An Outline of the Succession and Migration of Non-Crinoid Pelmatozoan Faunas in the Lower Paleozoic of Scandinavia.

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With 1 table and 4 figures in the text.

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Introduction.

The Pelmatozoa cannot be said on the whole to play a very important role in the fossil record of the Cambro-Silurian deposits of Scandinavia, either with regard to number of genera and species, or to individuals. This is true first and foremost of the non-crinoid forms, whereas crinoids are a fairly conspicuous element as rock-builders especially in the Silurian of Gotland.
Apart from a few horizons in which Hydrophoridea appear in great masses, non-crinoid pelmatozoans are as a rule found more or less fortuitously in Sweden. This also applies to Norway. The Old-Paleozoic echinoderm faunas of that country, however, are as yet somewhat less thoroughly investigated from a taxonomic point of view. As to Denmark, the Cambro-Silurian rock floor is exposed in the Island of Bornholm only. No statements of cystoids from Bornholm are to be found in the literature. Nor do the collections of the Paleontological Museum in Copenhagen contain any specimens, according to kind information (in litt.) from Professor Chr. Poulsen.

The reason why non-crinoid Pelmatozoa are found so relatively seldom can hardly be — as in the case of certain other animal groups — that their remains have been destroyed to a great extent. On the contrary, the calcified external skeleton of most echinoderms must have been especially resistant to the destructive power of environmental agencies. So it may be assumed, instead, that echinoderms are proportionally more frequent in the thanatoecenoses than in the biocenoses from which these were derived. The generally scarce occurrence of non-crinoid pelmatozoans, therefore, must be considered mainly a primary condition.

The migration of the sessile echinoderms now under discussion must have occurred during the stage of ontogeny in which the larvae were unattached, pelagic organisms. In recent crinoids the free-living existence of the larvae is of short duration. According to Delage & Hérouard (1903, p. 369) it lasts for two or three days only. In some cases it is considerably longer, however. Mortensen (1937, p. 61) found that the embryos of the comatulid Tropiometra audouini are free-swimming 5—6 days, or even longer, before attaching themselves. Of course we do not know what were the conditions in this respect in the non-crinoid pelmatozoans living in the Paleozoic seas. Yet it is most likely that their larvae had much the same cycle of development as have recent crinoids. If that be so, the shortness of the free-swimming stage in the larval development was a factor acting more or less unfavourably upon the migration of the individual species, which could hardly spread over long distances of the open sea. At any event this can not have been possible except under especially favourable conditions, in that the larvae were transported by currents rapid enough to carry them from one littoral zone to another in the course of a few days. For it must be kept in mind that all pelmatozoans, including the crinoids, so far known from Paleozoic deposits were living in fairly shallow water (cf. Deecke 1915, p. 1 seq., and Hadding 1933, pp. 51—52) as indicated by the lithologic character of the

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1 As regards the theory of the adult of Echinosphaerites as a planktonic form, cf. Regnéll (1945, p. 146).
rock and by the associated fauna. With regard to environmental conditions they were consequently very different from recent stalked crinoids, which are confined exclusively to the deep sea. But this implies, too, that the restraining effect of the special larval development just mentioned was selective to a certain degree, in so far as the crinoids, and the blastoids as well, were not affected to the same extent as the other Pelmatozoa, as indicated by their rich differentiation and development.

As mentioned above, the remains of non-crinoid pelmatozoans are embedded in sediments deposited in a shallow sea. But they do seldom occur in sediments of the actual shore-line, i.e. conglomerates and sandstones, as was already stated by Salter (1866, p. 272: «— the limestone has more or less of an aranaceous character, and it is the rarest thing for Cystidae to occur in such a rock»). Among forms originating from Scandinavia, one species only has been found in a sandstone, viz. the edrioasteroid Stromatocystites balticus Jaekel.1 They are extremely rare in pyrite-bearing sediments, and are almost absent in graptolite shales and other planktonic deposits2; nor are they common in other shales. In Sweden marly beds of the red Tretaspis shale of Dalarna, and the Staurocephalus shale and the so-called Cystoid shale of Scania have yielded some material. But species enclosed in limestone series rather often occur in marly or argillaceous layers (cf. Harding 1933, p. 53, foot-note 1). In the Oslo region, Norway, there are also shaly, lime-free sediments (especially in zones 4aZ—4bZ) bearing Hydrophoridea, which is also true of calciferous shales of zone 3cB (Regnell 1948 a, p. 23). Thus the non-crinoid Pelmatozoa cannot be said, as a whole, to be typical facies fossils. To what extent the individual species are dependent on lithologic facies, however, is a question which will not be discussed in this connexion.

The crinoids have survived up to the present time with a number of species, small in comparison with the vast amount of forms flourishing in ages past and especially during the Paleozoic. The non-crinoid pelmatozoans, on the other hand, became extinct in the Permian already (Blastoidea), most of its groups still earlier. The limited stratigraphic range of the non-crinoid pelmatozoans,

1 From other regions we have examples of cystoid faunas occurring in psammitic rocks, e.g. the Starfish Bed of Girvan and the Schistes quartzeux of Sombre-et-Meuse (Bather 1913, §§ 6, 559).

2 In one instance only has the writer noticed hydrophorid remains (Cheirocrinus sp.) associated with graptolites, viz. in a slab of a hard, lime-free shale from Fossum, Norway (spec. No. Ec 5165 in the Paleozool. Dept. of the State Museum of Natural History, Stockholm), probably originating from the Upper Didymograptus shale (4aZ). The Lower Devonian hydrophorids and carpoids described by Dehm (1933, 1934) occur in the Hunsrück slates of Bundenbach, which contain, however, a preponderantly benthonic fauna.
or, in other words, their short period of flourish, might be regarded as a function of the relatively feeble expansion power of most of the forms concerned.

**Previous Work on the Regional Distribution of the Non-Crinoid Pelmatozoans.**

The postulate of an attempt at analysing the migrations and history of development of a certain group of fossil animals within a definite area should be a thorough knowledge of the stratigraphic appearance all over the world of the several genera and species of the group which, in its turn, requires careful taxonomic investigations. It is evident that this demand is nothing but a vain wish: the fossil record is incomplete, and our research into the material available fragmentary or entirely wanting.

In the case of the non-crinoid Pelmatozoa, our present state of knowledge admits of but a rough outline of their history in the Cambro-Silurian seas covering part of the Scandinavian Peninsula of to-day. The bulk of the Swedish material available has been re-examined recently by the present writer (Regnéll 1945). Much of the old collections stored in the museums is not very fit for stratigraphical purposes, however, because of its inadequate labelling. The Norwegian material has not been studied in any detail as yet, but it has been thought worth while to consider in this connexion as far as it is known. Angelin (1878), Brögger (1882) (largely revised by the present author), Jækel (1926), and Regnéll (1948 a) have described a few forms. Some information on the matter can be gathered from some other papers as well, but these do not present any descriptions but mere statements on the occurrence of certain species.

The knowledge of the fossil record of the Ordovician-Silurian deposits of Estonia and the Leningrad district is notoriously of the utmost importance for the understanding of the Ordovician-Silurian faunas of Scandinavia. Good descriptions of non-crinoid pelmatozoans and observations on their stratigraphic range were given by several older authors (Pander 1830, Leuchtenberg 1843, Verneuil 1845, Volborth 1846 i. a., Eichwald 1860 i. a., F. Schmidt 1874 i. a.). In a paper published more than a hundred years ago Eichwald (1845 or 1846) made some special comments of the cystoid fauna of Scandinavia as compared with that of the East Baltic Provinces, and on paleogeographical conditions in Sweden. It is true that these remarks are primitive and unacceptable to-day, being based on false identifications of species and on confused ideas in general, but they may be quoted here as a first, and hitherto almost unique, attempt at discussing the
stratigraphical occurrence and regional distribution of the non-crinoid pelmatozoans in the Scandinavian-Baltic region:

»Mit dem Thonschiefer wechsellagert bei Christiania [Oslo] ein schwarzer Kalkstein, der ausser mehreren Arten von Asaphus, vorzüglich aus der Familie der Crinoideen die zu den ältesten Gattungen gehörigen Sphaeroniten enthält, die auch um Pawlowsk überall in so grosser Menge vorkommen; dahin gehört vorzüglich Sphaeronites aurantium und S. pomum [foot-note: »Die Art von Pawlowsk ist durch die Zeichnung der Täfelchen von Sphaer­nites pomum völlig verschieden und gehört offenbar mit meinem Proto­crinrites oviformis in eine Gattung, da in beiden die 5 rinnenartigen Spalten bemerkt werden«], die beide in denselben Schichten um Pawlowsk vorkommen. Auch ist die erstere Art schon von LINNÉ auf der Insel Oeland gefunden worden und dadurch diese Insel als Fortsetzung des Festlandes von Schweden anzusehen; sie kann also nicht, gleich Gottland, eine urweltliche Klippe oder ein Korallenriff in Meere der Vorwelt gebildet haben. Sphaer. pomum findet sich nicht in Norwegen, aber Sph. granatum nicht selten auf Gottland; diese ist bei uns noch nicht gefunden worden, während sich Sph. testudinarius HIs. auch selten um Pawlowsk, so wie auf Oeland findet. Ebenso wird Helicocrinus balticus in der Gegend von Christiania beobachtet, so wie um Pawlowsk und in Esthland, jedoch dort nirgends ein Hemicosmites, Cryptocrini­tes, Gonocrinites [= Echinoencerinites] oder ähnliche Arten, die unsere estländischen Schichten so sehr auszeichnen.» (EICHWALD 1845?, pp. 103—104.) In the same work (p. 93) he states that in Sweden »sphaeronites« are especially characteristic of the clay­shales. This, as we have seen, is definitely not the case.

A good deal of the material dealt with in JAEKEL's fundamental work of 1899 originated from Estonia and Russia, and much light was thrown upon the morphology and appearance of the Edrioasteroidea and Hydrophoridea.

More recently, most important contributions to our knowledge of the Ordovician non-crinoid pelmatozoan fauna of the East Baltic area have been published by HECKER in a series of papers (HECKER 1923, 1938, 1939, 1940). ORVIKU’s (1927) study on Echinosopharites may also be mentioned, as well as a paper by PHLEGER (1935) and a note by LUHA (1940) on a Silurian form.

Inconsiderable remains of Hydrophoridea were reported from Poland by e.g. CZARNOCKI (1928).

VĂȘCAȚUȚANU (1931) gave some information on hydrophorids in the Upper Ordovician of Romania.

What is known about the non-crinoid pelmatozoan fauna of Bohemia is due mainly to the work of BARRANDE (1887) (cf. also PERNER 1900). A survey of the geographical and stratigraphical distribution of these forms in general is also included in BARR-
RANDE's great monograph. On p. 220 there is a table showing the number of cystoid genera (24 in all) then known within the different stages of the Swedish series of strata. It is based on information from G. LINDBRÖM. — The papers of POMPECKJ (1896 a) and RUŽIČKA (1939) may also be referred to.

LORETTZ (1884) and FREYBERG (1923) described Hydrophoridea from the Ordovician of Germany, and RICHTER (1930) and DEHM (1933, 1934) have reported on Edrioasteroidea, Carpoidea, and Hydrophoridea from the Lower Devonian.

Apart from BATHER's (1913) admirable monograph on the Ashgillian Hydrophoridea and Carpoidea of Girvan, very little has been published on the taxonomy of non-crinoid peltazoans from the Lower Paleozoic of Great Britain after the memoir by FORBES (1848). This work, which thus appeared one hundred years ago, is quite naturally fairly out of date. SALTER (1866) described forms from North Wales. There is a short article of special interest in this connexion, however, viz. the summary by SPENCER (1938) on the distribution and migration of the starfishes and hydrophorids in the British Lower Paleozoic fauna. Part of this problem was touched upon slightly already by MARR (1882, p. 325). BEGG (1934, 1939) has dealt with Cyclocystoides. Of course there are a number of notes on cystoids in papers with mainly geological contents.

The Caradocian (sensu latu) cystoid material from Belgium is still insufficiently known, but will be studied by the present writer. MAILLIEUX (1926) published a note on a Devonian Cyclocystoides. A study by Dr. HERTHA DORECK on this and Rhine Devonian forms will appear in «Senckenbergiana».

Our knowledge of the Hydrophoridea and Carpoidea of France has increased considerably thanks to the important investigation carried out by CHAUVEL (1941). Other contributions have been made by KOENEN (1886), THORAL (1935 a, 1935 b) and by DREYFUSS (1939).

The considerable material of cystoids from the Lower Paleozoic of Italy has been reported on by BATHER (1910), PILOTTI (1924), and VINASSA DE REGNY (1941), of Spain by FAURA Y SANS (1913), and of Portugal by DELGADO (1908).

A description of the cystoid fauna of Morocco is being prepared by G. [DELPEY-]TEMPIER. A find of a Lower Devonian carpoid from South Africa was announced by RENNIE (1936).

BATHER (1906) and REED (1906, 1917 i.e.) reported on the fairly multiform hydrophorid fauna of India. SUN (1936) described Ordovician species from China and drew paleogeographical conclusions from the occurrence of certain European genera.

No non-crinoid peltazoans have been recorded from the Lower Paleozoic of Australia, as far as the writer is aware. The
so-called Cyamoidea (with the genus *Peridionites*) described by WHITEHOUSE (1941, p. 5 seq.) from the lowest Middle Cambrian of Queensland and recognized as the ancestral group of the Pelmatozoa cannot be accepted as echinoderms at all, according to GISLÉN (1947).

The contents of non-crinoid pelmatozoans in the Old Paleozoic deposits of North America have been elucidated by a number of authors: HALL (1852, 1867 i. a.), BILLINGS (1858 i. a.), SALTER & BILLINGS (1858), S. A. MILLER (1889 i. a.), SCHUCHERT (1904, 1919 i. a.), RAYMOND (1913 i. a.), FOERSTE (1914, 1916 i. a.), RUEDEMANN (1925), BASSLER (1935, 1936, 1943), A. E. WILSON (1946), and others. The importance of various cystoid genera for the intercontinental correlation between Europe and America is considered briefly in BASSLER 1943. Of considerable use to the student of Paleozoic pelmatozoans are the bibliographies published by the author just mentioned (BASSLER 1915, 1938). This is of course also true of the bibliographic and faunal index of Paleozoic pelmatozoans compiled by BASSLER & MOODEY (1943). This work presents useful faunal lists of different areas, arranged according to stratigraphic units. For reasons easily understood the faunal lists and the references suffer from certain unavoidable errors and shortcomings. Where Sweden and Norway are concerned, this is largely due to the fact that the recent revisions of the non-crinoid pelmatozoan faunas of these countries had not yet appeared when the index was published.

We have very meagre information about the appearance of non-crinoid pelmatozoans in the Lower Paleozoic of South America. Insignificant remains were mentioned by HARRINGTON (1937, p. 101; 1938, p. 117) and KOBAYASHI (1937, p. 417).

The Arctic has not yielded much material either. It has been recorded by POULSEN (1927, 1937, 1946)\(^1\), TROEDSSON (1928), and ROY (1941).

In this short review of our present information on the non-crinoid pelmatozoan faunas within various Lower Paleozoic areas such papers mainly have been considered as have more or less bearing on the subject to be dealt with below. Before concluding, it is appropriate to call attention to the magnificent work by JAEKEL (1899), briefly mentioned above. In that work JAEKEL treated the Edrioasteroidea and Hydrophoridae not only taxonomically but also, and in the first place, from general points of view, thus also with regard to distribution in time and space.

\(^1\) The remains of cystoids mentioned from the Lower Ordovician of Cape Clay, N.W. Greenland, by POULSEN 1927 (p. 282) and from Cape Webster, Ella Island, by POULSEN 1937 (pp. 27—28), may be related to *Macrocystella*, according to kind information from Prof. POULSEN (in litt.).
A survey of the evolution and distribution of the echinoderms in the Lower Paleozoic was presented recently by G. DELPEY [Termer] (1944). (N. B. the Addendum to Literature, p. 54 below.)

**Cambrian.**

Only a small number of pelmatozoans are known from the Cambrian deposits of the globe. From the Lower Cambrian there are two or three species (*Stromatocystites walcotti* Schuchert, *S. w. minor* Schuchert, *Lepidocystis wanneri* Forster); from the Upper Cambrian no more than one species has been described as far (*Trachelocrinus resseri* Ulrich; «Obscure remains of cystoids» were further reported from the Upper Cambrian of Andalusia by R. & E. Richter, 1940, p. 52, and of southern France, ibid., p. 64, after Miquel, mentioned by Thoral, 1935 a, pp. 90, 92, and 1935 b, p. 10 etc., as well). In comparison with this very meagre representation in the lower and upper parts of the system, the Middle Cambrian pelmatozoan faunas are remarkably well developed within a few areas, viz. Bohemia and southern France—Spain. Here the carpoids reached a vigorous flourish with a considerable differentiation of forms. No traces of these carpoid faunas have been discovered in the Scandinavian series of strata. But the single pelmatozoan genus known so far from the Middle Cambrian of Scandinavia, the edrioasteroid *Stromatocystites balticus* Jaekel, has congeneric forms in the areas mentioned, i.e. the Bohemian *S. pentangularis* Pompeckj and the Hérault species *S. cannati* (Miquel).

One of the first attempts at tracing the main features of Cambrian paleogeography is that by Frech in 1899. Since that time a wealth of facts has been accumulated regarding the Cambrian sequences and faunas within different areas. And yet the data available are not sufficient (and will of course never be) for the constructing of reliable paleogeographical maps. This is clearly demonstrated by Grabau’s magnificent attempt at a synthesis of an immense material, aiming at a general cosmography for the several periods of the Paleozoic (Grabau 1936—1938). The work was never accomplished but remains a gigantic and interesting torso. In 1940, however, Grabau published a comprehensive volume, in which the «pulse-beat» of the earth was followed from the pre-Cambrian up to the coming of Man.

What is of special interest to us in this connexion is to consider…

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1 Two specimens only have been found of this species, and not in bed rock but in the drift, of north Germany. From the lithologic character of the rock it seems to be possible to conclude, however, that the specimens originate from the Middle Cambrian of Sweden, and presumably from Öland (cf. Regnell 1945, pp. 198, 200).
for a while the map showing the paleogeography of Europe in Middle Cambrian time (Grabau 1936 a, Pl. II b) and the corresponding map of Pangaea (ibid., Pl. II) which may be the most recent maps of their kind published. One important correction was proposed by R. & E. Richter (1941 b, p. 34, textfig. 2) who showed that strong objections can be raised against the Tethys geosyncline as interpreted by Grabau. Of still greater importance to us is the shape given to the northern section of the map. The Caledonian geosyncline is taken in a sense different from that generally accepted. As is well known, the Caledonian geosyncline in Europe skirts the N.W. coast of the continent, from Ireland via Norway to Spitsbergen, the S.E. foreland being represented in Scandinavia by the Central Fennoscanian continental trunk. The Paleozoic sediments of the Baltic Shield S. and S.E. of this continental trunk are, quite naturally, typical shallow water deposits formed in an epicontinental sea (cf. e.g. Holtedahl 1920, textfig. 12; Frebold 1928; Asklund 1929, textfig. 1; Asklund 1938, textfig. 3; Bailey & Holtedahl 1938, textfigs. 1, 16). The Baltic Basin was an integral part of the sea-province characterized by the Acado-Baltic fauna, covering further Acadia, England, Bohemia, Middle Germany, Southern France, Sardinia, parts of Spain and North Africa (cf. R. & E. Richter 1940, pp. 71, 74; 1941 a, pp. 68, 69; 1941 b, p. 31). In view of this, it is not surprising to find representatives of Stromatocystites in the Middle Cambrian of Southern Scandinavia, Bohemia, and Southern France.

For this Acado-Baltic Basin Grabau (1936 a, Pl. II b) used the term »Caledonian geosyncline», which is of course illegitimate (cf. R. & E. Richter 1940, p. 72). The Scandinavian section of the true Caledonian geosyncline, on the other hand, coincides tolerably well with part of Grabau’s St. Lawrence geosyncline.

1 A synthetic map of the Cambrian in Europe is found on p. 99 in S. von Burnoff’s »Einführung in die Erdgeschichte», I, Berlin 1941. Somewhat modified reproductions of his maps of Pangaea were given by Grabau 1940.

2 We do not pay any attention to the fact that the map is drawn in polar projection with the North Pole in the region of modern Egypt, but let compass directions apply to modern maps. Nor is it necessary to discuss here Grabau’s supposition that, in Paleozoic times, the continents were in juxtaposition (Wegener position), forming one land-mass.

3 It should not be concealed, however, that in the text Grabau (1936 a, p. 634) declared that the »northern part of the Caledonian syncline [in the special sense of Grabau] i.e. the part involving southern Sweden and Bornholm, as well as that of the Oslo region, represents marginal shelf deposits, with repeated floodings as outlined in the text. Whether the central part of the geosyncline was more rapidly subsiding and has thicker deposits is unknown.» In their papers quoted repeatedly in this connexion, R. & E. Richter (1940, p. 72; 1941 b, pp. 36–37) object, rightly, against the wide-spread application of the term »geosyncline» in paleogeographical discussions. The term should be restricted to designate the zones from which the folded sedimentary mountain chains developed.
This is the northern extension of the Appalachian geosyncline, dismembered in Middle Cambrian time from the southern branch by the upheaval of the so-called Albany axis. The Appalachian trough (including the St. Lawrence geosyncline) must be supposed to have crossed the Atlantic west of, and almost parallel to, the Acado-Baltic province. We have to assume, further, that an exchange of faunal elements was possible between the Appalachian trough and the European part of the Acado-Baltic Basin, which communicated in an Arctic Sea. Known facts show (i. a. by the presence of a Middle Cambrian trilobite fauna in Bennett Island north of the New Siberian Group, described by Holm & Westergård 1930, closely related to that of southern Scandinavia) that the Baltic Basin was in connexion with the Siberian Sea, which, according to Grabau (1936 a, p. 495), may have been the centre of evolution and dispersal of the European Middle Cambrian faunas.\(^1\)

The presumed northern path-way from the Appalachian province to the Acado-Baltic would also explain the appearance of the American genus *Stromatocystites* in European series of strata. For *Stromatocystites* must be looked upon as an American element, as the oldest known representative of the genus originates from the Lower Cambrian of Newfoundland (*S. walcottii* Schuchert 1919). The migration in a northern direction from Newfoundland was of course initiated in Lower Cambrian time already, because the area now occupied by western Newfoundland seems to have been elevated over the sea in Middle Cambrian time (cf. maps I and II in Grabau 1936 a).\(^2\) It may be mentioned parenthetically, moreover, that the same migration route may have brought certain elements from the Appalachian province into the upper Lower Cambrian fauna of Aistjakk in Lappland, North Sweden, described by Kautsky (1945), as indicated by the close affinity between *Lingulella westergårdi* Kautsky and the East Greenland species *L. prisca* Poulsen. And it was suggested by Poulsen (1932, p. 65) that »the East Greenland geosyncline should be regarded as a continuation of the St. Lawrence geosyncline«. *Botsfordia* may as well have invaded from the north, being known from the Lower Cambrian of Northwest Greenland (Poulsen 1927, pp. 250, 339), but may also have arrived in Lappland from another direction, for the genus occurs also within the Atlantic coast region of North America (Poulsen 1927, p. 338), belonging to the Acado-Baltic faunal province.

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\(^{1}\) Cf. also the discussion of a possible Siberian Middle Cambrian strait connecting the Acado-Baltic and Western Pacific provinces in R. & E. Richter 1941 b, p. 38 seq.

\(^{2}\) It can also be imagined in this and similar cases that forms common to the Appalachian and Acado-Baltic faunal provinces have spread from a centre of evolution and dispersal in the Arctic (Boreal) Sea.
Ordovician.

In Scandinavia the Hydrophoridea are by far the most important group of the non-crinoid pelmatozoans. In this region, as well as in other areas, they reached their fullest development during the Ordovician period. As will appear from the following survey, they are very poorly represented in the Lower Ordovician, however, which may be a consequence of the decrease in the pelmatozoan stock as a whole in Upper Cambrian time.

In order to facilitate the comparison with foreign areas, the author has thought it wisest to review the contents of non-crinoid pelmatozoans in the Ordovician (and the Silurian) sequence according to the British standard section, although the correlation with Scandinavian strata is not quite definite throughout.

Tremadocian.¹

Cystoids of Tremadocian age are practically unknown from Scandinavia. The only statement of which the writer is aware is that of TULLBERG (1882 a, p. 230), who mentioned »Cystoid fragments» from the Ceratopyge limestone of southern Öland. In their monograph on the Ceratopyge fauna, MOBERG & SEGERBERG (1906, p. 107) did not pay any attention to the so-called cystoids referred to by TULLBERG, on account of insufficient information supplied by that author. Obviously they had no opportunity of studying the material alluded to, nor had the present writer. So the true nature of these fossils must be left undecided. But we can hardly doubt that they were remains of pelmatozoans.

The lower section of the Tremadocian of Scandinavia, the Dictyonema shale, has so far not yielded any fossils of this kind.

Thus, for the present, we lack actual data for considering the Tremadocian pelmatozoan fauna of Scandinavia in relation to that of other areas. As emphasized above, the total of non-crinoid pelmatozoans (and pelmatozoans in general) is most insignificant in Lower Ordovician deposits. The richest fauna hitherto discovered originates from the Upper Tremadocian zone of Asaphellina barroisi of Languedoc (THORAL 1935 b, p. 330). Macrocystella, and allied forms (Mimocystites etc.)², seems to have had a wide, possibly cosmopolitic distribution in the Tremadocian, being recorded from France (THORAL l. c.), England (STUBBLEFIELD & BULMAN 1927, pp. 113, 118), Bohemia (BARRANDE 1887, p. 164),

¹ Following LAPWORTH 1879 (On the tripartite classification of the Lower Palaeozoic rocks. — Geol. Mag. 6. Pp. 1—15), British stratigraphers usually classify the Tremadocian with the Upper Cambrian.
² Referred to the Eocrinoidea by JAÉKEL (1918, pp. 26—27) and, in accordance with him, by the present writer (REGNELL 1945, p. 37) as well.
Bavaria (Pompeckj 1896 b, p. 2), Greenland (cf. above, p. 7, foot-note 1), further from the South American Cordilleras (Kobayashi 1937, p. 417; Harrington 1937, p. 101; 1938, p. 117), and Korea (Kobayashi 1935, p. 59; the horizon, the Eoorth this zone, is taken by Kobayashi as the top-most zone of the Upper Cambrian sequence).

As mentioned above, the Tremadocian fauna of Scandinavia does not call for any discussion of paleogeographical conditions with regard to the distribution of the pelmatozoans. Maps relating to that epoch have been compiled e. g. by Grabau (1916, p. 621, text-fig. 10; 1936 b, Pl. III-a; 1937, Pl. III), Holtedahl (1920, p. 6, text-fig. 3), and Kobayashi (1936, p. 491, text-fig. 1). The several sea areas (and faunal provinces) seem to have been in closer connexion with one another than during the Cambrian (N.B. that the term »Caledonian geosyncline» is used by Grabau in the same improper sense as earlier). The main paleogeographical features and migration routes were summarized by Kobayashi (1936, pp. 490—492). As to Europe, a general survey of the distribution and relationships of the faunal elements was presented by Brögger (1896) in his well-known paper. Thoral (1935 b, p. 341), by his investigations of the Lower Ordovician of Southern France, also arrived at the conclusion that there existed an obvious affinity between the Tremadocian faunas of that region and of the part of the Acado-Baltic province ranging from eastern N. America to Scandinavia and Bohemia.

Skiddavian (Arenigian).

In the lowest Skiddavian strata of Sweden, made up of the Planilimbata stage (of the Asaphus series, or Orthoceratite limestone), Hydrophoridea are extremely uncommon. In fact one unique specimen only has been found, belonging to Cheirocrinus holmi Regnéll, from the green Planilimbata limestone of the Island of Öland.

From the superimposing division, the Limbata stage, no remains of non-crinoid pelmatozoans have been recorded in the literature, nor have such fossils been noted by the present writer. It would not be preposterous to suspect that the total lack, or at least utmost rarity, of cystoids and similar forms in these sediments is to some degree due to the special conditions under which the Limbata limestone was deposited. If we leave Scania and the Oslo region out of account, in which this zone (3cξ in Norway) is not very well developed, the rock is usually, though not always, a red limestone. Its red colour is due to the contents of iron oxide and/or its compounds. Moberg (1904), who made the problem the subject of a special investigation, arrived at the conclusion
(op. cit., p. 142) that the red colouring of certain divisions of the Cambro-Silurian sequence was effected thus that the mud was transported into a shallow and shelving sea. Then it was exposed to oxidation and complete red weathering during periods of emergence when the tide was low. Moberg (1904, p. 140) also pointed out that the red beds of the Orthoceratite limestone as a rule contain a smaller number of species than do the grey ones and are sometimes characterized by peculiar dwarf faunas. It cannot be altogether denied that the genesis of the red Limbata limestone thus outlined might have acted unfavourably upon the development of cystoids. It is true that Hydrophoridea and their allies are wanting in the upper, partially red-coloured portion of the Planilimbata limestone as well, but, on the other hand, there are a few forms which are confined to the red Platyurus limestone (cf. below). It should be remembered, too, that cystoids were represented very sparsely not only in Scandinavian deposits but in general at the time of the formation of the Planilimbata and Limbata limestones. In Norwegian equivalents to these divisions of the Swedish Orthoceratite limestone no non-crinoid pelmatozoans have been met with, as far as the author's knowledge goes.

The upper part of the Skiddavian is designated in Sweden (in shelly facies) as Asaphus limestone, and in Norway as 3cβ (Expanus shale and limestone). Here the hydrophoridean fauna reached its first flourish in Sweden, with several remarkable forms, and mass occurrence where Sphaeronites is concerned. In the Oslo region the first representatives of the group made their appearance.

In the south and middle of Öland two faunistically and lithologically characteristic divisions can be recognized within the Asaphus limestone, separated from each other by a bed crammed with thecae of Sphaeronites pomum (Gyllenhal). The Sphaeronites bed is further developed in Västergötland and, presumably, in Östergötland (Regnell 1945, pp. 166—167). Boulders of a grey limestone collected in 1947 at Lanna in Närke by Professor E. Stensiö, Stockholm, contain numerous poorly preserved specimens of Sphaeronites. The rock very likely derives from the Asaphus limestone, the youngest member of the Paleozoic sequence in Närke. The find may indicate that the Sphaeronites bed has been present locally in Närke as well.

As pointed out previously by the writer (Regnell 1945, p. 166), Sphaeronites pomum is undoubtedly a complex species comprising several forms. In most cases, however, the material of Sphaeronites of the pomum-group is in such a poor state of preservation as not to permit the investigator to recognize characters reliable enough for the establishing of separate forms.

It may be worth while to make some comments on two specimens of Sphaeronites pomum from Fägelsång in Scania (RM Ec
Provided that they were collected from the bed rock — the rock attached to the specimens agrees lithologically with the black Orthoceratite limestone found at Fågelsång — they have some bearing on the stratigraphy of the Orthoceratite limestone at that locality (cf. REGNELL 1945, p. 168, footnote 9). The Orthoceratite limestone in S.E. Scania, and at Röstänga as well (the small exposure in Kvarnbäcken is accessible at very low water only), is known to reach into the Asaphus limestone. But at Fågelsång, where the Orthoceratite limestone is in direct contact with the Upper Didymograptus shale, the limestone series does not include strata younger than the stage of *Megalaspis limbata*, according to the latest information available in the literature (FUNKQUIST 1919, p. 44; EKSTRÖM 1937, p. 49). However, *Sphaeronites pomum* indicates clearly that some part of the Asaphus limestone is present. Among the trilobites obtained from the Orthoceratite limestone of Fågelsång (cf. the lists published by TULLBERG 1883 b, p. 244, and MOBERG 1907, p. 257) there are also several pointing in the same direction, e.g. *Harpina scanica*, *Megalaspis extenuata*, *Pterygometopus sclerops*, *Ampyx volborthi* (the last-mentioned species associated with *Sphaeronites pomum*, a typical pygidium being present in the same hand-specimen as RM Ec 5026)*.

Consequently, the sub-zone of *Phyllograptus nobilis* (lowest sub-zone of the Upper Didymograptus shale) cannot be equivalent to at least the basal portion of the Asaphus limestone. According to EKSTRÖM (1937, p. 49, and the section on Pl. 10) there is, between the Limbata limestone and the Upper Didymograptus shale, a transition series (0.4—1.1 m thick) of limestone layers, interbedded with marl, shaly clay, and marl shale. This series has yielded a pygidium of *Megalaspis limbata* (not indicated whether from the lower or upper part of the transition series), and on ac-

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1 RM = Paleozoological Department of the State Museum of Natural History, Stockholm.

2 POUlsen (1936, pp. 50—51) also contributed to the characterization of the stratigraphic position of the Fågelsång Orthoceratite limestone but did not discuss its upper delimitation. It may be mentioned in this connexion that *Cyclopyge umbonata* (ANGELIN) has been found at Röstänga also (TULLBERG 1883 a, p. 5). In reproducing the stratigraphic scheme compiled by TULLBERG (1883 b, table facing p. 258) MOBERG (1911, p. 134) placed the Upper Didymograptus shale immediately above the black Fågelsång limestone with *Megalaspis limbata* S. & B.). In TULLBERG’s table, however, the limestone below the zone of *Phyllograptus cf. typus* was referred to as *Orthocerencalk*, with no further attribute. The dividing of this complex into faunistically characteristic zones was not done until 1890 by MOBERG.

3 In Öland these three species are confined to the Asaphus limestone (cf. WIMAN 1906, pp. 104, 105).

4 *Ampyx volborthi* F. SCHMIDT was found by POUlsen (1936, pp. 48, 51) in the Umbonata limestone of Bornholm, but as a rule seems to appear at higher horizons. It was recorded from the Lower Asaphus limestone of Öland by the present writer (REGNELL 1942, p. 4).
count of that it was referred by Ekström to the stage of *Megalaspis limbata*. It is not unreasonable to suggest, however, that the upper portion of the so-called transition series represents part of, or the total of, the Lower Asaphus limestone. A view of the correlation of the Upper Didymograptus shale similar to that advanced here has been, moreover, expressed by Troedsson (1928, stratigraphic table on p. 179; 1931, stratigraphic table on p. 327), who located the Upper Didymograptus shale above the Asaphus limestone and put its lower part as an equivalent of the Gigas limestone.

As mentioned above, the first hydrophorid to appear in the Skiddavian of Scandinavia was a species of *Cheirocrinus*. In the Upper Skiddavian, *Cheirocrinus* and other genera of the superfamily Glyptocystitida became the most significant pelmatozoan element along with *Sphaeronites pomum* (in Sweden). But contrary to that species all Glyptocystitida are rare forms in the Scandinavian fossil record, most of them being represented as yet by some few specimens only. In Swedish strata the following species have been met with: *Cheirocrinus leuchtenbergi* (Angelín), *Ch. cf. nodosus* (Jaeckel), *Echinoencrinites cf. reticulatus* Jaeckel, *E. senckenbergii* Meyer, and *Proctocystis monstruosa* Regnell. Zone 3cβ of the Oslo region has yielded *Cheirocrinus hyperboreus* Regnell, *Echinoencrinites senckenbergii acutangulus* Regnéll, and *Erinocystis bröggeri* Regnéll. Our list of species known so far from the Upper Skiddavian is complete after adding *Hemicosmites* sp. Regnell (1948 a) from the Oslo region¹, and a species from the Asaphus limestone of Röstånga, Scania, mentioned by Tullberg (1883 a, p. 5) as *«cystoid»*. The material upon which Tullberg based his statement could unfortunately not be re-found.

Like the extra geosynclinal shelly faunas of the Scandinavian Paleozoic in general, the Skiddavian non-crinoid pelmatozoan assemblage is decidedly East Baltic in aspect. It is true that *Sphaeronites pomum*², so characteristic of the Asaphus limestone

¹ The stratigraphic position of this species is not undisputed. According to Brögger (1882, p. 42), who referred to it as *Hemicosmites* sp., the single specimen available, an isolated thecal plate, originates either from the Upper Skiddavian (3cβ) or from the Lower Llandoillian (3cγ).

² In a review article, speaking of the Orthoceratite limestone at Röstånga, Tullberg (1883 b, p. 245) put it thus: »hier aber sind auch Cystideen angetroffen«.

³ No representative whatever of *Sphaeronites* has been described from the East Baltic area. Yet, according to kind information (in litt.) from Professor R. Hecker, Moscow, there are forms in the Leningrad province which have much in common with the Swedish *Sphaeronites*. It is due to a mistake, however, when Bassler & Moodley (1943, pp. 36, 190) report *Sph. pomum* from the Leningrad province. They refer to Volborth (1870, Pl.-fig. 1), who in the figure quoted reproduced a detail figure of *Sph. pomum* communicated by Lovén
of Sweden, has not been recorded from areas outside this country, but the Glyptocystitida show a close affinity to East Baltic forms. In stage B_{II} (Megalaspis limestone)\(^1\) in Estonia and the Leningrad district, corresponding to the stages of *Megalaspis planilimbata* and *M. limbata* in Sweden, we find species of the genera *Cheirocrinus* and *Echinoencrestites*\(^2\). These are represented by a multitude of forms in the subsequent stage, B_{III} (Vaginatum limestone, equivalent to the Asaphus limestone), which also contains *Erinoeystis* and, probably, *Proctoeystis*. Species common to the East Baltic area and Sweden are: *Echinoencrestites* cf. *reticulatus* JAEKEL and *E. senckenbergii* MEYER, and to the USSR and Norway: *E. senckenbergii* *acutangulus* REGNÉLL.\(^3\) No Skiddavian forms from Sweden are identical with such forms from Norway, nor is there any species common to Scandinavia and any other region but the East Baltic Provinces.

The Norwegian *Hemicosmites*\(^9\) sp. is a little surprising, if it can be trusted that it originates from the Upper Skiddavian. Neither in Sweden, nor with any certainty in the East Baltic area has the genus any representatives until in the Llandeillian (the Upper Llandeillian as far Sweden is concerned).\(^4\)

\(^{(1867)}\) VÖLBORTH (1846, p. 186) stated that *Sph. pomum* had not been met with in Russia, but had been identified erroneously with other species (cf. the list of non-synonyms in REGNÉLL 1945, p. 162). It is wrong as well to report *Sph. pomum* from the Oslo region (BASSLER & MOODEY 1943, pp. 37, 190). The statement must be due to the accidental misconception that the mountain Kinnekulle is situated in Norway. In a list of the Swedish Ordovician cystoid fauna *Sph. pomum* is reported properly from »Kinnekulle, Västergötland«.

1 The letter indices for the divisions in the Estonian geological column used in this paper are according to ÖPIK (1930).

2 As to the stratigraphic range of the East Baltic forms, see e.g. BASSLER & MOODEY (1943, p. 37 seq.) or ŠCUPIN (1928, pp. 171–172). In some cases the statements do not agree. Information on East Baltic forms is also found in REGNÉLL 1945.

3 The affinity between the Norwegian and the East Baltic echinoderm faunas is further accentuated by the presence of the ophiocistid *Volchovia* in both regions (cf. REGNÉLL 1948 a).

4 The stratigraphic range of the different forms is as a rule indicated vaguely in the writings of the older authors and cannot always be made out with certainty. According to JAEKEL (1899, p. 308), the oldest form of *Hemicosmites* known from the East Baltic area is *H. malum* (PANDER 1830; not 1840, as stated erroneously by JAEKEL 1899, p. 309, and REGNÉLL 1945, p. 100). BASSLER & MOODEY (1943, p. 165), however, report »*Hemicosmites elongatus* PANDER« from the »Kunda or Walchow fm.« which correspond, the former to the Vaginatum limestone, the latter to the Megalaspis limestone. In searching for information about *H. elongatus* in the original literature, the present writer arrived at the conclusion that such a species does not exist. The only place where the name in question is used, as far as the writer is aware, is in EICHWALD 1856 (p. 124), referred to by BASSLER & MOODEY (by a lapsus calami these authors give 1867 as the year of publication of EICHWALD's paper). All that is to be read here is as follows: »*Hemicosmites elongatus* PAND. Findet sich im unteren Grauwackenkalke von Pulkowa und Popofka.« Thus no description is given, and none was given
As just mentioned, no species of Skiddavian non-crinoid pelmatozoans of Scandinavia are known from other areas except the East Baltic Provinces. This is also true of the genera, with the possible exception of Cheirocrinus.\(^1\) Thoral (1935 a, p. 115) described, as a matter of fact, a species from the Lower Skiddavian of the Montagne Noir, which he designated as Ch.? languedoci anus. Judging from the figures published and the description, the determination would seem to be correct.

It can hardly be doubted that the Skiddavian echinoderm fauna invaded Scandinavia via the East Baltic Provinces. Contemporarily, certain elements migrated in a westerly direction along the northern border of the Caledonian—Hungarian barrier (or girdle of islands) thought to have separated intermittently the Bohemian Basin from the North-European Sea in Early and Middle Ordovician time (cf. e.g. Regnéll 1940, p. 11, with further references).

**Llandeillian.**

As the Lower Skiddavian, so the lower part of the Llandeilian is characterized by a very poor echinoderm fauna. In Sweden this section of the series of strata in limestone facies is made up of the red Gigas and Platyrurus limestones. With regard to lithologic development these stages are rather similar to the red limestones at the base of the Skiddavian barren of cystoid remains (cf. above, p. 13). It is possible that the same factors as acted unfavourably upon the flourish of echinoderm faunas in early Skiddavian time were of some importance in this instance as well.

The Gigas limestone in Sweden has yielded no non-crinoid pelmatozoans but *Sphaeronites?* sp. from Öland (Regnéll 1945, p. 171) and *Glyptosphaerites leuchtenbergi* (Volborth) from Östergötland. As regards the last-mentioned species, the stratigraphic

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1 In a previous paper (Regnéll 1945, p. 98) *Hemicosmites* was listed, with a mark of interrogation, to appear in the Lower Ordovician of France. The species upon which the statement was based may be of Upper Ordovician age, however (cf. Thoral 1935 a, p. 159).
determination is not quite conclusive (Regnell 1945, p. 156). Glyptosphaerites leuchtenbergi has a wide range in the East Baltic sequence (Vaginatum limestone—Uhaku), and is one of the two Hydrophoridea known from the stage of Asaphus platyrurus in Sweden. This stage is an equivalent of the Aseri (C1₃) in Estonia. The Swedish material has been derived mainly from Öland, further from Dalarna and, presumably, the North Baltic area. The second species occurring in this stage is Echinosphaerites aurantium suecicus Jaekel from Öland. As pointed out by Regnell (1945, p. 149), this form is very closely related to — if not identical with — the East Baltic Echinosphaerites aurantium infra Heck from the corresponding horizon. Thus the intimate connexion between the East Baltic and Swedish Ordovician pelmatozoan faunas is demonstrated again. Cheirocrinus, recorded from equivalent or somewhat younger strata of the Oslo region, has also East Baltic affinities, as we have seen. The genus is represented by Ch. nodosus (Jaekel) from the Ogygia shale (4αx) of Hedenstad (Jaekel 1899, p. 221). Further material has been obtained partly from the Ogygia shale of Törtberg at Frogner, Oslo (Grorud 1940, pp. 158, 159), and partly from the Ampyx limestone (4αβ) of Hovindsholm, Helgoya, Mjøsen (Angelin 1878, Pl. 12, figs. 16—17; Holtedahl 1909, p. 9). The species was referred by Angelin to Ch. leuchtenbergi (Angelín), by Jaekel (1899, p. 221) to Ch. nodosus (Jaekel), by Holtedahl to Ch. pennisiger Eichwald, and by Grorud to Ch. cf. leuchtenbergi. As stated by Regnell (1945, p. 76), we are probably concerned with a form which can be designated as Ch. cf. granulatus (Jaekel).

The Platyrurus limestone of the Swedish Orthoceratite limestone is superimposed by the stage of Illaenus schroeteri upon which follows, in Dalarna, the Crassicauda stage (Jaanussom 1947). This is equivalent with the Uhaku (C₁₆—C₂₉) of Estonia, and possibly with the Ancestroceras limestone of Öland (Moberg 1911, p. 104)² and in part with the Ampyx limestone of Norway. In Scandinavia non-crinoid pelmatozoans are as a rule scarce in this sequence, which is made up largely of grey limestones. The Norwegian Cheirocrinus cf. granulatus was just mentioned.³ According

1 Grorud’s paper (1940) was then not taken into account.
2 This question was left open by Jaanussom (1947, p. 50).
3 After the present paper was already completed, the writer had occasion to examine a few samples of limestone originating from 4αβ—4βx (Ampyx limestone—Lower Chasmops shale; locs.: Kullerud, Ringerike; Abbediengskollen, near Oslo) bearing remains of a Cheirocrinus (the specimens belong to the Palaeontological Museum in Oslo). Certain axial ridges of the thecal plates are provided with protuberances similar to those of Ch. nodosus, but the test is finely granulated, as in Ch. granulatus, a character which — as far as known — is not found in Ch. nodosus. This form very likely represents a new species which may be referred to as Ch. aff. nodosus until more complete material is available. It is evident that this species — as well as other Norwegian hydrophorid material — requires further attention.
to Brögger (1887, p. 17), *Echinoceras aurantium* (Gyllen- 
haal) appears rather frequently at the top of the Ampyx limestone 
(cf. also Stormer 1934, p. 25). Brögger (l. c.) also mentioned 
«numerous columnals of cystoids» (translated here), but of course 
«cystoids» must be taken as a synonym for «pelmatozoans» in this 
instance. From the upper Ancistroceras limestone of Öland and 
equivalent strata of Västergötland *Echinoceras aurantium*? 
has been reported (cf. Regnéll 1945, p. 147). Otherwise only two 
species seem to have been met with in the Swedish Schroeteri 
limestone, viz. *Cheirocrinus* cf. *nodosus* (Jaeckel) from Väster- 
götland, mentioned previously from the Skiddavian (Asaphus 
limestone) of that district, and *Cryptocrinites* sp. from Gräsgård in 
Öland.¹

It was emphasized by Jaanusson (1947, p. 48) that there is a 
remarkable difference in the composition of the fauna in the 
Crassicuda stage of Dalarna and the Uhaku, its equivalent in the 
East Baltic district, inasmuch as the rich cystoid fauna of the 
Uhaku is absent, or nearly so, in the Crassicuda beds. This dif-
fERENCE is supposed to be due to differences in facies.

If we turn to the upper part of the Llandeilian in Scandinavia, 
such a difference in faunal character is no longer predominant, 
especially not in Sweden (though it should be remembered that the 
majority of the Paleozoic pelmatozoans of Norway have as yet not 
been the subject of taxonomical investigation). In fact, an op-
timum of non-crinoid pelmatozoan development was initiated 
during the Upper Llandeilian. The abrupt changes in the fre-
quency of certain faunal elements — in this special case the non-
crinoid pelmatozoans — indicate that the series of strata does not 
represent a complete and uninterrupted sequence, but a complex 
formed during repeated transgressions separated by periods of 
upheaval. Very often the hiatuses are more or less masked dis-
conformities (Troedsson 1925, pp. 192—193). The stratigraphic 
gap between the middle and upper parts of the Llandeilian is 
demonstrated in certain districts of Sweden (Jämtland) by the 
presence of a conglomerate at the base of the Chasmops series (cf. 
Thorlund 1940, pp. 13, 69 seq., 121, 183).

The top of the Llandeilian is thus represented in Sweden by 
the lower part of the Chasmops series, made up mainly of the 
Cystoid limestone or Lower Chasmops limestone. Norwegian 
equivalents are the Lower Chasmops shale (4b2) and the Lower 
Chasmops limestone (4bβ).²

¹ The Swedish *Cryptocrinites* (one specimen only known) will be described 
in a forthcoming paper. The find of this genus is interesting, because the pre-
sence of Eocrinoidae in the Swedish series of strata has been indicated hitherto 
by *Bockia*? sp. only (Regnéll 1945, p. 67).
² Stormer (1934, p. 25) and Bailey & Holtedahl (1938, Pl. 1) place the 
Llandeilian—Caradocian boundary below the Lower Chasmops shale. Follow-
The correlation between shelly and graptolite facies in the Upper Llandeilian of Sweden was discussed at some length by Thorslund (1940, pp. 121—122). On geological grounds he suggested »that an upper part of the zone of Nemagraptus gracilis be considered equivalent in age to the basal Chasms series, instead of to the uppermost part of the Schroeteri limestone, i. e. the so-called Ancistroceras limestone« (Thorslund 1940, p. 121). The paleontological evidence wanted by Thorslund seems to be supplied by a graptolite associated with the shelly fauna of the Lower Chasms limestone at Böda, North Öland. In examining specimens collected by him at the locality mentioned, the present writer detected a fragment of a graptolite attached to the theca of a specimen of Echinospheerites aurantium. The graptolite fragment was determined, with a high degree of probability, as a branch of a species belonging to the form-group of Nemagraptus gracilis (Hall). If that be true, it seems to imply that the zone of Nemagraptus gracilis is equivalent, not only with the basal conglomerate and sandstone as indicated by Thorslund (l. c.; the sequences in Jämtland and Södermanland are considered), but with part of the Lower Chasms limestone as well. Some few fragments of graptolites, probably Glyptograptus sp., were also found associated with Echinospheerites aurantium in the flinty Lower Chasms limestone of Västergötland. These may not shed any further light on the problem of correlation, however.

The non-crinoid Pelmatozoa known from the Lower Chasms limestone in different districts of Sweden are as follows:


Öland: Cheirocrinus sp. (Regnell 1945, p. 77), Hemicosmites oelandicus Regnell, Caryocystites angelini (Haeckel), Helioicrinites granatum (Wahlenberg), H. ovalis (Angelin) (boulders), H. guttaeformis Regnell? (boulder), Echinospheerites aurantium (Gyllenhaal), Sphaeronites globulus (Angelin).

Gotland (drilling core): Echinospheerites sp. (Thorslund 1938, p. 28), Haplospheeris sp. (Thorslund, l. c.).

Västergötland: Cheirocrinus sp. (Regnell 1945, p. 77), Stichocystis alutacea (Angelin), Heliocrinites ovalis (Angelin), Echinospheerites gracilis

1 The material is in the Paleontological Institution of Lund University.
2 Janusson & Martna (1948, p. 190) suggest that the »Crassicauda limestone appears to be contemporaneous with the zone of Nemagraptus gracilis.«
3 Specimen in the Paleozoological Dept. of the State Museum of Natural History, Stockholm (No. Ec 3249).
4 Horizon not established with certainty.
sphaerites aurantium (Gyllenhal), Echinosphaerites sp. (Regnéll 1945, p. 152), Sphaeronites globulus (Angelin), Haplosphaeronis oblonga (Angelin), »cystoid» (Wallerius 1894, p. 300; cf. Regnéll 1945, p. 184).


Södermanland: Echinospaerites sp. (Thorslund 1940, p. 114).


Jämtland: Caryocystites sp. (Regnéll 1945, p. 118), Heliocrinites granatum (Wahlenberg) (boulders), Echinosphaerites aurantium (Gyllenhal), E. sp. (Thorslund 1940, pp. 68, 82), Haplosphaeronis sp. (Thorslund 1940, pp. 55, 91).

The North Baltic area (boulders): Heliocrinites prominens (Angelin), Echinospaerites aurantium (Gyllenhal).

The following species of non-crinoid Pelmatozoa originate from the Lower Chasmops limestone of Norway: Echinosphaerites aurantium (Gyllenhal) (Stormer 1934, p. 25; etc.), Glyptosphaerites sp. (Regnéll 1945, p. 154, foot-note 1)\(^5\), Sphaeronites globulus (Angelin)? (cf. Regnéll 1945, pp. 161, 171).

After this survey of the stratigraphic range and regional distribution within Scandinavia of the Llandeilian non-crinoid plematozoan faunas, we shall try to trace their relations to con-

\(^1\) Specimen from Fjäcka (coll. J. Martna 1945), not yet described (Paleontological Institution, Uppsala).


\(^3\) The holotype of H. prominens was found in the collections of the Paleozoölim. Dept. of the State Mus. Nat. Hist., Stockholm, after the author’s monograph of 1945 was already printed (cf. Regnéll 1945, p. 131).

\(^4\) Some forms have been recorded from strata above the Lower Chasmops limestone s. str. A specimen referred to Heliocrinites cf. ovalis (Angelín) has been collected by Jaanusson & Martna in the »beds of plastic clay (probably bentonite)». This section follows upon the Lower Chasmops limestone s. str. and is superimposed by beds of undetermined stratigraphic position but included provisionally in the Lower Chasmops limestone s.l. (Jaanusson & Martna 1948, p. 189). According to the authors mentioned, these beds have yielded i. a. Echinosphaerites aurantium.

\(^5\) On the label, written by G. Holm, who collected the specimen, the horizon is given as »Chasmops series». Locality: Baadbugten.
temporary extra-Scandinavian echinoderm faunas, which was briefly mentioned above.

Starting with the Lower Llandeilian, we have had occasion already to emphasize its affinity to the East Baltic area, as demonstrated by *Glyptosphaerites leuchtenbergi*, and by representatives of *Cheirocrinus, Echinosphaerites*, and *Cryptocrinites*. There is a statement (Pilotti 1924, p. 32) that *Glyptosphaerites*, and possibly *G. leuchtenbergi*, appears in Sardinia, which seems to require further confirmation, however. The genus was not mentioned by Vinassa de Regny (1941). If the statement be true, however, it would indicate an expansion towards the south of the Baltic echinoderm fauna. Then it seems most reasonable to assume that the migration was made possible by transgressions over the Caledonian-Hungarian barrier, in Middle Ordovician time (cf. above, p. 17). Ordovician strata of Baltic facies bearing *Echinosphaerites* are present in the St. Cross Mountain between Warsaw and Cracow (Čarnocki 1928, p. 557; as regards the distribution of Lower Paleozoic rocks in Poland, see also Sujkowski 1946, pp. 193—194, Pl. 14). It may be that the sea in which these were deposited reached as far as the Bohemian Basin, which, in its turn, stood in connexion with the sea covering parts of Britain (Spencer 1938), South Europe, and North Africa. As a whole, the rich hydrophorid faunas of Bohemia have not much in common with the Baltic ones. But it should be noticed that the very genus *Glyptosphaerites* that gave rise to this discussion is represented in Bohemia by *G. ferrigenus* (Barrande). According to Perner (1900, p. 145), the horizon of the single specimen known is Dd₁ (Komárov beds, of Skiddavian age; cf. Kettner and Bouček 1936, Table 4). This is admittedly an obstacle for the supposed Baltic origin of *Glyptosphaerites* in Bohemia. For in the East Baltic area the genus does not appear until in the Vaginatum limestone, as we have seen. This is equivalent to the lower part of the Šárka beds, which overlie the Komárov beds.

*Glyptosphaerites* has also been recorded from other areas, viz. from Thuringia, N.W. of the Bohemian Basin (Loretz 1884; Freyberg 1923, p. 265), and from Spain, S.W. of it (Jäckel 1899, p. 425). In the first-mentioned case, *Glyptosphaerites* is said to have been derived from strata equivalent to Dd₅ in Bohemia, i.e. the very top of the Ordovician sequence. If the specific determinations are correct, the genus is associated with hydrophorids appearing at considerably lower horizons, e.g. *Protocrinites fragum* (Eichwald) from the Vaginatum limestone. On the other hand, there are species such as *Orocystites helmhaeckeri thuringiae* (Jäckel) and *Heliocrinites confortatus* (Barrande), which are closely allied to, or identical with forms of Barrande's stage Dd₄. This is Caradocian-Ashgillian in age. Evidently some forms of the
Ordovician cystoid assemblage of Thuringia have not been determined properly and offer no reliable basis for the assumption of a connexion between the Baltic and the Bohemian Basin via Thuringia in Lower Llandeilian time. Such conditions may rather have been prevailing during the Upper Ordovician. — As regards *Glyptosphaerites* sp. from Spain, JAEKEL (1899, p. 425) stated only that it originates from the Upper Ordovician of Trasno.

It is well known that species belonging to the form-group of *Echinosphaerites aurantium* have an almost cosmopolitan distribution. This is true of *E. aurantium suecicus* as well, if FIELD’s statement (1919, p. 419) can be trusted that the species mentioned occurs in the Rodman formation of Pennsylvania.¹ In Sweden it is confined to the Platyrurus limestone; the most closely related *E. aurantium infra* appears in the equivalent Aseri of the East Baltic area. The North American form holds a considerably higher stratigraphic position, a fact which is in itself not quite unreasonable.² But hydrophorid genera of Baltic aspect have recently been reported from Oklahoma strata equivalent to the Lower Llandeillian (BASSLER 1943). These are *Cheirocrinus* (Cool Creek formation) and *Caryocystites* (Falls formation), both Cha­zyan. From the Bromide formation (Black River, probably equivalent to the Swedish Schroeteri stage) BASSLER (1943, p. 703) recorded *Echinoencrinites*. Of these, *Cheirocrinus* and *Echinoencrinites* are represented, as we have seen, already in the Skiddavian of the Baltic area. As far as our present knowledge goes, this cannot be said of *Caryocystites* (as defined by REGNELL 1945, p. 112), which does not appear until in the Upper Llandeillian of Sweden; the age of *C. esthoniae* (JAEKEL) is not known with any certainty, the unique specimen being obtained from an erratic boulder (JAEKEL 1899, p. 339—340). Anyhow, we can hardly doubt that the genera under discussion are either immigrants from the Baltic region — transformed (at least some of them) into other species, it is true — or else are descendants from common ancestors in some centre of faunal evolution connected with the Baltic area, on the one hand, and with North America, on the other.

¹ *Echinosphaerites aurantium suecicus* was not mentioned from USA by BASSLER & MOODEY (1943, p. 155).

² FIELD (1919, p. 419) took the Rodman formation as «the closing phase of Stones River time». According to WILMARTH (1938, p. 1837), it is the upper formation of Black River, overlying the Lowville limestone and underlying the Trenton. HUFFMAN (1945, Middle Ordovician correlation table on p. 173), finally, took it as the youngest formation of the Nealmont, which forms the lower part of the Trenton. Thus the Rodman would be equivalent to part of, or the whole of the Crassicauda stage in Sweden. It may be mentioned that — according to COOPER (1945, p. 275) — «Stones River as a general time-rock term should no longer be used, nor should the name be revived if a post-Chazyan, pre-Black River group is recognized.»
Then the question arises: What routes of migration did they use to arrive at their sites in the Western hemisphere, or, where was the common centre of evolution?

The general paleogeographical conditions of Middle Ordovician time were discussed i. a. by GRABAU (1923, p. 47 seq.), who published a map of Boreal paleogeography in Black River time (op. cit., fig. 31, p. 56). The same subject, with reference to the American and Eurasian circumpolar regions, was dealt with by HOLTEDAHL (1918, p. 93; 1920, pp. 5—6; 1924, p. 109 seq.), and by TROEDSSON (1928, p. 176 seq.). It seems likely that there existed a narrow Scandinavian-Scottish land barrier (HOLTEDAHL 1920, p. 5) separating the Baltic and the Arctic Sea provinces from each other (cf. TROEDSSON 1928, p. 183, who also reviewed the divergent opinions on the faunal connexion between North America and the East Baltic area arrived at by BASSLER on the basis of his studies on bryozoans). The migration of faunal elements, therefore, was effected across the Arctic Sea. A »true circumpolar distribution of the sea« in Lower Ordovician time was assumed by HOLTEDAHL (1924, p. 121), who further advocated the view that at a »somewhat younger [than Tetragraptus time] Ordovician time the Khabarova fauna of Northern Russia and the Pterygometopus selerops fauna of the Tunguska etc. tell of a more or less open connection with the South Scandinavian Baltic region, while the Black River—Trenton faunas of Bear Island, North Greenland, the American Arctic Archipelago and northwestern North America indicate a very wide distribution of the North American-Arctic Sea at this period, the sea reaching further south (across the Baffin Land—Hudson Bay area) than in the preceding, Lower Ordovician time« (HOLTEDAHL 1924, p. 122).

TROEDSSON (1928, p. 187) seems to be inclined to accept largely the views set forth by HOLTEDAHL and went a little more into details: »If — in this case — the geosyncline extending from Novaya Zemljja to Alaska means a coast-line this interpretation is in accordance with the statements made here. Furthermore, there was a central (deep) basin, the Arctic sea, which formed an obstacle in the way of the litoral fauna but, in return, made it easier for the pelagic forms or forms which were able of pelagic spreading.«

The present writer cannot see any possibility so far to decide conclusively whether the Hydrophoridea now under discussion are immigrants from the East Baltic area to North America via the Arctic sea, or whether the ancestral forms arose in the Arctic sea and from there invaded the Baltic area as well as North America. As far as the writer is aware, no Lower and Middle Llandeillian Hydrophoridea have been recorded from the Arctic. This fact — which may be due to our still imperfect knowledge of the Lower
Paleozoic faunas of these regions — cannot of course be used as an argument for either of these alternatives. The only species common to the Baltic area and North America, as we have seen, is *Echinospaerites aurantium suecicus*, provided that Field's determination is true (cf. above, p. 23). If any importance can be attached to this matter, it is rather in favour of the theory suggesting a Baltic origin, all the more as the species in question appears earlier in Sweden than in Pennsylvania. It should be noted, however, that according to Field, *E. aurantium suecicus* is associated i.a. with *E. grandis*, which appears in Sweden in the Upper Llandeilian and the Lower Caradocian. One of the two determinations, therefore, seems to be wrong.

Now we shall consider briefly the non-crinoid pelmatozoans of the Upper Llandeilian in Scandinavia, and their contemporaries. The Eocrinoida are probably represented by a species of *Bockia*. This genus is known otherwise from the East Baltic area only, appearing first in stage BII (Skiddavian) and ranging into stage C3, which is equivalent (at least in part) to the Swedish Lower Chasmops limestone.

Several of the Hydrophoridea have East Baltic affinities, but as to species, a number of them seem to be endemic to Sweden. Reviewing the genera in systematic order, *Cheirocrinus* is richly differentiated in the East Baltic area, where it has a considerable vertical range. It may be remembered, too, that there are earlier representatives of this genus in Sweden and in Norway as well. Further species are found in North America. In Scandinavia no post-Llandeilian forms of *Cheirocrinus* have been met with so far, but the genus reached a wide distribution, having been recorded from Caradocian, or younger, strata of the East Baltic area, Bohemia (Barrande 1887, p. 160), Great Britain (Girvan) (Bather 1913, p. 442), Portugal (Delgado 1908, p. 83), North America (cf. e.g. Bassler 1915), Baffin Land (Roy 1941, p. 80), and Greenland (Troedsson 1928, p. 105).

As regards the early occurrence of *Hemicosmites* in Norway and the East Baltic area, cf. above, p. 16. One species was described by Sun (1936, p. 481) from Kweichou, China. The age of the Shihtze pu shale, from which *Hemicosmites* (associated with other non-crinoid pelmatozoans) was collected, was said to be Llandeilian.1 Since the fauna also contains a species designated as *Sticho-
cystis sp. (cfr geometricus), it will hardly be older than the Upper Llandeilian. In Sweden Stichocystis geometrica (ANGELIN) appears in a somewhat younger horizon, the Macrourus beds (Caradocian). St. alutacea (ANGELIN), on the other hand, seems to have been derived from the Lower Chasmos limestome of Västergötland.

Caryocystites angelini (HAECKEL) is a significant element in the Lower Chasmos limestome fauna of northern Öland. A related form is known from corresponding strata of Dalarna. C. sp. from Jämtland shows more affinity to C. lagenalis REGNELL (cf. REGNELL 1945, p. 118). Some remarks on the genus have been given above (p. 23).

Whereas Caryocystites had a very restricted regional distribution during the Upper Llandeilian—Caradocian, Heliocrinites was widely spread, especially in Caradocian time. In Sweden there are at least five species in the Upper Llandeilian Chasmos limestome, but from younger Ordovician strata one species only has been recorded.\(^1\) If we have a general look at Heliocrtinites, it is evident that it approached Scandinavia from the east, for the East Baltic series of strata contains several species that are older than the Swedish ones. In the far East, too, Heliocrtinites has representatives, in part prior to those of Scandinavia (species originating from the Naungkangyi beds of Burma, which are equivalent to the so-called Echinosphaerites limestone, C\(_{13}\)—C\(_{19}\), of the East Baltic Provinces, according to REED 1906, p. 85), and in part fairly equivalent to them (a species from the Shihtzepe shale of China, cf. above, p. 25, foot-note 1). Later on, as we have seen, Heliocrinites reached far outside the Baltic Basin.\(^2\) Thus Caradocian, or Ashgillian, forms have been reported from the following extra Baltic-Scandinavian countries: Thuringia (FREYBERG 1923, p. 263, H. confortatus, sub Echinosphaerites), Bohemia (BARRANDE 1887, p. 153, as the preceding), Great Britain (BATHER 1913, p. 494), Belgium (BATHER, l. c.), France (KOENEN 1886, H. rouvillei, sub Caryocystites; cf. also REGNELL 1945, p. 137), Spain (FAURA Y SANS 1913, p. 112), and Portugal (JAEKEL 1899, p. 330). Of the Heliocrinites forms occurring within foreign areas none is identical specifically with any Swedish form, as far as known.

\(^1\) It should be noted, however, that the stratigraphic range of the two species of Heliocrinites mentioned below as Silurian is not quite conclusive.

\(^2\) Heliocrinites granaturn mentioned from Great Britain by FORBES (1848, p. 512) and by numerous subsequent authors might be designated as H. balticus EICHWALD? (cf. REGNELL 1945, p. 122).
The writer had occasion above (p. 23) to point out that *Echinospheerites aurantium*, and allied forms, had an almost world-wide distribution. The relations between the forms of the various areas are not very well known, however. The Scandinavian material, too, is fairly heterogeneous, as indicated also by the rather wide stratigraphic range of this form-group. We have seen that it was represented in strata below the Upper Llandeilian, and it appears in Caradocian beds as well. In Sweden there are also a few forms of *Echinospheerites* in the Upper Llandeilian, which are clearly distinguished from *E. aurantium*. One large species occurring in Östergötland and Dalarna (Upper Llandeilian—Lower Caradocian) was referred tentatively to *E. grandis* JAEKEL by the present writer (REGNELL 1945, p. 149). It was suggested that *E. pogrebowi* HECKER may be identical with *E. grandis*. If that be so, *E. grandis* is an example of a species common to Sweden and the East Baltic Provinces. Within the area last mentioned, *E. pogrebowi* was recorded from the Kukruse, which is equivalent to the Lower Chasmos limestone. A closely related form, designated by HECKER (1923, p. 37, Pl. 2, fig. 3) as *E. cf. pogrebowi*, originates from the Island of Vaigach, from Lower Llandeilian strata, since the horizon was said to be equivalent to the stage of *Asaphus platyurus*. Further, *E. grandis* was mentioned from the Rodman formation of Pennsylvania by FIELD (1919, p. 419), thus from a horizon somewhat below the Lower Chasmos limestone in Sweden (cf. above, p. 23, foot-note 2). The present writer has had no opportunity to form a personal opinion of the correctness of FIELD's determination.

Another species of *Echinospheerites*, with large pyriform theca, from Västergötland, was described and figured by REGNELL (1945, p. 152, Pl. 8, fig. 6), but not designated by a specific name on account of its unsatisfactory state of preservation. It is possible that this form is conspecific with a form from the Kukruse of Estonia, described by SCHMIDT [1858, p. 221 (223 of sep. print)] as follows: "Eine grosse, dieser Species [*E. aurantium*] nahestehende, birnförmige Art von 1 bis 2 Zoll Längsdurchmesser, gründet sich bisher auf nur unvollkommen erhaltene Exemplare."

FUNKQUIST (1919, p. 38) mentioned *E. aurantium* from the so-called Cystoid shale of Scania, which probably represents the Lower Chasmos beds. The present writer (REGNELL 1945, p. 153) is not inclined to confirm the determination, not even the genus, but preferred (l. c.) to refer to the species as "*Echinospheerites?* sp."

*Glyptospheerites?* sp. from the Chasmos limestone of the Oslo region is younger than the East Baltic representatives of the genus. Yet within other areas — in Sweden as well — there are species of *Glyptospheerites* comparable in age with the Norwegian one, or younger (cf. above, p. 22).
*Sphaeronites globulus* (Angelin) is very common in the Lower Chasmops limestone of northern Öland, but has been found also in a few other regions in Sweden (cf. above, p. 21). Apart from Brögger’s (1882, p. 42, foot-note 1) statement of a variety of *S. globulus* from the Oslo region, the reliability of which the writer has had no opportunity to control, the species has not been recorded from outside Sweden. The affinities of *S. shihienensis* (Reed) from West Yunnan (Reed 1917, p. 12) and Karakoram (Gortani 1934, p. 26), appearing at a stage with a supposed equivalence to the Platyrurus limestone, seem to be with *S. globulus* rather than with *S. pomum* (cf. Regnéll 1945, p. 170).

According to data published (cf. Regnéll 1945, p. 171), the genus *Haplosphaeronis* has been met with in Scandinavia and, possibly, in Yunnan (*Sphaeronis* lobiferus Reed), but is also present in the Leningrad Province, according to kind information (in litt.) from Professor R. Hecker of Moscow. The stratigraphic range of the East Baltic *Haplosphaeronis* is unknown to the writer. The contingent East Asiatic species is older than the Scandinavian ones. In Sweden, *Haplosphaeronis* appears first in the Lower Chamsops limestone, has its main distribution in the Macrourus beds (Caradocian), and still survived during the formation of the Lower Boda reef limestone of Dalarna (mainly Ashgillian). In Norway, *Haplosphaeronis* occurs in the Sphaeronid shale and limestone of Hadeland which constitute a northern facies of the Upper Chasmops limestone (4b§). These deposits have been suggested to be correlated with the Kullsberg limestone of Dalarna (Stormer 1945, p. 397), which is a reef facies of the stratified *»normal»* Macrourus beds.¹

Summing up the principal conclusions to be drawn from this review of the non-crinoid fauna of the Upper Llandeillian of Scandinavia, we find that the majority of its elements are of a distinct East Baltic type. It is true that certain forms stand fairly isolated and that the species common to Scandinavia and the East Baltic Provinces are easily counted, yet the assemblage of genera is largely the same. It may be mentioned that also the crinoids offer points of contact, as demonstrated by closely related forms of *Hoplocrinus* occurring in the Lower Chasmops limestone on the

¹ The writer takes advantage of the opportunity to correct a disturbing misprint on p. 174 in his memoir of 1945. In line 12 from above it is stated that the Norwegian *Haplosphaeronis* horizon forms the top of the *»Ordovician sequence*, which should of course read *»Middle Ordovician sequence*, according to the designations of the various portions of the Lower Paleozoic deposits adopted in that paper, Regnéll 1945, pp. 63—64. This also agrees with the view advocated by Stormer 1945, p. 396, that the Tretaspis shale should be regarded as the base of the Upper Ordovician of Scandinavia, since in the southern part of the Oslo Region, and probably also in Sweden, the typical black Tretaspis shale with *Tretaspis seticornis* forms a characteristic transgression zone following an interval of no sedimentation*}.
one hand, and in the Kukruse, on the other (Regnéll 1948b). We note further that a faunal communication existed between the Baltic area and the far East, via Central Asia, as indicated by the occurrence of genera common to the two regions (Hemicosmites, Stichocystis, Heliocrinites, Echinospaerites, Sphaeronites, ?Haplo-sphaeronis). On the basis of the Llandeilian cystoid fauna of Kweichou described by him, Sun (1936, p. 477) recognized a certain connection between Bohemia and China during Middle Ordovician time; and makes it probable that the fauna originated in the Indo-Pacific Ocean and then migrated westward to Bohemia, but never extended into the Baltic province [concluded at from the fact that Aristocystites is present in the East Asiatic and Bohemian faunas but absent from that of the East Baltic region]. This supposition is greatly strengthened by the fact that the Aristocystis fauna of S. China occurs earlier (Llandeilian) than that of Bohemia (Caradocian). The particulars of the account quoted may give rise to some discussion. First, the evidence of Hemicosmites, Stichocystis, and Heliocrinites must not be overlooked since they are characteristic of the Baltic cystoid fauna, but cannot be said to be characteristic of the Bohemian, the two first-mentioned genera not being represented at all. Secondly, as mentioned above (p. 22), the East Baltic and the Bohemian Basin may not have been separated altogether but seem to have communicated on some occasions, in Lower and Middle Ordovician time, presumably via Poland. Several East Baltic Llandeilian genera appearing in Caradocian and Ashgillian strata of western and south-western Europe may have migrated along this route. Sun may be right or not in assuming that the Aristocystites fauna originated in the Indo-Pacific Ocean. By bringing the East Baltic Basin, too, in connexion with the East Asiatic Sea, we must not take it for granted, however, that the fauna of the Baltic region is of Indo-Pacific origin. Both regions may have received immigrants from the Arctic Sea, from where faunal elements were brought to North America as well (cf. the map of Kobayashi 1936, p. 491; see also above, p. 24). Anyhow, the exchange of faunal elements between Europe and Central Asia is a significant feature of various periods of the Lower Paleozoic. Thus it was suggested e. g. by Kobayashi (1936, p. 490) for Middle Cambrian — Lower Ordovician faunas. The same was pointed out by Troedsson (1937, p. 14) for the Cambro-Ordovician faunas of Eastern Tien-shan, and is evident from the Middle Ordovician

1 According to Chauvel (1941, p. 64, etc.), all the Bohemian species of Aristocystites revised by him originate from d51, which may fall within the Upper Llandeilian.

2 Sun’s view was not corroborated by Chauvel (1941, p. 70), who pointed out that it does not agree with the fact that Aristocystites appears in the Armorican Llandeilian.
faunas of Karakoram described by Gortani (1934). Dealing with the Siluro-Devonian faunas of Eastern Tien-shan the present writer arrived at a similar conclusion (Regnéll 1941, p. 57).

Caradocian.

In Scandinavia, the Caradocian cystoid faunas are not very different from the Upper Llandeilian ones. A certain decrease is conceivable, however, less with regard to the quantity of individuals than with regard to the multitude of species. Most of the genera are the same, which is also true of several species. Yet a new element is brought in with the first representative of the Blastoidae.

All Caradocian Hydrophorida described hitherto from Sweden originate from the Macrourus beds of Dalarna (a cystoid fauna of Slandrom ls. age has not yet been studied). They are as follows: Hemicosmites extraneus Eichwald, Caryocystitites lagenalis Regnéll, Stichocystis geometrica (Angelin), Echinospaerites aurantium (Gyllenhaal), E. aurantium f., E. grandis Jaekel?, Glyptospaerites suecicus (Angelin), Sphaeronites? sp. (Regnéll 1945, p. 171), Haplosphaeronis oblonga (Angelin)?. »Megacystis ovalis» Angelin (cf. Regnéll 1945, p. 184) appears in the »Leptaena limestone», according to Lindström (1888, p. 23); we do not know, however, whether it was derived from the Ordovician or the Silurian portion of this complex.

The Upper Chasmops series (Macrourus beds) of Östergötland has yielded a unique specimen of Paracystis ostrogothicus Sjöberg. Quite recently, through the courtesy of Mr. Jaanusson of Uppsala, the present writer got the opportunity of examining an echinoderm fragment from Macrourus beds in the southern quarry at Amtjärn, Dalarna. This small fragment seems to be referable to Paracystis.

The only cystoids known so far from the Caradocian strata of Norway are Echinospaerites sp., Haplosphaeronis kiaeri Jaekel and H. kiaeri norvegicus Jaekel. For a discussion of their relations to the Swedish H. oblonga, see Regnéll 1945, pp. 173—174.

There is hardly any need to comment further upon Echinosphaerites aurantium, E. grandis, Haplosphaeronis oblonga, H. kiaeri (from the »Sphaeronid shale» of Hadeland), H. kiaeri norvegicus (from the superimposed »Sphaeronid limestone»), since all of them were treated above in discussing the Upper Llandeilian forms.

Hemicosmites extraneus is common to Sweden and the East Baltic Provinces. As stressed by the present writer (Regnéll 1945, pp. 101, 102), statements are not univocal concerning the stratigraphic distribution of this species in the East Baltic area. According to Jaekel (1899, p. 310) and Bassler & Moohey (1943, p. 165) it occurs in stage D1 (Jöhvi-Jewe). This stage has to be
correlated with a lower part of the Macourus beds, which seems to be the horizon of *H. extraneus* in Sweden as well. The species, which is the last representative of its genus in Scandinavia, is not known from any extra-Baltic area. In Estonia, *Hemicosmites* survived until Silurian time (*H. grandis* Jaekel, *F₂*, Porkuni-Borkholm). *H.? loczyi* Jaekel from Yunnan, based on some detached plates, was said to have been derived from an Upper Ordovician rock (Jaekel 1899, p. 315; Bather 1906, p. 29). Our information regarding this form is insufficient, however, *H.? loczyi* being in fact a nomen nudum. Some forms referred to *Hemicosmites* were described by Forbes (1848, pp. 510—511), and have been mentioned by several subsequent writers. Their systematic position is uncertain and requires a thorough revision, which is also true of the rest of the British cystoid material, except that treated by Bather (1913). According to Jaekel (1899, p. 314), *H.? squamosus* Forbes does not fit into the plan of organization of *Hemicosmites* and allied genera. As regards *H.? oblongus* (Pander) quoted by Forbes, cf. above, p. 16, foot-note 4. *H. rugatus* Forbes (syn. *H. pyriformis* Forbes) was referred to *Oocystites* by Dreyfuss (1939, p. 129).

Two specimens of *Stichocystis geometrica* (Angelin)¹ recently placed at the author’s disposal by Mr. Jaanusson come from the upper part of the Lower Macourus beds. The material available previously was not determined so exactly with regard to horizon. Apart from some specimens obtained from erratics in north Germany recorded by Jaekel (1899, p. 327), the only report on specimens possibly belonging to this species is that of Sun (1936, p. 483), from the Llandoelian of Kweichou in China (cf. above).

*Caryocystites lagenalis* Regnéll has been recorded from Dalarna only, but it is so characteristic of the Macourus beds (especially the lower ones) of that region that it should be regarded as an index fossil. The species seems to be endemic to Sweden.

*Glyptosphaerites suecicus* (Angelín) is not very well known, either with regard to morphology or to stratigraphic range. It occurs exclusively in Dalarna and is the last species of *Glyptosphaerites* in the Scandinavian—East Baltic region.

*Haplosphaeronis oblonga* (Angelín) is present at least in the lower and middle Macourus beds.

»*Megacytis ovalis* Angelín« is undefinable, since no material referable to it could be recognized (cf. Regnéll 1945, p. 184). Since its stratigraphic appearance is not known either, it was thought better not to record this form in the table showing the stratigraphic distribution of Scandinavian non-crinoid Pelmatozoa.

¹ In the author’s recent description of *Stichocystis geometrica* an error unfortunately crept in (Regnéll 1945, p. 109, line 12 from the top). In the line quoted, read hydropore for gonopore.
Finally, the coronate blastoid *Paracystis* has not been found outside Sweden and is extremely rare in this country, too, as mentioned just above. It seems to be fairly isolated, but its affinities are with the Stephanoblastidae (cf. Regnell 1945, pp. 189—190).

As we have seen, the general character of the Caradocian non-crinoid pelmatozoan fauna of Scandinavia is not very divergent from that of the Upper Llandeilian. Thus it follows that the echinoderm fauna is first of all comparable with that of the East Baltic Provinces, although it must be said to be definitely impoverished. A certain local development is also recognizable if we consider the predominance of *Caryocystites* and *Haplosphaeronis*, which play a very unimportant role in the East Baltic area.

The Scandinavian-Baltic Caradocian faunas now under discussion have little in common, however, with the contemporary echinoderm faunas of the rest of Europe and with those of Morocco. The Bohemian Basin and the Massif armorican of Brittany are characterized by an *Aristocystites* and *Craterina* fauna which is very much the same in the two districts (cf. Chauvel 1941, p. 252). Moreover, the latter fauna was essentially developed already in Upper Llandeilian time, being present in Portugal (Delgado 1908), Spain, and Morocco as well. According to Spencer (1938, p. 415), the Bala echinoderm faunas of Wales and Shropshire are related to Asiatic and Bohemian ones on the one hand and to Trenton faunas of Canada and Kentucky on the other. From Ireland two species of *Echinosphaerites* were mentioned by Jækel (1899, p. 337), viz. *E. granulatus* McCoy and *E. globosus anglicus* Jækel, the latter considered as closely related to *E. globosus* Jækel from Estonia. As to Wales, some species of Baltic aspect were listed by Bassler & Moodey (1943, p. 40). These are *Helio­crinites balticus* (Eichwald), *H. granatum* (Wahlenberg), *Echinosphaerites aurantium* (Gyllenhal), *Eucystis? litchi* (Forbes), and three species referred to *Hemicosmites* (as regards the so-called *Hemicosmites*, cf. above, p. 31).

The determination of *Helio­crinites balticus* may be correct. An impression of a part of the test in limestone shale from Bwlch-y-Gaseg, North Wales (the Törnquist collection, Paleontol. Inst., Lund), is the only specimen that the present writer has had an opportunity to examine. This, however, seems to be referable to the species mentioned. The forms of Forbes (1848) and subsequent authors denominated *Caryocystites granatum* and *C. davisii* McCoy probably also belong here (Jækel 1899, p. 330; Bather 1906, p. 17). As regards the British *Echinosphaerites aurantium*,

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1 It is possible that this is the specimen alluded to by Törnquist (1879, p. 71), who was inclined to refer it to *Echinosphaerites aurantium*. On the label written by him accompanying the specimen it is designated as »Echinosphaera baltica Eichw«, however.
the writer has had no opportunity to form a personal opinion. *Eucystis? litchi*, finally, is no typical *Eucystis*, but may be regarded — along with *Caryocystites pyriformis* and *C.? munitus* — as a species intermediate between that genus and *Sphaeronites* (Jaekel 1899, p. 406).

Though many points are still obscure concerning the British Caradocian echinoderm fauna, it does not seem unreasonable to assume that a communication existed between Great Britain and the Baltic region, principally on the evidence of *Heliocrinites balticus*. This species occurs in the Kukruse of the East Baltic Provinces, a stage which must be correlated with the Upper (although not the topmost) Llandeilian.\(^1\) It was observed by Törnquist (1879, p. 71) already that faunal elements common to the Scandinavian-Baltic region and Great Britain (where the easterly facies is concerned) appear earlier within the former area.\(^2\) Recognizing them as easterly migrants, he found this fact quite natural. The same problem was considered by Marr (1882, p. 325), who explained it by »the remoteness of Britain from land in Arenig and Lower-Bala times; for there are no shallow-water forms of Arenig age, and very few of Lower-Bala age, in the southern parts of Britain«. And he had just stated that »the migration of shallow-water forms seems to have taken place along the coast-lines, and to have proceeded much more slowly than that of the deep-water forms«.

**Ashgillian.**

In the Swedish Ordovician sequence, the Red Tretaspis shale and the Staurocephalus shale must be correlated with the Ashgillian, which is consequently true also of their equivalent in reef facies, the Lower Boda reef limestone of Dalarna. Whether the »Middle Tretaspis limestone« (Jaanusson & Martna 1948) should be included in the Ashgillian or the Caradocian is not settled as yet. From this horizon there is some undescribed cystoid material.

In Norway, the Ashgillian is represented by the Tretaspis limestone and Upper Tretaspis shale, the Isotelus beds, and the Uppermost Chasmosps zone (stages 4\(c\)\(f\)—5a).\(^3\)

\(^1\) _Fauna y Sans_ (1913, p. 97) mentioned »Echinospaerites cf. balticus d’Etchw.* from a Caradocian greywacke at Montcada, province of Barcelona. The present writer cannot judge to what extent this statement can be trusted, but it cannot be accepted unreservedly, since the same species (with a mark of interrogation, that is true) was listed (op. cit., p. 112) from Tremadocian strata.

\(^2\) Since the Ashgillian series was not yet recognized (established by Marr, in 1905) Törnquist (1879, p. 70) referred the Tretaspis shales to the Caradocian, which can be accepted only in part to-day. It should be noted that in the paper quoted Törnquist (l. c.) presented creditable ideas of the alternating East Baltic and British invasions in the Scandinavian fauna during the Lower Paleozoic.

\(^3\) The upper part of 5a (bearing i. a. *Dalmanitina mucronata*) probably belongs to the Silurian (cf. Stormer 1934, pp. 24, 30). As regards the lower boundary of the Ashgillian in Norway, cf. Stormer 1945, p. 397.
The impoverishment of the Scandinavian non-crinoid pelmatozoan fauna perceivable in the Caradocian proceeded, and is demonstrated clearly in the Ashgillian. The present writer is not inclined to ascribe this fact in the first hand to conditions of lithologic facies in this case either, but to a general tendency affecting the non-crinoid pelmatozoan stock in Upper Ordovician time within several areas. The Saunja and Vormsi stages, forming the top of the Ordovician sequence in Estonia (cf. Jaanusson 1944), have yielded the genus *Glaphyrocystis* only (two species), and the non-crinoid pelmatozoan fauna of the Bohemian Basin — housing previously a multiform assemblage — is remarkably poor. In North American Cincinnatian faunas Hydrophoridea are entirely absent, the non-crinoid pelmatozoans being represented by some genera of Edrioasteroidea and Cyclozystoidea (Bassler & Moodey 1943, pp. 32—33). Fairly rich non-crinoid pelmatozoan faunas are found, on the other hand, in Languedoc, in the Girvan district, and in Algiers.

The cystoids of the Ashgillian of the Montagne Noir were studied i. a. by Koenen (1886) and Dreyfuss (1939). This fauna contains genera such as *Juglandocrinus*, *Corylocrinus*, and *Oocystis*. Certain elements of the Languedoc fauna are known from other regions as well, namely Portugal, the Pyrenees, Sardinia, the Carnic Alps, and India (Dreyfuss 1939, p. 131, with further references; to these we have to add the Urals, from where *Corylocrinus* was recorded by Yakovlev, 1940, and Algiers). This suggests that a communication between these regions and Languedoc existed in Ashgillian time. Dreyfuss (1943, p. 132) found indications of a connexion with Great Britain as well.

According to Spencer (1938), the Starfish Bed fauna of Girvan is related to the Richmondiann of the Ohio Basin together with a new fauna, where the starfish are concerned, being quite different from the Welsh-Bohemian faunas. »Cystid fauna has same two constituents, i. e. American and a new fauna which is really an old fauna as developed in Languedoc. The number of peculiar genera common to both is very remarkable. An explanation might be an Eastern reservoir sending migrants by an Arctic route to Girvan. Starfish are not known from the contemporary Welsh, Irish or Baltic beds. Cystids in these three areas are as a whole different

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1 The author hopes to get an opportunity of discussing in a forthcoming paper the interrelations of fluctuations in the intensity of non-crinoid pelmatozoan faunas and major events in the earth's history.

2 Mme Termier has been so kind as to place at the writer's disposal a manuscript entitled »Découverte de l'ordovicien en Algérie Atlasienn« by A. Lambert, H. Termier and G. Termier. In this paper the following Hydrophoridea are announced: *Heliocrinites rouvillei* (Koenen), *Juglandocrinus* cf. *crassus* Koenen, *Echinopsphaerites* sp., and *Caryocystites* sp. They were associated with *Nicolella actoniae* (Sowerby).
from those of Girvan and have a common element, apparently Baltic in origin» (SPENCER, l. c.).

It was mentioned above (p. 28) that *Haplosphaeronis* persisted during the Upper Ordovician, *H. oblonga* appearing in the Lower Boda reef limestone. From Dalarna there are another two forms, *Caryocrinites septentrionalis* REGNÉLL and *C.?* sp. (REGNÉLL 1945, p. 106), both of which may come from strata belonging to the horizon of the Red Tretaspis shale. *Eucystis quadrangularis* REGNELL is known to appear in the Lower Boda reef limestone (REGNÉLL 1945, p. 183).

With our present knowledge, we must imagine that *Caryocrinites* is a migrant from East Asia, for the oldest known member of this genus is *C. aurora* (BATHER) from the Llandeilian Naung-kangyi beds of Burma (BATHER 1906, p. 29). *C.?* sp. (GORTANI 1934, p. 25) from Karakoram may be approximately contemporaneous with the species mentioned. A form designated as »*Caryocrinus ornatus* SAY» was reported by DELGADO (1908, pp. 62, 83) from the sections at Bucaco and in the Tage Basin (from here a »*Caryocrinus?* sp.» as well). The horizon was said to be Upper Ordovician, but judging from the associated echinoderm fauna it belongs to the Upper Llandeilian or Caradocian. In any case the Niagaran *C. ornatus* SAY of North America cannot be taken into account.¹ All other species of *Caryocrinites* known so far are Silurian. »*Caryocrinus* sp.» (KLER 1897, pp. 17, 75; cf. also REGNELL 1945, p. 105) from stage 5b in the Oslo region shows that the genus survived for some time in Scandinavia. According to a statement by F. SCHMIDT (1858, p. 221; 223 of sep. print), *Caryocrinites ornatus* appears in stage 7² of Estonia. This statement seems to have been overlooked altogether by subsequent writers, and it is impossible to judge of its value. SCHMIDT did not doubt the correctness of the generic determination, however, an incomplete theca being available to him »der wenigstens die Gattung sicher erkennen lässt». Apart from the forms just mentioned, all *Caryocrinites* are from the Niagaran of North America, being represented by a considerable number of species.

¹ BASSLER & MOOKEY (1943, p. 138) list a further Ordovician species, *C. buchianus* (HAECKEL, sub *Enneacystis*) from »Russia (vicinity St. Petersburg)«. However, the erection of this species (as well as of the genus *Enneacystis*) was a complete mistake, as pointed out by JAECKEL (1897, p. 392): »Die folgende neue Gattung *Enneacystis* stellt ihr Autor auf Formen auf, die angeblich von v. BUCH aus dem Untersilur von Russland beschrieben sein sollen, in Wahrheit aber gar nicht existieren, denn die citierten Exemplare, die v. BUCH beschrieb, gehören sämtlich dem typischen *Caryocrinus ornatus* SAY aus dem Obersilur von Lockport im Staaete New York an.« *C. buchianus*, therefore, is a synonym of *C. ornatus*.

² This corresponds (F. SCHMIDT 1882, p. 527) to stage I, or the Lower Oesel group, of Wenlockian age.
zone of *Staurocephalus clavirrons* at Tommarp in Scania. The present writer (REGNÉLL 1945, p. 137) referred the unique specimen to a new species of *Heliocrinites* (not named). A few more come from the Scanian Staurocephalus shale: »Echinospaerites sp.« (TROEDSSON 1918, p. 23), which is no *Echinospaerites* (REGNÉLL 1945, p. 153), and *Eucystis?* sp. (REGNÉLL 1945, p. 184). It is not necessary here to comment further on these forms.

The only species reported from the Ashgillian (5a)\(^1\) of Norway is *Heliocrinites cf. balticus* EICHWALD (KLØR 1901, p. 11, sub *Echinospaerites*), which was said to occur very commonly at Djupalstenen in Asker. In view of the divergent stratigraphic range of *Heliocrinites balticus* in the East Baltic area (cf. above, p. 33), it is better not to say anything definite until the actual fossil material has been examined.

Summing up, the Ashgillian cystoid fauna of Scandinavia does not show any close relationship to the contemporary fauna of the East Baltic Provinces, nor to that of any other region. But it may be suggested, in view of the stratigraphic range and regional distribution of *Caryocrinites* in Eurasia, that the richly differentiated Middle Silurian *Caryocrinites* fauna of North America developed from immigrants from the sea covering part of Scandinavia in Upper Ordovician time. This migration may have taken place via the Arctic route, but it is more likely that it went across the Atlantic, for there are reasons to believe that the barrier separating the South Scandinavian-Baltic region from the American Arctic one did not exist any longer (HOLTEDAHL 1920, p. 7; 1924, p. 122; TROEDSSON 1928, p. 186). A recent support of this view is the observation by STØRMER (1945, p. 398) that the Tretaposis faunas of Hadeland contain some North American trilobite genera. One form is identical even as to species.

**Silurian.**

The transition from the Ordovician to the Silurian system caused no great changes in the character of the non-crinoid pelmatozoan fauna of Scandinavia. Some elements are new but others are descendants from Ordovician ancestors within the South Scandinavian-Baltic Basin (cf., however, the reservation below).

As regards Sweden, a certain rise of the fauna just under consideration is noticeable in the Lower Silurian, with regard to both number of species and individuals. In Norway, however, this part of the sequence has yielded hitherto one species only, whereas no species have been recorded from younger strata. On account of the predominance of graptolite shales above the Dalmanitina series

\(^{1}\) N.B. above, p. 33, foot-note 3.
within most Silurian districts in Sweden, younger non-crinoid pelmatozoan faunas are known solely from Gotland. Contrary to expectation no material of non-crinoid pelmatozoans has been obtained from the so-called Pentamerus limestone of Jämtland (mainly of Lower Llandoveryian age); nor is there any material of non-crinoid pelmatozoans from the Öved-Ramsåsa series of Scania [Upper Ludlow—Downtonian?]).

Llandoveryian.

The only hydrophorid reported from the Silurian of Norway is Caryocrinites sp. (Klær 1897, pp. 17, 75) which was found in the basal Silurian stage 5b (N.B. above, p. 33, foot-note 3). This species has already been referred to above (p. 35).

The lowest portion of the Swedish Silurian sequence is made up of the Dalmanitina series. In Dalarna, from where the main part of the non-crinoid pelmatozoan material comes, the Dalmanitina shales are replaced partially by the Upper Boda reef limestone. The stratigraphic position of the reef limestone complex, formerly known as the «Leptaena limestone», was not fixed in its main features until fairly recently. The Leptaena limestone turned out to have been formed during various periods of reef-building, alternating with periods of «normal» sedimentation. Besides the Silurian part, as we have seen, it comprises two Ordovician parts: an Upper Ordovician part, the Lower Boda reef limestone, equivalent mainly to the Staurocephalus and Red Tretaspis shales, and a Middle Ordovician part, the Kullsberg reef limestone, equivalent to the principal part of the stratified Macrourous beds. From the old museum labels, bearing the designation «Leptaena limestone», it is often impossible to form a definite opinion on the age of the fossils concerned, especially in those cases where no locality is given. It must be admitted, therefore, that the forms from Dalarna referred to below may occur in the Upper Ordovician portion of the Boda reef limestone as well, or perhaps exclusively within that portion. If that be so, there would naturally be a fairly pronounced faunistical break between the Ordovician and the Silurian systems where the non-crinoid pelmatozoan fauna is concerned.

The following forms have been found in Dalarna: Heliocrinites stellatus Regnéll, H. variabilis Regnéll, Eucystis raripunctata Angelin, E. angelini Regnéll, E. acuminata Regnéll, E. quadrangularis Regnéll (cf. p. 35 above), E. sp. (Regnéll 1945, p. 183), Sphaeronites? sp. (Regnéll 1945, p. 184), «Sphaeronits? dalecarlica» Angelin, Tormoblastus bodae Jaekel, Cyathotheca suecica Jaekel, Cyathotheca? sp.1

1 This species from Boda (Törnquist collection, Paleontological Institution of Lund University) has not yet been described.
From the Dalmanitina series of Västergötland Holocystites? sp. (Regnéll 1945, p. 183, = »Megacystis alternata Hall var.«, Angelin 1878, p. 30), and an undeterminable »cystoid« (Troedsson 1921, p. 11; cf. Regnéll 1945, p. 184) have been reported.

Finally, in a boulder of so-called West Baltic Leptaena limestone from Hulterstad in Öland, there is an imperfect stem-fragment of Dendrocystites sp. (Regnéll 1945, p. 194).

Of the non-crinoid pelmatozoans just mentioned, the two species of Helioerinites are members of a genus well represented especially in the Middle Ordovician. H. stellatus and H. variabilis are somewhat different in type as compared with the Ordovician species, and are the youngest representatives of Helioerinites known. The general distribution in time and space of the genus was reviewed above (p. 26).

As pointed out by Thorslund (1936, p. 26), the hydrophorid Eucystis is as characteristic of the Boda limestone as is Haplosphaeronis of the Kullsberg limestone (we leave out of consideration the fact that Haplosphaeronis has been found also in the Lower Boda limestone). There are several species of Eucystis, and some of them occur abundantly. Eucystis may have an easterly origin, for the oldest species possibly referable to this genus is a form from Yunnan described by Reed (1917, p. 11) as Eucystis cf. raripunctata (Middle Llandeilian). The specific determination is of course incorrect. Another doubtful form, coming next in age, is E.Æ litchi (Forbes, sub Caryocystites; cf. above, p. 33), from the Caradocian of Great Britain. E.Æ sp. from the Staurocephalus shale has been referred to above (p. 36). In Dalarna the genus reached a rich development, but it has not been reported from the East Baltic area. From Scandinavia Eucystis spread over a good deal of central and western Europe, so that it is known (partially sub Proteocystites, Proteocystis, Carpocystites, and Carpocystis) from Lower Devonian deposits of Germany (Jaekel 1899, p. 407), Bohemia (Jaekel l.c.), and France (Ferronière 1922, p. 72). It occurs in the Devonian of Morocco as well (G. Termier, unpublished). Bulbocystis Ružička (1939, p. 292) from the Middle Devonian of Bohemia may be regarded as a descendant from Eucystis.

If the generic determination of Sphaeronites? sp. (Regnéll 1945, p. 184) can be trusted, it demonstrates that the stratigraphic range of Sphaeronites reaches considerably higher than the Middle Ordovician.

A very great number of species (about 50) of Holocystites have been described (mostly by S. A. Miller) from the Niagara of North America. H. alternata (Hall), which Angelin (1878, p. 30) was inclined to regard as closely related to the Swedish species, occurs in the Racine and Cedarville dolomites (Bassler & Moodie 1943, p. 167) of the Upper Niagara, corresponding to a middle or
upper part of the Wenlockian (Swartz et al. 1942). If the considerably older Swedish species is congeneric with the North American representatives of Holocystites, we must assume that these originate from migrants from north-western Europe.

The first blastoid entered the Swedish fauna in Caradocian time. In the Lower Silurian appeared the second representative of this subclass, which is one of the rarest of all fossil groups in the Swedish Paleozoic. Tormoblastus bodae Jäkel, as well as the Caradocian Paracystis, may be derived from ancestral forms in the Bohemian Basin (the Middle and Upper Ordovician genus Mespilo-cystites Barrande). Here the Stephanoblastidae survived, developing into the Ludlovian Stephanoblastus Jäkel. At an earlier stage they had reached North America, as demonstrated by the multiform Niagaran Stephanocrinus Conrad.

Also the Carpoidea and Edrioasteroidea are in Scandinavia confined chiefly to the Silurian part of the Paleozoic sequence. The only exception is the Middle Cambrian Stromato-cystites.

Dendrocystites — one of the two carpoids known from Sweden — was distributed almost all over the world during the Ordovician (see Regnéll 1945, pp. 194, 195—196). The oldest species recorded is D. vidali Thoral from the Upper Skiddavian of Hérault. There are also some stem fragments from the Skiddavian of Korea which may belong here (Kobayashi 1934, p. 525). Since the Swedish species seems to be fairly closely related to the Caradocian D. sedgwickii Barrande, it is possible that the genus invaded Sweden from the Bohemian Basin. But it may of course also have come either from the East Baltic Provinces, or from Scotland. The present species is one of the last members of Dendrocystites, being succeeded only by the Lower Devonian D. globulus Dehm of Germany (Dehm 1934, p. 20).

In the case of Cyathothea, its East Baltic origin cannot be doubted, the only congeneric form being C. corallum (Jäkel) from the Vaginatum limestone (Upper Skiddavian) of the Leningrad district.

We shall now have a look at the younger non-crinoid pelmatozoans of the Silurian of Sweden, all of them found in Gotland. A few of these may fall within the Upper Llandoverian, viz. those probably derived from the Upper Visby marl.1 The species concerned are Pyrgocystis cylindrica (Aurivillus) and P. procera (Aurivillus). The latter species occurs in younger strata as well where it is accompanied by a few more species belonging to the same genus. Pyrgocystis makes its appearance in the Skiddavian of the Leningrad Province (Hecker 1939).2 From the East Baltic

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1 According to Hedé (1942, p. 22), the Upper Visby marl is probably Upper Llandoverian in age.

2 A pyrgocystid, a very primitive form, as it seems (translated by the
area *Pyrgocystis* spread to North America (*P. sardesoni* BATHER; Black River, Middle Llandeilian; further *P. batheri* RUEDEMANN; Cayugan, Bertie waterlime, Aymestry), Scotland (*P. grayac BATHER*; Starfish bed, Ashgillian), England (*P. ansticei* BATHER; Wenlockian), Sweden, and Germany (*P. octogona* RICHTER; Lower Devonian).

To summarize what has been said above concerning the Llandoveryan non-crinoid pelmatozoan fauna of Sweden, we note that the Hydrophoridea and Edrioasteroidea have their affinities with East Baltic, or, at any rate, easterly forms, just as during the Ordovician. Only *Holocystites*? and, to a certain extent, *Eucystis* are fairly isolated. A remarkable feature is that the Swedish cystoid faunas are much more developed than the contemporary East Baltic ones. The Blastoidae and Carpoidea — two groups really foreign to the Scandinavian Paleozoic fauna — quite likely invaded Sweden from the Bohemian Basin.

**Wenlockian.**

The only hydrophorid hitherto recorded from Swedish Wenlockian strata is the diplopod *Gomphocystites gotlandicus* (ANGE-LIN). This species appears in the Högklint group (Lower Wenlockian) and the Slite group (Wenlockian, not younger than the zone of *Cyrtograptus ellesi*, both statements according to HEDE 1942, p. 22). Of the peculiar Cyclocystoidea a few species have probably been obtained from the Högklint limestone: *Cyclocystoides lindströmi* REGNELL, *C. insularis* REGNELL, and a third species not yet described. Finally, the Edrioasteroidea are represented by three species, viz. *Pyrgocystis procera* (AURIVILLIUS) — a survivor from the Llandoveryian —, *P. sulcata* (AURIVILLIUS), and *P. varia* (AURIVILLIUS). These are from the Mulde marl, which, according to HEDE (1942, p. 22) probably corresponds in age to the Wenlockian zone of *Cyrtograptus lundgreni* or, alternatively, forms transitional beds to the Ludlovian.

Apart from the species of *Pyrgocystis*, which are descendants from ancestors of East Baltic origin (cf. yet below), this Wenlockian fauna offers an entirely new aspect as compared with earlier non-crinoid pelmatozoan faunas. For both *Gomphocystites* and *Cyclocystoides* must be regarded as North American elements. In earlier instances where we have found genera, or even species, to be common to Europe and North America, we have invariably had reason to believe that they appeared earlier in Europe than they did in America. In the case just under discussion, on the other hand, the oldest North American representatives of the

Present writer) was mentioned from Norway by JAEKEL (1927 b, p. 4), who did not, however, say anything about its stratigraphic horizon.
genera in question are prior to the European ones. As regards *Gomphocystites*, which is confined to North America and Gotland, this fact is not very prominent, however. However, this fact is not very prominent, however, yet the Osgood formation of Indiana, from which *G. indianensis* S. A. Miller originates, is partially older than the basal Wenlockian (Swartz et al. 1942, correlation table). *G. tenax* Hall, from the Lockport-Shelby dolomite of New York and the Louisville limestone of Kentucky (Bassler & Moodey 1943, p. 161), seems to be fairly contemporaneous with the Gotland species. Three other Niagaran forms are younger.

We cannot ascertain what migration route *Gomphocystites* used to reach the waters covering Gotland of to-day. Perhaps we can form an opinion of this by considering the regional distribution of *Cyclocystoides*: Middle Ordovician—Lower Silurian forms in North America, Middle—Upper Ordovician forms, and a Lower* 

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1. It should be emphasized again that a common centre of evolution and dispersal could also be taken into consideration.

2. From the Middle Devonian of California the doubtful *Gomphocystites (?) californicus* Stauffer has been recorded (cf. Bassler & Moodey 1943, p. 161).
Silurian form in England, Upper Ordovician forms in Scotland, Middle Silurian forms in Sweden, and, finally, a Lower Devonian form in Belgium (Begg 1939, p. 21 seq.; Bassler & Moodey 1943, pp. 147—148; Regnéll 1945, p. 215 seq.). It seems justifiable to infer from these facts that the genus came to Gotland across the Atlantic. The systematic position of *Cyclocystoides* is disputable.

Also *Pyrgocystis*, in spite of its East Baltic origin, may fit into this pattern. As mentioned above, the genus spread over great areas, so as to be present in North America in Black River time. From here it may have been brought back to the Baltic Basin in Silurian time, via Scotland and England.

**Ludlovian.**

The gradual decrease of the non-crinoid pelmatozoan stock discernible in the Silurian of Gotland led to a complete extinction after the end of the Lower Ludlovian.

In Lower Ludlovian time the Hydrophoridea Rhombifera, which are absent in the lower strata of Gotland, became represented by the genus *Lovénicystis* Regnéll, including the single species *L. angelini* (Jaeckel). This species probably occurs in the Eke group (cf. Regnéll 1945, p. 92, foot-note 20).

The explanation of this sudden appearance of a member of the Callocystitidae in the Upper Silurian of Gotland is undoubtably that it is a migrant from the west, for the Apiocystinae are decidedly North American in origin. This subfamily commenced in the Upper Ordovician by *Lepadocystis*, followed in Lower Silurian time by *Brockocystis*. In Niagaran time, the Apiocystinae had split up into *Apiocystites*, *Tetracystis*, and *Hallicystis*, the first mentioned developing into *Lepocrinites* (Upper Silurian and Lower Devonian) and *Lipsanocystis* (Middle Devonian). *Jaekelocystis* (Lower Devonian) seems to have developed from *Tetracystis*. All the genera mentioned are North American. But in the course of time they extended their area of distribution. Thus *Apiocystites* and *Lepocrinites* are found in the Wenlockian of England.

From this it might easily be assumed that the British Wenlockian species had spread further eastwards, changing into the Lower Ludlovian *Lovénicystis* of Gotland. The morphological analysis shows, however, that *Lovénicystis* lies in the straight line of the Lower Silurian *Brockocystis* (cf. the scheme published by Regnéll 1945, p. 91). Luhu (1940, pp. 98—99) described an Upper Silurian callocystid from Oesel, which he called *Lepocrinites kailuka*. His report does not contain sufficient details to determine the exact taxonomic position of the species. It would not be surprising, however, if it turned out to be referable to *Lovénicystis*, demonstrating a migration of that genus eastwards. *Lepocrinites*
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Fig. 2. Diagram showing the regional distribution and approximate stratigraphic range of the known species of *Pisocrinus* (*P. glabellus* (Rowley), N. America (Bainbridge Is.: Wenlockian), and the doubtful *P.? yassensis* Etheridge and *P.? yassensis lobatus* Etheridge, Yass district, New South Wales (age of the Yass Is.: Upper Wenlockian—Lower Ludlovian, according to Hill 1943, p. 64), have not been recorded in the diagram). 1, *pyriiformis* (Ringueberg); 2, *bacula* Miller & Gurley; 3, *benedicti* S. A. Miller; 4, *campana* S. A. Miller; 5, *gemmiformis* S. A. Miller; 6, *globosus* (Ringueberg); 7, *gorbyi* S. A. Miller; 8, *granulosus* Rowley; 9, *quinquelobus* Bather; 10, *sphaericus* Rowley; 11, *tennesseensis* (Roemer); 12, *pilula* de Koninck; 13, sp. Bather 1893; 14, *pocillum* Angelin; 15, *ollula* Angelin.

*kailuka* was found in the Kaugatuma stage of the Upper Oesel group. According to Luha, this stage corresponds approximately to the Gotland strata bearing *Lovénicystis*.

It is hardly necessary to add anything to the remarks on *Lovénicystis*, since this genus is the only representative known of Ludlovian Hydrophoridea — and non-crinoid Pelmatozoa on the whole — in Sweden. It may only be pointed out once more that the Upper and Middle Silurian non-crinoid pelmatozoan faunas differ fundamentally from the Lower Silurian and Ordovician ones: Westerly elements have almost entirely replaced those of easterly origin. Taking the South Scandinavian—East Baltic province as a whole, the change in character may also be expressed thus (somewhat generalized, that is true): The province changed from an emigration area to an immigration one, as far as the group of animals now considered is concerned. Parallel to this process there occurred a gradual decrease in the non-crinoid Pelmatozoa, leading to their total extinction in these waters in Ludlovian time. Their role was finished; it was taken over definitely by the Crinoidea.

Let us in this connexion make a digression. It is quite instructive to consider the Crinoidea as well with regard to migration
directions, since they seem to conform very well with the ideas expressed above. The only crinoid group of the Ordovician of Sweden known tolerably well, the Hybocrinida, is decidedly East Baltic in origin (Regnell 1948 b; cf. also p. 28 above), whereas the Silurian Gotland crinoids may have immigrated mainly from the west. Time is not yet ripe for a general ventilation of this question — nor is this paper the forum for it — but the statement is supported by real facts in the few instances investigated. Some arbitrarily chosen examples will prove this, here plotted in diagrams for the sake of perspicuity. The diagrams are based mainly on records in Bassler & Moodey (1943), completed by data contained in Bouška 1942. The correlation between the North American and British sequences is in accordance with Swartz et al. (1942). Similar diagrams were constructed for Gissocrinus and Crotalocerinites (distribution in Bohemia according to Bouška 1943, 1946). They point in the same direction as those of Pisocrinus and Pycnosaccus reproduced here.

Our thesis is corroborated by an example from the Asteroidea as well, viz. Palasterina antiqua (Hisinger), which occurs in the upper parts of the Burgsvik sandstone in Gotland (cf. Munthe 1921, p. 40), of Upper Ludlovian age. The species, which, according to Spencer (1922, p. 220), passes directly into the Devonian \textit{P. follmanni} Stürtz, of Germany, is namely found in England and Scotland in Wenlockian and Lower Ludlovian strata (Spencer 1922, pp. 228—229).
Silurian Undefined.

Under this heading a few words may be said about *Placocystites* sp. from Gotland, since it is one of the two carpoids recorded from Sweden. The author has not examined the specimen himself, and the stratigraphic position is not clear from the statements in the literature (cf. Regnéll 1945, pp. 196—197). Yet, it contributes a little to the characterization of the Silurian non-crinoid pelmatozoan fauna in Scandinavia and its migrations. The Gotland species is, as a matter of fact, closely related to *Placocystites forbesianus* de Koninck from the Wenlockian of England. Recently, Chauvel (1941, p. 215) advocated that *Anomalocystites bohemicus* Barrande be referred to *Placocystites*. The species mentioned is from section d, (Ashgillian) of Bohemia and is thus the oldest representative of *Placocystites*. The migration history of *Placocystites*, therefore, is much the same as that of the Llandoverian *Dendrocystites*. In both cases, this foreign element was brought into the Swedish fauna by an episodic migration from the Bohemian Basin, conceivably via Great Britain.

Concluding Remarks.

The author is well aware of the impropriety in drawing conclusions concerning migration routes and paleogeographical conditions on the basis of one group of animals only. But he hopes that this review of the succession of the significant non-crinoid pelmatozoans within a restricted area and the discussion on their relations to contemporary assemblages will contribute to some extent to the understanding of the faunas contained in the Old Paleozoic sequence of Scandinavia.

In conclusion, the writer wishes to point out a few facts which have bearing on discussions like that presented on the preceding pages.

First, we have to remember that all results derived from a study of fossil faunas are liable to involve errors and mistakes due to the incompleteness of the geological record.

Secondly, we must realize that identical environmental conditions may produce similar morphological types independently in different areas. If such a phenomenon as that indicated here is not merely hypothetical, the very principle of drawing paleogeographical conclusions on the basis of identical (morphologically but not phylogenetically) forms appearing in different regions would be disturbed seriously. This matter was considered by Simpson (1947, p. 622, footnote 1), who was of opinion that it must be «highly exceptional and can be ignored in an over-all
Fig. 4. Graph of the stratigraphic distribution of the non-crinoid Pelmatozoa in the Paleozoic sequence of Sweden, with reference to the number of species.

view». The present writer cannot see any reason to object to this opinion.

Thirdly, geography of the past is conceived on the modern base of the continental areas. This, however, «is a greatly forshortened one in all the places where the roots of the ancient mountains and the peaks of the modern ones occur, and consequently the geo-
The stratigraphic distribution of the non-crinoid Pelmatozoa so far known in the Paleozoic sequence of Sweden has been summarized in fig. 4. The graphs would probably have had a somewhat different shape, had it been possible to represent the length of time required for the formation of the several stratigraphic divisions. Unfortunately, however, our present knowledge does not admit of the calculation of this factor.

The stratigraphic range of the individual species is in most cases restricted to one division only. So a graph showing the number of new species in each division is tolerably in conformance with the graph representing the total number of species.

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Addendum to the list of Literature: The writer wishes to call attention to certain papers which have some bearing on the subject dealt with above, but which had either escaped his notice when preparing the manuscript or had not appeared until the present paper was already in the press.

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