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ON THE LATERAL LINES AND DERMAL BONES IN THE PARIETAL REGION OF SOME CROSSOPTERYGIAN AND DIPNOAN FISHES

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CONTENTS

The current views on the relation between latero-sensory lines and dermal bones are briefly reviewed, and a modified version is proposed.

Published photographs of a number of parietal shields of crossopterygians other than coelacanths have been re-photographed, and enlarged outlines brought to a common frame of reference and compared. On this basis the significance of variations in *Osteolepis* that have two parietal bones on one side and the usual single parietal on the other is considered, the parietal shields of some genera of osteolepiforms, and also the equivalent area in ichthyostegids, are compared with one another, and the differences between the parietal shields of osteolepiforms, porolepiforms and rhizodontiforms are discussed. These last are believed to be due to the infraorbital lateral line having come to be situated at different relative locations at the beginning of skeletogenesis; the latero-sensory ossicles that it formed consequently came to act as foci for the development of different combinations of bones.

Published work on the skull-roof of dipnoans is also considered, with particular reference to the question of how bones I and B became latero-sensory. The variations in dipnoan pit-lines seem to have been similar in principle to those of the superficial sensory lines in placoderms.

A scheme relating the dermal skull-roofs of the main groups of gnathostomatous fishes is proposed.

1. INTRODUCTION

The present study may be regarded as a sequel to that on *Bothriolepis* and other placoderms (preceding paper); the approach is similar. A consideration of some intraspecific variations, and also of interspecific and other differences, is used to try to deduce inferences concerning underlying ontogenetic patterns and subsequent modes of growth, as indicated by the relevant bones and lateral lines. As before, the material considered is selective, not comprehensive, and in this case is largely confined to the parietal shields of crossopterygians and the comparable region of dipnoans.

The former work on placoderms differs from the present one on osteichthyans in two main respects. First, the former was concerned almost entirely with superficial sensory lines; the present one is concerned not only with the equivalent pit-lines but also with deep sensory lines that are housed in canals. This greatly complicates the issues that are involved. Brief notes on earlier ideas on these matters are given in the following section, along with a modified version developed by the present writer.

The second difference is that whereas the previous work on placoderms was to a considerable extent based on new descriptions of variations in *Bothriolepis*, the present one is based entirely on previous descriptions. In particular it is dependent on the many beautiful photographs of crossopterygian dermal skull-roofs reproduced in the works of Säve-Söderbergh, Jarvik and Jessen. The parietal shields of some of these have been re-photographed and enlarged to standard sizes, and have thus afforded a basis for quantitative and other comparisons somewhat similar to those developed in *Bothriolepis*. In dipnoans the individual bones are smaller and this approach has not been possible.

In this paper, as also in the previous one, the figures and tables are largely left to tell the story. The text merely attempts to extract and interpret some relevant features.

2. SOME VIEWS ON THE RELATION OF LATERAL LINES TO DERMAL BONES

Allis (1889) described in *Amia* the sinking of the neuromasts into the dermis, and the formation of a sensory canal through the union of separate sections, the primary pores being situated between the neuromasts. Bailey (1937) did interesting work on the regeneration of canals, particularly in goldfish, but as yet little seems to be known about how or why the sensory lines first take the course they do, or by what mechanism they come to join with one another. Already in 1889 Allis appreciated that there was a close relation between bones and lateral lines, and in 1898 he remarked: 'Furthermore, it is highly probable, though certainly not as yet established, that a bone or a part of a bone developed in any particular fish in relation to a particular part of the lateral-line system is always the homologue of the bone, or part of a bone, developed in relation to the same part of the lateral-line system in any other fish or animal.' This viewpoint was adopted by Goodrich for the interpretation of *Osteolepis* in 1919, and of *Dipterus* in 1925. It was transformed from an empirical observation to a more scientific concept by Pehrson's (1922) clear demonstration that during the ontogeny of *Amia* the sinking of the neuromasts into the dermis was associated with the initiation of ossification in their immediate vicinity. This seemed to explain the relation that Allis had observed between particular bones and corresponding parts of the sensory canals, and it also accounted for the observation that in maturity the canals passed through the centres of radiation of the bones. Allis's important concept came to be widely used by palaeontologists for the interpretation of homologies.

However this useful concept was found to be subject to certain limitations. One was already known to Allis. He remarked (1898) that canal-bearing bones could fuse with one another early in ontogeny, and (1905) that since one latero-sensory ossicle is normally associated with one neuromast it followed that when a bone contained more than one neuromast that bone was a product of fusion. Later Pehrson (1922) showed that in *Amia* the nasal bones for example are formed by the fusion of three bone rudiments each associated with a single sensory organ of the supraorbital canal. Moy-Thomas (1938) showed that the size and number of the postorbital and infraorbital bones in *Amia* varied from one specimen to another, and that these differences could be explained by assuming that the rudiments formed around the sensory organs had fused in different combinations in different individuals. Subsequent work on the ontogeny of other forms, particularly by Devillers (1947), confirmed this viewpoint; it became apparent that in different individuals of the same species, or even on the two sides of a single individual, fusions of adjacent bone rudiments might take place in different ways. Also some sensory organs might not induce ossifications. The individual bones resulting from such fusions and losses therefore could not be regarded as precisely homologous. They were, on the other hand, all products of a single homologous series of units; hence the concept of serial homology remained appropriate, whereas individual homologization was in this context inapplicable.

In palaeontology Westoll (1936) similarly showed that in *Osteolepis* the supraorbital canal in some cases traverses as many as seven small nasal bones; these could be regarded as derived from individual ossifications each associated with one of a series of supraorbital neuromasts. In most specimens the number of bones in this series was smaller, the reduction having taken place in different ways in different individuals, and these variations could readily be explained as due to appropriate fusions, or losses, of the serial bony rudiments. Jarvik (1944) showed that the nasal series of *Eusthenopteron* was very similar. The frontal bones of fishes are apparently formed by the fusion of a number of similar supraorbital rudiments, the particular elements involved varying from one type of fish to another.

Another complication was the need to take account of dermal bones that are not associated with sensory canals. In *Osteolepis*, for example, a network of small bones lies between the two series of nasal bones. They appear to be arranged in no particular order, and their pattern varies from one individual to another. Westoll (1936) gave to bones of this type the name anamestic, since their function appeared to be merely to fill space. In osteichthyans there are also a few non-canal bones that are quite large and not particularly variable, possibly because they have come to serve some special function in the architecture of the skull. There seemed to be no evidence (see for example, Westoll 1949) of the fusion of rudiments of latero-sensory and non-canal bones.

An important limitation applied in the case of neuromasts which remained relatively superficial instead of sinking well down into the dermis. Westoll (1949) showed that in *Dipterus* and *Scaumenacia* the course traversed by pit-lines sometimes varied widely from one individual to another, whereas the pattern of their dermal bones remained unchanged. It followed that Allis's generalization did not apply to these more superficial sensory lines. This conclusion was supported by ontogenetic evidence; Pehrson (1940, p. 9) showed that in *Amia* pit-line organs were not associated with the production of osteoblasts, and he expressed surprise that some palaeontologists should regard them as important morphogenetic units. Devillers (1947), working on *Salmo*, confirmed their inability to initiate ossification. Bystrow (1935) had observed that the floors of the sensory grooves of labyrinthodonts are pierced by foramina presumably for the nerves and blood vessels that supplied their sense organs, and that these foramina were circular near the centres of radiation of the bones and oval on passing away from these centres, indicating that here the nerves traversed an oblique course. He noted that these nerves and blood vessels would retain the sensory structures by anchoring them to the bottom of the groove. One consequence was that in the course of the development of water-breathing larvae into adults, which was often accompanied by extensive differential growth, the lateral lines would retain their association with the corresponding centres of bone radiation as these grew into relatively new positions. According to Westoll (see for example, 1937*a*, 1944, 1949, and Graham-Smith & Westoll 1937) such anchorages to bone rudiments, occurring at an early stage in skeletogenesis, would explain the various courses of the pit-lines in fishes. Subsequent growth by accretion at the peripheral margins of the bones would cause the pit-lines to traverse courses that passed relatively close to the eventual centres of radiation of the bones in question.

In the cheek region of actinopterygians Westoll (1937*a*) found the relation between pit-line and bone to be in some cases more incidental. In various members of this group the horizontal pit-line overlay, and left its imprint on, the peripheral region of various different bones – the maxilla, or the preopercular, or one of the postorbital or suborbital bones. In *Amia*, where ontogenetic evidence was available (Pehrson 1922), initiation of ossification of the postorbitals was known to be associated with the infraorbital sensory canal; from this centre a thin horizontal lamella grows backwards on a plane parallel with the skin, and it is this lamella which, in the lower postorbital, becomes associated with the pit-line. It seemed that in the cheek of actinopterygians this pit-line became associated with whatever bone happened, as a result of various phyletic contingencies, to grow into the area in question.

The occasional withdrawal of a canal from a bone also posed a problem. Dipnoans provide one example. In *Dipterus*, from the Middle Devonian, the supraorbital sensory canal extends into bone J and it presumably played a part in initiating its ossification. In a rather similar Upper Devonian dipnoan, *Scaumenacia*, the canal does not reach this bone, its place being taken by the anterior pit-line. However the bone continues to appear, and undiminished in size, and not only in *Scaumenacia* but in Carboniferous dipnoans as well. Westoll (1949) considered that the retention of a bone in such circumstances was due to its having assumed some special functional significance. However de Beer (1937, p. 489) had remarked that former canal bones appear in much the same positions in the higher vertebrates, though these have lost their lateral lines and the bones have ceased to be canal bones. He therefore suggested that the latero-sensory organs may not cause bones to arise, but may merely determine the localization of their rudiments.

Moy-Thomas (1941) removed the rudiments of the latero-sensory line from one side of the frontal area of a young trout, at a stage when there was still no sign of frontal bones or sensory organs. He found that on the operated side, where no sensory canal was formed, the bony gutter which would otherwise have formed around it was also missing. Nevertheless a frontal bone grew on this side quite normally, except that its development was slightly less advanced than on the other side. He concluded that, even though the lateral lines were apparently capable of stimulating bone development in their vicinity, nevertheless the actual origin of bone development must be due to some different cause. The value of lateral lines as guides to bone homology was therefore suspect. To this Westoll (1941) commented that this work was done on teleosts, in which fishes the dermal bones played an important part in the mechanical structure of the skull. Work on primitive osteichthyans, and on the development of *Amia*, had shown beyond doubt that in these forms, where the dermal bones were rather more superficial and did not take part in the mechanical structure of the skull, there was in fact a close relation between the sensory canals and the dermal bones.

Subsequent work on development, for example by Pehrson (1944), Devillers (1947) and Lekander (1949) has done much to clarify the position regarding teleosts. It appears that some teleost bones, for example the nasal bones of *Salmo*, develop in much the same way as the canal bones of *Amia*, that is by neuromasts sinking below the surface and forming an associated canal, by osteoblasts laying down bone at the sides of this canal and thus surrounding it with a tubular latero-sensory ossicle, and then, at a later stage, by lateral wings growing out from it along a plane parallel with the skin, these horizontal lamellae eventually forming the main body of the bone. This was described as the tubular method of development; it gave rise to typical latero-sensory bones. There was however a second category of teleost bones, represented for example by the frontals of *Salmo* and of *Leuciscus*, which developed in a different way. First a horizontal bone lamella formed a short distance below the epidermis; in some cases, as in the frontal of *Salmo*, the position of the initial foci of ossification had some association with the, still superficial, neuromasts; more often, as in the frontal of *Leuciscus*, there is apparently no such association. It is only at a later stage that the neuromasts sink into the dermis, that sensory canals are formed, and that cylindrical bony ossicles develop around them. If the horizontal lamella remains relatively superficial then the latero-sensory ossicle develops in close association with the bony lamella that lies immediately deep to it, and the two elements form a single closely integrated bone. However in some cases the membranous bone lamella rapidly sinks more deeply into the tissues and, becoming closely linked with the chondrocranium and its ossifications, comes to form a part of the mechanical structure of the skull. The latero-sensory ossicle may then be formed as a separate unit which is not connected with the horizontal lamella, since the latter is at this stage already relatively deeply placed; later the two elements may or may not unite.

This second method of bone formaton was termed by Devillers the method of two components. He recognized the horizontal lamella of a membranous element as equivalent to the horizontal lamellae that grow out as wings from a latero-sensory ossicle in the tubular method. Where, as in the frontal of *Leuciscus*, the membranous element is wholly independent of the neuromasts it is in all respects equivalent to a non-canal or anamestic bone. Such bones or bone components were said to be formed by membranogenesis, and were to be contrasted with the formation of latero-sensory bones. In the latter a latero-sensory ossicle, induced by a neuromast as a result of a process referred to as dermogenesis, provided a framework from which the horizontal bone lamellae spread. In teleosts the difference between the two types was essentially one of timing. He regarded the tubular method of bone formation as the more primitive, and noted that the possibility of its becoming dissociated into latero-sensory and membranous components provided a mechanism by which more or less the same bones could continue to be formed in tetrapods that had lost their lateral-line system.

More recently Branson & Moore (1962) have confirmed much of the ontogenetic evidence derived from teleosts, and they have also shown that the development of new deep-seated neuromasts is accompanied by the formation of new latero-sensory ossicles.

Although a sensory canal was usually found to be associated with the same bone, yet there were occasions when this relation broke down unexpectedly. The parietal shield of crossopterygians provided a classic example. In osteolepiforms the sensory canal on each side passes forwards through the centre of radiation of the supratemporal and intertemporal bones, leaving between them a pair of non-canal bones, namely the parietals. In porolepiforms, on the other hand, the canals pass through the supratemporals as before, but then, passing rather more mesially, they traverse a bone which is fairly similar in shape and occupies much the same region of the skull-roof as the parietal of osteolepiforms. If the canals are used to interpret homologies then this porolepiform bone would be the homologue of the osteolepiform intertemporal, and Westoll (1937*b*, fig. 9) assumed this to be the case. This view could find support in Pehrson's works (1947, 1958) on the development of the actinopterygian fish *Polypterus*. He showed that its parietal began to develop, presumably as a bone formed by membranogenesis although it is closely associated with the middle pit-line, but that presently this early ossification ceased growing and was then soon resorbed, its place being taken by the mesial spread of the horizontal lamella of the adjacent latero-sensory bone, which in this case developed from an early fusion of intertemporal and supratemporal bone rudiments. Parrington (1949) emphasized that this interpretation of homology was unsatisfactory; the parietal of osteolepiforms is matched by a bone of similar characteristic shape and in a similar topographical position in porolepiforms, and if homology is to have any meaning, these two bones should be regarded as homologous. To account for cases of this kind he suggested that the association usually observed between sensory canals and bones was not due primarily to the neuromasts stimulating osteogenesis, but to the existence of an osteogenetic precursor, already present before there was any sign of osteogenesis, which had the capacity of attracting to its vicinity the rudiments of lateral lines, as well as becoming the site of a subsequent ossification. This suggestion was based partly on a consideration of the experimental work of Harrison (1904) on amphibian tadpoles. In porolepiforms the precursor of the intertemporal would have failed to develop, with the result that the embryonic sensory line was drawn towards the precursor of the parietal instead. The corresponding bones in osteolepiforms and porolepiforms were therefore both parietals, and were homologous, even though their relation to the sensory canal had changed.

The Swedish school has approached these problems rather differently. Stensiö (1947, p. 101) considered that since superficial sensory lines and pit-lines were usually associated with the same bones, and in particular with the centres of radiation of these bones, in much the same way as were canal bones, it followed that all three types of latero-sensory structure had the same kind of morphogenetic influence during ontogeny; in each case they induced the initial ossification of the relevant bones, and this relation was retained thereafter. He (1947, p. 123) further remarked that the bones of the later labyrinthodonts were much the same as those of the earlier canal-bearing ichthyostegids, and that he was therefore inclined to agree with de Beer (1937) that latero-sensory structures were not responsible for the formation, but merely for the localization, of bone rudiments. He (1947, p. 117, 183) also came to the conclusion, contrary to Westoll, that non-canal bone elements frequently participated in the formation of the canal bones that developed.

Another problem was concerned with differences in the area of the skull-roof occupied by particular bones. Here early work proved misleading. Fell & Robinson (1929) showed that a rudiment of a chick femur grown in isolation in tissue culture developed into a bone with a characteristic femur form. This indicated that the character of such bones was in the main intrinsic and genetically determined. Also Troitsky (1932) found that if the parietal was removed from the skull of a dog then a new and more or less normal parietal developed. This case, which was more comparable with a primitive vertebrate skull-roof, also suggested that the size and form of the bones was intrinsically determined. Perhaps with such work in mind the Swedish palaeontologists have been inclined to suppose that each particular dermal bone occupies its own particular region of the skull-roof, and in cases where it does so only partially, they have postulated fusion between the bone that should, in their opinion, occupy the rest of the area and the bone that actually does so. Romer (1947), opposing this viewpoint, considered that an ossification spread from its centre until it met another, a sutural line then being established. The position of a suture depended on the relative time of establishment of the relevant centres, on their relative positions, and on the subsequent rate of growth of the bones concerned. Later work on the development of the bones of various mammals has shown Troitsky's work to have been misleading because, although he removed the parietal bone, some of the underlying osteoblastic tissue remained attached to the dura mater, and from this a parietal rapidly regenerated. If all the osteoblastic tissue is removed, for instance by using a cautery, the neighbouring bones grow in and fill the space (see for example, Girgis & Pritchard 1958). At some particular sites there does seem to have been an element of intrinsic limitation; on the whole however, there seems to be free competition among adjacent bones to fill any vacant space, growth in their area taking place principally by peripheral accretion at their margins, and sutures are formed merely where they happen to meet. Little comparable work seems to have been done on fishes, though Tatarko (1934) showed that if the opercular bone is removed from an adult carp the vacant space was filled by extensions from neighbouring bones. These observations support Romer's opinion.

It seems that two broad problems are involved. The first is concerned with the mechanism by which centres of ossification become established at particular times in particular places, and the second with the relative rates of horizontal growth from these centres and with the rate of growth of the dermis which forms the matrix in which this horizontal bone growth is taking place. The positions at which bones meet and sutures are formed will be determined by mutual interactions between these factors. The area occupied by a bone in maturity is only partially determined by the position of its initial centre of ossification. Parrington (1956) has explored the possibility of using sutural patterns to deduce the underlying ontogenetic changes that have given rise to them.

Ørvig (1971) has recently noted that in the bones of the head of placoderms the latero-sensory lines are housed in three main categories of channels. The deepest are canals in the bones; they open to the surface through tubes. Secondly there are deep undercut grooves which open to the surface by longitudinal slits. Thirdly there are shallow grooves without undercuts. The first category may grade into the second, and the second into the third. On the other hand in osteichthyans there is usually a sharp distinction between canals and pit-lines. The latter resemble the third category in being superficial structures, but they are much thinner. Ørvig (1971, 1972) has also demonstrated the presense of latero-sensory ossicles in ptyctodonts and in a number of other lower vertebrates, and has discussed the relation of these structures to the dermal skeleton.

Thus the force of Allis's original concept has been gradually reduced. On the other hand no comparable unifying concept has come to take its place. A minor modification of current views, which may however to some extent fill this need, can be formulated as follows.

It is reasonable to assume that in very early vertebrates the head was covered with small bony scutes (e.g. the 'micromeric scales made up of odontodes on basal bony plates' referred to by

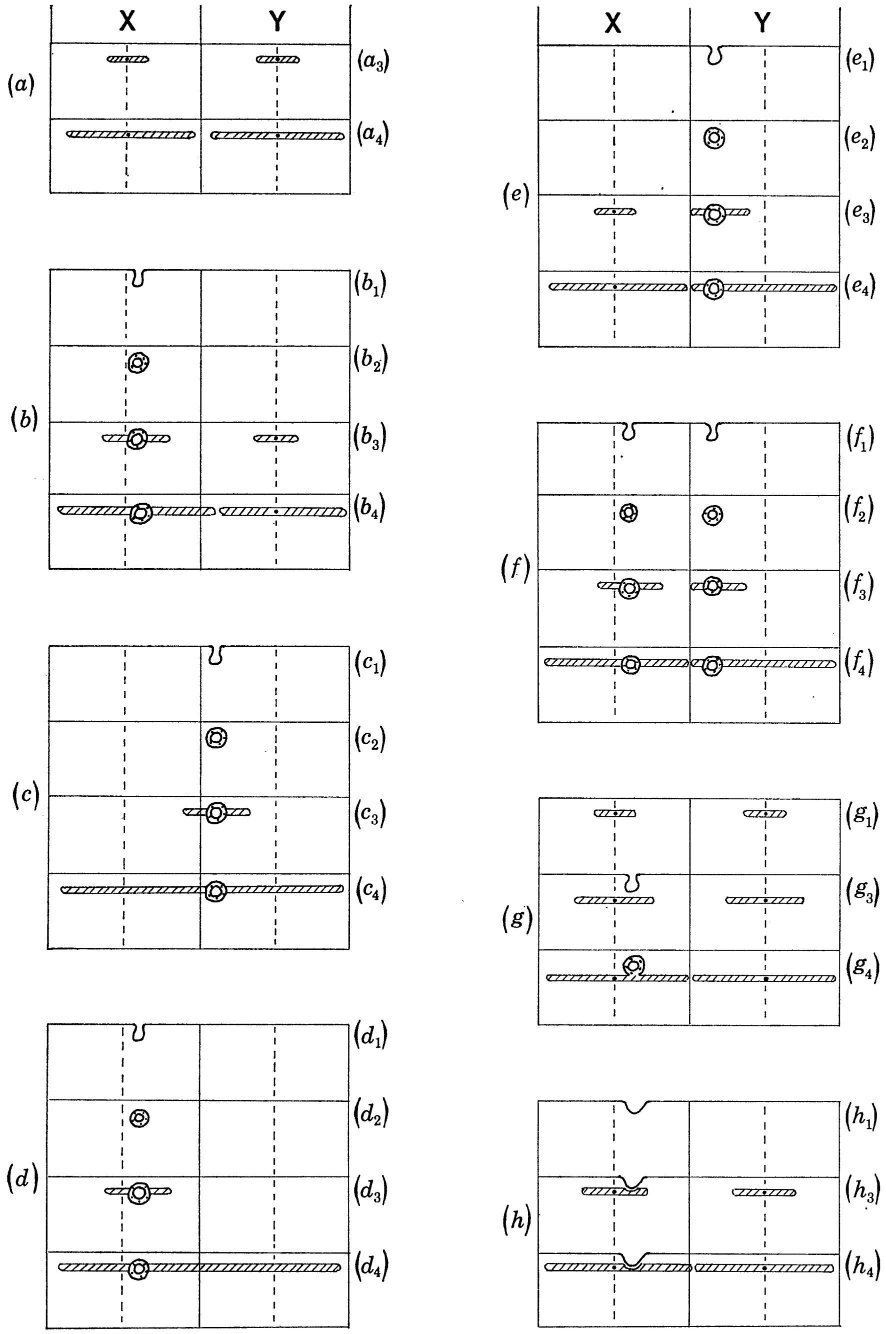

Figure 1. Schematic representation of modified version of bone-lateral line relations. For explanation see text.

Ørvig 1972, p. 152), and that with subsequent phyletic changes in some groups parts of this matrix became differentiated to form a number of relatively large definitive bones. Each such bone would presumably have been associated during ontogeny with a potential bone area within which processes would take place leading to the formation of the bone in question. In figure 1 two such potential bone areas, 'X' and 'Y', are shown schematically; (a_3) indicates the presence of two young bone lamellae ('x' and 'y') that have been formed by membranogenesis in the dermis in, respectively, these areas 'X' and 'Y'; later (a_4) horizontal bone lamellae are spreading outwards from these centres. It is postulated that all definitive dermal bones, whether latero-sensory or not, of all vertebrates develop essentially in this membranogenic way.

However this situation becomes more complex if a potential bone area comes to be traversed by a latero-sensory line whose neuromasts sink sufficiently deeply into the dermis to induce the formation around themselves of tubular bony ossicles. These minute tubular ossicles are of course to be distinguished from definitive bones. If the sinking of the neuromasts and the consequent formation of ossicles by dermogenesis occurs *before* membranogenic bone formation has begun (i.e. figure 1 b_1 and b_2) then this ossicle will come to act as a focus for the initiation of bone formation by membranogenesis (b_3); the definitive bone will later spread from this centre by the growth of horizontal wings (b_4). In figure 1 *b* 'x' will therefore become a lateral-line bone, whereas 'y' will remain a non-lateral-line one. They will develop at about the same time and in the same way, the only difference being that 'x' will develop from a ready-made bony focus, namely the ossicle; this may give its development an earlier start, as compared with 'y'. In figure 1 *b* the neuromast invagination is intentionally shown in a rather different position to that at which the membranogenesis of bone 'x' was shown as being initiated in figure 1 *a*, since wherever the neuromast happens to invaginate and dermogenesis to occur, there the initial membranogenesis will be focused. The centre of ossification is therefore likely to be transferred to a different position. The sensory canal will automatically come to lie at the centre of growth of the bone, and will at a later stage traverse its centre of radiation. In different organisms the same canal would be expected to pass through the centre of the same definitive bone; this would account for the homology relation that is usually observed.

If however the position of a neuromast (and hence also of the sensory canal and of the latero-sensory ossicle that is induced) for some reason changes its position in relation to the skull-roof as a whole, then the situation depicted by (*c*) in figure 1 can arise. The sensory line that in (*b*) was associated with area 'X' is shown in (*c*) as having now sunk into a region that lies within the normal province of bone area 'Y'. The latero-sensory ossicle that it induces would therefore be expected now to act as a focus for the membranogenic growth of bone 'y'; on the other hand area 'X' would have lost its latero-sensory focus.

In figure 1 *c* the definitive bone that develops from this centre is shown as occupying the territory previously occupied by both bones together. The differences in the bone pattern of different species of *Haplolepis* that have been described by Westoll (1944) are of interest in this respect. Those in which the posterior part of the skull-roof is formed by two bones can be represented by figure 1 *b*, 'x' being the dermopterotic and 'y' the parietal. Species with a single bone in this area can be interpreted in terms of figure 1 *c*; the infraorbital sensory line has become transferred to the parietal area and induced the formation of a latero-sensory bone there, which has come to occupy both areas. However this change can also be interpreted as by Westoll without any transference of the lateral-line canal, and thus as in figure 1 *d*; in the 'one-bone' species the parietal has failed to develop – this change possibly being associated with the withdrawal of the supraorbital canal from the area at an earlier stage in phylogeny – and the dermopterotic has spread into its area. However in the 'two-bone' species the parietal is a relatively large bone which shows no signs of reduction, so it could be argued that this apparently abrupt transformation is better accounted for in terms of figure 1*c*. On the other hand the ontogenetic work of Pehrson (1947, 1958) seems definitely to indicate that in *Polypterus* this region evolved from a normal actinopterygian by the kind of change envisaged by Westoll, shown here as from figure 1*b* to 1*d*. The parietal 'y' begins to ossify as usual, but soon regresses and then disappears (it is not represented in figure 1*d*) and the dermopterotic ('x') grows across to occupy area 'Y' as well as its own area 'X'.

The situation of figure 1*b* can also be transformed into that of 1*e*. Here the latero-sensory ossicle induced around the canal again acts as a focus for the membranogenetic component of bone 'y', but the resulting definitive bone does not come to include the area previously occupied by bone 'x'. Instead an independent ossification is established in this area by a reversion to an initiation by typical membranogenesis, as in figure 1*a*. A bone formed in this way is likely to be rather different to its previous latero-sensory counterpart. The relation between the parietal areas of osteolepiforms and porolepiforms can be considered in these terms.

A sensory canal which comes to provide a focus for a latero-sensory bone (i.e. bone 'x' in figure 1*b*) may also in a nearby part of its course come to lie within an adjacent, previously non-latero-sensory, area and form there an ossicle which acts as a focus for this bone as well, as indicated by figure 1*f*. In this case 'y' has no opportunity to invade area 'X', since this still retains its latero-sensory bone virtually unchanged. The parietal shield of *Rhizodus*, recently described by Andrews (1973), can be regarded as derived from an osteolepiform condition in this way. Bone I of dipnoans probably became a latero-sensory bone in a similar manner.

If the sinking of the neuromasts and the consequent dermogenesis occurs *after* a membranous ossification has begun, then no latero-sensory ossicle is available at an appropriate time to provide it with a focus. The definitive bone therefore develops independently of the latero-sensory system, and any subsequent union with a latero-sensory ossicle is secondary and incidental. This condition (figure 1*g*) is characteristic of teleost bones formed by the method of two components. Essentially it represents a reversion to the condition of figure 1*a*.

If the neuromasts sink *less deeply*, so that only a shallow gutter is formed and only a shallow groove on the surface of the underlying bone is produced, then both the embryological and the palaeontological evidence indicates that they do not induce latero-sensory ossicles and are not morphogenetic. This situation is represented by (*h*) in figure 1; the stage equivalent to (b_2) does not develop. This form of organization presumably applied to the more superficial sensory lines of placoderms, to the pit-lines of osteichthyans, and to all the sensory lines of post-Devonian labyrinthodonts. It can arise either de novo or as a regression from a canal system.

Finally if the sensory lines disappear, as in reptiles, the same bones as before are likely to be formed by the normal processes of membranogenesis. The situation in a bone area might therefore pass, in the course of phylogeny, from (*a*) to (*h*), to (*b*), back to (*h*) again, and so return to (*a*) (figure 1).

This minor reorganization of current concepts to form a modified system seems to accord with most of the results obtained by earlier workers, though not necessarily with their opinions. It is in agreement with de Beer's (1937) line of thought, which has been supported by Stensiö (1947, p. 123), with Moy-Thomas's (1941) experiments on *Salmo* and with Devillers's (1947) recognition that the horizontal lamella that grows out from a latero-sensory ossicle is equivalent to the lamella formed during membranogenesis. It does not accord with this last writer's view that the tubular method of bone formation is the more primitive. On the contrary, deep latero-sensory lines and their ossicles are seen as an intrusion on a membranogenetic process of bone formation which was functioning before their arrival, which continues to do so in a slightly modified form in their presence, and which returns to its former condition if they are formed too late to be effective, or become superficial or disappear altogether. The concept of transference of this intrusion from one bone area to another is used to try to account for the occasional sudden change in the relation between deep latero-sensory lines and the bones with which they are associated.

This modified system has made no reference to the frequent early fusions of latero-sensory elements. It is perhaps convenient to view the ontogenetic development of the skull-roof as divisible into two stages. At the very beginning of skeletogenesis certain sites of ossification are established; their precise form may vary from one individual to another. During this preliminary phase these small patches of bony tissue, whether of latero-sensory or membranogenic origin, may reorganize themselves by uniting, fading away or changing their form. At this stage the rudiments of the definitive bones have not yet been formed, so the concept of individual bone homologization is still not applicable. However from this unstable matrix there presently arise, presumably in relation to the potential bone areas postulated above, a relatively small number of more clearly defined sites of ossification. These can be regarded as definitive bone rudiments since from them horizontal bone lamellae will spread outwards and a definitive bone, circumscribed by connective tissue periosteum, will in due course become established. It is in this sense that the term rudiment is used. This approach largely avoids a difficulty raised by Devillers (1947, p. 76, footnote 2) that when a bone is formed from two or more centres of ossification the subsequent centre of radiation cannot correspond to both these points. This central area will not remain wholly 'frozen' while the bone spreads outwards by accretionary growth at its margins; there is evidence, for example, of bone resorption and redeposition; also in the case of canal bones the subsequent growth in diameter of the canals will cause complications. However the effect of such changes is largely unknown, and for the purposes of the present work it has been ignored.

3. The parietal shields of crossopterygians

(a) *Methods and abbreviations used*

The parietal shields of crossopterygians provide convenient material for the study of osteichthyan bones and latero-sensory lines. The bones are larger than in many regions of the skull-roof, and they have usually remained articulated in the fossil state. Also the shield forms a circumscribed area, demarcated anteriorly by the intracranial juncture apparatus and succeeded posteriorly by the relatively loose bones of the extrascapular region. Typically (see for example, figure 3*a* and *b*) each side of the shield consists of two latero-sensory bones, namely the intertemporal (It) and the supratemporal (St), which are traversed by the infraorbital sensory canal (ioc), and a single membranogenic bone, namely the parietal (Pa), which is marked by grooves formed by the middle (mp) and posterior (pp) pit-lines. In many actinopterygians and some dipnoans the supraorbital canal or its pit-line reaches back into the anterior part of the parietal region (see figure 25*f* and *h*), but it does not do so in crossopterygians; this reduction may be associated with the development of the intracranial juncture apparatus.

The number of units participating in the parietal shield is therefore small, and their variations and possible interactions can perhaps be studied the more effectively for this reason. Abbreviations, such as those given above, are used not only for the figures but also in the text; a key can be found on page 104.

Coelacanths differ in many ways from other crossopterygians (e.g. Bjerring 1973), and are not considered. As regards the remainder, osteolepiforms have a rather central type of shield with which those of the other three main groups can readily be compared. And within that group *Osteolepis* has a fairly generalized shield with which those of other genera can be compared. *Osteolepis macrolepidotus* Agassiz is a fairly common species, and a number of well preserved specimens have been described and illustrated by Säve-Söderbergh (1933, 1941) and by Jarvik (1948). Their published photographs have provided the core from which the present work has grown. Most of these shields have a single Pa on each side (figures 3, 4*a–e*); these are referred to as ss.Pa specimens. Six differ in having a single Pa on one side (the 's' side) and two bones (A.Pa and Pa) one in front of the other in the corresponding area on the other or 'd' side (figures 2, 5); these are sd.Pa specimens. There is also one specimen (figure 4*f*) with this double condition on both sides (dd.Pa).

It was important to try to determine accurately the position of the middle line, particularly in the sd.Pa shields. Here a digression is necessary. It is clear that in figure 2 A.Pa is considerably wider than Pa near the front of the shield. Parrington (1956) has observed that in sd.Pa individuals the A.Pa of the 'd' side has trespassed across the middle line into territory that would otherwise have been occupied by the single Pa of the 's' side. This interpretation is supported by the specimen represented in figure 5*b* in which the alignment of the skull-roof as a whole has been retained very exactly, and here the suture separating the frontals, which are symmetrical, reaches the front of the shield at a point midway between the It/Pa and It/A.Pa sutures, and appreciably to the 'd' side of the Pa/A.Pa suture. It seems likely that the ossification of A.Pa was proceeding before that of the single Pa of the other side had reached forward to this anterior region; this would have enabled it to encroach without hindrance into normal Pa territory on the 's' side. If the A.Pa thus developed early it might have encroached on It territory lateral to it, or the Pa, growing forward into a reduced field, might have compensated at the expense of the It on its own side. However, a quantitative comparison of the sd.Pa and ss.Pa specimens shows, contrary to a statement by Parrington (1967, p. 238), no evidence that the overall parietal width was greater in the former; on both sides the intertemporals seem to have resisted any disturbance that might have resulted from the unusual asymmetrical conditions, and the symmetry, relative to one another, of the sutures bordering their parietal neighbours was retained. The posterior region of the parietal shield of sd.Pa specimens also shows interesting asymmetries, which are considered later, but here also the symmetry of the equivalent St/Pa sutures seems usually not to have been affected. It is likely that during skeletogenesis the mesial margins of these temporal bones, closely supported by the sensory canals, formed a relatively strong framework which limited the lateral growth of the parietals.

The procedure adopted was therefore to re-photograph the more satisfactory shields of *Osteolepis macrolepidotus* illustrated by Säve-Söderbergh (1933, 1941) and Jarvik (1948), to prepare prints that brought the length of the shield to approximately 10 cm, to prepare from these tracings which showed the positions of the sutures and sensory lines, and then to manoeuvre these tracings over graph paper to determine a midline that lay as far as possible symmetrically between the two It/Pa sutures anteriorly, and the two St/Pa sutures posteriorly; the intermediate region where the sutures meet is relatively unstable and was ignored. Sizes were then adjusted to bring the length of this midline (mdl, figure 2) to precisely 10 cm. Lines drawn perpendicular to the front and back ends of this middle line are by definition 10 cm apart (a.p.p., figure 2), and bound the anteroposterior extension of the shield as portrayed at its middle line. On applying such tracings to centimetre graph paper the number of squares indicate immediately the distance of any point from the front of the shield in terms of percentage of the total midline length of the shield; this has been termed its anteroposterior position (a.p. position or a.p.p.); the anterior base-line is thus at a.p.p. 0 %, and the posterior one at 100 % (figure 2). The distance of a point from the middle line, referred to as its mesiolateral position (m.l. position, or m.l.p.), also expressed as a percentage of the length of the shield, is similarly easily measured. Results are shown in figure 2, and at half these linear dimensions in figures 3, 4 and 5, and in the data recorded in tables 1 and 2. The positions referred to as points A, B and C are indicated in figure 2. Abbreviations such as S.S. 13:2 or J. 1:3 indicate, respectively, Säve-Söderbergh 1933, pl. 13, fig. 2 and Jarvik 1948, pl. 1, fig. 3.

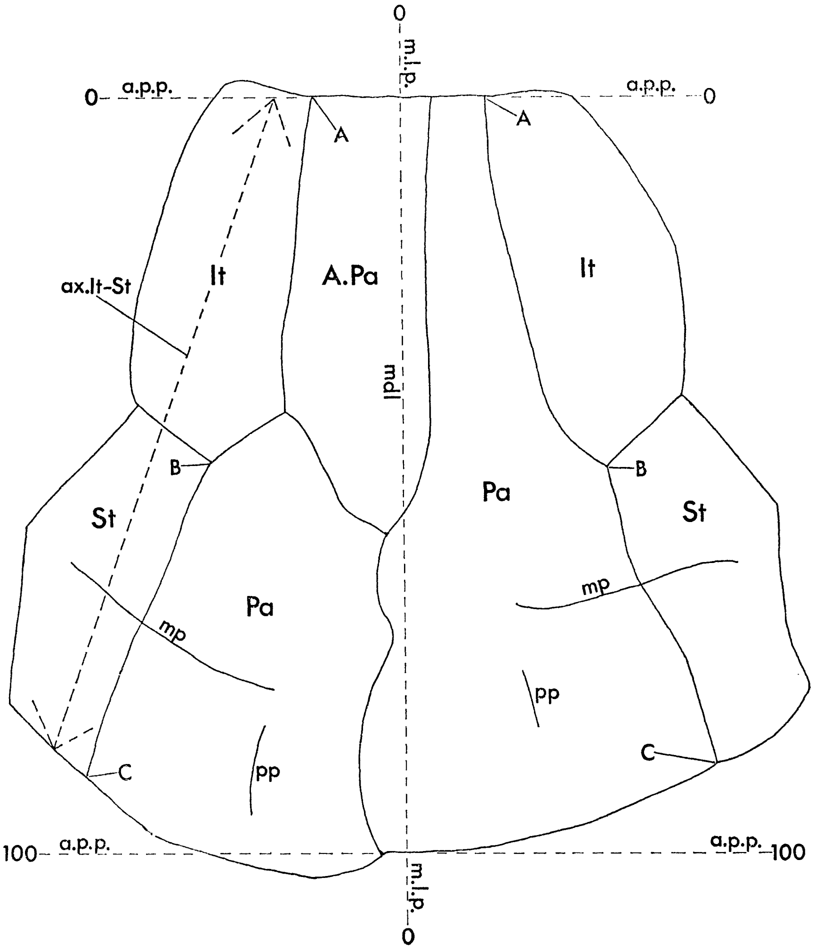

FIGURE 2. *Osteolepis macrolepidotus* Ag. Outline of parietal shield of sd.Pa specimen S.S. 13:2 with midline shield-length at 10 cm to illustrate methods of measurement, as shown by comparison with data on S.S. 13:2 in table 2.

Figures 3 and 4*a–c* show that in ss.Pa specimens the position of the middle line as determined in this way corresponds closely with that of the Pa/Pa suture in the anterior two-thirds of the shield; in the posterior third the course of this suture is less regular. In figure 4*d* there are two intertemporal bones on the left which has upset the symmetry; here the Pa/Pa suture has, anteriorly, been used as a guide instead.

It may be noted that the midline a.p. length of the shield has been used as a basis for comparison of shields of *Osteolepis macrolepidotus*. This, like other possible base-lines, is of course

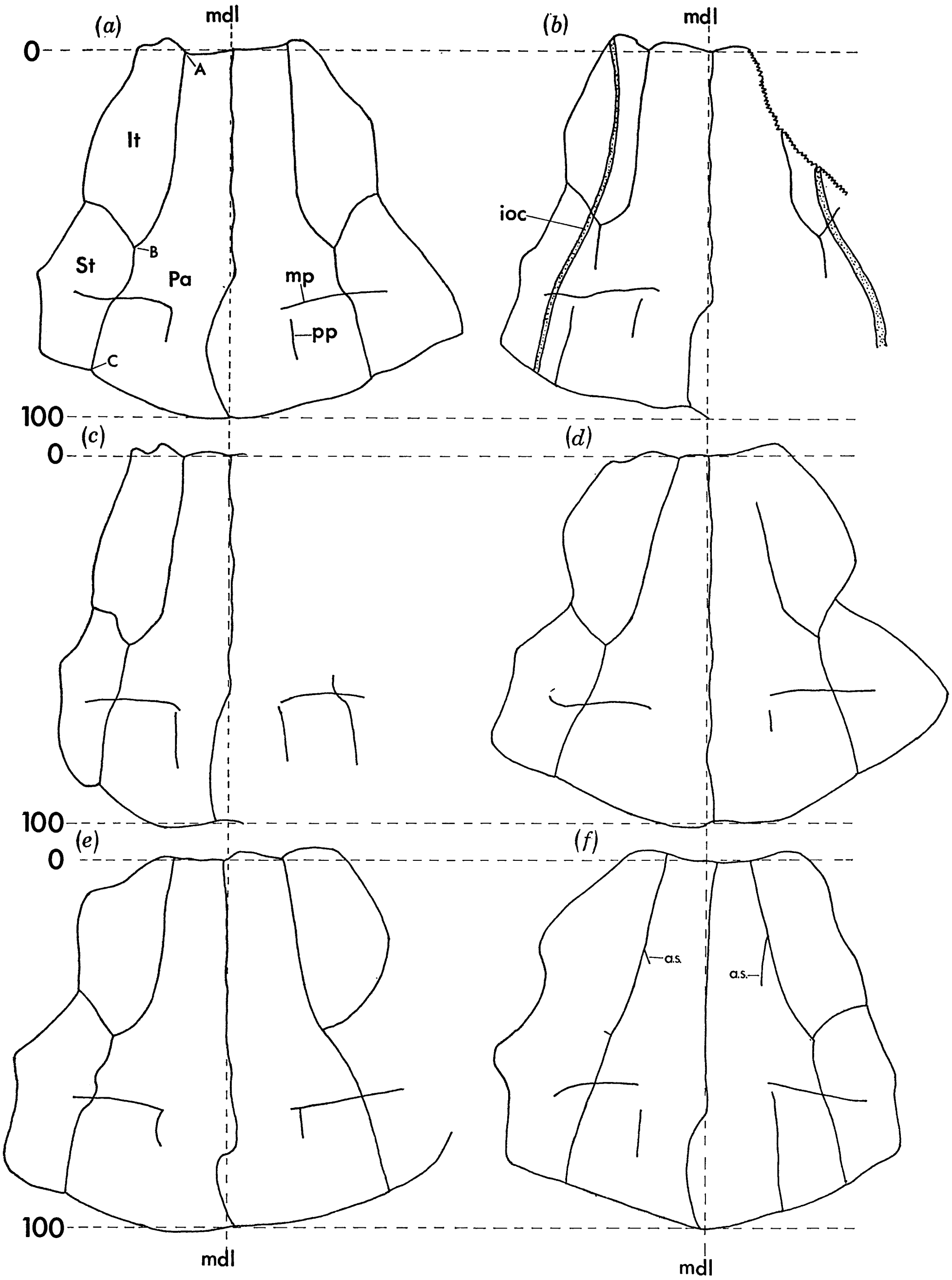

Figure 3. *Osteolepis macrolepidotus* Ag. Outlines of parietal shields of six ss.Pa specimens, brought to a common midline shield-length. After (*a*) S.S. 1:–; (*b*) S.S. 5/6/7; (*c*) S.S. 3:1; (*d*) S.S. 10:1; (*e*) J. 3:1; (*f*) S.S. 8:1.

itself liable to vary. In one case the posterior border of the shield is so much shortened that use of the midline length as a base clearly distorts all the percentages. If instead the point at which the St/Pa suture reaches the edge of the shield is placed at its average a.p. position (see table 1), as in figure 4*e*, this situation is rectified. However it seems that in most specimens the relative midline length of the shield was reasonably constant and can be used as a basis for comparison without introducing serious difficulties.

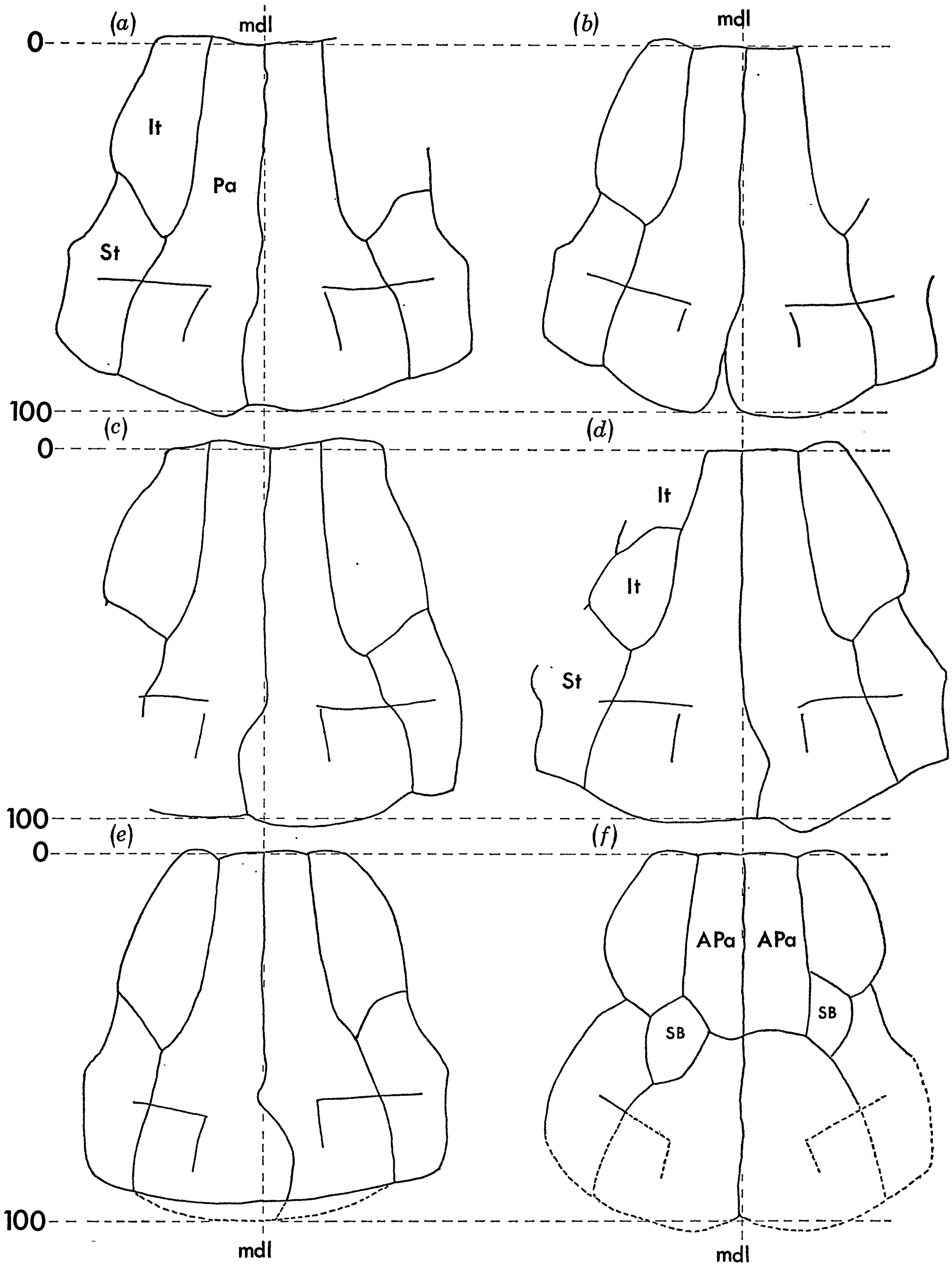

FIGURE 4. *Osteolepis macrolepidotus* Ag. Outlines of parietal shields of ((*a*) to (*e*)) five ss.Pa and (*f*) one dd.Pa specimens. (*a*), (*b*), (*c*), (*d*) and (*f*) brought to common midline shield-lengths. After (*a*) S.S. 11:2; (*b*) J. 4:2; (*c*) J. 9:–; (*d*) S.S. 4:–; (*e*) S.S. 12:2; (*f*) Säve-Söderbergh 1941, pl. 1.

When however the shield of *Osteolepis* is later compared with those of other genera of crossopterygians the situation is different, for the extent of the posterior regions of the shield varies widely and the midline length certainly does not provide a suitable basis for comparison. The architecture of the shield is probably built around the infraorbital canal and the two temporal bones associated with it. The base-line used to obtain outlines of comparable dimensions is therefore drawn through the length of this region, starting at the line representing a.p.p. 0 %, passing through the central regions of It and St, and ending at the posterior border of St. It is

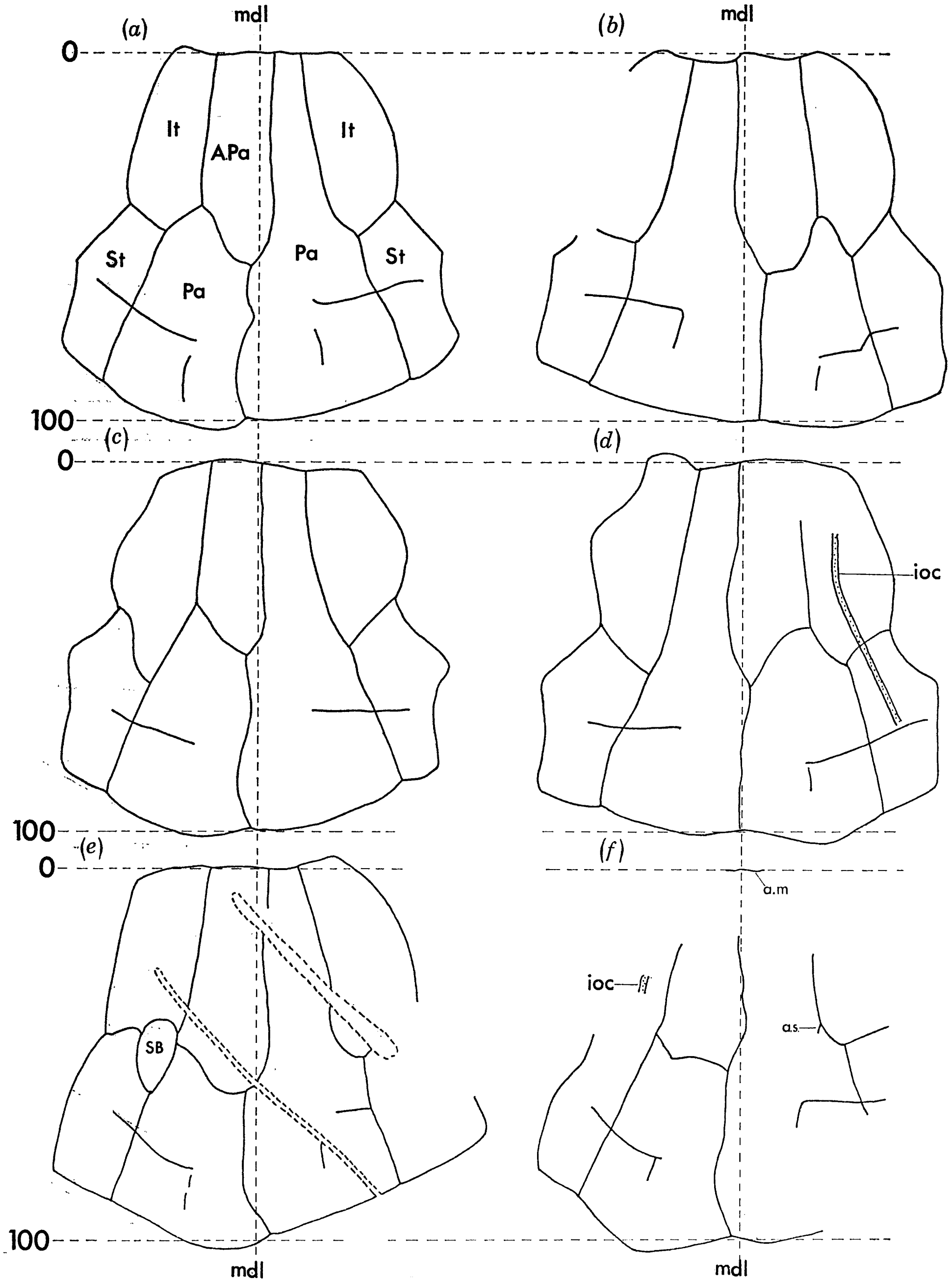

Figure 5. *Osteolepis macrolepidotus* Ag. Outlines of parietal shields of six sd.Pa specimens, brought to a common midline shield-length. After (*a*) S.S. 13:2; (*b*) J. 1:3; (*c*) J. 4:1; (*d*) J. 3:2; (*e*) S.S. 5:2; (*f*) S.S. 11:1.

referred to as the It-St axis, and is shown by a broken line on the left side of figure 2. The average length of this line in 10 cm shields of *O. macrolepidotus* is 9.1 cm (see tables 1 and 2). If the It-St axis of the shields of other crossopterygians are also brought to 9.1 cm, and if then the same a.p.p. 0 % and midline frame of reference is used, it becomes possible to compare the positions of equivalent points on these other shields in terms of a.p. and m.l. positions that are expressed not as percentages of their own midline shield-lengths, which are now one of the variables, but as percentages relative to shields of *Osteolepis* of midline length 10 cm which is

TABLE 1. POSITIONS OF CERTAIN POINTS ON THE PARIETAL SHIELDS OF SS.Pa SPECIMENS OF *OSTEOLEPIS MACROLEPIDOTUS* Ag., EXPRESSED AS PERCENTAGES OF THE MIDLINE SHIELD-LENGTH

			column								
source	side	text figure	1	2	3	4	5	6	7	8	9
S.S.	L	3*a*	13	66	43	70	16	33	87	38	90
1:–	R		15	65	42	70	16	33	89	38	90
S.S.	L	3*b*	17	66	45	65	17	—	90	42	91
5/6/7	R		—	—	—	—	—	—	—	—	—
S.S.	L	3*c*	12	67	39	68	14	31	89	35	91
3:1	R		—	66	38	67	13	31	—	—	—
S.S.	L	3*d*	8	65	44	69	15	34	87	41	90
10:1	R		—	64	45	66	16	35	86	41	88
J.	L	3*e*	14	65	42	68	18	39	90	44	93
3:1	R		15	63	47	67	20	39	90	44	91
S.S.	L	3*f*	11	65	42	61	—	30	88	39	90
8:1	R		12	65	44	61	18	31	88	38	88
S.S.	L	4*a*	14	65	45	66	15	34	90	40	92
11:2	R		16	64	46	66	16	34	91	40	92
J.	L	4*b*	14	63	43	70	15	33	87	38	90
4:2	R		15	68	42	71	13	32	92	37	93
J.	L	4*c*	15	—	—	68	16	33	—	—	—
9:–	R		15	68	47	70	15	33	93	41	95
S.S.	L	4*d*	9	68	40	69	17	36	91	43	94
4:–	R		15	66	44	70	16	35	90	43	90

Column 1. m.l. position of point A.
Column 2. a.p. position of lateral end of mp.
Column 3. m.l. position of lateral end of mp.
Column 4. a.p. position of the mesial end of mp, as indicated by the position at which pp meets mp, or would meet it if it were continued further forwards.
Column 5. m.l. position of mesial end of mp, located as above.
Column 6. m.l. position of the St/Pa sutures at the same a.p. level as the mesial end of mp.
Column 7. a.p. position of point C.
Column 8. m.l. position of point C.
Column 9. Length of It-St axis (p. 57).

being used as a common standard for comparison. If, for example, the a.p.p. of the mesial end of the middle pit-line of *Eusthenopteron* is stated to be 61 %, then this position is 7 % further forward as compared with an a.p.p. of 68 % for *Osteolepis* (figure 13*b*), all three dimensions being expressed as percentages of the midline shield-length of *Osteolepis*, not *Eusthenopteron*. On this basis relative positions can be compared not only with *O. macrolepidotus* but also with one another. The outlines and superimpositions of figures 8–13 and 16–19, and less directly also of figure 20, have been constructed in this way.

TABLE 2. POSITIONS OF CERTAIN POINTS ON THE PARIETAL SHIELDS OF sd.Pa SPECIMENS OF *OSTEOLEPIS MACROLEPIDOTUS* Ag., EXPRESSED AS PERCENTAGES OF THE MIDLINE SHIELD-LENGTHS

			column																		
source	side	text-figure	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19
S.S.	L	*5a*	12	—	—	—	—	—	61	44	78	17	39	50	4	1	—	89	42	—	91
13:2	R		11	62	44	67	15	32	—	—	—	—	—	—			88	—	41	91	—
J.	L	*5b*	14	65	43	69	16	33	—	—	—	—	—	—	5	6	90	—	41	91	—
1:3	R		15	—	—	—	—	—	74	42	82	21	36	52			—	96	42	—	97
J.	L	*5c*	12	—	—	—	—	—	67	39	76	17	35	45	4	3	—	89	41	—	93
4:1	R		13	67	41	67	15	32	—	—	—	—	—	—			86	—	39	90	—
J.	L	*5d*	11	70	42	71	17	32	—	—	—	—	—	—	4	2	93	—	38	95	—
3:2	R		—	—	—	—	—	—	69	51	81	18	35	53			—	95	38	—	95
S.S.	L	*5e*	13	—	—	—	—	—	65	—	81	18	36	54	7?	4?	—	89	39	—	90
5:2	R		11	—	—	66	—	—	—	—	—	—	—	—			85	—	39	86	—
S.S.	L	*5f*	—	—	—	—	—	—	64	40	78	23	39	49	—	—	—	—	—	—	—
11:1	R		—	62	40	62	17	33	—	—	—	—	—	—			—	—	—	—	—

Column 1. m.l. position of point A on both 's' and 'd' sides of the specimen.
Column 2. a.p. position of the lateral end of mp on the 's' side of the specimen.
Column 3. m.l. position of the lateral end of mp on the 's' side of the specimen.
Column 4. a.p. position of the mesial end of mp, located as for column 4 of table 1, on the 's' side of the specimen.
Column 5. m.l. position of the mesial end of mp on the 's' side of the specimen.
Column 6. m.l. position of the St/Pa suture at the same a.p. level as the mesial end of mp, on the 's' side of the specimen.
Column 7. a.p. position of the lateral end of mp on the 'd' side of the specimen.
Column 8. m.l. position of the lateral end of mp on the 'd' side of the specimen.
Column 9. a.p. position of the mesial end of mp on the 'd' side of the specimen.
Column 10. m.l. position of the mesial end of mp on the 'd' side of the specimen.
Column 11. m.l. position of the St/Pa suture at the same a.p. level as the mesial end of mp, on the 'd' side of the specimen.
Column 12. Overall a.p. position (see p. 60) of the A.Pa/Pa suture.
Column 13. Difference between a.p. positions of the posterior borders of the Pa on the 's' and 'd' sides at m.l. position 20%.
Column 14. Difference between a.p. positions of point C on the 's' and 'd' sides.
Column 15. a.p. position of point C on the 's' side of the specimen.
Column 16. a.p. position of point C on the 'd' side of the specimen.
Column 17. m.l. position of point C on both the 's' and 'd' sides of the specimen.
Column 18. Length of It-St axis (see p. 57) on the 's' side of the specimen.
Column 19. Length of It-St axis on the 'd' side of the specimen.

(*b*) *The parietal shield of* Osteolepis macrolepidotus *Agassiz*

This section is mainly concerned with the variation that is found in *Osteolepis macrolepidotus* within the restricted field circumscribed by the two pairs of temporal bones. Säve-Söderbergh (1933) stressed that in the three sd.Pa specimens of this species that were available to him the mesial ends of mp on the 'd' side were further back than those on the 's' side of the same individual, and also than those of normal ss.Pa specimens. Jarvik (1948) confirmed this as regards three additional sd.Pa specimens that he described. Outlines of the shields of these six specimens are shown in figure 5, and one of them also on a larger scale in figure 2. The relevant data are included in tables 1 and 2. An attempt is made to consider these differences quantitatively.

The lateral end of mp is situated at approximately the centre of radiation of St, though in some cases it seems to have a considerable loose end which passes laterally beyond this point (see figure 5*d*, right side). The ss.Pa specimens (table 1, column 2) have an a.p. range of 63–68 %, and a mean of 65.5 %. For the 's' side of the sd.Pa the range is 62–70 %, and the mean 65.2 %. For their 'd' sides the range is 61–74 %, but the 74% refers to J. 1:3 (figure 5*b*) which is an exceptional shield in a number of ways; for the remainder the range is 61–70 %. Thus there is probably no significant difference in the a.p.p. of the lateral end of mp between ss.Pa and sd.Pa specimens, whether on the 's' side or the 'd' side of the latter.

The mesial end of mp has in ss.Pa specimens a range of 61 % to 71 %. One individual (S.S. 8:1, figure 3*f*) is quite exceptional, with a.p.p. 61 % on each side; the lateral ends of its mp are normal at 65 %; it is referred to again later. For the remaining more typical specimens the range of 17 readings is 65–71 %, and the mean 68.2 %. On the 's' side of the sd.Pa specimens the mp, as Säve-Söderbergh has noted, is exceptionally far forwards in S.S. 11:1 (figure 5*f*), being at 62 %; this also is referred to later. For the remaining five the a.p.p. ranges from 66 to 71 %, with a mean of 68 %. On the 's' side therefore there is no difference between ss.Pa and sd.Pa. However on the 'd' side there is a great difference; a.p.p. ranges from 76 to 82 %, with a mean of 79.3 %. Thus the mesial end of mp is about 11 % of shield-length further back on the 'd' side of sd.Pa than on the 's' side. The two ranges do not meet, being separated by an interval of 5 %. This dimorphism in pit-line positions is clearly correlated with the dimorphism in the number of parietal bones on the side in question. An analysis of the data in tables 1 and 2 also shows that the mesial end of mp is in these cases situated slightly more laterally, as well as further back; the overall direction of their movement was approximately parallel with the St/Pa suture. Figure 5 also shows that the Pa on the 'd' side consistently extends further posteriorly than the single Pa on the 's' side (table 2, column 13). This is seen well in S.S. 13:2 (figures 2, 5*a*) which is excellently preserved.

In all the sd.Pa specimens except figure 5*f*, A.Pa has transgressed across the middle line; the amounts, at a.p.p. 25 %, vary between 1 and 3 %. This trespass usually reaches a maximum rather further back, after which the A.Pa/Pa suture soon crosses to the 'd' side of the middle line. Thereafter (except in figure 5*d*) the position is reversed, for in the posterior half of the shield it is the Pa of the 's' side that has crossed the middle line and occupied territory that would normally have belonged to its fellow Pa; in S.S. 13:2 this incursion reaches a depth of about 6 %. This posterior transgression is particularly interesting; it has presumably arisen owing to the Pa on the 'd' side developing later or more slowly than that on the 's' side, which consequently gained an opportunity to establish a trespass. This postulated late development of one of the parietals seems therefore to have been correlated with the development of an additional parietal ossification further forwards, and may have been the 'cause' of its appearance, and hence also of the sd.Pa condition. However some ss.Pa (see figure 3*a*) have comparable deviations of the Pa/Pa suture without having become sd.Pa.

A schematic pattern of ontogeny that endeavours to take account of these observations and of the implied timing of events is shown in figure 6. It is self-explanatory. There is sufficient evidence to permit the assumption that the mesial end of mp was closely tied to the centre of radiation of the bone, and it could therefore be used as a marker indicating the approximate position of this centre. The ossification of this Pa was presumably initiated in the usual place; from here it has on the 'd' side undergone an absolute movement, relative to the rest of the shield, backwards and slightly laterally, amounting on average to about 11 % of the shield's length (figure 6*f*). This is unlikely to have been due to a reorganization of bone structure within the parietal; also this would probably not have carried the pit-line backwards. Perhaps the anterior portion of the horizontal lamella of the bone, geared to extend rapidly forwards and meeting an obstacle in the form of the A.Pa, would by its continued growth have instead pushed bodily backwards the whole central region of the bone including its centre of radiation and the pit-lines anchored nearby.

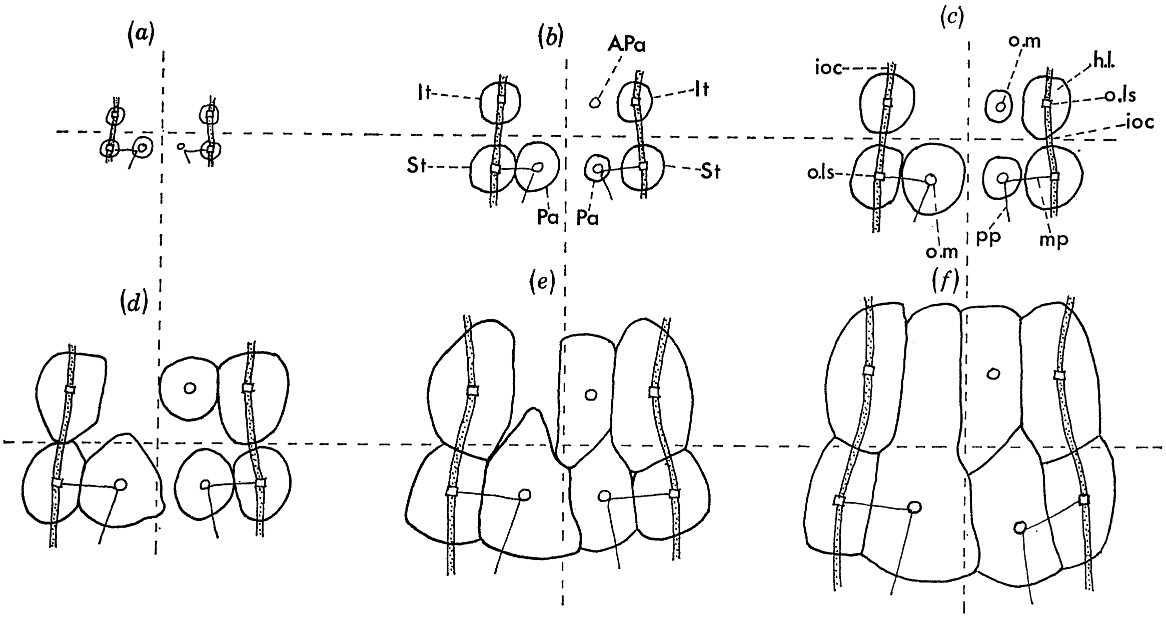

FIGURE 6. *Osteolepis macrolepidotus* Ag. Postulated patterns of growth of the parietal shield of sd.Pa specimens.

This line of thought suggests that the further the A.Pa grew backwards, as measured for instance by the a.p.p. of a point midway along its posterior suture (table 2, column 12), the more would the forward movement of Pa have been blocked, and therefore would its centre of radiation and the relevant pit-lines have been displaced backwards. There is some evidence that this was the case (figure 7). In ss.Pa, with zero extension of A.Pa, mp is at a.p.p. 68 % ((*a*), figure 7); in (*b*) (J. 4:1) the backward growth of A.Pa is 45 %, and mp position 76 %; the average of (*e*) (*f*) and (*g*) shows A.Pa at 53 % and mp at 81.6 %.

The s.d.Pa specimen of figure 5*f* is remarkable in showing no transgression by A.Pa across the middle line, the mesial end of mp on the 's' side unusually far forward (a.p.p. 62 %), and the remains of what may be an abortive suture (a.s.) diverging from the It/Pa suture at about the position where a suture separating an A.Pa from the Pa of its own side could have been expected. Is it possible that this individual initially developed an A.Pa. ossification on the right side, as well as on the left, which would have prevented the left A.Pa ossification from transgressing and could have begun to form a suture with the normal Pa behind it, and that then for some reason this ossification regressed and was replaced by, or was submerged by, a Pa behind it that swept forwards, demolishing the greater part of the juvenile suture, incorporating the area in front of this into its own bony structure, and carrying its own centre of radiation further forward in the course of this relatively sudden surge? This speculative comment brings to mind the parietal of *Polypterus* which regresses and has its place taken by the advancing lamella o.

the dermopterotic (Pehrson 1947, 1958), and also Miles's (1971, p. 182) account of a small anamestic bone in *Holonema* which usually becomes incorporated into the bone in front of it and sometimes retains a remnant of a suture there. The ss.Pa specimen of figure 3*f* may be a bilateral instance of the same condition; both sides show the mp abnormally far forwards (61 %) and possible abortive sutures (a.s.), which are however considerably further forward. It may have just missed becoming a dd.Pa.

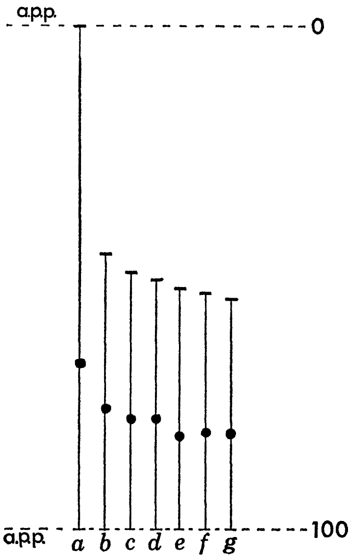

Figure 7. *Osteolepis macrolepidotus* Ag. Relation of a.p. length of parietal to a.p. position o mesial end of middle pit-line. For explanation see text.

The only dd.Pa specimen (Säve-Söderbergh 1941) is defective posteriorly, but it shows (figure 4*f*) that there was no trespass either anteriorly or posteriorly; also the mp grooves were probably similar to those on the 'd' side of sd.Pa specimens. An ontogeny in which both sides resembled that shown on the right in figure 6*a–c* would lead to this type of shield. There were also the supernumerary bones SB.

Commenting on the possible phylogenetic implications one may note that an A.Pa was formed occasionally in *Latvius* and *Eusthenopteron*, as well as in *Osteolepis*. A capacity to form a bone by membranogenesis in this position may therefore have been characteristic of osteolepiforms in general. This suggests that it was not a new feature, but more probably a relic of a time when a bone had regularly been formed in this position, perhaps as a part of a general pattern of the skull-roof such as that suggested for a generalized osteichthyan in figure 25*e*. At this stage it may well have been a latero-sensory bone formed in association with the supraorbital canal; later this sensory line no longer reached this region in crossopterygians, perhaps on account of the development of the intracranial juncture apparatus or, alternatively, through a change in orientation such as that postulated later (pages 88, 93). However it is unlikely that the loss of this bone was due in any important sense to the withdrawal of this latero-sensory stimulus; if the presence of the bone had been selectively advantageous it would presumably have continued to be formed, though now by membranogenesis, and this did in fact still occur occasionally among members of the *Osteolepis* population living in the Middle Devonian. This transition would have been from (*b*) to (*a*) on the X side of figure 1. Probably therefore a single bone proved more advantageous, perhaps through conferring greater strength to the shield; on the other hand the capacity to form the more anterior bone when developmental processes deviated somewhat from the normal was retained and was presumably advantageous to the population as a whole. This kind of phyletic history would account for the centre of radiation being so far back within the parietal bone; it has merely remained in the position indicated in figure 25*e* in spite of the bone having developed an anterior extension that occupied the territory of the bone that had been in front of it, as shown in figure 25*g*.

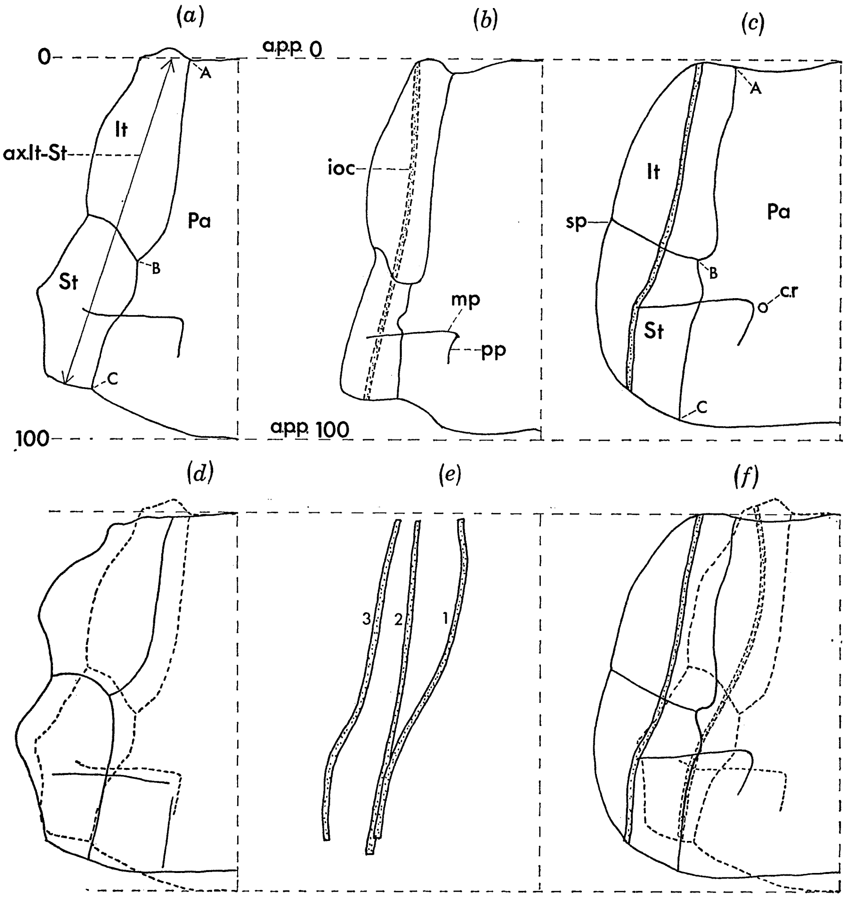

Figure 8. Parietal shield of *Gyroptychius*, and comparison with *Osteolepis*, on basis of equal lengths of It-St axis. (*a*), 'typical' *Osteolepis*. (*b*), *Gyroptychius agassizi* (Traill), after Jarvik 1948, pl. 29, fig. 1; the position of the lateral-line canal is postulated. (*c*), *Gyroptychius groenlandicus* Jarvik, after Jarvik 1950*a*, pl. 9, fig. 4. (*d*), *Osteolepis panderi* (Pander) after Jarvik 1948, pl. 13, Figure 2 (continuous lines) superimposed on 'typical' *Osteolepis* (discontinuous lines). (*e*), positions of lateral-line canals in (1) *Osteolepis macrolepidotus* (S.S. 5/6/7), (2) as postulated in *G. agassizi* and (3) in *G. groenlandicus*. (*f*), figure 8*c* (continuous lines) superimposed on 8*a* (discontinuous lines).

Jarvik (1948, pp. 82, 118, 119) considers that the single parietal of osteolepiforms is formed by a fusion of the two bones that are present on the 'd' side in the sd.Pa condition; he supports this view by noting that its centre lies between those of the two bones in question. However, though between them, it is by no means approximately midway between them, as might be expected in the case of fusion. This would bring the centre of radiation of the single parietal to about a.p.p. 52 %, whereas in *Osteolepis* it is usually about 68 %, and only exceptionally less than 65 %. In other words, Jarvik's supposition of fusion does not account for the centre of radiation of the single parietal being far back within the bone. Nor does the form of ontogeny that is implied account for either of the transgressions across the middle line that appear to be characteristic of sd.Pa specimens.

(*c*) *Comparison of parietal shields of osteolepiforms*

(i) Osteolepis *and* Gyroptychius

Table 1 indicates that the dimensions of the left side of the parietal shield of the specimen (figure 3*a*) of *Osteolepis macrolepidotus* illustrated by Säve-Söderbergh's (1933) pl. 1 correspond very closely with the average ss.Pa condition; with very slight modification it has been used (figure 8*a*) to represent the 'typical' condition found in this species. Comparison with other osteolepiforms, and also with other kinds of crossopterygians, have been made with this 'typical' *Osteolepis*, by using as a basis for this purpose an It-St axis of a common 9.1 cm length, in ways and for reasons that have already been explained (p. 57). All a.p. and m.l. positions are therefore expressed as percentages of the midline shield-length of this *Osteolepis*, and not of the shield of the species or individual to which the dimensions refer.

There is in *Osteolepis macrolepidotus* considerable mesiolateral variation in the position of the It/Pa and St/Pa sutures, and therefore in the width of the space occupied by the parietals. Point A at the front of the shield varies between m.l.p. 8 and 17 % (tables 1 and 2, column 1), with a mean of 13 %, and with most of the specimens between 11 and 15 %. There is no difference between ss.Pa and sd.Pa individuals. For point C at the back of the shield the corresponding range is 35 to 44 %, the mean 40 %, and most specimens between 38 % and 42 %.

Outlines of two well preserved shields of different species of *Gyroptychius* are shown, using the It–St axis, in figure 8*b* and 8*c*; in (*b*) ioc is not seen, but was doubtless in approximately the position indicated. In figure 8*b* point A is at m.l.p. 24 %, and in (*c*) at 28 %; the latter is therefore more than twice the mean (13 %) of *O. macrolepidotus*. It is interesting that in another species of *Osteolepis*, *O. panderi* (Pander), as represented by Jarvik 1948, pl. 13, figs 2, 4 and pl. 14, fig. 2, it is between 17 and 19 %, and therefore in an intermediate position. Thus for the two genera together the relative breadth of this anterior region extends between 8 and 28 %. At the back of the shield m.l.p. for point C are, in figure 8*b* about 39 %, in (*c*) 42 %, and in the three specimens of *O. panderi* between 40 % and 42 %. All these are therefore within the normal range of *O. macrolepidotus*. Thus at the anterior end of their parietal shields the *Osteolepis-Gyroptychius* series seem to have exhibited a very wide range of variation in the positions of their intertemporals and infraorbital canals; on the other hand at the back of their shields the corresponding range as regards the supratemporals was relatively small. These and other comparative features are demonstrated by the superimpositions of figure 8*d* and *f*, and by the indication of the relative positions of the sensory canals in figure 8*e*. The *Gyroptychius* of figure 8*c* shows that the pit-lines mp and pp have united at their ends, thus forming a single line that bends through a right angle; this occurs frequently in osteolepiforms. The centre of radiation (c.r.) of the parietal is also seen unusually well; it is very close to the union between the two lines, probably slightly mesial to it.

(ii) Latvius

Isolated parietal shields of *Latvius* have been described by Gross (1956) from the Baltic area; these belong to mature individuals, and in dorsal view the sutures are usually obscured by cosmine. More recently Jessen (1966) has described complete specimens from the Plattenkalk of Bergisch Gladbach in Germany; some of these are juvenile and show the sutures clearly. Two of these (figure 9*a* and *b*) are particularly interesting; in figures 9*c* and *d* their left sides are superimposed on that of the typical *Osteolepis* of figure 8*a*. In both of these the course of the It/Pa suture is very similar to that of *Osteolepis* down to about a.p.p. 45 %; it then swings abruptly lateralward for some 14 %, giving the appearance of a 'shoulder'. A much smaller

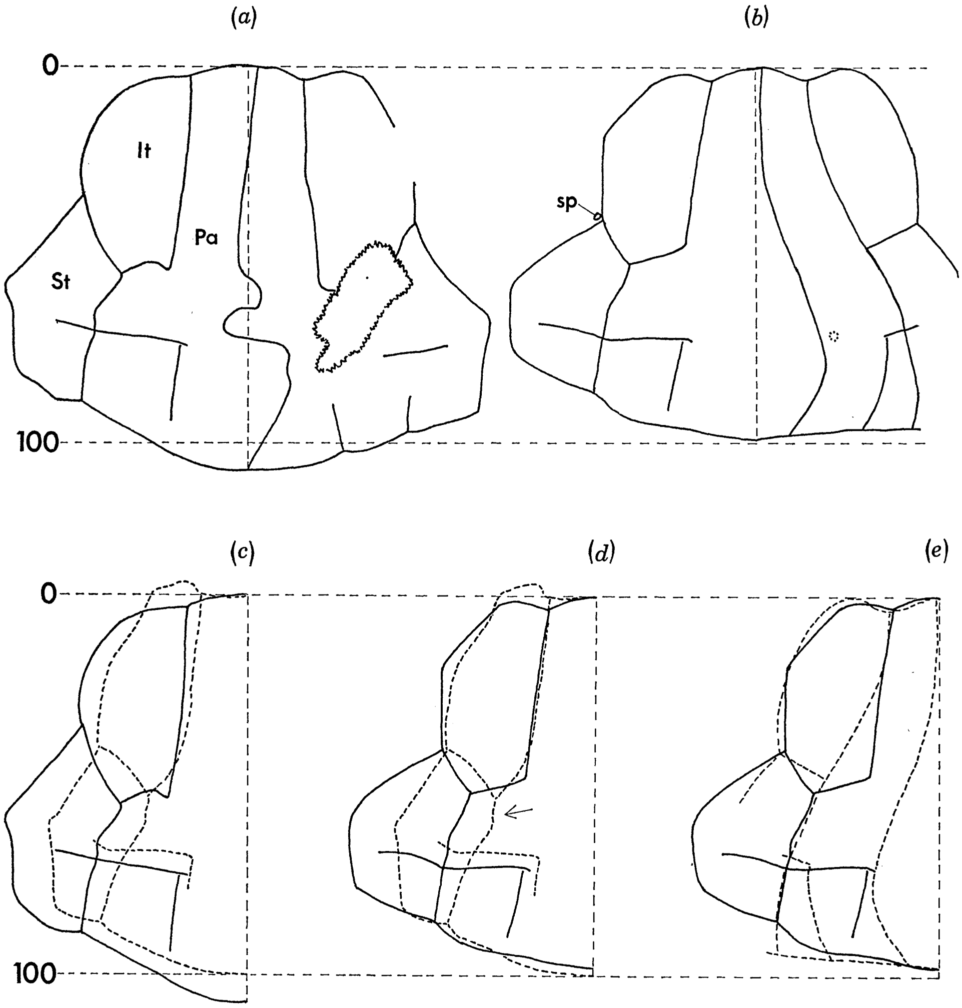

FIGURE 9. Parietal shield of *Latvius*, and comparison with that of 'typical' *Osteolepis*, on basis of equal lengths of It-St axis. (*a*) *Latvius*, after Jessen 1966, pl. 7, fig. 1. (*b*), *Latvius*, after Jessen 1966, pl. 8, fig. 3. (*c*) left side of figure 9*a* (continuous lines) superimposed on 'typical' *Osteolepis* (discontinuous lines). (*d*) left side of figure 9*b* superimposed on 'typical' *Osteolepis* (discontinuous lines). (*e*) right side of figure 9*b* (discontinuous lines) transposed to left side and superimposed on the left side of the same shield (continuous lines).

and more rounded 'shoulder' is present also in *Osteolepis*; in some specimens of *Gyroptychius* even this is missing. Also in these *Latvius* the St/Pa suture is further lateralward, by about 7 % at the level of mp, and about 4 % at point C. The centre of St is also clearly further lateral; figure 10*b* shows that in this *Latvius* the sensory canal deviates lateralward to a maximum of about 18 % from a line (l.c.) connecting the centres of It and Esc.l, whereas in *Osteolepis* this lateral excursion is relatively small (figure 10*a* and *c*). The general lateral extension has increased the length of mp, and the overall breadth of the shield at the corresponding level, as compared with *Osteolepis*.

This correlated set of changes, and in particular the divergence of the sensory canal, seems to imply an area of greater differential growth in the dermis. It caused a general broadening of the posterior half of the shield and by extending the amount of dermis available it altered the eventual dispositions of the relevant bones and sensory structures. It seems to have developed after the ossifications and sensory lines had become established. The superimpositions suggest that this postulated area of greater differential growth was centred in the parietal region in about the position of the arrow in figures 9*d* and 10*c*, that the increased rate of growth was mainly directed laterally, and that the range of its effect was sharply demarcated anteriorly, so giving rise to the 'shoulder'. The part of the shield in front of this 'shoulder' was not affected. The slight indication of a 'shoulder' in *Osteolepis* and in some specimens of *Gyroptychius* may indicate that in these also there was a small amount of similar growth. In *Latvius* itself the amount seems to have varied widely and was sometimes no greater than in *Osteolepis*, and then the two types of shield were very similar. The differential growth envisaged may have been similar in principle to that which apparently occurred in some labyrinthodonts (Bystrow 1935; Säve-Söderbergh 1937).

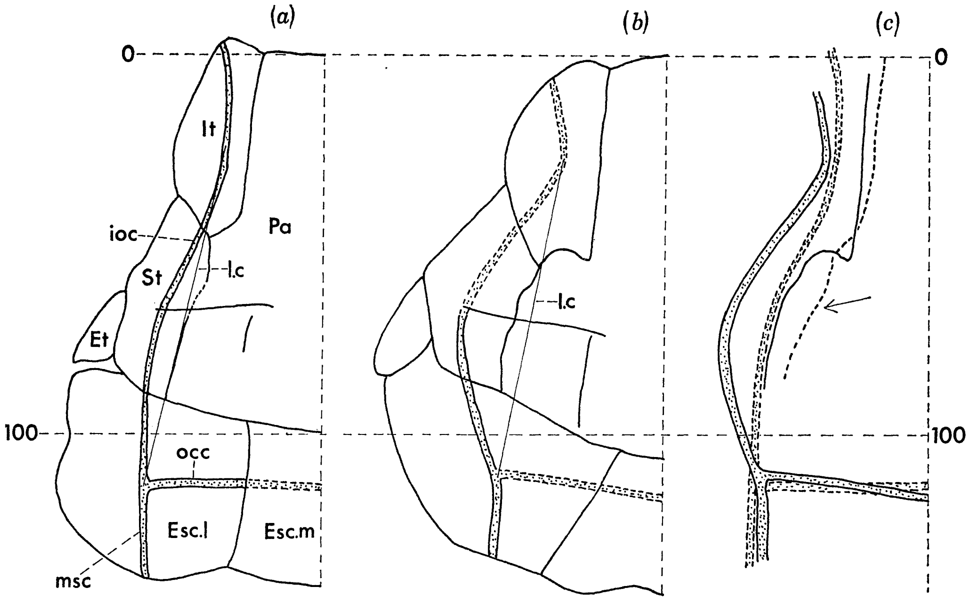

FIGURE 10. Comparison of courses of lateral-line canals in *Osteolepis* and *Latvius*, based on equal lengths of It-St axis. (*a*) *Osteolepis* after S.S. 5/6/7. (*b*) *Latvius* after Jessen 1966, pl. 7, fig. 1. (*c*) lateral-line canals and It/Pa and St/Pa sutures of figures 10*a* and 10*b* superimposed, *Latvius* with continuous lines.

Figure 9*b* shows other interesting features. The left Pa has made a huge excursion into the territory of the right Pa. Also the right It/Pa suture has no 'shoulder', and the asymmetry relative to that of the left side presents difficulties in determining the midline. A line was drawn on the left side which followed the same essentially direct course between points A and B as that traversed on the right side. The midline was then assessed as lying symmetrically between these two lines. The result paired up well with the midline as determined further back by reference to the two St/Pa sutures. The parietal excursion seems similar in principle to the much smaller deviations in Pa/Pa sutures seen in some ss.Pa *Osteolepis* (see figure 3*a*). In these the m.l. positions of the centres of radiation of both Pa, as indicated by the pit-lines, has remained unchanged. This applies also in figure 9*b* to the Pa that has done the transgressing; on the other hand the centre of radiation of the one whose growth has been restricted moved from the corresponding m.l.p. 20 %, shown by the dotted circle, a further 14 % lateralward to m.l.p. 34 %.

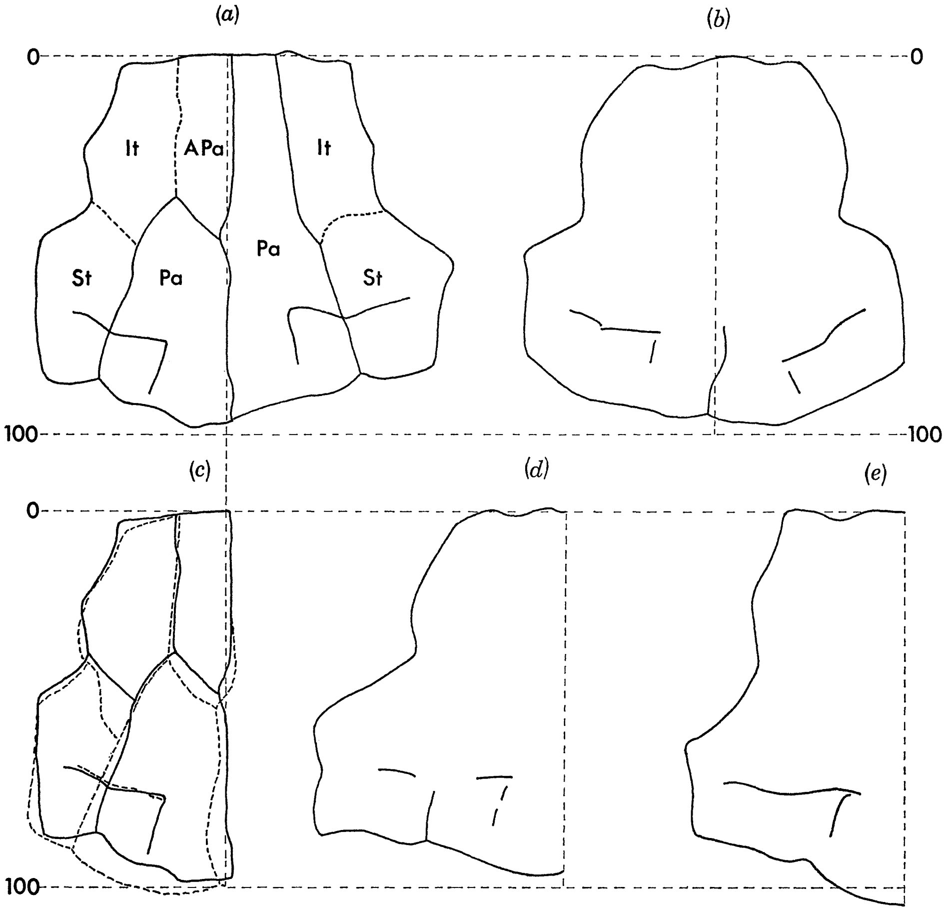

FIGURE 11. Parietal shields of *Latvius*. (*a*) sd.Pa specimen, after Gross 1956, pl. 2, fig. 3. (*b*) sd.Pa specimen, after Gross 1956, pl. 1, fig. 6. (*c*) left ('d') side of figure 11*a* (continuous lines) superimposed on left 'd' side of sd.Pa *Osteolepis* J. 4:1, figure 5*c*, (discontinuous lines). (*d*) after Gross 1956, pl. 1, fig. 4. (*e*) after Gross 1956 pl. 2, fig. 1.

This shift may have been comparable with that which occurred within the parietals on the 'd' side of sd.Pa *Osteolepis* (p. 59). Judging from figure 9*e* the only other important change associated with this gross parietal asymmetry was the infilling of the prominence in the posteromesial region of It that had developed as an indirect consequence of the more intensive lateral growth in the posterior part of the shield.

Gross (1956) has described two sd.Pa shields of *Latvius*. In one (figure 11*b*) the sutures are obscured by cosmine; the mesial end of the mp of the 'd' side is at about a.p.p. 81 %. In the other (figure 11*a* and *c*) some of the sutures are seen, though indistinctly. The suture separating A.Pa from the Pa of its own side is about 4 % further forward than in *Osteolepis* J. 4:1 (see figure 11*c*), and it is therefore even further forward (table 2, column 12) when compared with any of the other sd.Pa *Osteolepis*. Evidence already noted (see figure 7) has indicated that, if other circumstances were similar, the mesial end of this mp in this *Latvius* should be about 2 % further forward than in the J. 4:1 *Osteolepis*. However in ss.Pa *Latvius* the mesial end of mp seems usually to have been some 3 or 4 % further back than in typical *Osteolepis* (see figure 9*c* and *d*). It is likely that in this instance the effect on mp of these two contrary differences cancelled one another, since in both cases its mesial end is at a.p.p. 76 % and the two courses of the line are virtually coincident (figure 11*c*).

(iii) Glyptopomus

There are three important specimens of *Glyptopomus*, each of which is referred by Jarvik (1950*b*) to a different species. An outline of the parietal shield of the first is shown in figure 12*a*, with part of the sensory canal tentatively incorporated on the basis of the second. The third (figure 12*b*) represents an important variation.

The slender anterior extensions of the parietal bones (figure 12*a*) are characteristic of typical specimens. Figure 12*c* provides a comparison with *Osteolepis*. It seems that the sensory canals reach considerably nearer to the middle line in *Glyptopomus* (m.l.p about 18 %) than in *Osteolepis* (about 25 %); the intertemporal bones that develop around these canals consequently leave little space available for the forward growth of the parietals. Point A is at m.l.p. 9 %, compared with 13 % in *Osteolepis*, and at a.p. level 25 % the breadth of each parietal is 10 %, compared with 15 % in *Osteolepis*. The lateral end of mp was probably at about a.p.p. 66 %, much as in *Osteolepis*; however from there it passes posteromesially to a union with pp at a.p.p. 78 %, compared with 68 % in ss.Pa *Osteolepis*, as shown in figure 12*c*; this course is identical with that on the 'd' side of the sd.Pa *Osteolepis* shown in figure 12*e*. A possible explanation of this resemblance, which however is based only on a single side of a single specimen, is that in *Glyptopomus* the anterior extensions of the parietals were so slender that they played little part in the dynamics of the bone and that consequently its centre of radiation came to be located as far back as it would have been if, as in the equivalent 'd' side in sd.Pa *Osteolepis*, it had been entirely deprived of an anterior extension. This suggestion receives support from the variation (figure 12*b*) in which the parietals have failed to advance, for here the course of mp coincides both with the former *Glyptopomus* (figure 12*d*) and with that of a restricted parietal of an sd.Pa *Osteolepis* (figure 12*f*).

It is clear that in the specimen shown in figure 12*b* the parietals have not advanced and that in this contingency the organism has not responded by developing A.Pa ossifications, as would probably have occurred in other osteolepiforms under similar circumstances; it therefore seems likely that the failure to respond in this way was associated with the extreme restriction of the field that remained available between each intertemporal and the middle line. Instead the intertemporals have extended mesially to meet one another in the middle line, and also further back a median supernumerary bone (SB) has been formed. Intertemporals usually show no tendency to encroach on the parietal area and their response, as also the supernumerary ossification, may have been relatively late and occasioned by the absence of alternative procedures that would otherwise have filled the gap.

(iv) Eusthenopteron *with comments of ichthyostegids*

Eusthenopteron is known principally from abundant material of *E. foordi* Whiteaves obtained from the Upper Devonian of Escuminac Bay. Jarvik's (1948) fig. 16*b* is used to represent the standard condition of the shield (figure 13*a*), and photographs illustrating variations published by Jarvik (1944, fig. 10*b*) and by Säve-Söderbergh (1933, pl. 16) are also used (figure 13*d* and *g* respectively). A small amount of material of the allied genus *Eusthenodon* from the very late Upper Devonian of East Greenland has been described by Jarvik (1952); his fig. 24 has been used (figure 13*c*).

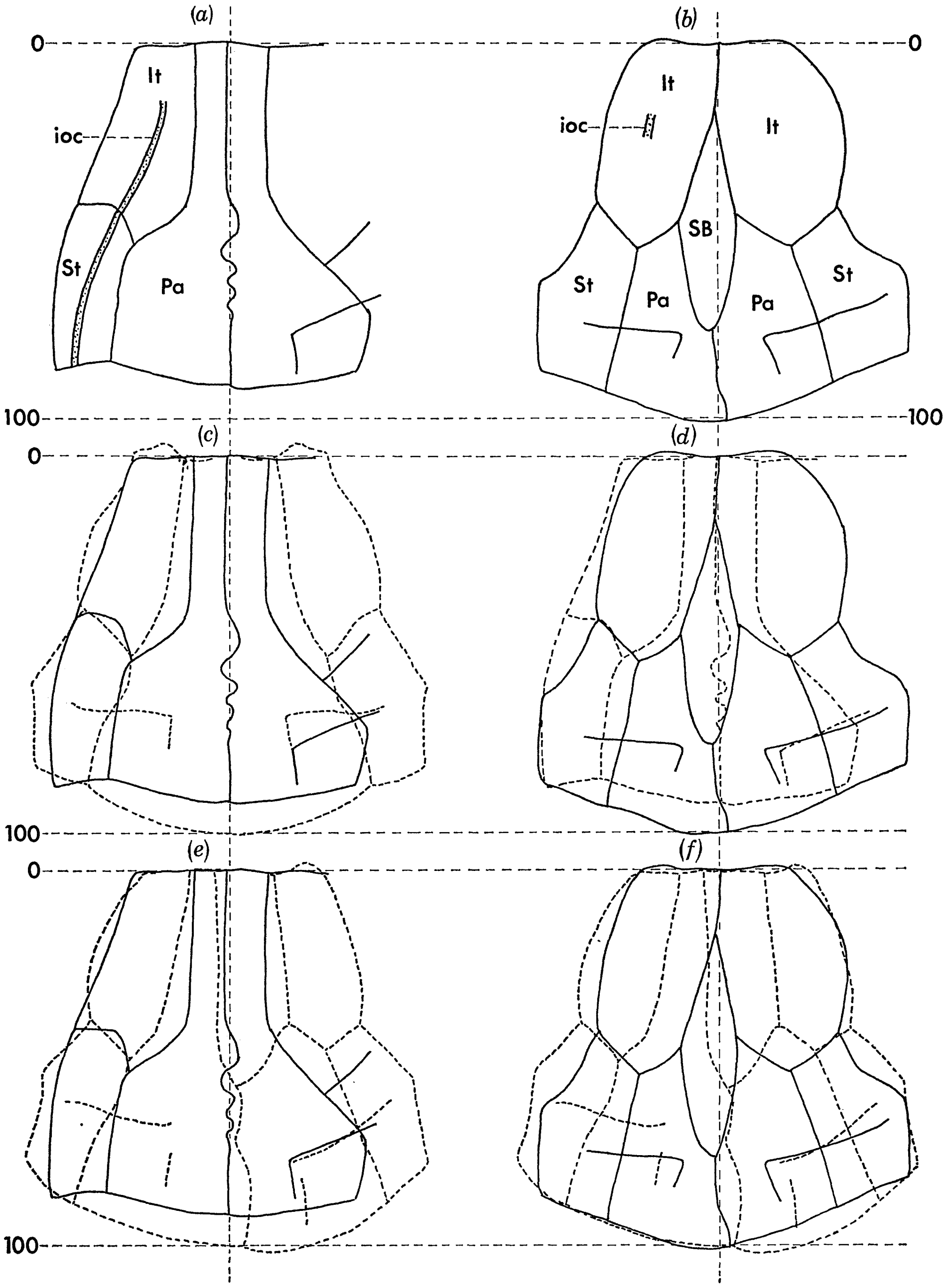

FIGURE 12. Parietal shields of *Glyptopomus* and comparison with those of *Osteolepis* on the basis of equal lengths of It-St axis. (*a*) *Glyptopomus* after Jarvik 1950*b*, pl. 5, fig. 1, except lateral-line canal, which after his pl. 2, fig. 1. (*b*) *Glyptopomus*, after Jarvik 1950*b*, pl. 2, fig. 2. (*c*) figure 12*a* (continuous lines) superimposed on 'typical' *Osteolepsis* (discontinuous lines). (*d*) figure 12*a* (discontinuous lines) superimposed on 12*b* (continuous lines). (*e*) figure 12*a*, and (*f*) figure 12*b*, each superimposed on sd.Pa *Osteolepis* S.S. 13:2 with sides transposed (discontinuous lines).

The superimposition of generalized shields of *Osteolepis* and *Eusthenopteron*, using the It-St axis, emphasizes (figure 13*b*) that its posterior border is markedly convex in the former and slightly concave in the latter; the overall reduction in the posterior part of the shield amounts, at the midline, to 21 % of the *Osteolepis* shield-length. The lateral ends of mp are at about

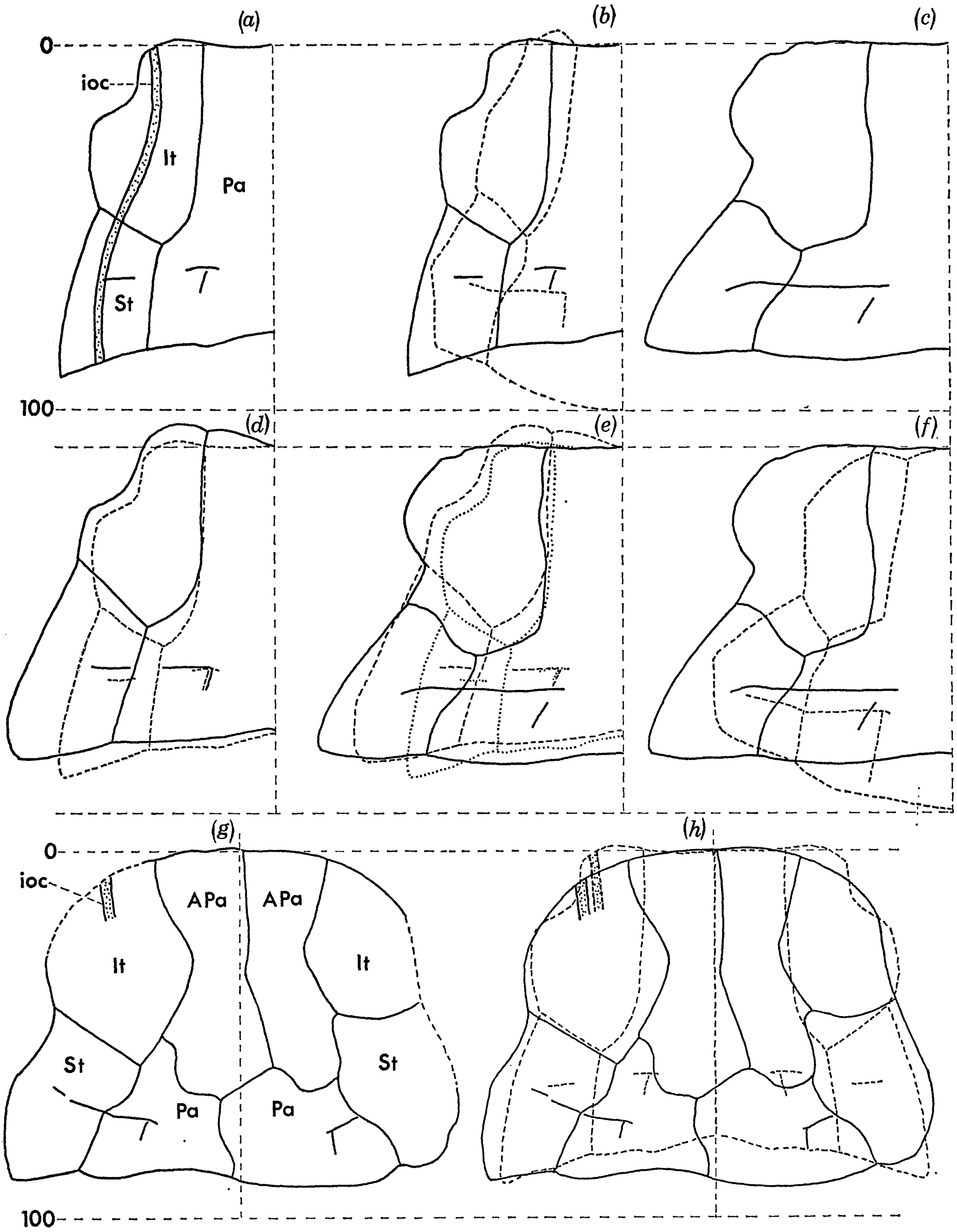

FIGURE 13. Parietal shields of *Eusthenopteron* and *Eusthenodon*, and comparison with *Osteolepis*, based on equal lengths of It-St axis. (*a*) generalized *Eusthenopteron* after Jarvik 1948, fig. 16*b*. (*b*) figure 13*a* (continuous lines) superimposed on 'typical' *Osteolepis* (discontinuous lines). (*c*) *Eusthenodon*, after Jarvik 1952, fig. 24. (*d*) *Eusthenopteron* variation, after Jarvik 1944, fig. 10*b* (continuous lines) superimposed on figure 13*a* (discontinuous lines). (*e*) figures 13*a* (dotted lines), 13*d* (discontinuous) and 13*c* (continuous lines) mutually superimposed. (*f*) *Eusthenodon* of figure 13*c* (continuous lines) superimposed on *Latvius* of figure 9*b* (discontinuous lines). (*g*) *Eusthenopteron* variation, after Säve-Söderbergh 1933, pl. 16. (*h*) this variation (figure 13*g*, continuous lines) superimposed on generalized *Eusthenopteron* shield (figure 13*a*, discontinuous lines).

the same positions, but its mesial end is at a.p.p. 61 % in *Eusthenopteron*, and so 7 % further forward than in *Osteolepsis*. Comparison of figure 14*a* with *b* suggests that in *Eusthenopteron* the backward growth of the parietals has been restricted by a relative forward movement, in the course of phylogeny, of the commissural canal (occ) and the extrascapular bones with which it is associated. The forward shift in the centre of radiation of the parietals may therefore have been comparable with, though in the reverse direction to, that which occurs in the parietal on the 'd' side of sd.Pa *Osteolepis*.

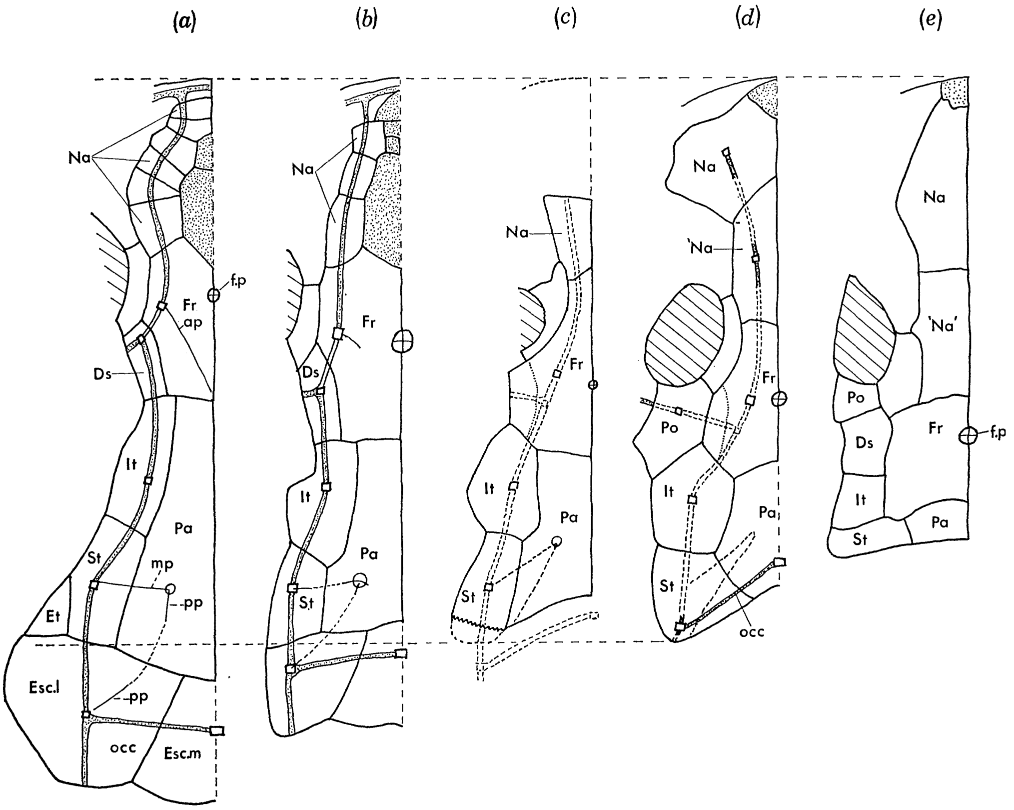

FIGURE 14. Comparison of some dermal skull-roofs of some osteolepiforms and labyrinthodonts. (*a*) *Osteolepis*, after Jarvik 1948, fig. 16*a*. (*b*) *Eusthenopteron*, after Jarvik 1948, fig, 16*b*. (*c*) *Elpistostege*, after Westoll 1938, fig. 1. (*d*) *Ichthyostega*, mainly after Jarvik 1952, fig. 35*b*. (*e*) *Seymouria*, after Romer 1947, fig. 47. For base lines and explanation see text. Known structures are indicated by continuous lines, and postulated ones by discontinuous lines.

It is interesting to consider whether this change played any part in the evolution of ichthyostegids from osteolepiforms. Jarvik (1948, fig. 16A and B) has shown outlines of the skull-roofs of *Osteolepis* and *Eusthenopteron* brought to a common overall length; in figures 14*a* and *b* these are again compared, but here using as a posterior base-line the position at which the sensory canal leaves the back of the supratemporal, which is equivalent to the posterior end of the It-St axis. In this way the variation referred to above is largely prevented from distorting the common base used for comparison. *Elpistostege* (figure 14*c*) is placed as far as possible in this framework; *Ichthyostega* (figure 14*d*) fits into it easily; an attempt is made also to include *Seymouria* (figure 14*e*), as a typical labyrinthodont.

This series appears to show certain trends. In figure 14 outlines (*a*), (*b*), (*c*), (*d*) and (*e*) are merely spaced at regular intervals; in figure 15 the same five types are represented by vertical lines on which the anteroposterior positions of certain equivalent points are shown; here the five types are spaced in such a way as, overall, to make these various equivalent points be arranged as nearly as possible in straight lines, or in other words to make the trends as smooth as possible.

It is the posterior part of the skull-roof that concerns us. As already mentioned, the posterior border of the parietal of *Eusthenopteron* is further forward than that of *Osteolepis* (figure 14*a* and *b*). It is still further forward, by nearly as much again, in *Ichthyostega* (figure 14*d*), and in figure 15 these three points lie almost exactly on a straight line (line 9). *Elpistostege* seems also to conform,

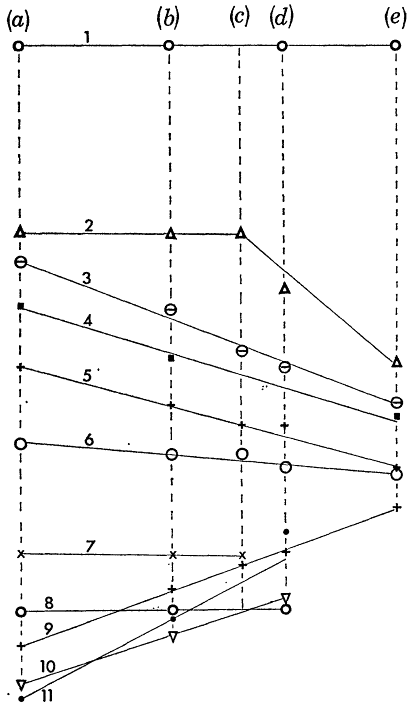

Figure 15. Comparison of certain corresponding positions on dermal skull-roof, based on figure 14. (*a*) *Osteolepis*. (*b*) *Eusthenopteron*. (*c*) *Elpistostege*. (*d*) *Ichthyostega*. (*e*) *Seymouria*. The base-line used for (*a*)–(*d*) is the posterior border of the supratemporal (line 8), and for (*e*) the extrapolated position of the posterior border of the parietal (line 9). For explanation see text.

though this is less certain. The junction of the main and commissural canals is similarly further forward in *Eusthenopteron*, and if the line (10) between the equivalent points is extrapolated it will, as seen in figure 15, pass in front of the base-line (line 8), and therefore into the supratemporal region, just before reaching *Ichthyostega*; and in fact in *Ichthyostega* the junction of the canals lies within and near the posterior corner of the supratemporal, and the centre of radiation of the bone has been transferred to that position (Jarvik 1952, fig. 35*b*– in the present paper the osteolepiform names have been retained for ichthyostegids, see Westoll 1943, p. 82). Similar extrapolation of the position at which the commissural canal crosses the midline, represented by line 11, would bring the crossing in *Ichthyostega* just behind the posterior border of the parietals. In fact (Jarvik 1952, fig. 35*b*) it crosses a little further forward, within but near the posterior border of the parietal.

The parietal of *Ichthyostega*, as thus shown by Jarvik, is of great interest. It is an unpaired bone which has its centre of radiation at the point where the commissural canal crosses the midline, and therefore close to its posterior border. In the osteolepiforms, and also in *Elpistostege*, the parietals are paired bones, and their centres of radiation are further forward within the bone (figure 14*a–c*). It is suggested that the trend referred to has brought the commissural canal within the potential field of the parietal bones, and that in this position they played the same role as they had once done for the median extrascapular in osteolepiforms. In other words, a medium latero-sensory ossicle, probably formed by an early union of a pair of ossicles, acted as a focus for the development of a horizontal lamella which thus came to form a median definitive bone, namely the unpaired parietal. In consequence the paired membranogenic centres of ossification from which the parietal bone had previously developed ceased to be operative. Here, therefore, a single latero-sensory focus was serving two bone areas that had previously ossified by membranogenesis. It is interesting that in later labyrinthodonts, as also in the Carboniferous ichthyostegid *Colosteus* (see Romer 1947), the sensory lines became shallow and non-morphogenetic, and here the parietals remained in, or reverted to, the same paired condition as in osteolepiforms. Thus it is only in Devonian ichthyostegids that there is the conjunction of a commissural canal that is relatively far enough forward to be within the parietal area and is sufficiently deeply situated to be morphogenetic; likewise it is virtually only in Devonian ichthyostegids that an unpaired parietal is found. This median parietal of *Ichthyostega* can thus be interpreted in terms of figure 1, and seems to provide useful support for the concepts that it incorporates. Westoll (1938) mentions the existence of a specimen of *Eusthenopteron* with a single median parietal; it would be interesting if in this instance the commissural canal had, so-to-speak prematurely, passed through the back of this bone, instead of through the median extrascapular, and had initiated its ossification. It apparently did not do so in *Elpistostege*.

Thus the reduction in the posterior part of the parietal shield of *Eusthenopteron*, as compared with *Osteolepis*, seems to have been part of a complex of changes which probably occurred at different rates in a number of rather similar groups. If the course from *Osteolepis* to *Ichthyostega* was allocated 100 units then (figure 15) it would seem that *Eusthenopteron foordi* had travelled some 57 units, and *Elpistostege* which was contemporary with it a further 27 units, along a similar route.

Returning to the parietal shield, figure 13*d* shows a variation of *Eusthenopteron* superimposed on the standard pattern. Figure 13*c* shows a shield of *Eusthenodon*. In figure 13*e* all three are superimposed on one another. These three demonstrated, to an increasing degree, the development of similar features to those seen in specimens of *Latvius* with a relative broadening of the posterior part of the shield, and they could result from a similar region of greater differential growth, also situated as in *Latvius* (figure 9*d*), but probably directed towards the posterolateral corner of the supratemporal rather than towards its centre. This, as in *Latvius*, would account for the pronounced 'shoulder', and for the position of the greater part of the It/Pa suture having remained unchanged. It is interesting that two different genera, namely *Eusthenopteron* and *Eusthenodon*, should show such similar types of modification developed to different degrees, and also that they should run parallel (figure 13*f*) with developments in a more remote genus, namely *Latvius*.

A remarkable variation of the parietal shield of *Eusthenopteron* illustrated by Säve-Söderbergh (1932, fig. 19; 1933, pl. 16) is shown in outline in figure 13*g*. In figure 13*h* it is superimposed on the generalized condition. It is clear that on both sides the parietals are restricted to the posterior part of the shield, and that extensive bones approximately equivalent to the A.Pa in certain *Osteolepis* and *Latvius* have developed. However it does not seem to be merely a dd.Pa *Eustheno-*

pteron; the extreme restriction of the Pa, the mesial bulges of both It, the asymmetry of the A.Pa/A.Pa suture and the absence of sd.Pa or typical dd.Pa among the many specimens from Escuminac Bay suggest that some different process had been at work. Perhaps early in skeletogenesis this individual suffered some injury or other pathological condition which was located just in front of the centre of growth of the parietals and prevented them from growing forwards in the usual manner. This restriction seems to have been particularly effective on the right side. One gets the impresssion that the response in the form of new A.Pa ossifications was long delayed and that in the meantime both It grew mesially, probably slowly, so tending to fill the deficiency left by the absence of the forward growth of the parietals. Such a sequence would seem to explain the form of the It/A.Pa sutures in terms of Parrington's (1956) observations.

Owing to the postulated injury the centres of radiation of the parietals may have found themselves close to the anterior margin of the territory that was left available to them. The horizontal lamella of each would have been unable to grow forwards and, deprived of this outlet, by its growth would have recoiled and in effect have exerted a pressure on the bone to extend in other directions. They apparently pressed posterolaterally into territory normally occupied by the supratemporals (figure 13*h*). They also pressed backwards extensively and on a broad front, carrying the posterior border of the shield about 10 % further back than normal. This has, to a lesser degree, its equivalent on the 'd' side of sd.Pa *Osteolepis*. Because the left Pa obtained some slight outlet anteriorly it exerted less pressure mesially than its fellow, so that the latter trespassed across the middle line by about 6 % into its territory. The centres of radiation would have been carried backwards from their original eccentric positions, and the relevant ends of the pit-lines would have provided markers. The mesial end of the left mp is at a.p.p. 74 %, the right at 76 %; typically it is at 61 %. It is significant that the lateral end of mp has remained at 64 %. This backward movement of the mesial end of mp was comparable with, but greater than, its movement on the 'd' side of sd.Pa *Osteolepis*. The assumption that pit-lines do provide convenient markers of the approximate positions of centres of radiation is confirmed by Jarvik's (1944, p. 20) statement to the effect that the centre of radiation of these parietals lies just below the place where the pit-lines meet, and thus is situated exactly as the centre of the normal parietal. The slightly more anterior position of the centre on the left side was presumably correlated with the relatively greater anterior extension of the parietal on that side.

Most of the features of this very interesting specimen can therefore be regarded as secondary consequences of a single primary event. The responses were similar in principle to those in sd.Pa *Osteolepis*, and they were complex and interacted with one another to form an integrated whole. The adaptability of its biological organization must have been considerable.

(*d*) *The parietal shields of porolepiforms*

In porolepiforms the latero-sensory canal does not pass from the supratemporal directly forwards into the intertemporal, as in osteolepiforms, but passes anteromesially through the centre of radiation of a bone which appears to correspond to the parietal, or to the parietal and intertemporal combined. Also further forward, in the fronto-ethmoidal region, there is a single latero-sensory bone in roughly the place occupied by two latero-sensory bones, namely the dermosphenotic and frontal, in osteolepiforms. The significance of these alternative patterns and their relation to Allis's concept has been a subject of much discussion, for example by

Westoll (1937*b*, 1944), Moy-Thomas (1938), Parrington (1949), Jarvik (1950*a*, 1972), Jardine (1969) and Andrews (1973).

Jarvik (1950*a*, pl. 24, fig. 1) has illustrated a parietal shield of a porolepiform from the Middle Devonian of East Greenland which is slightly worn and consequently shows the radiating structure of the bones, some latero-sensory tubes and a part of the latero-sensory canal, in addition to pit-line grooves. The interrelation of these structures, as seen on a single specimen, is important. The mesial end of the middle pit-line and anterior end of the posterior pit-line have apparently united end-to-end, forming a fairly open U. The right side, where a portion of the canal is visible, indicates that this U does not lie directly superficial to the canal, but is of the order of 8 % posteromesial to the position at which the canal traverses the centre of radiation. Figure 16*j* attempts to collate the information from both sides; the parts of the canals and pit-line grooves that can be seen are indicated by continuous lines, and their presumed approximate courses elsewhere by discontinuous ones. The principal difference between this

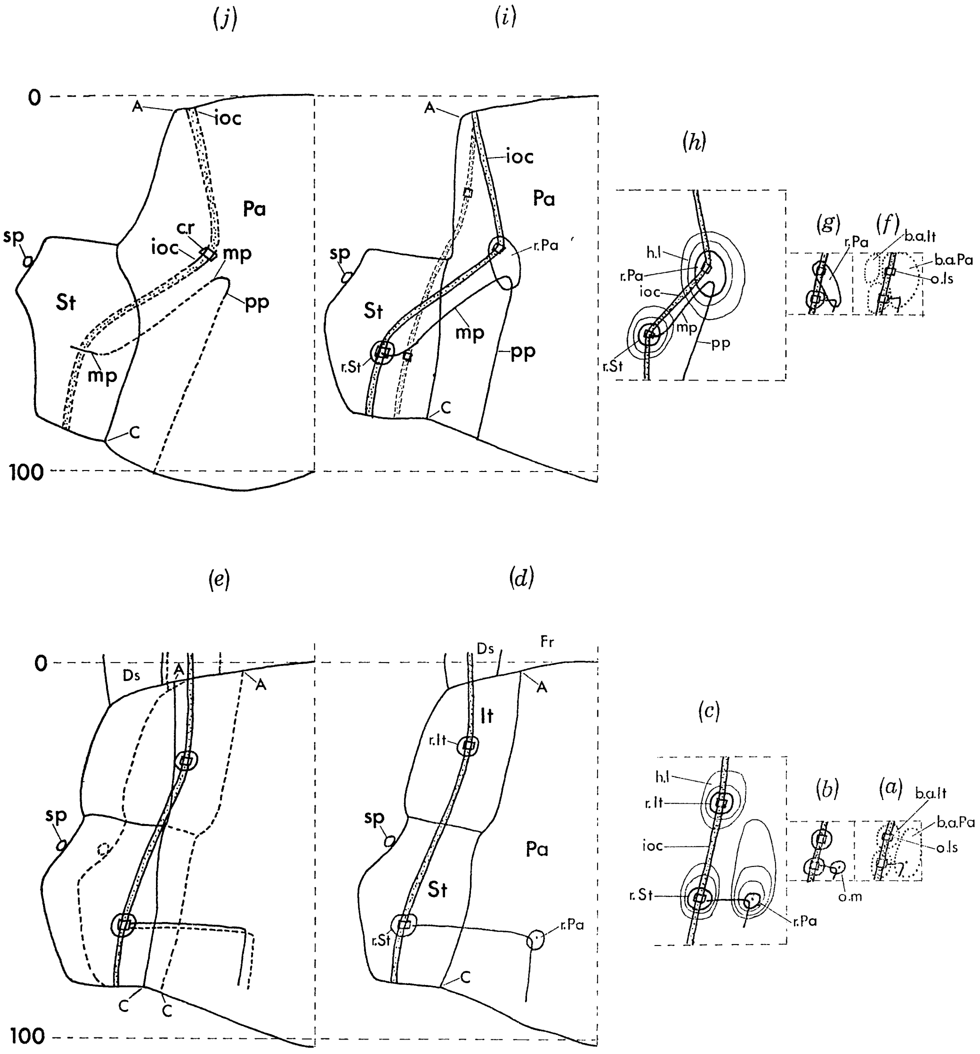

FIGURE 16. Comparison of porolepiform and osteolepiform parietal shields, and of their postulated ontogenies. (*d*) and (*j*) are based on equal lengths of It-St axis. (*d*) after Jarvik 1948, pl. 14, fig. 2. (*j*) after Jarvik 1950*a*, pl. 24, fig. 1. For explanation see text.

outline and Jarvik's (1950*a*, fig. 31*a*) outline representing *Porolepis* is that the union of the pit-lines is shown at some distance posteromesial to the lateral-line canal, instead of almost directly over it.

Figures 16 and 17 are constructed as before (p. 57). Intertemporals are not present, but the

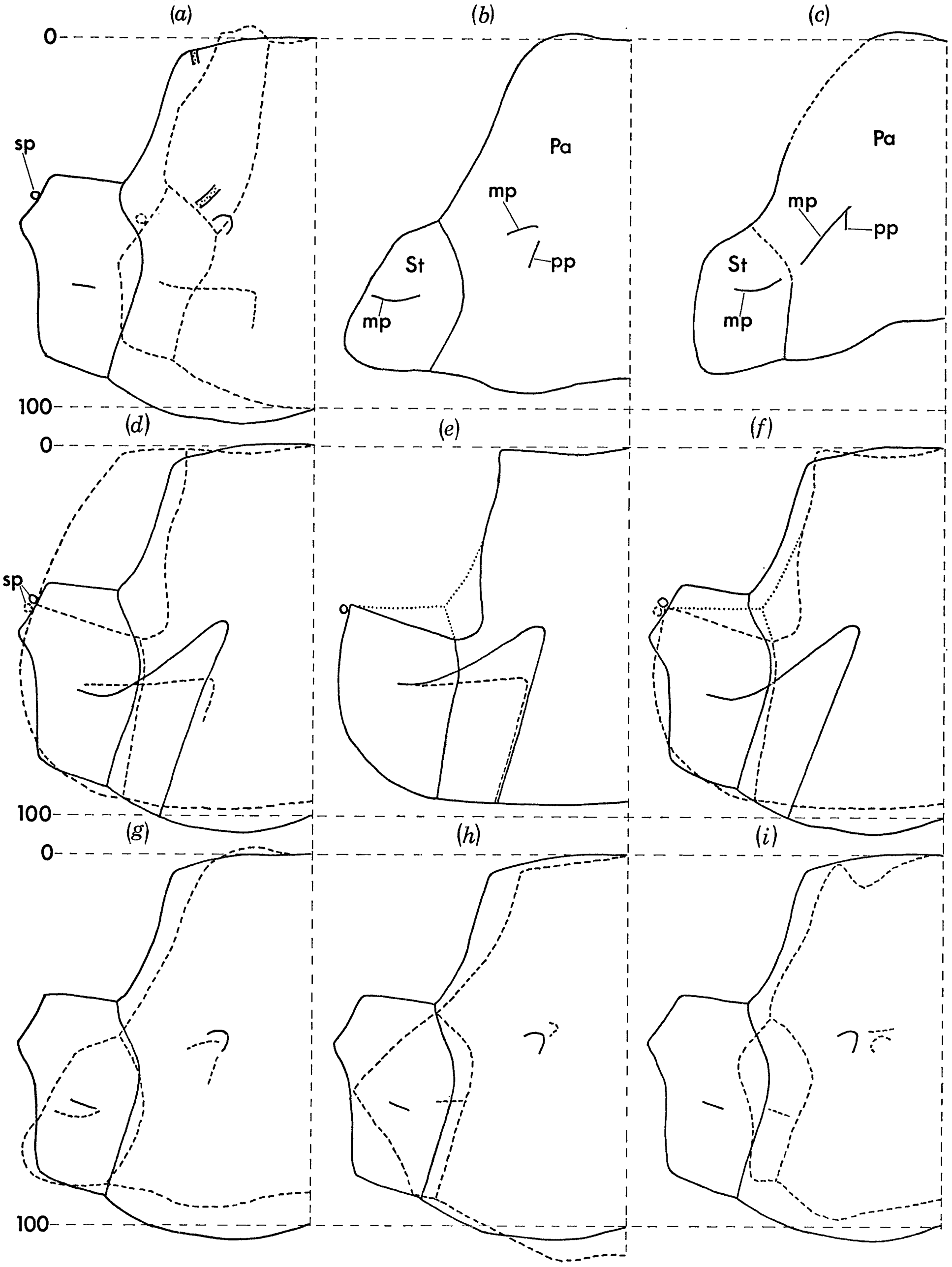

FIGURE 17. Porolepiform parietal shields, based on equal lengths of It-St axis. (*a*) porolepiform after Jarvik 1950*a*, pl. 24, fig. 1 (continuous lines) superimposed on 'typical' *Osteolepsis* (discontinuous lines). (*b*) and (*c*) *Porolepis*, after Jarvik 1972, fig. 57*a* and 57*b* respectively. (*d*) figure 17*a* (continuous lines) superimposed on 'broadened' *Gyroptychius* (discontinuous lines). (*e*) modified 'broadened' *Gyroptychius* (see text). (*f*) figure 17*a* (continuous lines) superimposed on 17*e* (discontinuous and dotted lines). (*g*) figure 17*a* (continuous lines), superimposed on 17*b*. (*h*) figure 17*a* (continuous lines) superimposed on *Glyptolepis* after Jarvik 1972, fig. 38 (discontinuous lines). (*i*) figure 17*a* (continuous lines) superimposed on *Holoptychius* after Jarvik 1972, fig. 57*d*, right side (discontinuous lines).

pattern of the bones is such that the position of top end of the It-St axis on the a.p.p. 0 % line can be reasonably judged. In figure 17*a* a porolepiform shield is superimposed on that of *Osteolepis* on this basis. Positions are, as previously, calculated as percentages of the midline shield-length of the 'typical' *Osteolepis*.

The approach adopted here is implied by figure 1. In this instance mesiolateral relations are clearly crucial. It seems reasonable to assume that at an earlier period there already existed osteolepiform ancestors with moderately broad parietal shields, such as that of *Osteolepis panderi*. A specimen of this species illustrated by Jarvik (1948, pl. 14, fig. 2) is used to represent this hypothetical earlier form (figure 16*d*). The lateral-line canal is not seen in this specimen, but its position can be reasonably deduced. As already noted, the breadth of parietal bone varies widely in osteolepiforms, particularly at its anterior end, and at an earlier period there would probably have been similar variations. Broadening would presumably have come to involve a greater relative breadth of the shield during the formative stages of ontogeny and, as the midline would have acted as a fixed point relative to mesiolateral changes, the presumptive areas for the various bones would also come to spread out lateralward from the middle line. The area of dermis potentially destined to become ossified by the parietals would therefore become broader, and that by the intertemporals more laterally placed. It seems that in the osteolepiforms the position of the lateral lines roughly kept pace with such mesiolateral changes, and so continued to act as foci for the same definitive bones. However such correspondence in the movement of these parts need not always have occurred. Latero-sensory lines are initially situated in the epidermis, not the dermis. They could have continued to develop in their previous positions without much reference to mesodermal tissues that, in the early formative stages, were perhaps multiplying, sliding and spreading out laterally beneath them, and so were broadening the head and the structures that would compose it. In this event when in due course the lateral lines sank into the dermis, their neuromasts would have been brought into relation with areas of mesoderm that now had different ossification potentialities, and so would through their latero-sensory ossicles have come to act as foci for the ossification of different bones.

Attempting to apply this viewpoint, figure 16*a* to *c* represents ontogenetic stages leading to the osteolepiform condition of figure 16*d*. They are comparable with the 's' (left) side of figure 6. In figure 16*e* the outline 16*d* is again shown, but here as discontinuous lines. The continuous lines show the result of broadening the shield in the manner referred to above. Point A has been moved 18 % lateralward, from m.l.p. 20 to 38 %; point C has been moved 4 %, from 41 to 45 %. In the *Osteolepis-Gyroptychius* series the variation is similarly greater at the anterior end of the shield. The resulting It/Pa plus St/Pa suture follows a very similar, though more lateral, course to that of the *Gyroptychius* of figure 8*c*. However in figure 16*e* – and this is the crucial point – the position of the lateral-line canal has been left unchanged. The result is that anteriorly the canal now for the most part traverses the parietal bone, not the intertemporal; its neuromasts would now be within the parietal area. Further forward the canal now passes straight into the frontal; the dermosphenotic (Ds) would have passed lateralward beyond its range. Further back, the canal still traverses the supratemporal, though rather near its mesial border.

When the canals come within the parietal area a crisis will occur, for then the ontogenetic condition of figure 16*a* will abruptly switch to that of 16*f*. The latero-sensory ossicle that had previously acted as a focus for the intertemporal will now act as a focus for the parietal instead. The question of the intertemporal is referred to later, but since it appears to take no part in the shield it is omitted from figure 16*g*, *h* and *i*. As regards the parietal, its site of ossification would have shifted from the site where it had previously been initiated to a latero-sensory site further forward and near the lateral edge of the parietal area. From here part of its horizontal lamella, growing out into the main body of the area, would soon have passed deep to the united ends of the two pit-lines, which would therefore have become anchored a short distance from and posteromesial to the eventual centre of radiation. The latter is apparently carried from its initially eccentric position some distance posteromesially towards a more central position in the bone, perhaps as a result of active growth of the lateral part of the lamella, and thus in a way comparable with changes in the parietal on the 'd' side of sd.Pa *Osteolepis*. Such changes will carry the lateral-line canal which is embedded in what will later become the centre of radiation of the bone away from its initial relatively straight course (figure 16*e*, and discontinuous lines in 16*i*) into a considerable mesial diversion (continuous lines in figure 16*i*). The ends of the pit-lines will bear the same relation to the centre of radiation as they did when they became anchored during skeletogenesis, and so will be a short distance posteromesial to it. Owing to the more anterior position of the centre of radiation within the bone they will, as the bone grows, be carried forwards from their original osteolepiform position; during this process their initial junction at a right angle will be transformed into an open U. The centre of ossification of the supratemporal, being now formed near the mesial border of its area, will tend to move laterally and will carry with it the lateral-line canal into, in this case, a lateral diversion. This postulated course of development would lead to a mature shield (figure 16*i*) which bears a reasonable resemblance to the porolepiform shield of figure 16*j*. The spiracle (sp) would come to be in the appropriate position. The bend on mp at the centre of St, noted by Jarvik (1972, p. 136) in the specimen represented by figure 17*c*, and correctly interpreted by him as due to the other end of mp having been dragged forwards, represents a relic of the sensory line's primary horizontal orientation and has been retained because here the line was held firmly in place by the anchoring tissue. Elsewhere the bone yielded. This relic provides useful evidence that the mesial end of mp moved in the course of the individual's ontogeny and was not merely formed from the first in the more anterior position. It is surprising that a similar relic has not been found in sd.Pa *Osteolepis*.

Figure 16*j* bears a certain resemblance to some shields of *Latvius* (figures 9*b*, 11*d*) which might support Jarvik's view that the large bone in porolepiforms is formed by the fusion of the intertemporal and parietal. However the position of the spiracular notch shows no correspondence on such comparison. On the other hand a broadening of a *Gyroptychius* shield (discontinuous lines in figure 17*d*) brings the spiracle to the same position as in *Porolepis*. A subsequent loss or disengagement of the intertemporal would result in figure 17*e* which, with a slight infilling of the consequent embayment as indicated by the dotted lines, brings it close to the actual condition in *Porolepis* shown by continuous lines in figure 17*f*. This still leaves a considerable embayment, which has come to be smoothed out in various ways (figure 17*g*, *h* and *i*, discontinuous lines) in different porolepiforms.

The latero-sensory line is therefore visualized as having become transferred from the intertemporal to the parietal area where it provided a focus for the ossification of a parietal which had previously been membranogenic. In terms of figure 1 it would have been a transference from (*b*) to (*e*). The pattern of comparisons of figures 16 and 17 give no indication that the shield still contained an intertemporal element. However there is a bone which, though separate from the shield, is in much the same topographical position as the intertemporal; Jarvik has stressed that this bone, which he calls the prespiracular, belongs to the bones of the cheek and is not to be confused with the intertemporal. This, up to a point, is accepted. It seems possible that when the tissue of the intertemporal area was deprived of its latero-sensory focus it formed a definitive bone by membranogenesis instead, this being the equivalent of bone 'x' in figure 1*e*, and that the reorganization of ontogenetic processes that was involved provided scope for readjustments which resulted in the severance of the previous association of this bone with the parietal shield; the reformed and different intertemporal came to function as a cheek bone instead. This readjustment may have been due in particular to a different localization of the new membranogenic centre of ossification relative to the position of the intracranial juncture apparatus.

As regards phylogenetic implications, one can visualize a long series of ontogenetic and adult phases, as in figure 16*a–d*, succeeding one another with little obvious change apart from a gradual broadening of the shield that resulted in an approach to the figure 16*e* condition. A time would eventually come when in some members of the population the lateral line would traverse the parietal area instead of that of the intertemporal. In these the set of changes beginning with figure 16*f* would then be set in motion, thus giving rise to adults with a porolepiform type of shield. Palaeontology, which necessarily deals only with relatively mature remains, would record an abrupt appearance of the new types, the term abrupt being used to denote an absence of intermediate conditions. There would presumably have been a transitional period, perhaps of long duration, when members of both categories would have been present in the population; it would probably have included unilateral variations with a broadened version of the pattern of figure 16*d* on one side and that of figure 16*i* on the other.

In principle such changes in phylogeny could have taken place either from an osteolepiform to a porolepiform condition, as envisaged here, or in the reverse direction. The latter seems to present certain marginal problems. It would, for instance, be difficult to explain why, when the lateral line ceased to provide a focus for the parietal, the centre of ossification that subsequently developed by membranogenesis should have been as far back as it is in osteolepiforms. This can however be accounted for (p. 62) if the osteolepiform type of shield is primary. Again, when the intertemporal ceased to be a cheek bone and became incorporated in the shield it is highly improbable that there would have been a suitable embayment waiting to receive it.

The present approach therefore suggests that the difference between the osteolepiform and porolepiform types of shield arose primarily as a result of the development during ontogeny of a different topographical relation between the lateral line and the presumptive bone areas. This represents a rather simple change in mesiolateral proportions, and probably has little relevance to the phyletic relations of the groups in question. This approach differs considerably from that of both Jarvik and Westoll. Jarvik (1972) believes that the large bone in the porolepiform shield is formed by a fusion of the intertemporal and the parietal. In this event the middle pit-line would presumably have become anchored to the developing parietal in its original posterior setting. The present writer finds it difficult to visualize what kind of reorganization of bone structure led to two separate centres of radiation becoming 'fused' into one, or the reason why this should have occurred, or to understand why such a reorganization of structure should have resulted in the relevant parts of the sensory lines being drawn forward to their more anterior positions. Westoll (1937*b*, fig. 9; 1944, p. 68) has taken the view that the parietal has regressed and the intertemporal, remaining a lateral-line bone, has spread throughout the area previously occupied by both bones. However the parietal of osteolepiforms is a large and apparently flourishing bone, even though devoid of any latero-sensory stimulus from a supraorbital canal, and there is no obvious reason why it should have regressed. Also it seems fairly certain that in the known porolepiforms this reduction did not take the form of a parietal ossification that developed for a time before regressing, as Pehrson (1947, 1958) has described in the parietal of *Polypterus*, and that was subsequently replaced or submerged by a horizontal lamella growing from the intertemporal, for then the middle pit-line would have become anchored to this parietal rudiment and would subsequently have retained its transverse orientation. Another difficulty is that the rhizodontiforms, which are referred to in the next section, appear to have a 'parietal' that is essentially similar to that of porolepiforms, but in this instance this bone cannot be a normal intertemporal that has taken over the parietal area, nor can it have been formed by a fusion of the intertemporal and parietal as Jarvik believes to have occurred in porolepiforms, for in *Rhizodus* the intertemporal is still present in the shield and is still a latero-sensory bone.

(*e*) *The parietal shields of rhizodontiforms*

The existence of a new group of crossopterygians, known as rhizodontiforms, has recently been demonstrated by Andrews and Westoll (1970), mainly on the basis of post-cranial characters. Andrews (1973) has given a preliminary description of the skull-roof of *Rhizodus*. Figure 18*a*, based on her (1973) fig. 2*d*, shows the parietal shield and the lateral extrascapulars; it is based on the same frame of reference as the previous figures. The more important features of this area of *Rhizodus*, as compared with osteolepiforms and porolepiforms, appear to be:

1. The sensory canal passes forwards from the supratemporal anteromesially through a part of the parietal, and then anterolaterally through the intertemporal.

2. The intertemporal remains a latero-sensory bone which is incorporated in the parietal shield, as in osteolepiforms. It is however rather small.

3. In traversing the parietal, the sensory canal makes a considerable mesial excursion rather similar to that in porolepiforms.

4. The mesial end of the middle pit-line and the anterior end of the posterior pit-line are located much further forward than in osteolepiforms. They come near to meeting, but instead trail away into conspicuous loose ends which are directed posteromesially. The probable positions of their anchorages are represented by dots in figure 18*b*; the anchorage indicated for the middle pit-line is at the position at which the posterior pit-line would have met it if its course had been prolonged forwards. It is at a.p.p. 49 %, which is similar to that of porolepiforms; also, as in the latter, it is a short distance mesial to the infraorbital canal.

5. The breadth of the parietals at their anterior ends (point A m.l.p. 19 %) is similar to *Osteolepis panderi* and much less than in porolepiforms.

6. The St/Pa suture passes backwards and somewhat mesially, so that the parietals become narrower from the middle of their length backwards, instead of broader as in most crossopterygians. Point C is consequently at m.l.p. 22 %, compared with a mean of 40 % in *Osteolepis*.

The following interpretation is suggested. The sensory canal is seen to traverse a part of the parietal. The centre of radiation is not shown by Andrews, but since the ends of the pit-lines are far forwards as in porolepiforms, and since they also bear the same relation to the sensory canal, it can be assumed that the pit-lines had a similar history and were drawn forward in the same manner in the two groups. The centre of radiation is presumably therefore on the canal, and in the same relative position as in porolepiforms. The canal would therefore have provided latero-sensory ossicles which acted as foci for the development of both the intertemporal and the parietal; the two intertemporals on the left side of the *Osteolepis* of figure 4*d* indicate that such foci would have been potentially available. At some stage the centre of ossification, and of subsequent radiation, of the parietal would have been transferred from the posterior membranogenic site that existed in osteolepiforms to a more anterior latero-sensory one; in this respect their phylogeny would have run a course parallel with that of porolepiforms, as also would the mesial excursion of the sensory canal and the drawing forward of the two pit-lines.

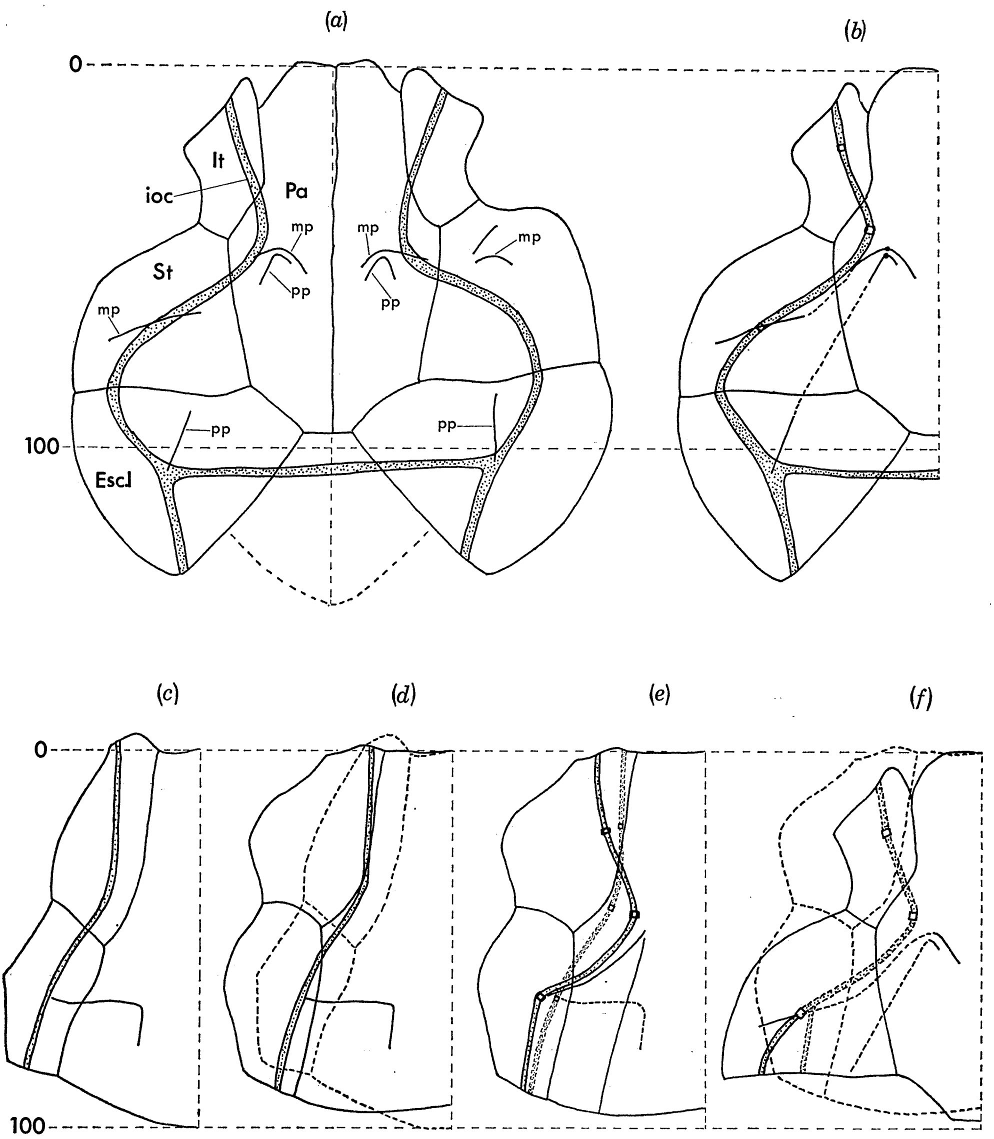

FIGURE 18. Parietal shield of *Rhizodus* and comparison with *Osteolepis*, based on equal lengths of It-St axis. (*a*) *Rhizodus*, parietal shield and lateral extrascapulars, after Andrews 1973, fig. 2*d*. (*b*) left side of figure 18*a*, but showing postulated positions of centres of radiation and of full courses and positions of anchorages of the pit-lines. (*c*)–(*e*) postulated type of change leading from osteolepiform to rhizodontiform condition. (*f*) superimposition comparing figure 18*e* with the actual condition in *Rhizodus*.

The transition from osteolepiform to rhizodontiform shields can be accounted for in terms of a process similar to that postulated for porolepiforms. The start in this case would have been a comparatively narrow shield, such as that of *Osteolepis macrolepidotus* (figure 18*c*), and it would be assumed that as a result of changes in the formative stages of ontogeny the parietal region became widened, again more anteriorly than posteriorly, to produce perhaps the kind of pattern found in *Osteolepis panderi*, but that this occurred without the lateral lines taking part in the widening (figure 18*d*); possible reasons for this have already been given. The results can be followed out in figure 18*d*, *e* and *f*, which can be compared with figure 16. In this case the transference in the relative position of the lateral-line canal resulted in the parietal area being entered, but not in the intertemporal one being vacated; consequently latero-sensory ossicles formed by the line provided foci for the development of both these bones. The sequence of events can be represented by the difference between figure 1*b* and *f*.

Figure 18*f* implies that the condition that would be expected to result from this process differs from that of *Rhizodus* itself mainly in two ways. First, the main sensory canal makes a wide lateral excursion as it passes from the centre of the supratemporal to that of the lateral extrascapular; this may have been due to a localized area of more intensive growth, such as has been postulated in some specimens of *Latvius* and *Eusthenopteron*. Secondly there is the different orientation of the St-Pa suture; perhaps the shift forward of the centre of growth of the parietal placed it at a disadvantage in restraining trespass by the supratemporal.

(*f*) *The parietal shields of onychodontiforms*

There are descriptions of the skull-roof of two genera of onychodontiforms, namely *Onychodus* and *Strunius*. For the former there is the recent preliminary description by Andrews (1973) of an uncrushed skull-roof from the Upper Devonian of Gogo in Western Australia. The left side is shown in figure 19*a*. The extratemporal is omitted and the extrascapulars included. *Strunius* is difficult because of its small size. Figure 19*c* is based on Jessen's (1966) pl. 11, fig. 1, which shows the shield unusually well; the lateral extrascapular and the lateral-line canal are based on Jessen's (1966, fig. 9*a*) representation of the generalized condition, slightly adapted to conform with the specimen referred to above.

Andrews (1973, p. 146) remarks that the main difference between the skull-table of osteolepiforms and onychodontiforms is the posterior extension of the parietals in the latter, which has displaced the extrascapular series; she further notes that the cross-commissural canal and the growth lines of the parietal shown by radiographs indicate this to be a secondary feature. Comparison of the *Osteolepis* of Säve-Söderbergh (1933, pls 5, 6 and 7) and *Onychodus* based on equal lengths of It-St axis (figure 19*b*) supports this opinion. The anteroposterior positions of most parts of the shield are very similar. In *Onychodus* the lateral end of the middle pit-line is at a.p.p. 66 %, and the mesial end at 67 %; both correspond closely with those of *Osteolepis*. The a.p. positions of the centres of radiation of the supratemporals and parietals therefore seem to have been virtually identical in the two forms; the difference lay in the greater extension of the posterior part of the shield. At the middle line the posterior border of the parietal of *Osteolepis* is, by definition, at a.p.p. 100 %; that of *Onychodus* is at 130 %. There is no great difference in the a.p.p. at which the main and commissural canals meet, and it is clear that the posterior extension is largely confined to the more mesial portion of the skull-roof. Presumably there was a zone of backwardly directed more intensive growth situated far back in the parietal region, which pushed back the median extrascapular and the canal embedded in it and caused the parietals themselves to grow back much further than usual to cover the area that was thus exposed. The centre of radiation of the parietals, established earlier in ontogeny, remained unchanged.

Regarding mesiolateral relations, it is noticeable (figure 19*b*) that the small 'shoulder' seen in *Osteolepis* is entirely absent in *Onychodus*; the St/Pa suture continues in alignment with the It/Pa one. In *Strunius* (figure 19*c*) however the It/Pa suture, which is much further lateralward (point A is at m.l.p. 19 % in *Onychodus*, 40 % in *Strunius*) runs the usual direct anteroposterior course until, at about a.p.p. 40 %, it changes to a posterolateral course which is more or less

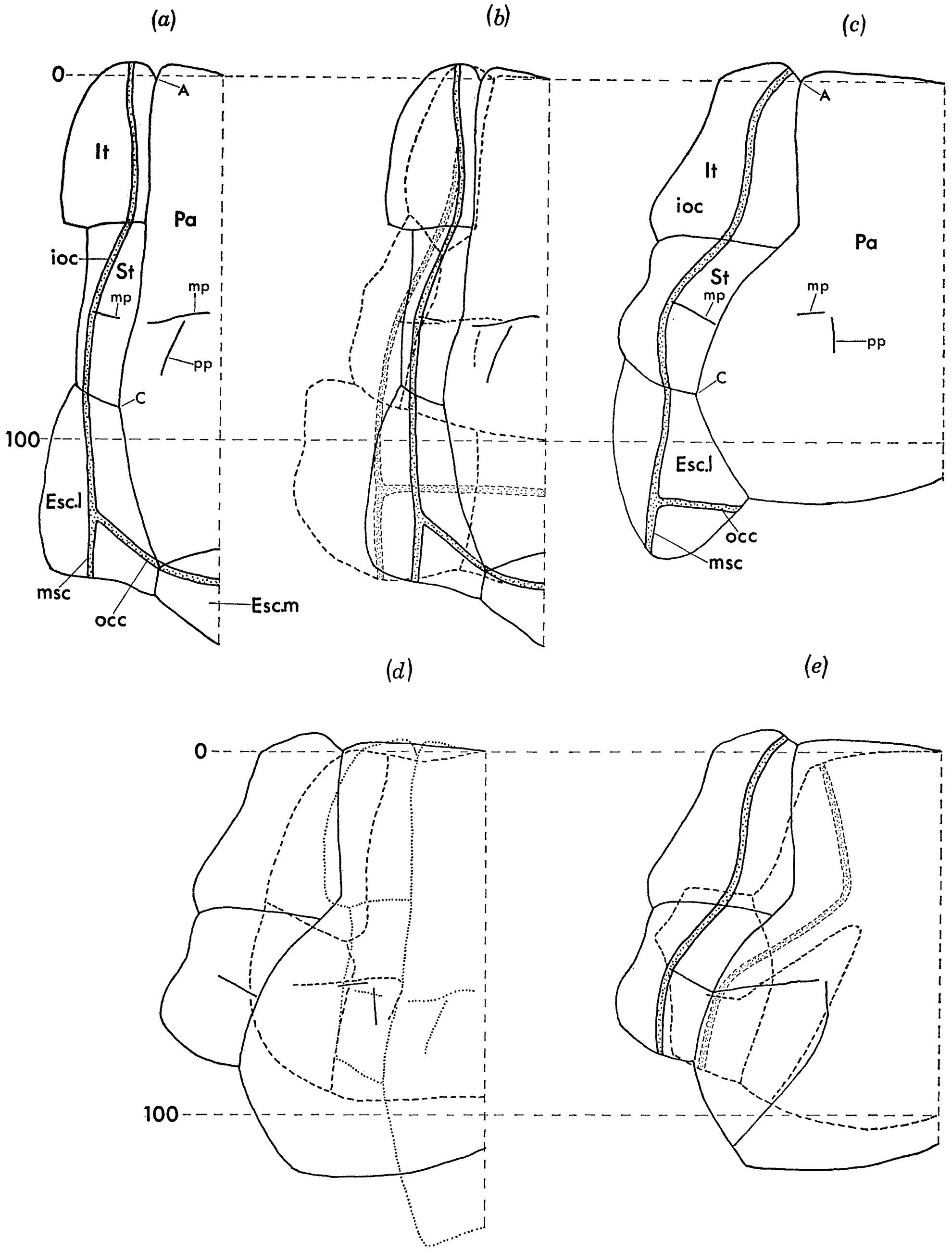

FIGURE 19. Parietal and extrascapular regions of onychodontiforms, and comparison with osteolepiforms and porolepiforms based on equal lengths of It-St axis. (*a*) *Onychodus*, after Andrews 1973, fig. 2*f*. (*b*) figure 19*a* (continuous lines) superimposed on *Osteolepis* S.S. 5/6/7. (*c*) *Strunius*, mainly after Jessen 1966, pl. 11, fig. 1. (*d*) superimposition of *Onychodus* (dotted lines), *Gyroptychius groenlandicus* (discontinuous lines) and *Strunius* (continuous lines). (*e*) *Strunius* (continuous lines) superimposed on porolepiform figure 16*j*.

continued by the St/Pa suture as far as point C, which is therefore situated at the remarkable m.l.p. 68 %; it gives the impression that the 'shoulder' seen in various osteolepiforms has been extended as far as this.

The relative anteroposterior dimensions of *Strunius* are rather similar to those of *Onychodus* (figure 19*d*). In the shield used the lateral end of the middle pit-line is at a.p.p. 62 %, and its mesial end at 64 %. The parietals extend further back than in *Osteolepis*, but not nearly as far as in *Onychodus*; at the midline its posterior border is at 109 %.

A superimposition of a *Strunius* shield with a porolepiform one is shown in figure 19*e*. The probable full course of the canals and pit-lines is shown. Anteriorly the latero-sensory canals entered the shield at much the same position, namely close to but on different sides of the lateral margin of the parietal. They then diverged on mesiolateral excursions in opposite directions. It seems likely that in *Strunius* the canal came to be just within the intertemporal zone and its latero-sensory ossicle acted as a focus for that bone; similarly in porolepiforms it came just within the parietal zone. In each case the centre of radiation so initiated became moved to a more central position within its respective bone, and in doing so drew the sensory canal in respective opposite directions. If in *Strunius* the sensory canal had come within the parietal area instead of the intertemporal, and if in the ensuing reorganization the intertemporal had become dissociated from the parietal shield, then a shield almost identical with the porolepiform shield of figure 16*j*, shown again in the superimposition of figure 19*e*, would be expected to develop. The only important difference would have been the posterolateral orientation of the St/Pa suture, which was probably secondary. This resemblance does not imply that porolepiforms and onychodontiforms were closely related; it probably points to a form of flexibility that was common to a wide range of crossopterygians and indicates that such differences in parietal shields are of little significance as regards phyletic relations.

(*g*) *The parietal shields of crossopterygians in general*

Differences in the parietal shields of crossopterygians are reflected in their different forms of parietal bones. Outlines of a number of these are shown in figure 20, in which the series (*a*) to (*e*) shows a decrease in breadth, particularly anteriorly; (*j*) can be regarded as a logical continuation of this process. This flexibility as regards breadth may have opened the way for the development of differences in the relation between lateral lines and bone areas, and hence the bones with which the lines subsequently became associated. It has been maintained that such a change in relationships occurred in porolepiforms (figure 20*f*) and, differently, in rhizodontiforms (figure 20*g*), and was associated with various secondary changes. Such changes may, at least in principle, have occurred rather freely among crossopterygians and are probably of little phylogenetic significance (cf. Andrews 1973, p. 171). Figure 20*h*, *i* and *j* show parietal bones that for one reason or another were not able to develop their usual anterior extensions; here a complex of interrelated secondary consequences arise among which the more posterior position of the mesial end of the middle pit-line is particularly significant. Comparison respectively of figure 20*k* and *l*, and of (*m*), (*n*) and (*o*) with one another is believed to show the results of a localized area of more intensive growth. Figure 20*m*, *n* and *o* also show reduction in the posterior extension of the parietal bones; this reduction seems to have been carried further in the ichthyostegid tetrapods.

Most of the features of the parietal shields of crossopterygians (other than coelacanths) thus seem to be explicable in terms of the following five types of change, or of secondary consequences arising from them. (1) Variations in the breadth of the parietal area, more particularly in the anterior part of the shield. (2) Differences in the relative positions of the lateral-line canals, involving their association with different bones. (3) The occasional occurrence of circumstances which prevent the development of the usual anterior extensions of the parietals.

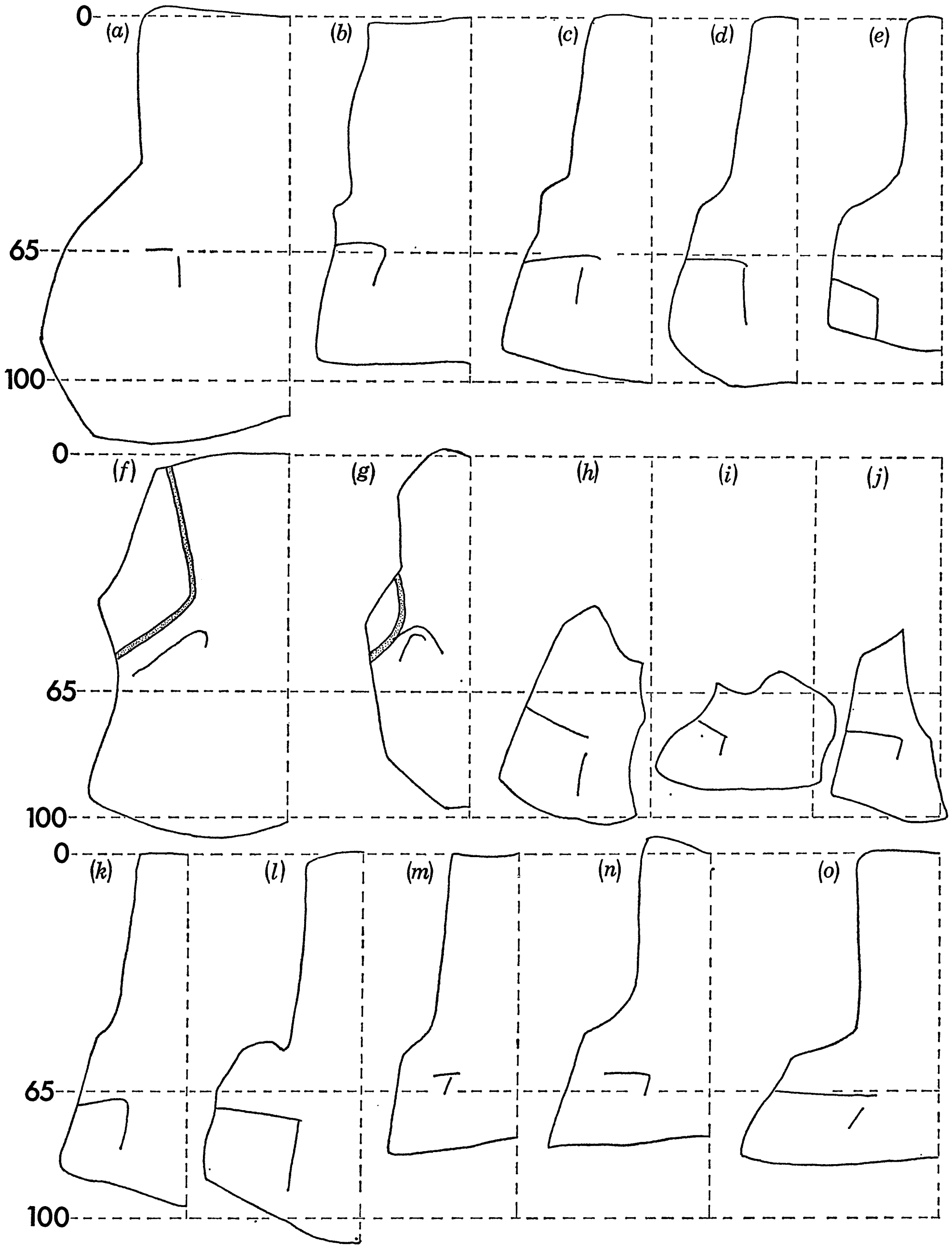

FIGURE 20. Comparison of some parietal bones of crossopterygians, on the basis of equal lengths of It-St axis of corresponding shields. The middle line is shown, but not the suture separating the parietals, except in (*h*), (*i*) and (*j*). The numbers in brackets indicate the figures showing the shields to which the parietals belong. (*a*) *Strunius* (19*c*). (*b*) *Gyroptychius* (8*c*). (*c*) *Osteolepis* (3*b*). (*d*) *Osteolepis* (3*c*). (*e*) *Glyptopomus* (12*a*, pit-lines transposed from right side). (*f*) porolepiform (16*j*, pit-lines partly from 17*c*). (*g*) *Rhizodus* (18*a*). (*h*) 'd' side of sd.Pa *Osteolepis* (5*a*). (*i*) *Eusthenopteron* variation (13*g*, right parietal transposed to left). (*j*) *Glyptopomus* variation (12*b*). (*k*) *Latvius* (11*a*, right transposed to left). (*l*) *Latvius* (9*a*). (*m*) *Eusthenopteron* (13*a*). (*n*) *Eusthenopteron* (13*d*). (*o*) *Eusthenodon* (13*c*).

(4) The occasional presence of localized areas of more intensive growth. (5) Reduction in the posterior extension of the parietals. The *Gyroptychius Osteolepis* group of shields (figure 20*b*, *c*, *d*), with their wide spectrum of breadth anteriorly, seem to form a central type from which other forms of shield could have been derived by fairly simple changes.

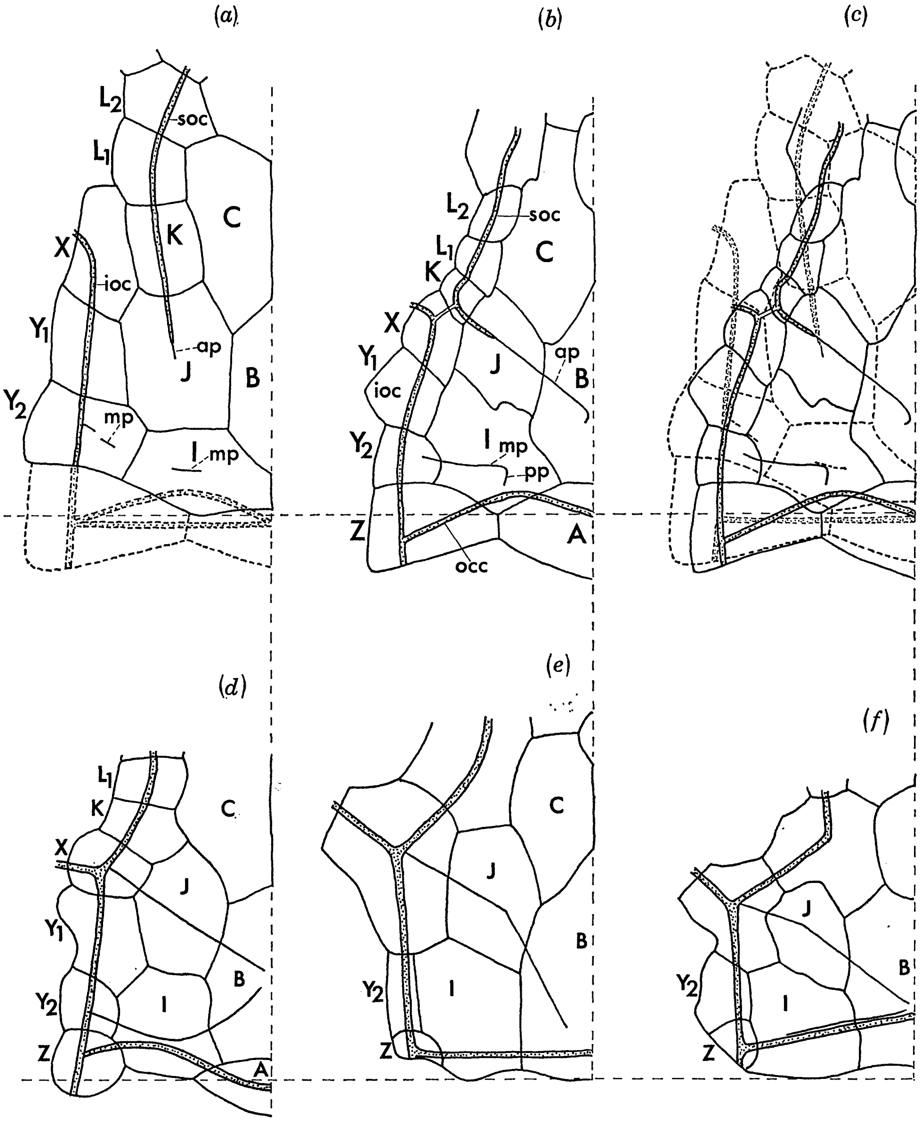

Figure 21. Comparison of parts of skull-roofs of some dipnoans, based on a common breadth from the centre of Y_2 to the midline, and on a common base-line passing through the most posterior part of I. (*a*) dipnorhynchid, after Denison 1968 and Thomson & Campbell 1971. (*b*) *Dipterus*, mainly after White 1965, fig. 18. (*c*) dipnorhynchid (21*a*, discontinuous lines) superimposed on *Dipterus* (21*b*, continuous lines). (*d*) *Scaumenacia*, after Westoll 1949, fig. 6*a*, right side. (*e*) *Uronemus*, after Westoll 1949, fig. 8*c*. (*f*) *Sagenodus* after Westoll 1949, fig. 8*a*.

4. The parietal region of dipnoans

A part of the skull-roof of *Dipterus* from the Middle Devonian is shown in figure 21*b*; the notation used by Denison (1968) is adopted. It is generally agreed (see for example, Westoll 1949) that bones X, Y_1, Y_2 and Z are equivalent, respectively, to the dermosphenotic, intertemporal, supratemporal and lateral extrascapular of osteolepiforms. The commissural canal (occ) does not take a straight mesiolateral course from Z to A, as in crossopterygians, but it loops forwards and traverses the posterior part of bone I; it passes through the centre of radiation of that bone and an ossicle derived from it presumably acted as a focus where its ossification began. Two specimens have been described by White (1965) in which the canal does go straight from Z to A and bone I is not involved.

Two genera of earlier and more primitive dipnoans are also known. Extrascapular bones have so far not been found in either. Thomson & Campbell (1971) state that the posterior border of the skull of *Dipnorhynchus* is curiously rounded and that there may have been room on each side for an additional extrascapular bone between Z and A. On the other hand Denison (1968) has shown that in *Uranolophus* this part of the skull closely resembles that of *Dipterus*, so the extrascapular bones, if present, were probably similar; they have been tentatively shown in this way in figure 21*a*. There is some evidence that in *Uranolophus* the commissural canal did pass through bone I and that in *Dipnorhynchus* it passed direct from Z to A. One specimen of *Uranolophus* shows the middle pit-line groove crossing parts of Y_2 and I. Figure 21*a* is probably a reasonable representation of a part of a dipnorhynchid skull-roof; it shows the two possible alternative courses of the commissural canal.

It seems clear that at any early stage in phylogeny the commissural canal passed straight from its union with the main canal in Z to meet its antimere in A. In this it would have resembled the crossopterygian and actinopterygian condition which was probably common to osteichthyans in general (figure 25). On the other hand in most specimens of *Dipterus* the canal loops forward and passes through bone I. On present evidence the dipnorhynchids may represent a threshold stage in which the canal may either pass direct from Z to A (*Dipnorhynchus*) or forwards and through I (*Uranolophus*). Westoll (1949, fig. 10*b* and *c*, p. 163), applying Allis's principles of the constancy of lateral line to bone relations considered that bone I in *Dipterus* is derived from a bone in the extrascapular series which has moved forwards away from this setting, carrying the canal forwards with it as a loop. However comparison of figure 21*a*, *b* and *c* suggests that the form and position of the bone in dipnorhynchids, there designated I but referred to by Westoll as J_3, is so similar to bone I in *Dipterus* that it is highly improbable that the latter is a different bone that has moved forwards from the extrascapular series and displaced the former. There is also the difficulty that there is little evidence that such a bone normally existed in the extrascapular series. It seems more satisfactory to suppose that in *Dipterus*, perhaps as an indirect result of the orbit being further back, the commissural canal came at an early stage in ontogeny to be located rather further forward relative to the skull-roof, and thus came to pass through the zone appropriate to the development of bone I (Westoll's J_3). A latero-sensory ossicle associated with one of its neuromasts would have come to act as a focus for its development, and its status would have changed from a membranogenic to a latero-sensory bone. It is probable that at first this focus was situated very close to the posterior margin of the area, and that later in ontogeny the resulting centre of radiation became transferred to a more central position within the bone, the canal consequently being diverted into an anterior loop. This loop is demonstrated particularly well by Schultze's (1969) work on *Griphognathus*. The variations described by White (1965, figs 23, 24), one of which is shown in figure 24*a*, show the canal passing direct from Z to A and indicate that in the Middle Devonian there were still some *Dipterus* individuals in which during their ontogeny the canal was not formed sufficiently far forward for it to become involved in bone area I. It is clear that in these there was no extrascapular bone between Z and A. Neuromasts and ossicles were doubtless present in this part of the canal, and there is some evidence (Westoll 1949, fig. 3*i*; White 1962) that occasionally one of them provided a focus for a small definitive bone. In general however it seems that extrascapular requirements were fully met by the latero-sensory ossicles that acted for bones Z and A, and usually no bones were formed around any of the others. However the transference of the canal into the zone of bone I brought its ossicles onto more fertile ground and, though previously usually non-effective, here one of them came to act as a latero-sensory focus for that bone. These variations described by White are of great interest, for they indicate how easily in the *Dipterus* population bone I could switch between a latero-sensory and a membranogenic condition, and without any obvious alteration in its form; however there is not sufficient evidence to show in what way the position of its centre of radiation or of the pit-lines that it carried may have been affected by these changes. The difference between the above interpretation and that by Westoll is significant, among other reasons, in relation to the comparison of the main groups of osteichthyans (see figure 25).

The change in the condition of bone I in dipnoans, as visualized above, is precisely comparable to that in the parietal of rhizodontiforms. In both cases a stretch of canal that extended between foci that acted for adjacent bones – in the one case the intertemporal and the supratemporal, and in the other bones Z and A – came to enter the area appropriate to a different bone that bordered on this stretch – here the parietal and bone I respectively – with the result that an ossicle which had previously usually remained dormant came to act as a focus for it and transformed it into a latero-sensory bone; in both cases the canal was consequently drawn into a deviation during later stages of growth. The dipnoan transference, like the rhizodontid, can be represented by the difference between figure 1*b* and *f*. It is interesting that in rhizodontiforms we do not yet have variations comparable with those of *Dipterus* described by White in which the canal did not enter this adjacent bone area, so that the earlier pattern was retained; one would expect that comparable rhizodontiform variations, if they should be found, would have parietal shields similar in principle to those of osteolepiforms.

It is interesting that in *Scaumenacia* (figure 21*d*) from the lower Upper Devonian the junction of the main and commissural canals was further forward than in *Dipterus*. Thus the relative forward movement of the commissural canal had at its lateral end developed a stage further. Later again, in the Carboniferous dipnoans (though not in *Conchopoma* from the early Permian) this further forward movement had taken place also in the mesial portion of the commissure, which resulted in the transfer of this canal from the area of bone A to that of B (figure 21*e* and *f*). Bone A, which in any case was becoming reduced in the Devonian, was no longer formed. Bone B, which in the Devonian was a membranogenic bone with its centre of radiation at its approximate centre, as is indicated by the pit-lines in figure 21*b* and *d*, responded to the entry of the commissural canal into the posterior part of its area by adopting its intruding latero-sensory ossicles as a focus for the initiation of its ossification and was thus transformed into a latero-sensory bone which had its centre of radiation situated far posteriorly, as in *Uronemus* (figure 21*e*) from relatively early in the Carboniferous. In the rather later genus *Sagenodus* (figure 21*f*) it is appreciably farther forward. This interpretation, which accords with that given above in relation to bone I, seems to the writer more satisfactory than either of the alternative interpretations given by Westoll (1949, p. 152). In terms of figure 1 it can be regarded as a change from (*b*) to either (*c*) or (*e*) in which however the bone of area 'X' (i.e. bone A) has ceased to develop, so that a distinction between them has become meaningless.

Some postulated ontogenetic patterns are shown in figure 22. The centre of ossification of bone I has been transferred from a membranous site in figure 22*a* to a more posterior latero-sensory one in figure 22*b*; the anterior loop in the commissural canal would have become more pronounced during later stages of growth. In *Uronemus* the postulated ontogeny of figure 22*e* would lead in maturity to a bone B as in figure 21*e*; the sharp bend in the anterior pit-line at its anchorage in bone J would mark a deviation from its primary orientation, seen in figure 21*b* and *d*, occasioned by the transference of the centre of ossification of bone B to a more posterior and latero-sensory site. It has been assumed that bone area A had ceased to exist as a relevant unit in Carboniferous dipnoans, and it has been omitted in figure 22*e*; it would have been directly behind area B. In *Scaumenacia*, and also in occasional specimens of *Dipterus*, the middle pit-line extends beyond bone I to reach the central region of bone B; in these presumably a loose end that had extended beyond the rudiment of I became anchored to rudiment B, and thus was eventually drawn to the vicinity of the centre of radiation of that bone.

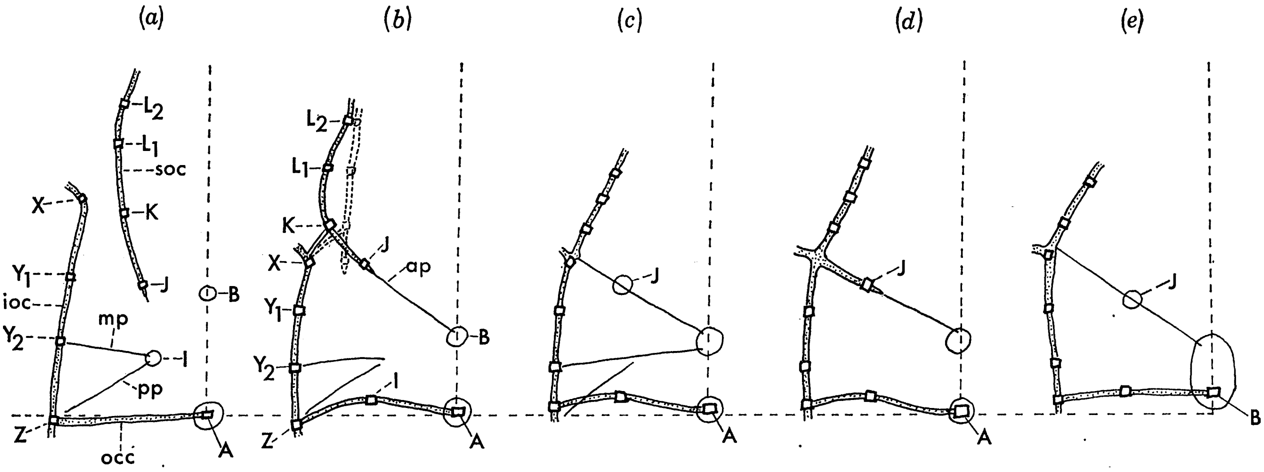

FIGURE 22. Postulated ontogenetic patterns of some dipnoans at about the beginning of skeletogenesis. (*a*) dipnorhynchid. (*b*) *Dipterus*. (*c*) *Scaumenacia*. (*d*) *Soederberghia*. (*e*) *Uronemus*.

The linkage between the supraorbital (soc) and infraorbital (ioc) latero-sensory canals is also interesting. In dipnorhynchids (figure 21*a*) these two canals run on more or less parallel courses a short distance from one another. A possible explanation of the different and strange course of the supraorbital line in *Dipterus* (figure 21*b*) is indicated by a comparison of figure 22*a* and *b*. The discontinuous lines in figure 22*b* show the supraorbital line in much the same position as in the dipnorhynchid. The position of the bend in the infraorbital line is further back because of the more posterior position of the orbit; hence although the neuromast responsible for J was opposite Y_1 in dipnorhynchids it was opposte X in *Dipterus*. It seems that when lateral lines are close to one another they exert some kind of mutual influence; this is indicated by the work of Bailey (1937) and helps to account for end-to-end unions. It is suggested that in this instance the proximity of the infraorbital line induced the young growing supraorbital line to change from a course like that in *Dipnorhynchus* by making a divergence towards the infra-orbital line, as indicated by the continuous lines in figure 22*b*. If the distal part of the line was already in some way tied to the dermis in region J then the orientation of this distal part would be abruptly altered as a result of the more proximal deviation towards the infraorbital line. This distal part would consequently be directed posteromesially rather than posteriorly and continued growth of the line in the form of a pit-line would result in it becoming anchored to the rudiment of B and so eventually being drawn to the vicinity of the centre of radiation of that bone. A further result is that the neuromast and the latero-sensory ossicle associated with K would then come to lie approximately between L_1 and X; bone K would therefore in due course develop in this position.

In this respect *Scaumenacia* (figures 21*d*, 22*c*) differs from *Dipterus* firstly, in the supraorbital line having from the position of its bend onwards the form of a pit-line, whereas in *Dipterus* it had continued as far as J as a canal; J has therefore changed from a probably latero-sensory to a definitely membranogenic bone. Secondly this bend is situated at or close to the bend in the infraorbital canal, instead of some distance in front of it as in *Dipterus*. Since the anterior pit-line is the continuation of the supraorbital canal one would expect that in *Scaumenacia* the union between the lines would be formed entirely, or almost entirely, by a junction of the canals themselves, rather than as in *Dipterus* by a union elaborated through their primary tubes. This is perhaps what Westoll (1949, p. 147) means when he speaks of the part of the supraorbital canal between K and J in *Dipterus* having been 'pirated' by bone X in *Scaumenacia*; however it seems likely that the crucial change in ontogeny took place before the ossification of bone X had begun. Judging from Westoll's (1949) outlines, individuals in both genera varied considerably and there was some overlap. In several other Devonian genera, and in those from the Carboniferous, the situation seems to have become stabilized with the anterior pit-line arising fairly precisely from the same position as the bend in the infraorbital canal. Thus it seems that in these cases the deflection of the supraorbital line brought the two canals into actual contact and a union was formed between them; thereafter the supraorbital line continued, usually in the form of a pit-line, to its pre-deflection destination in region J, and then onwards to B. *Soederberghia* (figure 22*d*) was exceptional (Lehman 1959) in that, as in *Dipterus*, the supraorbital line retained the form of a canal as far as J; here the supraorbital and infraorbital lines both make contact with one another as canals at the point where each makes a right-angled bend, so that a +shaped union of canals has resulted, with one horizontal and one vertical limb of the + formed by each of the canals.

The concept of the *Dipterus* depicted in figure 23*a* corresponds with figure 22*b* but includes an indication of the bone rudiments that would, as horizontal lamellae, have been growing outwards from the appropriate sites. There has been no systematic description of variations in the courses of the pit-lines, but Westoll (1949, p. 137) mentions that the anterior pit-line, instead of passing from J to B, may pass from J to Y_1 and then to Y_2, or from J to the suture between Y_2 and I, or from J to I. He (1949, fig. 3*b*) illustrates the first of these, as in figure 24*b*. If the supraorbital line was orientated as in figure 23*a* it is virtually impossible that, after traversing J, it could become involved with rudiments of Y_1 or Y_2. If however the line did not bend much towards the infraorbital line, and therefore did not change the more distal portion of its course from a posterior to a posteromesial direction, retaining therefore the course indicated by the discontinuous lines in figure 22*b*, then the kind of pattern shown in figure 23*b* could arise. In this event the anterior pit-line could have crossed the mesial portions of bone rudiments Y_1 and Y_2, to which it would have become anchored. Later, as a result of accretionary growth of these bones, such a pit-line would have passed relatively close to, and on the mesial side of, the centres of radiation of Y_1 and Y_2 on a course approximately parallel with the infraorbital canal, and thus as in figure 24*b*. If the supraorbital line had been slightly more mesially orientated it could well have become coincident with the suture between

Y_2 and I; if still more mesial it would have become anchored to rudiment I. These three alternative patterns are shown in figure 23*b*. Westoll (1949, fig. 8*c*) shows a specimen of *Uronemus* in which the left anterior pit-line had become anchored to rudiment I instead of that of B.

Westoll also mentions a middle pit-line of *Dipterus* which instead of passing direct from I to Y_2 runs approximately parallel with the posterior pit-line over Z and then turns sharply forwards onto Y_2. Presumably here the pit-line in the course of its traverse between rudiments Y_2 and I passed across a portion of rudiment Z and became anchored to it, as indicated in figure 23*c*. During subsequent growth it would have been pulled away from its normal course to a position relatively close to the centre of radiation of Z. The course of this line, and the presumed explanation, seem to correspond precisely with variation 'type 4' recently described in *Bothriolepis* (Graham-Smith 1978).

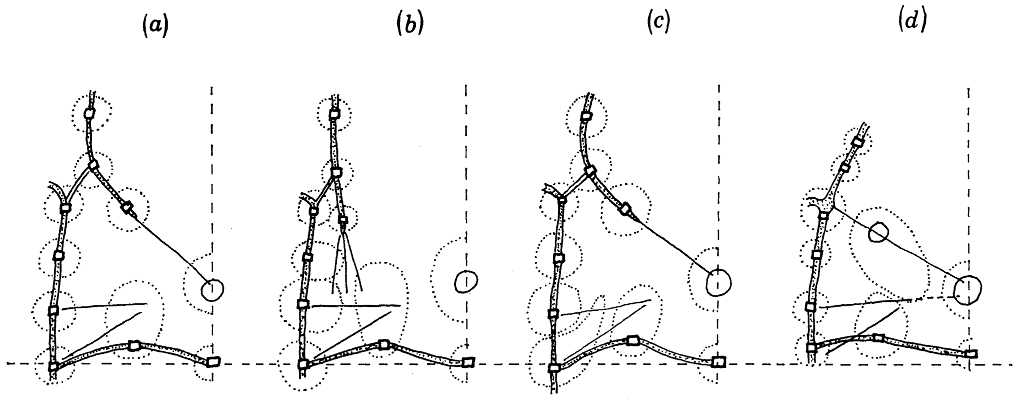

FIGURE 23. Postulated ontogenetic patterns of some dipnoans, showing bone rudiments. (*a*) typical *Dipterus* (*b*) and (*c*) to account for variations in pit-lines in *Dipterus* noted by Westoll 1949, p. 137, fig. 3*b*, see also figure 24*b*. (*d*) similarly in *Scaumenacia*, see Westoll 1949, fig. 6*d*, and figure 24*c*.

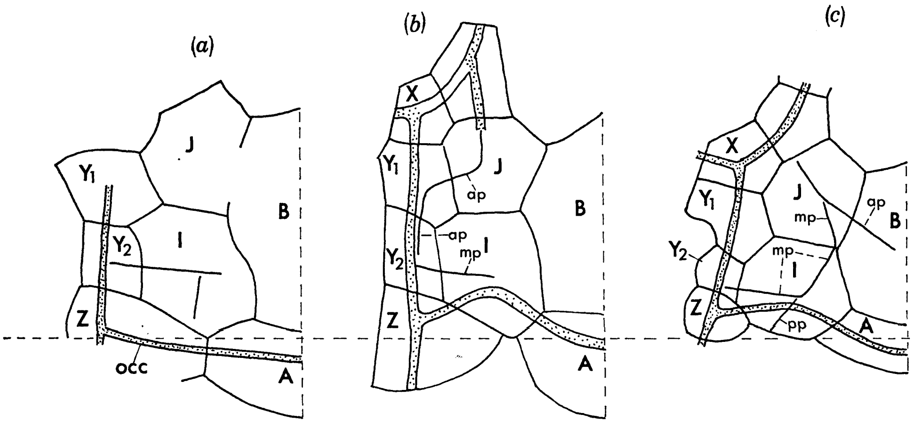

FIGURE 24. Variations in *Dipterus* and *Scaumenacia*. (*a*) *Dipterus*, after White 1965, fig. 23. (*b*) *Dipterus*, after Westoll 1949, fig. 3*b*, right side. (*c*) *Scaumenacia*, after Westoll 6*d*.

Westoll (1949, p. 137, fig. 6*d*) also refers to an interesting variation of *Scaumenacia*. The middle pit-line (mp, figure 24*c*) passes as usual from Y_2 to the central region of I, but then bends forwards to the junction of I, J and B, and then passes to the central region of J. Presumably during ontogeny this sensory line became anchored to a part of rudiment J instead of, or as well as, passing on to the normal anchorage on B (figure 23*d*). Such an association would in the course of its growth carry it to a position a relatively short distance posteromesial to the centre of radiation of J. A remarkable feature is that the groove does not pass fairly straight from the central region of I to J, but instead passes near to the adjacent corners of I and J where it makes an angulated turn. It seems that in this instance there was no yield, in the sense in which that word was used for *Bothriolepis*, and that in this respect it resembled course c. l. of Graham-Smith 1978, figure 34. This middle pit-line may well have been anchored to rudiment B, as well as to J, in which case one can anticipate that near the centre of J it would have undergone an almost complete reversal in its course to pass posteromesially to the central region of B. Here its course would have been very similar to, and perhaps indistinguishable from, that of the distal portion of the anterior pit-line.

Thus the various courses of the pit-lines of early dipnoans, as these have been indicated by Westoll (1949), present, though under less favourable circumstances, many of the features that were recently (Graham-Smith 1978) noted in the superficial sensory lines of *Bothriolepis* or discussed in other placoderms. Again we appear to be confronted with normal anchorages, alternative anchorages, additional anchorages formed along attached sectors, anchorages of loose ends, accretionary growth of bones which draws these anchorages apart, and sensory lines which usually traverse or terminate at the vicinity of the centres of radiation of bones instead of precisely at them. Again also there seem to be indications of the primary orientation of sensory lines being preserved near points of anchorage, and of various degrees of yield by bone to the tensions that are involved. Some of these concepts regarding superficial sensory lines have of course long been envisaged, but large and abundant placoderms like *Bothriolepis* seem to provide opportunities for new insights and clarification. A systematic and detailed study of the variations in the pit-lines of Devonian dipnoans might at this juncture prove rewarding.

5. Comparison of dermal skull-roofs of major groups

Zangerl (1973) has recently demonstrated that placoderms should probably no longer be regarded as having close affinities with holocephalians. Since placoderms and osteichthyans are the only gnathostomatous fishes with well developed definitive bones on the skull-roof a brief comparison of their roofing patterns, from the viewpoint developed in this paper, seems appropriate.

An outline of the skull-roof of a generalized dolichothoracid placoderm is shown in figure 25*a*. The main and infraorbital lateral line, the middle and posterior pit-lines and the commissural line all seem to have their equivalents in palaeozoic osteichthyans; so does the supraorbital line, which however is better developed in the latter. As regards bones, the paranuchals of dolichothoracids can be regarded as equivalent, among osteichthyans, to the lateral extrascapular of actinopterygians (figure 25*f*) and crossopterygians (figure 25*g*) and to bone Z in dipnoans (figure 25*h*); in each case there is a meeting near its centre of radiation of the main lateral line, the commissural line and the posterior pit-line. In the same four groups the central plate, the parietals and bone I are in similar relative positions and are associated with the middle and posterior pit-lines.

The main differences between typical dolichothoracid and osteichthyan skull-roofs can be viewed in terms of, firstly, mesiolateral proportions, secondly anteroposterior proportions and thirdly differences in the latero-sensory system. As regards the first, in figure 25*b* the various parts of the typical dolichothoracid skull-roof have been shifted mesially, thereby narrowing it. Figure 25*c* is based on this, but incorporates some anteroposterior differences. It seems that in osteichthyans, as compared with dolichothoracids, the whole preotic region has tended to elongate, this being greatest in the preorbital region. One result was that the central plate was in effect shifted backwards; this brought it closer to the commissural line. Associated with the anteroposterior extension an additional bone was interpolated along the infraorbital line. Figure 25*d* incorporates pattern 25*c* and is concerned with differences in the latero-sensory system. A principal feature is that the supraorbital line has extended into the long stretch of

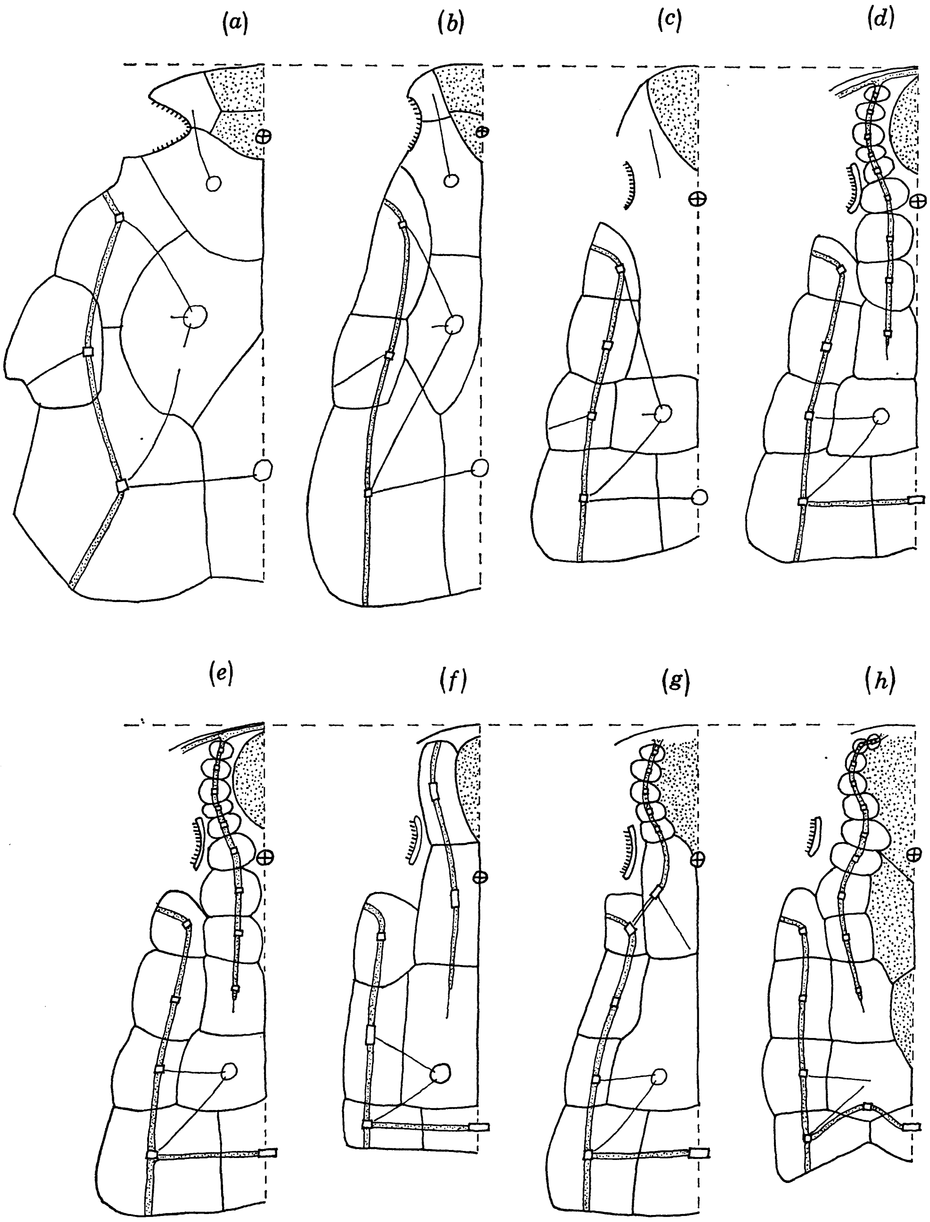

FIGURE 25. Schematic representation of possible relationships between dermal skull-roofs of some major groups of gnathostomatous fishes. For explanation see text. (*a*) skull-roof of the dolichothoracid *Kujdanowiaspis*, after Stensiö 1963, fig. 43*a*, but with commissural line added. (*b*) figure 25*a* narrowed. (*c*) figure 25*b*, but with changes in anteroposterior proportions incorporated. (*d*) (*e*) as in figure 25*c*, but with certain changes in the lateral-line system incorporated. (*f*), figure 25*e* modified to approximate to the skull-roof of an early actinopterygian. (*g*) figure 25*e* modified to approximate to an osteolepiform skull-roof. (*h*) figure 25*e* modified to approximate to the skull-roof of an early dipnoan.

territory that was opened to it as a result of the anteroposterior changes. It also deepened, establishing itself as a canal along which there was presumably formed a considerable number of latero-sensory ossicles which acted as foci for the formation of an extensive series of definitive bones. The main, the infraorbital and the commissural lines also became more deeply placed, forming canals. This general deepening of the system may have been correlated with a more active swimming habit (see Dijkgraaf 1962). On the other hand the dolichothoracid preopercular and central sensory lines are apparently not present in osteichthyans.

The type of skull-roof that could have resulted from such processes (figure 25*d*) would have provided a foundation from which the skull-roofs of the three main types of osteichthyans could have been derived. It is suggested that an ancestral type of skull-roof common to placoderms and osteichthyans might have been situated somewhere in the (*b*), (*c*) region of the figure 25*a*–*d* complex, and could have moved towards (*a*) or (*d*) depending largely on the type of swimming and feeding habits employed. The head of such a hypothetical ancestral form could have been covered with small bony scutes, and with its latero-sensory system disposed as indicated. This condition would approximate to that of acanthodians as described by Watson (1937), and could be linked with evidence provided by Miles (1973) indicating an affinity between acanthodians and osteichthyans. Definitive bones that were later evolved in the vicinity of the main and infraorbital sensory lines would have become centred on latero-sensory ossicles formed in association with these lines. The arthrodire postorbital, marginal and paranuchal could therefore approximately correspond to the osteichthyan dermosphenotic, intertemporal, supratemporal and lateral extrascapular even though these two sets of bones may, phyletically, have developed independently.

Figure 25*d* is repeated as (*e*). It is close to the actinopterygian condition, for fusions of bone rudiments along the supraorbital and infraorbital canal is virtually all that is required to result in figure *f*, which corresponds in principle to the skull-roof of an early actinopterygian such as *Moythomasia*.

To pass from figure 25*e* to a crossopterygian pattern would require the development of an intracranial juncture apparatus, the line of flexure passing, using dipnoan terms, between bones X and Y_1, and between K and J. Bone J (i.e. the 'anterior parietal') usually failed to develop, its place being taken by an extension forward of the parietal; the centre of ossification of the latter, remaining in its old position, gave rise to a centre of radiation that was relatively far back within the bone. The relation of the supraorbital and infraorbital lines to one another seems to have undergone a reorganization similar to that in *Dipterus* relative to dipnorhyncids (figures 21*a*, *b*, *c*, 22*a*, *b*), but this took place further forward, the anterior pit-line flexing across an area equivalent to K, instead of J. It may have been this development, rather than that of an intracranial juncture apparatus, that led to the supraorbital line no longer extending back to the J ('anterior parietal') region. Farther forward a reorganization of latero-sensory rudiments gave rise to a large frontal bone. By such modifications the skull-roof of figure 25*e* could become figure 25*g*, which corresponds approximately to that of a broad osteolepiform such as *Gyroptychius*.

The stippling of figure 25 serves to draw attention to the area between the series of supraorbital bones and the middle line. In dolichothoracids, actinopterygians and osteolepiforms this anamestic area is confined to a fairly small region near the front of the skull-roof. This is greatly reduced in ichthyostegids (figure 14*c* and *d*). In dipnoans however it extends further back. Figure 25*h*, which bears a reasonable resemblance to a dipnorhynchid, has been constructed from figure 25*e* by displacing the two sensory canals and their associated bones sufficiently lateralward to make room for this anamestic area. Thus the broadening of the skull of dipnoans may have made little other difference to the disposition of bones that were already present. At an appropriate stage of ontogeny there may have been a multiplication of the tissue near the middle line which spread laterally from there and, as it grew, displaced further lateralward the sensory lines and potential bone areas that lay across its path. Bone B is broader in *Dipnorhynchus* than in *Uranolophus*, and is broader still in *Dipterus* where it extends back as far as A and so prevents the two bones I from meeting one another at the middle line. These differences in successively younger genera may imply that, phyletically, the postulated lateral spread of tissue began in the pineal region and from there extended progressively further back.

A remarkably regular series of supraorbital bones was retained in dipnoans. Bone J was also retained, and consequently bone I did not extend forwards. The commissural canal became, relative to the skull-roof, progressively further forward, and had become involved in the formation of bone I by the early Devonian, and of bone B by the early Carboniferous. In this respect the changes in dipnoans ran somewhat parallel to those in the osteolepid, eusthanopterid, ichthyostegid series (figure 14, 15) in which the commissural line also came to be located progressively further forwards. In the latter however there had been no lateral spread from the mesial region and hence no bone B separated the pair of bones I (i.e. the parietals) from one another at the middle line, so that when eventually the commissural canal entered their zone it was possible for their areas to be reorganized conjointly to form a single, unpaired laterosensory bone.

6. Comments on lateral lines and dermal bones

It is widely accepted that deep-seated latero-sensory lines are in some way associated with the formation of the bones that develop around them. In the present paper it has been suggested that the small bony ossicles that ensheath the canals provide sites at which the formation of the bones proper by ordinary membranogenic processes becomes initially focused. The laterosensory structures thus merely determine the precise positions, and perhaps also influence the timing, of membranogenic ossifications that would in any case develop. A bone area may therefore change its status from one in which the latero-sensory system plays no morphogenetic part to one in which it does; this change will involve the entry of deep-seated sensory lines into the area in question. Their subsequent withdrawal will involve a reverse process. Entry may arise in principle as a result of an extension in length of a sensory canal so that it reaches a bone not previously involved (figure 1*a* to 1*b*), or as a result of a superficial sensory line or pit-line deepening sufficiently to become morphogenetic (figure 1*h* to 1*b*). These two processes are likely to be interrelated. Both can be reversed, leading to a withdrawal. In addition entry into a new area can arise through an alteration in relative positions of an established deep sensory line and an adjacent bone area, resulting in the former then exerting a morphogenetic influence on the latter. This may take the form of a simple transference (figure 1*b* to 1*f*); examples noted have concerned the parietal shield of rhizodontiforms (figure 18) and bone I of dipnoans (figure 21). Here a neuromast and its ossicle that had initially been potentially capable of acting as a focus, but had not normally done so, would in the changed circumstances have become operative in this respect. Figure 24*a* for example, which is also concerned with bone I, provides an instance that could be interpreted either as an absence of entry or as a subsequent withdrawal; the potentiality for non-entry still existed in the *Dipterus* population. On the other hand some changes in relative positions were more complex, the canal having moved away from one bone area, which was therefore no longer influenced by it, but having in the process at the same time moved into another bone area where it did exert an influence. Thus one area was substituted for another as regards its morphogenetic action; there was simultaneously an entry and a withdrawal (figure 1 *b* to 1 *e*). Three examples of transference involving such substitutions have been noted; these are concerned with the parietals of *Ichthyostega* (figure 14), the parietal shield of porolepiforms (figures 16, 17), and bones A and B in dipnoans (figure 21, 22). There is no necessary reason why entry and withdrawal in such cases should be different from those not involving substitution, but their simultaneous occurrence in adjacent areas affords an opportunity for interactions to occur between them.

The entry of a deep sensory line into a bone area will cause its site of ossification to be transferred from the location where it had been formed when there was no latero-sensory focus ('X' side of figure 1 *a*) to the position where a focus has been introduced (same side of figure 1 *b*). The territory occupied by the bone may remain unchanged, but the position of its centre of radiation will be different, as also presumably will be its construction, its strength and so forth. If the bone had previously provided anchorage to one or more pit-lines, then with the entry they will come to be anchored to a different part of a bone rudiment that is formed in a different place, and they will eventually be drawn to the vicinity of a centre of radiation that is located in a different part of the bone. Examples of such changes in the courses of pit-lines are seen in the parietals of porolepiforms and rhizodontiforms as compared with osteolepiforms (figures 16, 17, 18), and in bone B of Carboniferous dipnoans as compared with Devonian ones (figure 21, 22). Another complication is that a bone area that is entered may already be served by a latero-sensory ossicle. Something of this kind probably occurs when, for example, the part of the sensory canal that acted as a focus for the dermosphenotic in osteolepiforms becomes incorporated into the frontal area of porolepiforms (figure 16). In this case however it is merely serial ossicles along what amounts to a single stretch of canal that is involved, and it has long been known that serial osteoblastic elements have a considerable capacity for fusions or other integrations that give rise to variable bone patterns. More significant perhaps is a variation of *Polypterus* described by Jarvik (1947, fig. 6 *d*); since it is not a crossopterygian or a dipnoan it has not been referred to in the body of the paper. On the right side the commissural canal deviates away from the extrascapular area and enters the 'parietal' area instead. The bone which is thus entered is already served by a latero-sensory focus formed by a different sensory canal, namely the infraorbital, as a result of early fusion of intertemporal and supratemporal elements (Pehrson 1947, 1958); however the fact that the posterior part of this 'parietal' has transgressed both mesially into the territory of its antimere and posteriorly into normal extrascapular territory strongly suggests that a separate centre of ossification has developed at, and spread from, this new commissural focus. It would be interesting to know whether in this 'parietal' there are two separate bones each with a centre of radiation at the appropriate position, or whether the suture between two such bones has been partially or wholly obliterated, or whether there is a single bone with a single centre of radiation situated approximately midway between the two. This last would support Jarvik's view concerning the role of fusions in bone homologies.

Withdrawal from a bone area, like entry into one, can occur as a separate event or as a part of a substitution. The first can result from the reduction of a sensory line, so that a former canal comes to be represented in the area, if at all, merely as a pit-line, as in bone J during dipnoan phylogeny, or by a latero-sensory system as a whole becoming more superficial, as is that of labyrinthodonts as compared with their osteolepiform ancestors. It can also occur as a result of simple transference or re-positioning; this occurs in relation to bone I in some variations of *Dipterus*. In all these cases the bones seem to be formed as actively after the withdrawal as before; one can visualize the centre of ossification being formed by a membranogenesis now devoid of a specific focus in much the same place and manner as it may have been formed at an earlier stage in phylogeny before the advent of latero-sensory ossicles had complicated the scene. The instances quoted provide little information on this matter, but it is interesting to note that if any known labyrinthodonts are descended from ancestors which, like *Ichthyostega*, had had a median parietal formed through association with a commissural canal, then when later this became superficial there was a reversion to paired parietals each with a membranogenic centre.

Withdrawal can also represent the negative aspect of a transference that involves substitution. The extrascapular series of bones is missing in ichthyostegids, but presumably this was a part of general tetrapod adaptation and had little or nothing to do with the movement of the commissural canal to a more anterior position. In dipnoans bone A had become quite small before the withdrawal of the canal and one can argue nothing from its subsequent disappearance. The fate of the intertemporal in porolepiforms is open to various interpretations. Thus the three instances of substitution cited in this paper yield no definite information regarding the results of the withdrawal. However the variation of *Polypterus* described by Jarvik (1947, fig. 6*d*) and referred to above seems informative in this connection also. The commissural canal has withdrawn from the right median extrascapular and, as noted, has probably provided a focus for a latero-sensory ossification in the posterior part of the 'parietal' area. Two points seem interesting; firstly, this latter ossification has spread somewhat into right median extrascapular territory, indicating that there has been some interaction between the bone associated with the entry and the area involved in the withdrawal. Secondly, the latter has formed two separate membranogenic bones, which thus replace the normal latero-sensory right median extrascapular; the fact that two bones are formed instead of one perhaps indicates some instability resulting from the absence of the previous focus. Here the normal condition represented by figure 1*b* has been transformed into a combination of figure 1*c* and *e*. A specimen of *Acipenser* described by Jarvik (1948, fig. 18*c*) is also relevant; the setting is rather different, but the essential feature is that the right commissural canal has become transferred to the parietal area and the resulting bone has grown backwards to meet a more posterior bone that has grown forwards from behind the extrascapular series; no median extrascapular has developed on this side. In this case the change has been from figure 1*b* wholly to 1*c*. It seems that whether it is 'worth while' for a membranogenic centre of ossification to develop in an area following a withdrawal as part of a substitution may depend on whether, and if so how rapidly, the bone arising from the newly installed latero-sensory focus trespasses into the territory of the deprived bone. Here therefore timing may be involved, in addition to the transfer of location. This brings to mind the sd.Pa *Osteolepis*; here evidence afforded by the transgressions has suggested that it was 'worth while' for an 'anterior parietal' ossification to be formed only when the parietal of its side was unusually slow to develop. In the *Glyptopomus* variation of figure 12*b* it seems likely that anterior ossifications would have developed if in this genus the sensory canals and associated intertemporals had not been located so far mesially that little room was left. In general, it is probable that location and timing interact with one another in a complex manner.

It also seems that the idea of potential bone areas, which apparently forms a useful working concept, cannot be effectively pursued beyond an early stage in skeletogenesis.

In this general context it is interesting to consider the major changes experienced by the bone designated I in dipnoans. It probably began (figure 25*e*) as a typical membranogenic bone which gave anchorage to the middle and posterior pit-lines. In dipnoans it remained a small bone, but its region came to be entered from posteriorly by the commissural sensory line which presumably provided a latero-sensory focus which caused its centre of ossification to be transferred to a rather more posterior site. On the other hand in the crossopterygian lineage the bone in front (J) usually failed to develop, and bone I grew forwards and occupied its territory. The position of its centre of radiation apparently remained essentially unchanged, as seems usually to happen when a bone spreads into new territory, but not when territory that was previously available becomes curtailed. It is seen in this form, under the name parietal, in osteolepiforms. Within this group it underwent various modifications, some of which have been noted. Also in porolepiforms and rhizodontiforms this bone area with its expanded territory was entered fairly far forward from its lateral side by the infraorbital sensory line; in consequence a latero-sensory site of ossification was established well forward in the bone, at a relatively long distance from the previous membranogenic one, and the pit-lines were drawn to a considerably more anterior position within the bone (figure 20*f* and *g*). Lastly among ichthyostegids, which were also derived from osteolepiforms, the commissural canal entered the parietal region from behind and provided a latero-sensory focus in the middle line from which an unpaired parietal developed.

Many of the features of superficial sensory lines, represented in osteichthyans by pit-lines, correspond closely with those referred to in placoderms in an earlier paper (Graham-Smith 1978). In osteolepiforms unions of the middle and posterior pit-lines may or may not occur, this varying widely from group to group and from specimen to specimen; such unions are sometimes T-shaped, more often end-to-end. Loose ends are often evident. Examples of anchorage to alternative bones, to additional bones on the course between normal anchorages, and additional anchorage of loose ends that extend the pit-line beyond its former course, can all be inferred in dipnoans as well as in placoderms.

The symmetry of the It/Pa and St/Pa sutures on the two sides has, as previously explained, been used to determine the position of the middle line in parietal shields. This approximate symmetry may be disrupted by various factors. There is the obvious case of the *Osteolepis* of figure 4*d* with two intertemporals on the left side. The recoil of structures on the 'd' side of sd.Pa *Osteolepis* is usually almost confined to the parietal region, but in the specimen of figure 5*b* it has spread into the supratemporal region and affected the position of the St/Pa suture; this has occurred also in the *Eusthenopteron* of figure 13*g*. The right It/Pa suture of the *Latvius* of figure 9*b* has apparently been indirectly affected by the remarkable transgression of the left parietal. In specimens with areas of more intensive growth in the posterior parts of the shield the symmetry of the St/Pa sutures will depend on these growth patterns having been similar on the two sides. However it seems that in spite of various limitations a comparison of these sutures on the two sides can usually provide a satisfactory indication of the position of the middle line.

In some respects the courses of deep and superficial sensory lines resemble one another. The ossicles associated with the former provide foci from which the latero-sensory bones develop; their canals consequently become embedded at the centre of these bones. Superficial lines often become anchored to parts of bone rudiments early in skeletogenesis; their later courses consequently also become associated with the centres of radiation; in their case however the association is usually with the vicinity of the centre, in contrast to the precise centre itself. The courses of both types of sensory line are therefore in some respects related to the centres of radiation of bones. In addition if for various reasons the relative positions of the centres of radiation change during later stages of growth then both the canals and the pit-lines that are associated with them will be moved in similar ways. Their similar relation to centres of radiation, though far-reaching, is therefore only incidental; it arises in the two cases from quite different causes; these differences result in the canals playing a part in determining the positions at which the latero-sensory bones are formed whereas pit-lines and other superficial lines have no such morphogenetic role.

In the present work one particular approach has been applied to various problems. There are of course other quite different possible approaches. Jarvik (1948, 1972), who seems broadly to represent the views of a number of Swedish workers, considers that most changes are due to the fusion of bones. This, as already noted, seems to lead to difficulties with regard to the parietal of *Osteolepis*, and of porolepiforms. Also it seems impossible to apply it to the parietal of rhizodontiforms or to bone I of dipnoans. Another difficulty is that this concept, unless confined to the very early stages of skeletogenesis, involves a remodelling of the structure of the bone with the formation of a new centre of radiation. Jarvik (1972, p. 150) states that 'An interesting but still unexplained fact is that the sensory lines generally run through or close to the centres of radiation of the sensory line bones. This association with the centres of radiation is retained at the fusion of bones and the sensory lines of the bones that fuse will therefore move so as to pass close to the centre of radiation of the compound bone and this is true both of sensory canals and pit-lines.' He (1948, pp. 121, 122) considers that canals and pit-lines have the same value in homologizing dermal bones and that Westoll's (1937*a*, p. 380) view that pit-lines become anchored by their nerve supply to whatever bone develops deep to them cannot possibly be true. It seems to the present writer that Jarvik has been misled by the superficial resemblances between the courses of canals and pit-lines. The approach adopted in the present paper does explain the facts referred to in the above quotation, though without using the concept of fusion; it does this in terms of two different types of processes that are involved in, respectively, the case of canals and pit-lines, and it consequently leads to the conclusion that canals play an important part in determining the homologies of dermal bones, whereas pit-lines play no such part. Also variations type 4 and type 6 of *Bothriolepis* described in a recent paper (Graham-Smith 1978) would seem impossible to explain unless anchorages are involved.

It seems difficult to apply Parrington's (1949) approach, referred to on page 46, to some of the more recent evidence, such as that afforded by *Rhizodus*, or, again, by variations type 4 and type 6 in *Bothriolepis*.

The present approach is in accord with Westoll (e.g. 1937*a*, 1944, 1949) as regards the morphogenetic influences of deep sensory lines, its absence in superficial ones and the assumption of anchorages in the latter. However it differs as regards the interpretation of changes here regarded as due to alterations in the positions of deep lines relative to those of bone areas, whether involving substitutions or not. Thus Westoll (1937*b*, 1944) regards the large bone in the parietal shield of porolepiforms as derived phylogenetically through the regression and loss of a bone equivalent to the osteolepiform parietal and a spreading of the intertemporal to take its place. This is equivalent to a change from figure 1*b* to 1*d*. Pehrson (1947, 1958) has shown that during the ontogeny of *Polypterus* a parietal ossification develops for a time after which it regresses and disappears, its place then being taken by the mesial spread of the dermopterotic, this being a lateral-line bone resulting from an early fusion of intertemporal and supratemporal rudiments. It is therefore likely that the relevant bone in *Polypterus* has been derived from a typical actinopterygian condition by the kind of process envisaged by Westoll for porolepiforms from osteolepiforms. However it is unlikely that during the ontogeny of these the parietal progressed to a stage at which it would have provided anchorage for the pit-lines, for then they would not have been drawn forwards to their anterior position. According to Westoll the large bone in porolepiforms is an intertemporal that has come to occupy the territory of the parietal in addition to its own; the prespiracular is therefore necessarily a different bone. In some respects his interpretation differs little from that adopted here; thus in both cases skeletogenesis would consist essentially of ossification becoming established in association with the canal and its horizontal lamella spreading from there to occupy the territory of a bone that had previously developed by membranogenesis. Nevertheless the two approaches do involve differences in the mechanisms of change and in phylogenetic implications that are of considerable importance. Westoll is standing strictly by Allis; homologous neuromasts continue to be associated with homologous bones even though the latter are developing in a different setting; for the present writer the neuromasts concerned in a transference are approximately homologous, but they provide a focus for different, not homologous, bones. Because the two viewpoints in some respects run parallel with one another it may be difficult to find evidence that clearly establishes their relative validity, and this may well depend on critical specimens, either known now or to be discovered in the future.

One difference which may facilitate distinction is that Westoll's view seems to entail the existence of two bones before the change (figure 1*b*) and of only one afterwards (figure 1*d*). For the writer, with a simple transference there will be one bone at the beginning (figure 1*b*, right side), and the same bone at the end (figure 1*f*, right side); the only difference is that it has changed from a membranogenic to a latero-sensory ontogeny. In cases of substitution there are two bones at the beginning (figure 1*b*) and there may be the same two at the end (figure 1*e*), one of which has been vacated and become membranogenic, and the other has been entered and become latero-sensory; their roles have therefore been reversed. Alternatively the one that has been vacated may not be represented by a separate unit, in which case its territory may in some cases have been taken over by the one that has been entered, as in figure 1*c*. As noted above, the right side of the *Acipenser* of Jarvik 1948, fig. 18*c*, is probably an example of this. A demonstration that a membranogenic bone had developed in an area vacated by a canal would strongly support the present writer's approach. Among actinopterygians, the membranogenic right median extrascapulars in the *Polypterus* of Jarvik's (1947) fig. 6*d* seems to be one such instance. The evidence (Westoll 1944) afforded by the species of *Haplolepis* with a single bone in the parietal shield, as opposed to those with two, is indefinite, for it can be interpreted in terms of either figure 1*c* or 1*d*. However, as in most of the relevant cases, the relatively small size of the latero-sensory bone which Westoll regards as having done the taking over, as compared with that of the bone that is supposed to have regressed and been taken over, and also the absence of intermediate stages of this process, could be held to weigh against Westoll's viewpoint. Among crossopterygians, the evidence afforded by the porolepiforms is also indecisive, for the prespiracular can be interpreted either as a modified intertemporal or as a different bone. In the rhizodontiforms the large bone cannot be interpreted as a normal intertemporal, for this bone is still present; Westoll could perhaps argue that a second intertemporal, such as that in the *Osteolepis* of figure 4*d*, has taken over the field left vacant by the regression of the parietal; however this seems highly unlikely and there is no apparent reason for such a change. A simple transference, perhaps involving this same neuromast, seems to provide a simpler and more satisfactory working concept. As regards dipnoans, Westoll (1949, pp. 161, 163; fig. 10*b* and *c*) considers that bone I of *Dipterus* is derived from a bone of the extrascapular series that was situated between Z and A in dipnorhynchids; in the latter a bone (J_3) in front of it regressed and the latero-sensory bone I moved forwards leaving the extrascapular series and took its place. However as noted previously (e.g. figure 21 *a*–*c*) the bone that was already present in dipnorhynchids (Westoll's J_3) is so similar to the bone that is thought to have taken its place in *Dipterus* that it is highly improbable that two different bones are involved. Also there is no satisfactory evidence that an additional extrascapular bone was present between Z and A in dipnorhynchids; certainly there is no such bone in the two specimens of *Dipterus* described by White in which the canal passes direct from Z to A. These difficulties can be overcome by supposing that the commissural canal moved forward into a relatively more anterior position which brought it into association with a membranogenic bone, I, which was already present and was thereby converted into a latero-sensory bone. The latero-sensory ossicle which thus came to act as a focus for I would previously have been in the extrascapular region where, usually, it would have had no opportunity to function in this way. Thus with regard to both *Rhizodus* and bone I Westoll seems to have to rely on a bone that does not normally exist, though it is potentially capable of doing so, for the purpose of taking over the territory of an adjacent membranogenic bone which he believed to have regressed. Turning to dipnoan bones A and B, in this case Westoll (1949, p. 152) does not account for the differences between the Devonian and the Carboniferous genera in terms of B regressing and being taken over by A, perhaps because, by contrast, during the Devonian it was A that was regressing. Instead he offers two alternative explanations, one involving fusion and the other rather complex. However in this case also a forward movement in the relative position of the commissural canal seems to account for the differences satisfactorily. As far as I know Westoll has not given an explanation of the latero-sensory unpaired parietal bone of *Ichthyostega*. Thus Westoll's approach to this matter seems to involve a mixed assemblage of difficulties which can perhaps be uniformly avoided by using the concept of transference.

However critical comment of this kind has serious limitations. If advocates of different approaches could set out the consequent implications in some detail, as has been attempted here for one particular approach, then it would be possible to make more constructive comparisons and to know better where we stand. One advantage of the conceptual framework presented here, in which thresholds play a significant part, is that it permits prediction, even to some extent quantitatively, of the kind of results that would be expected to follow from other possible ontogenetic patterns; it thus provides opportunities for checking its own validity. One can for example appreciate from figures 14 and 15 that the *Eusthenopteron* with a median parietal mentioned by Westoll (1938) may possibly be a 'premature' instance of the commissural line having become transferred from the extrascapular to the parietal area, as in *Ichthyostega*. One can predict that such a specimen of *Eusthenopteron* would differ from *Ichthyostega* in having a membranogenic median (? paired) extrascapular, and one could superimpose on the typical *Eusthenopteron* condition of figure 13*a* an outline of the kind of parietal shield it would be expected to have. In general it is doubtless important that we should look out for variations that may for one reason or another be critical for our understanding, and so endeavour to make maximum use of the biological experiments in the business of living that were experienced by these animals so long ago.

7. SUMMARY

Some previous views on the relation of latero-sensory lines to bones are noted, and a modified version is suggested.

Published photographs of some parietal shields of crossopterygians have been re-photographed and enlarged, and their outlines compared, as far as possible quantitatively, using a common frame of reference.

Variations of *Osteolepis* with one parietal bone on one side and with two bones in the corresponding area on the other side are considered in some detail, particularly with reference to possible ontogenetic implications. The configuration of the sutures suggests that an ossification is formed in the anterior region only when the normal parietal is unusually slow to develop. The presence of an anterior bone prevents the forward growth of the normal one, and the growth changes in the latter then apparently result in its centre of radiation and associated structures being carried to a more posterior position.

The parietal shield of *Osteolepis* seems to hold a central position among osteolepiforms. In some of these there is evidence of a localized area of more intensive growth in the posterior part of the shield. In *Eusthenopteron* the posterior part of the shield is reduced and the commissural canal is relatively closer to its posterior border. This type of change has apparently led in ichthyostegids to the condition found in *Ichthyostega* where the canal has become involved in the parietal area, with the result that the paired membranogenic parietals of osteolepiforms have been replaced by an unpaired latero-sensory parietal that has its centre of radiation far back in the bone at the point where the commissural canal crosses the middle line.

In osteolepiforms there is much variation in the breadth of the parietals at the anterior end of the shield, and a case is made for the difference in relationship between the lateral lines and the relevant bones of the shield that is found in porolepiforms and rhizodontiforms, as compared with osteolepiforms, being due to the occurrence of similar difference in mesiolateral relations at an appropriate stage of ontogeny which however, importantly, are not accompanied by a similar change in the position at which the young sensory lines are formed; these consequently become associated with different bone areas.

The parietal region of dipnoans is considered from the same viewpoint. Most of the features of superficial sensory lines of placoderms noted in a recent paper are present also in the dipnoan pit-lines of this area.

The dermal skull-roofs of placoderms and of the three main groups of osteichthyans are tentatively compared.

Some conclusions concerning the relation of latero-sensory lines to bones are briefly considered and compared with those of other workers.

REFERENCES

Allis, E. P. 1889 The anatomy and development of the lateral line system in *Amia calva*. *J. Morph.* **2**, 463–540.

Allis, E. P. 1898 On the morphology of certain of the bones of the cheek and snout of *Amia calva*. *J. Morph.* **14**, 425–466.

Allis, E. P. 1905 The latero-sensory canals and related bones in fishes. *Int. Mschr. Anat. Physiol.* **21**, 401–502.

Andrews, S. M. 1973 Interrelationships of crossopterygians. In *Interrelationships of fishes* (ed. P. H. Greenwood, R. S. Miles & C. Patterson), pp. 137–177. London: Academic Press.

Andrews, S. M. & Westoll, T. S. 1970 The postcranial skeleton of rhipidistian fishes excluding *Eusthenopteron*. *Trans. R. Soc. Edinb.* **68**, 391–489.

Bailey, S. W. 1937 An experimental study of the origin of lateral-line structures in embryonic and adult teleosts. *J. exp. Zool.* **76**, 187–223.

de Beer, G. R. 1937 *The development of the vertebrate skull*, xxiv, 552 pages. Oxford: University Press.

Bjerring, H. C. 1973 Relationships of coelacanthiforms. In *Interrelationships of fishes* (ed. P. H. Greenwood, R. S. Miles & C. Patterson), pp. 175–210. London: Academic Press.

Branson, B. A. & Moore, G. A. 1962 The lateralis components of the acoustico-lateralis system in the sunfish family Centrarchidae. *Copeia* 1962, 1–108.

Bystrow, A. P. 1935 Morphologische Untersuchungen der Deckknochen des Schädels der Wirbeltiere. *Acta zool. Stockh.* **16**, 65–141.

Denison, R. H. 1968 Early Devonian lungfishes from Wyoming, Utah, and Idaho. *Fieldiana, Geol.* **17**, 353–413.

Devillers, C. 1947 Recherches sur la crâne dermique des téléostéens. *Annls. Palaeont.* **33**, 1–94.

Devillers, C. 1965 The role of morphogenesis in the origin of higher levels of organization. *Syst. Zool.* **14**, 259–271.

Dijkgraaf, S. 1962 The functioning and significance of the lateral-line organs. *Biol. Rev.* **38**, 51–105.

Fell, H. B. & Robinson, R. 1929 The growth, development and phosphatase activity of embryonic avian femora and limb-buds cultivated *in vitro*. *Biochem. J.* **23**, 767–784.

Girgis, F. G. & Pritchard, J. J. 1958 Effects of skull damage on the development of sutural patters in the rat. *J. Anat. Lond.* **92**, 39–51.

Goodrich, E. S. 1919 Restorations of the head of *Osteolepis*. *J. Linn. Soc.* (*Zool.*) **34**, 181–188.

Goodrich, E. S. 1925 On the cranial roofing-bones in the Dipnoi. *J. Linn. Soc.* (*Zool.*) **36**, 79–86.

Graham-Smith, W. 1978 On some variations in the latero-sensory lines of the placoderm fish *Bothriolepis*. *Phil. Trans. R. Soc. Lond.* B **282**, 1–39 (preceding paper).

Graham-Smith, W. & Westoll, T. S. 1937 On a new long-headed dipnoan fish from the Upper Devonian of Scaumenac Bay, P.Q., Canada. *Trans. R. Soc. Edinb.* **59**, 241–266.

Gross, W. 1956 Über Crossopterygier und Dipnoer aus dem baltischen Oberdevon im Zusammenhang einer vergleichenden Untersuchung des Porenkanalsystems paläozoischer Agnathen und Fische. *K. svenska VetenskAkad. Handl.* (4) **5**, 1–140.

Harrison, R. G. 1904 Experimentelle Untersuchungen über die Entwicklung der Sinnesorgane der Seitenlinie bei den Amphibien. *Arch. micr. Anat.* **63**, 35–149.

Jardine, N. 1969 The observational and theoretical components of homology: a study based on the morphology of the dermal skull-roofs of rhipidistian fishes. *Biol. J. Linn. Soc.* **1**, 327–361.

Jarvik, E. 1944 On the dermal bones, sensory canals and pit-lines of the skull in *Eusthenopteron foordi* Whiteaves, with some remarks on *E. säve-söderberghi* Jarvik. *K. svenska VetenskAkad. Handl.* (3) **21**, 1–48.

Jarvik, E. 1947 Notes on the pit-lines and dermal bones of the head in *Polypterus*. *Zool. Bidr. Upps.* **25**, 60–78.

Jarvik, E. 1948 On the morphology and taxonomy of the Middle Devonian osteolepid fishes of Scotland. *K. svenska VetenskAkad. Handl.* (3) **25**, 1–301.

Jarvik, E. 1950*a* Middle Devonian vertebrates from Canning Land and Wegeners Halvø (East Greenland). 2. Crossopterygii. *Meddr. Grønland* **96**, 1–132.

Jarvik, E. 1950*b* On some osteolepiform crossopterygians from the Upper Old Red Sandstone of Scotland. *K. svenska VetenskAkad. Handl.* (4) **2**, 1–35.

Jarvik, E. 1952 On the fish-like tail in the ichthyostegid stegocephalians with descriptions of a new stegocephalian and a new crossopterygian from the Upper Devonian of East Greenland. *Meddr. Grønland* **114**, 1–90.

Jarvik, E. 1972 Middle and Upper Devonian Porolepiformes from East Greenland with special reference to *Glyptolepis groenlandica* n.sp. and a discussion on the structure of the head in the Porolepiformes. *Meddr. Grønland* **187**, 1–307.

Jessen, H. 1966 Die Crossopterygier des Oberen Plattenkalkes (Devon) der Bergisch-Gladbach-Paffrather Mulde (Rheinisches Schiefergebirge) unter Berücksichtigung von amerikanischem und europäischem *Onychodus*-Material. *Ark. Zool.* (2) **18**, 305–389.

Lehman, J. P. 1959 Les Dipneustes du Dévonien du Groenland. *Meddr. Grønland* **160**, 1–58.

Lekander, B. 1949 The sensory line system and the canal bones of some Ostariophysi. *Acta zool. Stockh.* **30**, 1–131.

Miles, R. S. 1971 The Holonematidae (placoderm fishes), a review based on new specimens of *Holonema* from the Upper Devonian of Western Australia. *Phil. Trans. R. Soc. Lond.* B **263**, 101–234.

Miles, R. S. 1973 Relationships of acanthodians. In *Interrelationships of fishes* (ed. P. H. Greenwood, R. S. Miles & C. Patterson), pp. 63–103. London: Academic Press.

Moy-Thomas, J. A. 1938 The problem of the evolution of the dermal bones in fishes. In *Evolution, Essays on aspects of evolutionary biology* (ed. G. R. de Beer), pp. 305–319. Oxford: University Press.

Moy-Thomas, J. A. 1941 Development of the frontal bones of the Rainbow Trout. *Nature, Lond.* **147**, 681–682.

Ørvig, T. 1971 Comments on the lateral line system of some brachythoracid and ptyctodontid arthrodires. *Zool. Scripta* **1**, 5–35.

Ørvig, T. 1972 The latero-sensory component of the dermal skeleton in lower vertebrates and its phyletic significance. *Zool. Scripta* **1**, 139–155.

Parrington, F. R. 1949 A theory of the relation of lateral lines to dermal bones. *Proc. zool. Soc. Lond.* **119**, 65–78.

Parrington, F. R. 1956 The patterns of dermal bones in primitive vertebrates. *Proc. zool. Soc. Lond.* **127**, 389–411.

Parrington, F. R. 1967 The identification of the dermal bones of the head. *J. Linn. Soc.* (*Zool.*) **47**, 231–239.

Pehrson, T. 1922 Some points in the cranial development of teleostomian fishes. *Acta zool. Stockh.* **3**, 1–63.

Pehrson, T. 1940 The development of the dermal bones in the skull of *Amia calva*. *Acta zool. Stockh.* **21**, 1–50.

Pehrson, T. 1944 The development of the latero-sensory canal bones in the skull of *Esox lucius*. *Acta zool. Stockh.* **25**, 135–157.

Pehrson, T. 1947 Some new interpretations of the skull in *Polypterus*. *Acta zool. Stockh.* **28**, 399–455.

Pehrson, T. 1958 The early ontogeny of the sensory lines and dermal skull in *Polypterus*. *Acta zool. Stockh.* **39**, 241–258.

Romer, A. S. 1947 Review of the Labyrinthodontia. *Bull. Mus. comp. Zool. Harv.* **99**, 1–368.

Säve-Söderbergh, G. 1932 Preliminary note on Devonian stegocephalians from East Greenland. *Meddr. Grønland* **94**, 1–107.

Säve-Söderbergh, G. 1933 The dermal bones of the head and the lateral line system in *Osteolepis macrolepidotus* Ag. *Nova Acta R. Soc. Scient. Upsal.* (4) **9**, 1–129.

Säve-Söderbergh, G. 1937 On the dermal skulls of *Lyrocephalus*, *Aphaneramma*, and *Benthosaurus*, labyrinthodonts from the Triassic of Spitzbergen and N. Russia. *Bull. geol. Instn. Univ. Upsala* **27**, 189–208.

Säve-Söderbergh, G. 1941 Notes on the dermal bones of the head of *Osteolepis macrolepidotus* Ag. and the interpretation of the lateral line system in primitive vertebrates. *Zool. Bidr. Upps.* **20**, 523–541.

Schaeffer, B. 1965 The role of experimentation in the origin of higher levels of organisation. *Syst. Zool.* **14**, 318–336.

Schultze, H. P. 1969 *Griphognathus* Gross, ein langschnauziger Dipnoer aus dem Oberdevon von Bergisch-Gladbach (Rheinisches Schiefergebirge) und von Lettland. *Geol. Palaeont. Marburg* **3**, 21–79.

Stensiö, E. A. 1947 The sensory lines and dermal bones of the cheek in fishes and amphibians. *K. svenska Vetensk-Akad. Handl.* (3) **24**, 1–195.

Stensiö, E. A. 1963 Anatomical studies of the arthrodiran head. Pt. 1. Preface, geological and geographical distribution, the organisation of the arthrodires, the anatomy of the head in the Dolichothoraci, Coccosteomorphi and Pachyosteomorphi. *K. svenska VetenskAkad. Handl.* (4) **9**, 1–419.

Tatarko, K. 1934 Restitution des Kiemendeckels des Karpfens. *Zool. Jb.* (*Zool.*) **53**, 461–500.

Thomson, K. S. & Campbell, K. S. W. 1971 The structure and relationships of the primitive Devonian lungfish – *Dipnorhynchus sussmilci* (Etheridge). *Bull Peabody Mus. nat. Hist.* **38**, 1–109.

Troitsky, W. 1932 Zur frage der Formbildung des Schädeldaches. *Z. Morph. Anthrop.* **30**, 504–532.

Watson, D. M. S. 1937 The acanthodian fishes. *Phil. Trans. R. Soc. Lond.* B **228**, 49–146.

Westoll, T. S. 1936 On the structure of the dermal ethmoid shield of *Osteolepsis*. *Geol. Mag.* **73**, 157–171.

Westoll, T. S. 1937*a* On the cheek-bones in teleostome fishes. *J. Anat. Lond.*, **71**, 362–382.

Westoll, T. S. 1937*b* The Old Red Sandstone fishes of the North of Scotland, particularly of Orkney and Shetland. *Proc. Geol. Ass.* **48**, 13–45.

Westoll, T. S. 1938 Ancestry of the tetrapods. *Nature, Lond.* **141**, 127–128.

Westoll, T. S. 1941 Latero-sensory canals and dermal bones. *Nature, Lond.* **148**, 168–169.

Westoll, T. S. 1943 The origin of the tetrapods. *Biol. Rev.* **18**, 78–98.

Westoll, T. S. 1944 The Haplolepidae, a new family of Late Carboniferous bony fishes. A study in taxonomy and evolution. *Bull. Am. Mus. nat. Hist.* **83**, 1–122.

Westoll, T. S. 1949 On the evolution of the Dipnoi. In *Genetics, palaeontology and evolution.* (ed. G. L. Jepsen, E. Mayr & G. G. Simpson), pp. 121–184. Princeton: University Press.

White, E. I. 1962 A dipnoan from the Assise de Mazy of Hingeon. *Bull. Inst. r. Sci. nat. Belg.* **38**, 1–8.

White, E. I. 1965 The head of *Dipterus valenciennesi* Sedgwick & Murchison. *Bull. Br. Mus. nat. Hist.* (*Geol.*) **11**, 1–45.

Zangerl, R. 1973 Interrelationships of early chondrichthyans. In *Interrelationships of fishes* (ed. P. H. Greenwood, R. S. Miles & C. Patterson), pp. 1–14. London: Academic Press.

ABBREVIATIONS USED IN LINE DRAWINGS

A	in crossopterygians, position at which It/Pa or It/A.Pa suture meets anterior border of parietal shield. Referred to in text as point A
A	in dipnoans, bone A
A.Pa	anterior parietal
a.m.	anterior margin of parietal
ap	anterior pit-line or its groove
a.p.p.	anteroposterior position
a.s.	possible abortive suture
ax.It–St	intertemporal supratemporal axis
B	in crossopterygians, position at which It/Pa, It/St and St/Pa sutures meet. Referred to as point B
B	in dipnoans, bone B
b.a.	bone area of bone indicated
C	in crossopterygians, position at which St/Pa suture meets posterior border of parietal shield. Referred to as point C
C	in dipnoans, bone C
c.r.	centre of radiation
Ds	dermosphenotic
Esc.l	lateral extrascapular
Esc.m	median extrascapular
Et	extratemporal
Fr	frontal
f.p.	pineal foramen
h.l.	horizontal lamella of bone indicated
I	bone I of dipnoans
It	intertemporal
ioc	infraorbital sensory line or its canal
J	bone J in dipnoans
K	bone K in dipnoans
L_1	bone L_1 in dipnoans
L_2	bone L_2 in dipnoans
l.c.	line joining centres of radiation of intertemporal and lateral extrascapular
mdl	middle line
m.l.p.	mesiolateral position
mp	middle pit-line or its groove
msc	main sensory line or its canal
Na	nasal
‘Na’	bone derived from osteolepiform nasal series and referred to as frontal in tetrapod terminology
occ	occipital cross-commissural line or its canal
o.ls	latero-sensory ossicle, formed by dermogenesis
o.m	ossification initiated by membranogenesis of bone indicated
Pa	parietal

Po	postorbital
pp	posterior pit-line or its groove
r.	rudiment of bone indicated, or presumed subsequent site of rudiment at a later stage
SB	supernumerary bone
St	supratemporal
soc	supraorbital sensory line or its canal
sp	approximate position of spiracle
X	bone X in dipnoans
Y_1	bone Y_1 in dipnoans
Y_2	bone Y_2 in dipnoans
Z	bone Z in dipnoans