

A NEW CYCLOCYSTOID FROM THE LOWER ORDOVICIAN OF ÖLAND, SWEDEN

by VIVIANNE BERG-MADSEN

ABSTRACT. *Monocycloides oelandicus* gen. et sp. nov. is described from upper Arenig age beds on Öland, Sweden (Volkhov Stage, Langevoja Substage). The genus is monotypic and is the earliest known cyclocystoid echinoderm. Palaeogeographical origins of the cyclocystoids remain uncertain, but *Monocycloides* is regarded as a primitive sister group of the North American Ordovician *Cyclocystoides*.

FORTY years have elapsed since the first Swedish cyclocystoids were described from the Silurian of Gotland (Regnéll 1945). As the oldest cyclocystoids then known were from the Kirkfieldian (Middle Ordovician) of North America and the Ashgill (Upper Ordovician) of England and Scotland, the migration route seemed evident. The cyclocystoids apparently reached Sweden during the Silurian and Belgium-Germany in the Lower and Middle Devonian (Regnéll 1948; Sieverts-Doreck 1951).

Smith and Paul recently (1982) revised the class Cyclocystoidea thoroughly, now to include eight genera and twenty-five species. The early Middle Cambrian species from Australia (*'Cyclocystoides' primotica* Henderson and Shergold, 1971) was removed from the class, and the range in age thus re-established to Middle Ordovician-Middle Devonian. The stratigraphical and geographical distribution was discussed and the cyclocystoids regarded as probably having evolved in North America during the Lower Ordovician. This did not alter the assumed migration pattern.

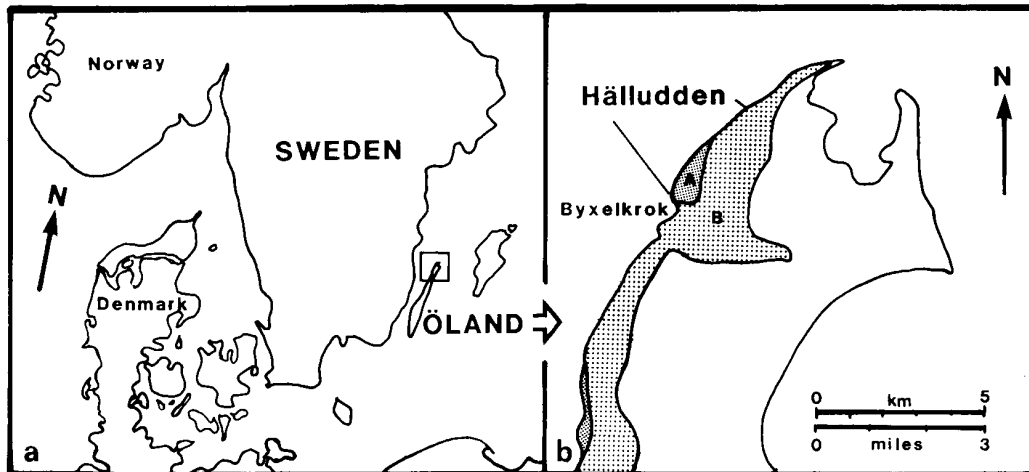
Now the presence of fragments of a new cyclocystoid from the high Lower Ordovician of Sweden extends the range considerably. The fragments represent a new genus with important features distinct from all known genera but most closely related to *Cyclocystoides*. Modern palaeogeographical research questions an early Ordovician migration from Baltoscandia to North America and the new genus *Monocycloides* is regarded as a primitive group of cyclocystoids which originated from an ancestor in common with *Cyclocystoides*. There is no evidence of a close genetic relationship with the genera from the Silurian of Gotland and thus the later migration theory still seems valid.

GEOLOGICAL SETTING

Öland is situated in the Baltic Sea, south-east of mainland Sweden (text-fig. 1a). Hälludden is an approximately 2 km long cliff section in the north of the island (text-fig. 1b). The name is generally used for the whole 5 km long beach section north of Byxelkrok. The Lower Ordovician strata here are about 20 m in thickness. The Hälludden section comprises the upper 'Limbata', Langevoja, Hunderum, and Valaste Substages (text-fig. 2) with a total thickness of 6.5 m (Grahn 1982; Jaanusson and Mutvei 1982).

The material described here was obtained from a level 10–20 cm below the oolitic bed whose base forms the boundary between the Langevojan and Hunderumian Substages. The boundary is accessible only at low-water level. For convenience the level is referred to as the E-level because of its content of echinoderm fragments.

Lithology, methods, and material. Lithologically the Hälludden sequence is identical to the similar interval in the Böda Hamn core where the fauna and microlithology were described by Bohlin and Jaanusson (*in* Bohlin 1955). Böda Hamn lies just outside the margin of the map, south-east of Hälludden (text-fig. 1b).



TEXT-FIG. 1. *a*, map showing the geographical location of Öland in southern Baltoscandia. *b*, the northernmost part of Öland and the bedrock geology at Hälludden. Limestones of (A) Latorp and Volkhov Stages, (B) Kunda Stage. The remaining part (white) is Middle Ordovician limestones. Modified from Jaanusson and Mutvei (1982).

The Langevoja limestone is a grey, predominantly sparitic calcarenite interbedded with marl layers and with a moderate to high glauconite content. The single beds are 2–5 cm thick. A regression starting in Latorp times (text-fig. 2) reached its maximum on Öland during the early Valasteian. The water depth during late Langevojan time is estimated to have been no more than 30 m, shallowing during the Hunderumian (Grahn 1982).

A series of limestone samples (45) covering the complete section, each between 50 and 100 g, was dissolved in 10 % acetic acid. The sampling levels correspond to those of Grahn (1982) who kindly provided most of the material.

In order to retain as much calcite as possible in partly glauconitized echinoderm fragments, the dissolution was interrupted twice a week, the residue removed, and cleaned. Once dried the phosphatized fossils become very fragile, and therefore the decanted sediment was used directly for manual extraction of fossils without sieving. Mechanical sieving was carried out during the first investigation of the Hälludden fauna (H. Mutvei, Swedish Museum of Natural History, Stockholm, pers. comm. 1983). This may explain why hardly any microfossils were obtained.

Microfossils do not occur in all samples. Large numbers are found in the samples just below and above the 'Limbata'–Langevoja and Langevoja–Hunderum boundaries. The Hunderum–Valaste boundary is practically unfossiliferous, chitinozoans and macrofossils excepted. In many cases microfossils are found at levels where macrofossils are absent.

THE FAUNA IN GENERAL

The Hälludden cliff section was sampled for fossils both qualitatively and quantitatively in 1948–1950 by H. Mutvei. Some of the results have been published by Jaanusson (1957), Skevington (1963, 1965*a, b*), and Grahn (1980, 1982) who also gave a short review of additionally described or unpublished fauna in general.

The macrofossils are mainly benthic and gradually become more diverse towards the end of Langevojan time, with a maximum diversity reached during the late Hunderumian. Both soft-bottom and hard-bottom forms occur in the shelly fauna. Predominantly fossils from the Kunda Stage have been described (text-fig. 2).

	Stages	Substages	Formational units on Öland	Graptolite Zones
LLANVIRN	KUNDA	Aluoja	GIGAS	<i>Didymograptus "bifidus"</i>
			OBTUSICAUDA	
		Valaste	RANICEPS	
		Hunderum	EXPANSUS	
ARENIG	VOLKHOV	Langevoja	LEPIDURUS ★	<i>Didymograptus hirundo</i>
		"Limbata"	LIMBATA	<i>Didymograptus extensus</i>
		Billingen	BILLINGEN	
LATORP		Hunneberg	HUNNEBERG	<i>(Tetragraptus approximatus)</i>

TEXT-FIG. 2. Diagram showing the stages and substages in Arenig and Lower Llanvirn of Sweden correlated with the British graptolite zones. The star indicates the position of the E-level. Modified from Grahn (1980, 1982).

Apart from chitinozoans (Grahn 1980, 1982) no fossils have been obtained previously from the E-level (H. Mutvei, pers. comm. 1985). Predominant among the fossils now found are conodonts, ostracodes, gastropods/monoplacophorans, and echinoderm fragments.

Anita Löfgren (Department of Historical Geology and Palaeontology, Lund) kindly identified the conodonts, all of which are known from the *Microzarkodina flabellum parva* Zone (Lindström 1984; Löfgren 1985). As the conodonts from the Hälludden section have not previously been described the taxa are recorded here: *M. f. parva*, *Prionodus (Baltoniodus) prevariabilis norrlandicus*, *Paroistodus originalis*, *Drepanoistodus? cf. venustus*, *D. basiovalis*, *Protopanderodus cf. rectus*, *Semiacontiodus corniformis*, *Drepanodus arcuatus*, *Scalpellodus latus*, and *Cornuodus longibasis*.

The ostracodes are preserved as internal moulds which are worn and difficult to determine. *Primitia* sp. and *Protallinnella* sp. were identified by Åke Bruun (Geological Survey of Sweden, Uppsala).

Coiled internal moulds are either gastropods or monoplacophorans or both; closer assignment is impossible due to the lack of muscle scars.

Echinoderms. Echinoderm macrofossils (*Cheirocrinus*, *Sphaeronites*) have been recorded from the 'Limbata' Substage and the upper part of the Hunderum Substage from other localities on Öland

(Regnéll 1945, 1948). The number of echinoderm microfragments increases from the topmost 'Limbata' to the early Hunderum, thereafter decreasing drastically to be totally absent in Valasteian samples. Most identifiable fragments can be assigned to inadunate crinoids but some belong to ophiuroids (A. B. Smith, British Museum (Natural History), London, pers. comm. 1985).

In the E-level about 50 % of the acid resistant residue consists of partly phosphatized, very fragile echinoderm fragments. Roughly 75 % of the fragments are poorly preserved and only identifiable as echinoderms due to their rather coarse stereom structure. Among the identifiable remaining 25 %, fragments of brachials and stem ossicles are dominant.

At least three main types of stem ossicles can be distinguished. 1, High, cylindrical forms without ornament on the latera, narrow to wide lumen and smooth, undifferentiated zygum. 2, High, pentalobate with variable lumen width. Areola subdivided in five discrete spoon-shaped fields with prominent culmina connecting the perilumen with the narrow crenularium midway along each side. Occasionally the culmina extend into minute spines. 3, High, circular with pentastellate narrow lumen, wide areola, and narrow peripheral crenularium. The ossicles are mostly found isolated but two or more together do occur. Single ossicles not referable to these types occur, for example quadrangular forms.

CYCLOCYSTOIDS

In all, thirty-five marginal ossicles from cyclocystoids have been found in the E-level. Additionally, two single marginal ossicles have been found in two lower levels, 108–117 cm and 159–162 cm below the Langevoja–Hunderum boundary. Unfortunately, the total of thirty-seven marginal ossicles diminished to twenty when picking and mounting for SEM, with the remaining left more or less fragmentary. Although additional fragments in the sample residue must belong to cyclocystoids, no attempt has been made to identify these. The presence of several echinoderm groups within the same sample prevents identification with reasonable certainty. Furthermore, the small size of the non-marginal plates of the cyclocystoids probably prevents any identification. All thirty-seven marginal ossicles are of almost equal size, about 500 μm long and 250 μm broad. Variations are due to etching. Two thin, awl-shaped ossicles without cupules represent newly initiated marginal ossicles. Etching has obliterated the outer structure and ornament in all specimens but has revealed the three-dimensional stereom structure.

In spite of the sample size (100 g before etching) and the size of the marginal ossicles the number make the presence of only one specimen likely. Due to the rarity of cyclocystoids recorded in general, and the distinct difference between any known genus and species and this material, it seems well founded to erect a new monotypic genus.

The type material is deposited at the Palaeozoology Section of the Swedish Museum of Natural History (Naturhistoriska Riksmuseet), Stockholm.

SYSTEMATIC PALAEOLOGY

Class CYCLOCYSTOIDEA Miller and Gurley, 1895

Family CYCLOCYSTOIDIDAE S. A. Miller, 1882

Genus *Monocycloides* gen. nov.

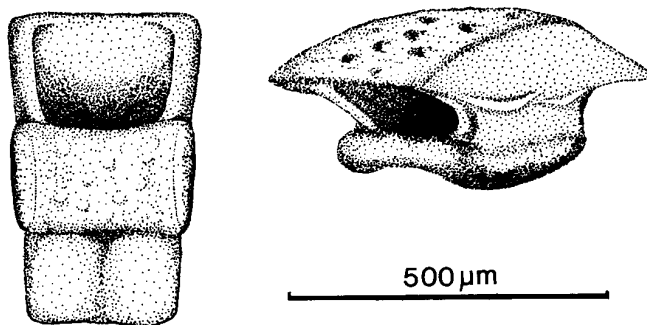
Type species. *Monocycloides oelandicus* sp. nov.

Derivation of generic name. Greek *mono* = alone, single.

Diagnosis. Cyclocystoid with > 35 marginal ossicles which are longer than broad, each with only one cupule without tubercle and prominent radial facets. Strongly convex dorsally. Crest broader than long, flat to saddle-shaped. Test and disc unknown.

Occurrence. Arenig (Lower Ordovician), Sweden. As currently known the genus is monotypic.

TEXT-FIG. 3. Reconstruction of a marginal ossicle of *Monocycloides oelandicus* seen from the ventral (left) and the dorsal side (in life position) to the right. Pits, pustules, and articulation ridges may have been slightly different in life from how they are reconstructed here.



Description. The marginal ossicles are twice as long as broad, the width almost equal distally and proximally. In radial cross-section they are rectangular to cuneiform, in lateral view characteristically submarine-shaped (Pl. 16, figs. 4 and 5) due to the convex dorsal surface and the high, almost flat-topped crest. The crest is broader than long and forms 35–40 % of the length of the marginal ossicle. The lateral margins are slightly raised, in lateral view convex to flattened, but the central part is always depressed, the distal and proximal edges gently curved. The cupule zone is slightly oblique to the crest, forming 35–40 % of the total length of the ossicle. The single cupule is squarish as seen directly from above but in fact is spoon-shaped as the straight cupule walls taper proximally below the overhanging crest. The distal edge is sharp, there is no tubercle or trace of any such structure. The circumferential canal is very narrow. The extended radial facets are horizontal to slightly oblique to the crest; they are separated by a shallow groove (Pl. 16, fig. 6). In most marginal ossicles the radial facets form 20–30 % of the entire length of the marginal ossicle but some of the best preserved ossicles suggests a tripartition (33 × 33 × 33 %) of equal size between cupule zone, crest, and radial facet. The gap between adjacent crests is less than 30 % of the breadth of the crest. The lateral surfaces have two series of articulation ridges, each with only a single ridge.

Remarks. The distinct shape of the marginal ossicles and the presence of only one cupule without tubercle readily distinguish *Monocycloides* from any other cyclocystoid genus.

Monocycloides oelandicus sp. nov.

Plate 15, figs. 1–5; text-fig. 3

Type material. Holotype RM Ec27420, paratypes RM Ec27421–27426.

Occurrence. Upper Arenig (Lower Ordovician), Langevoja Substage, Hälludden, northern Öland, Sweden.

Derivation of species name. Latin *oelandicus* = Öland.

Diagnosis. As for genus.

Description. In all, thirty-five marginal ossicles of almost equal size were studied and form the basis for this description. Average length and breadth based on the fifteen best preserved specimens: Length of marginal ossicle (ventral) 480 μm, breadth of marginal ossicle (proximal) 190 μm, (distal) 230 μm, length of crest 200 μm, breadth of crest 220 μm, height (top of crest perpendicular to dorsal surface) 210 μm. Measurements according to Smith and Paul (1982).

Based on the dimensions of the wedge-shaped marginal ossicle a hypothetical size and shape of the test has been calculated: diameter 3.8 mm, circumference 12 mm, and with approximately fifty marginal ossicles. The disc diameter should form more than 75 % of the test. Calculations of this kind should be accepted with some reservations. The test might have been ovoid. However, an imprint of a segment of a circle (Pl. 16, fig. 8) has been found in the acid resistant residue of the matrix. The size matches an imprint of the ventral surface, the ridges representing the gaps between crests. Unfortunately the sample disintegrated when removing it from the SEM.

The marginal ossicles may have been in contact along most of their entire length but the state of preservation prevents a reliable judgement. The dorsal surface is occasionally strongly convex (Pl. 16, figs. 2, 4, 5) and

continues into the radial facets without interjacent crescentic facets. This part is the thinnest and is most often incomplete (Pl. 15, figs. 1 and 3; Pl. 16, fig. 6). The outer surface is absent due to the etching; pustules and lateral striae obliterated.

Articulation ridges are seen in only a few ossicles, usually in the less well-preserved specimens, where the etching has thrown the ridges into relief (Pl. 16, fig. 4; text-fig. 3). The distal ridge follows the slope of the cupule wall upwards to the circumferential canal and from there bends gently downwards ending at a point in the middle of the crest length. The proximal ridge lies above the distal ridge, distally overlapping this. It is horizontal to gently arched and extends to the proximal end of the crest in line with the radial facet.

Remarks. The size of the marginal ossicles (and the estimated test) is small and the possibility that they belong to a juvenile specimen cannot be discounted. The presence of only one cupule seems to support this as the number of cupules seems to increase by growth in many other genera. Also, progressive growth is suggested by the presence of thin ossicles without cupules, and some of the largest marginal ossicles show evidence of growth in the cupule zone. Here the cupule walls become increasingly broader towards the lateral faces, flattening dorsally (Pl. 16, fig. 7). On the other hand, the additional two ossicles found at lower levels within the Langevoja Substage which contradict this, are exactly the same average size as the thirty-five from the E-level and also have only one cupule. It is hardly believable that only juvenile specimens should be represented in all three levels.

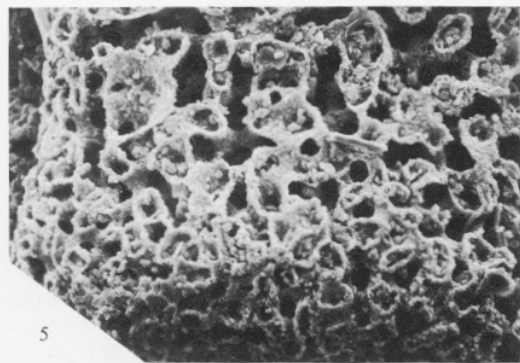
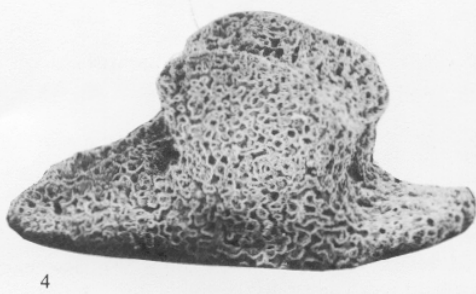
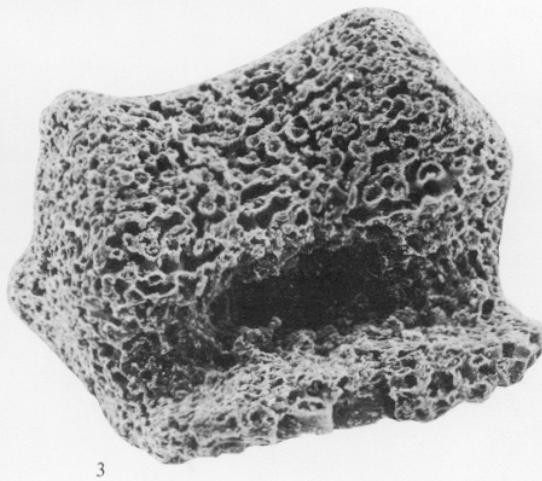
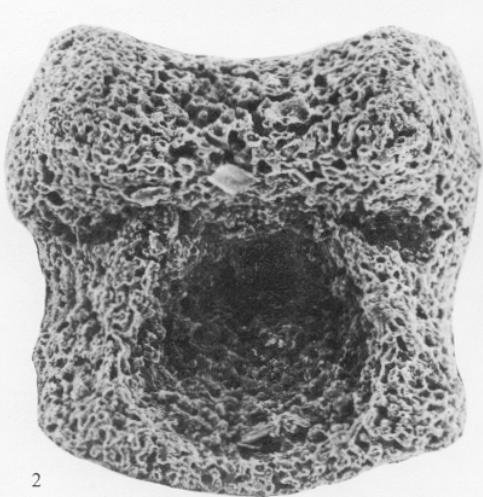
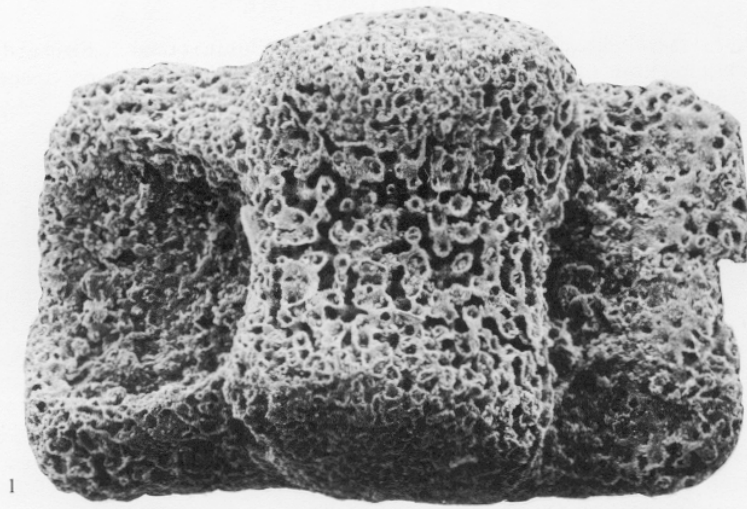
Although the methods for extraction of fossils used here is primarily aimed at the microfauna, larger fossils also occur in the samples. If larger marginal ossicles representing an adult stage existed they would probably have been found. Furthermore, the sequence at Hälludden and other localities on Öland, for example the Böda Hamn exposure and core, have been searched specifically for echinoderms. A large cyclocystoid would not have gone unnoticed. Finally, the size of the fauna in general in the Langevoja (and most other) samples is worth noting. All fossils are small: ostracodes, gastropods/monoplacophorans, inarticulate brachiopods, and the inadunate crinoids as estimated from the size of the fragments. For some reason the fauna seems starved, perhaps due to unfavourable environmental conditions. This may also explain the relative paucity of macrofossils in the Langevoja Substage (Grahm 1982), trilobites excepted. The supposition that *M. oelandicus* is adult in spite of its small size therefore seems well founded.

Microstructure. A characteristic of most lower Ordovician echinoderms from Hälludden is the rather coarse labyrinthic stereom (Pl. 15, figs. 1-5). The dorsal side of the marginal ossicles in *M. oelandicus* are especially coarse (Pl. 16, figs. 1-3) whereas the remaining part of the ossicle has a finer structure. It seems that the stereom gradually becomes more dense towards the centre of the ossicle. This can be seen in heavily etched ossicles (Pl. 16, fig. 4). The radial duct does not appear as an open channel, nor can any connection between the cupule zone and the radial facets be seen, for example in the form of especially thin stereom structure. If connected with the respiratory system the coarse stereom may indicate either an unfavourable environment (low oxygen content) or lack of the tube-foot/ampulla system used by most larger echinoderms. Both cases are in fact possible as the coarse stereom is found in almost all echinoderm fragments and *Monocycloides* is small enough to make do with diffusion alone (Paul 1977).

Preservation. The three-dimensional stereom is preserved during etching due to the presence of an acid-resistant component. This component is francolite (carbonate fluorapatite, $\text{Ca}_{10}(\text{PO}_4)_6$

EXPLANATION OF PLATE 15

Figs. 1-5. *Monocycloides oelandicus*, holotype RM Ec27420. 1, marginal ossicle in slightly oblique ventral view showing the cupule zone, the saddle-shaped crest, and the incomplete radial facets, $\times 200$. 2, cupule zone in distal view showing the narrow circumferential channel and the lateral slopes, $\times 200$. 3, oblique lateral-proximal view showing the radial duct and the incomplete radial facets, $\times 200$. 4, slightly tilted lateral view showing the raised lateral slopes and the depressed centre of the crest. The flat dorsal surface is due to etching, $\times 150$. 5, labyrinthic stereom of the lower left of the crest in fig. 1, $\times 400$.



BERG-MADSEN, *Monocycloides*

$\times (\text{CO}_3\text{F}) \times (\text{F,OH})_2$; XRD analysis by Ulf Sturesson, Palaeontological Institute, Uppsala). In some cases the francolite appears to be a 2–4 μm thick rind of cement in the pore space, in analogy with the Middle Cambrian echinoderms reported from Bornholm (Berg-Madsen 1986). Then, the acid-resistant structure is the *negative* of the original calcite stereom. Most often, however, a replacement/recrystallization of the original calcite matter seems to have taken place (Pl. 16, figs. 1–3) and the acid-resistant structure then is a true replica of the original skeleton. Phosphatization is believed to be an early diagenetic process gradually affecting the skeletons. Most of the unaltered calcite (the cores of the trabeculae) was lost during the dissolution in acetic acid.

It is interesting to note that the oolites at the Langevoja–Hunderum boundary are completely phosphatized to francolite (U. Sturesson, pers. comm. 1985). Phosphatization of the matrix also occurs (Pl. 16, fig. 8) although only very weakly as the samples are extremely fragile.

Phosphatization and glauconitization of microfossils have been described from the overlying Middle Ordovician strata at Hälludden by Eisenack (1978). He assumed that the original calcite dissolved completely leaving voids where the francolite was introduced. With regard to glauconitization he noted its occurrence especially in the echinoderm fragments. Glauconitized echinoderm fragments occur in the E-level but are much more common in the 'Limbata' Substage and the overlying Hunderum and lowermost Valaste Substages. The marginal ossicles of *M. oelandicus* show no trace of glauconitization but tiny glauconite grains are often squeezed into the cupule and the distal opening of the radial duct.

DISCUSSION

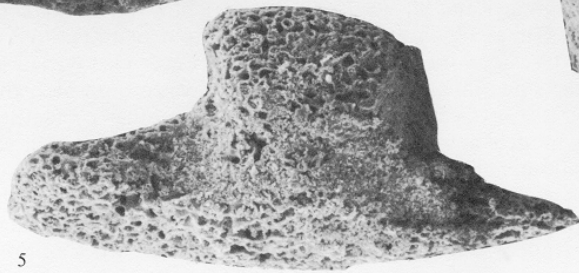
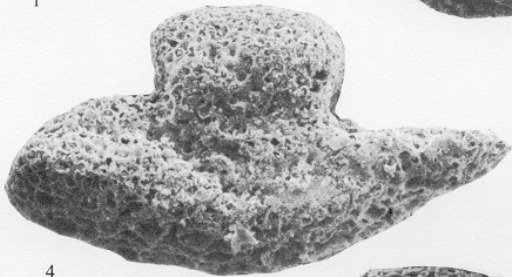
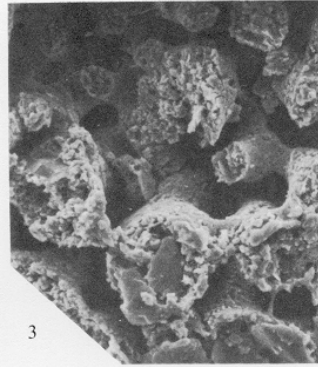
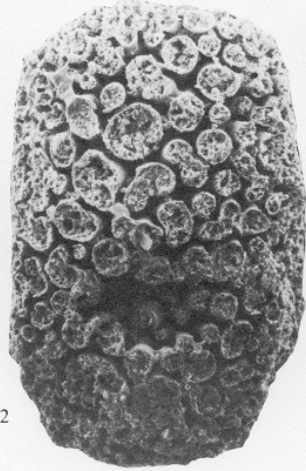
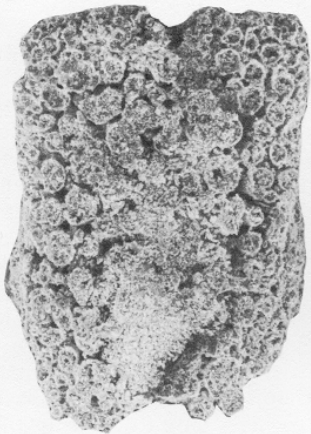
Palaeogeography. Since Regnéll (1945, 1948) proposed his view of migration routes it has been accepted generally that the cyclocystoids originated in North America, probably during early Ordovician time (Sievets-Doreck 1951; Kesling 1966). The known geographical and stratigraphical distribution is shown by Smith and Paul (1982, fig. 13) together with proposed details of their phylogeny (fig. 14). The occurrence of the cyclocystoid *M. oelandicus* in the Arenig of Baltoscandia demands a critical assessment of this view in the light of recent research in palaeobiogeography. A short review of the palaeogeography between the opening and closing of the Iapetus Ocean is compiled from McKerrow and Ziegler (1972), Jaanusson (1973*a, b*), Smith *et al.* (1973), McKerrow (1979), Ziegler *et al.* (1979), Cocks and Fortey (1982), Lindström (1984), and Schallreuter and Siveter (1985). Based on this the origin and possible migration will be discussed.

In early Cambrian times it appears that continental rifting began and the Gondwana, Laurentian, and Baltic plates drifted apart. The Gondwana continent stretched roughly 50° north and south of the equator during the Cambrian; it moved gradually polewards during Ordovician to early Devonian times.

Laurentia (including western Newfoundland, Greenland, north-west Britain, and Ireland) was already in late Cambrian time established across the equator, reaching from 20° S. to 20° N. Apart

EXPLANATION OF PLATE 16

Figs. 1–8. *Monocycloides oelandicus*, paratypes. 1, RM Ec27421, incomplete dorsal surface (distal part) of typical cuneiform marginal ossicle, $\times 140$. 2, RM Ec27422, rectangular and strongly convex dorsal surface, $\times 135$. 3, detail of fig. 2, showing the coarse labyrinthic stereom structure, $\times 475$. 4, RM Ec27423, lateral view of heavily etched marginal ossicle with convex dorsal surface, flattened crest and the articulation ridges revealed by the etching, $\times 160$. 5, RM Ec27424, lateral view of etched marginal ossicle with a more dense stereom structure showing towards the centre of the ossicle, $\times 150$. 6, RM Ec27425, ventral view of marginal ossicle with prominent radial facets, the break indicating the groove leading to the radial duct, $\times 150$. 7, RM Ec27426, the cupule zone of a marginal ossicle with narrow cupule walls and lateral growth (arrows) from the walls outward, $\times 110$. 8, imprint of the ventral surface of *M. oelandicus* in porous, acid resistant matrix, $\times 40$. Owing to the porosity the sample collapsed when it was removed from the SEM.



from a counterclockwise rotation during the Upper Cambrian through the Ordovician the position was maintained until late in the Silurian.

Regarding the Baltic plate, opinions differ considerably not only with regard to size but also to its degree of movement according to the authors cited above. Some authors include Baltoscandia, northern Poland, and the Russian Platform eastwards to Ural, others also the southern part of the British Isles, a large part of Central Europe, and eastern Newfoundland. However, more recent opinion suggests that the latter areas were attached to the Gondwana continent (Cocks and Fortey 1982). A third opinion advocates a separate microcontinent consisting of the southern part of the British Isles and eastern Newfoundland. From a position at cool, temperate latitudes in Middle Cambrian times Baltica either moved gradually towards the equator and Laurentia or moved polewards during the late Cambrian and early Ordovician and back towards low latitudes from Caradoc times onwards.

The continents were separated from each other by oceans. The Iapetus Ocean between Laurentia, Baltica, and Gondwana closed towards the end of Silurian times. Tornquist's sea is believed to have separated Baltica from Gondwana from the early Ordovician (or earlier?) until it closed in the Ashgill (Cocks and Fortey 1982). From then on the Rheic Ocean started opening. The maximum distance between the continents seems to have been in the early Ordovician, Baltica lying at least 3000 km, and perhaps as much as 8000 km from Laurentia.

Origin and diversification. Regnéll (1945, 1948, 1960a, b) reviewed the non-crinoid echinoderms, in particular from Baltoscandia. Both during the Ordovician and the Silurian about 98% of the echinoderm fauna was apparently developed from an eastern stock. Among the exceptions were the cyclocystoids *Apycnodiscus*, *Polytryphocystoides*, and *Sievertsia* (Smith and Paul 1982) which were thought to have migrated from North America to Baltoscandia.

Migration from Baltoscandia to North America is known to have taken place at least from Llanvirn times onwards (Schallreuter and Siveter 1985). There is, however, no evidence of migration either way in Arenig or earlier times which would be necessary to explain two out of three models of cyclocystoid evolution: a, *Cyclocystoides* existed back in the lower Ordovician and gave rise to *Monocystoides* as a specialized side branch, or b, *Monocystoides* was more widely distributed in the Lower Ordovician and gave rise to *Cyclocystoides* and hence the other cyclocystoid genera. Although not impossible both models imply benthic animals from a shallow shelf sea environment migrating across a wide (minimum 3000 km) ocean.

If large scale migration is excluded a third model is left: c, *Monocystoides* and *Cyclocystoides* stem from a common ancestor found in either of the continents Laurentia, Baltica, and Gondwana. Considering the still more advanced echinoderm groups recorded from the Cambrian the ancestral group may be as old as, for example, the Middle Cambrian. By this time the Iapetus Ocean was still fairly narrow and migration accordingly would have been more easy than in early Ordovician times. The cyclocystoids have much in common with edrioasteroids, although more with the Isorophida than Stromatocystitoidea (Smith and Paul 1982). The early Middle Cambrian cyclocystoid from Australia (Henderson and Shergold 1971) later excluded from the class is now redescribed as a new genus (*Edriodiscus*) of stromatocystitids (Jell *et al.* 1985).

Monocystoides shows similarities with several other cyclocystoid genera but is most closely related to *Cyclocystoides*. The articulation probably along the entire length of the marginal ossicle, the length and shape of the cupule zone, the smooth-floored cupule and absence of tubercle, the crest broader than long, and the prominent radial facets, are especially comparable with the Middle Ordovician *C. latus* and the Upper Ordovician *C. halli*. However, both these species have two cupules; in *C. latus* the cupules are squarish and not tapered proximally and in *C. halli* strongly tapered but ovoid. Both have convex crests but *C. latus* has prominent radial facets which are absent in *C. halli*. Also the shape in radial cross-section is different from that of *Monocystoides*, which has a flattened crest and more strongly convex dorsal surface. Although the outer details of this surface are not known, pits rather than a smooth or granular surface are suggested by the coarse stereom structure.

There are fewer features in common with other genera, for example *Apycnodiscus*, *Polytryphocycloides*, and an undescribed species of *Sievertsia* from the Silurian of Gotland (Smith and Paul 1982; Christina Franzén-Bengtson, Swedish Museum of Natural History, Stockholm, pers. comm. 1985). Whereas the dorsal surface tends to become flat or even concave, several cupules with tubercles are always present although they seem to disappear secondarily in the above mentioned species of *Sievertsia*. Even if flattened crests and radial facets occur the radial cross-section of the Silurian cyclocystoids differs more from *Monocycloides* than *Cyclocystoides* does from *Monocycloides*.

The presence of only one cupule in all marginal ossicles is the most significant difference between *Monocycloides* and *Cyclocystoides*. One cupule seems to represent a primitive feature, and if *Monocycloides* was the direct ancestor of *Cyclocystoides* at least a minor part of the marginal ossicles would have been expected to have two cupules. Until more (and older) genera or species have been found *Monocycloides* is regarded as a primitive 'sister' group of cyclocystoids, originating from an ancestor in common with *Cyclocystoides* and later genera. The ancestral form may have lived in either of the three continents, with the widening Iapetus Ocean separating the group, or an early migration may have taken place. There is no reason to believe that *Monocycloides* is the ancestral form of the genera found in the Silurian of Gotland; most possibly it became extinct before the end of Middle Ordovician.

SUMMARY

Marginal ossicles of a cyclocystoid occur in the uppermost of the Langevojan Substage (Arenig), Lower Ordovician, at Hälludden, northern Öland, Sweden. These represent the hitherto oldest known cyclocystoid. The thirty-five marginal ossicles are believed to belong to a single adult specimen estimated to have had at least fifty marginal ossicles. The cyclocystoid is also the smallest species ever recorded with an estimated diameter of 3.8 mm. The similarities with the genus *Cyclocystoides* are many but the distinct differences including only one cupule, the shape of the crest, the radial facets, and the articulation ridges warrant the erection of a new genus—*Monocycloides*. This is not regarded as the direct ancestor of *Cyclocystoides* nor of any other cyclocystoid genera but is thought to represent a more primitive genus living almost parallel in time with the more advanced *Cyclocystoides*, becoming extinct before a migration of cyclocystoids from North America to Europe started.

There is no evidence of migration from Europe (Baltica) to North America (Laurentia) during the early Ordovician and the common ancestor is believed to have lived in either of the three continents, Laurentia, Baltica, and Gondwana, lying separated by the Iapetus Ocean. An early migration may also have taken place from Baltica or Gondwana to Laurentia. This does not affect the migration theory of Regnéll (1945, 1948).

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