

The observational and theoretical components of homology: a study based on the morphology of the dermal skull-roofs of rhipidistian fishes

N. JARDINE*

King's College Research Centre, Cambridge

Accepted for publication March 1969

This paper is a study of the ways in which direct observation of the morphology of organisms, and indirect inferences about the kinds of morphological change that may take place in phylogeny, interact in the formation of judgements about homology. The dispute about the correct identification of dermal skull-roof bones in the osteolepiform and porolepiform rhipidistian fishes is used to illustrate the various issues. Some suggestions are made about the ways in which such disputes may be resolved.

CONTENTS

	PAGE
The empirical basis of homology	327
The determination of topographic homologies	332
The relations between topographic and phylogenetic homology	333
The homologies of the dermal skull-roof bones of the osteolepiform and porolepiform rhipidistian fishes	335
The facts	335
The beliefs underlying rival interpretations of the facts	340
The rival interpretations	347
Matching dermal skull-roof bones on the computer	350
Conclusions	351
General conclusions	357
Acknowledgements	358
References	358

THE EMPIRICAL BASIS OF HOMOLOGY

Recently there has been considerable debate about the meaning of the concept of homology in biology (see e.g. Boyden, 1947; Zangerl, 1948; Remane, 1956; Simpson, 1961; Sokal & Sneath, 1963; Inglis, 1966; Sattler, 1966; Jardine, 1967; Key, 1967). Many authors have pointed out that to define homology between parts of organisms in terms of derivation from a common ancestral part is inadequate, partly because such a definition is logically circular, and partly because it is unrelated to the way in which homologies are, in practice, established.

The logical circularity arises from the fact that homology itself is invoked in identifying the parts of descendant organisms with any part in a common ancestor; the irrelevance arises from the fact that even if we had some independent criteria for identifying parts of descendant organisms with parts in a common ancestor, this would seldom

*This work was carried out during the tenure of an S.R.C. Research Studentship and latterly during the tenure of a Royal Society Scientific Information Research Fellowship and an S.R.C. Research Grant.

enable us to determine homologies, for fossil series are rarely complete enough for us to identify common ancestors with any certainty, and even in such rare cases the morphology of the common ancestor may be incompletely known. In practice it is the homologies of parts of organisms that are used to infer something about the structure of ancestral organisms, rather than vice versa. The way out of this difficulty is to examine the ways in which homologies are in practice determined. The point has been expressed with great clarity by Woodger (1937: 137):

'Some authors have written as though homologies of parts could not be determined until the phylogenetic relations of their owners have been determined. But the determination of such phylogenetic relations presupposes the establishment of at least some homologies quite independently of all such considerations. In other words, we must possess some *criteria* of homology which the earlier morphologists also possessed before phylogenetic questions were considered at all. There is a primary sense of 'homology' which we all use intuitively and upon which all the more sophisticated senses of the word depend. Just because it is used intuitively we do not stop to analyse it, and are scarcely aware that we are using it.'

It has long been recognized that a basic empirical criterion of homology is correspondence in relative position (see e.g. Owen, 1847: 175-6; Darwin, 1859: 434-5; Boyden, 1947; Woodger, 1945; Remane, 1956: 30). The history of the concept of homology in biology is outlined in Tait (1928), Haas & Simpson (1946), and Jardine (1967).

There is a close historical parallel between the changes in biologists' attitudes to taxonomy and to homology. In the idealist morphology of St. Hilaire and Owen, taxonomy was supposed to be based upon the determination of a hierarchy of ideal types; with the advent of the theory of evolution it became orthodox to regard taxonomy as being based upon the determination of phylogenies. Similarly homology, which had formerly been supposed to be based upon the determination of the structure, or *Bauplan*, of ideal types, became supposedly based upon the determination of the structure of common ancestors. Yet the practice of both taxonomy and comparative anatomy was little affected by this conceptual revolution. Classification continued to be based on the observation of the homologies between parts of organisms and their relative dissimilarities, and homologies continued to be established largely on the basis of correspondence in relative position.*

In Jardine (1967) a logical model for correspondence between parts of things with respect to a set of relations was formulated, and a definition of homology in terms of correspondence with respect to a set of spatial relations was given. From the logical model a computable process for finding homologies was derived. Whilst the method for finding homologies has proved useful in comparative anatomical investigations (see Jardine & Jardine, 1967), I now believe the treatment of homology in that paper

*T. H. Huxley (see e.g. 1877: 23, 686) was almost alone amongst his contemporaries in realizing that the classification of organisms and the description of the common structure of groups of organisms is not based upon the evolutionary hypothesis, whereas the fact that organisms can be classified hierarchically and that the common structure of taxonomic groups of organisms can be described constitutes evidence for the hypothesis.

to have been oversimplified since several obvious objections to the definition of homology of parts in terms of correspondence in relative position were left unanswered. The most powerful objection is that correspondence in relative position does not *define* homology, but is simply one of several criteria used in determining homologies.

In Jardine (1967) it was suggested that common ancestral derivation of parts, common genetic determination of parts, and common embryological origin of parts should be regarded as hypotheses about homology rather than as criteria of homology. It was suggested that where homologous parts could be shown, directly or indirectly, to be derived from a homologous part in a common ancestor the homology should be described as a phylogenetic homology. In other words, it was argued that homology defined as a particular kind of correspondence in relative position is a *necessary condition* for parts to be said to be phylogenetic homologues.

An alternative course would be to coin some new term for correspondence in relative position (e.g. morphological correspondence, or isomorphism) and to reserve the term homology for phylogenetic homology. This was rejected on the grounds that it conceals the fact that phylogenetic homology is a special case of correspondence in relative position, and on the grounds that the proposed definition of homology, whilst conflicting with many biologists' beliefs about homology, is in line with the way in which the term is in practice used in comparative anatomy. The choice between the two courses is purely a matter of terminology, and in this paper I shall side-step the issue by using the terms *topographic homology* and *phylogenetic homology*, and by emphasizing that *phylogenetic homology* must be considered a special case of *topographic homology*.

To define topographic homology in terms of correspondence in relative position is, however, too sweeping, since there are certain conditions which a correspondence in relative position should fulfil if it is to correspond to the way in which the term 'homology' is used in comparative anatomy. One of these, pointed out by Dr Sneath (pers. comm.), is that the parts which correspond in relative position should correspond also in their composition, for most biologists would be reluctant to accept, for example, a bone as the homologue of a muscle. It is debatable whether any such criterion of similarity in composition should be built into a definition of topographic homology. Many cases are known where the histology of homologous parts varies quite widely, and it is at least conceivable that if organisms were discovered in which parts of very different composition were found to correspond consistently and precisely in relative position we should be forced to regard them as homologues. The generally accepted homology between the endostyle of *Amphioxus* and the thyroid of adult lampreys and hagfishes illustrates this point. An extreme version of the view that the homology of parts is determined by their composition, and other attributes, was expressed by Sokal & Sneath (1963) who suggested that homologous parts should be regarded as 'organ taxa', that is clusters of parts determined by mutual similarity measured in terms of shared attributes. This suggestion runs counter to common sense, for it would allow parts to be considered homologous which showed no correspondence in relative position, and would admit the notion of varying degrees of homology. A similar account which admits varying degrees of homology has been given by Sattler (1966, 1967), though in that account correspondence in relative position

is taken into account along with shared attributes of parts. Whilst this is clearly an inadequate account of biological homology, it seems a reasonable account of the relation of *analogy* between parts. On such an account we must regard homology and analogy as relations between parts which are determined by different empirical criteria, and must admit that all parts, whether or not they are homologues, may show varying degrees of analogy. A second point raised by Sneath, that difference in composition plays a crucial role in the initial demarcation of parts, prior to any decision about their homologies, is certainly valid.

It may be objected that in certain cases parts which are generally agreed to be homologous do not correspond in relative position. For example, the pelvic fin of primitive actinopterygians is behind the pectoral fin, whereas in advanced actinopterygians it is in front of the pectoral fin. In such cases the correspondence in relative position can be seen to be preserved when the spatial frame, by which the relations between parts are determined, is distorted. Examples of such grid transformations were given by D'Arcy Thompson (1942), and have been investigated in detail by Sneath (1967). Against this it might be argued that in order to find the appropriate distortion of the spatial frame it is necessary to find first the homologies of parts, so that the use of a distorted spatial frame in finding homologies involves circularity. This is untrue: the preliminary identification of axes, with or without distortion of the spatial frame, which is used to determine the homologies of parts will be that which yields the largest 1:1 matching of parts and this may, at least in principle, be found by experiment. A further objection might be that if a sufficiently complex spatial distortion were allowed we could successfully homologize any parts whatsoever. This also is untrue. If the pelvic fin in advanced actinopterygians did not occupy the same position relative to at least some other parts as that which it occupies in primitive actinopterygians, no amount of distortion of the spatial frame would determine the homology.

A second condition on homology which may be imposed is to stipulate that only those correspondences in relative position that are consistent with the developmental relations between parts of organisms should be allowed as homologies. Such a condition may be imposed by requiring:

(a) if a part x in one stage of the life-history of an organism is homologous with a part y in a comparable stage in the life-history of another organism, and if a part x' in a later stage of the life-history of the organism develops from x , then if x' is homologous with any part in a comparable stage in the life-history of the other organism, it must be homologous with a part that develops from y ;

(b) if a part x in one stage of the life-history of an organism is homologous with a part y in a comparable stage in the life-history of another organism, and if a part x'' in an earlier stage in the life-history of the organism develops into x , then if x'' is homologous with any part in a comparable stage in the life-history of the other organism, it must be homologous with a part that develops into y .

Due to relative migrations and reorientations of parts in the development of organisms this condition is often violated by the correspondences in relative position between parts of different organisms considered at various comparable stages in their life-histories. The only ways in which it could be ensured that the condition was fulfilled would be to take either the correspondence in relative position in the adult stages of

organisms, or the correspondence in relative position in some other stage in the ontogeny of organisms, as basic, and to allow correspondences in relative position to count as homologies only if they obeyed either condition (a) or condition (b) with respect to the basic correspondence in relative position. If the adult correspondence in relative position were taken as basic, embryonic parts would be counted as homologues only if they both occupied corresponding relative positions and also developed into adult parts occupying corresponding relative positions (i.e. only if they had the same *prospective significance*). If the correspondence in relative position in an embryonic stage were taken as basic, parts of adult organisms would be said to be homologous only if they both occupied corresponding relative positions and developed from parts occupying corresponding relative positions in the embryonic stage. Neither of these options is attractive. The former implies that homologous embryonic parts must have the same prospective significance; the latter implies that homologous adult parts must develop from embryonic parts occupying corresponding relative positions. Both alternatives are seen to run counter to the way in which the term 'homology' is in practice used by biologists.

Whilst it is clear that neither similarity in composition, nor consistency with the developmental relations between parts, should form part of a definition of topographic homology, it is equally clear that the attempt to *define* topographic homology in terms of correspondence in relative position was misguided, for it precludes under all circumstances the use of additional criteria in determining topographic homologies.* What is established by the arguments given here and in Jardine, 1967, is that correspondence in relative position is a *necessary condition* for parts to be said to be topographic homologues (i.e. every topographic homology is a correspondence in relative position with respect to some selection of parts and spatial relations). The arguments given above against the incorporation of criteria based upon similarity in composition, and the developmental relations between parts, into a definition of topographic homology, weigh equally against making any such criteria necessary conditions for parts to be said to be topographic homologues.

The conclusions about the empirical basis of homology may be summarized as follows. A basic criterion of homology is correspondence in relative position; that is, correspondence in relative position is a necessary condition for parts to be homologous. Topographic homology, the concept of homology which is fundamental to comparative anatomy, may be determined either on the basis of correspondence in relative position, or on the basis of correspondence in relative position together with such additional criteria as similarity in composition and similarity of origin or fate in ontogeny.† Topographic homologies from which it can be inferred that a common ancestor had parts standing in the same spatial relations to one another as in the descendant organisms are phylogenetic homologies. The determination of phylogenetic homologies is a very

*The attempt to define theoretical concepts in biology (e.g. homology) in terms of more directly observable concepts (e.g. parts and spatial relations) may be in general misguided. The definition is likely always to be narrower in scope than the concept allegedly defined (cf. Hempel, 1966: Ch. 7).

†The relations between the criteria used to identify parts in such fields as geology and protein chemistry and those used in comparative anatomy are discussed in papers by Sneath (1969), and Jardine & Jardine (1969). In both papers it is suggested that in a variety of fields the identification of parts often involves a compromise between matching in terms of correspondence in relative position and matching in terms of similarity with respect to some set of properties.

complex matter involving both direct evidence from fossil series, and evidence for hypotheses about the kinds of morphological and functional change that may take place in phylogeny. The ways in which topographic homologies may be determined are discussed in the next section, and some of the ways in which phylogenetic homologies may be established are discussed in subsequent sections.

THE DETERMINATION OF TOPOGRAPHIC HOMOLOGIES

In Jardine (1967) a computable method for finding topographic homologies was described. In the light of the weaker claim in this paper that correspondence in relative position is a necessary condition for topographic homology, but not definitive, the method should be regarded only as an aid in determination of topographic homologies. The first stage in the method is the identification of axes in the organisms studied. This may involve a distortion of the spatial frame by which the axes are determined (i.e. a grid transformation). Next the selected spatial relations which hold between the selected parts are recorded. The computer then seeks the largest 1:1 matching (i.e. the 1:1 matching which puts the greatest number of parts in 1:1 correspondence) in which all of the selected spatial relations are preserved. A relation such as 'anterior to' is said to be preserved in a matching if, whenever a part x is anterior to a part y in one organism, then any parts p and q in another organism which are matched with x and y respectively, are such that p is anterior to q .

The process described above may, for a given selection of parts and relations, yield several equally large 1:1 matchings between parts rather than a unique largest matching. This was the case in computing the topographic homology of the skull bones of *Clupea finta* and *Amia calva* using the relations 'anterior to', 'dorsal to', and 'distal to' (see Jardine & Jardine, 1967). Several equally large 1:1 correspondences were found which differed only in the ways in which the bones of the suborbital series were matched. In that case the obvious solution was to consider the entire suborbital series in *Clupea* as homologous with the entire suborbital series in *Amia*, since the suborbital series of bones in *Clupea* corresponds in relative position to the suborbital series of bones in *Amia*. It is, however, possible to construct artificial examples in which no such solution would be possible, since several equally large matchings differ radically in the way in which the parts are matched. If such cases were found in nature we should have to admit that, without using some additional criteria for topographic homology, there was no unambiguous solution.

There is likewise no guarantee that different selections of parts and relations from the same organisms will lead to the same matching of parts. For example, in computing the topographic homology of the skulls of the cat and rat the generally accepted homology is found if the relations 'anterior to', 'dorsal to', and 'distal to' are used. However, if in addition the relation 'adjacent to' is used, several equally large matchings of parts are found. The discrepancy arises from the fact that the frontal and squamosal bones of the rat are adjacent, whereas the frontal and squamosal bones of the cat are separated by the orbitosphenoid portion of the alisphenoid. Examples of the ways in which the matchings found may vary with different selections of parts are given in the next section.

Further flexibility is introduced into the process for finding topographic homologies by allowing for undecidability in the spatial relations between parts. In seeking the largest 1:1 matching between parts in which the spatial relations between parts are preserved an undecidable relation is allowed to map onto the relation, its converse, or undecidable in the relation. Examples of the use of undecidable relations are given in the next section.

THE RELATIONS BETWEEN TOPOGRAPHIC AND PHYLOGENETIC HOMOLOGY

The fact that the process for finding topographic homologies is flexible is of great importance in discussing the relations between topographic and phylogenetic homology. It has been emphasized that the topographic homologies found for various selections of parts and relations may differ widely. Implicit in the way in which parts and relations are selected are important assumptions about the kinds of matching which are admissible as homologies (either topographic or phylogenetic). An example of the way in which a prior assumption about the kinds of change which may take place in phylogeny may influence the selection of parts as candidates for topographic homology occurs frequently in computing the homologies of vertebrate skull bones. Either the set of parts selected may consist of individual bones, or the set of parts selected may include also as parts pairs, triplets, etc. of adjacent bones. If only individual bones are counted as parts, and a bone in one skull occupies a position corresponding to that of two adjacent bones in another skull, the topographic homology found may be one in which one of the two bones in the latter skull is matched with the bone in the former, the other bone in the latter skull being matched with no bone in the former. If pairs of adjacent bones are counted as parts, the topographic homology found may be one in which the pair of adjacent bones in the latter skull is matched with the single bone in the former. It is plausible to suggest that pairs, triplets, etc. of adjacent bones will be considered to constitute parts only if the hypothesis that fusion of adjacent bones may take place in phylogeny is accepted (see p. 343).

Similarly, assumptions about the kinds of change that may take place in phylogeny may be involved in the selection of spatial relations. As mentioned above, the inclusion of 'adjacent to' in the spatial relations used in computing the topographic homology between the skull bones of the cat and rat leads to a matching which does not correspond to the homology that is generally accepted. It is usual in the comparative anatomy of vertebrate skulls to allow that bones which are adjacent in the skulls of some forms may be homologous with bones that are not adjacent in the skulls of other forms. The assumption underlying this may be that whereas the relative positions of bones (determined by the relations 'anterior to', 'dorsal to', and 'distal to') are usually preserved in phylogeny, the interpolation of bones or parts of bones between formerly adjacent bones may occur quite frequently. Likewise, to allow in the preliminary identification of axes distortion of the spatial frame by which relations are determined may reflect the underlying assumption that such distortions may occur in phylogenetic sequences.

Assumptions about the extent to which the relative positions of bones are preserved in phylogeny may affect the way in which the spatial relations between bones are recorded. Consider the sequence **A-D** in Fig. 1. At what stage should part 1 be recorded

as anterior to part 2? **A** must certainly be recorded as undecidable and **D** as anterior, but whether **B** and **C** are recorded as undecidable or anterior may depend partly upon the amount of distortion that we suppose may have occurred in phylogeny.

Once a topographic homology has been established, further arguments may be used in an attempt to find out which matchings, if any, are to be considered as phylogenetic homologies. Thus Osborn (1893) presented evidence from the known fossil series of mammals to show that topographically homologous cusps and folds of mammalian teeth could not be used to infer the presence of corresponding cusps and folds in a common ancestor. Throckmorton (1962, 1965) has used cytological evidence for the branching sequence in the phylogeny of *Drosophila* to show that there has been

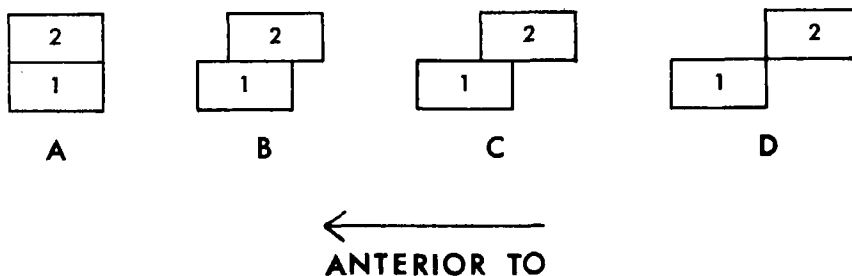


FIGURE 1. See text for explanation.

extensive parallel evolution of topographically homologous structures in the genitalia; and Inger (1967) has given evidence for the parallel development of topographically homologous structures in the phylogeny of the frogs.

It has been emphasized that phylogenetic homology must be considered a special case of topographic homology. Zangerl (1948) made a rather similar distinction between an 'observational' and an 'interpretative' stage in the determination of homologies. It seems, however, that such a clear-cut distinction does not correspond precisely to the distinction between topographic and phylogenetic homologies. The observation of topographic homologies is not direct observation, for, as shown above, the way in which such homologies are determined may be influenced by phylogenetic assumptions.* Nor is there any guarantee that phylogenetic homologies will form any kind of useful basis for the naming of parts for comparative anatomical purposes. The suggestion that phylogenetic homologies and the homologies most suitable as a basis for the naming of parts in comparative anatomy might not coincide was made by Osborn (1902). The same suggestion has been made by Moy-Thomas (1938), Westoll (1944), and Jarvik (1948).

In the following section the relation between the determination of topographic homologies and their interpretation is discussed in detail with reference to the question of the correct identification of dermal skull-roof bones in the osteolepiform and porolepiform rhipidistian fishes. Throughout the discussion, often at the cost of appearing pedantic, I have attempted to make explicit the evidence and arguments upon which the various proposed homologies are based. Use is made of a computer program for checking whether a matching of parts preserves a given set of spatial relations.

*The thesis that all observation is to some degree 'theory-laden', so that direct observation becomes a myth, has been persuasively presented by Hanson (1958: Ch. 2).

The input for the program is a list of possible matchings of parts, and a record of the spatial relations between each pair of parts in each organism. The output is a list of the matchings in the input in which the spatial relations are preserved.

The adequacy of the account of topographic homology given in Jardine (1967), and of the computable processes for finding and checking topographic homologies derived from the account, can be tested only by finding out by experiment whether in simple cases it yields the same matchings of parts as are obtained by eye. This was established in Jardine & Jardine (1967), and it is this that makes it reasonable to apply the processes in more complex cases where the determination of topographic homologies by eye is difficult.

THE HOMOLOGIES OF THE DERMAL SKULL-ROOF BONES OF THE OSTEOLEPIFORM AND POROLEPIFORM RHIPIDISTIAN FISHES

The facts

The terms osteolepiform and porolepiform are used here without taxonomic implications to cover genera having very different dispositions of bones in the dermal skull-roof. Many authors, e.g. Jarvik (1942), Vorobjeva & Obruchev (1967), and Jessen (1966), have treated the two groups as representing a valid taxonomic division of the Rhipidistia. The rank accorded to these groups has varied from familial to ordinal or even (Stensiö, 1963) class rank. Other authors, e.g. Moy-Thomas (1939), Berg (1940, 1958), and Thomson (1962, 1964*a*, 1967*b*), have divided the osteolepiform assemblage into two groups of the same rank as the porolepiforms, the rhizodontoids and the osteolepoids. Both Berg and Thomson have given the three groups super-familial rank. Of the genera considered here only *Eusthenopteron* and *Eusthenodon* have been assigned to the rhizodontoids. The disposition of dermal skull-roof bones in the other genera that have been referred to the rhizodontoids is not known. The taxonomy of the Rhipidistia is discussed in the light of the morphology of the dermal skull-roof on pp. 355–357.

The skull-roofs of the osteolepiforms studied are shown in Fig. 2, and of the porolepiforms studied in Fig. 3. The topographic homologies of the dermal skull-roof bones in the temporal and cheek regions within the osteolepiforms and within the porolepiforms are obvious, with the possible exception of the homologies of the temporal bones of *Glyptopomus elginensis* with those of the other osteolepiforms (see p. 346). The bones for which the correct homology between the osteolepiforms and porolepiforms has been disputed are numbered 1–7 in the osteolepiforms (Fig. 2) and 8–15 in the porolepiforms (Fig. 3). The bones whose homologies have not been disputed are labelled as follows in Figs 2 and 3: PO, postorbital; JU, jugal; QJ, quadratojugal; ESM, median extrascapular; ES, extrascapular; ET, extratemporal (tabular); OP, opercular; SOP, subopercular. The sensory canals are labelled as follows: so, supra-orbital; po, postorbital; ot, otic; st, supratemporal; ju, jugal; psp, prespiracular.

Certain differences of opinion about the correct reconstruction of the skulls of these rhipidistians are relevant to this study.

(1) The reconstructions of *Holoptychius flemingi* proposed by Westoll (1937*a*, Fig. 1C; 1937*b*, Fig. 9C) and Jarvik (in Stensiö, 1947; 1948, Fig. 33B; 1950*a*, Fig. 31D; 1963, Figs 4C and 11A) differ in several respects. Westoll's reconstruction was based upon specimens from Dura Den, Fifeshire. Jarvik's first (1948) reconstruction of *Holoptychius* was based partly on specimen A6028, and his second reconstruction (1950) was based on specimens A6027–6034 from Dura Den. These specimens are at the

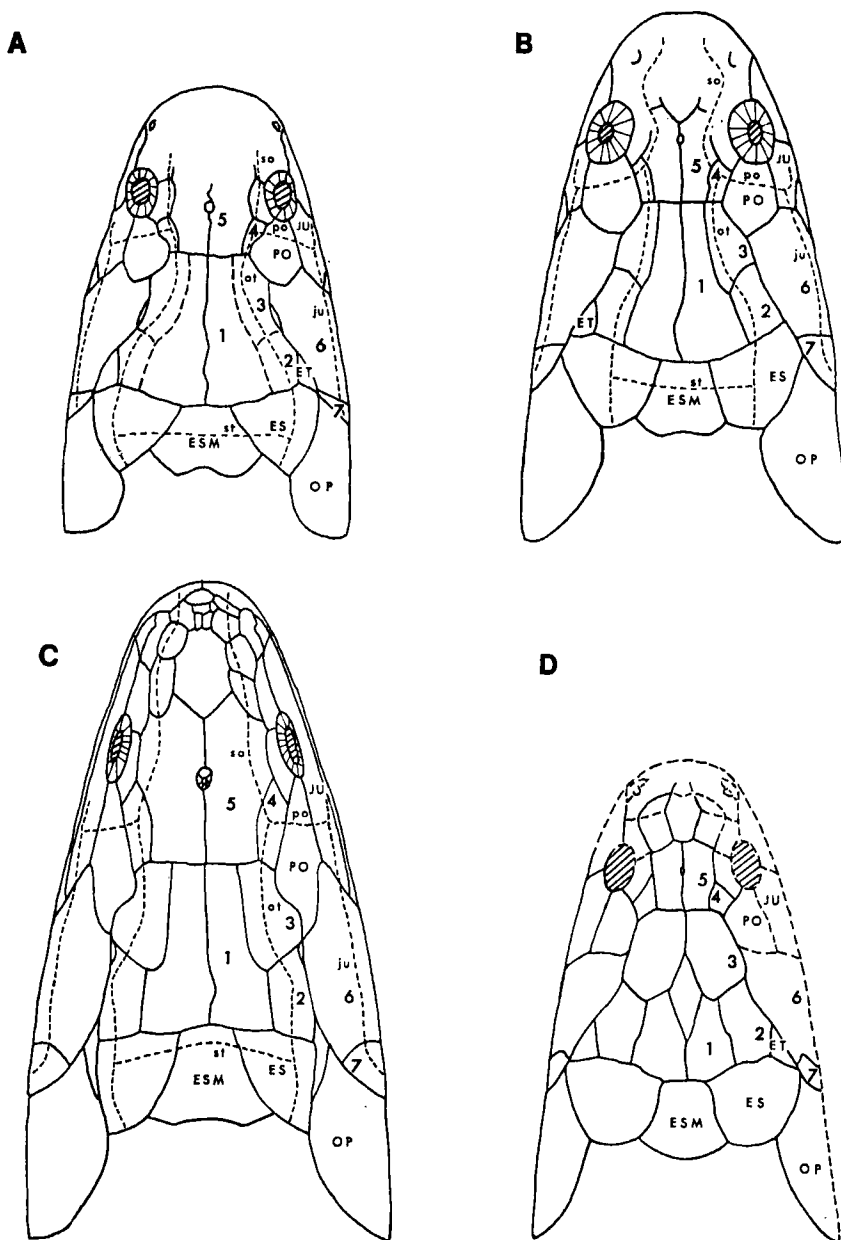


FIGURE 2

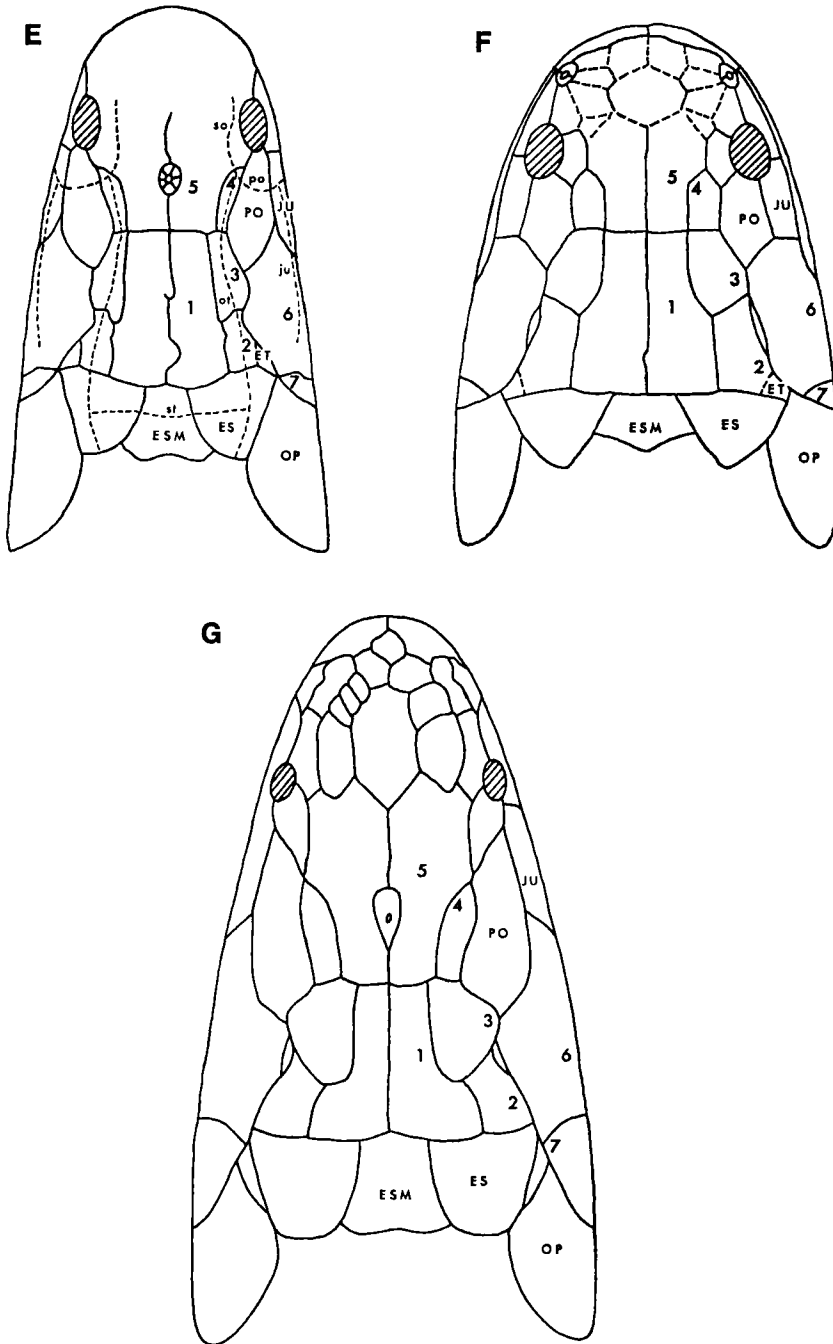


FIGURE 2. The dermal skull-roofs of osteolepiform fishes. **A.** *Latvius deckerti* Jessen (Middle Devonian), after Jessen (1966, Fig. 1B). **B.** *Osteolepis macrolepidotus* Ag. (Middle to Upper Devonian), after Säve-Söderbergh (1933, Fig. 19) and Jarvik (1948, Fig. 37B). **C.** *Eusthenopteron foordi* Whiteaves (Upper Devonian), after Jarvik (1944, Fig. 18B). **D.** *Glyptopomus elginensis* Jarvik (Upper Devonian), after Jarvik (1950b, Fig. 3). **E.** *Gyroptychius agassizi* Traill (Middle Devonian), after Jarvik (1948, Fig. 71B). **F.** *Ectosteorhachis nitidus* Cope (Lower Permian), after Thomson (1964b, 1967a Fig. 2A). **G.** *Eusthenodon wängsjöi* Jarvik (Upper Devonian), after Jarvik (1952, Fig. 26B). For explanation of symbols see text p. 335.

Sedgwick Museum, Cambridge. The respects in which Jarvik's and Westoll's reconstructions differ are as follows:

(a) In Jarvik's reconstruction bone 10 is shown as scarcely intruding between bones PO and 11, so that the suture between 11, and 9 and 10, is almost straight. In Westoll's

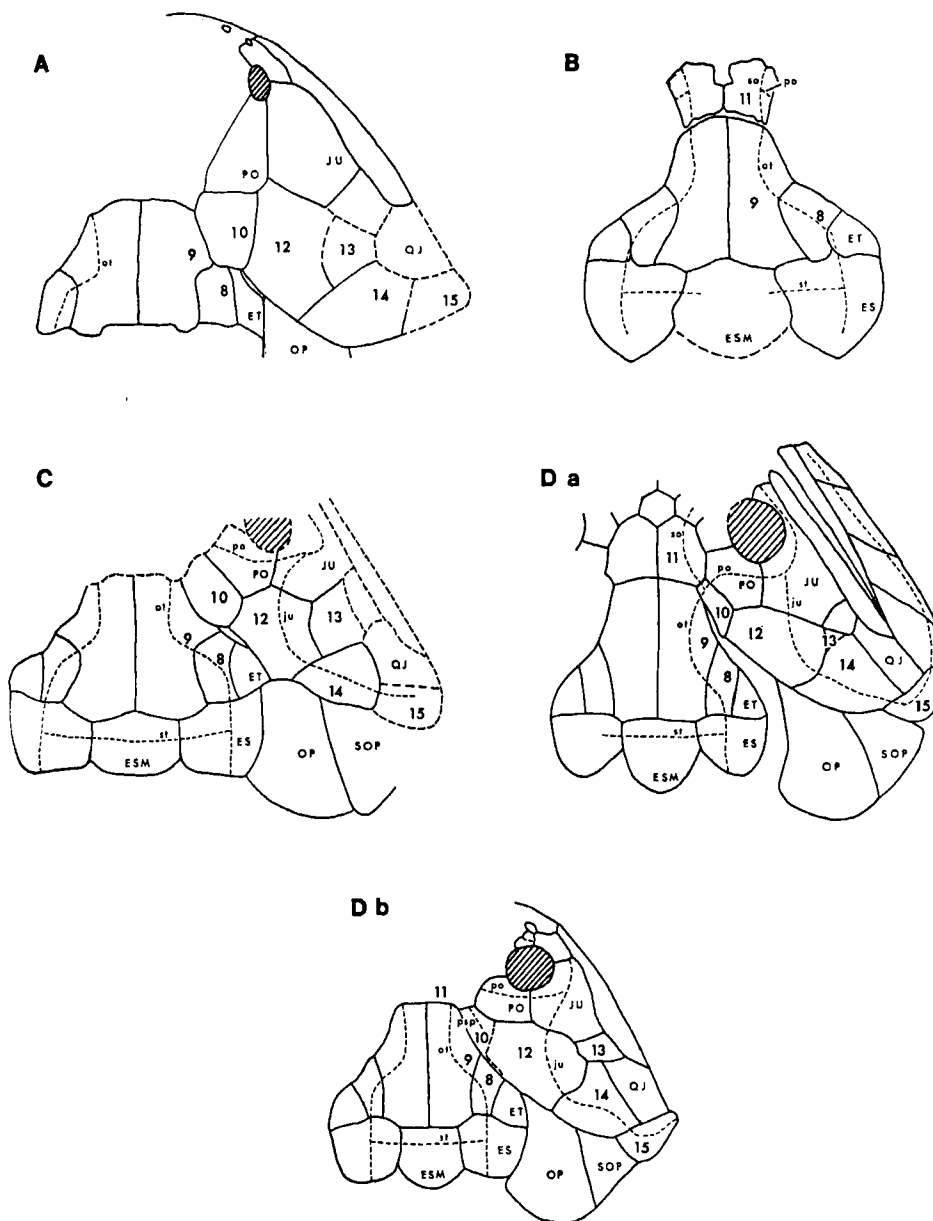


FIGURE 3. The dermal skull-roofs of porolepiform fishes. **A.** *Porolepis* sp. (Lower or Middle Devonian), after Jarvik (1950 a, Fig. 31 A). **B.** *Laccognathus panderi* Gross (Middle Devonian), after Jarvik (1950 a, Fig. 31 B). **C.** *Glyptolepis leptopterus* (Ag.) Woodward (Middle Devonian), after Jarvik (1950 a, Fig. 31 C). **Da.** *Holoptychius flemingi* Ag., after Westoll (1937 b, Fig. 9 C). **Db.** *Holoptychius flemingi* Ag. (Upper Devonian), after Jarvik (1950 a, Fig. 31 D). For explanation of symbols see text.

reconstruction bone 10 is shown as intruding between PO and 11. The relative position of bone 10 in Jarvik's reconstruction is distal to that in Westoll's reconstruction, and this is correlated with the fact that Jarvik reconstructed the skull of *Holoptychius* as being very much broader than in Westoll's reconstruction.

(b) The otic sensory canal, ot, is shown in Jarvik's reconstructions to run directly from bone 11 into bone 9 without passing through bone 10, whereas in Westoll's reconstruction it runs through bone 10. Jarvik (1948) claimed that Westoll had mistaken for a part of the otic sensory canal a small sensory canal, the prespiracular, which runs back from a point on the postorbital canal at, or near to, its junction with the otic sensory canal and terminates in bone 10. Parrington (1956) has written, 'if substantiated, this clash of opinion will indicate that the course of a canal can vary even within one genus'. In fact the specimens from Dura Den upon which these reconstructions are based are almost certainly conspecific. Jarvik (1948) claimed that his interpretation is supported by specimens of *Holoptychius* from East Greenland, one of which was figured in Jarvik (1942, Fig. 33, based upon specimen G.G.U. 496 from the Zoological Museum, Copenhagen). However, in Jarvik (1949) it is made clear that the reference of the East Greenland specimens to the genus *Holoptychius* is uncertain.

I have examined specimens of *Holoptychius flemingi* from Dura Den at the Royal Scottish Museum, Edinburgh, and at the Sedgwick Museum, Cambridge. It seems that Jarvik's reconstruction is correct. Specimen 1888.16.2 from Dura Den at the Royal Scottish Museum shows clearly the course of the otic canal, and specimen A6028 at the Sedgwick Museum shows the presence of more or less collinear pits in both bone 9 and bone 10. However, conclusions about the courses of sensory canals cannot be based on the positions of the pits with certainty for, as shown by Jarvik (1944) in *Eusthenopteron foordi*, the tubules running from the canals to the pits may cross the sutures between bones.

(2) Jarvik (1944) stated that in *Eusthenopteron* the posterior part of the jugal canal (there called the preoperculo-mandibular canal) 'pierces the ventral part of the preoperculum, ventrally to which it passes in soft tissue behind the articulation of the lower jaw and medially to the posterior part of the quadratojugal'. The course of the jugal canal was illustrated in two detailed figures (17B and C). Nevertheless Thomson (1966) wrote, 'In rhizodontoids, such as *Eusthenopteron*, as described by Jarvik (1944), the preoperculum is slightly smaller than in *Gyroptychius* and the lateral line now turns ventrally to pass through the posterior corner of the quadratojugal in its passage to the infradentary bone series'. He contrasted this situation with the situation in the osteolepoids such as *Osteolepis* and *Gyroptychius* in which the jugal canal does not pierce the quadratojugal. This mistake may have arisen from the fact that Fig. 16 in Jarvik (1944) would suggest, if the text were not read, that the lateral line passes through the quadratojugal rather than, as was intended, in the soft tissues medial to it.

To have called these reconstructions 'the facts' may seem odd, for there is little doubt that the kind of morphology that is expected of a fossil may influence the process of reconstruction itself. Thus Westoll's reconstruction shows the junction of the supra-orbital, postorbital, and otic sensory canals in bone 10 in *Holoptychius* which is what would be expected on the assumption that bone 10 is homologous with bone 4 in the osteolepiforms. Similarly Thomson's belief that the Rhipidistia fall into three groups

of superfamilial rank, the Rhizodontoideae, the Osteolepoideae and the Holoptychioideae may have led him to expect to find taxonomically significant differences between *Eusthenopteron* and the osteolepoids. This would be consistent with his misunderstanding of Jarvik (1944).

Such biasing of observation by expectation is, of course, understandable. Indeed the whole process of preparation and reconstruction of a fossil must depend upon an interplay between what is expected and what is observed. However, this kind of circularity differs from the kinds of circular reasoning involved in the interpretation of a reconstruction, for the former can, and should be, eliminated whereas the latter may be very much harder to eliminate.

The beliefs underlying rival interpretations of the facts

The various interpretations of the morphology of rhipidistian skulls have been influenced by hypotheses about the kinds of morphological change that may have taken place in the phylogeny of vertebrate skulls. First it is necessary to discuss briefly some of the evidential bases for such hypotheses.

Many such hypotheses are based upon direct or indirect inferences from the kinds of change that take place in ontogeny to the kinds of change that may have taken place in phylogeny. The more literal forms of the recapitulation theory are now in disfavour (see e.g. De Beer, 1937, 1958), yet as De Beer pointed out this does not in general invalidate all such arguments. The danger when we are dealing with fossils is, however, that in cases where ontogeny itself can only be inferred indirectly from adult morphology, the arguments may be presented in such a way that the argument from ontogeny to phylogeny is hidden. Thus Parrington (1956: 410), describing the specialization of the tetrapod skull, wrote, 'It is shown that the reduction of the supratemporal bone to a splinter is consistent with the assumption of its appearance only at a late stage in the growth of the parietal'. Here 'reduction' is reduction in phylogeny, 'growth' is growth in ontogeny. From the context it is clear that the statement may be so reformulated as to make clear the inference involved, thus: 'it is shown that the reduction in phylogeny of the supratemporal bone to a splinter is consistent with the assumption of its appearance at progressively later stages relative to the growth of the parietal in successive ontogenies'. The concealment of such inferences from ontogeny to phylogeny arises from the ambiguity of the terms 'reduction', 'loss', 'growth', and 'fusion' which may describe either phylogenetic or ontogenetic processes.

Many hypotheses about the kinds of morphological change that may take place in phylogeny are based upon morphological series. By a morphological series is meant a chain of organisms such that adjacent members of the chain are more similar to one another than to more distant members of the chain. The use of such series often enables us to establish topographic homologies that could not be established if only the terminal organisms were known (see e.g. Zangerl, 1948; Maslin, 1952; Inglis, 1966). For example, such sequences may, by indicating that distortion has occurred in phylogeny, suggest that a particular distortion of the spatial frame (grid transformation) should be used in determining the homology between parts of the terminal members of a sequence. Many sequences of contemporary organisms which suggest progressive

distortion of topography in phylogeny are illustrated in Gregory (1951). It is not always realized that homologies cannot simply be 'read off' such series. Firstly, the recognition of relative similarities upon which the establishment of such series depends will itself depend in part upon the establishment of the topographic homologies of parts. Secondly, many such series consist of contemporary organisms and the evidence they give about the kinds of change that may have taken place in phylogeny is indirect, often resting upon circular arguments about the relative primitiveness of characters (such sequences of contemporary organisms were called 'morphoclines' by Maslin, 1952). Even where a morphological series can reasonably be regarded as a phylogenetic sequence circular arguments may be involved in establishing the kinds of change that have taken place. For example, the series of dipnoans, *Dipnorhynchus*, *Dipterus*, *Neoceratodus*, figured by Westoll (1943, Fig. 7), shows conclusively a reduction in the numbers of dermal bones in phylogeny. But whether this should be interpreted as the result of loss or fusion of bones depends upon the homologies which are established between dermal bones of members of the sequence, and the homologies which are established will depend in turn upon whether the reduction in the number of bones is explained by loss or fusion.

Another kind of argument about the kinds of change which may have taken place in phylogeny is based upon evidence for the function of parts. A simple example arises in the discussion of the dermal skull-roof bones of the osteolepiforms and porolepiforms. Throughout the crossopterygians there is an articulation allowing dorsoventral movement of the anterior part of the skull relative to the posterior part (see e.g. Moy-Thomas, 1939; Schaeffer, 1965; Thomson, 1967a), though there is evidence that, at least in the adults of some forms, this kinesis may sometimes have been lost (see e.g. Jarvik, 1944). If bone 3 in the osteolepiforms is supposed to be the phylogenetic homologue of bone 10 in the porolepiforms, and if, as seems probable, the common ancestor of the osteolepiforms and porolepiforms had an intercranial kinesis, it must be assumed that in the phylogeny of one of the groups a bone has crossed the intercranial kinesis. It might be argued that this rules out the proposed homology since the presence at some stage in phylogeny of a bone straddling the intercranial kinesis would have prevented, or partially prevented, the kinetic movement of the skull. The functional argument appears to be weakened by the existence of osteolepiforms in which there can have no kinesis (see above). Further, the 'crossing' of the intercranial kinesis must not be taken too literally; the magnitude of the change involved would depend upon the order in which the ossificatory centres and the kinesis were established in ontogeny. Some light might be cast on this question by the investigation of the ontogeny of the intercranial kinesis in *Latimeria*.

Finally, it is important to note that many of the arguments used to support hypotheses about the kinds of morphological change which may have taken place in the phylogeny of a particular group of organisms are analogical arguments from the kinds of change which have taken place in groups of organisms that are similar in some respect. In other words many of the arguments depend upon underlying taxonomic judgments. Examples of such analogical inferences are the suggestion that the ontogeny of the intercranial kinesis in *Latimeria* might serve as a basis for a conjecture about its ontogeny in the osteolepiforms and porolepiforms (see above), and the argument of Parrington (1956) that the hypothesis that the bone corresponding to bone 4 in the osteolepiforms

(the intertemporal) has been lost in the porolepiforms is indirectly supported by the evidence for the reduction or loss of the intertemporal in many labyrinthodont amphibians and in the lepospondyls *Microbrachis* and *Hypoplezion*.

Some of the hypotheses about the kinds of morphological change which may have taken place in the phylogeny of the skulls of the osteolepiforms and porolepiforms which have influenced various authors in their judgments about the homology of the dermal skull-roof bones are listed below.

(1) It has generally been assumed that skull topography has been conserved, or at least partially conserved in evolution. Thus Parrington (1956) wrote, 'the identification of skull bones by their topography is an application of the general rule of the constancy of morphological relations, a well-tried rule which is fundamental to comparative anatomy and is quite undisputed'. It has been argued in the first section that correspondence in relative position with respect to some set of spatial relations is a necessary condition for parts to be said to be homologous, and the fact that skull topography is conserved, or partially conserved, is suggested by the fact that it is in practice possible to recognize homologies between the skull bones of successive members of fossil series. Indeed, if skull topography were grossly distorted in phylogeny we should not only be unable to recognize topographic homologies between successive members of fossil series, but might also be unable to recognize the series themselves.

(2) It has often been assumed that the courses of sensory canals are conserved in phylogeny. Allis (1898) wrote, '... a bone or 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'. As has been pointed out by Parrington (1956), such a criterion cannot be applied with complete disregard for skull topography, for the identification of homologous lateral lines must depend upon the establishment of at least some of the topographic homologies of bones. Säve-Söderbergh (1933, 1941) attempted to counter this objection by constructing a classification of sensory canals which is partially independent of skull morphology. He gave a primary classification according to innervation, and a secondary classification according to topographical and embryological criteria. Moy-Thomas (1938), Westoll (1938), Stensiö (1947) and Jarvik (1948, 1950*a*) have cited the observations of Pehrson (1922), showing that in *Amia* the ossificatory centres (blastemic primordia) develop in association with the neuromast cells, as evidence for the paramount importance of sensory canal courses in determining bone homologies. Jarvik (1948) cites also work by Neave (1936) in which it was shown that in *Salmo* the scale rudiments develop in association with neuromast cells. Neither Pehrson nor Neave gave evidence that the positions of the ossificatory centres are determined by the neuromast cells, and experiments by Moy-Thomas (1941) suggest that, on the contrary, in ontogeny the positions of the ossificatory centres play a part in determining the courses of the sensory canals. This suggestion has been developed convincingly by Parrington (1949).

Jarvik (1948) has cited as evidence for the hypothesis of sensory canal constancy the fact that in specimens of *Acipenser* in which the disposition of dermal skull-roof bones is abnormal the courses of the sensory canals are distorted so that they remain associated with the same ossificatory centres as in normal specimens. Although this

suggests a close association between bone and sensory canal development in ontogeny, it does not constitute evidence for the determination of bone disposition by the sensory canals.

It is well known that where the sensory canals form only superficial sulci in the dermal skull bones, as for example in the Rhachitomi, their courses may vary widely within a single genus (Westoll, 1943). The disagreement between Westoll and Jarvik about the course of the otic canal in *Holoptychius* is probably not an example of such variability (see p. 339), but such variability has been demonstrated in *Dipterus valenciennesi* in which the canals are enclosed in the dermal bones (see White, 1965).

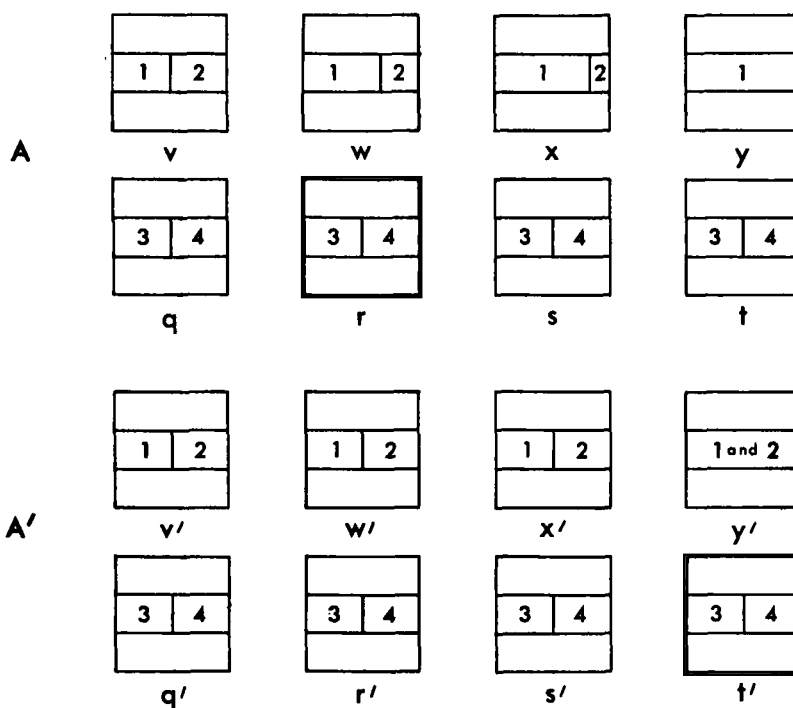
(3) Two apparently conflicting hypotheses about the kinds of change which may take place in phylogeny concern the interpretation of the well-established fact that in many vertebrate groups there has been a progressive reduction in the numbers of the dermal skull-roof bones. On one hypothesis this is explained by the relatively frequent occurrence of fusion of bones in phylogeny; on the alternative hypothesis fusion of bones in phylogeny is a relatively rare event and the reduction in numbers of bones is explained in terms of the loss of bones and the invasion of their territory by adjacent bones.

Unfortunately the meanings of the terms 'loss' and 'fusion' when applied to phylogenetic processes are obscure, since the terms are used only in loose analogy to their unproblematic use in describing processes in ontogeny. Figure 4(i) shows in diagrammatic form two pairs of phylogenetic series (A and A'). In the first series in each pair modification of adult morphology occurs. In A the first series shows gradual reduction followed by disappearance of bone 2, so that we might regard bone 3 in *t* as the homologue of bone 1 in *y*. In A' the first series shows fusion of bones 1 and 2 so that we might regard bones 3 and 4 in *t'* as the homologue of the bone labelled (1 and 2) in *y'*. But there are serious difficulties in the way of this naive account. We are never in possession of complete fossil series and the discovery of further intermediate forms might upset any hypothesis about loss or fusion. Discovery of forms intermediate between *x* and *y* might indicate that what had in fact occurred in the series was a gradual reduction of bone 2 to a splinter followed by fusion with bone 1. Similarly, the discovery of forms intermediate between *x'* and *y'* might indicate that in fact bone 2 had been reduced to a vestige and lost relatively rapidly.

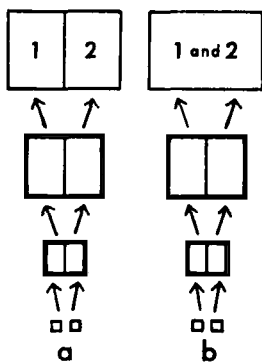
Perhaps the difficulty would be resolved if we were to consider phylogenetic changes not as sequential changes in adult morphology, but as sequential modifications of ontogenetic processes. We might then consider parts to show phylogenetic fusion only when there was evidence for fusion in ontogeny.* In Fig. 4(ii) such a case is illustrated. We should certainly consider bones 1 and 2 to have fused in phylogeny if we had evidence of the ontogenies *a* and *b*. We might consider evidence from adult morphology for fusion of ossificatory centres in the ontogeny of *b*, together with knowledge of the adult morphology of *a* and *b*, as conclusive evidence for phylogenetic fusion. Such cases are known; for example there are two centres of ossification in the postorbital-inter-temporal bone of the labyrinthodont *Dvinosaurus* (Bystrow, 1938, cited in Parrington, 1956). But to restrict the notion of phylogenetic fusion to cases where there is evidence

*Cf. Watson (1921), 'A term like supratemporo-extrascapularis implies that there has been an actual fusion of bones, and that we should expect to find that the bone so called develops from two centres.'

i



ii



iii

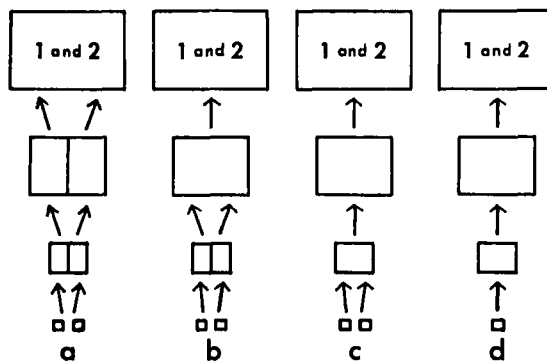


FIGURE 4. (i) A diagrammatic representation of two pairs of fossil series. The first series in the first pair is one in which the change in adult morphology suggests loss of a bone in phylogeny. The first series in the second pair is one in which the change in adult morphology suggests fusion of bones in phylogeny.

(ii) A diagrammatic representation of a sequence in which ontogenetic fusion is established.

(iii) A diagrammatic representation of a sequence in which fusion occurs at successively earlier stages in successive ontogenies until only a single ossificatory centre is present.

of fusion in ontogeny may sometimes lead to inconsistency. In the series shown in Fig. 4 (iii) the fusion of bones 1 and 2 occurs at successively earlier stages in the ontogenies *a-c* until finally only a single ossificatory centre is present in *d*. In such a case it would be unreasonable to regard only the stages in which fusion in ontogeny occurred as showing phylogenetic fusion. Yet such sequences may be of regular occurrence.* A definition of phylogenetic fusion which would cover such cases is suggested below.

Underlying any such use of ontogenetic evidence for phylogenetic processes is the hypothesis that embryonic structures (in this case ossificatory centres), are more consistently conserved in phylogeny than are adult structures. The evidence for this hypothesis can only be indirect since the ontogeny of parts of fossil organisms can usually be reconstructed only from their adult morphology, or by analogical argument from the ontogeny of contemporary organisms which are taxonomically related. For example, the demonstrations by Pehrson (1922, 1940) and Aumonier (1941) that the parietal bone in *Amia* develops from several ossificatory centres, and the demonstrations by Lekander (1949) and Weitzman (1962) that the frontal bone in cyprinoid fishes develops from several ossificatory centres, have been cited by Jarvik (1948, 1967) as evidence for the bone fusion hypothesis. If, however, the hypothesis that ossificatory centres were conserved in phylogeny were dropped, it would seem at least as reasonable to cite this as evidence for the multiplication of ossificatory centres in phylogeny, on the grounds that these bones are topographically homologous with bones in other fishes which develop from a single ossificatory centre.

Some conclusions are tentatively suggested. The meanings of the terms 'loss' and 'fusion' when applied to processes in phylogeny are unclear if applied solely on the basis of the changes in disposition of bones in adult forms. If the ontogeny of each member of a phylogenetic sequence were known it would be easy to apply the terms consistently. *Phylogenetic fusion* would describe cases where fusion of formerly distinct ossificatory centres had occurred in the ontogeny of some member of the fossil sequence, and either had occurred in the ontogeny of subsequent members, or had occurred at successively earlier stages in the ontogeny of subsequent members until eventually only a single ossificatory centre appeared in any stage at ontogeny. *Phylogenetic loss* would describe cases in which an ossificatory centre present in the ontogeny of some member of a sequence did not appear at any stage in the ontogeny of any subsequent member of the sequence, and in which there was no evidence for fusion of ossificatory centres in the ontogeny of any member of the sequence. Phylogenetic loss and fusion can be used as criteria in the determination of phylogenetic homologies only if it is true that the disposition of ossificatory centres is more strongly conserved in phylogeny than is the disposition of the bones of adults. If the disposition and numbers of ossificatory centres were more variable than that of adult bones, the only criterion for identification of ossificatory centres would be the topographic homologies of the adult bones to which they gave rise (i.e. their prospective significance), so that the use of

*Cf. Westoll (1943): 'During the obliteration of the transverse cranial division of an osteolepid the homologous elements ("dermosphenotic" and "intertemporal" of recent usage) being adjacent members of the same sensory-canal series, could easily fuse, and would thereby stiffen the joint region. It is perhaps permissible to regard them as having been for some time after this stage potentially separate, but often "phenotypically" fused, and to suppose that gradually a genotypic condition of a single ossification became habitual.'

phylogenetic fusion and loss, as defined above, as criteria of homology would involve a circular argument. In practice, in the study of fossil vertebrates we have to deal largely with incomplete phylogenetic sequences in which only the adult morphology is known. Except in these rare cases where juvenile forms are known or ontogenetic fusion is evident from the adult morphology (e.g. in the supratemporo-intertemporal of *Dvinosaurus* cited above) the kinds of evidence that have been cited in support of the loss and fusion hypotheses are indirect and open to alternative interpretation.

The view that reduction in the number of dermal bones in the phylogeny of the vertebrate skull should be explained by bone fusion was first systematically developed by Stensiö (1921, 1922, 1947). The consequences of this view in the interpretation of the homologies of the dermal skull-roof bones of the crossopterygians and early tetrapods have been developed in detail by Säve-Söderbergh (1933, 1935, 1941) and Jarvik (1944, 1948, 1950*a*, 1952). The converse view, that bone fusion is a relatively rare phenomenon in phylogeny, has been held by the majority of American and British palaeontologists (see e.g. Watson, 1921; Moy-Thomas, 1938; Parrington, 1949, 1956, 1967; Romer, 1945). Westoll (1938, 1943, 1949) held the intermediate view that phylogenetic fusion between bones through which the same sensory canal passes may have occurred, and that fusion between bones through which no sensory canal passes (anamnestic bones) may have occurred, but that fusion between sensory canal bones and anamnestic bones is unlikely.

The lateral-line constancy and bone fusion hypotheses are closely related since the lateral line constancy hypothesis, when used as a criterion of homology, is so restrictive that in many cases no topographic homology can be found unless it is assumed that bone fusions have occurred.

A further complication arises in the interpretation of the crossopterygian skull by Stensiö and Jarvik from the doctrine of conservative evolution (see Jarvik, 1960). According to this doctrine there is a sense in which all the ossificatory centres present in the hypothetical common ancestor of the crossopterygians are conserved in phylogeny. This leads to an extreme form of the fusion hypothesis in which bones are never lost, but 'elements' from them may be distributed in phylogeny to adjacent bones. From this follows the notion of partial homology of bones which are phylogenetically derived from some but not all the same elements. Thus Stensiö (1947) considered bones PO, JU, and QJ (see Figs 2 and 3) as only partial homologues between the osteolepiforms and porolepiforms, being derived from some but not all the same ossificatory centres, and Jarvik (1950*b*) suggested that bone 3 in *Glyptopomus elginensis* may be only partially homologous with bone 3 in other osteolepiforms (including other species of *Glyptopomus*) due to inclusion of elements which give rise to the anterior part of bone 1 in other osteolepiforms. The empirical content of this extreme form of the fusion hypothesis is obscure. If taken literally it implies that in the ontogeny of the forms with reduced numbers of bones many bones must be derived from a very large number of ossificatory centres. It is clear from what is known of the ontogeny of contemporary vertebrates that this is not always true. If the postulated fusion is phylogenetic fusion in the sense defined above then the hypothesis becomes vacuous, for the only possible basis for guesses about the disposition of the ossificatory centres in unknown ancestral skulls is the comparative anatomy of the skulls of known living and fossil forms. If a

sufficient number of primaeval ossificatory centres were postulated an allegedly phylogenetic justification for almost any proposed homology whatsoever could be found.

The rival interpretations

The dispute about the correct (phylogenetic) homology between dermal bones of the osteolepiforms and porolepiforms has concerned primarily the bones of the temporal region of the skull-roof. Alternative homologies have been suggested also for the bones of the cheek region, but since the morphology of the dermal cheek bones is imperfectly known for the porolepiforms these are discussed only briefly here.

Dermal cheek-bones

Westoll (1937) and Jarvik (1944) considered bone 6, the squamosal of the osteolepiforms, to be homologous with bones 12–14 of the porolepiforms, and bone 7, the pre-opercular, of the osteolepiforms to be homologous with bone 15 of the porolepiforms. Jarvik (1963) suggested that bone 7 of the osteolepiforms was in fact the homologue of bone 14 of the porolepiforms, and that bone 15, usually called the pre-opercular, of the

Table 1. The homologies between dermal skull-roof bones of the osteolepiform and porolepiform rhipidistian fishes which have been suggested by various authors

Author	Homology	Assumptions
Westoll (1937a)	2–8 Supratemporal	Westoll's reconstruction of <i>Holoptychius</i> Sensory canal courses constant
	3–9 Intertemporal	
	4–10 Dermosphenotic	
	5–11 Frontal	
Moy-Thomas (1938)	2–8 Supratemporal	Westoll's reconstruction of <i>Holoptychius</i> Sensory canal courses constant
	3–9 Intertemporal	
	4–10 Postfrontal	
	5–11 Frontal	
Stensiö (1947)	1 and 3–9 'Parieto'-dermopterotic 1	Jarvik's reconstruction of <i>Holoptychius</i> Bone fusions frequent Sensory canal courses constant
	2–8 Dermopterotic 2 and 3	
	4 and 5–11 'Frontalo'-dermosphenotic	
Jarvik (1948, 1950 a)	1 and 3–9 Parieto-intertemporal	Jarvik's reconstruction of <i>Holoptychius</i> Bone fusions frequent Sensory canal courses constant
	2–8 Supratemporal 1 and 2	
	4 and 5–11 Fronto-dermosphenotic	
Parrington (1949)	1–9 Interparietal	} Bone fusions allowed only with evidence for fusion in ontogeny Sensory canal courses variable
	2–8 Tabular	
	4–10 Intertemporal	
	5–11 Parietal	
Parrington (1956)	1–9 Interparietal	} Bone fusions allowed only with evidence for fusion in ontogeny Sensory canal courses variable
	2–8 Tabular	
	3–10 Supratemporal	
	5–11 Parietal	
Thomson (1966)	1 and 3–9 Postparietal	Not stated
	(or 1–9) and supratemporal	
	2–8 Tabular	
	5–11 Parietal	

Only Jarvik (1950 a) and Thomson (1966) considered porolepiforms other than *Holoptychius*. In each case the nomenclature used, and the assumptions about the kinds of change that may take place in phylogeny upon which the author's interpretation of skull morphology was based, are listed. Dermal bones are numbered as in Figs 2 and 3.

OSTEOLEPIFORM

POROLEPIFORM

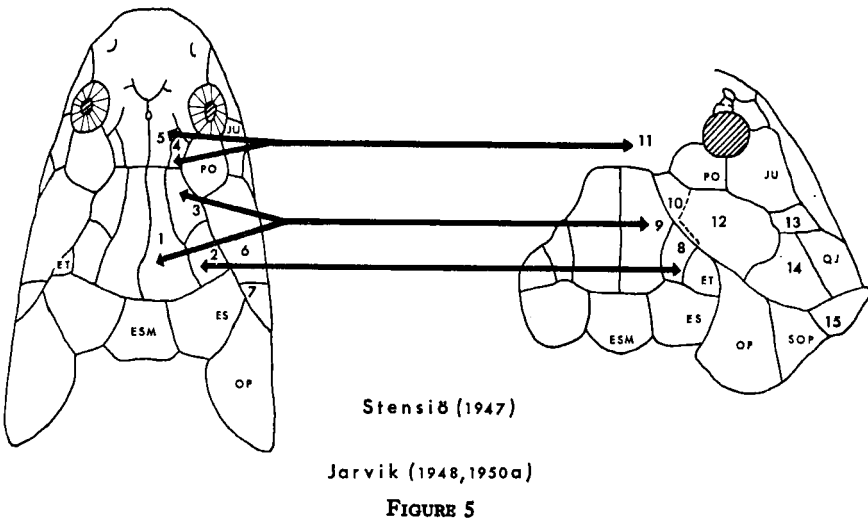
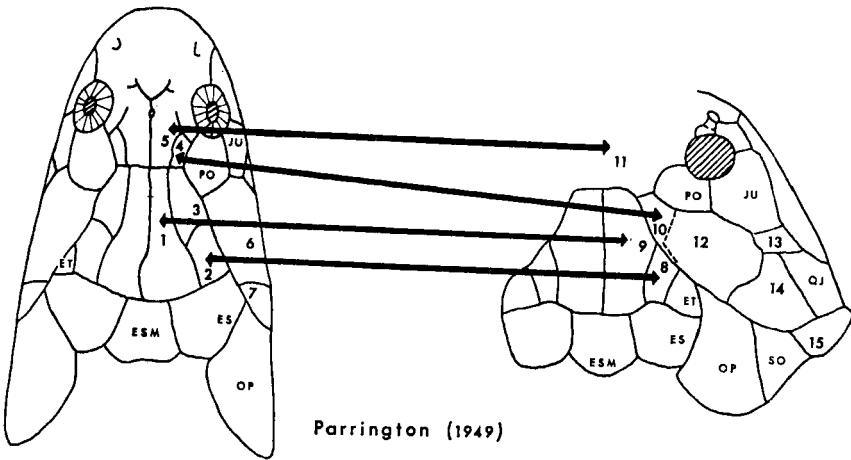
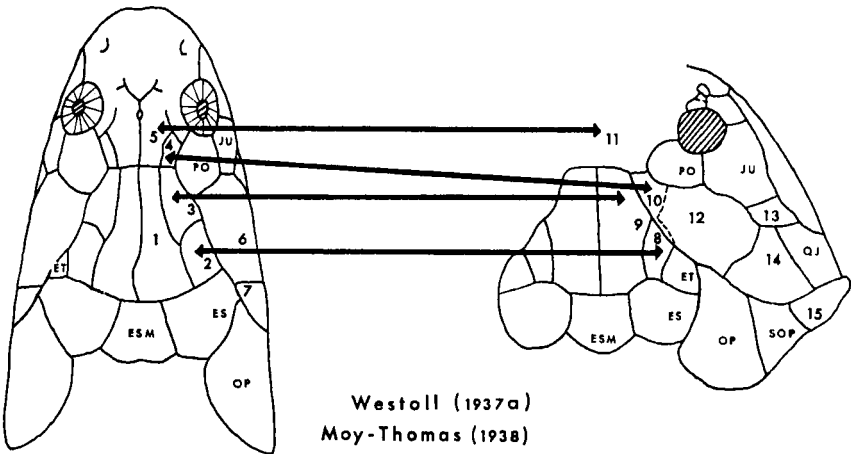


FIGURE 5

porolepiforms represented submandibular elements. The same suggestion was made by Thomson (1966). Both proposed homologies are consistent with skull-topography and with the lateral line constancy hypothesis. The latter seems to give a rather better topographic matching (see Jarvik, 1963 : Fig. 5A, B), but requires that a bone should have crossed the articulation of the jaw, a requirement that might be questioned on functional grounds (see p. 341).

Dermal skull-roof bones

The homologies proposed by different authors are shown in diagrammatic form in Fig. 5 and listed in Table 1 together with the nomenclature applied to the bones and the assumptions about the kinds of change which may have taken place in phylogeny which were held by the various authors.

The diversity in nomenclature of bones arises from the fact that Westoll (1938) revised the nomenclature of the dermal skull-roof of the crossopterygians, in the light of the morphology of the skulls of *Ichthyostega* and *Elpistostega*, so as to apply the

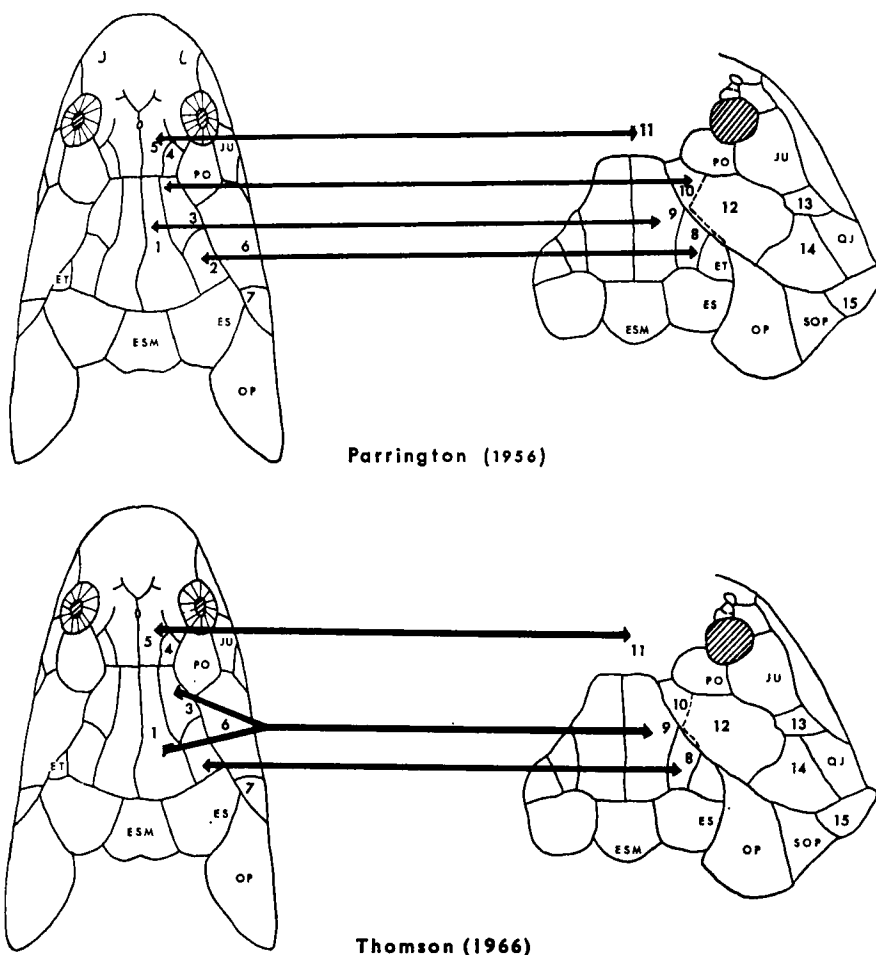


FIGURE 5. Suggested homologies between dermal skull-roof bones of osteolepiform and porolepiform rhipidistian fishes.

same names to the bones as are conventionally applied to their inferred homologues in the skulls of tetrapods. His revision was as follows :

<i>Old names</i>	<i>Revised names</i>
Frontal	Parietal
Parietal	Post-parietal (interparietal)
Dermosphenotic (post-frontal)	Intertemporal
Intertemporal	Supratemporal
Supratemporal	Tabular

The Swedish palaeontologists, Stensiö, Jarvik, and Säve-Söderbergh have followed the old nomenclature, and have also named bones according to their presumed components according to the bone-fusion hypothesis. Most other recent authors have used the revised nomenclature. The revised nomenclature is contrasted with the Swedish nomenclature by Westoll (1943).

Matching dermal skull-roof bones on the computer

The computer program described on p. 335 was used to find out the matchings of dermal skull-roof bones which are determined by various combinations of assumptions. The purpose of this experiment was to find out which of the proposed homologies are consistent with the assumptions made in their determination, and to find out if there are other possible topographic homologies not considered by any author.

The data for computing consisted in each case of a list of parts together with the spatial relations holding between them. It was assumed throughout that the topographic homologies within the osteolepiforms and porolepiforms are as shown in Figs 2 and 3, so that for each computation only two lists of parts and the spatial relations between them were prepared. In every computation the list of parts included the bones numbered 1–5 in the osteolepiforms and 8–11 in the porolepiforms, the bones lettered as PO, JU, QJ, ESM, ES, ET and SOP, and the sensory canals lettered as so, po, ot, st, ju and psp. The assumption that bone fusions may occur in the phylogeny of the dermal skull-roof was incorporated by including pairs of adjacent numbered bones in the lists of parts; the converse assumption, that bone fusion in phylogeny should not be postulated unless there is evidence for fusion of bones in ontogeny at some stage in the phylogenetic sequence, was incorporated by excluding pairs of adjacent bones from the lists of parts.

In every computation the relations 'anterior to' and 'distal to' were recorded between parts. It has been emphasized that the existence of a matching in which spatial relations are preserved is a necessary condition for the recognition of topographic homologies, and that the assumption that skull topography is at least partially conserved in phylogeny is a necessary condition for the interpretation of any topographic homology as a phylogenetic homology. Some of the homologies which have been proposed do in fact involve considerable distortion of the dermal skull-roof (e.g. that proposed by Moy-Thomas, 1938). The assumption that skull topography has been only partially conserved in

phylogeny is incorporated in the data for computation by recording the relations 'anterior to' and 'distal to' only where one part lies anterior or distal to another in its entirety, and recording 'undecidable' where one part is only partially anterior or distal to another. Strict conservation of skull topography is incorporated by recording 'anterior to' and 'distal to' not only where one part is entirely anterior or distal to another, but also where one part is only partially anterior or distal to another. The assumption that sensory canal courses have been constant in the phylogeny of the dermal skull-roof is incorporated by including in the data for computation the relation 'passing through' between sensory canals and dermal bones. In such cases the differences in sensory canal courses in Westoll's and Jarvik's reconstructions of *Holoptychius* are of crucial importance, and separate computations were carried out for the two reconstructions. In all computations the matching of the lettered bones was assumed to be beyond dispute.* This assumption was incorporated by including only a 'dummy' relation between each pair of lettered bones to ensure their correspondence in any matching found. The validity of this assumption was checked using the program for finding topographic homologies, described in Jardine & Jardine (1967), using data consisting of lists of numbered and lettered bones and the relations 'anterior to' and 'distal to'. This yielded matchings in which the lettered bones were paired and which differed only in the ways in which the numbered bones were paired.

It would have been more rigorous to use the program for finding topographic homologies in all cases, and to make no prior assumptions about the topographic homology of particular bones, since this ensures that no possible matching of parts consistent with the spatial relations selected can be overlooked. The method for checking the consistency of matchings of parts with a set of spatial relations between parts will yield all consistent matchings only if these were included in the initial list of possible matchings which, together with the specification of the relations holding between parts, forms the input for the program. The use of the less rigorous method is justified by the fact that the majority of possible matchings can be ruled out by eye without serious risk of error.

In Table 2 the ways in which the numbered bones were matched in the computations are shown. Only the matchings which are parts of matchings in which the lettered bones and sensory canals were also matched correctly are listed.† The parts and relations used in each computation, and the assumptions underlying the selection of parts and relations, are tabulated.

Conclusions

Comparison of Tables 1 and 2 shows that the phylogenetic homologies proposed by the various authors are indeed consistent with the assumptions that they made, and

*This is not entirely justified. Stensiö (1947) suggested that these bones may be only 'partially homologous' in the osteolepiforms and porolepiforms, being derived phylogenetically from some, but not all the same primitive ossificatory centres. As pointed out on p. 346, the concept of partial homology is ill-defined, and the hypothesis that the common ancestor of the osteolepiforms and porolepiforms had a large number of ossificatory centres in ontogeny, is valueless in determining homologies in the absence of evidence about the disposition of the hypothetical ossificatory centres.

†When sensory canal courses were allowed to be variable a number of matchings were found in which bones were matched with sensory canals! This illustrates the fact that whilst topographic matching is a necessary condition for parts to be considered topographic or phylogenetic homologues, such additional criteria as similarity of composition may be needed to determine a reasonable homology (see p. 331).

Table 2. The matchings between dermal skull-roof bones of the osteolepiform and porolepiform rhinidians in which skull topography is preserved or partially preserved

Assumptions	Parts selected	Relations selected	Matchings of four dermal skull-roof bones	Matchings of three dermal skull-roof bones
(1) Skull topography strictly conserved Sensory canal courses variable Bone fusions precluded	Bones Sensory canals	Partly or entirely anterior Partly or entirely distal	1-9 2-8 4-10 5-11	Many
(2) Skull topography strictly conserved Sensory canal courses variable Bone fusions allowed	Bones and pairs of adjacent bones Sensory canals	Partly or entirely anterior Partly or entirely distal	1&3-9 2-8 4-10 5-11	Many
(3) Skull topography strictly conserved Sensory canal courses constant Bone fusions precluded Westoll's reconstruction of <i>Holoptychius</i>	Bones Sensory canals	Partly or entirely anterior Partly or entirely distal Passing through	None	2-8 4-10 5-11
(4) Skull topography strictly conserved Sensory canal courses constant Bone fusions precluded Jarvik's reconstruction of <i>Holoptychius</i>	Bones Sensory canals	Partly or entirely anterior Partly or entirely distal Passing through	None	None
(5) Skull topography strictly conserved Sensory canal courses constant Bone fusions allowed Westoll's reconstruction of <i>Holoptychius</i>	Bones and pairs of adjacent bones Sensory canals	Partly or entirely anterior Partly or entirely distal Passing through	1&3-9 2-8 4-10 5-11	Many
(6) Skull topography strictly conserved Sensory canal courses constant Bone fusions allowed Jarvik's reconstruction of <i>Holoptychius</i>	Bones and pairs of adjacent bones Sensory canals	Partly or entirely anterior Partly or entirely distal Passing through	None	1&3-9 2-8 4&5-11
(7) Skull topography partially conserved Sensory canal courses variable Bone fusions precluded	Bones Sensory canals	Entirely anterior Entirely distal	Many	Many

(8) Skull topography partially conserved Sensory canal courses variable Bone fusions allowed	Bones and pairs of adjacent bones Sensory Canals	Entirely anterior Entirely distal	Many	Many
(9) Skull topography partially conserved Sensory canal courses constant Bone fusions precluded Westoll's reconstruction of <i>Holopttychius</i>	Bones Sensory canals	Entirely anterior Entirely distal Passing through	2-8 3-9 4-10 5-11	None
(10) Skull topography partially conserved Sensory canal courses constant Bone fusions precluded Jarvik's reconstruction of <i>Holopttychius</i>	Bones Sensory canals	Entirely anterior Entirely distal Passing through	None	2-8 3-9 4-11
(11) Skull topography partially conserved Sensory canal courses constant Bone fusions allowed Westoll's reconstruction of <i>Holopttychius</i>	Bones and pairs of adjacent bones Sensory canals	Entirely anterior Entirely distal Passing through	1&3-9 2-8 4-10 5-11	Many
(12) Skull topography partially conserved Sensory canal courses constant Bone fusions allowed Jarvik's reconstruction of <i>Holopttychius</i>	Bones and pairs of adjacent bones Sensory canals	Entirely anterior Entirely distal Passing through	None	1&3-9 1&3-9 3-9 2-8 2-8 2-8 4&5-11 4-11 4&5-11

The data used in each computation is indicated and the corresponding assumptions are listed (see text for explanation). The bones are numbered as in Figs 2 and 3 and the method of computation is described above. The computations are numbered 1-12 for reference in the text.

that in some cases the assumptions uniquely determine a particular matching of bones. Several points of interest emerge:

(a) The assumption that bone fusions should not be postulated without evidence for ontogenetic fusion at some stage in phylogeny, together with the assumption that skull topography is conserved in phylogeny and that sensory canal disposition is of no more importance than the disposition of other parts, determines the matchings suggested by Parrington (1949, 1956) (see Table 2(1)). At first sight the topographic correspondence between bone 10 in the porolepiforms and bone 3 in the osteolepiforms appears closer than that between bone 10 and bone 4 (see Fig. 5). There are however arguments for supposing that if either of these matchings is a phylogenetic homology it is more probably the matching in which bone 4 in the osteolepiforms is paired with bone 10 in the porolepiforms. As pointed out by Thomson (1966), bone 10 in the porolepiforms shows reduction in size and anterior extent in the series *Porolepis*, *Laccognathus* (inferred from the extent of the articular surface with bone 9, figured by Jarvik 1948, Fig. 31B), *Glyptolepis*, *Holoptychius*. Although this sequence cannot be regarded as a phylogenetic sequence it may reflect the phylogenetic modification of bone 10 (the status of such arguments is discussed on p. 341). The position of bone 10 in *Porolepis* and *Glyptolepis* matches that of bone 4 in the osteolepiforms more accurately than it does in the later porolepiforms. Further, if bone 10 were matched with bone 3, and if the common ancestor of the osteolepiforms and porolepiforms were assumed to have had an intercranial kinesis, it must be assumed that either bone 10 or bone 3 must have crossed the kinesis and the spiracular cleft in phylogeny (see p. 341 for a more detailed discussion).

(b) If bone fusions are precluded and sensory canal courses are constant in phylogeny, no matching of all dermal skull-roof bones in which skull topography is preserved is obtained. If skull topography is allowed to be only partially preserved and Westoll's reconstruction of *Holoptychius* is accepted, the matching proposed by Moy-Thomas and Westoll is obtained (see Table 2(9)). If Jarvik's reconstruction of *Holoptychius* is accepted an even stranger matching is obtained (see Table 2(10)). If the first of the matchings were interpreted as a phylogenetic homology it would have to be assumed that the porolepiforms had lost the post-parietals in phylogeny; if the second were interpreted as a phylogenetic homology it would have to be assumed that the porolepiforms had lost both the parietals and the post-parietals in phylogeny. Both the matchings would be precluded if the relations of the bones to underlying brain-case structures had been considered.

The only way in which the hypothesis that sensory canal courses are constant can be salvaged without gross distortion of skull topography is to allow that fusions of dermal skull-roof bones may have occurred.

(c) If both the bone fusion and sensory canal course constancy hypotheses are accepted, it is possible to find a matching between dermal skull-roof bones in which skull topography is strictly preserved. If the courses of the sensory canals were in all porolepiforms as in Westoll's reconstruction of *Holoptychius* then the matching 1 & 3-9, 2-8, 4-10, 5-11 is uniquely determined (see Table 2 (5)). If Jarvik's reconstruction of *Holoptychius* is correct, and as suggested by Jarvik (1948), and confirmed by Thomson (1966) for *Glyptolepis*, no sensory canal runs through bone 10 in the porolepiforms

other than *Holoptychius*, more extensive bone fusion has to be postulated in order to preserve sensory canal constancy. Under these assumptions the matching proposed by Stensiö (1947) and Jarvik (1948) is uniquely determined (see Table 2(6)).

It is concluded that, whilst the Swedish interpretation of the morphology of the dermal skull-roofs of rhipidistian fishes involves strong assumptions of questionable validity about the kinds of change which may take place in phylogeny (see pp. 343–346), and leads to a nomenclature of bones that is highly inconvenient for comparative anatomical purposes, it is a consistent interpretation.

(d) The matching suggested by Thomson (1966, 1967*b*) is one of the several matchings consistent with the assumptions that skull topography is strictly conserved, that bone fusions may occur, and that sensory canal courses are variable (see Table 2(2)). That Thomson (1966) allowed that sensory canal courses may vary is indicated by his mistaken assertion that in rhizodontoids the jugal canal passes through the quadratojugal whereas in osteolepoids it does not. It involves the assumption that the intertemporal, 4, is absent in the porolepiforms, but that a bone not homologous with the intertemporal, (bone 10, called by Jarvik the prespiracular plate) occupied a similar relative position in the porolepiforms. It is surprising that Thomson should accept a homology which implies a substantial difference in the morphology of dermal skull-roof bones since he has argued (see below) that the morphological differences within the osteolepiforms are as substantial as those between the osteolepiforms and the porolepiforms.

(e) The interpretation of the dermal skull-roof morphology of the osteolepiforms and porolepiforms may be relevant to the divergence of opinion about the way in which the osteolepiform and porolepiform crossopterygians should be classified. At one extreme it has been argued by Jarvik (1955, 1967) and Stensiö (1963) that the osteolepiforms and porolepiforms should be considered as distinct orders or even as distinct classes. At the other extreme Thomson (1962, 1964*a*, 1967*b*) has argued that they represent a single homogeneous group and that the differences within the osteolepiforms are as great as the differences between the osteolepiforms and porolepiforms. He therefore suggested that the osteolepiforms should be divided into two groups, the rhizodontoids (including *Eusthenopteron* and *Eusthenodon*) and the osteolepoids, and that the porolepiforms should be considered as a third group of equal rank.

The discussion has been complicated by disagreement about the phylogenetic relationship of the osteolepiform-porolepiform assemblage to the tetrapods. Jarvik (1955, 1967) and Stensiö (1963) have argued on the basis of comparison of the anatomy of the snout and intermandibular regions of the osteolepiforms and porolepiforms with that of present-day amphibians that the urodeles are derived from the porolepiforms, whereas the anurans and other tetrapods are derived from the osteolepiforms. Thomson (1962, 1964*b*) has argued that the characters supposed by Jarvik to differentiate the osteolepiforms and porolepiforms are relatively trivial and in some cases based upon misinterpretations of the fossil material. He has argued further that the morphological homogeneity of the osteolepiform-porolepiform assemblage is evidence against the diphyletic ancestry of the tetrapods. Jarvik (1966) has presented counter-arguments to many of Thomson's objections to his account of the anatomy of the osteolepiforms and porolepiforms.

A discussion of the details of this dispute would be out of place here, but some important issues which are illustrated will be discussed briefly. Three distinct issues are involved. One is the question of the relative magnitudes of the morphological differences within the osteolepiforms and between the osteolepiforms and the porolepiforms. Another is the question of the way in which these differences should be expressed within a classification. Finally there is the question of the phylogenetic relationships of the osteolepiforms and porolepiforms. The way in which these issues are related depends upon the nature of the relationship between classification and phylogeny.

At one extreme it has been argued that classification should be entirely phenetic; that is, that it should be based solely upon the relative morphological dissimilarities between groups of organisms (see e.g. Bigelow, 1958; Sokal & Sneath, 1963). At the other extreme it has been argued that classification should be entirely phyletic; that is, that it should be based as far as possible upon the cladistic relationships of organisms (see e.g. Hennig, 1950). On this view the ideal classification would be one in which all taxa were monophyletic in the sense that they included all and only organisms derived from a single ancestral population. In this extreme form of phyletic classification the taxonomic rank of groups of organisms would depend solely upon the order of their divergence in phylogeny without regard to their relative dissimilarities. The absurd consequences of this extreme form of phyletic (vertical) classification have been discussed by Bigelow (1961). If the porolepiforms gave rise to the urodeles and the osteolepiforms gave rise to the anurans and other tetrapods, the porolepiforms and urodeles would be grouped together in a taxon of the same rank as that containing the osteolepiforms, anurans and all other tetrapods. Stensiö (1963) has gone to this extreme in recognizing the osteolepiforms and porolepiforms as belonging to distinct classes.

Between these two extremes lies the view of Simpson (1961) that phenetic (horizontal) classification is basic, but that phenetic classifications may be modified so as to ensure a relation of consistency between classification and phylogeny. A classification is said to be consistent with a phylogeny if each taxon is monophyletic in the sense that the organisms referred to it are immediately derived from organisms referable to not more than one taxon of the same rank. The effect of this requirement is to allow that the rank of a taxon may differ within limits from that which it would be given on the sole grounds of its morphological dissimilarities from other taxa. This view appears to conform closely with usual zoological practice.*

Whilst the taxonomic weight to be attached to the morphological differences between the osteolepiforms and porolepiforms may be influenced by their phylogenetic relationships with the tetrapods, the magnitude of these differences is quite irrelevant to the dispute about the origin of the tetrapods. What is important in deciding whether the hypothesis of Stensiö and Jarvik is correct is the extent to which morphological differences between parts of the porolepiforms and osteolepiforms can be correlated with constant differences between homologous parts of the urodeles and anurans. Szarski (1962) and Parsons & Williams (1963) have argued that no such correlations can be found. Furthermore, Salthe & Kaplan (1966) have given convincing immuno-

*The logical basis of phenetic classification is discussed in Jardine (1949), and the relation between phenetic classification and phylogeny is discussed in Bader (1958), Simpson (1961), in several papers in Heywood & McNeill (eds. 1964), and in Jardine (in preparation).

logical evidence for the relatively recent (perhaps Permian) divergence of the anurans and urodeles.

The constancy of the disposition of dermal cheek and skull-roof bones within the osteolepiforms and the porolepiforms, and the fact that the disposition of bones in these regions differs considerably between the two groups, may be of taxonomic significance. All the various interpretations of the morphology of the skulls of the two groups lead to the conclusion that there are several dermal bones in each group which lack homologues in the other group. No such constant differences in homology have been demonstrated for the two groups recognized by Berg (1940) and Thomson (1962, 1964a) within the osteolepiforms. The differences cited by Thomson are differences only in the attributes of homologous parts. The dispositions of dermal skull-roof and cheek bones in the osteolepiform-porolepiform assemblage suggest that the division into osteolepiforms and porolepiforms is a natural one.

GENERAL CONCLUSIONS

It is suggested that attempts to define the relation of homology between parts of organisms in terms of common ancestry are misguided. A basic criterion of homology is correspondence in relative position, and computable methods for finding the largest 1:1 correspondence of parts in which given spatial relations are preserved may provide a valuable tool for the investigation of the comparative anatomy of organisms in which the disposition of parts is very complex.

It is useful to distinguish topographic homology, the kind of homology which is fundamental in comparative anatomy, and phylogenetic homology, the kind of homology which can be used to infer the disposition of parts in a common ancestor. Whether a given topographic homology, or part of a given topographic homology, can be considered to be a phylogenetic homology will usually depend upon a wide variety of hypotheses about the kinds of change that may take place in phylogeny. There can be no *a priori* guarantee that the topographic homologies which are most useful for comparative anatomical purposes will be phylogenetic homologies. Many of the hypotheses about the kinds of morphological change which may take place in phylogeny rest upon highly indirect evidence, and in many cases the arguments involve elements of circularity.

Amongst the questions which have been important in determining the phylogenetic homologies of dermal skull-roof bones are the following: Is skull topography strictly or partially conserved in evolution? Are sensory canal courses constant in evolution? Should the reduction of the numbers of dermal skull-roof bones in evolution be interpreted as the result of loss of bones in phylogeny? It is concluded that the hypothesis of at least partial conservation of skull topography in phylogeny is a *sine qua non* for the use of any homology as a basis for inference about the morphology of the skulls of ancestral organisms, and that the evidence for this hypothesis is overwhelming. It is argued that the evidence for strict sensory canal course constancy in phylogeny is unconvincing and open to alternative explanation. The question of dermal bone loss *versus* fusion is shown to depend upon the meanings assigned to phylogenetic loss and fusion. It is suggested that phylogenetic fusion should be supposed to have occurred

only when there is evidence for the occurrence of fusion of ossificatory centres in the ontogeny of some stage in a phylogenetic sequence, and that phylogenetic fusion and loss are relevant in determining the phylogenetic homologies of adult bones only if it can reasonably be assumed that the disposition of ossificatory centres is more strongly conserved in phylogeny than is the disposition of skull bones in adults. The extreme form of the fusion hypothesis proposed by Jarvik and Stensiö, in which bones may be partially homologous being derived from some but not all of the same ossificatory centres, is shown to be vacuous, since provided that sufficiently many ancestral ossificatory centres are postulated it can explain any conceivable disposition of bones without risk of refutation.

The homologies between dermal skull-roof bones of the osteolepiform and porolepiform rhipidistian fishes which have been proposed by various authors are shown to be consistent with the assumptions upon which they were based. Whilst the interpretation of dermal skull-roof morphology given by Stensiö and Jarvik is consistent with the hypotheses of sensory canal course constancy and bone fusion, it leads to a nomenclature of dermal bones that is inconvenient for comparative anatomical purposes. The interpretation of dermal skull-roof morphology suggested by Parrington is consistent with the assumptions that the courses of sensory canals may vary and that phylogenetic fusion of bones should not be postulated unnecessarily. It is suggested that this kind of interpretation is preferable both on the theoretical ground that the underlying assumptions are more reasonable, and on the practical ground that the resultant nomenclature of bones is more convenient.

ACKNOWLEDGEMENTS

It is a pleasure to acknowledge the helpful advice and criticism of Dr F. R. Parrington and Miss S. M. Andrews, the help of Mr A. G. Brighton (Sedgwick Museum) and Dr C. D. Waterson (Royal Scottish Museum) who guided me to relevant specimens, and the help of Mrs H. M. Hunt who drew the figures and Mr C. J. Jardine and Mrs B. Radford who helped in the preparation of the manuscript.

Especially I wish to acknowledge my substantial debt to Dr K. A. Joysey who first introduced me to the problems raised by biological homology and suggested the morphology of the rhipidistian skull as a subject for investigation, and who has helped and advised me throughout.

REFERENCES

- ALLIS, E. P., 1898. On the morphology of certain bones of the cheek and snout of *Amia calva*. *J. Morph.*, **14**: 425–476.
- AUMONIER, F. J., 1941. Development of the dermal bones in the skull of *Lepidosteus osseus*. *Q. Jl microsc. Sci.*, **83**: 1–31.
- BADER, R. S., 1958. Similarity and recency of common ancestry. *Syst. Zool.*, **7**: 184–187.
- BERG, L. S. 1940. Classification of fishes, both recent and fossil. *Trudy zool. Inst., Leningr.*, **5**: 87–577. (In Russian.)
- BERG, L. S., 1958. *System der rezenten und fossilen Fischartigen und Fische*. Berlin: Deutscher Verlag.
- BIGELOW, R. S., 1958. Classification and phylogeny. *Syst. Zool.*, **7**: 49–59.
- BIGELOW, R. S., 1961. Higher categories and phylogeny. *Syst. Zool.*, **10**: 86–91.
- BOYDEN, A. R., 1947. Homology and analogy. A critical review of the meanings and implications of these concepts in biology. *Am. Midl. Nat.*, **37**: 648–669.
- BYSTROW, A. P., 1938. *Dvinosaurus* als neotenische Form der Stegocephalen. *Acta. zool., Stockh.*, **19**: 209–295.

- DARWIN, C., 1859. *On the origin of species by means of natural selection*, 1st ed. London: Murray.
- DE BEER, G. R., 1937. *The development of the vertebrate skull*. Oxford University Press.
- DE BEER, G. R., 1958. *Embryos and ancestors*, 3rd ed. London: Oxford University Press.
- GREGORY, W. K., 1951. *Evolution emerging*, Vol. 1. New York: Macmillan.
- HAAS, O. & SIMPSON, G. G., 1946. Analysis of some phylogenetic terms with attempts at redefinition. *Proc. Am. phil. Soc.*, **90**: 319–349.
- HANSON, N. R., 1958. *Patterns of discovery: an inquiry into the conceptual foundations of science*. Cambridge University Press.
- HEMPEL, C. G., 1966. *Philosophy of natural science*. New Jersey: Prentice-Hall.
- HENNIG, W., 1950. *Grundzüge einer Theorie der phylogenetischen Systematik*. Berlin: Deutscher Verlag.
- HEYWOOD, V. H. & MCNEILL, J. (eds), 1964. *Phenetic and phylogenetic classification*. London: Syst. Assoc. Publ. No. 6.
- HUXLEY, T. H., 1877. *A manual of the anatomy of invertebrated animals*. London: Churchill.
- INGER, R. F., 1967. The development of a phylogeny of frogs. *Evolution, Lancaster Pa.*, **21**: 369–384.
- INGLIS, W. G., 1966. The observational basis of homology. *Syst. Zool.*, **15**: 219–228.
- JARDINE, N., 1967. The concept of homology in biology. *Br. J. Phil. Sci.*, **18**: 125–139.
- JARDINE, N., 1969. A logical basis for biological classification. *Syst. Zool.*, **18**: 37–52.
- JARDINE, N. & JARDINE, C. J., 1967. Numerical homology. *Nature, Lond.*, **216**: 301–302.
- JARDINE, N. & JARDINE, C. J., (1969). Is there a concept of homology common to several sciences? *Classification Bulletin*, **2**: 12–18.
- JARVIK, E., 1942. On the structure of the snout of crossopterygians and lower gnathostomes in general. *Zool. Bidr. Upps.*, **21**: 237–675.
- JARVIK, E., 1944. On the dermal bones, sensory canals and pitlines of the skull in *Eusthenopteron foordi* Whiteaves, with some remarks on *E. säve-söderberghi* Jarvik. *K. svenska VetenskAkad. Handl.*, **21**(3): 1–48.
- JARVIK, E., 1948. On the morphology and taxonomy of the Middle Devonian osteolepid fishes of Scotland. *K. svenska VetenskAkad. Handl.*, **25**(1): 1–301.
- JARVIK, E., 1949. Note on the Upper Devonian vertebrate fauna of East Greenland and on the age of the ichthyostegid stegocephalians. *Ark. Zool.*, **41A**(13): 1–8.
- JARVIK, E., 1950 a. Middle Devonian vertebrates from Canning Land and Wegeners Halvö (East Greenland). Part II: Crossopterygii. *Meddr Grönland*, **96**(4): 1–132.
- JARVIK, E., 1950 b. On some osteolepiform crossopterygians from the upper old red sandstone of Scotland. *K. svenska VetenskAkad. Handl.*, **2**(2): 1–35.
- JARVIK, E., 1952. On the fish-like tail in the ichthyostegid stegocephalians. *Meddr Grönland*, **114** (12): 1–90.
- JARVIK, E., 1955. The oldest tetrapods and their forerunners. *Scient. Mon., N. Y.*, **80**: 141–154.
- JARVIK, E., 1960. *Théories de l'évolution des vertébrés*. Paris: Masson.
- JARVIK, E., 1963. The composition of the intermandibular division of the head in fish and tetrapods, and the diphyletic origin of the tetrapod tongue. *K. svenska VetenskAkad. Handl.*, **9**(1): 1–74.
- JARVIK, E., 1966. Remarks on the structure of the snout in *Megalichthys* and certain other rhipidistid crossopterygians. *Ark. Zool.*, **19**(1): 41–98.
- JARVIK, E., 1967. The homologies of frontal and parietal bones in fishes and tetrapods. In *Problèmes actuels de paléontologie, Colloques int. Cent. natn. Rech. Scient.*, **163**: 181–213.
- JESSEN, H., 1966. Die Crossopterygier des Oberen Plattenkalkes (Devon) der Bergisch-Gladbach-Paffrather Mulde (Rheinisches Schiefergebirge) unter Berücksichtigung von amerikanischen und europäischen *Onychodus*-Materiel. *Ark. Zool.*, **18**: 305–389.
- KEY, K. H. L., 1967. Operational homology. *Syst. Zool.*, **16**: 275–276.
- LEKANDER, B., 1949. The sensory line system and the canal bones in the heads of some Ostariophysi. *Acta zool., Stockh.*, **30**: 1–131.
- MASLIN, T. P., 1952. Morphological criteria of phyletic relationships. *Syst. Zool.*, **1**: 49–70.
- MOY-THOMAS, J. A., 1938. The problem of the evolution of the dermal bones in fishes. In De Beer, G. R. (ed.), *Evolution*, pp. 305–319. Oxford: Clarendon Press.
- MOY-THOMAS, J. A., 1939. *Palaeozoic fishes*. London: Methuen.
- MOY-THOMAS, J. A., 1941. Development of the frontal bones of the rainbow trout. *Nature, Lond.*, **147**: 681–682.
- NEAVE, F., 1936. The development of the scales of *Salmo*. *Proc. Trans. R. Soc. Can. (ser. 3)*, **30**(5): 55–71.
- OWEN, R., 1847. Report on the archetype and homologies of the vertebrate skeleton. *Rep. Br. Ass. Advmt Sci.*, (1846), **16**: 169–340.
- OSBORN, H. F., 1893. The rise of the Mammalia in North America. *Proc. Am. Ass. Advmt Sci.*, **42**: 188–227.
- OSBORN, H. F., 1902. Homoplasy as a law of latent or potential homology. *Am. Nat.*, **36**: 259–271.
- 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.
- PARSONS, T. S. & WILLIAMS, E. E., 1963. The relationships of the modern Amphibia. A re-examination. *Q. Rev. Biol.*, **38**: 26–53.
- PEHRSON, T., 1922. Some points in the cranial development of teleostomian fishes. *Acta zool., Stockh.*, **3**: 1–63.
- PEHRSON, T., 1940. The development of dermal bones in the skull of *Amia calva*. *Acta zool., Stockh.*, **21**: 1–50.
- REMANE, A., 1956. *Die Grundlagen des natürlichen Systems, der vergleichenden Anatomie und der Phylogenetik*. Leipzig: Geest and Portig.
- ROMER, A. S., 1941. Notes on the crossopterygian hyomandibular and braincase. *J. Morph.*, **69**: 141–160.
- ROMER, A. S., 1945. *Vertebrate palaeontology*, 2nd ed. University of Chicago Press.
- SALTHER, S. N. & KAPLAN, N. O., 1966. Immunology and rates of enzyme evolution in the Amphibia in relation to the origins of certain taxa. *Evolution, Lancaster, Pa.*, **20**: 603–616.
- SATTLER, R., 1966. Towards a more adequate approach to comparative morphology. *Phytomorphology*, **16**: 417–429.
- SATTLER, R., 1967. Petal inception and the problem of pattern recognition. *J. theoret. Biol.*, **17**: 3–39.
- SÄVE-SÖDERBERGH, G., 1933. The dermal bones of the head and the lateral line system in *Osteolepis macrolepidotus* Ag., with remarks on the terminology of the lateral line system and on the dermal bones in certain other crossopterygians. *Nova Acta R. Soc. Scient. upsal.* (ser. 4), **9**(2): 1–123.
- SÄVE-SÖDERBERGH, G., 1935. On the dermal bones of the head in labyrinthodont stegocephalians and primitive Reptilia with special reference to Eotriassic stegocephalians from East Greenland. *Meddr Grönland*, **98**(3): 1–211.
- SÄVE-SÖDERBERGH, G., 1941. Notes on the dermal bones of the head in *Osteolepis macrolepidotus* Ag. and the interpretation of the lateral line system in certain primitive vertebrates. *Zool. Bidr. Upps.*, **20**: 523–541.
- SCHAEFFER, B., 1965. The rhipidistian amphibian transition. *Am. Zool.*, **5**: 267–276.
- SIMPSON, G. G., 1961. *Principles of animal taxonomy*. New York: Columbia University Press.
- SNEATH, P. H. A., 1967. Trend-surface analysis of transformation grids. *J. Zool., Lond.*, **151**: 65–122.
- SNEATH, P. H. A. (1969). Homology in geology and some related sciences. *Classification Bulletin*, **2**: 5–11.
- SOKAL, R. R. & SNEATH, P. H. A., 1963. *Principles of numerical taxonomy*. San Francisco and London: Freeman.
- STENSIÖ, E. A., 1921. *Triassic fishes from Spitzbergen*, Part I. Vienna: Adolf Holzhausen.
- STENSIÖ, E. A., 1922. Notes on certain crossopterygians. *Proc. zool. Soc. Lond.*, **1922**(2): 1241–1271.
- STENSIÖ, E. A., 1947. The sensory lines and dermal bones of the cheek in fishes and amphibians. *K. svenska VetenskAkad. Handl.*, **24**(3): 1–194.
- STENSIÖ, E. A., 1963. The brain and cranial nerves in fossil lower craniate vertebrates. *Skr. norske VidenskAkad.*, (N.S.), **13**: 5–120.
- SZARSKI, H., 1962. The origin of the Amphibia. *Q. Rev. Biol.*, **37**: 189–241.
- TAIT, J., 1928. Homology, analogy and plasis. *Q. Rev. Biol.*, **3**: 151–173.
- THOMPSON, D'A. W., 1942. *On growth and form*, 2nd ed. Cambridge University Press.
- THOMSON, K. S., 1962. Rhipidistian classification in relation to the origin of the tetrapods. *Breviora*, **177**: 1–12.
- THOMSON, K. S., 1964a. The ancestry of the tetrapods. *Sci. Prog., Lond.*, **52**: 451–459.
- THOMSON, K. S., 1964b. The comparative anatomy of the snout in rhipidistian fishes. *Bull. Mus. comp. Zool. Harv.*, **131**: 313–357.
- THOMSON, K. S., 1966. *Glyptolepis* from the Middle Devonian of Scotland. *Postilla*, **99**: 1–10.
- THOMSON, K. S., 1967a. Mechanisms of intercranial kinetics in fossil rhipidistian fishes (Crossopterygii) and their relatives. *J. Linn. Soc. (Zool.)*, **46**: 223–253.
- THOMSON, K. S., 1967b. Notes on the relationship of the rhipidistian fishes and the ancestry of the tetrapods. *J. Paleont.*, **41**: 660–674.
- THROCKMORTON, L. H., 1962. The problem of phylogeny in the genus *Drosophila*. *Studies in Genetics II. Univ. Tex. Publs*, **6205**: 207–343.
- THROCKMORTON, L. H., 1965. Similarity versus relationship in *Drosophila*. *Syst. Zool.*, **14**: 221–236.
- VOROBYEVA, E. I. & OBRUCHEV, D. V., 1967. In Obruchev, D. V. (ed.), *Fundamentals of palaeontology: a manual for the use of palaeontologists and geologists of the USSR*. Vol. 2, *Agnatha, Pisces*. Transl. from the Russian. Jerusalem: Israel Program for Scientific Translations.
- WATSON, D. M. S., 1921. On the coelacanth fish. *Ann. Mag. nat. Hist.* (ser. 9), **8**: 320–337.
- WEITZMAN, S. H., 1962. The osteology of *Brycon meeki*, a generalized characid fish, with an osteological definition of the family. *Stanford ichthyol. Bull.*, **8**(1): 1–77.
- WESTOLL, T. S., 1936. On the structures of the dermalethmoid shield of *Osteolepis*. *Geol. Mag.*, **73**: 157–171.
- WESTOLL, T. S., 1937a. On the cheek-bones in teleostome fishes. *J. Anat.*, **71**: 362–382.
- WESTOLL, T. S., 1937b. 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., 1943. The origin of the tetrapods. *Biol. Rev.*, **18**: 78-98.
- WESTOLL, T. S., 1944. The Haplolepididae, a new family of late Carboniferous bony fishes. A study in taxonomy and evolution. *Bull. Am. Mus. nat. Hist.*, **83**: 1-120.
- WESTOLL, T. S., 1949. On the evolution of the Dipnoi. In Jepson, G. L., Mayr, E. and Simpson, G. G. (eds), *Genetics, palaeontology, and evolution*, pp. 121-184. Princeton University Press.
- WHITE, E. I., 1965. The head of *Dipterus valenciennesi* Sedgwick & Murchison. *Bull. Br. Mus. nat. Hist. (Geol.)*, **11**: 1-45.
- WOODGER, J. H., 1937. *The axiomatic method in biology*. Cambridge University Press.
- WOODGER, J. H., 1945. On biological transformations. In Clark, W. E. Le Gros and Medawar, P. B. (eds), *Essays on growth and form*, pp. 95-120. Oxford: Clarendon Press.
- ZANGERL, R., 1948. The methods of comparative anatomy and its contribution to the study of evolution. *Evolution, Lancaster, Pa.*, **2**: 351-374.