MEDUSAE FROM UPPERMOST PRECAMBRIAN OR CAMBRIAN SANDSTONES, CENTRAL AUSTRALIA

by MARY WADE

ABSTRACT. Positive and negative moulds of circular bodies occur largely on depositional undersides of flaggy sandstones of the Central Mt. Stuart Beds, attributed to the Upper Proterozoic. Respectively they represent *Hallidaya brueri* gen. et sp. nov. and *Skinnera brooksi* gen. et sp. nov., two medusae with strikingly different gastrovascular systems, each of a scyphozoan grade of complexity but lacking pronounced fourfold symmetry. They do not closely resemble any form known from Ediacara, South Australia, but add to the slowly accumulating evidence that medusae in the past have been more varied than at present. *Hallidaya brueri* is also found in the lower part of the Arumbera Sandstone, WSW. of Alice Springs; this formation may bridge the Precambrian–Cambrian boundary.

IN the course of geological exploration near Mt. Skinner, Northern Territory, Australia, a sequence of maroon shales, sandstones, and quartzites was examined by Mr. A. L. Halliday, geologist, Kennecott Explorations (Australia) Pty. Ltd. He discovered a fossiliferous slab bearing six casts of an unknown fossil (Pl. 68, fig. 1) approximately $4\frac{1}{2}$ miles ENE. of Mt. Skinner, but was unable to trace it to its origin. During later work, Mr. M. M. Bruer, field assistant with the same company, discovered a sandstone and shale sequence containing a large number of these fossils approximately 1,100 ft. higher in the section, 3 miles NNW. of Mt. Skinner. There is a general dip of 15° SW. and the exposed structure is uncomplicated. No fossils have been found elsewhere in the sequence, save for a few doubtful 'worm casts' still higher. On the bases of regional reconaissance mapping and lithologic similarity this sequence is considered part of the Central Mt. Stuart Beds (Halliday, personal communication) of Upper Precambrian age. This formation is not known to contain fossils elsewhere, but at its northern extremity is overlain by the Grant Bluff Formation, to which a Cambrian age is assigned, since it contains a Lower Cambrian *Helcionella* (N. H. Fisher, pers. comm.). The Central Mt. Stuart Beds unconformably overlie a very rugged Archaean basement, as the beds at Mt. Skinner also seem to do (Halliday, pers. comm.) but the contact is here obscured by alluvium.
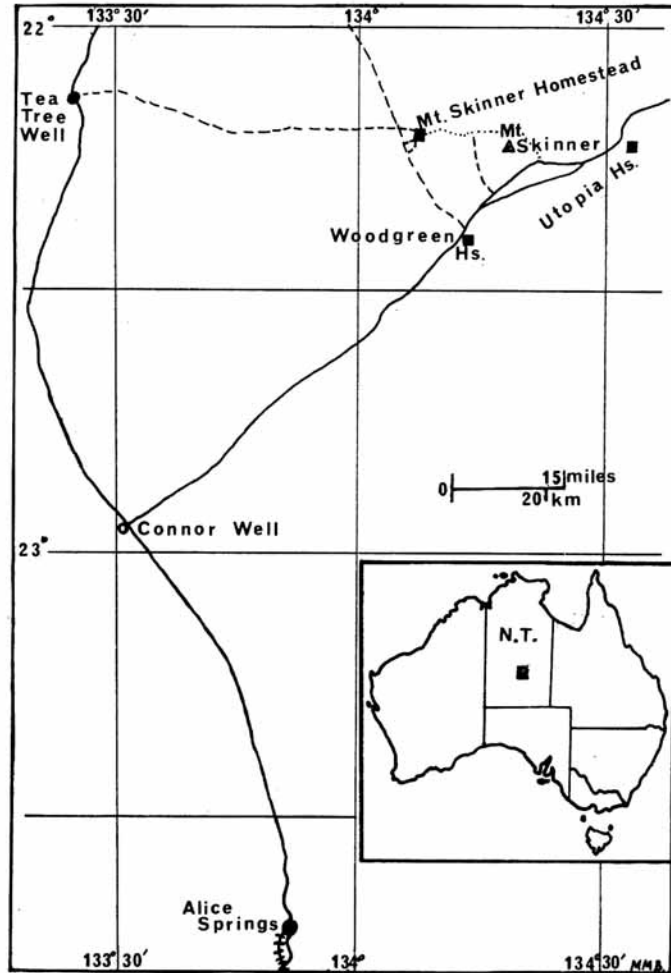
The material studied is deposited in the collections of the Geology Department, University of Adelaide, South Australia.

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TEXT-FIG. 1. Locality plan showing roads connecting the Mt. Skinner area to the main north–south (Darwin to Alice Springs) road. This portion of the Northern Territory is indicated on the inset map of Australia.

The monotonous succession of flaggy, maroon red-beds is occasionally interrupted by thin, widespread, pale greenish, flaggy beds, and by localized, coarse sediments such as the strongly cross-bedded, arkosic sandstones and grits that cap two prominent hill-tops overlooking the main fossil occurrence (text-fig. 2). In both the red and green flag-stones the coarser sediments are arkosic and sometimes include clay pellets. Small-scale
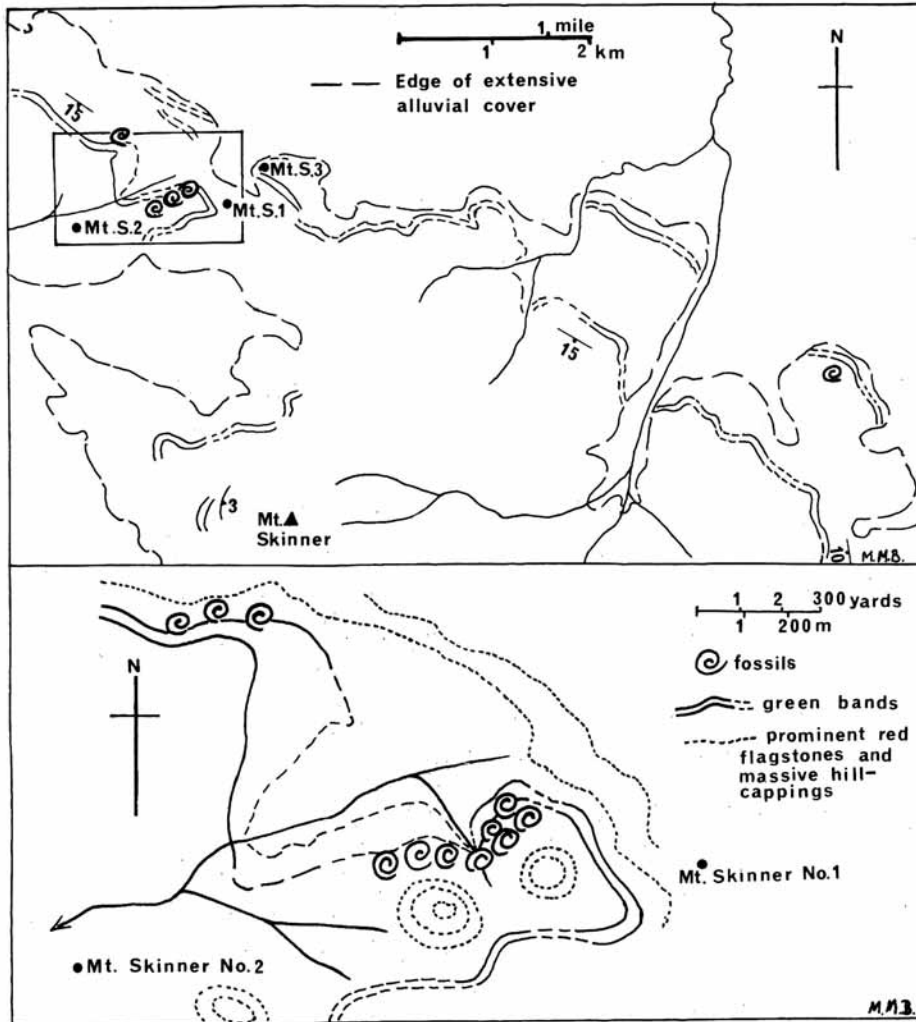
TEXT-FIG. 2. The Mt. Skinner area (after mapping by A. L. Halliday), showing the known fossil localities. The enlargement shows the main fossil localities on either side of the valley containing Mt. Skinner No. 2 drill-hole.

cross-bedding is very frequent, and scoured surfaces are often quite extensive. Rarely, masses of detrital mica are found.

A petrological report on samples of maroon and greenish, coarse and fine sediments was supplied to Kennecott Explorations by Australian Mineral Development Laboratories (Appendix to Kennecott final report, Mt. Skinner Examination, Northern Territory). It indicated that the sediments generally may be classified as subgreywackes and impure siltstones to claystones. The coarser sediments are more strongly cemented by authigenic quartz, and the red coloration is induced by iron oxides coating the detrital grains, whether of quartz, rock-fragments, or feldspar. The green bands contain copper minerals and lack iron oxide coatings on detrital grains. Where there is clay cement present (as, particularly, in the finer beds) there is less authigenic quartz. Laths of authigenic mica are present, and there is more evidence of stress and metamorphic change reported from the petrological study than would be expected from field evidence. The lithological setting has numerous parallels with the Precambrian fossiliferous deposits at Ediacara (Wade 1968), though these lack rock fragments and have much less detrital mica (Goldring and Curnow 1967).

Occurrence and fossilization. The main fossil occurrence lies almost on a direct line between Kennecott Explorations' drill-holes Mt. Skinner No. 2 and No. 3 (text-fig. 2), on the sides of a small valley running ENE.–WSW. On the south side of the valley, the fossils have been found through about 20 ft. of maroon sandstones and minor shales above a green band which measured 16 ft. thick (where it was intercepted by the drill-hole Mt. Skinner No. 2) and in the green band. On the north side they were encountered more sparsely below and in the green band which here forms a dip slope and is strongly weathered, outcropping poorly. Except on the steeper slopes of the valley, scree and rainwash material covers much of the outcrop. One piece of float containing a fossil was found in the creek between Mt. Skinner No. 2 and the main fossil outcrop; it is most probably from a further occurrence of the fossils along the strike of the beds.

The fossils occur in two major forms:

A. In the elevated relief on depositional lower surfaces of beds. These are discs, truncated at the edges, usually depressed in the centre. Their elevation ranges down from about one-eigth of their diameter to totally flat.

B. Impressions in depositional lower surfaces of beds. Latex casts of these are almost hemispherical in small specimens, to gently domed with elevation only about one-tenth of their diameter in large specimens.

Group A. Most of the fossils belong to group A and are sandstone discs, elevated to flat, and normally depressed in the centre, where the impressions of a number of concentrically ringed bodies (here called nuclei) are grouped. Quite a number of specimens appear as though the rock has broken away to expose the nuclei, and removal of the surface of one fossil with some partly exposed nuclei revealed their continuation inside it. In numerous specimens the nuclei are scattered from a grouping around the centre; in some the bodies seem to have been buried in a partly decomposed condition since they leave scarcely a mark on the sediment (Pl. 69, fig. 5), though the nuclei make firm impressions and occur also beyond the outline of the body. Clearly, the nuclei have been much more resistant to decay and to compression by sediment load than the bodies that enclosed them; nevertheless they can be flattened, giving rise to extra annular rings in

their outer parts. Their thickest portion, a central boss, is often more resistant to com-
pression but some are compressed excentrically. The common preservation, as a cast of
the body enclosing moulds of the more resistant nuclei, is best considered a *positive
composite mould* in the sense of McAlester (1962). Although the usual occurrence of
these fossils is on the depositional lower surfaces of flagstones as positive composite
moulds, they have been collected *in situ* with counterparts in complete reverse on the
upper surface of the underlying bed. In these the mould of the fossil body may be little
altered from the shape it had when the positive composite mould (projecting down from
the bed above) was formed. The nuclei, however, are cast by sediment which infills
their impressions in the overlying bed. It would be tempting to regard them as primary
infillings of hollows in the animals by mud, like the casting of medusa-gonads (Nathorst
1881; Walcott 1898) if it were not for the fact that nuclei can be scattered away from the
body and still make impressions in the sediment which covered them (Pl. 69, fig. 5).
These casts of nuclei are therefore secondary structures, *counterpart casts* (Glaessner
and Wade 1966; Wade 1968) set in the mould of the body. It is probably best to employ
the term *negative composite mould* (McAlester 1962) for the whole complex preservation.

The partial rings of sediment enclosing the identifiable specimen (Pl. 69, fig. 2a)
and its unidentifiable neighbour show that the specimens adhered tightly to the surface,
which is strongly scoured, while the sediment transport was in progress. Twenty or
thirty of these rings were observed on dismembered slabs of the one bedding plane, and
scattered individuals elsewhere, but only a few of the contained specimens were identi-
fiable. Perhaps a certain degree of decomposition caused dead bodies to adhere to the
substrate, for the preservation is exceptionally poor and only one depression that might
have sheltered such a creature in life is known. It is a gently curved hollow with a definite
circular outline, penetrating at least one lamina of sediment, and of the approximate
size to accommodate one of the smaller organisms. Alternatively, this hollow may
represent a specimen which chanced to be buried in the top of a bed; it lies in the
depression between small sedimentary ripples.

The nuclei may be scattered from the centre though still within the disc; many, few,
or none may be seen (Pl. 69, figs. 3, 4). Discs without nuclei are not, strictly speaking,
identifiable, as it cannot be proved that a cast with no nuclei, or a positive composite
mould with one or two displaced nuclei, is the same form as a specimen with nuclei
in place. In the field as well as in the collection, sharp-edged casts, flat to gently curved
very low domes, are a rare accompaniment of the positive composite moulds and may
well represent casts of the aboral side, unmodified except by flattening against the
substrate.

Group B fossils are only half as common as group A. All save one are impressions on
lower surfaces. A cast of the internal spaces (Pl. 69, fig. 12; text-fig. 5) occurs on an
upper surface. The amount of detail shown on latex casts of the moulds is very variable.
They tend towards a smooth, low, featureless dome but none of the larger specimens
have withstood sediment-load to the extent of being quite smooth, and they show
characteristic depressions. One of the least-flattened is illustrated (Pl. 69, fig. 8). Small
specimens, being much more steeply curved and having much smaller radii, withstood
sediment load better, and featureless moulds in this size-range are known. It thus appears
that the usual preservation of group B fossils is as negative composite moulds.

The only distinction between poorly preserved fossils of group A and group B is that they are in opposite relief on the same (upper or lower) surfaces; a few of the most flattened that are possibly group B cannot be distinguished from group A fossils.

Evidence of numerous minute, unidentifiable organisms was seen on slabs like that shown in Plate 69, fig. 7. Some small casts of medusiform shape (Pl. 69, fig. 6) are also known on the bases of slabs but they are not numerous. On the other hand, slabs with their lower surfaces literally covered with structures half way between this medusiform shape and the small load-casts seen on Plate 68, fig. 1 have been found. These minute load-casts are almost ubiquitous. They could have been initiated by hollows where small organisms decayed, but where there is evidence of variable thickness of the clay layers, the load-casts have formed only above the thicker clay. This evidence is supplied by the shape and particularly the texture (Wade 1968) of the undersurfaces of the sandstone slabs, which often indicate that clay was almost confined to ripple-mark troughs while neighbouring ridges were only thinly covered. Jüngst (1934) described a cratering of clay surfaces as clay dehydrates under water but the rather thin layers of clay involved here are not likely to have been able to form deeply indented surfaces. Dehydration could, however, have formed a surface dimpled enough to initiate the formation of these minute load-casts, which have not penetrated into any sedimentary layers below the clay in which they were formed. This supposition fits the confinement of the load-casts to the areas of thicker clay better than either the view that the initial surface-irregularities (and thus the load-casts) are all due to the decay of small organisms, or to scour marks. Their frequent lack of consistent orientation also seems to rule out formation of the initial irregularities by flow of water.

Fossil form A

Genus HALLIDAYA gen. nov.

Type species. Hallidaya brueri sp. nov.

Diagnosis. As for type species.

Hallidaya brueri sp. nov.

Plate 68, figs. 1, 3–6; Plate 69, figs. 1–5

EXPLANATION OF PLATE 68

Figs. 1, 3–6. *Hallidaya brueri* gen. et sp. nov. Positive composite moulds on the undersides of sandstone slabs.   1a–f, Paratypes F16461a–f, ×1; example a is the only one appearing to possess a marginal flange but this is probably due to the superposition of two individuals. Nuclei can be clearly seen in a–e and less clearly in f. Branched, radial canals appear at the left of c. The five-rayed depression at the centre of f may represent its mouth; its left and lower rays bifurcate, the lower of the two right-hand rays traverses one of the four visible nuclei.   3, F16463, ×2; specimen most clearly showing dichotomous branching of radial furrows, nuclei faint.   4, Holotype, F16464a, ×2; specimen with numerous, rather small nuclei; radial furrows show faintly and connect to a circum-central zigzag furrow which is only partly preserved.   5, Paratype F16465, approx. ×1·5; the other specimen which shows a zigzag circumcentral furrow with radial furrows connected to its outer points, and nuclei.   6a–c, F16471a–c, ×2; a, specimen with 13 nuclei; b, c, neighbouring well-preserved specimens with numerous nuclei.

Fig. 2. Lower surface of slab F16470, ×2·6; either the cast of a minute medusiform fossil similar to that shown on Plate 69, fig. 6, or the counterpart cast of an isolated nucleus of *H. brueri*.
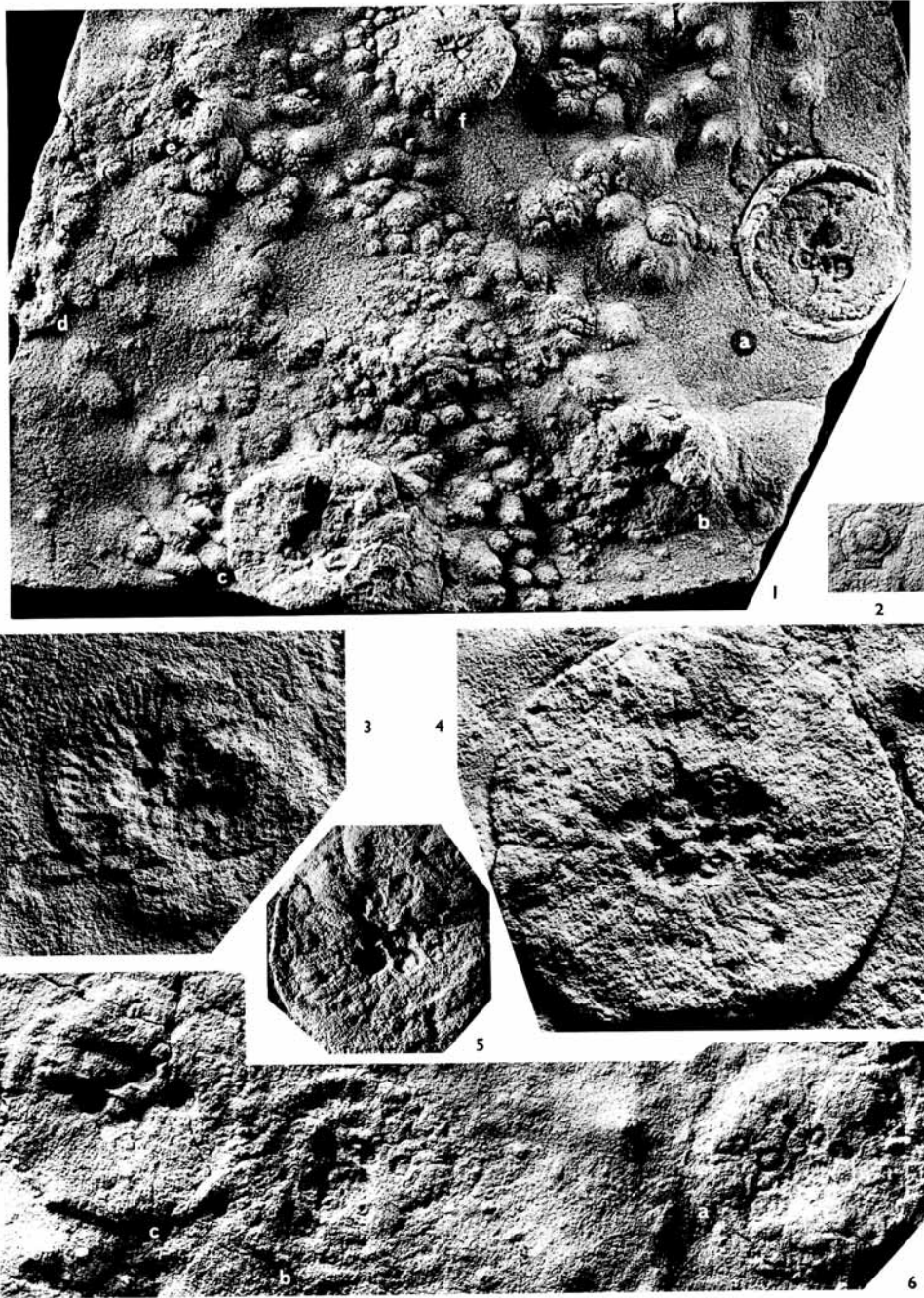
WADE, Medusae from central Australia

Diagnosis. Body disc-shaped, with truncated margin. Surface of elevated discs either flat, depressed in centre above discrete, ringed, inflated structures (here called nuclei), even more widely depressed, or (rarely) gently curved in a very low dome showing, at most, several, scattered nuclei. Branched, radial structure sometimes observed in those with central nuclei; it is clearly preserved only in one specimen where it consists of dichotomously branching, narrow furrows. Concentric corrugations very rare. Nuclei relatively resistant to compression and decay, round to oval in plan view; an inflated, equatorial 'tyre' forms a belt around a central, domed structure. Additional equatorial rings and ovate furrows on the central dome show on flattened specimens. Normal attitude of nuclei flat in one plane around centre of body but if crowded may be tilted and overlapping, 3–13 are known in different specimens.

Holotype. F16464a (Pl. 68, fig. 4).

Material. 49 well-preserved specimens in which both the over-all dimensions of the disc and the detail of at least some of the nuclei can be seen and a number of additional, moderately good to poor specimens; all these are positive composite moulds. Two identifiable negative composite moulds. A few smooth, featureless, casts may also belong here.

Subsequent to the completion of this paper, several specimens of *H. brueri* were collected about 23 km. WSW. of Alice Springs (133° 41′, 24° 37′), in a clayey siltstone approximately a quarter of the distance from base to top of the Arumbera Sandstone. This formation is about 600 m. thick here. It is mapped and recorded in numerous publications, mainly of the Bureau of Mineral Resources, Geology and Geophysics, Canberra, as uppermost Precambrian to Lower Cambrian, or more rarely as wholly Lower Cambrian.

Dimensions. The common size-range is between 10 and 30 mm. in a known range of 5–50 mm. On text-fig. 3 the over-all average diameter of each well-preserved specimen is plotted against the average diameter of the largest well-preserved nucleus present in it. This choice was made to minimize bias in the measurements; while flattening would tend to increase all diameters, the vagaries of tilting or a shallow impression could only act to minimize size, and it would never be possible to establish whether a small impression was the natural result of a small specimen or induced by preservation. The maximum size ratio of smallest to largest well-preserved nuclei in one individual is about 2:3 in this material. It has not been possible to recognize nuclei on specimens smaller than one of 5·5 mm., and specimens without nuclei cannot be identified with certainty. Even with the rather small number of points available to construct text-fig. 3, it suggests a direct relationship between the size of the over-all diameter and the size of the nuclei.

Description. The fossils present several aspects. A few are gently convex, very low domes that show, at most, a few nuclei scattered and tilted at any angle (Pl. 69, fig. 3, F16467). These could be aboral sides as they show no trace of a mouth, or tactile or locomotory organs, nor is there any structure which could obscure their presence. The most common aspect, whether the specimens are flattened or not, has a group of nuclei extending from the centre to occupy one-third to one-half of the diameter of the disc. They would tend to obscure a central mouth or any other insubstantial structure placed in this position. In unflattened specimens the surface is often depressed near the group of nuclei and always depressed where the nuclei are; it also seems decidedly flatter than the probable aboral side (Pl. 68, figs. 1c–f; Pl. 69, fig. 1). From these factors of shape and the association of scattered, tilted nuclei with the more convex side (Pl. 69, fig. 3) it appears that a planoconvex body with the nuclei lying nearer the flat side is the most natural original shape to assume. As the nuclei tend to lie horizontally in a group around the centre, they do not exclude the existence of a centrally situated mouth. Indeed, the

centre-top specimen (Pl. 68, fig. 1*f*) possesses a small, five-rayed depression in this position; it is not a compressed specimen and only faintly shows four nuclei situated between the rays and over one of them; two of the rays branch dichotomously (text-fig. 4*b*). A similar arrangement of three nuclei and a three-rayed impression is known from one other specimen. A number of the specimens with groups of nuclei also show a faint, branching, radial structure which is clearly seen only in F16463 (Pl. 68, fig. 3),
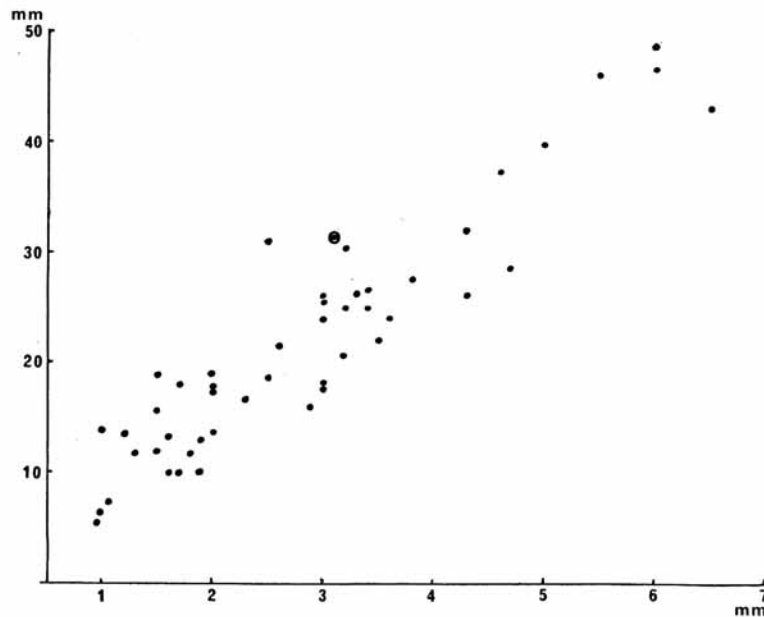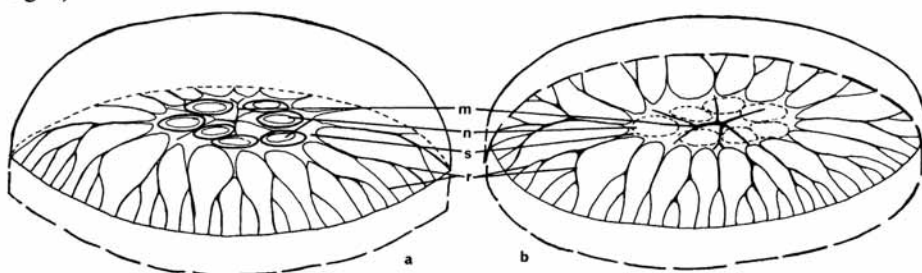

TEXT-FIG. 3. *Hallidaya brueri* gen. et sp. nov. Scatter diagram of the average diameters of the discs in millimetres plotted against the diameters of the largest nucleus in each disc. Holotype circled.

where it is seen to consist of dichotomous furrows. There is not enough structure preserved to tell whether the pattern of branching is regular in detail, but it is apparently always dichotomous. No trace of it has yet been observed on any wholly convex side (i.e. on any of the probable aboral sides), though it shows on some of the most convex of the specimens with nuclei grouped at their centres (Pl. 68, fig. 1*c*). In the holotype and in F16465 (Pl. 68, figs. 4, 5) some radial furrows can be seen to branch from the outer points of a zigzag furrow which partly encloses the centre and is partly obliterated by nuclei.

Some of the nuclei appear to have escaped the confines of ruptured or decayed bodies that may be faintly indicated on the same bedding plane (Pl. 69, fig. 5, F16468) but others are found completely free. Even when free of the discs, they normally held up the sediment long enough to form external moulds on the bottoms of overlying beds. Some casts of this general size have the proportions of nuclei (Pl. 68, fig. 2, F16470) and are

also found on the bottoms of beds; either they represent counterpart casts of nuclei which were partly buried in the top of a sediment layer, or the medusiform creatures responsible for such casts as that shown in Plate 69, fig. 6 can overlap the nuclei in proportions as well as size. Some casts which appear to represent uncrushed and partly crushed nuclei are present on a few bedding planes crowded with innumerable small, wrinkled, circular fossils which have the size range 3–6 mm. and could be either totally flattened nuclei or the minute medusiform creatures. They have the appearance of having been strongly inflated but are now flattened to an unidentifiable film (Pl. 69, fig. 7).

TEXT-FIG. 4. *Hallidaya brueri* gen. et sp. nov., approx. ×2. Restored as a translucent medusa showing the structures illustrated in Plate 68, figs. 1, 3–6; Plate 69, figs. 3, 5. *a*, oblique exumbrellar view; *b*, oblique subumbrellar view; *m*, mouth (Pl. 68, fig. 1*f*); *n*, nuclei (many figs.); *s*, central stomach (partially visible in Pl. 68, figs. 4, 5); *r*, radial canals (Pl. 68, figs. 1*c*, 3–5). The marginal flange shown here by dashed lines is seen only in Plate 68, fig. 1*a* and is probably due to superposition of a larger specimen on a smaller (several examples of partial superposition are known, e.g. Pl. 69, fig. 1*a*).

Interpretation. As these fossils are of soft-bodied animals of which no original material remains, we are left with a record only of the general shape and relative durability of some of the organs. Association of certain structures in the fossils allows us to assume their closeness, and dissociation their separation, in the undistorted animal. Besides circular outline, it is notable that the mass preservation of the discs is convex downward on lower sediment faces. Another feature is that the nuclei are present as moulds. From these factors we see that the animals were buried in, or adhered to, sediment surfaces, and were still present, either dead or alive, when the sand covered them but collapsed quickly allowing it to cast them. The nuclei, however, did not collapse but were tough enough to support the sediment until it set into moulds. The nuclei were discrete structures which could be displaced from their original position but probably would then also suffer relative displacement such as we observe. In elevated specimens, radial, branching furrows may show on the side of the disc that has the nuclei in orderly grouping, but not on sides with smooth, elevated contours in which only impressions of displaced nuclei can be seen. (Radial structure can also show, as do nuclei, in flattened specimens—in these the characters of the side with centrally grouped nuclei always prevail to some extent over the featurelessness of the side which shows displaced nuclei, or none.)

Assembling all these characteristics we have a circular body curved in a low dome on one side, the curve of the dome covering structureless material that disintegrated quickly

upon burial. The opposite surface is flatter. It is either naturally concave or poorly supported in the central region. It is most frequently smooth but in some specimens shows branched, radial furrows across its outer part; these may be related to a sub-surface system of canals which occasionally forms impressions on the casts, as their usual absence would be very difficult to explain if they were to be regarded as a system of surface markings. Their pattern is consistent with medusan—particularly scyphozoan —radial canals, and they branch from the outer points of a rather zigzag furrow around the centre, which could represent a central stomach. At about the same level as the canals we have to place the nuclei. Normally assembled around the centre and lying in one plane, they must also be beneath the epidermal layer, as they sometimes scarcely show (Pl. 68, fig. 1 *b*, *f*), but the actual depth is probably rather variable: in specimens in which they are very numerous they overlap somewhat. There is also the possibility that a central mouth is represented by the star-shaped slits, which are rarely observed in the centres (Pl. 68, fig. 1*f*). The structure of marginal and submarginal furrows seen in Plate 68, fig. 1*a* may represent two superimposed specimens or, perhaps, a nearly vertical marginal flange like a velarium.

In summary, the proposed reconstruction indicates a medusiform body almost certain to be a coelenterate medusa (text-fig. 4), whether Plate 68, fig. 1*a* is taken to represent a marginal flange or not. The nuclei are placed in a position which would allow them to be connected with the gastral epithelium, which is a common position for reproductive structures in modern medusae; these also grow throughout life. The behaviour of the nuclei as firm, discrete bodies cannot be equated with present day medusoid gonad struc-tures except, perhaps, those in which the embryos are incubated during early development. They are more probably the early stages of medusoid buds, but their later development is not known. The possibility of their being food material has to be considered also but


EXPLANATION OF PLATE 69

Figs. 2 and 12 are of the depositional tops of sandstone slabs; all others are from the bases of slabs.

Figs. 1–3, 5. *Hallidaya brueri*, gen. et sp. nov., paratypes.   1*a–c*, F16462*a–c*, ×1; *a*, superimposed specimens; *b*, the largest individual, showing the strongest development of concentric ridging, which is also seen on *c*.   2*a*, *b*, F16466*b*, ×1; negative composite moulds.   3, F16467, ×1; positive composite mould of probable aboral side showing 3 tilted and 1 horizontally-placed nuclei.   5, F16468, ×2, scattered nuclei, probably of 2 individuals, one of which is centred on the nucleus near the centre of the picture.

Fig. 4. cf. *Hallidaya brueri*, F16469, ×1; probable aboral side.

Fig. 6. Cast of minute medusiform fossil, F16471*d*, ×2.

Fig. 7. Minute fossils which appear to have been circular and inflated but very flattened during fossilization. F16472, ×1. Reverse side of slab shown in fig. 12.

Figs. 8–12. *Skinnera brooksi* gen. et sp. nov. 8, 9, ×1; 10–12, ×2;   8–11, negative composite moulds; 12, internal mould.   8, Paratype F16475*k*, relatively smooth, large specimen, centre undulating and partly surrounded by 8 secondary depressions spaced around half the perimeter.   9*a*, *b*, Paratypes, F16475*a*, *b*; *a*, irregularly flattened, large specimen; *b*, earliest identifiable growth stage with 3 large inner depressions and a fourth, smaller depression.   10, Paratype F16476; a small specimen with 3 inner depressions ringed by 13 visible secondary depressions and a small obscured area.   11, F16474*a*, *b*; *a*, holotype with 3 large, pouch-shaped inner depressions and 15 secondary depressions. *b*, Paratype with 3 inner depressions and 15 secondary depressions.   12, Paratype internal mould F16473, showing 3 inner pouches with broken canals at their inner ends, 15 secondary pouches attached by double canals to the inner pouches or the central area, and more complex structures placed between, and toward the margin from, the secondary pouches.
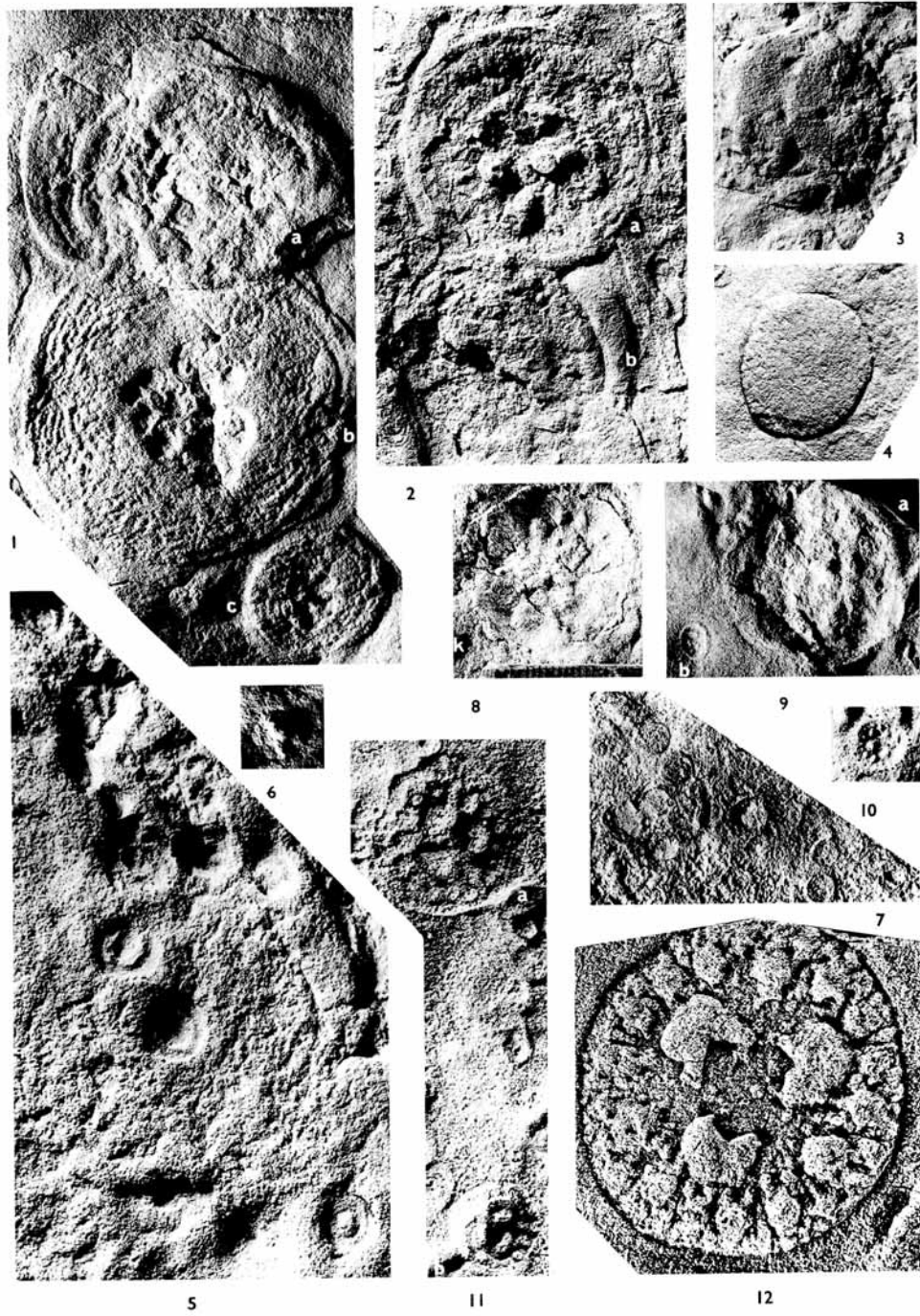
WADE, Medusae from central Australia

their rather small size range at any size of the body seems against this (text-fig. 3), as is the lack of oral sides without nuclei, and the lack of specimens that might be partly digested.

An early view that these bodies might represent some sort of embryo capsule with developing embryos, rather than an entire animal, seems negated by the constant growth-rates of the nuclei and the bodies, and the overall medusiform character of the bodies.

The system of radial canals in *H. brueri* is of a complexity very rarely reached in the Hydrozoa but frequently found in the Scyphozoa. The apparent depth of the nuclei within the body suggests also that they were more likely to have been related to the gastral epithelium than to have been invaginations in the sub-umbrella. The structure of the probable mouth resembles the bifurcating mouth-furrows of *Rhizostomites admirandus* Haeckel but is not as regular. Although it apparently had only blunt, finger-like lips like *Rhizostomites* and similarly lacked a manubrium, it shows no other similarities to *Rhizostomites* and stands apart as a primitive scyphozoan-like medusa without known, close relatives.

Fossil form B

Genus SKINNERA gen. nov.

Type species. Skinnera brooksi sp. nov.

Diagnosis. As for type species.

Skinnera brooksi sp. nov.

Plate 69, figs. 8–12

Diagnosis. Circular, low-domed, soft-bodied animals, relatively higher in proportion to width in smaller specimens. Probable original shape plano-convex. Body resilient but differentially compressible, revealing the pattern of major, internal, pouch-shaped spaces by its surface depressions, which form a group of 3 large inner depressions near the centre with a ring of 15 secondary depressions (wherever these can be counted) outside them. The 3 largest, inner depressions tend to be pouch-shaped with a concave curve toward the axial region like the inner pouches of a complete internal mould. In this, a network of paired canals connects the 3 inner pouches to the centre on one side and to 15 secondary pouches in a ring outside them but minor spaces and connections near the margin may be reticular. Only the 'inner' depressions are seen on the smallest individuals.

Holotype. F16467a (Pl. 69, fig. 10a).

Material. 26 negative composite moulds and 1 internal mould. Several small, smooth, external moulds and a number of very distorted specimens may belong here. They are described from latex casts of the natural moulds.

Dimensions. The ratio of height to width decreases markedly with increasing size. This is no doubt exaggerated by the larger specimens being more prone to sag against the substrate. Most of these are badly distorted (Pl. 69, fig. 9a). The range of average diameter is from 3·9 mm. to 32 mm. with a decided maximum frequency in the vicinity of 10 mm. Maximum height known is about 2 mm. regardless of diameter.

Description. The low-domed bodies were probably smooth prior to burial but tended to sag under load into a pattern of ridges and hollows which is standard for various growth stages, though more obscure in some specimens than others. The smallest specimen shows, in the cast, a pattern of three large, oval depressions and a fourth smaller one to one side, with prominent, smooth ridges between them (Pl. 69, fig. 9*b* shows the
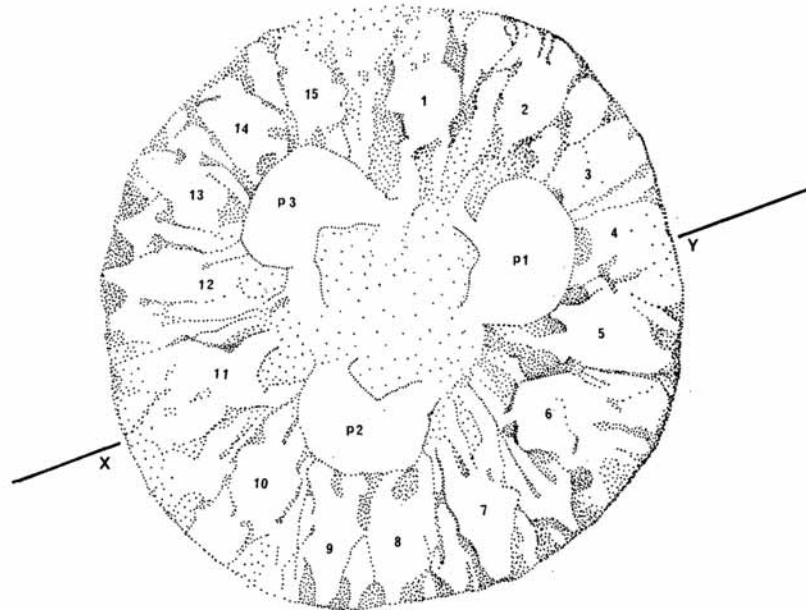
TEXT-FIG. 5. *Skinnera brooksi* gen. et sp. nov., F16473, paratype, ×3·1. Clear areas represent gently rounded prominences on this internal mould and stippled areas the depressions that bound the prominences. Depressed areas with obscure structures are lightly stippled. Coincidence of the dominant shear direction (x, y) in the rock and the radial canals partly obliterates the natural structure near the margin, as does chipping of the margin above. Inner pouches, p1–p3; secondary pouches, 1–15; of these, 1, 6, and 11, situated between the inner pouches, are larger than the others. They probably attached directly to the central area (?stomach) as their paired canals run radially and are much longer than those between inner and secondary pouches. There is no trace of structure derived from a ring canal in the plexus of small structures near the margin.

original). This characteristic ridging between the depressions is common to all identifiable small specimens. Numerous secondary depressions are lacking in the very smallest individuals; this may be an artifact of resistance to compression and not due to the structures they indicate forming at a later growth stage. The inner depressions are the largest and they are frequently pouch-shaped, concave on the axial side. No specimen has more than these 3 largest depressions possessing concave axial sides. In the holotype the 3 secondary depressions placed between the inner depressions are larger than the remaining 12 which occupy relatively more cramped positions. The accompanying

paratype (Pl. 69, fig. 11a, b) has the same number of depressions with similar proportions, and the structures are again evident in the internal mould (Pl. 69, fig. 12) where they are expressed as sand mounds, apparently casting a system of natural spaces. In this internal mould a third order of peripheral spaces is also cast by sand but the structures are small, and obscure in detail. Only the holotype, among the negative composite moulds, shows any evidence of these peripheral spaces, and that only by a few peripheral depressions exterior to the secondary depressions. In one or more sectors of several other specimens the number of secondary structures is 5 to each inner pouch (or depression). One specimen has only 3 secondary to one inner depression in the only sector in which they can be counted. In medium-large specimens (Pl. 69, figs. 11a, 12) the secondary structures may be radially elongate, to scarcely visible in relatively uncompressed specimens (Pl. 69, fig. 8). In a number of the larger specimens the centre is obscure but the pattern of depressions and ridges in the outer parts is radial. The most enlightening single specimen (Pl. 69, fig. 12; text-fig. 5) shows elevations of sandy sediment occurring in the relative positions of every depression known from fossils of the external surface. It seems this is an internal mould of a system of natural spaces in the body. The low, convex disc on which the internal mould is displayed may approximate the shape of the underside but it is more likely that the lower surface disintegrated, allowing the entry of sand to even small canals and spaces. The sand fill is identical with the substrate and the margin is a very sharply depressed furrow. Text-fig. 5 was drawn from the specimen onto a $5\times$ enlarged photo to achieve accurate proportions and overcome difficulties in illuminating the radial structure. Its lightly stippled centre indicates where the internal cast was either too shallow to form definite markings, or weathered or chipped away. 3 purse-shaped, inner pouches taper to canals at both axial ends. These canals appear broken off, as though once attached to a central stomach which is not delineated here because the numerous faint markings in the centre offer too many possible shapes for unprejudiced restoration. A system of paired canals attaches the 3 inner pouches (or, between them, the axial 'stomach' region) to 15 secondary pouches symmetrically placed in a ring nearer the margin. These are separated by, and give rise to, smaller connections and spaces too complex and small for clear preservation. These appear to be connected in a reticular manner. Canals do not multiply by branching.

Interpretation. The shape of the internal system of spaces and canals closely parallels the gastrovascular system of a medusa of the scyphozoan grade of complexity. The central area may be equated to the stomach, with double connections to the 3 large inner pouches and through these (or by-passing them in the inter-spaces) with double connections to the 15 secondary pouches and further connections to the still smaller subdivisions. The present evidence is of dominant 3-fold symmetry. It is tempting to regard the inner pouches as the direct homologue of the scyphozoan gastric pouches. They may be, but they differ from any modern scyphozoan system (see, e.g., Mayer 1910, Hyman 1940, Thiel *in* Rees 1966) in each pouch being connected to the central stomach by 2 widely separated canals; again, the canals to the secondary pouches are also double; even in the marginal plexus, minor spaces and narrower connections are still recognizable and the whole is distinctly different from the more uniform plexus development of a number of Semaeostomeae and Rhizostomeae. The similarities are probably due to convergence and it is not likely that *S. brooksi* is ancestral to any modern medusa.

Despite the initial impression of similarity produced by the similar size and curvature of *H. brueri* and *S. brooksi*, they have very little in common. *H. brueri* has narrow, dichotomously branched, radial canals. *S. brooksi* has its central stomach leading by paired canals into 3 inner pouches, and thence to numerous, more marginally placed pouches from which canals again branch. No example of a branching canal has been seen, though there may be reticulate connections near the margin. While in *H. brueri* reproduction by medusoid buds or incubation in the gonads appears to be firmly established, there is no evidence of this in *S. brooksi*. *H. brueri* has a normal texture to its mesogloea and collapses quickly when buried, forming casts. *S. brooksi* is much more resistant and under the same conditions forms moulds.

There is little evidence of 4-fold symmetry in these two species or among the medusoid forms from Ediacara (Upper Precambrian), nor is it a striking feature of the Cambrian medusoids (Nathorst 1881; Walcott 1898; Moore 1956), though in Mesozoic times it appears to have been well established. The taxonomic importance of 4-fold symmetry in medusae has been emphasized by the loss of the less regular forms and the diversification of the more regular forms to produce the modern aspect.

The few known fossils do not allow us to reconstruct scyphozoan phylogeny from fossil material, and the field has been left largely to workers on Recent forms who are in general agreement on the degrees of relationship within the modern scyphozoans but in notable disagreement about which gave rise to which (Thiel *in* Rees 1966). Thiel's careful assessment of characters in common leads back to an ever more strongly tetramerous ancestral form for the Scyphozoa. Chapman's work (*in* Rees 1966) verifies earlier placement (Kiderlen 1937, *vide* Moore 1956) of the Conulariida as ancestral to scyphopolyps and relatively close to Stauromedusae. The long range of the Conulariida, now extending to Upper Precambrian (Glaessner and Wade 1966) would provide ample time for the course of differentiation proposed by Thiel. In any discussion on the ancestral form of the Cnidaria the position of the early medusae, which are not Hydrozoa nor placeable among modern Scyphozoa, needs consideration. There seems no place in Thiel's scheme for the non-tetramerous fossil forms, even for those like *Hallidaya* and *Skinnera*, as complex (in the characters we know) as the younger scyphozoans. Extending the concept of Scyphozoa beyond its limitation to modern forms, however, it is reasonable to classify these new forms as parts of an early scyphozoan radiation.

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MARY WADE
Department of Geology
The University of Adelaide
Adelaide
South Australia