CYCLOCYSTOIDES FROM EARLY MIDDLE CAMBRIAN ROCKS OF NORTHWESTERN QUEENSLAND, AUSTRALIA

by R. A. HENDERSON *and* J. H. SHERGOLD

ABSTRACT. A new species of *Cyclocystoides*, *C. primotica*, is described from the early Middle Cambrian Ordian Stage of the Mt. Isa district, Queensland, Australia. It comprises the first record of the Cyclocystoidea from rocks older than Middle Ordovician, and from the Southern Hemisphere. Derivation of the class from the Cystoidea is unlikely on stratigraphic grounds; its earliest representative suggests no close affiliation with contemporaneous echinoderm taxa. It is suggested that undulation of the marginal ring provided feeding currents in life.

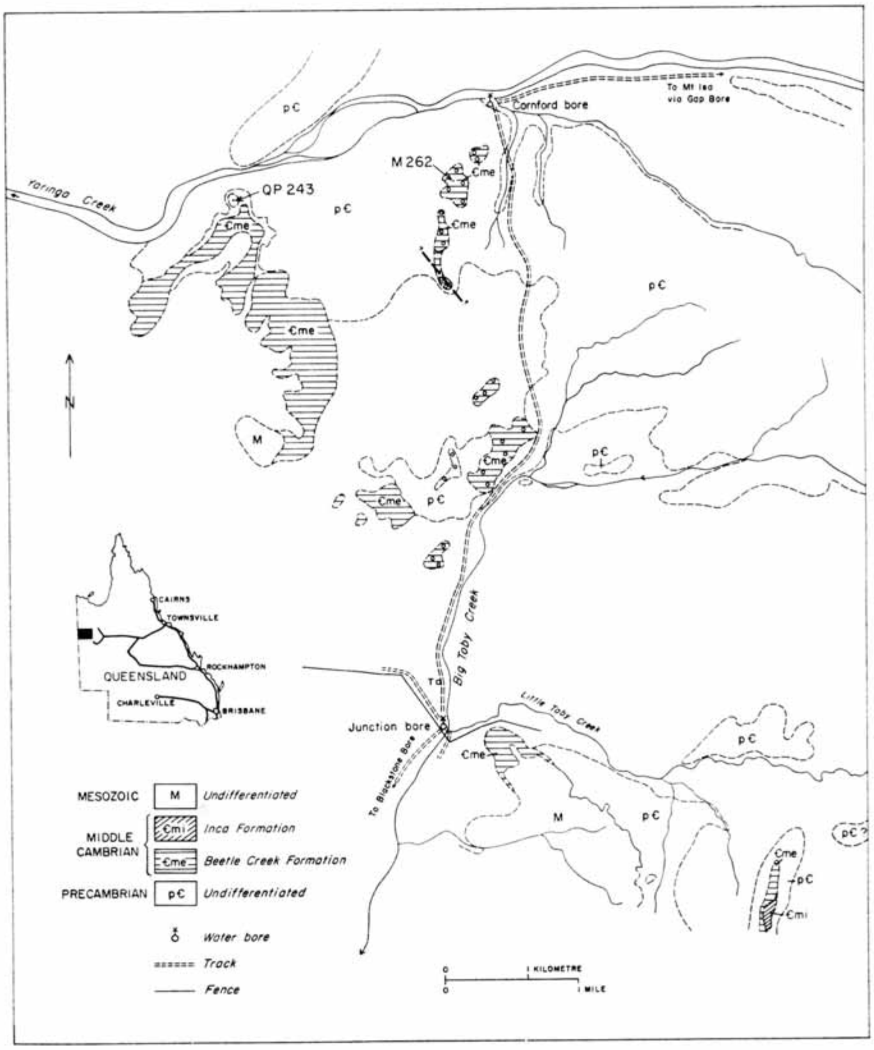
TWO well-preserved external moulds of the aboral surface of a single species of *Cyclocystoides* are represented in a fossil collection made by Mr. F. de Keyser (formerly of the Australian Bureau of Mineral Resources) during a detailed mapping programme promoted by the search for phosphorite in 1968. The specimens were picked out by one of us (JHS) following routine examination of the collection, and were identified as *Cyclocystoides* by the second author during a visit to the Bureau of Mineral Resources. In consequence, this report has been prepared as a joint project.

The specimens were found at locality QP 243, which is three miles WSW. of Cornford Bore, and approximately 28 miles WSW. of Mt. Isa, at latitude 20° 49·5′ S., longitude 139° 03·5′ E. (text-fig. 1). They are from the Yelvertoft Bed, the basal unit of the Beetle Creek Formation in this district. The cyclocystoids are preserved in laminated chert, associated with silicified coquinite, algal chert, and siltstone. These rocks overlie basal Cambrian sandstone and conglomerate, which are unconformable on Precambrian sediments (Mingera Beds). The fossiliferous horizon lies about 20 ft above the unconformity.

The cyclocystoids are associated with new species of the trilobite genus *Redlichia* (see Pl. 138, fig. 3) which are of late Ordian (early Middle Cambrian) age. Similar species of *Redlichia* occur at a neighbouring locality, M262, which is shown on the Bureau of Mineral Resources Mt. Isa 1:250,000 geological series sheet, F/54–1. Öpik (1967, p. 150) has listed fossils from this locality, and described the species of *Redlichia* (in press). The cyclocystoids are dated as older than the *Redlichia chinensis* fauna of western Queensland, which is of latest Ordian age, but younger than that of *Redlichia forresti* which occurs in the Northern Territory and Western Australia earlier in the Ordian (Öpik, personal communication). The late Ordian Stage of Australia correlates with the *Albertella* Zone of the North American Rocky Mountains, and pre-dates the paradoxidian Middle Cambrian of Europe (Öpik 1967, p. 144, table 1).

Following early description of *Cyclocystoides* as representative of a distinctive echinoderm grouping by Salter and Billings (1858), little progress has been made in describing its complete morphology as new material has been scarce. Thorough morphological analyses of the Cyclocystoidea in the light of all accumulated information, have been given recently by Kesling (1963, 1966). Until the discovery of the fossils reported here, the class was unknown outside of North America and north-western Europe, and its established geological range was from Middle Ordovician to Devonian, post-dating the appearance of most of the better known echinoderm classes. Phyletic relations of

[Palaeontology, Vol. 14, Part 4, 1971, pp. 704–10, pl. 138.]



TEXT-FIG. 1. Sketch map of the bedrock geology of part of the Mt. Isa 1:250,000 geological sheet (black on the inset map) showing the position of the cyclocystoid locality, QP243; based on air photograph 0105, Mt. Isa, run 7, and unpublished geological interpretation by F. de Keyser.

the group therefore require review in terms of the affinities of the species described here with contemporaneous free-living echinoderm taxa.

SYSTEMATIC DESCRIPTIONS

Class CYCLOCYSTOIDEA Miller and Gurley 1895
Genus CYCLOCYSTOIDES Salter and Billings 1858

Cyclocystoides primotica sp. nov.

(Plate 138, figs. 1–3)

Material. Holotype, Commonwealth Palaeontological Collection (CPC) 11395, external mould of an aboral surface. Paratype, CPC 11396, external mould of an aboral surface.

Occurrence. Yelvertoft Bed, basal Beetle Creek Formation, 3 miles WSW. of Cornford Bore, 28 miles WSW. of Mt. Isa, western Queensland, Australia.

Age. Late Ordian (early Middle Cambrian).

Diagnosis. Plate surfaces of the submarginal ring exposed on the aboral surface are slightly longer than wide, about twice the width of adjacent plates of the marginal ring and aboral disc. Plates of the aboral disc are arranged in a mosaic lacking a geometric pattern; they show no gradation in size from the centre to the periphery. All plates of the aboral surface bear a fine striation radiating from the disc centre and continuous to the periphery of the marginal ring.

Description. Known only from aboral surfaces which are large for the genus. Submarginal ring entire, consisting of subequal plates, often with indistinct sutures, numbering approximately 42 and 53 on the two specimens to hand. As exposed on the aboral surface the plates are rectangular in outline and slightly longer than wide. Marginal ring well developed, entire, of at least six, possibly eight, plates in thickness from the submarginal ring to the periphery. Plates adjacent to the sub-marginal ring are largest, form a regular circlet, and are subrectangular in outline; plate size, regularity of shape, and the geometric arrangement of plates all decline towards the periphery. Plates are separated by distinct sutures and there is no suggestion of a radial arrangement. Aboral disc composed entirely of plates, as far as can be seen, although the disc centre is imperfectly preserved on both specimens. Specimen CPC 11395 suggests some inclined, central plates, perhaps abutting a central aperture, but such structure cannot be confirmed. The remainder of the disc surface is covered in a mosaic of small irregularly polygonal plates separated by distinct interspaces and lacking geometric arrangement. Specimen CPC 11395 has the suggestion of a spiral plate arrangement but close examination shows it to be more apparent than real. Plates are mainly of uniform size but some smaller elements are intercalated in a random manner; there is no gradation in plate

---

EXPLANATION OF PLATE 138

Figs. 1–3. *Cyclocystoides primotica* sp. nov. 1, latex cast of holotype, CPC 11395. Aboral surface, ×2. 2, latex cast of paratype, CPC 11396. Aboral surface, ×2. 3, slab surface with paratype, CPC 11396, showing the orientation of *Redlichia* cephala, ×1·5.

size from the disc centre to the submarginal ring. A closely spaced striation is impressed on all plates of the aboral surface and is independent of individual skeletal elements; primary striae radiate from the disc centre but others are intercalated towards the periphery so that the density of striation is constant over the entire surface.

Dimensions. (in millimetres)

	CPC 11395	CPC 11396
Maximum diameter of aboral surface	*c.* 29·0	*c.* 32·2
Maximum diameter of aboral disc	*c.* 23·1	*c.* 25·9
Width of submarginal ring plates	1·1	1·0
Length of submarginal ring plates	1·6–1·9	1·3–1·5
Maximum diameter of plates of the aboral disc	0·5–1·5	0·6–1·8

Remarks. Some adjoining plates of the submarginal ring have separated slightly during preservation suggesting that in life they were connected by soft tissue rather than cemented together. In general, sutures between adjoining plates are not well marked, suggesting that articulation was limited, if possible at all. Distinct interspaces between plates of the aboral disc show that in life they were separated by distinct zones of soft tissue and the disc surface would undoubtedly have been capable of some inflation. A slightly inflated condition prior to fossilization is suggested by both specimens where the disc surface, as preserved, is raised centrally with indistinct radial rumples, rather than being planar in disposition. Distinct sutures bounding the plates of the marginal ring suggest that they too were capable of articulation on zones of connecting soft tissue in life. The radial striation ornamenting all plates of the aboral surface can be traced without interruption from one plate to the next from the marginal ring to the disc centre. It must reflect a similar patterning on the integument encasing the skeletal elements and completely covering the aboral surface.

Both specimens show a segment of the submarginal and marginal rings, comprising about one-fifth of the circumference, which is straight rather than curved. With only two specimens available, it is impossible to tell whether this indicates original bilateralism or whether it is a product of preservation. Bilateral symmetry in skeletal outline is not known from any other described cyclocystoid.

The external moulds of both cyclocystoid specimens are associated on the same slab surfaces with internal moulds of *Redlichia* cephala. The slab surfaces are therefore likely to represent the upper surfaces of beds or laminae, and the aboral surface of *C. primotica* probably lay against the substrate in life. Such an orientation of *Cyclocystoides* has already been inferred on morphological grounds by Sieverts-Doreck (1951, p. 10) and Kesling (1963, p. 163; 1966, p. 191). A small, undescribed fauna of inarticulate brachiopods and hyolithids is represented at the locality, and together with *Redlichia*, suggest shallow marine conditions of deposition for the host strata, a conclusion which is supported by the unconformable contact of the Cambrian succession on Precambrian basement a few feet below the fossiliferous horizon.

As already discussed by Kesling (1966, p. 205), generic classification of the Cyclocystoidea is uncertain because the complete morphology of so few species has been established. The basic aboral organization of *C. primotica* shows good general agreement with the type species of *Cyclocystoides*, *C. halli* Billings (Salter and Billings 1858, p. 86). In essence it differs only in possessing a radial striation, which is a unique feature among *Cyclocystoides*.

According to Sieverts-Doreck (1951, p. 24), the aboral disc of *C. devonicus* possesses radially arranged plates raised into radial ridges and separated in places by grooves. Such ridging is analogous to the striation of *C. primotica*, but plate arrangement suggests that *C. primotica* is more closely allied to *C. halli* than to *C. devonicus*. The latter may represent a separate genus (Kesling 1966, p. 205) on this account. *C. primotica* is distinguished from all other described species of *Cyclocystoides* in possessing narrower submarginal ring plates.

Phyletic Relationships of the Cyclocystoidea

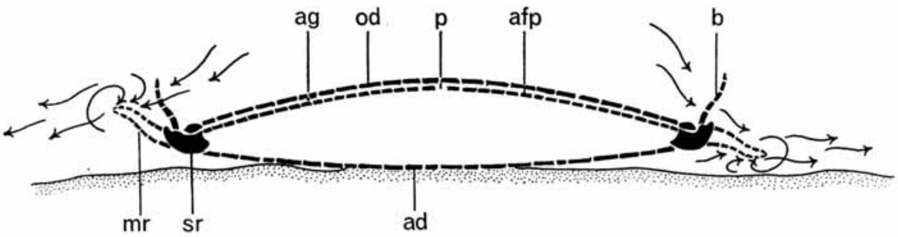
Cyclocystoides primotica is among the oldest known free-living echinoderms, being preceded only by the Lower Cambrian Helicoplacoidea (Durham and Caster, 1963) and the free-living edrioasteroid *Stromatocystites* which ranges from Lower Cambrian to Middle Cambrian in age. Robison and Sprinkle (1969) report the oldest Homalozoa, belonging to the classes Stylophora and Ctenocystoidea from the Spence Shale of northern Utah. In northwestern Queensland, Templetonian faunas with *Xystridura* and *Ptychagnostus gibbus* overlie the Ordian *Redlichia* faunas, and correlate with those of the Spence Shale. Hence *C. primotica* predates the oldest Homalozoa.

Kesling (1963, 1966) suggested that the class Cyclocystoidea was derived from a diplopore-bearing cystoid ancestor resembling the mid-Ordovician genus *Tholocystis* Chauvel. The oldest cyclocystoids then known were of mid-Ordovician age, and the hypothesis was in agreement with the known stratigraphic occurrence of the groups concerned. The Australian material shows that typical cyclocystoid structure was already developed by lower Middle Cambrian time, and predates by some 50 million years the earliest cystoid record. Derivation of cyclocystoids from cystoid ancestry therefore seems unlikely on stratigraphic grounds.

Cyclocystoides shows no close affinity with other Lower and Middle Cambrian echinoderm groups. On the basis of radial symmetry, flattened form, free living habit, and ambulacral structure (assuming this to be similar in *C. primotica* to the later *Cyclocystoides* for which it is known), it agrees with the earliest edrioasteroid family, the Stromatocystidae, but differs in the threefold concentric differentiation of test plates. The submarginal ring in *Cyclocystoides* is the dominant structural feature of the theca; it provides the principal skeletal support, and individual plates exhibit complex morphology on their oral surfaces. Its absence in Lower and Middle Cambrian Stromatocystidae suggests that if cyclocystoids and edrioasteroids shared a common origin, as suggested by Sieverts-Doreck (1951) and others, they experienced a considerable period of divergence prior to the lower Middle Cambrian.

Middle Cambrian Homalozoa of the classes Ctenocystoidea and Homostelea show some structural resemblance to *Cyclocystoides* in that they possess a relatively rigid peripheral system of strong plates, enclosing tessellated areas of small articulating plates on both the superior and inferior surfaces of the flattened theca, analogous to the submarginal and disc plate systems of *Cyclocystoides*. The same basic structure is true of Stylophora but the earliest (Middle Cambrian) representatives of this homalozoan class as yet described, belonging to the Ceratocystidae, differ in that the central plates are few in number and almost as large as the marginals. It may be that strong differentiation of marginals and centrals has been secondarily derived in the Stylophora and is not a primitive character. Even if basic thecal construction was inherited from a common ancestry of the Cyclocystoidea, Ctenocystoidea, and Homostelea, the asymmetry of the Homostelea, bilateral symmetry of the Ctenocystoidea, and the lack of ambulacral structure in both groups preclude a close phyletic connection with *Cyclocystoides*.

It can be concluded that the Cyclocystoidea, at the time of their earliest appearance in the fossil record, comprise a distinctive echinoderm grouping which displays no close affiliation with other contemporaneous echinoderm taxa and fully warrants class status as advocated by Kesling (1966). Origins of the group must be in the Lower Cambrian or, possibly, the Proterozoic.



TEXT-FIG. 2. Hypothetical cross-section of *Cyclocystoides* modified from Kesling (1963, text-fig. 5 in part) to show the function of the marginal ring in promoting feeding currents. Marginal ring at right beginning upward flexure, at left beginning downward flexure. *ag* = ambulacral groove; *od* = oral disc; *p* = peristome; *afp* = ambulacral flooring plates; *b* = brachiole; *mr* = marginal ring; *sr* = submarginal ring; *ad* = aboral disc.

Functional Significance of the Marginal Ring

Of the three concentric divisions of the cyclocystoid theca, the function of two have been explained by Kesling (1963, 1966) and Sieverts-Doreck (1951). It is generally agreed that food was transported to the mouth along the covered ambulacral rays of the oral (upper) surface, probably by means of ciliary currents. Food collection must have taken place in the region of the submarginal ring, probably on brachioles which attached to facets on the excavated oral surface of that structure. The submarginal ring is the main structural element of the theca, providing support for the aboral and oral discs which it encloses; in addition, it probably gives the base for the attachment of brachioles, although the presence of such structures is yet to be confirmed. The disc region enclosed and protected the soft parts, the ambulacral rays which lie within the oral disc being covered above and below by calcareous plates.

The third thecal division, the flap-like marginal ring, is a feature unique to cyclocystoids and its functional significance has never been adequately explained. It has been suggested by Kesling (1963, p. 164) that the animal was attached by muscular contraction of the marginal ring creating suction of the aboral disc on to the soft substrate in which it lived. Under normal current conditions, however, the flattened form of *Cyclocystoides* must have provided stability enough and the adoption of suctorial attachment would have only been useful when conditions of extreme turbulence prevailed. It seems more likely that the marginal ring was functional in causing feeding currents to sweep across the region of the submarginal ring which must have been the site of food collection. If the animal could raise its periphery slightly above the substrate by gentle inflation of the aboral disc, which is inferred to be extensile, undulation of the marginal ring would act to scull water away from the periphery, and draw a compensating water current across the region of the submarginal ring passing through the circlet of brachioles if such structures were indeed present (text-fig. 2).

Acknowledgements. Financial support for R. A. H. from the Australian Research Grants Committee grant 15/70 is gratefully acknowledged. J. H. S. publishes with the approval of the Director, Bureau of Mineral Resources, Canberra, A.C.T.

REFERENCES

DURHAM, L. W. and CASTER, K. E. 1963. Helicoplacoidea: a new class of echinoderms. *Science, N.Y.* **140** (3568), 820–822.

KESLING, R. V. 1963. Morphology and relationships of *Cyclocystoides*. *Contr. Mus. Paleont. Univ. Mich.* **18** (9), 157–176.

—— 1966. Cyclocystoidea: *in Treatise on invertebrate paleontology* (ed. R. C. MOORE). Part **U**, Echinodermata, **3**, 183–210. Univ. Kansas Press and Geol. Soc. Am.

MILLER, S. A. and GURLEY, W. F. E. 1895. Description of new species of Paleozoic Echinodermata. *Bull. Ill. St. Mus. Nat. Hist.* **6**, 1–62.

ÖPIK, A. A. 1967. The Ordian Stage of the Cambrian and its Australian Metadoxididae. *Bull. Bur. Miner. Resour. Aust.* **92** (7), 133–170, pls. 19–20.

—— (in press). *Redlichia* of the Ordian (Cambrian) of Northern Australia and New South Wales. Ibid. **114.**

ROBISON, R. A. and SPRINKLE, J. 1969. Ctenocystoidea: a new class of primitive echinoderms. *Science, N.Y.* **166** (3912), 1512–1514.

SALTER, J. W. and BILLINGS, E. 1858. On *Cyclocystoides*, a new genus of Echinodermata from the Lower and Middle Silurian rocks. *Canada geol. Surv., figures and descr. Can. org. Remains*, **3**, 86–90, pl. 10 bis.

SIEVERTS-DORECK, H. 1951. Über *Cyclocystoides* Salter and Billings und eine neue Art dem belgischen und rheinischen Devon. *Senckenbergiana*, **32**, 9–30, 2 pls.

R. A. HENDERSON
Geology Department
James Cook University of North Queensland
Townsville
Australia

J. H. SHERGOLD
Bureau of Mineral Resources
Canberra
Australia

Typescript received 18 February 1971

HENDERSON and SHERGOLD, *Cyclocystoides*