THE LOWER PALAEOZOIC ECHINODERM
FAUNAS OF THE BRITISH ISLES AND
BALTO-SCANDIA

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INTRODUCTION

A great many difficulties are involved in dealing with the relations between the British and the Balto-Scandian echinoderm faunas in Early Palaeozoic times. It is obvious that this is due mainly to two circumstances: the imperfect knowledge of the original composition of the faunas in different areas, and the insufficient exactitude in stratigraphic correlation between the British Isles on the one hand and Scandinavia, Estonia, and the Leningrad district on the other. It is not necessary to review here the various factors which in the course of time have acted upon the consecutive marine biota of different ecological niches and which have been decisive of the nature of the fossil record now available to us. Even Charles Darwin in his *Origin of Species*, the centenary of which is celebrated this year, devoted a special chapter to these questions which have subsequently received much attention in the literature. The essence of the dilemma was formulated by Wachsmuth and Springer (1897, p. 167) as follows: 'The trouble is that all our generalizations are necessarily based upon the Crinoids as they are represented in our museums, and not upon the Crinoids as they actually existed in geological time, which is a very different thing.' The term 'Crinoids' may of course be substituted by the name of any other group of echinoderms, or by the name of almost any other fossil group.

Wachsmuth and Springer introduced the human factor which should certainly not be neglected. It is a fact that some fossil groups have been subject to a more extensive collecting and a more penetrating study than other groups. Rather trivial matters have played a role in this respect. Henbest (1952, p. 204) observed, for instance, that the 'location of fossil records in relation to centres of education, research, industry, and mining is an important factor in the discovery and description of faunas'.

LITERARY BACKGROUND

Much basic knowledge of Palaeozoic echinoderms has come from London—in the first place I refer to the brilliant work of F. A. Bather. However, apart from the carpopods and cystoids from the Ashgillian Starfish Bed of Ladyburn near Girvan described in his magnificent and very important memoir of 1913, no British material of Old Palaeozoic echinoderms was treated monographically by Bather. But we are indebted to him for short but valuable papers on certain British edrioasteroids (Bather 1900, 1915). The work on the Silurian crinoids which he planned was never executed except for a series of minor problems.
contributions (Bather 1890–2; 1896; 1906; 1907). Much useful information about
British forms can, however, be obtained from the only part published of his monograph
of the Crinoidea of Gotland (Bather 1893). The non-crinoid Palæozoa have thus
attracted relatively slight attention after the middle of the nineteenth century when they
were described by Edward Forbes (1848) in a memoir which was very good for its time.
A certain number of species of the abundant crinoid fauna in the Wenlock Limestone
were illustrated by Murchison (1839) in *The Silurian System* and briefly described by
Phillips. In spite of Bather’s papers just referred to there is no doubt that the crinoids
still offer a fertile field of research, as evidenced by the recent publications by Dr. Rams-

The only Ordovician and Silurian echinoderms included in the monographs of the
Palæontographical Society are the Asterozoa. These have been treated in a comprehen-
sive volume—unfortunately not completed—by W. K. Spencer, published between 1914
and 1940. It tells us much about the difference in character between the British and the
Balto-Scandian echinoderm faunas of the Old Palæozoic that a corresponding work
could not have done on the basis of Balto-Scandian material. For fossil remains of
asteroids and ophiuroids are met with only occasionally in the deposits of Scandinavia
and of the East Baltic area.

On the other hand, where Balto-Scandia is concerned, cystoids have clearly been a
conspicuous element in certain Middle and Upper Ordovician faunas. Crinoids have
been found in great abundance particularly in the Silurian of Gotland. A first orienta-
tion as to the diversification in each group was presented by Angelin’s classical work,
edited posthumously in 1878. Through his monograph of the crinoids of Gotland,
Bather (1893) made a skilful and badly needed revision of the inadunate forms. The
articulate crinoids of Gotland (and of Britain) were accounted for by Springer, in 1920,
but the camerate have had to wait much longer. Lately, however, Professor Ubags, of
Liegé, has taken up their study. The work is well under way, and three parts have been
published (Ubags 1956–8). Other recent contributions to the knowledge of the Old
Palæozoic echinoderm fauna of Scandinavia mainly concern different non-crinoid
groups. It should be mentioned that even Jaekel drew on material in the Swedish Museum
of Natural History in Stockholm when preparing his great monograph of the Pelmatozoa
(1899).

The Ordovician of Estonia and of the Leningrad district is famous for excellently
preserved and, in part, unique echinoderms, first and foremost non-crinoid pelmato-
zoa. Many of these were early described in the classic works of Pander (1830), Leuch-
tenberg (1843), Volborth (1846, &c.), Eichwald (1860, &c.), and Friedrich Schmidt
(1874, &c.). Fresh light has been thrown on the morphology and taxonomy of many
remarkable forms by the eminent investigations of Professor Hecker (1923, 1940, 1958,
&c.), of Moscow. Two interesting genera of Ordovician crinoids have been commented
upon by Professor Opik (1934, 1935), then in Tartu, but the crinoids of the East Baltic
Palæozoic are comparatively poorly known so far.

What has been said now is of course in no way a complete review of the available
literature on Old Palæozoic echinoderms in Britain and Balto-Scandia. My intention has
only been to give a rough sketch of the literary background of our subject. It may be
added that summaries of the regional distribution of some groups of pelmatozoa are
included in general works, as those of Barrande (1887) and Jaekel (1899). Special men-
tion is due to the *Thesaurus siluricus* by J. J. Biggby (1868), which is a bold attempt to indicate the main traits of Cambro-Silurian palaeobiogeography on the basis of an extensive compilation of data in the relevant literature.

**FACTORS IN THE DISPERsal OF ECHINODERMs**

At a British Association meeting in 1938 a discussion was held on ‘The Distribution and Migration of certain Animal Groups in the British Lower Palaeozoic Faunas’. The opening contribution, published subsequently in the *Geological Magazine*, was given by Dr. Stubblefield. It gave most valuable details on the behaviour of trilobites in this respect. Dr. Stubblefield (1939, p. 49) observed that ‘any conclusions made at the present stage are tentative and are offered as an incentive to research’. Twenty years have passed since these words were uttered. But they are just as true now as then and will for many years to come stand as a motto for all discussions of this kind, irrespective of the group of animals dealt with.

In addition, Dr. Stubblefield drew attention to the fact that trilobites are favourable objects for the study of migration-paths, because they were presumably characterized by ecdisis. As a result, the number of potential fossils were several times greater than the number of individuals. The adult echinoderms, on the other hand, produce only one skeleton during their lifetime. It may be remembered, however, that the echinoderms have a remarkably high capacity of regeneration, which enables a rapid substitution of lost or cast-off parts of the body. Theoretically, this may have contributed to augment their share in the fossil record but in practice it may have been a rather negligible factor.

Another drawback is that the adult stages were capable of no, or a very restricted, shift of position. Like their recent representatives, the great majority of the early echinoderms were bottom-dwellers, either sedentary, as the bulk of the pelmatozoans, or moving sluggishly on the sea-floor or in the bottom ooze, or hiding in crevices of coral-reefs, and so forth. These habits may have been an advantage to potential fossils but did not favour a rapid distribution over wide areas by means of adult individuals. However, echinoderms have an extremely wide range of distribution in modern seas. The fossil record tells us that this was true also of echinoderm faunas from the Palaeozoic onwards. The explanation is, as in so many other cases where the adult generation is practically passive, that the migration to new areas of distribution and their colonization is chiefly performed by larvae. We do not know anything about the behaviour and resistibility of the larvae of primitive echinoderms. But it is reasonable to imagine that, in principle, they were much the same as those of the larvae of recent forms.

Because pelmatozoans predominated strongly among the echinoderms in the Old Palaeozoic faunas, attention should in the first case be given to their only existing representatives, the crinoids, which are likely to demonstrate conditions most nearly comparable to those of their Palaeozoic predecessors. The stage of active swimming is short in the crinoids, its duration being necessarily restricted by the fact that the larvae have no mouth and, accordingly, cannot take any nourishment. This stage lasts generally two or three days but may exceptionally be prolonged to twelve days (cf. Dawydoff 1948, p. 351). In the latter case especially the allotted time is enough for the spreading of a given species over great distances.¹ The larvae of certain other echinoderm groups,

¹ The transport of marine animals by sea currents has been discussed by Born (1920).
which were yet subordinate in Cambro-Silurian times, lead a pelagic life which may last for months.

There are very few examples of a pelagic, maybe epipelagic, habit in adult echinoderms; the most well known of fossil forms is the Upper Cretaceous crinoid *Ultracrinus*. In Middle Ordovician times no echinoderm reached a more universal distribution than the hydrophorid genus *Echinospherites*. The spherical theca of *E. aevanium* or closely related forms are found in many parts of the world. Bather (1928, pp. lxxvii et seq.) tried to account for its relative ubiquity by the alternative explanation that the thecae were occasionally torn off from their tiny stems and swept away by waves and currents. Bather also set forth the hypothesis that thecae of dead individuals floated in the plankton to be ultimately washed ashore. It goes without saying that a nekton plankton could not contribute to the dispersal of the living *Echinospherites*. In view of the fact that the *Echinospherites*-beds give the impression of being autochthonous, Bather’s theory seems to be supported by little actual evidence (see also Regnell 1945, p. 146).

It should be mentioned, finally, that in the free-living groups of echinoderms, dispersal may to some extent be due to active migration by adult individuals. Schindewolf (1950, p. 54) quoted an instance where marked specimens of asteroids had been stated to migrate more than a thousand kilometres in a remarkably short time.

On the whole, the ways in which echinoderms spread and which have secured them a prominent position in practically all types of biotopes in recent seas all over the world, are of little help to the sleuth who seeks to follow their track through the ancient seas. But the echinoderms have a quality which is much to their credit as potential fossils, that is to say the heavy skeleton characteristic of most of their representatives. This armour, which was in many cases disintegrated after the death of the animal, was no doubt extremely resistant to destructive agencies. Thus, we have reason to suppose that the quota of echinoderm remains in the fossil record is greater, rather than the reverse, than the quota of echinoderms in the faunal assemblages once living. This leads us to the conclusion that the numerous occasions in which a species is represented in our collections by a very small number of specimens, or maybe by a unique specimen, reflect an original condition: the species will have been of very scarce occurrence in the biota to which it belonged.

**EDRIOASTERIDS**

Edrioasteroids have never played any conspicuous role in the faunas inhabiting the Cambro-Silurian seas which covered the areas now under discussion. From the Cambrian there are only one or two isolated finds of *Stromatocystes balticus* Jäckel. This species has unfortunately not been encountered in the solid rock but in erratic boulders in north Germany. According to Jäckel (1899, p. 42), these boulders originate from the Middle Cambrian *Paradoxissimus* Sandstone of the Baltic Basin exposed on Öland. Previously the specimens were in museums in Germany, but it is to be feared that they have been lost. *Stromatocystes*, which has not been found in Britain, seems to be of North American origin, since it has been recorded in the Lower Cambrian of Newfoundland.

The evolution of the edrioasteroids reached its acme during the Middle Ordovician. This is due almost exclusively to the prolificity of the North American stock, mainly the Hemiasterellidae. The very scanty material from the East Baltic area includes mainly
Lower Ordovician forms. The peculiar Pyrgocystis is represented by three species, the age of which is not precisely known, but the specimens seem to originate from beds corresponding to the Arenig (Hecker 1939, p. 245). It is possible that Pyrgocystis was present in the Ordovician of the Oslo region as well. Unfortunately, it has not been possible to locate the specimen referred to incidentally by Jaekel in 1927 (cf. Reginl 1948, p. 39, footnote 2). Dr. G. Henningsmoen has kindly informed me that there is nothing of that kind in the collections of the Paleontologisk Museum in Oslo.

In Great Britain Pyrgocystis has been found in the Ashgillian Staurisch Bed in Girvan, and in the Wenlock Shales of Shropshire (Bather 1915, p. 16). By which migration routes Pyrgocystis arrived at the British area is not entirely evident, because the genus has also been found in Blackriverian beds of Minnesota, which may be correlated broadly with the basal Caradoc. But it is justifiable to state that the Ordovician centre of dispersal of Pyrgocystis was located in the East Baltic area. As has just been mentioned, the genus is represented in the Wenlock of England. Other Silurian localities exist on Gotland and in the State of New York. Whether the Silurian forms are descendants of their Ordovician predecessors within the respective regions, or whether they have been introduced by a new faunal invasion, is not known.

There is other evidence of the Baltic origin of the turret-shaped edrioasteroids. This is supplied by Cyathotheca, which is known from the Vaginatum Limestone, on the Arenig-Llanvirn boundary, and from the top of the Ordovician in Dalecarlia, North-Central Sweden. In addition, the Middle Ordovician of Estonia has yielded two species of Cyathocystis. Like Cyathotheca this genus is absent in the British fossil record, but there are two species of Cyathocystis in the American Ordovician (C. americana Bassler 1936, C. oklahomae Strimple and Graftham, in Strimple 1955). This would indicate a faunal interchange in Ordovician times between the Baltic area and North America via the Polar Basin.

It is interesting that the disk-shaped type of edrioasteroids, which is the predominating type in North America and Central Europe, is almost unrepresented in the areas now under discussion. The only exception is Edrioaster buchananus from a Bala sandstone in Denbighshire, North Wales. This find is remarkable also from the point of view that the four other known species of Edrioaster occur in the Trenton of North America. It is unadvisable to give any opinion of the direction of the migration, since E. buchananus and the American species seem to have been roughly contemporaneous.

In another context (Regnedl 1950, pp. 10–12) I have commented briefly on the biogeographical significance of edrioasteroids in general.

**CARPOIDS**

The stratigraphical and geographical distribution of the carpoids9 neatly display—or seem to do so—the existence of four subsequent faunas, each with a characteristic

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1. The exact locality was given by Bather (1900, p. 194) as 'two miles west of Ysbyty Evan [Ysbyty Evan, acc. to the Geol. Surv. "Quater-Inch" map, sheet 9 & 10]; that is to say, about two miles south of Rhoscolyn, [Penrhos Foelas], and therefore in Denbighshire and not in Caernarvonshire as stated by J. W. Salter—and by R. Etheridge; sen.----'. The present writer has not been able to find out if the 'Caradoc beds', referred to by Bather, are Caradoc in the modern sense of this term or if they belong to the Upper Bala or Ashgill.

9. The carpoids are here taken in the conventional sense of the term, thus including aberrant forms as Lingulocystis Thurial (cf. Chauvel 1941, p. 172).
regional localization. For the sake of convenience, these faunas will be designated by the names of predominating carpoid genera, as follows: 1, The Middle Cambrian *Trocho-
cystites* fauna; 2, the Ordovician *Dendrocytites* fauna; 3, the Silurian *Placocystites*
fauna; and 4, the Lower Devonian *Anomalocystites-Australocyrtites* fauna. Faunal
hiatuses occur in the Upper Cambrian, in the basal Silurian, and in the Ludlovian, but
these blanks are outstepped by some genera.

The oldest fauna, which comprises two or three genera beside *Trochoctistes*, is likely
to have originated in the Bohemian Basin but rapidly invaded the waters over south
France, Spain, and Morocco. The *Dendrocytites* fauna occupied a much larger area,
and the number of genera were multiplied. This fauna represents a high watermark of
carpoid evolution. From the faunal province inhabited by the Middle Cambrian forms,
carpoids spread to Estonia in early Ordovician times and reached North America in
Chazyan times (Llanvirn-Llandaf). This presumably took place via a Polar route, as
there are no records at all from Ireland, and only from Caradocian-Ashgillian deposits
in Scotland and England. All carpoids from Estonia described so far belong to *Rhipid-
ocyrtis*. This genus, which seems to be endemic to the East Baltic area, comprises six
or seven species, probably ranging from the Arenig to the Caradoc.

Carpoids are practically unrepresented in the Ordovician faunas of England. The only
published record seems to be a species from the Middle Ashgillian *Dalmanitina roberstii*
Beds in the Cautley District, Yorkshire, which, with a question-mark, was referred to
*Archeocyrtis* by Marr (1913, p. 4).

The famous Starfish Bed of Ladyburn in Girvan has yielded two species of *Cathur-
cystis* and one species which was described by Bather (1913) as *Dendrocytis scotica* but
which was later given the rank of an independent genus called *Dendrocytostele*. These
are among the last survivors of the Middle European *Dendrocytostele* fauna. *Dendro-
cystostele* developed from *Dendrocytostele*, and the remarkable *Cathurcyrtis* has an
early representative in *C. primavera* of Llandeilo which is probably of early Arenig age
(Thorle 1935, p. 100). It should be mentioned that remains of carpoids are practically
non-existent in the Ordovician rocks of Scandinavia. There is an isolated record of a
stem-fragment in a boulder—probably Ashgillian—found on Öland. This has been
assigned to *Dendrocytostele* (Regnell 1945, p. 194).

The next younger carpoid assemblage, the *Placocystites* fauna, is of particular interest
to us, being restricted to England on the one hand and Gotland on the other. Two
species have been described from the Wenlock Limestone in Dudley, namely *Pla-
cocystites forbesianus* Komnick 1869 (syn. *Ateleocyrtis georgianus* Haeckel 1896), and
*Ateleocyrtis fletcheri* Salter 1873. According to Woodward (1880, p. 195), the species
mentioned are identical, as was also stated by Barrande (1887, p. 90). No recent authors
seem to have commented upon *Ateleocyrtis fletcheri*, but the species has been entered
under this name in the well-known *Bibliographic and Faunal Index* by Bassler and Moodie
(1943, p. 132). Unfortunately, I have not seen any actual fossil material either of the
so-called *Ateleocyrtis fletcheri*, or of the Caradocian *Ateleocyrtis husleyi* Billings
type of the genus, from the Tournelian of Canada. But a comparison between the North

1 When studying material in the collections of the Geological Survey and Museum, London, the
present writer noticed, many years ago, two specimens from Shoalshook (presumably from the Lower
Ashgill Shoalshook Limestone), one of which is labelled "*Ateleocyrtis oblongus* Ms." and the other
*Ateleocyrtis n.s.p.*. The specimens have not been examined.
American type species as figured by Miss Alice E. Wilson (1946, pl. 2, figs. 1–4), and *Ateleocystites fletcheri* as figured by Salter (1873, p. 128), makes it clear that the two forms cannot possibly be congeneric. Instead, *Ateleocystites fletcheri* has to be transferred to *Placocystites*. It may well be that it is in fact identical with *P. forbesiannus*, as suggested by Woodward and Barrande. If this is true, there is only one carroid species from the English Wenlock.

If there be some doubt about the species erected by Salter, we have, so far, no substantial knowledge of the member of the *Placocystites* fauna found on Gotland. It is represented by one specimen. It is not known exactly from which stratigraphic unit it comes, but it is reasonable to assume that the specimen originates from a stratum equivalent to some part of the Wenlock Limestone. According to information received from the late Professor T. Gislén, of Lund, it should be assigned to a new species related to *Placocystites forbesiannus* (cf. Regnél 1945, pp. 196–7).

As mentioned, this uniform carroid fauna seems to have occupied a well-defined marine province in west and north-west Europe, no Silurian carroids being known from any other part of the world. It is a ticklish question to say from where the *Placocystites* fauna was introduced. Among pre-Silurian carroids there is not one which can be safely referred to *Placocystites*. It is true that *Anomalocystites bohemiensis* Barrande from Ashgillian beds of Bohemia belongs to this genus according to Chauvel (1941, p. 215), but Caster (1952, p. 88) believes it may prove to be an Ateleocystitidae. Be that as it may, the Bohemian form is the only member of the Placocystitida in the Ordovician of Europe, while these enjoyed a certain flourishing in North America. Taking into view the considerable difference in age between the Silurian *Placocystites* and their plausible Ordovician progenitors, we must leave the question whether the *Placocystites* fauna was of an easterly or of a westerly origin unanswered. The fauna appeared rather abruptly. Its closest affinity is with Lower Devonian forms. We are thus entitled to assume that England was the prime centre of dispersal of the widespread fourth carroid fauna (the *Anomalocystites–Australocystis* fauna), of early Devonian age, which meant a remarkable revival of the carroid stock before its final extinction.

**EOCRINODS AND PARACRINODS**

An analysis of the stratigraphic and regional distribution of the eocrinoids leads us to conclude that the mainly Middle Cambrian *Eocystites* fauna originated in North America in early Cambrian time. No members of this fauna have been traced in the areas now under discussion, although they were present in the Bohemian Basin and France. An interesting find of a new eocrinoid of late Middle Cambrian or early Upper Cambrian age from the Lena Basin in east Siberia was recently announced by Yakovlev (1956).

The eocrinoids rapidly colonized new marine provinces, however, and the *Macrocystella–Micromycystes* fauna seems to have been distributed nearly all over the world in Tremadocian time. But it is worth noticing that Balto-Scandia, which was later to become a refuge of the declining eocrinoid stock, does not seem to have been inhabited by the fauna just mentioned. In England this fauna is represented by *Macrocystella mariae* in the Shinton Shales, the only eocrinoid recorded so far from the British Isles.

The *Macrocystella–Micromycystes* fauna had laggards right up to the close of the Ordovician but was largely substituted by a fauna containing *Cryptocrinites*, *Bocilla*, *Asocystes*, and *Polypychella*, at the same time as the centre of eocrinoid distribution
was shifted to Balto-Scandia, and especially to the East Baltic area. There several species of *Cryptopteris* and *Buckia* are found, ranging from the Arenig to the Lower Caradoc.

In Europe the eocrinoids became extinct before the opening of the Silurian. They definitely terminated with two species of the inadequately known *Lysoeystites* in the upper Niagaran (Wenlock). This is, moreover, a strangely isolated occurrence of eocrinoids in North America, since *Lysoeystites* is separated from the next-older eocrinoids by a time-gap extending to the Middle Cambrian.

The pararocrinoids are an almost negligible quantity in the Lower Palaeozoic faunas outside east North America. Whereas there are a dozen American genera, ranging from the Chazyian Crown Point Formation (inclusive) (approximately on the Llanvirn-Llandeilo boundary) to the Trentonian Kirkfield Formation (Caradoc), the genus *Achradocystites* is unique in Estonia and in Europe as a whole. Thanks to a recent revision by Hecker (1958) based on fresh material, *Achradocystites* is now known in some detail. Its main affinities are with *Comarocystites* which belongs to the geologically youngest among American pararocrinoids. The Estonian species—there are two of them, one in Keila (D2) beds, the other in Vasalemmu (D3a) beds—are probably slightly younger than *Comarocystites*. It follows from the regional and stratigraphical distribution pattern of the pararocrinoids that *Achradocystites* may well be an Appalachian immigrant in the Middle to Upper Ordovician fauna of Estonia.

**HYDOPHORIDS**

Hydrophorids, or cystoids in a restricted sense, are a conspicuous element in the Lower Palaeozoic faunas of both the British Isles and Balto-Scandia. There is a difference, however, in that the Ordovician hydrophorid faunas of Balto-Scandia were abundant and prolific compared with those of the British Isles, whereas the reverse was true of the Silurian hydrophorid faunas.¹

The most ancient faunal assemblage of hydrophorids in Balto-Scandia appeared in late Arenig time after having been preceded by a few very early forms. Characteristic of this fauna are *Cheirocrinites* and *Echinoacrinus*, and, in addition, in Sweden, *Spinaecrinites pumilum*. The sequence on the east side of the Baltic is notable for a number of morphologically and phylogenetically remarkable genera, like *Asteroblastus*, *Asterocystis*, *Mesocyrtis*, *Blastocystis*, *Proterocrinites* (cf. Hecker and Hecker 1957), and others. A corresponding fauna is not present in the British fossil record.

The highest peak of the curve illustrating the representation of hydrophorids in the Ordovician of Balto-Scandia falls within the Llandeilo and the Lower Caradoc and is

¹ The basis of a comparison between the British Isles and Balto-Scandia would have been firmer, had the hydrophorids of the former region been the subject of a modern revision. My personal acquaintance with the actual material is fairly limited. About ten years ago I had an opportunity to skim over the collections kept in the Museum of the Geological Survey in London, and in the British Museum (Nat. Hist.). In addition, material from Grizedale has been placed at my disposal by the kind agency of the late Mr. J. L. Begg of Glasgow, Mr. M. V. O'Brien and Mr. G. J. Murphy have permitted me to study all the cystoids from the Irish Ordovician present in the collections of the Geological Survey of Ireland in Dublin. It is true that generally the material is not very attractive from a palaeontological point of view because of the poor state of preservation in many cases. But I hope that, in spite of this, somebody will take the trouble to make a general revision which will very likely prove to be worth while. Until such a revision is available we cannot go much beyond some rather generalized statements and assumptions.
caused by the *Echinospheiraerites aurantiun*–*Helicoerinites* fauna. There is a certain lagging of the Scandinavian forms in relation to the Estonian ones, which indicates a trend towards the west of the early Middle Ordovician hydrophorids. This migration wave probably carried East Baltic faunal elements into the waters covering parts of Wales and Ireland. As far as I have been able to find out, the fossil record of the Caradoc hardly substantiates a similar statement as regards England. The Tramore Limestones in Co. Waterford and more or less equivalent strata in Co. Wexford, south-east Ireland, have yielded a fairly rich harvest of hydrophorids. According to personal information from Mr. G. J. Murphy, of Dublin, the Tramore Limestones may be considered as being of *Nemagroupus gracilis* age. Main constituents of these oldest hydrophorid faunas of the British Isles are members of the genera *Echinospheiraerites*, *Helicoerinites*, and *Cheirocrinus*. It may be objected that these are rather cosmopolitan in distribution, and that few species are common to the British Isles and Balto-Scandia. But the idea of a gradual migration in a westerly direction fits well into the general pattern of distribution of the Balto-Scandian Ordovician hydrophorids, which seem to themselves to have come from the Far East (cf. Regnell 1948c, p. 29). In this connexion it will be appropriate to recall that, as demonstrated by Stubblefield (1939, pp. 58–60), the Caradocian trilobite faunas of south-east Ireland and Girvan have both North American and Scandinavian affinities. In the case of the bulk of the hydrophorids, an American origin is inconceivable, but, as we shall see, such an origin is evinced by the presence of representatives of *Pleurocygestes*.

There is no main difference between the faunas just referred to and the Ashgill faunas in Wales and England. The most fertile collecting-grounds have been Shoalsbook in South Wales and the Bala Country in North Wales. A list of fossils, including seven species of hydrophorids, has been published by Miss Elles (1922, p. 172). The correct interpretation of some species is still obscure. But I take it to be most fortuitous that *Cheirocrinus davisi* McCoy is identical with *Helicoerinites balticus* of the East Baltic area. It is probable that this is true also of *Caryocystites granatum* of Forbes and several subsequent authors. Further, it is likely that *Echinospheiraerites aurantiun* McCoy is closely related to *Echinospheiraerites aurantiun*. Both these species appear in the East Baltic area in lower horizons than in the British Isles. There is a third easterly element in the British Ashgill faunas, namely *Cheirocrinus interruptus* recorded by Bather (1913) in the Drummuck Group in Girvan. According to Jaekel (1899, p. 220), two specimens of *Cheirocrinus interruptus* available to him came from the vicinity of Leningrad, the stratigraphic horizon being unknown.

The East Baltic aspect of the faunas now under discussion cannot be disputed. But there are also threads leading to the western part of the European continent. Thecal plates similar to those of *Oocyystis rugata* (Forbes) (syn. *Hemicosmites rugatus* Forbes, *Hemicosmites pyriformis* Forbes), a species recorded from Ireland, Wales, and England, have been found in Ashgillian beds in Belgium (Regnell 1951, pp. 21–22) and Languedoc.

1 Both Shoalsbook (Shobie's Hook) and Bala were exploited for hydrophorids at the beginning of the nineteenth century by officers of the Geological Survey. The fossil-bearing strata at these localities were first classified as 'Llanddulas Flags'; this designation was used, e.g., by Forbes (1848). The Shoalsbook Limestone and the Rhivos Limestone and Mudstones are now ranged with the Lower Ashgill.

A couple of errors have crept into this list. It is not evident if *Caryocystites granulatus* Forbes refers to *Echinospheiraerites granulatus* McCoy, or to *Caryocystites (i.e. Helicoerinites) granatum* (Wahlenberg). For 'Sphaeroues', read *Sphaeroues*. 
(Dreyfuss 1939, pp. 129–30). And *Echinospheerites (‘Spheronerites’) arachnodoeus (Forbes)* may have a certain affinity to *Echinospheerites barrandei belgicus* (cf. Renné 1951, p. 30).

A few words may be said about *Carystocystites litchi* Forbes 1848 (see Renné 1951, pp. 34–35). According to my notes on the original material in the Geological Survey and Museum in London, the specimen pointed out by Salter (1866, p. 286) as the ‘true’ *Spheronerites litchi* can hardly be determined (Forbes 1848, pl. 21, fig. 2c; Mus. no. 7431). Other specimens associated with it recall the genus *Haplopheraconis* with regard to the nature of the thecal pores. But in contradistinction to *Haplopheraconis* they seem to be many-plated and approach in this respect *Eucystis*. *Carystocystites litchi* was tentatively assigned to *Eucystis* by Jaekel (1899, p. 406). The original of the specimen figured by Forbes (1848) in his pl. 21, fig. 2b (Geol. Surv. Mus. London no. 1430) is possibly a *Spheronerites*. *Carystocystites*? *munitus* Forbes 1848 should possibly be referred to *Eucystis*. The genera *Eucystis* and *Haplopheraconis* are found in Middle and Upper Ordovician rocks in Scandinavia. *Haplopheraconis* has also been recorded in the Gembloux Shales in the Brabant Massive in Belgium (Renné 1951, p. 31).

The Caradoc and Ashgill of Girvan are, if not exactly unique, so very characteristic among contemporary deposits in the British Isles in having yielded a hydrophorid fauna which has in part a definitely North American stamp impressed upon it by members of the genus *Pleurocystites*. Bather (1913) described four species from the Upper Ashgillian Drummuick Group and reviewed all species of *Pleurocystites* known up to then. Two species had previously been recorded from the British Isles, namely *P. rugeri* Salter and *P. anglicus* Jaekel. The precise horizon of the former is not known, but it has been collected at various Caradoc localities in Wales. *Pleurocystites anglicus* was so named by Jaekel, because he thought that it came from Scotland or, possibly, from South Wales! Bather (1913, p. 475, §§ 466, 466) demonstrated that it comes from Barddalgisagh, Co. Tyrone, Ireland, and concluded that it is a little younger than *P. rugeri* and a little older than the Girvan species from the Starfish Bed.

Subsequently, I have studied echinoderm material from the Caradoc Craighead Mudstone, of the Balclatchie Group, collected in Craighead quarry, Girvan, by Mr. R. P. Tripp. This material which has not yet been published, includes a new species of *Pleurocystites*.

All species of *Pleurocystites* older than those in the Caradoc and Ashgill of the British Isles are North American, with the exception of a somewhat dubious species from China, *P. bassleri* Sun (1948, p. 6), of Llanvirn age. In North America *Pleurocystites* survived in older Richardson (i.e. older Ashgill) times. But we must conclude that one part of the stock migrated eastward so as to reach European waters in Caradoc times. As emphasized by Foerste (*in* Slocom and Foerste 1924, p. 358), the ‘direction of migration of *Pleurocystites* into the British Isles is unknown’. Records of doubtful *Pleurocystites* in Ashgill rocks of Belgium indicate the extreme eastward extension of the American influence (Renné 1951).

If we take a general view of the European Middle Ordovician hydrophorid faunas two main geographical provinces can be recognized: one characterized by the predominance of Aristocystitidae; and a second one characterized by the absence of genera

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1 Jaekel (1918, p. 95) proposed a new genus, *Dipleurocystis*, for the reception of *P. rugeri* and *P. anglicus*. In my opinion, *Dipleurocystis* is weakly founded and should be rejected.
belonging to that family. The province first mentioned, which conforms with the
"province à Amphorides" of H. and G. Termier (1952, p. 381), occupied the sea south of
the hypothetical Scottish-Hungarian barrier and extended to Bretagne, the south-west
of Europe, and Morocco. The other province comprised the Balto-Scandian area. The
hydrophorid faunas of both provinces undoubtedly originated from the Far East.

No Aristocystitidae have been found in the Lower Palaeozoic deposits of the British
Isles. Nevertheless, a certain influx of Mid-European forms may have taken place,
especially to the Girvan area, as demonstrated by its carpoid fauna. On the whole,
Girvan has been the meeting-place of faunal elements of different origin: Balto-
Scandian, Mid-European, and North American. The Bohemian element in the Upper
Ordovician faunas of Britain and Ireland is borne out very strikingly by certain trilobites,
as observed by several authors, most recently by J. A. Weir (1959, p. 382).

As is the case with several other echinoderm groups, the early Silurian marks a period
of decline for the hydrophorids. The Wenlock Limestone in Dudley confronts us with
a hydrophorid fauna of an entirely different and much more uniform aspect. Six genera
have been recorded, namely Aplocystites, Lepocirites, Pseudocrites, Starcocystis,
Schizocystis, and Pronocystites. Of these, the last two are Echinocerinaeidae, while
the four others belong to the family Callocystitidae. Apart from two species in the Upper
Silurian of Balto-Scandia, the English genera are the only representatives outside North
America of that family, which arose in late Ordovician times. The European Callo-
cystitidae may be descended from North American forms. During the deposition of
the Wenlock Limestone the Callocystitidae flourished in Dudley whence they wandered to
Gotland and to the Island of Ösel (Regnell 1948c, p. 42). It would seem as if a few of the
immigrants returned to North America. For, both in the case of Lepocirites and of
Pseudocrites, the former of which has two, the latter eight species in the Lower Helder-
berg (Lower Devonian), the oldest representatives are those present in the Wenlock
Limestone.

Pronocystites and Schizocystis are specialized morphologically and isolated geo-
graphically. They have no doubt a north-easterly origin, however, because all other
members of the Echinocerinaeidae are Balto-Scandian.

Except Lovencystis (Callocystitidae) there is only one hydrophorid in the Silurian of

BLASTOIDS

I shall not here discuss the taxonomic position of certain Lower Palaeozoic genera,
which are considered by some authors to be blastoids while others define them in a
different way. I am referring to the so-called Coronata. I agree with Jaekel in placing
them among the blastoids. Coronate blastoids are very scarce in the fossil record of
the areas with which we are now concerned. In fact, only three genera have been mentioned
in the literature, each of them containing one or two species. From Sweden there are
the Middle Ordovician Paracystis and the Upper Ordovician Tornoblastus, from Britain
there is the Silurian Stephanoecrinus (see Regnell 1945, p. 193; 1948c, pp. 30, 32, 39).
Additional material both from England and Sweden is in the hands of Dr. Ramsbottom.

The oldest coronate blastoid known is Mespilocystites which appeared in the Llanvirn
in Bohemia. It is possible that the Swedish Paracystis and Tornoblastus were derived
from the Bohemian form. It is more difficult to give an opinion of the relations between
the English and the North American species of *Stephanocerinus* which were roughly con-
temporaneous, that is to say mainly of Wenlockian age.

**CRINOIDS**

The crinoids are by far the most comprehensive of all pelmatozoan groups. But they
will be dealt with very cursorily, chiefly because of my insufficient personal experience
of at least the Silurian forms.

We are still unable to point out the ancestors of the crinoids. Accordingly, we have
no idea of the place of origin of the group. But we can say that a differentiation into
principal branches must have taken place at an early date. For, it is a fact that the
most ancient crinoids in Eurasia and North America were already specialized into
camerate, inadunate, and flexible forms. Crinoid evolution in relation to major palaeo-
geographic changes has been summarized and illustrated by diagrams in a paper by
R. C. Moore (1950).

To the inadunates belong crinoid remains in Lower Arenig rocks (Lower Tremadoc
of Hicks) at St. David's and on Ramsey Island, South Wales, described by Hicks (1873,
p. 51, pl. 4, figs. 17–20) under the name of *Dendrocrinus cambriensis*. The generic
determination is hardly correct, but, though fairly imperfect, the fossil is of great interest
in being probably the oldest genuine crinoid recorded so far.¹ The Ramsey Island material
has not been subject to a modern revision. On the whole, little information on the
Ordovician crinoids of the British Isles can be gathered from the literature. It would be
fortunate indeed if this deficiency could be made up, and I think there is reason to expect
that it will be so in the comparatively near future.

As a matter of course, crinoid ossicles are frequently met with in various rocks of the
Ordovician sequence in the British Isles. A common Welsh Caradoc fossil is that
generally referred to as *Glyptocerinus basalis* McCoy. Marr (1883, p. 126) gives its horizon
as 'Middle Bala'. The species should be assigned to *Rhapheocrinus* whose oldest known
member has been recorded in the upper Chazyian of New York. Also *Mesocrinus subpictus*
Bather (1896), from Llandeilo rocks in Shropshire, has North American affinities, but
in this case the British species is the older one. It is possible that *Actinocrinus* wynnii
Baily and *Periechiocrinus laevis* (Portlock, non Angelin) provide other examples of an
interchange between the Ordovician crinoid faunas of North America and the British
Isles, but their generic status must be verified.

The Ordovician seas of Baltoscandia were inhabited by a group of inadunates called
the Hybocrinida. These are remarkable in so far as they demonstrate a retrograde
evolution of the brachial apparatus (Ragnell 1948a). The oldest representative of the
Hybocrinida, *Baerocrinus parvus*, appears on the Arenig-Llanvirn boundary in Estonia,
followed by *Revalocrinus* in the upper Llanvirn. *Hoplochirus* sets us in the Llandeilo
and reaches Sweden in early Caradoc time. *Cornucrinus*, finally, appears in the middle
Caradoc and ranges to the Ashgill, inclusive. Outside Baltoscandia, Hybocrinid have

¹ *Trichocrinites* from the Table Head Limestone of Newfoundland was supposed by Moore and
Laudon (Amer. J. Sci. 241, pp. 262–8) to be 'older than any other yet known' (p. 262). This is probably
not correct. In the correlation chart of the Ordovician published by the Geological Society of America
(Twenhofel et al., 1954), the Table Head Formation is placed on the level with the Llanvirn (chart,
column 3; text p. 284).
been found in North America only (Hybocrinus, Hybocystites). The oldest of these originates from late Chazyan rocks in Ottawa, and it is possible, therefore, that the North American Hybocriniida are immigrants from Baltoscandia.

Very few crinoid cups have been collected in the Ordovician of Sweden. This explains why its crinoid fauna is largely unknown. This applies also to other parts of Baltoscandia, though to a lesser degree to Estonia. A number of genera seem to be endemic, namely Eshoinocrinus, Metabolocrinus, Pentamerocrinus, Peritocrinus, Tetractocrinus (all of Jaekel, 1902, 1918), and the morphologically remarkable Ristnocrinus Opik (1934), while Carabocrinus esthomen Jaekel (Vasalamma, Middle Caradoc) is a member of an otherwise exclusively American genus. According to Jaekel (1918, p. 43), Porocrinus, which first appears in the Blackriveran of Illinois, is evidently a derivative of Peritocrinus (see also Forster, in Stiocom and Forster 1924, p. 358).

In his monograph of the inadequate crinoids of Gotland, Bather (1893, p. 7) remarked that out of forty species treated by him only six are common to Gotland and England. But it should be pointed out that of ten genera recognized on Gotland, six have also been found in England. In addition, all Gotland genera but two are represented in North America, and four species are even common to these two areas. One species, Myelodactylus ("Herpetocrinus") anomalus (Bather), has been recorded from both Gotland (the Sylt Group; Upper Middle Wenlock), Dudley (the Wenlock Shales), Tennessee, and Indiana (Laurel, Waldron, Beach River; Lower and Middle Wenlock). In a subsequent paper, Bather (1906) discussed species of Botrocricinus from Gotland, Dudley, North America, and Australia; and in another paper (Bather 1907), he commented on a Scyphocrinites from west Cornwall which has Bohemian affinities.

I am not going to give further details but will restrict myself to stating that a number of recent papers tend to show that the Silurian crinoid faunas of Europe had a largely North American origin, and that many genera and several species had a very wide regional distribution (Bouska 1942, 1943, 1946, 1956a, 1956b; Lowenstam 1948; Ramsbottom 1950, 1951, 1952, 1958; Ubaghs 1958; see also Regnell 1948e, pp. 43-44). As a matter of course more or less provincial crinoid faunas had developed, but it is apparent that conditions were favourable for an interchange of faunal elements between North America, Britain, Sweden, and Bohemia.

The apogee of Silurian crinoid development in England is marked by the prolific fauna in the Wenlock Limestone. As pointed out quite recently by Dr. Ramsbottom (1958, p. 105), this gave place to a much impoverished fauna in Ludlow times.

**ELEUTHEROZOA**

Eleutherozoa are very subordinate in the Lower Palaeozoic rocks of Baltoscandia, while asterozoans are remarkably abundant in the Ordovician and Silurian sequences in the British Isles. "Starfish Beds" occur in the Ashgillian Drummuack Group in Girvan; in Wenlock beds of Gutterford Burn, Pentland Hills; in Lower Ludlow shales at Church Hill, Leintwardine in the Welsh Borderland, and near Kendal, Westmorland; and in the Upper Llandovery Kirkby Moor Flags in the Lake District, &c. Thanks to the monograph by W. K. Spencer (1914-40) we have an excellent knowledge of the Ordovician

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1. The Melbourne Series, in which Botrocricinus longibrachiatus has been found, is placed by T. W. E. David (The Geology of the Commonwealth of Australia, London 1930, I, tab. xi facing p. 224; see also p. 186) in the Wenlock and Lower Ludlow.
and Silurian astrozoans of the British Isles. On two occasions Spencer (1938, 1950) discussed the palaeobiogeographical aspects offered by these forms. The main facts found to be relevant for the British astrozoan fauna can be summarized as follows: the scanty Arenig and Llanvirn fauna from Wales and the Welsh Borderland "shows a distinct affinity with that of Bohemia" (Spencer 1950, p. 396). The Middle Ordovician astrozoans covered a very wide area extending from Turkestania to the St. Lawrence valley. This was literally true of the Welsh and Irish Stenaster, and of Protopalaeaster, from the Welsh Borderland. Other genera occurring in the British Isles have also been met with either in the west or the east of this vast marine province. 'The centre of much of the new differentiation appears to be to the west of Britain' (Spencer 1950, p. 398). The basic difference between Welsh Ashgillian faunas and contemporary faunas of Girvan is apparent also from the fact that the latter have abundant starfish while the former have none. Spencer (1950, pp. 401–2) recognized four elements in the Girvan starfish fauna, namely forms derived from Middle Ordovician ancestors in the same basin; new forms derived from one or two centres, which supplied immigrants to North America as well; new forms derived from the Arenig faunas of South France; and 'immigrants with untraceable ancestry, found also in the Silurian of Australia'. The affinity to Australian faunas persisted during the Silurian.

Turning to Balto-Scandia we find that no information whatsoever about Ordovician astrozoans can be derived from the literature. I can add but little to this, but would like to mention that available to me is a poor specimen of an astrozoan (undescribed) from Upper Ordovician Tretaspis beds in Västergötland, Sweden. In an erratic boulder of a rock from the Caradoc Coelosphaeridium zone in the Oslo area, Norway, Dr. G. Henningsoen has detected remains of starfish (undescribed).

Three species have been recorded from the Silurian of Gotland. These are Neopalaeaster hesslandei H. W. Rasmussen (1952) from Upper Llandovery beds near Visby; Urasterella rathveni leitwardensis Spencer (1918, p. 147) from Wenlock beds; and Palasterina antiqua (Hisinger) (see Spencer 1922, p. 229) from the Lower Ludlow beds of south Gotland. Notable among material which still remains to be described is a magnificent specimen of an ophiuroid from the so-called Pterygotus Beds at the top of the Höglö Group (Lower Wenlock), Visby.

Rasmussen (1952, p. 23) is inclined to derive Neopalaeaster from the Ordovician Siluraster, represented in Bohemia and North Wales (S. caracaci (Gregory)). Urasterella is first found in the Middle Ordovician of North America (Spencer 1918, p. 136). It is also present in the Ashgill of Girvan, in the Wenlock of the Pentland Hills, and in the Upper Ludlow of the Lake District. Palasterina, finally, has been found in the Middle Silurian of Australia and England, and in the Upper Ludlow of the Lake District (Spencer 1950, p. 402; see also Regnell 1948, p. 44).

The remaining euteleostegous groups do not require any time-consuming comments. No remains of undoubted holothurians have been recognized in the Lower Palaeozoic rocks of our areas. We may expect, however, that sclerites of holothurians will be found in the residue of samples treated with acetic acid, or in wash samples.

1 Eothuria beggi MacBride and Spencer 1938, from the Ashgill of Girvan, described as a holothurian has by most subsequent authors been considered to be an echinoid. Gutschick (1954) evidently accepted the original interpretation as a holothurian. Durham and Melville (1957, pp. 262–3) classify the Megalopaoda (order containing Eothuria only) as 'Incertae sedis'.

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Both Britain and Balto-Scandia have yielded forms which have a bearing on the early phylogeny of the echinoids. From the Ashgill of Girvan come the remarkable Aulechius and Ectinechius, while Durham and Melville (1957, pp. 243–4) have recently presented evidence of a Silurian age of Myriasters, possibly from the Welsh Borderland. In any case, the Scottish genera mentioned are the most ancient of the Lepidocentroidae. It would seem that this order had a centre in Britain. Silurian representatives are ‘Wrightia’ philippinica, Lepidocentrus? sp., Echinocystites pumon, and Palaeodiscus ferox (listed by MacBride and Spencer 1938, p. 93; cf. Regnell 1956, p. 156). The only Silurian species from outside the British Isles is Koninckioecidaris silurica from the State of New York. This species was approximately contemporaneous with ‘Wrightia’ (Upper Llandovery) which is the oldest of the British species.

In their paper just referred to, Durham and Melville (1957, pp. 242–4) argue that the much-disputed Botriocidaris, from the upper Middle Ordovician and Upper Ordovician of Estonia, is a genuine echinoid. A common ancestor of the geographically isolated Botriocidaris and the lepidocentroides is not known. Irrespective of which interpretation we adopt for Botriocidaris we cannot doubt that this very singular unit ended in a blind alley.

A more prosperous line of development, namely that of the Melonechinoidea, can be traced back to the Silurian (probably the Lower Ludlow) of Gotland. Gotlandechius described recently (Regnell 1956) is the most ancient member of this order. In addition, spines of cidaroids and other echinoid remains not safely assigned to definite higher categories, have been found in the Silurian rocks of Gotland. We have no idea of the common source—if there was any—of the lepidocentroids and the melonechinoidea, nor, in consequence, of their breeding ground.

Much of the early history of the echinoids seems to have been enacted in the Old Palaeozoic seas of Balto-Scandia and Britain. This is true also of the Ophiocystoids, very rare eleutheroid forms which unite traits of several echinoderm groups. It is possible that they evolved in the East Baltic area, for the genus Voleholia appeared there as early as in Arenig times. Two species have been described from the Leningrad province (Hecker 1938, 1940), and a slightly younger one from the Oslo district, Norway (Regnell 1948b). There is a great discontinuity in the development of the Ophiocystoidea as known to us, as the next younger representative of the class, Euthemion, is not met with until in the Wenlock Limestone of the Malvern district (Sollas 1899, p. 696). Two more genera, each with one species, have come from British Silurian rocks, namely Eucladia from Sedgley, near Dudley (Woodward 1869, p. 241), and Sollasiana (genotype: Eucladia woodwardii Sollas 1899) from Leintwardine (Sollas 1899, p. 695). Both are probably Lower Ludlowian in age. A last survivor of the Ophiocystoidea (Rhenosquama R. Richter 1930) has been traced in the Middle Devonian of the Rhine Valley, Germany. The group became extinct without leaving any descendants.

**INCERTAE SEDIS**

Finally, a few words shall be said of Cyclocystoides and Bamboporites, echinoderms of problematic nature.

As regards Cyclocystoides it may suffice to refer to a diagram published by me (Regnell 1948c, p. 41), showing the regional distribution and approximate stratigraphic
range of the known species of Cyclocystoides. It is apparent that Cyclocystoides originated in North America in early Middle Ordovician time. Migrants moving in an easterly direction turned up in Caradoc faunas in England, and in Ashgill faunas in Girvan. The genus entered Gotland in the Wenlock.

Bolboporites has a very narrow stratigraphic range in Balto-Scandia, occurring in Arenig-Caradoc beds. It has been recorded both from the East Baltic area, Sweden, and Norway. A faunal interchange with North America is evidenced by the fact that Bolboporites has been found in the Chazyan and Blackriveran of Canada and the State of New York. The only additional record of Bolboporites relates to the Tramore Limestones (Caradoc) of south-east Ireland (Reed 1899, p. 732).

EPilogue

The various facts presented here will serve to illustrate the points of contact, and the differences, between the echinoderm faunas of the Lower Palaeozoic rocks in the British Isles on the one hand and in Balto-Scandia on the other. To be sure, it is no easy task to recognize the individual threads in this entangled web. An oversimplification would perhaps make us believe that much of the faunal migrations were directed towards the west in Ordovician times and towards the east in Silurian times. But the pictures of palaeogeographical and palaeoclimatological features in remote times which we endeavour to envisage are poor in details, on account of scanty information—not least of the role played by ecological factors—and vague in outline, on account of our inability to reproduce the subject in a correct perspective. Some few future finds may have far-reaching consequences. But isn’t it so that what makes Palaeontology such a fascinating study is, in part, the very fact that so much of the Past remains to be revealed in the Future?

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1 Additional Devonian material published subsequently by Dr. Hertza Sieverts-Doree (1931) does not affect the distributional pattern outlined in the diagram.
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