THE ENGLISH SILURIAN FOSSIL *PLACOCYSTITES FORBESIANUS* AND THE ANCESTRY OF THE VERTEBRATES

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CONTENTS

Placocystites forbesianus de Koninck, from the Silurian Dudley Limestone, near Dudley, West Midlands, is here interpreted as a primitive chordate with a calcite skeleton of echinoderm type. This agrees with earlier papers by the senior author and disagrees with the work of Ubaghs (1968 etc.). Applying Hennig's terminology, *Placocystites* probably belongs to the stem group of the vertebrates and therefore throws light on primitive vertebrate anatomy. It also belongs to the group Calcichordata, set up by one of us as a subphylum (Jefferies 1967). The Calcichordata, however, are not comparable in phylogenetic position with the living chordate subphyla, so the word calcichordate will henceforth be used only informally, for any chordate with a skeleton of echinoderm type. Ubaghs, who has developed a totally different interpretation, assigns *Placocystites* to the subphylum Homalozoa of the phylum Echinodermata. In assigning it to that phylum, Ubaghs's work is more traditional than ours.

Within the calcichordates, *Placocystites forbesianus* belongs to the more advanced group known as mitrates. These are distinguished from more primitive calcichordates (cornutes) by having right gill slits in addition to left ones. Within the mitrates it is possible to suggest the stem groups, in the Hennigian sense, of acraniates, tunicates and vertebrates. The term standard vertebrate is proposed to denote vertebrates in the usual sense, as contrasted with those stem vertebrates included in the mitrates.

The two obvious parts of a calcichordate, formerly called theca and stem, or body and tail, are best called head and tail by homology with standard vertebrates. Mitrates correspond to the tunicate-tadpole-like protovertebrate of 'antisegmentationist' morphologists such as Froriep, Starck and Romer. The uniformly segmented protovertebrate of 'segmentationist' morphologists such as Goodrich would represent a real but later stage in the ancestry of standard vertebrates, descended from a mitrate.

The somites of standard vertebrates and acraniates can be plausibly identified inside calcichordates. The premandibular and mandibular somites would be located in the head, along with the buccal cavity, pharynx, gill slits and viscera. The left and right mandibular somites were probably represented in mitrates by the left and right anterior coeloms. The paired premandibular somites would be represented by a crescentic body situated in the posterior part of the head just in front of the brain. The hyoidean somites would be the most anterior pair of somites of the tail, totally separated from gill slits and gill bars. More posterior somites would also be in the tail, behind the hyoidean somites.

The homologues of the paired eyes of standard vertebrates can also be recognized as having existed in mitrates (cispharyngeal eyes). The presumed premandibular, mandibular and hyoidean somites were grouped round them in an arrangement which could give rise to the extrinsic eye muscles of standard vertebrates. The ears of mitrates were lateral to the hyoidean somites as they are in living vertebrate embryos.

The nervous system of *Placocystites* and its relatives is comparable with that of a fish. The brain was divided into two parts broadly corresponding to the prosencephalon and rhombencephalon of an early standard vertebrate (though the rhombencephalon of vertebrates also includes derivatives of the mitrate tail). The cranial nerves are deduced to have included olfactory, perhaps terminalis, optic, trigeminal and acustico-lateralis complexes. The trigeminal complex included opthalmicus superficialis and ophthalmicus profundus branches and a single pair of ganglia. Contrary to classical theory, it was not divided into profundus and 'true' trigeminal subcomplexes.

The pharynx of *Placocystites* and related mitrates was like that of a tunicate, particularly in certain asymmetries. Details of the skeleton strongly indicate that the pharynx in life would have contained an endostylar mucous trap of tunicate or ammocoete type, as classical theory would predict. The neural gland ('hypophysis') seems to have had the same relations as in a fully formed tunicate tadpole, but was probably endodermal in origin, homologous with Seessel's pouch of a vertebrate. The anatomy of the head of the primitive calcichordate *Cothurnocystis*, which was a cornute, and like other cornutes and larval amphioxus had left gill slits only, is reconstructed by working backwards from mitrates and by direct evidence from its skeleton.

The hypothetical latest common ancestor of lampreys and gnathostomes is deduced. The parts derived from the mitrate head can be distinguished from those derived from the mitrate tail. The animal probably possessed a notochordal head region and a trunk. These would have formed when gill slits and viscera migrated backwards ventral to the anterior part of the mitrate tail. The pericardium would have arisen by ventral growth of mitrate tail somites down the gill bars and their fusion ventrally to form a cavity. The visceral coelom arose by the ventral growth of mitrate tail somites round the viscera, accompanied by the development and fusion of cavities in the ventral parts of these somites. The branchial nerves of standard vertebrates are a mixture of placodal elements, probably derived from the mitrate head, and neural crest elements, probably derived from the mitrate tail. This hypothetical animal probably evolved from the mitrates when one of them took to habitual forwards swimming.

Placocystites probably crept backwards through the sediment just below the sea bottom, pulled by the tail. A pair of spines near the mouth would serve to cut into the sediment, probably assisted by water squirted along them from the buccal cavity.

1. General introduction

The purpose of this paper is to describe and interpret the curious fossil *Placocystites forbesianus* de Koninck, known from the Silurian Dudley Limestone (Wenlock Stage) near the town of Dudley, West Midlands, England. We hope to show that this fossil, contrary to its interpretation as an aberrant echinoderm (see for example Ubaghs 1968), is closely related to the first accepted vertebrates. Its anatomy can be reconstructed in detail and throws light on the primitive vertebrate condition.

The methodology of Hennig (1966, 1969) is crucial in reconstructing phylogeny. Hennig considered that, to understand the phylogeny of a group, we should try to arrange its members on a dichotomously branching tree of descent. He argued that the lines of descent leading to any three animal species are very unlikely to have separated from each other simultaneously. It can be assumed that two of the species share a latest common ancestor (their stem species), more recent than the latest common ancestor of all three. These two species will be more closely related to each other, in the strict sense of the word 'related', than they are to the third species.

The reconstruction of a dichotomously branching tree of descent for a group depends on recognizing advanced features in certain of its members, these features having been absent in the latest common ancestral species of the whole group. If such a feature evolved within the group only once, it would have evolved in a line of descent, or segment of the phylogenetic tree, common to the animals that share the feature, but later than the stem species of the group as a whole. Thus in figure 1, if *n* represents a nightingale, *o* an ostrich and *s* a smooth snake, then the presence of feathers in the two birds implies a line of common descent (*j* to *m*) for them, within which feathers evolved. This line of descent for the two birds would be later than their featherless latest common ancestor (*h*) with the snake, but earlier than their feathered latest common ancestor with each other (*m*). In working out the phylogeny of a group it is therefore necessary to ignore features primitive for the whole group, while attending to more advanced features restricted to certain members of the whole group. (In order to ignore primitive features, however, it is necessary to know what they were.) Hennig recommends that systematists ought, so far as possible, to define groups by the presence of advanced features.

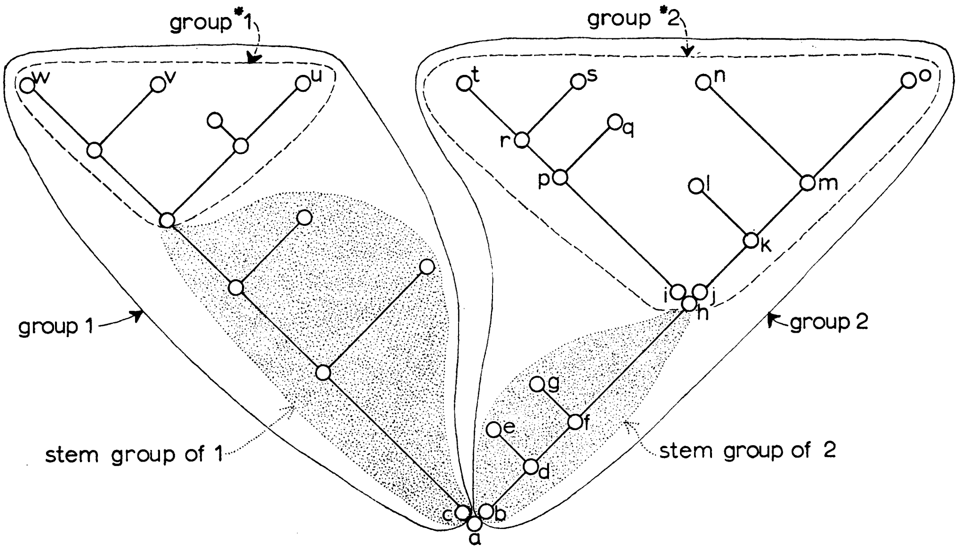

FIGURE 1. Hennig's stem-group concept. The letters are hypothetical species.

Each such group will be monophyletic in the strict or Hennigian sense, for it will include a stem species (presumed extinct) and all its descendants (e.g. groups 1 and 2, or groups *1 and *2 in figure 1). Monophyletic groups can be contrasted with polyphyletic and with paraphyletic groups. A polyphyletic group, as for example one comprising *w*, *t*, *s*, *o* and *n* in figure 1, but excluding *v* and *u*, excludes the latest common ancestor of itself and some descendants of this common ancestor which were ancestral to members of the polyphyletic group. All systematists would abhor it. A paraphyletic group is, in principle, a primitive part of a monophyletic group, and includes the stem species, but excludes certain advanced forms descended from its own members. Thus in figure 1 the group constituted by group 2, minus species *n*, *m* and *o*, would be a paraphyletic group. Such groups are acceptable to conventional systematists but, except for the stem groups discussed below, not to Hennig. Paraphyletic groups are defined partly by primitive and partly by advanced features. Thus amniotes are a monophyletic group, as also are mammals and birds. But reptiles, comprising all amniotes except mammals and birds, are a paraphyletic group. They are defined partly on advanced features, as having an amnion, but partly on primitive features, as having neither feathers nor fur.

The sister group is another important concept that Hennig has introduced to help in describing a dichotomously branching tree. When an ancestral species splits into two daughter species, each of these, plus all its descendants, will be the sister group of the other daughter species plus all *its* descendants. Thus in figure 1, group 1 is the sister group of group 2, while in figure 33 the echinoderms plus chordates are shown as the sister group of the hemichordates. The result of analysing a group according to Hennigian principles will therefore be a dichotomously branching tree, each segment of which corresponds to the evolution of a new feature, as in figure 33. The known members of the group will probably be at the ends of the twigs of the tree. For, at least when the fossil record is poor, known fossils will seldom be direct ancestors of other known forms, whether these be fossil or recent. Stratigraphical occurrence is consequently not very important in Hennig's methodology.

Hennig's stem-group concept (Stammgruppe) is an attempt to fit fossils into his method. It seems to have been ignored outside Germany (figure 1, see also Hennig 1969, pp. 32–53). Hennig points out that a group whose living members are monophyletically connected can be defined either in a narrow or a wide way when extinct relatives are taken into account. The narrow definition includes the latest common stem species of all living members and all descendants of this species. A group so defined is prefixed with an asterisk by Hennig e.g. *vertebrates. Thus group *2 in figure 1 includes species *h* and all its descendants, whether living or extinct. The wide definition, on the other hand, includes all descendants of the stem species which is common to the group and to the sister group, except all members of that sister group. Thus group 2 in figure 1 excludes species *a* and group 1, but includes the daughter species *b* and all *its* descendants. The stem group of a larger group comprises all species included by the wide definition but excluded by the narrow one. Thus, in figure 1, the stem group of 2 includes all descendants of species *a* which belong neither to group *2 nor to group 1. Stem groups are, by definition, paraphyletic and extinct. They are convenient because they can be set up without disturbing the systematic classification of living forms.

The group Calcichordata was set up by one of us in 1967 to include all chordates which retain a skeleton of echinoderm type, i.e. cornutes plus mitrates as shown in figure 33 (see also Jefferies 1968, 1969, 1973, 1975; Jefferies & Prokop 1972). It was given the rank of subphylum. It was a paraphyletic group, being defined partly by advanced features (notochord, dorsal nerve cord etc.) and partly by a primitive one (the calcite skeleton). In Hennig's terms it was an improper stem group (unechte Stammgruppe) since, if figure 33 is correct, it includes the earliest members of the living chordate subphyla, and also the stem group of tunicates plus vertebrates, in addition to true stem chordates. As research progresses the group Calcichordata is therefore splitting up. Eventually calcichordate systematics must be rewritten to take account of reconstructed phylogeny, but we do not propose to do this yet. It is clear that the Calcichordata do not constitute a subphylum logically comparable with the other chordate subphyla. We therefore proposed to use the word calcichordate in future only in an informal sense, for any primitive chordate with an echinoderm-like calcite skeleton.

The term 'standard vertebrate' is here proposed to comprise vertebrates as defined by custom. It includes the *vertebrates in Hennig's sense, but is widened to comprise all known fossil agnathans, some of which may have been stem vertebrates. It excludes all calcichordates. The oldest known standard vertebrate is *Anatolepis heintzi* (figure 2) from the Lowest Ordovician of Spitzbergen (Bockelie & Fortey 1976). This agnathan shows that the standard vertebrates had arisen from the calcichordates at an earlier date, presumably in the Cambrian. If the relations shown in figure 33 are correct, then the separation of acraniates from their tunicate-vertebrate sister goup, and the separation of tunicates from vertebrates, would also antedate *Anatolepis heintzi*, and would probably have happened during the Cambrian.

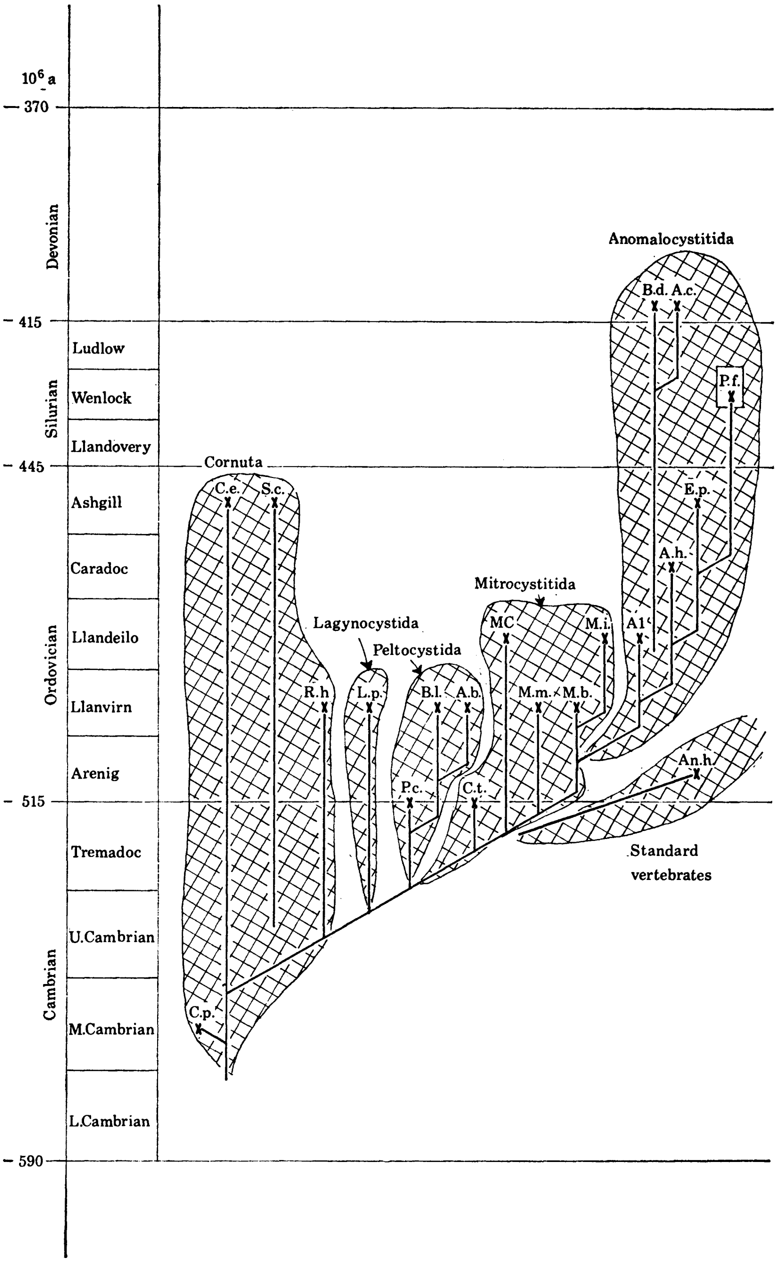

Figure 2. Stratigraphical distribution and probable phylogenetic relationships of fossils mentioned in text. A1 = first known Anomalocystitid (Prokop and Jefferies, personal observation); A.b. = *Anatiferocystis barrandei* Chauvel; A.c. = *Anomalocystites cornutus* Hall; A.h. = *Ateleocystites huxleyi* Billings; An.h. = *Anatolepis heintzi* Bockelie & Fortey; B.d. = *Basslerocystis disparilis* (Hall); B.l. = *Balanocystites lagenula* Barrande; C.e. = *Cothurnocystis elizae* Bather; C.p. = *Ceratocystis perneri* Jaekel; C.t. = *Chinianocarpos thorali* Ubaghs; E.p. = *Enoploura popei* Caster; L.p. = *Lagynocystis pyramidalis* Barrande; M.b. = *Mitrocystella barrandei* Jaekel; MC = Moroccan *Chinianocarpos* = *Mitrocystites* sp. of Chauvel (1971, p. 54); M.i. = *Mitrocystella incipiens* (Barrande); M.m. = *Mitrocystites mitra* Barrande; P.c. = *Peltocystis cornuta* Thoral; P.f. = *Placocystites forbesianus* de Koninck; R.h. = *Reticulocarpos hanusi* Jefferies & Prokop; S.c. = *Scotiaecystis curvata* (Bather).

The calcichordates are divided into two traditional major groups – the Cornuta Jaekel 1900 and the Mitrata Jaekel 1918. These have the rank of orders in the class Stylophora Gill & Caster 1960, which is coextensive with the subphylum Calcichordata Jefferies 1967. It is fairly certain that the Cornuta gave rise to the Mitrata and are therefore paraphyletic (Jefferies & Prokop 1972). It is also likely that the Mitrata gave rise to the *Acraniata, *Tunicata and standard vertebrates, and are therefore also paraphyletic. The genus *Placocystites* is an advanced mitrate and, being known from about 100 specimens, is the only common mitrate found in Britain.

The principal difference between cornutes and mitrates is that cornutes had left gill slits only, like larval amphioxus. Mitrates, on the other hand, are deduced to have had right as well as left gill slits, like adult amphioxus. All known living adult chordates share the advanced character of right gill slits with the mitrates. The latest common ancestor of tunicates, acraniates and vertebrates, which in Hennig's terms would be the latest common ancestor of the *chordates, was therefore probably a mitrate rather than a cornute.

All calcichordates consist of a massive part and an appendage. In most previous papers (Jefferies 1967–73 but not Jefferies 1975) we referred to these parts as 'theca' and 'stem' by supposed homology with crinoids and other stemmed echinoderms, while considering that they were also homologous with the 'body' and 'tail' of standard vertebrates. The supposed homology with theca and stem is in fact untenable. For Sprinkle (1973) has demonstrated that the stem, defined as a structure clearly distinct from the theca, arose at least twice within primitive echinoderms, among forms which, because of their pentameral symmetry and absence of gill slits, cannot be ancestral to calcichordates. The massive part and appendage of calcichordates are therefore not homologous with, but parallel to, the theca and stem of crinoids, as one of us had already admitted (Jefferies 1975), and as Eaton has argued on embryological grounds (1970).

To refer to the two parts as 'body' and 'tail', by homology with standard vertebrates, as in Jefferies (1975), is also somewhat unhappy. The term 'body', in reference to a standard vertebrate, may mean 'head + trunk + tail', or 'trunk + tail', or 'trunk' alone. It never means 'head' alone. And yet it is the head of a standard vertebrate to which the massive part of a calcichordate most closely corresponded. For in it were the pharynx, gill slits and buccal cavity, in contradistinction to the appendage or tail, which contained notochord, muscle blocks and dorsal nerve cord. In this paper we therefore propose to speak of 'head' and 'tail' (see also Jefferies, in the press) instead of 'body' and 'tail' (as in Jefferies 1975) or 'theca' and 'stem' (as in Jefferies 1967–73). Unlike standard vertebrates, the calcichordates had no trunk region, in which the notochord, dorsal nerve cord and muscle blocks would be dorsal to the coelom and the viscera, nor any notochordal part of the head, where these structures would be dorsal to the pharynx. Instead the head, which contained the viscera as well as the pharynx and buccal cavity, was entirely anterior to the tail.

Zoologists who have tried to reconstruct the ancestral standard vertebrate have been divided into two schools, which can be called 'segmentationist' and 'antisegmentationist'. The segmentationist school considers that the gill slits of this protovertebrate emerged between the most anterior muscle blocks. The antisegmentationist school, on the other hand, accepts that gill-slit segmentation and muscle-block segmentation are both real phenomena, but denies that they ever alternated in position. It sees the protovertebrate as like a tunicate tadpole in consisting of a head, with pharynx and gill slits, anterior to a tail, with notochord, muscle blocks and dorsal nerve cord. Both schools agree that muscle blocks primitively extended, on right and left, to the anterior end of the notochord. Both schools seem to have regarded their opponents' views as incompatible with their own.

At first sight the calcichordates, with their clearly distinct head and tail, strongly support the antisegmentationist view, as we formerly insisted (Jefferies 1968, pp. 299–302). In his recent presentation of the antisegmentationist case Romer (1972) referred to the protovertebrate head as the 'visceral animal' and the tail as the 'somatic animal' (figure 31). Romer's hypothetical protovertebrate in fact closely resembles a calcichordate, or in particular a mitrate, though he never said so.

However all standard vertebrates have a notochordal part of the head and a trunk region, which were therefore presumably present in their latest common ancestor. In evolving from the calcichordate to the standard vertebrate condition the coelom, viscera, pharynx and gill slits presumably migrated backwards ventral to the anterior part of what had previously been the tail. It is likely that muscle blocks and gill slits came to alternate in the notochordal head region of the resulting animal (figures, 34, 35 herein; Koltzoff 1901; Damas 1944, p. 221). But, if this had happened, both antisegmentationists and segmentationists would be partly right. The calcichordate-like and tunicate-tadpole-like 'antisegmentationists' animal' would be ancestral to the 'segmentationists' animal' which would have developed a notochordal head region, where gill slits were ventral to muscle blocks and alternated with them, and a trunk region where the viscera were contained in coelom ventral to the notochord and flanked by the muscle blocks. And the segmentationists' animal would be ancestral to all standard vertebrates.

The premandibular, mandibular and more posterior somites can be convincingly homologized in gnathostomes (Van Wijhe 1883; de Beer 1922, 1937), lampreys (Koltzoff 1901; Damas 1944) and acraniates (Koltzoff 1901; Damas 1944, p. 240). Homologues of these structures should therefore have existed in the mitrate latest common ancestor of gnathostomes, lampreys and acraniates and in this paper we try to demonstrate that such was the case.

As concerns feeding, we reconstruct the pharyngeal anatomy of *Placocystites* and its relatives in some detail. The pharynx can be closely compared, particularly in many curious asymmetries, with the pharynx of tunicates, in exact agreement with classical theory.

The nervous system of calcichordates, which can be reconstructed in detail on skeletal evidence, was fundamentally like that of a fish. By considering what would have happened when the trunk and notochordal head region of standard vertebrates arose it is possible to distinguish the elements in a fish's cranial nerves which derive from the mitrate head from those which derive from the mitrate tail. It is also possible to reconstruct the origin of the oculo-motor musculature and nerves and to recognize in mitrates the two fundamental divisions of the vertebrate brain as recognized by Starck (1975, pp. 369–372).

The mode of functioning of many features of the external anatomy of *Placocystites* can be explained by comparing it with its closest relatives.

We have studied *Placocystites forbesianus* by dissection and observation, and more particularly by constructing polystyrene models based on serial sections. Our study of *P. forbesianus* entailed a restudy of the related mitrate *Mitrocystella incipiens* (Barrande) *miloni* Chauvel from the Ordovician (Llandeilo) of Brittany by means of a polystyrene model and by examining internal moulds and latex casts. This study complements and modifies the account of the anatomy of this form given in Jefferies (1968). We have also restudied certain features of the mitrate *Mitrocystites mitra* Barrande from the Ordovician (Llanvirn) of Bohemia. Among the cornutes, we have restudied *Cothurnocystis elizae* Bather from the Ordovician (Ashgill) of Girvan in

Scotland. In the course of this work the junior author has mainly been involved in constructing the polystyrene models. The interpretation is the work of the senior author.

An alternative view of the calcichordates has been propounded by Ubaghs (1961, 1963, 1968, 1970, 1971, 1975) and incorporated in the 'Treatise of Invertebrate Paleontology' (Ubaghs 1968, and Caster therein). According to this view, which is by no means identical to the traditional interpretation of Bather (1913), what we call the tail of cornutes and mitrates was a feeding arm. A median groove in the tail, which we consider to have housed notochord and dorsal nerve cord, is seen by Ubaghs as accommodating a radial water vessel. Ubaghs further assumes that the obvious divisions of the cornute tail, known here as fore, mid and hind tail, are homologous with the like-named parts of mitrates. In our terms the cornutes have ventral ossicles and dorsal plates in the hind tail, whereas the mitrates have dorsal ossicles and ventral plates. But Ubaghs interprets the hind-tail ossicles and plates as homologous in the two groups. In consequence of this he considers as dorsal what we regard as the ventral surface of mitrates (for all workers agree which was the ventral side of cornutes).

Ubaghs has recently re-stated his views in polemical form (1975, pp. 84–87). His criticisms, and our answers, can be listed as follows:

1. Ubaghs rightly states that our interpretations are based on soft parts, which cannot be observed directly. This is true, but the same holds for his own views, which are based on the postulated presence of a water-vascular system in the tail.

2. Ubaghs rightly states that the skeleton of calcichordates is histologically identical with that of echinoderms, and unlikely to have originated twice. He then goes on to say, however, that they 'had an echinoderm-like skeleton because they were echinoderms' (Ubaghs 1975, p. 86). This is meaningless. Both we and Ubaghs assume that the skeleton in question only evolved once, and both views are, in this respect, equally parsimonious and equally likely. It is true that our view implies that the calcite skeleton was lost three times within the chordates, separately in the stem groups of acraniates, tunicates and vertebrates. In members of all three stem groups, however, there are signs of resorbtion of the skeleton in the adult. It is quite possible, therefore, that the actual initiation of the loss of skeleton only happened once, within the immediate common ancestry of these stem groups. In any case it seems that loss of the skeleton *had* begun in these stem groups. Ubaghs says that 'the skeleton of chordates, particularly vertebrates, is quite different'. But this statement is misleading, for vertebrates, and not all of *them*, are the only chordates that possess bone. There is no reason in comparative anatomy why the latest common ancestor of living chordates should have possessed it. On the question of bone see also Jefferies (1973, p. 420).

3. Ubaghs lists a number of non-histological skeletal features in which some calcichordates resemble some echinoderms and seems to imply, again, that therefore calcichordates are 'really echinoderms'. But these resemblances only signify phylogenetically if the features are homologous with those of calcichordates. With most of them this is very unlikely for they were probably not primitive for calcichordates. This is true for marginal plates, movable spines and 'plated coverings', none of which existed in the most primitive known cornute *Ceratocystis*. As to whether the plates at the anterior end of a cornute should be interpreted as an anal cone or an oral cone, the authority of Bather (1913) is irrelevant (see Ubaghs 1975, footnote p. 86). Bather's views have no more weight than his arguments for them, and these were based on a partly mistaken description of the gill-slit skeleton in *Cothurnocystis* (Bather 1913, pp. 403–405; cf. Jefferies 1968, p. 253).

4. Concerning the tail, which he calls the aulacophore, Ubaghs argues, as mentioned above, that the fore, mid and hind portions of the tails of cornutes are homologous with the like-named portions of mitrates. At first sight this seems an obvious interpretation, but one of us has argued elsewhere (Jefferies & Prokop 1972) that the whole tail of mitrates is homologous with only the fore tail of cornutes, the cornute mid and hind tail having dropped off. Ubaghs finds this explanation 'difficult to believe' (Ubaghs 1975, p. 87). However, to us it does not seem surprising, since autotomy appears to have been a regular feature in the ontogeny of calcichordates. For neither we, nor anyone else so far as we know, has ever seen an untruncated end to the tail. The termination is always abrupt, as if more distal segments had dropped off, but the observed, most distal segments are often specialized, suggesting that such autotomy was not accidental but regular (Jefferies 1973, p. 446; Jefferies & Prokop 1972, p. 94 ff). Moreover, in *Reticulocarpos* which is the most mitrate-like of known cornutes, the average number of segments observed in the hind tail is only about two (Jefferies & Prokop 1972, p. 91). The spiked and ventrally flattened ventral plates of the hind tail of the mitrate *Lagynocystis*, and the plated imbrication membranes of the hind tail of the mitrate *Chinianocarpos*, strongly suggest that the hind tail of mitrates should be compared and homologized with part of the fore tail of *Reticulocarpos* for this shows the same features. Ubaghs' view of the tail, in his own opinion, implies that the 'cover plates' of the hind tails could open in life. Against this is the way the plates articulate with the ossicles in *Scotiaecystis* (Jefferies 1968, p. 275, fig. 12, pl. 4, fig. 4) and the oblique overlap of the plates with the ossicles in *Chinianocarpos* (Jefferies & Prokop 1972, pl. 6C). These articulations and overlaps would have dislocated if the plates had opened outwards. The fact that the plates are often found separated from their antimeres can be explained by disarticulation after death.

These answers to Ubaghs' criticisms are naturally defensive. More constructively, however, our interpretation of the calcichordates has strengths. First, it agrees well with classical theory, in that echinoderms and chordates have long been seen as related, and in that mitrates are remarkably like the protovertebrate imagined by the antisegmentationist school of zoologists. Furthermore we attempt to show in this paper that, contrary to what we thought once, the calcichordate interpretation is compatible with most of the assertions of classical segmentation theory. Secondly, there are many conjunctions of features in calcichordates and primitive living chordates which are difficult, or in our view impossible, to explain by accident. Examples are the gill slits of cornutes (left gill slits only, as in larval amphioxus), the rectum opening into the left atrium in mitrates as in tunicate tadpoles, and, above all, a number of asymmetries in the deduced mitrate pharynx which recur in tunicates, as we try to show in this paper. In addition there is evidence of dorsal nerve cord, notochord, muscle blocks, and a fish-like brain and cranial nerves. The fact that Ubaghs has never produced a detailed and coherent interpretation of the features inside the mitrate head is not a strength but a grave weakness of his position. Note, however, that he too regarded the gill slits of *Lagynocystis* (Ubaghs 1968, pp. 552, 525 under ctenoid organ) as having a respiratory and food-filtering function with water flowing through them. He also suspected that what we call the nerve canals of mitrates carried nerves (Ubaghs 1968, p. 532).

The study of *Placocystites*, therefore, in our view throws light on a number of old problems of vertebrate comparative anatomy, suggests that the protovertebrates imagined by segmentationists and antisegmentationists are not incompatible with each other, and indicates how the adaptive radiation of the living chordate subphyla probably occurred.

2. Historical introduction, previous work on *Placocystites forbesianus*

Placocystites forbesianus, which is the only mitrate at all common in Britain, and the only known upper Silurian calcichordate, was first described by de Koninck (1869) on the basis of two specimens from the Wenlock Limestone of Dudley (i.e. what is now called the Dudley Limestone). The specimens at that time were in the collection of John Gray of Hagley, nr. Stourbridge. De Koninck referred to his new form as a remarkable echinoderm belonging to 'la famille des Cystidées' but he did not compare it with any previously known genus. The specimens described by de Koninck were shortly afterwards bought by the British Museum, together with others in the Gray and Ketley collections, and an English version of de Koninck's paper, translated by Henry Woodward of the British Museum, was published in the next year (de Koninck 1870). In a footnote to this English version Woodward remarked that *P. forbesianus* resembled *Ateleocystites huxleyi* Billings 1858, from the Upper Ordovician of Canada. In 1871 he published a paper synonymizing these two species, though he confessed later that this had been due to misunderstanding a letter that Billings had written to him (see Woodward 1880, p. 194). In his paper of 1871, Woodward described the oral spines and certain details of the head ornament and tail for the first time and also described the dorsal plating which de Koninck had not noticed. He also remarked a resemblance between *P. forbesianus* and two further North American species described by Hall as *Anomalocystites cornutus* and *Anomalocystites disparilis*. In this paper Woodward figured certain fragments (Woodward 1871, figs 6*a–c*) as portions of the 'stem' or hind tail of *Placocystites forbesianus*. These fragments were in fact machaeridians, being the original material of *Lepidocoleus ketleyanus* (Reed) (see Withers, 1926, p. 20).

In 1880 Woodward published a further paper, recognizing *P. forbesianus* as distinct at the specific and subgeneric level, contrary to his view of 1871, and placing *Placocystites* as a subgenus of *Ateleocystites*. He assigned *P. forbesianus* to the family Anomalocystidae Meek 1872. This paper also contains a fierce rebuke aimed at the American Wetherby, who in 1879 had placed the closely related genus *Enoploura* in the Crustacea, misled by the ornament. In 1888 Lindström recorded a form listed as *Ateleocystis huxleyi* Billings from the Silurian of Gotland. Regnéll (1945, p. 196) has suggested that this was probably a specimen of *Placocystites* and Gislén, who had seen the specimen, was of the same opinion.

In 1896 Haeckel described what purported to be the new species *Atelocystis gegenbauri* from the Wenlock Limestone of Dudley. This is a junior synonym of *Placocystites forbesianus* de Koninck, as Regnéll (1945, p. 197) has already pointed out. In this same paper Haeckel also introduced a piece of purely fanciful morphology into the group, in that he equipped *Anomalocystites balanoides* Meek, which he unaccountably called *Placocystis crustacea* Haeckel, with a pair of delicate, flexible, jointed and branched arms, instead of the oral spines (Haeckel 1896, figs 1, 2, p. 40). Haeckel was happier in suggesting that the tail was an organ of locomotion (1896, p. 34) rather as in crustaceans.

In 1900 Bather (p. 51) described *Placocystites forbesianus* in better detail than previously, particularly as regards the oral spines and the precise distribution of the ornament. He put it, along with a number of 'carpoid' forms, in the family Anomalocystidae, very broadly conceived.

Also in 1900, Jaekel placed *Placocystites*, along with other forms grouped by him in the family Anomalocystidae, in his new order Cornuta of his new class Carpoidea. Jaekel's classification was a great advance for its period, but one of his less happy ideas was his order Marginata, which included his conception of the family Mitrocystidae among other forms, and thus separated these from their relatives included by him in the Anomalocystidae.

This divorce of the Anomalocystidae in Jaekel's sense from the Mitrocystidae was criticized by Bather (1913) as unnatural and in 1918 Jaekel accepted Bather's criticism and placed Anomalocystidae, Mitrocystidae and Lagynocystidae (to use his spellings) in a new order Mitrata. This was a truly major advance. Dehm (1933, 1934) and Chauvel (1941) both accepted this classification.

In 1952 Caster, in connection with a detailed redescription of Wetherby's genus *Enoploura*, placed *Placocystites*, which he spelt *Placocystis*, in a new family Placocystidae of a new suborder Placocystida of the order Mitrata. This family and suborder he separated from his new suborder Anomalocystitida and the family Anomalocystitidae, in the mistaken belief, echoing Haeckel, that the Anomalocystitida had flexible oral appendages, rather than rigid oral spines. More recently Caster himself (in Ubaghs 1968) has shown that the Anomalocystitidae have rigid oral spines like *Placocystites*. For this reason the Placocystidae and Placocystida became indistinguishable from Anomalocystitidae and Anomalocystitida, and had to be abandoned. Ubaghs (1968) diagnosed *Placocystites*, redescribed it according to the morphological interpretation that he preferred, with the tail as an arm, and published drawings of it and various portions of its anatomy. He also described the oral spines much more precisely than before (his figs 331, 4a, b, c, fig. 332, 7, figs 359, 2a, b).

The most recent published reference to *Placocystites forbesianus* is by Cocks & Walton (1968, p. 395). These authors recorded the species from the Purple Shale (Llandovery series) of Devil's Dingle, Shropshire. The specimen in question (BMNH E 29331) is an external cast of most of the dorsal surface of the head. It should perhaps be referred to as *Placocystites* cf. *forbesianus* because its head is relatively less broad than in the Dudley specimens.

Pope (1975) has recently revived the suggestion that certain machaeridians are plates belonging to Anomalocystitid mitrates, though, unlike Woodward (1871) he sees them as perhaps enclosing the oral spines. It seems possible that some structures previously identified as short portions of machaeridians may be sleeves of plates in this manner, though many machaeridians are too long and sinuous for such an interpretation to be acceptable.

3. METHODS

All our previous investigations of calcichordates have been on material preserved as hollow moulds. By making latexes of these, and by examining the internal moulds direct, it has been possible to study the anatomy, both external and internal, in detail. By drawing reconstructions in several projections simultaneously on a drawing board we were able to obtain a coherent three-dimensional picture. In the present investigation, however, only the specimens of *Mitrocystella incipiens miloni* and *Mitrocystites mitra* were preserved as hollow moulds that could be studied in this way. *Placocystites forbesianus* itself is preserved as calcite plates of echinoderm type, embedded in a greenish marl of varying hardness. This demanded a different approach.

In studying the outside of *P. forbesianus* we used direct examination of many different specimens, making several projections simultaneously on a drawing board, much as in our previous work. It was necessary, however, to dissect certain delicate structures, especially the tail (plate 3, figures 67, 68). Dolomite or calcite powder in an airbrasive machine eroded the fossil almost as quickly as it did the matrix. Sodium bicarbonate in an airbrasive machine, on the other hand, removed only the softest parts of the matrix, leaving the fossil obstinately buried. Acting on a suggestion by Mr A. E. Rixon we therefore decided to soften the matrix artificially by leaving the specimen overnight in a strong solution of sodium hexametaphosphate (Calgon = $(Na_3PO_3)_6$), having protected the exposed parts of the fossil by painting them with latex or paraffin wax. After such soaking it always proved possible to blow away a little more of the matrix using sodium bicarbonate in the airbrasive machine. In this way, by repeated alternate blowing and soaking, we were able to expose fairly delicate structures. Large lumps of matrix which seemed unlikely to contain any part of the fossil were scratched away gently with a steel needle.

This method of dissection may be useful to other workers. When soaking the specimen it is absolutely essential to protect the already exposed parts of the fossil. Painting these parts with a solution of polybutylmethacrylate (Vinalac 5911) would give better protection than the latex or paraffin wax that we used. The varnish so formed could be removed with methyl ethyl ketone.

We also used ultrasonic cleaning when reconstructing the outside of *Placocystites*. This reveals differences in surface texture which cannot be seen otherwise, but it tends to disintegrate the fossil and must be used with great care.

We studied the internal anatomy of *Placocystites*, and also of *Mitrocystella*, by means of enlarged models in expanded polystyrene, based on serial sections. The use of expanded polystyrene to make models from serial sections was originally developed by Pedler & Tilley (1966). These workers used a × 3 pantograph, which was in some ways convenient, but led to inertial errors which had to be overcome by use of a servo-unit (Pedler 1968). We are very grateful to Dr Pedler for allowing us to use his machine at the Institute of Ophthalmology, London, in the early stages of our project.

In our own work we used a × 1 pantograph kindly lent to us by its designers, Ammonite Ltd, Llandow Industrial Estate, Cowbridge, Glamorgan (plate 15, figure 140). This is somewhat less convenient than Dr Pedler's machine, in that the photographs used must be enlarged to a greater magnification, but it is very much simpler and cheaper. It consists of a simple, hinged, steel-tube framework by means of which the point of a steel follower can be moved in a horizontal plane while a hot wire, held precisely beneath the follower in a vertical line, carries out an exactly similar series of movements in a lower horizontal plane, cutting a horizontal sheet of expanded polystyrene as it does so. The pantograph is mounted on a wooden base plate to which a perspex-topped table is also attached and the enlarged photograph of the relevant section is fixed to the table when the machine is in use. A hinged, wooden frame, designed to hold a horizontal sheet of expanded polystyrene, is clipped into position underneath the perspex table. Current to the hot wire in the pantograph is supplied from the mains through an adjustable D.C. power supply with an output of 12V and 0–5 A. This is a Clipper power-control unit produced by Hammond & Morgan Ltd and normally used in controlling model railways. The amount of heat produced should enable the wire to cut smoothly through the polystyrene without dragging or tearing, and yet without burning an aureole in the polystyrene round the cut. The hot wire is 40 S.G. Constantan high resistance wire, silk covered, with a resistance of 41 Ω/m. It is stretched vertically between two horizontal arms of the pantographs, one of which is just above the polystyrene and the other just beneath it. At the ends of each of these horizontal arms is a horizontal wing in which a brass sleeve is held by a grub screw. Each brass sleeve has a hole running through its central vertical axis, just big enough to accept the cutting wire. In this way the length of wire which remains unsupported is reduced to a few millimetres. The tension in the wire is adjusted by altering the height of the upper brass sleeve and its ring. It is desirable to put the wire under tension when cold, by pressing the two horizontal arms of the pantograph slightly together. In this way the wire does not become slack when hot. Slackness in the unsupported wire introduces an error into the polystyrene cut-out and also makes the wire break much more quickly than otherwise.

The expanded polystyrene sheet used was 2 mm thick Coatina, available in rolls 24 in wide. It is normally employed as an insulating backing for wall paper.

When the apparatus was in use, an enlarged photograph of the section to be copied was taped to the perspex table. The pointed steel follower was moved over the shape in the photograph, so that the hot wire cut out an exactly similar shape in the polystyrene beneath. Before beginning to cut, it was necessary to pencil in a series of brackets and struts on the photograph, which, when reproduced in the polystyrene, held the cut-out shape together. Brackets and struts thus cut in the polystyrene were coloured distinctively with water-soluble inks.

Specimens to be sectioned were set in blocks of dental plaster, or as later proved more satisfactory, in transparent resin (Trylon EM 301). The blocks were accurately squared up to ease alignment of sections. They were then sectioned at 100 μm intervals using the parallel grinding machine ('Nottingham grinder') described by Hendry, Rowell & Stanley (1963). Cellulose acetate sheet peels were taken of each section and when dry were mounted between two glass slides. The slides were photographed and prints made on unglazed paper to give a magnification of 20 times the original, so that magnification in the plane of section was equal to magnification perpendicular to it, i.e. magnification = (thickness of polystyrene/section interval) = 20.

In constructing the models, the cut-out polystyrene sections were joined together in bundles of 20 by means of entomological pins which were also inserted to give strength to delicate structures. A thin aqueous suspension of polyvinyl acetate was then brushed over the surface of the model to act as cement. In this way sufficient of the suspension ran between the polystyrene sheets to glue them together. It was not necessary to glue each sheet individually to its neighbours. When the cement was dry the pins were removed, where desirable, and the artificial brackets and struts that held the model plates together were gradually cut away with a sharp scalpel, as far as possible, so that the plates could be restored to their correct life positions. All the glues and inks applied to the models were water based. Other solutions would have destroyed the polystyrene. The models were mounted on thick polystyrene base plates, with the dorsal and ventral armour separated, and were kept in wooden boxes for protection.

Stacks of glass slides were useful in modelling certain features of the nervous system from serial sections. Relevant parts of the sections, as recorded on the cellulose acetate peels, were first drawn on to paper by using a camera lucida. The drawings so obtained were traced in Indian ink onto glass slides with a Rapidograph pen. The suspected positions of nerves were marked on these ink drawings in white ink and the slides were then fixed together in sequence, by using transparent resin (Trylon EM 301). In this way a three-dimensional view of complicated parts of the nervous system could be obtained (plate 8, figures 95, 96, 97). Unfortunately this method gave good results only for lines of vision almost perpendicular to the planes of section. The refractive index of the resin was too different from that of glass to obtain an adequate picture in aspects nearly parallel to the planes of section. Air bubbles between successive sheets of glass tended to form if the white ink was too thick. We have described these techniques in detail in the hope that other workers will use them.

4. HORIZON AND LOCALITY

Nearly all the known specimens of *Placocystites forbesianus* are from the Dudley Limestone near the town of Dudley, West Midlands (formerly in Worcestershire). The Dudley Limestone was known, until recently, as the Wenlock Limestone of Dudley (see for example, Butler 1939) but the name Dudley Limestone is now accepted. In the correlation chart of Cocks *et al.* (1971, fig. 4) it is shown as exactly equivalent in age to the Wenlock Limestone of Wenlock and as corresponding to part of the *Monograptus ludensis* zone of the graptolite sequence. More recent work, however, indicates that the Dudley Limestone is older than the Wenlock Limestone, ranging in age from the *linnarsoni* to *lundgreni* zones (L. R. M. Cocks, personal communication). It remains of Wenlock age, but extends from the Middle into the Upper Wenlock. The Dudley Limestone is exposed north of Dudley in the three small anticlines of Castle Hill, Wren's Nest and Hurst Hill (Butler 1939). These outcrops are now in West Midlands, but formerly were in Staffordshire. Nearly all the known specimens of *P. forbesianus* were collected between about 1850 and 1900. There is no precise stratigraphical information with the specimens and some, indeed, may have come from the Wenlock Shale beneath the Dudley Limestone (Butler 1939, p. 38). Usually, also, there is no information as to which of the three anticlines any given specimen came from, although most were probably from Wren's Nest. Fortunately detailed information as to locality and horizon is not very important for the present study.

The Dudley Limestone includes unstratified coral-bryozoan reefs embedded in contemporaneous stratified limestone. The specimens of *Placocystites forbesianus* are in a grey or greenish, rather silty marl and presumably come from inter-reef deposits. Scoffin (1972) has studied the similar reefs in the Wenlock Limestone of Wenlock and considers that they were deposited at a depth of 30 m or less. The depth of deposition of the Dudley Limestone reefs may have been similar, while the inter-reef deposits could have been laid down in rather deeper water.

In this study we have encountered only two specimens of *Placocystites forbesianus* which are recorded as not coming from the Dudley Limestone. One is the above-mentioned BMNH E29331 from the Purple Shale (late Llandovery) of Devil's Dingle, Shropshire (Cocks & Walton 1968). The other is BMNH E28690, recorded as from the Wenlock Shales, The Tunnel, Dudley.

5. MATERIAL AND LECTOTYPE

Specimens of *Placocystites forbesianus* examined during this investigation belong to the British Museum (Natural History), to the Geology Department, University of Birmingham, to the Sedgwick Museum, Cambridge and to the Natural History Museum, Nottingham.

British Museum specimens examined were: E417, E1462, E7513, E7514, E7539–E7544, E7545 (figured Bather 1900, p. 51, fig. 13, 2), E7546–7552, E7588 (the figured syntype of de Koninck 1869, fig. 2, 4, 5, 1870, pl. 7, fig. 2, 4, 5; also Woodward 1880, pl. 6, fig. 16; Haeckel 1896, pl. 2, fig. 10, here selected as lectotype plate 3, fig. 72), E7626, E16141, E16142, E16143 (used in making model), E16144, E16145, E16190, E16191, E28668 (figured Woodward 1880, pl. 6, fig. 18), E28669 (figured Woodward 1880, pl. 6, fig. 19). E28670 (figured Woodward 1880, pl. 6, fig. 20), E28671 (figured Woodward 1880, pl. 6, fig. 21), E28672 (figured Woodward 1880, pl. 6, fig. 17), E28673–E28683, E28689, E28690 (Wenlock Shale), E28691, E28692, E28693 (the unfigured syntype of de Koninck), E29331 (mentioned Cocks & Walton 1968), E29332–E29341.

Specimens possibly used by Woodward in restorations (1871, 1880) are not here recorded as figured.

Birmingham University specimens examined were: Holcroft Collection; 1–5, 7–15, 17–19, 21, 23, 24, 25 (used in making model), 27–29, 31, 32, 34–36, 38, 39, 43–45, 47–49, 54, 57, 60–62, 211–219, no number; 5 specimens in the Beale Collection; 6 other, unnumbered specimens.

Sedgwick Museum specimens examined were: A9011, A9013, A9015–A9023, A12570, A12932.

Fourteen specimens, numbered N1–14, from the Nottingham Museum of Natural History were also examined.

6. COMPARATIVE MORPHOLOGICAL DESCRIPTION OF *PLACOCYSTITES FORBESIANUS*

(*a*) *Introduction*

In describing *P. forbesianus* we shall often digress into the morphology of other mitrates. In doing so we have in mind the deduced phylogeny of the mitrates shown in figures 29 and 30 which is justified in a later section of this paper. The main mitrates used in comparison are *Mitrocystites mitra* Barrande from the Llanvirn (L. Ordovician) of Bohemia, and *Mitrocystella incipiens* Barrande *miloni* Chauvel from the Llandeilo (M. Ordovician) of Brittany. These two forms are informative for two reasons. First they are usually preserved as internal moulds, which allows many details to be observed by inspection rather than by making models. Secondly they are in most ways more primitive than *Placocystites*. If the phylogenetic relationships of these three forms are considered in isolation, *Mitrocystites* is the primitive sister group (=little changed descendant of the latest common ancestor) of *Mitrocystella* plus *Placocystites*, while *Mitrocystella* is the primitive sister group of *Placocystites*.

(*b*) *External morphology of the head; description and plate notation*

The head of *P. forbesianus* (figures 3 and 4 and plate 1, figures 40 to 44) is much the same shape as that of other mitrates, being relatively flat dorsally and convex ventrally. Dorsal and ventral surfaces meet at sharp, dorso-lateral, peripheral flanges. The head of *P. forbesianus* was more rigid than that of more primitive mitrates. Thus *Mitrocystella* had a fairly rigid dorsal shield, but the ventral surface of the head was largely made up of a flexible ventral integument, formed from an irregular number of imbricating plates (figure 5). *P. forbesianus* also had a rigid dorsal shield, but there was a rigid ventral shield as well, made up of a fixed number of plates that abutted against each other instead of imbricating. There was a wide mouth anteriorly and there is evidence of right and left gill openings posteriorly. The ventral shield was presumably slightly flexible near the gill openings to allow them to gape.

The dorsal surface of the head in *P. forbesianus* is less flat than in *Mitrocystella*. Posteriorly it slopes down much more steeply than in that genus, so that much of it is visible in posterior aspect (figure 3*f*). In dorsal aspect the peripheral flanges of *P. forbesianus* curve smoothly backwards towards the tail (figure 3*a*). Unlike *Mitrocystella* there are no postero-lateral angles (figure 3*a* and 5*a*). This is linked in *P. forbesianus* with the very small size of the posterior surface of the head (p sf in figure 3*c*), which is a tiny, sharply defined, smooth region, confined to the ventral plates just anterior to the tail and lacking the transverse ribs that occur on the rest of the head. In *Mitrocystella*, on the other hand, the posterior surface, defined by strong postero-

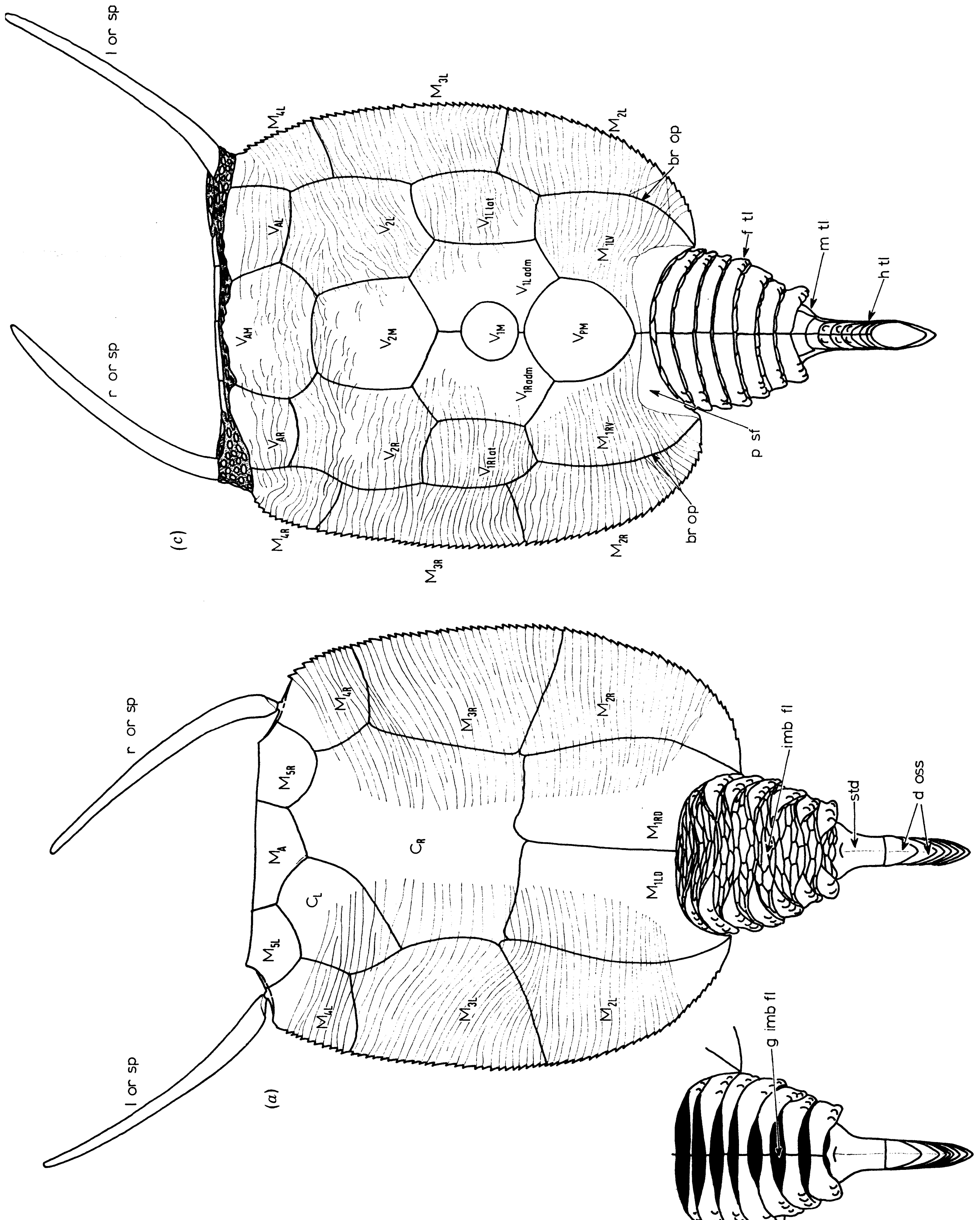

FIGURE 3(*a*–*c*). For description see following page.

ventral flanges, extends from the postero-lateral angles down to the ventral surface of the head and is developed on dorsal plates as well as ventral ones. It makes up much of the posterior aspect of the head in *Mitrocystella.* As in *Placocystites forbesianus,* it lacks transverse ribs. In the right ventral portion of the posterior surface of the head of *Mitrocystella, Mitrocystites,* Moroccan *Chinianocarpos* and *Chinianocarpos thorali,* there is a groove interpreted as a lateral line (lat 1 in figures 29, 30). There is no such lateral line in *Placocystites forbesianus.*

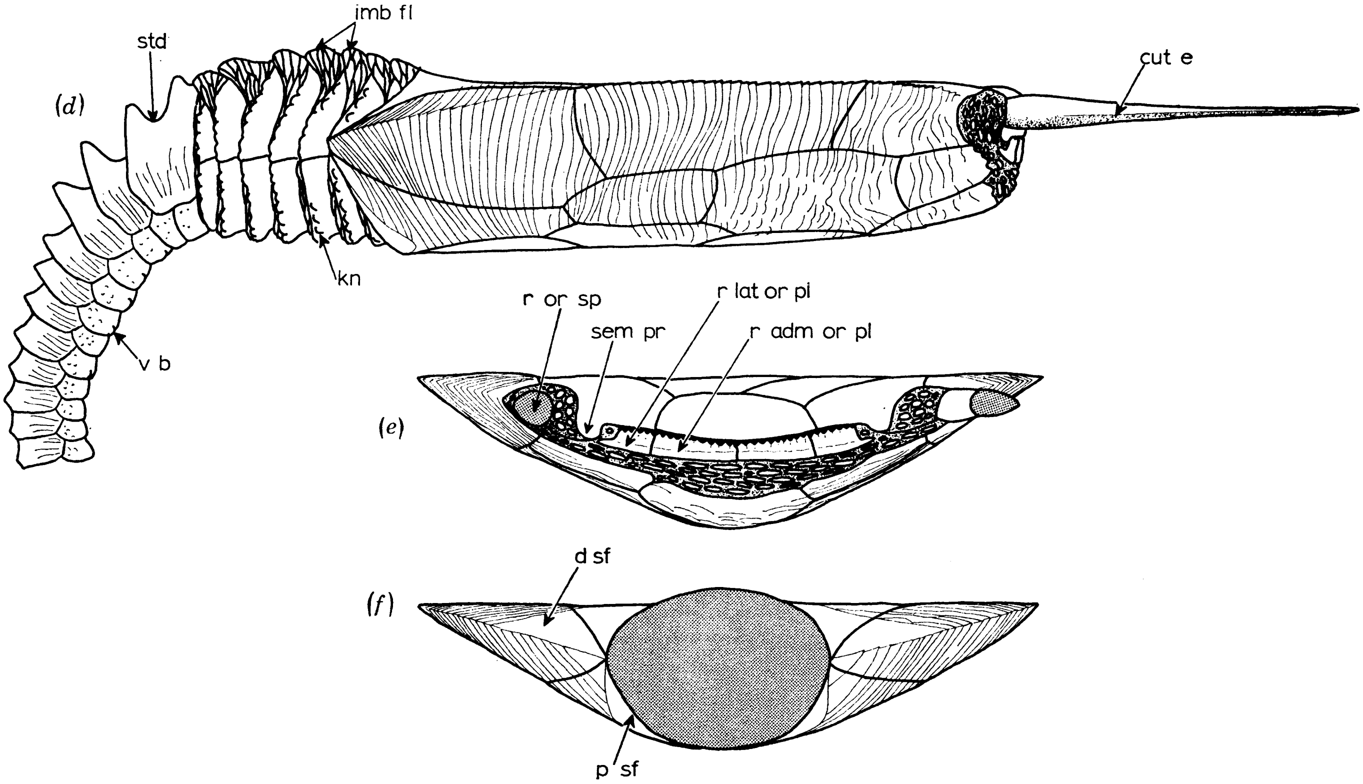

FIGURE 3. Reconstructions of external features of *Placocystites forbesianus* (see also figure 4 and plates 1–4). (*a*) Dorsal aspect, integuments round spine bases omitted. (*b*) Dorsal aspect of tail, integuments forming imbrication flaps omitted. (*c*) Ventral aspect. (*d*) Right lateral aspect; the tail was probably larger than shown here. (*e*) Anterior aspect; the precise relationships between the integuments and spine bases are conjectural. (*f*) Posterior aspect, tail omitted.

The ornament of the head of *P. forbesianus* is very striking. It consists of transverse ribs with cuesta-like profiles, steeper anteriorly than posteriorly. Unlike *Mitrocystella* or more primitive mitrates, these ribs are developed on the dorsal as well as the ventral surface of the head. On the dorsal surface they are confined to two broad areas at right and left, while a median area is smooth (figure 3*a*). There are precise limits between the ribbed areas of the dorsal surface and the smooth area between them, i.e. the ribs do not break up into segments when followed in a median direction, but simply stop as if at an invisible boundary line. The ribbed areas of the dorsal surface do not extend up to the oral spines, nor backwards to the tail. Instead, the median smooth area widens out anteriorly and posteriorly.

The oral spines are situated near the right and left anterior angles of the head (figures 3, 4; plate 2, figures 47, 49; plate 4, figure 71; plate 60, figures 79 to 82) and are the most striking difference between *P. forbesianus* and *Mitrocystella* (figure 5). Each spine is a single plate of calcite, straight in lateral aspect, but concave towards the median plane in dorsal aspect. The convex lateral margin of each spine is a cutting edge, except proximally. The median face is rounded. Each spine is articulated by an elongate socket in its base to a vertically elongate toroidal tubercle on the head. This articulation would allow the spine to sweep from side to side, probably mainly in a horizontal plane. The fact that the tubercle on the head is toroidal rather than cylindrical, however, suggests that the plane of sweep could be adjusted to slope upwards or downwards anteriorly. There is an areola round the tubercle on the head and there are facets on the base of the spine both lateral and median to the socket. Like the comparable structures round the articulation of an echinoid spine, the areola and facets probably served for muscle attachment. If so, the muscle pulling the spine laterally was much bigger than its antagonist, since it was attached to a larger facet on the spine (plate 2, figure 47). The power stroke of the spine was therefore outwards and would have forced its lateral cutting edge through the bottom sediment. We shall return to the subject of the spines later.

In considering the head plates it is necessary to use one objective and three comparative notations. The objective notation (figure 3), which does not imply homology between plates given the same notation in different species, has been used in previous work on calcichordates (Jefferies 1967, 1968, 1969, 1973; Jefferies & Prokop 1972). In it M = a marginal plate; C = a centrodorsal plate; V = a ventral non-marginal plate; arabic numeral suffixes 1–5 are given to plates in sequence, starting just anterior to the tail; suffix R = right; L = left; P = posterior; A = anterior; D = dorsal; V = ventral; M = median. M_{1LD}, for example, is the first left, dorsal marginal plate.

The first comparative notation (figures 29, 30) was introduced in Jefferies & Prokop (1972) to indicate probable plate homologies between rather primitive mitrates, such as *Peltocystis*, *Chinianocarpos* and *Lagynocystis*, and the mitrate-like cornute *Reticulocarpos hanusi*. In it the head plates of *Reticulocarpos* take lower case letters a–n, arranged as far as possible in clockwise alphabetical sequence in dorsal aspect, with plate a corresponding to M_{4L} of *Reticulocarpos* in the objective notation. In addition lower-case letters p and q are applied to plates which exist among primitive mitrates, but cannot be homologized in *Reticulocarpos*.

The second comparative notation (figures 29, 30) is introduced here for marginal and centro-dorsal plates that can be homologized between *Mitrocystella* and *Mitrocystites* and Anomalocystitids including *Placocystites*, but which cannot certainly be identified in more primitive mitrates. This notation starts from *Mitrocystites*, in which the plates in question are given arabic numerals, arranged in clockwise order in dorsal aspect firstly for the marginals (1 to 8), and secondly for the centro-dorsals (9 to 13).

The third comparative notation (figure 30) is introduced here for the ventral plates of *Placocystites* and *Enoploura*. It starts from *Placocystites* in which the plates are given small Roman numerals i to xi arranged as far as possible in clockwise order in ventral aspect, but converging inwards in a spiral. Plate *i* is underlined or italicized to distinguish it from plate i of the *Reticulocarpos* notation.

In dorsal aspect (figure 3*a*) nine marginal plates of the head are visible in *P. forbesianus*. There is an anterior marginal M_A; four marginals exist on the left side: M_{1LD}, M_{2L}, M_{3L} and M_{4L}; and four marginals on the right side: M_{1RD}, M_{2R}, M_{3R} and M_{4R}. In addition there are right and left oral spines. These marginal plates and spines are almost bilaterally symmetrical. Also visible in dorsal aspect are two centro-dorsal plates – a large, posterior right one C_R, and a small anterior left one C_L.

In ventral aspect (figure 3*c*) eight marginal plates are clearly visible, disregarding the curled-over edges of the most anterior marginal plates, dorsal to the mouth. These clearly visible plates are: the first, left and right, ventral marginals, M_{1LV} and M_{1RV}; three marginal plates of the left side: M_{2L}, M_{3L} and M_{4L}; and three marginal plates of the right side: M_{2R}, M_{3R}, M_{4R}. In addition there are the right and left oral spines. Six of the marginal plates visible in ventral aspect can also be seen in dorsal aspect i.e. M_{2L}, M_{3L}, M_{4L}, M_{2R}, M_{3R}, M_{4R}.

Anterior to the first ventral marginals there are twelve ventral plates which cover most of the ventral surface. These consist of a posterior median ventral plate, V_{PM}, deeply inserted between M_{1RV} and M_{1LV}, and three, more anterior, transverse rows. The most posterior of these rows has five plates – one median, two admedian and two lateral, i.e. $V_{1L\,lat}$, $V_{1L\,adm}$, V_{1M}, $V_{1R\,adm}$, $V_{1R\,lat}$. And the second and anterior rows each have three plates each i.e. V_{2R}, V_{2M}, V_{2L} and V_{AR}, V_{AM} and V_{AL}. Disregarding the post-oral integument plates and oral plates, but including the oral spines, there are thus twenty-nine major plates which make up the skeleton of the head of *P. forbesianus*. Unlike most other mitrates, only two of these, the centro-dorsals C_R and C_L, are strikingly asymmetrical.

It is interesting to compare the head plates of *Placocystites forbesianus* with those of related mitrates as shown in figures 29 and 30. *Mitrocystites mitra* has thirteen marginal plates visible in dorsal aspect. By using the appropriate comparative notations these can be listed as: i, 1, 2, 3, 4, and b on the left side of the head; n anteriorly in the mid line; and h, 8, 7, 6, 5 and c on the right side of the head. *Mitrocystella barrandei*, which is earlier and more primitive than *Mitrocystella incipiens* (stratigraphy in figure 2), has the same marginal plates as *Mitrocystites mitra*. The species *M. incipiens*, on the other hand has one plate less, having lost either 3 or 4 near the anterior left angle of the head. Both of the Anomalocystitidae shown in figures 29 and 30, i.e. *Placocystites forbesianus* and *Enoploura popei*, have at first sight eleven marginals visible in dorsal aspect. However, inspection of the figures strongly suggests that the oral spines of these forms are homologous with marginals 4 and 5 of *Mitrocystites mitra* and *Mitrocystella barrandei*. Furthermore the likely equivalents of plates 4 and 5 in the still more primitive Mitrocystitid *Chinianocarpos thorali* (i.e. plates *a* and *d*) are also marginal plates. It is therefore likely that the oral spines of Anomalocystitids were modified in the course of evolution from marginal plates homologous with and similar to plates 4 and 5 of *Mitrocystites mitra* i.e. from M_{5L} and M_{5R} to use the objective plate notation for *M. mitra*. The same figures suggest the likely homologies of the centro-dorsal and ventral plates of *Placocystites forbesianus* compared with its relatives.

The mouth of *Placocystites forbesianus* is a long slit at the anterior end of the head. Dorsally it is bordered by the down-turned edges of plates M_{5L}, M_A and M_{5R}, while it is limited at right and left by two downward-projecting semicircular processes on M_{5L} and M_{5R} (sem pr in figure 4*a*). Just median to these semicircular processes are two slight olfactory notches (olf n in figure 4*a*), each of which is connected by a shallow groove inside the head to an olfactory cup in the dorsal wall of the buccal cavity.

Ventrally the mouth is bordered by four oral plates: right and left, admedian, and right and left, lateral (figure 4; plate 2, figures 50 to 53; plate 6, figures 83, 86). The admedian oral plates are elongate rectangles. Their internal surfaces are smooth and flat; their anterior, dorsal, margins, forming the free edge of the lower lip, are serrated, with a series of fine points; and their outer surfaces are excavated postero-ventrally (tis f lp in figure 4) making a concave facet to which soft tissue was probably attached. The lateral oral plates are like the admedian ones through most of their length, but each one extends into a lateral process. The whole plate has roughly the shape of a meat cleaver with the lateral process for a handle and with serrations along the 'cutting edge'.

In whatever way the oral plates are assembled with respect to the head during reconstruction, there remains a little gap on each side (inh g in plate 6, figure 83). This is situated between the lateral oral plate with its process on the one hand, and the downwardly directed semicircular process of the fifth marginal plate, on the other. This gap includes the olfactory notch dorsally and was perhaps covered in life by a flap of soft tissue attached to a distinct facet on the antero-dorsal surface of the process of the lateral oral plate (tis f in plate 2, figure 52).

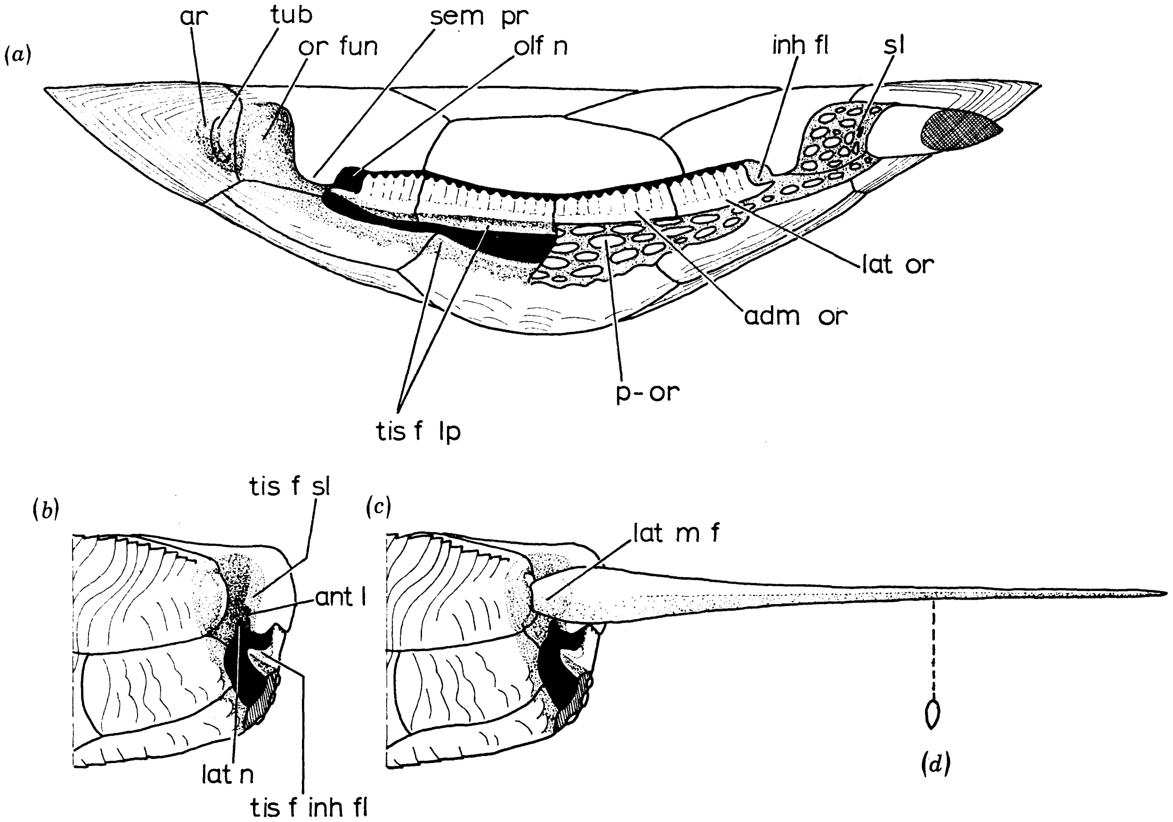

FIGURE 4. Anatomy of mouth region of *Placocystites forbesianus*. (*a*) Anterior aspect, with integument omitted from right half; the precise arrangement of integuments near the spine base is conjectural. (*b*) Right aspect; spine and integuments omitted. (*c*) Right aspect; spine inserted, integuments omitted.

On the anterior border of the rigid ventral armour, i.e. on V_{AR}, V_{AM}, and V_{AL}, another facet is developed (tis f lp in figure 4a). This is bounded ventrally by a blunt ridge surmounted by a row of rounded knobs. It probably represents the posterior attachment of the soft tissue of the lower lip which anteriorly would be fixed to the posterior facets of the oral plates. Elongate elliptical plates (p-or in figure 4*a*) were probably embedded in the skin of this soft tissue. The ventral limit of this anterior facet on the ventral armour passes right and left into a rounded ridge which runs outside the areolas (ar) of the oral spines into the dorsal borders of the oral funnels (or fun).

These oral funnels are well marked, shallow, conical depressions situated between the semi-circular processes and the areolas of the oral spines. The apex of each shallow cone lies at a lateral notch (lat n in figure 4*b*) which is posterior and lateral to the semicircular process. By this notch the shallow cavity of the funnel would communicate with the buccal cavity inside the head. Subtle differences in the surface texture of the inside of the funnel suggest that a flap of soft tissue was attached to the median margin of the funnel, anterior to the notch, i.e. attached to the lateral margin of the semicircular process (tis f sl in figure 4*b*). This soft flap would form an anterior wall to the cavity of the oral funnel (sl in figure 4*a*). It was plated and the plates have been found in position (plate 1, figures 37, 39). Occasional plates can also be observed lateral to the areolas of the oral spines, suggesting that plated integument was extensively developed lateral to the mouth, as suggested in figure 4*a*. The precise line of separation between dorsal and ventral parts of these plated integuments shown in figure 4*a*, representing, so to speak, lateral continuations of the mouth on each side, is conjectural, as also is the way in which the reconstructed flap surrounds the oral spine as a loose sleeve. A small concavity in the posterior margin of the attachment surface of the sleeve (ant l in figure 4*b*) marks an anterior lobe of the oral funnel.

When the mouth region of *Placocystites forbesianus* is compared with that of *Mitrocystella* (figure 5) a basic and presumably primitive resemblance is evident, with some differences superimposed. Thus the mouth of *P. forbesianus* is more ventral than that of *Mitrocystella*, because of a turning-down of the anterior edge of the dorsal shield. Also the oral plates of *P. forbesianus* could have arisen by the fusion, side-by-side, of the spike-shaped orals of *Mitrocystella*. In that case each of the points of the serrated dorsal free margins of the oral plates of *Placocystites* would correspond to an originally separate spike-shaped oral. The soft tissue of the lower lip of *Placocystites*, between the oral plates and the anterior facet of the rigid ventral armour, corresponds to the specially flexible post-oral integument of *Mitrocystella* (p–or in figure 5*b*) while an elaboration of the lateral parts of such an integument might produce the reconstructed integuments lateral to the mouth of *Placocystites*, including the plated flaps that formed a front wall to the cavities of the funnels. Finally the rigidly sutured, most anterior, ventral plates of *Placocystites* correspond broadly to the foremost ventral plates of *Mitrocystella*, which were held together less flexibly than the post-oral plates in front of them. On the other hand, *Mitrocystella* has no obvious equivalent to the funnels themselves, while the oral spines do not exist as such in *Mitrocystella* but are represented by normal marginal plates (at least in *M. barrandei*). This suggests that funnels and spines evolved together and were functionally related to each other. We shall return later to their functions and homologies.

The branchial openings, by comparison with other mitrates, would have been situated between M_{2R} and M_{1RV} on the right side, and M_{2L} and M_{1LV} on the left. Judging by the positions of nerves inside the head, the left branchial opening may have been about twice as long as the right one. For the branchial opening would lie between nerves n_2 and n_4 of the palmar complex, where these two nerves crossed from the ventral into the dorsal skeleton, and the relevant distance between these nerves on the left is about twice as long as on the right (figure 25*a*). This may be connected with the fact that the left pharynx is considerably bigger than the right pharynx. Also the rectum opened into the left atrium, not into the right one, so that faeces would have to leave the head through the left gill opening.

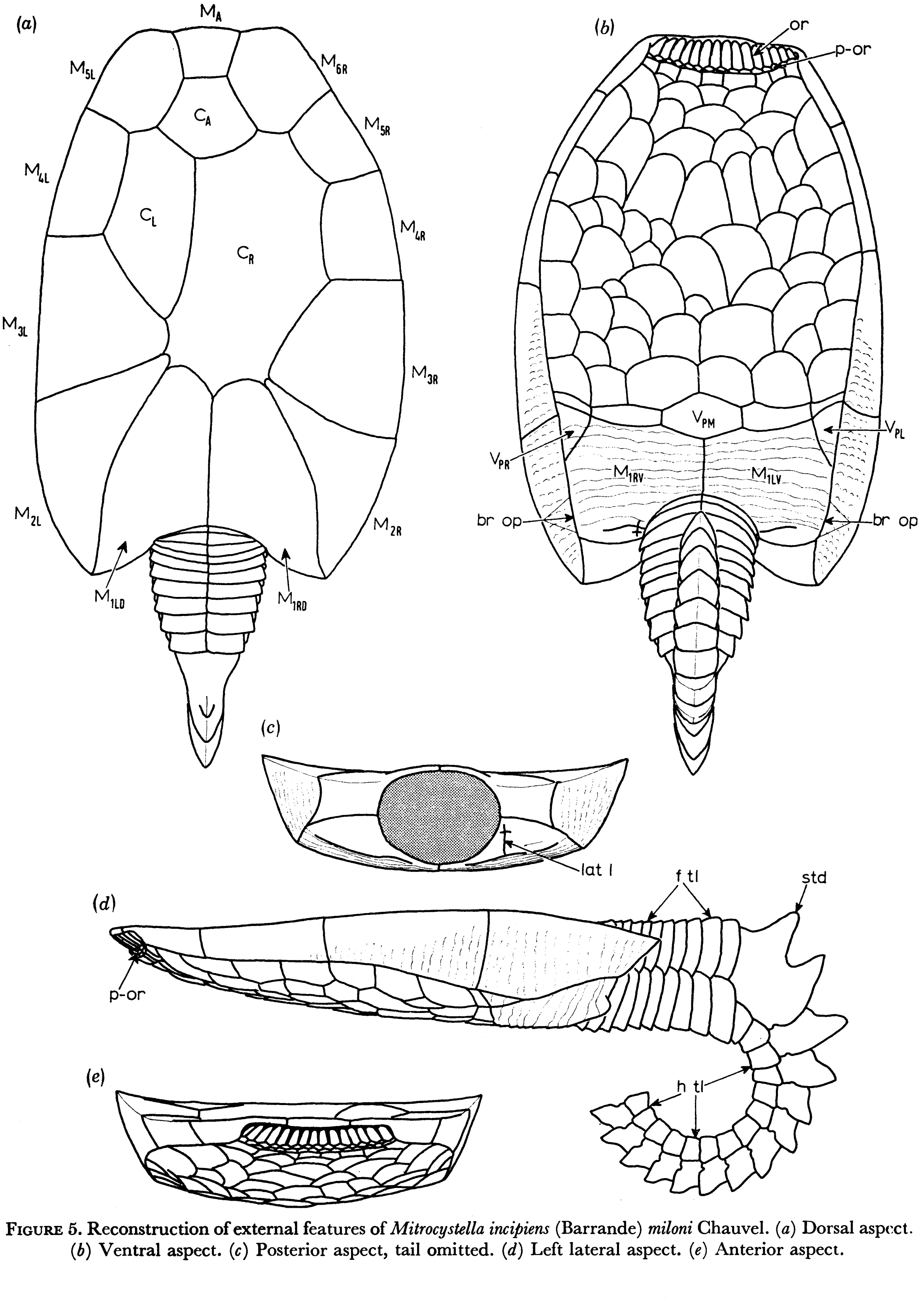

Figure 5. Reconstruction of external features of *Mitrocystella incipiens* (Barrande) *miloni* Chauvel. (*a*) Dorsal aspect. (*b*) Ventral aspect. (*c*) Posterior aspect, tail omitted. (*d*) Left lateral aspect. (*e*) Anterior aspect.

(*c*) *External and internal anatomy of the tail*

The anatomy of the tail, both internal and external, will now be described, since it is relevant to a functional interpretation of the external features of the head. As in all mitrates the tail is divided into fore, mid and hind portions.

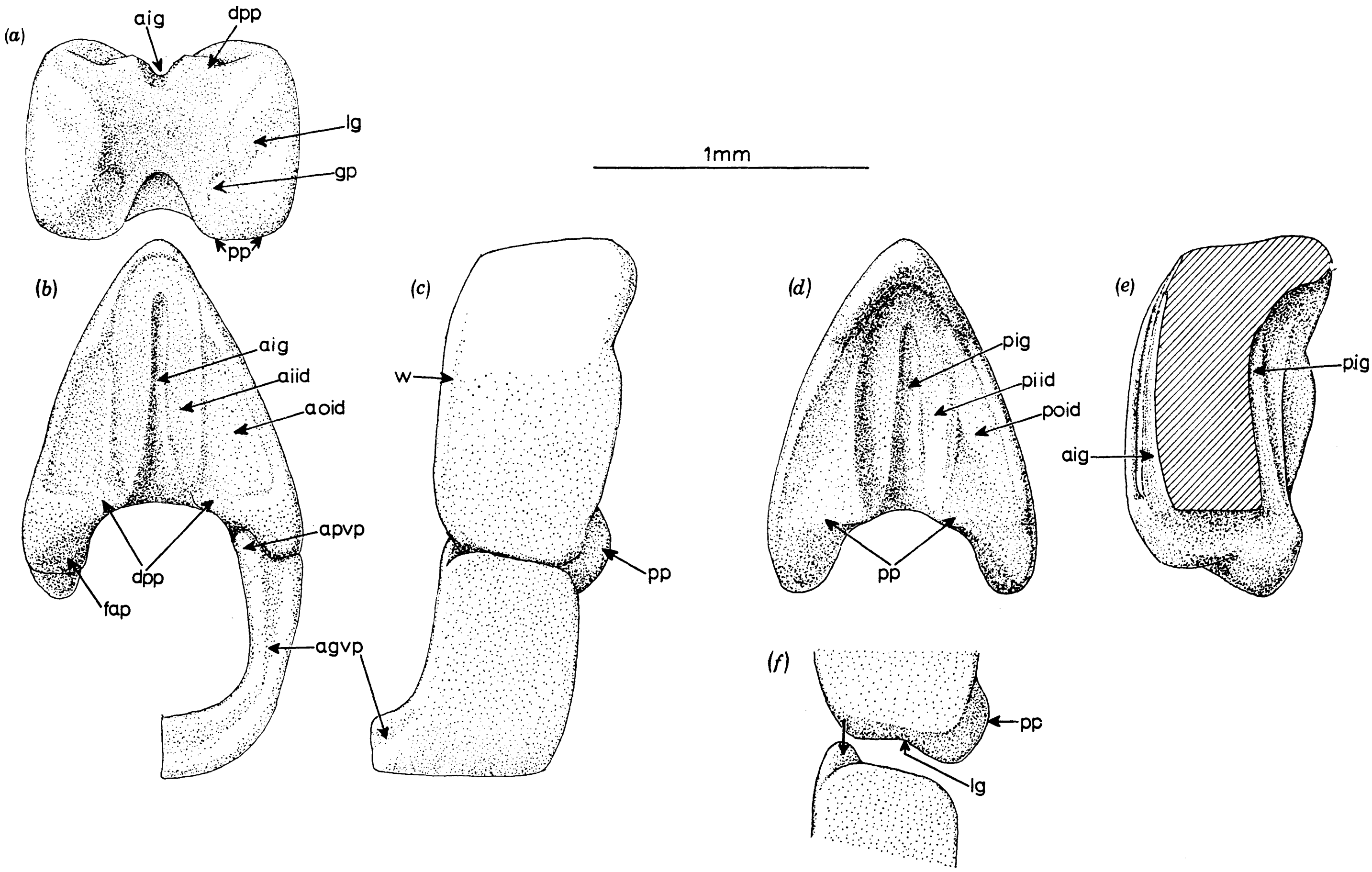

FIGURE 6. Reconstructed skeleton of one segment of the hind tail in *Placocystites forbesianus*. (Compare plate 1, figure 46; plate 2, figures 56–60; plate 3, figures 67, 68.) (*a*) Ventral aspect of dorsal ossicle. (*b*) Anterior aspect of dorsal ossicle and ventral plate. (*c*) Left lateral aspect of dorsal ossicle and ventral plate. (*d*) Posterior aspect of dorsal ossicle. (*e*) Median aspect of right half of dorsal ossicle cut through sagitally. (*f*) Interlocking mechanism between dorsal ossicle and ventral plate.

The fore tail is wide, as always in calcichordates (figure 3; plate 3, figures 64, 65, 67, 68). The skeleton consists of major plates and intercalaries and surrounds a large lumen. The major plates form about seven successive rings, made up of four plates each: left dorsal, left ventral, right dorsal and right ventral. The four plates of a ring are rigidly sutured to each other where they meet. The length of a major plate, measured parallel to the long axis of the animal, is greatest in the lateral and ventral parts of the fore tail. The major plates are shortest dorsally. As a result successive rings fit inside each other laterally and ventrally, with the proximal part of each ring inside the ring next anterior. But dorsally there are gaps between successive rings (figure 3*b*). The right and left portions of the posterior free edges of the rings are ornamented with a line of rounded knobs.

The intercalary plates were contained in the soft integument that connected the anterior ring to the head, the posterior ring to the styloid, and successive rings to each other. The plates were elongate parallel to the gaps between the rings. The plated integument was particularly well developed dorsally, covering the dorsal gaps between the rings of major plates (figure 3*a*; plate 3, figure 64, 68). In consequence, when the fore tail was extended horizontally, there would have been obvious recumbent folds of plated integument on its dorsal surface. These floppy dorsal imbrication membranes would have allowed the fore-tail to flex ventrally in a tight curve.

The skeleton of the hind tail consists of a series of dorsal ossicles with paired ventral plates as in all other mitrates (figure 5; plate 1, figure 46; plate 2, figures 56 to 60; plate 3, figure 68). It presumably ended abruptly as in every other known calcichordate. In *Placocystites forbesianus*, however, we have never seen a natural abrupt end, such as might have existed in life. The abrupt ends that we have seen are probably all due to breakage after discovery. The hind tail may really have been much longer than shown in the reconstructions.

As to external shape and sculpture, each hind tail ossicle has a dorsal apex. Anterior to this is a median cutting edge and posterior to it, in the more proximal ossicles, a triangular facet. The height of the apex, and therefore the height and area of the triangular facet, is greater on the more anterior ossicles than farther distally, where indeed the facets become indistinct with rounded edges and then disappear (plate 2, figure 56). There is sometimes an ornament of gentle vertical striae on the ventral parts of the ossicles, and of pits elsewhere on the ossicles and on the ventral plates. Some of the more proximal ventral plates have a rounded postero-ventral knob. The plates of opposite sides meet each other ventrally at a straight suture. Anteriorly the ventral plates imbricate inside the ventral plates next anterior. Posteriorly they embrace the next pair of plates behind.

The internal sculpture of the dorsal ossicles is complicated (figure 6). The anterior face of an ossicle is relatively flat and the posterior face relatively concave so that the anterior part of an ossicle fitted inside the posterior margins of the next ossicle in front. Both anterior and posterior faces have three main regions: there is a median, interossicular groove (aig, pig); an inner interossicular depression (aiid, piid); and an outer interossicular depression (aoid, poid). The inner interossicular depression of the anterior face is rather flat, while that of the posterior face is deeply excavated. The outer interossicular depression is of moderate depth, about equal on anterior and posterior faces. Unlike *Mitrocystella* or *Mitrocystites* there is no dorsal longitudinal canal passing through the ossicle to connect the dorsal ends of the anterior and posterior interossicular grooves (compare plate 2, figure 61; and Jefferies 1968, figs 18 and 26). There are blunt paired posterior processes (pp) in the ventral parts of the posterior face. These were received in depressions (dpp) in the anterior face of the next ossicle behind. The median part of the ventral face of each dorsal ossicle is concave. Near the lateral borders of this concave region are two indistinct pits on each side (gp). Lateral to the concave region the edges of the ossicle are bluntly rounded, each being divided into two hillocks by an oblique lateral groove (lg).

The ventral plates are relatively thin ventrally, ending in the narrow straight median suture. The plates are stouter dorsally to bear the groove which articulated with the ventral edge of the dorsal ossicle. An anterior process of the ventral plate (apvp) projected upwards against a corresponding facet (fap) on the dorsal ossicle. Each plate abutted anteriorly against its neighbour with an anterior groove (ag vp). Each plate overlapped the plate behind.

The mid tail has a dorsal styloid (st) to which two pairs of plates were articulated ventrally.

The styloid resembles, and is no doubt serially homologous with, two hind-tail ossicles fused together; it is deeply excavated anteriorly. As with the hind-tail ossicles the styloid is not penetrated by a dorsal longitudinal canal. The dorsal apices corresponding to the two constituent ossicles of the styloid differ from each other in shape. The more anterior is blade-like whereas the more posterior had a well developed posterior facet. The ventral parts of the external surface of the styloid are vertically striated, like the hind tail ossicles, while the remaining surface of the styloid (except the posterior facet) and of the ventral plates is pitted.

As to soft parts, the hind tail of *Placocystites* presumably did not greatly differ from that of *Mitrocystites* or *Mitrocystella* (Jefferies 1968, pp. 291–294, pp. 318–319; 1973, pl. 39, figs 32, 33). The hind tail seems to be adapted, as in other mitrates, for ventral flexion, though not to the same extent as in *Mitrocystites* or *Mitrocystella*. The lumen between the ventral plates and dorsal ossicles would have been filled with muscle blocks whose contraction would produce this flexion. The paired pits gp (ganglionic pits) presumably carried segmental ganglia situated between these muscle blocks, as in *Mitrocystites* or *Mitrocystella*. These ganglia would be connected with the dorsal nerve cord which would lie on the dorsal surface of the notochord as in *Mitrocystites* or *Mitrocystella* (photographs in: Jefferies 1973, pl. 39, figs 32, 33; 1968, pl. 9, fig. 5), though in *Placocystites* there is no direct evidence of notochord or dorsal nerve cord which presumably were not in contact with the ventral surface of the dorsal ossicles. If the hind tail flexed by contraction of ventral muscles, there would need to be a dorsal antagonist.

This antagonist could, in principle, have been either muscle or ligament between the dorsal ossicles. Indeed it probably included both types of tissue, for the following reasons. In the mitrates *Lagynocystis* and *Peltocystis*, which were presumably primitive in this respect, there are interossicular spaces entirely cut off from the lumen of the tail, i.e. there were no interossicular canals by which such spaces could have received a blood and nerve supply (for *Lagynocystis* see Jefferies 1973, p. 446, fig. 12, pl. 43, fig. 45–52; for *Peltocystis* see Ubaghs 1970, fig. 37, p. 90). These canal-less interossicular spaces therefore probably contained ligament. They correspond to the outer interossicular spaces, enclosed by the outer interossicular depressions (aoid, poid) in *Placocystites*, *Mitrocystites* and *Mitrocystella*. The inner interossicular spaces of these forms (filling aiid and piid), on the other hand, receive the interossicular canals, whose likely function would be to supply them with blood and to innervate them, for the canals ascend to the interossicular spaces by passing through the dorsal nerve cord, but are too wide to have carried nerves alone. The inner interossicular spaces were therefore probably filled with muscle. The absence in *Placocystites* of a dorsal longitudinal canal connecting the interossicular canals suggests that the presumed muscles were less well irrigated than in *Mitrocystites* or *Mitrocystella*.

Reconstructing the soft parts of the fore tail in *Placocystites* depends partly on comparison with its mid and hind tail. For the mitrate fore tail is homologous with the anterior part of the cornute fore tail relatively unchanged; while the mitrate mid and hind tail is homologous with the more posterior part of the cornute fore tail, considerably altered. The soft organs of the cornute fore tail would be either uniform along its length or metamerically repeated. Soft parts for which there is evidence in the mitrate mid and hind tail would therefore have had either continuations or serial homologues in the mitrate fore tail, unless, like the dorsal interossicular muscles, nerves and canals, they evolved within the mitrates.

The fore tail of *Placocystites* was evidently highly flexible. It would have contained large muscles which presumably formed muscle blocks corresponding to those in the hind tail and perhaps equal in number to the number of rings of major plates in the fore tail, i.e. about seven.

An anticompressional notochord would be required to prevent telescoping when these muscles contracted. This would be a forward continuation of the notochord of the mid and hind tail. The notochord would have been situated along the central axis of the fore tail, or principal axis in engineering terms, for this would be the only axis which neither shortened nor lengthened when it curved. The notochord would end anteriorly at the front end of the fore tail, i.e. at the transverse level of the brain. A dorsal nerve cord was presumably present on the dorsal surface of the notochord, connecting the brain with the dorsal nerve cord of the mid and hind tail. The muscle blocks of the fore tail would presumably fill the lumen from floor to ceiling. There would have been no coelom in the fore tail, for the viscera were entirely contained in the right anterior coelom inside the head.

There would probably have been paired, dorsal-root segmental ganglia between the muscle blocks of the fore tail, as in the hind tail. It is also likely that the muscle blocks were supplied by nerves, with motor end plates, going off to them from the dorsal nerve cord. For nerves with motor end plates exist in the tails of all vertebrates and in tunicates (Pucci-Minafra 1965) but not in acraniates. These motor end plates are probably a shared advanced feature suggesting that vertebrates plus tunicates are the sister group of acraniates (Jefferies 1973, p. 463). Furthermore in the tails of appendicularian tunicates the motor and sensory nerves alternate metamerically somewhat as in vertebrates (Martini 1909). If the latest common ancestor of tunicates and vertebrates possessed this pattern of innervation, then *Placocystites* would also probably have possessed it.* It will be argued later that the anterior pair of muscle blocks of the fore tail of a mitrate was homologous with the hyoidean somite of a vertebrate and that the non-placodal constituents of the facial nerve of vertebrates are derived from a neural-crest ganglion anterior to the hyoidean somite but posterior to the trigeminal ganglion. This facial ganglion presumably existed between the first tail somite of *Placocystites* and the posterior surface of the brain. The nervous system of the fore tail of *Mitrocystella* has been reconstructed on the basis of these comparative and functional arguments in figure 23*a*. The corresponding system in *Placocystites* would have been essentially the same.

The large anterior depression of the styloid of the mid tail presumably served as a socket receiving the more posterior muscle blocks of the fore tail. By means of this socket, the fore-tail muscles could move the mid and hind tail as a unit.

Compared with other mitrates the tail of *P. forbesianus* shows a mixture of advanced and primitive features. The fore tail differs from that of *Mitrocystella* or *Mitrocystites*, and from all other mitrates where the conditions are known, by: (1) having the dorsal major plates sutured to the ventral ones to form rigid rings, instead of imbricating with them; (2) by the exaggerated development of the dorsal imbrication membranes; and (3) by the development of knobby ornament near the free posterior edges of the major plates. These features are likely to be specializations peculiar to *Placocystites forbesianus* and perhaps some of its unstudied relatives.

The mid and hind tail of *P. forbesianus* differs from that of *Mitrocystella incipiens* and *Mitrocystites mitra* by the absence of well developed interossicular articulations, of a dorsal longitudinal canal and of dorsal posterior facets on all except the most proximal ossicles. Furthermore the external sculpture of the ventral plates in *Mitrocystella* (especially the species *M. barrandei*) suggests that the ventral plates of the hind tail could slip inside their proximal neighbours to a considerable extent, so that the hind tail could flex ventrally in a tight curve

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* *Note added in proof.* The argument based on Martinis's work is mistaken (see Bone & MacKie 1975).

as suggested in figure 5. The sculpture does not suggest the same power of overlap of the ventral plates in *P. forbesianus* which implies that the hind tail was relatively stiff, in agreement with the lack of interossicular articulations. All these features of the mid and hind tail of *P. forbesianus* could be primitive since they resemble the situation in the primitive mitrates *Peltocystis*, *Chinianocarpos* and *Lagynocystis*. If they are truly primitive, and if the phylogeny shown in figures 29 and 30 is correct, then the advanced peculiarities of the hind tails of *Mitrocystella* and *Mitrocystites* must have evolved twice and independently in these two genera. These peculiarities comprise well developed interossicular articulations, posterior facets on the ossicles and a dorsal longitudinal canal.

Placocystites forbesianus also differs from *Mitrocystites* and *Mitrocystella* by having an ornament of pits and striae on the mid and hind tail. This is probably a specialization of *P. forbesianus* since it cannot be paralleled in *Chinianocarpos*, *Peltocystis* or *Lagynocystis*. The postero-ventral knobs on some of the more proximal ventral hind tail plates of *Placocystites forbesianus* are probably also a specialization. They are unlikely to be homologous with the similarly situated postero-ventral spikes on the ventral hind-tail plates of *Lagynocystis*, seeing that such spikes or knobs are unknown in *Chinianocarpos*, *Peltocystis*, *Mitrocystites* and *Mitrocystella*, all of which are closer related to *Placocystites* than *Lagynocystis* is.

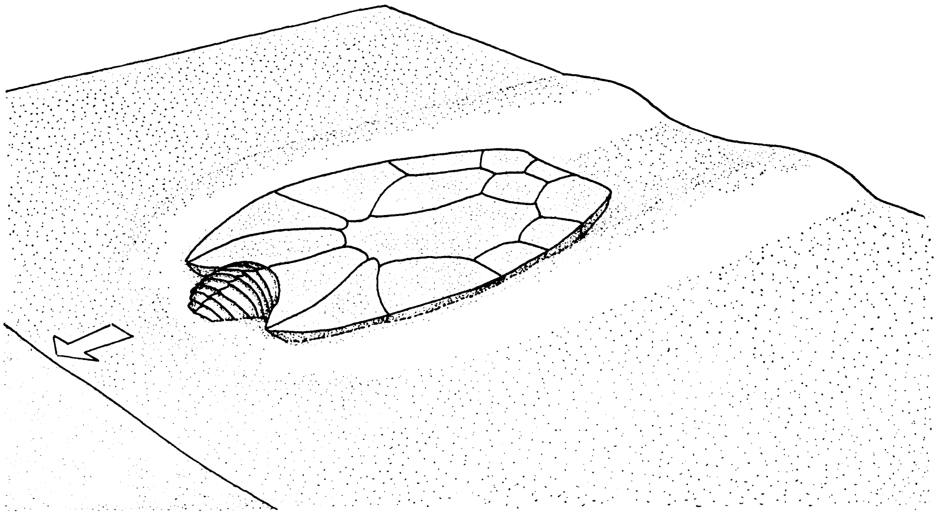

FIGURE 7. Suggested method of crawling in *Mitrocystella incipiens*.

(*d*) *The functional significance of the tail and external head anatomy of* Placocystites forbesianus

The functional significance of nearly all the differences in external anatomy between *Placocystites* and *Mitrocystella* probably lies in a difference in the mode of life. Mitrates primitively seem to have moved across the sea bottom, pulling themselves backwards by ventral flexion of their tails, with the ventral surfaces of their heads buried in the sea floor but their dorsal surfaces exposed (Jefferies & Prokop 1972). The peripheral grooves of *Mitrocystites*, innervated by large nerves (n_4 and n_5), probably arose to detect sediment on the dorsal surface of the head and so to prevent the animal from accidentally burying itself. The dorsally situated trans-pharyngeal eyes of *Mitrocystites*, *Chinianocarpos* or the cornute *Reticulocarpos* probably had this same function.

Mitrocystella is likely to have crawled in essentially the same manner as *Mitrocystites*, keeping its back exposed (figure 7). This is suggested by the fact that cuesta-shaped ribs, though well developed in the species *Mitrocystella incipiens*, are confined to the ventral and lateral surfaces of the head (figure 5). The posterior surface of the head, with its strong overhang, would slide upwards when pulled posteriorly by the tail, helping to prevent the animal from burying itself. The peripheral grooves, however, were covered in *Mitrocystella* with a layer of calcite to form peripheral canals, and the transpharyngeal eyes were internal instead of dorsal. These changes would have protected these organs when the dorsal surface accidentally became covered with sediment, but would also reduce their sensitivity. Crawling in *Mitrocystella* would have been very inefficient; the animal would tend to lift itself out of the sea bottom with each ventral or power stroke of the tail and push itself back in again with each dorsal or return stroke.

The cuesta-like ribs on the head of *Placocystites forbesianus* are of first importance in interpreting its habits. Remarkably similar ribs have been described in modern bivalves and crabs and in both these groups they function in helping the animal to move through sediment. For in contact with sediment the steep slopes of the cuestas resist movement more than the gentle slopes do.

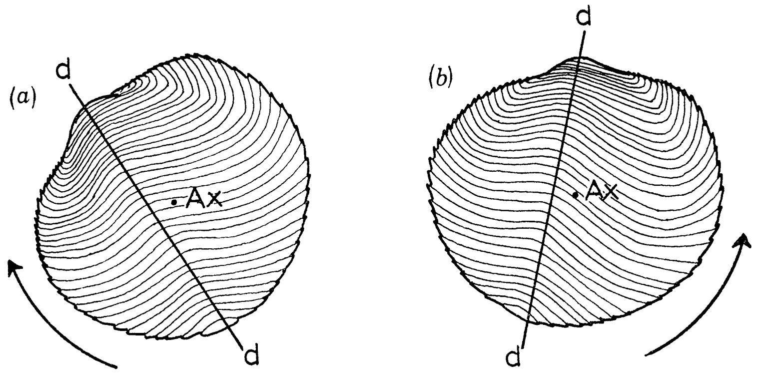

Figure 8. The use of cuesta-shaped ribs in burrowing in the bivalve mollusc *Divaricella quadrisulcata* (after Stanley 1970, fig. 27, p. 64). d–d = separation between anterior and posterior sets of ribs. Ax = axis of rotation during burrowing.

The functioning of cuesta-like ribs in bivalves has been studied by Stanley (1970). Several different groups of these molluscs have evolved a pattern of W-shaped or inverted V-shaped, 'divaricate' cuesta-like ribs, with the steep slopes of the cuestas facing dorsally. Such bivalves (figure 8) slide into the sediment by a rocking motion, pulled by the foot. This emerges between the two valves at the point of the divarication, where the anterior and posterior limbs of the ribs meet (i.e. at the ventral end of the line d–d in figure 8). In the first part of the rocking cycle the steep slopes of the ribs anterior to the foot resist movement dorsalwards by pushing upwards against the sediment (figure 8*a*). In this way the steep slopes act as a fulcrum, about which the ribs posterior to the foot slide ventralwards through the sediment by rotation of the shell. Then, by opposite rotation (figure 8*b*), the ribs posterior to the foot resist movement dorsalwards and act as a fulcrum, while the ribs anterior to the foot slide ventralwards through the sediment. These alternate rocking movements continue until the shell is buried. The edges of the valves are serrated by the cuesta-like ribs of these forms, and this helps the valves to cut through the sediment.

In crabs, cuesta-like ribs exist in the mole crab *Emerita* (figure 9 and Seilacher 1961). These crabs bury themselves in tropical sandy beaches with their posterior ends downwards but with their eyes and some anterior appendages clear of the sand. The cuesta-like ribs are best developed on the dorsal surface of the thorax and their steep slopes face anteriorly to assist the crab in burying itself tail-first in the sediment. It digs itself in by beating the walking limbs forward and upward (Pearse, Humm & Wharton 1942; Trueman 1970).

These analogies suggest that the cuesta-like ribs of *Placocystites forbesianus* were also adaptations for gripping the sediment during movement. Since their steep slopes face anteriorly, they would have favoured movement in a backwards direction, pulled by the tail, as was probably habitual in all calcichordates. Furthermore their presence on the dorsal surface of the head, as well as the ventral one, suggests that the dorsal surface, unlike *Mitrocystella*, was habitually covered by sediment, at least in part. If *P. forbesianus* habitually moved through sediment below the surface of the sea bed, as this suggests, then several other differences from *Mitrocystella* can be explained.

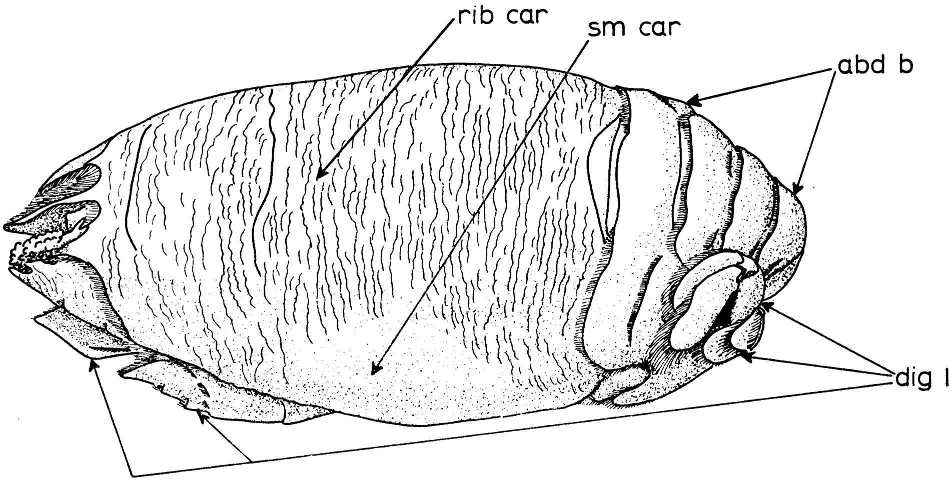

FIGURE 9. Distribution of cuesta-shaped ribs in the mole-crab *Emerita*. The steep slopes of the ribs are always anterior. Camera lucida drawing of specimen BMNH 79.32 from Madras. abd b = smooth abdominal boss; dig l = digging limb; rib car = ribbed carapace; sm car = smooth carapace.

Reduction of the posterior surface of the head and the development of a stronger downward slope of the posterior part of the dorsal surface would help to taper the head at the posterior leading end and also to make it more dorso-ventrally symmetrical, so that it could penetrate the sediment more easily, without bobbing up and down. The lateral line disappeared because, being always buried, it was of no use. The ventral wall of the head became rigid, to prevent the hollow head collapsing under the load of sediment on top of it. The major plates of the fore tail came to form rigid rings, perhaps to keep the muscles free to move inside the lumen.

However there are signs that *P. forbesianus* probably did not bury itself deeply, but slid through the sediment just below the sea bottom (figure 10). This is suggested by the distribution of ribs on the dorsal surface, confined to two precisely demarcated areas at right and left (figure 3*a*; plate 1, figure 43). If the animal habitually moved with the major part of the dorsal surface only slightly beneath the sea bottom, the downward sloping right and left posterior leading edges of the peripheral flanges would be deeper buried than the mid line of the dorsal surface. They would cut into the sediment and lift up a coherent slice of it on each side, with the serrations on the flanges helping the cutting action, much like the teeth on the valve edges of a bivalve with cuesta-like ribs, or the teeth on the cutting edge of a bread-knife. The fact that the ribs are not accurately transverse on the anterior part of the head, but arranged so as to converge posteriorly towards the median line, suggests that a certain amount of yawing motion may also have been involved. This would be analogous to the rocking action of a bivalve with divaricate ribs. The yawing motion may have been linked with side-to-side movement of the oral spines, as discussed later, and with the knobs on the major plates of the fore tail and the lateral striation of the dorsal ossicles of the hind tail. It would help the peripheral flanges of the head to slice through the sediment.

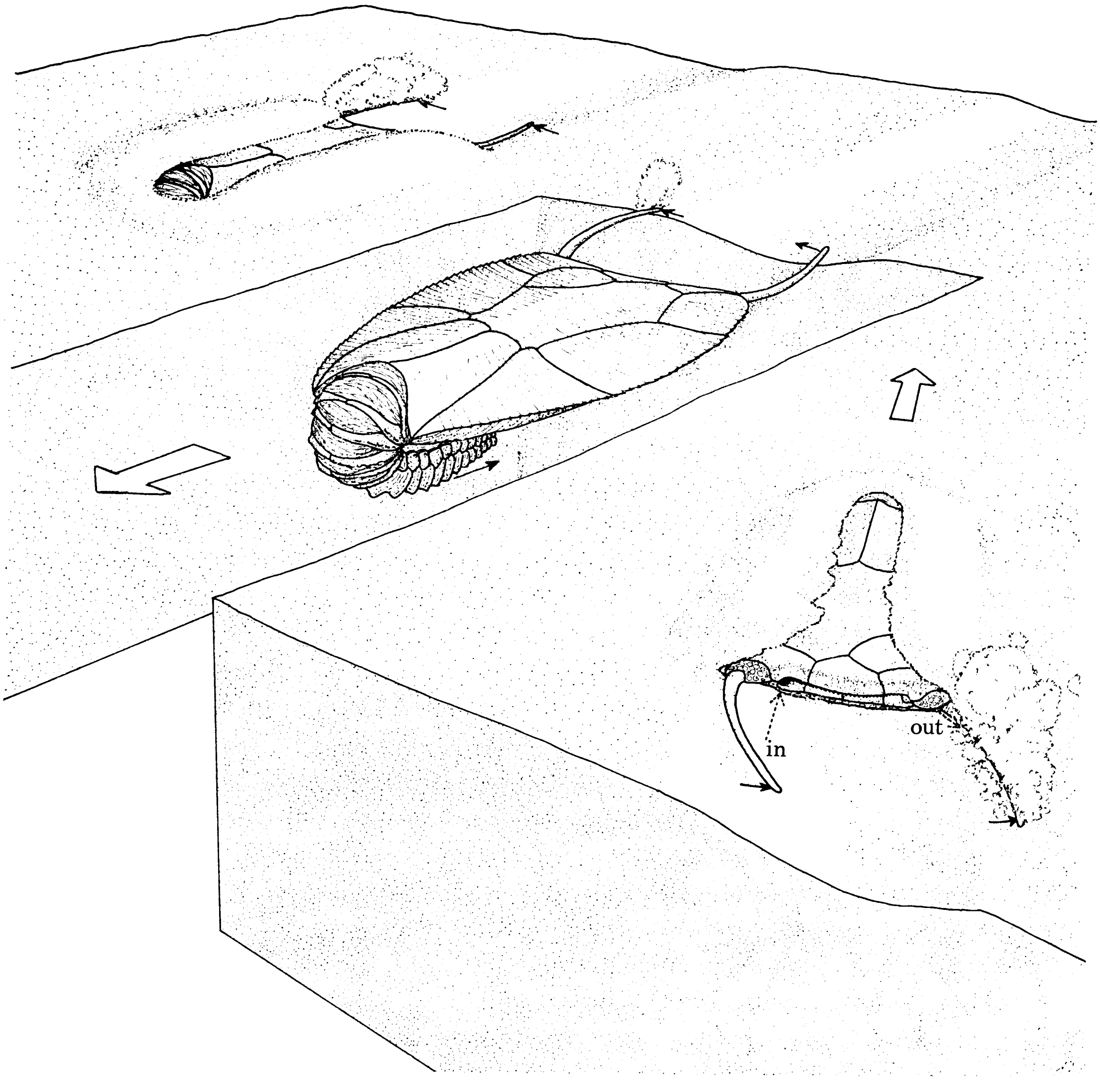

Figure 10. Suggested method of crawling in *Placocystites forbesianus*. The tail may have been longer than shown in the reconstruction; 'in' and 'out' refer to the inhalent and exhalent currents from the buccal cavity.

The slices of sediment cut out by the peripheral flanges, though not moving horizontally in absolute space, would pass forwards relative to the head as the latter moved backwards. If the animal was crawling only very slightly below the surface of the sea floor then these slices would rest on the head only where the ribs are developed, leaving the ribless median area free of mud. On the other hand ribs on the dorsal surface would only be useful if the slices of sediment above them remained coherent, retaining most of their initial strength, and also remained attached to the undisturbed sediment of the sea floor on each side of the animal. Otherwise the dorsal ribs would have had nothing to push against.

Habitual depth of burial was therefore probably rather critically adjusted. The animal buried itself shallow enough to leave a strip free of mud along the mid-line of the back and to keep the mouth free of mud by the methods discussed later. But, contrariwise, it buried itself deep enough for the slices of sediment which passed over its back to remain coherent and also firmly connected with undisturbed sediment on each side of the head.

The pattern of ribs on the ventral surface of the head (figure 3*c*; plate 1, figure 41; plate 4, figures 71, 72) is at first sight similar to that on the dorsal surface, since on both there is a median smooth patch. Different to the dorsal smooth patch, however, the ventral patch is not precisely demarcated, for the ribs tend to break up near it into arcuate segments. The likely explanation for it is also different. In crawling, the sediment touching the middle part of the ventral surface would have been stirred up by the tail, so losing most of its strength. If ribs had existed in this region, therefore, the sediment would not have been strong enough for them to push against. Indeed, they would have had the disadvantage of stirring it slightly and making it still weaker. In other words, the intensity of ribbing was probably adapted not to exceed the strength of the sediment in contact. The limits of the stirred area of sediment would not be precise, and so the limits of the smooth area on the ventral surface are also not precise. The ribs are broken up near it, to act on sediment whose strength was intermediate between the undisturbed and completely disturbed states.

A similar pattern exists in the crab *Emerita* where the ribs gradually weaken and then disappear in passing from the dorsal surface of the thorax to the sides (sm car in figure 9), where the adjacent sediment would be stirred up and weakened by the action of the limbs in digging. The analogy with *P. forbesianus* is completed in *Emerita* by the presence in that crab of a smooth boss, formed from the most anterior segments of the abdomen (abd b). This boss is presumably smooth because it is the first part of the body to be pushed through the sediment. Its position is analogous to the smooth, postero-ventral area of *P. forbesianus* which probably had the same function (p sf in figure 3*c*). There is no median smooth patch on the dorsal surface of *Emerita*. This correlates with the fact that the crab, unlike the reconstructed habits of *Placocystites*, buries its back completely instead of leaving a median strip clear of the sediment.

As to the tail, the presence of recumbent folds on the dorsal surface of the fore tail implies that this surface was very stretchable and suggests that the fore tail could flex ventrally into a tighter curve than in *Mitrocystella*. The muscles of the fore tail would be the main source of motive power so the increased power of flexion was probably a burrowing adaptation. The hind tail of *Placocystites forbesianus* on the other hand, was probably stiffer than that of *Mitrocystella* as already mentioned. The poor development of bearing surfaces on the observed part of the hind tail (no posterior facets on the ossicles) is puzzling. Perhaps the distal part of the hind tail, which we have never seen, had a bearing surface on its dorsal ossicles, as in *Chinianocarpos* (Jefferies 1973, p. 456, fig. 15*c*) or *Peltocystis* (personal observation). This might form a vertical hook at the end of the tail, pushing horizontally forwards, as was probably the case in these two primitive genera. However this may be, the posterior facets of the ossicles of the hind tail in *Mitrocystella* and *Mitrocystites* were probably adopted to push downwards as well as forwards against the mud (Jefferies 1973, p. 456, fig. 15*d*; 1975, p. 284, fig. 15). By doing so they pushed the head backwards and upwards and so helped to avoid self burial. Their weak development in *Placocystites forbesianus* suggests that self-burial was less of a danger, which is understandable in a shallow burrower. A horizontally pushing tail would in itself be more efficient in moving the animal across the sea bottom than one that pushed forwards and downwards.

Additional ornament on the tail of *P. forbesianus*, as compared with *Mitrocystella*, consisted of knobs on the major plates of the fore tail, and on the anterior ventral plates on the hind tail, and striae on the sides of the dorsal ossicles. The knobs of the fore tail and the striae of the hind tail were perhaps adapted to grip the sediment during lateral flexion, for some such flexion is probably implied, as mentioned above, by the divarication of the ribs on the head. The knobs on the ventral plates of the hind stem probably helped to grip the sediment in ventral flexion.

Various features associated with the mouth, including the oral spines, the oral funnels spreading out from the lateral notches, the integument anterior to the funnels, the olfactory notches and the associated gaps lateral to the oral plates, and the fusion of the orals into four large oral plates, are the most obvious differences between *Placocystites forbesianus* and *Mitrocystella*. It is likely that these features, also, were adaptations to a life spent crawling partly buried in sediment. The slices of sediment which slipped forwards over the dorsal surface of the head, as the latter was pulled backwards by the tail, would naturally fall off the anterior, trailing edge of the head. There they would be in danger of clogging the mouth which would have killed a filter-feeding animal like *Placocystites*. This danger was the greater since *P. forbesianus* having rigid ventral armour, could not squirt water out of the mouth by contracting the ventral wall of the head as *Mitrocystella* might have done.

The oral spines were probably part of the mechanism for removing mud from round the mouth. This is likely because the slices of sediment that fell off the anterior margin of the head would fall into the field of sweep of the spines. However the spines acting alone are ill adapted to serve as shovels. Indeed they are more like knives with a rounded median face and a single cutting edge along the lateral margin, convex along its length like the sharp edge of a sabre or a carving knife (plate 6, figures 79–82). Furthermore the articulations of the spines suggest that they moved mainly in a horizontal plane, although the plane of sweep could be adjusted to slope upwards or downwards anteriorly. A large site for muscle insertion exists on the proximal end of each spine, lateral to the socket. This implies a large muscle to pull the lateral, cutting edge of the spine outwards, presumably against considerable resistance from the mud. A much smaller muscle insertion, implying a much smaller muscle, exists on the proximal end of the spine median to the socket, although, during the return stroke, the blunt median surface of the spine would have been difficult to force through sediment (plate 2, figures 47, 49). The spines by themselves, therefore, would not have been effective in removing mud from near the mouth. Unaided they could have cut into it by swinging horizontally and outwards, but would have had difficulty in lifting the mud or returning in a median direction to their starting positions.

The oral funnels and their associated integuments, however, could well represent an additional part of the mud-shifting mechanism, for they probably evolved simultaneously with the spines and are in contact with them. The oral funnel on each side diverges from a notch that leads into the buccal cavity. The funnel seems to have been covered in front by a flap of plated integument that extended much or all of the distance to the spine. Perhaps, therefore, the funnel represents a channel carrying water, behind the flap of integument, from the buccal cavity to the spine base. If the integument of the funnel formed a soft sleeve round the base of the spine, as suggested in figure 4, then water could be squirted along the length of the spine as it swung outwards cutting the sediment (figure 10). This would make the spine enormously more effective as a mud shifter. It would also explain why the spine is blunt-backed, although the muscles acting during the return stroke were so small. With hydrodynamic assistance of the sort suggested, no mud would remain to resist the return stroke.

An analogy to this suggested mode of operation comes from the bivalve molluscs. The penetration of the bivalve foot into sediment is helped by squirting water out of the mantle cavity, along the surface of the foot into the sediment, which it momentarily liquidizes (Trueman & Ansell 1969, p. 339). The water is forced out of the mantle cavity by contraction of the adductor muscles that connect the two calcareous valves of the shell. Its exit along the surface of the foot is controlled by the soft mantle edges which form a sleeve loosely in contact with the base of the foot, like the postulated sleeve round the base of each oral spine in *P. forbesianus*. Dramatic photographs of this hydrodynamically assisted digging have been published by Ropes & Merrill (1966) for the American surf clam *Spisula solidissima*.

Hydrodynamic assistance for the oral spines, however, would require a powerful jet of water. Sufficient volume of water could probably not be supplied by contracting the integument anterior to the oral funnels. It is more likely that there was a strong pump inside the head. Unlike *Mitrocystella*, no jet could have been produced by contraction of the floor of the head, which in *P. forbesianus* was rigid. Perhaps the velum, between the buccal cavity and the pharynx, was highly muscular, as in agnathan fishes. It may have undulated in a sine wave, from one side to another and back again, like a billowing curtain. Such a velar pump could pull water into the right side of the buccal cavity while simultaneously expelling it from the left side and *vice versa*, without ever changing the total volume of water inside the head. This would imply that the spines swung leftwards or rightwards together, so that the outward exhalent, cutting stroke of one coincided with the inward, inhalent, return stroke of the other (figure 10). If, as implied by hydrodynamic assistance to the cutting action of the spines, the lateral notch leading to the oral funnel was an outlet from the buccal cavity, then the observed gap just lateral to the oral plates may have been an inlet. The groove connecting this gap to the olfactory cup inside the theca agrees with an inhalent function (plate 5, figure 78; inh gr).

Two features of the internal anatomy suggest that *P. forbesianus* probably did possess a more powerful velum than *Mitrocystella*. The more important is a well marked groove in the inner face of the dorsal skeleton of *P. forbesianus* in a position defining the posterior margin of the buccal cavity (vel in plate 4, figures 69, 70; plate 5, figure 77). This groove could well be the site of attachment of a muscular velum. Any such groove is much less definite in *Mitrocystella incipiens miloni*, *Mitrocystella barrandei* or *Mitrocystites mitra* in all of which the posterior limit of the buccal cavity is difficult to fix (see however figure 16 and plate 11, figure 111; figure 17 and plate 11, figure 113). The second feature which may be connected with a powerful muscular velum is a pair of big nerves n_x in *P. forbesianus*, running forward in the ventral skeleton (figure 25; plate 5, figure 75; plate 8, figure 95), for no homologous nerves existed in *Mitrocystella incipiens miloni* (figure 23; plate 9, figures 98, 99).

The divaricate pattern of ribs on the dorsal and ventral surface of the head could have been an adaptation to resist torsion in a horizontal plane as the oral spines cut sideways into the mud. This would be additional to any similar torsion produced by the tail. The fusion of small, primitive oral plates to form four large oral plates in *P. forbesianus* may relate to the rigidity of the ventral skeleton, which meant that the lower lip did not need to be so flexible as in *Mitrocystella*.

Perhaps the mud that fell off the anterior edge of the head during movement was not a mere nuisance to *P. forbesianus*, but useful to it. Like most mitrates its mouth would be approximately level with the sea bottom and so it was probably a deposit feeder, living on the layer of detritus that rested on the sea floor. It would be ecologically similar to many Tellinacean bivalves (Pohlo 1969; Yonge 1949). The mud that travelled forwards over the head would include this food-rich surface layer and the spines would represent a method of winnowing the mud, so that the resulting suspended food particles could be sucked into the mouth. By comparison with *Mitrocystella*, therefore, the burrowing habit of *P. forbesianus* would not be merely a better mode of locomotion, avoiding jerky, up-and-down movements of the head, but would also be a better way of grazing the food-rich surface layer of the sea floor.

If this were so, the spines of *Placocystites forbesianus* would be convergent with the right oral appendage of *Cothurnocystis*. This appendage also would have been able to swing from right to left in a horizontal plane presumably pulled by muscles (Jefferies 1968, p. 259; 1975, fig. 2) and would have served to churn up the surface layer of the sea floor so that the resulting suspension could be sucked in by the mouth. The right oral appendage of *Cothurnocystis*, however, was not hydrodynamically assisted and therefore had sharp edges on both sides. It cannot be homologous in any way with the oral spines of *P. forbesianus* which seem to have arisen from ordinary marginal plates as seen in *Mitrocystella* and *Mitrocystites*. In fact, the right oral appendage of *Cothurnocystis* is homologous with plate *c* of *Reticulocarpos*, *Mitrocystites* and *Mitrocystella*, and therefore with plate *c* of *P. forbesianus*, which is the marginal plate just median to the right oral spine (figures 29, 30). The laterally mobile spines of *P. forbesianus* developed independently to those of *Cothurnocystis* but probably had the same winnowing function.

Thus *Placocystites forbesianus* and its relatives, constituting the Anomalocystitida, were probably descended from a Mitrocystitid related and similar to *Mitrocystella barrandei*. This ancestral form was adapted to ploughing backwards through the topmost layer of sediment, with its dorsal surface unburied, in primitive mitrate fashion. The Anomalocystitids which descended from it, by contrast, took to sliding backwards through the sediment just beneath the sea bottom, so that the dorsal surface was largely, but not completely, covered with mud. Adaptations for this mobile but partly buried mode of life included: (1) evolution of a rigid ventral surface to the head, so that the whole head became box-like, and would not collapse under the load of sediment; (2) reduction in the posterior surface of the head, and acquisition of a strong downwards slope on the posterior part of the dorsal surface, so that the head rode more easily through the sediment without bobbing up and down and mud was lifted up over the dorsal surface; (3) acquisition of sediment-gripping ribs both dorsally and ventrally, to resist unwanted forward movement by pushing against the mud both above and below the animal; (4) development of hydrodynamically assisted oral spines by modification of two marginal plates (these spines served to clear mud away from the mouth and also served to winnow food from the surface layer of sediment; their evolution was correlated with the development of oral funnels and probably with the development of a thick muscular velum to act as a pump, of which there are some signs in the internal anatomy); (5) the major plates of the fore tail were sutured together to form rings, for better protection of the soft parts in the lumen against weight of sediment, and large imbrication flaps evolved dorsally, to increase the power of ventral flexion.

(*e*) *The non-nervous internal anatomy of the head*

(i) *The pharynxes of living primitive chordates*

Living primitive chordates that feed by means of a mucous trap inside the pharynx comprise the tunicates, the acraniates and the ammocoete larvae of lampreys. In all of these the pharynx has fundamentally the same structure. This is likely to have been inherited from the latest common ancestor, which would have been a mitrate.

The common elements in the anterior part of the alimentary canal in all chordates that feed by a primitive pharyngeal mucous trap are as follows. At the anterior end is an ectodermal buccal cavity. Behind this is a wall called the velum – a remnant of the embryonic stomodaeal membrane – penetrated by a hole called the velar mouth. Behind the velum is the pharynx which opens posteriorly into the oesophagus. The pharyngeal wall is penetrated by gill slits; usually these are paired on right and left but in early larval acraniates the gill slits that exist belong morphologically to the left side, though they penetrate the right wall of the pharynx. Somewhere in the wall of the pharynx, and except in larval acraniates always in the ventral mid line, is a gland known as the endostyle; this is usually a long groove with a flagellate strip forming its floor while alternating longitudinal gland strips and ciliated strips form its sides. From the anterior end of the endostyle go off the peripharyngeal bands of cilia, situated in peripharyngeal grooves. Usually there is a pair of peripharyngeal bands but early larval amphioxus appears to have a left peripharyngeal band only (Bone 1958).

The pharynx functions as follows. A current of water flows through the mouth, into the pharynx, and out through the gill slits; this current may be propelled by cilia on the edges of the gill slits (most tunicates, acraniates), by contraction of the body wall (salps) or by the pumping action of a muscular velum (ammocoete). The endostyle secretes mucus. In some forms this varies in quantity and can be produced in strands, in continuous sheets, or in intermediate abundance. The strands or sheets are carried out of the endostyle dorsalwards, being held at their front ends by the cilia of the peripharyngeal bands. Particles that have been brought into the pharynx by the water current become trapped in the mucus and are conveyed, by various methods, to the oesophagus and thence to the stomach. The mucus is often caused to rotate by cilia, either before entering the oesophagus or later. This rotation, curiously enough, seems to be always in the same direction: anticlockwise as seen from behind. This direction of rotation holds for benthonic tunicates (Werner & Werner 1954), salps (Carlisle, personal communication), doliolids (Fol 1872, fig. 4; Carlisle, personal communication), appendicularians (Fol 1872, fig 5; Carlisle, personal communication) and amphioxus (Barrington 1938).

The pharynx of tunicates requires special attention, because, as shown later, it presents particular points of comparison with mitrates. That of the benthonic tunicate *Ciona* has been well described by Millar (1953). The pharynx of this animal is enclosed laterally and dorsally, as in other tunicates, by a symmetrical ectodermal chamber, the atrium. This opens to the outside by an atrial siphon. Numerous gill slits penetrate the pharyngo-atrial wall, each slit fringed with cilia. These lateral cilia of the gill slits function in pumping the water current. This flows through the mouth (oral siphon), through the velar mouth into the pharynx, through the gill slits into the atrium, and thence out of the atrial siphon. The endostyle follows the mid-ventral line of the pharynx and is developed in the median walls of a pair of upstanding endostylar folds. The floor of the endostylar groove is flagellate. There are three longitudinal gland strips in either wall and between the gland strips the endostyle has longitudinal ciliated strips. Dorsal to the most dorsal gland strips, on the exposed edges of the endostylar folds, are the left and right marginal ciliated bands. Anteriorly these continue into the left and right peripharyngeal bands which pass round the pharynx, anterior to the gill slits to meet at a point in the dorsal mid line. Behind this point, along the dorsal mid line of the pharynx, there is developed a series of hooked, finger-like, dorsal languets which curve ventralwards and to the right. *Ciona* has a complex interbranchial basket made of blood vessels. This basket forms a sort of false wall, pierced by numerous large perforations, internal to the pharyngeal wall proper.

The right marginal band of the endostyle of *Ciona*, but not the left one, continues posteriorly into a pouch known as the endostylar appendage and passes from here, as the retropharyngeal band, into the oesophageal band. This runs in the wall of the oesophagus to the stomach. This asymmetry of the retropharyngeal band, in being connected to the right marginal band but not to the left one, is general for tunicates. It holds for benthonic tunicates, for salps, where the left marginal band never extends to the posterior end of the endostyle and the oesophagus opens into the pharynx well right of the mid line, and also in doliolids and pyrosomes (Neumann 1935, p. 252). In appendicularians, however, the whole internal surface of the oesophagus is ciliated and both marginal bands connect with this surface (Fol 1872, fig. 5). A generalized tunicate pharynx, rather similar to that of *Ciona*, is shown in figure 13. Excellent figures of *Ciona* are given by Millar (1953).

The method of feeding in benthonic tunicates has been described in *Ciona* (Millar 1953) and *Clavelina* (Werner & Werner 1954; figure 11, herein). The endostyle produces continuous sheets of mucus which pass into the pharynx at right and left, being kept separate by the flagella rooted in the floor of the endostylar groove. On leaving the endostyle the sheets pass dorsalward, being held away from the true pharyngeal wall by the interbranchial basket of *Ciona* and by special transverse hoops in *Clavelina*. Finally the sheets pass, from right or left respectively, to the right, concave side of the dorsal languets and are rolled up by the cilia of the dorsal languets to form a mucous rope. The rotation of the rope, anticlockwise as seen from behind, is consonant with the flow of mucus in the right half of the pharynx. The rope is pulled back into the oesophageal ciliated band, and so reaches the stomach.

Any particles in the water current, whether nutritious or not, will be filtered from it when the water passes through the mucous sheets. They will then be incorporated in the mucous rope and be passed through the oesophagus to the stomach. This method of feeding, by using mucous sheets, corresponds to what Carlisle (1950) called the fast method in the planktonic tunicates known as salps. (The slow method in salps involves the production of mucous strands which are fixed by their anterior ends to the peripharyngeal bands but posteriorly waggle freely in the water.) The retropharyngeal band of salps functions in conveying the posterior end of the mucous sheets to the oesophagus at the beginning of fast feeding (Carlisle, personal communication). It may have a parallel function in ascidians such as *Ciona*, serving to pass the posterior end of the mucous sheets back to the oesophagus when feeding begins. (Slow feeding, using mucous strands, has never been recorded in benthonic tunicates such as *Ciona* or *Clavelina* and the matter is further complicated by the fact that *Clavelina* has no retropharyngeal band, in that the right marginal band passes directly backwards into the oesophageal band).

Two further points in tunicate anatomy can be illustrated by *Ciona*. The first relates to the epicardia. These are a pair of pouches which exist in nearly all tunicates and arise as pouches from the posterior end of the pharynx i.e. the left epicardium arises from the left half of the pharynx and the right epicardium from the right half of the pharynx. In *Ciona*, but not in other tunicates, the epicardia remain connected with the pharynx in the adult by a pair of pharyngo-epicardial openings on either side of the retropharyngeal band (figure 12).

The second anatomical point relates to the arrangement of the ciliated bands of the pharynx. It is possible to see these bands in tunicates as arranged in a sequence which we here name the alimentary ciliated loop (figure 13). The distal end of this loop in *Ciona* can be taken at the posterior end of the left marginal band; from here the loop runs forward as the left marginal band, into the left peripharyngeal band, into the right peripharyngeal band, down the right marginal band, into the retropharyngeal band, into the oesophageal band, and ends proximally in the stomach. Seen in this light, the right peripharyngeal band is not so much a right antimere

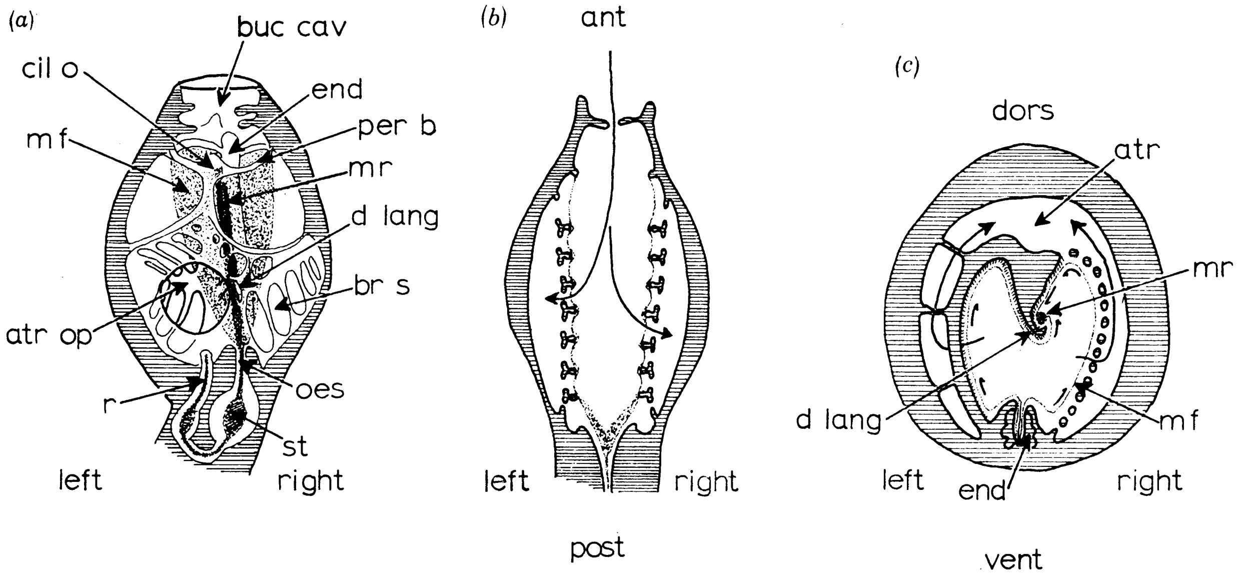

Figure 11. Structure and function of the pharynx in the ascidian *Clavelina lepadiformis* (redrawn after Werner & Werner 1954, figs 3, 6, 9). (*a*) General view, dorsal aspect. (*b*) Horizontal section. (*c*) Transverse section.

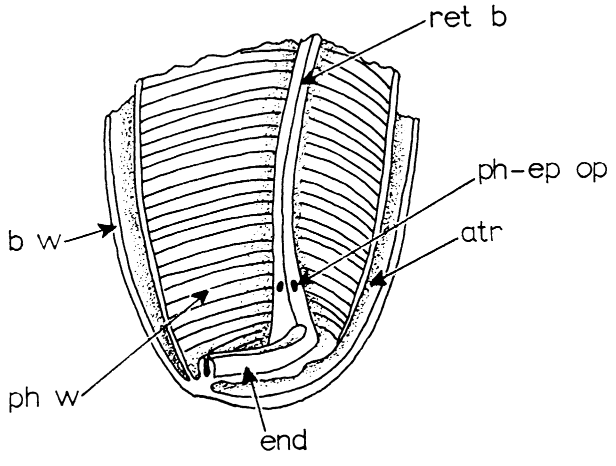

Figure 12. Diagram of posterior portion of pharynx of *Ciona intestinalis* anterior aspect (after Millar 1953, fig. 29). Note the retropharyngeal band (ret b) which is an extension, passing to the oesophagus, of the right marginal band of the endostyle (end). The pharyngo-epicardial openings (ph-ep op) are situated left and right of the retropharyngeal band.

of the left peripharyngeal band, as a continuation of it (figure 13). This is important because the deduced peripharyngeal bands of mitrates seem even less like antimeres than those of tunicates, except presumably in function, while cornutes, having no right pharynx, could not have had a right peripharyngeal band as such. They would be more like larval amphioxus in possessing only left gill slits and a left peripharyngeal band (Bone 1958).

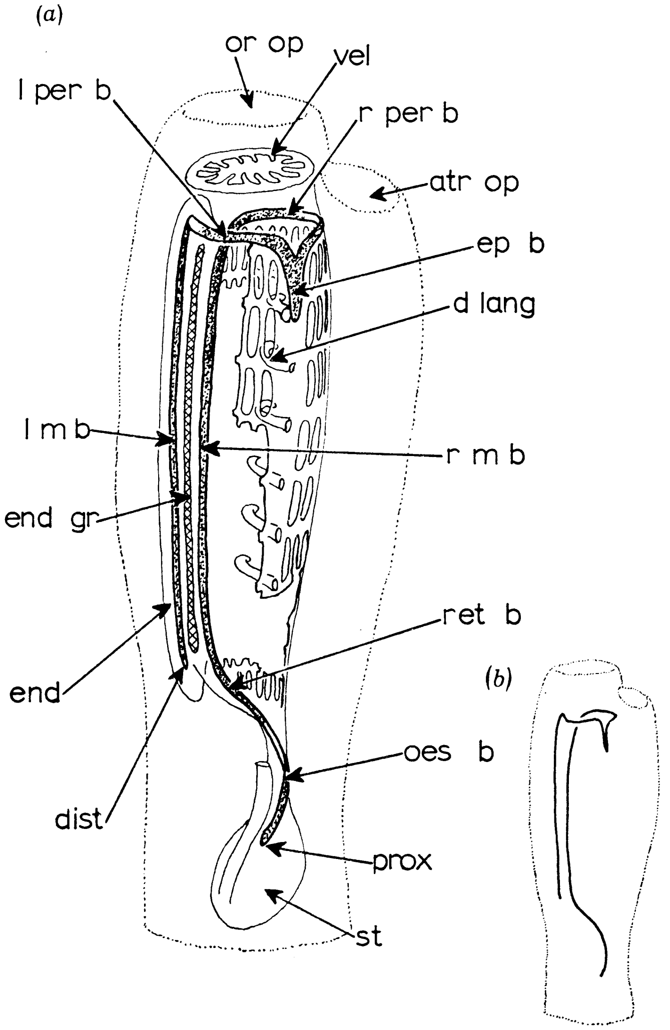

FIGURE 13. Diagram of the alimentary canal of a generalized ascidian. (a) General view. (b) The course of the alimentary ciliated loop in a.

Some other points of tunicate anatomy need mention. The first is that some tunicates have a fold of flesh called the dorsal lamina, instead of the series of dorsal languets. Like the languets, the lamina has the same curvature, ventralwards and rightwards, and presumably has the same function in rolling up the mucous rope. The second point concerns the neural gland. This is in contact with the ganglion of adult tunicates. It sends a duct forwards which opens, by a complicated ciliated organ, into the dorsal surface of the pharynx just anterior to where the left and right peripharyngeal bands meet each other. In the planktonic doliolids the duct is asymmetrical in position, passing dorsal to the left peripharyngeal band. A third point relates to the endostyle of some salps which is highly asymmetrical, with the right lip overlapping the left lip and no left marginal band, or only a very short one anteriorly (Garstang & Platt 1928).

The pharynx of adult amphioxus is too well known to need redescription. Its functioning was described by Orton (1913). Its very asymmetrical ontogeny is described later as concerns the mouth and gill slits (p. 267). The origin of the endostyle can be noted here, however. It arises as a bean-shaped structure in the right wall of the pharynx, anterior to any gill slits and with its greatest dimension vertical (figure 22*e*). Later, when the first group of right gill slits have appeared, the endostyle becomes V-shaped and grows back between the right and left gill slits so as to give the bilateral, median endostyle of the adult. The flagellated median strip of the adult endostyle probably arises from pharyngeal wall that originally lay anterior to the endostyle, but passed backwards as a salient between the extending arms of the V (Garstang 1928, p. 90). We suggest later that a similar change in the endostyle from a transverse to a bilateral, fundamentally V-shaped condition probably happened phylogenetically in passing from the cornute condition, with left gill slits only, to the mitrate condition, with right gill slits also. A similar V-shaped stage is passed through in ontogeny by the endostyle of salps (figure 14).

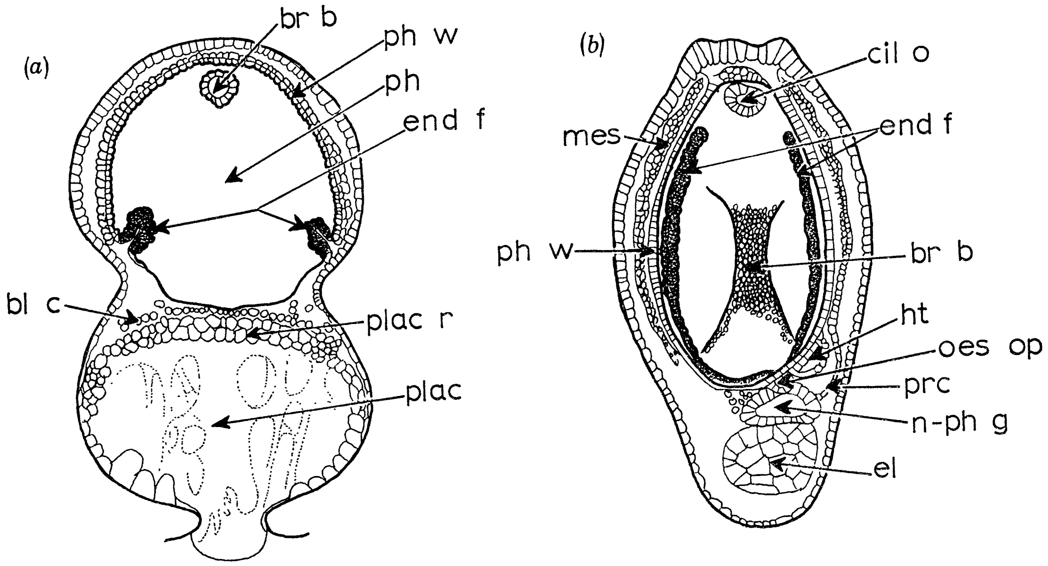

Figure 14. Early ontogeny of the endostyle in the salp *Salpa democratica*. (*a*) Transverse section showing widely separated endostylar folds (end f). (*b*) General dorsal aspect of embryo showing how endostylar folds converge backwards on the oesophageal opening (oes op). (After Salensky 1876, pl. 15, fig. 26, pl. 16, fig. 29.)

The pharynx of the ammocoete larva is known to function in much the same way as that of tunicates or amphioxus. The endostyle produces mucus which flows into the pharynx (Sterba 1962) and is carried dorsalward held anteriorly by the peripharyngeal bands. Within the pharynx the mucus is present either as threads (Whiting 1972, p. 2; Kieckebusch 1928, p. 353) or as a continuous cone (Balabai 1951, 1956; Newth 1930). The observers who saw a cone did so after feeding the ammocoete with particles of chalk or ink and assumed that this treatment had no effect on the mode of feeding. However it is known in salps that abundant particles will produce the fast mode of feeding, by mucous sheets rather than strands (Fedele 1934; Carlisle 1950) so perhaps the same is true of ammocoetes. The pharyngeal water current is pumped in ammocoetes by the paddling action of the muscular velum.

(ii) *Introduction to the internal anatomy of the head in calcichordates*

The reconstruction of the internal head anatomy of calcichordates is based partly on the skeletal details of the various forms and partly on comparisons between them. It is therefore necessary to review the whole subject before considering particular species.

Inside the head of a boot-shaped cornute such as *Cothurnocystis* (figures 15*b*, 27) there is direct evidence in the internal moulds for four chambers and circumstantial, comparative evidence for a fifth. The most obvious chamber was the buccal cavity which largely filled the buccal lobe behind the mouth (i.e. the 'ankle' part of the boot-shaped head). The evidence in the internal moulds for the buccal cavity of *Cothurnocystis* can be found in Jefferies (1968, p. 255) and see also Jefferies (1968, p. 271) for *Scotiaecystis* (= *Cothurnocystis curvata*), Jefferies (1969, p. 510) for *Ceratocystis*, and Jefferies & Prokop (1972, p. 87) for *Reticulocarpos* and *Galliaecystis*. Another obvious chamber was the posterior coelom, situated just anterior to the tail. In the 'foot' part of the 'boot' there is direct evidence for two further chambers, one lying above the other. The more dorsal of these two chambers had the gill slits opening through its roof, and was consequently the pharynx. The more ventral chamber, underlying the pharynx, was most capacious near the posterior right corner of the head. From it ran the gonorectal groove in the skeleton to the gonopore-anus just left of the tail (this groove corresponds to an obvious ridge on the internal mould, figure 26; plate 14, figures 127–132, 134, 135). The groove seems to have carried the rectum and gonoduct beneath the posterior coelom, so the chamber from which the groove emerged would have contained the gonad and most of the non-pharyngeal gut. It was therefore presumably a coelom, here called the right anterior coelom, as in Jefferies (1975, p. 261). It is the same as the anterior coelom of our earlier papers (e.g. Jefferies 1973, p. 425). There is also evidence that the right anterior coelom contained the heart, and homologues of the axial gland of echinoderms or neural gland of tunicates. The evidence in the internal moulds for the right anterior coelom and its contents, the pharynx and the posterior coelom of *Cothurnocystis* is discussed in a later section of this paper (p. 281).

The fifth chamber, based purely on comparative evidence, probably overlay the pharynx and had little or no cavity (figure 15). This virtual chamber can be called the left anterior coelom. The argument for its existence has already been given in outline in Jefferies (1975, p. 261). A cornute, and in particular the primitive form *Ceratocystis*, can be compared with a pterobranch hemichordate like *Cephalodiscus* lying on its right side. The stem of *Cephalodiscus* is presumed to be homologous with the tail of a cornute or at least to correspond to it in position. The pharynx, gonads and non-pharyngeal gut of *Cephalodiscus* are supported by mesenteries between the left and right trunk coeloms or metacoels. The right metacoel of a pterobranch, excluding its extension into the stem, is presumably homologous with the ventrally situated right anterior coelom of the head of a cornute, since the right side of *Cephalodiscus* corresponds to the ventral surface of a cornute. This suggests that, dorsal to the pharynx, the head of a cornute may also have contained a homologue of the pterobranch left metacoel, excluding the extension of the latter into the stem. This suggestion is strengthened by the situation in echinoderms. For these are probably the closest relatives of chordates, both phyla being descended from one and the same hemichordate ancestor that lay down on its right side and acquired a calcite skeleton (Jefferies 1969, 1975, p. 270), and echinoderms have left and right somatocoels homologous with the left and right metacoels of hemichordates.

Arguing from the descendants of calcichordates, rather than from their collateral relatives, the

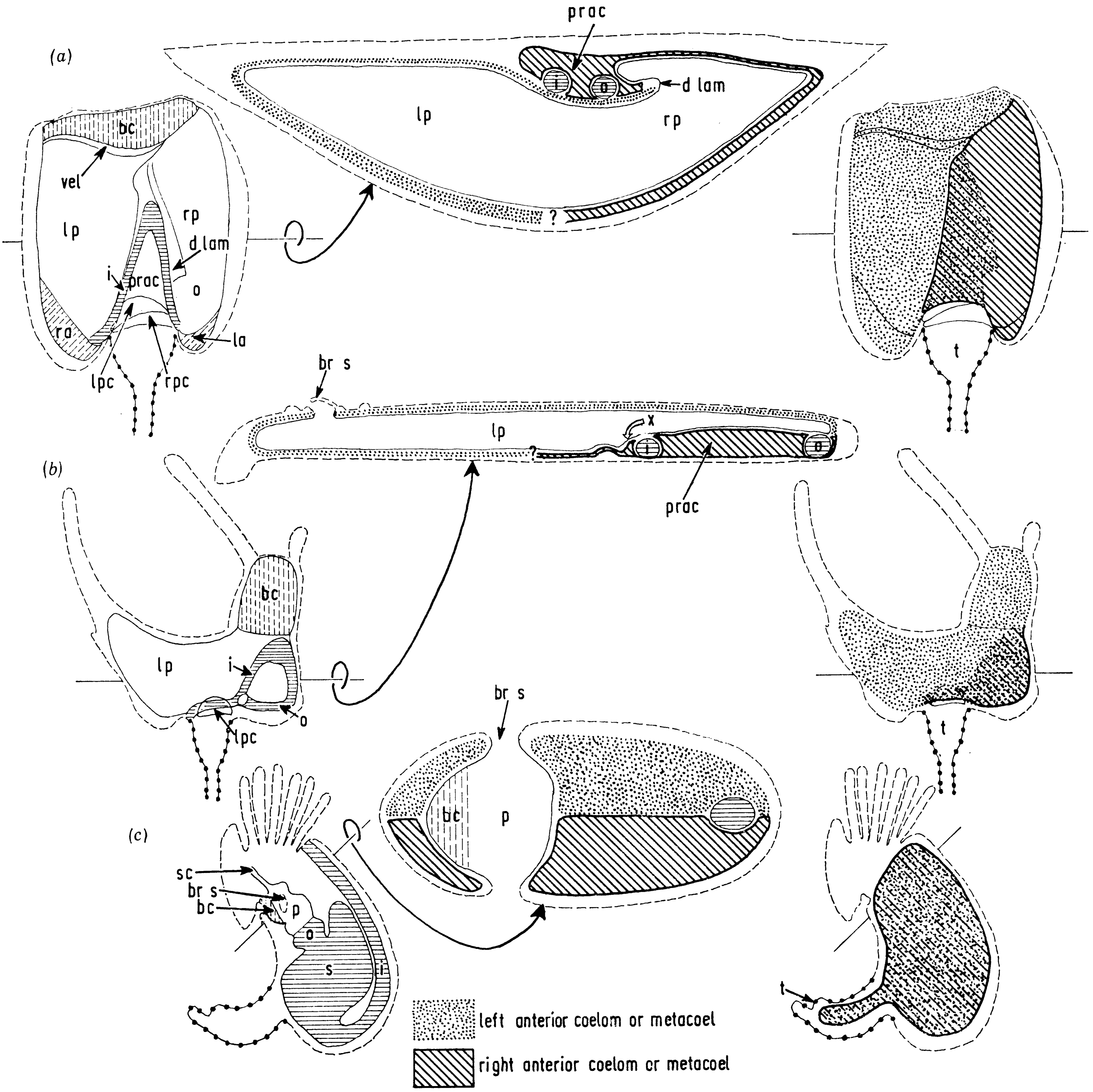

FIGURE 15. Comparison of the morphologies of: (*a*) mitrate (*Placocystites*); (*b*) a cornute (*Cothurnocystis*); and (*c*) a pterobranch (*Cephalodiscus*). The tails of cornutes and mitrates are presumed to be homologous with the stem of a pterobranch. A cornute can be compared with a pterobranch resting on its right side. The arrow at *x* indicates the approximate position from which the right pharynx grew out in mitrates. Compare figure 27.

conclusion that both left and right anterior coeloms existed in calcichordates is strengthened by the fact that the homologues of both chambers can be found in acraniates as well as vertebrates, as shown later. Tunicates, indeed, though likewise descended from calcichordates, do not have homologues of these coeloms, but this is probably due to secondary loss, the epicardia having replaced them functionally. (The epicardia of a tunicate are probably homologous with the posterior coelom of a mitrate, as argued below p. 257.) In summary it is therefore likely that the head of a cornute contained buccal cavity, pharynx and posterior coelom and right and left anterior coeloms. The latter were situated ventral and dorsal to the pharynx and were homologous with the right and left metacoels of the body region of pterobranchs, with the right and left somatocoels of echinoderms, and with right and left equivalents in standard vertebrates and acraniates whose nature will be discussed later. The use of the terms right and left in relation to anterior coeloms refers primarily to their positions in mitrates. By good luck it could equally well refer, however, to their positions in hemichordates.

In mitrates the chambers of the head are fundamentally as in cornutes, but with complications and additions (figure 15*a*). The internal natural mould of a mitrate head gives a positive replica of the soft parts, as if these had been modelled in rock. The most obvious feature of the dorsal surface of the internal mould is an oblique groove running from anterior right to posterior left (see for example figures 16, 17; *Mitrocystella* in plate 11, figures 110, 112, 113; plate 12, figures 114, 115, 117; and compare with the models of *Placocystites* in plate 5, figure 77; plate 10, figure 108). It divides the internal mould into an anterior left field and a posterior right one. The oblique groove of a mitrate corresponds in gross disposition with the line separating the left anterior coelom of a cornute from the right anterior coelom, which was also the line separating the pharynx of a cornute from the right anterior coelom. In cornutes, however, this line can be followed round the inside of the right lateral and right posterior walls of the head (see figure 26 and also Jefferies (1968, pp. 255–257) for *Cothurnocystis*), whereas in mitrates the oblique groove runs across the ceiling of the head. Comparison between cornutes and mitrates suggests that the field anterior to and left of the oblique groove of a mitrate should correspond to the left anterior coelom of a cornute, and would overlie the mitrate homologue of the cornute pharynx. And the field posterior to and right of the oblique groove should correspond to the right anterior coelom of a cornute (figure 15*a*, *b*).

This broad comparison is probably correct, but the oblique groove of mitrates varies along its length in strength and direction. Its anterior third often arches rightward and is weaker than the posterior two-thirds. Moreover it is necessary to explain why the oblique groove runs across the ceiling of the head, instead of being situated laterally as in the primitive cornute condition. The difference between mitrate and cornute situations can be explained by assuming the existence in mitrates of a right pharynx which, both in ontogeny and phylogeny, had pouched out of the left, primitive or cornute pharynx and extended towards the posterior right corner of the head, where gill slits would have existed between it and the right atrium. The anterior weak third of the oblique groove would indicate where the right pharynx emerged from the left one. Seen in transverse section, the right pharynx would have pouched out from the cornute left pharynx at the point marked x in figures 15*b*, 27*b*. It would pass through the right anterior coelom and ventral to its cavity and contents. These would have been lifted up, squashed against the ceiling of the head and forced in a median direction. As a result, the field posterior to and right of the oblique groove of the natural mould of a mitrate came to be divided into two regions. Laterally there is the region where the right pharynx was present, overlain by virtual right anterior coelom with no cavity. Median to this is a triangular region which corresponds to the cavity of the right anterior coelom and contained the viscera. This distinction shows particularly clearly in the internal mould of *Mitrocystites* (plate 11, figure 111). Consideration of how the outpouching of the right pharynx would have affected the primitive cornute situation suggests that the cavity of the right anterior coelom would overlie the rightmost part of the virtual left anterior coelom, and also the rightmost part of the left pharynx which would have been covered by virtual left anterior coelom (figure 15*a*). The oblique groove would therefore be a mesenteric trace where right and left coeloms met, which is a partial return to Chauvel's interpretation (1941, p. 232). There is no indication as to where the boundary between right and left anterior coeloms lay on the ventral face of a mitrate. Perhaps it was roughly median.

The gill slits of cornutes were external and penetrated the dorsal surface of the head on the left only. They seem to be clearly adapted as outlet valves in *Cothurnocystis* (Jefferies 1968, p. 253) and *Scotiaecystis* (Jefferies 1968, p. 266). The gill slits of mitrates were presumably internal, for there is evidence of left and right gill openings near the posterior corners of the head. Also the gill bars between the gill slits were calcitized in the mitrate *Lagynocystis* and are well preserved in the fossils; most of these gill bars are associated with a median atrium peculiar to *Lagynocystis* but the left-most gill bar shown in the photograph in Jefferies (1973, pl. 40, fig. 35) may well have belonged to the left atrium, as we now believe.

Left and right atria lay anterior to these openings in mitrates and presumably had gill slits in their anterior walls. The left atrium shows as a clearly defined chamber on the internal mould of *Mitrocystella* (plate 12, figure 118) and *Mitrocystites* (plate 15, fig. 138; Jefferies 1969, pl. 98, fig. 7, pl. 97, fig. 11, text-fig. 15). The existence of right gill slits, or at least of the first right gill slit to be evolved, is an all-or-nothing character which can only have evolved suddenly. The first mitrate, defined as the first chordate with right gill slits, would therefore have been a 'hopeful monster' and the child of cornute parents. It is conceivable that the right pharynx appeared before the right gill slits, but more likely that both appeared simultaneously, in one and the same individual.

The separation between buccal cavity and left pharynx on the dorsal surface of the internal moulds of the heads of mitrates is always much less obvious than the oblique groove (see for example *Mitrocystella* in plate 11, figure 113; *Mitrocystites* in plate 11, figure 111). It is therefore natural to suppose that the buccal cavity and the left pharynx, with the velum and velar mouth between them, all lay ventral to the left anterior coelom which would have covered the whole field left of and anterior to the oblique groove. (As already mentioned, there is no evidence as to how the left and right anterior coeloms were distributed on the ventral surface of the head.) The distribution of these structures beneath the left anterior coelom recalls the fact that the buccal cavity, the velum, the velar (or larval) mouth and the inner and outer lip coeloms of amphioxus are all organs of the left side. This is shown by their musculature and innervation (van Wijhe 1893; Franz 1927) and embryology (Legros 1898; van Wijhe 1914). Van Wijhe explained this asymmetry by supposing that the velar mouth of amphioxus was homologous with the left spiracle of a shark. A more likely explanation is that it derives, with little modification, from the mitrate condition, as will be discussed later.

Just anterior to the tail of mitrates was the posterior coelom (post c in plates 11, 12 (*Mitrocystella*) and plate 11, figure 111 (*Mitrocystites*)). We formerly assumed that this chamber was simply homologous with the posterior coelom of cornutes, with which it corresponds in position (see for example, Jefferies 1968, pp. 285), but this view now seems only half true (Jefferies 1975, p. 282). For there is evidence in *Placocystites* that the posterior coelom was homologous with right and left epicardia of a tunicate and direct evidence in *Mitrocystella* that it was a double chamber (photograph in plate 7, figure 89). Now the left epicardium of a tunicate arises as an outpouching from the left pharynx, while the right epicardium is an outpouching from the right pharynx. Since cornutes had a left pharynx, but no right one, their posterior coelom was presumably homologous only with the left epicardium of a tunicate. The right epicardium of mitrates was therefore presumably a new formation. It would have arisen in phylogeny at the same time as, or later than, the right pharynx.

In summary, the head of a mitrate is deduced to have contained: a left and a right anterior coelom separated by the oblique groove; a posterior coelom divided into right and left epicardia; right and left atria with presumed right and left gill slits anteriorly; and right and left pharynxes. These chambers are in many ways unsymmetrical, fundamentally as in cornutes. The main difference from cornutes was the first appearance of the right pharynx with right gill slits.

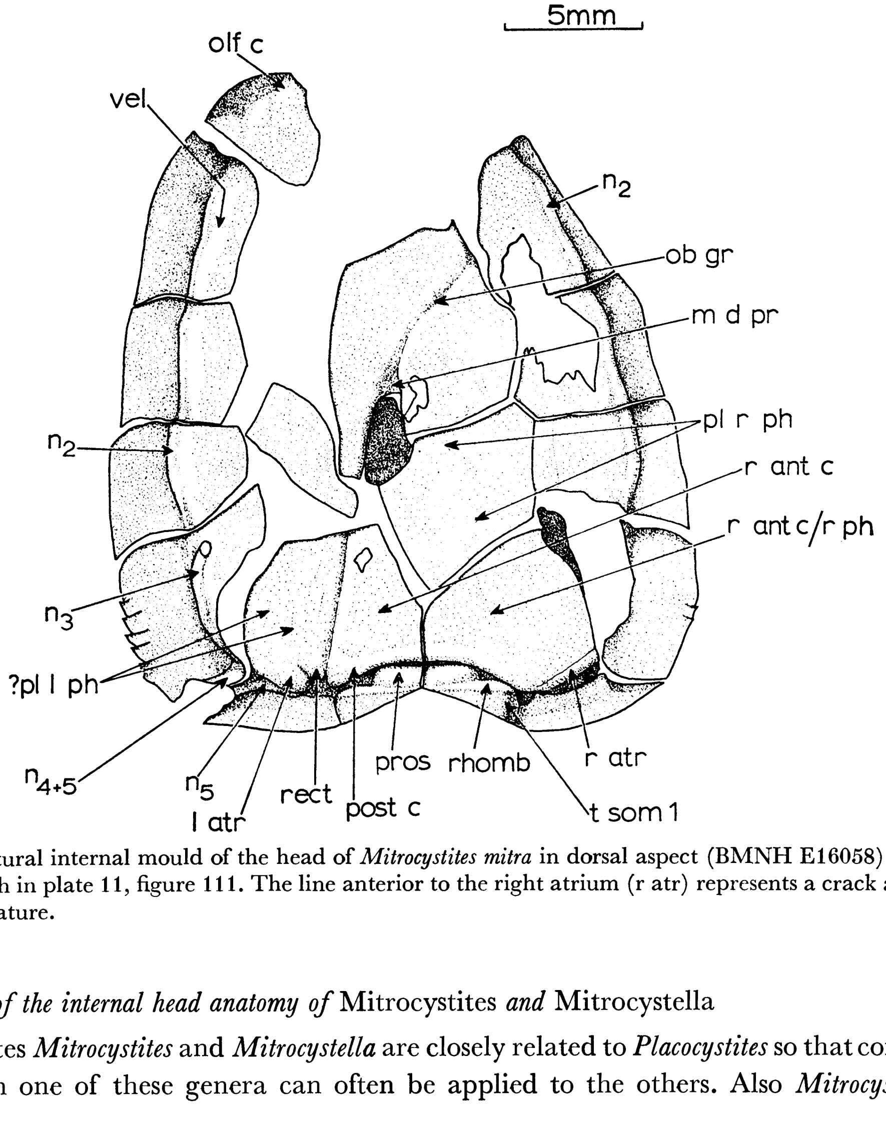

FIGURE 16. Natural internal mould of the head of *Mitrocystites mitra* in dorsal aspect (BMNH E16058). Compare photograph in plate 11, figure 111. The line anterior to the right atrium (r atr) represents a crack and not an original feature.

(iii) *Aspects of the internal head anatomy of* Mitrocystites *and* Mitrocystella

The mitrates *Mitrocystites* and *Mitrocystella* are closely related to *Placocystites* so that conclusions derived from one of these genera can often be applied to the others. Also *Mitrocystites* and

Mitrocystella are often preserved as internal moulds. This allows delicate structures to be observed which cannot be seen in *Placocystites*.

The dorsal aspect of the internal mould of *Mitrocystites mitra* Barrande (Lower Ordovician, Llanvirn, of Bohemia) is drawn in figure 16 and photographed in plate 11, figure 111. The specimen is incomplete anteriorly but clearly shows the oblique groove (ob gr) dividing the head into the fields of the left anterior coelom, anterior to it, and of the right anterior coelom posterior to it. The fact that the oblique groove is steeper on the right than on the left indicates that the left pharynx, and overlying left anterior coelom, dipped rightwards ventrally under the right anterior coelom. The mould also shows: the left atrium (l atr) (the right atrium occupied a corresponding position on the right, but in this particular specimen its dorsal boundary is not traceable); the posterior coelom (post c); the left olfactory cup (olf c) opening into the buccal cavity; and a possible trace of the velum (vel) between the buccal cavity and the left pharynx. A very important feature is a series of slight longitudinal corrugations in the region of the right pharynx (pl r ph). Anteriorly these corrugations extend near to the oblique groove. More posteriorly their leftward limit (r ant c/r ph) marks the boundary where virtual right anterior coelom, overlying the right pharynx, would have made contact with patent right anterior coelom. There are suggestions of similar corrugations in the left pharynx (? pl. l. ph). The corrugations cannot be growth lines, for they sometimes run across sutures without interruption.

A reconstructed, composite, internal mould of the head of *Mitrocystella incipiens miloni*, based on examination of a large number of individual specimens from the M. Ordovician (Llandeilo) of Brittany, is shown in figure 17*a*, *b* (cf. photographs in plate 8, figure 92; plate 11, figures 110, 112, 113; plate 12, figures 114, 115, 117 to 119). This reconstruction represents the surface of the soft parts in dorsal and posterior aspect. Broadly it is like the internal mould of *Mitrocystites mitra*. The oblique groove is again clearly visible, running from anterior right to posterior left. The field of the left anterior coelom would have included the buccal cavity, left pharynx and left atrium. The junction between buccal cavity and left pharynx would have been the velum which is perhaps indicated by a slight groove (vel in figure 17; plate 11, figure 113).

The left pharynx has two important peculiarities. The first of these is a series of slight longitudinal corrugations which end anteriorly as if against a sudden boundary (pl l ph) (photographs in plate 11, figures 112, 113; plate 12, figure 114). They recall the corrugations in the right pharynx of *Mitrocystites mitra*, and presumably have broadly the same structural significance. (There are also suggestions of one similar corrugation in the right pharynx of *Mitrocystella*, photograph in pl r ph in plate 11, figure 110.) The second peculiarity of the left pharyngeal region of *Mitrocystella* is the gentle ridge (g d), that passes from the region of the patent right anterior coelom backwards to the left atrium, becoming broader as it does so (photographs in plate 11, figures 110, 112; plate 12, figures 114, 115).

The longitudinal corrugations in the posterior part of the left pharynx of *Mitrocystella* and in the right pharynx of *Mitrocystites* suggest that these two parts were somehow functionally equivalent. (It is probably incidental that the two sets of corrugations have not certainly been found together in the same animal, for the preservation of such slight features is unusual and a matter of chance.) The individual corrugations suggest the original presence of longitudinal pleats in the pharyngeal wall. In interpreting them further it is necessary to recall the mucous pharyngeal traps of living chordates, briefly discussed above. In the filter-feeding pharynxes of living ammocoetes, acraniates and tunicates, whose latest common ancestor would have been

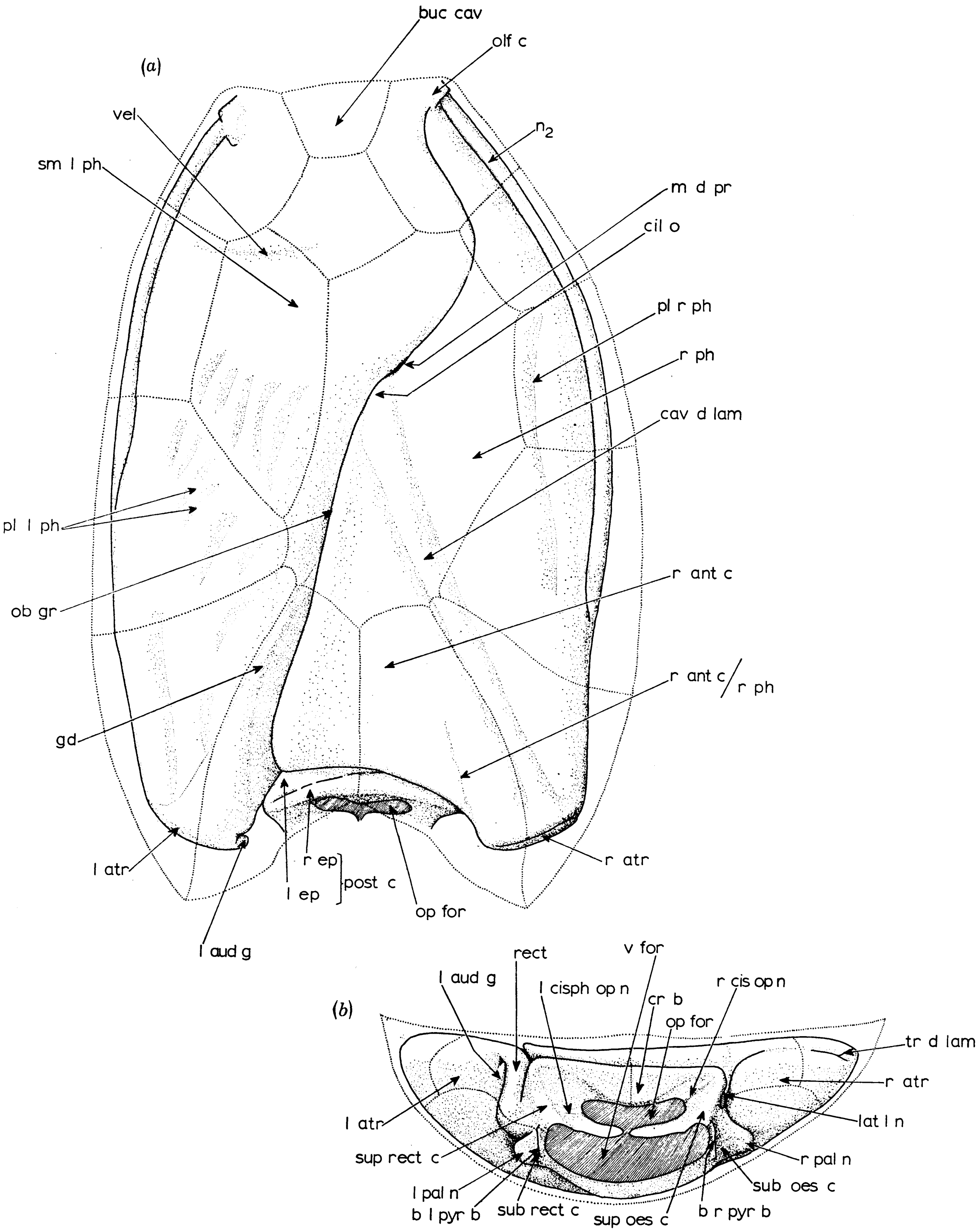

FIGURE 17. Reconstructed internal mould of the head of *Mitrocystella incipiens miloni*, based on many individual specimens. (*a*) Dorsal aspect. (*b*) Posterior aspect. Note especially: the oblique groove (ob gr) dividing the mould into the fields of the left and right anterior coeloms; the presence of longitudinal corrugations in the left pharynx, (pl l ph) comparable to those in the right pharynx of *Mitrocystites mitra* (figure 16). The rectum (rect) opening into the left atrium (l atr); the crescentic body (cr b); the cavity of the dorsal lamella (cav d lam); the gonoduct (g d); the division of the posterior coelom (post c) into left and right epicardia (l ep, r ep).

a mitrate, two regions can be recognized. The more anterior is behind the velum and in front of the peripharyngeal bands. The more posterior is behind the peripharyngeal bands, and in it various devices exist in tunicates to keep the strands of mucus produced by the endostyle away from the pharyngeal wall (e.g. the interbranchial bars of *Ciona*, the transverse hoops of *Clavelina*). This comparison suggests that the corrugated, and probably pleated, parts of the pharynx of mitrates would have been posterior to the peripharyngeal bands, while the smooth anterior part of the left pharynx would be anterior to them. The right peripharyngeal band would in that case have followed the anterior part of the oblique groove back to the left margin of the right pharynx near the mid-line (on the basis of the situation in *Mitrocystites*). The left peripharyngeal band, on the other hand, would cross the left pharynx at the anterior boundary of the corrugations (on the basis of the situation in *Mitrocystella*). The left and right peripharyngeal bands, if this suggestion is correct, would therefore meet dorsally at the oblique groove near the left boundary of the right pharynx. The suggested positions of the peripharyngeal bands are consistent with the situation in *Placocystites* (cf. figures 18, 20).

The gentle ridge gd probably has a different significance. In the primitive cornute *Ceratocystis* the gonopore opened directly out of the right anterior coelom, next to the anus, indicating that the gonad and non-pharyngeal gut were located in the cavity of this coelom, right of the tail (Jefferies 1969, text-fig. 2; 1975 fig. 6; photographs in 1969, pl. 95, fig. 1; pl. 96, figs 4, 6, 7, 8, 10). In *Cothurnocystis* the cavity of the right anterior coelom was still right of the tail but the gonopore and anus had shifted left of the tail, being connected to the cavity of the right anterior coelom by a groove in the skeleton. The details of this groove indicate that the gonoduct ran along the rectum and in contact with it (figure 26; photographs of internal moulds in plate 14, figures 128, 130, 134). In primitive mitrates conditions were probably the same, except that gonoduct and rectum would both open, not direct to the outside, but into the left atrium, as the rectum does in the tadpole of a modern tunicate. This is likely to have been the situation in *Mitrocystites* also, where the position of the rectum is indicated by a ridge on the internal mould (rect in figure 16; photograph in plate 11, figure 111). The same rectal ridge is even more prominent in *Mitrocystella* (figure 17*b*; photographs in plate 8, figure 92; plate 12, figure 118), indicating that the rectum opened into the left atrium in this genus also. The most likely explanation of the ridge gd in *Mitrocystella* is that it represents the course of the gonoduct, which no longer followed the course of the rectum, but ran direct from the gonad in the patent anterior coelom to the left atrium, across the ceiling of the left pharynx.

The field of the right anterior coelom of *Mitrocystella*, right of and posterior to the oblique groove, shows other complications. The line which is believed to mark the left boundary of the right pharynx in most mitrates (r ant c/r ph) is much weaker than in *Mitrocystites*, and indeed is only indicated doubtfully and in one specimen (photograph in plate 11, figure 112). More obvious, when once noticed, is a gentle but well defined ridge passing back from the oblique groove near the mid-line to the right posterior corner of the head (cav d lam; photographs in plate 11, figures 110, 112, 113; plate 12, figure 114). The nature of this ridge will be discussed later. Just to the right of it there is a deep pointed hole extending back almost horizontally into the internal mould from the oblique groove. This would represent a mid-dorsal process (m d pr; plate 12, figure 115) in the skeleton, corresponding to a process which is much better developed in *Placocystites*.

The posterior coelom of *Mitrocystella* shows signs, in one specimen, of being divided into two parts (l ep and r ep) by a groove in its dorsal surface, running from anterior right to posterior left (photograph in plate 7, figure 89). This division has already been mentioned above in discussing the homology of the posterior coelom with the right and left epicardia of tunicates.

The crescentic body (cr b), so-called because of its shape, is another noteworthy feature of *Mitrocystella*. It has never previously been mentioned in print. It is situated on the posterior face of the natural internal mould of the head, in the mid-line, just dorsal to the optic foramen, with the convex edge of the crescent downwards (figure 17*b*; photographs in: plate 8, figure 92; plate 9, figures 101 to 103; plate 12, figure 118; plate 15, figure 137). *Mitrocystella* is deduced to have had cispharyngeal optic nerves which would have extended up from the right and left part of the optic foramen to end in light-sensory organs (cispharyngeal eyes) below the presumably translucent calcite of the roof of the head (l cisph op n, r cisph op n in figure 17*b*; photographs of corresponding ridges, l cis, r cis, in: plate 8, figure 92; plate 9, figures 101, 103; plate 12, figure 118; plate 15, figure 137). These cispharyngeal optic nerves are indicated by ridges on the natural mould which are separated from the crescentic body by broad, flat-bottomed grooves. There is also evidence, discussed later, for the crescentic body and the right cispharyngeal optic nerve in *Placocystites* and *Mitrocystites mitra* (photograph in plate 15, figure 138).

In summary, the internal moulds of *Mitrocystites* and *Mitrocystella* show a number of details which are helpful in interpreting *Placocystites*. Perhaps the most important are indications that parts of the pharynx were pleated which suggests the likely positions of the peripharyngeal bands. Other features are the suggested position of the gonoduct in *Mitrocystella*, the probably double nature of the posterior coelom and, in particular, the existence of the crescentic body.

(iv) *The non-nervous internal anatomy of the head in* Placocystites forbesianus

The internal structure of the head of *Placocystites forbesianus* has been studied by means of two enlarged polystyrene models. One of these was based on a large specimen sectioned transversely (Holcroft 25, University of Birmingham, plates 5–8) and the other on a specimen of moderate size sectioned longitudinally (BMNH E16143; plate 7, figure 91; plate 10). There are a number of differences in details between the two models; these are probably not due to differences in the soft parts, but mainly to variations in the extent to which the soft parts were surrounded or penetrated by skeleton.

The ventral skeleton of *P. forbesianus* consists of an inner and outer layer of calcite which in most places were separated by a soft middle layer within which the cranial nerves spread out. The inner calcite layer is most extensive in the posterior half of the ventral skeleton. But it curls upwards to form a partial anterior rim to the posterior coelom, and is absent from the floor of the posterior coelom itself (inn l, out l in: plate 6, figure 86; plate 7, figure 90; plate 10, figure 107). Over the anterior part of the ventral armour the inner layer is represented only by 'buttons' (btn in plate 6, figure 86; plate 10, figure 107) fused to the outer layer near the centres of the plates. These buttons are flat- or concave-topped and concave-sided. Covering the areas between them there would have been extensive soft tissue which would have passed posteriorly into the soft middle layer of the skeleton and which probably represented ventral continuations of the left and right anterior coeloms (figure 19*b*, section 195).

The dorsal skeleton of *Placocystites forbesianus* is made up of only one calcitic layer, corresponding to, and at its edges contiguous with, the outer calcite layer of the ventral skeleton (plate 5, figure 75; plates 5 and 10). Unlike the outer layer of the ventral skeleton, however, the dorsal skeleton was extensively invaded by soft tissue as if calcite had been resorbed during the growth of the animal. Such areas of soft tissue are surrounded by 'resorbtion cliffs' (res cl in plate 5, figures 77, 78). When nerves were in contact with the dorsal skeleton they either ran inside definite or rather irregular canals, or else followed grooves in the inner surface of the skeleton. As regards the layers of which it was made, therefore, the skeleton of *P. forbesianus* did not differ from other mitrates (Jefferies 1968, p. 295 for *Mitrocystella*).

Dealing first with the dorsal skeleton, the oblique ridge, which would correspond to an oblique groove in an internal mould, runs as in other mitrates from anterior right to posterior left across the ventral surface of the roof of the head (ob r in plate 5, figures 75, 77, 78; plate 10, figures 107, 109). It shows the same variations along its length as in other mitrates; there is firstly an anterior, weak portion extending back to near the median line; immediately behind this weak portion a long, prominent mid-dorsal process (m d pr) goes off from the oblique ridge towards the posterior right; behind the origin of the mid-dorsal process the oblique ridge becomes much more marked and also asymmetrical with its right side steeper than its left side, and so continues, though with decreasing asymmetry, until it merges posteriorly into the left margin of the posterior coelom. This portion of the oblique ridge, posterior to the origin of the mid-dorsal process, is complicated in detail. There is a short portion just posterior to the process where, though the ridge is well marked, it is also rounded, as if some organ passed here into the pharynx (cil o in plate 5, figures 77, 78). Behind this rounded segment the ridge is so asymmetrical that it takes the form of an overhanging sheet of calcite which ends posteriorly in a little point. This little point is almost but not quite continuous with the long thin rectal process which extends up from the ventral skeleton and which is formed from the inner calcite layer (rect pr in plate 5, figure 77). The mid-dorsal process of the oblique ridge is D-shaped in section with a flattish facet, corresponding to the vertical stroke of the D, on its median side (f m d pr in plate 5, figure 78; plate 10, figure 108). Another ridge on the inner face of the dorsal skeleton, is weak but precise anteriorly, becomes strong but more rounded posteriorly, and runs backwards from near the anterior origin of the mid-dorsal process to a point just right of the tail (r ant c/r ph in plate 5, figures 75, 78; course indicated in plate 5, figure 77; see also sections 172–331 in figure 19*b*).

These features of the dorsal skeleton can be interpreted as in other mitrates. The oblique ridge would represent the dorsal line of contact between the left anterior coelom and the right anterior coelom. Ventral to the field of the left anterior coelom, left of the ridge, would have lain the buccal cavity, left pharynx and left atrium. Unlike most other mitrates the contact between the buccal cavity and left pharynx is marked in the skeleton by an obvious groove, visible in one of the models and in dissections, and to it the velum would have been attached (vel in plate 4, figures 69, 70; plate 5, figure 77). Ventral to the field of the right anterior coelom, right of the oblique ridge, would have lain the right pharynx, overlain by virtual right anterior coelom, and the patent part of the right anterior coelom. The weak anterior portion of the oblique ridge, in front of the mid-dorsal process, would represent the line of contact where the right, secondary pharynx pouched out of the left, primary pharynx. The other ridge in the skeleton, ie r ant c/r ph extending back from near the mid-dorsal process to just right of the tail, would mark the dorsal left boundary of the right pharynx, and likewise the line of contact between virtual and patent right anterior coelom (see e.g. figure 19*b*, section 270). Soft-tissue-filled spaces in the dorsal skeleton, presumably formed by resorbtion of calcite during the growth of the animal, are confined to areas dorsal to the right and left pharynxes and would have been separated from them only by virtual coelom. Soft-tissue-filled spaces are not found over the buccal cavity nor over the patent part of the right anterior coelom.

The buccal cavity, as already mentioned, would have been situated ventral to the anterior part of the field of the left anterior coelom and its posterior boundary is marked by an obvious groove that would have carried the velum. There were two large olfactory cups in the roof of the buccal cavity, left and right of the mouth (olf c in plate 4, figure 70; plate 5, figures 76 to 78). The cups are connected by grooves to the olfactory notches of the mouth (inh gr in plate 5, figure 78). In discussing the external anatomy we have already suggested that a flap of soft tissue, attached to the oral plates ventral to the olfactory notch, formed a valve over an inhalent opening. The groove (inhalent groove) could represent a channel in the soft parts by which a sample of inhaled water was carried from this inhalent opening to the olfactory cup. There is a short olfactory process (olf pr) in the anterior wall of each cup. Perhaps water was led out of the cup, ventral to this process, to the exhalent opening at the apex of the oral funnel. Olfactory fibres probably passed into the skeleton at an observed pit lateral to each cup, as in *Mitrocystites* and *Mitrocystella.*

The positions of the peripharyngeal bands in *P. forbesianus* can now be deduced by analogy with *Mitrocystella* and *Mitrocystites.* The right peripharyngeal band would have followed the anterior part of the oblique ridge back to the origin of the mid-dorsal process. The left peripharyngeal band would have crossed the left pharynx transversely to meet the oblique ridge near the origin of the mid-dorsal process. A very weak ridge, which may perhaps indicate its position, is present in the left pharynx in an appropriate place (per b in plate 4, figure 70; plate 5, figure 77). Longitudinal corrugations of the pharyngeal wall, whose distribution allowed the position of the peripharyngeal bands to be deduced in *Mitrocystella* and *Mitrocystites,* have not been found in *Placocystites.* However all these genera are close enough for arguments derived from one to be applied, with caution, to the others. The right and left peripharyngeal bands of *Placocystites* seem to have been thoroughly asymmetrical to each other though presumably they functioned as antimeres in the transport of mucus. This may be related to the fact that the right peripharyngeal band could not have existed as such in cornutes, in the absence of a right pharynx. It also recalls that, in tunicates, rather than being exact antimeres, they can be seen as consecutive segments of the alimentary ciliated loop.

The short rounded segment of the oblique ridge (cil o), just behind the origin of the mid-dorsal process, probably indicates where some organ passed into the pharynx. On tunicate analogies it probably represents the position of the ciliated organ, i.e. the opening of the duct of the neural gland, for this is always situated near the dorsal junction of right and left peripharyngeal bands. If this identification is correct the ciliated organ opened in *Placocystites* definitely into the left pharynx. We recall that in living doliolids the ciliated organ opens into the pharynx dorsal to the left peripharyngeal band, rather than in a median position.

The interpretation of the mid-dorsal process now becomes crucial. Its position suggests that it had something to do with the junction of the left and right pharynxes and with the junction of the virtual right anterior coelom, overlying the right pharynx, with the cavity of the right anterior coelom. However, as already remarked, it is consistently located right of and ventral to the ridge on the dorsal skeleton which should mark the left boundary of the right pharynx (r ant c/r ph). If an attempt is made to reconstruct in transverse section the chambers round the mid-dorsal process, as in the series of sections drawn from slides in figure 19*b* (sections 172–270), one is therefore obliged to draw a hook-shaped fold of flesh, curved downwards and rightwards, with the mid-dorsal process stiffening its free edge (see also figure 18*b*). Now this fold has the same direction of curvature in transverse section as the dorsal lamina of a tunicate.

Indeed it can almost certainly be identified with a dorsal lamina for, in addition to its direction of curvature in a transverse plane, it begins anteriorly at the dorsal junction of the deduced right and left peripharyngeal bands, and near the deduced position of the ciliated organ. Furthermore its free edge marks the reconstructed line of junction of the right pharynx with the left one.

We now turn to the ventral skeleton. The floor of the posterior coelom shows in this as a distinct semicircular area which, as already mentioned, lacks the inner layer of calcite (post c in plate 6, figures 85, 86; plate 7, figures 87, 90; plate 8, figure 94; plate 10, figure 106). The edge of the inner layer curls up where it meets the posterior coelom so forming a low rim beset with processes and re-entrants. At right and left, just lateral to the posterior coelom, near the contact of the head with the tail, the outer layer of calcite forms a triangular facet which in life would have articulated with a similar facet in the dorsal skeleton ($\mathrm{fM}_{1\mathrm{LD}}$, $\mathrm{fM}_{1\mathrm{RD}}$ in plate 6, figures 85, 86; plate 7, figure 90; plate 8, figure 94; corresponding to $\mathrm{fM}_{1\mathrm{LV}}$, $\mathrm{fM}_{1\mathrm{RV}}$ in plate 5, figure 77). Just lateral to the right one of these facets the transversely sectioned model has a distinct cup which is deduced to have contained, as shown later, two important ganglia (r aud g, r pyr b in plate 6, figures 85, 86; plate 7, figures 87, 90; plate 8, figure 94). There is no such cup on the left side of the transversely sectioned model nor on either side of the longitudinally sectioned model. The lateral wall of the cup is formed from the inner calcite layer of the skeleton. Canals, presumed to be for nerves, pass out of the anterior margin of the posterior coelom running in the soft layer between the inner and outer layers of calcite. These canals passing out of the posterior coelom will be dealt with in considering the nervous system. They included canals for the median nerves n_0 (plate 6, figure 86; plate 7, figure 90), and for the palmar complexes of which the big nerves n_x were part (n_x in plate 5, figure 75; plate 6, figure 85; plate 7, figures 87, 90; plate 8, figure 95).

Processes arising from the anterior wall of the posterior coelom, as seen in the transversely sectioned model, are the very prominent rectal process on the left, the tiny left adlateral process, the U-shaped retropharyngeal process near the mid-line, the tiny right adlateral process, the prominent oesophageal process, and the short, laterally compressed, post-oesophageal process on the right (see especially plate 7, figure 90). The names of theses processes imply an interpretation of the soft parts which is justified below.

The function of the dorsal lamina in modern tunicates is to roll up into a rope the strands or sheets of mucus conveyed to it by the peripharyngeal bands. The posterior end of the mucous rope is pulled from the dorsal lamina into the opening of the oesophagus by the oesophageal ciliated band. In *Placocystites*, therefore, the opening of the oesophagus into the pharynx would be expected somewhere behind the posterior end of the dorsal lamina.

The likely position of the oesophageal opening in *Placocystites* is indicated by a large semicircular re-entrant, with rounded edges, in the right wall of the anterior coelom. This re-entrant is situated between the processes referred to already as oesophageal and post-oesophageal. It is particularly obvious in the transversely sectioned model (oes op in plate 6, figures 85, 86; plate 8, figure 94). The position of the oesophageal opening well right of the mid line is comparable with the situation in living salps (see, for example, Fedele 1934, figs 4–13).

The retropharyngeal process of the anterior wall of the posterior coelom and the associated nerves canals n_0 near the mid line now become crucial. In the transversely sectioned model the paired canals for the nerves n_0 are very obvious (especially plate 7, figure 90). The retropharyngeal process is U-shaped and not symmetrical to the nerves n_0, but situated over the right one. In the longitudinally sectioned model the canals for the nerves n_0 are not shown, Presumably they existed in the living animal, but became filled after death with secondary calcite indistinguishable from the calcite of the skeleton. The retropharyngeal process in the longitudinally sectioned model is most striking (plate 7, figure 91; plate 10, figure 106). It is a large blade of calcite extending up from the floor of the head and curving over strongly towards the right. There are well marked notches on either side of the blade at its base (r & l adm ph-ep op). Also the end of the blade is notched, like the notch between the arms of the U of the retropharyngeal process of the transversely sectioned model. The position of the bases of the retropharyngeal processes is so similar in both models that the homology of the processes in the two models is virtually certain, despite their difference in shape.

The nerves n_0 probably supplied the endostyle. For this is the most important organ in the median ventral line of the pharynx in recent, primitive filter-feeding chordates and would probably therefore have been present in mitrates. Furthermore it is likely that the endostyle was a two-sided structure in *Placocystites*, both by comparison with recent primitive chordates, and from the existence of canals for two nerves n_0. This suggests that the retropharyngeal process, situated over the right canal n_0, was located just right of the posterior end of the endostyle. In curving over to the right the retropharyngeal process of the longitudinal model points towards the assumed position of the oesophagus. These pecularities of position and shape strongly suggest that the retropharyngeal process carried the retropharyngeal band on its anterior surface. For in tunicates the retropharyngeal band is a posterior extension, leading to the oesophageal opening, of the right marginal band of the endostyle (compare figure 13*a*, *b*).

The notches on either side of the base of the retropharyngeal process in the longitudinal model confirm that the process carried the retropharyngeal band. They probably correspond to openings that connected the left and right pharynxes with the posterior coelom. These suggested openings, the admedian pharyngo-epicardial openings, can be compared with the paired pharyngo-epicardial openings on either side of the retropharyngeal band of the tunicate *Ciona* (figure 12) and with the paired pharyngo-epicardial openings of the larvae of other tunicates. The left one of these openings in tunicates connects the left pharynx with the left epicardium while the right opening connects the right pharynx with the right epicardium. The posterior coelom of *Placocystites* is therefore equivalent to the left and right epicardia of tunicates. We have already mentioned this conclusion above, and noticed suggestive evidence that the posterior coelom was made up of two chambers in *Mitrocystella*.

The two tiny adlateral processes on the front wall of the anterior coelom are difficult to interpret. They suggest that adlateral pharyngo-epicardial openings existed in addition to the admedian ones (figure 18*a*, lat ph-ep op). These would have been bigger than the admedian openings and roughly elliptical in shape, situated beneath the bases of the rectal and oesophageal processes and defined on their median side by the adlateral processes. In *Cothurnocystis*, being a cornute, the posterior coelom would have been homologous with only the left epicardium of a tunicate, and seems to have opened into the pharynx by a left and a right aperture (as discussed below; compare figures 26, 27; photographs in plate 14). These openings in *Cothurnocystis* would correspond to the admedian and adlateral pharyngo-epicardial openings of the left epicardium of *Placocystites forbesianus*. The adlateral pharyngo-epicardial openings of *Placocystites* would be ventral to the rectum on the left and ventral to the oesophagus on the right. There is evidence in *Mitrocystella* that the left epicardium also communicated with the left pharynx by still a third opening dorsal to the rectum (Jefferies 1968, p. 285). The dorsal margin of the posterior coelom of *P. forbesianus* is indicated by a line on the dorsal skeleton of the longitudinal model (m post c in plate 10, figure 109; see also plate 10, figure 108). This is comparable in position with the dorsal margin of the posterior coelom in other mitrates.

The epicardia of tunicates are primarily excretory organs (Berrill 1950, pp. 28–29). This, therefore, was probably their function in calcichordates also. We have previously suggested that the nephridia of amphioxus were probably formed by extension of the gill slits to split the mitrate posterior coelom into segments each one above a gill bar. This is suggested by the situation in the mitrate *Lagynocystis* which we assign to the stem group of amphioxus (Jefferies 1973, p. 442). The new evidence, by confirming that the posterior coelom of mitrates was homologous with epicardia of tunicates, helps to strengthen this view of how the nephridia arose.

The right and left atria of *Placocystites forbesianus* would be located much as in *Mitrocystella* or *Mitrocystites*. It is likely, as already indicated, that the left branchial opening was much longer than the right one. For the branchial openings would be situated between the dorsal and ventral skeleton between the points where nerves n_2 and n_4 passed from one into the other. And the relevant distance between these two nerve canals is twice as great on the left as on the right. By analogy with *Mitrocystella* the rectum would have left the posterior coelom on the left side of the latter, just dorsal to the posterior end of the rectal process. There is a rectal opening on the left side of the posterior coelom (rect op in plate 6, figure 85; plate 8, figure 94) and in the longitudinally sectioned model there is a well marked groove, presumably for the rectum (plate 10, figure 109).

The course of the non-pharyngeal gut in *P. forbesianus* can be suggested in general terms. For obvious reasons it would have run between the oesophageal opening, on the right, and the point where the rectum left the posterior coelom, on the left. Reconstruction of the cranial nervous system, discussed in detail later, suggests that the big palmar nerve on each side was made up of a supra-alimentary component, which passed over the dorsal surface of the oesphagus or the rectum, and a sub-alimentary component, which passed under it. Now the most posterior portions of the inner faces of the oesophageal and rectal processes are distinctly concave as if to accommodate the supra-alimentary component pressed against the anterior surface of the oesophagus or rectum (sup oes c in plate 7, figure 90; plate 8, figure 94; missing label in plate 6, figure 85). And this requires that the oesophagus ran forwards from the oesophageal opening along the oesophageal process, and conversely that the rectum ran back along the rectal process to the rectal opening. The inner face of the rectal process is more weakly concave immediately anterior to the suggested position of the supra-alimentary nerve component, as if to accommodate the lateral surface of the rectum or intestine running forward along the median face of the process (i in figure 19*c*, section 325). And the inner face of the rectal process still farther forward becomes convex, suggesting that in this region the rectum or intestine had taken up a position mostly dorsal to the process, though still in contact with it (as suggested in figure 19*c*, section 300). The rectal process, as already mentioned, can be followed continuously forward almost as far as a posteriorly directed point on the oblique ridge of the dorsal skeleton. The rectum or intestine probably followed it the whole way. This implies that almost the whole length of the intestine was located inside the cavity of the right anterior coelom, apart from a portion, best called rectum, leading by way of the posterior coelom into the left atrium.

The oesophagus probably followed the much shorter oesophageal process in a similar manner. Indeed it would have to have done so to connect with the intestine, or some other part of the

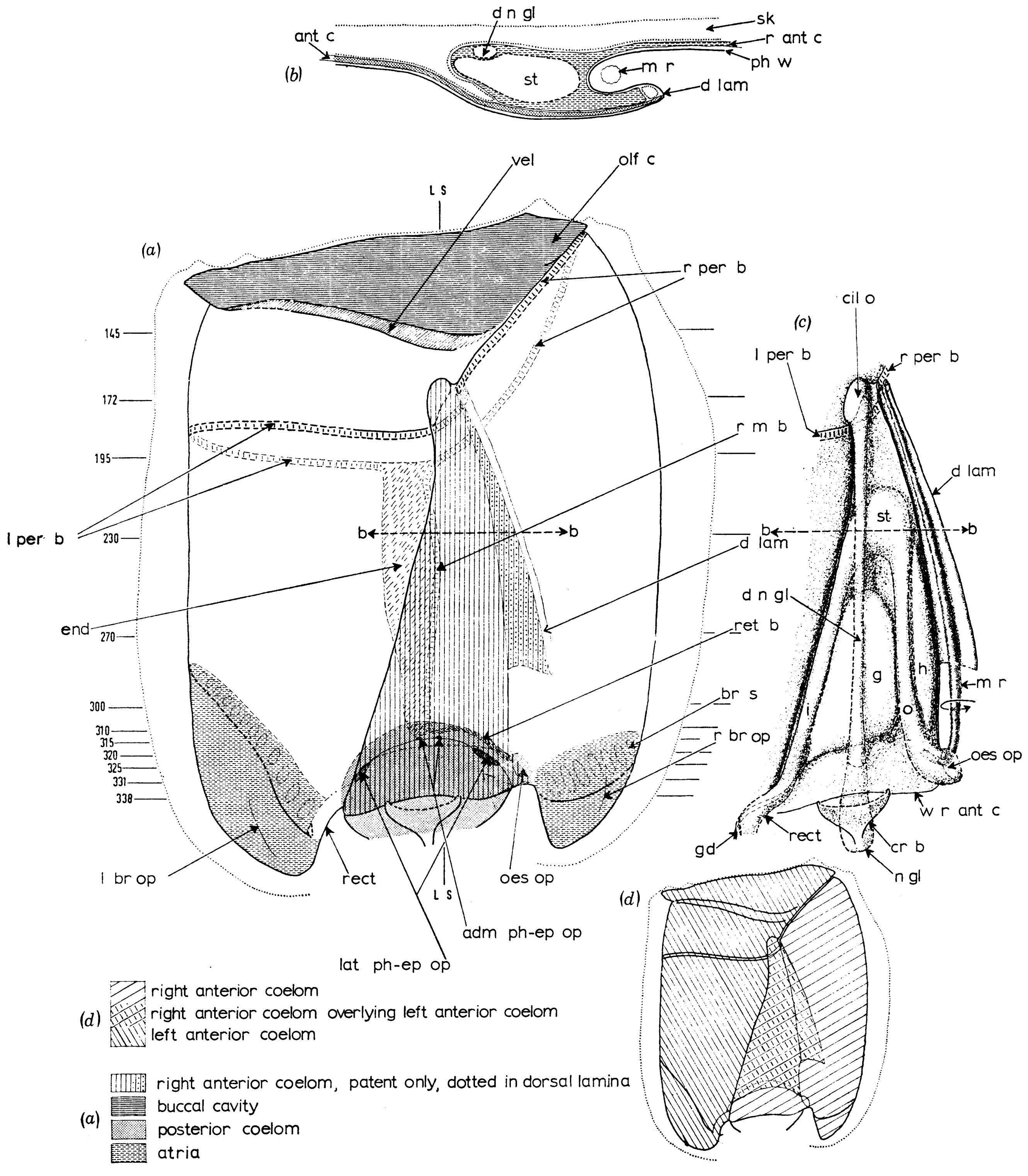

FIGURE 18. Diagrammatic representation of the reconstructed soft parts of the head in *Placocystites forbesianus*. (*a*) General dorsal aspect, also showing the positions of transverse sections (145 etc) and longitudinal section (L S) in figure 19. (*b*) Transverse section along the line b–b. (*c*) Reconstruction of viscera inside the cavity of the right anterior coelom. (*d*) Reconstructed relations of the left and right anterior coeloms. Solid lines are based on direct skeletal evidence (except in *d*); dashed lines are based on indirect evidence. Thin lines, whether solid or dashed, are more ventral than thick lines (except for stipple).

non-pharyngeal gut such as the stomach, somewhere inside the right anterior coelom. The reconstruction of the major part of the non-pharyngeal gut inside the right anterior coelom of mitrates has implications for the cornutes which will be discussed below.

The head chambers, pharyngeal structures and non-pharyngeal gut of *P. forbesianus* can therefore be reconstructed as shown in figures 18 and 19. These reconstructions arbitrarily assume that the asymmetrical structure of the endostyle seen today in certain salps, was primitive (Garstang & Platt 1928). These forms, as mentioned above in the section on living chordate pharynxes, have a right marginal band along the endostyle but no left marginal band. The reconstruction shows the various ciliated bands as forming an alimentary ciliated loop, beginning distally at the ventral end of the left peripharyngeal band, and passing into the right peripharyngeal band, right marginal band, retropharyngeal band and, inside the oesophagus, the oesophageal band.

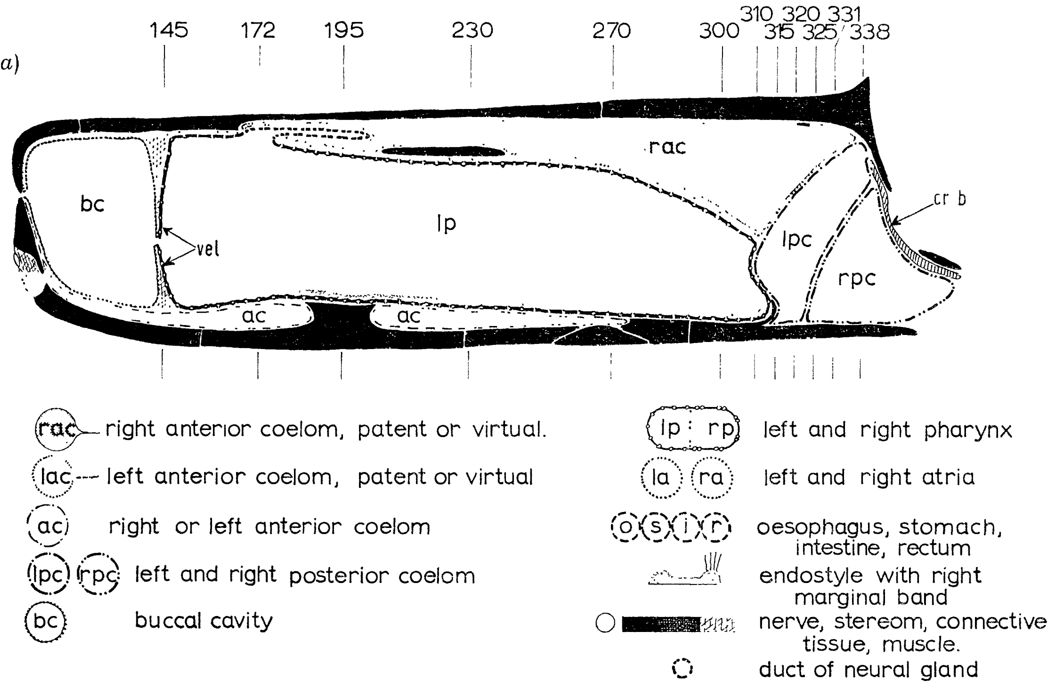

Figure 19. Sections through *Placocystites forbesianus* to show the observed skeleton and the reconstructed positions of head chambers and other soft parts. (*a*) Longitudinal section (LS in figure 18*a*). (*b*) Transverse sections numbered in sequence (section interval 0.1 mm); positions of sections are shown in figure 18*a*.

Certain features in the organization of the head of *Mitrocystella incipiens miloni* can now be considered. The straight gentle ridge (cav d lam in figure 17), running across the dorsal surface of the internal mould from near the origin of the mid-dorsal process to the posterior right corner of the body, is broadly comparable in position with the reconstructed dorsal lamina attached to the median dorsal process of *Placocystites forbesianus.* Indeed it probably represents the dorsal surface of the cylindrical cavity of the dorsal lamina in which the mucous rope would be rolled up. But the lamina seems to have been attached posteriorly to the inside of the body wall. One specimen seems to show the actual trace of this posterior attachment (tr d lam) dorsal to the right atrium (photograph in plate 8, figure 93). The straightness of the ridge implies that the edge of the dorsal lamina was also straight, as would be expected for a membrane stretched in this manner between two fixed points. This mode of suspension would mean that

(*b*)

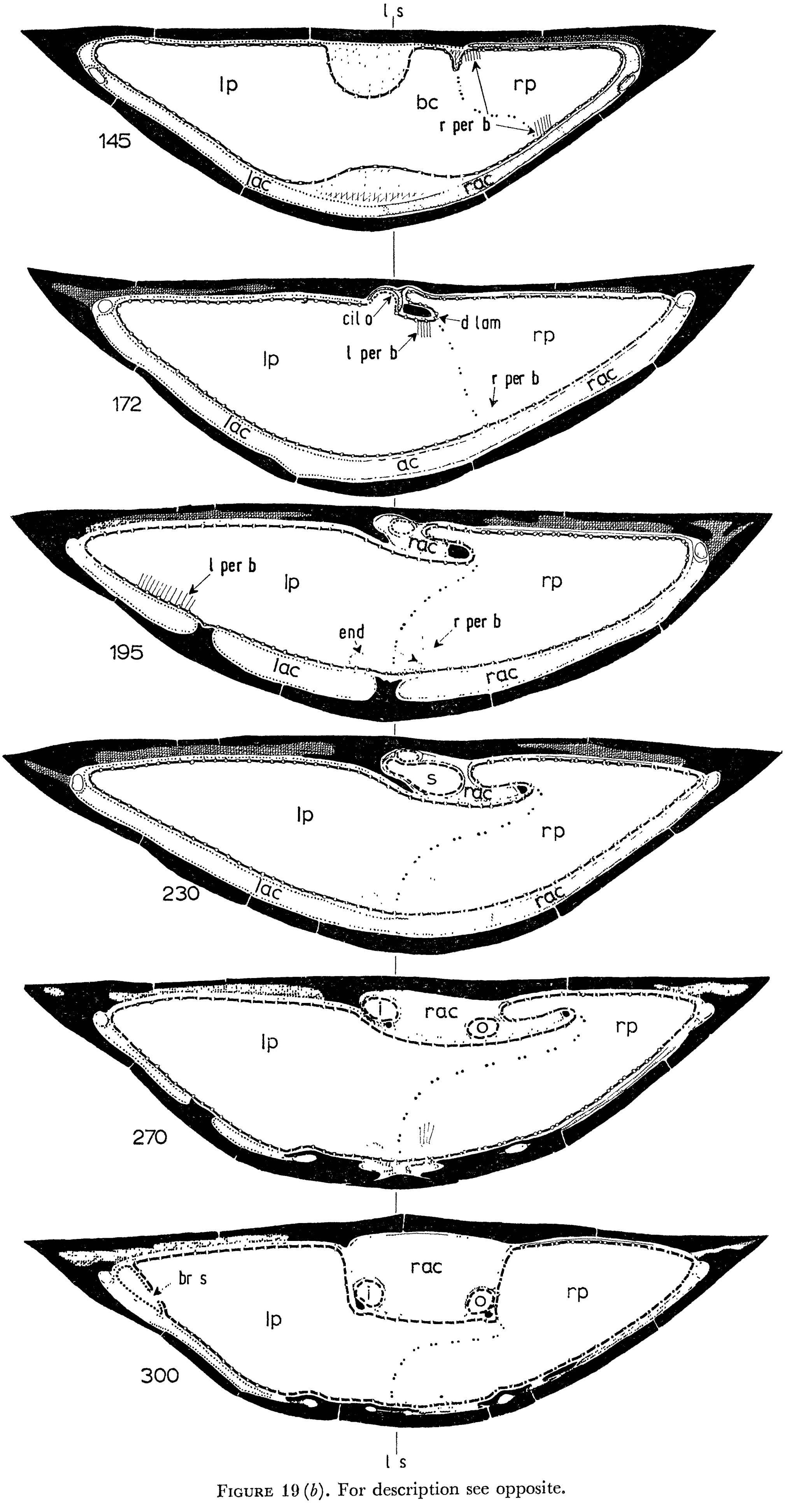

FIGURE 19 (*b*). For description see opposite.

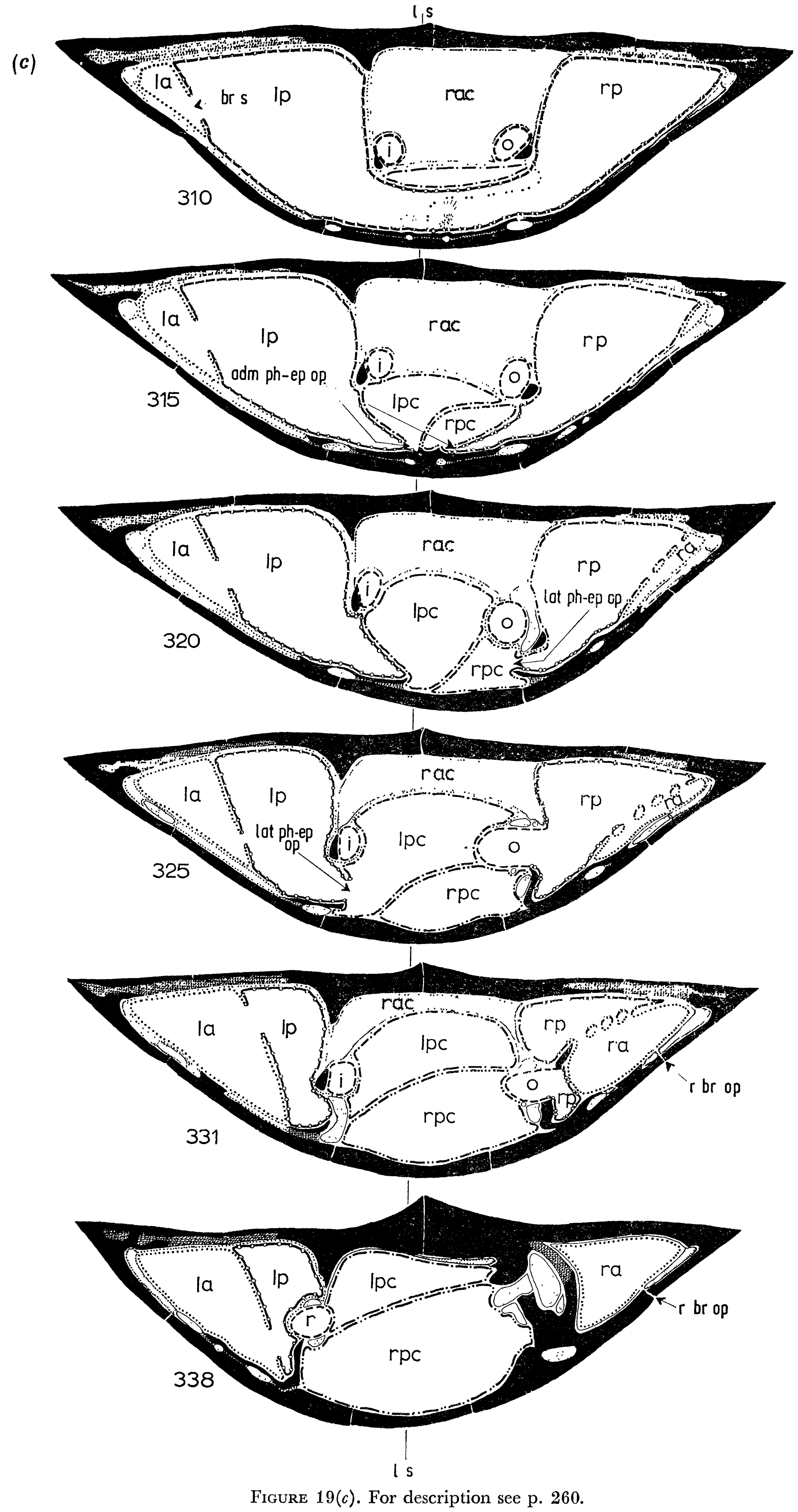

FIGURE 19(c). For description see p. 260.

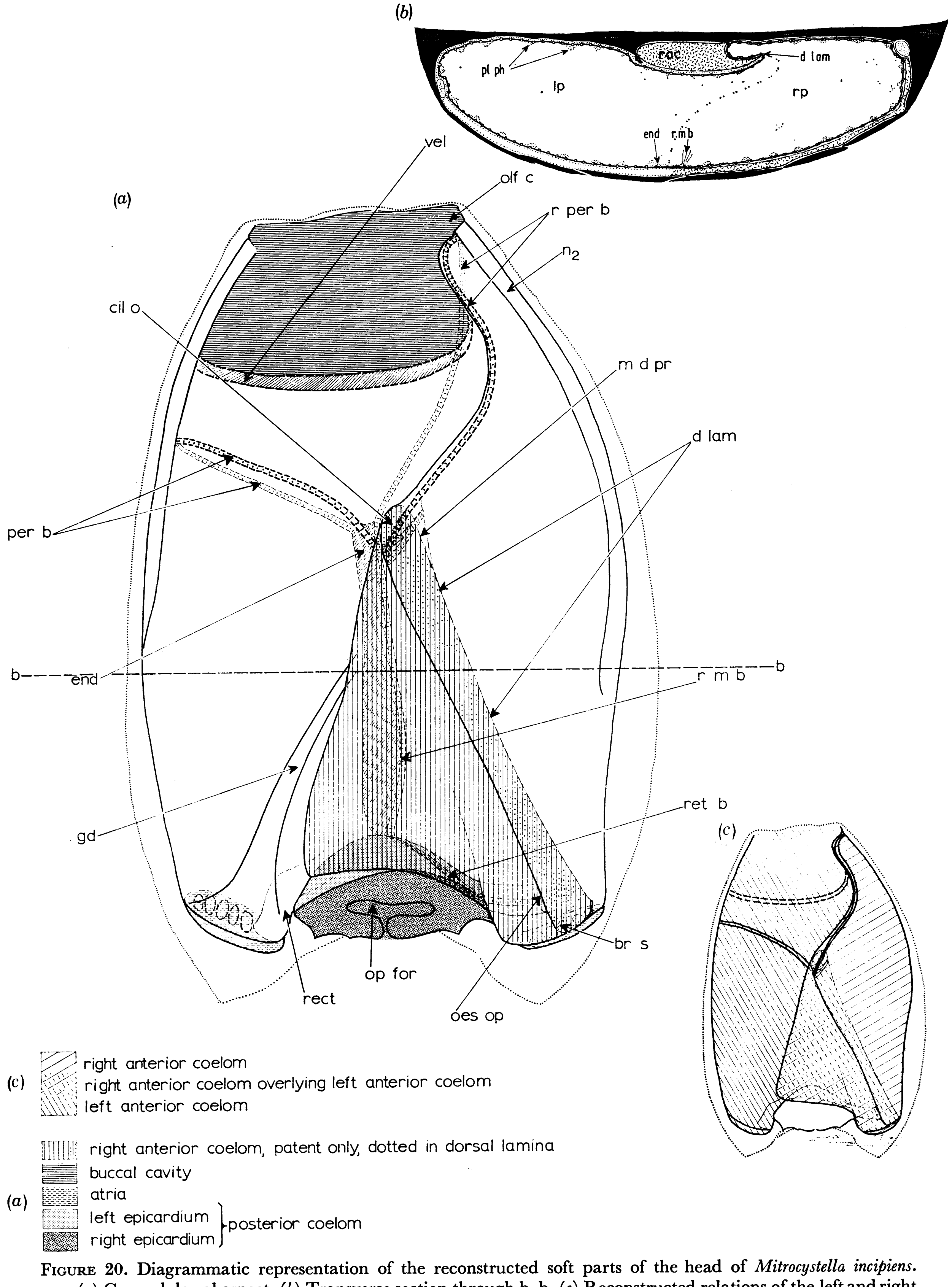

Figure 20. Diagrammatic representation of the reconstructed soft parts of the head of *Mitrocystella incipiens*. (*a*) General dorsal aspect. (*b*) Transverse section through b- b. (*c*) Reconstructed relations of the left and right anterior coeloms. Solid lines are based on direct evidence; dashed lines are based on indirect evidence. Thin lines, whether solid or dashed, are more ventral than thick lines.

the posterior end of the dorsal lamina was much farther to the right than in *Placocystites forbesianus*.

The relations of the dorsal lamina to the right pharynx in *Mitrocystella* would have been different from those in other mitrates, since both the left and the right margins of the lamina were farther rightwards. Moreover one specimen, as already mentioned, seems to show a trace of the boundary between the patent right anterior coelom and the right pharynx well left of the dorsal lamina, in the same position as in *Mitrocystites mitra* or *P. forbesianus* (r ant c/r ph in figure 17; plate 11, figure 112). Perhaps a thin extension of the patent part of the right anterior coelom passed to the dorsal lamina over the left part of the right pharynx as suggested in figure 20, invading what had ancestrally been the territory of the virtual right anterior coelom. In *Mitrocystella* the oesophagus would need to have opened direct into the cavity of the dorsal lamina, rather than being posterior to it, since the lamina extended posteriorly to the posterior right corner of the head. This would imply a position for the oesophageal opening much farther rightwards than in *Placocystites*. The condition of the dorsal lamina in *Mitrocystella* is less primitive than in *Placocystites*, being less like the condition in *Mitrocystites* and other mitrates. This contrasts with most of the other differences between *Placocystites* and *Mitrocystella*, in which *Mitrocystella* is the more primitive of the two genera.

The position of the heart in *Placocystites forbesianus* cannot be suggested from direct evidence. The evidence from comparative anatomy produces a tentative answer. The heart of tunicates arises as a tube invaginated within the pericardium (Berrill 1950, p. 23). The vessel from the anterior end of the heart passes into the subendostylar vessel while the vessel from the posterior end of the heart runs to the non-pharyngeal gut. Now among living benthonic tunicates (i.e. ascidians) *Ciona* is probably the most primitive genus. This was suggested by Berrill (1936) because adult *Ciona*, alone among tunicates, retains the pharyngo-epicardial openings seen in the larvae of nearly all tunicates. Berrill assumed that this was therefore a primitive feature, and his view is confirmed by the occurrence of the same situation in mitrates as deduced from the skeleton. *Ciona* is probably also primitive in having the non-pharyngeal gut situated immediately behind the pharynx. For this is more mitrate-like than having the non-pharyngeal gut in a long abdomen, as in the aplousobranch ascidians, or left of the left pharynx as in the genera *Molgula*, *Ascidia* and *Ecteinascidia*, or right of the right pharynx, as in *Corella*.

In *Ciona* (Berrill 1936) the posterior vessel of the heart runs to the right face of the stomach (figure 21). This is also true of the genus *Diazona* which Berrill saw as related to *Ciona*. Furthermore in *Molgula* and *Ecteinascidia* the heart is right of the pharynx though the non-pharyngeal gut is left of the latter. In *Ascidia* the heart is right of the non-pharyngeal gut, though both heart and non-pharyngeal gut are left of the pharynx. Finally in salps the heart is right of the posterior end of the endostyle, when the latter extends posteriorly into the heart region. All this suggests, particularly assuming that asymmetries seen in living primitive chordates are *prima facie* likely to be primitive, that the heart of the earliest tunicates was probably right of the loop of the non-pharyngeal gut.

Now the loop of the non-pharyngeal gut in *Placocystites* is deduced to have run forward from the oesophageal opening, whereas in *Ciona* it runs backward from it. In the evolution of *Ciona* from a mitrate the oesophagus would therefore have rotated through approximately 180° about a horizontal transverse axis passing through the oesophageal opening. To deduce the likely position of the heart in mitrates from that in *Ciona* it is necessary to imagine this rotation in reverse. This leaves the heart in mitrates right of the oesophagus, as shown in figure 18*c*, though turning it up-side-down with respect to *Ciona* and making its posterior end anterior. This assumed position of the heart in mitrates agrees, as explained later, with the situation in cornutes, if allowance is made for the non-existence of the right pharynx in that group.

The ciliated organ, or opening of the duct of the neural gland into the pharynx, seems to have been situated in *Placocystites* at the anterior end of the patent part of the right anterior coelom, just behind the origin of the mid-dorsal process from the oblique ridge, and just anterior to the likely meeting-place of left and right peripharyngeal bands, as mentioned above. The neural gland of tunicates, and of tunicate tadpoles, is in contact with the brain, so by analogy the duct should have extended backwards to make contact with the brain of *Placocystites*, as shown in the reconstruction in figure 18*c* (compare tadpole of *Amaroucium constellatum* in Grave 1921, fig. C; also shown in Jefferies 1968, fig. 22).

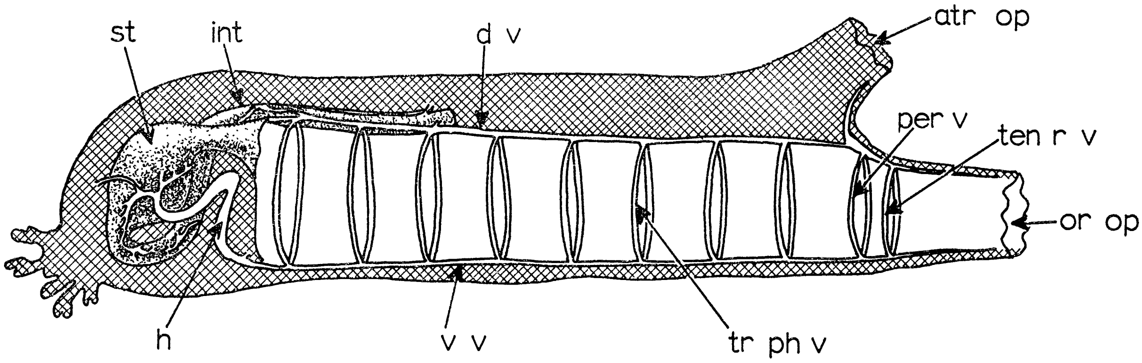

FIGURE 21. Vascular system of *Ciona intestinalis*. Note the heart (h) situated right of the stomach. After Millar (1953, fig. 74).

The same conclusion follows from vertebrate analogies, assuming that the neural gland of tunicates is homologous in some sense with the hypophysis of vertebrates, which it certainly resembles endocrinologically (Carlisle 1953). The brain of mitrates, as discussed later, can be divided into prosencephalon and rhombencephalon, broadly homologous with the two divisions recognized by Starck (1975, p. 369) in the brain of the very young embryo of a standard vertebrate. The mitrate prosencephalon (formerly called the medial part of the brain e.g. Jefferies 1975, p. 287) would be homologous dorsally with the telencephalon, and postero-ventrally with the diencephalon, of an older vertebrate embryo. Now the ventral diencephalar part of the prosencephalon of *Placocystites* and other mitrates seems to have connected to the inside of the head by an observed slit between the median ends of the left and right hypocerebral processes, which was postero-ventral to the foramen for the bases of the optic nerves (plate 5, figures 75, 77; plate 6, figure 84; plate 10, figure 109). This slit, by analogy with vertebrates, would connect the hypophysis to the brain.

There are embryological difficulties in these comparisons, however. The neural gland and its duct arises in tunicates by modification of the left anterior portion of the neural tube (Willey 1894). All authors agree that this portion breaks through into the alimentary canal to produce the definitive ciliated organ. Some consider that it opens into the buccal cavity (e.g. Willey 1894, p. 310 in *Clavelina*; Grave 1921 in *Amaroucium*). But Elwyn (1937) demonstrated with convincing photographs that, in *Ecteinascidia* at least, it breaks through into the roof of the pharynx and, since this corresponds to the observed adult position of the opening of the neural gland, it is likely to hold for all tunicates. It seems that the neural gland of ascidians therefore arises by interaction between the dorsal wall of the pharynx and the brain, though its actual substance is formed by modification of part of the brain. Berrill (1955, p. 245) has already argued that the adult ganglion, which is in contact with the neural gland, is homologous with the ventral part of the vertebrate diencephalon (hypothalamus).

The hyphophysis of standard vertebrates, however, arises by interaction between the diencephalon and Rathke's pouch. The latter is a pocket formed in the roof of the buccal cavity, and therefore ectodermal. There is in vertebrates an endodermal structure, known as Seessel's pouch or the preoral gut, which arises from the dorsal wall of the pharynx and extends up to the diencephalon just behind Rathke's pouch (de Beer 1926, p. 24; Starck 1975, p. 389) but it disappears without trace in the adult and has no known function.

The neural gland of *Placocystites* would have opened, in its deduced position, into the pharynx well posterior to the velum, separated from the latter by the junction of right and left pharynxes. It is therefore unlikely that the neural gland contained any ectodermal component from the buccal cavity. Perhaps it should be compared not with Rathke's but with Seessel's pouch. But in that case the 'hypophysis' of mitrates arose by interaction between the diencephalar part of the brain and the endoderm of the pharynx. This would represent the primitive condition from which the tunicate neural gland and the vertebrate hypophysis have separately arisen by divergence. Silén (1954) has suggested that the 'stomochord' of hemichordates, which he regards as glandular and endodermal, is homologous with Seessel's pouch. This suggests that the neural gland of mitrates may have been derived with little modification from the hemichordate stomochord.

Certain other comparisons should be mentioned. First we have argued elsewhere that the neural gland of tunicates is probably homologous with the axial gland of echinoderms (Jefferies 1975, p. 269; 1969, p. 515). Secondly, Hatschek's pit of amphioxus and the rostral coelom have also been homologized with the vertebrate pituitary and premandibular somite (Goodrich 1917, p. 546). We shall return to this later.

The evidence for the crescentic body in *Placocystites* consists of a flat-bottomed depression in the anterior surface of the dorsal skeleton just posterior to the posterior coelom. The margins of this depression are marked m cr b in plate 5, figures 75, 77. The margins of the depression pass dorso-laterally into a pair of narrow but deep pits, which presumably held the dorso-lateral angles of the crescentic body (same figures). We shall discuss the nature of this body later but here will emphasize its relations. It is unpaired, symmetrical in the mid line, just anterior to the prosencephalon, immediately dorsal to the posterior end of the neural gland (or Seessel's pouch) and median to the cispharyngeal eyes, which we assume to have been paired in *Placocystites*, since the cispharyngeal optic nerves, on the evidence of internal moulds, seem to have been paired in *Mitrocystella* (plate 8, figure 92; plate 9, figures 101, 103; and especially plate 15, figure 137). Its likely relations to the neural gland are shown in figure 18*c* and to the brain and cranial nerves in figure 25; compare figure 23 for the reconstructed situation in *Mitrocystella*.

In summary the head of *Placocystites* would have contained a pharynx like that of a tunicate with endostyle, peripharyngeal bands, dorsal lamina, retropharyngeal band (asymmetrical as in tunicates) and rightward-situated oesophageal opening. It had paired epicardia, also like a tunicate, and the admedian pharyngo-epicardial openings can be compared with those of *Ciona*. The buccal cavity, velum and left pharynx were in the field of the left anterior coelom at least dorsally. The non-pharyngeal gut probably formed a loop in the cavity of the right anterior coelom, with the heart probably right of it, while the gonad would also be in this coelom. The rectum opened into the left atrium as in a tunicate tadpole. A neural gland was present and opened into the pharynx in the same position as in a tunicate. It seems possible that the neural gland was strictly comparable with the Seessel's pouch of vertebrates, rather than with the hypophysis, having arisen by the interaction of the diencephalon with the pharynx, rather than with the buccal cavity. There was a crescentic body in a median position posteriorly. Many of these deductions will be mentioned again, in comparing mitrates with amphioxus and the vertebrates.

(v) *The homologies of the head coeloms of mitrates with living vertebrates and acraniates*

We have already emphasized that the buccal cavity, velum, velar mouth and left pharynx all lay in the field of the virtual left anterior coelom of *Placocystites*, *Mitrocystella* and other mitrates, at least in the dorsal part of the animal. This is curiously reminiscent of acraniates, where the buccal cavity, velum and velar mouth are fundamentally organs of the left side.

The mouth region of an adult amphioxus is superficially symmetrical. Its basic left-sidedness, however, was demonstrated by van Wijhe (1893, pp. 153–163; 1902). In particular he showed that the outer coelomic canal of the lip, outside the cirral skeleton, is continuous with the left pterygocoel (fin-fold coelom), but not with the right pterygocoel. (The left-sidedness of the *inner* lip coelom is demonstrated by embryology, as discussed below.) Also the nerve plexus of the buccal cavity is connected only with the left side of the dorsal nerve cord, not with the right. And the nerves of the velum come entirely from the fourth, fifth and sixth left spinal nerves. These observations of van Wijhe were confirmed by Franz (1927).

The embryology of the mouth region of amphioxus demands a digression. The best description up to the stage with one gill slit is still that of Hatschek (1881; see also Conklin 1932). Figures 22*a*, *b*, show a neurula larva. This has a series of eight dorso-lateral somites on either side of the notochord, and also a pair of anterior pouches from the archenteron. Hatschek referred to this pair of pouches as 'anterior gut diverticula' (vordere Darmdivertikeln) while he numbered the dorso-lateral somites from one to eight going backwards. We prefer to regard the 'anterior gut diverticula' as the first pair of somites, by homology with vertebrates, and to number the dorso-lateral somites in the figure from two to nine accordingly (in this we follow Koltzoff 1901, pp. 412–419; van Wijhe 1902, p. 170; 1906, p. 65; Damas 1944, p. 188). This first pair of somites are late to pouch out from the gut, for their first appearance coincides with that of somites 8 or 9 at the posterior end of the somitic series. The second pair of somites, i.e. the most anterior of the dorso-lateral series, differ from those behind them in being the earliest to pouch out from the archenteron, in developing anterior paired rostral extensions, and in retaining for a long time an open communication between their cavities and the archenteron (MacBride 1898, p. 599; Smith & Newth 1917).

A slightly later stage in development is represented in figure 22*c*, *d*. The dorso-lateral somites (i.e. 2–10) have started to grow ventralwards and have become distinctly offset with respect to each other, with the right intersomitic boundaries more posterior than the equivalent left ones. Eventually the ventral ends of these somites meet in the mid-line and the boundaries between the somites break down in this ventral region to form a continuous mesodermal lamella (figure 22*e*). In this lamella the ventral aorta arises. The lamella contains a virtual cavity which becomes the future general body coelom (splanchnocoel).

The first pair of somites of amphioxus (vordere Darmdivertikeln) have a very curious development. They first appear as symmetrical outpouchings from the gut, ventral to the rostral extensions of the second pair of somites (Hatschek 1881; Goodrich 1917). The right one

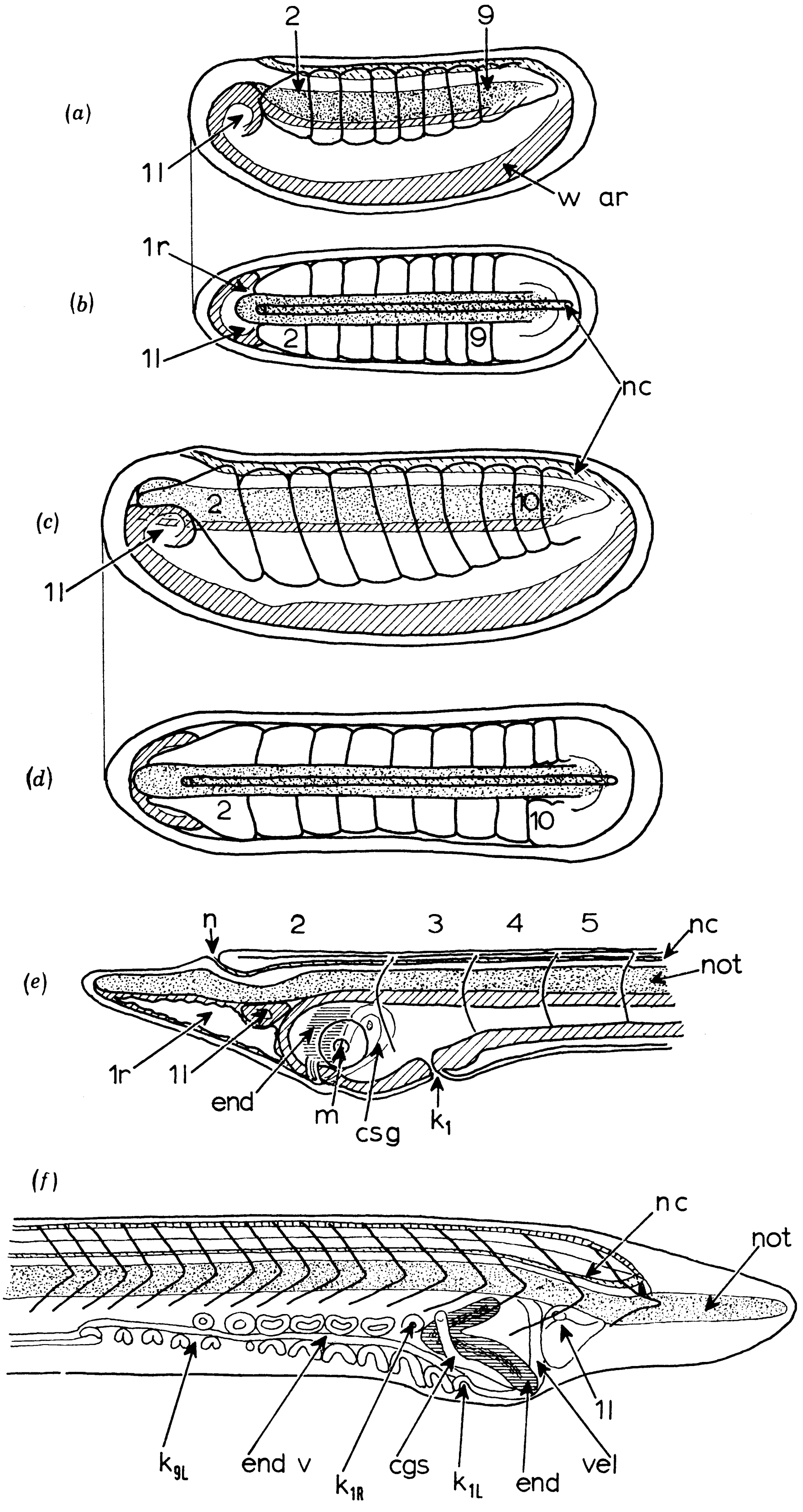

FIGURE 22. Ontogeny of amphioxus. (*a*), (*b*) Stage with 9 somites, lateral and dorsal aspect (after Hatschek 1881, figs 48, 49). (*c*), (*d*) Stage with 10 somites, lateral and dorsal aspect (after Hatschek 1881, figs 50, 52). (*e*) Stage with one gill slit, left aspect of anterior part (after Hatschek 1881, fig. 62, endostyle inserted after Conklin 1932, fig. 110). (*f*) Shortly after appearance of right gill slits; right aspect of anterior end (after Willey 1891, fig. 5). 1l, 1r = left and right anterior gut diverticula, or first somites; 2, 3, 4, 5, 9, 10 = second to tenth somites, belonging to dorsal-lateral series; csg = club-shaped gland; end = endostyle; end v = endostylar vessel; k_1, k_{1R}, k_{1L}, k_{9L} = gill slits, first to ninth on left and right; nc = neural cord; not = notochord; m = mouth (velar mouth); w ar = wall of archenteron.

remains epithelial and expands to form the ventral rostral coelom of the larva and adult (described in the adult by van Wijhe 1902, p. 167). The left one becomes thick-walled and its cavity develops an opening to the exterior, just anterior to the larval mouth. It thus forms what is known as the pre-oral pit (or Hatschek's pit), which becomes part of the ciliated and glandular wheel organ of the buccal cavity of the adult. This first pair of somites is probably homologous with the left and right premandibular somites of vertebrates. It resembles them in appearing late in ontogeny, in retaining for a long time a connection with the archenteron (Koltzoff 1901, p. 418) and in being at the anterior end of the somitic series.

The larval mouth of amphioxus, which is homologous with the velar mouth of the adult, arises in the lateral-plate region of the second left somite, ventral to the myotomic portion (m in figure 22*e*). Van Wijhe (1914) found, not surprisingly, that the coelom of the velum and the velar muscle arose from the lateral plate of this second left somite (in confirmation of Legros 1898, p. 533), as also did the inner lip coelom which in the adult is situated inside the cirral skeleton. The outer lip coelom, outside the cirral skeleton, was an anterior left extension of the splanchnocoel (see review by Franz 1927, p. 597 ff). The mouth later expands ventral to several myomeres (see e.g. Lankester & Willy 1890, pl. 29, fig. 1). The club-shaped gland (c s g) is another larval organ close to the mouth which deserves mention. It arises as an evagination of the pharynx and, when best developed, is a tube opening to the exterior at one end and into the pharynx at the other. Goodrich (1930) interpreted it as a modified gill slit, being the most anterior of the left or primary series.

The fact that the velum and velar mouth arise in the second left somite of amphioxus suggests that the left anterior coelom of mitrates, in whose field the velum, and therefore the velar mouth, were mainly included, should be equated with the coelom of the 2nd left somite of amphioxus. This would imply that the right anterior coelom of mitrates was homologous with the coelom of the 2nd right somite. It is interesting that the right anterior coelom of mitrates is posterior to the left one, just as the posterior boundary of the 2nd right somite of amphioxus is posterior to that of the left one (figure 22*d*).

The second pair of somites of amphioxus are probably homologous with the 2nd or mandibular somites of living vertebrates. This was argued by Koltzoff on the grounds that the lateral plate of the right and left mandibular somites of the ammocoete gave rise to the velum, like the 2nd left somite of amphioxus, that the cavities of the mandibular pair of somites in the ammocoete remained for an exceptionally long time in communication with the archenteron, like the 2nd somites of amphioxus, and that they were posterior to the premandibular pair of somites, which, as already mentioned, he regarded as homologous with the 'vordere Darmdivertikeln' or first pair of somites of amphioxus (Koltzoff 1901, p. 421; Goodrich 1917). Damas, whose study of the development of the ammocoete was as meticulous as Koltzoff's, agreed with these homologies (1944, p. 240). This implies that the left and right anterior coeloms of mitrates are homologous with the left and right second or mandibular somites (their lateral plate included) of living vertebrates.

This suggested homology between mitrates and living vertebrates is confirmed by direct comparison between the two groups, for the paired mandibular somites of living vertebrates are supplied by the trigeminal complex, like the anterior coeloms of mitrates (see also, pp. 70–76). Also the lateral-plate parts of the mandibular pair of somites of an ammocoete surround the mouth and buccal cavity and produce the muscles of the mouth (Damas 1944, p. 197), as in other vertebrates (van Wijhe 1883, p. 14 for sharks; Starck 1975, p. 619 for vertebrates in general).

In like manner the anterior coeloms of mitrates, probably principally the left one, surrounded the mouth and buccal cavity and presumably produced their muscles.

The premandibular pair of somites of living vertebrates was probably represented in mitrates by the crescentic body. Unlike more posterior somites, the right and left premandibular somites of living vertebrates are connected together in the mid-line and the crescentic body was correspondingly a median structure. Furthermore it was like the premandibular somites in being anterior to the front end of the notochord, anterior to the prosencephalon and medial to the cispharyngeal eyes, which are probably homologous with the paired eyes of vertebrates. Also it was dorsal to the posterior end of the duct of the neural gland which, as discussed above, is probably homologous with Seessel's pouch of a vertebrate. In like manner the premandibular somites of a lamprey extend left and right from the pre-oral gut (Seessel's pouch), with which they remain connected for a long time (Koltzoff 1901, p. 371).

The hyoidean pair of somites of vertebrates are probably represented by the most anterior pair of somites in the mitrate tail. For these would be closely associated with the rhombencephalon, and would be posterior to the mandibular and premandibular somites and medial to the left and right atria, whose most medial portions are probably homologous with the ears of living vertebrates. In the mitrates there could have been no close connection of the first pair of tail somites with the hyoid arch. The second pair of tail somites in mitrates would be homologous to the first branchial somites, and so forth.

The paired eyes of standard vertebrates were probably represented in mitrates by the cispharyngeal eyes, and the paired optic nerves by the cispharyngeal optic nerves (see discussion of cranial nerves below). These nerves seem to have left the brain of mitrates near the base of the prosencephalon and run dorsalwards to end just beneath the surface of the skeleton.

The oculo-motor muscles of vertebrates derive in ontogeny from the left and right premandibular somites, except the external rectus muscles which derive from the hyoidean somites, and the superior oblique muscles (= posterior obliques of lamprey) which derive from the dorso-lateral portion of the mandibular somites. The suggested mitrate homologues of these somites, as discussed above, would all pass very near to the cispharyngeal eyes. The premandibular somites (crescentic body) would be medial to them; the dorso-lateral portions of the mandibular somites (anterior coeloms) would be immediately lateral to them; and the hyoidean (first tail) somites would be immediately posterior to them. This mitrate arrangement could therefore easily have given rise to the oculo-motor muscles of vertebrates.

The homologies just suggested can be summed up in a table:

mitrates	amphioxus	living vertebrates
neural gland	median connection of 1st pair of somites with archenteron	Seessel's pouch or pre-oral gut
crescentic body	1st pair of somites (anterior gut diverticula)	1st or premandibular pair of somites
left and right anterior coeloms	left and right 2nd somites (1st of dorso-lateral series)	2nd or mandibular pair of somites
1st pair of tail somites	left and right 3rd somites (2nd of dorso-lateral series)	3rd or hyoidean pair of somites (myomeric portion only)
2nd pair of tail somites	left and right 4th somites (3rd of dorso-lateral series)	4th or 1st branchial pair of somites (myomeric portion only)

and so on

As already mentioned, the posterior coelom of mitrates is probably homologous with the left and right epicardia of tunicates and the nephridia of amphioxus. It probably has no equivalent in living vertebrates.

The implications of these homologies for the primitive morphology of vertebrates and acraniates will be discussed later.

(*f*) *The brain and cranial nerves*

(i) *Introduction*

In most previous papers (Jefferies 1967, 1968, 1969, 1973; Jefferies & Prokop 1972; but not Jefferies 1975 nor in press) we assumed that the tail and head of calcichordates were strictly homologous with the stem and theca of crinoids. Furthermore we assumed that the aboral nervous system of crinoids was homologous with the central nervous system of chordates, that the thecal nerves were broadly homologous with the cranial nerves, the aboral nerve centre with the brain and the peduncular nerve with the dorsal nerve cord. As explained in the introduction, these supposed homologies now appear to be only parallels, since it now seems likely that the crinoid stem and the chordate tail were independently evolved. It is necessary to consider how this change of opinion affects the reconstructions of the nervous system of calcichordates, since we originally identified the position of the brain of calcichordates, at the anterior end of the tail, by using its supposed homology with the aboral nerve centre of crinoids.

Leaving aside any features of the nervous system, the chordate nature of the calcichordate head is now strengthened by a great number of anatomical details, particularly in the pharynx as shown above. It is therefore reasonable to regard the jointed appendage as a chordate tail. This tail was adapted for movement and as such would have needed muscles and an anticompressional notochord in its proximal portion, where the calcite skeleton is loosest. On chordate analogies the brain would be located at the anterior, proximal end of this notochord, i.e. where the tail joined the head. And this was the same conclusion as was reached by comparison with crinoids. The crinoid comparison was therefore not misleading, although only an analogy. The aboral nerve centre of crinoids and the brain of chordates both arose where the apendage joined the rest of the animal, presumably because this position gave the best liaison between theca and stem or tail and head.

In discussing homologies of nerves between mitrates and vertebrates, the end organs and central relations are important but the intermediate courses are probably not. For embryological experiment has shown that nerves will grow out from the neural crest or neural tube to their end organs round obstacles artificially put in their path (Balinsky 1960, p. 426). The optic nerves are an exception to this rule since they are tracts of the brain whose end organs are partly induced by them and are partly the modified extremities of the optic nerves themselves.

(ii) *The brain and cranial nerves of* Mitrocystella incipiens miloni

We shall describe the brain and cranial nerves of *Mitrocystella incipiens miloni* (figure 23) before those of *Placocystites forbesianus*. We do this because *Mitrocystella* displays a more primitive condition which in some ways, though not all, is easier to read from the fossils.

The piece of rock which is deduced to represent the brain of *Mitrocystella* was divided into an anterior inflated portion (pros, pr) and a posterior, less inflated portion (rhomb, rh) (plate 7, figures 88, 89; plate 11, figures 110, 112, 113; plate 12, figure 116; plate 13, figures 121, 123, 124; for *Mitrocystites mitra* plate 11, figure 111). Both these portions were contained in a

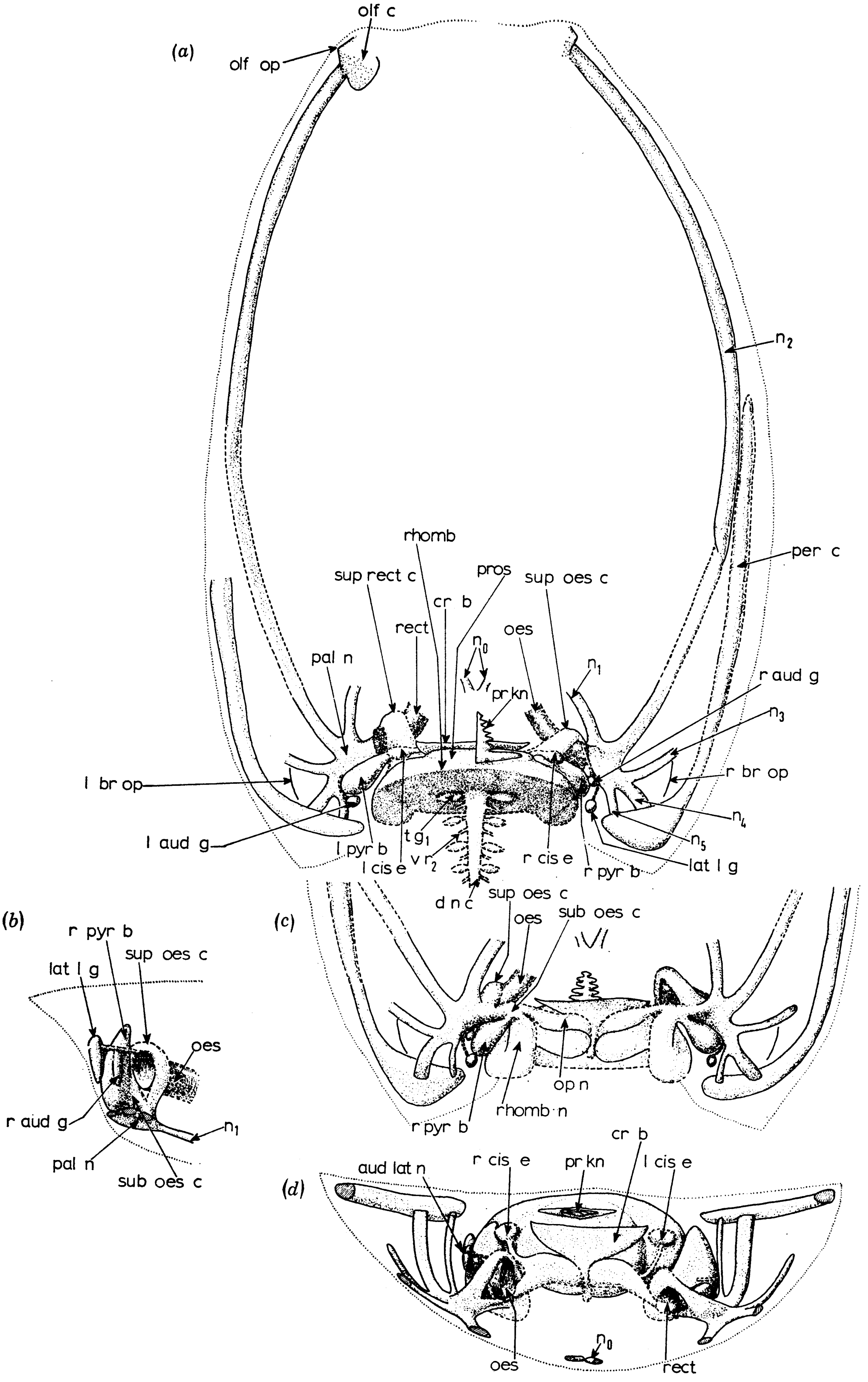

FIGURE 23. Nervous system of *Mitrocystella incipiens miloni*. Solid lines indicate direct skeletal evidence. Broken lines are based on indirect evidence. (*a*) Dorsal aspect. (*b*) Right aspect of region near oesophageal opening. (*c*) Ventral aspect of posterior part. (*d*) Anterior aspect of posterior part.

cerebral cup, excavated in the dorsal skeleton, in plates M_{1LD} and M_{1RD}. In the mid line, just anterior to the more inflated part of the brain (pros), there was an irregular structure, consisting of many cones pointing outwards from the median suture (pr kn in plate 12, figure 116). A figure-of-eight shaped foramen (op for) connected the antero-ventral face of the inflated part of the presumed brain to the inside of the head, and there was a slit in the mid-line, postero-ventral to this foramen, between the median ends of the hypocerebral processes (see especially plate 8, figure 92; plate 9, figure 101; plate 12, figure 118; plate 13, figure 123; plate 15, figure 137). In previous papers (e.g. Jefferies 1968, p. 296; 1973, pp. 450–451; 1975, pp. 287, 296) we spoke of the brain being divided into *three* parts called anterior, medial and posterior. The irregular structure (pr kn) counted as the anterior part of brain. We have long suspected, however, that this description was somewhat unnatural (Jefferies 1973, p. 451). Comparison with standard vertebrates confirms this suspicion and we therefore propose to change the nomenclature.

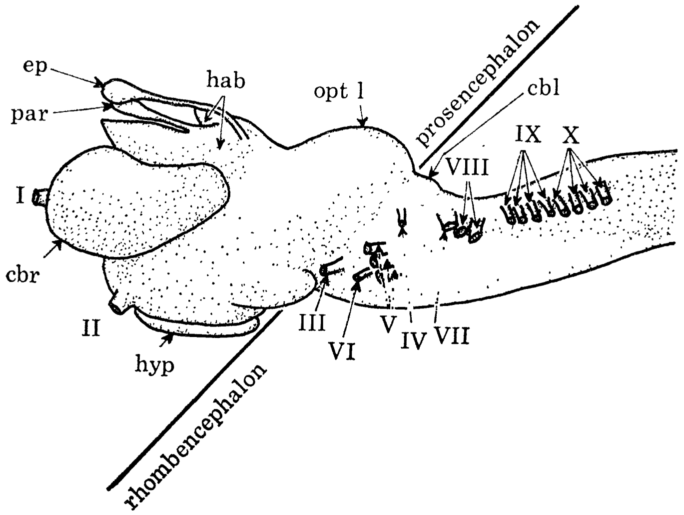

FIGURE 24. Left aspect of brain of *Petromyzon* (after Romer 1962, fig. 381) to illustrate Starck's conception of the primitively bipartite nature of the brain. cbl = cerebellum; cbr = cerebrum; ep = epiphysis; hab = habenular ganglia; hyp = hypophysis; opt l = optic lobes; par = paraphysis; I–X = cranial nerves.

Starck (1975, p. 369) has pointed out that in young vertebrate embryos the brain is divided into two portions: the fore brain or prosencephalon and the hind brain or rhombencephalon. The concept of a mid brain or mesencephalon, though widespread in the literature, is artificial according to Starck, for its dorsal part or tectum belongs naturally with the prosencephalon while its ventral part or tegmentum is a forward continuation of the rhombencephalon. Furthermore the same bipartition of the brain exists in a tunicate tadpole (Starck 1975, p. 356). This suggests that it existed also in the latest common ancestor of tunicates and vertebrates, which would have been a mitrate. The prosencephalon becomes differentiated in later vertebrate ontogeny into the antero-dorsal telencephalon, primarily concerned with olfaction, and the postero-ventral diencephalon, which is primarily optic and hypophyseal. The rhombencephalon, on the other hand, controls the branchial region, the mouth region, the viscera and the acustico-lateralis system. A basic division into prosencephalon and rhombencephalon is evident if the brain of an adult lamprey is viewed in lateral aspect (figure 24).

Starck's embryological intuition, that the brain of tunicates and vertebrates brain has two basic parts, fits the situation in *Mitrocystella*. The anterior inflated part of the brain would be the prosencephalon. The posterior less inflated part would correspond to the rhombencephalon, except that the rhombencephalon of standard vertebrates seems to have annexed certain structures which in mitrates belonged to the tail, as discussed later. The irregular structure antero-dorsal to the prosencephalon, formerly called the anterior part of the brain but henceforth called the precerebral knot, would represent a concentration mainly of olfactory fibres just before they entered the brain, as we have already suggested elsewhere (Jefferies 1973, p. 451; Jefferies & Prokop 1972, p. 99). It would not itself represent the telencephalon but would be in contact with the telencephalar part of the prosencephalon. It would receive olfactory fibres from the skeleton which had entered the skeleton by way of a pair of olfactory openings or pits in the roof of the buccal cavity (olf op in figure 23; see also plate 11, figures 112, 113). The precerebral knot may also have included touch-sensory fibres, as discussed below. The figure-of-eight shaped foramen anterior to the prosencephalon can be called the optic foramen (opt for) since a simple comparison with vertebrates suggests that the optic nerves passed through it. And the median slit in the skeletal floor beneath the prosencephalon, as already indicated, would connect the floor of the prosencephalon with a probably non-ectodermal 'hypophysis' or neural gland (Seessel's pouch or preoral gut).

The rhombencephalon of *Mitrocystella*, as we shall call it for simplicity, although it probably corresponds to only part of the rhombencephalon of standard vertebrates, shows signs of nerves leaving it medianwards and ventrally. We formerly referred to these as the posterior part nerves but we now call them the rhombencephalar nerves (rhomb n in plate 13, figure 121). Nerves leaving the rhombencephalon of a modern vertebrate include: the trigeminal to the mouth, velum and dorsal surface of the head; the oculomotor, trochlear and abducens to the extrinsic eye muscles; the acoustic and lateral-line nerves to the acustico-lateralis system; the facial, glosso-pharyngeal and vagus nerves to the gill bars, non-pharyngeal gut and endostyle (though these mainly branchial nerves are also closely associated with the acustico-lateralis system); and the hypoglossal nerves to the hypobranchial musculature. We should expect that the rhombencephalar nerves of *Mitrocystella* would include homologues of all of these, except for any components that belonged originally to the tail.

The paired 'pyriform bodies' lay just anterior to the rhombencephalon of *Mitrocystella* (pyr in plate 9, figures 98, 99, 102, 103; plate 11, figure 113; plate 13, figures 120, 123, 126; r pyr b in plate 13, figure 125; for *Mitrocystites mitra*, plate 15, figures 136, 138). We believe them to be homologous with the trigeminal ganglia of vertebrates, particularly by comparison with cephalaspids (Jefferies 1968, p. 307). Like the trigeminal ganglia of vertebrates they were situated between the ears (which were inside the atria in *Mitrocystella*) and the eyes (cispharyngeal eyes) and they were antero-lateral to the rhombencephalon.

The paired palmar complexes are the most obvious feature of the cranial nervous system of *Mitrocystella*. To judge by the canals, each consisted of a stout palmar nerve, like the palm of a hand, with five nerves or 'fingers' coming out of it peripherally (plate 9, figures 98, 99; plate 13, figure 126). The 'fingers' are numbered n_1, n_2, n_3, n_4, and n_5 counting outwards from the mid-line. These nerves, or rather their canals, can be followed in the fossils for a considerable distance because in life they spread out in the middle soft layer of skeleton and both the inner and outer calcite layers were excavated to receive them. Before actually giving rise to these five nerves the canals for palmar nerves broke up into two short, broad furcations. The anterior furcation gave rise to n_1 and n_2 while the posterior furcation gave rise to n_3, n_4 and n_5.

The paired nerves n_3 were probably optic. In *Mitrocystella incipiens miloni* they extended only to the suture between the dorsal and ventral skeletal and then stopped. In *Mitrocystites mitra*, however, they continued through wide cylindrical canals through the dorsal skeleton, through openings on the dorsal surface of the head, to end in little pits which probably carried vesicles (plate 11, figure 111; Jefferies 1968, pl. 8, figs 1, 10). The conclusion that these nerves were optic is based on this dorsal termination together with the fact that the prosencephalon was more inflated, and the optic foramen relatively larger, in *Mitrocystites mitra* which had these external eyes, than in *Mitrocystella miloni incipiens* which lacked them (compare, for example, plate 11, figure 111 with plate 11, figure 112). *Mitrocystites mitra* is also instructive in that a pair of grooves impressed in the ventral faces of the hypocerebral processes and passing outwards and downwards from the optic foramen, probably served to carry optic nerves from the optic foramen towards the palmar nerves (op n in plate 15, figure 136). There is evidence of similar external paired eyes in the primitive Mitrocystitid *Chinianocarpos* and in the advanced, mitrate-like cornute *Reticulocarpos* (Jefferies & Prokop 1972, p. 89; Jefferies 1973, p. 451). They can be called transpharyngeal eyes, being situated on the side of the pharynx farther from the brain. They cannot be homologous with the eyes of vertebrates, contrary to what we thought at one time (see for example, Jefferies, 1968, p. 336). The dorsal portion of the nerves n_3 had been lost in *Mitrocystella*. This was probably connected with a tendency to protect soft organs of the dorsal surface of the head from occasional contact with sediment.

Probably also related to the optic system are a pair of ridges in the internal cast (l & r cisph op n in figure 17*b*; l & r cis in photographs in plate 8, figure 92; plate 9, figures 101, 103; plate 12, figure 118; plate 15, figure 137). These diverge from the optic foramen. The right one can be followed to near the dorsal surface of the posterior coelom. (In *Mitrocystites mitra* it reaches this surface (plate 15, figure 138) and the same is true for *Peltocystis cornuta* (personal observation).) The left one cannot be followed so far, and bends down slightly before beginning to pass upwards. These ridges probably carried optic nerves and eyes situated on the same side of the pharynx as the brain, and hence called cispharyngeal eyes (Jefferies & Prokop 1972, p. 90; Jefferies 1973, p. 351). They would have received light that had come through the presumably translucent calcite of the skeleton. They were probably homologous with the paired eyes of vertebrates. Their relations to the probable homologues of the vertebrate premandibular, mandibular and hyoidean somites have been discussed in the preceding section of this paper.

Returning to the palmar nerves, in addition to the optic component, two other components seem to have entered them proximally. The first seems to have come out of the left or right trigeminal ganglion (pyriform body) and joined the left palmar nerve by passing under the rectum, and the right palmar nerve by passing under the oesophagus (sub-rectal and sub-oesophageal components = sub rect c and sub oes c in figure 17*b*, figure 23*b*, *c*, *d*). The second non-optic component of the palmar nerves seems to have passed over the rectum on the left or oesophagus on the right, probably without contact with the trigeminal ganglion from which it is always rather distant, and then entered the palmar nerve by passing lateralwards, ventralwards and somewhat posterior (supra-rectal and supra-oesophageal components = sup rect c and sup oes c). The two components of the left palmar nerve can be seen as replicas in rock in plate 13, figure 122 and of the right palmar nerve in plate 13, figure 125. More proximal parts of the supra-alimentary components can be seen as replicas in rock on the posterior face of the internal mould, passing dorsally upwards from the ventral foramen (plate 8, figure 92; plate 12, figure 118, left side only). The supra-alimentary components, since they do not pass near the trigeminal ganglia, were probably mainly motor. The subalimentary components, whose cell bodies probably occupied the trigeminal ganglia, were presumably mainly sensory.

The nerves leading from the palmar nerves, apart from the transpharyngeal optic nerves n_3, were probably all branches of the trigeminal. The biggest were the nerves n_2 which can be traced forward as ridges at right and left of the dorsal aspect of the internal mould, to enter the mouth region and buccal cavity (ventral portions in plate 9, figures 98, 99; dorsal portions in plate 11, figures 110, 112, 113; plate 12, figures 114, 117). These nerves were presumably homologous with the paired maxillary branches of the trigeminal of vertebrates, as maintained previously (see for example, Jefferies 1975, pp. 288, 296 and earlier papers). The nerves n_1 were probably the mandibular trigeminal nerves, for Lindström (1949, pp. 354, 384, 439) has shown that the trigeminal nerves of cyclostomes include maxillary and mandibular branches. These are presumably homologous with the like-named nerves of gnathostomes and would therefore have been represented by corresponding nerves in the latest common ancestor of agnathans and gnathostomes. It is therefore not surprising to find maxillary and mandibular branches of the trigeminal in mitrates. The nerves n_4 and n_5 passed up to the peripheral canals just beneath the dorsal surface in *Mitrocystella* (plate 13, figure 126) and to the peripheral grooves on the dorsal surface of the head in *Mitrocystites* (plate 11, figure 111; plate 15, figure 138). They were probably touch-sensory branches of the trigeminal. They can probably be equated with the paired ophthalmicus superficialis and ophthalmicus profundus branches of the trigeminal of vertebrates. The nerves n_5 would correspond to the profundus branches, since they are more median than n_4 and passed nearer to the premandibular somite (crescentic body). And the nerves n_4 would probably be homologous with the ophthalmicus superficialis branches, since they are more external than n_5 and lateral and posterior to the right or left mandibular somites (anterior coeloms). By comparison with the dorsal sensory branches of the trigeminal in a lamprey, nerves n_4 and n_5 would probably have arisen from placodes in the embryo (cf. Damas 1944, pp. 52, 81; Koltzoff 1901, pp. 518–523.)

Nerves n_4 and n_5 existed, among mitrates, only in advanced Mitrocystitida and Anomalocystitida. They are not found in *Lagynocystis*, *Peltocystis* or *Chinianocarpos thorali* (figure 29) and were therefore presumably absent from all the most primitive mitrates, as also from cornutes. These primitive forms would nevertheless require a sense of touch in the dorsal surface of the head. It is likely that the appropriate touch-sensory fibres would run to the brain through the dorsal skeleton and would enter the telencephalar part of the prosencephalon through the precerebral knot like the olfactory fibres, for there seems to be no other route available. This implies that the sense of touch in the head of these primitive forms was supplied by a terminalis nerve, homologous with that of vertebrates (cf. Goodrich 1930, p. 750; van Wijhe 1918).

A pair of presumed nerve canals, for the nerves n_0, left the posterior coelom of *Mitrocystella* near the mid-line, diverging outwards (plate 9, figure 100). Homologous nerves in *Placocystites* almost certainly supplied the endostyle (see p. 257) and this was presumably true in *Mitrocystella* also. Concerning their proximal connections there is no direct evidence. In an ammocoete, however, the endostyle is supplied by a branch of the facial nerve (Gaskell 1908, p. 311) so this ought also to have been true of mitrates, in so far as the facial nerve existed in them as a separate entity. There would also have been nerves supplying the non-pharyngeal gut, heart and other viscera. These would presumably be homologous with the intestinal branch of the vagus of standard vertebrates.

Finally there are indications of a number of small nerves and ganglia in *Mitrocystella incipiens miloni* which can be dealt with together because, as discussed later, they were probably related to each other functionally. The most obvious of these features is a long, carrot-shaped piece of rock interpreted as representing a ganglion (lat l g in plate 13, figures 125, 126). It is situated in the head plates on the right side of the tail just internal to a groove in the external surface (lat l in figure 5; plate 7, figure 88). This presumed ganglion was supplied by a flattened structure interpreted as a nerve. This approached the presumed ganglion and entered it, running posteriorly and slightly downwards (lat l n in plate 9, figures 101 to 103; in *Mitrocystites mitra*, plate 15, figure 138). There is evidence of another ganglion just right of and anterior to the right pyriform body or trigeminal ganglion (r aud g in plate 13, figures 125, 126). The presumed common nerve to lln and to these two minor ganglia would have been anterior to the skeleton. The presumed nerve to the carrot-shaped ganglion, however, seems to approach the latter from an antero-dorsal position, as if from the dorsal surface of the oesophagus. This suggests that the common nerve to the two minor ganglia passed over the anterior surface of the oesophagus from below to above, when followed out from the brain, i.e. in opposite direction to the supra-alimentary component of the palmar nerve. On the left side of the body there is evidence of a ganglion in the left atrium (l aud g in figures 17, 23; plate 13, figure 124). In *Mitrocystites mitra* (plate 15, figure 138) the lump presumed to represent this ganglion has a ridge entering it anteriorly. This ridge in that species runs round the anterior surface of the left pyriform body (trigeminal ganglion), between the latter and the rectum (Jefferies 1969, pp. 521–524). It presumably represents a nerve supplying the ganglion in *M. mitra* so the corresponding nerve in *Mitrocystella*, for which there is no direct evidence, probably had a similar course.

These presumed minor nerves and ganglia can probably be assigned to the acustico-lateralis system. This is suggested most forcibly on the right, where the long carrot-shaped body just internal to a groove can be interpreted as a lateralis ganglion internal to the lateral line. On the left side the nerve that seems to have swept round the left trigeminal ganglion, to supply a ganglion in the left atrium, recalls a deduced nerve in the primitive cornute *Ceratocystis* which supplied a groove on the surface. This groove presumably functioned as lateral line in *Ceratocystis* but became included in the left atrium when atria were evolved in the early mitrates and it would then have taken on an acoustic function (cf. Jefferies 1969, p. 522; 1975, p. 288). It is natural to interpret the presumed ganglion in the right atrium as an antimere of the ganglion in the left atrium, and therefore also acoustic. The fact that the ganglia seem to have been situated peripherally agrees with a fish's acustico-lateralis system in which the ganglia arise embryologically from placodes.

In summary, the deduced brain and cranial nerves of *Mitrocystella* were fundamentally like those of a standard vertebrate. The brain was divided into prosencephalon and rhombencephalon. The prosencephalon would be exactly homologous to that of a very young living vertebrate embryo. The rhombencephalon would correspond to that of a living vertebrate embryo, escept that the latter has annexed certain structures belonging to the nervous system of the mitrate tail. The prosencephalon seems to have received olfactory and probably terminalis fibres antero-dorsally, was connected antero-ventrally with optic nerves and ventrally with the hypophysis. The optic nerves are deduced to have comprised a cispharyngeal and a transpharyngeal pair, of which the former are probably homologous with the paired eyes of vertebrates. The rhombencephalon was presumably connected with paired trigeminal ganglia (the pyriform bodies). In the paired trigeminal or palmar complexes it is possible to recognize mandibular, maxillary, opthalmicus superficialis and opthalmicus profundus branches, with supra-alimentary, probably motor, components and sub-alimentary, probably sensory, ones. The acustico-lateralis system was developed, with acoustic ganglia inside the atria and with a lateralis ganglion, on the right side only, connected with a lateral-line groove. There is evidence of a nerve supply to the endostyle, presumably homologous with part of the facial nerve of an ammocoete, and there would presumably also have been a nerve supply to the non-pharyngeal gut, heart and other viscera, homologous with the intestinal branch of the vagus of standard vertebrates.

(iii) *The brain and cranial nerves of* Placocystites forbesianus

The cranial nerves and brain of *Placocystites forbesianus* were very like those of *Mitrocystella incipiens miloni*. They are best described by considering how the two species differed.

As regards the brain, the prosencephalon, as judged by the shape of the cerebral basin, was less inflated in *P. forbesianus* than in *Mitrocystella incipiens miloni*. Perhaps this was because *P. forbesianus*, as a partial burrower, was less concerned with light. The precerebral knot presumably existed in *P. forbesianus* but there is no fossil evidence of it. Olfactory and terminalis fibres presumably congregated at the posterior mid-dorsal suture, but are not associated with any detectable cavity there. In one specimen the cerebral basin shows signs that the prosencephalon was divided (plate 4, figure 73) into telencephalon and diencephalon, but in other specimens this distinction is not expressed (plate 4, figure 74).

In the cranial nerves the following differences are deduced between *Placocystites forbesianus* and *M. i. miloni*: (1) In the longitudinally sectioned specimen neither trigeminal ganglion (pyriform body) was in contact with skeleton, and in the transversely sectioned model only the right one was. The cup for the right trigeminal ganglion seems also to have contained the right auditory ganglion (glass model shown in plate 8, figures 95, 97; polystyrene models in plate 5, figure 75; plate 6, figure 86; plate 7, figure 90; plate 8, figure 94). (2) In neither specimen is there any sign of the nerves n_3 (transpharyngeal optic nerves). (3) Canals for a pair of large additional nerves(n_x) existed median to nerves n_1 of the palmar complexes (plate 5, figure 75; plate 6, figure 85; plate 7, figures 87, 90; plate 8, figures 94, 95). The nerves n_x can conveniently be seen as an extra branch of the palmar complex. (4) There was no external lateral line, and consequently no lateral-line ganglion or nerve.

The relations between the brain, the right palmar nerve and the right pyriform body, in the transversely sectioned specimen that showed them, are of interest. A reconstruction on glass sheets suggests a nerve from the ventral foramen (sup oes c in plate 8, figure 97), and ultimately from the rhombencephalon, going up to the pyriform body. It also suggests a nerve descending vertically (sub oes c in plate 8, figure 95) from the right trigeminal ganglion to the right palmar nerve. This latter would be the sensory sub-alimentary component of the palmar nerve having its cell bodies inside the pyriform body. The same reconstruction (plate 8, figure 97) also suggests that the supra-alimentary component of the palmar nerve went upwards from the ventral foramen, by-passing the pyriform body. It climbed up over the assumed position of the oesophagus and came down over the front surface of the latter (sup oes c in plate 8, figure 95). It sent one powerful branch forward as n_x in the soft middle layer of the ventral skeleton. This was presumably almost entirely motor since most of its fibres do not seem to have run near

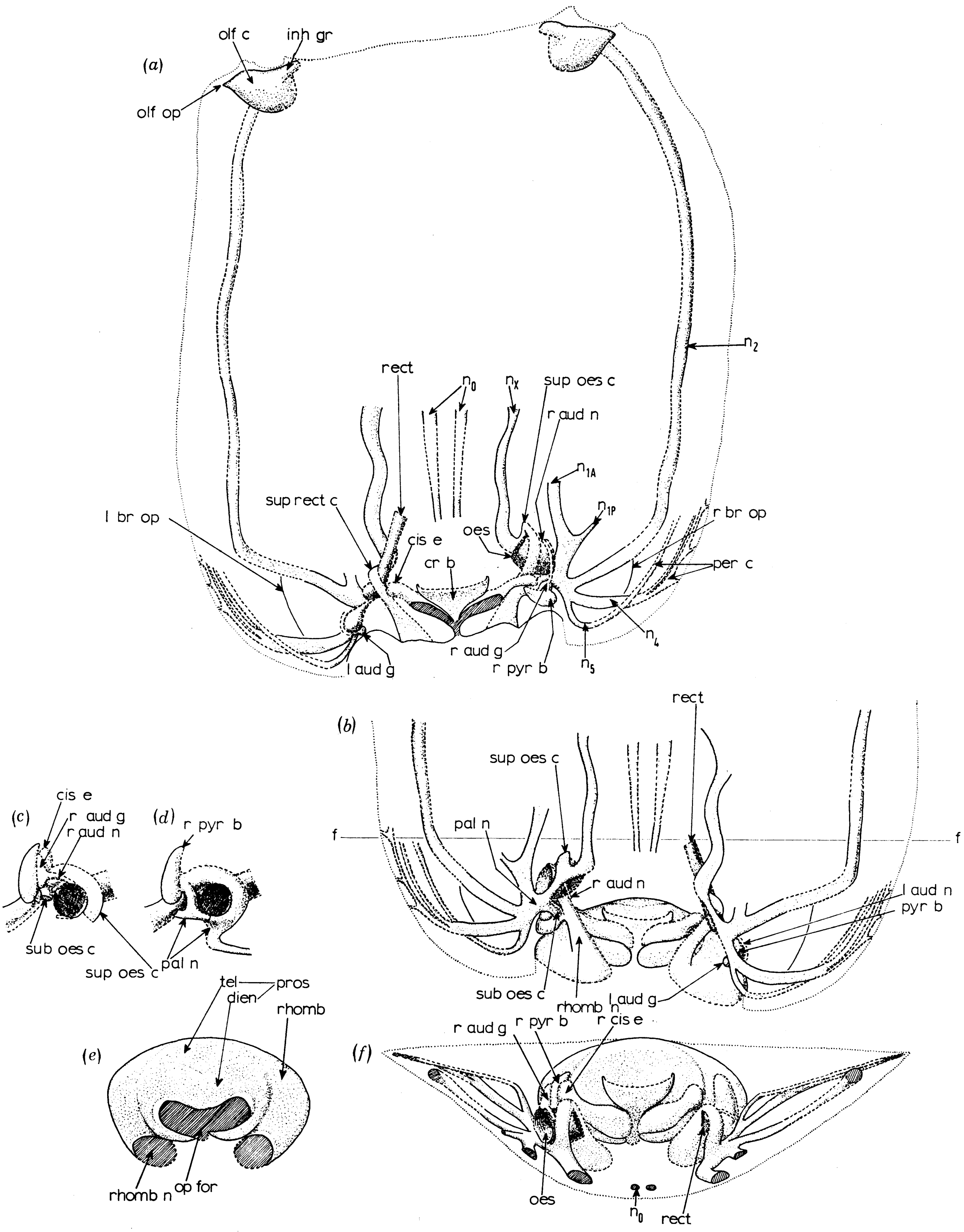

FIGURE 25. Nervous system of *Placocystites forbesianus*. (*a*) Dorsal aspect, brain omitted. (*b*) Ventral aspect of posterior part. (*c*) Region of oesophageal opening with the right auditory ganglion and nerve included (r aud g, r aud n), the cispharyngeal eye included (cis e) and the palmar nerve cut away. (*d*) Region of oesophageal opening including the palmar nerve but omitting auditory parts and eye. (*e*) Anterior aspect of brain. (*f*) Anterior aspect of nervous system behind f–f in figure 25*b*.

the pyriform body. The remainder of the supra-alimentary component ran backwards and passed into the palmar nerve proper (pal n). This then sent off: nerve n_1 (or mandibular trigeminal) which passed forwards inside the ventral skeleton; n_2 (or maxillary trigeminal) which ran laterally through the ventral skeleton, and joined a groove running forward in the dorsal skeleton towards the mouth; n_4 (or ophthalmicus superficialis) which was a large trunk going up to the peripheral canal in the dorsal skeleton (plate 8, figure 97 for right side; compare plate 8, figure 96 for left side); and n_5 (or ophthalmicus profundus) which likewise supplied the peripheral canal. The X-ray picture (plate 15, figure 139) suggests that nerves n_4 and n_5 were continued forwards by several longitudinal nerves in the peripheral canals and that transverse twigs went off from these to supply the edge of the peripheral flange. Rich innervation of the peripheral flange would be important to an animal which needed to live just below the surface of the sediment and was therefore in danger of accidentally emerging.

Nerves n_4 and n_5 would have been purely sensory and were well placed to receive all, or almost all, of their constituent fibres from the presumably sensory sub-alimentary component which would come out of the trigeminal ganglion. Nerve n_2 (the maxillary trigeminal) was probably mainly motor, since it probably supplied the lower lip, oral funnels and oral spines. Being thus connected with the surface of the body, however, it may have been partly sensory also. Its proximal end is well placed to receive both a motor component, from the supra-alimentary component of the palmar nerve, and a sensory component, from the sub-alimentary component of the palmar nerve. Nerves n_1 and n_0, to judge by the positions of their proximal ends of their canals, would have been supplied mainly by the supra-alimentary component of the palmar nerve. They were probably mainly motor. As already suggested, nerve n_x, which was very strong in *Placocystites forbesianus* but did not exist in *Mitrocystella incipiens miloni*, was perhaps evolved to supply a muscular pumping velum.

The acustico-lateralis system of *Placocystites forbesianus* was simpler than that of *Mitrocystella incipiens miloni* in having no lateral line. The cup ventral to the right trigeminal ganglion of the transversely sectioned model contains a big depression presumed to be for this ganglion. This is partly confluent with a small depression, opening anteriorly by a slit (plate 7, figure 90). This small depression presumably contained the right acoustic ganglion connected with the right atrium. The glass-slide reconstruction suggests that the nerve supplying this ganglion through the anterior slit came off the dorsal surface of the oesophagus as already suggested for *Mitrocystella* (r aud n in plate 8, figure 95). The probable position of the left auditory ganglion can be seen in the appropriate glass reconstruction (plate 8, figure 96; compare polystyrene model in plate 7, figure 90).

The optic system is not well recorded in the skeleton. There seem to have been no nerves n_3 but there are indications of a large right cispharyngeal optic nerve ending in a bulb (r cis e in plate 5, figure 75; plate 8, figures 95, 97). A left cispharyngeal optic nerve presumably existed also. The optic system would retain some use in a partial burrower which needed to know whether it had accidentally become either exposed or totally buried.

The nerves n_0 to the endostyle have been dealt with in considering the pharynx. In addition to definite canals for them just anterior to the posterior coelom, there are also possible indications of their position farther forward, in the form of two gaps between the inner and outer calcite layers of the small median ventral plate V_{1M} (compare plate 7, figure 90).

The picture of the cranial nerves of mitrates which now emerges is therefore even more complicated than in previous reconstructions (cf. Jefferies 1967, figs 10, 14; 1968, figs 19, 27;

1969, fig. 16; 1973, fig. 14). Since *Placocystites* and *Mitrocystella*, as we believe, belong to the stem group of living vertebrates, the new reconstructions have great comparative-anatomical significance.

7. THE INTERNAL ANATOMY OF THE CORNUTE HEAD

The change which signalled the emergence of the mitrates from the cornutes was the appearance of gill slits on the right side of the head. Since the presence of a single gill slit is an all-or-nothing character, the first appearance of these right gill slits, or at least of the first one of them, would have been a sudden event, happening between one generation and the next, presumably due to a single important mutation. The first mitrate would have had cornute parents.

The first appearance of right gill slits probably coincided with the first appearance of the right pharynx. It is possible, however, that the chamber of the right pharynx evolved slightly before the right gill slits which would be subsequently perforated in its wall. Clearly the right pharynx could not have evolved later than these slits. The right pharynx would have ballooned out of the left or primary pharynx through the right anterior coelom and underneath its cavity and contents. In so doing the right pharynx would have lifted up the cavity of the right anterior coelom, with its contained organs, and squashed it against the roof of the head. As a result the cavity and its organs would be forced leftwards into a median position, hanging from the ceiling (figure 15).

Two anatomical features would have arisen either simultaneous with the origin of the right pharynx or subsequent to it. They are: (1) the right epicardium, which, by homology with tunicates, sprouted out of the right pharynx; and (2) the oblique ridge of the skeleton, which presumably arose on the inner face of a dorsal strut that was formed by processes of marginal plates i and c, after the right anterior coelom had been forced against the roof of the head by the right pharynx.

Some anatomical features would have arisen either simultaneous with the origin of the right gill slits or subsequent to it. These include: (1) the right atrium, which enclosed the right gill slits; and (2) the right auditory ganglion, situated in the right atrium.

If, as seems likely, right pharynx and right gill slits originated simultaneously, as a single event in the birth of the first mitrate, then the right epicardium, the oblique ridge, the right atrium and the right auditory ganglion originated simultaneously with, or subsequent to, this single event.

Still other features are characteristic of all known mitrates, but not intimately associated with the right pharynx or right gill slits. Their time of origin shows no obvious causal link with that of the right pharynx or slits but they seem to have arisen in the evolutionary line that included the first mitrate itself, its close ancestors and its immediate descendants. The most important such changes include the following. (1) The acquisition of a flat dorsal surface to the head and a convex ventral surface, whereas the immediately ancestral cornutes had a flat ventral surface and a convex dorsal one; this change presumably happened before the formation of the oblique ridge, since the latter arose as a strut crossing flexible integument, and a strut following a curved surface would be mechanically useless. (2) The development of a left atrium to protect the left gill slits; if this happened before the gill slits arose, then the right atrium probably came into existence simultaneous with the right gill slits. If the left atrium originated subsequent to the development of the right gill slits, then it and the right atrium probably evolved simultaneously.

(3) The loss of the old mid and hind tail and the regionation of new fore, mid and hind tail from the remaining stump.

The purpose of the present section of this paper is mentally to reverse the changes associated with the appearance of the right gill slits. In this way, starting with the detailed reconstruction of the mitrate head given above, it should be possible to make deductions about the ancestral cornute condition. The results of this applied geometry can be used to interpret the internal natural moulds of cornutes. The mitrates almost certainly arose from a cornute similar to *Reticulocarpos*. However, we prefer to test our deductions by using the natural moulds of *Cothurnocystis elizae*, because this was bigger than *Reticulocarpos*, and many more specimens of it are known.

The non-pharyngeal gut of mitrates, as already argued, was mostly included in the patent right anterior coelom (figure 18*c*). It would have started at the oesophageal opening, have run

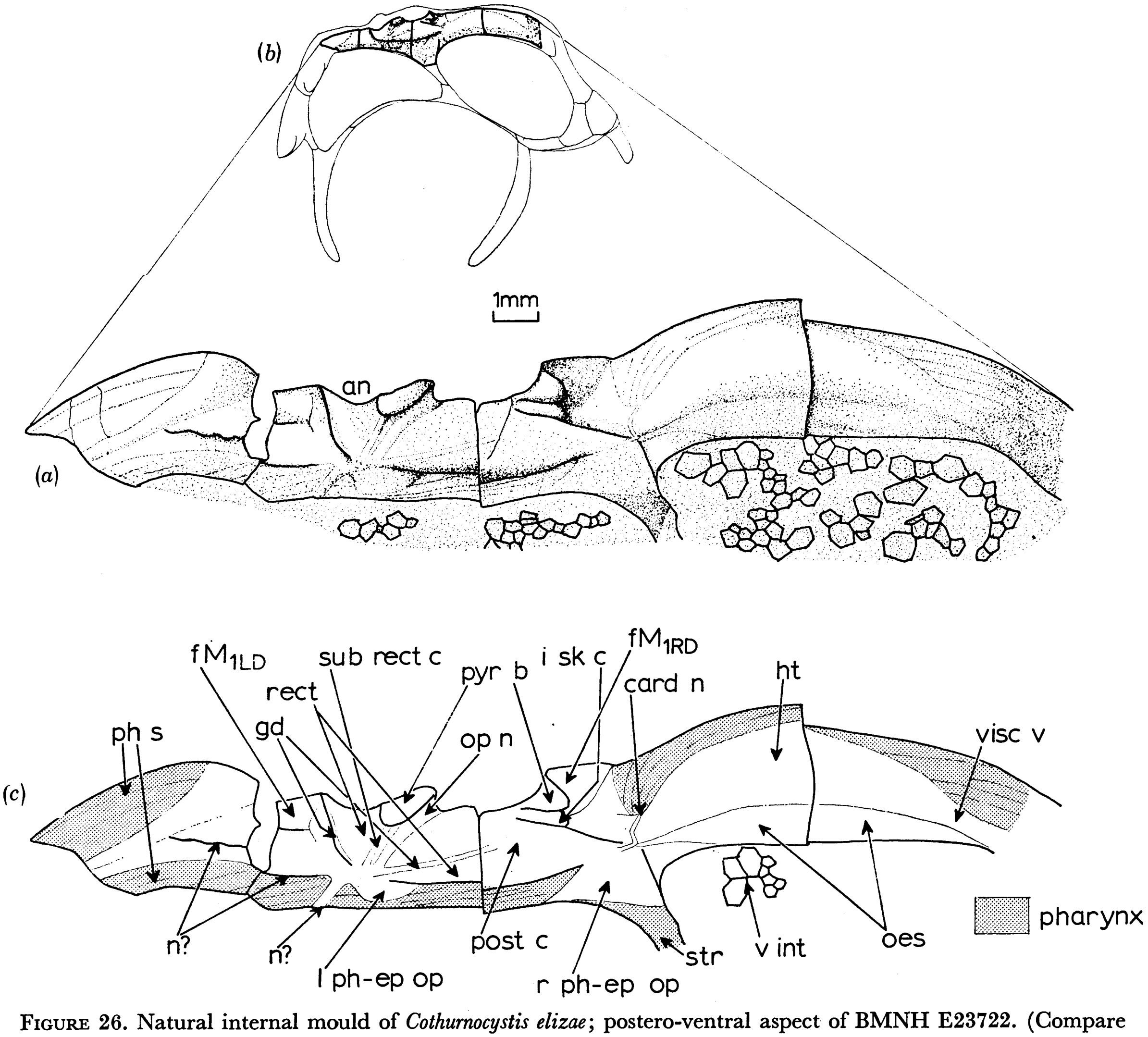

FIGURE 26. Natural internal mould of *Cothurnocystis elizae*; postero-ventral aspect of BMNH E23722. (Compare plate 14, figures 127, 130, 133). (*a*) Camera-lucida drawing. (*b*) Position within animal. (*c*) Interpretation. Note the positions of the heart (ht) and oesophagus (oes), of the right and left pharyngo-epicardial openings (rph-ep op, l ph-ep op) connecting the epicardium or posterior coelom (post c) with the pharynx, and the gonoduct (gd).

forward along the right margin of the cavity of the right anterior coelom, turned through an angle, run back along the left margin of the coelom as far as the posterior coelom, and thence have passed, as the rectum, into the left atrium.

In nearly all cornutes there is direct evidence in the fossils that the rectum emerged from the right anterior coelom, ran across the floor of the posterior coelom (equivalent to only the left epicardium of mitrates) and then climbed vertically to emerge at the anus just left of the tail. This statement holds true of *Cothurnocystis* and *Reticulocarpos* among other forms, and therefore held for the particular cornutes which gave rise to the mitrates. The only exceptions to it are the primitive *Ceratocystis*, where the anus was right of the tail, and the specialized *Scotiaecystis curvata* and other Scotiaecystidae where the anus opened into gill slits just left of the tail; neither of these two exceptions is relevant to our argument.

If the right pharynx is mentally extracted from a mitrate, so as to return the cavity of the right anterior coelom, with its contents, to its cornute position on the floor of the head, then the intestine would follow the left margin of the cavity of the right anterior coelom, obliquely backwards and leftwards over the floor of the head (figure 27*a*, *c*), back to a point just right of the tail. Here it would join the rectum which turns leftwards on the internal mould to run beneath the posterior coelom. The oesophagus would follow the right margin of the right anterior coelom round the inside of the marginal plates of the right posterior corner of the head, to join the intestine or some other part of the gut near the anterior end of the right anterior coelom. The oesophagus would open into the left and only pharynx in a posterior position, presumably right of the posterior coelom, since the oesophageal opening of mitrates was right of the equivalent left epicardium.

Turning to the internal moulds of *Cothurnocystis elizae* we find this suggested position of the non-pharyngeal gut somewhat strengthened (figure 26 and plate 14, figures 127, 130, 132). For the most posterior portion of the intestine in contact with the skeleton appears to have approached the skeleton, and the rectum, from a right anterior position (especially plate 14, figure 132), suggesting that the intestine followed the left margin of the cavity of the right anterior coelom across the floor of the head.

To interpret the internal moulds of *Cothurnocystis elizae* farther, even as concerns the non-pharyngeal gut, it is now necessary to consider the likely positions of the pericardium and its contained organ the heart. The problems of locating these organs in *Cothurnocystis elizae* can be approached from two opposite directions, starting from more primitive cornutes or from the mitrates.

The heart and pericardium of mitrates, as we have tentatively concluded by comparison with tunicates, might have been situated on the right-hand side of the loop of the non-pharyngeal gut i.e. on the right surface of the oesophagus (figure 18*c*).

The posterior end of the heart in mitrates would presumably lead into a sub-endostylar vessel and its anterior end into a visceral vessel. (It must be remembered that anterior and posterior, as concerns the heart, were the opposite way round in mitrates to tunicates.) Mentally removing the right pharynx to obtain the cornute condition, the heart and pericardium would therefore have been located on the posterior surface of the oesophagus of cornutes, between the latter organ and the marginal plates of the right posterior part of the frame. On the internal surface of these plates we might hope to find traces of this arrangement.

Approaching the problem from the opposite direction, the heart and pericardium of the primitive cornute *Ceratocystis* would be expected to be located somewhere near the hydropore, for the equivalent madreporic vesicle (dorsal sac) of echinoderms is located near the hydropore (Jefferies 1969, pp. 513–515; Jefferies 1975, pp. 265–270). In *Ceratocystis* the hydropore was situated in the posterior right-hand portion of the head. Now *Cothurnocystis elizae* had no hydropore, but there is no reason to suppose that its heart and pericardium would be situated very differently from those of *Ceratocystis.* Working backwards from mitrates and forwards from *Ceratocystis,* therefore, we should expect to find the heart and pericardium of *Cothurnocystis elizae* in the posterior right-hand corner of the head, probably squashed between the marginal plates and the oesophagus.

The internal moulds of *Cothurnocystis elizae* strengthen this conclusion for, particularly in very large individuals, a distinct, spindle-shaped swelling is visible on the posterior right-hand surface of the internal mould (ht in figure 26*c*; compare plate 14, figures 127, 130). One end of this spindle runs leftwards towards the inferred position of the oesophageal opening. The other end runs rightwards towards the ventral right posterior corner of the head. This spindle-shaped swelling presumably represents the pericardium with its included heart, with the subendostylar vessel coming out of it leftwards, and the visceral vessel coming out of it rightwards. This supposed pericardium is much the same shape as the pericardium, with included heart, of a salp (compare Fedele 1934, figures 5, 6, 8, 9). It is also the same shape as the pericardium and heart of ascidians, except that in many of these the basic spindle-shape is bent into a V, probably so as to accommodate it better in the abdomen (figure 21).

Having thus circumstantially located the pericardium and heart on the natural mould of *Cothurnocystis elizae* it becomes possible to distinguish a cylindrical structure, mainly ventral to, but partly anterior to, the presumed pericardium, and to suggest that it represents the oesophagus, in the expected position just internal to the marginal plates of the posterior part of the body (figure 26*a*, *c*). Followed leftwards the oesophagus seems to turn upwards slightly, dorsal to the rectum, towards the previously inferred position of the opening of the oesophagus into the pharynx. After having received the visceral vessel from the heart at the right posterior angle of the head, the oesophagus would be expected to run forward along the right side of the right anterior coelom. The trace of this coelom on the internal mould gradually increases in depth forwards from the posterior right corner, or, in other words, the line of separation between the overlying pharynx and the right anterior coelom steadily ascends on the inner faces of the marginals, when followed forwards (Jefferies 1968, fig. 4). The deep anterior part of the right anterior coelom perhaps accommodated a stomach to which would be connected the oesophagus on the right and the intestine on the left, as suggested in figure 27.

Turning now to the reproductive system, the position of the gonoduct is probably indicated by a narrow ridge on the internal mould of some specimens of *Cothurnocystis elizae* (gd in figure 26*c*; plate 14, figures 128, 130, 134, 135). The most distal part of this ridge ran left of the rectum where both ran vertically upwards to the gonopore-anus left of the tail. Proximal to this vertical portion however, the ridge for the presumed gonoduct ran posterior to the rectum and can be followed, maintaining this relationship, slightly beyond the vertical suture between plates M_{1LV} and M_{1RV}, as shown in figure 26*a*, *c*. Farther rightwards than this the gonoductal and rectal ridges on the internal mould fuse into a common gonorectal ridge, which runs into the cavity of the right anterior coelom.

Now in *Ceratocystis* the gonopore and anus are separate and are both situated just right of the tail with the gonopore right of the anus (Jefferies 1969, text-fig. 2*d*; 1975, fig. 6*b*). In the evolution of *Cothurnocystis* from *Ceratocystis* the gonopore-anus had migrated leftwards from the primitive position, and so had come to lie left of the tail, in the outwash current from the gill slits. If the gonoduct of *Cothurnocystis elizae* continued to run posterior to the rectum farther rightwards than where their separate ridges can be distinguished on the natural moulds, then the gonoduct would enter the right anterior coelom right of the rectum i.e. rectum and gonoduct would have the same mutual relationship at this point as the anus and gonopore of *Ceratocystis*. It follows from this that the gonad would probably have been situated inside the loop of the non-pharyngeal gut in *Cothurnocystis elizae* (g in figure 27*c*), as presumably in *Ceratocystis* also. This is the position of the gonads in enterogonous tunicates such as *Ciona*. According to Berrill (1936, p. 58) the enterogonous condition of ascidians is more primitive than the pleurogonous condition, in which the gonads are in the wall of the atrium. The cornutes confirm Berrill's conclusion.

It follows that the mitrates were probably enterogonous also, with the gonad or gonads inside the loop of the non-pharyngeal gut, inside the cavity of the right anterior coelom, as suggested above (figure 18*c*). We have already mentioned evidence that the gonoduct of *Mitrocystella incipiens miloni* emerged from the cavity of the right anterior coelom to run dorsal to the left pharynx into the left atrium (gd in figures 17, 20). This strengthened the conclusion that the gonads were situated in the right anterior coelom but in itself was an exceptional condition. In most mitrates the gonoduct would presumably run along the surface of the rectum with its terminal portion running left of the rectum as in cornutes. In the evolution of tunicates from mitrates the terminal portions of the rectum and gonoduct have rotated through about 140°, associated with the backward migration of the non-pharyngeal gut from its mitrate position dorsal to the pharynx. This rotation resulted in the end of the gonoduct coming to be right of the rectum in tunicates (Jefferies 1969, p. 507).

The location in cornutes of the neural gland (or hypophysis or Seessel's pouch) and its duct, will now be considered. It is likely that the neural gland of tunicates is homologous with the axial gland of echinoderms (Jefferies 1969, pp. 513–515). For both probably have an endocrine function (Godeaux 1964; Carlisle 1953, for the neural gland; Millott 1967 for the axial gland). Both mainly function in expelling the degeneration products of coelomocytes (Godeaux 1964, Pérès 1943, Millar 1953 for the neural gland; Millott 1966 for the axial gland), and both are connected by strands of tissue to the gonads (dorsal strand of tunicates, genital strand of echinoderms). As with the heart, therefore, the problem of where the neural gland and its duct were situated in cornutes can be approached from two opposite directions.

The most direct evidence comes from *Ceratocystis* which has a hydropore. By way of this the axial sinus of the axial gland would presumably have issued to the outside, which suggests that the axial sinus and axial gland would both have been located in the right anterior coelom. No other known cornute has a hydropore. This perhaps means that in all cornutes except *Ceratocystis* the axial sinus opened into the left and only pharynx. In other words the axial sinus had become the duct of the neural gland.

In *Placocystites forbesianus* the duct of the neural gland seems to have opened into the left pharynx from the anterior end of the cavity of the right anterior coelom, anterior to the left peripharyngeal band. The gland itself was probably situated beneath the brain, and would be connected to the floor of the prosencephalon, as argued above. If the right pharynx is mentally removed to obtain the cornute condition then the duct would have opened into the left pharynx at the anterior end of the right anterior coelom, anterior to the peripharyngeal band, immediately behind the velum (figure 27*a*, *c*).

The pharynx is indicated by a characteristic sculpture on the internal moulds of *Cothurnocystis elizae*. This sculpture, found on the internal faces of the marginal plates of some large individuals, consists of horizontal striae (ph s in figure 26*a*, *c*; plate 14, figure 130), crossed perpendicularly by corrugations (pl ph in plate 14, figures 127, 132; Jefferies 1969, pl. 98, fig. 4). The horizontal striae are probably growth lines, indicating that the marginal plates grew in height after they had ceased to grow in length. The corrugations, here recorded for the first time, are probably homologous with the pharyngeal corrugations of mitrates.

The posterior coelom of *Cothurnocystis elizae* is smoothly sculptured on the internal mould. Anteriorly it would be in contact with the pharynx, which is marked, on the internal surface of marginal plates M_{1LV} and M_{1RV}, by the characteristic pharyngeal sculpture. There are two funnel-shaped areas, one on the left and one on the right of the posterior coelom, which probably represent openings between the posterior coelom and the pharynx (l ph-ep op and r ph-ep op in figure 26*c*; see also plate 14, figures 127, 131, 134). Since the posterior coelom would correspond to the left epicardium of a mitrate, the left opening of *Cothurnocystis* would correspond to the left adlateral pharyngo-epicardial opening of *Placocystites* while the right opening of *Cothurnocystis* would correspond to the left admedian opening of *Placocystites*.

In reconstructing the cornute pharynx it is necessary to imagine an anatomy which would allow the animal to feed by a pharyngeal mucous trap in its single left pharynx and which also, by sudden appearance of the right pharynx, would give rise to the reconstructed tunicate-like pharynx of mitrates. The picture so obtained is very hypothetical, but the cornute pharynx has such a strategic importance in chordate evolution that an attempt to visualize it is justified.

Cornutes presumably had a non-bilateral endostyle, to produce mucus, and a left peripharyngeal band to carry the mucus away from the endostyle round the walls of the left pharynx. They would have had no right peripharyngeal band as such, no right side to the endostyle, and no flagellated endostylar floor such as serves in tunicates and amphioxus to separate the left stream of mucus from the right. Presumably they possessed an oesophageal band to pull the mucus into the oesophagus. By analogy with the continuous alimentary ciliated loop of tunicates, which probably existed in mitrates also, it is likely that the left peripharyngeal band in cornutes was connected to the oesophageal band by an intermediate band of cilia which can best be called the protoretropharyngeal band. Indeed at least the anterior part of this protoretropharyngeal band would presumably have existed in the immediate cornute ancestors of mitrates, to give rise to the right peripharyngeal band when the right pharynx arose. For without a right peripharyngeal band the right pharynx of mitrates could not have functioned.

Furthermore the cornute pharynx could probably not have functioned without a complete protoretropharyngeal band, running the whole way from endostyle to oesophagus, to carry the posterior ends of mucous strands into the oesophagus. For the branchial current, flowing towards the gill slits, would not carry the strands towards the oesophageal opening.

The endostyle of a cornute could have been a transverse band of alternating gland strips and ciliated strips, like the transverse endostyle of larval acraniates, which are the only living chordates which feed by using left gill slits alone. Such a transverse endostyle would function in cornutes by producing mucus from its left end. It could function in the first mitrate by producing mucus from the right end also. It could convert itself into the more efficient bilateral endostyle deduced to have existed in *Placocystites* by growing backwards in a V, as happens in the ontogeny of amphioxus. Ciliated pharyngeal floor anterior to the transverse endostyle

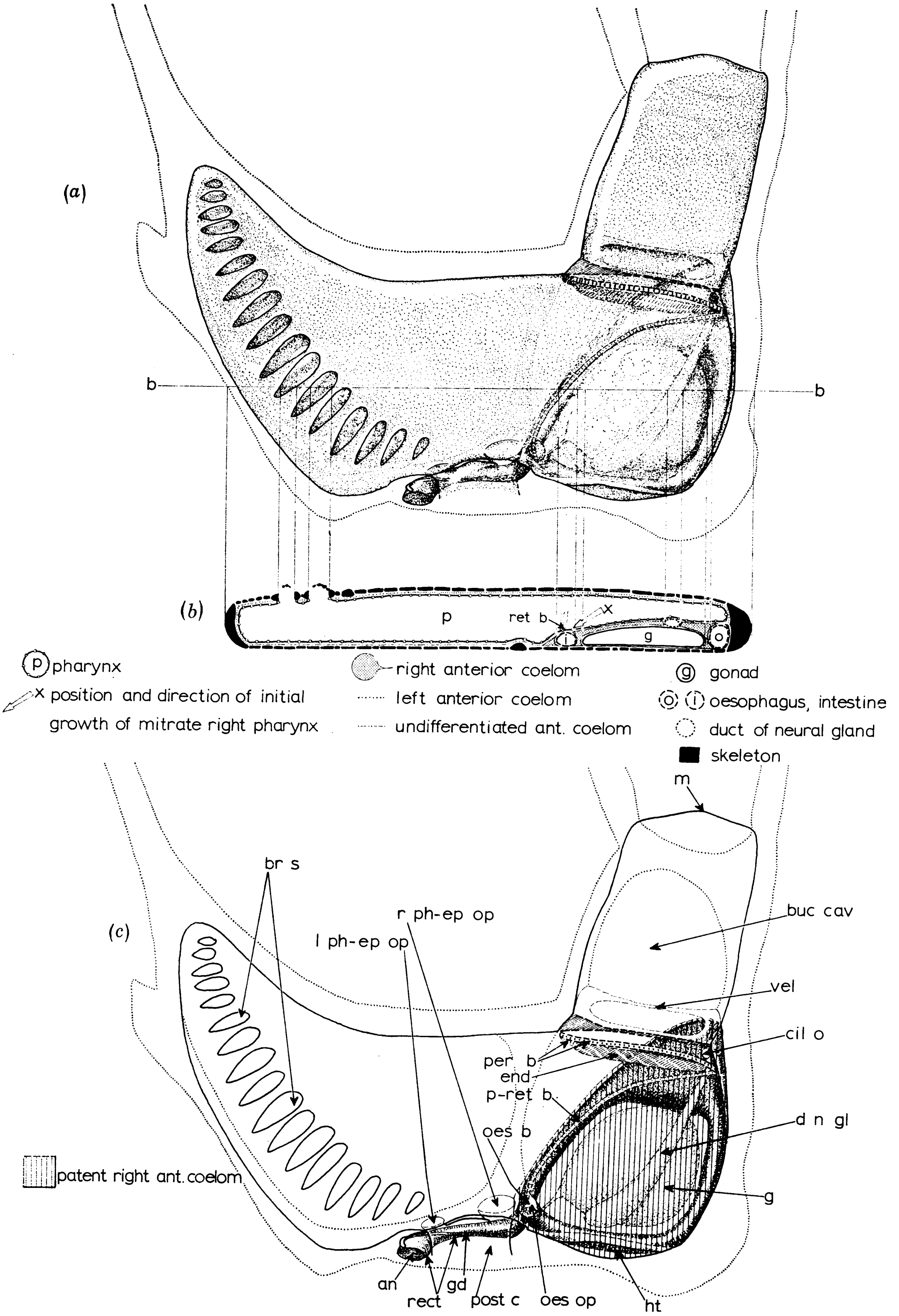

FIGURE 27. Reconstruction of the soft parts in the head of *Cothurnocystis elizae*. (*a*) Visual representation. (*b*) Transverse section through b–b. (*c*) Diagramatic representation (ret b in *b* refers to the protoretropharyngeal band (p-ret b)). After first appearing at x in the origin of the mitrates the right pharynx would expand between the protoretropharyngeal band and the intestine, then penetrate rightwards and posteriorly beneath the latter and the other viscera, lifting them up, squashing them against the ceiling, and pushing them into a median position (cf. figure 15).

would become the flagellated floor of the bilateral endostyle. Such a V-shaped endostyle exists in the ontogeny of both salps and amphioxus (figures 14, 22f). This suggests that it also existed in the ontogeny of their latest common ancestor, which would have been a mitrate.

The postulated pharyngeal anatomy of a cornute is therefore as shown in figure 27 for *Cothurnocystis*. The transverse endostyle would be situated on the floor of the pharynx shortly behind the velum. At its left end it would give rise to the peripharyngeal band which ran across the ceiling of the pharynx and passed into the proto-retropharyngeal band. This would run across the floor of the pharynx to connect with the oesophageal band at the oesophageal opening. The protoretropharyngeal band would be situated where it could give rise in a mitrate to the right peripharyngeal band (round the right pharynx) the right marginal band (right of the endostyle) and the retropharyngeal band (behind the endostyle). This would happen by the pouching out of the right pharynx just right of it, under the cavity and contents of the right anterior coelom, and by the subsequent backward growth of the endostyle, in a V, on the left side of the protoretropharyngeal band. The neural gland would open into the left pharynx just anterior to the peripharyngeal band at the anterior end of the cavity of the right anterior coelom, and just anterior to the meeting place of left peripharyngeal band and protoretropharyngeal band as in a mitrate. The cornute pharynx so deduced can only be a hypothesis. Perhaps it can be tested by observing the ontogeny of the alimentary ciliated loop in living tunicates. In some tunicates the left peripharyngeal band is known to arise before the right one in ontogeny (Professor Carlisle, personal communication).

A number of features probably related to the nervous system can be discerned on the internal moulds of *Cothurnocystis elizae* just anterior to the brain (figure 26; plate 14, figures 127, 130 to 133). There is a pair of pyriform bodies anterior to which are groups of intra-skeletal cones. Diverging outwards and downwards, partly from the pyriform bodies and partly from the region median to these bodies, are ridges on the internal mould which probably represent what we previously called the median-line nerves (see for example, Jefferies 1968, p. 264; Jefferies & Prokop 1972, p. 89). The left median-line nerve seems to have passed under the ventral surfaces of the gonoduct and rectum in *Cothurnocystis elizae*, but cannot be traced thereafter. The ridge representing the right median-line nerve goes towards the right anterior coelom, but cannot be followed as great a distance as the left one. One specimen shows a delicate ridge which could be the trace of a cardiac nerve running to the heart and pericardium (card n in figure 26; plate 14, figures 127, 133).

As to interpretation, the pyriform bodies are presumably equivalent to those of mitrates and would therefore represent the trigeminal ganglia. The intra-skeletal cones correspond to the cones of the precerebral knot of mitrates. They would represent the places where presumed olfactory fibres running from the buccal cavity, and also terminalis fibres from the skin of the head, came out of the skeleton on their way to the brain. In *Ceratocystis perneri* these cones can be more precisely related to the brain than in *Cothurnocystis*, and their identity with the cones of the mitrate precerebral knot can thus be confirmed (Jefferies 1969, pp. 518–521, 'anterior brain' = precerebral knot). The parts of the median-line nerves emerging from the brain median to the pyriform bodies would probably correspond to the bases of the transpharyngeal optic nerves of mitrates. The parts of the median-line nerves coming out of the pyriform bodies would perhaps represent the sensory fibres forming the subalimentary component of the palmar nerves of mitrates. It seems likely that the right anterior coelom of cornutes would be supplied mostly or completely from the right side of the brain, and that the possible delicate cardiac nerve of *Cothurnocystis elizae* was part of this supply. The visceral nerve of ascidians tends to arise from the right side of the adult ganglion of ascidians (Metcalf 1900, p. 533) which may possibly be an inheritance from the cornute conditions.

To sum up, therefore, comparison with mitrates allows cornutes to be interpreted in more detail than before. Some of the detailed interpretations seem to be partly confirmed by examining the internal moulds of cornutes. This is true of the location of heart and pericardium, the openings of the posterior coelom or left epicardium into the pharynx, the general position of the gonad and the positions of parts of the non-pharyngeal gut and cranial nerves. Other deductions about the cornute condition, drawn purely by comparison with mitrates or modern protochordates, are without direct evidence and presented as hypotheses which are worth putting because of the central importance of cornutes for chordate comparative anatomy. Such hypotheses include the suggested positions of the ciliated bands and endostyle in the pharynx and of the neural gland and its duct.

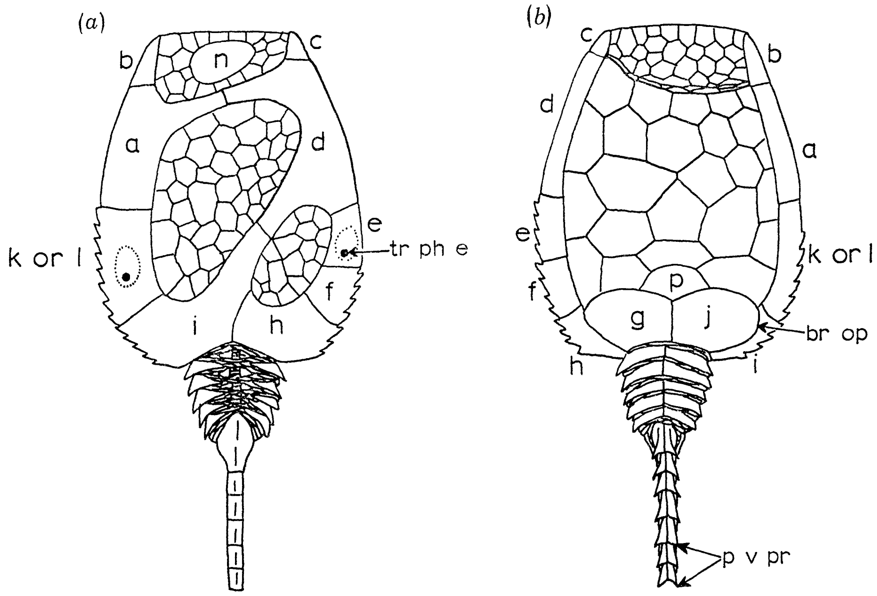

FIGURE 28. The animal q, being the reconstructed latest common ancestor of *Lagynocystis*, *Peltocystis* and *Chinianocarpos*, and therefore the latest common ancestor of all living chordates: Compare also Jefferies (1973, fig. 4). Letters refer to the comparative plate notation based on *Reticulocarpos*. (*a*) Dorsal aspect. (*b*) Ventral aspect.

8. THE PHYLETIC POSITION OF *PLACOCYSTITES* AND THE EVOLUTIONARY DIVERGENCE OF THE LIVING CHORDATE SUBPHYLA

It is possible to reconstruct the phylogeny of the mitrates in some detail. The resulting diagram records the evolutionary divergence of the stem groups of the chordate subphyla from each other. In particular it bears on the evolution of the stem vertebrates. All living adult chordates have right gill slits as well as left ones. Their latest common ancestor is therefore likely to have been a mitrate rather than a cornute. We have worked out the phylogeny of the mitrates by using Hennigian methods, as discussed in the introduction.

One of us (Jefferies 1973, p. 421) has reconstructed the latest common ancestor of the three rather primitive mitrates *Lagynocystis*, *Peltocystis* and *Chinianocarpos*. This reconstructed animal which for convenience we refer to as q, is shown as we now conceive it in figure 28. In contrast to fig. 4 of Jefferies (1973) we have introduced a right posterior patch of integument in the dorsal head skeleton. We have observed such a patch in a new species of *Chinianocarpos* from Morocco (*Mitrocystites* sp of Chauvel 1971, fig. 3*a*, *b*; Moroccan *Chinianocarpos*, figures 29, 30). It is a cornute-like feature, and therefore probably primitive, as is confirmed by the fact that it corresponds in position to the right centro-dorsal plate of *Peltocystis*. The principles used in reconstructing this animal are the same as those used in reconstructing the latest common ancestor of Petromyzontids and gnathostomes (see below).

The hypothetical animal q would have had a small head, about 10 mm long, dorsally plane and ventrally convex. The dorsal surface of the head would have had three patches of integument – oral, central and right posterior. These three patches of integument would be separated by two bars – an oral bar, formed of plates a and d and somewhat more anterior on the right than the left, and an oblique bar, bearing the oblique ridge internally, and much more anterior on the right than on the left. A specially large plate n would exist within the oral integument. There would be transpharyngeal eyes situated on the dorsal surface of the head, but there would be no dorsal touch-sensory branches of the trigeminal (n_4 and n_5) such as exist in *Mitrocystites mitra*, *Mitrocystella* and *Placocystites*. There would be no external lateral line. The ventral surface of the head would mainly be covered by plated integument which would have been particularly flexible anteriorly. Paired gill openings would be present near the right and left posterior angles of the head. There would be nine dorsal marginal plates – a, b, c, d, e, f, h, i and (k or l), and other plates as indicated. The tail would be divided into, fore, mid and hind portions with a styloid in the mid tail and dorsal ossicles and paired ventral plates in the hind tail. The fore tail would have four series of major plates, separated by integument with intercalary plates. No ventral plates would be sutured to the styloid. Intercalary plates would exist on the imbricating membranes between the ventral plates throughout the length of the hind tail. There would be ventral bearing surfaces and posteroventral processes (p v pr) on the ventral plates of the hind tail, used for pressing against the mud when crawling backwards, but there would be no dorsal bearing surfaces on the dorsal ossicles. The arguments on which this reconstruction is based can be found in Jefferies (1973, pp. 420–421). Inside the head, q would have had: a right pharynx as well as a left one; right and left anterior coeloms with the patent cavity of the right anterior coelom suspended from the ceiling; a left posterior coelom (left epicardium) and probably a right one also; left and right atria but no median atrium; and a buccal cavity. q would be the latest common ancestor of the extant chordate subphyla, as well as the latest common ancestor of *Lagynocystis*, *Peltocystis* and *Chinianocarpos*. The phylogenetic position of q is indicated in figure 33.

Lagynocystis would have evolved from q by acquiring a median ventral atrium with a median ventral atrial opening. Also the head became much more elongate and the cranial nerves and brain were simplified. *Lagynocystis* retained many primitive features in its tail. The median ventral atrium and atrial opening were advanced features absent from q and connecting *Lagynocystis* with modern cephalochordates (Jefferies 1973, pp. 459–465).

Peltocystis and *Chinianocarpos* both differ in common from the hypothetical q by having bearing surfaces on the dorsal ossicles of the hind tail, no bearing surfaces on the ventral plates of the hind tail, and two pairs of ventral plates articulated with the styloid. These shared advanced features point to a line of common ancestry for these two forms subsequent to q. Within this line of common ancestry, motor end plates on the muscle blocks probably evolved, as explained below.

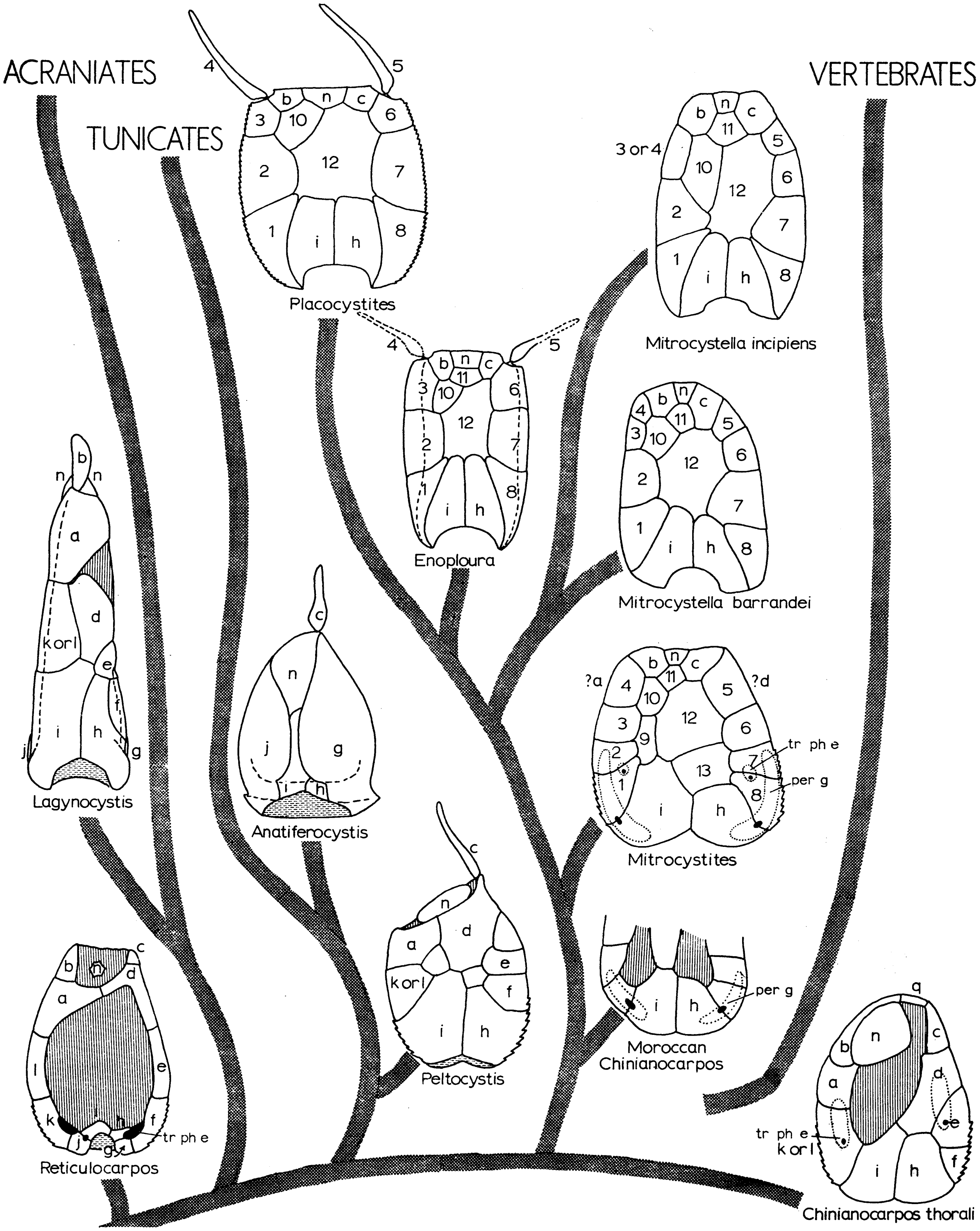

FIGURE 29. Suggested phylogenetic relations of the mitrates, the cornute *Reticulocarpos*, and the extant chordate subphyla; dorsal surfaces of the heads; a, b, c etc = plates in *Reticulocarpos* notation; 1, 2, 3 etc = plates in *Mitrocystites* notation; compare figure 30. *Anatiferocystis*, *Enoploura* and *Mitrocystella barrandei* after Ubaghs (1968).

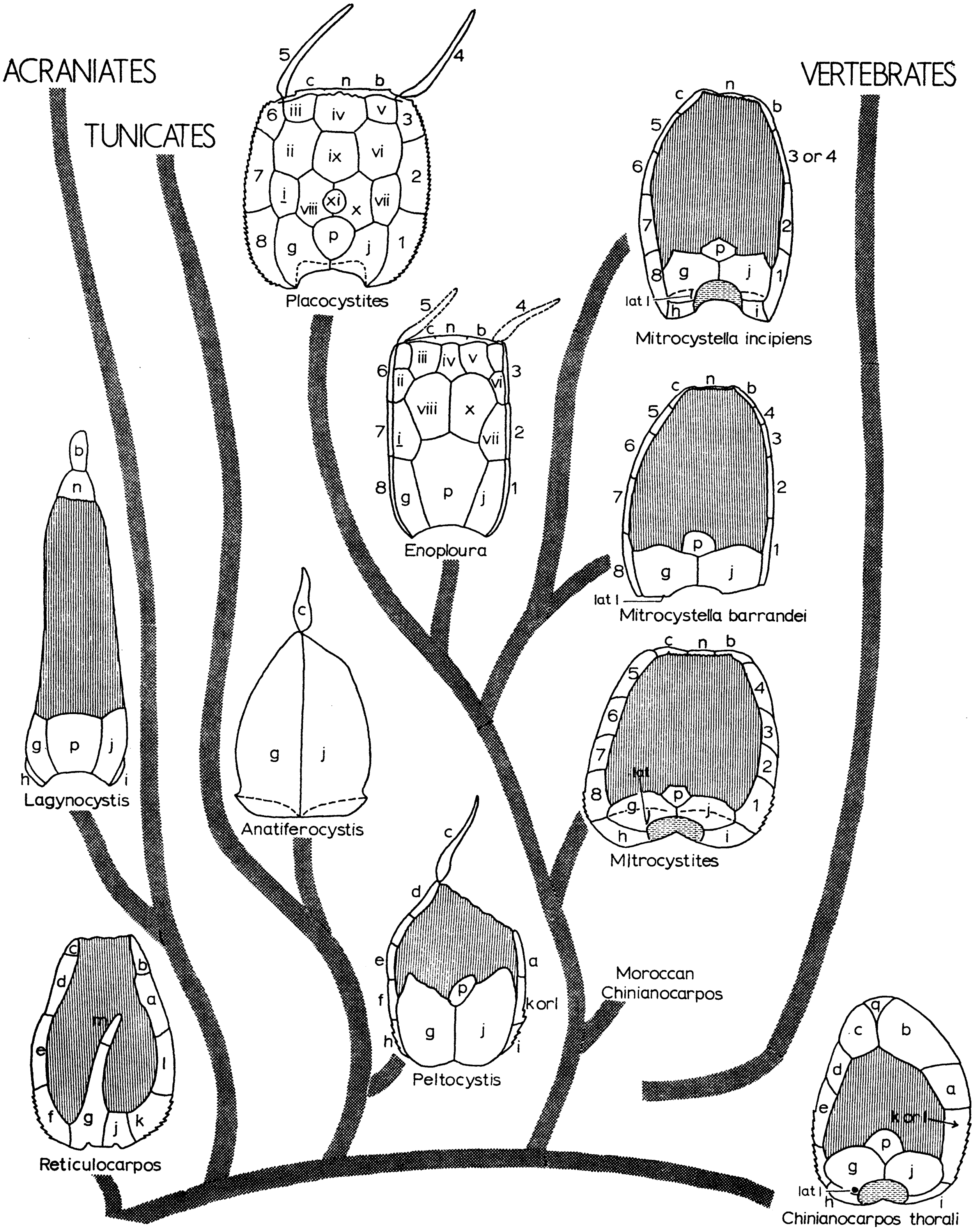

FIGURE 30. Phylogenetic relations of the mitrates, the cornute *Reticulocarpos* and the extant chordate subphyla. Ventral surfaces of heads. i, ii, iii etc = plates in *Placocystites* notation. For other symbols see figure 29.

Peltocystis differs from q, apart from tail features, by: the loss of plate b; the modification of plate c to form a spine; reduction of the oral integuments to form two separate centro-dorsal plates; and a great enlargement of the gill openings and adjacent plates. The genera *Balanocystites* and *Anatiferocystis*, placed together with *Peltocystis* in the suborder Peltocystida Jefferies 1973, resemble each other furthermore in that the ventral skeleton has grown over the dorsal skeleton so that the gill openings, as well as being very large, were dorsal (personal observation R.P.S.J.). Such dorsal gill openings resemble the condition in modern tunicates, to the stem group of which *Balanocystites* and *Anatiferocystis* therefore probably belonged.

Chinianocarpos thorali differs from its latest common ancestor with the Peltocystida in a number of ways. The most striking is that plates b and c have grown together to form a rigid lower lip functionally replacing the post-oral strut (plates a and d) which has broken down. Less obvious, but more important, is the presence of a lateral-line pit on the right posterior marginal (plate g = M_{1RV}). This lateral line is a new specialization in common with standard vertebrates (defined in introduction). The genus *Chinianocarpos*, as represented by its type species *C. thorali* from the South of France, seems to have no dorsal nerves n_4 or n_5.

Moroccan *Chinianocarpos*, which unfortunately is not well known, shows the rigid lower lip and the lateral-line pit of *Chinianocarpos thorali*. On the dorsal surface, however, it has openings corresponding in position to those for nerves n_4 and n_5 in *Mitrocystites mitra*, but has no external transpharyngeal eyes. We have already argued that n_4 and n_5 were the ophthalmicus superficialis and profundus branches of the trigeminal, so, if it possessed these nerves, Moroccan *Chinianocarpos* was more closely related to standard vertebrates than *Chinianocarpos thorali* was. The standard vertebrates are more likely to have arisen from the Mitrocystitida, which retained a lateral line, than from the Anomalocystitida, which had lost it.

Moroccan *Chinianocarpos* therefore shares the rigid lower lip of *Ch. thorali* with advanced features (n_4 and n_5) found in *Mitrocystites*, *Mitrocystella* and *Placocystites* but not in *Ch. thorali*. This suggests that the rigid lower lip as seen in *Chinianocarpos* had existed in the ancestors of *Mitrocystites*, *Mitrocystella* and *Placocystites*, but had been lost in these genera themselves. Thus the flexible lower lip as seen in *Mitrocystella* and *Mitrocystites* is probably not homologous with the flexible lower lip primitive to the mitrates and found in *Peltocystis*, *Lagynocystis* or the cornute *Reticulocarpos*. This is confirmed by the fact that the condition of the rigid upper lip seen in *Mitrocystites*, *Mitrocystella* and *Placocystites*, with plate n rigidly sutured to plates b and c, can more easily be derived from the *Chinianocarpos* condition than direct from the primitive rigid upper lip of *Peltocystis*, with plate a sutured to d and plate n loose in the upper lip (contrast Jefferies 1973, p. 421).

The genera *Mitrocystella* and *Mitrocystites*, commonly placed in the sub-order Mitrocystitida, and *Placocystites* and *Enoploura*, placed together in the Anomalocystitida, are all connected together by a number of features which *Chinianocarpos thorali* does not share. (Moroccan *Chinianocarpos* is too badly known to compare most features beyond what has been said above.) Such features in common include: two extra left marginal plates and one right one; the suturing of plate n with plates a and b dorsal to the mouth; the loss of the dorsal integument; the loss of the rigid lower lip formed by suturing a and b; the presence of many oral plates in a loose, lower-lip integument; and greater size, with a head length of 20–30 mm instead of about 10 mm. In addition *Mitrocystites* and *Mitrocystella* have the lateral line developed as a groove instead of a pit. (Anomalocystitida, as already mentioned, have no lateral line.) The latest common ancestor of *Mitrocystites*, *Mitrocystella* and the Anomalocystida was therefore more recent than their latest common ancestor with *Chinianocarpos thorali* and within this line of exclusive common ancestry all these common distinctive features were probably acquired.

Mitrocystites shares the external dorsal openings of n_4 and n_5 with the Moroccan *Chinianocarpos.* Both differ in this respect, not only from *Chinianocarpos thorali* which was more primitive than either, but also from *Mitrocystella* and the Anomalocystitida. *Placocystites,* among the latter, possesses n_4 and n_5 but they led into peripheral canals, precisely as in *Mitrocystella,* and the same is presumably true of all other Anomalocystitida. Thus it seems likely that external peripheral grooves supplied by n_4 and n_5, as seen in *Mitrocystites* and probably in the Moroccan *Chinianocarpos,* are more primitive than peripheral canals. Such grooves became buried beneath a thin layer of calcite to produce the peripheral canals of *Mitrocystella* and the Anomalocystitida. The burial of the peripheral grooves indicates a line of common ancestry of *Mitrocystella* and the Anomalocystitida which *Mitrocystites* did not share. Such a line of exclusive common ancestry probably also saw the loss of a number of centro-dorsal plates. For *Mitrocystites mitra* has five such, and this is more like *Chinianocarpos* and the cornutes, and therefore more primitive, than in *Mitrocystella* or most Anomalocystitida which have only three, or *Placocystites forbesianus* which has only two. If, however, *Mitrocystites* thus represents the primitive sister group of *Mitrocystella* plus the Anomalocystitida, then the dorsal longitudinal canal in the hind tail must have evolved twice. For it is present in *Mitrocystites* and *Mitrocystella* but not in any other mitrates so far as known, and in particular not in *Chinianocarpos thorali* nor in *Placocystites.*

A great number of features separate all known Anomalocystitida from *Mitrocystella.* These include: oral spines modified from marginals 4 and 5 (? = a and d); absence of the external lateral line; cuesta-like ribs on the dorsal and ventral surfaces of the head, rather than on the ventral or ventro-lateral surfaces only; and rigid ventral armour. As already explained, these differences can be interpreted as adaptations for shallow burrowing. They were probably acquired within a line of common ancestry which all Anomalocystitida share, but which *Mitrocystella* did not. They imply that *Mitrocystella* is the primitive sister group of the Anomalocystitida. It should be mentioned that in some ways the species of this genus which has been best studied (i.e. *Mitrocystella incipiens* from the Llandeilo) differs from the earlier *Mitrocystella barrandei* (Llanvirn). Thus *M. incipiens* seems to have lost a plate near the anterior left angle of the head (either 3 or 4) though this plate occurs in *M. barrandei, Mitrocystites mitra* and the Anomalocystitida. Also *M. incipiens* has extensive cuesta-like ribbing on the postero-ventral surface of the head, while *M. barrandei* is smooth in that place like *Mitrocystites mitra.* This postero-ventral cuesta-like ribbing is almost certainly a convergence between *M. incipiens* and Anomalocystitida, rather than a primitive resemblance. The latest common ancestor of *Mitrocystella* and the Anomalocystida would resemble *Mitrocystella barrandei* in that it would retain both 3 and 4 and would be smooth postero-ventrally. Also it would have no dorsal longitudinal canal in the hind tail.

The resulting phylogenetic tree (figures 29, 30) implies that the suborders of Mitrata are not all of the same status. In particular the order Mitrocystitida (represented by *Chinianocarpos, Mitrocystites* and *Mitrocystella*) is ancestral to the Anomalocystitida (represented by *Placocystites* and *Enoploura*) in the sense that some members of it are closer related to the Anomalocystitida than others are. The major groups of mitrates ought eventually to be redefined to conform with the reconstructed phylogeny, but we do not intend to do this yet.

In a previous paper (Jefferies 1973, p. 463) we argued that tunicates are probably closer related to vertebrates than cephalochordates are. Our argument was that in tunicates and vertebrates the tail muscles are innervated by motor end plates. This is unlike cephalochordates which innervate the equivalent muscles by means of extensions of the muscle cells passing to the dorsal nerve cord. Such muscular extensions are echinoderm-like and therefore probably primitive for chordates. Motor end plates were probably acquired, therefore, within the line of common evolution of tunicates and vertebrates which cephalochordates did not share. As mentioned already, this would also be the segment of the phylogenetic tree leading to the latest common ancestor of the Peltocystida and Mitrocystitida, after the Lagynocystida had separated.

As concerns timing, q would be older than the Lower Arenig (earliest Ordovician) in which *Chinianocarpos thorali*, *Peltocystis* and the earliest standard vertebrate *Anatolepis heintzi* (figure 2) occur. *Chinianocarpos* was probably a stem vertebrate and *Peltocystis* a stem tunicate. The vertebrates, in both broad and standard senses, would therefore already have been separate from the tunicates at the beginning of the Ordovician. This implies that cephalochordates were also distinct by then, since tunicates and vertebrates probably shared a line of of common ancestry later than q which the cephalochordates did not. The divergence of the extant chordate subphyla from each other must be later than the divergence of chordates from echinoderms. And this latter event was probably later than the beginning of the Cambrian, since early chordates share with echinoderms a skeleton homologous in both phyla which does not occur in the hemichordates and which is unlikely to have evolved before the beginning of the Cambrian, when hard skeletons commence. The divergence of the living chordate subphyla from each other therefore would have happened during the Cambrian. Other time relations of the phylogeny of the mitrates are suggested in figure 2. In general it is possible to give a minimum age for a divergence, which must be as old as, or older than, the rocks in which its products are first found. To give a maximum age for a divergence is seldom possible. The earliest known member of the Anomalocystitida is an undescribed form from the Llandeilo of Bohemia (A1 in figure 2; personal observation by R.P.S.J. in collaboration with R. J. Prokop). The separation of Anomalocystitida from *Mitrocystella* must be older than that horizon.

9. The evolution of standard vertebrates from mitrates

Zoologists who have reconstructed the ancestral vertebrate have fallen into two schools which can be called antisegmentationist and segmentationist.

The antisegmentationist school is represented by such workers as Froriep (1882, 1902), Veit (1947), Romer (1972) and Starck (1963, 1975). They consider that the distinction between head and tail was a primitive feature of vertebrate organization and that branchiomery was not primitively related to myomery. Their imagined protovertebrate, which we call 'Froriep's animal', closely resembles a tunicate tadpole, and Romer's conception of it is shown in figure 31. In our opinion Froriep's animal is essentially a mitrate.

The segmentationist school, on the other hand, considers that the first vertebrates were formed of segments which were exact or almost exact serial equivalents, except that the more anterior ones were separated by gill slits. This conception of the protovertebrate was developed by many famous anatomists including van Wijhe (1883), Koltzoff (1901), Damas (1944) and Goodrich (1918; 1930; figure 32 herein). We shall call it 'the segmentationists' animal'. Figure 32, after Goodrich, can be said to illustrate approximately 'the segmentationists' animal' although Goodrich himself only put this figure forward as a generalized scheme of the selachian head. Also the figure shows jaws which the segmentationists' animal would have lacked.

In our view the assertions of the segmentationists and antisegmentationists are largely compatible. It is likely that Froriep's animal, a mitrate, was ancestral to the segmentationists' animal which in turn was ancestral to all living vertebrates, or possibly to all living vertebrates except the myxinoids. Amphioxus was derived, independently to the standard vertebrates, from a mitrate with a clearly distinct head and tail. We did not formerly believe that classical segmentationist views could be reconciled either with the antisegmentationist position, or with the calcichordates (Jefferies 1968, pp. 300–302).

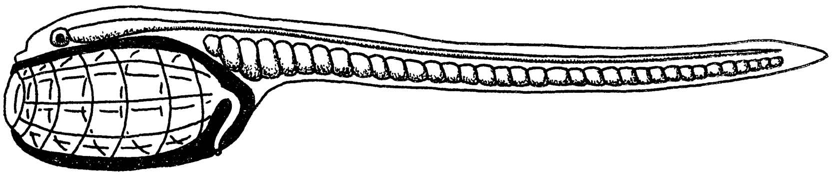

FIGURE 31. Romer's 'somatico-visceral animal' (after 1972, fig. 8*a*). This is a representation of the imagined tadpole-like protovertebrate of the antisegmentationists, referred to in the text as Froriep's animal. It is very like a mitrate.

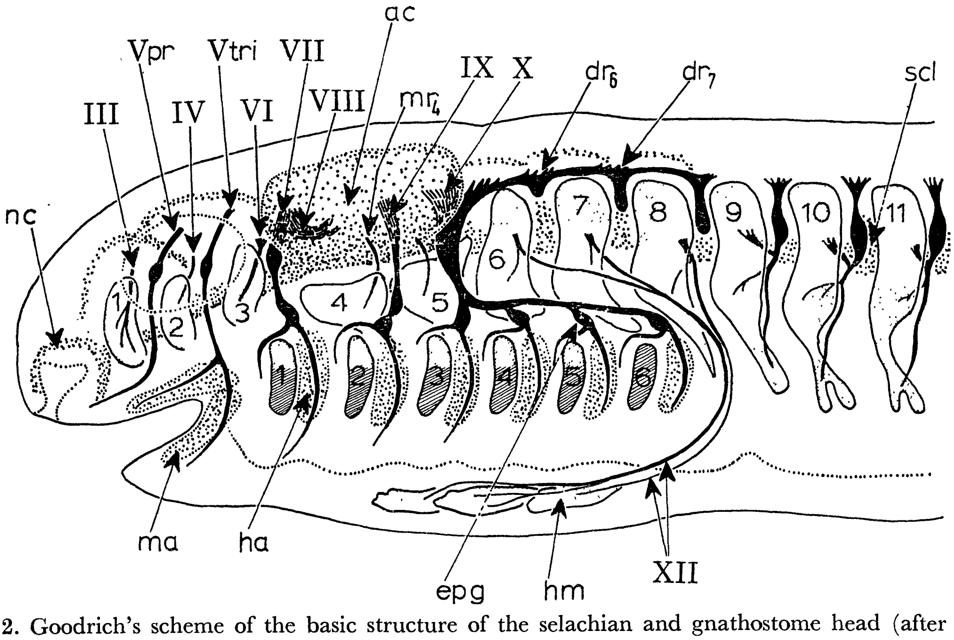

FIGURE 32. Goodrich's scheme of the basic structure of the selachian and gnathostome head (after Goodrich 1930, p. 240). Apart from the presence of jaws this can be taken as representing the imagined uniformly segmented protovertebrate of the segmentationists. 1, 2, 3–11 = first to eleventh somites; 1–6 = spiracle and normal gill slits; III–XII cranial nerves omitting the olfactory (I) terminalis (O) optic (II) and accessory (XI); V pr and V tri are the profundus and 'true' trigeminal parts of the trigeminal complex, conceived as intersegmental between somites 1 and 2, and 2 and 3. ac = auditory capsule; dr$_6$, dr$_7$ = dorsal roots posterior to somites 6 and 7. epg = epibranchial ganglion; ha = hyoid arch; hm = hypoglossal musculature; nc = nasal capsule; ma = mandibular arch; mr$_4$ = motor or ventral root to the fourth somite.

The latest common ancestor of lampreys and gnathostomes (animal x, figure 35, facing p. 316), can be reconstructed by assuming the phylogenetic relations with mitrates shown in figure 33. The animal so reconstructed does not much differ from the segmentationists' animal but represents a conceptual advance since features derived from the mitrate head (colour) can be distinguished from those derived from the mitrate tail (black). Such features as the kidney and its duct, or the oculo-motor muscles, could not have existed as such in mitrates, but we believe that we can indicate whether they were elaborated from mitrate tail material or head material, and they are coloured accordingly.

In reconstructing x we pay special attention to *Placocystites* and *Mitrocystella* since these forms are well known and belong to the particular group of mitrates from which standard vertebrates probably descended. Like other authors we base our picture of primitive gnathostome embryology largely on sharks. We ignore the myxinoids in reconstructing x, because their phylogenetic position is so uncertain. However it is quite possible that myxinoids are the sister group of all other living vertebrates, including the lampreys.

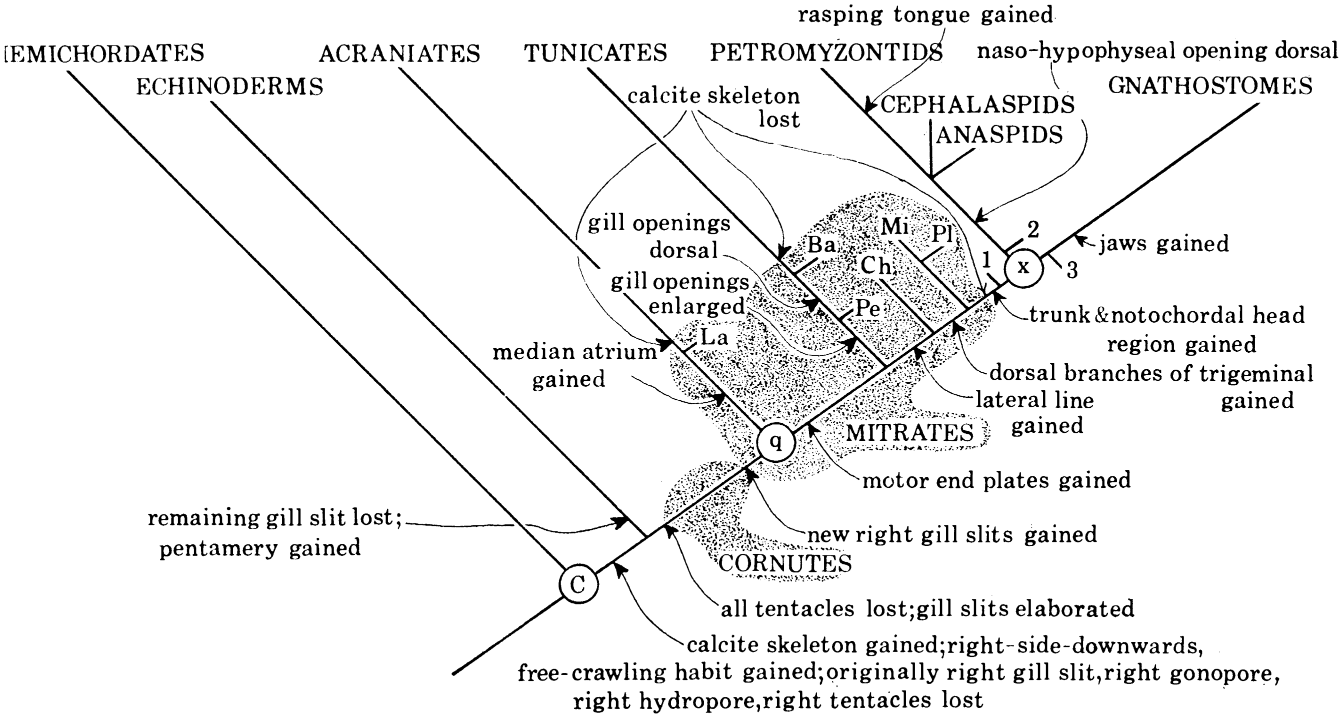

FIGURE 33. Phylogeny of the deuterostomes with evolutionary events. C is the postulated *Cephalodiscus*-like ancestor of all deuterostomes; q is shown in figure 28; x is shown in figure 35. 1, 2 and 3 represent three possible positions for the heterostracans. Ba = *Balanocystites lagenula* (a close relative of *Anatiferocystis* shown in figures 29, 30); Ch = *Chinianocarpos thorali*; La = *Lagynocystis pyramidalis*; Mi = *Mitrocystella incipiens*; Pe = *Peltocystis cornuta*; Pl = *Placocystites forbesianus*.

The principles used in reconstructing x are as follows. It would have possessed those features shared by Petromyzontida, gnathostomes, *Mitrocystella* and *Placocystites*. It would also have possessed those features which Petromyzontida and the gnathostomes have in common, but which the two mitrates did not have. If, however, a feature is found in one, but not both, of the two mentioned standard vertebrate groups, and also in one or both of the two selected mitrates, then it is likely to be a primitive feature which existed in x, having been inherited by it from the mitrates, but which was lost by one of the two daughter groups. A similar process of argument has already been used in reconstructing the latest common ancestor (q) of *Lagynocystis*, *Peltocystis* and *Chinianocarpos*, and therefore of acraniates, tunicates and vertebrates, in Jefferies (1973, p. 420, compare figure 28 herein). The hypothetical animals reconstructed in this manner are morphotypes in Nelson's sense (1970, p. 379). We signify that a feature is present in

Placocystites by Pl, in *Mitrocystella* by Mi, in Petromyzontida by La (for lamprey) and in gnathostomes by Sh (for shark).

Notochord and somites of x. The animal x would have possessed a notochord (Pl, Mi, La, Sh). In the embryo of x the paired premandibular somites would have existed anterior to the notochord (adult Pl, adult Mi, embryo La, embryo Sh). The mandibular somites in the embryo of x would have been situated on either side of the front end of the notochord (La, Sh, they were anterior to the notochord in Pl, Mi). The post-mandibular somites in the *embryo* of x would have formed a complete series in each side of the notochord, extending back from the mandibular somite to the posterior end of the tail (Pl adult, Mi adult, La embryo, Sh embryo). The premandibular pair of somites would have produced the extrinsic eye muscles, except for the superior oblique (posterior oblique of cyclostomes) and the external rectus (La, Sh, not Pl nor Mi). The mandibular pair of somites would have produced the superior oblique eye muscles (La, Sh, not Pl nor Mi) and also the muscles of the velum and mouth (La, Sh, probably Pl and Mi). These buccal and velar muscles would have arisen equally from left and right mandibular somites, rather than predominantly from the left one (La, Sh, probably unlike Pl or Mi). The hyoidean pair of somites would produce the paired external rectus muscles of the eye (La, Sh, not Pl nor Mi), but would otherwise largely be suppressed by the otic capsule (La, Sh, not Pl nor Mi). The post-hyoidean somites would all be developed as muscle blocks in the adult (La, Mi, Pl, but not Sh).

Gill slits. The gill slits, including the homologue of the spiracle, would be ventral to the anterior part of the muscle-block series (La, Sh, but not Pl nor Mi), with the most anterior one between the mandibular and hyoidean somites (La, Sh, but not Pl nor Mi). There may have been about 8 gill slits on each side (La, 6 in primitive sharks, no information for Pl nor Mi). It is likely that each gill bar was ventral to a muscle block or that such a situation had existed in the post-mitrate immediate ancestors of x (Sh embryo, La embryo, see argument in Damas 1944, pp. 222–225 and figure 34 herein; Koltzoff 1901, p. 434, not Pl nor Mi). Supposing, for purposes of argument, that eight gill slits existed, the most posterior would have been situated between somites 9 and 10, if the premandibular somite is counted as somite 1 (La embryo, Damas 1944, p. 204; Sh embryo, de Beer 1922, p. 473; not Pl nor Mi). The gill slits perhaps opened into paired opercular cavities, rather than direct to the outside (atria of Mi, Pl, opercular cavities of many gnathostomes, but not La nor Sh).

Pericardium and Blood Systems. The suprabranchial portions of somites 3 to 9 (assuming 8 gill slits) would presumably send ventral extensions down each gill bar, this being the reason why the gill slits and myocommata coincided in the branchial region. Ventral to the gill slits these extensions would fuse with each other and with the ventral parts of the mandibular somite to form the pericardium (La, Sh, not Pl nor Mi where the pericardium, being inside the head, was presumably formed entirely by the mandibular somites). The heart was presumably situated in the pericardium posterior to the gill bars (La, Sh, but not Pl nor Mi where it would have been anterior to them). It would have forced blood into a ventral aorta and up the gill bars (i.e. afferent and efferent vessels) to the dorsal aorta and so into the trunk (La, Sh, no information in Pl nor Mi). (It is a very curious fact that in the myxinoid *Bdellostoma* the heart in very young embryos is anterior to the gill slits and branchial vessels, as it would have been in a mitrate (Pasteels in Grassé 1958, p. 137).)

Trunk Region. The non-pharyngeal gut, gonad or gonads, and other viscera of x would be posterior to the pharynx, not dorsal to it, and the anus and gonopore would open into a cloaca in the ventral mid-line, i.e. there would have been a trunk region (La, Sh, not Pl nor Mi). The non-pharyngeal gut and gonad would be contained in a post-pharyngeal, perivisceral coelom (La, Sh, not Pl nor Mi). This would probably be formed by the development of cavities in the ventral part of some of the mitrate tail somites, and the breakdown of the myocommata between these cavities, for this is what happens in the lamprey (Damas 1944, pp. 189–190). In sharks, the lateral plate from the beginning is not divided by myocommata. The lamprey mode of coelom development, by cavitation and fusion of somites, is therefore more like the adult mitrate condition, in which all the corresponding tail somites were presumably solid muscle blocks, separated from each other by complete dorso-ventral myocommata. It is therefore more likely to have existed in x than the shark mode of coelom development.

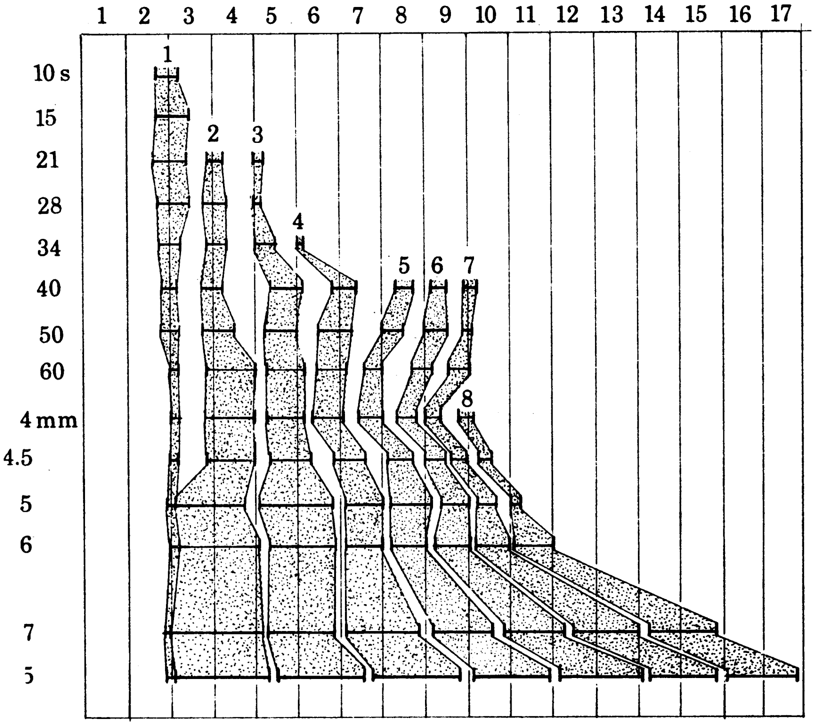

FIGURE 34. The relation between gill pouches and myocommata in the ontogeny of *Lampetra* (after Damas 1944, p. 223). The ordinal numbers of the somites are given along the top margin. The ontogenetic stage is given down the side (from 10 somite stage to total length 125 mm). The positions of gill pouches 1 to 8 at these different stages are compared with the position of the somites. Damas believed that there was a fundamental topographical correspondence between the gill pouches and the myocommata of the branchial region on the following grounds: the third somite was observed to grow ventralwards between the first and second gill pouches (by the time more posterior pouches had appeared the ventral parts of the somites had fused together); at their first appearance the first, second, third, and fourth gill pouches were immediately ventral to myocommata; when the eighth pouch appeared the pouches were spread out between the second and tenth somites, i.e. over a length representing eight myocommata (though by this stage the first gill pouch has disappeared). All the gill pouches except the first give rise to gill slits.

Hypobranchial musculature. There would have been hypobranchial muscles in x formed by anterior extensions of the more anterior post-pharyngeal somites (La, Sh, not Pl nor Mi).

Excretory System. A kidney would exist in x, with a pronephric duct (La, Sh, not Pl or Mi). A kidney could not have existed in the mitrates, for nephrotomes arise in vertebrates between dorsal myotomes and ventral lateral plate, and the latter would have been lacking in the mitrate tail. There would be no epicardia (La, Sh, not Pl or Mi).

Tails and Fins. The tail would be complete, rather than broken off posteriorly, and would have had a vertical caudal fin (La, Sh not Pl nor Mi). It would not have been divided into the fore, mid and hind regions of mitrates (La, Sh, not Pl nor Mi). There would be no paired fins (La, Pl, Mi, unlike Sh).

Pharynx, hypophysis and Seessel's pouch. The pharynx of x, at least in the young animal but probably in the adult also (see below), would contain a mucous trap, produced by an endostyle and held anteriorly by peripharyngeal bands (La when young, Pl, Mi, not Sh). The pharynx would be symmetrical, the right side being a mirror image of the left (La, Sh, unlike Pl or Mi). A Seessel's pouch (pre-oral gut) probably existed in the embryo of x (La, Sh, probably adult Pl and adult Mi) but did not help to form the adult hypophysis (La, Sh, probably unlike Pl or Mi). A Rathke's pouch probably existed (La, Sh, probably not Pl nor Mi) and helped to form the adult hypophysis by interaction with the hypothalamus (La, Sh, presumably not Pl nor Mi).

Nervous System; Brain. The animal x would have had a brain, cranial nerves and dorsal nerve cord (La, Sh, Pl, Mi). The brain would have been divided into prosencephalon and rhombencephalon (La, Sh, Pl, Mi, though the rhombencephalon of x would have included parts which had belonged to the dorsal nerve cord of mitrates). The prosencephalon would have been obviously divided further into telencephalon and diencephalon (La, Sh, some specimens of Pl but not Mi). The diencephalon would have given rise dorsally to the pineal and parapineal bodies (La, Sh and other gnathostomes, not Pl nor Mi).

Cranial Nerves. The olfactory nerves would have opened into olfactory cups in the dorsal surface of the buccal cavity, or just anterior to that cavity (Pl, Mi, Sh not La). There was probably a terminalis nerve (Pl, Mi and more primitive mitrates, Sh, not La). There would have been a trigeminal complex (La, Sh, Pl, Mi) with a single pair of ganglia and no obvious division of the complex into profundus and 'true' trigeminal portions (Sh, Pl, Mi, not La where there are two pairs of ganglia). The trigeminal nerve would have been divided into mandibular, maxillary, opthalmicus superficialis and opthalmicus profundus branches (La, Sh, Pl, Mi). The oculomotor, trochlear and abducens nerves would exist as such, with their oculomotor function (La, Sh, not Pl nor Mi). There would be an acustico-lateralis complex with both acoustic and lateralis divisions (La, Sh, Mi, acoustic system present but lateral line lost in Pl). The lateral line would extend from the head, over the trunk and tail (La, Sh, not Pl nor Mi) and the ears would be in separate otic capsules, not continuous with the left and right atria (La, Sh, not Pl nor Mi). There would have been a branchial nervous complex consisting of facial, glossopharyngeal and vagus nerves. These would be made up of a placodal epibranchial constituent (La, Sh, no information in Mi nor Pl, suggestive evidence in *Peltocystis*, see below) and a neural crest constituent formed by modification of the neural crest of somites 3, 4 and 5 and 6 (La, Sh, but not Mi nor Pl, where the homologous somites were entirely post-branchial). (Epibranchial constituents probably existed in mitrates, for *Peltocystis cornuta* seems to have had nerves passing from the dorso-lateral angles of the rhombencephalon direct to the likely positions of the dorsal ends of the gill slits (personal observation of internal moulds by R.P.S.J.).) The nerves to the viscera would be the intestinal branch of the vagus (La, Sh, no information in Pl nor Mi).

Dorsal nerve cord and embryology of nervous system. The dorsal nerve cord of x would have been connected with segmental ganglia (La, Sh, Pl, Mi). It would also have been connected with ventral motor roots (La, Sh, no information in Pl nor Mi). The neural crest of x is likely to have appeared as a portion (Koltzoff's primary portion) separated or almost separated from a more posterior portion (Koltzoff's secondary portion) that produced the neural crest constituents of the branchial and spinal nerves (Koltzoff 1901, p. 456 ff for La, Sh; no information in Pl nor Mi). This separation of the neural crest of standard vertebrates into trigeminal and post-trigeminal (primary and secondary) portions coincides with the division between head and tail in mitrates. There would also have been dorso-lateral placodes giving rise to the acustico-lateralis system (La, Sh, presumably Pl and Mi) and epibranchial placodes (La, Sh, no information in Pl nor Mi, suggestive evidence in *Peltocystis*).

Skeleton. The skeleton of x would include cartilage (La, Sh, perhaps Pl and Mi in the resorption spaces of the dorsal skeleton) and probably dentine or bone (Sh, other gnathostomes, and Cephalaspida, but not La, nor Pl or Mi). Calcium carbonate would be absent (La, Sh, unlike Pl or Mi), except perhaps as otoconiae in the ears (Sh, not La, no information for Pl nor Mi, though it is possible that the acoustic calcium carbonate of vertebrates is inherited from the mitrates (see Jefferies 1968, p. 331)).

In further connection with the pharynx, x probably had an endostylar mucous trap throughout life, as in mitrates, rather than only when young like a lamprey. For lampreys, cephalaspids and anaspids all have the naso-hypophyseal opening on the dorsal surface of the head. This is an advanced feature which x probably did not possess. It was presumably acquired within a line of common ancestry subsequent to x, as suggested in figure 33. Adult cephalaspids do not show signs of the rasping tongue by which an adult lamprey feeds itself. Indeed they probably had peripharyngeal bands (Wangsjö 1952, p. 159, fig. 15B). Also there are corrugations behind these bands reminiscent of the pharyngeal corrugations of mitrates. These corrugations perhaps held pleats which served to hold the mucous trap away from the pharyngeal wall. This suggests that x had an endostylar trap in the adult, in common with its mitrate ancestors and its cephalaspid descendants.

The reconstructed animal x, as already mentioned, is much like the 'segmentationists' animal' (figure 32). The main differences concern the mandibular and premandibular segments of x which, in many respects, are not serial homologues of these behind them. Indeed the premandibular and mandibular segments of living vertebrates seem to have had distinctive phylogenetic origins. The premandibular segment perhaps represents the protocoel of pterobranchs. The mandibular segment, on the other hand, probably represents the anterior part of the metacoel of pterobranchs, i.e. the part that in *Cephalodiscus* contains the viscera and is not included in the tail or stem. All post-mandibular somites, by contrast, derive from mitrate tail somites and therefore perhaps from the tail or stem of the *Cephalodiscus*-like ancestor of all deuterostomes (compare figure 15).

The classical segmentationist conception that the trigeminal complex of vertebrates was primitively divided into a profundus portion and a 'true' trigeminal, each corresponding to a segment (van Wijhe 1883; Goodrich 1918, 1930), is probably incorrect. For it depends on the assumption that the premandibular and mandibular segments are serial homologues of those behind them. To be more precise, the profundus is probably not the dorsal root posterior to the premandibular segment, with the oculo-motor as the corresponding ventral root, nor is the 'true' trigeminal the dorsal root posterior to the mandibular segment, with the trochlear nerve as the ventral root. It is more likely that all the branches of the trigeminal nerve of lampreys and gnathostomes, together with the trigeminal and profundus ganglia and the oculo-motor and trochlear nerves, derive from particular parts of the trigeminal complex of mitrates and this, observedly, was not segmentally arranged. Froriep (1891) argued on embryological grounds that the trochlear was a branch of the trigeminal.

Concerning the branchial nerves, the segmentationist and antisegmentationist schools contradict each other. The classical segmentationist view is that they are phylogenetically derived from the neural crest anterior to the hyoidean segment (facial), posterior to the hyoidean segment (glossopharyngeal), and posterior to the 4th, 5th and perhaps 6th somites (vagus). There is likely to be some truth in this view, for this derivation is seen to occur in the ontogeny of a lamprey (Damas 1944; Koltzoff 1901). The opposite, antisegmentationist view was first expressed by Froriep (1882, 1885). It regards the branchial nerves as properly belonging to the head for two reasons: (1) they contain a placodal epibranchial constituent closely connected with the gills (which latter have presumably always been part of the head); (2) because the hypoglossal nerves, which are little-modified spinal nerves with transitory segmental dorsal ganglia, sweep round the branchial region on their way to the hypoglossal musculature, as if avoiding a region of totally different origin. The mechanical cause of this circuitous track is the placodal connection of the branchial nerves with the ectoderm, for this connection pushes the hypoglossal nerve backwards. It should be mentioned that Froriep made his observations on mammals which have no lateralis components. In agnathans, fishes and amphibians such components, of placodal origin, are involved also in forming the branchial nerves.

Remembering the mitrates, however, it is likely that both views are partly right and that the branchial nerves are of mixed head and tail origin. If the hyoidean somite is homologous with the 1st mitrate tail somite then the neural-crest constituent of the facial ganglion was presumably situated in mitrates between this somite and the posterior face of the brain (as reconstructed in figure 23*a*). The neural-crest constituent of the glossopharyngeal ganglion would be between the 1st and 2nd mitrate tail somites. And the neural-crest constituent of the vagus ganglion would be between the 2nd and 3rd, 3rd and 4th, 4th and 5th, and perhaps 5th and 6th, mitrate tail somites. Any epibranchial constituent in mitrates, however, would have passed direct to the gill slits, remaining always inside the head. (As already mentioned, the situation in *Peltocystis* suggests that this constituent already existed in mitrates.) The lateralis component also belonged to the head in mitrates. It is therefore likely that the branchial nerves, as observed in the embryos of modern vertebrates, could not exist as entities until the branchial slits had grown backwards underneath the anterior part of the mitrate tail, and the anterior tail somites of mitrates had each come to overlie a gill bar. Only then could the epibranchial, lateralis and neural-crest constituents unite to form the branchial nerves as we now see them.

The segmentationist interpretation of the oculo-motor muscles is that they are anterior serial homologues of the trunk somites. This implies, as already mentioned, that the oculo-motor, trochlear and abducens nerves would be the corresponding somitic ventral roots. The mitrates suggest, however, that only the external rectus muscle (derived from the paired hyoidean somites and supplied by the abducens nerve), would have this origin, being evolved from the 1st pair of mitrate tail somites. The superior oblique muscle, supplied by the trochlear and derived from the mandibular pair of somites, would have been evolved from part of the mitrate head (part of the left and right anterior coeloms). And the inferior oblique, and superior, anterior and inferior rectus muscles, supplied by the oculo-motor nerve and derived from the premandibular pair of somites, would also be derived from the mitrate head (crescentic body).

The atria of mitrates probably gave rise to several structures in standard vertebrates, including the ear capsules, the opercular cavities and the cloaca, which latter would have derived from the left atrium only.

The evolution of the animal x from a mitrate related to *Mitrocystella* or *Placocystites* probably involved the adoption of habitual forward swimming, by wagging the tail from side to side. Perhaps this swimming habit first developed as a way of grazing the superficial, food-rich layer of sediment more efficiently. A mitrate that started to swim forwards would be ill-adapted in several ways: its sense organs and brain would be situated too far from the new leading edge; its shape would be very badly streamlined; and the mechanical link between head and tail would be weak and liable to crick when the tail pushed, so that directional stability would be poor and brain damage likely. For all these reasons, but principally to stiffen the head-tail connection, the tail began to grow forwards over the posterior part of the head, to produce the notochordal head region and the trunk. This overgrowth involved the extension of the more anterior post-mandibular somites down the gill bars, to produce the pericardium ventral to the pharynx (the pericardium of mitrates was presumably entirely mandibular). Also the viscera migrated out of the pharyngeal region and occupied a new coelom that was formed by cavitation and fusion of the ventral parts of some of the mitrate tail somites. The anus came to open into a cloaca derived from the mitrate left atrium. This cloaca was situated in the ventral mid-line, just posterior to this new trunk region. The gonads probably released gametes through abdominal pores as in lampreys. For the gonoducts of gnathostomes, being nephric in origin, cannot be homologous with those of mitrates. There were probably two reasons for the backward migration of the viscera. First it was no longer necessary, in an actively moving animal, for faeces and gametes to be flushed away by the current through the left gill slits. Indeed it was better to expel them nearer the trailing posterior end of the animal. Secondly the migration of the viscera led to an increase in symmetry inside the pharynx.

The kidney could develop only when the perivisceral coelom had been acquired and lateral-plate mesoderm had arisen by the cavitation and fusion of the ventral parts of the trunk somites. It arose in the embryo just ventral to the myotomes and dorsal to the lateral plate so that the excretory products of the muscle blocks, now much increased by active swimming, could be removed more effectively. When the kidney had evolved, the old epicardial excretory system became unnecessary, and was lost entirely.

Active swimming required a caudal fin at the end of the tail, so the mitrate habit of losing the tip of the tail by autotomy was given up. Active swimming was also facilitated by loss of the calcite skeleton. If x had a phosphatic skeleton it had probably evolved after the calcitic skeleton had disappeared.

Elaboration of the sense organs and brain also resulted from active swimming. The lateral line extended from the head over the whole surface, as a way of detecting movements in the surrounding water. The ears became detached from the atria or opercular cavities, so that accelerometry, equilibration and hearing would be undisturbed by the branchial current. As part of the process of stiffening the contact between head and tail, and stream-lining the animal, the otic vesicles moved medianwards and crushed the hyoidean somites. The eyes acquired lenses and became mobile by developing extrinsic eye muscles from the premandibular, mandibular and hyoidean somites. Pineal and parapineal eyes developed. The nerves to the gill complex evolved from a mixture of mitrate head and tail nerves. The epibranchial placodes of the facial, glossopharyngeal and vagus would have derived from the mitrate head. The intestinal branch of the vagus and endostylar branch of the facial also derived from the mitrate head. To these were added neural-crest elements that had previously given rise to dorsal roots: (*a*) just behind the brain but anterior to the hyoidean or mitrate first tail somite (facial nerve): (*b*) between the 1st and 2nd mitrate tail somite (glossopharyngeal); (*c*) between the 2nd and 3rd, 3rd and 4th, and 4th and 5th tail somites (vagus nerve). The lateralis nerve became associated near its root with all these three branchial nerves. The olfactory system changed very little except that the prosencephalon developed a well differentiated telencephalon to coordinate its olfactory activities, and also the brain migrated nearer the olfactory sense organs, as a result of its forward movement.

As to the hypophysis, the backward migration of the pharynx relative to the brain meant that the diencephalar region of the prosencephalon was situated over the junction between buccal cavity and pharynx, instead of being posterior to that junction. In consequence the diencephalon induced a pouch in the roof of the buccal cavity (Rathke's pouch) as well as the one in the pharynx which was the pre-existing Seessel's pouch or pre-oral gut. The hypophysis came to develop where Rathke's pouch touched the diencephalon, while Seessel's pouch lost its hypophyseal function probably being retained only for its embryological function in producing the premandibular somites.

The animal resulting from all these changes would be clearly recognizable as a very primitive vertebrate, much like an ammocoete but with nasal cups inside the buccal cavity and probably opercular cavities and a bony skeleton. When this animal lived is difficult to decide. It was presumably older than the Lower Silurian, when the earliest certain Osteostracans occur (Thelodonts in Aldridge & Turner 1975), but may have been much older than that. Since it probably possessed bone there is a chance that it may be found fossil, or indeed that it has been found already. Recognizing it for what it was, however, would certainly be difficult and might be impossible. It should be emphasized that the animal x is not necessarily the stem species of all living vertebrates, for myxinoids may possibly be the sister group of petromyzontids plus gnathostomes.

Some morphologists suppose that the chordate tail first developed in the tunicate tadpole, and was retained as a neotonous feature in the adults of vertebrates and acraniates (Veit 1947; Berrill 1955; Starck 1963; Romer 1972). This seems unlikely, for the latest common ancestor of acraniates, tunicates and vertebrates was probably a primitive mitrate. And all mitrates, like all cornutes, have the head and tail distinct and well developed in the adult.

10. The head in heterostracans

The heterostracan agnathan fishes are still of uncertain phyletic position, for they lack advanced characters which might distinguish them from the animal x, which indeed they may include. They may belong in any of the positions 1, 2 or 3 in figure 33, or possibly they include all three positions. Comparison with mitrates, however, helps to interpret heterostracan head anatomy.

The heterostracans probably had an endostylar mucous trap, for the inside of the ventral head shield sometimes shows a long median impression, which probably represents the endostyle (Tarlo & Whiting 1965). On right and left sides of the internal surfaces of the dorsal and ventral shields there are also serially repeated paired impressions which, for most authors, represent the positions of gill chambers. Tarlo & Whiting, however, argue that these paired impressions represent the position of head somites associated with the pharynx. One argument that they adduce is the presence of corrugations on these impressions, approximately parallel to the long axis of the animal. If the impressions represented gill chambers, these corrugations would be perpendicular to the likely flow of water. Tarlo & Whiting therefore deduce that they cannot represent lamellae in the gill chambers, and are more likely to represent the divisions between blocks of longitudinal fibres in suprabranchial myomeres. These deductions are probably not correct, however. In the first place there is sometimes a distinct line on the inside of the dorsal shield of Pteraspidomorphs which can best be interpreted as making a sharp junction between trunk somites and the pharynx. In the second place the corrugations inside the paired impression are not exactly longitudinal to the animal, but in *Simopteraspis* converge backwards towards an imaginary point in the mid-line near the posterior end of the head shield (p in figure 36). This point is situated in a likely position for the opening of the oesophagus into the pharynx. If pteraspidormorphs had an endostylar mucous trap these corrugations could represent lamellae converging on the oesophageal opening at p and serving, like the similar pleats which probably existed in mitrates, to keep mucus away from the pharyngeal wall. The traditional interpretation of these impressions as representing gill chambers could therefore well be correct.

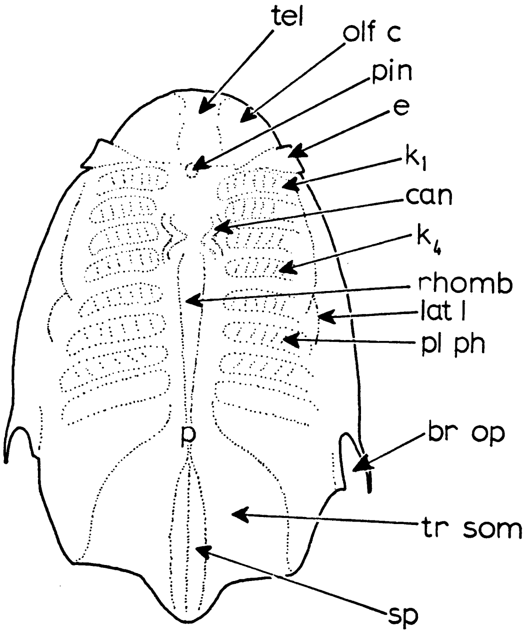

FIGURE 36. Natural internal mould of the dorsal shield of the Pteraspid *Simopteraspis primaeva* (Kiaer) (after Stensiö 1958, fig. 197*b*). The pleats of the pharynx (pl ph) are not longitudinal but converge backwards towards the point p. Other features: br op = branchial opening; can = semicircular canal; e = eye; k_1, k_4 = first and fourth gill pouches; lat l = lateral line; olf c = olfactory cup; pin = pineal body; rhomb = rhombencephalon; sp = base of nuchal spine; tel = telencephalon; tr som = trunk somites.

11. THE EVOLUTION OF ACRANIATES FROM MITRATES

The picture of the origin of acraniates from mitrates given in Jefferies (1973 pp. 461–465), can now be made more precise. The genus *Lagynocystis*, with its median ventral atrium and well preserved gill bars, was a member of the stem-group of acraniates within the mitrates. Like all other mitrates it had the head clearly distinct from the tail. The fact that a head region cannot easily be recognized in amphioxus is therefore a specialization of acraniates, not a primitive condition shared with the ancestors of vertebrates. Contrary to the classical segmentationist view (see for example, Goodrich 1930, p. 217), the notochordal head region and the trunk of vertebrates are therefore not inherited from a headless amphioxus-like ancestor from which vertebrates arose by cephalization. Instead there has been, both in acraniates, and vertebrates, a blurring of a previously clear distinction between head and tail. The trunk of acraniates is an evolutionary parallel to the trunk and notochordal head region of vertebrates.

The right and left anterior coeloms of the head of *Lagynocystis* have much the same distribution as in other mitrates. The velum was in the field of the left anterior coelom, which would also have included most or perhaps all of the buccal cavity (compare Jefferies 1973, figs. 6, 7). The left anterior coelom would correspond to the left 2nd somite of amphioxus in figures 22*a–e* (left mandibular somite of vertebrates). And the right anterior coelom would correspond to the right 2nd somite (right mandibular somite).

The first pair of somites in amphioxus arise as the right and left anterior gut diverticula of Hatschek in the neural larva (1l and 1r in figure 22). The left first somite gives rise to the Hatschek's pit of the adult, while the right one gives rise to the rostral coelom. Goodrich (1917) suggested that Hatschek's pit and the rostral coelom of amphioxus were together homologous with Rathke's pouch plus the premandibular somite of vertebrates. He therefore saw them as including a homologue of the ectodermal adenohypophysis of vertebrates, although the structures in question arise in amphioxus entirely from archenteron. We think it more likely that Hatschek's pit and the rostral coelom together represent Seessel's pouch plus the pre-mandibular somite of vertebrates, which likewise arise from archenteron. They would also correspond respectively to the neural gland and duct and the crescentic body of mitrates, which again are likely to have been archenteric derivatives unconnected with the ectoderm of the buccal cavity. The neural gland, its duct and the crescentic body may well have existed in *Lagynocystis* as in other mitrates, though there is no direct evidence of them in that genus. The neural gland, if it existed, would not have been directly connected with the brain for, alone among mitrates, this animal had no slit in the skeleton in the mid-line ventral to the prosencephalon (Jefferies 1973, fig. 13, pp. 453–455). The brain and neural gland would have been separated from each other by the intervening median atrium. In a similar way Hatschek's pit is not directly connected with the 'brain' of amphioxus, although Seessel's pouch of vertebrates is connected with the brain. In amphioxus the notochord extends forward dorsal to the first pair of somites which does not happen in vertebrates and could not have been true in *Lagynocystis*.

The evolution of amphioxus from a form like *Lagynocystis* would therefore involve: (1) the forward growth of the notochord between the left and right anterior coeloms, dorsal to the crescentic body and neural gland. This forward growth would follow the oblique groove of mitrates, pushing the velar mouth even more onto the left side than in *Lagynocystis*. It seems also to have made the crescentic body and neural gland more unsymmetrical so that Hatschek's pit (= Seessel's pouch = neural gland of mitrates) is formed in amphioxus entirely from the left anterior gut diverticulum while the rostral coelom (= premandibular somite = crescentic body of mitrates) is formed entirely from the right one. In this respect amphioxus is more unsymmetrical than its mitrate ancestors. (2) Concomitant with the forward growth of the notochord the second pair of somites (= mandibular somites = left and right anterior coeloms) developed a myotomic region next to the notochord, like that of somites behind. The dorsal nerve cord also grew forwards with the notochord but the formation of the brain was inhibited, for brain cannot develop in contact with myotome (Newth 1951, p. 256). The second pair of somites also diminished in size, so that they were not much larger than the somites behind them. (3) In this way the gill slits came to be entirely ventral to the notochord and to several of the more anterior myotomes. These myotomes dorsal to the gill slits grew ventral extensions, and coelomic cavities developed in these and fused with each other. Also the non-pharyngeal gut, as in vertebrates, moved out of the right mandibular segment (right anterior coelom), and extended behind the pharynx. As it did so the myotomes now dorsal to it cavitated in their ventral parts and the cavities fused with each other both in a longitudinal direction and in the mid line. The major cavity so formed, whether associated with the pharyngeal or the post-pharyngeal region, was the trunk coelom or splanchnocoel. In its mode of ontogenetic and phylogenetic development it is parallel to, but not homologous with, the pericardium and trunk coelom of vertebrates. As a result of these developments the anus of amphioxus has come to lie near the posterior end of the animal on the left side near the mid-ventral line. (4) The median atrium, which had existed in *Lagynocystis*, grew forwards till it covered those gill slits which had formerly opened into the left and right atria, and these paired atria disappeared. (5) The posterior coelom (left and right epicardia) grew forwards dorsal to the gill slits and was split into portions, each one above a gill bar. These individual portions became the nephridia of amphioxus. (6) Because of the decrease in size of the 2nd pair of somites, Hatschek's pit came to open into the buccal cavity, whereas the equivalent neural gland and duct of mitrate had opened into the pharynx. This was parallel to the development of Rathke's pouch in the buccal cavity of vertebrates, which was likewise due to the forward migration of the anterior end of the central nervous system relative to the velum. Rathke's pouch, however, is a new formation whereas Hatschek's pit would be an old mitrate structure whose position has shifted. (7) The tail lost the habit of autotomy and became complete, with a terminal fin. (8) The calcite skeleton was lost.

The forward growth of the notochord in the evolution of amphioxus was probably a burrowing adaptation, as most authors have assumed. Indeed it is probable that *Lagynocystis*, like *Placocystites* but unlike more primitive mitrates or cornutes, crawled slightly below the surface of the sea bed. For in both *Lagynocystis* and *Placocystites* the dorsal surface of the head is visible in posterior aspect (cf. Jefferies 1973, fig. 5*b*) so that, when pulled backwards by the tail, mud would slide over the dorsal surface of the head. We have changed our view on this (cf. Jefferies 1973, pp. 456–459). The first suggestion that *Lagynocystis* was fossorial was made by an anonymous correspondent to 'Nature' (Anonymous 1973). Loss of skeleton may also be a burrowing adaptation, for the mud in which *Lagnyocystis* lived may have been cold and acid.

Knowledge of *Lagynocystis*, therefore, allows us to distinguish parallels between acraniates and vertebrates from primitive resemblances between the two groups.

12. CONCLUSIONS

(*a*) The stem-group concept of Hennig is briefly discussed and its use suggested in such problems as the origin of the chordates. The group Calcichordata of Jefferies 1967, though proposed as a subphylum, is not a subphylum comparable with the other chordate subphyla. Instead it occupies a special position comprising the stem group of the chordates as a whole, and parts of the stem groups of acraniates, tunicates and vertebrates. The word 'calcichordate' will henceforth be used only informally, to include all chordates which retain a calcite skeleton.

Placocystites forbesianus, the particular object of the present study, can be regarded as a stem vertebrate. As such it throws light on the primitive vertebrate condition. The vertebrates as usually defined are here called standard vertebrates.

(*b*) The two obvious parts of calcichordates are best called head and tail, rather than body and tail or theca and stem. For they are not homologous with the theca and stem of crinoids and correspond best to the head and tail of standard vertebrates. The mitrates represent the hypothetical, tunicate-tadpole-like protovertebrate postulated by the antisegmentationist school of vertebrate anatomists (Froriep, Veit, Starck, Romer). The uniformly segmented protovertebrate of the segmentationist school (Gegenbaur, van Wijhe, Koltzoff, Damas, Goodrich) represents a real stage in the ancestry of the vertebrates descended from the antisegmentationist protovertebrate. The trunk and notochordal head regions of standard vertebrates are new formations, not present in calcichordates. They are parallel to the trunk of amphioxus but not homologous with it, for in amphioxus the trunk evolved independently out of the trunkless mitrate condition.

(*c*) The somites of a standard vertebrate were already present in mitrates and cornutes, with the following likely homologies: premandibular somites = crescentic organ; left mandibular somite = left anterior coelom; right mandibular somite = right anterior coelom; hyoidean somites = 1st calcichordate tail somites; 1st branchial somites = 2nd calcichordate tail somites etc. In calcichordates there could have been no topographical alternation between gill slits and somites. This alternation only arose later within the immediate ancestry of petromyzontids and gnathostomes. The premandibular, mandibular and hyoidean somites are grouped round the cispharyngeal eyes of mitrates much as they are round the paired eyes of vertebrates. These paired eyes are therefore probably homologous with cispharyngeal eyes and the extrinsic eye muscles of standard vertebrates could easily have arisen from the mitrate condition. Similarly the ears of mitrates, deduced to have existed inside the right and left atria, would be just external to the hyoidean somites. These somites were therefore crushed when the ears moved inwards towards the notochord in the origin of standard vertebrates.

(*d*) The pharynx of mitrates was fundamentally like that of tunicates and would have functioned as an endostylar mucous trap of the type considered primitive for chordates by classical anatomists. Among the structures whose position can be deduced are: the velum; the left peripharyngeal band; the right peripharyngeal band; the endostyle and its nerves; the dorsal lamina; the retropharyngeal band; the oesophageal opening, right of the mid line as in salps; the opening of the duct of the neural gland; and the pharyngo-epicardial openings, right and left of the retropharyngeal band as in *Ciona*. The posterior coelom of mitrates would be homologous with the right and left epicardia of tunicates. The non-pharyngeal gut of mitrates seems to have run as a loop within the cavity of the right anterior coelom. It would connect the oesophageal opening on the right with the rectum on the left and this opened into the left atrium. The heart of mitrates was probably just right of the oesophagus. The gonad was probably situated in the loop of the non-pharyngeal gut.

(*e*) The neural gland of mitrates was probably situated beneath the prosencephalar part of the brain and its duct would have run forward to open into the left pharynx just anterior to the dorsal meeting-place of the left and right peripharyngeal bands. It was therefore situated very much as in a tunicate tadpole. It probably corresponded physiologically to the neural gland of tunicates and, to lesser degree, to the hypophysis of vertebrates. However, it is likely to have been formed by interaction of the prosencephalon with the pharynx rather than with the buccal cavity, i.e. it is probably homologous to an endodermal Seessel's pouch (pre-oral gut) rather than to an ectodermal Rathke's pouch, which probably did not exist in mitrates. Its relationship to the crescentic body, so far as can be worked out, is like that of Seessel's pouch with the premandibular somites of vertebrates. From such an endodermal hypophysis the homologous structures of amphioxus are also probably derived (Hatschek's pit of amphioxus = Seessel's pouch of vertebrates = neural gland and its duct of mitrates; rostral coelom of amphioxus = premandibular somites of vertebrates = crescentic organ of mitrates). The neural gland and duct of mitrates are like those of a tunicate tadpole in deduced position, but in tunicates the substance of the gland duct is formed from the neural tube. This neural origin is probably not primitive for chordates, since an endodermal probable homologue of Seessel's pouch – the stomochord – exists in hemichordates.

(*f*) The nervous system of a mitrate was fundamentally like that of a fish, but more clearly divided into head and tail elements. The brain of mitrates was divided into prosencephalon and rhombencephalon homologous with those of an early standard vertebrate embryo (Starck 1975, p. 369) except that the standard vertebrate rhombencephalon has annexed certain parts of the mitrate dorsal nerve cord. The prosencephalon gave rise to paired optic nerves antero-ventrally, was probably connected with a hypophyseal neural gland (Seessel's pouch) mid-ventrally, and with olfactory and perhaps terminalis elements antero-dorsally.

The olfactory nerves opened into the roof of the buccal cavity. The trigeminal nerves in advanced mitrates such as *Placocystites* had mandibular, maxillary, ophthalmicus profundus and opthalmicus superficialis branches. The proximal parts of the trigeminal nerve passed partly under and partly over the oesophagus and rectum. Motor fibres probably followed the supra-alimentary route while sensory fibres, connected with the trigeminal ganglia, followed the sub-alimentary one. There was a single pair of trigeminal ganglia, i.e. the profundus ganglia, unlike living cyclostomes, were not separate. An acustico-lateralis system was present with acoustic ganglia in the right and left atria. Some advanced mitrates also had an external lateral line (e.g. *Mitrocystella*) but *Placocystites* had lost it. A pair of nerves supplied the endostyle.

The nervous system of the tail of mitrates included a dorsal nerve cord with paired segmental ganglia.

(*g*) The stem groups (Hennig 1969, pp. 32–35) of the living chordate subphyla can now be suggested in so far as they were included within the mitrates. The Lagynocystida would be the mitrate stem group of amphioxus; they are distinguished from the hypothetical latest common ancestor of mitrates, and linked with amphioxus, mainly by the presence of a median ventral atrium opening by a median ventral atriopore. The Peltocystida were probably the mitrate stem group of the tunicates; they are distinguished from the latest common ancestor of mitrates, and linked with the tunicates, by probable elongation of the atria (suggested by elongation of the branchial openings) and, in advanced forms, by the dorsal position of the branchial openings. The Mitrocystitida plus Anomalocystitida are probably the stem group of the vertebrates, in so far as it was contained in the mitrates; they are distinguished from the latest common ancestor of mitrates, and linked with standard vertebrates, by the presence of an external lateral line and, in advanced forms, by the presence of two pairs of dorsal touch-sensory branches of the trigeminal nerve (ophthalmicus superficialis = n_4 and ophthalmicus profundus = n_5). The vertebrates are probably more closely related to tunicates than to acraniates (Jefferies 1973, p. 463).

(*h*) The latest common ancestor of lampreys and gnathostomes (known as x) can be reconstructed with more confidence than before, assuming that it was descended from a member of the Mitrocystitida, and taking account of the segmentation studies of Koltzoff (1901) and Damas (1944) on lampreys. The reconstructed animal is shown in figure 35. Compared with the mitrates, the posterior part of the mitrate head had grown backwards in x underneath the anterior part of the mitrate tail, giving rise to the notochordal head region. Also the non-pharyngeal gut had migrated backwards out of the head, coming to lie in a new coelomic cavity posterior to the pharynx and formed from mitrate tail somites. This new coelom was the trunk coelom, and the region containing it was the trunk of standard vertebrates.

In the reconstructed animal x it is possible to distinguish elements probably derived from the mitrate head from those derived from the mitrate tail. Elements derived from the mitrate head probably included: the mandibular and premandibular somites and the extrinsic eye muscles derived from them, i.e. all except the external rectus; the prosencephalon and the part of the rhombencephalon that is connected with the ear, with the lateral-line, with the epibranchial placodes, and with the trigeminal complex including the trochlear and oculo-motor nerves; the trigeminal, optic, olfactory and terminalis nerves; the buccal cavity, pharynx, gill slits, non-pharyngeal gut and gonads.

Elements derived from the mitrate tail would include the hyoidean pair of somites and the external rectus muscles derived from them; the notochord and all myotomes behind the hyoidean; the dorsal nerve cord, the segmental ganglia behind the trigeminal ganglia and the abducens nerves together with motor roots posterior to them.

In the animal x the supra-branchial myotomes had grown down the gill bars and developed cavities ventrally which fused with each other and with the ventral part of the mandibular somite to form the pericardium, which had formerly been entirely mandibular. In this way an alternation of gill slits with myotomes arose within the exclusive ancestry of the standard vertebrates. Because of this alternation, the facial, glossopharyngeal and vagus nerves of vertebrates derive partly from the mitrate head, and partly from the mitrate tail. The facial pair of nerves were probably formed when a pair of ganglia posterior to the mitrate brain, but anterior to the first pair of mitrate tail somites, fused with placodal epibranchial and lateralis fibres from the mitrate head. The glossopharyngeal pair of nerves were formed when the pair of ganglia between the first and second tail somites of mitrates fused with epibranchial and lateralis fibres from the mitrate head. And the vagus pair of nerves were formed when the pairs of ganglia between the second and third, and third and fourth, mitrate tail somites fused with each other and with epibranchial, lateralis and intestinalis fibres from the mitrate head. The kidney of x arose where the new perivisceral coelom was in contact in the embryo with the myotomes. The animal x would have had a vertical caudal fin, probably a bony skeleton (or in any case not a calcite one), probably an opercular cavity covering the gill slits, and an endostylar pharynx acting as a mucous trap. The olfactory nerves of x would have opened into the buccal cavity or immediately anterior to it. The atria of mitrates were probably represented in it by the opercular cavities, the ears and the cloaca (this being derived from the left atrium only).

This hypothetical animal, which was a primitive standard vertebrate, but not necessarily the latest common ancestor of all living vertebrates since it was perhaps not ancestral to the myxinoids, would have lived before the Silurian Period and probably after the first part of the Cambrian. The differences between it and the mitrates are probably due mainly to the adoption of the habit of forward swimming. Perhaps this served initially as a more efficient way of grazing the food-rich surface layer of the sea bottom.

(*i*) Heterostracan agnathans probably also fed by an endostylar mucous trap inside the pharynx.

(*j*) The evolution of acraniates from mitrates involved forward growth of the notochord between the left and right anterior coeloms (mandibular somites) and dorsal to the crescentic organ (premandibular somites). The splanchnocoel of acraniates arose by cavitation of the ventral parts of mitrate tail somites and fusion of the cavities with each other. It is a parallelism with the pericardium and trunk coeloms of standard vertebrates. The origin of acraniates may be primarily connected with the adoption of a burrowing mode of life, which probably began within the mitrate stem group of the acraniates.

(*k*) The cornute head differed from the mitrate one mainly by lacking right gill slits and right pharynx. The cornute condition can, therefore, be reconstructed by mentally subtracting these organs from a mitrate. In this way it is possible to suggest how the heart, non-pharyngeal gut and cranial nerves of a cornute were arranged, and partly to confirm some of these suggestions by direct fossil evidence. It is also possible to reconstruct how the pharynx of cornutes operated, partly by analogy with recent larval amphioxus.

(*l*) The Anomalocystitida (including *Placocystites*), were adapted for crawling just beneath the surface of the sea bed. The oral spines of Anomalocystitids are marginal plates modified to cut sideways into the sediment. This cutting action was probably assisted by squirting water along them as they sliced outwards, the water probably being pumped by the velum.

Detailed study of *Placocystites* and its relatives therefore answers a number of fundamental questions concerning the primitive anatomy of vertebrates. Also it shows the importance of fitting phylogeny to a dichotomously branching tree as advocated by Hennig. This leads to the circle-squaring conclusion that segmentationist and antisegmentationist standpoints are both largely correct.

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REFERENCES

Aldridge, R. J. & Turner, S. 1975 Britain's oldest agnathans. *Geol. Mag.* **112**, 419–420.

Anonymous 1973 Ancestry of Chordates. *Nature, Lond.* **245**, 123–124.

Balabai, P. P. 1951 [Observations on the feeding of the ammocoete]. *Dokl. Akad. Nauk. SSSR* **77**, 341–344.

Balabai, P. P. 1956 [*Morphology and phylogenetic development of the agnatha*]. Kiev: Akademii Nauk Ukrainskoi SSR.

Balfour, F. M. 1878 A monograph on the development of elasmobranch fishes. London: MacMillan.

Balinsky, B. I. 1960 *An introduction to embryology*. Philadelphia & London: Saunders.

Barrington, E. J. W. 1938 The digestive system of *Amphioxus* (*Branchiostoma*) *lanceolatus*. *Phil. Trans. R. Soc. Lond.* B **228**, 269–311.

Barrington, E. J. W. & Sage, M. 1972 The endostyle and thyroid gland. In *The biology of lampreys* (ed. M. W. Hardisty & I. C. Potter), vol. 2, pp. 105–134. London: Academic Press.

Bather, F. A. 1900 In *A Treatise on Zoology Pt. III Echinoderma* (ed. E. R. Lankester), chaps 8–12, pp. 1–216. London: Black.

Bather, F. A. 1913 Caradocian Cystidea from Girvan. *Trans. R. Soc. Edinb.* **49**, 359–529.

Berrill, N. J. 1936 Studies on tunicate development. V. Evolution and classification. *Phil. Trans. R. Soc. Lond.* B **226**, 43–70.

Berrill, N. J. 1950 *The Tunicata with an account of the British species.* London: Ray Society.

Berrill, N. J. 1955 *The origin of vertebrates.* London: Oxford University Press.

Bjerring, H. C. 1970 Nervus tenuis, a hitherto unknown cranial nerve of the fourth metamere. *Acta zool., Stockh.* **51**, 107–114.

Bockelie, T. & Fortey, R. A. 1976 An early Ordovician vertebrate. *Nature, Lond.* **260**, 36–38.

Bone, Q. 1958 Observations upon the living larva of amphioxus. *Pubbl. Staz. zool. Napoli*, **30**, 458–471.

Bone, Q. & Mackie, G. O. 1975 Skin impulses and locomotion in *Oikopleura* (Tunicata: Larvacea). *Biol. Bnll. mar. biol. Lab., Woods Hole*, **149**, 267–286.

Butler, A. J. 1939 The stratigraphy of the Wenlock Limestone of Dudley. *Q. J. geol. Soc. Lond.* **95**, 37–74, pl. 3.

Carlisle, D. B. 1950 Alcune osservazioni sulla meccanica dell'alimentazione della *Salpa*. *Pubbl. Staz. zool. Napoli*, **22**, 146–154.

Carlisle, D. B. 1953 Origin of the pituitary body of chordates. *Nature, Lond.* **172**, 1098.

Caster, K. E. 1952 Concerning *Enoploura* of the Upper Ordovician and its relation to other carpoid Echinodermata. *Bull. Am. Paleont.* **24**, 5–56.

Cocks, L. R. M., Holland, C. H., Rickards, R. B. & Strachan, I. 1971 A correlation of Silurian rocks in the British Isles. *J. geol. Soc. Lond.* **127**, 103–136.

Cocks, L. R. M. & Walton, G. 1968 A large temporary exposure in the Lower Silurian of Shopshire. *Geol. Mag.* **105**, 390–397.

Chauvel, J. 1941 Recherches sur les cystoides et les carpoides armoricains. *Mém. Soc. géol. minér. Bretagne* **5**, 1–286.

Chauvel, J. 1971 Les echinodermes carpoides du paléozoique inférieur marocain. *Notes Mém. Serv. Mines Carte géol. Maroc.* **31**, 49–60.

Conklin, E. 1932 The embryology of Amphioxus. *J. Morph.* **54**, 69–151.

Damas, H. 1944 Recherches sur le developpement de *Lampetra fluviatilis* L. Contribution à l'étude de la céphalogenèse des vertébrés. *Archs. Biol.* **55**, 1–284.

De Beer, G. R. 1922 The segmentation of the head in *Squalus acanthias*. *Q. Jl microsc. Sci.* **66**, 457–474.

De Beer, G. R. 1926 *The comparative anatomy, histology and development of the pituitary body.* Edinburgh & London: Oliver & Boyd.

De Beer, G. R. 1937 *The development of the vertebrate skull.* Oxford: University Press.

Dehm, R. 1933 Cystoideen aus dem rheinischen Unterdevon. *Neues jb. Miner. Geol. Paläont. BeilBd.*, **69** B, 63–93, pl. 2.

Dehm, R. 1934 Untersuchungen an Cystoideen des rheinischen Unterdevons. *Sber. bayer. Akad. Wiss. Jahrg.* 1934, 19–43, pls 1, 2.

Eaton, T. H. 1970 The stem-tail problem and the ancestry of chordates. *J. Paleont.* **44**, 969–979.

Elwyn, A. 1937 Some stages in the development of the neural complex in *Ecteinascidia turbinata*. *Bull. neurol. Inst. N.Y.* **6**, 163–177.

Fedele, M. 1934 Sulla nutrizione degli animali pelagici III – Ricerche sui Salpidae. *Boll. Soc. Nat. Napoli*, **45**, 49–117.

Fenaux, R. 1968 Le mécanisme alimentaire chez les tuniciers. *Année Biol.* **7**, 345–368.

Fol, H. 1872 Études sur les appendiculaires du Détroit de Messine. *Mém. Soc. Phys. Hist. nat. Genève* **21**, 445–499.

Franz, V. 1927 Morphologie der Akranier. *Ergebn. Anat. Entw Gesch.* **27**, 464–541.

Froriep, A. F. 1882 Über ein Ganglion des Hypoglossus und Wirbelanlagen in der Occipitalregion. *Arch. Anat. Physiol.* (1882), 279–301.

Froriep, A. F. 1885 Über Anlagen von Sinnesorganen am Facialis, Glossopharyngeus und Vagus, über die genetische Stellung des Vagus zum Hypoglossus und über die Herkunft der Zungenmuskulatur. *Arch. Anat. Physiol.* (1885), 1–55.

Froriep, A. F. 1891 Zur Entwickelungsgeschichte der Kopfnerven. I. Über die Entwickelung des Trochlearis bei Torpedo. *Verh. anat. Ges., Jena.* (Suppl. *Anat. Anz.*) **6**, 55–60.

Froriep, A. F. 1902 Zur Entwicklungsgeschichte des Wirbeltierkopfes. *Verh. anat. Ges. Jena* (Suppl. *Anat. Anz.*) **21**, 34–46.

Gaskell, W. H. 1908 *The origin of vertebrates.* London: Longmans.

Garstang, W. 1928 The morphology of the Tunicata, and its bearing on the phylogeny of the Chordata. *Q. Jl microsc. Sci.* **72**, 51–187.

Garstang, W. & Platt, M. I. 1928 On the asymmetry and closure of the endostyle in *Cyclosalpa pinnata*. *Proc. Leeds phil. lit. Soc.* **1**, 325–334.

Gegenbaur, C. 1874 *Grundriss der vergleichenden Anatomie.* Leipzig: Engelmann.

Gill, E. D. & Caster, K. E. 1960 Carpoid echinoderms from the Silurian and Devonian of Australia. *Bull. Am. Paleont.* **41**, 1–71, pl. 1–10.

Godeaux, J. 1964 Que connaissons-nous de la glande neurale des tuniciers? *Publ. Univ. off. Congo Elisabethville*, **7**, 51–64.

Goodrich, E. S. 1917 'Proboscis pores' in craniate vertebrates, a suggestion concerning the mandibular somites and hypophysis. *Q. Jl microsc. Sci.*, **62**, 539–554.

Goodrich, E. S. 1918 On the development of the segments of the head in *Scyllium*. *Q. Jl microsc. Sci.* **63**, 1–13, pls 1–2.

Goodrich, E. S. 1930 *Studies on the structure and developments of vertebrates*. London: Constable.

Grave, C. 1921 *Amaroucium constellatum* (Verrill). 2. The structure and organisation of the tadpole larva. *J. Morph.* **36**, 7–91, pls 1–4.

Haeckel, E. 1896 Die Amphorideen und Cystoideen. Beiträge zur Morphologie und Phylogenie der Echinodermen. *Festschr. Siebzigsten Geburtstage. Carl Gegenbaur* vol. I, 1–179, pls 1–5.

Hatschek, B. 1881 Studien über die Entwickelung des Amphioxus. *Arb. zool. Inst. Univ. Wien* **4**, 1–88, pls 1–9.

Hendry, R. D., Rowell, A. J. & Stanley, J. W. 1963 A rapid parallel grinding machine for serial sectioning of fossils. *Palaeontology* **6**, 145–7, pl. 20.

Hennig, W. 1966 *Phylogenetic systematics*. Chicago & London: University of Illinois Press.

Hennig, W. 1969 *Die Stammesgeschichte der Insekten*. Frankfurt am Main: Waldemar Kramer.

Jaekel, O. 1900 Über Carpoideen, eine neue Klasse von Pelmatozoen. *Z. dt. geol. Ges.* **52**, 661–677.

Jaekel, O. 1918 Phylogenie und System der Pelmatozoen. *Paläont. Z.* **3**, 1–128.

Jefferies, R. P. S. 1967 Some fossil chordates with echinoderm affinities. *Symp. zool. Soc. Lond.* **20**, 163–208.

Jefferies, R. P. S. 1968 The subphylum Calcichordata (Jefferies 1967) – primitive fossil chordates with echinoderm affinities. *Bull Br. Mus. nat. Hist. (Geol.)*, **16**, 243–339, pls 1–10.

Jefferies, R. P. S. 1969 *Ceratocystis perneri* Jaekel – a Middle Cambrian chordate with echinoderm affinities. *Palaeontology* **12**, 494–535, pls 95–98.

Jefferies, R. P. S. 1973 The Ordovician fossil *Lagynocystis pyramidalis* (Barrande) and the ancestry of amphioxus. *Phil. Trans. R. Soc. Lond.* B **265**, 409–469, pls 37–46.

Jefferies, R. P. S. 1975 Fossil evidence concerning the origin of the chordates. *Symp. zool. Soc. Lond.* **36**, 253–318.

Jefferies, R. P. S. (in press) Calcichordata. In *Encyclopaedia of Paleontology* (ed. D. Jablonski). New York: Reinhold.

Jefferies, R. P. S. & Prokop, R. J. 1972 A new calcichordate from the Ordovician of Bohemia and its anatomy, adaptations and relationships. *Biol. J. Linn. Soc.* **4**, 69–115.

Jollie, M. 1973 The origin of chordates. *Acta Zool., Stockh.* **54**, 81–100.

Jørgensen, C. B. 1966 *The biology of suspension feeding*. London: Oxford University Press.

Kieckebusch, H. H. 1928 Beiträge zur Kenntnis des Baues und der Entwicklung der Schilddrüse bei den Neunaugenlarven (*Lampetra fluviatilis* L und *Lampetra planeri* Bl). *Z. Morph. Ökol. Tiere* **11**, 247–360, pls 4–12.

Koltzoff, N. K. 1901 Entwickelungsgeschichte des Kopfes von *Petromyzon planeri*. *Byull. mosk. Obshch. Ispyt. Prir.* **15**, 259–598, pls 1–7.

Koninck, M. L. de 1869 Sur quelques échinodermes remarquables des terrains paléozoiques. *Bull Acad. r. Belg. Cl. Sci.* (2) **28**, 544–552, pl. 1.

Koninck, M. L. de 1870 On some new and remarkable echinoderms from the British Palaeozoic rocks. *Geol. Mag.* (1) **7**, 258–263, pl. 7.

Lankester, E. R. & Willey, A. 1890 The development of the atrial chamber of Amphioxus. *Q. Jl microsc. Sci.* **31**, 445–446, pls 29–32.

Legros, R. 1898 Développement de la cavité buccale de *l'Amphioxus lanceolatus*. Contribution à l'etude de la morphologie de la tête. *Archs Anat. microsc.* **1**, 497–542, pls 21–23; 2, 1–43, pls 1–2.

Lindström, G. 1888 *List of the fossil faunas of Sweden. Edited by the Palaeontological Department of the Swedish State Museum (Natural History). 2. Upper Silurian.* Stockholm: Riksmuseum.

Lindström, T. 1949 On the cranial nerves of the cyclostomes, with special reference to n. trigeminus. *Acta. zool., Stockh.* **30**, 315–458.

MacBride, E. W. 1898 The early development of Amphioxus. *Q. Jl microsc. Sci.* **40**, 589–612, pls 42–45.

Martini, E. 1909 Über die Segmentierung des Appendicularien-Schwanzes. *Verh. dt. zool. Ges.* **19**, 300–307.

Metcalf, M. M. 1900 Notes on the morphology of the Tunicata. *Zool. Jb. (Anat. Ont. Tiere)* **13**, 495–602, pls. 1–7.

Millar, R. H. 1953 *Ciona. L.M.B.C. Mem. typ. Br. mar. Pl. Anim.* **35**, 1–84, pls 1–19.

Millott, N. 1966 A possible function for the axial organ of echinoids. *Nature, Lond.* **209**, 594–6.

Millott, N. 1967 The axial organ of echinoids. Reinterpretation of its structure and function. *Symp. zool. Soc. Lond.* **20**, 53–63.

Nelson, G. J. 1970 Outline of a theory of comparative biology. *Syst. Zool.* **19**, 373–384.

Neumann, G. 1935 2. Ordnung der Thaliaceae: Cyclomyaria. In Kükenthal, W. & Krumbach, T. *Handbuch der Zoologie* (ed. W. Kükenthal & T. Krumbach), 5ter Band, 2te Hälfte. Tunicata. pp. 324–400. Berlin & Leipzig: de Gruyter.

Newth, H. G. 1930 The feeding of Ammocoetes. *Nature, Lond.* **126**, 94–95.

Newth, D. R. 1951 Experiments on the neural crest of the lamprey embryo. *J. exp. Biol.* **28**, 247–260, pls 3–4.

Orton, J. H. 1913 The ciliary mechanism of the gills and the mode of feeding in Amphioxus, ascidians and *Solenomya togata*. *J. mar. biol. Ass. U.K.* **10**, 19–49.

Pasteels, J. 1958 Développement des agnathes. *Traité de Zoologie* (ed. P. P. Grassé), Tome 13, fasc 1. Pp. 106–144. Paris: Masson.

Pearse, A. S., Hamm, H. J. & Wharton, G. W. 1942 Ecology of sand beaches at Beaufort, N. C. *Ecol. Monogr* **12**, 135–190.

Pedler, C. M. H. 1968 A computerised system for the three-dimensional reconstruction of serial electron micrographs. *4th European Regional Conference on Electron Microscopy* (ed. D. S. Bocciarelli), vol. 1, pp. 573–574.

Pedler, C. M. H. & Tilley, R. 1966 A new method of serial reconstruction from electron micrographs. *Jl R. microsc. Soc.* **86**, 189–197.

Pérès, J. M. 1943 Recherches sur le sang et les organes neuraux des Tuniciers. *Annls. Inst. océanogr., Monaco* **21**, 229–359.

Pohlo, R. 1969 Confusion concerning deposit feeding in the Tellinacea. *Proc. malac. Soc. Lond.* **38**, 361–364.

Pope, J. K. 1975 Evidence for relating the Lepidocoleidae, machaeridian echinoderms to the mitrate carpoids. In *Studies in Paleontology and Stratigraphy, dedicated to K. E. Caster* (ed. J. Pojeta & J. K. Pope), *Bull. Am. Paleont.* **67**, 385–402, pl. 13.

Pucci-Minafra, I. 1965. Ultrastructure of muscle cells in *Ciona intestinalis* tadpoles. *Acta Embryol. Morph. exp.* **8**, 289–305.

Reese, A. M. 1902 Structure and development of the thyroid gland in *Petromyzon. Proc. Acad. nat. Sci. Philad.* **54**, 85–112, pls 4–7.

Regnéll, G. 1945 Non-crinoid Pelmatozoa from the Palaeozoic of Sweden. *Meddn Lunds geol.-miner. Instn* **108**, 1–255, pls 1–14.

Romer, A. S. 1962 *The vertebrate body*. 3rd edition. Philadelphia and London: Saunders.

Romer, A. S. 1972 The vertebrate as a dual animal – somatic and visceral. *Evol. Biol.* **6**, 121–156.

Ropes, J. W. & Merrill, A. S. 1966 The burrowing activities of the surf clam. *Underwat. Natur.* **3**, 11–17.

Salensky, W. 1876 Über die embryonale Entwicklungsgeschichte der Salpen. *Z. wiss. Zool.* **27**, 179–237, pls 14–16.

Scoffin, T. P. 1971 (or 2) The conditions of growth of the Wenlock reefs of Shropshire, England. *Sedimentology* **17**, 173–219.

Seilacher, A. 1961 Krebse im Brandungssand. *Natur Volk* **91**, 257–264.

Silén, L. 1954 Reflections concerning the 'stomochord' of the Enteropneusta. *Proc. zool. Soc. Lond.* **124**, 63–7.

Smith, K. M. & Newth, H. G. 1917 A note concerning the collar cavities of the larval amphioxus. *Q. Jl microsc. Sci.* **62**, 243–251.

Sprinkle, J. 1973 Morphology and evolution of blastozoan echinoderms. *Spec. Publ. Mus. Comp. Zool. Harvard Univ.* 1–196, pls 1–43.

Stanley, S. M. 1970 Relation of shell form to life habits in the Bivalvia (Mollusca). *Mem. geol. Soc. Am.* **125**, 1–296, pls 1–40.

Starck, D. 1963 Die Metamerie des Kopfes der Wirbeltiere. *Zool. anz.* **170**, 393–429.

Starck, D. 1975 *Embryologie. Ein Lehrbuch auf allgemein biologischer Grundlage*. 3rd edition. Stuttgart: Thieme.

Stensiö, E. A. 1958 Les cyclostomes fossiles ou ostracodermes. In *Traité de Zoologie* (ed. P. P. Grassé), Tome 13, fasc 1, pp. 173–432. Paris: Masson.

Sterba, G. 1953 Die Physiologie und Histogenese der Schilddrüse und des Thymus beim Bachneunauge als Grundlage phylogenetischer Studien über die Evolution der innensekretorischen Kiemendarmderivate. *Wiss. Z. Friedrich Schiller-Univ. Jena* **3**.

Sterba, G. 1962 [On the importance of the Petromyzonidae in the evolution of the Chordates.] *Vest. Leningr. Gos. Univ.* (Biol. Ser.) **15**, 58–65.

Tarlo, L. B. H. & Whiting, H. P. 1965 A new interpretation of the internal anatomy of the Heterostraci (Agnatha). *Nature, Lond.* **206**, 148–150.

Trueman, E. R. 1970 The mechanism of burrowing of the mole crab, *Emerita. J. expl. Biol.* **53**, 701–710.

Trueman, E. E. & Ansell, A. D. 1969 The mechanisms of burrowing into soft substrate by marine animals. *Oceanogr. Mar. Biol.* **7**, 315–366.

Ubaghs, G. 1961 Sur la nature de l'organe appelé tige ou pedoncule chez les Carpoïdes Cornuta et Mitrata. *C.r. hebd. Sèanc. Acad. Sci. Paris* **253**, 2738–2740.

Ubaghs, G. 1963 *Cothurnocystis* Bather, *Phyllocystis* Thoral and an undetermined member of the order Soluta (Echinodermata, Carpoidea) in the Uppermost Cambrian of Nevada. *J. Paleont.* **37**, 1133–1142.

Ubaghs, G. 1968 *Stylophora*. In *Treatise on invertebrate paleontology* (ed. R. C. Moore), pt. S *Echinodermata* **1**, 3–60. New York: Geological Society of America.

Ubaghs, G. 1970 Les echinodermes carpoides de l'ordovicien inférieur de la Montagne Noire (France). *Cahiers de Paléontologie*, Paris, pp. 1–112.

Ubaghs, G. 1971 Diversité et spécialisation des plus anciennes echinodermes que l'on connaisse. *Biol. Rev.* **46**, 157–200.

Ubaghs, G. 1975 Early Paleozoic Echinoderms. *Rev. Earth planet. Sci.* **3**, 79–98.

Veit, O. 1947 *Über das Problem Wirbeltierkopf*. Kempen: Thomas.

Wängsjö, G. 1952 The Downtonian and Devonian vertebrates of Spitzbergen, IX. Morphologic and systematic studies of the Spitzbergen cephalaspids. *Skr. norsk. Polarinst.* **9**, 1–616, pls 1–118.

Werner, E. & Werner, B. 1954 Über den Mechanismus des Nahrungserwerbs der Tunicaten, speziell der Ascidien. *Helgoländer Wiss. Meeresunters.* **5**, 57–92.

Wetherby, A. G. 1879 Description of a new family and genus of Lower Silurian Crustacea. *J. Cincinn. Soc. nat. Hist.* **1**, 162–166, pls 7, figs 1–1g.

Whiting, H. P. 1972 The cranial anatomy of ostracoderms in relation to the organisation of larval lampreys. In *Studies in Vertebrate evolution: Essays presented to Dr F. R. Parrington, F.R.S.* (ed. K. A. Joysey & T. S. Kemp), pp. 1–19. Edinburgh: Oliver & Boyd.

Wijhe, J. W. van 1883 Über die Mesodermsegmente und die Entwickelung der Nerven des Selachierkopfes. *Verh. K. Akad. Wet.* (2 Afd.) **22**, 1–50, pls 1–5.

Wijhe, J. W. van 1893 Über Amphioxus. *Anat. Anz.* **8**, 152–172.

Wijhe, J. W. van 1902 Beiträge zur Anatomie der Kopfregion des *Amphioxus lanceolatus. Petrus Camper ned. Bijdr Anat.* **1**, 109–194, pls 8–11.

Wijhe, J. W. van 1906 Die Homologisierung des Mundes des *Amphioxus* und die primitive Leibesgliederung der Wirbelthiere. *Petrus Camper ned. Bijdr. Anat.* **4**, 61–102, pl. 2.

Wijhe, J. W. van 1914 Studien über Amphioxus I. Mund und Darmkanal während der Metamorphose. *Verh. K. Akad. Wet.* (2 Afd) **18**, 1–84, pls 1–5.

Wijhe, J. W. van 1918 On the nervus terminalis from man to Amphioxus. *Proc. K. ned. Akad. Wet.* **21**, 172–182, pl. 1.

Willey, A. 1891 The later larval development of amphioxus. *Q. Jl microsc. Sci.* **32**, 183–234, pls 13–15.

Willey, A. 1893 Studies on the protochordata 2. The development of the neurohypophysial system in *Ciona intestinalis* and *Clavelina lepadiformis* with an account of the origin of the sense organs in *Ascidia mentula*. *Q. Jl microsc. Sci.* **35**, 295–333, pl. 18–20.

Willey, A. 1894 *Amphioxus and the ancestry of the vertebrates.* New York: MacMillan.

Withers, T. H. 1926 *Catalogue of Machaeridia (Turrilepas and its allies) in the Department of Geology.* London: British Museum (Natural History).

Woodward, H. 1871 Note on a new British Cystidean. *Geol. Mag.* (1) 8, 71–2.

Woodward, H. 1880 Notes on the Anomalocystidae, a remarkable family of Cystoidea found in the Silurian rocks of North America and Britain. *Geol. Mag.* (2) 7, 193–202, pl. 6.

Yonge, C. M. 1949 On the structure and adaptations of the Tellinacea, deposit-feeding Eulamellibranchia. *Phil. Trans. R. Soc. Lond.* B **234**, 29–76.

DESCRIPTION OF PLATE 1

Placocystites forbesianus from Dudley Limestone, Dudley. External anatomy.

FIGURE 37. Integument plates round left tubercle (Birmingham University, Holcroft Coll. 62).

FIGURE 38. Integument plates apparently still articulated to left side of left semicircular process (Birmingham University, Holcroft Coll. 59).

FIGURE 39. Integument plates round left tubercle (Birmingham University, Holcroft Coll. 13).

FIGURES 40–44. External anatomy of head (Birmingham University, Holcroft Coll. 35); 40. anterior aspect; 41. ventral aspect; 42. posterior aspect; 43. dorsal aspect; 44. right lateral aspect. Compare figure 3.

FIGURE 45. Serrations on peripheral flange of head (Birmingham University, Holcroft Coll. 219).

FIGURE 46. Right aspect of a ventral plate of the hind tail (Nottingham Natural History Museum N8). Note anterior process of ventral plate (ap) and anterior groove (ag). Compare figure 6.

DESCRIPTION OF PLATE 2

FIGURES 47–60. *Placocystites forbesianus* from Dudley Limestone, Dudley.

FIGURE 61. *Mitrocystella incipiens miloni*, Schistes à Calymènes, Le Traveusot.

FIGURE 47. Anterior aspect of right oral funnel and right oral spine of *P. forbesianus* (BMNH E7547). The spine has the ventral face upward so that the admedian face is still admedian. Note that the lateral muscle facet (lat m f) on the spine is much bigger than the admedian muscle facet (adm m f).

FIGURE 48. Right anterior aspect of same oral funnel as in figure 47.

FIGURE 49. Anterior aspect of right portion of head and posterior aspect of right oral spine (Nottingham Natural History Museum N9). The spine has the dorsal surface upward, and the lateral edge consequently admedian. Note that the lateral muscle facet (lat m f) is much bigger than the admedian muscle facet (adm m f). Compare figure 4, figure 47 above, and plate 6, figures 79, 80.

FIGURE 50. Dorsal aspect of dissected mouth region, to show oral plates still in place (Birmingham University, Holcroft Coll. 5).

FIGURE 51. Dorsal aspect of right lateral oral plate (Nottingham Natural History Museum N11).

FIGURES 52, 53. Ventral and dorsal aspects of left lateral oral plate from same specimen as figure 50. The plate has been fractured at fr. Note tissue facet for inhalent flap (tis f in) and for the lip (tis f l). Compare figure 4.

FIGURE 54. Mouth anatomy and oral funnels (Birmingham University, Holcroft Coll. 29).

FIGURE 55. Mouth features (Birmingham University, Holcroft Coll. 23).

FIGURE 56. Right lateral aspect of portion of hind tail (Birmingham University, Holcroft Coll. 55). Note the absence of posterior facets on the dorsal ossicles.

FIGURES 57–60. A dorsal ossicle of the hind tail (Nottingham Natural History Museum N8) in left lateral, ventral, anterior and posterior aspects. Compare figure 6.

FIGURE 61. *Mitrocystella incipiens miloni.* Natural internal mould of hind tail in left lateral aspect (Université de Rennes 15436). Note the dorsal longitudinal canal (d l can) connecting the interossicular canals (int can) and also the segmental ganglia (gan) leading to dorsal root nerves (dr n).

DESCRIPTION OF PLATE 3

Placocystites forbesianus from Dudley Limestone, Dudley.

FIGURES 62, 63. Dorsal and ventral aspects of smallest known specimen (Birmingham University, Holcroft Coll. 60). As compared with the definitive condition note the relatively large distance between the cuesta-shaped ribs and the prominence of the mid-ventral plate V_{1M}.

FIGURES 64–66. Fore and mid tail in dorsal, right lateral and ventral aspects (BMNH E28671). Note especially the well developed imbrication membranes in figures 64 and 65.

FIGURES 67, 68. The twisted tail of specimen (Sedgwick Museum A12570); figure 67 shows the fore tail in dorsal and hind tail in left lateral aspect; figure 68 shows the fore tail in left lateral aspect.

DESCRIPTION OF PLATE 4

Placocystites forbesianus, from Dudley Limestone, Dudley.

FIGURES 69, 70. Specimens showing ventral internal aspect of parts of the dorsal skeleton. Note especially the velar groove (vel) in 69 and 70 and the mid-dorsal process (m d pr) especially in 69. The specimen in figure 69 is BMNH E7549 and in figure 70, Nottingham Natural History Museum N2. The latter specimen has been heavily scored with a knife but the scratches can easily be distinguished from original features of the internal anatomy.

FIGURE 71. Ventral aspect of head to show ornament, and oral spines parallel to each other (Birmingham University, Holcroft Coll. 24).

FIGURE 72. Ventral aspect of head of lectotype (BMNH 7588). The dorsal aspect is covered with matrix.

FIGURE 73. Posterior aspect of cerebral cup to show division of the prosencephalon into telencephalon and diencephalon (Birmingham University, Holcroft Coll. 45).

FIGURE 74. Posterior aspect of the cerebral basin in which the division between telencephalon and diencephalon is not expressed (Birmingham University, Holcroft Coll. 34).

DESCRIPTION OF PLATE 5

Placocystites forbesianus; transversely sectioned model based on Birmingham University, Holcroft Coll. 25. The models in all figures are 20 times as big as the specimens and the section interval is 100 µm. Scales refer to specimens.

FIGURE 75. Anterior aspect of posterior portion of head. Note especially the deduced position of the crescentic body, whose margins are indicated by m cr b and culminate dorsally in two deep holes in the skeleton, the groove for the right cispharyngeal eye (r cis e) and the low-ridge separating the patent right anterior coelom from the right pharynx (r ant c/r ph). Scale as in plate 6, figure 83.

FIGURE 76. Dorsal skeleton. The left olfactory cup in postero-ventral aspect.

FIGURE 77. Ventral aspect of dorsal skeleton. Note the velar groove (vel, compare plate 4, figures 69, 70), the possible position of the left peripharyngeal band (per b compare plate 4, figure 70), the position of the ciliated organ (cil o). A low ridge (r ant c/r ph) consistently median to the mid-dorsal process (m d pr) probably marks the line of contact of the patent right anterior coelom with the right pharynx (compare figures 75 and 78 on this plate, and also sections in figure 19). Note also the deep holes believed to mark the dorso-lateral ends of the crescentic body (m cr b). Resorbtion cliffs (res cl) mark the edges of the areas over the left and right pharynxes where the skeleton seems to have been removed by resorbtion.

FIGURE 78. Dorsal skeleton. The right olfactory cup in postero-ventral aspect. Note the inhalent groove (inh gr) and the facet on the ademedian surface of the mid-dorsal process.

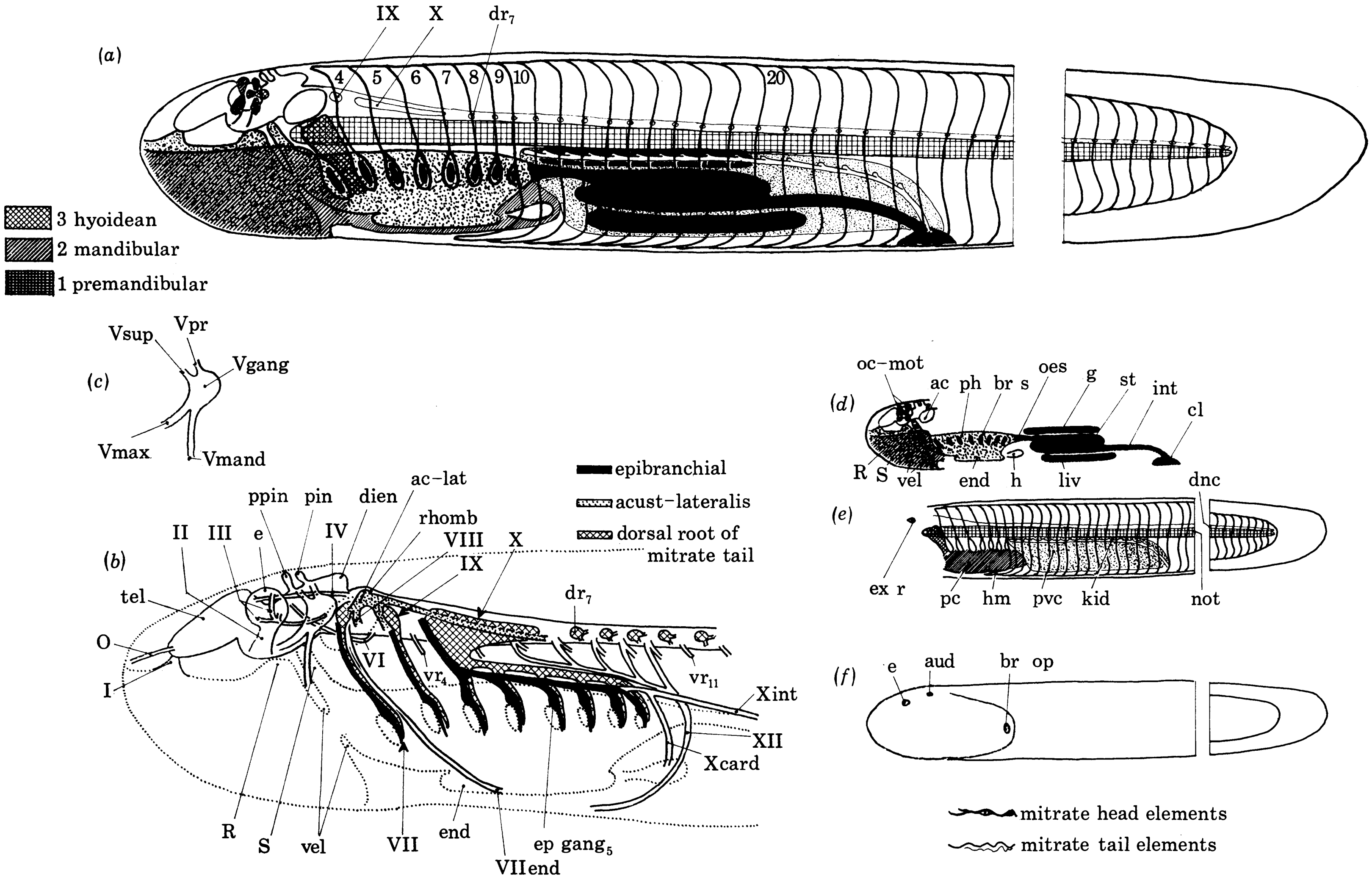
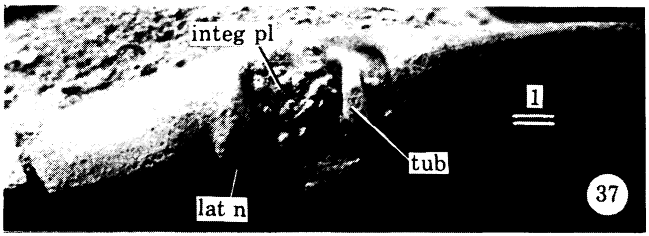
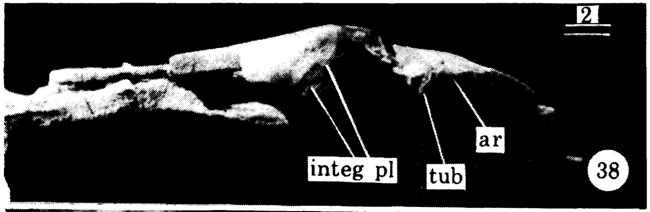
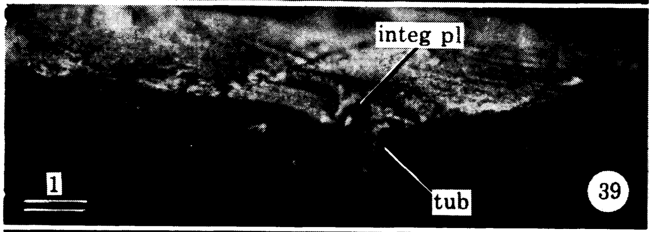
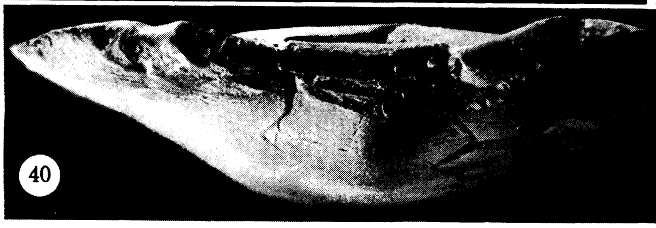


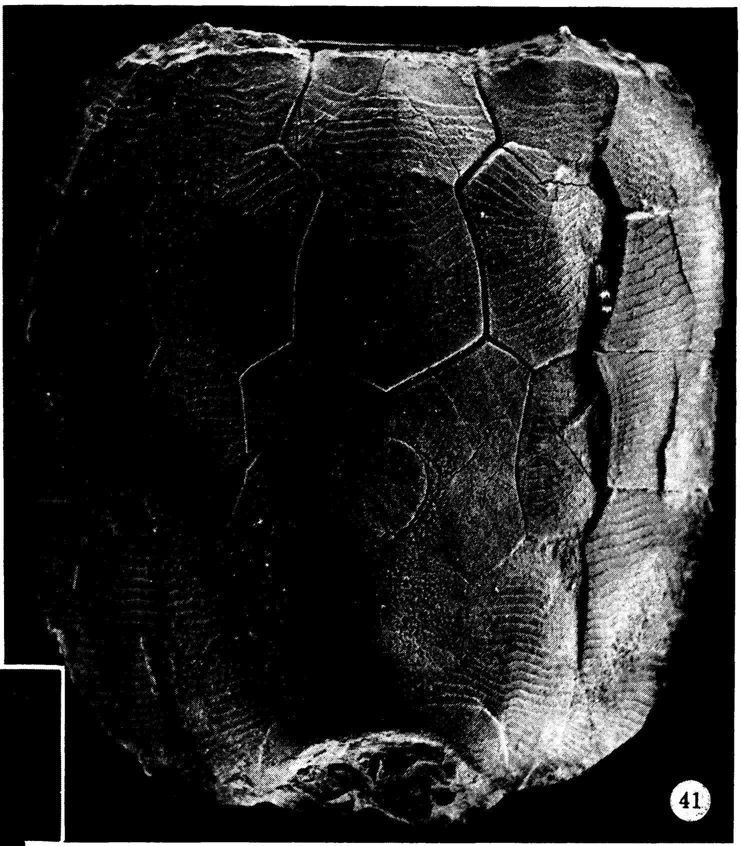
FIGURE 35. The animal x, being the reconstructed latest common ancestor of Petromyzontida and gnathostomes (for phylogenetic position see figure 33). (*a*) Entire animal; IX, X and dr$_7$ represent the bases of the corresponding nerves. (*b*) Anterior end to show cranial nerves. (*c*) Trigeminal ganglion and nerves. (*d*) Elements derived from mitrate head. (*e*) Elements derived from mitrate tail. (*f*) External features. The division into mitrate head elements (colour) and tail elements (black) is based on their presumed phylogenetic derivation from mitrate head or tail tissue, but does not imply that the elements existed as such in mitrates. For example, mitrates would have had no kidneys. O = terminalis nerve; I = olfactory; II = optic; III = oculo-motor; IV = trochlear; V gang, mand, max, pr, sup = trigeminal ganglion and mandibular, maxillary, profundus and superficialis branches; VI = abducens; VII, VII end = facial with endostylar branch; VIII = auditory; IX = glossopharyngeal; X, X_{int}, X_{card} = vagus with intestinal and cardiac branches; XII = hypoglossal. 4, 5, ... 20 = fourth to 20th somites. ac = auditory capsule; ac-lat = acustico-lateralis component; aud = auditory opening; br op = branchial opening; br s = branchial slit; cl = cloaca; dien = diencephalon; dnc = dorsal nerve cord; dr$_7$ = dorsal root posterior to seventh somite; e = eye; end = endostyle; ep gang 5 = fifth epibranchial ganglion; ex r = external rectus muscle; g = gonad; h = heart; hm = hypoglossal musculature; int = intestine; kid = kidney; liv = liver; not = notochord; oc-mot = oculo-motor muscles except the external rectus; oes = oesophagus; pc = pericardium; ph = pharynx; pin = pineal; p pin = parapineal; pvc = perivisceral coelom; R = Rathke's pouch; rhomb = rhombencephalon; S = Seessel's pouch (pre-oral gut); st = stomach; tel = telencephalon; vel = velum; vr$_4$, vr$_{11}$ = ventral root to the fourth and eleventh somites (the existence of a ventral root to the fourth somite has been established in shark embryos by Bjerring, 1970).

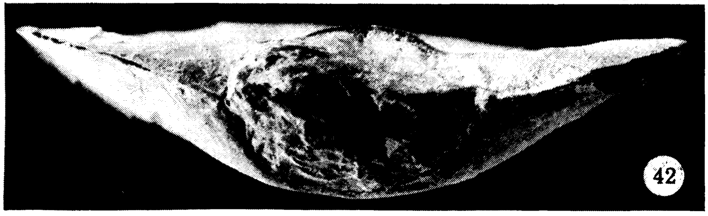


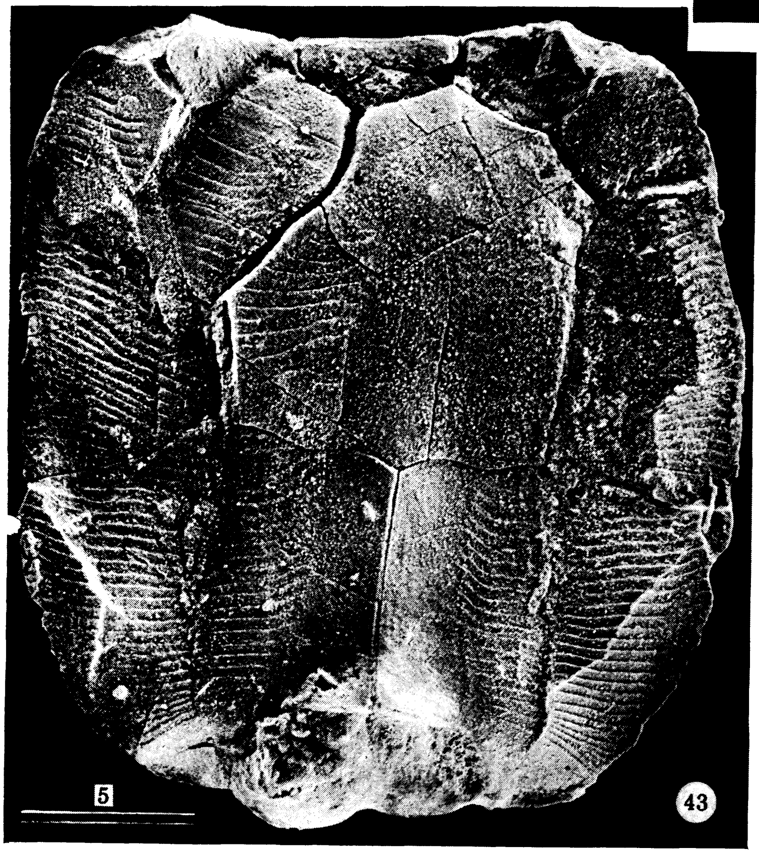


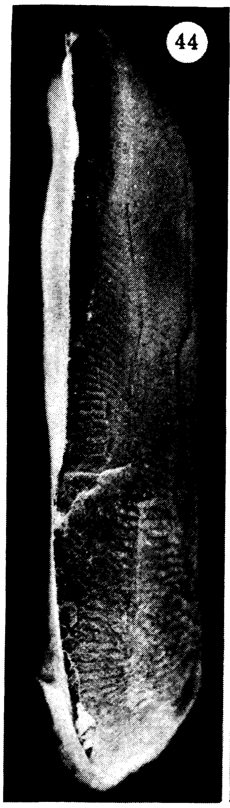


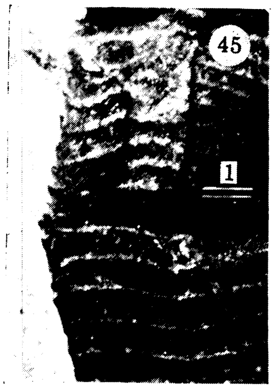


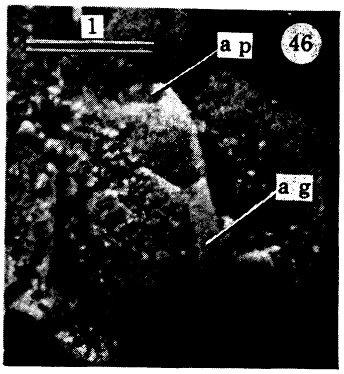




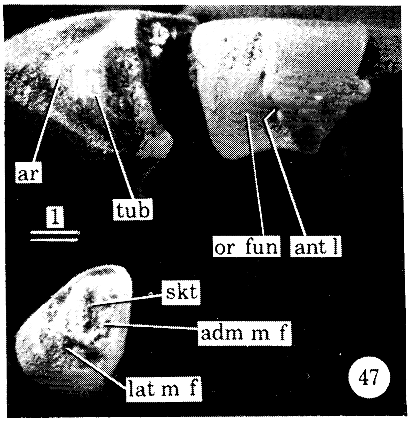


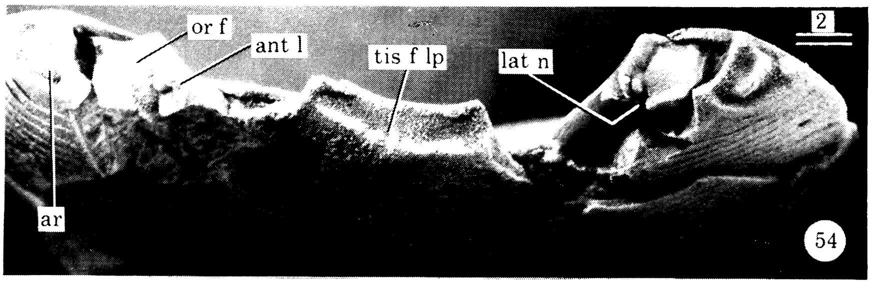


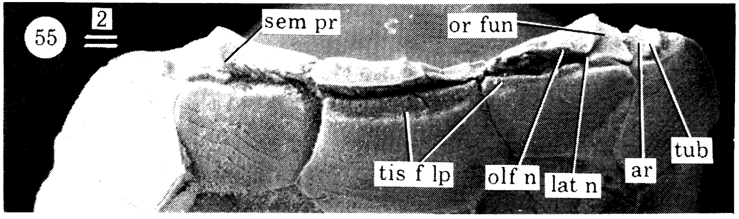


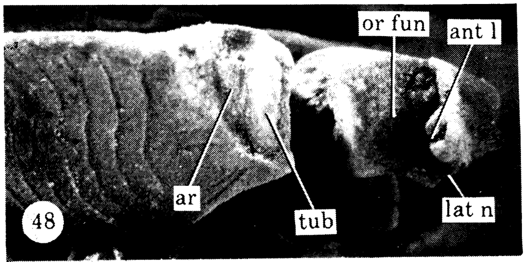


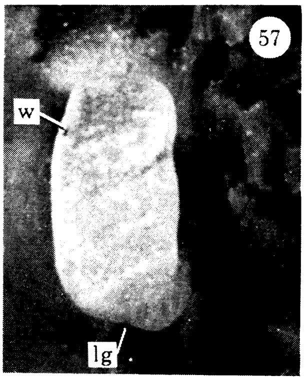
FIGURES 37–46. For description see p. 315.

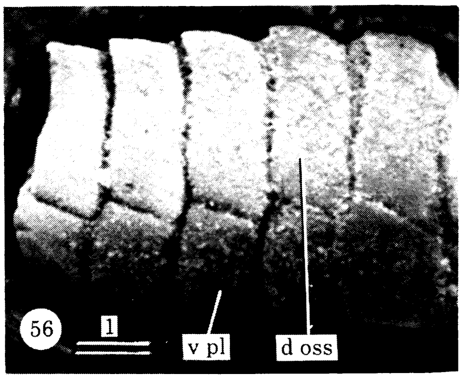


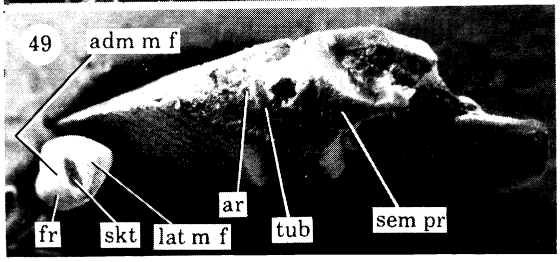


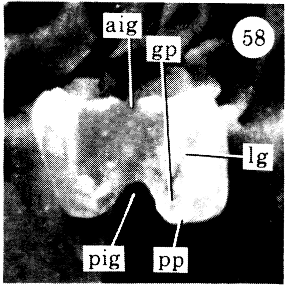


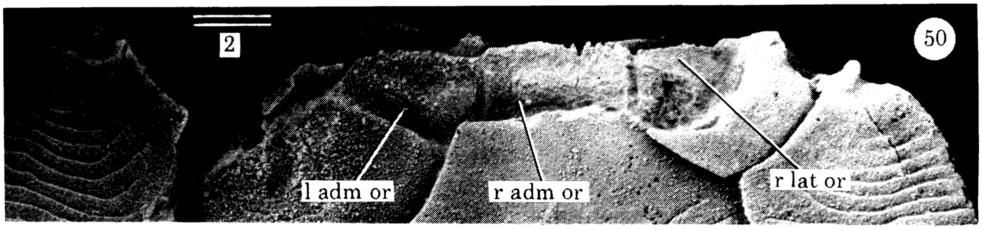


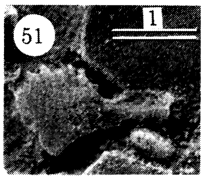


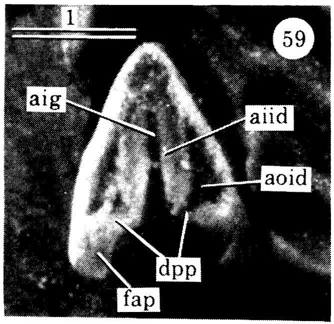


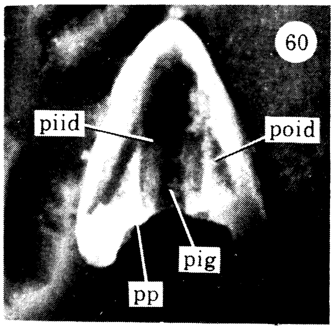


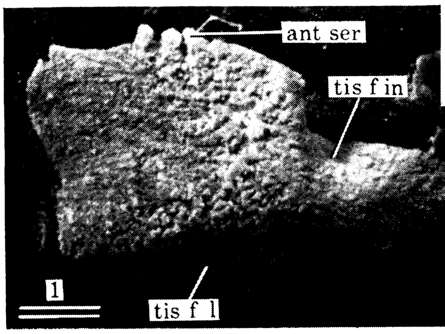


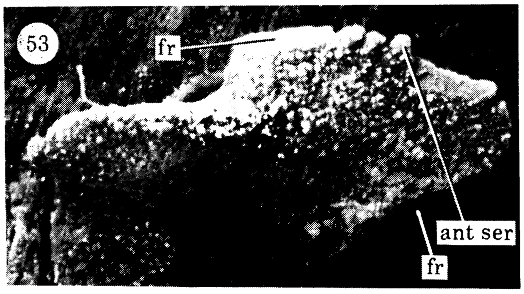


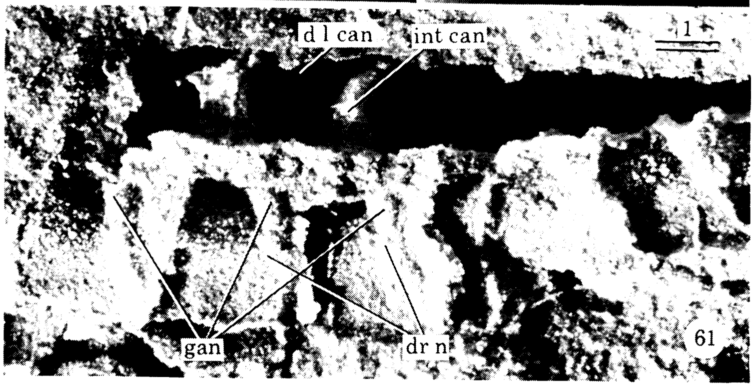




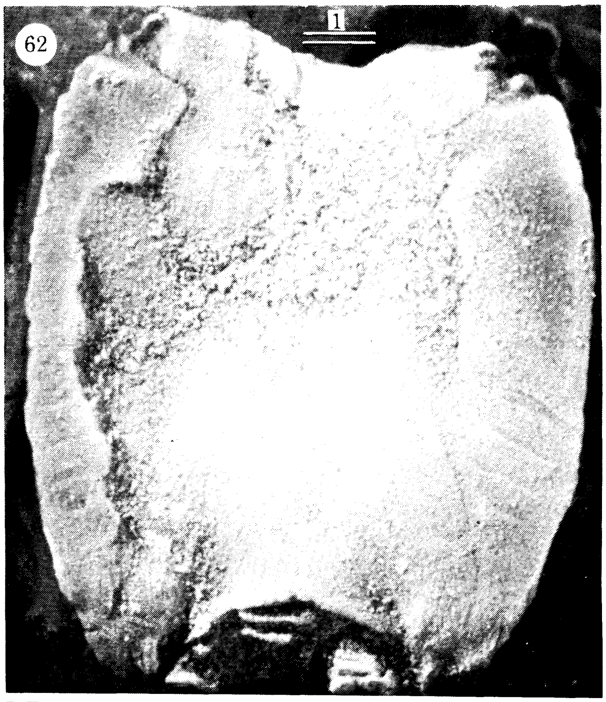


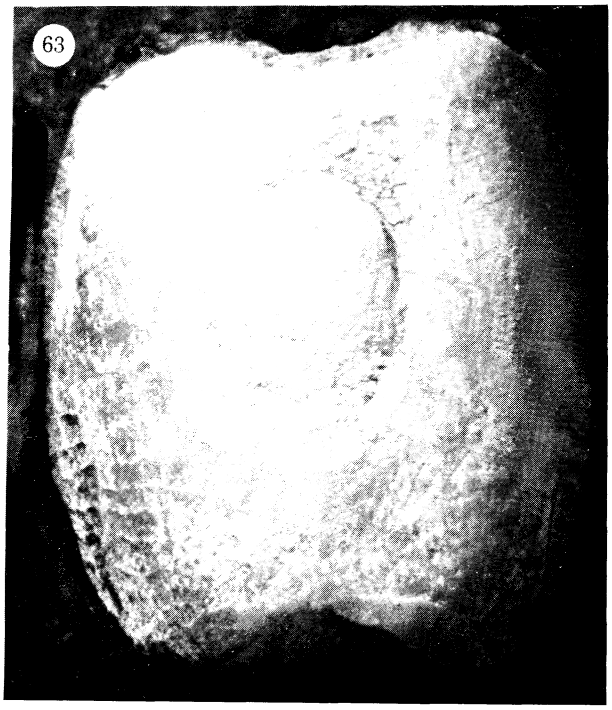


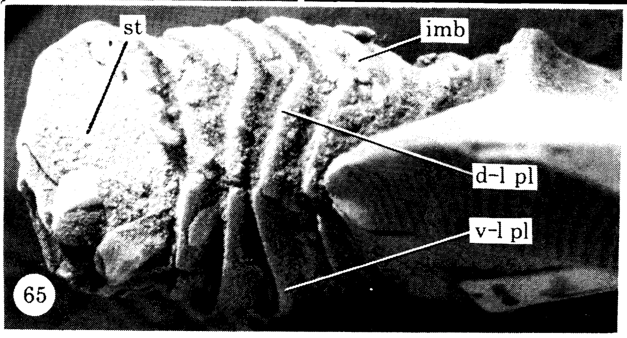


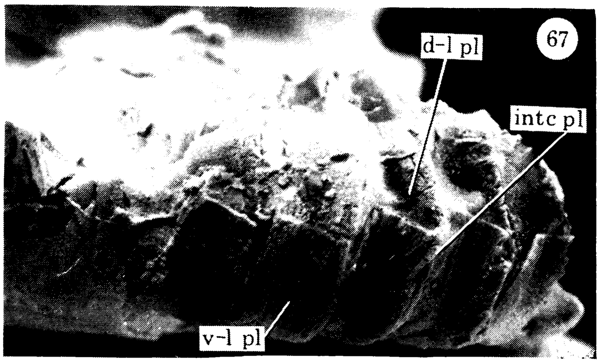


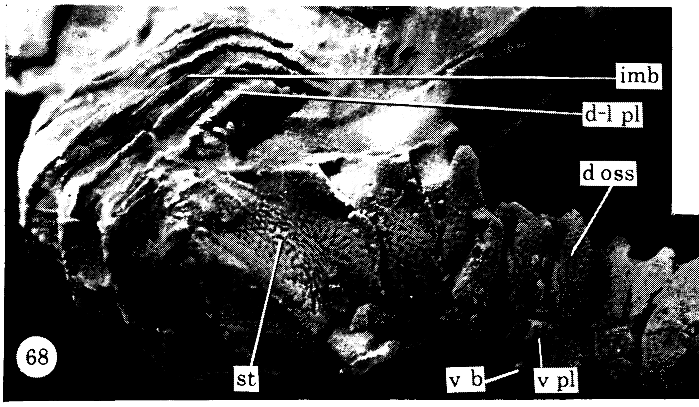
FIGURES 47–61. For description see pp. 315–316.



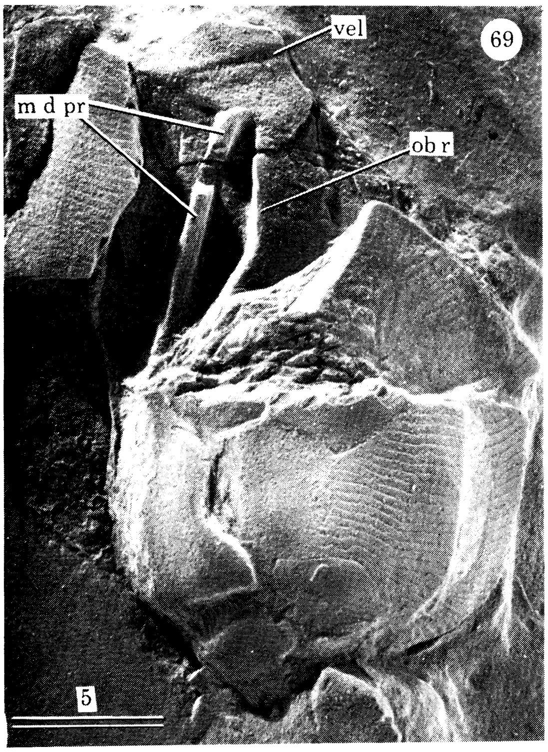


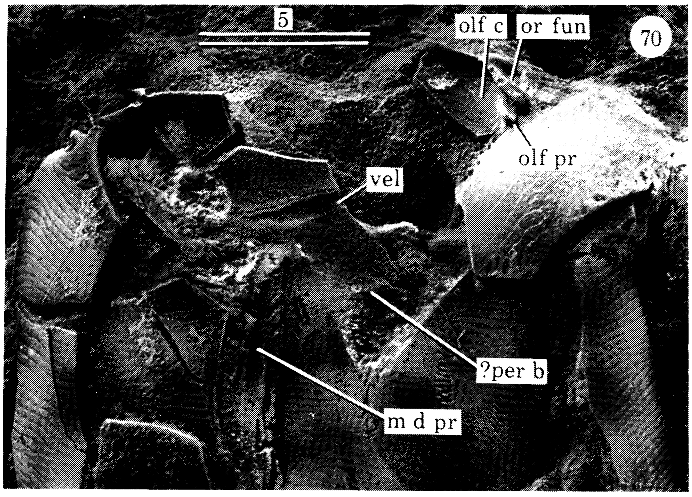


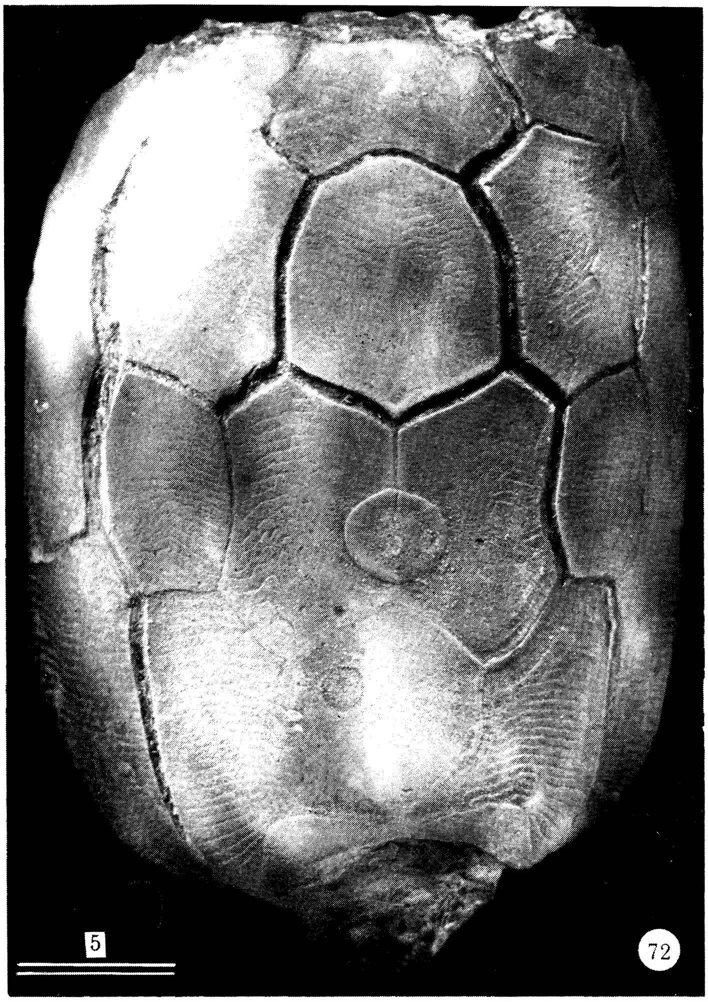


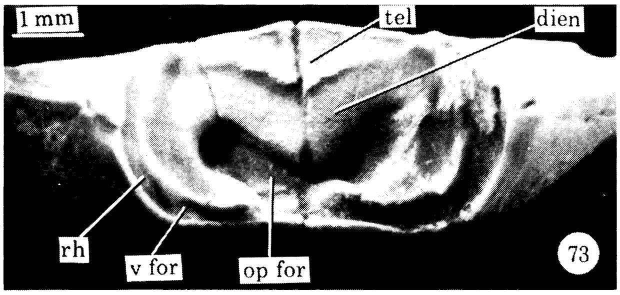


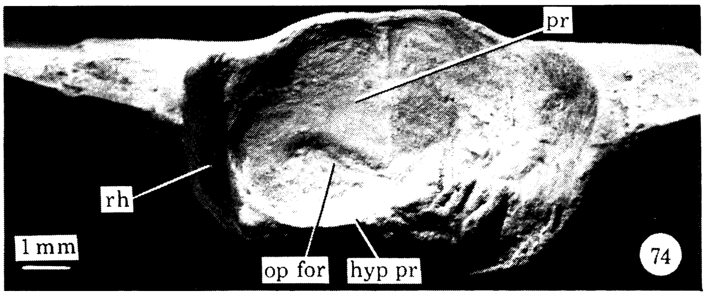
FIGURES 62–68. For description see p. 316.



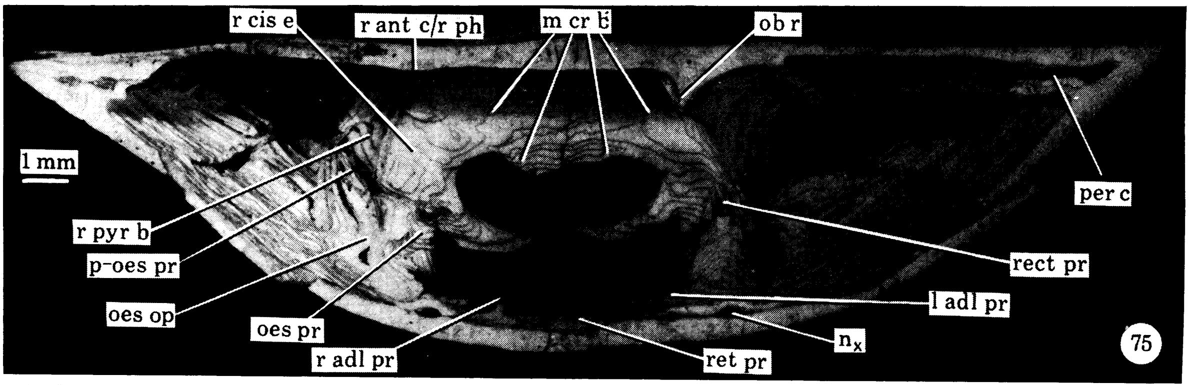


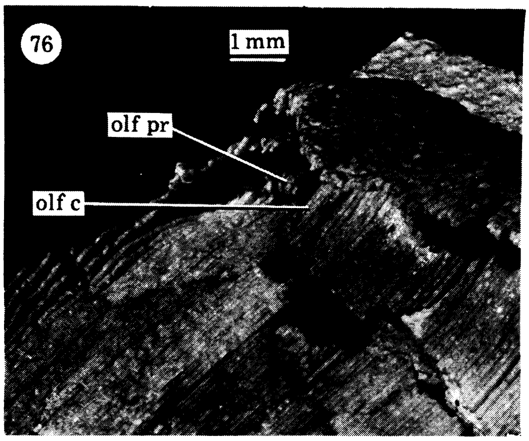


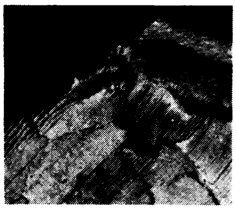


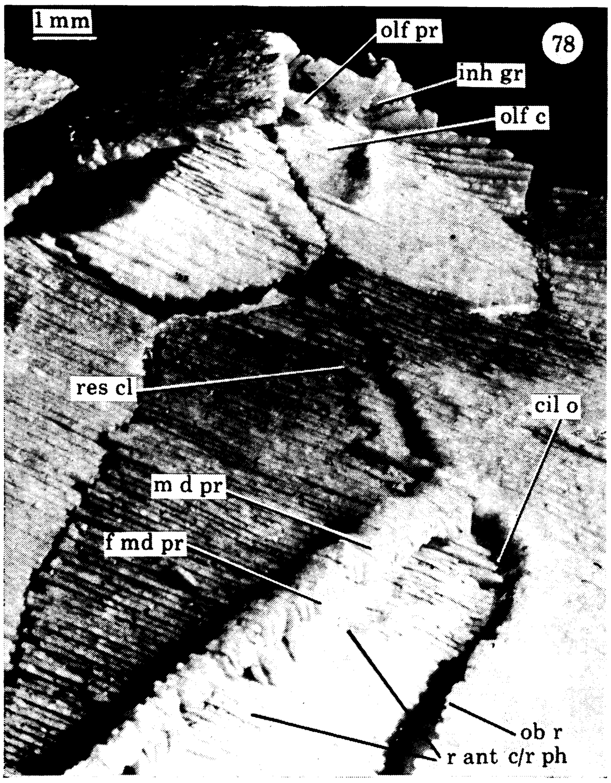


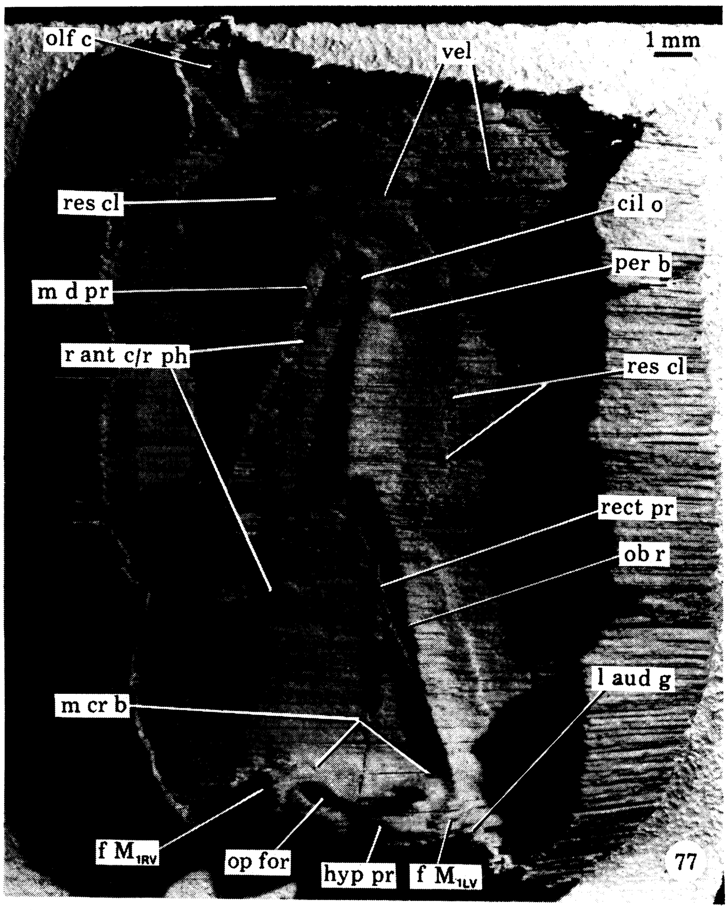
FIGURES 69–74. For description see p. 316.



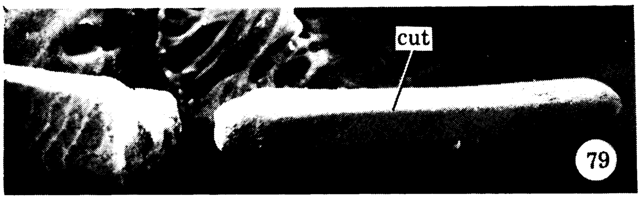


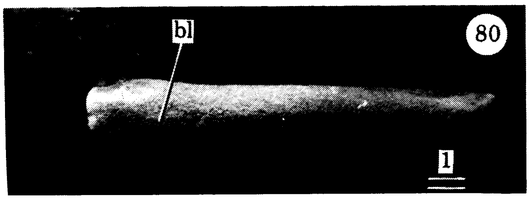


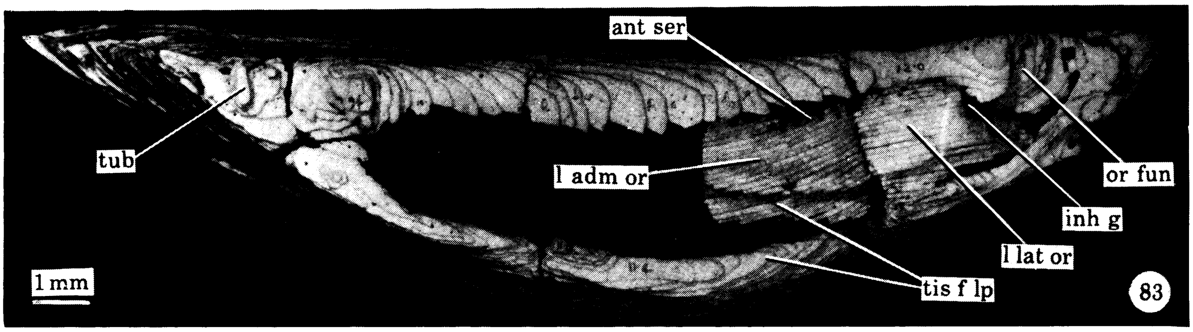


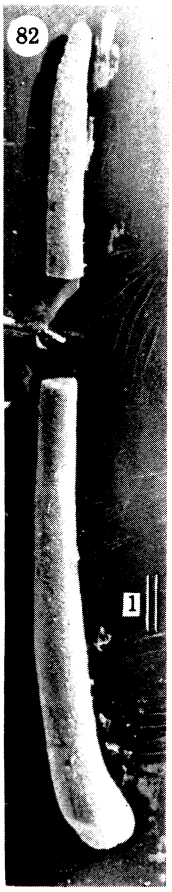


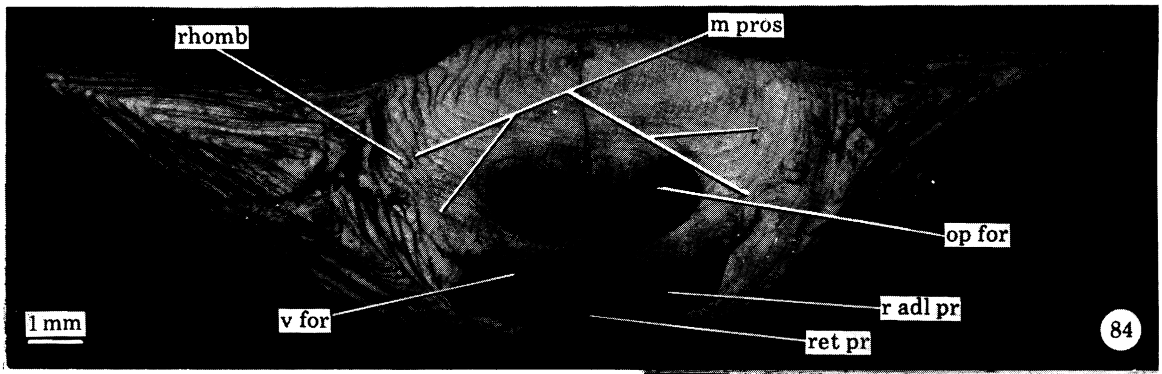
FIGURES 75–78. For description see p. 316.

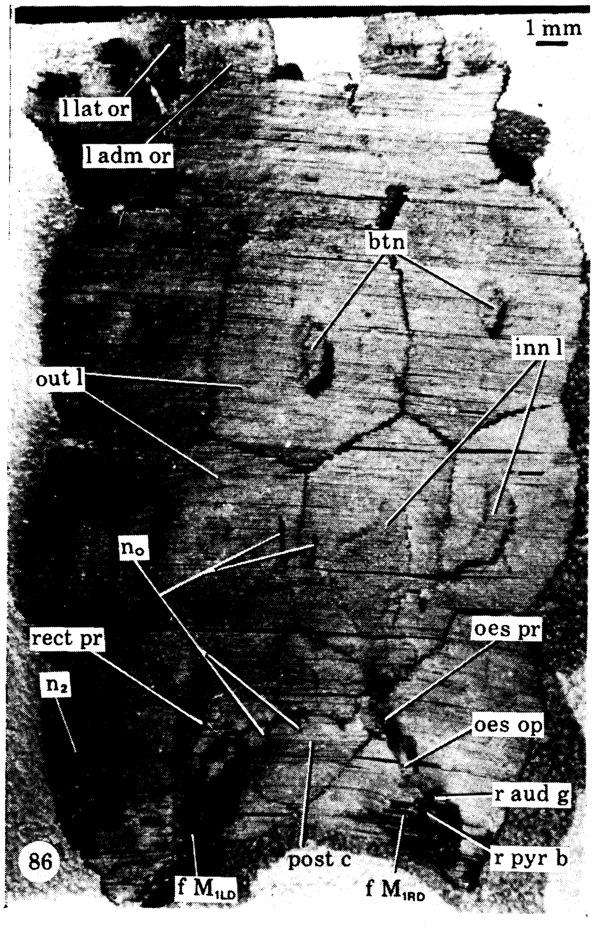


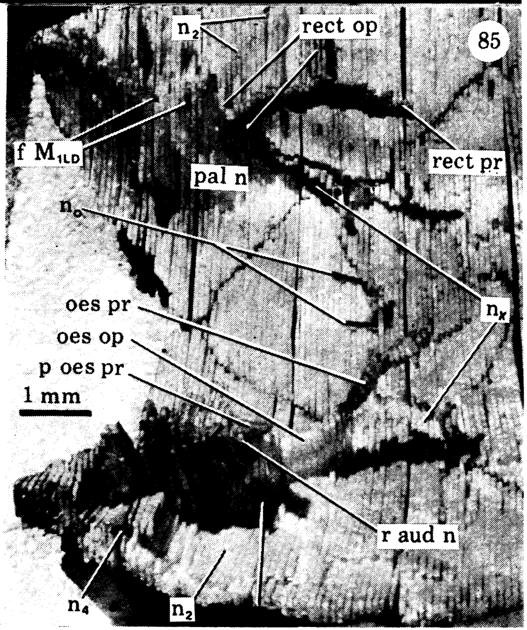


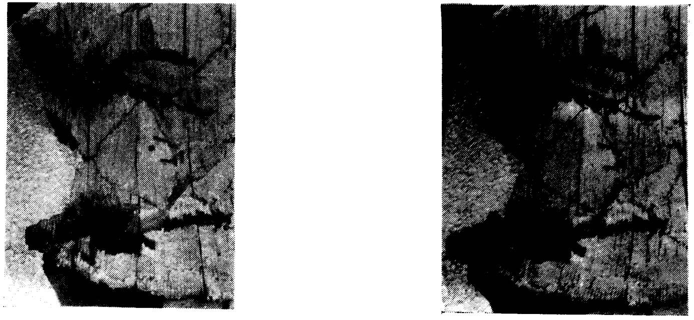




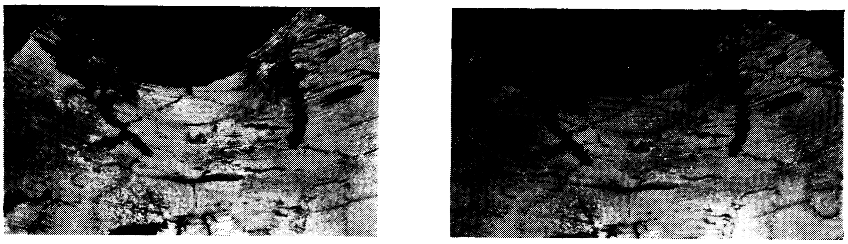


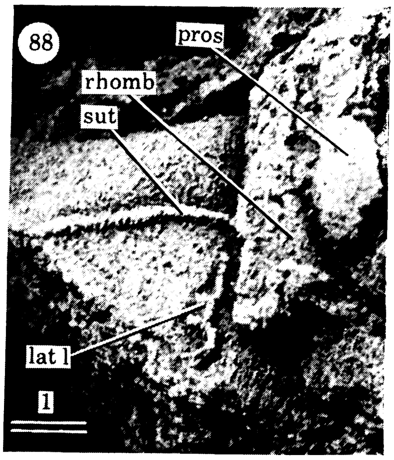


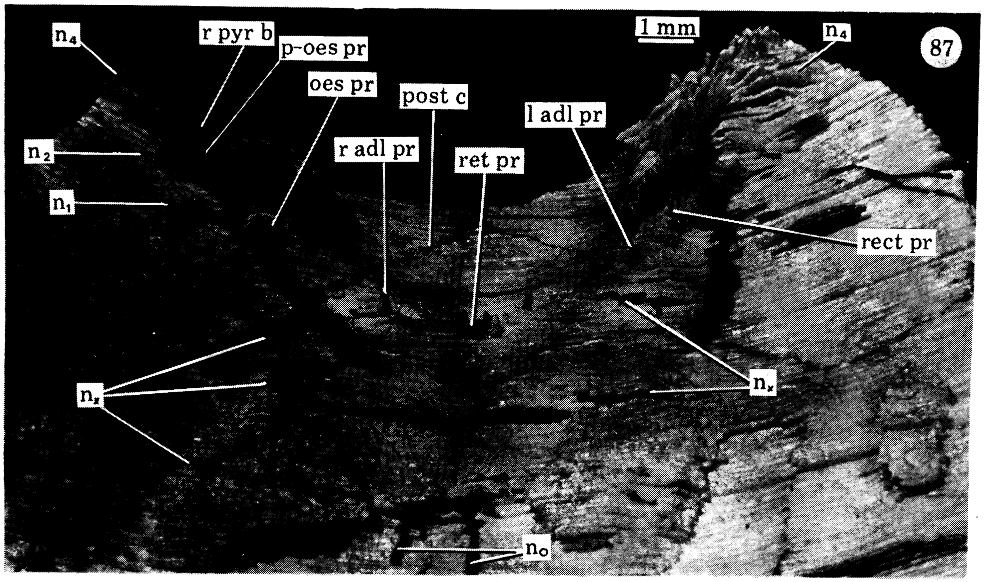


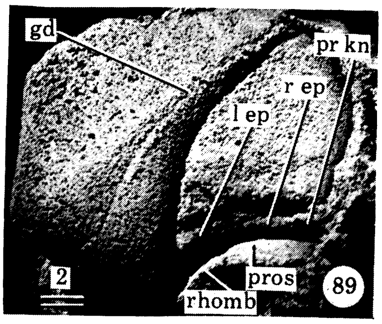


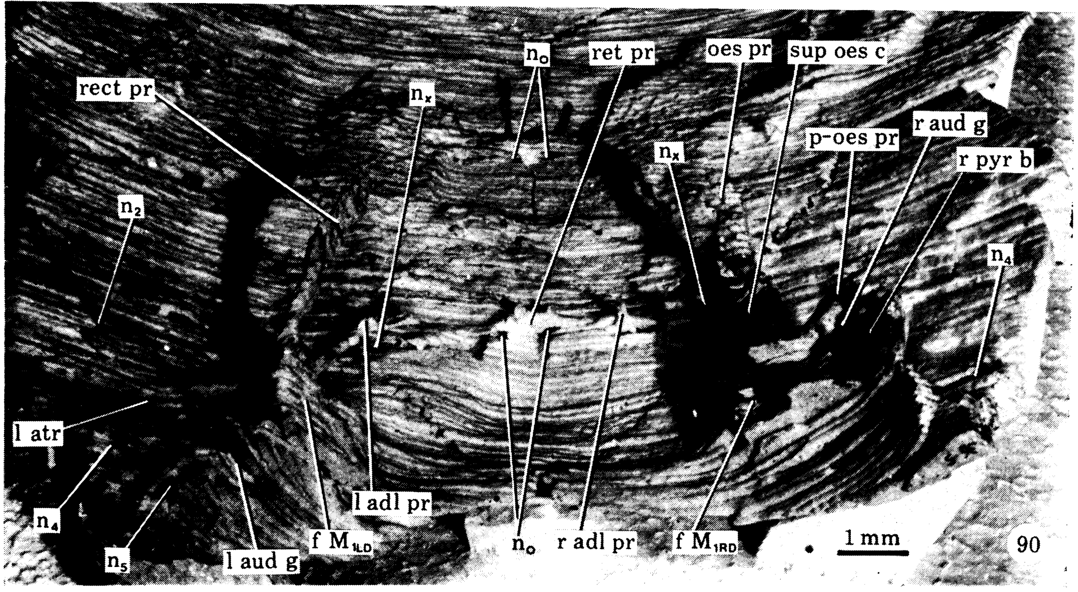
FIGURES 79–86. For description see p. 317.

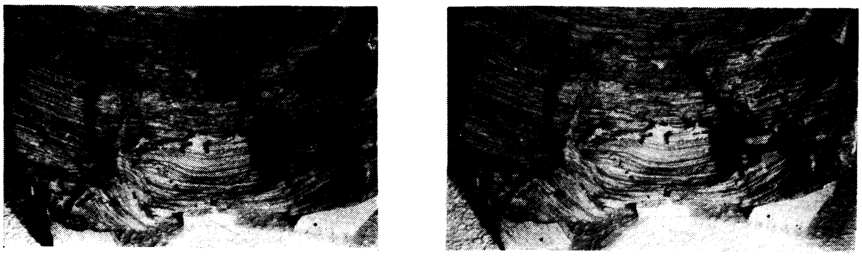


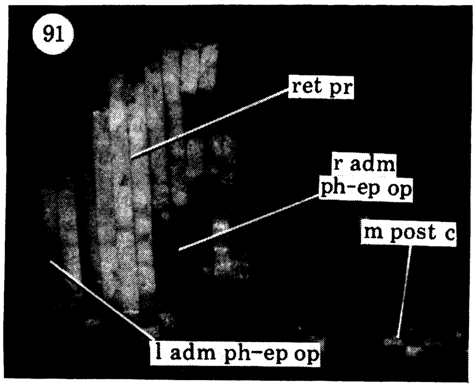




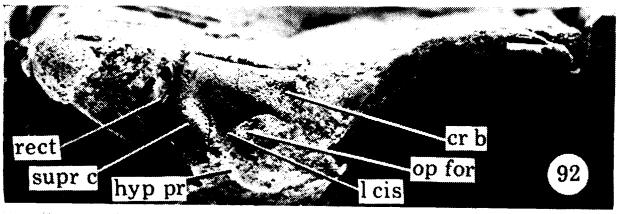


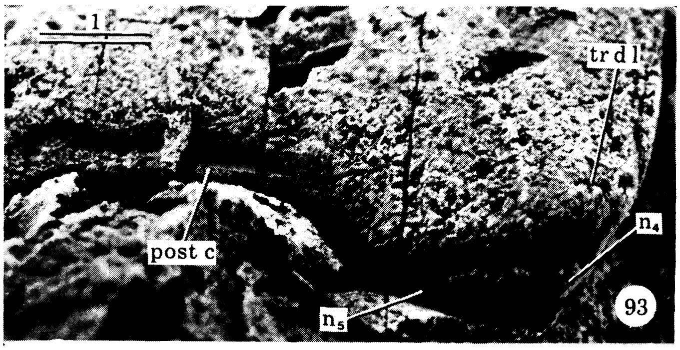


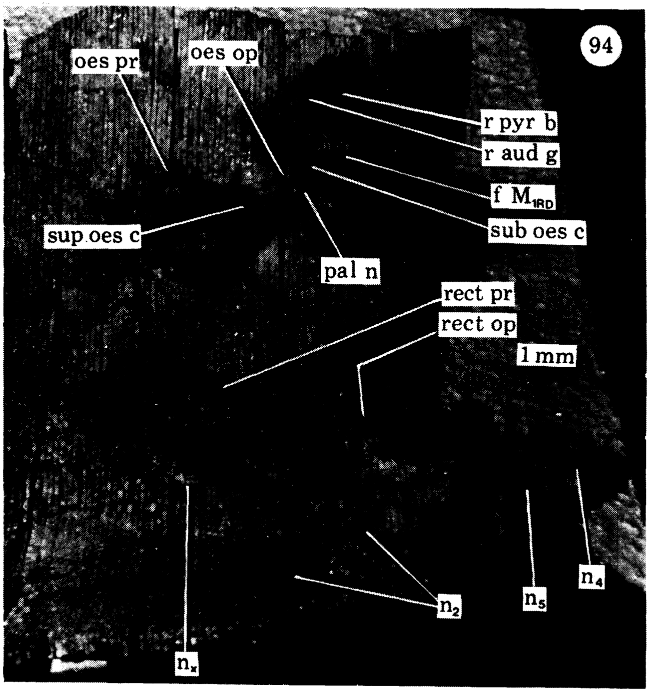


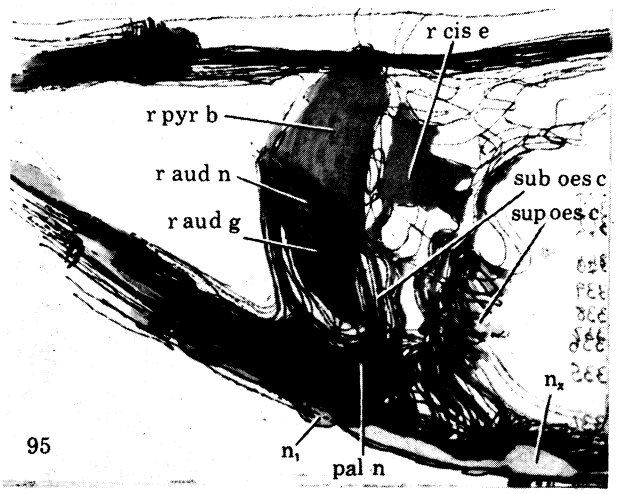


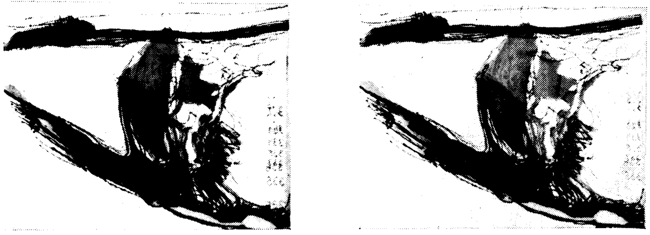
FIGURES 87–91. For description see p. 317.

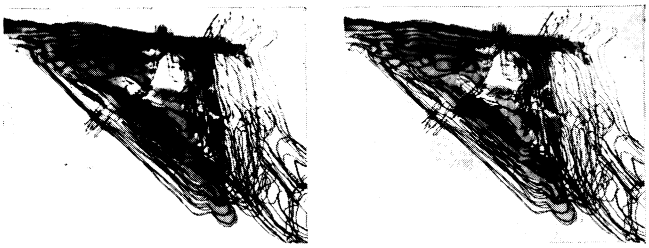


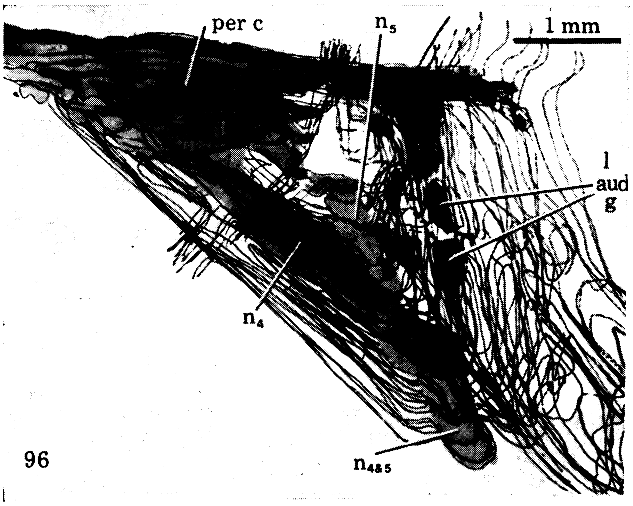


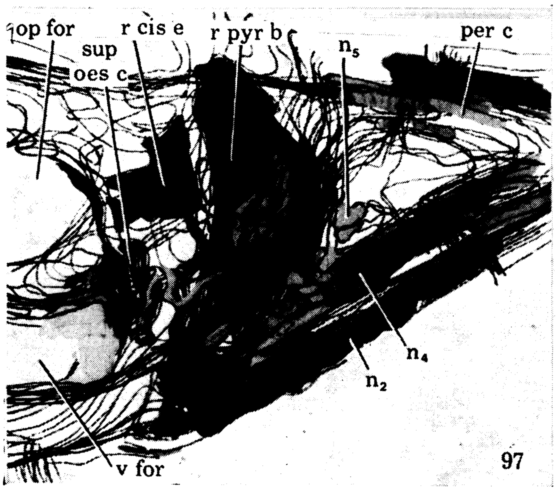


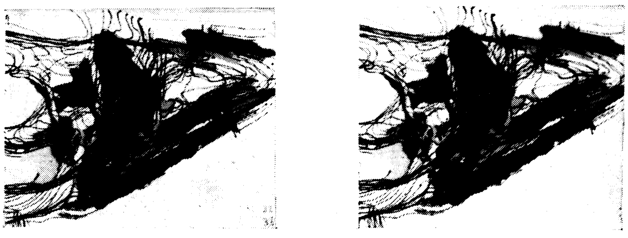




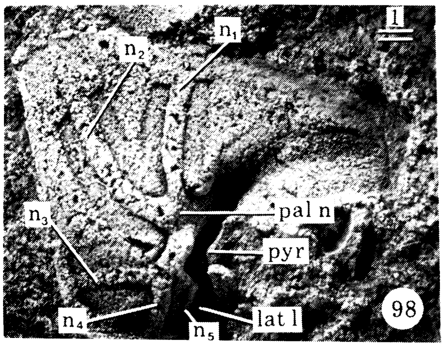


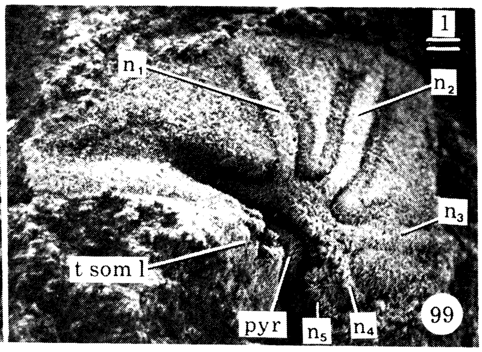


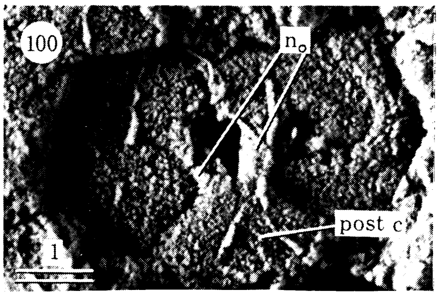


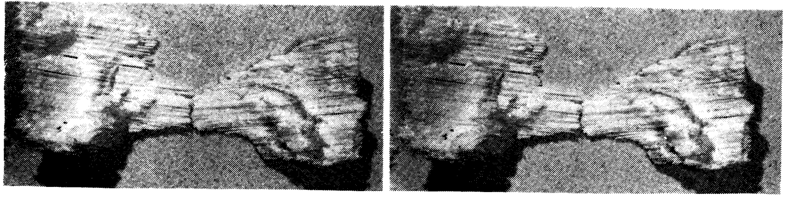


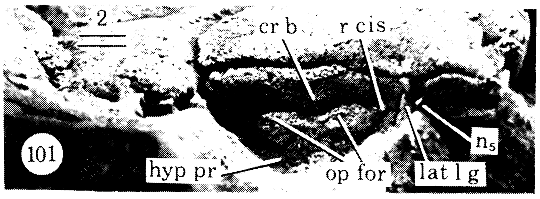
FIGURES 92–97. For description see pp. 317–318.

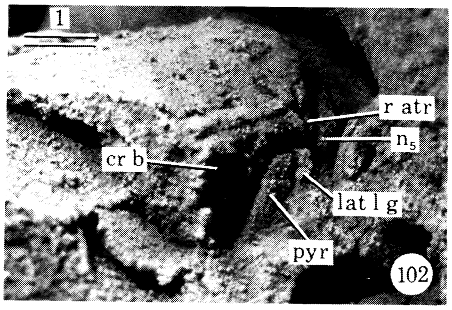


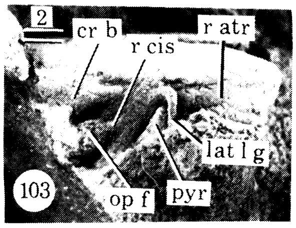


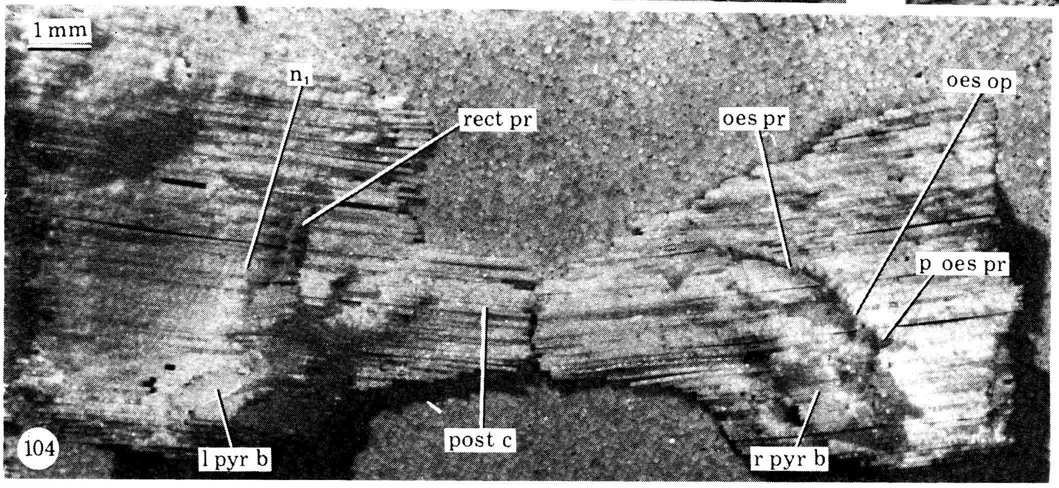


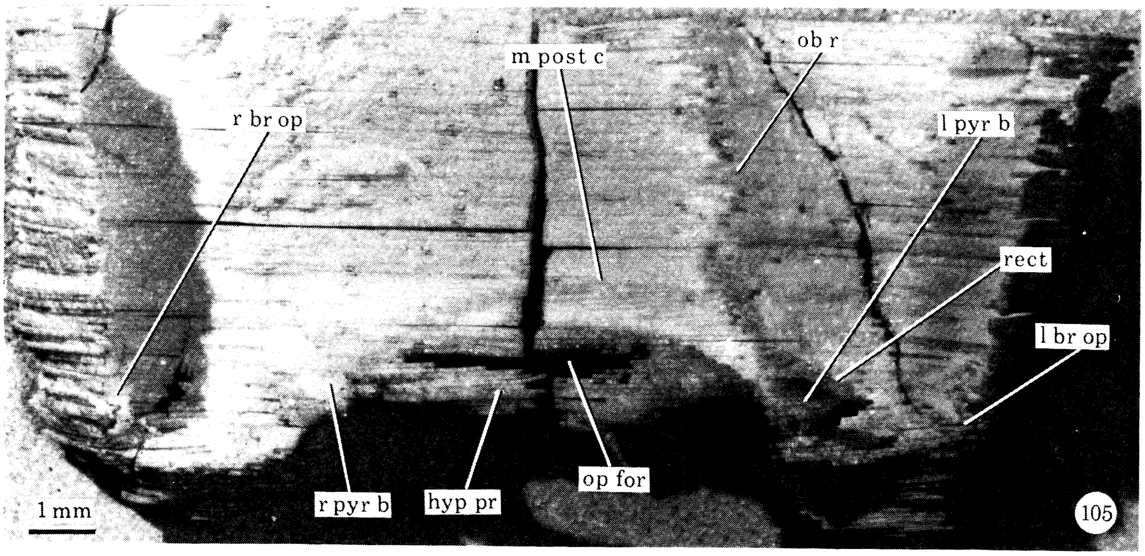




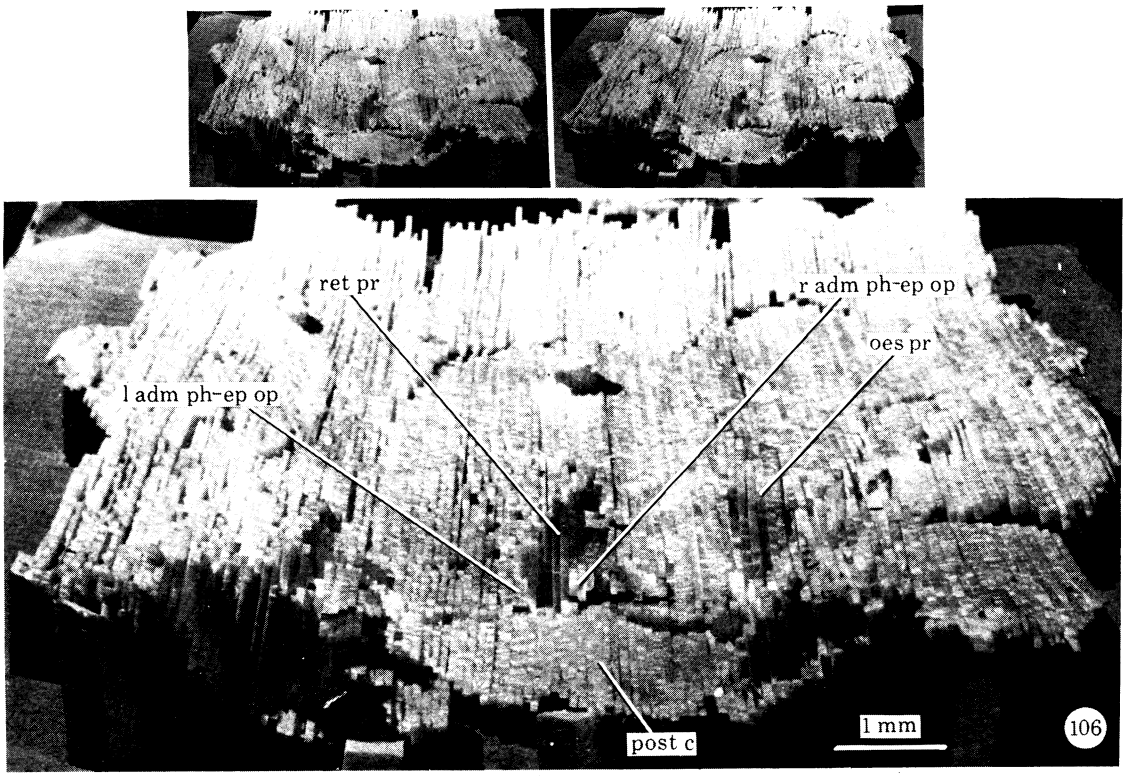


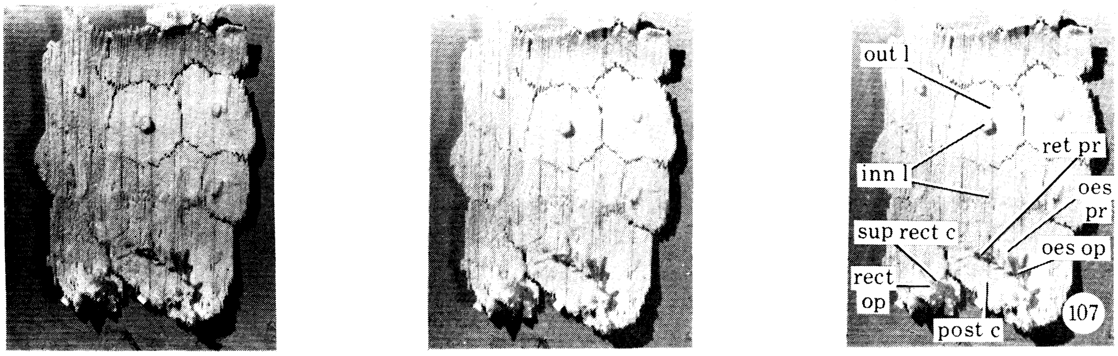




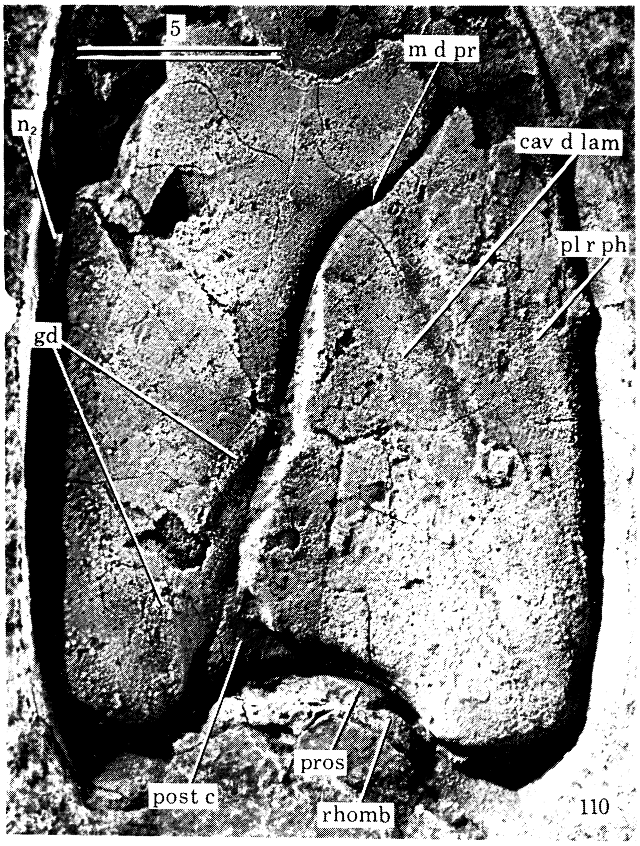


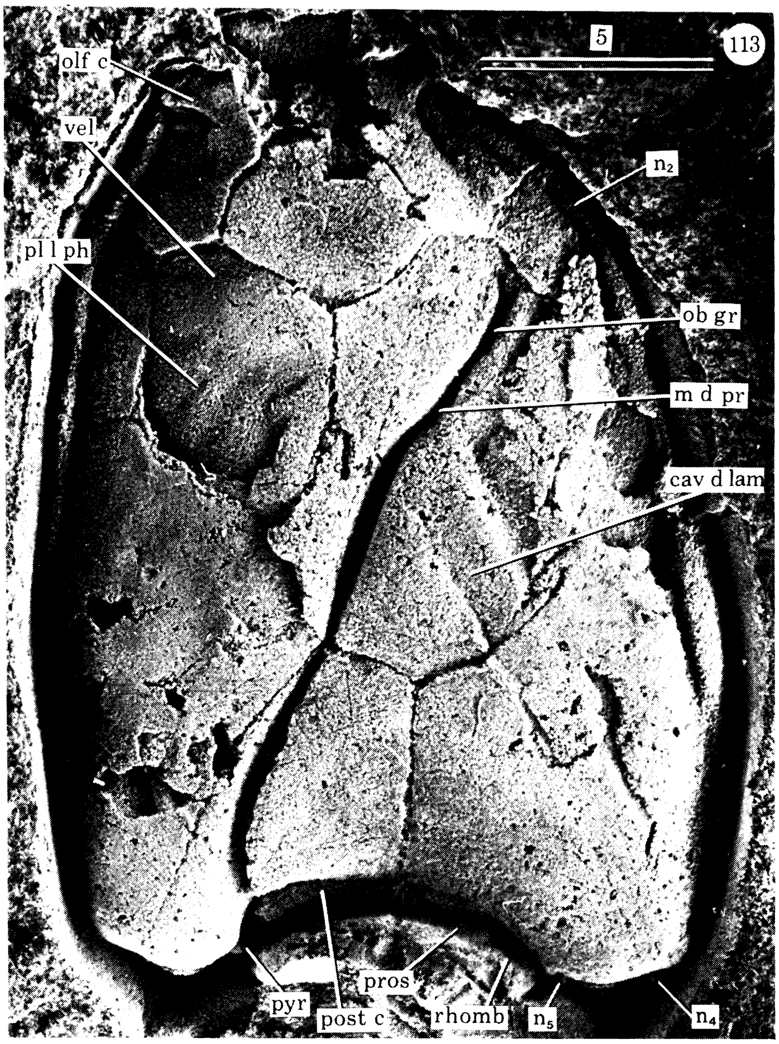
Figures 98–105. For description see p. 318.



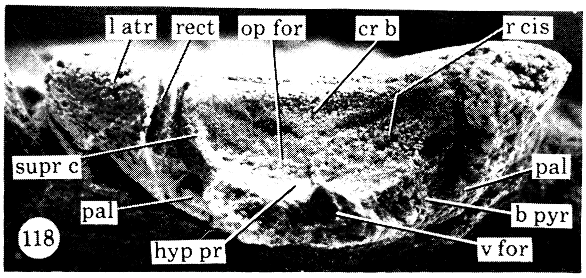


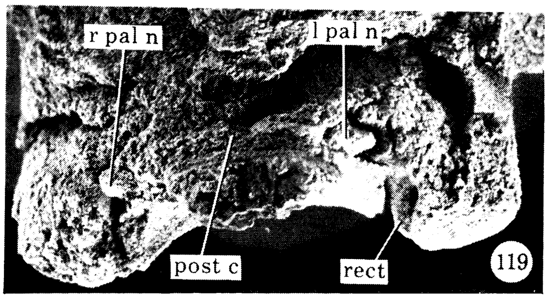
FIGURES 106–109. For description see p. 318.



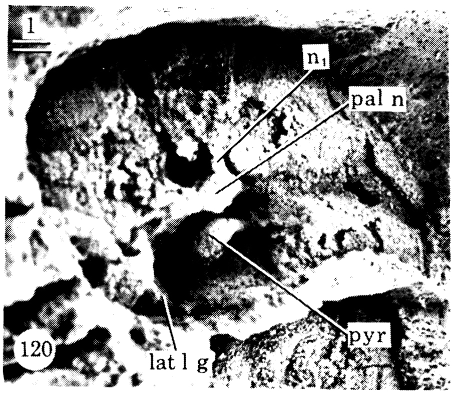


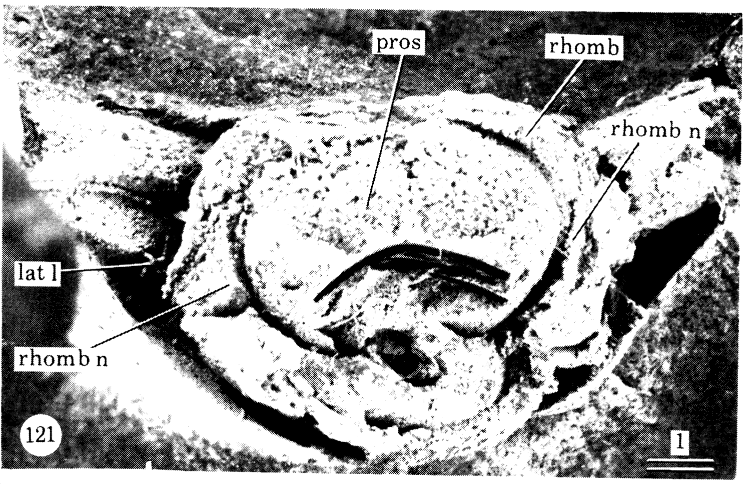
FIGURES 110–113. For description see p. 318.

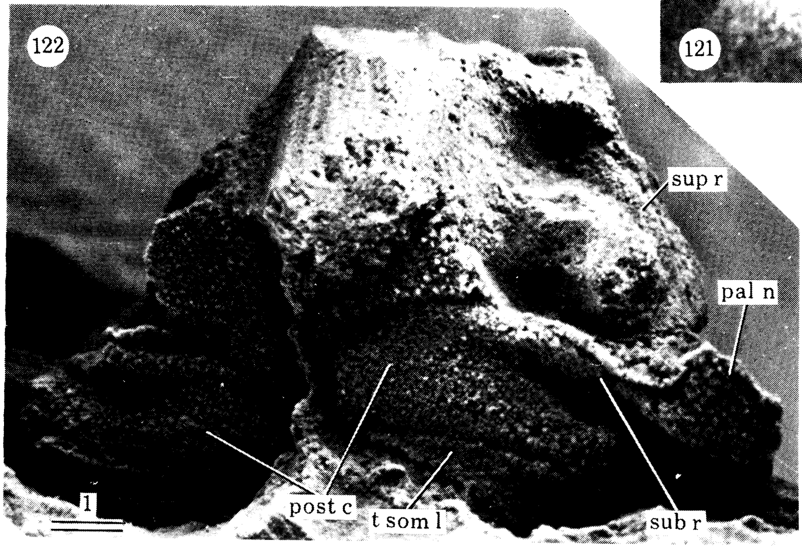


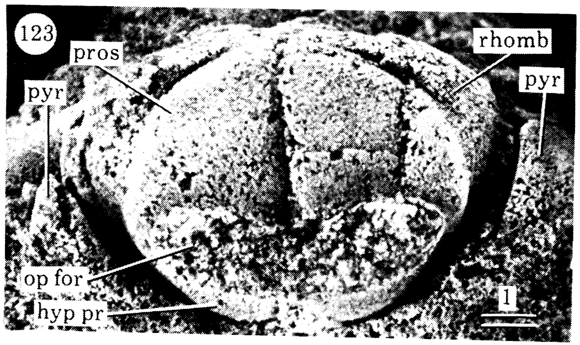


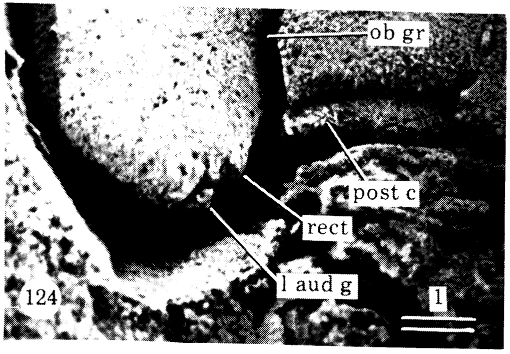
FIGURES 114–119. For description see pp. 318–319.

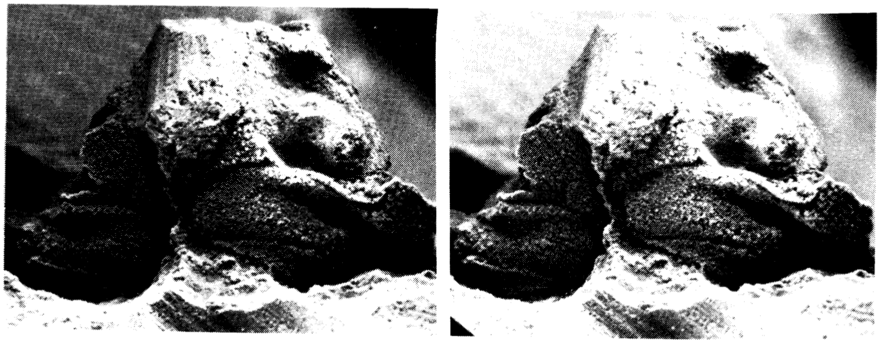


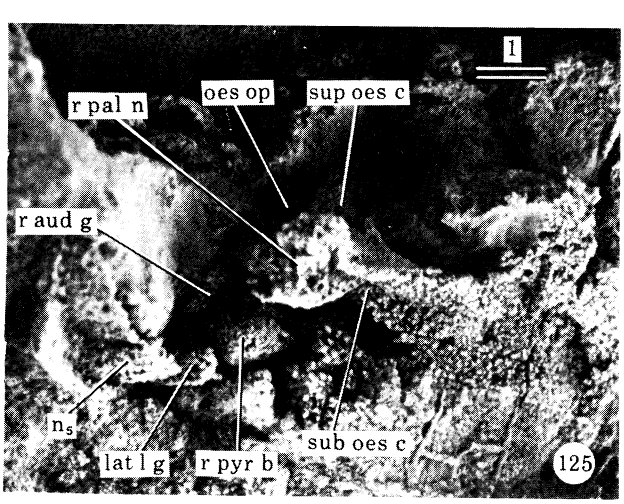


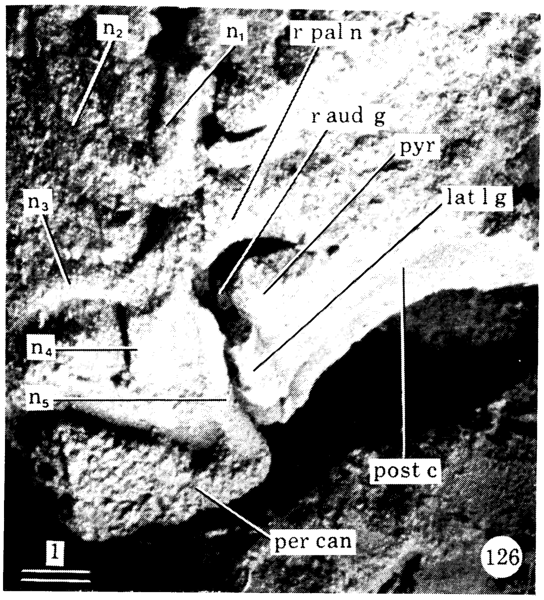




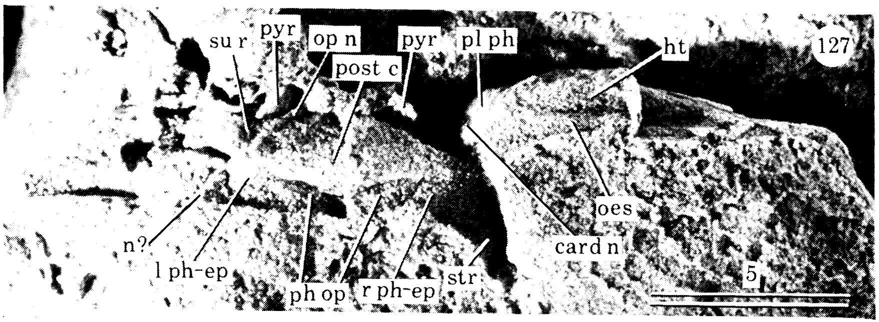


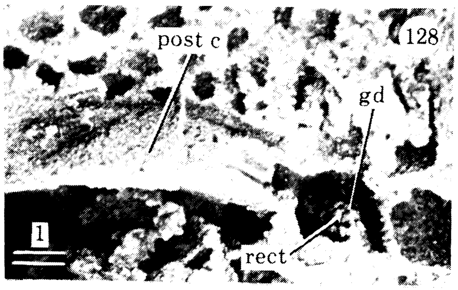


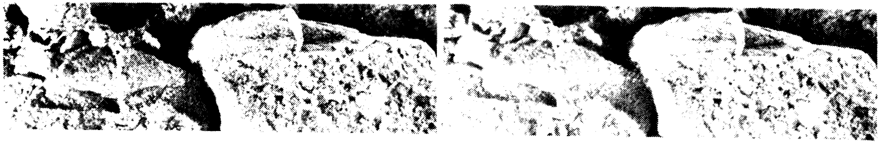


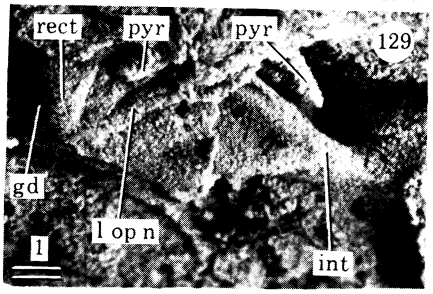


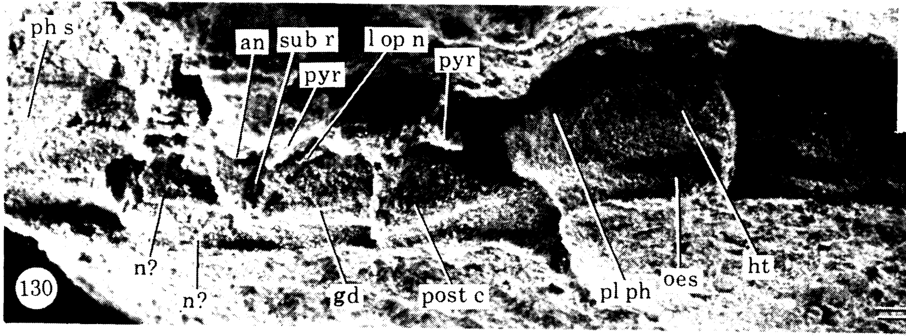
FIGURES 120–126. For description see p. 319.

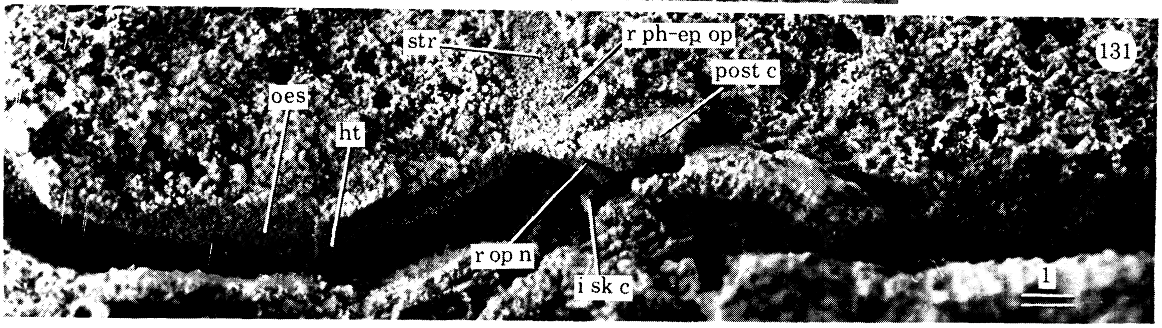


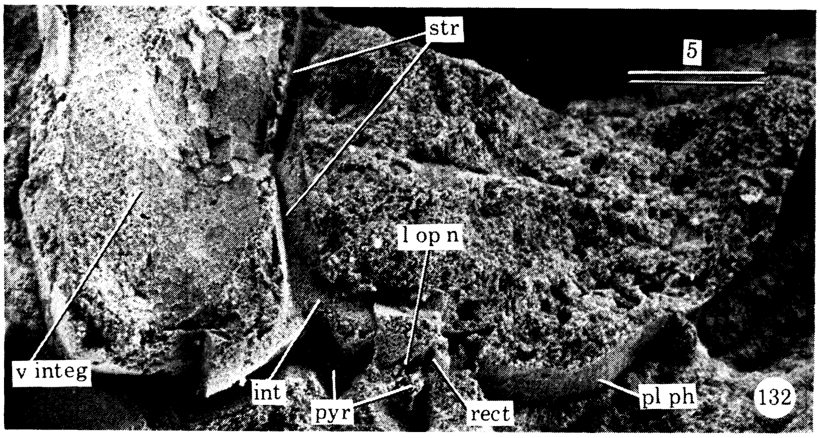


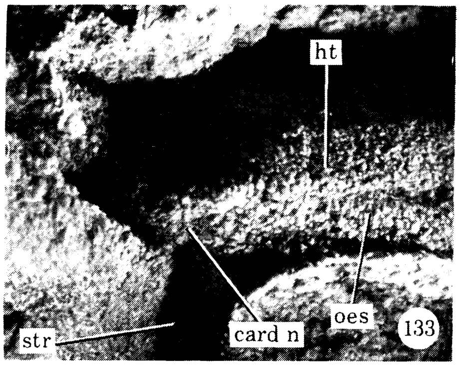


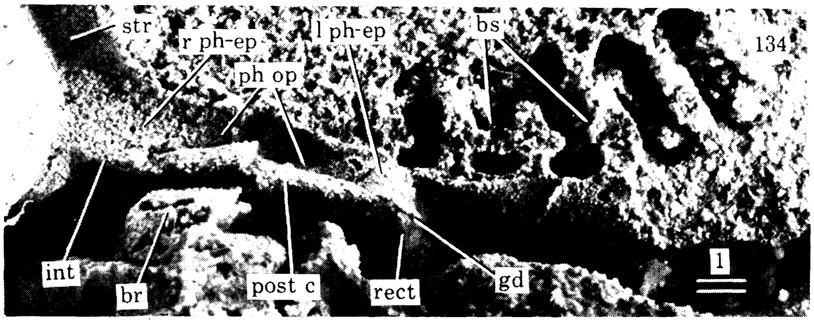


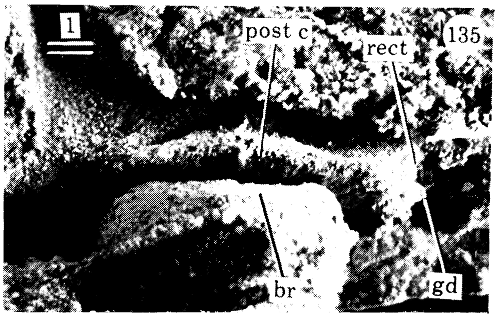




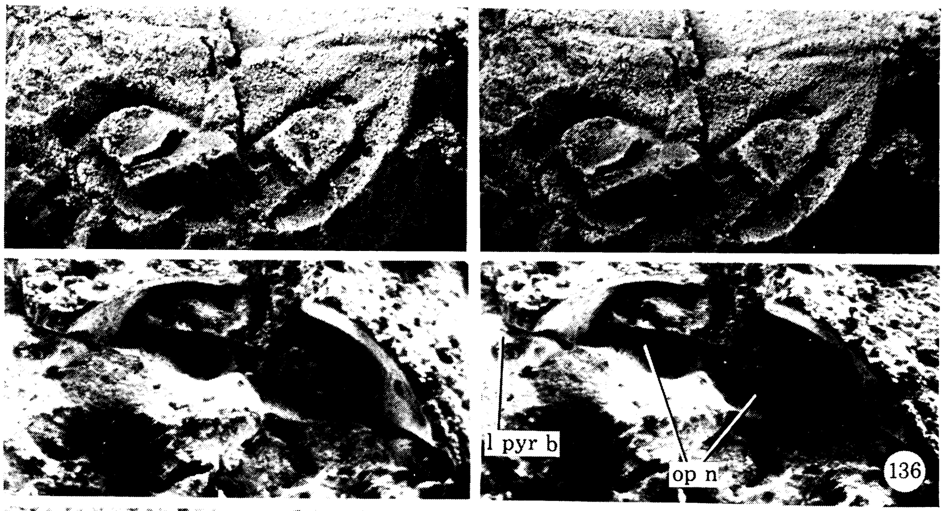


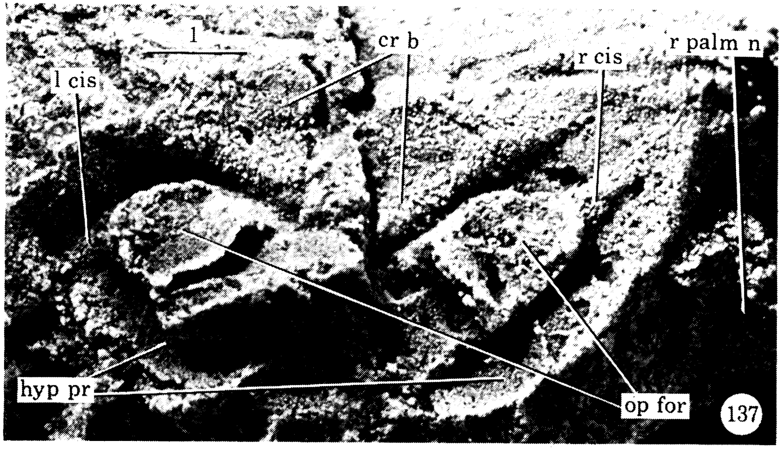


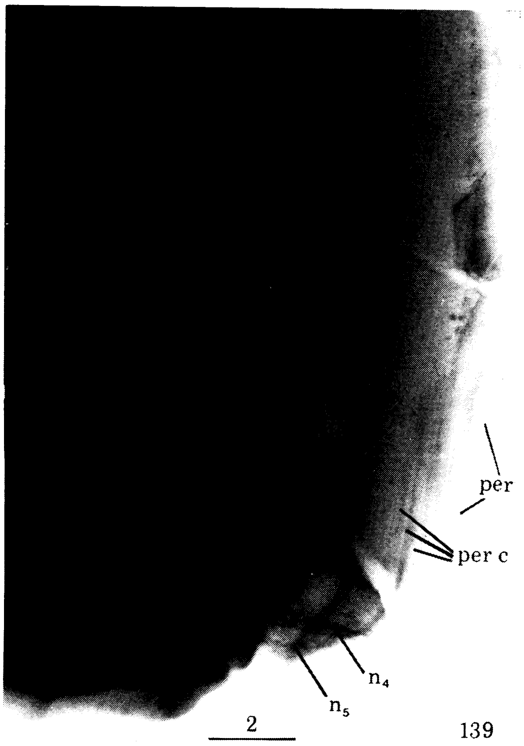


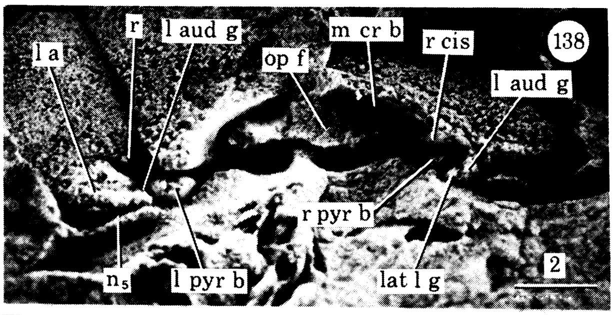


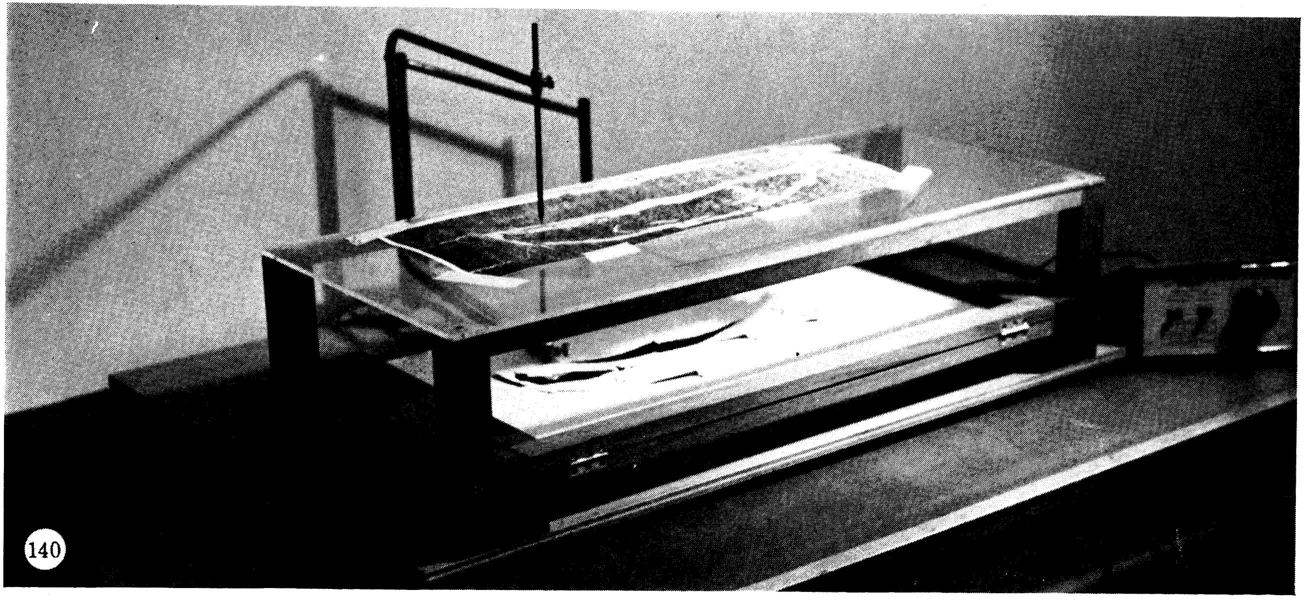
FIGURES 127–135. For description see p. 319.











FIGURES 136–140. For description see p. 319.

DESCRIPTION OF PLATE 6

Placocystites forbesianus from Dudley Limestone, Dudley.

FIGURE 79. Lateral aspect of tubercle and oral spine of same specimen as plate 2, figures 47, 48.

FIGURE 80. Median aspect of tubercle of same specimen. Note that the cutting edge is confined to the outer face of the spine and the facet for muscle attachment is much larger on the lateral than on the median face.

FIGURE 81, 82. Right oral spine (Birmingham University, Holcroft Coll. 27) in ventro-distal and ventral aspect.

FIGURE 83. Transversely sectioned model. Anterior aspect of anterior part of head, with oral plates.

FIGURE 84. Same model. Posterior aspect of head to show cerebral basin. Note the optic foramen (op for), ventral foramen (v for) and the outer margin of the prosencephalon (m pros) in the cerebral cup.

FIGURE 85. Same model. Right anterior aspect of posterior coelom as shown in ventral skeleton. Note the deduced position of the opening of the oesophagus into the pharynx (oes op). The missing label should read: sup rect c. Compare plate 7, figures 87, 90.

FIGURE 86. Same model. Ventral skeleton in dorsal aspect. The inner and outer layers of calcite (inn l, out l) are distinguishable, the inner layer being represented anteriorly by 'buttons' (btn) at the centres of plates. Pieces of string have been inserted in the canals for n_0 and n_2.

DESCRIPTION OF PLATE 7

Placocystites forbesianus from Dudley Limestone, Dudley (figures 87, 90, 91) and *Mitrocystella incipiens miloni* from Schistes à Calymènes, Le Traveusot (figures 88, 89).

FIGURE 87. Antero-dorsal aspect of posterior part of ventral skeleton of transversely sectioned model of *P. forbesianus*.

FIGURE 88. *M. incipiens miloni* (Université de Rennes 15433). Natural mould of part of brain and of external posterior surface. Note branched lateral line (lat l) and brain divided into prosencephalon (pros) and rhombencephalon (rhomb).

FIGURE 89. *M. incipiens miloni*. Dorsal aspect of natural internal mould of left posterior part of the head (BMNH E29238). Note the division of the posterior coelom by a groove probably into left and right epicardia (l ep, r ep); note also precerebral knot (pr kn).

FIGURE 90. Postero-dorsal aspect of posterior part of ventral skeleton of transversely sectioned model of *P. forbesianus*. Note the retropharyngeal process (ret pr) situated more over the right than over the left canal n_0 (the piece of string in the left canal has been shifted leftwards). Note the concave proximal portion of the oesophageal process (sup oes c). This portion is deduced to have borne the supra-oesophageal component of the right palmar nerve.

FIGURE 91. Postero-dorsal aspect of the retropharyngeal process of the longitudinally sectioned model of *P. forbesianus* (compare pl 10, figure 106). This leans rightwards towards the oesophageal opening and has the left and right admedian pharyngo-epicardial openings on each side of it (r & l adm ph-ep op).

DESCRIPTION OF PLATE 8

Mitrocystella incipiens miloni from Schistes à Calymènes, le Traveusot (figures 92, 93) and *Placocystites forbesianus* from Dudley Limestone, Dudley (figures 94 to 97).

FIGURE 92. *M. incipiens miloni* (BMNH E28888). Posterior aspect of internal natural mould of head (see also plate 12, figure 114). Note crescentic body (cr b), left cispharyngeal optic nerve (l cis) and rectum. Compare figure 17, plates 11 and 12, and plate 15, figure 137.

FIGURE 93. *M. incipiens miloni*. Postero-dorsal aspect of internal mould of right posterior portion of head to show probable trace of dorsal lamina (tr d l) where it was attached to the inside of the wall of the head (Université de Rennes 15449).

FIGURE 94. *P. forbesianus*. Left dorsal aspect of posterior part of ventral skeleton in transversely sectioned model. For explanation see plate 7, figure 90.

FIGURES 95, 96, 97. Glass models of nervous system based on transversely sectioned specimen (Birmingham University, Holcroft Coll. 25). Compare reconstructions in figure 25.

FIGURE 95. Anterior aspect of right posterior part of head, sections 309 to 344 only. Note supra- and sub-oesophageal components of palmar nerve (sup oes c, sub oes c, pal n), the right auditory nerve to the right auditory ganglion (r aud n, r aud g), the right pyriform body (r pyr b) and the right cispharyngeal eye (r cis e). As regards the supra- and sub-alimentary components of the palmar nerves compare plate 13, figures 122, 125 (*M. incipiens miloni*).

FIGURE 96. Posterior aspect of left posterior part of head. Sections 353 to 376 only. Note the left auditory ganglion (l aud g).

FIGURE 97. Posterior aspect of right posterior part of head, sections 327 to 360 only. Note right cispharyngeal eye (r cis e) and supra-oesophageal component of palmar nerve (sup oes c).

DESCRIPTION OF PLATE 9

Mitrocystella incipiens miloni from Schistes à Calymènes, le Traveusot.

FIGURE 98. Internal natural mould of plate M_{1RV} showing the right palmar complex in ventral aspect (Université de Rennes 15070).

FIGURE 99. Left palmar complex showing as internal mould of plate M_{1LV} in ventral aspect (Université de Rennes 15693).

FIGURE 100. Internal natural mould of the small median ventral plate V_{PM} (Université de Rennes 15091). Note the paired endostylar nerves (n_0) running forwards out of the posterior coelom (post c).

FIGURE 101. Postero-dorsal aspect of natural internal mould of posterior part of head (BMNH E28886). Note the right cispharyngeal optic nerve (r cis), the crescentic body (cr b) and a crinkle in the dorsal margin of the posterior coelom, perhaps connected with the division of this coelom into two epicardia.

FIGURE 102. Natural internal mould of posterior right portion of head, postero-median aspect (Université de Rennes 15436).

FIGURE 103. Posterior aspect of right portion of internal natural mould (Université de Rennes 15602). Note the right atrium (r atr), right cispharyngeal optic nerve (r cis), the crescentic body (cr b), the right pyriform body (pyr) and the lateral-line ganglion (lat l g).

FIGURES 104, 105. Polystyrene model of *M. i. miloni* based on a natural mould (BMNH E29246). The left pyriform body was broken away and its position is consequently filled by solid polystyrene in the model. The right pyriform body was not entirely surrounded by skeleton, and also was partly broken away. Note that the oesophageal opening (oes op) is farther rightwards than in *P. forbesianus* (compare plate 6, figures 85, 86).

FIGURE 104. Dorsal aspect of posterior part of ventral skeleton (plates M_{1LV}, M_{1RV}).

FIGURE 105. Ventral aspect of posterior part of dorsal skeleton.

DESCRIPTION OF PLATE 10

Longitudinally sectioned model of *Placocystites forbesianus* from Dudley Limestone, Dudley (BMNH E16143).

FIGURE 106. Postero-dorsal aspect of ventral skeleton. Note the retropharyngeal process (ret pr) in the anterior wall of the posterior coelom. Compare plate 7, figures 90, 91.

FIGURE 107. Dorsal aspect of ventral skeleton.

FIGURE 108. Ventral aspect of dorsal skeleton.

FIGURE 109. Antero-ventral aspect of dorsal skeleton to show margin of posterior coelom (m post c) and position of rectum.

DESCRIPTION OF PLATE 11

Mitrocystella incipiens miloni from Schistes à Calymènes, le Traveusot (figures 110, 112, 113) and *Mitrocystites mitra* Šarka Shales, Osek near Rokycany, Bohemia (figure 111).

FIGURES 110, 112, 113. Dorsal aspects of internal moulds of *M. i. miloni.* Note the pleats of the left pharynx in 112, 113 (pl l ph), the possible position of the velum (vel) in 113, the oblique groove dividing the head into the fields of the left and right anterior coeloms (ob gr), the gonoduct (g d), the brain divided into prosencephalon (pros) and rhombencephalon (rhomb), the cavity of the dorsal lamella (cav d lam), and the posterior coelom (post c). Figure 110 is BMNH E29428. Figure 112 is Université de Rennes 15030. Figure 113 is Université de Rennes 15022.

FIGURE 111. Dorsal aspect of internal mould of *M. mitra* (BMNH E16058). Compare figure 16.

DESCRIPTION OF PLATE 12

Mitrocystella incipiens miloni, Schistes à Calymènes, le Traveusot.

FIGURE 114. Dorsal aspect of internal mould of BMNH E28888 (see also plate 8, figure 92). Note the pleats of the left pharynx (pl l ph), gonoduct (gd) and the cavity of the dorsal lamella (cav d lam). Compare plate 11 and figure 17.

Figures 115, 116. Dorsal aspect of internal mould and ventral aspect of mould of dorsal surface of Université de Rennes 15458. Note the median dorsal process (m d pr), the precerebral knot (pr kn), the peripheral canal (per c) and traces of calcite cleavage (calc cl).

Figures 117, 118, 119. An internal natural mould of the head in dorsal, posterior and ventral aspects. (Université de Rennes 15018). Compare figure 17. In figure 118 note the rectum (rect) leading into the left atrium (l atr), and the crescentic body (cr b).

Description of plate 13

Mitrocystella incipiens miloni, Schistes à Calymènes, le Traveusot.

Figure 120. Internal natural mould of plate M_{1RV} in postero-ventral aspect (BMNH E28887). Note the pyriform body and the posterior sub-oesophageal component of the palmar nerve (pal n).

Figures 121, 123. Antero-dorsal aspects of brains (i.e. of rock infilling of cerebral basins) to show division into prosencephalon (pros) and rhombencephalon (rhomb). Note also the lateral line (lat l). Specimens are respectively Université de Rennes 15623 and BMNH E29245.

Figure 122. Dissection of internal mould to show the supra-rectal and sub-rectal components (sup r, sub r) of the left palmar nerve (BMNH E28889). Left ventral aspect.

Figure 124. Dorsal aspect of posterior left portion of head to show left auditory ganglion (l aud g). (Université de Rennes 15623).

Figure 125. Antero-ventral aspect of right palmar nerve (r pal n) to show the supra-oesophageal and sub-oesophageal components (sup oes c, sub oes c) on either side of the oesophageal opening (oes op). Note also the right auditory ganglion (r aud g) and lateral-line ganglion (lat l g) (Université de Rennes 15058).

Figure 126. Right posterior portion of internal natural mould in postero-ventral aspect (Université de Rennes 15110). Note right palmar nerve (r pal n), the nerves branching off it (n_1-n_5) and the right auditory ganglion (r aud g) anterior to the right pyriform body (pyr) and the lateral-line ganglion (lat l g).

Description of plate 14

Cothurnocystis elizae, Starfish Bed, Thraive Glen, Natural internal moulds.

Figures 127, 130, 133. Internal mould of posterior part of the head in postero-ventral aspect (BMNH E23722). Compare Figure 26. In Figure 130 the aspect is more posterior than in Figure 127. Figure 133 is a detail of the region of the right part of the posterior coelom to show the possible cardiac nerve (card n).

Figure 128. Internal mould of region of posterior coelom in ventral aspect (BMNH E23161). Note especially the gonoduct and rectum (gd, rect) inside plate M_{1LD}.

Figure 129. Posterior coelom, posterior aspect (BMNH E23761).

Figure 131. Internal mould of posterior part of head in ventral aspect, lying on its dorsal surface (BMNH E28425).

Figure 132. Postero-ventral aspect of internal mould of BMNH E28667. Note the intestine (int) passing out of the right anterior coelom into the posterior coelom and also the pharyngeal pleats (pl ph).

Figure 134. Posterior coelom and associated structure in ventral aspect (BMNH 28417). Note the gonoduct (gd) and right and left pharyngo-epicardial openings (r ph-eph, l ph-ep).

Figure 135. Ventral aspect of posterior coelom and brain in BMNH E28560. Note gonoduct (gd).

Description of plate 15

Mitrocystites mitra from Šarka Shales, Osek, *Mitrocystella incipiens miloni* from Schistes à Calymènes, le Traveusot, and *Placocystites forbesianus* from Dudley Limestone, Dudley.

Figures 136, 138. *M. mitra*. Postero-dorsal aspect of posterior part of natural internal mould of head (BMNH E7517). Figure 136 is a scanning electron micrograph and figure 138 is a light micrograph. Figure 136 shows the optic nerves (op n) running ventrally backwards from the optic foramen. Figure 138 shows details of nervous system, especially the right cispharyngeal eye (r cis).

Figure 137. *M. incipiens miloni*. Posterior aspects of internal natural mould of the head (Université de Rennes 15065). Note the left and right cispharyngeal optic nerves (l cis, r cis) extending from the optic foramen (op for) and the crescentic body between them (cr b). Compare figure 17.

Figure 139. *P. forbesianus*. X-ray photograph of right posterior part of head (Birmingham University, Holcroft Coll. 32). Note n_4 and n_5, the peripheral canals (per c) and twigs innervating the peripheral flange (per).

Figure 140. Hot-wire pantograph used in constructing polystyrene models (by courtesy of Ammonite Limited, Cowbridge). The vertical steel follower is 182 mm long.

EXPLANATION OF ABBREVIATIONS USED IN FIGURES

A list of abbreviations used in figures other than figures 1, 2, 8, 9, 10, 22, 24, 32, 33, 34, 36 which have their own legends. Figures 37 to 140 are on plates 1 to 15. Shorter or longer abbreviations for the same structure are sometimes used according to available space.

a, b, c, d, e, etc.	head plates in *Reticulocarpos* notation
adm m f	admedian muscle facet of oral spine
adm or	admedian oral plate
adm ph-ep op	admedian pharyngo-epicardial opening
a g, agvp	anterior groove of ventral plate of hind tail
aig	anterior interossicular groove of dorsal ossicle of hind tail
aiid	anterior inner interossicular depression of dorsal ossicle of hind tail
an	anus
ant l	anterior lobe of oral funnel
ant ser	anterior serration of oral plate
aoid	anterior outer interossicular depression
ap, apvp	anterior process of ventral plate of hind tail
ar	areola
atr	atrium of ascidians
atr op	atrial opening of ascidians
bc	buccal cavity (or buc cav)
bl	blunt face of oral spine
bl c	blood corpuscles of salp
b l pyr b, b pyr	base of left pyriform body
br	brain
br b	branchial bar of salp
br s	branchial slit
btn	button of ventral head skeleton
buc cav	buccal cavity (or bc)
b w	body wall of tunicates
C_A etc	centro-dorsal plates in objective notation
calc cl	calcite cleavage
card n	cardiac nerve of *Cothurnocystis*
cav d lam	cavity of dorsal lamella of *Mitrocystella*
cil o	ciliated organ i.e. opening of duct of neural gland into pharynx
cis e	cispharyngeal eye
cr b	crescentic body
cut e, cut	cutting edge of oral spine
dien	diencephalon
dist	distal end of alimentary ciliated loop in ascidians
d lang	dorsal languets of tunicates
d l can	dorsal longitudinal canal of *Mitrocystella*
d-l pl	dorso-lateral plate of fore tail
d n c	dorsal nerve cord
d n gl	duct of neural gland
d oss	dorsal ossicle
d pp	depressions in anterior face of hind-tail ossicle to receive the posterior process.
dr n	dorsal root nerve in *Mitrocystella*
d sf	dorsal surface of head
d v	dorsal vein of ascidian
el	elaeoblast or budding tissue in salps
end	endostyle
end f	endostylar fold of ascidian
end gr	endostylar groove
ep b	epibranchial band of tunicates
f ap	facet on dorsal ossicle for anterior process of ventral plate of hind tail
f m d pr	facet on mid-dorsal process
f M_{ILD}, M_{ILV}, M_{IRD}, M_{IRV}	facets on head skeleton for plate M_{ILD} etc.
f tl	fore tail
fr	fractured surface
g	gonad
gan	hind-tail ganglion of *Mitrocystella*
gd	gonoduct
g imb fl	gap for imbrication flaps between major dorsal plates of fore tail
g p	ganglionic pit in dorsal ossicle of hind tail
h, ht	heart
h tl	hind tail
hyp pr	hypocerebral processes
i	intestine (or int)
imb, imb fl	imbrication flaps of fore tail
inh fl	inhalent flap, supposedly attached to lateral oral plate.
inh g	inhalent gap for inhalent flap
inh gr	groove in dorsal skeleton leading from inhalent gap to olfactory cup
inn l	inner calcite layer of ventral skeleton
int	intestine (or i)
int can	interossicular canal in *Mitrocystella*
intc pl	intercalary plate
integ pl	integument plate
i sk c	intra-skeletal cone of cornute
kn	knob on major plate of fore tail
la	left atrium (also l atr)
l adm or	left admedian oral plate
l adl pr	left adlateral process of anterior border of posterior coelom in *Placocystites*
l adm ph-ep op	left admedian pharyngo-epicardial opening
l ant c	left anterior coelom
lat l	lateral line
lat l g	lateral line ganglion
lat l n	lateral line nerve
lat m	lateral muscle facet of oral spine
lat n	lateral notch leading to oral funnel of *Placocystites*

lat ph-ep op	lateral pharyngo-epicardial openings
l atr	left atrium (also la)
l aud g	left auditory ganglion
l aud n	left auditory nerve
l br op	left branchial opening
l cis e	left cispharyngeal eye
l ep	left epicardium
l g	lateral groove of dorsal ossicle
l lat or	left lateral oral plate
l m b	left marginal band of endostyle
l op n	left optic nerve
l or sp	left oral spine
l p	left pharynx (or l ph)
l pal n	left palmar nerve
l pc	left posterior coelom
l per b	left peripharyngeal band
l ph-ep, l ph-ep op	left pharyngo-epicardial opening of cornutes
l pyr b	left pyriform body
m	mouth
m cr, m cr b	margin of crescentic body
m d pr	mid-dorsal process
M_{1LD}, M_{1LV} etc	marginal plates in objective notation
mes	mesoderm in salps
m f	mucous funnel
m post c	margin of posterior coelom
m pros	margin of prosencephalon
m r	mucous rope
m tl	mid tail
n_0	endostylar nerves of mitrates
n_1, n_2, n_3, n_4, n_{4+5}, n_5	nerves of palmar complex of mitrates
n?	possible nerves in cornutes
n_x	supplementary nerve of palmar complex in *Placocystites*
n gl	neural gland
n-ph g	non-pharyngeal gut in salps
o	oesophagus (or oes)
ob gr	oblique groove of mitrates
ob r	oblique ridge of mitrates
oes	oesophagus (or o)
oes b	oesophageal band of cilia
oes op	oesophageal opening into pharynx
oes pr	oesophageal process of mitrates
olf c	olfactory cup of mitrates
olf n	olfactory notch in *Placocystites*
olf op	olfactory opening carrying olfactory nerves into buccal cavity
olf pr	olfactory process inside olfactory cup of *Placocystites*
op for	optic foramen in mitrate skeleton, anteroventral to prosencephalon
op n	optic nerve
or	oral plate
or fun	oral funnel
out l	outer layer of ventral skeleton in mitrates
p	pharynx (or ph)
pal, pal n	palmar nerve
per	peripheral twigs innervating peripheral flange
per b	peripharyngeal band
per c, per can	peripheral canal
per g	peripheral groove of *Mitrocystites* etc.
per v	peripharyngeal vessel of tunicates
ph	pharynx (or p)
ph-ep op	pharyngo-epicardial opening
ph op	pharynx between pharyngo-epicardial openings in *Cothurnocystis*
ph s	pharyngeal striae of *Cothurnocystis*
ph w	pharyngeal wall
pig	posterior interossicular groove
piid	posterior inner interossicular depression
plac	placenta of salp
plac r	placental roof of salp
pl l ph	pleats of left pharynx
pl ph	pleats of pharynx
pl r ph	pleats of right pharynx
p-oes pr	post-oesophageal process
poid	posterior outer interossicular depression
p or	post-oral plate
post c	posterior coelom
p p	posterior process of dorsal ossicle
pr	prosencephalon (or pros)
p-ret b	proto-retropharyngeal band
prac	patent right anterior coelom
prc	pericardium of salp
pr kn	precerebral knot
pros	prosencephalon (or pr)
prox	proximal end of alimentary ciliated loop
p sf	posterior surface
p v pr	postero-ventral process of ventral hind-tail plates in some mitrates
pyr, pyr b	pyriform body
r	rectum (or rect)
r a	right atrium (or r atr)
r adl pr	right adlateral process
r adm or, rad m or pl	right admedian oral plate
r adm ph-ep op	right admedian pharyngo-epicardial opening
r ant c	right anterior coelom (or rac)
r ant c/r ph	boundary between right anterior coelom and right pharynx
r atr	right atrium (or ra)
r aud g	right auditory ganglion
r aud n	right auditory nerve
r br op	right branchial opening
r cis, r cis e	right cispharyngeal eye
r cis op n	right cispharyngeal optic nerve
rect	rectum (or r)
rect op	rectal opening, where the rectum passes out of posterior coelom
rect pr	rectal process
r ep	right epicardium

res cl	resorbtion cliff in dorsal skeleton of *Placocystites*
ret b	retropharyngeal band
ret pr	retropharyngeal process
rh, rhomb	rhombencephalon
r lat or, r lat or pl	right lateral oral plate
r mb b	right marginal band of endostyle
r op n	right optic nerve
r or sp	right oral spine
r p	right pharynx (or r ph)
r pal n	right palmar nerve
r p c	right posterior coelom
r per b	right peripharyngeal band
r ph	right pharynx (or rp)
r ph-ep, r ph-ep op	right pharyngo-epicardial opening of cornutes
r pyr b	right pyriform body
s	stomach (or st)
sc	stomochord of *Cephalodiscus*
sem pr	semicircular process
sk	skeleton
skt	socket
sl	postulated sleeve round base of oral spine
sm l ph	smooth left pharynx
st	stomach
std	styloid
st ph	striations of pharynx
str	strut of cornutes
sub oes c	sub-oesophageal component of palmar nerve
sub rect c, sub r, su r	sub-rectal component of palmar nerve
sup oes c	supra-oesophageal component of palmar nerve
sup r, supr c, sup rect c	supra-rectal component of palmar nerve
sut	suture
t	tail
tel	telencephalon
ten r v	tentacle ring vessel of *Ciona*
t g	first tail ganglion (facial ganglion) in *Mitrocystella*
tis f in, tis f inh fl	tissue facet for inhalent flap
tis f l, tis f lp	tissue facet for lip
tis f sl	tissue facet for sleeve
tr d l, tr d lam	posterior trace of dorsal lamina of *Mitrocystella*
tr op n	transpharyngeal optic nerve (or n_3)
tr ph e	transpharyngeal eye
tr ph v	transverse pharyngeal vessel of *Ciona*
t som 1	first tail somite
tub	tubercle
v b	ventral boss on ventral plate of hind tail
vel	velum
v for	ventral foramen beneath hypocerebral processes of mitrates
v-l pl	ventro-lateral plate of fore tail
v int	ventral integument
visc v	visceral vessel of *Cothurnocystis*
v pl	ventral plate
v r_2	ventral root of tail somite 2 in *Mitrocystella*
v v	ventral vessel of tunicates
w	welt of dorsal ossicle of hind tail
w r ant c	wall of right anterior coelom
x	point at which the left pharynx first pouched out of the right pharynx in the origin of mitrates from cornutes.

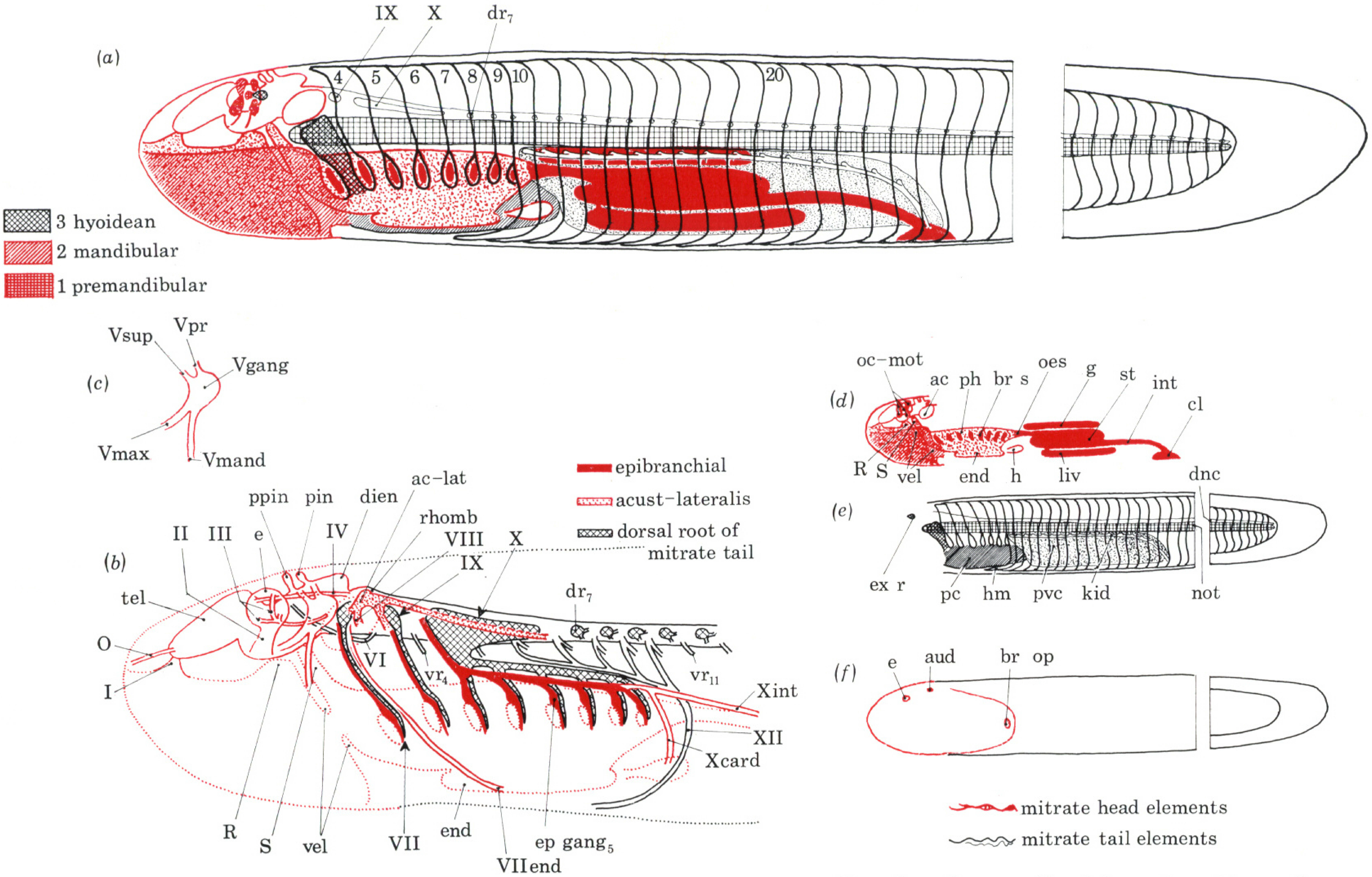
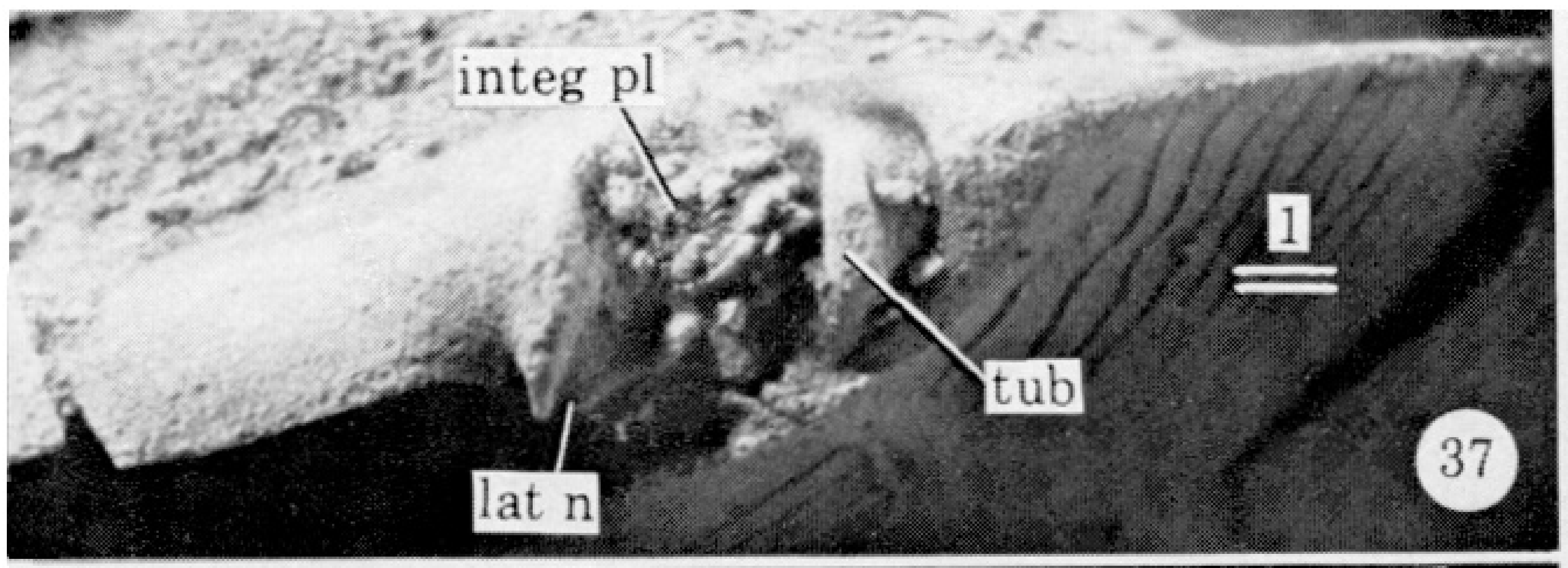


FIGURE 35. The animal x, being the reconstructed latest common ancestor of Petromyzontida and gnathostomes (for phylogenetic position see figure 33). (*a*) Entire animal; IX, X and dr$_7$ represent the bases of the corresponding nerves. (*b*) Anterior end to show cranial nerves. (*c*) Trigeminal ganglion and nerves. (*d*) Elements derived from mitrate head. (*e*) Elements derived from mitrate tail. (*f*) External features. The division into mitrate head elements (colour) and tail elements (black) is based on their presumed phylogenetic derivation from mitrate head or tail tissue, but does not imply that the elements existed as such in mitrates. For example, mitrates would have had no kidneys. O = terminalis nerve; I = olfactory; II = optic; III = oculo-motor; IV = trochlear; V gang, mand, max, pr, sup = trigeminal ganglion and mandibular, maxillary, profundus and superficialis branches; VI = abducens; VII, VII end = facial with endostylar branch; VIII = auditory; IX = glossopharyngeal; X, X$_{\mathrm{int}}$, X$_{\mathrm{card}}$ = vagus with intestinal and cardiac branches; XII = hypoglossal. 4, 5, … 20 = fourth to 20th somites. ac = auditory capsule; ac-lat = acustico-lateralis component; aud = auditory opening; br op = branchial opening; br s = branchial slit; cl = cloaca; dien = diencephalon; dnc = dorsal nerve cord; dr$_7$ = dorsal root posterior to seventh somite; e = eye; end = endostyle; ep gang 5 = fifth epibranchial ganglion; ex r = external rectus muscle; g = gonad; h = heart; hm = hypoglossal musculature; int = intestine; kid = kidney; liv = liver; not = notochord; oc-mot = oculo-motor muscles except the external rectus; oes = oesophagus; pc = pericardium; ph = pharynx; pin = pineal; p pin = parapineal; pvc = perivisceral coelom; R = Rathke's pouch; rhomb = rhombencephalon; S = Seessel's pouch (pre-oral gut); st = stomach; tel = telencephalon; vel = velum; vr$_4$, vr$_{11}$ = ventral root to the fourth and eleventh somites (the existence of a ventral root to the fourth somite has been established in shark embryos by Bjerring, 1970).



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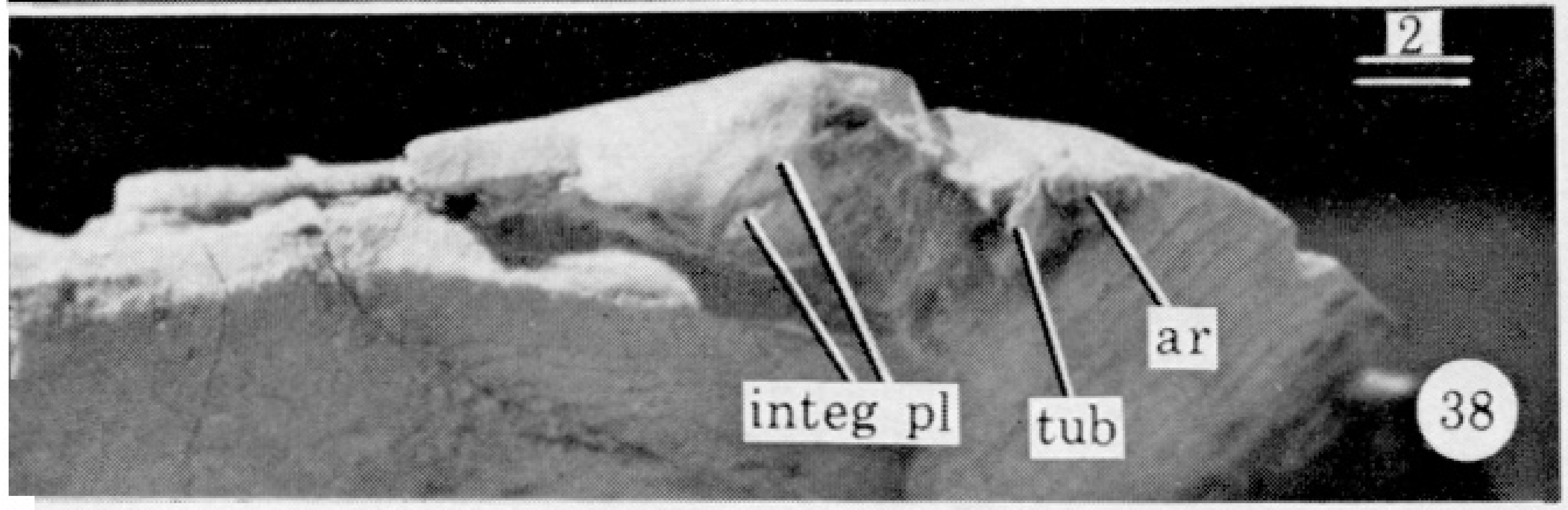

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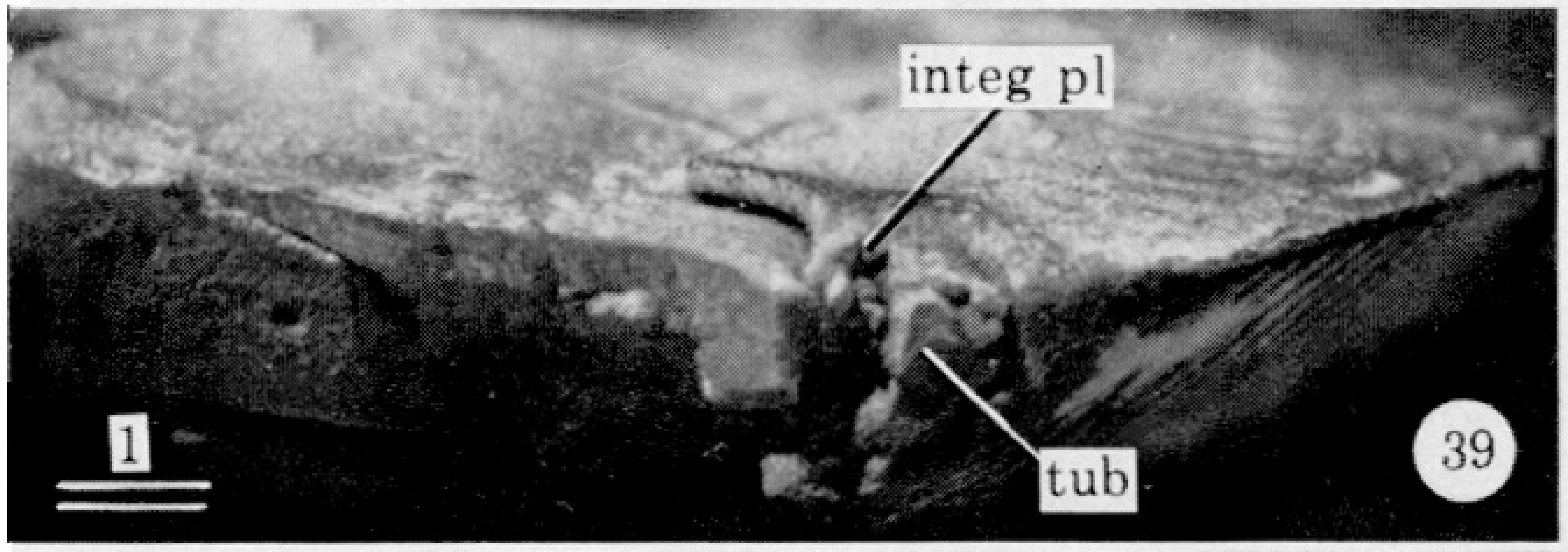

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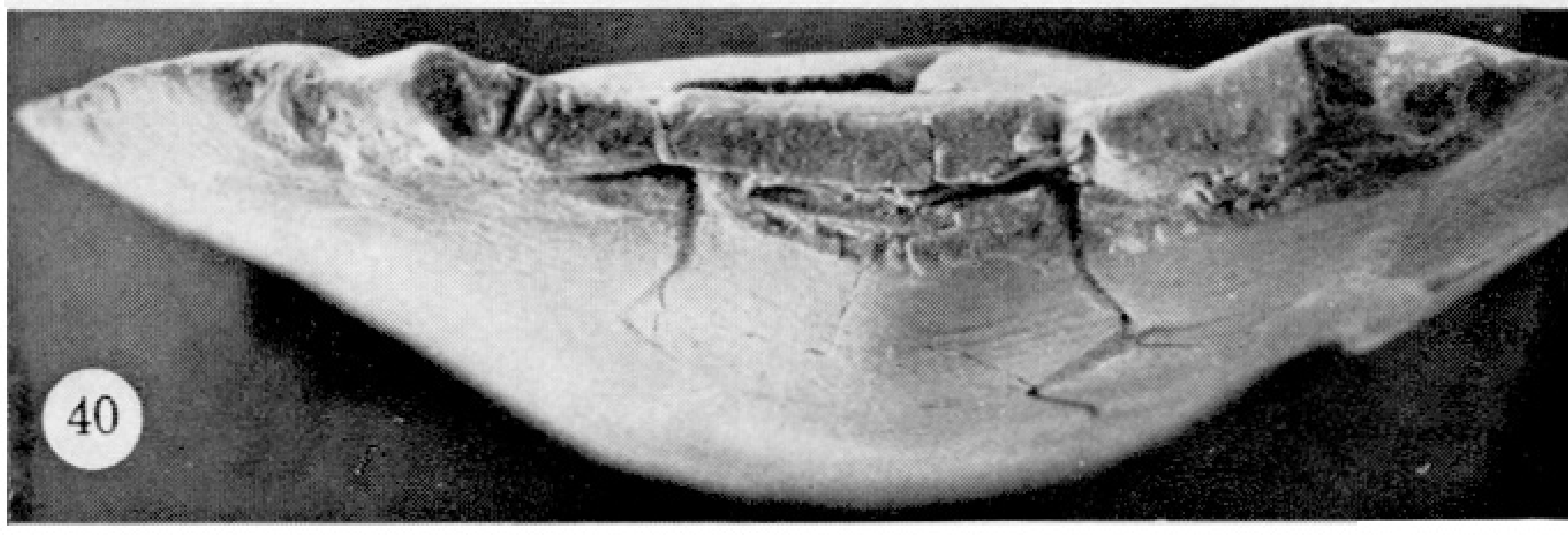

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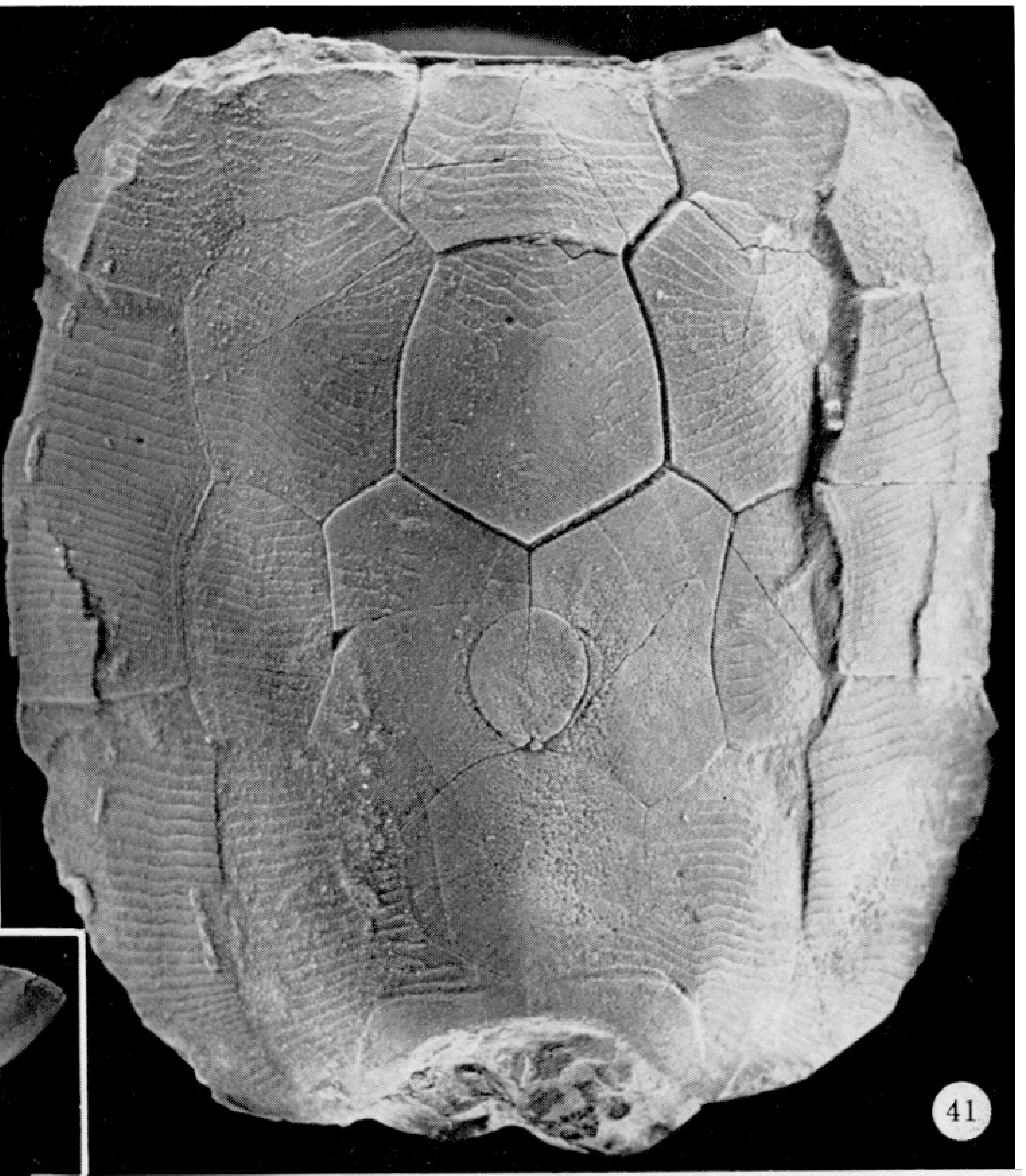

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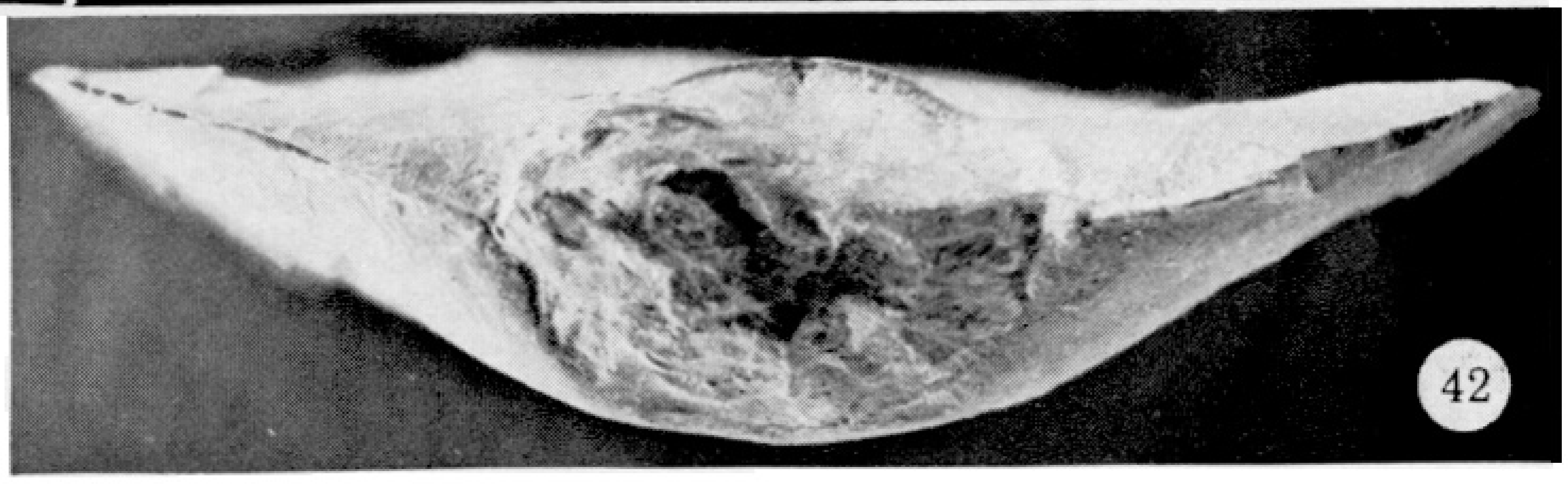

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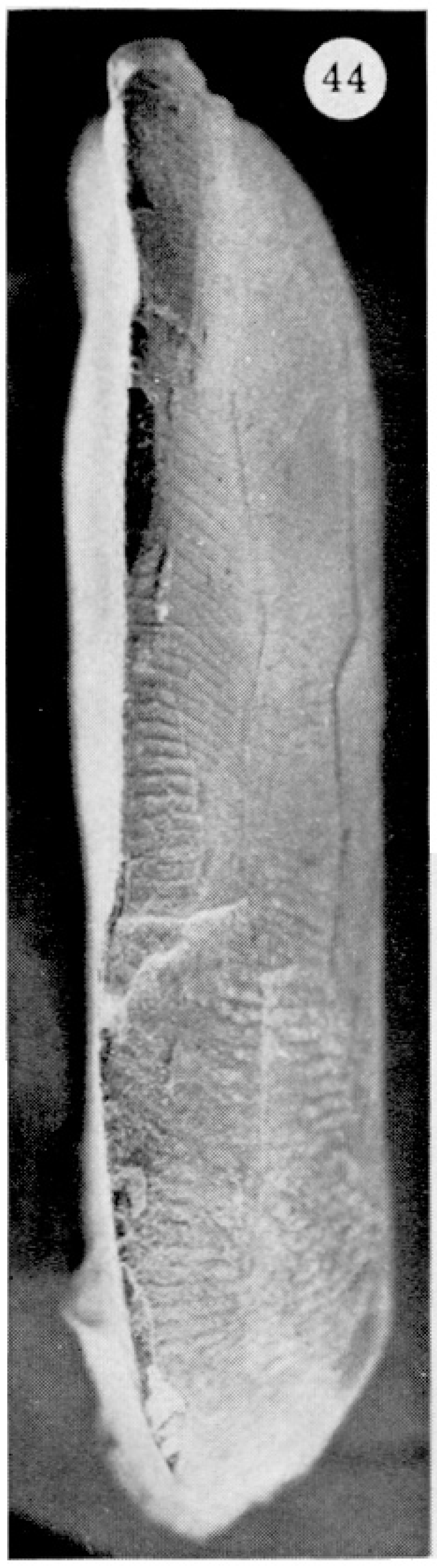

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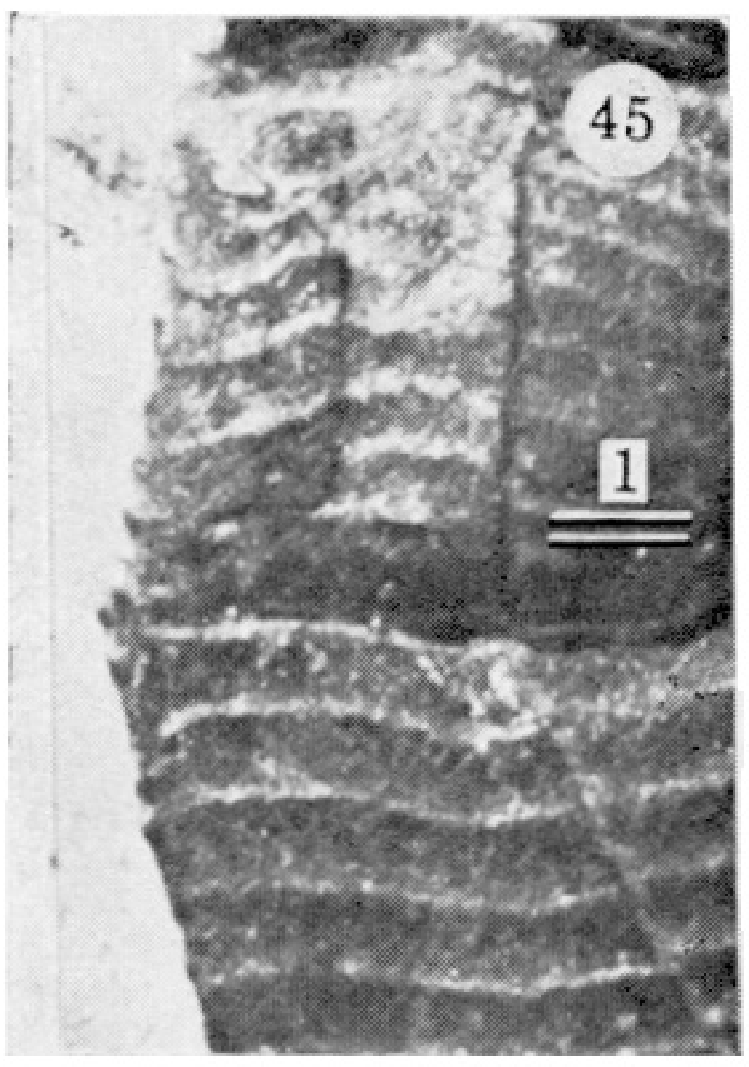

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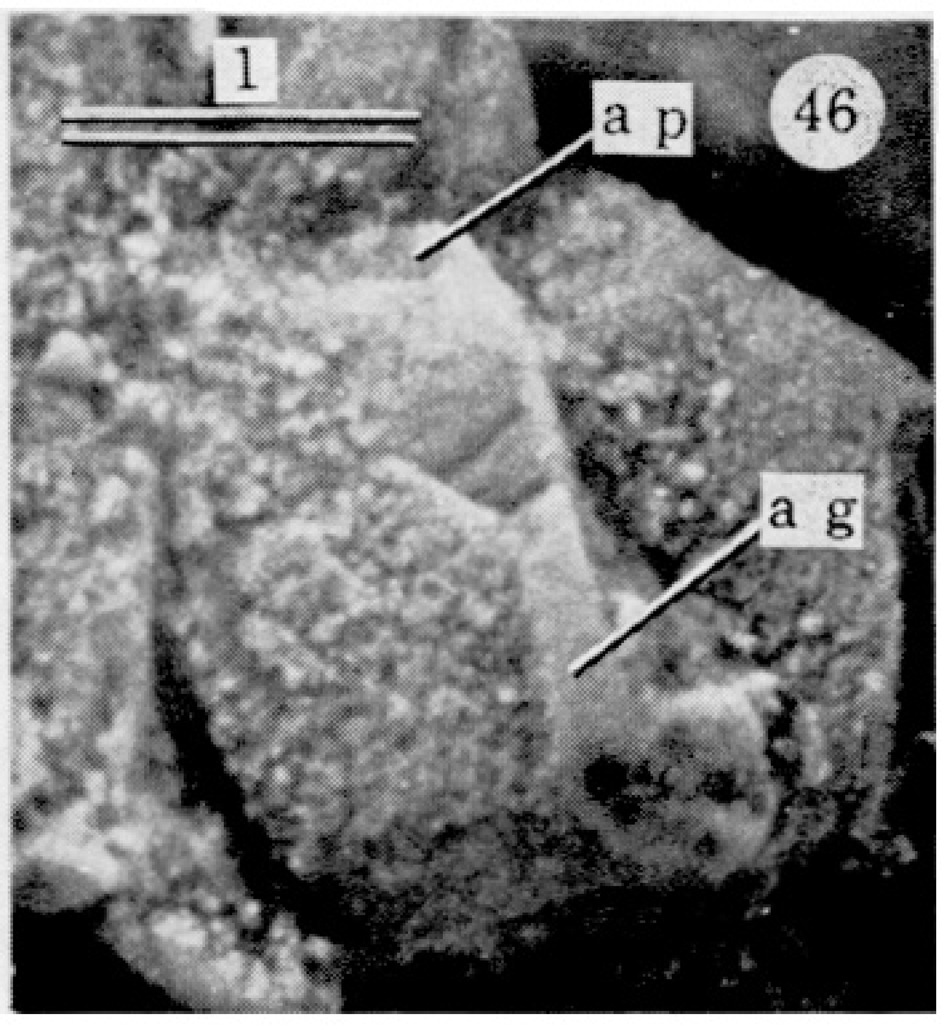

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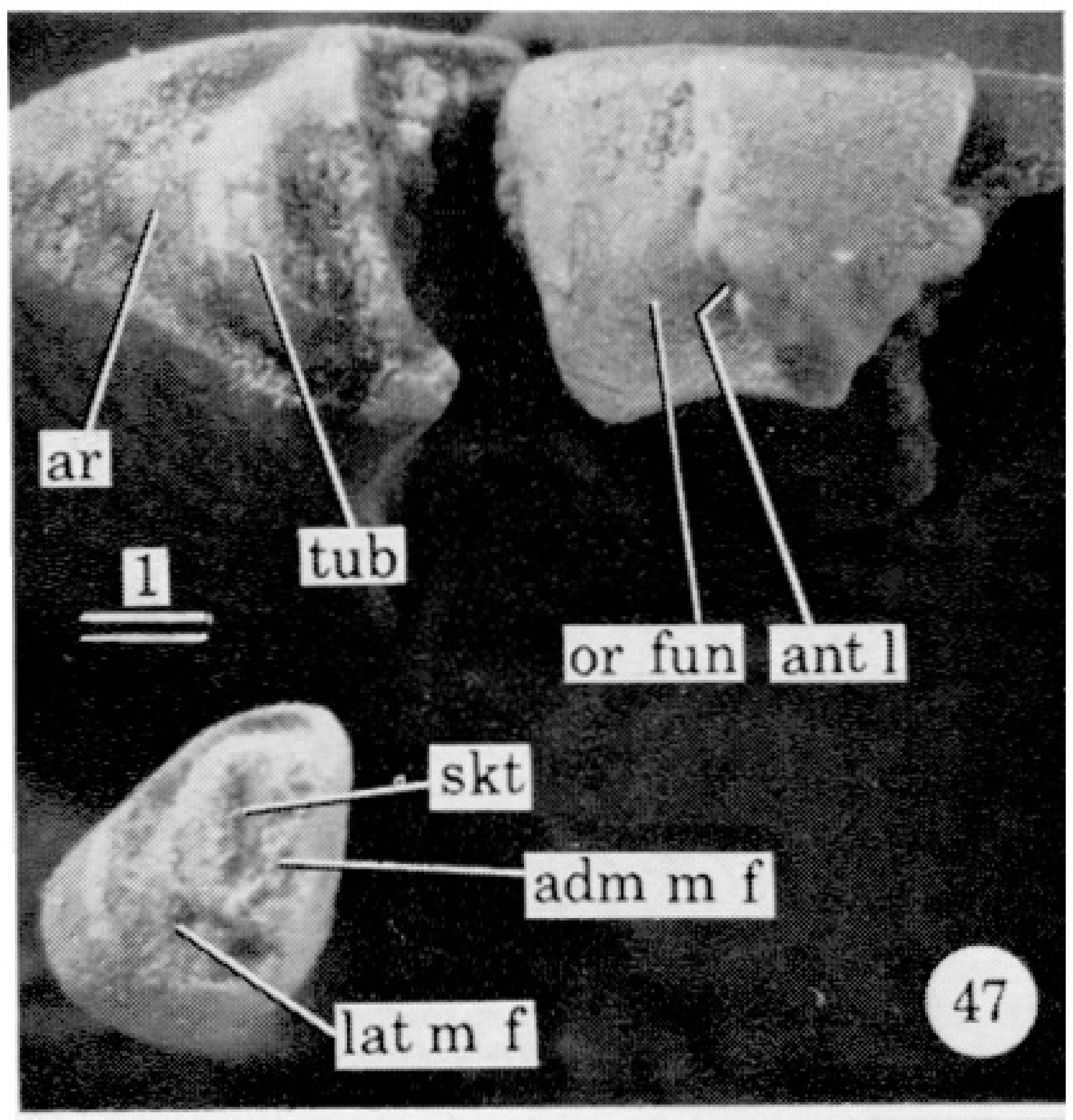
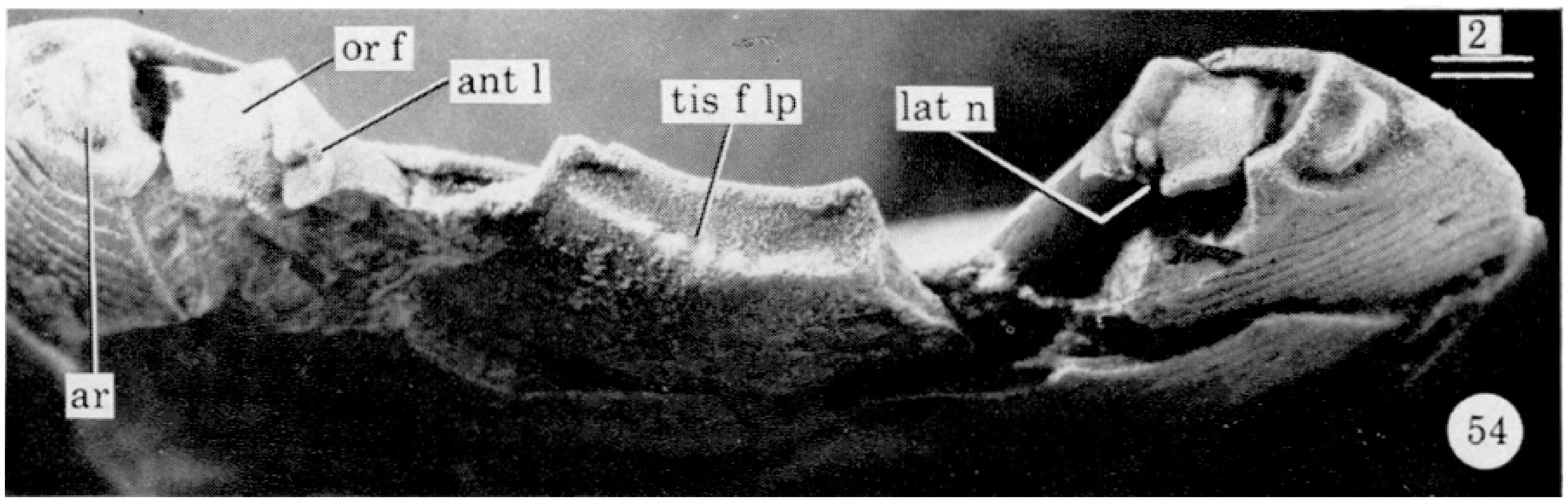
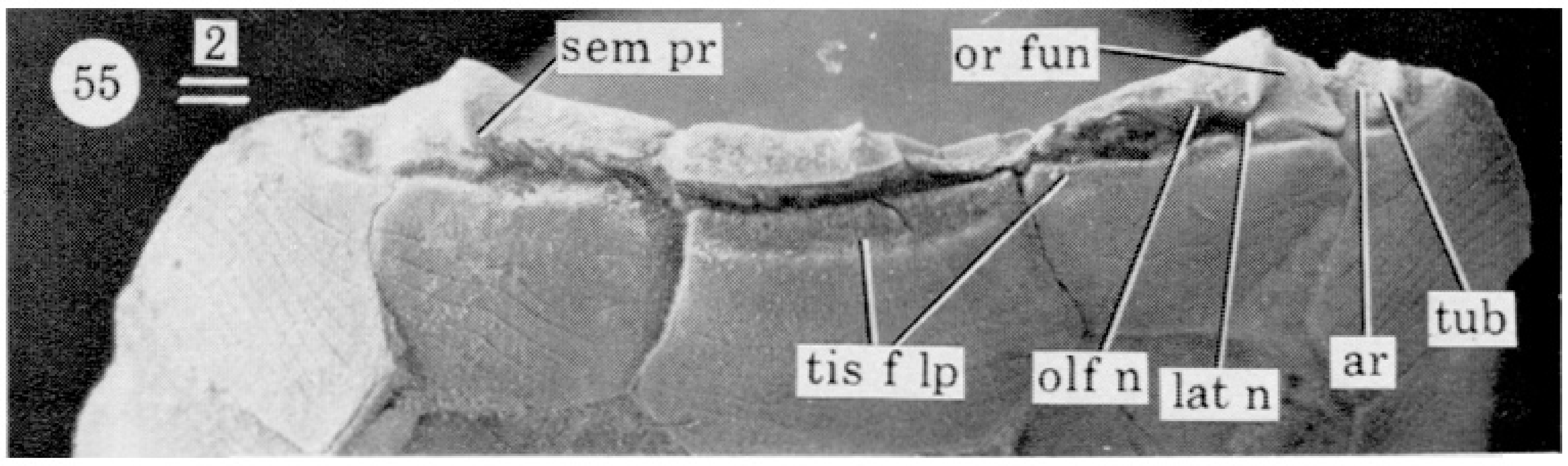
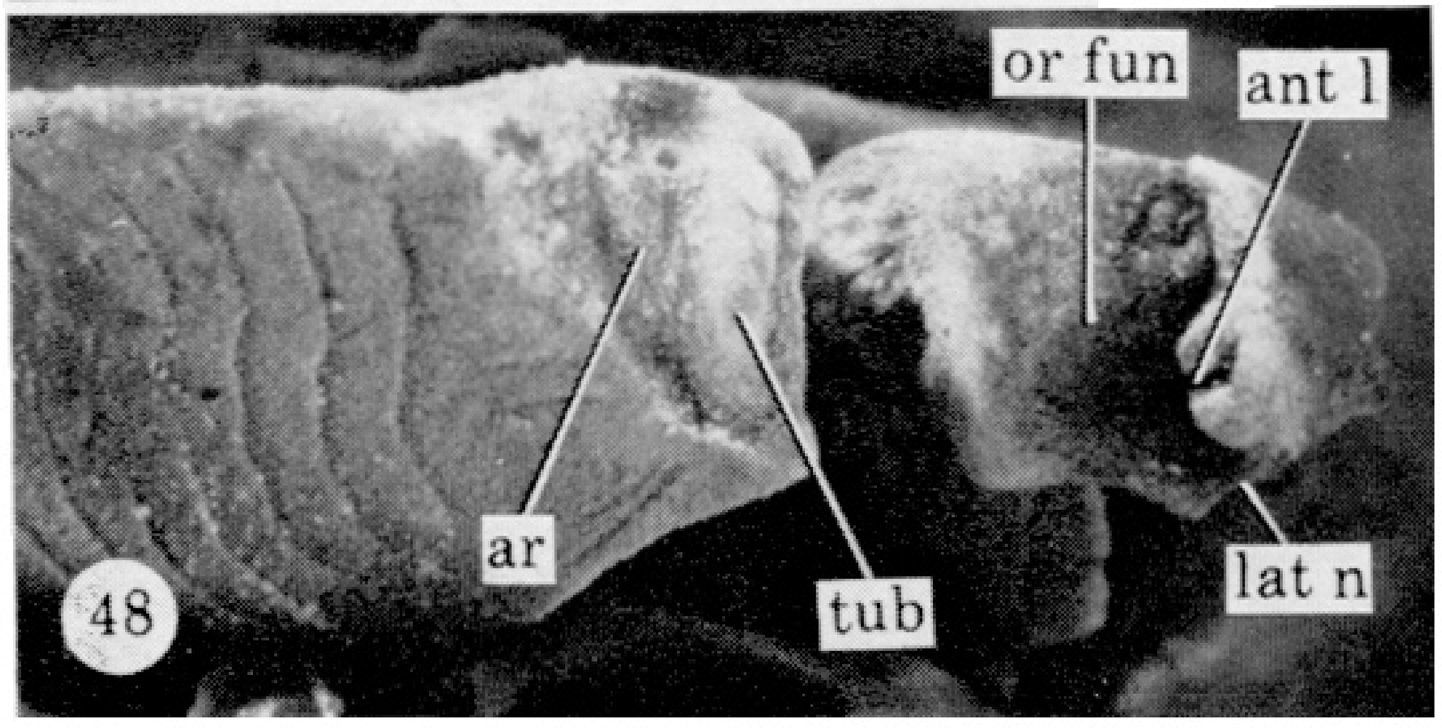
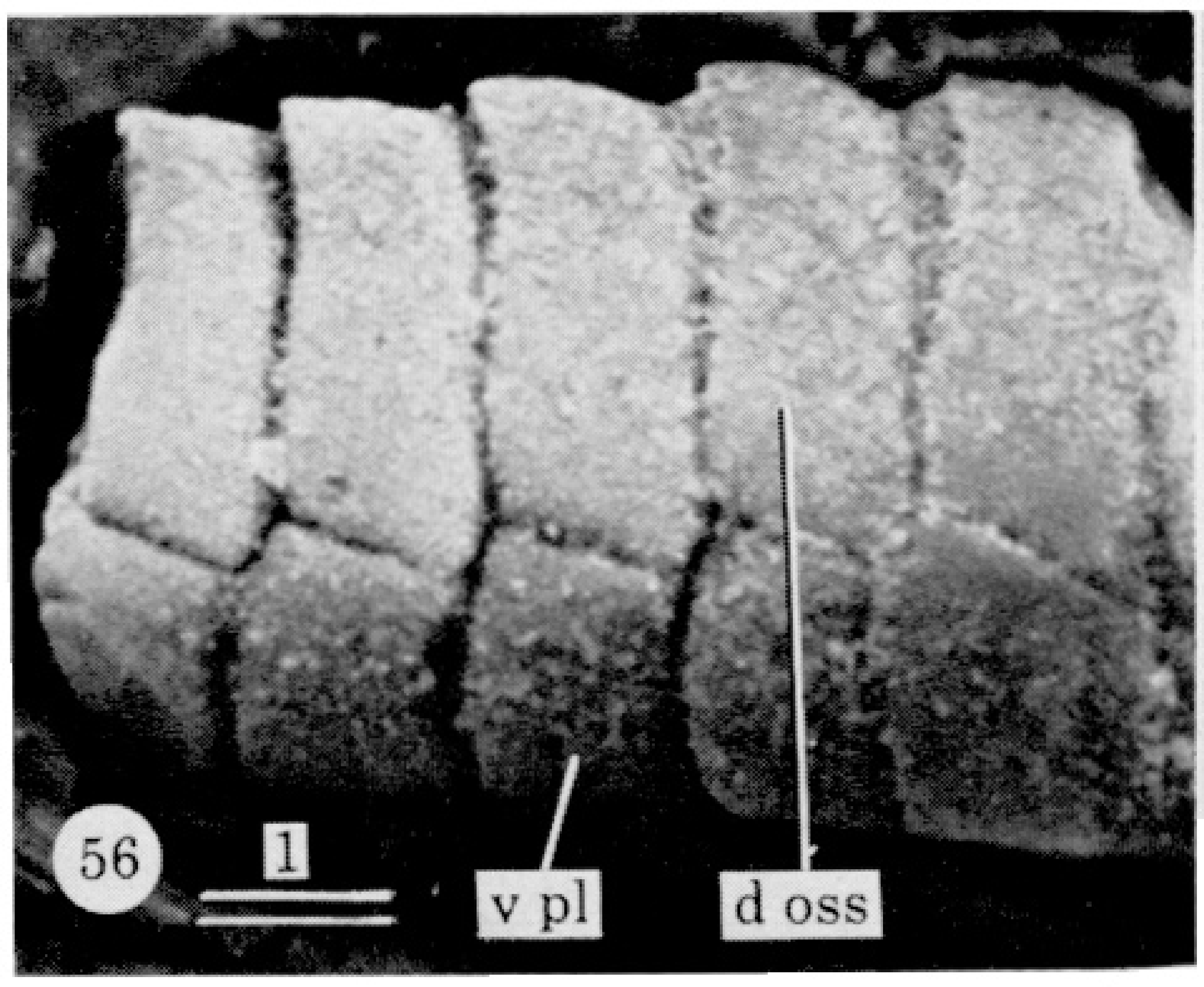
FIGURES 37–46. For description see p. 315.

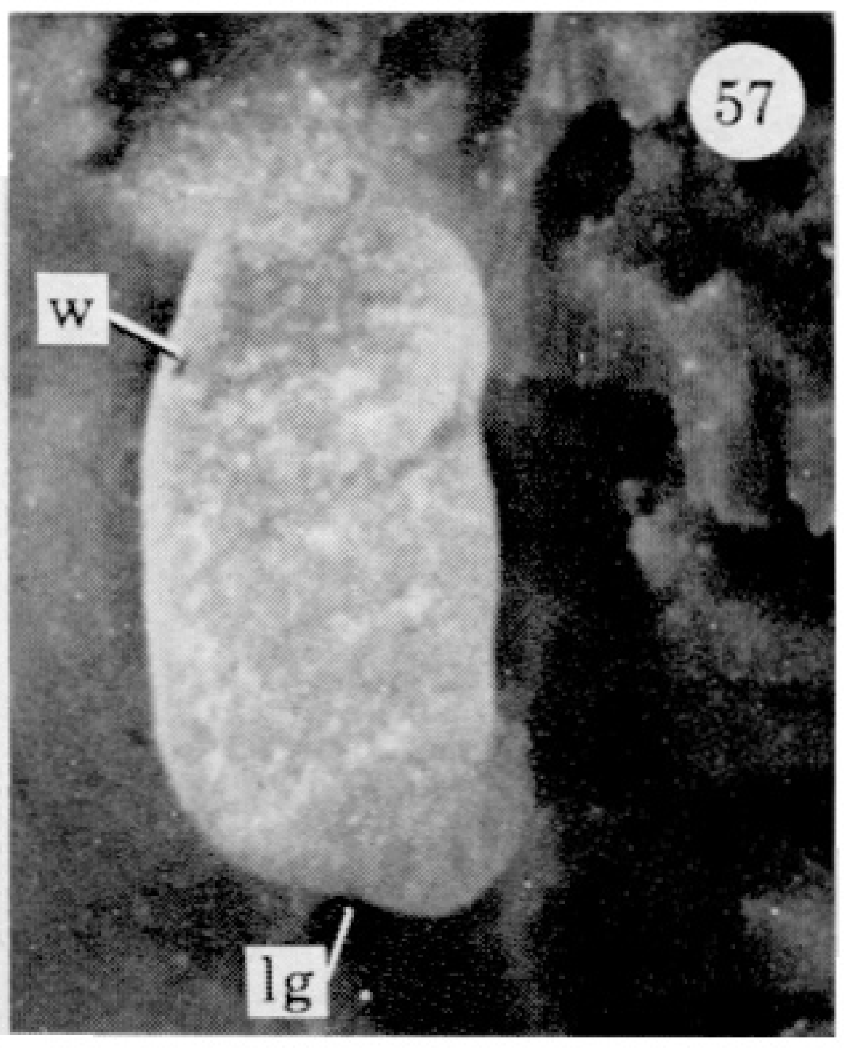


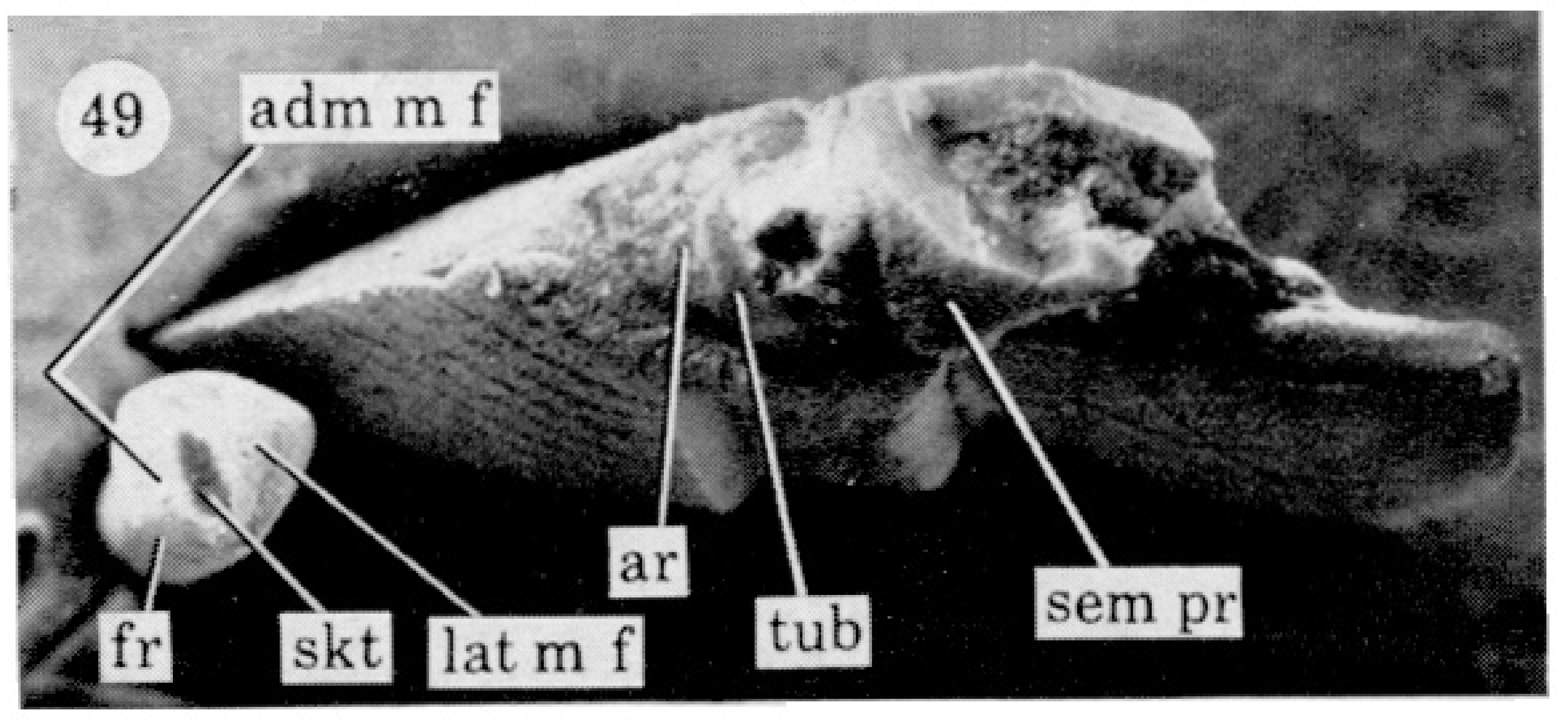


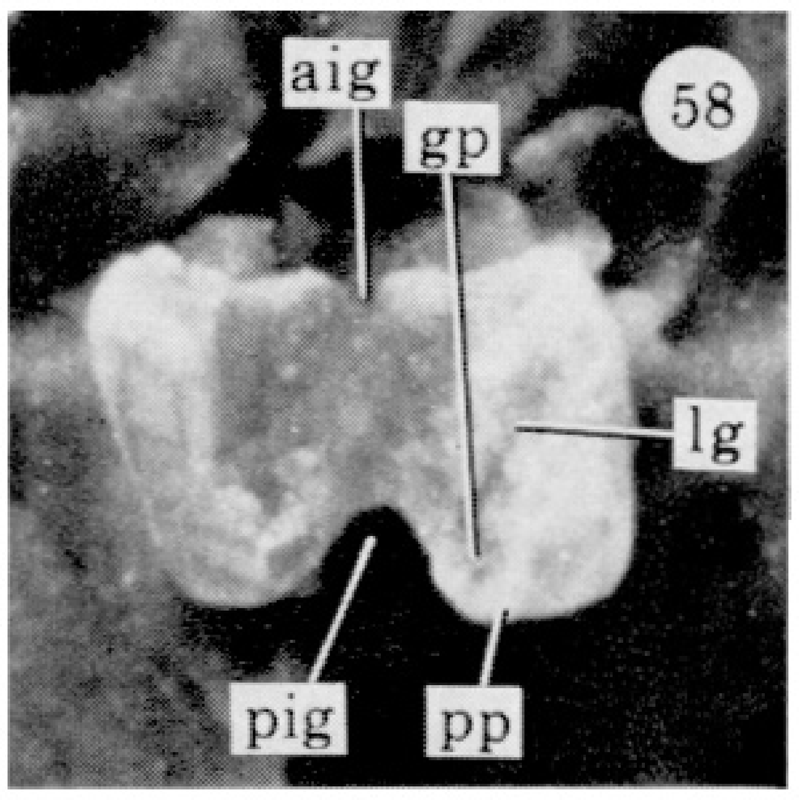


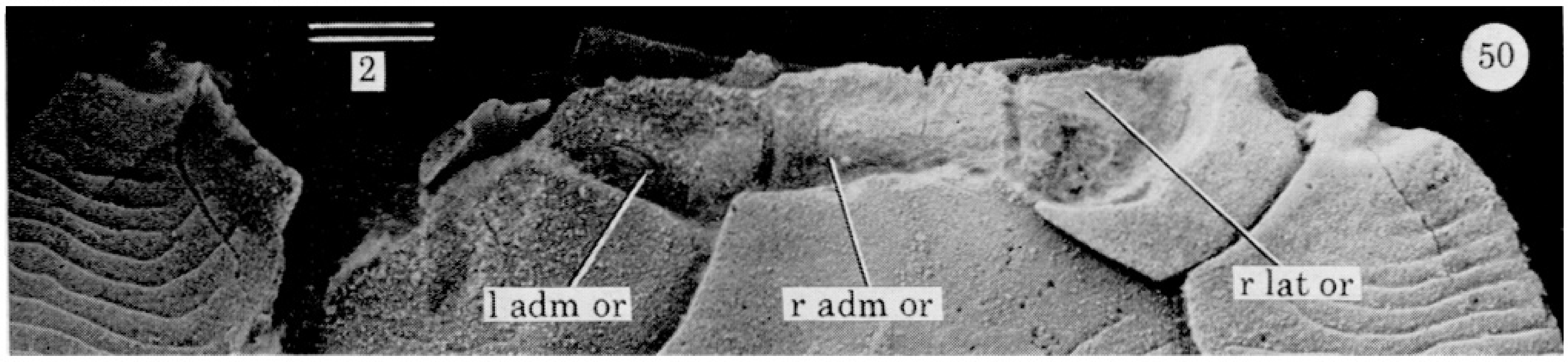


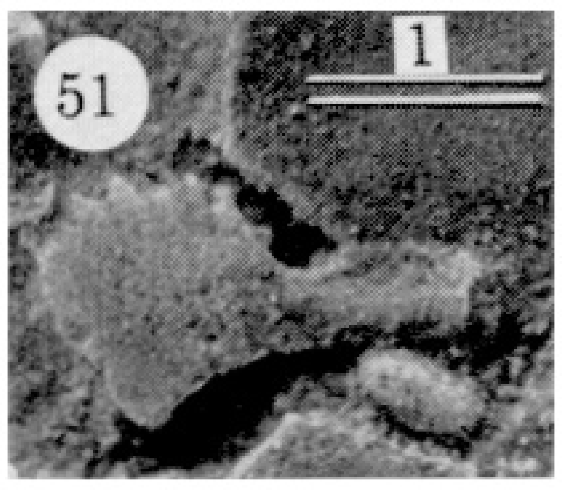


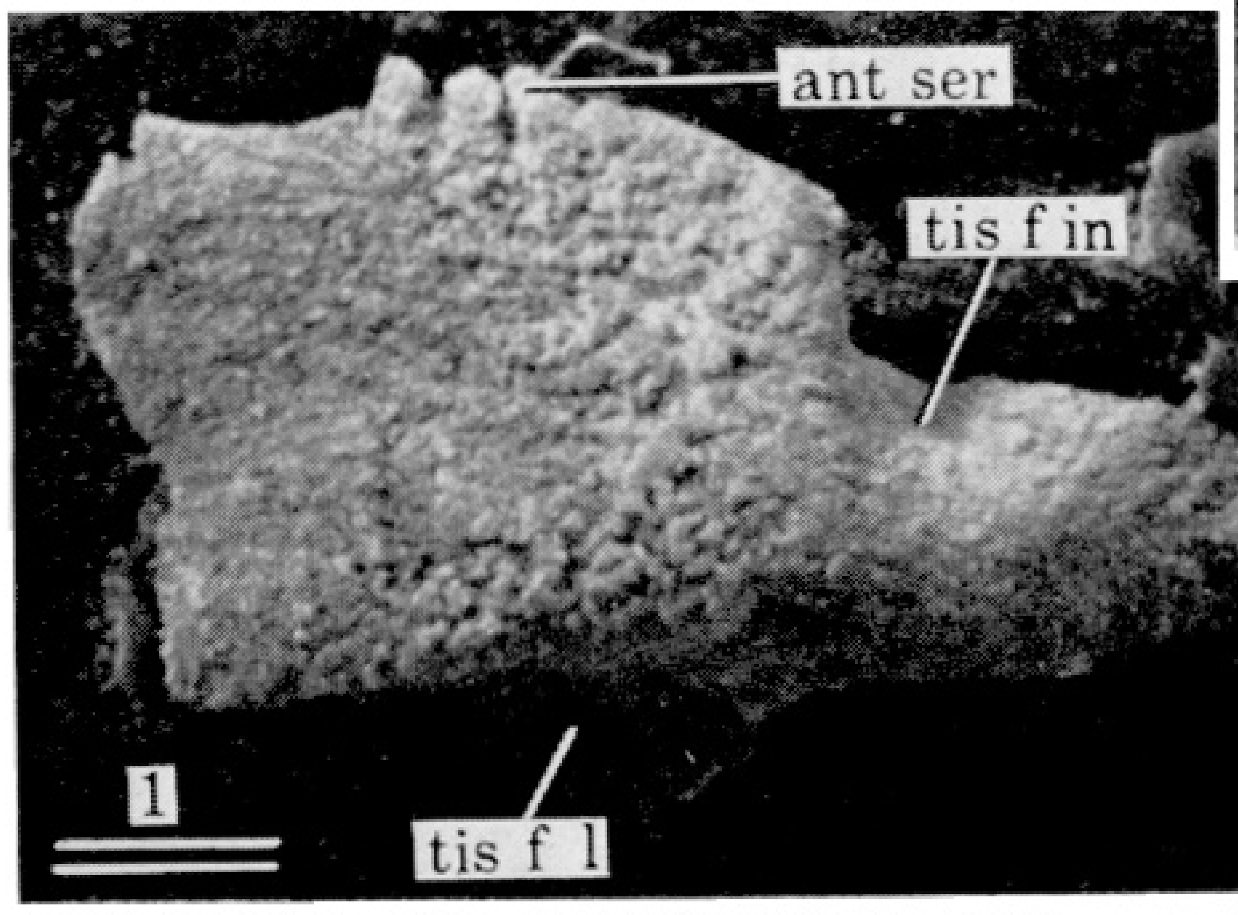


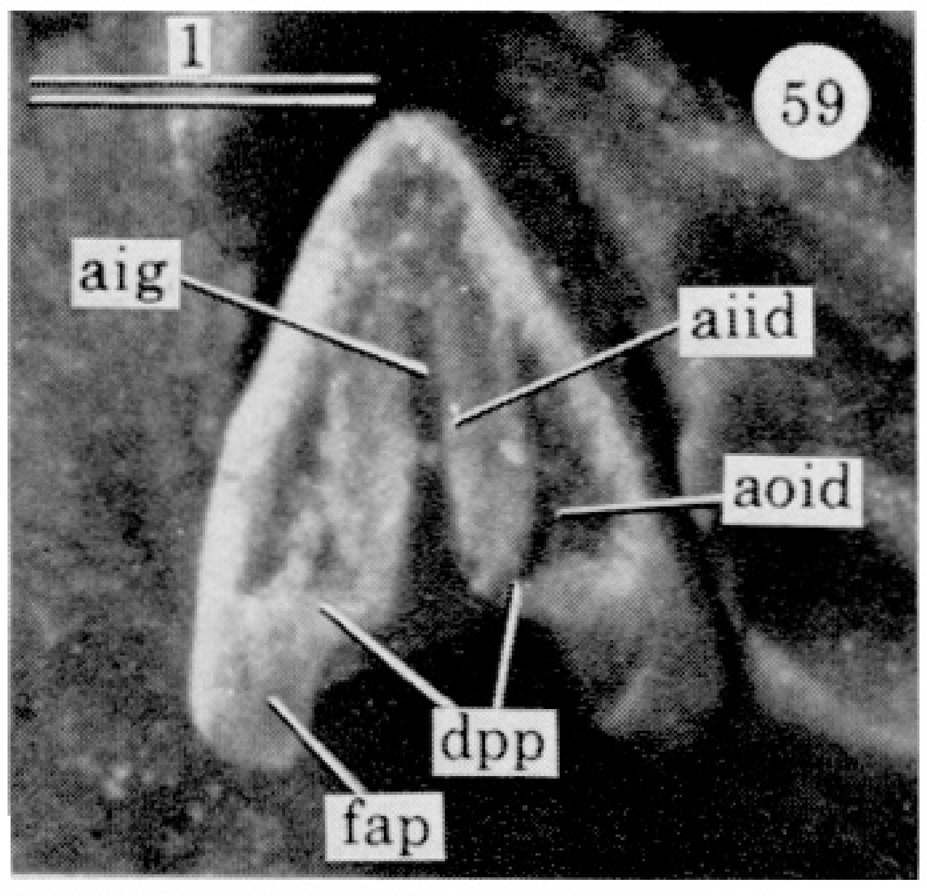


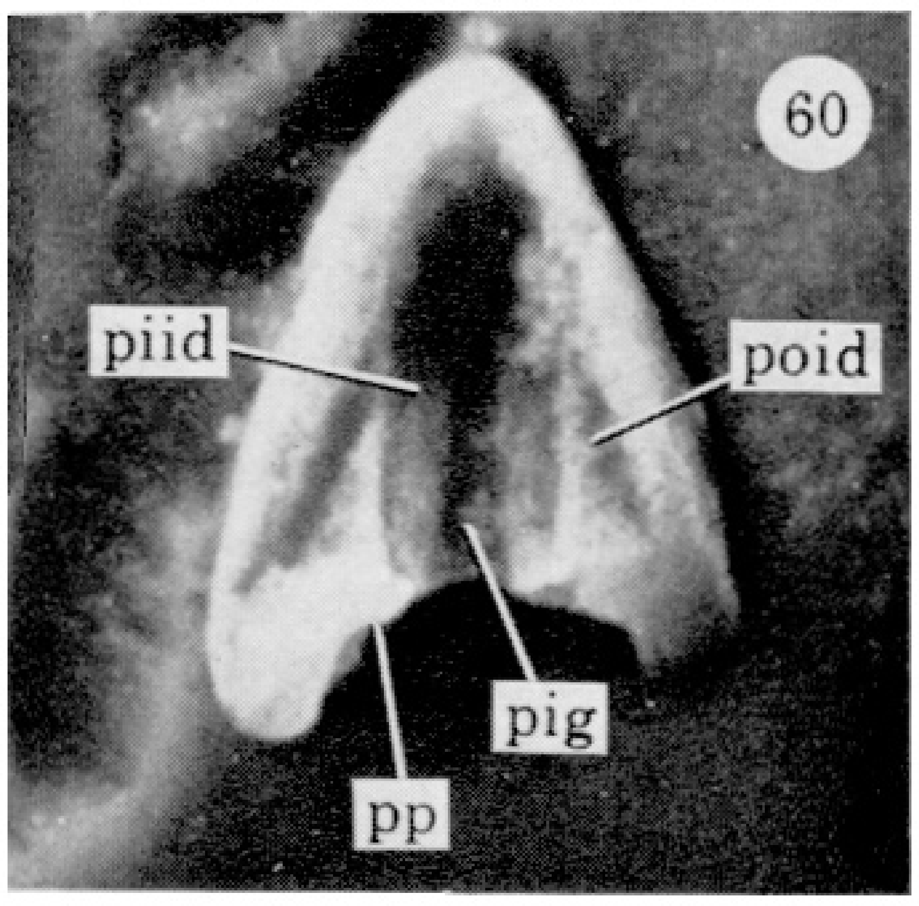


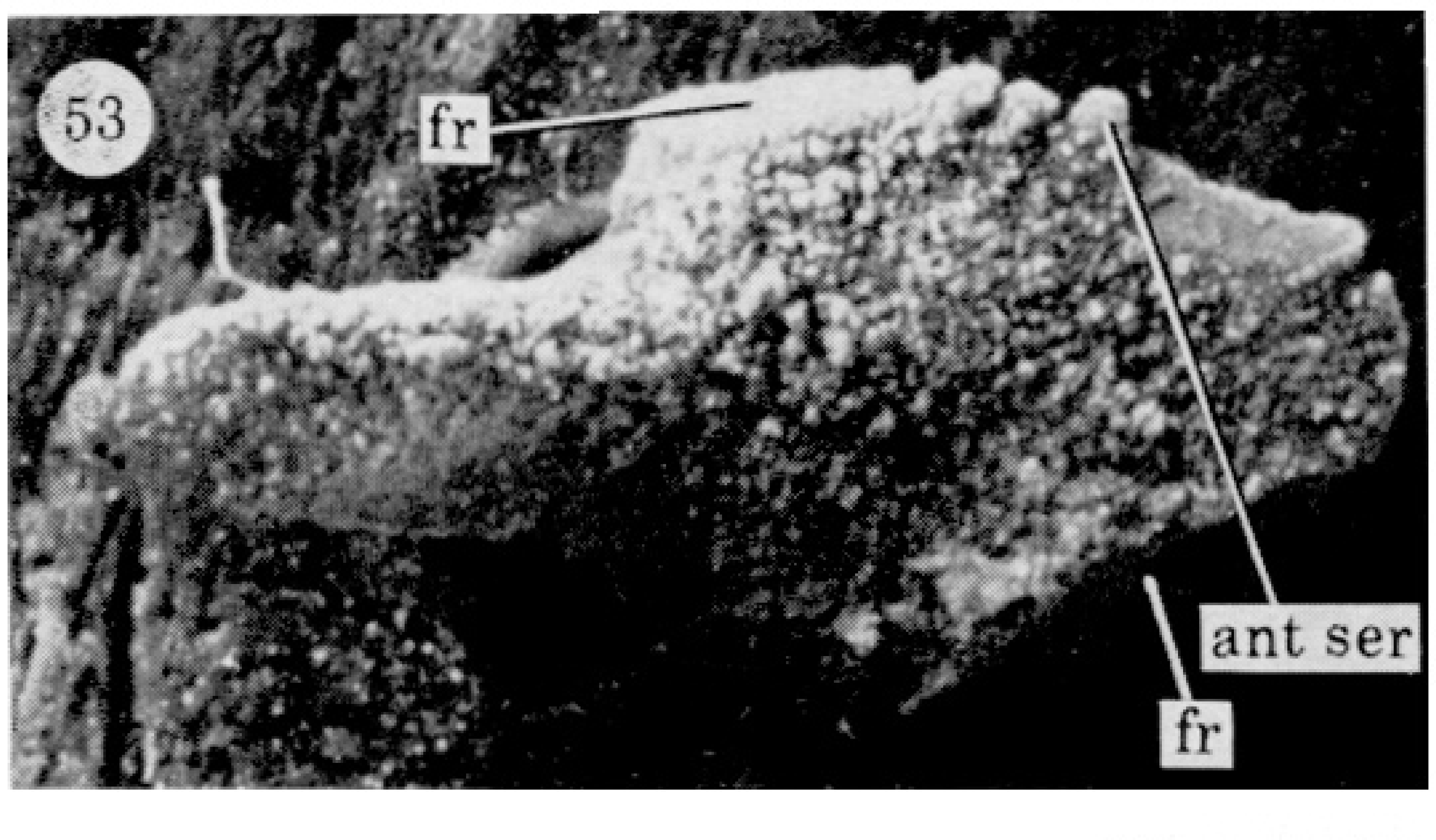


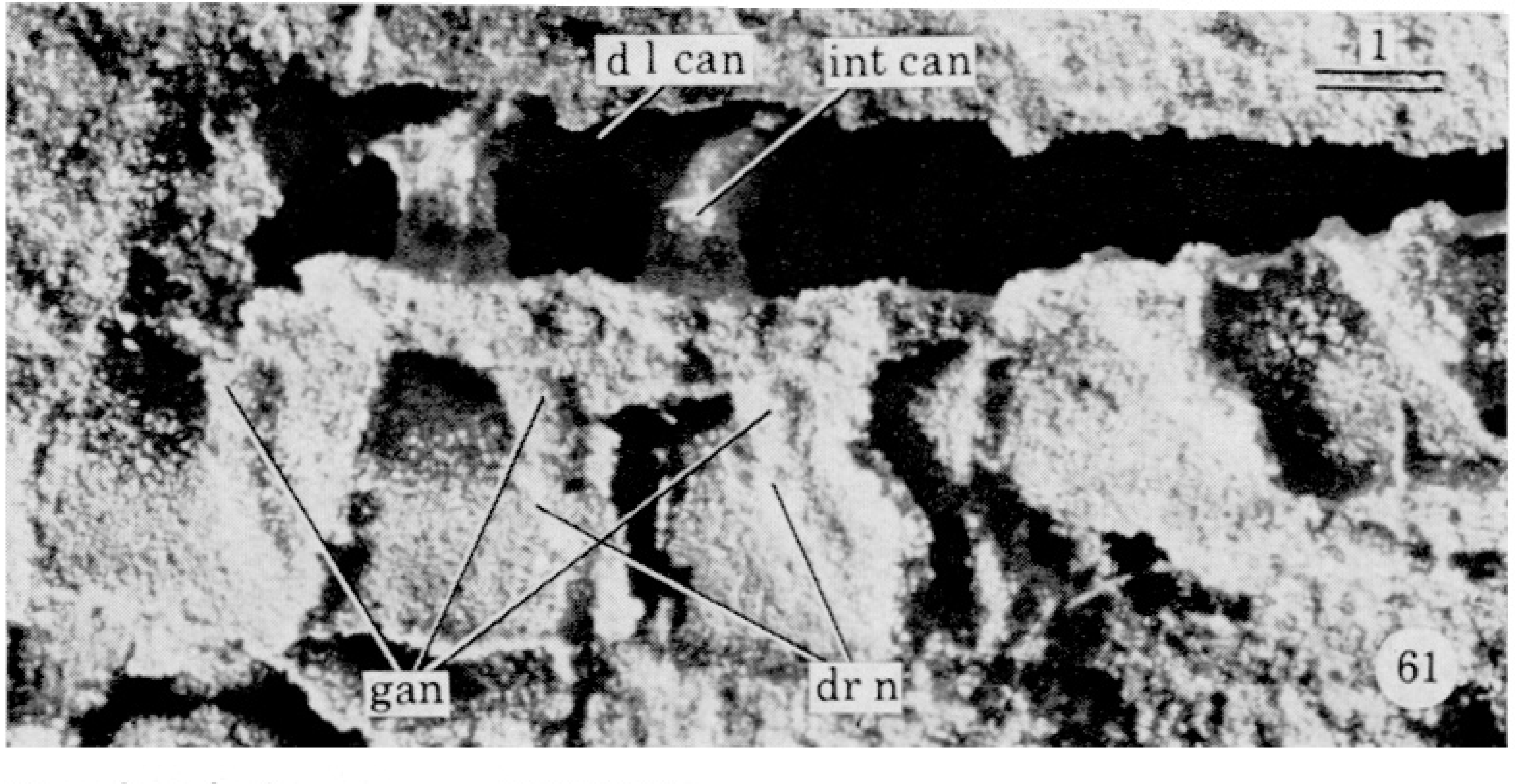




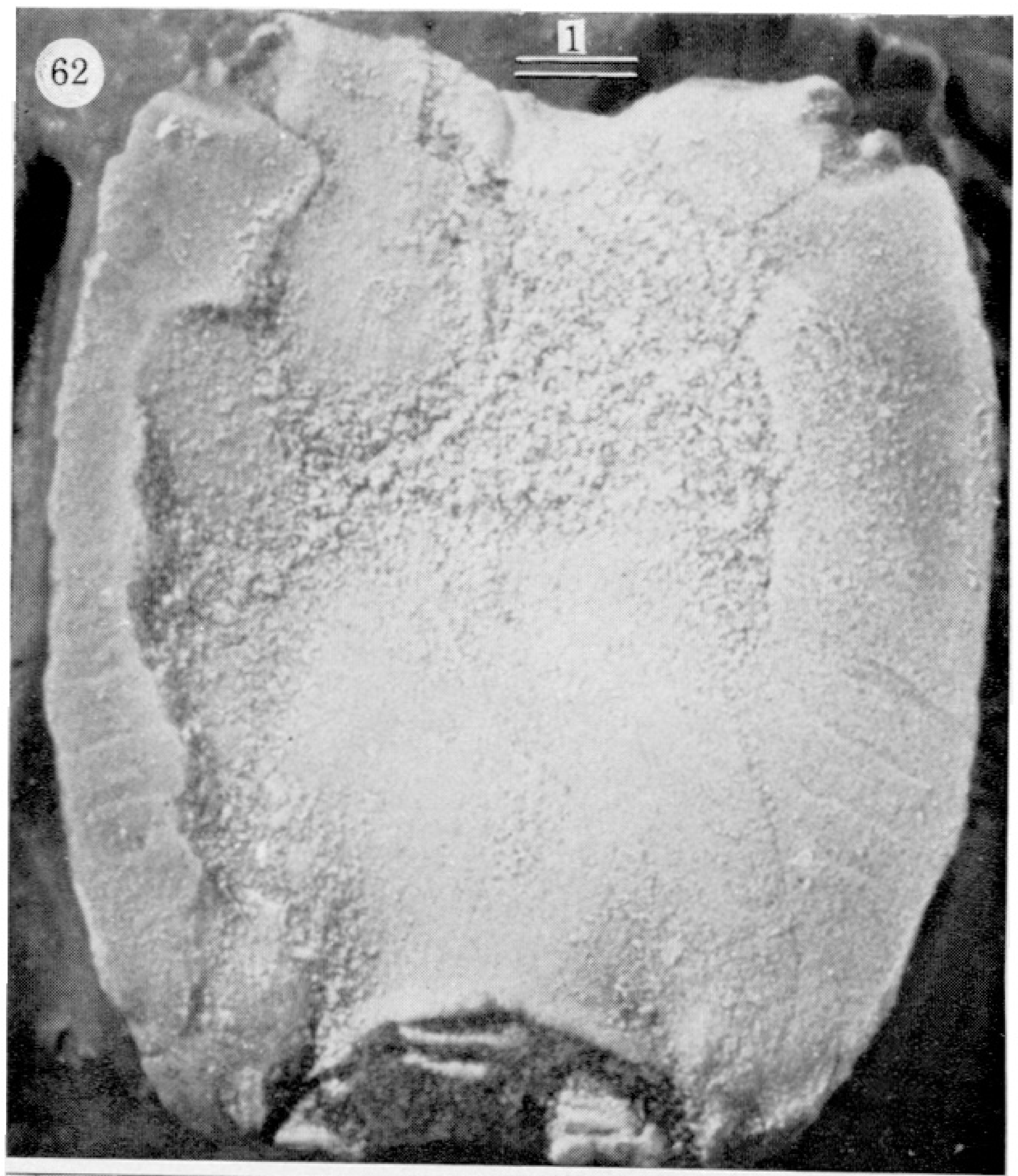


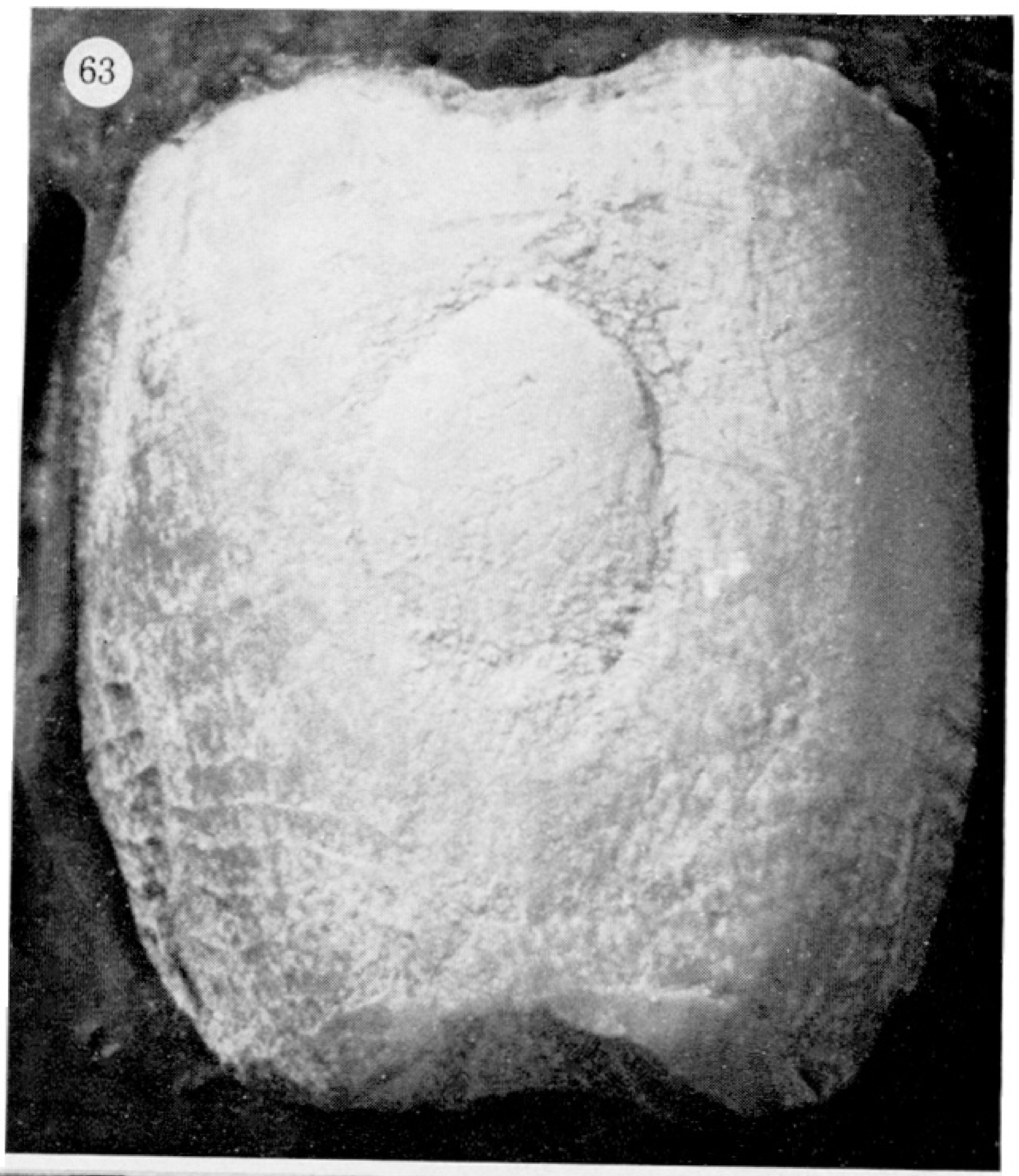


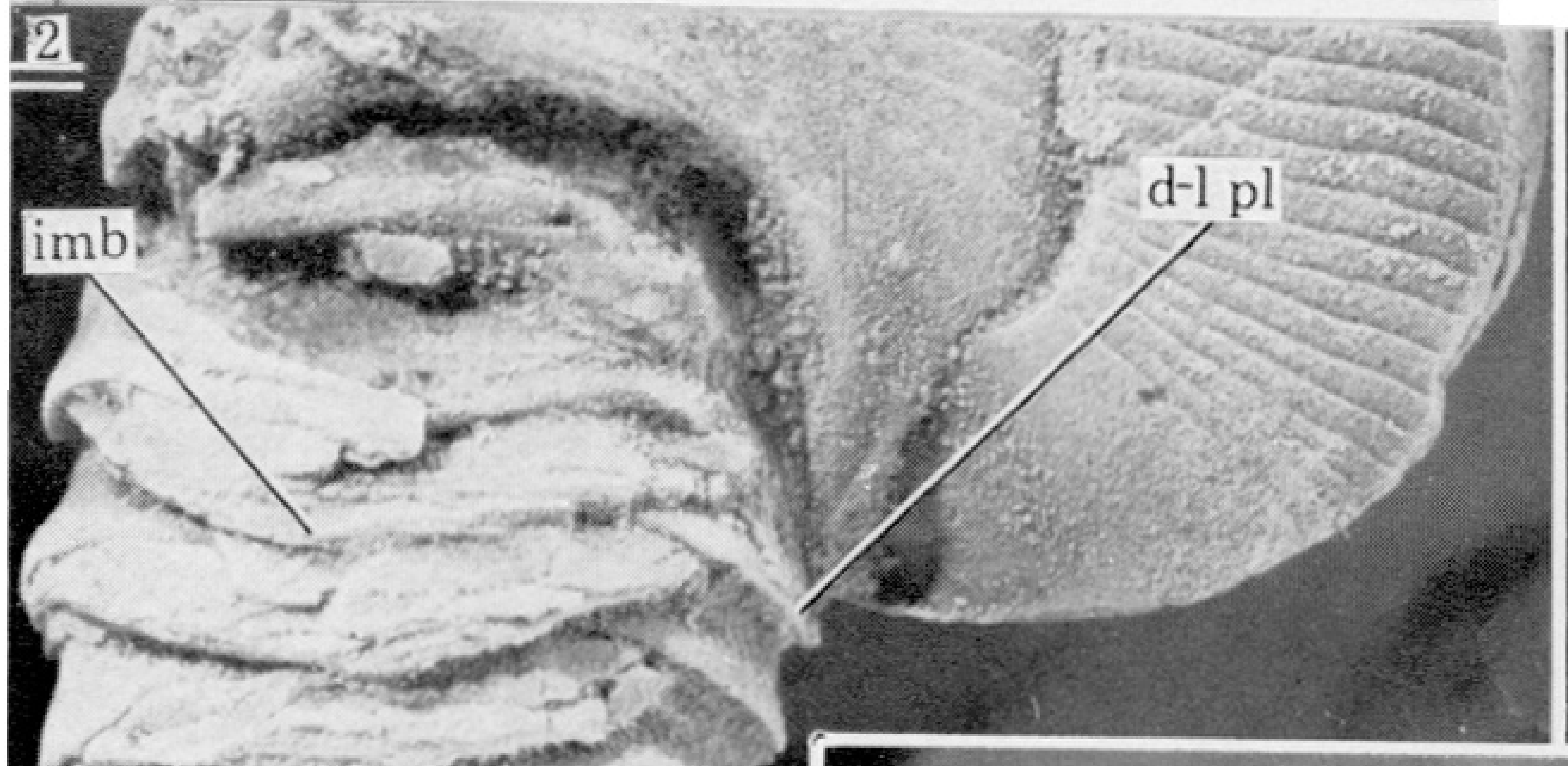


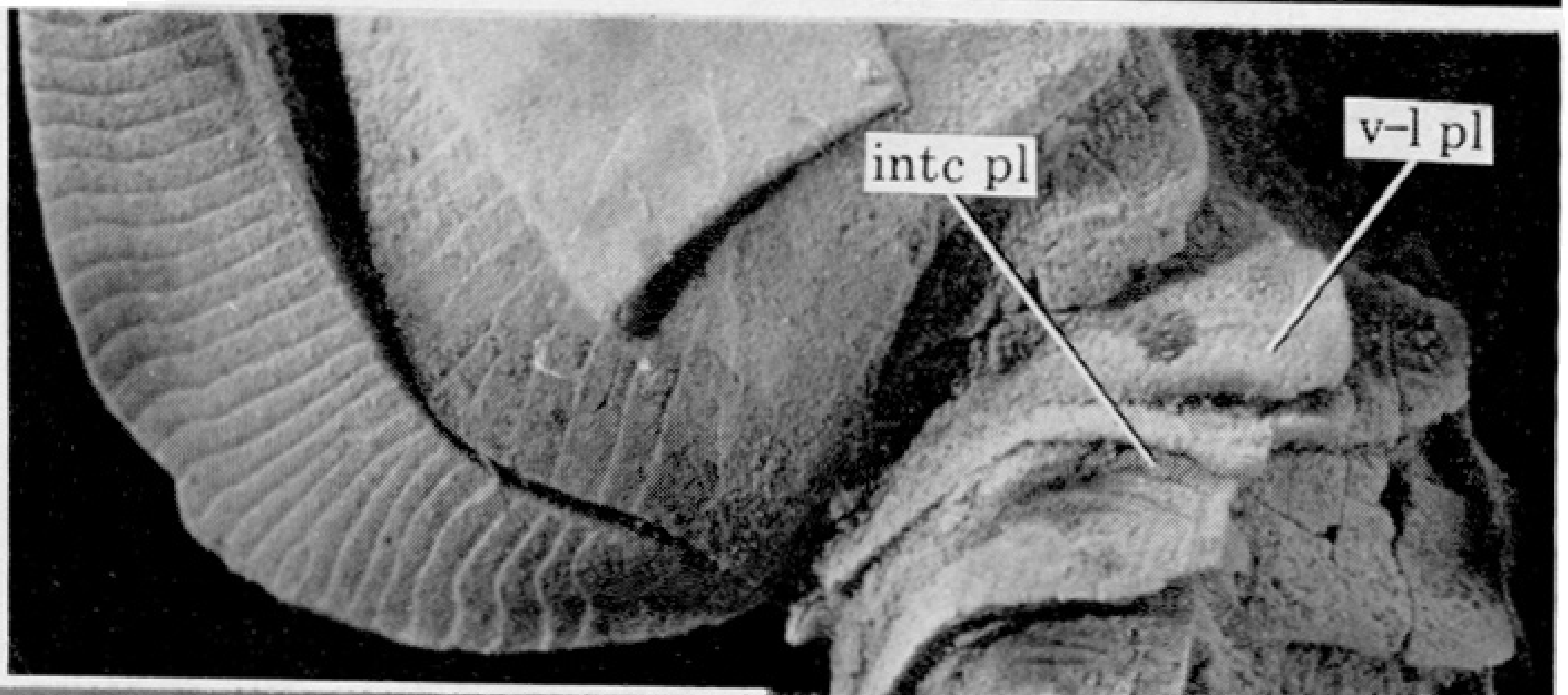


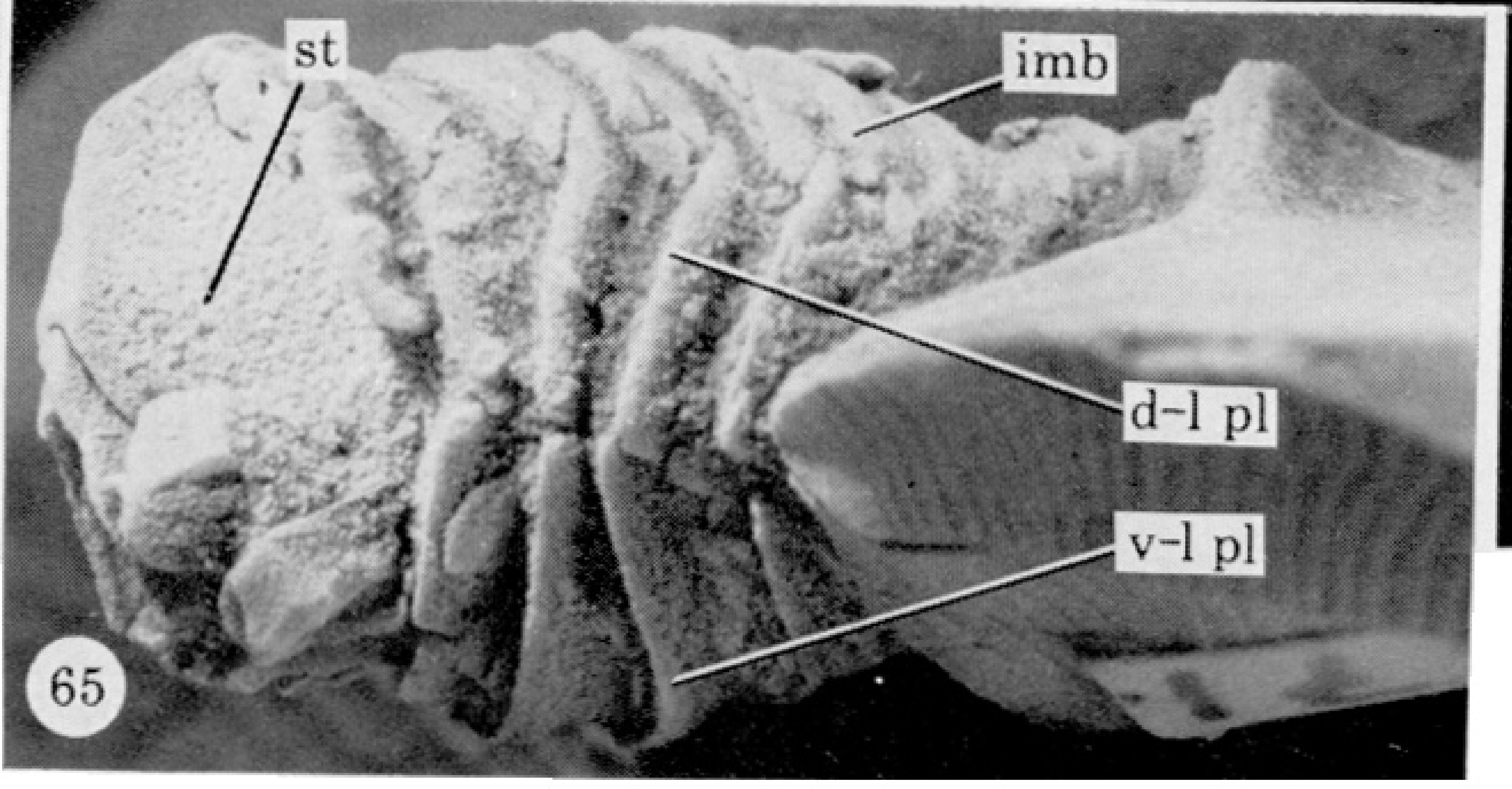
FIGURES 47–61. For description see pp. 315–316.

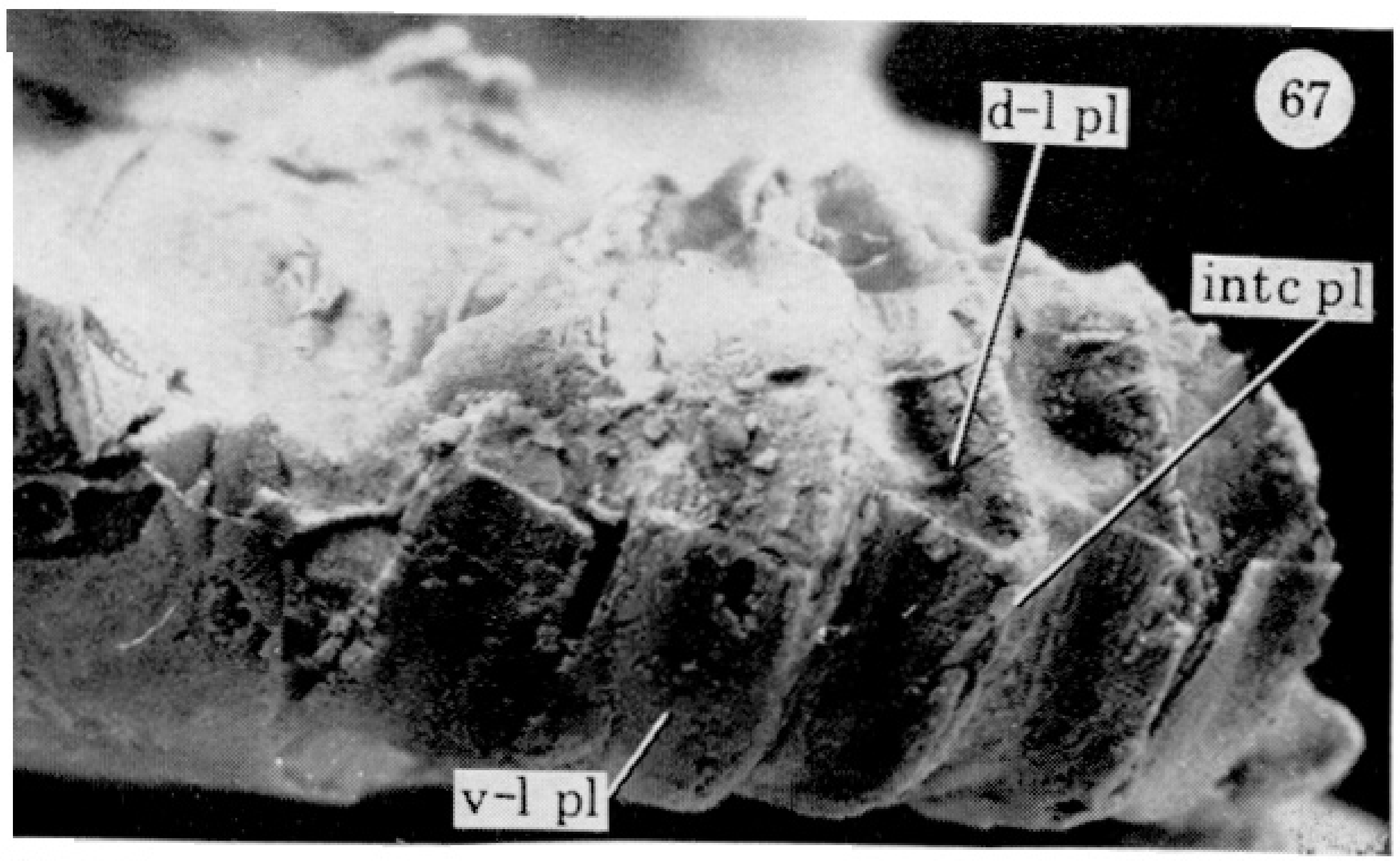


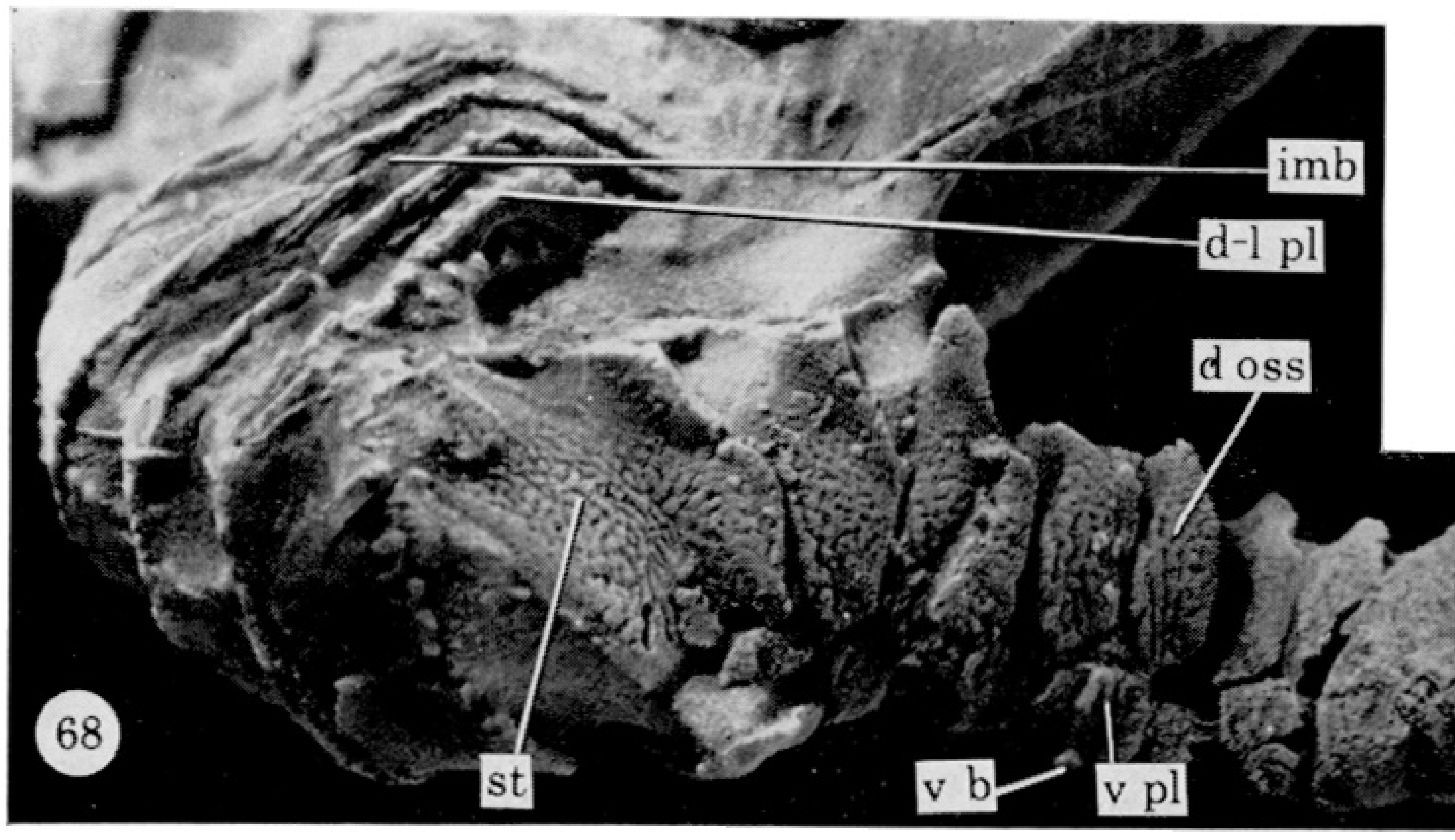




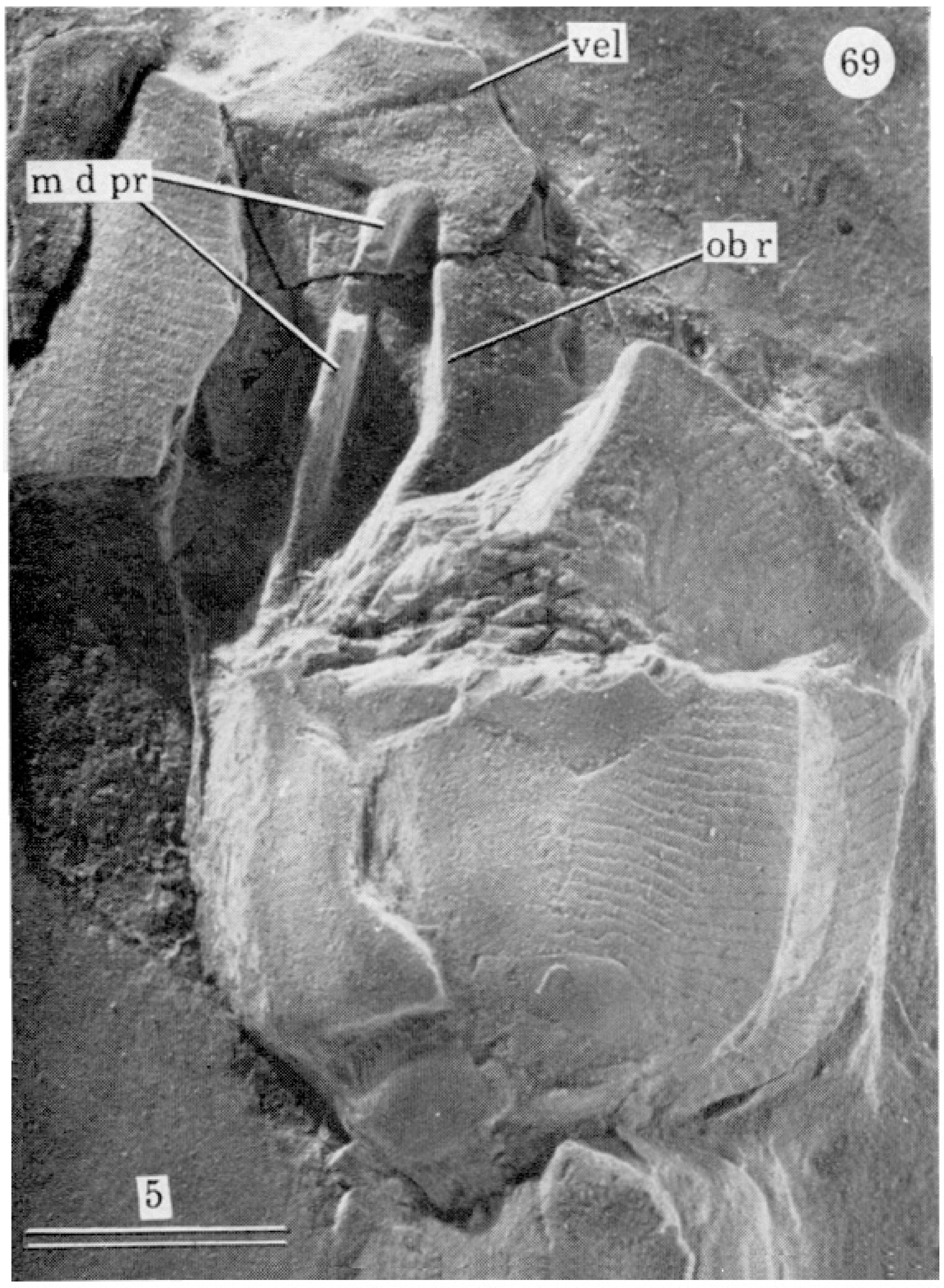


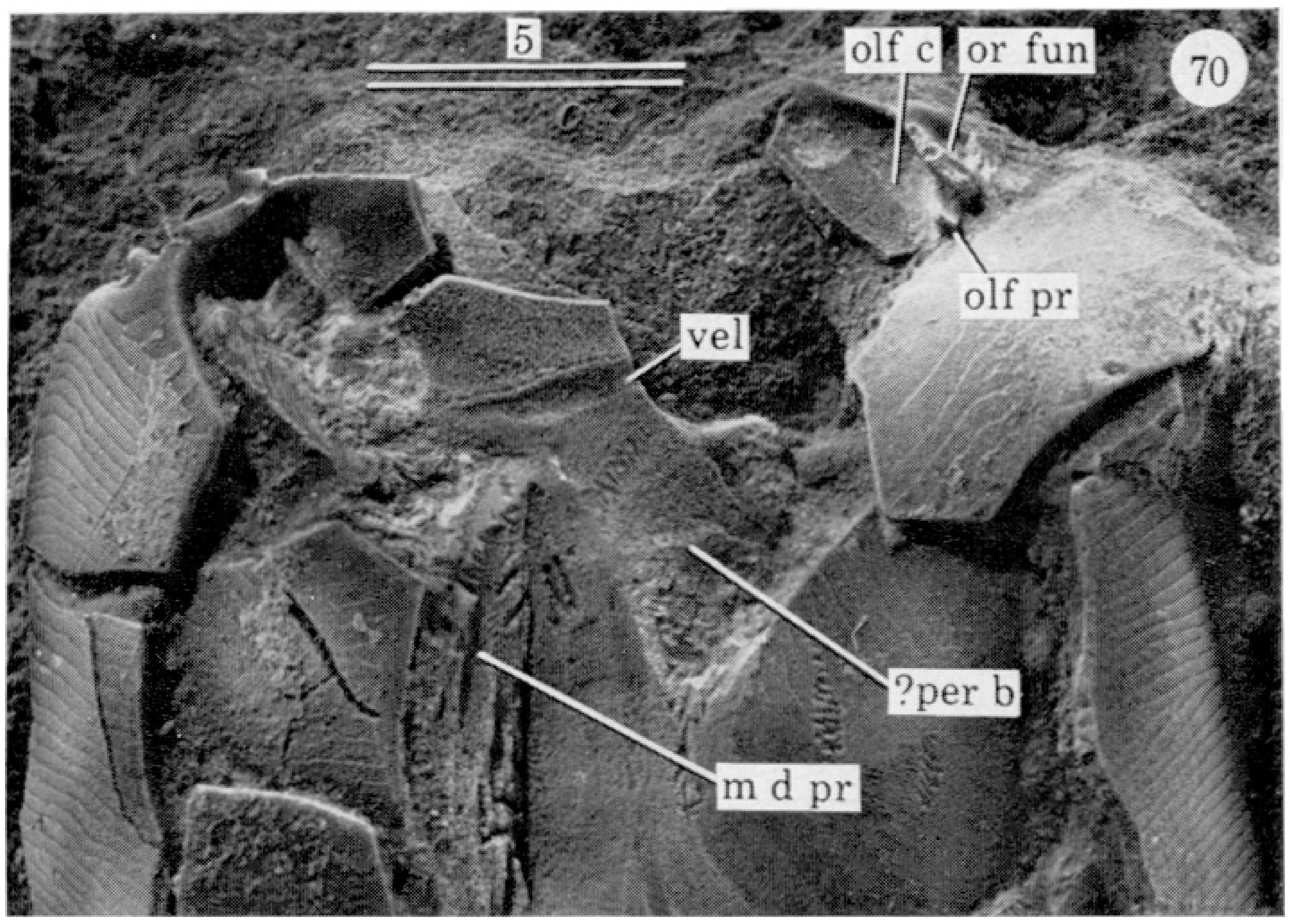


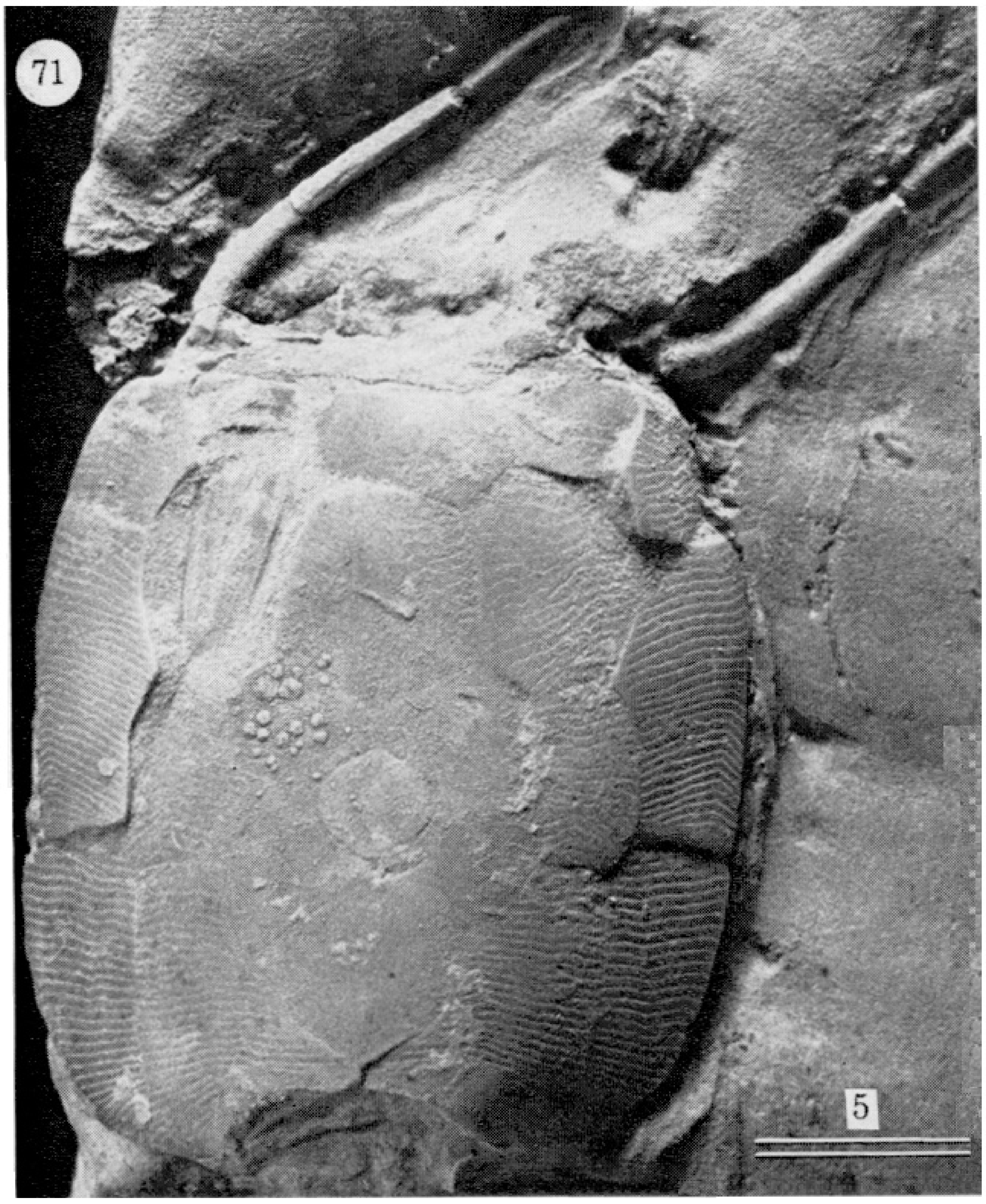


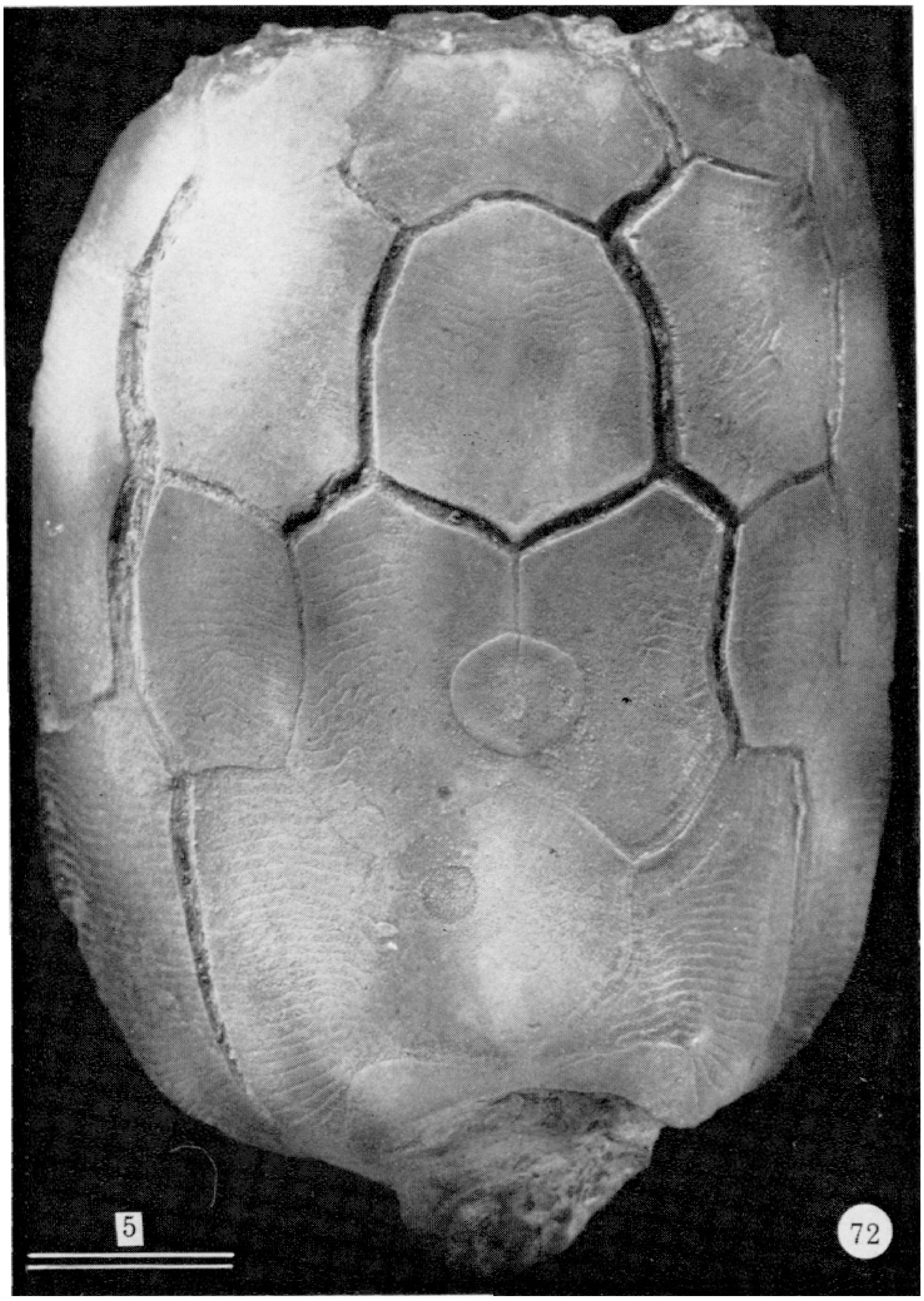


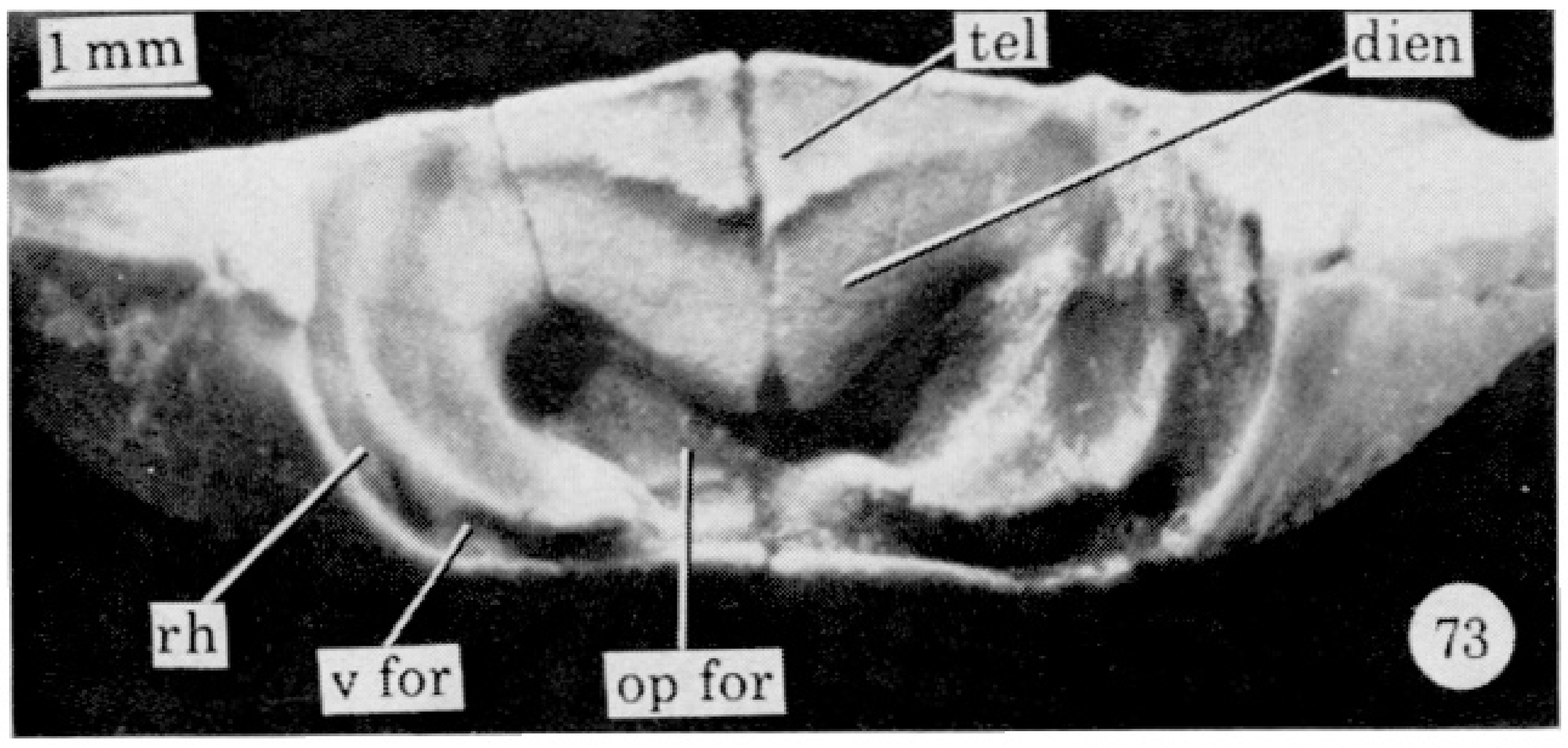
Figures 62–68. For description see p. 316.

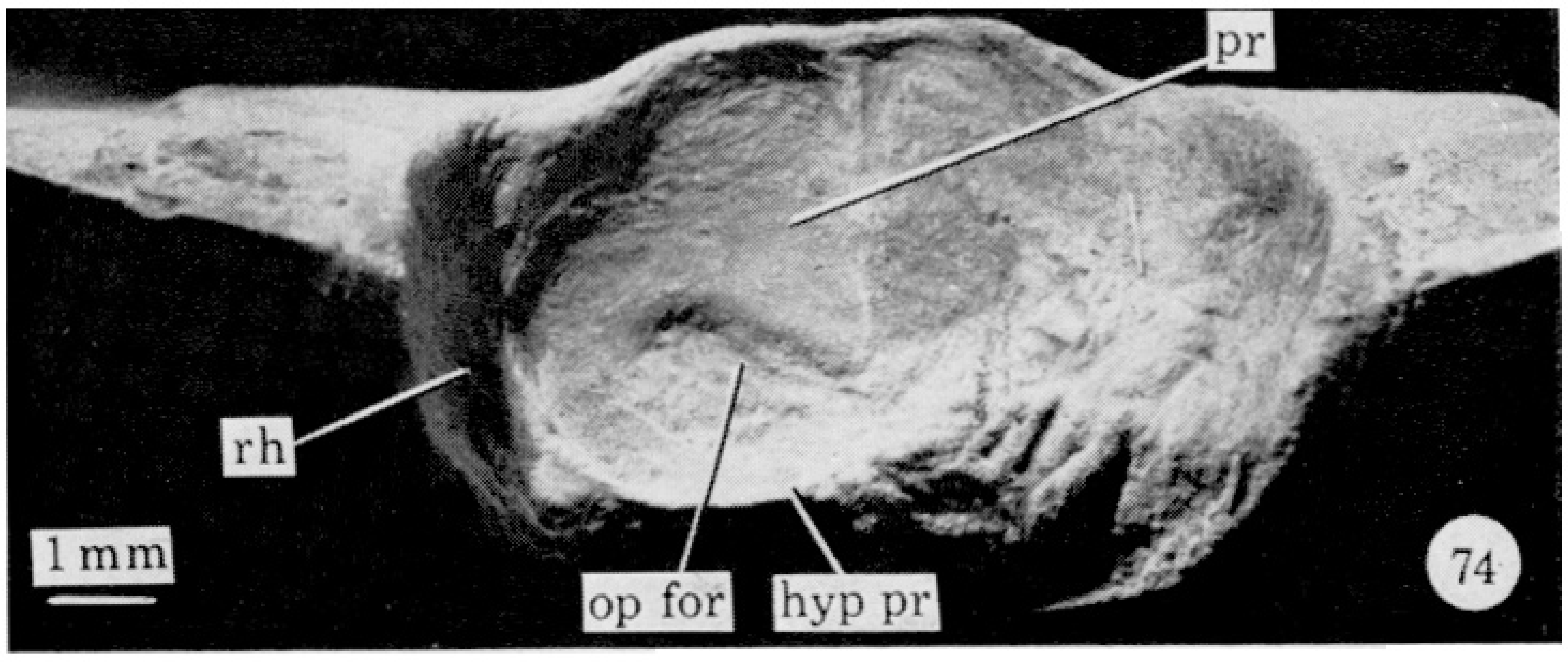




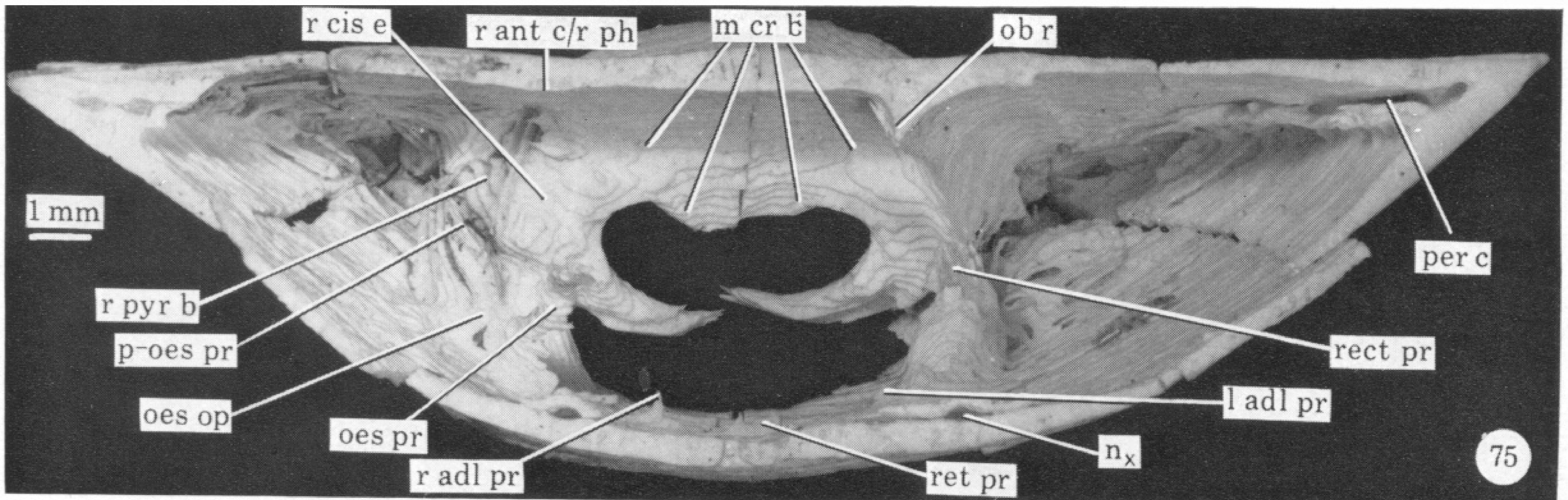


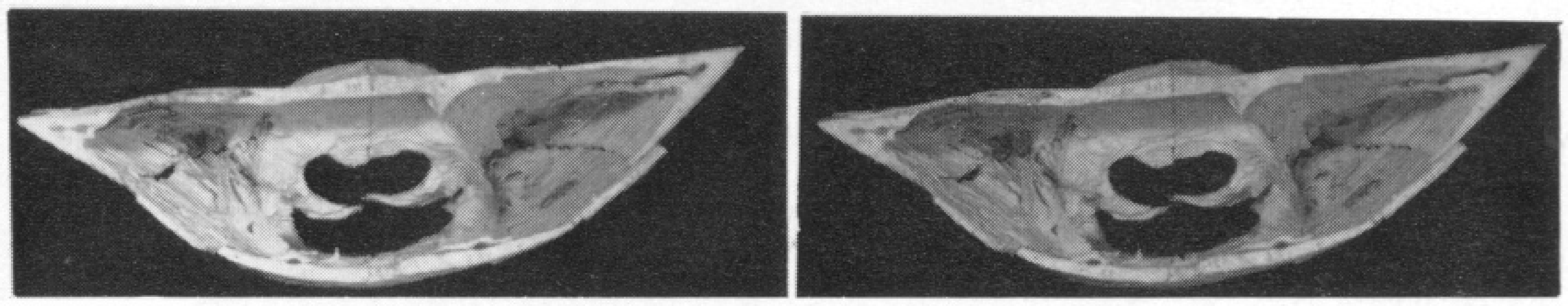


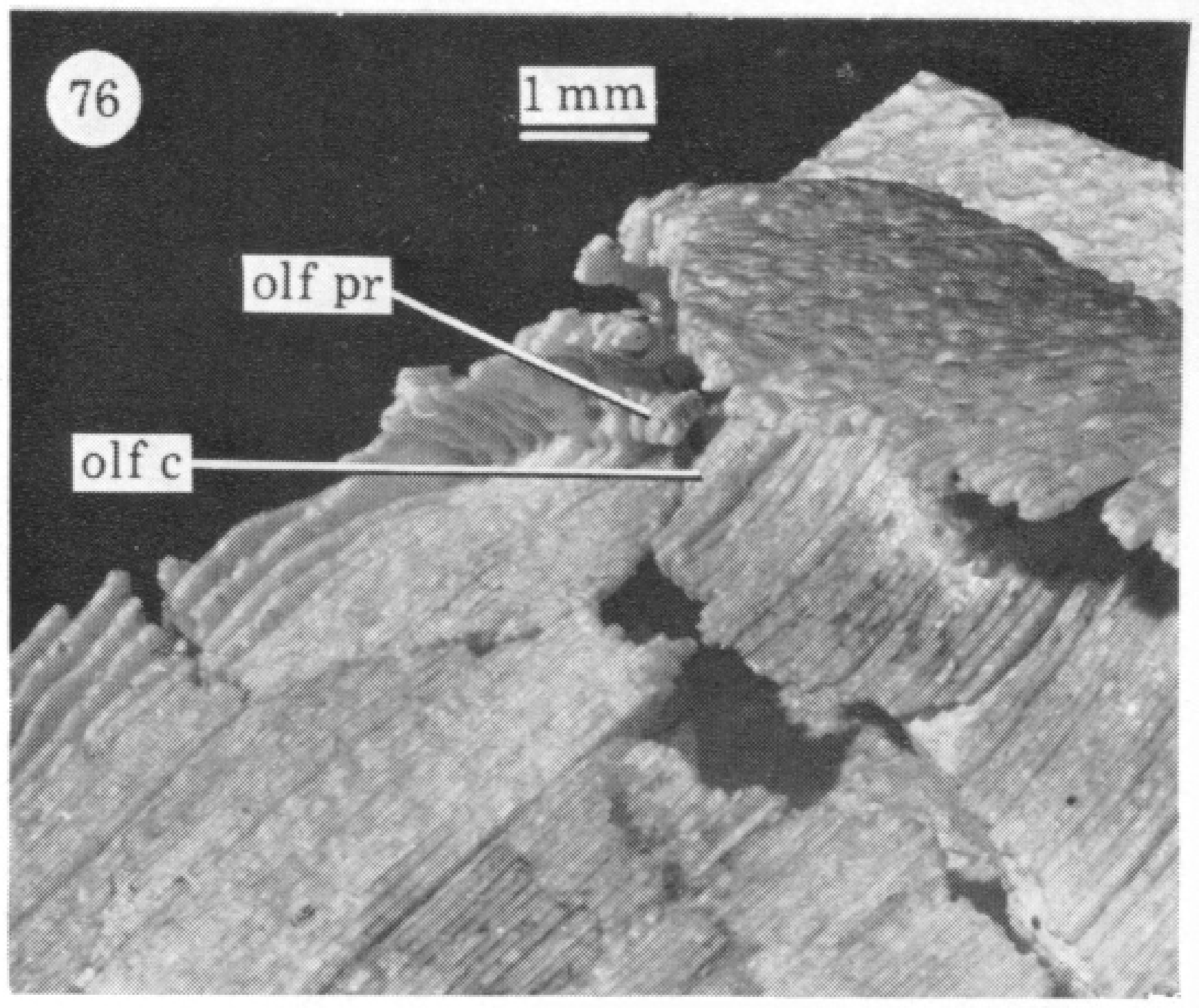


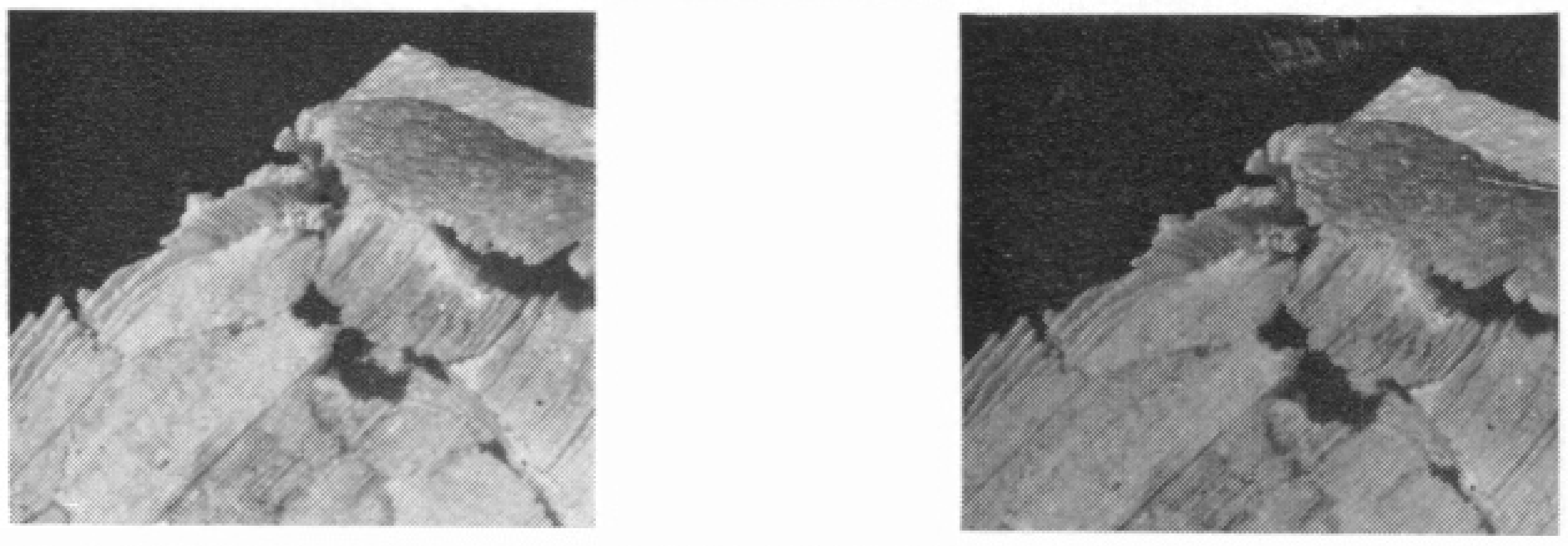


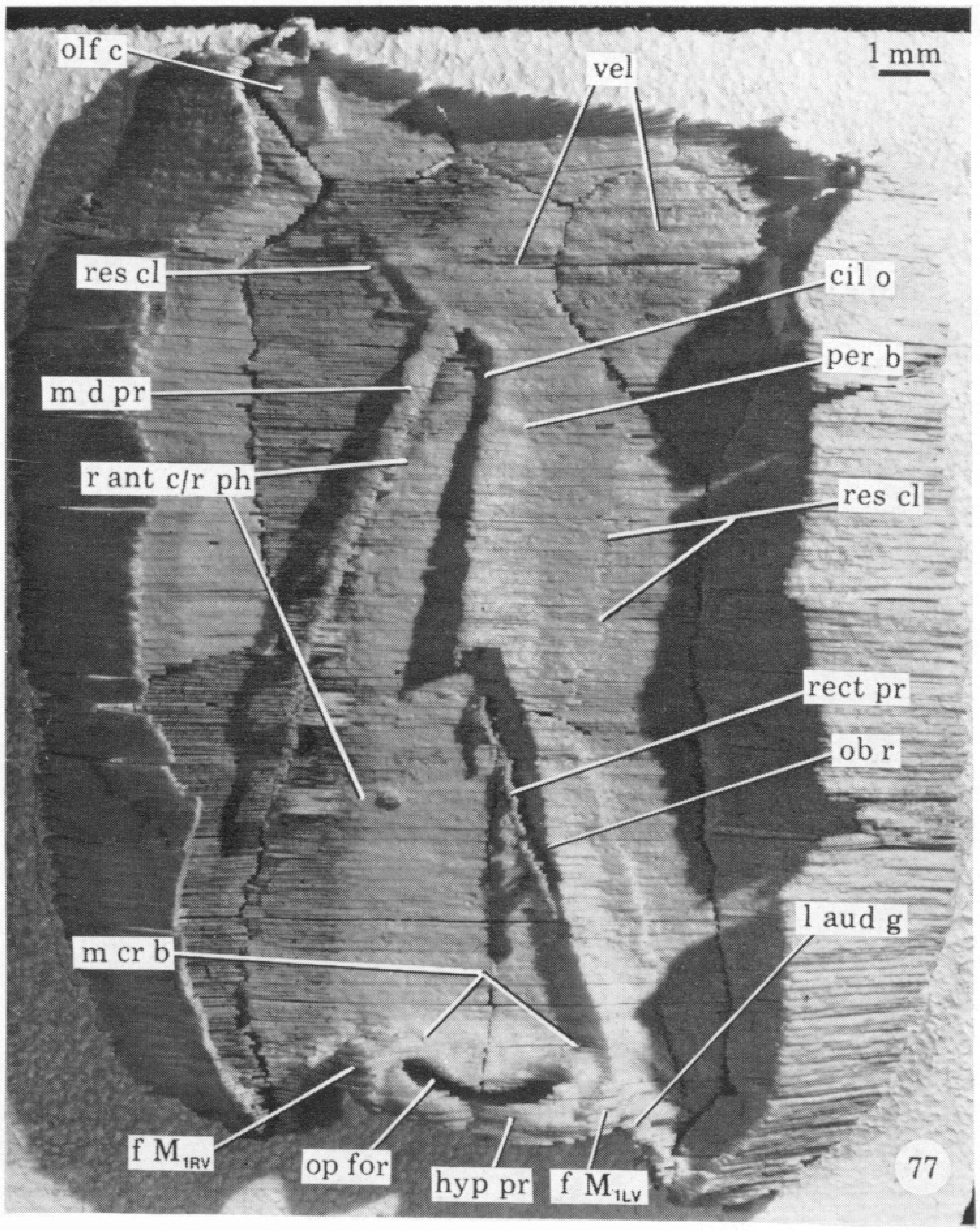
FIGURES 69–74. For description see p. 316.

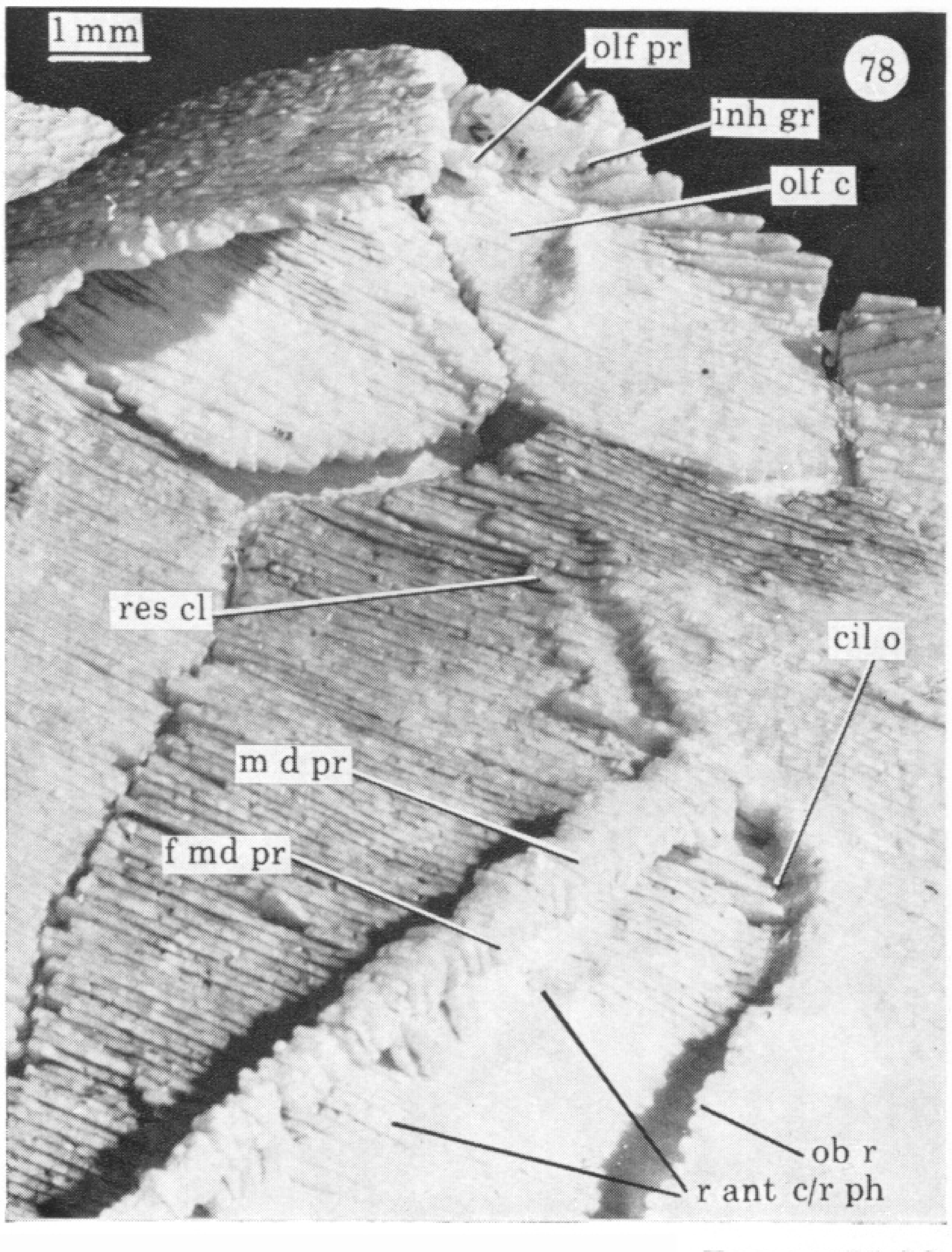


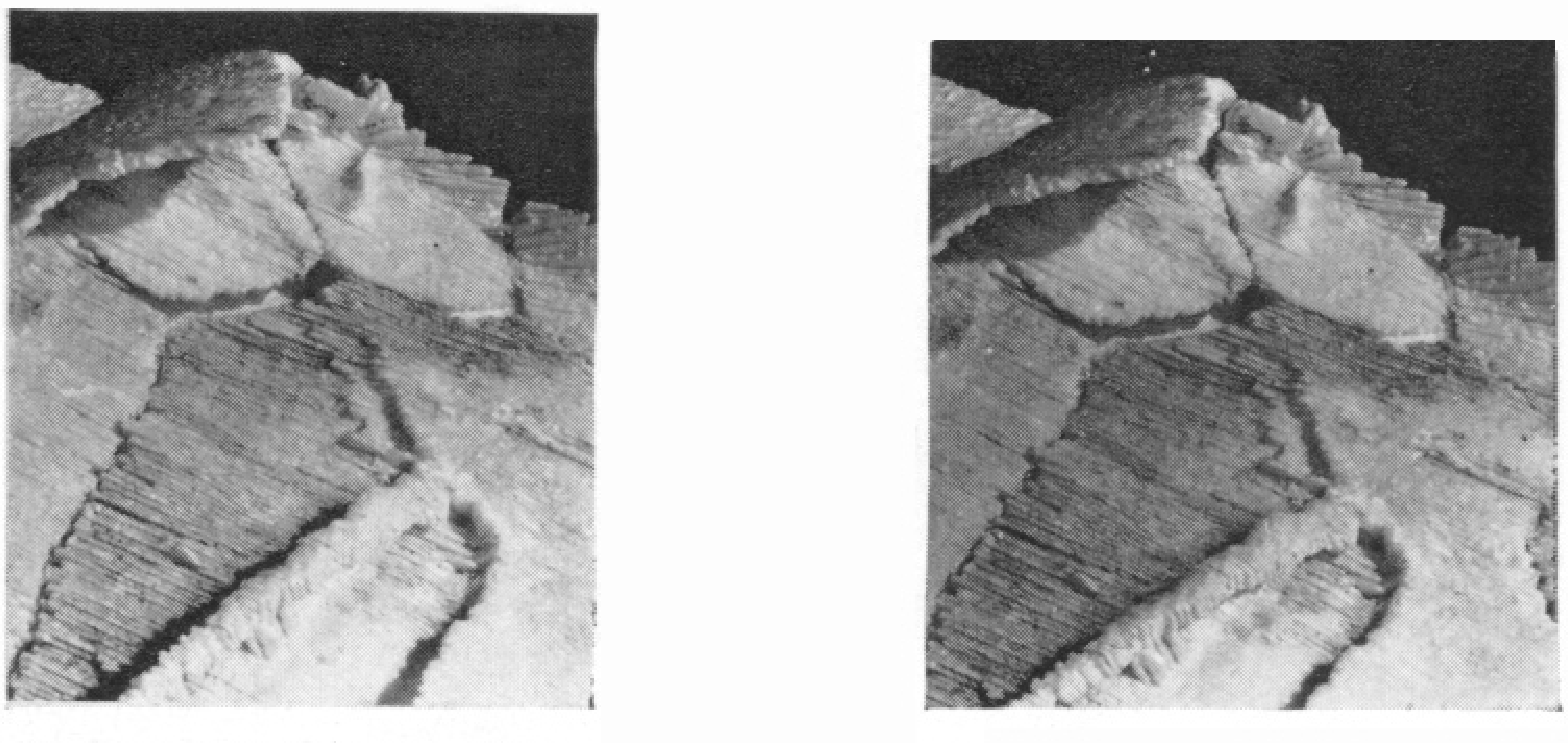




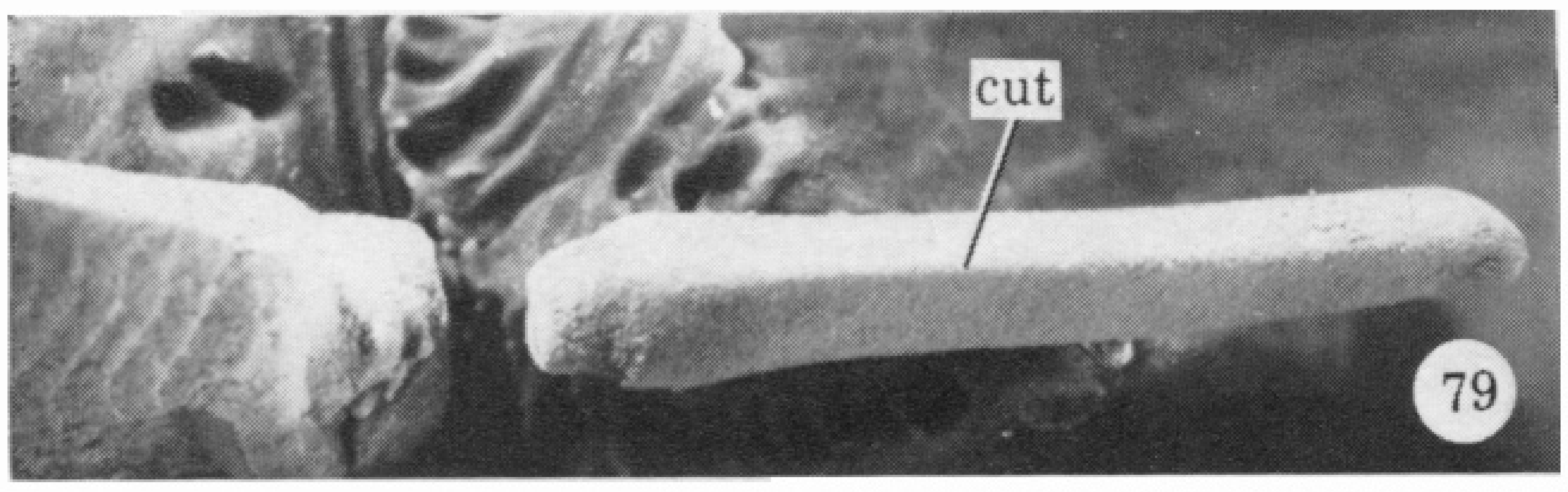


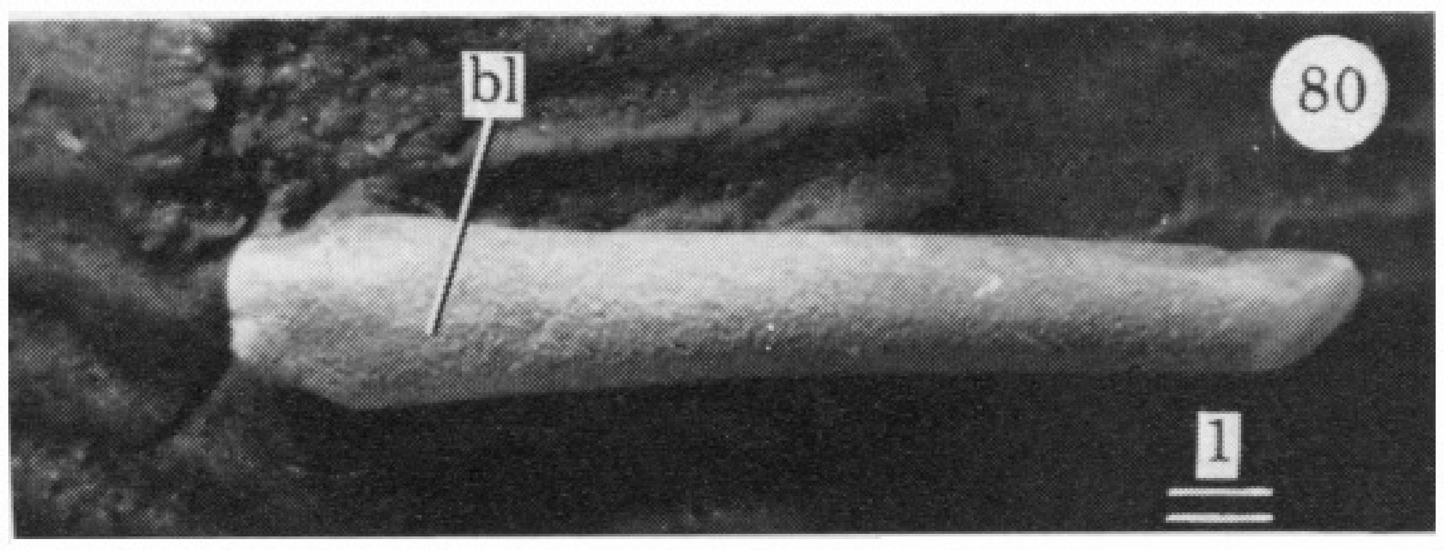


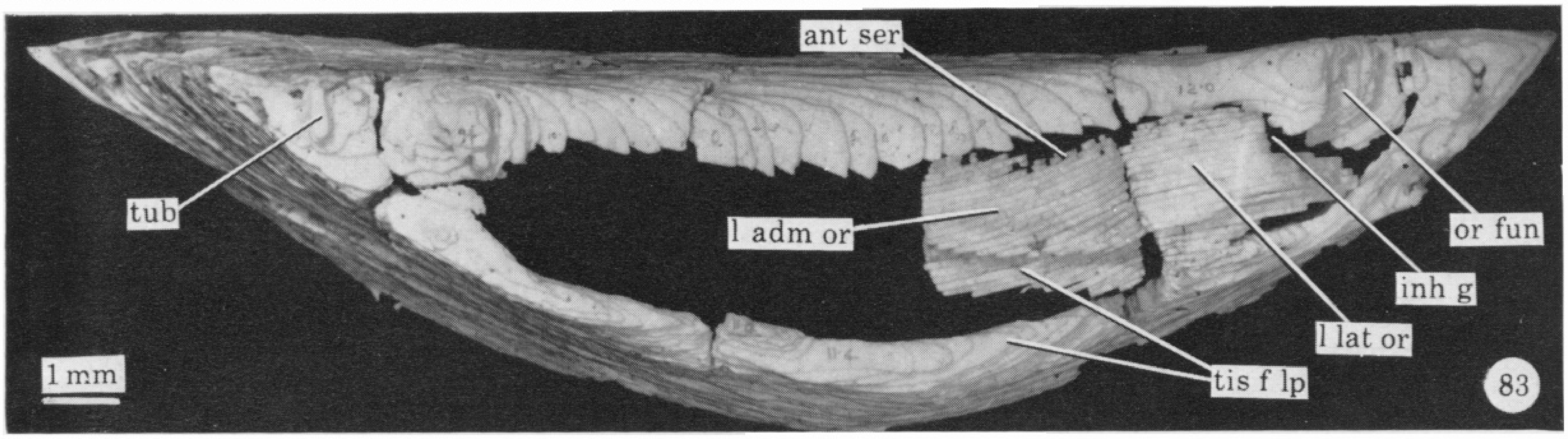


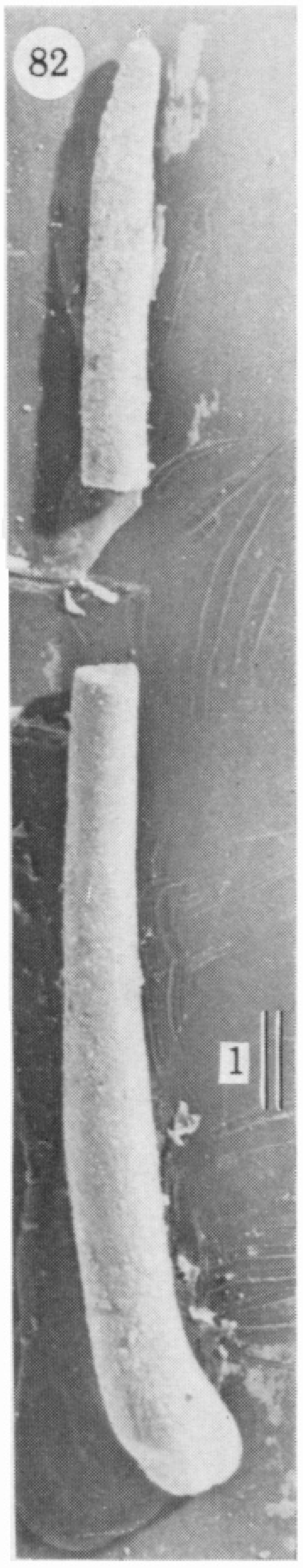


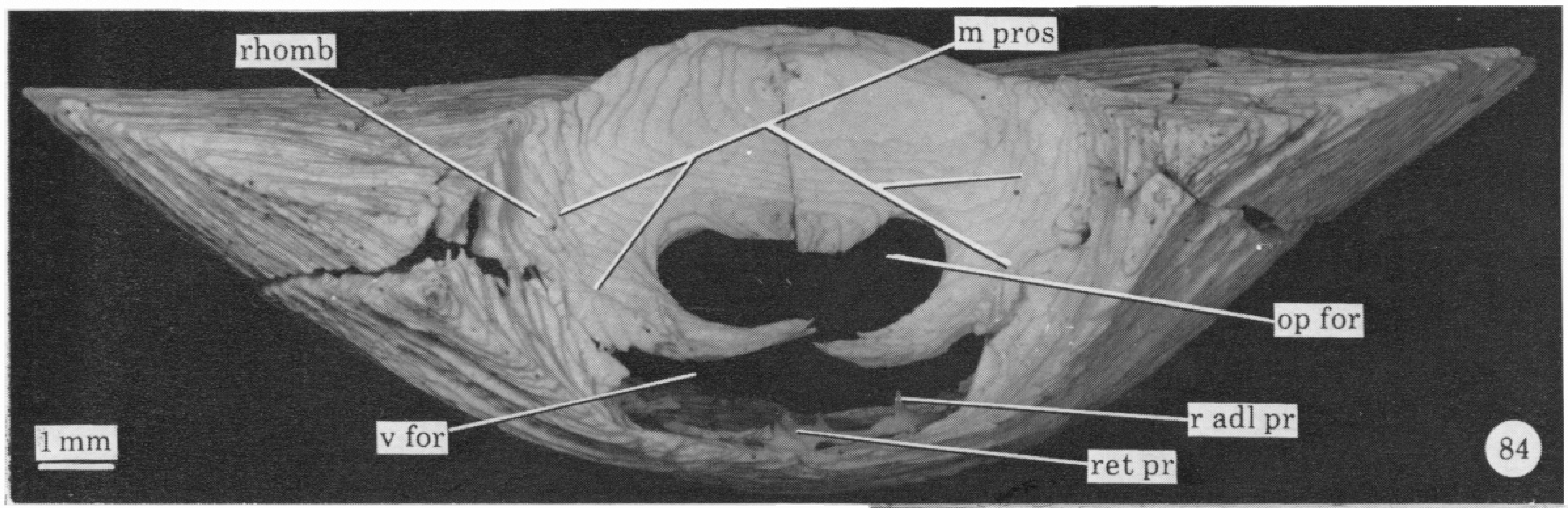
FIGURES 75–78. For description see p. 316.

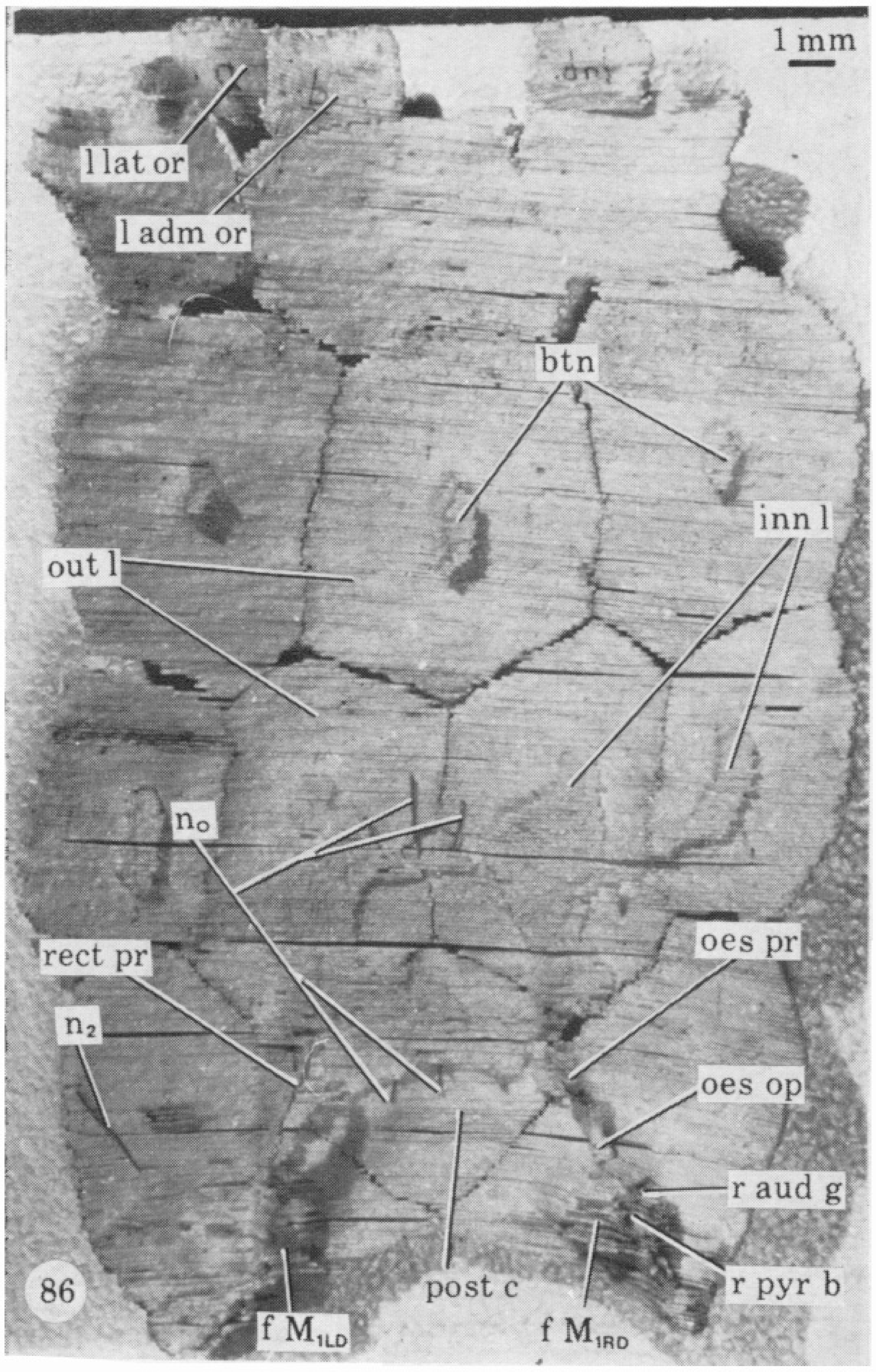


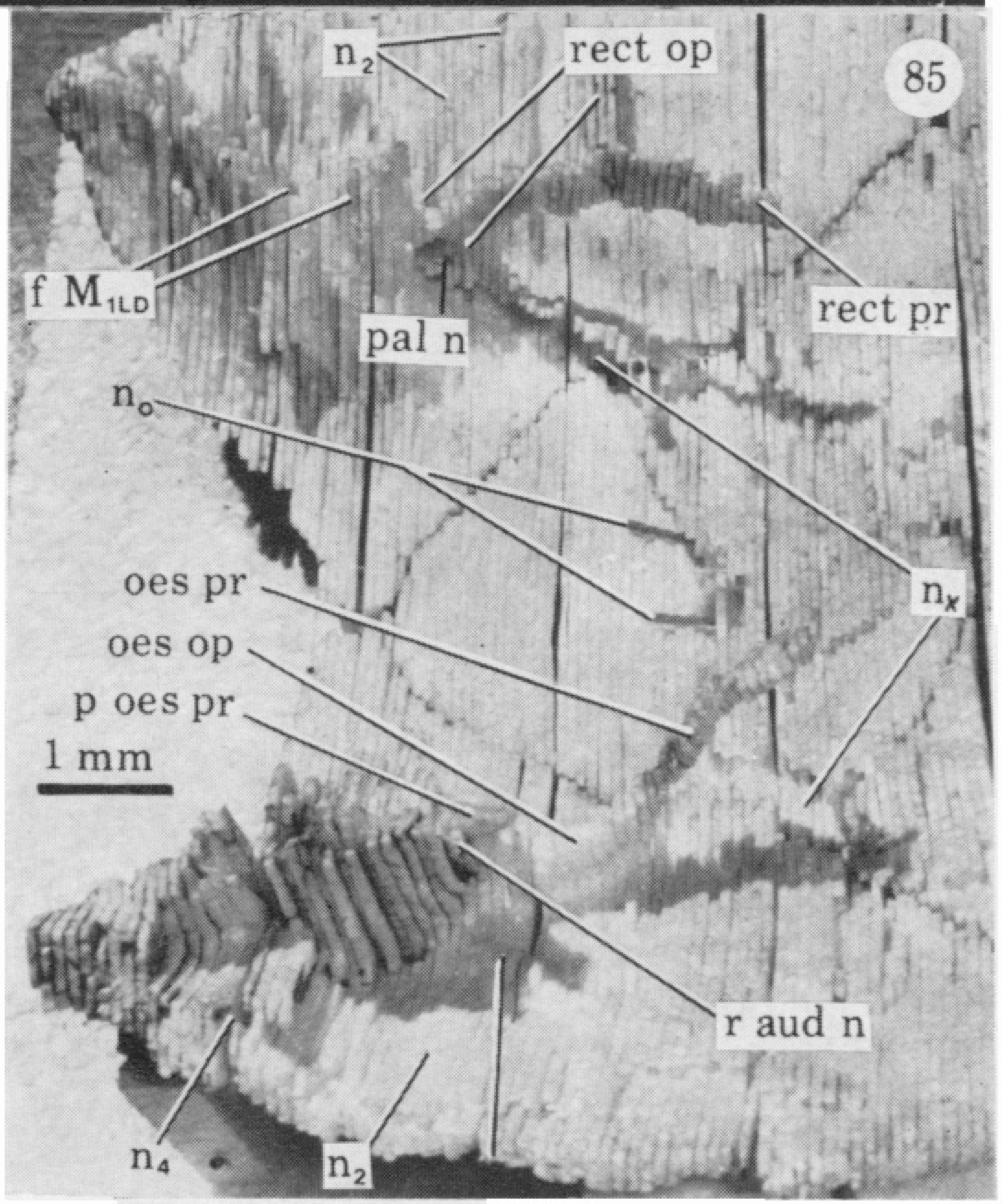


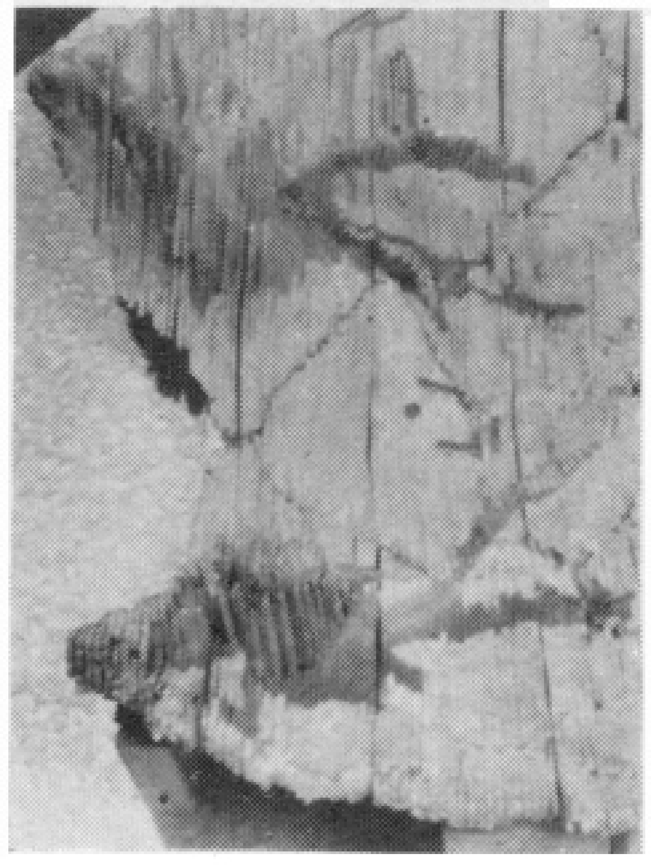




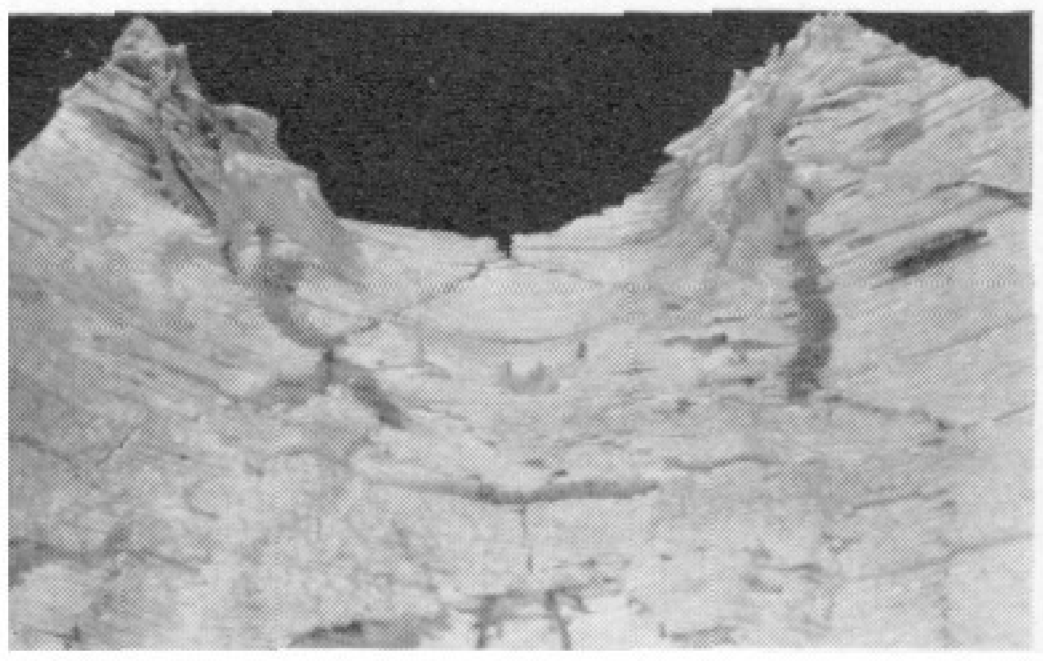


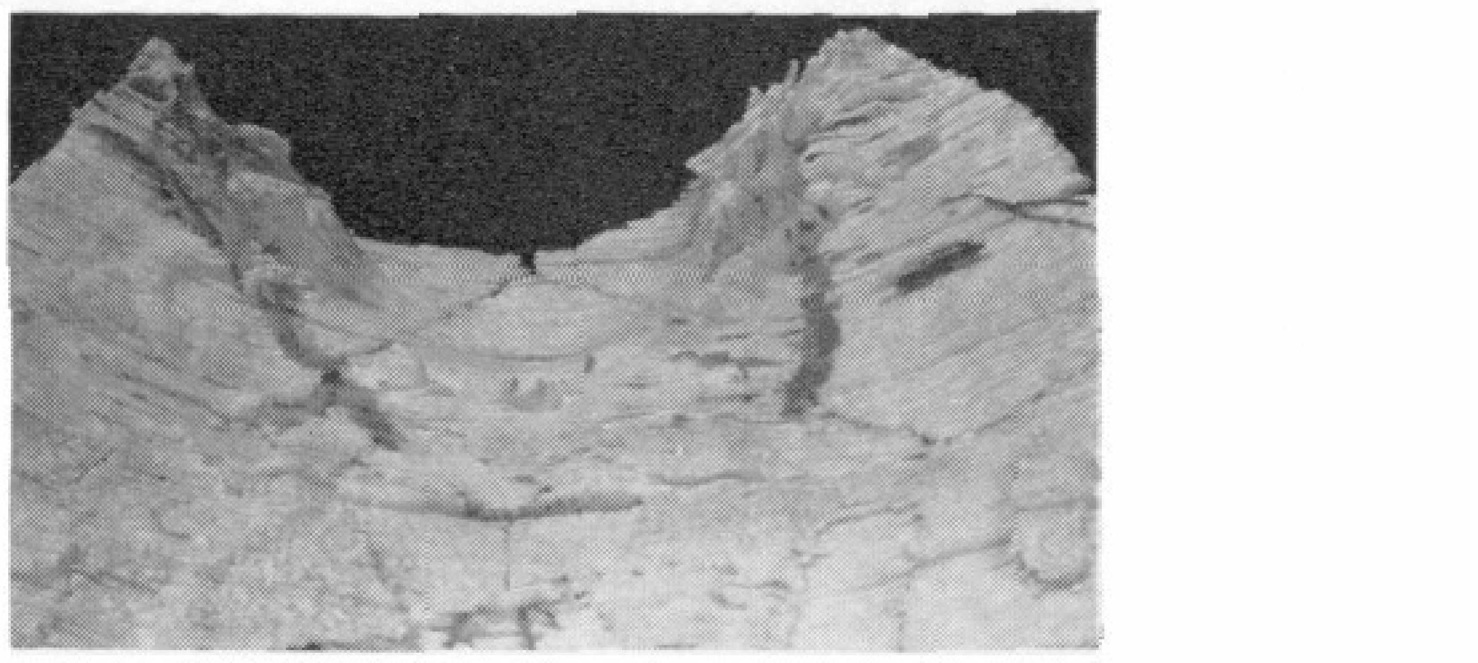


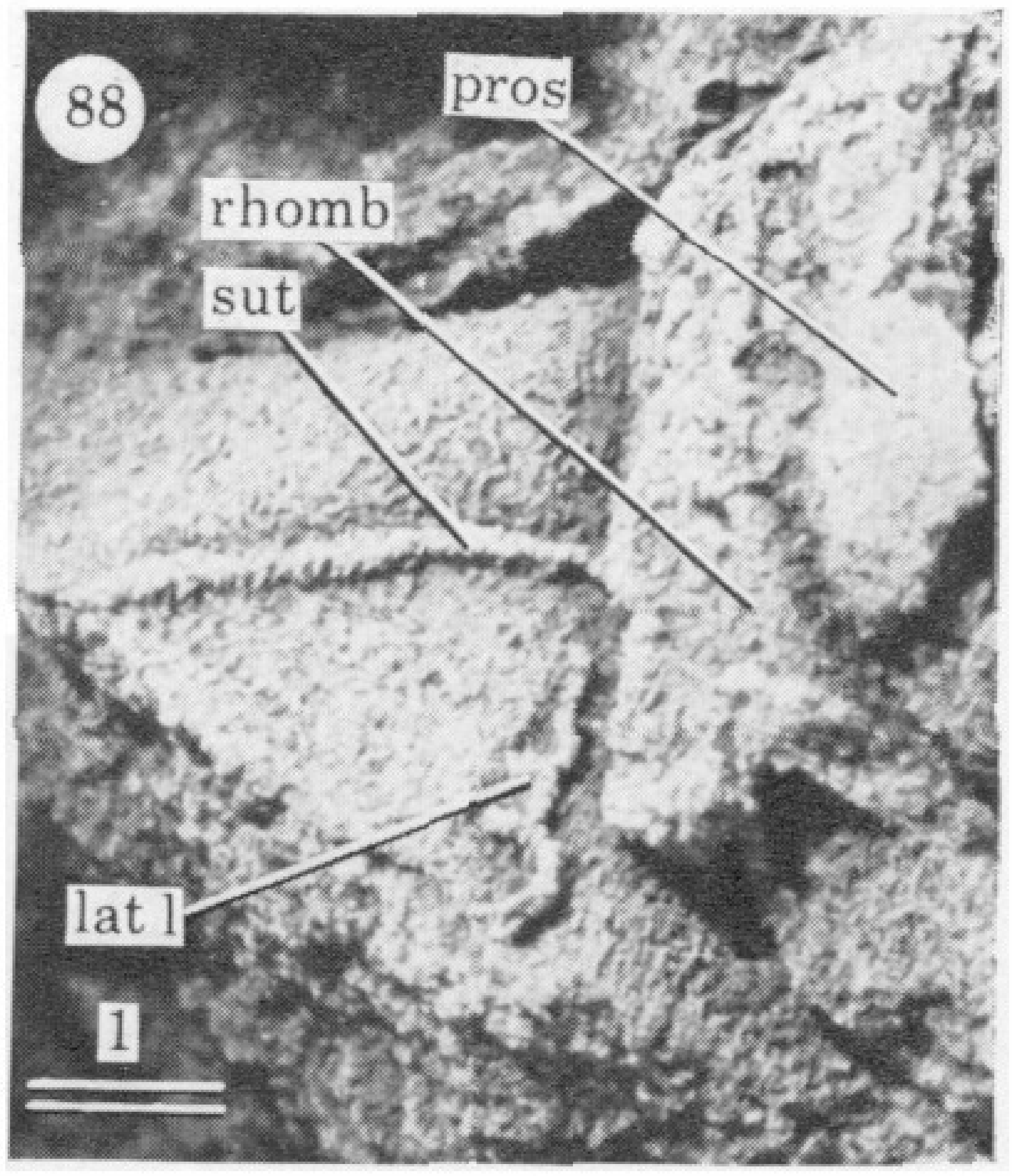


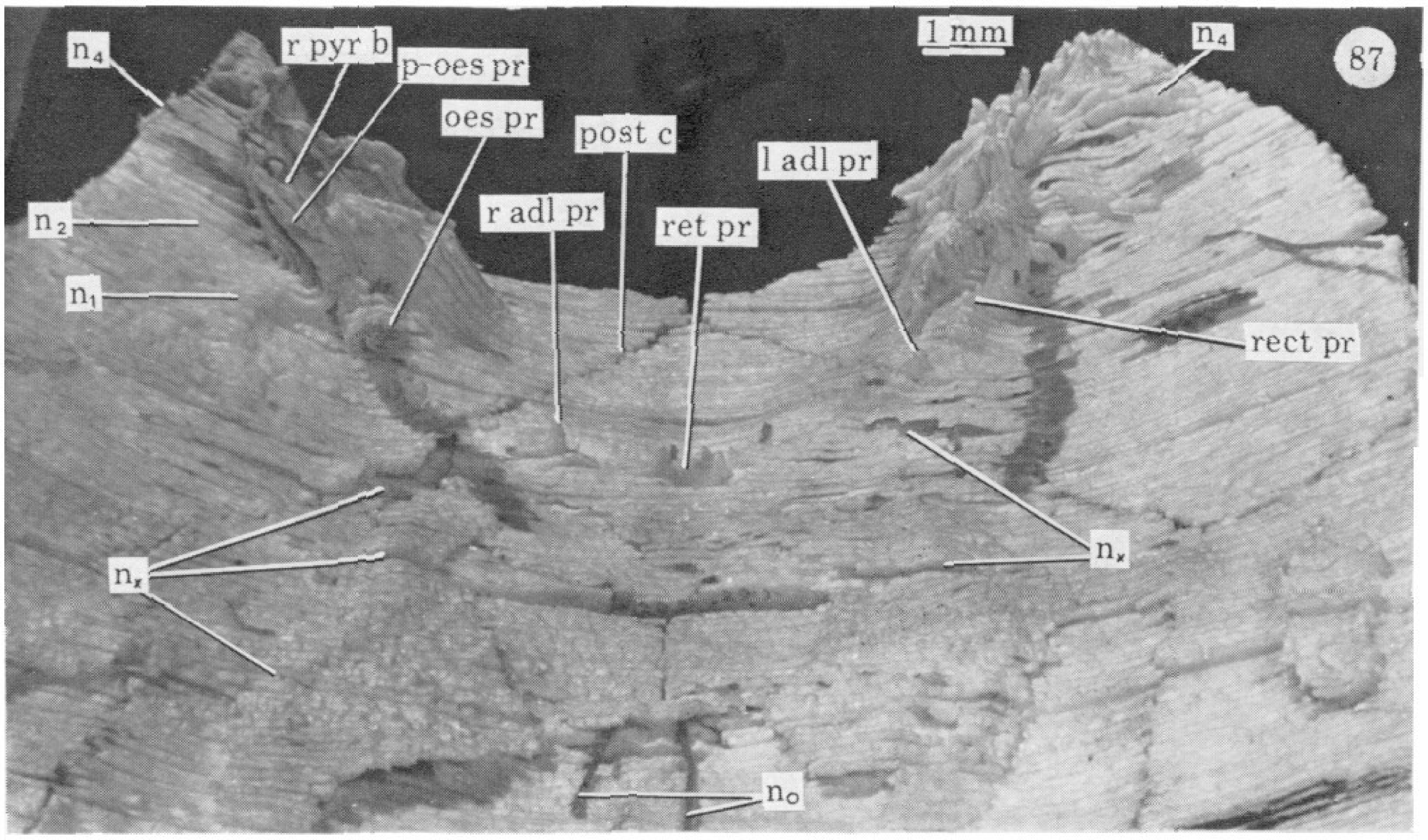


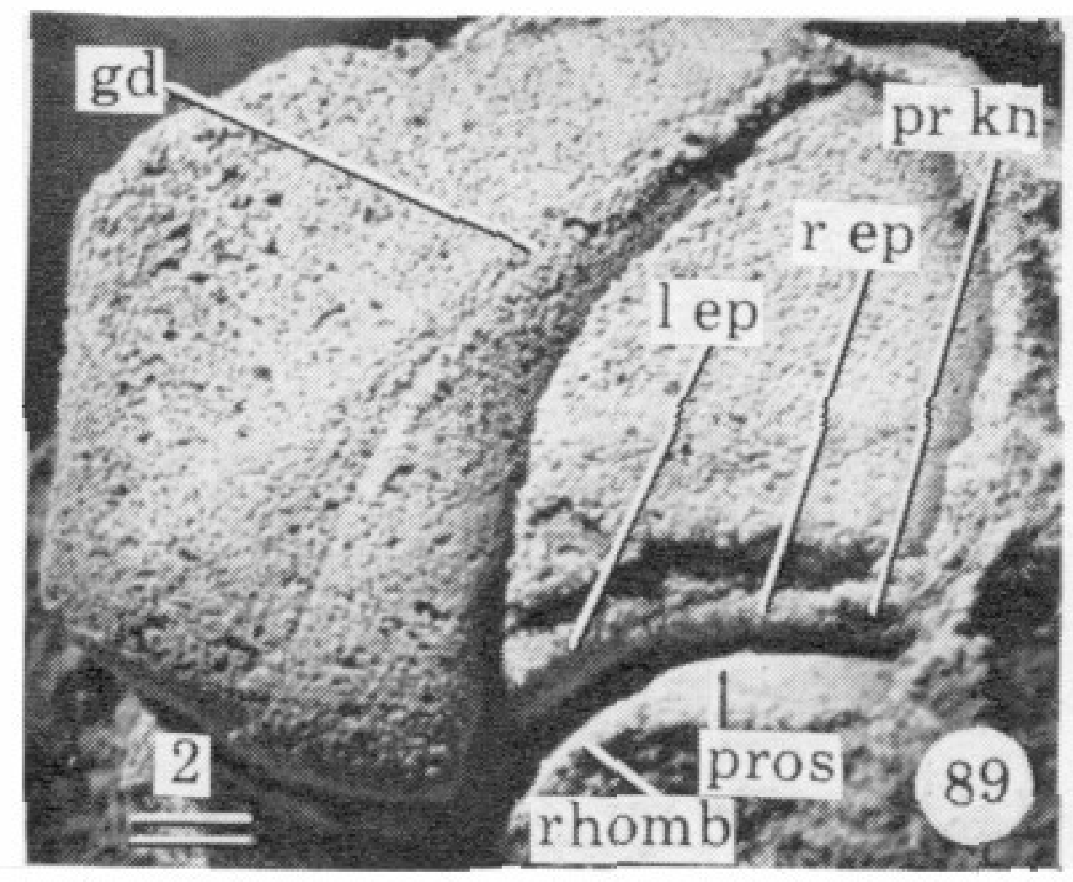
FIGURES 79–86. For description see p. 317.

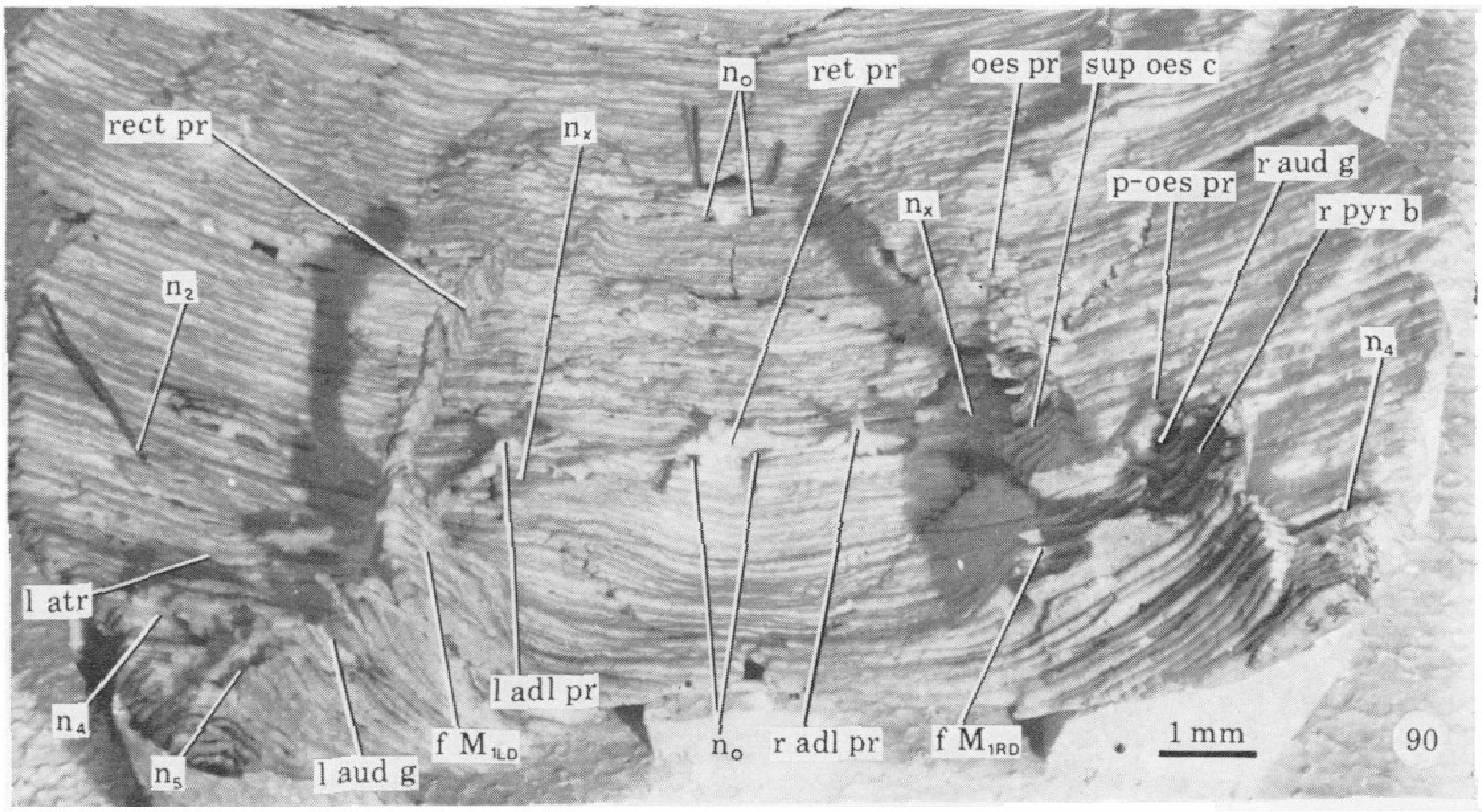


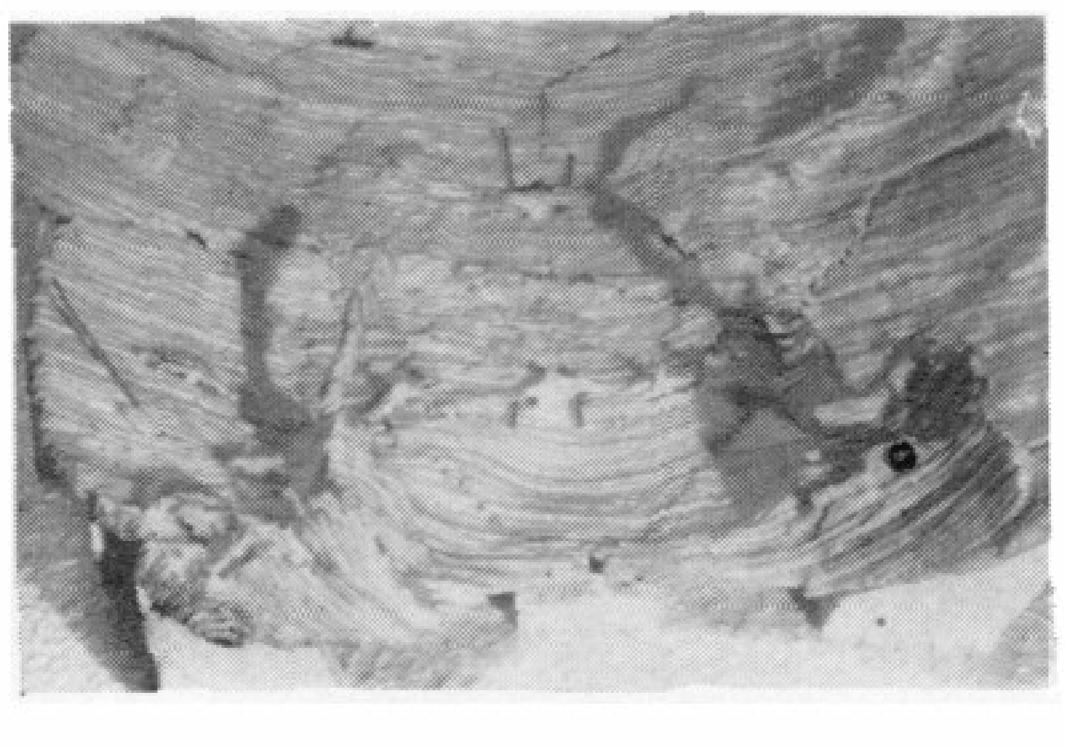


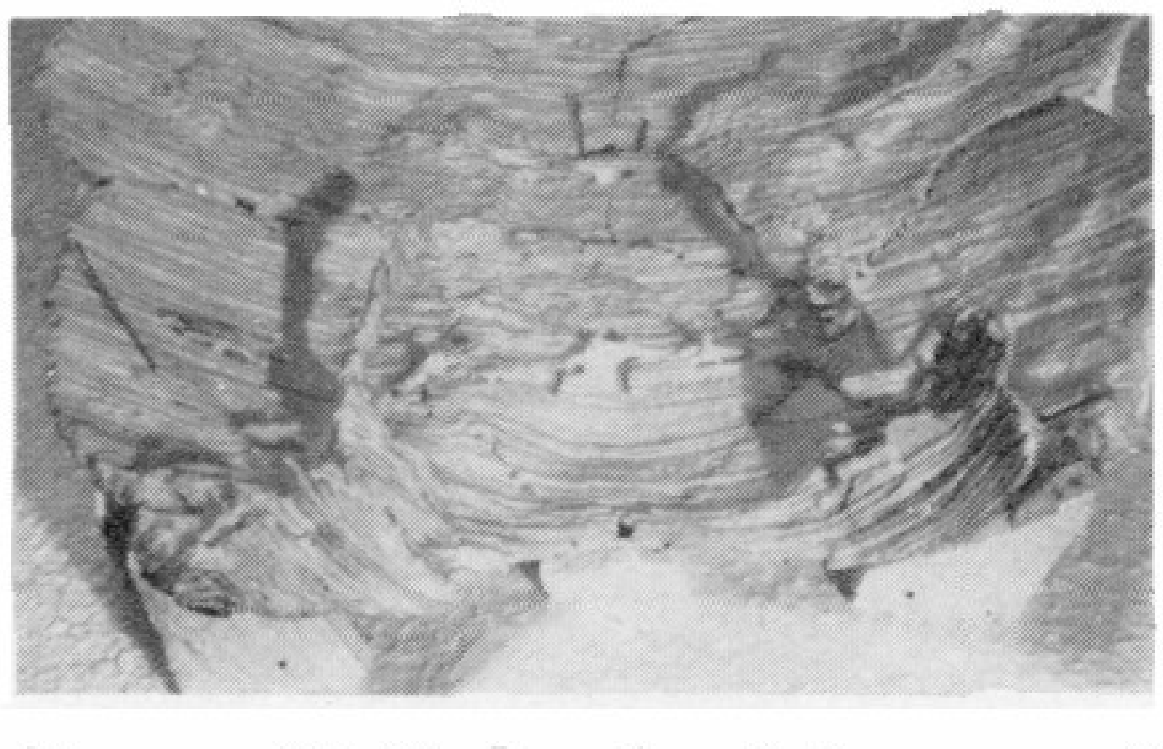


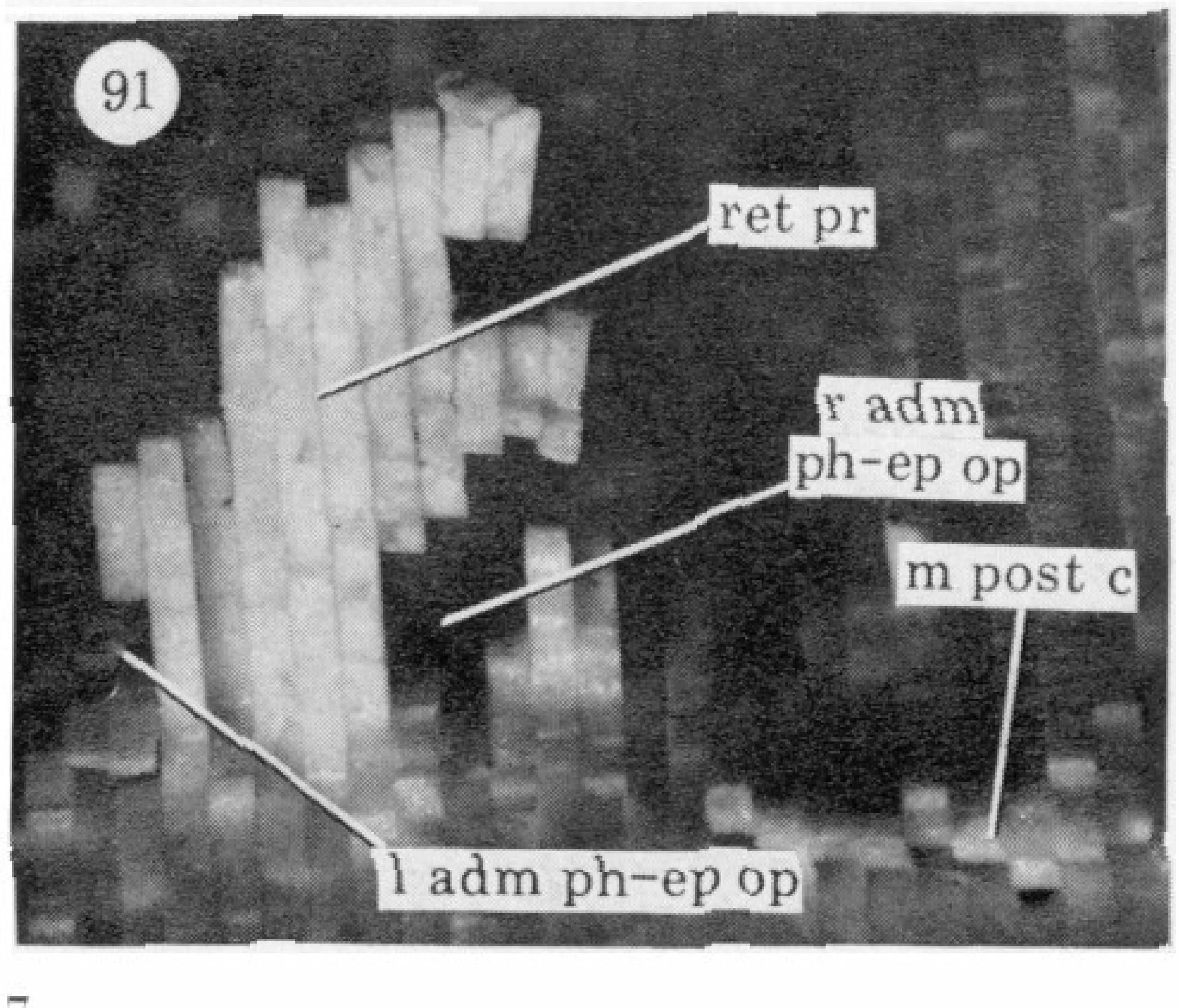




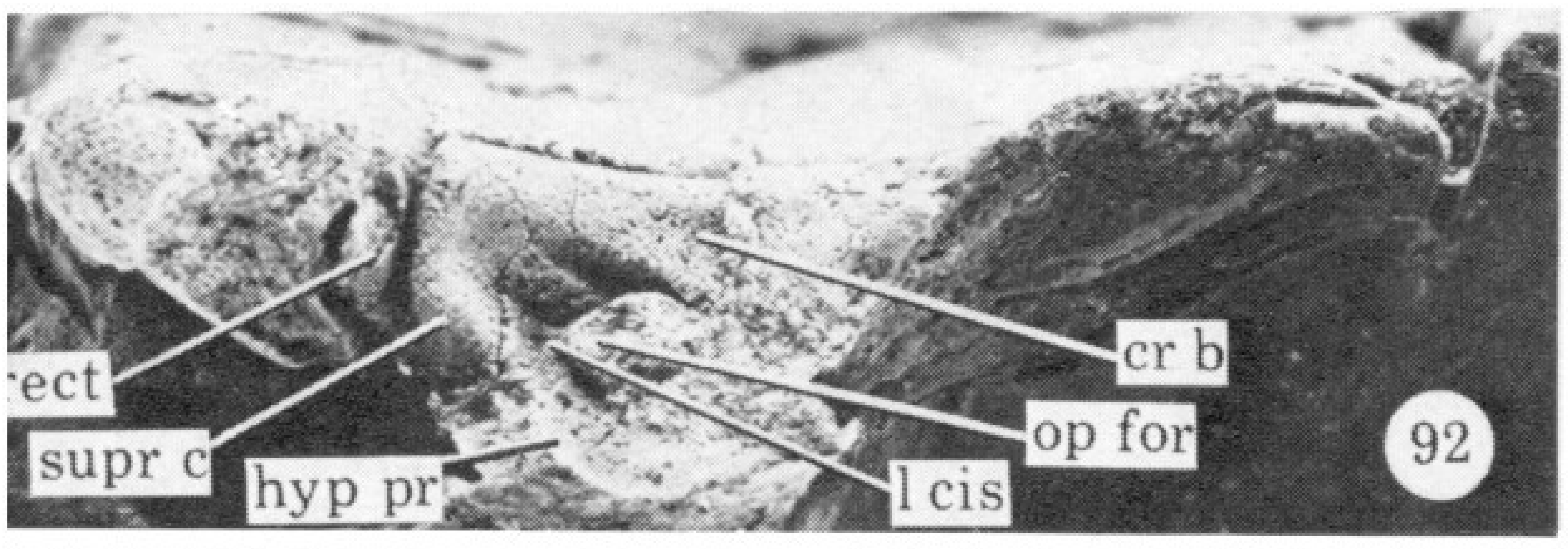


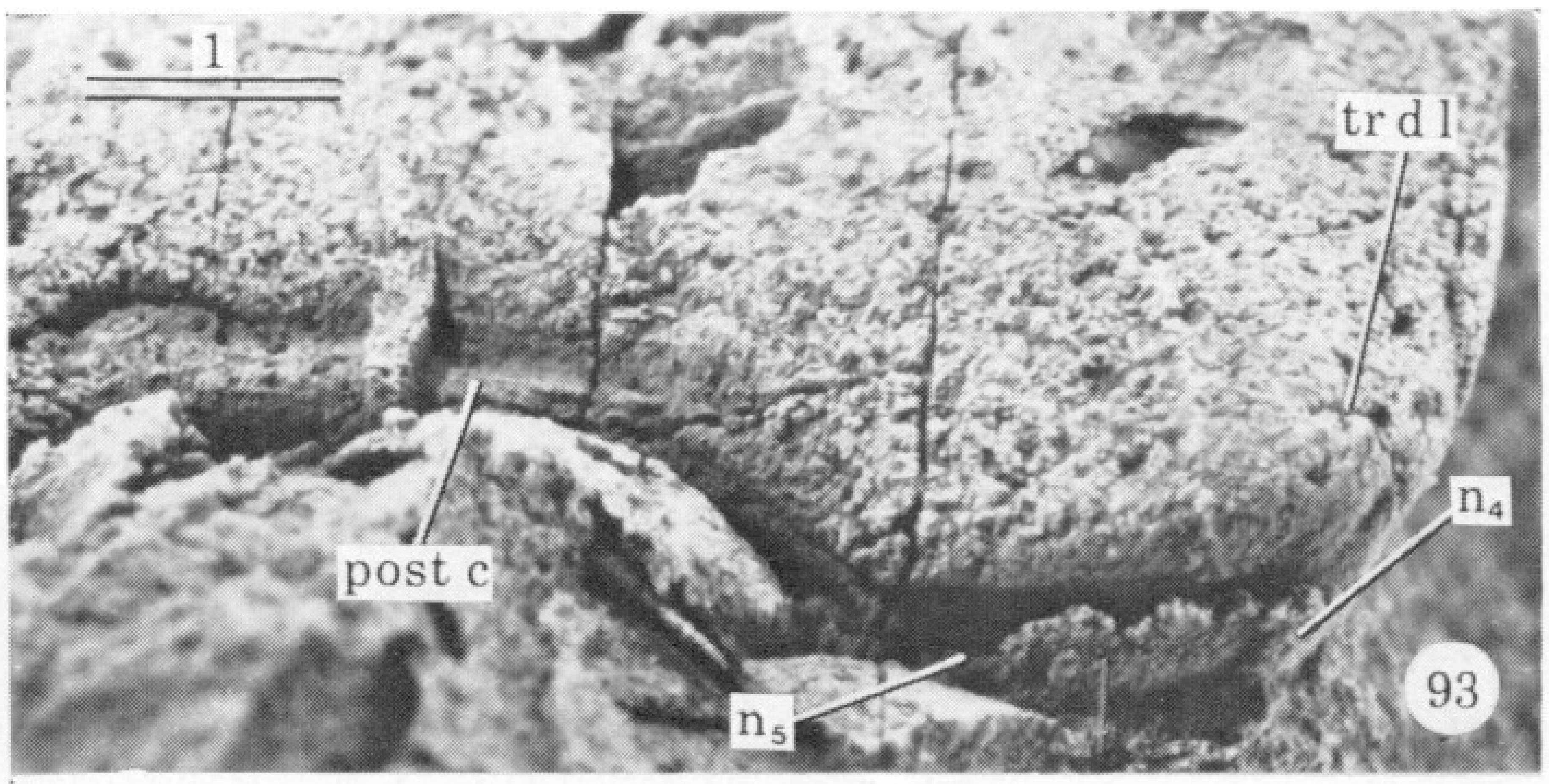


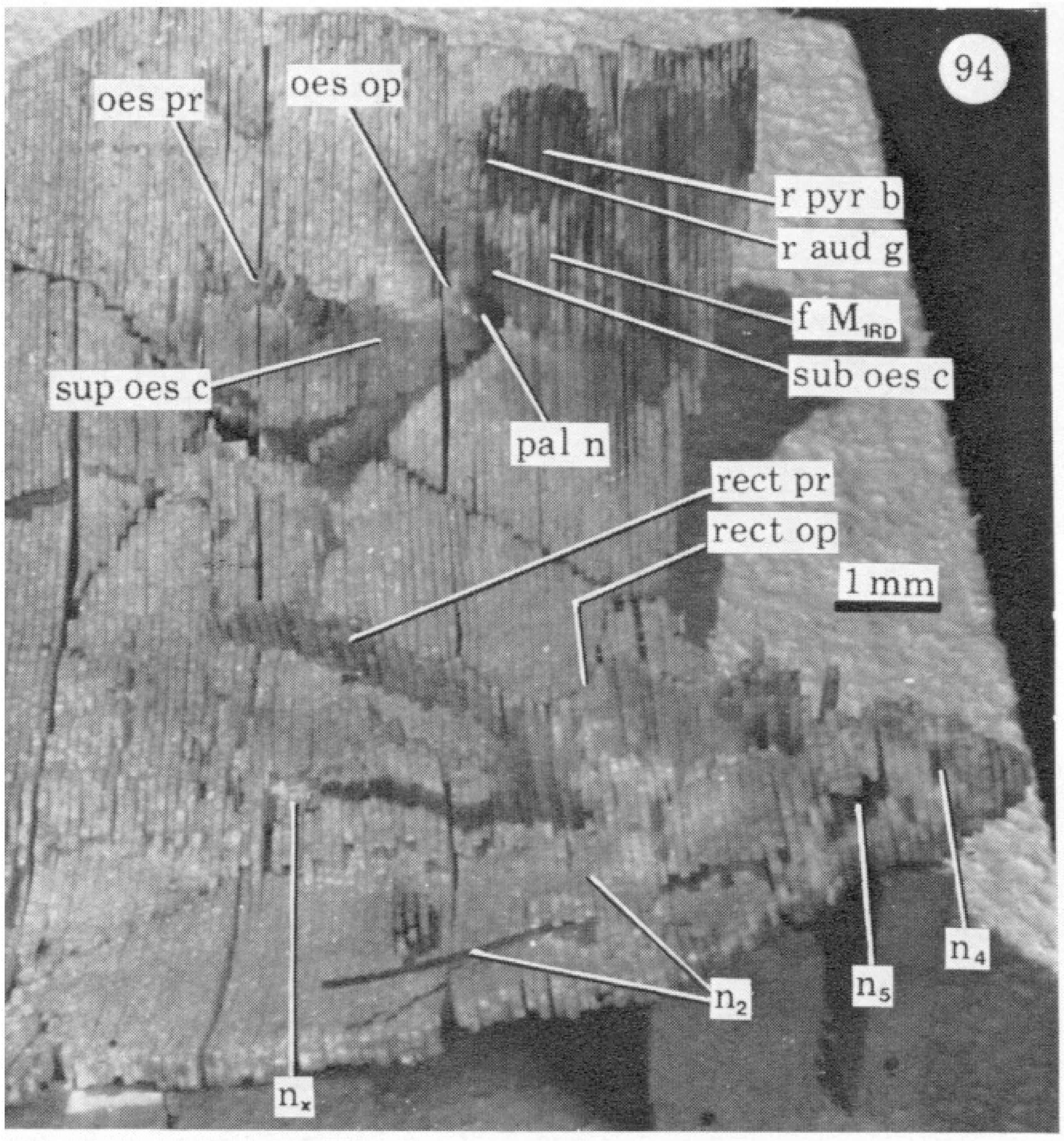


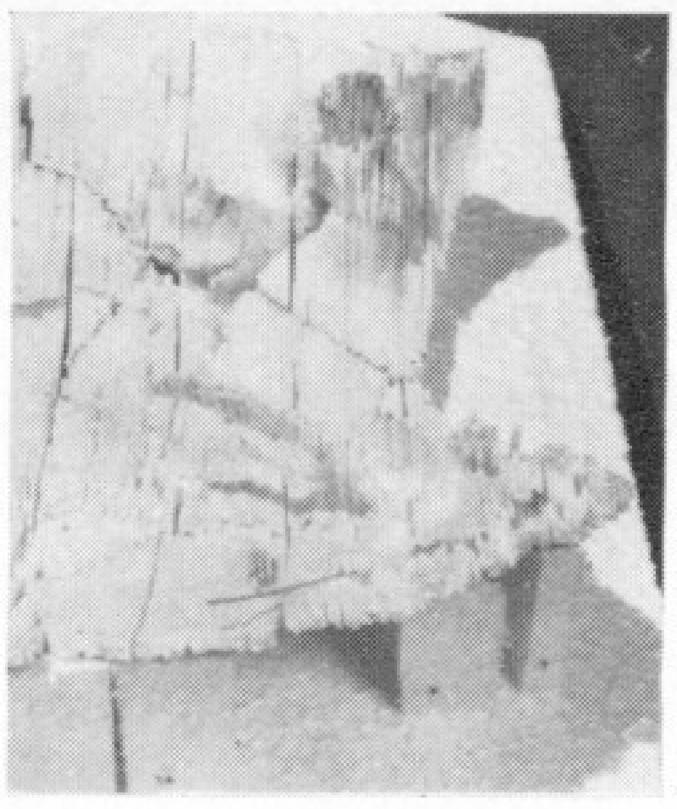


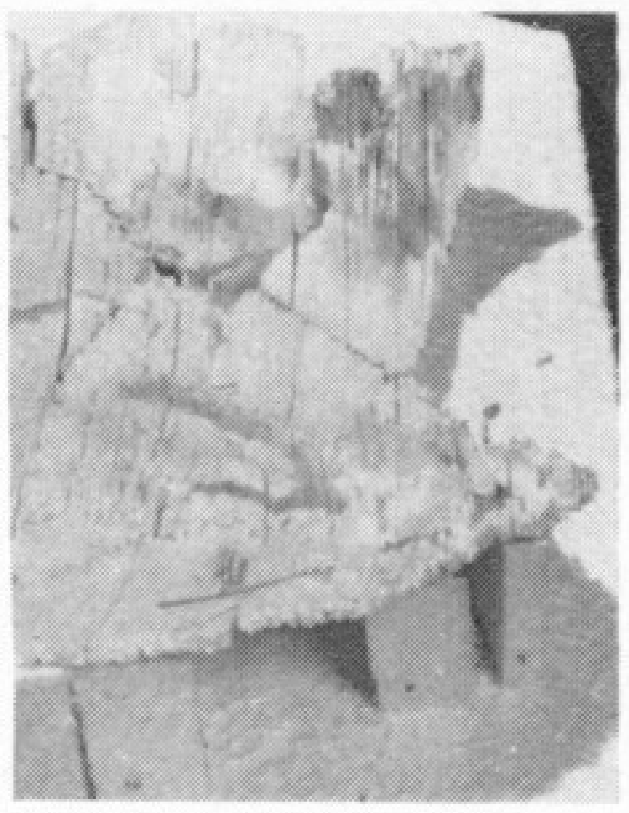
FIGURES 87–91. For description see p. 317.

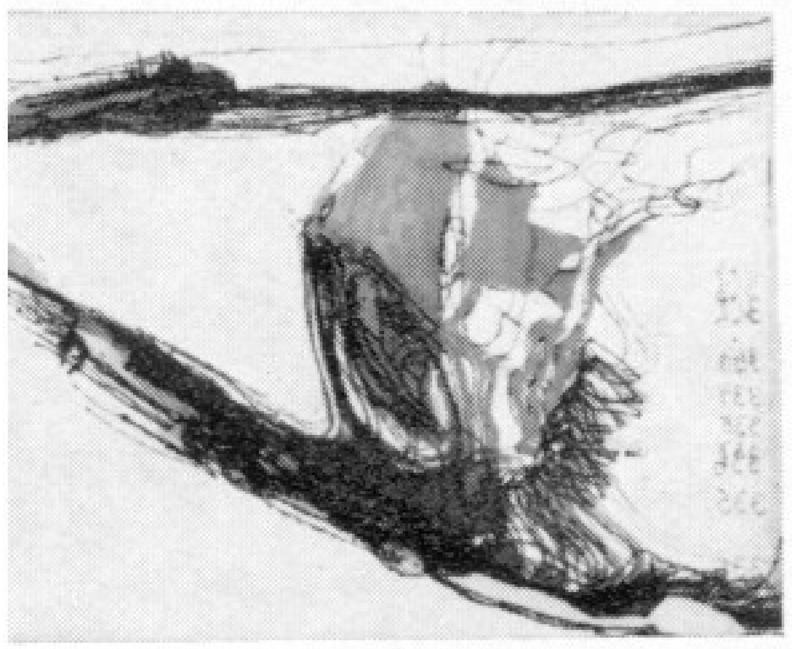


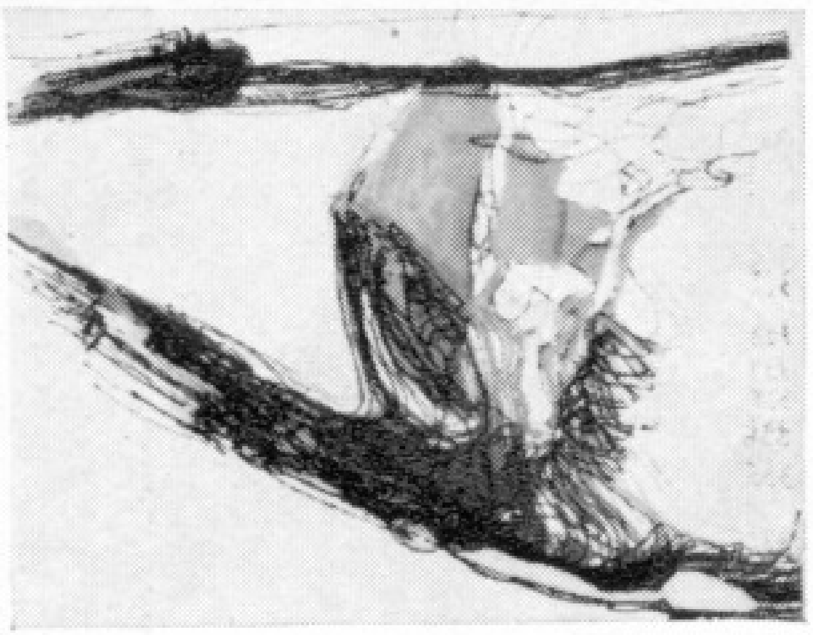


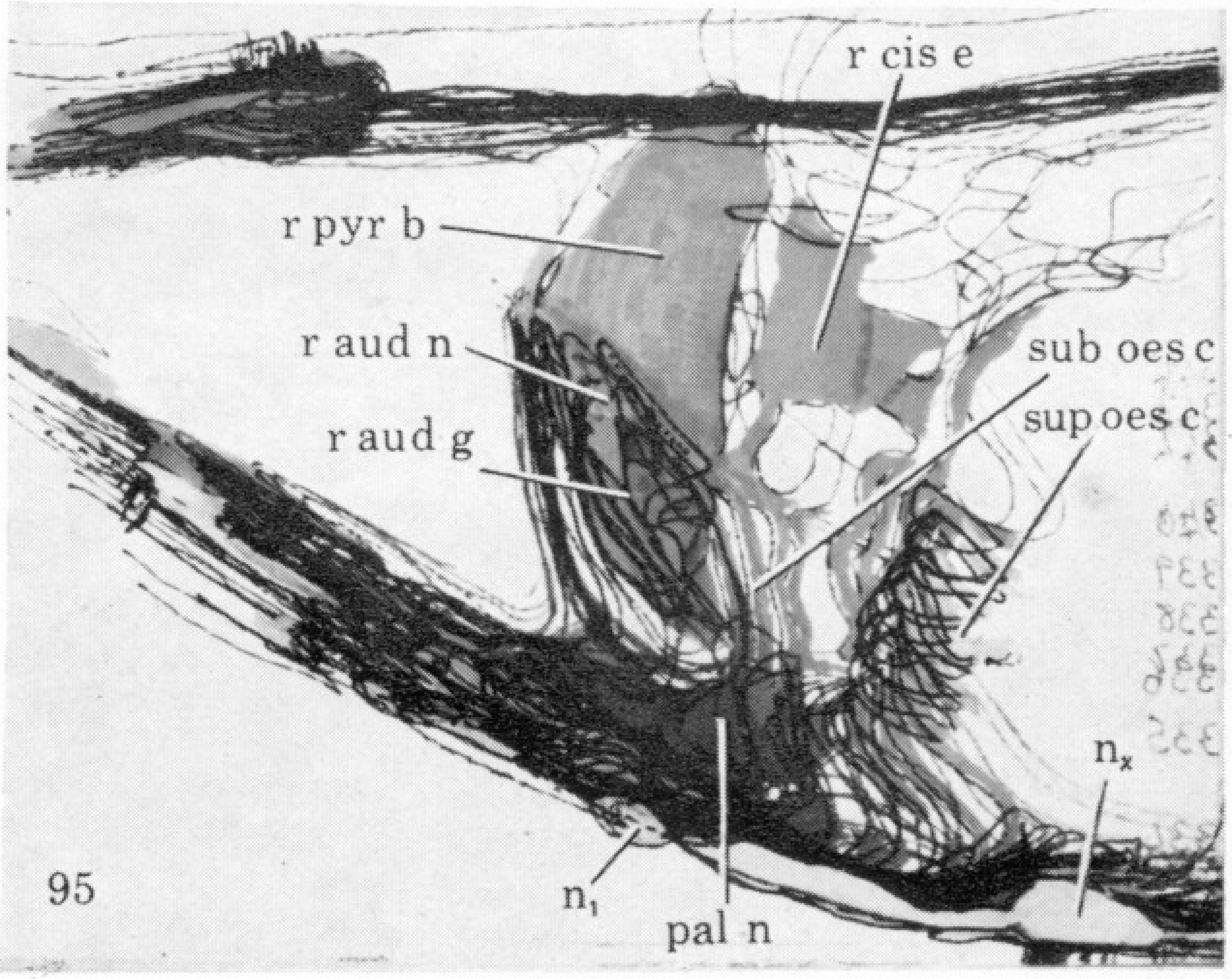


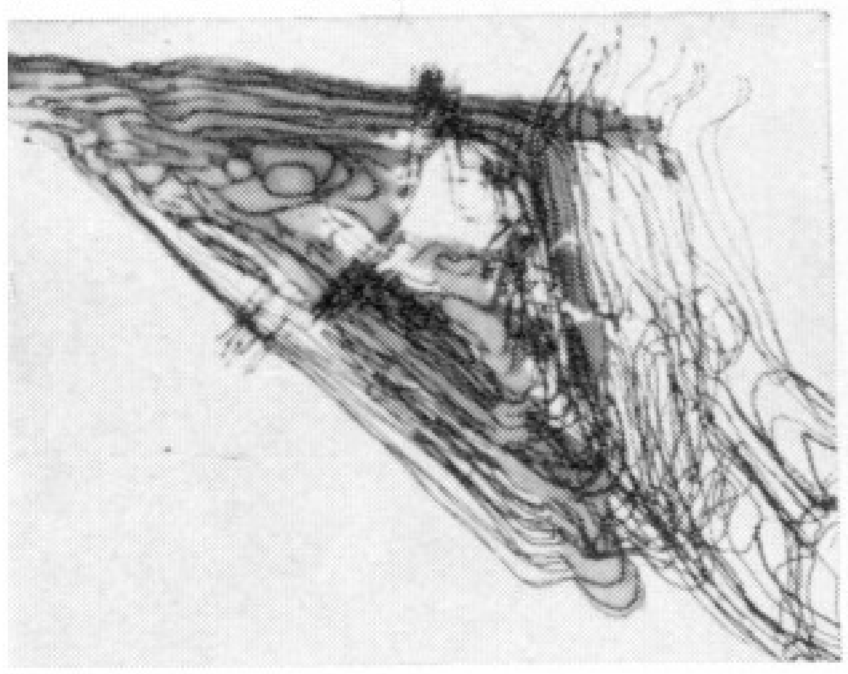


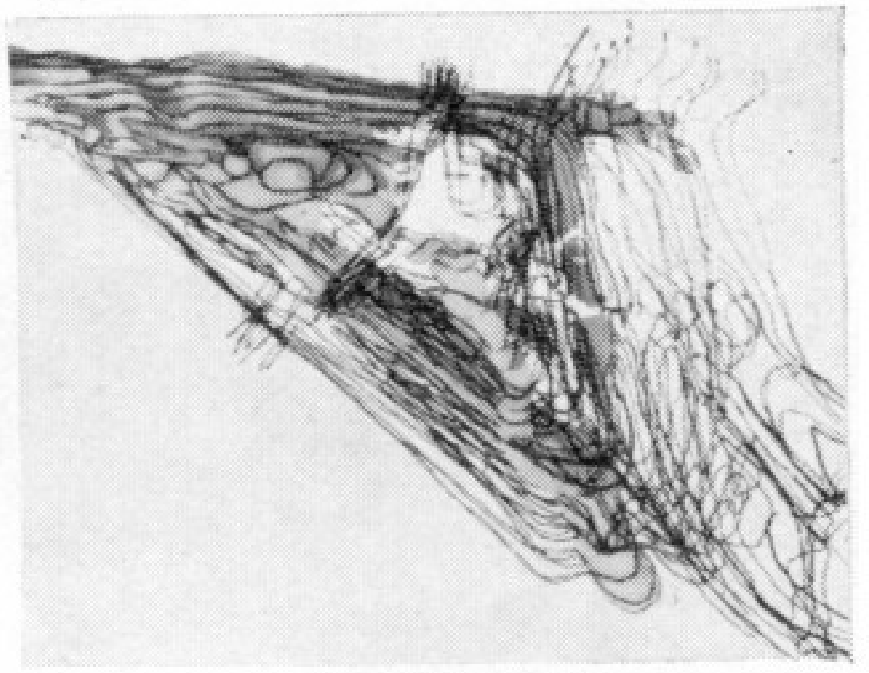


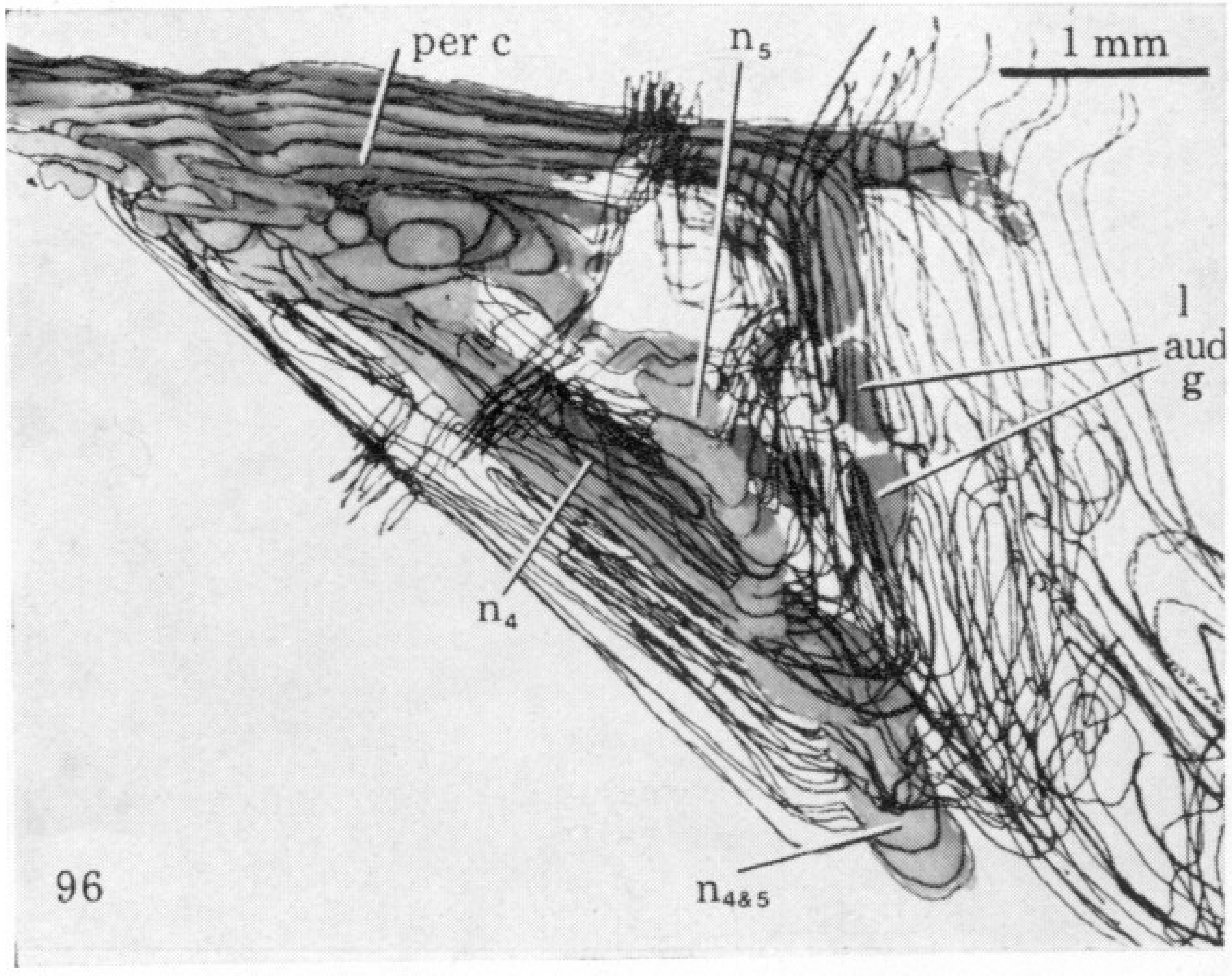


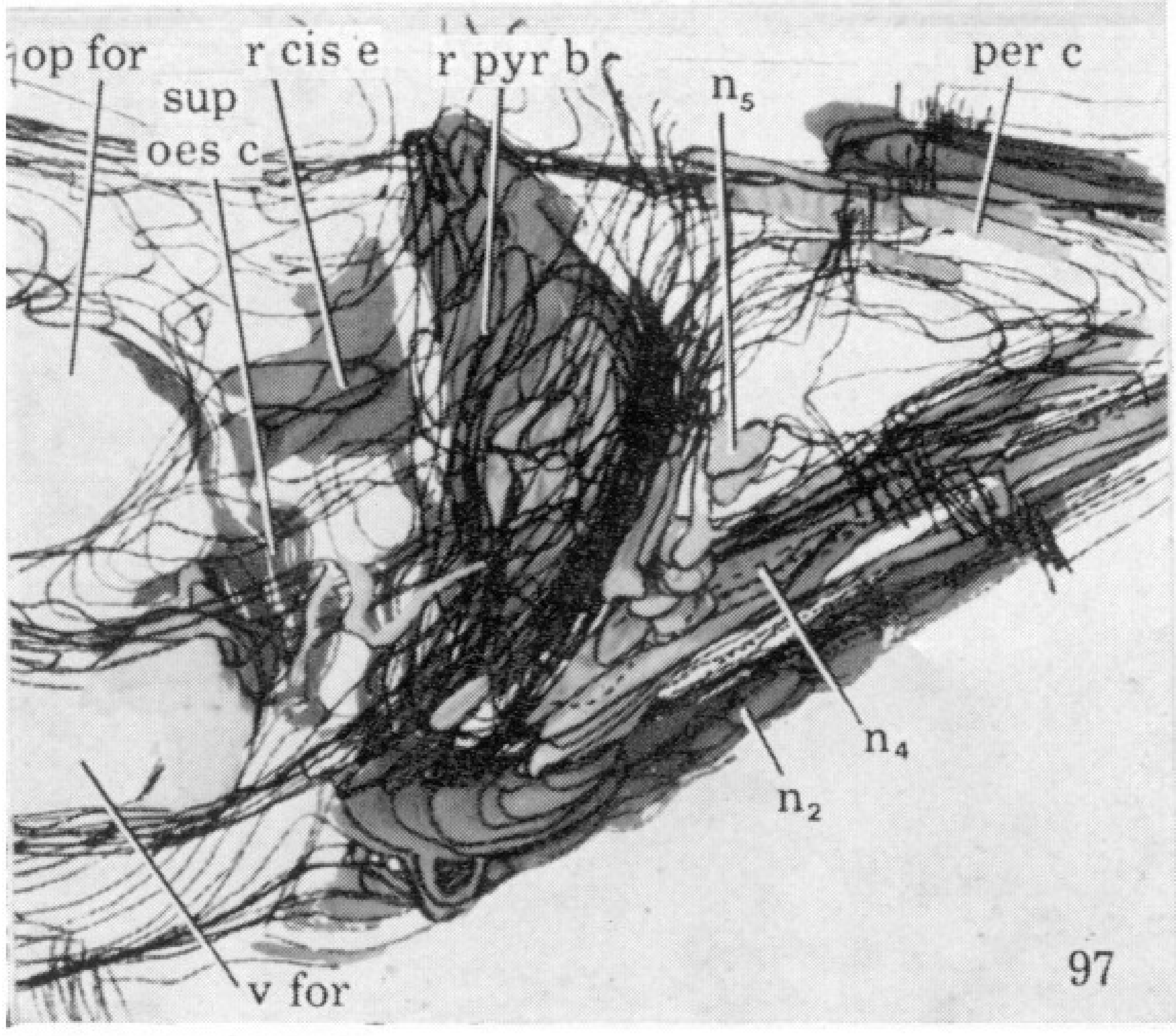


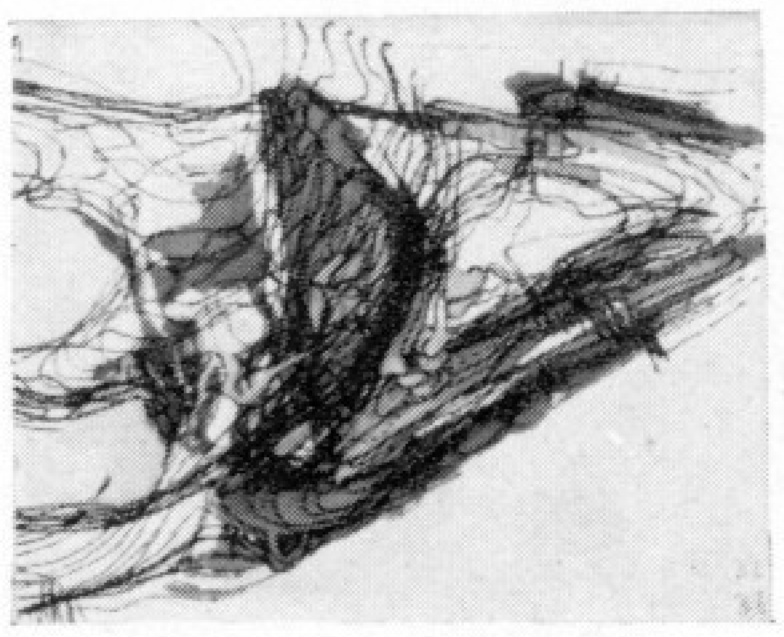


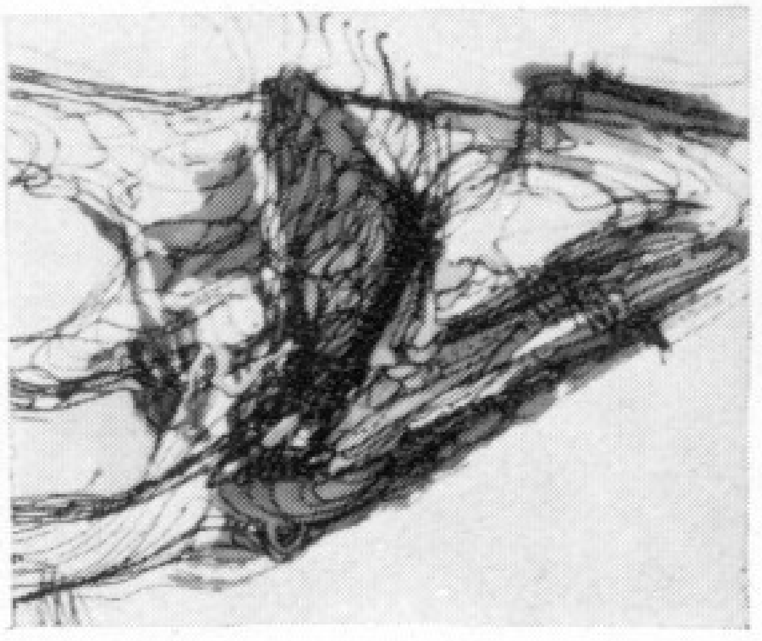




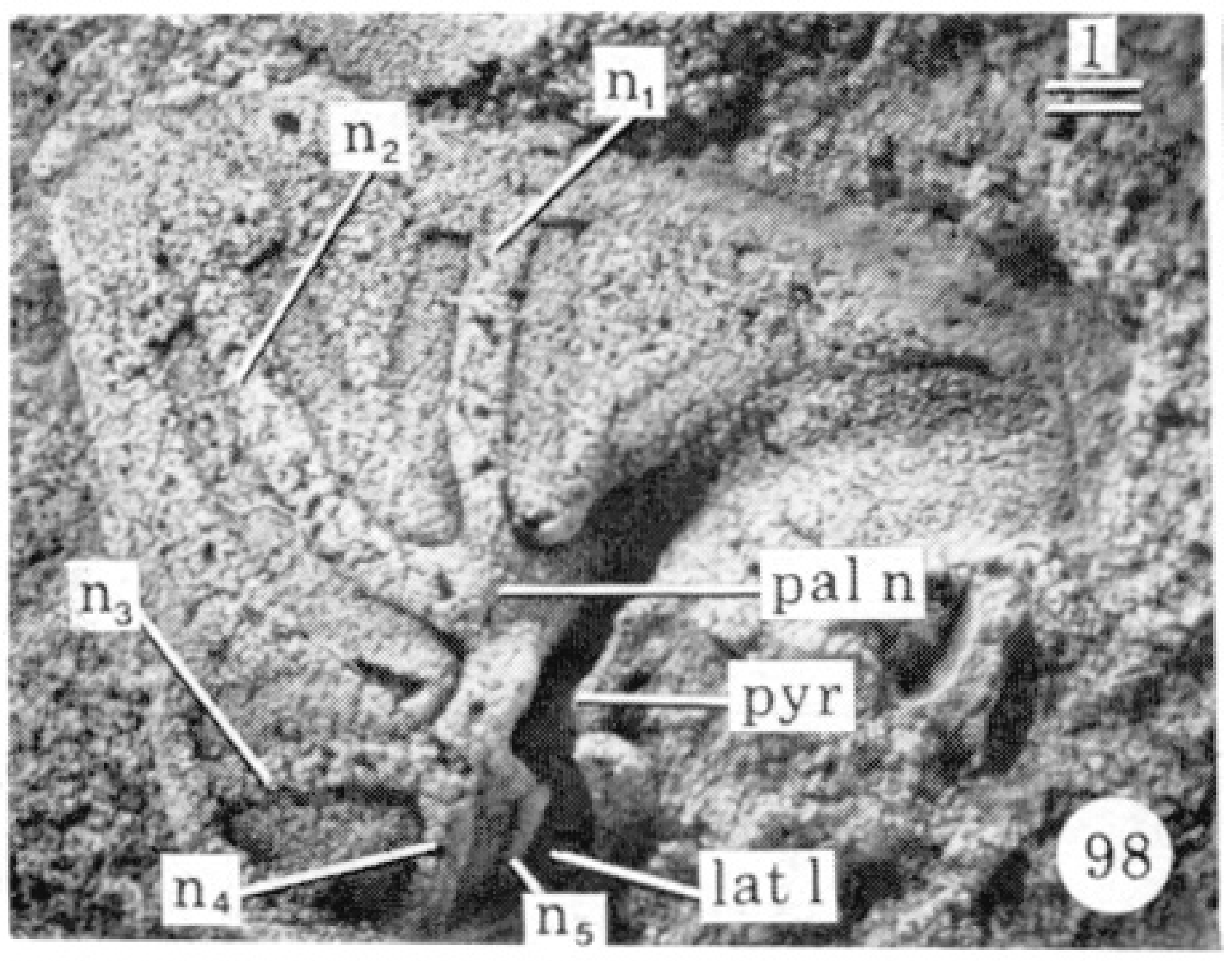


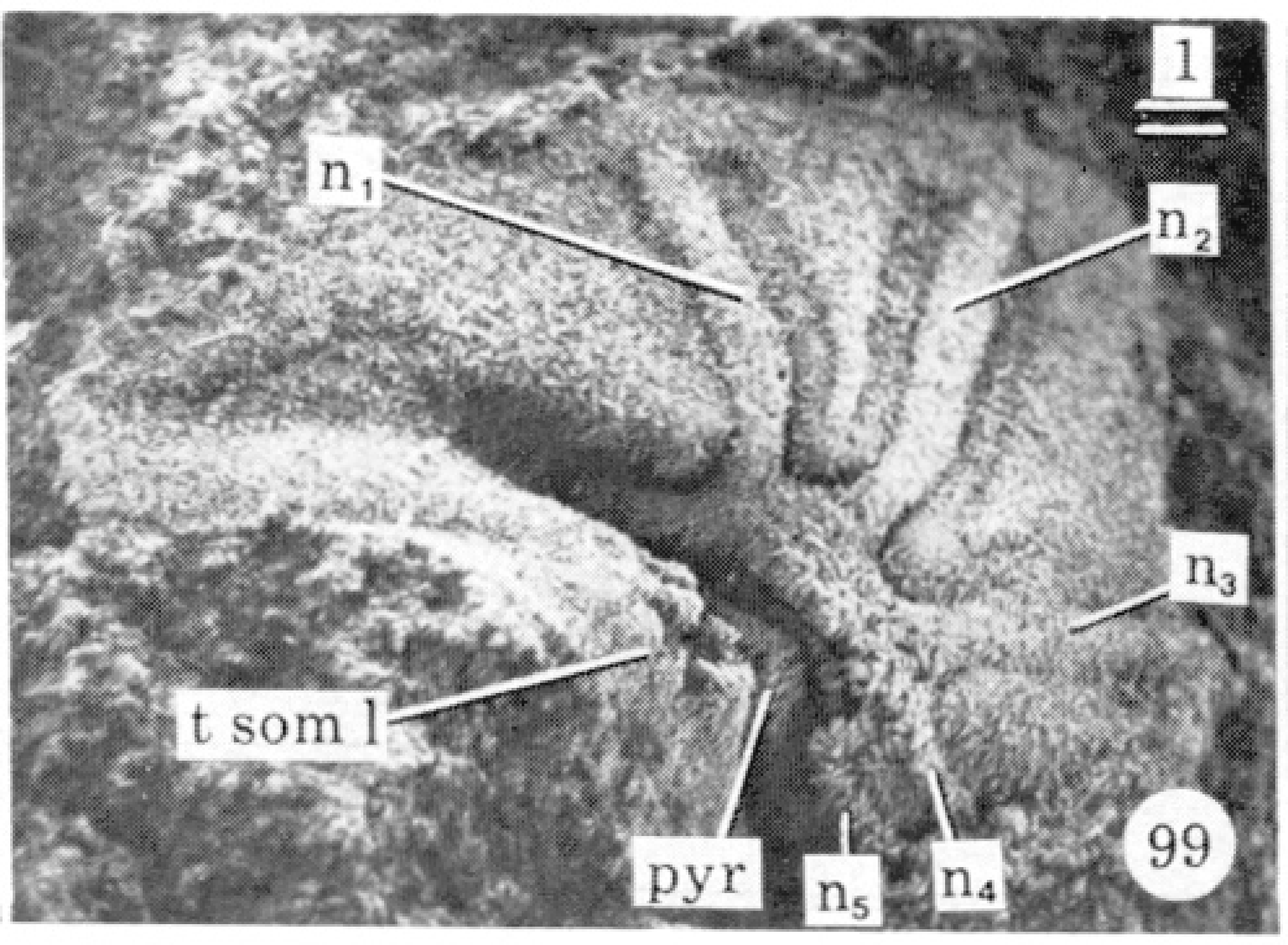


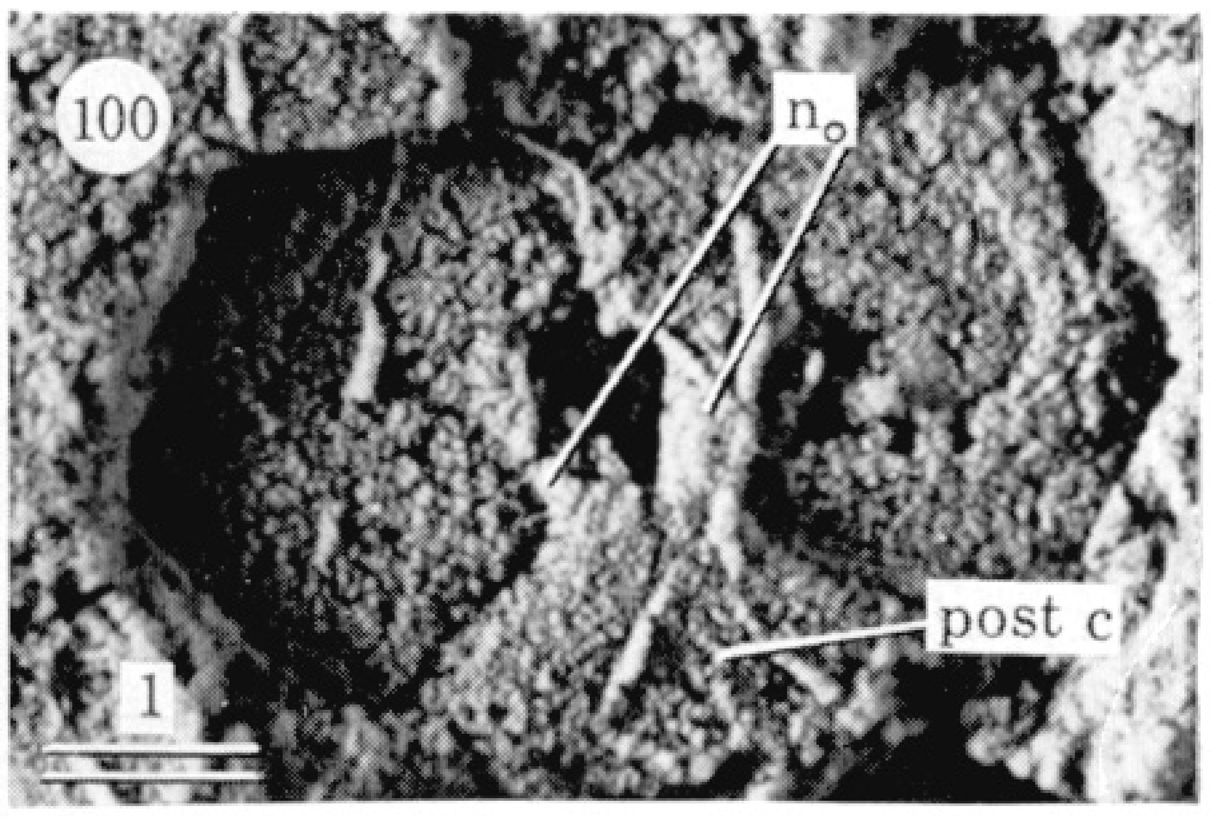


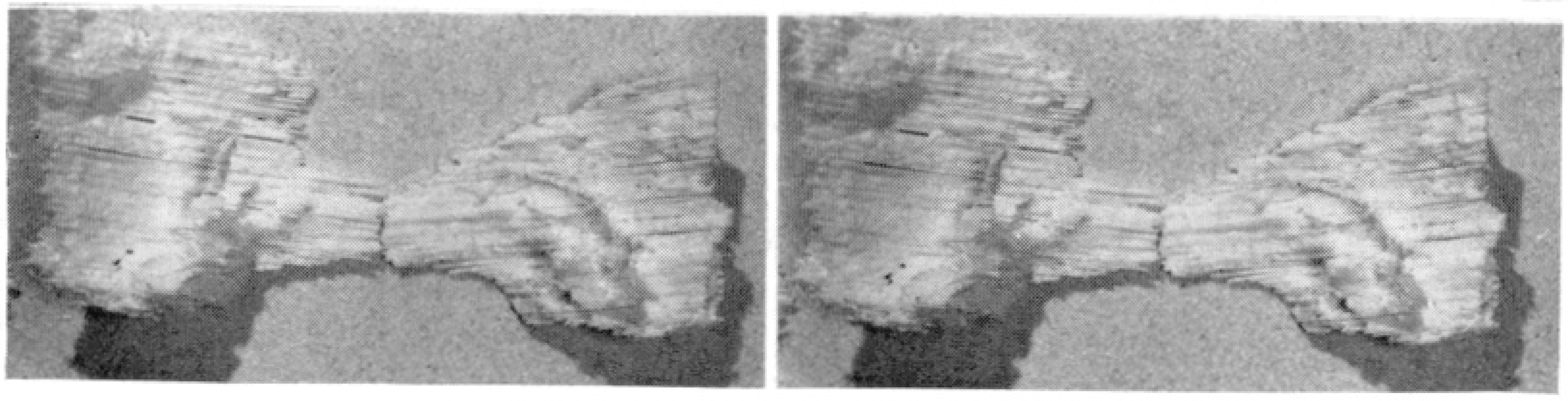


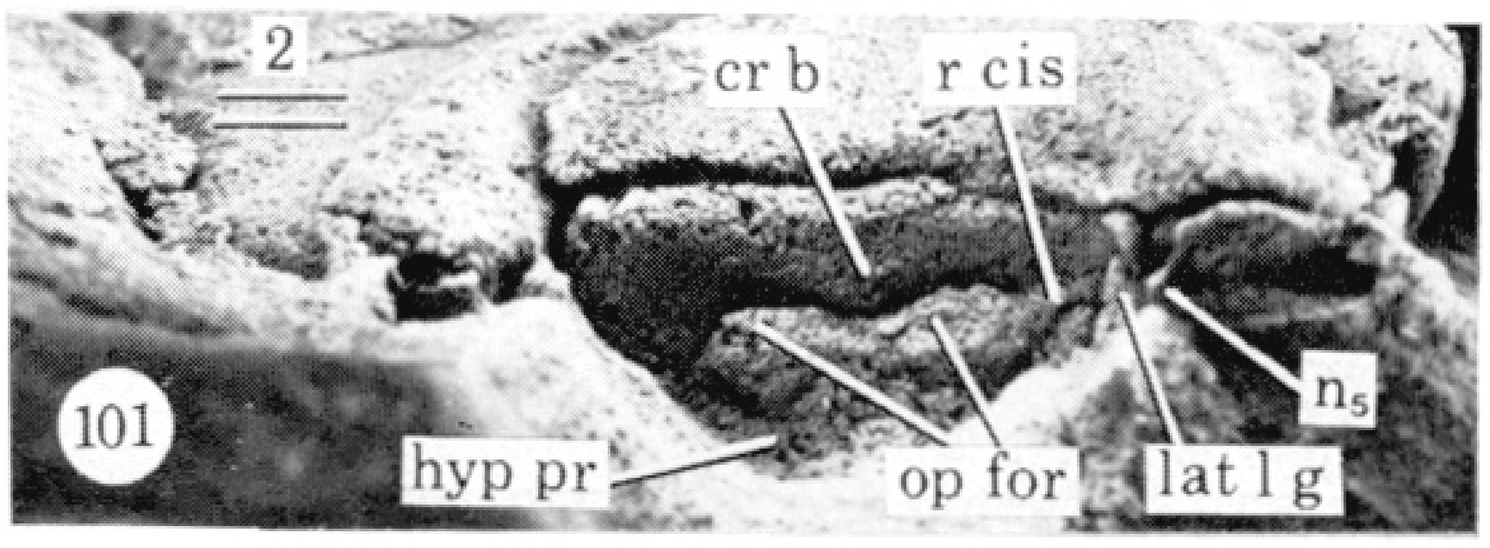
FIGURES 92–97. For description see pp. 317–318.

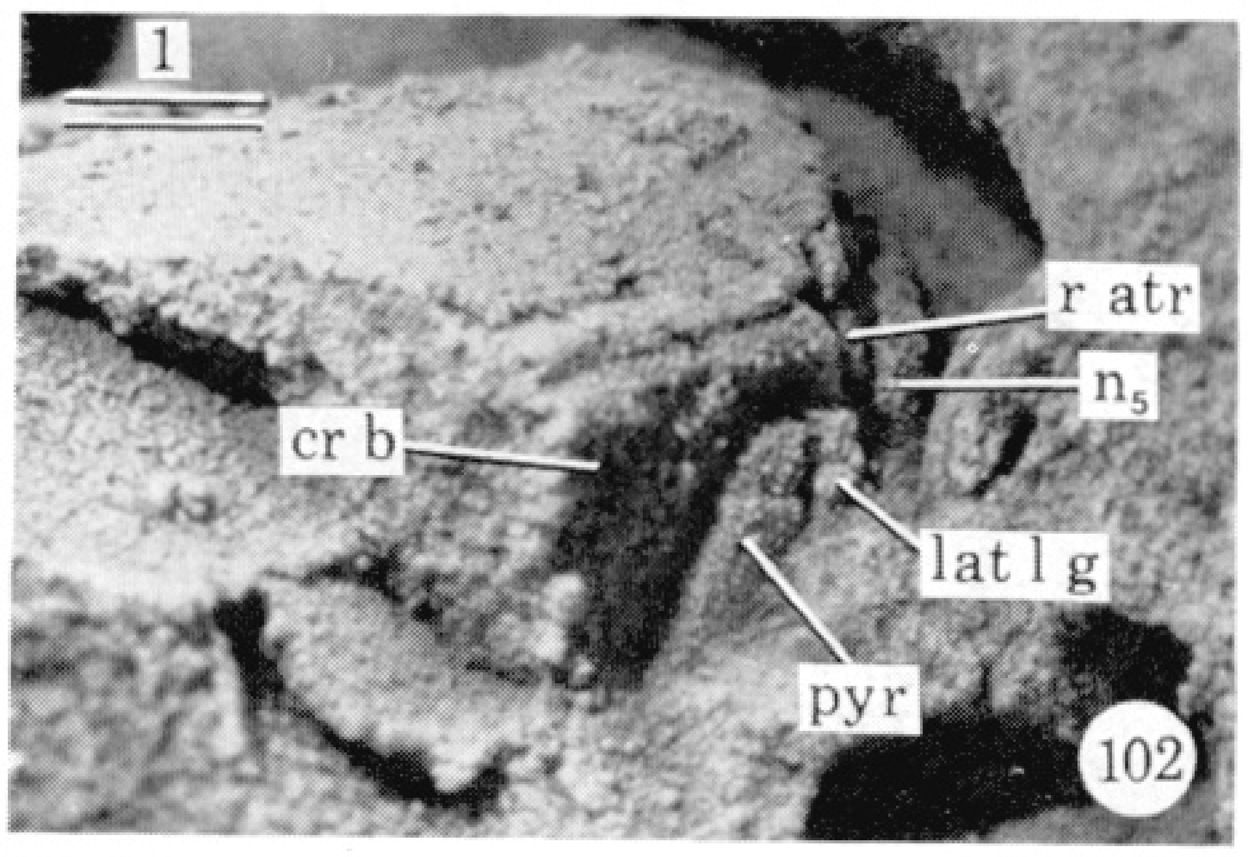


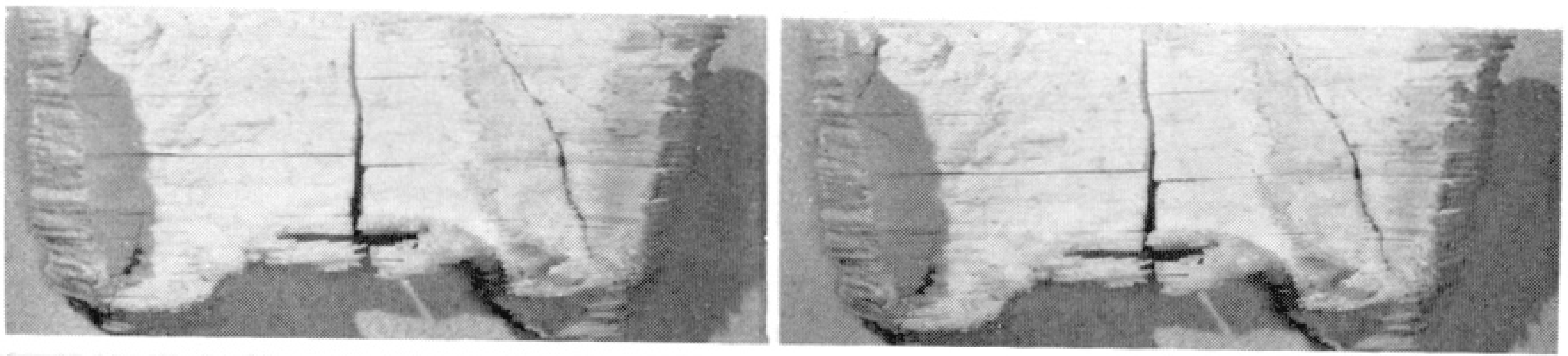


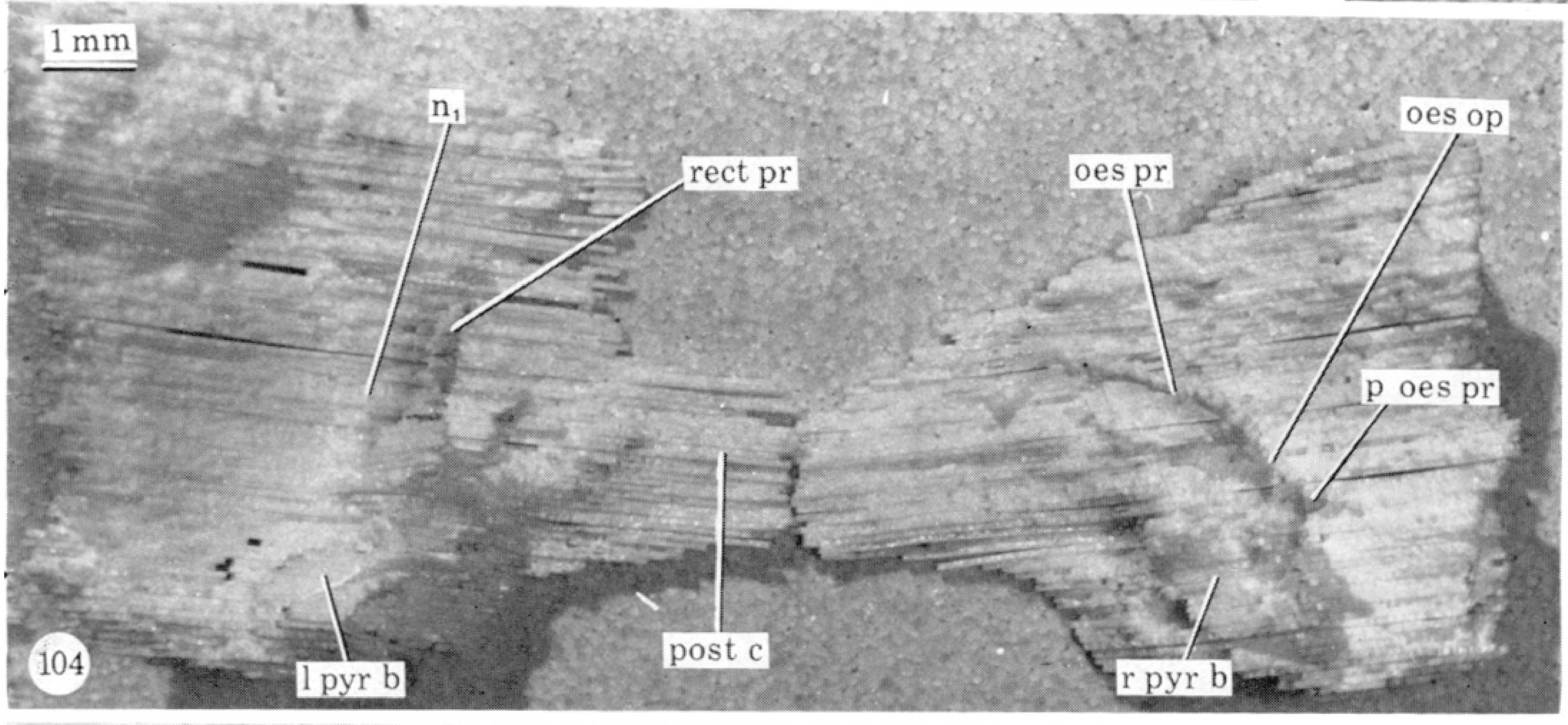


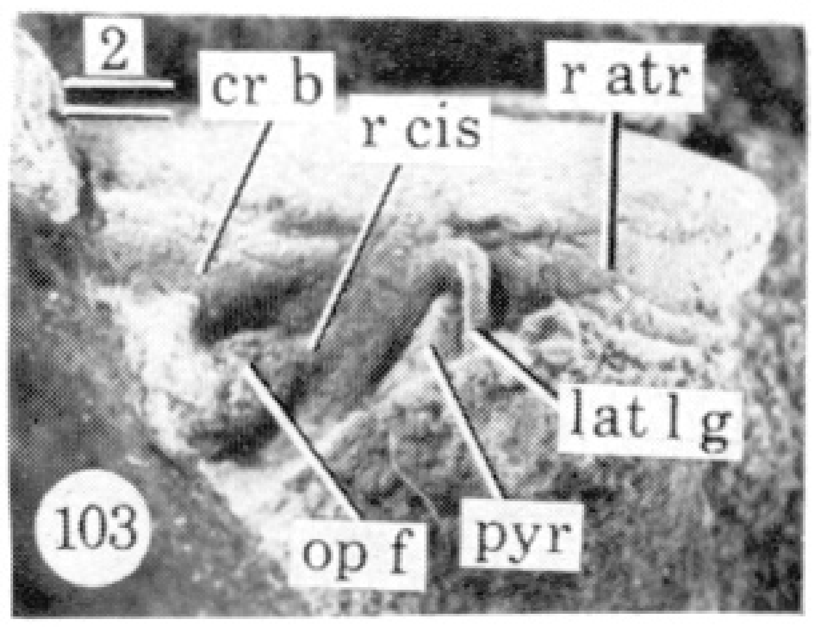


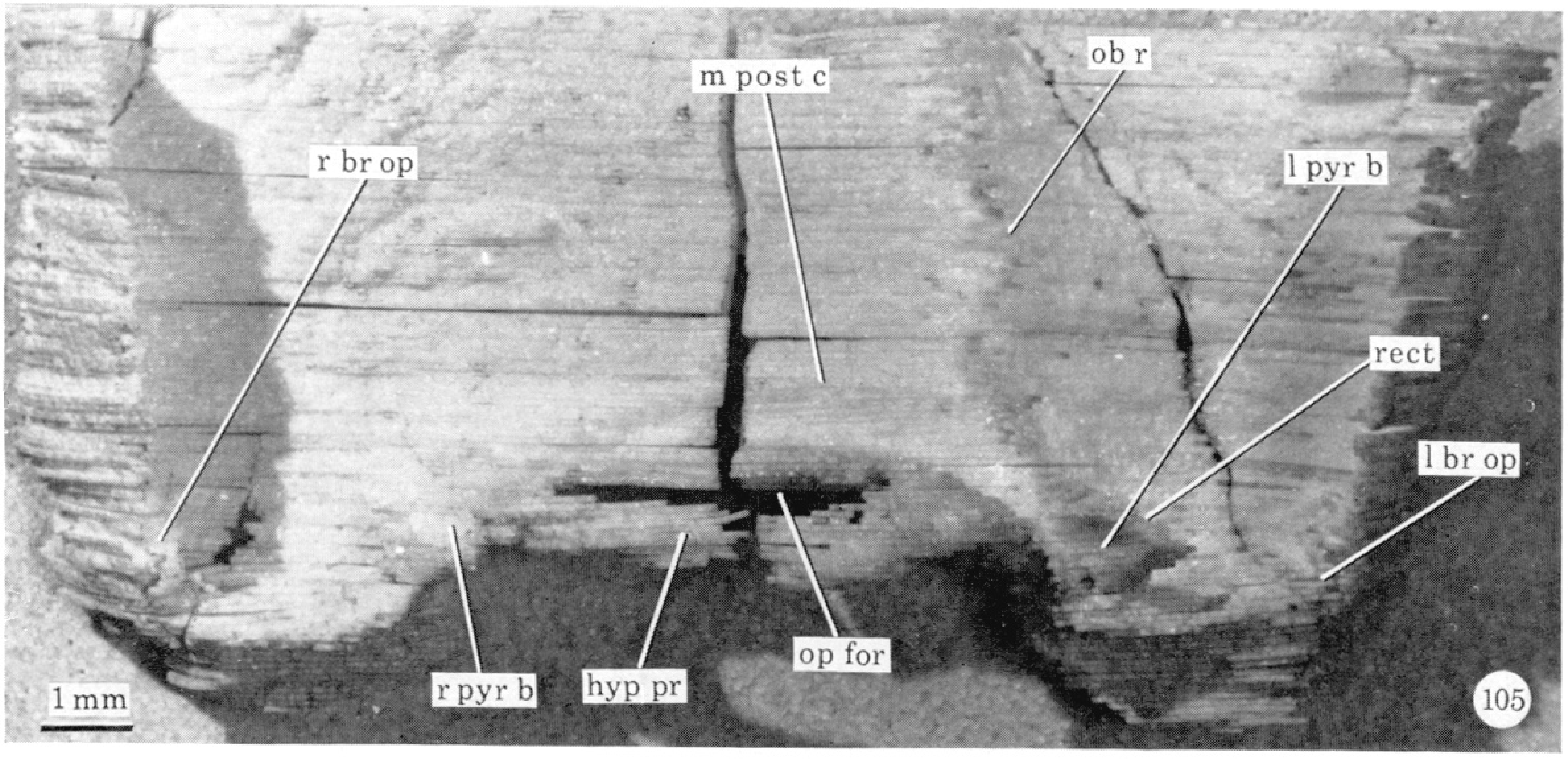




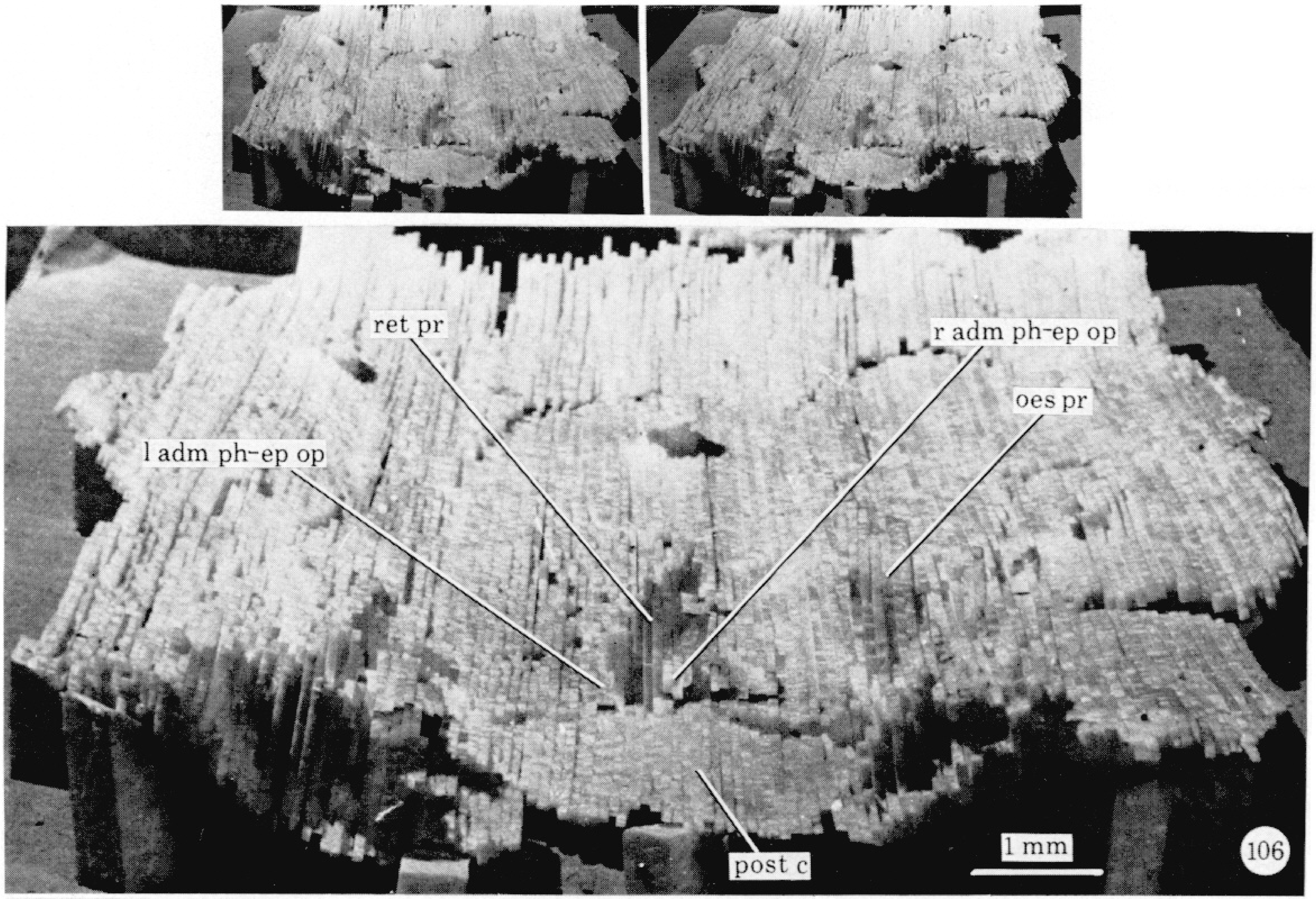


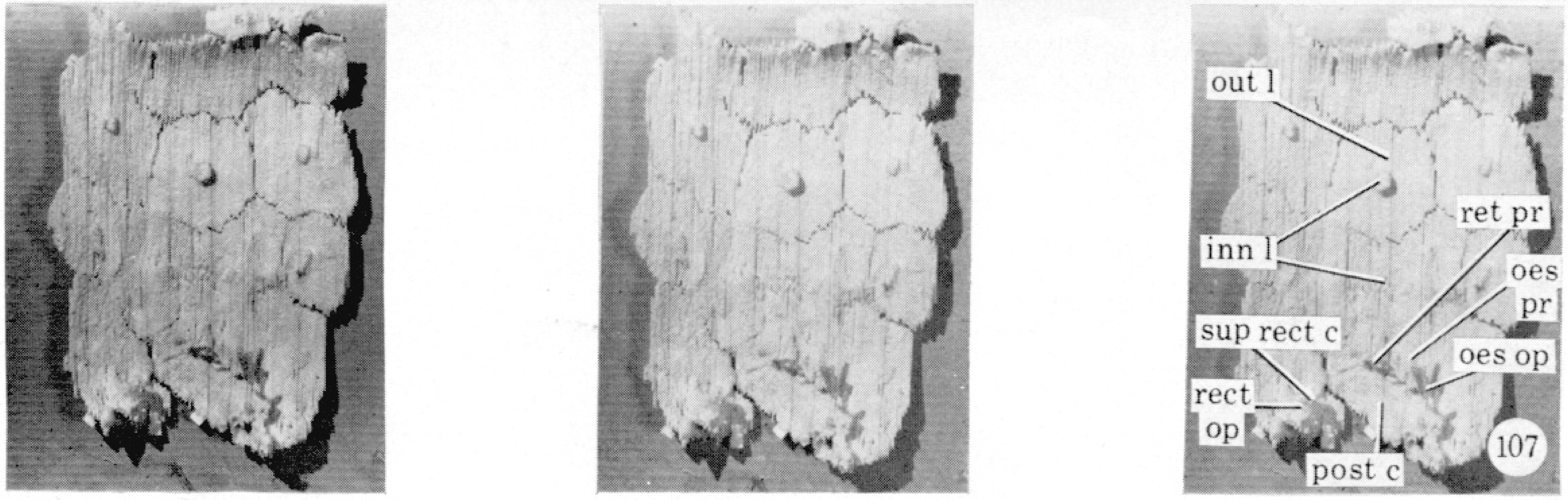


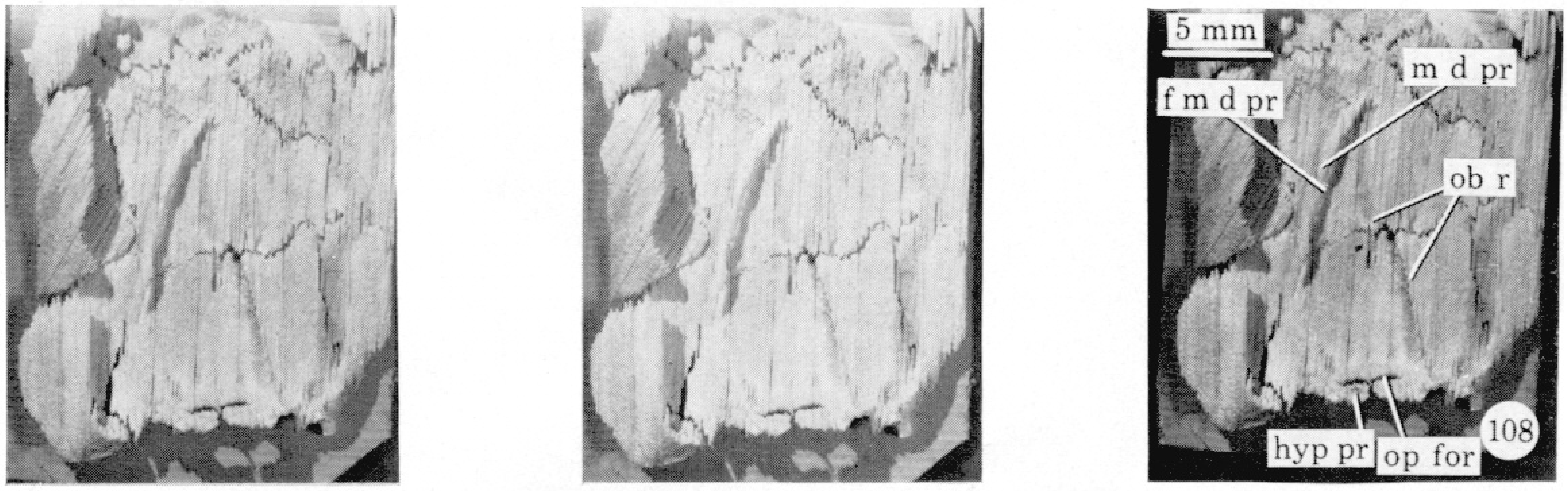


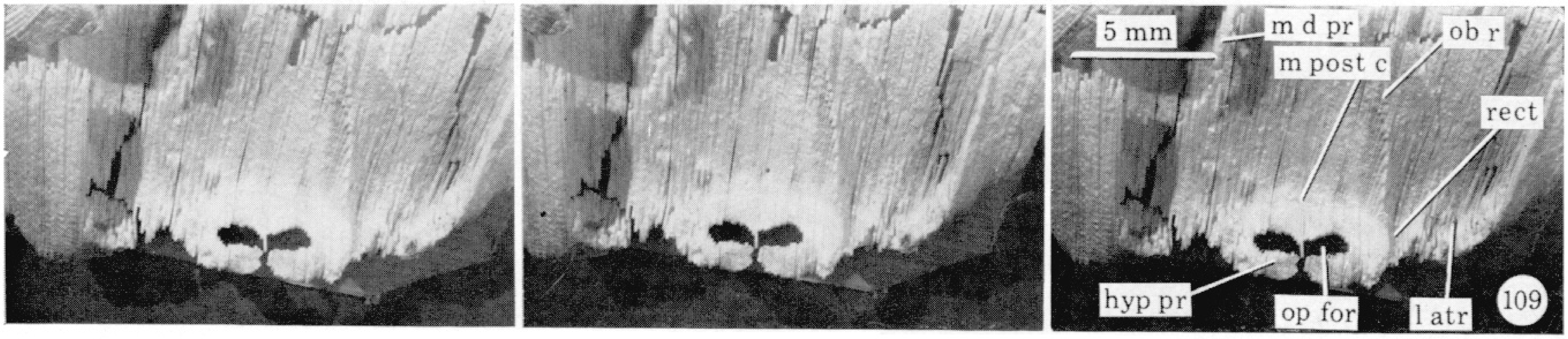


Figures 98–105. For description see p. 318.

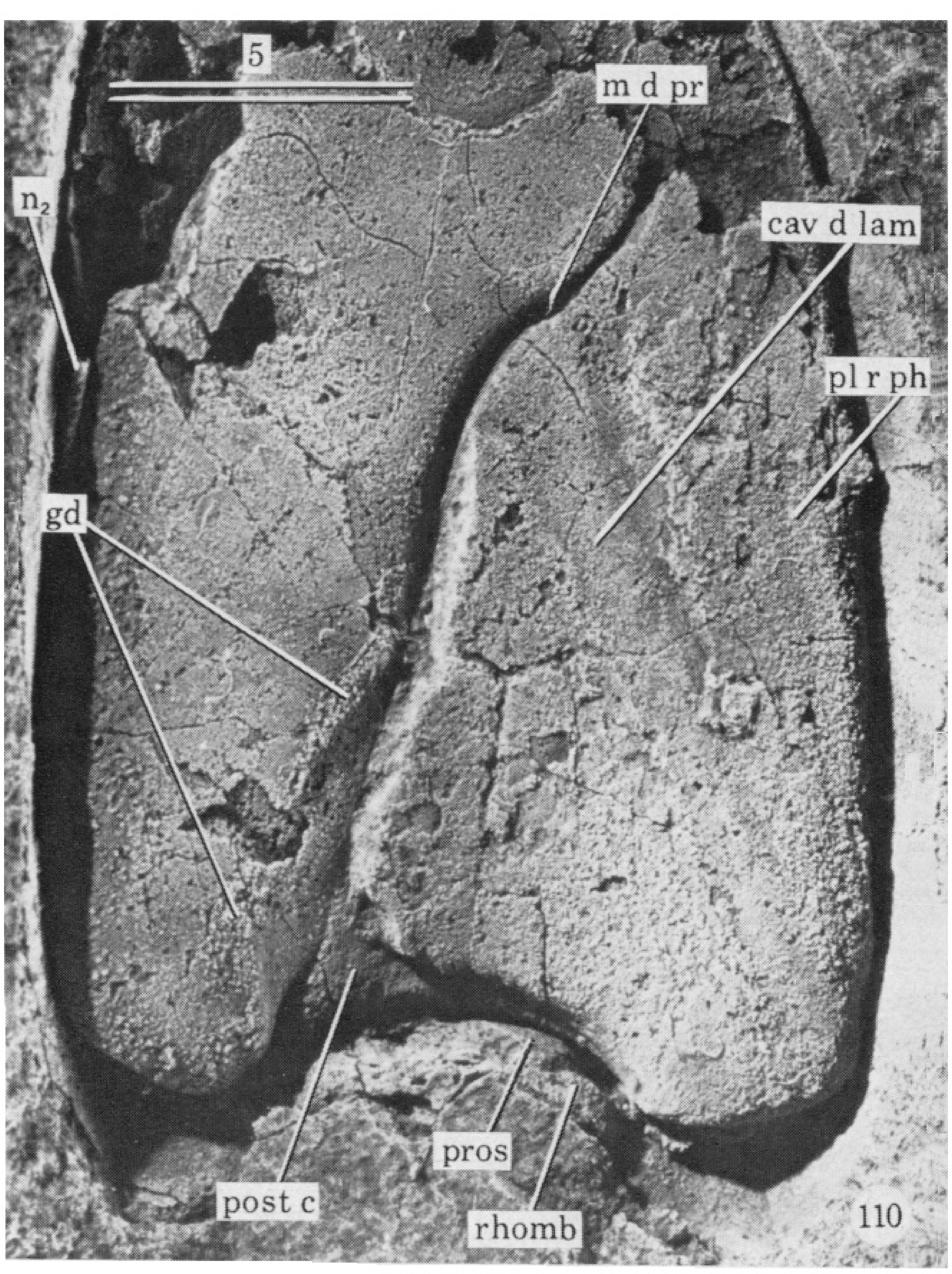


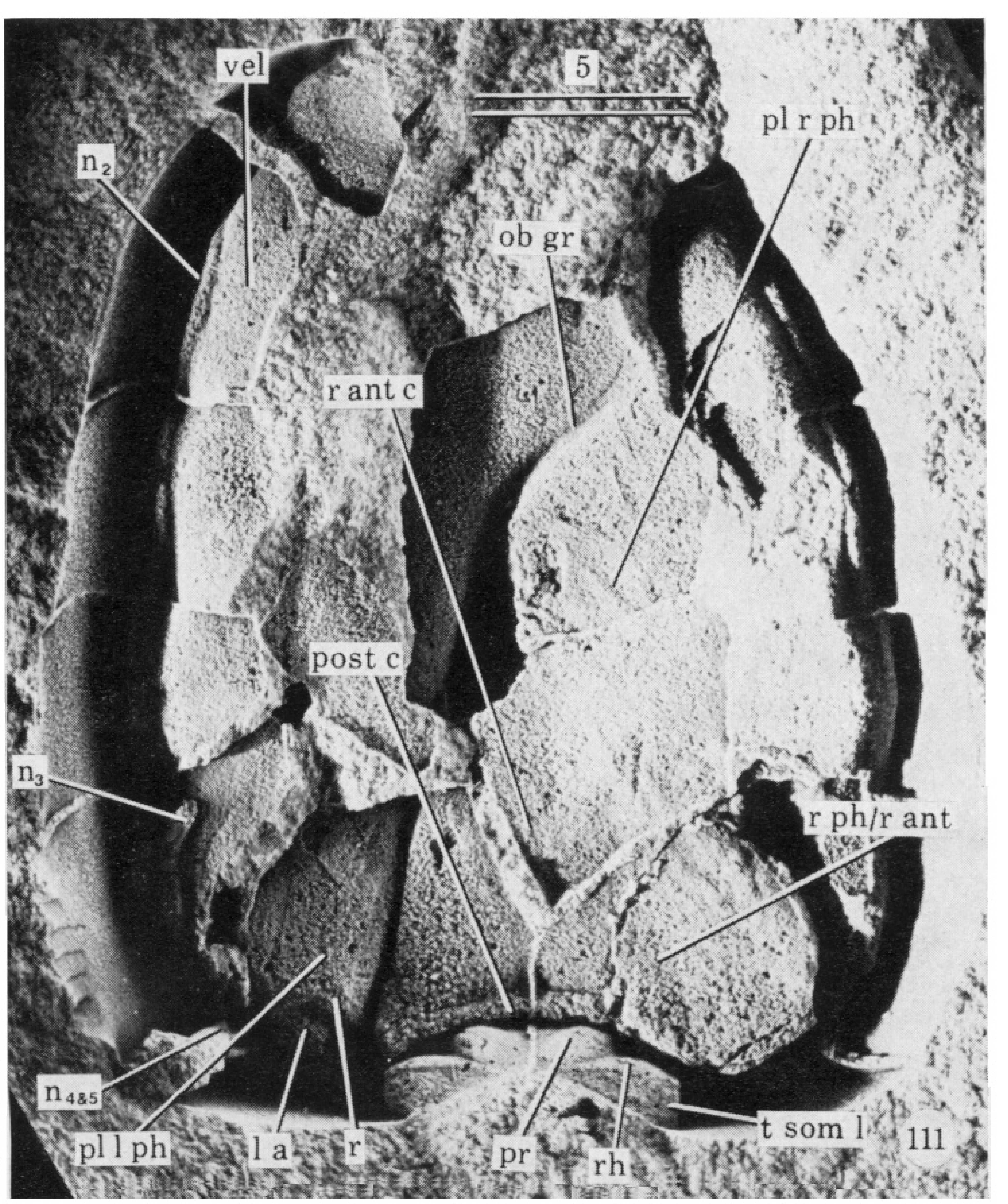


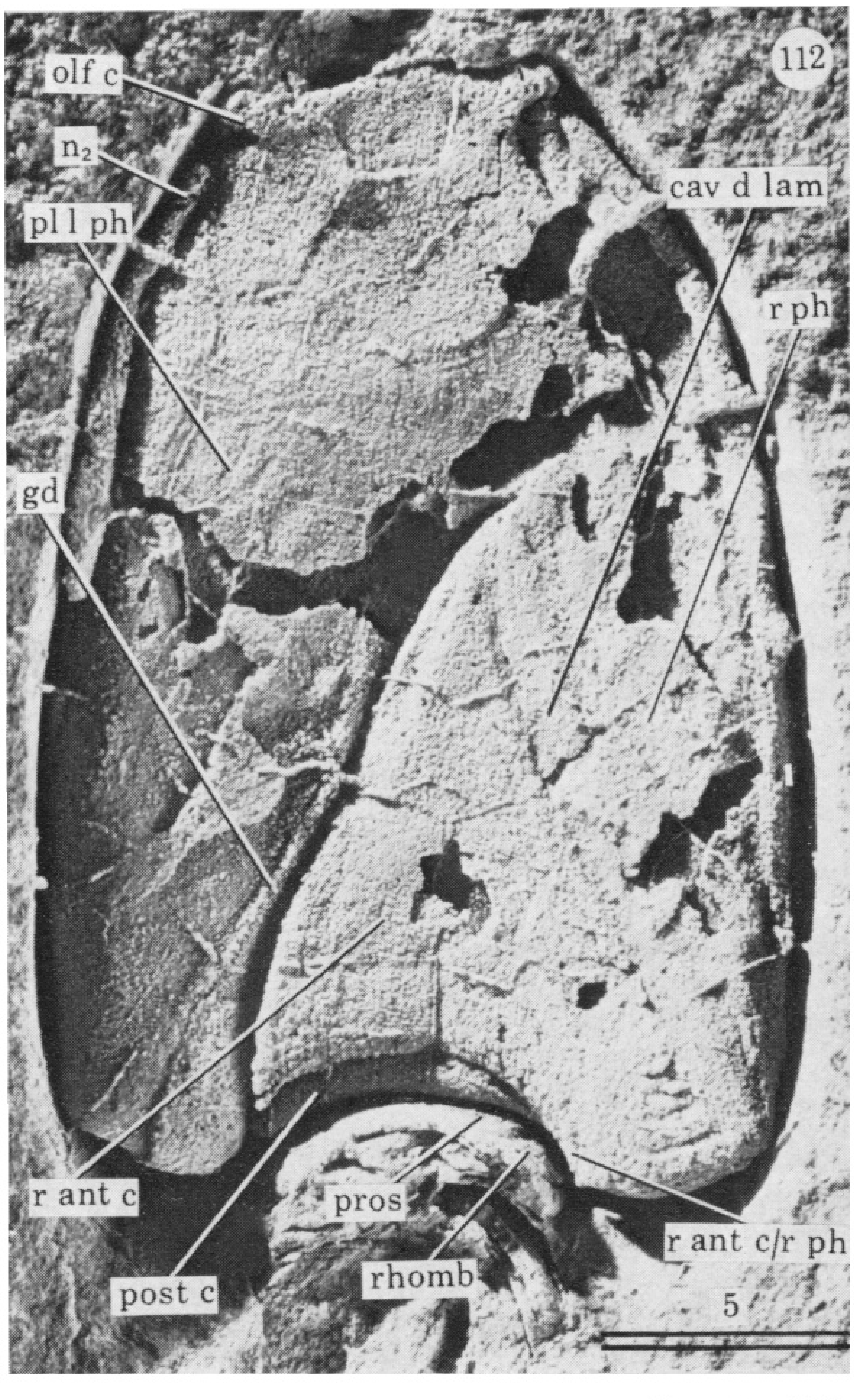


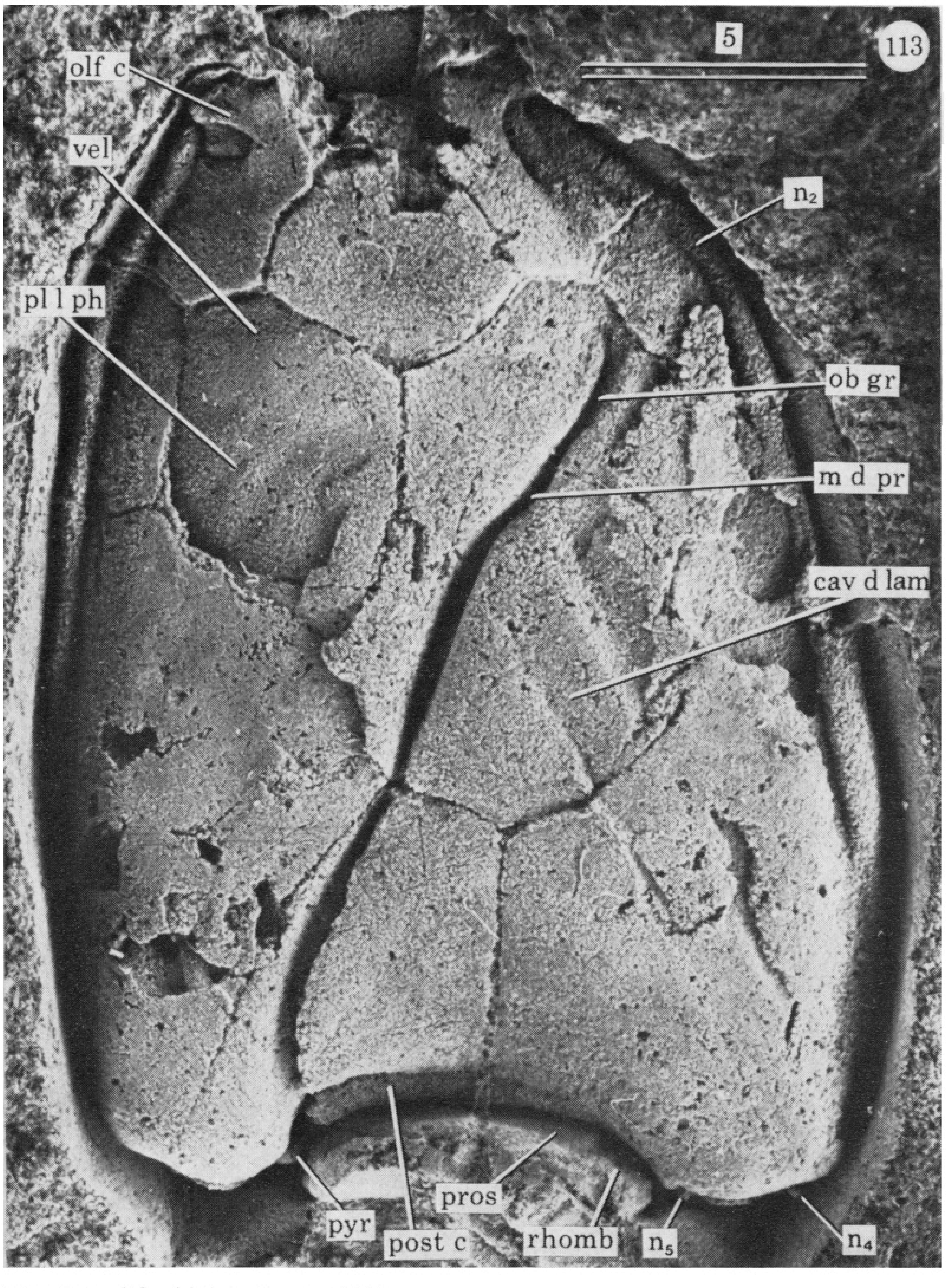


FIGURES 106–109. For description see p. 318.

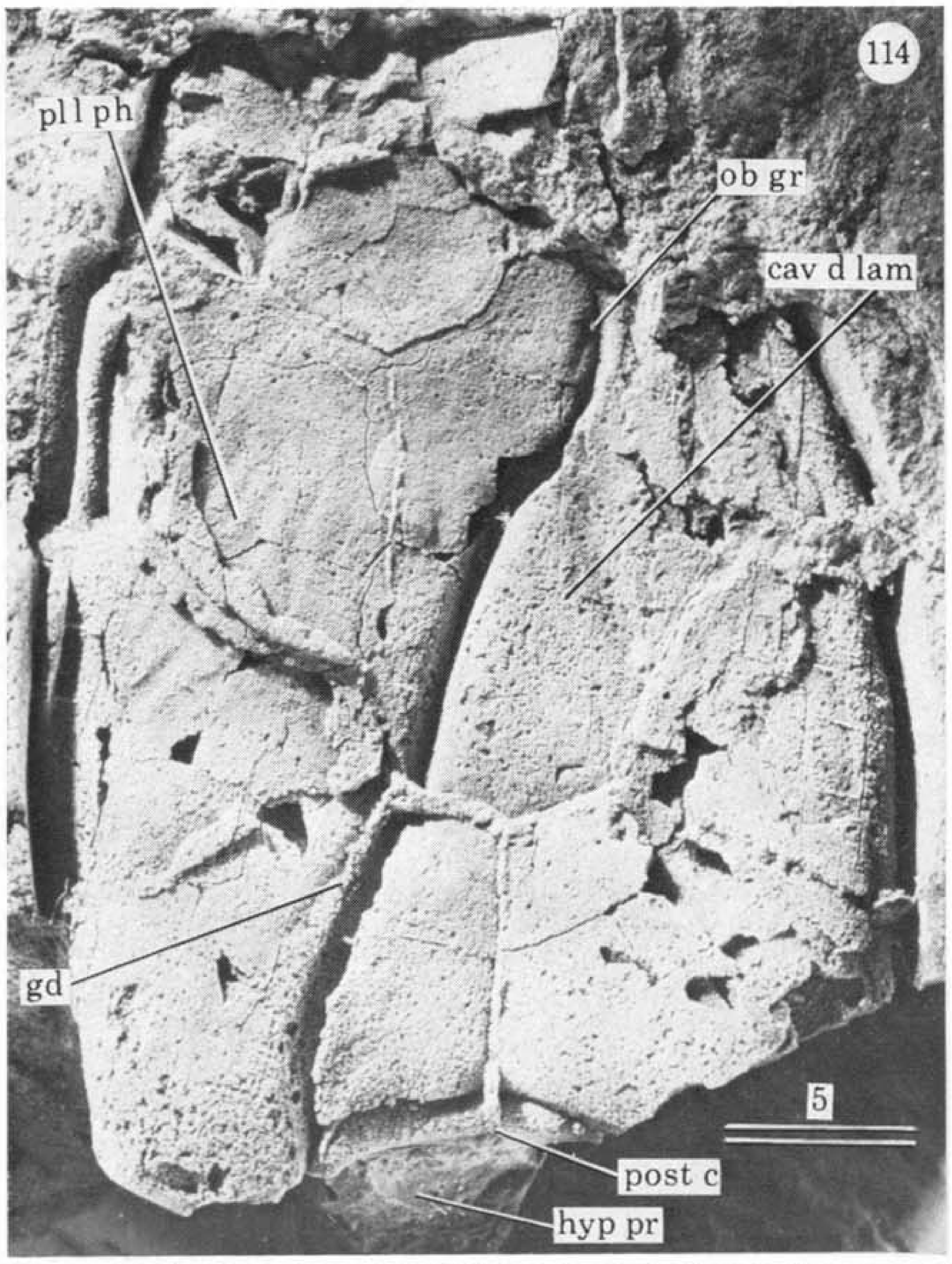


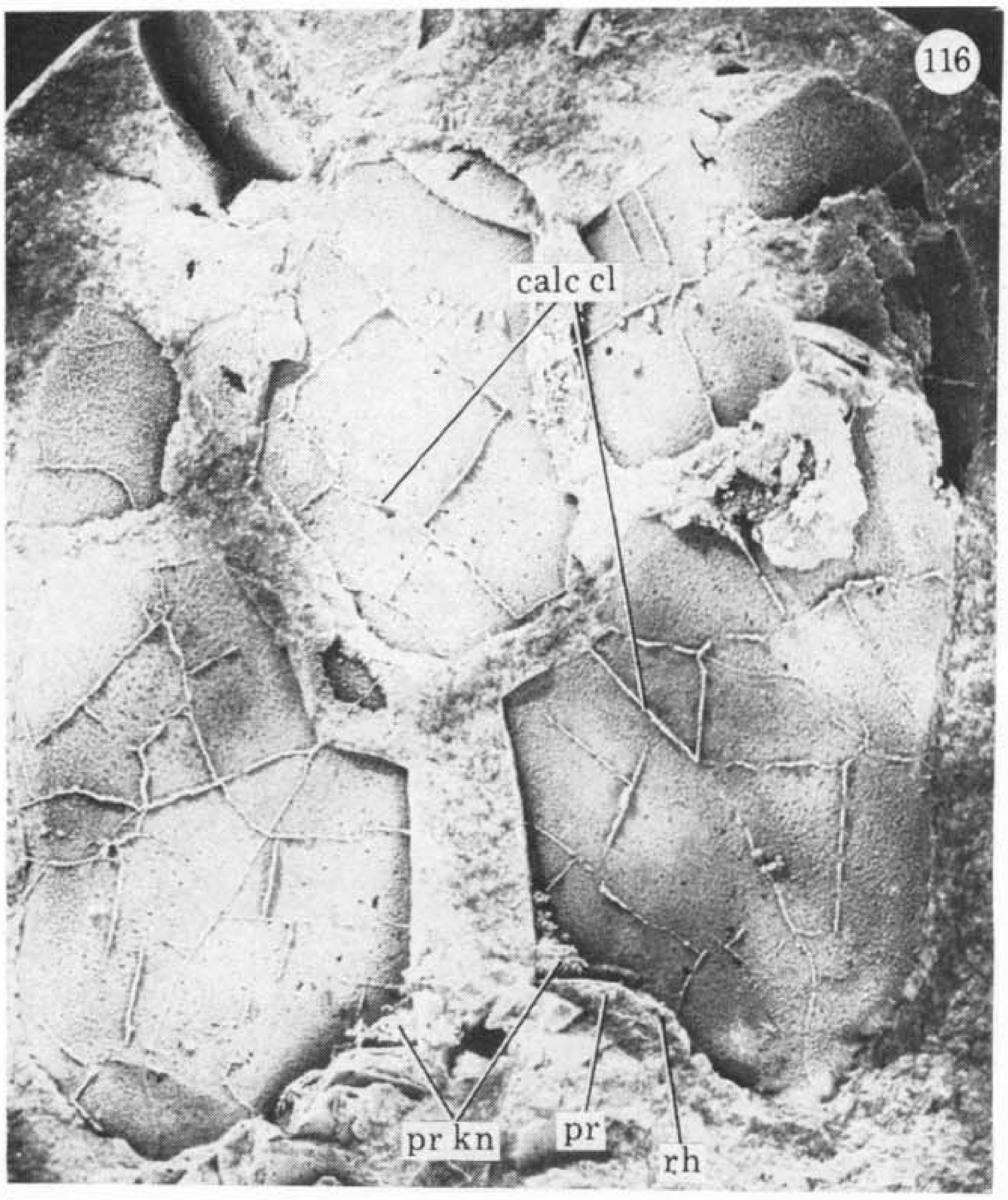


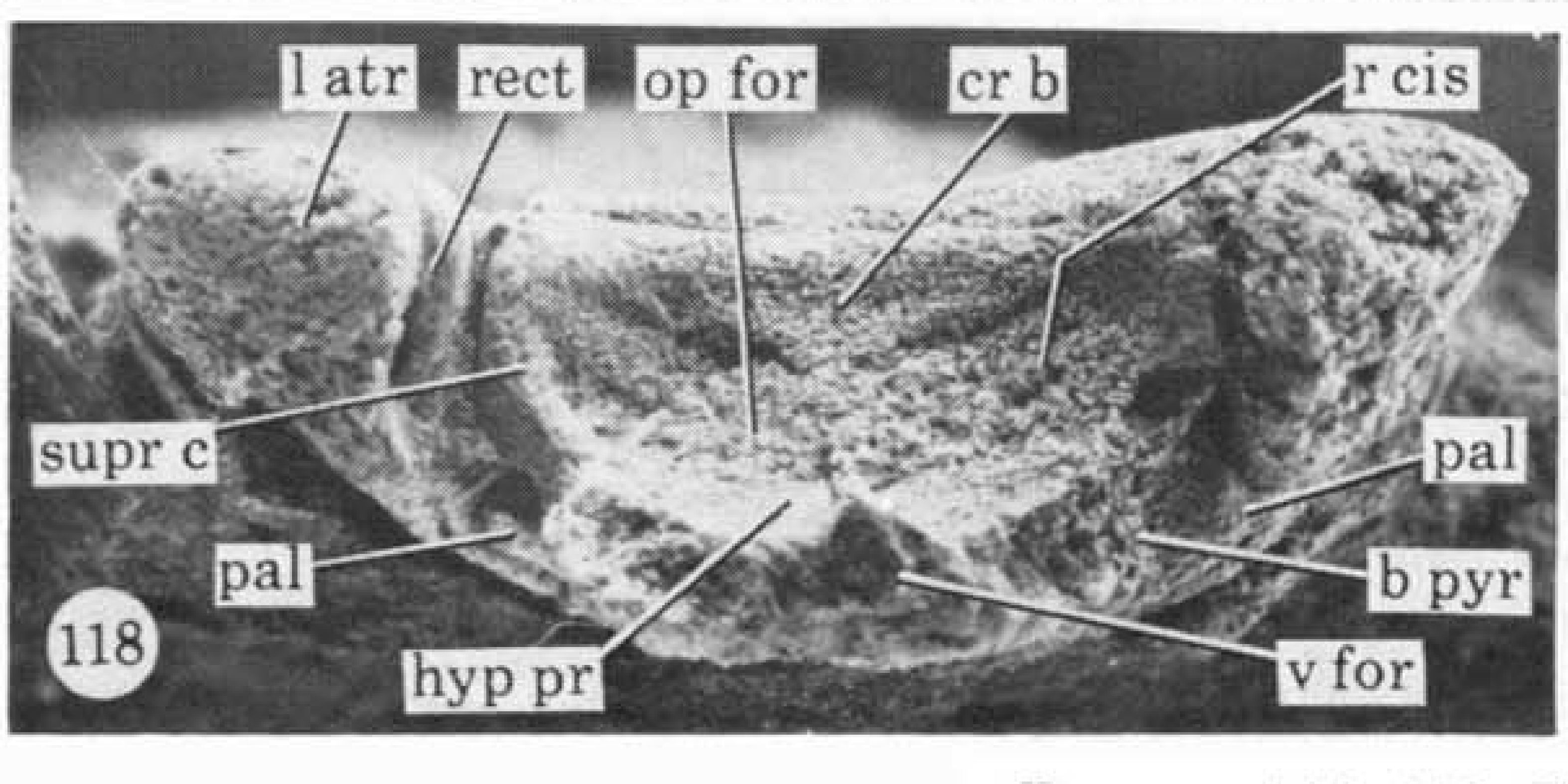


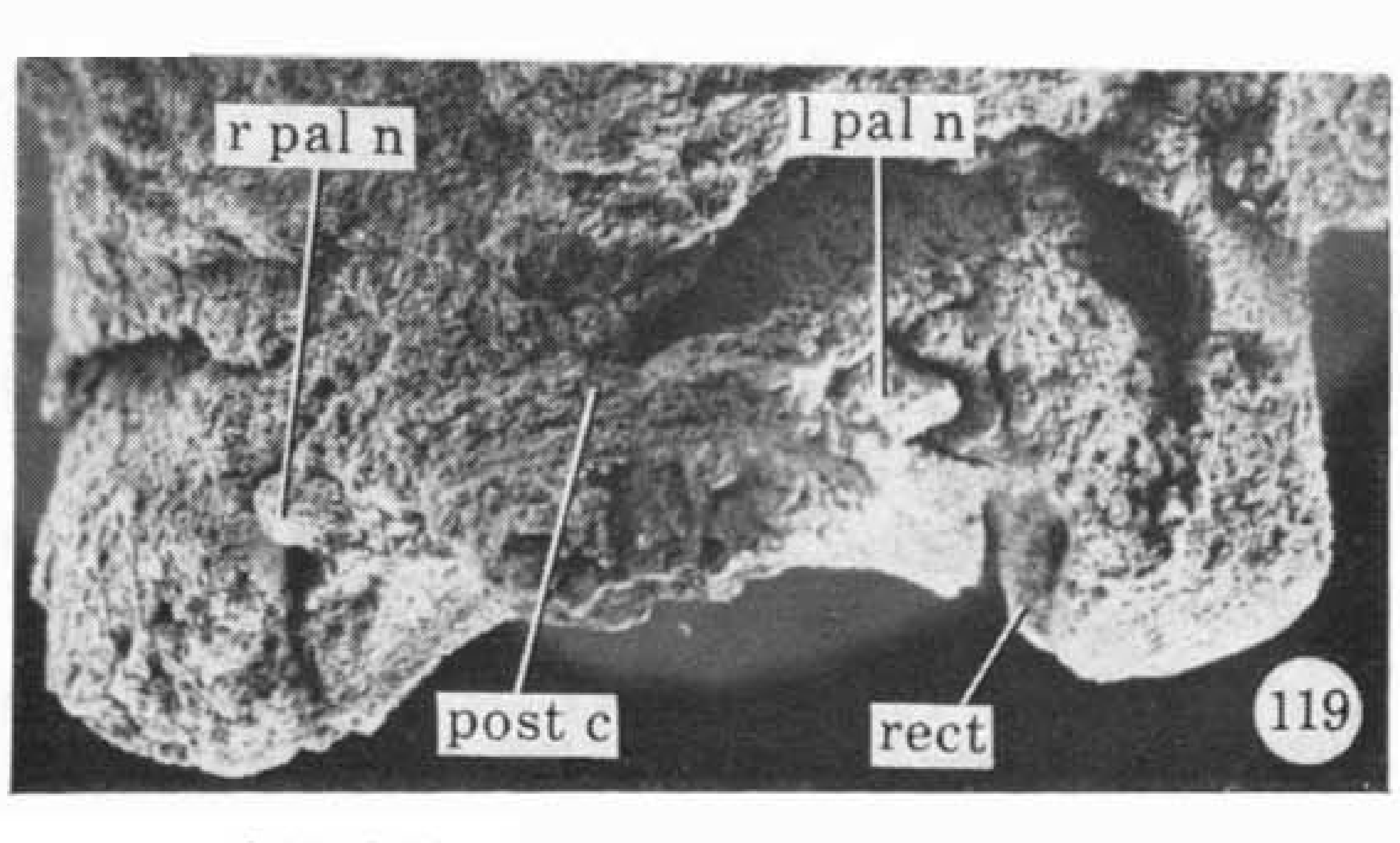


FIGURES 110–113. For description see p. 318.

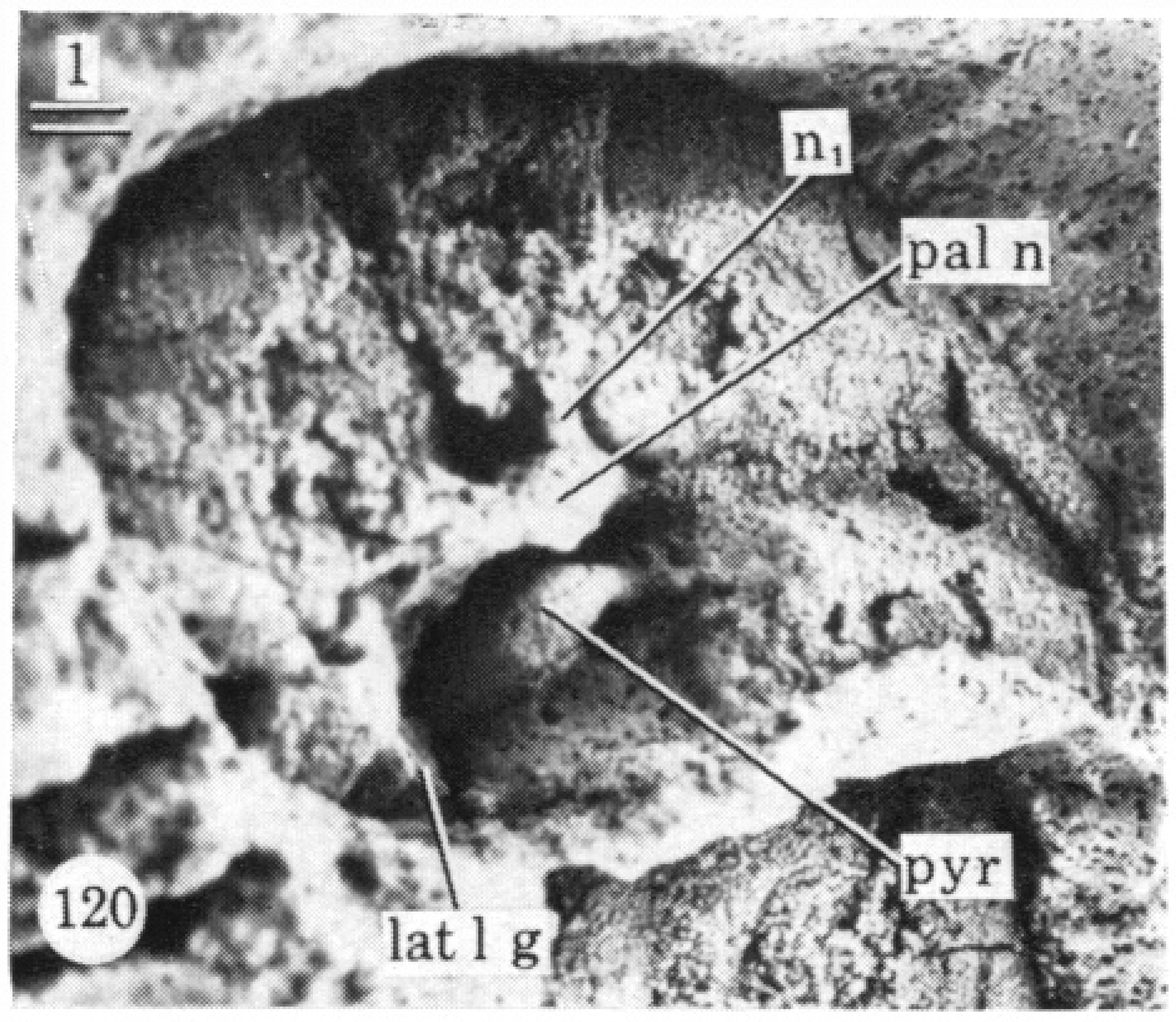


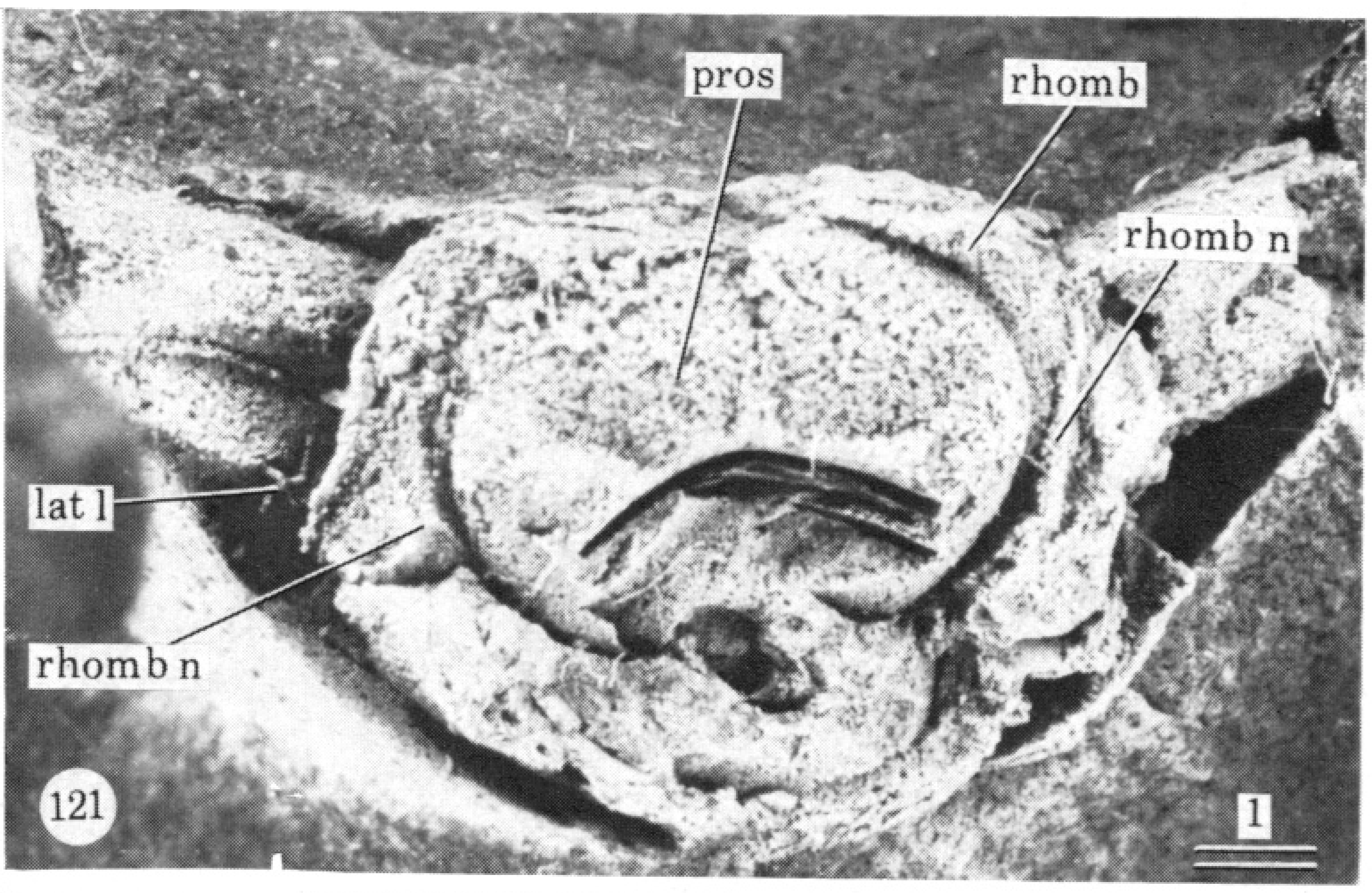


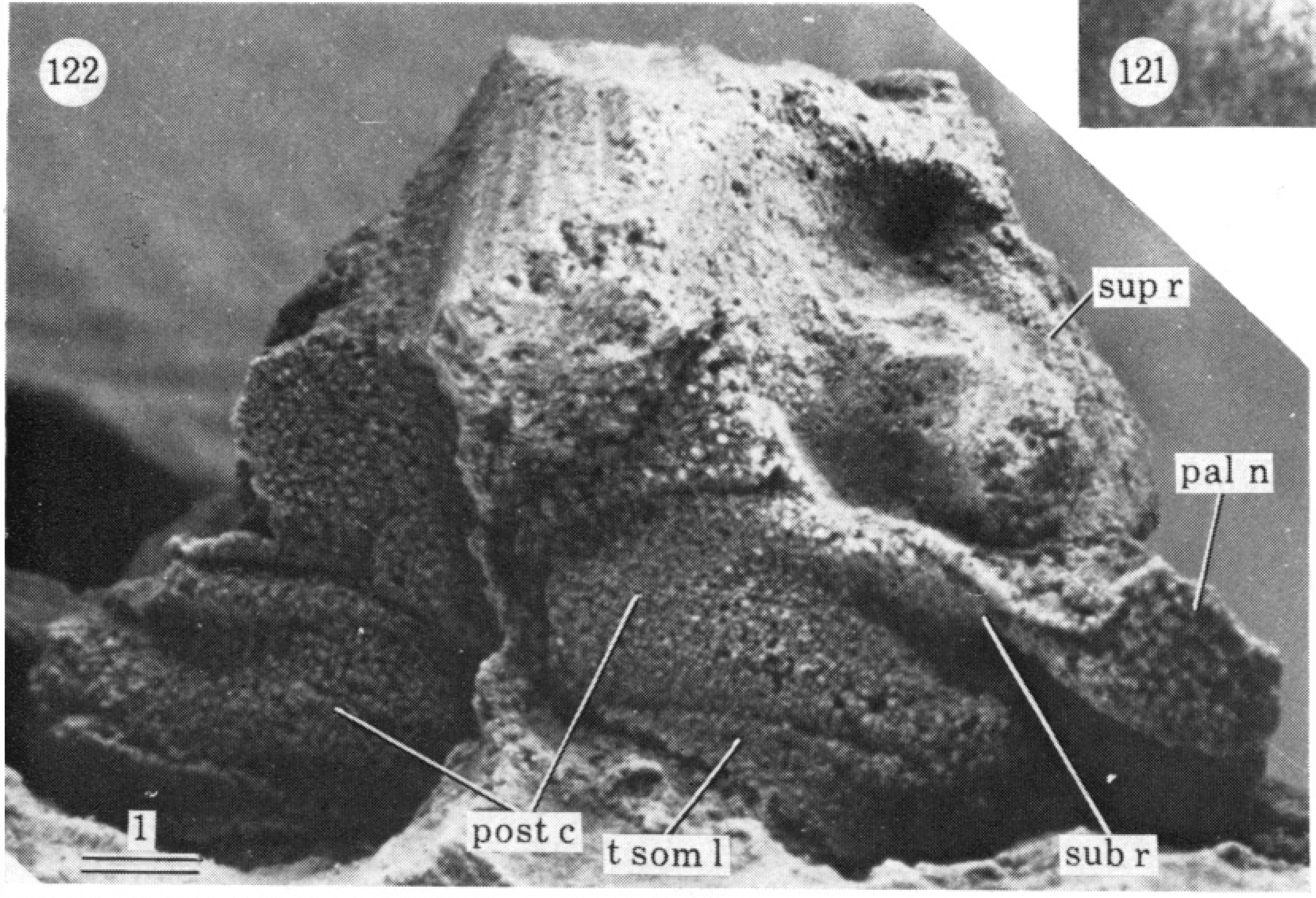


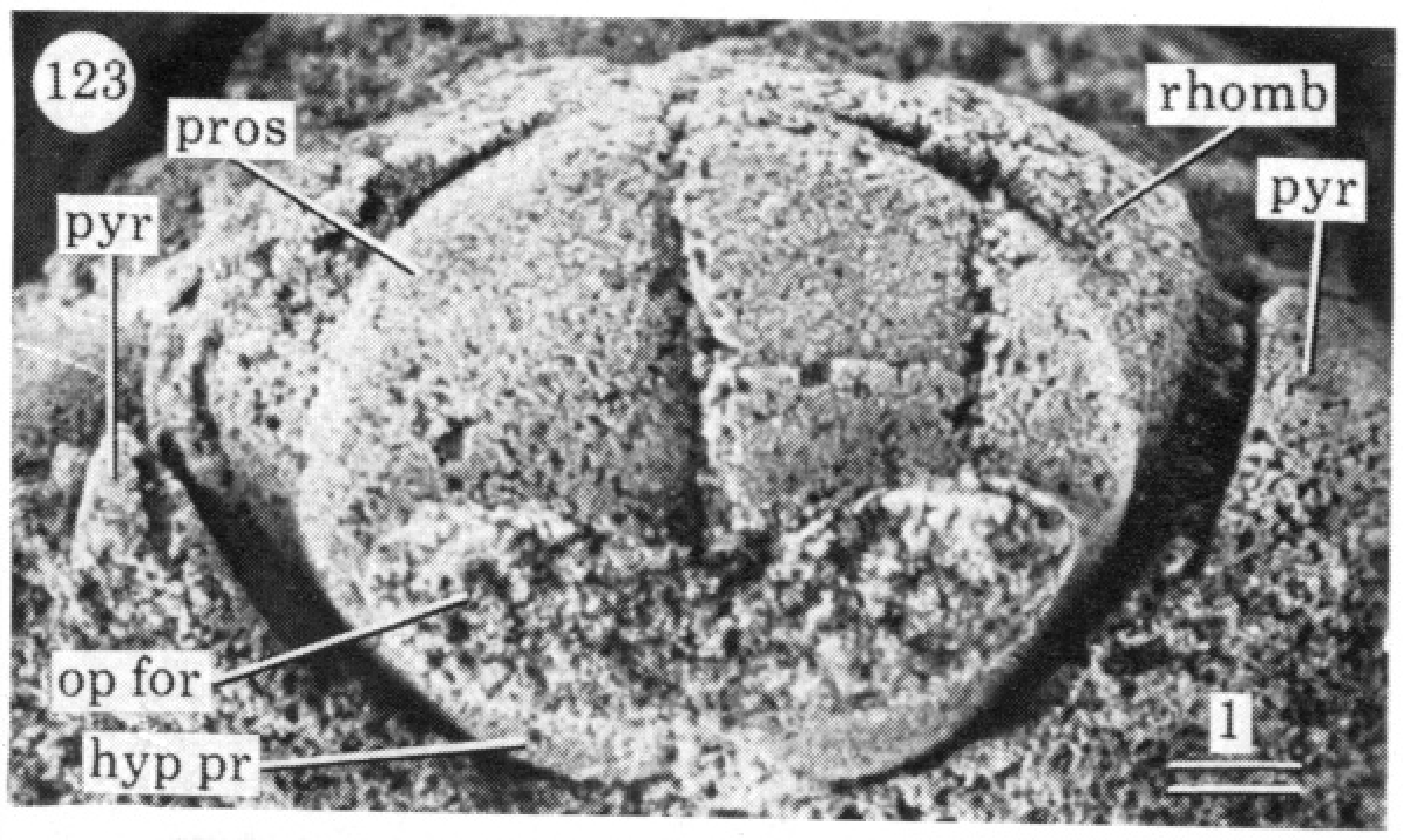


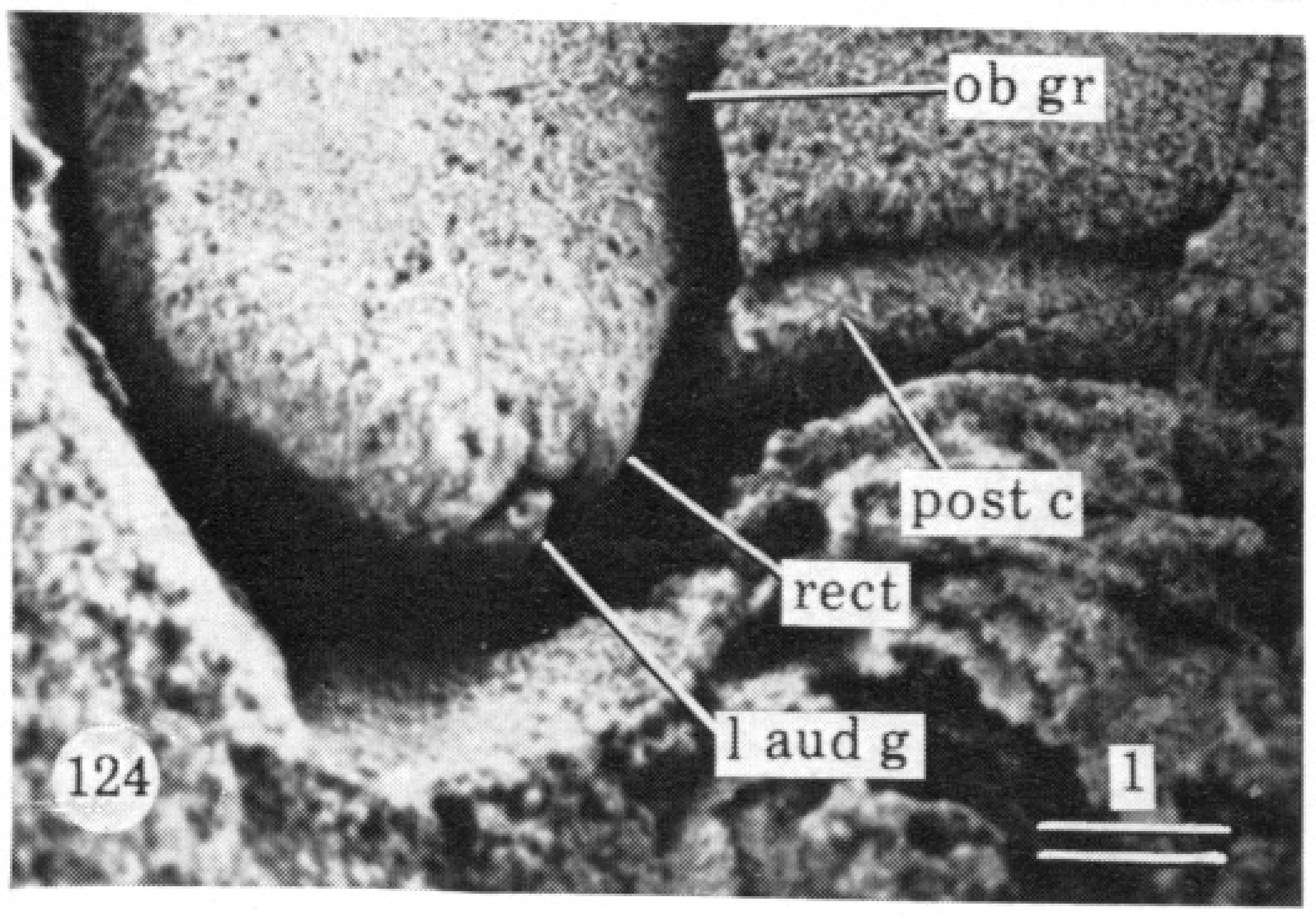
FIGURES 114–119. For description see pp. 318–319.

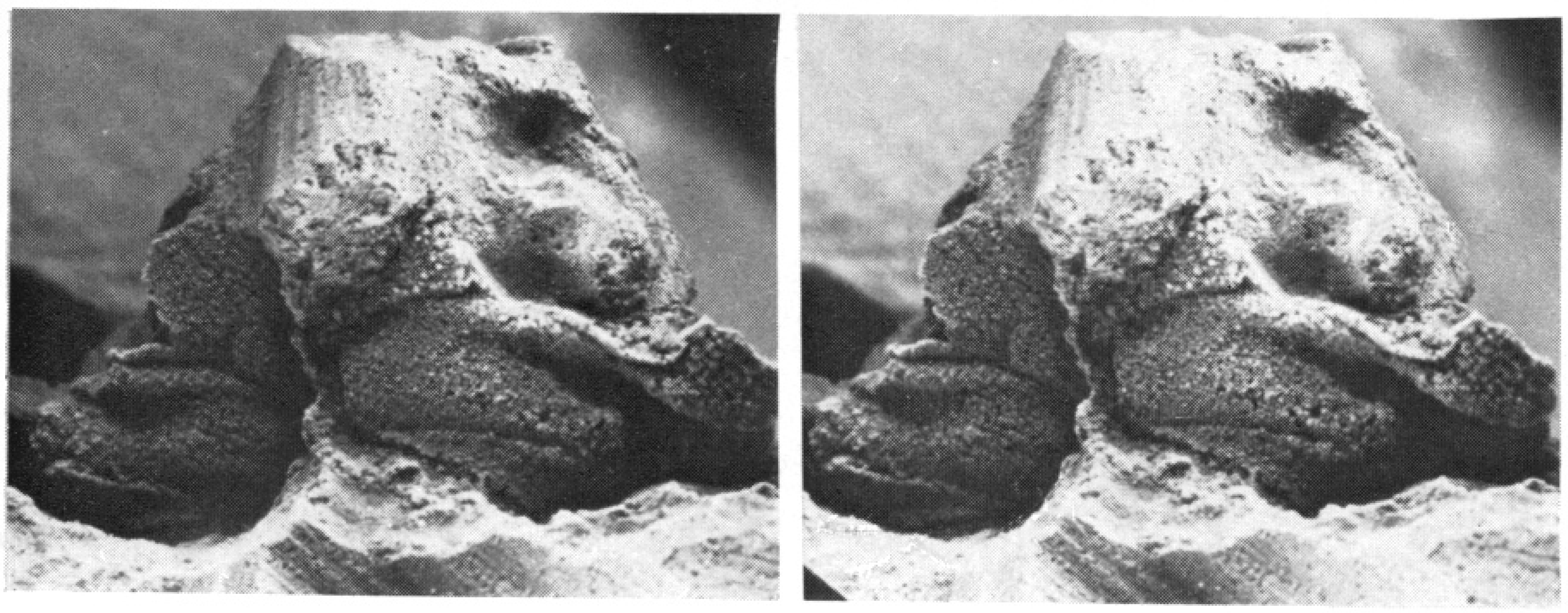


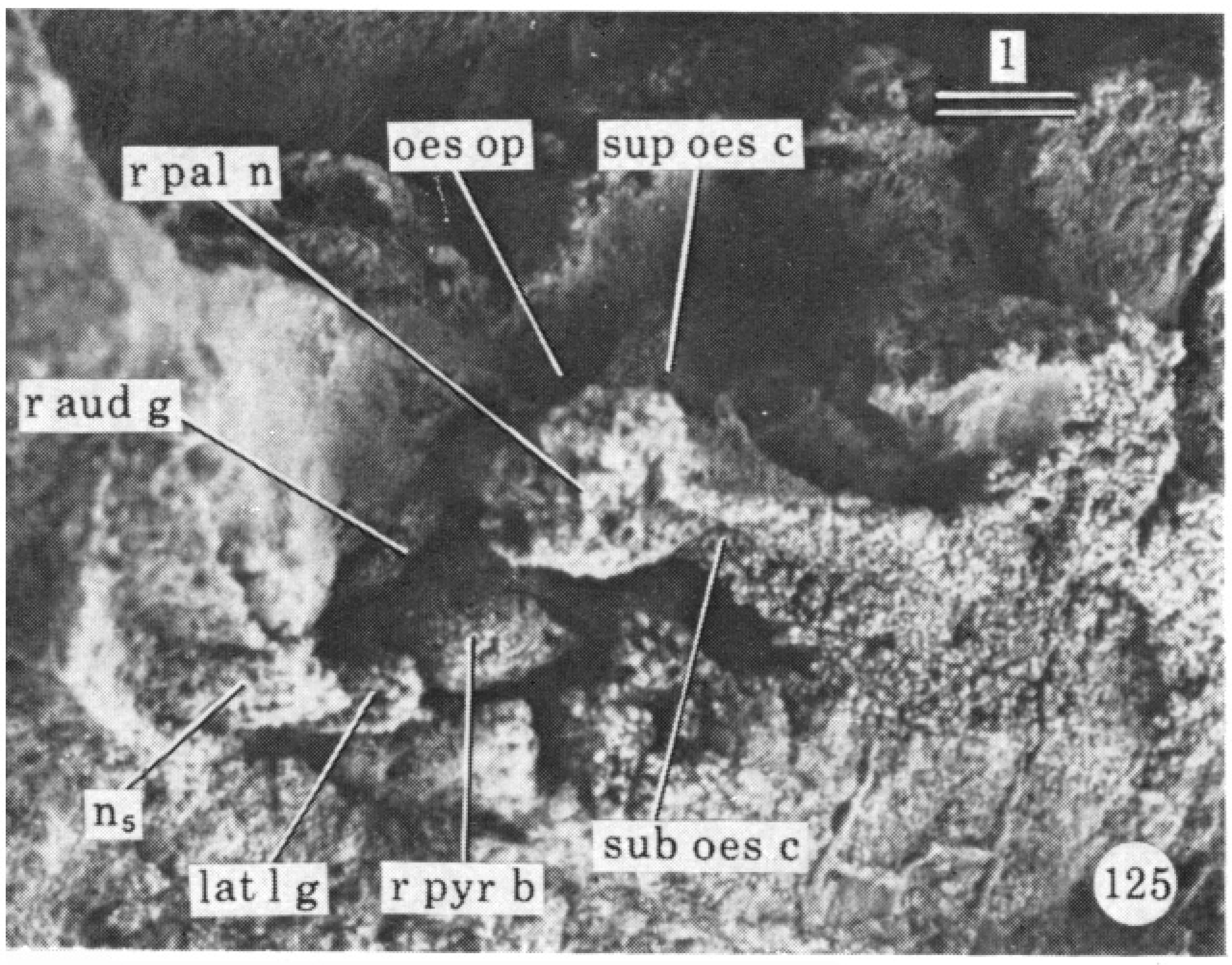


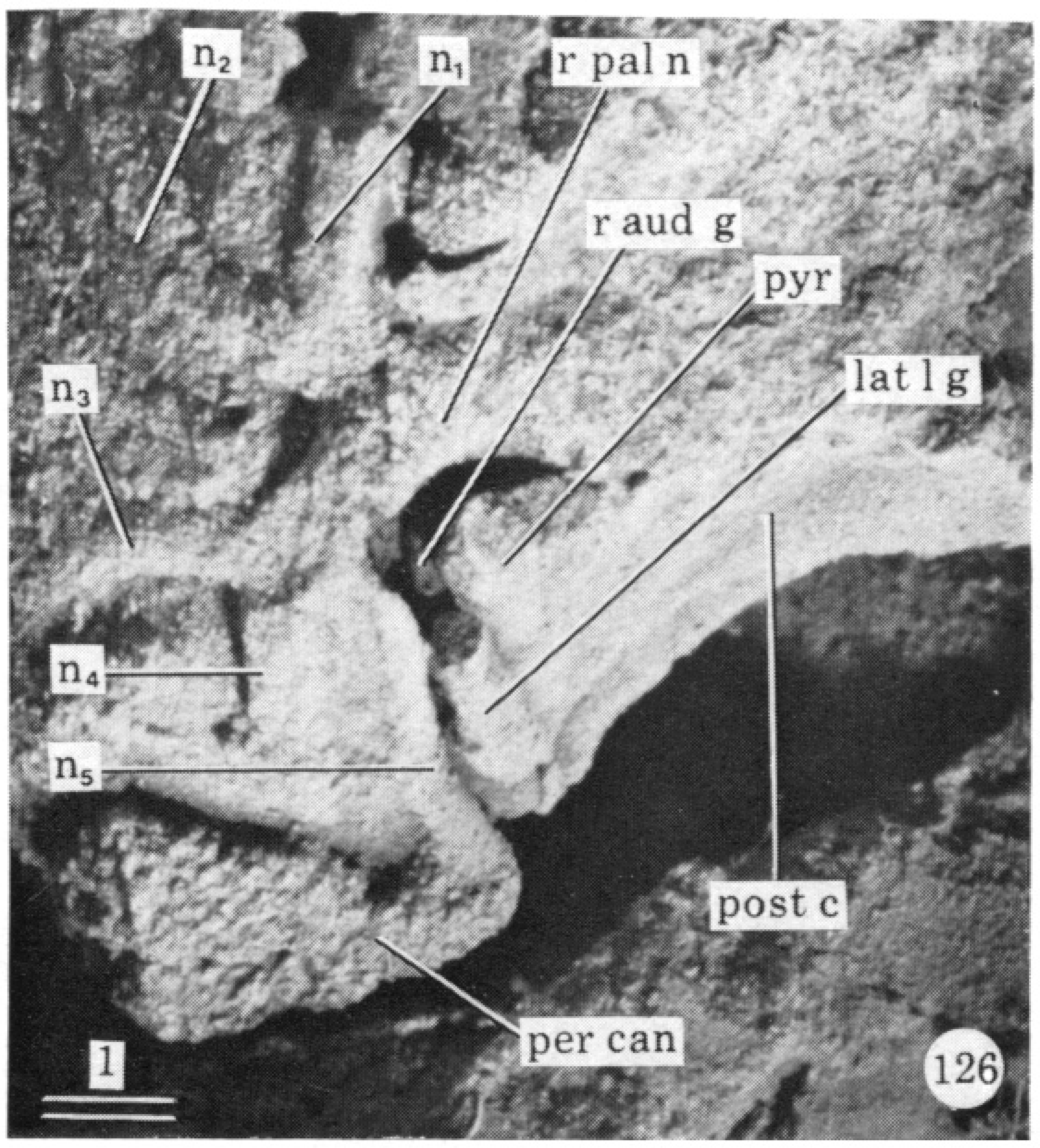




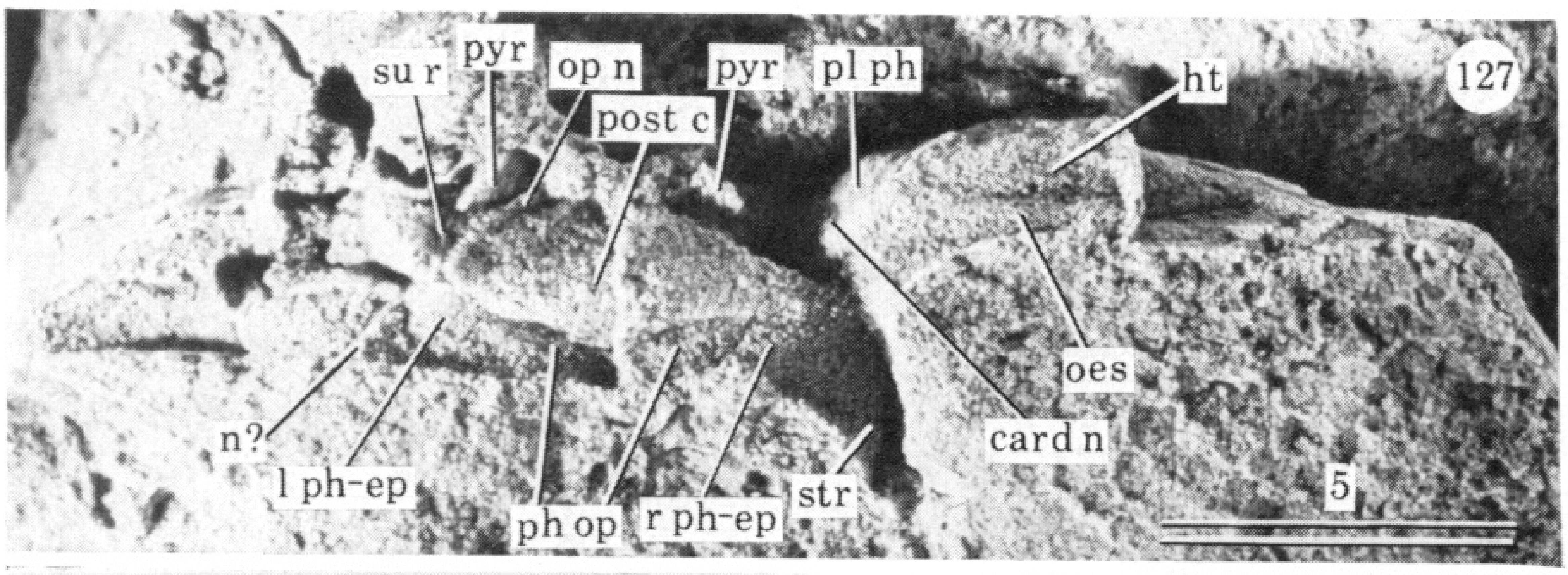


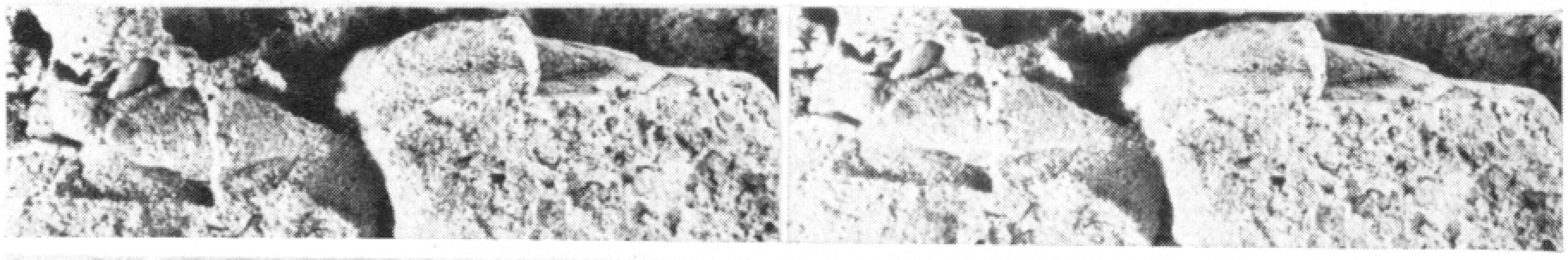


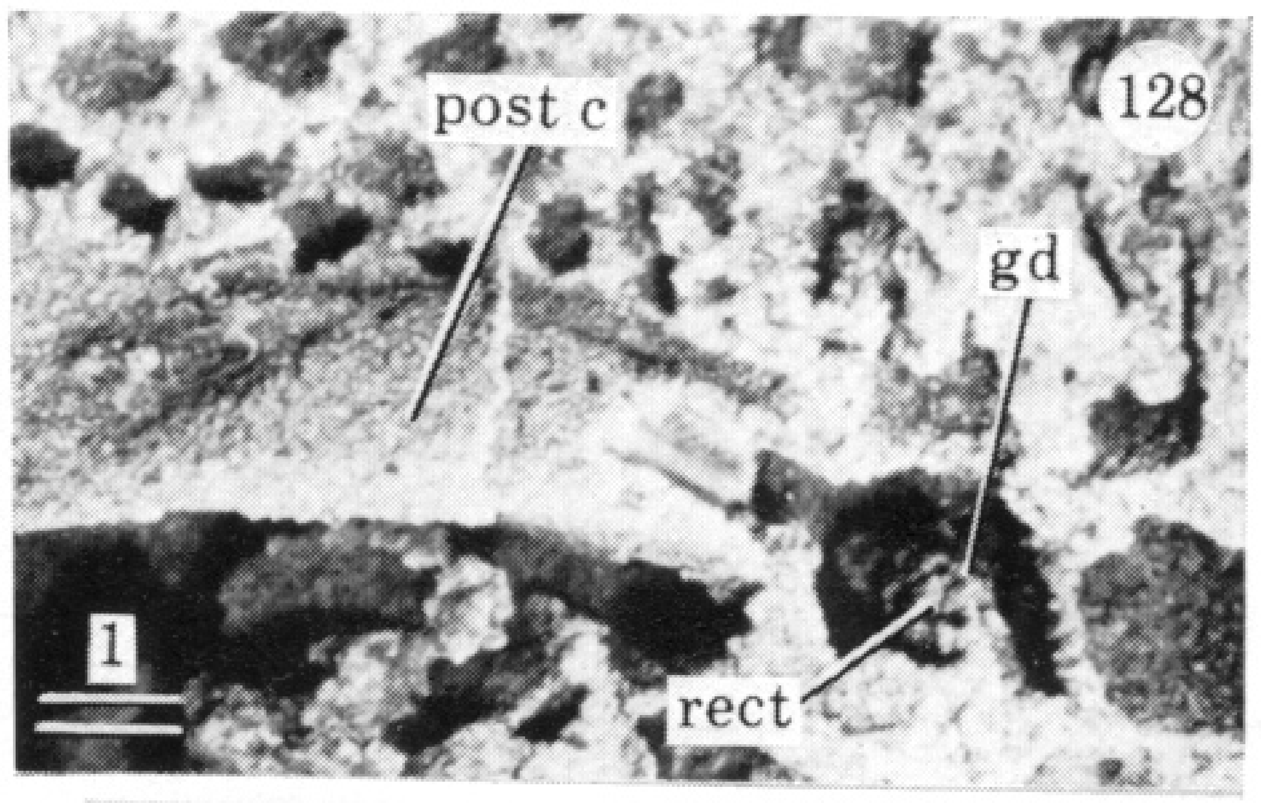


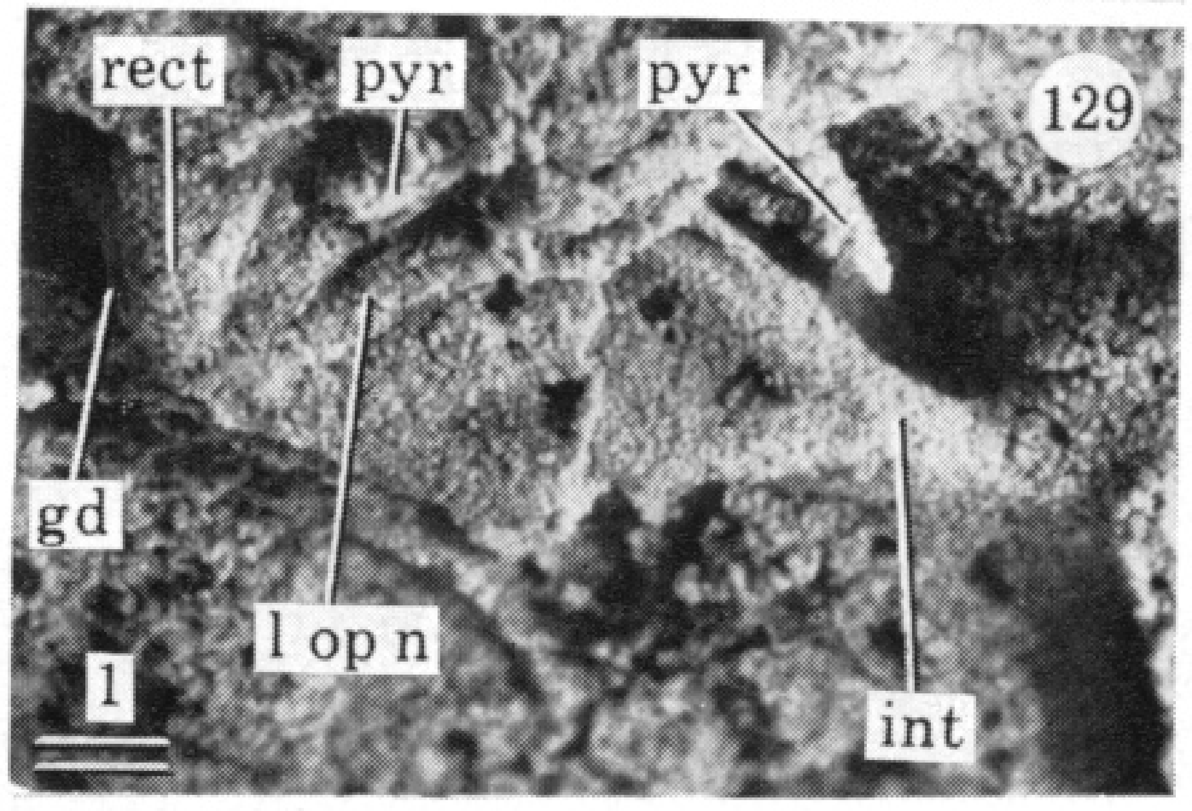


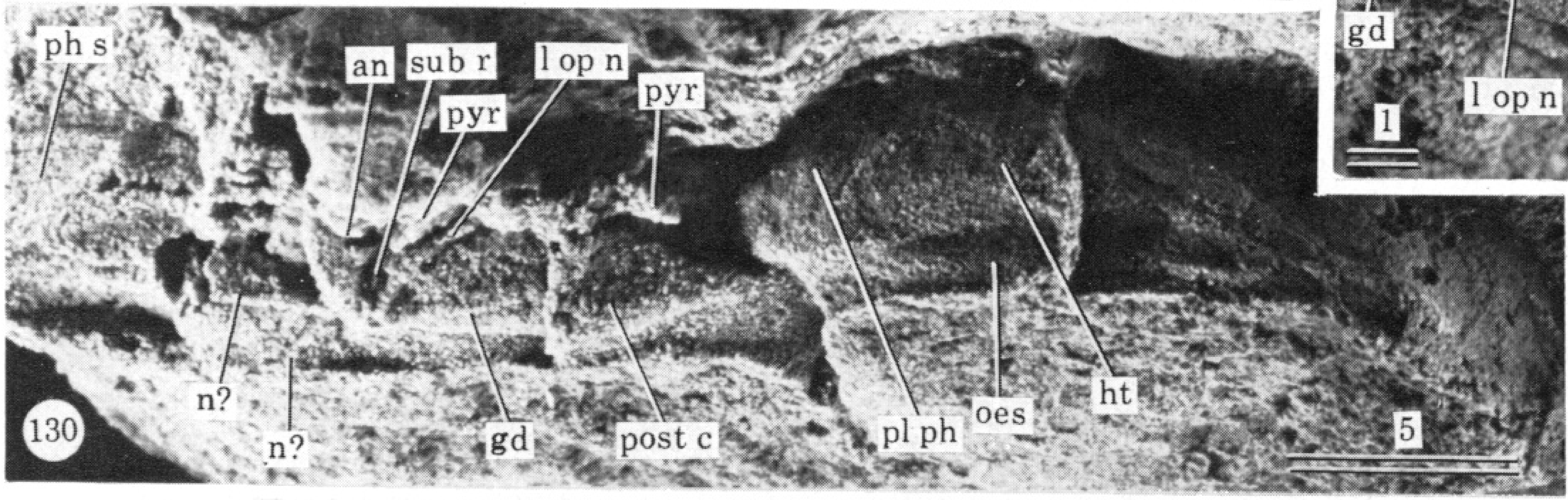
FIGURES 120–126. For description see p. 319.

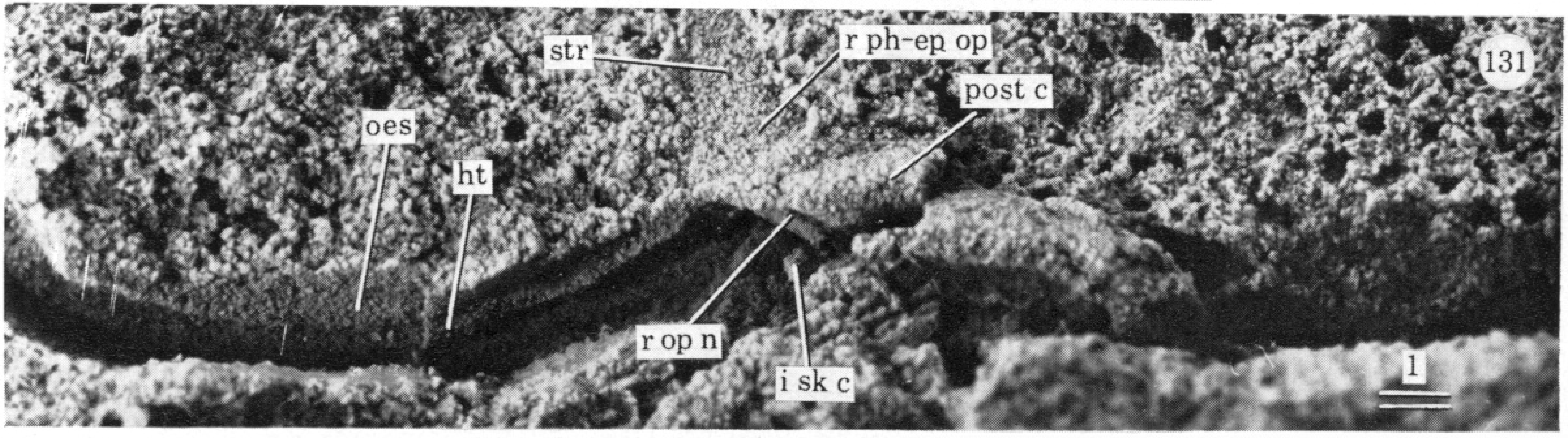


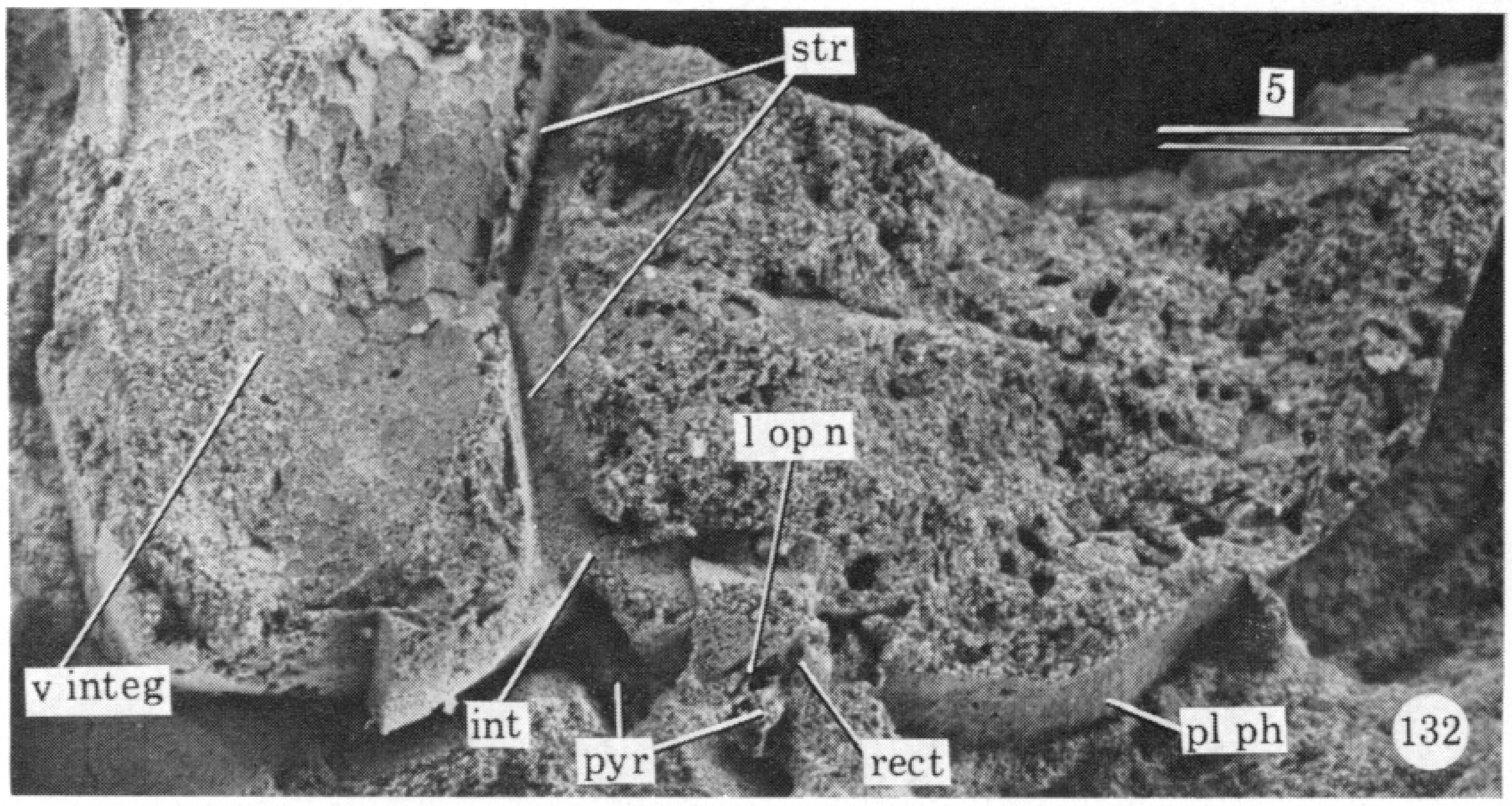


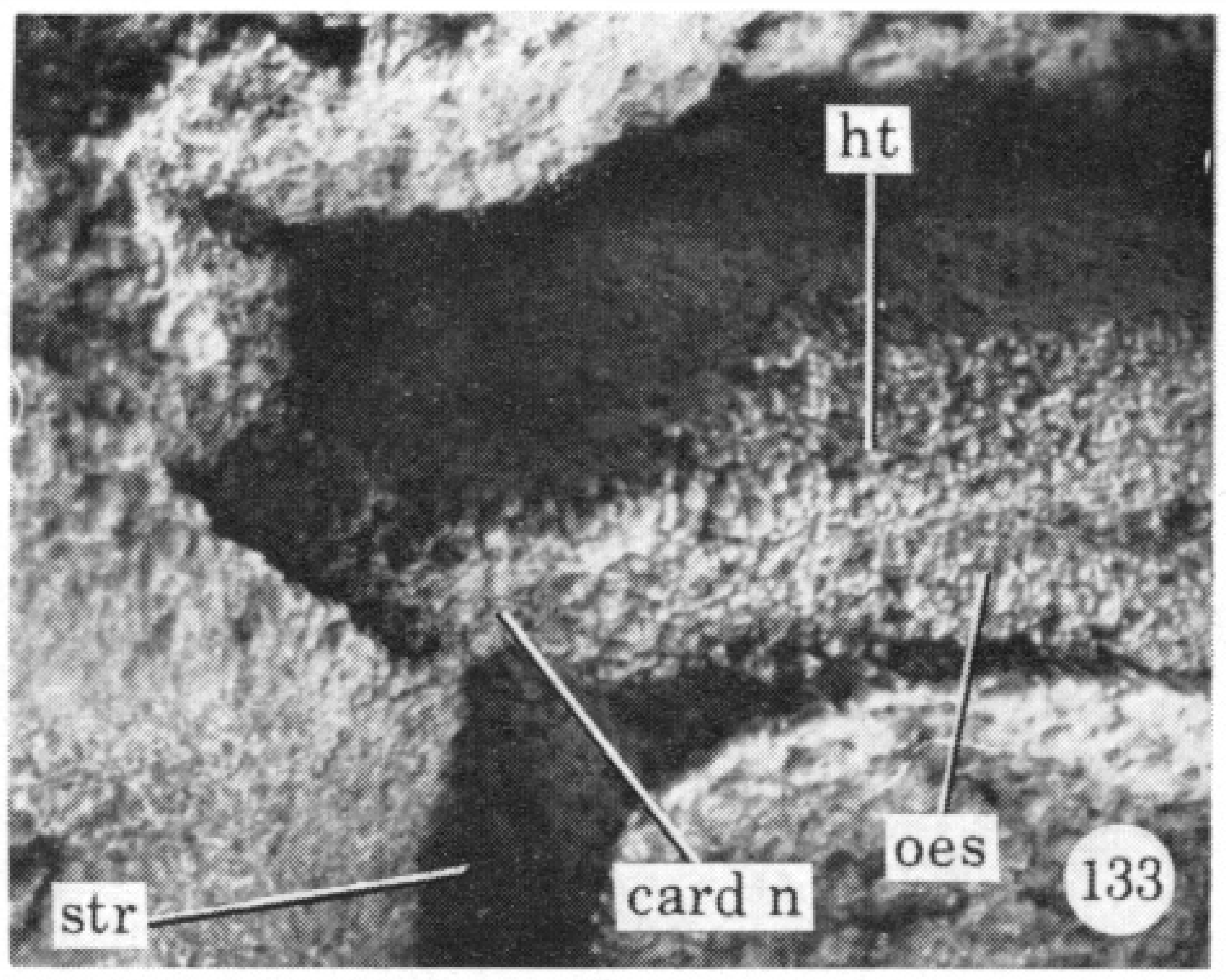


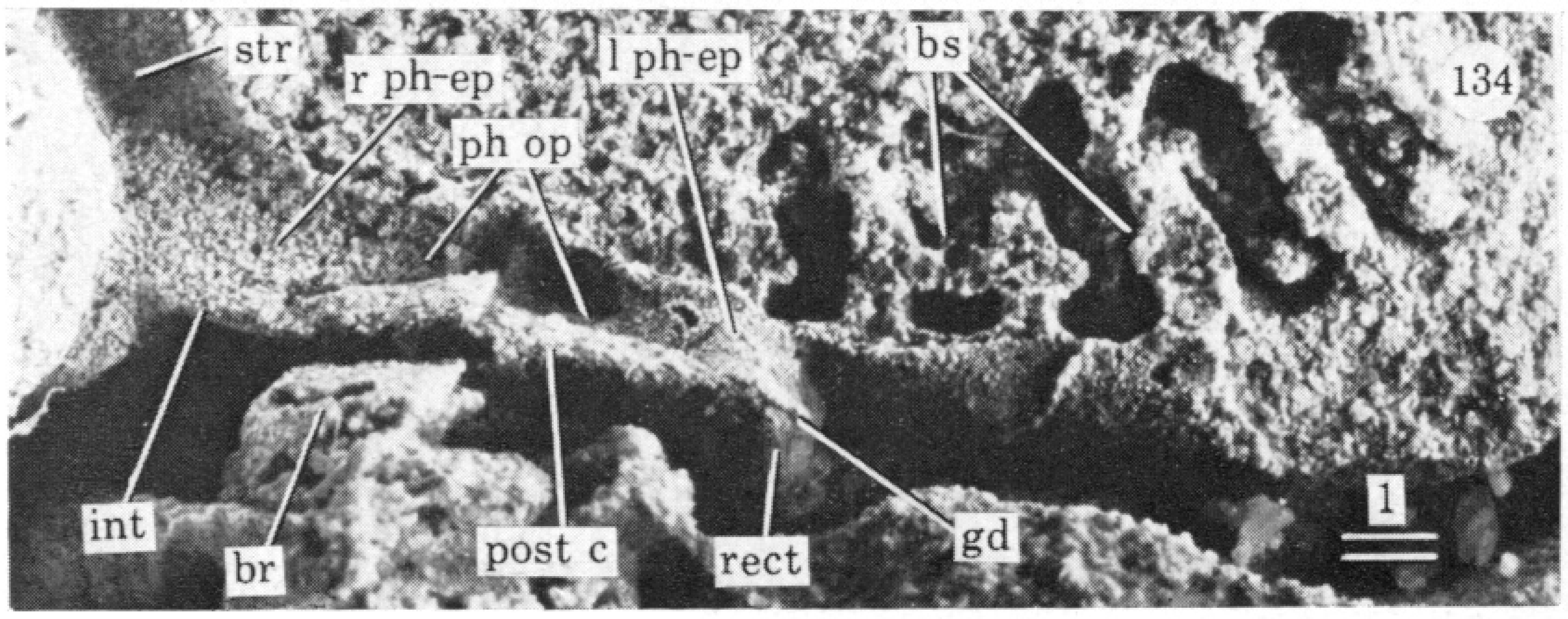


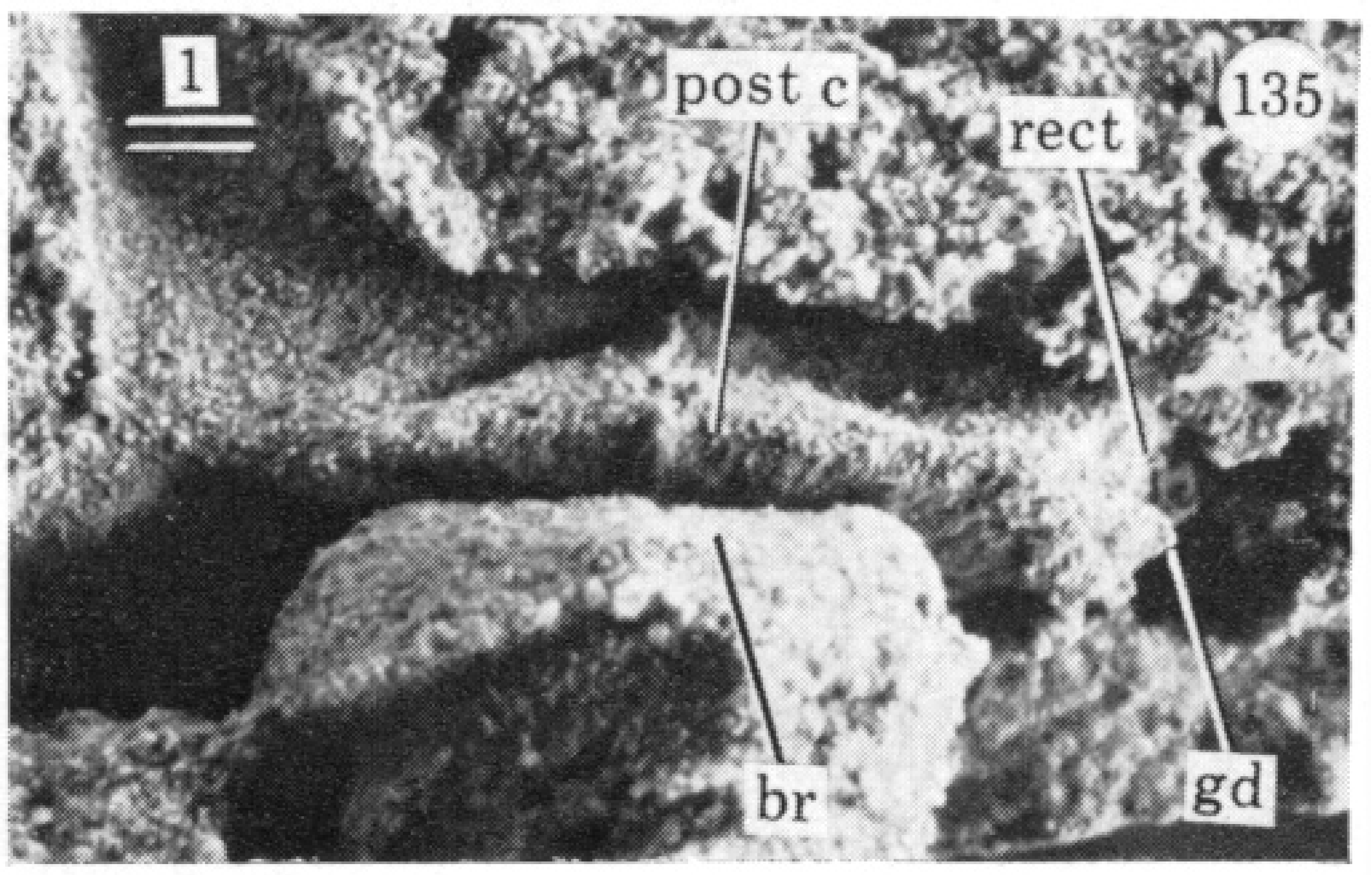




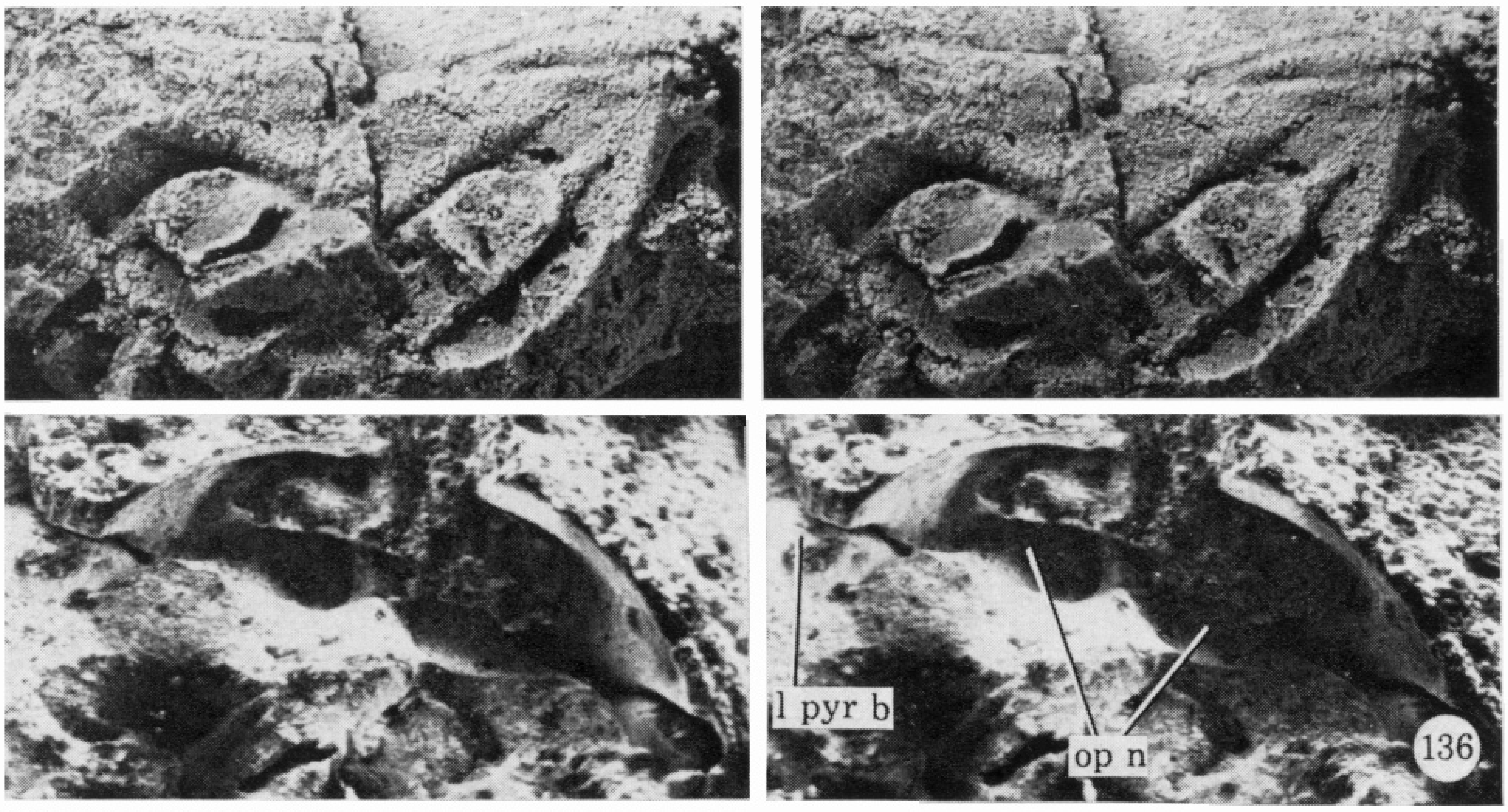


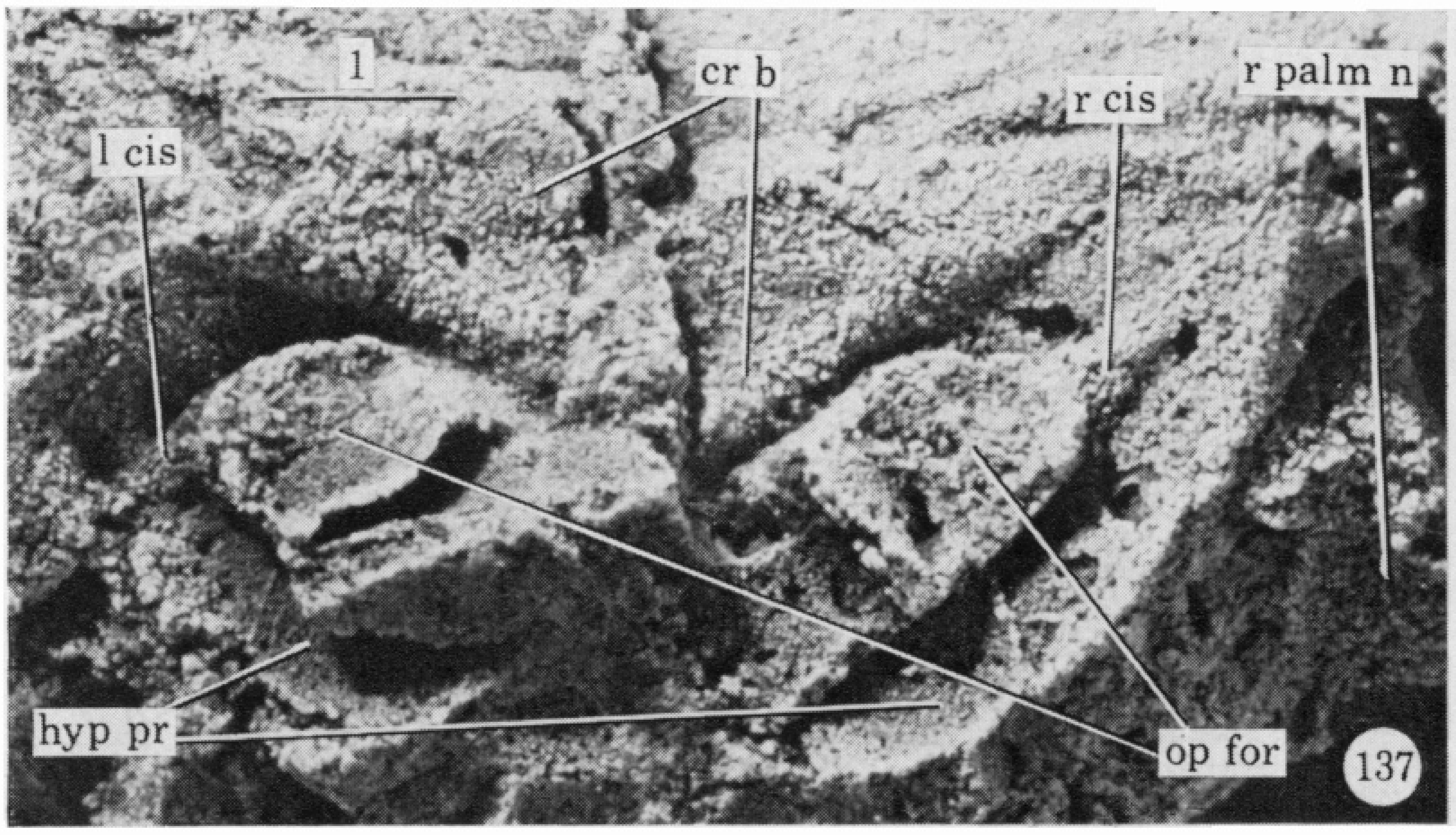


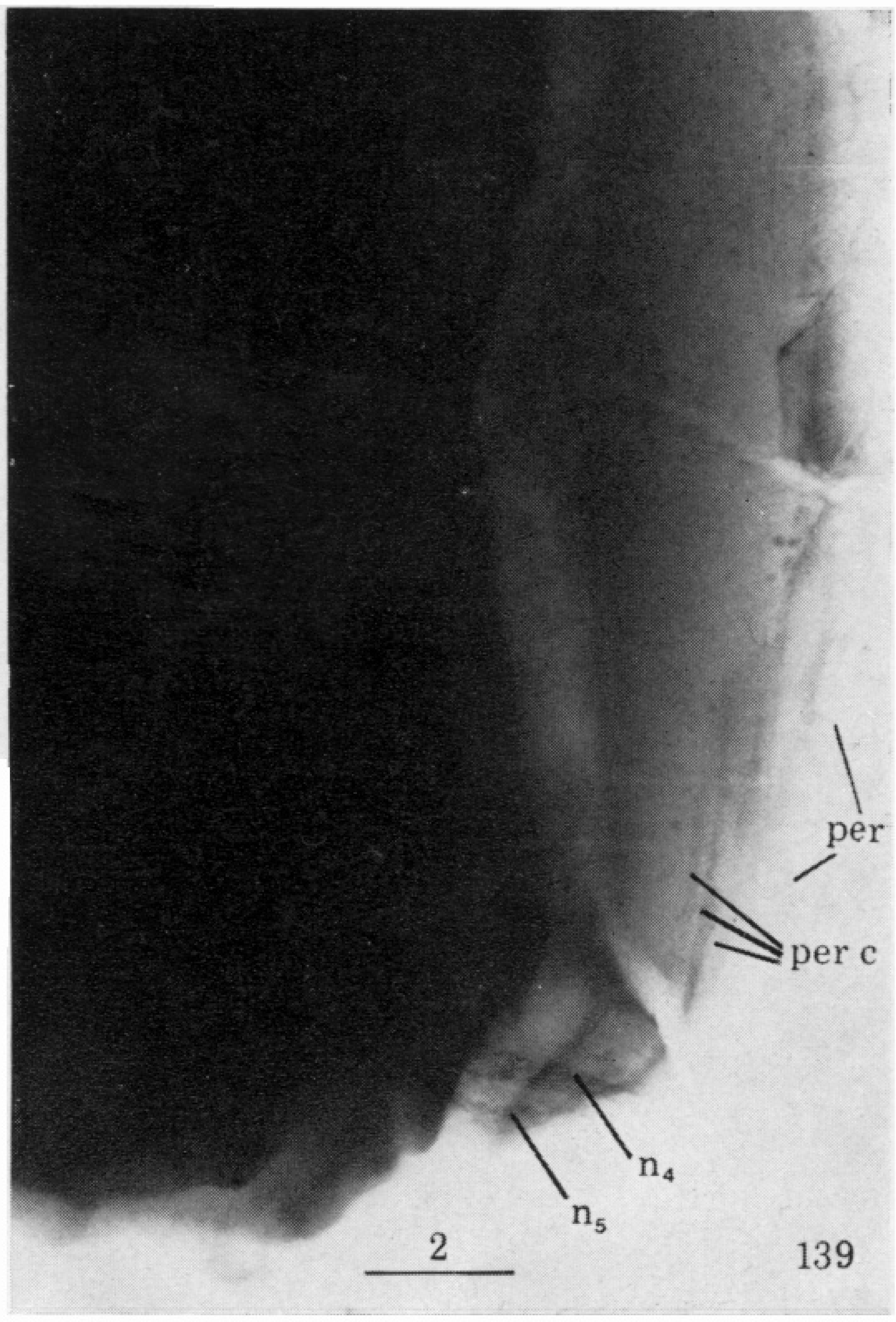


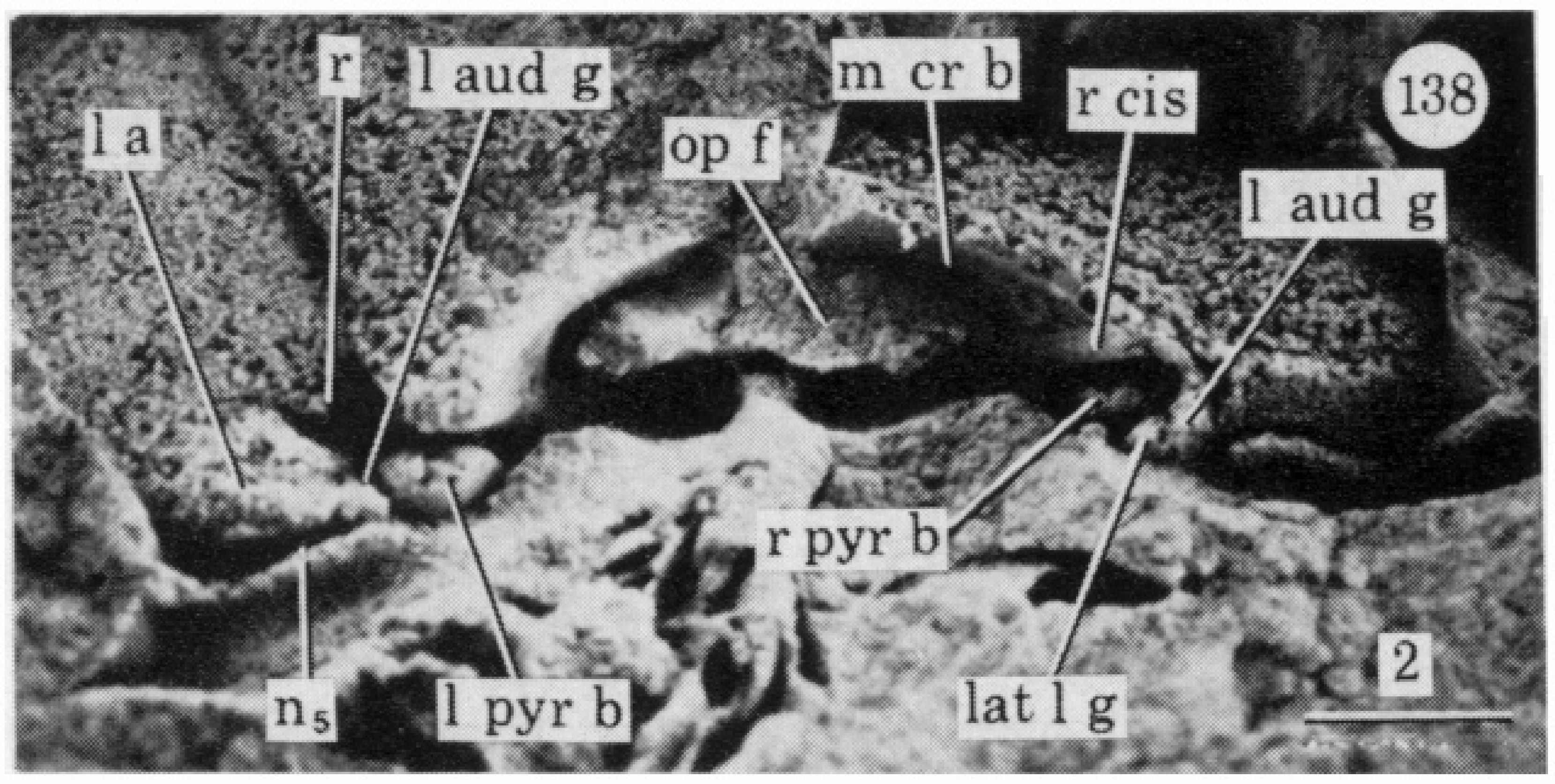


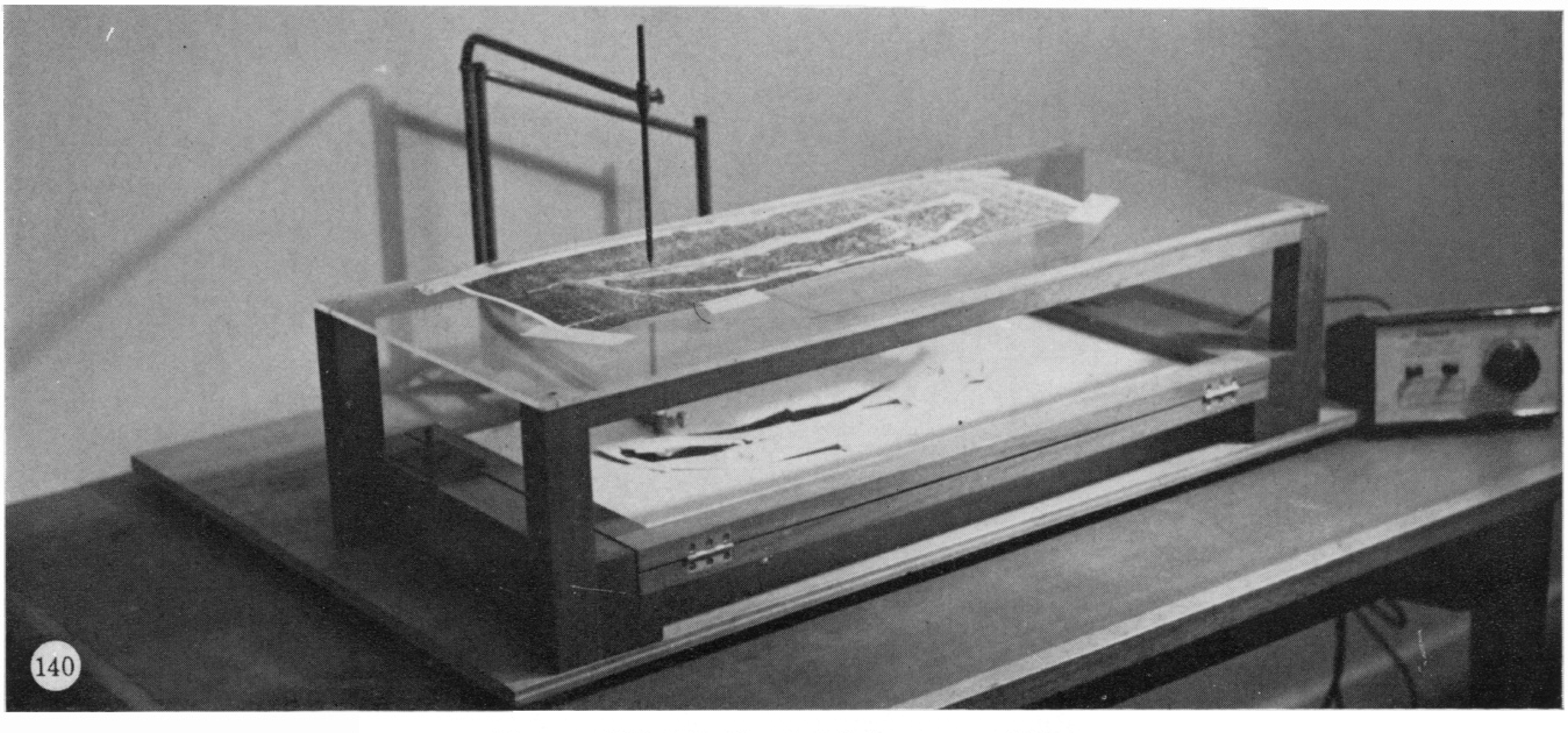
FIGURES 127–135. For description see p. 319.











Figures 136–140. For description see p. 319.