

HOMOLOGIZATIONS OF SKULL ROOFING BONES BETWEEN TETRAPODS AND OSTEOLEPIFORM FISHES

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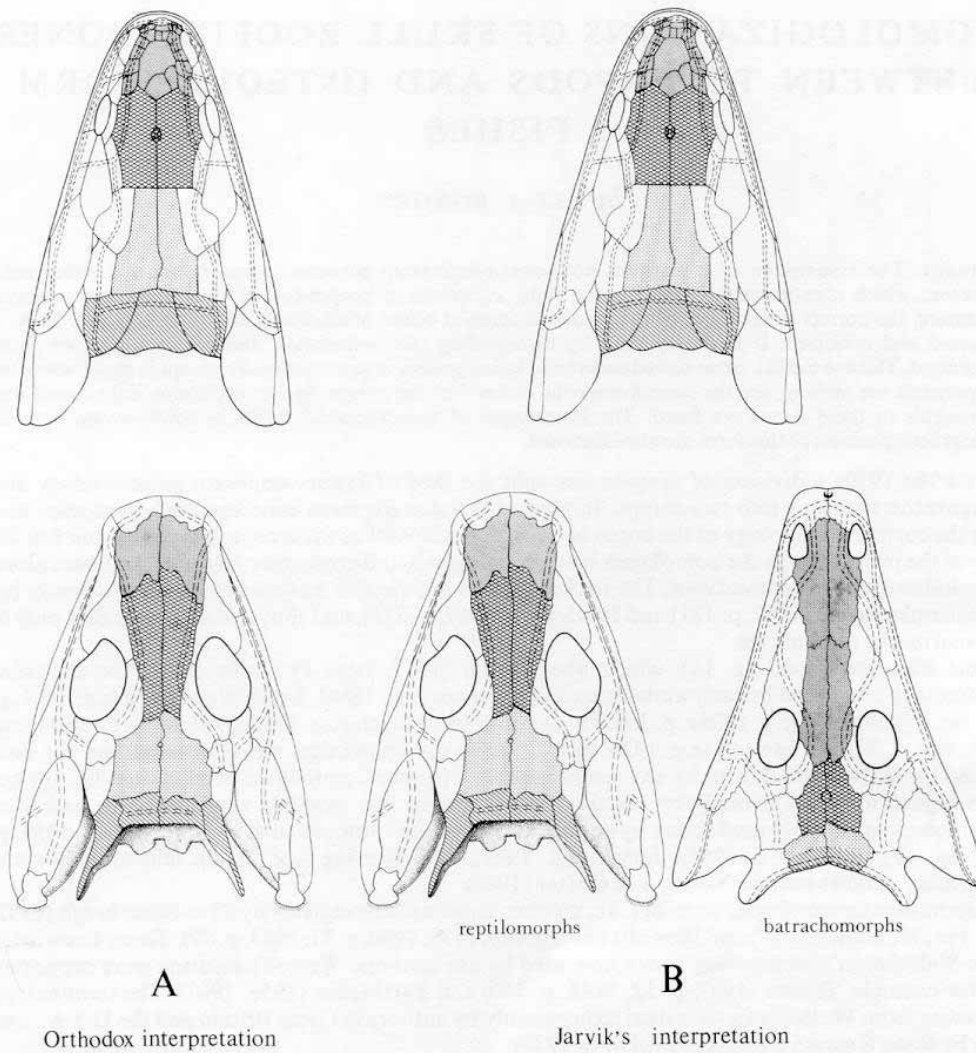
ABSTRACT. The assumption of a constant positional relationship between dermal bones and endocranial structures, which constitutes the basis for the main arguments of proponents of three suggested solutions concerning the correct homologies of the medial exocranial bones of tetrapods and osteolepiform fishes, is discussed and criticized. It is shown that, by disregarding this assumption, these homologies are easily understood. The five medial, often paired exocranial bones present in most tetrapods, except in those where the postparietals are missing, are the same five medial bones that are present in osteolepiforms if the nasals and postrostrals in these forms are fused. The homologies of the exocranial bones in *Ichthyostega*, and the phylogenetic position of this form are also discussed.

SINCE the 1930s a division of opinion has split the field of lower vertebrate palaeontology and comparative anatomy into two camps. In general this disagreement concerns the homologies, and thus the correct terminology of the bones in the exocranial roof of the crossopterygian fishes, but the core of the problem is in the homologies between tetrapods and crossopterygians of the bones along the midline of the exocranial roof. The background to this conflict has been reviewed previously by, for example, Jarvik (1967, p. 181) and Parrington (1967, p. 231), and thus it is necessary here only to summarize the alternatives.

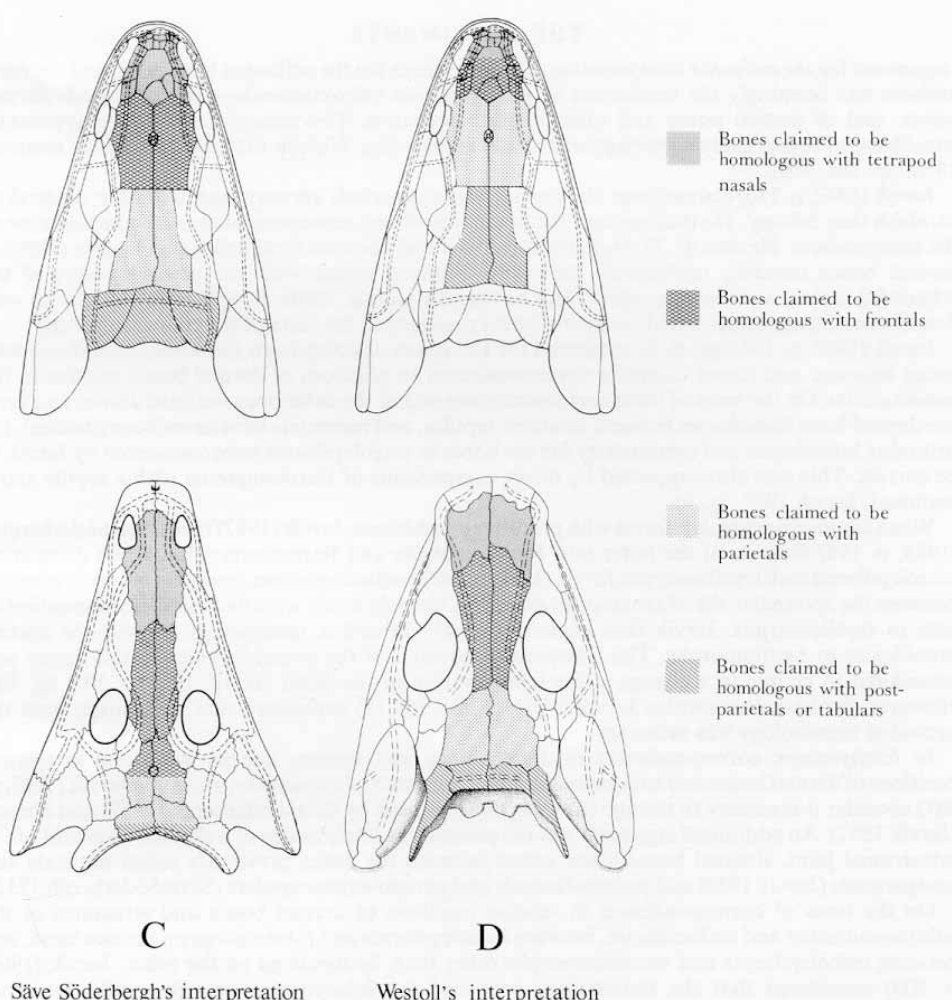
One alternative (text-fig. 1A), which like Westoll (1943, table 1) I refer to as 'the orthodox terminology', was used by early authors such as Traquair (e.g. 1884), Smith Woodward (e.g. 1891, p. 318, fig. 47), Watson (e.g. 1926a, p. 196, fig. 2), Säve-Söderbergh (e.g. 1933, p. 9), Moy-Thomas (e.g. 1935, figs. 1, 2), and Westoll (e.g. 1936, figs. 1, 3). To my knowledge, this alternative has not been argued for in its original form by any recent authors. However, a modified version (text-fig. 1B) has been argued for most strongly by Jarvik (1967). More or less modified versions of the orthodox terminology are mainly used today by continental European authors such as Lehman (e.g. 1959, p. 110, fig. 49), Jessen (e.g. 1966), Jarvik (e.g. 1967), and Bjerring (e.g. 1979), and also by some Australian authors such as Young and Gorter (1981).

Alternative terminologies (text-figs. 1C, D) were suggested respectively by Säve-Söderbergh (1932, figs. 16A, 18, table 2, p. 92) and Westoll (1936, p. 166; 1938, 1940, p. 71; 1943, p. 79). To my knowledge Säve-Söderbergh's terminology is not now used by any authors. Westoll's solution were supported by, for example, Romer (1937, p. 52; 1941, p. 150) and Parrington (1956, 1967). The terminology following from Westoll's views is used today mainly by authors in Great Britain and the U.S.A., and also by some Russian authors (Vorobyeva 1977).

This dispute needs to be discussed for several reasons. 1. In their arguments, the proponents of the different alternatives have employed general assumptions concerning the positional relationship between the endocranium and dermal bones in general, with very far-reaching impacts on the methods of comparative vertebrate anatomy. These assumptions thus need to be checked. 2. Osteolepiforms and stegocephalians presumably include links in the transition between tetrapods and the assemblage that we call fishes. Since the names of the main cranial roof bones are defined in man, and their homologies among tetrapods are generally accepted, it is necessary to clarify what happened to these bones at this transition, in order to place correct names on these bones in fishes. Obviously this knowledge is important when establishing phylogenies between fishes and tetrapods, not the least since these bones are prominent among determinable fossil finds of vertebrates.



TEXT-FIG. 1. View of the alternative homologizations and terminologies for the medial exocranial roof bones of osteolepiforms and stegocephalians. The upper row shows alternative terminologies in osteolepiforms, represented by *Eusthenopteron foordi* (from Bjerring 1979, fig. 5). The lower row shows alternative terminologies in stegocephalians. Under A and D the reptilomorph *Paleoherpeton decorum* (from Panchen 1970, fig. 1)



represents tetrapods generally. Under c the batrachomorph *Benthosaurus sushkini* (from Bystrow 1935, fig. 12) represents tetrapods generally. This latter form is used here since Säve-Söderbergh (1936) used batrachomorphs to demonstrate his interpretations. Under b, *P. decorum* and *B. sushkini* represent each other's respective group of tetrapods.

3. Obviously this dispute is also unfortunate since different terminologies make communication between scientists more difficult.

THE ARGUMENTS

Arguments for the orthodox interpretation. The main basis for the orthodox terminology of the early authors was seemingly the similarities in the positional interrelationships of the various dermal bones, and of dermal bones and other cranial structures. The sensory canals were apparently considered to be especially important in the latter context (e.g. Watson 1926a, p. 196, fig. 2; Goodrich 1958, pp. 284, 309).

Jarvik (1967, p. 186) claimed that 'the dermal bones as a whole are anchored to the part of the skull to which they belong'. He thus rejected the possibility of any movement of dermal bones relative to the endocranium. He also (p. 82) stated that frontals and parietals were defined by Gaupp (1905) as dermal bones covering respectively the orbitotemporal region with the adjoining part of the ethmoidal region, and the otic region, and he recently (Jarvik 1980b, p. 101) followed this up with definitions of these bones based on their relative positions to the tecta of the endocranial roof.

Jarvik (1967, p. 194, figs. 8, 9) compared the Devonian osteolepiform *Eusthenopteron foordi* with living anurans, and found extensive correspondences in positions of dermal bones relative to the endocranium. On the basis of these correspondences and of the definitions outlined above, and since the dermal bone homologies between anurans, reptiles, and mammals have never been doubted, the orthodox homologies and terminology for the bones in osteolepiforms were considered by Jarvik to be correct. This was also supported by direct comparisons of *Eusthenopteron* with a reptile and a mammal (Jarvik 1967, fig. 9).

When comparing osteolepiforms with primitive amphibians, Jarvik (1967) used Säve-Söderbergh's (1935, p. 198) division of the latter into Reptilomorpha and Batrachomorpha. When comparing osteolepiforms with reptilomorphs Jarvik (1967, p. 197) pointed out close correspondences in position between the spiracular slit of crossopterygians and the otic notch with its anterior continuation as seen in reptilomorphs. Jarvik thus claimed that the orthodox terminology showed the correct homologies in reptilomorphs. The interparietal position of the pineal foramen in this group was considered to be due to a change in the configuration of the brain (Jarvik 1967, p. 199, fig. 13). However, for batrachomorphs, Jarvik (1967, p. 201, fig. 11) considered that a deviation from the orthodox terminology was necessary.

In *Ichthyostega*, correspondences in dermal bone and sensory line patterns, and in relative positions of dermal bones and endocranial regions, with that of osteolepiforms, made Jarvik (1967, p. 201) consider it necessary to change the terminologies used by Säve-Söderbergh (1932) and himself (Jarvik 1952). An additional argument was the presence in *Ichthyostega* of a claimed rudiment of the intracranial joint, situated beneath the suture between the bones previously called parietals and postparietals (Jarvik 1952) and parieto-frontals and parieto-extrascapulars (Säve-Söderbergh 1932).

On the basis of correspondences in relative positions of dermal bones and structures of the palatoquadratum and endocranium, between osteolepiforms and *Ichthyostega* on the one hand, and between osteolepiforms and batrachomorphs other than *Ichthyostega* on the other, Jarvik (1967, p. 203) considered that the terminology proposed for *Ichthyostega* was also valid for other temnospondyls.

Arguments for Säve-Söderbergh's interpretation. As evidence for the presumed fused components in the dermal bones, Säve-Söderbergh (1932, p. 96, fig. 19) illustrated a specimen of *Eusthenopteron foordi* in which the parietals were divided into anterior and posterior components. The position of the borders between the components fused into the dermal bones were based on positions of sutures between adjacent dermal bones (Säve-Söderbergh 1932, p. 90). He also claimed support (1932, p. 94) from similarities in cheek plate and anterior part of the skull roof.

Arguments for Westoll's interpretation. Westoll's alternative (text-fig. 1D) was based on comparisons between osteolepiforms and stegocephalians, which were claimed to show a relative shortening of the

otico-occipital part of the endocranium at the transition from fish to tetrapods (Romer 1937, p. 52; 1941, p. 156; Westoll 1943, p. 83, fig. 3). This observation, together with assumed needs to have the same dermal bones situated above the otico-occipital part of the endocranium (e.g. Westoll 1943, pp. 81, 83, fig. 3), and to have the pineal foramen situated between homologous bones in osteolepiforms and stegocephalians (e.g. Romer 1937, p. 51), led to the assumption that the dermal bones that covered the relative short otico-occipital region in stegocephalians, had gone through a relative shortening at the transition from fishes to tetrapods that corresponded to the shortening of the otico-occipital region. On the assumption that the postparietals (or dermo-supraoccipitals) are homologous among tetrapods generally (e.g. Westoll 1961, p. 608), as was also stated in the orthodox terminology, Westoll's terminology (text-fig. 1D) seemed probable. A claimed lack of postparietals, or the presence of small such bones, in reptiles, was considered to be an end result of this trend of reduction (Romer 1937, p. 52; 1941, p. 159).

The cranial shield of the Devonian form *Elpistostege* (Westoll 1938) was considered as supporting evidence for the posterior transfer of dermal bones. This was found to fit between osteolepiforms and *Ichthyostega* in an evolutionary series from osteolepiforms to stegocephalians and also pelycosaurs (e.g. Westoll 1943, fig. 4). Westoll (1943, p. 81) also used as an argument the mode of formation of large bones, which he claimed had taken place in the frontal and nasal regions of dipnoans (*Fleurantia*), and which thus, he claimed, could also have taken place in crossopterygians. He thus considered the problem arising from his scheme as solved, which of the dermal bones in the osteolepiform skull roof, the nasals and frontals of tetrapods had developed from.

DISCUSSION OF THE ARGUMENTS

A discussion of homologies must be based on an unambiguous concept of homology. The only criterion that I find to be useful in a definition of such a concept is that of phylogenetic continuity or common ancestry. Criteria such as similar relative positions to other structures, common embryological origin, similar structure, etc., can merely be indications of varying importance. It is necessary to emphasize this since concepts referred to as homology are sometimes used in the literature, concepts in which phylogenetic continuity is considered to be of minor importance relative to, for example, relative position, common embryological origin, etc. It may also be useful to emphasize that when a name is given to a dermal bone, this name denotes a unity of bone tissues delimited from other dermal bones by sutures, and not, for example, a region of the whole dermal skeleton.

Since the assumption that there is a constant positional relationship between dermal bones and endocranial structures is basic to the arguments for all three alternatives that differ from the orthodox view, I will first discuss this assumption in some detail, and then successively discuss the other arguments of the main proponents of these alternatives.

Discussion of allegation of constant relative positions between dermal bones and endocranial structures. Jarvik (1952, p. 52, fig. 22; 1967, p. 194, figs. 8, 9) showed clearly that the parietals and frontals in certain reptiles and mammals covered approximately the same regions in the endocranium as the bones which in the orthodox terminology were called parietals and frontals in osteolepiforms. From the principle of constant positional relations between dermal bones and endocranial structures, since the 'type locality' of the names Parietal and Frontal is in man (Westoll 1961, p. 608; Jarvik 1967, p. 181; Patterson 1977, p. 83), and since the homologies of these bones are generally accepted from man to early reptiles, the terminology used by Jarvik for these bones in osteolepiforms must be correct.

However, what Jarvik has not taken into consideration is that it is not only in batrachomorphs that the bones called postparietals in orthodox terminology covered the otic region of the endocranium, but that also, according to reconstructions by Watson (1926a, figs. 12, 13, 15) and by Panchen (1970, figs. 1, 2), this feature is present in the reptilomorph *Paleoherpeton* (= *Paleogyrinus*) (text-fig. 2C). *Paleoherpeton* is an anthracosaur, here used as defined by Säve-Söderbergh (1934, p. 9; 1935, pp. 12, 104) and used by, for example, Panchen (1970, p. 1). The exocranial bone pattern of *Paleoherpeton* is

fairly typical for anthracosaurs (Panchen 1970, fig. 11). If following the allegation discussed here, the terminology generally used in this group must also be changed accordingly. For example, should the posteriormost exocranial pair of bones be called parietals, not postparietals. Anthracosaurs have been considered a suitable link between reptiles and rhipidists (e.g. Romer 1967, fig. 1; Panchen 1970, p. 1), and the main difference between the exocranial bone patterns of anthracosaurs and a cotylosaur like *Captorhinus* is that the supratemporal and intertemporal have disappeared as separate bones in *Captorhinus* (text-fig. 2A, C). If the allegation discussed here is followed, we thus get the situation that in two groups, which are considered comparatively close to each other in phylogeny, and which have very similar exocranial bone patterns, corresponding bones in these patterns should have different names. This must be considered a discrepancy.

The same type of discrepancy is even more distinct if comparing anthracosaurs with seymouriamorphs. The latter are often grouped with anthracosaurs (e.g. Säve-Söderbergh 1932, p. 202; Romer 1966, p. 363; Panchen 1975, p. 609; 1980, pp. 343–344). The exocranial bone patterns of, for example, *Seymouria* and *Paleoherpeton* are virtually identical (text-fig. 2B, C), the differences being restricted to the relative lengths of nasals and lacrymals, a posteriorly longer cheek plate in *Paleoherpeton*, and the shapes of some bones. However, the positional relationship between the medial exocranial bones and endocranial structures in the two forms are different (text-fig. 2B, C). Thus also here, the result of the principle of constant positional relations between dermal bones and endocranial structures is that corresponding bones in nearly identical exocranial patterns in supposed phylogenetically close forms should have different names.

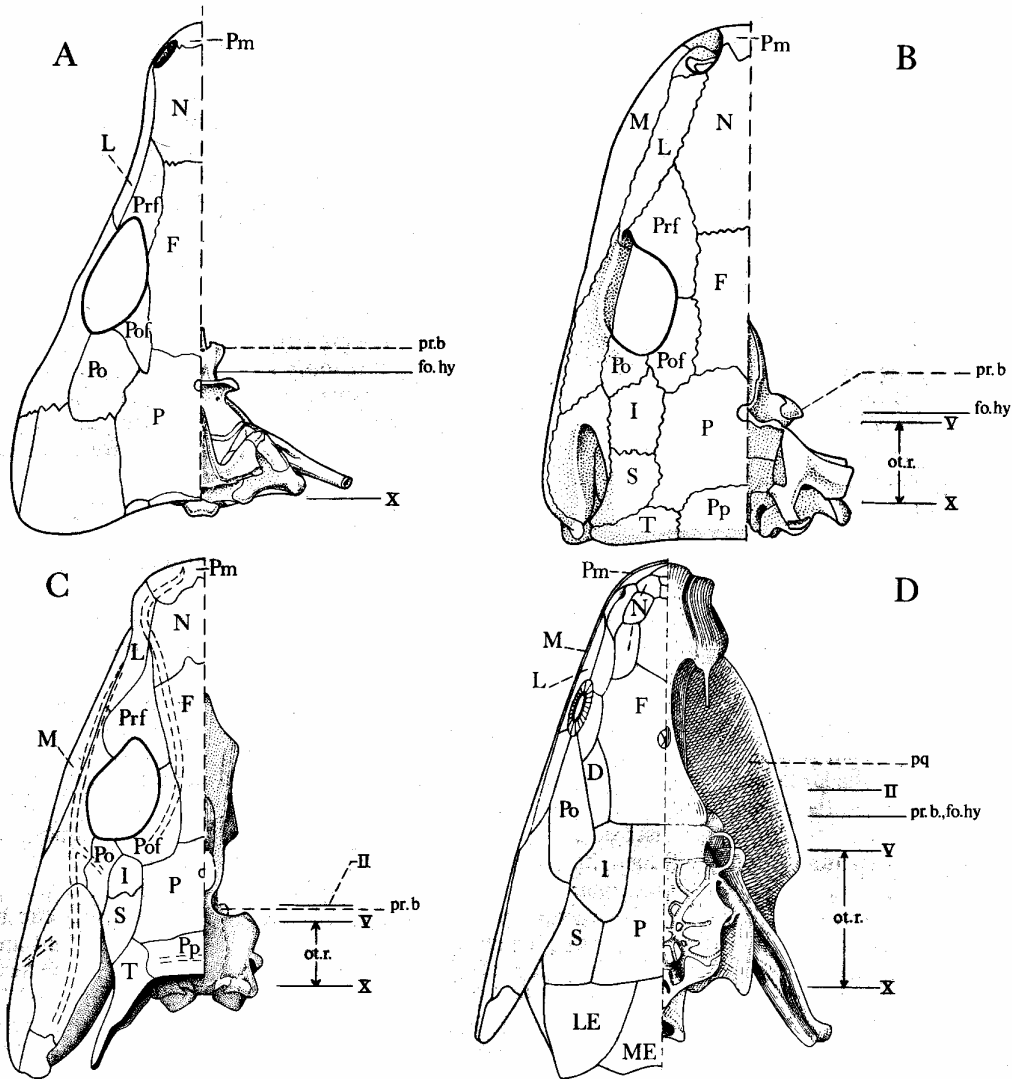
From the above reasoning it is clear that Jarvik's way of using the allegation discussed here leads to discrepancies.

In Westoll's and Romer's use of the postulate of constant relative positions between dermal bones and endocranial structures there are also discrepancies. Both these authors did not consider the clear fact emphasized by Jarvik (1967), that in mammals the otic region is often covered by the parietals, and thus if the allegation discussed here is valid, the terminology for the osteolepiforms must be as stated in the orthodox terminology. However, although they disregard this alleged constancy in this sense, they did use it when they claimed that the relative shortening of the endocranium in the evolution from fish to tetrapods was connected with a reduction of the bones they called postparietals. Westoll and Romer thus sometimes disregard and sometimes use this allegation. Their reasoning is also somewhat strange when the absence of the postparietals in some reptiles is considered to be the end result of this trend. If the connection between endocranium and dermal bones is assumed strong enough to deduce a reduction of the latter because of a relative reduction of the former, the lack of postparietals in some tetrapods (e.g. Romer 1941, p. 159) should mean that the otical part of the endocranium should be missing in these forms. Since this part is not missing in these forms, this reasoning of Westoll and Romer is illogical.

The above discussion shows that the uses by proponents of both main alternatives, i.e. those of Jarvik and Westoll, of an alleged constancy in position between dermal bones and endocranial structures, lead to discrepancies. A possible existence of such a constancy can also be discussed in more general terms. It may be examined by (1) studying how in ontogeny the relative position between dermal bones and endocranial parts are determined, and (2) by comparing the relative positions between dermal bones and endocranial structures in forms where the dermal bone homologies are generally accepted.

The crucial problem with respect to point (1) is whether there are any interdependencies between the ontogenetic processes determining the positions of dermal bones and those determining the positions of endocranial structures. If any such interdependencies exist and are unchangeable during phylogeny, an absolute constancy in relative positions can be said to exist between dermal bones and endocranial structures, but only then. However, if these interdependencies can be changed during phylogeny, e.g. as an adjustment to what is functionally beneficial, an absolute constancy cannot exist.

Two types of interdependencies between dermal bones and chondrocranial structures can be



TEXT-FIG. 2. Crania of A, a cotylosaur (*Captorhinus*, based on Romer 1956, fig. 36A; and Price 1935, pls. 6, 7); B, a seymouriamorph (*Seymouria*, based on White 1939, fig. 1, pl. 1B); C, a reptilomorph (*Paleoherpeton*, based on Panchen 1970, figs. 1, 2); D, an osteolepiform (*Eusthenopteron*, based on Bjerring 1979, fig. 5; Jarvik 1954, figs. 1, 24). The left side of the crania shows the exocranial bones, and the right side the endocranium. Interrupted lines point to certain cranial structures, whole lines mark the antero-posterior level of cranial structures. Abbreviations are explained on p. 752.

considered. 1. The genetic process directing the ontogenetic development of a specific dermal bone is dependent on the presence of specific chondrocranial structures, or tissues that develops into such structures. 2. There is a functional interdependency where, for example, a dermal bone is dependent on some chondrocranial structure to be able to fulfil its function.

With respect to the first point, it seems doubtful that there is an inductive dependency between

chondrocranium and dermal bones. Moss (1968, p. 366) claimed that dermal bone ossification is the result of a series of inductive interactions between the basal layer of the epidermal cells and the ectomesenchym in the dermis. In contrast, the experimental works of Schowing (1968*a, b, c*) and Benoit and Schowing (1970) indicate that some cranial roof bones of birds were formed through induction by parts of the brain. Frontals were the results of induction by prosencephalon and mesencephalon, parietals were formed through induction by rhombencephalon and mesencephalon, and occipitals through induction by rhombencephalon. Hall (1978, p. 51) stated that similar results had also been obtained in forms other than birds, e.g. tests with regeneration of dermal bones in dogs had shown that this was dependent on induction by dura mater. Schowing (1968*a*, p. 51) also mentioned the possible importance of dura mater. According to Hall (1978, p. 51), the results of Schowing and Benoit indicate some sort of site specificity of the interactions between brain and dermal tissues. However, this site specificity can seemingly be determined not only by the brain, since if it was, the 180° turn of the developing brain (Benoit and Schowing 1970, fig. 23) should have led to the development of complete frontals, etc., in the neck. One or more still unknown factors must probably therefore also be effective. An experimental work of relevance in this context is also that of Leibel (1976) who studied the relationship in ontogenetic development between the otic capsule and dermal bones, and stated (p. 88) 'a parietal plate of normal proportions invariably forms in the complete absence of an otic capsule'.

With regard to the second point, functional interdependencies between endocranial parts and dermal bones apparently may exist. Lebedkina (1968, p. 318) demonstrated that the premaxilla receives support from the ethmoidal part of the endocranium in some holosteans and brachiopterygians. Such relationships are also indicated by Leibel (1976, pp. 89, 95) who stated that 'fine adjustments of parietal bone morphology, however, seem to depend in large part on the neighboring otic capsule, particularly the extent of posterior spreading of the otic process and planar orientation of the entire parietal base', and 'the otic capsule apparently functions as a substrate or surface for the condensation of osteo- and chondrogenic mesenchym'. However, such interdependencies appear to be changeable through phylogeny. This was demonstrated in the work by Lebedkina (1968). She showed that the support for the premaxilla by chondrocranial structures in the larva of some fishes did not exist in the larvae of urodeles. In the latter, this function had been taken over by the dermal bones posterior to the premaxilla.

As a conclusion to the above discussion of how relative positions between dermal bones and endocranial structures are determined in ontogeny, it can be stated that nothing indicates a mechanism leading to a constant positional relationship between parts of the skeleton.

The variation in relative positions between cranial roof bones and endocranial structures can be studied also by comparing them in forms in which the dermal bone homologies are evident and generally accepted. The best endocranial structures for such comparisons would have been the tecta which constitute the endocranial roof, and on which Jarvik (1980*b*, p. 100) based his definition of the exocranial roof bones. However, these tecta are often missing as complete mineralized structures in amniotes where the homologies are generally accepted (Goodrich 1958, p. 246, figs. 263, 264, 274, 275, 281), and are thus difficult to study in fossil material. This makes them inconvenient for such comparisons. Because of this, and also because structures like the otic capsules and the fossa hypophyseos were used in the arguments for the different homology alternatives (Säve-Söderbergh 1936, p. 145; Romer 1941, p. 158; Westoll 1943, p. 83, figs. 3-4; Jarvik 1967, pp. 194, 196), comparisons based on these latter structures are also of interest, and they have been used here.

Interesting comparisons can be made, for example, between *Bos* and *Equus* (Ellenberger-Baum 1943, figs. 830, 831). The frontal-parietal suture is situated far more posteriorly in *Bos* than in *Equus*. In *Equus*, like in man, the parietals constitute the cranial roof above the otic capsules, while in *Bos* they make part of the nuchal and lateral surfaces of the brain case. The hypophysis is situated beneath the anterior part of the parietals in *Equus*, and the middle part of the frontals in *Bos*. *Equus* is thus not so different from man in these respects, while *Bos* is. This difference is probably due to an adaptation to the presence of horns in *Bos*. In another mammal, *Ornithorhynchus* (Jollie 1962, figs. 3-8), the fossa hypophyseos is situated beneath the middle or posterior part of the parietals,

and in a baleen whale the cranial roof is mainly made of maxillaries and supraoccipitals (e.g. Slijper 1962, fig. 34).

The above descriptions of relative positions between dermal bones and endocranial structures show that they are variable. However, this variation can be interpreted as variation around a specific positional interrelationship that seem to be fairly common, and in which the postparietals cover the occipital region, the parietals cover the otic region, the frontals the orbitotemporal region, and the nasals the main part of the ethmoidal region. The seemingly frequent occurrence of this pattern may possibly be the reason for the notion that there is a fixed positional relationship between certain dermal bones and endocranial structures. However, this apparent stable positional relationship probably merely reflects the constancy of structures when there is no selective pressure working for changes. Put in other words, the parietals usually cover the otic region because they usually constitute the main posterior part of the exocranial roof, and the otic region constitutes the main posterior part of the endocranium. Changes in this configuration occur when there is a selective pressure for changes. I discuss evidence below to suggest that the disagreement regarding the homologies of the exocranial roof bones of crossopterygians and tetrapods is due to different misunderstandings of a deviation from this seemingly common positional relationship. However, before this, I will briefly discuss some other arguments used by the proponents of the different alternatives.

Discussion of additional arguments for Westoll's alternative. Westoll's use (1943, p. 81) of the possible fusion of bones in dipnoans is a weak argument. That bones may fuse during phylogeny is now, I believe, generally accepted (e.g. Patterson 1977, p. 92). It is thus evident that the osteolepiform nasals and postrostrals may have fused into both the nasals and frontals of tetrapods. However, the interesting point is whether the former bones fused into both these latter pairs of bones or only one pair. To the solution of this problem, this reasoning of Westoll contributes little.

The restricted value of the pineal foramen has been pointed out by Jarvik (1967, p. 185) and by Parrington (1967, p. 233).

The value of the exocranial bone patterns of *Elpistostege* and *Ichthyostega* has probably also been somewhat exaggerated. The patterns in these two forms seem to me a rather weak basis for stating general trends in the evolution of the vertebrate cranial roof. At the transitional stage from water to land, it is easy to imagine that a great deal of variation occurred.

Discussion of additional arguments for Jarvik's alternative. Jarvik's (1967, p. 197) homologization of the spiracular slit in osteolepiforms with the anterior continuation of the otic notch in reptilomorphs seems reasonable. However, Panchen (1970, p. 9) considered the otic notch of antracosaur as homologous with the spiracular slit of osteolepiforms, and the anterior continuation of the otic notch, which Panchen called 'kinetic edge', as homologous with a presumed postero-lateral continuation of the transverse intracranial joint connecting this joint with the spiracular slit. Since this interpretation of Panchen's is possible and not disproved, Jarvik's argument is not conclusive. Since, however, the spiracular is a much more distinct opening than the assumed connection between the transverse joint and the spiracular, the transfer of the latter into the anterior continuation of the otic notch is a larger change than transferring the spiracular slit into this structure. On this basis the interpretation of Jarvik seems most probable.

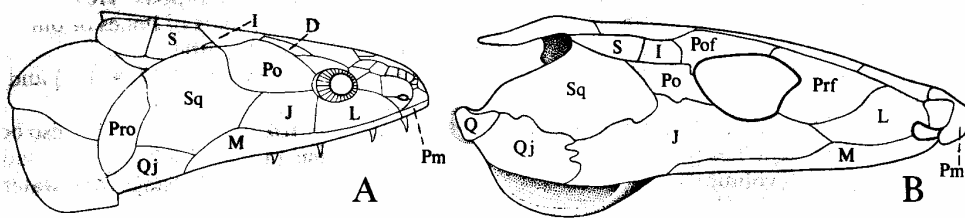
Jarvik's interpretation (1952, fig. 35B; 1967, p. 203; 1980a, p. 241) of the postero-medial bone in *Ichthyostega* as a parieto-extratemporal seems sensible on the basis of the position of the bone and the presence and course of the occipital transverse sensory canal. The position of the claimed rudiment of the intracranial joint in *Ichthyostega* may also be important, but the conclusion reached from its position is again based on the assumed constant positional relationship between dermal bones and endoskeleton. Jarvik's transfer of the terminology of *Ichthyostega* to other batrachomorphs is based solely on this assumption, and is thus questionable.

Discussion of arguments for Säve-Söderbergh's alternative. Säve-Söderbergh's (1932, p. 90) reconstructions of components of compound exocranial bones on the basis of sutures between neighbouring bones seem questionable to me. Dermal bones often change positional interrelations,

and differences may even exist between left and right sides of the same individual, e.g. as in *Acipenser* (Jarvik 1948, p. 68, figs. 18, 19). The specimen of *Eusthenopteron foordi* referred to (Säve-Söderbergh 1932, fig. 19, p. 96) indicates that the parietals are compound bones. However, neither this nor claimed similarities in the dermal bone patterns of the cheek plate and the snout between ichthyostegid and crossopterygians (1932, p. 94), make the reconstructions of the components in the compound dermal bones more reliable.

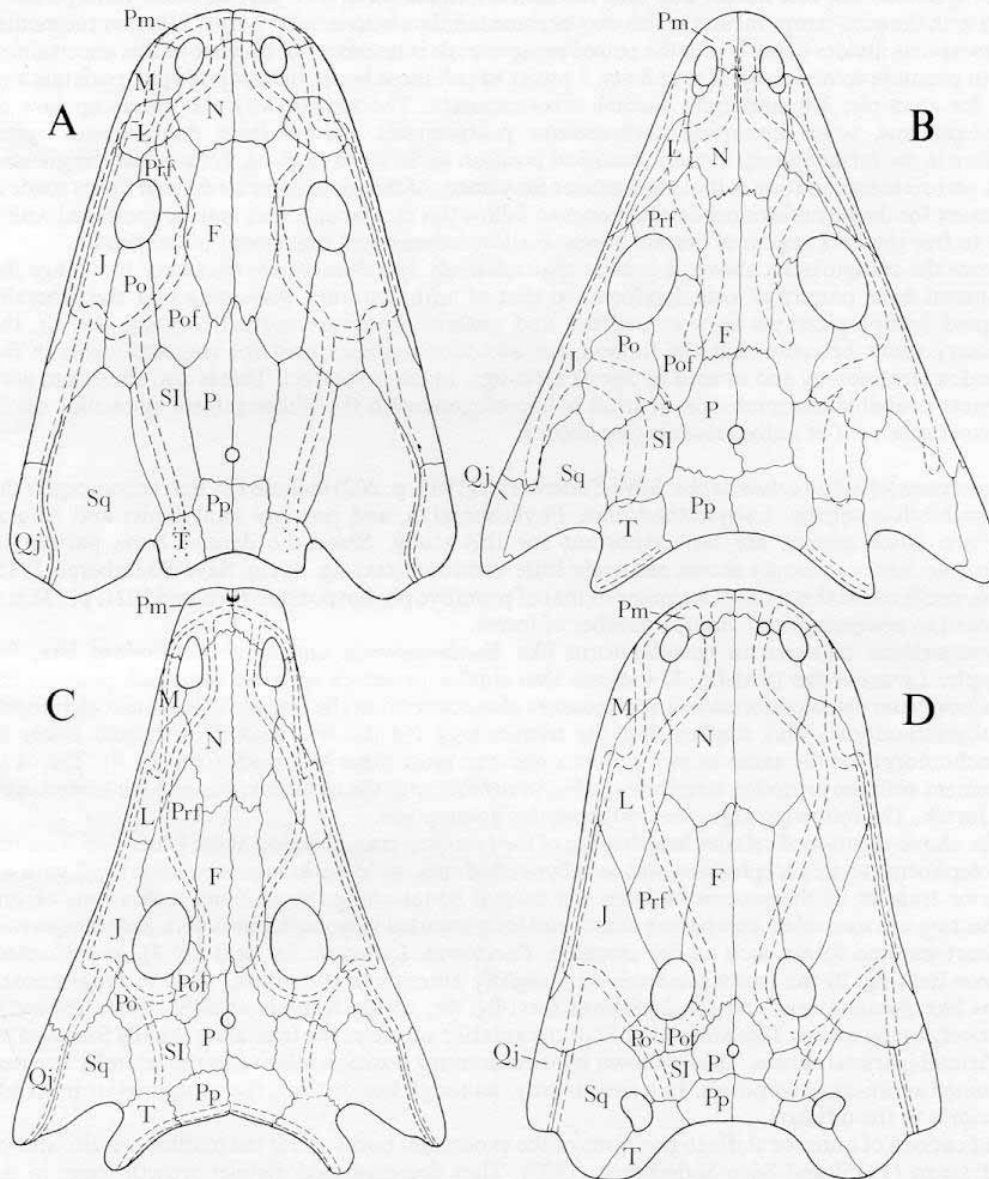
THE PROBABLE SOLUTION

Since in my view the basic criterion for homology is that of evolutionary continuity, it is necessary to study the exocranial roof bones in the transitional groups between osteolepiforms, in which the correct homologies and thus terminology is disputed, and reptiles in which the terminology used is generally accepted as correct. These transitional groups are presumably included in the assemblage of early amphibians denoted as stegocephalians. As mentioned above, these were divided by Säve-Söderbergh (1935) into reptilomorphs and batrachomorphs. I will in this article use this division as a basis for comparisons even if the correctness of Säve-Söderbergh's system may be disputed. I do so because this division is basal to Jarvik's (1967) interpretation, and also since major assemblages equivalent to those of Säve-Söderbergh are present also in other taxonomic systems for the stegocephalians, e.g. in that of Romer (1966). The more detailed systematics of the stegocephalians are probably not important to the conclusions drawn from the comparisons below.



TEXT-FIG. 3. Crania of A, an osteolepiform (*Eusthenopteron*, based on Bjerring 1979, fig. 1), and B, a reptilomorph (*Paleoherpeton*, based on Panchen 1970, fig. 1B), viewed from the right side, and showing antero-posterior lengthening of the dermal cheek bones at the transition from the former to the latter group. Abbreviations are explained on p. 752.

Comparisons with reptilomorphs. In comparing the Carboniferous anthracosaur *Paleoherpeton* with the Devonian osteolepiform *Eusthenopteron* it can be seen that their exocranial bone patterns are very similar (text-figs. 1, 2, 3). The main changes necessary to transfer the bone pattern of *Eusthenopteron* into that of *Paleoherpeton* include (1) a transfer of the nasals and postrostrals of the former into the nasals of the latter, (2) a relative increase of the orbital fenestra, and (3) the possibly most important in this context, a lengthening and flattening of the exocranium. As noted previously by several authors (e.g. Romer 1966, p. 80; Jarvik 1967, p. 188), a cranial lengthening is distinct in the preotical region of the cranium at the transition from osteolepiforms to stegocephalians. In the exocranium of *Paleoherpeton* this is shown clearly in the relatively increased length of the frontals, the anterior sutures of which become situated anterior to the orbital fenestrae. Also apparently the parietals have been slightly expanded anteriorly, having their anterior sutures situated anteriorly to the intertemporals. *Paleoherpeton* also has the jaw articulation situated more posteriorly relative to the neurocranium than *Eusthenopteron* (text-fig. 2). This is the result of an antero-posterior expansion of the cheek plate which, like the expansion of the frontals and parietals, is presumably connected with a general antero-posterior stretching of the dermal cranium. The stretching of the cheek plate is also shown in the lengthening of squamosum, jugal, and quadrato-jugal (text-fig. 3). Other changes at the transition from *Eusthenopteron* to *Paleoherpeton* include the disappearance of the operculars, which



TEXT-FIG. 4. Exocrania of four batrachomorphs placed in a succession of increasing snout lengths showing that this increase largely coincides with an increase in anterior extensions of the medial exocranial bones. A, *Buettneria* (based on Bystrow 1935, fig. 22); B, *Lyrocephalus* (based on Säve-Söderbergh 1937, fig. 3); C, *Benthosaurus* (based on Bystrow 1935, fig. 12); D, *Cyclotosaurus* (based on Bystrow 1935, fig. 23). Abbreviations are explained on p. 752.

leaves space for the otic notch, and that the lateral extrascapulars, or part of them, have possibly fused with the post-temporal and in this way become tabulars with tabular horns. Whether the medial extrascapular divides directly into the paired postparietals is unclear, but because of this uncertainty, and to promote terminological simplicity, I prefer to call these bones in tetrapods postparietals and not, for example, left and right medial extrascapulars. The reason why the extrascapulars of osteolepiforms, when becoming anthracosaur postparietals, moved from their supraoccipital position in the former group to the supraotical position in the latter (text-fig. 2c) can only be guessed at. A plausible explanation is that the anterior movement of the more anterior dermal bones made it necessary for the posteriormost dermal bones to follow this movement. This may be combined with a need to free the neck region of dermal bones to allow independent movement of the head.

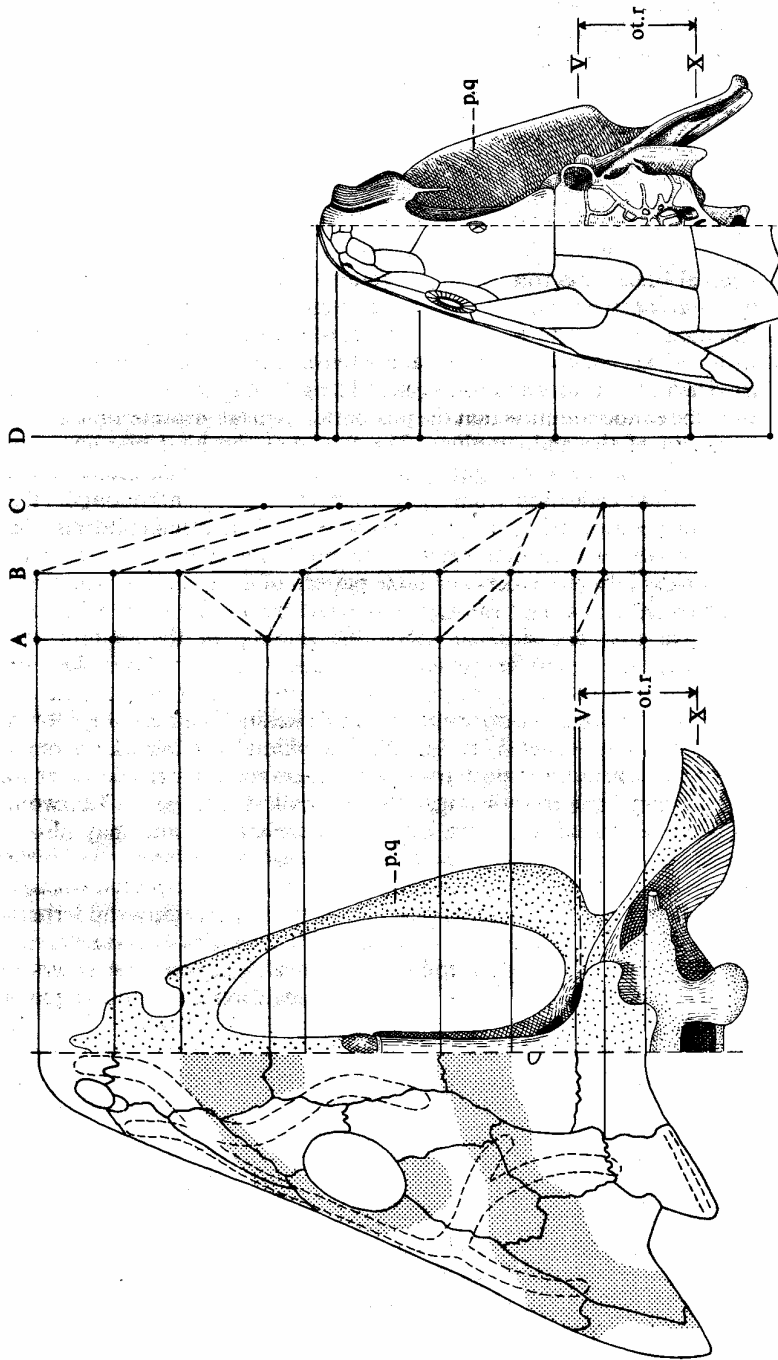
From the comparisons above, it is clear that relatively few changes are necessary to change the exocranial bone pattern of osteolepiforms to that of anthracosaurs. Assuming that the generally accepted homologizations between reptiles and anthracosaurs are correct (text-fig. 2A, c), the necessary result becomes that the homologies and terminologies used for osteolepiforms in the orthodox terminology and as used by Jarvik (text-figs. 1A, B) are correct. This is also consistent with the most probable interpretation of what is homologous with the osteolepiform spiracular slit in the exocranial roof of anthracosaurs (see above).

Comparisons with batrachomorpha. Säve-Söderbergh (1935, p. 202) included in Batrachomorpha the groups Ichthyostegalia, Labyrinthodontia, Phyllospodyli, and possibly Pantyloidei and Anura. The two latter groups are not important for this study. Since the dermal bone pattern of labyrinthodonts seemingly shows relatively little variation (text-fig. 4; e.g. Säve-Söderbergh 1935, 1936), and because this pattern is similar to that of primitive phyllospodyls (Watson 1921, p. 73), it is sufficient to compare with a limited number of forms.

Comparisons between an osteolepiform like *Eusthenopteron* and a labyrinthodont like, for example, *Lyrocephalus* (text-fig. 5) indicate that similar processes to those that took place at the transition from osteolepiforms to anthracosaurs also occurred at the transition from osteolepiforms to labyrinthodonts. This implies that the terminology for the five medial exocranial bones in batrachomorphs is the same as in reptilomorphs and most other tetrapods (text-fig. 4). This is in agreement with the orthodox terminology, but in conflict with the terminologies of Säve-Söderbergh and Jarvik. The following arguments support this assumption.

The above-mentioned relative lengthening of the preotical cranial region at the transition from the osteolepiforms to stegocephalians was in labyrinthodonts, as in anthracosaurs, connected with an anterior transfer of the sutures between the dermal bones along the midline. Indications of this connection are seen when comparing short- and long-snouted stegocephalians with *Eusthenopteron*. In short-snouted forms such as, for example, *Buettneria*, *Lyrocephalus* (text-fig. 4), and *Eusthenopteron* (text-fig. 2) the frontals stretch only slightly anterior to the orbits, while in long-snouted forms like *Benthosaurus* and *Cyclotosaurus* (text-fig. 4C, D) the frontals usually stretch distinctly anteriorly to the orbits. This anterior shift of the anterior suture of the frontals is usually followed by the frontal-parietal suture. This is shown by their anterior position relative to the laterally situated presumed supra-intertemporals. In a similar way, although less distinct, the postparietals protrude anteriorly to the tabulars.

Indications of anterior shifts in positions of the exocranial bones along the midline are also shown by Bystrow (1935) and Säve-Söderbergh (1937). They demonstrated distinct growth zones in the surface sculpture of the cranial roof bones. Even if the growth indicated by these zones shows ontogenetic growth, it must also indicate a phylogenetic change from adult stages of *Eusthenopteron* to adult stages of more or less long-snouted labyrinthodonts. In this connection it is interesting to note that if the lengths of the medial exocranial bones in a labyrinthodont were to be reduced with the lengths of the growth zones (stages A-B, text-fig. 5), and thereafter these reduced bones were placed in the natural succession from the posterior end forwards (stages B-C, text-fig. 5), the sutures between these reduced frontals and nasals, and between frontals and parietals, would be approximately level with the corresponding sutures in a cranium of *Eusthenopteron* where the otic region (ot.r., text-fig. 5)



TEXT-FIG. 5. Illustration of relative differences in antero-posterior extensions of exocranial bones and endoskeletal features of a labyrinthodont (*Lyrocephalus euri*, from Säve-Söderbergh 1936, fig. 14; 1937, fig. 3), and an osteolepiform (*Eusthenopteron foordi*, from Jarvik 1954, figs. 1, 24; Bjerring 1979, fig. 1). The crania are figured with equally long optical regions. Their left sides show the exocrania, and the right sides the endoskeleton. On the exocranium of *Lyrocephalus* are the growth zones marked by shading. The antero-posterior extension of the medial exocranial bones of *Lyrocephalus* are projected on to stage A. In stage B these lengths, minus the lengths of the respective growth zones, are shown. The transfer of this reduction is marked by interrupted lines. In stage C the lengths set out in stage B have been placed adjacent to each other, in natural succession from the level of the posterior margin of the postparietals of *Lyrocephalus*. The transfer of bone positions that change in this step is marked by interrupted lines. In stage D is projected the antero-posterior extensions of the medial exocranial bones of the cranium of *Eusthenopteron*. Abbreviations are explained on p. 752.

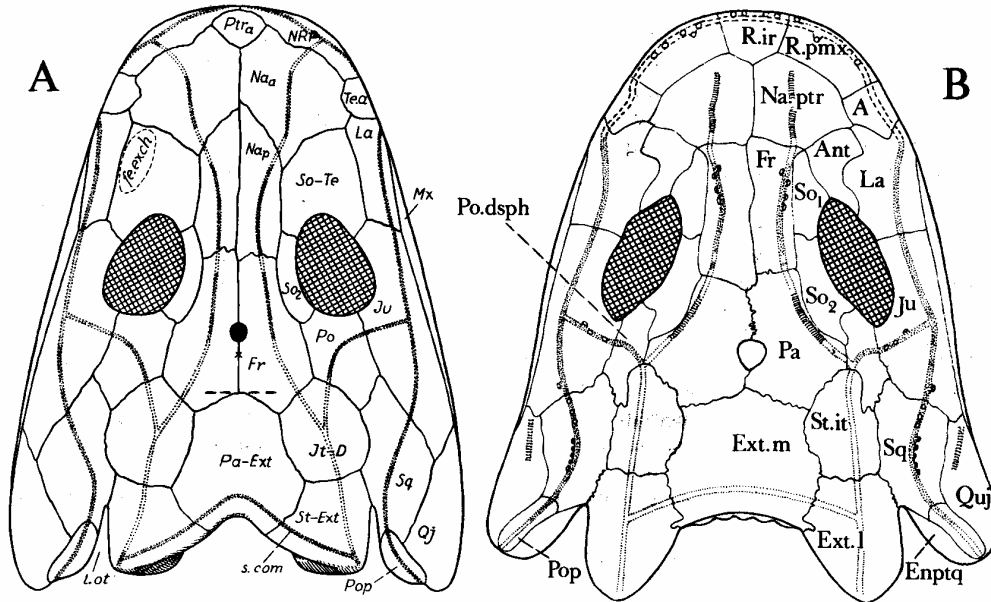
is of the same length as in the labyrinthodont (stages C–D, text-fig. 5). This result necessitates a growth zone also in the postparietals. No growth zones have been claimed in this bone by Säve-Söderbergh (1937), but Bystrow (1935, table p. 24) indicated a slight growth. A lack of distinct traces of growth zones on the postparietals may be explained by the gradual transformation of the surface sculpture from oblong grooves to rounded pits (Bystrow 1935, p. 84, fig. 11g–h; Säve-Söderbergh 1937, p. 197, figs. 7, 8). It should also be pointed out that the anterior pits on the postparietals often are distinctly more oblong than the posterior pits (Bystrow 1935, figs. 12, 15, 27; Säve-Söderbergh 1937, figs. 1, 4A, 5, 10A). An anterior expansion of the postparietals is indicated also by the posterior position in these bones of the transverse occipital canal, and from the succession of ontogenetic stages in *Sclerophagus* and *Archegosaurus* shown by Romer (1939, figs. 2, 3). It is thus clear that the sutures between probably all the medial exocranial bones was transferred more or less anteriorly at the transition from osteolepiforms to labyrinthodonts in connection with a lengthening of the cranium. The corresponding endocranial lengthening is, as shown by comparing otical and preotical proportions of the endocranium and palatoquadrate of osteolepiforms and labyrinthodonts (text-fig. 5), mainly restricted to the preotical part. The necessary result of this general lengthening of the medial dermal bones and limited lengthening of the endocranium is that the postparietals in labyrinthodonts occupy a position covering the otic region of the endocranium. The fact that the hind margin of the postparietals is concave in labyrinthodonts and straight or convex in osteolepiforms indicates that this margin has moved forward at the transition from osteolepiforms to labyrinthodonts. These bones thus left the supraoccipital position they, as extrascapulars, had in osteolepiforms. The adaptive reason for this change probably was to allow the head to move independently of the body.

From the above reasoning it is clear how the exocranial bone pattern of osteolepiforms probably developed into that of labyrinthodonts, and that the five exocranial bones along the midline in labyrinthodonts are the same five that are situated along the midline in the reptilomorph exocranium. The exocranial terminology for the batrachomorphs following from this is shown in text-fig. 4.

The only batrachomorph that possibly makes an exception to the above-stated terminology for the five medial exocranial bones, is the Devonian *Ichthyostega*. The transition from osteolepiforms to *Ichthyostega* presents the problem of whether the postero-medial exocranial bone in the latter is a medial extrascapular which has expanded anteriorly as suggested by Jarvik (1952, fig. 35). This would make the bones along the midline the same five as in other stegocephalians, and may also be considered supported by similarities in the dermal bone patterns of *Ichthyostega* and other batrachomorphs (text-figs. 4, 6). If the parietals in certain labyrinthodonts like, for example, *Lyrocephalus* (text-fig. 5), *Peltosaurus*, *Capitosaurus*, *Heptasaurus*, *Wetlugasaurus* (Säve-Söderbergh 1935, figs. 26, 36A, 37, 38) were to move forward somewhat, they would occupy a position very similar to the paired dermal bones which in *Ichthyostega* surrounds the pineal foramen. The anteriorly protruding part of the postero-medial bone may be due to an anterior expansion corresponding to the anterior expansion of the postparietals of many labyrinthodonts (text-fig. 4). However, if so, this anterior expansion has gone very far in *Ichthyostega*, and the fact that such large anterior expansions mainly are found in long-snouted labyrinthodonts, while *Ichthyostega* is short snouted, speaks against this interpretation.

The alternative solution, that the postero-medial bone in *Ichthyostega* results from a fusion between the parietals and the medial extrascapular, was suggested by Säve-Söderbergh (1932, p. 78, figs. 2, 4) and Jarvik (1967, p. 203, fig. 11c). However, these authors differed in their views in that Säve-Söderbergh considered that only the posterior part of the parietals had fused with the medial extrascapular, while Jarvik considered that the whole parietal did so. Säve-Söderbergh's alternative is unlikely because it would mean both that the parietals in *Ichthyostega* are unusually large, and that they are positioned unusually far anteriorly. As already mentioned, the latter is unlikely in a short-snouted form like *Ichthyostega*. Jarvik's alternative (text-fig. 6A) is supported by the following similarities between the posterior interorbital bone in *Ichthyostega*, which in Jarvik's scheme must be the frontals, and the frontals in *Eusthenopteron*. 1. These bones in the two forms have the approximate same position relative to the orbital fenestra, the bones in *Ichthyostega* being situated

slightly more posteriorly. 2. If the frontals and dermosphenotics in *Eusthenopteron* fuse, the result are bones which in shape and position are nearly identical to the bones in *Ichthyostega*. 3. In both forms these bones surround the pineal foramen. 4. The supraorbital sensory canal runs through both the discussed bones in *Ichthyostega*, and the frontals in *Eusthenopteron*, while the postero-medial exocranial bone in *Ichthyostega* and the parietals in *Eusthenopteron* lack sensory canals. 5. The



TEXT-FIG. 6. Exocrania of *Ichthyostega* showing respectively A, Jarvik's (1967, fig. 11c) interpretation of dermal bone and sensory canal pattern, and B, Säve-Söderbergh's (1932, fig. 15) interpretation of the same. Abbreviations: A, anterior antorbital; Ant., posterior antorbital; Enptq., quadrate ramus of entopterygoid; Ext.l., lateral extrascapular; Ext.m., parietoextrascapular; fe.exch., fenestra exchoanal; Fr., frontals; i.ot., otic notch; It-D., intertemporo-dermosphenotic; Ju., jugal; La., lachrymal; Mx., maxillary; Na_a, anterior nasal; Na_p, posterior nasal; Na.ptr., naso-postrostral; NRP., naso-rostro-premaxillary; Pa., parietal; Pa-Ext., parieto-extrascapular; Po., postorbital; Po.dsph., postorbito-dermosphenotic; Pop., preopercular; Ptr_a, anterior median postrostral; Qj. and Quj., quadratojugal; R.ir., rostro-interrostral; R.pmx., rostromaxillary; So₁, anterior supraorbital; So₂, posterior supraorbital; So-Te., supraorbito-tectal; Sq., squamosal; St-Ext., supratemporo-extrascapular; St.it., supratemporo-intertemporal; Te.a., anterior tectal.

claimed rudiment of the intracranial joint in *Ichthyostega* is also a possible support for this alternative. The significance of these correspondences between the bones in *Ichthyostega* and *Eusthenopteron* is indicated by the presumed primitiveness of *Ichthyostega*. On the basis of the arguments discussed above, Jarvik's alternative (text-fig. 6A) seems to me the most probable.

The bones antero-lateral to the parieto-extrascapulars were called supratemporo-intertemporals by Säve-Söderbergh (1932; text-fig. 6B), and intertemporo-dermosphenotics by Jarvik (1967; text-fig. 6A). The postero-lateral bones were thus called lateral extrascapulars and supratemporo-extrascapulars, respectively. While Jarvik thus considered the dermosphenoticum to be fused with the intertemporals, Säve-Söderbergh considered it to be fused with the postorbital. In a later study, Jarvik (1980a, p. 241) mentioned the possibility of a fusion between dermosphenotics and frontals. These alternatives may be judged from the viewpoints of relative positions to the surrounding dermal bones, the sensory canals, and the otic notch.

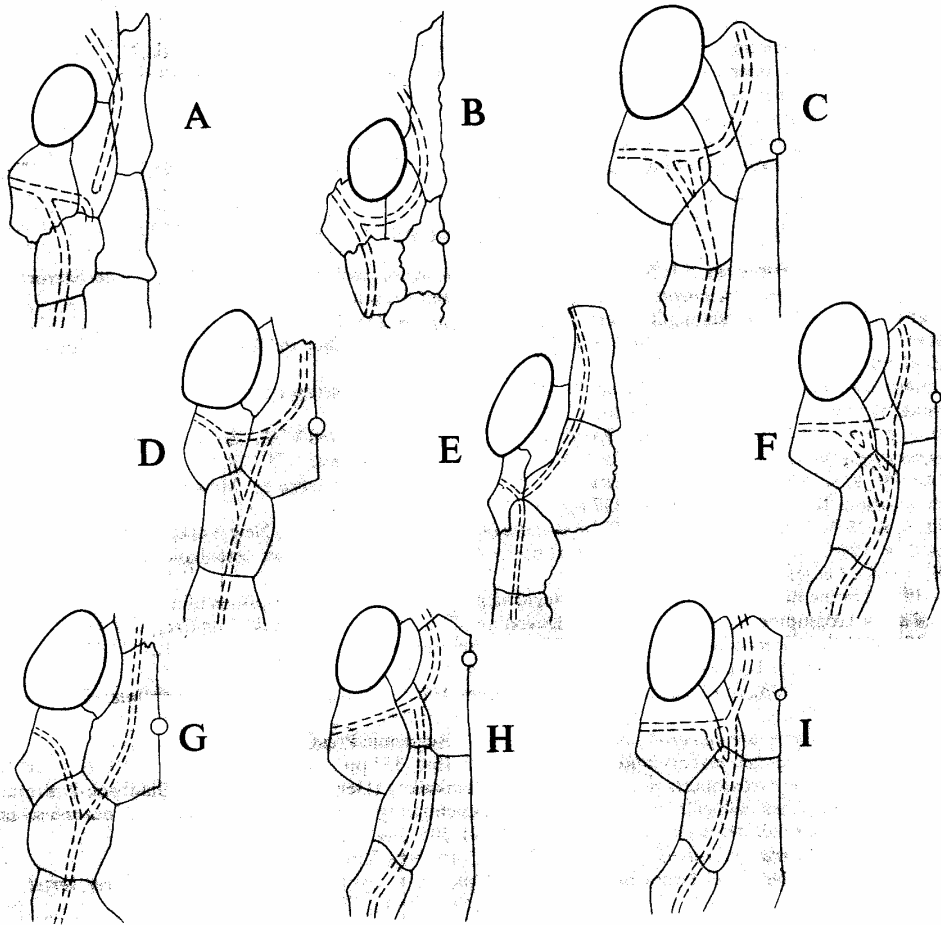
The dermosphenotics in *Eusthenopteron* are situated between the postorbitals and the posterior parts of the frontals, and borders anteriorly on the posterior supraorbital (text-fig. 2D). Together with the fact that a fusion in *Eusthenopteron* between frontals and dermosphenotics would lead to bones very similar both in shape and position to the presumed frontals in *Ichthyostega* (text-fig. 6A), this indicates that this bone in *Ichthyostega* is a fronto-dermosphenotic. A possible counter-argument to this is the position of the junction between infraorbital and supraorbital canals, which in *Eusthenopteron* is situated in the dermosphenotics. This was presumably the basis for the interpretations of both Säve-Söderbergh and Jarvik, since they interpreted the course of the sensory canals, which are very indistinct in the known specimens, differently (text-fig. 6). However, both these interpretations of the position of this junction may fit the presence of a fronto-dermosphenotic bone. This is due to an apparent transfer of this sensory canal junction from the dermosphenoticum to the postorbitals, in the transition from osteolepiforms to the labyrinthodonts. This makes the position of this junction a weak argument in determining bone homologies in this region and in these forms. That this change in position of this junction occurred is indicated by: (1) that the dermal bone containing this junction in labyrinthodonts is, judging from its position relative to both the orbit and the surrounding dermal bones, clearly a postorbital; and (2) that several stegocephalians have sensory canal patterns that may be interpreted as intermediate stages in such a transition. Examples of such forms are *Trematosaurus* (Bystrow 1935, figs. 18D, 25), *Lyrocephalus* (Säve-Söderbergh 1935, figs. 61, 66), and *Aphaneramma* (Säve-Söderbergh 1935, fig. 56; 1936, fig. 31).

Theoretically there are several ways in which this change may have taken place, and it is interesting to note that both Säve-Söderbergh's and Jarvik's interpretation of the position of the junction in *Ichthyostega* may fit as an intermediate stage in some theoretical succession. If the junction gradually moved from the dermosphenoticum to the postorbital (text-fig. 7H → E → B) Säve-Söderbergh's interpretation of the position of the junction would fit as an intermediate stage between osteolepiforms and labyrinthodonts. Another alternative is that a connection developed directly between postorbital and intertemporal (text-fig. 7H → D). Examples of specimens approximately at this stage are given by Bystrow (1935, fig. 18A, C). From this stage there may either be a reduction of the postorbital-dermosphenotic connection, or a reduction of the dermosphenotic-intertemporal connection. The first leads to a sensory canal pattern like Jarvik's interpretation of *Ichthyostega* (text-figs. 6A, 7G), the latter to the pattern that is common in labyrinthodonts (text-fig. 7B). A possible intermediate in the latter process is shown in a specimen of *Lyrocephalus* (text-fig. 7A). A third alternative is that a series of branchings took place, which gradually 'moved' the junction on to the postorbital (text-fig. 7H → I → F → C → B). The presence of branched sensory canals in this region is shown by Bystrow (1935, p. 115, figs. 18B, D, 25).

To solve the problem of which way the position of the junction changed, a more detailed study, and probably more material, is needed. However, the existence of so many specimens with branching canals makes the first of the three alternatives, that the junction gradually 'wandered' to its new position, somewhat less probable. This again can theoretically be considered to reduce somewhat the probability for Säve-Söderbergh's interpretation of the position of the junction in *Ichthyostega*. No matter how this change took place, however, the reasonings above leave no doubt that the change in position occurred, and thus that there are no valid arguments against the existence of a fronto-dermosphenotic. This also supports Jarvik's interpretation concerning which bones are frontals and parietals in *Ichthyostega* (text-fig. 6A).

A very tentative interpretation of the phylogenetic position of *Ichthyostega* based on the estimated bone homologies, and also partly on the above theoretical discussions on the sensory canal patterns, is that it is in several aspects a primitive tetrapod belonging to a side-branch from a line between osteolepiforms and other stegocephalians.

Two other forms possibly on the tetrapod side of the osteolepiform-tetrapod transition, that should be mentioned briefly, are the Devonian *Elpistostege* and *Acanthostega*. To my knowledge *Elpistostege* is known only from a single specimen (Westoll 1938, fig. 1), showing only some of the medial exocranial bones. It seems similar to *Ichthyostega*, but too little is known to warrant any further discussion. *Acanthostega* is also a relatively little known form (Jarvik 1952, p. 68; 1980a, p.



TEXT-FIG. 7. Sketches of temporal regions of exocrania showing possible transitional stages of the junction of infraorbital and supraorbital sensory canals between that of osteolepiforms (H) and a common labyrinthodont pattern (B). A, *Lyrocephalus euri* (from Säve-Söderbergh 1937, fig. 1); B, *Benthosaurus sushkini*, (from Bystrow 1935, fig. 12); C, D, theoretical intermediate stages; E, *Ichthyostega* (from Säve-Söderbergh 1932, fig. 15); F, theoretical intermediate stage; G, *Ichthyostega* (from Jarvik 1967, fig. 11c); H, *Osteolepis* (from Jarvik 1967, fig. 11A); I, theoretical intermediate stage. The orbit is marked by a thick line.

242), and thus does not allow any thorough analysis of homologies or relationships. The exocranial sutures of the specimens of *Acanthostega* are very indistinct, but granting that Jarvik's interpretations of these are correct, I find his reasonings well founded. To his statements I will only add that, in its position relative to the squamosum, and to the skull table generally, the process positioned posteriorly on the skull roof is very similar to the tabular process of the anthracosaurs.

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ABBREVIATIONS

The following abbreviations are used in all text-figures except text-fig. 6: D, dermosphenotic; F, frontal; fo.hy., fossa hypophyseos; I, intertemporal; J, jugal; L, lachrymal; LE, lateral extrascapular; M, maxillary; ME, medial extrascapular; N, nasal; ot.r., otic region; P, parietal; Pm., premaxillary; Po., postorbital; Pof., postfrontal; pq, palatoquadratum; Pp, postparietal; pr.b., processus basiptyergoideus; Prf., prefrontal; Pro., preopercular; Q, quadratum; Qj., quadratojugal; S, supratemporal; SI, supra-intertemporal; Sq, squamosum; T, tabular; II, nervus opticus; V, nervus trigeminus; X, nervus vagus.

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