
Classification and the Bivalve Gill

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Classification and the bivalve gill

BY G. OWEN

Department of Zoology, Queen's University, Belfast, U.K.

[Plates 1 and 2]

The proposal by Atkins (1938), that the Bivalvia can, on the basis of the composition of the latero-frontal ciliated tracts, be divided into two groups, the Macrobranchia and the Microbranchia, is examined. It is concluded that the Ostreidae, in which the latero-frontal tracts consist of compound cirri together with subsidiary simple cilia, should not be grouped with the Microbranchia. The remaining families in this group are characterized by the possession of latero-frontal tracts consisting of simple cilia only; the Pinnidae show some modifications of the latero-frontal tracts, the precise details of which are still to be determined. The form of the gill in the Anomiidae, Pectinidae, Limidae and Pinnidae is reviewed. It is suggested that in these families, possibly correlated with latero-frontal tracts consisting of simple cilia only, the collection and transport of particles by the gill for possible ingestion is primarily dependent upon the flow of water currents rather than direct ciliary action as in those bivalves which possess compound eu-latero-frontal cirri. The families possessing latero-frontal tracts consisting of simple cilia only are all included in the subclass Pteriomorpha, together with two families, the Mytilidae and Ostreidae, which possess compound latero-frontal cirri. Some workers already exclude the Mytilidae from the Pteriomorpha. It is suggested that before discounting the value of the latero-frontal tracts in indicating relations there should be a reappraisal of the position of the Ostreidae.

INTRODUCTION

Atkins (1936, 1937 *a, b*, 1938) found that all the bivalves examined by her (117 species representing 51 families) could be separated into one or other of two main groups on the basis of the composition of the latero-frontal ciliated tracts. In one group the latero-frontal tracts are composed of compound eu-latero-frontal cirri together with one or more rows of subsidiary pro-latero-frontal cilia. Atkins termed this group the Macrobranchia and included in it the three families of protobranch bivalves, all the eulamellibranch families excluding those included by Pelseneer (1911) in the Pseudolamellibranchia, and the Mytilidae and possibly the Trigoniidae among filibranch bivalves. In the second group, consisting mainly of bivalves previously considered as lacking latero-frontal cilia, Atkins found the latero-frontal tracts, with the exception of the Ostreidae and possibly the Pinnidae, to consist of a single row of cilia only which she termed micro-latero-frontal cilia. She called this group the Microbranchia and included in it those families placed by Pelseneer (1911) in the Pseudolamellibranchia and Filibranchia, excluding the Mytilidae and the Trigoniidae.

The expression of doubt by Atkins concerning the Pinnidae simply reflected the difficulty she experienced in determining whether the latero-frontal cilia in this family are arranged in a single row, as in other members of the Microbranchia, or are present in a double row. The Ostreidae, on the other hand, presented Atkins with a more difficult problem. In this family the latero-frontal tracts are composed of compound cirri and a double row of subsidiary cilia but, from 'a consideration of phylogenetic relationships based on other characters', Atkins claimed they could not be regarded as homologous with the eu-latero-frontal cirri and

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pro-latero-frontal cilia of the Macrociobranchia. She therefore described them as 'anomalous' and 'para-latero-frontal cilia' respectively and included the Ostreidae in the Microciobranchia.

It is against this background that the latero-frontal tracts of a number of bivalves and particularly those placed by Atkins in the Microciobranchia have been re-examined by using the techniques of scanning (s.e.m.) and transmission (t.e.m.) electron microscopy.

THE COMPOSITION OF THE LATERO-FRONTAL TRACTS

The degree of development of the latero-frontal tracts varies in different bivalves but essentially they consist either of compound eu-latero-frontal cirri with, to the frontal side of these, simple pro-latero-frontal cilia or of simple micro-latero-frontal cilia only.

Eu-latero-frontal cirri

Representatives of the families Nuculidae, Mytilidae, Semelidae, Petricolidae and Pholadidae, of those included by Atkins (1938) in the Macrociobranchia, have been previously examined under the scanning electron microscope (Moore 1971; Hughes 1975; Owen, 1974, 1976) and during the present study members of the Nuculanidae, Solemyidae, Cardiidae, Solenidae, Arcticidae, Glossidae, Veneridae and Myidae have also been examined. In each case, the general form and composition of the compound eu-latero-frontal cirri resemble those described in detail for *Mytilus edulis* (Owen 1974). Each cirrus arises from a single cell, elongated in the transverse plane of the ctenidial filament (figures 1 and 4, plate 1) and consists of cilia arranged in two parallel rows (e.l., figure 3, plate 1). The number of cilia comprising each cirrus varies from species to species (20–22 pairs in *Nucula sulcata*; 22–26 in *Mytilus edulis*; 27–29 in *Venus casina*) but, in all, the individual cilia bend to one side or other of the main axis at regular intervals along the length of the cirrus (figure 4). In *Mytilus edulis*, each cilium where it bends to leave the cirrus shaft contains a well developed stiffening element which extends distally toward the free tip of the cilium (Owen 1974). A similar structure is present in *Venus casina* (s.r., figure 2, plate 1) and *Arctica islandica* and probably other eulamellibranch bivalves but is lacking in the protobranch *Nucula sulcata*.

Pro-latero-frontal cilia

In all the families noted in the previous section, with the possible exception of the Solemyidae where it was not possible to confirm their presence, the latero-frontal tracts include simple

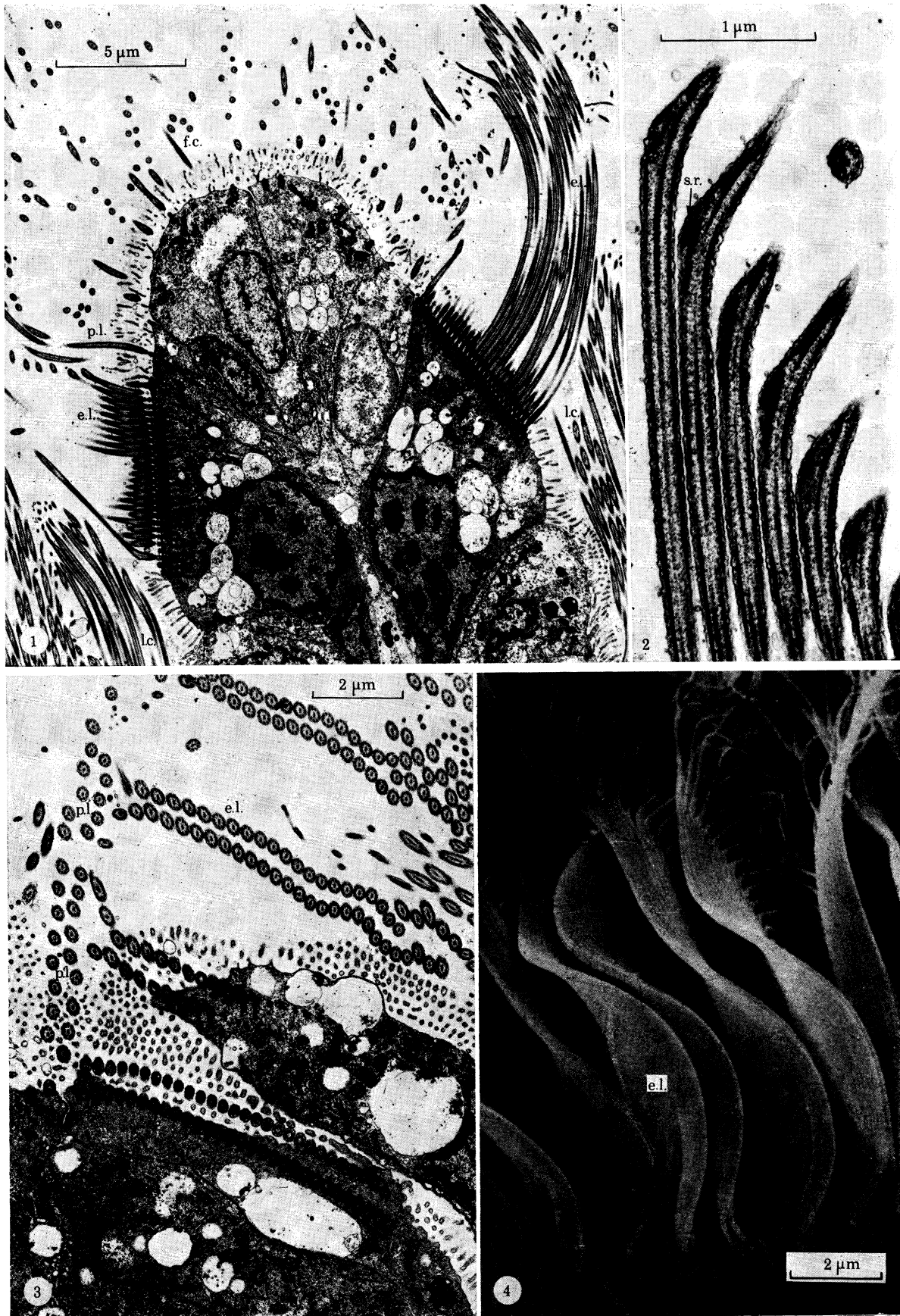
DESCRIPTION OF PLATE 1

FIGURE 1. Electron micrograph of a transverse section through the frontal region of a gill filament of *Venus casina* showing the compound eu-latero-frontal cirri (e.l.), pro-latero-frontal cilia (p.l.), lateral cilia (l.c.) and frontal cilia (f.c.).

FIGURE 2. Electron micrograph of a longitudinal section through a eu-latero-frontal cirrus of *Venus casina* in the region where the individual cilia bend to leave the main axis of the cirrus; electron dense stiffening elements (s.r.) occur in the region of the bend.

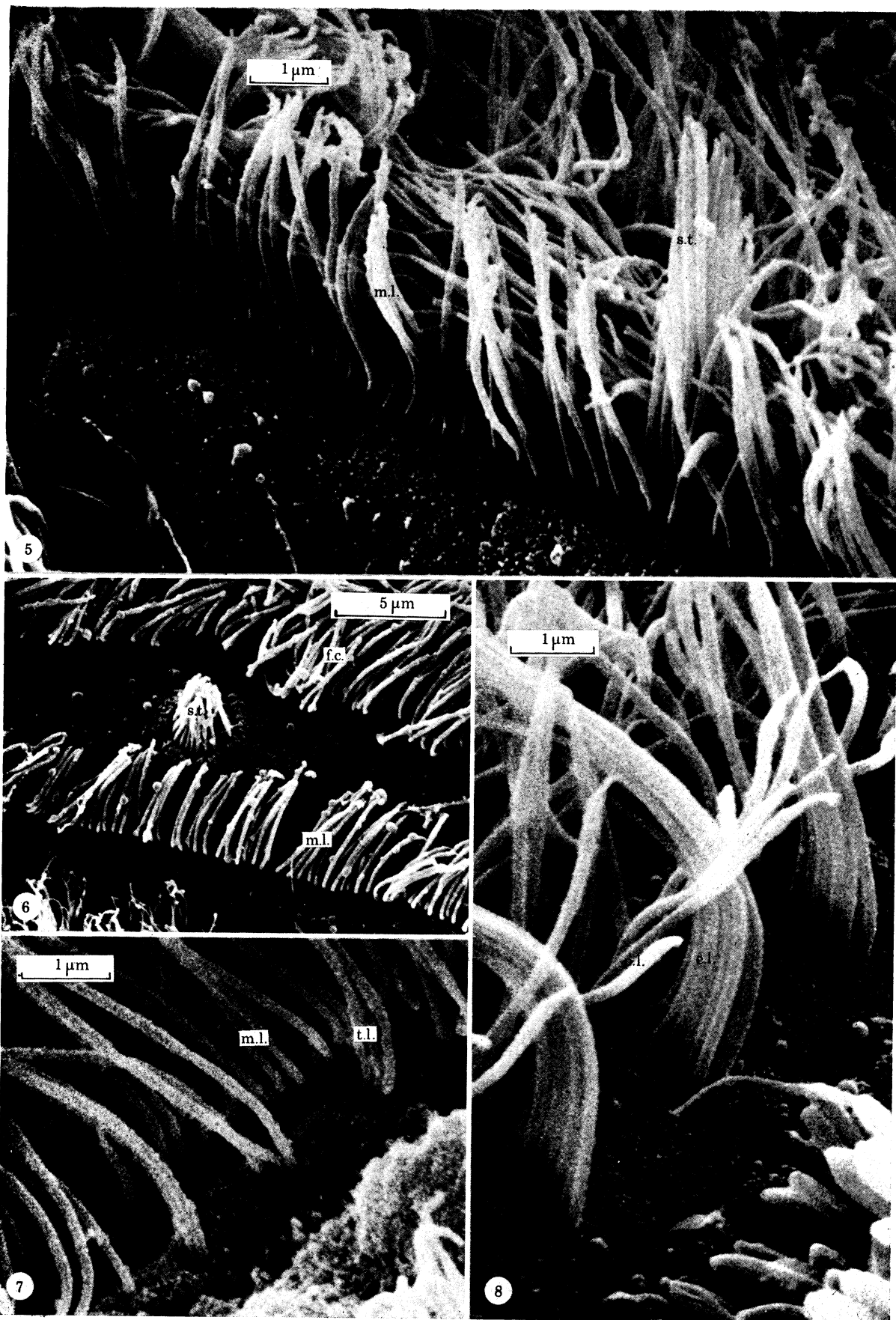
FIGURE 3. Electron micrograph of a section through the latero-frontal face of a gill filament of *Venus casina*. Each cirrus (e.l.) is composed of some 28 pairs of cilia and to the frontal side of these are two alternating rows of pro-latero-frontal cilia (p.l.).

FIGURE 4. Scanning electron micrograph of the eu-latero-frontal cirri of *Venus casina*. Each cirrus is borne by a single cell and is composed of two rows of cilia.



FIGURES 1-4. For description see opposite.

(Facing p. 378)



FIGURES 5-8. For description see opposite.

pro-latero-frontal cilia in addition to compound eu-latero-frontal cirri. They are arranged to the frontal side of the compound cirri and arise from narrow cells elongated in the direction of the length of the ctenidial filament. In *Nucula sulcata*, the pro-latero-frontal cilia are arranged in four rows but in all the other bivalves examined they are arranged in two closely packed alternating rows (p.l., figure 3).

Micro-latero-frontal cilia

An account of such cilia in *Chlamys varia* has already been given (Owen 1976) and during the course of this work representatives of the Glycymeridae, Anomiidae, Limidae and Pinnidae were also examined. In *Pododesmus (Monia) patelliformis*, as in *Chlamys varia*, the latero-frontal tracts consist of only a single row of micro-latero-frontal cilia arranged on each side of the frontal ciliated tracts (m.l., figure 5, plate 2) and a similar arrangement is present in *Glycymeris glycymeris* and *Lima hians* (m.l., figure 6, plate 2).

Atkins (1938) was uncertain of the arrangement of the latero-frontal tracts in *Pinna fragilis* but suspected that they might consist of two rows of cilia arranged on each side of the frontal tracts. It was not possible to obtain fresh material but an examination of preserved material of *Atrina vexillum* and *Pinna muricata* confirmed that the arrangement of the latero-frontal tracts in the Pinnidae differs from that in the families noted above, although not in quite the way suspected by Atkins. The appearance under the s.e.m. of what is admittedly poorly preserved material suggests that in both *Atrina* and *Pinna* the latero-frontal ciliated tracts are borne by two rows of cells on each side of the frontal ciliated tracts (figure 7, plate 2). The cilia borne by the inner (i.e. nearer the frontal surface) row of cells are arranged in a single row (m.l.) while those borne by the outer row of cells are arranged in a series of triplets (t.l.). The triplets are spaced some 2 μm apart, each forming a row lying in the transverse plane of the ctenidial filament. It was not possible to tell whether each triplet functioned as a cirrus or compound cilium and the precise arrangement requires confirmation from living material and suitably preserved material examined under the t.e.m.

Ostreidae (anomalous latero-frontal cilia)

Atkins (1938) described the latero-frontal tracts of the Ostreidae as comprising anomalous latero-frontal cirri and subsidiary para-latero-frontal cilia but as shown in figure 8, plate 2, the arrangement is essentially similar to the eu-latero-frontal and pro-latero-frontal tracts of the Mytilidae (Owen 1974, 1976) and Veneridae (cf. figure 4). As in the latter, the latero-frontal tracts of *Ostrea edulis* consist of compound cirri (e.l.) and, to the frontal side of these, two alternating rows of simple cilia (p.l.). Although the number of cilia comprising each cirrus is

DESCRIPTION OF PLATE 2

FIGURE 5. Scanning electron micrograph of the latero-frontal face of a ctenidial filament of *Pododesmus (Monia) patelliformis* showing the single row of micro-latero-frontal cilia (m.l.) bordering the frontal cilia (f.c.).

FIGURE 6. The latero-frontal face of an ordinary gill filament of *Lima hians*. A non-ciliated region separates the micro-latero-frontal cilia (m.l.) from the frontal cilia (f.c.).

FIGURE 7. The latero-frontal tract of an ordinary gill filament of *Pinna muricata* consisting of a single row of cilia (m.l.) and cilia arranged in triplets (t.l.). The latter are in single rows and not double rows as for eu-latero-frontal cirri.

FIGURE 8. The latero-frontal tract of an ordinary gill filament of *Ostrea edulis* showing the compound eu-latero-frontal cirri (e.l.) and to the frontal side of these the simple pro-latero-frontal cilia (p.l.).

small (6–11 pairs) they are arranged as in *Venus casina* in two parallel rows and the individual cilia bend to one side or other at regular intervals along the length of the cirrus. Finally, again as in *Venus casina*, each cilium where it bends to leave the cirrus shaft contains an electron dense stiffening element (Owen 1976).

DISCUSSION

The effect of Atkins's (1938) proposals are to separate a large group of bivalves in which the latero-frontal tracts consist of compound cirri together with simple subsidiary cilia from a smaller but still large group in which the tracts, with the exception of the Ostreidae and possibly the Pinnidae, are composed of simple cilia only. An interesting feature of this division is that the smaller group, that is the Microciliobranchia, correspond closely with the sedentary branch as conceived by Douvillé (1913) and the sub-class Pteriomorphia as outlined by Newell (1965, 1969). The main difference lies in the position of the Mytilidae, included in the Pteriomorphia by Newell but excluded from the Microciliobranchia by the possession of compound eu-latero-frontal cirri. There would appear, however, to be some doubt about the inclusion of the Mytilacea in the Pteriomorphia (Cox 1960; Taylor, Kennedy & Hall 1973; Babin 1977) and clearly, if the nature of the latero-frontal tracts has any phylogenetic significance, they should be excluded.

A more difficult problem is that presented by the nature of the latero-frontal tracts in the Ostreidae. The family, included in the Ostreacea, is usually grouped with the Anomiacea, Pectinacea, Limacea and Pinnacea in the order Pterioidea, and Atkins (1938), despite the fact that the Ostreidae possess compound latero-frontal cirri, included the family in the Microciliobranchia. As already discussed, there does not appear to be any real distinction between the so called 'anomalous' latero-frontal cirri of the Ostreidae and the eu-latero-frontal cirri of those bivalves included by Atkins in the Macrociliobranchia (Owen 1976). Moreover, as indicated by Purchon (1958), if it is necessary in this one case to ignore the evidence supplied by the form of the latero-frontal tracts in order to accommodate relations based on other characters then the value of the latero-frontal tracts as a whole in determining relations is suspect.

Owen (1976) suggested that in those bivalves in which the latero-frontal tracts consist of simple cilia only, that is the Microciliobranchia excluding the Ostreidae, the collection of particles by the gills for possible ingestion is dependent upon the flow of water currents rather than the direct filtration and transport of particles by cilia, traditionally regarded as the basic mechanism of the lamellibranch gill. It is thus relevant to compare the form of the gills in the Ostreidae with that of representatives of those families usually grouped with the Ostreidae in the order Pterioidea, namely the Anomiidae, Pectinidae, Limidae and Pinnidae.

Descriptions of the structure and ciliation of the gills of members of the Anomiidae have been given by Atkins (1936); they are flat, filibranch and homorhabdic. The latero-frontal tracts consist of a single row of cilia (p, figure 5) disposed on each side of the frontal cilia (f.c.). The latter are arranged in two tracts, a broad densely packed tract of ventrally beating cilia and cirri along the anterior side of each filament and a narrow tract of more widely spaced, dorsally beating cilia. Despite the presence of the latter, Atkins rarely observed particles on the gill surface being carried dorsally. She considered that the gills seemed to be concerned chiefly with rejection since all particles are carried ventrally to the free margins of the demibranchs where the currents are directed posteriorly. As shown diagrammatically in figure 9, Atkins

concluded that members of the Anomiidae subsist largely on particles brought by the main water current directly to the dorsal grooves of the gills where the currents are directed anteriorly.

The gills of *Chlamys varia* while filibranch are, in contrast to those of the Anomiidae, plicate and heterorhabdic. In the relaxed gill the principal filaments form a pronounced gutter at the bottom of the grooves between adjacent plicae (figure 10). The frontal ciliation of these principal filaments is divided into a broad median tract (f.m.) occupying the floor of the gutter

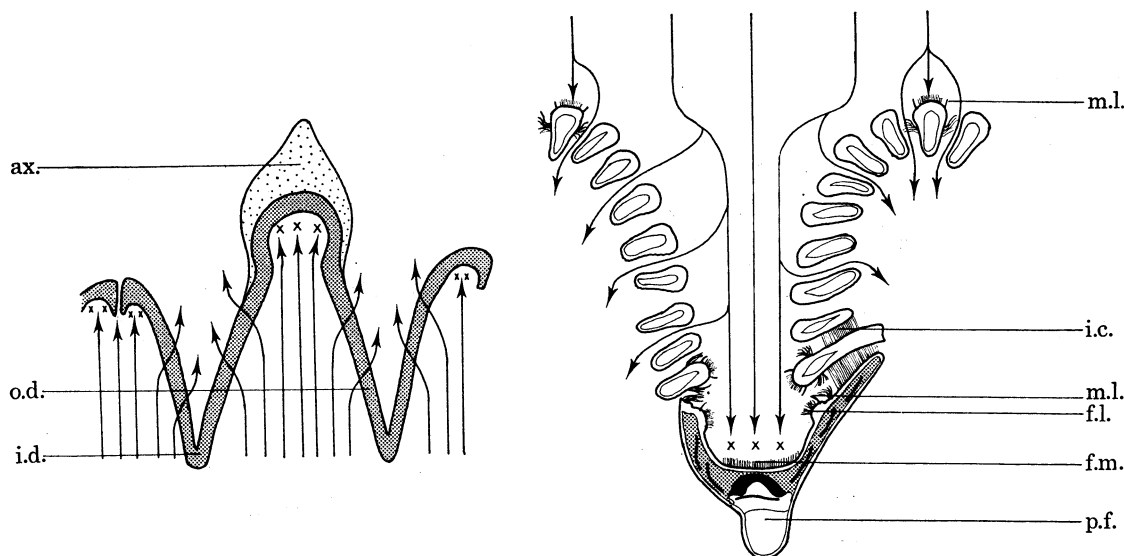


FIGURE 9

FIGURE 10

FIGURE 9. Diagrammatic transverse section of a gill of *Pododesmus (Monia)* after Atkins (1936) to show the flow of water toward and through the gill (arrows); X indicates an anteriorly directed flow.

FIGURE 10. Diagrammatic horizontal longitudinal section through a relaxed gill lamella of *Chlamys varia* after Owen (1976). The arrows indicate the flow of water toward and through the lamella; X indicates a dorsally directed flow in the gutters formed by the principal filaments (p.f.).

and, on each side and extending the length of the walls of the gutter, a narrow tract of cilia (f.l.) borne on raised ridges. All three tracts of frontal cilia beat dorsally in contrast to the ventrally beating frontal cilia of the ordinary filaments forming the crests of the plicae. It is suggested (Owen 1976) that in such a gill the form of the plicae, the U shape of the principal filaments, and the dorsally directed flow of water created by the frontal ciliated tracts, all combine to form a region of low pressure which tends to attract particles into the gutters formed by the principal filaments. Here the particles are transported dorsally *in suspension* to join the anteriorly directed currents between the bases of the two demibranchs and along the edges of all the ascending lamellae. The concept is illustrated in figure 10. Figure 11 *a*, on the other hand, shows the form of the principal filaments in a contracted gill; they are T-shaped in section. This change is accompanied by a marked reduction in the degree of plication of the gill and, as a consequence, the collection of particles by water currents postulated above can no longer operate. There is an increase in the secretion of mucus and all material on the gill surface is carried ventrally by the action of the frontal ciliary tracts of the ordinary filaments.

The gills of *Lima hians* are eulamellibranch, deeply plicate and markedly heterorhabdic (figure 12 *a*). In the relaxed gill the principal filaments (p.f.) are U-shaped but with the ridges bearing the lateral tracts of frontal cilia (f.l.) more pronounced than in *Chlamys varia*. The

principal filaments thus enclose a well defined tubular gutter (p.f.). The filaments forming the crests of the plicae are considerably enlarged (a.f.). The frontal ciliary currents are similar to those of *Chlamys varia*, that is they are directed dorsally in the channels formed by the principal filaments but ventrally on those forming the crests of the plicae. Contraction of the gill, possibly because of its eulamellibranch structure, does not produce the same results as in *Chlamys varia*. The plication remains pronounced but adjacent plicae are more closely apposed so that the

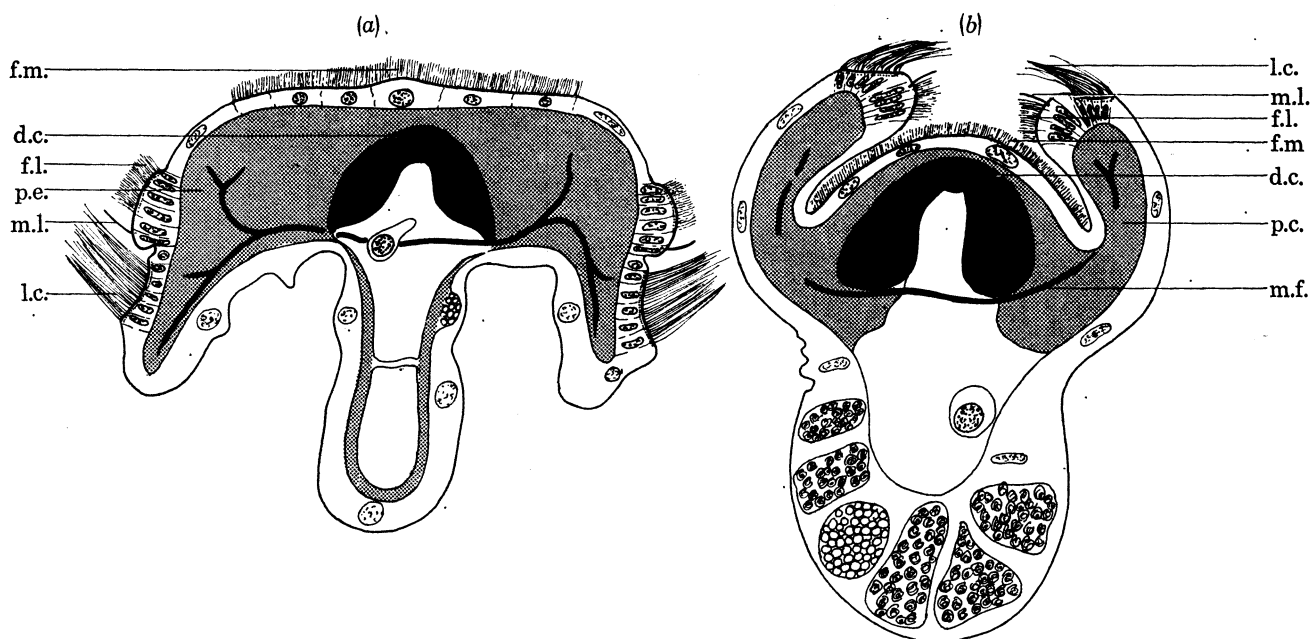


FIGURE 11. Semi-diagrammatic drawings of sections through contracted principal filaments of (a) *Chlamys varia* (after Owen 1976) and (b) *Lima hians*. Compare the form of the filaments with those of the relaxed lamellae shown in figures 10 and 12a respectively.

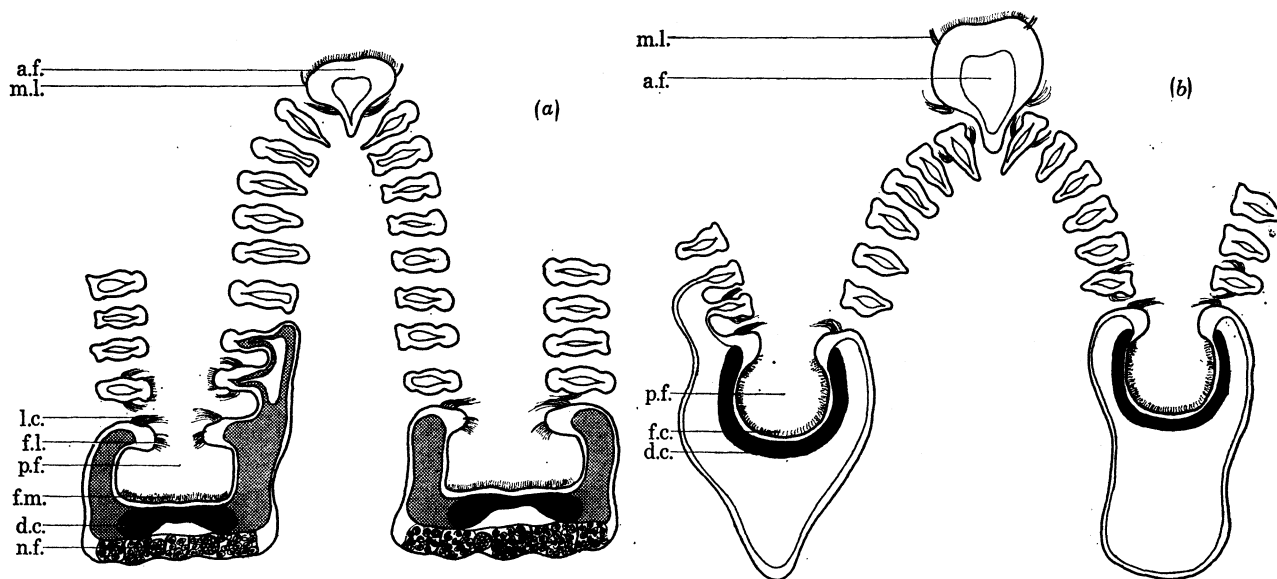


FIGURE 12. Diagrammatic horizontal longitudinal sections through relaxed gill lamellae of (a) *Lima hians* and (b) *Pinna muricata*. Note the form of the principal filaments (p.f.) and the enlarged apical filaments (a.f.).

exposed surfaces of the gill lamellae are formed mainly by the enlarged apical filaments. As for the principal filaments, the floor of the gutter is raised and the side walls curved inward to obliterate the channel present in the relaxed gill (figure 11*b*). It is reasonable to assume that in *Lima hians*, as in *Chlamys varia*, particles destined for ingestion are drawn in to the channels formed by the principal filaments and there carried dorsally in suspension by the water currents produced by the frontal ciliated tracts. In the contracted gill such water currents cannot operate and most of the material drawn to the gill surface will be carried ventrally on the crests of the plicae.

It was possible to examine only preserved material of the gills of *Atrina vexillum* and *Pinna muricata*. In both the gill is eulamellibranch, plicate and heterorhabdic and in both the frontal face of the principal filaments has the form of a deep semi-cylindrical groove (p.f., figure 12*b*). The apical filaments (a.f.) forming the crests of the plicae are greatly enlarged. Owing to the state of preservation of the material available it was not possible to determine the distribution of the frontal cilia on the principal filaments nor was it possible to determine the consequences of contraction of the gill. The eulamellibranch structure of the gill, the form of the principal filaments and the skeletal elements associated with them, suggest that contraction does not, as in *Chlamys varia* and *Lima hians*, result in any marked change in the form of the frontal faces of the principal filaments. Rather, the selection of material for possible ingestion is achieved by changes in the nature of the plication and the form of the marginal groove. Useful descriptions of the living gill of *Pinna fragilis* and *P. carnea* are given by Atkins (1937*a*) and Yonge (1953) respectively. The frontal ciliary currents on all the filaments are directed ventrally. Particles carried ventrally in the channels formed by the principal filaments readily enter the very deep marginal groove while material carried ventrally on the crests of the plicae is unable to do so. Both authors comment on the ability of the gill to contract and approximate the plicae to an extent where the exposed surfaces are presumably formed by the enlarged apical filaments only. Thus it would appear that in the Pinnidae, as in the Pectinidae and Limidae, the main method of collecting particles for ingestion is dependent on the flow of water currents associated with the form of the principal filaments rather than the filtration and transport of material by direct ciliary action.

As in *Lima hians* and *Pinna muricata*, the gills of *Ostrea edulis* are eulamellibranch, plicate and heterorhabdic. The frontal currents are similar to those of *Chlamys varia*, that is dorsal on the principal filaments, ventral on the apical filaments with intermediate filaments possessing both dorsally and ventrally beating tracts (Yonge 1926; Atkins 1937*a*). An obvious difference, however, lies in the form of the principal filaments. The frontal faces of these are not U-shaped but show an inverted V or U shape in sections of both contracted and relaxed gills. A similar form is shown by the principal filaments of *Ensis siliqua*, a species which undoubtedly possesses well developed compound eu-latero-frontal cirri and in which, although not related to *Ostrea edulis*, the form and ciliation of the gill is similar. Given such a shape for the principal filaments and bearing in mind the presence of ostia on each side of these filaments, water currents of the type postulated for *Chlamys*, *Lima* and *Pinna* could not be produced. It is suggested that in *Ostrea edulis*, and unlike *Chlamys*, *Lima* and *Pinna*, the collection of particles for possible ingestion is not dependent on the flow of water currents but, as in bivalves such as *Mytilus edulis* and *Ensis siliqua* which possess compound latero-frontal cirri, particles are collected by the straining effect of these cirri and the retained material is transported by the direct action of the appropriate ciliary tracts.

Thus it would appear both from the nature of the latero-frontal tracts and the mode of functioning of the gill that the Ostreidae should not be included in the Microciliobranchia. Like the Mytilidae, the family should be regarded as possessing compound eu-latero-frontal cirri and subsidiary pro-latero-frontal cilia rather than anomalous and para-latero-frontal cilia as suggested by Atkins (1938).

The question can now be asked whether the nature of the latero-frontal tracts has any value in indicating relations. Compound eu-latero-frontal cirri occur in a large number of divergent families and, apart from the absence of stiffening elements and the greater number of rows of pro-latero-frontal cilia in the Nuculidae (Owen 1976), there appears to be little to indicate possible sub-divisions of this large group. As for the Microciliobranchia, Purchon (1958) has suggested that while compound eu-latero-frontal cirri may once have been widely distributed through the class, they could have been lost on numerous occasions in different lineages. If this did occur then the occurrence of latero-frontal tracts composed of simple cilia only could not be relied upon as an indicator of phylogenetic relation. It cannot be overlooked, however, that the families which possess simple micro-latero-frontal cilia only are essentially those usually grouped in the sub-class Pteriomorphia, generally accepted by palaeontologists as a phylogenetic unit. Moreover, if the mode of functioning of the gill proposed here is also taken into account, then these families can be further sub-divided into three sub-groups: first, the Arcidae and Glycymeridae in which the flow of water currents does not appear to play a major rôle in the collection and transport of particles although the latero-frontal tracts are composed of simple cilia only; second, the Anomiidae, Pectinidae and Limidae in which the flow of water currents plays a significant rôle in the collection and transport of particles with the Anomiidae somewhat intermediate between the Arcidae and Glycymeridae on the one hand and the Pectinidae and Limidae on the other; and third, the Pinnidae in which, as in the previous group, the flow of water currents is important but the latero-frontal tracts show some significant differences, the details of which have still to be determined.

There are, of course, other recent families possessing simple latero-frontal cilia included in the Pteriomorphia but only those of which representatives have been examined during the present work are noted. The three sub-groups into which these fall correspond closely to the three orders given by Newell (1965, 1969) as comprising the Pteriomorphia, the Arcoida, the Mytiloida and the Pterioida. The main differences are the inclusion by Newell of the Mytilidae with the Pinnidae in the Mytiloida and of the Ostreidae in the Pterioida. As already indicated there appears to be some doubt about the origin of the Mytilidae and their inclusion in the Pteriomorphia. Thus it is the position of the Ostreidae which presents the main difficulty in accepting that those families which possess latero-frontal tracts composed of micro-latero-frontal cilia do represent a phylogenetic unit. Nevertheless, there is sufficient merit in the concept to justify not only further work on the nature of the latero-frontal tracts of bivalves but also a reappraisal of the position of the Ostreidae.

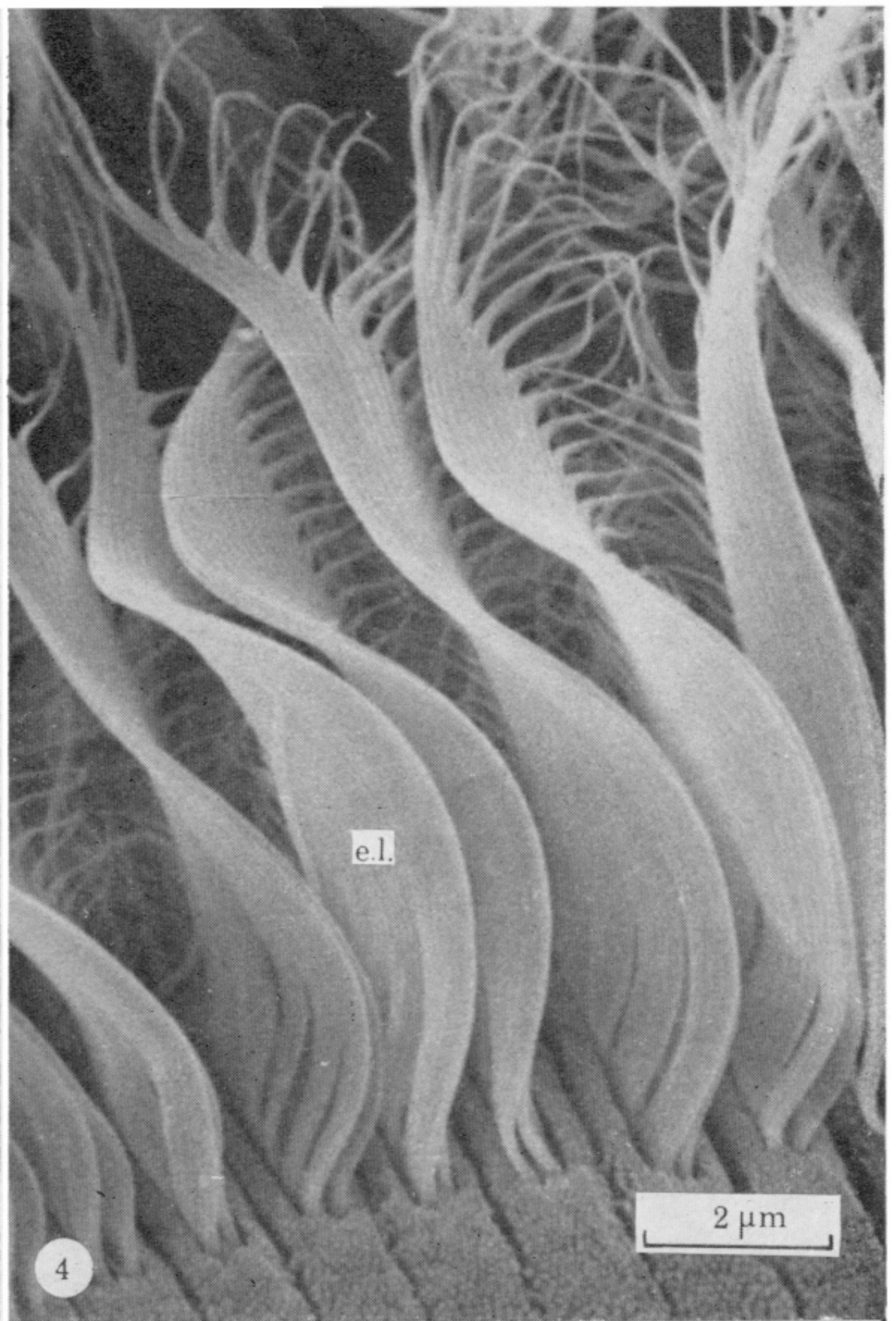
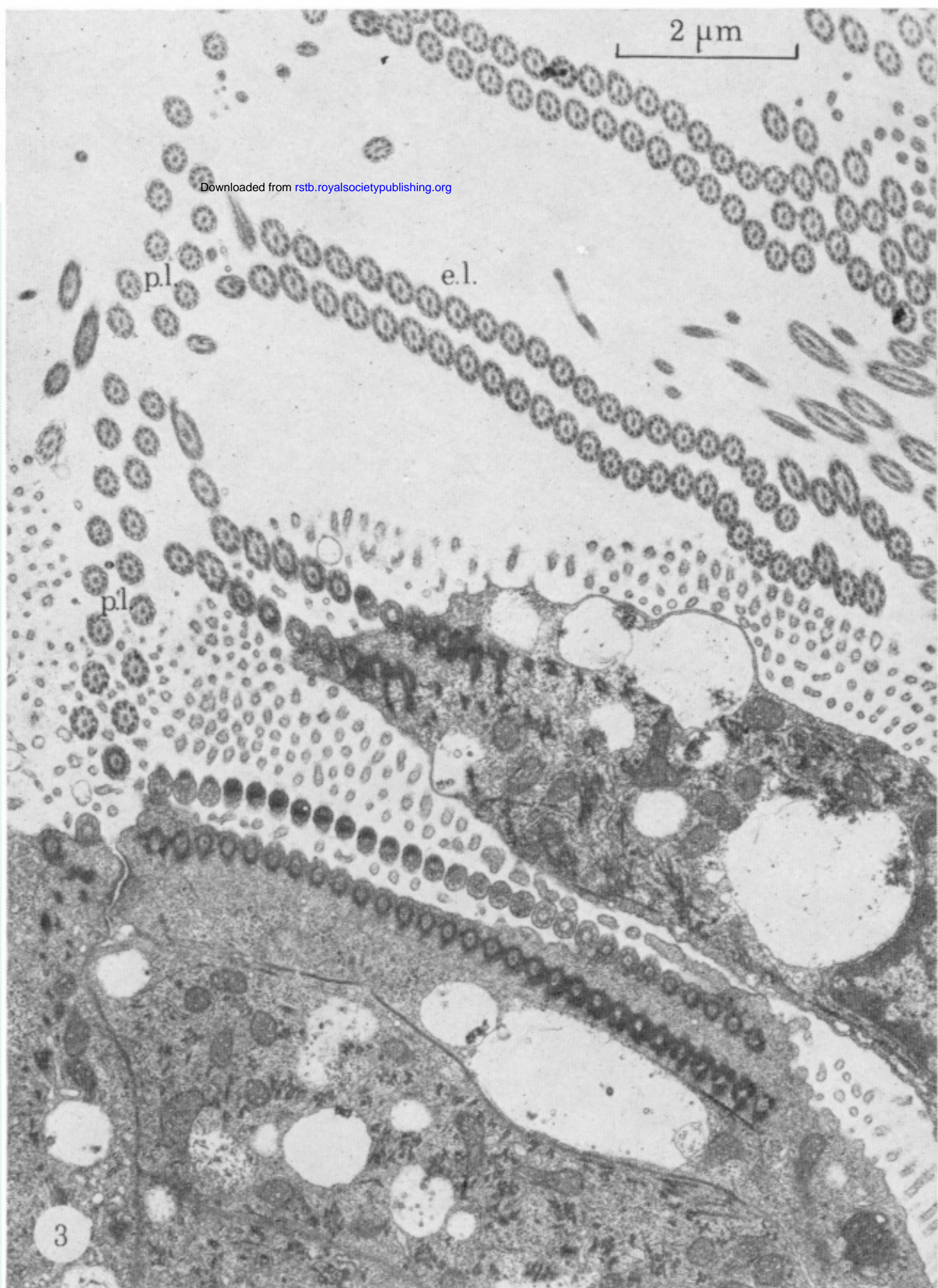
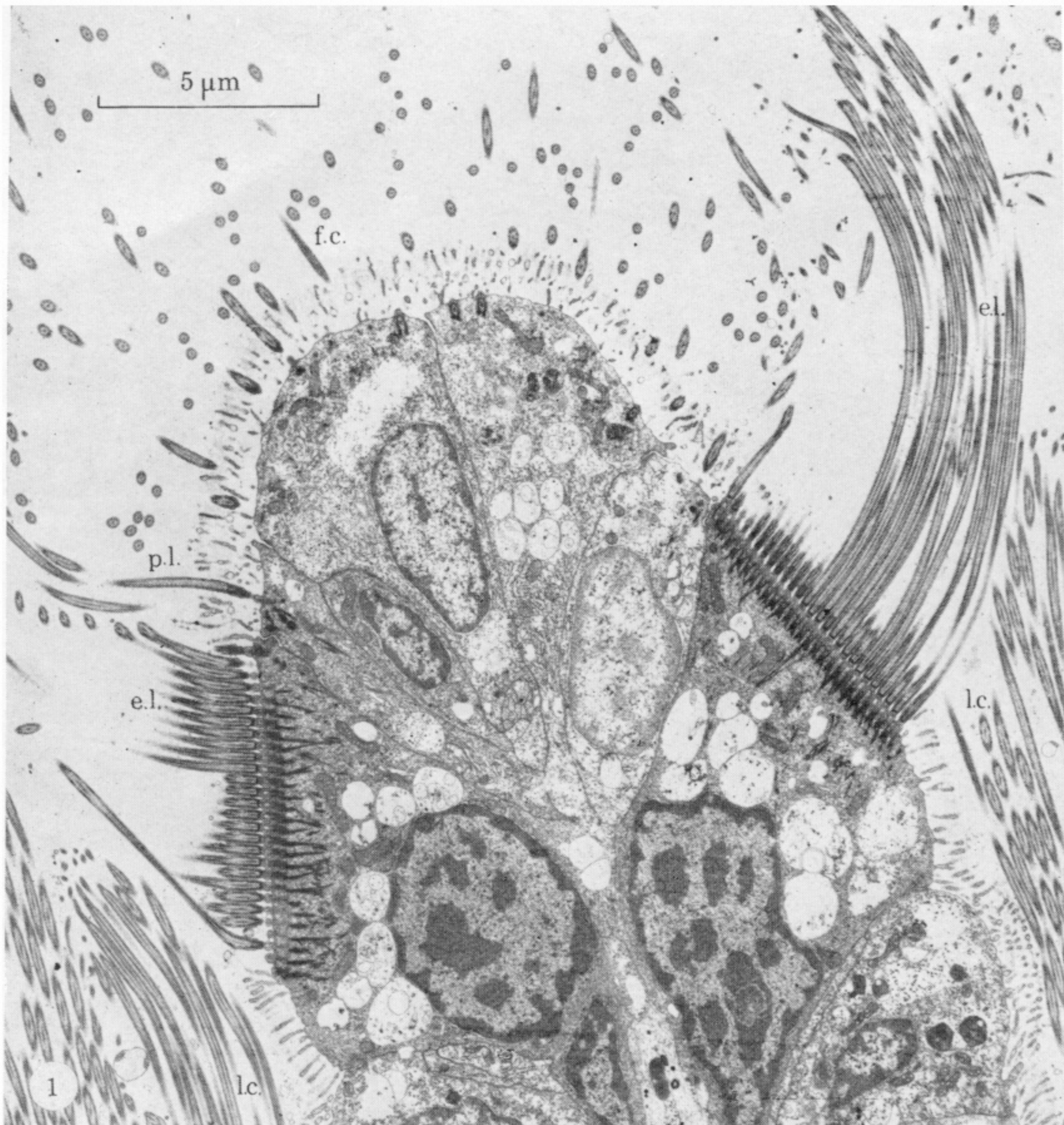
LIST OF ABBREVIATIONS USED IN FIGURES

a.f.	apical filament	f.c.	frontal cilia
a.x.	ctenidial axis	f.l.	lateral tract of frontal cilia
d.c.	dense staining chitin	f.m.	median tract of frontal cilia
e.l.	eu-latero-frontal cirri	i.c.	interlocking cilia

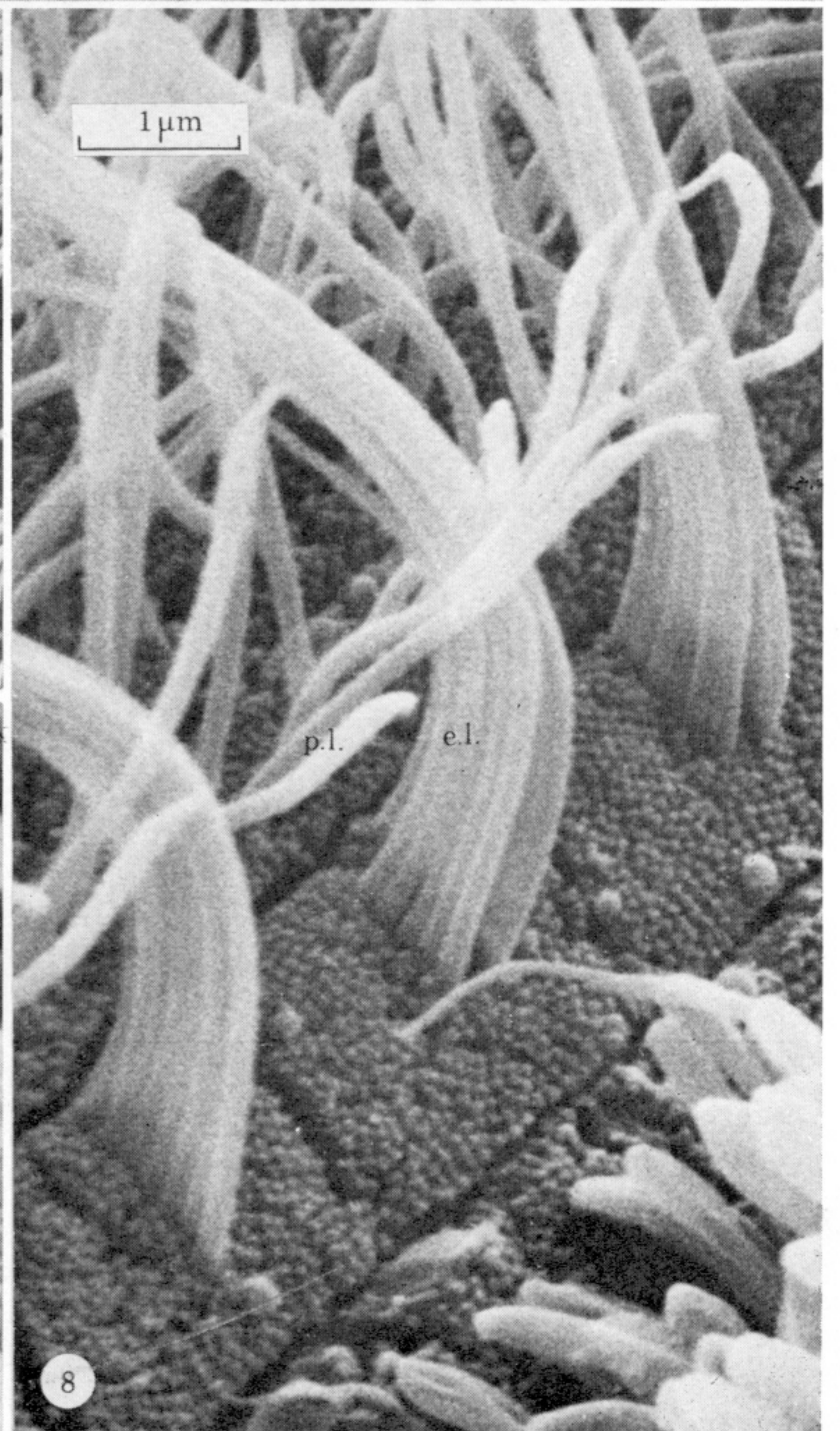
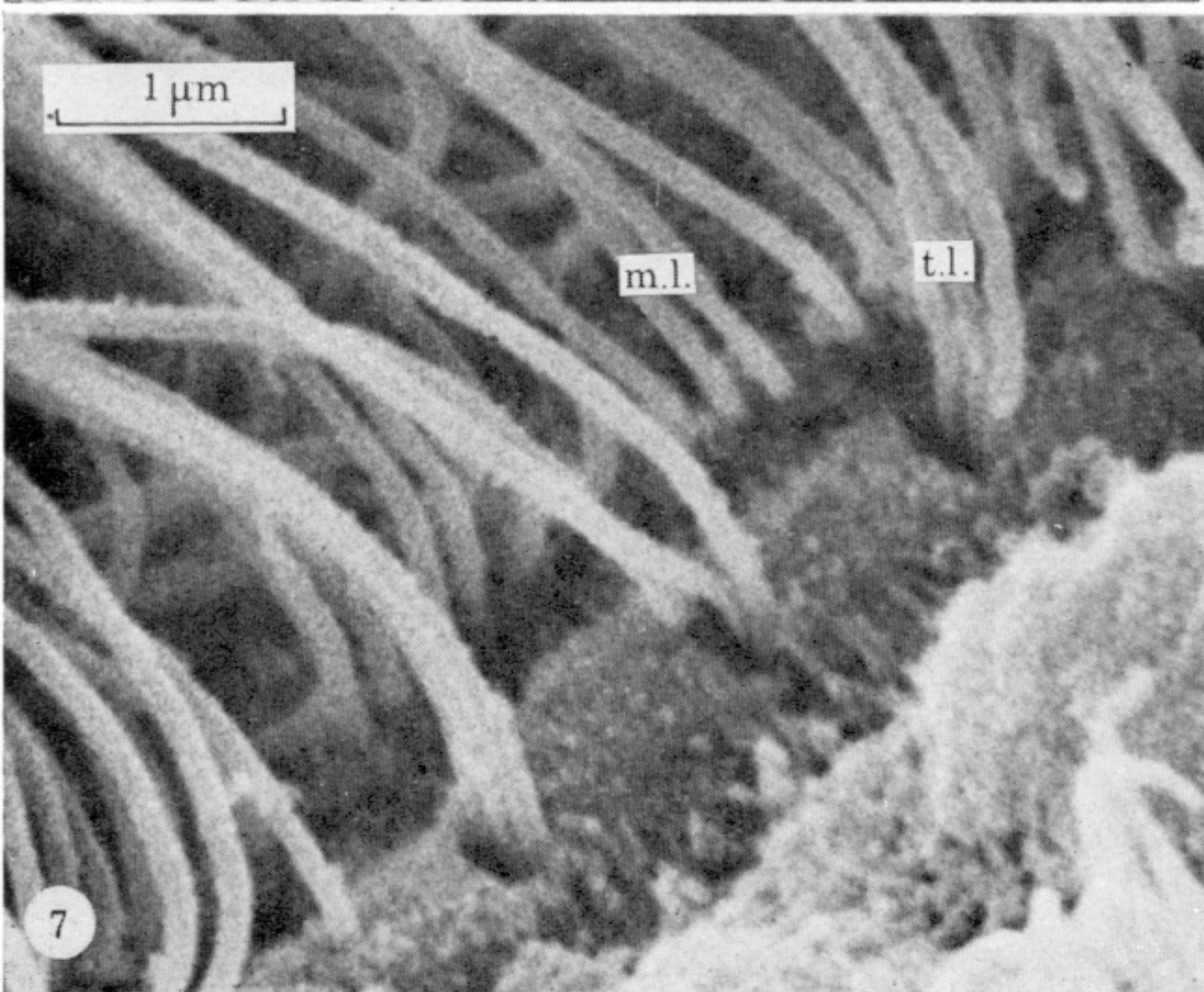
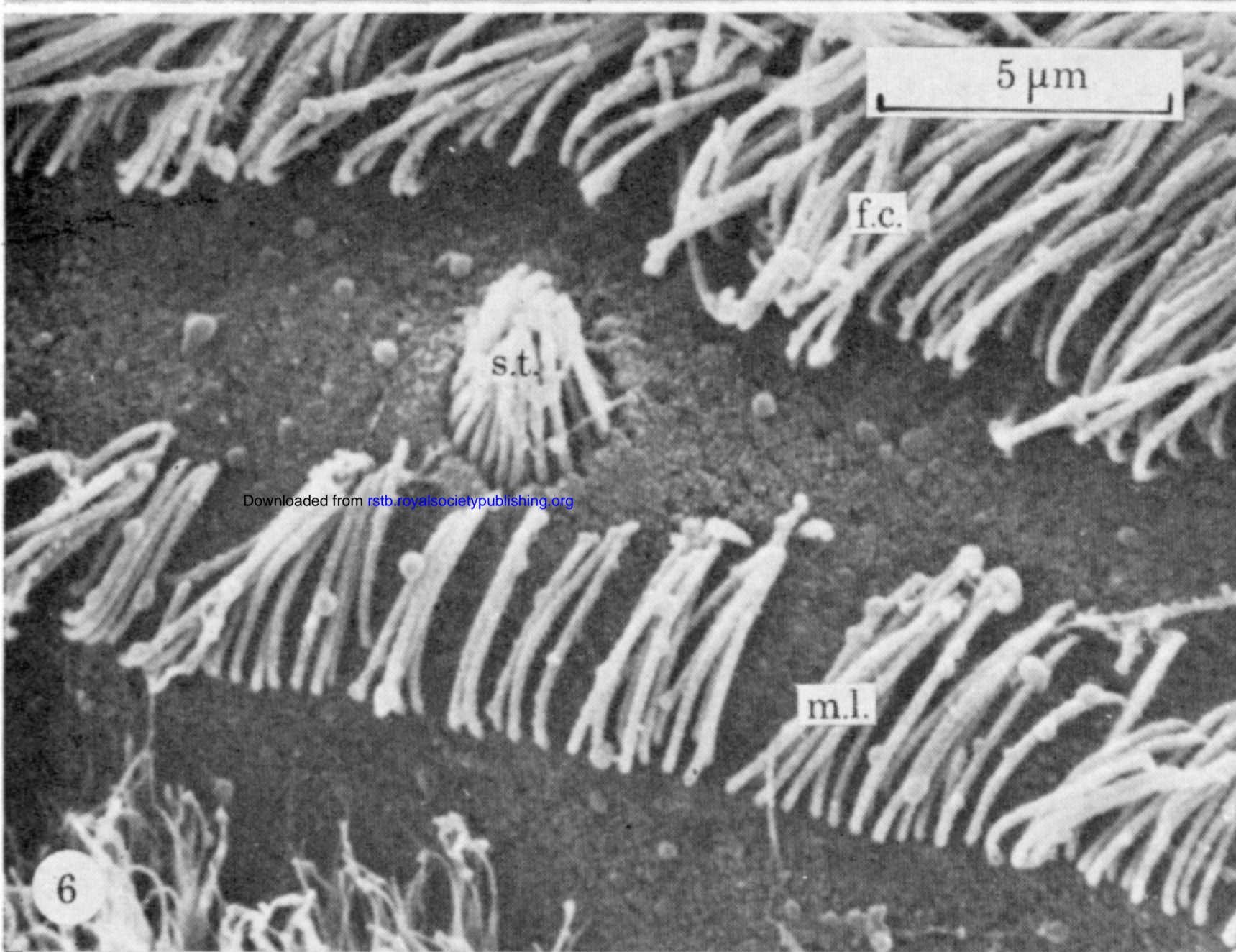
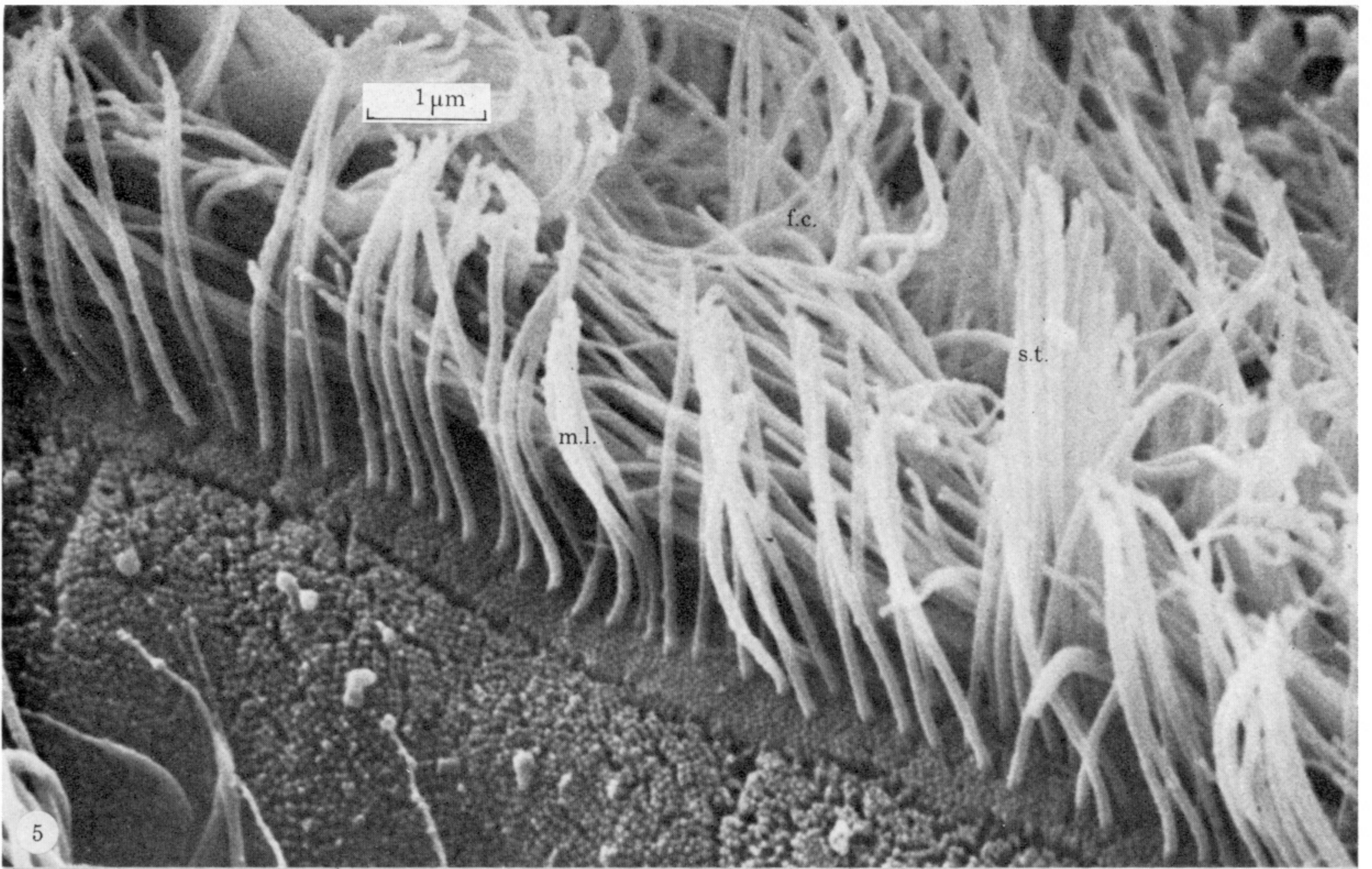
i.d.	inner demibranch	p.c.	pale staining chitin
l.c.	lateral cilia	p.f.	principal filament
m.f.	muscle fibre	p.l.	pro-latero-frontal cilia
m.l.	micro-latero-frontal cilia	s.r.	stiffening element
n.f.	nerve fibres	s.t.	sensory ciliary tuft
o.d.	outer demibranch	t.l.	latero-frontal cilia arranged in triplets

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FIGURES 1-4. For description see opposite.



FIGURES 5-8. For description see opposite.