Phil. Trans. R. Soc. Lond. B. **282**, 1–39 (1978) [1]
Printed in Great Britain

ON SOME VARIATIONS IN THE LATERO-SENSORY LINES OF THE PLACODERM FISH *BOTHRIOLEPIS*

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(*Communicated by F. R. Parrington, F.R.S. – Received* 11 *June* 1975, *revised* 28 *March* 1977)

[Plates 1–6]

CONTENTS

Some variations of the superficial latero-sensory lines of the antiarch fish *Bothriolepis* are described. These are considered to be due to the sensory lines having become anchored to different combinations of bone rudiments at an early stage in skeletogenesis; during later growth they were consequently drawn along different courses. Some effects of the tensions involved in this process are considered. Loose ends of sensory lines extending beyond their normal points of anchorage are regarded as important, partly because they themselves may become sites of further anchorages and partly because they may form unions with other sensory lines.

A similar approach is applied to some problems in arthrodires. The central sensory line of *Bothriolepis* may be derived from a posterior pit-line of the normal arthrodire type as a result of a transference of anchorage at both its ends.

In another kind of variation in *Bothriolepis* a sensory line appears to have channelled the growth of advancing horizontal bone lamellae in such a way that the suture formed between adjacent bones becomes coincident with the sensory line for a short part of its course.

1. Introduction

The purpose of this paper is to describe and to consider the implications of some variations in the latero-sensory lines in specimens of *Bothriolepis canadensis* Whiteaves obtained from Escuminac in Canada by the writer on his own in 1934 and conjointly with Dr T. S. Westoll (now Professor T. S. Westoll, F.R.S.) in 1937. These specimens, which are referred to as 1934/37 material, have subsequently been transferred to the British Museum (Natural History). The following abbreviations are used to designate institutions to which specimens referred to belong: B.M., British Museum (Natural History); N.Y.S.M., New York State Museum; R.S.M., Royal Scottish Museum; S.M.N.H., Swedish Museum of Natural History.

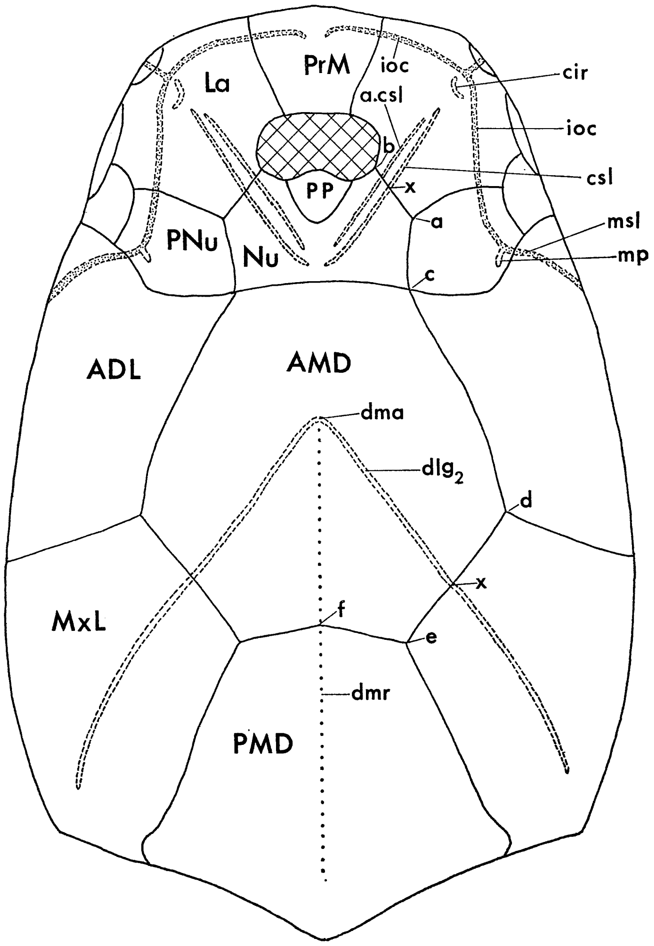


FIGURE 1. *Bothriolepis canadensis* Whiteaves. Outline showing in dorsal view some aspects of the head-shield and trunk-armour of a typical specimen.

2. Some variations in the latero-sensory lines of *Bothriolepis*

Miles's (1968) recent monograph on Scottish Bothriolepididae gives an account of earlier work on *Bothriolepis*. He adopted Stensiö's (1947, 1948) terminology, apart from a few minor modifications cited in his introduction. In addition Miles discontinued the use of the term 'posterior pit-line groove' which Stensiö had applied to what appears to be essentially a posterior extension of the central sensory line groove. Miles's terminology has been used virtually unchanged in the present paper, except that the term supraoccipital cross-commissural pit-line groove has been replaced by occipital cross-commissural sensory line (occ) which has been used more recently by Miles (1971) for the equivalent line in *Holonema*. The homologies of the sensory lines of *Bothriolepis* are discussed later; in some cases the interpretation suggested there does not accord with the names currently used.

Figure 1 shows in dorsal view an outline of the head and armoured portion of the trunk of a typical specimen of *Bothriolepis canadensis* Whiteaves. For convenience the abbreviations used in the figures are frequently used also in the text in place of the actual names of the bones and sensory structures, which are shown on page 38. Also for convenience certain positions are designated by letters, inverted commas being used in the text but not in the figures. Their meanings are also listed in the 'abbreviations used in line drawings', page 38. Point 'a' is crucial; it is the point at which the sutures separating Nu and La, Nu and PNu, and La and PNu meet one another. Point 'x' is used to refer to the points at which the relevant sensory lines cross certain sutures.

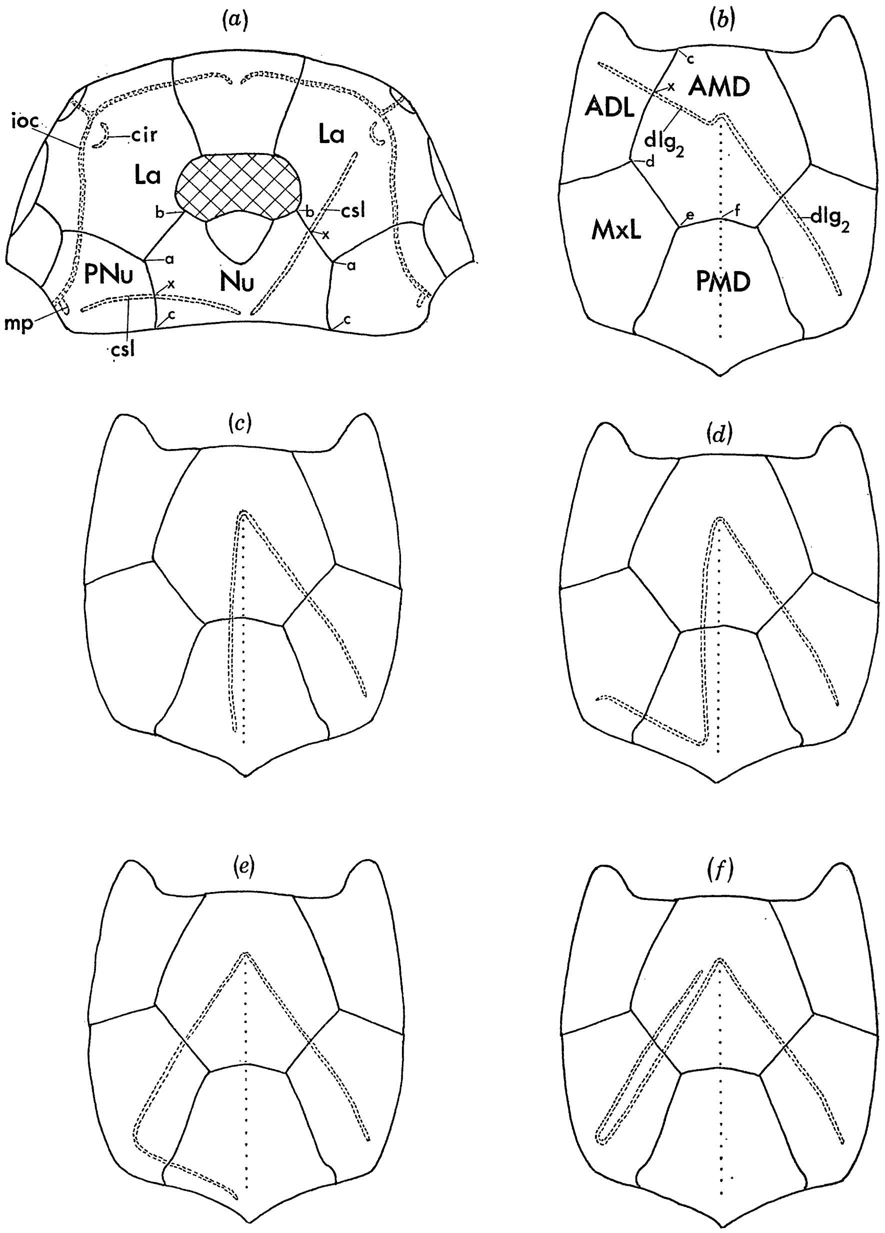


FIGURE 2. *Bothriolepis canadensis* Whiteaves. (*a*) variation 'type 1'. (*b*) 'type 2'. (*c*) 'type 3'. (*d*) 'type 4'. (*e*) 'type 5'. (*f*) 'type 6'. In each case the variation is shown on the left side.

Stensiö (1931) has shown that groove ioc was a relatively deep structure which opened to the surface by a longitudinal slit. It therefore corresponded to the second type of groove described by Ørvig (1971). There are also a number of relatively shallow but fairly wide sensory grooves; these belong to the third category described by Ørvig, and are to be distinguished from pit-line grooves, even though pit-line forms part of the name used for some of them. Variations in the courses of two of these shallow grooves, namely csl and dlg_2, are considered in the present paper.

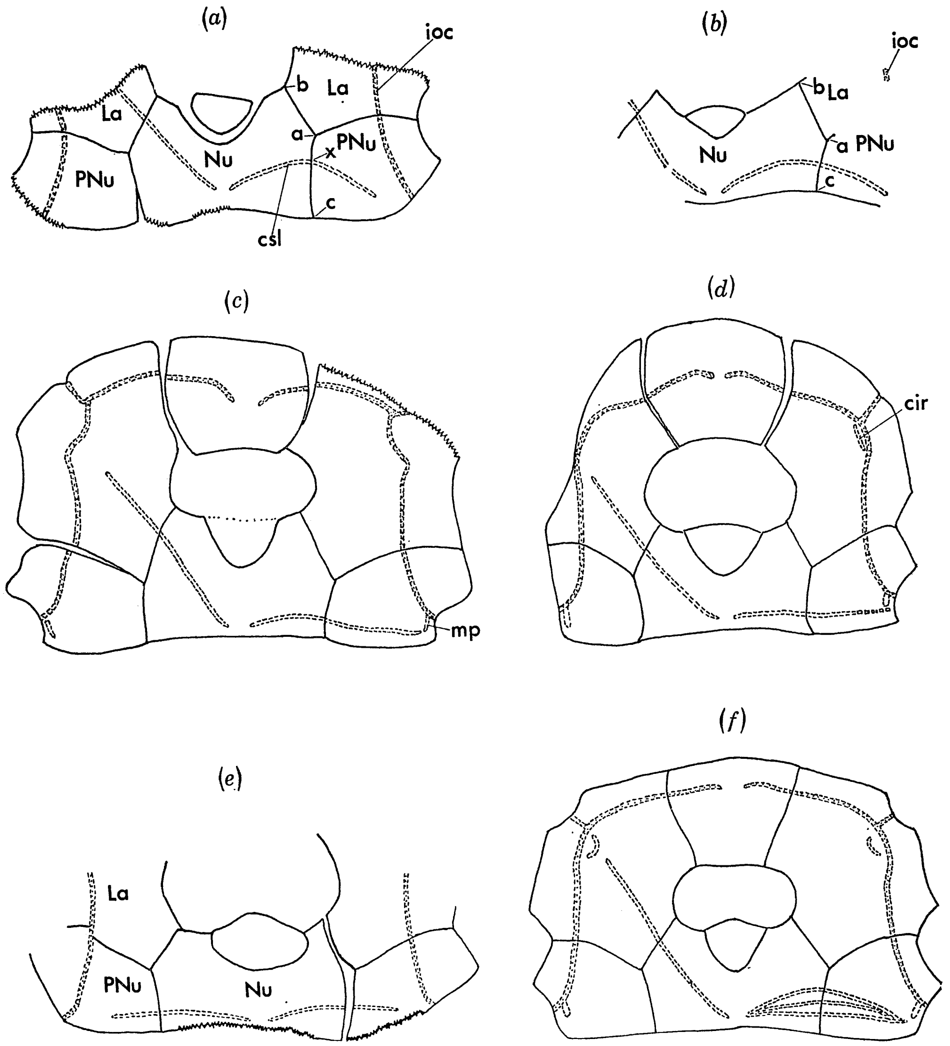
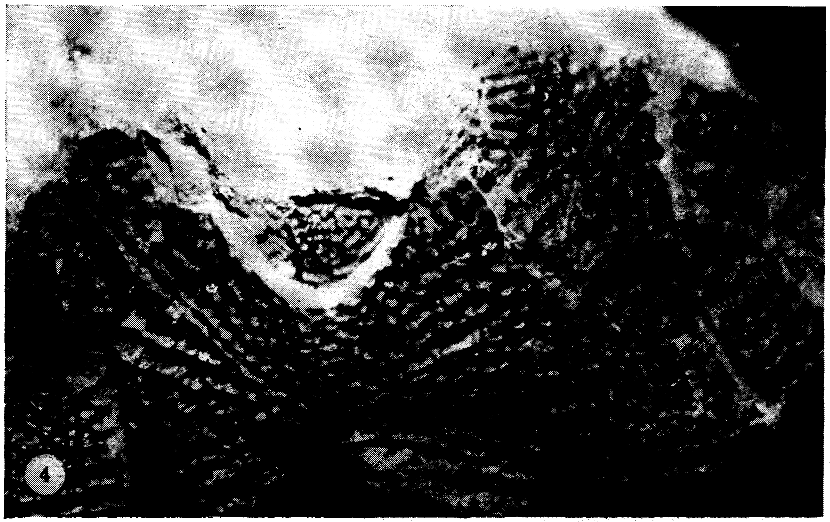
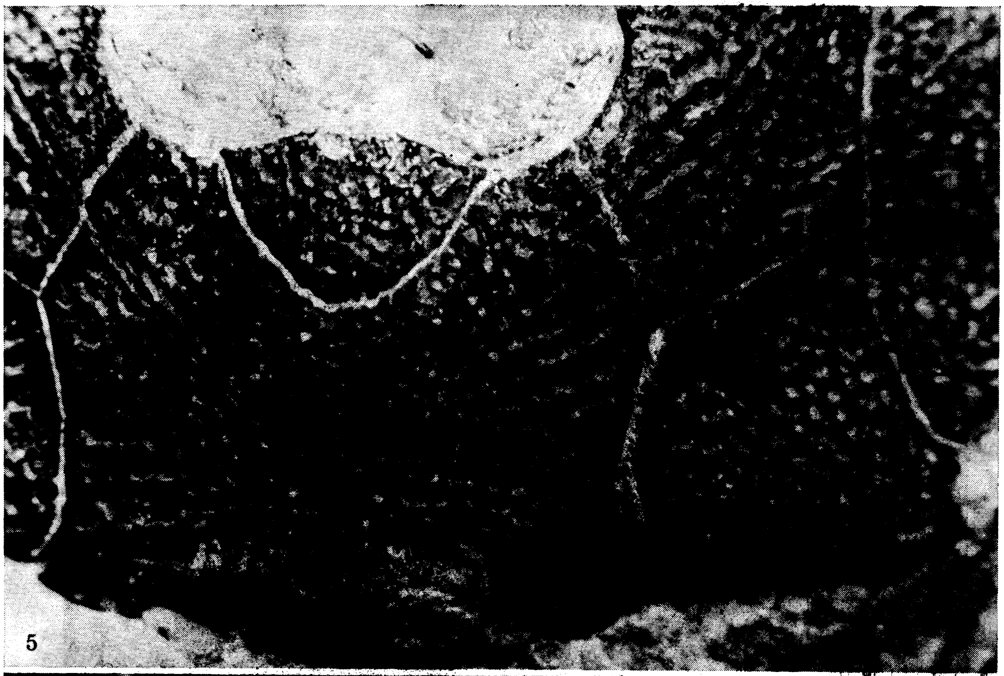


FIGURE 3. *Bothriolepis canadensis* Whiteaves. Variation 'type 1'. (*a*) B.M. P. 52091. (*b*) N.Y.S.M. 3775. (*c*) S.M.N.H. P. 2181, after Stensiö 1948, fig. 209. (*d*) B.M. P. 52084. (*e*) B.M. P. 52109. (*f*) schematic representation of alternative courses of the central sensory line.

In his monograph Stensiö (1948) does not consider the positions of the centres of growth of the individual bones, but he expresses the definite opinion (p. 384–386) that the zonal growth of the bone is often indicated by both the concentric and the radiating form of the external ornamentation; this is clearly seen in some of his illustrations. The general area from which the growth of the bone proceeded can usually be determined in this way, though with no great precision. In addition the centres of radiation are indicated, perhaps more precisely, by the radiating striae sometimes seen on the internal surface of the bones (see for example, Stensiö





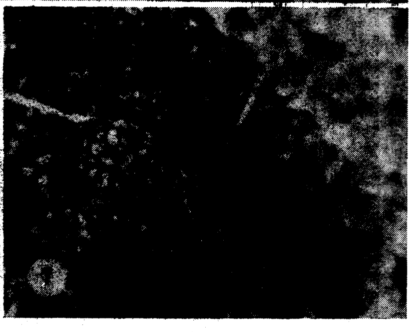
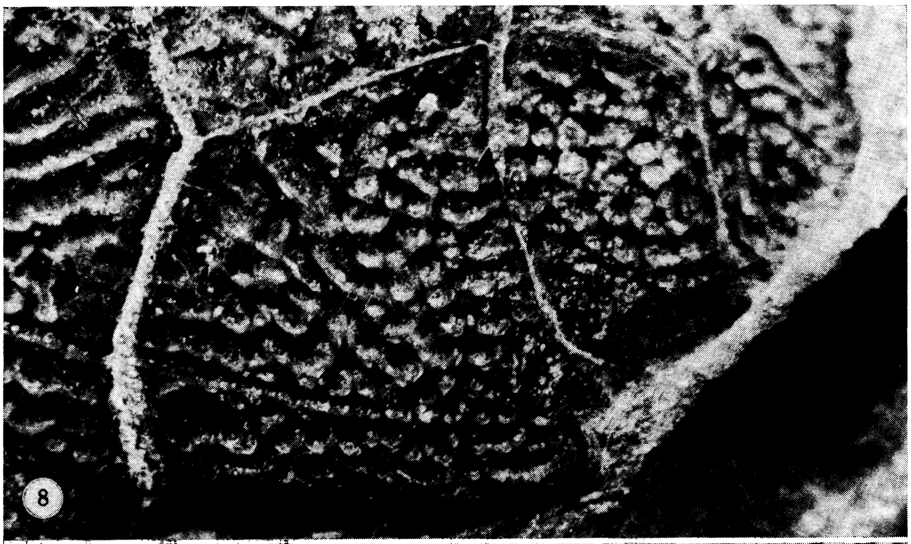
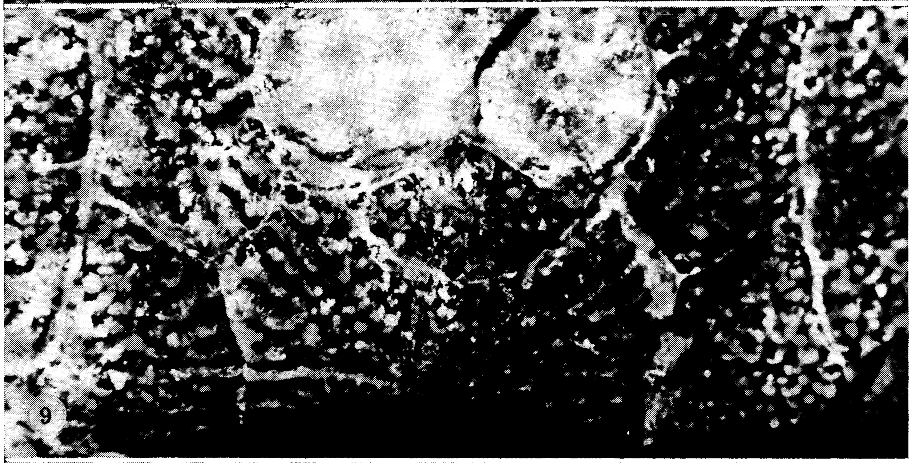


FIGURE 4. Posterior part of head-shield. B.M. P.52091 (magn. × 2).
FIGURE 5. Posterior part of head-shield. B.M. P.52084 (magn. × 3).
FIGURE 6. Central part of nuchal plate. B.M. P.52084 (magn. × 6).
FIGURE 7. Part of right lateral plate. B.M. P. 52084 (magn. × $\frac{5}{2}$).





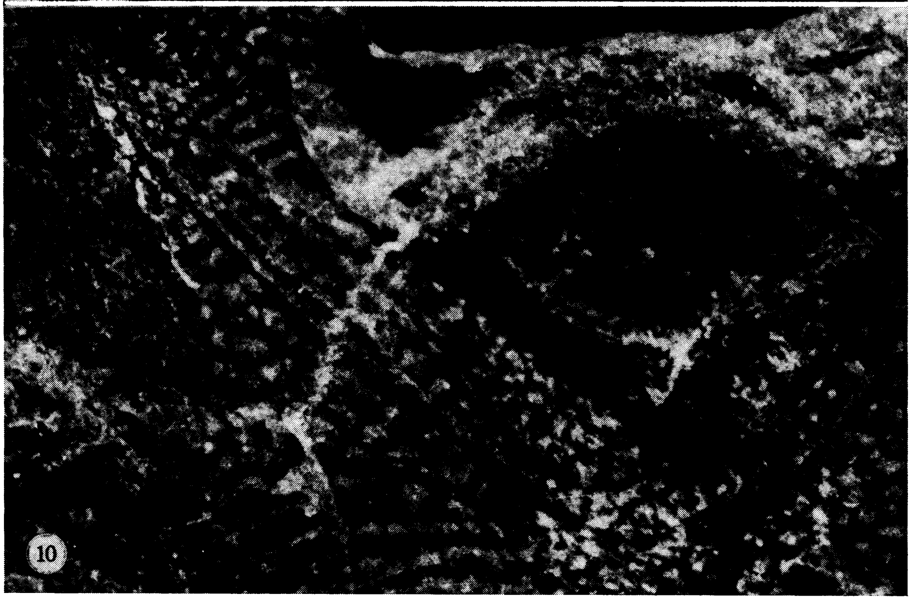


FIGURE 8. Right paranuchal plate. B.M. P. 52084 (magn. × 4).

FIGURE 9. Posterior part of head-shield. B.M. P. 52109 (magn. × 5).

FIGURE 10. Impression of posterior part of head-shield. B.M. P. 52086 (magn. $\times\frac{11}{2}$).

1948, fig. 12). The infraorbital sensory line (ioc) and its continuation as the main sensory line appears to bear a constant relation to the relevant bones associated with it, namely La, PNu, ADL and MxL. Being relatively deep it may have been morphogenetic. If this was so, then the centres of growth and the subsequent centres of radiation of these bones could be expected to be situated on it. In this connection it may be noted (Stensiö 1931, fig. 6*a*) that ioc slopes in such a way that its deeper portion, from which any initiation of ossification would have come, is situated appreciably mesial to the external opening of the longitudinal slit, which is the part seen in dorsal view. The relevant bones not associated with this deep groove, namely Nu, AMD and PMD, are all median bones, and in each case the centre of radiation appears to be located on the middle line, as would be expected.

The principal types of variation considered in this paper are referred to as variation 'type 1', involving csl (figure 2*a*), and variations 'type 2' to 'type 6', involving dlg_2 (figure 2*b*–*f*); in each case the course of the variant groove is shown on the left and the typical condition on the right. Specimens of types 1, 2 and 3 have already been described, principally by Stensiö (1948), but their possible significance has not been considered in any detail. Types 4, 5 and 6 do not seem to have been previously recognized.

Variation 'type 1'. Five specimens of this type of variation have been noted in *Bothriolepis canadensis*. One (S.M.N.H. P. 2181) described by Stensiö (1948, p. 388, fig. 209) is shown in figure 3*c*, and another (N.Y.S.M. 3775) kindly loaned by the New York State Museum in figure 3*b*; the other three were obtained at Escuminac Bay in 1934 and 1937; these are B.M. P. 52091 (figure 3*a* and figure 4, plate 1), B.M. P. 52084 (figures 3*d*, 8 and figures 5, 6 and 7, plate 1) and B.M. P. 52109 (figures 3*e*, and figure 9, plate 2) in which the variation is bilateral.

Figure 3*a* shows the right csl starting from the usual position on Nu; its initial anterolateral course is directed less anteriorly than usual, along a course which, if extrapolated, would pass somewhat behind point 'a'. As the groove continues across the surface of Nu it curves gradually more posteriorly, so that it crosses the suture separating Nu from PNu at a point such that 'ax' is about 30 % of 'ac'. On PNu the groove continues on the same general course, so that it runs in a posterolateral direction until it terminates in the central region of PNu, but some distance mesial to the probable centre of radiation of that bone. The head represented by figure 3*b* is rather poorly preserved, but shows clearly that the right csl groove crosses the Nu/PNu suture about midway along its length, 'ax' being approximately 50 % of 'ac'. In figure 3*c* the right csl crosses this suture further back, 'ax' being betweeen 60 % and 65 % of 'ac'. The groove then continues laterally across PNu, running almost a straight course approximately parallel with the posterior border of that bone and apparently terminating in its central region. Here however it appears to be more or less continuous with the middle pit-line (mp). Stensiö considered the groove in question to be an unusual extension of mp, which is normally a short structure confined to the posterolateral corner of the head-shield. There is in this specimen a faint groove on the right side of Nu in about the position where the right groove csl would be expected, which Stensiö interprets as due to this. However it seems more probable that the groove which Stensiö regards as an unusual extension of mp is the csl of the right side which, as in other examples of variation type 1, has deviated from its normal course and passes across PNu, where in this instance it has become closely associated with a normal mp. The faint groove on Nu which Stensiö believes to represent the right csl is probably merely a groove in the ornamentation which has no sensory line significance. The large and well preserved head represented by figure 3*d* is very similar; 'ax' is about 70 % of 'ac'. The groove can be clearly traced to a position about half way across PNu, and its probable further course is represented by a row of pits (figure 8), which would bring its lateral end to almost exactly the same position as in figure 3*c*; mp is only doubtfully seen on this side. In B.M. P. 52109 (i.e. figure 3*e*) the posterior part of Nu and of the right PNu is missing, but it seems to be possible to locate position 'c' on both sides; on the left 'ax' is about 70 % of 'ac', and on the right 55 %.

These five specimens indicate that in variation type 1, csl may pass on a curved course which carries it fairly close to point 'a', or the curvature may be less pronounced, or lastly and perhaps more frequently after a slight anterior inclination, it may traverse a virtually straight-line course between its terminal positions on Nu and PNu. These three possible courses are shown schematically on the right side of figure 3*f*.

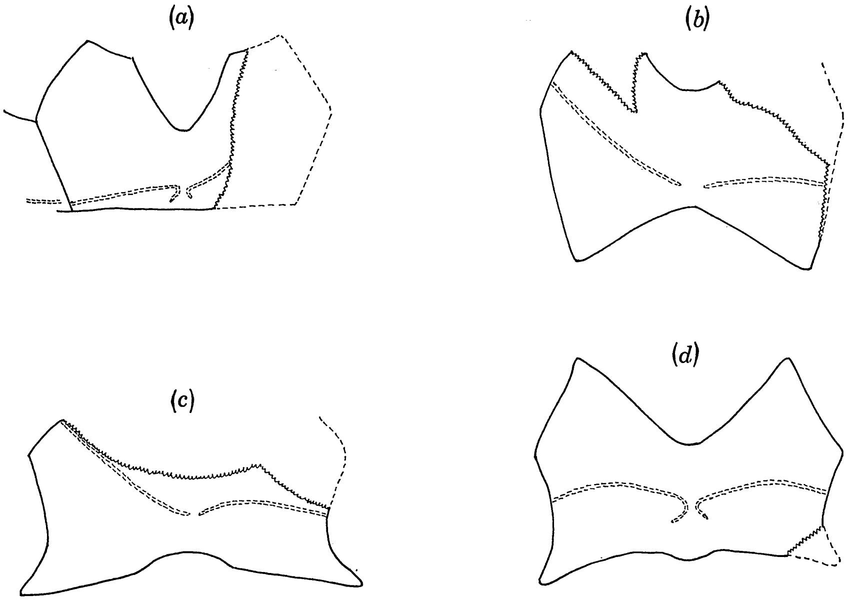


Figure 11. Variation 'type 1'. (*a*) *Bothriolepis groenlandica* Heintz, after Stensiö 1948, pl. 9, fig. 1. (*b*) *Bothriolepis paradoxa* (Agassiz), isolated nuchal plate, after Miles 1968, pl. 6, fig. 8. (*c*) *Bothriolepis cellulosa* (Pander), isolated nuchal plate, after Gross 1941, pl. 4, fig. 8. (*d*) *Grossilepis tuberculata* (Gross), isolated nuchal plate, after Gross 1941, pl. 19, fig. 10.

As regards other species of *Bothriolepis*, Stensiö (1948) has illustrated an impression of a specimen of *B. groenlandica* Heintz in which the right csl groove passes from Nu to PNu (figure 11*a*). Its course across Nu is almost straight, and 'ax' is about 90 % of 'ac'. In this case also Stensiö interprets the groove, though only tentatively, as an unusual extension of mp. Miles (1968) has illustrated an excellent, though incomplete, isolated nuchal plate of *B. paradoxa* (Agassiz) in which the right csl reached the lateral margin of the bone well behind the lateral process (figure 11*b*), which indicates the position of point 'a'. Presumably therefore, as Miles tentatively suggested, csl passed onto PNu instead of La. Gross (1941) gave a similar explanation to an isolated nuchal plate (figure 11*c*) of *B. cellulosa* (Pander); he seems therefore to have been the first to recognize this type of variation.

Lastly in *Grossilepis*, a genus closely allied to *Bothriolepis*, Gross (1941) has described an isolated nuchal plate in which csl reaches the margin of the plate on both sides well behind the lateral process (figure 11*d*); the individual concerned was presumably the equivalent of a bilateral variation type 1 in *Bothriolepis*.

Variation 'type 2'. The relevant parts of Stensiö's (1948) fig. 210 and of one of three specimens designated N.Y.S.M. 3775 are shown respectively in figure 12*a* and figures 12*b*, 17 and 18. In both cases for approximately the first 2 mm the aberrant dlg_2 follows a normal posterolateral course; if it had continued in this direction it would have reached suture AMD/MxL about midway along its course in figure 12*a*, and rather closer to point 'd' in figure 12*b*. This short initial stretch was therefore normal. However during the next 2 mm, the groove swings round abruptly, becoming directed anterolaterally; in this short length its course is reorientated by 75° in the first specimen, and by 70° in the second. From this point it proceeds in a straight line, crossing the AMD/ADL suture far forward, 'cx' being about 45 % and 30 % of 'cd' in the respective specimens. In both cases much of the relevant ADL plates are missing, but comparison of the two sides of N.Y.S.M. 3775 shows that its course was directed towards the region from which the growth of that bone had spread. Stensiö (1948, p. 390, fig. 123*c*) mentions an AMD plate in which the right dlg_2 also presumably passed onto ADL. He shows the initial course of the groove to be directed more laterally than in the specimens referred to above; if prolonged it would not have crossed the AMD/MxL suture, but instead the AMD/ADL one a short distance in front of point 'd'. In this case a less acute bend, of about 45°, sufficed to redirect it to much the same course as in the other two specimens.

Variation 'type 3'. Stensiö (1948, fig. 211) illustrates a good bilateral example of this variation (figure 12*c*). The dlg_2 starts on AMD in much the usual way, but soon sweeps backwards in a gentle bow-shaped curve which carries it across the AMD/PMD suture about midway between points 'e' and 'f'; it appears to end an appreciable distance from the middle line and somewhat in front of the centre of radiation of PMD which, in figure 12*c*, is probably at the position at which the line of dots representing the dorsal median ridge (dmr) has been brought to an end. However on the right side there is a short broad groove which may represent its continuation, though this seems unlikely; it is represented by a continuous line in 12*c*. The right side of the 1934/37 specimen B.M. P. 52085 A and B also belongs to this type of variation. Part of the fossil is badly crushed, but the posterior part of the deviant dlg_2 can be seen to follow a course approximately parallel with the middle line, and relatively nearer to it than in the last specimen; it also seems to terminate anterolateral to the centre of radiation of PMD. One of the N.Y.S.M. 3775 specimens is another unilateral example, which however is rather defective (figure 12*d*). These three specimens are preserved in ways that demonstrate that they did belong to variation type 3, not type 4. Robertson (1938) refers to a specimen which was probably a unilateral type 3. Gross (1941) illustrates an AMD plate of *Grossilepis* (figure 22*d*) which was a bilateral type 3, or possibly type 4.

Variation 'type 4'. Three specimens of *Bothriolepis canadensis* can be referred to this category. In the 1934/37 specimen B.M. P. 52090 (figures 19, 22*a*) the left dlg_2 passes across AMD to the AMD/PMD suture as in variation type 3, and then passes on a backward and slightly mesial course across PMD. The posterior part of this plate is unfortunately missing, but the more anterior portion of the general central region from which the growth of the bone spread is clearly indicated by the ornamentation (figure 19, plate 4). The dlg_2 groove is seen to traverse the left side of this area. At the last position at which dlg_2 can be seen before the break in the rock, its distance from the middle line is about 17 % of the breadth of the left half of the PMD measured to the tip of its lateral process (prl); this is slightly more than the point of termination of dlg_2 in variation type 3 as measured on the left side of figure 12*c*. About 4 mm lateral and slightly posterior to this break a sensory groove is seen extending laterally from the broken edge of the bone. It passes on a lateral and slightly anterior course across the remainder of PMD, and continues on MxL in the same general direction until it reaches the central region of the bone, which is also clearly demarcated by the ornamentation. Here it changes to a lateral and slightly posterior course immediately before its termination.

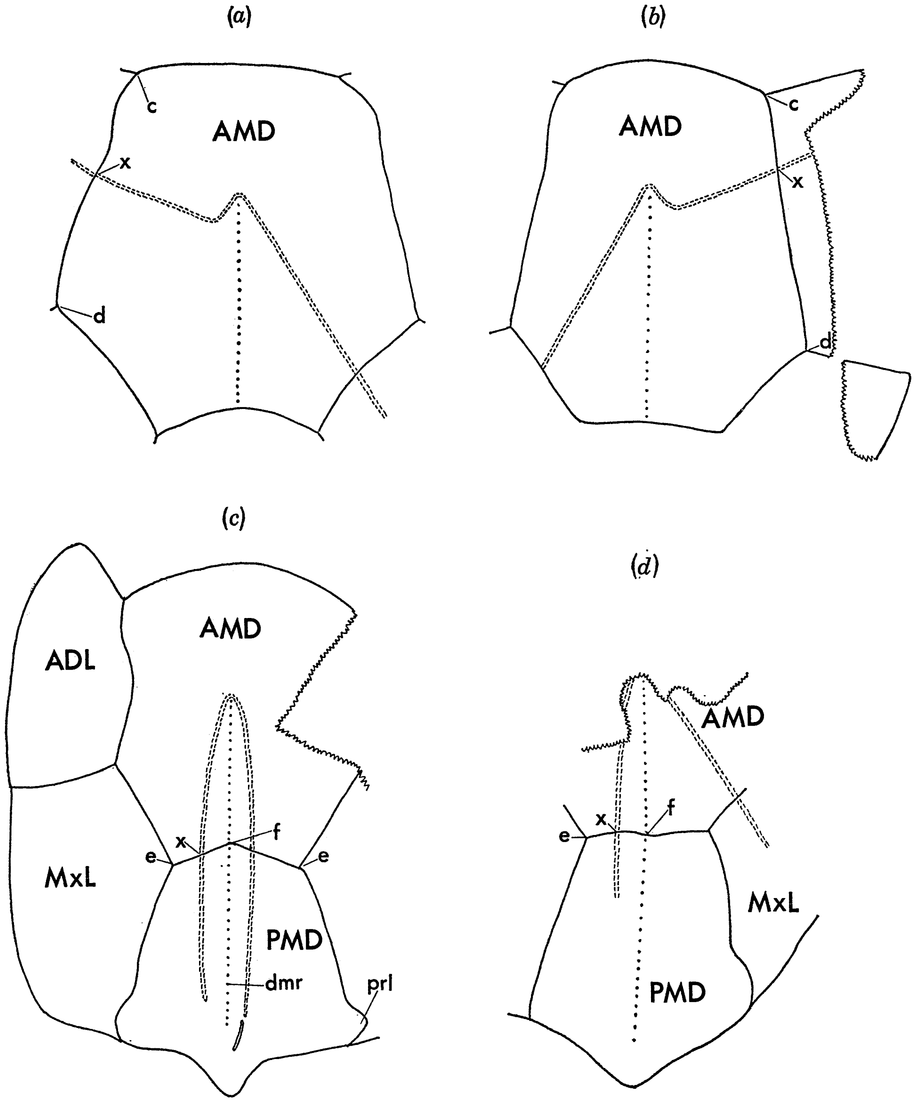
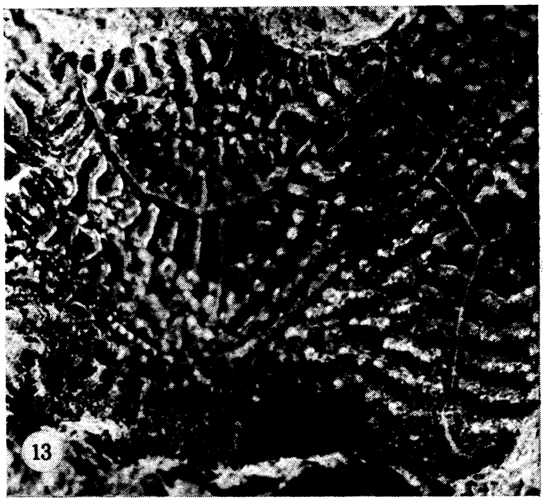
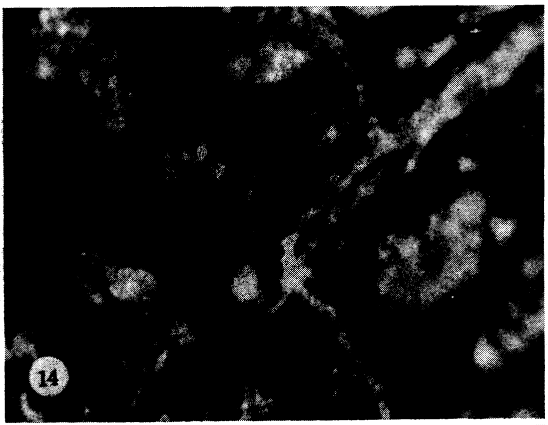
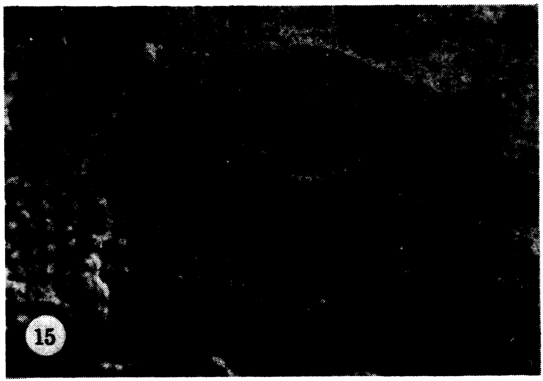


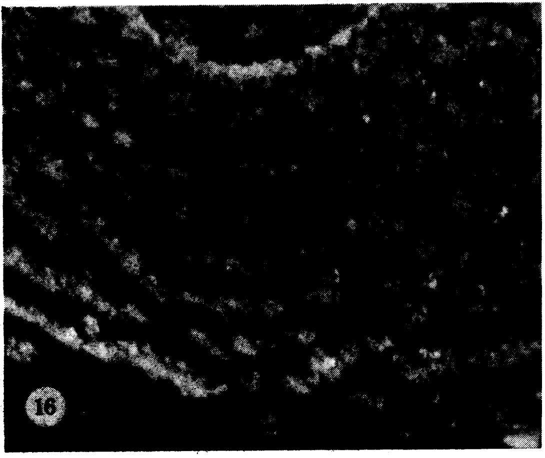
FIGURE 12. *Bothriolepis canadensis* Whiteaves. (*a*) variation 'type 2', after Stensiö 1948, fig. 210. (*b*) variation 'type 2', N.Y.S.M. 3775. (*c*) variation 'type 3', after Stensiö 1948, fig. 211. (*d*) variation 'type 3', N.Y.S.M. 3775.

The significance of these two separate lengths of sensory groove becomes clear in the light of the beautiful isolated PMD plate (R.S.M. 1887.20.6E) at the Royal Scottish Museum. The Museum has kindly supplied photographs. The left side is normal, having no sensory line groove; however it is clear (figure 20, plate 4, figure 22*c*) that on the right side an aberrant dlg_2 has reached the anterior margin of this PMD from a missing AMD, apparently at a position at which 'ex' is about 66 % of 'ef'. From there it passed posteriorly and slightly mesially across PMD on a remarkably straight course. After traversing about three quarters of the length of PMD this posteriorly directed course is abruptly transformed into an anterolateral one as a









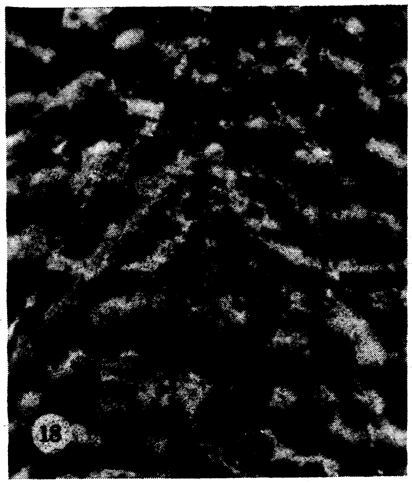


Figure 13. Part of head-shield. B.M. P. 52093 (magn. × 2).

Figure 14. Part of nuchal and lateral plates. B.M. P. 52093 (magn. × 10).

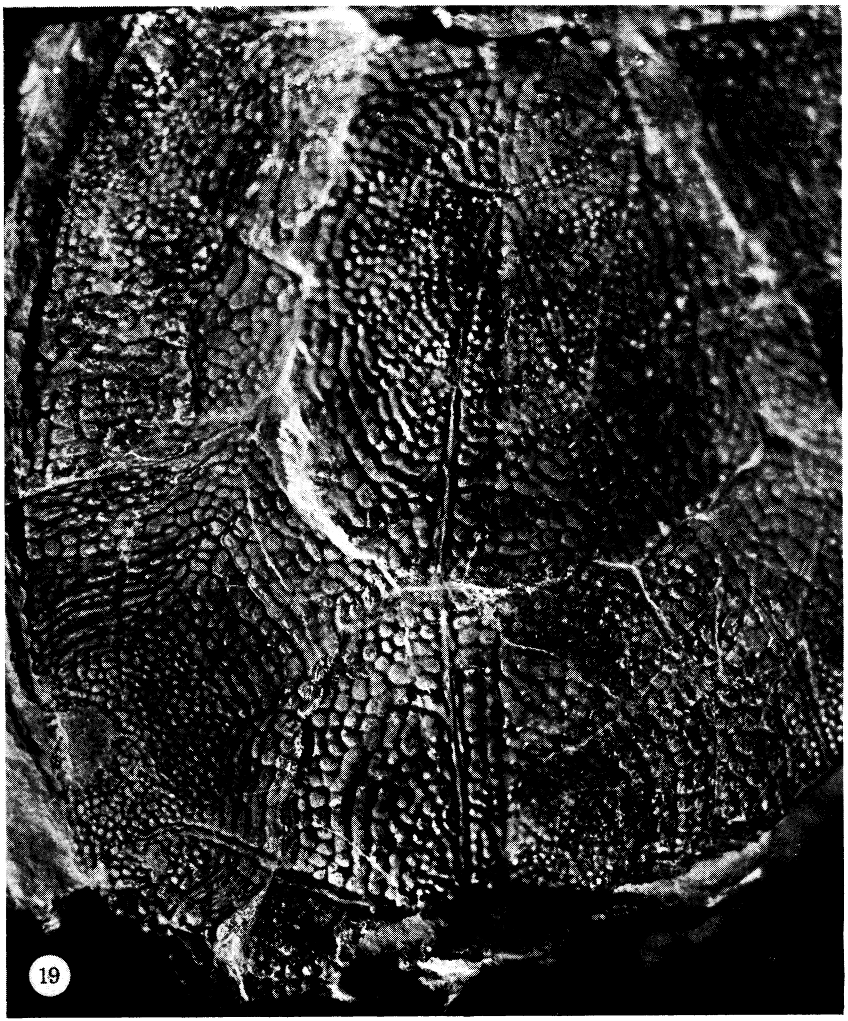
Figure 15. Posterior part of head-shield. B.M. P. 52098 (magn. × 3).

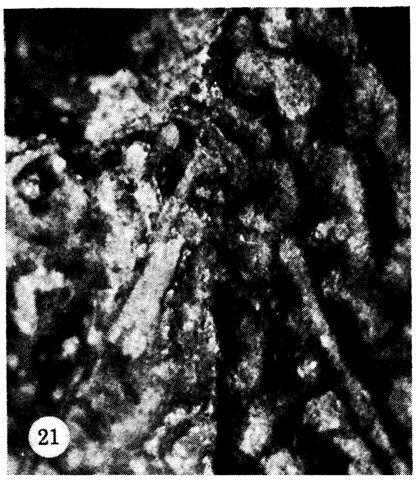
Figure 16. Part of nuchal plate. B.M. P. 52098 (magn. × 7).

Figure 17. Anterior part of trunk-armour. N.Y.S.M. 3775 (magn. × 3).

Figure 18. Tergal area of anterior median dorsal plate. N.Y.S.M. 3775 (magn. × 9).

(*Facing p.* 8)





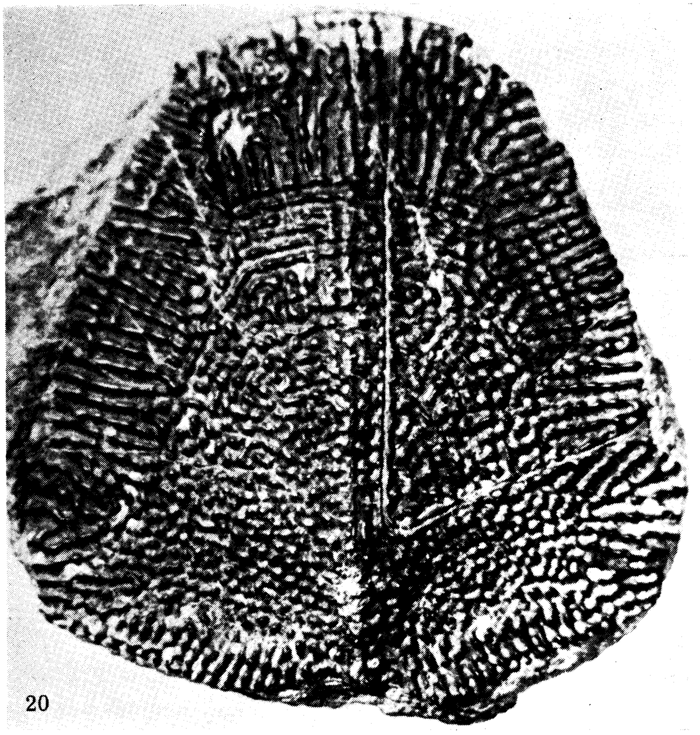


FIGURE 19. Part of trunk-armour. B.M. P. 52090 (magn. × $\frac{5}{2}$).

FIGURE 20. Posterior median dorsal plate. R.S.M. 1887.20.6E (magn. × 2).

FIGURE 21. Tergal area of anterior median dorsal plate. B.M. P. 52104 (magn. × 4).

result of an acute bend. To judge from the ornamentation of this PMD it seems likely that the bend was located some distance anterolateral to the centre of radiation of the bone. The bend began about 2 mm from the middle line, and was therefore certainly not less than this distance from the centre of radiation. This distance is about 10 % of the breadth of the right half of PMD. The position at which the groove makes this bend seems to be much the same as that in which it terminates in variation type 3. Within about the following 1 mm, the groove makes an acute bend at an angle of 70°, the alteration in its course therefore being 110°. Thereafter dlg_2 passes anterolaterally across PMD, again in a straight line, so reaching its lateral margin a short distance in front of the lateral process (prl), as in the previous specimen; from there it doubtless similarly passed onto MxL. This specimen compliments the deficiency in B.M. P. 52090 in a very satisfactory way. It is clear that in the latter the two separate grooves were

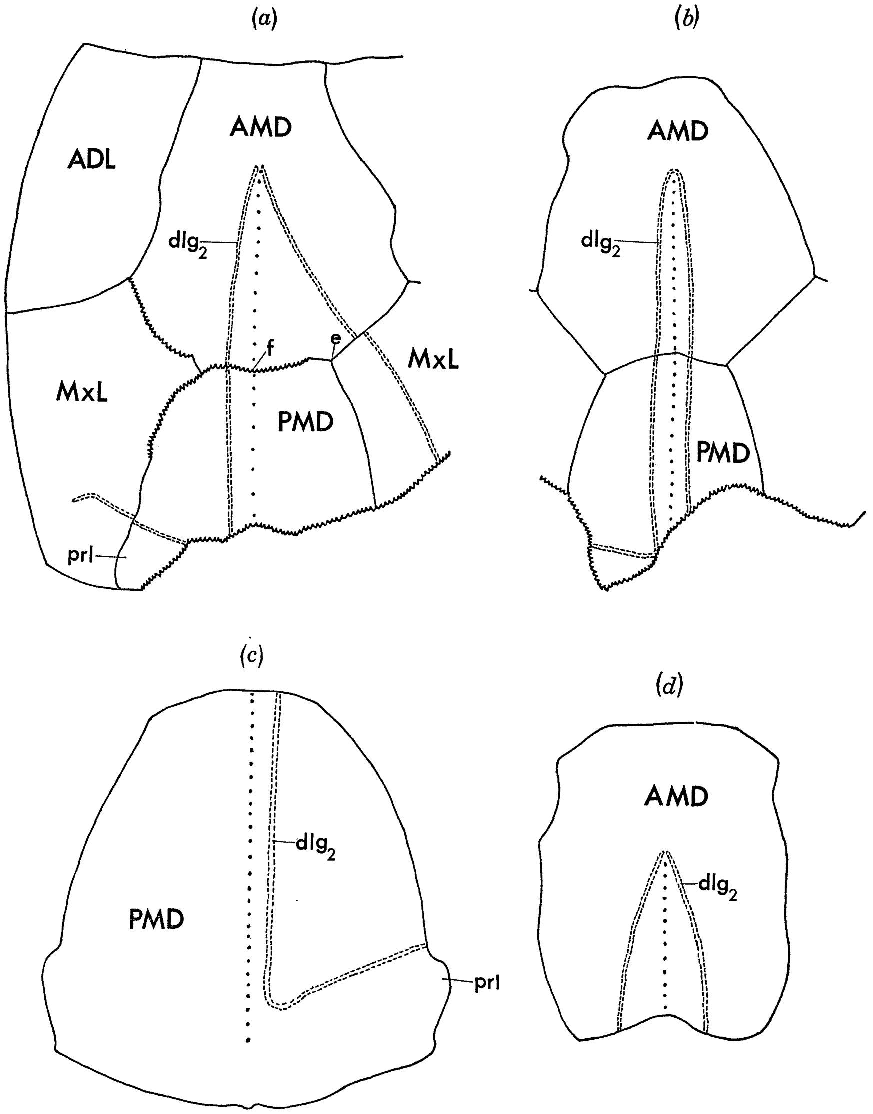


FIGURE 22. (*a*), (*b*), (*c*) *Bothriolepis canadensis* Whiteaves, variation 'type 4'. (*a*) B.M. P. 52090. (*b*) N.Y.S.M. 3775. (*c*) R.S.M. 1887.20.6E isolated, posterior median dorsal plate. (*d*) *Grossilepis tuberculata* (Gross), variation 'type 3' or 'type 4', isolated anterior median dorsal plate, after Gross 1941, pl. 21, fig. 1.

parts of a dlg_2 which made a similar abrupt turn in a corresponding position in the part of PMD that is now missing.

Lastly a third N.Y.S.M. 3775 specimen is of interest (figure 22*b*). The courses of the two dlg_2 grooves, as far as preserved, are similar. They diverge at the tergal angle in the usual way, but soon swing into posteriorly directed straight-line courses which cross the AMD/PMD suture rather close to the middle line; they thus differ appreciably from those of figure 12*c*. On the left side dlg_2 can be traced back on PMD to a position at which it makes an abrupt turn and can then be seen passing laterally across a part of PMD; beyond this the bones are missing. The actual turn is at the edge of the bone breakage. The equivalent area on the right side is missing.

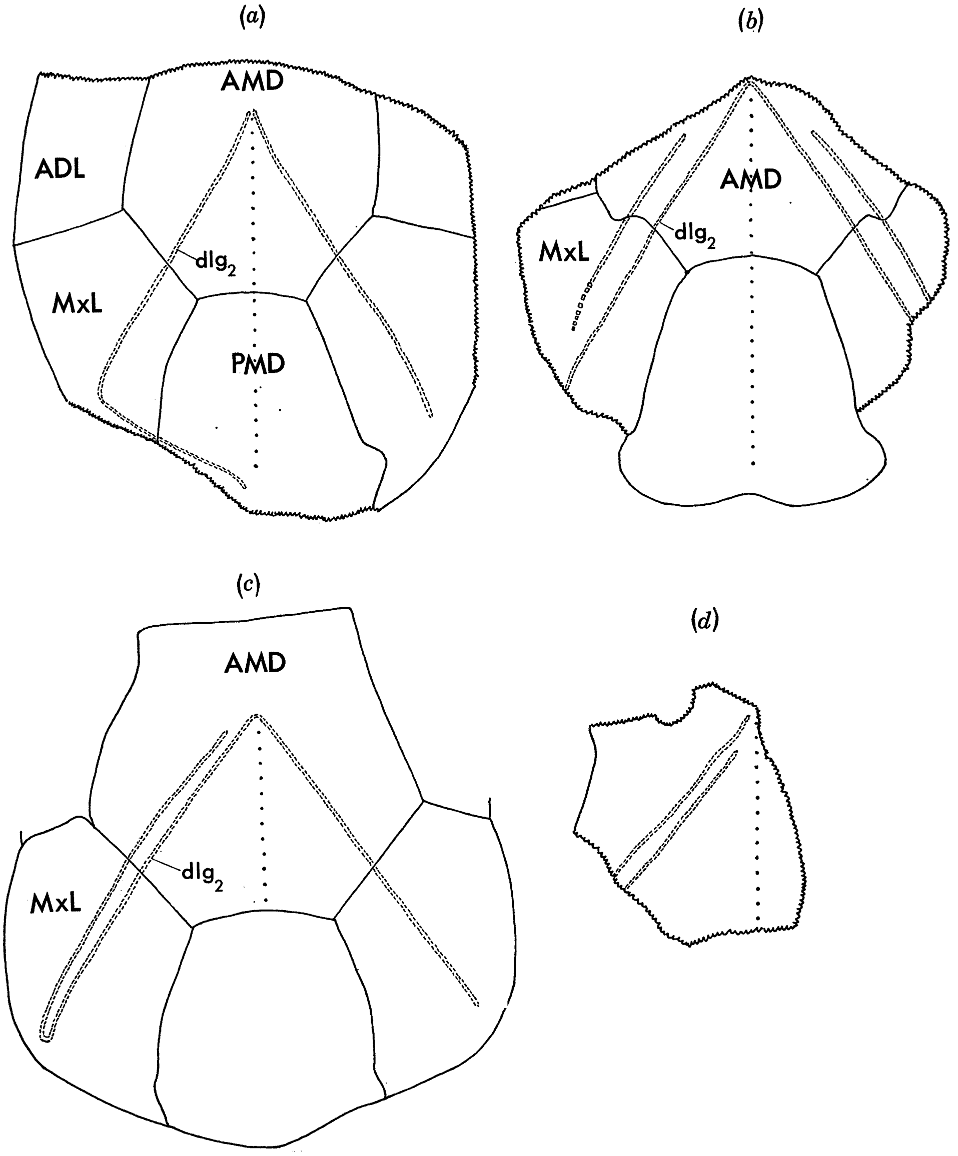
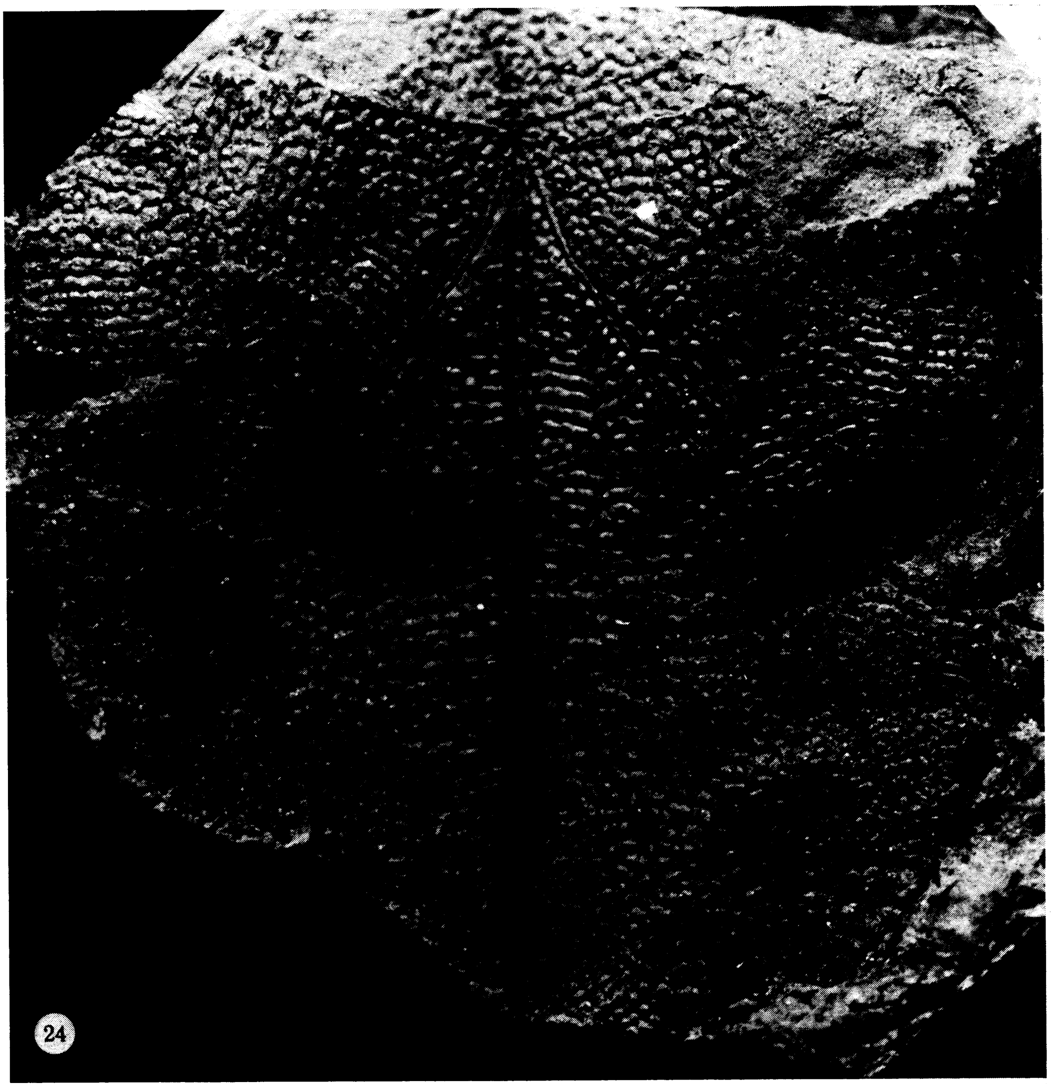
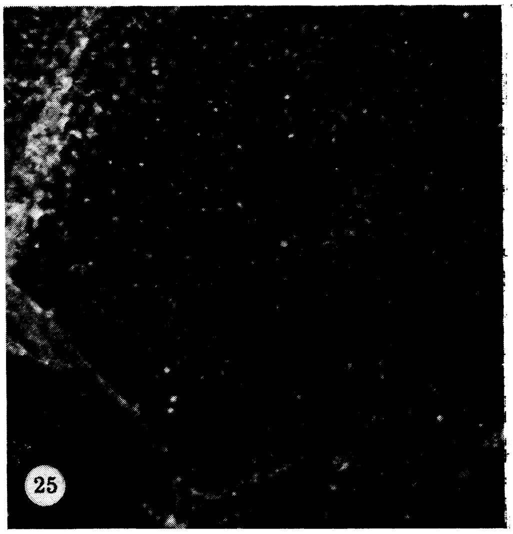


FIGURE 23. (*a*), (*b*), (*c*) *Bothriolepis canadensis* Whiteaves. (*a*) variation 'type 5', B.M. P.52087. (*b*) possible variation 'type 6', after Stensiö 1948, fig. 207. (*c*) variation 'type 6', B.M. P.52092. (*d*) *Bothriolepis hayi* Miles, possible variation 'type 6', isolated fragmentary anterior median dorsal plate, R.S.M. 1967.34.72.





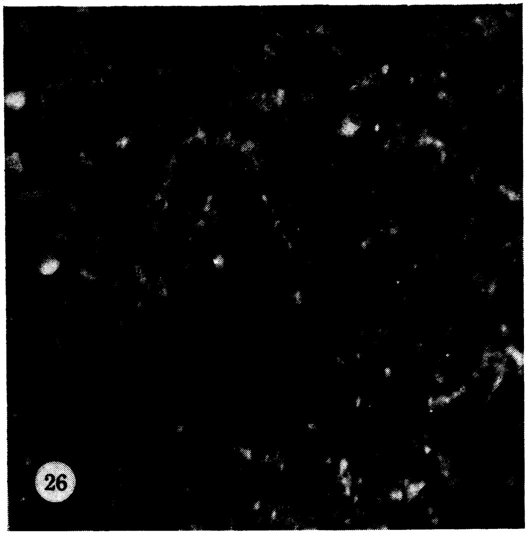
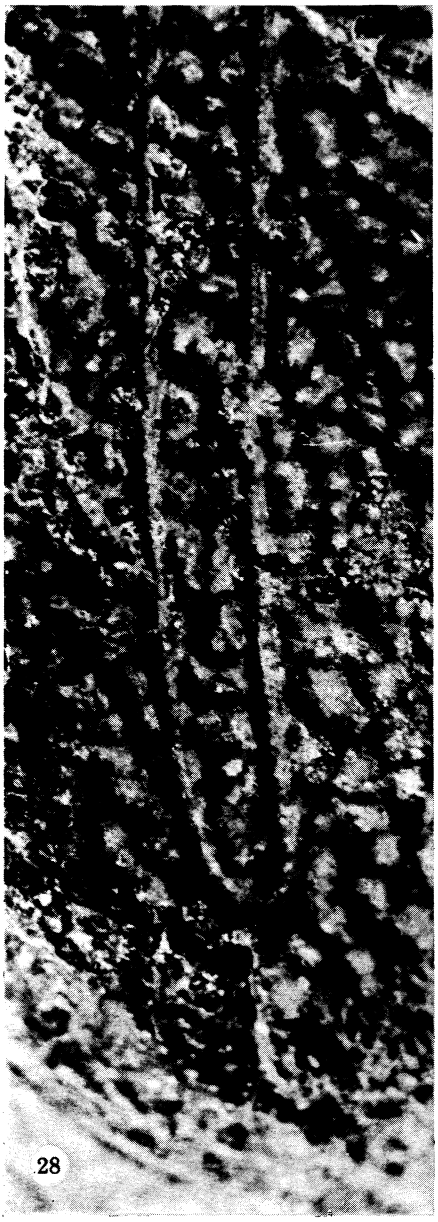


FIGURE 24. Impression of trunk-armour. B.M. P. 52087b (magn. × 3).

FIGURE 25. Impression of anterior median dorsal plate. B.M. P. 52103 (magn. $\times \frac{5}{2}$).

FIGURE 26. Impression of tergal area of anterior median dorsal plate. B.M. P. 52103 (magn. × 12).



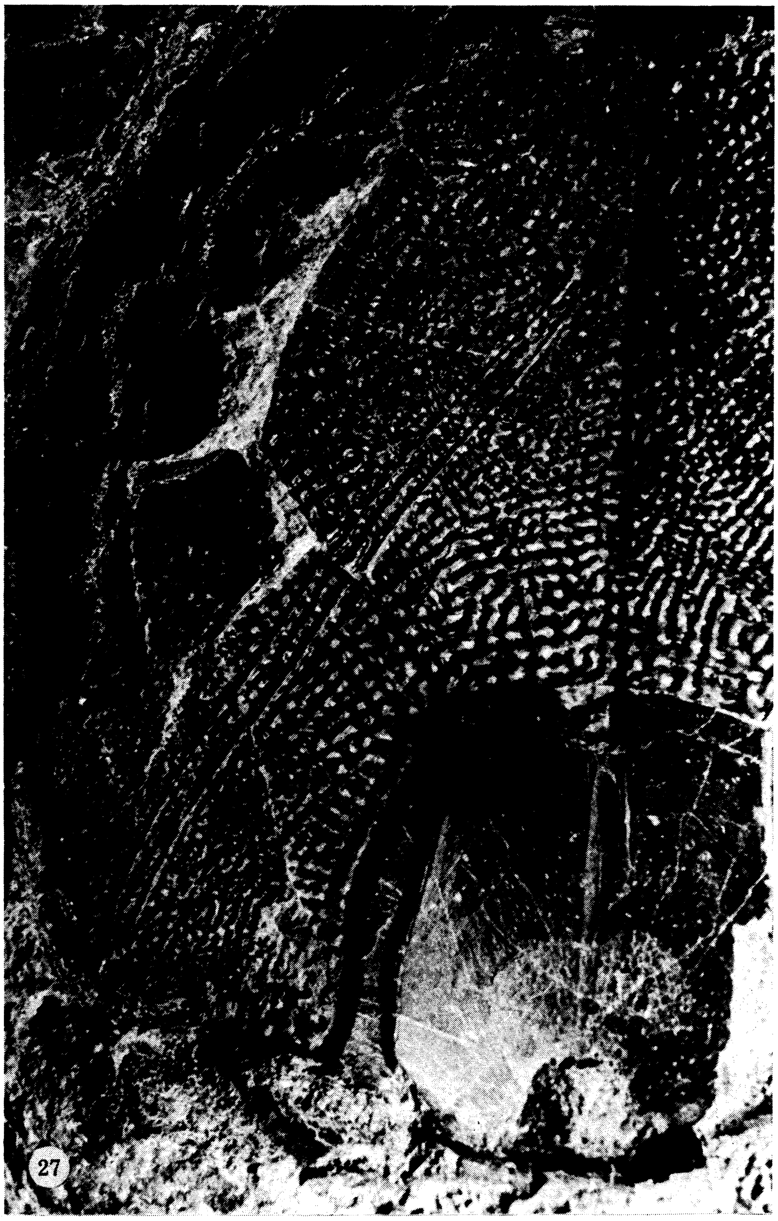


FIGURE 27. Impression of part of trunk-armour. B.M. P. 52092 (magn. × 2).

FIGURE 28. Impression of part of mixilateral plate. B.M. 52092 (magn. × 8).

FIGURE 29. Impression of tergal area of anterior median dorsal plate. B.M. P. 52092 (magn. × 3).

All photographs were taken by the author, except figure 20 which (the negative) was taken by the Royal Scottish Museum.

Variation 'type 5'. This variation is represented only by the 1934/37 specimen of *Bothriolepis canadensis* B.M. P. 52087, seen in counterpart. The impression is shown in figure 23*a* and figure 24, plate 5. Both dlg_2 pass on normal courses to the central region of MxL, which is well demarcated by the ornamentation. Here the left dlg_2 (right side of impression) terminates in the usual way; however the right dlg_2 does not terminate, but instead swings through an angle of 90° and passes posteromesially in a straight-line course across MxL and PMD to its point of termination, which is precisely seen and is about 3 mm posterolateral to the probable centre of radiation.

Variation 'type 6'. The crucial example is the 1934/37 specimen B.M. P. 52092. The relevant part is preserved as an impression (figure 23*c*, figures 27, 28, 29, plate 6). The two dlg_2 grooves pass to the central region of MxL in the usual manner, and the left one (right side of impression) duly terminates there. However the right dlg_2 instead makes a tight U-turn in this central region, and its course is thus redirected through an angle of 180°. The specimen demonstrates the existence of this U-turn with complete certainty. From there it traverses a reverse course passing anteromesially parallel with, and a short distance anterolateral to, the normal primary part of dlg_2. This recurrent groove terminates at a position which can be located exactly; it is about 4 mm posterolateral to the tergal angle, which is the position from which it began its course.

On the left side of the smaller 1934/37 specimen B.M. P. 52094 a similar pair of parallel grooves is seen on adjacent parts of AMD and MxL; in the critical area of MxL there are numerous small dislocations, and it has not been possible to show whether a U-turn was present also in this case.

Stensiö (1948, p. 391) states that dlg_2 'in *B. canadensis* may sometimes be double on both sides throughout its length (text-fig. 207).' This specimen (figure 23*b*) may be a bilateral variation type 6. On both sides, the region where the U-turn would be expected is missing. If this interpretation is correct, then the primary and recurrent portions are further apart, and the recurrent portion ends further from the tergal angle, than in the specimen represented by figure 23*c*.

Miles (1968) refers to an isolated fragmentary AMD plate (R.S.M. 1967.34.72) of *Bothriolepis hayi* Miles on which dlg_2 'is doubled'. This specimen (figure 23*d*) has been re-examined, and has kindly been photographed by the authorities at the Royal Scottish Museum. It seems likely that the apparent doubling is due to one of the grooves, in this case possibly the more mesial one, being recurrent, though of course since MxL is missing this cannot be demonstrated.

Gross (1941, pl. 22, fig. 1) illustrates an isolated AMD plate of *Grossilepis* on which, near its posterolateral corner, there is an impression of two parallel dlg_2 grooves. The remainder of its external surface is obscured by the plate itself, seen in internal view. One of these grooves may have been recurrent.

3. COMMENTS ON THE LATERO-SENSORY LINES OF *BOTHRIOLEPIS*

There has been a tendency (see for example, Stensiö 1948, Ørvig 1971) to interpret lateral-line variations in terms of the presence of additional lines, or of a doubling of lines. However it seems clear that neither of these causes are involved in the variations previously considered; these arise instead as deviations of csl or dlg_2 from their normal course. These variations, in other words, represent alternative courses.

These grooves appear always to pass from the vicinity of the centre of radiation of one bone to that of another. They do not go to some intermediate position. Clearly therefore, the courses of these sensory lines are in some way related to the general region surrounding the centres of radiation of the relevant bones. This association might in principle have arisen as a result of the sensory lines providing foci at which the ossification of these bones was initiated. However it seems fairly certain that this was not the case. For one thing the lines in question were relatively superficial, and therefore probably did not induce ossifications (see for example, Devillers 1947). Secondly, although the courses of these sensory lines varied widely, the bone pattern remained remarkably constant; this virtually precludes them from having acted as morphogenetic foci. Lastly, if the sensory lines had been morphogenetic they would have been expected to pass rather precisely to, or across, the centres of radiation of the bones. However, with the exception of dlg_2 on AMD which may be a special case and is considered later, they pass instead merely to the vicinities of these centres. This is shown particularly clearly by the midline bone PMD of figures 20 and 22*c*.

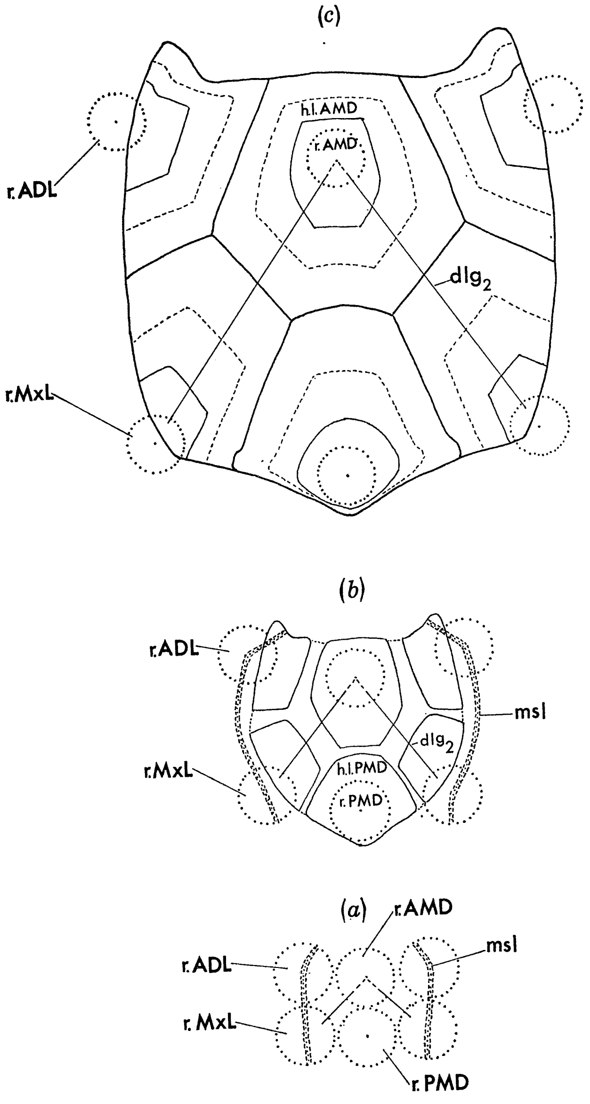


FIGURE 30. Schematic representation of postulated growth of trunk-armour of *Bothriolepis*. (*a*) at beginning of skeletogenesis. (*b*) somewhat later. (*c*) mature. The dotted circles represent bone rudiments, or equivalent areas at a later stage. For explanation see text.

The evidence therefore indicates that lines csl and dlg_2 were not morphogenetic. The close association of these lines with the vicinities of the centres of radiation of bones was presumably due to the sensory lines having become tied by the nerves and blood vessels that supplied them to some portion of the bone rudiments that formed deep to them. This process has been considered particularly by Bystrow (1935), and also referred to in various papers by Westoll (e.g. 1937). The importance of such anchorage, which would have been established at a very early stage in skeletogenesis, has perhaps been underrated.

Figure 30*a–c* indicates the kind of changes that are therefore postulated during the growth of the dorsal body-armour of a typical specimen of *Bothriolepis*. The main sensory line (msl), and also dlg_2, would already have been established, though in a rudimentary form, before definitive bones began to ossify. The rudiments of ADL and MxL may have formed around ossicles derived from msl. Nerves and blood vessels supplying dlg_2, already present before ossification had begun, would become embedded in the osseous tissue that developed deep to it, and would thus anchor the sensory line to whatever bone rudiment was formed below it. During the early stages, the dermis would have been growing faster than the young bones, which would therefore have tended to 'float' away from one another (figure 30*b*); later the bones would have grown faster than the dermis, and sutures would have been formed (figure 30*c*). The bone rudiments, initially close together, would have necessarily diverged from one another as the area of the bones in question was extended as a result of accretionary growth at their margins; the ends of the main part of dlg_2 anchored respectively to parts of bone rudiments AMD and MxL, would have been drawn apart, and the sensory line would have had to accommodate itself to this divergence of its anchorages by an equivalent growth in length. In most cases a juvenile sensory line would have become anchored to a more or less peripheral part of a bone rudiment; later, even though still attached to the corresponding site, its distance from what would now presumably be the centre of radiation would have become quite small in comparison with the size of a bone that had increased vastly in area. This would account for these sensory lines reaching to the vicinities of the centres of radiation of the bones, and also for them not being associated with the precise centres. The concepts underlying figure 30 assume that conditions in the central region of the bones remained relatively fixed; it is the growth at the periphery of the bones that has been emphasized. Such 'freezing' would doubtless not have been absolute; there would have been some bone resorption and redeposition, the sensory lines would have increased in size, and so forth. However, the overall effect of such changes is unknown, and the fact that figure 30, when applied also as a model for the variations, as in figures 31 and 32, can result in expectations which correspond closely with the variations in *Bothriolepis* seen in maturity, indicates that changes of this kind were probably not very important in this context.

As indicated above, this model can be extended to account for variations types 2 to 6. The left side of the typical condition is shown again in figure 31 a_1 and a_2; stages 1 and 2 in figure 31 correspond respectively to the stages shown in figure 30*a* and *b*; figure 32 corresponds to figure 30*c* in representing the adult condition. In variation type 2 the juvenile dlg_2 presumably overlay the rudiment of ADL instead of that of MxL; it became anchored to it and in due course was drawn to the central region of that bone instead (figures 31 b_1, b_2, and 32). In type 3 it similarly became anchored to rudiment PMD. Variation type 4 is particularly interesting; it would seem that here dlg_2 became attached, from before backwards, first to rudiment AMD, then to the anterolateral part of rudiment PMD and lastly to the anteromesial part of rudiment MxL. With the subsequent growth of the bones dlg_2, instead of being merely extended between the diverging anchorages of AMD and MxL, was in addition drawn posteromesially on account of its attachment to the central region of PMD. The course of the sensory line could be likened to a piece of elastic stretched between two pins and at the same time drawn sideways by a third. Instead of following a straight line it traversed two sides of a triangle; this necessitated a further increase in its length. In variation type 5, the relative positions of attachments to PMD and MxL are reversed. The sensory line became anchored to AMD and MxL in the usual way, but beyond this point its distal end became in addition anchored to rudiment PMD, probably on its posterolateral side. Here, then, the AMD-MxL sector has grown in the usual way, but distally beyond this zone it has been pulled out and drawn far mesially due to an accessory attachment to PMD. Lastly in variation type 6 (figure 31*f*) the recurrent course of the distal part of dlg_2 can be accounted for if the most distal part of the juvenile line, beyond rudiment MxL, overlay and became anchored to another part of rudiment AMD. As these rudiments withdrew from one another the point at which the line was attached to MxL would be drawn

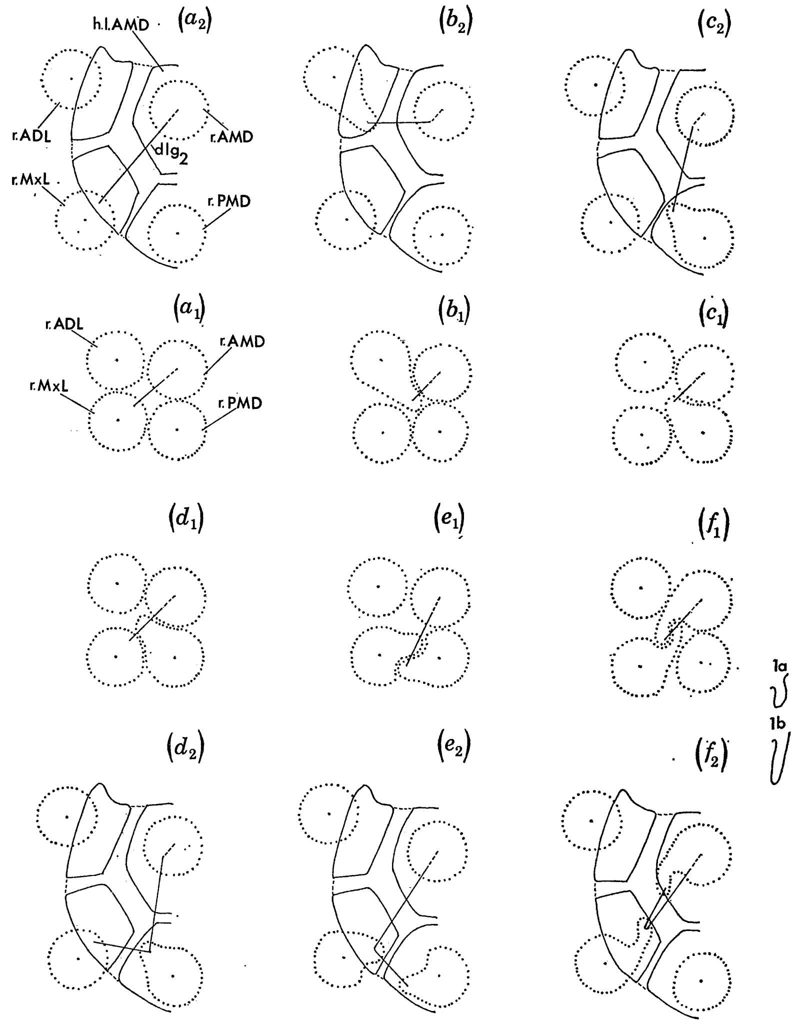


FIGURE 31. Postulated development of trunk-armour of *Bothriolepis*. (a_1), (b_1) etc. at beginning of skeletogenesis, (a_2), b_2) etc. somewhat later. (a_1), (a_2) typical specimens. (b_1), (b_2) variation 'type 2'. (c_1), (c_2) 'type 3'. (d_1), (d_2) 'type 4'. (e_1), (e_2) 'type 5'. (f_1), (f_2) 'type 6'.

first to the bottom of a shallow loop (figure $31f_{1a}$), then to a deeper loop (f_{1b}) and presently to the U-turn at the bottom of a long narrow loop, as in figures $31f_2$ and 32.

It is therefore suggested that differences in the courses of dlg_2 depend on which bone rudiment the juvenile sensory line became anchored to. This in turn depends on the relative positions of the juvenile line and the bone rudiments at the critical stage in development. Either, or both, may have been variable. Variation type 2, for example, could have been due to the juvenile line being orientated more laterally, and type 3 more mesially, with the bone rudiments remaining as in figure 31*a*. On the other hand variation types 4, 5 and 6 cannot be explained in terms of different orientations of the sensory line, nor by its having a curved course, unless it were involved in impossible contortions. At least in these cases it would therefore seem that differences in the relative positions, and perhaps more particularly in the shapes, of the bone rudiments were responsible.

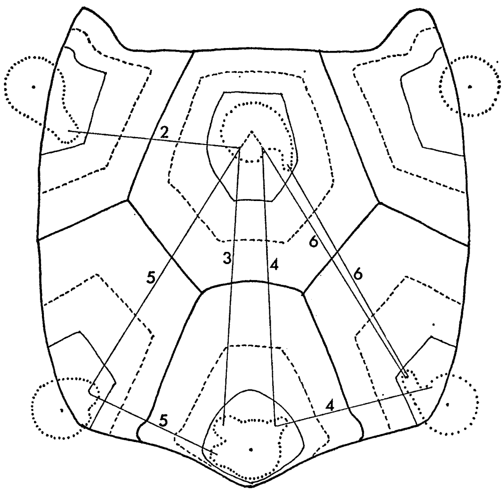


FIGURE 32. Trunk-armour of *Bothriolepis* showing the different courses of dlg_2 that would have been expected on the basis of the assumptions postulated in figure 31 for variations 'types 2 to 6'.

It is difficult to visualize a set of ontogenetic relations that will account for variations types 4, 5 and 6 unless the bone rudiments were closely packed together. At this early stage they would presumably not have been surrounded by a connective tissue sheath, so their osteoblasts would have been liable to mingle. Yet the adult condition indicates that the rudiments remained discrete. The postulated bunching of these rudiments therefore suggests that their cells had some means of recognizing an affinity with fellow cells of their own rudiment, in contrast to those of others. Devillers & Corsin (1968), discussing the fusion or non-fusion of adjacent latero-sensory elements in teleosts, have postulated an affinity between cells of some of the rudiments, and an avoidance reaction between those of others. It is relevant also that the variable pattern postulated for the early bone rudiments stands in marked contrast to the relatively constant bone patterns of the mature stage. Lastly, since many of these variations were unilateral, it would seem that ontogeny differed somewhat on the two sides of such individuals, even though the cells on the two sides would have contained the same genes. Minor phenotypic variations arising on the two sides would have given rise to different bone rudiment patterns, these to different anchorages, and these to the different sensory line courses observed in the fossils.

Variations types 2 to 6 also raise problems of another kind. It has been assumed, for reasons already stated, that in all these variations the juvenile dlg$_2$ passed posterolaterally along much the same alignment, as in figure 31a_1–f_1. This may be called its primary orientation. Normally this brought it into association with rudiment MxL, and this anchorage would subsequently have drawn it along much the same alignment. However in variation type 2 it became associated with rudiment ADL and was drawn anterolaterally instead, and the position at which the line swung round presumably indicated the point at which it was firmly anchored to AMD by nerves and blood vessels. This anchorage acted as a fixed point, like a pin with elastic swinging round it. Its firmness saved the most anterior part of dlg$_2$ from being pulled round, and so it retained its original orientation. Near the point of anchorage, where the tension due to the

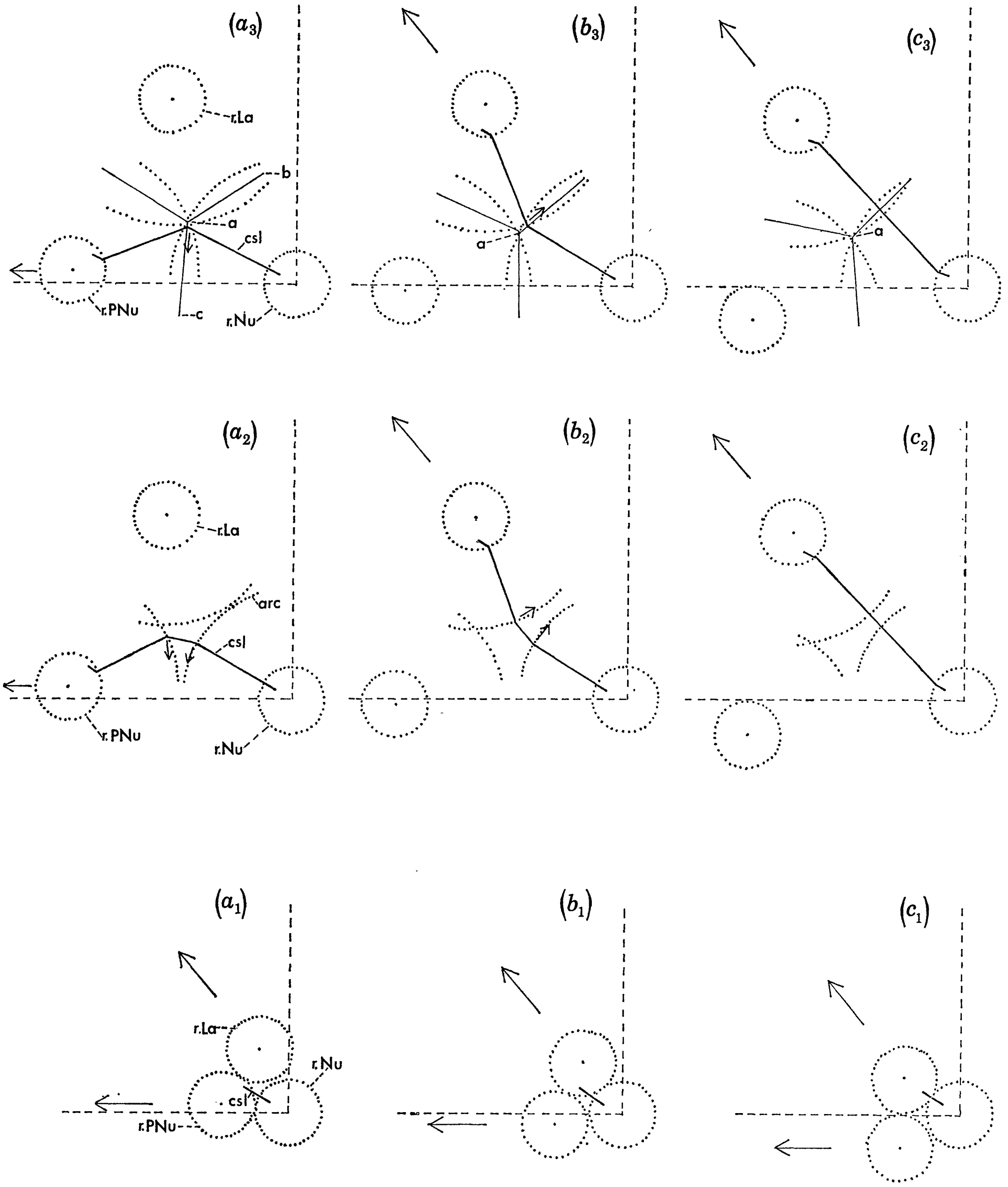


FIGURE 33. Representation of three alternative relations [(a_1) to (a_3), (b_1) to (b_3), (c_1) to (c_3)] between the central sensory line and bone rudiments postulated as existing in *Bothriolepsis*.

alteration in the direction of the pull would have been maximal, the yield was total. Here the line swung round abruptly in a tight curve, and then traversed a straight course towards its new destination. In this connection the third specimen referred to (Stensiö 1948, fig. 123*c*) is interesting, for here the anchorage itself seems to have yielded somewhat to the lateral tension; the shielding of the most anterior part of the line was therefore incomplete and it has been drawn into a more lateral orientation. The abruptness of the turn has consequently been reduced. It follows, according to this interpretation, that the anchorage of dlg_2 was not at the centre of radiation of AMD, which was on the midline at the tergal angle, but took the form of a pair of anchorages which was 2 or 3 mm posterolateral to that centre. It may be noted that the dlg_2 of the two sides do not always reach and unite with one another at the tergal angle.

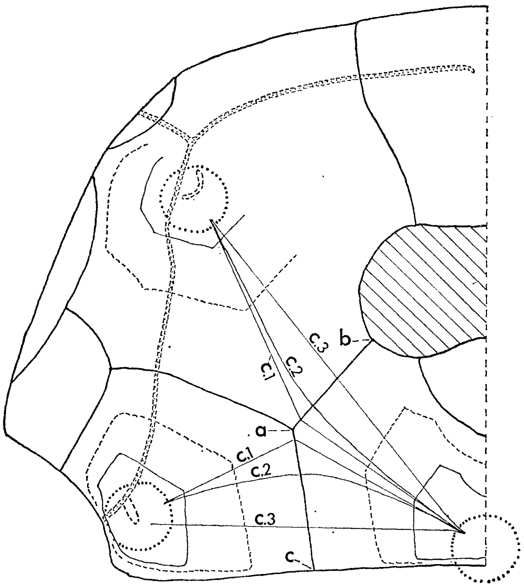


FIGURE 34. Diagram showing six possible courses of the central sensory line in *Bothriolepis*.

Thus in B.M. P. 52087a and P. 52090 the two grooves remain separated by a high narrow extension of the dorsal median ridge, and in B.M. P. 52104 (figure 21, plate 4) the right dlg_2 appears to terminate about 3 mm posterolateral to the angle, the region of its expected further course being occupied by normal ornamentation. Thus the passage of dlg_2 across the centre of radiation of AMD seems to have been somewhat incidental and was not invariable.

The same reasoning can be applied where the line was carried to PMD (i.e. types 3 and 4), but here the degree of deviation from the primary orientation was much smaller. In some cases there is (figure 22*b*) a sharp turn at the AMD anchorage, but alternatively (figure 12*c*), instead of the change in direction being concentrated at this point, it is distributed in the form of a gentle curve; this suggests that the bone's yield was a gradual process that continued throughout growth.

The abrupt bends on PMD and MxL in variations types 4, 5 and 6 can be visualized in similar terms. In each case forces were introduced which concentrated tensions at the points of anchorage and led to extreme deviations of course, amounting respectively to 110°, 90°, and 180°. In each case the bone yielded completely to the resulting tensions at the point where they would have been at a maximum. Elsewhere dlg_2 proceeded in straight lines between its points of attachment. It thus took the shortest possible course compatible with its anchorages, and so reduced the tensions involved, and also its own inevitable lengthening, to a minimum.

Turning to the head, groove csl often starts on Nu a short distance from the middle line (see figures 3*a*, *d*, 6, 11*b*), and it was probably anchored at this position. Posterior extensions from there occur fairly often (see figures 11*a*, *d*, 35*c*), and are considered later (p. 33). On passing lateralward from this presumed anchorage the first part of the course is usually directed towards or slightly in front of point 'a'. However in typical specimens it thereafter almost immediately bends to a more anterior orientation, and then follows this course more or less straight to its termination on La. In variation type 1 it may start in much the same direction, and then makes a similar bend, but in this case to a posterior direction (see figure 3*a*). Thus it seems likely that the juvenile line was first directed towards or slightly in front of a position later equivalent to point 'a', as it is shown in figure 33a_1, b_1 and c_1. This would have been its primary orientation. If the line became anchored to La it was drawn to a somewhat more anterior course, and if to PNu to a more posterior one, as indicated by the large arrows, as a result of the subsequent relative movements of these points of anchorage. In both types there was a tendency for the line to be held firmly in the first part of its course close to the Nu anchorage, with the result that here an indication of the primary orientation has been preserved. It is interesting to compare these courses with those of dlg_2.

This evidence of a primary orientation, though slender, suggests that, as in dlg_2, it was differences in the forms or locations of bone rudiments, rather than those of the juvenile sensory line, that determined whether csl should become anchored to La or PNu. As the latter anchorage was relatively uncommon there may have been a graded variation of the ontogenies, a few individuals having csl anchored to the PNu rudiment (figure 33a_1), a larger number to the adjacent (i.e. posterolateral) part of the La rudiment (b_1), and a still larger number to a more central position in this rudiment (c_1). It seemed likely that such differences might in some way be reflected in the positions at which csl crossed the Nu/PNu and Nu/La sutures. Information regarding the former, which are type 1, has already been given. As regards the latter or 'typical' condition the position at which csl crossed the suture was measured, and 'ax' was calculated as a percentage of 'ab', in all suitable 1934/37 specimens of *Bothriolepis canadensis*. The two sides of each individual were treated separately; in many cases, therefore, a single specimen yielded two units of measurement. Table 1 shows the number of instances in which the position of the csl crossing fell within each successive 5 % sector passing from 'a' towards 'b' in these 1934/37 specimens and also, separately, in those previously present in the British Museum (Natural History), and in the Royal Scottish Museum. The frequency was highest in the 50–60 % regions; the fall off below 45 % was rather gradual, but there was a notable paucity of specimens with crossings close to point 'a'. The few examples of type 1 available indicate that also on this side of 'a' there was a similar avoidance of crossings close to 'a'.

It is interesting that nevertheless there are occasional specimens of *Bothriolepis* in which csl has an angulated course with the angle at or very close to point 'a'. In the 1934/37 series there is only one such case, namely the left side of B.M. P. 52098 (with impression counterpart B.M. P. 52101). PNu overrides Nu slightly (figures 15, 16); however in the impression the portion of the groove on La can be seen to meet that on Nu at the suture; both parts are straight, and they meet at a sharp angle of about 140°. The sensory line therefore changes its course abruptly at the suture at a position very close to 'a', 'ax' being only about 8 % of 'ab'. Stensiö (1948) has illustrated a similar specimen of *B. gigantea* Traquair (figure 35*a*), and one of his illustrations (pl. 3, fig. 2) of *B. groenlandica* probably represents a similar condition. Gross (1941, p. 8, pl. 6, fig. 2), referring to a small specimen of *B. cellulosa*, states that csl goes precisely to the corner between La and PNu and there makes a sharp bend at its continuation onto La. Here 'ax' was virtually 0 % of 'ab'; in the *B. gigantea* it was only about 5 %.

Table 1

'a'	0–5	5–10	10–15	15–20	20–25	25–30	30–35	35–40
1934/37	0	1	0	0	2	3	3	7
B.M.	0	0	0	0	0	0	1	1
R.S.M.	0	0	0	0	0	1	0	1
total	0	1	0	0	2	4	4	9

	40–45	45–50	50–55	55–60	60–65	65–70	70–75	'b'
1934/37	14	21	35	39	19	5	0	
B.M.	2	4	10	4	5	1	0	
R.S.M.	2	5	13	8	4	0	0	
total	18	30	58	51	28	6	0	

The first row of figures shows 'ab' divided into 5% blocks, starting at 'a', progressing towards 'b' and terminating at 75%. The next three rows shows the number of measurements in which 'ax' expressed as a percentage of 'ab' falls within each of these 5% sectors in, respectively, the 1934/37, B.M. and R.S.M. specimens.

Table 2

'e'	0–5	5–10	10–15	15–20	20–25	25–30	30–35	35–40
1934/37	0	0	0	0	1	2	6	24
B.M.	0	0	0	0	0	0	0	1
R.S.M.	0	0	0	0	0	0	0	0
total	0	0	0	0	1	2	6	25

	40–45	45–50	50–55	55–60	60–65	65–70	'd'
1934/7	47	77	40	8	1	0	
B.M.	6	17	8	3	0	0	
R.S.M.	7	12	8	0	0	0	
total	60	106	56	11	1	0	

The first row of figures shows 'ed' divided into 5% blocks, starting at 'e', progressing towards 'd', and terminating at 70%. The next three rows show the number of measurements in which 'ex' expressed as a percentage of 'ed' falls within each of these 5% sectors in, respectively, the 1934/37, B.M. and R.S.M. specimens.

Such courses can be interpreted developmentally in terms of figure 33 b_1–b_3; the small arrows represent horizontal tensions, and the sensory line develops a sharp angle at the suture. The outcome of such changes is represented by course 1 (c. 1) in figure 34. It is of considerable interest that in these four specimens the initial part of csl on Nu has a straight course. This is seen in figure 16, in which the straight initial course on the left angulated side can be compared with the typical initial bend on the right normal side. The absence of a bend supports the contention that in such specimens the primary orientation of the sensory line has been retained unchanged throughout its whole course on Nu.

There are occasional specimens of *B. canadensis* in which csl crosses suture La/Nu about half way between point 'a' and the most frequent 50–60 % region, and has a gentle curved course throughout. Examples are the left side of Stensiö's (1948) fig. 77 *b*, shown in outline in figure 35 *c*, and also the 1934/37 specimens B.M. P. 52087 (right side) and P. 52090 (right side); in each of these 'ax' is about 25 % of 'ab'. Massler & Schour (1951) have shown that in mammals the bone growing at the sutural margins is sensitive to small forces acting on it. It is suggested that in these individuals the anchorages were much the same as in the previous four, but that here the margins of the growing bones yielded somewhat to the resulting tensions represented by the small arrows (figure 33b_2 and b_3) and that consequently the sensory line came to assume a

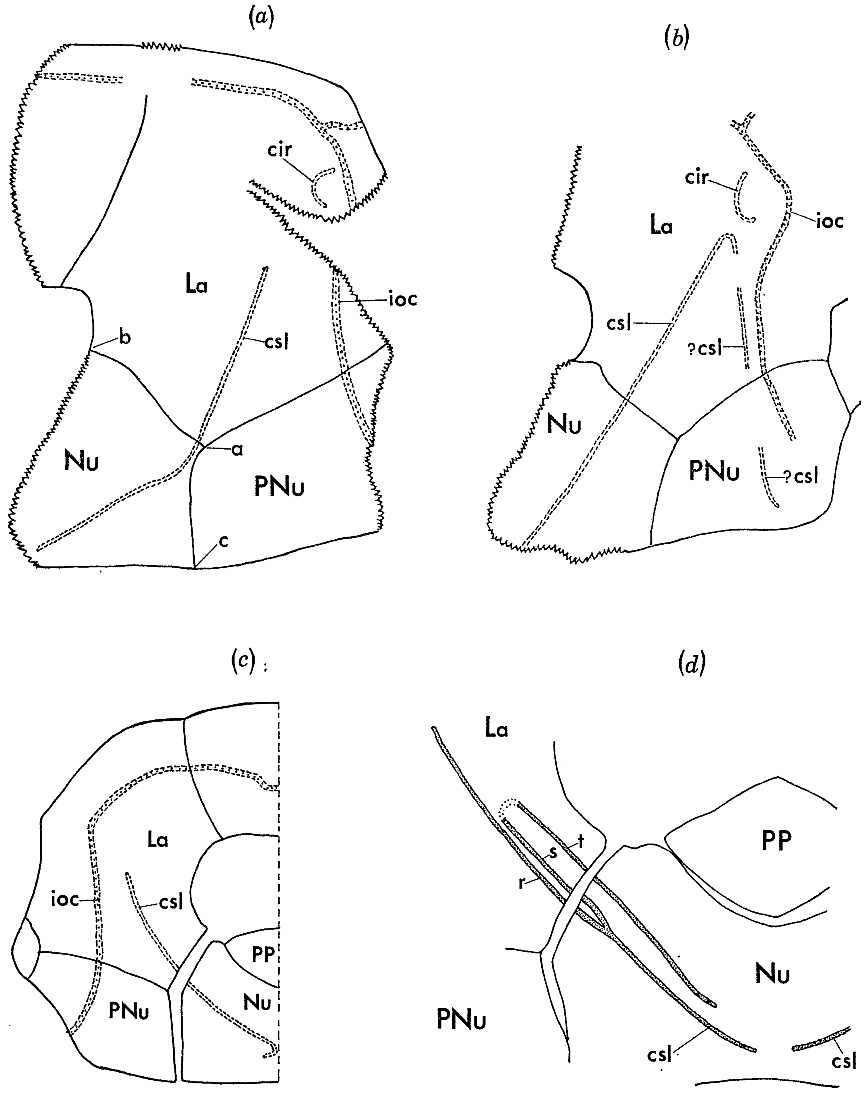


FIGURE 35. Variations of the central sensory line in *Bothriolepis*. (*a*) *B. gigantea* Traquair, after Stensiö 1948, fig. 252*b*. (*b*) *B. groenlandica* Heintz, after Stensiö 1948, pl. 2. (*c*) *B. canadensis* Whiteaves, after Stensiö 1948, fig. 77*b*. (*d*) *B. canadensis* Whiteaves, B.M. P.52086.

curved course in which the angulation had been smoothed away and the line itself carried some distance towards point 'b'. This is represented by course 2 (c. 2) in figure 34. If in such specimens yield had been rapid and complete the courses that resulted in maturity would have been indistinguishable from those shown in figure 33c_3, though this is envisaged as having started from the different type of anchorage shown in figure 33c_1; both are represented by c. 3 in figure 34. The existence of some specimens in which there has been no yield is important, for they provide evidence regarding ontogenetic background which has been obscured when yield was considerable. Figure 34 also shows comparable courses c. 1, c. 2 and c. 3 on the variation type 1 side of point 'a'; c. 1 has not been found; it would require the conjunction of two unusual conditions, namely anchorage to PNu and no yield.

Table 2 shows the results of similar measurements of the positions at which dlg_2 crossed suture AMD/MxL. The setting is rather different, since here the alignment of the primary orientation of dlg_2 and of its subsequent extension by anchorage to MxL probably approximately coincided. It seems (Gross 1941; Stensiö 1948) that in *Grossilepis* dlg_2 became anchored to PMD more frequently than in *Bothriolepis*; its primary orientation may have been more mesial.

The ontogenies postulated schematically in figures 31 and 33 indicate that other anchorages could possibly take place, and it is easy to predict the approximate courses that the lines would then follow. A specimen of *B. groenlandica* illustrated by Stensiö (1948, pl. 2) has the appearance (figure 35*b*) of groove csl making a rather open U-turn at the position on La where it would normally have terminated, and then of passing backwards across La, and possibly also across PNu, on a course mesial to and approximately parallel with ioc. This is the course that would have been expected if the juvenile csl had become anchored to the rudiment of PNu in addition to those of Nu and La; it would have been comparable to variation type 5. However the appearance in the photograph may be due merely to grooves in the ornamentation.

Another possible ontogenetic development is for csl to have become anchored in the usual way to Nu and La, and then in addition to a different position on Nu; this would be comparable with variation type 6. In this respect the unusual 1934/37 specimen B.M. P. 52086 is of interest (figures 10, 35*d*). One part (r) of the csl on the left side of the impression has a normal course; however it gives off a branch (s) which has the appearance (which is possibly misleading) of swinging round a tubercle and so being continuous with a recurrent sensory line (t) which is clearly seen to end on Nu at a point a short distance anterolateral to that at which csl begins. Explanation is difficult. It is suggested that the tension caused by an additional anchorage to Nu resulted in some kind of splitting of the line. This specimen brings to mind the possibility that the shallow sensory groove (a.csl, figure 1) sometimes seen in front of csl, particularly in juvenile specimens, may be a recurrent extension of csl of a type 6 kind which has developed normally instead of 'splitting'.

While making these measurements a note was also kept of instances in which csl or dlg_2 could be seen to pass to the usual bone, namely La or MxL, even though the position at which it crossed the suture could not be measured. There were in this series 339 instances where csl was seen to pass to La, as compared with 4 where it passed to PNu; in this sample there were therefore about 1 % of variation type 1. On the trunk there were 425 instances of dlg_2 taking the normal course to MxL, none of variation type 2, 1 of type 3, 1 of 4, 1 of 5, and 1 definite and 1 probable example of type 6.

Defective or missing grooves were also noted. Both are rare. In two heads (R.S.M. 1897.51.149 and B.M. P. 52102) groove csl is missing on one side. This frequency is half that of variation type 1 in the comparable sample. In B.M. P. 52102 both the right csl and the right dlg_2 are missing; since absence is so rare it is fairly certain that the two losses in this specimen were not coincidental. As regards defective grooves, there are two 1934/37 specimens, and two important instances in *Grossilepis* described by Gross (1941). Figures 25, 26 and 36 are self-explanatory. Perhaps these defective lines were the result of their distal ends not becoming anchored to any bone rudiment and so not being extended in the usual way; they sometimes grew for short distances in directions that were poorly determined. This lack of extension might also account for the remarkable breadth of the dlg_2 stumps.

This analysis indicates that the superficial sensory lines of *Bothriolepis* are divisible into regions of rather different kinds. First there are the sectors that were anchored at both their ends.

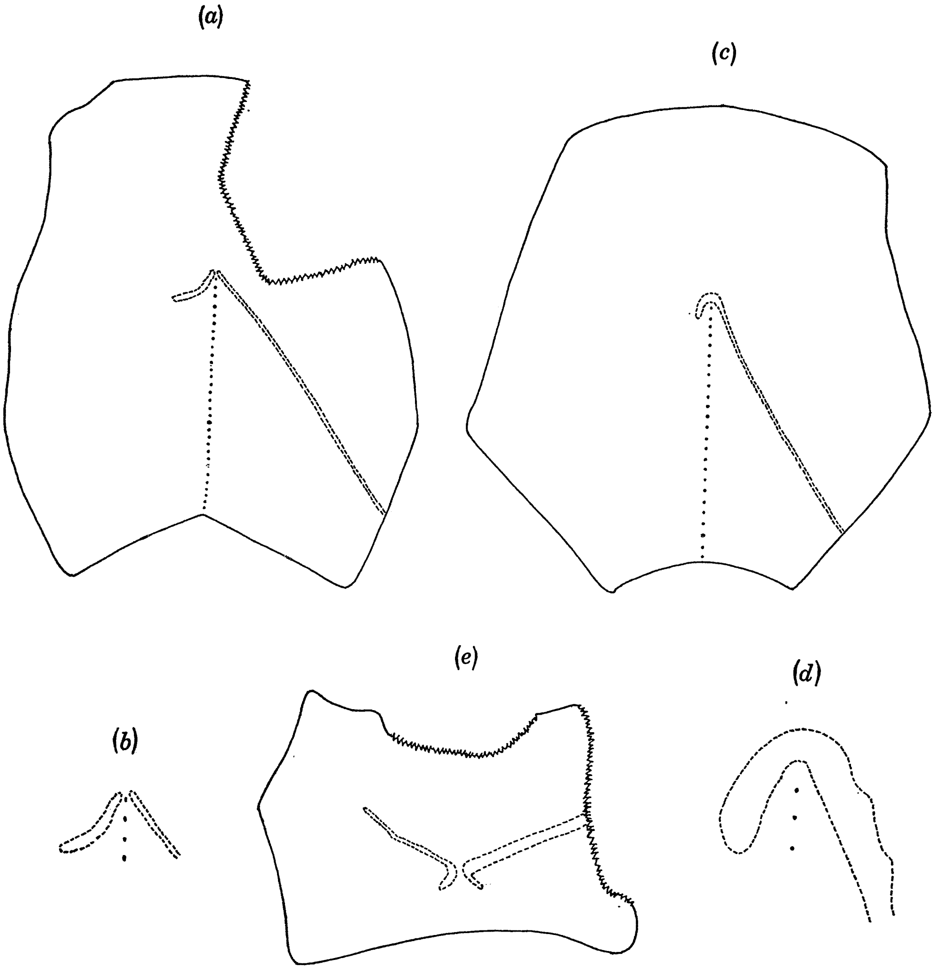


FIGURE 36. Defective sensory lines (*a*) (*b*) *Grossilepsis tuberculata* (Gross). (*a*) isolated anterior median dorsal plate and, (*b*) tergal area of the same enlarged, after Gross 1941, pl. 20, fig. 1. (*c*) (*d*) *Bothriolepis canadensis* Whiteaves. (*c*) isolated anterior median dorsal plate and, (*d*) tergal area of same enlarged, B.M. P.52103. (*e*) *Grossilepis tuberculata* (Gross), isolated nuchal plate, after Gross 1941, pl. 19, fig. 13.

These may be called 'attached sectors'. Secondly there are the parts of sensory lines that extend beyond the last point of anchorage; these are referred to as 'loose ends'; they are often present at the mesial end of a csl, usually at the anterior end of a dlg_2, where they often unite with their antimeres, and are probably also present at the distal end on MxL, though here they are likely to be recognized only when the normal alignment of the attached portion has been modified, as in variation type 4 (figures 19, 22*a*). Variations types 5 and 6 can be regarded as due to this loose end having extended beyond rudiment MxL, so becoming anchored, respectively, to rudiment PMD and AMD; in each case a loose end has thus been converted into an additional attached sector. In variation type 4 an additional anchorage, to rudiment PMD, has developed along the course of the attached sector AMD-MxL; two attached sectors consequently resulted.

An essential difference between attached sectors and loose ends is that the former are extended by the growth of the bones, and the latter are not. The loose ends probably became more or less fixed to whatever bones underlay them at a fairly early stage, but they were not subjected to the same stretching, so that the vagaries of the courses established early in ontogeny are likely to have been subsequently preserved.

A third kind of region can also be present. If attachment of dlg_2 to MxL or to some alternative rudiment fails to materialize then a region that would otherwise have become an attached sector will be left without an attachment at one of its ends. Such a region could be called an 'unattached sector'. Such sectors could in principle arise: (*a*) through a fortuitous failure to become attached, as suggested above, (*b*) through the topographical relation between a bone rudiment and a sensory line changing in the course of phylogeny, with the result that a former anchorage ceased to become established (p. 26); (*c*) through a bone rudiment which had formerly provided an anchorage ceasing to develop as a result of phyletic changes, and so no longer providing an anchorage site (p. 33); and (*d*) lastly, and rather differently, through a failure to establish continuity, or to a subsequent break-down of continuity, in the part of a sensory line that would otherwise have become an attached sector; the peculiar courses of the sensory lines in the postfrontal region of some trematosaurid labyrinthodonts (see Säve-Söderbergh 1937) may have arisen in this way.

A minor variation, which may however be significant, is well exemplified in *Bothriolepis canadensis* by the right side of the 1934/37 specimen B.M. P. 52093 (figures 13 and 14, plate 3, and figure 37). In this case the sensory line follows a normal course and it is a suture that deviates. On reaching groove csl the Nu/La suture turns abruptly through a right angle and runs along the centre of the sensory groove (i.e. the deepest part of its valley) for about 2 mm; it then turns through a second right angle and so resumes its normal direction. Similar variations are seen in some other specimens of *B. canadensis*, and also in *B. hayi* and *B. gigantea*. Some of these amount merely to a minor disturbance of the suture's course as it crosses csl. Stensiö's (1948) figs. 10 and 12 show clearly that the variant course of the suture seen on the external surface of the bone is not present on its internal surface; also his fig. 76*b* shows two deviations of the Nu/La suture, one associated with csl and the other with a.csl. Gross (1941) has illustrated specimens of *B. cellulosa* in which precisely similar deviations are developed, but in this case by a different suture, namely La/PNu, and in relation to a different and deeper sensory groove, namely ioc. It is therefore a type of variation that occurs fairly widely in *Bothriolepis*.

The interpretation advanced below owes much to various papers on the development of the bones of the skull-roof of mammals, particularly one by Pritchard, Scott & Girgis (1956). In *Bothriolepis* the sensory lines have left grooves on the external surface of the bones, which indicates that both structures were on much the same horizontal plane. Also in juvenile specimens the sensory grooves extend relatively deeply into the surface of the bone, indicating that the horizontal lamellae were at first quite thin as compared with the depth of the sensory gutters. The crucial stage would have been when the young bones were still separated by areas devoid of bone, as indicated in figure 30*b*. In typical specimens the relation of sensory line to bone would have been simple; the bone La, extending by accretionary growth, would have advanced at the same rate on either side of csl, as also would have been the case with Nu. Where the two bones met the suture would have passed straight across the sensory line in the usual way. If however for any reason the advance of either bone became out of phase on the two sides of the sensory gutter, then it is suggested that the advancing periosteal front would have been prevented

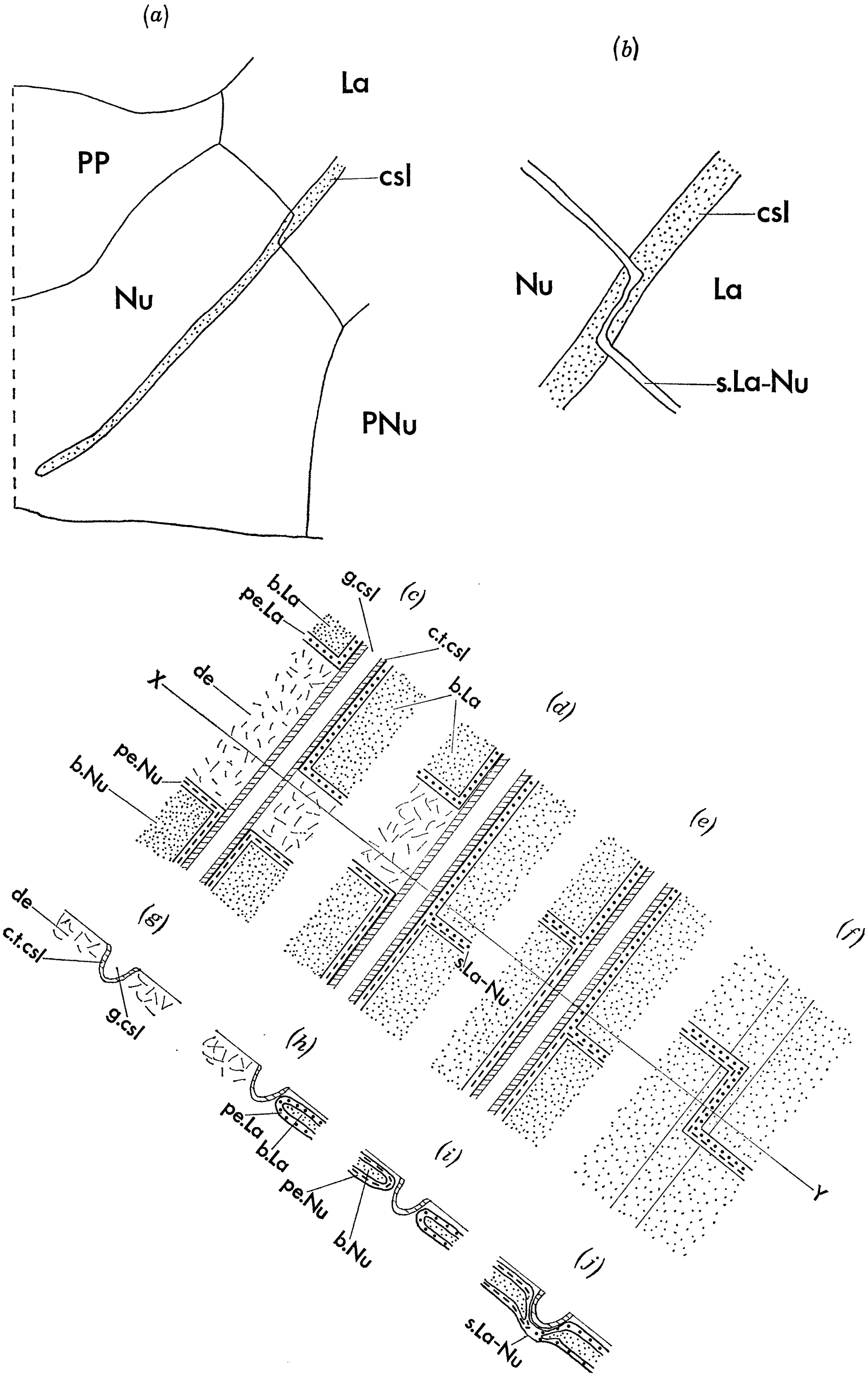


FIGURE 37. *Bothriolepis canadensis* Whiteaves, B.M. P.52093, showing unusual relation between the central sensory line groove and the suture separating the lateral and nuchal plates. (*a*) outline of relevant area. (*b*) enlarged outline of the critical area. (*c*)–(*j*) postulated development orientated as in (*a*) and (*b*), and also as in figures 13 and 14, plate 3, so that (*c*)–(*f*) can be compared directly with (*b*); for explanation see text.

from growing across and reducing the discrepancy by the presence of the gutter. The periosteal connective tissue would in a sense have been guided or channelled by the sensory line connective tissue, and the bone lamella would therefore have advanced as separate portions on either side of it. This discrepancy is shown schematically as regards La in figure 37*c*. The continued growth, as visualized, is shown in figure 37*d*, *e* and *f*, and by schematic transverse sections (*g*, *h*, *i*, *j*) through the crucial XY area. La and Nu will meet one another in different positions on the two sides of the sensory gutter; when eventually the bones grow deep to the gutter they will meet one another below it, and will form a suture which runs midway along its length (figure 14) for the extent of the discrepancy and then reverts to its normal course.

This interpretation implies that a sensory line may in certain circumstances channel the course of advancing bone lamellae in such a way that the suture eventually formed between them is caused to follow the same course as the sensory line, and this can occur even though the sutures and the sensory lines normally grow at right angles to one another.

4. COMMENTS ON THE LATERO-SENSORY LINES OF PLACODERMS

Since *Bothriolepis* is an antiarch and antiarchs are specialized placoderms, it may be useful to consider to what extent the conclusions reached in the previous section are more widely applicable. The material used has been drawn from the numerous recent descriptions of placoderms and selected because they appear to be relevant in this context; these comments are therefore in no way comprehensive. It has been assumed that arthrodires, which form a central group within the placoderms, can be regarded as comprising two large and rather indefinite groups, the dolichothoracids and brachythoracids. Of these, the former extended further back into geological time and were the more generalized. The figures (38–44) are regarded as largely self-explanatory, and the text merely comments on the relevant features they are believed to display.

Figure 38*b* represents in outline a generalized dolichothoracid skull-roof. Small dotted circles have been drawn round the centres of radiation of the bones; these are regarded as equivalent to the similar circles in figures 30*c* and 34. Groove ioc was relatively deep and may have been morphogenetic. Grooves soc and csl were also rather deep, whereas mp and pp were open and shallow. Ørvig (1971) has pointed out that the depths of the sensory lines of placoderms are not rigidly maintained; they tend to grade as between shallow and deep along various portions of their courses.

The positions of the sensory grooves on the central plate (Ce) are interesting. The ends of csl, mp and pp are grouped round the approximate centre of radiation of this bone. It is clear that not more than one terminated at or crossed the precise centre of radiation, for then they would have met one another at that point; it is probable that all three terminated merely in its vicinity. It follows that, at least as regards Ce, they were not morphogenetic. The pattern suggests that these sensory lines became anchored to rudiment Ce at an early stage in skeletogenesis, as indicated in figure 39*b*, this figure bearing the same relation to 38*b* as does figure 30*a* to 30*c*. Thus anchorage again seems to have been important in determining the courses of non-morphogenetic sensory lines; in this case however a single paired rudiment provided anchorage for three sensory lines as compared with, usually, only one in *Bothriolepis*.

The positions of the bones of the skull-roof of dolichothoracids is on the whole very uniform. However Denison (1958) has shown that in *Aethaspis* Nu extends exceptionally far forwards;

in *A. ohioensis* Denison it meets PtO, so excluding Ce from contact with PrO. In figure 38*a* an outline of this skull-roof has been superimposed on that of a typical dolichothoracid, using the front of PrO and the opening of the ductus endolymphaticus to establish common base-lines. In *A. ohioensis* the centre of radiation of Ce is farther back by more than 10 % of the length of the skull-roof, and the point of interest is that in this species of *Aethaspis*, csl does not approach this centre of radiation. It seems likely that the bone rudiment Ce formed too far back for the juvenile line to become anchored to it (figure 39*a*); if anchorage had occurred then the line would have been drawn back to this more posterior position. Instead it apparently came to assume the status of an unattached sector which grew for some distance in more or less the usual direction.

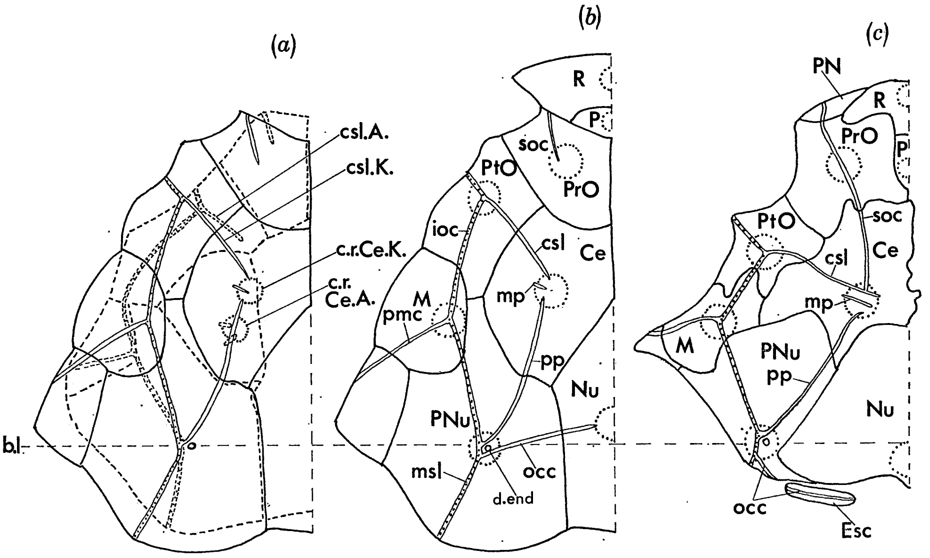


FIGURE 38. Outlines of arthrodire head-shields. (*a*) *Kujdanowiaspis* (continuous lines) superimposed on *Aethaspis ohioensis* Denison (discontinuous lines – after Denison 1960, fig. 143). (*b*) the dolichothoracid *Kujdanowiapsis*, after Stensiö 1963, fig. 43*a*, but with the commissural line added and without separate postnasals (see p. 30). (*c*) the brachythoracid *Coccosteus cuspidatus* Miller ex Ag., After Miles & Westoll 1968, fig. 1*b*.

In dolichothoracids soc does not usually extend farther back than the central region of PrO (figure 38*b*), but in brachythoracids it normally reaches the centre of radiation of Ce. It has therefore taken up a position along the other three sensory lines anchored to Ce, though, as might be expected, it typically terminates a short distance in front of these. This is shown in figure 40*a*. It is also shown in principle in figure 38*c*; here however csl has extended further mesially and soc has united with it, forming an inverted T-shaped junction. It is suggested that in dolichothoracids there was often a loose end of soc extending backwards some little distance beyond its anchorage to rudiment PrO, and that in brachythoracids it came to overlie and become anchored to the anterior portion of rudiment Ce, as indicated in figure 39*c*; this would in due course draw it to a position a short distance in front of the centre of radiation of that bone. On this interpretation a loose end has in the course of phylogeny been converted into an attached sector. Miles (1962) is relevant in this context. It may also be noted that with a slightly different ontogenetic pattern the loose end of soc could become anchored instead to PtO; this could account for the occurrence of a 'profundus' groove in some dolichothoracids.

Stensiö (1963) has illustrated numerous brachythoracids (see figure 40*a*) in which the relation of the sensory grooves is essentially of this type. In a few cases the tips of soc (figure 40*b*), or of both soc and csl, lie at an angle to the rest of the line; these may imply that loose ends extending beyond points of anchorage had 'drifted' into positions that were out of alignment with the main part of the sensory line. The sensory grooves of *Coccosteus* and allied genera have recently been studied in some detail. Miles & Westoll (1968, p. 456) have found in *Coccosteus cuspidatus* Miller ex Agassiz instances in which mp extends laterally onto PtO (figure 40*c*) so that it runs into, or almost into csl; they consider that it usually had this course, but its lateral portion was often too superficial to leave a groove on the bone. They also note that in a few cases mp turned towards bone M and would probably have passed to it if the full course were seen. Also in the only known specimen of the allied genus *Rhachiosteus* Miles (1966*a*) has shown

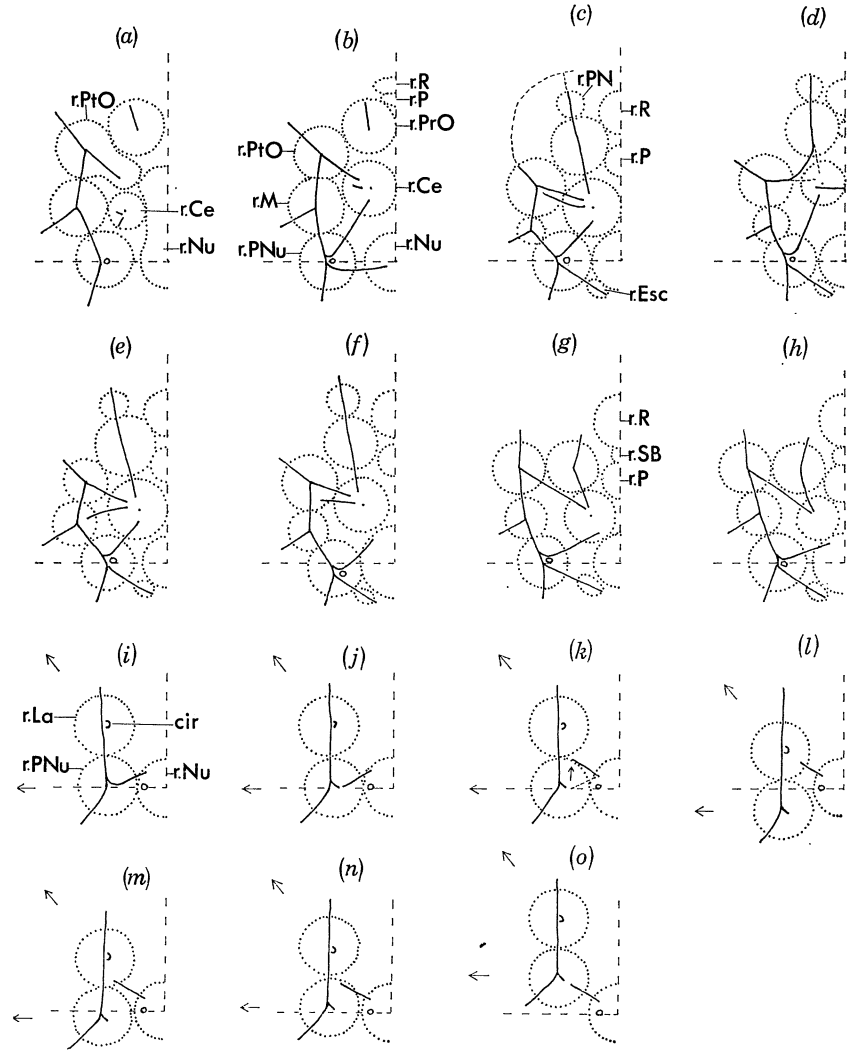


FIGURE 39. Postulated ontogenetic patterns in some arthrodires and antiarchs at about the beginning of skeletogenesis. The figures that show the equivalent mature forms are indicated by the numbers in brackets. (*a*) *Aethaspis ohioensis* Denison (fig. 38*a*). (*b*) typical dolichothoracid (38*b*). (*c*) typical brachythoracid (38*c*). (*d*) a variation of the brachythoracid *Pholidosteus* (41). (*e*) brachythoracid (posterior pit-line as in continuous line of 42*a*). (*f*) brachythoracid (posterior pit-line as in discontinuous line of 42*a*). (*g*) *Holonema* (posterior pit-line as in continuous line of 42*b*). (*h*) *Holonema* (posterior pit-line as in discontinuous line of 42*b*). (*i*) asterolepiform (42*c*). (*j*) asterolepiform, with postulated break in posterior pit-line. (*k*) postulated movement of distal part of posterior pit-line rudiment indicated by arrow. (*l*), (*m*), (*n*), (*o*) bothriolepiforms, showing some postulated different relative positions of rudiments (see text).

that mp definitely passed onto M. It follows that mp probably included an attached sector; also at its lateral end it could be anchored to alternative bones, namely PtO and M, as indicated in figure 40*c*.

Miles & Westoll (1968) also found that in most specimens of *Coccosteus cuspidatus* soc forms an inverted T-shaped union with csl. In juvenile specimens the groove for csl can be seen to reach the middle line, where it forms an end-to-end union with its antimere; in effect, therefore, a single line passes right across the centrals. Judging from other arthrodires (see figure 40*a*) it seems likely that the anchorages were in approximately the positions marked by black dots in figure 40*c*; the extension of the lines beyond these points, indicated by transverse shading, would initially have been loose ends. Union between the ends of the csl antimeres would have led to the formation of a new attached sector.

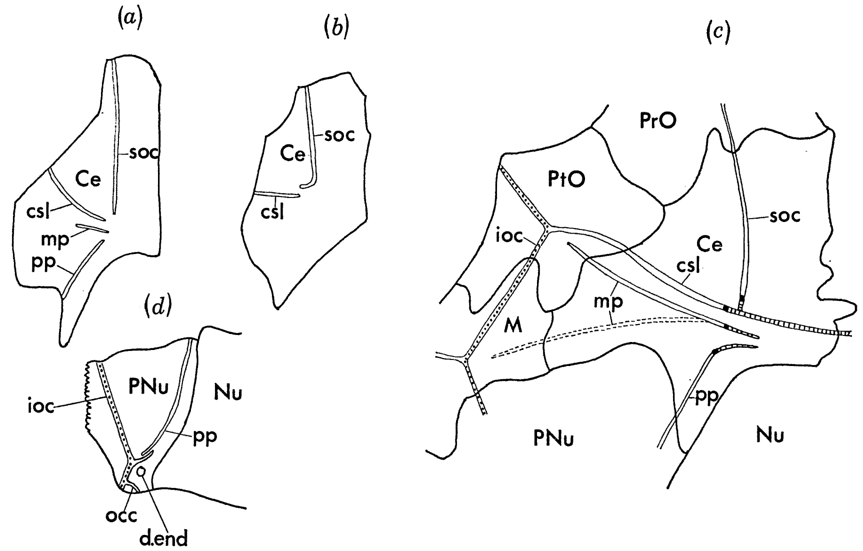


FIGURE 40. Variations in the superficial lines of brachythoracids. (*a*) left central plate of *Rhinosteus*, after Stensiö 1963, pl. 17, fig. 1. (*b*) left central plate of *Ottonosteus*, after Stensiö 1963, pl. 15, fig. 4. (*c*) schematic representation (see text) of sensory lines of *Coccosteus* and allied genera, mainly after Miles & Westoll 1963, fig. 1a; 1968, fig. 1b and after Miles 1966*a*. (*d*) paranuchal plate of *Dickosteus threiplandi* Miles & Westoll after Miles & Westoll 1963, fig. 2*a*.

Such unions may be important as regards phylogeny. Where two lines approach one another they may cease to grow further (note the two mp in figure 41) or they may form end-to-end, T-shaped or other unions, possibly as a result of a mutual tendency for lines to nose towards one another and unite (Bailey 1937). Restrictions on size and depth due to the need to bring loose ends to a termination will be removed when unions occur, for terminal ends will thereby be transformed into a locally continuous system. The neuromasts can then sink more deeply into the dermis, and can become housed in canals instead of in grooves, if (note Dijkgraff 1962) this is selectively advantageous. This does not seem to have occurred in the central region of *Coccosteus*, but may have done so in ptyctodonts. Here the sequence, both phyletic and ontogenetic, may have been, first, an extension of loose ends of soc and pp both towards one another and towards their fellows of the opposite side, resulting in more or less end-to-end unions where they mutually met at the middle line. Secondly, a sinking of this closed system more deeply into the tissues; consequently pp, which in most placoderms is shallow, and soc became housed in canals. Thirdly, the neuromasts would probably in these circumstances have induced latero-sensory ossicles which would have provided foci for the formation of the two Ce bones and also for the new bone that arose at the middle line where the four canals met. A series of changes of this kind could in principle proceed in either direction.

The beautiful variation of the brachythoracid *Pholidosteus friedeli* Jaekel illustrated by Stensiö (1963, pl. 5, fig. 2) is of great interest; I thank Dr Miles for first drawing my attention to it. The left side of the specimen (figure 41) shows the usual pattern. On the right side sensory lines soc and csl do not pass onto Ce; instead they have apparently joined end to end to form a single sensory line which sweeps round on a curved course between the central regions of PrO and PtO. The suggested explanation in terms of ontogeny is that neither the embryonic soc or csl reached and became anchored to rudiment Ce; instead they formed an end-to-end union at some point beyond its limits. Presumably through turning aside towards one another they deviated beyond its range. It is shown in this way in figure 39*d*; the postulated ontogenetic situation for the normal left soc and csl is indicated by discontinuous lines, and the united soc and csl of the right side, transposed to the left, by a continuous line. The result of this development was that two separate attached sectors, which could be represented as $\mathrm{PrO}\overset{\mathrm{soc}}{\text{—}}\mathrm{Ce}$ and $\mathrm{PtO}\overset{\mathrm{csl}}{\text{—}}\mathrm{Ce}$, has been replaced by a single new attached sector, $\mathrm{PrO}\overset{\mathrm{soc\ csl}}{\text{——}}\mathrm{PtO}$. However early in skeletogenesis this new sensory structure would not have passed directly between its points of attachment, but would have made a mesial detour that would have brought it close to rudiment Ce (figure 39*d*). During subsequent growth the points of attachment to PrO and PtO would have been drawn apart and the usual tensions, already discussed for *Bothriolepis*, would have tended to draw the sensory line into a straight course. The union between the two parts of the confluent line was strong enough to withstand this tension. Yield to the tension was partial and diffuse, as in c. 2 of figure 34, for in maturity the line did not pass straight between its two anchorages, but made a wide, gently-curved mesial diversion as it passed between them. It is in fact only the retention of this detour that clearly demonstrates the origin of this line.

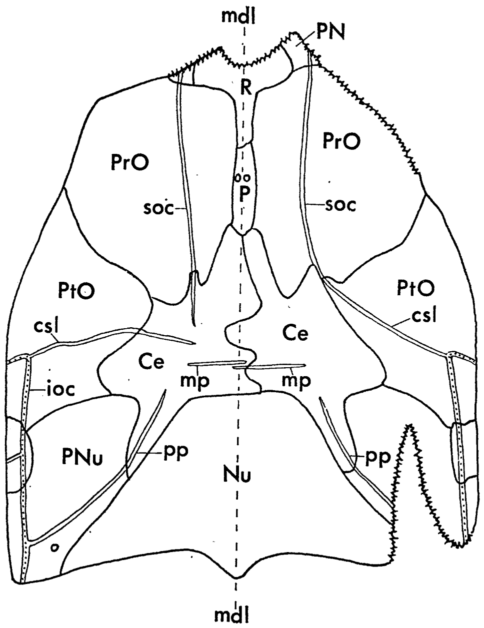


FIGURE 41. Variation of brachythoracid *Pholidosteus friedeli* Jaekel, after Stensiö 1963, pl. 5, fig. 2.

Miles (1971) has recently discussed the possible homologies and development of the bones covering the snout of *Holonema*. His interpretation is based on the assumption that a postnasal was present in dolichothoracids. However his observations seem to indicate that there is no satisfactory evidence for the existence of a postnasal bone in *Arctolepis*, and that this may apply also to *Kujdanowiaspis* and possibly to other dolichothoracids. In *Holonema* also there is no direct evidence for the existence of this bone. If there was in fact no postnasal in these forms, then much of the front of the snout would have been covered by the large median bone known as the rostral (R); soc could have extended forward from PrO as a loose end some distance onto it (figure 38*b*), as it is seen to do in *Holonema* (figure 42*b*). On the other hand in brachythoracids a postnasal bone (PN, figures 38*c*, 42*a*) is certainly present; soc passes across it, and beyond it forms a T-shaped junction with the anterior part of ioc. It is suggested that PN in brachythoracids originated as a new centre of ossification. The anterior end of soc became anchored to this rudiment, and was consequently drawn forwards during later growth; any further extension would have brought it into close proximity with ioc (figure 39*c*). This interpretation, which depends on the absence of PN in dolichothoracids, has the advantage of involving less complex types of change than are required by Miles; it would imply that in this region the bones of dolichothoracids and *Holonema* are similar to one another, except that in the latter there is a small anamestic bone, only partially differentiated into a separate entity, situated between the rostral and pineal bones.

As regards the back of the skull-roof, in figures 38 and 42 the bend in the main sensory line on PNu has been used to provide a common posterior base-line. In dolichothoracids the centre of radiation of PNu is placed fairly centrally within this bone; also, at least in *Actinolepis*, line occ passes (Gross 1940), across Nu towards its centre of radiation (figure 38*b*). In brachythoracids these centres of radiation are in much the same positions, but the posterior extensions of both bones are much reduced; also usually occ passes posteromesially, so reaching the posterior border of PNu and its groove is sometimes seen crossing a small paired bone (Esc) situated in the nuchal gap (figure 38*c*). Presumably therefore, as Miles & Westoll (1963, p. 146) have implied, there was a change in the relative positions of the ontogenetic units which led to line occ becoming anchored to rudiment Esc instead of Nu (figure 39*b* and *c*).

Variations in the course of the posterior pit-line (pp) are of interest. Its normal course in brachythoracids is shown in figure 38*c*. Ørvig (1971) cites various instances where a groove on PNu passes towards Nu, instead of towards Ce. He considers that this is due to a different sensory line, but he has not been able to find convincing evidence of both lines being present on the same side of the same specimen. To the present writer it seems more likely that they represent alternative courses of pp; usually the anteromesial end of the embryonic line becomes anchored to bone rudiment Ce, as in figure 39*e*, but occasionally to that of Nu instead, as in figure 39*f*. The normal course is shown by a continuous line in figure 42*a*, and the presumed alternative course by a broken line, though a relevant groove on Nu has not yet been observed. The case of *Holonema* (figure 42*b*) is very similar; pp usually passes towards Ce, as has been shown very clearly by Miles (1971) in *H. westolli* Miles; however Obruchev (1932) figured an isolated PNu of *Holonema* in which the groove arched mesially towards Nu. Miles considers this to be an alternative course of pp; Ørvig again regards it as representing a separate sensory line. The same type of alternative ontogenesis is suggested (figure 39*g* and *h*). However, clearly more information is needed, and in particular, specimens showing grooves on Nu.

There are occasional specimens (e.g. Ørvig 1971, fig. 2*c*; Miles & Westoll 1963, fig. 2*a*; Miles

1966*b*, fig. 26, pl. 8; Miles 1971, figs. 29*a*, 30*b*) in which pp has the appearance of having separated into two parts which sometimes overlap (see, for example, figure 40*d*). Ørvig considers that each of these two portions represents one of the two branches of his pit-line complex. However it seems more likely that they arise either as a break-down in the continuity of the sensory line soon after it was formed, or through the failure of individual sensory units to locate one another and form unions in the usual way at the time when the sensory line was being constructed. Little displacement of the parts is involved, and since the disjunctions are fairly close to the centre of radiation of PNu, each part may have become anchored separately to the rudiment of that bone.

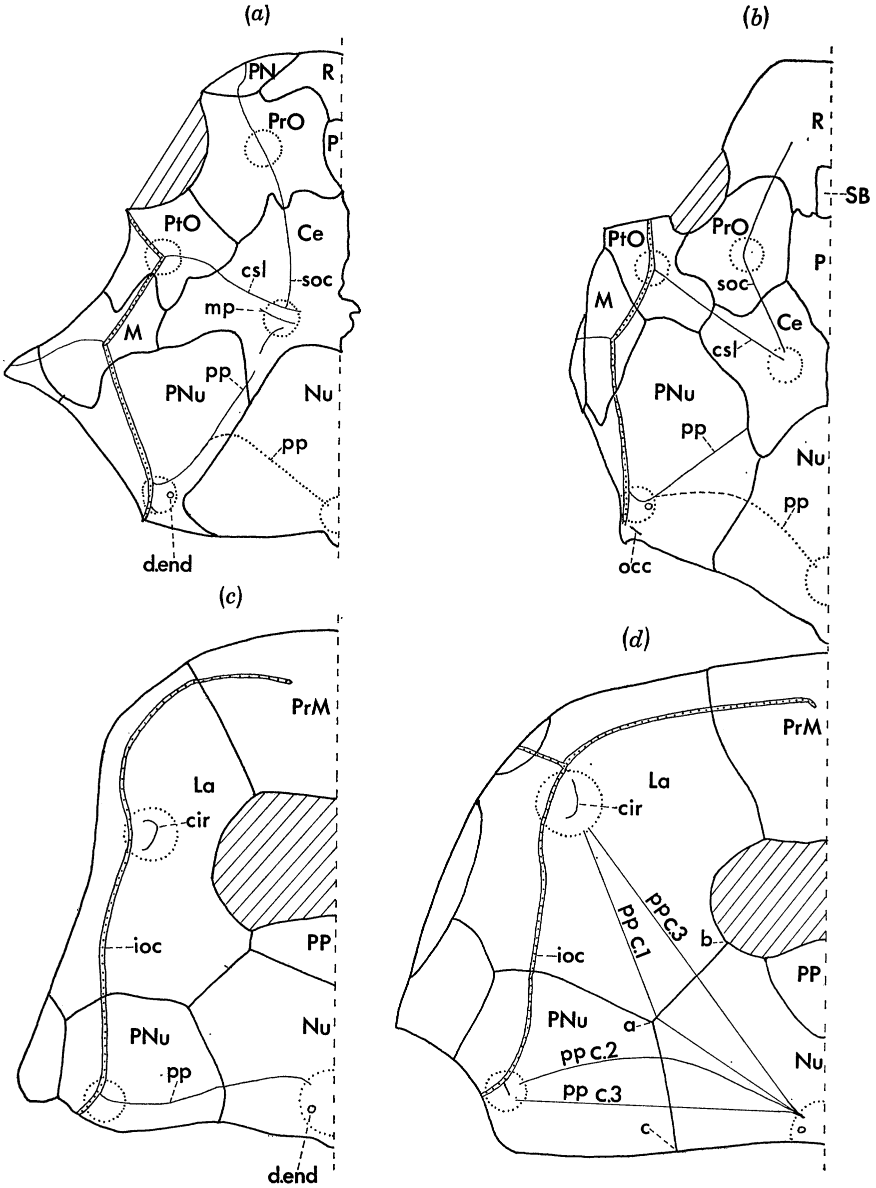


FIGURE 42. Various courses of the posterior pit-line. (*a*) typical brachythoracid and (*b*) *Holonema* after Miles 1971, fig. 4, both showing normal course of posterior pit-line towards central plate (continuous line), and alternative course towards nuchal plate (discontinuous line). The further course shown as a dotted line across the nuchal plate is conjectural. (*c*) asterolepiform, after Gross 1965, fig. 3*b*. (*d*) bothriolepiform, showing four alternative courses of what is here regarded as the posterior pit-line.

There is a close resemblance between the posterior part of the skull-roof of brachythoracids (figure 42*a* and *b*) and antiarchs (42*c* and *d*). Nu, PNu and the main and infraorbital sensory lines are comparable. The external opening of the ductus endolymphaticus is much nearer to the middle line in antiarchs. Further forward however their skull-roofs differ widely. The eyes of brachythoracids were at the sides of the head, those of antiarchs further back and near to the middle line; structures formerly lying between or a short distance behind the orbits have consequently been reduced or lost. PrO, and presumably also Ce, have been lost, and soc greatly reduced. Passing forward along the infraorbital line, PNu is followed in antiarchs by La; this may correspond to PtO of brachythoracids, M having been lost. A transverse sensory line, shown as pp in figure 42*c*, is present in asterolepiform antiarchs, but not in 'typical' specimens of bothriolepiforms. In these however there is instead the oblique sensory line usually referred to as csl. The only antiarch in which both these lines have been described as present is a specimen of *Asterolepis orcadensis* Watson (Watson 1932); however a re-examination of this specimen has indicated that the supposed oblique groove for csl may be merely a groove in the ornamentation.

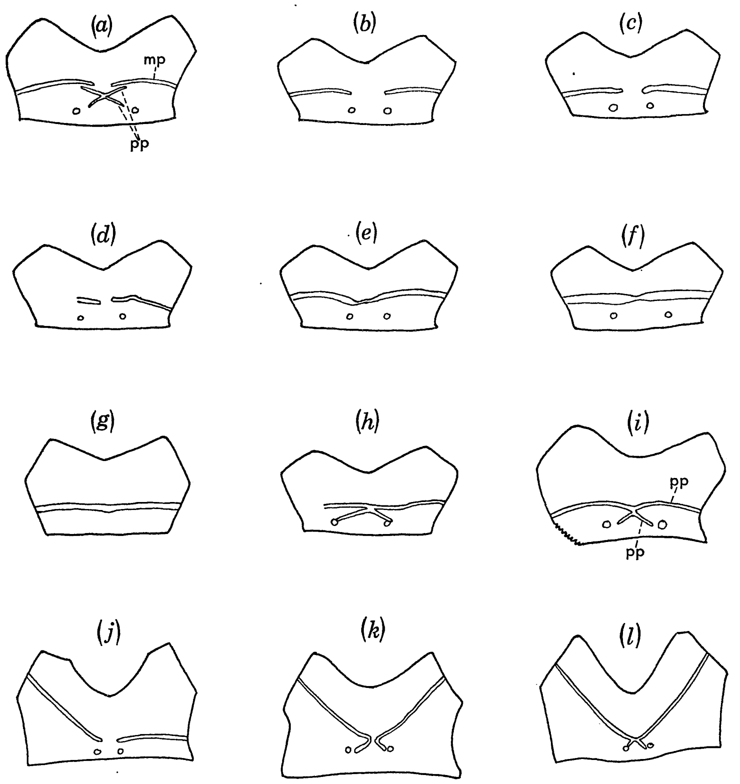


FIGURE 43. Nuchal plates of asterolepiforms and bothriolepiforms. (*a*) *Asterolepis säve-söderberghi*?, as interpreted by Stensiö, after Stensiö 1938, fig. 2. (*b*), (*c*), (*d*), (*e*), (*f*), (*h*) *Asterolepis ornata*, after Stensiö 1931, figs. 13*a*, *b*, *c*, *i*, *h*, *f* respectively. (*g*) *Remigolepis* after Stensiö, 1931, pl. 4, fig. 2. (*i*) *Asterolepis säve-söderberghi*?, after Stensio 1938, pl. 3, fig. 1, as interpreted here. (*j*) *Bothriolepis canadensis*, B.M. P.52084. (*k*) *Grossilepis tuberculata*, after Gross 1941, pl. 19, fig. 14. (*l*) *Bothriolepis groenlandica*, after Stensiö 1948, e.g. pl. 4, fig. 1.

The current views on the homologies of the sensory lines of antiarchs depend largely on Stensiö's (1947, 1948) works. He has stressed his view that a detached nuchal plate (Stensiö

1938, pl. 3, fig. 1) of probably *Asterolepis säve-söderberghi* Stensiö has a separate > shaped sensory line behind the transverse sensory line, as shown in figure 43*a*. This > shaped line, as also the similar grooves seen in many bothriolepiforms, he regards as equivalent to pp in brachythoracids. He regards the transverse sensory line as an mp, and as homologous with the very similar line seen on the right side of a specimen of *Bothriolepis* (figure 3*c*) here referred to as variation type 1. Stensiö thinks that in most specimens of *Bothriolepis* this mp is represented only by the short stump that diverges from the main line close to its bend on PNu. The line that passes from La to Nu in typical bothriolepiforms he refers to as csl, and he considers the peculiar short semi-circular groove cir to be an anterior extension of this line.

Stensiö (1931, 1948) has illustrated a number of nuchal plates of *Asterolepis ornata* Agassiz. The external ornamentation makes interpretation rather difficult. However it seems that the transverse groove may terminate some distance from the middle line (figure 43*b*), or may continue and thence make varying degrees of end-to-end union with its antimere (figure 43*c–f*). This tendency has reached completion in *Remigolepis*, where the grooves unite with virtually no constriction or alteration in their course (figure 43*g*). In some *A. ornata* the transverse line curls round on a > shaped course which brings it close to the external opening of the ductus endolymphaticus (figure 43*h*), and it probably makes contact with its antimere at the apex of the > . Judging from Stensiö's illustration, it seems that the isolated Nu of *A. säve-söderberghi* could also be interpreted in this way, as is indicated in figure 43*i*. It is suggested, therefore, that in asterolepiforms this transverse line became anchored to Nu at a point corresponding to its termination in figure 43*b*. In such individuals there would have been little or no loose end. In others there were loose ends with variable courses; they might pass towards, or reach, or unite with their antimeres and might also curl round towards the opening of the ductus endolymphaticus. In bothriolepiforms the situation was similar in principle. The line referred to as csl often terminated on Nu a short distance from the middle line (figure 43*j*); alternatively it might be continued by curling round to or near to the opening of the ductus (figure 43*k*), as is seen well in some of Gross's (1941) illustrations; or it might both meet its antimere and curl round (figure 43*l*), as shown particularly in Stensiö's (1948) illustrations of *B. groenlandica*.

Figure 42 shows that pp joins the main sensory line in brachythoracids at about the same position as the transverse line, here also designated pp, joins it in asterolepiforms; in both cases the union is at about the centre of radiation of PNu. This drawing also shows that the less usual presumed alternative course of pp in brachythoracids, and particularly in *Holonema*, is similar in principle to that of this transverse line in asterolepiforms. It is therefore suggested that the latter is a posterior pit-line which has become anchored to Nu, instead of to Ce as in most brachythoracids. Some change would in any case have been required owing to the loss of Ce during antiarch phylogeny. The ontogenetic pattern (figure 39*i*) would have resembled that of brachythoracid variations (figure 39*f* and *h*), but would have been without a Ce rudiment. Again the position of the anchorage would have been expected to be in the anterolateral region of the Nu rudiment.

In asterolepiforms this pp is orientated transversely, and its lateral end is connected to the main sensory line. On the other hand in bothriolepiforms there is usually no transverse line, but instead a more superficial line which is orientated obliquely so passing to La instead of PNu; it stops a short distance from the centre of radiation of La, and does not unite with ioc. Since both these lines pass to about the same position on Nu, and since both have a similar range of varied endings, they probably demonstrate alternative courses of the same sensory line, namely the posterior pit-line. Comparison with brachythoracids indicates that the asterolepiform condition was the more primitive. The transition to a bothriolepiform one could have taken place in two stages. In the first an asterolepiform type of pp would have become more superficial, and would have lost its connection with the main sensory line. This separation seems to have occurred a short distance from the main sensory line, as indicated in figure 39*j*. This would have been approximately the position at which the brachythoracid pp was sometimes disunited (see for example, figure 40*d*). Disjunction at this point would have left a stump (i.e. mp, figures 1, 3) attached to the main sensory line.

The second stage would have been concerned with the transfer of this anchorage from PNu to La. The pattern of figure 39*j* would have led to an adult virtually identical with the more extreme forms of variation type 1. However it does not provide a model that can easily be modified to account for more typical specimens of *Bothriolepis*. It is therefore suggested, somewhat arbitrarily, that after detachment the main portion of the embryonic pp swung round in the manner indicated in figure 39*k*. This would have brought it to a course that corresponded with the primary orientation postulated earlier (p. 18); it would also have directed it to a position more or less intermediate between rudiments La and PNu. Small changes in the positions of these rudiments, relative to that of Nu and of the juvenile pp, would account for many of the observed courses. In figure 39*l* the La-PNu-ioc complex is shown relatively further back; this will lead to pp c. 3 (figure 42*d*). If these rudiments are slightly further forward (figure 39*m*), and there is no yield, one would expect an adult with the angulated course pp c. 1; if there was complete yield the course would be indistinguishable from the previous pp c. 3. Figure 39*n*, with these rudiments again further forward, would with slight yield result in the pp c. 2 form of variation type 1. Figure 39*o*, where they are still further forward, would lead to variation type 1 with a pp c. 3 course; this would bring the detached portion of pp very close to its original stump.

This short groove or stump is seen clearly in many specimens of *Bothriolepis*, and also in *Grossilepis*. It is referred to by Gross (1941) as pp, and by Stensiö (1948) and by Miles (1968) as mp. It is interpreted above as a stump of pp still attached to the main sensory line. This groove does not seem to have been described in asterolepiforms; in these, pp has not become disjointed, so the absence of the stump provides negative evidence that supports the interpretation.

One feature of this analysis is that it gives a definite indication of the direction of the change in question. There presumably was a stage early in bothriolepiform phylogeny when pp was attached to PNu in all the individuals; in other words, 100 % of the population would have approximated to the variation type 1 condition, and 0 % would have been 'typical'. It has been shown that in *B. canadensis* there were about 1 % variation type 1 and 99 % 'typical'. A problem, then, would be to account for this quantitative shift. At the time when the Scaumenac beds were deposited the gene pool seems still to have covered a wide ontogenetic spectrum ranging, in terms of figure 39, from (*l*) to (*o*). A reversal of this phylogenetic trend towards the 'typical' condition could presumably still have occurred, if it had been selectively advantageous.

According to the above view the bothriolepiform sensory line that was previously regarded as csl is a pp instead. What then has become of the placoderm csl? The loss of Ce during antiarch phylogeny would have deprived csl, as well as pp, of its mesial anchorage. Line pp probably obtained compensating anchorage to Nu, but there is no evidence that csl obtained any similar alternative footing. It may instead have curled up on itself, so giving rise to cir; this could account for the shortness, breadth and crescentic form of this peculiar sensory groove; it could thus be comparable with the dlg_2 of figure 36*b*. It is relevant that groove cir is present in cases of variation type 1 (figures 3*d* and 7), for here pp (previously designated csl) has been drawn on a different course; it follows that cir is not an extension of this line, as Stensiö 1947 supposed, but is a separate unit. The presence of cir could, on this interpretation, also be expected in asterolepiforms, since in these a normal csl is likewise missing. Usually no such groove is seen, but Gross (1941, p. 11) states that cir is sometimes observed in *Asterolepis ornata*; he (1965, fig. 3*b*) also reproduces a figure by Karatajute-Talimaa (1960) of the asterolepiform *Byssacanthus dilatatus* (Eichw.) which shows this sensory groove; it is shown in figure 42*c*.

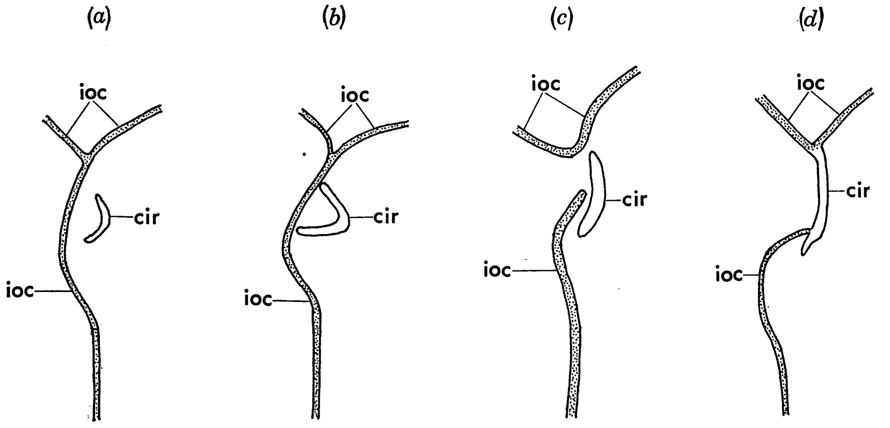


FIGURE 44. The relation of the semicircular pit-line groove to the infraorbital sensory groove. (*a*), (*b*), (*d*) *Bothriolepis cellulosa* (Pander) after Gross 1941, pl. 3, fig. 1, pl. 2, fig. 1. and pl. 4, fig. 6 respectively. (*c*) *Grossilepis tuberculata* (Gross), after Gross 1941, pl. 19, fig. 15.

Another feature of this sensory line, noted by Gross (1941) and Stensiö (1948), is indicated in figure 44. The typical pattern is shown in figure *a* and *b*; here cir apparently has no influence on ioc. In (*c*) there is a considerable gap in ioc just behind the position at which it branched; cir, which is aligned close by, may have had a disruptive effect on its formation. In (*d*) ioc again appears to have been disrupted, but in this case cir has become rather fully integrated into the gap, forming a full union with ioc anteriorly and a partial one posteriorly. It rather looks as if the presence of this latero-sensory element cir could on occasion influence and disturb the behaviour of the latero-sensory units from which ioc was normally constructed.

5. SUMMARY

Certain variations in the courses of two of the superficial sensory lines of *Bothriolepis* are described. Some of these have been briefly noted by earlier workers, but their significance has not been considered in detail.

These superficial sensory lines apparently resemble those of various other vertebrates in having been anchored to bone rudiments at an early stage in skeletogenesis. Later, with the accretionary growth of the bones, these sites grew away from one another. The anchorages therefore necessarily played an important part in determining the courses of the lines. The relatively large size of the bones in *Bothriolepis*, and the occurrence of anchorages both to alternative and to additional bone rudiments, has displayed this relationship unusually well. It has been found convenient to regard the sensory lines as composed of attached sectors that stretched

between points of anchorage and loose ends which extended beyond them; the attachment of a loose end to a bone rudiment resulted in an additional attached sector.

The tensions created by the divergence of anchorage sites, and the extent to which the bone yielded to these tensions, are considered, particularly in the light of the variations. The concept of the primary orientation of a sensory line has been employed.

In some instances a superficial sensory line has apparently limited the spread of the growing bone lamellae in such a way that for a short stretch the suture between adjacent bones follows the course of the sensory line.

Some features of the sensory lines of other placoderms are viewed in the light of the inferences derived from *Bothriolepis*. A rudiment of each central plate probably gave anchorage to three sensory lines in dolichothoracids, and to four in brachythoracids. Some postulated patterns of ontogeny which could have given rise to various observed patterns in maturity are considered both in *Bothriolepis* and in other placoderms, partly with reference to their possible phyletic significance. The significance of unions between sensory lines is similarly considered.

Some variations in the posterior pit-line of brachythoracids suggests a failure of some of the separate units to link together initially to form a sensory line, or alternatively later to maintain it. The semicircular sensory line of *Bothriolepis* may have been derived from the central sensory line of arthrodires as a result of the loss of one of the anchorages by which it had previously been extended. The proximity of this semicircular line to the infraorbital line seems sometimes to have disrupted the normal formation of the latter.

Some evidence suggests that the 'central sensory line' of *Bothriolepis* is derived from the posterior pit-line of arthrodires. The 'middle pit-line' may be a stump of this posterior pit-line which has remained joined to the main sensory line.

I am grateful to the authorities in charge of a number of institutions in North America for an opportunity to examine material in their charge in 1937, and in particular to the New York State Museum, Albany, for the loan of three important specimens of *Bothriolepis*. At a more recent date I am indebted to Dr R. B. Wilson, Institute of Geological Sciences, Scotland, for an opportunity to examine a specimen of *Asterolepis*, and to Dr C. D. Waterston and his staff at the Royal Scottish Museum for opportunities to examine material and for their kindness in photographing certain specimens. At the British Museum (Natural History) I am particularly indebted to Dr R. S. Miles for his constructive criticism of some earlier versions of my ideas and for guidance on important literature. Also crucial has been the advice so willingly given by Mr N. Wood, of Appleford, regarding photographic procedure. This work has required considerable time and effort, and not least I am grateful to my wife for her patience and understanding.

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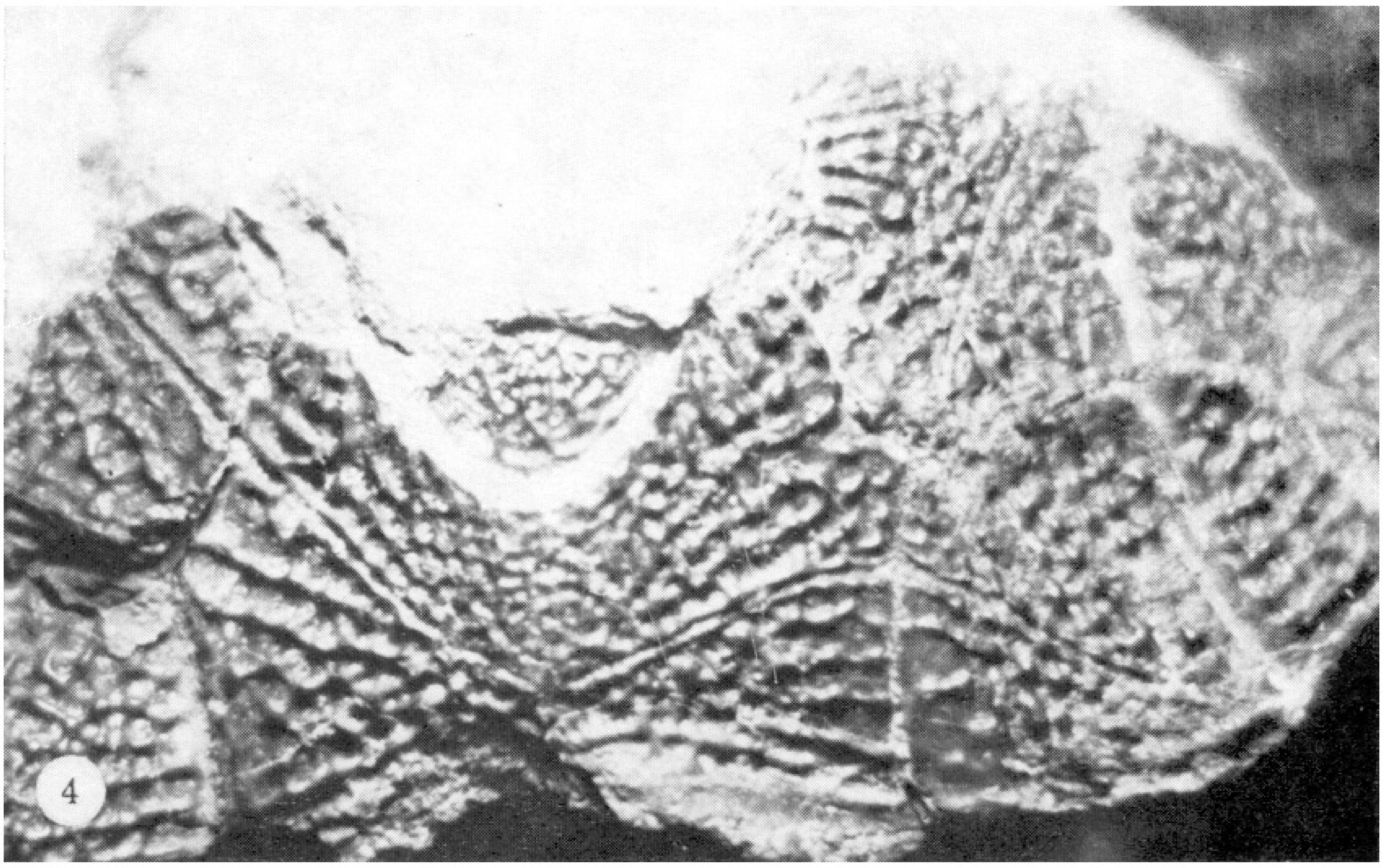
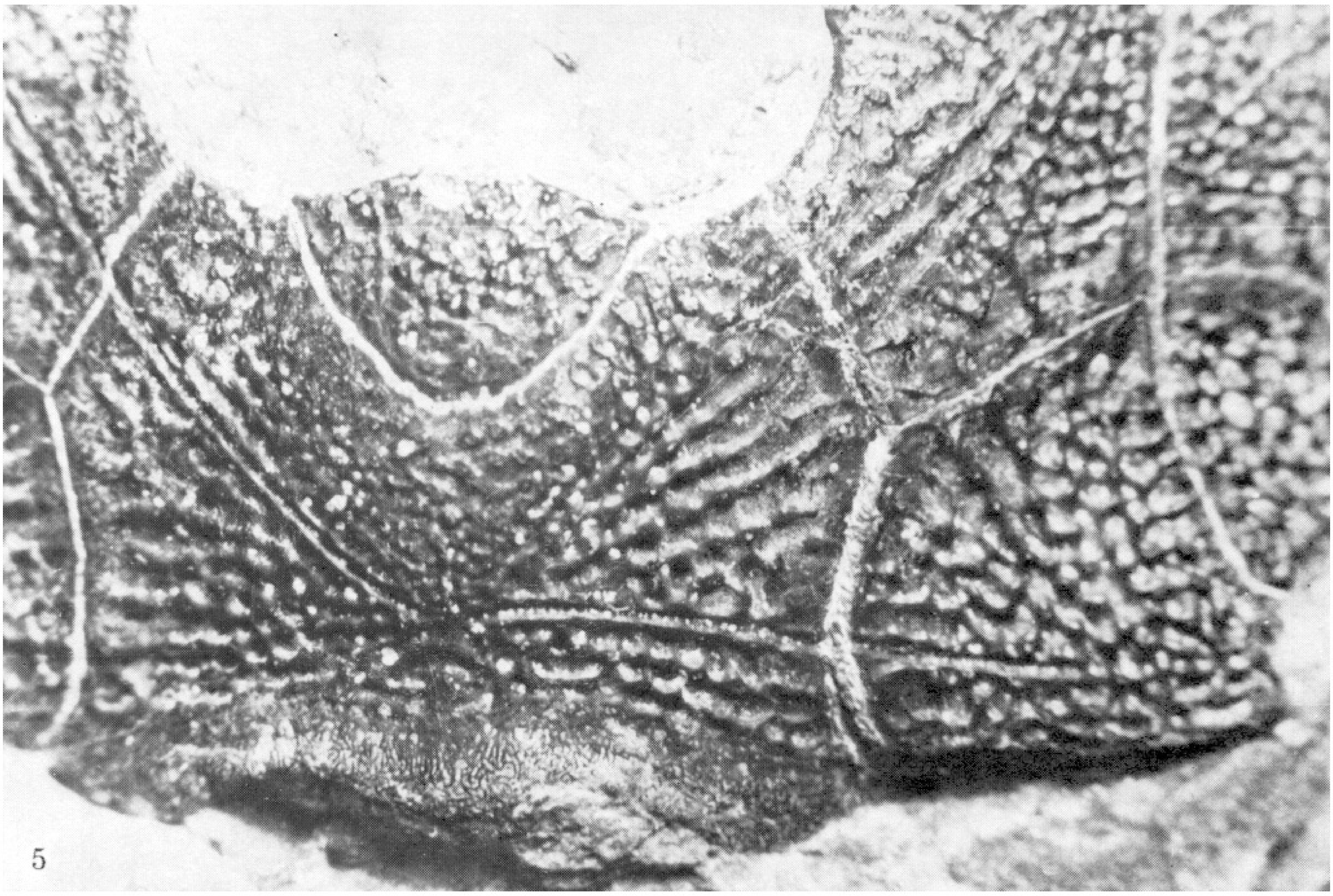
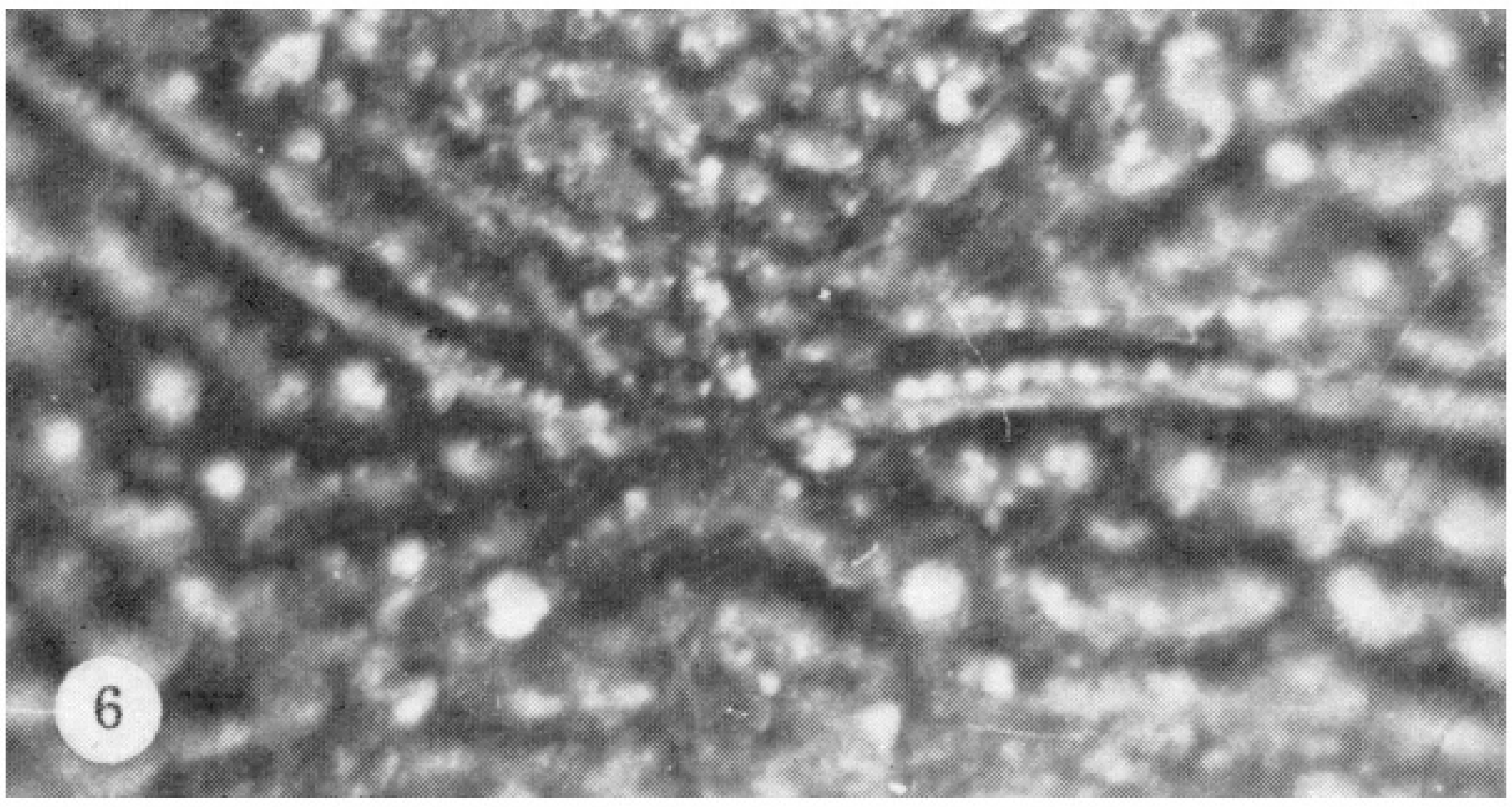
Abbreviations used in line drawings

ADL	anterior dorsolateral plate
AMD	anterior median dorsal plate
a	position at which sutures Nu/La, Nu/PNu and La/PNu meet
a.csl	accessory central sensory line groove
arc	postulated arc formed by advancing horizontal bone lamella
b	position at which Nu/La suture meets margin of orbit
b. l	base line
b.La	bone of lateral plate
b.Nu	bone of nuchal plate
Ce	central plate
c	position at which Nu/PNu suture reaches posterior margin of external ornamentation, and at which AMD/ADL suture reaches anterior margin of trunk
c. 1, c. 2, c. 3	some possible alternative courses of central sensory line
cir	semicircular pit-line groove
c.r.Ce.A.	centre of radiation of Ce of *Aethaspis*
c.r.Ce.K.	centre of radiation of Ce of *Kujdanowiaspis*
csl	central sensory line or its groove
csl.A.	central sensory line groove of *Aethaspis*
csl.K.	central sensory line groove of *Kujdanowiaspis*
c.t.csl	connective tissue of central sensory line
d	position at which sutures AMD/ADL, ADL/MxL and AMD/MxL meet
de	dermis
d.end	external opening of ductus endolymphaticus
dlg$_2$	posterior oblique dorsal sensory line or its groove
dma	tergal angle
dmr	dorsal median ridge
Esc	extrascapular
e	position at which sutures AMD/MxL, MxL/PMD and AMD/PMD meet
f	position at which AMD/PMD suture crosses middle line
g.csl	groove for central sensory line
h.l.AMD	horizontal lamella of AMD or of other bone as indicated by abbreviation
ioc	infraorbital sensory line or its groove
La	lateral plate
M	marginal plate
MxL	mixilateral plate
mdl	middle line
mp	middle pit-line or its groove
msl	main sensory line or its groove
Nu	nuchal plate
occ	occipital cross-commissural line or its groove
P	pineal plate
PMD	posterior median dorsal plate
PN	postnasal plate

PNu	paranuchal plate
PP	postpineal plate
PrM	premedian plate
PrO	preorbital plate
PtO	postorbital plate
pe.La	periosteum of lateral plate
pe.Nu	periosteum of nuchal plate
pmc	postmarginal sensory line groove
pp	posterior pit-line or its groove
pp.c. 1 etc	possible alternative course of 'csl', here now regarded as the posterior pit-line.
prl	lateral process of PMD
R	rostral plate
r, s, t.	latero-sensory grooves in figure 35. See text
r.AMD	bone rudiment, or its presumed subsequent site at a later stage, of AMD, or of other equivalent bone as indicated
SB	supernumerary bone
s.La-Nu	suture between La and Nu in figure 37*j*
soc	supraorbital sensory line or its groove
x	position at which sensory line groove csl or dlg_2 crosses relevant suture







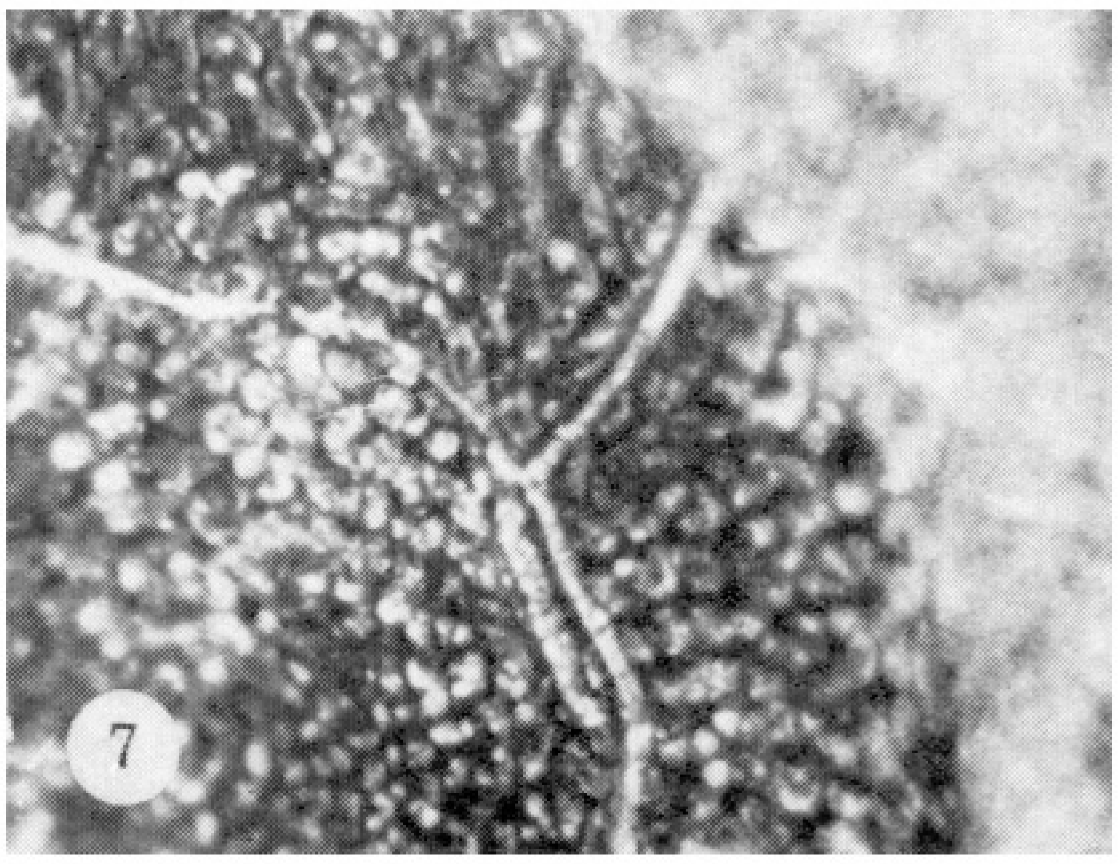
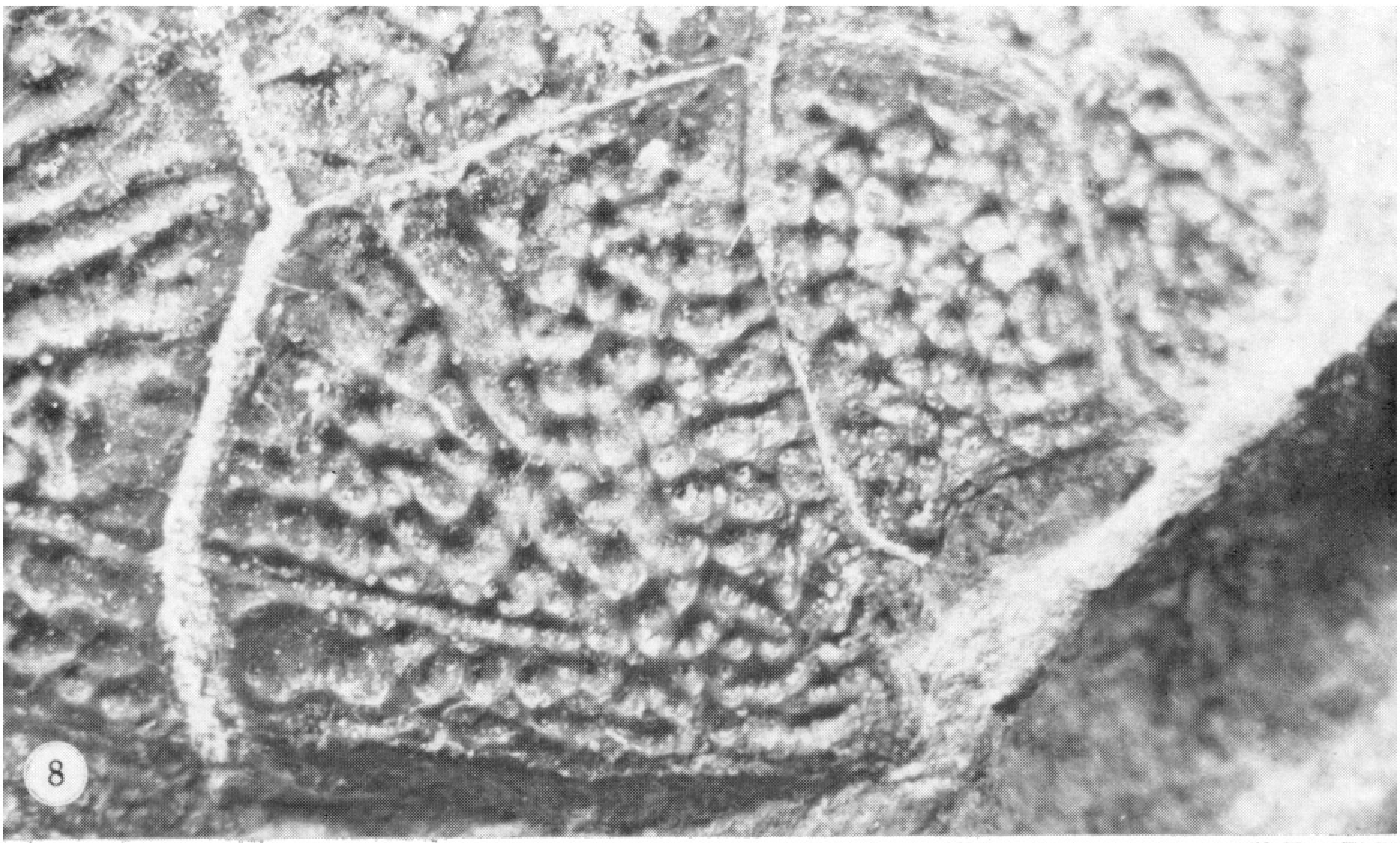


FIGURE 4. Posterior part of head-shield. B.M. P.52091 (magn. × 2).

FIGURE 5. Posterior part of head-shield. B.M. P.52084 (magn. × 3).

FIGURE 6. Central part of nuchal plate. B.M. P.52084 (magn. × 6).

FIGURE 7. Part of right lateral plate. B.M. P. 52084 (magn. $\times\frac{5}{2}$).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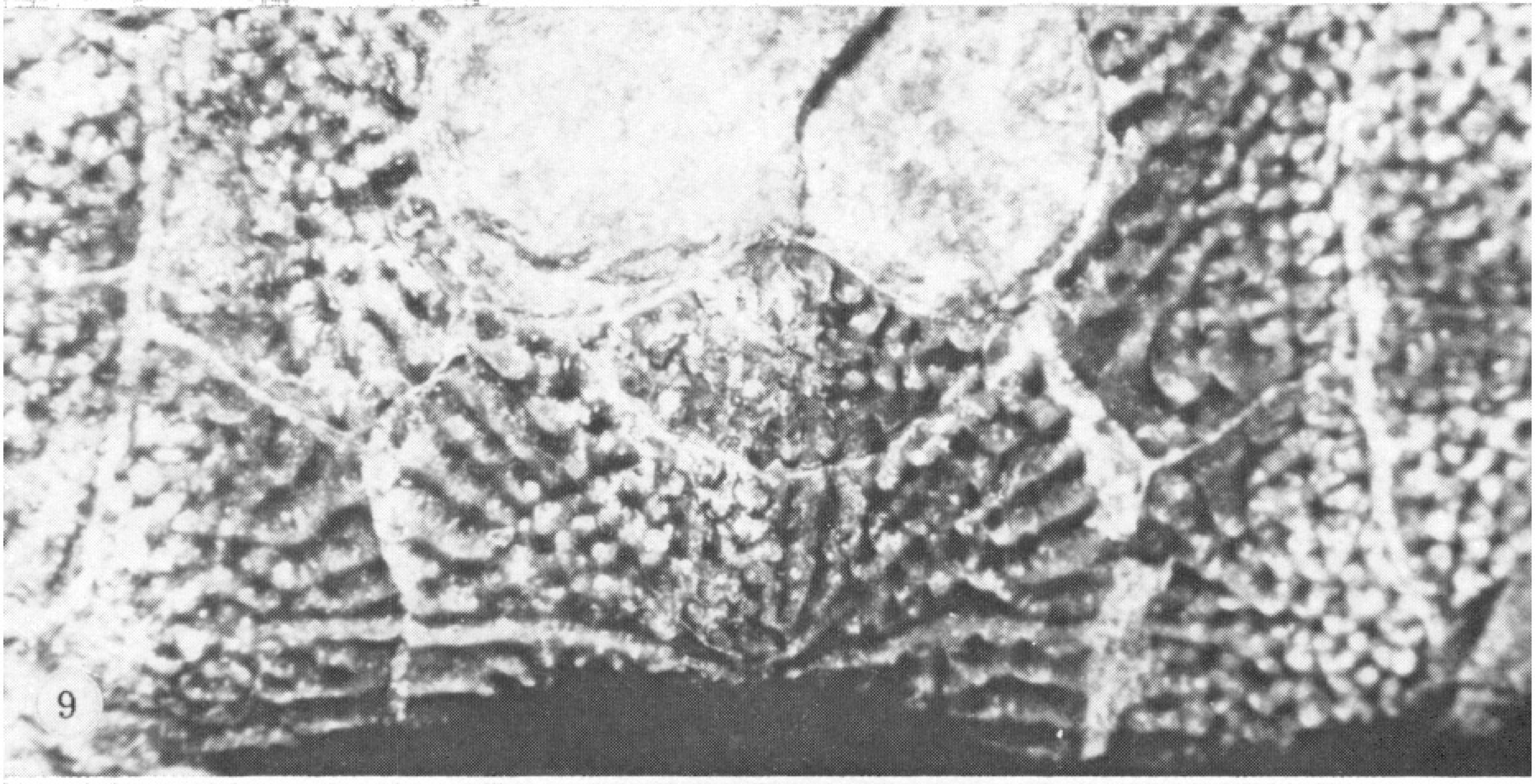
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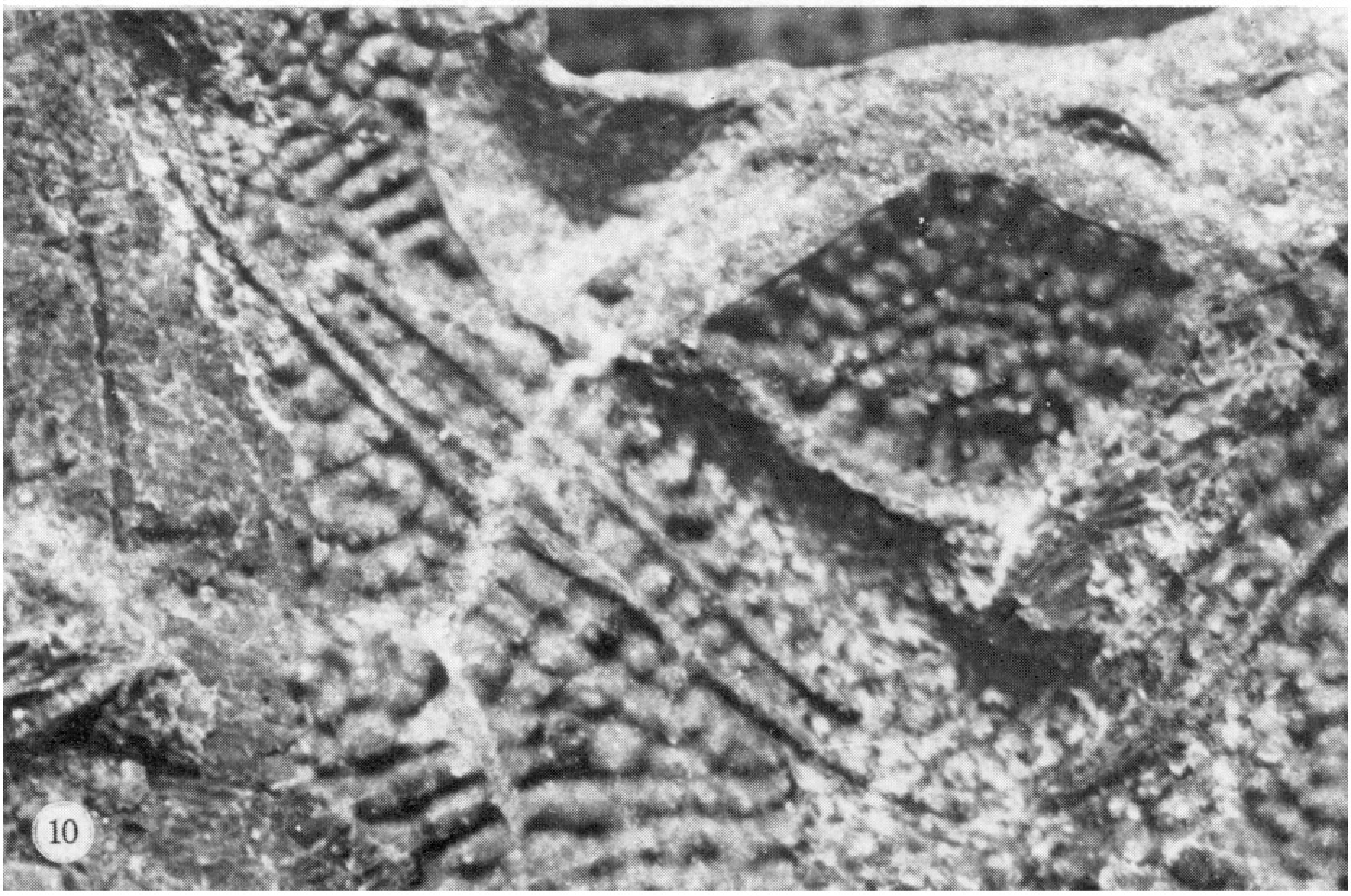
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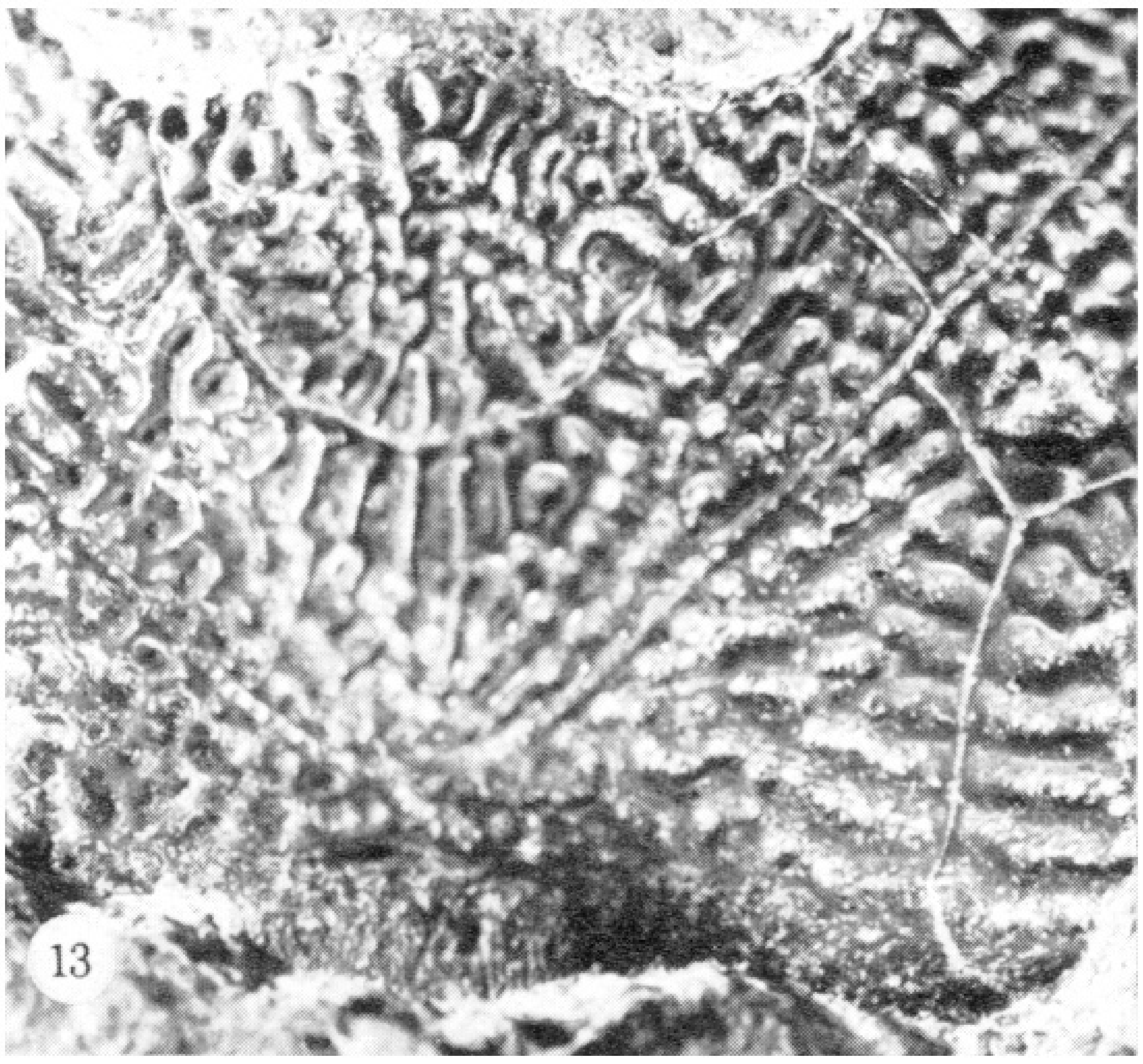
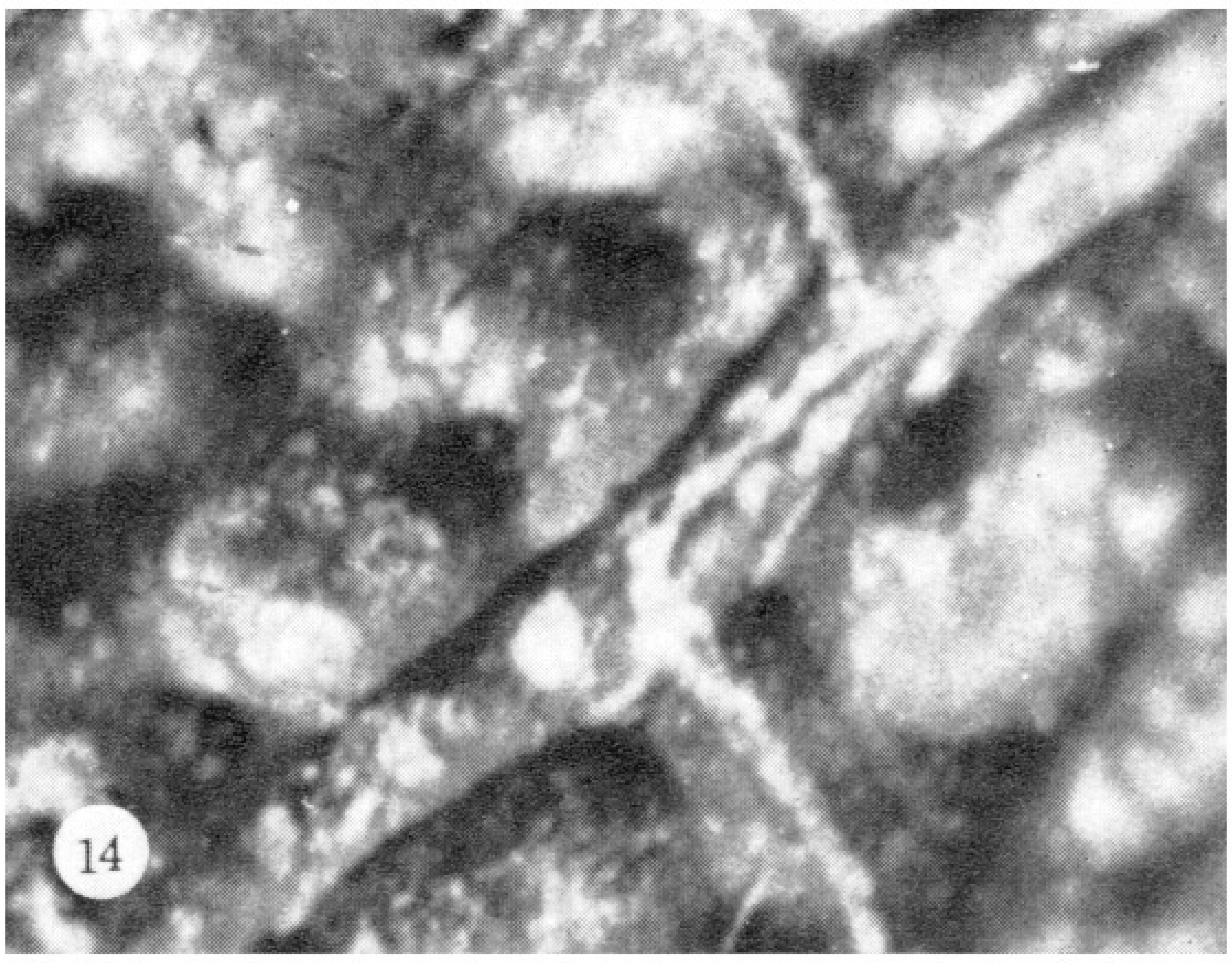
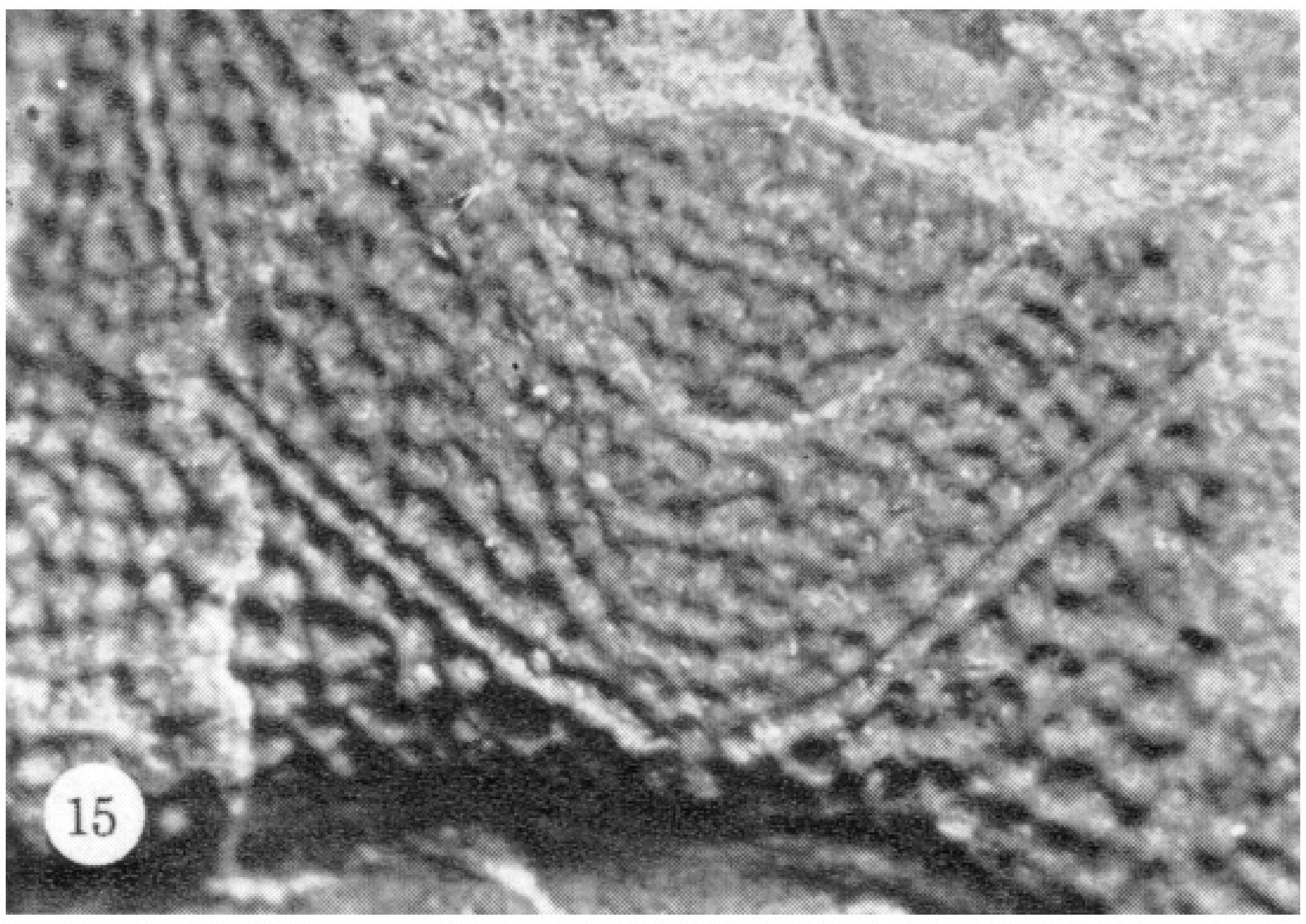
FIGURE 8. Right paranuchal plate. B.M. P. 52084 (magn. × 4).

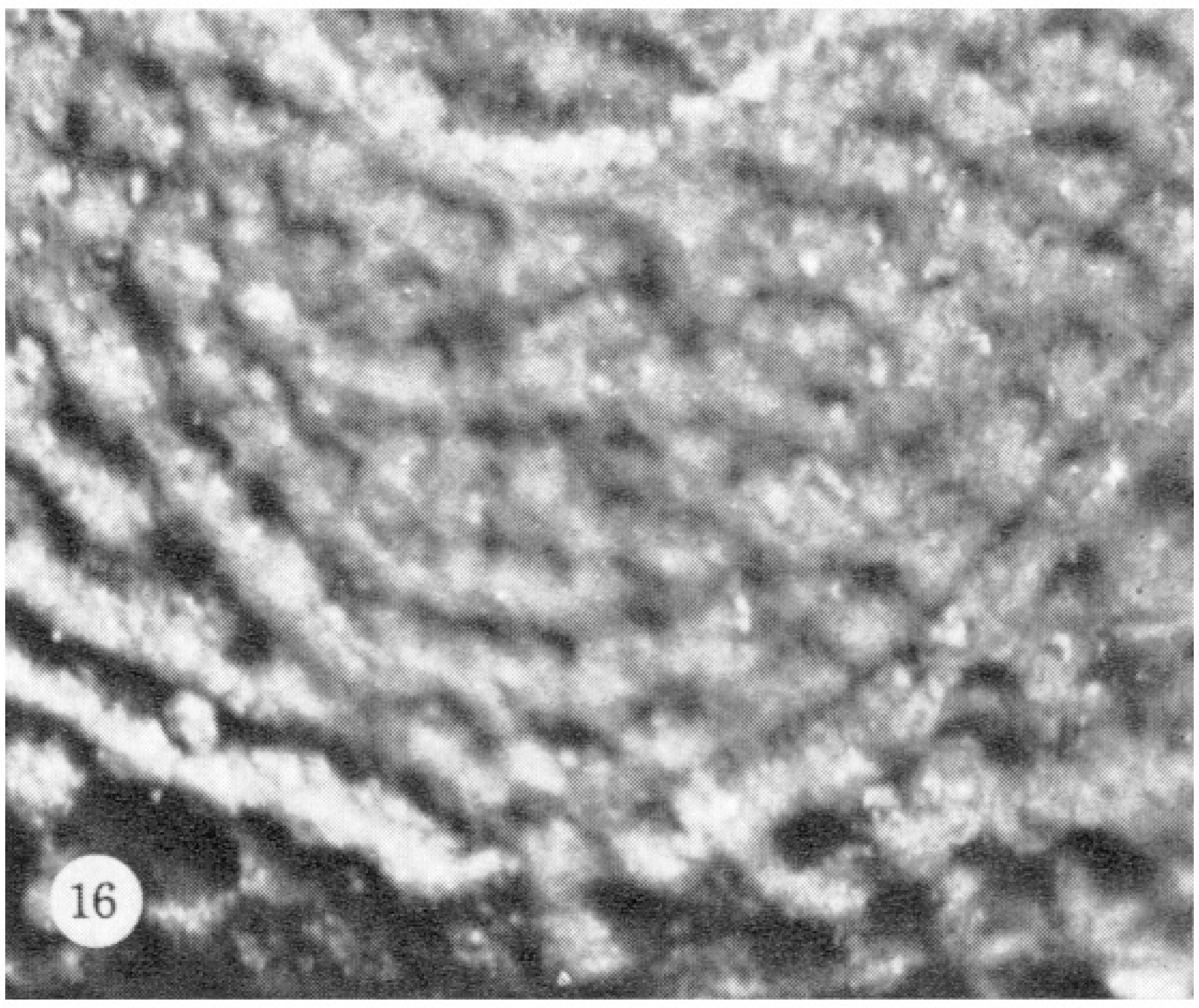
FIGURE 9. Posterior part of head-shield. B.M. P. 52109 (magn. × 5).

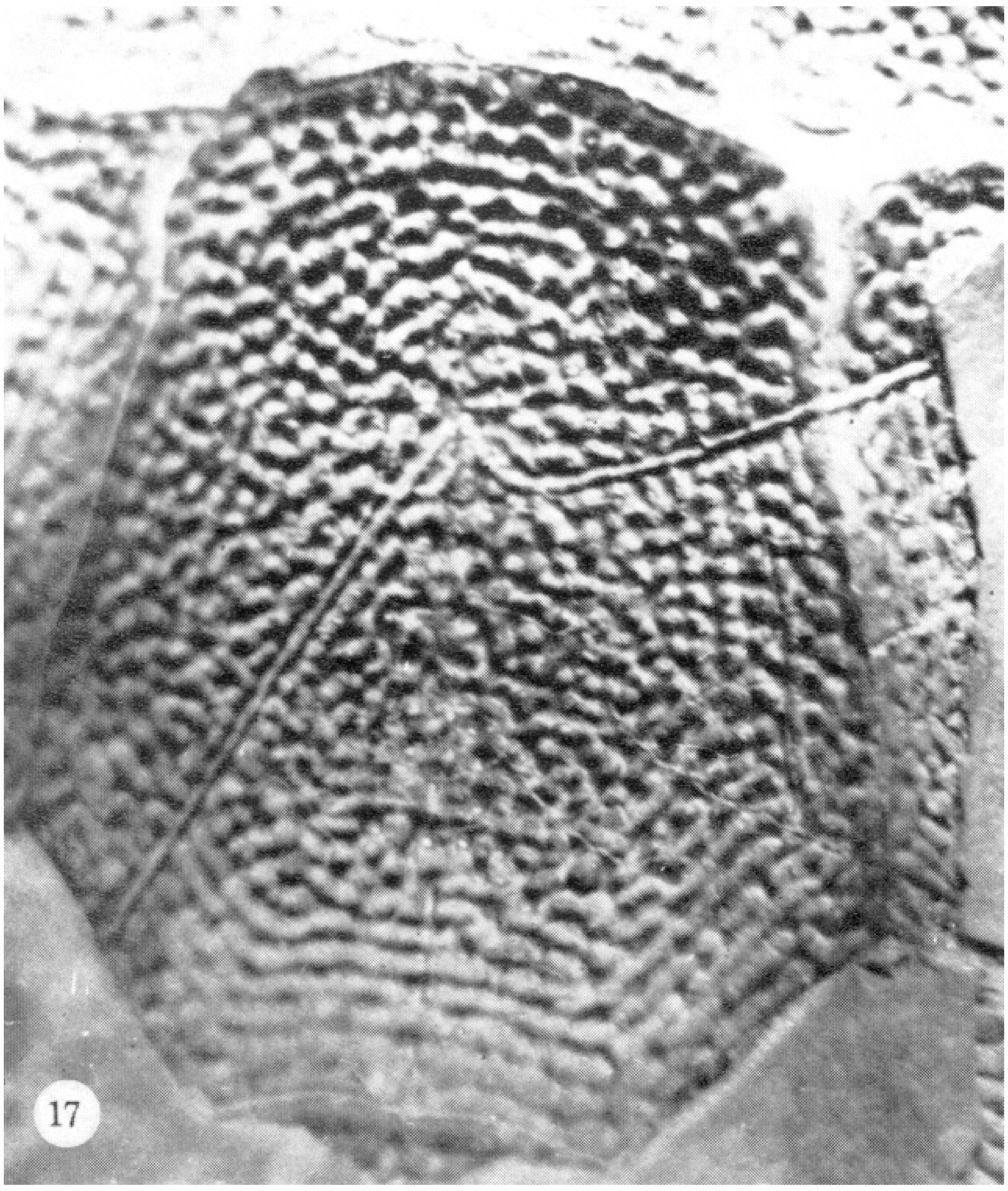
FIGURE 10. Impression of posterior part of head-shield. B.M. P. 52086 (magn. × $\frac{11}{2}$).











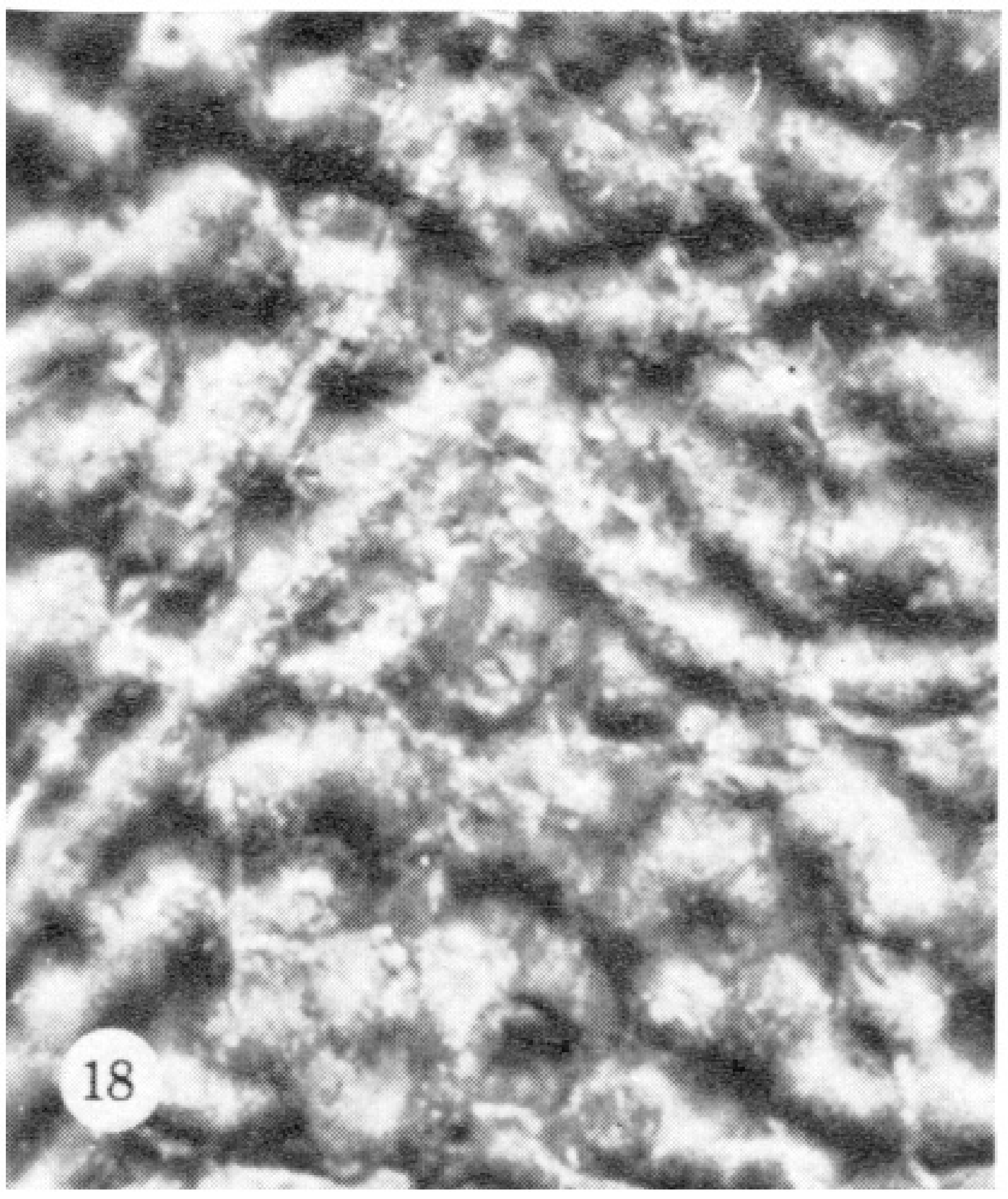


FIGURE 13. Part of head-shield. B.M. P. 52093 (magn. × 2).

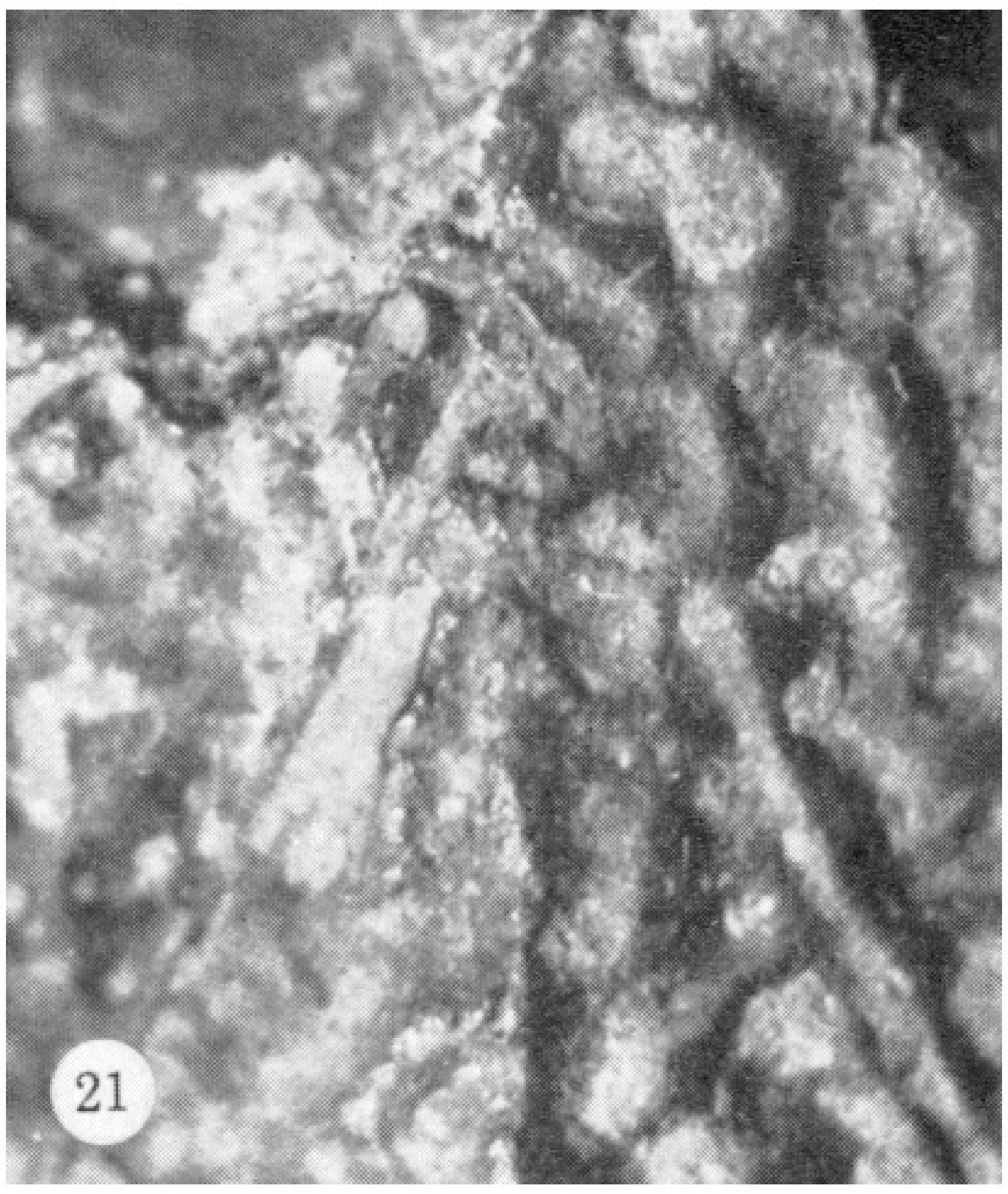
FIGURE 14. Part of nuchal and lateral plates. B.M. P. 52093 (magn. × 10).

FIGURE 15. Posterior part of head-shield. B.M. P. 52098 (magn. × 3).

FIGURE 16. Part of nuchal plate. B.M. P. 52098 (magn. × 7).

FIGURE 17. Anterior part of trunk-armour. N.Y.S.M. 3775 (magn. × 3).

FIGURE 18. Tergal area of anterior median dorsal plate. N.Y.S.M. 3775 (magn. × 9).



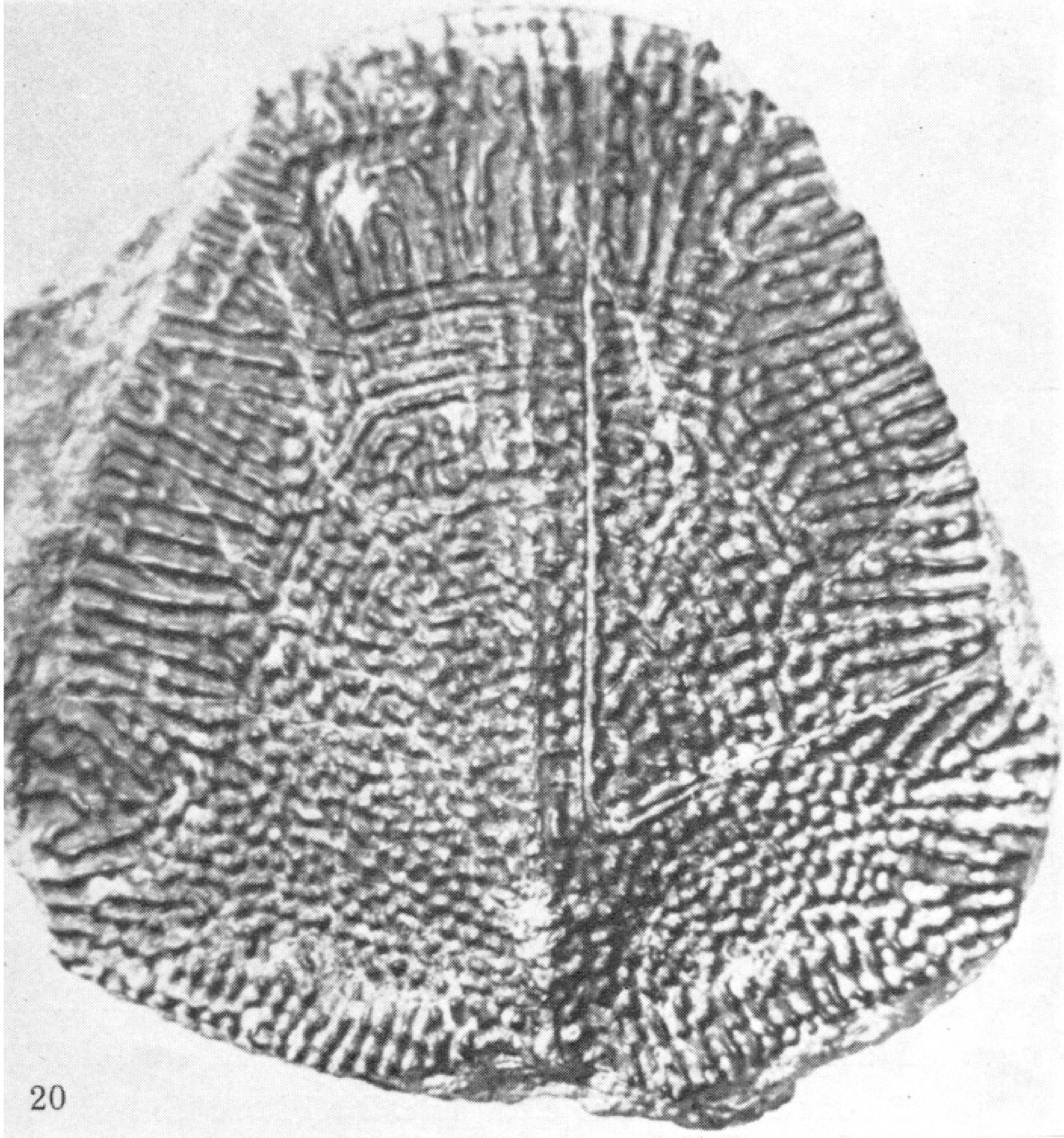
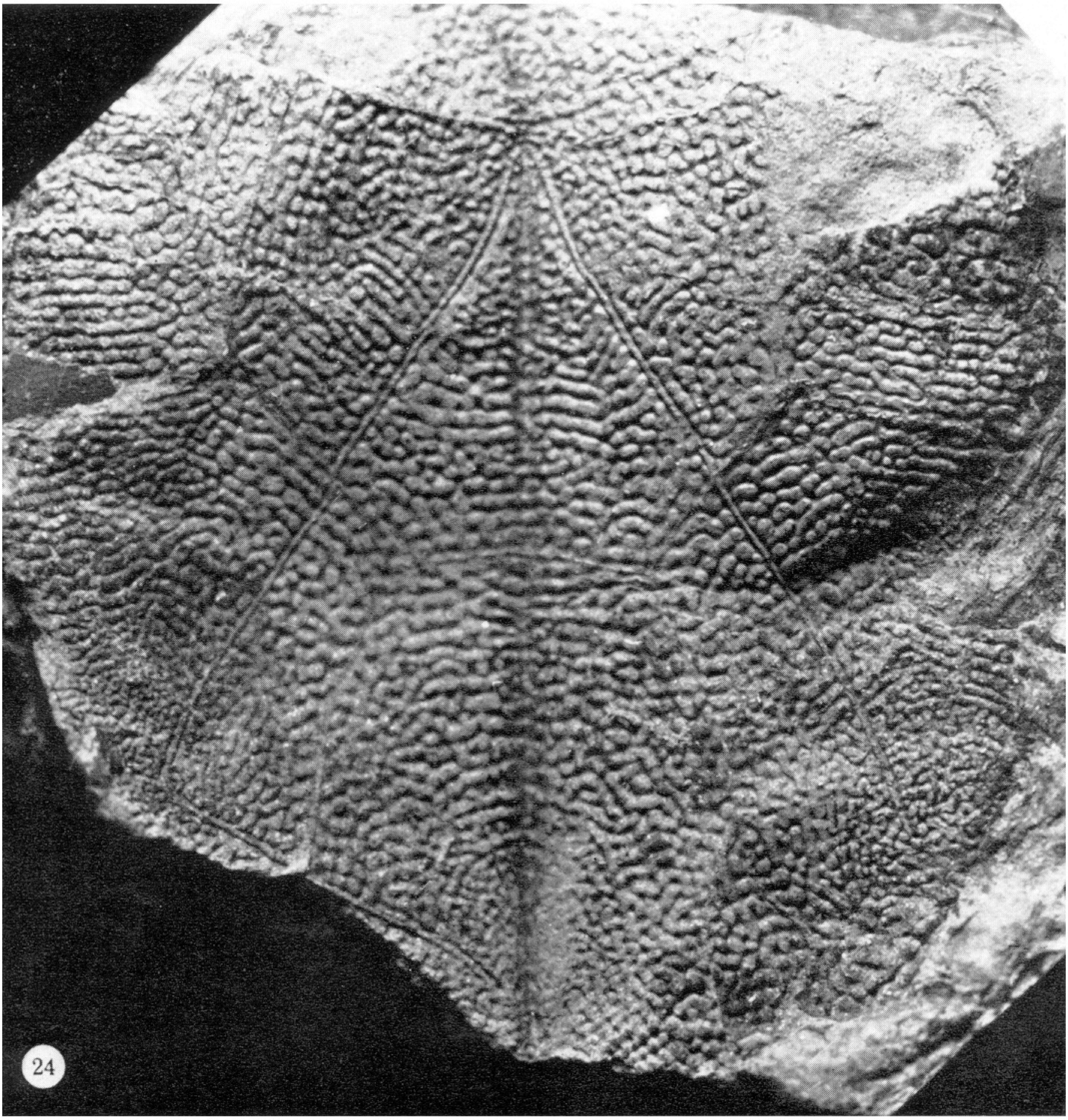
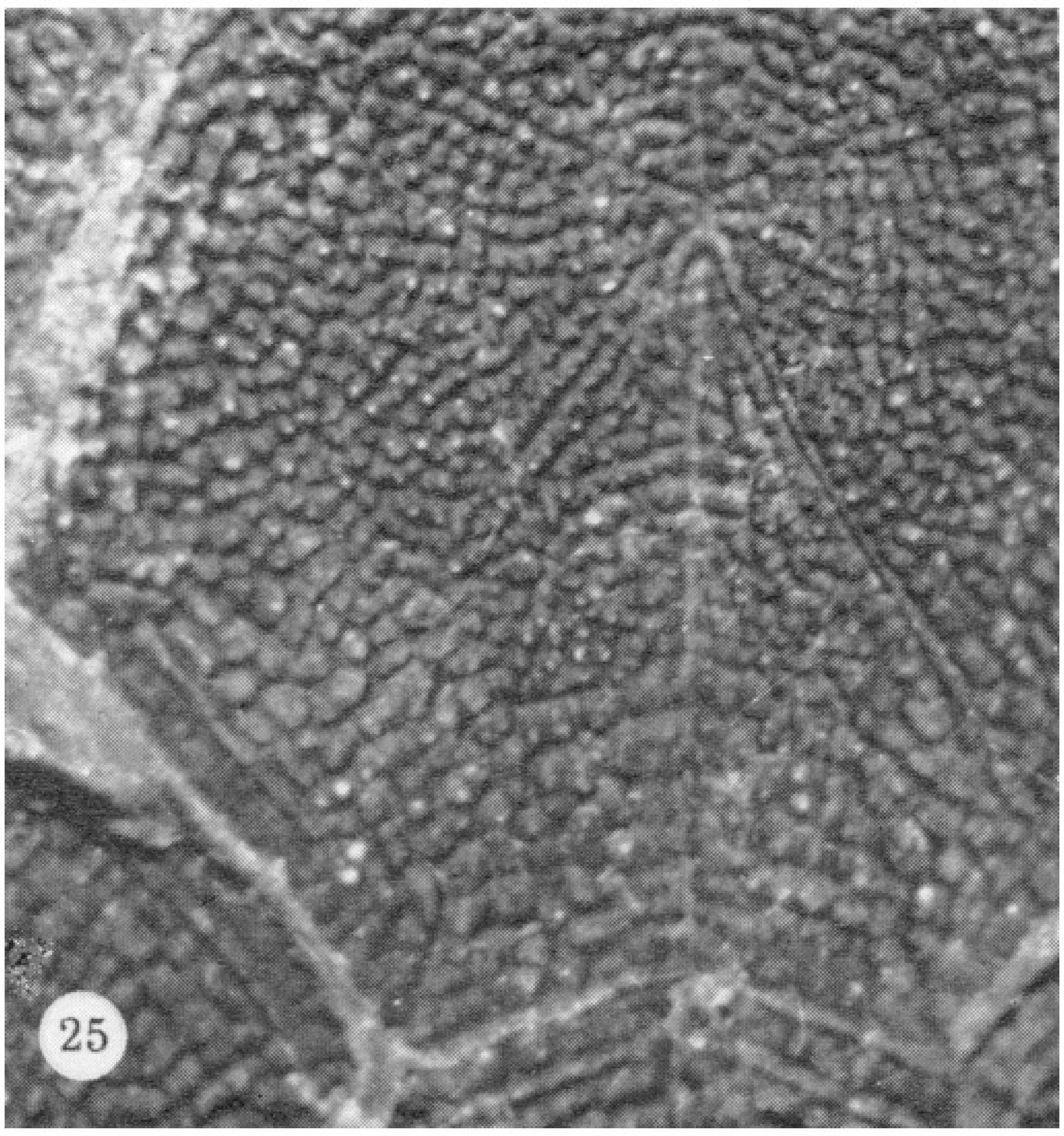


FIGURE 19. Part of trunk-armour. B.M. P. 52090 (magn. $\times \frac{5}{2}$).

FIGURE 20. Posterior median dorsal plate. R.S.M. 1887.20.6E (magn. × 2).

FIGURE 21. Tergal area of anterior median dorsal plate. B.M. P. 52104 (magn. × 4).





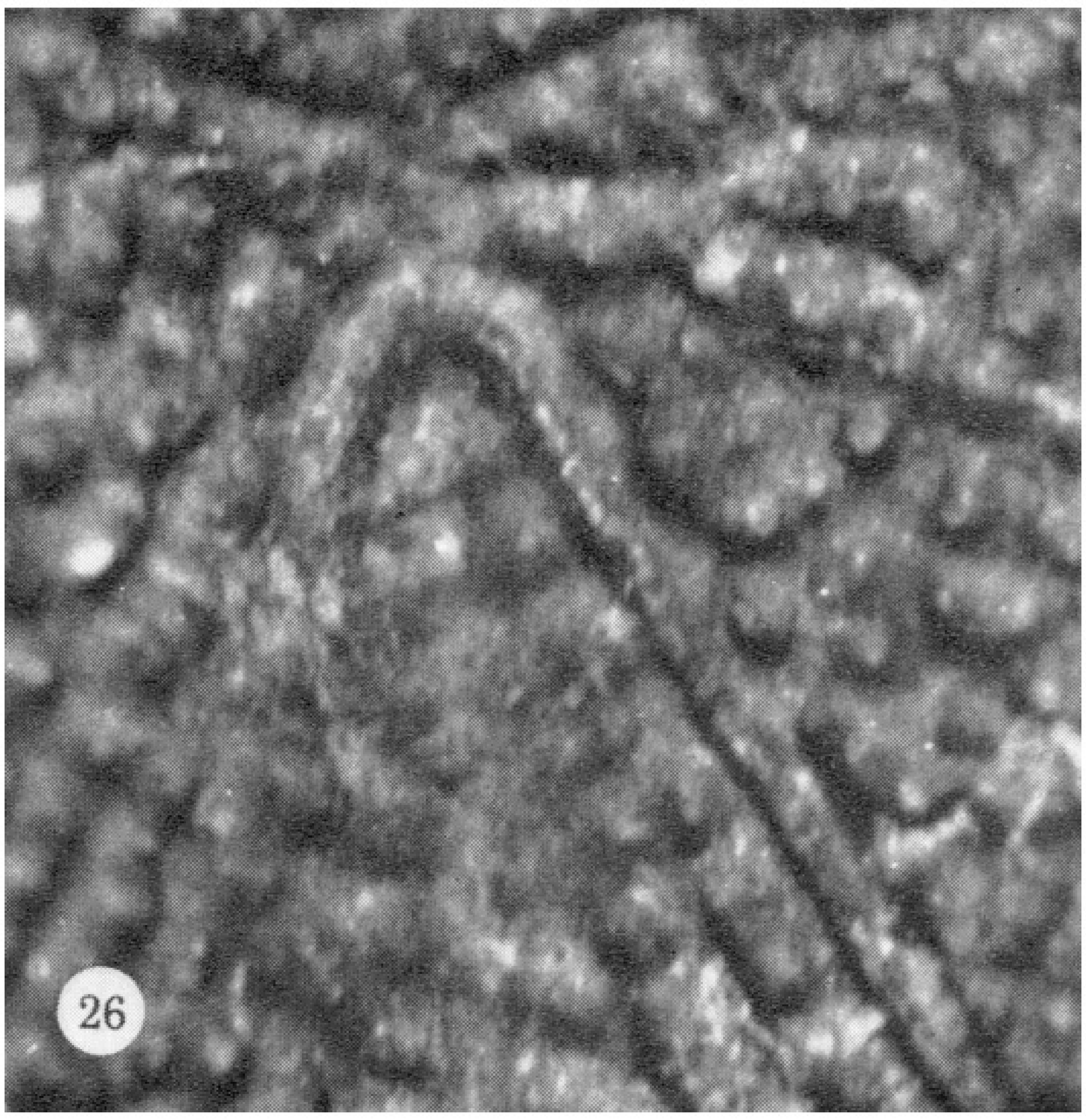
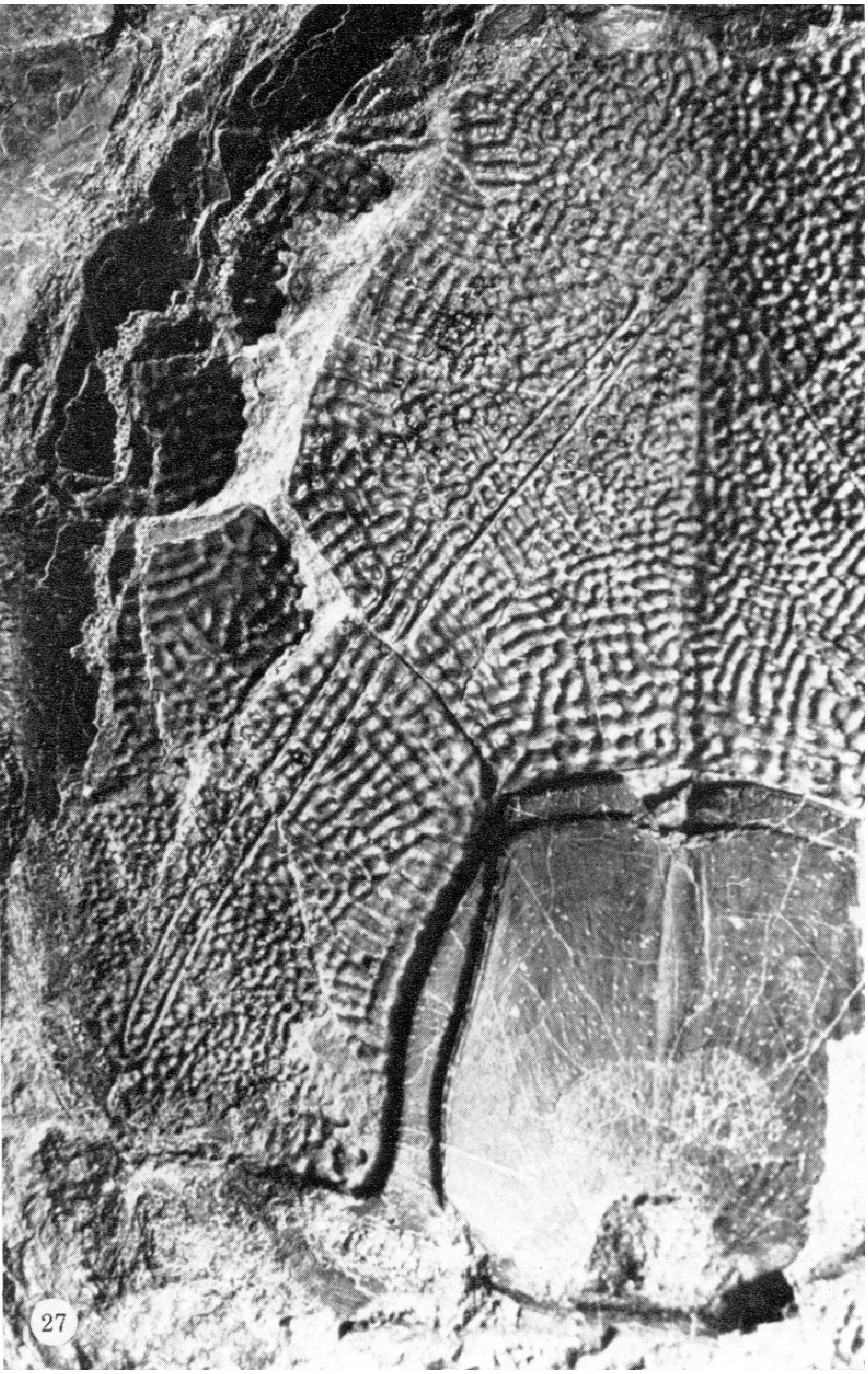


FIGURE 24. Impression of trunk-armour. B.M. P. 52087 b (magn. × 3).

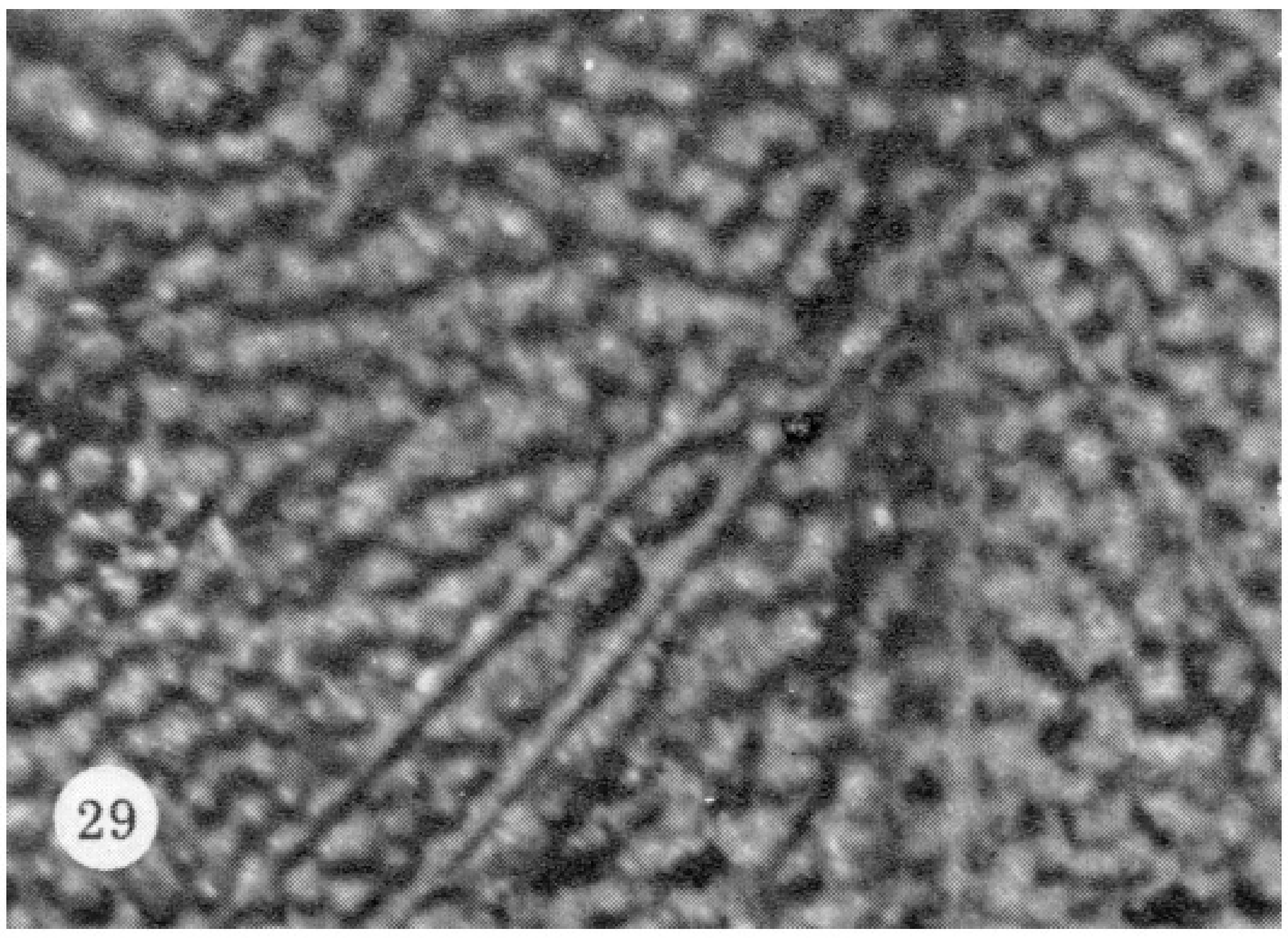
FIGURE 25. Impression of anterior median dorsal plate. B.M. P. 52103 (magn. × $\frac{5}{2}$).

FIGURE 26. Impression of tergal area of anterior median dorsal plate. B.M. P. 52103 (magn. × 12).

28



27



29

Figure 27. Impression of part of trunk-armour. B.M. P. 52092 (magn. × 2).

Figure 28. Impression of part of mixilateral plate. B.M. 52092 (magn. × 8).

Figure 29. Impression of tergal area of anterior median dorsal plate. B.M. P. 52092 (magn. × 3).

All photographs were taken by the author, except figure 20 which (the negative) was taken by the Royal Scottish Museum.