THE ORDOVICIAN FOSSIL *LAGYNOCYSTIS PYRAMIDALIS* (BARRANDE) AND THE ANCESTRY OF AMPHIOXUS

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CONTENTS

Lagynocystis pyramidalis (Barrande) from the marine Lower Ordovician of Bohemia (Šárka Formation (Llanvirn)), has features which suggest that it is ancestral, or nearly so, to living cephalochordates such as amphioxus (*Branchiostoma*).

L. pyramidalis belongs to a strange group of fossils classified by some workers as 'carpoid' echinoderms (phylum Echinodermata, subphylum Homalozoa, class Stylophora). They are better seen, however, as primitive chordates with echinoderm affinities (phylum Chordata, subphylum Calcichordata Jefferies, 1967, class Stylophora). The most striking echinoderm-like feature of the calcichordates is their calcite skeleton with each plate a single crystal of calcite. Their chordate characters include: (1) branchial slits; (2) a postanal tail (stem) with muscle blocks, notochord, dorsal nerve cord and segmental ganglia; (3) a brain and cranial nervous system like those of a fish; and (4) various asymmetries like those of recent primitive chordates. The calcichordates are divided into a more primitive order, Cornuta, and a more advanced order Mitrata, which evolved from Cornuta. *L. pyramidalis* is a specialized member of the order Mitrata. Forms up till now associated with it in the suborder Lagynocystida of the Mitrata are better separated from it to form a new suborder Peltocystida (Kirkocystidae plus Peltocystidae).

The features which ally *L. pyramidalis* to amphioxus are as follows: (1) a median ventral atrium opening by a median ventral atriopore; (2) a probably excretory posterior coelom which could give rise to the nephridia of amphioxus by upward growth of the gill slits; (3) evidence that the anus opened externally on the left; (4) evidence that the mouth and buccal cavity was innervated more strongly from the left than from the right; (5) evidence suggesting that, if it swam, *L. pyramidalis* would rotate about its long axis, clockwise as seen from behind, like late larval amphioxus and larval tunicates.

The amphioxus-like features of *L. pyramidalis* are imposed on the pattern of a very primitive mitrate. There existed thus: (1) a well-developed brain and the cranial nerves were more of the vertebrate pattern than those of amphioxus; (2) left and right branchial openings in addition to the median atriopore; and (3) the tail or stem had paired segmental ganglia. The latest common ancestor of vertebrates and amphioxus would be a primitive mitrate. It follows, since *Lagynocystis* had a calcite skeleton, that such a skeleton has been lost at least twice in the evolution of the chordates.

1. Introduction

Lagynocystis pyramidalis, from the marine Lower Ordovician of Bohemia, was either directly ancestral to amphioxus, or closely related to such an ancestor. This is shown by a number of anatomical features, of which the most important is the presence of a median ventral atrium, with well-preserved gill slits (plate 40).

L. pyramidalis belongs to the group of fossils which I have called Calcichordata (Jefferies 1967, 1968*a*, *b*, 1969, 1971; Jefferies & Prokop 1972; Eaton 1970). I have argued that this group constitutes a basal chordate subphylum with echinoderm affinities from which are descended the living subphyla of chordates, i.e. the tunicates, cephalochordates and vertebrates. In its essentials this view was first suggested by Gislén (1930), but many workers still regard the calcichordates as primitive, 'carpoid' echinoderms (Ubaghs 1961, 1963, 1968, 1970, 1971).

It is now necessary to explain what I have so far deduced about the calcichordates, so that the arguments in the rest of the paper will be easier to follow (see Jefferies (1967) for a concise account). The Calcichordata can be briefly defined as a primitive subphylum of fossil marine chordates with a calcite skeleton of echinoderm type. They all have a stem, or tail, and a flattish theca, or body, which was adapted to lie on one surface on the sea floor. Among the chordate features which can be established in various members of the group are a dorsal nerve cord and notochord located in a postanal tail (or stem), branchial slits in the wall of the theca and a fish-like system of cranial nerves. Furthermore, the Calcichordata were very asymmetrical animals and some of the asymmetries resemble those of recent, primitive chordates. Thus in some calcichordates the rectum opened into a left atrium, as it does in a tunicate tadpole. The existence of calcichordates confirms an old suspicion that echinoderms and chordates are closely related to each other. It means in particular that the chordates are closer related to echinoderms than to hemichordates, which would constitute a separate though related phylum, as Hyman (1955) and Barrington (1965) suggested.

Chordates and echinoderms probably evolved from a common ancestor resembling the hemichordate *Cephalodiscus*, which had taken to crawling on the sea floor, right side down, and acquired a calcite skeleton (Jefferies 1969).

The skeleton of calcichordates was echinoderm-like, in that each plate was a single crystal of calcite and had a carious structure, like the stereom mesh of echinoderms. In fact this skeleton is almost certainly homologous with the skeleton of echinoderms, and argues that the calcichordates and echinoderms are closely related. It is also sometimes seen as an argument for thinking that the calcichordates had nothing to do with the chordates, on the grounds that most vertebrates have a hard skeleton made of bone, dentine or 'calcified' cartilage mineralized with hydroxyapatite (Halstead-Tarlo and Hill in discussion of Jefferies (1968*b*) and Ubaghs (1971, p. 170)).

However, there are three living subphyla of chordates, not just one. A phosphatic skeleton is developed in most vertebrates, but not in tunicates or cephalochordates. On comparative grounds there is therefore no reason to assume that the latest common ancestor of tunicates, vertebrates and cephalochordates need have had a phosphatic skeleton. The calcite skeleton of calcichordates is probably a primitive feature of chordates, inherited from the latest common ancestor of echinoderms and chordates. It can be compared with the teeth of *Archaeopteryx*, which indicate reptile affinities in a primitive bird, or the hard-shelled eggs of *Ornithorhynchus*, which indicate reptile affinities in a primitive mammal. But if a calcite skeleton was a primitive feature of chordates, it must have been lost in the evolution of the extant chordate subphyla.

I do not think it likely that the calcite skeleton of calcichordates was lost by being transformed directly into vertebrate bone or dentine, athough Eaton (1970) has suggested just such a transformation. My reasons are: (1) It is crystallographically impossible to insert phosphorus ions in a calcite lattice, which makes it unlikely that a chemical change from calcite to apatite could occur gradually. (2) The earliest vertebrates known, in the Ordovician, seem to be in the process of acquiring a totally new hard skeleton, having directly descended from forms without one, rather than transforming a calcite skeleton (see Jefferies 1968*a*, p. 331). (3) The way in which the skeletal minerals are first seeded is completely different in echinoderms and vertebrates (Jefferies 1968*a*, p. 331). (4) An extensive soft layer existed in the dorsal skeleton of some calcichordates and this suggests that the calcite was in part being replaced by connective tissue, perhaps by resorption (Jefferies 1968*a*, p. 296). (5) It is obviously possible for an echinoderm-type skeleton to be lost since some Molpadid holothurians have no skeleton, though a skeleton of normal echinoderm type was presumably present in their ancestors.

The calcite skeleton was therefore probably lost in the early evolution of the extant chordate subphyla, giving rise to forms with no hard skeleton. Later, in the vertebrates alone, a new, phosphatic, skeleton evolved. The argument developed later in this paper suggests that the loss of calcite must have occurred at least twice – once in the line leading toward the cephalochordates and once in the line leading towards the vertebrates and tunicates. The loss may, in both cases, have been due to the adoption of a swimming mode of life.

The calcichordates can be divided into two orders – the more primitive Cornuta and the Mitrata which arose from Cornuta.

The cornutes were bizarre animals and extremely unsymmetrical. The first known representatives are Middle Cambrian in age (*Ceratocystis*) and the last were Upper Ordovician (*Cothurnocystis*, *Scotiaecystis*). The more primitive cornutes, such as *Cothurnocystis* and *Ceratocystis*, had thecas resembling medieval ankle boots in outline, with the stem attached to the sole of the 'boot'. The 'boot' was adapted to lie with one, ventral, 'side' downwards on the sea floor, and the other, dorsal, 'side' upwards. The skeleton was entirely of calcite. That of the theca usually consisted of a frame of marginal plates with upper, dorsal, and lower, ventral flexible integuments. The ventral integument was divided into two parts by a strengthening strut.

There were a number of openings in the cornute theca. Thus a row of gill slits, often with the mechanical structure of outlet valves, penetrated the dorsal integument on the left side of the theca. A gonopore-anus (anus in Jefferies (1967, 1968*a*) but see 1969) was present in all cornutes, and in all except the most primitive form (*Ceratocystis*), it lay just left of the stem, behind or opening into the gill slits. At the anterior end of the theca was the mouth, being the largest opening of all.

Four chambers existed inside the theca of cornutes. These were: the buccal cavity, behind the mouth; the posterior coelom, just in front of the stem; the pharynx, from which the gill slits opened; and the anterior coelom, which lay beneath the pharynx in the posterior right part of the theca.

The stem of a cornute can be interpreted by comparison with the stem of a crinoid, with which it is probably homologous. It is probably also homologous with the tail of a fish or of a tunicate tadpole. The stem had a fore-, a mid- and a hind-portion (formerly called anterior, medial and posterior), and always ended abruptly, as if a more distal portion had broken away.

Precisely where the breakaway occurred was probably not accidental, however, because the stem often shows special modifications in the region of the observed distal end.

The hind-portion of the stem of cornutes had a series of ventral ossicles roofed over by paired dorsal plates. A groove in the dorsal surface of the ventral ossicles probably contained organs homologous with those down the middle of a crinoid stem, i.e. a tubular, tumid chambered organ and a peduncular nerve. In chordate terms these would be respectively the notochord and the dorsal nerve cord.

The fore-stem had a large lumen which probably contained muscle blocks and would also have contained the anterior part of the notochord or chambered organ, functioning as an anticompressional organ, to prevent telescoping of the fore-stem. The skeleton of the fore-stem consisted of a series of rings of major plates with four plates in each ring, i.e. left and right, dorsal, and left and right, ventral.

The mid-stem contained a large ventral element, the stylocone, resembling two or more hind-stem ossicles fused together and deeply excavated anteriorly. The stylocone probably served as a socket for the insertion of the muscles of the fore-stem, whereby these muscles could move the mid- and hind-stem as a unit.

The cornute brain was probably lodged in a large depression that existed in the skeleton at the front end of the stem, where the latter joined the theca. This brain was probably homologous with the brain of other chordates, and also homologous with the aboral nerve centre or brain of crinoids, whose position is similar.

Primitive cornutes lived on a sandy sea bottom, and seem to be adapted for pulling themselves backwards across it by side-to-side movements of the stem, sticking the end of the stem into the bottom to secure purchase. Spikes on the ventral surface of the theca point anteriorly. They would have damped down yaw and prevented unwanted forward movement.

The mitrates were externally much more symmetrical than primitive cornutes. The first known representatives (*Peltocystis* and *Chinianocarpos*, figure 3) are lowest Ordovician in age, and the last known representative (*Dalejocystis*) is Middle Devonian. The mitrate theca was convex ventrally and flat dorsally. A large mouth was present anteriorly. There were no external gill slits, but there was a right, as well as a left, gill opening and right as well as left gill slits probably existed internally. The dorsal integument was inherited by the most primitive mitrates from the cornutes, but was entirely replaced in most mitrates by a rather rigid dorsal shield. This was made partly of flat ingrowths of the marginal plates and partly of big central plates. Most mitrates retained a flexible ventral integument from the cornutes.

Several chambers can be recognized inside the mitrate theca. Some of these chambers are homologous with those of cornutes, and some additional. The chambers were in close contact with the skeleton. A distinct idea of them can therefore be obtained by examining internal moulds where the skeleton has been dissolved away and the chambers are represented, as if in positive, by rock.

There was thus a buccal cavity at the anterior end of the theca, behind the mouth (figure 8), and a posterior coelom at the posterior end of the theca, just in front of the stem. There were right and left atria anterior to the gill openings. These atria presumably had gill slits opening into them in front. The rest of the theca, as in cornutes, was divided between anterior coelom and pharynx. The situation was more complicated than in cornutes, however, for there is evidence of a left or primary pharynx, an anterior coelom and a right or secondary pharynx (figure 2*f*). The way these three chambers are geometrically related to each other in the adult mitrate allows certain deductions about their order of appearance during the life history. Their observed relations can be explained if, at the earliest ontogenetic stages, only the left pharynx and anterior coelom existed but not the right pharynx. Furthermore, the condition in adult mitrates suggests that, at this very early stage, the left pharynx and anterior coelom would have had the same asymmetrical relationship to each other as in cornutes (figure 2*e*). That is to say the left pharynx would be anterior and to the left and the anterior coelom posterior, to the right, and presumably lying on the floor of the theca. Later in ontogeny the right pharynx pouched out from the left pharynx towards the posterior right corner of the theca. In doing so it distorted the pre-existing line of separation between the primary or left pharynx and the anterior coelom and lifted the anterior coelom up, pushing it against the ceiling of the theca. Consequently the lumen of the anterior coelom was eliminated above the new, right pharynx and the contents of the anterior coelom squashed into a median position against the ceiling of the theca instead of lying on the floor. There is evidence that the anus lay left of the stem in mitrates as in most cornutes. Instead of being external, however, it opened into the left atrium. This arrangement, as mentioned already, persists in modern tunicate tadpoles.

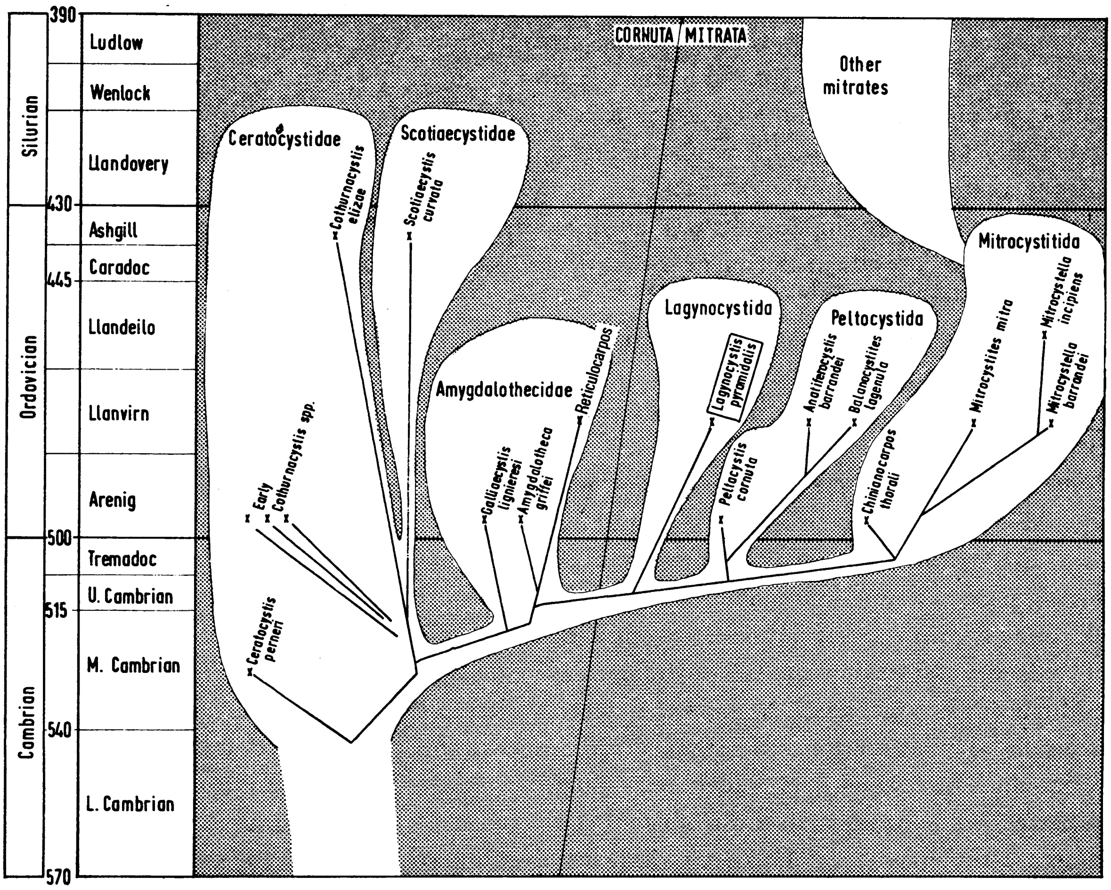

FIGURE 1. Stratigraphical position and probable phylogeny of forms mentioned in text.

The ventral parts of the right and left pharynxes of mitrates can often not easily be separated from each other, and it is then sometimes appropriate to speak of a ventral pharynx, as well as a left and right pharynx. This is essentially a matter of convenience however. The fundamental division of the mitrate pharynx is into two parts – right and left – and not into three.

The calcite of the dorsal shield of mitrates usually fills the asymmetrical gap between the left pharynx and anterior coelom producing a prominent, asymmetrical oblique ridge, running from posterior left to anterior right, on the ventral, inner surface of the shield (or in figure 2*f*). It is the relationships of this oblique ridge, which has been disturbed by the pouching out of the right pharynx, which show that the right pharynx appeared later than the left pharynx in ontogeny.

The stem or tail of mitrates was divided into fore, mid and hind portions like the stem of cornutes, though it now seems unlikely that like-named portions are homologous in cornutes and mitrates. As in cornutes, the mitrate stem always ends abruptly. The hind-stem has dorsal ossicles and paired ventral plates. A groove along the ventral surface of the dorsal ossicles probably contained the chambered organ and peduncular nerve, in echinoderm terms. In chordate terms these would be the notochord and dorsal nerve cord. And in fact there is evidence in some mitrates for the existence in the soft structures filling the groove of a flattish structure, presumably the dorsal nerve cord, overlying a cylindrical structure, presumably the notochord. The presumed dorsal nerve cord was connected in each segment with what look like ganglia (figures 32, 33, plate 39).

The fore-stem, as in cornutes, had a large lumen. The fore-stem was presumably activated by muscle blocks and would have needed an anticompressional notochord inside it to prevent telescoping. This would have been a forward continuation of the notochord that seems to have existed in the hind-stem.

The mid-stem of mitrates contained a large dorsal element, the styloid, which resembles two dorsal hind-stem ossicles fused together and excavated anteriorly. The styloid probably served as a socket for the insertion of the muscles of the fore-stem, whereby these muscles could move the hind-stem as a unit. It was similar in function, and somewhat similar in shape, to the ventral stylocone of cornutes, but not homologous with it.

The brain and cranial nerves of mitrates are extremely complex (figure 14). They can be reconstructed in some detail because they were buried in the skeleton to a considerable extent. The brain lay just anterior to the stem, as it did in cornutes, and as the aboral nerve centre does in crinoids. The cranial nerves included olfactory, optic, trigeminal, auditory and lateral line complexes, homologous with those of fishes. The reasons for thinking that the cranial nerves of mitrates were nerves, are: (1) They radiate out from the region where the stem joins the theca, like the aboral nerves of crinoids. (2) They vary in cross-section, as a nerve can, from flat to circular in the same canal. (3) They often end at the surface of the theca like sensory nerves, or at structures, such as the mouth, which would need a strong nerve supply.

As concerns habits, many mitrates have transverse ribs with a characteristic cross-section, steeper anteriorly than posteriorly. Such ribs resemble those used by bivalve molluscs for gripping the sediment when crawling. They would have helped the mitrate to move backward and hindered it from moving forward. Usually these ribs are restricted to the ventral or ventrolateral parts of the thecal surface and forms with the ribbing confined in this way presumably sank down with their convex bellies in the sea bottom, leaving only their backs exposed. The distribution of sediment-gripping ribs in these forms confirms that the ventral surface was indeed ventral. Other mitrates, however, have asymmetric ribs on both the back and the belly and these forms were probably burrowers, at least occasionally. All mitrates probably crawled backwards by ventral flexion of the stem (see §5).

It is now necessary to summarize at length some recent work which indicates how mitrates

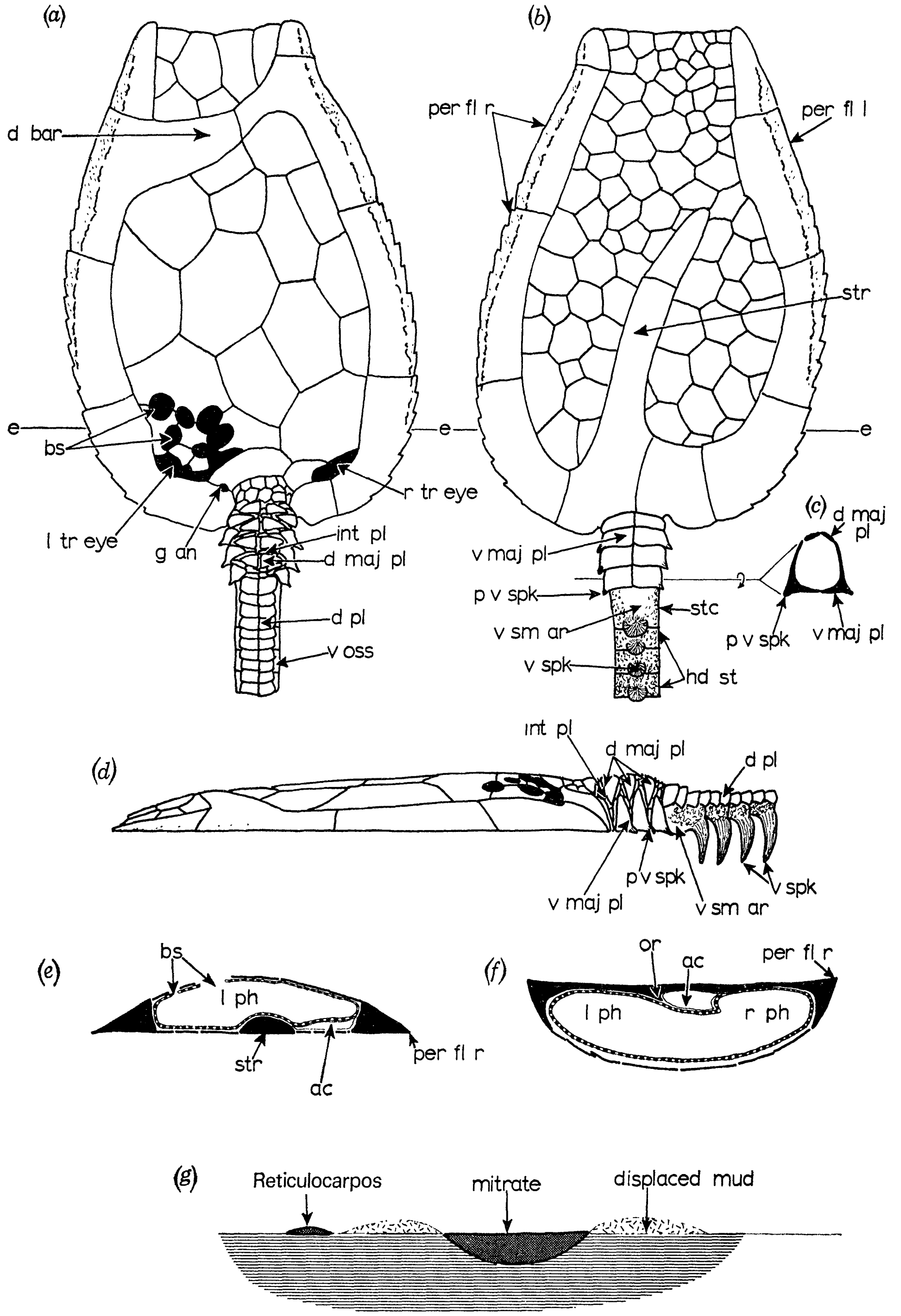

Figure 2. The Amygdalothecid cornute *Reticulocarpos*, closely related to the origin of the mitrates, Šárka Formation (Llanvirn) of Šárka near Prague, Czechoslovakia (Jefferies & Prokop 1972). (*a*) Dorsal aspect; note the dorsal bar, branchial slits confined to the posterior left part of the dorsal integument as in other cornutes, the transpharyngeal eyes, the gonopore-anus, and the presence of intercalary as well as major plates in the fore stem. (*b*) Ventral aspect; note the incomplete strut, the peripheral flanges, the postero-ventral spikes on the ventral major plates of the fore-stem and the ventral smooth area on the stylocone of the mid-stem. (*c*), Silhouette of the most distal ring of major plates in the fore-stem. (*d*), Left lateral aspect; note ventral spikes on the mid- and hind-stem. (*e*), Transverse section of *Reticulocarpos* through the line *e–e* in figures *a*, *b*. The left pharynx fills most of the thecal cavity and overlies the anterior coelom which is restricted to the right side of the theca, lying on the floor. (*f*), Transverse section through a typical mitrate (*Mitrocystella*). The condition of the chambers of such a mitrate can be derived from that of *Reticulocarpos* if the right pharynx sprouted out from the left pharynx underneath the anterior coelom, so lifting the anterior coelom up, pushing it against the ceiling of the theca, and displacing it in a median direction. (*g*) How *Reticulocarpos* and a mitrate would have supported themselves on soft mud. Mitrates sank into the mud and compensated their weight by displacing a certain weight of mud. *Reticulocarpos* relied entirely on the very weak strength of the mud. Consequently *Reticulocarpus* had a convex back and a flat belly, whereas mitrates had a convex belly and a flat back.

arose from cornutes (Jefferies & Prokop 1972). This work throws light on the primitive characters of mitrates and is relevant to the interpretation of *Lagynocystis*. It suggests that the mitrates had their origin in the cornute family Amygdalothecidae Ubaghs 1970. This family contains three genera namely *Amygdalotheca* Ubaghs, *Galliaecystis* Ubaghs and *Reticulocarpos* Jefferies & Prokop. The latter genus is represented by only one species – *Reticulocarpos hanusi* Jefferies & Prokop 1972 – which comes from the Lower Ordovician of Bohemia, from the same horizon and locality as *Lagynocystis pyramidalis*, i.e. the Šárka Beds of Šárka. Of the three genera, *Reticulocarpos* is probably the most closely related to the latest common ancestor of the mitrates.

Reticulocarpos (figures 2, 3) has many features which distinguish it from a fairly primitive cornute such as *Cothurnocystis*. These can be listed as follows:

(1) The theca is almost bilaterally symmetrical in outline, smoothly convex dorsally and flat ventrally (figure 2*e*).

(2) The marginal plates are without ventral spikes and are prolonged into peripheral flanges (per fl r and l in figures 2*a*, *b*, *e*).

(3) The strut does not extend the whole distance across the ventral integument but stops short anteriorly (str in figure 2*b*).

(4) The marginal plates are carious and the integument plates reticulate, in a way which would reduce the weight of the skeleton to a minimum.

(5) The theca is small, about 1 cm long, as opposed to 2 or 3 cm in most cornutes.

(6) There is no ventral mouth frame of marginal plates behind the mouth (figure 2*b*).

(7) Instead there is a dorsal bar (d bar in figure 2*a*) which replaces the ventral mouth frame mechanically and divides the dorsal integument into two parts. Comparison with the homologous dorsal bar of the boot-shaped, primitive Amygdalothecid *Galliaecystis* suggests that this dorsal bar lay just posterior to the buccal cavity.

(8) The skeleton of the gill slits has been lost so that these slits, situated in the usual position in the left posterior portion of the dorsal integument, are retained merely as circular holes between the integument plates (bs in figure 2*a*).

(9) Excavations inside the posterior marginal plates probably carried transpharyngeal eyes like those of the mitrates *Chinianocarpos* and *Mitrocystites* (l tr eye, r tr eye in figures 2 and 4).

(10) The hind-stem, which ends abruptly as in all calcichordates, retains between one and four ventral ossicles (hd st in figures 2*a*, *b*, *d*), whereas all other known cornutes have more than 10, and some of them have more than 50. These ventral ossicles, and the stylocone of the mid-stem of *Reticulocarpos*, carry big, hollow, curved spikes postero-ventrally (v spk in figures 2*b*, *d*).

(11) Between major plates like those of other cornutes the fore-stem has intercalary plates inserted (int pl in figure 2*a*, *d*). The ventral major plates (v maj pl) have a flat ventral surface ending in posteroventral spikes (p v spk) at right and left.

(12) On the ventral surface of the stylocone there is a ventral smooth area (v sm ar in figure 2*b*, *d*) which could have slid inside the fore-stem, in such a way as to flex the stem downwards. The direction of curvature of the ventral spikes on the stem confirms that this was the preferred direction of flexion. More primitive cornutes by contrast, probably flexed the stem sideways.

A change in mode of life will explain many of these differences between *Reticulocarpos* and more primitive cornutes. Thus primitive cornutes lived on a sandy sea bottom. The Amygdalothecids, on the other hand, lived on mud, and *Reticulocarpos* seems to be adapted for life on very soft mud indeed. Like more primitive cornutes, however, it stayed up on the sea bottom by relying on the strength of the bottom material. But on soft mud this was a very precarious method of support, that brought many extreme adaptations with it. Thus the weight imposed on the mud was reduced to a minimum by small size, by the carious nature of the skeleton and reducing the length of the stem. The weight that remained was spread over as large an area as possible by the flat ventral surface of the theca and the peripheral flange round its edge. It can be calculated that the load imposed on the bottom was only about 10 mg cm^{-2}. The ventral spikes on the theca of other cornutes, which served to present yaw during movement, would be ineffectual on soft mud, and would also tend to disturb and weaken it, so increasing the risk of self-burial. These spikes were therefore lost and *Reticulocarpos* was adapted instead to *avoid* yaw. To this end it had acquired bilateral symmetry and flexed the stem vertically downwards, when crawling backwards, instead of right and left horizontally. The spikes in the ventral surface of the mid- and hind-stem, and on each side of the ventral surface of the fore-stem, would help to grip the extremely slippery mud, like the spikes on a running shoe. The broad ventral surface of the ventral plates of the fore-stem was well adapted to push downwards and forwards against the mud when the stem flexed ventrally. Together with the ventral surface of the hind-stem, it would have acted as the bearing surface used by the animal to push against the mud when crawling. The acquisition of bilateral symmetry made the frame of marginal plates stronger, and the ventral strut lost its original function, which was to prevent the collapse, under tension from the muscular integuments, of a boot-shaped frame with a large, weak anterior re-entrant. The strut consequently became incomplete.

Reticulocarpos resembles mitrates in many of the features which distinguish it from more primitive cornutes. These features can be listed as follows:

(1) The bilaterally symmetrical theca.

(2) The dorsal bar, which is homologous with the front of the dorsal shield of mitrates (cf. *Peltocystis* in figure 3).

(3) The absence of the ventral mouth frame.

(4) The peripheral flange round the marginals, though this is ventro-lateral in position, rather than dorso-lateral as it is in mitrates (cf. figure 2*e*, *f*).

(5) Evidence that the stem acted by ventral flexion, like the stem of mitrates, rather than by horizontal flexion as in more primitive cornutes.

(6) The incompleteness of the strut, which in mitrates is absent.

(7) The small size of the theca, comparable with that of the primitive and early mitrates *Chinianocarpos* and *Peltocystis*.

(8) The presence of transpharyngeal eyes.

(9) The shortness of the hind-stem. (The cornute hind-stem was absent in mitrates, as discussed below.)

These specializations shared with mitrates are enough to indicate that the new cornute is closely related to the original mitrate. It is noteworthy that most mitrates, like *Reticulocarpos*, lived on a mud sea bottom.

The stem of *Reticulocarpos* consisted mechanically of two parts. A more proximal portion, i.e. the fore-stem, was highly flexible and its skeleton consisted of both major and intercalary plates. A more distal portion, i.e. the mid- and hind-stem, was rigid and its skeleton consisted of stylocone, ventral ossicles and paired dorsal plates without intercalaries. The stems of mitrates, on the other hand, were flexible throughout their length. That is to say the mitrate fore-stem was probably flexible in all planes, while the mitrate mid- and hind-stem was strongly flexible ventrally in a vertical plane. Furthermore, in *Chinianocarpos*, which in most ways is the most primitive mitrate known, intercalary as well as major plates can be found throughout the length of the stem, i.e. in the mid- and hind-stem as well as in the fore-stem. It is therefore likely that the fore-, mid- and hind-stem of mitrates correspond only to the flexible fore-stem of cornutes. This would mean that the mid- and hind-stem of cornutes was lost in the early

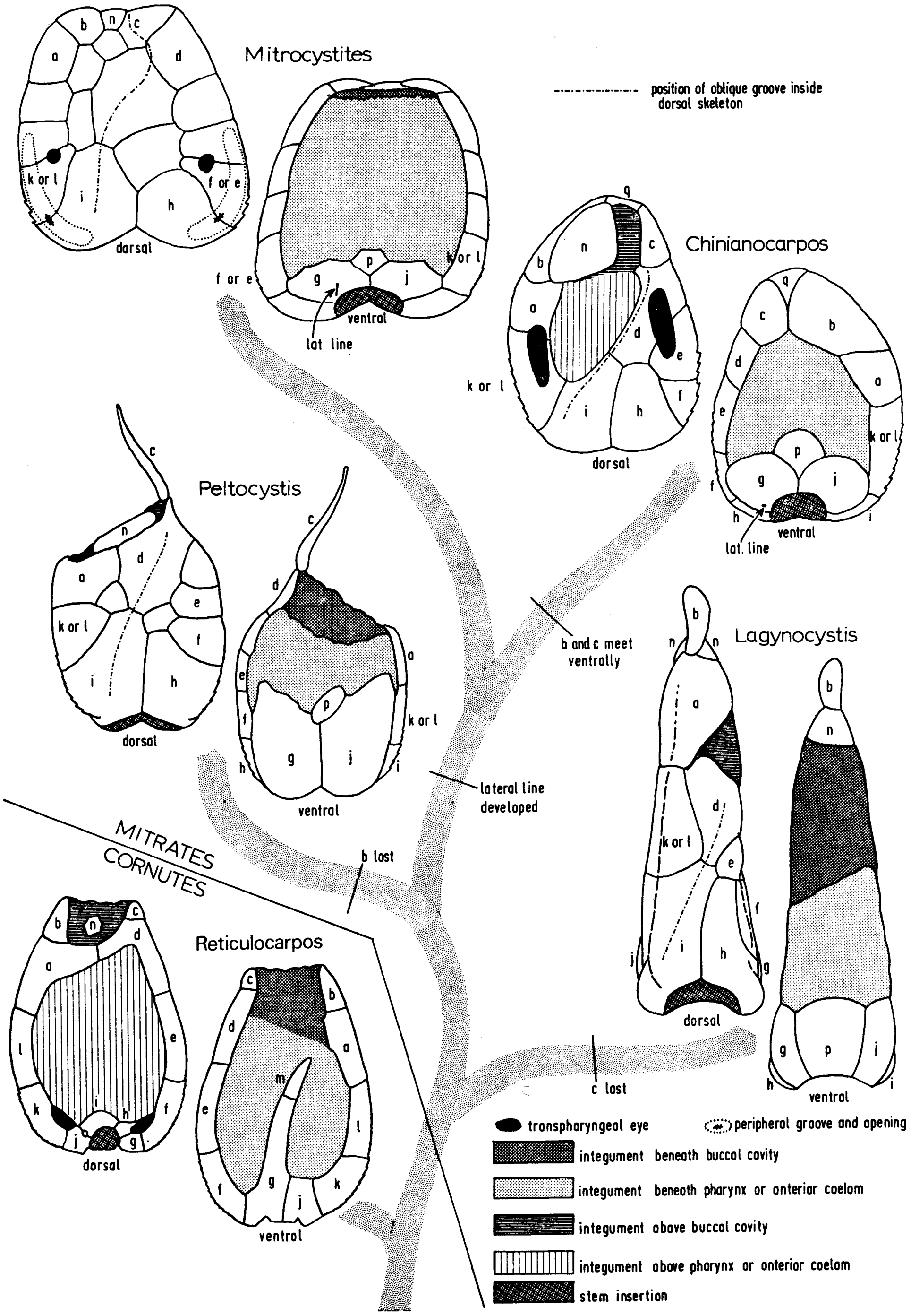

FIGURE 3. Homologies of plates and integuments in some mitrates and *Reticulocarpos*.

evolution of mitrates and the new fore-, mid- and hind-stems elaborated from the remaining flexible stump. It is therefore no surprise that the hind-stem ossicles and styloid of mitrates are dorsal, whereas the massive elements of the cornute mid- and hind-stem were ventral, for the respective parts of the stem are not homologous in cornutes and mitrates. It follows that the shortness of the hind-stem of *Reticulocarpos*, with between one and four ossicles, also represents a mitrate-like feature, as listed above. The paired ventral plates of the mid- and hind-stem of mitrates are probably serially homologous with the major ventral plates of the mitrate fore-stem, and specialized from the major ventral plates of the distal parts of the unregionated stump-stem of the primitive mitrate. As shown below (see §§4*c* and 5), this is important in interpreting the stem of *Lagynocystis*.

The thecal plates of *Reticulocarpos*, especially the marginal plates, can be homologized with those of mitrates (figure 3), as well as with those of other cornutes (Jefferies & Prokop 1972). For this purpose, plates that can be homologized have been given lower-case letters, arranged as near as possible clockwise when *Reticulocarpos* is seen from above. Plates with the same letter in figure 3 are probably homologous in all the forms indicated.

Many features obviously separate *Reticulocarpos* from all mitrates. These can be listed as follows:

(1) *Reticulocarpos* has gill slits opening externally and restricted to the left side. All mitrates, on the other hand, have hypothetical gill slits, opening on right and left sides into right and left atria. By implication, the right pharynx will also have been absent from the new cornute.

(2) *Reticulocarpos* is convex dorsally and flat ventrally, whereas mitrates, according to the interpretation here adopted, are convex ventrally and flat dorsally.

(3) *Reticulocarpos* has no dorsal shield. It must be remembered, however, that unlike most mitrates, the dorsal shield is incomplete in the primitive mitrate *Chinianocarpos* (figure 3).

(4) *Reticulocarpos* has a strut, though an incomplete one.

(5) *Reticulocarpos* retains the cornute mid-stem and a short hind-stem, whereas the first mitrates had probably lost them.

Most of the differences between mitrates and *Reticulocarpos* probably resulted from an improvement in the way the animal supported itself on soft mud (figure 2*g*). The convex belly of a mitrate would sink into soft mud, expelling it sideways. Under these conditions, the load imposed by the mitrate on the sea bottom would equal the weight in sea water of the mitrate, less the weight in sea water of the displaced mud. The animal therefore compensated its weight, staying up by a method resembling buoyancy. This was fundamentally more reliable than the method of support used by *Reticulocarpos*, since soft mud can easily loose strength by stirring, but cannot so easily change in density. It explains why the mitrates were convex ventrally and flat dorsally rather than the opposite.

Using the new method of support, it was no longer necessary to have a very light skeleton and it became possible to elongate the stem. Indeed this became necessary, because the theca now had to plough through the top layer of mud when the animal crawled, instead of sliding over its surface. The final loss of the old mid- and hind-stem probably resulted because, if these portions of the stem flexed beyond the vertical, they would pull the animal down into the sea bottom (see §5). The regionation of the remaining stump into new fore-, mid- and hind-stems was a direct adaptation to better crawling. Sheltering the gill slits inside atria prevented them being clogged with the mud stirred up by crawling, for the gill slits, near the posterior leading edge of the theca and level or nearly so with the sea floor, would otherwise be in a very vulnerable position.

The appearance of gill slits on the right as well as the left, which must have been a sudden event and can be taken as marking the true beginning of the mitrates, was probably not connected with the improved method of staying up on mud. It was, instead, an adaptation to make the flow of water through the pharynx more symmetrical.

An alternative interpretation of the homologies between mitrates and *Reticulocarpos* is also possible, in many ways opposite to the one adopted here. According to this alternative interpretation the flat, ventral surface of mitrates, which I consider dorsal, would be homologous to the flat surface of *Reticulocarpos*, which I consider ventral. Consequently the strut would be homologous to the oblique ridge; the ossicles of the hind-stem would be homologous in both mitrates and cornutes; the spikes on the stem ossicles of *Reticulocarpos* would be homologous with the blades on the stem ossicles of mitrates; the stylocone of cornutes would be homologous to the styloid of mitrates; and the paired plates of the mid- and hind-stem would also be homologous in cornutes and mitrates.

The arguments against this alternative interpretation rest on the basic asymmetries of the chambers inside the cornute and mitrate thecas, with the primary pharynx anterior to and left of the anterior coelom. This basic arrangement is still discernible in mitrates, though greatly modified by the appearance for the first time of the right pharynx, which lifted the anterior coelom up from the floor of the theca, squashed it against the ceiling and pushed it in a median direction. The oblique ridge of mitrates, as already said, has the appearance of an intercameral feature, formed by calcite filling the space between two chambers, i.e. the anterior coelom and the left pharynx. The strut of cornutes, its supposed equivalent, does not look like an intercameral feature, but merely resembles a strut. The fact that *Reticulocarpos* had evolved a dorsal bar, which can readily be homologized with the front of the dorsal shield in the primitive mitrate *Peltocystis*, being made of the same plates (*a* and *d* in figure 3) with the same asymmetry (more posterior on the left) and the same relations with the buccal cavity, strongly favours the interpretation developed here. The fact that asymmetrical, sediment-gripping ribs, when restricted to only one face of the mitrate theca are restricted to the ventral and ventro-lateral face, confirms the orientation here advocated.

It is now possible to reconstruct a primitive mitrate such as could have been the latest common ancestor of the mitrates *Peltocystis*, *Lagynocystis* and *Chinianocarpos*, bearing the features of *Reticulocarpos* in mind (see figure 4). Such a reconstruction makes for clarity of thought and is not overhypothetical, since much relevant information now exists. This primitive mitrate can be supposed to have possessed the features which these three mitrates share with the cornute *Reticulocarpos*, and also to have possessed those common features of the three mitrates which *Reticulocarpos* did not have (shared mitrate specializations). But if some feature is present in only one or two of the three descendant mitrates but also present in *Reticulocarpos*, then this feature is probably a primitive feature of the mitrate concerned, and would have existed in the latest common ancestor of the three descendant mitrates. In what follows I shall signify that a feature is present in *Reticulocarpos* by *R* (italicized to show it has a distinctive phyletic position to the others), in *Lagynocystis* by L, in *Chinianocarpos* by C and in *Peltocystis* by P.

The theca of the hypothetical primitive mitrate would have been about 1 cm long (*R*, C, P, not L, but the theca of L is exceptionally elongate rather than large). It would have had peripheral flanges (*R*, L, C, P) and these would have been dorso-lateral rather than ventro-lateral in position (L, C, P, not *R*) and symmetrical on right and left (*R*, C, P, not L). The theca would have been broad rather than elongate in outline (*R*, C, P, not L). It would have been convex ventrally and flat dorsally (L, C, P, not *R*), with no strut (L, C, P, not *R*). The lower lip would have been flexible (*R*, L, P, not C) and the ventral integument flexible (*R*, L, C, P). Most of the marginal plates of the theca of *Reticulocarpos* would have been present (figure 3); plate m would have been absent however (L, C, P, not *R*), and either k or l would have disappeared (L, C, P, not *R*). In particular, plate b would have existed (*R*, L, C, not P) and also plate c (*R*, P, C, not L). Plates b and c would have been free from each other, not meeting ventral to the mouth (*R*, P, L, and also *Mitrocystites*, not C). One of the plates (n) of the dorsal buccal integument would have grown in size to cover most of the upper lip (L, C, P, not *R*), but some upper lip integument would have remained (*R*, P, C, not L). The dorsal integument would have been diminished by the growth of the dorsal shield (L, C, P, not *R*), but integument would still persist over the left pharynx (*R*, C, not L or P). There would have been a dorsal bar posterior to the buccal cavity, dividing the dorsal integument into two parts and disposed asymmetrically, more posterior to left than to right (*R*, P, not C or L) – this assumes that the dorsal bar has been lost secondarily in *Chinianocarpos*. Inside the theca, the right pharynx would have existed (L, C, P, not *R*). There would have been right and left gill slits and right and left gill openings and atria (L, C, P, not *R*). It is important to note that there would have been no median atrium (*R*, C, P, not L), and the posterior coelom would have extended from the floor to the ceiling of the theca (*R*, C, P, not L). The buccal cavity would have extended farther back on the left than the right (*R*, P, C, not L). Transpharyngeal eyes would have been present (*R*, C, not L or P). In the stem, the cornute mid- and hind-stem would have been lost (L, C, P, not *R*). Regionation of the old fore-stem into new fore-, mid- and hind-stem would have begun and the dorsal ossicles and styloid would already exist (L, C, P, not *R*). The ventral plates of the new hind-stem, as in *Reticulocarpos*, would have retained ventral bearing surfaces with postero-ventral spikes (*R*, L, not C or P). Intercalary plates would be present between the major plates throughout the length of the stem (*R*, C, not L or P). This reconstructed hypothetical form

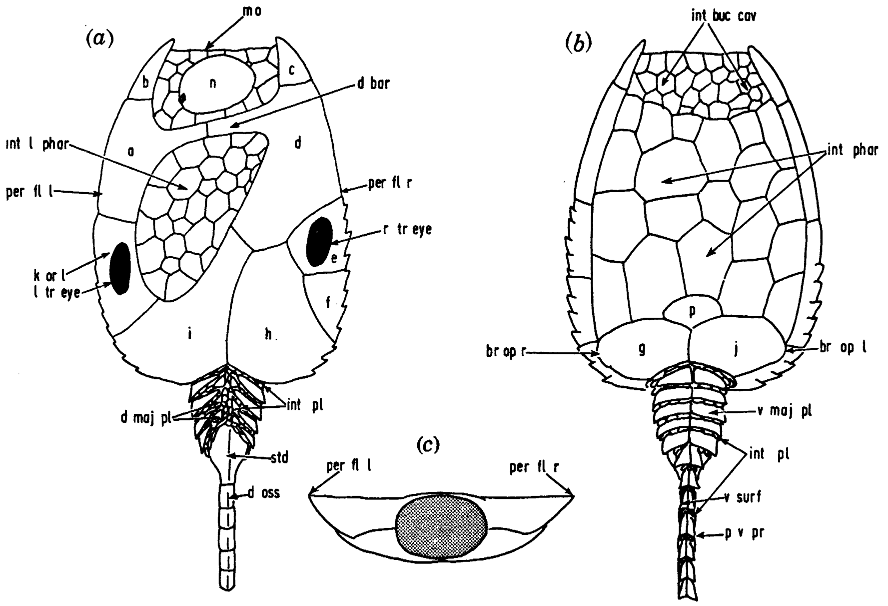

FIGURE 4. A hypothetical primitive mitrate, being the recontructed latest common ancestor of *Chinianocarpos*, *Peltocystis* and *Lagynocystis*. It probably also represents the latest common ancestor of vertebrates and amphioxus.

does not greatly differ from *Chinianocarpos* but is less specialized round the mouth and has ventral bearing surfaces on the hind-stem.

From this hypothetical form *Chinianocarpos* would evolve by making the anterior marginal plates (a + b) meet under the mouth and loss of the dorsal bar behind the buccal cavity. *Peltocystis* would evolve by loss of the left anterior marginal plate (b), development of the right anterior marginal plate (c) into a right oral appendage and the elimination of the dorsal integument over the left pharynx. *Lagynocystis* would evolve by elongation of the theca, great loss of symmetry, the loss of the right anterior marginal plate (c), the development of the left anterior marginal plate (b) into the anterior appendage, and, most importantly, the development of a median ventral atrium, additional to right and left atria already present. The evolution of the median atrium produced other important changes, mainly in the thecal chambers and the nervous system.

Knowledge of the primitive mitrate condition is thus extremely useful in interpreting the subsequent evolution of mitrates.

Lagynocystis pyramidalis was first described and figured by Barrande (1887, p. 94, pl. 5, case III, figures 1 to 8) under the name *Anomalocystites pyramidalis*. Jaekel (1918, p. 122) proposed the genus *Lagynocystis* to include only the species *L. pyramidalis*. He included it, along with *Balanocystites* Barrande and, with some doubt, *Ateleocystites* Billings in his new family Lagynocystidae. Chauvel (1941, p. 200 ff.) added a number of morphological details concerning *L. pyramidalis* and noticed the presence of structures, 'crêtes aborales', which are here interpreted as calcitized gill bars in the wall of the median ventral atrium. Caster (1952) set up the suborder Lagynocystida to include Jaekel's Lagynocystidae less *Ateleocystites* Billings. He divided the Lagynocystidae into the Lagynocystinae, including *Lagynocystis* only, and the Kirkocystinae to include *Kirkocystis* Bassler 1950 (= *Anatiferocystis* Chauvel 1941) and *Balanocystites*. Ubaghs (1968) described *Lagynocystis pyramidalis* in much more detail than previously. He noticed a number of important anatomical facts and described the calcitized gill bars (ctenoid organ) in greater detail than Chauvel. Ubaghs interpreted *Lagynocystis* in the same way as he interpreted other cornutes and mitrates, and quite differently to the way they are interpreted here. Thus what I call the stem was for him an arm. Accordingly, the stem for Ubaghs was anterior, instead of posterior. Ubaghs and I also disagree on most other points of interpretation, including which is the upper and which the lower side of the theca. Interestingly, however, Ubaghs suspected that the calcitized gill bars may indeed have been branchial (1968, p. 541). Ubaghs followed Caster in placing the Lagynocystidae in the suborder Lagynocystida, together with the families Peltocystidae and Kirkocystidae.

There is no evidence to suggest a specially close relationship between *Lagynocystis*, on the one hand, and Kirkocystidae plus Peltocystidae on the other. The features common to all three families are either adaptations to a life on very soft mud or are derived from a primitive mitrate. As against this, the Peltocystidae and Kirkocystidae are probably closely related to each other. Both have a single homologous oral appendage right of the mouth (plate c) which is probably not homologous with the anterior appendage of *Lagynocystis*, left of the mouth (plate b). I therefore place Peltocystidae plus Kirkocystidae together in a new suborder Peltocystida of the Mitrata. The suborder Lagynocystida therefore contains only the family Lagynocystidae with one genus *Lagynocystis* and one species *L. pyramidalis*.

I have reconstructed *L. pyramidalis* from natural moulds and rubber casts. As with my previous work, several projections were drawn simultaneously on a drawing board. The outside was reconstructed first, followed by reconstructions of the internal cast of the theca, of the brain and nervous system and of parts of the stem.

Throughout this paper I use 'amphioxus' as the English name for the animal correctly called *Branchiostoma* (cf. Barrington 1965, p. 109).

2. TERMINOLOGY

The terminology applied here to *Lagynocystis* is similar to that used for other calcichordates in my previous papers. I give a guide here, to make the description easier to follow.

(*a*) *External features* (*figure* 5)

(i) *Notation of marginal plates* (*figures* 2, 5)

Two notations are used, one objective and the other comparative and implying homology. In the objective notation: M = marginal plate, suffixes $_1$ to $_4$ indicate position in sequence counting forward from the stem, suffix $_L$ indicates left, $_R$ right, $_D$ dorsal, $_V$ ventral, $_P$ posterior, and $_A$ anterior. There is an anterior appendage (ant ap). Sutures are indicated by a solidus (/). Thus M_{1LD}/M_{1RD} is the suture between plates M_{1LD} and M_{1RD}. In the comparative notation the plates take lower case letters. Letters a to l imply homology with marginal plates in the cornute *Reticulocarpos* and also with other mitrates. Letters n, p, imply homology with other mitrates (figure 5).

(ii) *Mechanical units among marginal plates* (*figure* 5*g*, *h*)

The marginal plates of *Lagynocystis* can be divided mechanically into three rigid groups, with articulations between the groups (figure 5*g*, *h*). Thus there are the anterior group (ant gr), the postero-dorsal group (post dors gr), and the postero-ventral group (post ven gr). Articulations are (art) and axis of articulation is (ax art).

(iii) *Flanges* (*figure* 5)

On the marginal plates there are left and right peripheral flanges (per fl l and r), left and right postero-dorsal flanges (post d fl l and r) and left and right postero-ventral flanges (post v fl l and r).

(iv) *Integument plates and oral plates* (*figure* 5)

Integument plates belong to the integument of the pharynx (int phar), or the ventral or dorsal integument of the buccal cavity (int buc cav v, int buc cav d). Some of the plates of the buccal cavity have bosses in the middle (bos). Oral plates (or pl) form the lower lip. One, the 'keystone plate' (kst pl), is different to the others.

(v) *Thecal openings* (*figure* 5)

Openings in the theca are the mouth (mo), anterior to the oral plates, the left and right branchial openings (br op l and r) and the opening of the median atrium (med atr op). The groove for the left nerve to the buccal cavity (n_{BCL}) is externally visible.

(vi) *External features of stem* (*figure* 5)

The terms fore-, mid- and hind-stem (proposed in Jefferies & Prokop (1972)) replace anterior, medial and posterior stem as used in Jefferies (1967, 1968*a*, 1969). The new terms do not imply that fore-, mid- and hind-stems are homologous in cornutes and mitrates. The fore-stem has major plates (maj pl), intercalary plates (int pl) and spikes (spk). The mid-stem carries the styloid (std). The hind-stem has dorsal ossicles in series (d oss 1, 20, etc.) and ventral plates (v pl) with external ventral surfaces (v surf) and postero-ventral processes (p v pr).

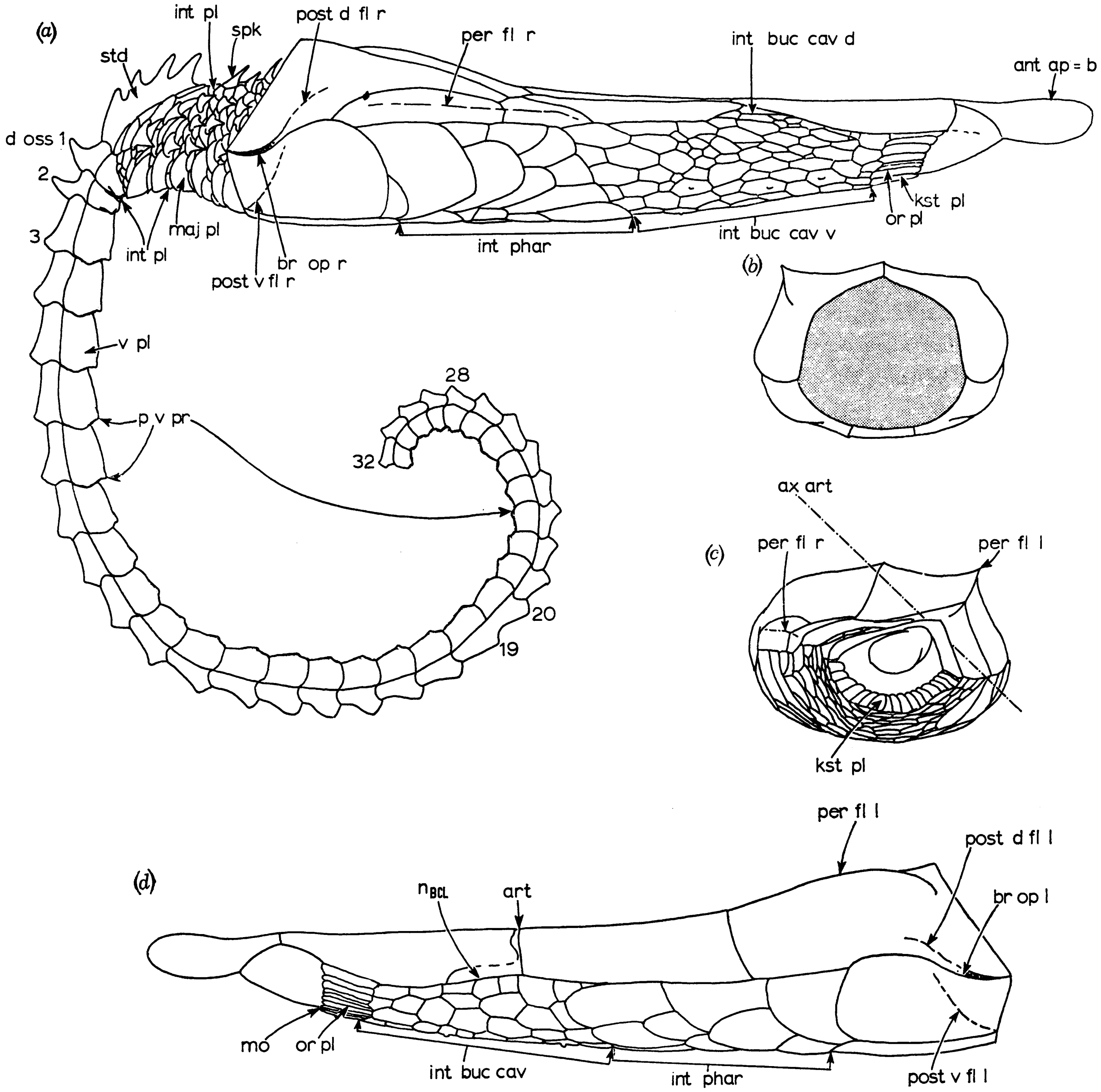

FIGURE 5. Reconstruction of the external features of *Lagynocystis pyramidalis*. (*a*) Right lateral aspect. (*b*) Posterior aspect of theca. (*c*) Anterior aspect of theca. (*d*) Left lateral aspect. (*e*) Ventral aspect. (*f*), Dorsal aspect. (*g*, *h*) Functional groupings of marginal plates and divisions of integument (shaded) and postulated direction of rotation during swimming (*h*).

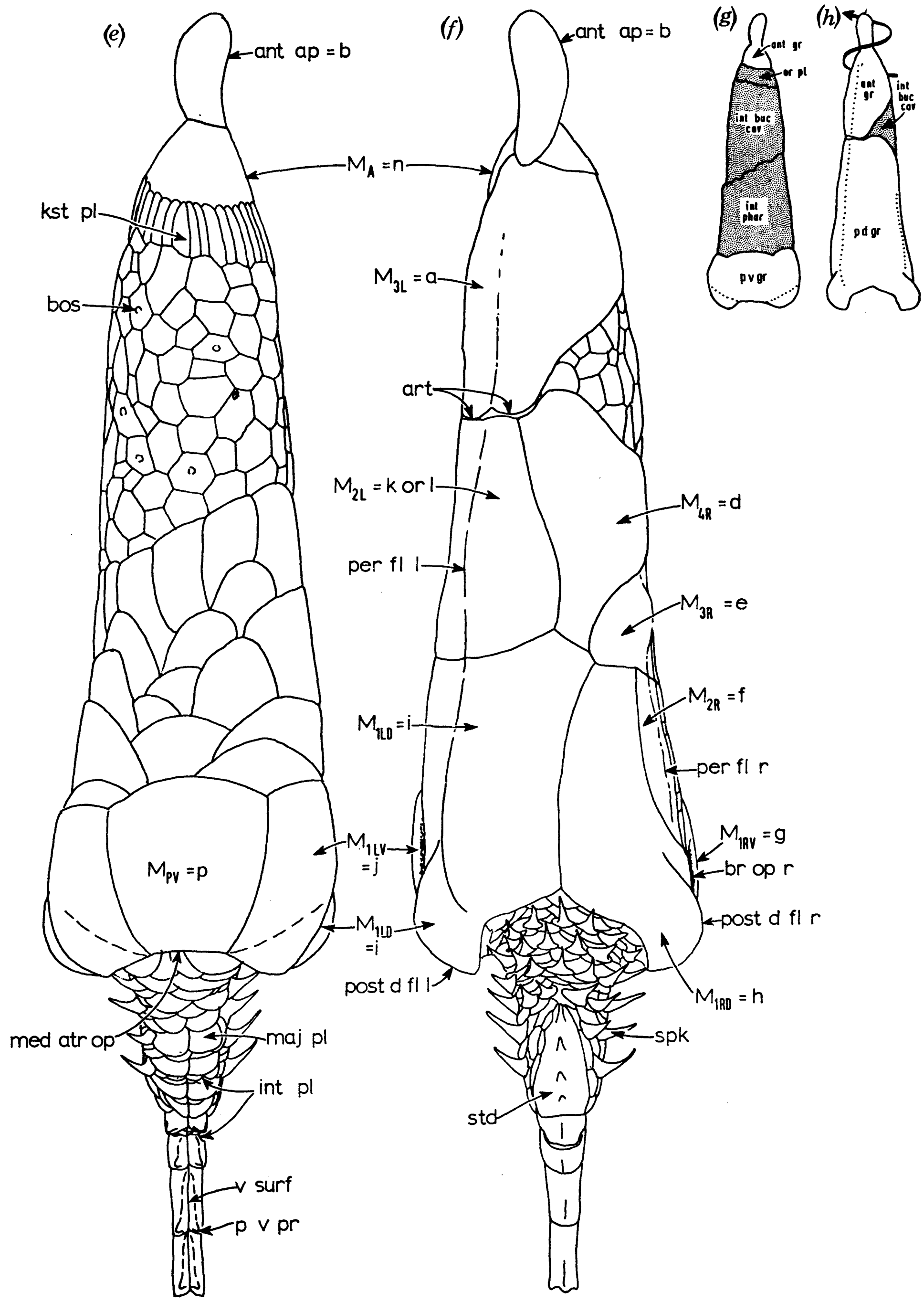

FIGURE 5*e–h*. For description see opposite.

(*b*) *Internal features*

(i) *Chambers of the theca* (*figures* 6, 7, 9)

These are: the buccal cavity (b cav or bc), the anterior coelom (ant c or ac) the left pharynx (l ph), the ventral pharynx (v ph) which is recognized as a matter of convenience, because right and left pharynxes cannot readily be separated in the ventral part of the theca, the right pharynx (r ph), the posterior coelom (pc), the right atrium (r atr or ra), the median atrium (m atr or ma) and the left atrium (la), which is deduced to have existed by comparison with other mitrates. Well-preserved branchial slits of the median atrium (bs med at in figure 7) penetrated the front wall of the median atrium (see also figure 6). The rectum (rect or r) opened directly at the left branchial opening.

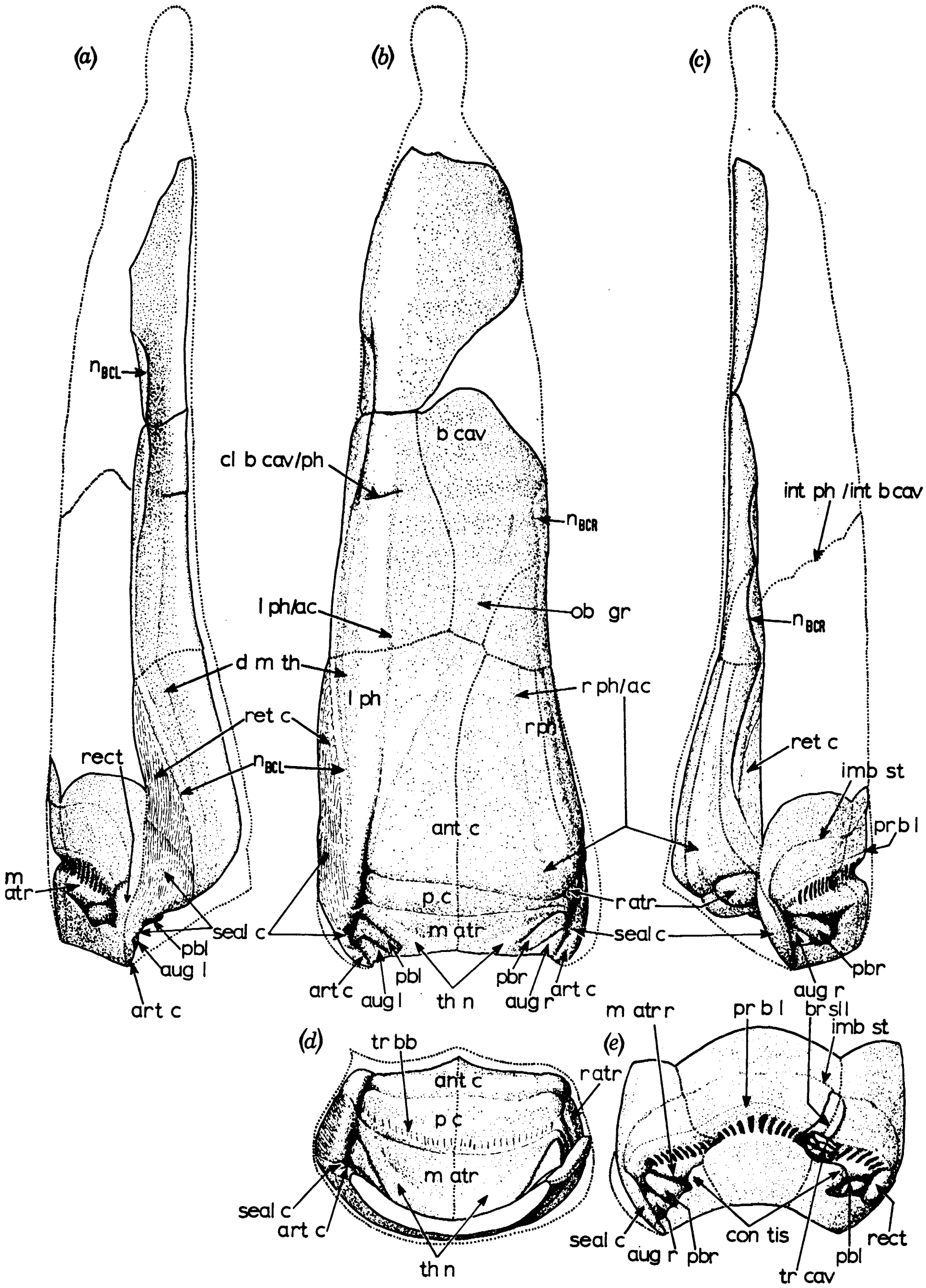

FIGURE 6. Reconstruction of the internal mould of *Lagynocystis pyramidalis*, based on observations from many specimens. Growth lines of plates and the growth tracks of plate corners have been omitted. (*a*) Left. (*b*) Dorsal. (*c*) Right. (*d*) Posterior. (*e*) Ventral aspect of posterior part of theca.

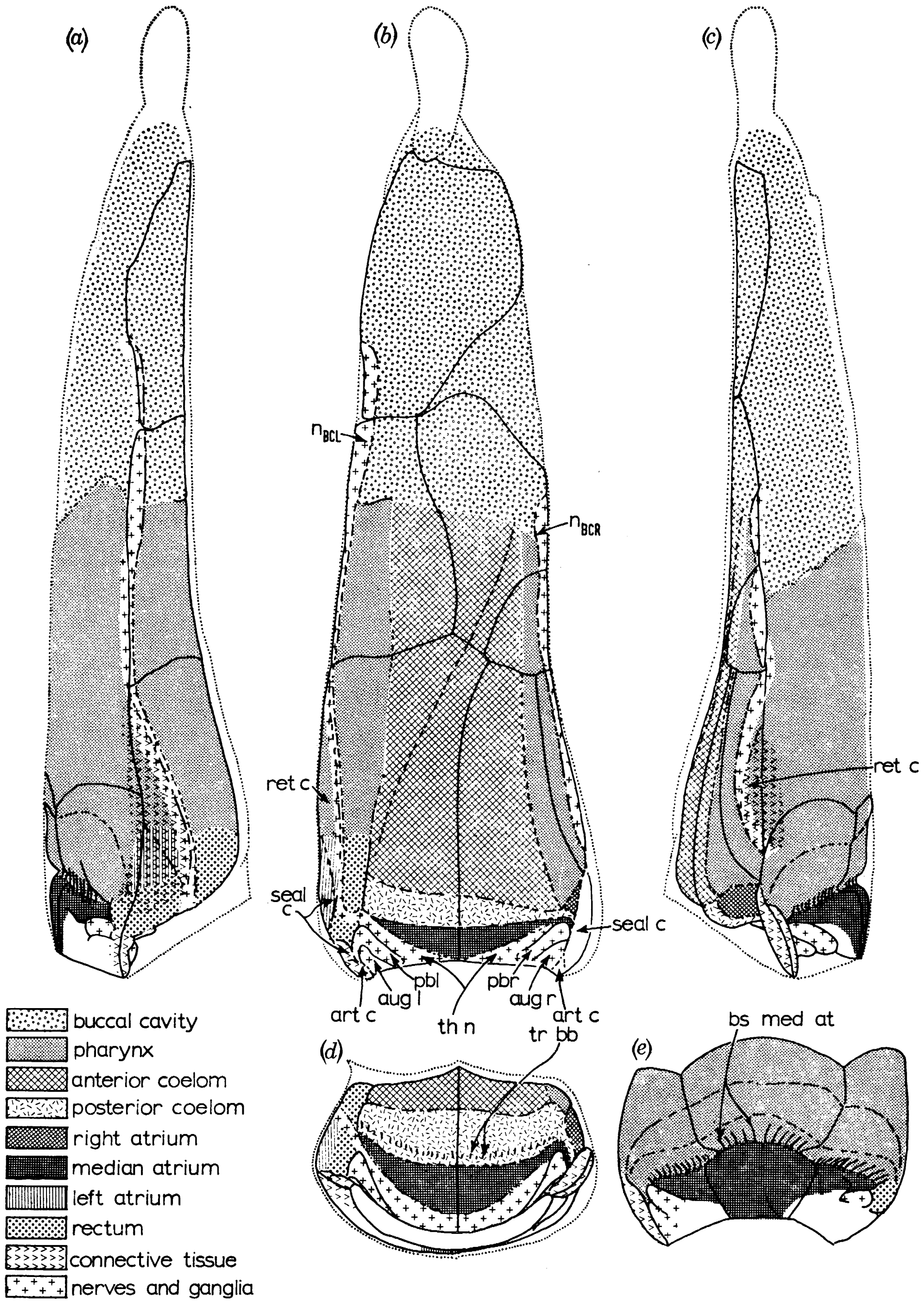

Figure 7. Internal chambers of the theca: an interpretation of the reconstructed internal mould.

(ii) *Junctions between chambers*

These are indicated on the diagrams by a solidus (/). Thus l ph/ac and r ph/ac are the junctions of the left and right pharynxes with the anterior coelom; cl b cav/ph is a cleft between buccal cavity and pharynx; int ph/int b cav is the junction between integument beneath the pharynx and integument beneath the buccal cavity.

(iii) *Oblique groove and oblique ridge*

The oblique groove (ob gr) on the dorsal surface of the internal mould, or of the soft parts, has more complicated relations with the chambers than in other mitrates. The oblique ridge (or) is the ridge on the skeleton that filled the oblique groove.

(iv) *Structures near left and right branchial openings*

Structures to do with the left and right branchial articulations consisted of retaining connective tissue (ret c) holding the dorsal and ventral skeleton together in front of the branchial openings, sealing connective tissue (seal c) dorsal and ventral to the branchial openings and articular connective tissue (art c) holding the dorsal and ventral skeletons together posterior to the branchial openings.

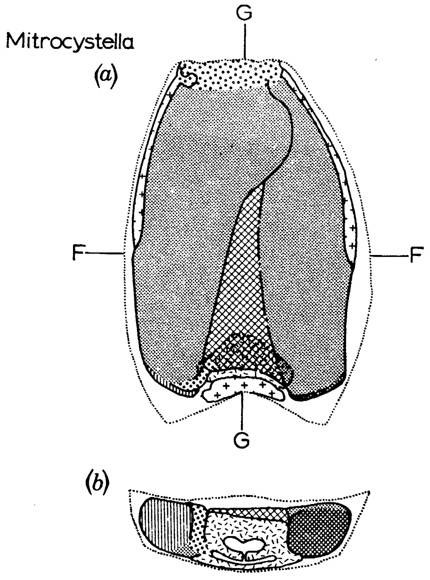

FIGURE 8. The internal chambers of *Mitrocystella*: (*a*) Dorsal. (*b*) Posterior aspect. Legend as in figure 7. Sections F-F, G-G, refer to figure 9.

(v) *Other probable connective tissue*

The ventral skeleton seems to have been resorbed posteriorly and probably replaced by connective tissue (con tis). Similarly, there are transverse cavities in the skeleton, presumably filled with connective tissue in life and transverse to the sutures of the branchial buttresses (tr cav). There was a branchial soft layer in the branchial region (br s l) between inner and outer layers of calcite.

(vi) *Structures connected with the median atrium* (*figures* 10, 11)

Structures connected with the median atrium are mainly branchial in nature. Most important are the branchial slits which are separated ventrally by calcitic branchial bars (calc br b). The more dorsal parts of the branchial bars must have been soft and were connected to dorsal traces of the branchial bars (tr bb). The course of the soft parts of the bars can therefore be reconstructed (rec br b). The calcitic branchial bars are fixed to the top of branchial buttresses (br but). There is a prebranchial line (pr bl) just anterior to the branchial buttresses. The branchial bars formed the front wall of the median atrium whose right and dorsal margins can readily be

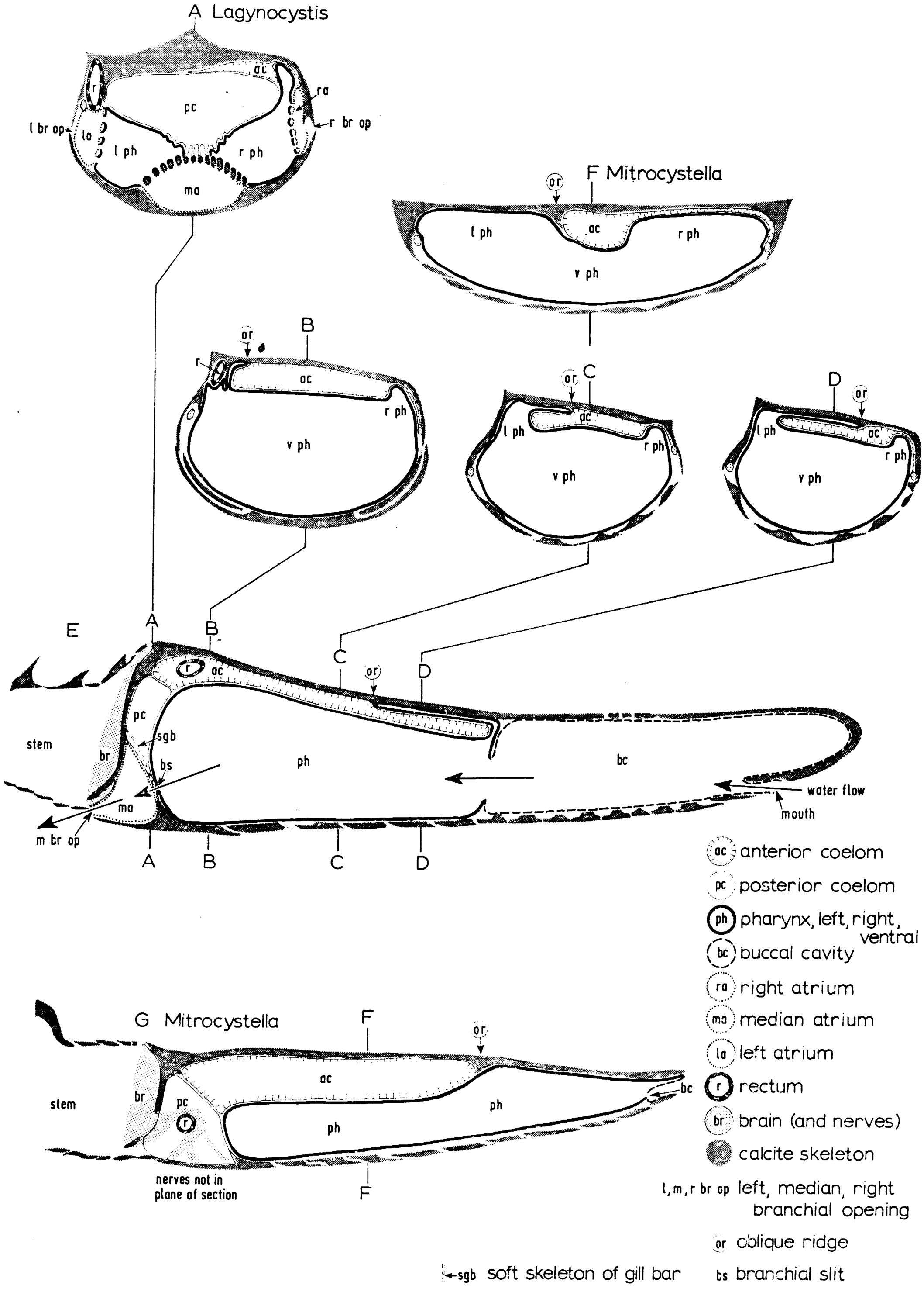

FIGURE 9. Reconstructed sections showing the internal chambers of *Lagynocystis* and *Mitrocystella*. The situation in *Lagynocystis* is peculiar in the existence of a median atrium. The pharynx had pushed back to meet this, so lifting the posterior coelom off the floor of the theca and squashing the anterior coelom against the ceiling. The anterior coelom has spread out sideways in consequence and become more symmetrical in position. In its chambers *Mitrocystella* is very close to the primitive mitrate condition.

determined (r m m atr, d m m atr). The dorsal margin of the posterior coelom is also visible (d m pc). The posterior surface of the branchial cage (pos sf br cage) (i.e. of the calcitic bars plus the buttresses) is made up of branchial bars separated by branchial slits (br sl) and of the buttresses which carry growth traces of the branchial slits (gr tr bs) and growth traces of the bars. There are cavities inside the branchial buttresses (cav br but).

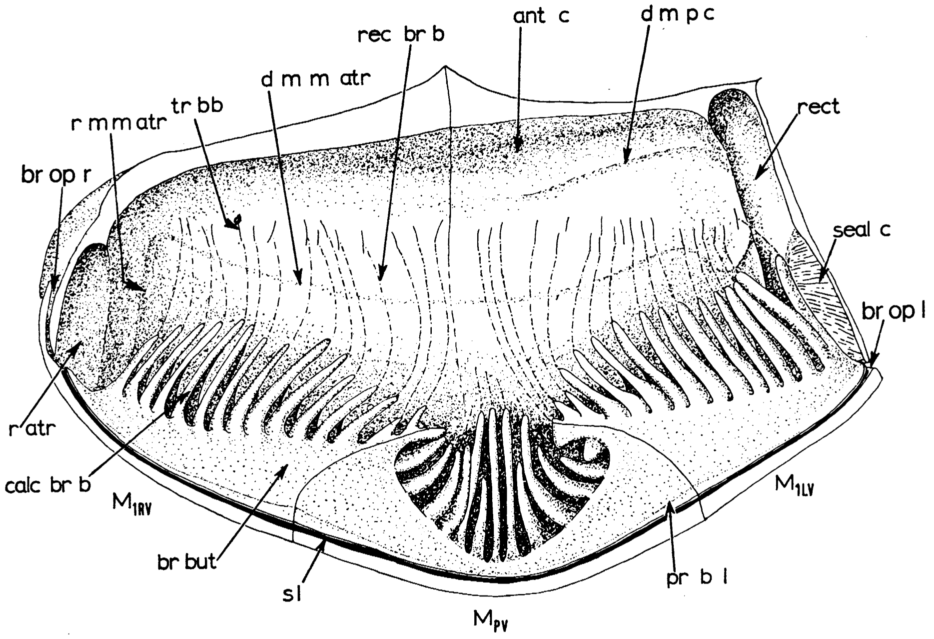

Figure 10. Reconstruction of the skeleton inside the posterior part of the theca, showing the branchial bars in the front wall of the median atrium (cf. plate 40, especially figure 35).

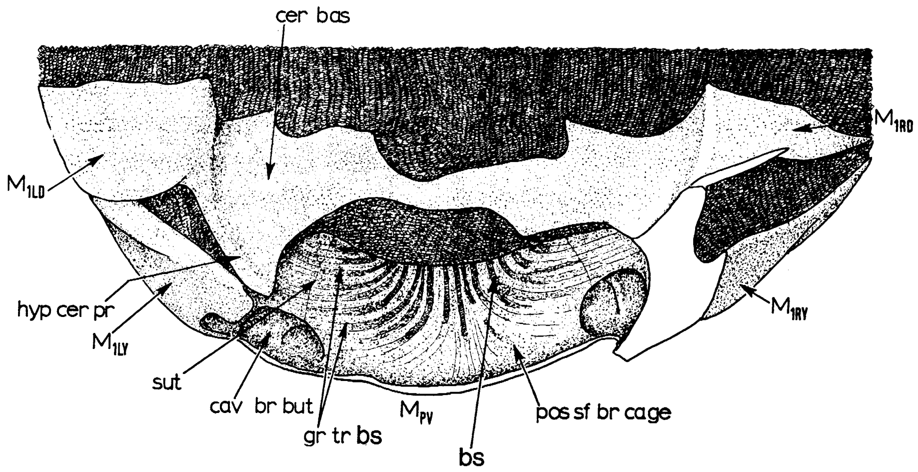

Figure 11. The posterior surface of the front wall of the median atrium. Camera lucida drawing of NM 311/69 (cf. figure 36, plate 40). It is often hard to tell where branchial slits pass into growth traces of branchial slits.

(vii) *Internal features and other details of the hind-stem* (*figure* 12)

The dorsal ossicles of the hind-stem were separated by pads of soft interossicular tissue (int tis), lodged in anterior and posterior interossicular depressions (a and p int dep). Ossicles were articulated together by posterior processes (p pr) fitting into anterior sockets (a skt). The ventral surface of each ossicle has a median groove (m gr) flanked by lateral grooves (lat gr) which are flanked in turn by facets for ventral plates (f ven pl). The ventral surface of the dorsal ossicles also has ganglionic pits (gan p) and ventral processes (v pr). The median groove has a widening (w mgr) near the ganglionic pits.

The ventral plates of the hind stem have a distinct ventral surface (v surf) ending in a postero-ventral process (p v pr). There is an anterior imbrication facet (a imb f) fitting into a posterior

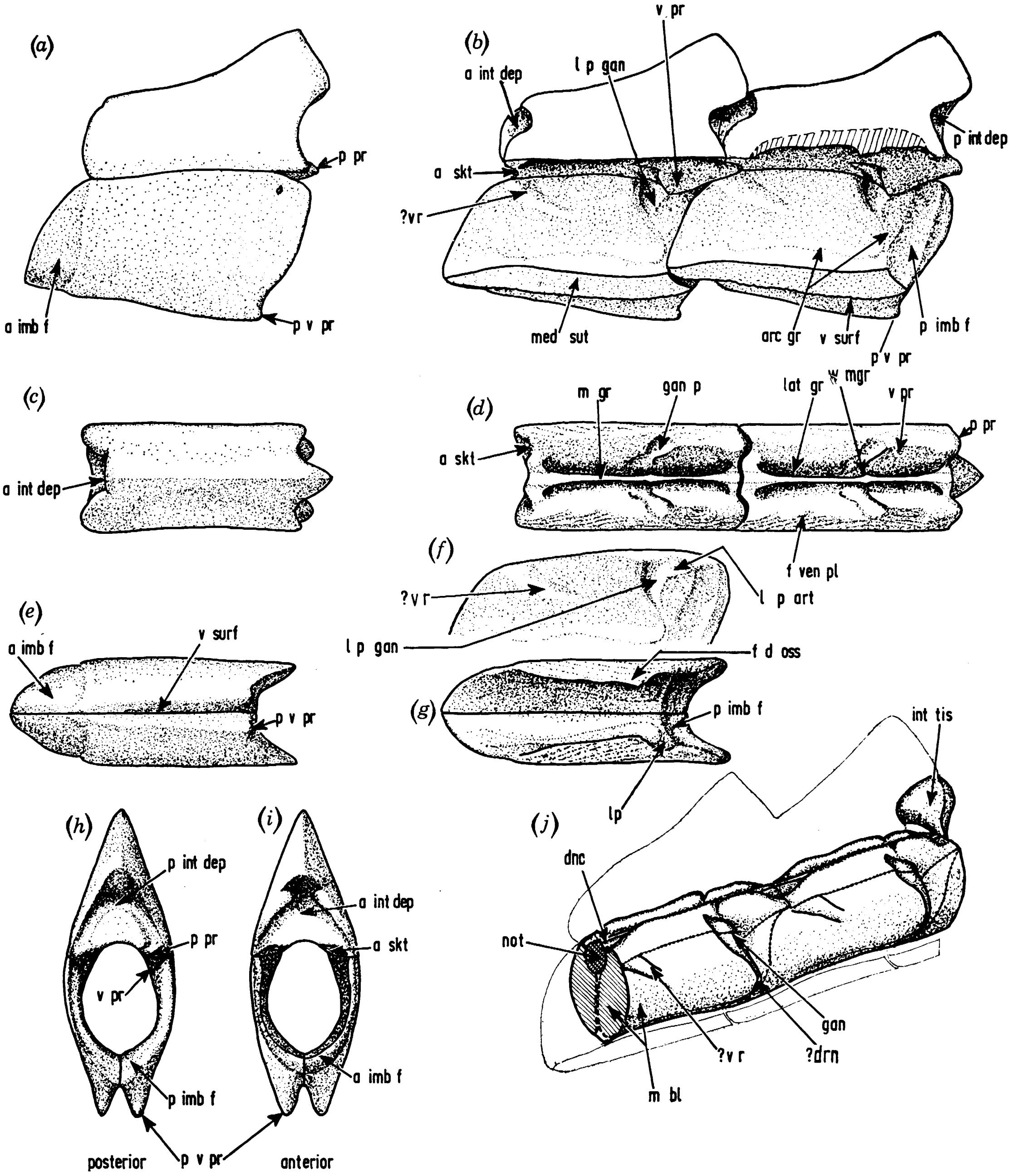

Figure 12. Skeleton and soft parts of the hind stem (cf. plates 42 and 43). (*a*) Left aspect of dorsal ossicle and ventral plate. (*b*) Two segments cut through the median plane, in median aspects. (*c*) Dorsal ossicle in dorsal aspect. (*d*) Dorsal ossicles in ventral aspect. (*e*) Ventral plates in ventral aspect. (*f*) Dorsal part of a ventral plate in median aspect. (*g*) Ventral plates in dorsal aspect. (*h*) Dorsal ossicle and ventral plates in posterior aspect. (*i*) Dorsal ossicle and ventral plates in anterior aspect. (*j*) Reconstruction of the soft parts in two segments.

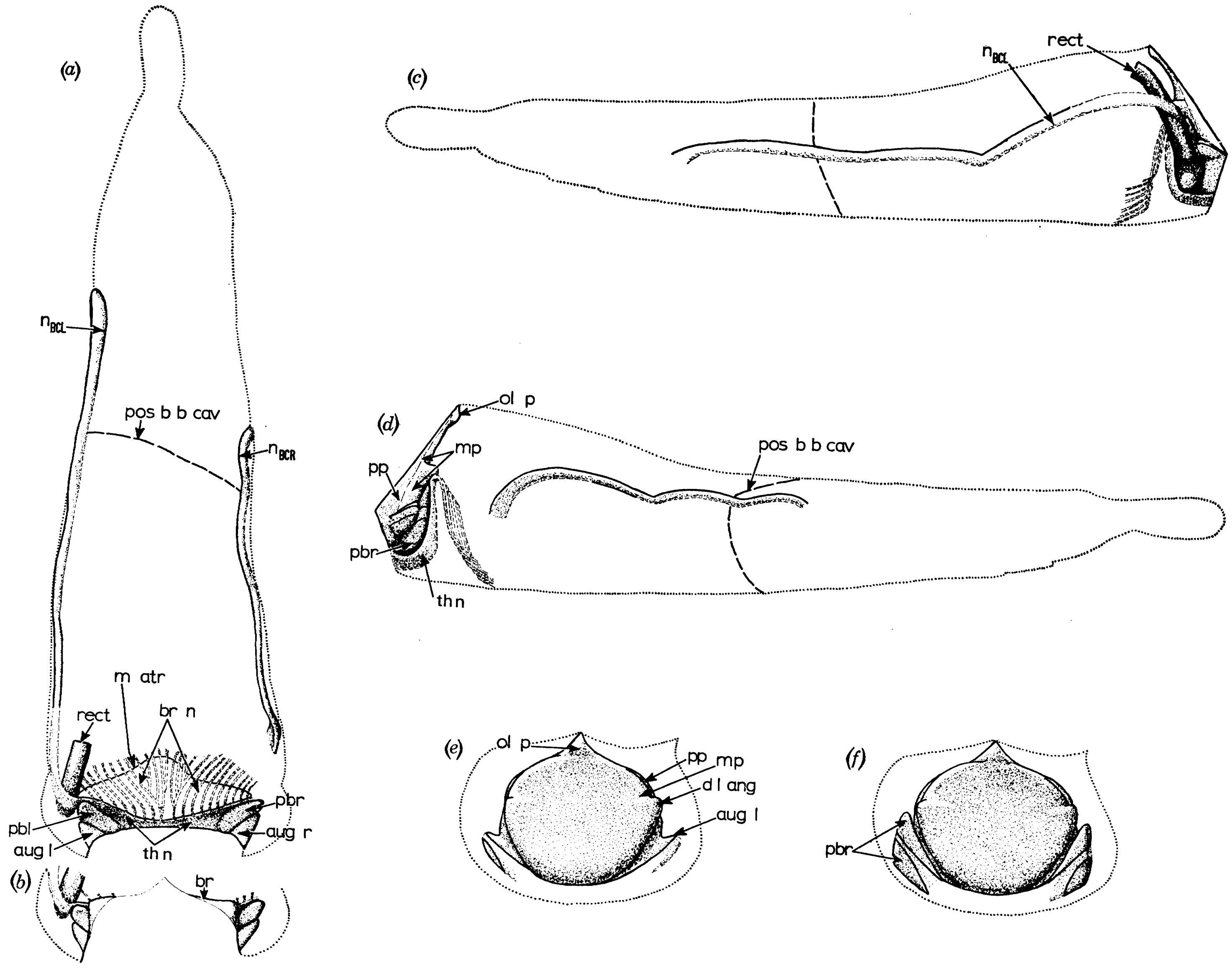

FIGURE 13. Reconstruction of the cranial nerves and brain; anterior part of brain omitted (figure 30, plate 39). (*a*) Dorsal aspect of whole theca, without brain. (*b*) Dorsal aspect of posterior part of theca, with brain. (*c*) Left aspect. (*d*) Right aspect. (*e*) Anterior aspect of brain without pyriform bodies. (*f*) Anterior aspect of brain, with pyriform bodies.

imbrication facet (p imb f) in the next plate in front. The dorsal surface of each plate bears a facet for the dorsal ossicle (f d oss). Lateral pits (l p) partly accommodate ganglia (l p gan) and partly articulated with the ventral processes of the dorsal ossicles (l p art). An arcuate groove (arc gr) goes out from the bottom of each lateral pit and may have carried the dorsal root nerve (? drn). Weak grooves in the ventral plate may have accommodated the ventral root (? v r) which may have been muscular. A median suture (med sut) joined right and left ventral plates together in each segment.

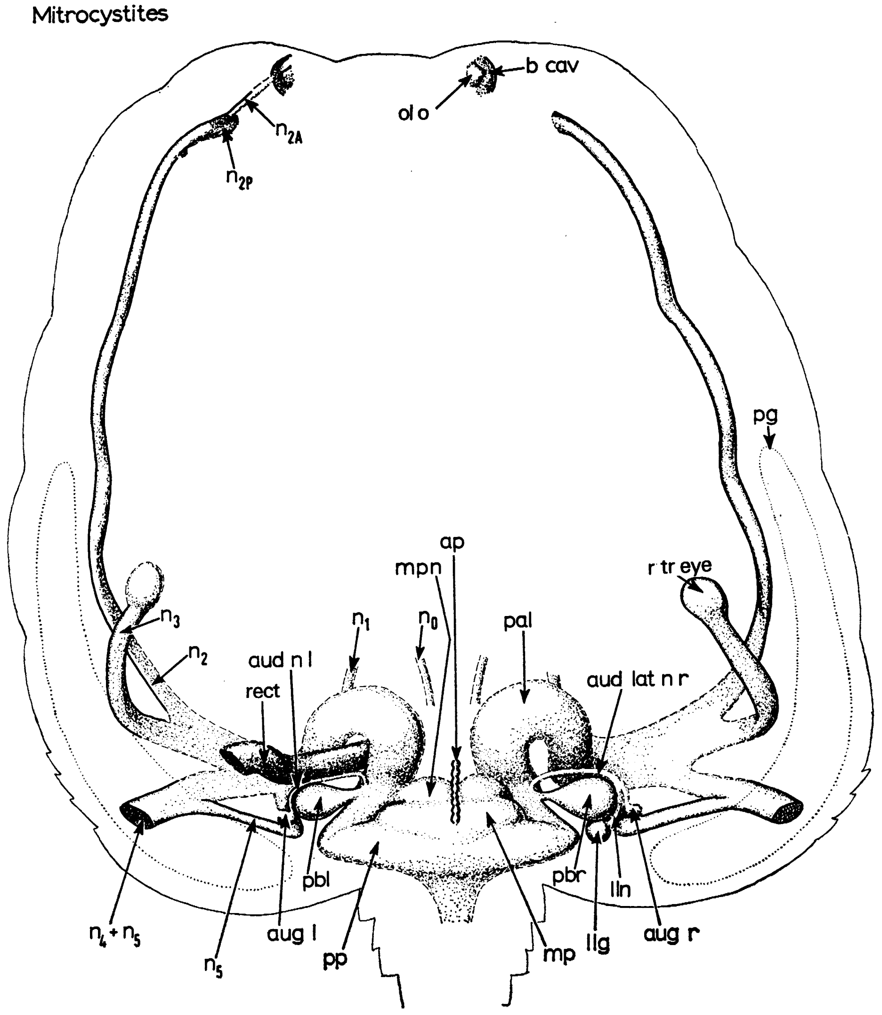

FIGURE 14. Reconstruction of cranial nerves and brain in *Mitrocystites mitra* (cf. Jefferies 1968, 1969). In most ways this nervous system represents the primitive mitrate condition, from which the situation in *Lagynocystis* has been derived by simplification.

Soft parts in the hind-stem probably included dorsal nerve cord (d n c), notochord (not), muscle blocks (m bl), paired ganglia (gan), dorsal root nerves (? drn) and ventral roots (? vr), probably made of muscle.

(viii) *Brain and nervous system in the theca of Lagynocystis* (*figure* 13).

The anterior part of the brain was probably represented by ill-defined cones of rock on some of the internal casts (ap in figure 30, plate 39). The cerebral depression in the skeleton carried the medial part (mp) of the brain and a posterior part (pp). The medial part had a dorsal olfactory portion (ol p) and dorso-lateral angles (d l ang). Nerves in the theca, taken in sequence from back to front, included thecal nerves (th n) leaving the brain, left and right auditory ganglia (aug l, aug r) left and right pyriform bodies or trigeminal ganglia (pbl, pbr), probably branchial nerves (br n) and left and right buccal cavity nerves (n_{BCL}, n_{BCR}).

(ix) *Brain and nervous system in theca of normal mitrates*

The normal mitrate brain and cranial nerves can be illustrated from *Mitrocystites* (figure 14). The brain had anterior, medial and posterior parts (ap, mp, pp).

The anterior part of the brain was probably connected by olfactory fibres in the skeleton to olfactory openings (ol o) in the buccal cavity (b cav).

The medial part gave off big, probably optic, medial part nerves (mpn) antero-ventrally. These joined posterior part nerves from the posterior part of the brain and the nerves formed by their junction, the palmar nerves (pal), passed median to the left and right pyriform bodies (pbl, pbr, trigeminal ganglia) and then looped upwards and down again. The left palmar nerve probably looped over the rectum (rect) and the right one over the oesophagus (not shown). The palmar nerves are so called because they are connected to five 'fingers' peripherally, these being nerves n_1, n_2, n_3, n_4 and n_5 of the right and left palmar complexes. Nerves n_1 supplied the ventral skeleton, nerves n_2 (maxillary trigeminal) went to the buccal cavity and mouth, and the left one divided into anterior and posterior portions (n_{2A}, n_{2P}). Nerves n_3 or transpharyngeal optic nerves went to the dorsal surface and ended in optic bulbs or transpharyngeal eyes (l and r tr eye). Nerves n_4 and n_5, behind the branchial opening joined together (n_4+n_5) and went to the dorsal surface to supply probably touch-sensory peripheral grooves (pg).

Outside the palmar complexes nerves n_0 probably supplied the posterior end of the endostyle.

The acustico-lateralis nerves on the left side include: a left auditory nerve (aud n l) supplying a left auditory ganglion in the left atrium. On the right side there was probably a common auditory and lateralis nerve (aud lat n r) supplying a presumed right auditory ganglion (aug r) in the right atrium and also a lateral line nerve (lln) ending in a lateral line ganglion (llg) that underlay a lateral line groove in the surface of one of the plates.

This picture of the nervous system of *Mitrocystites* is based on information from *Mitrocystella*, *Peltocystis*, *Placocystites* and the cornute *Ceratocystis* (Jefferies 1969) as well as from *Mitrocystites* itself. The lateralis system, on the right, was only present in Mitrocystitid mitrates. Some mitrates had cispharyngeal optic nerves going directly up inside the theca from the medial part of the brains to end beneath the inner surface of the dorsal skeleton. In *Peltocystis* the nerve supply to presumed auditory ganglia went to right and left atria by a very direct route

Description of plate 37

Latexes of *Lagynocystis pyramidalis* from Šárka Formation of Šárka. All scale lines are 1 mm long. All latexes and specimens in this and subsequent plates are coated with NH_4Cl.

Figure 18. Dorsal aspect of theca. NM 320/69.

Figure 19. Ventral aspect of theca. Specimen as figure 18. (cf. figure 5*e*, *g*.)

Figure 20. Ventral aspect of theca. NM 325/69.

Figure 21. Dorsal aspect of theca. NM 312/69.

Figure 22. Right aspect of posterior portion of theca. NM 324/69.

Figure 23. Posterior portion of theca looking in through the roof; also fore- and mid-stem. NM 325/69.


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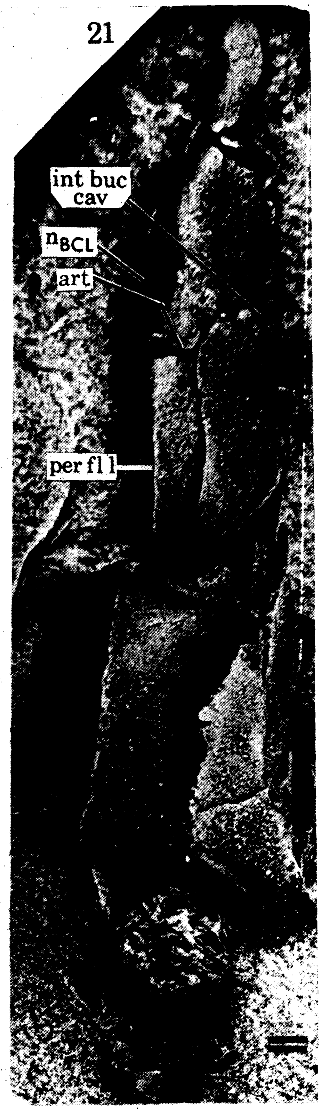
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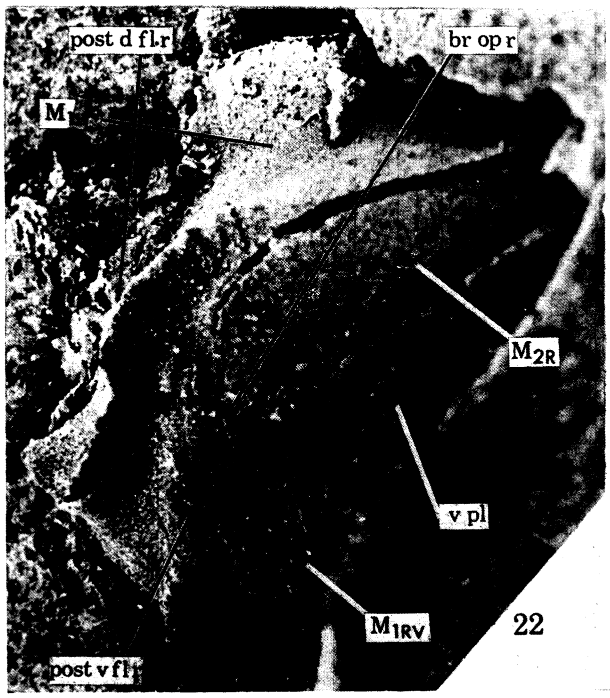
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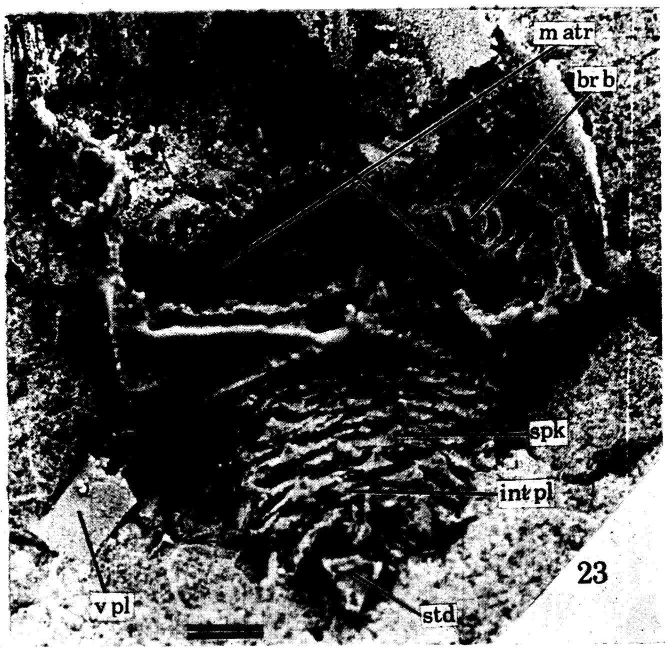
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FIGURES 18 to 23. For legends see facing page.

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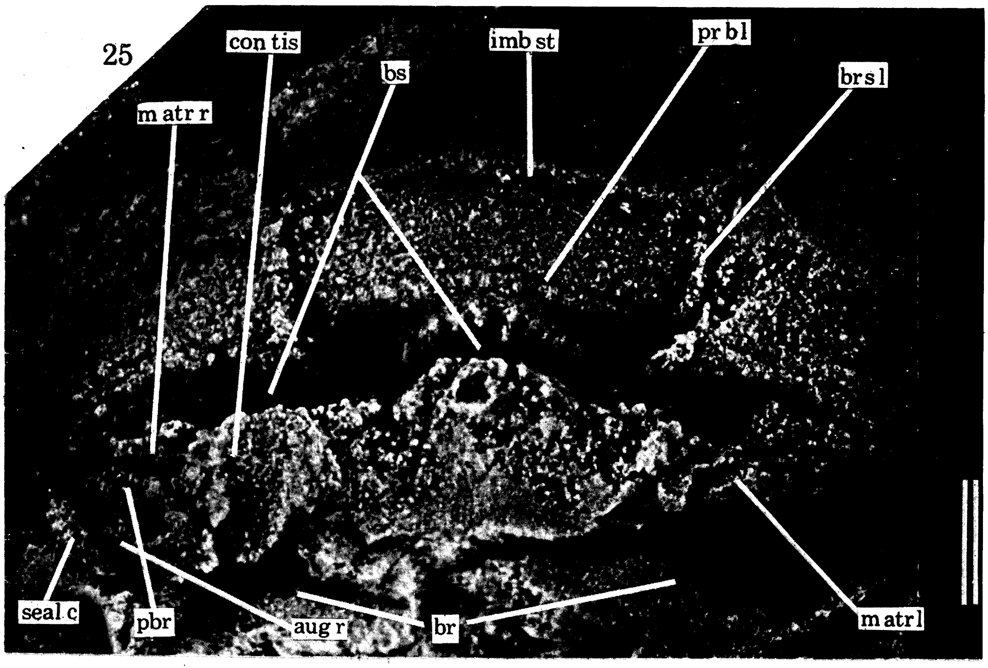

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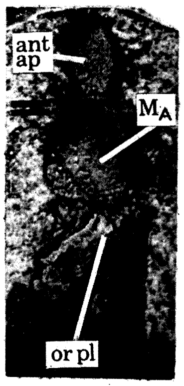

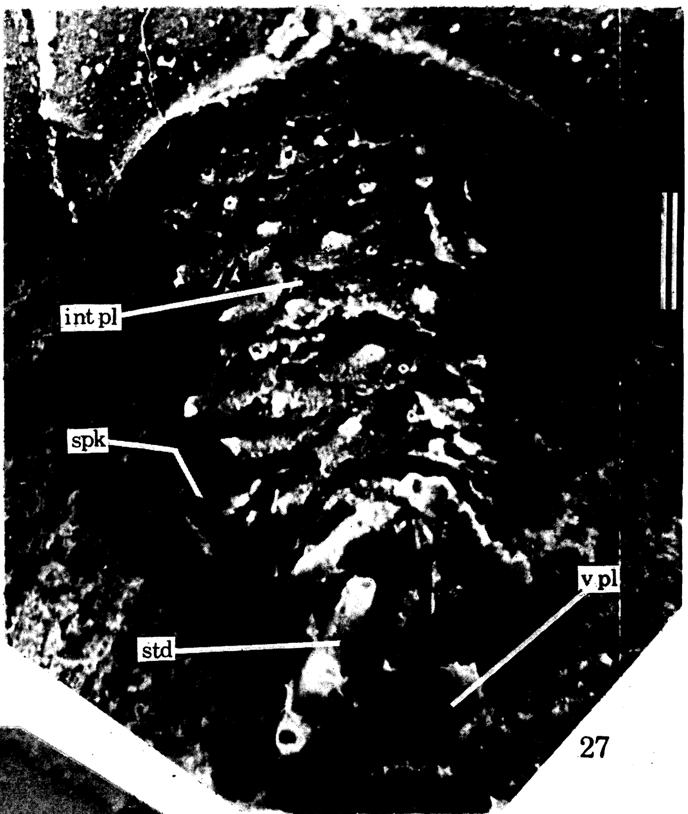

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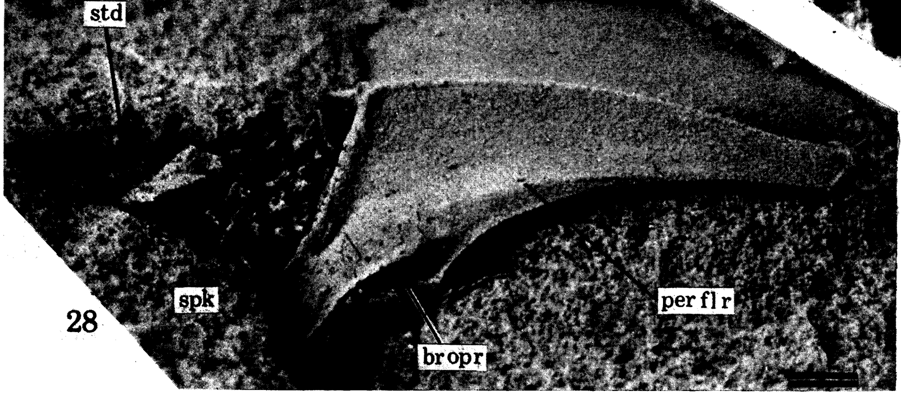

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FIGURES 24 to 28. For legends see facing page.

from the dorso-lateral angles of the posterior part of the brain (medulla oblongata). These nerves thus had their origin at the points where the auditory centres would be expected by analogy with fishes and agnathans.

3. MATERIAL, LOCALITY AND HORIZON

Lagynocystis pyramidalis is known from the shales of the Šárka Formation of Bohemia which is Llanvirn in age (Havlíček & Vaněk 1966). The only useful material is preserved as uncrushed and scarcely disarticulated moulds in siliceous nodules with the plates represented by empty holes. There is no doubt that the Šárka Beds are marine in origin, for other elements of the fauna include trilobites, brachiopods, cephalopods, graptolites, hyolithids, ophiuroids and asteroids.

The species was first described by Barrande on the basis of two specimens from the Šárka Formation of Osek (Wosek) near Rokycany. It is much commoner, however, in the Šárka Formation of Šárka near Prague. The most important locality was the fields round Šárka (Šárka pole) on the surface of which the siliceous nodules used to be thrown up by the plough, before the area was built over. The collections of the Národní Muzeum in Prague contain about 190 specimens of the species from this locality, collected by the notable amateur F. Hanuš in the early years of this century. All of these specimens have been examined for this investigation.

Specimens used in detailed reconstruction of *L. pyramidalis* are as follows: British Museum (Natural History); E 16104 (from Osek), E 16105–E 16109 (from Šárka), E 29040–E 29049 (from Šárka): Národní Muzeum, Prague, Hanuš collection from Šárka pole; akz. cat. no. 308/69 = Hanuš 157 ±, 309/69 = 151 ±, 310/69 = 57 ±, 311/69 = 156 ±, 312/69 = 1 ±, 313/69 = no Hanuš number, 314/69 = no Hanuš number, 315/69 = no Hanuš number, 316/69 = 165 ±, 317/69 = 161 ±, 318/69 = 155 ±, 319/69 = 3 ±, 320/69 = 55 ±, 321/69 = 22 ±, 322/69 = 11 ±, 323/69 = 190 ±, 324/69 = 187 ±, 325/69 = 153 ± : Sedgwick Museum, Cambridge; A48928*a*, *b*, *c*, (from Šárka): Mus. Comp. Zool. Harvard; MCZ 982 (locality given as Bohemia).

4. MORPHOLOGY

(*a*) *Theca: external features*

Like other calcichordates, *Lagynocystis pyramidalis* consists of a theca and a stem (see figures 5*a* to *h*; figures 18 to 21, plate 37; figure 24, plate 38; figures 40, 42, plate 42). The animal is here oriented with the stem posterior, as in my other works, and with the dorsal side upwards. This is the same orientation as that of a fish. Two separate notations are used for the thecal plates. One is intended to be objective and the other comparative (as explained above, see § 2).

In shape the theca is elongate for a mitrate and tapers forward to end in an anterior appendage, somewhat left of the median line (ant ap = *b* in figure 5). The dorsal surface of the theca

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DESCRIPTION OF PLATE 38

Latexes (figures 24, 26 to 28) and internal mould (figure 25) of *Lagynocystis pyramidalis* from the Šárka Formation of Šárka. All scale lines 1 mm long.

FIGURE 24. Dorsal aspect of theca and stem. BMNH, E 29043.

FIGURE 25. Internal mould of posterior part of theca in ventral aspect (cf. figure 6*e*). NM 316/69.

FIGURE 26. Ventral aspect of anterior part of theca, mouth region. NM 312/69.

FIGURE 27. Dorsal aspect of fore- and mid-stem. BMNH, E 16107.

FIGURE 28. Right dorsal aspect of posterior part of theca, fore-stem and mid-stem. NM 308/69.

is fairly flat but tends to slope downwards, forwards and to the right, particularly near the front end of the theca, and especially just right of the anterior appendage. The dorsal surface is limited by left and right peripheral flanges developed on marginal plates and homologous with at least the major portions of the peripheral flanges of other mitrates and amygdalothecid cornutes. The left peripheral flange (per fl l) is much better developed than the right (per fl r), which is shorter, and rather blunt for part of its length (figure 24, plate 38). The ventral surface of the theca is strongly convex downward, almost conforming to part of a cone. The theca was widest ventral to the peripheral flanges. The shape of the theca therefore departs greatly from the primitive mitrate condition in being larger and deeper relative to its width, in having an anterior left appendage, developed from the anterior left marginal (b) of the ancestral cornute, in the reduction of the right peripheral flange compared with the left, and in the rightward and downward slope of the dorsal surface.

These changes of thecal shape to something approaching a solid of revolution affected by certain special asymmetries must be related to the mode of life of *L. pyramidalis*. More precisely they would have the effect, if *L. pyramidalis* swam forwards, of making the theca rotate about its long axis, clockwise as seen from behind, with the anterior appendage in the axis of rotation (figure 5*h*).

It is interesting that the late larva of amphioxus rotates in the same manner and direction when swimming by muscular action (Wickstead 1967, p. 54). In the adult the same rotation has also been reported (Franz 1927, p. 523; Gislén 1930, p. 224ff.) but does not always occur since cinematographic studies have not confirmed it (Professor J. E. Webb, personal communication). As against this, the early larva of amphioxus rotates mainly anticlockwise as seen from behind, by using its cilia (Bone 1958, p. 459). Tunicate tadpoles are also known to rotate clockwise as seen from behind when swimming by waving their tails (Grave 1920, p. 240, Mast 1921, p. 153). The function of such rotation is probably to even out irregularities in the trajectory in animals whose sensory and control mechanisms are rather poor. It can be compared with the slow rotation that was given to early rockets so as to cancel out chance asymmetries in the jet and make the flight-path more predictable (P. Minton, personal communication). Rotation became unnecessary when rockets became more sophisticated. It seems that, if *Lagynocystis* swam, it would rotate in the same manner and direction as modern tunicate tadpoles, late amphioxus larvae, and perhaps, sometimes, amphioxus adults.

The plates of the theca, as in other calcichordates, are of two types – marginal plates and integument plates. Much as in other mitrates the marginal plates form most of the dorsal and the posterior part of the ventral surface. Integument plates cover the rest of the theca. They form most of the ventral surface, but also extend on to the anterior right part of the dorsal surface.

The marginal plates can be divided into three groups, each of which probably behaved as a rigid unit in life (figure 5*g*, *h*). These were: (1) A postero-ventral group made of plates M_{1LV}, M_{PM} and M_{1RV}. This group carried right and left postero-ventral flanges, homologous with those of other mitrates. (2) A postero-dorsal group made up of plates M_{1LD}, M_{1RD}, M_{2R}, M_{3R}, M_{4R}. This group forms most of the more dorsal part of the theca. It carried the right and left peripheral flanges and also right and left postero-dorsal flanges (post d fl l and r in figure 5*f*). The latter may correspond to the posterior parts of the peripheral flanges of other mitrates, or may be an independent development. (3) An anterior group made up of the anterior appendage (ant ap) and M_A and M_{3L}. This group carried the anterior part of the left peripheral flange. It is largely separated from the postero-dorsal group of plates by the dorsal piece of integument already mentioned.

There was an articulation between the anterior group of marginal plates and the postero-dorsal group where the posterior edge of M_{3L} touched the anterior edge of M_{2L} (art in figure 5*f*; figure 21, plate 37). This articulation would have allowed a slight movement of the anterior group, about an axis of rotation which slopes leftwards and downwards (ax art in figure 5*c*). By this movement the anterior appendage could approach or move away from the long axis of the animal.

There would also have been articulations (branchial hinges) between the postero-ventral and postero-dorsal group of plates, to left and right of the stem, where M_{1RV} touched M_{1RD} and M_{1LV} touched M_{1LD}. These hinges would allow the postero-ventral group of plates to rock downwards and backwards with respect to the postero-dorsal group, so that right and left branchial openings, corresponding to those of other mitrates, would appear as long slits along the dorsal edges of M_{1LV} and M_{1RV} (br op r in figure 5*a*, *f*, left branchial opening in corresponding position on left; figure 22, plate 37; figure 28, plate 38; figure 42, plate 42). These openings were probably guarded by strips of connective tissue, above and below, that served to seal the openings when these were closed. Other strips of connective tissue, held the dorsal and ventral sets of plates together. On each side there was one such strip behind the gill opening, just anterior to the hinge, and another strip anterior to the gill opening. These strips of connective tissue are recorded by holes in the skeleton, corresponding to ridges on the internal cast. Their anatomy and significance will be discussed below.

The integument plates cover most of the ventral and part of the dorsal surface of the theca. They can be divided into three groups, i.e. the plates beneath the pharynx, the oral plates, and unspecialized plates dorsal and ventral to the buccal cavity (figure 5*g*; figures 19 to 21, plate 37; figures 61, 62 plate 45). The pharyngeal plates imbricate with each other in the usual mitrate manner, i.e. each plate tucks inside its more posterior neighbours. The most posterior of the pharyngeal integument plates are inserted inside the postero-ventral group of marginals. To left and right the plates of the pharyngeal integument overlap the marginals of the postero-dorsal shield. As a result of these insertions and overlaps, the pharyngeal integument plates would be given a rather rigid shape in life, convex downwards.

The most anterior of the integument plates are specialized as orals, forming the lower lip of the mouth. These oral plates are elongate, imbricate with each other sideways and overlap the ventral surface of the anterior marginal M_A. They fall into a left and a right series, separated by a 'keystone' plate (kst pl in figure 5*e*; figure 62, plate 45). Each plate imbricates inside its neighbour on the keystone-plate side while the neighbours of the keystone plate imbricate inside that plate. In the only specimen that shows a complete lower lip (figure 62, plate 45) the oral plates are not symmetrical, i.e. there are nine plates left of the 'keystone' and only six right of it. This suggests a predominance of the left side of the mouth which can be better established in the innervation (see below). It may be significant that the buccal cavity of amphioxus likewise shows a predominance of the left side in its muscles, coeloms and nerves (Franz 1927, pp. 507, 529). The sideways imbrication of the oral plates would allow the lower lip to increase or decrease in length so opening or closing the mouth.

Finally, between the orals and the pharyngeal plates was another group of integument plates forming with some of the marginals the walls of the buccal cavity (int buc cav in figure 5*g*; figures 18 to 20, plate 37; figures 61, 62, plate 45). This group is mainly ventral in distribution but also forms part of the thecal roof, between the anterior and postero-dorsal group of marginal plates. These integument plates of the buccal cavity are in contact with their neighbours round the edges, but do not imbricate. They are smaller than the pharyngeal plates. Some of them carry a boss near the centre (bos in figure 5*e*; figure 20, plate 37). They do not overlap the adjacent marginals and the integument which they covered would have been capable of bending inwards or outwards, so raising or depressing the floor of the buccal cavity. The dorsal portion of the integument of the buccal cavity was perhaps derived from the right portion of the dorsal buccal integument of the ancestral cornute judging by the marginal plates which touch it (figure 3).

The boundary between the integument plates of the buccal cavity and the integument plates of the pharynx is oblique, being more posterior at right than at left. This is probably a specialization, for both in the advanced cornute *Reticulocarpos* and in the primitive mitrate *Peltocystis cornuta* (figure 3) the posterior margin of the buccal cavity is more posterior at left than at right, and this probably represents the primitive mitrate condition, as explained in §1. The explanation for the buccal cavity of *Lagynocystis* extending further back at right than at left probably lies in the postulated mode of swimming, with rotation about the long axis clockwise as seen from behind. The junction of the plates of the buccal cavity and the pharyngeal plates produced a step in the external ventral surface. In its presumed primitive condition, farther back at left then right, such a step would resist the direction of rotation caused by the gross morphology of the theca. By evolving to a condition more posterior at right than at left, it would come to assist such a motion.

The openings of the theca number four, three of which have been mentioned already, i.e. the mouth and the left and right gill openings. The fourth opening was a median gill opening between the ventral side of the stem and the dorsal side of plate M_{PM} (med atr op in figure 5*e*). The evidence for this opening comes from the internal structure (see below). Briefly, it served as outlet for the median ventral atrium which existed in *L. pyramidalis*, but is unknown in any other mitrate. This atrium could not have issued by right or left gill openings, with which it did not make contact. Its structure indicates that it issued by a postero-median opening in the position indicated. The presence of a median branchial opening, or atriopore, serving to release water from a median ventral atrium, strongly links *Lagynocystis pyramidalis* with the cephalochordates, for these are the only other known animals with a similar arrangement of parts.

(*b*) *The chambers of the theca*

The arrangement of thecal chambers in *L. pyramidalis* can be deduced from the internal cast, bearing in mind what is known about the chambers in other mitrates. The internal

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DESCRIPTION OF PLATE 39

Lagynocystis pyramidalis (figures 29 to 31) and *Mitrocystites mitra* Barrande (figures 32, 33). Internal casts coated with NH_4Cl. Scale lines 1 mm long.

FIGURE 29. Brain of *L. pyramidalis*, anterior aspect (cf. figure 13*e*). NM 320/69. Šárka Formation, Šárka.

FIGURE 30. Anterior part of brain of *L. pyramidalis* in ventral aspect. BMNH, E29049. Šárka Formation, Šárka.

FIGURE 31. Internal cast of posterior part of theca of *L. pyramidalis* in left ventral aspect. To show particularly the left part of the median atrium and structures within the branchial buttress (cf. figure 6*e*). NM 313/69.

FIGURES 32, 33. *Mitrocystites mitra*. Natural mould of ventral surface of dorsal ossicles of hind-stem, giving a representation of the soft parts (cf. Jefferies 1968*a*, p. 318). MCZ 569, Von Schary Collection. Šárka Formation, Osek near Rokycany. Figure 32 shows a more distal and figure 33 a more proximal part of the stem. The proximal end of each fragment is upwards on page.

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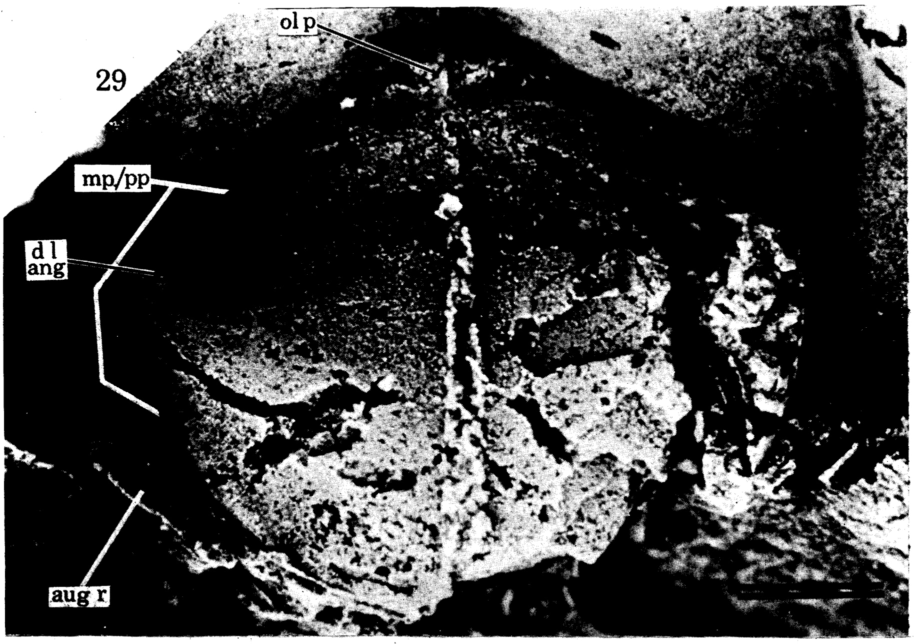

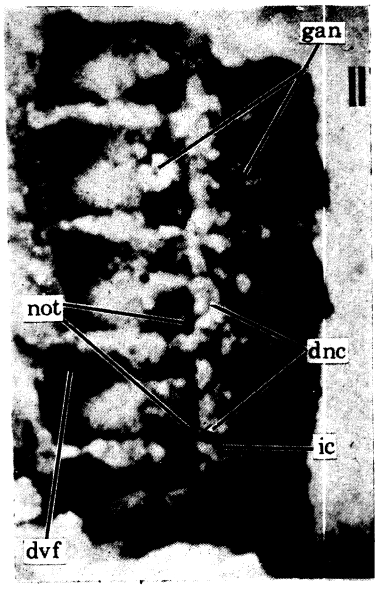

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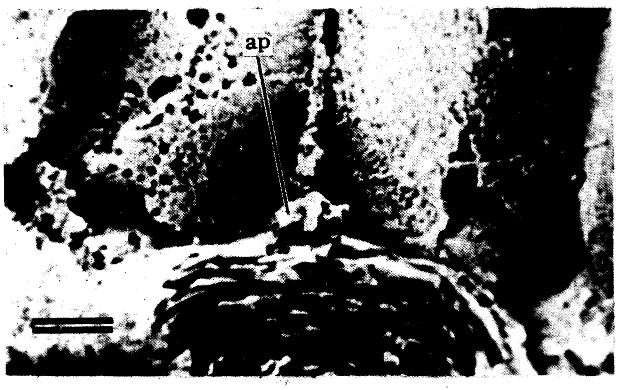

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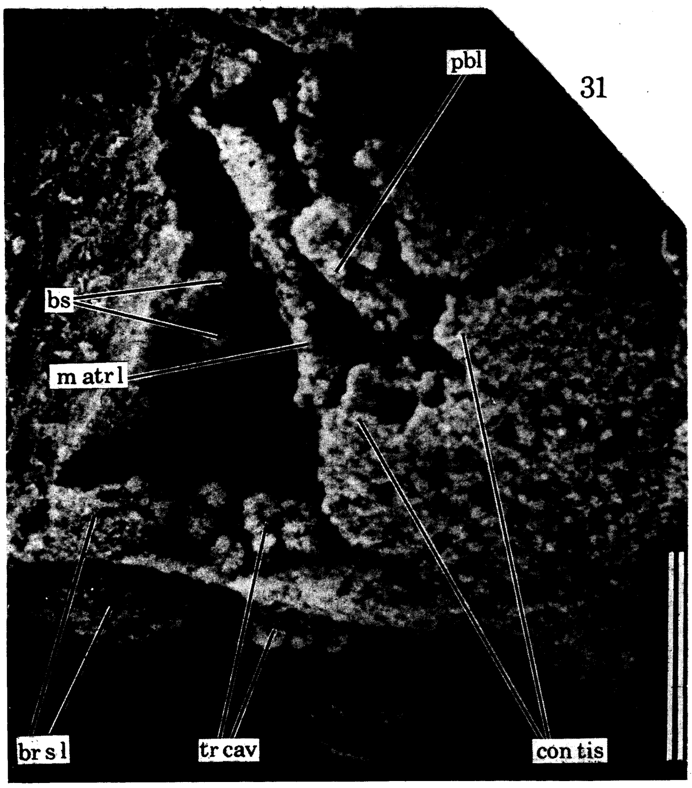

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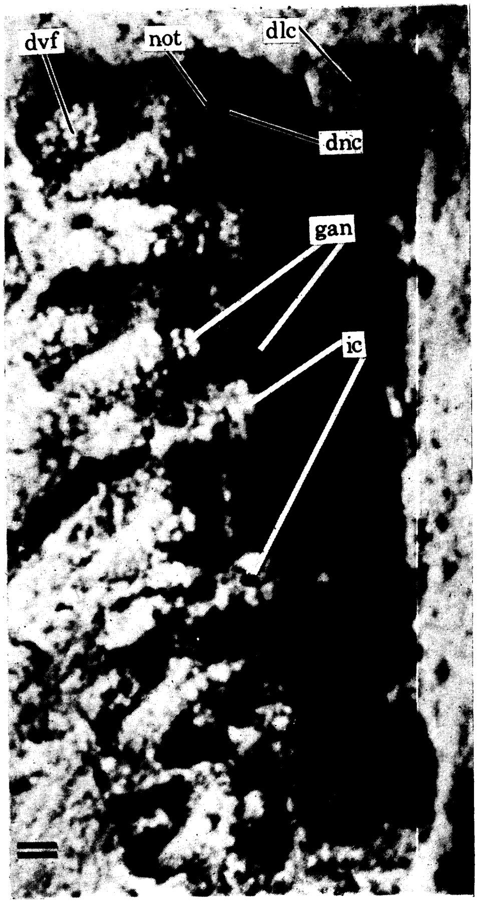
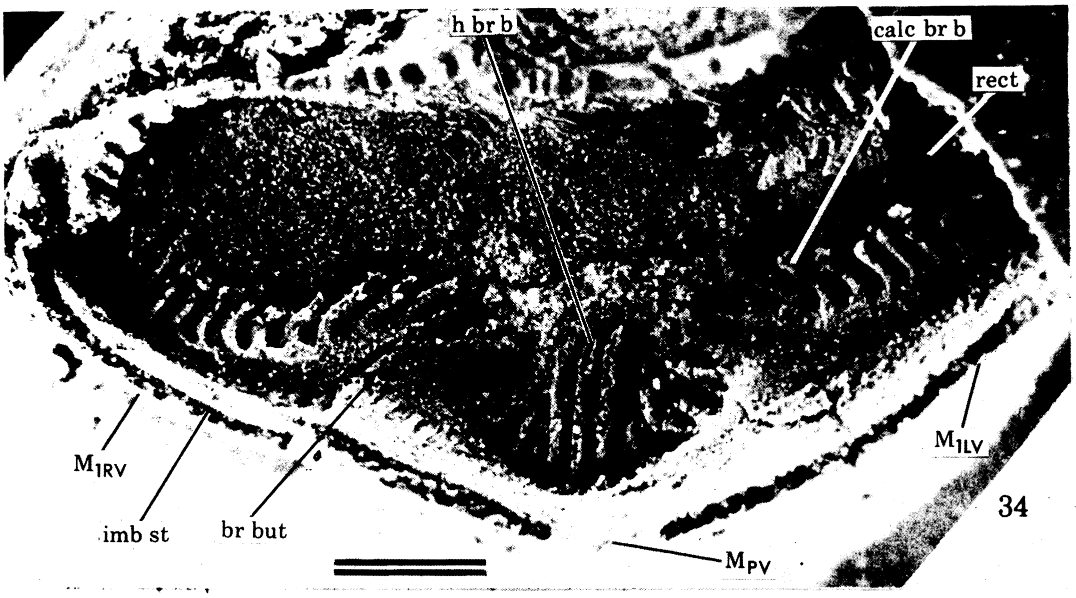


Figures 29 to 33. For legends see facing page.



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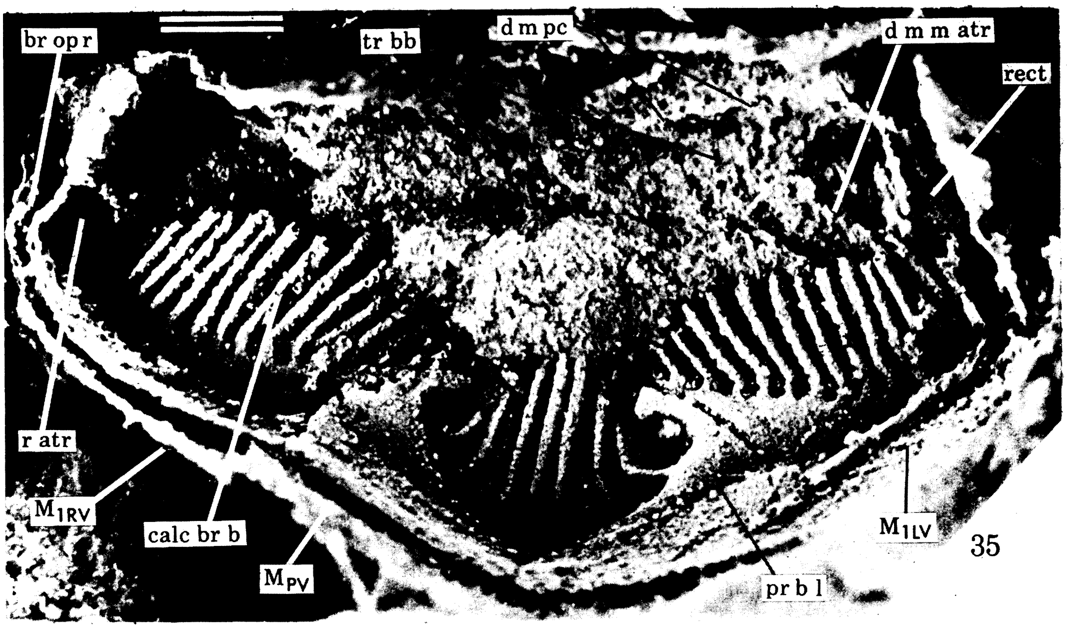

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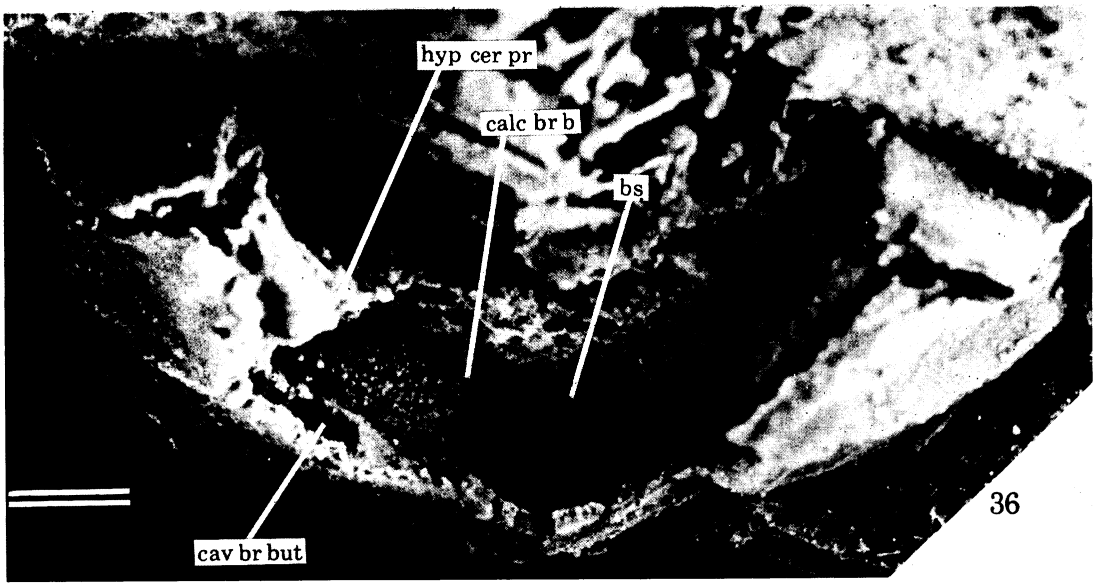

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Figures 34 to 36. For legends see facing page.

cast carries a great number of growth lines parallel to the edges of plates. These have to be discounted when examining the cast for indications of chambers. It is also necessary to discount growth tracks corresponding to plate corners and caused by the meeting of two sets of growth lines parallel to adjacent edges of a plate. Figures 6*a* to *e* represent a reconstructed internal cast, obtained by examining many individual specimens. Figures 7*a* to *e* give an interpretation of this reconstruction (see figure 25, plate 38; figure 31, plate 39; figures 37 to 39, plate 41; figures 56 to 60, plate 44; figures 62 to 64, plate 45; figures 65 to 69, plate 46).

Before discussing the chambers in *Lagynocystis* it is fitting to discuss in more detail than in § 1 the situation in other mitrates, as exemplified by *Mitrocystella* (figures 8*a*, *b*, 9*f*, *g*; cf. Jefferies 1968*a*, p. 283, 1969, p. 508). The following chambers exist in normal mitrates: (1) A buccal cavity just inside the mouth. (2) A posterior coelom in front of the stem and extending from the roof to the floor of the theca. (3) Left and right atria, inside the left and right branchial openings. (4) The anterior coelom, which was situated in a posterior right position, hanging from the ceiling of the theca; part of it was obliterated by the right pharynx. (5) The pharynx, divided into left, and right (and ventral) portions. The left pharynx, which issued by hypothetical gill slits into the left atrium, was primary, being first to appear in ontogeny and phylogeny. The right pharynx pouched out from the left pharynx towards the posterior right corner of the theca, and issued through hypothetical gill slits into the right atrium. In pouching out from the left pharynx it pushed upwards against the right portion of the anterior coelom.

It thus eliminated the cavity of the anterior coelom in this region, and pushed the viscera contained in the anterior coelom towards the left, into a median residual anterior coelom (ac in figures 2*e*, *f*, 9*f*). The ventral pharynx is merely a convenient name for the ventral portions of the left and right pharynxes, which cannot readily be separated from each other. The rectum ran across the posterior coelom near the floor to issue into the left atrium, as it does in a tunicate tadpole. The most prominent groove on the internal cast of a normal mitrate is the oblique groove corresponding to the oblique ridge in the skeleton (or in figure 9) and running from near the right side of the buccal cavity to just left of the posterior coelom. It separates the primary or left pharynx from the anterior coelom.

The chambers of *Lagynocystis pyramidalis* have fundamentally the same arrangement as in other mitrates, but are modified by the presence of the median atrium in front of the front end of the stem. The presence of this chamber has somewhat altered the mutual relations of the posterior coelom, anterior coelom and pharynx.

The buccal cavity, posterior to the mouth, is very large for a mitrate. This is a primitive, cornute-like character. The posterior border of the buccal cavity is marked by: (1) A change in the plating of the ventral integument, as already mentioned. This change is similar to a corresponding change in the ventral integument of the primitive mitrate *Peltocystis cornuta* (figure 3). (2) A cleft in the internal cast on the inside of plate M_{2L} (cl b cav/ph in figure 6; figure 61,

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Description of plate 40

Lagynocystis pyramidalis, latexes showing branchial apparatus in front wall of median atrium. Scale lines 1 mm. All specimens from Šárka Formation, Šárka.

Figure 34. Anterior aspect of branchial bars, to show, especially, hollowness of bars (h br b). NM 318/69.

Figure 35. Anterior aspect of branchial bars and buttresses (cf. figure 10). Note especially the dorsal traces of the branchial bars (tr bb). NM 311/69.

Figure 36. Posterior aspect of branchial bars and buttresses. Same specimen as figure 35 (cf. figure 11).

plate 45; figure 68, plate 46; obscurer junction in figure 65, plate 46). (3) The anterior end of the oblique groove (ob gr in figure 6; figures 65 to 68, plate 46). As pointed out already, the oblique groove ends at the posterior border of the buccal cavity in normal mitrates. The posterior margin of the buccal cavity is more posterior at right than at left. As already mentioned, this may be an adaptation to rotational swimming.

The median atrium lies just anterior to the stem (m atr and m atr r in figure 6*a*, *e*, see also figures 10 and 11; figure 23, plate 37; figure 25, plate 38; figure 31, plate 38; figures 36, 38, plates 40, 41; figure 59, plate 44; figure 69, plate 46). Its floor is made up of the postero-ventral marginal plates, i.e. M_{1LV}, M_{PM}, M_{1RV}. A complicated partition on the internal surface of these makes up the anterior wall of the median atrium. This partition consists of right and left branchial buttresses (br but in figure 10; figures 34 to 36, plate 40) with gill bars above. The buttresses are roughly triangular and are crossed by the sutures on each side of M_{PV} (sut in figure 11). The calcitized parts of the gill bars are arranged like the bars of a cage along the upper edge of the buttresses (calc br b in figure 10; figures 34 to 36, plate 40). They are divided into three groups corresponding to the three marginal plates. Thus there are about 15 gill bars on M_{1LV}, 15 on M_{PV}, and 15 on M_{1RV}.

It is fairly certain that the gill slits are gill slits in fact. First, by comparison with cornutes, gill slits are deduced to have existed in the posterior part of the mitrate theca, though only in *Lagynocystis* were they median in position. Secondly, the parallel-sided nature of the slits resembles that of living tunicates and amphioxus. The gill slits of these animals are lined with cilia which drive water through the slit. These cilia are fairly uniform in length and the slits are parallel-sided so that there shall be no dead water between the cilia on opposite sides of a slit i.e. the slit is wide enough to accommodate two sets of cilia almost touching each other (Berrill 1955, p. 88; Jørgensen 1966, p. 117). Presumably the slits of *L. pyramidalis* functioned in the same way, and also owe their shape to being ciliated in life.

The observed distance between the calcite bars of *Lagynocystis pyramidalis* is 60 to 100 μm (figure 10; figures 34, 35, plate 40). This is unexpectedly large since the commonest width for ascidian gill slits, to judge from drawings in Herdman (1882–8) is 25 μm, and the greatest width about 60 μm. Likewise, the functioning gill slits of amphioxus are about 40 μm wide (Bone 1961, measurements from figure 20). However, as well as the cilia, the observed slits of *L. pyramidalis* had to accommodate epithelia and perhaps other soft tissues to support the cilia. These soft tissues could easily have decreased the width of the living slit to what is seen in modern animals. The median atrium touched the distal part of the rectum on the left. Unlike the posterior coelom and the posterior part of the anterior coelom, however, it is not separated from the rectum by a deep cleft in the internal cast, i.e. by the posterior part of the oblique groove (figures 56, 58, plate 44). This is probably due to the nervous anatomy, for the internal cast in this region gives the impression that the left thecal nerve (th n in figure 6; figures 56, 58, plate 44) passed out of the dorsal left corner of the median atrium to run over and behind the rectum before continuing forward along the left side of the thecal cavity. In leaving the median atrium it blurred the contact on the internal cast between that chamber and the rectum.

Dorsally and to the right the boundary of the median atrium is marked by a slight furrow on the internal cast, or ridge on the skeleton (r m m atr, d m m atr in figure 10; figure 35, plate 40; figures 56, 58, plate 44; figure 69, plate 46). The dorsal ends of the gill bars are marked by traces in the form of short vertical striae on the internal cast, arrayed in a transverse row (tr bb in figures 6*d*, 7*d*, 10; figure 35, plate 40; figures 56, 58, 59, plate 44; figure 69, plate 46).

These traces roughly equal in number the total of calcitized gill bars developed on M_{1LV} and M_{1RV}.

The order of emplacement of the gill bars of the median atrium during life can partly be deduced. The posterior surfaces of the branchial buttresses are marked by a set of nearly horizontal grooves, running obliquely across the suture (gr tr bs in figure 11).

Each groove runs to the bottom of a gill bar, or to the bottom of a gill slit. If it runs to the bottom of gill bar it then turns through an angle and runs up the back of the bar. In this way the buttresses and attached gill bars are formed from a series of L-shaped or reversed L-shaped elements. The horizontal limbs of these elements are superimposed on each other to make up the buttress, while the more nearly vertical limbs form the gill bars. The horizontal limbs are growth traces of the bottom of gill bars or gill slits. It follows from this, that the gill bars whose bases are nearest the sutures were formed more recently than those farther away. Also new gill bars were still being formed in the adult animal up to the moment when it stopped growing or died. The way in which new gill bars appeared in ontogeny is further discussed below.

Bearing this in mind it is possible to connect the calcitized part of the gill bars with the corresponding dorsal gill bar traces. These traces are distributed across only two plates (M_{1LD}, M_{1RD}), not three like the ventral portion of the bars. Growth lines on the internal surfaces of all the marginal plates suggest that they grew by accretion. It follows that the gill bar traces must increase in age away from the dorsal median suture (M_{1LV}/M_{1RD}). This indicates that the dorsal gill bar traces would connect in life only with the calcitized gill bars of the two lateral ventral plates (M_{1LV}, M_{1RV}), which they equal in number, not with those of the central plate (M_{PM}). For it is impossible to connect the calcitized parts of the gill bars of the central plate with one of the more central of the dorsal gill bar traces without connecting old gill bars to new gill bar traces. The complete gill bars must thus have been arranged roughly as in the reconstruction (figure 10).

In ventral view the median atrium is nearly symmetrical (figures 6*e*, 7*e*; figure 25, plate 38; figure 37, plate 41). It is wide just behind the slits, but rapidly becomes narrower posteriorly since other structures fill the posterior right and left corners of the theca, i.e. pyriform bodies, auditory ganglia, rectum, etc. The median atrium is separated from the right gill opening by a considerable space inside the theca and from the left gill opening by the rectum. It could not therefore have issued by either of these openings. Furthermore, the gill slits in ventral view are arranged in a radial pattern, and converge admedian and posteriorly. This arrangement strongly suggests that water escaped from the median atrium by a posterior mid-ventral opening ventral to the stem and dorsal to the posterior, median, ventral plate M_{PM} as already mentioned.

The presence of a median ventral atrium with a median ventral gill opening or atriopore connects *L. pyramidalis* with living cephalochordates, which are the only other animals known that have such an arrangement. It seems likely that the gill slits of *L. pyramidalis* were long continuous slits from top to bottom, for there is no sign of division by a tongue bar fixed dorsally, i.e. the gill slits are likely to be primary gill slits in amphioxus terms.

The posterior coelom lies immediately in front of the median atrium (pc in figure 6*b*, *d*; figure 7; pc and d m pc in figure 35, plate 40; figures 56, 58, 59, plate 44; figure 64, plate 45; figures 67, 69, plate 46). Its boundary is marked dorsally by a groove in the internal cast and this groove curves downward to the right where it separates the posterior coelom from the right atrium (r atr in figure 6*b*, *c*; figure 35, plate 40; figure 59, plate 44; figure 64, plate 45; figure 69, plate 46). The boundary of the posterior coelom on the left is a posterior continuation of the deep cleft labelled lph/ac (figure 6*b*; figures 58, 59, plate 44; figure 64, plate 45; figures 65 to 69, plate 46). Dorsally the posterior coelom bears much the same relationship to adjacent chambers as in other mitrates. However, it does not seem to have extended down to the floor of the theca, as it does in all other cornutes and mitrates. This is presumably a specialized condition, related to the presence of the median atrium. The posterior coelom contains the dorsal gill bar traces (tr bb in figures 6*d*, 7; figure 35, plate 40; figures 56, 58, 59, plate 44; figure 69, plate 46) and in life must have included the upper, uncalcitized parts of the gill bars, which presumably consisted of connective tissue (sgb in figure 9*e*).

The inclusion of the tops of the gill bars in the posterior coelom is highly interesting. In *Mitrocystella* and *Mitrocystites* there is evidence that the posterior coelom communicated with the left pharynx (Jefferies 1968*a*, pp. 285, 317) and this suggests that the posterior coelom was homologous with an epicardium of a tunicate, for the epicardia pouch out from the pharynx during the life history of all modern tunicates, and in *Ciona* they remain connected with it in the adult. The epicardia are probably primarily excretory organs (Berrill 1955, p. 103). By analogy the posterior coelom of mitrates and cornutes in general, including that of *Lagynocystis*, was probably excretory. Now the nephridia of amphioxus are situated at the tops of the primary gill bars, resting in the primary coelom and opening into the atrium (Franz 1927, p. 566; Drach 1948, p. 972). The nephridia of amphioxus could easily have evolved from the presumably excretory posterior coelom of *Lagynocystis* by upward lengthening of the gill slits, so as to split the posterior coelom into segments corresponding each to a gill bar. Indeed it is possible that in *Lagynocystis* the posterior coelom already had an undulating lower edge, with each downward extension corresponding to a gill bar.

Turning now to the pharynx and anterior coelom, the relations in *L. pyramidalis* are somewhat different to those in other mitrates. Most mitrates have a very strong oblique groove in the dorsal surface of the internal cast running from posterior left to anterior right (figure 8). The right slope of the oblique groove is steeper than the left slope so that the groove separates a left more ventral and anterior chamber (left pharynx) from a right, more dorsal and posterior one (anterior coelom). As well as this, the anterior coelom of normal mitrates has been partly obliterated by a right pharynx pouching out from the left one (figure 2*f*, 9*f*). The same oblique groove is recognizable in the internal cast of *L. pyramidalis* (ob gr in figure 6*b*; figure 59, plate 44; figure 64, plate 45; figures 65 to 69, plate 46). As in other mitrates it runs from posterior left to anterior right and is entirely supported by the same two plates (i and d) as in *Chinianocarpos* and *Peltocystis* (cf. figure 3). Unlike other mitrates, however, the oblique groove of *L. pyramidalis* is variable in strength between individuals, and always very weak. Also its left and right

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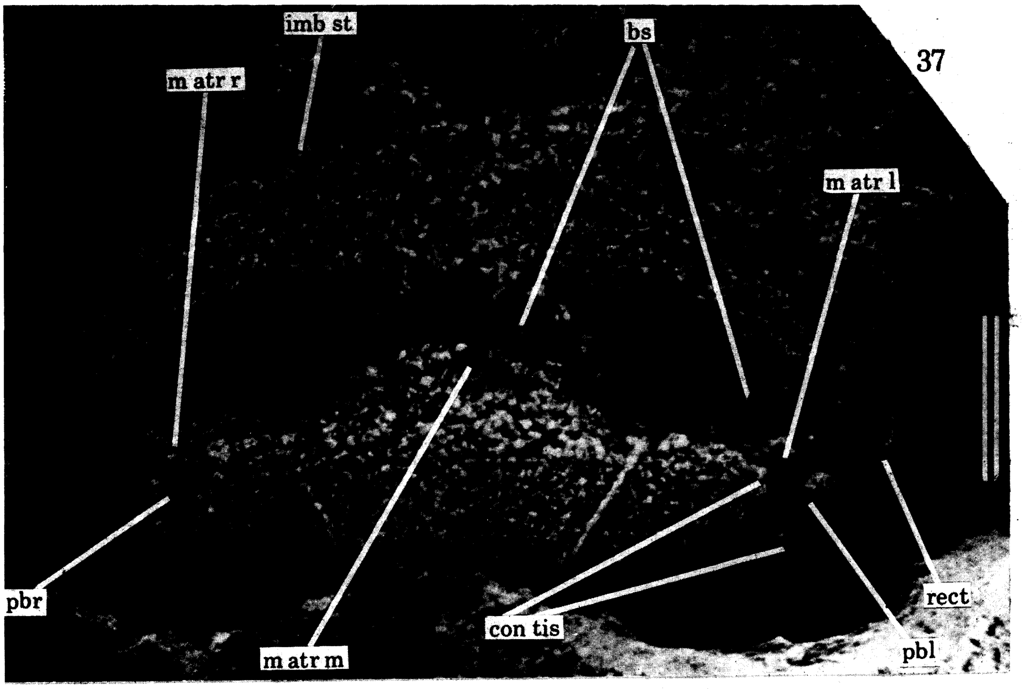
DESCRIPTION OF PLATE 41

Lagynocystis pyramidalis. Internal casts representing the soft tissues of the posterior part of the theca (cf. figure 6). All from the Šárka Formation of Šárka. Scale lines 1 mm.

FIGURE 37. Ventral aspect showing the median atrium and the branchial slits in front of it. NM 317/69.

FIGURE 38. Left aspect of same specimen as figure 37. To show especially the end of the rectum.

FIGURE 39. Left dorsal aspect of E 16107. Note how the dorsal border of the ridge of rock representing retaining connective tissue is rounded instead of rough as in figure 38. This probably indicates that the nerve n_{BCL} was partly buried in the thecal wall, unlike figure 38.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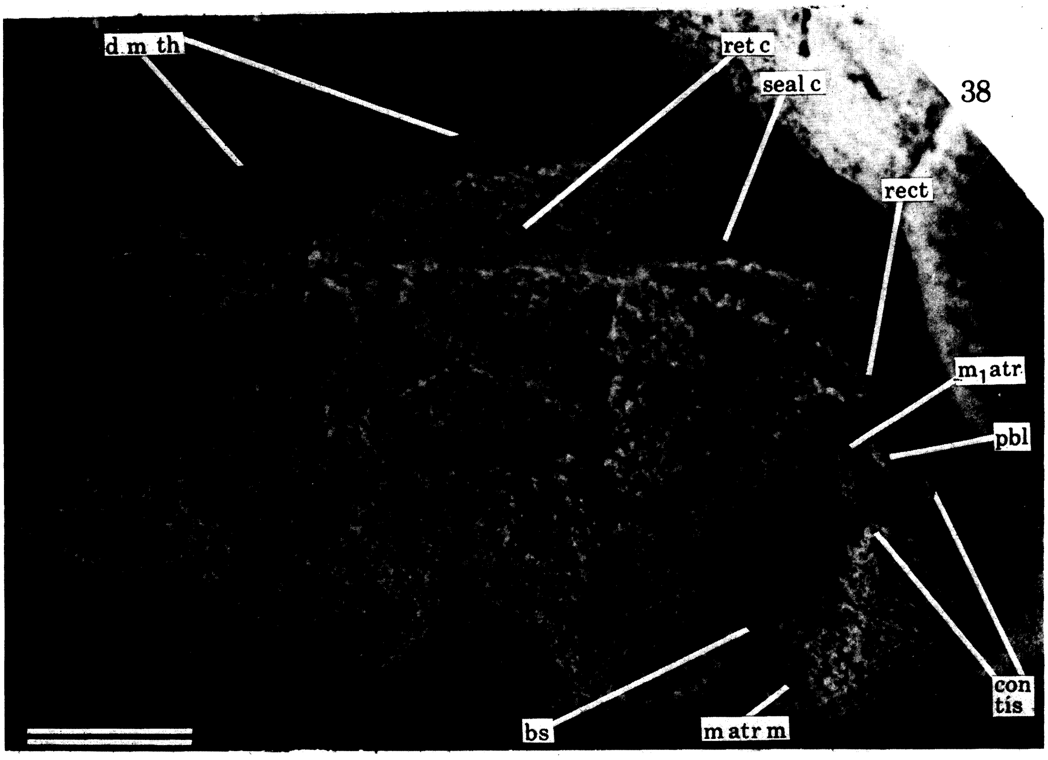
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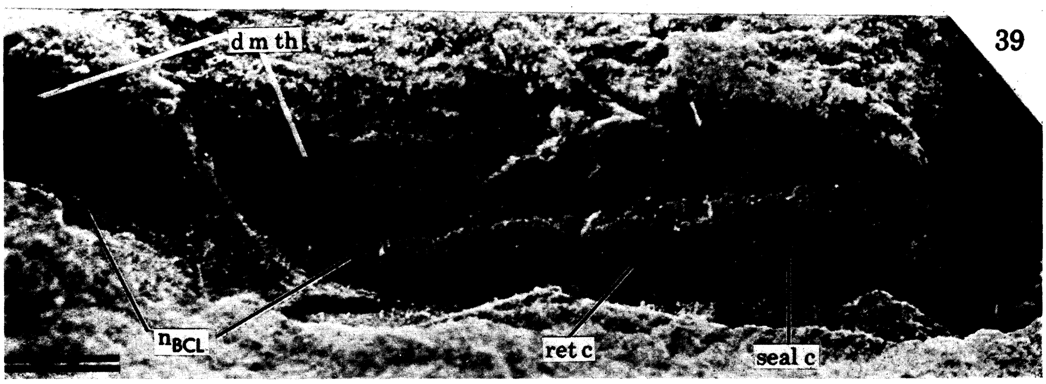
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FIGURES 37 to 39. For legends see facing page.

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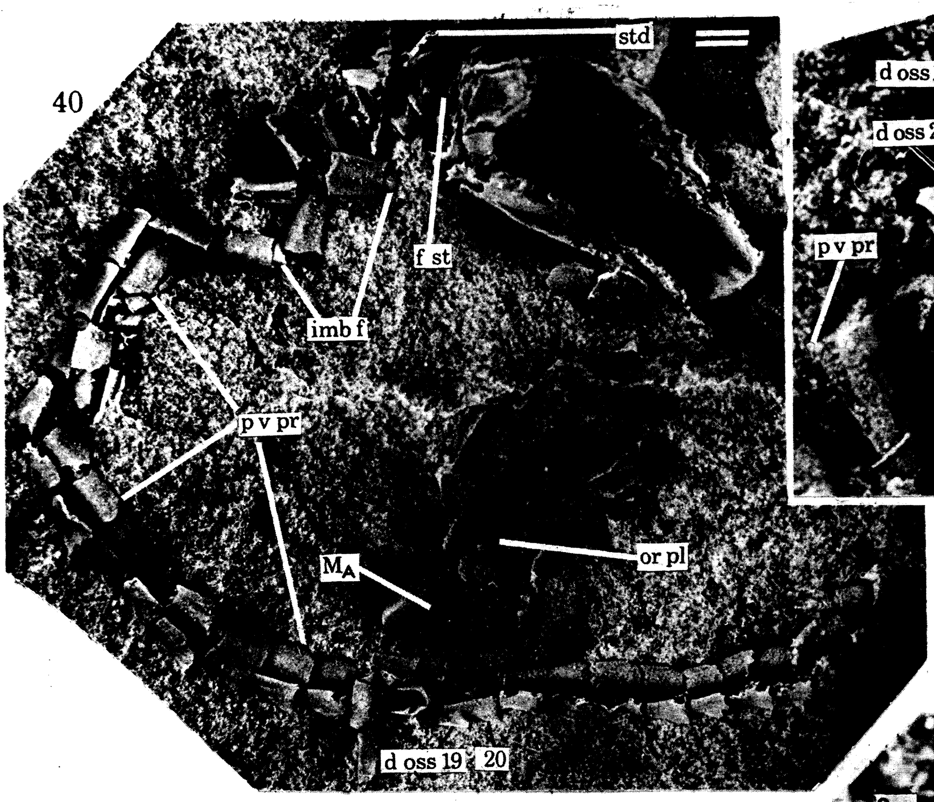

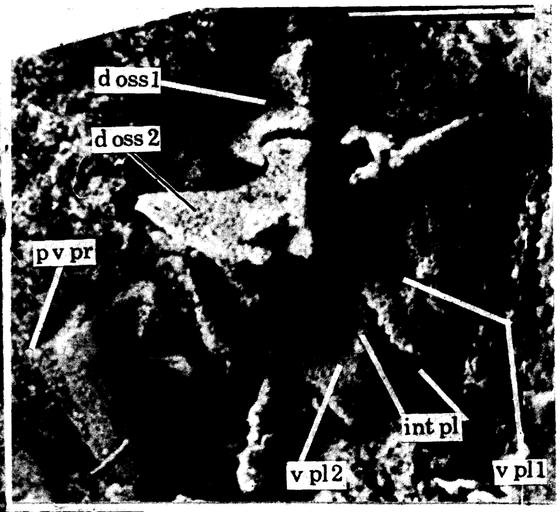

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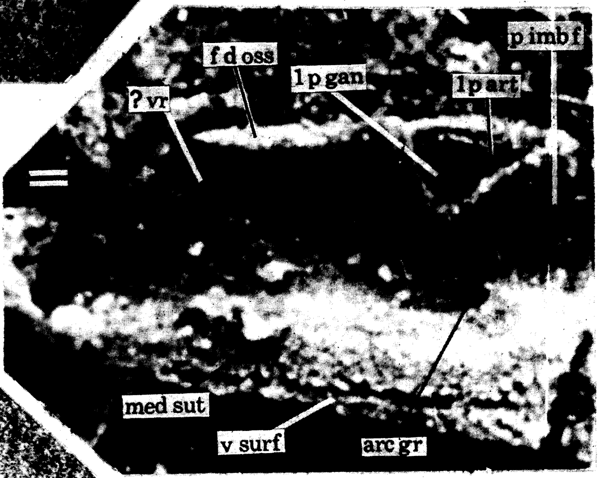

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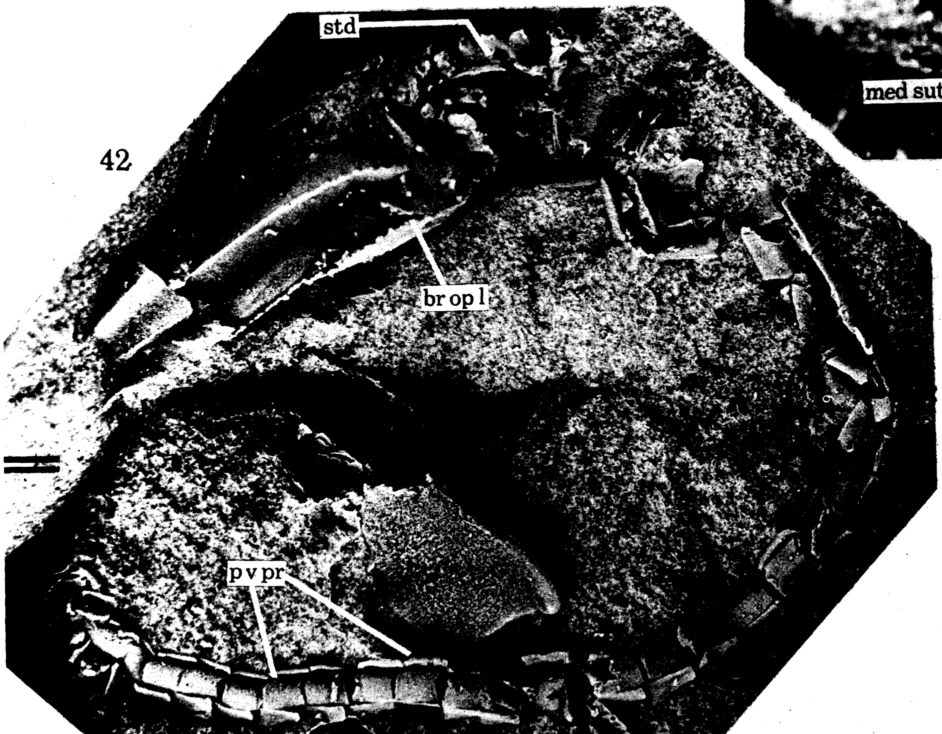

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FIGURES 40 to 44. For legends see facing page.

slopes are about equal in steepness as if the chambers that it separated did not lie one above the other. The oblique groove, in fact, gives the impression of being basically as in other mitrates, but almost smudged out.

Posteriorly the oblique groove runs back to join the deep cleft just left of the posterior coelom. In its relations this cleft is much like the posterior part of the oblique groove in other mitrates. However, the cleft can be followed forward not only into the vestigial oblique groove, but also into a weak line on the dorsal face of the internal cast which is clearly distinct from the oblique groove (l ph/ac in figure 6; figures 65, 67, 68, plate 46). Furthermore, this weak line seems to have a right counterpart (r ph/ac in figure 6; figure 64, plate 45). These two lines have no equivalent in other mitrates.

The relations seen in the internal cast of *L. pyramidalis* strongly suggest that the basic mitrate arrangement of chambers was modified as shown in figure 9. The pharynx had pushed back towards the median atrium so that gill slits could penetrate the intervening wall. The backward and upward growth of the pharynx would have squashed the anterior and posterior coeloms upwards (cf. figures 9*g*, *e*). In consequence the posterior coelom would be lifted off the floor of the theca and the anterior coelom would have been squeezed outwards, so that it lay partly left of the oblique ridge (or, see especially figure 9*c*), while the oblique ridge itself would become weak, vestigial and more or less symmetrical. The weak lines labelled l ph/ac and r ph/ac would represent the new dorsal lines of contact of the left and right pharynxes against the anterior coelom.

Such an explanation of the grooves and lines in the internal cast implies that in the earliest life stages the chambers of *Lagynocystis* were arranged much as in *Mitrocystella.*

Later during ontogeny, the median atrium appeared and the pharynx pushed backwards and upwards squashing the anterior and posterior coeloms into their new shapes. These changes were parallel to what happened in phylogeny, for the hypothetical primitive mitrate, like the ancestral cornute, would have had no median atrium and the posterior coelom would have extended from the floor to the ceiling of the theca.

The right atrium was a little chamber defined by grooves in the internal cast (r atr in figure 6*b* *c*, *d*; figure 9; figure 35, plate 40; figure 59, plate 44; figure 69, plate 46). It presumably had gill slits between itself and the right pharynx, but as in other mitrates these are hypothetical.

The left atrium in other mitrates is the chamber that receives the rectum, as it does in a tunicate tadpole (Text-figure 7*a*, *b*, in Jefferies 1968*a*, p. 285ff., 1969, p. 509ff.). In such mitrates the terminal portion of the rectum is almost vertical, running up from near the floor of the posterior coelom. In *L. pyramidalis* the posterior coelom has been lifted upwards by the ventral pharynx and median atrium, so the proximal end of the rectum would probably have been lifted up as well. It is likely, in fact, that the rectum ran downwards just left of the posterior portion of the

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Description of plate 42

Lagynocystis pyramidalis. Latexes of specimen NM 323/69 mainly to show features of the stem (cf. figure 12). Scale lines 1 mm in figures 40 to 42; scale lines 0.1 mm in figures 43, 44. Šárka Formation, Šárka.

Figure 40. General view of theca and stem, right side.

Figure 41. Detail of figure 40 to show especially the skeleton at the front end of the hind-stem.

Figure 42. General view of theca and stem, left side.

Figure 43. Internal surface of right ventral plate, probably ventral plate 5 of hind-stem. See also figure 45.

Figure 44. Ventral surface of dorsal ossicle, probably third dorsal ossicle of hind-stem.

oblique groove as shown in figure 7 to open at the left gill opening. The end of the rectum (rect in figure 6*a*, *e*) is represented by a bump on the ventral side of the internal cast (rect in figure 38, plate 41). Presumably the left atrium existed round the rectum, as in other mitrates, but there is no direct evidence of it, probably because the skeleton was covered internally by connective tissue in this region. It appears that the rectum opened nearer the gill opening than in other mitrates, and, indeed, the left gill opening had come to serve, at least partly, as anus. It is well known that the anus of amphioxus is on the left side of the animal (Franz 1927, pp. 476, 615; Drach 1948, p. 933).

Three groups of gill slits can therefore be inferred in *L. pyramidalis*, i.e. hypothetical slits opening into the left atrium, hypothetical slits opening into the right atrium, and observed slits opening into the median atrium. The group opening into the median atrium was itself divided into right, left and median subgroups, corresponding to thecal plates. The likely order of appearance of the groups opening into the three atria is of interest. The geometrical relations of the left pharynx, right pharynx and anterior coelom in other mitrates lead to the conclusion that the left pharynx appeared earlier in ontogeny than the right pharynx since the oblique groove, between left pharynx and anterior coelom, has been disturbed by the pouching-out of the right pharynx. It is therefore likely that the left gill slits of normal mitrates appeared in ontogeny before the right gill slits. *L. pyramidalis* possesses an oblique groove, and this suggests that the left gill slits appeared before the right gill slits as in other mitrates. However, the oblique groove is weakened, as already mentioned, probably by upward pressure of the median part of the pharynx, connected with the appearance of gill slits between the pharynx and the median atrium. Most probably therefore the median atrium appeared later than did the anterior coelom or the left and right pharynxes and atria. It has been shown above that gill slits of the median atrium continued to be laid down till the animal reached full size. In summary, the most likely sequence of appearance for the gill slits in *L. pyramidalis* was therefore: (1) gill slits of left atrium; (2) gill slits of right atrium and (3) gill slits of median atrium which continued to be produced probably till death.

Now this inferred sequence is very similar to the observed sequence in amphioxus. The first gill slits to appear in this animal are the more anterior gill slits of the left side of the definitive animal (ontogenetically primary gill slits). The next group to appear are the more anterior gill slits of the right side of the definitive animal (ontogenetically secondary gill slits), and afterwards gill slits are added on both sides posterior to those already there (Willey 1894 p. 230ff.).

There is evidence of soft tissue associated with the contact between dorsal and ventral skeleton in the posterior part of the theca and probably related to the right and left branchial openings. This tissue was probably mainly connective but included some nerve, and perhaps muscle. The evidence for it consists of grooves in the skeleton, expressed as ridges in the internal cast (figure 6*a* to *e*).

On the right side there is a small lump on the internal cast of M_{1RD} just in front of the branchial hinge (art c in figure 6*b*; figures 59, 60, plate 44). This probably represents articular connective tissue holding dorsal and ventral plates together at the hinge. It is probably continuous with connective tissue covering the inside of the ventral skeleton. Anterior to this lump on the right side of the internal cast there is a ridge included in the dorsal skeleton dorsal to the gill opening, and a corresponding ridge ventral to the gill opening (seal c in figure 6*b* to *e*; figure 25, plate 38; figures 59, 60, plate 44; figure 67, plate 46). These probably represent connective tissue that bulged slightly out of the containing grooves when the gill opening gaped and consequently sealed it when it closed. Similar connective-tissue seals have been postulated round the gill slits of *Scotiaecystis curvata* (Jefferies 1968*a*, p. 282). Anterior to the gill opening on the right side of the theca is another ridge on the internal cast of the dorsal skeleton which continues forward into plate M_{4L} (figure 63, plate 45; figures 65, 67, plate 46). It has an undulating course, going up in the plates and down at the sutures. Its dorsal surface is gently rounded transversely and probably represents a nerve to the right side of the buccal cavity (n_{BCR}) corresponding to the nerve n_{2R} of other mitrates (Jefferies 1968*a*, pp. 296ff., 319ff., 1969, p. 523). The nerve would have passed into the dorsal skeleton from the soft layer inside the ventral skeleton. Ventral to the presumed position of the nerve there is an area on this ridge characterized by strong growth lines on its surface (ret c in figure 6*c*). By analogy with other mitrates it probably represents a dorsal extension of the ventral soft layer of muscle and connective tissue, serving to hold the dorsal and ventral skeletons together anterior to the gill opening (cf. *Mitrocystella* and *Mitrocystites*, Jefferies 1968*a*, pp. 259, 314).

On the left side of the theca, there is most posteriorly a small lump on the internal cast of M_{1LD} (art c in figure 6*b*, *d*; figures 56, 58, plate 44) just in front of the branchial hinge and corresponding to the similar lump already noticed on the right side. It probably represents connective tissue with a corresponding function of holding the left branchial hinge together. Anterior to it is a small ridge that reaches forward to the position of the rectum (seal c in figure 6*a*, *b*, *e*; figures 56, 58, plate 44).

Anterior to the inferred position of the rectum is another ridge, strongly covered with growth lines, and hence reminiscent of a structure already seen on the right (ret c and seal c in figure 6; figures 38, 39, plate 41; figure 58, plate 44; figure 68, plate 46). The dorsal margin of this ridge is sometimes rough, the roughness corresponding to the ends of growth lines (figure 38, plate 41). In other specimens the ridge has a rounded dorsal margin, much like the structure on the right (figure 39, plate 41). This rounded dorsal margin probably represents the position of the nerve n_{BCL} to the buccal cavity, being a forward continuation of the left thecal nerve that came out of the dorsal left corner of the median atrium. Whether the dorsal margin of the ridge is rounded or rough probably depends only on whether the nerve was partly buried in the skeleton or not. The part of the ridge with prominent growth lines can be divided into a more posterior part, where the lines arch gently upwards (seal c) and a more anterior part (ret c) where they are straight.

The part with the arched growth lines could represent the position of connective tissue dorsal to the left gill opening and acting as a seal (seal c in figure 6*a*, *b*). The part with the straight growth lines would then represent retaining connective tissue, holding ventral and dorsal skeleton together anterior to the gill opening (ret c). On this assumption the left gill opening, which also functioned as anus, would have been about the same length as the right gill opening.

So far as the soft tissue connecting dorsal and ventral skeletons is concerned, therefore, *Lagynocystis* has an arrangement that makes good mechanical sense, with articular portions holding the branchial hinges together behind the branchial openings, portions sealing the branchial openings when these were closed, and retaining portions holding ventral and dorsal skeletons together anterior to the branchial openings.

(*c*) *The stem*

As in other calcichordates the stem has three parts, i.e. the fore-, mid- and hind-stems. These correspond to what I have called the anterior, medial and posterior stems in earlier papers (see Jefferies 1967, 1968*a*, 1969). The new less formal names have been adopted to accord with the view that the three parts in cornutes are not homologous with the like-named parts in mitrates (Jefferies & Prokop 1972). As explained in § 1 the cornute that gave rise to the mitrates had probably lost its mid- and hind-stem, so that the entire stem of mitrates is an elaboration of the fore-stem of cornutes. I shall describe the stem in the order hind-stem, fore-stem, mid-stem, since the mid-stem is transitional between the other two portions.

The skeleton of the hind stem (figure 5*a*, *e*, *f*, and plates 42 and 43) contained 32 dorsal ossicles overlying 32 pairs of ventral plates in the only specimen where the entire length could be seen (NM 323/69 = Hanuš 190). As in other calcichordates, it ended abruptly. The observed position of the end of the stem is not likely to be chance, since the last few segments quickly decrease in height towards the end.

The skeleton of each segment of the hind-stem (figure 12) consists of a dorsal ossicle and two ventral plates. Along the median dorsal line each ossicle has a sharp edge, culminating in a point near the posterior end. These points give the dorsal edge of the hind-stem a serrated profile (figure 5*a*). The ventral plates are different from those of other mitrates in external shape (figure 55, plate 43). In other mitrates the right and left ventral plates of each segment meet at a sharp edge ventrally. In *L. pyramidalis*, on the other hand, the ventral portion of each plate is truncated, so that a distinct, slightly concave, ventral surface is developed (figures 5*e*, 12*e*). At the outer, posterior corners the ventral surface is produced into postero-ventral processes (p v pr).

The ventral plates of the hind-stem of *L. pyramidalis* can be compared with the homologous ventral plates of the fore-stem of the advanced cornute *Reticulocarpos*. These plates have a similar, though much wider, flat ventral surface (figure 2*c*) with paired postero-ventral spikes in each segment. As regards function, the ventral surface of the fore-stem of *Reticulocarpos* was probably used to press downwards and forwards on the sea bottom, so pulling the theca backwards during crawling (Jefferies & Prokop 1972, see also § 5). It is likely that the homologous ventral surface of the hind-stem of *L. pyramidalis* was likewise used as a bearing surface. All other known mitrates probably pulled themselves backwards by bearing surfaces on the dorsal ossicles,

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DESCRIPTION OF PLATE 43

Lagynocystis pyramidalis, detail of stem. Scale lines 0.1 mm in figures 45 to 54, 1.0 mm in figure 55. All specimens from the Šárka Formation of Šárka except figure 55, which is from the Šárka Formation of 'Bohemia'. Cf. figure 12

FIGURE 45. Internal cast of the ventral plate shown in figure 43. NM 323/69.

FIGURE 46. Left aspect of internal cast of a dorsal ossicle, probably the 4th in the hind-stem. NM 323/69.

FIGURE 47. Oblique view of specimen shown in figure 46.

FIGURE 48. Natural mould of dorsal, anterior, posterior surfaces of dorsal ossicle in ventral view. (Same ossicle as figures 44, 49 to 52.) NM 323/69.

FIGURE 49. Latex of same dorsal ossicle in dorsal aspect.

FIGURE 50. Latex of same dorsal ossicle, left lateral aspect. Apex damaged.

FIGURE 51. Latex of same dorsal ossicle, antero-dorsal aspect.

FIGURE 52. Latex of same dorsal ossicle. Posterior aspect.

FIGURE 53. Natural mould of ventral surface of one of the most anterior ossicles of the hind-stem, probably the first dorsal ossicle. Left anterior part broken away. NM 319/69.

FIGURE 54. Natural mould of ventral surfaces of portions of three dorsal ossicles. NM 321/69.

FIGURE 55. Latex of hind-stem in oblique, ventral aspect, to show ventral surfaces of ventral plates and postero-ventral processes. MCZ 982.

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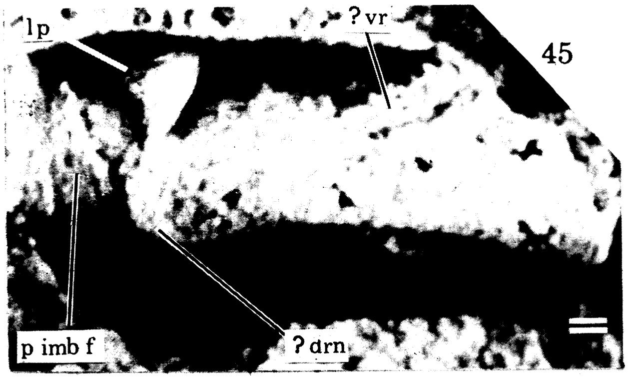

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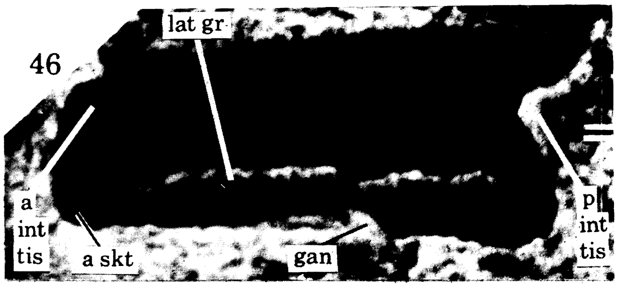

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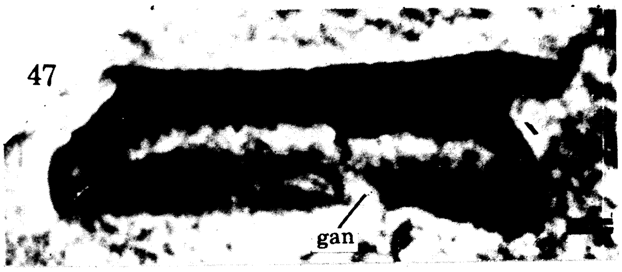

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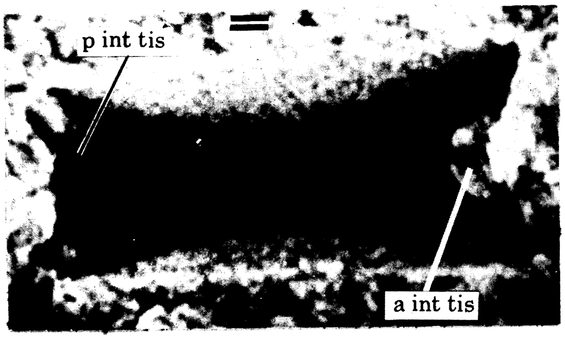

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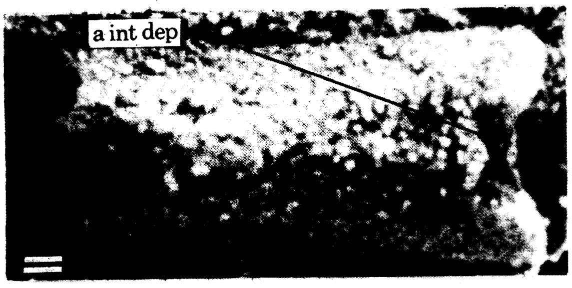

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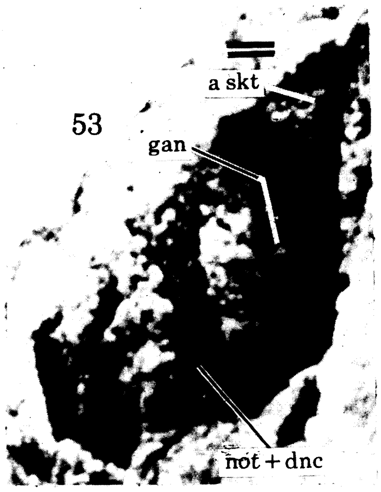

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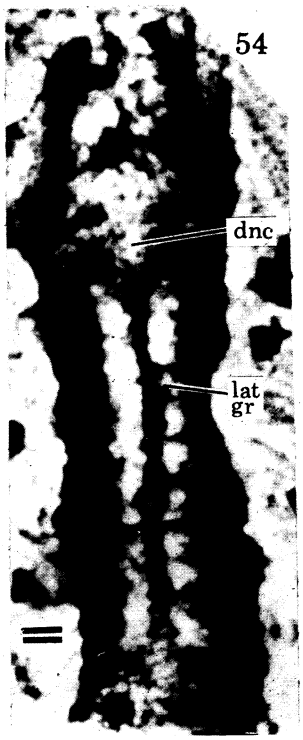

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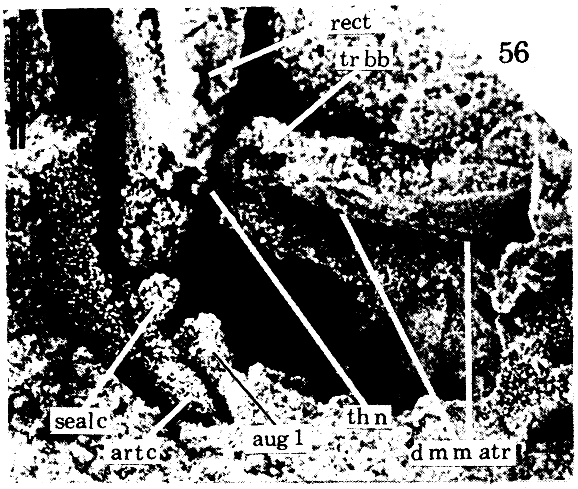
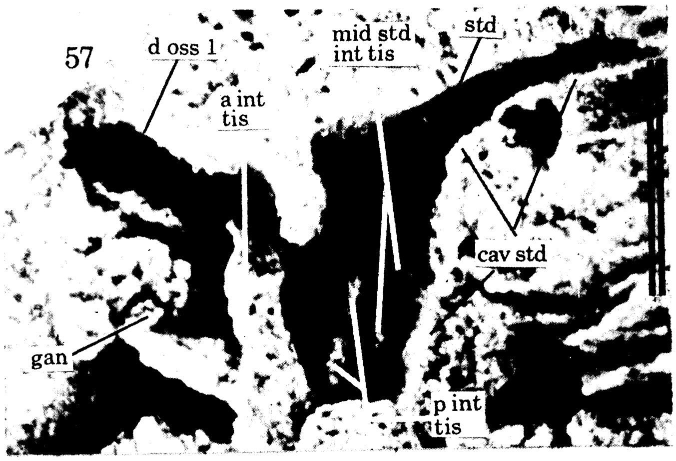
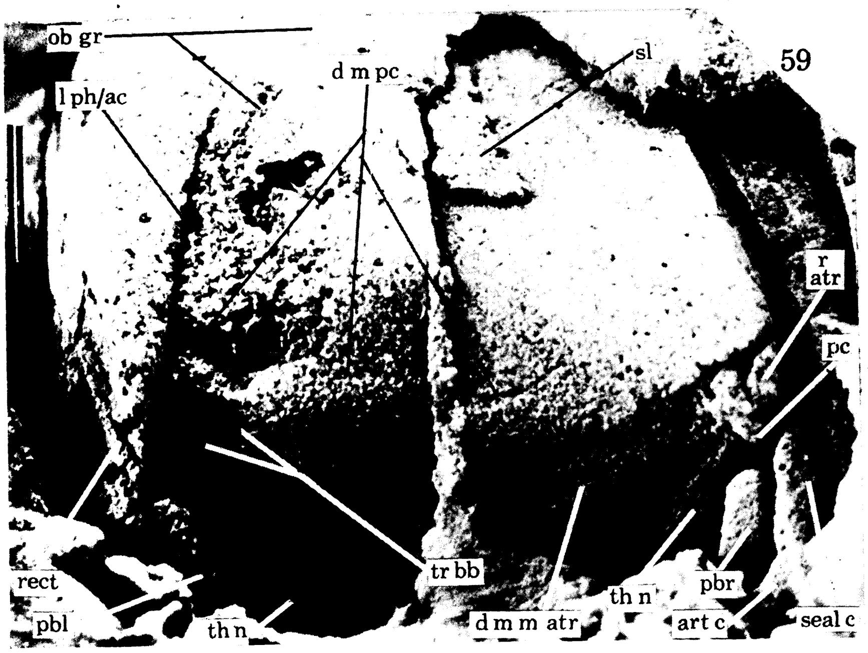
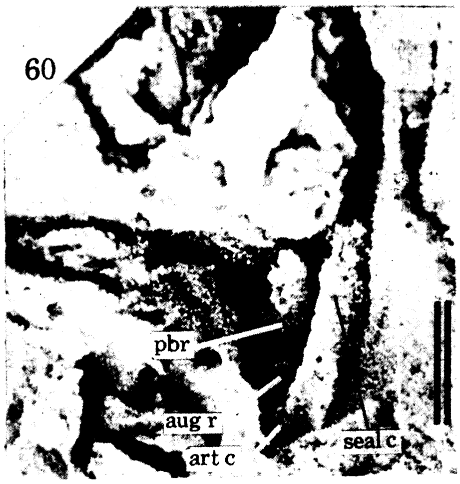
FIGURES 45 to 55. For legends see facing page.









FIGURES 56 to 60. For legends see facing page.

as explained below (§5). In using ventral bearing surfaces, the stem of *L. pyramidalis* was cornute-like, and more primitive than the stem of any other known mitrate.

The internal structure of the hind-stem is represented in figure 12. Each ossicle had an anterior and a posterior interossicular depression (a int dep, p int dep, figures 49, 51, 52, plate 43). The depressions between successive ossicles came together to form interossicular cavities, presumably filled with soft tissue (int tis in figure 12*j*; figures 46 to 48, plate 43). In *Mitrocystella* and *Mitrocystites* the interossicular cavities are divided into an outer and an inner portion. Also they communicated in these genera by vertical canals with the main cavity of the stem and were connected to each other by a dorsal longitudinal canal running through the ossicles. All these canals probably carried blood and the vertical canals passed through the dorsal nerve cord in a way unknown in other chordates (Jefferies 1968, pp. 289ff., 317ff.). The interossicular cavities of *L. pyramidalis*, however, were not divided into inner and outer portions and have no associated canals. The tissue that filled them probably corresponded to the tissue filling the outer interossicular depressions of Mitrocystitids and did not need a blood supply. The tissue was therefore probably ligament, rather than muscle, and opposed the muscles of the main cavity of the stem by elasticity. The absence in *Lagynocystis* of vessels passing through the dorsal nerve cord could well be primitive for mitrates. Such vessels were probably absent in the closely related mitrate that led to amphioxus and need not have existed in the mitrate ancestors of vertebrates and tunicates.

Paired posterior processes of each ossicle (p pr) fitted into paired anterior sockets in the next ossicle behind (a skt in figure 44, plate 42; figures 46, 47, 53, plate 43). The interossicular articulations so produced were in the same position as those of *Mitrocystella* and *Mitrocystites*. They were converse in structure, however, since in Mitrocystitids paired bosses on the anterior surface of an ossicle fitted into pits in the next ossicle in front.

The ventral surface of the dorsal ossicles is complicated (figure 44, plate 42; figures 46, 47, 53, 54, plate 43). Laterally there are facets which received corresponding facets of the ventral plates (f ven pl, f d oss). These facets are marked by longitudinal striae which would have strengthened the connexion between ossicle and plates. Median to the facets are deep lateral grooves (lat gr in figure 12*d*; figure 46, plate 43) which are separated by a median groove (m gr). The median groove justifies its name by being slightly concave, but appears as if on a high wall between the deep lateral grooves on each side of it. The median groove continues from one ossicle to the next, whereas the lateral grooves do not. By comparison with other mitrates the median groove probably indicates the position of the dorsal nerve cord (dnc in figure 12*j*; figure 54, plate 43). The notochord, which would have been a broader structure, probably touched the skeleton only near the interossicular articulations (not in figure 12*j*).

DESCRIPTION OF PLATE 44

Lagynocystis pyramidalis, natural internal moulds of postero-dorsal parts of theca. (cf. figure 6*b*, *d*) and styloid region of stem. All from Šárka Formation of Šárka. Scale lines 1.0 mm.

FIGURE 56. Dorsal aspect of posterior left portion of theca. The left pyriform body has broken away, leaving a hole. NM 319/69.

FIGURE 57. Natural mould of styloid and first dorsal ossicle: right, dorso-lateral aspect. BMNH, E29048.

FIGURE 58. Natural internal mould of posterior part of the theca; postero-dorsal aspect. NM 312/69.

FIGURE 59. Natural internal mould of posterior part of the theca; postero-dorsal aspect. NM 314/69.

FIGURE 60. Natural internal mould of right posterior part of theca. BMNH, E16109.

The ventral surfaces of all ossicles carried a pair of ventral processes posteriorly (v pr in figure 12*b*, *d*, *h*; figure 44, plate 42). These helped to hold the ventral plates in position. In front of the ventral processes the more anterior ossicles had distinct pits, which by analogy with other mitrates, probably held ganglia (gan p). In *Mitrocystites* and *Mitrocystella* the ganglionic pits communicate by canals or grooves with the groove that held the dorsal nerve cord (figures 32, 33, plate 39). The ganglia in the pits of *Lagynocystis* were presumably also connected with the dorsal nerve cord, but the connecting points would not have been in contact with the skeleton. A widening of the median groove near the ganglionic pits, however, may show where nerves went off to the ganglia (w m gr in figure 44, plate 42).

The internal surfaces of the ventral plates also have features of interest. The dorsal margin of each plate forms a flattened but striated facet that made contact with the facet of the ossicle above (f d oss in figure 12*g*; figure 43, plate 42). There is also a posterior imbrication facet (p imb f in figure 12*b*; figure 43, plate 42) which fitted against the anterior imbrication facet of the next plate behind (a imb f in figure 12*a*, *e*; imb f in figure 40, plate 42). In the ventral medial line there is a broad flat suture (med sut) by which each plate made contact with its counterpart.

The lateral pits are striking features of the dorsal part of the internal surface of the ventral plates (figure 12*f*). Each such pit has a posterior articular part and an anterior ganglionic part (l p art and l p gan, figure 43, plate 42). The articular part received, and was braced against, the ventral processes of the dorsal ossicles while the ganglionic part, which is continuous with the ganglionic pits of those dorsal ossicles which have them, presumably helped to house the segmental ganglia.

An arcuate groove comes out of each lateral pit ventrally (arc gr in figure 12*b*; figure 40, plate 42). Each groove probably represents the boundary, or myocomma, between two muscle blocks, curving round ventrally into the ventral boundary of the muscle blocks. This is likely, because the ganglia seem to have lain between the muscle blocks of other mitrates (Jefferies 1968*a*, p. 293). Also the lateral grooves, which presumably housed the dorsal portions of the muscle blocks, are partly subdivided near the ganglionic pits (figures 46, 47, 54, plate 43). In lying between muscle blocks the ganglia of *Lagynocystis* and other mitrates resembled the dorsal root ganglia of lampreys (Romer 1949, p. 541) and the dorsal roots of amphioxus (Franz 1927, p. 526). It may also be that the arcuate groove carried a dorsal-root nerve.

By apparently possessing dorsal root ganglia *L. pyramidalis* differed from amphioxus which has no well-defined ganglia in its dorsal nerves, but instead has the cell bodies of the sensory fibres scattered in the dorsal nerve cord and in the proximal parts of the dorsal root nerves (Goodrich 1930). The ganglionated condition found in vertebrates, appendicularian tunicates and mitrates is presumably more primitive than that of amphioxus, which is secondarily simplified in this respect, as in others.

The grooves marked ? vr in figure 12*b*, *f*, *j*; figure 43, plate 42; figure 45, plate 43 were faint but constant. They seem to have run from the middle of muscle blocks towards the dorsal nerve cord and could very well represent the positions of ventral roots. If they do so, the 'ventral roots' concerned are more likely to have been made of muscle than of nerve, since Flood (1966) has shown that the so-called ventral roots of amphioxus are muscular, and, histologically speaking, muscle-tails of this sort are a primitive, echinoderm-like characteristic.

The hind-stem segments are not all identical. The ossicles and plates shown in figure 12 represent the fourth or fifth segment of the hind-stem. The first two hind-stem segments are much shorter than the ones behind and the ventral plates of segment 1 of the hind-stem are triangular (figure 5*a*; figure 41, plate 42). Also the articulations between the ossicles are very well developed in the first two segments of the hind-stem, and the interossicular depressions are less high than usual, so that the ligaments in them would have been low and strap-like (figure 57, plate 44). In addition, the articular membrane between the plates of the segments 1 and 2 of the hind-stem was covered with intercalary plates, which is not the case farther behind (figure 5*a*, *e*; figure 41, plate 42). All these features suggest that this region of the stem was particularly capable of ventral flexion. Another region of strong ventral flexion probably existed near the tip of the stem, distal to segment 24 (figure 5*a*). The function of these regions of strong ventral flexion will be dealt with below (§5). Ossicles 19 and 20 are fused together in the specimen on which the reconstruction is based (NM 323/69) but this may be pathological (figure 40, plate 42).

The intercalary plates between segments 1 and 2 of the hind-stem resemble those in the fore-stem. They probably derive from the hypothetical advanced cornute or primitive mitrate ancestor which had alternating intercalary and major plates throughout the length of the fore-stem and had lost the old mid- and hind-stem. The primitive mitrate *Chinianocarpos* had intercalary plates between the ventral plates along the whole length of the hind-stem (Ubaghs 1970, p. 80, figure 31; Jefferies & Prokop, 1972, text-figure 9).

The fore-stem, as in other mitrates, was presumably more flexible in all directions than the rest of the stem, since it had a big lumen enclosed in a skeleton of loose plates. These plates are of three types – major, intercalary and spiked (maj pl, int pl, spk in figures 5*a*, *e*, *f*; figure 23, plate 37; figures 24, 27, plate 38). The major plates are not always easy to recognize as such and sometimes become rather spiky. They are presumably homologous with the major ventral plates of the fore-stem of cornutes and serially homologous with the ventral plates of the hind-stem in *Lagynocystis pyramidalis*. The spiked plates are developed dorsally and laterally, and lie at the intersections of two sets of imaginary helical lines. The individual spikes are thorn-like and curve forwards. They are probably serially homologous with the dorsal ossicles of the hind-stem and the ossicles that fused to form the styloid. The intercalary plates fill the gaps between the other plates.

The soft parts of the fore-stem presumably included muscles, probably divided into muscle blocks, and an anti-compressional notochord (chambered organ) continuous with the structure in the hind-stem. At the front end of the fore-stem was the brain, as in other calcichordates. There was presumably a dorsal nerve cord with paired segmental ganglia as in the hind-stem.

The mid-stem is less well defined than in other mitrates (figures 40, 42, plate 42). A dorsal styloid exists, but no ventral plates articulate with it. The styloid has four or five spikes down its back. There is a posterior interossicular depression which abuts against the anterior depression of the first ossicle of the hind stem (figure 57, plate 44). Both depressions are low, and the contained ligament would have been strap-like, for strong ventral flexion. A vestigial interossicular cavity exists within the styloid suggesting that the posterior part of the styloid was formed by the fusion of two dorsal ossicles. The more anterior spikes of the styloid perhaps represent spiked fore-stem plates that also fused into the styloid.

Speaking generally, the fore-stem is the most primitive part of the stem of *Lagynocystis*, i.e. it is most like the undifferentiated stem of the hypothetical ancestor, which had lost the old mid- and hind-stem, but had not yet regionated the stem into new fore-, mid- and hind-portions. The hind-stem ossicles probably developed from spiked plates, which became articulated to each other for ventral flexion and developed dorsal cutting edges. To form the styloid the two anterior dorsal ossicles so formed would fuse together and perhaps also fuse with two or three spiked plates which had not transformed into dorsal ossicles. The styloid was a socket, by which the muscles of the fore-stem could move the mid- and hind-stem as a unit. The ventral plates of the hind-stem would develop from the more posterior ventral major plates of the old fore-stem of the ancestral cornute. The intercalary plates of the old fore-stem would disappear in most of the hind-stem region.

Professor Ubaghs has interpreted the stem of mitrates differently, i.e. he regards it as an arm, with the median groove housing a water vessel and the ganglionic pits housing the tube feet. Furthermore, he considers that what are here called dorsal ossicles represent flooring plates of the arm while the ventral plates represent cover plates that were able to open (Ubaghs, 1961, 1963, 1968, 1970, 1971, p. 168; see also Jefferies 1967, 1968*a*, *b*, 1969, 1971; Jefferies & Prokop 1972). He also considers that what is here called the dorsal side of mitrates was ventral.

The broad, striated facets of contact between ossicles and plates in *Lagynocystis*, and the way in which the ventral processes are braced inside the lateral pits, indicate, against Ubaghs's view, that any movement of the plates relative to the dorsal ossicle was very limited indeed, and the flat median sutures of the ventral plates suggest that the plates would not separate in life. The massiveness of the plates, with their distinct ventral surfaces and postero-ventral processes, is also difficult to reconcile with their being cover plates, but easy to understand if they represent modified ventral plates of the fore-stem of the ancestral cornute.

In summary, the stem of *L. pyramidalis* was basically like that of other mitrates. There are signs in the hind-stem of ventral segmental muscle blocks with segmental ganglia between them. The dorsal nerve cord and notochord probably did not much differ from those of other mitrates, but are less well recorded in the skeleton. There were interossicular dorsal ligaments, but probably no dorsal blood vessels and no sign of vessels passing up through the dorsal nerve cord as in other mitrates. The absence of such vessels may well be primitive for mitrates. Since they did not exist in *Lagynocystis* they would probably also be absent in the closely related mitrate that is assumed to have given rise to amphioxus. Also, they need not have existed in the mitrate ancestors of vertebrates or tunicates. The hind-stem of *Lagynocystis* is in some ways very primitive, having ventral bearing surfaces like the fore-stem of the ancestral cornute that gave rise to it.

(*d*) *Brain and cranial nerves*

The brain and cranial nerves of *L. pyramidalis* resemble those of other mitrates in basic plan, but are modified, mainly by the presence of the median atrium.

DESCRIPTION OF PLATE 45

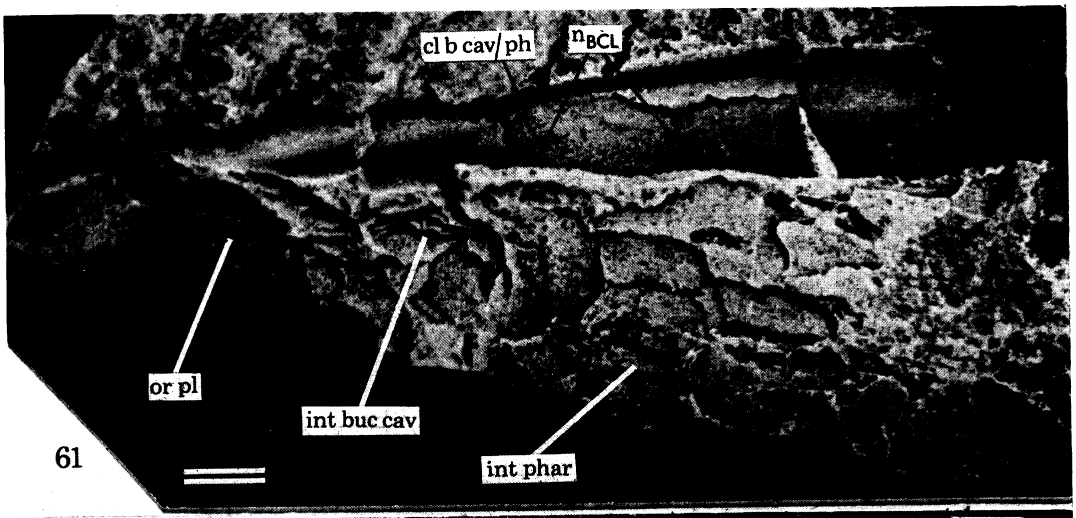
Lagynocystis pyramidalis. Šárka Formation. From Šárka and Osek. Scale lines 1 mm.

FIGURE 61. Internal cast of theca, left ventro-lateral aspect. NM 321/69. Šárka. To show especially the cleft between the buccal cavity and the left pharynx.

FIGURE 62. Latex of ventral surface of theca of same specimen and from same aspect. Note how the groove for the left nerve to the buccal cavity continues forward from its position in figure 61. The oral plates and the anterior marginal have been displaced backwards from their correct position.

FIGURE 63. Natural mould of the internal surface of plate M_{2R} of BMNH E 16104. Osek, near Rokycany.

FIGURE 64. Natural mould of inside of posterior part of the theca, dorsal aspect. Same specimen as figure 59. Note especially the boundary between right pharynx and anterior coelom.



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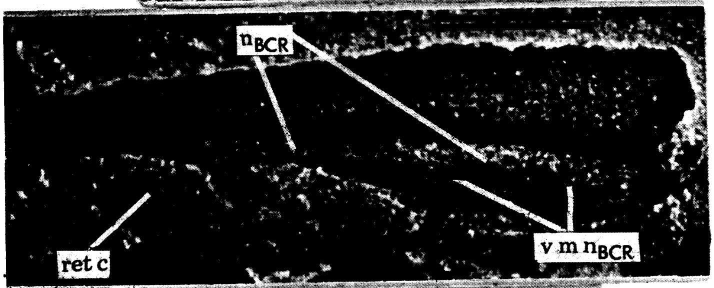

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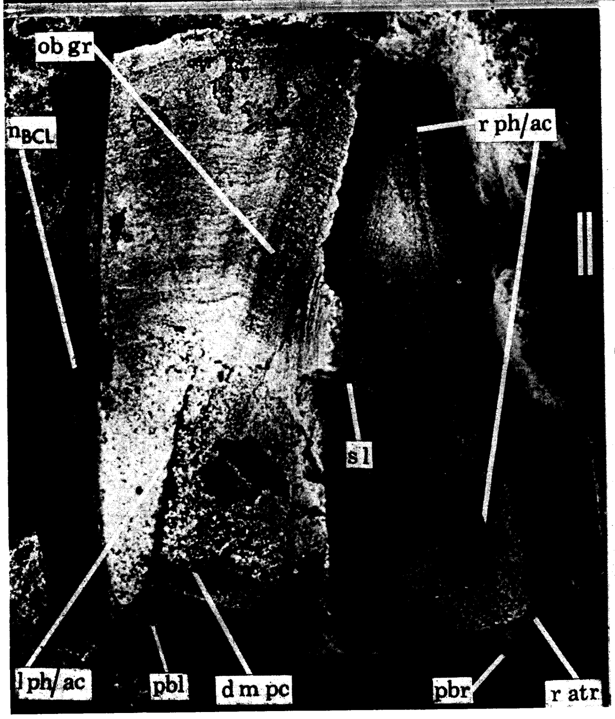

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Figures 61 to 64. For legends see facing page.

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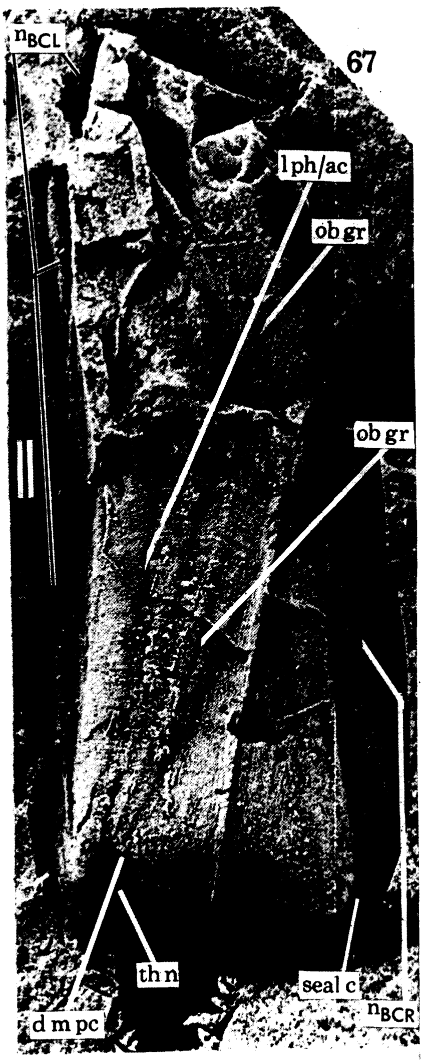

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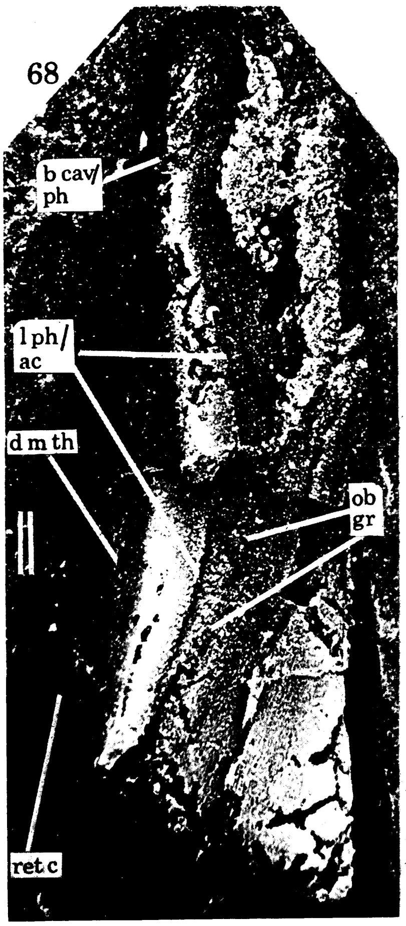

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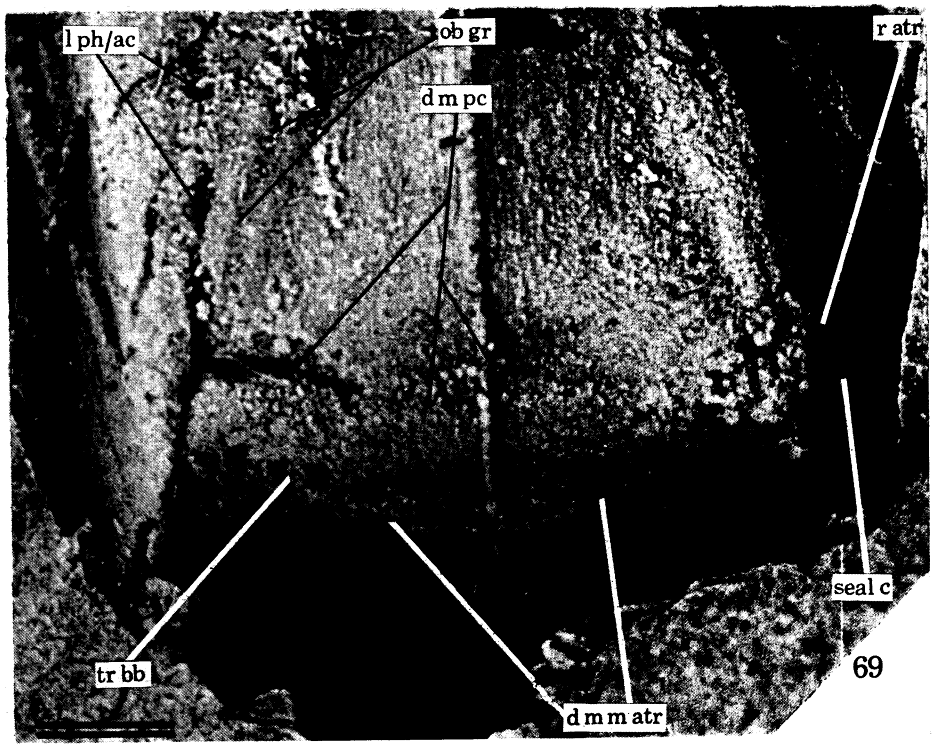

Figures 65 to 69. For legends see facing page.

Before describing them it is necessary to summarize the situation in other, more normal mitrates, partly because recent work has modified my ideas on some details (cf. Jefferies 1968*a*, pp. 295, 319, 1969, p. 520). *Mitrocystites mitra* represents the normal situation (figure 14). The structures shown in hard lines in figure 14 are based on direct observation in *M. mitra*. Structures shown in dotted lines are, deduced from other mitrates, such as *Mitrocystella*, *Peltocystis* and *Lagynocystis*. As in other calcichordates, the brain was at the anterior end of the stem, like the aboral nerve centre of crinoids which is probably homologous. Cranial nerves radiated out from the brain.

The brain of *Mitrocystites mitra* was divided into three parts – anterior, medial and posterior (ap, mp, pp). The anterior part of the brain probably received fibres from the dorsal skeleton. These fibres were probably olfactory and entered the dorsal skeleton through paired olfactory openings (ol o) in the buccal cavity. I previously supposed that the anterior part of the brain of mitrates was homologous with the telencephalon of fishes. I have now modified this view, however, since the telencephalon is the part of the fish brain that *receives* the olfactory fibres. It probably arose, therefore, from the portion of the mitrate brain immediately behind the anterior part.

The medial part of the brain of *Mitrocystites* probably corresponded to the diencephalon *plus* optic lobes of a fish's brain and was therefore optic and hypophyseal in function. Through a slit in the skeleton beneath it, the medial part of the brain probably communicated with the adenohypophysis. Medial part nerves (mpn) left the medial part of the brain anteriorly through a bilobed hole in the skeleton and went outwards and downwards to join the palmar nerves (pal). The medial part nerves were probably optic in function and were connected with the nerves n_3 which ended on the dorsal surface of the skeleton in little optic vesicles (r tr eye and corresponding structure on left).

I formerly considered that the nerves n_3 were strictly homologous with the paired optic nerves of fishes, but I now think this view is too simple. The nerves n_3 pass under the pharynx and finish on the dorsal surface of the skeleton on the far side of the pharynx from the brain. Because of this path, they cannot be homologous with the optic nerves of fishes. They are probably optic, however, because of where they end, and because the forms that possess them have an especially large diencephalon (medial brain). The nerves n_3 can be referred to as transpharyngeal optic nerves, and as such they already existed in *Reticulocarpos*.

Some mitrates, however, have a different pair of optic nerves which leave the antero-ventral surface of the medial brain in the same place as the medial part nerves, but climb immediately upwards inside the theca, to end beneath the dorsal skeleton. This was presumably transparent enough to let through sufficient light. These nerves can be called cispharyngeal optic nerves

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Description of plate 46

Lagynocystis pyramidalis. Natural moulds of the interior of the dorsal surface. Scale lines 1 mm. All from Šárka Formation of Šárka.

Figure 65. Same specimen as figure 57. Note the unusual clarity of the oblique groove, of the boundary between anterior coelom and left pharynx and of the right nerve to the buccal cavity.

Figure 66. Dorsal aspect. BMNH E29042. The fossil has been dissected away near the posterior left corner to show how the boundary between the left pharynx and anterior coelom can be followed down into the fossil.

Figure 67. Dorsal aspect. NM 310/69.

Figure 68. Dorsal aspect. BMNH, E16106.

Figure 69. Postero-dorsal aspect. Same specimen as figure 67. To show especially the dorsal margin of the median atrium.

because they are not separated from the brain by the pharynx. They existed in the primitive mitrate *Peltocystis* and probably also in *Mitrocystella* and *Placocystites* (personal observation). There seems no reason why cispharyngeal optic nerves should not be homologous with the paired optic nerves of fishes. It seems that, at the calcichordate stage of evolution, the optic system was very labile, so that any upward extension of the diencephalon could function as a photo-receptor. This supposition is consistent with the mode of origin for eyes proposed by Studnička, who derived the light-sensitive cells of the retina from the ciliated cells of the ependymal lining of the diencephalon (see Walls 1942). It is likely that such light-sensitive upward extensions have come into existence at least five times. These are: first, the median eye of primitive cornutes like *Ceratocystis*; secondly, transpharyngeal paired eyes; thirdly, cispharyngeal paired eyes that may be homologous with the paired eyes of fishes; fourthly and fifthly, the pineal and parapineal eyes of vertebrates.

The posterior part of the brain of *Mitrocystites* was equivalent to the medulla oblongata plus the ventral part of the mesencephalon of a fish. Paired posterior part nerves went off from it downwards and inwards, passed the left and right pyriform bodies (pbl, pbr) and joined with the medial part nerves to form the palmar nerves (pal). The left palmar nerve curved over the rectum (rect). The right one curved up and down in a similar manner, perhaps over the oesophagus, which I previously mislocated (Jefferies 1968*a*, p. 285). After entering the skeleton the palmar nerves split up into n_1, to the floor of the theca, n_2 to the buccal cavity, n_3 or the transpharyngeal optic nerves to the dorsal surface of the skeleton running in front of the gill opening, and n_4 and n_5 to the dorsal surface of the skeleton, running up behind the gill opening. Other structures that probably connected with the posterior part of the brain had to do with the acustico-lateralis system. These were: first, the left auditory nerve and its ganglion in the left atrium (aud n l and aug l); secondly, a right auditory and lateral line nerve (aud lat r) supplying a lateralis ganglion (llg) beneath a lateral-line groove in the external surface; and thirdly, an auditory ganglion in the right atrium which probably existed, but which I have not proposed before (cf. Jefferies 1969, p. 521ff.). The nerves n_0 to the median posterior part of the thecal floor may also have connected with the posterior part of the brain and perhaps supplied an endostyle in the pharynx.

The nerves n_1 and n_2 probably represent the mandibular and maxillary branches of the trigeminal nerves of fishes and the pyriform bodies represent the trigeminal ganglia (Jefferies, 1968*a*, p. 295ff., p. 319ff.). As already mentioned, the nerves n_3 were transpharyngeal optic nerves. Nerves n_4 and n_5 were probably touch-sensory nerves, conveying information from the dorsal surface.

The history of the acustico-lateralis system in calcichordates is complicated, and becomes more so. The first manifestation of the system is an external groove, just left of the stem on the ventral side of the primitive cornute *Ceratocystis*. This was supplied by a nerve round the left pyriform body and probably functioned as lateral line. In mitrates this groove presumably became enclosed in the left atrium and took on an auditory function (Jefferies 1969, p. 521). In figure 14 aug l and aud n l represent its ganglion and nerve supply in *Mitrocystites*. The reasons for thinking that mitrates had a similar ganglion in the right atrium rest largely on the condition in the mitrate *Peltocystis* (personal observation). From the right and left atria nerves ascend direct to the brain of this form, without going round the pyriform bodies. These nerves enter the posterior brain at its right and left dorsal angles, i.e. at the points which in fishes house the acustico-lateralis centres. This suggests, since *Peltocystis* had no external lateral line, that there was an auditory ganglion in the right atrium, as well as in the left atrium. It also confirms that the structures identified as acustico-lateralis in other mitrates and cornutes, were so in fact. *Peltocystis* is an early and rather primitive mitrate. Right and left ganglia directly connected to the brain also existed in *Lagynocystis*, as discussed below. Right and left auditory ganglia therefore presumably existed in the latest common ancestor of *Lagynocystis* and *Peltocystis*, which would have been a very primitive mitrate indeed similar to figure 4 or perhaps identical to it. It is therefore likely that there was also a right auditory ganglion in the right atrium of *Mitrocystites* as shown in figure 14. As compared with *Peltocystis* and *Lagynocystis*, the Mitrocystitid situation was further complicated by the development of the lateral line groove and ganglion. These appeared just right of the stem on the ventral surface and were supplied by a nerve which presumably connected with the right auditory nerve. The lateral line of Mitrocystitids is first known in *Chinianocarpos*, where it is only a tiny pit. It is a long groove in *Mitrocystites* and *Mitrocystella*. This picture of the acustico-lateralis system of calcichordates is self-consistent. The evidence for it is not complete in any single form, but ties together in a way that seems natural. The anatomy of *Peltocystis* will be the subject of a later paper.

Turning now to *Lagynocystis pyramidalis* (figure 13; figures 29, 30, plate 39) the brain was again divided into anterior, medial and posterior parts. The anterior part (ap in figure 30, plate 39) is represented only by little cones of rock on each side of the dorsal, postero-median suture (M_{1RD}/M_{1LD}) as in other mitrates. There is no sign of specialized areas in the buccal cavity where olfactory fibres gathered before entering the skeleton, and the lack of such areas is a cornute-like and probably primitive feature. The situation in the primitive mitrate *Peltocystis* supports this view, for the olfactory fibres of this form seem to have entered the skeleton through a diffuse, sausage-shaped area above the buccal cavity – a condition which is more cornute-like than the paired olfactory pits of *Mitrocystites*.

The posterior and medial parts of the brain in *Lagynocystis pyramidalis* (pp, mp) were lodged in a cerebral depression formed from plate M_{1RD} and M_{1LD} (h and i), just as in other mitrates. The medial part of the brain, however, is markedly different from that of other mitrates. The skeleton that enclosed it lacked antero-ventral openings for the bases of the optic nerves, and had no median ventral slit by which the medial part of the brain could communicate with an adenohypophysis ventral to it. It is likely that the optic nerves had been eliminated, and the adenohypophysis had either been eliminated or pushed out of the way, by the growth of the median atrium. An additional peculiarity of the medial part of the brain is the way it is drawn out into right and left dorso-lateral angles (d l ang in figure 13; figure 29, plate 39; figure 65, plate 46). These perhaps represent yet another form of simple, paired light receptor formed by outpouching from the diencephalon. They probably compensated for the loss of the optic nerves. The medial brain has a swollen portion in a median dorsal position (ol p in figure 13*e*; figure 29, plate 39). This may have been an olfactory portion, specialized to connect with fibres from the anterior brain.

The posterior part of the brain is much as in other mitrates. Just anterior to it are right and left pyriform bodies, (trigeminal ganglia, pbl, pbr in figure 13*a*, *b*, *d*, *f*; figure 25, plate 38; figure 31, plate 39; figures 37, 38, plate 41; figures 58 to 60, plate 44; figure 64, plate 45) closely resembling those of other mitrates. They were enclosed, as is usual, by cups in M_{1RV} and M_{1LV} ventrally and cups in M_{1RD} and M_{1LD} dorsally. Posterior to the pyriform bodies are conical lumps, one on each side, which are directly connected to the posterior part of the brain (aug l, aug r in figure 6*b*, *c*, *e*; figure 13*a*, *b*, *c*; figure 29, plate 39; figures 56, 58, 60, plate 44). The positions of these and the way they are connected to the brain identify them as auditory ganglia like those of *Mitrocystites* and *Peltocystis*. Their existence on both sides confirms the conclusion drawn from *Peltocystis*, that paired auditory ganglia were primitive in mitrates. It is to be expected that the auditory ganglia connect to the brain behind the trigeminal ganglia.

There are shallow grooves in the internal surface of the posterior wall of the theca represented by elongate swellings on the internal cast (th n in figure 6*b*, *d*), which probably indicate thecal nerves coming out of the brain and leading upwards and away from the median plane towards the right and left dorsal angles of the median atrium (figures 56, 58, 59, plate 44). It is likely that these correspond to the posterior part nerves of other mitrates. The parts of the palmar complexes of other mitrates which can most clearly be recognized in *Lagynocystis pyramidalis* are the left and right nerves to the buccal cavity (n_{BCL} and n_{BCR} in figure 6*a*, *b*, *c*; figure 13*a*, *b d*; figure 39, plate 41; figures 61 to 64, plate 45; figures 65 to 67, plate 46) which correspond, to judge by their relations to the buccal cavity and the thecal plates, to the nerves n_2 of other mitrates (figure 14). Nerve n_{BCR} enters the dorsal skeleton just in front of the right branchial opening. Since n_{BCR} already forms a well-marked trunk when it is first seen to climb into the dorsal skeleton, it must have existed as a trunk or as tributary nerves in the adjacent part of the soft layer that coated the inside of the ventral skeleton. This shows that the nerves from the brain had already entered the soft layer of the ventral skeleton in this region. Left nerve n_{BC} did not run in the ventral skeleton in the posterior part of the theca. It seems to have run dorsal to the retaining and sealing cartilage on the left side (ret c and seal c in figure 6*a*, *b*; figure 39, plate 41), having passed over the rectum from the left thecal nerve (figures 56, 58, plate 44).

It is now necessary to consider how the development of a median atrium will have modified the nervous anatomy of a normal mitrate. Figure 9*g* shows diagrammatically the positions of the thecal chambers in a sagittal section of such a form (*Mitrocystella*). The left palmar nerve in the diagram is projected rightwards on to the sagittal plane. It has an arched course, as a result of passing over the rectum, whose position is indicated on the diagram. The right palmar nerve arched in a similar way, perhaps over the oesophagus. In the evolution of *Lagynocystis* a fold of skin developed at the anterior end of the stem and expanded forwards and upwards to form the median atrium, so as to come in contact with the back of the pharynx. The wall between median atrium and pharynx came to be broken by gill slits. In its expansion, as discussed above, the median atrium would push the posterior coelom upwards and with it the palmar nerves, the rectum and presumably the oesophagus.

As a natural result of the growth of the median atrium beneath the palmar nerves of the ancestral, normal mitrate, the left palmar nerve would be lifted up with the rectum and pass forward over it into the left nerve to the buccal cavity (n_{BCL}) as suggested in figure 13*a*. The reconstructed anatomy of this nerve can largely be confirmed from the internal casts. On the right the situation is less clear. The observed proximal end of n_{BCR} comes out of the soft layer that covered the ventral skeleton on the inside, so the right thecal nerve to supply it presumably passed over or round the median atrium to get into the soft layer covering the ventral skeleton. It may have split and gone down the gill bars, or without splitting have passed downwards in the small segment of posterior coelom between the median and right atria (the portion labelled pc in figure 59, plate 44). It is not likely that nerves passed beneath the median atrium to the ventral wall of the theca since: (1) they would have to have gone round the median branchial opening, which was probably a wide slit; (2) such a path would not naturally result from expanding the median atrium beneath the nerves in the posterior theca of a normal mitrate;

and (3) there are transverse cavities in the thecal floor beneath the median atrium (tr cav in figure 6*a*, *c*, *e*; figure 31, plate 39) which run perpendicular to the path of any such postulated fibres.

Nerves to the floor of the theca just in front of the median atrium probably ran down the gill bars, irrespective of how n_{BCR} may have been supplied. This is likely since: (1) the gill bars are hollow (h brb in figure 34, plate 40); (2) there is evidence of a branchial soft layer (br s l) just beneath the anterior surface of the branchial buttresses, dorsal and anterior to the transverse cavities (figure 6; figure 25, plate 38; figure 31, plate 39). This layer leads into the soft tissue inside the plates of the thecal floor and could well have received nerves passing down the gill bars; (3) such nerves passing down the gill bars would be expected to result from the development of the median atrium beneath the nerves n_0 of normal mitrates. Amphioxus has similar nerves going over the median atrium and down the gill bars (Bone 1961, p. 250).

The relationships of the nerves to the buccal cavity (i.e. n_{BCR} and n_{BCL}) are of great interest. Figure 13*a*, *c*, *d* shows these nerves as highly unsymmetrical, with the left one extending much farther forward, and farther into buccal cavity, than the right one. This is based on skeletal evidence (figure 6*a*, *b*, *c*; figures 61, 62, plate 45; figures 65 to 67, plate 46). It is therefore likely that the muscles which controlled the lower lip would predominantly have been innervated from the left. This feature recalls a similar asymmetry in amphioxus, in which the left side of the buccal cavity of oral hood and the velum is supplied entirely by left spinal nerves, while the right side is supplied by nerves of both left and right sides (Franz 1927, p. 528ff.). It has been remarked above that the oral plates of *Lagynocystis pyramidalis* seem also to be unsymmetrical with a predominance of the left side.

Innervation of the buccal cavity mainly from the left is probably an inheritance from the primitive mitrate. In *Reticulocarpos* the mouth is nearly symmetrical, but the posterior margin of the buccal cavity is much farther back on the left than on the right (see figures 2, 3 and § 1). In the primitive mitrate *Peltocystis cornuta* the same basic asymmetry persists, with the left side of the buccal cavity more posterior than the right. In this form, however, the mouth has acquired the same asymmetry, and is farther back on the left than on the right (figure 3). The points where the nerves n_2 of the palmar complex left the dorsal skeleton can be observed in this form. On the left and right sides these points are almost the same distance forward from the posterior end of the theca. Because of this and the obliquity of the mouth and buccal cavity, left n_2 leaves the dorsal skeleton much nearer to the buccal cavity than does right n_2. It is therefore likely that the velum and buccal cavity in *Peltocystis cornuta* was mainly innervated from the left. In *Lagynocystis pyramidalis* the situation is changed in some respects, since the posterior margin of the buccal cavity is more posterior on the right than on the left. As already mentioned, the reason for this is probably hydrodynamic and connected with rotation of the theca while swimming. The innervation of the mouth predominantly from the left, however, is retained from the primitive mitrate condition.

In summary, therefore the brain and cranial nerves of *L. pyramidalis* are much more complex than those of amphioxus, but simpler than those of other mitrates. The simplification was probably caused by the presence of the median atrium. There may have been a nerve supply to the gill bars running over the median atrium rather like that of amphioxus. The asymmetrical innervation of the oral hood (buccal cavity) seen in amphioxus was probably inherited from the condition seen in *L. pyramidalis*, which inherited it in turn from a more primitive mitrate.

5. MODE OF LIFE

The first mitrates lived on soft mud and were probably adapted for crawling over it backwards (see Jefferies & Prokop 1972; also Jefferies 1968*a*, pp. 309, 322 and § 1 above). In this they resembled their immediate cornute ancestors among the Amygdalothecidae. In the way it crawled *Lagynocystis pyramidalis* was probably more cornute-like and primitive than other known mitrates, so its functional morphology is important.

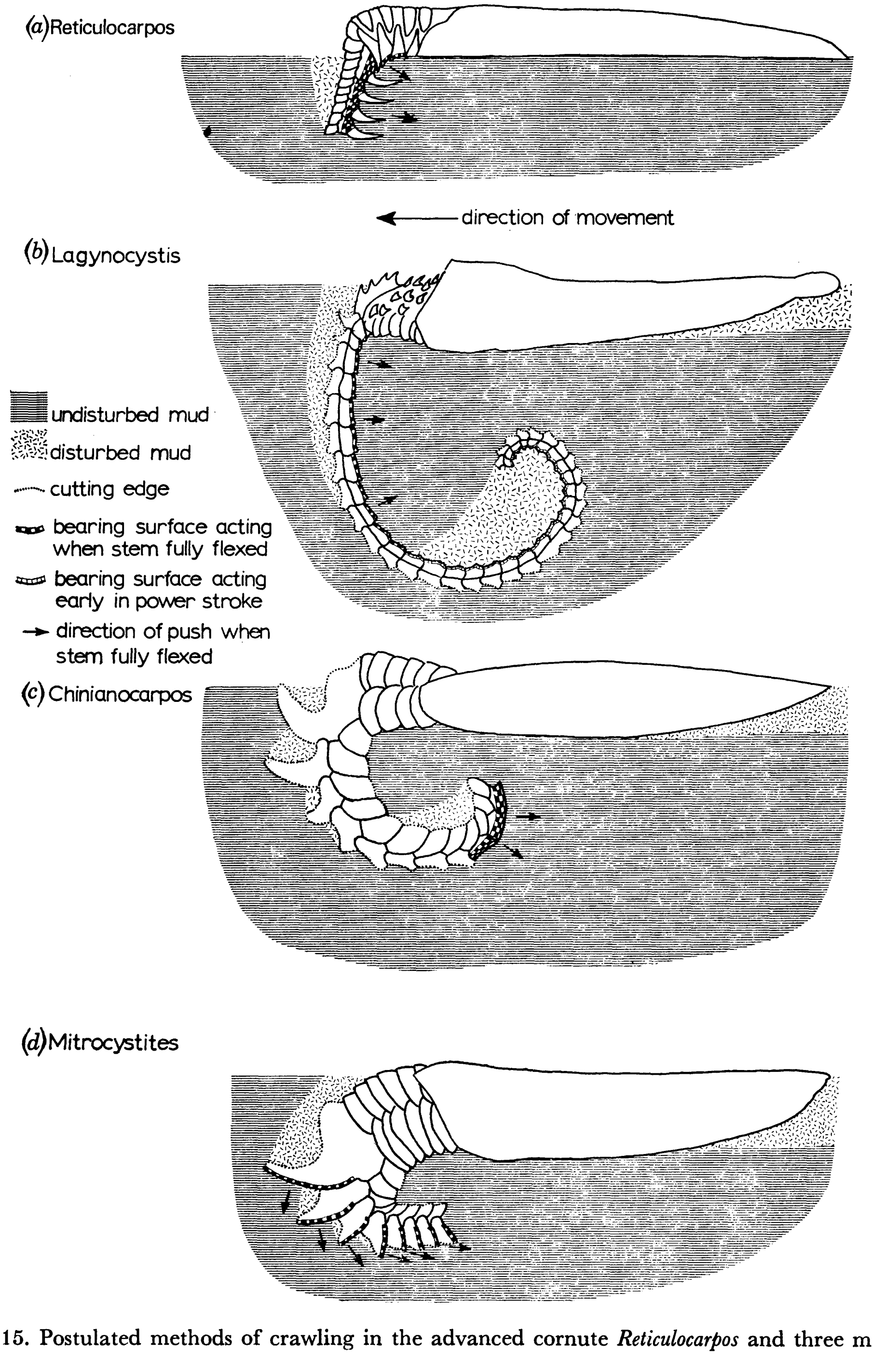

FIGURE 15. Postulated methods of crawling in the advanced cornute *Reticulocarpos* and three mitrates.

The group of cornutes from which mitrates arose is represented by *Reticulocarpos* in figure 15*a* (see also figure 2 and Jefferies & Prokop 1972). As it happens, this form occurs at Šárka in the same beds as *Lagynocystis*, but its close relatives that gave rise to the mitrates must have been older. *Reticulocarpos* was adapted to support itself on soft mud, using only the strength of the mud (figure 2*g*). To this end, lightness and a big, flat area of contact are desirable. Accordingly, the theca is very small, the skeleton is very lightly built indeed, and the ventral surface of the theca is flat. Calculation suggests that the animal would exert a pressure of only about 10 mg cm^{-2} on the sea floor but even so, if natural selection operated, the mud would probably sometimes collapse beneath it and bury it. (It is possible to produce a mud as weak as this in the laboratory (Jefferies & Prokop 1972, p. 101)). *Reticulocarpos* probably crawled backwards like all other calcichordates pulling itself by the stem. Unlike other cornutes, but like mitrates, it probably did so by flexing the stem ventrally, rather than sideways. The mid- and hind-stem were very wide and carried big ventral spikes. These parts of the stem were therefore well able to grip the bottom mud in ventral flexion. The fore-stem was also wide and flat ventrally, to provide an additional bearing surface. So long as the stem was not flexed ventrally much beyond the position shown in figure 15*a*, it would exert a forwards and downwards force on the mud. This would pull the theca backwards and upwards, in the desired direction, without risk of burying it. Difficulties would arise, however, if the hind-stem flexed beyond the vertical, for then it would pull the theca backwards and downwards into the mud, with the possibility of killing the animal. This was the more likely, because the leading, posterior edge of the theca was sharp and would not resist the downwards pull. The danger of self-burial in this manner was probably the reason why the form that gave rise to the mitrates had lost the old mid- and hind-stem completely.

The mitrates adopted a different approach to the problem of staying up on mud (figure 2*g*). Instead of simply resting on the mud, relying on its precarious strength for support, they became ventrally convex and 'floated' in the top of the mud like boats. By displacing a weight of mud equal to their own weight, they could neutralize completely any downward force exerted on the mud. Or by displacing a lesser weight of mud, they could neutralize the part of their weight which the strength of the mud would not carry (Jefferies & Prokop 1972). Using this method, it was much less critical that the animal should be light in weight. It was more difficult to crawl, however, because the theca now had to plough through the top layer of mud instead of sliding over it. This meant that a larger stem became both necessary, for crawling, and possible, because its extra weight did not matter. The old fore-stem developed new fore-, mid- and hind-stem regions, simulating those of cornutes, but not homologous. The new hind-stem was specialized for ventral flexion and came to consist of sharp-backed, inter-articulated dorsal ossicles and plates ventral to them. The dorsal ossicles were sharp-backed to cut backwards through the mud in the power stroke, and to make the stem easy to extract in the return stroke. The most proximal ossicles of the hind-stem were fused to form a socket or styloid by which the fore-stem could move the rest of the stem as a unit.

Lagynocystis (figure 15*b*) represents such a mitrate crawling stem in a very primitive state. The main bearing surface was the ventral surface of the new hind-stem which was slightly concave and equipped with a pair of spikes or posterior ventral processes in each segment for better grip. This ventral bearing surface was a direct development of the ventral bearing surface of the fore-stem of the ancestral cornute as represented in figure 15*a*. Each part of the hind-stem would work best when it was vertical in the mud so that it exerted an exactly horizontal force to pull the theca backwards. In the early stages of the power stroke, the tip of the stem would press forwards and downwards on the mud. As more and more of the stem was pushed downwards, however, the bearing surfaces of the distal parts of the stem would start to push forwards and upwards. Consequently the animal, like its cornute ancestor, would be in danger of pulling itself down into the mud. This was the more unfortunate, because, towards the end of the power stroke, the proximal parts of the hind-stem, where the biggest bearing surfaces were, would be nearly vertical and pulling backwards most effectively.

Lagynocystis probably overcame this danger by bending the tip of the stem ventrally and upwards as shown so that the dorsal cutting edges of the stem tip pushed upwards at the end of the power stroke. These cutting edges would exert very little effective pressure on the mud but would disturb and weaken it, so that the somewhat more proximal bearing surfaces were made ineffective at the end of the power stroke, and did not pull the animal under.

This method of crawling was inefficient, however, because the distal part of the stem, which moved farthest in each stroke, nullified itself during part of each stroke. Such a form as *Chinianocarpos* (figure 15*c*) represents an improved type of crawling in which the flexed tip of the stem has come to push directly forwards. Instead of being without effect, the dorsal ossicles have developed a rounded, dorsal bearing surface, which in fact is the only one in the stem. The animal would consequently push against a distal anchor. The dorsal cutters of the hind-stem are much bigger than in *Lagynocystis* and would have been at their most effective in the position shown. They would also have been useful in extracting the stem from the mud in the return stroke. *Peltocystis* crawled in a similar way to *Chinianocarpos* but had an even clearer separation of the stem into functionally distinct parts including a dorsal bearing surface near the tip.

Mitrocystites used a still more advanced type of crawling (figure 15*d*). Its stem was much more flexible and the dorsal ossicles had developed distal, slightly concave bearing surfaces all of which would have pushed downwards and forwards, so pulling the animal backwards with no risk of burying it. The proximal edges of the dorsal ossicles are still sharp, for ease of extraction. The proximal segment of the styloid, which could only push backwards and downwards, is the only segment of the mid- and hind-stem that has no bearing surface. It would have cut through the mud like the prow of a ship through water.

As regards crawling and posture, therefore, *Lagynocystis* probably lay in the top layer of the bottom mud, with the dorsal surface level with the bottom, supporting itself like other mitrates by displacing a weight of mud. It crawled backwards by ventral flexion of the stem but unlike other mitrates and like advanced cornutes, used ventral-bearing surfaces.

Turning now to swimming, it is likely that primitive mitrates were the first chordates that could swim (Jefferies & Prokop 1972). From the cornutes they inherited thecas that were small, broad, flat, and symmetrical with very light skeletons, all of which features pre-adapted than for swimming (cf. Gould 1971). Unlike the cornutes which gave rise to them, however, they had developed muscular, laterally compressed stems for crawling and these, by being waved from side to side, could be used as engines and propellers. They probably swam theca foremost, by analogy with fishes or tadpoles. Arguing from a different standpoint, swimming by waving a muscular tail occurs in living tunicates, cephalochordates and vertebrates. It is therefore likely to have existed in their latest common ancestor, which would have been a primitive mitrate, as argued below.

The special asymmetries of *Lagynocystis*, as mentioned above, must be related to the mode of life of this form since they are absent in other mitrates and amygdalothecid cornutes. They can be explained if *Lagynocystis* could swim, rotating about its long axis as it did so, clockwise as seen from behind, like larval amphioxus and tunicate tadpoles. Conversely, if features of *Lagynocystis* suggest that it swam like the larvae of its recent cephalochordate relatives, it is the more likely that primitive mitrates in general could swim.

As to feeding, the gill bars of *Lagynocystis pyramidalis* suggest a ciliary pump. In living tunicates such a ciliary pump works by pulling water through a mucus bag inside the pharynx, so that the bag filters off food particles (Werner & Werner 1954). A similar mucus bag exists in the larval lamprey (Newth 1930; Balabai 1951) and very probably exists also in amphioxus (Jørgensen 1966, p. 128). In tunicates the bag is produced continuously by the endostyle, taken up by the dorsal lamina, held in front by the peripharyngeal grooves and pulled backwards with the food in it by the oesophagus. It is likely that *Lagynocystis* fed by a mucus bag of the same sort, drawing water through it by cilia in the gill bars. *Lagynocystis* may also have been able to 'cough' like tunicates and amphioxus (Jørgensen 1966, pp. 116, 129). It would do so by contracting the muscles inside the floor of the pharynx and buccal cavity.

Lagynocystis therefore lived like other mitrates, except that it rotated as it swam and crawled in an unusually primitive way.

6. THE POSITION OF *LAGYNOCYSTIS* WITHIN THE CALCICHORDATES

The most probable phylogenetic position of *Lagynocystis* among mitrates and amygdalothecid cornutes is suggested in figure 3. Some parts of the tree shown are more certain than others, but fortunately the uncertainties are not very important.

I have already argued in the introduction that the Amygdalothecid cornute *Reticulocarpos* (figure 2) was more closely related to the mitrates than any other cornute known. Assuming this, and knowing the morphology of a number of mitrates, it was therefore possible to make several statements about the hypothetical primitive mitrate which might have been the latest common ancestor of *Lagynocystis*, *Chinianocarpos* and *Peltocystis* (figure 4).

Detailed morphological study shows that *Lagynocystis* differed from that primitive mitrate in the following main ways: (1) The existence of the median atrium, the fact that the posterior coelom no longer rested on the floor of the theca, the change in the relation of the residual anterior coelom to the oblique groove, and the lifting up of the proximal end of the rectum. (2) The simplification of the nervous system with the loss of the medial part nerves and of the slit in the skeleton which existed ventral to the brain of most mitrates and which probably connected the brain of those forms with the adenohypophysis. (3) Considerable loss of external symmetry and the elongation of the theca. The loss of external symmetry expressed itself by the weakening of the right peripheral flange relative to the left one, and the loss of the right marginal plate c. Also, the back of the buccal cavity became more posterior at right than left, instead of the converse. (4) The dorsal integument over the left pharyx, such as persisted in *Chinianocarpos*, no longer occurred in *Lagynocystis*. The dorsal integument over the buccal cavity, left of plate n, was also lost, though that right of plate n remained. (5) Plate a became articulated to the plate behind it. The ventral plate p migrated backward, separating plates g and j.

The most important of these changes relate to the appearance of the median atrium. This represents an infolding of skin just ventral to the front end of the stem of the ancestral mitrate. This inpouching dilated and grew forward, so that it touched the posterior end of the pharynx. Gill slits developed in the wall separating it from the pharynx. The dilatation of the median atrium, and a corresponding dilatation of the posterior part of the pharynx backwards to meet it, lifted the posterior coelom off the floor of the theca and squashed the residual anterior coelom upwards so that it splayed out on both sides of the oblique groove and acquired a more symmetrical relationship to the thecal cavity in general. The same dilatation of the pharynx to meet the median atrium lifted up the proximal end of the rectum.

Much of the simplification of the nervous system may also be due to the coming into existence of the median atrium. Thus the medial part nerves, which *Lagynocystis* had lost, would have emerged from the brain of the ancestral form just where the median atrium appeared. The median atrium was presumably also responsible for severing the direct connexion of the adenohypophysis with the brain. The dilatation of the median atrium, by lifting up the rectum, also lifted up the left palmar nerve where it passed over the rectum, giving the disposition seen in *Lagynocystis*. What happened to the right palmar nerve is not clear. It is likely that the nerves n_0, probably to the endostyle, would have been split up by the gill slits of the median atrium. If anything remained of them, it would have to pass over the median atrium and down the gill bars to reach the ventral wall of the pharynx.

The loss of symmetry in the theca of *Lagynocystis*, relative to the rather symmetrical theca deduced to have existed in the primitive mitrate, can best be explained as due to rotational swimming. The development of plate b as an anterior appendage in the presumed axis of rotation can be explained in the same way, as also can the change in the asymmetry of the posterior margin of the buccal cavity from more posterior on the left to more posterior on the right. Rotational swimming would be favoured by an elongate rather than flattish theca.

The phylogeny shown in figure 3 indicates that the mitrates split at an early stage into a line leading to *Lagynocystis*, on the one hand and a line leading to *Peltocystis*, *Chinianocarpos* and *Mitrocystites* on the other. This is based on the observation that *Lagynocystis*, despite numerous advanced features separating it from the hypothetical latest common ancestor with *Peltocystis*, *Chinianocarpos* and *Mitrocystites*, retains two primitive characters that the other forms have lost. These are the ventral bearing surfaces in the hind-stem and the absence of distinct olfactory openings in the buccal cavity. In both these features, *Lagynocystis* was similar to the cornute *Reticulocarpos*.

As regards bearing surfaces, this means that *Peltocystis*, *Chinianocarpos* and *Mitrocystites* have dorsal bearing surfaces in the stem. These are a shared specialization which, on the most parsimonious assumption, only developed once, and which the latest common ancestor of these forms with *Lagynocystis* would not have had.

As regards olfactory openings, the situation is more complicated. *Mitrocystites* has well-developed olfactory openings in the buccal cavity; *Peltocystis* has specialized areas (personal observation) which could well be homologous with the olfactory openings of *Mitrocystites*; the situation in *Chinianocarpos* is not known; and *Lagynocystis* has neither olfactory openings nor specialized areas. The most parsimonious assumption, in this case also therefore, is that olfactory openings or areas represent a shared specialization, present in the latest common ancestor of *Mitrocystites* and *Peltocystis*, but not present in the latest common ancestor of these two forms with *Lagynocystis*. The latest common ancestor of *Mitrocystites* and *Peltocystis*, would also have been the latest common ancestor of *Chinianocarpos*, *Mitrocystites* and *Peltocystis*.

The most parsimonious phylogeny for the mitrates is therefore as shown in figure 3. This means that, at a very early stage, the mitrates split into two lines. One of the lines evolved towards *Lagynocystis* and developed rotational swimming and a median atrium, but retained ventral bearing surfaces and developed no olfactory openings in the roof of the buccal cavity. The other line evolved forwards *Peltocystis*, *Mitrocystites* and *Chinianocarpos* and did not develop rotational swimming or a median atrium, but did develop dorsal bearing surfaces and olfactory openings or areas in the buccal cavity.

As against this, further work may very well show that the mitrates first split into a line leading towards *Chinianocarpos* and *Mitrocystites* on the one hand, and another line leading to *Peltocystis* and *Lagynocystis* on the other. But in this case, dorsal bearing surfaces and olfactory openings or areas in the buccal cavity evolved twice.

Chinianocarpos and *Mitrocystites*, and also *Mitrocystella*, share one important specialization which neither *Peltocystis* nor *Lagynocystis* had. This is the lateral line, developed just right of the stem, in the plate $M_{1RV} = g$. This shared specialization makes it likely that the latest common ancestor of *Chinianocarpos*, *Mitrocystites* and *Mitrocystella* was more recent than that of these three forms with *Lagynocystis* or *Peltocystis*. As shown below, this deduction is important in considering the possible age of the latest common ancestor of vertebrates and cephalochordates.

7. The position of *Lagynocystis* within the Chordates

The evidence for thinking that *Lagynocystis pyramidalis* is specially related to amphioxus can be summarized as follows:

(1) *Median atrium.* There is a median ventral atrium, opening by a median ventral atriopore and provided with gill slits anteriorly. The only known animals with a similar arrangement are the living cephalochordates. What is more, the inferred order of appearance of the gill slits (left, then right, then median, with median gill slits continuing to be produced till a late stage) resembles the order of appearance of the groups of gill slits in amphioxus.

(2) *Origin of nephridia.* By analogy with other mitrates the posterior coelom of *L. pyramidalis* is probably homologous with a tunicate epicardium, and therefore basically excretory in function. Its position dorsal to the gill bars suggests that it could easily give rise to the nephridia of amphioxus, if the gill slits increased in length upwards so as to split it into small pieces, each piece above a gill bar.

(3) *Innervation of the theca.* The mouth and anterior part of the buccal cavity of *L. pyramidalis* was innervated mainly from the left, like the same region in amphioxus. This feature was probably inherited by *L. pyramidalis* from the primitive mitrate condition, and does not in itself ally amphioxus with *L. pyramidalis* more than with other primitive mitrates. It, none the less, confirms the origin of amphioxus from this general group of animals. The plates of the lower lip of *Lagynocystis* also suggest a dominance of the left side, perhaps connected with the dominance of the coeloms and muscles of the left side in the buccal cavity of amphioxus.

It is also likely that nerves from the brain went over the median atrium and down the gill bars as in amphioxus.

(4) *Asymmetry of the anus.* The rectum of *L. pyramidalis* opened directly into the left gill opening, which functioned, at least in part, as the anus. This is a specialization of the primitive mitrate condition, where the rectum opened into the left atrium. It recalls the fact that the anus in amphioxus opens on the left side.

(5) *Rotation during swimming.* The special asymmetries of *Lagynocystis* suggest that it rotated as it swam, clockwise as seen from behind. The same behaviour is seen in larval tunicates, late

larval amphioxus and perhaps adult amphioxus in some cases. It connects *Lagynocystis* with tunicates and cephalochordates but separates it from the vertebrates.

Before discussing the evolution of amphioxus from a form near *Lagynocystis* it is desirable to mention three fairly recent studies in the anatomy of amphioxus whose results are highly surprising, but undoubtedly correct. The first of these is the work of Flood (1966) who showed that the so-called ventral-root spinal nerves of amphioxus, which are described as such in many text books (see, for example, Young 1950, p. 37), are in fact not nerves at all. They are instead 'tails' of muscle coming from the muscle blocks to the dorsal nerve cord. This is an arrangement similar to what occurs in echinoderms (Cobb & Laverack 1967). It is presumably more primitive than the tunicate situation, for the tail muscles of a *Ciona* tadpole are innervated by means of nerves ending in motor end-plates of mammalian type (Pucci-Minafra 1965). The second study is the work of Welsch (1968) and Flood, Guthrie & Banks (1969). These workers showed that the notochord of amphioxus is not a mere passive anticompressional organ, but is largely made up of muscle connected by muscle-tails to the dorsal nerve cord. The third study is the work of Skramlik (1938) and Wolf (1940) which was confirmed by Azariah (1966). These authors showed that the fish-like, unidirectional circulation of blood traditionally ascribed to amphioxus (Young 1950, p. 34) does not exist. Indeed, amphioxus can live for long periods without the blood circulating and there is little regularity in the flow when it does occur. Circulation seems to be controlled from three different centres, one in the region of the gills, one in the intestine and one anteriorly in the glomus right of the mouth. These regions circulate blood quite independently of each other, and it moves equally easily, and almost equally often, in reverse as forward directions. All these results shown that the simple view of amphioxus as an ideal proto-vertebrate is misleading.

In the evolution of amphioxus from a form like *Lagynocystis* a number of changes must have occurred, the most important of which are as follows:

(1) The muscle blocks and notochord grow forward over the pharynx and buccal cavity. This forward growth probably eliminated the brain, which cannot form in contact with myotome (Newth 1951).

(2) The median atrium increased in size and joined up with right and left atria, which lost their separate gill openings. In this way a single, large, median ventral atrium was formed opening only by a median ventral atriopore.

(3) As a result of the forward growth of the myotomes, nerves to most organs could only leave the dorsal nerve cord by way of the myocommata between the myotomes. This disrupted still further the original mitrate nervous system, though traces of the primitive asymmetrical innervation of the buccal cavity and mouth were retained. The forward growth of the median atrium meant, furthermore, that nerves to the floor of the pharynx had to reach it by passing over the atrium and down the gill bars. This condition may have existed already in *Lagynocystis* or, in any case, could easily arise from the condition in that animal.

(4) The posterior coelom grew forward, concomitant with the median atrium, and was split into pieces by upward growth of the gill slits, so as to produce the nephridia. These came to excrete into the atrium – what the posterior coelom excreted into in *Lagynocystis* is unknown.

(5) The calcite skeleton disappeared.

(6) The stem lost its division into fore- mid- and hind-portions, and the segmental ganglia degenerated by migration of cell bodies down the spinal nerves and into the dorsal nerve cord.

(7) The metapleural folds developed, perhaps by modification of the keels that existed

already in *Lagynocystis*. It is at least possible that the oral lobe of amphioxus was developed from the anterior appendage of *Lagynocystis* by the forward growth of the notochord to support it.

The latest common ancestor of the living chordate subphyla, i.e. of vertebrates, tunicates and cephalochordates, would have been a mitrate. This is likely because all living chordates have both right and left gill slits, like mitrates, but unlike cornutes. Furthermore, the latest common ancestor of vertebrates and cephalochordates was probably a very primitive mitrate. This conclusion can be argued as follows:

(1) Several of the features which ally *Lagynocystis* with amphioxus also disqualify it as an ancestor of the vertebrates. The most important of these are the median atrium opening by a median ventral atriopore, the loss of the optic nerves and probably the anus opening direct to the left branchial opening.

(2) It follows that the vertebrates must derive from some mitrate other than *Lagynocystis*. Origin of the vertebrates from within the family Mitrocystitidae seems the most likely possibility, since among mitrates only Mitrocystitidae share with the vertebrates the possession of an external lateral line. The Mitrocystitidae include the genera *Mitrocystites*, *Mitrocystella* and *Chinianocarpos*, the latter being one of the earliest and in most ways one of the most primitive mitrates known.

(3) The latest common ancestor of vertebrates and amphioxus, therefore, would also be the latest common ancestor of *Chinianocarpos* and *Lagynocystis*. Such a form would have been very like, or perhaps identical with, the hypothetical primitive mitrate postulated in the introduction as the latest common ancestor of *Peltocystis*, *Chinianocarpos* and *Lagynocystis*. *Chinianocarpos* is known from the lower Arenig stage, i.e. from very near the base of the Ordovician. The latest common ancestor of vertebrates and amphioxus would be older than *Chinianocarpos* and therefore of lower Arenig age or earlier.

It is also possible to suggest a maximum age for this latest common ancestor of vertebrates and amphioxus. I have argued elsewhere (Jefferies 1969), that the sister-group relationships of echinoderms, chordates and hemichordates are as shown in figure 16. The latest common ancestor of echinoderms and chordates would have had a calcite skeleton of echinoderm type, and would therefore have lived later than the beginning of the Cambrian, when animals with hard skeletons start to occur. The latest common ancestor of vertebrates and amphioxus would have been still more recent. Since it therefore lived after the beginning of the Cambrian, but before *Chinianocarpos*, it was probably Cambrian in age.

The origin of the tunicates relative to that of the vertebrates and cephalochordates is not easy to define. I have already said that the latest common ancestor of tunicates, vertebrates and cephalochordates would have been a mitrate, since cornutes had no right gills. Also *Lagynocystis* is probably disqualified as an ancestor of the tunicates by possessing a median atrium. Another possibly relevant feature concerns the innervation of the trunk muscles from the dorsal nerve cord. Amphioxus, as just explained, innervates the trunk muscles by muscle-tails going up to the dorsal nerve cord, and histologically speaking such muscle-tails are an echinoderm-like and primitive feature. Tunicates and vertebrates, on the other hand, innervate their trunk or tail muscles by means of motor end plates. This leads to three logical possibilities for the relation between tunicates (urochordates) vertebrates and cephalochordates as shown in figure 17 *a* to *c*. The possibility shown in figure 17*c* is somewhat more likely than the other possibilities, because it requires motor-end plates to have evolved only once. But this possibility implies that the latest common ancestor of tunicates and vertebrates was either a descendant

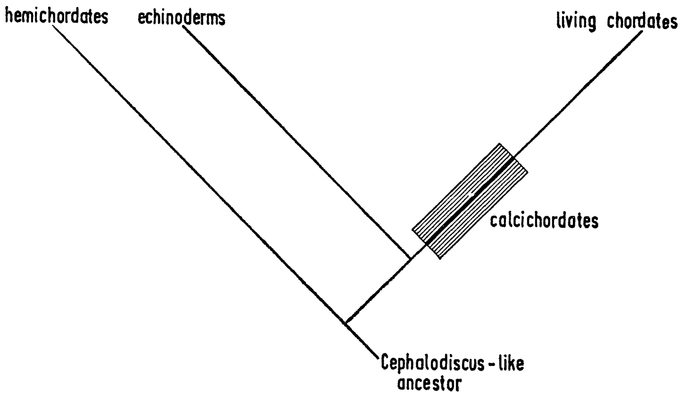

Figure 16. Phylogenetic relations of the deuterostome phyla.

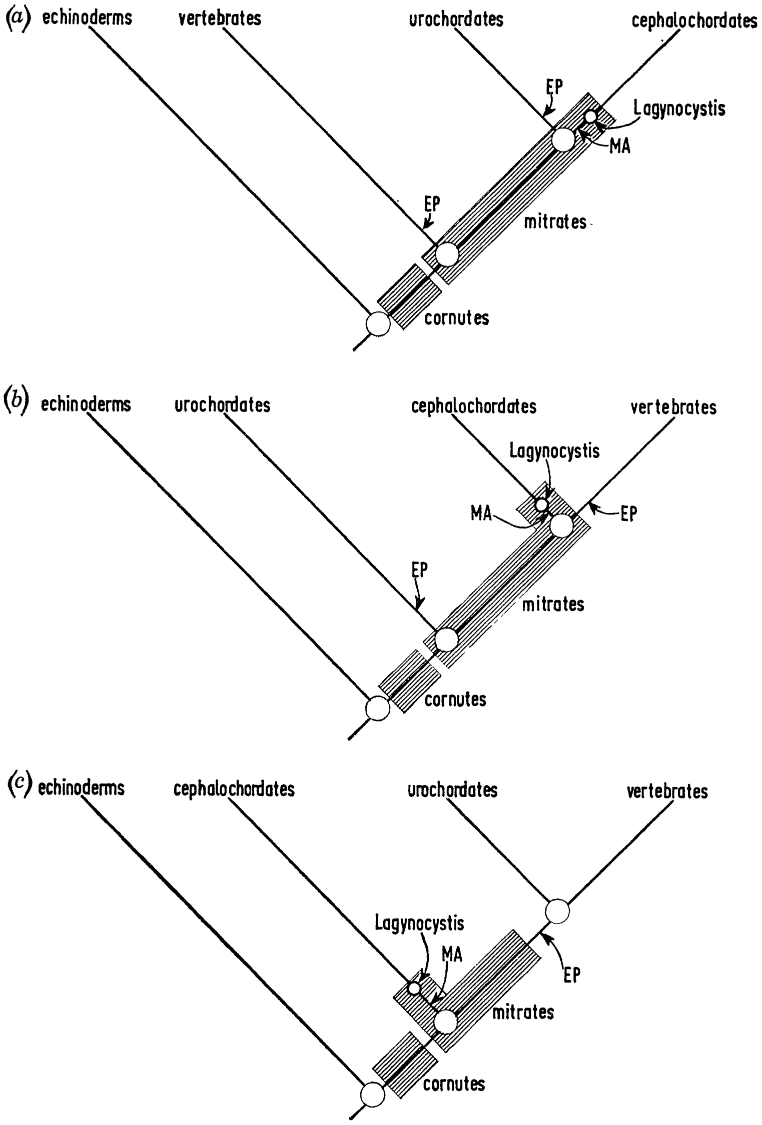

Figure 17. Three possible phylogenies for the echinoderms and chordates. EP, appearance of motor-end plates controlling the trunk muscles; MA, appearance of median atrium.

of the mitrates, or else a mitrate more advanced than the latest common ancestor of vertebrates and amphioxus. Figure 17*c* implies, in Hennigian terms, that vertebrates plus tunicates are the sister group of the cephalochordates.

To sum up, *Lagynocystis* shows that amphioxus is far from being the ideal text-book ancestor of vertebrates. Many of the most peculiar features of amphioxus, such as the absence of a brain, the presence of muscle blocks and notochord extending throughout the length of the animal, the median atrium opening by the median ventral atriopore, the absence of segmental ganglia, and the presence of nephridia over the gill bars, are specializations which the ancestors of vertebrates never had. The proximate ancestors of the vertebrates would have been more like a giant tunicate tadpole, with a brain, a complex nervous system and a body clearly separate from the tail. Apart from having lost their calcite skeletons, these proximate ancestors would be almost identical to normal mitrates.

It is now possible to write a history of the mitrate-like cornutes and their descendants somewhat as follows. Probably in late Cambrian times, or anyway during the Cambrian, there existed certain Amygdalothecid cornutes which were adapted to staying up on very soft mud, relying for support only on the strength of the mud. These forms, which derived ultimately from sand-dwelling ancestors resembling *Cothurnocystis*, had extremely small, light, bilaterally symmetrical thecas with flat ventral surfaces and crawled mainly by ventral flexion of the stem.

From such animals evolved others which developed a convex ventral surface and stayed up on mud by displacing a certain weight of it. This 'design' of theca represented a basically sounder approach to the problem of staying up on mud, since it depended far less on very light weight and was less likely to fail. A long muscular stem now became possible, because extreme lightness was no longer essential. It also became necessary, because the boat-shaped theca had to be dragged through the top layer of mud. This muscular stem was elaborated from the old fore-stem, which was all of the cornute stem that remained. At about this stage the left gills became enclosed in an atrium, probably as protection against clogging by mud, and corresponding right gills with right pharynx and right atrium were produced. The appearance of gills on the right side, which must have happened suddenly, can be taken as marking the beginning of the mitrates.

It is very likely that the early mitrates were able to swim. For they inherited small size and a light skeleton from the advanced cornutes that gave rise to them and they were also rather flat-bodied and wide, all of which features would help them in swimming. Furthermore, the stem was muscular and laterally flattened and would make an effective paddle if waved from side to side.

Tunicates and vertebrates probably descend from an unspecialized mitrate of this sort which took to swimming continuously and lost its skeleton as a result. Vertebrates probably descend from the group of mitrates (Mitrocystitidae) which had developed an external lateral line.

Some other early mitrates, however, became deep bodied as an adaptation to life on very soft bottom, developed a median atrium and evolved the habit of rotation round the long axis when swimming, clockwise as seen from behind. Such a form was *Lagynocystis*. The descendants of it, or of a close relative, took to burrowing, lost their skeletons and increased the length of the notochord and of the columns of muscle blocks. From such a form were descended the modern cephalochordates, including amphioxus.

I would like to acknowledge the help of curators who have made available specimens in their charge. In particular, I would like to thank Dr V. Zázvorka, Dr R. Horný and Dr R. J. Prokop of the Národní Muzeum, Prague, who have shown patience and hospitality during my visits, Mr A. G. Brighton of the Sedgwick Museum, Cambridge, and Dr B. Kummel of the Museum of Comparative Zoology, Harvard. Dr D. Hardwick and Mr P. Minton of the Civil Engineering Department, Imperial College, London, have contributed many valuable discussions on functional morphology. Finally, the study would have been impossible if the great Czech collector, F. Hanuš, had not long ago amassed the specimens on which it was based.

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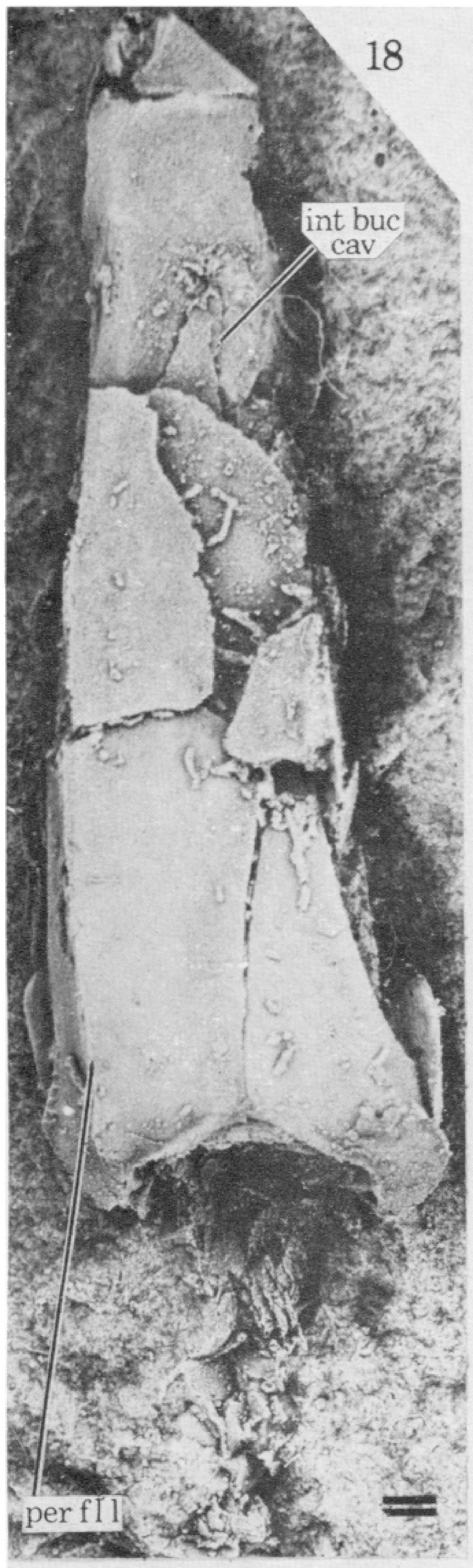
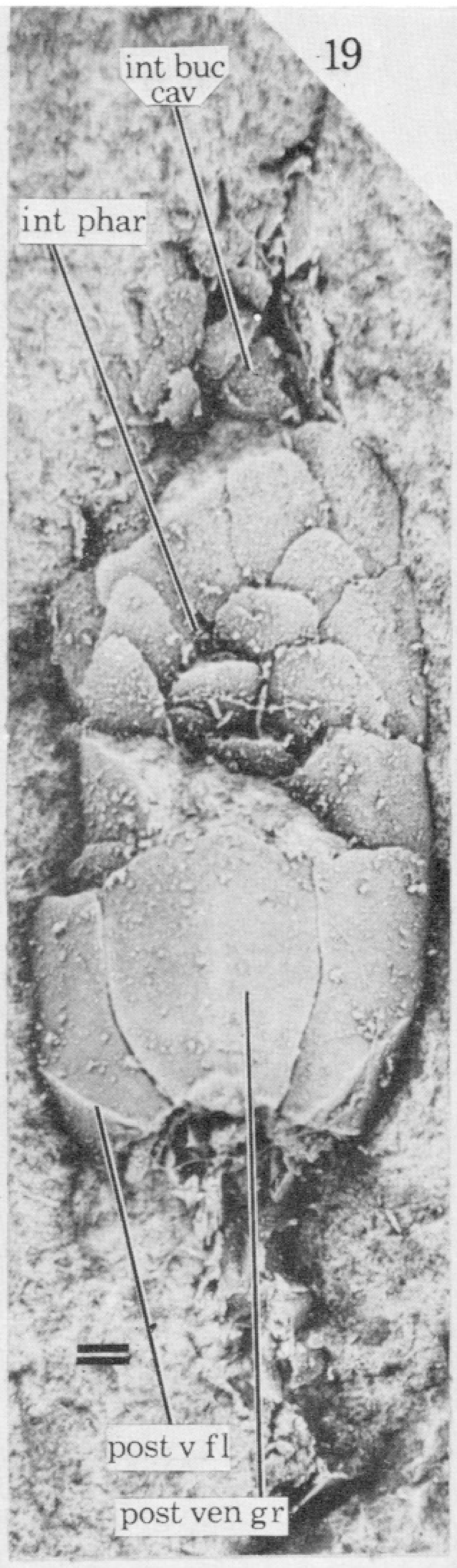
A LIST OF THE ABBREVIATIONS USED ON FIGURES 1 TO 8 AND 10 TO 69 (FIGURE 9 HAS ITS OWN LEGEND); FIGURES 18 TO 69 ARE ON PLATES 37 TO 46.

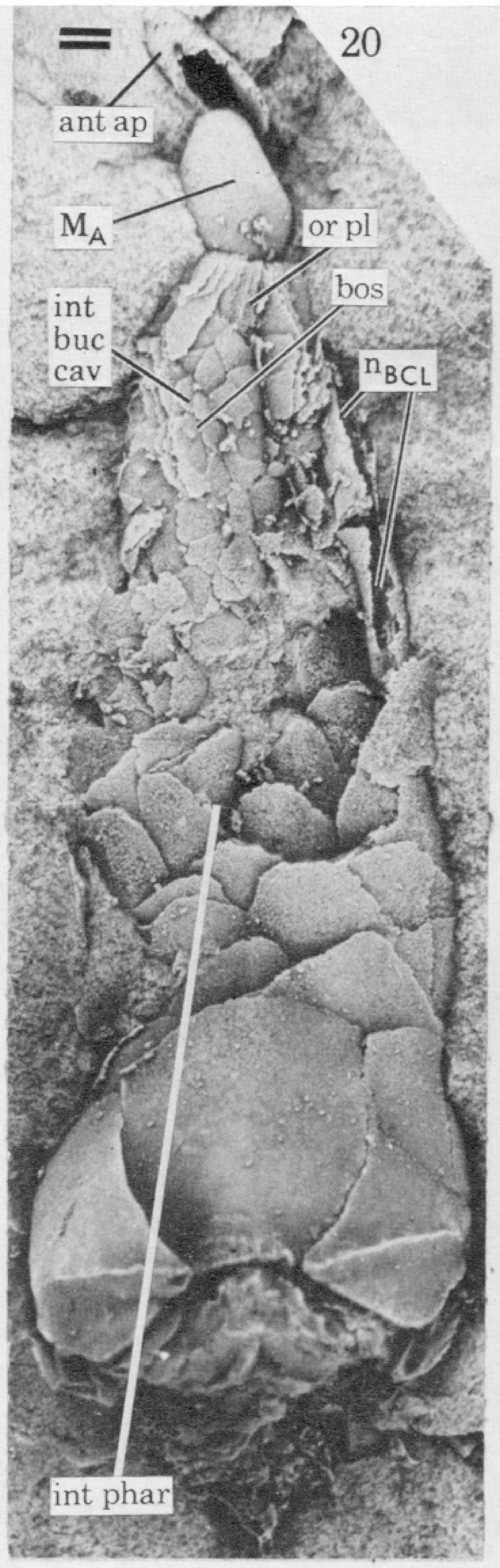
(a, b, c, d, e, f, g, h, i, j, k, l, m, n, p, q are marginal plates lettered according to comparative notation (see §2.))

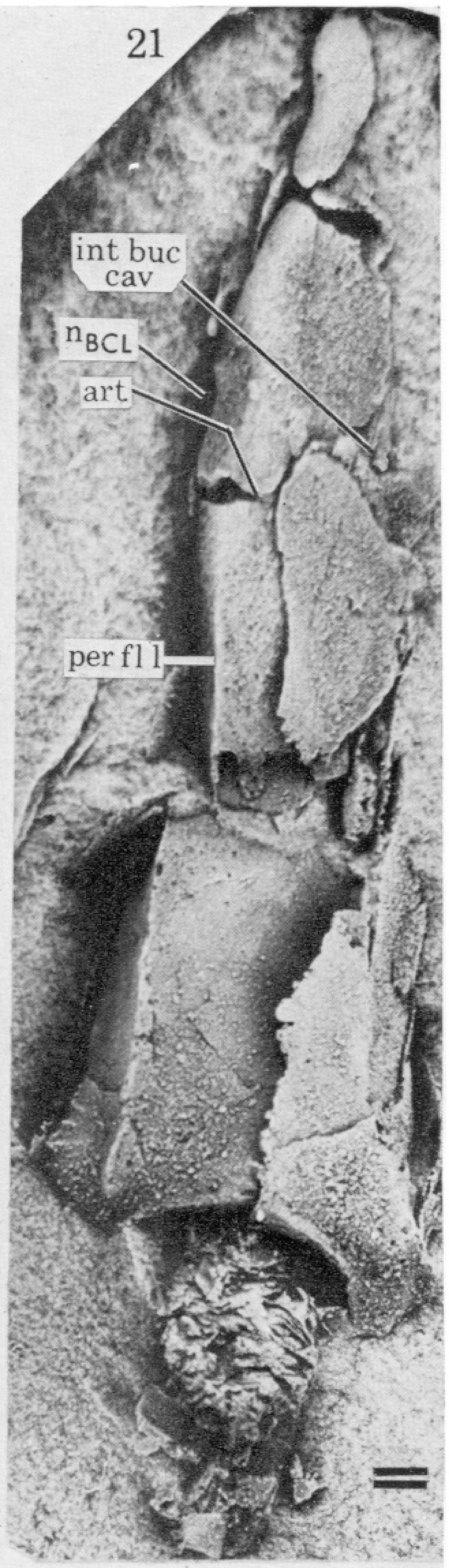
ac	anterior coelom
a imb f	anterior imbrication facet of ventral hind-stem plate
a int dep	anterior interossicular depression of dorsal hind-stem ossicle
a int tis	anterior interossicular tissue of dorsal ossicle of hind-stem
ant ap = b	anterior appendage
ant gr	anterior rigid group of marginal plates
ap	anterior part of the brain
arc gr	arcuate groove inside ventral hind-stem plate
art	articulation between anterior and postero-dorsal groups of marginal plates
art c	articular connective tissue
a skt	anterior socket of dorsal hind-stem ossicle
aud lat n r	right auditory and lateral nerve (*Mitrocystites*)
aud n l	left auditory nerve (*Mitrocystites*)
aug l, r	left and right auditory ganglia
ax art	axis of articulation between anterior and postero-dorsal rigid groups of marginal plates
b cav	buccal cavity
b cav/ph	junction between buccal cavity and pharynx
bos	boss on integument plate of buccal cavity
br	brain
br b	branchial bar of median atrium
br but	branchial buttress
br n	branchial nerves
br op l, r	left and right branchial openings
bs	branchial slits
br s l	branchial soft layer
bs med at	branchial slits of median atrium
calc br b	calcitized branchial bar
cav br but	cavity of branchial buttress
cav std	anterior cavity of styloid
cer bas	cerebral basin
cl b cav/ph	cleft in internal mould between buccal cavity and pharynx
con tis	connective tissue invading ventral skeleton
d bar	dorsal bar (of *Reticulocarpos* etc.)
d l ang	dorso-lateral angle of medial part of the brain
dlc	dorsal longitudinal canal through dorsal ossicles of *Mitrocystites*
d maj pl	dorsal major plates of fore-stem (of *Reticulocarpos* etc.)
d m m atr	dorsal margin of median atrium
d m pc	dorsal margin of posterior coelom
d m th	dorsal margin of thickened region of left thecal wall
dnc	dorsal nerve cord
d oss 1, 2, 3, etc.	dorsal ossicles of hind-stem, numbered backwards
d pl	dorsal plate of mid- and hind-stem of *Reticulocarpos*
? drn	? dorsal root nerve
dvf	dorso-ventral facet to receive ventral plates in dorsal ossicles of *Mitrocystites*
e–e	line of section in figure 2
f d oss	facet on ventral plate for dorsal ossicle of hind-stem
f st	fore-stem
f ven pl	facet on dorsal ossicle of hind-stem to receive ventral plate
gan	ganglion
g an	gonopore-anus (*Reticulocarpos*)
gan p	ganglionic pit
gr tr bs	growth traces of branchial slits
h br b	hollow branchial bar of median atrium
hd st	hind-stem (*Reticulocarpos*)
hyp cer pr	hypocerebral process
ic	interossicular canal (*Mitrocystites*)
imb f	imbrication facet of ventral plates of hind-stem
imb st	imbrication step for posterior integument plates in postero-ventral group of marginal plates
int buc cav	integument of buccal cavity
int buc cav d, v	dorsal and ventral integument of buccal cavity
int l phar	integument of left pharynx (in primitive mitrates)
int phar	integument of pharynx
int ph/int b cav	junction between integuments of pharynx and buccal cavity
int pl	intercalary plates
int tis	interossicular tissue between dorsal ossicles of hind-stem
kst pl	'keystone' plate of oral plates
lat gr	lateral groove of dorsal ossicle of hind-stem
llg, n	lateral line ganglion and nerve (*Mitrocystites*)
l p	lateral pit (in hind-stem)
l p art, gan	articular and ganglionic parts of lateral pit
l ph	left pharynx

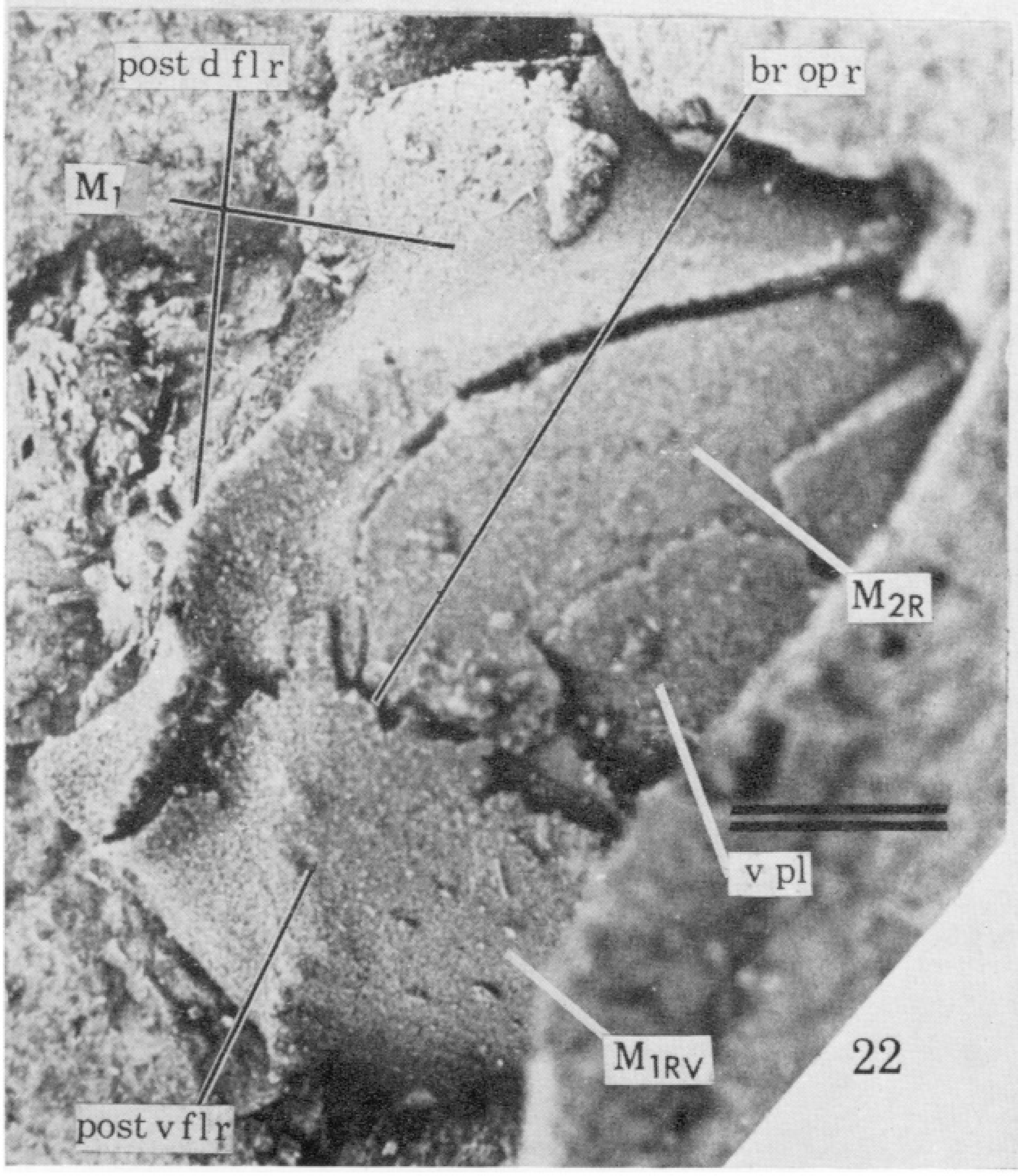
l ph/ac	junction between left pharynx and anterior coelom
l tr eye	left transpharyngeal eye (*Reticulocarpos*, *Mitrocystites* and primitive mitrates)
M_A, M_{3L}, M_{1RV} etc	marginal plates lettered according to objective notation (see §2)
maj pl	major plate of fore-stem
m atr	median atrium
m atr l, m, r	left, median and right portions of median atrium
m bl	muscle blocks
med atr op	opening of median atrium
med sut	median suture, between two ventral plates of hind-stem
m gr	median groove on ventral surface of dorsal ossicle of hind-stem
mid std int tis	mid-styloidal interossicular tissue
mp	medial part of brain
mpn	medial part nerve (*Mitrocystites*)
mp/pp	junction between medial and posterior parts of brain
n_{BC}	nerve to buccal cavity of *Lagynocystis*: right or left
n_{BCL}	nerve to left side of buccal cavity of *Lagynocystis*
n_{BCR}	nerve to right side of buccal cavity of *Lagynocystis*
not	notochord
not + dnc	notochord plus dorsal nerve chord
n_0	nerves in *Mitrocystites*, probably supplying endostyle
n_1, n_2, n_{2A}, n_{2P}, n_3, n_{4+5}, n_5	nerves of palmar complex of *Mitrocystites*. Nerve n_2 corresponds to n_{BC} of *Lagynocystis*
ob gr	oblique groove in dorsal surface of internal cast
ol o	olfactory openings in buccal cavity (*Mitrocystites*)
ol p	possibly olfactory portion of medial brain of *Lagynocystis*
or	oblique ridge on skeleton, filling oblique groove
or pl	oral plate
pal	palmar nerve (*Mitrocystites*)
pbl, pbr	left and right pyriform bodies
pc	posterior coelom
per fl l, r	left and right peripheral flanges of theca
pg	peripheral groove, on dorsal surface of theca of *Mitrocystites*
p imb f	posterior imbrication facet of ventral plate of hind-stem
p int dep	posterior interossicular depression of ossicle of hind-stem
p int tis	posterior interossicular tissue of dorsal osside of hind-stem or of styloid.
pos b b cav	posterior border of buccal cavity
pos sf br cage	posterior surface of branchial cage
post d fl l, r	left and right postero-dorsal flanges
post dors gr, p d gr	postero-dorsal group of marginal plates
post ven gr, p v gr,	postero-ventral group of marginal plates
post v fl l, r	left and right postero-ventral flanges
pp	posterior part of brain
p pr	posterior process of dorsal ossicle of hind-stem, fitting into anterior socket
pr b l	pre-branchial line
p v pr	postero-ventral process of ventral plates of hind-stem of *Lagynocystis*
p v spk	postero-ventral spike of hind-stem of *Reticulocarpos*
r atr	right atrium
rec br b	reconstructed portion of branchial bar
rect	rectum
ret c	retaining cartilage anterior to branchial openings
r m m atr	right margin of median atrium
r ph	right pharynx
r ph/ac	boundary between right pharynx and anterior coelom
r tr eye	right transpharyngeal eye (*Reticulocarpos*, *Mitrocystites*)
seal c	sealing connecting tissue of branchial openings
s l	soft layer inside skeleton
spk	spike of fore-stem of *Lagynocystis*
stc	stylocone (*Reticulocarpos*)
std	styloid
str	strut (*Reticulocarpos*)
sut	sutures, on each side of M_{PV}
th n	thecal nerves
tr bb	dorsal trace of branchial bar
tr cav	transverse cavities inside branchial buttress
v m n_{BCR}	ventral margin of right nerve to buccal cavity
v maj pl	ventral major plate of fore-stem (primitive mitrate and *Reticulocarpos*)
v oss	ventral ossicle of hind-stem (*Reticulocarpos*)
v pl	ventral plate of hind-stem
v pr	ventral process of dorsal ossicle of hind-stem
? v r	possible ventral root 'muscle-tail' or containing groove, in ventral plates of hind-stem
v sm ar	ventral smooth area of stylocone (*Reticulocarpos*)
v spk	ventral spike on stylocone and hind-stem ossicle of *Reticulocarpos*
v surf	ventral surface developed on hind-stem plates of *Lagynocystis* and hypothetical primitive mitrate
w mgr	widening of median groove of dorsal ossicles, possibly indicating where segmental ganglia were connected to dorsal nerve cord

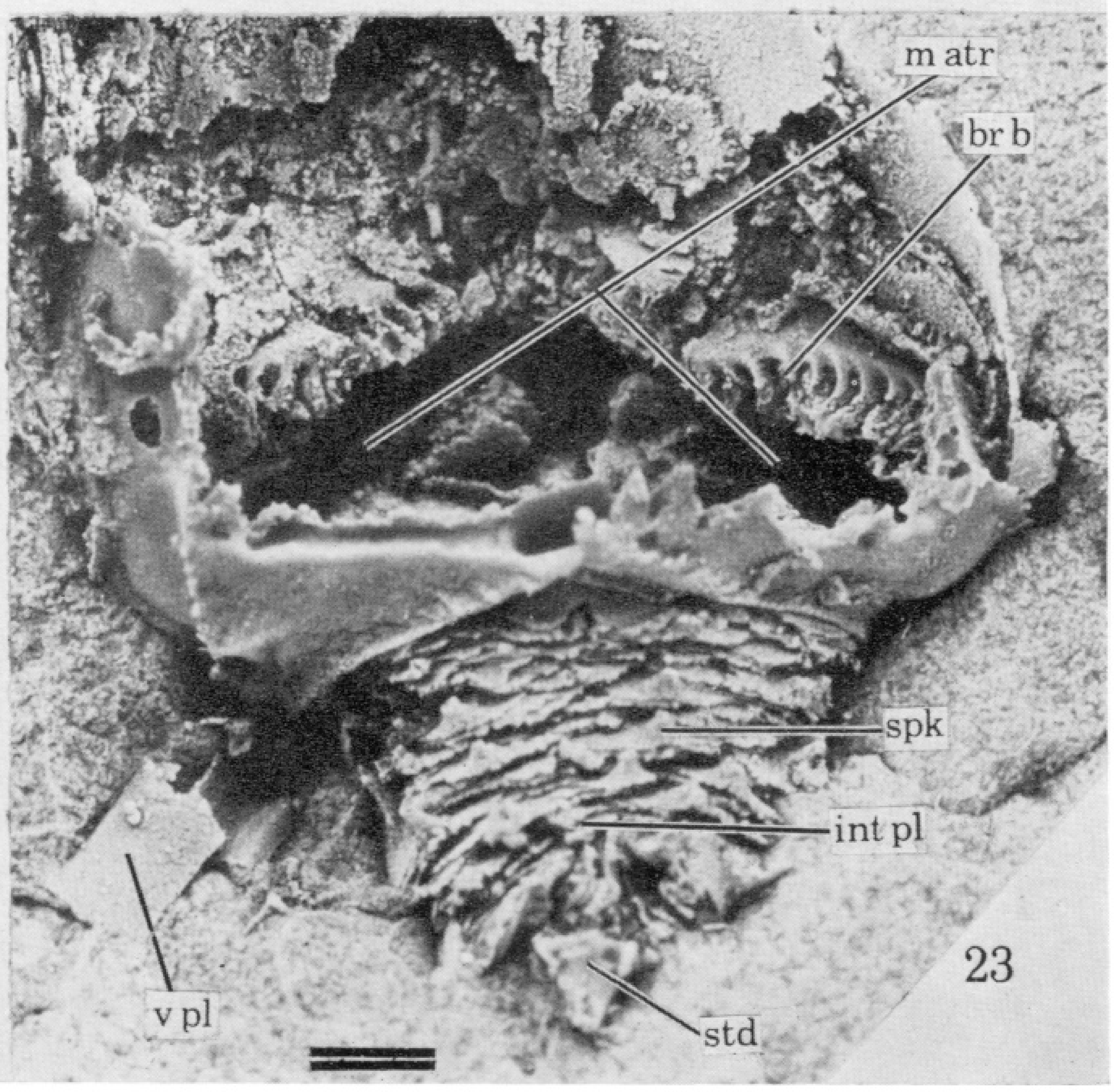












FIGURES 18 to 23. For legends see facing page.

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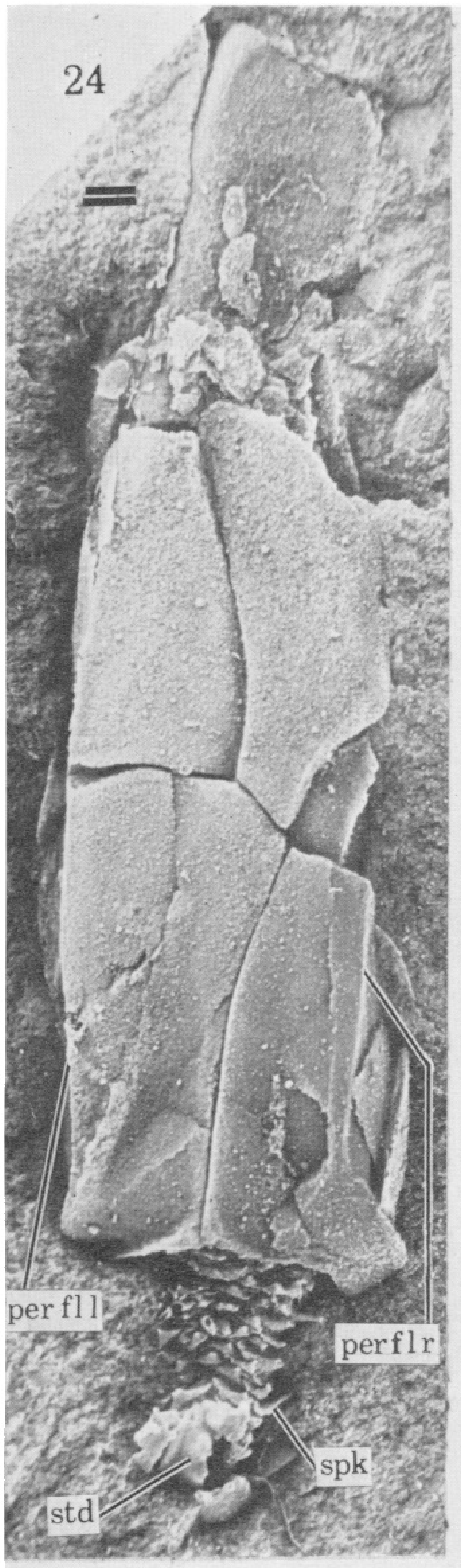

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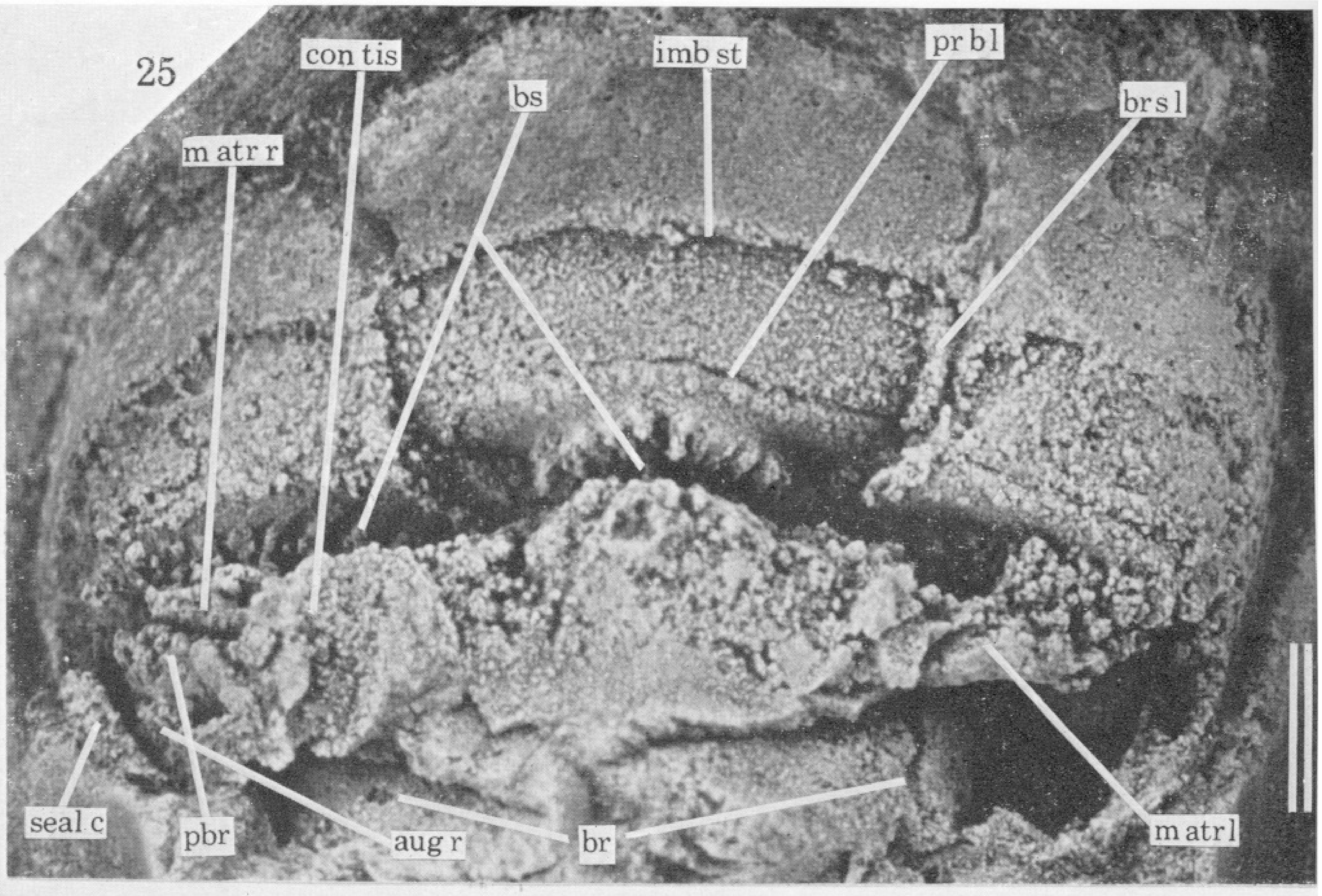

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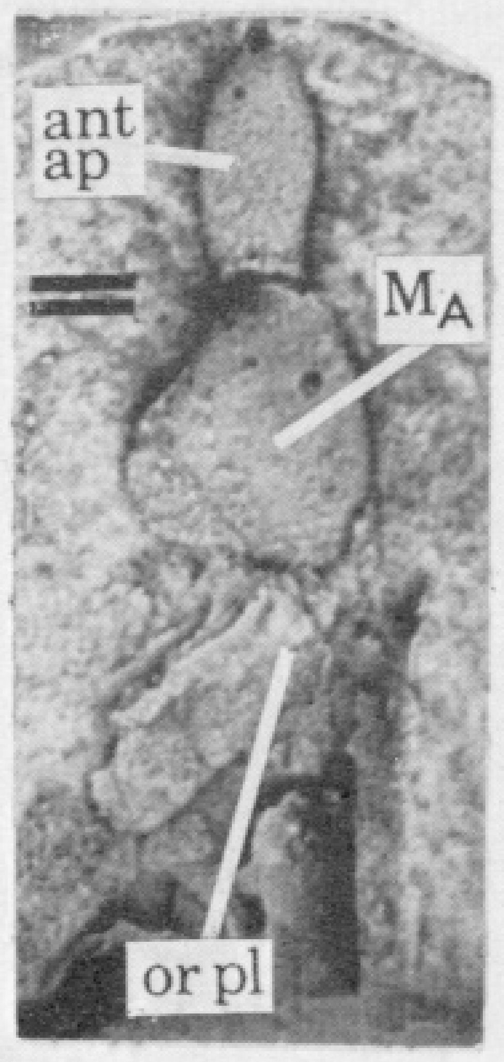

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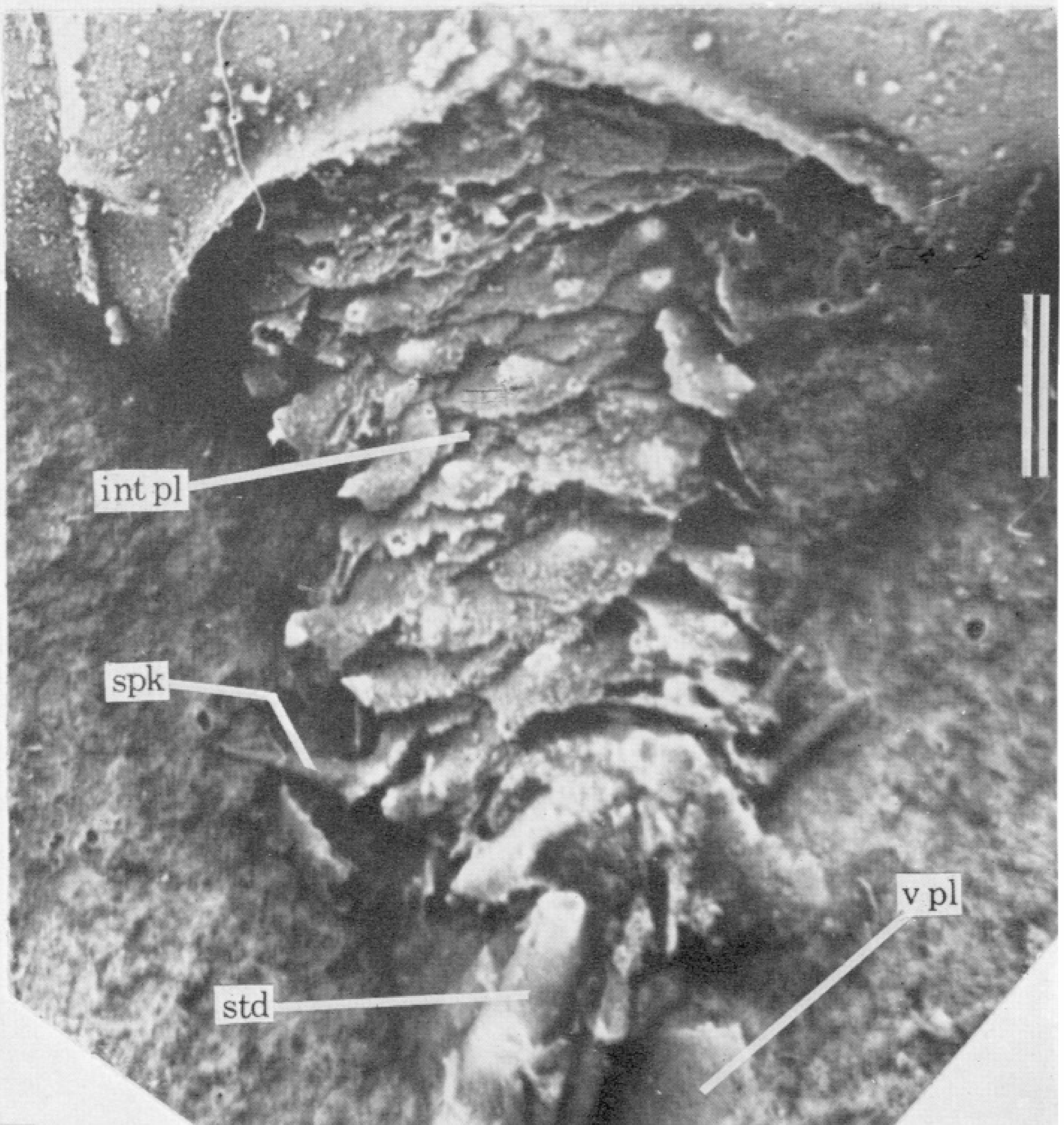

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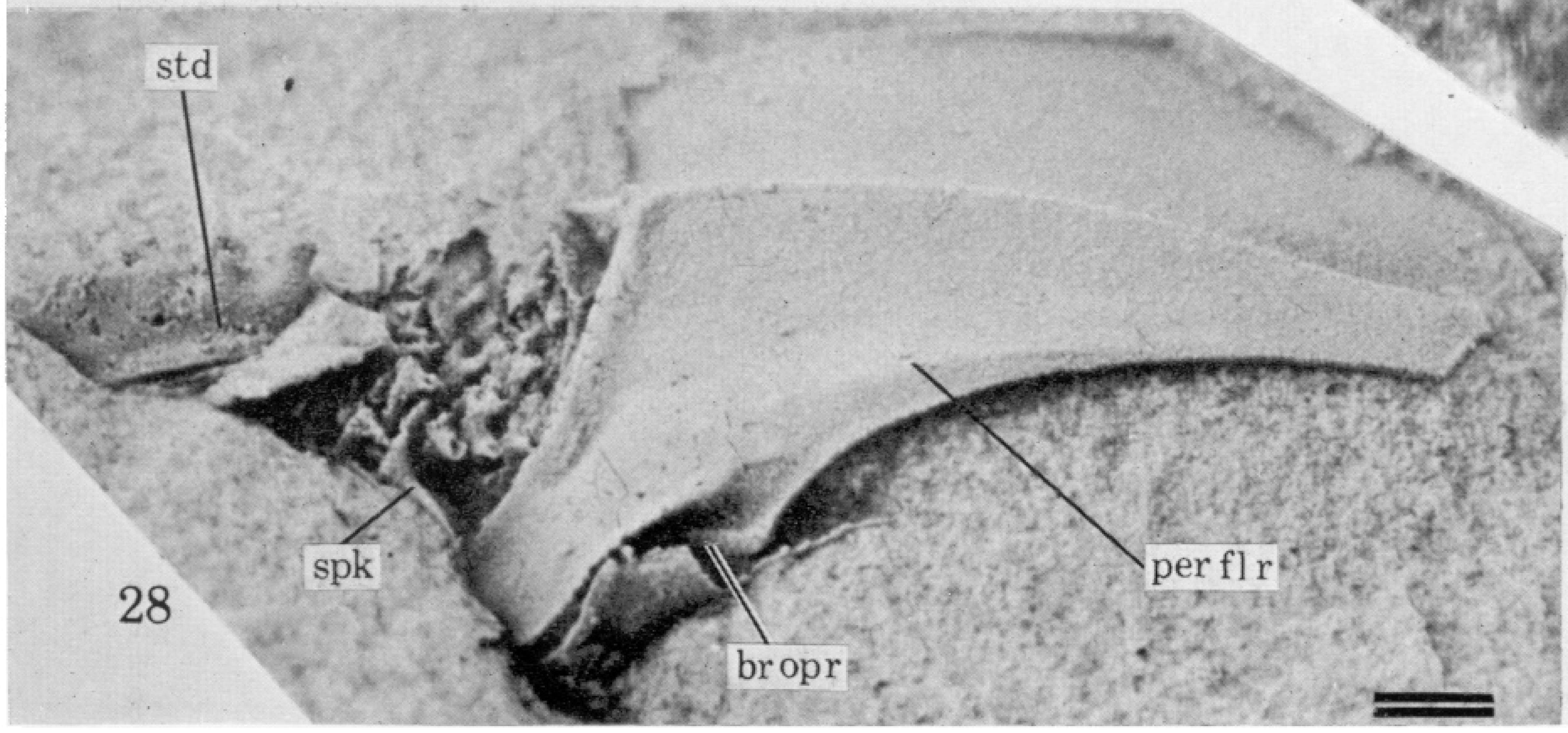

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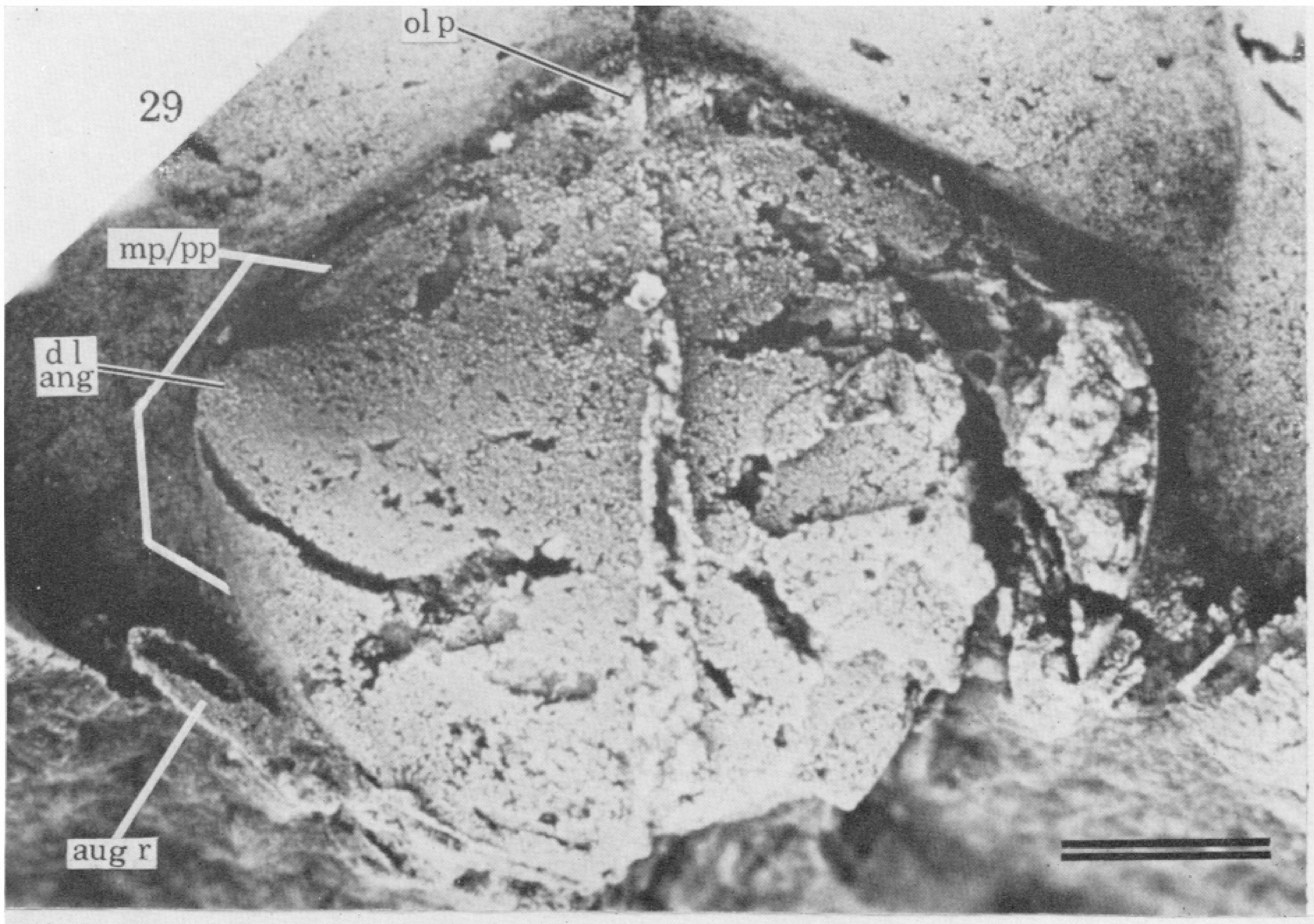

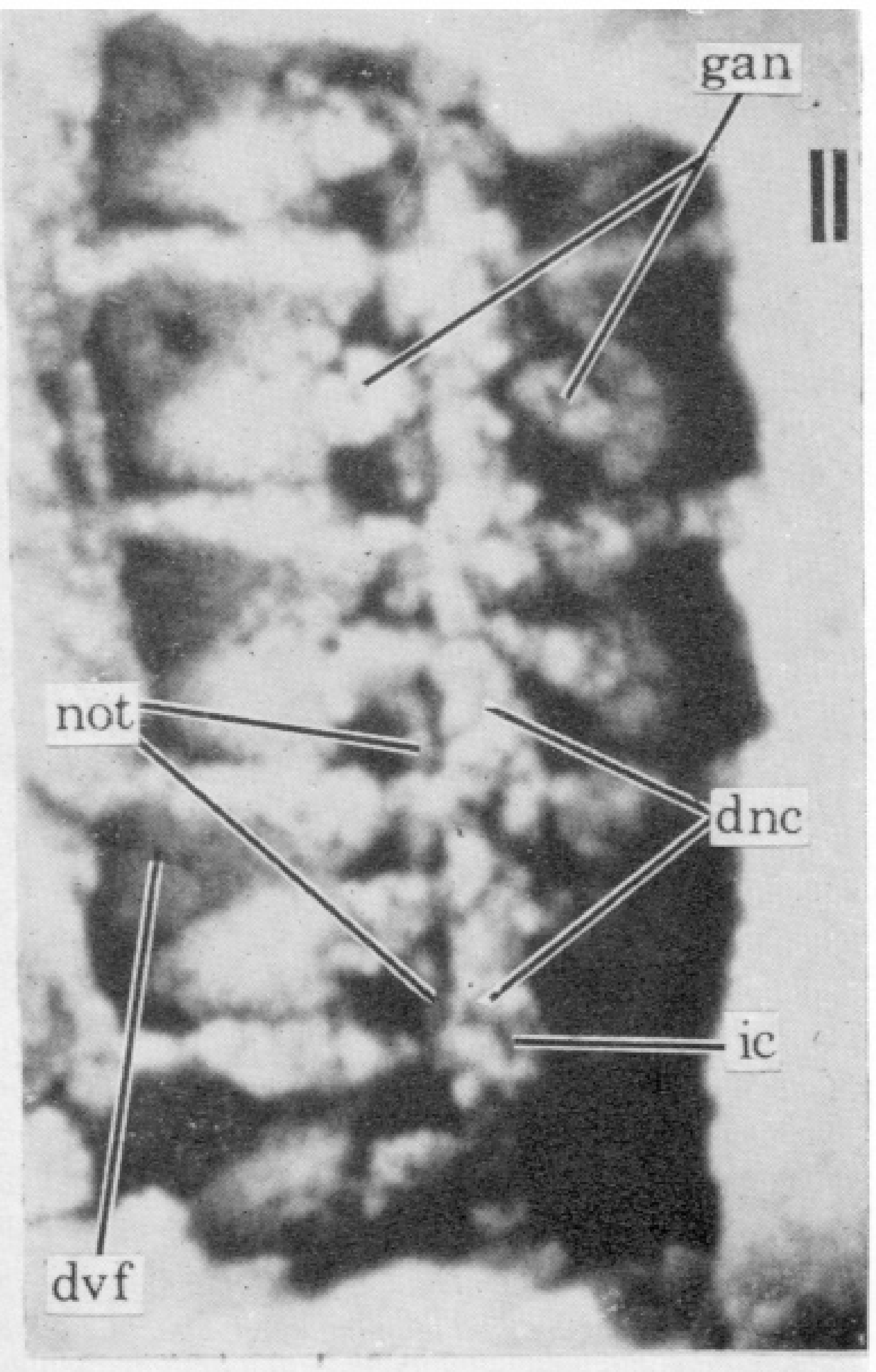

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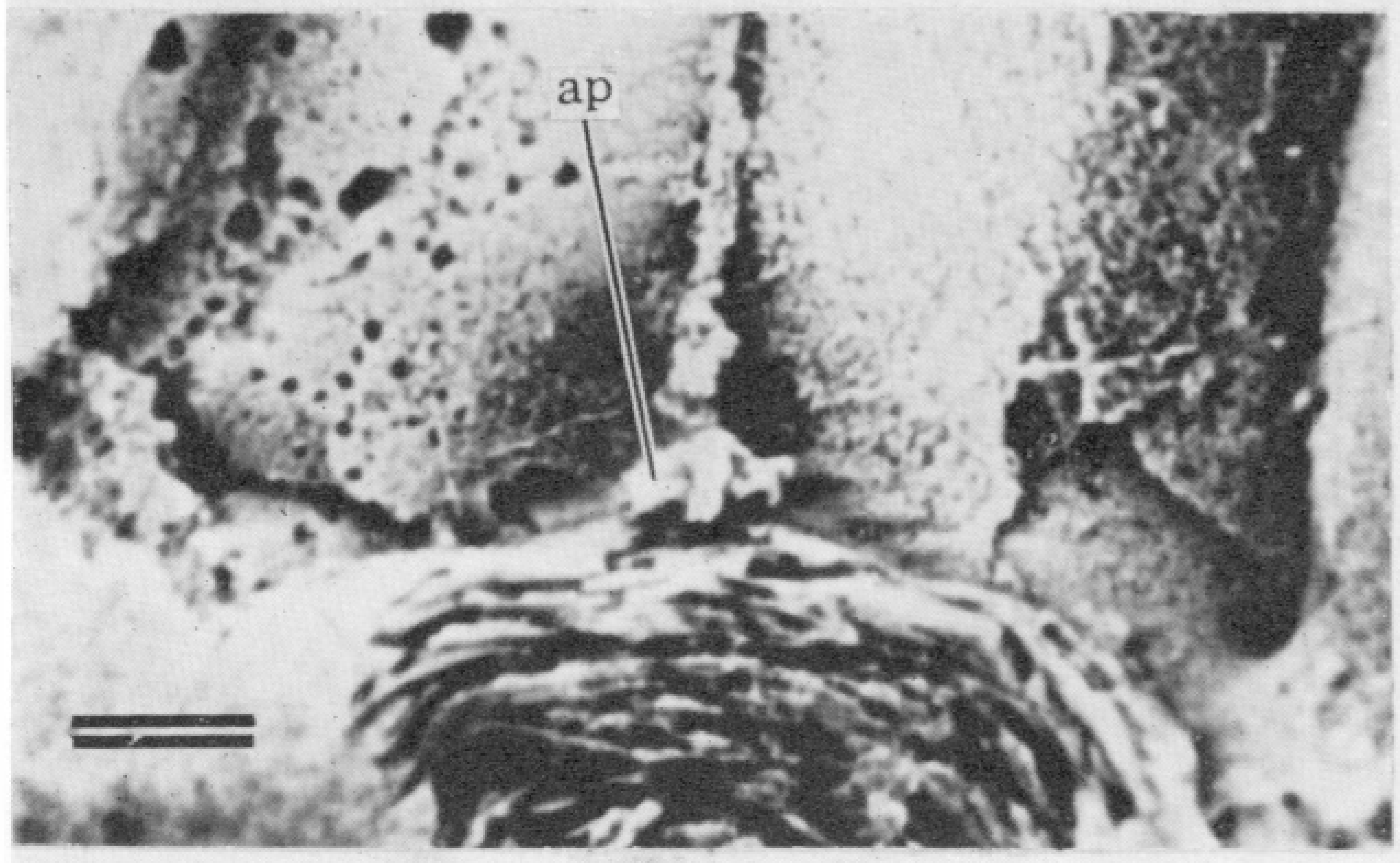

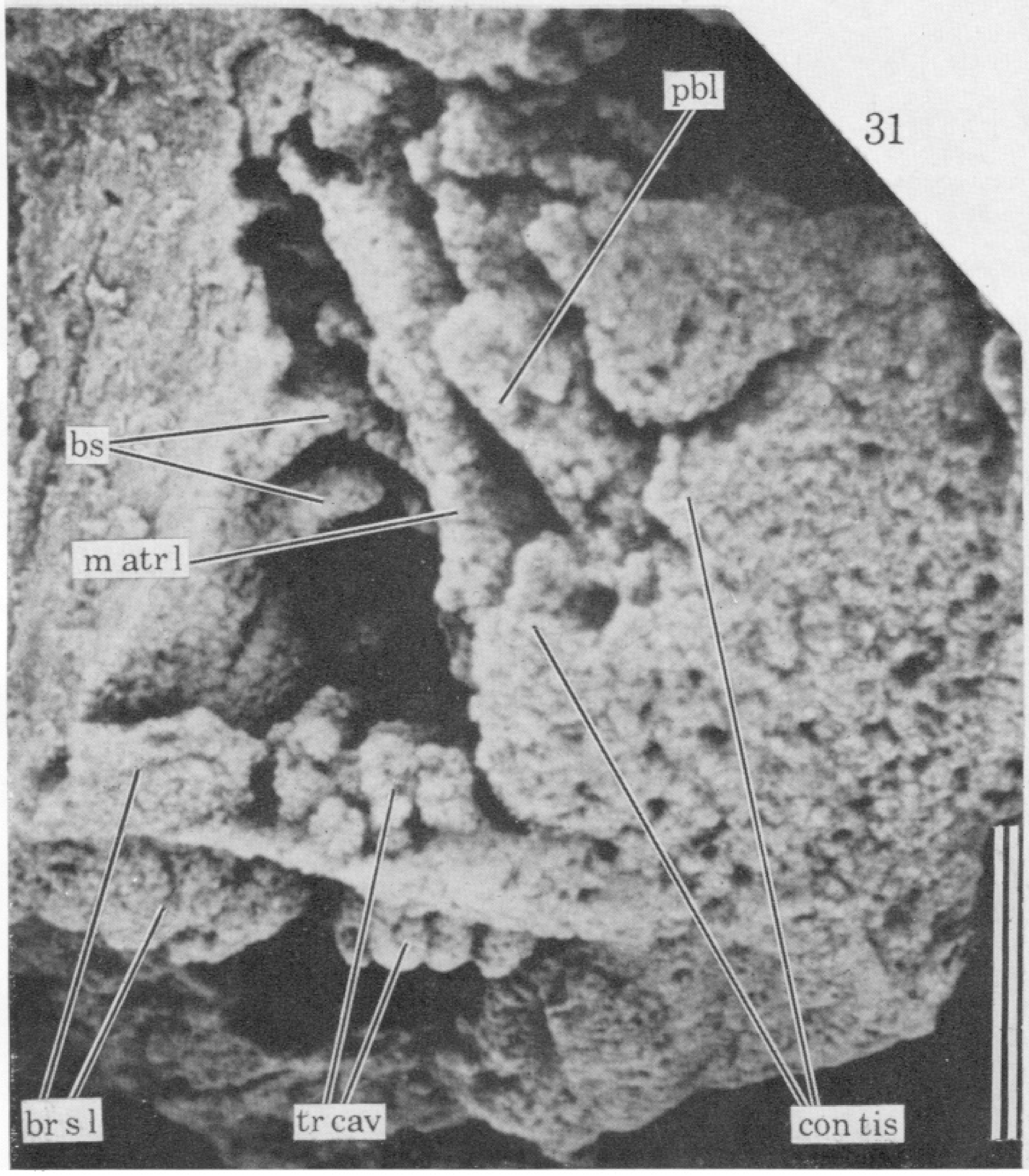

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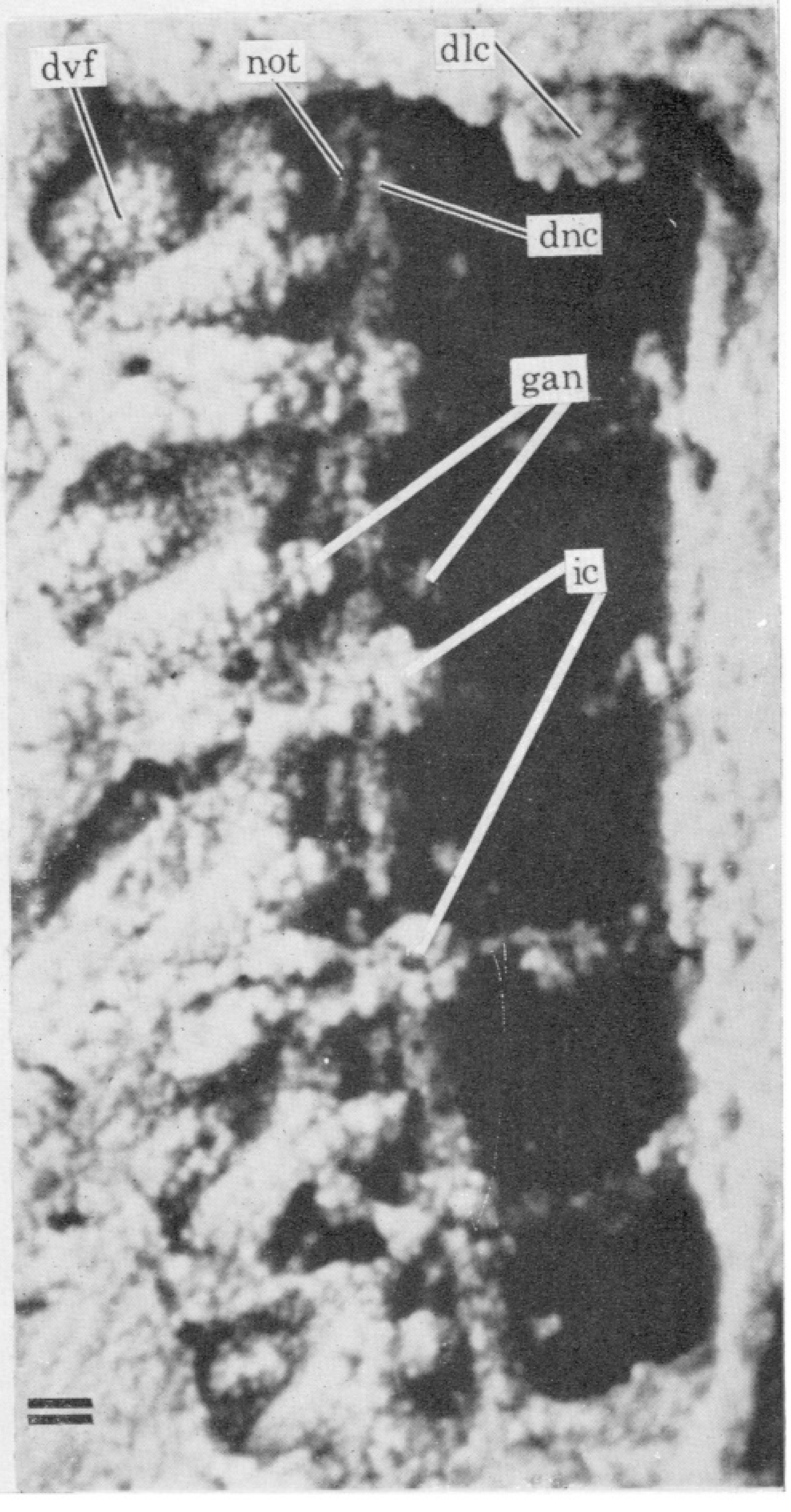
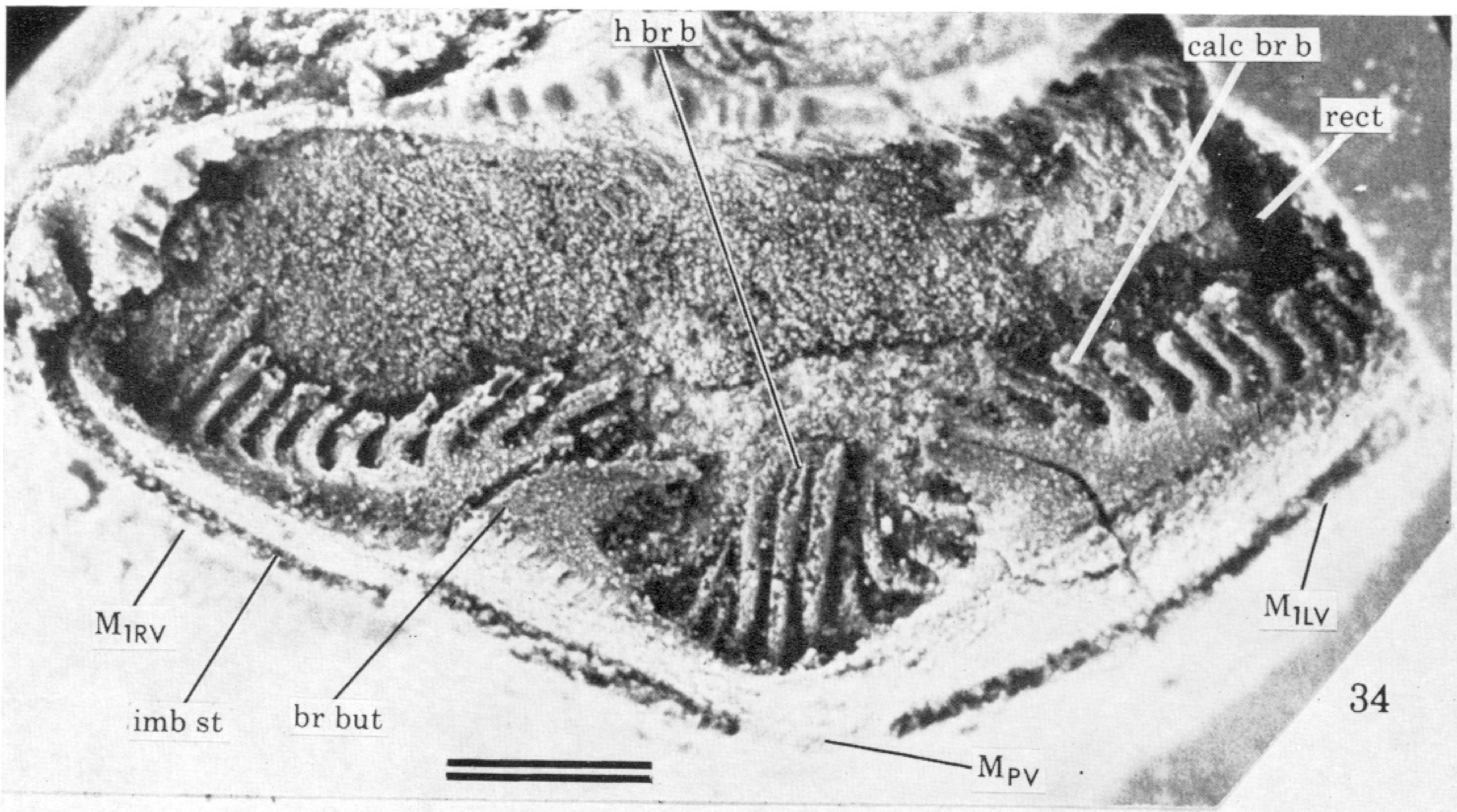


Figures 29 to 33. For legends see facing page.



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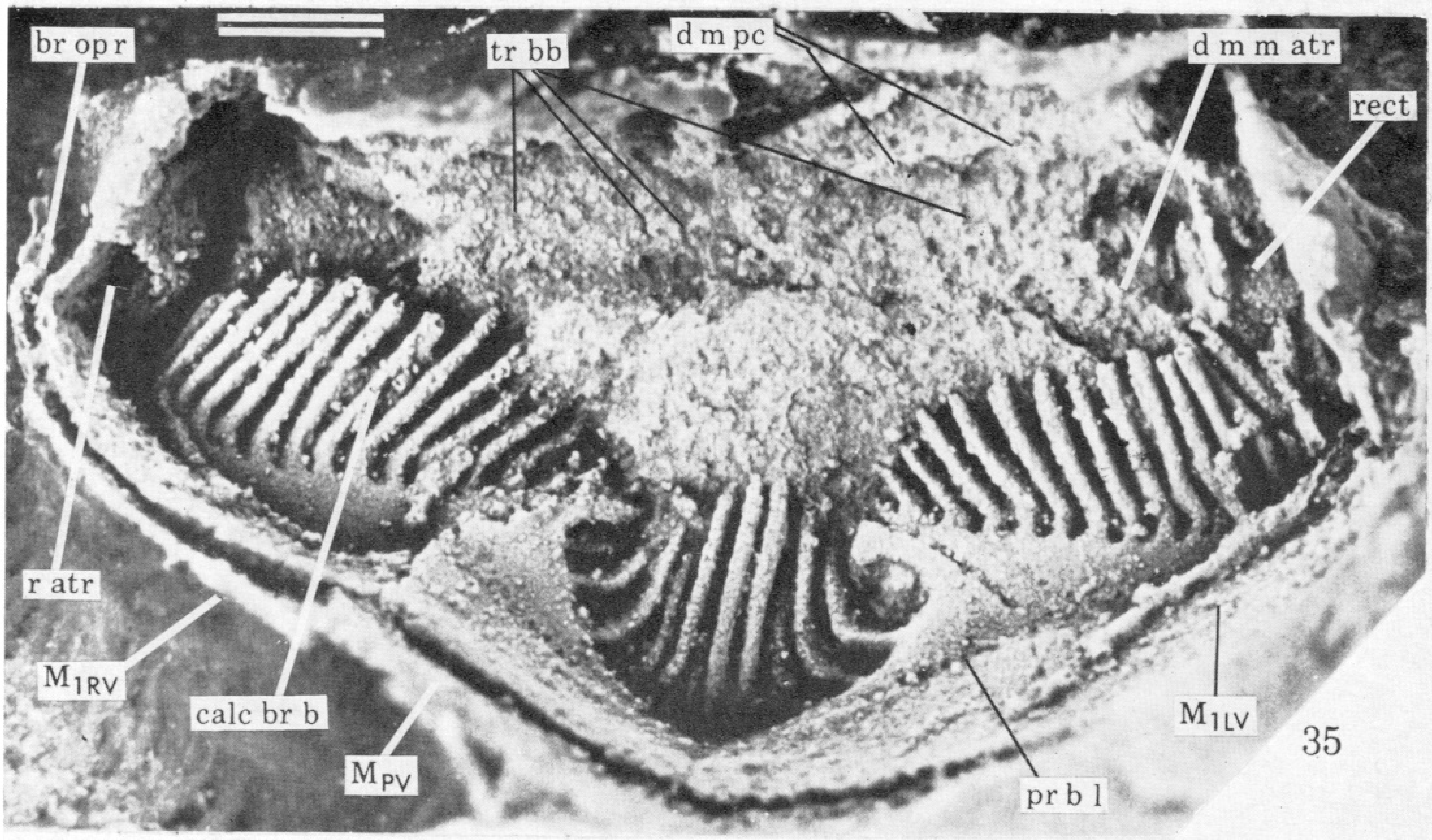

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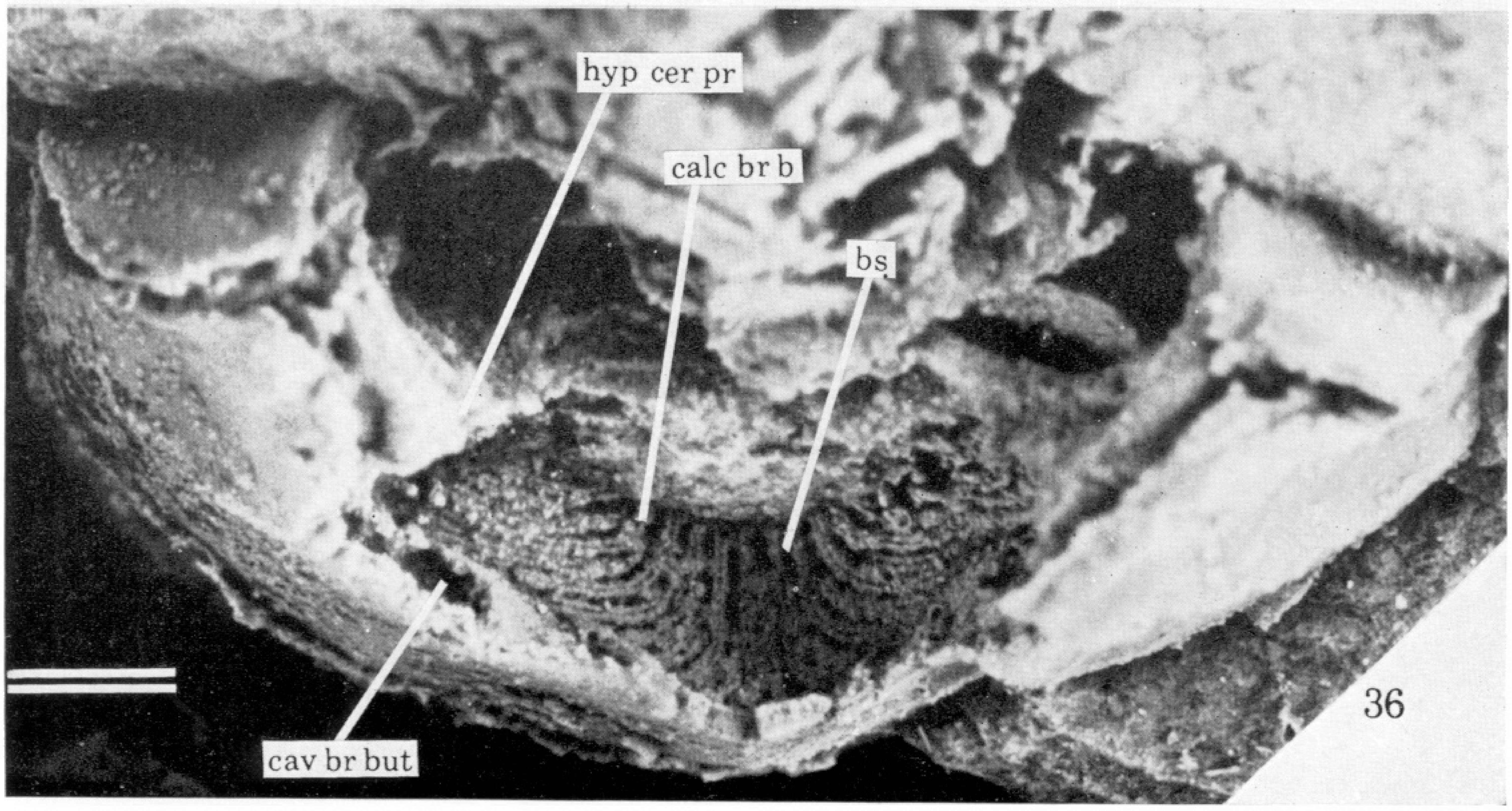

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Figures 34 to 36. For legends see facing page.

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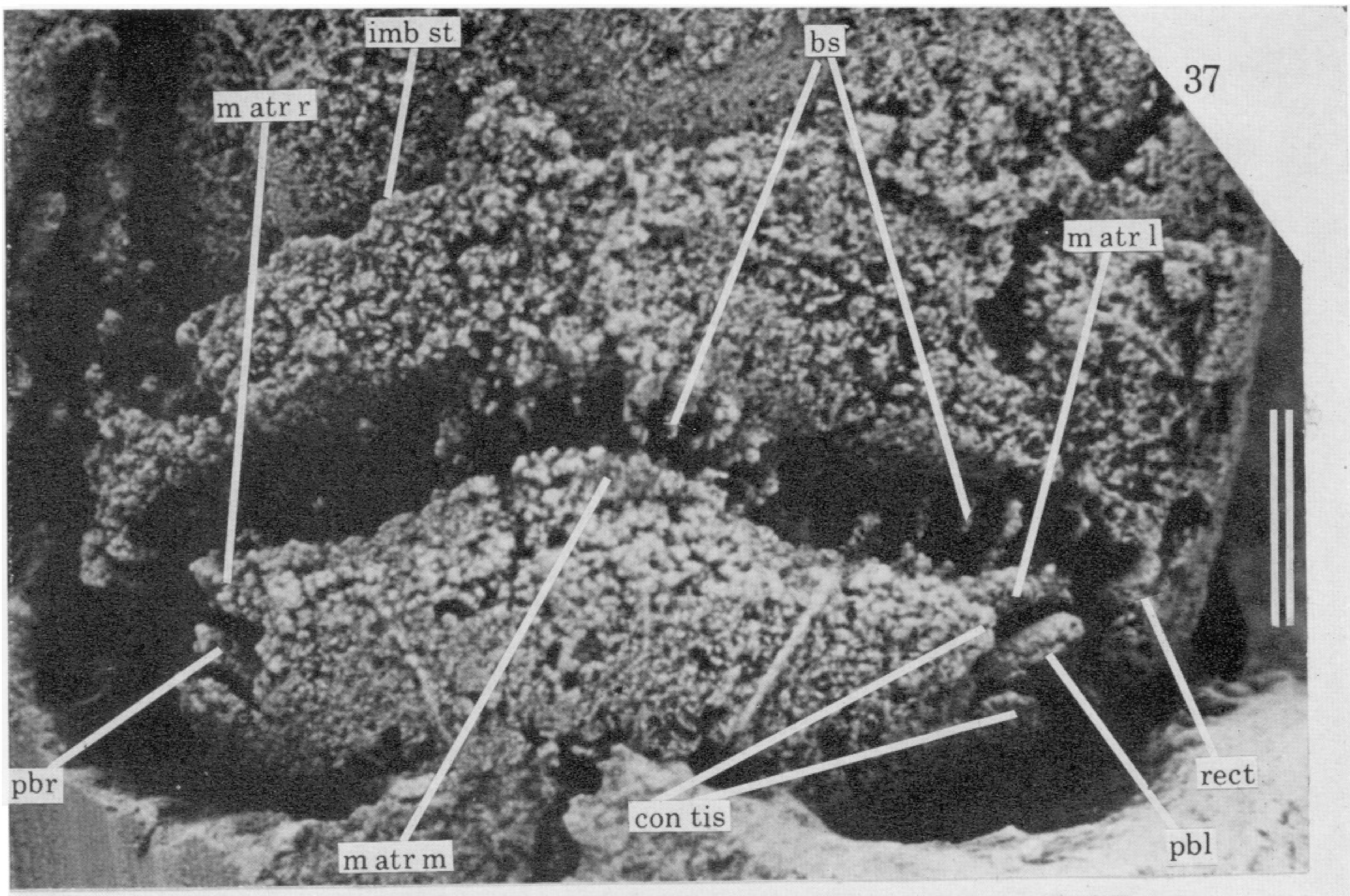

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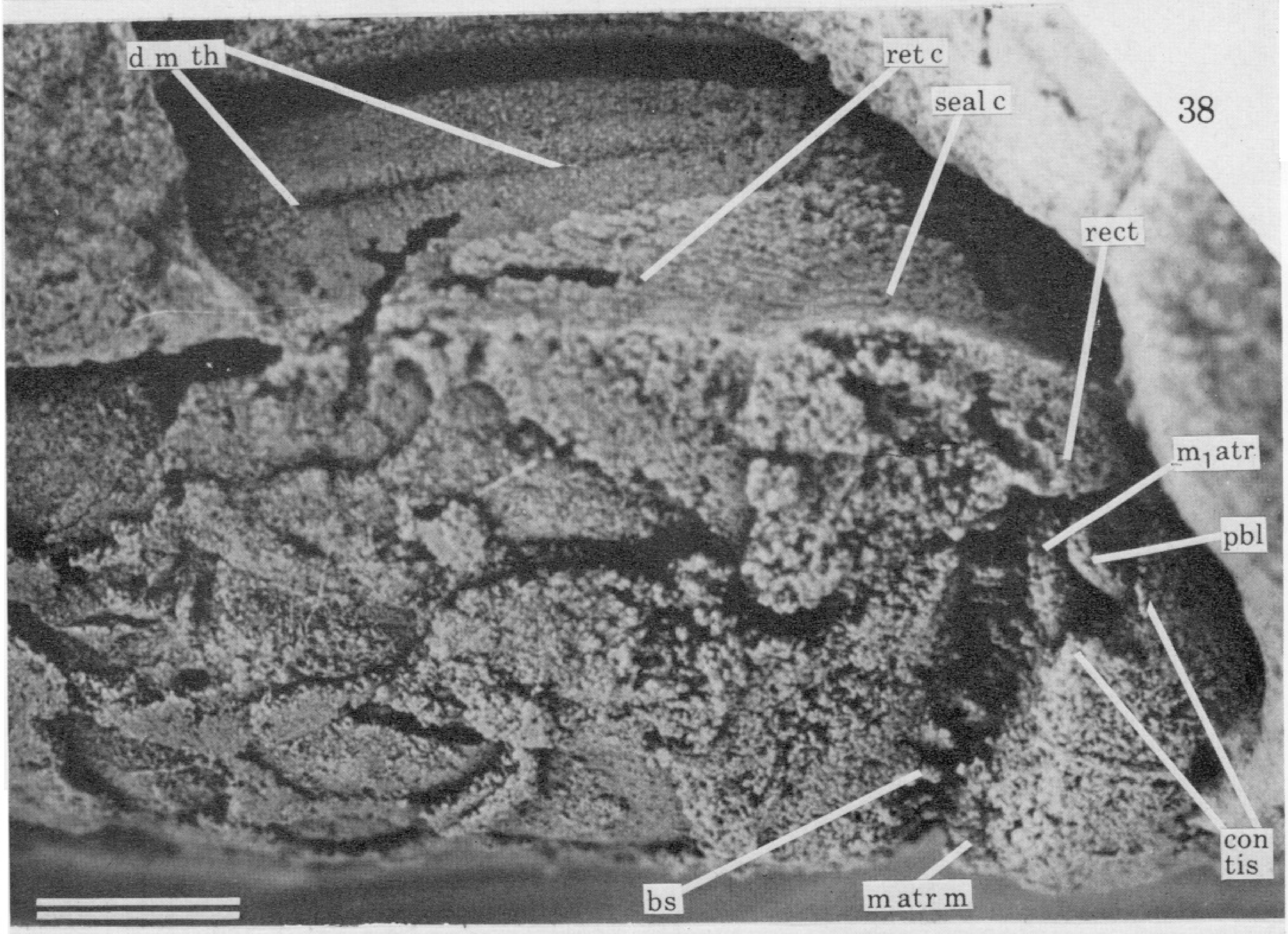

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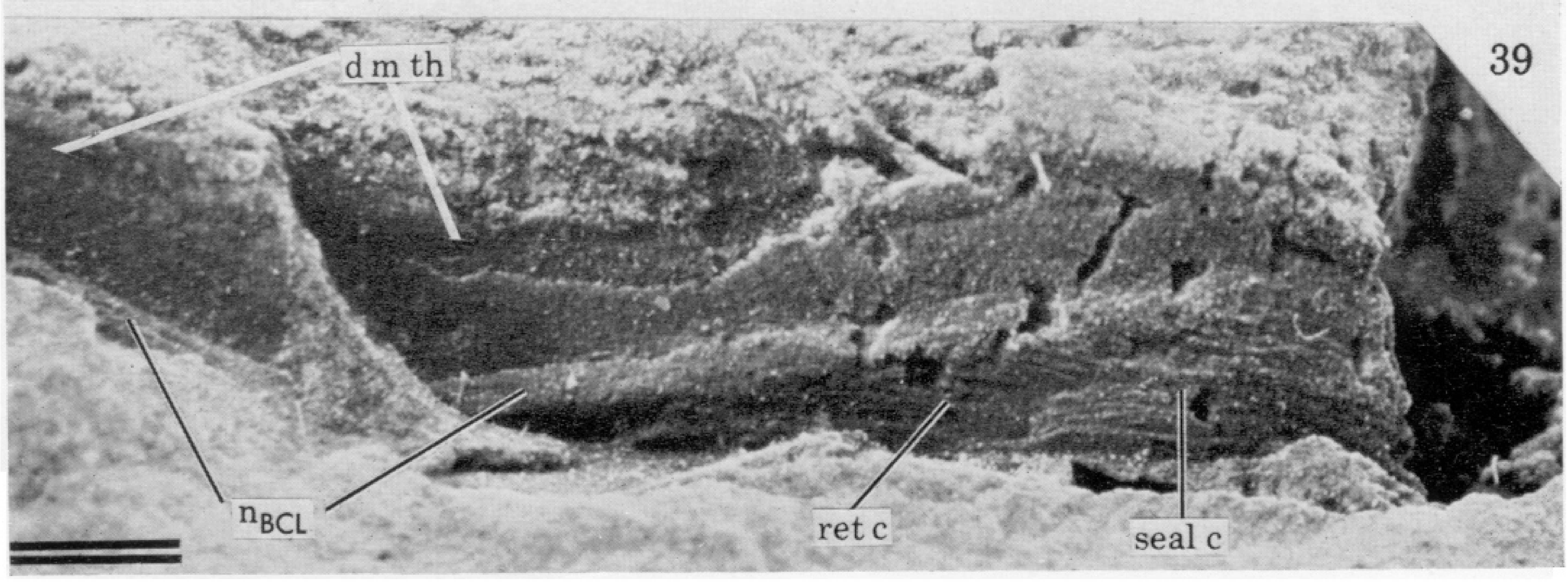
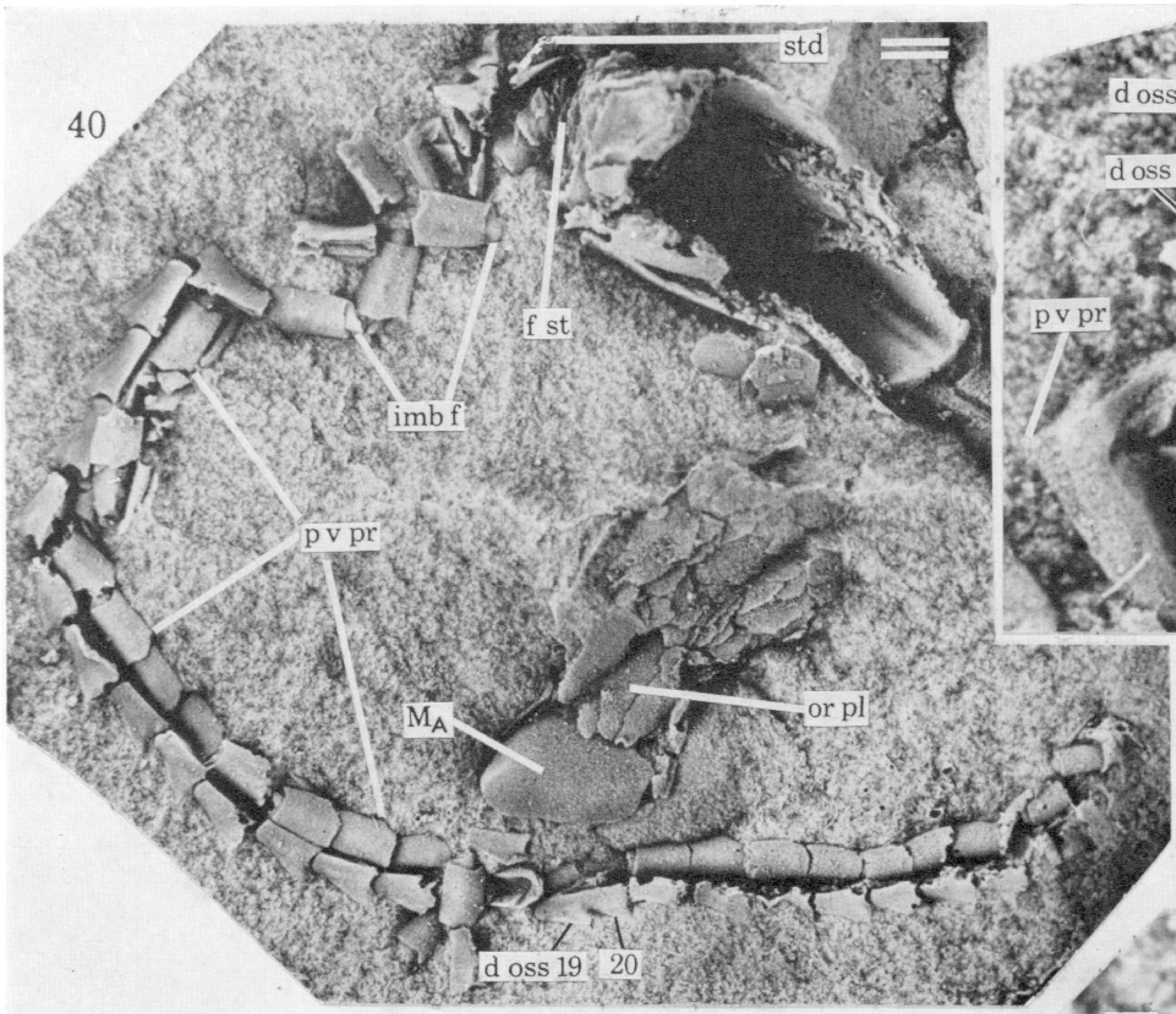
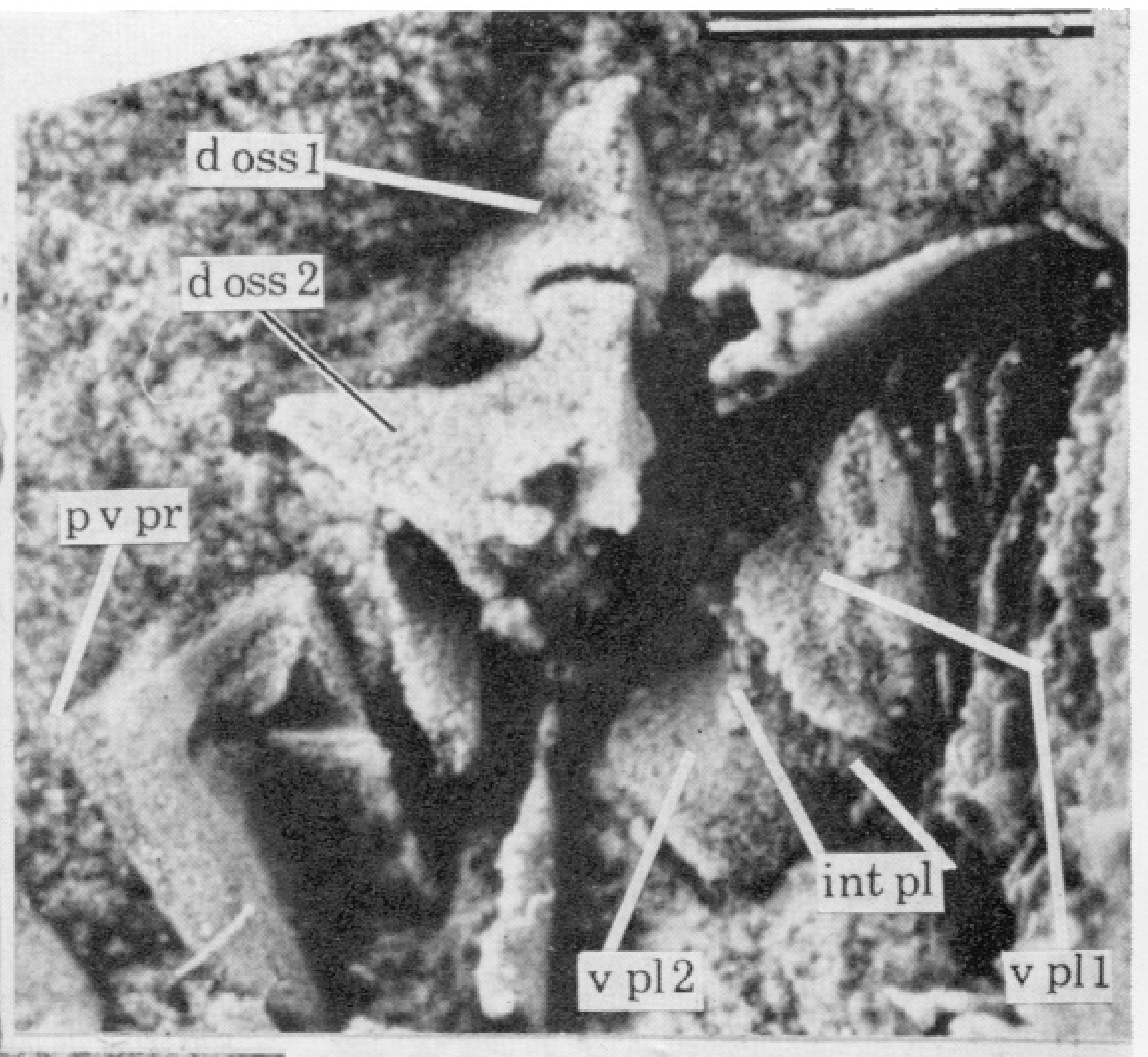


FIGURES 37 to 39. For legends see facing page.

40





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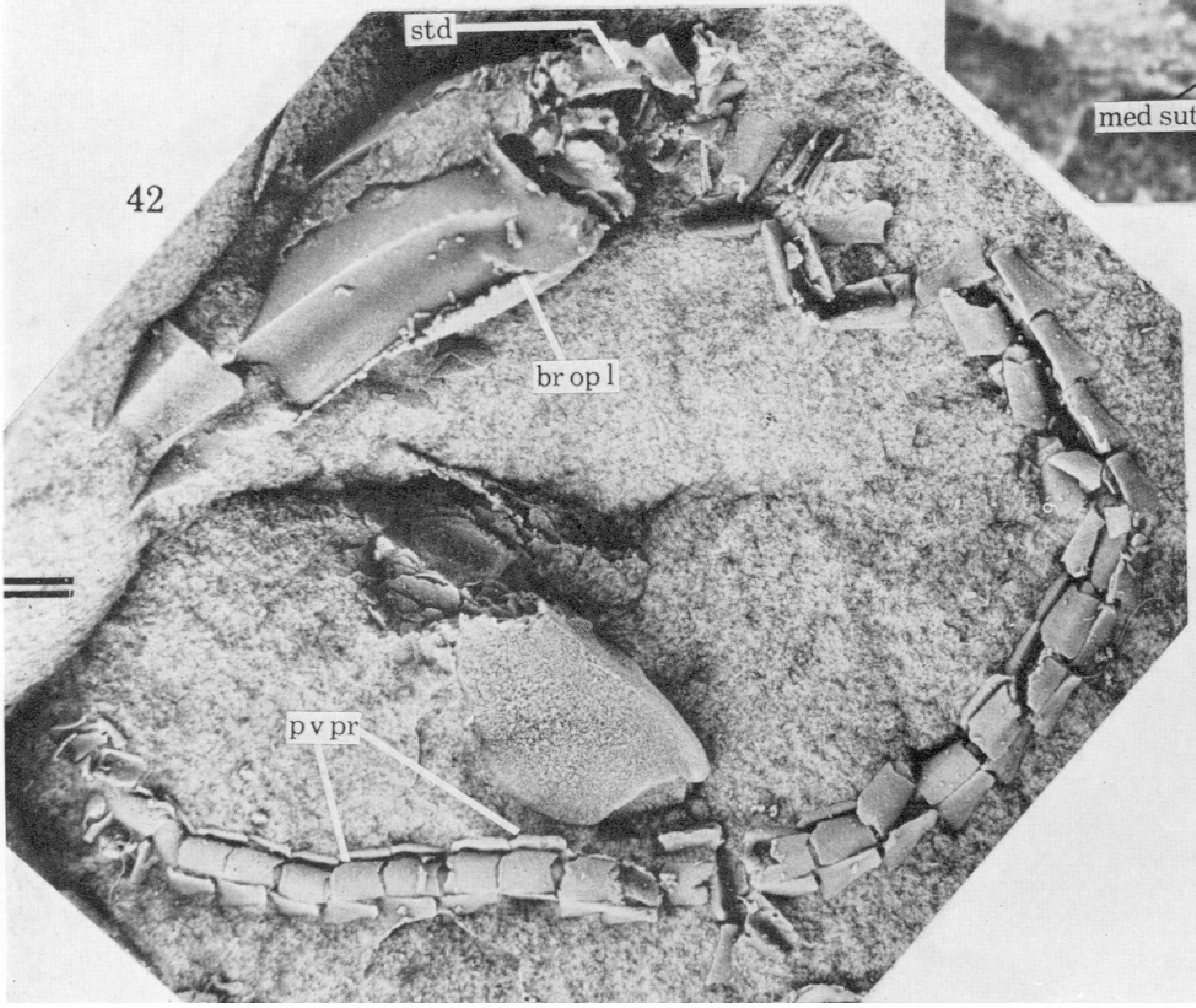

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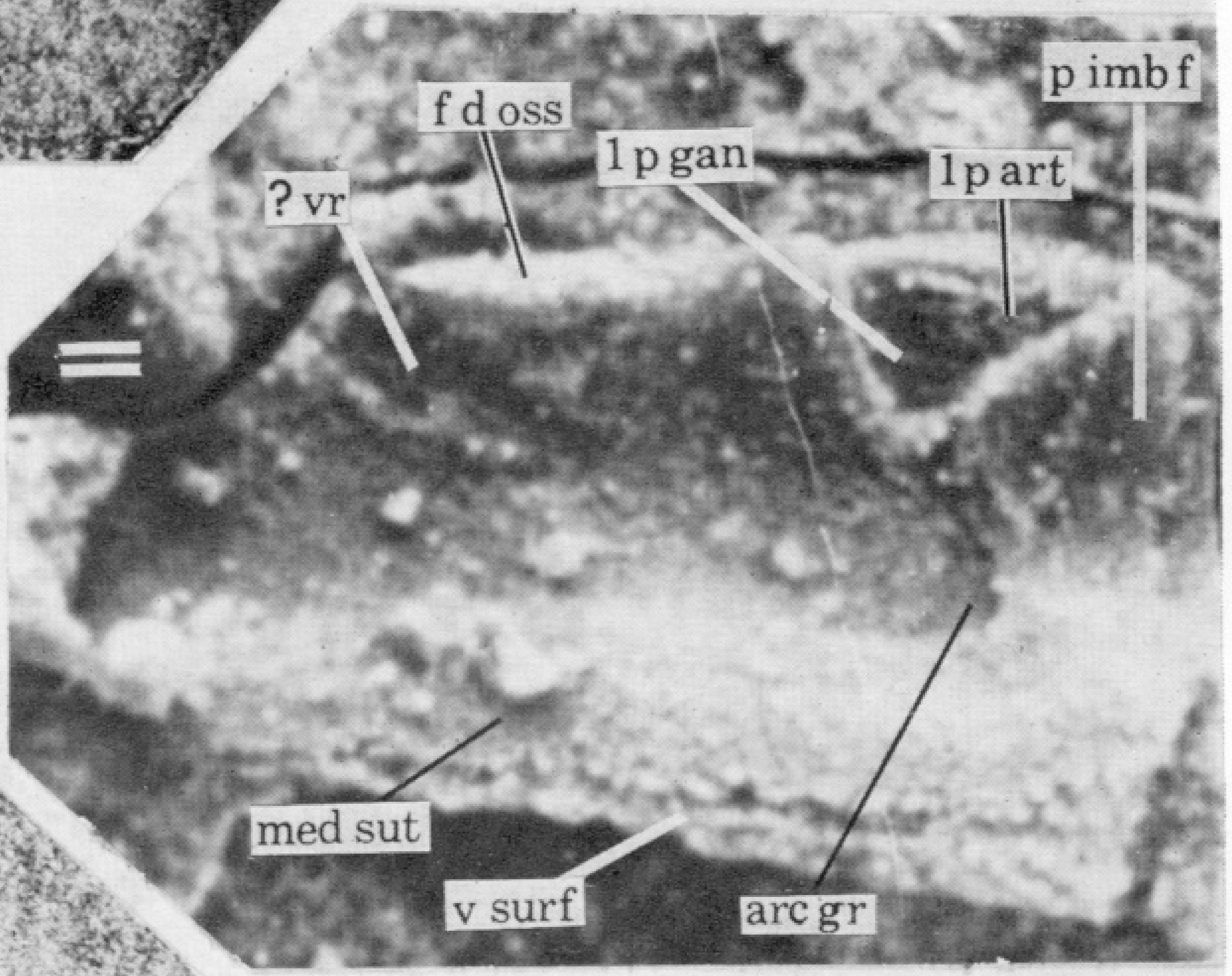

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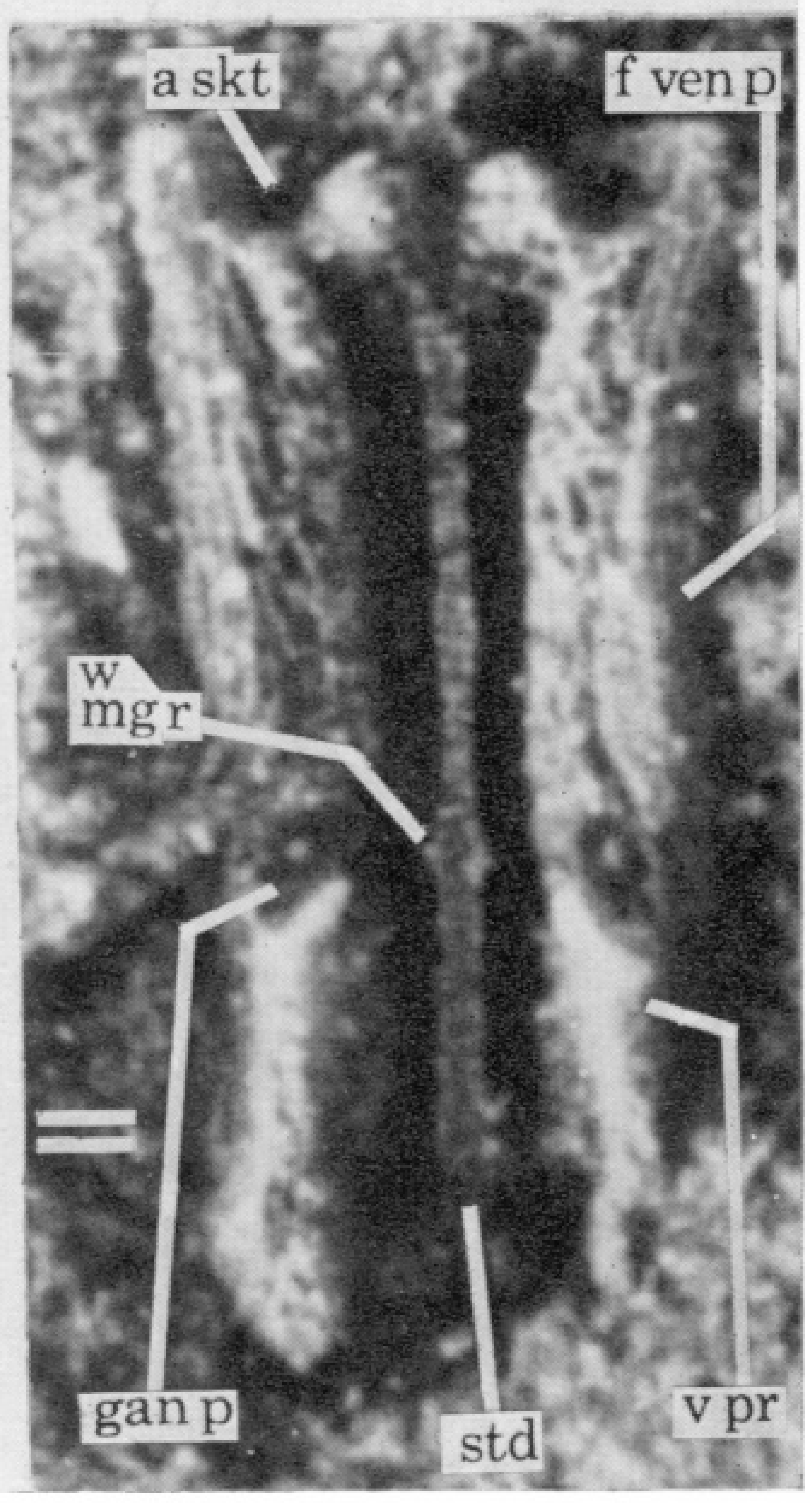
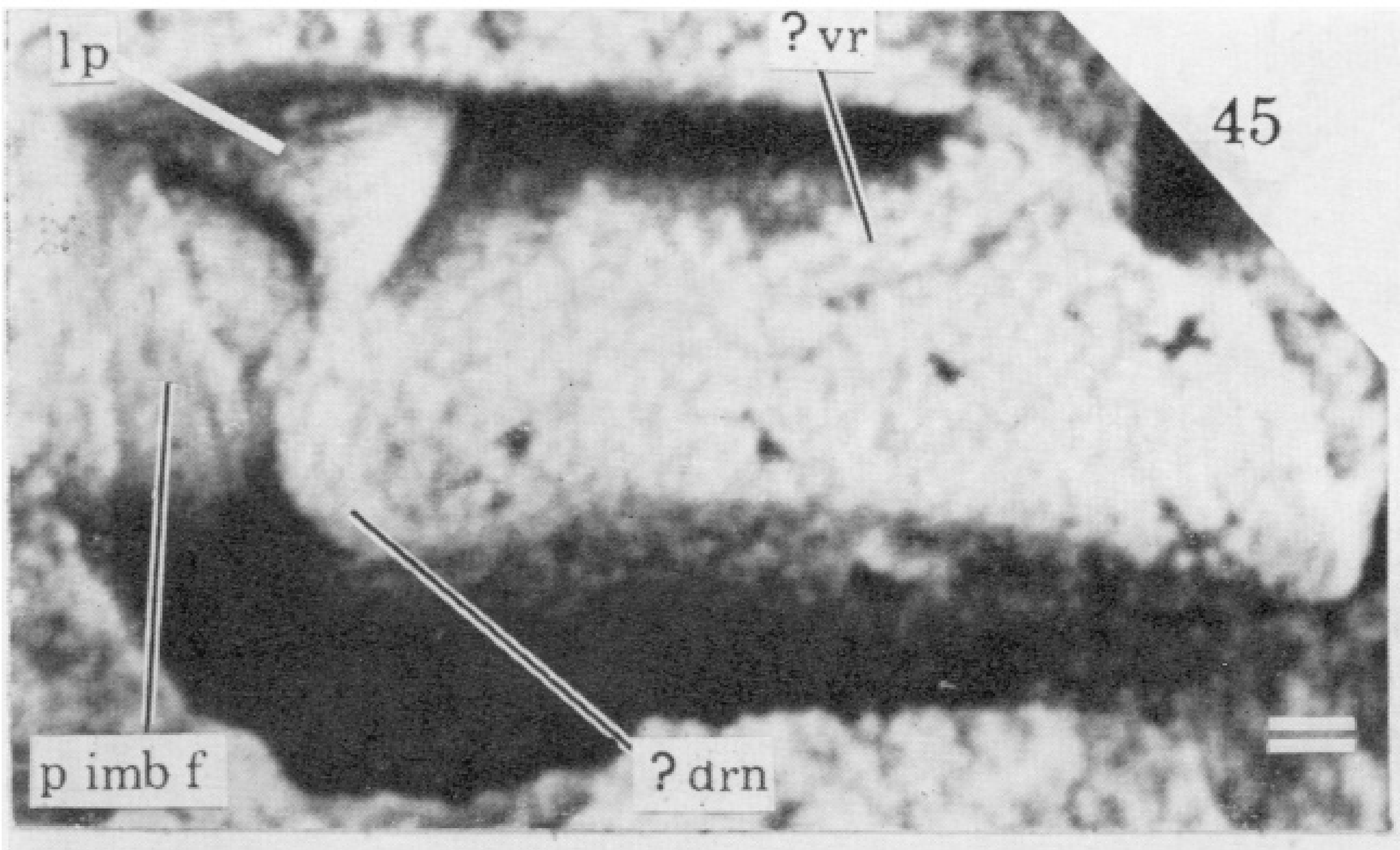


FIGURES 40 to 44. For legends see facing page.

45



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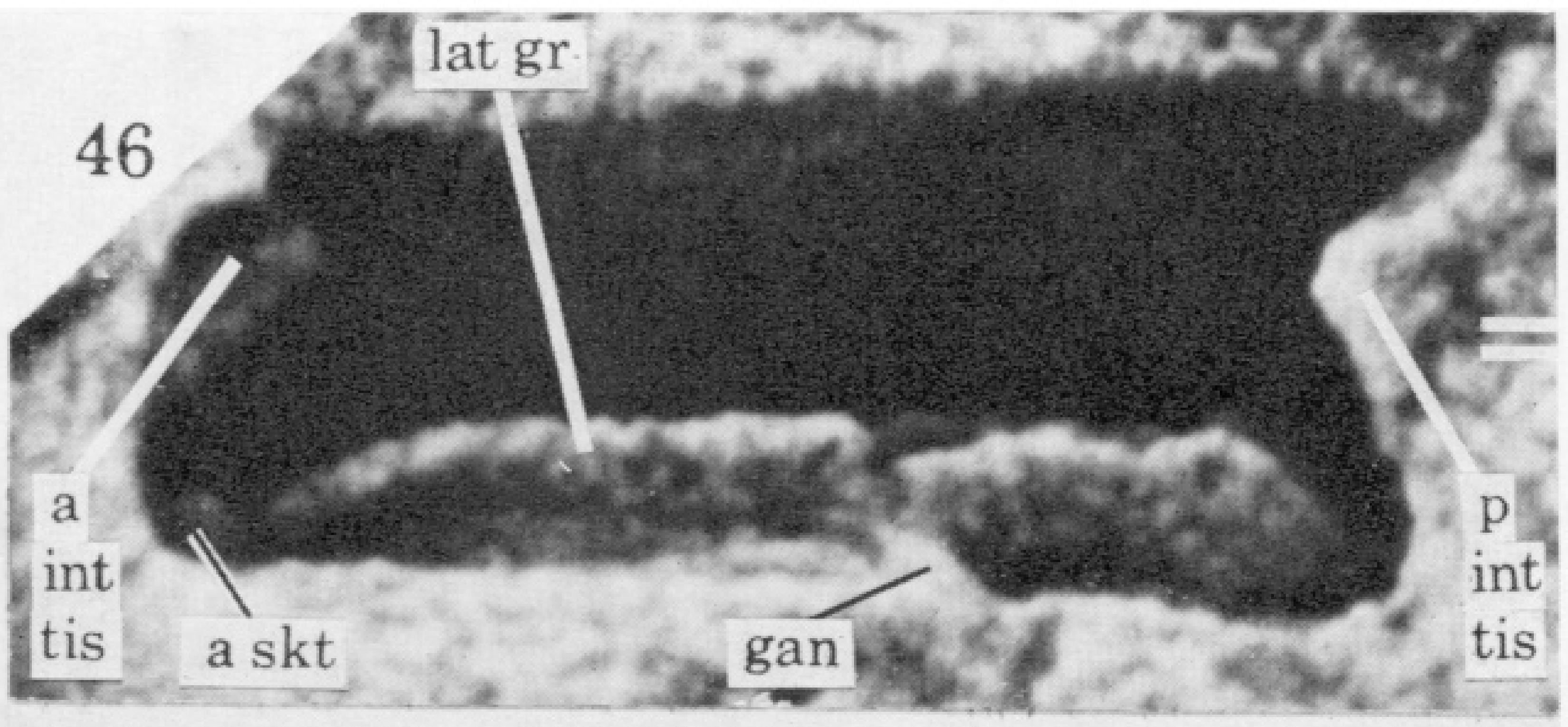

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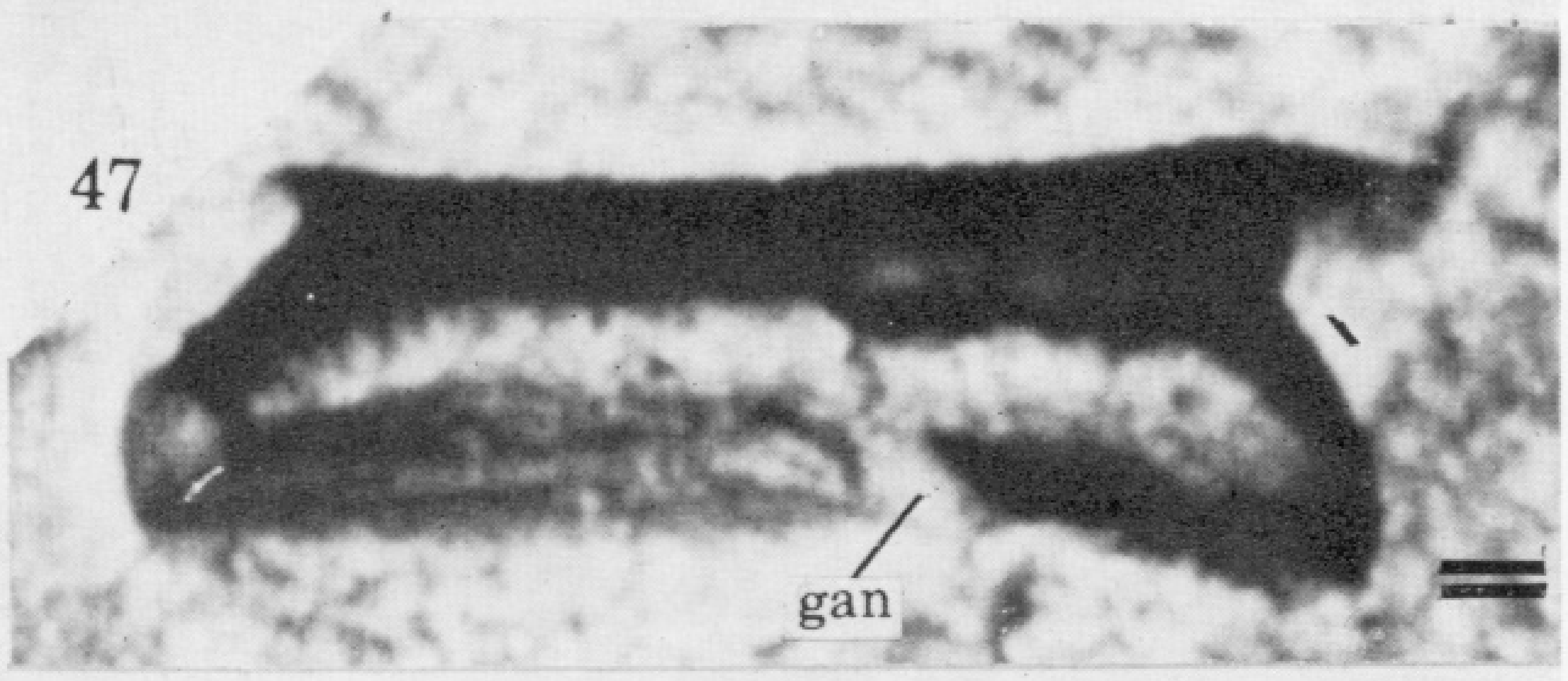

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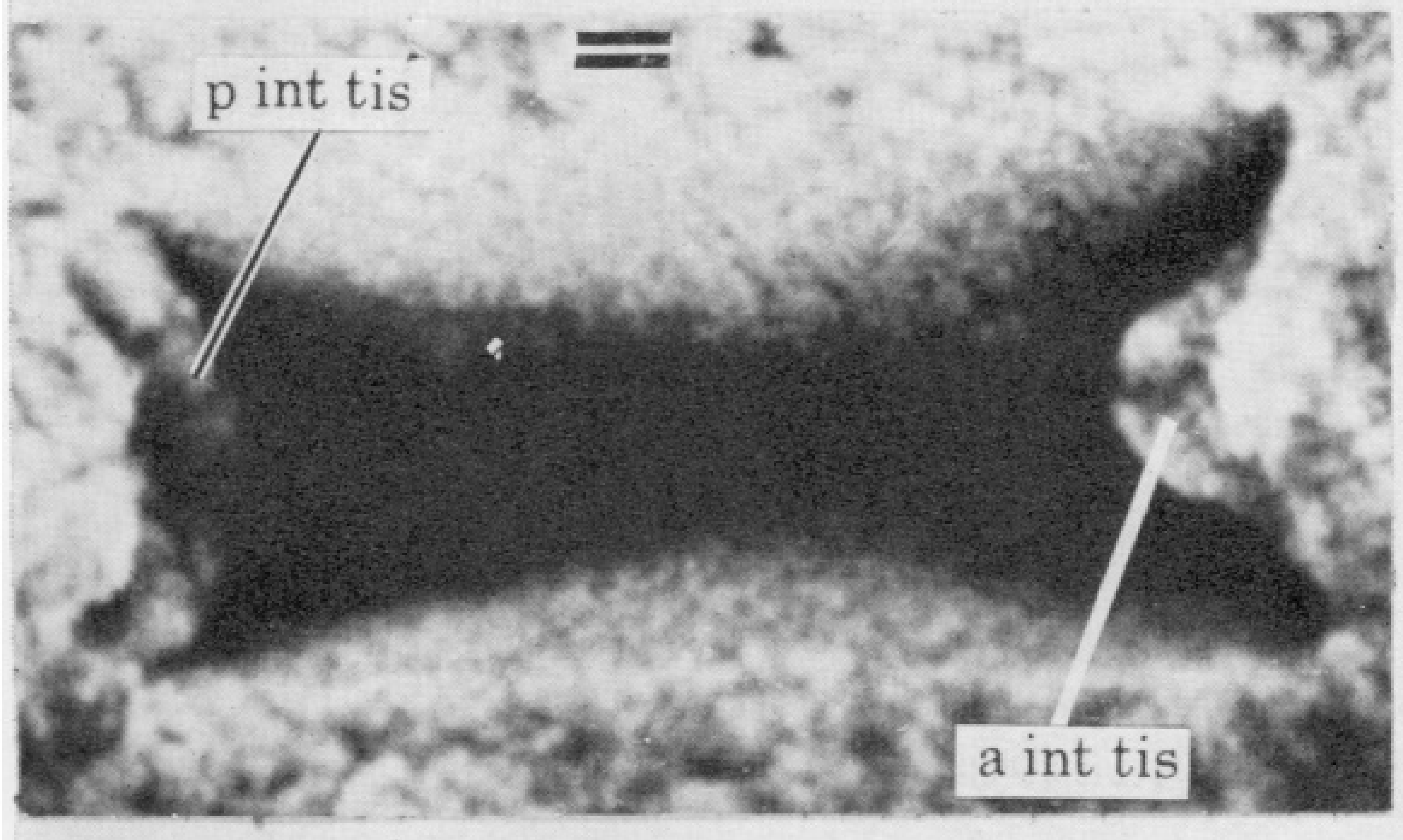

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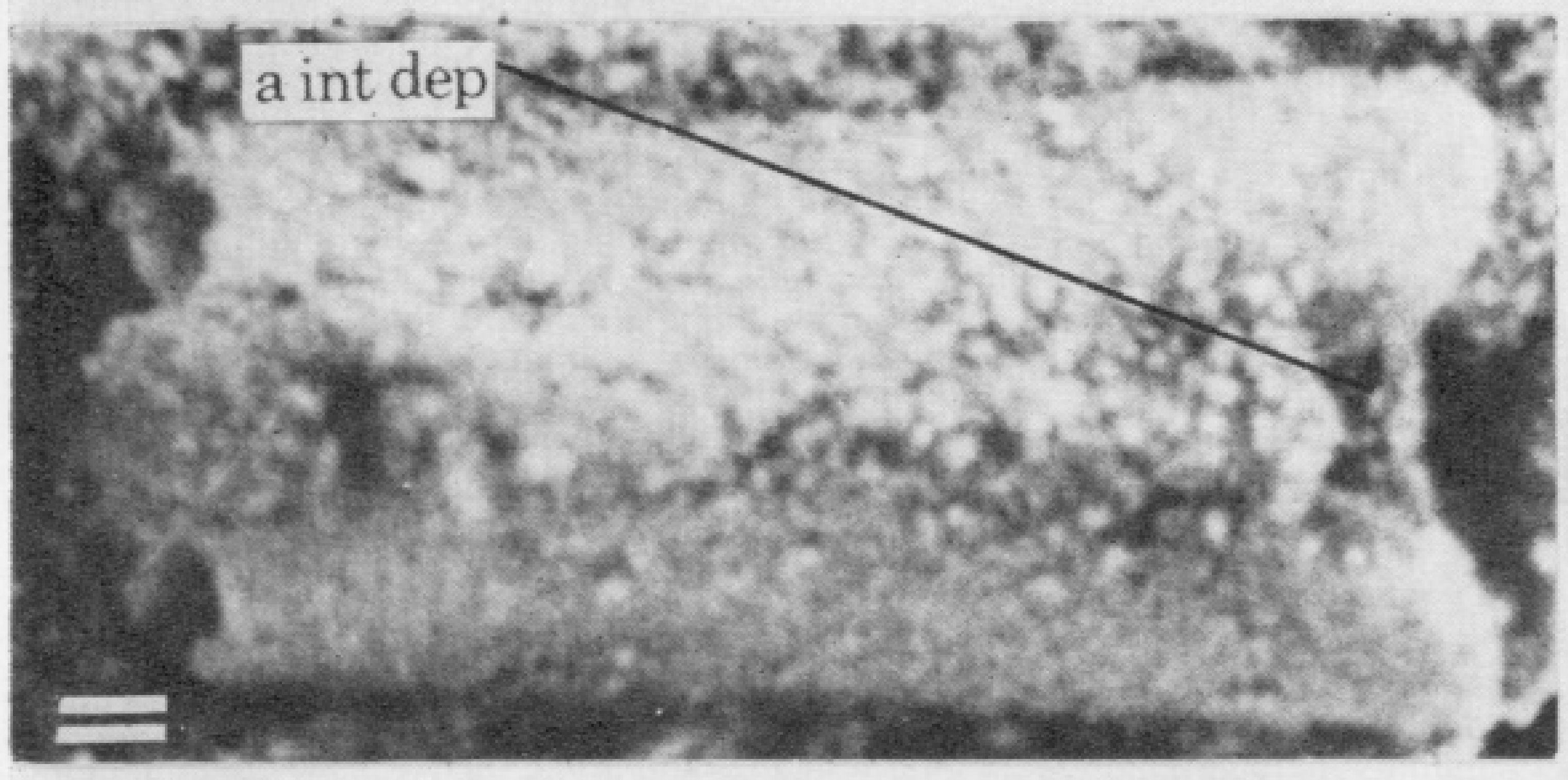

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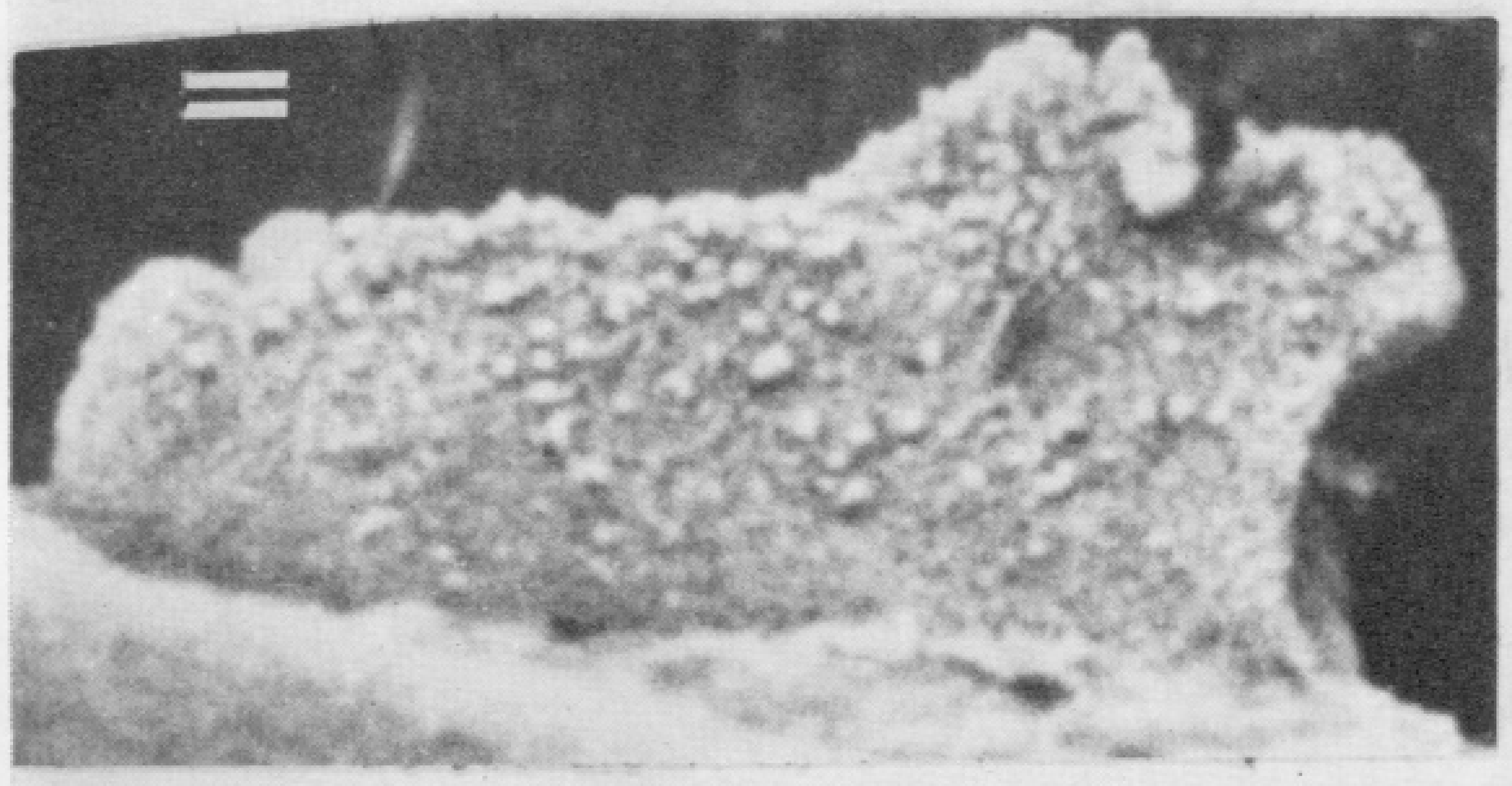

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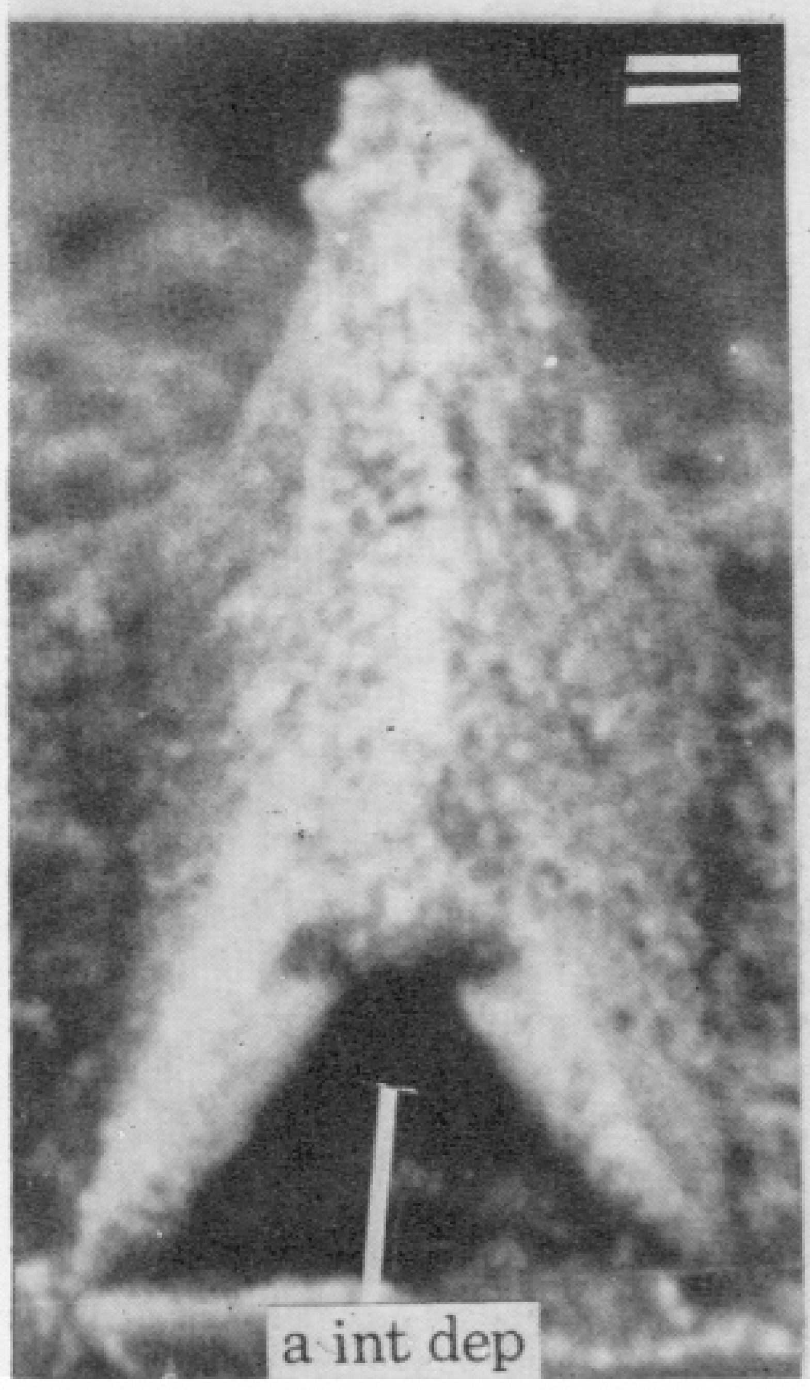

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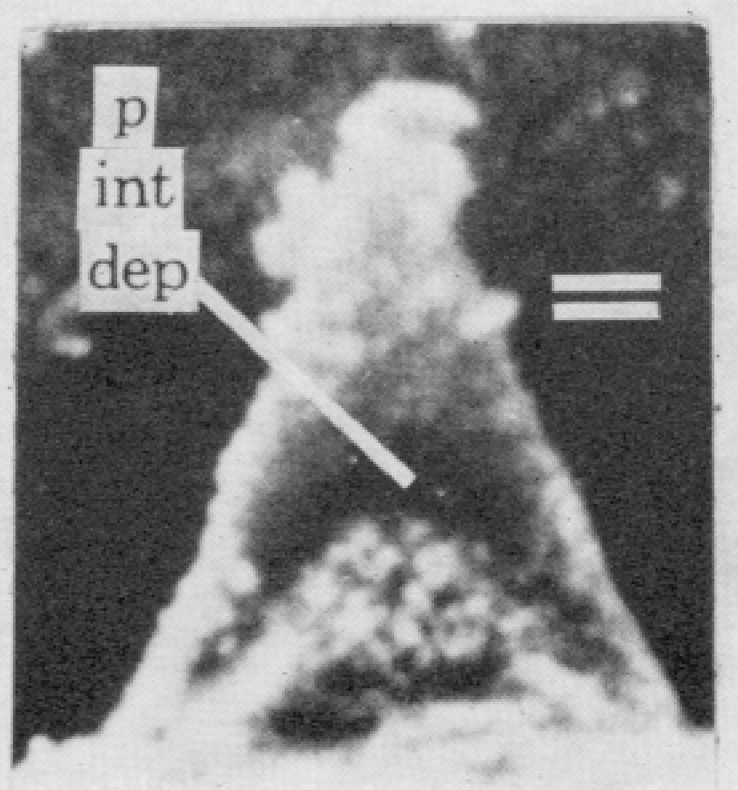

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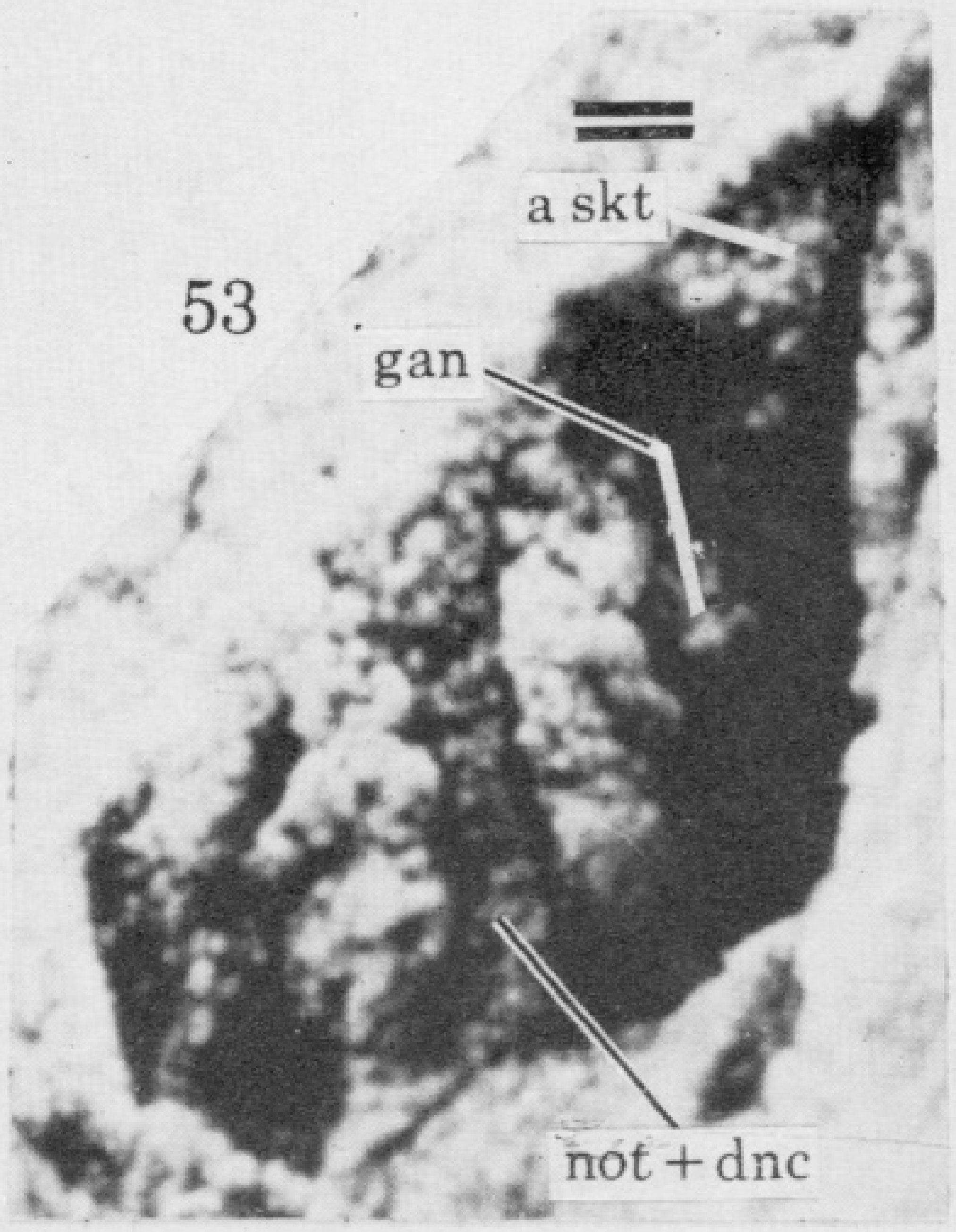

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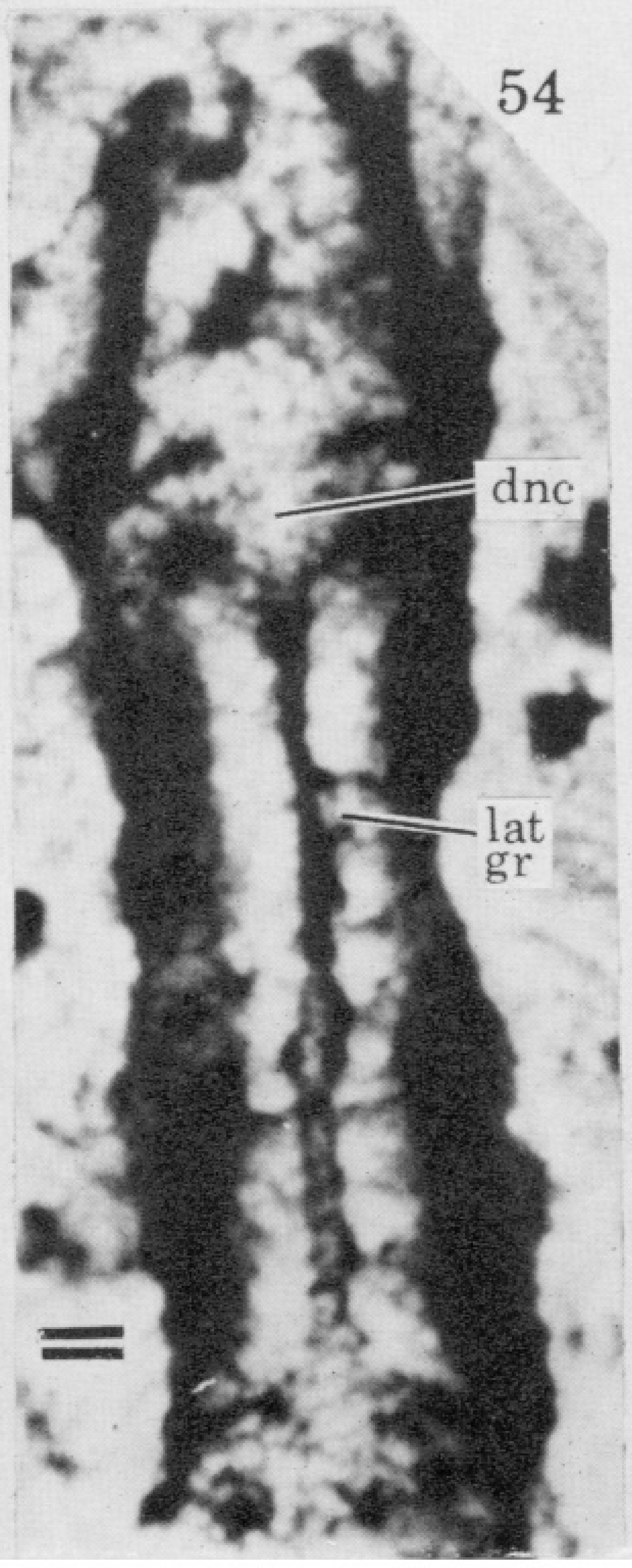

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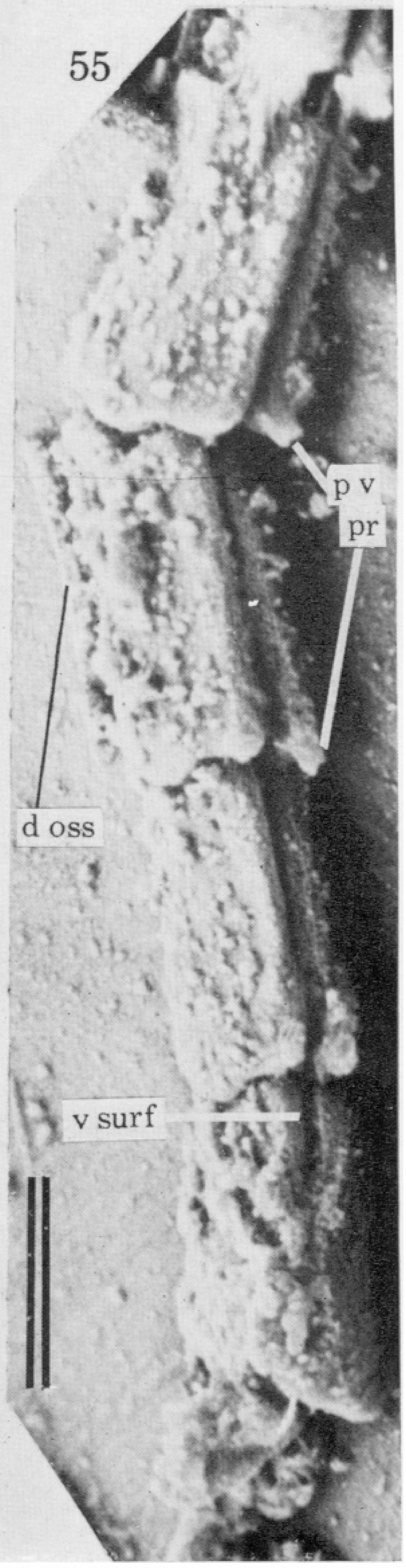
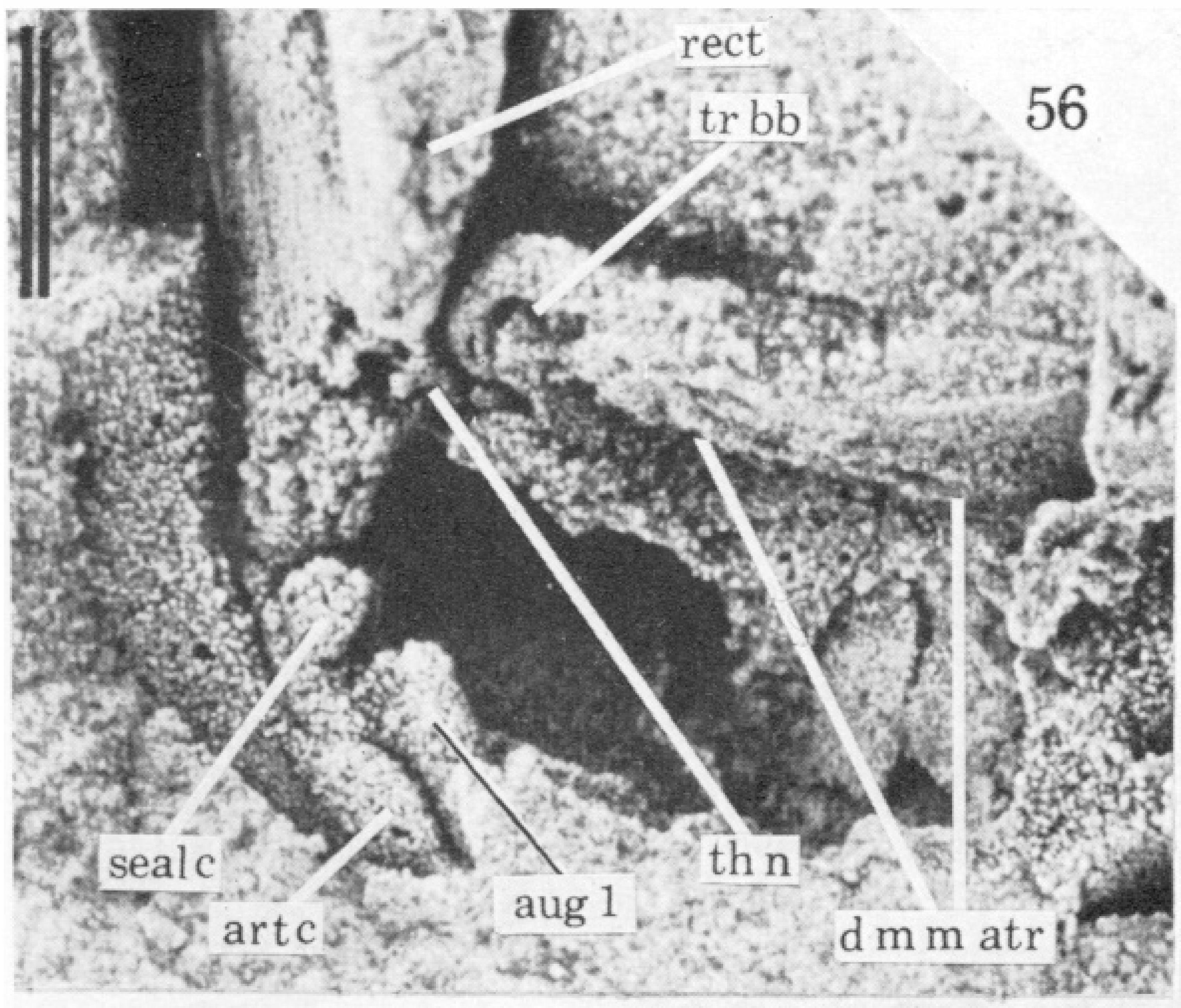


FIGURES 45 to 55. For legends see facing page.

56



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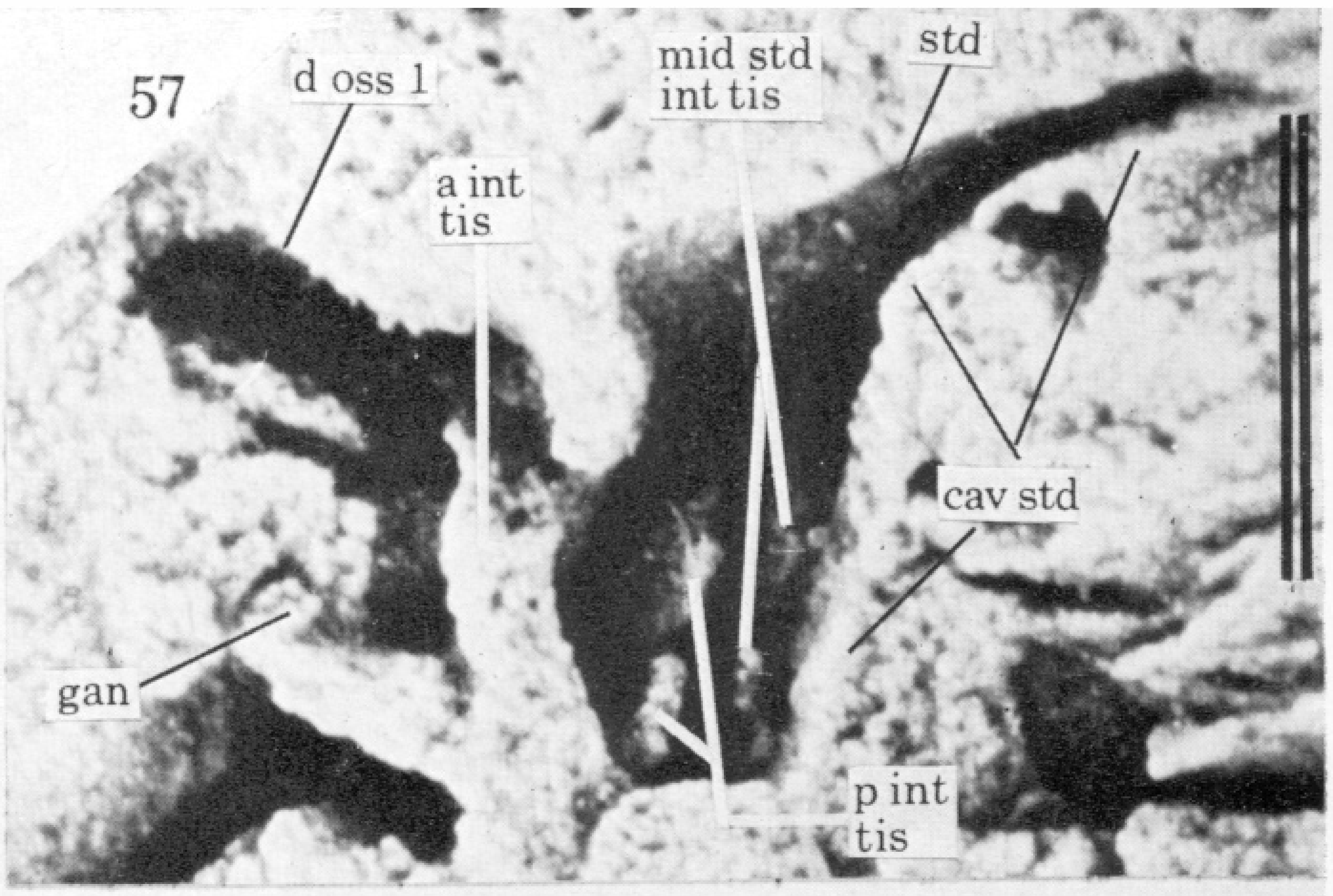

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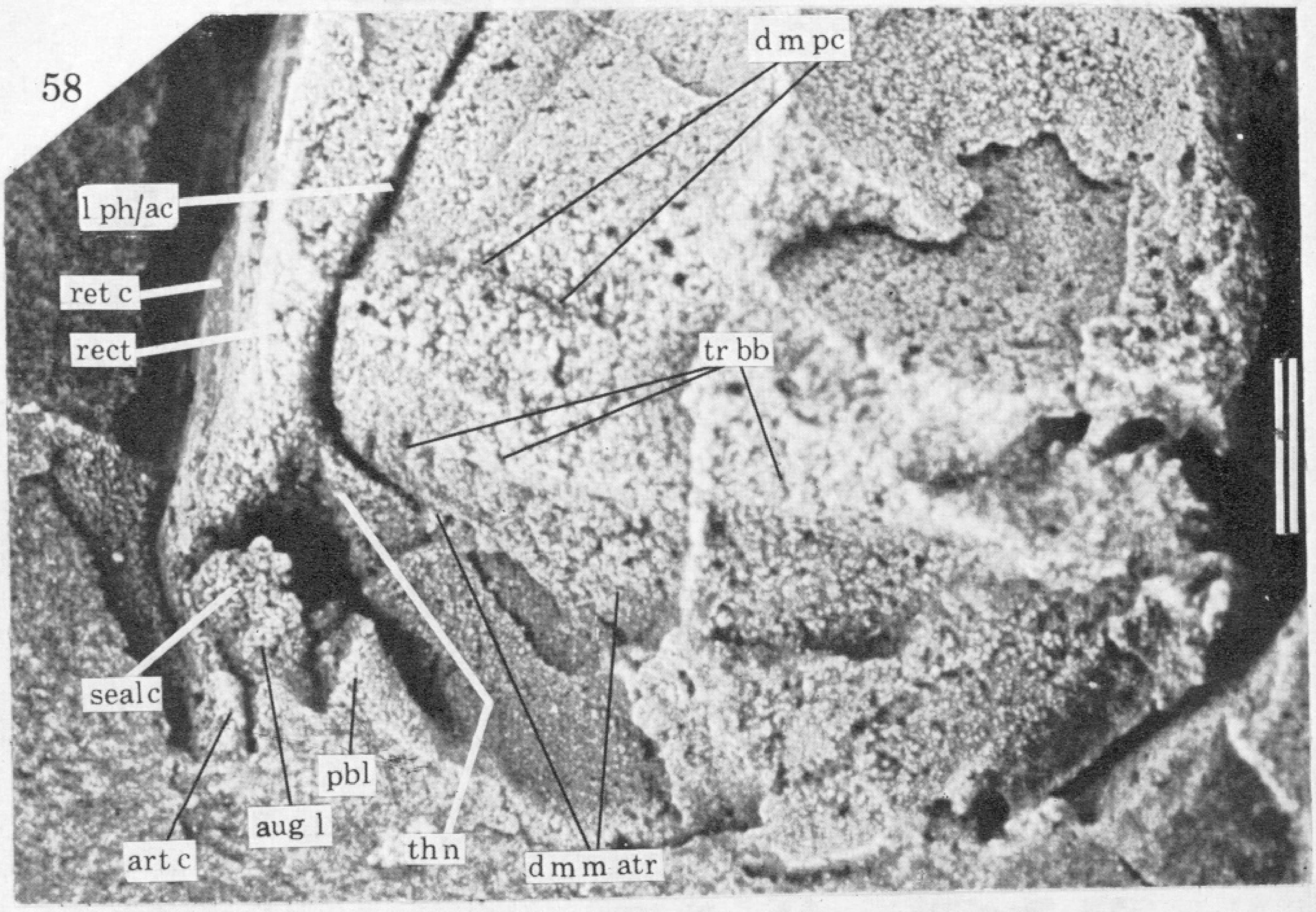

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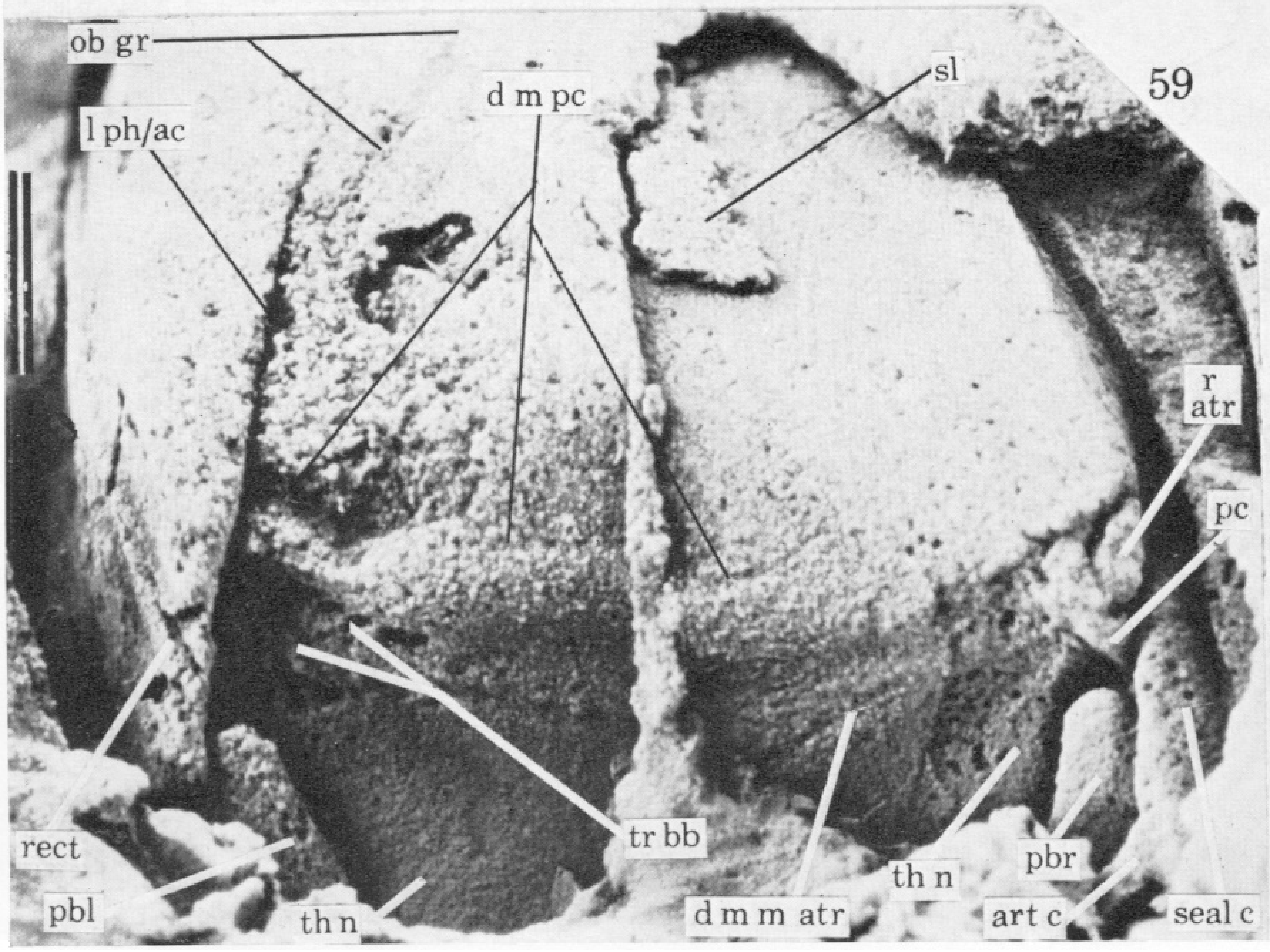

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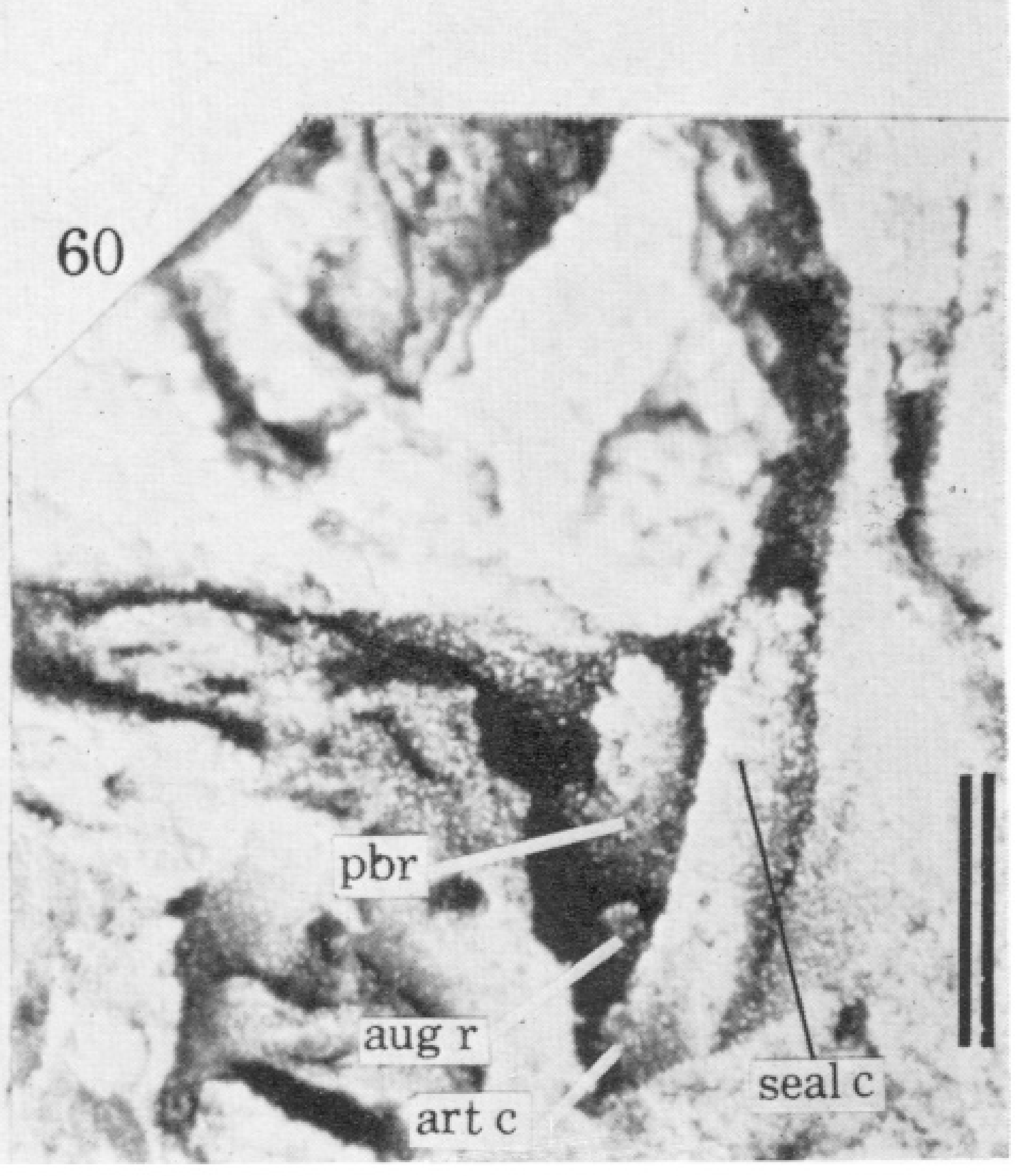
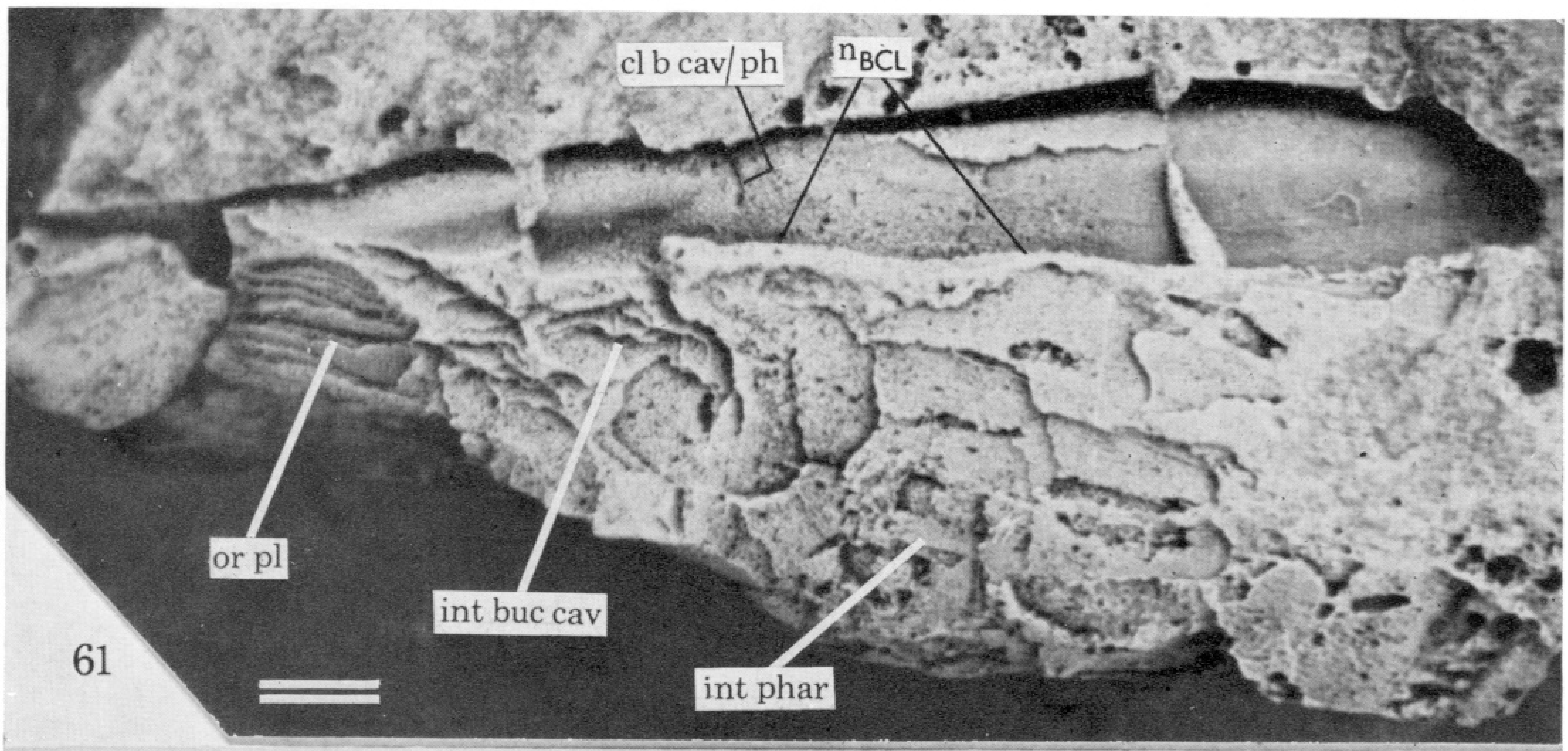


Figures 56 to 60. For legends see facing page.

61



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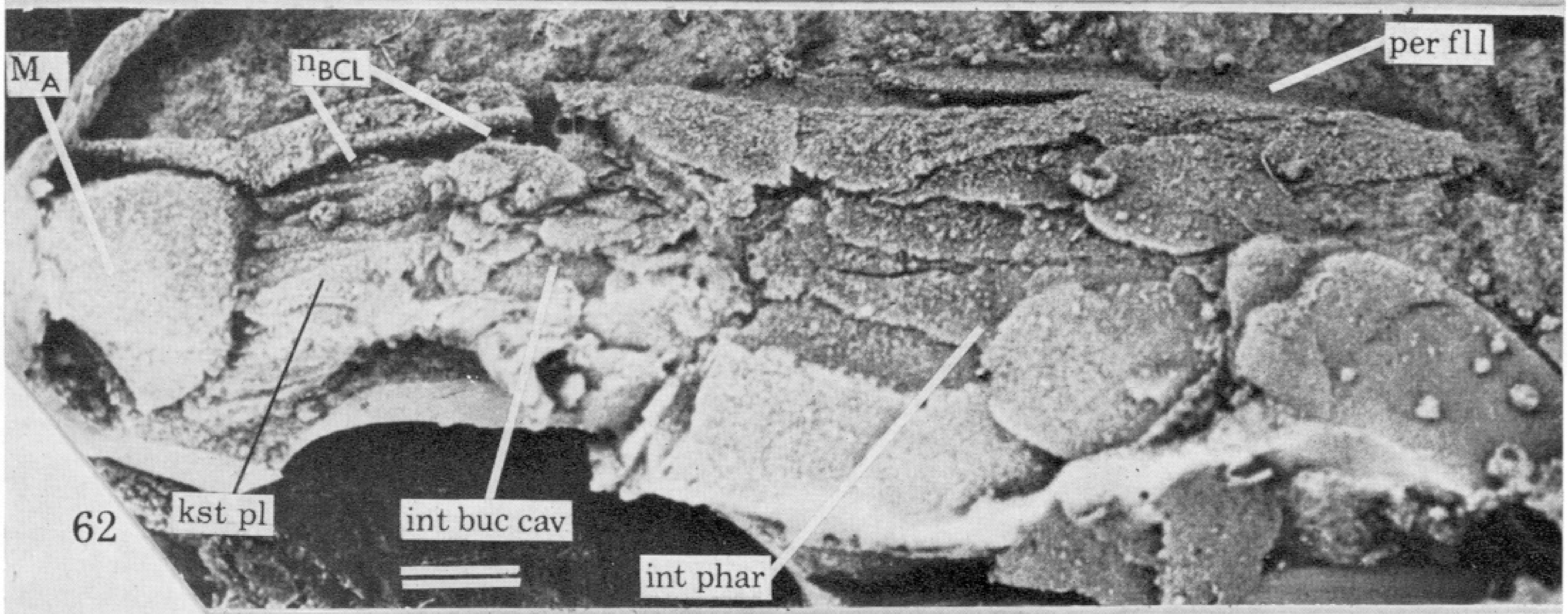

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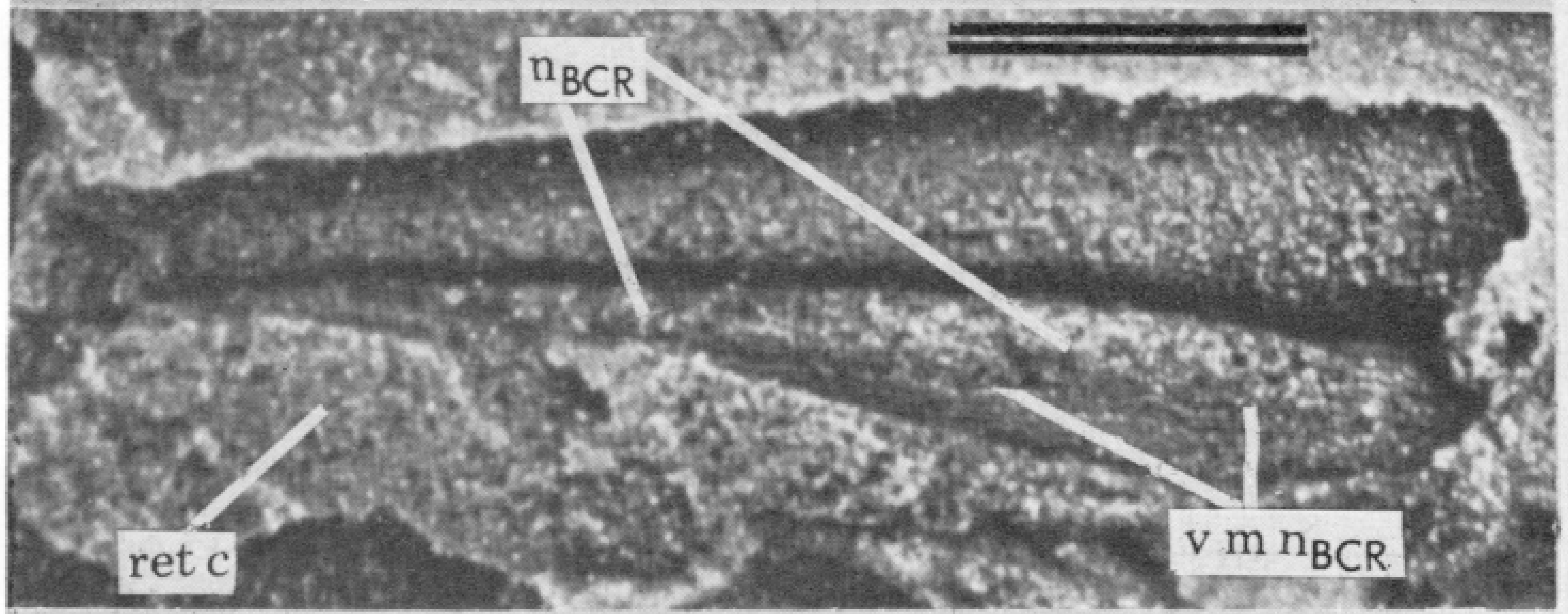

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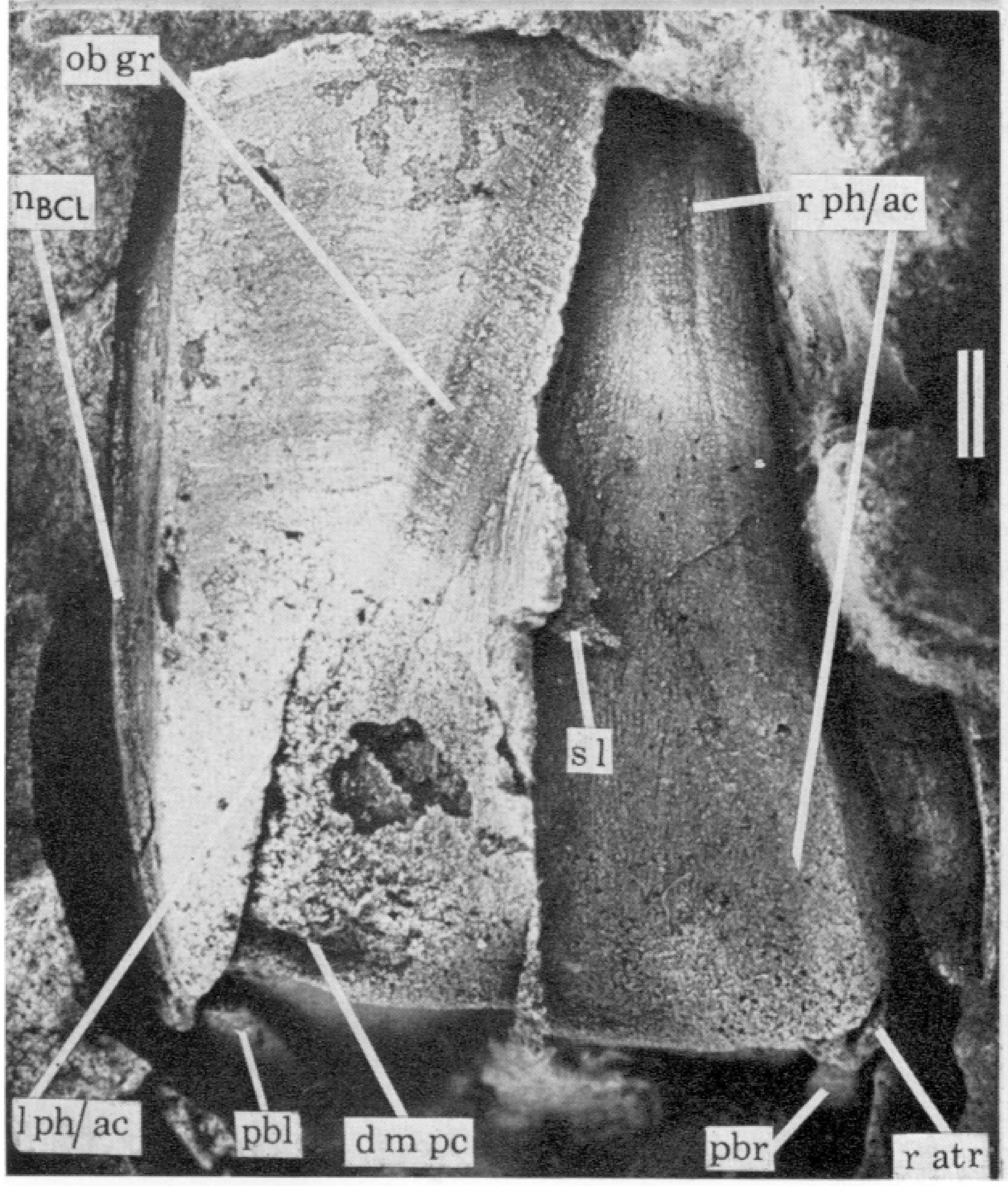
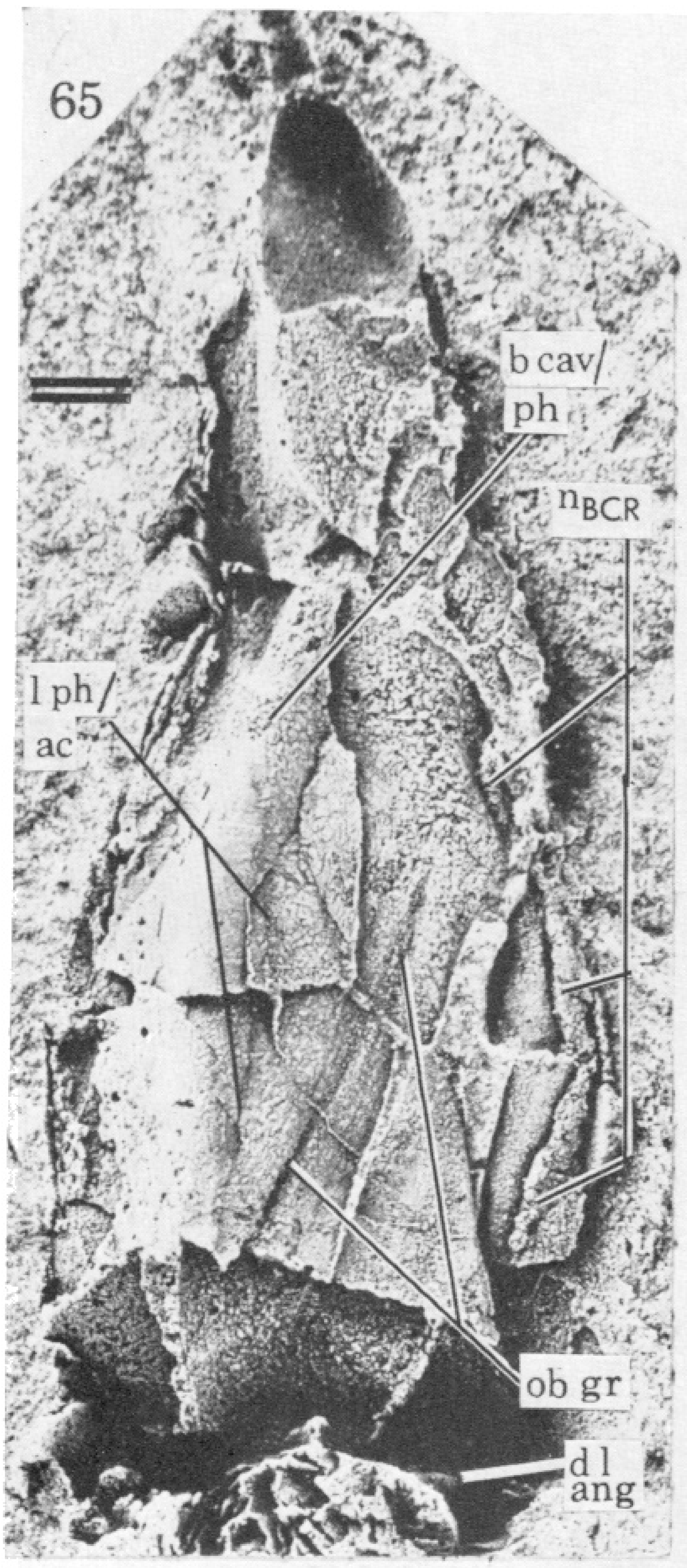
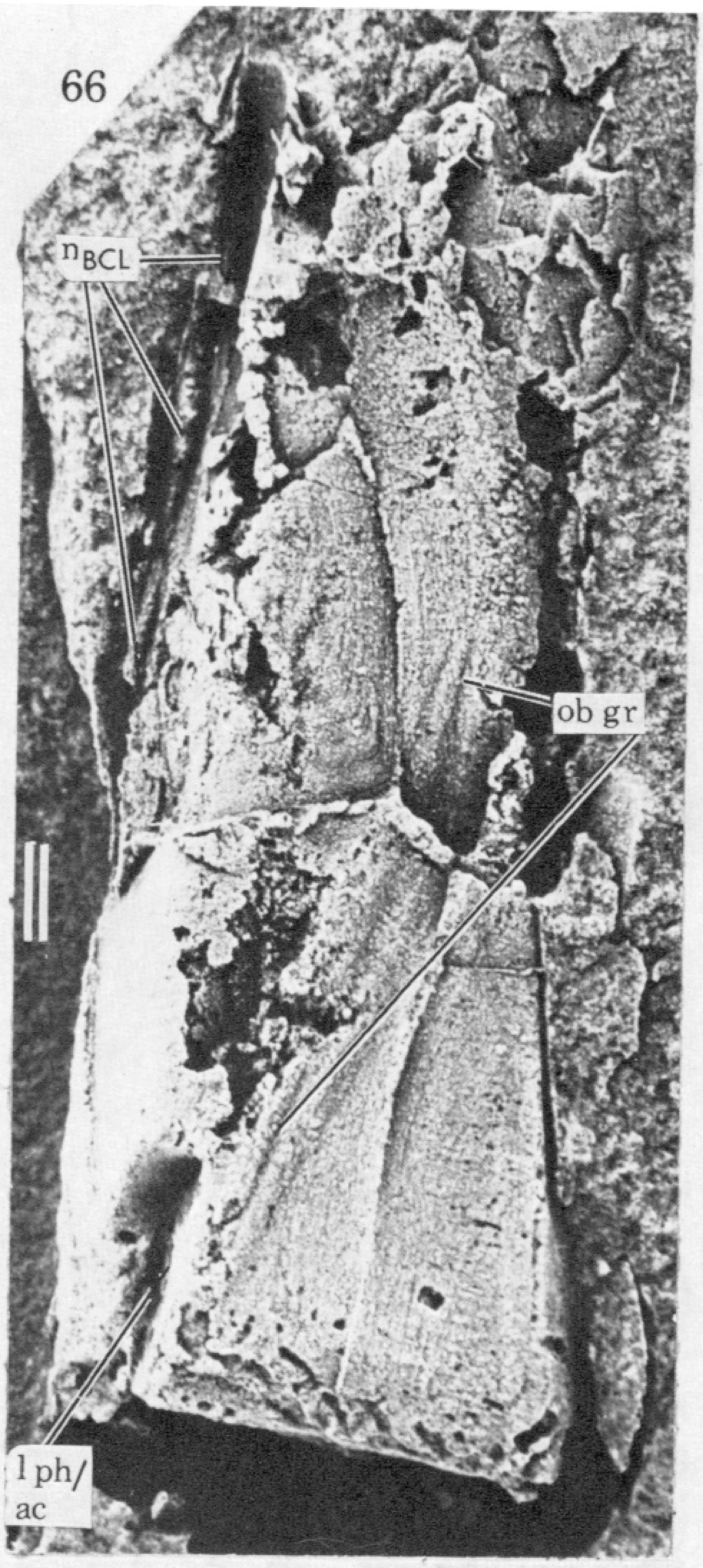
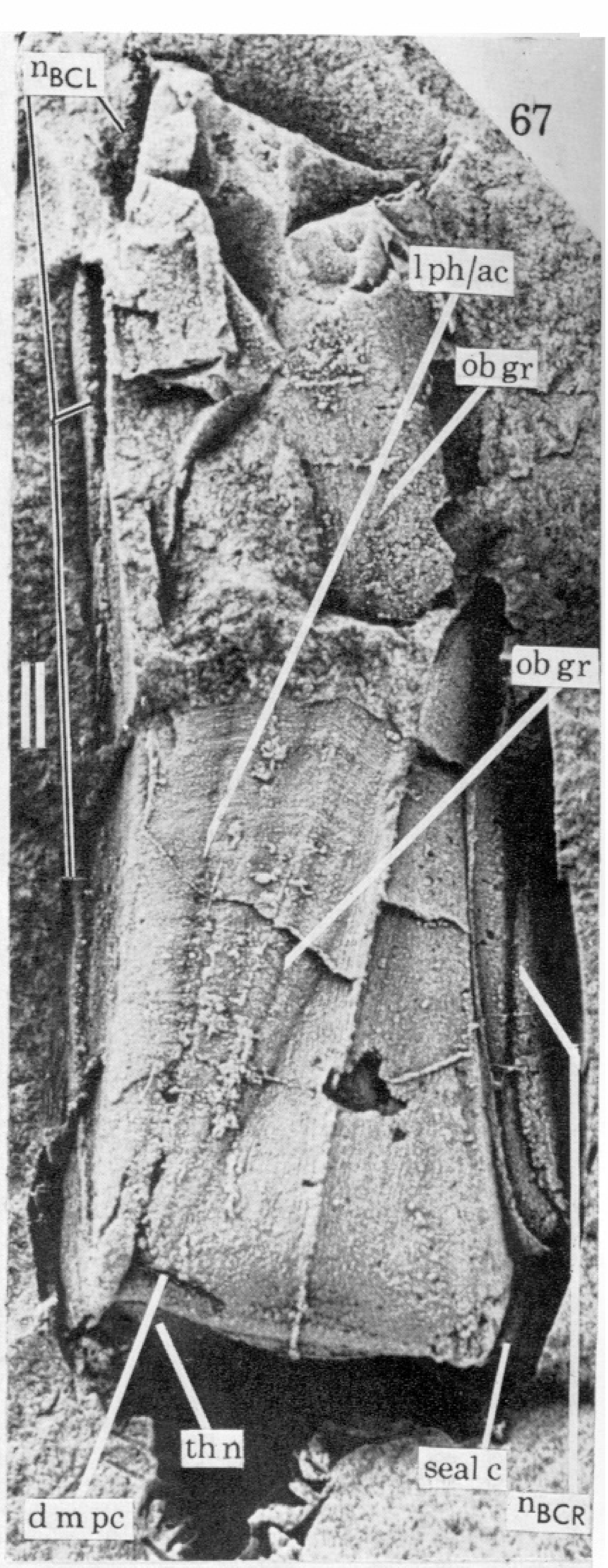


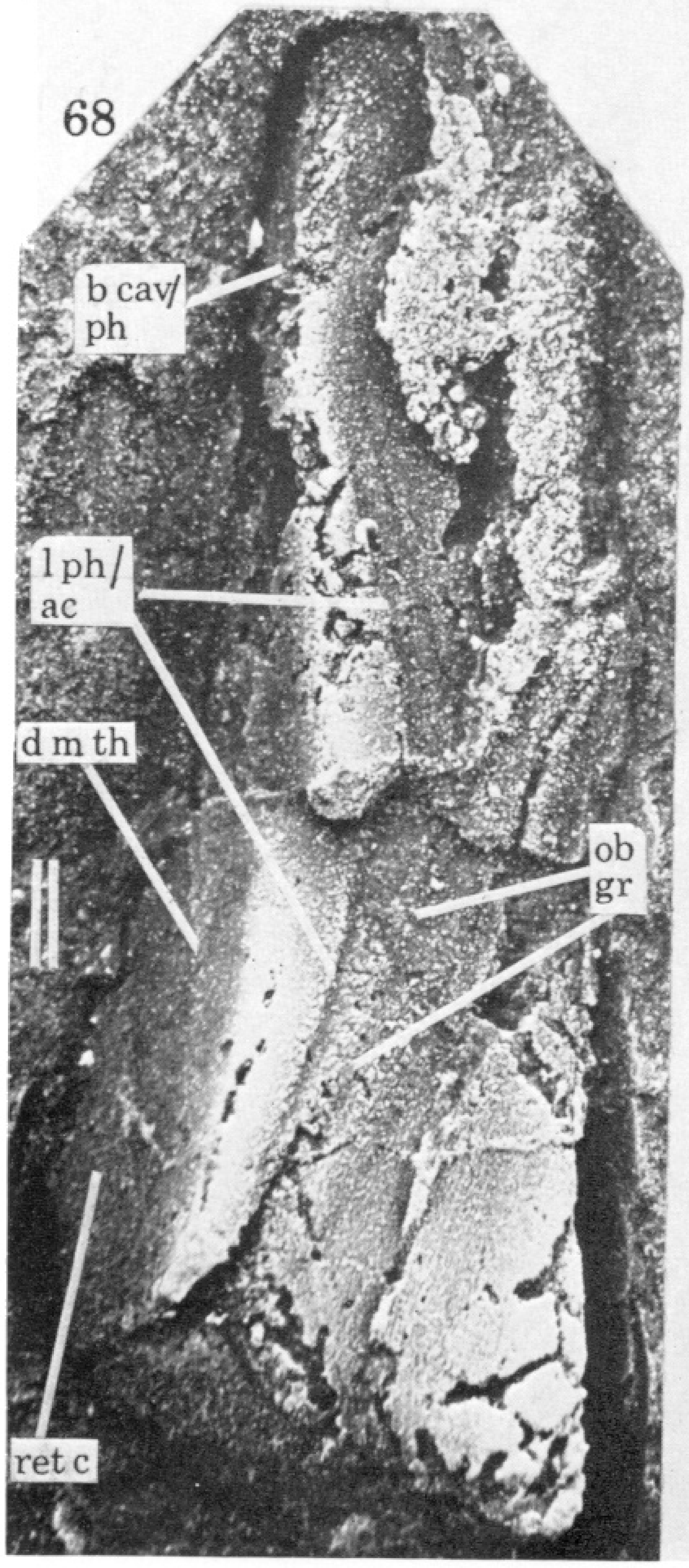
FIGURES 61 to 64. For legends see facing page.

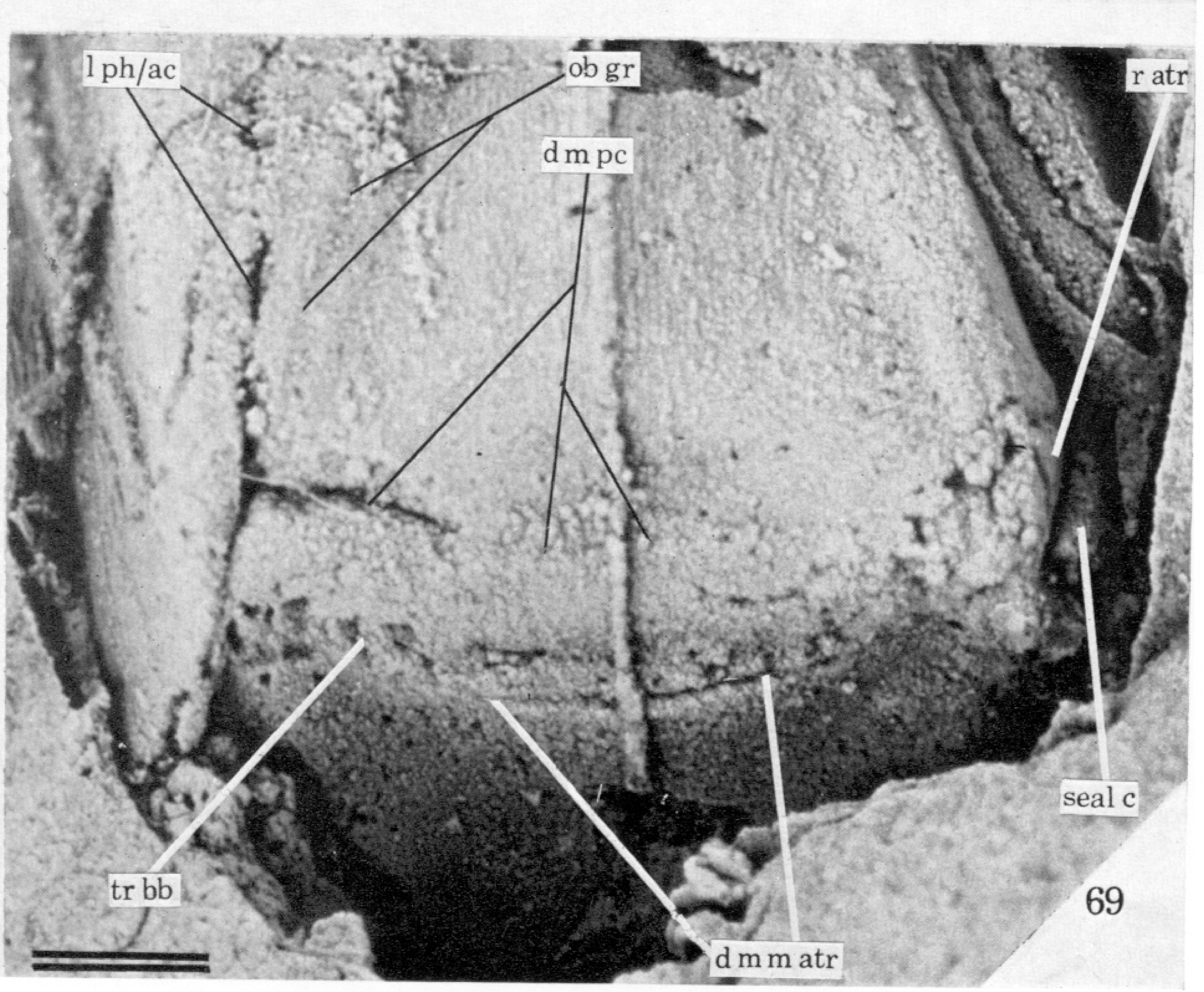
(*Facing p.* 450)











FIGURES 65 to 69. For legends see facing page.