

LUNGFISHES, TETRAPODS,
PALEONTOLOGY, AND
PLESIOMORPHY

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ABSTRACT

We conclude that the internal (excurrent) nostril of Recent lungfishes is a true choana, as judged by its comparison with (1) the internal nostril of a Devonian lungfish species which opens through the bony palate internal to an arcade of maxillary and premaxillary teeth; (2) the choana of the Devonian ichthyostegid amphibians, and (3) nostril development in Recent urodeles. The idea that lungfishes might therefore be the sister group of tetrapods is compared with the competing, deeply entrenched theory that rhipidistian fishes and eusthenopterids in particular include the ancestor of tetrapods. Our own theory, derived from study of Recent and fossil material, and an analysis of literature spanning 140 years, is framed in the context of a classification of the main groups of fossil and living gnathostomes: acanthodians, chondrichthyans, cladistians, actinopterygians, rhipidistians, actinistians, dipnoans, and tetrapods. In formulating our proposal we have reviewed the anatomy of the nasal capsule, nostrils and related structures, paired fins and their girdles, dermal bones of the skull, palate and jaw suspension, hyoid and gill arches, ribs and vertebrae, and scale and tooth structure. We

hypothesize, in agreement with most nineteenth- and many twentieth-century biologists, and in disagreement with the current paleontological view, that lungfishes are the sister group of tetrapods, and further that actinistians are the sister group of those two, and that *Eusthenopteron* is the sister group of those three. We also conclude that the characters used formerly to link *Eusthenopteron* with tetrapods either (1) are primitive for all bony fishes (including cladistians and actinopterygians) or for living gnathostomes (including chondrichthyans); (2) are convergent with those of several groups of gnathostomes; (3) only justify the inclusion of *Eusthenopteron* in a group with actinistians, dipnoans and tetrapods; or (4) are spurious. We attribute the century of confusion about the structure and position of lungfishes to the traditional paleontological preoccupation with the search for ancestors, to the interpretation of *Eusthenopteron* in the light of tetrapods and the reciprocal interpretation of fossil amphibians in the light of *Eusthenopteron*, and to the paleontological predilection for using plesiomorphous characters to formulate schemes of relationships.

“The convictions of our palaeontological colleagues are very real to them, and under the drive of these convictions they have quite honestly contended for their theories. The colour-blind man sees the scarlet robe and the green lawn the same colour, to him they *are* the same colour, but he is wrong.”

Kesteven, 1950, p. 99

INTRODUCTION

Miles's (1977) descriptions and illustrations of the head of the Devonian lungfish, *Griphognathus*, caused the independent realization in London (BGG) and New York (DER) that the internal nostrils of lungfishes are true choanae. This conviction meant to us that the only synapomorphy of Miles's (1977, p. 316) Choanata (tetrapods and rhipidistians; cf. Gaffney, 1979b, p. 93) is also present in lungfishes. It also meant to us that Allis's (1919, 1932a, 1932b) arguments for rejecting the internal lungfish naris as a choana, based partly on the interpretation of certain folds of soft tissue as primary, secondary, and tertiary upper lips, might be faulty. With the idea of reviewing the struc-

ture of the two outermost lip folds discussed by Allis, our attention was drawn to a large opening in the outermost fold of *Neoceratodus* near the corner of the mouth that was first described by Günther (1871, p. 515): “At the angle of the mouth, and hidden below a duplicature of the skin, there is an opening wide enough to admit an ordinary quill (pl. XXX, fig. 2, a); it leads into a spacious cavity (b), irregular in shape, clothed with a mucous membrane, and containing coagulated mucous in which an immense number of mucous corpuscles are deposited. This cavity is separated from the cavity of the mouth by the membrana mucosa only, and there is no direct communication be-

tween them; a branch cavity runs forward into the interior of the upper lip."

The extent of this rostral structure, which Günther called the labial cavity, is from the anterior wall of the orbit forward to the anterolateral part of the nasal capsule (fig. 18). It is subtriangular, narrow anteriorly near the nasal capsule and wider posteriorly in front of the orbit where the internal wall of the cavity is thrown into a series of folds. The opening of the labial cavity to the outside is through a short and broad tube that leads directly to the pore in the outermost accessory lip (fig. 19). Visual examination of the same region of the snout in premetamorphic *Neoceratodus* of about 2 cm. in total length (prior to development of pelvic fins) revealed neither a pore nor a labial cavity, but, in larger young, serial sections show these structures (fig. 20). The presence in larger young and adults of an apparently mucous-secreting organ extending between the nasal capsule and the orbit and its opening to the outside on the side of the head not far in front of the eye, and its absence in premetamorphic young, suggested to us the anatomical relations and ontogenetic history of the nasolacrimal organ of living amphibians.

These two kinds of observations, and their interpretations, that dipnoans may have a choana and nasolacrimal structure synapomorphic with such features in tetrapods, caused us to look critically at the dipnoans, and also the rhipidistians, Paleozoic fishes now universally regarded as the closest relatives of tetrapods. In searching for synapomorphies that would justify the latter opinion, we have also reviewed the interrelationships of the main groups of fossil and living gnathostomes.

Schaeffer (1965, p. 115), discussing the history of ideas about tetrapod origins, wrote that Cope (1892) "broke through the 'dipnoan barrier.'" By "dipnoan barrier," Schaeffer meant the late nineteenth-century view that dipnoans are the closest relatives ("nearest allies"—Huxley, 1876, p. 56) of tetrapods. Cope and his successors have succeeded so well that our problem has been to break through the "rhipidistian barrier," today's unquestioned doctrine that rhipidis-

tians, and osteolepiforms in particular, are the closest relatives, or direct ancestors, of tetrapods. This doctrine is so pervasive that a researcher seeking the primitive tetrapod condition of some structure turns automatically to the rhipidistians, usually to *Eusthenopteron*, forgetting that *Eusthenopteron* has been interpreted in the light of tetrapods and that tetrapods have been interpreted in the reciprocal light of *Eusthenopteron*. Our assault on the "rhipidistian barrier" begins with an account of the history of opinion on lungfishes, tetrapods, rhipidistians and other crossopterygian fishes. We believe that this account shows that current beliefs about rhipidistians have grown up among a thicket of preconceptions and wishful thinking, especially the belief that processes can be demonstrated in the fossil record. To give one classic example, Watson, in his Croonian lecture on amphibian origins, wrote (1926, p. 189) "It is possible to view the problem as one of purely formal morphology, the establishment of a series of stages which show intermediates between typical fish structures and those of the homologous organs in Amphibia. . . . But such studies . . . are now satisfying to few men: the centre of interest has passed from structure to function, and it is in the attempt to understand the process by which the animal's mechanism was so profoundly modified . . . that the attraction of the problem lies." Watson emphasized process both in morphology ("establishment of . . . intermediates") and in "the attempt to understand the process" through which morphology is modified. Our approach is simpler. It rests on the assumption that morphological pattern must be recognized before one can speculate about process.

We have accepted a number of assumptions or axioms. First, that tetrapods are monophyletic. Gaffney (1979a) listed 11 synapomorphies which characterize living and fossil tetrapods as a monophyletic group. Four of these also occur in lungfishes (Gaffney's numbers 1, 8, 10, and 11: absence of intracranial joint; pectoral girdle not joined to skull; pelvic girdle with well-developed ischiac ramus and pubic symphysis; well-developed, ventrally directed ribs), but we re-

gard the remainder, especially the carpus, tarsus, and dactyly as uncontradicted evidence of tetrapod monophyly.

Second, we accept Gaffney's (1979a) characterization of *Ichthyostega* as the sister group of the remaining tetrapods (Gaffney's Neotetrapoda). He listed five synapomorphies which distinguish all neotetrapods¹ from *Ichthyostega*, and we accept all those but the last (ethmosphenoid and otico-occipital portions of braincase not separated by suture), preferring to wait until the reputed division in the braincase of *Ichthyostega* is described. Accepting *Ichthyostega* as the sister group of all other tetrapods, we turn to it in seeking primitive tetrapod conditions in the skull roof, nostrils, etc. But there are many structures which are still unknown in ichthyostegids (e.g., manus, braincase, details of vertebral column and course of sensory canals, all soft parts), and we have to look elsewhere for information on primitive tetrapod conditions. At present, there is no acceptable phylogeny of tetrapods (see Løvtrup, 1977, p. 176; Gaffney, 1979a, 1979b; Carroll and Holmes, 1980). Lack of such a phylogeny leaves us three alternatives: to follow Gaffney (1979b) in regarding lepospondyls as the sister group of other tetrapods; or to survey Paleozoic "amphibians" and select what appear to be primitive conditions; or to select a living tetrapod group. In any case our selection could be justified only by outgroup comparison, i.e., comparison with non-tetrapod groups, and would therefore depend on a previous solution to the problem we are trying to solve. Of course, all previous attempts to solve that problem have depended on similar though rarely acknowledged circular arguments. Whichever alternative we choose we can be

accused of bias, but since most previous discussions of the problem have relied largely on one or another Paleozoic amphibian, we shall select a living group, the urodeles. As is well known (Kerr, 1932; Holmgren, 1933, 1949a, 1949b; Kesteven, 1950; Lehman, 1956; Fox, 1965), urodeles share many features of soft anatomy with lungfishes. Our selection of urodeles as primitive tetrapods means that we rate these features as synapomorphies of choanates, sympletiomorphies of tetrapods.

Third, rhipidistians are not a monophyletic group, so that no unique statements can be made about their structure. So far as we know, the same is true of osteolepiforms. This means that osteolepiforms have to be treated as a series of nominal taxa, among which *Eusthenopteron foordi* Whiteaves is most completely known, and is selected for discussion. The porolepiforms are united by one derived character, dendrodont tooth structure (Schultze, 1970a), known in *Porolepis*, *Glyptolepis*, *Holoptychius*, and *Laccognathus*. On the basis of this one synapomorphy, we regard the group as monophyletic.

Fourth, Dipnoi are monophyletic. The form of the snout and dentition (radiate toothplates or marginal tooth ridges—Miles, 1977, p. 288) are synapomorphies of all those Recent and well-preserved fossil fishes currently placed in the Dipnoi. Whether other Paleozoic fishes, such as *Powichthys* (Jessen, 1975), are dipnoans we cannot say.

Fifth, osteichthyans are monophyletic, and their sister group is the Chondrichthyes. Sixth, actinopterygians are monophyletic, and include the Chondrostei and Neopterygii; seventh, the Cladistia (= Brachiopterygii; *Polypterus* and *Erpetoichthys*) are monophyletic; and, eighth, actinistians (coelacanth) also are monophyletic.

Finally, almost every topic discussed in this paper is already embedded in deposits of theory and interpretation—vertebral theory of the skull, fin-fold theory, gill-arch contributions to the skull and forelimb skeleton, bone fusion versus bone loss, constancy of bone/sensory canal relationships, and so on. In dealing with these topics, we do not claim

¹ We do not, however, endorse the use of Gaffney's term Neotetrapoda, or any other named taxon for Recent organisms formulated for, or because of, the cladistic position of a fossil; elsewhere (Patterson and Rosen, 1977) reasons were advanced for believing that allowing fossils to affect the taxonomic structure of classifications of extant organisms is inevitably self-defeating.

to have eyes unclouded by theory. But we have tried to be guided by one principle, that agreed interpretations of soft parts are only attainable among living animals, and that the

only changes in anatomical relationships that are demonstrable are those which occur in the ontogeny of one or another living species.

HISTORICAL SURVEY

When living lungfishes were first discovered, lepidosirenids (Fitzinger, 1837; Natterer, 1837) and neoceratodontids (Krefft, 1870) were both recognized as amphibians. The purpose of this review is to map the path from those first thoughts to recent opinions such as that found in today's textbooks, that lungfishes are more remote from amphibians than are coelacanth, or those of von Wahlert (1968) and Bjerring (1977), that lungfishes are more remote from amphibians than are actinopterygians, or of Jarvik (1968a), that they may be chondrichthyans.

Lungfishes are now universally regarded as fishes (Kesteven, 1950, was the most recent exception), but in the middle of the nineteenth century there was a controversy over the class of vertebrates to which they belonged. The first detailed account of *Lepidosiren* was Bischoff's (1840a, 1840b). He agreed with Fitzinger that the animal was an amphibian, and since several zoologists disagreed, judging it to be a fish, Bischoff gave the reasons for his belief in full (table 1).

Løvtrup (1977, p. 43), in his axiomatization of phylogenetics, gave as one theorem "If, in a basic [i.e., three-taxon] classification, one . . . taxon has several characters in common with both of the other taxa, then one of the two sets of characters will represent the presence of plesiotypic characters absent, and/or the absence of teleotypic [i.e., apomorphic] characters present, in the third taxon." If the three taxa were *Lepidosiren*, a salmon and a cow, we see that in table 1 the four salmon-like characters (fishlike, nos. 1, 2, 4, 5) consist of three primitive characters absent in cows (1, 2, 4) and one derived character (5) absent in fishes, as Løvtrup's theorem predicts.

While Bischoff's work was in press, Owen (1839) published a preliminary account of the

African *Protopterus*, followed by a detailed account in 1841. Owen was the first (1839, p. 331) to notice the resemblance between Recent lungfish toothplates and the Mesozoic *Ceratodus* Agassiz (1838). Owen disagreed with Fitzinger's and Bischoff's opinion that lungfishes were amphibians and differed from Bischoff on two particulars, the auricle and internal nostril, finding both the auricle and nostril to be single. He gave an interesting and thorough discussion of the systematic position of *Protopterus*, considering every system of the body in a search for the essential character that distinguishes fishes from tetrapods. After surveying the skeleton and the respiratory, digestive, reproductive, and nervous systems Owen concluded that none of these is essentially different in fishes and tetrapods, and wrote (1841, p. 352) "In the organ of smell we have, at last, a character which is absolute in reference to the distinction of Fishes from Reptiles. In every Fish it is a short sac communicating with the external surface; in every Reptile it is a canal with both an external and an internal opening. According to this test, the *Lepidosiren* is a Fish: by its nose it is known not to be a Reptile . . . so that at the close of our analysis we arrive at this very unexpected result, that a Reptile is not characterized by its lungs, nor a Fish by its gills, but that the only unexceptionable distinction is afforded by the organ of smell."

Having seen Owen's 1839 paper, Bischoff added a supplement to his own, commenting on the differences between his own observations and Owen's. In particular he reiterated his opinion on the divided auricle and the internal nostril. Milne Edwards (1840) added some remarks to the French translation of Bischoff's paper, pointing out that dissection of a Paris specimen of *Protopterus*

TABLE 1
Characters of *Lepidosiren paradoxa*
(From Bischoff, 1840b, pp. 144–151)

| Fishlike | Amphibian-like |
|---|---|
| 1. Scales | 1. Internal nostril |
| 2. Sensory canals | 2. Large paired lungs, connected with the oesophagus by a large glottis |
| 3. No ossified vertebrae, and notochord penetrating base of cranium | 3. Gills much reduced, most blood bypasses them |
| 4. Opercular bones | 4. Heart with two auricles, one receiving blood from lungs |
| 5. No external ear | 5. Conus with two valves which separate the pulmonary and branchial blood |
| 6. Labial and nasal cartilages | |

confirmed Bischoff’s observation of a divided auricle and internal nostrils.

In this first exchange in the controversy, we see Bischoff correctly interpreting synapomorphies, and Owen basing his opinion partly on a mistaken observation, and partly on primitive characters. Owen never (e.g., 1846, p. 256; 1866, p. 474) agreed that the auricle was divided in lungfishes. He later (e.g., 1846, p. 201) allowed that there were two nostrils, but argued that neither opened into the mouth. This first exchange set the pattern for the next 20 years. Those workers who believed lungfishes to be amphibians (Milne Edwards, 1840; Hogg, 1841; Heckel, 1845; Melville, 1848, 1860; Vogt, 1845, 1851; Asmuss, 1856; Gray, 1856) relied on the same characters as Bischoff, and included those who had observed living animals (Gray, Melville). Those who put lungfishes among fishes (Müller, 1840, 1844; Oken, 1841; Fitzinger, 1843—a change of mind; Agassiz, 1843; Hyrtl, 1845; Newman, 1857; and others—see Duméril, 1870) were, when they gave reasons, weighting primitive characters.

A third viewpoint was possible, that it was futile to search for an essential distinction between fishes and amphibians. Heckel (1851) took this view, as did M’Donnell (1860, p. 18) in these words: “our present knowledge . . . leads us to regard it [*Protopterus*] as a form so transitional as to support the view taken by some systematizing zoologists in later days, that no distinctly defined line of demarcation exists between

Fishes and Reptiles . . . an order uniting fishes with the amphibian reptiles, seems to be the true mode of giving it its proper place.” By “systematizing zoologists” M’Donnell might have been referring to Owen (1859), who named a group *Haemacrymes* for cold-blooded vertebrates (equivalent to his 1866 *Haematocrya*) and wrote that within this group “*Archegosaurus* conducts the march of development from the fish-proper to the Labyrinthodont type: the *Lepidosiren* conducts it to the perennibranchiate batrachian type.” Or M’Donnell might have been referring to Darwin and Wallace. In either case, such views as his were readily adapted to the evolutionary doctrine, and in Haeckel’s first trees (1866) the Dipnoi are placed as the sister group of the tetrapods, with a line of “Dipnoi ignoti” extending back into the Devonian. In Haeckel’s later versions (e.g., fig. 1) lungfishes are placed as the direct ancestors of tetrapods. Thus with acceptance of evolution, the problem of distinguishing tetrapods from fishes, i.e., the problem of characterizing tetrapods, disappeared, since difficulties in distinguishing the two groups were agreeable to evolutionists.

In 1870, Krefft announced the discovery of *Neoceratodus*, “a gigantic Amphibian.” As with the lepidosirenids a third of a century before, such opinions found no support in the British Museum, where Günther wrote the first detailed account of *Neoceratodus* (1871). Before reviewing Günther’s conclusions, it is worth recalling that he was, like most of the senior naturalists in the British

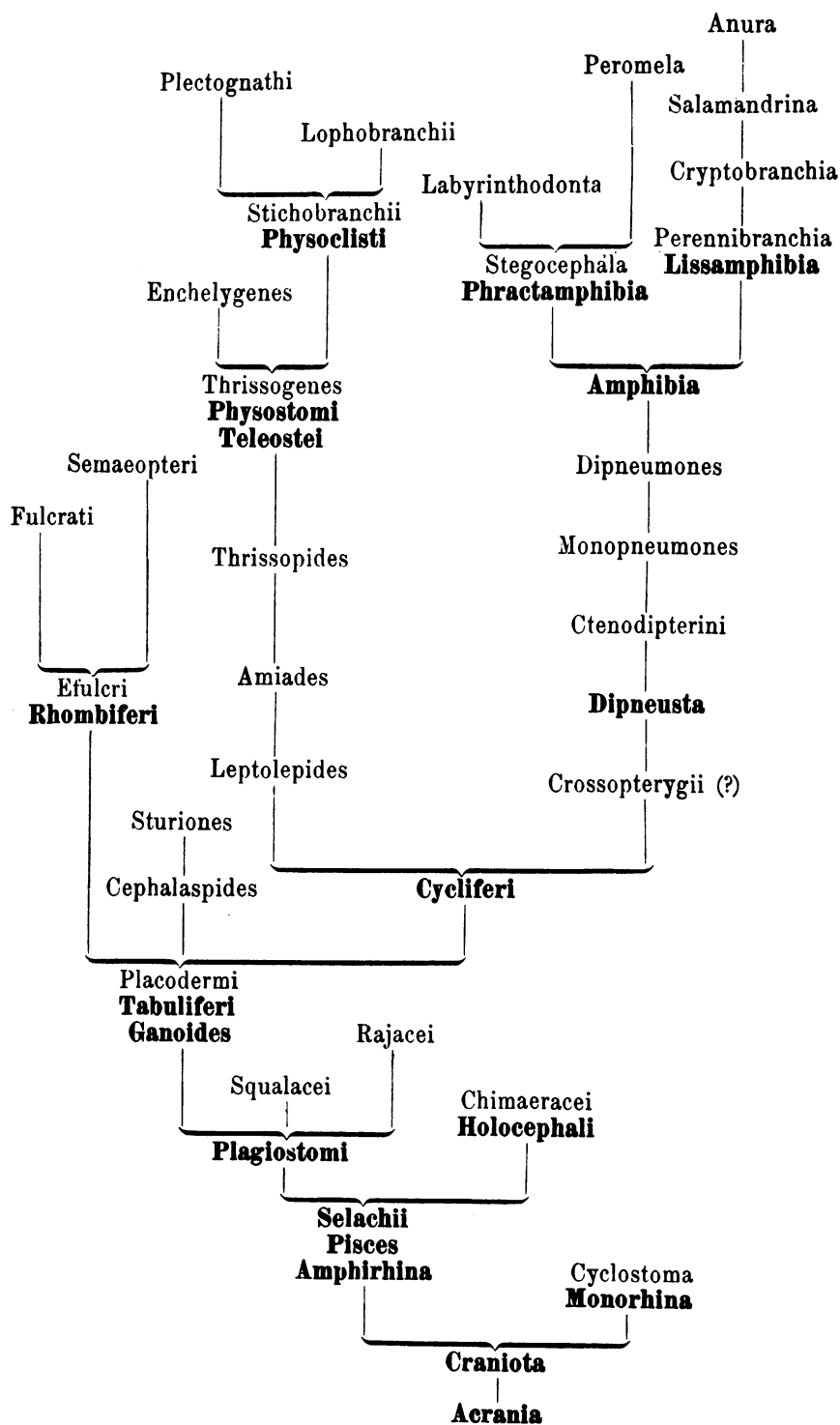


FIG. 1. Phylogeny of lower vertebrates, from Haeckel (1889, p. 613).

Museum at that time, an opponent of evolution. Günther's most recent biographer remarks that in the memoir on *Neoceratodus* he "had taken the opportunity to trail his coat before the evolutionists" (A. E. Günther, 1975, p. 335).

Günther (1871) found that *Neoceratodus* was less amphibian-like than the lepidosirenids, since it had ganoid valves in the conus, a single lung, well-developed gills, and so on. Concerning the nostrils of lungfishes, it would be hard to find a better illustration of the idea that all observation is theory-laden than the contrast between Günther's view (1871, p. 517) that both the anterior and posterior nostrils open inside the mouth, and Owen's (1866, p. 329) that neither opens within the mouth. Günther concluded that lungfishes were ganoid fishes, and named a new subclass Palaeichthyes to include all fishes except teleosts. Günther was the first to realize that Paleozoic fishes such as *Dipterus* and *Phaneropleuron*, included by Huxley (1861) in his Crossopterygii, were lungfishes. Although his discovery carried the dipnoans back into the Devonian, as Haeckel's trees demanded, Günther saw this not as evidence of evolution, but as "a proof of the incompleteness of the palaeontological record" and as "the most remarkable example of persistence of organization, not in Fishes only, but in Vertebrates."

Huxley, through whose Crossopterygii Günther had trailed his coat, replied in 1876. He distinguished autostylic, hyostylic, and amphistylic skulls, showed that lungfishes had the same autostyly as amphibians, and discussed the paired fins of *Neoceratodus* as forerunners of tetrapod limbs. On classification, he argued against Günther's Palaeichthyes, and for Müller's original (1844) groups (Dipnoi, Ganoidei, etc.). Huxley maintained that Dipnoi are the "nearest allies of the Amphibia" (p. 56), whereas in 1861 (p. 27) he had argued that they are "next of kin" to the crossopterygian ganoids. This ambiguity was not cleared up in Huxley's next contribution (1880). There he wrote of *Neoceratodus* (p. 660), "This wonderful creature seems contrived for the illustration of the doctrine of Evolution. Equally

good arguments might be adduced for the assertion that it is an amphibian or a fish, or both, or neither." In this paper, Huxley proposed the names Chondrichthyes and Osteichthyes, but included in the latter only the ganoids and teleosts, placing dipnoans in a group Herpetichthyes named "for that particular stage of vertebrate evolution of which both the typical Fishes and the typical Amphibia are special modifications." Huxley's diagram seems to imply that he regarded the crossopterygians as descendants of dipnoan-like fishes. Thus, in contrast to Günther, Huxley sought to blend lungfishes with both crossopterygians and tetrapods.

Similar uncertainties about the status, and content, of the Crossopterygii are evident in the publications of other workers during this period (see Schaeffer's 1965 review). For example, Gill (1872; pp. xxxii, xliii) had the crossopterygians as the sister group of coelacanth in one of his genealogical trees, and as the sister group of actinopterygians, with a question mark, in the other (our fig. 2); Haeckel's question mark against the crossopterygians in figure 1 is also symptomatic. Cope (1872, 1885, 1887, 1892) vacillated on the content of the Crossopterygii [Woodward (1891, p. xxii), whose *Catalogue* stabilized things, complained of "the somewhat fluctuating classifications of Cope"]. In 1887 Cope removed the Rhipidistia (Tristichopteridae) and Actinistia (Coelacanthidae) from the Crossopterygii, leaving in the latter only the Holoptychiidae, Osteolepididae, Polypteridae, and *Phaneropleuron* (a dipnoan that he had formerly excluded). By 1892 the holoptychiids and osteolepids had also joined the rhipidistians and actinistians, leaving the polypterids as the only crossopterygians.

A passage from Cope's 1892 paper is cited by Schaeffer (1965, p. 115) as the source of "our present understanding of amphibian origin." Like Gill, Huxley, Haeckel, and other evolutionists of this period, Cope had previously believed that tetrapods were descended from dipnoans (e.g., Cope, 1884, p. 1256, "The Batrachia have originated from the sub-class of fishes, the Dipnoi, though not from any known form"). But in 1892 he emphasized the lack of the maxillary arch in

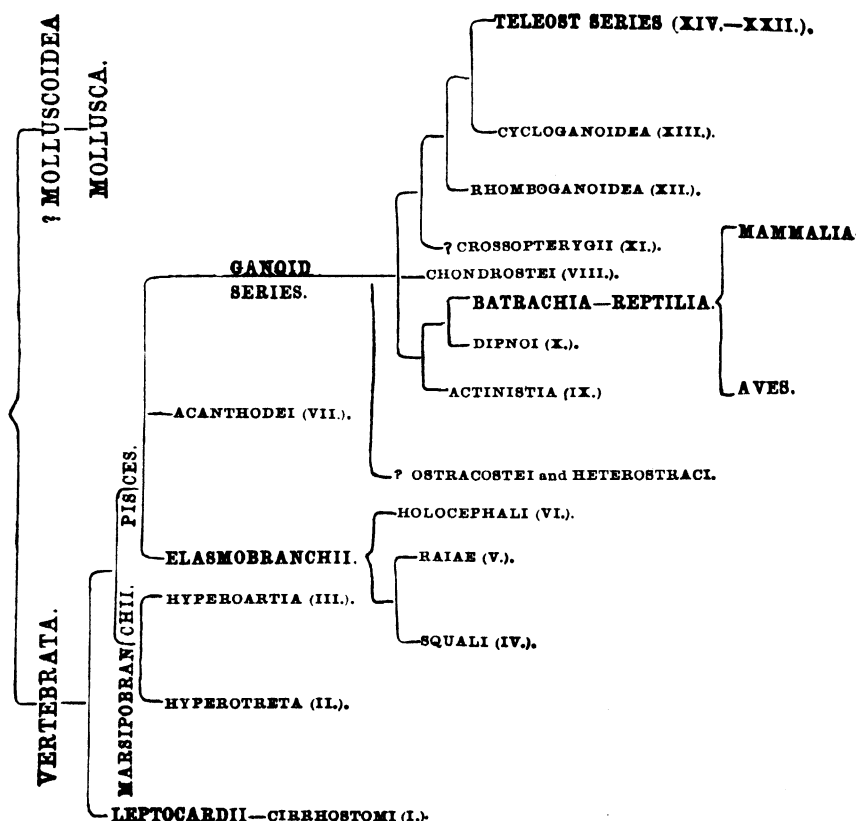


FIG. 2. A genealogical tree of the relations of major groups of vertebrates, from Gill (1872, p. xliii).

Dipnoi, their large dorsal and anal fins, and the fact that autostyly developed during ontogeny in amphibians, and concluded that amphibians therefore originated from a hyostylic fish with a complete maxillary arch, feeble median fins, and amphibian-like paired fins. The rhipidistians, and *Eusthenopteron* in particular, were offered as such fishes.

Pollard's (1891, 1892) papers on *Polypterus* are a forthright attack on dipnoan-tetrapod relationships. He argued that *Polypterus* resembles the urodeles in features of the inner ear, braincase, palate, musculature, nerves and ribs, and concluded that "the ancestry of the Urodela must be sought among the Crossopterygian forms now represented only by *Polypterus* and *Calamoichthys*"

(1891, p. 341). Pollard also asserted that the posterior nares of dipnoans are not homologous with the choanae of urodeles. Kingsley (1892) argued in the same vein, that since autostyly developed during ontogeny in urodeles, they could not be descended from dipnoans. Baur (1896) reached similar conclusions from a study of labyrinthodonts, and was the first to suggest (p. 670) that the resemblances between dipnoans and amphibians are merely parallelisms.

Dollo (1896) produced the first detailed phylogeny of dipnoans, and summarized earlier work on the interrelationships of dipnoans, crossopterygians, and tetrapods. He expressed his conclusions in a diagram (fig. 3) which places the dipnoans as the sister group of tetrapods, and crossopterygians as

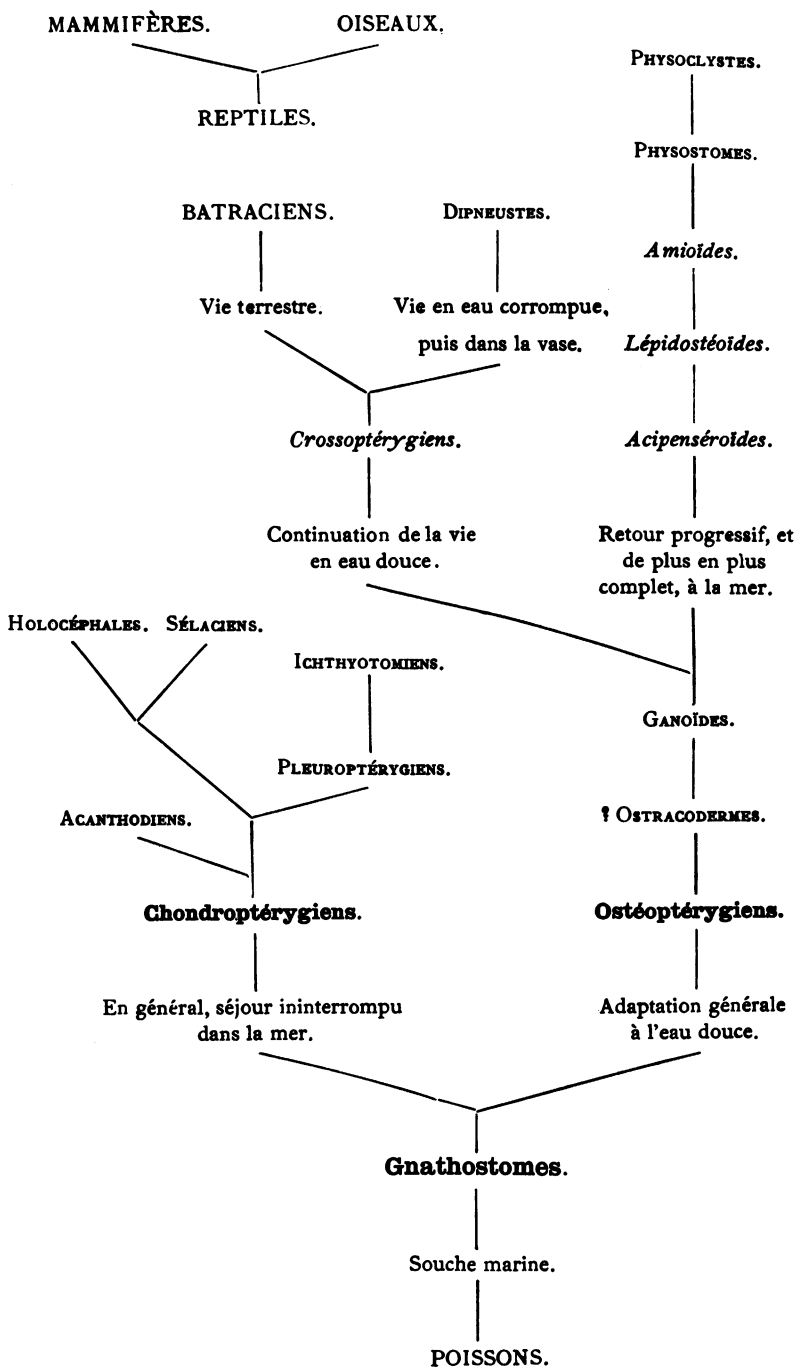


FIG. 3. Phylogeny of gnathostome vertebrates, from Dollo (1896, p. 113).

the group ancestral to both. This was the generally accepted scheme for the next 40 years, though with many variants. Thus, by the end of the nineteenth century, the dipnoan ancestry of tetrapods favored by early evolutionists (fig. 1) had been replaced by a crossopterygian ancestry (fig. 3). In cladistic terms, figure 3 implies that dipnoans are the sister group of tetrapods (i.e., those two groups share synapomorphies), whereas the crossopterygians are a paraphyletic group, some members of which share synapomorphies with dipnoans and tetrapods, but whose relationships are yet to be worked out. Of course, we find nothing to quarrel with in that statement. It is worth summarizing the evidence so far produced to cause the conceptual change from figure 1 to figure 3: the following characters were used by late nineteenth-century biologists to relate tetrapods, dipnoans, and crossopterygians in the way shown in figure 3:

I. Characters excluding dipnoans from tetrapod ancestry

1. Dentition too specialized (Boas, 1882, p. 557: cf. Miles, 1977, fig. 157—the tooth plates are a synapomorphy of higher dipnoans)
2. No maxillary arch (Cope, 1892: for our view see p. 180)
3. Autostyly develops during ontogeny in amphibians (Cope, 1892; Kingsley, 1892)
4. Ribs not homologous in dipnoans and tetrapods (Pollard, 1892; Baur, 1896: for our view see p. 242)

II. Characters relating crossopterygians to tetrapods

1. Large maxilla, dentition not modified (Cope, 1892; Pollard, 1892: cf. actinopterygians—a synapomorphy of osteichthyans?)
2. Hyostyly (Cope, 1892: cf. sharks—a synapomorphy of gnathostomes?)
3. Most of the bones can be homologized in *Polypterus*, fossil crossopterygians and labyrinthodonts (Pollard, 1892; Baur, 1896; Woodward, 1898, p. 123—for our view see p. 221, 227)
4. Many sclerotic plates in fossil crossopterygians and tetrapods (Woodward, 1898, p. 123—a synapomorphy of sarcopterygians: cf. Miles, 1977, p. 249)
5. Pineal foramen present in fossil crossop-

terygians and labyrinthodonts (Woodward, 1898, p. 123—a synapomorphy of bony vertebrates)

6. Paired fins of *Eusthenopteron* more like tetrapod limbs than are those of dipnoans (Cope, 1892; for our view see p. 209)
7. *Polypterus* has dorsal ribs (Pollard, 1892; Baur, 1896: for our view see p. 242)
8. Fossil crossopterygians and labyrinthodonts have an infradentary (splenial) in the mandible (Woodward, 1898, p. 123—so have all non-actinopterygian osteichthyans)
9. The median fins are reduced in Paleozoic crossopterygians (Cope, 1892; Baur, 1896: no comment necessary)
10. Fossil crossopterygians and labyrinthodonts have folded teeth

As is clear from the above list, the characters so far offered in support of the relationship between crossopterygians and tetrapods were a melange of primitive characters, characters of *Polypterus* alone, and vague assertions about Paleozoic crossopterygians. Concerning fin structure, Goodrich's (1901) account of the pelvic fin and girdle ends with the statements that *Polypterus* "probably belongs to the actinopterygian line" and that *Eusthenopteron* is "very far removed from *Polypterus*."

Nevertheless, the belief that the Crossopterygii, containing polypterids and rhipidistians, was a natural group, and that this group gave rise to the tetrapods, continued to gain strength. Since *Polypterus* lacks many of the derived features in which dipnoans agree with tetrapods, it followed that these dipnoan/tetrapod similarities must have arisen in parallel, as Baur (1896) had realized. This was acceptable to some (e.g., Boulenger, 1901, p. 30; Bridge, 1904, p. 520), but not to others (e.g., Semon, 1901, who listed more than 20 resemblances between dipnoans and amphibians; Jordan, 1905, p. 600; Goodrich, 1909, p. 230). Goodrich (1909) believed that dipnoans "present many striking points of resemblance to the Amphibia, which cannot all be put down to convergence." In his phylogenetic diagram (p. 29) Goodrich reverted to an unfashionable view in placing dipnoans as the sister group of teleostome fishes, with the tetrapods entered, with a query, as a tri-

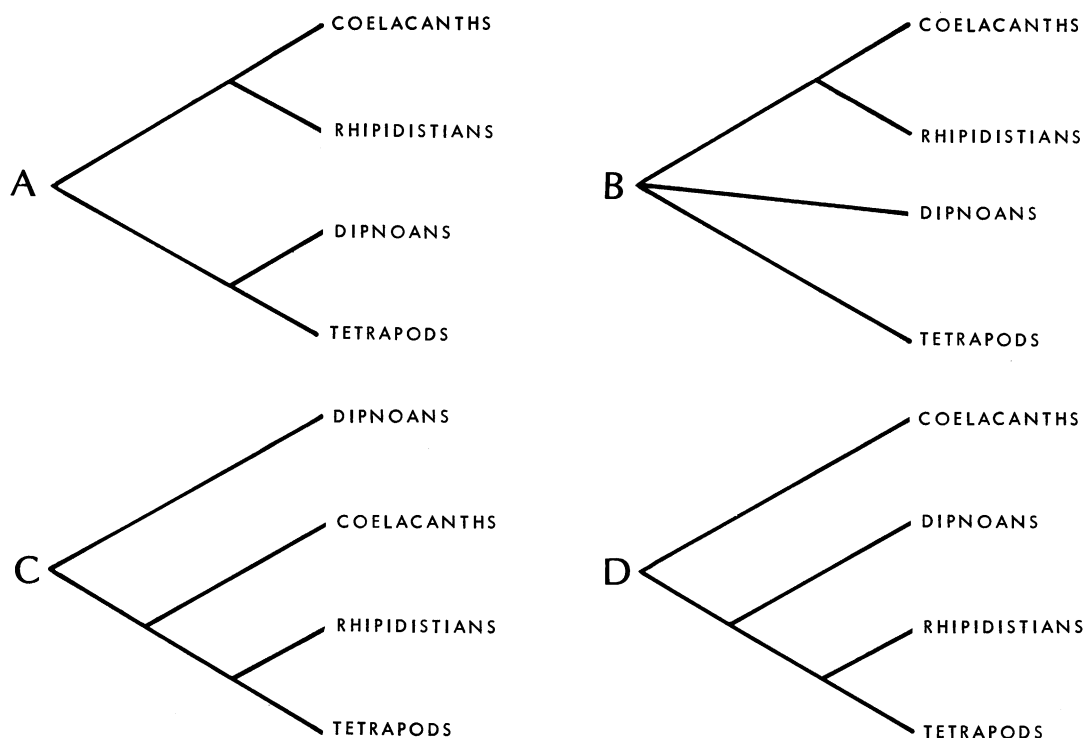


FIG. 4. Cladograms to show evolution of opinion on interrelationships of crossopterygians, lungfishes, and tetrapods. A, Goodrich (1924); B, Watson (1926), Romer (1933); C, Säve-Söderbergh (1935), Westoll (1961, etc.), Miles (1975); D, Miles (1977), Wiley (1979).

chotomy with those two groups. In that diagram, polypterids are also marked by a query, since Goodrich's assessment was that they are closer to actinopterygians than to coelacanth and rhipidistians. Goodrich's opinions were clearer by 1924. In that paper, he still insisted that the resemblances between lungfishes and tetrapods "can scarcely be due to convergence" and wrote "the earliest Osteichthyes diverged into teleostome and dipnoan branches and that the tetrapods arose from the base of the latter" (cf. fig. 4A). Goodrich is often cited as one of the architects of the theory of the crossopterygian ancestry of tetrapods (e.g., Romer, 1956, p. 159; Schaeffer, 1965), but in our reading his work shows nothing of the sort.

After Goodrich's 1909 work, *Polypterus* played a less central role in discussions of tetrapod origins. For example, Watson (1912) used "crossopterygian" as synonym-

ous with "rhipidistian," in a paper including new information on *Megalichthys*, and the observation that the mode of tooth replacement was identical in rhipidistians and labyrinthodonts.

Gregory (1915) published the first detailed review of the question of tetrapod origins. On dipnoans, Gregory believed that while their similarity with tetrapods, and urodeles in particular, "might be ascribed to convergence" they implied "a similarity in the 'potential of evolution,' that is, of structural possibilities, in the forerunners of these groups" (p. 322). Gregory argued that "The only crossopterygians that can claim even remote relationships with the Amphibia are the Devonian Rhipidistia, especially the Osteolepidae and the nearly allied Rhizodontidae" (p. 326). In his review he concentrated on seeking homologies in the dermal bones of the skull and in the forelimb skeleton be-

tween rhipidistians and labyrinthodonts. Concerning the forelimb, Gregory tried to settle the much-discussed question of the relative status of the fin of *Neoceratodus* and of rhipidistians. Unlike many of his predecessors, Gregory rejected "the traditional view that the 'archipterygia' of Dipnoi are primitive structures and [regarded] the imperfect archipterygium of the Devonian *Osteolepis* as more primitive" (p. 350). Thus Gregory imagined that tetrapods are descended from rhipidistians, and argued for a "common origin of the Dipnoi and Crossopterygii" (p. 325).

Gregory did not describe exactly how he envisaged the interrelationships of rhipidistians and dipnoans, but this was made clear by Watson (1926), the next major reviewer of tetrapod origins. He wrote (p. 195) "the most primitive known Dipnoan is . . . *Dipterus valenciennesi* . . . this fish presents so many resemblances in structure to the contemporaneous Osteolepids as to show that the two groups arose from a common ancestor not much earlier in date. It is from this hypothetical fish that I believe the Amphibia to have arisen." Thus Watson envisages a trichotomy of dipnoans, rhipidistians, and tetrapods (fig. 4B), this arrangement, rather than derivation of dipnoans and tetrapods from rhipidistians (fig. 3), being necessitated by the intracranial joint of rhipidistians (cf. Watson and Gill, 1923, p. 210), which Watson regarded as a specialized feature. On the resemblances between dipnoans and urodeles, Watson wrote (1926, p. 190) "it is certain that the existing resemblances depend on the parallel evolution of not distantly related stocks." Romer (1933) followed Watson in adopting a trichotomous diagram of the relationships between dipnoans, tetrapods and rhipidistians (his fig. 51), but Romer preferred to regard the similarities between dipnoans and amphibians as "retention of characters present in their crossopterygian ancestors." Given the trichotomous pattern of relationships inferred by Watson and Romer (fig. 4B), it should be pointed out that special similarities between rhipidistians and tetrapods are open to just the same interpretations as those applied by Watson and Ro-

mer to dipnoan/tetrapod similarities: they may be parallelisms or retained primitive characters.

In 1932 Säve-Söderbergh announced the discovery of the Devonian ichthyostegids. These animals have had a profound effect on subsequent discussions of tetrapod origins, because they are both stratigraphically older and anatomically more primitive than the Carboniferous amphibians that Watson had used to demonstrate similarities between osteolepids and early tetrapods. As Parrington (1967, p. 231) put it, "It was to be expected, therefore, that any Amphibia from the Upper Devonian would be intermediate in their structures between the Middle Devonian osteolepids and the Carboniferous labyrinthodonts, but when discovered the ichthyostegids did not conform at all well to this expectation. While their skulls showed some very primitive features which might have been expected, the pattern of the dermal bones did not conform to plan." In attempting to explain the differences in the skull roof between osteolepids and ichthyostegids, Säve-Söderbergh adopted an explanation involving differential fusions from an ancestral pattern which, as he said (1934, p. 5), is "astonishingly" dipnoan-like. After the discovery of the ichthyostegids, discussions of the dermal skull roof shifted away from the search for homologies between rhipidistians and tetrapods, toward discussions of the fusion theory and of Westoll's (1938) alternative explanation requiring changes in proportion (see Jarvik, 1967; Schmalhausen, 1968; and section on Dermal Bones).

Of his 1932 paper, Säve-Söderbergh wrote (1935, p. 201) "the investigations of the Devonian Ichthyostegids . . . show that these . . . are more nearly related to the Crossopterygians [i.e., rhipidistians and coelacanth] than to the Dipnoans." Thus he had adopted the scheme of relationships shown in figure 4C, though it is not clear to us what characters of ichthyostegids or crossopterygians prompted this conclusion. In any case, this opinion was short-lived, for in 1933, after elaborating on the characters common to dipnoans, crossopterygians, and tetrapods and naming the group Choanata for them,

Säve-Söderbergh suggested (p. 118) that the tetrapods were polyphyletic, urodeles being related to dipnoans, and the labyrinthodonts possibly being polyphyletic. The idea of tetrapod polyphyly, and of direct dipnoan/urodele relationships, was taken up by Holmgren (1933; see also 1939, 1949a, 1949b), at first on the structure of the limbs. He concluded (1933, p. 288) "regarding the limbs there is a greater agreement between a dipnoan and an urodele, than between an urodele and an anuran."

Säve-Söderbergh adopted Holmgren's views on urodele/dipnoan relationships (1934, 1935) and so began the central theme of modern discussions of tetrapod origins, the dispute between the advocates of polyphyly, and the advocates of monophyly. Holmgren's original advocacy of urodele/dipnoan relationships can be seen as an attempt to reconcile the conflicting claims of neontology (resemblances between Recent dipnoans and amphibians, especially urodeles) and paleontology (resemblances between labyrinthodonts and rhipidistians). However, Holmgren's views received little support (see references cited in Holmgren, 1949a), and the emphasis soon passed back to paleontology, with Jarvik's (1942) monumental work on the snout. In that monograph, Jarvik gave incomparable accounts of the morphology of the snout in *Eusthenopteron* and porolepiforms. Like Holmgren and Säve-Söderbergh, he advocated a diphyletic origin of tetrapods, but as urodele ancestors he replaced the dipnoans by the porolepiforms. Jarvik's principal reason for excluding the dipnoans from consideration was his argument that they have no choanae (see section on Nostrils).

Westoll's 1943 review of tetrapod origins, though published after Jarvik's monograph, was written without knowledge of it, because of wartime conditions. Westoll's paper is in the tradition of Watson's (1926) review. Like Watson, Westoll emphasized process, both in his discussion of the significance of the change from fish to tetrapod, and in his morphology, where sequences of fossils are selected to illustrate trends. Westoll's general conclusion was that tetrapods are monophy-

letic, and "that all known tetrapods can be derived from a single basic structural pattern, which resembles osteolepid crossopterygians in so many details that this group is the only possible source of proto-tetrapods" (p. 79). This conclusion is not surprising, for Westoll's discussion was much influenced by his (1938) discovery of *Elpistostege*, "an important proto-tetrapod" (Westoll, 1943, p. 78) now interpreted as a panderichthyid fish (Vorobyeva, 1977a), or, in Westoll's classification, an osteolepid. Later, Westoll wrote (1958b, p. 100; 1961, p. 605) of "overwhelming evidence" of the descent of tetrapods from osteolepid rhipidistians. On lungfishes, Westoll (1949; Lehmann and Westoll, 1952) did not accept Jarvik's argument that the posterior nostrils of dipnoans are not choanae, and maintained that dipnoans, like tetrapods, are descended from osteolepids. Westoll's scheme of relationships (e.g., 1961, fig. 1) is like that introduced by Säve-Söderbergh (fig. 4C), with coelacanth closer to tetrapods than are dipnoans, but the coelacanth is regarded as descendants of porolepiforms, and, following Jarvik, the possibility of urodele descent from porolepiforms is allowed. Romer's views (e.g., 1968) and his trees (e.g., 1956, fig. 19) are similar to Westoll's; like Westoll he did not accept Jarvik's argument that dipnoans have no choanae, but unlike Westoll he never allowed the possibility that tetrapods are non-monophyletic.

On the relationships of dipnoans, crossopterygians, and tetrapods most authorities have followed the pattern shown in figure 4C (e.g., Trewavas et al., 1955—"the closer relationship of [tetrapods to] Osteolepidoti and Coelacanthini than to the Dipnoi"), and so today's textbook view became established.

As for the dipnoans, they were free to wander farther down the family tree, since coelacanth, now known (*Latimeria*) to lack choanae, and judged to show nothing in common with amphibians, were interposed between lungfishes and tetrapods. White (1965) argued that dipnoans were distinct from other osteichthyans; Schaeffer (1968) that they formed a trichotomy with actinopt and crossopt; Bertmar (1966) that they are related to

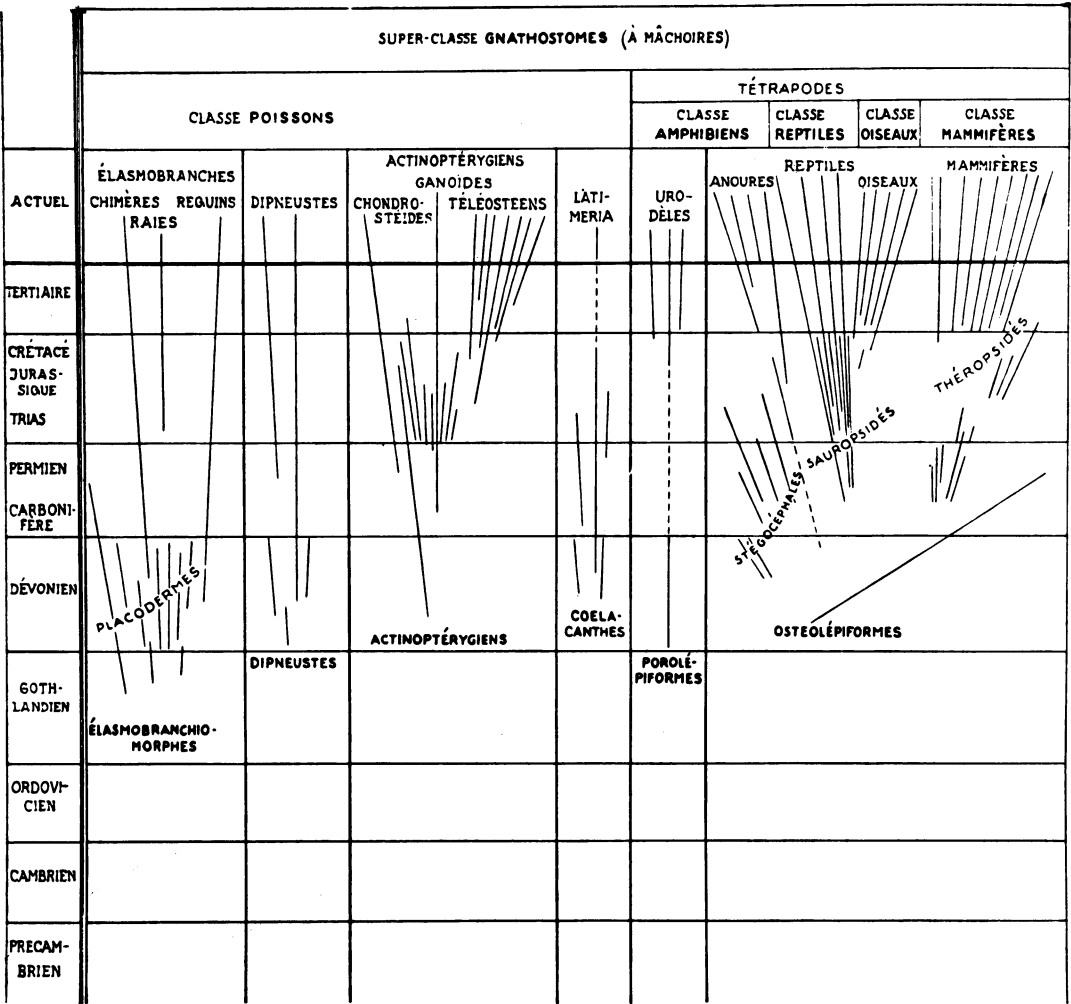


FIG. 5. Phylogeny of gnathostomes, modified from Jarvik (1960, fig. 28).

actinopts; von Wahlert (1968) that they are the sister group of all osteichthyans; and Jarvik (1968a, 1968b), citing resemblances between dipnoans and holocephalans, concluded (1968b, p. 518) "if we ask which of the recent vertebrate groups is the sister group of dipnoans (holocephalians? coelacanthiforms?) no answer can be given." Thus the fossils had taken over. Dipnoans, placed as amphibians or the closest relatives of tetrapods by nineteenth-century neontologists, had been ousted by the rhipidistians, and relegated to a limbo between osteichthy-

ans and chondrichthyans (cf. fig. 5). Despite a few dissenting neontologists (e.g., Fox, 1965), it is now accepted that the resemblances between dipnoans and amphibians are convergent, and that the resemblances between rhipidistians, especially osteolepiforms, and tetrapods are evidence of relationship (i.e., synapomorphies). What, then, are these resemblances? Above, those used by nineteenth-century biologists are listed; the following list contains characters emphasized by twentieth-century workers to relate osteolepiform rhipidistians and tetrapods,

additional to or amplifying those of nineteenth-century biologists:

1. Detailed correspondence between bones of skull roof and cheek (e.g., Westoll, 1943; cf. Jarvik, 1967; Parrington, 1967)
2. Intracranial joint is immobilized in some osteolepiforms (e.g., Westoll, 1943; Vorobyeva, 1977a)
3. Dermal bones of palate "practically identical" in osteolepids and primitive tetrapods (Westoll, 1943, p. 84)
4. Choana present, with the same relationship to the dermal bones in both groups (Jarvik, 1942; Westoll, 1943)
5. Mandible "almost identical" in early tetrapods and osteolepids (Westoll, 1943, p. 85)
6. Tetrapod septomaxilla is found in osteolepiforms (Panchen, 1967)
7. Opercular and preopercular present in ichthyostegids (Jarvik, 1952)
8. Suture in braincase of ichthyostegids represents intracranial joint (Jarvik, 1952)
9. Notochord penetrates base of braincase in ichthyostegids (Jarvik, 1952)
10. Cranial cavity and its inferred contents similar in *Ectosteiorachis* and amphibians (Romer, 1937)
11. Osteolepiforms have ethmoid, basal, ascending and otic processes on the palatoquadrate (Jarvik, 1954)
12. Hyomandibular double-headed, like tetrapod stapes, in osteolepiforms (Jarvik, 1954)
13. Distribution of dentition, and mode of replacement of fangs, similar in the two groups (Westoll, 1943; Jarvik, 1954, 1963)
14. Osteolepiforms have folded teeth of the same type as labyrinthodonts (Schultze, 1970a)
15. Vertebrae of osteolepiforms are "protorachitinous" (Andrews and Westoll, 1970a, 1970b)
16. *Eusthenopteron* has bicipital dorsal ribs (Andrews and Westoll, 1970a)
17. Scapulocoracoid of *Eusthenopteron* like that of early tetrapods, with a screw-shaped glenoid (Andrews and Westoll, 1970a)
18. Humerus of *Eusthenopteron* and *Strepsodus* comparable with tetrapod humerus (Andrews and Westoll, 1970a, 1970b)
19. *Eusthenopteron* may have a sacral attachment (Andrews and Westoll, 1970a)
20. *Ichthyostega* has a fishlike tail (Jarvik, 1952)

This list may seem short to those who recall the extraordinarily detailed comparisons with tetrapods in Jarvik's papers (1942, 1952,

1954, 1963, 1964, 1966, 1967, 1972, 1975) on osteolepiforms. But it must be emphasized that Jarvik never pretended to cite characters common to osteolepiforms and tetrapods; instead, he cited characters common to *Eusthenopteron* and frogs. Our main task in this paper is to review the characters listed above, in osteolepiforms, tetrapods, and dipnoans. Some of them (nos. 7, 9, 20) may be immediately discarded as primitive for osteichthyans or gnathostomes. Others may be discarded because of lack of published evidence (nos. 8, 19), or because dipnoans are known to share the same features (nos. 2, 10, 12; cf. Miles, 1977). The remainder are discussed in subsequent sections.

During the last few years, there has been a changed approach to dipnoan relationships, stemming mainly from cladism. Miles (1975) reviewed the question and concluded that the textbook solution (fig. 4C) was correct, but later (1977) changed his mind, after studying the Devonian Gogo lungfishes, and adopted a new scheme (fig. 4D). Meanwhile, others had suggested that coelacanth belonged elsewhere (Løvtrup, 1977—sister group of chondrichthyans; Wiley, 1979—sister group of osteichthyans) on evidence from the anatomy, physiology, and biochemistry of *Latimeria*. In other words, further investigation of *Latimeria* repeatedly turns up primitive osteichthyan or chondrichthyan-like characters. Further investigation of Recent lungfishes, on the other hand, repeatedly produces characters which seem to be synapomorphous with tetrapods; e.g., lens proteins and bile salts (Løvtrup, 1977), ciliation of the larva (Whiting and Bone, 1980) and gill-arch muscles (Wiley, 1979). It is unfortunate that, so far as we know, no proteins of lungfishes or *Latimeria* have yet been sequenced. In any case, the number of apparent synapomorphies between lungfishes and tetrapods continues to increase. Proponents of the rhipidistian ancestry of tetrapods have continued to rate such characters as convergent, following Baur (1896). Alternatives are to rate these characters as synapomorphies, either of tetrapods and dipnoans, or of some more extensive group. Since most of these characters are in soft

anatomy and embryology, they can, when assumed to have occurred in rhipidistians, be rated as synapomorphies of a group comprising tetrapods, lungfishes, and rhipidistians. As a paraphyletic group, rhipidistians might then include members of the stem-groups of tetrapods, of dipnoans, and of tetrapods plus dipnoans. That statement recalls our comment on Dollo's (1896) diagram (p. 170), implying that remarkably little progress has been made during the last eighty years.

In our view, the reason for that lack of progress is plain enough. It is acceptance of evolution, which has directed attention away from the unsolved problem that occupied pre-Darwinians—what are the characters of tetrapods, how are they distinguished from fishes, and from lungfishes in particular—and toward a search for sequences of fossils which will fit the evolutionary doctrine, and toward an interest in process rather than pattern. The search for fossils has produced superficially acceptable sequences, as it was bound to, for few transformations, however fantastic, are forbidden by the Darwinian or

Neo-Darwinian picture of the evolutionary process. Yet the sequences consist of nothing more than abstractions from paraphyletic groups such as rhipidistians, osteolepiforms, and labyrinthodonts. As for the pattern, very few plausible derived characters have yet been presented to link some rhipidistians and some tetrapods (e.g., folded teeth). For the rest, the characters used by twentieth-century biologists seem to us little different from those of nineteenth-century workers—a melange of primitive characters, and assertions of identity or general similarity whose precise content is still to be established.

Acceptance of cladistic methodology during the last few years has begun to direct attention back towards pre-Darwinian problems, problems of pattern. How are choanates and tetrapods characterized (e.g., Miles, 1977; Szarski, 1977; Schultze, 1977a; Gaffney, 1979a, 1979b)? With the realization that some generally accepted groups (rhipidistians, osteolepiforms, labyrinthodonts) are uncharacterized, or uncharacterizable, the way is open for a new attack on the problem.

CHOANA, NOSTRILS, AND SNOUT

(A) INITIAL COMPARISONS AND INFERENCES

Our interpretation of the dipnoan internal nostril as a choana (fig. 6) has already been alluded to in the Introduction. This interpretation has resulted from the rejection of a comparative anatomical argument by Allis (1919, 1932a, 1932b) concerning living lungfishes from which he deduced that the true upper lip and excurrent, external nostril had migrated together into the oral cavity. Allis's reasoning predicts that if marginal upper jaw teeth were present in lungfishes, these teeth (which are absent in extant and most fossil species) would lie medial to the internal nostril. The prediction, however, is inconsistent with Miles's (1977) account of several more or less complete skulls of the Devonian lungfish, *Griphognathus whitei* Miles, in which the internal nostril is clearly marked and in

which marginal jaw teeth are present lateral, rather than medial, to this opening (fig. 7).

In vertebrate systematics identification of a choana must satisfy not only anatomical criteria, but other criteria of homology as well. To do this, the lungfish choana either must be indistinguishable from the choana of tetrapods, or one must be regarded as a modification of the other. Primary comparisons are, therefore, made between Miles's (1977) excellent specimens of *Griphognathus whitei*, as interpreted partly on the basis of our own dissections of *Neoceratodus forsteri* and ichthyostegid amphibians, which we consider to be the sister group of all other tetrapods (see Introduction). Our comments on ichthyostegids are based on *Ichthyostega* sp. as described by Säve-Söderbergh (1932) and Jarvik (1952) and on two casts of well-preserved palates (fig. 10).

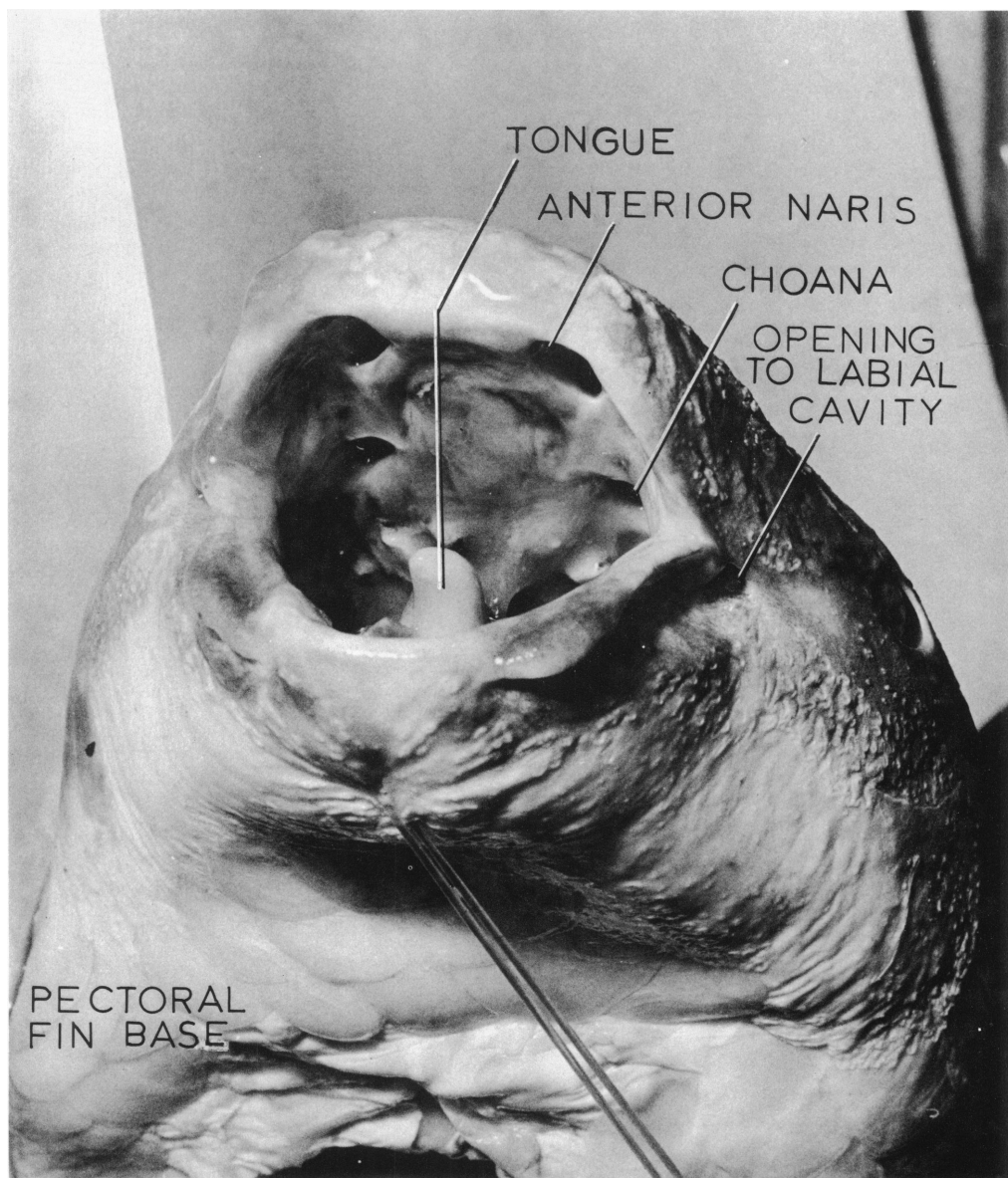


FIG. 6. *Neoceratodus forsteri* (Krefft), approximately 120 cm. total length, AMNH 40800, showing head and bases of pectoral appendages.

In *Griphognathus* the preoral region of the snout medial to a pair of nasal recesses bears a pair of tooth ridges fused with the rostrum and covered with enamel. Miles (1977, p. 187) refers to these tooth ridges as premaxillae because, when the lower jaw is in place, the mandibular symphysis closes just behind

them. Although Miles seemed to have some reservations that these elements are either tooth plates or premaxillae, for he identified them in his figures only as preoral eminences, their interpretation as dentigerous on the one hand and as paired elements on the other is supported by the presence of a

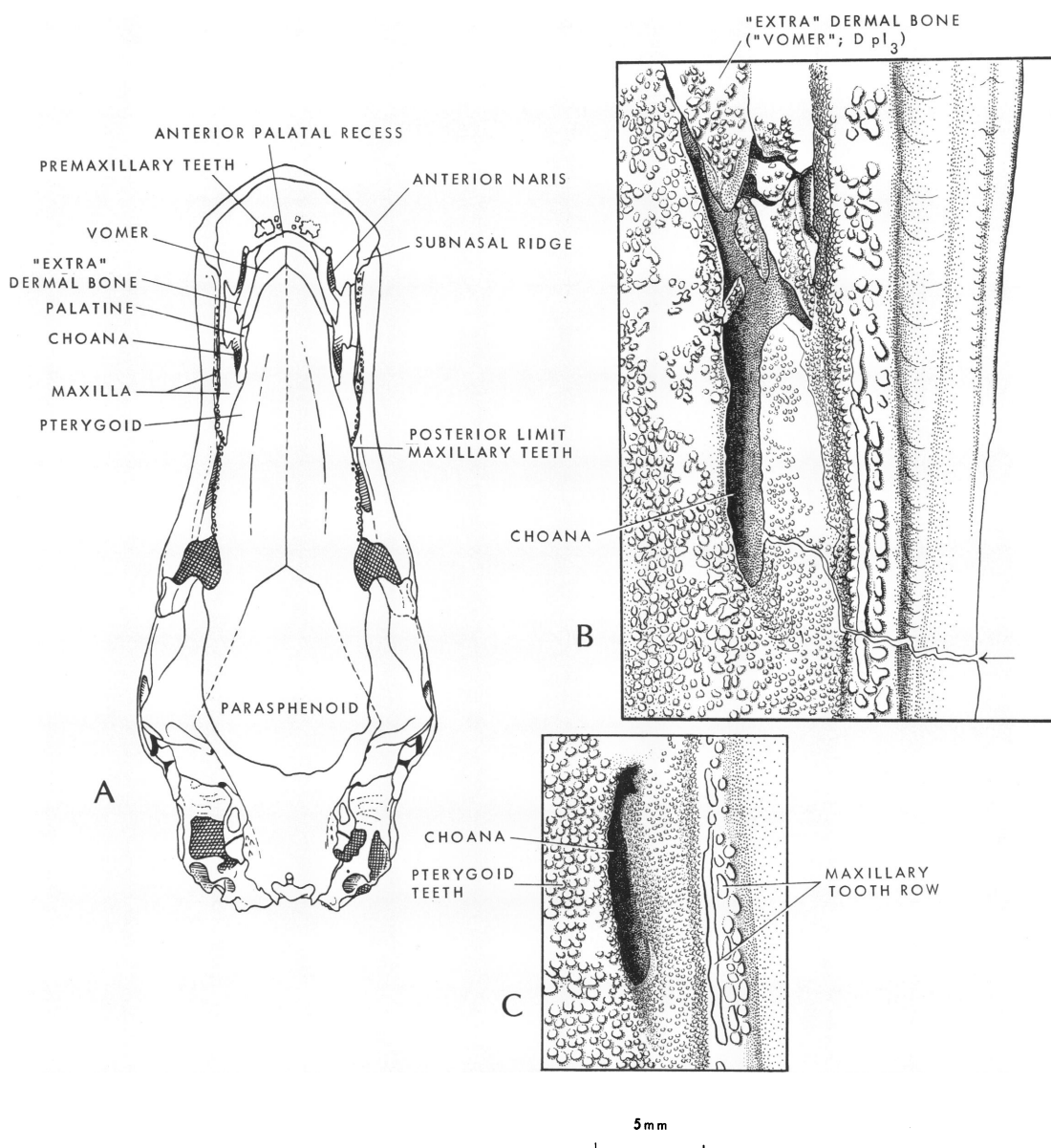


FIG. 7. *Griphognathus whitei* Miles. A, ventral view of skull, from BMNH P. 56054, after Miles (1977, fig. 6); B, camera lucida drawing of left choana and surrounding dermal bones in BMNH P. 56054; arrow indicates a crack not a suture; C, camera lucida drawing of left choana in BMNH P. 50996 (holotype), an individual in which the bones surrounding the choana are fused.

similar but more distinct pair of toothed elements medial to the nasal recesses in *Ganorhynchus woodwardi* (fig. 8). Our conclusion that they represent premaxillae that

have fused with the bone of the snout is based on the observations that they are paired, are in series with a more posterior marginal upper jaw dentition (as are premax-

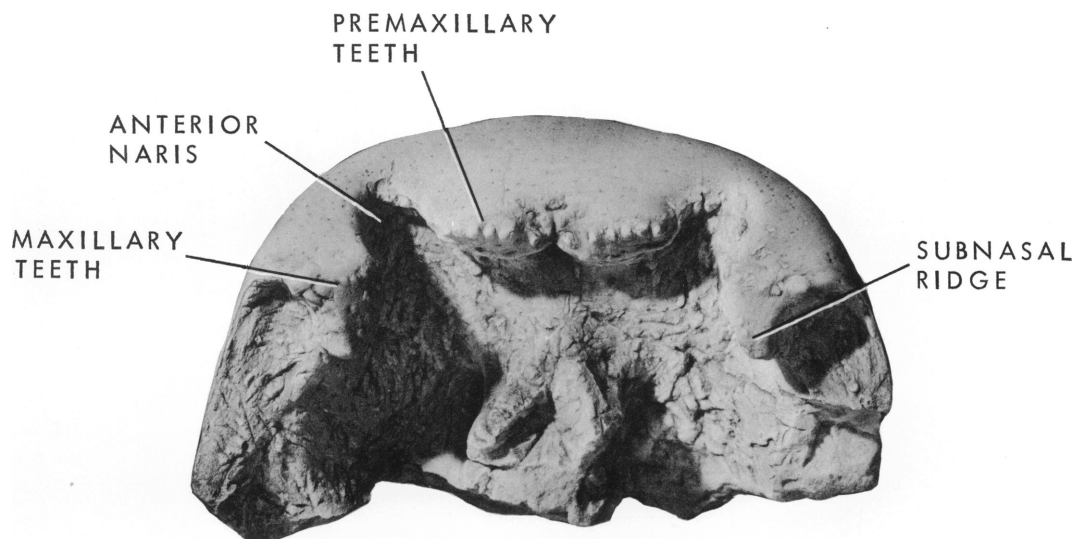


FIG. 8. *Ganorhynchus woodwardi* Traquair. Snout of a Devonian "hard-snouted" lungfish in ventral view (holotype, BMNH 44627, whitened with ammonium chloride). A paired row of premaxillary teeth on the preoral area (Miles, 1977, p. 179) and a patch of maxillary teeth on the subnasal ridge lateral to the notch leading to the anterior nostril are shown. $\times 1.5$.

illae with maxillae), are the most anterior teeth in the upper jaw, and are immediately in front of an anterior palatal recess that, in osteichthyans, normally follows the concave oral border of the premaxillae, as it does in *Griphognathus* (figs. 7, 10, 14). Lateral to each premaxilla there is a sulcus or nasal recess in the consolidated ethmoid block and the latter is notched along its oral margin where the sulcus extends obliquely toward the palate. Posterolateral to the sulcus is a high tooth-bearing knob (the subnasal ridge, figs. 7, 8), also enamel-coated, and this is followed in *Griphognathus* by a long, low tooth-bearing ridge (the maxilla) that is ankylosed with the bones of the cheek (fig. 7B, C). We interpret the high, tooth-bearing knob as the anterior part of the maxilla since its enamel coating continues posteriorly onto the low dentigerous surface behind.

The maxilla has a medially directed flange posteriorly which is sutured to the pterygoid (fig. 7). This flange forms the posterior boundary of an elongate, oval opening into what was probably the nasal capsule. The anterior part of the oval opening is bounded laterally by the maxilla, medially and ante-

riorly by a series of dermopalatines (fig. 7). The series of dermopalatines and the vomer extend forward around the pterygoid and meet in the midline. An additional paired, toothed dermal bone ("extra" dermal bone, fig. 7) is present between the dermopalatines and the inner, hind, edge of the nasal recess and this element may represent a supernumerary dermopalatine as suggested by Miles (1977) or a vomer (but see p. 230). Between the anterior end of the pterygoids and the encircling vomers and the ethmoid block with its ankylosed premaxillae there is a long, shallow depression which, in other sarcopterygian fishes and tetrapods, has been termed the anterior palatal recess. The position of the nasal capsule between the elongate, oval posterior opening in the palate and a region just behind the inner end of the nasal recess is suggested by the position and termination of the canal for the olfactory tracts and by the course of various canals (fig. 9) that are comparable with those for nerve and blood vessels in extant fishes and amphibians. The posterior oval opening in the palate is therefore interpreted as the fenestra exchoanalis, and the nasal recess, present in

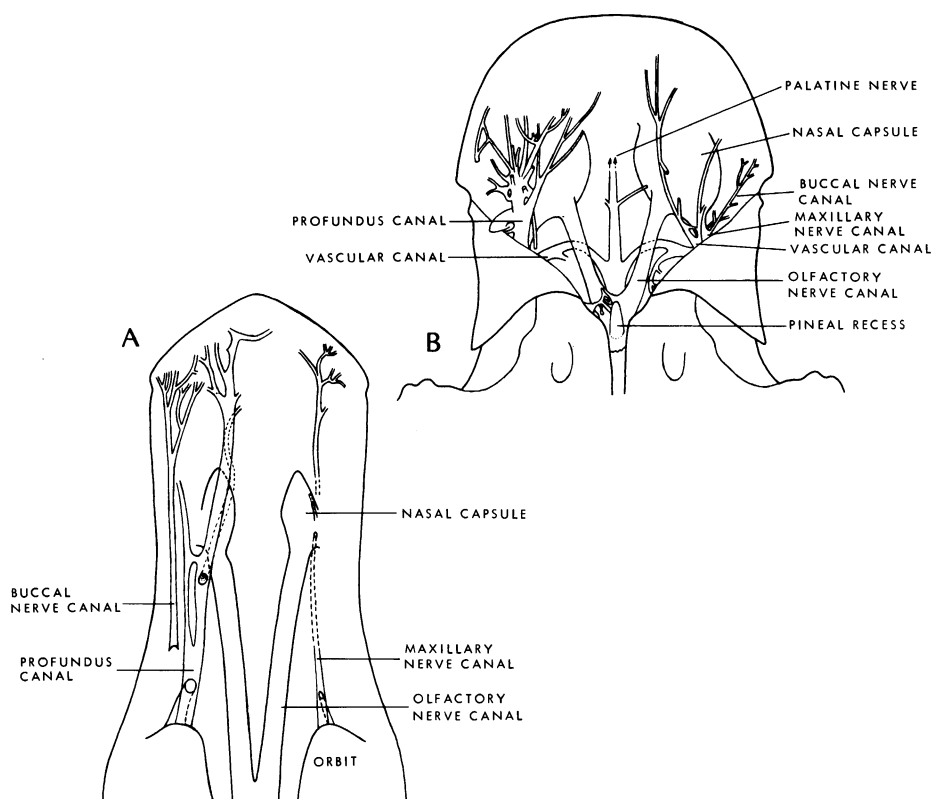


FIG. 9. Plans of snout of two Devonian dipnoans to show major canals as interpreted by Miles. A, *Griphognathus whitei* Miles (after Miles, 1977, fig. 63); B, *Chirodipterus australis* Miles (after Miles, 1977, fig. 66).

some form in all fossil and extant lungfishes, as housing the anterior, external, incurrent nostril. When the lower jaw is in place in *Griphognathus* the mandibular symphysis is seated in the anterior palatal recess just behind the premaxillae, as in all osteichthyans, and the anterior tip of the nasal recess is just visible beyond the lower jaw margin as in living lungfishes.

The essential features of *Griphognathus* for comparison with tetrapods are (1) the ventrally opening anterior nostril and choana; (2) the oval outline of the fenestra exochoanalis (choana); (3) the interruption of the dentigerous border of the upper jaw (between the premaxilla and maxilla) at the site of the anterior nostril; (4) the formation of the fenestra exochoanalis by the maxilla and the dermal bones of the palate that encircle

the pterygoids anteriorly, and (5) the junction of the broad pterygoids in the midline under the anterior part of the parasphenoid. Each of these features may be seen also in *Ichthyostega* (cf. figs. 10 and 46B).

(B) NASAL CAPSULE

There are basically four major openings in the wall of the endoskeletal nasal capsule of gnathostomes that transmit water or air currents, nerves, and blood vessels. One is for the olfactory tract, and this is situated posteromedially. Another, anterolateral opening is for the nostrils extending to the outside. This opening may be subdivided by soft tissue, dividing it into an incurrent and excurrent port. These two ports may each form separate tubes that open remotely from each

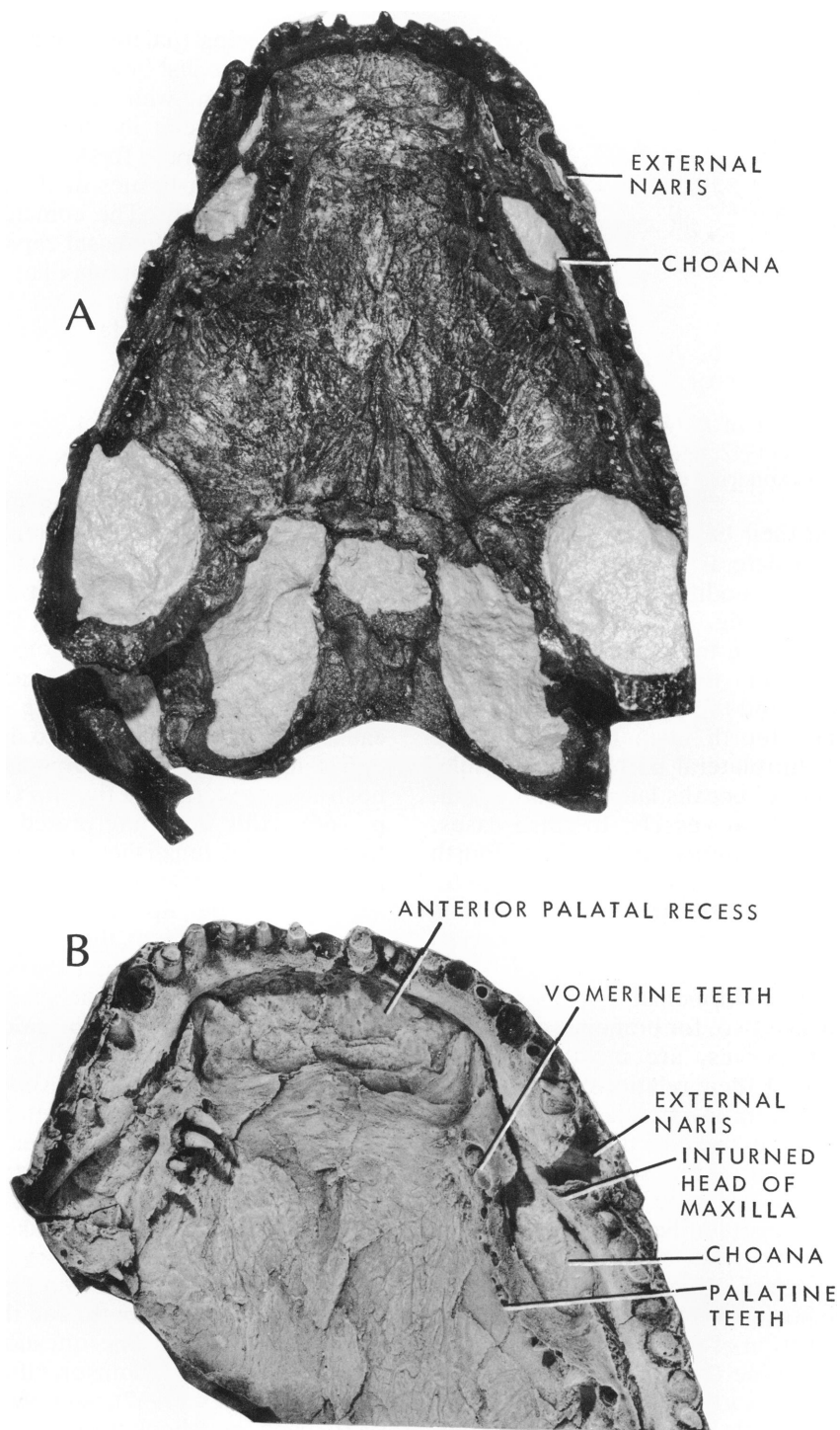


FIG. 10. Casts of ventral surface of snout in specimens of *Ichthyostega* sp., to show choana. A, AMNH P. A756a; B, BMNH R. 9469.

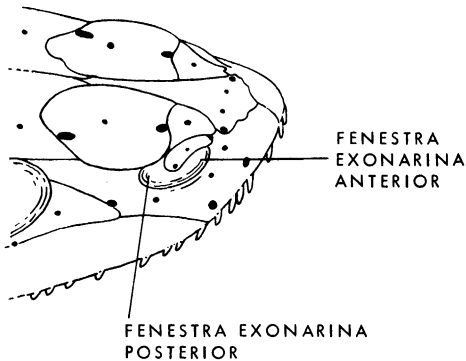


FIG. 11. Snout of *Polypterus senegalus* Cuvier, after Jarvik (1942, fig. 84), showing bony limits of fenestra exonarina communis.

other, but at their bases they come together into the anterolateral wall of the nasal capsule. The latter condition is found in cladistians [*Polypterus* (fig. 11) and *Erpetoichthys*]. A third opening, in the posterior wall of the capsule, transmits the maxillary branch of the fifth nerve and the palatine branch of the seventh. The fourth main opening, in the ventral or ventrolateral part of the capsule, is for the ramus buccalis lateralis and, often, one or more blood vessels. In some cases, for example, *Polypterus*, the third and fourth openings are represented by only a single fenestra. In other cases there are numerous smaller perforations in the capsule for nerves and blood vessels.

Of the various principal openings in the capsule, the last two, for branches of the fifth and seventh nerves, are most interesting here because of their relations to surrounding bony structures. In cladistians these nerves enter the capsule through a single, large, posteroventral fenestra, but the ramus buccalis and at least one of the main blood vessels pass together between the capsule and the anteroventral wall of the orbit dorsal to the bony palate. Where they turn dorsally to enter the posteroventral capsule wall there is a triple junction of the premaxilla, maxilla, and dermopalatine (fig. 12). The premaxilla is notched posteriorly just below the fenestra in the nasal capsule and the maxilla and dermopalatine fail to cover completely the premaxillary notch. The result is an oval or tri-

angular opening (palatal fenestra, fig. 12) in the bony palate just below a large fenestra in the ventrolateral wall of the nasal capsule which can be seen in cleared and stained specimens, but not in fresh specimens unless the covering soft tissues of the oral mucosa are dissected away. The coincidence of the palatal fenestra in the nasal capsule and dermal palate involving premaxilla, maxilla, and dermopalatine is similar to the "choana" of *Eusthenopteron* as described by Jarvik (1942).

(C) CHOANA AND NOSTRIL IN DIPNOANS

The internal nostril of living lungfishes was regarded as a choana by all nineteenth-century anatomists, and by virtually all in the first half of the twentieth (references in Jarvik, 1942, p. 273). Allis (1932a, 1932b) argued that this nostril was homologous with the excurrent nostril of chondrichthyans and actinopterygians, but not with the choana, because the choana lies medial to the secondary upper lip, whereas the dipnoan excurrent nostril lies external to that lip (Allis, 1932a, p. 666). Allis here interpreted the anterior toothplates of lungfishes, usually called vomers, as premaxillary, and so identified the secondary upper lip, which always lies immediately external to the premaxillary and maxillary teeth. Allis had earlier (1919) argued that dipnoans have no secondary upper lip, but a tertiary upper lip, unique to them, lying external to both nostrils.

Jarvik (1942) developed Allis's argument further, bringing in interpretations of the subnasal cartilage of lungfishes, the course of the maxillary nerve, and the interruption of the infraorbital sensory canal opposite the nostrils. Jarvik concluded, like Allis, that dipnoan nostrils are ordinary fish nostrils which have migrated back so that one opens into the roof of the mouth, and that dipnoans are not choanates. The question has since been reviewed by Thomson (1965), Bertmar (1966), Panchen (1967), and Miles (1977, p. 147), each of whom disagreed with Jarvik over the interpretation of one structure or another, while agreeing with his conclusion.

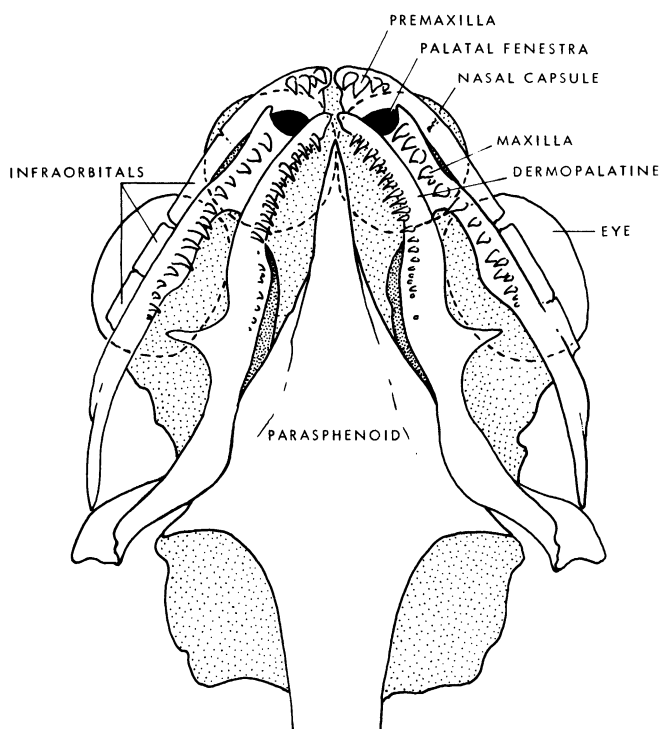


FIG. 12. *Polypterus ornatipinnis* Boulenger, ventral view of roof of mouth of juvenile (4 cm. standard length), still with large external gills, to show fenestra beneath nasal capsule, between premaxilla, maxilla, and dermopalatine. Note that maxilla and infraorbital bones are still recognizably discrete. Eye and nasal capsule are indicated by broken lines. Cartilage stippled.

Thus Panchen (1967, p. 379) wrote "the evidence for the homology of the dipnoan posterior nares with those of actinopterygian fishes and their non-homology with tetrapod choanae seems conclusive." Rather than re-view these interpretations yet again, we refer the reader to pages 376–379 in Panchen's paper, and suggest that the conclusion quoted comes as a surprise if the whole passage is read with an open mind.

Miles's (1977) figures of the Devonian lungfish *Griphognathus* show an outer dental arcade (premaxillary-maxillary dentition in other osteichthyans), identifiable by its position outside the lower jaw when the mouth is closed. This tooth row is external to the posterior nostril, which is completely enclosed by dermal bone in some individuals (Miles, 1977, fig. 80; fig. 7C). The tooth row

is interrupted anteriorly by a notch (fig. 7A) which is identifiable as the anterior margin of the anterior nostril, by comparison with Recent lungfishes. The same notch is evident in other fossil "hard-snouted" dipnoans (e.g., White, 1962, pl. 2—*Dipterus*, *Rhino-dipterus*, *Ganorhynchus*; Miles, 1977, fig. 4—*Holodipterus*, *Chirodipterus*; fig. 8). As argued above (pp. 180–181), we identify the teeth anteromedial to this notch (e.g., in *Griphognathus* and *Ganorhynchus*, figs. 7, 8) as premaxillary, as did Miles (1977, p. 187), since they bite outside the lower jaw, are the most anterior teeth in the upper jaw, and lie immediately in front of an anterior palatal recess similar to that which normally lies behind the premaxillae in osteichthyans (figs. 7, 10, 14). Posterolateral to the anterior nostril, *Griphognathus* has a tooth row which

runs back on a series of bones which Miles (1977, fig. 57) interprets as lateral nasal toothplates and ectopterygoid. These teeth bite outside the lower jaw (Miles, 1977, p. 181), and we therefore interpret them as maxillary, since in no known gnathostome do palatal teeth bite outside the lower jaw. Maxillary teeth occur in some other Devonian lungfishes (*Holodipterus*, *Dipterus*; Miles, 1977, p. 186), but in most hard-snouted dipnoans they are represented only by the subnasal ridge (Miles, 1977, p. 185), a denticulated or enameled knob lateral to the anterior nostril (fig. 8).

The posterior nostril is, as noted above, completely bone-enclosed in some specimens of *Griphognathus* (fig. 7). In these specimens, the opening is a rostro-caudally elongate ellipse, with smoothly inturned, toothed margins (fig. 7C). The opening is bordered laterally by Miles's ectopterygoid, our maxilla, and medially by Miles's dermopalatine 2, our palatine. Miles noted (p. 175) that the opening has the position of a choana, but rejected that homology in favor of "chance similarity." This is because he (p. 147) interpreted dipnoan nostrils to bring "dipnoans into line with other fishes." But since his overall conclusion (p. 313) was that dipnoans are the sister group of choanates, it is with them, not other fishes, that we should expect dipnoans to fall in line.

The outer dental arcade of *Griphognathus*, which lies external to the posterior nostril and is notched or interrupted by the anterior nostril, meets Allis's (1919, 1932a) criteria for choanates, and removes his reason for denying the homology of the lungfish posterior nostril and the choana. This interpretation carries the implication that the two nostrils of choanates (lungfishes and tetrapods) are homologous with those of other gnathostomes, so that the choana is the homologue of a fish nostril. We note Bertmar's (1966, p. 140) conclusion on the origin of the dipnoan condition—"The posterior nostril migrated ventrally simultaneously with a reduction of the maxillary, the premaxillary and the anterior part of the infraorbital sensory canal"—and Panchen's (1967, p. 379) pro-

viso—"it is very unlikely that there was ever in the ontogeny or phylogeny of the Dipnoi an actual physical ventral migration of the nares. Rather there was a failure of the dorsal migration of the nasal placode normal in the ontogeny of other bony fish." If the dipnoan posterior nostril is a choana, this explanation should also apply to tetrapods.

Panchen (1967, p. 380) reviews this hypothesis: that the tetrapod choana is the homologue of a fish nostril. He specifies one prediction from it, that primitive tetrapods would have "a single external naris on each side, situated at or very near the jaw margin and almost confluent with a laterally placed choana inside that margin. Thus the condition in the amphibian *Ichthyostegalia* (Säve-Söderbergh, 1932; Jarvik, 1952) would be regarded as primitive." Later (1967, p. 407) Panchen concluded that this condition was indeed primitive for tetrapods, a view he still holds (Panchen, personal commun.). Panchen also pointed out the choana/fish nostril homology would be refuted if any fish had two external nostrils in addition to a choana, and noted that this was the basis for Westoll's (1943) doubt that porolepiforms have two external nostrils, since porolepiforms are the only fishes described as having two nostrils and a choana. Panchen went on to summarize Jarvik's more recent interpretations of porolepiforms as removing Westoll's doubts, and refuting the choana/naris homology. But even if two external nostrils were demonstrated beyond any possible doubt in porolepiforms, we do not agree that the choana/naris hypothesis would be refuted, for we would question the existence of a choana in porolepiforms. To explain why, it is necessary to review the choanae of rhipidistians. Before doing so, we emphasize that the varied interpretations of lungfishes show that even in living animals, with full ontogenetic information, identification of choanae can be a matter for debate. In fossils, where soft anatomy can only be interpreted after some Recent model, and where vagaries of preservation lead to disputed interpretation even of hard parts, there is endless room for debate.

(D) CHOANA AND NOSTRIL IN RHIPIDISTIANS

Dollo (1896, p. 109) suggested that if osteolepid crossopterygians were ancestral to lungfishes and tetrapods, they would have a choana. Such an aperture was first reported by Watson (1912, p. 9) in *Megalichthys*, as an opening whose front margin is formed by the vomer, and then by Watson and Day (1916, p. 11, pl. 1, fig. 5) in *Glyptopomus*, where it was said to lie entirely within the palatine. Bryant (1919, p. 18), perhaps influenced by Watson and Day, described a similar internal nostril, enclosed within the palatine, in *Eusthenopteron*. Stensiö (1918, p. 120) suggested that a choana might be present in *Dictyonosteus*, a Devonian fish since interpreted as a coelacanth by Jarvik (1942, p. 579, pl. 17), with the opening in question labeled as the fenestra endonarina communis.

In 1921, Stensiö referred (p. 136) to choanae in the rhipidistians *Dictyonosteus*, *Osteolepis*, *Diplopterus* (= *Gyroptychius*), *Rhizodopsis* and *Megalichthys*, but the last four are clearly due to misreadings of Dollo (1896) and Watson and Day (1916), who mentioned these names in discussing nostrils, but referred only to their *external* nostrils. In 1922 Stensiö (p. 195) suggested that the coelacanth *Diplocercides* had a choana, and this suggestion seems to be the only source of Watson's (1926, p. 200) statement "The original conclusion that the internal nostrils of Osteolepids imply an air-breathing habit is confirmed by the fact that whilst the Old Red Sandstone Coelacanth *Diplocercides* possessed similar internal nostrils, the marine Triassic and Cretaceous Coelacanth possess only an external nostril" [italics ours; air-breathing is, of course, not implied by the possession of internal nostrils—see Broman, 1939, on lungfishes, and Szarski, 1977, on teleosts]. In the same paper, Watson (1926, fig. 4) restored a choana in *Eusthenopteron*, on the basis (p. 249, figs. 34, 35) of two disarticulated specimens in the Royal Scottish Museum, and described (p. 246) a choana in *Megalichthys*, on the basis of disarticulated

specimens in the Hancock Museum. On this evidence, he wrote (p. 198) "The internal nostril found in all Osteolepids is identical in position, size and borders with that of certain Embolomeri."

Stensiö (1932, fig. 30) figured two undetermined crossopterygian snouts from the Devonian of Spitsbergen, and described them as showing two external nostrils and an internal nostril, the latter confluent with the posterior external nostril. Romer (1933, fig. 53B) illustrated the choana in *Eusthenopteron*, on data from Bryant, Watson, and Stensiö. Säve-Söderbergh (1933) mentioned internal nostrils in *Dictyonosteus* and *Osteolepis*, referring to Stensiö (1922) and Watson (1926), and named a group Choanata, comprising Dipnoi, Crossopterygii, and tetrapods. Nielsen (1936, p. 32, figs. 14, 15) restored an internal nostril in an undetermined coelacanth from the Triassic of East Greenland. Jarvik (1942, figs. 80, 81) reproduced Nielsen's figures and reinterpreted the "choana" as the canal for the buccal nerve.

Holmgren and Stensiö (1936) reproduced Watson's (1926) figure of *Eusthenopteron* and Stensiö's (1932) figures of the Spitsbergen crossopterygians, now determined as *Porolepis*, both showing an internal nostril. In a footnote (p. 348) they referred to Watson and Day's identification of a choana in the middle of the palatine of *Glyptopomus*, and said that Säve-Söderbergh has found that the opening "ihre normale Lage hat."

Westoll (1937, p. 28) wrote of crossopterygians "there is typically a single external nostril and an internal nostril on each side: in early forms (e.g., *Thursius*, *Diplopterus* [= *Gyroptychius*]) the external and internal nares may be confluent, the former being merely notches in the dermal bones of the lip." Also in 1937, Jarvik described the nasal capsule of two species of *Eusthenopteron* from the Baltic, and showed a large ventral opening identified as the fenestra choanalis. Finally, in 1937 Romer described the nasal capsule of *Ectosteorachis* with a ventral opening "to the choana." He named a group Choanichthyes to include lungfishes and crossopterygians.

So far as we know, this review covers all the primary literature on crossopterygian choanae prior to Jarvik's 1942 monograph. Before commenting on that, it is worth summing up this early work. By 1940, the literature contained references to internal nostrils in 12 genera of Paleozoic crossopterygians: *Megalichthys*, *Glyptopomus*, *Dictyonosteus*, *Osteolepis*, *Gyroptychius*, *Rhizodopsis*, *Diplocercides*, *Eusthenopteron*, *Porolepis*, Nielsen's undetermined coelacanth, *Thursius* and *Ectosteorachis*. Three of these (*Dictyonosteus*, *Diplocercides* and Nielsen's fish) are coelacanths, and the openings concerned were reinterpreted after the discovery of *Latimeria*. In *Osteolepis* and *Rhizodopsis* no internal nostril had been described—the references were mistaken. In *Glyptopomus* the only illustrated specimen was wrongly interpreted. In *Gyroptychius* and *Thursius* Jarvik later (1948, p. 36) maintained that Westoll's observations were based on broken specimens. In *Porolepis*, *Ectosteorachis*, and Jarvik's Baltic *Eusthenopteron* all that had been described was a ventral opening of the endoskeletal nasal cavity, not an opening in the roof of the mouth. But all these names surely contributed to a climate of opinion in which Watson could write "the internal nostrils found in all osteolepids," Säve-Söderbergh and Romer could name the Choanata and Choanichthyes, and so on. The only unchallenged information that had been presented was Watson's restoration of *Eusthenopteron* and his account of *Megalichthys*. And in the museums of the world no single specimen had been reported that might be shown to the skeptical enquirer anxious to judge the size and position of this opening for himself.

Jarvik (1942) presented uniquely detailed accounts of snout structure in *Porolepis* and *Eusthenopteron*. In *Porolepis* no palate was described, so that the opening in the palate, the fenestra exochoanalis (p. 372) could not be described. In *Eusthenopteron* he gave an extraordinarily thorough and well-illustrated description of the fenestrae endo- and exochoanalis, and the structures surrounding them. This account was based primarily on two serially-ground specimens, one of which

(series 1) lacked the palate, while the other was complete only on one side, and there the palate was thrust up into the nasal capsule (Jarvik, 1942, pls. 11, 12). Jarvik's restoration of the fenestra exochoanalis was based mainly on this second series, but that opening is labeled in one other specimen (pl. 8, fig. 1).

We have prepared four BMNH specimens of *Eusthenopteron foordi* to show the nasal capsule and surrounding structures. The most informative of these is P. 60310 (figs. 13, 14), an acid-prepared specimen consisting of a snout, both palates, and the maxilla and cheek bones of one side. Our specimens confirm the accuracy of Jarvik's account of these bones, and we will comment only on the choana.

Our restoration of the fenestra exochoanalis and surrounding bones (fig. 14) differs in several ways from Jarvik's (1942, fig. 56—since much reproduced and redrawn, e.g., Jarvik, 1954, fig. 25; 1966, fig. 17B; 1972, fig. 73B; Romer, 1966, fig. 101; Panchen, 1967, fig. 3; Thomson, 1968, fig. 2B; Vorobyeva, 1977a, fig. 3C). In his restoration the fenestra exochoanalis is a drop-shaped opening bounded anteromedially and anterolaterally by the notch between the vomer and premaxilla, posterolaterally by the maxilla, and posteromedially by the dermopalatine. The opening has a maximum width (at the dermopalatine/vomer junction) of about 12 (1942) to 15 (1972) percent of the total width of the snout at that point, and a maximum length about equal to the greatest width of the vomer (1942) or somewhat more than that (1966, 1972). In our restoration, the opening has the same boundaries as in Jarvik's, but its medial border is irregular, and it is much smaller, almost equal in length to Jarvik's, but with a maximum width of only about 5 percent of the width of the snout at the dermopalatine/vomer junction. This difference is due almost entirely to the form of the head of the dermopalatine in the two reconstructions. Jarvik (1942, p. 453, figs. 54A, 56) described the head of the dermopalatine as articulating with the vomer by one surface, a roughened depression facing anteroventrally, and overlapping the posterolateral

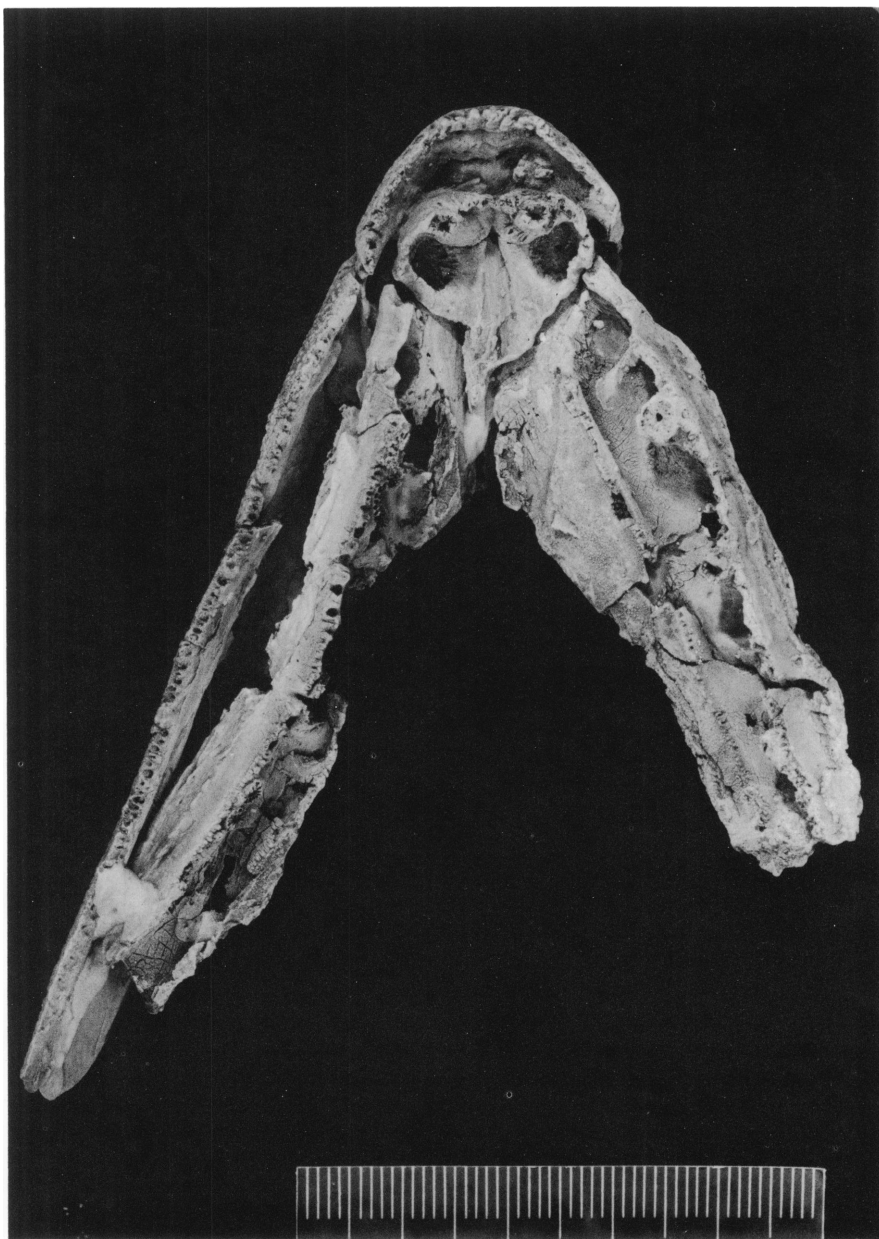


FIG. 13. *Eusthenopteron foordi* Whiteaves. Ventral view of an acid-prepared specimen (BMNH P. 60310, whitened with ammonium chloride) comprising snout, incomplete palates, and left cheek. Compare figure 14.

corner of the vomer. He also argued (1942, p. 457), and has since insisted (1954; also Bjerring, 1967, 1973), that the joint between the palate and the snout was immobile. In

our specimens (P. 60310, acid-prepared, P. 6807, mechanically prepared) the head of the dermopalatine ends in a thumblike process which bears three articular surfaces. The

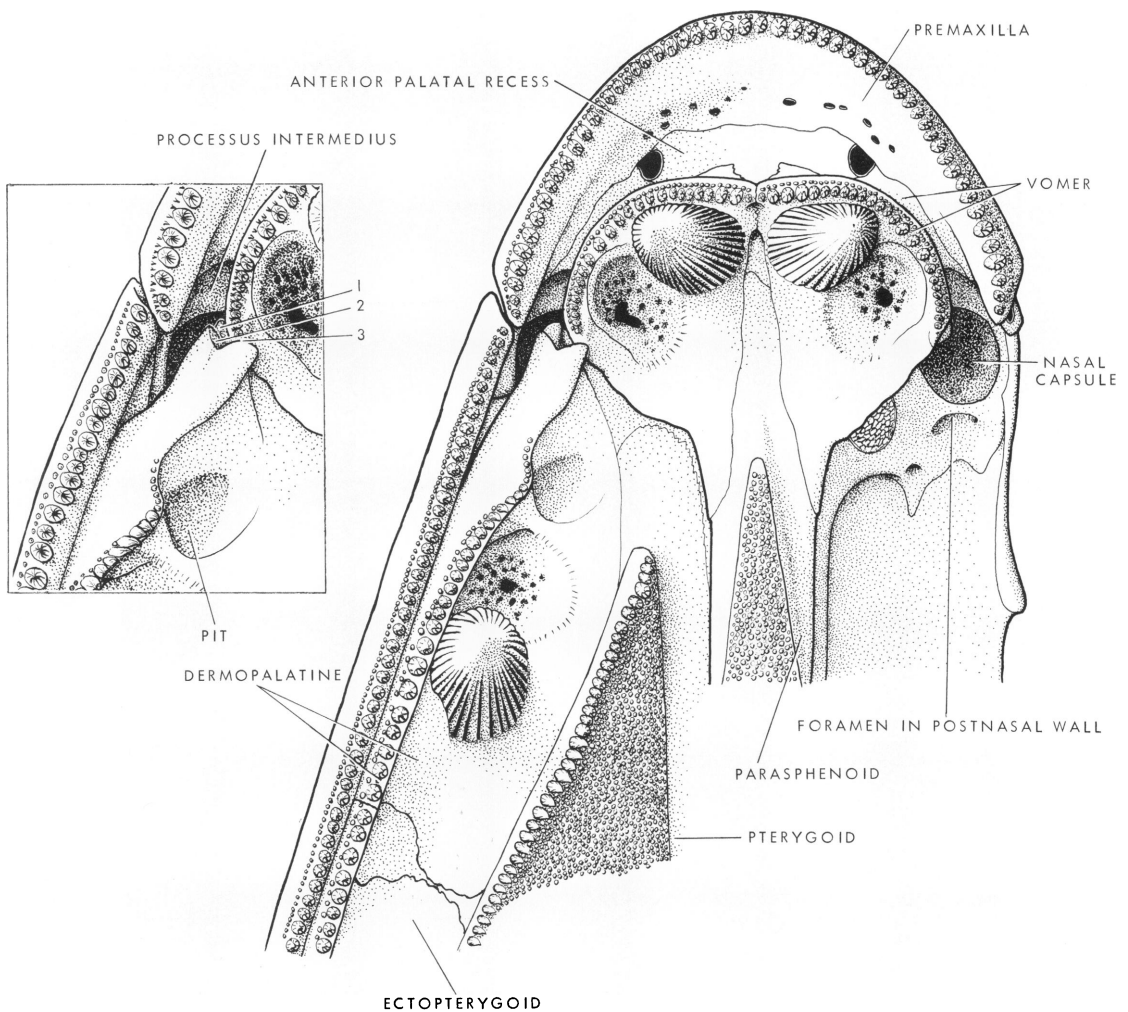


FIG. 14. *Eusthenopteron foordi* Whiteaves. Snout with left palate and maxilla in articulation in ventral view, based mainly on camera lucida drawings of BMNH P. 60310 (fig. 13). Body of parasphenoid and ventral margin of postnasal wall (damaged in P. 60310) drawn from other BMNH specimens. Otherwise, the only restoration in figure is by matching two sides of specimen, restoring damaged teeth, and in articulation of palate and maxilla with snout. Inset, drawn on a slightly larger scale, is an earlier attempt at restoring maxilla and palate in articulation with snout, made before left palate and maxilla of specimen were completely free from matrix and each other. Head of dermopalatine is more closely articulated with vomer and dermopalatine is turned medially more than in the main figure. Numbers 1, 2, and 3 identify three articular facets on the head of the dermopalatine (see text); foramen in postnasal wall is inferred to have been for nerves and vessels (fenestra endonarina posterior of Jarvik); processus intermedius is endoskeletal lining of processus dermintermedius; pit in dermopalatine (labeled on inset) is inferred to have accommodated fang of first coronoid. For other structures, see Jarvik (1942).

most dorsal of these (1, fig. 14) corresponds with the one described by Jarvik. It faces anteroventrally and articulates with a flat surface on the dorsal side of the posterolater-

al corner of the vomer. The second articular surface (2, fig. 14) lies ventrolateral to the first, faces anteromedially, and articulates with a facet on the lateral face of the vomer,

separated from the dorsal surface by a crest. The third surface (3, fig. 14) is the most ventral, faces anterolaterally, and articulates with a facet on the posteromedial face of the vomer, above the hind end of the vomerine tooth row. In Jarvik's figures, the external and internal tooth rows on the dermopalatine extend forward to the junction with the vomer, and are continuous with the corresponding tooth rows on the vomer so that the fenestra exochoanalis has a toothed medial margin, as in *Ichthyostega* (fig. 10; Jarvik, 1952). In our specimens, the external tooth row of the dermopalatine is absent on the anterior part of the bone, and the larger, internal teeth decrease in size and fade out on the upward-sloping part of the bone behind the fenestra exochoanalis, and the thumblike articular process of the dermopalatine is toothless.

Because of these differences in the head of the dermopalatine, the fenestra exochoanalis is much smaller in our reconstruction than in Jarvik's. When the dermopalatine is placed in articulation with the vomer, it rocks in the dorsoventral plane and in the horizontal plane, pivoting on the articulation between the processus apicalis of the palatoquadrate and the lateral ethmoid (fig. 14; Jarvik, 1942, figs. 54, 55). The lateral surface of the dermopalatine and ectopterygoid was closely and apparently immovably bound to the maxilla and lacrimal (cf. Jarvik, 1942, pl. 13, figs. 3-5). If the rostral end of the palate was mobile, the rostral end of the maxilla and lacrimal must also have been movably articulated with the snout. That this was so is indicated by the fact that the two joints (dermopalatine/vomer and lacrimal + maxilla/premaxilla + lateral rostral) are in the same transverse plane (figs. 13, 14), and by the form of the joint surfaces on the medial face of the anterior part of the lacrimal and on the lateral face of the lateral rostral and supraorbito-tectal (Jarvik, 1944a, fig. 7B, od. La + Mx). These two surfaces are a poor match, and that on the lateral rostral and supraorbito-tectal shows blurred margins, quite different from the sharply defined overlap areas of immobile dermal bones such as the supraorbital. We therefore believe that

the palatoquadrate/cheek unit was movably articulated with the snout.

Thus our interpretation of the fenestra exochoanalis differs from Jarvik's in two particulars: our opening is smaller, and is traversed by a mobile joint-plane. Nevertheless, the opening does communicate with the nasal capsule in the fossils, and could still be a choana (though we are aware of no choanate with a joint through the choana). But if we attempt to restore a choanal tube leading from the fenestra exochoanalis to the nasal capsule, the passage is severely restricted by the processus intermedius (endoskeletal; fig. 14) and the processus dermintermedius of the lateral rostral, which occlude the anterior and widest part of the opening (cf. Jarvik, 1942, figs. 47, 48, 52, 53, 56, 58). This means that a choanal tube would have had to turn medially to enter the nasal capsule beneath the posterior part of the processus intermedius. But here we meet another problem. In the lateral ethmoid (postnasal wall, Jarvik) of *Eusthenopteron* there is a large foramen (fig. 14). In 1937 Jarvik interpreted this as having "most probably transmitted the truncus infraorbitalis (the ramus maxillaris trigemini and the ramus buccalis of the nervus facialis) and its accompanying vessels" (Jarvik, 1937, p. 98, fig. 13). This is a reasonable interpretation, since it brings *Eusthenopteron* into line with other primitive fishes, in which there is a large canal in the postnasal wall (*Porolepis*, Jarvik, 1942, fig. 36; *Glyptolepis*, BMNH P. 47838), presumably transmitting the orbitonasal sinus, in addition to nerves. But in 1942 Jarvik reinterpreted the opening in *Eusthenopteron* as the fenestra endonarina posterior, or nasolacrimal duct. This interpretation raises certain difficulties (Thomson, 1964; Schmalhausen, 1968), principally, in our view, because it leaves no room for the substantial venous drainage of the snout which one would expect (cf. Jarvik, 1942, p. 481; Thomson, 1964, p. 330). Furthermore, the nasolacrimal duct does not pass through the endoskeleton in primitive tetrapods: in living amphibians, the duct passes through the fenestra endonarina communis except in the plethodontids *Plethodon*, *Hydromantes*, and *Batrachoseps*, and

in postmetamorphic *Breviceps adspersus* among anurans (Jurgens, 1971; Presley, personal commun.); in primitive fossil tetrapods the duct penetrates the lacrimal from end to end, like a sensory canal (Watson, 1940, fig. 22; Panchen, 1977, fig. 8; Heaton, 1979, fig. 15). In *Eusthenopteron*, Jarvik's (1942, fig. 57) reconstruction of the cavities in the snout shows the canal in the postnasal wall (labeled f. enp.) to be directly in line with a canal of roughly equal size, the nasobasal canal (c.n.-b.) running into the rostrum from the anterior wall of the nasal capsule, and breaking up into three branches. It is the same in our acid-prepared specimen: looking forward through the opening in the postnasal wall, one looks directly into the posterior opening of the nasobasal canal. If we restore the truncus infraorbitalis and vessels running through the ventrolateral part of the nasal capsule, from the opening in the postnasal wall to the nasobasal canal, they occlude the only space available for a choanal tube (cf. Jarvik, 1942, fig. 57).

We do not suppose that these remarks will convince the reader that *Eusthenopteron* had no choana, and that is not our intention. We wish only to show that interpretation of the opening in the palate as a choana raises certain difficulties, and is at least debatable. And there are other, non-choanate fishes with a comparable opening in the palate. In *Polypterus* the opening (fig. 12, palatal fenestra) lies beneath the anterior part of the nasal capsule, between the premaxilla, maxilla, and dermopalatine, and is large in young fishes. In paleoniscoids such as *Mimia* (Gardiner and Bartram, 1977, fig. 2) there is a notch between the premaxilla and vomer, similar to the notch between those bones in osteolepiforms (fig. 15), and when the dermopalatine and maxilla are in place, there is a drop-shaped opening between the four bones, as in *Eusthenopteron*. This opening lies behind the nasal capsule, and does not communicate with the latter as it does in *Eusthenopteron*. But our main reasoning for questioning the existence of a choana in *Eusthenopteron* is that the nose does not match the condition in other primitive choanates (dipnoans, ichthyostegids, and other primi-

tive tetrapods—temnospondyls, lepospondyls, anthracosaurs, hynobiids). In these, the two nostrils are separated only by a narrow bar of tissue (in ichthyostegids, loxomatids, and anthracosaurs by the inturned anterior end of the maxilla; fig. 10, cf. Panchen, 1967, p. 407), and the infraorbital sensory canal is interrupted. Instead, if *Eusthenopteron* is a choanate, it shows a derived condition of the snout, with the external nostril well above the edge of the mouth, and an uninterrupted infraorbital canal beneath it, as in advanced amphibians (Schmalhausen, 1968; see p. 226 on the infraorbital canal of *Ichthyostega*).

If *Eusthenopteron* had no choana, then both external nostrils must have opened through the single fenestra exonarina, as Panchen (1967, p. 402) suggested. We note that this is also the case in *Polypterus* (fig. 11), *Laccognathus* (Vorobyeva, 1980), and, according to Jarvik (1966) in *Holoptychius* (fig. 17D).

Since Jarvik's 1942 account of the fenestra exochoanalis in *Eusthenopteron*, a similar fenestra has been illustrated (see fig. 15) in the osteolepiforms *Glyptopomus kinnairdi* (Jarvik, 1950, pl. 5, fig. 2; 1966, fig. 16C, D), *Eusthenodon waengsjoei* (Jarvik, 1952, pl. 16, fig. 2, text-fig. 29), *Panderichthys rhombolepis* (Vorobyeva, 1975, fig. 2), *Thursius estonicus* (Vorobyeva, 1977a, fig. 3) and *Gyroptychius pauli* (Vorobyeva, 1977a, figs. 3, 29). Among these five genera *Glyptopomus*, *Panderichthys*, and *Eusthenodon* have fangs at the tip of the dentary and differ from *Eusthenopteron*, *Latvius*, and *Thursius* which lack them (Jarvik, 1966, p. 57). The dentary fangs of *Glyptopomus*, *Panderichthys* and *Eusthenodon* fitted into the anterior palatal recess when the mouth was closed (Jarvik, 1966, fig. 16C), and this suggested the possibility that the other opening in the palate, the fenestra exochoanalis, might have been occupied by the fangs of the anterior coronoid. We have examined the specimen of *Glyptopomus* illustrated by Jarvik (1966, fig. 16C), and find that the tip of the first coronoid fang is preserved beneath the dermopalatine in about the same position as the depression in the dermopalatine of *Eusthe-*

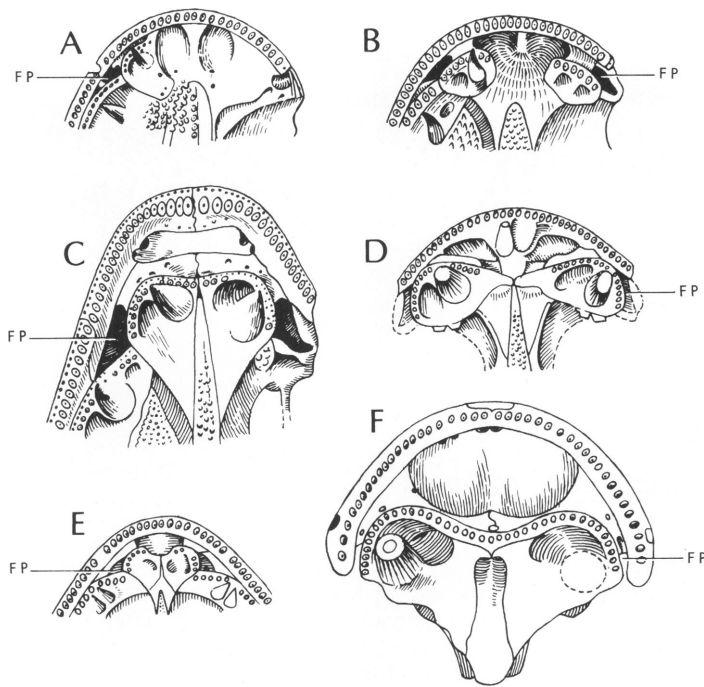


FIG. 15. Reconstructions of snouts of rhipidistians in ventral view to show variations in fenestra in palate (fp). A, *Porolepis brevis* Jarvik; B, *Thursius estonicus* Vorobyeva; C, *Eusthenopteron foordi* Whiteaves; D, *Megalichthys hibberti* Agassiz; E, *Gyroptichius pauli* Vorobyeva; F, *Panderichthys stolbovi* Vorobyeva. After Vorobyeva (1977a, fig. 3).

nopteron which we assume housed a coronoid fang (pit, fig. 14). However, the specimen is dorsoventrally flattened, and the jaws displaced laterally. Janvier (personal commun.) informs us that in an undetermined osteolepiform which he obtained in the Upper Devonian of Turkey the opening in the floor of the nasal capsule is in the matching position to some fangs in the lower jaw. And Jessen (1966, fig. 5B, C) illustrated an undetermined osteolepid lower jaw in which the fangs of the first coronoid are placed laterally, just inside the dentary tooth row, and posterolateral to the pit for the vomerine fang. If Jessen's picture is accurate, the coronoid fangs would surely fit into the fenestra exochoanalis (fig. 16A). In *Panderichthys*, where the opening lateral to the dermopalatine appears very large (Vorobyeva, 1973, pl. 36, fig. 4), the lateral articulation between the palatoquadrate and ethmoid is absent (Vorobyeva, 1980) and there is no pit in the der-

mopalatine. The coronoid fangs must have fitted into the "choana" (fig. 16B).

In porolepiforms, Jarvik had no information on the fenestra exochoanalis in 1942 (p. 372). In 1966, he restored the fenestra in *Porolepis brevis* (his fig. 2A), adding information from *Glyptolepis*. Since the porolepiform dermopalatine is well known only in *Glyptolepis groenlandica* (Jarvik, 1972, p. 189) we assume that the restoration of *Porolepis* includes the dermopalatine of *Glyptolepis*, so that the shape and size of the fenestra exochoanalis are conjectural.

In *Glyptolepis*, the fenestra exochoanalis (Jarvik, 1972, figs. 30, 31, pl. 22, fig. 1) is restored as a triangular opening, with a smooth outer border formed by the premaxilla and maxilla, and an angled inner margin formed by the junction of the vomer and dermopalatine. The opening is very small, with a maximum width of about 3 percent of the breadth of the snout at that level. This res-

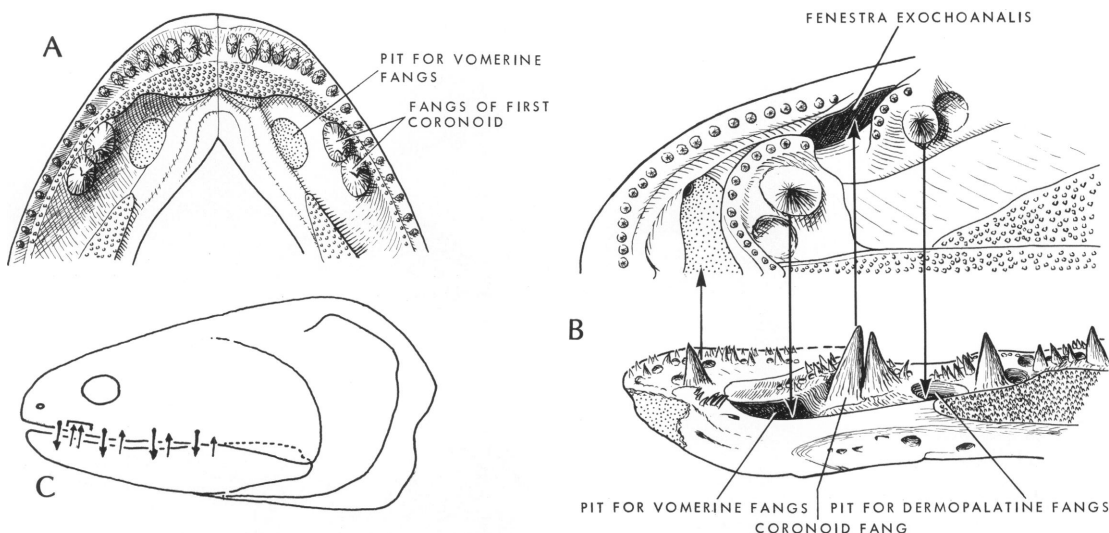


FIG. 16. Possible occlusal relationships between coronoid fangs and fenestra exochoanalis in osteolepiforms. A, reconstruction of anterior part of lower jaw, in dorsal view, of an undetermined osteolepidid from the Frasnian of Bergisch Gladbach, West Germany, after Jessen (1966, fig. 5B). Note positional relationships of coronoid fangs and pit for vomerine fangs, compare figure 14; B, *Panderichthys rhombolepis* (Gross). Reconstruction of left half of snout in ventral view (after Vorobyeva, 1975, fig. 2) and of anterior part of right lower jaw in medial view (after Vorobyeva, 1962, fig. 30, reversed). Arrows mark approximate boundaries of pits or openings expected in opposing jaw to house fangs. Endoskeleton stippled in A and B; C, *Eusthenopteron foordi* Whiteaves, outline of head (after Jarvik, 1944a, fig. 2), with upper and lower fangs (represented by arrows) added (after Jarvik, 1944a, figs. 11B, 13). Bracket covering tips of fangs of first coronoid is position of choana in Jarvik's reconstruction (1944a, fig. 13).

toration is based primarily on Jarvik's serially ground specimen. In the published sections, the right fenestra exochoanalis is not present in no. 50 (1972, fig. 8B), is shown in nos. 58 and 62 (1972, figs. 66C, 8C), and has disappeared by no. 67 (1972, fig. 32A). The left fenestra exochoanalis is not present in no. 58, is shown in nos. 61, 62 and 67 (1972, figs. 76B, 8C; 1963, fig. 13A) and has disappeared by no. 72 (1966, fig. 1A). This gives the opening a maximum rostrocaudal extent of less than 1.5 mm. (section interval 100 μ .) in a fish of head length about 75 mm. We note that the dermal bones are displaced on both sides of the sectioned head, and suggest that one would expect some sort of notch in the margin of the palate at the junction of four dermal bones (cf. Jarvik, 1972, pl. 22, fig. 1), and that there are no grounds for regarding such a notch as the choana.

The only other supposed porolepiform in

which a choana has been described is *Powichthys* (Jessen, 1975). The palate of this fish is unknown, and all that has been described is an opening in the floor of the nasal capsule.

In summary, we regard statements like "the choanate condition of the Rhipidistia has been regarded as firmly established" (Panchen, 1967, p. 381) as wholly unwarranted. No satisfactory evidence of a choana in porolepiforms has been produced. In osteolepiforms, the only well-known example is *Eusthenopteron*, and we find the fenestra exochoanalis to be much smaller than in previous restorations. Possible interpretations of that opening are that it was part of a mobile joint between the cheek/palate unit and the snout; and/or that it transmitted nerves and vessels branching from the adjacent truncus infraorbitalis and its accompanying vessels; and/or that it accommodated a coronoid fang (fig. 16).

(E) CHOANA AND NOSTRIL IN TETRAPODS

Our theory is that the choana is the homologue of a fish nostril. Dismissing that theory, Panchen (1967, p. 380) wrote "Arguments against this theory follow closely those used in the rejection of the choanate condition of the Dipnoi and are reinforced by description of the snout in Rhipidistia and the embryology of tetrapods." Arguments concerning the choanate condition of the Dipnoi and the snout of Rhipidistia are discussed in the two preceding sections.

In his comment on "the embryology of tetrapods" Panchen referred to his own summary of the facts (1967, pp. 389–391). He noted that the amniote and apodan choana forms at the oral end of a nasobuccal groove similar to that formed in the ontogeny of Dipnoi and Chondrichthyes. Urodeles and anurans differ in that their choanal tube develops in two portions, an anterior choanal process, reasonably homologized with the nasobuccal groove, and a gut process that grows forward to meet the choanal process. Panchen accepts that this condition is secondary, and cites Medvedeva's and Bertmar's work on the possible relationship between this mode of development and the influence of the infraorbital sensory canal. He concludes that the anuran and urodele mode of development is "probably . . . due . . . to a precocious development of the [infraorbital sensory] canal in the larvae of the ancestral forms" (1967, p. 391).

The theory of the tetrapod choana that we advocate is that it is the homologue of the dipnoan choana, and hence of the excurrent nostril of chondrichthyans. The chondrichthyan excurrent (posterior) nostril lies external to the primary upper lip which, in turn, borders the external edge of the dental arcade of the palatoquadrate. When a secondary upper lip extends forward from the angle of the mouth to the nasal region, this fold of tissue will abut against the nasobuccal groove that connects the excurrent (posterior) and incurrent (anterior) nostrils in chondrichthyans. Given such a development of primary and secondary upper lips as primi-

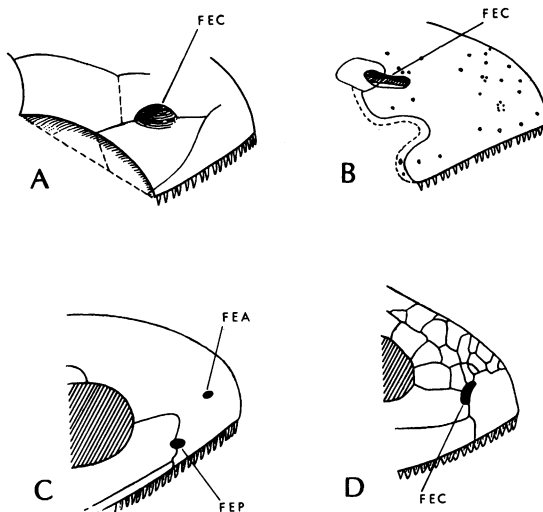


FIG. 17. External nostrils in rhipidistians. A, *Glyptopomus kinnairdi* (Huxley) and B, *Megalichthys hiberni* Agassiz, are osteolepiforms showing our interpretation of a fenestra exonarina communis (fec, cf. fig. 11); C, *Porolepis brevis* Jarvik; and D, *Holoptychius* sp., are porolepiforms, the first with separate anterior (fea) and posterior (fep) fenestrae exonarinae, the second with a fenestra exonarina communis, as in A and B (A, B after Jarvik, 1966, fig. 14B, C; C, D after Jarvik, 1972, fig. 7A, C).

tive for osteichthyans, the dorsal migration of the nasal placode during embryogenesis displaces both nostrils external to the secondary upper lip, which includes the dermal bones of the maxillary-premaxillary arch and its dental arcade. This migration from the primitive ventral position of the placode explains the position of the nostrils on the side of the snout in front of the eye in cladistians, actinopterygians, rhipidistians and actinistians.² The choanate condition (dipnoans,

² We note Panchen's (1967, p. 380) summary of the controversy over whether the teleostean nasal placode migrates up the tip of the snout, so reversing its rostro-caudal direction, the anterior nostril becoming the posterior and vice versa, or migrates up the side of the snout, so that the orientation of the nostrils is unchanged. Since, as Panchen says, it is the placode not the nostrils that migrates, and the nostrils differentiate subsequently, we consider it immaterial whether the choana is homologized with the excurrent or incurrent nostril of other osteichthyans.

tetrapods) arose by a modification of this primitive osteichthyan pattern, in which the placode failed to migrate, and the excurrent nostril came to open in the roof of the mouth, between the primary and secondary upper lips. As one consequence of this modification, the secondary upper lip and outer dental arcade were interrupted in primitive choanates. This condition is shown by the "hard-snouted" dipnoans (figs. 7, 8), and is hardly modified in larval urodeles (e.g., Schmalhausen, 1968, fig. 90) and in primitive fossil tetrapods such as *Ichthyostega* and other genera reviewed by Panchen (1967, pp. 402-407), where the choana and external nostril are separated only by an inturned prong of the maxilla (fig. 10B). A second consequence of this modification was interruption of the infraorbital sensory canal, as in dipnoans and primitive tetrapods. One prediction of our interpretation is therefore that the lateral rostral of *Ichthyostega* (Jarvik, 1952), a tubular ossicle carrying the infraorbital sensory canal between the nostrils, does not exist. In more advanced tetrapods, the

distance between the choana and the external nostril increased, and in those forms with aquatic larvae, restoration of continuity of the infraorbital sensory canal entailed a further modification of choanal ontogeny, the development of a gut process.

Other predictions of our hypothesis (see fig. 17) are that the porolepiforms, if correctly restored with two external nostrils, had no choana; and that osteolepiforms, if correctly restored with one external narial opening, either had two narial tubes emerging from that opening (like *Polypterus*) and no choana, or were choanates exhibiting an advanced condition of the nostrils, with a secondarily intact infraorbital canal between the choana and external nostril. Since the second interpretation demands the independent acquisition of an uninterrupted infraorbital canal, we favor the first. *Panderichthys* is restored as an osteolepiform with two external nostrils. If correct, this would corroborate our view that other osteolepiforms had a fenestra exonarina communis.

NASOLACRIMAL DUCT, LABIAL CAVITY, ROSTRAL ORGAN, AND JACOBSON'S ORGAN

As noted above in the Introduction, the nasolacrimal duct of amphibians and the labial cavity of *Neoceratodus* (figs. 18-20) have similar anatomical relations and ontogenetic histories (figs. 18, 19). The only other structure in gnathostomes anatomically similar to these dipnoan and tetrapod features is the rostral organ of actinistians. The rostral organ, which is known in some detail in *Latimeria* (fig. 22) (Millot and Anthony, 1965) is, like the labial cavity in *Neoceratodus*, filled with a cavernous mucosa, partly fills the region of the snout between the orbit and the nasal capsule, and opens by pores to the outside. The rostral organ, however, is very extensive, the right and left ones are interconnected in the midline and, on each side, there are three pores opening to the outside, one on the snout and two between the orbit and the posterior external nostrils.

Jarvik (1942) followed Allis (1932a) in pro-

posing that the nasolacrimal duct of tetrapods is homologous with the posterior external nostril in bony fishes. He saw in *Eusthenopteron* a canal in the endocranial postnasal wall connecting the nasal capsule with the orbit approximating the course of the nasolacrimal duct of tetrapods, that *Eusthenopteron* has but a single external narial opening in the dermal bones of the snout and that *Porolepis* lacks the canal but has a normally developed posterior external nostril as well as an anterior one. From this he concluded that the posterior external nostril of *Eusthenopteron* has sunken into the endocranium of the snout to form a primitive nasolacrimal duct, but that in *Porolepis* the posterior external nostril is essentially unmodified. What, to us, seems basically unconvincing about Jarvik's proposal is that the canal in the endocranium of *Eusthenopteron* exactly parallels the course of the

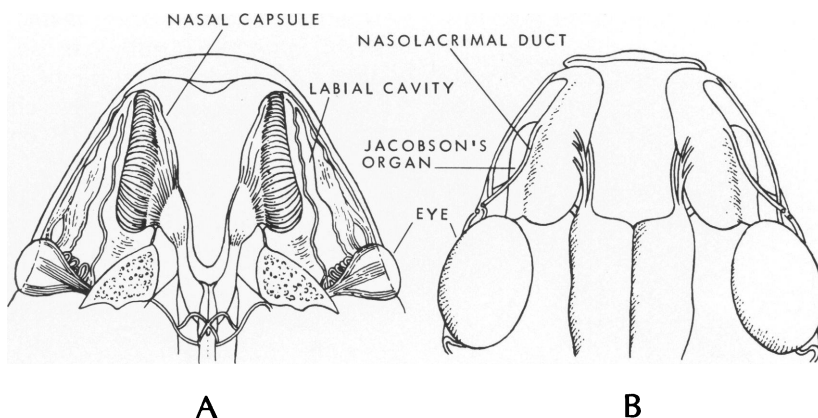


FIG. 18. Dissected snouts, in dorsal views, of A, *Neoceratodus forsteri* (Krefft) and B; larval *Triturus alpestris* (Laurenti), to show position of lungfish labial cavity and tetrapod nasolacrimal duct (A, after Jarvik, 1942, fig. 11A; B, after Jarvik, 1942, fig. 19B).

maxillary and buccal nerves and accompanying vessels as they emerge from the anterior orbital wall and pass forward into the posterior wall of the nasal capsule in elasmobranchs, *Polypterus*, *Amia*, dipnoans, and urodeles and that there might well have been an anterior and posterior nostril separated only by soft tissue as was probably true of *Laccognathus* (Vorobyeva, 1980) and *Holoptychius* (the nariodal bone shown by Jarvik within the external nasal opening has been included in the nasal opening of *Holoptychius* by supposition, not by observation). At best, Jarvik's proposal ignores a simpler interpretation of the *Eusthenopteron* canal based on frequently observed and widespread anatomical relations of gnathostomes.

Although Schmalhausen (1968), like Jarvik (1942) before him, had accepted Allis's (1932a) theory of the transformation of the fish posterior nostril into the nasolacrimal duct and the development of the choana as a neomorph (hence, a third functional opening in the nasal sac of choanates), Schmalhausen disagreed with Jarvik and Allis by proposing that the nasolacrimal duct incorporates material from the cephalic lateral line system, resulting in an interrupted infraorbital canal.

We have two major objections to Schmal-

hausen's theory, as well as to all others (e.g., Allis, 1932a; Jarvik, 1942; Bertmar, 1965, 1968) postulating a former occurrence of two pairs of posterior nares. One is that a theory in which the nasolacrimal duct is said to form from a seismosensory canal and a nostril is inconsistent with the fact that the nostrils are fully developed in urodeles prior to metamorphosis, whereas the nasolacrimal duct appears later and, except in salamandrids, becomes confluent with the nasal sac. Schmalhausen's and Allis's theory requires the presence of a posterior external nostril prior to metamorphosis and this is not observed in any choanate animal. The second objection is that no vertebrate animal is known to have had three pairs of nostrils.

We see our own theory, in which the nasal placode fails to migrate outward and upward to the side of the snout as in other fishes, as more simply accounting for the presence of the two nostrils (an anterior one and a posterior one, or choana) in tetrapods, and in dipnoans. This theory, as outlined above (pp. 195–196), interprets the external nostrils of actinopterygians, actinistians, and rhipidistians as a result of ontogenetic migration of the nasal placode.

Nevertheless, we find much merit in Schmalhausen's ideas, particularly as they pertain to the homologies of the nasolacrimal

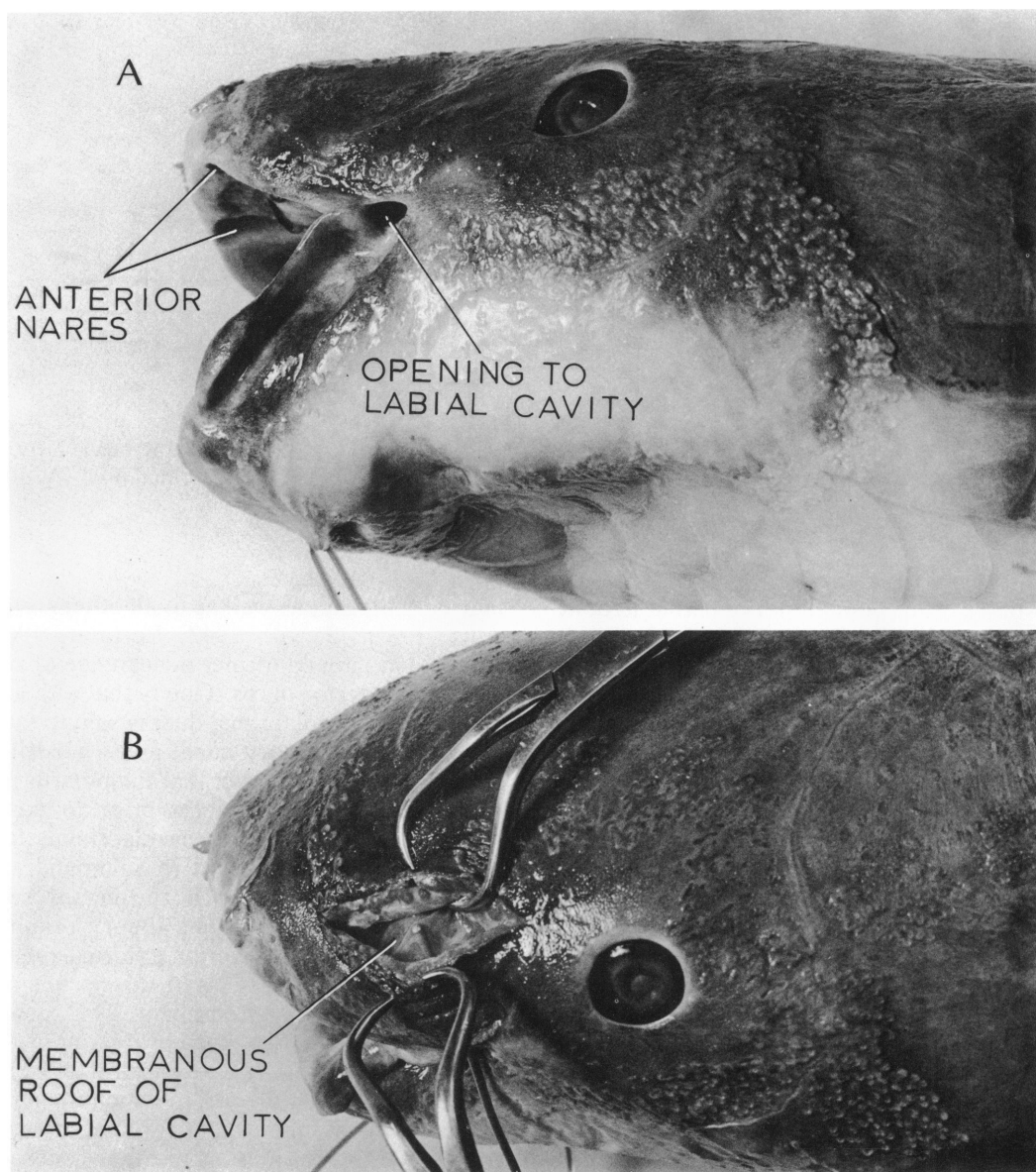


FIG. 19. *Neoceratodus forsteri* (Krefft), approximately 120 cm. total length, AMNH 40800. Photographs of head to show A, opening of labial cavity; and B, membranous roof of cavity with a probe inserted.

duct. We find interesting, for example, the topological and dependent developmental relations between the duct and the lacrimal and septomaxillary bones (fig. 23), as well as the fact that extensions of the infraorbital canal can become confluent with the nasal sac, as

indications that the duct could have had a seismosensory origin.³ If, as discussed

³ Schmalhausen argued that the nasolacrimal duct forms from a detached extension of the infraorbital lateral line canal that has become confluent with the nasal

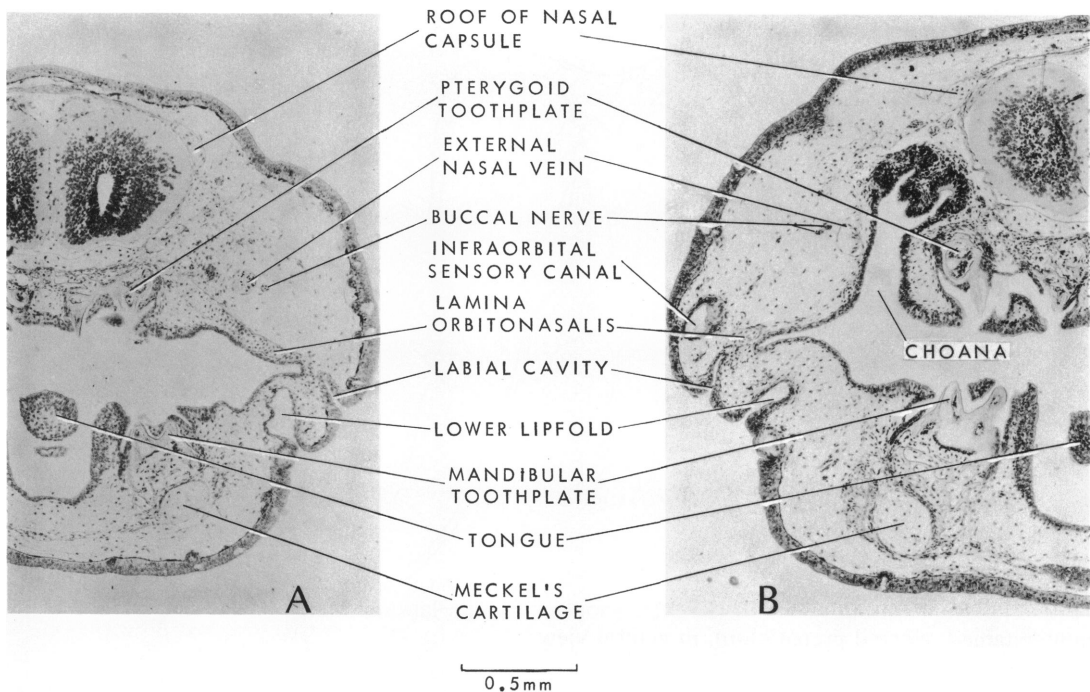


FIG. 20. *Neoceratodus forsteri* (Krefft). Transverse sections through deepest part of labial cavity in 27 mm. (A) and 34.5 mm. (B) larvae (series F120, F121, Hubrecht Laboratory, Utrecht; same series used by Fox, 1965). Labial cavity at these stages is a deep pit at angle of mouth, whose apex is close to distal end of lamina orbitonasalis, and is attached to latter by connective tissue. This relationship is maintained in the adult, where cavity is greatly enlarged by increase of gape.

above, the labial cavity of *Neoceratodus* and the rostral organ of *Latimeria* might be homologues of the tetrapod duct, and if the duct has a seismosensory origin, then one should expect to find in the labial cavity, rostral organ, and in the primitive tetrapod duct,

sac because: (a) the formation of the lacrimal and septomaxillary bones is dependent on the presence of the nasolacrimal duct (Schmalhausen cites the experiments of Medvedeva, 1959, 1960, in which the anlage of the duct was removed and the two bones failed to develop); (b) the lacrimal and septomaxillary bones are membrane bones that, at metamorphosis, come to surround completely the nasolacrimal duct but underlie the duct at first—thereby closely resembling the development of seismosensory canal bones in bony fishes (Schmalhausen's fig. 103 shows these relations in a larva of the urodele *Onychodactylus*); and (c) parts of the infraorbital canal are known to become confluent with the nasal sac in some fishes (Schmalhausen illustrates this, fig. 104, in an individual of *Amia*).

sense organs comparable with neuromasts and an appropriate innervation. So far as presently known, the rostral organ of *Latimeria*, according to Millot and Anthony (1965), has an extensive innervation entirely from the n. ophthalmicus superficialis (V) which is characteristically associated with lateral line innervation (see, e.g., Strong, 1895; Norris, 1913). Fibers from at least the ventral branches of the n. buccalis would not be expected in the rostral organ since *Latimeria* has a well-developed and uninterrupted infraorbital canal; n. buccalis innervates neuromasts of the posterolateral snout region between the eye and anterior nostril. Do the nerve fibers in *Latimeria* go to some form of seismosensory organ? Are there such organs in the labial cavity of *Neoceratodus* and are they innervated by n. ophthalmicus superficialis? Do the nasolacrimal ducts of the anuran *Xenopus* and apodans,

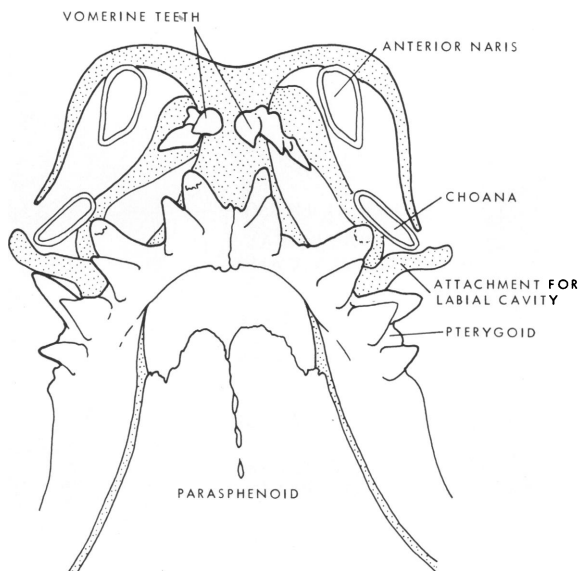


FIG. 21. *Neoceratodus forsteri* (Krefft). Snout of 15 mm. larva, AMNH 40801 (alcian blue/alizarin counterstained, cleared preparation), in ventral view.

which are associated with tentacular organs of presumed sensory function, have a similar innervation and are there seismosensory organs in the nasolacrimal ducts which, in the

Salamandridae, do not become confluent with the nasal sac? Future work will decide. If Schmalhausen's theory is correct, however, the duct should be associated ontoge-

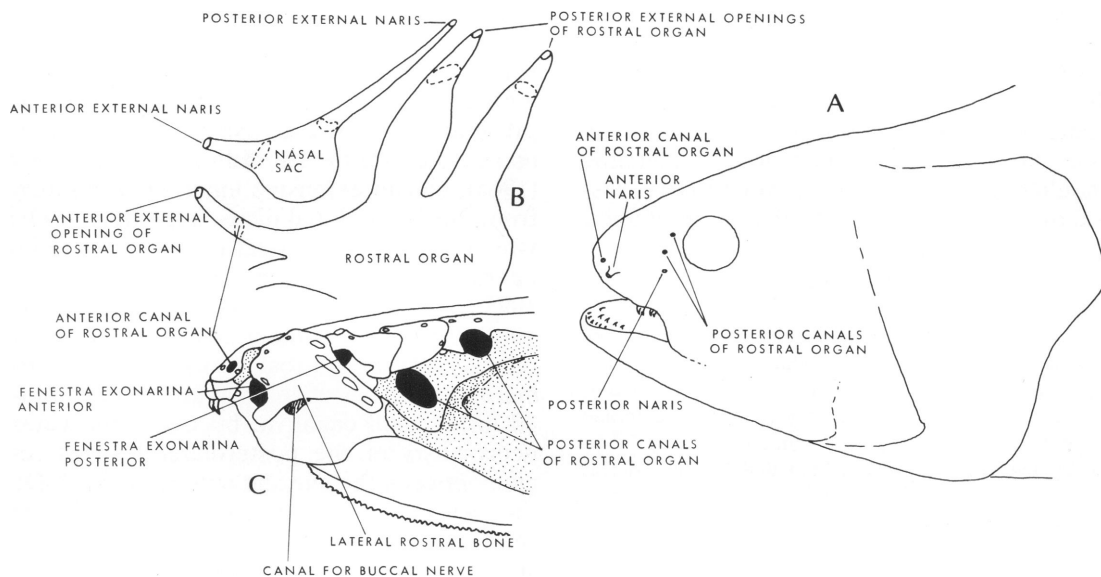


FIG. 22. *Latimeria chalumnae* Smith. A, outline of head to show nostrils and openings of rostral organ; B, diagram of rostral organ and nasal sac of right side in dorsal view; C, snout in lateral view (A, after Millot and Anthony, 1958; B, C, after Millot and Anthony, 1965).

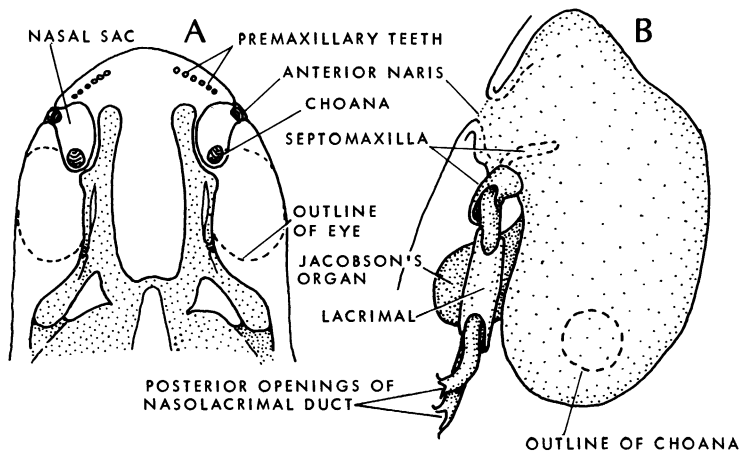


FIG. 23. Nasal structure in hynobiid urodeles. A, *Ranodon sibiricus* Kessler, diagrammatic reconstruction of snout of a 22 mm. larva, ventral view; B, *Onychodactylus fischeri* (Boulenger), diagrammatic reconstruction of left nasal sac of 85 mm. (postmetamorphic) individual in dorsal view. After Schmalhausen (1968, figs. 98A, 103).

netically with the infraorbital system and, hence, with n. buccalis, and, if that proves to be the case, it would appear to rule out the n. ophthalmicus superficialis innervated rostral organ of *Latimeria* as a homologue.

We find ourselves in disagreement with one other feature of Schmalhausen's analysis, and that concerns the explanation of the interruption of the infraorbital canal. The interruption typically is at the point where, in lungfishes and tetrapods, the canal meets the nostril and does not appear to be associated with the ontogenetic history of the choana, whatever that history might be. In both groups, the infraorbital canal bends downward toward the oral border [in dipnoans, temnospondyls, lepospondyls, and in those anthracosaurs with a ventrally situated external nostril, and in larval *Necturus* and *Ranodon* (see, e.g., Stensiö, 1947, figs. 2, 24A; Schmalhausen, 1968, figs. 100, 101; Miles, 1977, figs. 18, 35, 111, 112)] and the similarity in the courses of the supraorbital and infraorbital lateral lines is particularly striking between lungfishes and such larval hynobiid urodeles as *Ranodon* (Schmalhausen, 1968, fig. 90). Differences between lungfishes and urodeles in the external form of the snout appear to be associated primarily with turning under of the tip of the snout in

lungfishes. But even this difference appears to be minimal when lungfishes are compared with 22 mm. *Ranodon* larvae in which, according to Schmalhausen's (1968) figure 98A (fig. 23A), the external nostril opens ventrally on the margin of the lip as in lungfishes and ichthyostegids. It is the snout in modern urodeles, anurans, and amniotes that appears to have turned upward, carrying the external nostril into a more dorsal position.

One additional similarity between the nasal apparatus of lungfishes and tetrapods concerns a lateral diverticulum of the nasal sac. In lungfishes it has generally been given the neutral term of diverticulum laterale, whereas in tetrapods it is often identified as a vomeronasal organ or Jacobson's organ. In both groups the diverticulum is a lateral outpocketing of the posterior part of the nasal sac (fig. 24) and consists largely of olfactory epithelium. In the more terrestrial amphibians Jacobson's organ is better developed and is associated with the nasolacrimal duct. In some forms it includes a narrow strip of respiratory epithelium along its dorsal part (Jurgens, 1971, fig. 31). In this dorsal position in at least some *Protopterus* the epithelium appears to be somewhat differentiated and is less nucleated (Bertmar, 1965, fig. 18D). A comparison of Bertmar's (1965) figure 18C of

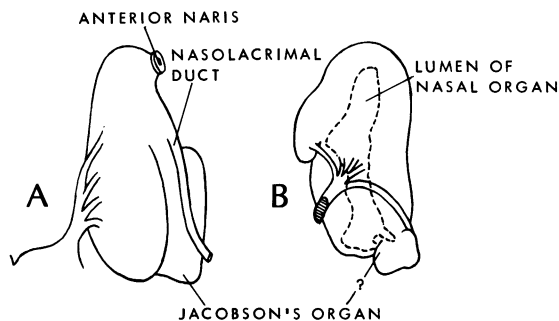


FIG. 24. The nasal sac in A, *Triturus alpestris* (Laurenti); and B, *Protopterus annectens* Owen. A, diagram of right sac in dorsal view, after Jurgens (1971, fig. 39A); B, diagram of right sac, in dorsal view, of 20 mm. larva, after Bertmar (1965, fig. 18B).

a transverse section of the nasal sac and lateral diverticulum of *Protopterus* with comparable sections in various urodeles (Jurgens, 1971, fig. 32; Higgins, 1920, pl. 8, fig. 55; Medvedeva, 1968, fig. 1 showing *Triton* and *Ranodon*) makes it clear why the dipnoan structure has been likened to the tetrapod vomeronasal organ. The similarity is heightened by a comparison of Bertmar's (1965) reconstruction of the whole nasal sac of *Protopterus* (his fig. 18B) and with Jurgens's (1971) of the sac in *Triturus* (his fig.

39A) (fig. 24). Bertmar (1965, 1968) has argued that a large diverticulum laterale is certainly formed in all three dipnoan genera but that "it develops into an olfactory fold as do other lateral diverticles of the nasal sac, and therefore it does not seem to be homologous with the vomeronasal organ . . . in tetrapods." Since the lateral diverticulum is, in fact, an outpocketing of olfactory epithelium in both dipnoans and tetrapods, Bertmar's reasoning escapes us. Perhaps he is saying, however, that because dipnoans have other diverticula, the large posterolateral one cannot be homologous with the tetrapod diverticulum in the same position. We are equally mystified by this argument. The question is: do other gnathostomes besides dipnoans and tetrapods have a lateral diverticulum of this type and in this position on the nasal sac? If the answer is negative, and Bertmar has not suggested that such a modification of the nasal sac occurs elsewhere, the structure in the two groups is most simply regarded as synapomorphic. Bertmar (1965) does not refute Rudebeck's (1945) claim in his study of the forebrain of *Protopterus* that Jacobson's organ is present in the genus as a rudimentary accessory olfactory bulb and that a rudimentary vomeronasal nerve may be formed.

PAIRED FINS AND GIRDLES

(A) PAIRED FIN SKELETON

Although the paired appendages of lungfishes have been cited as precursors of tetrapod limbs (Braus, 1901 and many earlier workers; Holmgren, 1933, 1949a, 1949b, as a precursor of urodele limbs), the osteolepiform crossopterygian fins are today assumed to be closer to the tetrapod structure (Gregory, 1911; Watson, 1913; Westoll, 1943, 1958a; Jarvik, 1964, 1965; Thomson, 1968, 1972; Andrews and Westoll, 1970a, 1970b; Rackoff, 1976, 1980). The favored comparison of osteolepiforms is attributable to their possession of a pair of distal bones (one short and stout, the other long and slender) articulating on a single stout basal radial with a

dorsal process that has been likened to a tetrapod humeral process. The terms humerus, ulna, radius and femur, tibia, and fibula are in general use for the three radial elements in the osteolepiform pectoral and pelvic fins. Preference for the osteolepiform structures seemed to be reinforced by the observation that, at the base of lungfish fins, the principal radials are in a single series with smaller ones radiating outward from each side of the central axis as do the barbs on the rachis of a feather. Moreover, *Neoceratodus* fins were seen to be very similar to those of Paleozoic xenacanth sharks and Gegenbaur (1895) had represented this "archipterygial" fin as the primitive type for gnathostome fishes. It ap-

parently went unnoticed that, during Gegenbaur's era, Semon (1898), in a study of the embryology of the pectoral fin of *Neoceratodus*, showed that the second axial radial element is ontogenetically double.

In reviewing the skeletal anatomy of the paired appendages and their girdles in gnathostomes we have concluded that lungfish fins include synapomorphies with tetrapod limbs and that there are synapomorphies of the fins and girdles in all chondrichthyans and osteichthyans.

Osteichthyan paired fins, as pointed out by Goodrich (1930), are of two kinds, those of sarcopterygians in which pectoral and pelvic fins are constructed according to the same basic plan, and those of actinopterygians in which the pectoral and pelvic differ. The differences between the two groups of bony fishes may be understood by examining the fin skeletons of other gnathostome fishes. In acanthodians all that is known about endoskeletal fin supports is that in *Acanthodes bronni* the pectoral fin has a few small nodules arranged irregularly at the fin base (Miles, 1973). In arthrodires a condition more nearly like that of chondrichthyans has been found, especially in *Brachyosteus dietrichi* Gross, in which the pectoral fin includes a segmented metapterygial axis articulated with a posterior process on the scapulocoracoid and a series of radials arranged along the articular surface of the scapulocoracoid anterior to the metapterygium (Stensiö, 1959, pl. 15, figs. 1–3). The term metapterygium as used here refers simply to one or more basipterygial cartilage or bone segments aligned in series, joined to a posterior articulatory process or surface on the scapulocoracoid, and forming the posterior or trailing endoskeletal support of the fin. In the fin of *Brachyosteus*, as in all primitive shark fins, the metapterygium appears to be a main axis of fin support. An arrangement of fin supports like that of *Brachyosteus* occurs also in the arthrodire *Enseosteus jaekeli* Gross (Stensiö, 1959, pl. 2). In another group of placoderms related to arthrodires, the petalichthyomorphs (Miles and Young, 1977), pectoral radials are also present. In *Gemuendina sturtzi* Traquair, radials are arranged

around the fanlike shoulder girdle, in one row laterally and in three or more rows posteriorly (Stensiö, 1959, fig. 14A). In *Pseudopetalichthys problematicus* Moy-Thomas, all that is known of the endoskeletal support is a pair of somewhat triangular basal elements each of which articulates separately in a notch in the shoulder girdle (Gross, 1962, fig. 7). This last fossil also shows that pelvic radials were present in placoderms, in this case 10 or 11 rods parallel to each other and, as a group, parallel to a more medial elongate bone. Gross (1962, p. 76 and fig. 7) interpreted this elongate bone as a basipterygium (=metapterygium). He described it as having a longitudinal ridge, which makes it unlike the metapterygial axes of other fishes. It seems to us that the row of parallel radials is most simply interpreted as a primitive series of basal radials, and the medial bone lying against the radials on one side, and at the anterior end of the series of radials on the other, as a pelvic girdle. A summary of acanthodian and placoderm fin anatomy indicates that the former have nothing comparable with the rodlike radials of other gnathostomes and that the latter have basal radials but lack the details of endoskeletal anatomy of sharks and bony fishes.

The pectoral fin of living chondrichthyans has often been characterized as tribasal because there are three distinct cartilages articulating with the shoulder girdle that support three or more rows of distal radials. In fossil chondrichthyans the fin anatomy may be much simpler in lacking a definite propterygium along the fin's leading edge and a central cartilage, the mesopterygium, between the former and the metapterygium at the fin's trailing edge (fig. 26A, B). The tribasal fin seems to be characteristic only of some euselachians.⁴ Among non-euselachian chondrichthyans present in the Paleozoic the modern tribasal condition did not exist (Zangerl, in press). Instead, the most general condition, as exemplified by species of *Cladoseleache* (fig. 25A), *Cladodus*, *Cobelodus* (fig. 25B), *Fadenia*, and *Xenacanthus* is the

⁴ Euselachians include all modern sharks and rays, and some fossil groups (Zangerl, in press).

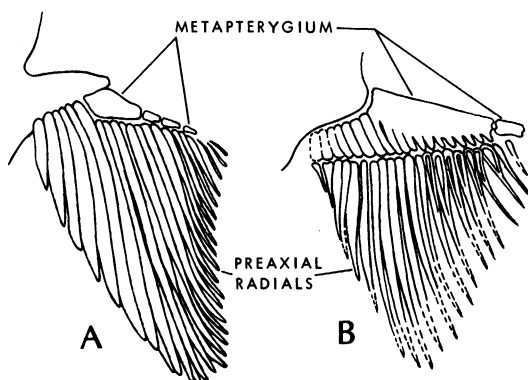


FIG. 25. Left pectoral fin skeleton of A, *Cladoselache brachypterygius* Dean; and B, *Cobelodus aculeatus* Zangerl and Case (after Zangerl, in press, fig. 34).

presence of a well-defined metapterygial axis made of an elongate basal segment that articulates with the girdle followed by one to 13 cuboidal or rectangular segments. On the preaxial side of the metapterygium (facing the fin's leading edge) there are numerous parallel radials arranged at an angle between 70 to 90 degrees with the metapterygial axis. Zangerl (in press) regarded those species with unsegmented radials and a long whiplike metapterygium as being somewhat specialized. He constructed what he considered to be a generalized non-euselachian pectoral (his fig. 35A) in which there are only four metapterygial segments, and proposed that the earliest transition toward the pectoral of modern sharks involved segmentation of radials (his fig. 34). We would state the generalized condition of the pectoral somewhat differently by observing that in Zangerl's cladogram of the main groups of sharks (his fig. 52), in which euselachians and hybodonts are depicted as the sister group to all other sharks, segmented radials are present in both sister groups and that long whiplike metapterygia occur only in groups with cladistically apomorphic positions among non-euselachians. Also characteristic of these primitive shark pectorals is the presence of radials anterior to the base of the metapterygium as in some arthrodires. As many as 10 of these anterior radials attach along the posteroventral mar-

gin of the scapulocoracoid in front of the metapterygium. Various morphologically transitional conditions in some non-euselachians suggest that anterior radials enlarge or fuse to form the propterygium and mesopterygium of euselachians (cf. figs. 25–27). Correlated with the development of a tribasal fin is the shift in the main point of fin articulation from the metapterygium in non-euselachians to the propterygium in euselachians. It is clear, therefore, that cladistic comparisons involving chondrichthyan fin structure should be with a *Cobelodus*-like fin in which there are no more than four or five segments in the metapterygium, seven or eight segmented preaxial radials articulating on the scapulocoracoid anterior to the metapterygial base, and the main axis of fin support on the trailing (metapterygial) rather than leading (propterygial) side of the fin.

The pelvic fin skeleton of chondrichthyans has apparently had a history similar to, but less complex than, that of the pectoral. A metapterygium, also the main axis of fin support, has numerous radials attached along its preaxial surface. In the pelvic skeleton, however, only a few radials extend anterior to the metapterygial base, the metapterygium has only one to three segments distal to the basal articular segment, the metapterygium retains its function as the main axis of support for the fin even in euselachians in which a small propterygial element develops (fig. 26B), and the fin is characteristically either unibasal or (in some euselachians) dibasal. In male chondrichthyans the terminal metapterygial segments (fig. 26B) form internal support for a clasper (claspers are not known to be present in some cladodont sharks).

In the discussion that follows we will interpret actinopterygian paired fin structure as a transformation of a primitive (chondrichthyan) metapterygial fin into a propterygial type, paralleling the development of the euselachian fins, and sarcopterygian fin structure as an alternative transformation of a primitive metapterygial fin into an exclusively metapterygial structure primarily by the loss of all radial elements anterior to the metapterygial base. We feel justified in pursuing these comparisons because the basic

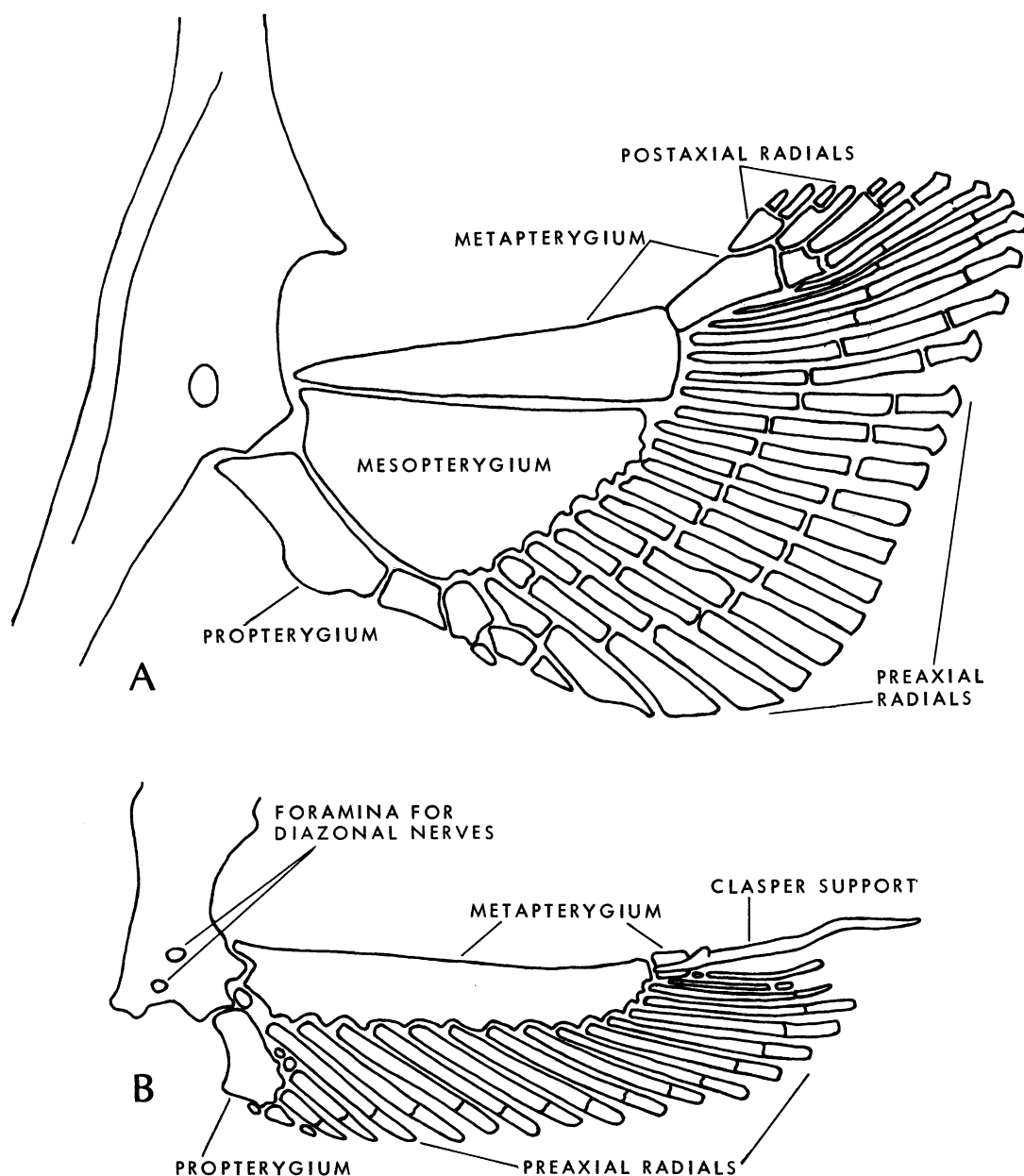


FIG. 26. Left pectoral (A) and pelvic (B) fin skeleton, in dorsolateral view, of 17 cm. ♂ *Squalus acanthias* Linnaeus, AMNH 40804.

structural elements of the pectoral and pelvic fins of osteichthyans are present in primitive sharks and placoderms as well (e.g., *Brachyosteus* and *Pseudopetalichthys*). To infer a

transformation series between osteichthyan fin structure and that of acanthodians, as would be required by Miles's (1973) theory of relationships, requires the assumption that

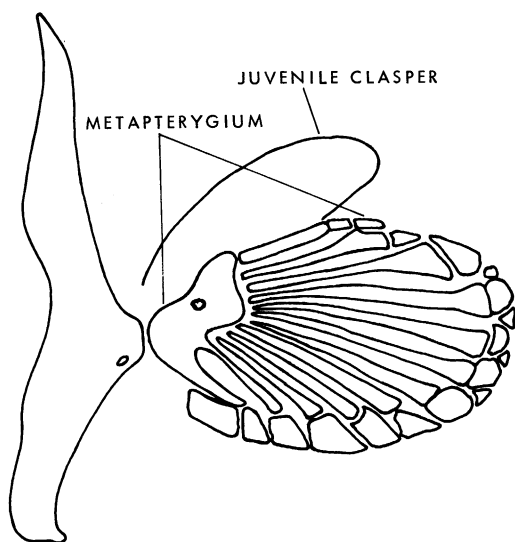


FIG. 27. Left pelvic fin skeleton of 20 cm. ♂ *Hydrolagus colliei* (Lay and Bennett) in dorsolateral view, AMNH.

complex similarities between osteichthyans and chondrichthyans were attained independently.

The difference between actinopterygians and sarcopterygians in pectoral and pelvic structure can be appreciated by contrasting the paired fin endoskeletons of *Acipenser* and *Eusthenopteron* (fig. 28). Even a cursory comparison shows that the most complete of the pectoral and pelvic fin skeletons of *Eusthenopteron* illustrated by Andrews and Westoll (1970a, fig. 8J) have branching patterns that resemble in detail the arrangements of metapterygial elements and their preaxial radials in *Acipenser*. *Acipenser* fins appear to differ from those of *Eusthenopteron* only in the presence of three sets of radials anterior to the metapterygial axis and of a heavy, fenestrated pectoral propterygial segment that Jessen (1972) identified as a character of actinopterygians. It is also evident that the fins of *Acipenser* resemble, in considerable detail, the paired fins of chondrichthyans, differing from the primitive shark fins (fig. 25), but resembling those of euselachians (fig. 26), in the development of a strong propterygial articulation. The fins of

both *Acipenser* and *Eusthenopteron* differ from those of chondrichthyans and resemble one another in the lower number of distal radials anterior to the metapterygial base, and the alignment on the metapterygial axis of one basal preaxial radial per metapterygial segment. The metapterygial axes in *Eusthenopteron* may be distinguished from those of *Acipenser* by having posterodorsal processes (=entepicondyles of Andrews and Westoll, 1970a) in the first and third, second and third (AMNH P. 3871), or second (AMNH P. 8095) pectoral metapterygial segments (although some specimens have none at all; Holmgren, 1933, fig. 18) (fig. 29) and by having a greatly reduced pelvic skeleton in which there are only two metapterygial segments with three basal radials attached to them. Hence, *Acipenser* appears to have retained a primitive chondrichthyan arrangement of radials but has paralleled euselachians by shifting part of the fin support to the propterygial side, and *Eusthenopteron* appears to have retained the primitive chondrichthyan pattern of four pectoral metapterygial segments and two pelvic ones and, by losing all radials anterior to the metapterygium, to have retained a primitive metapterygial support for the pectoral and pelvic fins.

With respect to fin structure in general, Jessen (1972) has shown that *Acipenser* is typical of the members of other plesiomorph groups of actinopterygians, including various paleoniscids (and see also Nielsen, 1942, 1949), as Andrews and Westoll (1970b) have shown that *Eusthenopteron* is similar to other "rhipidistian" fishes such as *Sauripterus* (known only from part of a shoulder girdle and fin) and *Megalichthys*. According to Thomson (1972) and Rackoff (1980) *Sterropterygion brandei*, of which both pectorals and pelvics are known, is, again, much like *Eusthenopteron*.

Although for more than a half-century *Eusthenopteron* fin structure has been considered antecedent to tetrapod limbs, and the most recent interpreter of this doctrine has even identified elbow and ankle joints in the fins of *Sterropterygion* (Rackoff, 1980), we believe that Goodrich's (1930, p. 161) cau-

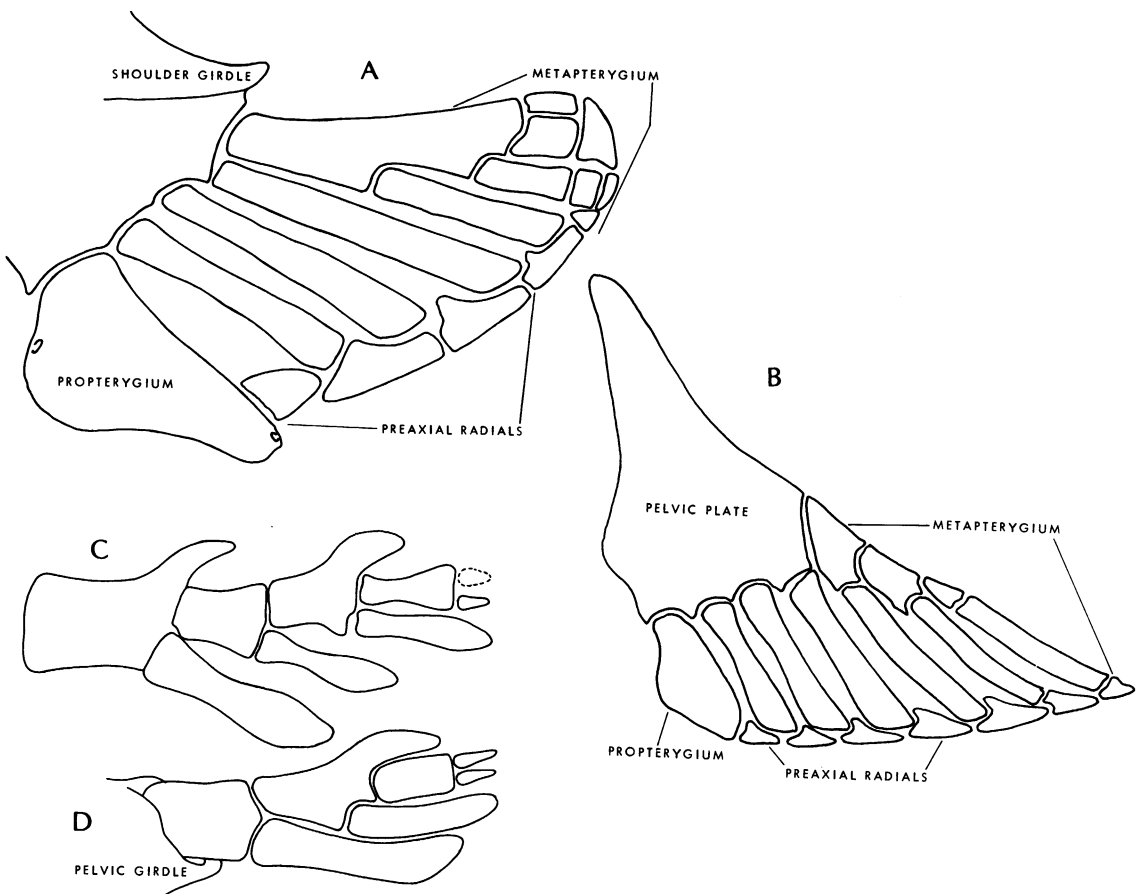


FIG. 28. Left pectoral (A) and pelvic (B) fin skeleton, in dorsolateral view, of adult *Acipenser sturio* Linnaeus, BMNH E. 170-1, distal elements in A from Jessen (1972); C, D, left pectoral (C) and pelvic (D) fin skeleton of *Eusthenopteron foordi* Whiteaves, in lateral view, after Andrews and Westoll (1970a, figs. 8H, J, 27).

tionary comments are still appropriate. It was clear to Goodrich that we should expect a fishlike relative of the tetrapods to possess "pectoral and pelvic fins alike in structure, with outstanding muscular lobe, extensive endoskeleton with at least five radials [=metapterygial segments], small web, and few if any dermal rays. But . . . the fin (especially the pelvic fin) is too specialized [in *Eusthenopteron*] . . . with short endoskeleton, large fin-web, and powerful dermal rays."

We specify below seven general conditions of the tetrapod limb that we believe

must be met, including some of the points made by Goodrich:

1. An unpaired basal element (humerus or femur) supporting entire appendage.
2. Paired, subequal subbasal elements (ulna-radius and fibula-tibia) that are functionally joined distally.
3. Two primary joints (shoulder or hip and elbow or knee) in each appendage.
4. Distal bony elements (carpals or tarsals and digits) arising on postaxial side of appendage (see p. 211).
5. Pectoral and pelvic appendages alike in

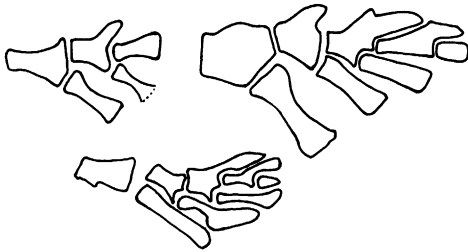


FIG. 29. *Eusthenopteron foordi* Whiteaves, left pectoral fin endoskeletons, showing variable development of processes on postaxial (dorsal) margin of metapterygial segments (compare fig. 28). Upper left, AMNH P. 8095; upper right, AMNH P. 3871; lower, from Holmgren (1933, fig. 18). Note spread radials of upper two fins and contracted radials of lower fin.

structure (i.e., structurally similar and with at least four or five primary segments).

6. Extensive muscular lobe that can be extended well below the ventral body wall.
7. Reduction or loss of dermal rays.

Of these seven criteria, osteolepiforms satisfy only the first and part of the second, that is, they have an unpaired basal element (the first segment of the metapterygial axis) and they have a second axial segment with the proximal end of which a large radial articulates. The second criterion is only partly met because the second axial segment and associated radial are decidedly unequal in length and the two bones diverge distally. In some specimens of *Eusthenopteron*, the two bones are more closely aligned than in others (e.g., in the specimens illustrated by Andrews and Westoll, 1970a, as compared with two specimens seen by us; see figs. 28D, 29) and this suggests to us that the *Eusthenopteron* fin, like those of other fishes, could be spread and contracted, corresponding with a motion of the radial away or toward the second axial segment. In turn, this means that the distal tips of the two bones are not functionally joined. The third criterion is not met because there is no joint of tetrapod type between the first and second axial segments (but Rackoff, 1980, disagrees). The fourth is rejected for osteolepiforms because all radials are on the preaxial side of the me-

tapterygial axis, and the fifth is also, because the osteolepiform pectoral has three or four axial elements and the pelvic only two. The sixth criterion is rejected because osteolepiforms have very short muscular lobes as judged by the posterior limits of the radials (when known), scale cover and position of the fin-ray bases, and the seventh criterion is also denied because of the extensive fin web.

In porolepiform "rhypidistians" criteria six and seven are met with respect to the pectoral fins only. Internal skeletal anatomy of porolepiform paired fins is virtually unknown, however (see Jarvik, 1972).

Dipnoans, on the other hand, meet all of the seven criteria (fig. 30A, B), many of which were previously discussed by Holmgren (1933). There are some minor points of disagreement between Holmgren's and our analysis which require some comment. The second criterion is not evident in adult lungfishes, though, because ontogenetically paired sub-basal elements fuse to form a single broad cartilage (fig. 31). But there is no indication either in early or late development of a significant inequality in length of these elements and the two sub-basal pelvic fin cartilages fuse incompletely and show no indications of the divergent angle between the second pelvic metapterygial segment and the first preaxial radial that occurs in *Eusthenopteron* (figs. 28, 29). In early development of the pectoral fin, the radial associated with the second metapterygial segment actually curves down toward that segment at its distal end (fig. 31; and see also Holmgren, 1933, fig. 11). It will be noticed by comparing figures 30A and 30B of the pectoral and pelvic fins of *Neoceratodus* that the pectoral is structurally the obverse of the pelvic, although the two fins are constructed according to exactly the same plan. In other words, the larger radials, which stand in a one-to-one relationship with the metapterygial segments, are postaxial (dorsal) in the pectoral and preaxial (ventral) in the pelvic. Likewise the radial that is functionally and ontogenetically associated with the second metapterygial segment is postaxial in the pectoral and preaxial in the pelvic. Semon (1898, p. 68),

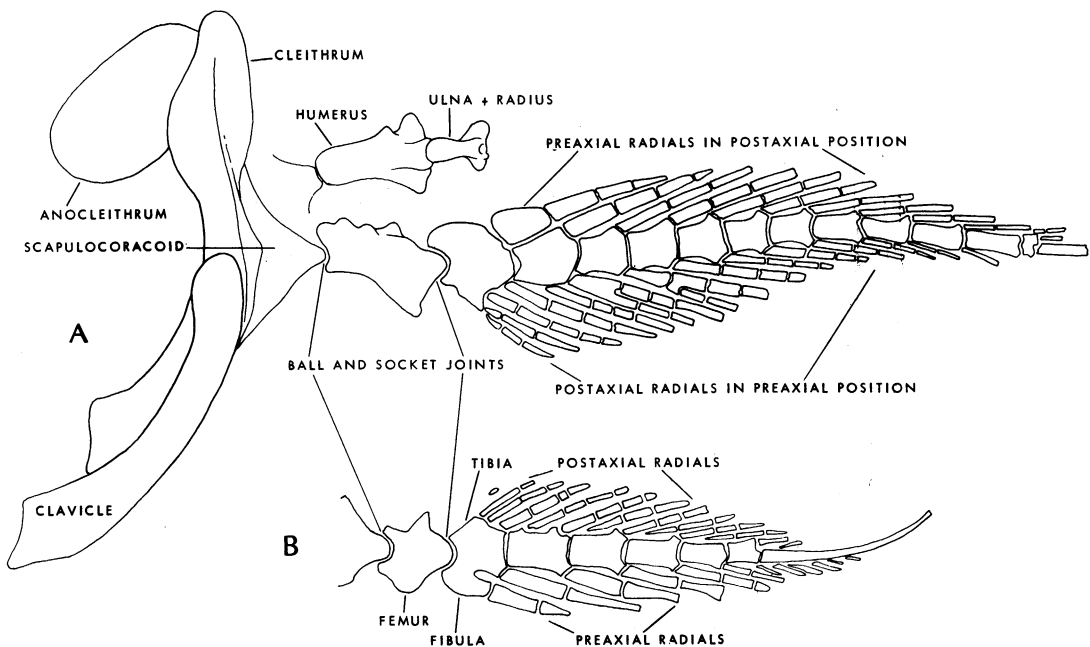


FIG. 30. *Neoceratodus forsteri* (Krefft), left pectoral (A) and pelvic (B) fin endoskeletons in positions of rest against body. AMNH 36982, 18 cm. total length.

as mentioned earlier, described the developmental sequence at ontogenetic stage 45 of how the pectoral anlage rotates dorsalward 90 degrees from the horizontal, and the pelvic anlage ventralward 90 degrees from the horizontal, so that the preaxial margins of the two fins have a 180 degree different orientation. Part of Holmgren's argument for drawing a comparison between the two paired appendages of *Neoceratodus* and urodeles is his inference that the carpals and tarsals and digits of urodeles are preaxial radials now in the postaxial position (presumably also requiring that in a lungfish-like ancestor of the urodeles the pelvic anlage has rotated dorsalward together with the pectoral). He made this inference for two reasons: (1) in *Neoceratodus* and urodeles the unpaired basal and paired sub-basal elements of the paired appendages (the first two metapterygial segments and the radial associated with the second segment) in *Neoceratodus* and the humerus (femur) and radius and ulna (tibia and fibula) of urodeles all appear in the primary blastema of the limb endoskeleton

prior to the formation of the prochondral anlage of the radials in *Neoceratodus* and carpals (tarsals) and digits in urodeles; and (2) by identifying the segments of the primitive metapterygial axis in the developing urodele limb, one could discover whether the carpals (tarsals) and digits are pre- or postaxial and are therefore homologous with pre- or postaxial lungfish radials. Holmgren's argument is complex, but reduces to a conclusion that the limbs of urodeles include both pre- and postaxial radials. We believe that Holmgren's goals are worthy but that his analysis is contrived, and that the problem can be reduced to a set of simple comparisons.

For our primary comparisons with *Neoceratodus* we select the same urodeles as did Holmgren. We choose the hynobiid salamanders because the hynobiids are considered to be among the most primitive of all living urodeles (e.g., in their reproductive methods, arterial system, unfused lacrimal, septomaxilla, angular and prearticular bones, size of columella and correspondence in position to the lungfish hyomandibula in ad-

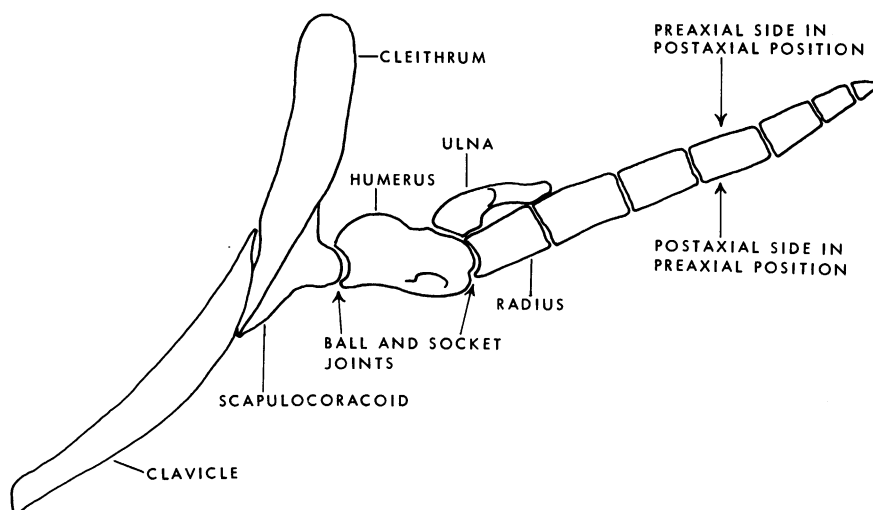


FIG. 31. *Neoceratodus forsteri* (Krefft), left pectoral fin endoskeleton of 15 mm. larva in which pelvic fins are not yet present. AMNH 40801.

vanced larvae; Schmalhausen, 1968, pp. 184–187, figs. 110–113). We choose hynobiids also because in the earliest stages of limb development the paired appendages appear as leaf-shaped fins with a strong muscular lobe as in larval *Neoceratodus* (fig. 32). We agree with Holmgren that the occurrence in *Neoceratodus* and *Hynobius* of an unpaired basal and paired sub-basal elements in the primary blastema of the appendicular endoskeleton prior to the formation of more distal elements is probably significant since in primitive gnathostomes the fin endoskeleton first appears as a procartilagenous plate continuous with the primary girdle and later separates from the girdle and then subdivides into radials (Goodrich, 1930). But what strikes us as being a more complete, and therefore more informative, comparison is that the radial associated with the second metapterygial segment of *Neoceratodus* and the ulna of *Hynobius* and other urodeles are joined to the basal segment (humerus) in the same way, viz., mainly along the postaxial (dorsal) surface of the humerus, and that their paired sub-basal segments (radius and ulna) form a definite joint surface with the humerus not found between more distal segments or in any other gnathostome pectoral endoskele-

ton (figs. 31, 33). The existence of this second joint in lungfishes is easily appreciated in cleared and stained preparations of small specimens which show that the fin is cocked at this juncture and in large and small specimens by the presence of a ball and socket joint surface between the first and second metapterygial segments (figs. 30A, 31). These observations therefore satisfy criterion number 3, above.

The application of the fourth criterion, whether the distal elements of the fin endoskeleton are postaxial, depends on discovering the position in tetrapods of what remains, if anything, of the metapterygial fin axis. In *Neoceratodus*, the metapterygium extends distally to the pointed tip of the fin. In developing *Hynobius* no skeletal element extends to the tip of the fin membrane, but instead the first digit extends ventrally to the preaxial margin and digits two to four (in the pectoral) or five (in the pelvic) extend dorsally to the postaxial fin margin. Holmgren assumed that three parts of the *Hynobius* limb are important for this question, the radius (tibia), the ulna (fibula) and the central carpals (tarsals); the lateral carpals (tarsals) and digits he considered to be secondary elements. He reasoned, since there are three

primary branches and, since the urodele limb must have arisen phylogenetically from an archipterygium with preaxial and postaxial radials on a central metapterygium, that the middle of the three branches in *Hynobius* must be homologous with the dipnoan metapterygium. Holmgren's argument is clearly loaded by the assumption of what is primary and secondary for these comparisons and by his assumption that each of the three elements of a lungfish fin is represented in the tetrapod limb. Our own study of developing *Hynobius* limbs suggests to us that (1) there are only two morphological units, a ventral unbranched series of segments (radius + radiale + prepollex) and a dorsal branched series (ulna + carpals + digits) (fig. 33); (2) the ventral unbranched series is composed of more robust segments; (3) a line drawn through the axis of the ventral unbranched series intersects at or very near the pointed tip of the larval fin; (4) the base of the first element of the dorsal series (the ulna) has a dorsal contact with the humerus as does the dorsal radial in the primary fin blastema of *Neoceratodus*; and (5) the base of the first element of the ventral series (the radius) has a socket for the ball joint of the humerus as does the second metapterygial segment in *Neoceratodus*. We conclude, as did Romer and Byrne (1934, p. 44), that the ventral unbranched series (radius + radiale + prepollex) represents the primitive metapterygium, and that the dorsal branched series (ulna + carpals + digits) represents preaxial radials that are in the rotated postaxial position. The synapomorphy that we therefore specify between *Neoceratodus* and *Hynobius* is the ontogenetically rotated appendage with its preaxial radials on the postaxial side, and this would satisfy criterion number 4, as given above. We must also point out, however, if we are wrong and Holmgren is right, then our fourth criterion, restated in Holmgren's terms, would still relate dipnoans and tetrapods and exclude *Eusthenopteron*. We simply feel that our interpretation is more closely bound to simple morphological comparisons and carries a smaller burden of assumptions.

Lungfish fins certainly satisfy the fifth cri-

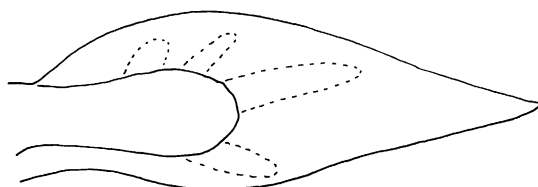


FIG. 32. *Hynobius chinensis* Günther, left pelvic "fin" of 3 cm. larva. AMNH 30616. Positions of anlagen of first four of five digits shown by dashed lines.

terion by being of similar form and constructed along virtually identical lines (although they are 180° out of alignment with each other). The high number of axial elements in living and many fossil dipnoans and the presence of true postaxial radials are probably derived, however, and are autapomorphic for these species. In more primitive lungfishes, such as *Griphognathus*, the muscular fin bases are stout and neither so long nor so slender as in *Neoceratodus* (Schultze, 1969a, fig. 31).

Criteria 6 and 7 relate to features that are well known in lungfishes and their significance is enhanced by the use of the fins, particularly in *Neoceratodus*, for walking across a substrate by their alternate side-to-side motions in connection with sinusoidal motions of the trunk and tail as in urodeles.

The close similarity in paired appendages between dipnoans and tetrapods does not imply, of course, that *Eusthenopteron* fins are without significance for this problem, but that, cladistically speaking, their significance lies at a higher level of generality which specifies only that *Eusthenopteron* is the sister taxon to a group that includes dipnoans and tetrapods and perhaps also porolepiforms as the sister taxon to those two.

Since osteolepiforms have a probably primitive number of metapterygial segments in both fins but fewer preaxial radials than chondrichthyans, actinopterygians, dipnoans and tetrapods, we infer that osteolepiforms exhibit a trend in radial reduction. Radial reduction is especially evident in the pectoral fin of *Panderichthys* (Vorobyeva, 1975, fig. 3). Coelacanth also have a single radial associated with the first two metapterygial segments, and these radials are reduced

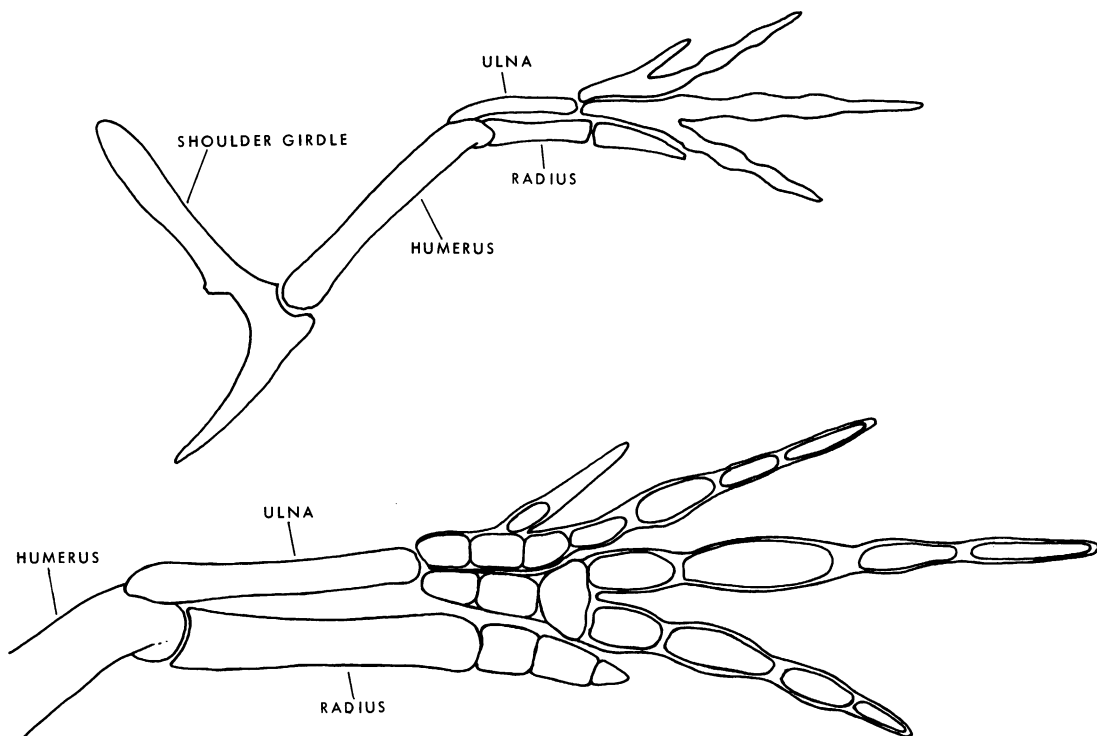


FIG. 33. *Hynobius chinensis* Günther, left pectoral appendage of 3 cm. larva. AMNH 30616. Upper figure, diagram of girdle and limb showing four digits clustered into two distinct developmental fields. Lower figure, detail of cartilaginous anlagen of segments of digits within the two fields. Ulna and prepollex are hypothesized to be homologues of fish metapterygium, and radius, carpals and digits, homologues of fish preaxial radials now in postaxial position (compare figs. 30, 31).

to tiny nubbins embedded in connective tissue (fig. 34). Such reduction suggests their membership in a group including osteolepiforms. But contrasting with this interpretation is the presence of four metapterygial segments in the pelvic fin and the mirror-image complete similarity of pelvic and pectoral endoskeletons (fig. 34), features which are presumably derived and suggest that coelacanth fit near dipnoans and tetrapods. Also indicative of coelacanth-dipnoan-tetrapod relationship is the evident rotation of the preaxial side of the coelacanth pectoral to the postaxial position so that, like dipnoans, the pectoral and pelvic fins are out of phase. Millot and Anthony (1958) illustrated the pectoral fin of *Latimeria* wrong way up in their illustration of the skeleton, but their stated purpose was to show its similarity to the fin of *Eusthe-*

nopteron in which the "humeral processes" for muscle attachment have the primitive osteichthyan orientation (cf. figs. 28, 30, 34). Thus, whereas one character (radial reduction) somewhat ambiguously aligns coelacanth with osteolepiforms, a second (four pelvic radials) and a third (pectoral rotation) align them as a sister group of dipnoans plus tetrapods. Although one might wish to argue the exact cladistic placement of coelacanth by using alternative interpretations of paired fin characters, the placement of these fishes with the sarcopterygians is unambiguous: coelacanth completely satisfy the first criterion, as do osteolepiforms, and, like *Eusthenopteron*, they have entirely metapterygial fins, thus rejecting theories of relationship that would place them as the sister group either of actinopterygians, of all other os-

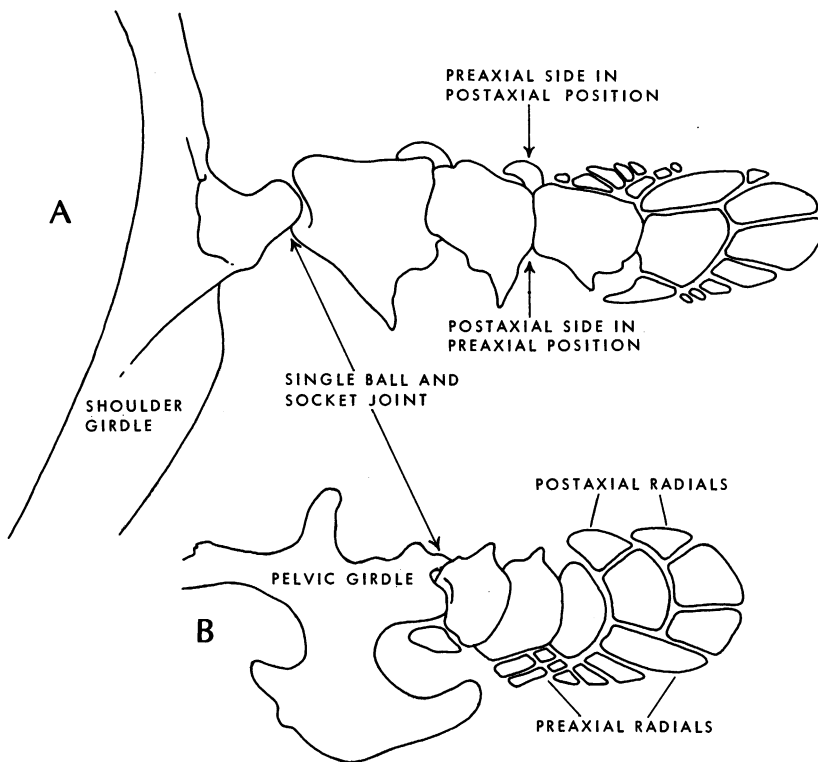


FIG. 34. *Latimeria chalumnae* Smith, left pectoral (above) and pelvic (below) fin endoskeletons of unborn juvenile of 34 cm. total length (AMNH 32949) shown in positions of rest against body.

teichthyans (e.g., Wiley, 1979), or of chondrichthyans (as suggested by some workers with a penchant for treating shared primitive characters as evidence of relationship; cf. Forey, 1980). We also reject the conclusion of Bjerring (1973) that the relationship of coelacanths to actinopterygians and sarcopterygians, or to chondrichthyans and osteichthyans, is unresolved.

This discussion would be incomplete without some comment on the position of cladistians within the Osteichthyes, since *Polypterus*, as the "type" crossopterygian, has often been compared with tetrapods (e.g., Pollard, 1891, 1892), and Klaatsch (1896) even tried to relate its fin structure to the tetrapod limb. *Polypterus*, however, has the propterygial margin of the pectoral fin strongly developed (fig. 35) which, within the Osteichthyes, is a characteristically actinopterygian feature.

Pelvic anatomy also contributes to an understanding of cladistian relationships. Stensiö (1921, 1925) was the first to recognize that the pelvic girdle of actinopterygians may have a unique ontogenetic history. He suggested that the girdle has a compound structure, consisting of the pelvic plate to which the metapterygium is fused. We agree with Stensiö in substance if not in detail. Our own conclusion that actinopterygians might not have a primary pelvic girdle derives from a comparison of the endoskeletal fin supports in gnathostomes generally. In acanthodians the only known skeletal support of the pelvic fin is a heavy spine along the fin's leading edge. All other gnathostomes have a complex internal fin skeleton primitively without a leading spine. In sharks the pelvic is structured much like the pectoral; there are two, or sometimes three, rows of radials joined to the preaxial side of the metapterygium (fig.

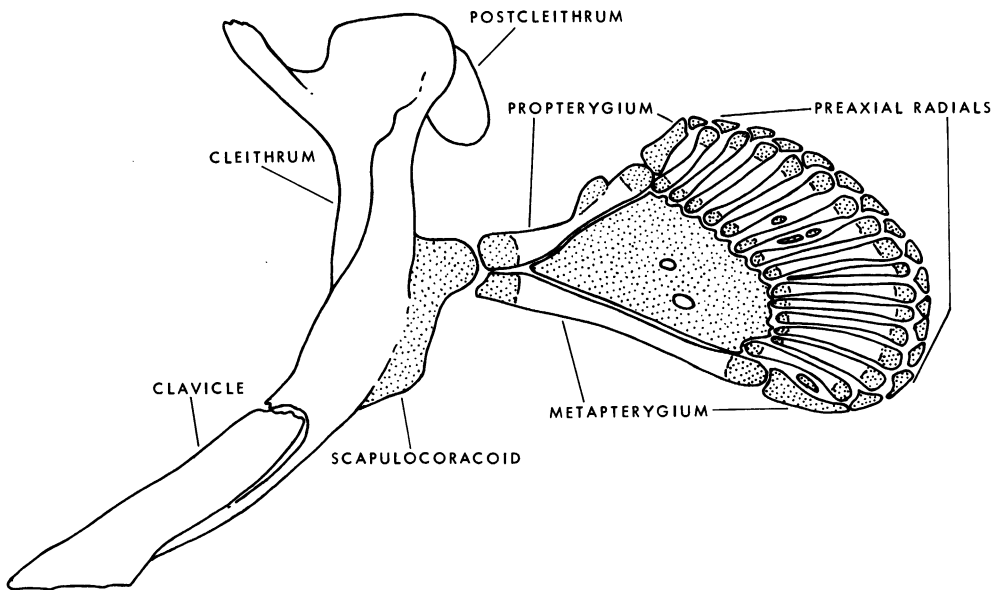


FIG. 35. *Polypterus ornatipinnis* Boulenger, left shoulder girdle and pectoral fin endoskeleton. AMNH 40802, 14 cm. standard length.

26B). In primitive actinopterygians such as *Polyodon* (fig. 36A) and *Acipenser* (fig. 36B) (and some paleoniscids as well; Lehman, 1966), there is a series of radial-like cartilages that either fuse (in most adult forms) or remain separate (in juveniles and some adult forms). Two rows of radial elements are joined to the outer surface of these internal cartilages, an inner row of elongate radials and an outer row of shorter ones, the whole thus closely resembling a metapterygium and its preaxial radials in chondrichthyans and sarcopterygians; no other recognizably separate structure lies anteromedial to these internal cartilages. The various conditions in actinopterygians suggest that there is a trend toward consolidation of the internal cartilages both ontogenetically and phylogenetically, and a reduction in the length of the series and number of radials it supports. Among the most primitive living and fossil actinopterygians (see Nielsen, 1942, 1949) varying degrees of reduction are already apparent (fig. 37A, B). Since *Polypterus* has a simple triangular girdle along which two rows of radials are arranged in parallel (an

inner row of long radials and an outer row of very short ones) comparable with the preaxial radials of chondrichthyans and osteichthyans, we conclude that the surface along which they attach is at least, in part, metapterygial (fig. 38).

Goodrich (1930) objected to arguments like those of Stensiö's on the grounds that the pelvic girdles of actinopterygians are pierced by foramina for diazonal (=spinal) nerves as are the girdles in other gnathostomes, thus indicating a common plan of development. These foramina are explained by the fact that in most gnathostomes the girdle is primarily outside the myotomes in early development and is merely an extension inwards from the base of the fin skeleton with which it initially forms a continuous procartilaginous plate. As the girdle grows inward it comes to surround the nerves that pass from the myotomes outwards to supply the fin. But exactly the same developmental history would be expected even if a girdle were reduced, combined with the metapterygium of the fin endoskeleton, or replaced entirely by the metapterygium. In the latter case, the

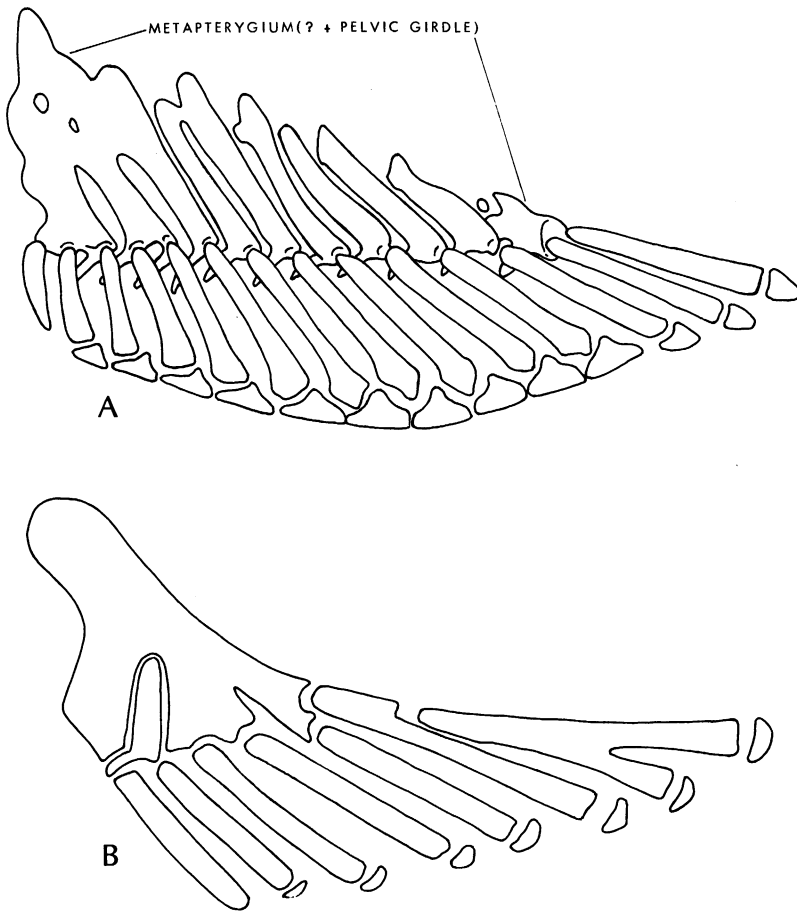


FIG. 36. Left pelvic girdle and fin endoskeleton in A, *Polyodon spathula* (Walbaum), juvenile, 12 cm. total length (AMNH 40803); and B, *Acipenser oxyrhynchus* Mitchill, juvenile, 11 cm. total length (AMNH 37296).

metapterygium, in consolidating and enlarging to form a support for the preaxial radials, would also come to surround one or more diazonal nerves.

The alternative explanation, that the parallel series of radials lying outside the body wall is a remnant of the metapterygium (i.e., that they are not preaxial radials at all, but metapterygial segments that have assumed the form of such radials) seems to us contrived, and is rejected by the observation that in sturgeons the external metapterygial axis is continuous with internal segmented cartilage so that the metapterygial segments

appear to lie on both sides of the body wall (figs. 28B, 36B), and that, when the external part of the metapterygium is finally lost altogether in more advanced actinopterygians (see Lehman, 1966), all that is left is a series of parallel radials such as those found in *Polypterus*. We conclude, therefore, that the pelvic fin radials of *Polypterus* are of a derived, typically actinopterygian type and that its girdle, which lies entirely between the body wall and the myotomes and lacks the dorsal processes that are primitively present in chondrichthyans (e.g., *Cladoselache* and chimaeras, fig. 27) and sarcopterygians, but

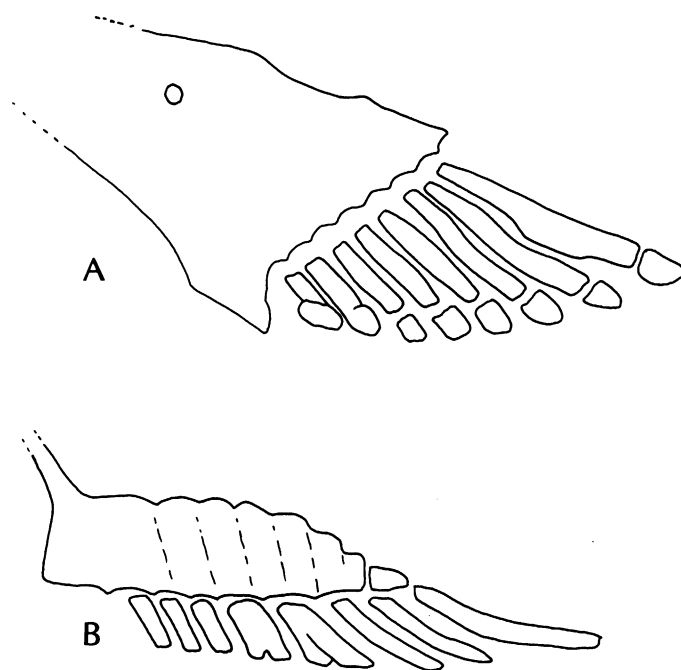


FIG. 37. Pelvic girdle and fin endoskeleton in A, *Boreosomus piveteaui* Nielsen; and B, *Pteronisculus gunnari* (Nielsen), both from Nielsen (1942).

absent in chondrosteans, is also of actinopterygian type.

(B) PECTORAL GIRDLE

Characters of the dermal bones of the pectoral girdle have been used by several workers to support ideas of relationships between

sarcopterygian groups and also to distinguish one group from another (Jarvik, 1944b, 1948, 1972; Andrews and Westoll, 1970a, 1970b; Andrews 1973).

In osteolepiforms (the Rhizodontidae *sensu* Andrews and Westoll are very poorly known and will be dealt with separately), porolepiforms and primitive lungfishes such as *Chirodipterus* the girdle consists of five paired dermal bones arranged in an overlapping series (fig. 39C–G). A median interclavicle is present ventrally. Primitive actinopterygians show a series of four paired bones plus a median interclavicle (fig. 39A, B; Jensen, 1972). We may assume therefore that the primitive osteichthyan had a girdle which consisted of, at least, a post-temporal, supracleithrum, cleithrum, clavicle and interclavicle and that successive elements in the series overlapped one another from dorsal to ventral. The main lateral line runs through the post-temporal and descends through the supracleithrum before running through the body scales. *Polypterus* is unusual in that the

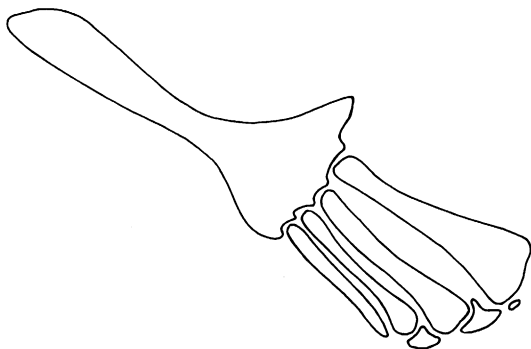


FIG. 38. *Polypterus ornatipinnis* Boulenger, left pelvic girdle and fin endoskeleton. AMNH 40802, 14 cm. standard length.

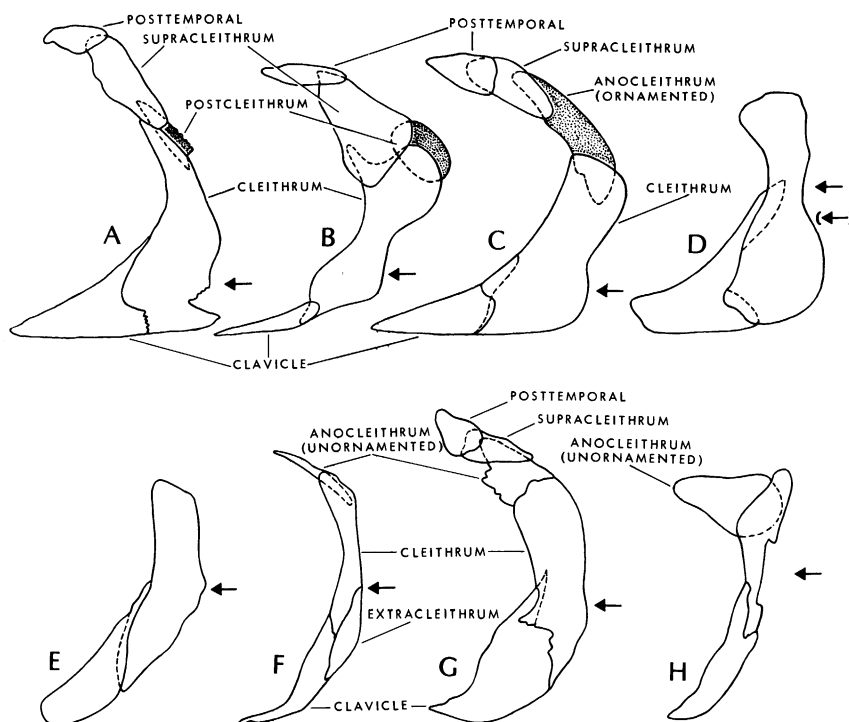


FIG. 39. Diagrams of dermal shoulder girdles (interclavicle omitted) of osteichthyans to show development of anocleithrum (actinopterygian postcleithrum) in sarcopterygians and transformation series in the increasing importance of clavicle and dorsal migration of fin insertion (arrow). Stipple distinguishes ornamented postcleithrum and anocleithrum. A, *Mimia toombsi* Gardiner and Bartram (original, BMNH specimens); B, *Polypterus bichir* Saint-Hilaire (from Jarvik, 1944b); C, *Eusthenopteron foordi* Whiteaves (from Jarvik, 1944b); D, *Rhizodus hibberti* (Agassiz) (from Andrews and Westoll, 1970b); E, *Holoptychius* sp. (from Jarvik, 1972); F, *Latimeria chalumnae* Smith (from Millot and Anthony, 1958); G, *Chirodipterus australis* Miles (original, BMNH P. 52560, P. 52586); H, *Neoceratodus forsteri* (Krefft) (from Wiedersheim, 1892).

sensory canal does not penetrate the supracleithrum but runs directly from the posttemporal to the first lateral line scale.

The skull-girdle connection is provided by the post-temporal which abuts against the hind wall of the braincase and is partially overlain by the extrascapular series. In Recent actinopterygians and in *Polypterus* there is a pronounced anteroventral process on the post-temporal which provides a firm union with the braincase. This process is absent from the post-temporal of *Mimia* and *Moythomasia* and therefore it is considered as a synapomorphy of all actinopterygians except those most primitive genera.

The sarcopterygian girdle differs from that

of the actinopterygians in the incorporation of the anocleithrum which lies between and separates the cleithrum and supracleithrum (where present) and is overlapped by both of these elements. The overlap relationships of the anocleithrum suggest that it is not a part of the primitive series in the osteichthyan girdle. The homologous bone in actinopterygians is the dorsalmost postcleithrum which lies slightly behind the supracleithrum and cleithrum, which are in contact, but is nevertheless overlapped by both of these bones (fig. 39A, B; Jessen, 1972). Although the postcleithrum may develop a ventral process in some neopterygians it remains fundamentally scalelike, a condition well dis-

played in the paleoniscid *Mimia* where a typical scale peg-and-socket is still present.

The anocleithrum of *Eusthenopteron* (Jarvik, 1944b; fig. 3) shows a small ornamented area which lay superficially but most of the bone is represented as overlap surfaces. The anocleithrum of porolepiforms is very poorly known but there are indications (Jarvik, 1972, pl. 18, fig. 2) that in *Glyptolepis* it is large and platelike and deeply embedded, bearing no ornament. In fact, it looks very similar to the anocleithrum of *Chirodipterus* (fig. 39G), both showing anterior processes. In Recent lungfishes and in coelacanth the anocleithrum is the most dorsal functional element in the girdle. It varies in shape from an ovoid plate in *Neoceratodus* (fig. 39H), to splintlike in *Latimeria* (fig. 39F) and *Protopterus* (Wiedersheim, 1892), while it is absent in *Lepidosiren* (Bridge, 1897).

The incorporation of the anocleithrum/postcleithrum as a functional unit in the girdle is a feature common to osteolepiforms, coelacanth, porolepiforms and lungfishes, and this stands in contrast to the scalelike postcleithrum in actinopterygians. Jarvik (1944b, p. 27) took the view that, since the incorporation of an anocleithrum occurs in rhipidistians, then "it must be assumed to have undergone a regressive development in Actinopterygians and Brachiopterygians." In other words, according to Jarvik the anocleithrum condition is primitive for osteichthyans. We would argue that the converse is more plausible; that is, the anocleithrum condition is derived and can be considered as a synapomorphy for sarcopterygians, later lost in tetrapods. Which of the two character states is derived cannot be decided simply on outgroup comparison, since the only other group with a well-developed dermal shoulder girdle is the Placodermi. Despite attempts of Stensiö (1959) to list detailed homologies between the bones of the trunk shield and the bones of the osteichthyan girdle the differences seem too great to allow any but the most tenuous comparison. But even if we allow Stensiö's suggestion that the placoderm posterior lateral is equivalent to the postcleithrum/anocleithrum, then the condition in the primitive out-

group, where the posterior lateral lies wholly behind the supracleithrum and cleithrum equivalents, only reinforces the view that the actinopterygian postcleithrum exemplifies the primitive character state.

It does, in fact, seem more reasonable to assume that the superficial, scalelike postcleithrum represents the primitive condition and that the anocleithrum was developed by a forward migration and sinking inward of the postcleithrum. The stages in this hypothesis would be represented by *Polypterus*–*Eusthenopteron*–coelacanth, lungfishes, and possibly porolepiforms. A similar hypothesis can be suggested for another bone of the shoulder girdle, the interclavicle, which has also apparently sunk inward to become part of the teleostean urohyal (Patterson, 1977). The coelacanth interclavicle has also sunk inwards to come to lie between the urohyal and the clavicles.

Recent lungfishes have lost both the supracleithrum and the post-temporal and the former element is absent from coelacanth (the anocleithrum is often mislabelled as the supracleithrum). Furthermore, the anocleithrum lies deep within the epaxial musculature and this means that like tetrapods, which have lost the anocleithrum as well, there is no bony connection between the skull and the girdle.⁵ The absence of such a connection cannot be regarded as a synapomorphy of these three groups since at least *Chirodipterus* retains a skull connection by way of a post-temporal and a supracleithrum (fig. 39G).

⁵ Watson (1926) maintained that a skull-girdle connection exists in primitive tetrapods such as *Pholidropteron* and *Eogyrinus attheyi*; the former was said to possess a post-temporal and the latter a complete series of connecting bones. However, Romer (1957, p. 112) reinterpreted the post-temporal as a cleithrum of *Pholidropteron* and suggested that the supposed specimen (DMSW.34) of *E. attheyi* is in fact a fish. The specimen has been subsequently reinterpreted as a rhizodont, possibly *Strepsodus*, by Andrews (1973). At the very best, therefore, the evidence of a skull-girdle connection in tetrapods by way of a post-temporal, supracleithrum, and anocleithrum is equivocal. Specialized secondary connection between the dorsal tip of the cleithrum and the "tabular" horn in some neotrideans has been reported (Angela Milner, personal commun.).

The absence of a skull-girdle connection remains a similarity between coelacanth and tetrapods but in the light of other synapomorphies between lungfishes and tetrapods this must be assumed to have developed in parallel, in these two groups and in Recent lungfishes. The skull-girdle connection is also absent in some teleosts such as eels.

The cleithrum and clavicle, the dominant elements in the primitive dermal shoulder girdle, always have a complex interlocking suture between them. In primitive members of the Actinopterygii, Osteolepiformes, and Porolepiformes the clavicle bears an ascending process which fits along the inner face of the cleithrum. In coelacanth and lungfishes the dorsal part of the clavicle is not clearly demarcated from the main body of the bone but nevertheless it rises to wrap around the anterior margin of the cleithrum. It is therefore misleading to consider that coelacanth lack an ascending process (cf. Jarvik, 1944b, p. 27).

Jarvik (1944) sought to distinguish a particular type of double overlap between the clavicular ascending process and the cleithrum in porolepiforms from a simple overlap of the clavicle by the cleithrum in osteolepiforms (*Eusthenopteron*). But Andrews and Westoll (1970b, p. 407) rightly pointed out that *Osteolepis* shows an essentially porolepiform pattern and intermediate conditions are seen in *Rhizodus*.

The relative sizes of the cleithrum and clavicle differ considerably between primitive members of osteichthyan groups. A transformation series of the ratio of exposed surface area of the cleithrum to exposed surface area of the clavicle would read: *Polyperterus*, 7; *Eusthenopteron*, 3.7; *Mimia*, 3.4; *Holoptychius* and *Latimeria*, 1.5 (the latter combines the area of the extracleithrum with the cleithrum); *Chirodipterus*, 1.25. The ratio in a primitive tetrapod such as *Archeria* is approximately 0.9, measured from Romer's (1957) restoration. The ratio in *Neoceratodus* is 0.93, whereas in adult *Protopterus* no ratio can be calculated since there is only one bone present which represents the result of ontogenetic fusion between an embryologically separate clavicle and cleithrum

(Schmalhausen, 1917). These figures demonstrate that there is a progressive increase in the size of the clavicle. On this basis, the traditional position of *Eusthenopteron* as the most tetrapod-like fish cannot be supported.

The position of the fin insertion follows a similar sequence, showing a dorsal migration of the point of fin articulation through the series primitive actinopterygian–*Eusthenopteron*–porolepiforms/lungfishes/coelacanth. It is difficult to quantify the relative positions of fin insertion in fossil material, particularly for round-bodied sarcopterygians in which preservation nearly always distorts the true position.

The rhizodontiforms (*Sauripterus*, *Rhizodus*, and *Strepsodus*) are not our immediate concern here but since this group is recognized on distinctive features of the shoulder girdle (Andrews and Westoll, 1970b) it is appropriate to add a note. The surface area ratio between the cleithrum and clavicle is 2.2 (*Rhizodus*); that is a value between *Eusthenopteron* and *Holoptychius*/*Latimeria*. The fin insertion is high in *Rhizodus*, apparently comparable with that in *Holoptychius*, coelacanth and lungfishes, but considerably lower in *Sauripterus*. So, on the basis of shoulder girdle morphology, rhizodontiforms could be placed on our cladogram immediately above *Eusthenopteron*.

Our interpretation of the dermal shoulder girdle can be summed up as follows. The incorporation of the anocleithrum as a functional element in the girdle is a synapomorphy of *Eusthenopteron*, *Latimeria*, *Holoptychius*, and dipnoans. We assume this to have been lost, with the skull-girdle connection, in tetrapods. The ratio of cleithrum to clavicle area follows a similar sequence except that it is not possible to discriminate between *Latimeria*, *Holoptychius*, and dipnoans. The high fin insertion is a synapomorphy of *Latimeria*, *Holoptychius*, dipnoans, and tetrapods (paralleled by many acanthopterygians and paracanthopterygians among teleost fishes). The anocleithrum of coelacanth, *Holoptychius* and dipnoans has sunk beneath the surface and lost all trace of ornament.

The endoskeletal shoulder girdle sheds lit-

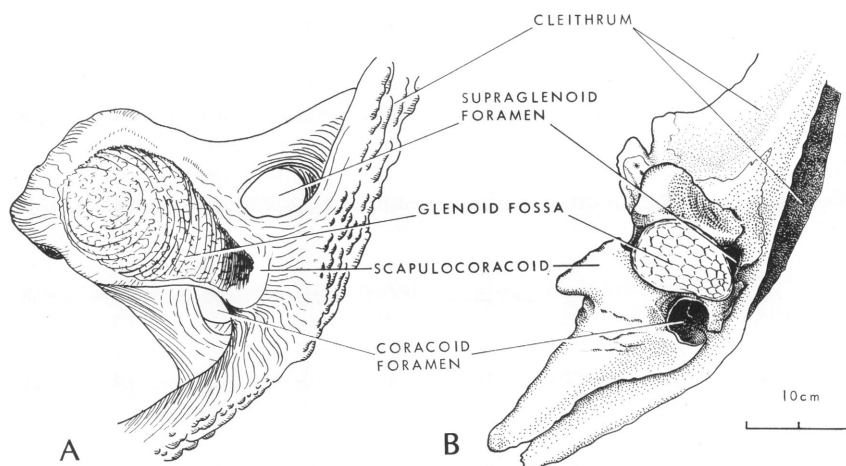


FIG. 40. "Screw-shaped" glenoid and scapulocoracoid in *Eusthenopteron* (A) and a Devonian lungfish (B). Posterior view of scapulocoracoid of A, *Eusthenopteron foordi* Whiteaves (modified from Andrews and Westoll, 1970a, fig. 4a, reversed); and B, *Chirodipterus australis* Miles (BMNH P. 52576). Note especially strong processes, presumably for muscle attachment, developed on scapulocoracoid of *Chirodipterus*. Andrews and Westoll (1970a) commented on several similarities between scapulocoracoid of *Eusthenopteron* and that of early tetrapods, including a screw-shaped glenoid. Features of such a glenoid are that it is pear-shaped, with articular surface twisted, so that narrow lateral end faces downward, and broad medial end faces upward. In the lungfish, the glenoid fossa is pear-shaped, as in *Eusthenopteron*. It shows no transverse twist, and is much less thoroughly ossified than glenoid in large individual of *Eusthenopteron* figured by Andrews and Westoll (1970a, figs. 4, 6), where a twist is not easy to detect. In living lungfishes, glenoid is a convex knob (figs. 30, 31), not a hollow as it is in tetrapods (cf. Jarvik, 1968a, p. 228). In Gogo lungfishes (the only fossil lungfishes in which the endoskeletal girdle is accessible) both glenoid and head of humerus are too weakly ossified for us to comment on the form of the joint, though figured specimen suggests that the glenoid was convex.

tle light on the interrelationships of the bony fishes under discussion. Romer (1924) noted the basic similarity in the construction of the scapulocoracoid in primitive actinopterygians and primitive tetrapods, with *Neoceratodus* differing in the possession of an unfenestrated scapulocoracoid (the nerves, blood vessels and muscles pass entirely outside the skeleton). *Latimeria* shows an unfenestrated scapulocoracoid similar to that of the Recent lungfishes.

The scapulocoracoid of *Eusthenopteron* has been favored (e.g., Andrews and Westoll, 1970a) over that of other bony fishes as being of tetrapod type because the glenoid fossa is said to be screw-shaped as in early tetrapods (Miner, 1925). The significance of this resemblance is, however, brought into question in the light of the structure of the scapulocoracoid in the primitive

lungfish, *Chirodipterus* (fig. 40). Here the scapulocoracoid, which is attached to the cleithrum by three contact areas as in *Eusthenopteron*, bears a large pear-shaped glenoid facet entirely comparable with that in *Eusthenopteron* (Andrews and Westoll, 1970a, fig. 4a). It seems to us therefore that the same tetrapod-like conditions (Romer, 1924) seen in *Eusthenopteron* can be matched in *Chirodipterus*. The shoulder girdle of *Chirodipterus* is of further interest because the scapulocoracoid is relatively much larger than that of *Eusthenopteron* and because of the development of a broad transverse flange, developed along the anterior edge of the cleithrum (fig. 40). The rugose nature of the bone surface suggests that a very large muscle sheet, comparable with the *deltoideus scapularis* of tetrapods, inserted at this point.

DERMAL BONES OF THE SKULL

Attempts to derive a useful nomenclature for the dermal bones of the skull involve some of the most confused, and confusing, episodes in the history of comparative studies of fishes and tetrapods. Today, consensus on bone homology is still lacking, as we try to make evident in the following brief review.

The nomenclature of the skull roof and cheek bones in osteichthyans has for the most part been derived from that originally applied to tetrapods, in particular, man. Thus, the early anatomists confidently homologized the frontals and parietals of mammals with similar bones in bony fishes. These homologies were based on positional relationships to other bones and underlying internal structures, as well as embryonic development. Consequently, over several decades the terminology of the dermal bones of advanced mammals was applied to reptiles, amphibians, and fishes (with the exception of the Dipnoi—see later) without anyone doubting that the bones were homologous throughout these groups.

Then in 1932 Säve-Söderbergh proposed that the dermal skull roof of fossil crossopterygians and ichthyostegids had been derived from a common ancestor with two pairs of frontals and two pairs of parietals and so concluded (his fig. 5) that the tetrapod parietal and post-parietal should be regarded as frontoparietal and parieto-extrascapular, respectively. He developed this terminology further in his 1935 paper on labyrinthodonts where he introduced a set of compound names for additional, inferred bone fusions, viz., lacrimo-maxillary, supratemporo-inter-temporal, supraorbito-dermosphenotic, etc. By the assumption of different fusion patterns, Säve-Söderbergh was then able to explain the varying conditions of the skull roof seen in osteolepid fishes, ichthyostegids, and labyrinthodonts.

A year later Westoll (1936, p. 166) working on *Osteolepis* suggested that the frontals and nasals of this fossil fish included homologues of the tetrapod nasals, frontals, and parietals. Then in 1938, with the discovery of the

skull table of the Devonian fossil *Elpistostege* (now thought to be a panderichthyid fish), Westoll decided that the crossopterygian frontal was homologous with the tetrapod parietal and that both the classical homologies and Säve-Söderbergh's (1935) revision were misleading. He concluded (1938, p. 127) that the tetrapod names of bones have largely been misapplied in fishes, and suggested that the parietal of crossopterygians was homologous with the post-parietal of tetrapods and that the latter bones diminished in size passing from crossopterygian fishes to amphibians and to reptiles. He therefore imagined that there was a corresponding backward movement of the parietals.

Romer (1941, 1945) subsequently championed Westoll's theory and today many British and North American texts (Jollie, 1962; Moy-Thomas and Miles, 1971) and authors (Thomson, 1965; Parrington, 1967; Andrews, 1973) have adopted Westoll's terminology and consider the bone previously named as frontal in crossopterygians to be the parietal and the parietals to be post-parietals.

The underlying reason for Westoll's radical change in terminology was his belief (1938, p. 128) that "the pineal foramen is absolutely homologous in position in all forms," a view with which Romer (1941, fig. 1) agreed, stating that in the transition from fish to amphibian to reptile there "has been no shift in the pineal eye, but a gradual shift in bone positions." In order to substantiate his theory Westoll (1943) pointed out that the osteolepid frontal not only included the pineal foramen but also lay above the optic foramen, pituitary fossa, and basipterygeroid process, all of which he claimed were covered by the parietal in early tetrapods. Moreover, the parietals of osteolepids covered the otic capsule, hyomandibular facet, and the exits of the trigeminal and facial nerves, all of which in early tetrapods were covered by the post-parietals.

The pineal foramen may occupy different positions in vertebrates (Jarvik, 1967, fig. 3) and even within the osteolepids it may be

situated between the eyes (*Osteolepis*; Jarvik, 1967, fig. 4a) or behind them (*Eusthenodon*; Jarvik, 1967, fig. 4c). The foramen may lie between the parietals, or between the parietals and frontals, or between the frontals, or even anterior to the latter (*Powichthys*; Jessen, 1975, fig. 2). In *Captorhinus* (Parrington, 1967, fig. 3c) the frontals lie above the basiptyergoid process and the optic foramen, whereas in the urodele *Molge* (Reynolds, 1913) and in *Sphenodon* (Säve-Söderbergh, 1946) both this foramen and the hypophysis lie beneath the junction of frontals and parietals.

The frontal/parietal controversy is associated with the problem of whether or not homologues of the tetrapod tabulars and post-parietals may be recognized in any other group of osteichthyans. There are two points of view. The first owes its inception to Watson and Day's 1916 paper in which the authors homologized the crossopterygian median extrascapular with the post-parietal and the lateral extrascapular with the tabular (their figs. 1, 5). These homologies were accepted by Goodrich (1919, 1930), Schmalhausen (1950, 1968) and most Russian, French, and Swedish workers but with Säve-Söderbergh (1936, fig. 14) and Jarvik (1967, fig. 13B) later maintaining that the post-parietal in temnospondyls represented a composite parieto-extrascapular and the tabular a supratemporo-extrascapular. The second hypothesis (Westoll, 1938) is that the crossopterygian parietal is a post-parietal and the posterior supratemporal a tabular.

Schmalhausen (1968, p. 82), in accepting the theory of Watson and Day (1916), pointed out that the lateral line furrows in fossil amphibians pass unchanged over the same bones as in fishes, whereas Westoll's (1938) hypothesis presumed that the fish extrascapular series had vanished. Schmalhausen (1968, p. 83) cited in support the works of Watson (1926) and Bystrov (1935), in which he believed it had been demonstrated that the cephalic division of the main lateral line (infraorbital canal) joined the transverse supratemporal canal in the tabular. In none of the examples chosen by Schmalhausen, however (viz., *Benthosaurus*; Bystrov, 1935,

fig. 12; *Trematosaurus*; Bystrov, 1935, fig. 25; *Dolichopareias*; Watson, 1926, fig. 24b) does the lateral line groove actually connect with that of the supratemporal canal. Moreover, in the majority of stegocephalians the groove for the cephalic division of the lateral line terminates posteriorly in the supratemporal and only in such forms as *Metoposaurus* (Romer, 1937), *Trematosaurus*, *Lyrocephalus*, *Lonchorhynchus*, and *Dolichopareias* (Bystrov, 1935) does the canal leave a furrow on the anterior limits of the tabular. Further, in many temnospondyls the supratemporal canal is confined to the tabular (*Aphaneramma*, *Lyrocephalus*; Säve-Söderbergh, 1935, figs. 31, 60, 61), whereas in others, where the furrow is continued onto the post-parietal, it rarely if ever meets its counterpart medially (*Trematosaurus*, *Benthosaurus*; Säve-Söderbergh, 1937, figs. 4, 9).

In his criticism of Westoll's (1936) theory, Jarvik (1967, p. 186) found it difficult to imagine how the bones of the skull roof could move backward, independently of the underlying neural endocranium, yet in accepting in its place the theory of Watson and Day (1916) or its modification proposed by Säve-Söderbergh (1936) he demanded the reverse—that a transverse series of bones moved forward onto the endocranium.

In osteichthyans many of the dermal bones of the skull roof are tightly attached to the underlying neural endocranium by ventral outgrowths of membrane bone from their centers of growth (descending laminae). The extrascapulars are clearly recognizable as a transverse series of scalelike bones variable in number and arrangement (4 in *Polypterus*, 7 in *Diplurus*, 3 in *Osteolepis* and *Dipterus*) and never intimately connected with the neurocranium. In many fossil amphibians the tabulars and post-parietals show extensive descending laminae (*Benthosaurus*; Bystrov and Efremov, 1940, fig. 23). And from this we must conclude that there is no unambiguous way to recognize the homologues of the tetrapod post-parietal and tabular in the skull roof of fishes.

Regarding lungfishes, Säve-Söderbergh (1932, pp. 97–98) commented that, in the

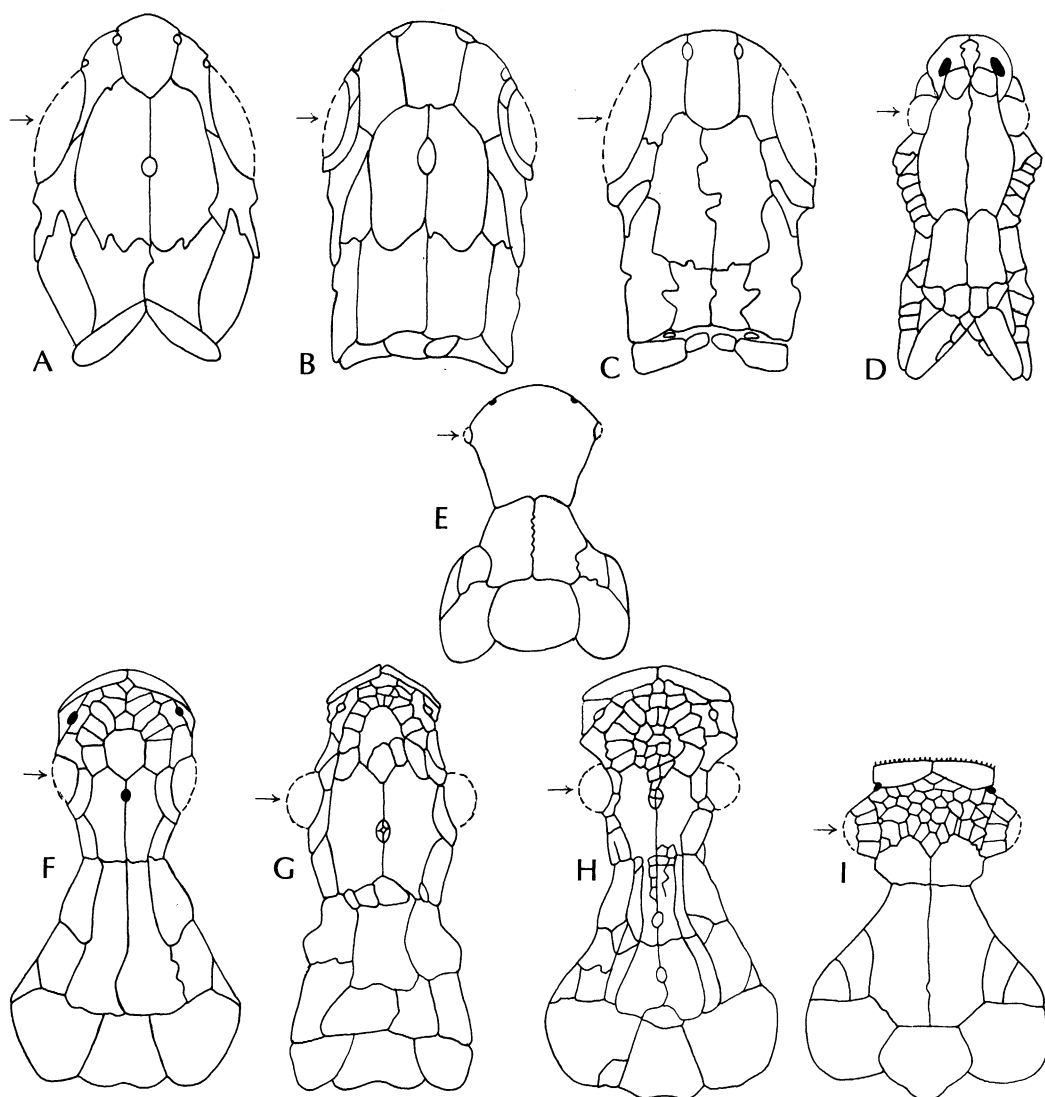


FIG. 41. Skull roofs. A-C, Actinopterygians: A, *Kentuckia deani* (Eastman) (from Rayner, 1951); B, *Moythomasia nitidus* Gross (from Moy-Thomas and Miles, 1971); C, *Pteronisculus magna* (Nielsen) (from Nielsen, 1942). Cladistian: D, *Polypterus* sp. (from Schmalhausen, 1968). E-I, Rhipidistians: E, *Porolepis brevis* Jarvik (from Jarvik, 1972); F, *Eusthenopteron foordi* Whiteaves (from Jarvik, 1967); G, *Eusthenopteron*, composite, showing variations in bone patterns (from Jarvik, 1944a); H, composite, showing maximum number of separate bones observed in *Osteolepis*, *Thursius*, and *Gyroptychius* (from Jarvik, 1948); I, *Holoptychius* sp. (from Jarvik, 1972). Arrows show position of eye.

morphology of the skull roof, *Dipterus* appeared more nearly related to ichthyostegids than were crossopterygians. But most British and American authors (White, 1965; Denison, 1968a, 1968b; Thomson and Campbell,

1971; Miles, 1975, 1977) have given up attempts at dermal bone homology and use instead a system of letters and numbers. This custom stems from Romer (1936) who, finding it impossible to reconcile the two mu-

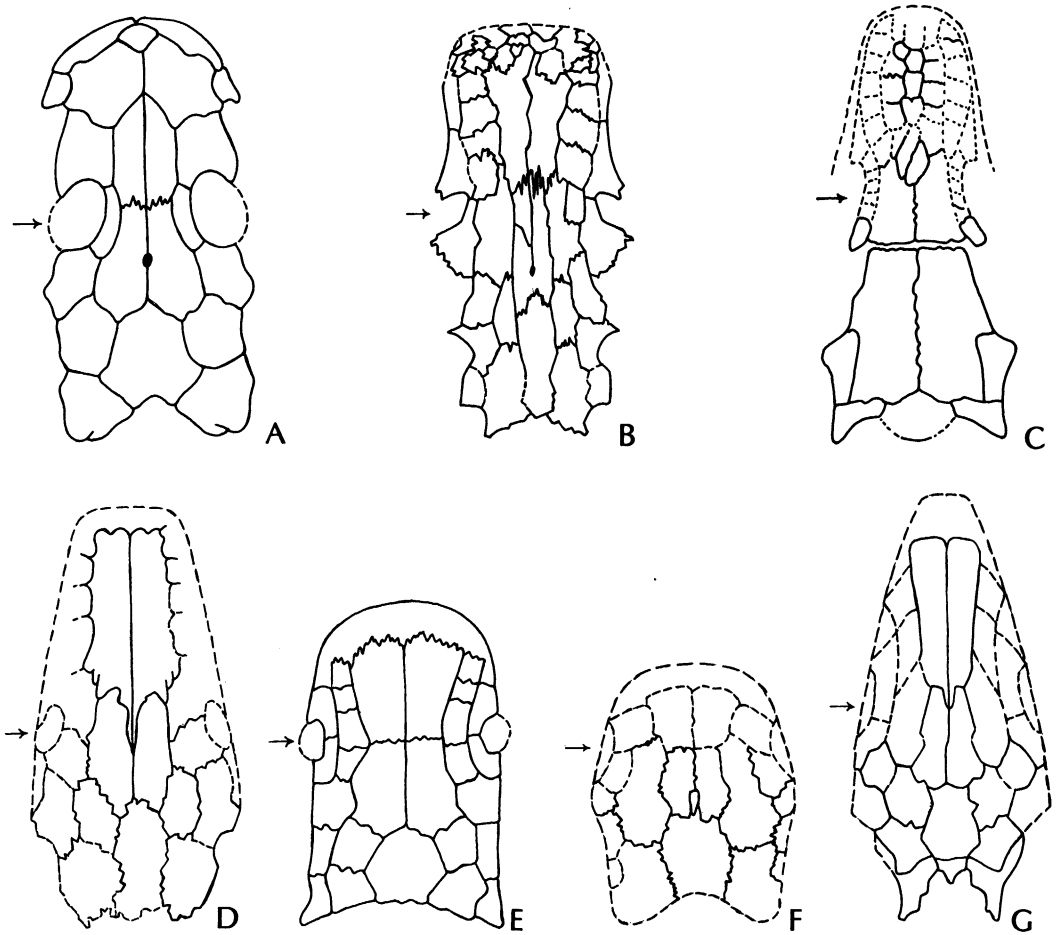


FIG. 42. Skull roofs. A, tetrapod; B, D, E, F, G, dipnoans (all but E from Lehman, 1959); C, actinistian. A, *Ichthyostega* (from Romer, 1966); B, *Soederberghia groenlandica* Lehman; C, *Diplocercides kayseri* (von Koenen), after Stensiö, showing condition intermediate between A, B, D-G (this figure) and fig. 41; D, *Soederberghia* sp.; E, *Scaumenacia* (various sources); F, *Nielsenia nordica* Lehman; G, *Oervigia nordica* Lehman. Arrows show position of eye.

tually contradictory systems of Watson and Day (1916) and Goodrich (1925, 1930), abandoned the use of names. He was subscribing to a view put forward by Gregory (1915, p. 327) that the primitive dipnoan had a skull consisting of a mosaic of small and variable plates. Forster-Cooper (1937) formulated a similar nomenclature of letters and numbers which was used by Westoll (1949), White (1965), and Thomson and Campbell (1971).

Disagreements and uncertainties in the use of bone names have several different causes. The most obvious source of disagreement is application of different criteria of homology

(e.g., bone fusion, relation of bones to pineal position or to a part of the cephalic lateral-line canal system). Seemingly irresolvable differences have arisen when anatomists have applied the same criterion (the lateral line) and yet obtained different results. A further difficulty has been that the evidence for choosing among the different criteria, or for applying any one criterion in specific cases, has been of a very indirect, circumstantial kind. The last, perhaps the major source of difficulty, is that the exposition of pattern and process have been inextricably bound together so that assumptions about certain

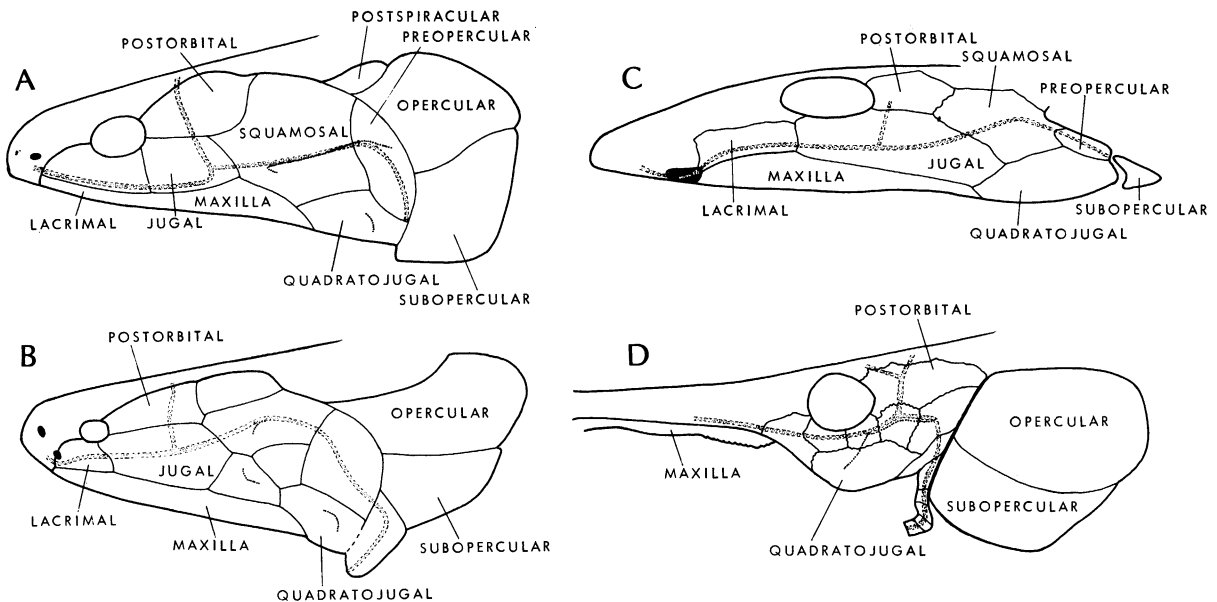


FIG. 43. Cheek in A, *Eusthenopteron foordi* Whiteaves (after Jarvik, 1944a, fig. 18); B, *Porolepis brevis* Jarvik (after Jarvik, 1972, fig. 43); C, *Ichthyostega* sp. (after Jarvik, 1952, fig. 35); D, *Griphognathus whitei* Miles (after Miles, 1977, fig. 112). In A and C there are seven bones in the cheek plate, and the same bone names can be applied. This pattern is usually treated as synapomorphous, uniting osteolepiforms with tetrapods. In B there are 11 bones in the cheek, and in D 14. Using A as a model, bone names can be applied in B and D only by giving the same name to more than one bone (e.g., squamosals 1–3 in B; preoperculars 1–6 in D). The different patterns in B and D must be autapomorphous or primitive, given that the pattern in A and C is synapomorphous. That synapomorphy may be tested by considering other patterns—see figure 44.

processes have had the effect of denying patterns that were readily apparent to the earliest investigators of the problem. For example, if we assert that a pattern exists with respect to the position of the eye in relation to the junction between two pairs of large bones on the skull roof, actinopterygians, cladistians, and “rhipidistians” form one group and primitive dipnoans, and tetrapods form another (figs. 41, 42). But if we also assert that the bone pattern has been more or less stable and that in early development the eye can migrate anteriorly or posteriorly, we imply that accepting the pattern is dependent upon accepting this developmental explanation. Our confidence in the significance of the pattern then comes into question because we lack information on whether one process (shifting of the eye in early development) explains the pattern better than another process, say elongation of the snout, which carries the roofing bones

with it. The issue then degenerates into an irresolvable argument over process and the reality of the observed pattern becomes secondary. Thus, Säve-Söderbergh suggested that a pattern exists to unite osteolepids and tetrapods if one accepts a specific process of bone fusion. Or, in the case of Westoll’s assertion of pattern based on pineal position, one must accept a process of bones shifting backward, or, in the case of Jarvik’s theory, their shifting forward. Jarvik’s hypothesis of pattern also involves the assumption of a process of interaction of the placodes of the cephalic lateral-line system and dermal bone formation such that the latter is invariably dependent on the former. There is, of course, evidence that, in some instances, eyes can assume different relative positions in the head (flatfishes), that bones can fuse in ontogeny or fragment in phylogeny (infraorbital bones of characoid fishes), that the pineal maintains a stable relationship to cer-

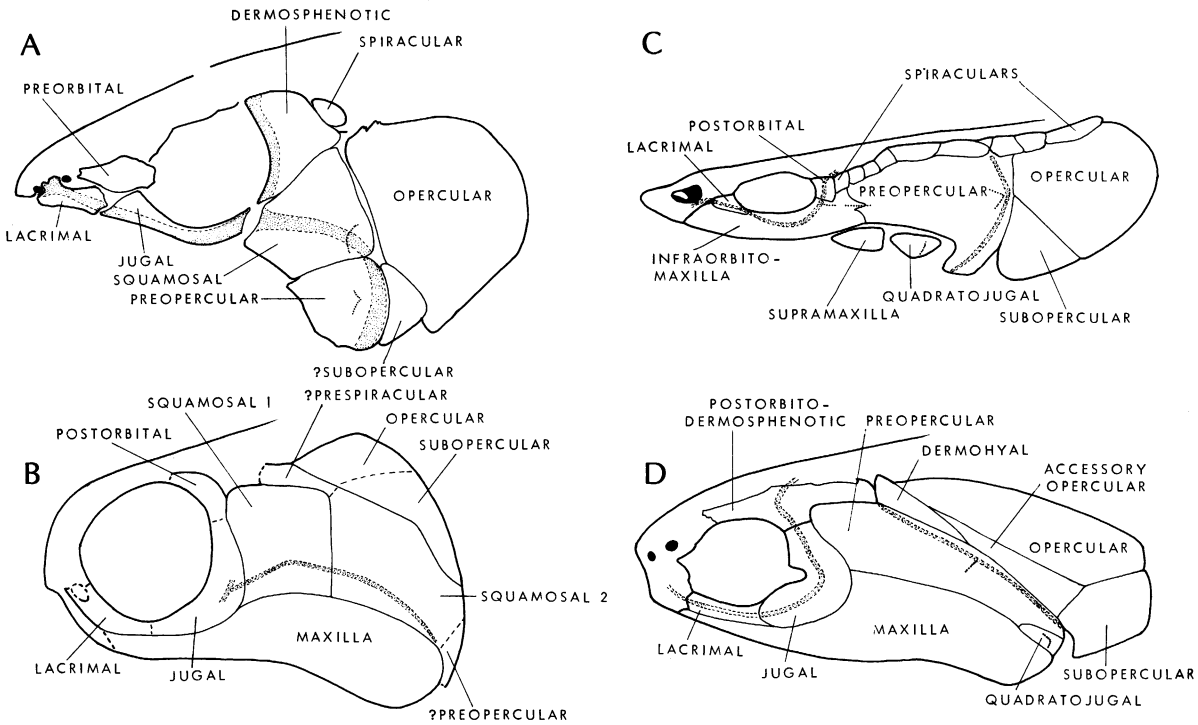


FIG. 44. Cheek bones and operculum in coelacanth (A), an onychodont (B), a cladistian (C), and a Devonian actinopterygian (D). A, *Rhabdoderma elegans* (Newberry) (after Forey, in press); B, *Strunius walteri* Jessen (after Jessen, 1966, fig. 6); C, *Polypterus bichir* Saint-Hilaire (after Daget, 1950, fig. 26); D, *Cheirolepis trailli* Agassiz (after Pearson and Westoll, 1979, fig. 20A). Bone names are those used by authors cited. The pattern in *Eusthenopteron* and *Ichthyostega* (fig. 43A, C) is best matched in B (quadratojugal missing) and D (squamosal missing). The quadratojugal (present in C and D) is apparently a primitive osteichthyan feature, lost or not found in onychodonts (Andrews, 1973, p. 146); and the squamosal is a primitive sarcopterygian feature (present in A, B and fig. 43). The features common to the cheek plate of *Eusthenopteron* and *Ichthyostega* (fig. 43A, C) seem therefore to be primitive for sarcopterygians; the extra bones in porolepiforms (fig. 43B) and dipnoans (fig. 43D) are autapomorphous, as is the absence of maxilla and quadratojugal in coelacanth (A).

tain bones (some tetrapods), and that the neuromasts can influence dermal bone ontogeny or fail to do so. But the occasions on which we should call forth these various "explanations" are unknown, especially in Devonian fishes and tetrapods where experimental investigation is not possible. As we see the problem, the patterns suggested by Säve-Söderbergh, Westoll, and Jarvik are not actually observable and can be said to exist only if one first assumes the reality and general applicability of a process of questionable relevance to the problem at hand. We therefore eschew such lines of argument and suggest, instead, that there are three observable patterns that can be recognized re-

gardless of what causal agents might be invoked to explain them. Two of these patterns concern dermal roofing bones, and, one, the cephalic lateral-line system. The first is the position of the eye in relation to the large paired bones on the skull roof which, as mentioned above, groups dipnoans and tetrapods. The second is a cluster of five bones in the occipital region of the skull of dipnoans and *Ichthyostega*. And the third is the interruption of the infraorbital canal near the incurrent (external) nostril in dipnoans and tetrapods (see p. 196). An interpretation of the dermal cheek bones is suggested in figs. 43, 44.

PALATE AND JAW SUSPENSION

(A) HISTORICAL

The earliest comparisons of Recent lungfishes with Recent amphibians, particularly urodeles, noted an obvious similarity in the palates and braincases (Huxley, 1876; Cope, 1885). But the late nineteenth century search for amphibian ancestors meant that the many derived features of dipnoans excluded these fishes from immediate relationship with tetrapods (see Historical Survey) and placed, in our view, unwarranted emphasis on the fossils. It was reasoned that lungfishes could not be ancestral to Recent Amphibia because, among other features, they lack a maxillary arch (Cope, 1885) and the dentition is too highly specialized (Baur, 1896; Gregory, 1915). Pollard (1891, p. 343) argued that "... Presuming the Dipnoi to be in the ancestral line of the Urodela such [autostyly *sensu* Huxley, 1876] should be the condition in young and primitive Urodeles. Such is not the case." He believed, like Jarvik (1968a), that lungfishes were close relatives of holoccephalans. Kingsley (1892, p. 679) maintained that "the autostylic condition [in urodeles] arises comparatively late in development, and never attains the completeness which a Dipnoan ancestry would require." The embryology of lungfishes was not known to either Kingsley or Pollard so this view expresses the same opinion as that given by Dollo (1896), that the dipnoans are *more* autostylic than urodeles and cannot therefore be considered ancestral to Recent amphibians (see also Schmalhausen, 1968, and pp. 233–234 below).

Pollard (1892) went on to suggest a scheme of homology between the palatal bones of *Polypterus* (then considered as a crossopterygian) and those of a frog.

The paleontological arguments for dismissing lungfish as amphibian ancestors were taken up by Watson from Baur (1896) and Cope (1892). Watson (1912, p. 10) compared the palate of *Megalichthys* with that of the temnospondylous amphibians *Loxomma* and *Eogyrinus*. He concluded that not only

was the arrangement of the bones of the palate very similar but also that "the ordinary idea of the autostylysm of the Tetrapoda is incorrect in postulating a connection between the palato-quadrato cartilage and the otic region. It is, I think, quite certain that there never was such a connection in primitive forms, except through the dermal bones of the temporal region."

That is still the current view (Kesteven, 1950) and may be summed up as follows: crossopterygians (with or without *Polypterus*), rather than lungfishes, are related to amphibians because of similarities in palatal dentition, a closer correspondence with fossil amphibians⁶ in jaw suspension and the persistence of palatal kineticism, and because it is easy to draw homologies between the dermal bones of the palate of a crossopterygian and those of both Recent and fossil amphibians.

Yet, Dollo (1896), Kesteven (1950), and Thomson and Campbell (1971) recognized that the tritoral dentition and the absence of maxillae, dermopalatines, and ectopterygoids in Recent lungfishes are simply unique dipnoan specializations and are therefore irrelevant for establishing their relationships.

(B) DERMAL BONES OF PALATE

We are concerned here with the presence or absence and the pattern formed by the paired pterygoid (entopterygoid or endopterygoid), ectopterygoid (transpalatine or transverse of tetrapods), dermometapterygoid (dermal metapterygoid), and the dermopalatine (palatine of tetrapods) which are associated with the palatoquadrato, and the vomer (prevomer) and the median parasphenoid which are associated with the neurocranium (figs. 45, 46). A variety of names has been used for the bones of the dermal palate; these

⁶ For our purposes in this section we take fossil amphibians to include ichthyostegids, lepospondyls, temnospondyls, and anthracosaurs. It is unlikely that they form a monophyletic group (Gaffney, 1979a).

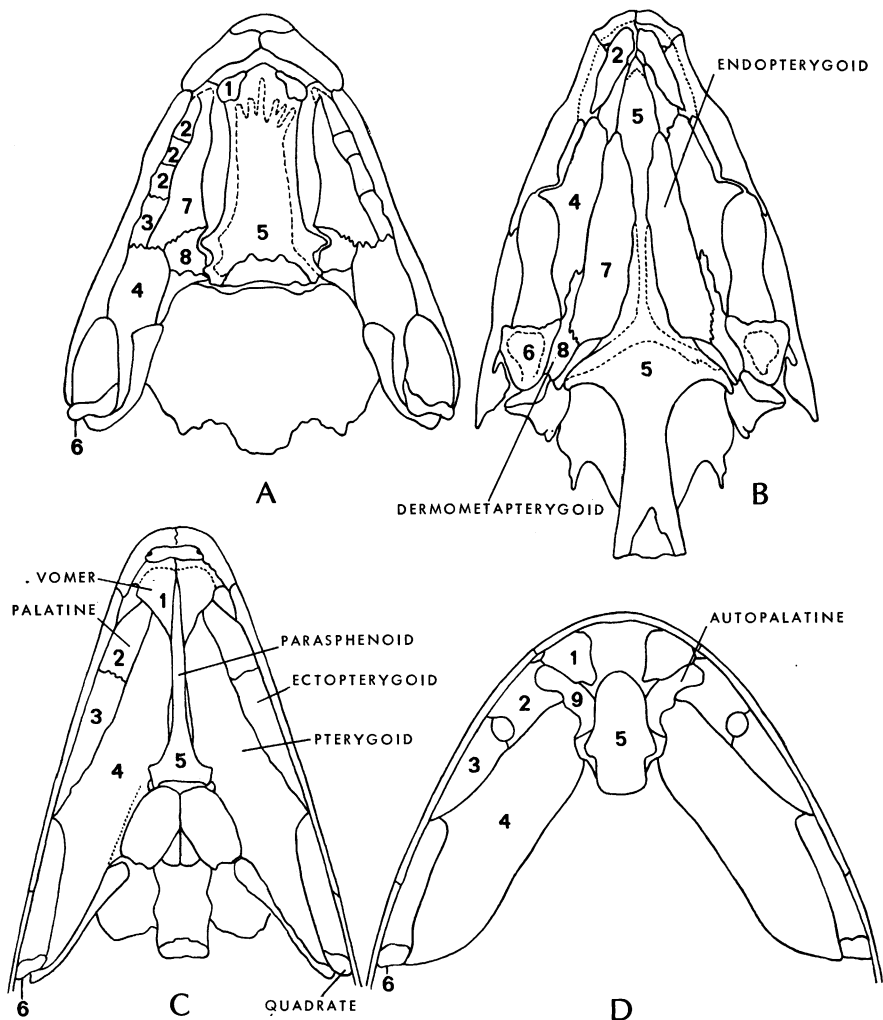


FIG. 45. Palates in ventral view and suggested homology of dermal bones and their relation to palatoquadrate. Actinopterygian: A, *Mimia toombsi* Gardiner and Bartram (BMNH specimens). Cladistian: B, *Polypterus bichir* Saint-Hilaire (BMNH specimens). Rhipidistians: C, *Eusthenopteron foordi* Whiteaves (from Jarvik, 1954); D, *Glyptolepis groenlandica* Jarvik (from Jarvik, 1972). Compare figure 46. Code 2 refers to dermopalatine in all figures.

are listed in table 2. The dermal palatal bones are thought to have been derived from condensations within a uniform lining of denticles within the buccal cavity (Nelson, 1970). We regard the presence of such tooth-bearing bones (except the parasphenoid, present in placoderms) as a synapomorphy of osteichthyans.

Many authors have stressed the close sim-

ilarity in number and arrangement of the bones between the palate of *Eusthenopteron* and primitive amphibians. In both (figs. 45C, 46B, C), the parasphenoid is flanked by a large pterygoid which extends from the posterolateral contact with the quadrate to the vomer. The dermopalatine and ectopterygoid are sutured to the lateral edge of the pterygoid but a considerable portion of the

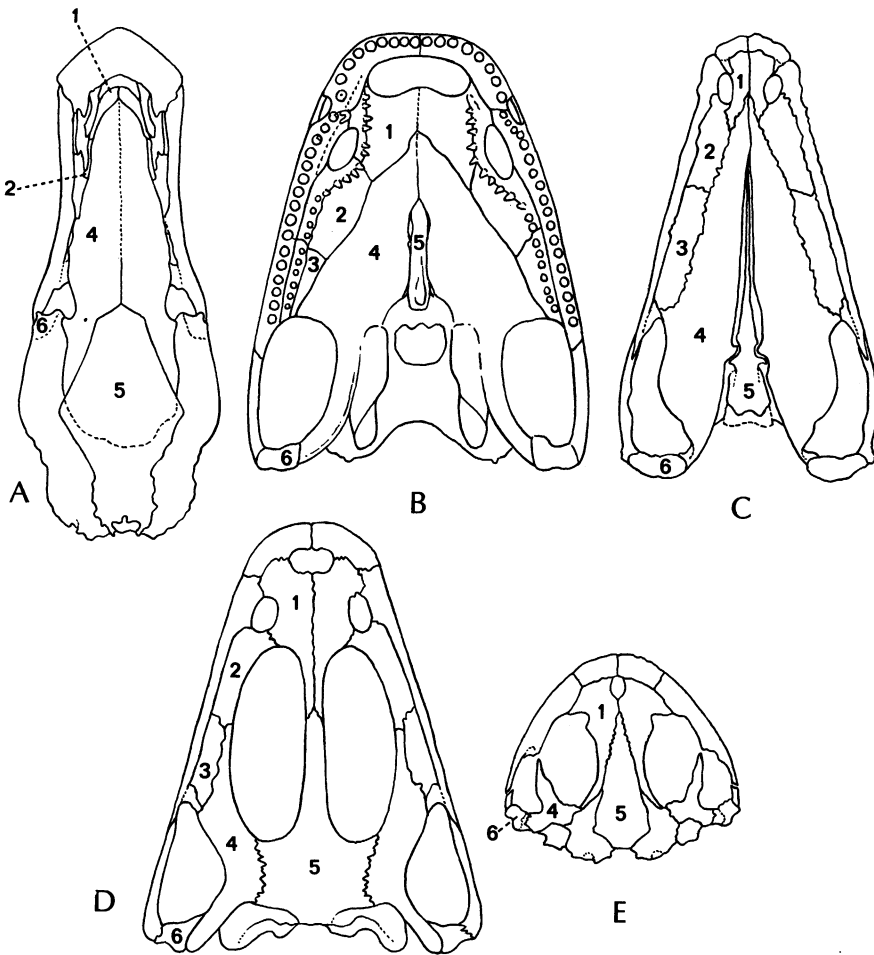


FIG. 46. Palates in ventral view and suggested homology of dermal bones and their relation to palatoquadrate. Dipnoan: A, *Griphognathus whitei* Miles (from Miles, 1977). Tetrapods: B, *Ichthyostega* (from Romer, 1966); C, *Eogyrinus attheyi* Watson (from Panchen, 1972a); D, *Benthosuchus sushkini* Efremov (from Bystrov and Efremov, 1940); E, *Tylotriton verrucosus* Riese (from Noble, 1931). Compare figure 45 for bone names.

latter extends posteriorly beyond the ectopterygoid. The dermopalatine and ectopterygoid lie in series with the vomer and are securely attached to the maxilla laterally. In fossil amphibians there is no possibility of movement between the dermopalatine, ectopterygoid and maxilla. The choana, or its presumed homologue in *Eusthenopteron*, is bordered medially by the vomer and dermopalatine. Achoanate *Latimeria* is very similar except that there are three bones in series in place of the dermopalatine

and ectopterygoid of *Eusthenopteron* and primitive amphibians. This difference is of unknown significance since actinopterygians have a variable number of bones in this position (below). Also, fossil amphibians have been described with two ectopterygoids (*Megalocephalus*, Watson, 1926) and some have a single bone occupying the territory of the vomer and dermopalatine [*Trematosaurus brauni* (Owen)—Watson, 1919; *Batrachosuchus*—Säve-Söderbergh, 1935]. The palate of anurans and urodeles (fig. 46E)

differs from that described above chiefly in the development of large palatal vacuities and absence of the ectopterygoid. The palatal vacuities are present in more advanced temnospondyls; they are developed between the pterygoid-dermopalatine and the parasphenoid, in contrast to those found in amniotes between the pterygoids and the maxilla-jugal. Palatal vacuities and absence of the ectopterygoid are both derived features within certain tetrapod subgroups.

There are two important differences between the palatal structure of crossopterygians (including coelacanth) and tetrapods. In crossopterygians the pterygoids do not meet and suture with one another in the midline and the parasphenoid ends posteriorly at the ventral fissure, as in primitive actinopterygians (fig. 45). This contrasts with medially united pterygoids and a long parasphenoid in tetrapods (we are uncertain about the condition of the parasphenoid in *Ichthyostega*; see Jarvik, 1952).

In all dipnoans, like tetrapods, the pterygoids and vomers meet in the midline and the parasphenoid is long.⁷ Kesteven (1950) noted the close similarity in shape and arrangement of the vomers and pterygoids between *Dipterus* and *Ichthyostega* and went on to say (p. 125) “. . . The essential simi-

larity of these bones is only partly disguised by the peculiar teeth on those of Dipnoans, and this difference in the teeth should not be deemed of phylogenetic importance because we observe marked differences in the teeth of relatively closely related Elasmobranchs.” Since Kesteven wrote that sentence we have discovered a great deal about the primitive lungfish palate (Denison, 1968a, 1968b, 1974; Thomson and Campbell, 1971; Miles, 1977). Our current knowledge strengthens the correctness of Kesteven's view. The specialized dentition of the Recent lungfishes has clearly arisen within the group (Denison, 1974) and there are several genera (*Griphognathus*, *Uranolophus*, *Holodipterus*, *Fleurantia* and *Conchopoma*) in which the palate is covered by a shagreen of tiny teeth. The pterygoids are also primitively long (Miles, 1977, p. 173) as in crossopterygians and primitive tetrapods. *Griphognathus whitei* Miles shows long pterygoids which, in some specimens (e.g., BMNH P. 56054) are flanked anteriorly by two paired bones identified here as vomer and dermopalatine (figs. 7A, 46A). They are equivalent to dermopalatine 1 and 2 of Miles. The vomers meet in the midline anteriorly and the dermopalatine forms the medial margin of the choana. There is a third paired palatal bone which lies anterolateral to the vomer (dermopalatine 3 of Miles; “extra” dermal bone, fig. 7). This could be interpreted as a dermopalatine, in which case the bone we have labeled by that name would be interpreted as the ectopterygoid. Be that as it may, there are marginal palatal bones and at least the posterior member of this series is firmly sutured to a maxilla (see p. 181). It is possible that *Holodipterus gogoensis* also shows a separate palatine and ectopterygoid since there are several small tooth plates in this area (Miles, 1977, fig. 72). We do, however, agree with Miles that it is very difficult to restore these plates to their mutual position and they equally well might represent fragments of the maxilla or premaxilla as seen in *Griphognathus* (fig. 7B).

In *Griphognathus* therefore, we can see the same so-called special similarities between the crossopterygian palate and the palate of a primitive tetrapod. The lungfishes

⁷ Three Lower Devonian lungfishes have been described as having short (“stalkless”) parasphenoids and this is presumed primitive for dipnoans (Miles, 1977). The precise condition of the parasphenoid in each of these forms is, however, uncertain. For *Dipnorhynchus lehmanni* Lehman and Westoll (1952, p. 410) stated that “The details, however, are not well shown, and a very small posterior expansion may be present.” In *Dipnorhynchus sussmilchi* there is no separate parasphenoid (Thomson and Campbell, 1971) although it is presumed to have fused with the pterygoids (Miles, 1977). The parasphenoid of *Uranolophus* has a large toothed area, behind which is a smooth flange, broken posteriorly (Denison, 1968b, figs. 8, 9). Here too, there is doubt about the posterior limit of the parasphenoid. The crucial fact is, not so much whether there is a “stalk” or not, but whether the parasphenoid has grown back sufficiently to occlude the ventral cranial fissure, as it has in all other dipnoans. The relative position of the ventral fissure and parasphenoid is unknown in both *D. lehmanni* and *Uranolophus*.

TABLE 2
Synonymy of Bone Names for Dermal Palate
(Those in brackets are less commonly used.)

| This paper (figs. 45, 46) | Actinopterygians + <i>Polypterus</i> | Crossopterygians and Lungfishes | Tetrapods |
|--|--|---------------------------------------|--|
| Dermopalatine (2) Ectopterygoid (3) | dermopalatine posterior dermopalatine | dermopalatine ectopterygoid | palatine transpalatine (transverse, ectopterygoid) |
| Pterygoid (4) | ectopterygoid | entopterygoid (endopterygoid) | pterygoid (entopterygoid) |
| Dermometapterygoid (8) | dermometapterygoid (dermal metapterygoid) | — | — |
| Endopterygoid (7) | endopterygoid | — | — |
| Vomer (1) | vomer (prevomer) | vomer (prevomer) | prevomer (vomer) |

show an additional feature of tetrapods, namely the medially united pterygoids.

In porolepiforms (fig. 45D) the palate, as restored by Jarvik (1972), is similar to that of osteolepiforms. The vomers do not apparently meet in the midline, in at least *Porolepis* or *Glyptolepis*, and this is a reflection of the broad snout of porolepiforms. Unlike dipnoans and tetrapods the pterygoids do not meet in the midline.

The vertebrates dealt with so far show a similar number and arrangement of palatal dermal bones to which a consistent system of names can be applied. The varied names which have been used resulted from the application of names coined for actinopterygians or, in the case of the prevomer, from a presumed difference in mammals.⁸ We em-

ploy terminology commonly used for fishes (table 2).

Actinopterygians and *Polypterus* show a rather different arrangement of dermal bones on the palate: some homologies can be drawn between these and the palatal bones discussed above but this group has additional elements. The Gogo paleoniscid *Mimia* shows what we believe to be the primitive condition for the group. There is a paired vomer⁹ followed by two series (fig. 45A); an outer row of dermopalatines and an inner row of endopterygoid followed by one or more dermometapterygoids. The dermomet-

viewed this problem with particular reference to *Ornithorhynchus* and showed that the palatine process (prevomer) is ontogenetically part of the premaxilla. They concluded (p. 104) “*There is therefore in no mammal an additional pair of elements between the vomer and the premaxilla, and thus the vomer(s) in all mammals occupy an homologous position to those of reptiles*” [italics theirs].

⁹ A special problem surrounds the identification of the vomer of *Polypterus*. Several authors identify the vomer as that bone here called dermopalatine (2, fig. 45B). It resembles the vomer of *Griphognathus* (cf. Miles, 1977, fig. 81; Allis, 1922, fig. 25) and lies close behind and parallel to the premaxilla. It is here identified as a dermopalatine because it is associated with the palate in disarticulated skulls (a true vomer is always closely attached to the floor of the nasal capsule) and because in early ontogenetic stages of *Polypterus* an identifiable vomer is recorded (Holmgren and Stensiö, 1936; Pehrson, 1947).

⁸ In non-mammalian vertebrates the bones which are clearly homologues of fish vomers are often called prevomers (Watson, 1926; de Beer, 1937) following a recommendation by Broom (1895). The history of the problem has been outlined by de Beer (1937, pp. 433–435) and Parrington and Westoll (1940). Broom noted that the premaxilla of several primitive mammals developed as two parts; a marginal tooth bearing portion and a palatine process. The latter remains separate in *Ornithorhynchus* (the dumbbell bone) and apparently fuses very late in ontogeny in several others (e.g., *Erinaceus*, *Tatusia*). Since this separate process lay anterior to the mammalian vomer Broom called this the prevomer. Broom considered this palatine process to be the topographic homologue of the vomer of non-mammalian vertebrates. However, Presley and Steel (1978) have re-

apterygoid is a primitive characteristic of the group *Polypterus* + actinopterygians. One or several are found in paleoniscids (Watson, 1925; Nielsen, 1942, 1949). *Polypterus* is the only living fish with a (single) dermometapterygoid.

The endopterygoid lies anterior to the dermometapterygoid and traditionally is the bone considered homologous with the pterygoid (sometimes called entopterygoid) of rhipidistians and coelacanth, lungfishes, and tetrapods. However, there is reason to believe that the endopterygoid is unique to *Polypterus* and actinopterygians and that the homologue of the pterygoid is the bone called ectopterygoid in actinopterygians and *Polypterus*.

The ectopterygoid of actinopterygians and *Polypterus* (bone 4; fig. 45B) is the posterior member of a series with the dermopalatines to which it is related embryologically (Pehrson, 1922, 1947). It reaches back to the quadrate, borders the adductor fossa and primitively contacts the maxilla anterolaterally. These are precisely the relationships of the pterygoid of *Eusthenopteron* (Jarvik, 1954), porolepiforms (Jarvik, 1972), lungfishes (Miles, 1977), urodeles (Goodrich, 1930), fossil amphibians (e.g., Panchen, 1964; Beaumont, 1977; Säve-Söderbergh, 1935, 1936), and *Latimeria* (Milot and Anthony, 1958) although in the last a maxilla is absent. In the pterygoid of all these forms and in the actinopterygian ectopterygoid, the ossification center lies near the ventral (lateral) margin. In contrast, the ossification center of the endopterygoid lies near the dorsal or medial margin.

The pterygoid of sarcopterygians is very large and reaches along the medial edge of the more anterior members of the series where it may overlap the ectopterygoid (coelacanth) or the ectopterygoid and the dermopalatine (*Eusthenopteron*, porolepiforms, *Ichthyostega* and many temnospondyls, and anthracosaurs; similar overlaps are shown by the ectopterygoid of *Polypterus* and actinopterygians such as *Lepisosteus*, *Amia*, and *Saurichthys*).

It is difficult to decide if the endopterygoid and dermometapterygoid are synapomor-

phies of *Polypterus* + actinopterygians for two reasons. First, a dermometapterygoid has been figured in a specimen of *Eusthenopteron* (BMNH P. 6807, Woodward, 1922). We have examined this specimen and remain undecided whether or not there is a separate bone. Second, if we assume that the group *Polypterus* + actinopterygians are the most primitive osteichthyans and if we also assume that the dermal skeleton has taken an assimilative route (Nelson, 1970) then the extra bones in primitive actinopterygians could be the primitive osteichthyan condition. If so, the absence of an endopterygoid and dermometapterygoid are sarcopterygian synapomorphies.

(C) PALATOQUADRATE

The gnathostome palatoquadrate cartilage primitively ossifies from three centers; an anterior autopalatine; a posteroventral quadrate at the lower jaw articulation; and a dorsal metapterygoid (epipterygoid of tetrapods) at the basal articulation. This primitive condition may be seen in diverse fishes: *Acanthodes* (Miles, 1973) where these ossifications are perichondral only; juvenile *Mimia*, *Moythomasia*, some specimens of *Pteronisculus* (Nielsen, 1942), and *Acropholis* (Aldinger, 1937), many teleosts, and coelacanth. In osteolepiforms and porolepiforms, as, in large specimens of the actinopterygians *Mimia*, *Moythomasia*, and *Pteronisculus*, the palatoquadrate is ossified throughout as a single bone. Our knowledge of the growth stages of the actinopterygians mentioned and the condition in coelacanth suggests that the palatoquadrate of rhipidistians also ossified from three centers representing sites of articulation between the palate and the braincase and lower jaw.

Reduction or loss of ossification centers is therefore regarded as a derived condition. Thus, among actinopterygians, *Lepisosteus* and some teleosts have lost the autopalatine (Patterson, 1973) and only the quadrate seems to have survived in *Birgeria* (Nielsen, 1949). *Polypterus* has lost the metapterygoid (Allis, 1922).

The palatoquadrate of *Neoceratodus* contains only a quadrate ossification, as in frogs and urodeles, and even this is absent in *Lepidosiren* and *Polypterus*. Fossil lungfishes appear to show more extensive ossification of the palatoquadrate in which it is not possible to recognize centers of ossification (Miles, 1977, p. 24) but, since an ascending process is well ossified in many of these lungfishes, we assume that at least a metapterygoid center was present. Temnospondyls (Bystrov and Efremov, 1940), anthracosaurs (Panchen, 1964, 1970), turtles, lizards, and *Sphenodon* have both a quadrate and a metapterygoid (epipterygoid).

The picture which emerges is that choanates (lungfishes and tetrapods) have the palatoquadrate foreshortened anteriorly so that it no longer contacts the ethmoid region. This is associated with the loss of an autopalatine. Loss of an autopalatine is also seen in some actinopterygians but it is never associated with a foreshortening of the palatoquadrate.

(D) RELATION BETWEEN PALATE AND BRAINCASE

The similarity between lungfishes and amphibians in the relation between the palate and the braincase was pointed out long ago by Huxley (1876) and Cope (1885), and more recently by Kesteven (1950) and Fox (1965). This type of jaw suspension was designated autostylic by Huxley (1876, p. 40) who noted that autostyly also occurred in holocephalans and Recent agnathans. These authors regarded the union of palate with braincase as evidence of relationship between lungfishes and amphibians. Other authors have regarded autostyly as evidence of a lungfish-holocephalan relationship (Jarvik, 1968a; Edgeworth, 1935). Jarvik's view can be falsified by several other characters which suggest that elasmobranchs and holocephalans are sister groups (Schaeffer and Williams, 1977). The "autostyly" of holocephalans differs considerably from that of lungfishes which, in turn, is very similar to that of amphibians.

The contact between the palate and the braincase of dipnoans and lissamphibians is

effected by three processes: basal,¹⁰ ascending and otic (defined by de Beer, 1937) and the anterior projection of the palatoquadrate beneath the neurocranium (pterygoid process) is reduced or absent (Fox, 1965; Bertmar, 1968). The relationships of the nerves and blood vessels to these processes and to the extracranial cavities which they enclose (cavum epiptericum and cranioquadrate passage) in the two groups and the form and size of these processes are very similar (Goodrich, 1930; de Beer, 1937; Fox, 1965, figs. 21, 34, 38). The otic and ascending processes are fused to the neurocranium; the basal process is fused in dipnoans and some urodeles, but not in anurans and apodans. The hyomandibular is reduced in comparison with the first epibranchial and takes no part in jaw suspension.

The autostyly of holocephalans is different, a fact which led Gregory (1904) to propose the term holostyly for these fishes. The palatoquadrate is attached throughout its length from the nasal capsule to the occiput, there is no ascending process and the identification of the otic process is questionable (Goodrich, 1930, fig. 444). The hyomandibular takes no part in jaw suspension but is unreduced. With Gregory we agree there is little ground for comparison between the autostyly of holocephalans and dipnoans + tetrapods and accept that fusion of the palate with the braincase has occurred convergently.

Consideration of the palate/braincase relationship in primitive amphibians and in crossopterygians has profoundly favored crossopterygians over lungfishes as tetrapod relatives since it is believed that the primitive amphibian palate is kinetic and that this could only have been inherited from a crossopterygian ancestor. It is assumed that the palate of primitive amphibians is movable on

¹⁰ There has been considerable argument (see de Beer, 1937, pp. 207, 214; Jarvik, 1954) as to whether there is a true basal process in anurans (except *Ascaplus*), since the relation of the palatine nerve to the process is rather different to that in dipnoans and urodeles. This is of little significance to the arguments here since, if one wishes to argue for non-homology this would simply be an autapomorphy of anurans.

the braincase (e.g., Watson, 1912; Panchen, 1970; Beaumont, 1977). The palate is certainly movable in *Latimeria* (Thomson, 1966) and this was probably true of *Eusthenopteron* and porolepiforms. In fact, in *Eusthenopteron*, there is a very complex and, in our view, movable joint between the dermopalatine and the vomer (fig. 14). The palate and ectopterygoid are keyed to the maxilla and must have moved with it. The condition of our *Eusthenopteron* specimen suggests that the maxilla, palate, and the circumorbital bones moved as a unit against the snout: there are distinct sliding joints between the lacrimal and the supraorbito-tectal/lateral rostral.

A kinetic palate in primitive amphibians is more difficult to believe. Anteriorly the skull is very solid, with dermopalatine, ectopterygoid, vomers, and pterygoids firmly keyed to one another and to the cheek bones, and the cheek bones are keyed to the skull roofing bones, at least to those lying anterior to the pineal. There is no evidence of sliding joints. So, with the palate firmly fixed anteriorly, the kineticism must be located posteriorly, at the basal articulation, or at the point where the ascending process contacts the braincase. *Ichthyostega* may or may not retain the intracranial joint but kinesis at this point is apparently impossible because of "a remarkably precocious consolidation of the skull roof" (Panchen, 1972b, p. 78). The comments of two amphibian workers are pertinent at this point. Panchen (1970), writing about anthracosaurs, denies the existence of kineticism in temnospondyls (primitive relatives of lissamphibians, Gaffney, 1979b). Certainly the members of this group generally accepted as advanced, the stereospondyls, have the palate firmly fixed at the basal articulation (Säve-Söderbergh, 1935, 1936). But according to Beaumont (1977) the more primitive loxomatids have palatal kineticism which to us requires bone-bending. The bending would take place in the transverse plane. In anthracosaurs (Panchen, 1970) a gap between the squamosal and the supratemporal is thought to enable the palate to move up and down but since the palate is fixed anteriorly this may mean no more than

bone-bending in the longitudinal plane. These remarks are not intended to be facetious but there does seem to be a case for questioning the existence of palatal kineticism in primitive amphibians. Perhaps there was some movement but the alleged remnant of kineticism was not of the crossopterygian kind.

To sum up this section on the palate and jaw suspension we propose the following outline of character phylogeny. The primitive gnathostome condition is an amphistylic jaw suspension with a fully developed suspensory hyomandibula and a palate which articulates with the braincase at the basal articulation and rises dorsally from this point as a cleaver-shaped process (Schaeffer, 1975). The palatoquadrate of either side curves inward anteriorly and meets its antimeres beneath the nasal capsules. The palatoquadrate ossifies from three centers and is covered with a shagreen of teeth; a vomer is absent. These conditions are met in *Acanthodes* and in primitive sharks, except that sharks have an unossified palatoquadrate (derived sharks show hyostyly and rays euhyostyly; holocephalans are holostylic). Synapomorphies of osteichthyans are: palatoquadrate of either side not meeting in the midline anteriorly (chondrosteans parallel more plesiomorph groups in this respect) but articulating with the postnasal wall; paired vomer, dermopalatine, ectopterygoid and pterygoid tooth plates present (actinopterygians + *Polypterus* show additional tooth plates and methostyly is developed within the group). Sarcopterygians show an articulation between the metapterygoid (epipterygoid) and the dorsal portion of the orbitotemporal region of the braincase, hyomandibular straddling the jugular canal, pterygoid enlarged and forming the chief bone of the palate. Choanates show a reduced hyomandibula playing no direct part in jaw suspension, absence of an autopalatine associated with an anterior reduction of the palatoquadrate, an immobile dermopalatine-snout contact, pterygoids meeting in the midline, and autostyly (but not necessarily involving fusion of bone as opposed to cartilage fusion).

HYOID AND GILL ARCHES

In comparing the gill arches of the main groups of gnathostomes we have accepted, in part, Nelson's (1968), rather than Miles's (1964, 1965) and Moy-Thomas and Miles's (1971), interpretation of the branchial skeleton of *Acanthodes*, and we have accepted Jarvik's (1954) reconstruction of the parts of the *Eusthenopteron* skeleton preserved in his specimens (viz., the first three arches and part of the fourth). Nelson's and Miles's interpretations of the *Acanthodes* visceral skeleton are out of phase by one element, namely whether the gill arches are supported ventrally on a copula with two ossified basibranchials between arches one and two and two and three (Nelson's inference, fig. 47A) or whether the basibranchials identified by Nelson are really hypobranchials of the second and third arches, and the hypobranchials and ceratobranchials of Nelson are really the two parts of a segmented ceratobranchial (Moy-Thomas and Miles's inference). We favor Nelson's view because (1) there is no particular reason to postulate an unusual condition of a bipartite ceratobranchial (see, below, comments on Miles's postulate of a bipartite epibranchial); (2) the structures identified as basibranchials by Nelson are small elements of about equal length oriented at an angle to the gill arch as one might expect them to be if they were median elements; and (3) in a photograph published by Miles (1973, plate 7), the plainly visible gill rakers on the inner side of the arches are present all along what Nelson identified as hypobranchials and ceratobranchials but are absent on the small ventral elements, as would be true of ceratobranchials, hypobranchials, and basibranchials in other fishes. Nelson (1968) commented on the dorsal gill arches of *Acanthodes*: "Watson and Miles apparently erred in showing the epibranchial divided in two pieces, and in terming one of these either a pharyngobranchial (Watson) or an infrapharyngobranchial (Miles) . . . the suprapharyngobranchial of Miles appears to be part . . . of the same pharyngobranchial figured by Reis and possibly also by Dean." In addition, Miles (1964, 1965) figured the pharyn-

gobranchials extending forward as in bony fishes, whereas Nelson (1968), by studying the details of paired articular surfaces on the epibranchials in relation to corresponding points on the pharyngobranchials, concluded that the pharyngobranchials are directed posteriorly as in chondrichthyans. From these, and other observations of the hyoid arch, Nelson (1969) concluded that "the visceral apparatus of acanthodians appears to be more primitively organized than that of any other gnathostome group."

If Nelson's interpretation of acanthodian gill arch structure is correct, then *Acanthodes* resembles chondrichthyans in three important respects: the ventral articulation of the first two gill arches fore and aft of a small basibranchial element, the absence of a suprapharyngobranchial element articulating with the basicranium, and the posterior orientation of the pharyngobranchials (fig. 47). Further, if these are primitive conditions of gnathostome gill arches, then the Osteichthyes are defined by three derived conditions: the ventral articulation of at least the first two gill arches on a single basibranchial, the presence of a suprapharyngobranchial articulation with the basicranium, and the forward orientation of the infrapharyngobranchials. These three conditions are illustrated (fig. 48) in the sarcopterygian *Eusthenopteron* (in which the first suprapharyngobranchial apparently arises from the proximal end of the first infrapharyngobranchial), the paleoniscid *Pteronisculus* (in which there is a suprapharyngobranchial on the first and second epibranchials, as in Recent chondrosteans), and the Recent cladistian *Polypterus* (in which the only suprapharyngobranchial present appears to have fused with the first epibranchial). Nelson (1969) suggested that a condition not unlike that of *Eusthenopteron* may be present on the first arch of *Latimeria* in which the pharyngobranchial is a slender, dorsally directed rod (fig. 49A); it suggests the interpretation that a compound supra-infrapharyngobranchial has been reduced distally, leaving only the erect dorsal process proxi-

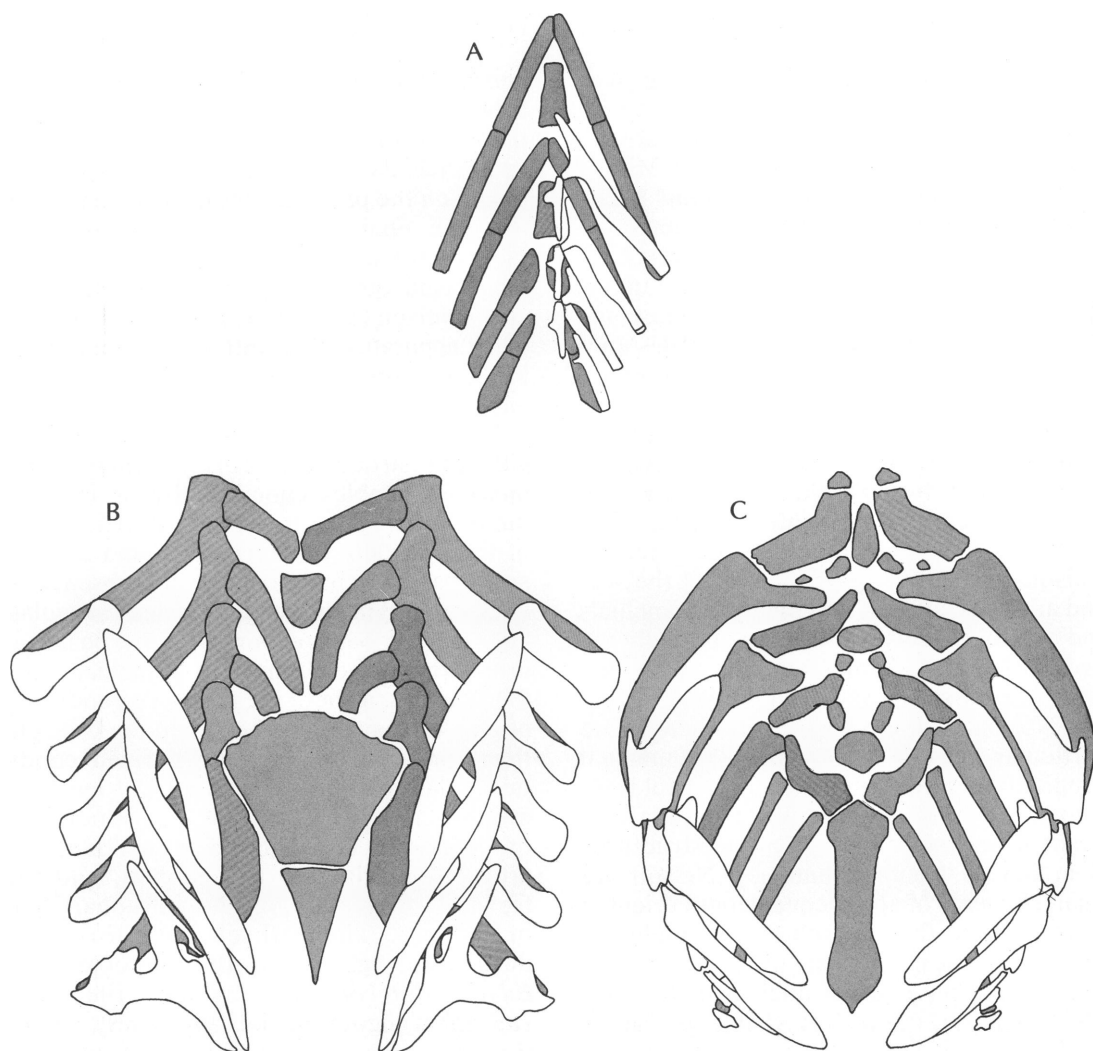


FIG. 47. Gill arches, dorsal view. A, *Acanthodes bronni* Agassiz (from Nelson, 1968; compilation of figs. 3 and 4a; fifth arch not shown). B, *Squalus acanthias* Linnaeus (AMNH 40804); C, *Hydrolagus colliei* (Lay and Bennett) (AMNH 40805). Dorsal gill arches unshaded.

mally. The suprapharyngobranchial of the second arch in *Latimeria*, like that in *Eusthenopteron* and *Pteronisculus*, is articulated, not fused, with the epibranchial.

Eusthenopteron and *Pteronisculus* and other actinopterygians share with acanthodians and chondrichthyans the apparently primitive condition of having the right and left gill arches coming together in the ventral midline on a long, narrow copula, the arch

elements of one side extending forward and downward more or less parallel with each other. In *Polypterus* the arches also run parallel and articulate against a copula, but the copula, as in *Mimia*, is undivided into separate basibranchials (Sewertzoff, 1927, figures a specimen of *P. delhezi* as having two basibranchials, but our material of this species, AMNH 31013, shows only a single basibranchial); the single basibranchial is also

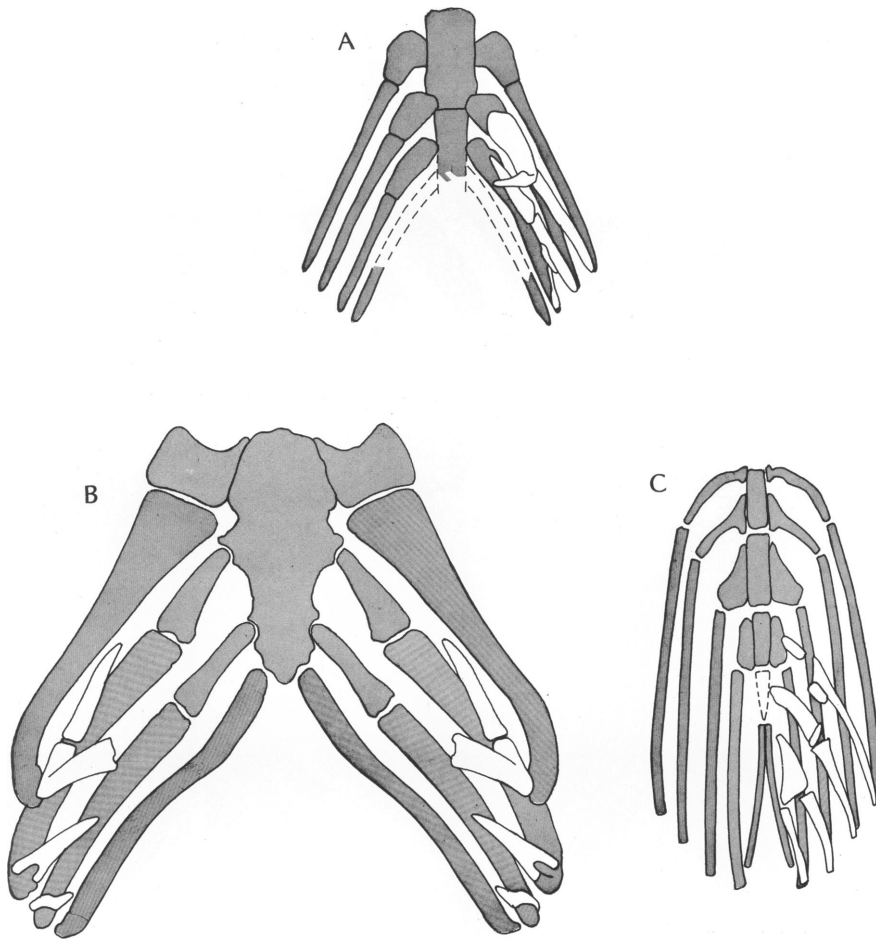


FIG. 48. Gill arches, dorsal view. A, *Eusthenopteron foordi* Whiteaves (modified from Jarvik, 1954); B, *Polypterus ornatipinnis* Boulenger (AMNH 40802); C, *Pteronisculus stensioei* (Nielsen) (modified from Nielsen, 1942). Dorsal gill arches unshaded.

somewhat broader than in actinopterygians but is perhaps similar in outline to what is known of the basibranchials of *Eusthenopteron* (fig. 48A). In addition, the copula of *Polypterus* may be secondarily foreshortened in connection with the loss of a gill arch (Nelson, 1969, has argued that an intermediate arch has been lost and his proposal is supported by the similarity in structure and associated dorsal arch elements on the first arch and the absence of dorsal elements on the fourth and last arch with the first and fifth arches of other fishes).

In *Latimeria* and *Neoceratodus* (fig. 49A, B) five arches are present, but the copula is greatly foreshortened (*Latimeria*) or reduced (*Neoceratodus*) and hypobranchials are absent (*Latimeria*) or absent anteriorly and greatly reduced posteriorly (*Neoceratodus*). The supposition that *Neoceratodus* has small hypobranchials present on arches three and four is suggested by the presence of small, forwardly directed proximal processes which closely resemble similar elements in the hypobranchial position of larval urodeles (see, for example, *Hynobius*, fig. 49C) and by the

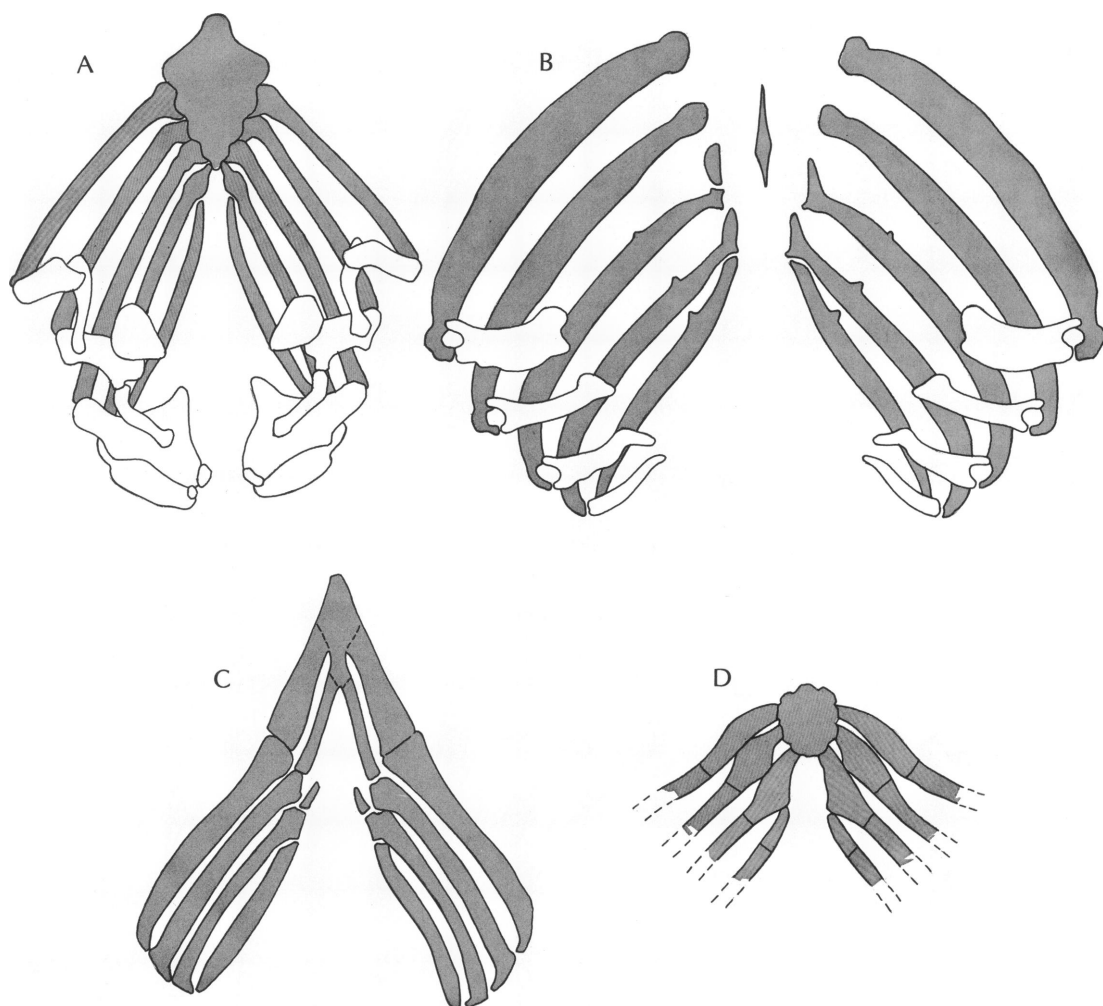


FIG. 49. Gill arches, dorsal view. A, *Latimeria chalumnae* Smith (AMNH 32949); B, *Neoceratodus forsteri* (Krefft) (AMNH 36982); C, *Hynobius leechi* Boulenger (AMNH 58792); D, *Glyptolepis groenlandica* Jarvik (modified from Jarvik, 1972). Dorsal gill arches unshaded.

fact that one of these processes is free from the ceratobranchial on one side of one specimen. *Latimeria*, *Neoceratodus*, and *Hynobius* have the copular region reduced to a short triangular area with the apex of the triangle posterior, so that the anterior gill arch bases are noticeably farther apart than those of the posterior arches, and consistently have the posteriormost arch articulating directly with the base of the preceding arch rather than lying free or articulating with the

copular region.¹¹ *Latimeria*, *Neoceratodus* and urodeles also show an apparent transi-

¹¹ The gill arch bases of *Griphognathus*, as restored by Miles (1977, fig. 137) are not farther apart anteriorly than posteriorly, but Miles has restored the bases of the first two arches on the posterior end of a specialized basihyal. If the known arches were restored entirely on the triangular basibranchial (on which they would all fit), the arrangement of gill arch bases would be similar to those of *Neoceratodus*. We have no good clue as to which is the preferable solution.

tion series in reduction of gill arch elements. In *Latimeria* the anterior epibranchials are reduced in length relative to posterior ones, the first pharyngobranchial is represented by a slender rod (cf. the first arch in *Eusthenopteron*), the second pharyngobranchial is a simple, round nodule loosely associated with the epibranchial, and the third pharyngobranchial is either absent or, if present, is represented only by one or two tiny, irregular bits of cartilage. In *Neoceratodus* the anterior epibranchials are reduced relative to the posterior ones and there are no pharyngobranchials. In urodeles there are neither epibranchials nor pharyngobranchials. *Eusthenopteron foordi*, if correctly interpreted by Jarvik (1954), might be considered to be part of this transformation series in lacking a posterior pharyngobranchial. This loss may be a unique reductional feature of the species because it is associated with a very small third and no fourth epibranchial in combination with very well-developed epibranchials and pharyngobranchials similar to those of actinopterygians on the first and second arches. Or the loss may be apparent and reflect only poor preservation (see Jarvik, 1954, pp. 22–23). A fifth arch was postulated by Jarvik, but is not actually known. Jarvik (1972) has also reconstructed the ventral part of the gill arches of the porolepiform *Glyptolepis groenlandica*, in which, again, elements of only four arches have been found (fig. 49D). In the porolepiform *Laccognathus*, however, there are five (Vorobyeva, 1980). Jarvik shows the copula as suboval, greatly foreshortened, and supporting all but the last arch; this reconstruction strongly resembles the condition in *Latimeria*, except that Jarvik has identified hypobranchials in *Glyptolepis*. A further resemblance between Jarvik's reconstruction and the ventral gill arch structure in *Latimeria*, *Neoceratodus* and urodeles is the articulation of the posterior arch base with the base of the preceding arch rather than with the copular region, but unlike those three groups and other osteichthyans, the posterior arch has a hypobranchial. In *Laccognathus* the bases of each of the last two arches (fourth and fifth) articulate with the preceding arch (Vorobyeva,

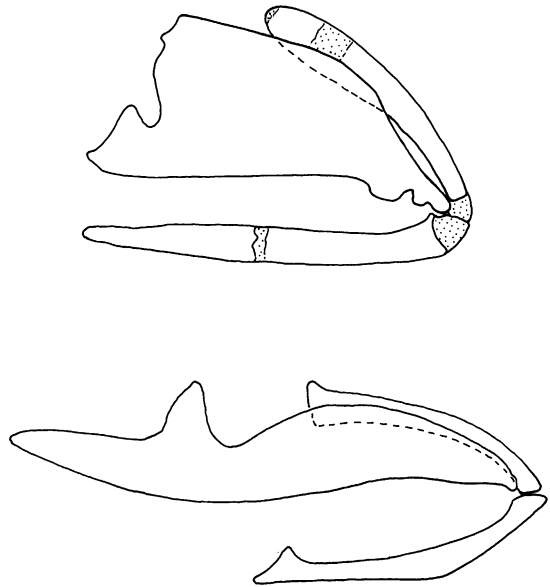


FIG. 50. Hyoid arch in relation to palatoquadrate. Above, *Acanthodes bronni* Agassiz (various sources). Below, *Chlamydoselachus anguineus* Garman (from Allis, 1923).

va, 1980). The Devonian dipnoan *Griphognathus* is also described (Miles, 1977) as having only four gill arches, but, as in modern lungfishes, the last arch articulates with the base of the preceding arch and there are no hypobranchials. In general, it does seem to us that there exists reason here, as in a number of other features discussed in other sections, to place porolepiforms in a group including coelacanth, lungfishes, and tetrapods. On the basis of its primitive visceral arch anatomy, *Eusthenopteron* is excluded from the above group and is not even unambiguously assignable to the Sarcopterygii. *Polypterus* likewise cannot be placed within a subgroup of the Osteichthyes on the basis of its visceral arch structure. Living and fossil chondrosteans appear to have the most primitive osteichthyan gill arches in showing the greatest general similarity to chondrichthyans and *Acanthodes*.

Reorientation and reduction of dorsal elements is characteristic also of the hyoid arch of coelacanth, dipnoans, and tetrapods but not of *Eusthenopteron*, actinopterygians,

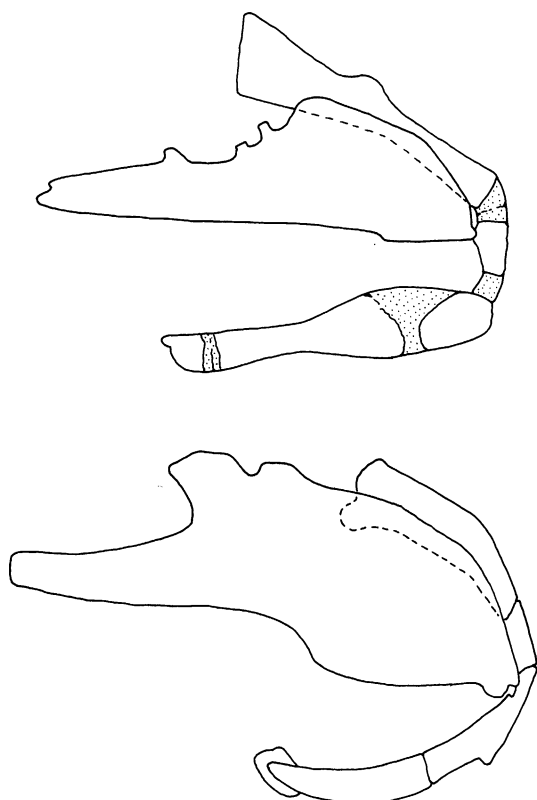


FIG. 51. Hyoid arch in relation to palatoquadrate. Above, *Pteronisculus stensioei* (Nielsen) (from Nielsen, 1942). Below, *Eusthenopteron foordi* Whiteaves (from Jarvik, 1972).

chondrichthyans, or acanthodians. In the last four groups (figs. 50, 51) the hyomandibula is long and slender, closely associated with both the ceratohyal and palatoquadrate, and conforms in orientation with the sharp forward slope of the posterodorsal margin of the latter. In coelacanth, dipnoans, and tetrapods the hyomandibula and the posterior part of the palatoquadrate have a more nearly vertical or backward orientation, and the hyomandibula shows a progressive reduction in size in the series, and evidence of increasing functional decoupling from the hyoid bar and palatoquadrate. In *Latimeria* (fig. 52) the hyomandibula is a relatively small, flat, subtriangular element that is displaced posteriorly away from the palatoquadrate. Ventrally the hyomandibula articu-

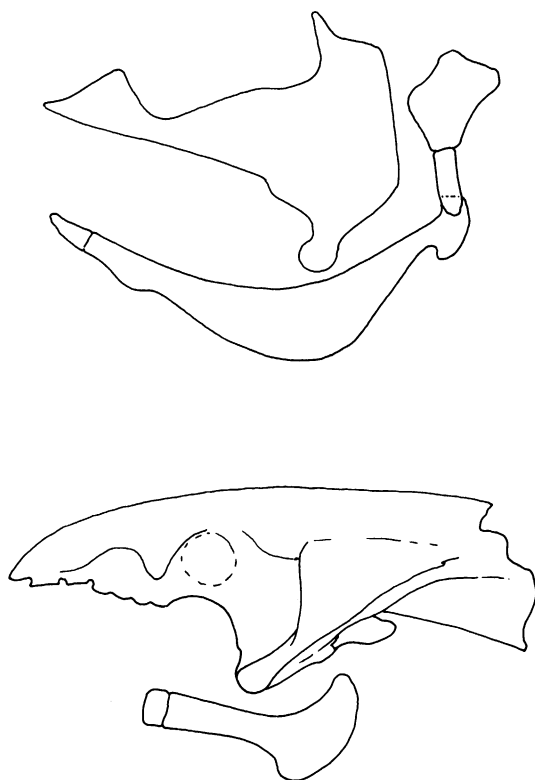


FIG. 52. Hyoid arch in relation to palatoquadrate. Above, *Latimeria chalumnae* Smith (modified from Millot and Anthony, 1958). Below, *Neoceratodus forsteri* (Krefft) (various sources; showing fusion of palatoquadrate with neurocranium).

lates with a rodlike interhyal (stylohyal of authors). The interhyal, which in *Eusthenopteron* and actinopterygians is in series with and directly articulates between the hyomandibula and hyoid bar, is in *Latimeria* laterally offset from the distal end of the hyoid bar and attached to it only by a bed of ligaments. In *Neoceratodus* (fig. 52) the hyomandibula is also a small, flat, triangular plate, but the interhyal is absent and a connection between the ventral part of the hyomandibula and the hyoid bar is made only by an oblique ligament. But in dipnoans (figs. 52, 53) the hyomandibula is completely reoriented, its ventral end directed anteriorly toward the quadrate and, at least in *Neoceratodus*, its dorsomedial process fused with the capsular wall of the otic region of the cranium (de

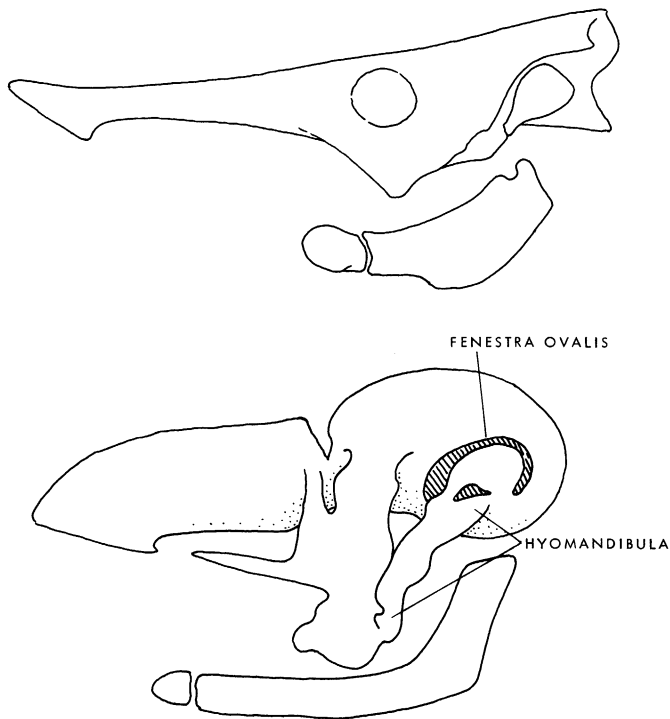


FIG. 53. Hyoid arch in relation to palatoquadrate and neurocranium. Above, *Griphognathus whitei* Miles (from Miles, 1977). Below, hynobiid urodele (modified from Schmalhausen, 1968; *Hynobius leechi* Boulenger, AMNH 58792, and *H. chinensis* Günther, AMNH 30616).

Beer, 1937, p. 412). The hyoid bar is expanded posteriorly and turned sharply upward toward the otic region, a structural modification also present to some degree in *Latimeria*. In hynobiids (fig. 53), the hyomandibula has exactly the same orientation as in dipnoans except that here the hyomandibula is fused anteroventrally with the quadrate and its dorsomedial process is greatly expanded and occludes an unossified region, the fenestra ovalis, in the capsular wall. Again, as in dipnoans, there is a hyoquadrate ligament between the sharply upturned distal end of the hyoid bar and the ventral part of the hyomandibula that fuses with the quadrate (this ligament is all that remains of the primitive osteichthyan interhyal joint).

Thus, the anatomy of both the hyoidean and branchial arches supports a sister group relationship between dipnoans and tetrapods

with coelacanth as the sister group of those two. *Eusthenopteron* appears to have a primitive hyoidean and gill arch anatomy similar to that of actinopterygians. Porolepiforms appear to have retained the primitive hyomandibular orientation, as judged by the arrangement of dermal cheek bones, and thus lack one of the two classes of visceral arch synapomorphies that unite coelacanth with dipnoans and tetrapods. *Polypterus* shows a jaw suspension of intermediate type: the hyomandibula is only slightly expanded dorsally, is strongly oblique dorsally and nearly vertical ventrally where it lies against the vertical posterior face of the palatoquadrate, but remains intimately associated with both the hyoid bar and palatoquadrate as in chondrosteans. The cladistic position of *Polypterus* is therefore problematical not only with respect to the branchial apparatus but with

the hyoid arch as well. Hence, the combined information derived from hyoid and gill arch anatomy specifies that porolepiforms are the sister group of coelacanth and dipnoans/tetrapods, that actinopterygians, cladistians and *Eusthenopteron* form an unresolved tet-

rachotomy with those four, that chondrichthyans are the sister group of bony fishes and that acanthodians, using Nelson's (1969) argument, are the sister group of other gnathostomes.

RIBS AND VERTEBRAE

(A) RIBS

One of the earliest reasons given for excluding lungfishes from close relationship with tetrapods was that lungfishes have pleural ribs, whereas tetrapods have dorsal ribs (Pollard, 1892; Goodrich, 1909). And the identification of dorsal ribs, possibly bicipital, in *Eusthenopteron* (Jarvik, 1952; Andrews and Westoll, 1970a) seemed an important confirmation of the relationship between osteolepiforms and tetrapods.

Devillers (1954) gave an excellent account of the interpretation of ribs, on which the following summary is based. The presence of two kinds of ribs on each vertebra in the middle part of the trunk of *Polypterus* was the foundation for the recognition of two distinct categories of ribs, dorsal ribs in the horizontal septum, and ventral (pleural) ribs in the wall of the coelom. Many teleosts also have these two types of ribs, and in addition, epineural ribs in the epaxial musculature. In other groups of gnathostomes, with only one series of ribs, the problem is to find decisive criteria for allocating the ribs to one series or another. Topographic criteria fail, because in actinopterygians and chondrichthyans the ribs vary in position, from species to species, and from one part of the vertebral column to another in the same fish, "wandering" within the transverse septum. In tetrapods the problem is aggravated by the fact that the horizontal septum is absent in the trunk of all except urodeles.

Seeking a more reliable criterion, Emelianov (1935, 1936) found that the ventral ribs of *Polypterus* and teleosts develop centrifugally, from cartilaginous anlagen close to the vertebra, whereas the dorsal ribs of those fishes develop centripetally, from cartilagi-

nous anlagen beneath the lateral line, at the outer junction of the horizontal and transverse septa. According to this criterion, the ribs of elasmobranchs, previously thought to be dorsal, are ventral ribs, as are those of dipnoans and non-teleostean actinopterygians; the ribs of urodeles, previously taken to be dorsal, are indeed dorsal; and those of apodans and amniotes, previously thought to be dorsal, are ventral. However, in urodeles the characteristic centripetal development of dorsal ribs is seen only in the anterior vertebrae. Passing back down the trunk, the later the ribs appear, the closer their anlagen are to the vertebral column, so that the most posterior ribs develop as ventral ribs. Because of this, Devillers doubted that Emelianov's criterion was as trenchant as its author supposed and noted that the anterior ribs of urodeles are the only exception to the universal presence of pleural ribs.

From this summary, it is clear that identification of ribs as dorsal or ventral is no simple matter. Topographic criteria (position of the articulation with the vertebra; orientation of the rib; relationship to the musculature) do not suffice. In fossils, unless more than one series of ribs is present, the ribs can therefore be identified as dorsal or ventral only by a comparative argument (showing that the fossil is a member of a group characterized by one type of rib), or by evidence of mode of growth (centripetal or centrifugal).

The original reason for recognizing two categories of ribs was the presence of both types in cladistians and teleosts. In Cladistia the dorsal ribs are peculiar, borne on hypertrophied parapophyses and firmly tied distally to the lateral line scales, an arrangement

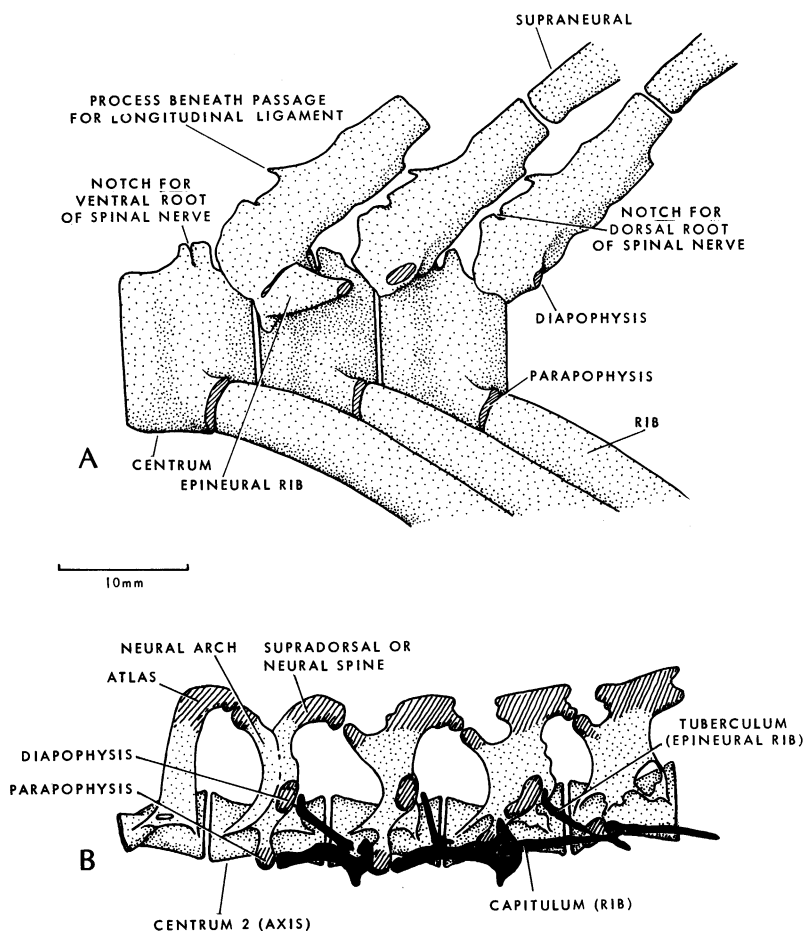


FIG. 54. A, *Griphognathus whitei* Miles. Sketch of three vertebrae (approx. nos. 9–11) in left lateral view, based on BMNH P. 60420. B, *Gyrinophilus porphyriticus* (Green), vertebrae. Ribs, black. Unsurfaced areas hatched.

interpreted by Pearson (in press) as a specialization enhancing the flexibility of the trunk. In teleosts, dorsal (epipleural) ribs are now thought to be a derived feature characterizing higher (elopocephalan) teleosts (Patterson and Rosen, 1977, p. 126) and certain osteoglossomorphs (*Heterotis* and notoptyrids; Taverne, 1979, p. 61). The alternative, to regard dorsal ribs as a primitive attribute of actinopterygians, would be unparsimonious, requiring their independent loss in many lineages. By the same argument, dorsal ribs are not a primitive attribute of osteichthyans. Instead, we should expect prim-

itive osteichthyans to have ribs of chondrichthyan type—short, oriented like dorsal ribs, but developing like ventral ribs. In our view, this is the simplest interpretation of the ribs of *Eusthenopteron* (figs. 55, 56). The thickening or anterior process on the ribs in the middle part of the trunk of *Eusthenopteron*, identified by Andrews and Westoll as a tuberculum, is matched in various elasmobranchs (e.g., *Notorynchus*, Daniel, 1928, fig. 51; *Somniosus*, *Dalatias*, Helbing, 1904, figs. 27, 28), and the absence of ribs on the first three to seven vertebrae (Andrews and Westoll, 1970a, fig. 22; Jarvik,

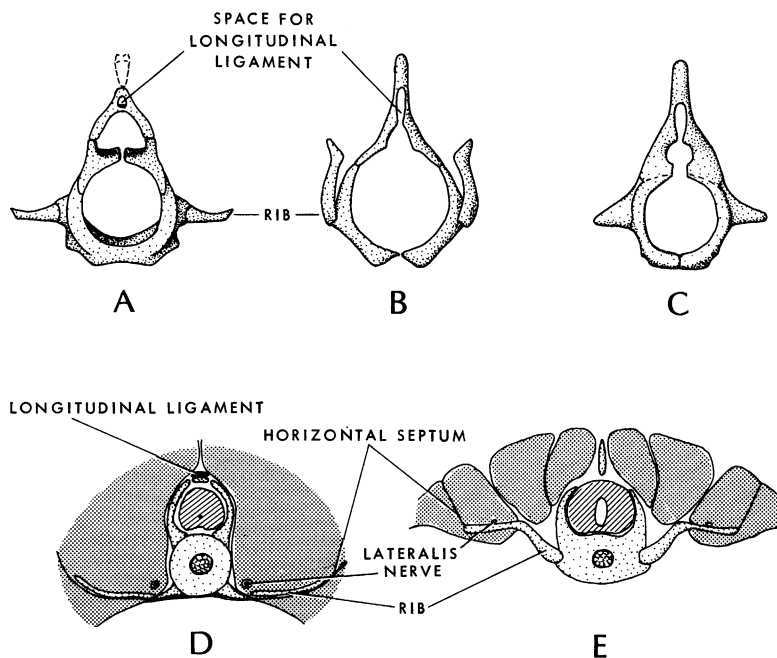


FIG. 55. Form of ribs in *Eusthenopteron* and elasmobranchs. A–C, restorations of three vertebrae of *Eusthenopteron foordi* Whiteaves. A, fifth in posterior view, after Jarvik (1975, fig. 10); B, about eighteenth in anterior view, after Andrews and Westoll (1970a, fig. 21C); C, about twenty-sixth in anterior view, after Jarvik (1952, fig. 13); D, E, reconstructed thick sections of a mid-trunk vertebra of D, *Mustelus laevis* Risso, 100 mm.; and E, *Torpedo* sp., 30 mm., after Emelianov (1935, figs. 49, 52). In D and E muscle is stippled, nerve cord hatched.

1975, fig. 10) also agrees with sharks (fig. 56A, B).

An assessment of the primitive condition of the ribs in tetrapods (dorsal ribs, pleural ribs, or both) requires a reasoned phylogeny of tetrapods, and, as Devillers (1954) suggested, investigation of a more extensive suite of urodeles than the two genera studied by Emelianov. But one synapomorphy of tetrapods is the bicipital rib, articulating with a diapophysis on the base of the neural arch, and a parapophysis on the centrum. The diapophysis of tetrapods recalls the articulation of the epineurals in teleosts. The separate epineurals of teleosts are a derived feature within actinopterygians, where the primitive condition seems to be an outgrowth or process of the neural arch in the diapophysial position (Patterson, 1973, p. 237; these outgrowths are also present on the anterior

neural arches of the Gogo paleoniscoids). Such outgrowths are also present in the dipnoan *Griphognathus* (fig. 54A), and appear to be independently ossified. They are absent in *Eusthenopteron* (figs. 55A–C, 56B), as are any identifiable diapophyses on the rib-bearing vertebrae (Andrews and Westoll, 1970a). These diapophysial outgrowths in *Griphognathus* and primitive actinopterygians are most completely developed on the foremost vertebrae; that is, they show a morphogenetic gradient which decreases with distance from the occiput. The ribs of *Eusthenopteron*, sharks and primitive actinopterygians (fig. 56C) show a different gradient, which decreases rostrally and caudally from the middle of the trunk. The ribs of primitive tetrapods (fig. 54B) and Recent lungfishes (fig. 57) show the first type of gradient, decreasing from the occiput. The expanded head of

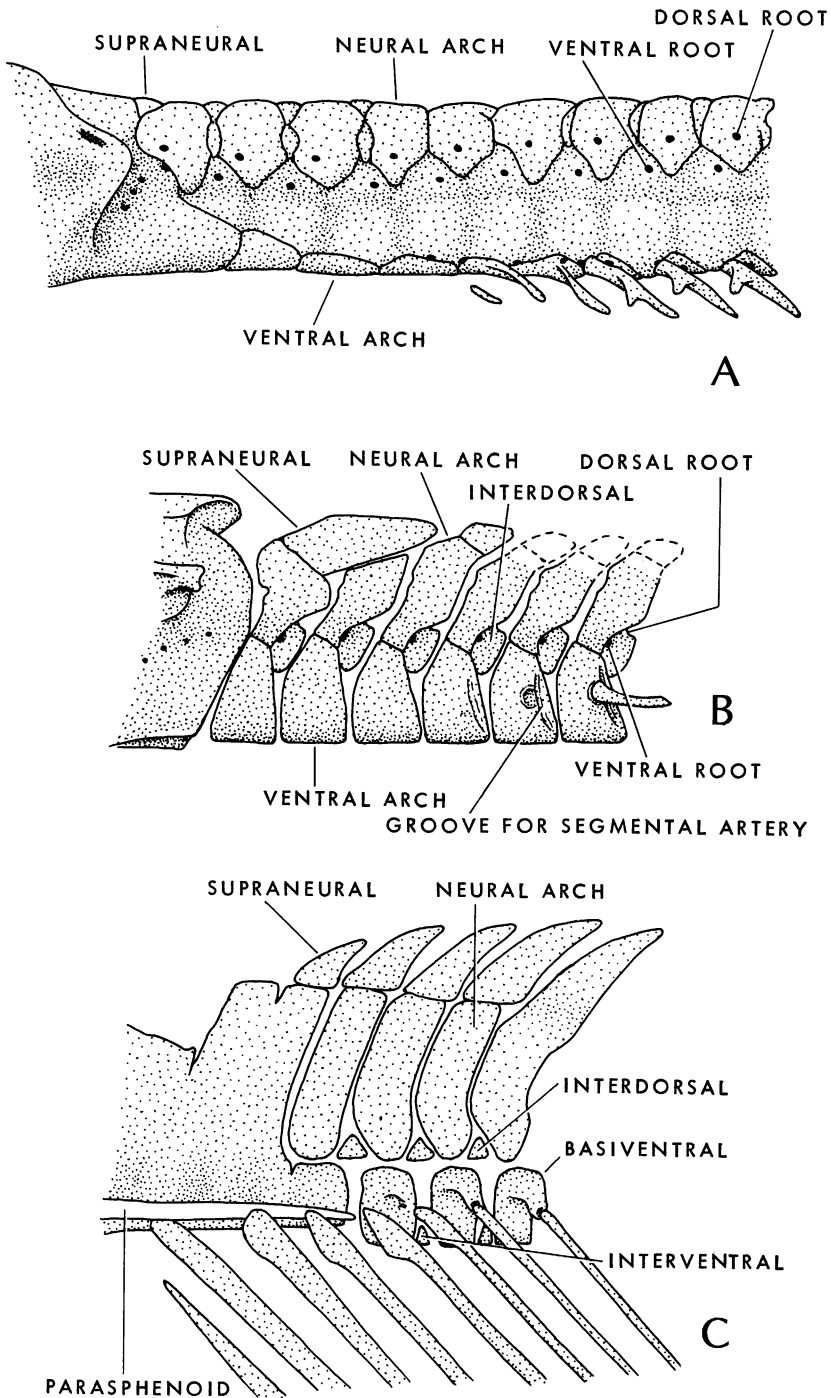


FIG. 56. Occiput and anterior vertebrae in left lateral view of A, *Notorynchus maculatus* Ayres, after Daniel (1928, figs. 47, 51); B, *Eusthenopteron foordi* Whiteaves, after Jarvik (1975, fig. 10); C, *Acipenser oxyrhynchus* Mitchill, 150 mm. total length, from AMNH 37296. Cartilage stippled in A and C, bone stippled in B.

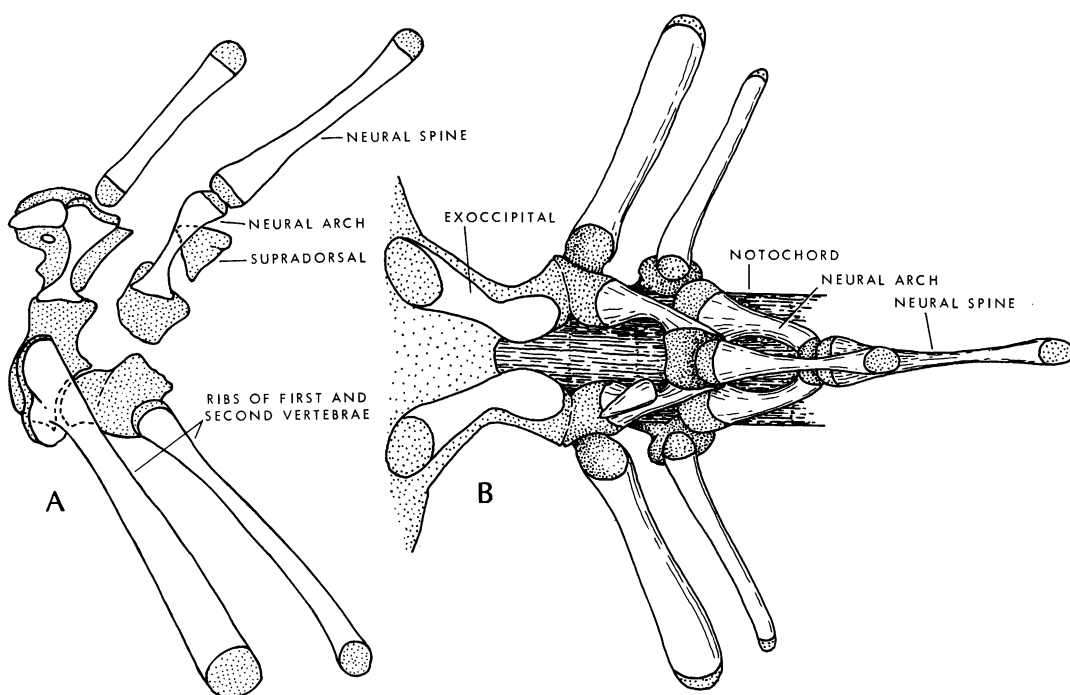


FIG. 57. *Neoceratodus forsteri* (Krefft). A, anterior vertebrae and ribs, left lateral view; B, skull-vertebral articulation, dorsal view. Small bone in front of first neural arch, in the position of the tetrapod "preatlas," is present on only left side of this specimen, AMNH 36982.

the first rib of young *Neoceratodus* (fig. 57; this rib becomes the cranial rib in full-grown animals) is evidence of this gradient in lung-fishes. In urodeles (fig. 54B) modification of the heads of the foremost ribs is more pronounced, with the dorsal struts to the diapophysis decreasing in size away from the occiput. We suggest that the anterior vertebrae and ribs of *Neoceratodus* fit the tetrapod morphocline far better than those of *Eusthenopteron*, which seem to be primitive in all respects.

(B) INTERPRETATION OF GNATHOSTOME VERTEBRAE

Four pairs of arcualia are present in the development of many elasmobranchs, holocephalans, actinopterygians, unborn juvenile *Latimeria*, and *Neoceratodus*. These arcualia are also retained in some adult elasmobranchs (*Chlamydoselachus*, fig. 58A) and

holocephalans (*Callorhynchus*), and, within the Osteichthyes, they are represented by ossified or cartilaginous elements in at least a part of the vertebral column: e.g., in actinopterygians (*Acipenser*, fig. 56C; *Polyodon*, fig. 58B; *Pteronisculus*, *Caturus*, fig. 59; *Pholidophorus*, Patterson, 1968), in actinistians (*Latimeria*, fig. 58C), in dipnoans (*Neoceratodus*, fig. 58D, E) and in tetrapods (*Archegosaurus*, *Chelydosaurus* and "*Sphenosaurus*" *sternbergii*, Fritsch, 1883-1895, pp. 25, 28). In many bony fishes and primitive tetrapods (loxommatids, temnospondyls) however, the ventral, caudal pair of arcualia (interventrals) are wanting, they have either failed to develop or have fused with the more anterior basiventrals. Thus, in the trunk and abdominal regions of *Caturus* (fig. 59A, B), *Pholidophorus*, *Latimeria*, and the temnospondyls *Archegosaurus*, *Chelydosaurus*, and "*Sphenosaurus*" there is only one pair of ventral elements, the ventral ver-

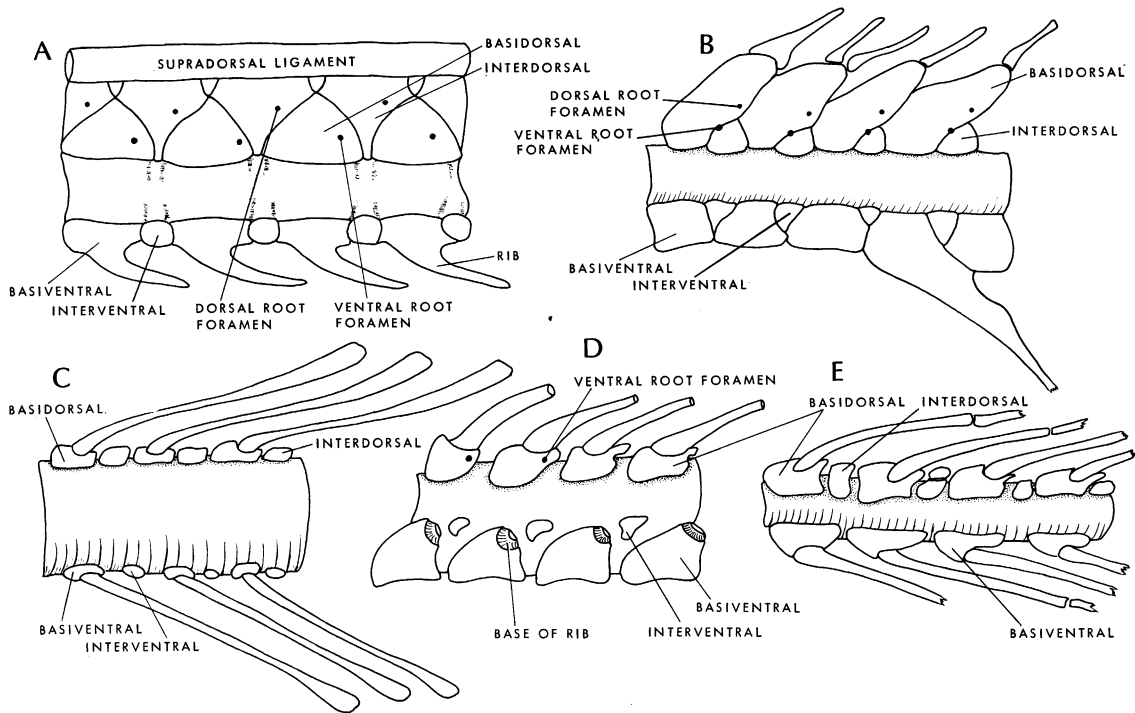


FIG. 58. Vertebrae. A, *Chlamydoselachus anguineus* Garman, trunk region (from Goodey, 1910); B, *Polyodon folium* Lacépède, region of trunk-caudal transition (from Schauinsland, 1906); C, *Latimeria chalumnae* Smith, caudal region (from Andrews, 1977); D, *Neoceratodus forsteri* (Krefft), anterior trunk region (from Fürbringer, 1904); E, *N. forsteri*, posterior trunk region (from Andrews, 1977).

tebral arch, in each segment. In *Neoceratodus* (fig. 58D), on the other hand, intervertebrals have only been described in one small portion of the thoracic region (Fürbringer, 1904), whereas in *Glyptolepis* (Andrews and Westoll, 1970b, fig. 23), *Eusthenopteron* (Andrews and Westoll, 1970a, fig. 23) and *Osteolepis* (Andrews and Westoll, 1970b, fig. 5) ossified intervertebrals are invariably absent.

Previously (Jarvik, 1952, 1975; Andrews and Westoll, 1970a), the vertebral column of *Eusthenopteron* was considered very similar to that of *Ichthyostega*. For *Eusthenopteron* there are four very different reconstructions of the vertebral column. The earliest is that of Gregory, Rockwell and Evans (1939); Jarvik (1952, fig. 13C) figured vertebrae from the anterior part of the tail and from the most anterior trunk region (Jarvik, 1975, fig. 10A); Andrews and Westoll (1970a, figs. 19, 20) fig-

ured the first 26 vertebrae. In all of these reconstructions the interdorsal is interpreted as being smaller than that of *Ichthyostega* (Jarvik, 1952, fig. 14A, B, C). In addition, the occurrence of a notch in the interdorsal for the presumed passage of the ventral nerve root in *Eusthenopteron* (figs. 56B, 60B) and *Ichthyostega* (Jarvik, 1952, fig. 14C) is matched by a similar notch for the passage of the ventral root in the interdorsal of *Neoceratodus* (fig. 58D).

The pre- and postzygapophyses of *Eusthenopteron* (Jarvik, 1952, fig. 13, pr.a, pr.p.) are here presumed to be no more than expansions of the neural spine associated with the passage of the dorsal ligament and correspond with similar projections in *Griphognathus* (fig. 54A), *Latimeria* (Andrews, 1977, fig. 1) and many actinopterygians (*Caturus*, fig. 59). Zygapophyses, in the sense of processes with articular surfaces that join

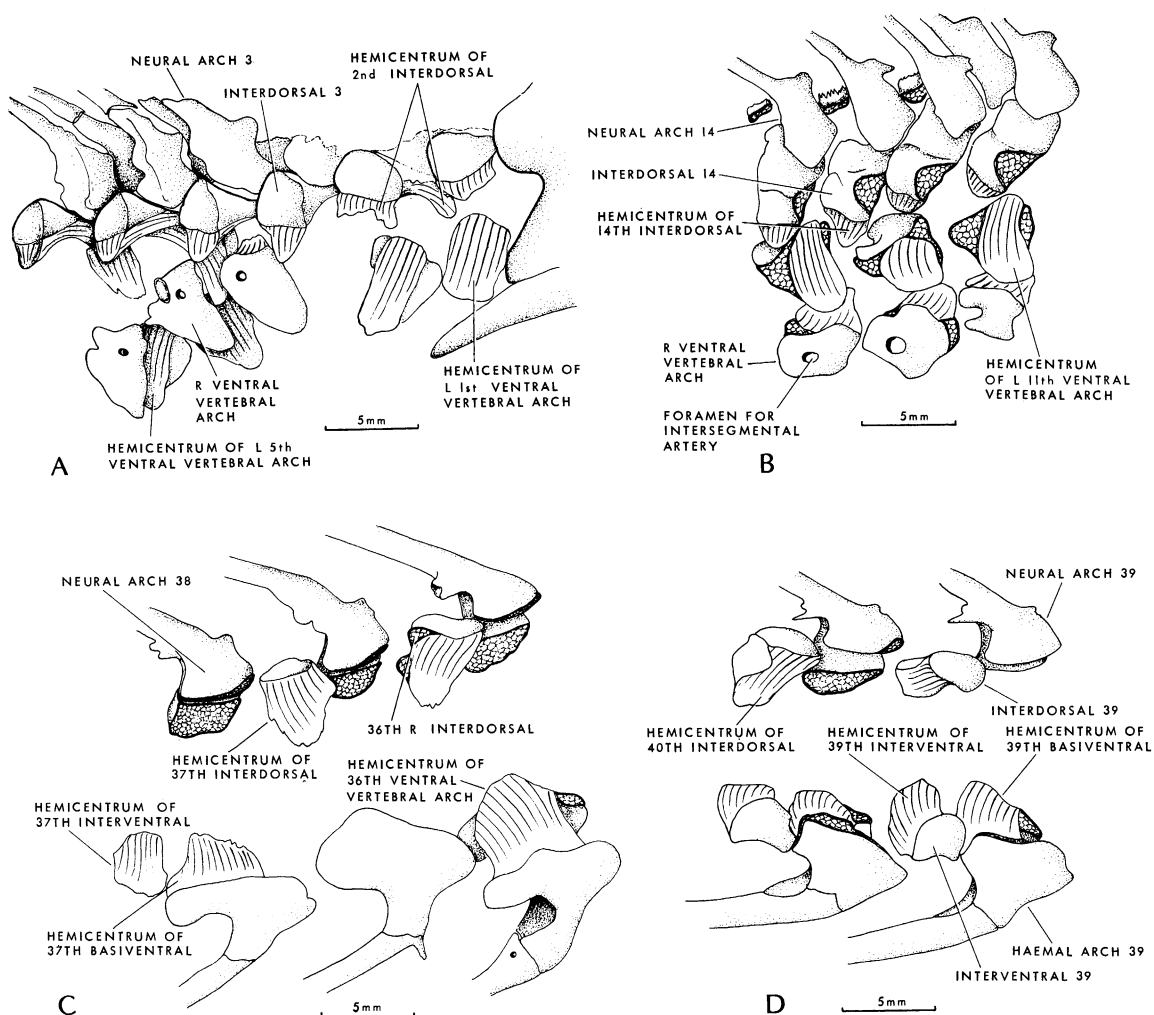


FIG. 59. Vertebrae of *Caturus furcatus* (Agassiz), as preserved in BMNH P. 20578, anterior to right. A, anterior trunk; B, trunk; C, posterior trunk; D, anterior caudal.

successive neural arches, are found only in tetrapods.

Complete centra occur within the elasmobranchs (*Chondrenchelys*, euselachians), holocephalans, actinopterygians, osteolepiforms (*Strepsodus*, *Rhizodus*, Andrews and Westoll, 1970b, fig. 7), dipnoans (*Griphognathus*, fig. 54, *Protopterus*, Mookerjee, Ganguly, and Brahma, 1954), and tetrapods. Within the actinopterygians true (complete) centra have arisen on at least four separate

occasions (*Polypterus*, *Lepisosteus*, *Amia*, and teleosts), whereas within the tetrapods we conclude that true centra have formed on at least two occasions (Recent amphibians and amniotes). This latter conclusion is based on the fact that the amniote vertebral column, unlike that of anurans, apodans, and urodeles, is often composed of more than one part per segment (viz., intercentrum and centrum) and is ossified not only perichondrally, but endochondrally as well.

(C) HETEROSPONDYLY IN *CATURUS FURCATUS*, AND VERTEBRAL HOMOLOGIES

An almost complete specimen of *Caturus furcatus* (BMNH P. 20578) was acid-prepared by one of our colleagues, Alan Bartram. This specimen has a complete and uncrushed vertebral column (fig. 59). Throughout the column individual ossification centers comprising perichondral shells surrounding endochondral bone are clearly recognizable and there are four such pairs per segment from the thirty-ninth vertebra posteriorly. Furthermore, these ossifications may be directly compared with the four pairs of cartilages known to be present in *Chlamydoselachus* and in the developing vertebral column of *Amia*. We shall therefore call these ossifications basidorsals, basiventrals, interdorsals, and interventrals in accordance with Gadow's (1933) terminology.

Throughout the column the basidorsals are continuous with the bases of the neural spines and sit between the interdorsals. The pairs of interdorsals are joined to one another by half-rings of calcification of the notochordal sheath as in the caudal region of *Pholidophorus* (Patterson, 1968, fig. 3). Similar calcifications of the notochordal sheath are seen in the development of *Clupea* (Ramanujam, 1929, p. 377) and *Salmo* (François, 1966, p. 292). Elsewhere calcifications of the notochordal sheath are seen in some holocephalans, *Chondrenchelys*, various elasmobranchs, and *Australosomus*.

In the trunk region of *Caturus* (anterior to vertebra 39) the basiventrals and interventrals of each side are presumed to have fused together, their point of junction being marked by the foramen for the intersegmental artery. A similar fusion of basiventral with interventral is deduced to have also occurred in the ventral element of *Eusthenopteron* (Jarvik, 1952, fig. 13E) where a dorsoventral groove marks the passage of the intersegmental artery.

In the caudal region of *Caturus* these two elements remain separate as in the tail of *Pholidophorus* (Patterson, 1968, fig. 1). In the anterior trunk region partial chordacen-

tra form in association with the fused basiventrals and interventrals, but the ossifications of either side remain separate as in *Glyptolepis*, *Osteolepis* (Andrews and Westoll, 1970b, figs. 4, 20), and *Eusthenopteron* (Jarvik, 1952, fig. 13D). Farther back along the trunk the fused ossifications of either side (basiventral + interventral) are joined into a hemicentrum by the addition of a median ventral crescentic calcification in the sheath of the notochord (chordacentrum). Thus, these ventral ossifications resemble the condition seen in the trunks of many holosteans and *Pholidophorus*. Fusion of the ventral elements in the midline has also occurred in the tail region of *Eusthenopteron* (Jarvik, 1952, fig. 13E) and anterior trunk (Jarvik, 1975, fig. 10) and throughout almost the entire column in temnospondylous amphibians.

More posteriorly in the tail region of *Caturus* (vertebra 39 onward) two ventral hemicentra are formed in each segment. An anterior chordacentrum links the basiventrals of either side while a posterior chordacentrum joins the two interventrals. Thus, the middle part of the caudal region of *Caturus* shows diplospondylous hemicentra as in *Pholidophorus*, *Australosomus* (Stensiö, 1932, pls. 35–37) and many holosteans and parallels the condition seen in the entire vertebral column of primitive amniotes. From this study we conclude that Schaeffer (1967) and Thomson and Vaughn (1968) were probably correct in homologizing the pleurocentra of crossopterygians with the dorsal intercalaries of *Amia* and furthermore that these dorsal intercalaries may be directly homologized with temnospondylous pleurocentra.

(D) VERTEBRAE OF RHIPIDISTIANS, LUNGFISHES, AND TETRAPODS

As was the case with the interpretation of dipnoan ribs, dipnoan vertebrae were also taken to be of an extremely primitive type that has no bearing on the question of tetrapod affinities. This was partly based on the supposition that dipnoans lack ossified centra and that their neural and hemal arch components are extremely simple and primitive

for gnathostomes generally. Schmalhausen (1968) has written, for example, that the "primitiveness of the Dipnoi is displayed in the retention of a permanent notochord even in the modern forms" and the "vertebrae consisted only of cartilaginous elements, the bases of the upper and lower arches." This widespread opinion is due, in large part, to the repetition of an old illustration in Goodrich (1909) showing several poorly differentiated vertebral segments from the posterior part of the axis in *Neoceratodus*, and, in part, from failure to realize that the vertebral centra, ossified in some Devonian forms such as *Griphognathus*, are represented in modern forms by a few barely ossified ring centra or hemicentra in the posterior part of the skeleton. Nevertheless, a study of the first few vertebrae of young *Neoceratodus* shows that the column articulates with the skull on two exoccipital processes (fig. 57B) that closely resemble the exoccipital condyles of the bicipital first vertebral articulation of modern and fossil amphibians (see Schmalhausen, 1968, figs. 136, 137). In contrast, actinistian and rhipidistian fishes, so far as known, have only the primitive, single, basioccipital contact of the first vertebra that also characterizes chondrosteian actinopterygians and chondrichthyans.

Until now, however, it has been assumed that the vertebrae of *Eusthenopteron* and tetrapods (as represented by *Ichthyostega*, fig. 60A) are significantly alike and that the similarity signifies close relationship. The assumption goes back to several statements made by Jarvik (1952) in his review of the ichthyostegids: "each vertebra, both in the trunk and in the tail, is composed of three elements, two dorsal and one ventral very suggestive of those in *Eusthenopteron*" (p. 36), and "neural spines [in the sacral region] gradually become narrower and more inclined backwards and are converted into the comparatively narrow spines, round in section, which in the tail articulate with the radials. The latter strongly resemble the neural spines in *Eusthenopteron*" (p. 38). Jarvik also compared the interdorsal vertebral segments in *Eusthenopteron* and ichthyostegids and concluded that their segments are simi-

larly notched for the dorsal and ventral roots of the spinal nerves. But Jarvik also noted (p. 36) that "The vertebral column in the ichthyostegids . . . is on the whole imperfectly preserved in the material available." When one compares the published photographs of the columns of ichthyostegids and *Eusthenopteron* there is, in our opinion, little specific resemblance between the trunk and tail vertebrae of *Eusthenopteron* (Andrews and Westoll, 1970a, pls. 4, 5) and *Ichthyostega* (Jarvik, 1952, figs. 2, 3, 14, 15) except insofar as they are all unconsolidated vertebrae with ossified neural and hemal arches, bits of hemicentra, and structures of questionable identity called interdorsals: "The interdorsal [of *Ichthyostega*] is well shown [in two specimens] whereas in other specimens showing the neural arches it generally is imperfectly preserved or missing [Jarvik, 1952, p. 36]." Only one of these structures is identified in one specimen and perhaps three or four can be made out in the second; they are of varying sizes and shapes, although somewhat hemispherical and, to us, their relationship to other structures is unclear. These features in the two specimens of *Ichthyostega* contrast with the positionally similar structures of *Eusthenopteron* which are smaller, more dorsal in position (behind the neural spine base), and round, nodular or hemispherical (but with a different orientation from those of *Ichthyostega*). Hence, both taxa seem to be similar at most in having present in the column three of the four possible arcual elements, basidorsals and basiventrals (neural and hemal arches) and interdorsals, and incomplete ring (*Ichthyostega*) or hemicentra (*Eusthenopteron*) that are primitive for chondrichthyans and osteichthyans. The only derived character they might share, therefore, is the absence of intervertebrals (see, for example, fig. 56C, of *Acipenser*).

Panchen (1977), however, rejected Jarvik's comparisons because he believed that the interdorsal of *Osteolepis* is a better match with those of ichthyostegids than that of *Eusthenopteron* in being larger. But in *Osteolepis* the interdorsals, in being large triangular bones, are not only larger and more

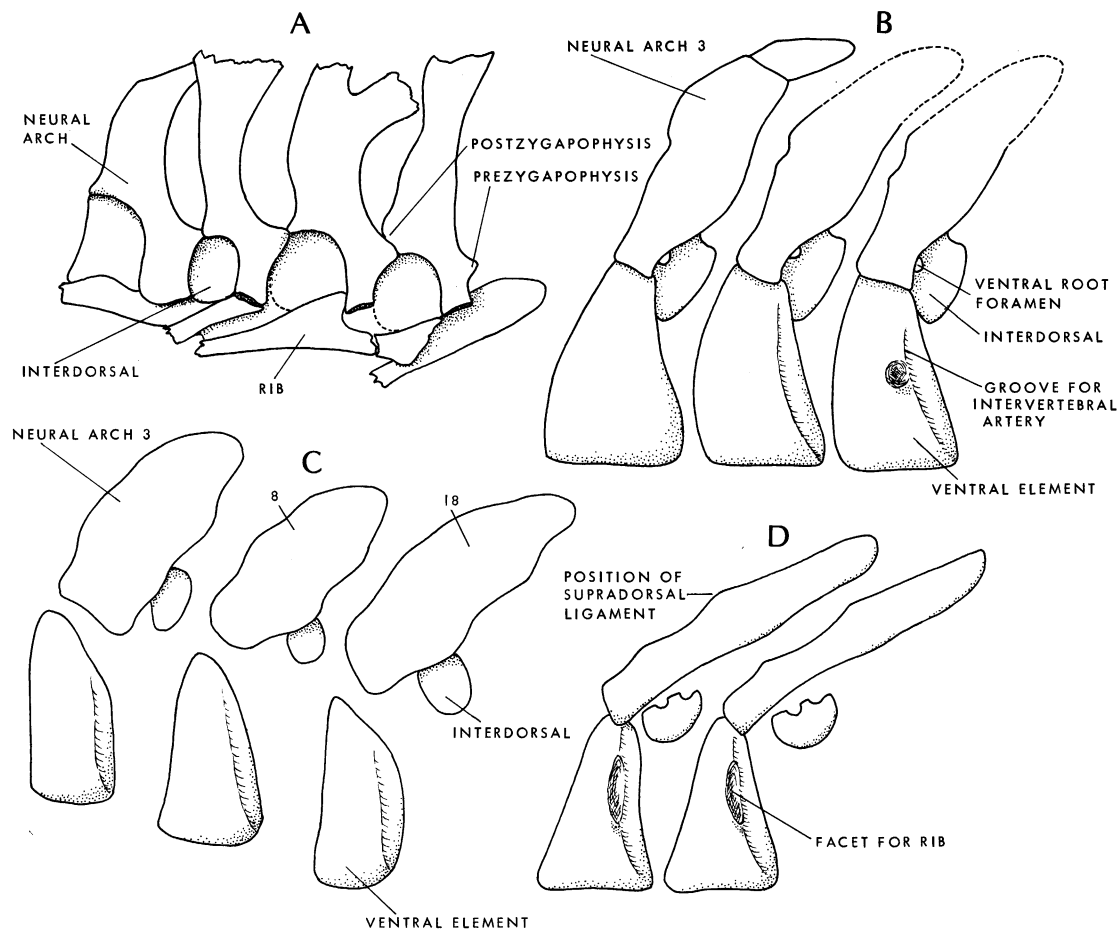


FIG. 60. Trunk vertebrae. A. *Ichthyostega* sp. (from Jarvik, 1952, fig. 14B, anterior to right); B–D, *Eusthenopteron foordi* Whiteaves, anterior to left; B, anterior trunk vertebrae, from Jarvik, 1975; C, from Andrews and Westoll, 1970a; D, from Jarvik, 1952.

heavily ossified than those of *Eusthenopteron*, they are also larger, better ossified, and better differentiated than those of *Ichthyostega*. In other words, *Osteolepis* has a condition of the interdorsals not present in either of the other taxa. Interestingly, Panchen's argument, unlike Jarvik's apparent use of symplesiomorphous features for formulating relationships, is also an appeal to stratigraphic position (*Osteolepis* is older than *Eusthenopteron* and is therefore a better ancestor) and convergence (*Osteolepis* resembles more advanced tetrapods with large, triangular interdorsals). He writes that *Osteolepis*

"is generally regarded as [a] primitive [osteolepiform], characterized by heavy ossification" and is therefore a better ancestor, and that the convergent development of ring centra in some more advanced members of the Osteolepididae and Tetrapoda indicates a relationship between them. Perhaps Panchen's line of argument might also be used to propose a relationship between those two assemblages and the halecomorph actinopterygian *Caturus furcatus* (Agassiz), since different parts of the column of *Caturus* show most of the main features of the column of osteolepids and primitive tetra-

pods and amniotes (fig. 59; Baur, 1896; Andrews, 1977; and p. 249 above). Baur (p. 663) wrote: "In the Crossopterygii we find unossified and well ossified vertebrae . . . it is very probable that some of the crossopterygians showed a condition like *Archegosaurus* and *Caturus*." And Andrews (p. 284) observed: "Fossil chondrosteans and especially holosteans show very diverse conditions of the vertebrae, but in some forms at least (*Caturus*, *Eurycormus*) the centra appear to be composed, in a similar manner to *Osteolepis*, from 'alternating dorsal and ventral crescentic hemicentra' " (Schaeffer, 1967, p. 192).

Each of the proposals, by Jarvik and Panchen, reminds us of our methodological goal in undertaking this study: to avoid the loose style of argument that has often characterized investigations of gnathostome relationships (Nelson's 1969 work is one exception), and to approach the problem in an explicitly cladistic fashion. To accomplish this in dealing with the vertebrae we must first specify the condition of the vertebrae primitive for each group. In attempting this, we observe that all but one of the recognizable groups, chondrichthyans, actinopteryg-

ians, actinistians, dipnoans, and tetrapods (as represented by *Ichthyostega*) are primitively with unconsolidated cartilaginous or ossified arcualia and unossified or poorly ossified centra. We note that the same is true of *Acanthodes*, *Osteolepis*, and *Eusthenopteron*. The Cladistia are the single exception. Features that have been used in the past to unite groups representing patterns of fusion of arcual elements and their co-ossification with centra are therefore secondarily derived for each group (i.e., convergent). We are left in doubt about the structure of the vertebrae in *Ichthyostega*, and we reject Panchen's reasoning which uses every undesirable feature of past phylogenetic argumentation in paleontology and neontology—symplesiomorphy, stratigraphic position, and convergence—as evidence of relationship. We do not rule out the possibility that some unique derived characters will be discovered in better material to unite *Ichthyostega* with one or another "rhpidistian," but our own study has revealed only a single derived vertebral character, a bicipital type of exoccipital joint with the first vertebra (fig. 57B), that unites only dipnoans and tetrapods.

DERMAL SKELETON

(A) COSMINE

Cosmine is a superficial hard tissue containing a pore-canal system. It is found on the dermal bones of some cephalaspidomorphs, rhipidistians and Paleozoic dipnoans. No living fish has cosmine or a pore-canal system, and the function is unknown (Thomson, 1977). The cosmine of cephalaspids differs from that of osteichthyans in so many ways (Ørvig, 1969a; Schultze, 1969a, p. 56) that we agree with Ørvig (1969a) that cosmine is not a primitive feature of a group containing cephalaspids and osteichthyans; in other words, we do not regard cephalaspid and osteichthyan cosmine as homologous. Schultze (1969a) and Thomson (1975, 1977) accept that the pore-canal system (not necessarily enclosed in cosmine) is a primitive feature of vertebrates. It is true that a pore-canal system also occurs in some acantho-

dians (*Poracanthodes*), but the architecture of the system is so different in cephalaspids, acanthodians, and osteichthyans (Gross, 1956) that it is difficult to recognize any homologies. We therefore regard the cosmine and pore-canal system of dipnoans and rhipidistians as a synapomorphy (Schultze, 1977b, fig. 1, seems now to agree, indicating the pore-canal system as a synapomorphy in his cladogram). The problem is to decide what group is characterized by this synapomorphy.

In rhipidistians, cosmine occurs in porolepiforms (Porolepididae—*Porolepis*, *Heimania*—and *Powichthys*, if *Powichthys* is a porolepiform) and in osteolepiforms (Osteolepididae *sensu* Vorobyeva, 1977a; *Rhizodopsis*, Andrews and Westoll, 1970b, p. 403). In dipnoans cosmine occurs in *Uranolophus*, *Dipnorhynchus* and dipterids (*sen-*

su lato). In onychodonts the only report of cosmine is a small patch on the premaxilla (Jessen, 1966, pl. 16, fig. 4) and parietal (Jessen, 1967, pl. 2B) of *Strunius*. This tissue has not been studied histologically, and might be only superficially cosmine-like, as are patches of porous enameloid on the head of the dipnoan *Holodipterus* (Smith, 1977, p. 48, fig. 66). Cosmine has not been reported in coelacanth, though Westoll (e.g., 1979, p. 346) has referred to "modified cosmine" in undescribed Devonian specimens from Scaumenac Bay. We have examined those specimens, and did not see anything recognizable as cosmine.

The pore-canal system of cosmine-bearing dipnoans, osteolepiforms, and porolepiforms has the same layout (Schultze, 1969a, fig. 42). In some osteolepiforms the mesh canals linking the flask-shaped pore-canals are divided by a horizontal partition into upper and lower divisions (Gross, 1956). Schultze (1969a) and Thomson (1975, 1977) have taken that condition to be primitive, since it recalls the perforated "sieve-plate" dividing the mesh-canal in cephalaspids. We regard this as a far-fetched homology, since it depends on the assumption that the pore-canal system is primitive for vertebrates. Horizontal division of the mesh-canals, which has not been found in any dipnoan or porolepiform, might be a synapomorphy of osteolepiforms, or its absence might be a synapomorphy of dipnoans and porolepiforms. In some porolepids the enamel extends inward to line the pore-canal (Ørvig, 1969b, p. 294). This condition is also found in some dipnoans (Gross, 1956, fig. 69) but not in others (Smith, 1977, fig. 18).

"Westoll-lines" are a prominent feature of the cosmine of dipnoans (Gross, 1956; Ørvig, 1969a). Such naked strips are not recorded in porolepiform cosmine, or, according to Gross (1956) and Jarvik (1968a) in any osteolepiform. However, Thomson (1975) believes that Westoll-lines occur in some osteolepiforms, and illustrates skull bones of *Megalichthys laticeps*. Jarvik (1966, pl. 4, fig. 3) has also illustrated these lines on a maxilla of *Megalichthys*, and said (1968a, p. 227) that their "nature . . . is uncertain." Thomson suggests that the difference be-

tween his interpretation and Jarvik's is a matter of how Westoll-lines are defined, and depends on some theory of the ontogeny of cosmine. In any case, such lines have been reported, and observed by us, only on skull bones of *Megalichthys*. They are unknown on osteolepiform scales. Evidence of resorption of cosmine (as distinct from Westoll-lines) is found in dipnoans and osteolepiforms, but not in cosmine-bearing porolepiforms (Ørvig, 1969b).

According to Miles's (1977) phylogeny of dipnoans, cosmine is a primitive feature of the group, independently lost at least three times. In any alternative dipnoan phylogeny, it seems that cosmine must either be lost or developed more than once, or dipnoans cannot be treated as monophyletic. In osteolepiforms, Vorobyeva's recent phylogenies (1977a, 1977b) require that cosmine be independently lost five or six times, or that it develop more than once within the group. In porolepiforms, it is generally assumed (largely on stratigraphic grounds) that cosmine is primitive, and is lost in holoptychiids.

In dipnoans, Smith (1977) has made thorough comparisons of the histology of cosmine-bearing (*Chirodipterus*) and cosmine-free (*Griphognathus*, *Holodipterus*) dermal bones. Of particular interest is her report on superposed generations of tubercles in *Griphognathus* and *Holodipterus*. Unless cosmine developed independently on several occasions, these genera have to be regarded as having secondarily lost cosmine. Yet they show a pattern of superposed tubercles (generations of odontodes; Ørvig, 1969a) resembling the tubercles of *Latimeria* (Smith, 1977, p. 41) and like that in other primitive fishes (Schultze, 1977b). We therefore lack any anatomical criterion which will distinguish "pre-cosmoid" (cosmine assumed never to have been present) and "post-cosmoid" (cosmine lost) dermal bones. Discrimination between those two conditions depends on the position of the animal in question in a phylogeny, and that phylogeny must be established on grounds other than cosmine. We also therefore reject arguments that *Latimeria* is the primitive sister group of other osteichthyans because it possesses scale odontodes.

To sum up, we believe that cosmine is a synapomorphy of some taxon, but cosmine alone cannot tell us whether animals that lack it (such as coelacanth and tetrapods) belong in that taxon or not, because we cannot distinguish pre-cosmoid and post-cosmoid dermal bones. Cosmine is therefore irrelevant to the monophyly of Sarcopterygii, or any other taxon. Resorption of cosmine, found only in cosmine-bearing dipnoans and osteolepiforms, could be a synapomorphy relating those taxa. But if the primitive dipnoan pattern is shown by *Uranolophus* (scales and skull bones with Westoll-lines, superposed generations of tubercles in the scales, mesh-canals without a horizontal partition, Denison, 1968a, 1968b), it does not match the pattern generally assumed to be primitive for cosmine-bearing osteolepiforms (no Westoll-lines, no buried tubercles, mesh-canals with horizontal partition). We have to conclude that, as yet, cosmine provides no phylogenetically useful information.

(B) FOLDED TEETH

Schultze (1969b, 1970a) made a very thorough survey of the histology of folded teeth in fishes and tetrapods. He found that true plicidentine occurs only in porolepiforms, osteolepiforms, labyrinthodont amphibians, a few reptiles, and in lepisosteids. He showed that these teeth could be separated into several categories according to the mode and complexity of folding. All porolepiforms (except *Powichthys*, Vorobyeva, 1977c) have dendrodont teeth, with very complex folding and the pulp cavity filled with osteodentine. The most primitive amphibians (ichthyostegids, loxommatids) have polyplocodont teeth, with simple branching of the folds in the dentine. Among fishes, polyplocodont teeth are found only in osteolepiforms, *Powichthys* and lepisosteids. Within osteolepiforms, there are genera with simple, unfolded teeth (*Osteolepis*, *Thursius*, *Latvius*), with polyplocodont teeth (*Gyroptychius*, *Megalichthys*, *Tristichopterus*, *Eusthenopteron*, *Panderichthys*, *Rhizodopsis*, *Rhizodus*, *Strepsodus*), and with the more complicated, eusthenodont teeth (*Eusthenodon*, *Platycephalichthys*, *Litoptychus*, *Sauripte-*

rus). Among osteolepiforms with polyplocodont teeth, only *Panderichthys* has the same type as primitive tetrapods (Vorobyeva, 1977c, table 1).

Schultze (1969b, p. 128) summarized the significance of these facts neatly: either one must accept the detailed correspondence in tooth structure between *Panderichthys* and *Ichthyostega* as evidence of close relationship (or direct ancestry), or one must push tetrapod ancestry back to animals with simple, unfolded teeth, and interpret the folded teeth of tetrapods and osteolepiforms as convergent. Schultze preferred the first of these alternatives, as does Westoll (1979), who envisaged a direct stratigraphic lineage from *Panderichthys*, through *Elpistostegia*, to *Ichthyostega*, and writes (p. 347) "Late Devonian intermediates are confidently awaited."

When Schultze discussed the teeth of *Panderichthys*, the animal was known only by isolated fragments—lower jaws, scales and bones of the skull roof and pectoral girdle. Since then, more or less intact individuals have been found (Vorobyeva, 1973, 1975, 1980). These serve as a test of Schultze's and Westoll's hypothesis, which predicts that *Panderichthys* will be more tetrapod-like than other osteolepiforms. In some respects, this is true: the head is ichthyostegid-like in dorsal view (Vorobyeva, 1980, fig. 1), with "brow-ridges" and a long snout, and the skull roof pattern is somewhat ichthyostegid-like (Vorobyeva, 1973, fig. 1). But in other characters *Panderichthys* does not fit. It has two external nostrils (Vorobyeva, 1973), a very short pectoral fin skeleton, of only three segments (Vorobyeva, 1975, fig. 3), pelvic fins which are "very small, and set far back close to the caudal fin" (Vorobyeva, 1980, p. 194), and ring-vertebrae in the thoracic and caudal regions. Vorobyeva's conclusions from her work on *Panderichthys*, and on folded teeth (1977c), are that "at present *Panderichthys* and *Ichthyostega* are practically proved to belong to divergent evolutionary lines" (1977c, p. 17), and that the resemblances between the two are convergent (1974).

Thus, after studying more complete spec-

imens of *Panderichthys*, Vorobyeva has discarded her earlier opinion (1962, fig. 34) that *Panderichthys* is the closest relative of tetrapods among fishes, and now concludes that tetrapods are the sister group of Osteolepididae (1977a, fig. 22). The same conclusion, that tetrapods are best compared with osteolepidids rather than more specialized osteolepiforms, has been reached by Panchen (1977) on vertebral structure, Rackoff (1980) on fin structure, and by Andrews and Thomson (personal commun.).

The polyplocodont teeth of *Panderichthys*

and tetrapods do not, therefore, appear to be synapomorphous. Nor are polyplocodont teeth synapomorphous within osteolepiforms, since their distribution (Vorobyeva, 1977c, table 1: Gyroptychiinae, Megistolepididae, Eusthenopteridae, Rhizodopsidae, Rhizodontidae) cuts across every classification (e.g., Andrews, 1973; Vorobyeva, 1977a). Occurrence of such teeth in lepisosteids and other actinopterygians such as *Anarhichas* (personal observ.) only emphasizes this.

SYNAPOMORPHY SCHEME

Comparisons are among cladistically pleisiomorphic or the only well-known members of each group: *Acanthodes bronni* (for acanthodians), *Eusthenopteron foordi* (for osteolepiforms), *Latimeria chalumnae* (for actinistians), *Polypterus* (for cladistians), chondrosteans (for actinopterygians), Hynobiidae and Ichthyostegidae (for tetrapods), *Neoceratodus forsteri* (for living lungfishes) and *Griphognathus whitei* (for fossil lungfishes). Chondrichthyan characters are selected from both sharks and chimaeras, excluding from the comparisons apparently derived characters of each (pelvic bridge and posteriorly directed hypobranchials in sharks; fin endoskeleton in chimaeras; etc.). Placoderms are not included; at least one, *Pholidosteus*, has a complex pectoral fin endoskeleton without a definite metapterygial axis (part of character B.7.), and another, *Coccosteus*, has a sclerotic ring of four plates (character C-I.13.) (Moy-Thomas and Miles, 1971).

A. *Acanthodes* shares with other gnathostomes:

1. The presence of a lower jaw supported by a palatoquadrate and hyomandibula.
2. A hyoid bar connecting the branchial apparatus with the hyomandibula.
3. Anterior branchial arches consisting of basibranchial, hypobranchi-

al, ceratobranchial, epibranchial and pharyngobranchial elements.

4. A cephalic lateral-line system that includes the following canal sections: a supraorbital, infraorbital, supratemporal, mandibular, supramaxillary (jugal) that joins the infraorbital (absent in cladistians and actinopterygians), and preopercular that rises toward the supratemporal canal (connection absent in sarcopterygians).

5. Paired pectoral and pelvic appendages with internal supporting girdles.

6. Three semicircular canals in the otic capsule.

B. Chondrichthyans also have the following derived feature which they share with osteichthyans:

7. Complex endoskeletal support of the paired appendages consisting of a metapterygial axis and radials articulating with the metapterygium and girdle.

C-I. Actinopterygians have the foregoing characters and share with other osteichthyans:

8. Dermal skull bones with internal processes (descending laminae) attaching to endocranium, and various toothed dermal bones on the palate (see pp. 222, 227ff).
9. Endochondral bone.

10. The presence of lepidotrichia in addition to ceratotrichia in the fins.
 11. Radials of the fins never extending to the fin margin.
 12. With two or fewer preaxial radials associated with the first two metapterygial segments of the pectoral fin endoskeleton.
 13. Dermal sclerotic ring (primitively of four plates (see below, section D).
 14. The presence of marginal upper and lower jaw teeth (dental arcades) on dermal bones lateral to palatoquadrate (as contrasted with teeth fused with, or attached to, the palatoquadrate and Meckel's cartilage in A and B).
 15. Interhyal (=stylohyal) present.
 16. A forward, rather than backward, orientation of the infrapharyngo-branchials.
 17. Suprapharyngobranchials present on first two gill arches.
 18. Gill arches 1 and 2 articulating on the same basibranchial.
 19. A pneumatic or buoyancy organ as an outpocketing of the anterior gut (swimbladder, lung).
- C-II. Cladistians (=Brachiopterygii) also uniquely share with primitive actinopterygians:
20. The absence of the supramaxillary (jugal) canal joining the infraorbital canal.
 21. A differentiated propterygium in the pectoral fin.
 22. Modification of the pelvic fin metapterygium to form part or all of the pelvic girdle, and the endoskeletal support of the pelvic fin exclusively by preaxial pelvic radials.
 23. Acrodin caps on all teeth (Ørvig, 1976).
- D. *Eusthenopteron* has the characters of A, B and C-I (but character 19 not known) and shares the following derived features with actinistians, porolepiforms, dipnoans and tetrapods:
24. An exclusively metapterygial pectoral and pelvic fin (loss of all radials anterior to base of metapterygium) supported by a single basal element, and an anocleithrum in the shoulder girdle suspension (see pp. 206, 207).
 25. Absence of the connection between the preopercular and supratemporal lateral-line canal.
 26. Enamel on teeth (Smith, 1979).
 27. Sclerotic ring composed of more than four plates (see Miles, 1977, pp. 249–250).
- E. Actinistians have the characters of A, B, C-I, and D and share with dipnoans and tetrapods:
28. Anocleithrum of dermal shoulder girdle sunken beneath dermis and with no trace of surface ornamentation.
 29. Clavicle large relative to cleithrum, and pectoral appendage insertion high as compared with these conditions in C-I, C-II, and D.
 30. Pectoral and pelvic appendages each with long, muscular lobes that extend well below ventral body wall and with structurally similar endoskeletal supports.
 31. Preaxial side of pectoral fin endoskeleton rotated to postaxial position (Braus, 1901; Romer and Byrne, 1931).
 32. A series of canal-bearing bones (for the supraorbital canal) lateral to large, paired, roofing bones between orbits.
 33. Absence of hyostyly in the jaw suspension (the reduced, subtriangular hyomandibula and interhyal decoupled from, and not in direct sequence with, the hyoid bar, and only loosely connected to the symplectic).
 34. Posterior margin of palatoquadrate erect or sloping backward rather than sharply forward from the jaw articulation.
 35. Presence of a rostral organ (a possible synapomorphy with the la-

bial cavity of dipnoans and nasolacrimal duct of tetrapods, as discussed above, but recognized here as an ambiguous character).

36. With only a single, broad, triangular basibranchial (cladistians have a similar basibranchial, perhaps associated with the loss of one gill arch; a single elongate basibranchial is present also in primitive paleoniscids; Gardiner, 1973).
37. Last gill arch articulates with base of preceding arch rather than with basibranchial.
38. Reduction or loss of hypobranchials.
39. Reduction or loss of pharyngobranchials.
40. An inferior vena cava (Lauder, 1979).
41. A pulmonary vein.

Porolepiforms (*Porolepis*, *Glyptolepis*, *Laccognathus*, and *Holoptychius* are the best known of these fishes) are very incompletely known but have characters reported in the literature some of which would place these fishes in a position plesiomorphous, and others, apomorphous, to actinistians. Nothing is known of their dorsal gill arches and almost nothing is known of their endoskeletal fin supports. They might be regarded as plesiomorphous to actinistians because of eye position in relation to paired dermal roofing bones and because the pelvic appendage is very much shorter than the pectoral, although the scale-covered (and presumably fleshy) fin bases are longer than those of ostelepiforms and extend well below the ventral body wall. They agree with actinistians, dipnoans and primitive tetrapods (e.g., ichthyostegids) in having a relatively large clavicle and an embedded unornamented anocleithrum, a high pectoral appendage insertion, an expanded parasphenoid, only a single, compact basibranchial, and the last gill arch (or the last two in *Laccognathus*; Vorobyeva, 1980) articulating with the base of the preceding arch, not with the basibranchial where these structures are known.

They agree only with dipnoans in having a long, leaf-shaped pectoral, and in details of the cosmine pore-canal system (in a comparison of *Porolepis* and *Dipterus*; Schultze, 1969a, fig. 42). At most, one can say that they form an unresolved trichotomy with actinistians and dipnoans + tetrapods.

- F. Dipnoans have all the foregoing characters excluding those of C-II, and uniquely share with primitive tetrapods:
 42. A choana.
 43. A labial cavity (a possible synapomorphy of the nasolacrimal duct, as discussed above, but regarded here as an ambiguous character).
 44. Second metapterygial segment of paired appendages composed of paired, subequal elements that are functionally joined distally.
 45. Two primary joints in each paired appendage, between endoskeletal girdle and unpaired basal element and between basal element and paired elements of second segment. In pectoral appendage, preaxial member of paired elements with a ball and socket joint with basal element and postaxial member articulating on dorsal (postaxial) margin of basal element.
 46. Reduction in ratio of dermal fin rays to endoskeletal supports in paired appendages.
 47. Tetrapodous locomotion in living representatives (Dean, 1903; Lindsey, 1978; personal observ.).
 48. Muscles in paired fins segmented (Braus, 1901, pl. 21; in contrast to the non-segmented muscles in actinistians, actinopterygians, cladistians and chondrichthyans).
 49. Fusion of right and left pelvic girdles to form pubic and ischial processes (fig. 61).
 50. Hyomandibula plays no part in jaw suspension. De Beer (1937) described the condition of *Neoceratodus*, as follows: "The orbi-

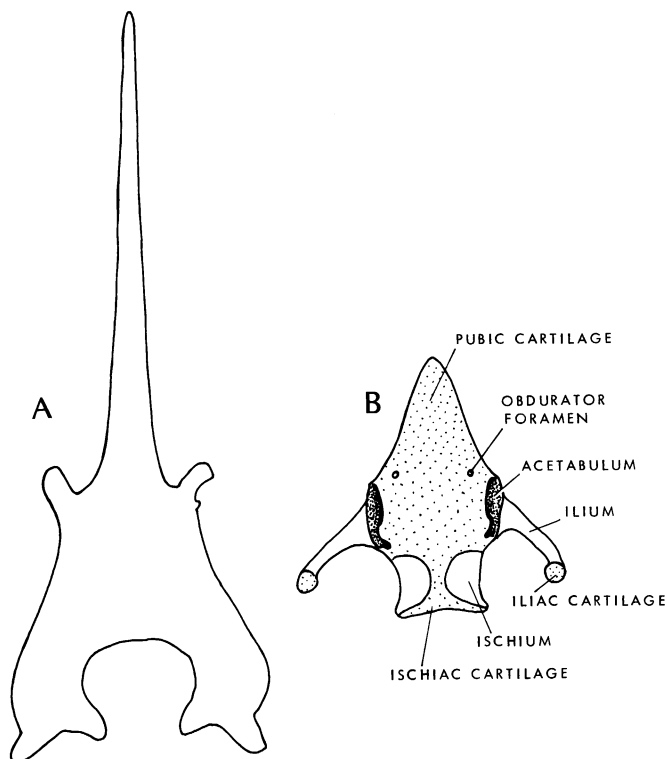


FIG. 61. Pelvic girdle of A, *Neoceratodus forsteri* (Krefft), 18 cm. total length (AMNH 36982); and B, *Necturus maculosus* (Rafinesque), (from Gilbert, 1973). A is entirely cartilaginous.

totemporal region is different from that of any other (non-Dipnoan) fish owing to the autostylic attachment of the quadrate by means of basal, otic, and ascending processes. The basal connexion is ventral to the head vein and dorsal and anterior to the palatine branch of the facial nerve. The otic connexion is lateral to the head vein and orbital artery, posterior to the trigeminal nerve (and ophthalmic and buccal branches of the facial nerves), and anterior to the hyomandibular branch of the facial nerve. The ascending connexion is lateral to a branch of the head vein, postero-lateral to the abducens nerve and the ophthalmic profundus nerve (V_1), but antero-medial to the maxillary and mandibular branches of the tri-

geminal nerve (V_2 and V_3), and to the orbital artery. All these relations are typical and practically constant throughout Tetrapods."

51. Loss of interhyal (=stylohyal).
52. Hyomandibula reduced and, at least in extant forms, joined dorsally by ligament and closely associated with an otic recess in the braincase, and ventrally with quadrate.
53. Loss of dorsal gill arch elements (pharyngobranchials).
54. Opercular bone, in extant forms, reduced and joined posteriorly by a division of the epaxial musculature to the upper half of the primary shoulder girdle.
55. Right and left pterygoids joined in midline, excluding the parasphenoid anteriorly from the roof of the mouth.

56. Loss of autopalatine.
57. Elongation of the snout region.
58. Eye somewhat posterior in skull, at level of junction between two principal bones in skull roof.
59. Pattern of five dermal bones covering otic and occipital regions of braincase.
60. Resorption of calcified cartilage and subsequent deposition of bony tissue in the vertebrae of the Devonian *Griphognathus* is identical with the formation of bony tissue in uncalcified cartilage in Tetrapoda, according to Schultze (1970b, p. 329).
61. There are, of course, numerous features of soft anatomy, development, and physiology in which dipnoans uniquely resemble urodeles and other tetrapods. Some of the more striking of these features are the internal structure of the lung (Johansen, 1970), the presence of a pulmonary circulation, the development of a two-chambered auricle and the ventral aorta as a truncus, the telolecithal development of the jelly-coated bipolar egg, ciliation of the larva (Whiting and Bone, 1980), presence of a glottis and epiglottis, flask glands, pituitary structure and a tetrapod neurohypophysial hormone (Perks, 1969; Archer, Chauvet, and Chauvet 1970), lens proteins and bile salts (Løvtrup, 1977), and gill arch muscles (Wiley, 1979).

Within the framework of this theory of relationships (fig. 62), three features of sarcopterygians deserve some comment: the intracranial joint, ventral gill arch muscles, and the rhipidistian "choana."

When present, the intracranial joint separates the anterior part of the neurocranium, including the orbit, from the posterior part, including the brain minus the olfactory lobes, and it corresponds, at least ventrally, to an embryonic division of the neurocranium into

trabecular (anterior) and parachordal (posterior) cartilaginous primordia. In "rhipidistian" crossopterygians, the joint may be kinetic (as in *Ectosteorhachis*, where a peg-and-socket are present in the skull roof), akinetic (as in *Eusthenopteron*, where no hinge mechanism has been found), or perhaps even absent (as in *Panderichthys*, *Elpistostege* and *Powichthys*, where there is no external indication that a joint exists; Jessen, 1975). In actinistians there is a well-developed kinetic joint that moves on a ventrally situated groove and track, but dorsally the joint separates the cranium more posteriorly than it does in rhipidistians (Bjerring, 1973), and the claim has been made that the actinistian joint arose independently of that in "rhipidistians." Gardiner and Bartram (1977; also Gardiner 1973), on the other hand, in a discussion of the primitive subdivision of the actinopterygian cranium along a cartilage-filled, staggered groove, claimed that the ventral part of this groove (the ventral otic fissure) is homologous with the ventral part of the intracranial joint. Both a ventral otic fissure and a lateral occipital fissure are also present in *Acanthodes* so that the actinopterygian condition might be primitive for gnathostomes. Bjerring's claim that the joints are fundamentally different in actinistians and rhipidistians is unconvincing because in both groups the dorsal part of the joint is just anterior to the emergence of the fifth and seventh nerves from the endocranium and because, ventrally, the joint is either at or slightly in front of the end of the notochord. Differences between the two are perhaps most easily related to the probably different degrees of, and certainly radically different mechanisms for, kineticism. The two kinds of joints are either synapomorphic, thus specifying a sister-group relationship between "rhipidistians" and actinistians, or some form of a joint is primitive for sarcopterygians and has been lost in dipnoans and tetrapods (the claim that a remnant of the joint is present in *Ichthyostega* is not yet supported by published evidence). We cannot ourselves resolve these questions on the basis of a study of the anatomical features of the joint in different animals, but we observe that if there are different degrees of

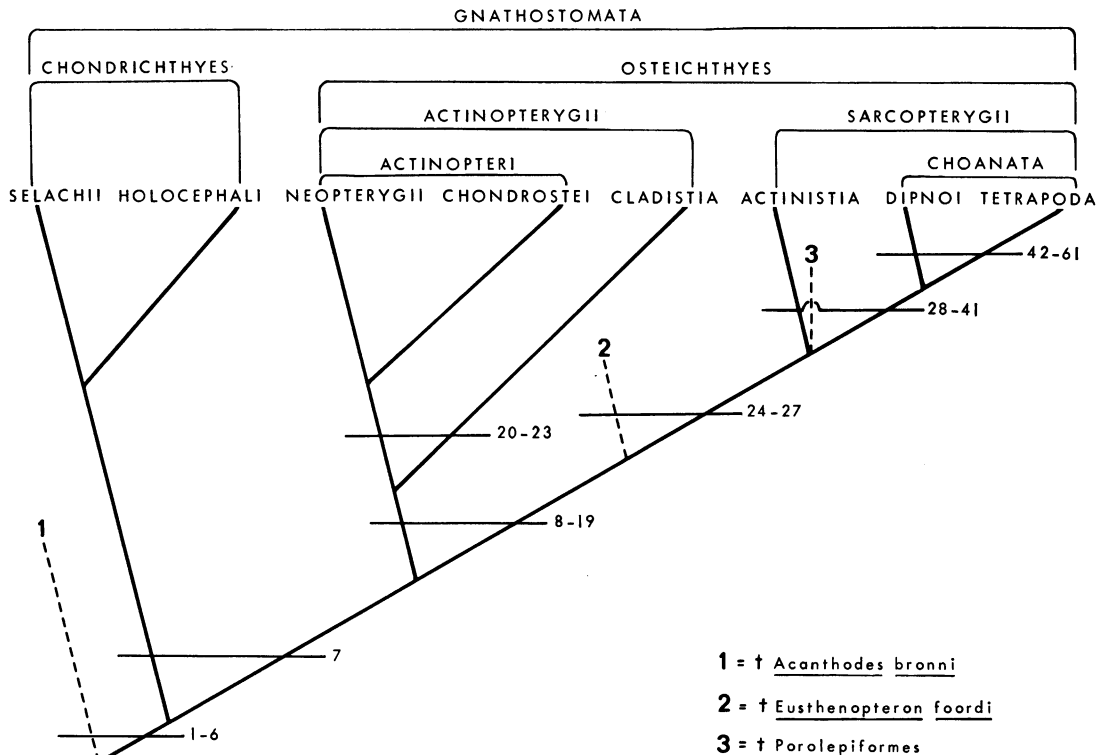


FIG. 62. Character-state tree of major groups of gnathostomes. Numbered characters refer to synapomorphy scheme in text. Unresolved cladistic position of porolepiformes is discussed in synapomorphy scheme.

joint development in rhipidistians, and rhipidistians are not a monophyletic group as we have every reason to suspect, then actinistians would simply represent the last of a perhaps large series of sister groups whose positions relative to each other in the hierarchy would be specified by the degree of kineticism. A parsimony argument would, therefore, require that the joint be considered either an autapomorphy of actinistians, as suggested by Bjerring (1973), or a primitive feature of sarcopterygians (Miles, 1977). Wiley (1979) also reviewed the problem and concluded (p. 171) "that both Bjerring and Miles are partly correct. Bjerring (1973) is correct in his assertion that the dorsal part of the intracranial joint is non-homologous [in rhipidistians and actinistians]. Miles (1977) is correct in accepting the ventral part of the intracranial joint as homologous. Bjerring is incorrect in asserting that the entire intra-

cranial joint is non-homologous and, as a matter of parsimony, Miles is incorrect in asserting that the entire intracranial joint is homologous."

Wiley (1979) also proposed in a study of ventral gill arch muscles that dipnoans and tetrapods are sister groups but that actinistians are excluded from membership in either the Sarcopterygii or Actinopterygii. He advocated that the Actinistia are instead the sister group of all other osteichthyans. The latter conclusion was based on his observation that three conditions of the musculature are present as a synapomorphy of actinopterygians plus sarcopterygians but are absent in actinistians. These three conditions are (1) an obliquus ventralis 1; (2) a transversus ventralis 4; and (3) the pharyngocla- viculars. Although we have not ourselves studied this musculature, we admit to some surprise at the absence of three myological

features of *Latimeria* that occur in dipnoans and urodeles, primarily because four of the 14 synapomorphies we propose for uniting actinistians with dipnoans and tetrapods are in gill arch characters, three of which are features of the ventral gill arch skeleton. For the present, it is parsimony rather than a study of Wiley's "absence" characters that forces us to interpret the absence of these muscles in *Latimeria* as autapomorphic. Wiley's evidence that "refutes" a link between *Latimeria* and our Choanata includes not only the three "absence" characters, but also two muscles uniquely shared by dipnoans and urodeles: a subarcualis rectus and multiple pharyngoclaviculars. For us, however, these last two conditions of the musculature only further corroborate our Choanata and say nothing about the position of *Latimeria*.

Finally, a word about the "choana" of *Eusthenopteron* is in order. We have tried to show that study of new material of the *Eusthenopteron* palate allows other interpretations of the palatal fenestra which is notably smaller in our specimens than in Jarvik's: (1) as a space for the passage of nerves and vessels as seen in some Recent fishes; (2) as a space allowing movement along a joint surface; and (3) as a space for receiving the tip of a coronoid fang when the mouth is closed. One might even suppose, since the palatines and pterygoids were displaced anteriorly under the vomer in Jarvik's specimen, probably a result of dorsoventral crushing, that the much larger palatal fenestra observed by Jarvik was caused mechanically by an abnormally deep penetration of a coronoid fang into the palate. Whatever the reality of the *Eusthenopteron* palate might have been, there is another view of the problem which it is helpful to remember: to accept the position of *Eusthenopteron* as a sister group of tetrapods based on this feature and even the alleged "septomaxilla" and "nasolacrimal duct," it would be necessary to reject at least 33 characters (nos. 28 through 61 in our synapomorphy scheme) which unite actinistians, dipnoans and tetrapods. Some of these 33 characters would also dichotomously resolve the position of

porolepiforms in this sequence if more could be learned about details of their anatomy—and that porolepiforms belong somewhere in this sequence seems evident to us. What this has meant to us, since actinistians and some porolepiforms have two external narial openings in the snout, is that the single narial opening in the snout of osteolepiforms, and *Eusthenopteron* in particular, is reasonably interpreted as having housed a common chamber for superficial membranous canals of two external nostrils, as in Recent *Polyp-terus* (compare figs. 11 and 17A, B). Accepting this interpretation, there is no longer a reason to search for a missing fenestra exonarina posterior in the palate of *Eusthenopteron* and other osteolepiforms. Application of parsimony in constructing theories of relationships among tetrapods, dipnoans, actinistians and "rhypidistians" could long ago have resolved the question of the rhypidistian "choana" with the ample data already in the literature.

Our conclusions, based on the foregoing synapomorphy scheme are depicted in figure 62, and summarized in the classification below; fossils are incorporated according to the method described by Patterson and Rosen (1977).

- SUPERCLASS Gnathostomata Gegenbaur, 1874
 - plesion †*Acanthodes bronni* Agassiz, 1832
 - CLASS Chondrichthyes Huxley, 1880
 - SUBCLASS Selachii Latreille, 1825
 - SUBCLASS Holocephali Bonaparte, 1832
 - CLASS Osteichthyes Huxley, 1880
 - SUBCLASS Actinopterygii Cope, 1891
 - INFRAClass Cladistia Cope, 1871
 - INFRAClass Actinopteri Cope, 1871
 - SERIES Chondrostei Müller, 1844
 - SERIES Neopterygii Regan, 1923
 - DIVISION Ginglymodi Cope, 1871
 - DIVISION Halecostomi Regan, 1923
 - SUBCLASS Sarcopterygii Romer, 1955
 - Sarcopterygii *incertae sedis* † Porolepiformes Jarvik, 1942
 - plesion †*Eusthenopteron foordi* Whiteaves, 1881
 - INFRAClass Actinistia Cope, 1871
 - INFRAClass Choanata Sæve-Söderbergh, 1934
 - SERIES Dipnoi Müller, 1844
 - SERIES Tetrapoda

In the classification above we use two very similar names intentionally: Actinopterygii, Actinopteri. Actinopteri is Cope's original name for actinopterygians *sensu stricto*, excluding Cladistia. Actinopterygii is today commonly used *sensu* Goodrich (1930), to

include Cladistia. The distinction we suggest will allow continued use of the vernacular "actinopt," and it will only be necessary to specify Actinopterygii or Actinopteri when the inclusive (+Cladistia) and exclusive (-Cladistia) groups are to be distinguished.

CONCLUSIONS

Goodrich (1909, p. 230), writing of the "many striking points of resemblance" between lungfishes and amphibians, commented that they "cannot all be put down to convergence." Goodrich was careful to distinguish primitive and derived characters, and the "many striking points of resemblance" were, in his view, derived. Since Goodrich's time, the number of apparent synapomorphies between lungfishes and tetrapods has increased rather than decreased, and the question still remains, can they all be put down to convergence? The consensus today is that these resemblances are convergent or adaptive, since they are outweighed by detailed correspondence between Paleozoic amphibians and osteolepiform fishes. Our purpose in this paper has been to oppose that view, by reemphasizing the shared derived characters of lungfishes and tetrapods, and by proposing alternative explanations of the similarities between osteolepiforms and tetrapods—that they are convergent or primitive.

Eusthenopteron is, after all, a very primitive fish, as Jarvik (e.g., 1968b, p. 506) has often said. Even so, it seems not to be primitive enough to serve as a morphotype of the ancestral tetrapod, since others who have surveyed a wide range of osteolepiforms (Vorobyeva, Andrews, Thomson, Panchen) have concluded that it is osteolepiforms as a whole, or the earliest osteolepidids, that are closest to tetrapods, rather than any derived osteolepiform subgroup. These theories of tetrapod origins follow the traditional paleontological method of the search for ancestors—reliance on paraphyletic groups. In the approach we have followed, the search for synapomorphies specifying sister-

group relationships, there is nothing to say about osteolepiforms as a whole, or osteolepidids, since they seem to lack synapomorphies, and therefore present the problems peculiar to extinct paraphyletic groups. Previous attempts to specify the relationship between osteolepiforms and tetrapods in terms of synapomorphies (Szarski, 1977; Schultze, 1977a; Gaffney, 1979a, 1979b) have avoided the problem of characterizing osteolepiforms, and have relied almost exclusively on the choana, a character which we have found to be open to other interpretations. If we select *Eusthenopteron foordi* as the best known osteolepiform, we can take that paleospecies, lungfishes, and tetrapods as three monophyletic groups, and list the apparent synapomorphies between each pair. *Eusthenopteron* and lungfishes share no plausible synapomorphies apart from the elongate basihyal (sublingual rod, also found in *Griphognathus*). Among the apparent synapomorphies between *Eusthenopteron* and tetrapods (p. 177), those that have withstood our criticism best are the pattern of dermal bones on the cheek (fig. 43), and the structure of the humerus. Lungfishes and tetrapods share derived features of the choana, dermal roofing bones of the skull, palate and jaw suspension, hyoid arch, gill arches, skull-vertebra articulation, ribs, dermal shoulder girdle, and paired appendages, in addition to numerous features of soft anatomy, physiology, embryology, and behavior which are not checkable in *Eusthenopteron*. The principle of parsimony leads us to accept these numerous derived features as synapomorphies. It follows that the characters shared by *Eusthenopteron* and tetrapods are primitive for sarcopterygians, conver-

gent or spurious. Abstracting from the list of those characters which were claimed to be exclusive to *Eusthenopteron* and tetrapods (p. 177), our assessment is as follows: primitive—cheek pattern, “protorhachitinous” vertebrae; convergent—polyplocodont teeth, structure of humerus; spurious—fenestra exochoanalis, septomaxilla.

In those assessments, we mean to argue an alternative view, not to insist that we are right. Those who are still impressed by resemblances between *Eusthenopteron*, or other osteolepiforms, and tetrapods, may amplify and enumerate those resemblances, and seek to show that they outnumber or outweigh the lungfish/tetrapod synapomorphies that we cite. We hope they will do so. In the course of this paper we have criticized many people and many ideas. Our criticisms stem from our viewpoint, that of phylogenetic systematics. Some of those we criticize have already published their opinion of that viewpoint (e.g., Panchen, 1979; Westoll, 1979, p. 346). We suggest that little will be gained by denigrating logic (Westoll), or denying the principle of parsimony (Panchen). Nor will progress come from simply reasserting general similarities between particular osteolepiforms and particular tetrapods, or between an osteolepiform morphotype and a tetrapod morphotype, unless those similarities are justified as synapomorphies by means of an explicit scheme of relationships, covering tetrapod subgroups and other relevant groups such as lungfishes and coelacanths.

In the 140 years since living lungfishes were first discovered, there has been evidence of a consistent pattern of derived characters shared by lungfishes and tetrapods. Nevertheless, during this century, that pattern has been treated as irrelevant or has been explained away, since the problem of tetrapod relationships has become one of origins, the property of paleontology, solved by the process approach: following back stratigraphic series of tetrapods and finding that they converge on a morphotype plausibly attributed to osteolepiforms. But when lungfishes are treated by the same method, they also converge on osteolepiforms (Den-

ison, 1968a); so do actinopterygians (Westoll, 1979, p. 345). Ancestors are slippery things, but ancestral groups are very accommodating, for their only attributes are plesiomorphous.

It seems fitting, therefore, to end our assault on the “rhpidistian barrier” by recording some personal observations, made near the completion of this study, of five particular locomotor and feeding behaviors of two large lungfishes (a *Protopterus annectens* and *Neoceratodus forsteri*, each over a meter long)¹² and a small *Neoceratodus* of about 5 centimeters.¹³ Needless to say, we record them because of their similarity to behaviors of aquatic urodeles. (1) Swimming is accomplished by undulations of the caudal peduncle while the paired fins are held loosely near the body rather than being used as maneuvering planes, although *Neoceratodus* will sometimes extend the pectorals somewhat. (2) Stopping is accomplished by sinking to the substrate on the extended paired fins; the pectorals are moved forward to an angle of 90 degrees, or slightly more, with the body axis, and the pelvics are often moved forward sharply (as much as 120°). Thus at rest, with the pelvics firmly down on the substrate, the fish may raise the entire precaudal region, sitting in this raised position for some minutes, with the pectorals hanging loosely downward. (3) When progressing forward slowly, the weight of the body is transferred to the paired fins which lift the body and pull it forward by moving in a side-to-side alternating diagonal pattern. During each cycle of fin movement, the body changes in curvature (when LF-RH fins are protracted the right side of the body is concave, whereas when RF-LH fins are protracted the right side of the body is convex). (4) When performing special movements across the substrate, such as turning or backing, right and left fins can be moved forward and backward synchronously or one fin can be moved independently of the other three. (5) When feeding from the substrate, the fore-

¹² In the New York Aquarium of the New York Zoological Society.

¹³ In the Department of Ichthyology of the American Museum of Natural History.

part of the body is elevated on the pectoral fins and the head is bent down toward the food; if the food consists of live worms in the substrate, small *Neoceratodus* will grasp the worms in its mouth and push backward with its pectorals until the worms are dislodged. None of the above observations is original with us; the same or similar behaviors were noted and recorded many times by late nineteenth-century and early twentieth-century biologists who were no less impressed than we by the remarkable behavioral likenesses of lungfishes and urodeles. We record our own fascination with these likenesses for a particular reason—the conviction that, had the study of lungfish relationships developed directly from comparisons among living gnathostomes without interruption by futile paleontological searches for ancestors, there would have been no “rhypidistian barrier” to break through, this review would have been written decades ago, and we would all have been spared a generation of anatomical misconstruction, dispensable scenarios about the fish-amphibian transition, and hapless appeals to plesiomorphy. Finally, it should be obvious from the nature of this review that our argument is not with the use of fossils, but with the use of the traditional paleontological method.

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