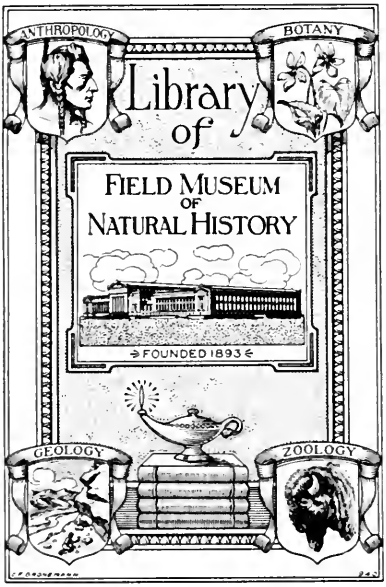
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A REVIEW OF THE HABITAT OF THE EARLIEST VERTEBRATES

ROBERT H. DENISON

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INTRODUCTION

The first reasonably comprehensive and objective study of the habitat of early vertebrates was published by Romer and Grove in 1935. For many years there had been considerable interest in this problem, at first centered around the British Old Red Sandstone fishes, which at the time of their discovery were the oldest known vertebrates. In an influential, purely theoretical paper by Chamberlin, which appeared in 1900, it was concluded that the primitive chordate form was a specific response to stream conditions, and that the chordates arose in this fresh-water environment. Chamberlin's paper is still quoted, although his arguments have been refuted by Berry (1925) and Gunter (1941). A physiological approach to the problem was proposed by Smith in 1932, and, as later developed by him in 1953, has been considered to support the fresh-water origin of vertebrates. The 1935 work of Romer and Grove was largely paleontological; they reviewed all the known North American pre-Mississippian vertebrate occurrences and concluded that early vertebrates were fresh-water forms, some of which later migrated into the seas. Their conclusions are widely accepted today and appear in many geological and paleontological textbooks. Only Walter Gross (1950) has cast some doubt on this theory; after a comprehensive tabulation of all the pre-Carboniferous vertebrate species, he concludes that the sea must be taken into consideration as the original home of Agnatha and Pisces.

My own interest in this problem was aroused during work on early vertebrate faunas when I found that I could not agree with Romer and Grove in specific cases. For some years I have been accumulating information from the literature, and on field trips for Chicago Natural History Museum I have visited most of the early vertebrate localities in North America. In 1953 and 1954 I was able to study in Europe, by means of a grant from the John Simon Guggenheim Memorial Foundation. There I had an opportunity to see collections and visit a large number of fossil localities in Norway, Sweden, and Great Britain. I am indebted to the Guggenheim Foundation, without whose help it would have been impossible to complete this work. I am also indebted to those European colleagues who helped in many ways to make my work abroad simple and pleasant. I wish to thank particularly: Professor Anatol Heintz and Professor Leif Størmer of the Paleontologisk Museum in Oslo; Professor Erik Stensiö, Dr. Erik Jarvik, and Dr. Tor Örvig of Naturhistoriska Riksmuseet in Stockholm; Dr. Errol I. White, Dr. H. W. Ball, and Mr. H. A. Toombs of the British Museum (Natural History) in London; and Professor D. M. S. Watson of University College, London.

In paleoecological studies, details of the manner of occurrence may be of the greatest significance, but in a comprehensive review of this sort it is not practical to present all of the available evidence. An attempt has been made to include the most pertinent information as a basis for discussion and to give references to the latest or most important papers on the various occurrences. This study has been restricted to the Ordovician, Silurian, and Early Devonian finds, since later ones can have little bearing on the original habitat of most major groups of Agnatha and Pisces. On the other hand, no geographical limitations have been set, although some recent finds, particularly in Asia, have not been included for lack of sufficient data. Although conodonts may represent a group of vertebrates (W. Gross, 1954), no attempt has been made to discuss their occurrences, since, as far as I know, they are limited to marine deposits (Ellison, 1944).

DETERMINATION OF EARLY VERTEBRATE ENVIRONMENTS

Salinity of the Environment of Deposition

The first problem for the paleoecologist is the determination of the environment of deposition of the sediments in which the fossils are found. In the study of the earliest vertebrates, we are concerned only with aquatic deposits and are interested first of all in the salinity of the water. In the determination of the salinity, the characteristics of the sediments, although they may be helpful, are rarely conclusive; one exception is saline evaporites that necessarily indicate hypersaline waters. The early vertebrates themselves are too far removed from living forms of known habits to furnish any reliable clues. This leaves the nature of the faunal assemblage as the chief evidence of the salinity of the depositing waters.

The determination of marine deposition is often simple and conclusive. Many groups of invertebrates are, and presumably always were, restricted to the sea, and only rarely, under exceptional circumstances, can they be transported into and preserved in fresh-water or terrestrial environments. The marine groups of particular importance in this study include stromatoporoids, corals, brachiopods, bryozoans (except Phylactolaemata), cephalopods, Conulariidae, Tentaculitidae, trilobites, and echinoderms. Some of these, especially stromatoporoids, corals, echinoderms, and cephalopods, are stenohaline forms that cannot tolerate reduced salinity. Others can live in brackish waters, and of course many can be transported into marginal, possibly brackish, zones. Other invertebrate groups commonly found associated with early vertebrates are not restricted to the sea. Pelecypoda today live in all salinities, even in extremely hypersaline waters. The early Paleozoic pelecypods were probably all marine forms, but some of them invaded brackish and fresh waters by the middle Paleozoic. Most Paleozoic Gastropoda are marine, but some of them got into fresh waters and onto land during the latter half of the era. Ostracoda today live in salt, brackish, and fresh waters, and the same may have been true during the middle and latter part of the Paleozoic, although the earliest ones were all marine. Most Phyllocarida are marine, but a brackish habitat was not uncommon, and a few may have lived in fresh waters. The habitat of the Eurypterida has been the subject of a controversy that is intimately connected with the question of the environment of early vertebrates; for this reason they cannot be used as evidence of vertebrate habitats. The Xiphosura lived at various times in all salinities.

Fresh-water deposits of the Ordovician, Silurian, and Early Devonian are not easy to recognize, largely because a fresh-water invertebrate fauna of this age either did not exist or was not clearly distinctive. In fact, the determination of many formations as fresh-water sediments has been based on the presence of ostracoderms or primitive fishes, and on the absence of other fossils. Obviously the presence of any particular vertebrate is a line of evidence that cannot be used in this study, and the absence of invertebrates is far from conclusive. There are marine environments today which support little or no invertebrate fauna, and it is not uncommon for all traces of marine forms to disappear after death because of the action of scavengers, mechanical abrasion, or chemical decay. Thus negative evidence, although it may be significant, must be used with caution. There can be no question, however, that at least by the Late Silurian or Early Devonian, a fauna and flora were developing in fresh waters and on land. Invertebrate groups that probably had fresh-water representatives at this time are the pelecypods, gastropods, branchiopods, ostracods, xiphosurans, eurypterids, and worms. Myriapods appear to have inhabited fresh waters or land at their earliest appearance in the Late Silurian, and scorpions probably got into terrestrial habitats by the Devonian. The fresh waters of the Late Silurian and Early Devonian were probably occupied by Algae (Nematophytales) and primitive vascular plants (Psilophytales), while more advanced vascular plants, including Lycopsida and Sphenopsida, may have lived on land.

The fauna of brackish waters is made up largely of marine forms that can tolerate low salinities. There may be relatively few species, but the euryhaline species may be represented by abundant individuals. The individuals may be small in size, although this is not definitely determined to be caused by the low salinity. Generally there are relatively few fresh-water forms, and the stenohaline marine groups are absent.

Deposits of extremely hypersaline waters may often be recognized by the presence of rock salt, gypsum, anhydrite, and other evaporites. The fauna of such waters is always greatly reduced, and may be derived from that of fresh waters or the sea, depending on the history of the particular body of water.

In addition to the characteristics of a single thanatocoenose, the sequence of faunal assemblages may be very instructive. A gradual change in lithology and invertebrates, accompanied by a corresponding change in the associated vertebrates, may lead to a better understanding of the ecological implications than will isolated occurrences. Perhaps the most convincing evidence is what Romer and Grove (1935, p. 850) refer to as faunal contrast. Sharp differences between essentially contemporaneous faunal assemblages clearly imply ecological differences.

Depositional Facies

After the salinity of the water in which deposition took place has been decided, it is important in an ecological study to determine more specifically the nature of the sedimentary environment. The major facies include: in fresh waters: stream channels and flood plains, lakes, and swamps; in brackish waters: bays, deltas, estuaries, and lagoons; in salt waters: littoral and neritic environments (deeper water environments do not play an important part in the fossil record). Within these environments certain physical features are important: the nature and depth of the bottom; proximity to shore; presence or absence of currents, waves, and tides; temperature; and oxygen content. For the determination of the lithofacies, sedimentary features are most useful. Important evidence comes from the nature of the sedimentary body and its relationship to other bodies, as well as the structures, texture, color, and composition of the sediment. A general paleogeographic reconstruction is helpful. Additional information may be furnished by the character and sequence of fossil assemblages.

Post-Mortem Transportation

Benthonic forms, especially those that are sessile, may under favorable conditions be preserved where they lived. In exceptional cases this may be true of bottom-dwelling vertebrates. The majority of Agnatha and Pisces are free-swimming forms that are particularly liable to transportation after death. For this reason the depositional environment in which they were buried and preserved may give little direct information about their place of life. If post-mortem transportation is indicated, an evaluation of its amount and significance is one of the most important aspects of paleoecological studies.

The exceptional cases where little or no transportation is involved furnish the most valuable clues to the actual habitat of fossil vertebrates. They may be recognized by common, well-preserved, articulated remains. Examples of this type of occurrence are found in the Late Silurian of the Island of Oesel, Norway, and Scotland, and in the Early Devonian of England and Germany. Trackways, indicating the life habitat, are not certainly identified for any of the earliest vertebrates.

Transportation is indicated in a number of ways. It may be assumed when the fossils are fragmentary, scattered, or worn, if they are mechanically sorted or oriented, or if they occur in coprolites. Rarity of a fossil may suggest transportation but does not prove it. The nature of the sediment is also important: if it is coarse-textured, or shows evidence of currents such as cross-bedding and ripple marks, transportation of any contained fossils is probable. While it is generally easy to determine whether transportation of fossils has occurred, there is no simple rule for assessing its amount. A fossil may be rolled, worn, and broken on the bottom of a shallow sea without being moved any appreciable distance. On the other hand, a fresh-water fish may be carried into the sea and buried among marine invertebrates. Thus, when transportation is indicated, the faunal associations in a single thanatocoenose may have little ecological meaning. But when there are a number of occurrences that conform to a pattern, this pattern begins to take on considerable significance. Where there is consistently strong contrast between different types of faunal assemblages, this may be assumed to have ecological importance.

A few simple and obvious rules are useful in determining the source of fossils. (1) Marine forms are not found in fresh-water deposits except under the most unusual conditions. (2) Fresh-water forms may be found in fresh-water or marginal marine deposits; only rarely, possibly excepting plants, will they be found in the sea at any great distance from the shore. (3) Marginal marine deposits will contain mostly marine forms, but perhaps with some admixture from fresh waters. (4) Abundance of a certain fossil is strongly suggestive that transportation was for no great distance, especially if preservation is good. (5) Rarity or absence of fossils is not necessarily significant because of the vagaries of preservation.

Adaptation of Early Vertebrates to Their Environment

Because most Ordovician, Silurian, and Early Devonian vertebrates are so remote from any living forms, it is usually possible to make only general comparisons of their adaptive features. The locomotor adaptation is most easily determined because it is generally indicated by preservable hard parts. Bottom-dwelling forms, at least in extremes of specialization, are determinable, and may be distinguished from free-swimming types. The significance of the presence or absence of paired fins and of the development of all the fins may be deduced from comparisons with living forms and from the study of experimental models. Some indication of the manner of feeding may be gained from the nature of the mouth parts. An exoskeleton may be interpreted as a defensive adaptation against predators. The position and development of the sense organs, particularly the eyes, nostrils, and lateral line canals, have great adaptive significance. The structure of the gills may sometimes be determined, and suggests in certain Agnatha their use in feeding as well as in respiration.

The adaptation of soft parts that are rarely or never preserved in fossils may sometimes be inferred. Thus, the functions of the kidneys of living forms indicate a fresh-water habitat for their ancestors. The composition of the blood has led to a belief in the marine habitat of early vertebrates. The presence of lungs in some early vertebrates is suggested by the morphology and embryology of living forms. The presence of a spiral valve in the intestine may be indicated by the shape of coprolites.

REVIEW OF EARLY VERTEBRATE OCCURRENCES

Ordovician Vertebrates

Fragmentary remains of vertebrates have been found in Ordovician rocks in the following four regions:

(1) Early Ordovician, Glauconite Sand, near Leningrad, Russia (Rohon, 1889). The vertebrate remains are small, tooth-like structures, perhaps some sort of denticles, named *Archodus* and *Palaeodus*. Histologically, they consist of tissues resembling dentine, enamel, and perhaps bone, so there can be no doubt of their vertebrate origin, but they cannot at present be referred to any better-known groups of Agnatha or Pisces.

(2) Middle Ordovician, Harding Formation, at a number of localities in central-western Colorado (Walcott, 1892; Behre and Johnson, 1933; Sweet, 1954). Two genera, *Astraspis* and *Eriptychius*, show many histological similarities to the Heterostraci, and *Eriptychius* has been compared closely to the Drepanaspidae. It is most unlikely that either of these genera belong to the same families as Silurian and Devonian Heterostraci. In addition, Stetson (1931, p. 153) has reported scales of *Thelodus* from the Harding Sandstone. Since he found it difficult to distinguish them from basal Devonian (Ludlow Bone Bed) scales of this genus, it is possible that the Coelolepida were already present in the Ordovician. However, before this is accepted, it should be demonstrated that these are not denticles belonging to *Astraspis* or *Eriptychius*.

(3) Middle Ordovician, sandstones and shales lying above the Cambrian Deadwood Formation and below the Late Ordovician Bighorn Formation, in the Bighorn Mountains of Wyoming (Darton, 1906; Amsden and Miller, 1942). The vertebrates, which as yet have not been described, appear to be referable to *Astraspis* and *Eriptychius*.

(4) Middle Ordovician, Icebox Shale and Roughlock Siltstone, of the Black Hills of South Dakota (Darton, 1909; Furnish, Barragy, and Miller, 1936; McCoy, 1952). The vertebrate fragments have not been determined.

The best known of these occurrences is that of the Harding Sandstone in the quarries near Cañon City, Colorado, from which came the specimens first described by Walcott in 1892. Here the Harding Formation is about 90 feet thick and rests on pre-Cambrian gneiss. Overlying a thin basal conglomerate and coarse sandstone, it consists of gray or reddish sandstones, separated at two levels by shales or argillites. Vertebrate fragments occur throughout the sandstones. Relatively smaller fragments occur abundantly at two horizons in "bone beds."

For the purposes of this study, there are two important questions: What was the environment of the sands? Were the vertebrates introduced from another environment? The first question is answered in part by the associated invertebrates. With the vertebrate fragments in the sandstones are found common *Dictyorhabdus*, which is believed by Flower (1952, pp. 516–517) to be an hexactinellid sponge, *Lingula*, annelid borings, gastropods, pelecypods, and conodonts. The shales contain the same forms with the exception of the annelid borings, but *Dictyorhabdus* is less common, and conodonts are abundant; many pelecypods (*Ctenodonta*, *Modiolopsis*, *Orthodesma*, *Vanuxemia*) and gastropods (*Ecculiomphalus*, *Liospira*) occur here, as well as rarer cephalopods (*Ormoceras*, *Kionoceras*), trilobites (*Isalaux*, *Törnquistia*), and ostracods (*Isochilina*). All of the invertebrates are surely marine, but the preponderance of pelecypods and gastropods, and the absence or rarity of such forms as corals, articulate brachiopods, cephalopods, and trilobites, indicate some special environment. This is probably shallow, turbid waters near the shore, with a bottom of loose, shifting sand or mud, a situation unsuitable for most bottom-dwelling, marine invertebrates.

If the marine deposition of the Harding Formation is accepted, is there any support for the theory of Barrell (1916, p. 393) and Romer and Grove (1935, pp. 810–811) that the vertebrates lived in streams or estuaries and were introduced from them into this near-shore marine environment after death? Romer and Grove believed that the fragmentary nature of the remains and the absence of vertebrates in "typical" marine formations of this age supported this theory, but against it are the following facts: (a) The abundance of the fragments. It seems highly improbable that they would have been introduced from streams in such great numbers. Without considering the bone beds, which were probably secondarily concentrated, vertebrate remains preponderate over those of the invertebrates that presumably inhabited these sea margins. (b) The size of the fragments. The vertebrate fragments in the sandstones may be as large as one inch or more, but the grains of sand are of medium size and fairly well sorted. It is obvious that the currents that transported the sand grains could not have carried the vertebrate fragments in suspension. If the latter were transported by these currents, they must have been rolled along the bottom. The relatively slight wear and imperfect rounding of the vertebrate fragments in the sandstones indicate that they could not have been carried far by this method. Thus, if the vertebrates were introduced, it must have been as floating corpses, and this is unlikely because of their abundance. (c) The distribution of the vertebrate remains. If they came from streams to be deposited in the sea, their occurrence would be local, at and near the mouths of streams. But vertebrate fragments have been found, usually abundantly, in every exposure over a wide area of the Harding Sandstone that has been studied by Behre and Johnson (1933, p. 480) and Johnson (1944, p. 320). Their occurrence in similar formations in Wyoming and South Dakota makes the argument against the fluviatile origin of the vertebrates almost conclusive.

The Harding Formation was probably deposited during the advance of the sea into an elongate depression called the Colorado Sag, lying between two positive areas (Sweet, 1954, p. 303). The basal unfossiliferous conglomerate and coarse sandstone may represent an actual beach deposit, as Walcott suggested (1892, p. 156). The succeeding sands were deposited not far from shore in shallow water on an exposed bottom of low relief. The size of the sand grains argues for transport by moderate currents, and these together with scavengers would account for the fragmentary nature of the fossils. Relatively few invertebrates were adapted for life on the mobile sandy bottom.

The bone beds probably formed at times when, because of rapid deposition of sand or minor fluctuations of sea level, the bottom came to be above wave base; or they might be the result of increased current action. Either waves or currents might be competent to remove previously deposited sand grains, but not the larger fragments of vertebrates or invertebrates. The hard parts would be broken, rolled, and worn, and would become more and more concentrated over a period of non-deposition.

Overlying the upper bone bed at Cañon City is a three-foot layer of argillite containing *Lingula*, pelecypods, and conodonts, but no vertebrates. This may represent a mud flat, deposited in shallow water near the shore. It is succeeded by more sandstones, with abundant fragments of vertebrate dermal armor.

The general picture of the Harding Formation deposition is of a fluctuating advance, leaving a record of beach, mud flat, and offshore sand bottoms, the latter containing the vertebrate fragments. At times the sand bottoms were the site of rapid deposition and at other times of non-deposition or slight erosion when the bone beds were formed. With further advance of the sea in post-Harding times, the source of clastic material was at a greater distance, and the waters were presumably somewhat deeper. In these conditions the Fremont Limestone was deposited and a great variety of marine vertebrates thrived, but not a single fragment of a vertebrate has been discovered.

The pre-Bighorn sandstones and shales of Wyoming were probably deposited under conditions similar to those in which the Harding Formation originated. In the Black Hills of South Dakota vertebrate remains occur in shales and siltstones, indicating a muddy rather than a sandy bottom. But in the Icebox Shale the associated fauna is similar to that of the Harding Formation; it consists of pelecypods, gastropods, linguloids, scolecodonts, and conodonts (Furnish, Barragy, and Miller, 1936, p. 1332). The overlying Roughlock Siltstone is sandy in the lower part but is transitional lithologically to the overlying Whitewood Dolomite in its upper part. It includes a fauna similar to that of the Harding Formation, but also a greater variety of marine invertebrates (including echinoderms, articulate brachiopods, and bryozoans), due perhaps to its transitional nature.

The Glauconite Sand of Russia, which yielded *Archodus* and *Palaeodus,* is only about one meter thick. Associated with the vertebrates are inarticulate brachiopods (*Lingula* and *Obolus*), simple conodonts, and Foraminifera. These fossils, as well as the glauconite, indicate that this is a marine deposit. It may have been laid down near shore in a situation not dissimilar to that of the Harding Formation.

Romer and Grove (1935, p. 811) implied that the absence of vertebrates in "the abundant typical marine formations of the Ordovician" was an argument against their marine habitat. The known vertebrate occurrences indicate, however, that at least certain Heterostraci did inhabit the margins of the sea during the Middle Ordovician in regions where, due perhaps to the turbidity or the nature of the bottom, the typical varied marine invertebrate fauna could not survive or flourish. It is possible that additional vertebrates will be found in other formations of a similar facies.

Silurian Vertebrates

During the Silurian Period vertebrates continue to be rare except at a few localities. The number of occurrences is quite sufficient, however, to permit some fairly satisfactory inferences regarding habitat. In the Late Silurian it becomes obvious for the first time that different groups of vertebrates were adapted for life in different ecological zones. This was undoubtedly true for some considerable previous time, but is not demonstrable because of the incompleteness of the paleontological record. It is perhaps most clearly shown in the Upper Oesel Group of the Island of Oesel in the Baltic. The lower or K_1 horizons contain abundant and varied Osteostraci, a few Anaspida, common eurypterids, and very rare marine invertebrates; Heterostraci and Acanthodii are completely absent. The upper or K_4 horizons contain Heterostraci, Acanthodii, and a variety of marine invertebrates; there are no Osteostraci or Anaspida. Although K_1 and K_4 are different in age, the striking faunal difference is due to ecological factors. The Osteostraci–Anaspida–Eurypterida assemblage occurs at this time in brackish or fresh-water habitats, while the Silurian Heterostraci (Cyathaspinae) and Acanthodii are largely or entirely limited to a marine environment. These two distinct faunal assemblages will be discussed separately.

OSTEOSTRACI AND ANASPIDA

Island of Oesel: The lower part of the Upper Oesel Group, or K_1 Beds, is represented on Oesel by two distinct facies. The eastern or Kaarma facies, occurring in the middle of the island, consists of dolomitic limestones containing cephalopods and ostracods; it is considered by Hoppe (1931, pp. 40, 44) to have been deposited in warm, shallow, marine waters not far from shore. The western or Wita facies consists of three cyclic repetitions of (1) ostracod limestone, (2) clay and dolomitic limestone, and (3) fine-grained, light, dolomitic "*Eurypterus* Gestein" (Luha, 1930, fig. 2). It is in the *Eurypterus* stone that abundant vertebrates and eurypterids have been collected at three localities: at Wita (or Rootsiküla) they occur in the lower cycle; at Wesiko in the middle cycle; and at Himmiste near Hoheneichen in the upper cycle. Although the faunal assemblages differ in detail at these three localities, they are of the same general type. Detailed lists may be found in papers by Luha (1930, pp. 10–15), Hoppe (1931, pp. 40–41), and Bölau (1949, table 1). The age of the K_1 Beds is probably Lower Ludlow.

As far as the vertebrates are concerned, the *Eurypterus* stone is characterized particularly by abundant and often excellently preserved Osteostraci belonging to the following primitive genera: *Tremataspis*, *Dartmuthia*, *Saaremaaspis*, *Witaspis*, *Oeselaspis*, *Thyestes*, and *Procephalaspis*. Anaspida are rare in Oesel and are known only from a few incomplete, though partially articulated specimens of *Saarolepis*. Scales of Coelolepida, referred to *Coelolepis* and *Thelodus*, occur in all zones. Near Himmiste abundant articulated specimens of *Phlebolepis* have been collected; although generally referred to the Coelolepida, this genus may not be closely related to typical members of this group such as *Thelodus*, *Coelolepis*, and *Lanarkia*.

Among the invertebrates, Eurypterida (*Eurypterus*, *Stylonurus*, and *Pterygotus*) and Xiphosura (*Bunodes*) are common and beautifully preserved. The phyllocarid, *Ceratiocaris*, is reported. Typically marine invertebrates are very rare and generally poorly preserved; *Orthoceras*, *Pterinea*, *Conchidium*, and *Favosites* have been found. In addition there are occasional ostracods (*Leperditia* and *Primitia*), conodonts, inarticulate brachiopods (*Pseudolingula*), and gastropods (*Platyschisma*).

The rarity of marine invertebrates under conditions suitable for their preservation suggests that the deposition of the *Eurypterus* stone did not take place in the open sea. Their occasional presence, however, demonstrates that this particular environment was close enough to the sea to permit their introduction under unusual conditions. Hoppe (1931, p. 43) believed that the western or Wita facies was deposited in a brackish shore lagoon, while the eastern facies represents the deposits of the open shallow sea outside the lagoon. Judging from their abundance and good preservation, the following forms probably lived in the brackish waters of the lagoon: Osteostraci, Anaspida, *Phlebolepis*, Eurypterida, *Bunodes*, and perhaps *Platyschisma*. On the other hand, *Orthoceras*, *Pterinea*, *Conchidium*, and *Favosites* were undoubtedly introduced from the open sea, perhaps carried by storm waves over a barrier reef. The remaining forms (*Coelolepis*, *Thelodus*, ostracods, *Ceratiocaris*, conodonts, and *Pseudolingula*) were probably either euryhaline or adapted to life in brackish water.

Ringerike, Norway: In the region of Ringerike, northwest of Oslo, there is an excellent early Paleozoic section, described in detail by Kiaer (1908). Marine rocks containing a varied invertebrate fauna include at their top Stage 9 of Kiaer, which he assigned to the Ludlow.

They are overlain by reddish-brown, grayish-brown, or green sandstones and shales, generally unfossiliferous, but exhibiting ripple marks, mud cracks, false bedding, and probable eurypterid trails. These strata were called Stage 10 and assigned to the Downtonian by Kiaer. In 1909 Kiaer discovered a rich fauna of vertebrates and arthropods in the lower part of Stage 10 at Rudstangen on Kroksund. Almost all of his collection came from a thin (3 cm.) lenticle of greenish-gray, fine sandstone about 10 meters above the base of Stage 10, or above the highest occurrence of marine invertebrates. The most recent study indicates that its age is probably Upper Ludlow (Størmer, 1954).

The fauna of the greenish-gray sandstone lenticle at Rudstangen has been described by Kiaer (1924), Størmer (1934, 1935), and Heintz (1939). Among the vertebrates, Osteostraci (*Aceraspis* and *Hirella*) and Anaspida (*Pterygolepis, Pharyngolepis*, and *Rhyncholepis*) are common, entire, and articulated. Coelolepids are rare, but include a few articulated specimens referred to *Thelodus*. Among the Eurypterida, *Hughmilleria* is common, while *Pterygotus, Stylonurus*, and *Mixopterus* are represented by a few specimens; they are generally cast exuviae and are rarely preserved entire. *Dictyocaris*, probably a phyllocarid, is abundant. The Xiphosura, *Bunodes* and *Kiaeria*, are very rare.

The similarity of this assemblage to that of the K_1 Beds of Oesel is striking. Partly because of the difference in age most of the genera are different, but the same orders and in some cases the same families are found in both places. *Eurypterus*, the common eurypterid in K_1 Beds, does not occur at Rudstangen, while *Hughmilleria* is not found in K_1 Beds. *Dictyocaris* is the most abundant fossil at Rudstangen, while Phyllocarida are probably rare in the K_1 Beds. Heterostraci and Acanthodii are absent in both. In Ringerike marine invertebrates disappear within a few feet of the top of the gray shales and limestones that form Stage 9, thus 10 meters below the Rudstangen lenticle.

The absence of marine forms suggests that this is a fresh-water deposit. There are many indications of shallow water deposition, such as rapid alternation of sediments, shale pellets in the sandstones, ripple marks, trails, and mud cracks. Kiaer (1924, pp. 13–15) believed that this was a river flood-plain deposit in which the Rudstangen lenticle represented a pool. The fact that the fossils occur at such a short distance above marine beds indicates that deposition was not far from the sea margins. It may well have been deltaic, but it is almost impossible to be certain whether this part of the section was deposited on the sub-aerial portion of the delta in fresh waters or at the margin of the delta in the submarine portion where conditions may have been brackish because of the volume of water brought in by streams.

In 1953 another vertebrate-bearing horizon was discovered in Ringerike along the shores of Kroksund. To date only a preliminary note on this locality has been published by Størmer (1954). It occurs in the upper part of Stage 9 (9g of Kiaer, 1908) in strata that still contain marine invertebrates. This has been correlated with the Middle Ludlow by Størmer. The vertebrates are mostly Osteostraci, provisionally identified as *Hirella*, cf. *Aceraspis*, and cf. *Oeselaspis* (Heintz, in litt.). The majority are complete, articulated specimens. Scales of the coelolepid, *Thelodus*, occur in calcareous bands at a slightly lower horizon. The vertebrates are closely associated, but not in the same bed with well-preserved eurypterids (*Eurypterus*, *Pterygotus*, *Hughmilleria*, and *?Mixopterus*). The vertebrate- and eurypterid-bearing beds alternate with a marine facies containing ostracods and the bryozoan, *Amplexopora*. One must assume from this preliminary information that Stage 9g was deposited near the margins of the sea where at certain times a higher salinity, though perhaps still brackish water, permitted a few marine forms to live, and at other times a reduced salinity, perhaps even fresh water, was favorable for the Osteostraci and Eurypterida. The habitat may have been on the seaward margin of the same delta in which is found the Rudstangen fauna at a higher level.

Lesmahagow and Hagshaw Hills inliers, Scotland: These two adjacent inliers in the Carboniferous of Lanarkshire and Ayrshire exhibit rocks of Silurian and Devonian age. Lying below the Early Devonian Old Red Sandstone, is a series of conglomerates, sandstones, graywackes, shales and mudstones, divided into eleven beds by Peach and Horne (1899). Bed 3 (*Ceratiocaris* beds) and Bed 9 (including the Downtonian fish beds) contain well-preserved vertebrates. Conventionally (MacGregor and MacGregor, 1948, p. 10), Bed 3 has been assigned to the Ludlow and Bed 9 to the Downtonian. However, recent opinion is that they are older; Heintz (1939, p. 109) assigned them to the Middle or Upper Ludlow, Westoll (1951, p. 7) to the Late Wenlock to Middle Ludlow, and Lamont (1947, p. 296; 1952, p. 30) to the Wenlock or earlier. In my opinion they are of Ludlow age, but there is little basis for an exact correlation at present.

Both Bed 3 and Bed 9 contain the anaspid, *Birkenia elegans*, the coelolepid, *Thelodus scoticus*, the eurypterid, *Slimonia*, myriapods, and the phyllocarids, *Ceratiocaris* and *Dictyocaris*. However, in Bed 3 the only common vertebrate is *Thelodus*. *Ceratiocaris* is abundant, and there are a number of invertebrates that indicate marine or brackish conditions (*Orthonota*, *Pterinea*, *Modiolopsis*, *Platyschisma*, *Lingula*, *Beyrichia*, and *Spirorbis*). Bed 3 is notable as the source of *Jamoytius*, considered by White (1946) to be the most primitive of known vertebrates, and of the early scorpion, *Palaeophonus*. In the fish beds of Bed 9, vertebrates are the most common fossils and are preserved entire. Anaspida (*Birkenia* and *Lasanius*) and Coelolepida (*Thelodus* and *Lanarkia*) are the most usual, while Osteostraci (*Ateleaspis*) are relatively rare. Eurypterida (*Eurypterus*, *Slimonia*, and *Stylonurus*) are not common but may be excellently preserved. Phyllocarida are not common, but a number of plants (*Pachytheca*, *Parka*, etc.) are reported. There is nothing in this assemblage suggestive of marine deposition.

If we consider the whole section, it appears that deposition of the lower beds was marine and that in ascending the section there is a gradual dropping out of the marine elements. From Bed 1 few fossils are reported, but in Bed 2 there are many molluscs, including cephalopods, and a few articulate brachiopods, bryozoans, crinoids, and corals; this is a marine, muddy bottom, pelecypod facies, deposited perhaps in a bay. In Bed 3 the cephalopods, articulate brachiopods, crinoids, and corals have gone, and only a few marine types survive, particularly pelecypods and *Lingula*. This appears to be a near-shore marine or brackish-water assemblage. *Jamoytius* and *Thelodus* may have lived in this habitat together with phyllocarids and perhaps scorpions, but the rare *Birkenia* and myriapods were more probably introduced from near-by fresher waters or land. The shales and mudstones of Bed 4 are characterized by their many excellently preserved eurypterids, with which are associated the xiphosuran, *Neolimulus*, and phyllocarids; remnants of the marine fauna surviving into this brackish, marginal habitat are *Beyrichia*, *Spirorbis*, *Platyschisma*, and *Lingula*. Bed 5 contains an abundance of the gastropod, *Platyschisma*, as well as common pelecypods (*Orthonota*, *Modiolopsis*, and *Goniophora*) and ostracods (*Beyrichia*) and a few phyllocarids, eurypterids, and *Spirorbis;* this still has the aspect of a marginal marine assemblage. Bed 6 is unfossiliferous graywackes, Bed 7 is a local, perhaps littoral, conglomerate, and Bed 8 is barren, red and yellow, cross-bedded sandstones and red mudstones, also perhaps littoral. Bed 9 consists of barren mudstones, shales, and graywackes in which occurs the "fish band," 12 to 15 feet of brown, carbonaceous shales with green mudstones. There is not a single form in its faunal assemblage that could be taken to indicate marine conditions. On the other hand, proximity to the sea is suggested by the presence of certain forms that occur also in the underlying marginal marine beds. These include *Thelodus*, *Birkenia*, eurypterids and phyllocarids; *Birkenia* may be a fresh-water form that was carried occasionally into the sea margins, but the others probably could tolerate considerable differences in salinity. Another indication of proximity to the sea is the presence of abundant bryozoans, *Glauconome disticha*, at a level above the "fish band" of Bed 9; if this is correctly identified, it certainly is a marine species, occurring elsewhere in the Dudley Limestone, Gotland Silurian, and Pentland Hills Silurian. The sediments of the "fish band" are fine-grained, evenly and thinly bedded, indicative of quiet water deposition. The environment may have been a fresh or brackish lake close to the margins of the sea.

Conclusions: The faunal assemblages discussed above are clearly of a similar type. From them we can conclude that in the Late Silurian the Osteostraci and Anaspida inhabited marginal brackish or fresh-water habitats such as lagoons, deltas, and lakes. Coelolepida are not characteristic of this assemblage but are also found commonly in marine associations; they may have been euryhaline forms, inhabiting both the sea margins and brackish or fresh-water environments near the sea. The fact that well-preserved Eurypterida and Xiphosura are regularly associated with these vertebrates indicates that some of them lived in brackish or fresh-water habitats also. Typical Phyllocarida appear to be most abundant in saline waters, as in Bed 3 of the Lesmahagow inlier, but they were not restricted to the sea, and *Dictyocaris* may have been a fresh-water form.

CYATHASPINAE AND ACANTHODII

Cyathaspinae are known from a number of occurrences, usually of isolated specimens, in Europe, Canada, and the United States. Such occurrences may have no great ecological significance when considered alone, but since most of them conform to a pattern, the probability that they indicate the habitat of this group is much increased. In some cases Cyathaspinae are found without associated vertebrates; in others they are found with Acanthodii and Coelolepida. The various recorded occurrences will be discussed briefly.

Cornwallis Island, Canada, Allen Bay Formation: Thorsteinsson and Fortier (1954, pp. 8–9) report ostracoderms from the two marine facies of this formation. They have not yet been described, but represent a new genus and species of Cyathaspinae. Some have been found in the southern part of the island in the shelly facies, which is characterized by biostromes of corals and stromatoporoids and by coquinas of *Conchidium.* Others occur in the graptolitic facies at Disappointment Bay, where they are associated with graptolites, inarticulate brachiopods, and other invertebrates. The age is lowermost Wenlock, just below the *Cyrtograptus rigidus* zone.

Cornwallis Island, Canada, Read Bay Formation: This formation overlies gradationally the Allen Bay Formation and consists of a shelly facies to the south, a graptolitic facies to the north, and a reef facies between (Thorsteinsson and Fortier, 1954, pp. 9–12). In the shelly facies, associated with graptolites, articulate brachiopods, gastropods, etc., occurs another new genus of Cyathaspinae. Its age is Upper Wenlock, the *Cyrtograptus lundgreni* zone.

North Germany, Graptolithengestein: This greenish-gray limestone is known in northern Germany from glacial erratics, a number of which have yielded specimens of *Archegonaspis integer* (Kunth). One from Rostock described by Geinitz (1884) contains a well-preserved dorsal shield. Another from Schönberg, near Berlin (Kunth, 1872, pl. 1) shows dorsal and ventral shields, branchial plates and a few scales, and may represent a partially articulated individual. *Monograptus, Orthoceras,* and probably other marine invertebrates are associated with *Archegonaspis.* This rock resembles the *Colonus* Shales of southern Sweden, and may be derived from there. Its age is Lower Ludlow, the *Monograptus nilssoni* zone.

Gotland, Hemse Group: Lindström's (1895) well-preserved specimen of *Archegonaspis lindstromi* Kiaer probably came from this group on the Lau Canal. Later Munthe (1902, p. 231) found fragments belonging to this species in the lower part of the Hemse Group at the same locality.

Acanthodians (*Gomphodus* scales and undetermined fin spines) and coelolepid scales are reported from the lower or middle part of the Hemse Group at Hammarudd in the parish of Kräklingbo (Spjeldnaes, 1950, pp. 213–215). This group contains a large and varied invertebrate fauna, dominantly of brachiopods, and was deposited in comparatively shallow, quiet, muddy waters in a warm sea, probably not far from a coast to the northwest that was fringed by barrier reefs (Hadding, 1950, pp. 406–407). Its age is Lower Ludlow, the *Monograptus nilssoni* zone (Hede, 1942).

Island of Oesel, Upper Oesel Group (K_4): At Ohesaare Pank on the Sworbe Peninsula the limestones and calcareous shales of K_4 have yielded scattered vertebrates throughout the section and abundant fragmentary vertebrates in three "bone bed" horizons. Two excellently preserved dorsal shields of the Cyathaspine, *Tolypelepis undulata* Pander, came from this section but probably not from the bone beds; one is figured by Kiaer (1932, pl. 10), the other by Rohon (1893, pl. 1, fig. 45). This species does occur as fragments in the lower bone bed (Beds 9–10 of the section of Hoppe, 1931, p. 56). Here it is associated with the following vertebrates, all fragmentary: A probable Cyathaspine, *Strosipherus* (=*Oniscolepis*); a variety of Acanthodii, including scales of *Nostolepis* and *Gomphodus*, spines of *Climatius* and *Onchus*, and probably also the fragments called *Lophosteus, Monopleurodus, Chelmodus,* and *"Eukeraspis"* (Rohon, 1893, pl. 1, figs. 28–29, not of Agassiz); also coelolepid scales referred to *Thelodus*. The invertebrates in Beds 7–13, including the lower bone bed, are articulate brachiopods, cephalopods, and gastropods. All of K_4 is marine, and the lower bone bed is considered by Hoppe (1931, pp. 59–60) to be a concentration formed near the shore. Its age is probably Upper Ludlow, although Lungerhausen and Nikiforova (1942, p. 64), Lamont (1952, p. 30), and Northrop (1939, p. 119) argue for an earlier age.

Southern Urals: An incomplete shield of *Cyathaspis* sp. is described by Obruchev (1938, p. 42) from the River Sirengupan in the basin of the River Belaja in the southern Urals. It occurs in dark shales that also contain trilobites and brachiopods, and thus are marine. The invertebrates suggest a correlation with the Wenlock, but Obruchev believes that *Cyathaspis* indicates a Ludlow age.

North Germany, Beyrichienkalk: Glacial erratics of the Beyrichienkalk have been discovered in northern Europe from East Prussia to Holland, but the formation is known in place only in a deep boring at Leba in northeast Pomerania (W. Gross, 1950, p. 53). The source of the glacially transported stones is thought to be under the Baltic between Oesel and Gotland. The rocks are limestones and dolomites that vary somewhat in lithology and fossil content because of different lateral facies or different horizons. Gross (1947, p. 151) distinguishes two zones, an older one resembling the K_4 Beds on Oesel and characterized by *Thelodus parvidens*, and a younger one, possibly Downtonian in age and characterized by *Thelodus scoticus*. It is not possible from published information to consider these zones separately, so only a general account of the fauna can be given.

Only fragmentary remains are known. The Heterostraci are represented by *Strosipherus*, which probably belongs to the Cyathaspinae, and *Orthaspis*, which is of uncertain affinities. Among the Acanthodii, scales are referred to *Nostolepis*, *Gomphodus*, and *Poracanthodes*, spines to *Onchus* and *Climatius*, jaws to *Plectrodus*, and teeth to *Protodus; Chelmodus* and *Lophosteus* probably are acanthodian fragments. Coelolepida are represented by common scales of *Thelodus* and *Lanarkia*. Osteostraci are possibly absent, although Gross (1947, p. 111) believes that some fragments, including *Lophosteus*, belong to this group. It is difficult to determine from published accounts just what invertebrates are actually associated with the vertebrates. Gross (1947, p. 150) says that certain types of Beyrichienkalk, named after their most common invertebrate, the Pholidopskalk, Choneteskalk, and ostracod-rich limestone, contain numerous fish remains. Reuter (1885) lists vertebrates in association with articulate brachiopods, crinoids, and ostracods. There can be no question of the marine origin of the Beyrichienkalk, while the presence of the limestone-pebble conglomerates, as well as the rolled and worn condition of the vertebrate fragments, suggests that deposition took place in shallow waters, possibly near shore. The age of this formation is Upper Ludlow, and perhaps in part Lower Downtonian.

Southern Sweden, Öved-Ramsåsa Beds: In Scania the Öved-Ramsåsa Beds overlie the *Colonus* Shales, and include at the top reddish sandstones and clay shales that contain vertebrate remains, especially in "bone beds." The vertebrate fauna, described by Lehman in 1937, is in need of revision. Probable Cyathaspinae occur as unidentified fragments. Among the Acanthodii are scales of *Nostolepis* (including *Diplacanthoides*, *Dendracanthus*, and *Dontacanthus* of Lehman), *Gomphodus*, and *Poracanthodes*, spines of *Onchus* and *Climatius*, jaws of *Plectrodus*, and teeth of *Protodus*. Coelolepida are represented by numerous scales of *Thelodus* and *Lanarkia*. A few fragments certainly belong to the Osteostraci on the basis of their histology (Lehman, 1937, pl. 6, figs. 6, 7; pl. 7, fig. 10), but cannot be identified more closely. Lehman also identified one fragment as arthrodire (1937, pl. 5, fig. 1), but this requires confirmation. Associated invertebrates (Grönwall, 1897, pp. 213, 219–220, 224, 235–238) include brachiopods, pelecypods, gastropods, cephalopods, *Tentaculites*, ostracods, and *Ceratiocaris*. The occurrence is marine, similar to the K_4 Beds of Oesel and to the Beyrichienkalk. Its age is Upper Ludlow or Lower Downtonian.

England, Mocktree Shales: The Church Hill quarry, east of the village of Leintwardine, Herefordshire (Symonds, 1872, pp. 93–94), has yielded the cyathaspine, *Archegonaspis ludensis* (Salter), represented by the type ventral shield, and three doubtful specimens, all rather poorly preserved. The quarry is famous for its well-preserved starfishes, echinoids, and crinoids, which occur in local bands (Hawkins and Hampton, 1927). In addition, there are common brachiopods, molluscs, and graptolites, as well as bryozoans, worms (*Serpulites, Trachyderma,* and *Metaconularia*), xiphosurans (*Limuloides*), eurypterids (*Pterygotus, Eurypterus,* and *Carcinosoma*), and phyllocarids (*Ceratiocaris*). Deposition was probably in a rather shallow sea with gentle currents, perhaps sheltered to some extent by the submarine ridge of the Aymestry Limestone, though the latter was removed by erosion at Church Hill itself (Alexander, 1936, p. 112). The age is, of course, typical Middle Ludlow.

England, Upper Whitcliffe Flags: There is little detailed information available on specific vertebrate occurrences, and published identifications are not always to be relied upon. For these reasons, only a general listing of the records of vertebrates in Shropshire and Herefordshire in these uppermost Ludlow or *Chonetes* beds will be provided. *Cyathaspis banksi* (Huxley and Salter) is known from two specimens from Whitcliffe, opposite Ludlow, Shropshire (White, 1950a, p. 54). The same species probably occurs in the *Chonetes* beds at Bradnor Lane, Kington, Herefordshire (CNHM–PF 1290). Acanthodian spines, usually identified as *Onchus*, are reported from Dean Brook, Wenlock area, Shropshire (Robertson, 1927, pp. 85–86); from near Patton, Corvedale, Shropshire (op. cit., p. 93); from Norton, Shropshire (Straw, 1927, p. 88); from Mathon Court, Malverns, Herefordshire (Phillips, 1848, pp. 97–98); and from Bradnor Lane, Kington, Herefordshire (CNHM–PF 1291). Strangely enough, I find no records of acanthodian scales, so perhaps some of the scales identified as *Thelodus* belong to acanthodians. Coelolepid scales referred to *Thelodus* have been discovered at Clive Cottages, near Ludlow, Shropshire (Straw, 1927, p. 88); at Patton, Corvedale, Shropshire (Robertson, 1927, p. 93); at Norton, Shropshire (Straw, 1927, p. 88); and at Hagley, Herefordshire (Strickland, 1852, p. 384). The marine invertebrate fauna of these Upper Ludlow beds is considerable; it is listed by Elles and Slater (1906, pp. 219–220).

New York, Vernon Shale: The purplish-red Vernon Shales are generally unfossiliferous but have yielded fossils in intercalated gray or buff shales at two localities. From one of these, near Kenwood, Oneida County, Flower and Wayland-Smith (1952) have described the following Cyathaspinae: *Vernonaspis allenae, V. leonardi, Archegonaspis drummondi,* and *A.* sp. They are associated with abundant pelecypods (*Pterinea, Modiolopsis, Nuculites*), less common cephalopods, brachiopods (*Lingula* and *Camarotoechia*), ostracods, annelid jaws, abundant but fragmentary eurypterids, and a colonial, pelagic siphonophore. During preceding Niagaran time this part of New York state was covered by a widespread coral sea, but at the end of the Niagaran there are indications of increasing salinity, accompanied by the Guelph fauna. The waters became more salty during Pittsford-Vernon times, and this is followed by deposition of gypsum and then thick salt (Camillus Shale and Syracuse Salt); a few remnants of the marine fauna were able to persist in the Camillus. The salt deposition was followed by decreasing salinity until more normal marine conditions were attained (Alling, 1928). The Vernon Shale invertebrate fauna undoubtedly consists of marine forms that managed to live at least temporarily in waters of higher than normal salinity. The salinity indicates some enclosure of an arm of the sea, perhaps a lagoon, in which evaporation was considerable. Mud cracks in the Vernon Shale show that the lagoon was shallow and that part of its bottom was exposed at times. The Pittsford and Vernon Shales form the bottom of the typical Salina Group, correlated by Swartz et al. (1942) with the lower part of the Ludlow.

New York, Shawangunk Conglomerate: The base of the Silurian section in Orange County, southeastern New York, is the thick Shawangunk Conglomerate. Its conglomeratic beds are unfossiliferous and its grits contain only trails of *Arthrophycus harlani,* but intercalated black shales contain many eurypterids, which are generally dismembered except for small individuals. The upper part of this formation, known as the Otisville Shale Member, consists of arkosic sandstones and arenaceous shales with little conglomerate. From gray shales in this member came a number of vertebrates, presumably Cyathaspinae (Clarke, 1907, p. 298), whose taxonomic history is extremely confused. They were recorded by Clarke (op. cit., p. 310, pl. 8, figs. 14–21) as phyllocarids, and later described by Ruedemann (1916, pp. 102–105) as a new species of *Anatifopsis,* a phyllopod or cirripede. Bryant (1926, pp. 266–270) realized that they were vertebrates, referred them to *Cyathaspis,* and erected a second species. His own material, however, came from red shales (op. cit., p. 260), and is thus presumably from the overlying High Falls Shale; moreover, none of his material is conspecific with that of Ruedemann and Clarke. Kiaer (1932, p. 24) referred Ruedemann's and Bryant's species to a new genus, *Eoarchegonaspis*, which is undefined and has no validity. Flower and Wayland-Smith (1952, pp. 369–370), in order to avoid further taxonomic confusion, designated an unrecognizable fragment as lectotype of Ruedemann's species, *Anatifopsis wardelli*. At the present, and until this fauna is revised, the vertebrates from the Shawangunk Conglomerate cannot properly be referred to either *Cyathaspis* or *Eoarchegonaspis*, but must be considered as undetermined. According to Clarke (1907, p. 298) they are associated here with the same eurypterid fauna that occurs in the lower black shales. Whether this is a marine or a fresh-water deposit is a much debated question. The age of the Shawangunk Conglomerate has been the subject of much controversy. Swartz and Swartz (1930) have given quite convincing arguments for its Early Silurian (Albion and Clinton) age, but the Otisville Member may possibly be Middle Silurian.

New York and New Jersey, High Falls Shale: As much as 1,350 feet of red shales and mudstones, with some green bands and occasional red sandstones, overlie the Shawangunk Conglomerate in Orange County, New York, and Sussex and Warren counties, New Jersey. In New Jersey they are sometimes called the Longwood Shale. Cyathaspidae have been discovered at a number of localities in these counties, but for the most part have not been determined or described. The material described by Bryant (1926, pp. 266–270) presumably came from the lower part of this formation, near Otisville, New York. His species *"Cyathaspis" vaningeni*, is valid, but does not belong to this genus. The Chicago Natural History Museum collection from this area includes forms close to *Vernonaspis*, as well as others possibly representative of one or more new genera; specimens from one locality approach the Poraspinae in the pattern of the dentine ridges. What evidence there is indicates that this is a fresh-water deposit. The evidence is, however, largely negative, namely, the absence of marine fossils. If this were deposited in the sea, it must have been in littoral mud flats, since mud cracks indicate frequent exposure to the air.

Pennsylvania, Perry County: Three different formations in the Silurian of this county contain vertebrates, including Cyathaspidae and Acanthodii. Since there is little detailed information available regarding the occurrences, only a general account of the section and its contained vertebrates will be given. At the base of the Silurian section is the Tuscarora Sandstone, which is equivalent to part of the Shawangunk Conglomerate, and farther east contains eurypterids of the same species as occur in southeastern New York. It is overlain by the Rose Hill Formation, consisting mostly of olive shales with some calcareous sandstones, and containing brachiopods, trilobites, and ostracods. The Rose Hill Formation includes the Center Iron Sandstone Member, a massive red-brown sandstone with some shale, containing abundant ostracods of the genus *Bonnemaia*, as well as the trilobite, *Calymene* (Claypole, 1885, p. 50; Swartz and Swartz, 1931, p. 628). In this sandstone have been found broken vertebrate plates with a superficial striation similar to that of the cyathaspid, *Americaspis* (= *Palaeaspis*), and spines of the acanthodian, *Onchus clintoni* (Claypole, 1885, p. 58). The age of these beds is Lower Niagaran, perhaps equivalent to the Upper Llandovery of Great Britain.

Overlying the Rose Hill Formation is the Rochester Shale with the Keefer Sandstone Member at the base; it contains marine invertebrates, including brachiopods, pelecypods, gastropods, *Cornulites, Tentaculites,* trilobites, and ostracods. This is followed by the McKenzie Formation, with brachiopods, pelecypods, cephalopods, and ostracods. Then comes the Bloomsburg Formation of red shale and sandstone, with some green bands in the lower part; this contains few fossils except for ostracods, identified as *Leperditia* and *Beyrichia* by Claypole (1885, p. 51). From the Bridgeport Sandstone Member of this formation Claypole (op. cit., p. 58) reported comminuted fish scales that lack bone cell lacunae and resemble the basal layer of *Americaspis.* The age of the Bloomsburg Formation in this region is probably lowermost Cayugan—thus approximately equivalent to the Lower Ludlow of Britain.

The overlying rocks are referred to the Wills Creek Formation, which consists chiefly of greenish shales with some limestone and sandstone and many beds of red shale, especially in the lower part. At its top is the Landisburg (formerly Bloomfield) Sandstone Member, a red and gray sandstone with minor shales, containing *Onchus pennsylvanicus* and abundant Cyathaspidae. The cyathaspids were described by Claypole (1885, pp. 61–63) as *Palaeaspis americana* and *P. bitruncata;* recently they have been referred to *Americaspis.* The type material is lost and it is impossible from Claypole's description to be sure of the systematic position of this form. The Chicago Natural History Museum collection from the Landisburg Sandstone contains at least two types: one, probably *Americaspis,* is intermediate in its ridge pattern between the Cyathaspinae and Poraspinae; the other, a new genus, probably belongs to the Cyathaspinae. Adjacent beds contain numerous ostracods belonging to *Leperditia* and *Kyammodes;* Bryant (1926, p. 265) reports *Lingula* in these beds, but this has not been confirmed. The age of the Landisburg Sandstone is probably Upper Salinan and equivalent to the Middle or Upper Ludlow of England.

Perry County lies in a region in which marine Silurian formations interfinger with relatively barren beds that usually have been considered to be continental. The environment of deposition of the Tuscarora Sandstone is uncertain, since it contains only eurypterids and *Arthrophycus* trails. The Rose Hill Formation is clearly marine, as is indicated by its invertebrate fossils, and this is true also of the Center Iron Sandstone Member; thus the early Cyathaspidae that are found in it were buried in a marine environment. Both the Rochester and McKenzie Formations are marine, but the overlying Bloomsburg Formation, with its relatively barren red beds, has a continental aspect. The most important evidence for its fresh-water deposition is the absence of definitely marine fossils, but its ostracods may be marine, and its deposition may have taken place in a marginal environment where the waters were possibly brackish and were certainly extremely muddy; these conditions may account for the absence of the usual marine fauna. The same remarks apply to the overlying Wills Creek Formation, from which have come most of the Perry County vertebrates. This is succeeded by limestones and shales with marine invertebrates, referred to the Tonoloway Formation.

Maryland, Tonoloway Formation: Swartz (1923a, p. 43) reports "fragments of fish scales" and *Lingula* from the Bloomsburg Formation of Maryland. No vertebrates have been found in the Wills Creek Formation in this state. From the overlying Tonoloway Formation, Swartz (1923b, p. 220) lists *Palaeaspis americana* but gives no information about the horizon or locality. In Maryland the Tonoloway Formation consists mainly of argillaceous limestones and calcareous shales with marine invertebrates, but in the east it also includes a sandstone, the Indian Springs Red Beds; this sandstone is correlated with the Landisburg Sandstone of Perry County, Pennsylvania, but its fossils, if any, are not separately listed.

New Brunswick, Long Reach Formation: The Long Reach Formation in Kings County consists of a variety of intrusive and extrusive volcanics, together with interbedded gray shales, argillites, and small amounts of shaly limestone (MacKenzie, 1951). A large part of the sediments are marine deposits; their invertebrate fauna (Bailey and Matthew, 1872, p. 165) is as yet largely undescribed, but includes brachiopods, bryozoans, corals, etc. On Cunningham

Brook there are dark, fissile shales with a different assemblage of fossils interbedded in the marine sediments. The dark shales contain abundant *Ceratiocaris*, a few conodonts (*Lonchodus*), and *Thelodus* scales. Associated thicker-bedded, dark gray, siliceous shales contain the cyathaspine, *Diplaspis acadica* (Matthew), acanthodian spines of undetermined genus related to *Climatius*, not uncommon large coelolepids, *Thelodus macintoshi* Stetson (1928), which are either complete and articulated or in coprolites, and rare *Ceratiocaris*. Two other fossils are reported from this locality, but their exact horizon and association are not given; they are *Ctenopleuron nerepisense* Matthew (1907), which is probably an anaspid, and *Bunodella horrida* Matthew (1888), which is a xiphosuran. The absence of the typical marine invertebrates that occur elsewhere in this formation, together with the presence of conodonts and *Ceratiocaris*, is best explained by deposition in a marginal marine habitat where the waters were muddy and possibly brackish. The vertebrate assemblage is mixed and includes members of the Cyathaspinae–Acanthodii assemblage (*Diplaspis*, acanthodian, and *Thelodus*), as well as of the Osteostraci–Anaspida assemblage (*Ctenopleuron* and *Bunodella*). The age of the Long Reach Formation may be Middle Silurian (G. S. MacKenzie, in litt.).

Miscellaneous records of Acanthodii: The following occurrences of Acanthodii are based on fragments and will only be noted briefly. They are all marine.

Oesel, K_3 Beds: *Gomphodus* scales and *Onchus* spines occur with a varied marine fauna, especially crinoids. Their age is probably Middle or Upper Ludlow (Hoppe, 1931, pp. 50–55).

Gotland, Eke Group: From the basal part, Spjeldnaes (1950, pp. 211–213) reports acanthodian scales (*Nostolepis* and *Gomphodus*) and coelolepid scales (including *Lanarkia*) associated with a varied marine invertebrate fauna. The age is Middle or Upper Ludlow.

Bohemia: *Onchus* and *Nostolepis* have been found in the Liteň Beds ($e\alpha$) of Llandovery or Wenlock age. *Onchus* and scales of acanthodians occur in the Budňany Limestones ($e\beta$) of Lower or Middle Ludlow age. Both are in a completely marine section (W. Gross, 1950, pp. 64–65).

Portugal: The vertebrate fauna of Ludlow age listed by Priem (1911) is largely misidentified. It includes acanthodian fragments and is found associated with marine invertebrates.

England, Sedgley Limestone: An impersistent bone bed at the top of the Sedgley Limestone contains *Onchus* spines, *Thelodus* scales, and marine invertebrates; it occurs at the base of the Upper Ludlow (Ball, 1951, p. 228).

Conclusions: The majority of occurrences of Silurian Cyathaspinae are in undoubted marine strata, and in one case, the Vernon Shale, there is evidence of higher than usual salinity. In certain of these, where there are indications that deposition took place in shallow waters or near shore, Acanthodii and Coelolepida are associated; these include the K_4 Beds, the Beyrichienkalk, the Öved-Ramsåsa Beds, and the Upper Whitcliffe Flags. Osteostraci are notable by their absence, occurring only as fragments in the Öved-Ramsåsa Beds and doubtfully in the Beyrichienkalk. Anaspida are found in association only in the Long Reach Formation of New Brunswick, which is considered to be a mixed marginal assemblage. Eurypterids, which are common associates of contemporaneous Osteostraci, are found in the Mocktree Shales, Upper Whitcliffe Flags, Vernon Shale, and Shawangunk Conglomerate, but only in the last is there any doubt of the marine environment of deposition.

The occurrences in southeastern New York, New Jersey, and Pennsylvania are usually considered to be fresh-water deposits, and if this is true, they do not fit into the picture presented by the other localities. There are three possible explanations of this discrepancy: The first is that the habitat of Silurian Cyathaspinae was fresh waters, and the occurrences in Canada, Europe, and the Vernon Shales represent individuals washed into the sea. Against this is the number of occurrences in marine deposits, the probable distance from the coast in many cases, and the absence of any indication of Cyathaspinae and Acanthodii in the marginal brackish or fresh-water deposits that contain Osteostraci. A second explanation is that the vertebrate-bearing formations in southeastern New York, northern New Jersey, and central Pennsylvania were not continental but marginal marine deposits. The argument for their continental origin is based largely on the negative evidence of the absence of marine invertebrates, although there is the doubtful positive evidence of the presence of some supposed fresh-water plants in the Bloomsburg Formation (Willard, 1938), and the presence of abundant mud cracks locally. It is not improbable, however, that marine fossils were absent because of such unfavorable conditions as turbid waters and muddy bottoms, reduced salinity, and failure of preservation. In Perry County, Pennsylvania, the presence of ostracods and trilobites shows that the Center Iron Sandstone was marine, and the ostracods of the Bloomsburg Formation and Landisburg Sandstone may also have been marine, though probably marginal. The similarity and proximity of some of these formations to the Vernon Shale supports the possibility of their marine origin. The third explanation is that Cyathaspinae were, in general, marine forms during the Silurian, but in some localities invaded marginal, brackish, or fresh-water habitats. The resemblance of some Cyathaspidae from the High Falls Shale and the Landisburg Sandstone to the Poraspinae suggests that these forms may have been not only structurally distinct but different in habits from typical Cyathaspinae. This explanation must be retained as a possibility at present, pending the closer study of the New York, New Jersey, and Pennsylvania Silurian red beds.

The survey of this Silurian faunal assemblage leads to the following conclusions: The Cyathaspinae were marine forms, inhabiting shallow epicontinental seas, including habitats near the shore; it is possible, though not definitely proved, that some of them invaded marginal brackish or fresh-water habitats. The Acanthodii were also marine forms in the Silurian, but seem to be more typical of near-shore zones. The Coelolepida (*Coelolepis, Thelodus,* and *Lanarkia*) were euryhaline forms that lived in the sea margins as well as in the brackish and possibly fresh-water habitats near the shore.

Early Devonian Vertebrates

EARLY DEVONIAN SUCCESSION OF THE ANGLO-WELSH AREA

In England and Wales the base of the Devonian is taken to correspond to the change in faunas and lithologies that heralds the advent of the Old Red Sandstone. The minor changes that have been made in the boundary have been reviewed recently by White (1950a), and I shall follow him in considering the Ludlow Bone Bed as the base of the Devonian. The current zoning of the Early Devonian Passage Beds and Lower Old Red Sandstone in this region is as follows (White, 1950a, fig. 1; Croft, 1953, p. 429):

Breconian Stage	Brownstones	
	Senni Beds	*Rhinopteraspis dunensis* Zone
Dittonian Stage	Upper	*Rhinopteraspis leachi* Zone
	Middle	*Pteraspis crouchi* Zone
	Lower	*Pteraspis leathensis* Zone

Downtonian Stage	Red Marl Group	*Traquairaspis symondsi* Zone
		Traquairaspis pococki Zone
		Lower Red Marl Group
	Temeside Shales	*Lingula cornea* Zone
	Downton Sandstone	*Lingula minima* Zone
	Ludlow Bone Bed	

Ludlow Bone Bed: This thin bed or beds of concentrated vertebrate and invertebrate fragments is widespread over the Welsh borderland. White (1950a, p. 63), in selecting it as the base of the Devonian, states that it is in this "stratum that the incoming of the vertebrate faunas in the type area is most marked. . . ." My own analysis of its faunal assemblage leads to a somewhat different conclusion. Its vertebrates include Cyathaspinae belonging to *Cyathaspis* and perhaps to other genera. Acanthodii are prominent; there are spines of *Onchus* and *Climatius*, scales of the *Gomphodus* type, jaws (*Ischnacanthus*), and teeth (*Protodus*). Coelolepid scales of the genus *Thelodus* are conspicuous. Osteostraci of a peculiar type, *Sclerodus*, are not uncommon. Among the invertebrates, the most prominent are inarticulate brachiopods (*Lingula* and *Discina*), fragments of worm tubes (probably *Serpulites*), phyllocarid fragments (*Ceratiocaris*), and conodonts. Less common are eurypterids (*Eurypterus*, *Hughmilleria*, and *Pterygotus*), ostracods (*Leperditia* and *Beyrichia*), articulate brachiopods (*Chonetes*, *Dalmanella*, and *Rhynchonella*), gastropods (*Platyschisma* and *Holopella*), pelecypods (*Modiolopsis*, *Goniophora*, *Orthonota*, and *Cucullella*), and cephalopods (*Orthoceras*). There are also plants belonging to *Pachytheca* as well as undetermined remains.

One remarkable thing about this assemblage is that there are very few species in it that do not occur in the underlying Upper Ludlow rocks. The species of *Lingula* are new, and *Platyschisma helicites* is not reported in earlier rocks in this region, although it is elsewhere. The only new vertebrate is *Sclerodus*, and there is the possibility that it does occur in the Upper Ludlow but has escaped detection.

Another feature of the typical Ludlow Bone Bed is that the abundant forms are those with phosphatic hard parts, including vertebrates, inarticulate brachiopods, phyllocarids, conodonts, and worm tubes. The invertebrates with shells of calcium carbonate are almost invariably preserved as molds. The larger preserved fragments are also for the most part relatively dense and hard parts. It is clear from these facts that the Ludlow Bone Bed is composed of fragments of animals that were able to resist solution and abrasion, and the absence of many Upper Ludlow invertebrates may be due to these factors.

While there is little suggestion of the introduction of any new fauna, there was at least a change in the conditions of deposition. This was probably brought about by an increase in bottom currents, perhaps, though not necessarily, caused by a shallowing of the waters, and resulted in the non-deposition or even removal of the silts and fine sands that had been accumulating in the Upper Ludlow. Larger particles, including parts of animals, coprolites, and concretions, would be left by the currents on the bottom where they would be rolled and broken and the calcium carbonate dissolved. Under these conditions the resistant fossils would accumulate over a period of time as a bone bed. It is also possible in some cases that there was actual removal of previously deposited sediment, concentrating any resistant fossils that had been buried before. This bone bed formation was probably a local phenomenon, requiring specific conditions for its accomplishment. While it is found in one form or another over a wide area, it probably was not formed everywhere at the same time. It is apt to be lenticular and may reappear at a slightly higher level. Theoretically, since uplift was taking place to the west, it should occur somewhat earlier there. It is interesting to note, however, that an impersistent bone bed occurs at the top of the Sedgley Limestone in south Staffordshire, thus at the base of the Upper Ludlow (Ball, 1951, p. 228).

Little can be learned from accounts of present-day deposition about the conditions in which bone beds form. Brongersma-Sanders (1949) found fish remains to be generally scarce in recent marine sediments; where there are accumulations she attributes it to periodic mass mortality, and perhaps in some cases to the absence of scavengers due to toxic bottom conditions. Lyell (1868, pp. 773–774) records two occurrences of recent bone beds, one on Rockall Bank at a depth of 80 to 90 fathoms, the other just east of the Faroe Islands in 45 fathoms. In these cases they are associated with an abundance of broken shells, and there is no suggestion of either mass mortality or foul bottoms. In the case of the Ludlow Bone Bed the bottom waters were certainly well aerated, and I do not believe that mass mortality is necessary to explain the abundance of vertebrate remains. If it is, as I believe, a lag concentrate, it must have formed in an area where there was little or no deposition. Such areas are found today over large parts of the continental shelves, including the tops and sides of most banks (Shepard, 1941).

The Ludlow Bone Bed vertebrate fauna is the same as the marine, near-shore, Cyathaspinae–Acanthodii–Coelolepida assemblage of the Silurian. The only new element is *Sclerodus*. As we have seen, the Osteostraci are characteristic of brackish or fresh waters in the Late Silurian. But *Sclerodus* is a form of such peculiar specialization that it must be placed in a family of its own; thus it may well have been adapted to an entirely different manner of life and represent a stock that remained in or migrated into the sea.

Downton Sandstone: This formation consists largely of yellowish sandstones that may be very similar to the Upper Ludlow beds, although they are often more micaceous; there are also thin shaly beds. The total faunal list, assembled from records in various parts of the Welsh borderland, is very similar to that of the Ludlow Bone Bed and includes quite a number of marine Ludlow invertebrates, including brachiopods, gastropods, pelecypods, cephalopods, a trilobite, and even a coral. But the general faunal aspect is very different from that of the Upper Ludlow or the Ludlow Bone Bed. Typical marine vertebrates are generally rare or absent, although this may be caused in part by solution in sediments ill adapted to preserve molds. *Ceratiocaris* and conodonts are not reported, *Lingula* is the only common brachiopod, ostracods may be abundant in some levels, and eurypterids are now an important part of the assemblage, being not uncommon in sandstones and sometimes abundant in shales, as at Perton, Herefordshire. Locally an argillaceous bed near the base may be composed largely of shells of the gastropod, *Platyschisma helicites*, and the pelecypod, *Modiolopsis complanata*. Remains of plants are common for the first time, especially in shales, and include *Pachytheca*, *Cooksonia*, and *Actinophyllum;* some or all of these may have been transported from fresh waters or land (Lang, 1937, pp. 281–283).

Among the vertebrates the usual forms are members of the same marine Cyathaspinae–Acanthodii–Coelolepida assemblage that is found in the underlying beds. *Cyathaspis* occurs at several localities and was once commonly found at Kington, Herefordshire. The Acanthodii, Coelolepida, and *Sclerodus* are essentially the same as in the Ludlow Bone Bed. They occur in the sandstones as well as in local bone beds. There are, however, rare representatives of the brackish or fresh-water Osteostraci–Anaspida assemblage. *Hemicyclaspis murchisoni* is known from a complete, articulated specimen from the Gornal Sandstone, the equivalent of the Downton Sandstone in south Staffordshire (Ball, 1951, p. 232); other records of this species have not been confirmed (White, 1950a, p. 54). *Thyestes* cf. *salteri* occurs near Durlow Common, Herefordshire (CNHM–PF 1289). Anaspid scales are doubtfully recorded by Stamp (1923, pp. 335, 385) from two localities.

The Downton Sandstone appears to have been a marine formation, but the waters may have been somewhat brackish, as is indicated by the reduction of the marine invertebrate fauna and perhaps also by the abundance of eurypterids and *Platyschisma*. The presence of *Hemicyclaspis*, *Thyestes*, Anaspida, and possible land or fresh-water plants suggests that it was deposited near to shore.

Temeside Shales: This formation consists mostly of shales, generally olive, but includes some thin, local grit bands, which may contain abundant vertebrate fragments and are often referred to as bone beds. Lithologically this is quite distinct from the Downton Sandstone, although similar thin shales do occur in the latter. Along with the change in lithofacies, there is some faunal change, though it is not profound. In the shales the most prominent invertebrates are eurypterids, ostracods, and inarticulate brachiopods (*Lingula*), all of which are abundant; the phyllocarid, *Physocaris*, is reported to be common in the Ludlow region, and a xiphosuran, *Limuloides* (=*Hemiaspis*), is recorded (Elles and Slater, 1906, p. 220). Most of these forms are presumably tolerant of brackish waters. There are no typical marine invertebrates in the shales; the only molluscs are undetermined pelecypods. Among the vertebrates there is not a single record of any Heterostraci. However, Acanthodii continue to be common and include scales (*Nostolepis* and *Gomphodus* types), spines (*Onchus* and *Climatius*), jaws (*Plectrodus* and *Ischnacanthus*), and tooth spirals (*Protodus*). Coelolepids have not been previously reported, but *Thelodus* scales do occur near Downton Castle, in Herefordshire. The marine osteostracian, *Sclerodus*, has disappeared, except for one record at Turners Hill, south Staffordshire. Other Osteostraci are still relatively rare, but more have been discovered than in the Downton Sandstone; they include two species of the ateleaspid, *Hemicyclaspis*, as well as the cephalaspid, *Thyestes salteri*.

The Temeside Shales must have been deposited near the margins of the sea. The absence of typical marine invertebrates and Cyathaspinae and the abundance of ostracods and *Lingula* suggest that the waters were brackish. The assemblage is probably mixed, including marine animals tolerant of brackish water and muddy bottoms (ostracods, *Lingula*, pelecypods, *Thelodus*, and acanthodians), as well as forms that lived in fresher waters and could tolerate brackish waters or were washed into the sea margins (Osteostraci, eurypterids, and plants).

Lower Red Marl Group: The Temeside Shales give way to red and green, spotted mudstones, indicating the passage into the base of the typical Old Red Sandstone. There are some beds of red, green, and gray sandstone, pellet bands, and occasional light-colored siltstones. Cross-bedding is common in the sandstones, indicating strong current action, and in one place traces of sun-crack markings have been noted, indicating probable exposure of a shallow bottom (Ball and Dineley, 1952, p. 209). Yet there are many fossils that indicate that deposition was still taking place in the sea, though probably in a marginal environment. These include *Lingula*, the pelecypods, *Modiolopsis*, *Grammysia*, and *Leptodesma*, the ostracod *Leperditia*, one trilobite (from Ledbury, Herefordshire, Bed 7 of Piper, 1898), and possibly *Sclerodus*. But there are none of the Heterostraci or Coelolepida that occur in earlier marine beds. Acanthodii, belonging to the same genera as are found earlier, are not unusual in the Red Downtonian; this group appeared to be characteristic of near-shore, marine habitats in the Silurian, but it is found in non-marine deposits in the succeeding Dittonian, so it is hardly to be relied upon as an indicator of environment at this time. The most striking thing in these beds is the appearance for the first time in some abundance of the Osteostraci, *Hemicyclaspis* and *Thyestes*. With them may be associated the anaspid, *Birkenia*. A new type of osteostracian, *Didymaspis*, makes its first appearance in these beds.

The mixed nature of this assemblage is apparent. This, together with the evidence of shallow water (mud cracks, pellet bands, etc.), suggests that the Lower Red Marl Group was deposited at the margin of the sea. Either it includes interfingering brackish and fresh-water deposits, or fresh-water Osteostraci and Anaspida were washed into and buried in the sea margin.

Upper Red Marl Group, Traquairaspis Zones: The characteristic faunal assemblage of the upper part of the Anglo-Welsh Downtonian includes the following forms: *Traquairaspis*, the zone fossil, a heterostracian belonging to a family of its own; *Anglaspis* and possibly *Poraspis*, belonging to the Poraspinae; a small and primitive

Pteraspis, among the earliest known pteraspids; *Corvaspis,* a heterostracian of uncertain affinities; and various at present undeterminable heterostracian fragments referred variously to *Oniscolepis, Tolypelepis,* etc. The Osteostraci include the first representatives of *Cephalaspis,* as well as *Didymaspis,* which has survived from earlier times. *Tesseraspis* may be an osteostracian. Acanthodian spines, scales, jaws, and teeth are not uncommon, but coelolepids are rarely recorded. There are plants belonging to *Parka, Pachytheca,* and *Zosterophyllum.* The vertebrates are most commonly found in conglomeratic rocks, usually consisting of mudstone or calcareous pellets in a sandy matrix, and often called "cornstones"; in a number of cases they are found in sandstones, in two localities they occur in clay, and in only one in a red marl. Generally the remains are fragmentary, and never is there articulated preservation. It is clear that most of these forms have been transported by rather strong currents.

It is perhaps significant that in no case have marine invertebrates been found in association with this vertebrate assemblage, although they are reported in other localities and horizons in the Upper Red Marl Group. From green silts at Ammons Hill, Herefordshire, and from a few other localities, there have been described the pelecypods, *Modiolopsis* and *Eurymyella,* the gastropod, *Polytropina,* the ostracod, *Leperditia,* and a few eurypterids (King, 1934, pp. 533–534; Reed, 1934, p. 571). The molluscs belong to species elsewhere clearly marine, so their discovery points to persistence, at least at times, of marine deposition in this area into the late Downtonian. The vertebrates and plants may be of fresh-water origin, however; the presence of *Cephalaspis* suggests this, if we may judge from the earlier and later history of the Osteostraci.

It is probable that the Upper Red Marl Group was deposited in marginal, perhaps deltaic, environments. The rare occurrence of marine molluscs indicates occasional marine or brackish deposition, while the appearance of a largely new vertebrate assemblage in otherwise barren beds may well indicate deposition in fresh-water streams on the sub-aerial portion of the delta.

Lower Dittonian, Pteraspis leathensis Zone: The faunal difference between this zone and the underlying Red Marl Group may be due more to evolutionary than to ecological changes. *Traquairaspis* and *Tesseraspis* are no longer found, and *Pteraspis* (subgenus *Protopteraspis*), which was rare in the Upper Downtonian, is now common enough to be used as an index fossil. Otherwise the general aspect of this poorly known fauna is similar, with *Poraspis*, *Cephalaspis*, *Didymaspis*, acanthodian fragments, and rare coelolepid scales. In one locality, Ammons Hill, Herefordshire, invertebrates, some of which are marine or brackish-water forms, have been found in green silts and marls with *Pteraspis*, *Didymaspis*, and acanthodians; they include the pelecypods, *Modiolopsis* and *Carditomantea* (*Pleurophorus*), the ostracod, *Leperditia*, and the eurypterid, *Pterygotus* (King, 1934, p. 534; Reed, 1934, p. 571). Presumably deposition is still marginal and may include interfingering marine and fresh-water deposits.

Middle Dittonian, Pteraspis crouchi Zone: Although "marls" still form the major part of the deposits, beds of sandstone are more common. The sandstones are reddish, green, or brown, are often lenticular and cross-bedded, contain pellet bands, and show ripple marks, sun cracks, and supposed trails of animals (Ball and Dineley, 1952, p. 210). For the first time in this Anglo-Welsh succession there are no reports of invertebrates indicative of marine deposition. In fact, no invertebrates have been collected except for a very few eurypterids, *Stylonurus* and *Pterygotus*, and the problematical arthropod, *Praearcturus*. Plants include *Cooksonia*, *Parka*, and *Pachytheca*. Vertebrates are common locally. Among the Heterostraci, *Poraspis* is rather rare, but *Pteraspis* (*P. crouchi*, *P. rostrata*, *P. jackana*, and *P. stensioi*) is widespread and common. A new type of heterostracian of uncertain affinities, *Weigeltaspis*, makes its first appearance. Among the Osteostraci, *Cephalaspis* is widespread, though common only locally; more specialized Osteostraci, *Securiaspis*, *Stensiopelta* and *Benneviaspis*, appear for the first time. Acanthodii are in general rare, but at the Wayne Herbert quarry, near Newton, Herefordshire, several complete, articulated specimens (cf. *Diplacanthus*) have been found in association with similar specimens of *Pteraspis* and *Cephalaspis* in a single small lenticle of siltstone. There is only a single unconfirmed record of coelolepids. A notable new element in the faunal assemblage is the euarthrodires, represented by the genus *Kujdanowiaspis*. The evidence suggests that we are dealing here with fresh-water deposits, for the first time without any marine incursions. Deposition was presumably in stream channels and flood plains.

Upper Dittonian and Breconian: Fossils are rare in the upper part of the Anglo-Welsh Lower Old Red Sandstone, and none at all have been found in the Brownstones of the Upper Breconian. The same groups of vertebrates occur as in the *Pteraspis crouchi* Zone. Pteraspidae are now represented by *Rhinopteraspis* and *Protaspis*.

Osteostraci, including *Benneviaspis,* have been reported at two localities. Only a single fragment of Acanthodii is recorded. The arthrodire, *Kujdanowiaspis,* persists. No invertebrates have been found. Well-preserved plants have been described from the Senni Beds of the Lower Breconian; they include probable fresh-water algae (*Prototaxites, Nematothallus, Taitea,* and cf. *Pachytheca*), a member of the Psilophytales that may have been aquatic or semi-aquatic (*Gosslingia*), and a lycopsid (*Drepanophycus* = *Arthrostigma*) that was almost certainly a terrestrial plant. It is clear that these strata are stream deposits of the Anglo-Welsh deltas.

Conclusions: The Anglo-Welsh region is extremely important, not only for its classic section of the Silurian-Devonian boundary, but also because it exhibits a gradual transition from marine to fresh-water, deltaic deposition. There can be no question that the Ludlow Bone Bed and Downton Sandstone, with their Cyathaspinae, Acanthodii, Coelolepida, and *Sclerodus,* are marine. It is almost certain that the Middle and Upper Dittonian and Breconian, with their Osteostraci, Pteraspidae, and Arthrodira, are fresh-water stream deposits. Between these two facies there is not a sharp boundary, but a series of transitional sediments that were deposited near the margins of the sea. By themselves the latter would be difficult to interpret ecologically, but when considered in relation to the rest of the section, they may be better understood. They show alternation of marine and fresh-water deposition on the delta and include fossils derived from both the sea and fresh waters. In the Upper Red Marl Group there is a rather distinct vertebrate assemblage characterized by *Traquairaspis, Anglaspis, Corvaspis, Tesseraspis,* and *Cephalaspis,* most of which may be fresh-water genera, although some were surely euryhaline.

DOWNTONIAN AND LOWER OLD RED SANDSTONE OF SCOTLAND

A sequence of passage beds from marine Silurian into fresh-water Devonian is either absent or poorly displayed in Scotland. The so-called "Downtonian Fish Beds" of the Lesmahagow and Hagshaw Hills inliers (see p. 374) are probably Ludlow in age. They are succeeded by conglomerates and sandstones with volcanic rocks in the upper part, which, above a marked unconformity, are called the Lower Old Red Sandstone. The only fossil discovered in the latter is *Cephalaspis;* it is presumably a fresh-water deposit of Dittonian age (Richey et al., 1930).

Cowie Harbour, near Stonehaven in Kincardineshire, has the only section in Scotland that includes certain Downtonian, the

Stonehaven Beds. They consist of 2,760 feet of sediments and volcanic rocks that rest unconformably on Cambrian or Early Ordovician strata and are succeeded conformably by the Lower Old Red Sandstone, Dunnottar Group (Campbell, 1913, pp. 930–933). The Stonehaven Beds are unfossiliferous except for Bed 6, which consists of 600 feet of gray sandstone and sandy shale with green and gray mudstones. The only common vertebrate is *Traquairaspis campbelli*, which, by comparison with Anglo-Welsh and Spitsbergen occurrences of this genus, indicates the Downtonian age of this horizon. There is a single specimen of the osteostracian, *Hemicyclaspis* (*Hemiteleaspis heintzi* Westoll), as well as probable anaspid scales (Westoll, 1945). The associated invertebrates include only *Phyllocarida* (abundant *Dictyocaris*, less common *Ceratiocaris*), Eurypterida (*Hughmilleria* and *Pterygotus*), and Myriapoda (*Archidesmus* and cf. *Kampecaris*). There are also undetermined fragmentary plant remains. Clearly marine elements are absent in this assemblage. On the other hand, the previously discussed occurrences of *Traquairaspis*, *Hemicyclaspis*, and Anaspida indicate that these are fresh- or brackish-water types. The same is true of *Dictyocaris* according to Størmer (1935, pp. 284–286), although *Ceratiocaris* appears to be more common in near-shore marine formations. The habitat of Downtonian myriapods is uncertain, but it was probably either land or fresh waters. The evidence indicates that Bed 6 of the Stonehaven Beds was deposited in fresh waters, but the sedimentary environment is not more closely determinable at present.

The Lower Old Red Sandstone occupies considerable areas on the northern and southern sides of the Midland Valley (MacGregor and MacGregor, 1948, pp. 17–22), as well as a smaller outlier on the Lorne Plateau, near Oban, Argyllshire (Kynaston and Hill, 1908). On the northern side of the Midland Valley, vertebrates are known from the middle part of the series, the Carmyllie and Cairnconnon Beds of Forfarshire, and their equivalents, the Arbuthnott and Garvock Groups in Kincardineshire. Exact correlation with the Anglo-Welsh section is difficult, but these beds certainly represent some part of the Dittonian. The most common vertebrates are the Acanthodii, which are represented by a large number of small but entire, articulated specimens from shales at many famous localities; the following genera are recorded: *Brachyacanthus*, *Mesacanthus*, *Ischnacanthus*, *Parexus*, *Climatius*, and *Euthacanthus*. At least six species of *Cephalaspis* have been found, many represented by complete, articulated specimens; they occur in shaly beds, but more commonly in sandstones. A single specimen of a coelolepid, *Turinea* (=*Cephalopterus*) *pagei*, has been found in sandstones at Turin Hill; as suggested by Westoll (1945, pp. 346–347), this form may be related to the Osteostraci. A striking thing about this fauna, at least by comparison with the Anglo-Welsh Dittonian, is the usual absence of *Pteraspis;* it has been found only near Bridge of Allan, Stirlingshire, and Newtyle, Forfarshire. Associated invertebrates include not common, but sometimes well-preserved eurypterids (*Pterygotus* and *Stylonurus*), and myriapods (*Kampecaris* and *Archidesmus*). In the Lorne area (Read and MacGregor, 1948, p. 60), ostracods are reported (*Aparchites, Isochilina,* and *Beyrichia* or *Drepanella*). Plants include common *Parka* and *Zosterophyllum* (Lang, 1927, pp. 443–452). This has generally been considered to be a fresh-water assemblage; certainly it contains nothing indicative of a marine or brackish-water origin. The presence of ostracods is interesting as being one of the earliest records of a fresh-water occurrence of that group.

The Scottish Lower Old Red Sandstone is believed to have been deposited in a wide depression or Graben between the Highland Boundary and Southern Upland faults (MacGregor and MacGregor, 1948, pp. 21–22). The sandstones were partly fluviatile and partly lacustrine, and the shales were lacustrine. The Acanthodii, which are small, often probably young individuals, are common in the shales, and it may be that this group was characteristic of the lacustrine habitat, though larger individuals may have entered the streams. *Cephalaspis* is more usual in sandstones, and may have been more typically a stream dweller. It is difficult to account for the usual absence of *Pteraspis,* which is the commonest genus of the fluviatile deposits of the Anglo-Welsh Dittonian. It is possible that this genus inhabited the lower reaches of streams and that we are dealing in Scotland with deposits laid down some distance from the sea. The arthrodires are another group that occurs in the fresh-water Lower Old Red of England and Wales but is absent in the corresponding beds of Scotland. It is nowhere a common group in the British Early Devonian, so its absence here is not necessarily significant ecologically.

DOWNTONIAN OF OTHER REGIONS

Schmidt (1939, pp. 36–47) has expressed the opinion that the Downtonian vertebrate fauna represents a paleontological facies, not limited to a certain period of time, and that where the section is marine no Downtonian is recognizable. There is no doubt that this part of the British section is a poor standard for correlative purposes, whatever its ecological interest. On the other hand, the Anglo-Welsh Downtonian does represent a certain period of time, and this time is marked by the various vertebrate zones of White (1950a, p. 53). Since this is a type section, it is important to determine its equivalents in other regions.

Outside of Great Britain there are relatively few vertebrate-bearing formations of Downtonian age. The Fraenkelryggen Division of the Red Bay Series of Spitsbergen is Downtonian in its lower part; this will be discussed later. The Czortków Stage of Podolia has generally been correlated with the Downtonian, but its vertebrates clearly indicate a Dittonian age. The upper part of the Sandstone Series (Stage 10) of Norway has yielded on Jeløya a number of specimens of the osteostracian, *Hemicyclaspis kiaeri*, as well as acanthodian spines; the former suggests an early Downtonian age for these presumably fluviatile deposits (Kiaer, 1931).

Most of the marine deposits that can be correlated with the Downtonian have not yielded any vertebrates, but there are a few exceptions. As was mentioned above (pp. 378–379), the Beyrichienkalk and the Öved-Ramsåsa Beds may include Downtonian equivalents. The Little Missenden borehole in Buckinghamshire, England, penetrated into marine Downtonian, where a number of vertebrate fragments were found in association with marine pelecypods, gastropods, and other invertebrates. The vertebrates have been identified (Woodward, *in* Straw, 1933, pp. 132–134) as Coelolepida (*Thelodus*), Acanthodii (*Climatius*), and Drepanaspidae (*Psammosteus*); the latter is most improbable, and it is suggested that this specimen may be a part of an acanthodian jaw. This occurrence resembles some of the marginal marine assemblages of the Late Silurian, except for the absence of Cyathaspinae.

In Bohemia there is a marine section extending from the Cambrian to the Middle Devonian. The Lochkov Limestone (eγ), which contains vertebrates, is generally considered to be of Upper Ludlow age. However, the upper part of this limestone contains an invertebrate fauna of distinctly Devonian aspect, so its lower part is probably Downtonian. The vertebrates are still inadequately described (W. Gross, 1950, pp. 64–65), but they include not uncommon specimens of *Radotina*. probably the earliest known arthrodire, and a member of a distinct group showing resemblances to the Macropetalichthyida, Rhenanida, and Euarthrodira. Other vertebrates include acanthodian spines resembling the Early Devonian *Machaeracanthus*, acanthodian scales of the *Nostolepis* type, and fragments of the shields of undetermined Heterostraci. There are no Osteostraci, Anaspida, or Coelolepida. Gross also reports *Radotina* from the overlying Early Devonian Konjeprus Limestone. The Lochkov Limestone exhibits a limestone ("reef") facies and a shaly facies. The vertebrates come from the lower part of the shaly facies and apparently have few fossils in association (Perner, 1918, p. 320). The middle part of the Lochkov Limestone is characterized by common eurypterids and phyllocarids in some beds, and a variety of marine molluscs in others. The highest beds have a rich marine fauna. According to Prantl and Přibyl (1948, p. 110) the sediments are "of the neritic type which by their petrographic nature do not indicate at all an immediate proximity to the coast." Assuming that the Heterostraci of the Lochkov Limestone are descendants of the Cyathaspinae, this assemblage resembles the Silurian marine vertebrate fauna, with of course the important addition of early arthrodires.

Elsewhere there has been considerable difficulty in recognizing the typical marine equivalents of the Anglo-Welsh Downtonian. In northeastern France the Psammites de Liévin, at the base of the Gedinnian, contain a *Pteraspis, P. gosseleti*, that is very close to the British *P. leathensis;* they may be correlated with the Lower Dittonian (White, 1950b, p. 86). The underlying marine Schistes de Mèrincourt are certainly Downtonian, and this may be true of some or all of the Couches de Drocourt, Calcaire d'Angres, and Calcaire de Liévin (Shirley, 1938, p. 358). In Podolia, the Czortków Stage is clearly Dittonian on the basis of its vertebrates, so one may look for Downtonian equivalents in the underlying Borszczów Stage. The upper part of the marine section of Gotland, the typical Gotlandian, may extend into the Downtonian (Spjeldnaes, 1950, p. 218). In North America, *Pteraspis whitei* from the Knoydart Formation of Nova Scotia is comparable to *P. leathensis*, and indicates a Lower Dittonian age; so presumably the underlying Stonehouse Formation includes Downtonian equivalents (Denison, 1955, p. 460). This is supported by the resemblance of the invertebrate fauna of the Stonehouse Formation to that of the Downtonian of the Little Missenden borehole in England and to the Beyrichienkalk of Germany (Straw, 1933, pp. 138–139). The precise correlation of the Stonehouse Formation with other North American formations is difficult (McLearn, 1924, p. 29).

EARLY DEVONIAN OF SPITSBERGEN

Large collections from the Spitsbergen Devonian have added much to our knowledge of early vertebrates, but there is still no detailed stratigraphic description of any of these important deposits, nor has much attention been given to their ecological implications. The Early Devonian history is related to the Caledonian orogeny, which resulted in the folding and metamorphism of the earlier Heckla Hoek sediments and in the deposition of a great thickness of Devonian clastics.

Red Bay Series: The lower or Fraenkelryggen Division of the Red Bay Series begins with conglomerates and coarse sandstones, 600 to 800 meters thick. Overlying these, the lowest fossiliferous level, the *Psammosteus* Horizon, is a yellowish-gray sandstone characterized by common remains of an undescribed species of *Traquairaspis,* similar in size to the British *T. symondsi,* and thus suggesting an Upper Downtonian age. The only associated fossils are *Cephalaspis, Corvaspis,* and a form related to *Ctenaspis.* This assemblage recalls that of the upper part of the Anglo-Welsh Downtonian and, like the latter, probably consists of fresh-water forms that lived in the lower reaches of streams.

In many of the succeeding fossiliferous horizons of the Red Bay Series, vertebrates are found in association with pelecypods (*Carditomantea, Prosocoelus, Cypricardinia, Modiolopsis,* and *Pterinea*), and in some levels there are also gastropods, ostracods (*Isochilina* and *Leperditia*), eurypterids (*Pterygotus* and *Eurypterus*), *Lingula, Spirorbis,* and plants. Quenstedt (1926, pp. 52–56) has made a valuable study of the molluscs, in which he concluded (1) that they were benthonic types preserved in most cases where they lived, and (2) that they were marine species, although they may have invaded brackish waters near shore. It is clear from this, and the presence of *Lingula* and perhaps *Spirorbis,* that much of the Red Bay Series was deposited in the sea, though probably near its margin. In some horizons no invertebrates have been reported, and in these cases fresh-water deposition is possible; this is true of the *Psammosteus,* Plant, and *Primaeva* Horizons of the Fraenkelryggen Division, and of levels H, I, P, Q, R, S, T, and the *Vogti* Horizon of the Ben Nevis Division. There is no published information about the nonfossiliferous strata between the named horizons. Holtedahl (1914, p. 710) believed that the Red Bay Series was deposited in a large delta that was covered at certain times by brackish waters. Possibly there is an alternation of marine and fresh-water deposits, but the fact remains that the majority of the vertebrates occur in horizons that are clearly marine.

While many of the molluscs were buried in their natural habitat, this is probably rarely true of the vertebrates, eurypterids, and plants. Usually there is clear evidence of transportation, and the problem is to determine which vertebrates may have inhabited the sea margins and which may have been introduced from fresh-water streams. Excellently preserved, articulated specimens that may have undergone little or no transportation are extremely rare. These include: (1) from Ben Nevis a loose block of uncertain horizon containing six complete specimens of *Pteraspis vogti* (Kiaer, 1928, p. 119); (2) the type of *Irregulareaspis hoeli* from the *Benneviaspis* Horizon (Kiaer, 1932, pl. 5); (3) two individuals of *Anglaspis heintzi* (Pal. Mus., Oslo, D382) probably from the upper part of the Fraenkelryggen Division; and perhaps (4) a specimen of *Cephalaspis pinnifera* lacking only the caudal, second dorsal, and pectoral fins, from somewhere in the *Benneviaspis* Horizon (Wängsjö, 1952, pl. 42). Unfortunately in none of these occurrences is it possible to determine the depositional environment. *Carditomantea* and *Modiolopsis* do occur in the *Benneviaspis* Horizon, but not necessarily at the same level as the articulated specimens of *Irregulareaspis hoeli* and *Cephalaspis pinnifera*. Some horizons contain transported ostracoderm plates in such abundance and in such an excellent state of preservation that it is probable that they were not carried any great distance. Notable examples are *Poraspis polaris* in the *Polaris* Horizon (Kiaer and Heintz, 1935, pl. 1), and *Anglaspis* and *Poraspis* in the *Anglaspis* Horizon. Both of these horizons contain marine pelecypods.

If we approach the problem by considering the occurrence of each group of vertebrates, it appears first of all that the Traquairaspidae are limited to the lowermost or *Psammosteus* Horizon, where there are no indications of marine deposition; this suggests a fresh-water habitat for this family. The Poraspinae (Kiaer and Heintz, 1935) and *Ctenaspis* (Kiaer, 1930) occur throughout the Red Bay Series excepting the lowermost beds, the *Psammosteus* and *Corvaspis* Horizons. Their greatest abundance is in the *Primaeva, Polaris,* and *Anglaspis* Horizons, in the last two of which marine pelecypods occur. Poraspinae are rare in the upper part of the Ben Nevis Group, where marine vertebrates are not reported. This distribution indicates that the Poraspinae and *Ctenaspis* usually inhabited marginal marine, perhaps brackish habitats, though it is probable that some of them were able to enter fresh waters. *Cor-*

vaspis, which is known only from fragments, is common in the *Corvaspis* Horizon, where it is associated with marine pelecypods; it is found also in all the other horizons of the Fraenkelryggen Division, and rarely at two levels (B and *Vogti* Horizons) in the Ben Nevis Division (Dineley, 1953). This distribution shows it to be most usual in marginal marine deposits, but its presence in the non-marine *Psammosteus* and Plant Horizons and the doubtfully marine *Primaeva* and *Vogti* Horizons suggests that it may have lived in fresh-water streams. The first primitive Pteraspidae appear in the *Corvaspis* Horizon, and they are found in all the later horizons of the Red Bay Series. From the little information that is available to me concerning their distribution, there is no suggestion of their preponderance in either marine or fresh-water levels; they may have been euryhaline forms inhabiting both the sea margins and the lower reaches of streams. Osteostraci occur throughout the Red Bay Series and the succeeding Wood Bay Series. Judging from the number of specimens collected, they are by far the most abundant in the fresh-water Wood Bay Series, where 472 specimens are recorded (Stensiö, 1927; Wängsjö, 1952). In the Red Bay Series they are most common in the following: 52 specimens in the *Primaeva* Horizon, where no invertebrates are known; 32 specimens in the *Anglaspis* Horizon, where marine invertebrates occur, though rarely; 31 specimens in the *Benneviaspis* Horizon, where marine invertebrates are not common. The horizons with common marine invertebrates have yielded very few or no specimens of Osteostraci. Thus there is a suggestion of a negative correlation between the abundance of Osteostraci and marine invertebrates, and this supports the presumption of fresh-water habitat indicated elsewhere for the Osteostraci. The only Acanthodii that I have seen in the Red Bay Series collections are spines in the *Primaeva* Horizon. Whether their rarity is real or due to lack of discovery is not certain, so any conclusion from their Spitsbergen occurrence would be questionable.

Wood Bay Series: There are some significant faunal differences between the Wood Bay and Red Bay Series. The Wood Bay Series has yielded no definitely marine invertebrates; in fact, the only invertebrates reported are the ostracods, *Isochilina* (*Hogmochilina*) and *Holtedahlina* (Solle, 1935). Two fresh-water or land plants, *Hostimella* and *Psilophyton,* have been found (Hoeg, 1942). As for the vertebrates, Osteostraci are apparently much more abundant than in the Red Bay Series and include *Cephalaspis* and *Benneviaspis,* carried over from the underlying beds, as well as some new genera, particularly *Boreaspis.* Among the Heterostraci, no

Poraspinae or *Ctenaspis* are found above the Red Bay Series, although this may be due as much to evolutionary extinction as to ecological factors. Pteraspidae continue with the specialized descendants of *Pteraspis—Gigantaspis* and *Doryaspis* (Føyn and Heintz, 1943, pp. 14–16). Few Acanthodii have been found. The most striking thing about the Wood Bay Series fauna is the sudden appearance of euarthrodires in considerable abundance and variety (Heintz, 1929a, b). Along with them come Crossopterygii of the *Porolepis* type. The total aspect of this series is that of a fresh-water stream deposit, preserving Osteostraci, Arthrodira, and perhaps Crossopterygii as typical inhabitants of the streams, and the Pteraspidae as euryhaline forms that often entered the streams.

Grey Hoek Series: The Grey Hoek Series generally overlies the Wood Bay Series conformably, but this simple relationship leaves many unexplained problems of correlation. It is possible that the Grey Hoek Series, at least in its lower part at Gråhuken, is a lateral facies of some of the Wood Bay Series. The lithology is typically gray sandstones and dark arenaceous shales. Pelecypoda are often abundant, though of limited variety (*Ctenodonta, Nucula, Myalina, Montenaria,* and *Avicula*), and there are also gastropods (*Bellerephon* and *Palaeotrochus*) and ostracods. According to Quenstedt (1926, pp. 97–98) the molluscs were purely marine species. At Gråhuken the only vertebrates discovered are a few specimens of euarthrodires (*Arctolepis* and *Mediaspis*) that may be closely related to those of the Wood Bay Series (Heintz, 1937, p. 16). On the west side of Wijde Fjord, in presumably younger beds, the characteristic vertebrates are the macropetalichthyid, *Lunaspis,* and the euarthrodire, *Huginaspis;* associated are two specimens of Osteostraci (*Cephalaspis* and *Acrotomaspis*) and crossopterygian scales and teeth. In the Grey Hoek Series of Huginaspiskardet there occur *Huginaspis* and a probable drepanaspid, "*Psammosteus.*" *Lunaspis, Huginaspis,* and "*Psammosteus*" may represent marine forms, but it is probable that the rare Osteostraci and crossopterygians, as well as a few fragments of plants, were introduced from fresh-water streams.

EARLY DEVONIAN OF PODOLIA AND BUCOVINA

Czortków Stage: Although a few acanthodian spines have been found in the marine Borszczów Stage (Kozlowski, 1929, p. 8), the earliest important vertebrate fauna of Podolia occurs in the overlying Czortków Stage. This has generally been correlated with the Downtonian, but the pteraspids indicate that it is Dittonian, perhaps

Middle Dittonian. The lower part consists of alternating limestones and shales that contain a typical, varied, marine invertebrate fauna. According to Kozlowski (1929, pp. 11–12), this is a deposit of a shallow sea whose muddy bottom was occupied by thin-shelled pelecypods; locally there were large colonies of brachiopods, pelecypods, and other calcareous-shelled organisms, which were at times covered with mud and preserved as lenticular limestones. A few eurypterids and phyllocarids have been found. The vertebrates (Brotzen, 1933b, 1934) occur in all lithologies, and include several species of *Pteraspis,* as well as *Poraspis,* coelolepid scales, acanthodian scales and spines, and rare *Cephalaspis* (Zych, 1937); in addition, there is an arthrodire, *Palaeacanthaspis,* belonging to a group quite distinct from the Euarthrodira (Stensiö, 1944).

The upper part of the Czortków Stage is distinguished as Passage Beds or Übergangsschichten (Brotzen, 1936, p. 5). It contains interfingering green, micaceous sandstones that become more frequent upwards. The shales and limestones still contain the Czortków marine fauna, although in the upper beds ostracods, pelecypods, and eurypterids become dominant and brachiopods become rare, except for *Lingula.* As before, vertebrates occur in all lithologies and include the same genera, though with different species, as in the typical Czortków Stage. In addition, *Irregulareaspis, Ctenaspis,* and *Corvaspis* have been found.

Old Red: This consists mainly of red sandstones and shales without any of the marine layers that persist in the Passage Beds. Marine invertebrates have disappeared entirely. The Old Red is divided into three stages, characterized by their vertebrates. In Stage 1 there are several species of *Pteraspis,* some of which are comparable to those of the Anglo-Welsh Middle Dittonian. *Poraspis* is not uncommon, and the problematical heterostracian, *Weigeltaspis,* appears (Brotzen, 1933a). Osteostraci are now common and include *Cephalaspis, Securiaspis, Stensiopelta,* and *Benneviaspis* (Wängsjö, 1952, p. 584). Acanthodii are present but have not been described. A single fragment of a crossopterygian of the *Porolepis* type has been found. Euarthrodires of the genus *Kujdanowiaspis* appear in some numbers. This assemblage resembles that of the *Pteraspis crouchi* Zone of the Anglo-Welsh area, and there can be little question that it is similar in age and ecology. These are clearly fresh-water, stream deposits without any marine elements, except for certain euryhaline forms.

Stages 2 and 3 show no significant ecological change. In Stage 3 the pteraspids include more specialized forms such as the longsnouted *Rhinopteraspis*, and very broad-shielded *Pteraspis* ("*Brachypteraspis*") and *Protaspis* (Brotzen, 1936). These suggest a late Dittonian or perhaps early Breconian age. The species of *Benneviaspis* (Wängsjö, 1952, p. 585) and *Kujdanowiaspis* indicate that Stage 3 is similar in age to the lower Wood Bay Series, Kapp Kjeldsen Division, of Spitsbergen.

Stage 3 is overlain to the north by sandstones and shales with intercalated marls. These contain undescribed vertebrates, fresh-water or land plants, and eurypterids. They are correlated with the Eifelian by Samsonowicz (1950), but may well be Early Devonian.

Bucovina: A similar section occurs in Bucovina south of the Dneister River in Rumania (Văscăutanu, 1931; Arabu, 1941; Paucă, 1941). Since the vertebrates are still inadequately described and for the most part incorrectly identified, they cannot be considered in comparison with those of the other areas.

Conclusions: The Czortków Stage represents shallow-water marine deposits. Its upper part, or Passage Beds, is marginal marine, and contains an increasing amount of sandstone, derived no doubt from near-by streams. The Old Red is a fresh-water deposit, probably deltaic. Pteraspidae, *Poraspis*, and probably Acanthodii are found not uncommonly in all lithologies in both the marine and fresh-water parts of the section; this suggests, as elsewhere, that they were euryhaline forms, living in the sea margins and in the lower reaches of streams. *Corvaspis*, *Ctenaspis*, and *Irregulareaspis* are known only in the marginal marine Passage Beds; this may have been their habitat, but because of their rarity here, their occurrence is not ecologically significant. Coelolepida, presumably *Thelodus*, are known certainly only from the Czortków Stage; they are probably marginal marine forms. *Palaeacanthaspis* may represent a marine group of arthrodires, since it occurs only in the marine part of the section. The Osteostraci are common in the Old Red and rare in the Czortków Stage; as elsewhere, they are presumably fresh-water stream-dwellers, and the specimens in the marine layers may have been introduced into the sea. *Weigeltaspis*, *Kujdanowiaspis*, and *Porolepis* are probably inhabitants of fresh-water streams and are not known in the marine beds.

CORNWALL–ARDENNES–RHINELAND GEOSYNCLINE

In the Late Silurian there was Caledonian folding of Silurian and older rocks in Cornwall, Devon, Belgium, and the Rhineland. In much of the region this resulted in a major unconformity below the earliest Devonian (Gedinnian) deposits. In northeastern France, near Liévin, this unconformity is slight or absent. Here in faulted subsurface sections pre-Gedinnian, Downtonian and probably Ludlovian, marine sediments are present (p. 399).

Gedinnian: The Gedinnian began with a marine transgression that is indicated by littoral conglomerates and sandstones in the southern part of the geosyncline in Belgium. These are succeeded by marine shales (Schistes de Mérincourt in France, and Schistes de Mondrepuits in Belgium) deposited in deeper water farther from shore. Heavy deposition of clastics from the Old Red Continent to the north then filled much of the geosyncline in this area. Near Liévin, the Schistes de Mérincourt are succeeded by the Psammites de Liévin, a series of marls and shales alternating with red and greenish sandstones (Leriche, 1906, p. 18; Barrois, Pruvost, and Dubois, 1921, pp. 183–184). The marls and shales contain a limited invertebrate fauna, *Ctenodonta, Modiolopsis, Orbiculoidea,* and *Lingula,* all of which might have lived in brackish water. The sandstones contain *Poraspis, Pteraspis gosseleti,* and eurypterids (*Stylonurus*), and may be marginal marine or fresh-water stream deposits. *Pteraspis gosseleti* is Lower Dittonian in age, as is indicated by its similarity to the British *P. leathensis* (White, 1950b, p. 86); the underlying lower part of the Lower Gedinnian must have been deposited during some of the Downtonian.

Upper Gedinnian sediments are more extensive in the geosynclinal area, and include some marine formations. Finds of vertebrates, however, have been restricted to non-marine or marginal-marine deposits in the following localities:

(1) In northeastern France overlying the Psammites de Liévin are the Grès de Pernes. These consist of grits alternating with red and green shales and contain *Pteraspis crouchi, P. rostrata,* and *Cephalaspis* (Leriche, 1948, p. 295; Dollé, 1950). This formation corresponds in age and ecology to the Anglo-Welsh, fluviatile Middle Dittonian. It is followed by the Grès de Vimy, which contains plants and a *Rhinopteraspis* referred, though possibly incorrectly, to *R. dewalquei* (Barrois, Pruvost, and Dubois, 1921, p. 184). This is probably a fresh-water deposit also, and is considered to be Upper Gedinnian in age.

(2) In Belgium on the north side of the Basin of Dinant there is no Lower Gedinnian. The Upper Gedinnian begins with conglomerates and arkoses, which are followed by the Psammites et Schistes de Fooz. The latter contain, at Ombret and Vitrival

(Leriche, 1924, p. 143; 1948, p. 296), plants, *Pteraspis crouchi*, and *P. rostrata*. No invertebrates are associated, and this may be a fresh-water occurrence. In Hainaut the lower part of the Grès de Wihéries (f_2 of Leriche, 1948, p. 283) contains a *Rhinopteraspis* that is close to *R. leachi* (White, 1938, p. 96), and *Protaspis wiheriesiensis* (Brotzen, 1936, p. 20). This horizon is probably Upper Gedinnian, rather than Siegenian, in age. The associated plants and *Modiolopsis* suggest that this may be a marginal marine, brackish-water deposit.

(3) In Belgium and France in the Ardennes, to the south of the Basin of Dinant, the Assise d'Oignies, which overlies the marine Schistes de Mondrepuits, consists of variegated shales containing *Pteraspis crouchi*, and arkoses that may contain a limited marine invertebrate fauna (Pruvost, 1914; Asselberghs, 1946, p. 63; Dubar, 1947). This is apparently a marginal marine facies. It is overlain by the Assise de St. Hubert, probably continental red and green shales with greenish sandstones, which at Carlsbourg have yielded "*Pteraspis*" *dewalquei* but no other fossils (Leriche, 1924, p. 145); this species probably belongs to *Rhinopteraspis*.

(4) In Germany, red shales derived from the Old Red Continent on the north spread at this time to the southern part of the Rheinischen Schiefergebirges. From generally unfossiliferous variegated shales and sandstones on the north slope of the Hohe Venn, Wolfgang Schmidt (1954, pp. 2–35) reports the characteristic forms of the fresh-water Middle Dittonian *Pteraspis crouchi*, *P. rostrata*, *P.* cf. *jackana*, *Cephalaspis*, and acanthodian spines (*Onchus*). The only associated fossils are undeterminable plants in the green sandstones. In Sauerland, the Gedinnian Bunten Ebbe-Schichten have yielded *Pteraspis* cf. *crouchi*, but no fossils are associated (op. cit., pp. 35–37).

Siegenian: Vertebrates are reported in a few cases in marine geosynclinal sediments, deposited at some distance from the shore. In the first three of the following four localities, only the pteraspid, *Rhinopteraspis dunensis*, has been found:

(1) In the Ardennes in the southern facies of the Lower Siegenian (Facies d'Anlier of Asselberghs, 1946, p. 114), near Bertrix and at Mande-Saint-Étienne. Other fossils in this facies include marine invertebrates and plants (*Taeniocrada* and *Asteroxylon*).

(2) In Siegerlands, in the Tonschiefer at the lower part of the typical Siegen beds (Karl Gross, 1948, p. 383). The Tonschiefer contain a varied marine fauna and plants resembling *Taeniocrada*.

(3) In the Herdorfer Schichten of later Siegenian age. In addition to *Rhinopteraspis,* these beds contain a considerable invertebrate fauna and a few plants (Gross, loc. cit.).

(4) An important and varied early vertebrate fauna has been found in the Hunsrückschiefer in the Hunsrück, where the sediments of a muddy bottom have preserved many vertebrates not known elsewhere (W. Gross, 1937, pp. 74–76). *Rhinopteraspis dunensis* occurs here. Probably the commonest vertebrate is *Drepanaspis,* a specialized, flat-bodied, bottom-dwelling heterostracian. *Nessariostoma,* which is known from a single specimen, has been referred to the Stegoselachii but may be a heterostracian. No Osteostraci are known, but the Anaspida are possibly represented by one specimen of *Paraplesiobatis,* although its affinities are still uncertain. There are acanthodian spines belonging to *Machaeracanthus.* A few Euarthrodira occur, mostly described as *Phlyctaenaspis.* The Macropetalichthyidae are represented by two species of *Lunaspis.* The only Early Devonian Stegoselachii (*Pseudopetalichthys* and *Stensioella*) and Rhenanida (*Gemundina*) have been found in the Hunsrückschiefer. There is also a single specimen of a dipnoan, *Dipnorhynchus* (Lehmann and Westoll, 1952). The commonest invertebrates are trilobites, echinoderms, pelecypods, and cephalopods, but there are also xiphosurans, phyllocarids, a scorpion, brachiopods, gastropods, corals, conulariids, and sponges (Richter, 1931). Plants are uncommon. The Hunsrückschiefer were deposited at some distance from shore, in water probably not much more than 100 to 200 meters deep (von Koenigswald, 1930).

Formations deposited nearer the margin of the geosyncline, but still in a marine environment, have yielded vertebrates at two localities:

(1) The Taunusquarzit was deposited near the southern edge of the basin, along the north coast of the German Island (or Mitteldeutsche Schwelle of Wolfgang Schmidt, 1952, p. 165). It is, in part at least, a lateral facies of the Hunsrückschiefer, and the two are seen to interfinger locally. It has a varied marine fauna, but one with dominant pelecypods. The vertebrates have been found in the upper part at Rüdesheim, where they are associated with gastropods, pelecypods, brachiopods, and *Tentaculites* (H. Schmidt, 1933; W. Gross, 1937, pp. 74–76; 1950, pp. 57–58). There is a large species of *Rhinopteraspis,* probably not identical with *R. dunensis. Drepanaspis* was reported by Hermann Schmidt (1933, p. 230) but has not been confirmed. Acanthodian spines have been identified as

Machaeracanthus, Gyracanthus, and *Onchus.* Euarthrodires include *Phlyctaenaspis, Taunaspis,* a form of uncertain relationships, and *Euleptaspis,* the earliest of known Brachythoraci. There is a placoderm that may be related to the Bohemian *Radotina,* and the macropetalichthyid, *Lunaspis,* may be present. Jaws, teeth and scales of the crossopterygian, *Porolepis,* are not uncommon. There are many similarities between this assemblage and that of the Hunsrückschiefer, and it is probable that most of the vertebrates in both were inhabitants of the sea.

(2) The Grès et Schistes de Solières of the Middle Siegenian of Belgium were deposited at the north side of the geosyncline, not far from the coast of the Old Red Continent. The more calcareous beds contain marine invertebrates, and *Rhinopteraspis dunensis* has been found associated with articulate brachiopods. A euarthrodire (*"Coccosteus"*) is also reported (Asselberghs, 1946, p. 154).

There are three occurrences of vertebrates in marginal deposits laid down near the coast of the Old Red Continent. In some cases they may represent brackish-water sediments.

(1) The Facies du Bois d'Ausse (Asselberghs, 1946, pp. 116–120) of the Lower Siegenian, consisting of purplish, green, and variegated shales with some blue or black shales and lenticular sandstones, occurs along the northern border of the Basin of Dinant and the Massif of Stavelot. At Nonceveux, *Rhinopteraspis dunensis* is found in association with eurypterid fragments, abundant pelecypods (*Modiolopsis*), and rare plants (*Zosterophyllum*) (Raynaud, 1942). In the upper level of the Grès de Wihéries (f_1) at Wihéries, *Rhinopteraspis dunensis* and the euarthrodire, *?Prosphymaspis,* are associated with *Pterygotus, Lingula,* and *Modiolopsis* (Leriche, 1948). At two localities near Huy, *Rhinopteraspis dunensis* occurs with no listed associates (Leriche, 1924, pp. 143–146).

(2) The Facies du Bois de Fraipont (Asselberghs, 1946, pp. 187–188) consists of shales and sandstones with red beds and represents some of the Upper Siegenian of Belgium. The only vertebrate reported is the euarthrodire, *Euleptaspis.* Plants occur at many localities (*Taeniocrada, Pachytheca, Nematophyton, Psilophyton*), and brachiopods, pelecypods, *Tentaculites,* and ostracods have been found.

(3) In the Wahnbachschichten of the Upper Siegenian of Overath, Bergischeland (W. Gross, 1933b, 1937; Schriel, 1933), vertebrates occur in association with eurypterids (*Pterygotus* and *Rhenopterus*), trilobites, brachiopods, several pelecypods, and *Tentaculites;*

plants are common in adjacent beds (*Drepanophycus* and *Prototaxites*). The vertebrates include the Heterostraci, *Rhinopteraspis dunensis*, *Pteraspis rotunda* (=?*Protaspis*), and *Drepanaspis*. There are rare fragments of a large species of the osteostracian, *Cephalaspis*. Acanthodii are represented by spines of *Machaeracanthus*, *Gyracanthus*, and *Onchus*, the Euarthrodira by *Phlyctaenaspis*, *Prosphymaspis*, and *Euleptaspis*. The macropetalichthyid, *Lunaspis*, occurs, as well as the crossopterygian, *Porolepis*. This assemblage is very similar to that of the Taunusquarzit, except for the presence of *Cephalaspis*, which has rarely been found elsewhere in the Rhineland Devonian and may have been introduced from fresh waters.

Emsian: Vertebrates have been found in a number of localities in the Emsian of Germany, and in all but one they are in formations of undoubted marine origin, associated with large and varied marine invertebrate faunas. The marine occurrences are: (1) Bendorfer Schichten near Koblenz (Mauz, 1935, pp. 19–23); (2) Nellenköpfchen-Schichten near Koblenz (op. cit., pp. 10–16); (3) Upper Emsian near Koblenz (W. Gross, 1937, p. 64); (4) Stadtfelder Schichten in the Eifel (Mauz, 1935, pp. 19–23); (5) Schleidener Schichten at Gemünd in the Eifel (W. Gross, 1933a, p. 64); (6) Wiltzer Schichten at Daleiden (Lippert, 1939, pp. 37–40); (7) Upper Emsian at Prüm (W. Gross, 1937, pp. 64–65); (8) Upper Emsian at Krekelkirch in the Eifel (W. Gross, op. cit., p. 64); (9) Remscheider Schichten in Bergischeland (Spriestersbach and Fuchs, 1909, pp. 2–7; W. Gross, 1937, p. 25). The vertebrates include *Rhinopteraspis dunensis* (1, 2, 4); acanthodian spines, *Nodacosta* (5) and ?*Machaeracanthus* (9); several euarthrodires including *Prosphymaspis* (2, 4), *Diadsomaspis* (3, 9), and an undetermined form (6). The macropetalichthyid, *Lunaspis*, is the most widespread (2, 3, 4, 7, 8), and crossopterygian fragments of *Porolepis* occur (1, 2).

The Lower Emsian Klerfer Schichten contain marine horizons, but vertebrates occur in levels in which typical marine invertebrates are absent. The vertebrate localities are in the Eifel at: (1) Willwerath (W. Gross, 1937, p. 20; Reuling, 1937, p. 61); (2) Kreuzweingarten (W. Gross, 1937, p. 11; Lippert, 1937, pp. 284–286); (3) Zweifelscheid (Lippert, 1939, p. 14); and (4) Euskirchen (W. Gross, 1937, p. 7). The associated invertebrates are Conchostraca (*Pseudestheria* and ?*Palaeolimnadiopsis*), ostracods (*Leperditia* and *Hogmochilina*), eurypterids (*Tarsopterus*, *Rhenopterus*, *Eurypterus*, and *Pterygotus*), phyllocarids, pelecypods (including *Modiola*), and inarticulate brachiopods. There are also fresh-water or land plants (*Prototaxites*, *Psilophyton, Drepanophycus,* and *?Dawsonites*). The vertebrates are mostly forms that are found in marine rocks of this area, *Rhinopteraspis dunensis* (2), *Drepanaspis* (1, 3), *Phlyctaenaspis* (1, 3), an undetermined euarthrodire (2), and *Porolepis* (3); there is also the osteostracian, *Cephalaspis* (2, 4), which is generally rare or absent in the marine Early Devonian and may have been introduced from fresh waters. The Klerfer Schichten are marginal deposits, possibly brackish and estuarine (Asselberghs, 1946, p. 245; Richter, 1952, p. 344).

Cornwall and Devon: The Early Devonian sections are rather obscure, due in part to the Amorican folding which has made it difficult to determine the sequence of strata and has resulted generally in poor preservation of fossils. In south Devon and Cornwall (Dewey, 1948, p. 17) the base of the Devonian is not seen, the lowest beds exposed being the Dartmouth Slates. These contain the marine gastropods, *Bellerephon trilobatus* and *Loxonema;* King (1934, p. 545) reports *Spirifer mercurii,* but this has not been confirmed. No other invertebrates have been definitely determined, but there are common brown patches that suggest decomposed calcareous organic matter (Ussher and Lloyd, 1933, pp. 30–31). Most of the vertebrates are so poorly preserved that they are difficult to identify. *Rhinopteraspis dunensis* is probably represented by some of the specimens earlier referred to *Pteraspis cornubica. Protaspis* and possibly *Drepanaspis* occur, as well as fragments that may belong to *Cephalaspis.* Acanthodian spines have been referred to *Parexus, Climatius, Onchus,* and *Ctenacanthus* (Reid and Scrivenor, 1906, pp. 8, 11). There are also undetermined Euarthrodira and possibly Macropetalichthyidae. The Dartmouth Slates are Siegenian, or perhaps in part Upper Gedinnian in age, and are probably marine, though the few preserved invertebrates are not sufficient to give a clear picture of the depositional environment.

The overlying Meadfoot Beds (Dewey, 1948, pp. 17–18) have a considerable marine invertebrate fauna that indicates an Emsian or perhaps in part Siegenian age. Pteraspids and undetermined arthrodire fragments are the only vertebrates reported.

In the north Devon section, deposited near the northern edge of the geosyncline (Dewey, 1948, p. 19), the oldest datable Devonian strata are the Lynton Beds. These contain marine invertebrates of Upper and perhaps Lower Emsian age (Simpson, 1951, p. 62). Vertebrates, including probable pteraspids, occur but have not been certainly identified (Hall, 1876; Hamling and Rogers, 1910, p. 468).

The Foreland Grits are generally considered to be older than the Lynton Beds, but this is not proved; they contain obscure fish remains and plants (Evans, 1922, p. 207).

Conclusions: Vertebrate-bearing, marine Early Devonian deposits are best displayed in the Cornwall–Ardennes–Rhineland geosyncline and have yielded an assemblage of forms that are distinctive of the seas of this time. *Rhinopteraspis dunensis* is probably to be considered a member of this fauna because of its wide occurrence in marine rocks; it does occur, however, in marginal deposits, and in Britain in probable fresh-water deposits, so it may be a euryhaline form. *Drepanaspis* is restricted to marine deposits, except for the marginal Klerfer Schichten. Certain Euarthrodira, which belong to genera distinct from those of the fresh-water Wood Bay Series of Spitsbergen, appear to be marine forms; these include *Prosphymaspis, Taunaspis, Diadsomaspis, Euleptaspis,* and possibly *Phlyctaenaspis.* The Macropetalichthyidae (*Lunaspis*) are known only in marine rocks, and it is interesting to note the presence of a possible relative of the marine *Radotina* in the Taunusquarzit. The Stegoselachii and Rhenanida are known in the Early Devonian only in the marine Hunsrückschiefer. Outside of the geosyncline, the members of this assemblage can be recognized only in the Grey Hoek Series of Spitsbergen.

The marginal and fresh-water deposits of the geosynclinal area also contain presumed non-marine and euryhaline vertebrates such as *Pteraspis, Rhinopteraspis, Protaspis, Poraspis,* and *Cephalaspis.* The habitat of certain other forms that occur in the marine Early Devonian is open to some question. The crossopterygian, *Porolepis,* is found in marine formations in Germany and Spitsbergen, yet is perhaps most abundant in the non-marine Wood Bay Series. The single specimen of the dipnoan, *Dipnorhynchus,* is hardly sufficient to indicate the early habitat of the group. Acanthodian spines are found in both marine and fresh-water deposits at this time. The Hunsrückschiefer *Paraplesiobatis,* if it is an anaspid, belongs to a group that is known otherwise only from non-marine deposits.

NORTH AMERICAN EARLY DEVONIAN

Nova Scotia: The Knoydart Formation of Nova Scotia, consisting mainly of red sandstones, siltstones, and shales, contains what is probably the earliest Devonian vertebrate fauna in North America. The commonest form, *Pteraspis whitei,* is similar to *P. leathensis* of Britain and indicates a Lower Dittonian age. Also reported are

Cephalaspis, as well as acanthodian spines and scales (Denison, 1955). The only invertebrates associated are the eurypterid, *Pterygotus,* and the ostracod, *Herrmannina.* The absence of typical marine invertebrates and the similarity of this assemblage to that of the Anglo-Welsh Dittonian suggest that this is a fresh-water deposit. The Knoydart Formation probably grades down into the underlying Stonehouse Formation, which also contains much red sandstone and shale, though it is largely marine. Both formations may be deltaic, one deposited on the submarine portion of the delta, the other on the subaerial part.

Percé, Quebec: A dental plate of *Dipterus* has been reported by Clarke (1913, p. 98) from the Mont Joli Formation at Percé. This specimen has not been described and requires confirmation. The Mont Joli Formation contains marine invertebrates (Schuchert and Cooper, 1930, p. 173) and is of Helderbergian age, thus possibly equivalent to the Gedinnian of Europe.

Wyoming and Utah: The largest Early Devonian vertebrate assemblages occur in the Beartooth Butte Formation of northwestern Wyoming (Bryant, 1932; 1933; 1934; 1935) and in the Water Canyon Formation of northern Utah (Denison, 1952; 1953). They are very similar and include among the Heterostraci a large poraspine, *Allocryptaspis,* common representatives of the pteraspid, *Protaspis,* belonging to several species, and *Cardipeltis,* a specialized derivative of the Poraspinae belonging to a family of its own. Osteostraci are rare, but include three species of *Cephalaspis.* Fragmentary remains of acanthodians include a variety of spines, jaws, and scales. Euarthrodires are among the commonest vertebrates; those from Wyoming belonging to *Bryantolepis, Anarthraspis,* and *Murmur;* those from Utah have not been described but occur in considerable variety. Crossopterygian fragments are found rarely in Utah. Bryant (1932, p. 254) reported a poorly preserved dipnoan skull from Wyoming, and a better one in the Chicago Natural History Museum collections (PF 1427) is referrable to *Dipnorhynchus.*

While the vertebrate assemblages from Utah and Wyoming are very similar, there are important differences in their geological occurrence and in the associated fossils. The Beartooth Butte Formation is a lenticular channel-like deposit consisting of a basal limestone conglomerate, overlain by red or gray limestones and calcareous shales. Besides the vertebrates, the only fossils are eurypterids (*Strobilopterus* and *Eurypterus*) and fresh-water or land plants (*Psilophyton, Bucheria, Hostimella, Sphondylophyton,* and

?Broggeria). According to Dorf (1934, pp. 735–736) this is a channel fill, deposited in fresh or brackish water under estuarine conditions in a drowned river valley.

The Water Canyon Formation, on the other hand, is an extensive, rather uniform deposit of gray, impure, slightly sandy limestone with local calcareous siltstone or sandstone. No invertebrates were reported by Williams (1948, pp. 1138–1139), but they do occur in association with the vertebrates, in considerable abundance on some bedding planes. The commonest form is a pelecypod, not yet determined; in addition there are gastropods, ostracods, and *Lingula*. The phosphatic shell of *Lingula* is preserved, but the molluscs and ostracods are only casts. No plants or eurypterids have been found. The invertebrates, particularly *Lingula*, indicate that the Water Canyon Formation was deposited in a marine environment, but the absence of many typical marine forms suggests that conditions were in some way unfavorable for them. Because of the wide extent of the Water Canyon Formation, brackish-water conditions seem unlikely, unless deposition took place in a large bay with limited access to the sea, as in the Baltic today. It is possible that the restricted variety of invertebrates is due to turbid waters and muddy bottoms.

The great similarity between the Beartooth Butte and Water Canyon Formation vertebrate faunas implies some similarity in depositional conditions. Proximity to land is indicated by the abundance of land or fresh-water plants (and possibly of eurypterids) at Beartooth Butte. The indications of near-shore deposition are less clear in Utah, but the presence of *Lingula* suggests this (Craig, 1952). It is probable that the waters were marine in both states, and that the absence at Beartooth Butte of invertebrates, except for eurypterids, is due in part to non-preservation, and in part to unfavorable conditions for life. As Dorf himself points out (1934, pp. 735–736), above the basal beds there are none of the characters of fluviatile deposits, and the uniform texture and even bedding indicate quiet waters infrequently disturbed. The Beartooth Butte lenticular deposit may represent an arm of a marine bay, rather than a brackish-water estuary.

The similarity in vertebrate faunas extends not only to the presence of the same genera, and in some cases of the same species (as far as these faunas have been studied), but also to the relative abundance of the various groups. In both, *Protaspis* and Euarthrodira are dominant, and *Allocryptaspis* and *Cardipeltis* occur regularly, if not commonly. These forms may all have inhabited the sea margins. On the other hand, *Cephalaspis* is rare and, judging by its occurrence elsewhere, may have been introduced from fresh waters. The rarity of Crossopterygii and Dipnoi in the Early Devonian makes any ecological inferences from these occurrences of little value. Likewise, the small size of acanthodian fragments may account to some extent for their rarity in collections.

The presence of *Protaspis* in these faunas suggests a correlation with the Upper Dittonian and Upper Gedinnian of Europe, although it is possible that they are slightly younger.

Gaspé Sandstone, Quebec: The Gaspé Sandstone has for years been considered to be Middle Devonian by the Canadian Geological Survey. The vertebrates suggest an Early Devonian age, and this is supported by a recent restudy of the invertebrates (Boucot and Cumming, 1954). South and west of the town of Gaspé, the Gaspé Sandstone is now called the York River Formation, and it contains abundant marine invertebrates, especially molluscs, in some levels. On the northeast side of Gaspé Bay, the York River Formation may not occur; here the Gaspé Sandstone is called the Battery Point Formation (McGerrigle, 1946, pp. 44–45). Apparently the latter is, to some extent at least, a lateral facies of the York River Formation.

The Battery Point Formation contains abundant plant remains, but other fossils are generally rare or absent. Lankester (1870) described a *Cephalaspis* that Dawson found in a shale associated with common *Psilophyton;* an adjacent sandstone contained a *Machaeracanthus* spine and stems of *Prototaxites.* Recently Russell (1947; 1954a, b) has described additional forms from shales and mudstones near the d'Aiguillon Postoffice, a locality that he considers to be close to, though not identical with, that of Dawson. The vertebrates are *Cephalaspis* and *?Phlyctaenaspis.* Associated with them are eurypterids (*Pterygotus*), abundant pelecypods (cf. *Modiomorpha*), and undetermined gastropods and plants. At d'Aiguillon Wharf, Kindle (1938, p. 27) reports what he considers to be a marine fauna, including *Lingula* and a few species of small pelecypods; this is presumably at a slightly higher horizon than the vertebrates. The Gaspé Sandstone is considered to be deltaic, and the Battery Point Formation is believed to represent the non-marine portion of the deposits. This may be true for the most part, but the *Lingula* and possibly the pelecypods suggest that marginal marine deposits are included in the Battery Point Formation.

New Brunswick: At Campbellton, New Brunswick, the base of the Gaspé Sandstone can be seen in contact with the eroded surface of underlying volcanic rocks (Alcock, 1935, p. 86). The lower beds consist of a dark gray argillite, a breccia of fragments of tuff in an argillitic matrix, and sandstone. These contain a well-known vertebrate fauna (Romer and Grove, 1935, pp. 813–814) including the following: common *Cephalaspis* belonging to three species; spines and teeth of Acanthodii assigned to various genera; and common Euarthrodira, *Phlyctaenaspis*. Associated fossils are identified as eurypterids (*Pterygotus*), gastropods (*"Cyclora"*), *Spirorbis*, "Entomostraca," and fresh-water or land plants (including *Psilophyton*). In the absence of a critical study of the invertebrates, or of a detailed study of the local geology, there is little on which to base any conclusion on the manner of deposition of these beds. They are generally believed to be of fresh-water origin, and there is certainly nothing known that indicates marine deposition.

SYSTEMATIC REVIEW OF THE HABITAT AND ADAPTATION OF EARLY VERTEBRATES

Heterostraci

Ordovician Heterostraci: These are known only from Colorado, Wyoming, and South Dakota, in sandstones and siltstones that were deposited not far from the shore of the sea. The evidence indicates that they were not introduced into this environment after death, but inhabited the marginal marine zone.

Cyathaspinae: Most Cyathaspinae are found in Silurian and Lower Downtonian marine rocks, usually in shallow-water shelly facies, and occasionally in graptolitic and near-shore facies. This, and their absence in the contemporary brackish and fresh-water assemblages of Oesel, Norway, and Scotland, point toward shallow seas as their habitat. In southeastern New York, New Jersey, and perhaps in Pennsylvania, Cyathaspinae are preserved in what are generally believed to be fresh-water deposits. However, the latter may be marginal marine sediments formed in a shallow water, muddy environment, unfavorable either for the life or preservation of marine invertebrates; it is also possible that locally Cyathaspinae were invading fresh waters in the latter half of the Silurian.

Poraspinae: This subfamily of the Cyathaspidae is characteristic of the Upper Downtonian and Dittonian, and surely did not survive far into post-Dittonian times. Poraspinae are not found in typical marine deposits, although they do occur in marginal marine formations such as the Red Bay Series of Spitsbergen, the Czortków Stage of Podolia, and the Water Canyon Formation of Utah. Their greatest abundance and variety are in the Red Bay Series, where thousands of specimens of *Poraspis* have been found in the near-shore marine *Polaris* Horizon. Articulated specimens are known only from the *Benneviaspis* Horizon (*Irregulareaspis hoeli*) and probably the *Anglaspis* Horizon (*Anglaspis heintzi*) of the Red Bay Series. A disarticulated but partially associated specimen of *Allocryptaspis utahensis* has been found in the Water Canyon Formation. All of these are probably near-shore marine occurrences and suggest that this was the habitat of many Poraspinae. Upper Downtonian and Lower Dittonian finds in England are in sediments that were very probably deposited in fresh or brackish waters, and the Middle Dittonian *Poraspis* of England and Wales and of the Podolian Old Red are clearly in fluviatile deposits. All of the occurrences of Poraspinae indicate either that they were euryhaline forms or that they were originally a group of the sea margins, some of which became adapted to life in the lower reaches of streams.

Possible relatives of the Poraspinae occur in the marginal marine or fresh-water deposits of the Silurian of Pennsylvania and New Jersey. *Ctenaspis,* which should not be included in the Poraspinae, is similar to the latter in its occurrence and probably in its habitat.

Traquairaspidae: Traquairaspis, the only known genus, is perhaps limited to the Downtonian, and is particularly characteristic of its upper part. The most important occurrences are: (1) the Stonehaven Beds of Scotland; (2) Earnstrey Hall Farm, Gardeners Bank, Onon, and other localities in the upper part of the Anglo-Welsh Downtonian; (3) the *Psammosteus* Horizon near the base of the Red Bay Series of Spitsbergen. It is not found in association with definitely marine fossils. At Stonehaven, eurypterids, myriapods, and probably phyllocarids are associated, and elsewhere there are only occasional eurypterids and plants. The vertebrates commonly associated include *Cephalaspis* or *Hemicyclaspis, Corvaspis, Tesseraspis, Anglaspis,* and acanthodians. *Traquairaspis* probably inhabited the lower reaches of streams and perhaps other fresh-water environments.

Pteraspidae: The earliest pteraspids of the Upper Downtonian approach very closely to certain Cyathaspinae, from which they were undoubtedly derived. In the Dittonian they are probably the most prominent vertebrate family, but in post-Dittonian times they decline, leaving only one doubtful descendant to survive into the

Middle Devonian. The majority of pteraspids have been found in fresh-water deposits, particularly in the Middle Dittonian of England and Wales, the Old Red of Podolia, the Wood Bay Series of Spitsbergen, various localities in the Gedinnian of France, Belgium, and Germany, and the Knoydart Formation of Nova Scotia. However, their remains are not restricted to fresh-water sediments; they are common in marginal formations that may have been laid down in brackish or salt waters. Some pteraspids have been found in definitely marine sediments. *Rhinopteraspis dunensis*, for example, has been found in the following marine formations: Tonschiefer, Hunsrückschiefer, Herdorfer Schichten, Stadtfelder Schichten, Nellenköpfchen-Schichten, and Bendorfer Schichten in Germany, and the Facies d'Anlier in Belgium; it is known in near-shore marine formations as follows: Taunusquarzit in Germany, Grès et Schistes de Solières in Belgium, and Dartmouth Slates in Cornwall. Well-preserved, articulated pteraspids are known only from the Wayne Herbert quarry in the Middle Dittonian of England (*Pteraspis rostrata*), from an undetermined horizon in the Ben Nevis Group of Spitsbergen (*P. vogti*), and from Beartooth Butte, Wyoming (*Protaspis*); the first is in fresh-water sediments, the second is uncertain, and the third is possibly marginal marine.

When all the pteraspid occurrences are taken into consideration, it is clear that many inhabited fresh-water streams. Their absence in most of the Lower Old Red Sandstone of Scotland may signify that they were restricted to the lower reaches of rivers. Some pteraspids almost certainly lived in the seas. *Rhinopteraspis*, which is common in marine deposits, yet occurs in the fresh-water Upper Dittonian and Breconian of England and Wales, was probably a euryhaline genus. This may be true also of *Pteraspis* and *Protaspis*, which occur in both fresh-water and near-shore marine deposits.

Drepanaspidae: The Early Devonian drepanaspids are characteristic of marine deposits. *Drepanaspis* is the commonest vertebrate in the Hunsrückschiefer, and probably occurs also in the Taunusquarzit, as well as in the marginal-marine Klerfer Schichten and Wahnbachschichten. Undetermined drepanaspids are probably present in the Dartmouth Slates of Cornwall, and "*Psammosteus*" is reported from the Grey Hoek Series in Spitsbergen. By the Middle and Late Devonian this family has left the seas and is common in fresh-water sediments.

Corvaspis: This genus is a probable derivative of the Cyathaspinae that may represent a distinct family of its own (Dineley, 1953,

p. 179). In Great Britain it is one of the characteristic forms of the Upper Downtonian, where it is associated with *Traquairaspis, Tesseraspis,* and *Anglaspis;* it is also reported from the Middle Dittonian (op. cit., p. 167). Both of these are presumably fresh-water occurrences. In Spitsbergen, it is found in all levels of the Fraenkelryggen Group and in three horizons of the Ben Nevis Group but is abundant only in the *Corvaspis* Horizon, where it is associated with *Cephalaspis, Pteraspis,* and the marine pelecypod, *Carditomantea.* This and some other Spitsbergen occurrences are marginal marine, but the genus does occur also in presumably non-marine levels, such as the *Psammosteus* and Plant Horizons. In Podolia it has been reported, but is rare, in the near-shore marine Passage Beds at the top of the Czortków Stage. *Corvaspis* certainly inhabited fresh waters, but may have been a euryhaline form that was not uncommon in marginal marine habitats also.

Weigeltaspis: This heterostracian of uncertain affinities is known certainly only in the fluviatile sediments of the Middle Dittonian of the Anglo-Welsh area, and from the similar Old Red, Stage 1, of Podolia.

Cardipeltis: This genus is a specialized derivative of the Poraspinae and represents a distinct family. It has been found only in the Beartooth Butte Formation of Wyoming and the Water Canyon Formation of Utah, where its occurrences suggest that it was an inhabitant of the sea margins.

Summary of heterostracian habitat: The early Heterostraci of the Ordovician and Silurian lived in the sea, many of them near the shore. In the Late Silurian some Cyathaspinae may have begun the invasion of fresh or brackish waters. In the Early Devonian the sea margins continued to be an important habitat of the Heterostraci, though members of most families penetrated into streams, at least into their lower reaches. Some of these stream dwellers may have been euryhaline forms (Poraspinae, *Ctenaspis,* Pteraspidae, *Corvaspis*); others possibly became definitely adapted to fresh-water life (*Traquairaspis, Weigeltaspis*). The Drepanaspidae remained in the sea during the Early Devonian and did not get into fresh waters until later.

Adaptation of Heterostraci: Of the habitus of Ordovician Heterostraci nothing is known except that they had a heavy exoskeleton, which of course is more or less true of all members of the order. The Cyathaspidae of the Silurian and Early Devonian were free-swimming forms, judging by their rather fusiform shape. The body shows dorso-ventral compression anteriorly, lateral compression posteriorly, and rounding at the anterior end. The ventral shield sloped up in front to form a surface that provided lift to the anterior end in swimming. The only locomotor organ was the posterior part of the body, which was provided with relatively few large scales, indicating limited flexibility. The tail, at least in *Anglaspis*, was of a modified protocercal type in which the axis turned slightly downward and ended in a ventrally placed lobe. In the absence of a well-developed, flexible, epichordal lobe, the downward component of thrust may have made this tail functionally slightly epibatic. Some of the Poraspinae developed small lateral and dorsal keels, but there were no paired fins in these or in any other Heterostraci. Essentially the Cyathaspidae were tadpole-like swimmers, possibly the primitive vertebrate method of locomotion. The eyes were laterally directed and extremely small, and the paired nostrils were situated inside the mouth. The mouth faced ventrally and was provided, if we may judge from the situation in *Pteraspis*, with small, dermal, oral plates, but of course with no true jaws. They may have been nibblers but not biters. These early Heterostraci were probably only moderately active, non-predaceous forms, feeding on plants, small invertebrates, or bottom debris.

The Pteraspidae show no very great modification of the cyathaspid adaptation. In *Pteraspis* and *Rhinopteraspis* the anterior end develops a more or less elongate rostrum, and the posterior part of the body becomes more flexible as a result of the reduction of scale size. The tail is hypocercal and presumably hypobatic, an adaptation for increasing the angle of attack and the lift on the anterior part of the body in swimming. Some pteraspids developed large dorsal and lateral keels, particularly *Doryaspis*. *Protaspis* shows benthonic adaptation in its broad, flattened carapace and nearly protocercal, isobatic tail.

The Drepanaspidae were benthonic Heterostraci with bodies very broad and flat anteriorly, and relatively slender tails. The orbits, though far lateral in position, were directed dorsally. These were probably mud-grubbing, bottom feeders. *Corvaspis* and *Cardipeltis* may have been somewhat similar, broad, rather flat, bottom-living Heterostraci.

Coelolepida

The typical members of this group—*Thelodus*, *Coelolepis*, and *Lanarkia*—may possibly be related to the Heterostraci (Westoll, 1945, p. 347). Articulated specimens have been found in the marginal marine sediments of Bed 3 of the Lesmahagow inlier, Scotland, and of the Long Reach Formation of New Brunswick; they are also known in Bed 9 of the Lesmahagow inlier, and in the lower part of Stage 10 in Ringerike, Norway, both fresh or brackish-water sediments deposited near the sea. Scattered scales occur in many localities and are particularly characteristic of near-shore, marine facies. In a few cases scales are found in brackish-water sediments, but apparently they are very unusual in typical fresh-water deposits. These coelolepids lived near the shore of the sea but were sufficiently euryhaline to survive in brackish and perhaps temporarily in fresh water. The members of this group are too poorly known to permit any speculations regarding their adaptations and manner of life.

Osteostraci

With the exception of *Sclerodus*, the Osteostraci appear to have been restricted to fresh and brackish waters during their recorded history. There are occasional finds in marginal marine deposits, but in such they are always rare and usually fragmentary. These include the Beyrichienkalk of Germany, the Burgsvik Sandstone of Gotland (Spjeldnaes, 1950, p. 211), the Öved-Ramsåsa Beds of Sweden, the Lower Downtonian of England, the Red Bay and Grey Hoek Series of Spitsbergen, the Czortków Stage of Podolia, the Wahnbachschichten and Klerfer Schichten of Germany, the Dartmouth Slates of Cornwall, the Water Canyon Formation of Utah, and the Beartooth Butte Formation of Wyoming. In all these cases the Osteostraci are considered to be individuals carried by streams into the sea.

The earliest known Silurian Osteostraci, those of the K_1 Beds in Oesel, inhabited a marginal lagoon in which the waters were probably brackish. Other Silurian Osteostraci inhabited fresh or brackish rivers or lakes. In the Early Devonian this group is most common in typical stream deposits, such as the Old Red of Podolia and Scotland, the Middle Dittonian of England and Wales, and the Wood Bay Series of Spitsbergen. The few that are known from the Middle and Late Devonian seem to have persisted in this habitat. It is interesting that the coelolepid, *Turinea*, which Westoll (1945, p. 346) believes to be related to the Osteostraci, occurs with them in the fluviatile deposits of the Lower Old Red Sandstone of Scotland.

Sclerodus is known only from the Lower Downtonian of England, always in marine or marginal marine deposits. As was stated above, this is probably a specialized side-branch of the Osteostraci that remained in or returned to a marine habitat.

Tesseraspis, which was considered by Wills (1935, p. 439) to be a drepanaspid, very possibly belongs to the Osteostraci. It is found only in presumed fresh-water, deltaic sediments of the Upper Downtonian of England and Wales.

The Osteostraci show adaptation to bottom life in their dorsally placed eyes and nasal opening, the ventrally facing mouth, and usually in their flattened ventral surface. The well-developed exoskeleton served as a defensive armor. In the absence of true jaws, they probably fed on bottom detritus, and their relatively huge pharyngeal cavity and numerous gills may have served in part as a mechanism for filtering the food particles from the water. The most primitive forms, *Tremataspis*, *Oeselaspis*, and *Dartmuthia*, were less extremely specialized for bottom life. In the absence of paired fins, and with a relatively short, flexible, scaled, posterior body, they can be compared in their locomotion only to the Cyathaspidae and to tadpoles. Most of the later forms possessed pectoral fins, had well-developed lateral and dorsal keels, and had a more elongate, more flexible, post-cranial locomotor organ; these features must have given them more control in swimming. The Cephalaspidae, which are characterized by the presence of cornua lateral to their pectoral fins, show a striking similarity to certain recent Loricariidae; the latter, like the cephalaspids, are stream dwellers.

Anaspida

Like the Osteostraci, the Anaspida appear to be restricted to non-marine habitats during their known history. The genus *Paraplesiobatis*, known only from a single specimen from the marine Hunsrückschiefer, shows resemblances to the anaspids in its dorsal ridge scales but in other features does not agree well with known members of this group. Very rare and usually fragmentary anaspids may occur in marginal marine deposits, into which they were probably washed from fresh waters. These include the Long Reach Formation of New Brunswick, Bed 3 in the Lesmahagow inlier of Scotland, and the Lower Red Marl Group at Baggeridge Colliery, Staffordshire. On the other hand, the two outstanding anaspid occurrences, in the lower part of Stage 10, Ringerike, Norway, and Bed 9 of the Lesmahagow inlier, are not marine. They are found in sediments probably deposited on the sub-aerial portion of a delta (Norway), or in a fresh or brackish lake near the sea margin (Scotland). A few anaspids are found in brackish lagoonal deposits of the K_1 Beds of Oesel. These same deposits contain the coelolepid, *Phlebolepis,* which differs considerably from typical coelolepids of the *Thelodus* type and, as Westoll suggested (1945, pp. 347–348), may be related in some way to the Anaspida. Rare anaspids have been found in the Stonehaven Beds of Scotland and in the Lower Red Marl Group of Ledbury, Herefordshire (Bed 3 of Piper, 1898); both of these occurrences are probably non-marine, though the latter may be marginal marine. The only other Anaspida known are *Euphanerops* and *Endeiolepis,* which occur in Late Devonian fluviatile deposits at Escuminac Bay, Quebec.

The anaspids were adapted for an entirely different mode of life from that of their associates, the Osteostraci. Their body shape indicates that they were nectonic forms, and the Silurian anaspids were, for their time, rapid swimmers. This is shown by their fusiform shape, strongly metameric body, well-developed caudal fin, and relatively large eyes. The dorsal ridge scales and perhaps the pectoral spines acted as keels, but their swimming could not have been as well controlled as in most modern fishes because they lacked paired fins, except in the Late Devonian survivors. Their outstanding specialization was the hypocercal tail, which must have functioned to depress the posterior part of the body. The adaptive significance of this feature is not clear, but, as suggested by Harris (1936, p. 492), it may indicate that they were surface feeders. This is in keeping with their possession of a nearly terminal mouth. In the probable absence of gill-arch jaws, the anaspids were surely not predaceous forms, but they may have fed on plankton and small nectonic invertebrates.

Miscellaneous Agnatha

The denticles of *Archodus* and *Palaeodus* from the Early Ordovician of Russia were found in the marginal marine Glauconite Sand, an occurrence similar to that of the North American Ordovician Heterostraci. Presumably they belonged to marine Agnatha.

Conodonts are believed by Walter Gross (1954, p. 84) to represent the skeletal parts of otherwise unknown Agnatha. They occur from the Ordovician to the Triassic in marine and perhaps in brackish-water deposits, but apparently do not occur in fresh-water sediments. Their distribution suggests that they were nectonic forms, possibly in some cases pelagic (Ellison, 1944). They are particularly common in near-shore marine facies.

Jamoytius, from the Late Silurian of Scotland, was believed by White (1946, p. 93) to be the most primitive of known vertebrates, and a form that was close, structurally at least, to the ideal ancestor of Agnatha and perhaps even *Amphioxus*. I am inclined to interpret this form quite differently, considering it to be for its time an advanced, though not necessarily highly specialized, vertebrate. The absence of dermal armor, the fusiform body, the presence of long lateral and dorsal fin folds (if they really do exist), the highly developed metamerism, and the large eyes are all characters of a very active, fast-swimming vertebrate, functionally more progressive than most of its contemporaries. Whatever its evolutionary position, its occurrence in Bed 3 of the Lesmahagow inlier indicates that the habitat of *Jamoytius* was probably in near-shore marine environments.

Acanthodii

Romer and Grove (1935, p. 844) concluded that the Acanthodii were "essentially fresh water forms throughout their history." This does not agree with their occurrence as interpreted here. Silurian Acanthodii appear to be restricted to marine sediments, and largely to those deposited near shore. This is certainly true in the K_3 and K_4 Beds of Oesel, the Hemse and Eke Groups of Gotland, the Öved-Ramsåsa Beds of Sweden, the Beyrichienkalk of Germany, the Borszczów Stage of Podolia, the Liteň Beds (eα), Budňany Limestones (eβ), and Lochkow Limestones (eγ) of Bohemia, the Late Silurian of Portugal, the Upper Whitcliffe Flags of England, and the Center Iron Sandstone of Pennsylvania. In the Long Reach Formation of New Brunswick acanthodians occur in a mixed assemblage that probably accumulated in a marginal marine zone. In the Landisburg Sandstone of Pennsylvania they are found in a marginal deposit, possibly though not certainly marine.

Silurian Acanthodii are known only as fragments such as spines, scales, teeth, and jaws. This implies post-mortem transportation, and Romer and Grove believe that they were introduced from rivers. This is not necessarily so, because the marginal marine environments generally are ill-suited for good preservation; their currents and waves would probably disarticulate and scatter any carcasses. There is, however, direct evidence of their absence in Silurian non-marine deposits, for not a single trace of any acanthodian has been found in the K_1 Beds of Oesel, in the lower part of Stage 10 in Ringerike, Norway, and in Bed 9 of the Lesmahagow inlier of Scotland. These are all brackish or fresh-water deposits that have been intensively collected, and it is unlikely that acanthodians would have been overlooked if they were present. It is most improbable that they could have been introduced frequently from fresh-water streams or lakes into the sea margins and yet not appear in some of these three deposits. The conclusion is that in the early part of their history they were a marine group characteristic of near-shore habitats.

In the Early Devonian, Acanthodii are still found in marine and marginal marine formations, but in addition there is evidence that many of them lived in fresh waters. The well-preserved specimens of the Lower Old Red Sandstone of Scotland occur in clays that probably represent lake deposits. The majority of them are small, perhaps juvenile individuals, so it is possible that lakes were their spawning and nursery grounds. Large articulated acanthodians have been found in the siltstone lenticle of the Wayne Herbert quarry of Herefordshire, in a deposit that probably represents a dried-up pool on a river's flood plain. Thus it is clear that at least by Dittonian times some acanthodians had left salt waters.

In their later history, which extends to the Early Permian, Acanthodii are found in both marine and non-marine deposits. Probably they were euryhaline forms, but it is possible that different forms became adapted to different salinities. In any case, it appears that as a group the Acanthodii never completely left the marine habitat.

The early Acanthodii, the first gnathostomes to appear, were perhaps the most active and speedy swimmers of their time. The Silurian genera were probably similar to Early Devonian forms in possessing a fusiform, highly flexible body, a well-developed heterocercal caudal fin, and relatively large eyes. In the more primitive forms the paired fins were often numerous and, like the median fins, functioned as little more than keels, although the relatively large pectoral fins undoubtedly acted as aerofoils to balance the effects of the heterocercal tail. Later forms had the paired fins reduced to the usual number of two pairs, and developed various characters that indicate they were capable of some controlled movements, leading to better directional control in swimming. The Acanthodii possessed well-developed gill-arch jaws, a large subterminal mouth, and sometimes relatively large conical teeth—features that indicate a predaceous habit. A specimen in the British Museum (Natural History), P19999, suggests that Osteostraci may have formed part of the diet of fresh-water acanthodians. This large individual from the siltstone lenticle of the Wayne Herbert quarry apparently contains within its body cavity the head shield of a small *Cephalaspis*. That this *Cephalaspis* had actually been eaten is supported by the fact that it is the only small individual and the only non-articulated specimen of this genus in the lenticle, and also by the poor preservation of its surface, which suggests that it had been acted on by digestive juices.

Placodermi

When they first appeared, the placoderms were already diversified into several orders, the majority of which occur only in marine deposits. Probably the earliest known member of this class is *Radotina*, which is found in the marine Lochkov and Konjeprus Limestones of Bohemia; a placoderm in the marine Taunusquarzit of Germany may belong to the same genus. *Radotina* has been placed in an order of its own, the Radotinida, by Walter Gross (1950, p. 117). A better-known group is the order Macropetalichthyida, whose Early Devonian representative, *Lunaspis*, is characteristic of marine deposits of that age. In addition to the localities discussed in pages 403–411 of this paper, *Lunaspis* occurs in marine formations in the Taymir Peninsula, Siberia; near Lake Balkash, Turkestan; and on the River Kosva in the Urals (Obruchev, 1939; 1940). The Middle and Late Devonian Macropetalichthyidae, *Macropetalichthys*, *Notopetalichthys*, and *Epipetalichthys*, are all marine forms. The third early order of marine placoderms, the Acanthothoraci, is represented by *Palaeacanthaspis*, a genus known only from the marine Czortków Stage of Podolia. There is a possibility that it is related to the Ptyctodontidae, a family that occurs in both marine and fresh-water deposits in the Middle and Late Devonian. Other marine placoderms appearing in the Early Devonian are the Stegoselachii (*Stensioella* and *Pseudopetalichthys*) and Rhenanida (*Gemundina*, *Asterosteus*, and *Jagorina*).

The Euarthrodira (in the sense originally used by Walter Gross, 1932, p. 10) are notable for their strikingly sudden appearance in considerable numbers in fresh-water deposits of Gedinnian (Dittonian) and Lower Siegenian age. They are completely absent in the marginal marine Red Bay Series of Spitsbergen but are common in all divisions of the overlying fresh-water Wood Bay Series. They are absent in the Czortków Stage of Podolia but are relatively common in the overlying Old Red. They are absent from the Anglo-Welsh Downtonian and Lower Dittonian (except perhaps for one fragment in the latter) but appear at several localities in the Middle and

Upper Dittonian. In these three cases there is a sequence of strata passing from marine to non-marine, and the appearance of euarthrodires is correlated with the transition to fresh-water, fluviatile sediments. This indicates that the earliest known euarthrodires made their home in rivers. In Great Britain and Podolia, *Kujdanowiaspis* is found; in Spitsbergen there are primitive genera in the lower part of the Wood Bay Series (*Arctaspis, Svalbardaspis*), while higher beds include more specialized forms such as *Arctolepis* and *Actinolepis.*

In Siegenian and Emsian times the Euarthrodira were no longer restricted to fresh-water sediments. Some of them did remain in streams, including *Arctolepis* and *Actinolepis* of the Wood Bay Series and probably *Phlyctaenaspis* of the Gaspé Sandstone of New Brunswick and Quebec. But other genera are characteristic of the marine and marginal marine Siegenian and Emsian of Germany and Belgium; these include *Prosphymaspis, Diadsomaspis, Taunaspis,* and *Euleptaspis; Phlyctaenaspis* is also reported in German marine beds, but in no case is identity with this genus certain. In the marine Grey Hoek Series of Spitsbergen, *Huginaspis* is the most characteristic euarthrodire. Presumably the euarthrodires of the Beartooth Butte Formation of Wyoming and the Water Canyon Formation of Utah are marginal marine forms. The Early Devonian record thus indicates that early Euarthrodira lived in rivers, while some migrated into the seas in the Siegenian. In the Middle and Late Devonian they are found in both habitats.

This review shows that the original habitat of each order of placoderms is suggested by its geological occurrence, but there is little indication of the ancestral home of the whole class.

Radotina and *Palaeacanthaspis* are too poorly known to allow much speculation about their manner of life. Other Early Devonian placoderms exhibit two major adaptive types, the first of which is seen in the early Euarthrodira and Macropetalichthyida. As in most placoderms, these have a heavy exoskeleton that probably functioned in part as a defensive armor. This is divided by an articulation in the post-cranial region into a head and trunk shield, the latter serving as a shoulder girdle. This peculiar articulation allows only vertical movements of the head with respect to the posterior part of the body; whatever its other functions may have been, it offered a means of controlling the angle of attack in swimming. With the exception of this articulation of the skeleton, the early Euarthrodira and Macropetalichthyida are very similar adaptively to the Cephalaspidae. The body has a flattened ventral surface, the head is broad and flat, there are large pectoral spines firmly attached to the trunk shield, and mediad to the spines are narrow-based pectoral fins, directed posteriorly. These features suggest a benthonic habit, comparable to some extent to that of the recent Loricariidae. The bottom-dwelling adaptations are less extreme than in the Cephalaspidae, for the eyes, though small, are directed laterally, and the nasal openings are directed ventrally. The placoderms possessed true gill-arch jaws, although little is known about them in Early Devonian forms. Presumably in the latter the mouth was ventrally situated, much as in sharks, and the jaws, while capable of biting, were used for feeding on small, benthonic invertebrates. Many latter marine Euarthrodira developed into nectonic, rapid-swimming, highly predaceous types, comparable to sharks.

The second major adaptive type in Early Devonian placoderms is exhibited by the marine Rhenanida, which were strikingly similar adaptively to the rays. The head and anterior part of the body were broad and flat, and the pectoral fins became enormously expanded so as to become the most important locomotor organ. The tail, at least in the Early Devonian *Gemundina,* was not reduced to the same extent as in rays. The mouth was terminal and faced somewhat upward, and the eyes and nostrils were both dorsally directed and not far from the midline. Their habits may have been essentially benthonic, as in most rays. *Pseudopetalichthys,* a stegoselachian, possibly represents an early stage in this adaptation.

Osteichthyes

The first Osteichthyes are found in the Early Devonian, but their remains are so rare and fragmentary that it is not possible to come to definite conclusions regarding their original habitat. Most common in the Early Devonian are Crossopterygii, which at present are referred to *Porolepis.* The earliest record is a single fragment from the Old Red, Stage 1, of Podolia, of Middle Dittonian age. The largest number of specimens have been obtained in the Wood Bay Series of Spitsbergen. Both of these are fluviatile deposits. On the other hand, Crossopterygii occur in marine and marginal marine formations at a number of places, as follows: Grey Hoek Series of Spitsbergen; Taunusquarzit, Wahnbachschichten, Klerfer Schichten, Bendorfer Schichten, and Nellenköpfchen-Schichten of Germany; Early Devonian of the Taimyr Peninsula, Siberia (Obruchev, 1940);

and the Water Canyon Formation of Utah. These few, scattered finds do not establish the original habitat of the group. Middle and Late Devonian Crossopterygii, however, are exclusively fresh-water forms with the exception of some coelacanths.

Of Dipnoi there are only five specimens recorded from the Early Devonian. A tooth identified as *Dipterus* has come from the marine Mont Joli Formation of Quebec. A dipnoan dental plate, as yet undescribed, occurs in the marginal marine Water Canyon Formation of Utah. Two cranial roofs, one referable to *Dipnorhynchus*, have been found in the Beartooth Butte Formation of Wyoming in possibly marginal marine deposits. A head of *Dipnorhynchus* is described from the marine Hunsrückschiefer. With the possible exception of the Beartooth Butte record, these are all marine occurrences. In the Middle and Late Devonian, lungfishes are found in both marine and fresh-water deposits, and presumably they lived in both habitats during those times. Later Dipnoi were largely if not entirely restricted to fresh waters. The early occurrences do not offer any support for the often presumed original fresh-water habitat of this group; in fact, they suggest a marine origin.

No Actinopterygii are known from the Early Devonian. In the Middle Devonian well-preserved specimens occur in the fresh-water Old Red Sandstone of Scotland and the Shetland Islands, and also in the marine Plattenkalk of Germany (W. Gross, 1953). In the Late Devonian they are found in both marine and fresh-water habitats. Again, their early occurrence gives no indication of their original habitat.

The fresh-water origin of the Osteichthyes has been argued on theoretical grounds (Romer and Grove, 1935, p. 847). Lungs are present in modern Dipnoi, and presumably Devonian lungfish possessed them also. They must have been present in those Devonian rhipidistian crossopterygians that gave rise to land vertebrates. If we accept the homology of lungs and air bladders, they were probably present in some form in early coelacanths and actinopterygians. Now, either lungs were independently acquired in each of these groups of bony fishes, or else they were present in their common ancestor, probably of Silurian age. If the first alternative is true, lungs may have been acquired at any time in the fresh-water history of each group. If the second alternative is correct, it implies that the common ancestor must have lived in fresh waters in the Silurian. For lungs in fishes are an adaptation for life in poorly oxygenated waters, and since such are unlikely in the sea they are almost certainly an adaptation for life in stagnant fresh water. Either of these arguments is possible, though it is unlikely that lungs would be independently acquired in the three groups of Osteichthyes.

The early Osteichthyes were essentially similar to many modern teleosts in their adaptation, and they must be reckoned among the best swimmers of their time. The crossopterygians had powerful jaws and well-developed, pointed marginal teeth, indicating that they were predaceous. They may have fed largely on other fishes. The Dipnoi are characterized particularly by the reduction and loss of marginal teeth, the development of dental plates borne on the pterygoids and prearticulars, and the fusion of the palatoquadrates with the cranium. The original adaptive significance of these features is not clear. The primitive lungfish dental plate probably had distinct conical teeth arranged in rows but not fused into ridges; this is the situation in the Water Canyon Formation dipnoan and probably in *Dipnorhynchus*. Such a dental plate is not at all adapted for crushing mollusc shells, the food commonly assumed for these fishes. They may have been omnivorous forms or may have fed on relatively soft-bodied invertebrates or on plants. The bracing of the skull and upper jaws perhaps is best correlated with crushing, though not grinding, plant food. In their locomotor adaptation, the early Dipnoi are very similar to the first Crossopterygii.

DISCUSSION OF EARLY VERTEBRATE HABITATS

Early Habitats as Indicated by the Geological Record

The earliest known vertebrates of the Ordovician were marine forms, apparently restricted to habitats near shore.

In the Silurian, the Cyathaspinae lived in the sea, although it is possible that some were invading brackish or fresh-water marginal habitats in the latter part of the period. The Coelolepida, Euphanerida (*Jamoytius*), and Acanthodii were marginal marine groups; the Coelolepida, however, were probably euryhaline forms and could tolerate brackish water and probably even fresh water for a time. The earliest known Osteostraci and Anaspida lived in brackish lagoons, while later ones inhabited brackish or fresh-water streams and lakes.

In the Early Devonian, fresh-water environments were colonized extensively by vertebrates. The Heterostraci had radiated into several families, most of which included stream dwellers. However, they appear to have been restricted to the lower reaches of streams and to have remained to a large extent euryhaline forms, not leaving the sea entirely. The Drepanaspidae did not leave the sea until the Middle Devonian, by which time most other Heterostraci had become extinct. The coelolepid, *Thelodus*, continued to be a marginal marine form, euryhaline to some extent. The Osteostraci, *Turinea*, and Anaspida were typical of fresh-water streams, only one osteostracian, *Sclerodus*, remaining in the seas. The Acanthodii were for the first time definitely inhabitants of fresh waters, where they lived in lakes and streams; but some members of the group remained in the sea. Among the placoderms, the Macropetalichthyidae, *Palaeacanthaspis*, *Radotina*, Stegoselachii, and Rhenanida were all marine groups; only the Euarthrodira inhabited fresh waters, and many of these entered the seas during this time. The early habitat of the Osteichthyes is not clear from their occurrence; there is some indication that the earliest Dipnoi may have lived in the sea, but as far as the Crossopterygii and Actinopterygii are concerned, the record is non-committal. No Chondrichthyes are known until later in the Devonian.

Conodonts, which probably represent a special branch of the Agnatha, appear never to have left the sea.

Taken as a whole, the record suggests that vertebrates were originally near-shore, marine forms, that they did not start to invade brackish and fresh waters until the latter part of the Silurian, and that during the Devonian all classes and most orders of vertebrates lived to a greater or lesser extent in fresh waters. This is contrary to the conclusions of Romer and Grove (1935, pp. 838–839), who believed that the early Paleozoic vertebrates were fresh-water forms and in support of this belief laid great stress on the absence of vertebrates in marine formations of this age. In this connection the following points are important: (1) Ordovician vertebrates, as well as Silurian Heterostraci, Coelolepida, and Acanthodii, do occur in marine sediments; (2) the rarity of these groups and the absence of other vertebrates in marine deposits are not surprising when one considers that the early history of all major groups of animals is either unrecorded or obscure. In the case of early vertebrates, it is not necessary to suppose, as did Romer and Grove, that they lived in fresh-water streams and were preserved in sediments that were particularly subject to subsequent erosion. It is more probable that they were relatively few in number and small in size, and thus not easily discovered. In addition, many early vertebrates may have occupied special ecological zones in the sea, resulting in their preservation only in particular geological facies. An example is the abundant preservation of vertebrate fragments in the Harding Sandstone, and their complete absence in the "typical" marine facies of the overlying Fremont Limestone.

It is necessary in this study not to lose sight of the fact that the paleontological record is far from complete. Of particular importance, in view of the conclusions of Romer and Grove, is the rarity of continental deposits of early Paleozoic age. Such deposits are probably not completely absent, however. In the Late Ordovician of the eastern United States two deltaic fans built out westward from the land mass, Appalachia, during and after the Taconic revolution (Grabau, 1913). The northern delta consists of the Queenston Shales in New York and the Bald Eagle Conglomerate and Juniata Sandstone in Pennsylvania. The southern delta is made up largely by the Bays Sandstone. Further erosion of Appalachia in Silurian times resulted in the continued deposition of deltaic sediments, some of which may have been laid down sub-aerially. These include the Shawangunk Conglomerate near the source, and the Tuscarora and Clinch Sandstones farther west from Appalachia. It is possible that the Bloomsburg and High Falls Shales were, in part at least, deposited in fresh waters on these deltas. The deltaic sediments are generally completely barren of fossils, and the few that do occur are difficult or impossible to place ecologically. The sandstones may contain the presumed worm borings, *Scolithus,* and in the Silurian there are not uncommon trails of an undetermined animal, *Arthrophycus.* The Shawangunk Conglomerate locally contains *Arthrophycus,* has yielded a considerable eurypterid fauna from interbedded dark shales, and contains Cyathaspinae in its upper sandy and shaly member. The Tuscarora Sandstone contains *Arthrophycus* and eurypterids, while the Clinch Formation typically yields only *Scolithus* and *Arthrophycus.* The Late Silurian High Falls and Bloomsburg Shales contain only Cyathaspidae except to the west, where the Bloomsburg interfingers with beds containing marine invertebrates.

Other possible continental deposits of early Paleozoic age occur in Siberia and India. In the Lena region of Siberia there are Silurian red beds, sometimes saliferous, from which no fossils are reported. In the Salt Range of the Punjab, early Paleozoic red beds and salines are largely unfossiliferous. There is then some evidence for the absence of vertebrates from continental deposits during the Ordovician and most of the Silurian. Only in the latter part of the Silurian in New York and New Jersey are vertebrates present in possible continental deposits. The evidence, being negative, is far from conclusive, and considering the uncertainties and incompleteness of the geological record in general, it must be admitted that it is possible, if not probable, that vertebrates entered fresh waters at an earlier date than the record indicates. This does not mean, however, that it is necessary to jump to the extreme conclusion that vertebrates originated in fresh waters.

Bearing of the History of Fresh-Water and Land Plants On the Habitat of Early Vertebrates

Since plants are at the base of the food cycle, it is obvious that their migration into fresh waters must have preceded that of animals. In this connection it is important to review the history of early plants with special reference to the occurrence of forms that might have lived in fresh waters or on land.

Considering first the macroscopic remains, the oldest definitely non-marine flora occurs in the Late Silurian, probably Lower Ludlow, of Australia (Lang and Cookson, 1935). Similar floras are found in the Early Devonian of Europe and North America. They consist mostly of primitive Psilophytales that were surely plants of streams, marshes, and lakes. Associated with them are a number of algae (Nematophytales), such as *Prototaxites* and *Pachytheca*, that were probably fresh-water types. More advanced, possibly terrestrial plants, related to the lycopods, are recorded from the Late Silurian of Australia, but do not appear elsewhere until late in the Early Devonian. Finally, possible Sphenopsida (scouring rushes) are recorded in the Early Devonian. In the Middle Devonian more groups are represented, but it is not until the Late Devonian that a large and diversified fresh-water and land flora is found. This contains lycopods, scouring rushes, ferns, seed ferns, and Cordaitales, all groups that had their climax in the Carboniferous.

As far as megaflora is concerned, records of possible fresh-water and land plants are extremely rare and still uncertain in rocks older than the Late Silurian. In recent years a few fragments of woody elements have been reported from the Cambrian of India (Jacob, Jacob, and Shrivastava, 1953). Kryschtofowitch (1953) has described fragments of shoots of lycopsids from the Middle Cambrian of Siberia. These records, if confirmed, may be taken to indicate that vascular plants were in existence for a long time before they appear commonly as fossils.

The recent, widespread interest in plant spores and pollen because of their value for correlation, promises to add to the knowledge of early floras. The spores and pollen described from the Late Devonian are diversified, as would be expected from the known megaflora. In the Middle and Early Devonian it is not surprising that less complex spore assemblages are found. Radforth and McGregor (1954, p. 615) indicate this in their studies of Devonian and Late Silurian spores from Canada. Thomson (1952, p. 158) found a strong contrast between Middle and Early Devonian spore assemblages of Europe, paralleling that between known megafloras. So far the records of mega- and microfloras are rather well in agreement. On the other hand, spores have been described from the Cambrian that by some are believed to indicate the presence of vascular plants belonging to groups otherwise unknown at this early time. Reissinger (1939, p. 16) described spores from the Early Cambrian Blue Clay of Esthonia that he believed belonged to land plants because of their heavy membrane. Jacob, Jacob, and Shrivastava (1953) attributed spores from the Cambrian of India to Pteridophyta, Pteridospermae, and possibly primitive Gymnospermae; as they themselves point out, these spores are poorly preserved and the suggested affinities must be taken with reserve.

The records from the Early Paleozoic are suggestive, though not yet conclusive proof, that vascular land plants existed at this time. Because of the general agreement of micro- and megafloras in Devonian and later times, and their rapidly decreasing complexity as one passes from Late to Early Devonian, there is need for caution in coming to the conclusion that a complex and diverse fresh-water or land flora existed in the Cambrian. Vascular plants are easily transported for long distances and easily preserved. Many Devonian fresh-water and land plants, as well as those from the Silurian of Australia, occur in marine deposits. For this reason there are good possibilities for the preservation of such plants, even where there are no continental deposits. The absence of their macroscopic remains in most early Paleozoic sediments is a strong argument against their existence in any numbers in the fresh waters or on the lands of that time. Of course, if we may judge by the early history of most groups of animals, land or fresh-water plants may have existed in small numbers for some time previous to their common appearance as fossils. This is suggested by the Cambrian spores and wood fragments, and by the relatively high development of certain plants from the Late Silurian of Australia. But this is of little importance to the theory of the late invasion of fresh waters by vertebrates, because plants must have been present in considerable abundance before offering a stable source of food for the early animal colonists of fresh waters. There is no indication from the fossil record that this was the case until late in the Silurian and in the Devonian.

Invasion of Fresh Waters and Land by Invertebrates

The time at which various invertebrate groups were first able to adapt to life in fresh waters or on land has a definite bearing on the problem of the habitat of early vertebrates, since it furnishes evidence of the availability of these environments for animal colonization. This is a large problem, in details beyond the scope of this paper, and it will be reviewed only briefly.

Many invertebrate groups have always been restricted to the sea. Of those that left the sea early, a number of groups of Arthropoda are most important. The most striking of these are the Eurypterida, about whose habitat there has been much difference of opinion. O'Connell (1916) has taken the extreme view that throughout their entire history they lived in rivers. Clarke and Ruedemann (1912, p. 112) believed that they inhabited the sea from the Cambrian to the Silurian, became euryhaline and thus adapted for life in marginal lagoons and estuaries in the Silurian, and later lived in fresh waters. Later, Ruedemann (1924, p. 231) and Størmer (1934, p. 69) considered that they were typically fresh-water forms but were euryhaline and able to invade the sea at times. If their geological record is examined, it appears that all of the Ordovician and many of the Silurian eurypterids are found in marine deposits; in the Late Silurian and Early Devonian they are common in marine, marginal marine, and brackish water deposits; and in some Early Devonian and in all later occurrences they are found in fresh-water sediments. This suggests that they were originally marine, and that only in the Late Silurian and Early Devonian did they become adapted to life in brackish and fresh waters. It is perhaps significant that this is the time when they attained their greatest abundance and diversity. During their subsequent decline until their extinction in the Permian they were restricted to fresh-water swamps and lakes. This is essentially the view of Waterlot (1953, pp. 550–551).

The earliest known Xiphosura belong to the order Aglaspida and are found in Cambrian and Ordovician marine rocks (Størmer, 1952). The order Xiphosurida appears in the Silurian. Its more primitive suborder, the Synxiphosurina, occurs during this period in marine deposits (*Limuloides* and *Bembicosoma*), and in lagoonal, estuarine, and bay sediments, deposited in some cases in brackish waters (*Bunodes, Bunodella, Bunaia, Pseudoniscus, Neolimulus,* and *Cyamocephalus*); the only Devonian genus (*Weinbergina*) has been found in the marine Hunsrückschiefer. The earliest representative of the other suborder, the Limulina, is *Kiaeria* from the fresh or brackish-water, deltaic sediments of the Late Silurian of Norway. Most other Paleozoic Limulina are fresh-water forms, while many Mesozoic and all the recent genera are marine. The history of the Xiphosura is not well documented, but what is known shows considerable similarity to that of the Eurypterida. It suggests a marine origin, an invasion of brackish and fresh waters in the Late Silurian and Devonian, and preference for fresh-water habitats during the latter half of the Paleozoic. The marine Mesozoic genera, as well as the surviving forms (*Limulus, Tachypleus,* and *Carcinoscorpius*) may have returned secondarily to the sea.

Living scorpions are strictly air-breathing, land-living animals, yet the four earliest species from the Silurian occur in marine deposits. These are referred to *Palaeophonus* (Bed 3 of Lesmahagow inlier of Scotland; Högklint Limestone of Gotland), *Dolichophonus* (Wenlock, Bed A, Pentland Hills of Scotland), and *Proscorpius* ("Waterlime" of Waterville, New York). Introduction of these individuals from land is unlikely, except perhaps for the Lesmahagow inlier specimen. In spite of this highly suggestive occurrence, there has been considerable controversy regarding the habitat of these Silurian scorpions. Unfortunately, anatomical evidence that would settle the question is either lacking or not conclusive. Neither gills nor spiracles are preserved in any of the specimens (Petrunkevitch, 1953, p. 5), and the claw-like termination of the tarsi that occurs in *Palaeophonus* is suggestive of a marine habit but does occur also in terrestrial arthropods. Petrunkevitch (op. cit., p. 6) believes that Silurian scorpions were air-breathers, although he does concede that they may have led a marine life, similar to that of crabs. His chief reason for this is that no recent or fossil Arachnida are known to possess respiratory organs other than book lungs or tracheal tubes. Since this is negative evidence, the possibility must be considered that Silurian scorpions were water-breathers that had not yet acquired the adaptations for land life. The geological record certainly suggests a marine origin for this group, and a change to life on land only in the Devonian or Carboniferous.

The earliest known Myriapoda, which are found in Scotland, are the Diplopoda, *Kampecaris* and *Archidesmus.* The latter occurs in the Late Silurian, near-shore, marine Bed 3 of the Lesmahagow inlier, but all the other occurrences—in Bed 9 of the Lesmahagow inlier, the Stonehaven Beds, the Carmyllie and Cairnconnon Groups, and the Lower Old Red Sandstone of the Oban district—are in fresh-water deposits. It is possible that the specimen in Bed 3 of the Lesmahagow inlier was washed in from land, and that myriapods were already inhabiting the land, or perhaps fresh waters, by the end of the Silurian. Of course, this does not give any information about their original habitat or the time of their departure from the sea.

Branchiopoda are restricted almost entirely to fresh and brackish waters. However, the earliest known representatives, Conchostraca from the Early Devonian and perhaps Silurian, are found in marginal marine or marine deposits (Raymond, 1946). *Euestheria* is doubtfully recorded from the Lower Emsian Grès et Schistes de Wépion in Belgium, associated with land or fresh-water plants and *Spirorbis;* the latter is not certainly a marine genus at this time, but the geological evidence suggests that this is a marginal marine deposit (Asselberghs, 1946, pp. 224–225). *Pseudestheria* and *Palaeolimnadiopsis* occur in the Lower Emsian Klerfer Schichten at Willwerath in Germany; this is a marginal marine, possibly brackish-water deposit. *Rhabdostichus* is found in the Silurian or Devonian Schistes de Moulin de Régereau in the Amorican massif; here it is in definitely marine beds. The same genus is found in the Middle Devonian, marine Hamilton Group of New York. In the Grès et Schistes de Wépion and in the Klerfer Schichten the conchostracans may have been washed in from fresh waters, but this is unlikely in the two occurrences of *Rhabdostichus.* Raymond (1946, p. 305), in summarizing their history, says "Conchostracans descended from some of the [marine] bivalved crustaceans of the Cambrian and Ordovician, and like so many other animals, got into fresh waters in late Silurian or early Devonian times. The genus *Rhabdostichus* appears to have remained in the original marine environment."

Throughout their history the Phyllocarida are largely restricted to marine habitats, but they are often most common in non-typical, perhaps marginal, marine assemblages. It is possible that some phyllocarids preferred brackish waters, but there are few records of members of this group from fresh-water deposits (e.g., *Gwyneddocaris* from the Triassic Newark Series of Pennsylvania). In the Late Silurian and Early Devonian, phyllocarids are commonly associated with vertebrates in marginal marine deposits, in a few cases probably deposited in a brackish-water environment. They are almost always absent in fresh-water, vertebrate-bearing deposits of this age. But, in the lower part of Bed 10 at Ringerike, Norway, and in Bed 6 of the Stonehaven Beds, Scotland, *Dictyocaris*, a probable phyllocarid, is abundant in presumably fresh-water deposits (Størmer, 1935). *Ceratiocaris* occurs rarely in Bed 9 of the Lesmahagow inlier, a fresh or possibly brackish-water sediment. Thus it is possible that in the Late Silurian a few phyllocarids did leave the sea, perhaps temporarily, but it cannot be said that as a group they ever became adapted to the fresh-water environments.

Present-day Ostracoda are found in all salinities and in a wide variety of habitats, but the earliest forms of the Ordovician and Silurian are known only from marine deposits. The time of their first successful invasion of fresh waters has never been clearly demonstrated. There were certainly a number of genera adapted to life in fresh-water habitats by the Pennsylvanian (Agnew, 1948). The ostracods, *Aparchites, Isochilina,* and *Beyrichia* or *Drepanella* are reported from the Early Devonian Lower Old Red Sandstone of the Oban district, Scotland (Read and MacGregor, 1948, p. 60), and there is little reason to doubt that they lived in fresh waters. *Isochilina* (*Hogmochilina*) and *Holtedahlina* are found in the Early Devonian fresh-water Wood Bay Series of Spitsbergen (Solle, 1935). It is possible that the Bloomsburg Formation and Landisburg Sandstone of the Pennsylvania Late Silurian, with their vertebrates and ostracods, may be fresh- or brackish-water deposits. It appears, then, that perhaps by the latter part of the Silurian, and certainly by the Early Devonian, some ostracods had succeeded in leaving the seas and making their life in fresh waters.

The molluscs have always been dominantly marine, and the Cephalopoda, Amphineura, and Scaphopoda never left the sea. A few pelecypods and gastropods became adapted to life in fresh and brackish water, probably during the Devonian Period. Air-breathing, terrestrial Gastropoda appear during the latter half of the Paleozoic. The possibility that certain Silurian and Devonian pelecypods and gastropods may have been euryhaline makes it difficult to determine the time of their earliest invasion of fresh waters.

Some of the various groups of worms may have moved into fresh waters during the middle or late Paleozoic, but so few of them are capable of preservation that their history is obscure. Some

Spirorbis of the Carboniferous were certainly fresh-water forms, and this may also be true in the Devonian.

This review indicates that it was during the Late Silurian and Devonian that certain invertebrate groups first left the seas for fresh waters. Their history agrees with that of the early vertebrates and is strong support for the view that it was not until the Silurian that fresh waters contained sufficient plant life to be available for animal occupancy.

Physiological Evidence of Early Vertebrate Habitat

The important studies of Homer Smith (1932; 1953) on the functions of the vertebrate kidney furnish an extremely interesting physiological approach to the problem of early vertebrate habitat. The devices used by different groups of fishes to regulate the osmotic pressure in the body fluids have led Smith to believe that the first vertebrates arose in brackish or fresh waters. According to his theory, the excretory system of the vertebrate ancestor consisted of a series of tubules, opening into the body cavity and serving to drain the fluid in the cavity to the exterior. When the ancestral vertebrates first entered fresh waters, physiological adjustments were necessary, since the osmotic pressure would result in self dilution through the absorption of water through permeable gills and oral membranes. The glomerulus, a tuft of capillaries at the mouth of the tubule, was evolved according to Smith in connection with the necessity of excreting the large quantities of water that were absorbed by the early vertebrate in fresh water. This is the first and most important point of Smith's argument.

The construction of the glomerulus makes it ideally suited for the rapid filtration of the body fluids, and it is easy to assume that it is an adaptation for fresh-water life. Moreover, its presence in all major groups indicates that it was acquired very early in vertebrate history, unless we assume its independent acquisition in various groups, which is unlikely. But in spite of these considerations, Smith has not demonstrated that this character was evolved in the fresh-water habitat. The early marine vertebrates may have been functionally hypertonic to sea water, and the glomerulus may have originated in response to this condition. If this were so, these early vertebrates could be said to be preadapted for life in fresh water. They possessed the necessary mechanism for osmo-regulation in that environment and could move into it as soon as plants had invaded it and made it suitable for animal life. It can be argued also that vertebrates could not survive in fresh waters until a glomerular kidney had been acquired; in other words, this character must have evolved in the seas and not in fresh waters.

Smith also shows that certain groups of fishes, after living in fresh waters, returned to the seas, where they were subject to reversed osmotic pressure. Thus, marine elasmobranchs retain both salts and urea in the blood until its osmotic pressure is above that of sea water, enabling them to absorb sufficient water. The teleosts that have returned to the sea get the necessary water by gulping it in, and their problem is to get rid of excess salts, which they do by excreting them through the gills. Since the glomeruli are no longer advantageous, they may degenerate or disappear in marine teleosts. Some Cyclostomata maintain hypertonic blood largely by conserving salts, but this may not be true of all.

The demonstration of a fresh-water ancestry for these fishes does not necessarily imply that vertebrates as a group arose in fresh waters. If Stensiö (1950, pp. 37–39) is correct in believing that elasmobranchs were closely related to and perhaps derived from placoderms, their fresh-water ancestry may be represented by some of the Devonian or earlier arthrodires. Much of the history of the Actinopterygii from the Devonian on took place in fresh waters, so there is no difficulty with regard to the fresh-water origin of teleosts. The cyclostomes are derived presumably from ostracoderms, which, as is shown above, entered fresh waters in the Late Silurian and Devonian.

SUMMARY AND CONCLUSIONS

The criteria for the determination of the depositional environment have been discussed, with particular attention to the salinity of the depositing waters. The difficulties in making decisions regarding the habitat of particular fossil vertebrates because of post-mortem transportation have been considered.

The Ordovician, Silurian, and Early Devonian vertebrate occurrences have been reviewed, and indicate the following: (1) Known Ordovician vertebrates were near-shore, marine forms. (2) In the Silurian, the Cyathaspinae, Euphanerida, Acanthodii, and typical Coelolepida (*Thelodus*, etc.) lived in the sea, while the Osteostraci and Anaspida were established in brackish and fresh waters. A few Cyathaspidae may have invaded brackish or fresh waters in the Late Silurian. (3) By the Early Devonian, fresh waters had acquired a considerable vertebrate fauna. The Osteostraci, *Turinea*, and

Anaspida were almost exclusively fresh-water forms, while many Acanthodii and Crossopterygii, and the earliest Euarthrodira also lived in fresh waters. Most Heterostraci were euryhaline types, capable of living either in the seas or in the lower reaches of streams. The Early Devonian seas were characterized particularly by the presence of Drepanaspidae, Macropetalichthyidae, Radotinida, and Acanthothoraci. Some Acanthodii still remained in salt waters, and a number of Euarthrodira and Crossopterygii either returned to or remained in marine habitats. The coelolepid, *Thelodus*, was largely restricted to the sea margins. The habitat of the earliest known Osteichthyes is not clearly indicated by their occurrence, although there is a suggestion that the Dipnoi lived in the Early Devonian seas.

It is concluded that vertebrates originated in the sea and did not begin to enter fresh waters until some time in the Silurian. The fresh-water invasion may have been somewhat earlier than is indicated by known fossils, for the geological record is imperfect, especially as regards early Paleozoic continental sediments.

The recorded history of plants indicates that it was not until the Silurian that they became sufficiently abundant in fresh waters and on land to offer a stable source of food for animals.

The first appearance of fresh-water invertebrates approximately coincides with that of vertebrates. Eurypterids, xiphosurans, myriapods, and ostracods are found in fresh-water deposits only in the latter part of the Silurian, while scorpions, conchostracans, pelecypods, gastropods, and worms may not have left the sea until the Devonian.

The glomeruli of the kidney were probably acquired in the sea early in vertebrate history. This character was preadaptive in that it enabled vertebrates to invade fresh waters as soon as they were sufficiently colonized by plants. The fresh-water ancestry of cyclostomes, elasmobranchs, and teleosts, which is indicated by their physiology, was of Silurian or later age.

ADDENDUM

While this paper was in press, there appeared a new work by Professor Romer (1955) that defends his earlier hypothesis of the fresh-water origin of vertebrates. He discusses various general considerations, which he interprets as support for his belief. These include the paucity of continental deposits in the early Paleozoic, the usual absence of vertebrates in Ordovician and Silurian marine sediments, the effects of post-mortem transportation, and the implications of kidney structure and function. All of these have been discussed above. He stresses the need for detailed information on exact horizon and locality, an obvious refinement that has been the purpose of most of my research on this subject. He repeats his earlier belief that plants were probably present in fresh waters early in the Paleozoic; this may be true, but at present is largely speculative. He stresses the common association of eurypterids and ceratiocarids with early vertebrates, and apparently considers this as support for his theory. However, as shown above, the ceratiocarids (with the exception of the problematical *Dictyocaris*) are almost exclusively marine (p. 438), and this may be true of most pre-Devonian eurypterids (p. 435).

The rest of the paper is a frank attempt to reconcile Walter Gross' (1950) conclusion that the majority of Silurian vertebrates were marine, with the results of the study of Romer and Grove (1935), which indicated that as far as North America was concerned they were all fresh-water forms. First of all, it should be emphasized that my work does not support the conclusions of Romer and Grove. There are now known in North America ten Silurian vertebrate occurrences, all containing the Cyathaspinae–Acanthodii assemblage. Four of these are definitely marine, one is a mixed assemblage in a probably marginal marine deposit, three are possibly fresh-water but may also be interpreted as marginal marine, and two are uncertain.

Professor Romer considers a number of European Silurian and Downtonian vertebrate occurrences and finds that he can interpret them so that they are in agreement with his hypothesis. A discussion of his interpretations follows:

Great Britain: The marine Ludlow vertebrates are lightly disposed of as strays floated out to sea from land. The Ludlow Bone Bed is considered to mark the arrival of continental conditions, but this is clearly not the case (p. 388). The Downtonian is considered to be deltaic, and I would agree with this in a broad sense, though it contains many marine horizons, and, I believe, many marine vertebrates.

Norway: The fish record of Stage 10 is considered by Romer to indicate a fresh-water habitus. This may be true of Kiaer's Ringerike Osteostraci, Anaspida, and Eurypterida, but the new discovery in Stage 9 in Ringerike is suggestive of brackish conditions for these groups (p. 374).

Bohemia: Romer emphasizes the fact that the fishes of the Lochkov Limestone occur with eurypterids and ceratiocarids, and that there is little or no indication of a marine invertebrate fauna. This, he believes, suggests a near-shore and possibly deltaic deposit. There is no suggestion of delta development here at this time, and Prantl and Přibyl (1948) concluded that they were not near-shore deposits. What evidence is available indicates marine deposition and supports a marine habitat for the contained vertebrates (p. 399).

Podolia: Romer states that "fishes appear in numbers only as continental conditions are approached." This is true, but his conclusion that this "strongly supports the thesis that fresh waters were the center of Silurian vertebrate life" does not necessarily follow. Firstly, these are not Silurian in age, and secondly, many Podolian vertebrates occur in definitely marine beds (p. 404), and some of them were probably either inhabitants of the sea margins or marine euryhaline forms.

France: Romer is perfectly correct in stating that the vertebrates found near Liévin are not associated with marine invertebrates and may well be fresh-water forms. But these are post-Downtonian Pteraspidae and Poraspinae, both groups that were in part clearly inhabitants of fresh waters at this time (p. 406).

Scania: Romer believes the Öved-Ramsåsa Beds to be estuarine or deltaic, but he did not know that there are marine invertebrates associated with the vertebrates (p. 379). This is certainly a marine occurrence, and the introduction of most of the vertebrates from fresh waters is unlikely.

Beyrichienkalk: This is a marine deposit. The transportation of the vertebrates from a continental habitat, which Romer suggests, is purely speculation.

Oesel: Romer pictures lagoonal conditions of deposition for the K_1 Beds and favors fluctuating salinity, with vertebrates and eurypterids occurring in fresher waters and the few marine invertebrates in more saline waters. The accounts of Hoppe (1931) and others do not support this suggestion of varying salinity but indicate that the "*Eurypterus* fauna," including the vertebrates, is an assemblage formed under very particular ecological conditions. In regard to the K_4 Beds on Oesel, Romer states that the invertebrates and fish are not found in the same layer. This is supposition, based upon inadequate published data. Invertebrates do occur, though perhaps not commonly, in the bone bed horizons of K_4, and at least one of the nearly complete *Tolypelepis* dorsal shields (that figured by Kiaer, 1932, pl. 10) is associated with brachiopods and crinoids in a non-bone-bed horizon. Thus the marine origin of the whole of K_4 is indicated.

In conclusion, the Silurian Osteostraci and Anaspida probably lived in brackish or fresh waters, but the Ordovician Heterostraci and the Silurian Cyathaspinae–Acanthodii assemblage occur with few exceptions in sediments whose marine origin is beyond doubt. Professor Romer's hypothesis requires in these cases that the vertebrates be transported from fresh waters into the seas. While such drifting undoubtedly took place, it is putting too great a strain on credulity to invoke this interpretation where vertebrate remains are abundant, and where they conform with considerable consistency to a marine pattern of occurrence.

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