HYDROZOA AND SCYPHOZOA AND OTHER MEDUSOIDS FROM THE PRECAMBRIAN EDIACARA FAUNA, SOUTH AUSTRALIA

by MARY WADE

ABSTRACT. *Eoporpita medusa* gen. et sp. nov., is a chondrophore with annular float chambers. Simple dactylozooids and details of its gonozooids differentiate it from modern Porpitidae but its affinities are closest to these. The enigmatic group *Cyclomedusa* Sprigg has characters in common with *Eoporpita* but typically lacks a float. They could represent a form close to the hydrozoan root stock from which chondrophores arose but no certainly-assignable oral side is known. Two species of Scyphozoa are recognized from positive composite moulds including internal structures. *Brachina delicata* gen. et sp. nov. is radial and annular in structure and *Kimberella quadrata* (Glaessner and Wade), new name, is tetramerous radial. *Ediacaria flindersi* Sprigg and *Rugoconites* Glaessner and Wade are restored but it is still not certain what their structures mean in terms of coelenterate history.

THE study of 'medusoids' in the Ediacara fauna has lagged behind the study of more distinctive forms, both because of the great number of indifferently preserved specimens, and the morphologic intergrading of the simple outlines preserved. This paper is a progress report on forms that have become better known since their original description, and on new material.

The greatest source of new knowledge comes from the discovery and study of composite moulds showing internal and external characters on the same specimen. Until they are found, any interpretation or restoration remains provisional. Composite moulds have been invaluable in linking the oral surface of a new chondrophore, *Eoporpita*, to its float and to its aboral side. Similar moulds allow description of *Brachina delicata* gen. et sp. nov. and its assignment to the Scyphozoa. *Kimberella quadrata* (Glaessner and Wade) (new name for *Kimberia quadrata* Glaessner and Wade) is also probably a Scyphozoan. *Rugoconites enigmaticus* Glaessner and Wade appears only as a composite mould; it has an unusual preservation in which ridges appear to have occupied the position of radial canals whether observed from the exumbrellar or subumbrellar side of the body. The necessity to explain this structure introduces a note of speculation into the restoration of this species and genus, of which a second species is described. The external morphology of *Ediacaria flindersi* Sprigg is now known in some detail but as none of its internal structures are known, it remains *incertae sedis* (Glaessner and Wade 1966). The lack of extensive composite moulding hinders our understanding of *Cyclomedusa*.

From time to time medusoids are observed with one or more sharp re-entrants in the margin leading into deep creases across the body (pl. 42, fig. 1, centre right margin). These are reminiscent of the radial tears deep into the mesogloea which are often found in Recent medusae. Such tears appear to be the result of physical battering. I have mostly observed stranded Semaeostomatida and only noted tears on these but while battering during stranding is doubtless more severe than fully submarine battering, the structures in the fossils are closely similar to those in the Recent specimens. This

[Palaeontology, Vol. 15, Part 2, 1972, pp. 197–225, pls. 40–43.]

re-entrant and furrow effect is not confined to any one form but is widespread in the Ediacara fauna; also, it occurs without regular spacing in an individual, or regular occurrence in a species. As such it cannot be satisfactorily considered an original structure but must be an artifact.

Late in 1968 the Ediacara fauna was located in the main Flinders Ranges, 320 km north of Adelaide, a short distance above the base of the upper of two members which make up the Pound Quartzite. During the following year it was traced 140 km north and south from Mt. Scott Range, north of Ediacara Range, to Yappala, west of Hawker (text-fig. 1). All these occurrences proved to be at the same stratigraphic level and it was possible to show that the occurrences at Red Range (Beltana Station) and Ediacara Range also were deposited at this time (Wade 1970). Other workers are presently extending the discoveries to the east in the major syncline of which Mt. Scott is part, and to the southeast side of the central Flinders Ranges.

Repositories. Specimens with numbers prefixed 'F' or 'T' or without prefix are deposited in the collections of the Geology Department, University of Adelaide. Those prefixed 'P' are deposited in the South Australian Museum.

SYSTEMATICS

Class HYDROZOA
Order CHONDROPHORIDA
Family PORPITIDAE?
Genus EOPORPITA nov.

Type species. Eoporpita medusa sp. nov.

Diagnosis. As for type species.

Eoporpita medusa sp. nov.

Plate 40, figs. 1–6; Plate 41, fig. 6a, b; text-fig. 2

Material and occurrence. About 20 specimens from Ediacara Range. One from Mayo Gorge was shattered during collection.

Holotype. T27; 2019, from Ediacara Range.

Preservation. All of the fossils are preserved wholly or mainly in convex relief, on the depositionally lower surfaces of rock slabs. The actual preservation represents the complex interplay of a structure sometimes resistant enough to hold the sediment up until it had consolidated, forming an impression, with invariably non-resistant structures which disintegrated before the overlying sediment set and thus allowed the sediment to form casts. This combination of negative and positive preservations on one surface is a type of composite mould. The modes of preservation in these sediments have been discussed at length (Wade 1968).

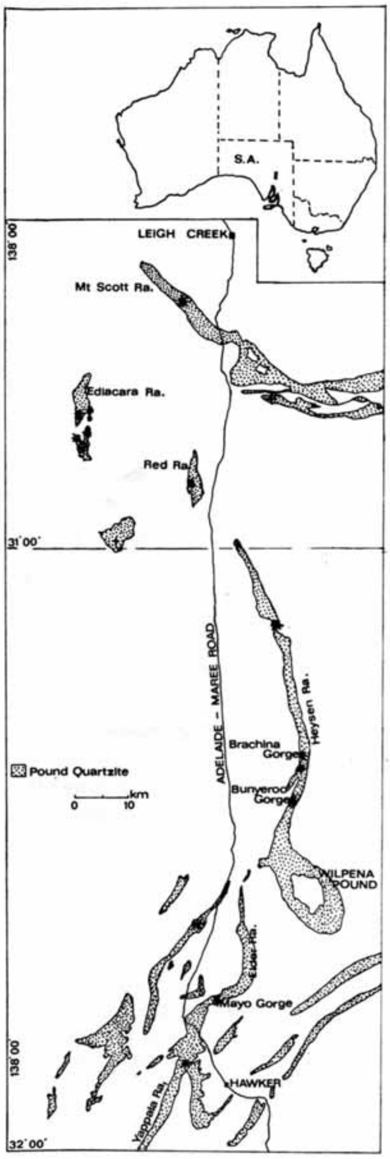
The fossils are circular and raised in the centre. They display several aspects which could not be combined without the presence of composite moulds, so they will be discussed under five preservational types and summarized in a diagram of the structure:

1. One, perhaps two specimens (Pl. 40, fig. 4); almost flat cast with smooth, entire surfaces with a very faint radial structure, and a slight central dome.
2. Two specimens, almost flat positive composite moulds like (1) at the centre but

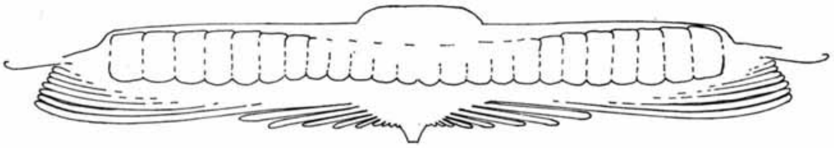
surrounded by flat, broad rings with depressed sutures between them. The whole annular structure is slightly depressed (see Pl. 40, fig. 6). This is a composite mould dominated inwardly by a low, domed centre as in (1) and outwardly by a resistant, ringed structure, with ridged sutures between adjacent rings. Prior to fossilization this annular structure must have underlain a smooth outer surface such as that seen in Pl. 40, fig. 4, because it was higher (depositionally) in the rock, than the centre it encircles.

3. Two specimens; casts of annulate discs made of rings of comparable size to those seen in (2). The smaller specimen is figured in Pl. 40, fig. 2, and shows slightly depressed sutures. The larger specimen (P12720) has one end covered (on the depositionally lower side) by inwardly tapering strips of sand like those seen in (4).

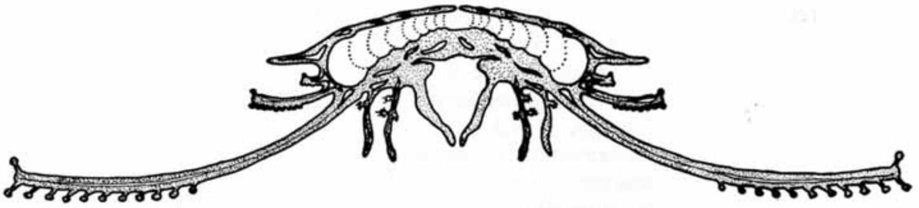
4. Fifteen specimens; discoid bodies including those seen in Pl. 40, figs. 1, 5. These are all casts. The specimen seen in fig. 5 has been sectioned and confirms the impression gained by viewing it entire, that the radially sculptured layers of sand are individually distinct to varying depths, but lose distinctness inwardly and merge in a structureless sand-mass. The chipping of layers from the specimen seen in fig. 1 and others shows that the normal preservation of these specimens is as layers of sand marked by furrows into irregularly disposed, inwardly tapering, rounded strips. Several specimens beside those in Pl. 40, figs. 1, 5 show 2 series of strips, several outer ones all approximately the same length and several inner ones of inwardly decreasing length. The greatest known length of strips is from the margin to the inner series of strips. On the evidence of the larger specimen (3) these layers or whorls of strips cover one side



TEXT-FIG. 1. Locality plan showing the distribution of the Pound Quartzite in the central Flinders Ranges. Fossiliferous deposits are found along the strike of the beds in the named ranges, a short distance above the base of the upper, or white, member of the Pound Quartzite. Only the section in Brachina Gorge was as rich as any comparable area at Ediacara Range. Fossiliferous sections recorded by Wade (1970) are indicated by asterisks if the fossils were found *in situ* or by crosses if only float is yet known.



TEXT-FIG. 2. *Eoporpita medusa* gen et sp. nov., natural size. The structures exhibited by the specimens shown in Plate 40, and additional specimens, have been scaled to one body-size and assembled in natural order without any further attempt to restore the original animal, or reconstruct the life position of the several structures illustrated. *Upper surface*: Pl. 40, figs. 4, 6. *Float*: Pl. 40, figs. 6, 2. Fig. 6 preserves the annules as a mould and the depressions between annules indicate original sutural ridges but the amount of distortion due to compression prior to moulding is unknown; the cast, Pl. 40, fig. 2, shows depressed sutures between convex annules like a larger, unfigured, annular disc with tentacles attached to one end, and the lower surface of the float has therefore been shown with depressed sutures. *Lower surface of body*: based on 15 specimens including those illustrated in Pl. 40, figs. 1, 5. *Number of whorls and length of overlap*: based mainly on the specimens seen in Pl. 40, figs. 1, 5. *Individual separation of 'strips' marking the surfaces of whorls*: small areas seen Pl. 40, fig. 1, and on unfigured specimens, in which the outer strips or tentacles are few and sometimes very widely separated. *Possible upper surface of mantle flap*: Pl. 40, fig. 4 'm'. *Lower surface of mantle flap*: Pl. 40, 1 'm'. *Association of upper and lower surfaces*: Pl. 40, fig. 3.



TEXT-FIG. 3. *Porpita porpita* Linné, transverse section of a young specimen, after Mackie (1959).

of the annulate disc. Necessarily, this is the opposite side from the smooth, centrally domed side.

At the centre whorls of inwardly tapering strips cease against the base of a central mound. This mound can appear as a truncated cone (one specimen) or, because of eccentric wrinkling, as a rather flattened cone. It is always single. Pl. 40, fig. 1, shows

EXPLANATION OF PLATE 40

Figs. 1–6. *Eoporpita medusa* gen. et. sp. nov., 1–3, 6 × 1; 4, 5 × 0·5. 1, T27; 2019, holotype, oral surface; 'm' possible mantle flap; 1–3, tentacles of outer series (dactylozoids), 4–8, tentacles of inner series (gonozooids) and 9, incipient tentacles, surround a flattened centre. 2, F17453, paratype, float showing narrow annular chambers traversed by radial furrows which are irregular in position, length, and definition and thus do not appear to result from sulci. 3, F17454, paratype, aboral side, composite mould showing tentacles near four-fifths of margin. 4, P14283, paratype, aboral side showing central mound and faint, radial striae. 5, F17455, paratype, oral surface showing seven inner whorls of tentacles and (at edge) six outer whorls, gonozoids and dactylozooids respectively. 6, P14286, paratype, aboral side, composite mould showing central mound, faint radial striae, and impressions of annular chambers.

(at 'm') a relatively smooth area, depositionally above the radiating strips, marked off from the general rock surface by a shallow furrow.

5. One specimen (Pl. 40, fig. 3), which appears to be partly equivalent to (1), and partly radiating strips which form a surface uniquely smooth for the strips. They are crossed (upper left side) by faint, equidistant annulations. This is a positive composite mould of upper and lower surfaces with some hint of an annulate disc between them.

The smooth, centrally domed side had no hiding place for unobserved openings and is thus aboral; from the fact that it was also a much thinner covering to the float than the 'whorls of strips' and conical centre, it was presumably the upper side in life. In compiling text-fig. 2, the structures observed are placed in order of superposition with the aboral surface at the top. This diagrammatic cross-section indicates what is actually seen rather than representing a restoration for (apart from the fact that the overall shape was lenticular) vertical control is lacking and there has been no attempt to restore original shape. This was done with the model in Pl. 41, figs. 6a, b. The only 'restoration' in the diagram is the scaling of all structures to the same body size and the joining of the annulate structures mentioned under preservations (2), (3) and (5) as one, annular-chambered float. This structure must have been very lightly sclerotized as it was more prone to collapse under load than to form external moulds. Only its outer portion supported sediment (preservation 2) in two specimens: the inner portion gave way completely in these same specimens and allowed the centre of the specimen to be cast. In two other specimens the whole depositionally upper surface gave way while the lower surface still remained intact (preservation 3) and complete casts of the depositionally lower surface resulted. At least one of these casts is of the side with whorls of strips, the lower side in life. Some of these strips have been separated from neighbours and reveal other strips in the gap between them, while neither side of the gap has lost the strip shape (Pl. 40, fig. 1). This suggests that the strips had individual walls and were tentacle-like, like the internal mould figured as a possible *Cyclomedusa* (Pl. 41, fig. 2–'*a*'). On the other hand there is the tendency for the strips to merge into sheets or whorls of sand. Such a tendency would arise from very slight compaction during diagensis, if whorls of sand-casts overlay each other, but it is also possible that dragging of the body on the sea-floor caused sand to be caught between whorls of tentacles, and that the strips arise from external moulds of almost flattened tentacles. Whichever explanation of preservation is considered, only whorls of tentacles seem adequate to explain the behaviour of the numerous 'strips'; up to 6 whorls are known in the outer series, while the inwardly-diminishing series had 6 or 7 more whorls. The whole layout is so like that of a porpitid chondrophore (text-fig. 3) that subjectively deciding to coin new terms to describe it 'objectively' seems unreasonable.

P14289 is the second specimen referred to in preservation (1), it has a relatively broad 'central dome' which is slightly depressed in its centre; this fragment is only questionably assigned to *Eoporpita* and not used in compiling the description.

Diagnosis. A circular or elliptical chondrophore with radial symmetry. Two series of club-shaped 'tentacles' form several outer whorls (dactylozooids) of near constant length, and several inner whorls (gonozooids) of inwardly reducing size, encircling a single, large central cone (gastrozooid). Aboral surface smooth except for very fine radial striae; with a small, low, central dome. Float delicate, with numerous narrow, annular chambers enclosing a small, circular, central chamber. Some radial creases reach from near centre to margin.

Description. The average radius ranges from approximately 2 to over 8 cm. That of the smaller float (Pl. 40, fig. 2) is about 2·5 cm and of the larger roughly 4·5 to 5 cm (the largest radius, probably about 6 cm., is obscured by a positive mould of some tentacles.)

The holotype (Pl. 40, fig. 1) shows the supposed tentacles most clearly. The central area is not very distinct but has overlapping 'concentric' folds, the outermost two of these are slightly corrugated (whorls 9 and 8) and (at maximum preserved radius) the distance from centre, across the corrugated folds or incipient tentacles to the base of the first well developed tentacles (whorl 7) is 1·6 cm. From here to 3·7 cm the whole span of five whorls of tentacles, each whorl larger than the one before, is crossed. Roughly the same number of tentacles is present in equal sectors of each whorl. From 3·7 to 7 cm no further edges of whorls are observed though chipping shows that at least three whorls of tentacles are superposed at the outer edge. The thickness of the fossil suggests more than 3 layers here. The centre of the paratype in Pl. 40, fig. 5 is not clear but at least seven whorls of tentacles are involved in the elongating series of tentacles and at least six whorls overlap at the outer edge. No differences except in relative length could be observed between the inner series of tentacles and the outer series. In both, the tentacles appear to have been club-shaped. Two or three other specimens also hint at this sort of tentacle-distribution. The largest, P 12753, has the best preserved centre. A small, truncated, inverted cone projects from among the inner tentacles. This has a fine, X-shaped furrow on its truncated end. The structure appears to be due to tiny creases radiating from the centre. In this specimen well-developed tentacles approach closer to the central cone than in the holotype and they may have approached as closely in several of the specimens damaged predepositionally. Plate 40, fig. 3 shows a positive composite mould. It has a tilted, low, truncated mound of radius 7–8 mm at the centre, with two arcuate ridges on the more depressed side. Around four-fifths of the circumference rows of tentacles show in convex relief. A sharp crease separates them from the remainder of the disc. It extends from the margin, encircles the centre but not at a regular distance from it, and returns to the margin. The surface within this line is smooth except for the centre and except for extremely fine radial striae all over it. This specimen was buried to a maximum depth of 9 mm and the margin seen at the upper right side of Pl. 40, fig. 3 is very smooth where it was most deeply impressed in the enclosing sediment; in fact, it is everywhere smoother than any other specimen. The remaining two aboral composite moulds are fragmental and show no margins. The larger fragment consists of a central dome 1·2 cm in radius and one quarter of the disc. About nine annuli show intermittently between 1·2 and 5 cm and remnants are seen on the poorly-preserved surface further out. The edge is vague but the complete radius was probably about 10 cm. Faint radial striae occur in small patches. The smaller fragment (Pl. 40, fig. 6) is of little more than the central disc and parts of three annuli a short distance outside it. These are clearly defined by narrow grooves between flat surfaces. The fragmental cast of the aboral surface (Pl. 40, fig. 4) is just over 8 cm at its greatest preserved radius. The centre is occupied by a low, rather flattened mound with a radius of just over 1 cm. The surface is partly smooth but mainly covered by numerous fine to very fine radiating striae. These can be traced across the main expanse of the disc and up the gentler slopes of the dome to its top (which is broken at the centre). As far as can be seen, striae are multiplied by the interpolation of extra furrows radially outward, and maintain a fairly constant spacing. A sharp groove (under 2 cm long, and at a slight angle to the striae) runs up the less steep side of the dome and disappears before the centre. It has no equivalent in the three composite moulds and is presumably accidental. A concentric groove (at bottom) may indicate the edge of the float.

The smaller float (Pl. 40, fig. 2) consists of a circular innermost chamber (2 mm in diameter) with at least 12 annular chambers (probably several more) around it. The centre of the innermost chamber is marked by a pinpoint depression. The float is dented at one side and asymmetric but there is no observable narrowing of individual, undistorted chambers as the shorter radius is approached: the shortening is possibly due to the denting. The larger specimen is also asymmetric but this has some of the soft parts preserved, overlapping the more elongate radius and projecting beyond its possible boundary. This elongation is also suspect but there is a possibility that the natural shape is elliptical, with the centre approximately at one pole of the ellipse. A third, almost round, float is now known.

Restoration. The smooth, very finely striate surfaces of the four aboral (or partly aboral) specimens are taken as representing the fleshy surface layer on the aboral side of the float. The central, truncate mound is a naturally domed centre slightly flatter than that of the preserved *Porpita* figured by Hyman (1940, fig. 154D). The striae appear to show more coarsely with compression. They can be equated to coenosarc between aboral, radiating, gastrodermal canals, which are very regular in young *Porpita porpita* Linné. The smoothness of the margin in the one composite mould which shows it, is attributed to the coenosarcal disc-edge or mantle flap, folding over the outer ends of the tentacles. The impressions of tentacles near four-fifths of its outer edge would thus be due to composite moulding. The restoration of the oral surface is also securely based on numerous specimens. For simplicity Pl. 41, fig. 6 has been restored as an adult considerably smaller than the holotype. It has only three whorls of 47 tentacles in the outer series and three well-developed and two incipient whorls in the inner series. In view of the similarity of arrangement to the Recent chondrophores, it seems reasonable to consider the outer series dactylozooids, the inner series gonozooids, and the larger central cone the gastrozooid.

Remarks. The endoderm cells of the tentacles are vacuolated in *Porpita* and form a resilient 'skeleton' that returns them to the 'resting' position seen in text-fig. 3, whenever muscular control is relaxed (Mackie 1959). As musclature is virtually all radial ('longitudinal'), movement is almost entirely in the vertical plane. It is interesting to note that there is remarkably little crossing-over of tentacles in *Eoporpita*, even though those of the outer series are long. Fossil chondrophores showing 'tentacles' are rare. The only form attributed to the Porpitidae is *Paropsonema* Clarke (Silurian to Devonian) but this form has apparently branched tentacles (Ruedemann, 1916; Chapman, 1926; Harrington and Moore, 1956). The vellelid *Palaeonectris discoidea* Rauff (1939) has dactylozooids of the simple, tapering broad-tipped form seen in *E. medusa*. One of Rauff's three specimens has a thick ridge across the body which has been interpreted as a sail and is the reason for the placement of this Lower Devonian form in the Vellelidae. Another specimen appears to be viewed from the dorsal side with the coenosarcal disc-edge folded upwards and inward, so that the inner edge of a hollow oval is formed of the mantle flap, showing concentric furrows due to muscular contraction, and the dactylozooids are attached to the body outside the mantle flap. It would be interesting to have this specimen X-rayed to find if the remainder of the body is still within the rock below the apparent 'hole' in the centre. The third specimen shows branched structures interpreted as gonozooids.

The structure of the float in *Eoporpita* is strongly annular and bears no close resemblance to that in the Ediacaran bilateral chondrophores *Ovatoscutum concentricum* Glaessner and Wade and *Chondroplon bilobatum* (Wade 1971), which were resistant enough to form external moulds. The chamber sutures are much less sharply defined in most specimens of *Eoporpita* and this tends to substantiate the much softer material of the float suggested by the usual preservation as casts. The aboral views show the fleshy surface more than the floats. As the centres are quite clear it is certain that there was no sail or elongate crest but only a low, round mound in this region. The coarsest of the radial striae (explicable as due to relatively fine dorsal gastrodermal canals above) are as coarse as those of *Cyclomedusa plana* Glaessner and Wade or *C. gigantea* Sprigg (1949); see also Harrington and Moore, 1956, fig. 122). In the centre of *C. plana* small, concentric furrows and ridges indicate no broad, low, central dome but a conical peak, which may be twinned (Glaessner and Wade, 1966, pl. 98, figs. 1–3). In *C. gigantea* the centre is preserved as a broad, low dome though it could have been conical before flattening as ring markings are not concentric, the mid- and out-fields of the disc being strongly corrugated concentrically. Though *Palaeoscia floweri* Caster (1942) is equally corrugated it is probably not a chondrophore (Osgood, 1970, p. 395–397). Though it is possible *C. gigantea* is a chondrophore there is no proof, and its strongly corrugated disc offers a substantial reason for regarding it as distinct from *E. medusa*, for it was either initially corrugated or much more convex than the aboral side of *E. medusa*.

The shape of the float is a critical consideration in classifying chondrophores. *E. medusa* appears to have had narrow, circular chambers with a few radial creases and no definite bilateral symmetry. Not only does it differ from the other Ediacaran chondrophores, but it is morphologically closer to the Recent *Porpita* than to Palaeozoic Porpitidae (Harrington and Moore, 1956). While it may seem unlikely that the same family could be present for over 600 m.y., only two positive characteristics distinguish *Eoporpita* from modern Porpitidae: (i) the tentacles or dactylozooids are invariably simple and club-shaped; shorter sizes have not been observed but this is to be expected for the growth of *Porpita* adds the younger whorls outside the older whorls (text-fig. 3, after Mackie 1959, fig. 1D; Delsman 1922), (ii) Mackie showed that the whorls of gonozooids are also added to by outward growth in *Porpita* whereas the inner whorls of the inner series of tentacles are the smaller ones in *Eoporpita*. The inner series is also club-shaped except where very small (Pl. 40, fig. 1 (4–9), 8 and 9 are incipient). No medusa-buds have been seen but these could have been lost or failed to be preserved. Whether the concensus of views ultimately places *Eoporpita* in the Porpitidae or not, it provides evidence of a long history of little change in the Chondrophorida which are much more conservative than the Scyphozoa. Indeed, Garstang (1946) and Mackie (1959) have shown how the modern members of this family can be compared to Recent Tubulariidae, *Corymorpha* in particular. The parallel is perhaps overstressed in view of the great time gap between *Corymorpha* and the earliest known chondrophores, and the complete lack of reduction of stem in *Corymorpha*, which belongs to a group characterized by oral tentacles, unlike the chondrophores.

Class HYDROZOA?

Genus CYCLOMEDUSA Sprigg 1947

Plate 41, figs. 1–5; plate 42, figs. 1, 2; text-fig. 4

Type species. Cyclomedusa davidi Sprigg 1947.

A synonymy to the genus was given by Glaessner and Wade (1966). *C. plana* Glaessner and Wade is now known from the Ukraine and is thus the most widely distributed medusoid of the Ediacara fauna (Zaika-Novatskii *et al.* 1968; Glaessner 1971). Wade (1968, figs. 14, 15) figured specimens showing the flexibility of *C.* cf. *davidi*. After re-examining all the *Cyclomedusa* specimens in the South Australian Museum and the University of Adelaide in the course of this work, I now accept these forms as *C. davidi*.

Material and occurrence. C. davidi is the commonest known. All species are known from Ediacara, *C. radiata* and *C. davidi* from Brachina Gorge and only *C. davidi* from Red Range.

Preservation. On the bases of rock slabs; specimens always have some convex relief even in the flattest species, *C. radiata*. It is thought that all specimens showing radial structures are positive composite moulds of exumbrellar and internal structures; some specimens are smooth except for concentric rugosities and these are casts of flattened exumbrellar sides (Pl. 41, fig. 1). Only Pl. 41, fig. 2 (right side—*a*) may represent *Cyclomedusa* in subumbrellar view as an internal mould.

Remarks on described species. C. davidi is usually concentrically rugose, as originally described. The central structure is very like that of *C. radiata* (below) but usually smaller and often more prominent. Its radial furrows are very variably developed; as far as can be seen they never extend right to the central peak but may cross the entire body from the second ring furrow outside the central peak to the margin. No regularity in the addition of furrows has been observed but if well expressed, they tend to maintain

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EXPLANATION OF PLATE 41

Figs. 1, 2 (left side—*b*), 3–5. *Cyclomedusa davidi* Sprigg, ×1. Flattened casts of aboral sides. 1, P12775, 2, *b*, F16720B. Composite moulds showing zones or patches of radial furrows, fig. 4 (right) apparently where compressed; 3, T5, holotype; 4, P14176; 5, F17456.

Fig. 2 (right side—*a*). Oral surface, possibly *Cyclomedusa davidi*, ×1; *m*, mantle flap, *t*, tentacles and bases of tentacles, *g*, gastrozooid.

Fig. 6, a, b. *Eoporpita medusa* gen. et sp. nov., plasticene model of small adult, approximately ×1, viewed, respectively, from oral surface and, slightly obliquely from the side.

a relatively constant spacing except on the outer ring or rings where new furrows are rarely inserted. These are interpolated between older furrows in forming the radial structure. On other specimens furrows may be few or none (Pl. 41, figs. 1, 2 (left side), 4, 5). Fig. 4 shows a specimen with a patch where they occur quite close-spaced, though generally absent. Such patches may appear to have been at a lower level than the smooth surface of the body, e.g. on the holotype of *Spriggia annulata* and Pl. 41, fig. 4. Furrows may be localized in zones as in Pl. 41, fig. 5 and the holotype of *C. davidi* (Pl. 41, fig. 3) where an inner annular zone shows more closely spaced radial furrows than are found in its outer zone.

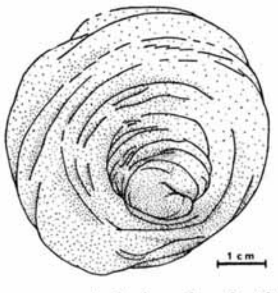
C. radiata contains several large specimens of which the best preserved is that shown in Pl. 42, fig. 1, an oval specimen of maximum radius just over 7 cm and minimum a little under 6 cm. The best preserved centre is still that of the paratype illustrated by Sprigg (1949, pl. 14, fig. 3) (refigured here Pl. 42, fig. 2). It has an oval, central, flat dome measuring 8·3 by 4·6 mm; this is surrounded by a deep, sharp furrow, marking the inner edge of a broad ridge. Its inner edge carries a slight ridge, and a fainter, slightly excentric furrow. The broad ridge is delimited on the outside by another sharp furrow and a narrow, rather smooth, zone. Radial furrows traverse the broad ridge in one place, and most of its outer margin is notched by the inner ends of the radial furrows which run to the margin of the fossil. Increase of furrows is by interpolation. They mostly commence outside the narrow, smooth zone. This specimen has been refigured and described in detail because its appearance seems to clearly represent the structure less well-preserved specimens appear to have had. The holotype (T23; 2037) deviates from this plan only in having a faint furrow nearer the outside than the inside of the broad ridge, in both specimens this faint furrow is probably due to flattening; several furrows are developed in some other specimens. Concentric folds can also be developed on the outer disc (Pl. 42, fig. 1). Some developing near the margin of the holotype and a paratype were interpreted as 'an epimarginal groove or (?) ring canal' (Sprigg 1949; refigured Harrington and Moore, 1956, fig. 60 (4, 5)).

C. gigantea has only one preserved radius, 6·7 cm. In general shape the centre is an oval platform about 20 by 22 mm radius, surrounded by a deep, wide, annular sulcus, and a concentrically ridged outer region. Radial striae show clearly in part of a zone from about 3·5 to 4·5 cm from the centre but can be traced more faintly to the margin and very faintly, almost to the centre of the bell. The centre of the bell is a flat oval 10 by 8 mm; not concentric with this is a circular, partly double ridged, furrow 31 to 32 mm across which is not concentric with the edge of the central platform either. There is no way of deciding how much elevation has been lost by flattening against the substrate, one side of the platform has a gently rounded surface but much is almost totally flat. No specimen duplicates the appearance of the holotype. *In toto*, its affinities are close to *C. davidi* with which it may be conspecific, as its radial striae are of similar dimensions at their coarsest.

Cyclomedusa plana Glaessner and Wade is the only *Cyclomedusa* in which specimens with two centres exist without a furrow that *completely* traverses the bell from one side to the other passing between the centres (Glaessner and Wade 1966, pl. 98, fig. 3). Thus it is the only species of *Cyclomedusa* in which twinning appears a genuine possibility. Although a furrow has to completely divide two present-day medusae before they separate, it seems unlikely that medusae dying at such a moment would stay together and be deposited and fossilized together. *Cyclomedusa* must have been very supple (Wade 1968, figs. 14, 15) and any specimens with complete furrows between two centres could be two individuals juxtaposed in death. This must be suspected when, as in the *C. davidi* figured by Sprigg (1949, pl. 14, fig. 4, or text-fig. 8F), the centres are separated from the furrow by notably different distances, and the curvature of the concentric furrows suggests two complete bells with their adjacent free edges folded away from each other. The smaller specimen of these also bears a near-radial fortuitous crease which displaces structures that can still be matched across it, as tears in Recent medusae often do.

Remarks on Cyclomedusa. The commonest medusoids in the whole fauna are those collectively referred to as '*Cyclomedusa*'. They share the characteristics of a circular marginal outline and several to many near-concentric rugae which indicate, by their excentricity, a generally conical shape for the centre or even most of the body. Many but not all of these have radial structures of varying degrees of coarseness. *Eoporpita* was initially thought to belong in this plexus but was removed to the Chondrophora on the discovery of its float.

There remains one other specimen, F16720A (Pl. 41, fig. 2 right side) giving evidence of 'tentacles' generally similar to those of *Eoporpita*. The specimen (as deposited) partly overlies a *Cyclomedusa* of the *C. davidi* kind (left side). Due partly to breakage and partly to compression against the *Cyclomedusa*, only about one third of the body is seen; it is generally flat, including the central region, though this is commonly high in *Eoporpita*. Its 'tentacles' are represented by a few, individual cones of sand regarded as fillings of rounded tubules. These occur in the mid-field of the disc, and the outlines of several more show toward the outside edge with the disc marginal zone 'm' exposed bare and smooth on each side of them. This marginal zone is apparently a mantle flap; in natural section at the rock edge it is seen to extend inward, depositionally above the mid-field tentacles. All the inner tentacles have been infilled, as is shown by their individual, rounded bases, and fairly recently broken off during weathering, as differential staining shows. Only a few, doubled-over tentacles remain between the *Cyclomedusa*, the centre of F16720A and the broken edge. The many freshly-truncated, round bases are roughly arranged in concentric whorls around a larger, truncate, conical, central 'zooid'. The specimen is thus the internal mould of a chondrophore-like animal. The mould is flatter, and its tentacles are less regularly placed than would be expected of an internal mould of *Eoporpita* (to judge from examination of the centre of its holotype). The alternative explanation is that the specimen may represent the oral surface of a *Cyclomedusa* similar to the adjacent specimen of an exumbrellar side. These two specimens are so alike in proportions that it was at first thought that they were twinned, but on closer examination it is certain that one shows the subumbrellar and the other the exumbrellar side. They are not just different levels in bodies with similar orientation because the base of most and the full length of some of the tentacles is exposed. The central cones are respectively the gastrozooid of the right side '*a*' and the aboral conical centre of the left side '*b*'.



TEXT-FIG. 4. *Cyclomedusa davidi* Sprigg. Tracing from photograph of a moderate-sized specimen which appears to have been steeply conical throughout. The apex was weathered and rather indistinct.

The outer edge of *Cyclomedusa* spp. is normally much more distorted than the remainder of the bodies (Wade 1968, fig. 14); the flexibility increases gradually and did not coincide with the development of 'concentric' rugae, as if rugae coincided with a change in structure like the difference between disc and outer ring in *Ediacaria* or *Brachina*. Rather, the flexibility lessens gradually toward the more elevated centre but text-fig. 4 shows that the whole bell may be compressed obliquely. One group of '*Cyclomedusa*', however, is not high in the centre but lower than the edge zone of the body. This is seen on many of 49 specimens on one bedding plane from Brachina Gorge, and several Ediacara specimens. The central two-thirds tends to hold a circular outline even when the edge zone is folded over it (two specimens). This evidence of an unusually resilient, though flattened, centre may also be evidence of a (collapsed) float in this group. The majority of once conical and wholly flexible forms, however, can scarcely be envisaged as possessing a float. Both dorsal and ventral gastrodermal canals of porpitid chondrophores are remarkably strongly radial, as prepared specimens show. Similarly regular canals may cause the ridges and furrows of *Cyclomedusa*, which may run from near their centres to their margins or be patchily distributed, or not occur at all, as though structures naturally at depth in the bodies are represented.

Reconstruction of *Cyclomedusa* is not possible while the oral surface remains unknown. Its conical, rugose, flexible body indicates that it did not swim like a medusa, with the muscles reacting against a mesogloeal 'skeleton'. On the contrary, the rugae suggest radial contractility, and it makes sense as a contractile animal only if attached in life by the apex which is truncate in all specimens where it can be observed (see Pl. 41, figs. 1–5; Pl. 42, fig. 2; Wade 1968, fig. 15). Thus the probability is that like the *Aurelia* scyphistoma, *Stephanoscyphus* and *Conularia* described by Chapman (1966) *Cyclomedusa* developed (or retained, in a phyletic sense) chitin at the point of attachment. A broad, low conical form with a marginal zone of coenosarc continuous in structure with the aboral wall, with a strongly radial structure comparable to gastrodermal canals and similarly at depth in the body, and probably secreting chitin at its apex, seems to have more adaptations leading toward chondrophores (and particularly porpitid chondrophores) than any better known form. Until the oral surface of *Cyclomedusa* is definitely known, however, it will not be known whether it was allied to the chondrophores or merely a convergence. The larval stages of Recent chondrophores are so strongly modified as vehicles for the developing pneumatophore that their development does not cast light on their immediate ancestry (see Delsman, 1922; LeLoup, 1929) despite the similarities to Tubulariidae emphasized by Mackie (1959).

The aboral truncate cone of *C. plana* is only a small portion of the whole animal, and the greater portion lacks the rugae that suggest contractility in the other species of *Cyclomedusa*. Taken together, these characters suggest that this species was not attached in adult life. Presumably swimming with the aid of the disc-edge (or mantle flap) was a possibility, or its near-flat shape may have enabled it to lie free on the sea floor as some modern medusae do. These two modes are not mutually exclusive.

While it is possible to speculate that *Cyclomedusa* was a persistent ancestral type of the Chondrophora, a functional intermediate between normal, attached Hydrozoa and the pelagic forms with a float, it is necessary to remember that hydrozoan affinities for *Cyclomedusa* are not yet proved. Knowledge of this 'genus' is in such a primitive state that for the present suitable specimens can only be placed in the morphotypic species already described and, although these groups are reasonably clear, many *Cyclomedusa* remain outside them. Many of these are poorly preserved and may never be placed.

Class SCYPHOZOA
Order undescribed
Genus BRACHINA nov.

Type species. Brachina delicata sp. nov.

Diagnosis. As for type species.

Brachina delicata sp. nov.

Plate 42, figs. 3–5, text-figs. 5a–c

Madigania annulata Sprigg (part), 1949, pl. 17, figs. 1, 2, possibly pl. 16, fig. 2.
Ediacaria flindersi Sprigg. Glaessner and Wade (part), 1966, p. 602.

Material and occurrence. Six, possibly seven, large specimens and possibly one small specimen from Ediacara Range, two specimens from Brachina Gorge, South Australia.

Holotype. F17343 (Pl. 42, fig. 3) from Brachina Gorge.

Preservation. The holotype is a fragment of maximum width 3 cm, maximum length 5·3 cm. The natural edge is somewhat crumpled but consists of small marginal lappets attached to a narrow, smooth band. Lappets and band are very faintly imprinted in the rock and form an external mould. The remainder of the fossil is preserved in convex relief and appears to be the mould of internal spaces in the original animal. To be, instead, the cast of the external (subumbrellar) surface, it would have had to be relatively deeply buried in the sediment. The adherent depositionally underlying matrix is a finely-laminated siltstone which was irregular enough to have caused distortion in the fossil of an elevation several times greater than the thickness of a lamina. The fossil clearly was not deeply buried in this siltstone as it did not penetrate even one lamina. Its margins were not buried at all in the siltstone as they formed an external mould in the overlying sand layer. The fossil as a whole is thus a composite mould (Wade, 1969; McAlester, 1962) dominated by the internal mould. The second specimen from Brachina Gorge is also dominated by the internal mould. Although this is a larger specimen it is very badly distorted by a contemporaneous lineation which penetrates the whole rock, and also weathered.

The specimens from Ediacara Range are all dominantly casts of the exumbrellar sides but most show some degree of impression of the mouth-funnel through the disc, and less definite indications of other structures. These are positive composite moulds dominated by the exumbrella, in specimen T16; 2025 dominance is less than in the other three. Specimen T9 (Sprigg 1949, pl. 17, fig. 2; this paper Pl. 42, fig. 5) is partly divided in two by a wedge of coarse sand and appears to show the centre of the stomach from the inside, folded depositionally upward at a steep angle to the cast of its external surface. The two surfaces merge on the lower bedding plane and the disc is thus largely a composite mould. (A second specimen '*b*' which impinges on this individual is very badly preserved, it shows only the margin of the disc and the inside-top of the mouth-funnel.) Specimen T14 (Sprigg 1949, Pl. 16, fig. 2) shows more complete composite moulding of the disc than any other individual discussed here, but is so badly preserved in other respects that it is not really generically identifiable.

EXPLANATION OF PLATE 42

Figs. 1, 2. *Cyclomedusa radiata* Sprigg, F16729, ×0·5, largest specimen known. 2, T21; 2032, paratype, ×1·3, small well-preserved specimen figured by Sprigg 1949, pl. 14, fig. 3.

Figs. 3–5 *Brachina delicata* gen. et sp. nov. All positive composite moulds. 3, F17343, holotype, from Brachina Gorge, ×1·5, mainly internal mould (numbers 1–6, see text). 4, F17457, paratype from Ediacara, ×0·5, mainly exumbrellar cast, markers indicate portion of margin shown as 4*b*, ×1·3, detail of marginal lappets. The inner edge of the annulus possibly shows mid-way across the outer ring and possibly both its edges can be seen near the markers. Within the ridge and double furrows of the disc margin the furrow attributed to the stomach '*s*' is not concentric with the ridge '*r*' attributed to surface 'ornamentation'. 5, T9, paratype from Ediacara, ×0·6, oblique view; the annulus occurs midway across the outer ring and disc markings resemble 4a except in the central region where a wedge of sand '*w*' separates the exumbrella from a portion curved depositionally upward through 90°. This shows the inside view of the mouth funnel. The three fragments '*b*' appear to be portions of a second specimen.

Diagnosis. A moderately large, discoid medusa with numerous, small, spatulate lappets attached to a broad outer ring of width about equal to the radius of the disc it encloses. On the exumbrella the outer ring joins the disc margin in a groove from which a rounded ridge arises abruptly. This is followed by a second groove which has a rounded bottom. Another rounded groove occurs about one third of the distance across the disc (this may represent the stomach margin). A sharp elevation of the surface occurs nearer the centre of the disc. The centre was occupied by a slight peak (except where compressed against the mouthparts). On the subumbrella the manubrium was small and conical. Radial passages (gastrovascular canals) within the subumbrellar wall reach almost to the outer edge of the outer ring and appear to have ended blindly. They increase in number outwardly by occasional dichotomous branching and anastomose inwardly forming a wide ring complex around the stomach. A large, pouched annulus occurs about midwidth of the outer ring on the subumbrellar side of the radial passages (it appears to have been an annular gonad within the subumbrellar wall).

Description. The structures of the holotype may be described as six zones occupying concentric arcs. From the natural edge inward these zones 1–6 are numbered in Pl. 42, fig. 3.

1. A line of small, spatulate impressions about 2 mm long and wide. Indications of these *marginal lappets* are seen at several places but they are complete only where numbered at the left side of the photograph.
2. A narrow, smooth zone just within the lappets. This *sub-peripheral band* was at least 1 mm wide.
3. The first zone of convex relief is about 8 mm wide and consists of radially arranged ridges and depressions, 10–11 pairs/cm. The ridges present blunt, roundish ends to zone 2 and become gradually less distinct toward zone 4 which cuts them off at right angles.
4. This is a raised *annulus* 1 cm across which shows occasional, shallow, dimpled depressions as if rather compressed. Its inner curve is smooth while its outer curve is cut by irregularly spaced, short, deep depressions which appear to have divided it into shallow *pouches*, unconstricted on their inner sides. The outer edge is more elevated above its surroundings than the inner.
5. This is again a zone of radial ridges and depressions; the ridges about the same size as in zone 3 but more closely packed. The ridges sometimes fuse inwardly.
6. Zone 5 grades irregularly into 6 by the breaking up of the radial depressions into pits and the anastomosing of the ridges which gradually lose their radial alignment and form a *ring complex* with a uniform, pitted surface.

The second internal mould (from Brachina Gorge) clearly shows the junction of zones 5 and 6. Most of the surface is covered by zone 6 but a furrow, which distorts the whole thickness of the rock slab, and erosion have the effect of obscuring any central structures which might have been present. There is a hint of the annulus, zone 4, and slight indications of zone 3 and, in one spot, zone 1. The specimen confirms the supposition that zone 6 is relatively wide.

Two of the four better-preserved positive composite moulds have small, spatulate marginal lappets. These are closely similar individuals about 9 cm in radius. The larger piece (Pl. 42, fig. 4a, b) has part of its margin folded over towards the subumbrella but elsewhere has 12 or 13 lappets in 5·5 cm. Most are about 4 mm long and a little wider than long. One is slightly smaller and more tapered than most, and supported by a very small, elongate lobe at either side (Pl. 42, fig. 4b). This structure is unique but the present material is not adequate to show occasional repetition. The structure may be fortuitous but may be sensory. The other, smaller piece, has a rather battered margin but its spatulate lappets are longer than wide at its maximum radius (10 cm) and a little shorter than wide in at least one of the places, on either side of the maximum, where the margin forms an arc of radius just under 9 cm.

The largest specimen is T9 (Sprigg 1949, pl. 17, fig. 2; this paper, Pl. 42, fig. 5). This is over 11 cm in radius from its mouth to the base of the lappets (if a slight crenulation of the margin is taken as evidence of these). Its margin is inturned and no lappets are seen. The fourth specimen (T16; 2025, Sprigg, 1949, pl. 17, fig. 1) is broken off short of its margin at maximum radius 10·6 cm. All four specimens have a relatively flat *outer ring* ranging from 4 to at least 5·7 cm broad; on all except T16; 2025, this is ridged by very fine, discontinuous, concentric striae. In T9 and 379 these fine striae are interrupted across an annulus about 1·5 cm across. A similar structure exists on T16; 2025 where its outer edge appears to be broadly lobate; as it is clearer here, where there are no surface striae, it presumably represents a subsurface structure. Its presence on F17457 (Pl. 42, fig. 4a) is disputable; a faint, broad ridge is present in places, but does not interrupt the concentric striae. This annulus lies parallel to the edges of the outer ring at about the middle of its subumbrellar side in two specimens; and a little closer to the disc in the third specimen. The ring is of about the same width as the disc-radius or a little greater. It is thus possible to estimate the radius of the holotype fragment as 5–6 cm. An attempt to restore the size of the original by projecting the radial structures was not very satisfactory but suggested a circular body with radius 5–8 cm. The central structures of the original body are thus not observable on the fragmental internal mould of maximum radial width 3 cm. Erosion and the pleating of the thin rock-lamina have removed evidence of the central structures of the second internal mould.

The margin of the disc is the most prominent feature of the exumbrella. The outer ring meets the disc in a groove (which is probably accentuated by flattening) and the disc edge rises sharply from the groove and forms a rounded ridge closely followed by a rounded groove which is often more distinct than that where disc and outer ring meet. The striae may continue on to the edge of the disc but the discs have more strongly marked concentric 'ornamentation' with considerable individual variation (see Table 1). On four specimens two concentric elements are present, a shallow, rounded groove about one third of the distance in from the margin, and a sharp elevation nearer the centre. The centre is expressed in a variety of ways: in T9 (pl. 42, fig. 5) it is likely to be viewed from inside (above). It consists of a narrow, annular furrow enclosing a rounded ridge which folds down into a shallow, central pit, irregularly closed at the base. Contrasting Pl. 42, fig. 4a with fig. 5, the central depression is more arcuate, as if a slight mound occupied the side and centre of a pit. In T16; 2025 a depressed area is filled with coarse, arkosic sand which is in remarkable contrast to its fine-grained surround, but similar to the layer of sand depositionally just above the surface of the fossil. 379 is broken across its centre; it shows no evidence of a depression but only a slight mound, which appears to have been central.

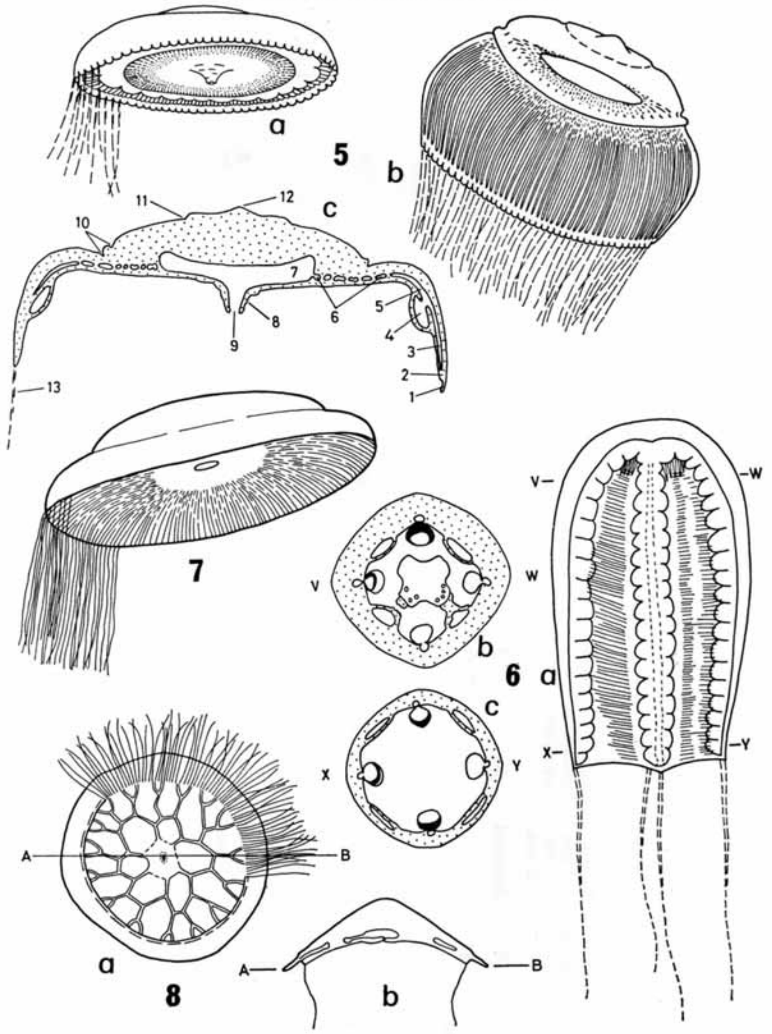
A comparison of all seven specimens is given in Table 1.

Restoration. The characters in common between the largely internal composite moulds and the exumbrellar-dominated composite moulds are principally the small, spatulate lappets attached to an otherwise entire outer ring, and the broad annulus, pouched on its outer side, placed about midway across the outer ring, and towards the subumbrellar side. These characters define a group which is isolated from all other medusae so it is reasonable to combine both preservations in the one restoration. Text-fig. 5a–c is based on all 7 specimens, with the zones 1–6 numbered in the restored section 5c as in Pl. 42, fig. 3.

They are interpreted as: (1) a ring of small, *marginal lappets*, (2) the edge of the *outer ring*, (3) the internal moulds of *radial passages* which are traversed on the subumbrellar side by (4) a broad, inflated *annulus* with large *pouches* on its outer side, and re-emerge as (5) the internal moulds of radial passages sometimes showing fusion in an inward direction or *dichotomous branching* in an outward direction. These passages can be traced into (6) a *ring complex* of anastomosing spaces which, in its outer parts, shows remnant dichotomous branching. This ring complex presumably encloses (7) the stomach which is restored as if its outer edge is responsible (upon compression) for the shallow groove one third of the way across the disc. The small, conical manubrium (8) is most reliably shown by T9 (Pl. 42. fig. 5) but is also shown by the very incomplete specimen that abuts it. The concentric rings around it are sometimes crossed by short radial markings interpreted as due to the musculature for operating it and (9) the mouth. The disc margin (10) is interpreted as a ridge separating a double groove in life as in the

TABLE 1. Comparison of all known specimens of *Brachina delicata* gen. et sp. nov.

Specimen No.	*Preservation composite mould*	*Amount of animal*	*Lappets*	*Radial Structures*	*Annulus*	*Outer ring*	*Disc margin*	*Disc markings*	*Centre*	*Radius*
F 17343 (holotype)	Dominantly internal mould	⅕ outer portion	Length 2 mm., width 2 mm.	Ridges, anastomosing ridges	Pouched	Mostly hidden	—	—	—	5–6 cm.
1279	do.	?	Distorted	do.	?	—	—	—	—	—
T9 and adjacent fragment '*b*'	Dominantly exumbrellar external mould but subumbrellar internal mould at centre	⅗	—	—	Present	With striae	Typical: adjacent spec. also typical	Typical, few extra corrugations	Pit with raised ring surround; adjacent spec. similar, but more flattened	11–12 cm.
379	Dominantly exumbrellar external mould	¼	Width 4–5 mm.	—	?Pouched	With striae	Typical	Extra incomplete rings, striae at outer edge	?Slight mound	Just under 9 cm.
F17457	Dominantly exumbrellar external mould	Most of disc, ⅓ of outer ring	Length 4 mm. Width just over 4 mm.	—	?	With striae	Typical	Extra incomplete rings, striae in outer third	Slight peak at side of partly double arcuate depression. The inner arc is extended into a faint ring	9 cm.
T16;2025	Exumbrellar external mould just dominant over internal mould	⅓ of disc, little of outer ring	—	—	Pouched	Without striae	Usual inner groove poorly developed 2nd groove present	Groove at ⅓ width poorly developed	Depression filled with coarse sand	Over 10·6 cm.



TEXT-FIGS. 5–8. Restorations. 5 a–c, *Brachina delicata* gen. et sp. nov. Approximately ×0·5, tentacles hypothetical. *a*, Moderately expanded small specimen in oblique, subumbrellar view showing the annular gonad and radial gastrovascular system through the wall. The manubrium was small and conical. *b*, Moderately contracted larger specimen viewed from side top of exumbrella. *c*, Restored section. For numbers see text. 6 a–c, *Kimberella quadrata* (Glaessner and Wade), slightly enlarged, tentacles hypothetical. *a*, Side view, *b*, *c*. Cross-sections at the levels indicated by *v–w* and *x–y*. The gonads adhered to the radial canals and projected into the lumen of the bell. Gastric pouches alternating with the canals are hypothetical, as is the shape of the stomach at level *v–w*. Gastric filaments inside apex pass below puckering of bell wall. 7, *Ediacaria flindersi* Sprigg. Approximately ×0·5. Oblique subumbrellar view of moderate-sized specimen. Tentacles observed on only one fragment. Radial striations believed to be a surface feature. 8 *a*, *b*. *Rugoconites enigmaticus* Glaessner and Wade, canal system and tentacles based on specimen in Pl. 43, fig. 3, ×0·57, outer flange and general shape based on both figured specimens, and others.

fossil. The sharp elevation toward the centre of the disc (11) is also interpreted as an external feature while the centre of the disc (12) is a low conical mound after specimens F17457 and 379. The presence of a central depression (hollow, ring or arc) is considered the effect of compression against the mouthparts. The tentacle (13) is the only structure for which there is no evidence.

Text-fig. 5a shows a moderately expanded, small specimen obliquely from below while a moderately contracted larger specimen is seen from the side top in 5b. As in 5c, the tentacles are hypothetical, but the remainder of the structures have been restored by comparison of drawings from life of modern medusae with the structures of the fossils. The functional comparison of the new form with modern discoid Scyphozoa is very close but the detailed morphology shows significant differences. Although the marginal lappets have many parallels, the edge of the outer ring they attach to does not take part in the internal mould and so the radial passages appear to end blindly instead of being united by a ring canal, but as ring canals are lacking in many recent forms radial passages are still to be regarded as gastrovascular canals. They communicate with one another in the ring complex which presumably surrounded the stomach, and, as relict dichotomous branching is present in its outer parts (adjacent to zone 5, Pl. 42, fig. 3; text-fig. 5) presumably represents phyletically increasing communication between the passages.

The pouched annulus is a unique character. It is distorted in the same sense and places as the other zones of the body, and is constant in its spatial relationships with the other zones, and in its attitude. It thus appears to have been confined within the same body wall, a conclusion supported by its preservation in the holotype as an internal mould. Hence, its connection with the radial passages may be inferred from the fact that, like them, it was evenly filled with fine sand before the body decayed, though it shows no direct connection to the exterior. Admittedly, the holotype fragment is too small to prove that there were not rare external openings but the mould is evenly filled. In general appearance the pouched annulus is more like a simple gonad than any other medusa-structure. The four gonads of the recent *Poralia rufescens* Vanhöffen form an almost complete annulus but here, as in other Semaeostomatida, the gonads are positioned at the junction of the gastrovascular canals and stomach. The pouched annulus, by comparison, is situated well away from the stomach toward the outer end of the gastrovascular canals. Its size and structure are radically different from any known gastrovascular canal and it is not on the same plane as the radial passages, as a ring canal should be. As the four factors of its size, pouched structure, level in the body, and position part way across the outer ring, militate against its interpretation as a ring canal, and only its unusual position (in comparison with modern medusae) is against its interpretation as a gonad, the latter interpretation is favoured. The annulus could have covered a ring canal of normal dimensions as it is several times wider (by modern standards) than a ring canal of width commensurate with the radial passages. Support for a hidden change of structure is weak, merely that the radial passages do not branch outside the annulus; this is an observable reduction in the frequency of branching, and does not prove the unbranched outer ends to be a structure like the unbranched canals external to the ring canal which serve large lappets in many Semaeostomatida (see, for example, Mayer, 1910, text-figs. 388, 392–396). Even if present, a ring canal hidden by the annulus could hardly be homologous with the structure in modern

Scyphozoa or Hydrozoa because that would require the annulus to be marginal and zones 1–3 to represent lappets—an inherently unlikely proposition. Ring canals are not present in *Hallidaya brueri* or *Skinnera brooksi* Wade (1969) which are only slightly younger than *Brachina* (Wade, 1970). A ring canal or its morphologic substitute, a ring sinus, is not necessary to all kinds of water-vascular circulation, for numerous modern medusae have dispensed with it wholly or functionally, as many authors have noted since Browne (1904) discussed *Proboscidactyla* [as '*Willia*']. Mayer (1910) described it as variable in Narcomedusae, and absent in Pelagiidae and Cyaneidae; Hyman (1940, p. 454) noted that in 'Narcomedusae . . . the ring canal is often reduced to a solid strand or absent' (see also further discussion in Hyman op. cit., pp. 508, 519, 521). Russell (1953, p. 6) gave a short general statement on its morphology in Hydromedusae. Gonads in modern medusae are sited in diverse well-oxygenated positions so it is necessary to consider possible water circulation through the annulus. As the smooth surface of the internal mould is not interrupted in about one fifth of its circumference, as seen from the subumbrellar side, or in two fifths of the exumbrellar side, the annulus can have had few or no external openings. The infilling with sand (in the holotype) could have taken place through connections to the similarly filled radial passages. In all, communication through the radial passages seems most likely from the preservation, and the undivided inner half of the broad annulus would allow considerable lateral water circulation. It may well have served both the functions of ring canal and gonad.

Remarks. Brachina delicata is about the common size range of *Ediacaria flindersi* Sprigg but is differentiated from this species by its marginal lappets, its uniformly wide outer ring, its striking disc-margin with a circular ridge between double grooves, and more concentric grooves on the disc. Only one more groove is consistently present (see text-fig. 5b) but adventitious grooves are frequent. The concentric grooving caused Sprigg (1949) to place the first two specimens collected in '*Madigania*' *annulata* as neither showed the true margin with lappets. However, they both have the print of the annulus in the centre of the outer ring and all the disc grooves of *Brachina*; also, the strong conical projection in the centre of T9 (Sprigg, 1949, pl. 17, fig. 2; this paper, Pl. 42, fig. 5) projects down from the subumbrella and not up from the exumbrella, as is shown by the oblique edge view which indicates a wedge-shaped layer of sand '*w*' between the two surfaces. T9 and T16; 2025 were incorrectly transferred to *E. flindersi* when the holotype of '*Madigania*' *annulata* [= *Spriggia annulata* (Sprigg) Southcott 1958] was transferred to *Cyclomedusa* Sprigg (Glaessner and Wade, 1966).

A composite mould of a discoid medusa was described from the Nama System of Southwest Africa as *Paramedusium africanum* Gürich, 1933; re-illustrated in Harrington and Moore, 1956. This was about the same age as *Brachina* (Glaessner, 1963; Germs, 1968). W. Häntzschel informed M. F. Glaessner that the specimen was lost during the war. No further specimens have been collected (pers. comm. Germs, dated 4 Feb. 1970). Its description was illustrated by an extremely unsatisfactory photo and a wash drawing which showed a half-specimen with a practically featureless centre and, in its outer one third, radial ridges (presumably gastrovascular canals) which occasionally branch dichotomously and are only slightly more widely separated than those of *Brachina*. They are connected to each other by narrow cross ridges, forming an irregular network. A patch of slight, fine radial markings is all the structure described for the central area.

The margin is not clearly described but two small portions of the figure show what might have been a smooth, natural margin with one niche. The specimen probably never was generically identifiable. Its resemblance to *Brachina* is only that its main radial passages run parallel, relatively close together, and maintain their spacing by occasional dichotomous branching. In *Paramedusium* they are united by cross-passages in the region where there are no cross-connections in *Brachina*. That *Paramedusium* certainly and *Brachina* probably lacked ring canals cannot be assumed to be significant as so many unrelated forms lack them too (above).

In *Brachina* we have a medusa of the scyphozoan grade of complexity, like *Hallidaya* and *Skinnera*, which also does not fit a definition of Scyphozoa based solely on tetramerous forms. *Brachina* is morphologically closer to *Hallidaya* than to *Skinnera* but they have little in common but dichotomous branching of the radial canals. Their gastrovascular systems are not similar for there is frequent dichotomous branching in *Hallidaya* and few canals extend from the stomach, in contrast to the ring complex and rare branching in *Brachina*. The annulus in *Brachina* has no parallel in *Hallidaya* and the nuclei of *Hallidaya* have no parallel in *Brachina*.

Genus KIMBERELLA, nom. nov.

= *Kimberia* Glaessner and Wade, 1966, non *Kimberia* Cotton and Woods, 1935.

Type species. *Kimberella quadrata* (Glaessner and Wade).
(= *Kimberia quadrata* Glaessner and Wade, 1966, pl. 97, figs. 6, 7).

Dr. N. H. Ludbrook kindly drew attention to the fact that the name *Kimberia* is preoccupied by *Kimberia* Cotton and Woods, a subgenus of *Turritella* Lamarck. Accordingly the new name *Kimberella* is proposed.

Diagnosis. As for type species.

Kimberella quadrata (Glaessner and Wade)

Plate 43, figs. 2a, b; text-fig. 6a–c

1959 'Problematic fossil, possibly belonging to the Siphonophora' Glaessner, *in* Glaessner and Daily, p. 391, pl. 47, fig. 9.
1966 *Kimberia quadrata* Glaessner and Wade, pp. 611–612, pl. 97, figs. 6, 7.

Material and occurrence. Four almost complete specimens and three fragments from Ediacara Range. All are positive composite moulds, laterally compressed.

Preservation. All specimens appear in convex relief on the bottoms of rock slabs. Their preservation is not as simple, external moulds, for an elongate zone of transverse puckering of the surface may or may not traverse the edges of most obvious, radially elongate, convex structures. While the puckering can be viewed either as an exumbrellar or subumbrellar feature, the elongate convex structures were necessarily inside the puckered structure. Internal structures which also pass below the puckering occur inside the apex of the bell, these are filaments that occur in negative relief. These filaments must have been tougher than any other portion of the body, as they are the only structures in negative relief. On these two counts, then, the preservation is as positive composite moulds.

Diagnosis. An elongate, slender, perhaps squarish, bell-shaped Scyphozoan with 4 pouched gonads attached to radial canals and projecting into the cavity of the bell and to each side of the canal. The centre of the area between the canals is often transversely puckered (probably by the contraction of 8 muscle zones on the subumbrella). Gastric filaments are present adapically. Tentacles possibly are few, and broad near the bell.

Description. The elongate bodies appear to have been bluntly rounded at one end and reach their maximum diameter near this end; from there, they taper gradually for the remaining two-thirds or three-quarters of their length and are then truncated. The shape is best seen in P12739 (Glaessner and Wade, 1966, pl. 97, fig. 7; this paper, Pl. 43, fig. 2a, b). In the other specimen in which the truncate end is unbroken the positive mould fades out. No certain appendages to this body are preserved, though at least two broad tentacles could be present at the margin of P12739 (Pl. 43, fig. 2a, marked as '?'). These structures are also open to interpretation as fortuitious markings, and no definite statement as to their organic or inorganic nature can be justified from this specimen. Within the body the most strongly-marked features are elongate, convex, segmented zones which run from the truncated margin up the sides of the body and converge near the apex. These present two aspects, either a slight, smoothly-rounded median keel which is not segmented, with a lobulate, less elevated portion on both sides, or a lateral smooth area (the keel) and one more deeply lobulated area on one or the other side of the smooth keel. Adjacent to the segmented zones is usually a narrow, elongate, smooth area; in one specimen (P13771) (unfigured) the smooth area extends right across the centre to the segmented zones on the other side but in the remainder it is followed by a puckered zone with transverse, narrow, ridges and furrows. In P12739 the puckered zone is interrupted by a fortuitous fold which distorts the specimen. In this specimen the inner curve of the segmented zones, where they come together adapically has sharp, deep furrows and ridges appended at right angles. Previously these were assumed to be part of the 'frilled' or puckered region although they are a little larger and at right angles to it except at the edges (Pl. 43, fig. 2a, b '*g*'). Three or four of these adapical ridges and depressions are present on P13775, however, and here they pass below the puckered zone. Casts suggest they are, in fact, external moulds of tentacular structures inside the apical end of the bell.

Specimen P13775 (unfigured) has the segmented zones of the left and right sides asymmetric in the opposite sense. Both have smooth keels facing in toward the puckered zone and deeply lobulate areas facing outwardly. In this the puckered zone is adjacent to the keel of the right segmented zone and near the apex reaches across to the keel of the left segmented zone. Lower down, this area is smooth on the left side, and still lower, it is deeply creased parallel to the puckers. It has a diagonally stretched appearance in this sector. Near the adapical end slight grooves on both sides extend obliquely up from

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EXPLANATION OF PLATE 43

Fig. 1. Subumbrella attributed to *Ediacaria flindersi* Sprigg, ×0·8; specimens overlie each other on a crowded bedding plane. Structures thought to be the mouth are indicated by *m* and the possible stomach-edges by *s*.

Fig. 2a, b. *Kimberella quadrata* (Glaessner and Wade), P12739, paratype. 2a, ×1, where marked with '?' two structures delimited by faint double lines; these could represent tentacles. 2b, Apex ×1·8, gastric filaments, *g*.

Figs. 3, 4. *Rugoconites enigmaticus* Glaessner and Wade, ×1 and ×0·5 respectively. 3, latex cast from Brachina Gorge showing tentacles *t* and marginal flange *f*. The dichotomous ridges show more clearly in lighting unfavourable to the tentacles. This specimen is the main basis of text-fig. 5. 4, F17458. Shallow, conical depression with narrow, smooth, marginal flange and a weakly doubled marginal impression.

Figs. 5–7. *Rugoconites tenuirugosus* sp. nov. 5, F17461 holotype, ×1, Bunyeroo Gorge. The dichotomous furrows sometimes reticulate. They focus on a near-circular central furrow to weak depression thought to represent the stomach. The '?' indicates a smaller circular furrow possibly due to the mouth. 6, F17460, paratype, ×0·5, Brachina Gorge. Specimen showing little or no reticulation of its dichotomous furrows. Possible tentacles are seen at *t*, F17459, paratype, ×0·7. Dichotomous furrows occasionally reticulate. Furrows near the centre form a coarse mesh which is partly circumcentral. It is not known whether any of these furrows delimit the stomach.

the respective creases at the edges of the segmented zones and are lost to view below the adapical ridges and furrows. As the puckered zone is also present here, the structure is obscure; it is seen in no other specimen.

The width of featureless material between the outer membrane and the internal structures is always least near the truncated end and greatest toward the apical end, though not necessarily at the apex.

Restoration. The reasons for believing there are four segmented zones present were advanced at the time the species was described. The structure of the segmented zones is now recognizable in the positive moulds as an individually variable number of discrete lobes with rather broad connections to radially arranged keels. These are interpreted in text-fig. 6 as deeply pouched gonads attached by their outer-central region to radial canals. The keel is interpreted as a radial canal rather than a septum because it presents a smooth curve to the outer wall and is itself convex like the gonad, which was presumably hollow in life. As the gonads can be folded either to the left or right, showing the radial canal at either the right or left side, they must have projected into the cavity of the bell. They could be paired but this is not likely as the pouches are usually deeper if the keel is to one side than if it is centrally placed. The adapical ridges and furrows which appear to be tentacular are interpreted as gastric filaments which are described as having solid mesogloea inside an entodermal covering (Hyman 1940). These are a scyphozoan characteristic found in the Carybdeida which have similar overall shape. In the Carybdeida elongate gonads attached to the septa are paired, however, and though possible, this is not likely for *Kimberella*. Gonads in Carybdeida are also lamellar and confined in broad gastric pouches on either side of the interradial septa. Both cannot be folded to one side of the same septum as in *Kimberella*. There are now five specimens in which there are smooth areas adjacent to the radial canals and one fragment of one side; only in the specimen in which both gonads are folded outward (leaving the radial canals back to back) does the puckered zone give some evidence of extending from canal to canal. In this specimen the area between the radial canals appears stretched and the puckers are directed obliquely. Possibly they are creases on the subumbrellar wall due to the pull of muscles. No puckers are present in one of the seven specimens. The normal localization of the puckers in the centres of the sectors between the radial canals must be due to the placement of the radial muscles, but their abrupt line of commencement indicates a structural change as well. This could be produced by large gastric pouches in this position, as shown in the cross-sections, text-figs. 6b, c. The fact that the puckers are normally most strongly developed at one side or the other, suggests that they are an inert response of the subumbrellar surface to the contraction of muscle zones with a definite edge adjacent to the smooth zone between them and the adjacent radial canals, that is, they represent eight strips of muscle-fibres. This is a normal number for modern scyphozoan and hydrozoan medusae.

Remarks. Glaessner and Wade (1966) pointed out that the positioning of the gonads suggested elongate gonads on radial septa or canals such as can be found in Carybdeida or Trachymedusina and Leptomedusina, and that the simplicity of the structure was more like the hydrozoans mentioned than the scyphozoan. On the other hand, the gastric filaments seem proven by position, dimensions and texture, i.e. they are a reliably established character considered strictly scyphozoan (Mayer, 1910; Hyman, 1940). Among structures found in Recent medusae, only gastric pouches seem to offer a ready explanation for the puckered zone. These are known in Carybdeida and

Narcomedusae (Mayer, 1910) in inter-radial and radial positions respectively. In *Kimberella* the presumed gastric pouches alternate with the radial canals from which they are broadly separated. Though this cannot be used in defining radial and inter-radial in an unknown group, it indicates that, if present, gastric pouches are not of the narcomedusan type. It appears that *Kimberella* is another primitive scyphozoan. Its tetramerous shape raises the question of whether it is an early member of the modern scyphozoan radiation. *Kimberella* is not a member of the order Carybdeida but all its known characters are found in this group except that *Kimberella* does not share the pairing, lamellar shape and placement of the gonads in the gastric pouches. This is the closest morphological similarity to modern forms found among the Precambrian Scyphozoa. All others, *Brachina*, *Hallidaya* and *Skinnera*, are more different from one another and from *Kimberella* than *Kimberella* is from the Carybdeida. It is possible that this form derives independently from the same root stock as modern Scyphozoa. It is coeval with *Conomedusites* Glaessner and Wade, the earliest known member of the Conchopeltida. Glaessner (1971) has reviewed the modern views on the placement of the Conulata (= Conchopeltida+Conulariida) and regards them as polypoid animals, the earliest members of the group probably being ancestral to the polyps represented by the now reduced polypoid stages of modern Scyphozoa. He further drew attention to similarities between the chondrophore conaria larva and *Conomedusites*, and to the advanced differentiation of the bilaterial chondrophores by the time of the Ediacara fauna. He thus inferred a considerable pre-Ediacaran evolution of this group, an inference that is borne out by the discovery of another kind, the circular chondrophore *Eoporpita*. The time involved in this much differentiation, at least, is by inference available for the differentiation of the early Conchopeltida. The original differentiation of the early Scyphozoa, as shown by the genera described here, had probably proceeded further by Ediacaran times than was previously known.

Medusa *incertae sedis*

Genus *Ediacaria* Sprigg 1947

Type species. *Ediacaria flindersi* Sprigg 1947.

The genus is monotypic and the characters as diagnosed by Glaessner and Wade (1966, p. 603) except that the removal of several more extreme specimens to other genera (mostly to *Brachina*) has reduced the known variation in the proportionate width of the disc to the outer ring. The disc is usually about two-thirds to three-quarters of the total radius.

Ediacaria flindersi Sprigg 1947

Plate 43, fig. 1; text-fig. 7

1947 *Ediacaria flindersi* Sprigg, p. 215, pl. 5, figs. 1, 2, text-fig. 3.
?1947 *Beltanella gilesi* Sprigg, p. 218, pl. 6, fig. 1, text-fig. 4.
1949 *Ediacaria flindersi* Sprigg, p. 83, pl. 10, fig. 2, text-fig. 5.
1949 *Protodipleurosoma wardi* Sprigg, p. 79, pl. 9, fig. 2, text-fig. 3E.
1956 *Ediacaria flindersi* Sprigg (partim); *Protodipleurosoma wardi* Sprigg; Harrington and Moore, *in* Moore, p. F47, fig. 60(1); p. F79, fig. 64.
?1956 *Beltanella gilesi* Sprigg; Harrington and Moore, p. F70, fig. 56.
1959 *Ediacaria flindersi* Sprigg; Glaessner *in* Glaessner and Daily, p. 378.
?1959 *Beltanella gilesi* Sprigg; Glaessner *in* Glaessner and Daily, p. 378.
1962 *Ediacaria* Sprigg; Glaessner, p. 483.

?1962 *Beltanella gilesi* Sprigg; Glaessner, p. 483, pl. 1, fig. 3.
1966 *Ediacaria flindersi* Sprigg; Glaessner and Wade, p. 602, pl. 99, fig. 6.
?1966 *Beltanella gilesi* Sprigg; Glaessner and Wade, p. 604.

Preservation. Typical *Ediacaria* are low exumbrellar casts, and subumbrellar casts are now attributed to this specimen, but some specimens of either side show a furrow which is interpreted as the stomach margin, and these must be considered positive composite moulds, as must any in which the mouth shows through the disc on the exumbrellar side.

Restoration. Sprigg (1947) associated an incomplete subumbrellar mould with *Ediacaria flindersi* (as *Ediacaria* cf. *flindersi* on the plate reference and as *Ediacaria* sp. in the text). This type of subumbrella is thought to be that of *E. flindersi* (Glaessner and Wade 1966, p. 602, 603). Pl. 43, fig. 1, shows parts of at least three subumbrellar impressions. All have a round to oval central mouth without any appendages or lips but in the most constricted, with a slight, circumoral furrow a short distance outside the mouth. Several other specimens beside these also show a similar mouth and a decided circular groove at about one third of the radius. Outside this groove, fine, radial striae extend to the margin. Sometimes they extend across this groove toward the mouth but very rarely reach to it. These radial striae increase in number outward by interpolation more often than by branching, and appear to be a surface structure.

The size-range of these medusae coincides with the exumbrellar surfaces of *E. flindersi* and *Brachina delicata*. If the distinct groove at about one third width is taken as the edge of the disc, only *B. delicata* has the correct proportions, but this species has a small, funnel-shaped manubrium. Its annular gonad, also, though placed on the subumbrellar side of the gastrovascular canals shows on several of the exumbrella-dominated moulds. This kind of structure does not show on any of the subumbrellar surfaces here described nor do any have the regular lappets of *B. delicata*. It seems that comparison with *B. delicata* is not valid. There remains the comparison with *E. flindersi*. The groove at one third of the radius is about the right size to match the groove on the exumbrella-dominated composite moulds thought to represent the stomach. This interpretation would also explain the dying-out of the radial striae at, or soon after, this groove. The outer zone of radial striae is wider than the outer ring of *E. flindersi* but as it shows no internal structures it cannot be expected to show those of the opposite side. One specimen of an outer ring occurs on a very fine-grained sandstone slab which apparently broke off at the disc margin (though none of the disc is present). This has the dimensions of the outer ring of *Ediacaria* and appears to have had long, fine, numerous tentacles appended. All of these characteristics have been assembled in the reconstruction, text-fig. 7.

A careful search was made for any trace of an annular gonad like that of *B. delicata*. The holotype of *Ediacaria flindersi* Sprigg has a number of partial concentric furrows and broad ridges on its outer ring but nothing delimiting a continuous band. The specimen morphologically closest of all to the holotype similarly has an incomplete band. Other medium to small-sized specimens also show no annulus but both of the large specimens mentioned by Glaessner and Wade (1966) show an annular depression near the centre of the outer ring. In the low cast 21 cm in radius this is not sharply defined, though clearly continuous, and in the fragment of a much larger specimen, it is under

1 cm wide and an observable maximum of 3 mm deep. As the outer edge of this depression is not lobulate in either specimen, it is not suggested that this annular depression actually is an annular gonad. It may be present only by chance, or it may represent a real structure approximately the width of the annulus in specimens of *Brachina* of less than one third the radius of these *Ediacaria*.

Genus *Rugoconites* Glaessner and Wade 1966

Type species. Rugoconites enigmaticus Glaessner and Wade, 1966, p. 611.

New material has made the type species fairly well known, and enables description of a new species previously represented by inadequate material.

Diagnosis. Moderate-sized medusa with a low, conical disc which often shows a double ring at the disc margin. Rarely, a narrow marginal flange is preserved and more rarely, very fine, numerous tentacles. Several to many furrows extend from the corners of a small, indistinct, polygonal to rounded centre (? stomach region) and repeatedly branch dichotomously. Mouth probably circular, apparently without appendages. Where furrows meet they anastomose. The furrows may be rather coarse and relatively few, to fine and numerous, depending on the species.

Preservation. Save for one natural counterpart cast of *R. enigmaticus* on the top of a bed, all specimens are impressions on the bases of beds. *R. tenuirugosus* sp. nov. is always flat with fine, incised, branching furrows radiating from an indistinct centre, but the whole disc edge of *R. enigmaticus* is usually deeply incised and the impression of the fossil continues to deepen to its centre which may be severely distorted. Radiating, branched furrows run from near the centre to the margin. In latex casts they form ridges which indicate the sculpture of the bodies at the time of fossilization, which is not necessarily their life-shape. In *R. enigmaticus* they are clearest in a few, naturally rather flat specimens: small specimens are low conical and the ridges on them are very broad; large specimens are often extremely confused in the centres as if a conical shape had collapsed, but their outer edges are undistorted. These are the only medusae in the Ediacara fauna which had sufficiently tough mesogloea to constantly form impressions in the overlying beds but they are not uniquely tough, for they show comparable resilience to *Skinnera brooksi* Wade (1969, p. 355, 361) from a slightly younger portion of the Central Mt. Stuart Beds, Northern Territory, Australia. As in this species, 'ornamentation' may result from differential compression and the normal preservation also may be as negative composite moulds. This is emphasized by *R. tenuirugosus* which is more easily compressed, and yet shows a comparable pattern of furrows. This can only be regarded as a slightly negative composite mould. The presence of sharp furrows in this more compressible species shows that the resilience and resulting 'ornamentation' are not likely to be effects of an external cuticle.

Rugoconites enigmaticus Glaessner and Wade

Plate 43, figs. 3, 4; text-fig. 8a, b

Rugoconites enigmaticus Glaessner and Wade, 1966, p. 611, pl. 100, figs. 2, 3.

Material and occurrence. Twenty-one specimens from Ediacara Range and five from Brachina Gorge (the original of Pl. 43, fig. 3 is still *in situ*). The Brachina Gorge specimens are extremely well preserved and most of the additional information comes from these.

Restoration. The new material of *R. enigmaticus* allows the original animal to be reconstructed with a fair degree of confidence. Small specimens are the most conical and have a pattern of relatively coarse, dichotomously branched furrows radiating from a central area of obscure structure. Many larger specimens are greatly distorted in the centre, as if the original material was not strong enough to support sediment-load across the greater span. The deeply impressed edges of the disc indicate a truncate margin which probably sloped inward on the subumbrellar side. This truncate margin, rather than a marginal canal, is the probable cause of the double-ringed 'disc' margin seen in Pl. 43, fig. 4 and in parts of several specimens; in this the radial structures cross the inner of these rings as they would if they were radial canals servicing the marginal flange among other portions of the body.

The few larger specimens in which the furrows are relatively clear toward the centre are exceptionally flat. In the flattest specimen (Pl. 43, fig. 3) they are only slightly depressed, but can be traced quite clearly (by lighting which does not favour the tentacles) and shown to anastomose, two giving rise to only one branch, where repeated dichotomous branching brings two furrows into contact. As this happens regularly, the branches were all in the one plane (text-fig. 8a). This one, undistorted specimen is two-thirds of quite a flat, depressed disc, and has a narrow, smooth zone with a slightly wavy edge encircling it. Very fine, unbranched striae radiate from the faint, inner ring of the disc margin and across the smooth area; in one place they extend beyond it. While four specimens show parts of such a smooth zone or marginal flange around the disc (e.g. Pl. 43, fig. 4) only a fifth specimen shows similar striae. Here also the striae arise from the inner edge of the truncate margin (as can be seen in latex casts); they thus may be interpreted as very fine tentacles arising from the inner edge of the disc margin, while the outer flange arises from the outer edge (text-fig. 8a, b).

Clearly the fossil is of a strongly medusiform animal but as its mouth has not yet been observed other structures must be invoked to decide its orientation. As seen in latex casts, it seems unlikely that the conical surface harboured a mouth, and its convex shape suggests it is the exumbrella. Of the flatter specimens only the two which have tentacles are well enough preserved to have shown a mouth and the larger of these is broken at the centre. The other shows very slight puckering at the centre but no definite mouth.

Marginal flanges are associated with three conical sides and one flat surface with tentacles depositionally overlying the flange. In every example, marginal flanges seem to attach to the periphery as they have no inner structures of their own and do not obscure the outer ends of the radial ridges between the inner concentric ridge and the margin. Both specimens with tentacles have them attached in a ring that is about as far within the periphery as the inner ring seen in conical specimens. From these factors we can be sure that the tentacles are not marginal but slightly within the margin, while the flange is marginal. While the specimens are too few to be certain that the correlation of flat surface and tentacles is constant, all the evidence we have points this way. It seems most probable that conical surface and flat surface represent exumbrella and subumbrella respectively.

The radial structures show equally clearly all over the flattish surfaces, but not equally clearly all over the conical surfaces. From this it is legitimate to assume that they lie in a plane (above) parallel to the flatter surface, equally close to both surfaces near the margin, but at inwardly increasing depths below the conical surface. The radiating system thus occupies the position of gastrovascular canals. What is not explained by this comparison is the fact that the radiating system is clearly even more resilient than the tough mesogloea of this toughest medusa in the fauna. The idea that the impressions might be due to counterpart casting (Wade 1968) of (in this case) natural moulds of the subumbrella, formed in the underlying incompetent beds falls before the facts that (1) the fine ridges of *R. tenuirugosus* are as clear or clearer than any of *R. enigmaticus*, and (2) the impression in the bottom of the upper bed is often deeper than the thickness of incompetent material that may be inferred from lithology as having been present below the fossiliferous surface. Another cause for the resilience should be sought. The filling of radial canals with frothy material that kept them distended while the remainder of the body shrank, has been described, but in stranded material. We have no reason for regarding any of the Ediacara fauna as stranded material (Goldring and Curnow 1967; Wade 1968). It is feasible, however, that the release of gaseous material within radial canals could have kept them distended without disruption for this medusa must have been exceptionally tough and slow to decay, as its preservation as imprints demonstrates. It seems quite likely that any food material would decay more rapidly than the medusa, particularly so if its canals contained symbiotic algae.

Rugoconites tenuirugosus sp. nov.

Plate 43, figs. 5–7

Material and occurrence. Three specimens are known from Ediacara Range, two from Brachina Gorge and one from Bunyeroo Gorge.

Holotype. F17461, Pl. 43, fig. 5, from Bunyeroo Gorge.

Preservation. The holotype alone shows a composite of internal and external characters. The remainder consist of radial furrows incised like those of *R. enigmaticus* on the bases of rock slabs. Unlike *R. enigmaticus* every specimen is flat; though not so destructible as to form casts like other medusae, they were not resilient enough to form impressions.

Diagnosis. *Rugoconites* with very fine radial furrows which branch dichotomously about 3–5 times, diverging at a very low angle and tending to curve parallel; reticulation rare to common in different individuals; furrows reach smooth central area (? stomach).

Description. The largest specimens known have discs just under 5 cm average radius. The holotype is just under 4 cm. It is broken across at one side of the probable stomach but presumably lost only radially repeated structures. The centre is occupied by a circle 4 mm across which is presumably the mouth as it is almost central in a smooth, oval to polygonal area about 15 by 12 mm. From the furrow delimiting this area, the probable stomach, radial furrows arise and repeatedly branch dichotomously, the branches diverging only slightly and rapidly curving to become almost parallel. In some individuals the outer branches may be reticulate but often their shape prevents them from meeting. The number of branches reaching the stomach cannot be clearly ascertained in any specimen but by extrapolation from the better preserved areas of several specimens it appears to have been about 10 to possibly 20. The specimen with least initial branches has the most divergent branching and branches four to five times, while on another specimen only 3 divisions could be seen. As a result, all specimens have terminal branches meeting the margin of the disc at right angles and less than 1 mm apart. Outside the disc margin even finer furrows, closer together, are seen on parts of two specimens (Pl. 43, figs. 5, 6 '*t*'). In fig. 6 they are seen to die out, but in the holotype fig. 5 they are present within a narrow area delimited by an arcuate furrow here interpreted as a small portion of its outer flange which was mostly folded under the body. These fine and closely-spaced outer furrows are interpreted as tentacles.

Remarks. The close resemblance of structure between *R. tenuirugosus* and *R. enigmaticus*, and the fact that both have a similar, exceptional preservation resulting from textures less destructible than the other medusae, are the basis for uniting them in one genus. They are differentiated principally by the finer, more numerous radial furrows in the new species, and the less divergent angles between their branches. Though forming shallow impressions unlike species of other genera, the disc is less resistant in the new form than *R. enigmaticus*, for all specimens are flat (apart from the furrows) and the margin is often indistinct. An initially more flat disc could not alone account for this.

The orientation suggested here for the disc of the two best preserved *R. enigmaticus*—oral side to the rock—is not supported by a clear view of the orifice nor denied by its clear absence. If the surface of these two is a flat equivalent of the usually conical exumbrellar surface, the tentacles must arise on the exumbrellar side of the marginal flange which is thus comparable with the structures of some hydrozoans, Trachymedusae in particular. On the other hand, if the orientation suggested here is correct, the tentacles will prove to be a subumbrellar feature on the oral side of the marginal flange, and the overall sum of characters tends to scyphozoan, as illustrated in the restoration, text-fig. 8.

Among Recent medusae the morphologically closest form is, at first sight, *Proboscidactyla*. This hydrozoan has both specifically and to some extent individually variable numbers of radial canals which branch and (in some) re-branch. Reticulation of canals is a rarely-seen teratologic phenomenon in the Recent species. It is not suggested that there is a close relationship between the two genera because, apart from the time factor, the anthomedusan type of velum is clearly not closely similar to the outer flange of *Rugoconites*. The mouth also is quite large and has angles and lips in *Proboscidactyla*. Another factor in which the two converge is that *Proboscidactyla* has no circular canal, no lumen in its circular endoderm strand. No detailed description is to hand of the circulation of water through the radial canals of medusae lacking circular canals but Browne (1904) described 'active circulation' in the radial canals and basal bulbs of tentacles in '*Willia*' *stellata* (= *Proboscidactyla stellata* (Forbes)). This form has tentacles only opposite radial canals. It is hard to see how such a form could function without excretory pores but these were not mentioned by Browne, who noted them in Aequoridae; or by Mayer (1910) or Russell (1953) who noted them in Aequoridae and some Eirinidae on papillae on the circular canals, opposite each tentacle or tentacular bulb. Hyman (1940, p. 396) did not specify which scyphomedusae have radial canals with pores opening near the tentacles. Clearly pores are usually far from obvious in Recent medusae, and the lack of evidence in fossil forms is less surprising than their presence would be. A Semaeostomatida without circular canals and with a dichotomously branched canal system similar in complexity to *Rugoconites* is *Drymonema* Haeckel (Mayer 1910) though in this also the canal system is not reticulated. The complexity of the canal system is not sufficient to place the genus in class or order, and gonad structures are lacking. Ultimately the position of the mouth will probably reveal the orientation, and the class and order may well be new.

CONCLUSIONS

The Chondrophora are the only group among those discussed here which can be placed in taxonomic perspective. The floats of the circular and the bilateral Precambrian forms are more strongly differentiated than those of the modern forms *Porpita* and *Vellela*. The whole record consists of two widely differing bilateral forms which represent the family Chondroplidae Wade (1971); *Eoporpita* gen. nov. which represents, or is closely allied to, the Porpitidae, several Palaeozoic Porpitidae (or close allies), Recent Porpitidae, and Palaeozoic and Recent Vellelidae which can be morphologically derived from porpitid ancestry. The concentric float of *Archaeonectris* Huckriede presumably could have derived from the partly embracing early chambers of either porpitids or vellelids. The Ediacara fauna is too young to cast light on whether the circular or bilateral floats are a primitive character but a single kind of chambered float is not the only possible derivative of a probably single chambered ancestral type. Taking the divergence of these early forms into account, a likely view is that the two bilateral forms and the circular form are two or three answers to the problem of how to increase the volume of a single float chamber without sacrificing overall strength or greatly increasing weight.

Cyclomedusa may represent a hydrozoan form sharing common ancestry with the Chondrophora as its low conical form thins to an outer edge which is a prolongation of the coenosarcal disc-edge (i.e. a mantle flap) rather than a separate outer flange like the medusae possess: its internal radial structure resembles the radial gastrodermal canals of young *Porpita* in shape and position: the probability that it was adherent by the apex suggests the secretion of chitin in the place where the float rudiment appears in the development of Recent chondrophores. The small central cone of *C. plana* suggests the loss of attachment in the adult stages of this species.

Scyphozoa are represented by *Brachina delicata* and *Kimberella quadrata*, *B. delicata* is not close to any other known form unless *Ediacaria flindersi* Sprigg belongs here; the gastrovascular and gonad systems of this form are still unknown. The tetramerous *K. quadrata*, which does not belong in any presently recognized order of Scyphozoa, is closer in morphology to the Carybdeida than *Brachina delicata*, *Hallidaya brueri* or *Skinnera brooksi*, the other early Scyphozoa, are to it, to one another or to any modern medusa. *Kimberella* was probably derived from the same line as the modern forms. The position of the other three is more obscure, but it is noteworthy that the oldest of the three has the structures most easily comparable to modern medusa. The diversification of Scyphozoa must have commenced prior to the Ediacaran.

As yet the oral side of *Rugoconites* Glaessner and Wade has not been conclusively identified and its provisional restoration as scyphozoan rather than hydrozoan rests on the interpretation of two rather flat specimens with tentacles as representing oral sides. The peculiar ridged 'ornamentation' is interpreted as distended radial canals.

Acknowledgements. The work on which this paper is based was carried out at the University of Adelaide. Mr. I. M. Thomas kindly provided comparative material of *Porpita porpita* Linné as microscopic preparations and preserved specimens. Field work was partly supported by an Australian Research Grant to Professor M. F. Glaessner who has also read the manuscript. I have benefited from discussions with him at various stages of the work. Miss A. M. C. Swan redrew most of the text-figures.

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Typescript received 24 June 1971


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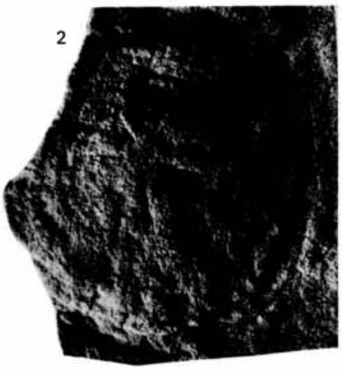
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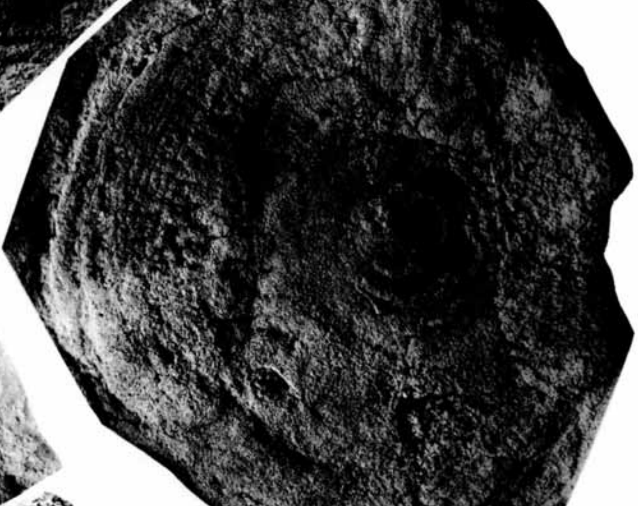
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WADE, *Eoporpita medusa*

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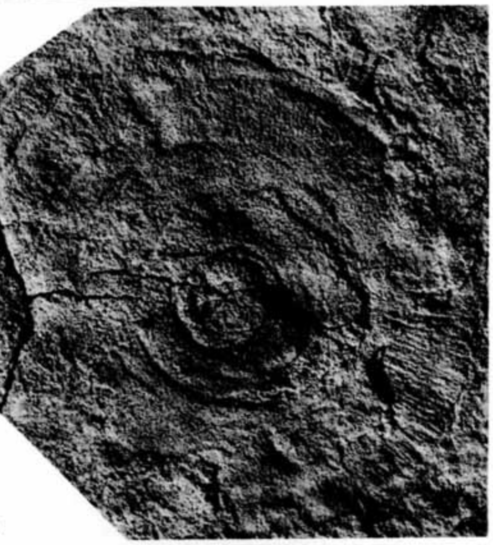

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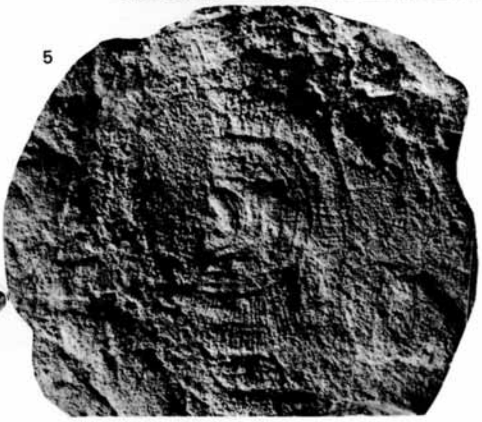

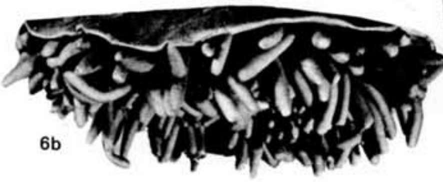

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WADE, *Cyclomedusa* and *Eoporpita medusa*


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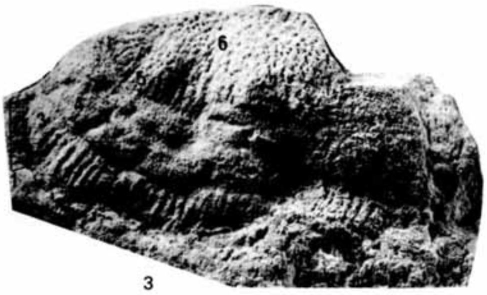

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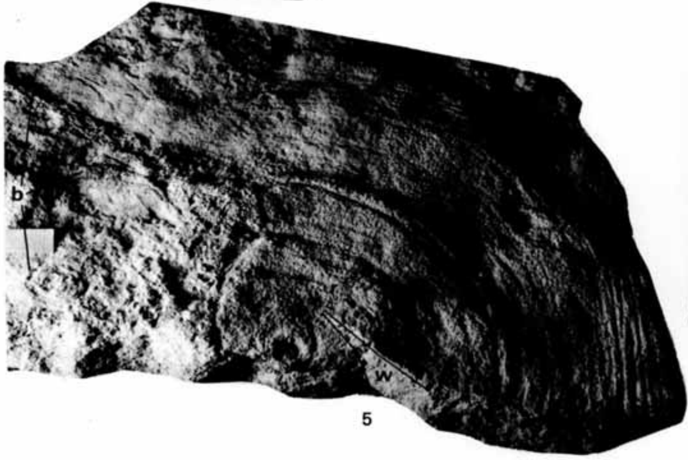

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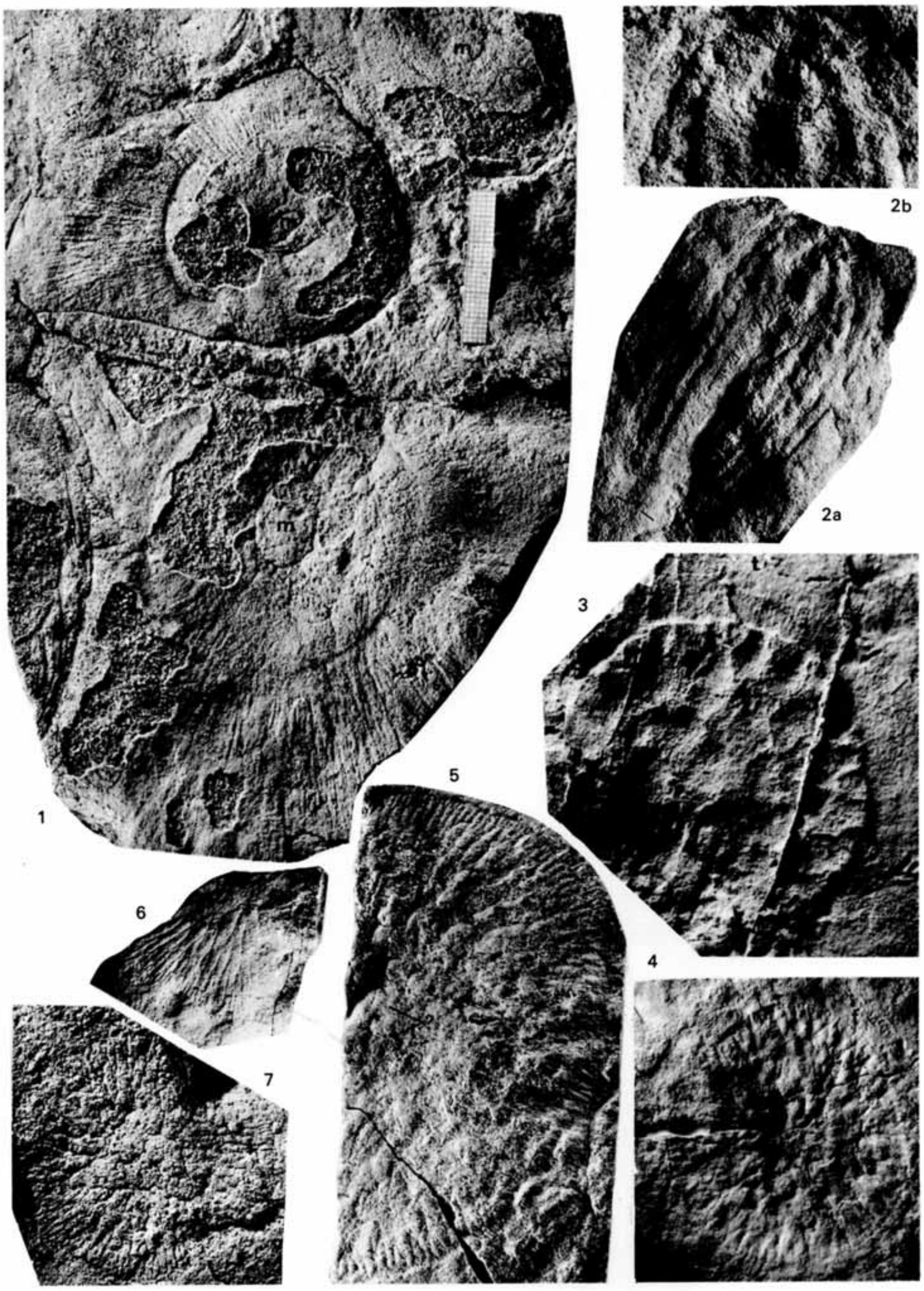
WADE, *Cyclomedusa* and *Brachina*



WADE, *Ediacaria*, *Kimberella*, and *Rugoconites*