioned a secondary vessel is seen through both fenestrae. Towards the centre of the picture is shown another secondary vessel running in the plane of the lamella. The filamentary frontal channels of the shoulder are seen ending close to the blood spaces from which they are filled.

Figure 7. SEM. Critical-point dried preparation. Dorsal view of the junction between the two demibranchs of a gill. The dorsal walls of the two primary vessels have been removed. The outer afferent primary vessel is seen making two connections to afferent vessels of the shoulder (loop vessels), which have the status of primary vessels. Three secondary vessels in the plane of the suspensory membrane join the efferent primary vessel. The openings into this vessel of two secondary vessels from the lateral demibranch are also shown.



FIGURES 10–14. For description see opposite.

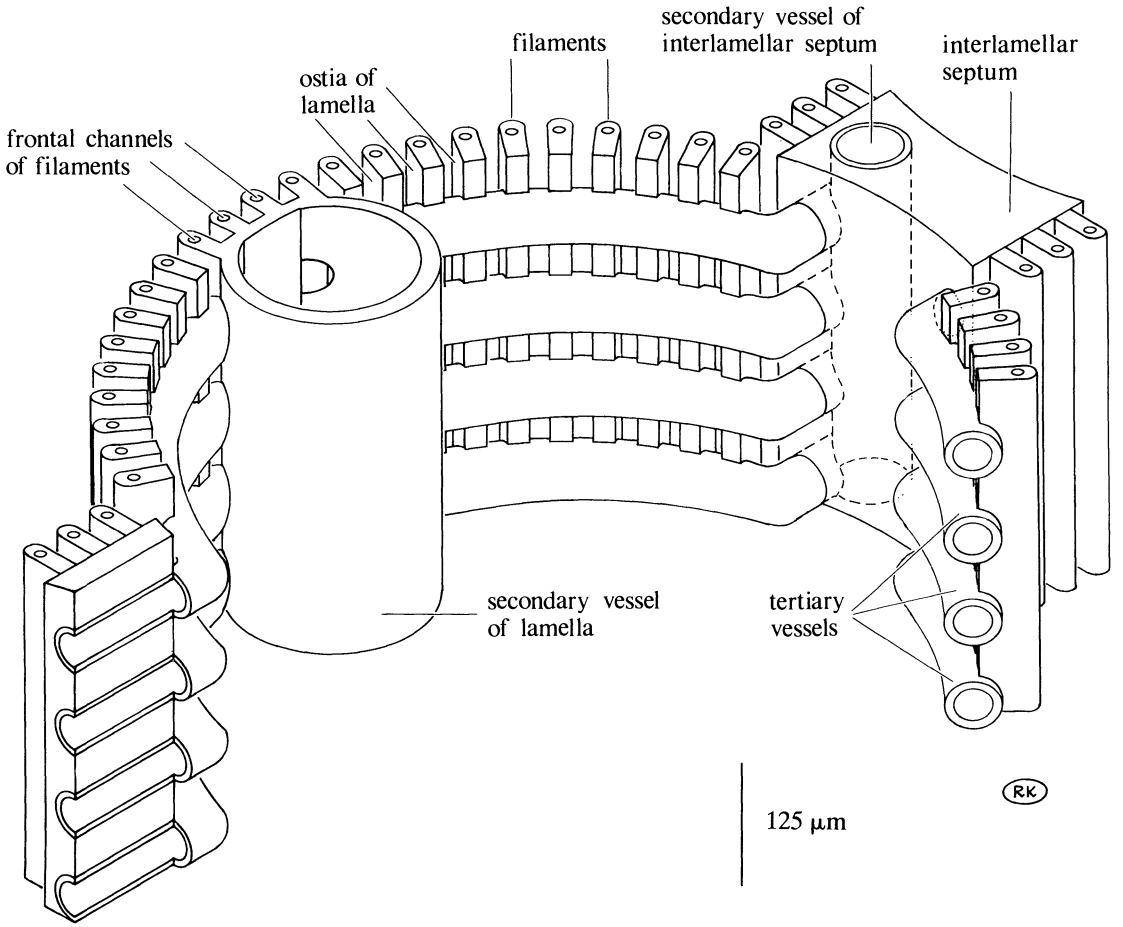


FIGURE 8. Diagrammatic isometric projection of part of one sacculus of a demibranch.

The filamentary frontal channels extend from the region of the primary vessels to the food grooves of the demibranch (figures 2, 5, 9 and 10). On each side of a food groove the channels terminate in a vessel that runs the length of the food groove (figures 9 and 10). Immediately dorsal to the food groove is situated a third longitudinal, and much less regular, channel, which makes multiple connections with the two lateral longitudinal channels (figure 12).

DESCRIPTION OF PLATE 3

FIGURE 10. SEM. Corrosion cast. Ventral aspect of two adjacent demibranchs showing how the filamentary frontal channels end in the vessels lateral to the food groove. In places the highly irregular vessel running dorsal to the food groove can be seen.

FIGURE 11. SEM. Corrosion cast. Part of the shoulder viewed along an antero-posterior axis. The abfrontal surface shows tertiary vessels joined by the straight side of the dees. The frontal surface (above and to the right) shows the curved sides of the dees topped by the often incomplete filamentary frontal channels.

FIGURE 12. SEM. Corrosion cast. Detail of the highly irregular dorsal vessel of the food groove flanked by the lateral vessels of the food groove, to which it makes multiple connections.

FIGURE 13. SEM. Corrosion cast. Frontal aspect of a lamella showing two tertiary vessels. Very prominent are the grooves that are occupied in life by the fibrous bands of the tertiary vessels. The filamentary frontal channels have not been completely filled with polymer.

FIGURE 14. SEM. Corrosion cast. An oblique view of the frontal aspect of a lamella showing the somewhat irregular nature of the lumen of the dees and the filamentary frontal channels.

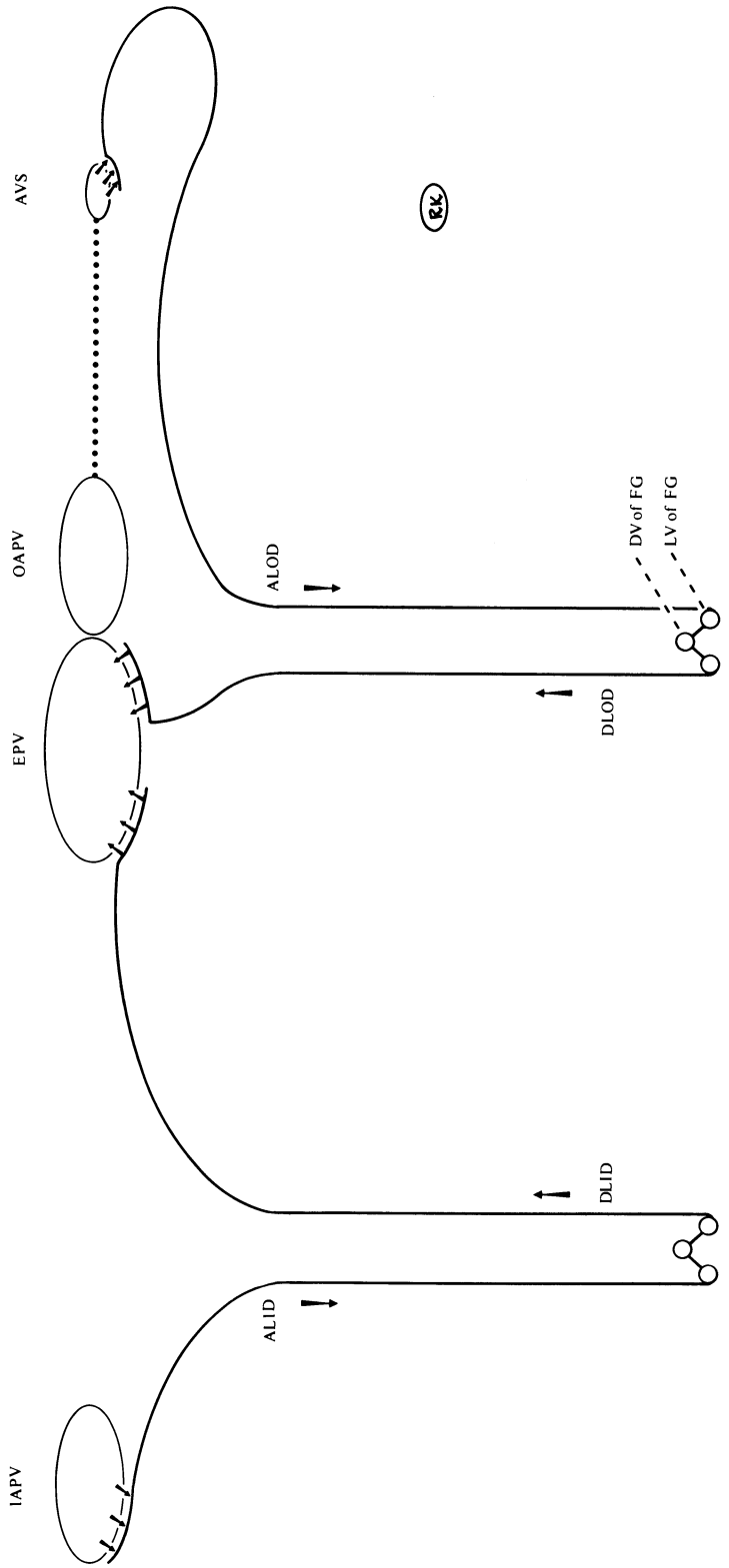


FIGURE 9. A diagrammatic section of a gill showing the path of blood (arrows) between afferent and efferent primary vessels in the filamentary frontal pathway. The small arrows represent the passage of blood through the perforations in the ventral walls of the vessels. The dotted line represents the path in the afferent vessel of the shoulder, which is not in the plane of the section. Note that the net flow of blood is descending in the ascending lamella and ascending in the descending lamella.

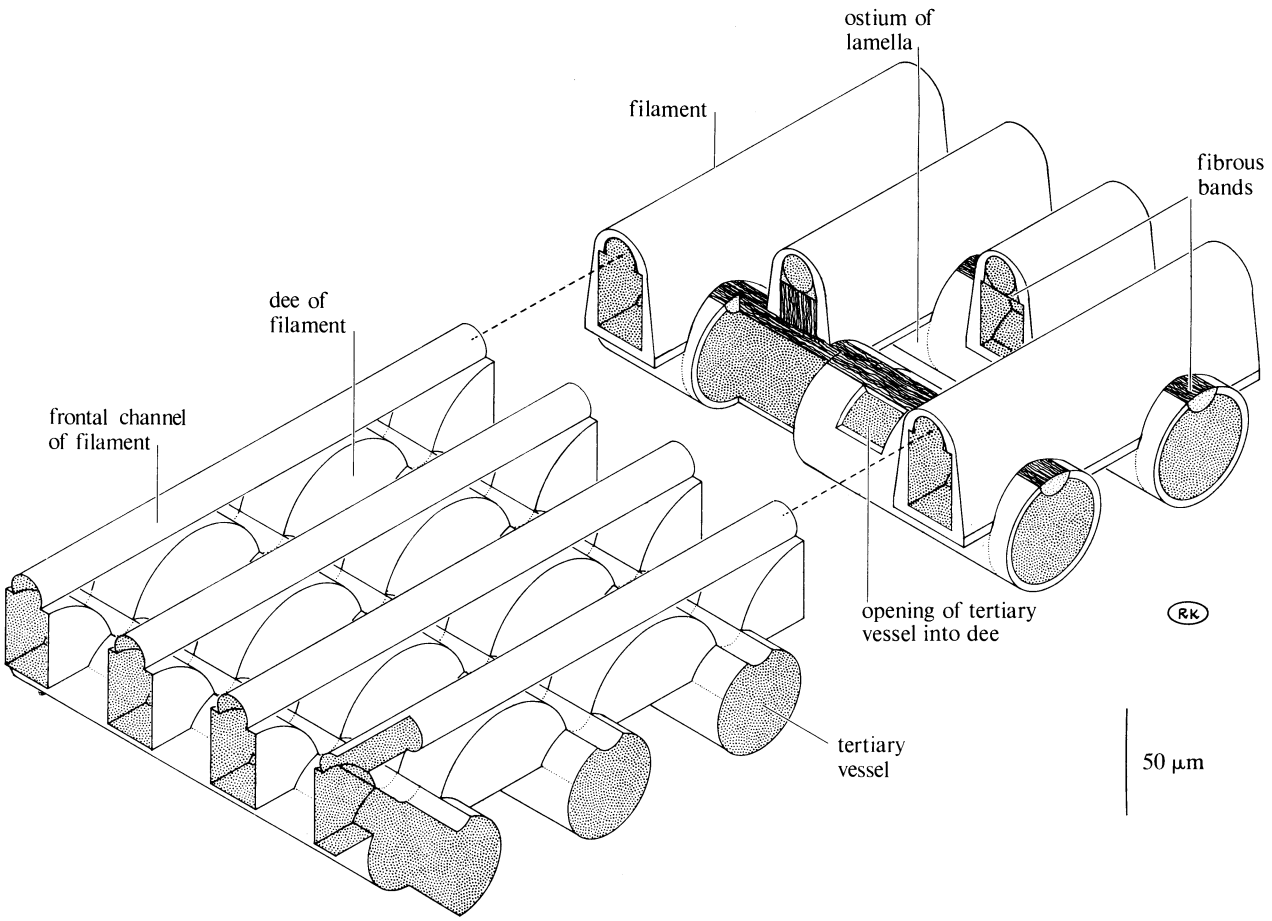


FIGURE 15. Diagrammatic isometric projection of (left) a corrosion cast of part of a lamella and (right) the preparation before corrosion.

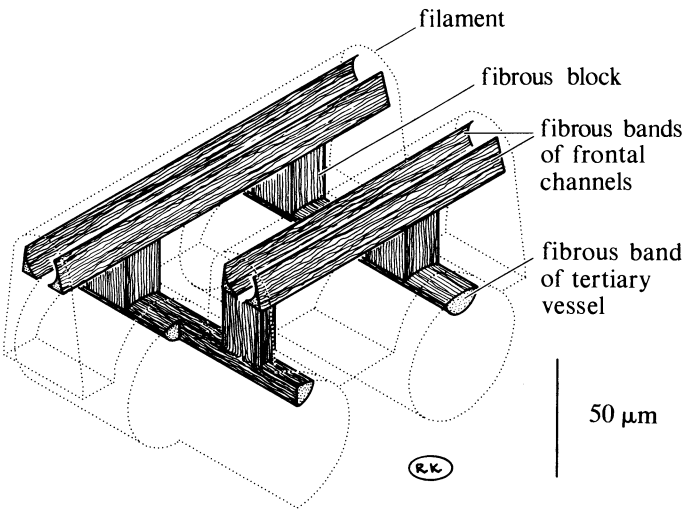


FIGURE 16. Diagrammatic isometric projection of part of a lamella to show the disposition of the fibrous skeleton in relation to the components of the lamella.

3.7. *Blind tubes*

At its proximal end each filament of the gill lies close to and approximately parallel to the suspensory membrane (figure 2) and in this region it is split longitudinally through the frontal channel into two halves in a plane at right angles to the frontal surface (figure 26). Adjacent halves of adjacent filaments then unite so as to enclose between them a cylindrical space continuous with the seawater; the tube formed in this way is short and is sealed at its free end (figures 17–21 and 26). The regions dorsal and ventral to the split filaments are covered with the labyrinthic blood spaces into which the filamentary frontal channels empty. Thus the blood is separated from the seawater dorsally and ventrally by the tissue of the labyrinthic blood spaces and laterally by the blind tubes that project into these spaces.

3.8. *Labyrinthic blood spaces*

In addition to vessels with a discrete wall, and blood channels between tissues (filamentary frontal channels and dees), there is a third type of tissue in the gills through which blood passes. This consists of clusters of labyrinthic spaces which together have definite shape and distribution. Such blood spaces are associated with the inner afferent primary vessels, the efferent primary vessels and the afferent vessels of the shoulder (figures 6 and 20). They are in each case at the proximal termination of the filamentary frontal channels.

There are no labyrinthic blood spaces closely associated with the outer afferent primary vessels.

3.9. *The two circulatory systems*

There are two systems for the circulation of blood between afferent and efferent primary vessels in the gills of *P. dactylus*: the filamentary frontal system (see figure 9 for route) and the abfrontal system in which blood travels in the secondary and tertiary vessels. These two circulations are not independent, in so far as blood may proceed partly by one and partly by the other route. The filamentary dees allow the passage of blood from one system to the other as well as between adjacent tertiary vessels.

Description of plate 4

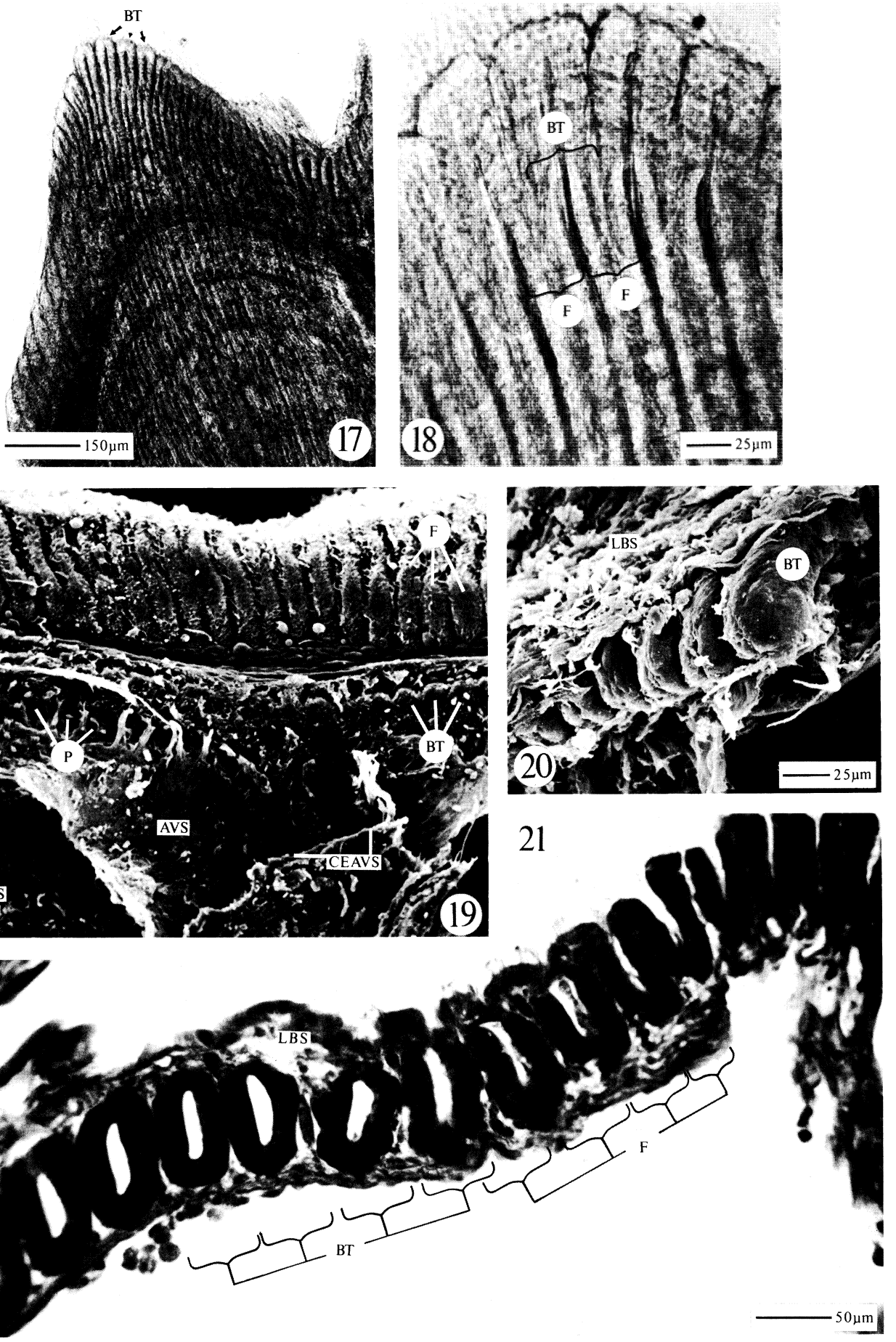
Figure 17. LM. Frontal aspect of a proximal portion of the ascending lamella of an inner demibranch of a dissected, living gill. Three blind tubes formed between adjacent filaments are indicated. The sinusoidal shape of the proximal edge of the lamella conforms to the undulations of the primary vessels.

Figure 18. LM. Detail of a similar preparation to that in figure 17 showing how adjacent halves of adjacent filaments unite to form blind tubes. The braces define the limits of two adjacent filaments and the blind tube formed from them.

Figure 19. SEM. Critical-point dried preparation. Dorsal aspect of part of the shoulder of an outer demibranch. The dorsal surface of the afferent vessel of the shoulder has been largely removed to reveal the perforations in its ventral wall in close proximity to the blind tubes.

Figure 20. SEM. Critical-point dried preparation. A row of blind tubes revealed by the removal of some of the associated labyrinthic blood spaces.

Figure 21. LM. A slightly oblique transverse section (Mallory's trichrome stain) through the proximal portion of a lamella in which the formation of the blind tubes from adjacent halves of adjacent filaments can be traced. Seawater, which was on the outside of the filaments to the top right of the picture, is within the blind tubes on the left. Blood, which was in the frontal channels of the filaments on the right of the picture, is released into the labyrinthic blood spaces on the left.



FIGURES 17–21. For description see opposite.

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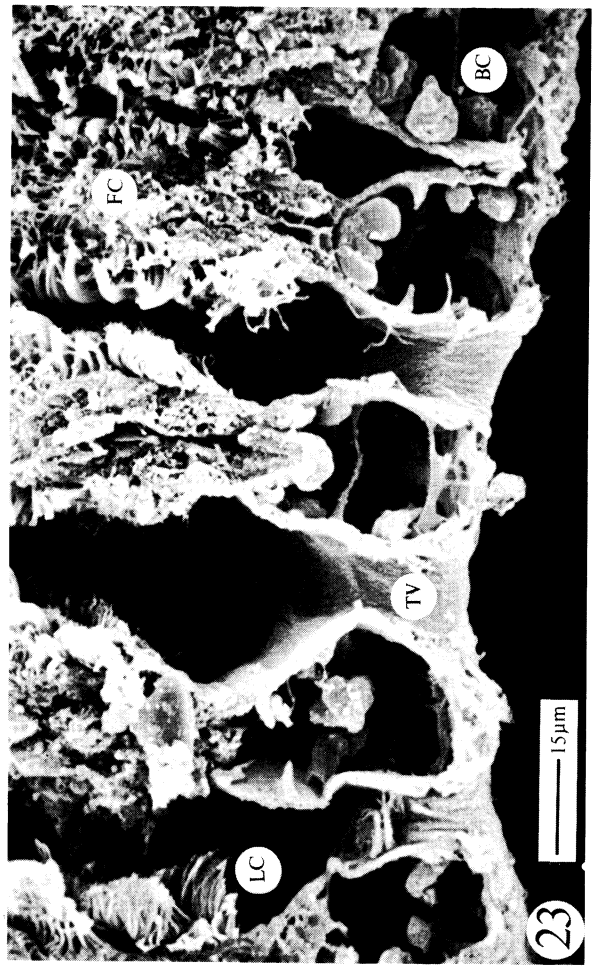

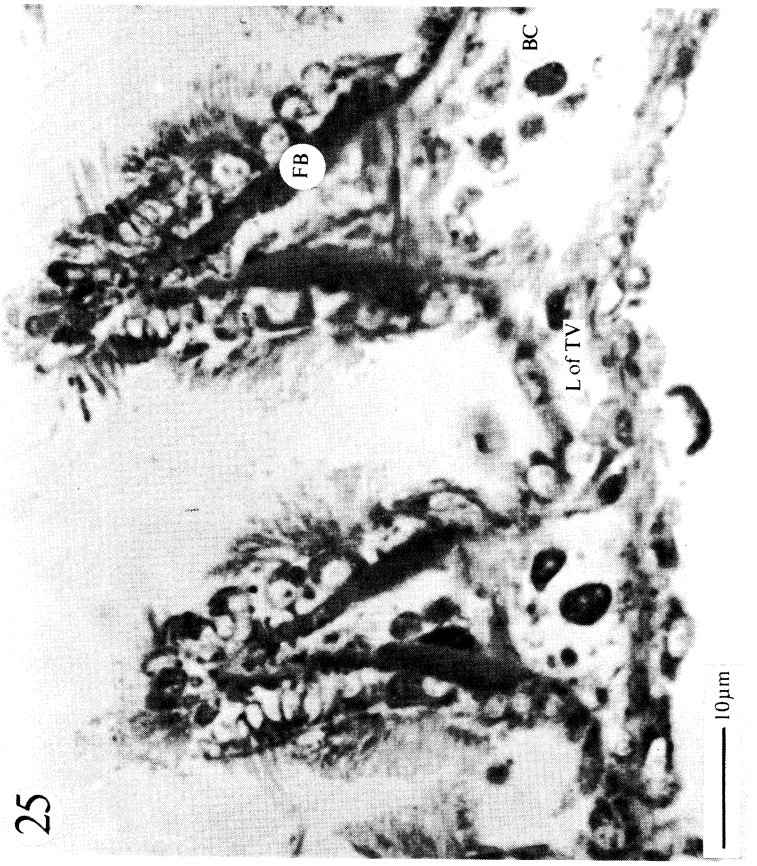

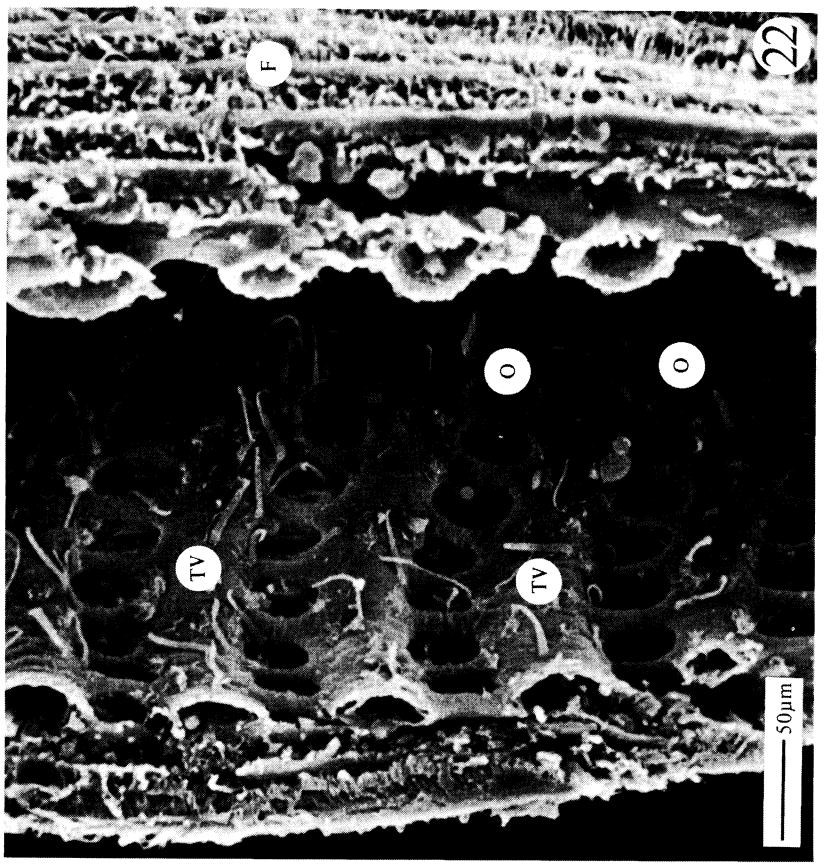

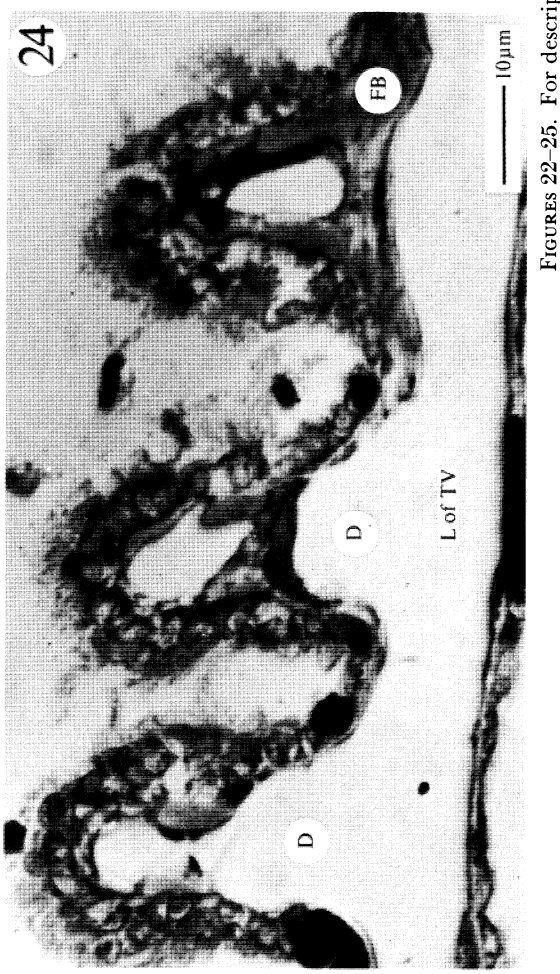

FIGURES 22–25. For description see opposite.

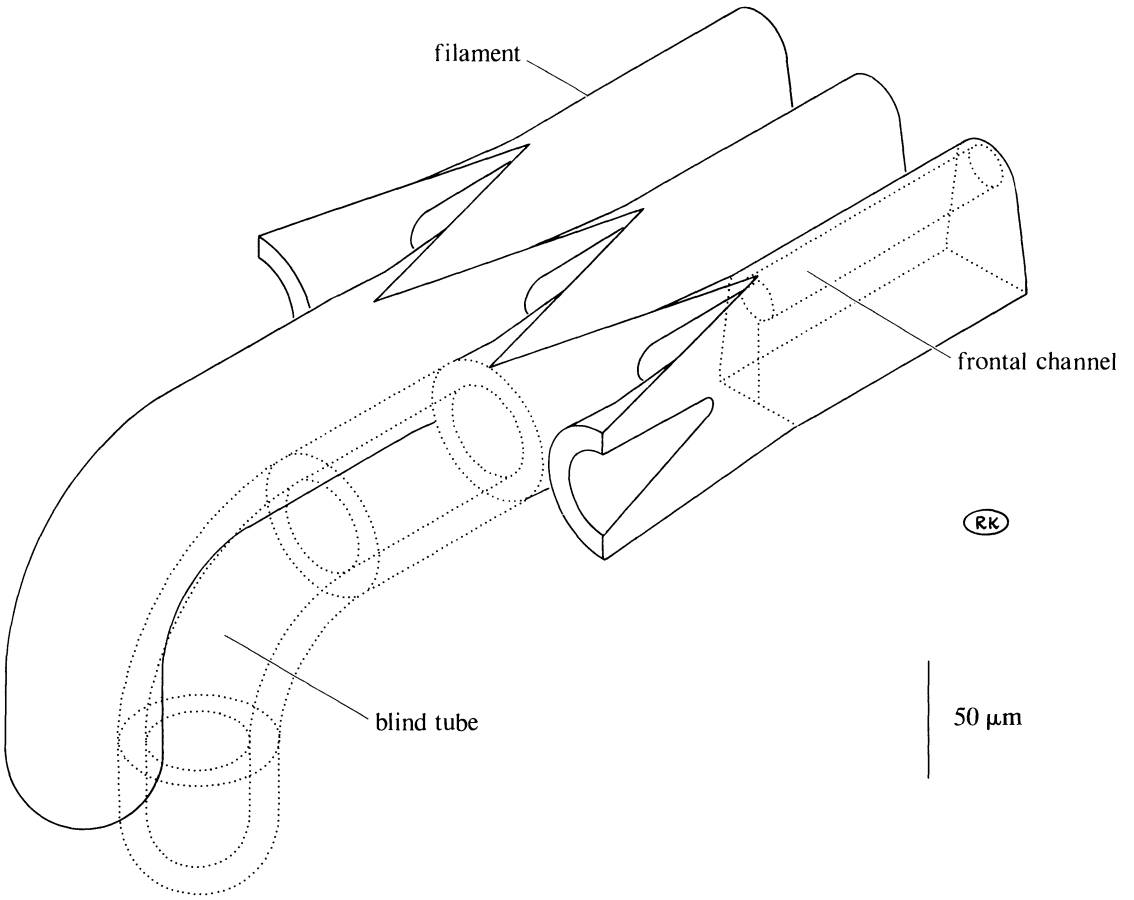

FIGURE 26. Diagrammatic isometric projection of the proximal end of three filaments to show the formation of blind tubes between adjacent halves of adjacent filaments. Not shown in this diagram are the labyrinthic blood spaces that cover both sides of the blind tubes and the split parts of the filaments. Note that this figure represents the termination of the filaments of the two inner demibranchs. The course of the filaments of the descending lamellae of the outer demibranchs is turned through 180° close to the suspensory membrane (see also figures 2, 5 and 9) and the blind tubes formed at the proximal ends of these filaments bend towards, and not away from, the frontal surface of the filaments.

DESCRIPTION OF PLATE 5

FIGURE 22. SEM. Critical-point dried preparation. A demibranch dissected to show both frontal and abfrontal aspects.

FIGURE 23. SEM. Critical-point dried preparation. A section at right angles to the longitudinal axis of five filaments for comparison with figures 24 and 25.

FIGURE 24. LM. Thick resin section stained with toluidine blue (see also figure 25). Part of a gill that contained polymerized methylmethacrylate. A tertiary vessel has been sectioned longitudinally and slightly obliquely and the space occupied by the polymer in each of three filaments is shown. Because the section is slightly oblique each filament is different. The filament on the right shows the filamentary frontal vessels only as the section here passes through the fibrous bands of the tertiary vessel; the centre filament shows a frontal channel and part of a dee; the filament on the left shows the lumen of a frontal channel continuous with that of a dee.

FIGURE 25. LM. Thick resin section stained with toluidine blue. A part of the same gill as in figure 24 into which the injected monomer did not penetrate, showing the presence of blood cells in regions that might otherwise have been filled with polymer. The appearance of the filaments differs from that of the filaments in figure 24 as the section is again oblique but in a different plane.

3.10. *Fibrous skeleton of lamellae of demibranchs*

Successive dees on the long axis of a filament do not touch each other but are separated by a band of fibrous connective tissue that follows the course of each tertiary vessel on the side of it in contact with the filaments (figures 13 and 15). This band is the fibrous part of the interfilamentary tissue bridge characteristic of eulamellibranchs. The filamentary frontal channels (which are not uncommonly seen to be collapsed) lie between two bands of fibrous connective tissue. The frontal bands are joined to the band on a tertiary vessel by a block of fibrous tissue; in this way a continuous and united fibrous 'warp and weft' is present in each lamella of each demibranch (figure 16).

4. Discussion

4.1. *Direction of flow of blood*

Our observations of the movements of haemocytes in primary, secondary and tertiary vessels as well as in the frontal channels of filaments have shown that the direction of flow is determined to a large extent by the frequent and extensive movements of the gills and the siphons. The relatively small net directional flow produced by the heart is thus superimposed on an essentially random movement of blood within and between the two systems of the gills.

4.2. *Absorption of oxygen*

There is mention in the literature of the countercurrent flow of blood and seawater in lamellibranch gills (Ghiretti 1966; Leake 1975). The functional advantages of countercurrent flow discussed by Yonge (1947) for the gills of the gastropod *Haliotis tuberculata*, which extracts into the blood 56% of the oxygen dissolved in the seawater flowing through its mantle cavity, would not be evident in a bivalve mollusc that extracts much less (*Mya arenaria*, 3–10% (Van Dam 1935); *Cardium tuberculatum*, 6–10% (Hazelhof 1939); *Pecten irradians*, 2.5–6.85% (Van Dam 1954); *Mytilus californianus*, 3.6–10.4% (Bayne *et al.* 1976); *Pholas dactylus* 6–10% (Knight 1984)). In these animals the major function of the gills is the acquisition not of oxygen but of particulate food by filter-feeding.

If in the light of the present findings both feeding currents and the mass movement of water through the gills are considered, then countercurrent flow is seen to occur only between:

(*a*) blood in the frontal channels of the filaments of the descending lamellae and the frontal feeding currents that convey particles towards the food grooves;

(*b*) blood in the afferent secondary vessels and the water passing up the sacculi; and

(*c*) blood in the primary efferent vessels and water being directed towards the exhalant aperture.

Taken together with the findings in §4.1 above, these results show that there is only a very limited amount of countercurrent flow present, and indeed possible, in *P. dactylus*. However, there are so many sites of respiratory exchange within the mantle cavity and on the body of *P. dactylus* that the presence or absence of countercurrent flow is not likely to be of significance, especially in such an inactive animal. This limited amount, however, may be of some significance in other lamellibranchs with a similar ctenidial blood vascular system.

4.3. *Air-gaping*

One aspect of the respiration of *P. dactylus* that must be accounted for by any satisfactory theory of blood flow in the gills is that which occurs when the animal is 'air-gaping' (Knight 1984). This condition occurs as follows. When, in the laboratory, the oxygen tension in the surrounding water is low, or when, in the field, the tide has receded from an animal in its hole, the aperture on the inhalant siphon is opened wide, in the former case in a siphon that has extended above the water level, and in the latter case in a siphon that has opened so as to touch the sides of the hole in which the animal lives and is consequently exposed to the air in the hole. A pool of water is retained in the siphon and kept oxygenated by the ciliary currents of the exposed wall of the siphon.

The lateral cilia of the gills account for 47 % of the oxygen consumption of the whole animal (Knight 1984) and it is most unlikely that they would be active when water could not be pumped through the system. Under these circumstances it is probable that blood in the filamentary frontal channels would play the major part in absorbing oxygen from the pool. However, the possibility still exists that passage of blood would occur from the filaments, through the filamentary dees into the circumferential vessels and then into the secondary vessels, and that the transport of oxygenated blood back to the efferent primary vessels would thus occur in both circulatory systems. The main function of the gills of *P. dactylus* is the extraction of particulate food from the large volumes of seawater passing through them (up to 100 l per day in a large animal (Knight 1984)) and much more oxygen is contained in this water than is needed for the functioning of the animal. However, in an air-gaping animal, which is under some stress because it no longer has access to a renewable supply of water, the extraction of oxygen from a fixed volume of water and its transport to the tissues may be of much greater importance.

4.4. *Shutdown of posterior parts of the gill*

A specimen of *P. dactylus* in which the siphons are fully extended may be three times as long as the shell; when the siphons are completely withdrawn into the shell they are no more than a quarter the length of the shell. The gills extend as the siphons extend and become puckered as the siphons contract. When the siphons are fully contracted the posterior parts of the gills are so puckered that it is unlikely that any significant flow of blood occurs in them. The anterior parts of the gills do not undergo such changes and in them the flow of blood could be maintained at all times.

4.5. *Conclusions*

The present work has shown how blood travels from an afferent primary vessel to a filamentary frontal channel and returns to the primary efferent vessel. It has also shown the nature of the connections between the filamentary frontal circulation and the abfrontal circulation. These new findings would appear to complete the picture of the blood vascular system of *P. dactylus*. The relation between the fibrous reticulum of the lamellae of the gills of this species and the blood vascular system has also been determined.

We have as yet made an acrylic corrosion cast of the vessels of the gills of only one other species, *Barnea parva*. This shows pronounced similarities to *P. dactylus*, as might be expected

from their close relationship. However, we recognize in the drawings of Ridewood (1903) and others structures in certain other eulamellibranchs that appear to be identical to the dees and tertiary vessels of *P. dactylus*. The results of an application to other species of lamellibranchs of the techniques described in this paper might well help in the elucidation of the evolution of the bivalve gill.

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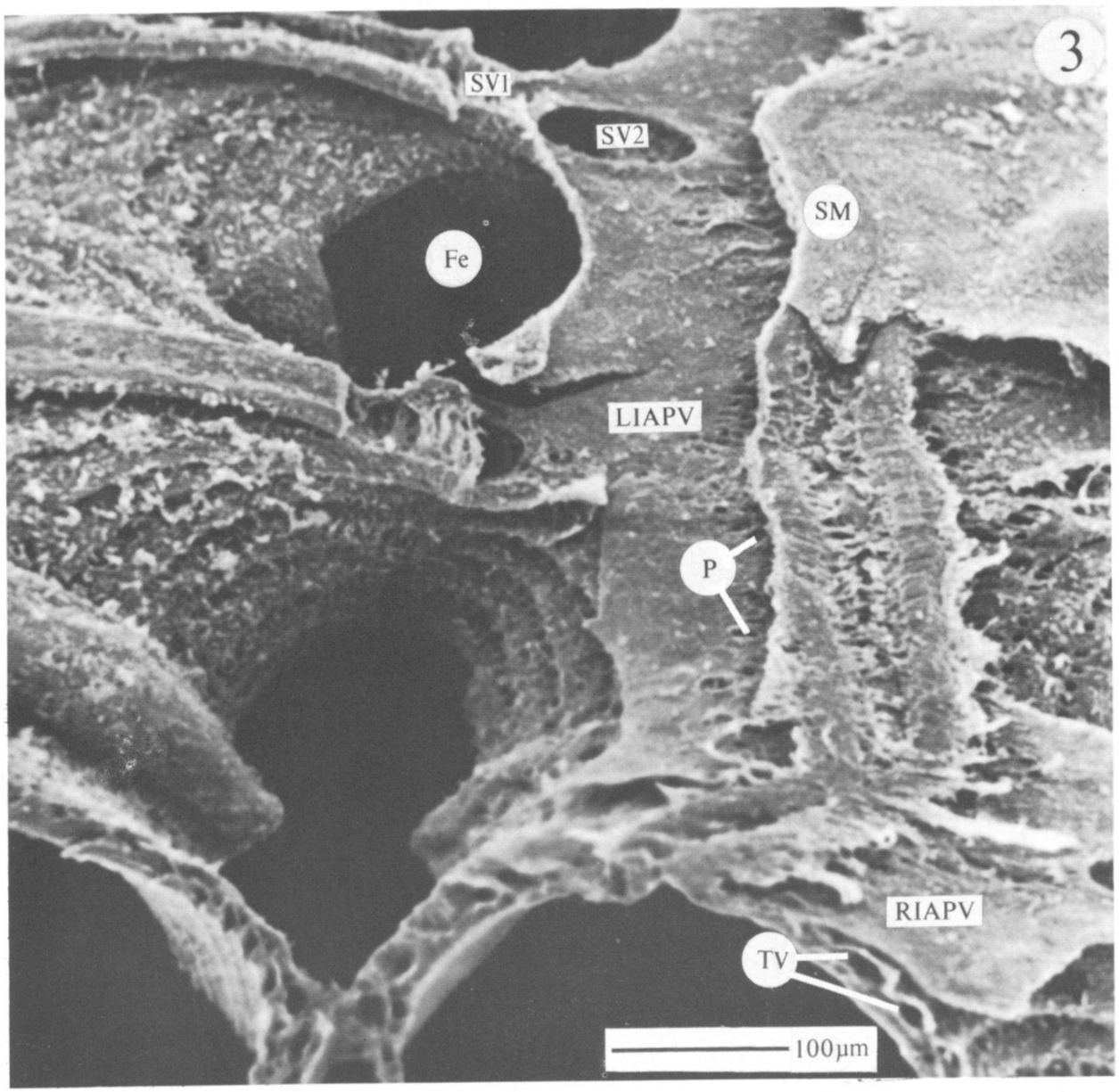
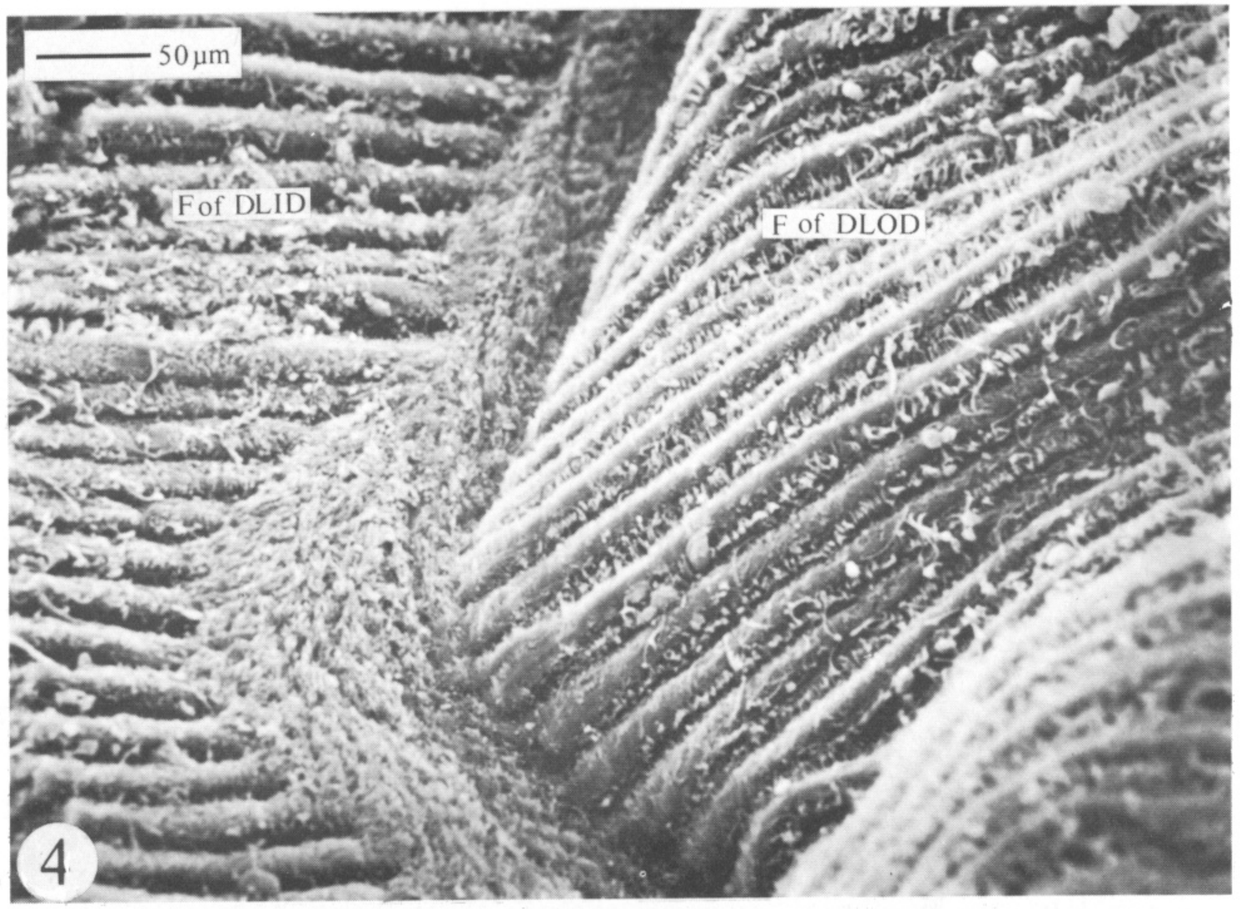
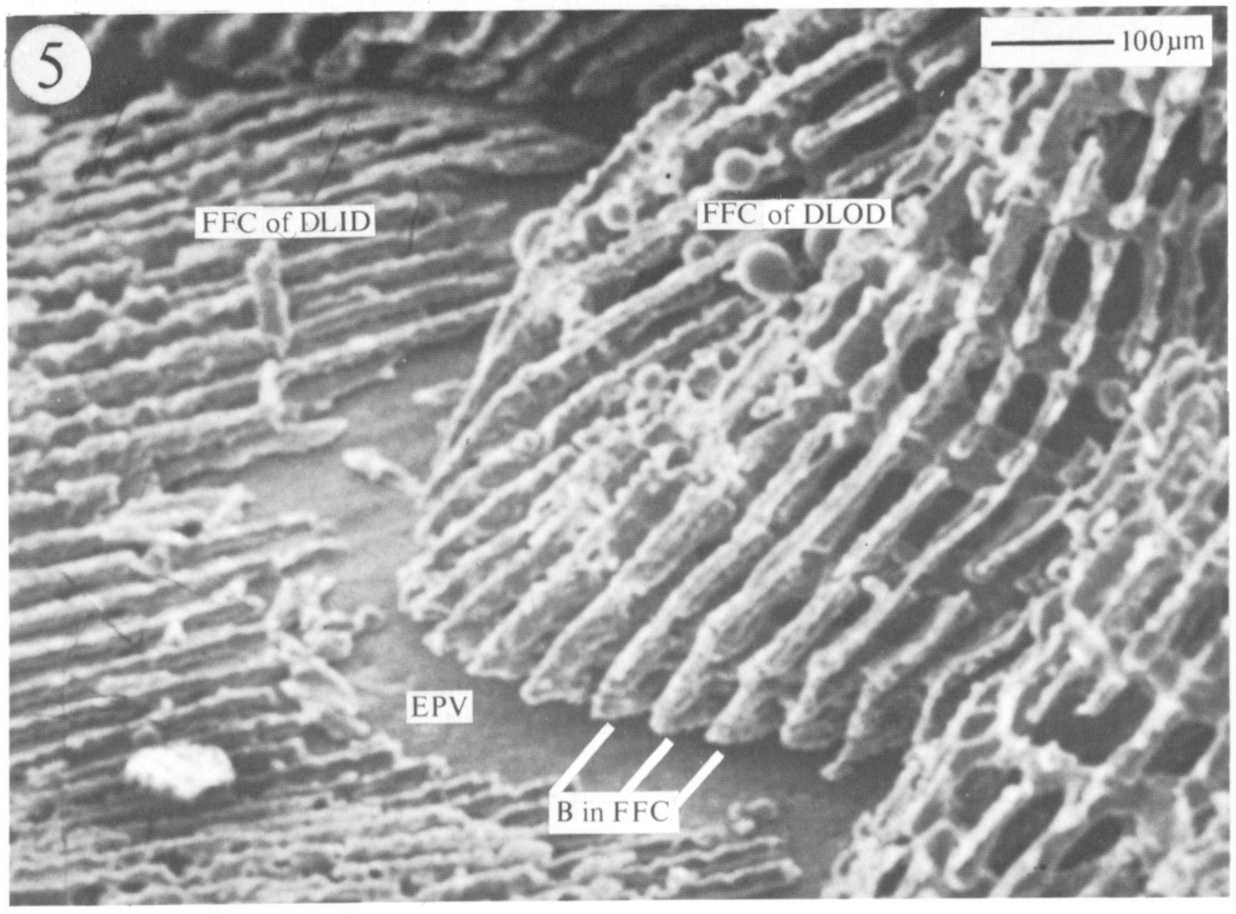
Abbreviations

ALID	ascending lamella of inner demibranch
ALOD	ascending lamella of outer demibranch
AVS	afferent vessel of shoulder (loop vessel)
ASV	afferent secondary vessel
B	bend
BC	blood cell
BT	blind tube
CEAVS	cut edge of afferent vessel of shoulder
D	dee
DLID	descending lamella of inner demibranch
DLOD	descending lamella of outer demibranch
DV	dorsal vessel
EPV	efferent primary vessel
ESV	efferent secondary vessel
F	filament
FB	fibrous band
FC	frontal cilia
Fe	fenestra
FFC	filamentary frontal channel
FG	food groove
GFB	groove of fibrous band
IAPV	inner afferent primary vessel
L	lumen
LBS	labyrinthic blood space
LC	lateral cilia
LIAPV	left inner afferent primary vessel
LM	light microscopy
LV	lateral vessel
O	ostium
OAPV	outer afferent primary vessel
P	perforations
RIAPV	right inner afferent primary vessel
S	shoulder
SEM	scanning electron microscope
SM	suspensory membrane
SV	secondary vessel
SV1	secondary vessel of suspensory membrane (dorsal surface partly removed)
SV2	secondary vessel of lamella
TV	tertiary vessel







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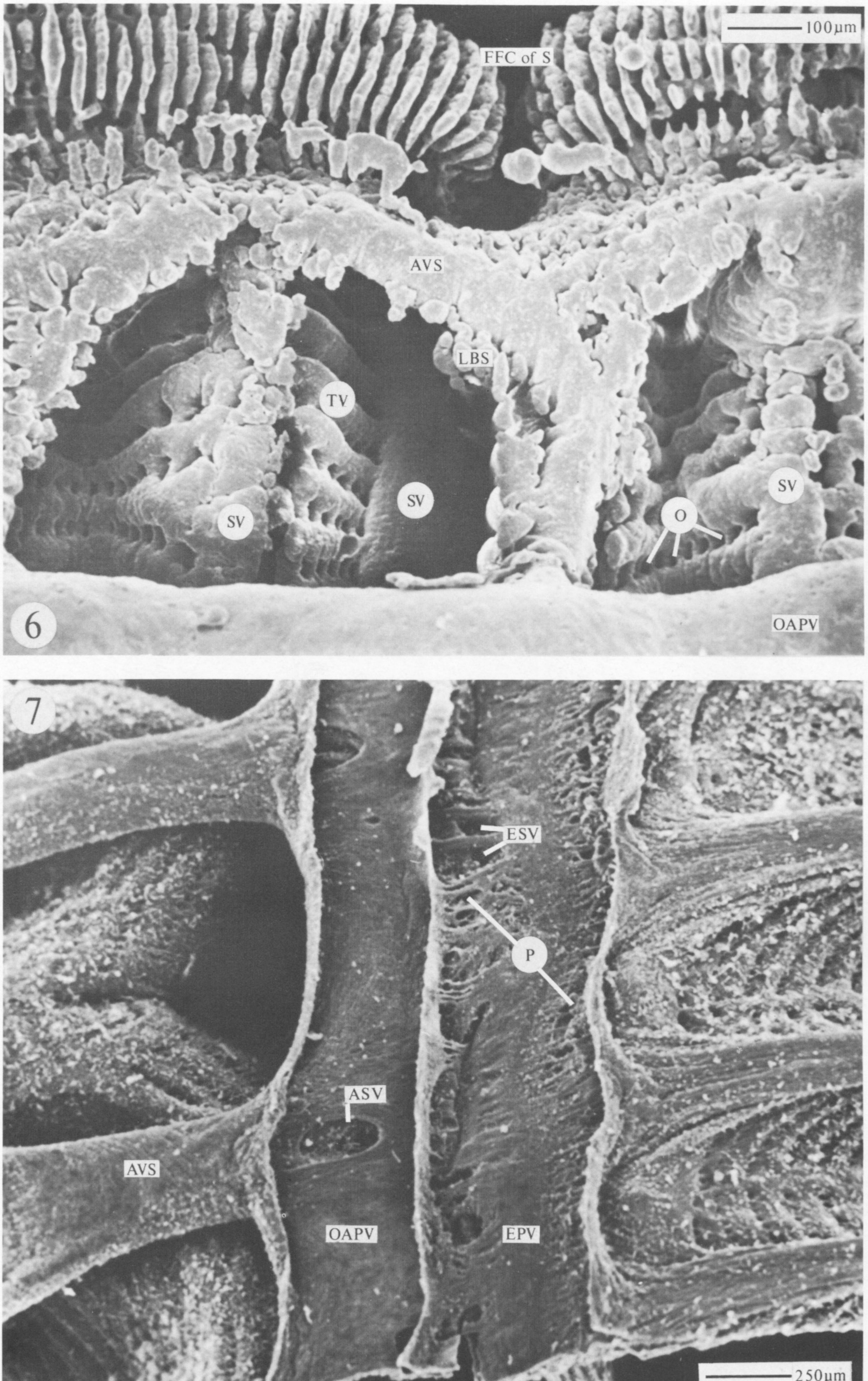

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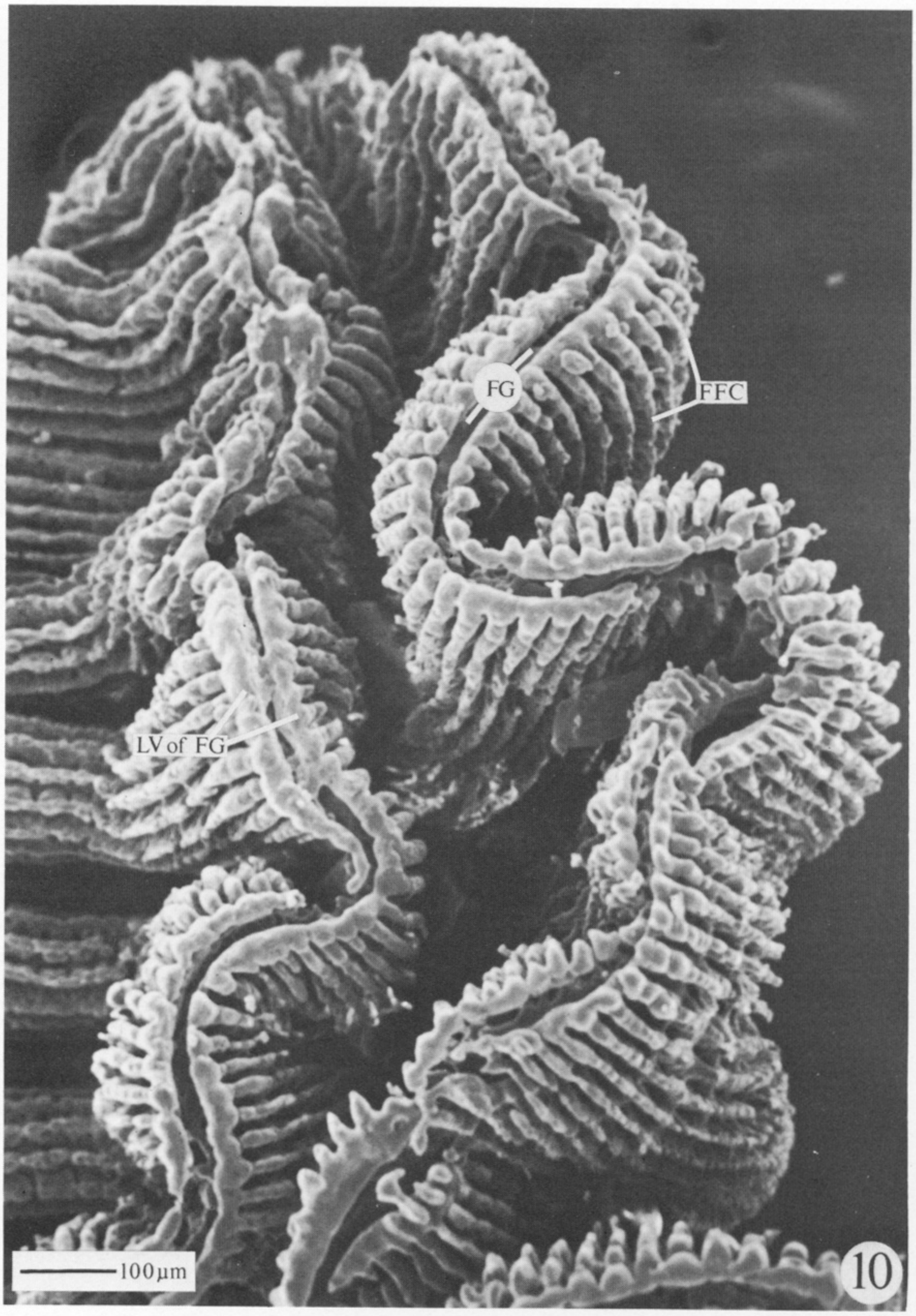
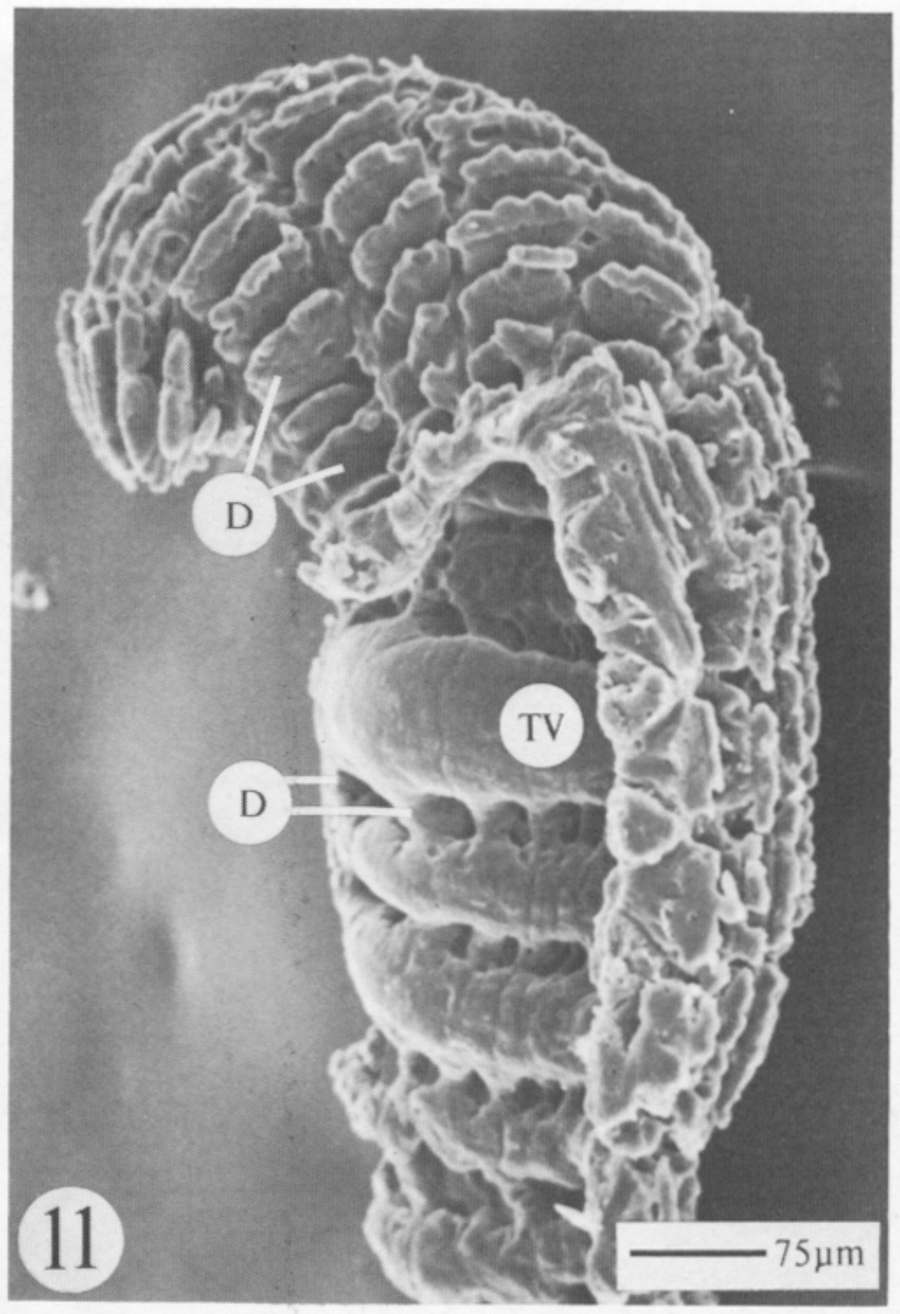
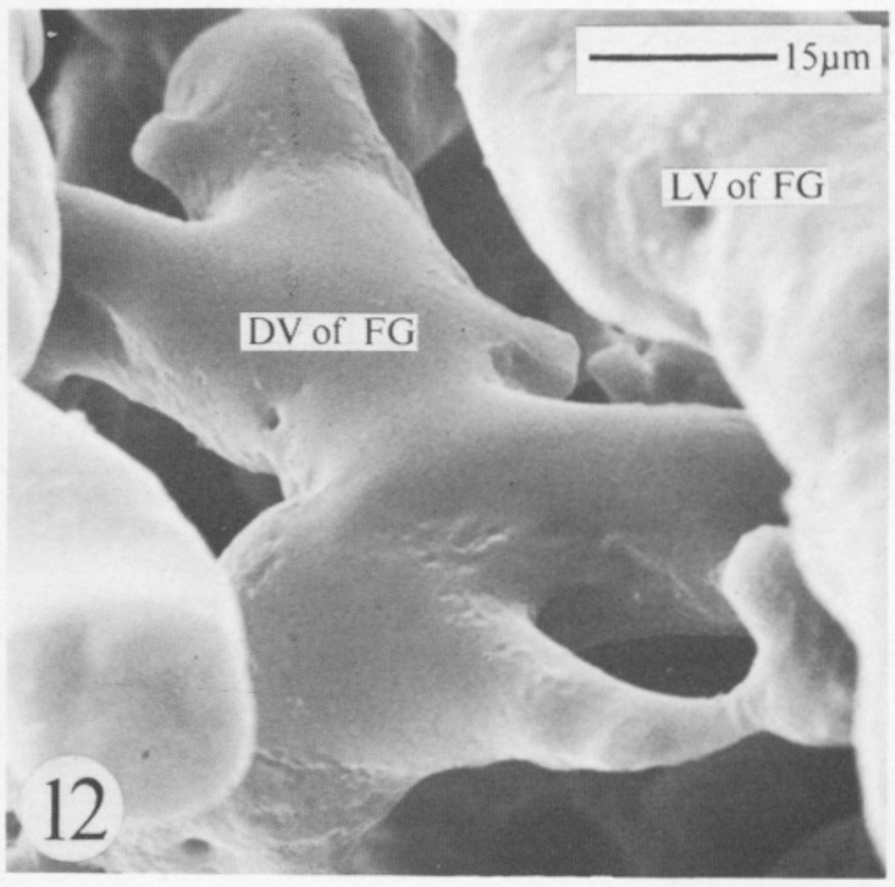
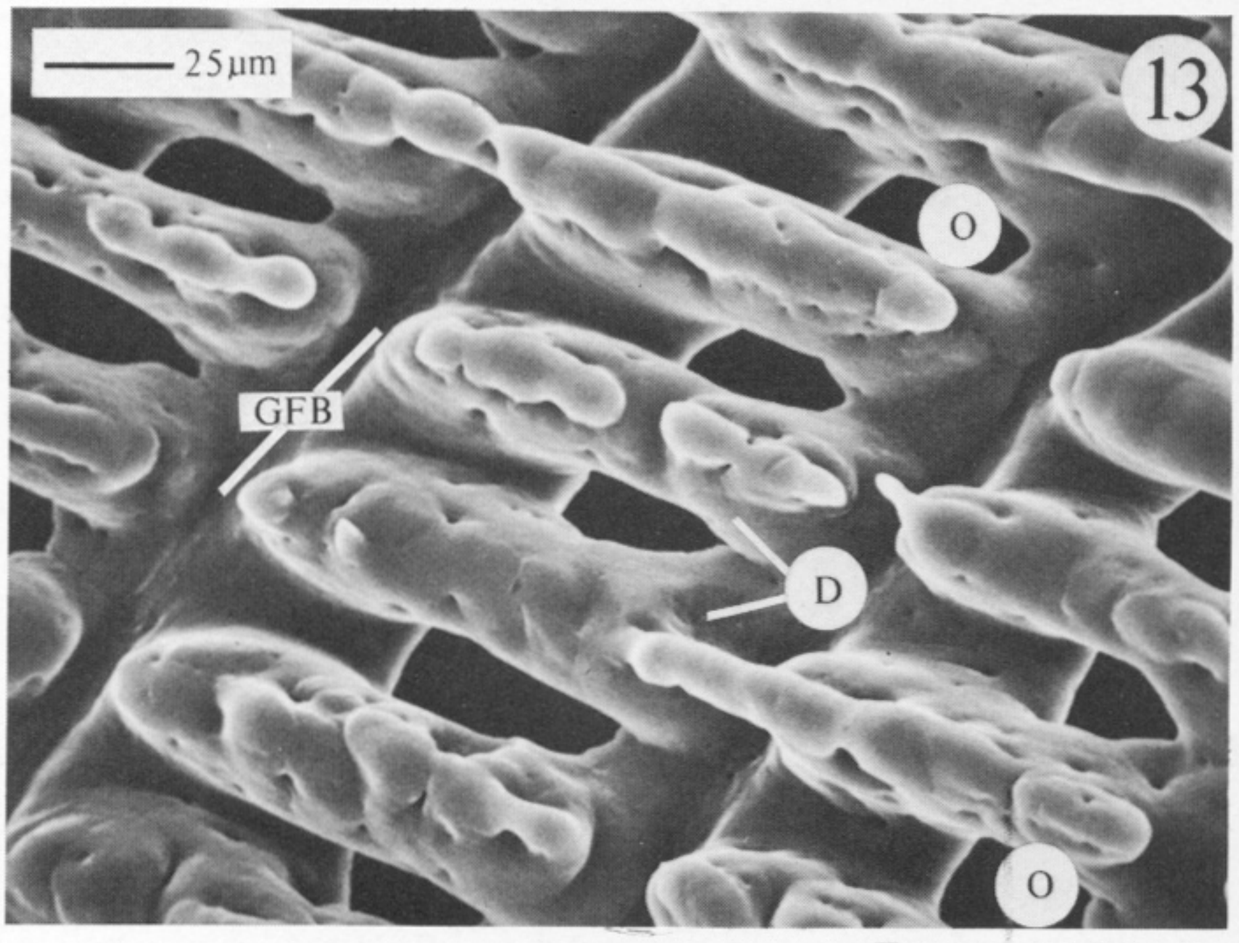
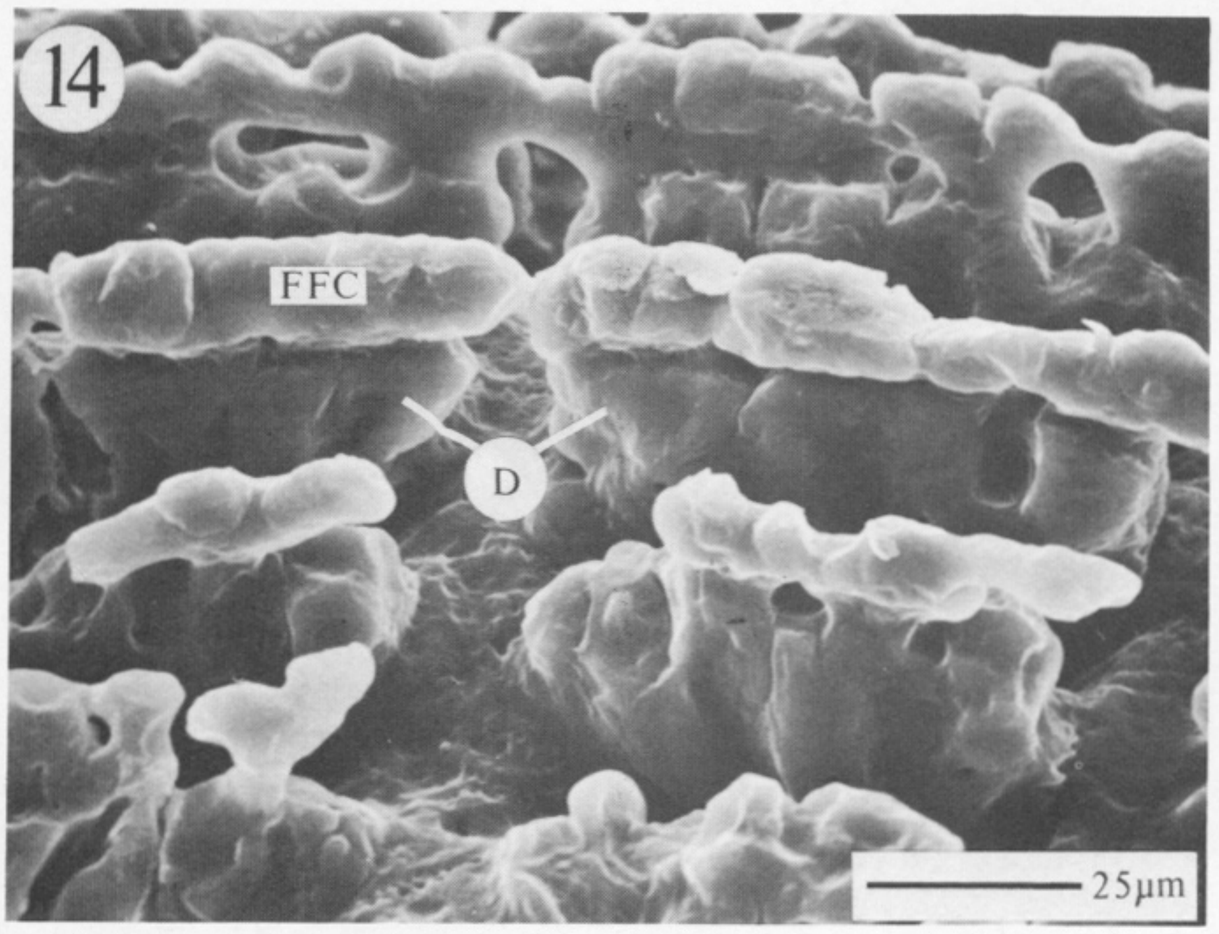


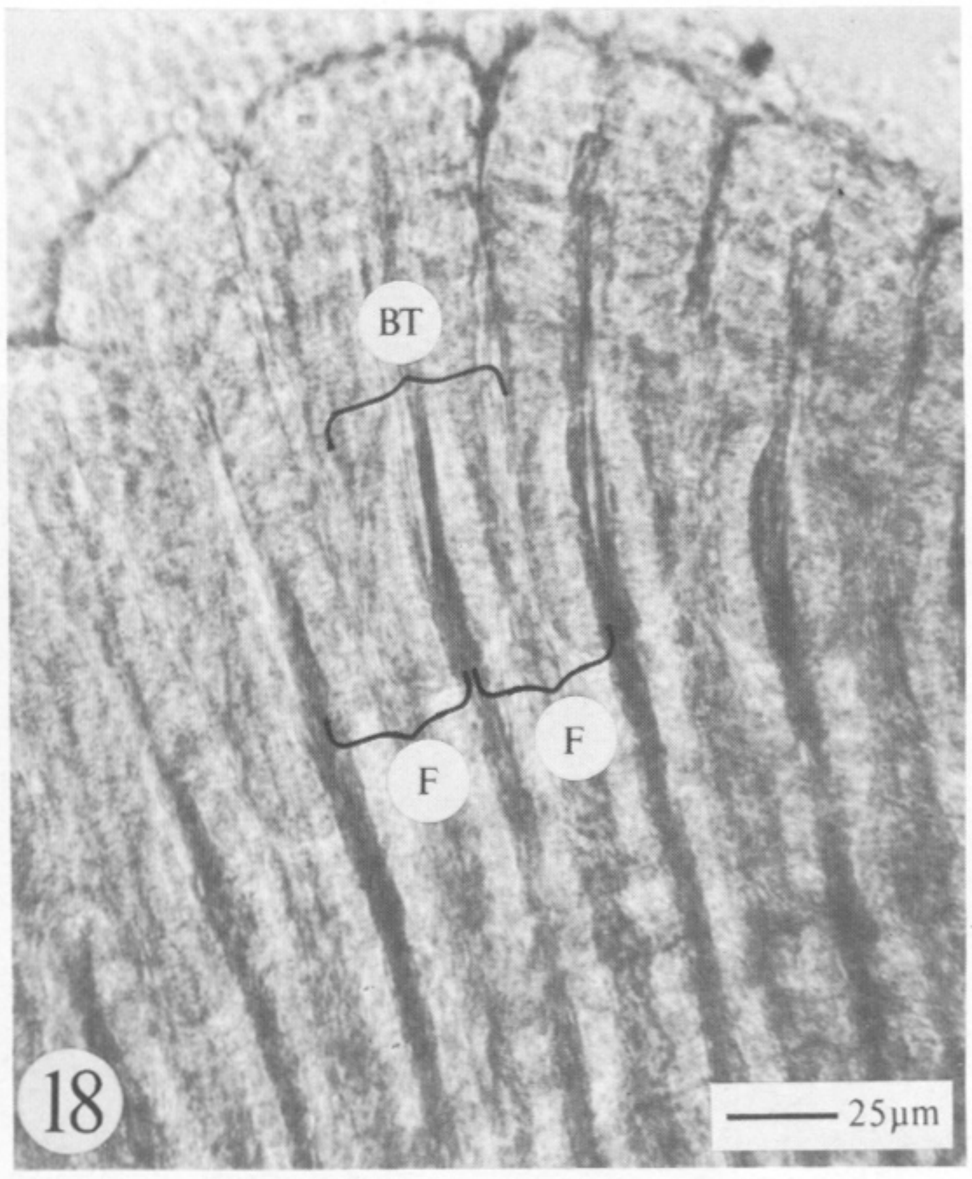


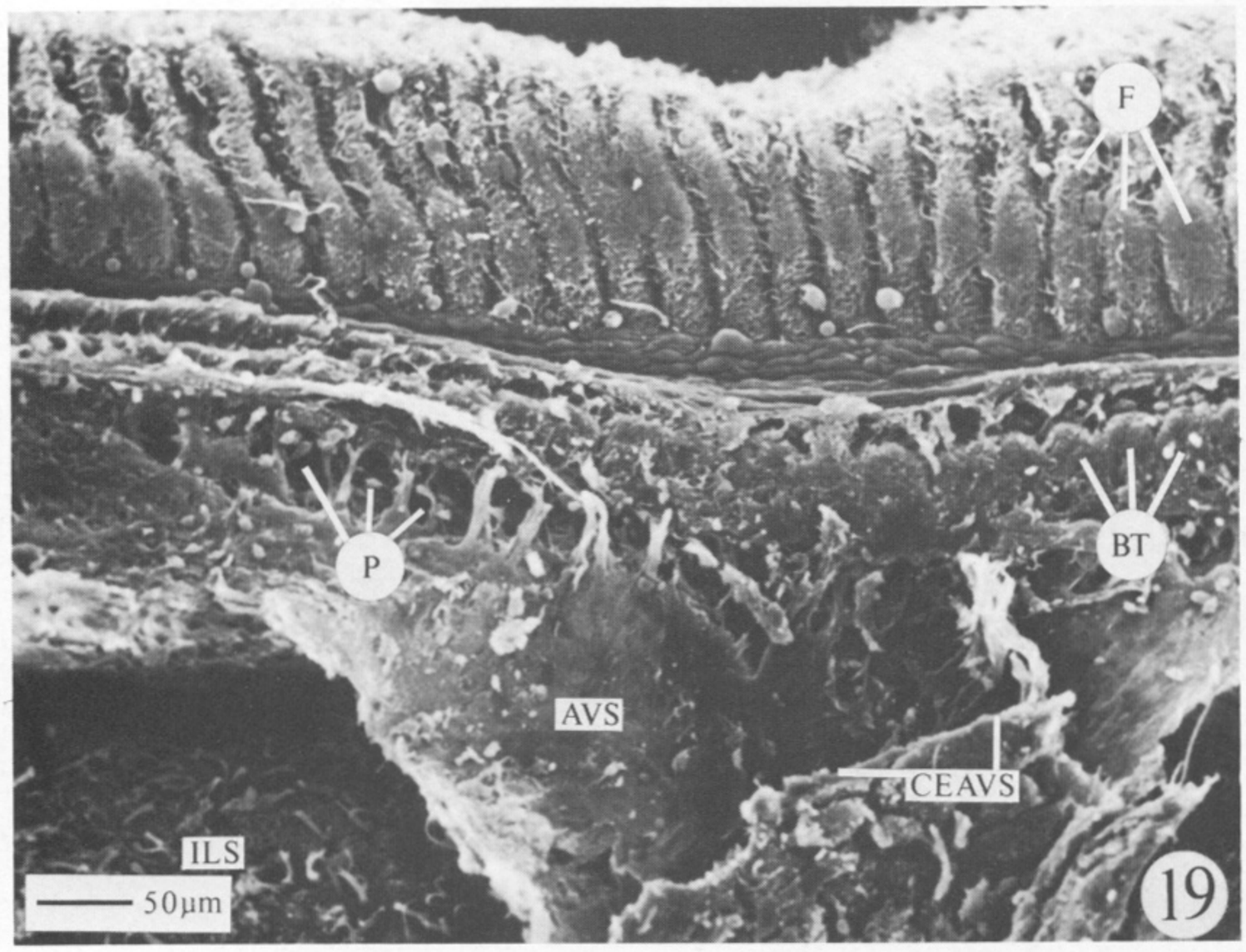


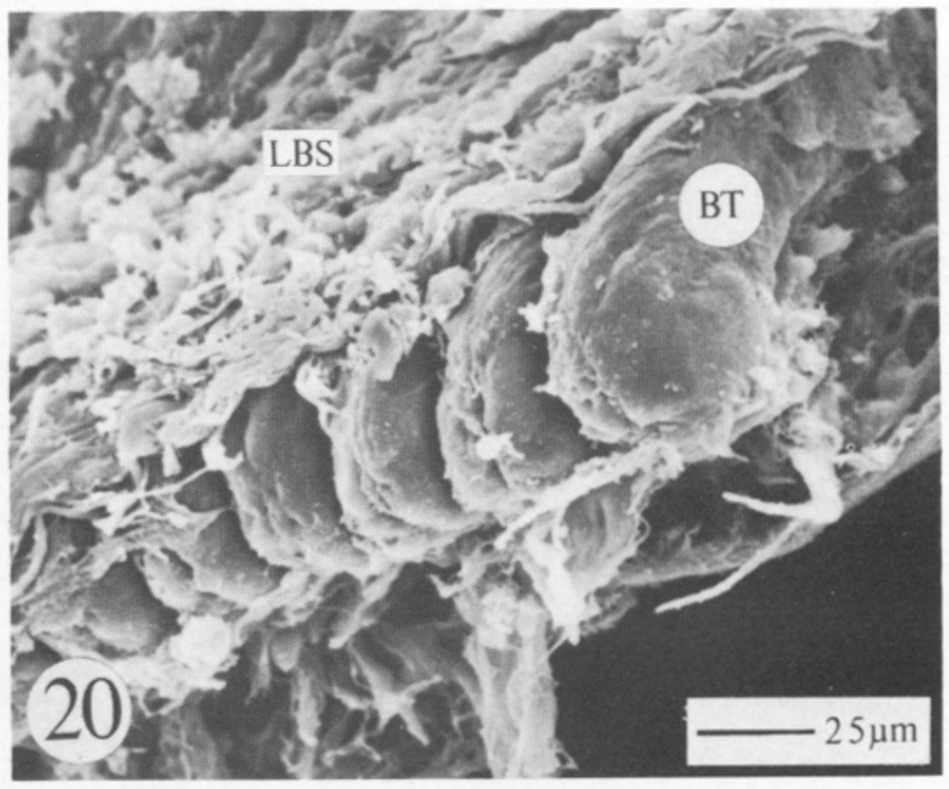


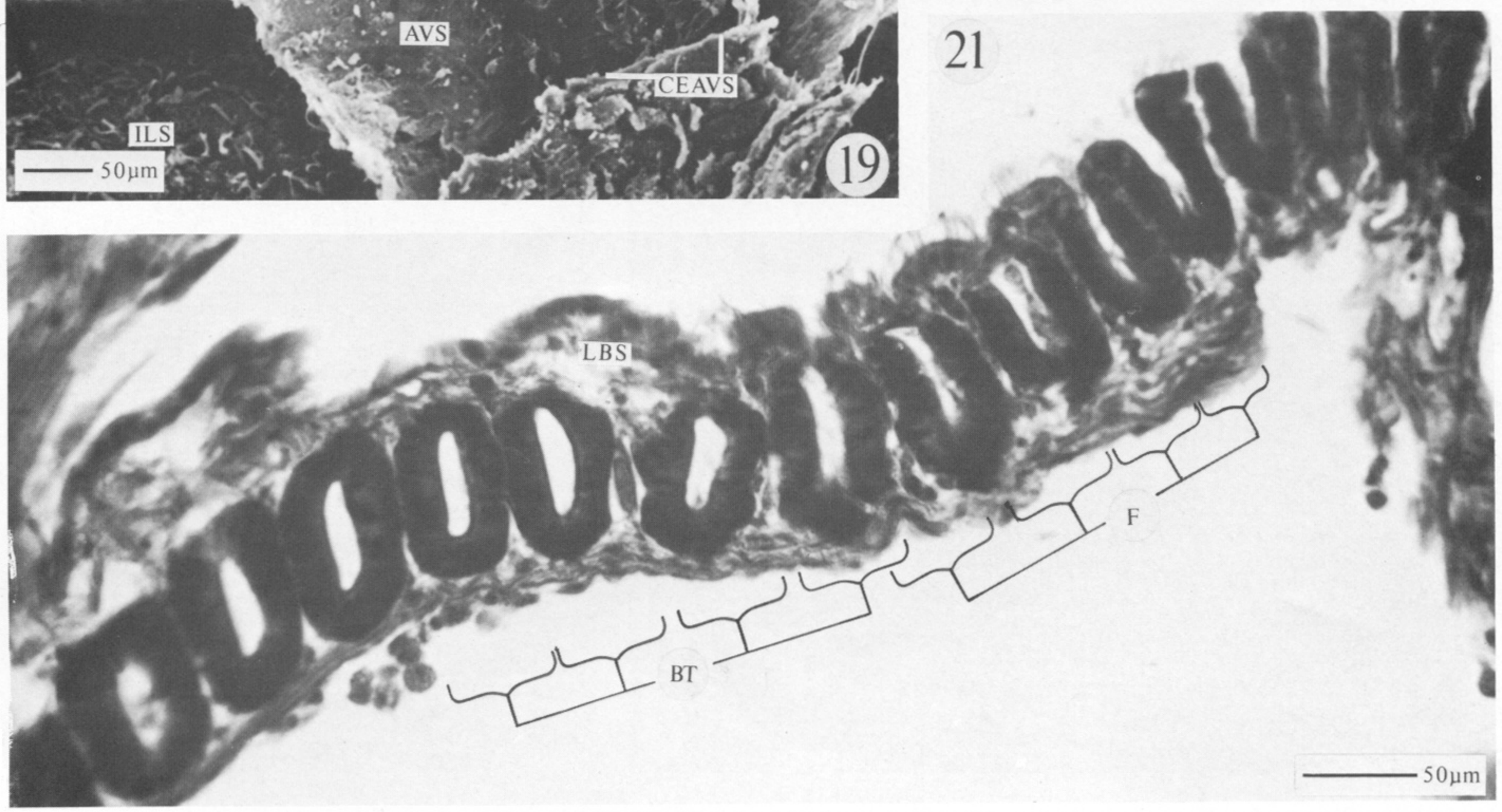


FIGURES 10–14. For description see opposite.









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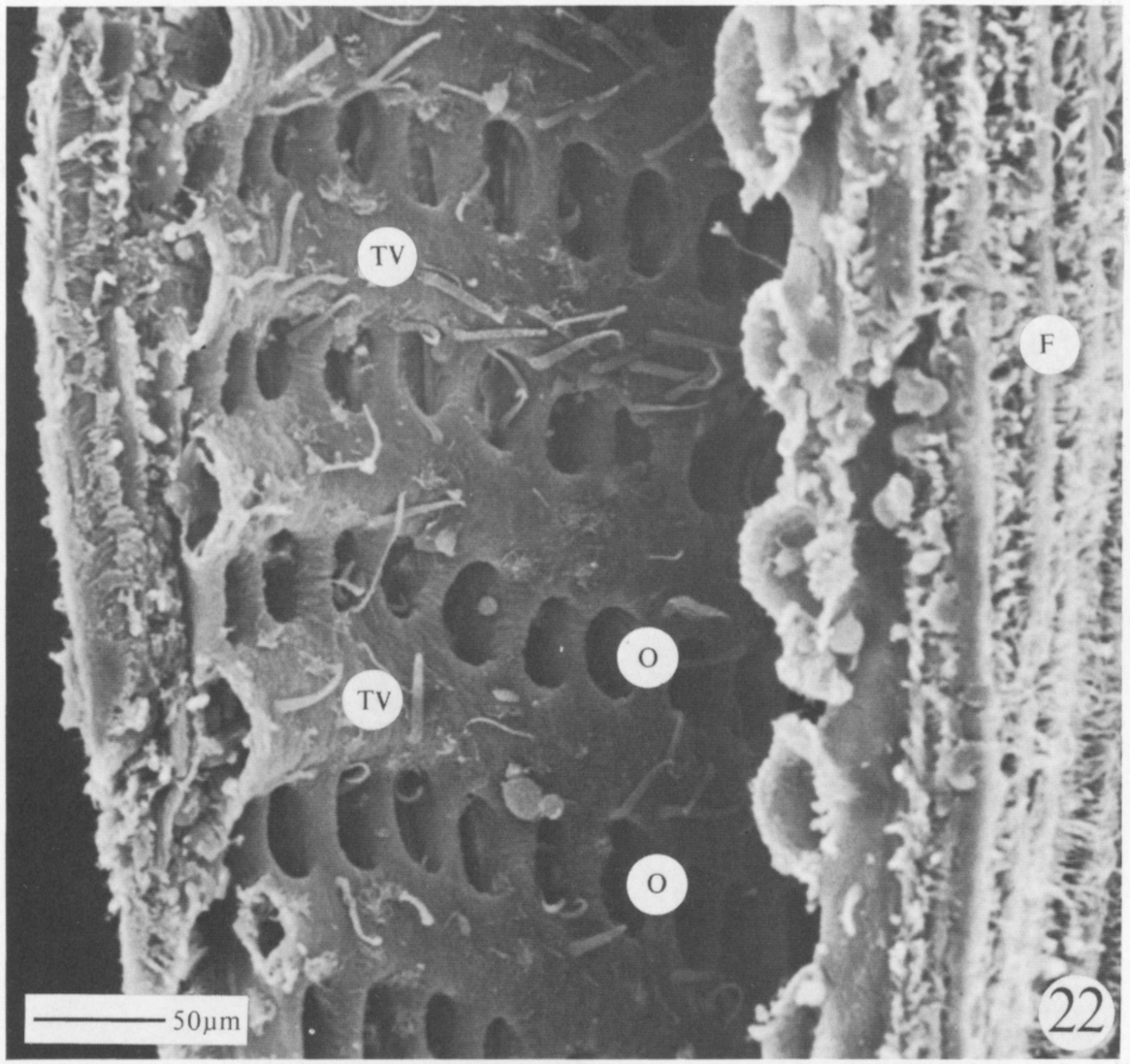

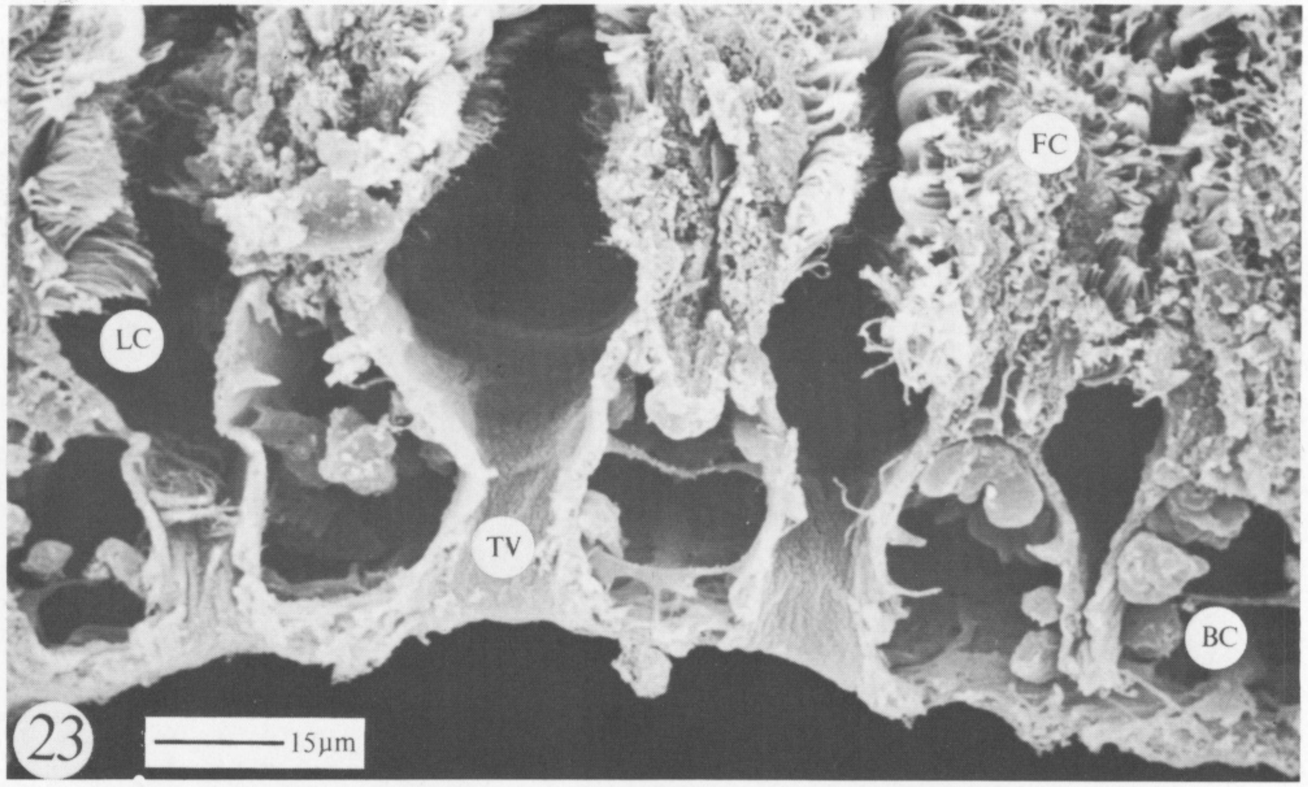

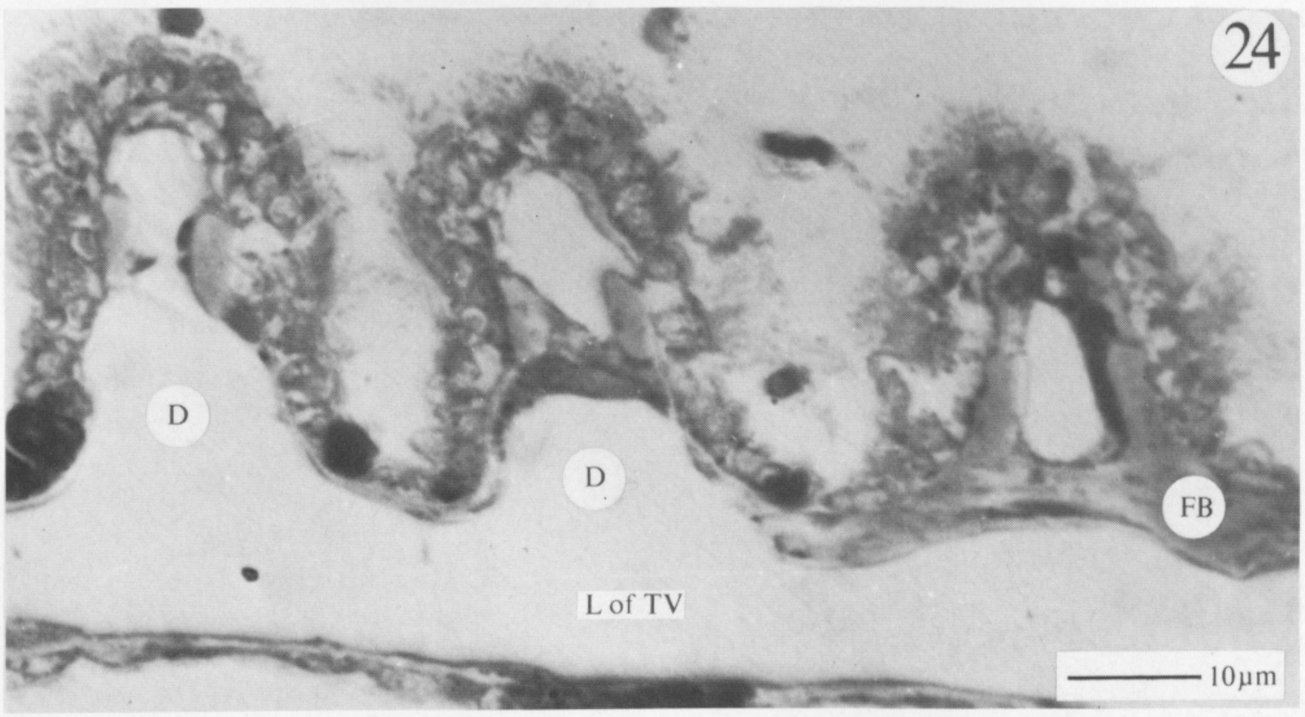

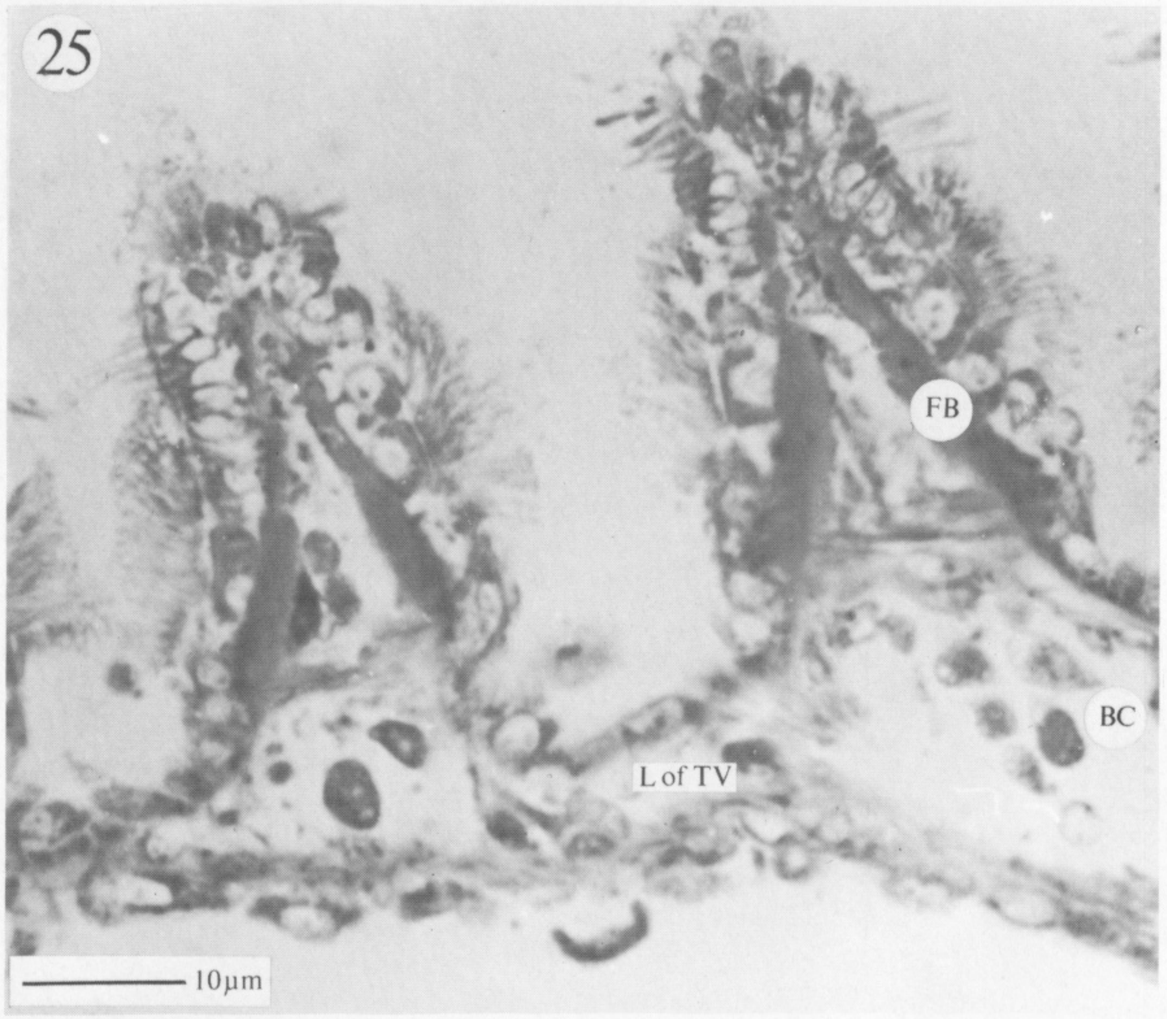

FIGURES 22–25. For description see opposite.