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THE ENVIRONMENT AND DISTRIBUTION OF PALEOZOIC SARCOPTERYGIAN FISHES

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ABSTRACT. A survey of available data concerning the environment and distribution of the Paleozoic sarcopterygian fishes shows that, although this group has been thought to have had a strictly fresh-water ancestry, there is considerable evidence that the ancestral stock was either marine or at least euryhaline. However, with the exception of the Coelacanthini, which generally persisted in more saline conditions, the later (Carboniferous and Permian) sarcoptergyians are all fresh-water fishes. The overall pattern of paleogeographic distribution of the Sarcopterygii is complex but offers considerable support for the theory that what are now the North American and Eurasian continents were closely adjoined in Paleozoic times.

INTRODUCTION

The paleogeographical distribution of organisms has long been a subject of close interest to biologists and geologists, often in connection with the question of movement of the continents. While many studies have concerned Mesozoic or younger distribution, the biogeography of Paleozoic vertebrates also offers valuable evidence on this subject. White (1958) in a paper dealing with the possible fresh-water or marine origin of vertebrates pointed out the similarities between Devonian fish faunas on both sides of the North Atlantic. More recently, Dineley (1967) has indicated the presence of members of the same species of Devonian fish in Canada and Britain. Attention is drawn here to an interesting problem (suggested by a previous study (Thomson, 1969)) concerning the distribution of Paleozoic sarcopterygian fishes on the North American and Eurasian land masses.

The Sarcopterygii are an important group of living and fossil fishes. They include the oldest osteichthyan fishes (Early Devonian) and during the Devonian as a whole they were, in both numbers and diversity, the most abundant representatives of the class. They comprise two main groups, the Crossopterygii and the Dipnoi. During the Mesozoic, the coelacanth Crossopterygii underwent a second broad diversification. The rhipidistian Crossopterygii (which gave rise to the Amphibia) became extinct by the Early Permian. Three genera of Dipnoi and one coelacanth survive to the Present. The distribution of living Dipnoi (lungfish), one genus each in Australia, South America, and Africa, has often been cited as evidence for Continental Drift. The living Dipnoi are freshwater forms, but the coelacanth is marine in occurrence.

Latimeria, the living coelacanth, is a marine fish and shows the interesting physiological specialization of maintenance of osmotic balance through urea retention (Pickford and Grant, 1967). The urea is produced via the ornithine cycle (Brown and Brown, 1967). This specialization is known elsewhere only in the elasmobranchs but has probably evolved independently in the two groups. It is interesting, however, that estivating lungfishes (*Protopterus* and *Lepidosiren*) show a similar accumulation of urea in the tissues.

The Sarcopterygii have generally been considered to be primarily fresh-water fishes, evolved from a fresh-water ancestor (see, for example, Romer and Grove, 1935; Denison, 1956). This judgement is based in large measure on the presence in all Osteichthyes of lungs—an accessory respiratory system usually considered to be an adaptation that could only have evolved in fresh water. However, the geological evidence concerning the environments of known fossil Sarcopterygii throws some doubt on the supposed fresh-water origin of these fishes. (This is, of course, not related to the separate problem of the fresh-water or marine origin of the first vertebrates.) Not only do the Sarcopterygii include forms of both marine and fresh-water occurrence, but, as noted below, there are significant differences in the patterns of distribution of these fishes. These differences are of direct relevance to the biogeographic problem because, while marine fishes may be widely distributed around the globe, the dispersal of fresh-water fishes is extremely limited, being restricted to contiguous land masses and often within these to particular drainage systems.

The purpose of this paper is to analyze the available published geological evidence concerning both the environment and distribution of the Paleozoic lobe-finned fishes. Earlier studies on the environment of fossil fishes include those of Gross (1950), Romer (1955), Romer and Grove (1935), Denison (1956), White (1958), and Obruchev and Mark-Kurik (1965). The data used here are drawn from these sources, from the summary account of Lehman (1966), or original observations. In all such work it is difficult to be completely precise with respect to the nature of the original environment (compare, for example, Romer, 1955, and Denison, 1956), and such problems as transport of carcasses after death need very careful consideration. I do not claim any special expertise in this regard, having drawn my data almost entirely from published sources. Many deposits yielding fossil sarcopterygians are of relatively unequivocal nature; for example, the Upper Devonian Scaumenac Bay locality in Canada, the British Devonian localities, Spitzbergen, and East Greenland. I have taken the data on Asia from Gross (1950), Obruchev and Mark-Kurik (1965), and Vorobjeva (personal commun.). The records from continental Europe have been reviewed by Lehman (1966) whose assessments are followed here. For the North American record I have followed Romer and Grove (1935), except as modified by Denison (1956). In the summary of data (table 1) occurrences are classified as "marine" or "fresh water" where the evidence seems conclusive and "intermediate" in other cases (such as estuarine or lagoonal conditions). It is unlikely that full agreement on these matters is yet possible. However, I believe that the conclusions reached from these data have solid status as generalities.

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DISCUSSION

Table 1 is a survey of the environment and distribution of the Sarcopterygii. We must bear in mind, in attempting to interpret these data, that, even at the generic level, identification of fossil fishes may be only tentative. We should be particularly cautious in the case of the dipnoan "genera" *Dipterus, Conchodus, Ganorhynchus,* and *Paleadaphus* and in any case where identification is based on isolated elements such as tooth plates or scales. Also, collections from North America and Eurasia can scarcely be considered complete. For example, the lack of records of Devonian osteolepid Rhipidistia and Coelacanthini from North America certainly affects our analysis of the distributional pattern of these groups and may not reflect an original situation. Due to the very small fauna and the fact that much material remains undescribed, Australia is not included in this discussion. We may note here that at present no genera are described that are unique to Australia and the Antarctic (but see below, Distribution).

We may consider the two main problems—environment and distribution—separately.

Environment.—Of twenty-nine genera of Rhipidistia (fig. 1), there appear to be none that are wholly marine in occurrence, but at least nine genera have representatives in both fresh-water and marine, or fresh-water and intermediate, deposits. More striking is the fact that of the eleven genera from Early or Middle Devonian deposits, seven occur in saline as well as fresh-water conditions. Of nine genera of Paleozoic coelacanths (fig. 1), five are wholly marine, and two more are of mixed occurrence. Of the twenty-seven Dipnoi (fig. 1), eight are fully marine, and two more are of mixed occurrence. As in the case of the Rhipidistia, none of the Carboniferous and Permian forms are of marine or intermediate occurrence. Only nine of the twenty Devonian dipnoan genera are solely from fresh-water deposits. Summing all lineages, of fifty Devonian sarcopterygian genera, twenty-four are found in saline conditions. Of all lines, nine out of thirty-three North American genera and twenty-five out of forty-three Eurasian genera occur in saline conditions.

In view of the fact that the lobe-finned fishes are widely considered to be primarily fresh-water forms, the proportion of non-fresh-water forms, especially in the Devonian, is surprising. The contrast is emphasized if the earliest forms are censused separately. Of nineteen genera of Sarcopterygii occurring in Early or Middle Devonian deposits, only seven (four rhipidistians and three dipnoans) are known solely from

Table 1

Summary of data on environment and distribution of Paleozoic Sarcopterygii. The genera marked with a single asterisk have been reported by Lehman (1966) as occurring occasionally (as isolated scales) in marine conditions, but in all probability this represents secondary transport of the materials. The genera marked with a double asterisk are only tentatively identified (see text). Abbreviations used: LD, MD, UD–Lower, Middle and Upper Devonian, C–Carboniferous, P–Permian, M–marine, FW–fresh water, I–intermediate conditions. For detailed information concerning the geographical occurrence of individual genera the reader is referred to the source literature listed in the text and to the summary by Obruchev and Vorobjeva (1966).

Age	Fish	NAm	Eur	As	Gr	Spz
Rhipidistia						
LD-MD	Porolepis		M-F	M		F
MD	Canningius				F	
	Gyroptychius		M-F			
	Hamodus		F			
	Thursius		M-F			
	Tristicopterus		F			
MD-UD	Glyptolepis	I-F	M-F	F	F	F
	Glyptopomus	F	F			
	Holoptychius	M-F	M-F	F	F	
	Latvius		M-F			
	Osteolepis		M-F	F		
UD	Bogdanovia			F		
	Callistiopterus	F				
	Eusthenodon	F	F		F	
	Eusthenopteron	F	I-F			
	Hyneria	F				
	Laccognathus		I-F			
	Litoptychius	F				
	Megistolepis				F	
	Panderichthys		F			
	Platycephalichthys		F			
	Pseudosauripteris		F			
	Sauripteris	F	F			
	Thaumatoplepis			F		
C	Rhizodopsis	F	F*			
	Rhizodus	F	F			
C-P?	Megalichthys	F	F*			
P	Ectosteorhachis	F				
	Lohsania	F				
Coelancanthini						
MD-UD	Euporosteus		M			
UD	Chagrinia	M				
	Devonosteus		M			
	Dictyonosteus					F
	Diplocercides		M			
	Nesides		M			
C	Rhabdoderma	M-F	M-F			
C-P	Coelacanthus		M-F			
P	Spermatodus	F				

TABLE 1 Continued

Age	Fish	NAm	Eur	As	Gr	Spz
Dipnoi						
LD	Uranolophus	F				
LD?	Melanognathus	F				
MD	Dipnorhynchus		M			
	Pentlandia		F			
LD-UD	Dipterus**	M-F	M-F	M-F		
MD-UD	Conchodus**	M	M			
	Ganorhynchus**	I-M	I-M			
UD	Chirodipterus		M			
	Fleurantia	F				
	Griphognathus		M			
	Holodipterus		M			
	Jarvikia				F	
	Oervigia				F	
	Paleadaphus**	M	M			
	Rhinodipterus		M			
	Rhynchodipterus		F			
	Phaneropleuron		F			
	Scaumenacia	F				
	Soderberghia				F	
	Sunwapta	M				
C	Ctenodus	F	F			
	Tranodis	F				
	Uronemus	F	F			
C-P	Conchopoma	F	F			
	Proceratodus	F				
	Sagenodus	F	F			
P	Gnathorhiza	F	F(Triassic)			

fresh-water deposits. In contrast, of fifteen post-Devonian genera, only two (both coelacanths) occur in saline conditions. The available geological evidence seems to indicate quite clearly that the early lobe-finned fishes had a tolerance of salt water, that a majority of the known earlier forms actually lived in waters of high salinity, and that the vast majority of the Carboniferous and Permian forms were restricted to fresh waters. Only in the Coelacanthini did the main course of evolution continue in saline conditions. There are two principal alternative explanations of this situation: either (1) the Sarcopterygii evolved from a marine or euryhaline stock, and the Rhipidistia and Dipnoi progressively became more restricted to, and adapted for, life in fresh waters; or (2) the Sarcopterygii evolved from a fresh-water stock that was able early to adapt to more saline conditions and enjoyed a small radiation in such conditions in the Devonian (continued by the Coelacanthini) before returning to more completely fresh-water conditions. Because marine and "mixed" forms are found in all three lines of Sarcopterygii and a similar physiological adaptation—urea production via the ornithine cycle and urea retention—occurs in both coelacanths and dipnoans as a device to avert excess water loss to the environment. I am inclined to consider the first alternative the more likely. For further consideration of the evolutionary significance of the nitrogen metabolism of Sarcopterygii, see Thomson (1969).

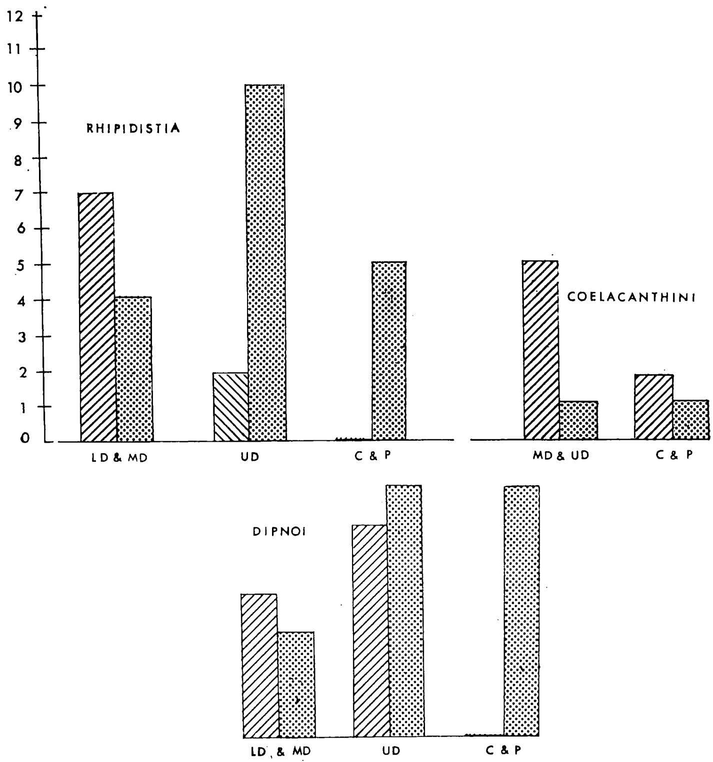

Fig. 1. Histograms showing relative number of genera found in solely fresh-water (stippled columns) or marine and intermediate or "mixed" (diagonal striped columns) occurrence.

Whichever of the two above alternatives is favored, it remains virtually certain that very many of the Devonian Sarcopterygii were tolerant of high salinity. It is therefore possible that some of the forms presently known from fresh-water deposits were anadromous forms, moving between the seas and rivers.

Distribution.—As noted previously, in general, the dispersal of marine or salt-tolerant fishes is likely to be wider than that of strictly fresh-water forms. However, even given the fact that many Sarcopterygii had a high tolerance of saline conditions, the distribution of the Paleozoic genera presents problems. The Devonian record is particularly interesting. There are ten Devonian "genera" with a bi-continental distribution (modern North America and Eurasia). Three of these are wholly fresh-water forms, two are wholly marine, five are mixed. Two of the mixed and both the marine records are unreliable because the generic identifications are highly dubious (see above). There are eleven marine, four mixed, and twenty-two fresh-water genera that do not show a bi-continental distribution. In the Carboniferous and Permian records, all the Rhipidistia and Dipnoi are fresh-water forms, and three out of five Rhipidistia and four out of six Dipnoi have a bi-continental distribution.

While the Australian record is as yet incomplete (see above), it is made up of materials of zoogeographic significance—*Dipnorhynchus* (Lower or Middle Devonian, marine), *"Dipterus"* (Middle Devonian, marine and fresh water), and *"Strepsodus"* (probably Rhizodus, Carboniferous, fresh water). I am confident that there will eventually be found several sarcopterygian genera unique to Australia (such as the "perfect crossopterygian" from the Upper Devonian of New South Wales, mentioned by Hills, 1958), but the total fauna nonetheless shows a basic pattern in common with all other parts of the world.

Dispersal of a wholly fresh-water fish requires contiguous land masses or continuity of river drainages. The wide distribution of the post-Devonian Rhipidistia and Dipnoi (apparently all fresh-water forms) over the present North American and Eurasian land masses seems therefore to accord with the theory that these continents were connected in some way during the Carboniferous and Permian. The distribution of the Devonian forms, on the other hand, is much more complicated. Our interpretation of the general biology of sarcopterygians (Thomson, 1969) suggests that they were virtually all tropical shallow-water fishes, and it may well be that the restricted distribution of marine sarcopterygians in the Devonian reflects this situation. The general fossil record suggests that large areas of what is now eastern North America and western Eurasia (where the principal fossil-bearing deposits are found) were subject to extensive marine incursion during the Devonian, and it is possible that the open water constituted a barrier to the broad dispersal of marine sarcopterygians. Strong latitudinal zoning in the distribution of these fishes (as in modern marine shore fishes, see Ekman, 1953) may also have been involved. However, the fact that the forms found in both mixed and fresh-water conditions are somewhat less restricted in distribution is extremely puzzling and possibly will only be interpreted in the light of further, more detailed, paleogeographic studies. At the present time, it may suffice to indicate the general nature of the problem and to suggest that the distributional patterns of Devonian genera from fresh-water or mixed environments seem also to argue for a relatively close approximation of the North American and Eurasian continents during this period. It would be of interest to extend this type of study to a consideration of the distribution and environment of the early actinopterygian Osteichthyes, although unfortunately many of the interesting early forms are known only from isolated scales, the mechanical and environmental history of which is difficult to decide.

CONCLUSIONS

Our current knowledge of the environment and distribution of Paleozoic sarcopterygian fishes presents a complicated picture involving both fresh-water and salt-tolerant fishes. The fossil record offers strong evidence that the Sarcopterygii evolved from a marine or at least euryhaline ancestor. Salt-tolerance probably played a major role in the distribution of the Devonian genera but, in contrast, the Carboniferous and Permian members of the Rhipidistia and Dipnoi seem to have been strictly fresh-water forms. The coelacanths persisted in the marine environment with occasional invasion of more fresh-water habitats by post-Devonian groups. The distributional patterns of the group, while complex, largely argue in favor of the theory of close association or contiguity of what are now the North American and Eurasian continents in the Paleozoic.

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