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On the Relationships of the Triassic-Liassic Redfieldiiform Fishes

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ABSTRACT

A survey of character distributions among the extinct lower actinopterygians has corroborated the hypothesis that the freshwater, Triassic-Liassic redfieldiiform fishes form a monophyletic group. This proposal is based mainly on the pattern of the dermal snout, loss of anterior nares, and pre-

sumably independent reduction of the branchios-tegal series.

The sister group of the redfieldiiforms among the other extinct lower actinopterygians remains unknown, but a survey of the dermal skull in these fishes has provided a hypothetical "sister" pattern.

INTRODUCTION

Character analysis in the palaeonisciforms and other extinct lower actinopterygian groups has lagged well behind that for the extinct neopterygians. The reasons for this include the absence of close living relatives, the apparent paucity of useful characters in taxa that are frequently represented by compressed and inadequately preserved dermal skeletons, the fragmentary fossil record, and the not inconsiderable problems of morphological interpretation. More or less three dimensional specimens that can be prepared chemically or by air abrasion may yield a great deal of information, but they represent only a small fraction of the nearly 200 genera in this paraphyletic assemblage.

The primary purpose of the present paper is to attempt a cladistic analysis of one group of extinct lower actinopterygians that has long been regarded as a "natural" one, namely, the Redfieldiiformes. They are Triassic and early Jurassic freshwater fishes (fig. 1) whose remains have been found in continental sediments in Australia, South Africa, Zambia, Morocco, eastern and western United States, and questionably in Madagascar. The design of the redfieldiiform skeleton has suggested affinity with several other extinct lower actinopterygian groups, but there has been no consensus about relationship.

In regard to the living lower actinopterygians, Patterson (1982) has recently defined

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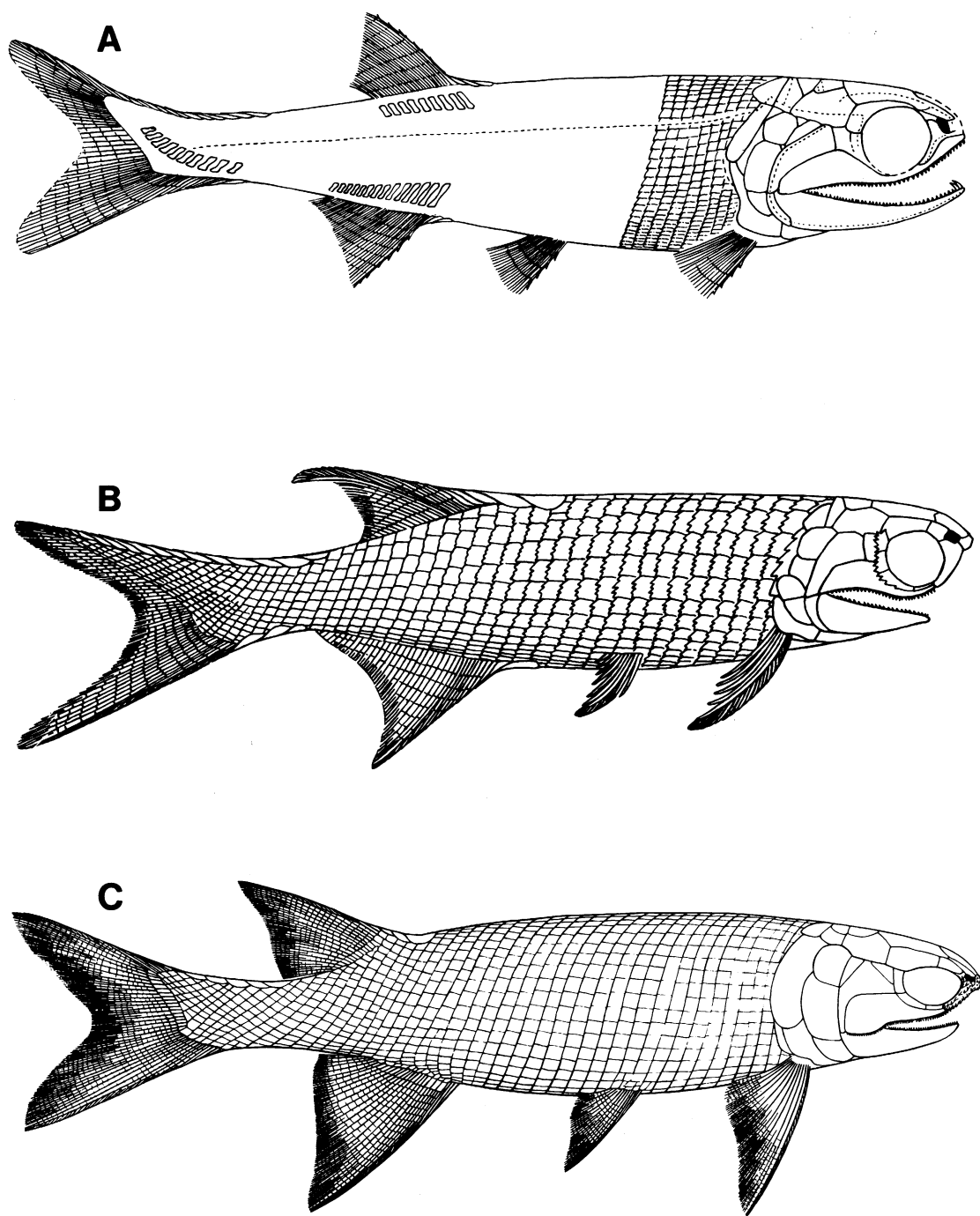


FIG. 1. Restorations of three redfieldiiforms. A. *Brookvalia*. After Hutchinson, 1973 and AMNH 4706, 9254. Flank squamation omitted. B. *Daedalichthys*. After Brough, 1931 and BMNH 17532-3. C. *Cyonichthys*. From Schaeffer, 1967.

two monophyletic groups, the Cladistia for the polypteroids, and the Chondrostei for the acipenseroids and polyodontoids plus their fossil relatives. This restricted use of the term Chondrostei makes it still more imperative that the various taxa of extinct lower actinopterygians be restudied. The suspected paraphyly of numerous fossil non-neopterygian categories is emphasized by Patterson's (1982, fig. 3B) decision to include the palaeonisciform genus *Pteronisculus* in a trichotomy with the Chondrostei and the Neopterygii on the basis of five shared characters. In addition, Gardiner (in press) has concluded that the Devonian palaeonisciform genera *Mimia* and *Moythomasia* are successive sister taxa to the remaining actinopterygians. As such, they should provide us with information on the primitive state for the actinopterygian braincase (*Mimia* is represented by abundant three-dimensional material), palate, dermal skull, axial skeleton, fins, and squamation. This information, much of it recently acquired, is obviously of considerable importance in working out the patterns of character distribution within the palaeonisciforms and the redfieldiiforms, and in relation to seeking a sister group for the latter.

Discussion of redfieldiiform relationships (see summary in Schaeffer, 1967, p. 329) effectively began with Stensiö's (1921) opinion that the catopterids (=redfieldiids) and the colobodontids (=perleidids) should be grouped in the family Catopteridae, which, he believed, is closely related to the palaeoniscids. Lehman (1966) placed both families in the order Perleidiformes, which he considered to be one of numerous orders of fossil, non-teleost actinopterygians (*ibid.*, p. 71). Brough (1931, 1934) first considered the Catopteridae to be "closely related to, and derived from, the Palaeoniscidae," and, in 1936, to be derived from another palaeonisciform family, the Dicelopygidae. Schaeffer (1967, 1973) has favored derivation from generalized palaeoniscids, while Lowney (MS) has tentatively proposed a sister-group relationship with the rhadinichthyid palaeonisciforms. Hutchinson (1973, p. 345), suggested that the redfieldiiforms and the perleidiforms had a common ancestor (*ibid.*,

fig. 54), and that the two groups arose from a palaeonisciform complex including the Elonichthyidae, Acrolepidae, and the Rhadinichthyidae (*ibid.*, p. 346). In recent precladistic classifications of the extinct and living actinopterygians (e.g., Andrews et al., 1967; Romer, 1967) the Redfieldiiformes are listed as a suborder or order of the Chondrostei without comment on relationship.

Hutchinson's (1978) last paper on the redfieldiiforms, which is mainly concerned with the genus *Helichthys*, includes alternative cladograms for the relationships of this genus to the three redfieldiiform families that he defined in 1973 (the Brookvaliidae, Schizurichthyidae, and Redfieldiidae). Prior to his death in 1978, Peter Hutchinson and I had planned to write a joint paper on redfieldiiform affinities and interrelationships.

The present paper is dedicated to his memory.

ABBREVIATIONS

AMNH, The American Museum of Natural History
 BMNH, British Museum (Natural History)
 UTVPC, University of Texas Vertebrate Paleontology Collection

Anatomical abbreviations are included in the legend for figure 4.

SYSTEMATIC RESUME

In order to facilitate later discussion, a diagnosis of the Redfieldiiformes is included in this section along with a list of genera arranged, as far as practicable, by character distribution (fig. 6), relative age and source area. The vertical distribution of the Newark supergroup genera is summarized in Olsen, McCune and Thomson (1982, fig. 7).

DIAGNOSIS: Lower actinopterygians (non-neopterygians) with a terminal or subterminal gape, fusiform body outline and an equilobate, hemiheterocercal tail. The braincase is typically palaeonisciform with an open otico-occipital fissure and a nearly vertical hyomandibular facet. The parasphenoid is short, with well-developed ascending processes. The vomerine area is covered by elongated paired tooth plates (in *Ichnelepis*). The endoptery-

goids are relatively large and dentigerous. The dermal snout is composed of a median rostral and postrostral, paired nasals and paired "premaxillae" (=premaxillo-antorbital of some authors). The single nostril is surrounded by the nasal, adnasal and the enlarged "premaxilla." The nasal is excluded from the orbit by the adnasal. The maxilla is fixed and expanded posteriorly. The preopercular is angled; the subopercular is larger than, or about equal to, the size of the opercular. Both a dermohyal and an antopercular are present in the more generalized taxa. There is a single, platelike branchiostegal (two in *Daedalichthys*) and a single median gular. The dermopterotic is large and rectangular. The shoulder girdle includes a clavicle, postcleithrum, and a presupracleithrum (observed in *Helichthys*). Fringing fulcra are probably present on all fins. Basal fulcra border the unpaired fins, including both lobes of the caudal. The rays of the remote, opposite dorsal and anal fins are more numerous than the basals. The scales are rhomboidal, with peg-and-socket articulation, and with dentine and ganoin layers.

Hutchinson's (1973, 1978) division of the redfieldiiforms into the Brookvaliidae, Schizurichthyidae and the Redfieldiidae left the genus *Helichthys* (*ibid.*, 1978) in an indeterminate status. The potential monophyly of these families and the affinities of *Helichthys* will be considered in the section on cladistic analysis.

The redfieldiiform genera that I presently recognize are:

1. *Atopocephala* Brough, 1934. Lower Triassic (Scythian), Lower Cynognathus Zone, Karroo Series, Orange Free State, South Africa.
2. *Schizurichthys* Wade, 1935. Middle Triassic (?Ladinian), Hawkesbury Sandstone, New South Wales, Australia.
3. *Ischnolepis* Houghton, 1934. Lower Triassic (Scythian), Madumabisa Shales, Zambia.
4. *Brookvalia* Wade, 1933. Middle Triassic (?Ladinian). Same locality as *Schizurichthys*.
5. *Phlyctaenichthys* Wade, 1935. Middle Triassic (?Ladinian). Same locality as *Schizurichthys*.
6. *Helichthys* Broom, 1909. Lower Triassic (Scythian). Same locality as *Atopocephala*.
7. *Geitonichthys* Wade, 1935. Middle Triassic (?Ladinian). Same locality as *Schizurichthys*.
8. *Molybdichthys* Wade, 1935. Middle Triassic (?Ladinian). Same locality as *Schizurichthys*.
9. *Daedalichthys* Brough, 1931. Lower Triassic (Scythian). Same locality as *Atopocephala*.
10. *Cionichthys* Schaeffer, 1967. Upper Triassic (Middle-Late Carnian) Chinle Group and Dockum Formation, western USA; Newark Supergroup, eastern USA.
11. *Redfieldius* Hay, 1899. Lower Jurassic (Hettangian-Sinemurian), Newark Supergroup, eastern USA.
12. *Dictyopyge* Lyell, 1847. Upper Triassic (Middle Carnian), Newark Supergroup, eastern USA.
13. *Mauritanichthys* Martin, 1982. Upper Triassic, Argana Valley, Western Atlas, Morocco.
14. *Lasalichthys* Schaeffer, 1967. Upper Triassic (?Carnian), Chinle Group and Dockum Formation, western USA.
15. *Synorichthys* Schaeffer, 1967; Schaeffer and Mangus, 1970. Upper Triassic (?Carnian), Chinle Group and Dockum Formation, western USA; Newark Supergroup, eastern USA.

Genera 1 through 5 were included by Hutchinson (1973) in his Brookvaliidae and 12, 14 and 15 in the Redfieldiidae. *Schizurichthys* was the only genus assigned to the Family Schizurichthyidae.

CHARACTER ANALYSIS

The characters discussed below are arranged as follows: neurocranium, snout, circumorbital series, skull roof, cheek area, opercular series, palate, mandible, paired and unpaired fins and squamation.

NEUROCRANIUM: The only three-dimensional redfieldiiform neurocranium (UTVPC 31089-44) comes from the Upper Triassic Dockum Group in Howard County, Texas. On the basis of the incomplete skull roof, it can be assigned either to *Lasalichthys* or *Synorichthys* (Schaeffer, 1967, p. 315 and pl. 19). As noted in the diagnosis (above), the general aspect of this braincase is palaeonisciform with an open otico-occipital fissure and a nearly vertical hyomandibular facet. Although it is considerably weathered, comparison of the lateral surface with Patterson's (1975, fig. 115) restoration of an incompletely ossified *Perleidus* neurocranium indicates that the Dockum specimen is composed of large opisthotic elements, somewhat smaller prootic ones, as well as pterotic and sphenotic ossifications. There is apparently a small in-

tercalar. The epioccipital-exoccipital-basioccipital complex is also similar to that of the immature *Perleidus*. As discussed by Schaeffer (1971) and Patterson (1975), these ossifications form a pattern that was undoubtedly typical of the palaeonisciform and other extinct lower actinopterygian neurocrania. It also represents the basic pattern that, with modifications, gave rise to the neurocrania of the higher actinopterygians.

The parasphenoid is known in *Redfieldius* (Schaeffer and McDonald, 1978, fig. 3). It apparently ended at the ventral otic fissure, and has narrow, well-developed ascending processes, as in the "more advanced" palaeonisciforms (cf. Patterson, 1975, p. 533) including *Paramblypterus* (Heyler, 1969, fig. 13).

SNOUT: A review of the snout pattern in generalized, extinct, lower actinopterygians by Gardiner (1963, and in press) and by Patterson (1975) has led them to conclude that this pattern consists of a single, median, canal-bearing rostral bone situated between paired nasals, and of paired dentigerous "premaxillae" (premaxillo-antorbital) that carry the infraorbital canals. The "premaxillae" usually meet in the midline, but may be separated by the rostral, which is dentigerous when it enters the jaw margin. This snout pattern (with or without the rostral in the jaw margin) occurs in the Devonian genera *Cheirolepis* (Gardiner, in press), *Mimia* (Gardiner, in press), *Moythomasia* (Jessen, 1968; Gardiner, in press), a palaeoniscoid from the late Devonian of Australia (Long, 1983), various later palaeonisciforms, and in the adult *Polypterus*. On the basis of present evidence, the redfieldiiform snout differs from that of the primitive one only in having a horizontally subdivided rostral bone. The ventral, canal-bearing element is here called the rostral, and the more posterior, anamestic element is named the postrostral (fig. 4B).

Gardiner (1963, and in press) and Patterson (1975) have proposed that the "premaxilla" of the generalized actinopterygians was subdivided in more advanced forms into a separate, dentigerous, anamestic premaxilla and an antorbital with its characteristic tri-radiate canal pattern. This is essentially the condition in the larval *Polypterus* (24 mm),

which has distinct toothed, anamestic premaxillae and several sensory canal ossifications that can be reasonably regarded as antorbital precursors (Pehrson, 1947). An economical explanation for these observations is that the pattern in the 24 mm *Polypterus* represents the primitive actinopterygian larval condition, whereas that in the mature *Polypterus*, and in the extinct, generalized actinopterygians mentioned above, may be regarded as the primitive adult condition. A second, but less favored interpretation in view of the fossil evidence, is that the condition in the larval *Polypterus* is the primitive one.

With some reservation, Nielson (1942, pp. 136 and 155) restored the snout of *Pteronisculus* with separate premaxillae and canal-bearing antorbitals. According to Lowney (MS), these elements are separate in the palaeonisciforms *Canobius*, *Mesopoma*, and *Phanerosteon*, as well as in the majority of the palaeonisciforms from the Upper Mississippian Bear Gulch Formation in Montana. There is also evidence for their separation in the perleidiiforms (Stensiö, 1921, fig. 80; Lehman, 1952; Schaeffer, 1955; Hutchinson, 1973a and 1973b). This is, of course, the case in all neopterygians (Patterson, 1975). Pending further investigation, it appears that the primitive larval condition was independently retained in the adult stage of some extinct lower actinopterygians of unknown relationship, and also in the neopterygians.

The relationships of the prominent redfieldiiform "premaxilla" with its neighboring bones, along with its distinctive shape, its major contribution to the orbital border, and the presence of a single naris on each side of the snout represents a complex of synapomorphies for the entire redfieldiiform group (fig. 4B). To this list must be added the presence of separate median rostral and postrostral elements. Although a complete separation between the canal-bearing and the anamestic portions of the primitively single rostral bone (Patterson, 1975, pp. 511–512) can be confirmed in most of the redfieldiiforms, the distribution of this condition among other lower actinopterygians is less certain. Lowney (MS) found evidence for it in

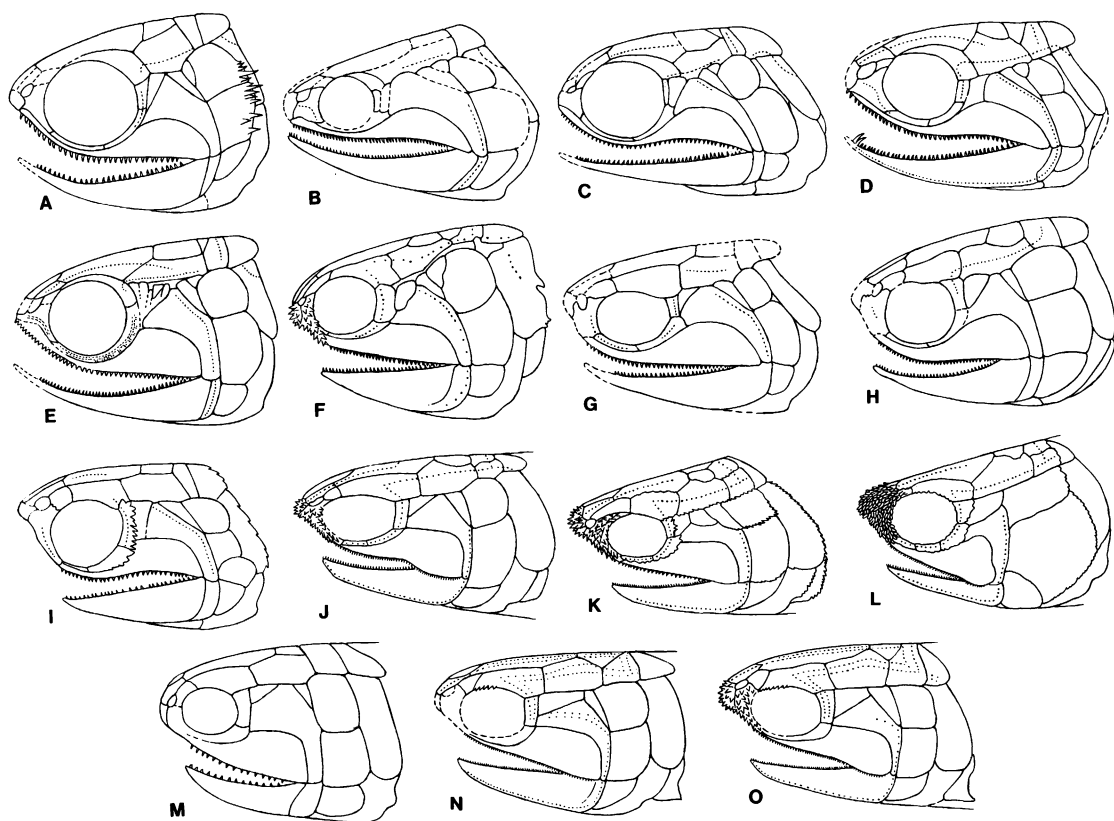


FIG. 2. Restorations of redfieldiiform skulls and shoulder girdles in lateral aspect. A. *Atopocephala*. After Hutchinson, 1973 and BMNH P.16083. B. *Schizurichthys*. After Hutchinson, 1973 and BMNH P.15892. C. *Ischnolepis*. After Hutchinson, 1973 and BMNH P.27577 and 27578. D. *Brookvalia*. After Hutchinson, 1973 and AMNH 4705, 4706, 4707, 9254. E. *Phlyctaenichthys*. After Wade, 1935; Hutchinson, 1973. F. *Helichthys*. After Hutchinson, 1978 and AMNH 8063, 11212, 11213. G. *Geitonichthys*. After Wade, 1935 and Hutchinson, 1973. H. *Molybdichthys*. After Wade, 1935; Hutchinson, 1973. I. *Daedalichthys*. After Brough, 1931; Hutchinson, 1973. J. *Cionichthys*. After Schaeffer, 1967. K. *Redfieldius*. After Schaeffer, 1967; Schaeffer and McDonald, 1978. L. *Dictyopyge*. After Schaeffer and McDonald, 1978. M. *Mauritanichthys*. After Martin, 1982. N. *Lasalichthys*. After Schaeffer, 1967. O. *Synorichthys*. After Schaeffer, 1967. For bone identifications see figure 4B.

several palaeonisciforms from the Bear Gulch Formation. Stamberg (1978) has noted a separate rostral and postrostral in some specimens of the haplolepid palaeonisciform *Pyritocephalus sculptus*, but apparently not in all individuals. Separation of the anamestic and canal-bearing parts of the rostral bone in various groups of extinct lower actinopterygians, however, only can be demonstrated in exceptionally well-preserved specimens. The postrostral is reduced in *Lasalichthys* and absent in *Synorichthys*. According to Hutchinson (1973, p. 385) the postrostral is also

absent in *Schizurichthys*, but the snout (BMNH P.15891, USGD 305) is very poorly preserved. What is known about the skull suggests relationship with *Ischnolepis* and other genera with an anteriorly elongated maxilla (figs. 2, 3).

In order to reduce confusion in snout dermal bone terminology, the term postrostral should be used only for the separate anamestic rostral element when it exists behind the rostral bone that carries the ethmoid canal. The canal-bearing rostral may be relatively small as in *Polypterus* and in most

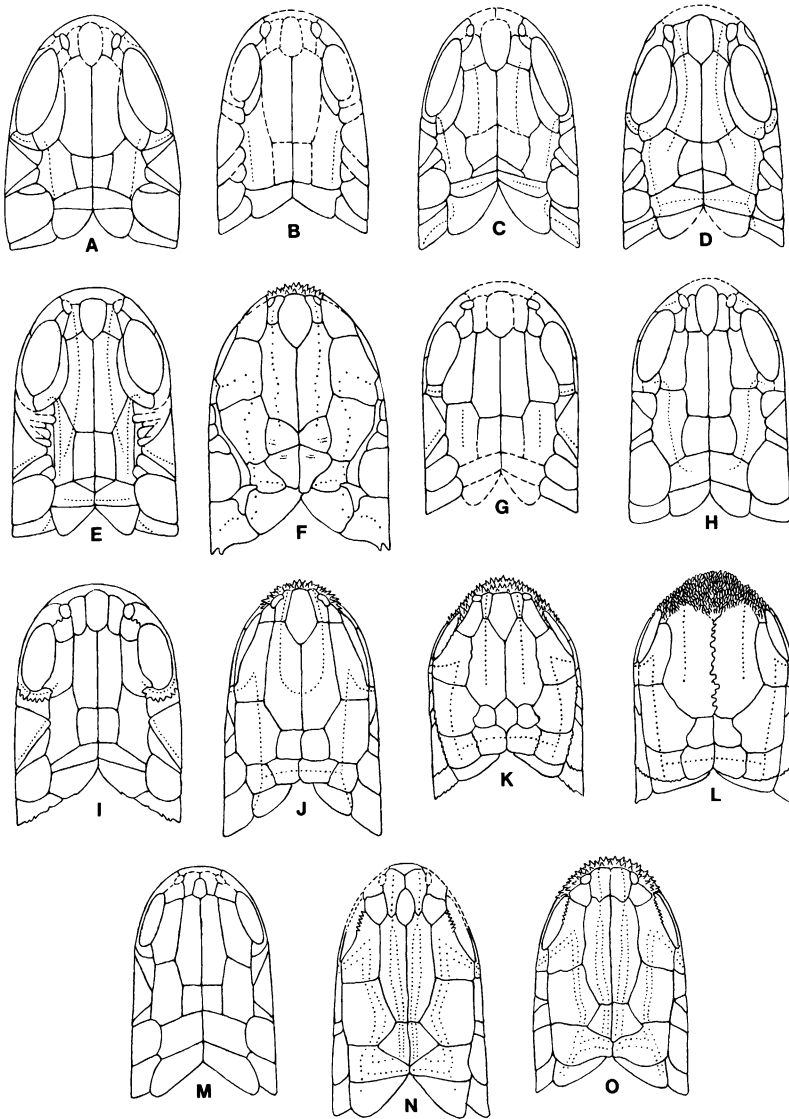


FIG. 3. Restorations of redfieldiiform skulls in dorsal aspect. Identifications and sources as in figure 2. For A through E and G through I, the dorsal views have been drafted by projection from the lateral aspect and are therefore partly diagrammatic. For bone identifications see figure 4B.

neopterygians which still retain it, but it may also be large and extend posteriorly between the nasals to the frontals as in the teleost *Elops* (Nybelin, 1967) and in *Polypterus*.

The presence of separate, anamestic premaxillae in the Scythian-Ladinian redfieldiiforms was proposed by Hutchinson (1973), who showed (correctly) that the upper marginal dentition extends forward below the rostral and nearly to the midline. This is par-

ticularly evident in some specimens of *Brookvalia* (e.g., AMNH 4705). However, recent examination of specimens in the British Museum previously studied by Hutchinson has not confirmed the presence of separate anamestic premaxillae in any of the South African or Australian taxa, and there is no evidence of these elements in the American genera (Schaeffer, 1967). The maxillae in the more generalized forms are attenuated an-

teriorly and to some extent must underlie the rostral. I have found no indication that the rostral is dentigerous or that it enters into the functional jaw margin. In most or all the redfieldiiform genera there is evidence that the rostral bone is covered with strong, bluntly pointed tubercles or denticles that resemble those on the "premaxilla." These tubercles are usually larger than the marginal teeth of the maxilla and the dentary, and there is no reason to believe that the ventral ones functioned as teeth.

Except for *Lasalichthys* (fig. 3N), possibly *Mauritanichthys* (fig. 3M), and *Synorichthys* (fig. 3O), the nasals are slim bones situated between the adnasals and the postrostral. In the first two genera, the nasals meet in front of the reduced postrostral; I have found no indication in *Lasalichthys* that the nasals actually covered the postrostral posteriorly. According to Hutchinson (1973) the nasals also meet in *Manlietta*, which is presently regarded as a perleidid.

CIRCUMORBITAL BONES: The ventral rim of the redfieldiiform orbit is framed in part by the enlarged "premaxilla" and by one or two narrow infraorbitals. There is usually a single bar-like postorbital; according to Hutchinson (1973), *Daedalichthys* has two (fig. 2I). The upper border of the orbit is formed by the so-called adnasal and the dermosphenotic, which is more or less sickle-shaped. The dermosphenotic, which is situated in front of the spiracle, contains the bend in the infraorbital sensory canal as it follows around the ventral border of the orbit. In palaeonisciforms that have numerous separate supraorbital bones such as *Elonichthys serratus* (Moy-Thomas and Dyne, 1938), *Perleidus* (Lehman, 1952), and various groups of extinct neopterygians, the dermosphenotic is typically reduced in size and resembles the anamestic supraorbitals. In some of the Ladinian, and all the late Triassic-Liassic redfieldiiforms (fig. 2F-O), the dermosphenotic is widened and has a broader contact with both the adnasal and the dermopterotic. It is also subequal in size with the dermopterotic.

The homology of the redfieldiiform adnasal bone remains somewhat in doubt. It was called the prefrontal by Brough (1931) and, for topographic reasons, the adnasal by Schaeffer (1967). Hutchinson (1973, p. 345)

suggested that it represents an anterior fragment of the dermosphenotic (fig. 5C). However, the adnasal is barely in contact with the falcate dermosphenotic in the more generalized redfieldiiforms. It does, however, eliminate the nasal from the rim of the orbit, a condition that has been regarded as a redfieldiiform synapomorphy. Poor preservation has made it difficult to confirm the presence of the adnasal in *Ischnolepis*, *Atopocephala*, and *Phyctaenichthys*, but the occurrence of this bone in *Brookvalia* and in the more advanced genera make this probable (fig. 2).

There are three other possibilities regarding the identity of the adnasal. It might represent a neomorph, which seems unlikely. It could represent a "fragment" of the dorsal, postnasal part of the enlarged "premaxilla," or it might be a relic supraorbital (fig. 5D). The last interpretation is suggested by the position of an anterior supraorbital in the palaeonisciforms *Cheirolepis* (Pearson and Westoll, 1979; BMNH P.60533) and *Paramblypterus* (fig. 4A, 5B; Blot, 1966; Heyler, 1969; and BMNH P.607), which is in contact with the anterior border of the dermosphenotic and is situated lateral to the nasal bone.²

The diagrams in figure 5 illustrate the progressive enlargement of the "premaxilla," plus the hypothesis that the redfieldiiform adnasal is derived from the dermosphenotic (C) or from the dorsal part of the "premaxilla" (E). The sequence B-D-F begins with a form such as *Paramblypterus* (B), and shows a progressive reduction of the anterior supraorbital along with enlargement of the "premaxilla." A few other palaeonisciforms (e.g., *Palaeoniscus* and *Oxygnathus*) have a series of small anamestic supraorbitals in series with the dermosphenotic. It may be assumed that in some taxa, such as *Paramblypterus*, the supraorbital ossifications extended anteroventrally behind the nasal until they reached the "premaxilla." In this regard, it should be noted that the *Paramblypterus* supraorbital is in contact posteriorly with the subdivided dermosphenotic.

As noted by Patterson (1982, p. 250), the

² *Lawnia* (Wilson, 1953) and *Coccocephalichthys* (*Cocconiscus*; see Poplin, 1974) may have the same basic pattern but the evidence is still equivocal.

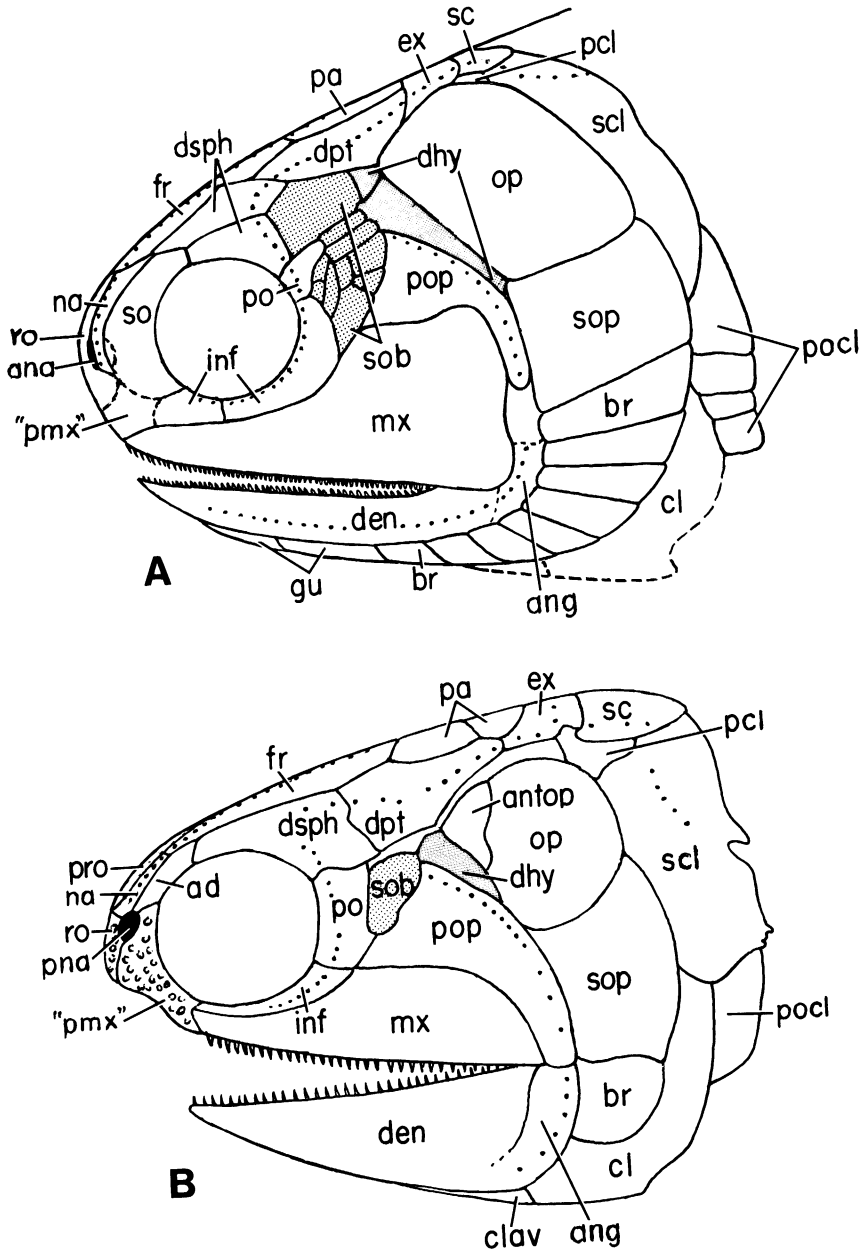


FIG. 4. Skull restorations in lateral aspect. A. *Paramblypterus*. (Modified after Blot, 1966, Heyler, 1969 and BMNH P.607. B. *Helichthys*. After Hutchinson, 1978 and AMNH 8063, 11212, 11213. Abbreviations: ana, anterior naris; ang, angular; br, branchiostegal; cl, cleithrum; den, dentary; dhy, dermohyal; dpt, dermopterotic; dsph, dermosphenotic; ex, extrascapular; fr, frontal; gu, gular; inf, infraorbital; mx, maxilla; na, nasal; op, opercular; pa, parietal; pcl, presupracleithrum; "pmx," premaxillo-antorbital; pna, posterior naris; po, postorbital; pocl, postcleithrum; pro, postrostral; ro, rostral; scl, suprascapular; so, supraorbital; sop, subopercular.

nasal bone in generalized actinopterygians is notched for the anterior and posterior nares.

In the redfieldiiforms there is no evidence of an anterior narial notch. The single, large nar-

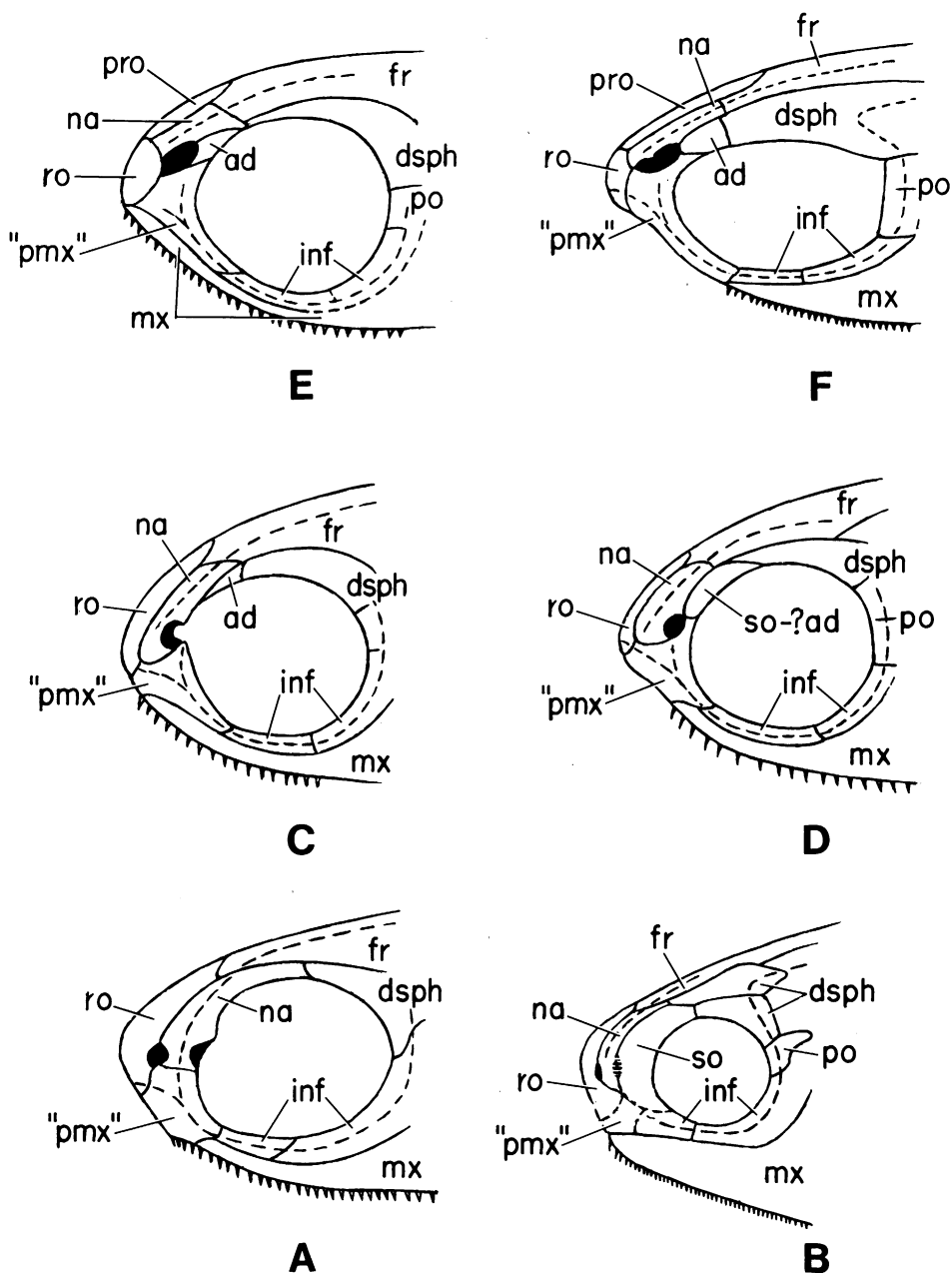


FIG. 5. Snout pattern diagrams arranged to illustrate the origin of the adnasal bone from the anterior part of the dermosphenotic, as in hypothetical stage C, or from a supraorbital, as in hypothetical stage D. Diagram A is essentially the snout pattern of *Mimia* (after Gardiner, 1963). B represents *Paramblypterus*. After Blot, 1966 and Heyler, 1969. E. *Brookvalia*. After Hutchinson, 1973 and AMNH 4706. F. *Cionichthys*. After Schaeffer, 1967. Bone identifications as in figure 4.

ial opening is framed in part by the posterior border of the nasal bone on each side of the

snout (slightly indented) and by the rostral. It is also behind the supraorbital sensory ca-

nal. It follows, therefore, that the narial opening in these fishes is the posterior naris of other lower actinopterygians.

SKULL ROOF: As discussed by Hutchinson (1978, p. 889), three genera assigned by him to the family Brookvaliidae (*Ischnolepis*, *Brookvalia* and *Phlyctaenichthys*) have two pairs of rectangular parietals (figs. 3C–E). *Atopocephala* (fig. 3A) and *Schizurichthys* (fig. 3B), both of which are incompletely known, have been restored with one pair of parietals (the primitive actinopterygian number). *Helichthys* (fig. 3F) has two pairs of parietals, but otherwise this genus shows no particular resemblance to Hutchinson's brookvaliids.

A broad abutment between the dermosphenotic and the dermopterotic is characteristic of most generalized actinopterygians. A falcate dermosphenotic is known outside of the Redfieldiiformes in *Pteronisculus* (Nielson, 1942) and in some other palaeonisciform genera whose relationships are presently unknown (Schaeffer, 1973). The wider, nearly rectangular dermosphenotic, which approaches the size of the dermopterotic, is peculiar to *Helichthys*, *Daedalichthys*, *Geitonichthys*, *Molybdichthys*, *Mauritanichthys* and the North American taxa (fig. 3). All the redfieldiiforms seem to have the usual single pair of extrascapulars except for *Cionichthys* and *Redfieldius*, which have these elements doubled on each side of the midline.

CHEEK AREA: The cheek pattern resembles that of a palaeonisciform with a nearly vertical suspensorium. There is, however, an extra bone, the antopercular, between the dermohyal and the opercular in those redfieldiiforms with a relatively narrow, falcate dermosphenotic (figs. 2A–E) and in *Helichthys* (fig. 2F), which has a widened dermosphenotic. Otherwise an antopercular has been noted only in *Pteronisculus* (Nielson, 1942, figs. 27 and 30). In the redfieldiiforms, the antopercular, in its shape and position, resembles an ossification that has separated from the anterodorsal part of the opercular bone rather than a wedge-shaped element that appears to be quite distinct from the opercular as in *Pteronisculus*. In the latter, the antopercular (which is sometimes doubled in *P. magna*; Nielson, 1942, p. 181, fig. 30) is situated in front of the straight anterior bor-

der of the opercular. Although this distinction may seem superficial, it, at least, does not falsify the hypothesis that the antoperculars of *Pteronisculus* and the more generalized redfieldiiforms are non-homologous. This presumed parallelism is also corroborated by other character distributions.

Most redfieldiiforms have a single suborbital bone that is more or less separated from the dermohyal by the preopercular (fig. 2, fig. 4B). *Phlyctaenichthys* is distinctive in having this element subdivided into six small bones and *Redfieldius* into two. *Dictyopyge*, on the other hand, has no suborbitals. It is evident that the number, shape, and arrangement of these elements varies considerably among the extinct lower actinopterygians. Suborbitals are absent in representatives of the stem-group actinopterygians, and the origin of these bones is obscure (see Gardiner, 1967, p. 199).

OPERCULAR SERIES: The single, platelike branchiostegal (two in *Daedalichthys*) has long been regarded as a unique redfieldiiform character (Brough, 1934, p. 563). As in the case of the antopercular, the distribution of other characters favors independent reduction of the branchiostegal series, even though it is also reduced to one or two elements in the distinctive haplolepid and in the aeduellids (Westoll, 1944; Heyler, 1969). The opercular bone is smaller than, or about equal in size to, the subopercular in the redfieldiiforms—as in various other lower actinopterygians. *Sakamenichthys* (Lehman et al., 1959) from the Lower Triassic of Madagascar has a small opercular and a single platelike branchiostegal. It may be a redfieldiiform, but unfortunately the snout area remains unknown and, as noted, the opercular-branchiostegal pattern in the redfieldiiforms has by itself a limited value in cladistic analysis.

PALATE: The dermal bones of the redfieldiiform palate are fairly well displayed in a specimen of *Brookvalia gracilis* (BMNH P.15813; figured somewhat diagrammatically by Hutchinson 1973, fig. 10). Although the dermometapterygoid is partly covered by the right opercular and the sutures are nearly obliterated, it is evident that the generalized actinopterygian pattern is present, as recently discussed by Rosen et al. (1981) and Patterson (1982). The bone fragment labeled by

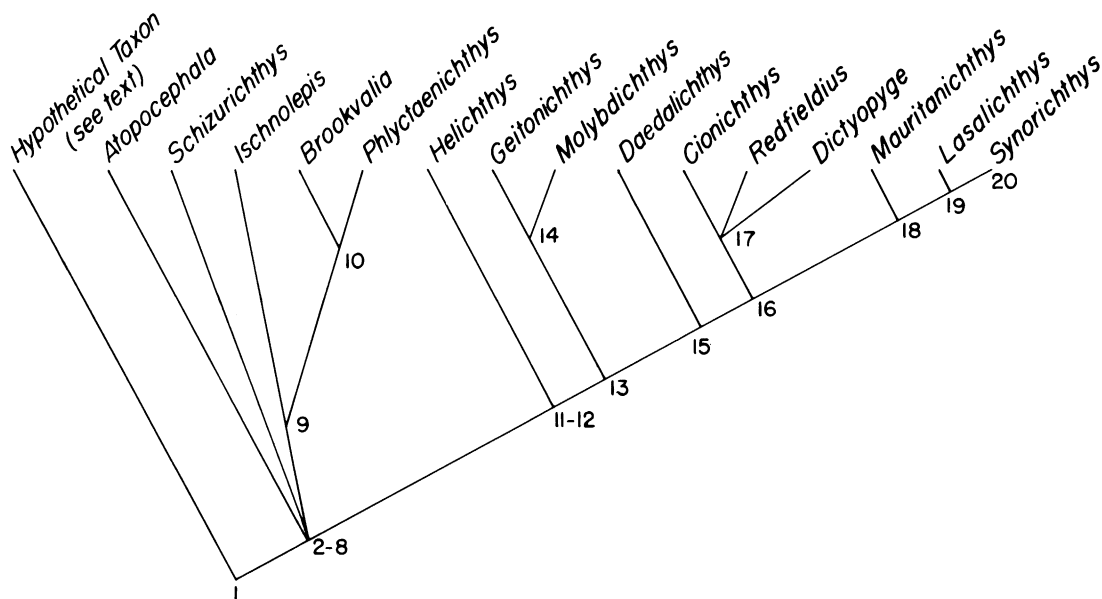


FIG. 6. Proposed cladogram of the hypothetical taxon discussed in text plus the 15 genera of redfieldiiforms. Numbers refer to characters in the lists on pages 14 and 15.

Hutchinson (1973, fig. 10) “?pmx” is probably part of the attenuated anterior portion of the maxilla, as the associated teeth seem too large for the dermopalatine.

MANDIBLE: In agreement with their many other generalized aspects, the redfieldiiforms lack a coronoid process on the mandible. The angular, which is small and confined to the posterior part of the mandible, is rarely evident in the American forms because of the prominent ornamentation. The supra-angular may be absent, or it may be very small and obscure as in *Mimia* (see Patterson, 1982, p. 248). The pores of the mandibular sensory canal are usually obvious in spite of the ornamentation.

PAIRED AND UNPAIRED FINS: Most of the girdle and fin characters are generalized actinopterygian ones such as the retention of the clavicle, the presupracleithrum (positively identified in *Helichthys*, fig. 2F, but it must be more generally distributed), and the excessive number of fin rays over basals. There may be an increase in ray segmentation and subdivision between the Scythian and the late Triassic–early Jurassic genera, but this is equivocal. It is probable that most or all the

fins in all genera have both basal and fringing fulcra. Patterson (1982, p. 247) notes that basal fulcra occur on the dorsal margin of the tail in the most generalized actinopterygians, whereas the presence of fringing fulcra is a more advanced condition. The hemiheterocercal tail is a common advanced lower actinopterygian character, also without usefulness in this connotation. There are differences, however, in the relative length of the caudal axis in some redfieldiiform genera (fig. 1A–C). Also *Schizurichthys* has a distinctive “epaxial lobe” (Hutchinson, 1973, fig. 28; Patterson, personal commun.) which is bordered dorsally and ventrally by fringing fulcra. Actually this lobe represents a modification in the first six upper principal rays. The most unusual aspect is the presence of fringing fulcra partway along the lower border of the sixth ray. Although Hutchinson (1973, pp. 323–324) assigned *Schizurichthys* to a separate family, mainly on the basis of this specialization in the caudal fin, I regard it as an autapomorphy for this genus, which is otherwise a generalized redfieldiiform (fig. 2B and fig. 3B).

SCALES: Redfieldiiform scales have been

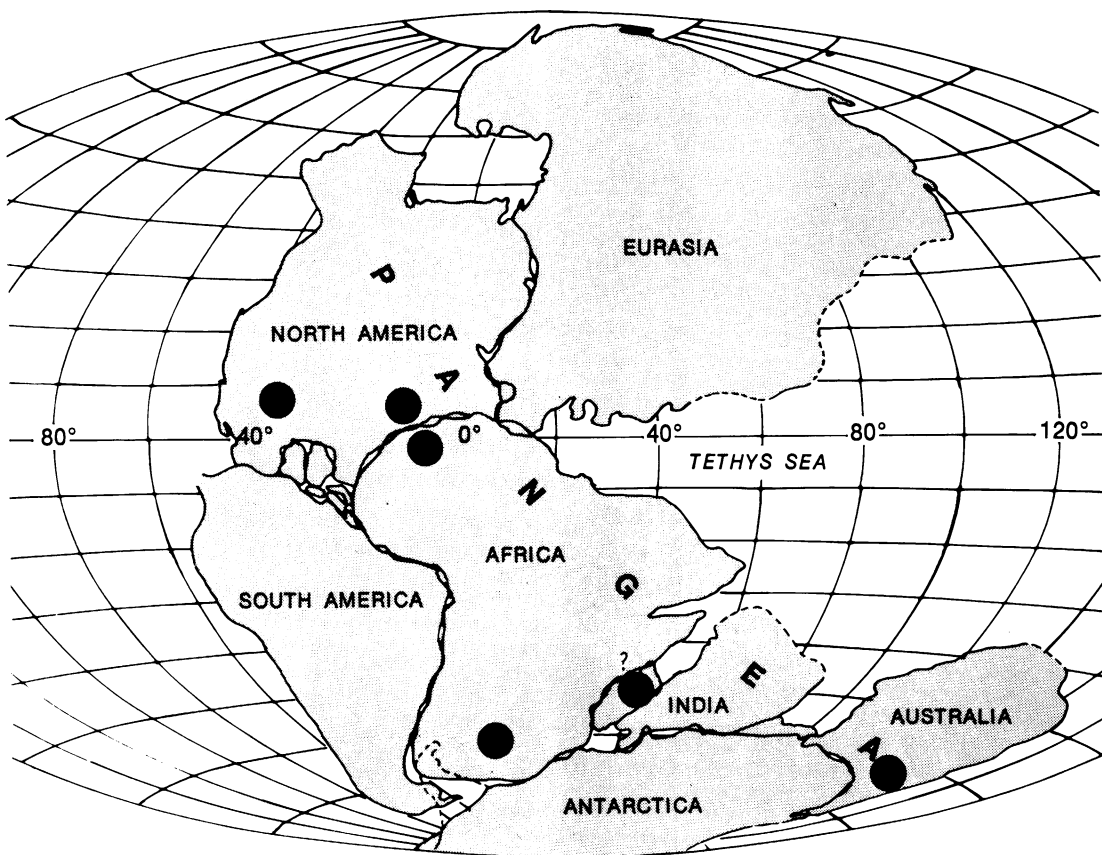


FIG. 7. Redfieldiiform localities related to a reconstruction of Triassic Pangea (Based on Dietz and Holden, 1970)

successfully sectioned in *Redfieldius* and *Dictyopge* (Schaeffer and McDonald, 1978). True ganoin and dentine layers are present, and both presumably exist in the scales of the other genera. No specialized scale characters have been detected aside from ornamentation that may be meaningful at the generic or specific level. The prismatic structure of the ganoin (Orvig, 1967), which is characteristic of many late Paleozoic and Mesozoic lower actinopterygians, can be observed with polarized light in thin sections of both *Redfieldius* and *Dictyopge*.

CLADISTIC ANALYSIS

It is not surprising in view of our insufficient knowledge of the extinct lower actinopterygians, that it is difficult to designate a more specific sister group for the redfieldiiforms than “some or any other lower actinopterygians.”

On the basis of the previous discussion, however, a possible candidate might be expected to have at least one supraorbital that excludes the nasal bone and the posterior naris from the orbital rim. The suspensorium should be around 40 degrees, with a fairly sharp angle between the horizontal and vertical arms of the preopercular. The cheek should include one or more suborbitals and a dermohyal. As discussed above, the antopercular was probably independently acquired by the redfieldiiforms.

This description of a hypothetical redfieldiiform sister taxon is based on a current review of the dermal bone skull pattern in all extinct lower actinopterygians in which this pattern is adequately known. Although exclusion of the nasal bone and the posterior naris from the orbital rim by an anamestic

supraorbital occurs in *Cheirolepis* (Pearson and Westoll, 1979), *Paramblypterus* (Blot, 1966; Heyler, 1969; BMNH P.607) and the redfieldiiforms, there is no evidence that these taxa are closely related. *Cheirolepis* is a most generalized actinopterygian (Gardiner, in press), and its "anterior suborbital" may have a sarcopterygian homologue. *Paramblypterus* is a derived palaeonisciform-level genus with several specializations, such as the relatively large anterior supraorbital and marginal teeth implanted in deep sockets. It is not closely related to the redfieldiiforms, but it does provide clues about the origin of the redfieldiiform snout pattern.

On the basis of the preceding section, it is possible to recognize (as might be expected) characters in the redfieldiiforms that are synapomorphic for the Osteichthyes, the Actinopterygii, the Actinopteri, the Redfieldiiformes plus their hypothetical sister group, and finally the Redfieldiiformes alone. An additional list has been added before the final redfieldiiform one for characters of uncertain position that are more advanced than those of stem-group actinopterygians.

- A. Osteichthyan:
 - Maxilla fixed to cheek and expanded posteriorly
 - Mandible without coronoid process
 - Clavicle present
- B. Actinopterygian:
 - Generalized, fused braincase with single, vertical hyomandibular facet
 - Parasphenoid with ascending process, but elongated as in more advanced lower actinopterygians
 - Nasal bones separated by rostral
 - "Premaxilla" (premaxilla-antorbital)
 - Boomerang-shaped preopercular
 - Mandibular sensory canal
 - Dermohyal
 - Presupracleithrum (presumably present in at least more generalized redfieldiiforms)
 - Rays of median fins more numerous than basals
 - Scales with ganoin and dentine layers
 - Scales with peg-and-socket articulations
- C. Actinopteran:
 - Basal fulcrum on dorsal margin of caudal

fin (also on ventral margin in *Daedalichthys*)

Fringing fulcrum

- D. Characters present in redfieldiiforms and various other lower actinopterygians that belong to unrecognized groups at some undetermined hierarchical level:
 - Cheek pattern reflecting a more vertical suspensorium than in stem-group actinopterygians
 - Separate postorbital, presumably derived from large "jugal" in stem-group actinopterygians
 - Suborbitals, which are absent in the stem-group actinopterygians
- E. Redfieldiiforms plus hypothetical sister group (numbered characters refer to the cladogram, fig. 6).
 - 1. Nasal bone more or less excluded from orbit by an anterior supraorbital proposed as homologue of the redfieldiiform adnasal
- F. Redfieldiiforms:
 - 2. Distinctive shape and size of "premaxillae" which may be in contact with rostral
 - 3. Separate rostral and postrostral bones
 - 4. Adnasal (?supraorbital) between "premaxilla" and demosphentic
 - 5. Single external naris surrounded by "premaxilla," rostral, nasal and adnasal bones
 - 6. Orbit bordered anteriorly by adnasal and "premaxilla"
 - 7. Antopercular present, possibly representing subdivision of opercular
 - 8. Branchiostegals reduced to one or two platelike bones, probably independently of other extinct lower actinopterygian groups that show the same condition

The characters listed under D also emphasize some of the character distribution problems that clearly involve the redfieldiiforms and other extinct lower actinopterygian groups but cannot be presently resolved. There is, nevertheless, sufficient information about various characters among the extinct lower actinopterygians to propose that the Redfieldiiformes represent a monophyletic group. Although the Redfieldiiformes are still *incertae sedis* among the extinct lower acti-

nopterygians, it is now possible to provide a reasonable description of the hypothetical sister group. The fact that this group has not been recognized supports the conclusion that it is unknown.

The proposed cladogram for the redfieldiiforms (fig. 6) is based on the above deliberations plus the character states listed below that are unique to particular genera or groups of genera.

9. Two pairs of parietals
10. Supraorbital canal reaching the dermopterotic
11. Jaws and tooth rows shortened, maxilla not extended below "premaxilla"
12. Dermosphenotic broadened, rectangular, suture with dermopterotic broad and transverse
13. Antopercular absent
14. "Premaxillae" broadened and relatively shorter
15. "Premaxillae" relatively narrow and recurved ventrally
16. Maxilla further shortened and snout profile lowered
18. Postrostral reduced, nasals meeting anteriorly
19. Supra and infraorbital canals with double row of pores
20. Postrostral absent and nasals meeting throughout their length

I have not found it possible to resolve several polychotomies in this cladogram. The number of parietals in *Atopocephala* and *Schizurichthys* is uncertain (the former is described by Hutchinson (1973, p. 249) with some reservation as having one pair. *Ischnolepis*, *Brookvalia*, and *Phlyctaenichthys* have two pairs. The last two genera are unique in having the supraorbital canals extending into the dermopterotics. *Phlyctaenichthys* alone has four or five suborbitals. Together these genera are the most plesiomorphic of the redfieldiiform taxa in terms of conserving relatively long jaws and a wide gape. One pair of parietals is obviously the primitive actinopterygian as well as the primitive osteichthyan number. Although the parietal number in *Atopocephala* and *Schizurichthys* remains to be confirmed, the presence of two pairs in certain other redfieldiiforms including *Helichthys* is surely a derived condition.

In addition to two pairs of parietals, *Helichthys* has antoperculars, shortened maxillae that do not extend forward under the "premaxillae," and widened dermosphenotics that meet the dermopterotics in a nearly transverse suture. The most economical hypothesis is to regard the extra pair of parietals in this genus as an independent acquisition. Interpreted in this way, *Helichthys* fits neatly between Hutchinson's "brookvaliids" and "redfieldiids." The pattern of the skull roof is clearly of the "redfieldiid" type (fig. 3). *Geitonichthys* and *Molybdichthys*, along with the succeeding taxa, have no antoperculars. Their maxillae are about the same length as in *Helichthys*, and the "premaxillae" are distinctively broad and stocky. *Daedalichthys* and the remaining genera have relatively narrow "premaxillae" that are recurved ventrally. The two branchiostegals and a nearly heterocercal tail are distinctive features (fig. 1C) of *Daedalichthys*.

Although the dermal skull pattern of *Daedalichthys* closely resembles that of the American taxa, the ventral arm of the "premaxilla" is longer and more vertical, and the snout profile is correspondingly higher than in the American redfieldiiforms. I have not been able to resolve a trichotomy consisting of *Cionichthys*, *Redfieldius*, and *Dictyopyge*. All three have four extrascapulars in a transverse row. *Redfieldius* alone has three parietals in a transverse row. *Dictyopyge* (Schaeffer and McDonald, 1978) has the entire front of the skull covered with tubercles, unusually broad frontals, and no dermohyal.

The Moroccan genus *Mauritanichthys* (Martin, 1982), appears to have a reduced postrostral, which suggests that the nasals meet in front of this bone as in *Lasalichthys* (fig. 3M). Few specimens have been found, however, and further confirmation is desirable. *Lasalichthys* and *Synorichthys* are clearly related in having double rows of sensory canal pores that cross triangular parietals to meet the extrascapular commissure (fig. 3N and O). *Synorichthys* is the only redfieldiiform known to lack a postrostral. Its possible absence in *Schizurichthys* (Hutchinson, 1973, p. 385) cannot be confirmed because the snout area of BMNH P.15891 is too poorly preserved.

In general, the hypotheses of relationship

proposed in this character analysis corroborate the cladogram proposed by Hutchinson (1978, fig. 4a) in which he assumes that *Helichthys* is more closely related to redfieldiids than to the brookvaliids. Also, by implication, he relates *Schizurichthys* to the brookvaliids.

CONCLUSIONS

1. The Triassic–Early Jurassic redfieldiiform fishes are part of a large complex (nearly 200 genera) of extinct lower actinopterygians (non-neopterygians) that includes the palaeonisciforms and an array of more advanced groups whose relationships are essentially unresolved.

2. The evidence in favor of redfieldiiform monophyly is based on a survey and an economical interpretation of certain character distributions among the more adequately known extinct lower actinopterygians. As noted earlier, the generally useful characters are limited to those in the dermal skeleton (skull, fins, squamation).

3. The uniqueness of these fishes is demonstrated by a complex of characters mostly in the snout-postorbital region of the skull. These include “subdivision” of the medial rostral bone, exclusion of the nasal bone from the orbit by the enlarged “premaxilla,” loss of the anterior naris, exclusion of the posterior naris from the orbit by the adnasal (?supraorbital) and the “premaxilla,” and reduction of the branchiostegal series to one or two platelike elements.

4. Subdivision of the Redfieldiiformes into the Brookvaliidae and Redfieldiidae (Hutchinson, 1973, 1978) is more or less supported by this cladistic analysis. The problematical *Helichthys* is regarded as the sister taxon of the more derived taxa as arranged in figure 6. At this stage of analysis, however, I can find no useful purpose in recognizing Hutchinson’s families except in a vernacular sense. Although the relationships of the genera within the Redfieldiiformes are based mostly on single characters, no contradictions have been found that might alter the configuration of the cladogram.

5. The problem of discerning the sister group of the Redfieldiiformes is obviously impeded by our insufficient and imprecise

knowledge of the extinct lower actinopterygians. The selection of the palaeonisciforms *Paramblypterus* (Blot, 1966; Heyler, 1959), which was my original decision, has proved to be difficult to substantiate, and its designation as such might be misleading. Nevertheless, the redfieldiiform outgroup must have shared, probably in more generalized form, some or most of the redfieldiiform snout synapomorphies. If this were not the case, it obviously could not be recognized. As *Paramblypterus* does not fill the sister-group role, we may conclude that the latter remains unknown.

6. In order to test the hypothesis of redfieldiiform monophyly, it will be necessary to provide a more detailed and objective analysis of character distributions in the actinopterygians. The recognition of stem-group actinopterygians by Patterson (1982) and Gardiner (in press), plus the redefinition of the Chondrostei by Patterson (1982), are significant steps in this direction. In regard to the relationships of the redfieldiiforms to other extinct lower actinopterygians, most of the characters in Patterson’s recent cladogram (1982, fig. 3B) have not been observed in the redfieldiiforms. However, the robust ascending processes on the parasphenoid and the presence of both basal and fringing fulcra places the redfieldiiforms above the generalized stem-group level, but certainly not within the neopterygians. Furthermore, redfieldiiform scales, as noted above, have prismatic ganoin.

7. Attempts to deal with the historical biogeography of the redfieldiiforms have been thwarted by the absence of cladistic data for other groups of aquatic and terrestrial organisms that occupied some part of Pangea during the Triassic Period. This additional evidence is required to corroborate a particular distributional pattern in terms of separating random from non-random (vicariant) distribution. The fact that the earliest and most generalized redfieldiiforms have been found in Australia and South Africa and the most specialized in North America and Morocco (fig. 7) tells us little about a possible distributional pattern. Redfieldiiforms are still unknown, but not necessarily absent, from the continental Lower Triassic rocks of North America (e.g., the Moenkopi Formation). It

should also be noted that we are concerned here with distribution on a single, great land mass—Pangea. Assuming that the redfieldiiforms were primary freshwater fishes, the distributional barriers would be within the boundaries of this mass and unrelated to later continental movements.

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