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Fish origins—fresh or salt water?

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Summary—There are discussed various general considerations entering into palaeontological study of the problem as to whether the early evolution of fishes took place in fresh or salt water. Opposite conclusions as to the typical habitat of Silurian fishes have been reached by the author and Grove on American evidence, on the one hand, and Gross, mainly concerned with European material, on the other. An attempt is made to reconcile this difference. Part may be due to the very different histories of the two continents in Silurian times. Close examination of the stratigraphy of European fossil fish localities suggests that many deposits which are often regarded as marine are of continental or near-continental nature. It is concluded that the evidence, taken as a whole, points strongly towards fresh waters as the common Silurian fish habitat.

INTRODUCTION

It is generally agreed that the early chordates originated, as in the case of all major animal groups, in the sea. But many of the more ancient geological records of fishes are from sediments of continental type, and the possibility that fish evolved in inland waters was long ago seen as a distinct possibility. T. C. Chamberlin in 1900 noted theoretical considerations favouring a fresh water origin, but failed to give any detailed consideration of the actual fossil evidence. In 1923 MacFarlane (a botanist!) wrote an entire volume attempting to prove the fresh water origin of fishes; but this cannot be taken too seriously as proof of the case, for the argument is a forced one in many regards, and MacFarlane's general attitude is that of the King of Hearts in *Alice in Wonderland*—" Verdict first, evidence afterwards ".

Two decades ago I determined to make a study of at least a considerable body of the available fossil evidence. In this I associated myself with Dr. Brandon H. Grove. My own inclinations at the time were mildly in favour of the hypothesis of a fresh water origin; Dr. Grove (a student of invertebrate palaeontology) favoured, on the contrary, an early marine habitat. Under the circumstances any conclusion, one way or the other, which we could jointly reach, might be reasonably considered as attained in objective fashion. We decided to restrict our study to an attempt to determine the environmental conditions surrounding all fish finds recorded from North American pre-Carboniferous rocks. Our upper time boundary was set for the reason that by the end of the Devonian there definitely existed both fresh and salt water fish faunas and there was no need to go further. We limited ourselves to North America in a belief that the American record would give us a representative sample of the total world assemblage without our being forced to a consideration of European localities—localities with which we were personally unfamiliar and concerning many of which we would have had difficulty in obtaining exact data.

The results of our study (Romer and Grove, 1935) led both of us strongly to the belief that the early vertebrates were continental forms and that Devonian and later marine types had invaded the seas from fresh waters. As summarized in the left-hand column of Table I, all American Silurian finds were indicative of a fresh water environment; during the Devonian, however, there was an increasing trend toward the sea, so that by the end of that period a truly marine as well as a continental fish fauna had been established.

At the time that we were considering the fossil evidence, the same general question was approached from an entirely different direction through the kidney studies of HOMER SMITH; these are to be found summarized in various papers and books by that author (1932, 1936, 1953, etc.); his conclusions are briefly discussed in my text, "The Vertebrate Body" (1955). His studies furnish extremely strong proof that the early history of vertebrates was passed in fresh waters. It is well known that typical vertebrates cannot exist unless their blood and body fluids contain a specific series of salts in a given concentration which is considerably lower than that of sea water. The most generalized type of vertebrate kidney is a structure that functions most especially as a " pump " to rid the body of excess water rather than merely furnishing (as in the case of many invertebrate nephridia) a means for disposal of metabolic wastes.* Such kidneys are found in all fresh water fishes and amphibians. These animals live in an environment where death would ensue, owing to osmotic dilution of the salt content of their blood and body fluids, were not such a " pump " present to rid the body of excess water, thus keeping up a proper salt concentration. Salt water fishes live, on the other hand, in a water medium containing a higher concentration of salt than their body fluids and hence equally dangerous to existence. A marine fish must avoid the danger of becoming too salty in its body fluid content; it may do this either by conserving water or by excreting excess salt, or both. Actually two very different methods are found in the two major groups of marine fishes. Salt water bony fish have solved the problem by (1) the development of salt excretion in the gills, and (2) in many instances by kidney modification which reduces the water outflow. Sharks, in contrast, have retained the " pump " type of kidney present in fresh water forms, but nevertheless prevent excess salinity of the blood by a most unusual specialization—the retention of considerable amounts of urea in the blood, so that blood and sea water are in osmotic balance and hence loss of water through surface membranes (and consequent dehydration) does not occur.

These two contrasting types of marine adaptations are not derivable one from the other; the two can have as a common origin only the kidney type found in fresh water forms. This is, therefore, the ancestral type. Hence the ancestral fishes must have lived in inland waters, and sharks and bony fishes must have independently invaded the sea.

I had hoped, since the time of our earlier publication, to be able on some occasion

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* *Amphioxus* is remarkably similar to the vertebrates in almost every basic feature, and practically every student of vertebrate history agrees that this little marine chordate is closely related, in some fashion or other, to the primitive vertebrates. *Amphioxus*, however, does not have a kidney of vertebrate type, but in contrast has nephridia comparable to those of certain marine organisms quite unrelated to the vertebrates. For this reason SMITH (1953) has felt forced to deny the relationship of *Amphioxus* to the vertebrates—this despite the strong evidence to the contrary seen in almost every other structural regard. This attitude seems to me quite unnecessary; in fact this contrast in kidney structure can be fitted satisfactorily into the assumed history. Although I am not aware of any precise functional study of the *Amphioxus* nephridia, these little organs appear to be (like comparable structures in many other invertebrates) primarily for the elimination of nitrogenous wastes, and not too efficient as eliminators of water. With the invasion of fresh water by the ancestral vertebrates, water elimination in quantity was a basic necessity, and the vertebrate kidney was evolved *de novo* as a water pump. But the kidney can also act as an eliminator of waste, and if nephridia were present in the fish ancestors, they could be done away with in safety once the new kidney mechanism was established. Thus the presence of nephridia in *Amphioxus* need not debar this animal from the vertebrate " family circle ".

to extend our palaeontological study to the European deposits, much richer in Silurian and Devonian fish localities than North America, but had hesitated to do so because of the amount of time it would have taken to familiarize myself with the complex stratigraphic situation involved. To my delight, this topic is now covered in an excellent comprehensive work by GROSS (1950). In this he summarizes the pre-Carboniferous fish faunas of the entire world; since but few finds have been made in continents other than Europe and North America, the major new contribution is his careful review of the numerous and varied European assemblages. As one topic, GROSS considers the fresh *vs.* the salt problem. Although he had previously voiced his belief in a marine origin for fishes (GROSS, 1933, 134, etc.), he nevertheless treats the matter in a properly objective fashion. All finds from each locality are listed by genus or species, his conclusion as to the marine or continental nature of the desposit is stated, and totals for the two environments are computed.

For comparison, I have listed his summarized figures for the Silurian and the three subdivisions of the Devonian parallel to my own in Table I. For the Devonian stages we are in complete agreement. We both find that in the early Devonian, fishes were dominantly continental in habitat, but that there was a strong trend toward establishment of an important marine fauna before the end of the period.

As regards the Silurian, however, there is radical disagreement between our two studies. The American " sample " suggested that Silurian fishes were nearly or completely fresh water in habit, with the first marine invasion taking place only about the beginning of the Devonian. GROSS, on the other hand, believes Silurian fishes to have been predominantly marine; following this, his figures indicate that there was a sharp shift to a fresh water life in the early Devonian and then a strong reverse trend toward the sea.*

It is to a more detailed consideration of the European Silurian record that (following consideration of some general questions) the present paper is devoted. Not so much

Table I

Percentage of forms in seemingly fresh water deposits at successive horizons. Left, ROMER *and* GROVE (1935) *for finds from all North American localities*, right, *for world totals by species as given by* GROSS (1950, *table IV*)

	ROMER *and* GROVE	GROSS
U. Devonian	29	50
M. Devonian	13	64
L. Devonian	77	81
U. Silurian	100	36

* The sharp marine-continental shift indicated by GROSS's figures would be further accentuated if the American finds were excluded and if, as is done by many workers today, the Downtonian and its equivalents were included in the Devonian. In this case, the apparent increase in fresh water fishes from Upper Silurian to Lower Devonian instead of being from 36 per cent to 81 per cent would have been from close to 0 per cent to about 90 per cent!

because of my own limited work on the fossil evidence as because of the seemingly conclusive nature of the evidence from kidney studies, I find it difficult to accept the conclusion to be drawn from GROSS's figures that fishes were entering fresh waters in major numbers for the first time at such a late period in the evolution as the end of the Silurian. Further, I find it difficult on ecological grounds to conceive of circumstances under which a sudden and almost unanimous surge of fishes from the ocean into the streams at the end of the Silurian would be immediately followed by a Devonian reverse migration of nearly as strong an intensity. An inquiry into the nature of the supporting evidence seems warranted. The reader, however, must be warned that this present inquiry lays no claim to the objectivity in treatment which I believe was true of the work in the ROMER–GROVE paper. Our conclusions there favoured a fresh water origin, but were, of course, far from definitive; the evidence for this same conclusion based on kidney structure is, however, of so substantial a nature that I am firmly convinced of its validity and hence find it difficult to believe that the palaeontological evidence truly indicates the opposite conclusion. The present discussion is thus, frankly, an attempt to reconcile GROSS's presentation of the Silurian fauna with the—to me—more probable thesis that the ancestral vertebrates (and hence presumably those of this period) were in the main fresh water forms.*

GENERAL CONSIDERATIONS

There may be noted here certain of the problems and difficulties encountered in attempting to evaluate the environment of early fishes. Most of the factors concerned (to my anguished regret) increase the difficulty of gathering evidence in favour of a fresh water origin.

Paucity of early continental sediments

If we were concerned with Tertiary deposits, a solution might be much more readily attained. From the late Cretaceous onward the fossil record includes not only abundant marine beds but also numerous formations of a definitely continental nature. But, as even an elementary consideration of geologic history would suggest, the continental record becomes increasingly scanty as we travel backwards in time. Period by period, successive cycles of erosion have tended to do away with inland and upland deposits, so that for the older epochs the sediments preserved include very few truly continental beds. The Mesozoic record of fresh water and terrestrial life is a fragmentary one. In the Upper Palaeozoic, extensive continental beds are rare, although they may be preserved in a few relatively stable areas, such as the South African Karroo. Going back to the Lower Palaeozoic, the elapsed time for the operation of diastrophic and erosional forces has been so great that practically no truly continental beds of that age survive today; the record is almost entirely marine. Our knowledge of the possible continental life of the Silurian and older periods is thus

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* It would be unfair to be unduly sceptical of the reality of the " double shift ", salt-to-fresh-to-salt, which GROSS's statistics would indicate, unless the data be broken down into its components. Might it be that this seeming anomaly has no real existence, and that the shift in the statistical totals is caused by changes in abundance of various groups and by the appearance of new groups which alter the total complex of the fauna without themselves changing notably in their environment? If the faunal components in GROSS's Table IV be considered separately, it will be seen that of the major groups present in the Silurian, the ostracoderms (Agnatha), show no reversal of trend. However, the two remaining Silurian groups, the acanthodians and arthrodires which together form a large percentage of the statistical material, show, in GROSS's table, a very sharp reversal.

essentially confined to the inferences which may be drawn from such few marginal deposits, of deltaic and other coastal regions, which have alone survived.

But while the rarity of ancient deposits of typically continental type makes it difficult to establish the presence of fishes in early fresh water, this very condition in itself affords strong support to the fresh water hypothesis. A startling feature of early fish history is the way in which, in late Silurian and Devonian times, one major group after another appears on the scene quite suddenly and yet fully differentiated, with little or no trace of ancestors in earlier deposits. The most reasonable explanation of this remarkable situation is that the early evolution took place in inland waters, and that our dearth of knowledge is due to the dearth of ancient continental sediments.

Importance of negative evidence

Seeing our newspapers filled with reports of murders, robberies, suicides and the like, we sometimes lament the fact that the reader of such journals tends to gain the impression that all men lead lives of violence, whereas in reality nearly all are peaceable citizens leading humdrum lives that are not at all newsworthy. The case of the pre-Devonian vertebrates is quite comparable. Proponents of a marine origin point with pride to the occurrences of vertebrates in relatively small numbers in a limited series of Silurian marine—or supposedly marine—deposits. What is not remarked is the much more important fact that in the vast majority of Lower Palaeozoic marine formations there is not the slightest trace of any vertebrate. Such marine deposits are widespread and highly developed, and frequently carry abundant invertebrate faunas—but no vertebrates.

If the early vertebrates were marine, why are they not commonly found in such beds? A variety of possible explanations has been advanced by proponents of marine origins and may be briefly discussed, seriatim. (1) *Since vertebrates are relatively rare in marine beds, lack of specimens is due to the chances of random collecting.* But this is unsatisfactory; in all post-Silurian periods, vertebrates, although seldom common, are nevertheless found in a great variety of marine beds. (2) *Vertebrates did not evolve until the time when we begin to find them in marine beds.* But vertebrates are known well down in the Ordovician. (3) *Vertebrates were present earlier, but did not develop a hard skeleton until late Silurian times.* But the few known Ordovician vertebrates were already well ossified. (4) *Vertebrates were present in the ancient oceans, but acquired a bony skeleton capable of preservation only when they invaded fresh waters.* This is a rather better argument. One thesis is that there might have arisen on entrance to fresh waters some physiologic condition causing deposition of calcium salts in the dermis. But the armour of ancient ostracoderms and placoderms is of varied and complex patterns, not a mere random deposition of calcium, and later fishes show no sign of physiologic discrimination between fresh and salt water as regards degree of ossification. I have myself aided the argument somewhat by the suggestion (ROMER, 1933) that vertebrate armour was important in defence against eurypterid enemies. Perhaps armour did arise on entrance into fresh water in connection with defence. But unless we believe that bone arose independently a very considerable number of times in the vertebrates, this does not aid the marine argument. And finally, under this sub-topic: if it be argued that presence of bone and fresh water life are correlated in early vertebrate history, claims that most Silurian vertebrates with armour were marine must be abandoned—" one cannot eat one's cake and have it too ".

Although believing strongly in a fresh water origin for vertebrates, I must confess I am surprised, not at the fact that there are a certain number of reports of reputed marine vertebrates from the Silurian, but rather at the fact that, when such reports are carefully scrutinized, there are so few instances of unquestionable marine occurrences. During the Devonian and later periods there were various incursions from fresh water into the sea; similar incursions of ostracoderms may well have occurred earlier. The record suggests that, on the whole, the Heterostraci were a relatively euryhaline group and may have had marine representatives in the Silurian, as appears rather definitely to be true in the Devonian.

Biocenosis vs. *necrocenosis*

Our object is to determine the conditions under which the early fishes lived. Study of the beds in which fossil remains are found does not necessarily tell us this. Habitat in life and place of burial may be far removed from one another. If a cadaver is destroyed by predators, its remains may be buried on the spot. But if the trunk of a dead fish remains intact, gradual decomposition results in buoyancy, and the cadaver may be transported by currents far from its proper habitat before settling to the bottom. The fact that water runs down hill works strongly to the detriment of one advocating a fresh water origin. An inland stream-dweller will tend to be carried down to lower reaches of a river system; forms living in a coastal region may be carried out to sea, with resulting ecological confusion. If fish specimens in a given formation are abundant and well-preserved, a life habitat in or close to the spot where they are found is strongly indicated. If rare and fragmentary, remains in a marine deposit strongly suggest transportation by currents; but whether transportation from another marine locality or from fresh water cannot, of course, be proven.

Identification of fresh water deposits

Marine sediments are frequently identifiable in ready and positive fashion; there is generally an abundance of invertebrates of dominantly marine groups. Identification of Palaeozoic fish-bearing beds as continental in nature is a much more difficult task, for the evidence is essentially negative in nature. Sediments are no sure guide. While limestones are highly suggestive of marine conditions, calcareous deposition may take place in inland waters, but on the other hand shales and sandstones, although presumably derived ultimately from continental areas, have been in large measure deposited under marine conditions. It is only in the case of coarse clastics and conglomerates that continental conditions, or an approach to them, are strongly suggested by sediments. As to the associated fauna, the absence of typical marine invertebrates suggests continental conditions. This does not, however, prove the case, for there are numerous marine areas today in which invertebrates capable of fossil preservation are absent, and there are numerous geologic formations which were obviously laid down in a marine situation and yet contain few or no invertebrate remains. Further, absence of marine fossils in fish beds may be attributed by those advocating salt water environment to diagenetic removal, by solution, of carbonate shells once present. But this argument is one of which one may be reasonably sceptical if used too frequently.

In many Devonian beds which are generally agreed to be of a continental nature we find fishes associated with a sparse fauna including eurypterids, ceratiocarid crustaceans and very little, if anything, else (plant remains of probable fluviatile or terrestrial nature may be present as well). There are various Silurian deposits with a similar assemblage, and in default of evidence to the contrary, it is reasonable to consider them likewise continental in nature.

Need for detailed stratigraphic study

If a geologic formation or group is dominantly marine (or continental) in nature, it is frequently claimed that the fossil forms contained in it at every horizon must be entirely marine (or continental) in origin. Such statements should not be made or accepted without careful consideration of stratigraphic detail and possible facies differences. For example, the early Permian Redbeds of north central Texas in which I have worked extensively, are predominantly continental, with a wealth of terrestrial reptiles and fresh water amphibians and fishes. But it would be absurd for me to make a sweeping claim that all the fossil content of these beds (which includes, for example, a number of cephalopods) is of a continental nature. The deposit is a deltaic one, and from time to time the delta was invaded for a brief period by waters from a sea which lay not far away. When in doubt, it is thus important to know, in the case of such a continental formation, the exact horizon and locality from which a fossil has come before attempting to reach conclusions as to its ecologic position.

The same caution should be observed in the case of fossils contained in a dominantly marine formation or zone—particularly so for fossils of the time under special consideration, the late Silurian, when over much of Europe there was occurring a transition from marine conditions to the continental " Old Red " of Devonian times. We are dealing with " Passage Beds ", tending toward and reaching deltaic conditions, where fluctuations of a very minor nature could readily cause alternations of salt and fresh water environments. Close examination of stratigraphic detail is requisite if the truth is to be sought for.

Fresh and brackish water invertebrates

Most invertebrate palaeontologists working in the Palaeozoic are dealing with marine faunas, and hence generally tend to assume, unthinkingly, that all Palaeozoic invertebrates are unquestionably marine. This was obviously not the case; there is an acknowledged, if small, fresh water fauna of invertebrates in the Carboniferous, and there is every reason to believe, on theoretical grounds, that at whatever earlier date a basal plant food supply had been established, an invertebrate fauna would have soon evolved to occupy this ecological niche. Before the close of the Devonian a continental flora of rather advanced and diversified nature was present. This must have had an antecedent history of some length. It is not necessary, however, to wait for the development of land floras to establish a fresh water biocenosis, and it may well be that fresh waters may have contained, as far back as the Cambrian, at least, a basal element in a potential food chain in the form of simple algae.

Two problems, among many, which must be " solved " by any type of animal which attempts to leave the ocean and avail itself of the opportunities offered by a life in fresh waters, are: (1) physiological adaptations to counteract dilution of body liquids (with resulting death) in non-saline waters, and (2) some method—preferably active locomotion—for maintaining the population in an inland environment and preventing adults or young from being carried downstream, back the ocean.

The modern fresh water invertebrate fauna is relatively sparse as compared with that of the ocean, but contains a considerable variety of types. As would be expected, sessile forms, and those with relatively poor locomotor ability, such as sponges, coelenterates, bryozoans and brachiopods are rare or absent; the molluscs, however, have achieved success by means of highly specialized modifications of developmental processes. More common are active-swimming bilaterally symmetrical forms including (in addition to fishes) a variety of members of the worm phyla and, most especially, diversified crustaceans, mainly phyllopods, cladocerans, copepods and ostracods. In addition to truly fresh-water assemblages, there are, of course, a variety of other invertebrates derived from both marine and inland faunas which are euryhaline, able to live in brackish water deposits of the sort which may be encountered in estuarine and deltaic regions (cf. O'Connell, 1916, 70–76).

Although it seems certain that a fresh-water invertebrate fauna containing elements analogous to those present today was developed at an early stage, little attention has been paid to this subject by invertebrate palaeontologists. As in recent times, however, most of the forms present would probably have been soft-bodied, and hence not likely to be fossilized, or of small size and hence liable to escape observation. In the Devonian and Silurian fish-bearing beds which are reasonably suspected of being of fresh-water origin recorded invertebrates are few in number. There are occasional reports of lingulids, *Leperditia* and a few other forms which may indicate a brackish layer or a brief incursion of salt waters. Two invertebrate types, however, occur time after time with fishes—ceratiocarids and eurypterids. It may be reasonably claimed that they are fresh water in habitat or are euryhaline forms which were able to inhabit, with fishes, fresh water streams into which typical marine life could not extend.

The ceratiocarids are small crustaceans, apparently of phyllopod affinities, which have attracted little scientific attention. Study of them from an ecological point of view should prove interesting. *Dictyocaris* is another phyllopod which has a distribution likewise suggestive of fresh waters (Størmer, 1934).

The eurypterids are the one group of Palaeozoic invertebrates which exhibit such distinctive features in their apparent ecological surroundings that students of invertebrate palaeontology have had to hesitate, at least, in their habitual tendency to claim a marine environment for all fossils. The eurypterid environmental picture is comparable in many ways to that for the older fishes, but with somewhat less evidence for fresh water habitats. We can here but briefly note the main points in the discussion; among the major papers concerned are those of O'Connell (1916), Pompeckj, Versluys and other discussants in a 1923 symposium, and Ruedemann (1934, etc.); a recent resumé is that of Prantl and Přibyl (1948, 108–111). Eurypterids are most abundant in the Silurian; they are rare earlier, and although surviving until the Permian become increasingly uncommon from the Middle Devonian onward. The post-Silurian forms are definitely fresh water, and these, together with certain of the Silurian finds, are often associated with fish faunas which likewise appear to be fresh water in nature. In the Silurian, however, the eurypterids occur in a number of situations in which the evidence for a fresh-water habitat is far from certain (as the " water limes ") and, further, are present to some degree in beds of definitely marine nature. As Prantl and Přibyl note, the " almost universally accepted opinion " today is that the eurypterids were fresh water organisms throughout their history. It appears to be rather generally accepted that occurrences of eurypterid remains in deep water deposits, such as graptolitic shales, are due to necrocenosis, the floating outward of cadavers or shed armour. But to RUEDEMANN and a minority of other workers, the number of occurrences of eurypterids in lagoonal and near-shore deposits suggests that the older Palaeozoic eurypterids were euryhaline, capable of living in sublittoral and neritic marine environments.

" *No decision?* "

The work on kidney structure and function makes it reasonably certain that fresh waters were the original fish environment. However, it is obvious from the discussion above, that it is difficult to reach a positive confirmation of this conclusion from palaeontological studies, no matter how carefully conducted. Additional points are sometimes advanced which tend towards the discouraging conclusion that attainment of palaeontological proof is not only difficult but perhaps impossible.

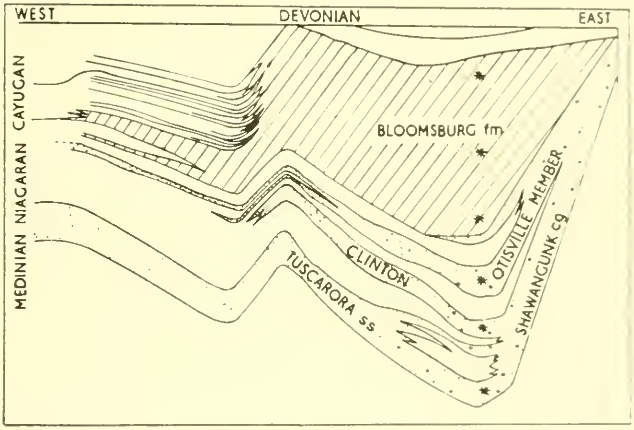

Fig. 1. Diagrammatic east–west section through the Silurian of Pennsylvania, showing the transition from sediments of continental type at the east to an essentially marine section at the west. Known Silurian vertebrate occurrences are all in the eastern continental region, and although not confined to a single area, are here shown in approximately their vertical and horizontal position. Conglomerates and sandstones stippled; redbeds (essentially continental) hatched; limestone and other typical marine beds unshaded. (Modified from Moore; data from C. K. and F. M. SWARTZ.)

It may well be, for example, that the available material of early fishes is too late in date to be of great value. We have little evidence to go on before very late Silurian days, while the Ordovician scrap material shows that ostracoderms were well developed by the middle of that period and probably originated at a much earlier time. There may, therefore, have been considerable ecological shifting between streams and sea by Silurian times, so that evidence from that period may have little meaning in terms of truly primitive vertebrate environments. Again, it is possible that Silurian fishes may have been to a considerable degree euryhaline in nature, with an ecologically cosmopolitan range; if such were the case, a distributional study would be meaningless. Still further, ontogenetic development must be considered. As WESTOLL (1945) has pointed out, it is probable that young ostracoderms had little or no armour, and hence cannot be found under normal conditions as fossils. In consequence we cannot tell where these " fry " lived; they may have stayed in the same environment throughout their lives, or may have migrated from salt to fresh waters or vice versa at the end of the larval period.

These are discouraging thoughts. But despite them, I feel it is nevertheless profitable to follow the known evidence as far as it can lead us.

THE EUROPEAN SILURIAN RECORD

We now come to the specific problem under discussion—the fact that, while the North American Silurian fish fauna, although limited in extent, includes a series of finds extending over the greater part of the duration of the Silurian which is almost purely fresh water in apparent origin, the European record of fishes is confined almost entirely to the closing phases of the period and, according to GROSS's interpretation, is dominantly marine in origin. How can these contrasts be reconciled?

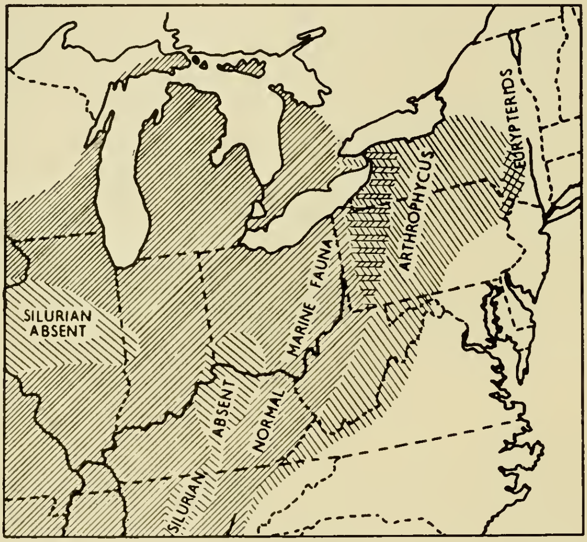

Fig. 2. A map of the north-eastern United States area in Lower Silurian times to show the distribution of some major faunal elements. The midwestern region was one of typical marine conditions, with limestone deposition dominant. Farther east, toward the presumed land area, is a transitional zone with few fossils except the problematical *Arthrophycus*. The most easterly zone in which Silurian sediments are preserved is a seemingly continental deposit of conglomerates and sandstones with a eurypterid-fish fauna. (From AMSDEN.)

Part of the differences may be readily accounted for if we review the differences in the Silurian history of the two areas. In North America, as may be seen from the summaries in any standard text (as, for example, MOORE, 1933, 159–177) the Mississippi Basin region was occupied throughout the Silurian by a sea. Along the eastern border of the present continent, however, there is believed to have been an area or areas of high land—the land mass of " Appalachia ", or an island chain. Throughout nearly the length of the Silurian period materials from this region were carried westward, to be deposited along the sea margins as conglomerates, sandstones and—particularly in late Silurian times—red shales. The gradual lateral change in sediments from eastern deposits dominantly continental in nature to western marine shales and limestones is well illustrated in the east-to-west section of deposits in Pennsylvania shown in Fig. 1, and the palaeogeography of the Silurian as a whole is well exemplified by the map for the early part of the period given by Amsden (1955) and reproduced in Fig. 2. The known vertebrates are present only in the most eastern and more definitely continental formations; there is no trace of any vertebrate in the marine beds to the west. This situation is in perfect agreement with the theory that the centre of distribution of the vertebrates of that day lay in fresh waters.

In Europe, the Silurian geologic story is in strong contrast with that of North America. For most of the period much of Europe was occupied by a widespread ocean, in which were perhaps a few small islands; the shores of this ocean lay far to the north and east (Fig. 3). Toward the end of the Silurian, however, the oncoming of the Caledonian Revolution brought about an advance of the shore-line to the south, over the areas indicated by cross-hatching on the map. This brought about the development in Downtonian times of beds of nearshore, estuarine and deltaic nature, leading to the characteristic Devonian continental deposits of " Old Red Sandstone " type. It is in this area of advance of the shore-lines and oncoming of continental conditions that nearly all of the European Silurian fish-bearing deposits, indicated by figures on the map, are to be found. The late appearance of fishes in the European Silurian is thus closely correlated with the late appearance of " transitional " or truly continental beds in which remains of fresh-water dwellers would be expected.

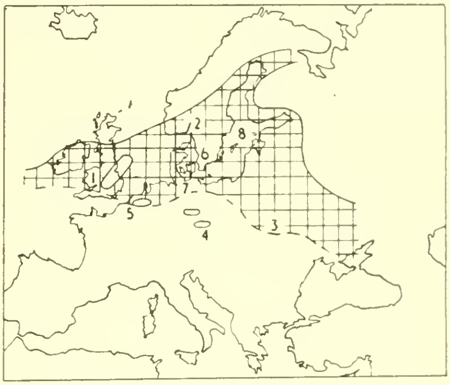

Fig. 3. Map of Europe to show changes in land–sea relations in late Silurian times. At the end of the Middle Silurian much of Europe was covered by a sea. Its northern shoreline (full line) is believed to have run along the northern part of the British Isles to central Scandinavia and then south-eastward through Finland and central Russia: islands are believed to have existed in England, in the region of the present Belgian coast, and in Saxony and Bohemia. By the end of the Downtonian, continental conditions had extended southward over much of northern Europe (cross-hatched area). The Silurian vertebrate localities (numbered) all lie within the area of advance of continental sediments or close to the island areas. (Modified from Born.)

Of the deposits numbered on the map, numbers 1 and 2 are recognized by Gross as continental. The remainder are considered by him as definitely marine. Let us briefly review the stratigraphic evidence concerning these deposits to test the validity of such a conclusion. In doing so, I will restrict discussion to the materials considered in GROSS's paper. As he has done, we will here include the Downtonian as part of the Silurian, although recognizing the growing tendency on the part of many stratigraphers to include it in the Devonian.

1. *Great Britain*

In Great Britain (JONES, 1929; KING, 1934, etc.) the Silurian was for most of its duration a time of marine deposition (Valentian, Wenlockian), and in correlation with this there are no vertebrates recorded until fairly late in the period. The upper Silurian Ludlow beds are likewise marine, but there are a few records of fragmentary vertebrate remains; English stratigraphers generally agree, however, that these are " strays " floated out from the shore-line of the advancing land areas at the summit of the Ludlow.

Vertebrates first appear in numbers in the famous Ludlow Bonebed, marking the arrival of continental conditions and the transition to the Downtonian. This last is obviously a deltaic formation. There are occasional eruptions of brackish to salt waters (as indicated by the presence of *Lingula*, etc.), but essentially it is a fresh-water deposit, with a paucity of invertebrates and a diversified fish fauna. As in many other Silurian and early Devonian continental deposits, the fishes are accompanied by eurypterids and ceratiocarids. The British record is thus consistent with beliefs as to the general fresh water nature of early fish faunas: fishes appear only as continental conditions are approached or reached.

2. *Norway*

Here again the fish record is clearly one indicating a fresh-water habitus. The Norwegian Silurian is restricted in area, and found mainly in the Oslo fiord region, as at Ringerike (KIAER, 1908, 1924; HEINTZ, 1939). In Norway, marine Silurian beds are, as in England, succeeded by continental " redbeds " comparable to the English Downtonian but possibly somewhat earlier in age. In these beds typical marine fossils are absent; as usual, the vertebrates are accompanied by eurypterids and ceratiocarids. There are no vertebrates in the marine part of the section; fishes appear when continental deposits appear.

3. *Podolia*

The late Gotlandian and " Passage Beds " of Podolia contain a considerable fauna of vertebrates—about 24 types, described by ZYCH (1927), BROTZEN (1933 A, 1936), and STENSIÖ (1944)—which are similar to those of the continental Downtonian. However, there is a considerable marine fauna in the Podolian beds as a whole, and hence these forms are classed by GROSS (46–49) as marine.

Let us, however, examine more closely the stratigraphic situation as described by KOZLOWSKI (1929, 1–23; more recently summarized by SAMSONOWICZ, 1950, 499–503). KOZLOWSKI distinguishes three successive Silurian stages. The lowest, the Skala stage, has a good marine invertebrate fauna; no vertebrates are present. In the second, Borszczów, stage there is likewise a good marine fauna. There are no reports of vertebrates except that BROTZEN (1936) mentions that indeterminate acanthodian scales have been found. The fish remains are thus almost entirely confined to a final stage, the Czortków, which is many ways comparable to the Downtonian, and is succeeded by typical continental Old Red deposits. KOZLOWSKI cites a considerable marine invertebrate fauna from the Czortków as a whole, but we should not jump to the conclusion that the fishes are intimately associated with this fauna. To cite (in translation) KOZLOWSKI's description (1929, 14) of the Czortków, in part: " In the lower beds . . . the fauna is composed mainly of brachiopods, tentaculites, little ostracods and pelecypods. In the upper beds . . . the tentaculites and the brachiopods diminish progressively in number, while the leperditiids and the fishes become more and more numerous. Finally, in the terminal beds . . . the brachiopods are very rare (with the exception of lingulas), the fauna being principally made up of ostracods, among which the leperditiids dominate, filling entire beds, and of fishes; here one also finds fragments of *Pterygotus.* This difference between the fauna of the lower part of the stage and that of its upper part has been remarked on by most of the authors occupying themselves with the Silurian of Podolia. . . . However, the passage from one fauna to the other occurs in a gradual manner, and certain species characteristic of the first continue in the second until its disappearance. . . . This underlines the unity of the Czortków fauna from its commencement until the moment when continental conditions have invaded the marine basin and put an end to its existence."

KOZLOWSKI further states, *in litteris:*

" Dans l'étage de Czortków, en allant de sa base vers le sommet, on constate un développement de plus en plus accentué du facies schisto-gréseux. Ce que BROTZEN appelle ' Uebergangsschichten ' et ' Schichten mit grünen Sandsteinen ' correspond à la partie supérieure de la série de Czortków qui est séparée de sa partie moyenne par un épais banc de grès micacé. A partir de ce banc les grès et schistes dominent de plus en plus sur les calcaires à faune marine, ces derniers ne formant que de minces intercalations dans la série schisto-gréseuse. Il me semble qu'on y a à faire à un empiétement de plus en plus accentué du milieu continental sur le milieu marin. Et il est significatif qu' à ceci correspond un enrichissement progressif des sédiments en restes de Vertébrés, surtout de Ptéraspidés. Aujourd'hui—toutes mes notes ayant disparu pendant le guerre—je ne saurais dire si ces Vertébrés se rencontrent seulement dans les couches de schistes et de grès ou s'ils se présentent également dans les intercalations calcaires à faune marine. Quoiqu'il en soit on a l'impression que leur présence dans le série de Czortków est essentiellement liée aux avancements périodiques des dépôts deltaïques dans le domaine marin. On y observe aussi que dans les intercalations marines, en allant du bas vers le haut de la série, les Brachiopodes sont progressivement remplacés par les Lamellibranches et surtout par les Ostracodes."

No extensive comment is, I think, needed. We have here an excellent example, in an area towards and over which continental Old Red deposition was advancing, of a transition from typical marine beds to brackish, presumably estuarine deposits, and to continental redbeds, much as in England or Norway. As in those countries, fishes appear in numbers only as continental conditions are approached. Far from indicating a marine fish habitat, the Podolian situation strongly supports the thesis that fresh waters were the centre of Silurian vertebrate life.

4. *Bohemia*

We are here beyond the limits of the Downtonian advance of continental deposits from the north, but it appears that although much of Bohemia was covered by seas during the Silurian, there was present here an island area (cf. Fig. 3) which was the nucleus from which a larger land mass emerged in Devonian times. The Bohemian

Silurian includes " Bandes " Ee_1, Ee_2, and Ff_1 of Barrande, termed eα, eβ and eγ by KETTNER and KODYM (1919) and BOUČEK (1934). A certain amount of fish material is present which, as GROSS notes (1950, 64–65), is as yet insufficiently described. GROSS states that the beds containing fishes are " all of purely marine origin " and hence counts all the Bohemian fish as part of his Silurian marine assemblage. A closer examination of the actual sequence, however, suggests a somewhat different interpretation. The stratigraphy has been most recently reviewed by PRANTL and PŘIBYL (1948, 67–73). Zones eα and eβ, which cover most of the extent of the Silurian, appear to be typically marine. There are no described fish except for one and possibly two spines of *Onchus*, with one of which some scales are associated; these are most reasonably regarded, like the equally rare fragments in the English Ludlow and in the Borszczów of Podolia, as strays from the adjacent land area.

In eγ, the " Lochkov Limestones " there is a diversified fish fauna, although specimens are not abundant. Much of the Lochkov exposures show a typically marine reef facies; the fish, however, occur instead in a shaly facies in which a series of successive zones are present (PERNER, 1918 A, 1918 B; PERNER and KODYM, 1919, 1922; PRANTL and PŘIBYL, 1948, 73). This facies is stated to be limited chiefly to a seam in the Radotin Valley between Prague and Kosor. The fish described by PERNER occur in the lowest zone. PERNER and KODYM (1922, 67) state that in this zone " other fossils are also rare "; since they give detailed faunal lists of invertebrates from all other Silurian horizons but name no invertebrates from this zone, it would seem that any non-vertebrate material present is inadequate to give evidence regarding ecological conditions. Following the fish zone is a layer of black bituminous limestones with thin intercalated shales, the lower part of which contains eurypterids and ceratiocarids but no other fossils. Above this, the remainder—and greater part—of the shaly facies contains typical marine invertebrate assemblages.

We have, thus, in the lower zones of the shaly facies of the Lochkov the familiar story of fishes, eurypterids and ceratiocarids with little or no indication of a marine invertebrate fauna. Far from indicating a typical marine environment for the Lochkov fishes, the evidence strongly suggests that their place of entombment was a near-shore and possibly deltaic deposit.*

5. *Pas-de-Calais*

A second " island " region, independent of the advance of the main Downtonian continental shore-line, is that of the Pas-de-Calais region of northern France. Here, LERICHE (1906) has described from the late Silurian or Downtonian of pit number 6 of the Liévin mining company of Pas-de-Calais two species of Heterostraci which GROSS appears to include in his marine list. The beds *as a whole* do contain good marine fossils; but LERICHE (18–21) gives the section in detail, as shown below. This definitely

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* Mr. RADVAN HORNÝ, of the Geological-Palaeontological Institute of the Charles University and Dr. FERDINAND PRANTL, Vice-Director of the Národní Museum (Prague), in letters received after completion of this paper, have furnished further information with regard to this situation. They feel certain that these beds are all marine in nature, but that, on the other hand, the fragmentary and isolated condition of the fish remains indicates a necrocenosis, with post-mortem transportation from another habitat—quite possibly, of course, fresh water. It is obvious that the Bohemian fish faunas are of great interest, and it is to be hoped that our Czech colleagues will make a thorough study of them

indicates that the fishes are not associated with the marine invertebrates. The figures given are depths from the surface, in metres:

to 270·70 Typical Old Red sandstone (Gedinnian) with ostracoderms
270·70 to 295·80 Sandstones more drab than those above, micaceous, somewhat calcareous; *Cyathaspis barroisi* at 278–281; no other fossils reported
295·80 to 296·30 Dark blue schistoid sandstone with marine shells
296·30 to 298 Pale grey sandstone with *Pteraspis gosseleti*
298 to 318·20 Dark blue schistoid sandstone with marine shells
318·20 to 331·70 Pale grey sandstone with *Pteraspis gosseleti*; a bonebed at base
331·70 to 350 Dark blue schistoid sandstone with marine shells
350 to 473 Marine beds of Ludlow age, with *Dayia navicula*, etc.

The section here is clearly comparable in its general nature to a typical English section—first marine Ludlow beds; then " Passage beds " in which final marine phases alternate with non-marine ostracoderm layers, including an initial bonebed; these are followed in turn by a typical Old Red sandstone of continental type.

6. *Scania*

The remaining European vertebrate localities are from the Baltic region. There are here excellent Silurian sections in the main typically marine in nature. As was true both to the north and west in Great Britain and Norway, and to the south in Podolia, we are in a region in which there was a change from marine to continental deposits at about the end of Silurian times. But although it is probable that typical " Old Red " deposits were formed in this area, none is preserved, and in consequence we are left to interpret the story from decapitated Silurian stratigraphic columns from which the terminal Old Red has been secondarily removed. Although the island of Gotland is the classic locality for study of the Baltic Silurian we shall use that of adjacent Scania instead, since but a single vertebrate specimen (not mentioned by Gross) has been found in Gotland, whereas Lehman (1937) has described numerous scales, spines and other fragments from Scania.

In Scania we find a Silurian sequence comparable in nature to those we have described in other regions. For most of its vertical extent the Silurian is purely marine in nature, including *Rastrites*, *Cyrtograptus* and *colonus* stages covering the Valentian and Salopian. The last is succeeded by the Öved-Ramsåsa stage, generally equated with the Downtonian. As Born notes (1926, 160), this stage contains few invertebrates. " Es handelt sich hier um eine typische verarmte Fauna der Übergangsschichten, die zum kontinentaler Old Red überleitet." The Öved-Ramsåsa is composed mainly of coarse clastics. Limestone is found only in the lowest of four zones; it is followed by barren white and yellow sandstones; then by grey-blue clays containing fishes and eurypterids and also a variety of invertebrates; finally by red sandstones containing nothing but *Lingula* and ostracods. The Öved-Ramsåsa is, thus, ecologically a Downtonian type of deposit. It is certainly no more marine in nature than an estuarine–deltaic situation, and even so, the fragmentary nature of the fish remains strongly indicates an upstream origin, with the remains, as Lehman suggests, brought to the area of deposition by currents. As far as I am aware, there are no published data showing the exact stratigraphic relation of the fish scales to the marine fossils contained in the same zone.

7. *The Beyrichienkalk erratics*

Among the numerous glacial erratics of the north German plain, a large percentage are derived from an upper Silurian formation termed the Beyrichienkalk which presumably was once widely developed in the west Baltic region but is now known only from erratics and deep borings (KRAUSE, 1877; ROEMER, 1885, etc.). A percentage of the erratics have yielded scales and other fragmentary fish remains, best described by GROSS (1947). From the nature of the case, the general stratigraphic situation cannot be determined, but the age is certainly quite late Silurian, and a general equivalence to the transitional Öved-Ramsåsa beds is indicated. This is further suggested by such ecological data as can be derived from the erratics themselves. In some cases, as the conglomeratic boulder described by BROTZEN (1933 B), there may be no fossils other than the scales themselves; in other instances the scales are interbedded with invertebrate fossils. The remains are always fragmentary and the situation suggests, as in Scania, transport from a more continental type of habitat into an estuarine or near-shore deposit.

8. *Oesel*

Most famous, most interesting, and most controversial of all Silurian vertebrate deposits are those of the Baltic island of Oesel, Esthonia, famous since the days of EICHWALD, PANDER, SCHRENK and FR. SCHMIDT. The stratigraphy has been reviewed by HOPPE (1931). The lower to middle Silurian beds of Esthonia—the G, H and I stages—are purely marine in nature and, as would be expected, have yielded not the slightest trace of a vertebrate. The uppermost beds are those of the K stage of Oesel. The fauna is particularly interesting from an evolutionary point of view as the only notable vertebrate assemblage in the world which is clearly pre-Downtonian in age. Considered as a whole, K has an abundant invertebrate fauna, and hence GROSS classes the numerous Oesel vertebrates as marine. As is generally the case, however, closer examination casts strong doubt on the truly marine nature of the vertebrate occurrences.

K is divided into four zones. K_1, the Rootziküll–Karmel Zone, is a dolomitic formation which varies considerably in facies both vertically and horizontally. At several horizons in the western end of the island, notably at Rootziküll and Wita, there are layers which carry an abundance of the familiar assemblage of eurypterids, *Ceratiocaris*, and a variety of ostracoderms—mainly cephalaspids with *Tremataspis* as the most common form. In the K_1 zone as a whole only nine species of presumably marine invertebrates are recorded. HOPPE (43) notes that in the *Eurypterus* deposits proper the only definitely marine forms recorded are an *Orthoceras* and very rare specimens of *Favosites* and *Conchidium*; whether these are exactly in the fish-eurypterid layers or merely stratigraphically close to them is not stated by him. O'CONNELL (1916, 143–147), after reviewing the earlier literature on this point says: " In summary, it may be said that the detailed sections bring out the sporadic occurrence of the eurypterids in very thin beds, rarely intimately associated with the typical marine forms which occur in beds above and below the eurypterid marls."

Quite in contrast is K_2, the Padel Zone. Here there is an abundant marine invertebrate fauna, mainly of brachiopods and stromatoporites; forty-five species are listed. It is not surprising to find that eurypterids are unknown and that of fishes there are only isolated and apparently very rare scales of one species of *Coelolepis*.

K_3, the Kaugatoma Zone, is, again, typically marine, with a fauna of forty-one invertebrate species. Eurypterids are absent; fishes are found somewhat more commonly than in K_2, but only in the form of isolated scales of *Gomphodus* and a few spines of the *Onchus* type.

In the K_4 or Ohesaare Zone, exposed only in a very restricted area of the island, we leave the limestone–dolomite formations typical of the lower zones, and find ourselves in a deposit characterized for most of its extent by a rapid alternation between thin limestones, typically crystalline and red in colour, and equally thin clay conglomerates: in a profile little more than 3 metres in thickness HOPPE distinguishes no less than 70 such alternating layers. The situation, as HOPPE notes, indicates that we are very close to the shore-line. There is a fairly good marine fauna in K_4 as a whole, including 34 species of invertebrates. There are no eurypterids. There are, on the other hand, numerous remains of fishes. But nowhere are there articulated specimens, the whole material consisting of isolated scales, spines and fragments of various types, and HOPPE notes that the fish remains are not normally associated with the marine invertebrates, but occur only in bonebeds at three specific horizons.

In attempting to review this interesting Oesel series, the most striking general feature of the story is the fact that the fishes and marine invertebrates are (so to speak) " allergic " to one another. The beds here follow the " rule of thumb " which we have seen to apply in the Silurian in general: *the more abundant the fishes, the fewer the marine invertebrates*, and vice versa. Zones K_2 and K_3 are typically marine, and fish are found rarely and only in fragmentary form; in K_4 invertebrates and fish are both abundant but are not found in the same layers; in K_1 fish (and eurypterids) are abundant and well preserved, while marine invertebrates are rare.

With regard to the scale and spine findings of Zones K_2–K_4, we have a situation comparable to that of the roughly contemporaneous Beyrichienkalk and the Scanian scale-bearing beds farther west in the Baltic. The fragmentary nature of the remains might be attributed to the work of scavengers if these fishes are considered marine or to disintegration during transportation from stream mouths if they are believed to be of fresh water origin. On the whole, however, consideration of the Oesel situation in its entirety seems to me to throw the balance rather strongly towards fresh water origin for these scales and spines.

The critical problem is that of Zone K_1, with its abundant and well-preserved fauna. The assemblage here of fishes, eurypterids and ceratiocarids is one which we have seen repeatedly in Silurian and early Devonian localities which are clearly of fresh water nature, and O'CONNELL would have it that we are dealing here with a fluviatile deposit. I fail to be convinced that this is the case. The conditions of deposition suggest quiet waters, and the presence of at least a few definitely marine invertebrates strongly indicates that, for the beds as a whole, the region certainly lay no farther inland than could be reached by salt tidal waters.

On the other hand, claims that the eurypterid-fish beds are typically marine seem no better founded. The marine invertebrates reported are limited in variety and very limited in numbers and there is no published evidence, as far as I am aware, that they are closely associated with the eurypterids and fishes. Resort may be had to the supposition that the fauna was originally a typically marine one, and that diagenetic processes have removed most of the invertebrates. There has been a process of solution of carbonate shells in at least certain instances in the K_1 Zone, but the known invertebrate forms are adequately identifiable from the moulds remaining; considering the long series of students of these beds, had a richer marine fauna been present, indications of it would surely have been discovered and described. Here, as in other instances, I find myself sceptical—reasonably, I think—of hypotheses which propose diagenetic disappearance of marine invertebrates exclusively in those beds of a series which carry fish.

On the whole, the evidence suggests that the eurypterid-fish beds of K_1 are deposits laid down in lagoons in which *on the average* the water was of low salinity. With this much, I think most students of the subject would agree. From this point onwards advocates of fresh- or salt-water fish origins may reasonably disagree. (1) It may be assumed by those who favour marine origins that the lagoonal conditions were uniformily brackish during the time of deposition of the K_1 beds and that the fishes were marine forms but euryhaline, tolerant enough of brackish conditions to exist here as well as in a normal marine environment. (2) Again assuming uniformity of brackish conditions, fresh water advocates may argue that the fishes of the time were normally inland dwellers but sufficiently euryhaline to descend to brackish waters. (3) A third possibility is that the lagoons were deltaic and fluctuated from time to time in salinity, with the fauna shifting from time to time between one of fish and eurypterids when the waters were relatively fresh, and one with sparse invertebrates replacing them when the salt content increased.

All three assumptions are equally reasonable as far as the evidence from Oesel alone is concerned. I am strongly disinclined to accept the first hypothesis and tend to favour the second, and more especially the third; this not alone because of my admitted prejudice, but particularly because the complete lack, as we have seen, of any comparable fauna of fish of this age in any typical marine bed.

CONCLUSIONS

I have above reviewed all fish occurrences from the European Silurian (and Downtonian) cited by Gross; these include all described pre-Devonian vertebrate finds except for those from the relatively few American continental localities previously studied and a few scattered European finds omitted by Gross or described too late to be included in his review. They may be grouped under the following headings:

(1) From typical marine deposits (as in England, Podolia, Bohemia) a very few rare and generally fragmentary remains, mainly scales or spines, which may most reasonably be regarded as strays.

(2) Finds in beds of Downtonian or " Old Red " facies of transitional or continental type, as in Great Britain, Norway, Podolia, Bohemia and Pas-de-Calais.

(3) Isolated scales and spines from late Silurian Baltic deposits (as the Beyrichienkalk, Scania, Zones K_2–K_4 of Oesel) which are of somewhat questionable nature but on the whole reasonably interpreted as materials drifted out from the advancing shore-line.

(4) The Oesel K_1 fauna of eurypterids and fish, which in itself can be used as an argument for either fresh- or salt-water origins, but when viewed in the light of the whole picture is most reasonably interpreted on the hypothesis of continental origins.

In sum, the European record is in entire agreement with the thesis that the primary home of the vertebrates in Silurian times lay in fresh waters, and adds confirmatory evidence to the proof of fresh water vertebrate origins given by study of kidney structure and function. It is not at all improbable that evidence may be forthcoming that some vertebrates at least were euryhaline or even definitely marine in habitus as early as the Silurian. But unless or until a very considerable body of data of this sort—now lacking—be accumulated, I see no reason for serious consideration of a marine history for the early vertebrates. As I have said on an earlier occasion, " A consideration of selected portions of the evidence might permit of such an interpretation; but examination of the entire body of facts . . . leads unmistakably to the conclusion that the early vertebrates were dwellers in fresh water."

REFERENCES

AMSDEN, T. W. (1955), Lithofacies map of Lower Silurian deposits in central and eastern United States and Canada. *Bull. Amer. Assoc. Petrol. Geol.*, **39** (1), 60–74.

BORN, A. (1926), Das Gotlandium. *In* Salomon, W. *Grundzüge der Geologie*, **2**, 143–193.

BOUČEK, B. (1934), Bemerkungen zur Stratigraphie des böhmischen Gotlandien und seinen Faziesverhältnissen. *Centralbl. f. Mineral.*, 1934, 477–494.

BROTZEN, F. (1933 A), Die silurischen und devonischen Fischvorkommen in Westpodolien. *Palaeobiologica*, **5**, 423–466.

BROTZEN, F. (1933 B), Erster Nachweis von Unterdevon im Ostseegebiete durch Konglomeratgeschiebe mit Fischresten. *Zeitschr. f. Geschiebeforschung*, **9**, 55–63.

BROTZEN, F. (1936), Beiträge zur Vertebratenfauna des westpodolischen Silurs und Devons. I. *Protaspis arnelli* n.sp. und *Brachipteraspis* n.gen. *latissima* Zych. *Arkiv f. Zool.*, **28A** (22), 1–52.

CHAMBERLIN, T. C. (1900), On the habitat of the early vertebrates. *Jour. Geol.*, **8** (5), 400–412.

GROSS, W. (1933), Die phylogenetische Bedeutung der altpaläozoischen Agnathen und Fische. *Palaeont. Zeitschr.*, **15**, 102–137.

GROSS, W. (1947), Die Agnathen und Acanthodier des obersilurischen Beyrichienkalks. *Palaeontographica*, **96A**, 91–158.

GROSS, W. (1950), Die paläontologische und stratigraphische Bedeutung der Wirbeltierfaunen des Old Reds und der marinen altpaläozoischen Schichten. *Abh. deutsch. Akad. Wiss. Berlin. Math.-natur. Kl.*, 1949 (1), 1–127.

HEINTZ, A. (1939), Cephalaspida from Downtonian of Norway. *Norske Vidensk. Akad. Oslo Skr.* I, *Mat.-Naturw. Kl.*, 1939 (5), 1–119.

HOPPE, K.-H. (1931), Die Coelolepiden und Acanthodier des Obersilurs der Insel Ösel. Ihre Palaobiologie und Paläontologie. *Palaeontographica*, **76**, 35–94.

JONES, O. T. (1929), Silurian system. *In:* Evans, J. W. and Stubblefield, C. J., *Handbook of the geology of Great Britain*, pp. 88–127. London.

KETTNER, R. and KODYM, O. (1919), Nová stratigraphie Barrandienu. *Cas. Nár. Musea*, **93**, 48–59

KIAER, J. (1908), Das Obersilur im Kristianiagebiete. *Skr. Vidensk.-Sels. Christ.*, I, *Math.-naturv. Kl.*, 1906 B (2), 1–595.

KIAER, J. (1924), The Downtonian fauna of Norway. I. Anaspida with a geological introduction. *Vidensk. Skr.* I. *Mat.-naturv. Kl.*, 1924 (6), 1–139.

KING, W. W. (1934), The Downtonian and Dittonian strata of Great Britain and north-western Europe. *Quart. J. Geol. Soc. London*, **90**, 526–570.

KOZLOWSKI, R. (1929), Les Brachiopodes gothlandiens de la Podolie Polonaise. *Palaeont. Polonica*, **1**, 1–254.

KRAUSE, A. (1877), Die Fauna der sogen. Beyrichien- oder Choneten-Kalke des norddeutschen Diluviums. *Zeits. deutsch. geol. Ges.*, **29**, 1–49.

LEHMAN, J.-P. (1937), Les Poissons du Downtonien de la Scanie (Suède). Rennes. (*Thèse, Faculté des Sciences de l'Université de Paris.*) 98 pp.

LERICHE, M. (1906), Contribution a l'étude des poissons fossiles du Nord de la France et des regions voisines. *Mém. Soc. Géol. Nord*, **5**, 1–430.

MACFARLANE, J. M. (1923), *The evolution and distribution of fishes*. New York. 564 pp.

MOORE, R. C. (1933), *Historical geology*. New York. 673 pp.

O'CONNELL, M. (1916), The habitat of the Eurypterida. *Bull. Buffalo Soc. Nat. Sci.*, **11** (3), 1–277.

PERNER, J. (1918 A), Vorläufiger Bericht über die Fischfauna des bohmischen Obersilur und die Fossilen verteilung in den F_1-Schichten. *Centralbl. f. Mineral.*, 1918, 318–322.

Perner, J. (1918 b), O rybách z pásma Ff$_1$ (Lochkovské vápence) a vertikálním rozšíření zkamenělin v těchto vrstvách. *Cas. Nár. Musea Cesk.*, **92**, 72–76.

Perner, J. and Kodym, O. (1919), O rozclenení svrchního siluru v Cechách. *Cas. Nár. Musea Cesk.*, 93, 3–19.

Perner, J. and Kodym, O. (1922), On the zonal division and correlation of the Silurian of Bohemia. *Amer. Jour. Sci.*, (5) **4**, 53–72.

Pompeckj, J. F. (1923), Gigantostraca und Scorpionida. *Palaeont. Zeitschr.*, **5**, 319–338.

Prantl, F. and Přibyl, A. (1948), Revision of the Bohemian Silurian Eurypterida. *Rozpravy Stát. Geol. Ůstavu Ceskoslov. Rep.*, **10**, 60–116.

Roemer, F. (1885), Lethae erratica. *Palaeont. Abh.*, **2** (5), 1–173.

Romer, A. S. (1933), Eurypterid influence on vertebrate history. *Science*, (n.s.) **78**, 114–117.

Romer, A. S. (1955), *The Vertebrate Body*. 2nd ed., Philadelphia. 644 pp.

Romer, A. S. and Grove, B. H. (1935), Environment of the early vertebrates. *Amer. Midl. Natur.*, **16** (6), 805–862.

Ruedemann, R. (1934), Eurypterids in graptolite shales. *Bull. New York State Mus.*, **27**, 374–385.

Samsonowicz, J. (1950), The Devonian in Volhynia. *Acta Geol. Polonica*, **1**, 401–518.

Smith, H. W. (1932), Water regulation and its evolution in the fishes. *Quart. Rev. Biol.*, **7**, 1–26.

Smith, H. W. (1936), The retention and physiological role of urea in the Elasmobranchii. *Biol. Rev.*, **11**, 49–82.

Smith, H. W. (1953), *From Fish to Philosopher*. Boston. 264 pp.

Stensiö, E. A. (1944), Contributions to the knowledge of the vertebrate fauna of the Silurian and Devonian of western Podolia. II. Notes on two arthrodires from the Downtonian of Podolia. *Arkiv f. Zool.*, **35A** (9), 1–83.

Størmer, L. (1934), Merostomata from the Downtonian sandstone of Ringerike. *Norsk Vid.-Akad. Skr.* I, *Mat.-Naturv. Kl.*, 1933 (10), 1–125.

Størmer, L. (1935), *Dictyocaris*, Salter, a large crustacean from the Upper Silurian and Downtonian. *Norsk Geol. Tidsskr.*, **14**, 267–298.

Versluys, J. (1923), Die Abstammung und Differenzierung der Gigantostraken. *Palaeont. Zeits.*, **5**, 292–319.

Westoll, S. J. (1945), A new cephalaspid fish from the Downtonian of Scotland, with notes on the structure and classification of ostracoderms. *Trans. Roy. Soc. Edinburgh*, **61**, 341–357.

Zych, W. (1927), Old-red de la Podolie. *Trav. Serv. Géol. Pologne*, **2**, 1–65.