KIRKLANDIA TEXANA CASTER— CRETACEOUS HYDROZOAN MEDUSOID OR TRACE FOSSIL CHIMAERA?

by F. T. FÜRSICH and W. J. KENNEDY

ABSTRACT. A re-examination of *Kirklandia texana* Caster, 1945 described originally as a medusoid hydrozoan, revealed stratinomic, preservational, and morphological features incompatible with interpretations as a body fossil. An alternative interpretation, with the 'bell' of *Kirklandia* as a feeding trace of *Gyrophyllites* type and the 'arms' as fecal-pellet-lined burrows comparable with *Granularia*, satisfactorily explains these anomalous features. The genus *Kirklandia* and the family Kirklandidae should be removed from the Coelenterata and the medusoid hydrozoans (order Trachylinida) thus have no unequivocal fossil representatives.

THE last hundred years has seen the description of a variety of actual or supposed fossil hydrozoan medusae. These range from mere stellate impressions on the top surfaces or soles of sandstones, through lobate concretions and composite moulds to material retaining details of internal organs, tentacles, and umbrellar ornament (Rüger and Rüger-Haas 1925; Kühn 1937; Rüger 1933; Kiderlen 1935; Lörcher 1931; Huene 1901; Caster 1945; Kolb 1951; Sprigg 1947, 1949; Harrington and Moore 1956; Glaessner 1961, 1962, 1966; Glaessner and Wade 1966; Wade 1968). These fossils have in turn been used to draw conclusions on topics as distant as coelenterate phylogeny (e.g. Rüger 1933; Caster 1945) and intertidal exposure (Rüger 1933).

In the Treatise (Harrington and Moore 1956) some eight fossil genera are tentatively classed as hydrozoan medusae. Of these, Beltanella Sprigg, 1947 and Ediacaria Sprigg, 1947 from the late Precambrian Ediacara fauna of South Australia are undoubted medusoids, but cannot be referred with confidence to any of the coelenterate classes (Glaessner and Wade 1966). Acalepha Beyrich, 1849, Acraspedites Haeckel, 1869, and Hydrocraspedota Kolb, 1951 are doubtfully classed as Trachylinid medusae, whilst Atollites Maas, 1902 and Palaeosemaeostoma Rüger, 1933 are definitely trace fossils (Seilacher 1955, 1962; Vialov 1968; Häntzschel 1970 with references; Grubić 1970 with references). Thus only the genus and species Kirklandia texana Caster, 1945 remains as a hitherto undisputed fossil record of the medusoid hydrozoans, the Trachylinida, and the sole member of the Family Kirklandidae Caster, 1945. This species is known from scores of individuals from the Albian Paw Paw Formation of Texas, and there is an additional doubtful record of the genus from the German Dogger (Lörcher 1931). The Cretaceous material occurs typically as sharp sandstone external moulds preserved in full relief. Caster recognized a remarkable degree of structure interpreted as a lobate body typically divided by eight adradial sulci, petaloid stomach pouches, genital sacs with paired gonads, a quadrate, functional mouth, and eight apparently rod-like tentacles covered in pustules, interpreted as nettling structures.

During the summer of 1974 we had the opportunity of studying the holotype and [Palaeontology, Vol. 18, Part 4, pp. 665-679, pls. 78-80.]

paratype material preserved in the Smithsonian Institution, Washington, D.C., and a large number of additional specimens housed in that institution and the Texas Memorial Museum, Austin, Texas. With the paratype material preserved in the University of Cincinnati Museum, Princeton University Museum, and other collections (Caster 1945, p. 186) over a hundred individuals are available for study. They suggest that, on the basis of preservation and morphology, *Kirklandia* is not a medusoid, but rather a chimaera—a chance association of a feeding burrow of *Gyrophyllites* type and a fecal-pellet-lined or stuffed burrow-*Granularia*.

THE MATERIAL

Preservation. The Kirklandia material studied here consists predominantly of depressions—described as natural moulds by Caster (1945)—on the top surfaces of thin-bedded, ripple cross-laminated fine sandstones with a calcareous cement. The sandstone slabs are generally less than 10 cm in thickness, and laminations are generally well preserved, although showing some biogenic disturbance. These are cylindrical burrows both normal and sub-parallel to bedding, some being empty (although originally clay infilled), others with meniscus-like back fills. Escape structures are frequent. Bottom surfaces bear common sole markings; some of these are of inorganic origin, while others are meandering and branching burrows preserved in positive hyporelief. Top surfaces are often covered in diverse burrows in addition to Kirklandia (Caster 1945, p. 186, pl. 4, fig. 6). There are also three supposed natural casts of Kirklandia preserved as ellipsoidal sideritic and pyritic concretions (Caster 1945, pl. 5, figs. 1–5).

Occurrence. The bulk of the Kirklandia material originates from the area around Roanoke in Denton County, Texas. The supposed natural casts are from Gainesville, Texas. The former region coincides with what Sellards et al. (1966) describe as their second facies of the Paw Paw, a blackish lustrous clay with ironstone and jasper-like concretions and occasional sandstone ledges. The facies around Gainesville is somewhat similar (Hill 1901). The sandstones occur interbedded with clays which yield an extensive normal marine fauna, including diverse ammonites (Adkins 1920, 1928; Clark 1965). The whole is interpreted as representing a relatively offshore environment.

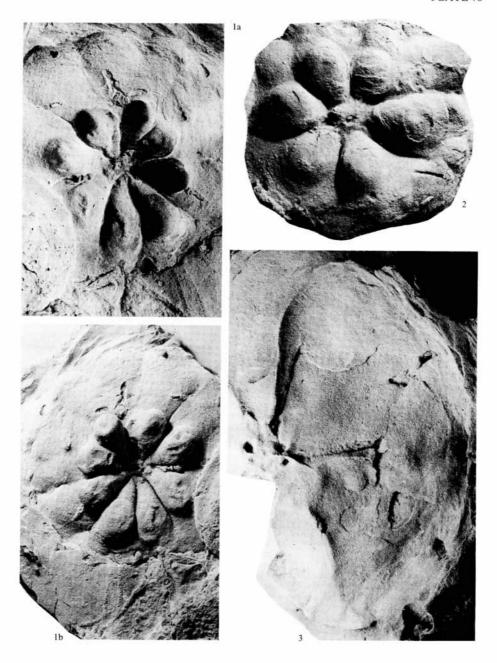
Morphology. Caster (1945) provides a lengthy description and extensive illustrations of Kirklandia and only an outline is therefore needed here. Kirklandia consist of scalloped depressions, generally from 40 to 100 mm in diameter and up to 35 mm depth. There is, in our view, no consistent symmetry other than radial. Up to three

EXPLANATION OF PLATE 78

Fig. 3. A further specimen, preserved as a negative epirelief, from the same locality.

Fig. 1a-b. The holotype of Kirklandia texana Caster. 1a, the negative epirelief, from the Paw Paw Formation (Albian), 2 miles west of Roanoke, Denton County, Texas, USNM 136131a. 1b, silicone mould of same, OUM KT 8/P.

Fig. 2. Silicone mould of a specimen from the Paw Paw Formation (Albian) at USGS Mesozoic Locality 22258. Blue Mound, 5 miles south of Haslet, Tarrant County, Texas. OUM KT 9/P.



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cycles, each with from five to sixteen lobes, are present within the structure (Plate 78, figs. 1–3; Plate 79, figs. 1–3; Plate 80, fig. 3; text-fig. 1), six or seven being the commonest lobe number. Lobes vary enormously in relative development within cycles, and may be equal or highly unequal. The divisions between lobes, preserved as tapering walls of sandstone (Caster's radial sulci), are likewise variable in development, whilst the depressions between vary from deep and narrowly rounded (Plate 78, fig. 1*a*–*b*) to the shallowest of scoops (Plate 78, fig. 2; Plate 79, fig. 2; text-fig. 2). One of the most critical features of these lobes is that many are associated with definite overhangs—partial roofs of sandstone (text-fig. 2).

The outermost cycle of lobes is in general the shallowest and most poorly differentiated. The intermediate, generally deeper, cycle consists of two lobe types. There are elongate petaloid structures extending to the centre of the disc (Caster's insert lobes) and those which are reduced, triangular, and peripheral (Caster's exsert lobes; see text-fig. 1). The lobes of the innermost cycle are deep inflated structures corresponding approximately with the position of the longer petaloid 'insert' lobes of the middle cycle. Lobe surfaces commonly show distinct, subparallel concretic striations (Plate 79, figs. 2–3). Caster regarded these as wrinkles resulting either from desiccation shrinkage prior to burial, or rigor mortis contraction (Caster 1945, pp. 176, 180).

In the centre of the disc there may be depressed areas with a conical protuberance and an axial and tubular pit (Plate 78, fig. 1a-b; Plate 79, figs. 2-3). The 'arms' of Kirklandia described by Caster are tubular, sometimes branching cavity systems extending through the sandstone slabs (Plate 80, fig. 7a-b), or mere depressions on top surfaces (Plate 80, fig. 6). The tubes are about 10 mm diameter, and their surfaces are covered in randomly orientated ellipsoidal depressions up to 1.5 mm in length (Plate 79, fig. 5 and Plate 80, figs. 6 and 7 show silicone rubber moulds of these).

THE MEDUSOID INTERPRETATION

The original view. Text-fig. 1a-b shows Caster's original interpretation of Kirklandia as natural moulds of the oral or subumbrellar surfaces of trachylinid medusae. The outer cycle of lobes are interpreted as the peripheral zone of the umbrella, the central cycle as the gastric lobes, and the inner cycle as gastrogenital sacs. Obscure structures on some specimens are interpreted as paired gonads within genital sacs. The central area, conical protuberance, and central pit are interpreted as the mouth and associated

EXPLANATION OF PLATE 79

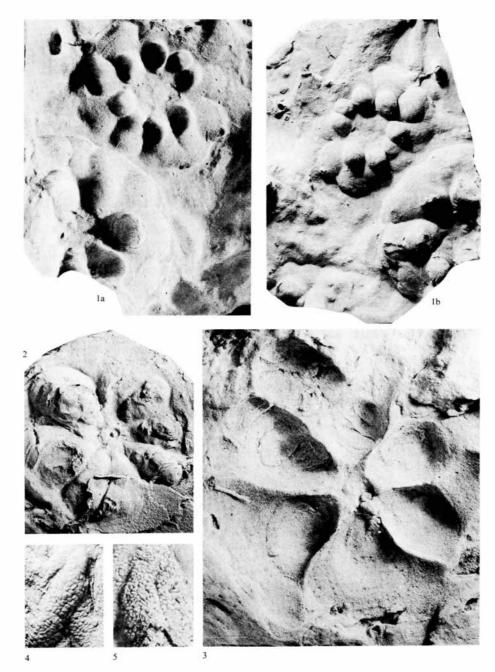
Fig. 1a-b. A paratype of Kirklandia texana Caster. 1a, the negative epirelief, USNM 136131b, from the Paw Paw Formation (Albian), 2 miles west of Roanoke, Denton County, Texas. 1b, silicone mould of same, OUM KT 11/P.

Fig. 2. A silicone mould of Kirklandia texana, from the Paw Paw Formation of USGS Mesozoic Locality 22258, Blue Mound, 5 miles south of Haslet, Tarrant County, Texas. OUM KT 13/P.

Fig. 3. Same locality as fig. 2, preserved as a negative epirelief.

Fig. 4. Surface details of a specimen of the fecal-pellet-lined burrows *Granularia* from the Atherfield Clay Series (Lower Aptian), Atherfield, Isle of Wight, Hampshire. BMNH A6208 (Stinton Collection), × 2. Fig. 5. Surface details of a silicone mould of the 'arms' of *Kirklandia texana* from the same locality as

fig. 2; compare with the *Granularia* shown in fig. 4, OUM KT 12/P, ×2.



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organs, the mouth being quadrate (text-fig. 1a). The granules on the 'arms' are interpreted as stinging cells.

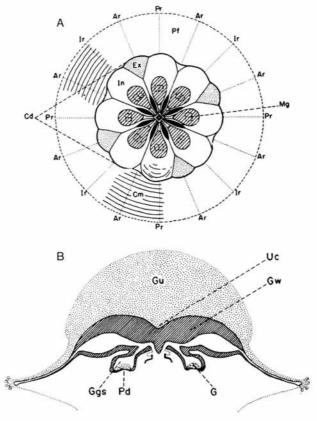
Objections. 1. Preservation potential of medusoids. There are three chief situations in which medusoids can become fossilized. (1) In the intertidal zone, (2) associated with very fine grained sediments in restricted environments and burial by special mechanisms, as is the case of the Solnhofen Limestone and Burgess Shale occurrences, and (3) as a result of rapid burial by clastic influx in exceptional conditions, as at Ediacara

Observations on the preservational potential of medusoids, albeit brief, are widespread. The early studies and experiments of Walcott (1898) are now classic; there are more recent observations by Trusheim (1937), Wagner (1932), Schäfer (1941), Lincke (1956), Müller (1970), experiments by Hertweck (1966), and extensive biostratinomic discussion by Schäfer (1962, pp. 212-216; available in English translation 1972, pp. 157-190, pls. 37b-39a). Medusoids can be preserved only as moulds, and exposure and desiccation are a prerequisite; they cannot occur as body fossils. The mould is produced by body and organs within a few hours of stranding, and the precise organs identifiable on moulds depend on sediment grain size, water content, and rate of decomposition amongst other factors. As the buried bell decays and subsides the overlying sediment collapses, and all that remains is a composite mould, perhaps picked out by a thin clay veneer, above which is a region of disturbed and crumpled lamination. In some cases the gastrovascular cavity and genital pouches can fill with sediment, either passively, or as a result of inadvertent ingestion during pumping motions as the stranded organism tries to escape. These 'stomach stones' have preservation potential, and indeed Walther (e.g. 1910) and others have described such objects.

The second category of fossilization again results in the preservation of the medusoid as a composite mould, or mere film of organic material. The best-known examples are the Solnhofen Limestone, Germany (Barthel 1964, 1970; Van Straaten 1971) and Burgess Shale, Canada (Whittington 1971; Piper 1972a, b). In both cases the medusoids (and indeed other fauna) were buried in very fine-grained material, apparently by turbiditic mud clouds (microturbidites) in local euxinic basins.

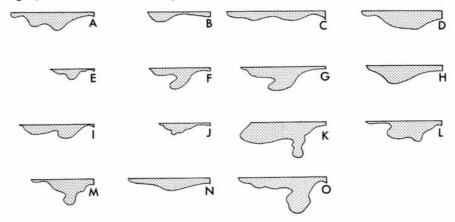
The Ediacara occurrences of Australia (Wade 1968; Goldring and Curnow 1967) are in relatively coarse-grained sediment. Medusoids occur as moulds in two situations. The commonest is in positive relief on the bottom of sandstone laminae; after rapid burial tissues decayed, and sediment collapsed into the void to produce a species of composite mould. If a clay lamina was present between quartzitic laminae, a counterpart mould may also occur on the subadjacent lamina (Wade 1968, figs. 7, 9, 11). In all cases the mould has an extremely low relief.

2. Comparisons with Kirklandia. The Kirklandia material shows none of the features of preservation and preservational environment seen in undoubted fossil medusoids. The fauna, sedimentology, and palaeogeographic setting of the Paw Paw in the area yielding the specimens studied are offshore, normal marine, with no evidence of intertidal exposure, nor of restricted bottom conditions nor burial in fine-grained sediment. The material occurs with full three-dimensional relief on the top surfaces of



TEXT-FIG. 1. The medusoid interpretation of Kirklandia. A, oral or sub-umbrellar view showing the basic four-part symmetry. According to Caster, the mutability of the species is attained by asymmetrical centripetal insertion of exsert lobes and perhaps by splitting of the canaliculate radii. B, axial section through the restored disc of Kirklandia. Known features are shown in solid outlines; all others inferred from similarities to the trachyline hydrozoa. Ar, adradius; Cd, central disc; Cm, delicate circular corrugations or rugae of the peripheral zone (possibly ring-muscles or velar muscles); Ex, exsert lobes; G, inferred internal gonads; Ggs, gastrogenital sacs on the radial canals; Gu, implied gelatinous umbrella; Gw, gastric wall or shrunken residue of gelatinous umbrella; In, insert lobe; Ir, interradius; Mg, low carina between ovoid depressions on the swollen protuberances (perhaps indications of the gonads within the gastro-genital pouches); Pf, peripheral field (subumbrella or velum); Pr, perradius; Uc, umbral concavity of aboral surface (modified from Caster 1945, fig. 1 and fig. 4).

sandstones and therefore cannot be compared with the Ediacara material. Furthermore, sections show the *Kirklandia* cutting across laminations, rather than distorting laminae, which suggests a post-depositional emplacement. Perhaps the most serious objection to a medusoid origin is the presence of overhangs in many sections (text-fig. 2). These could survive only if cementation occurred prior to decomposition of



TEXT-FIG. 2. Cross-sections of *Kirklandia* lobes (after Caster 1945, fig. 5). Note overhanging rims and partial roofs of sediment to lobes in many specimens.

the coelenterate tissue. In the environment indicated for the Paw Paw, such decomposition would take only hours or days; there is none of the petrographic evidence of early cements reviewed by Bathurst (1971), whilst the distortion by compaction of some burrows and the obvious cross-cutting relations of others suggest a relatively late date for cementation. Finally, if these indeed are medusoids, the absence of material preserved on bottom surfaces is curious. The supposed

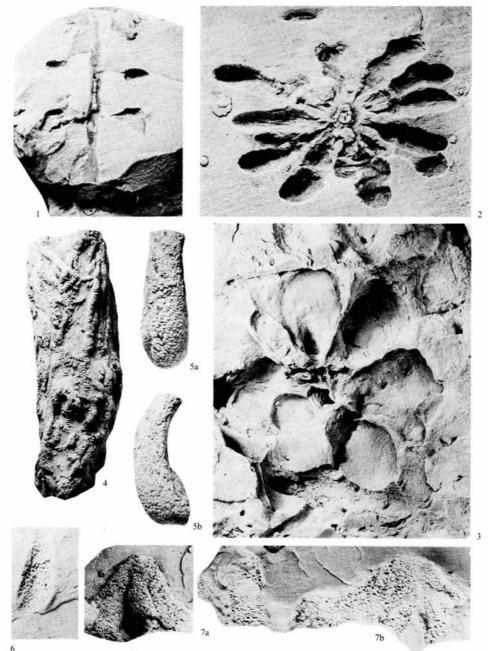
EXPLANATION OF PLATE 80

Figs. 1-2. 'Caulerpa carruthersi'—Gyrophyllites preserved in three dimensions. Fig. 1 is BMNH 25 (Damon Collection) a section normal to bedding; fig. 2 is BMNH V 2546 (Damon Collection) a section parallel to bedding. These specimens have been preserved by early diagenetic cementation of the clay matrix they were excavated in (compare text-fig. 3a). Kimmeridge Clay (Kimmeridgian) of Sandsfoot, Dorset, × 2

Fig. 3. Kirklandia texana Caster. Specimen preserved as a negative epirelief on the upper surface of a sandstone slab from the Paw Paw formation (Albian) of USGS Mesozoic Locality 22258, Blue Mound, 5 miles south of Haslet, Tarrant County, Texas.

Fig. 4. Granularia sp. BMNH A789 (Wethrell Collection) from the London Clay (Yprisian) of Chalk Farm, London.

Fig. 5. Granularia sp. BMNH A6154, a club-shaped specimen from the Atherfield Clay Series (Lower Aptian) of the Lower Greensand, Atherfield, Isle of Wight, Hampshire. Compare with fig. 6 of this plate. Figs. 6, 7a-b. Moulds (6, 7b) and silicone impression (7a; OUM KT 10/P) of Kirklandia arms from the Paw Paw formation (Albian) of USGS Mesozoic Locality 22258, Blue Mound, 5 miles south of Haslet, Tarrant County, Texas.



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'natural casts' of *Kirklandia* are equally unlikely to be medusoids, since all other workers have concluded that body fossils of medusoids cannot be preserved.

We stress that the depositional environment of the Paw Paw, where Kirklandia is found, is neither one of fine-grained substrate and rapid burial under restricted conditions, nor is it intertidal. In addition there is no stratinomic or petrographic evidence to suggest that these were body fossils buried in sediment and preserved in three-dimensions by rapid cementation; they are a post-deposition phenomenon and their matrix was cemented at a relatively late date.

The biological problems of accepting *Kirklandia* as a medusoid were discussed by Caster (1945, pp. 187 et seq.). Thus his genus not only mingles features of the Narcomedusidae and Trachymedusidae, but also includes many unique traits, the most striking of which is the enormous variation in the number of body lobes and symmetry.

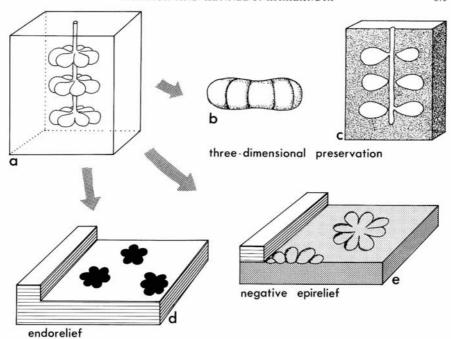
KIRKLANDIA AS TRACE FOSSILS

What we believe to be the true nature of *Kirklandia* is suggested by Caster's (1945, p. 184) comment, where he notes two specimens which 'show either arms or worm burrows emanating from the central area of the mould. In one the burrow-like structure enters the rock, and its termination is unknown. In the illustrated specimen, the two "burrows" terminate in large fusiform expansions, unlike anything seen on any of the worm spoor interlacing the matrix of most slabs."

We have sectioned a number of specimens, and some of these clearly show an open, or sediment filled, vertical cylindrical burrow extending down into the sandstone slab from the centre of the 'mouth' of *Kirklandia*. This feature recalls the relationship demonstrated by Häntzschel (1970, p. 207, pl. 2) in very similar stellate depressions on the top surfaces of Lower Jurassic sandstones. Häntzschel interpreted these structures as a surface trace, produced by the surface grazing of an animal dwelling in the central tube. The difficulty in applying this interpretation to *Kirklandia* is that it does not explain the overhangs associated with many of the deeper lobes, the presence of several cycles of lobes, or the observation that a central burrow is not always present. We would therefore suggest that *Kirklandia* in fact represents the preservation of the distal parts of a much more extensive feeding burrow of *Gyrophyllites* type. *Gyrophyllites* consists of a vertical shaft from which arise rosettes of short, simple, tear-shaped lobes, interpreted by Seilacher (1955) and Häntzschel (1962) as feeding structures. Some typical 'three-dimensional' *Gyrophyllites* are shown in Plate 80, figs. 1–2 and schematically in text-fig. 3.

The preservation potential of Gyrophyllites (text-fig. 3). The preservation of a burrow in the sedimentary record depends mainly on the following factors: (a) the nature of the infilling, (b) the sedimentary interfaces through which the trace fossils cut, and (c) the subsequent diagenetic history of the sediment.

The Gyrophyllites animal seems to have preferred fine-grained substrates, presumably because of their high organic content. A large percentage of the known occurrences of Gyrophyllites are therefore in mudstones, silts, or even clays. In these cases the burrow fill usually does not differ a great deal from the matrix, and after diagenesis the burrows will be difficult to pick out, especially as compaction will



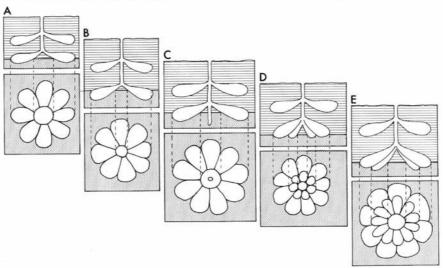
TEXT-FIG. 3. The preservation potential of Gyrophyllites. a, reconstruction of the complete burrow; b, c, three-dimensional preservation of the burrow or parts of it by early diagenetic mineralization. The formation of concretions can be confined either to the burrow fill (b) or to the surrounding sediment (c); d, preservation as compacted endoreliefs in fine-grained sediments as in most Flysch and Molasse occurrences; e, preservation as negative epirelief at clay/sandstone interfaces.

largely destroy their three-dimensional nature. If the fill differs from the matrix, thin impressions of rosettes can be found on the upper or lower surfaces of slabs—the common preservation of Flysch and Molasse specimens (text-fig. 3d). To guarantee a three-dimensional preservation of Gyrophyllites differential diagenesis must take place. This can either be an early cementation of the infilling, resulting in a concretion whilst the surrounding sediment remains uncemented (text-fig. 3b). Such seems to have been the case in, for instance, the three-dimensional specimen of Medusina liasica of Rüger and Rüger-Haas (1925). Alternatively, the matrix can have been cemented early in diagenesis, while the burrow infillings remained soft. Damon's (1888) specimens of Caulerpa carruthersi from the Kimmeridge Clay of Dorset illustrate the latter case (text-fig. 3c; Plate 80, figs. 1-2). Here, calcareous/sideritic mudstone concretions formed around the burrows which are filled with soft clay. Finally, parts of the Gyrophyllites system can be preserved at sedimentary interfaces, usually at clay/sand junctions. This is the mode of preservation of the bulk of the 'Kirklandia' and many other fossil 'medusoids'. In these cases, parts of the burrow system,

especially the more or less horizontal rosettes of lobes, are found as negative epireliefs on sandstone surfaces (text-fig. 3e), which usually seem to have set the lower limit of sediment penetration.

Kirklandia as Gyrophyllites. As a deposit feeder, the producer of Gyrophyllites mined the sediment for food, probably inhabiting a vertical shaft from which the sediment was explored in a radial fashion. The preservation of Gyrophyllites at a sedimentary interface suggests the burrows were excavated primarily in clays. These were exploited for food by the animals shifting their burrows downwards when a rosette was completed to start a further series of radial excavations at a lower level (text-fig. 4). When a clay/sand interface was reached, mining generally terminated, for the sands were low in nutrients due to their larger grain size. In some cases a probing shaft was extended down into the sand (text-fig. 4c), but always abandoned; the 'bell' of Kirklandia thus represents the lowest rosette or rosettes of tunnels produced immediately before abandoning the excavation.

Text-fig. 4 illustrates how the great variety of *Kirklandia* can be explained by a combination of slight variations in burrowing behaviour and by preservational phenomena associated with the position of the rosette/rosettes of feeding lobes relative to the clay/sand interface. The size of the central 'disc' depends on the position of the axial tube of the burrow system (text-fig. 4), from where the radial feeding lobes originate, relative to the buried sedimentary interface. When well above the interface (text-fig. 4a), only the distal parts of the feeding lobes reach the sand, and the result is a large central 'disc'. As the distance decreases (text-fig. 4a-b) the central



TEXT-FIG. 4. Generalized features of *Kirklandia* interpreted as a feeding burrow of the *Gyrophyllites* type. Vertical sections are reconstructions; only the negative epireliefs are preserved. Horizontal shading is clay, stippling is sand.

disc becomes smaller, and the lobes deeper and their more proximal parts are also preserved (text-fig. 4b). If the animal extended an exploratory shaft down into the sandstone, then the specimen will bear a central sandstone plug and associated features—Caster's (1945) manubrial apparatus (text-fig. 4c).

The presence of two or three rosettes suggests that lobes were in some cases closely stacked; this is clearly an efficient means of exploiting the sediment (text-fig. 4d-e), whilst crowding may also have been produced by final intense exploitation of the clay above the top of the sand layer before the burrow system was abandoned. The variation in relative development of rosettes can be explained by the position of the termination of the axial tunnel to clay/sand interface (compare text-figs. 4a and 3e), whilst shape and depth of lobes depend on the angle between the axis of feeding lobes and the central shaft. With an angle of 90° , the lobes will be very elongate (text-fig. 4a-b); as the angle decreases the lobes become deeper, increasingly circular in section, and, in general, will lack their proximal portions (text-fig. 4d-e).

By combining these variables, it is thus possible to generate the variety of structures described in the original account of the 'bell' of *Kirklandia*.

Kirklandia 'arms' as Granularia. The nature of the 'arms' of Kirklandia is equally explicable in trace-fossil terms; they are simple or branched burrows which were lined or stuffed with clay pellets, referable to the ichnogenus Granularia Pomel, 1849. The 'utricating structures' of Caster (1945) are no more than individual pellets. The association with Gyrophyllites is thus no more than chance; we do not regard them as necessarily products of the same animal. Specimens of Granularia from the English Eocene and Cretaceous are figured for comparison in Plate 79, fig. 4 and Plate 80, figs. 4, 5a-b. The remaining Kirklandia material can also be interpreted as trace fossils. The supposed natural casts (Caster 1945, pl. 5) represent no more than concretions developed around Gyrophyllites systems (text-fig. 5b).

Apart from *Kirklandia*, it is clear that the supposed medusoid *Palaeosemaeostoma* geryonides (von Huene) is also part of a *Gyrophyllites*, preserved at a sedimentary interface. The overhanging rim of the lobes in the type species (Kiderlen 1935, fig. 3) suggests that an origin at a sediment/water interface is unlikely. Lörcher's (1931, pl. 1, figs. 1-3) *Medusina*, from the German Dogger α , referred to *Kirklandia* in the *Treatise* (Harrington and Moore 1956, p. 870) is again part of a *Gyrophyllites*, preserved as a negative epirelief at a clay/sand junction. Identical '*Kirklandia*' stellate traces in the same preservation in interbedded clay/sandstone successions of Carboniferous age from central Texas have been shown to us by Professor J. E. Warme of Rice University.

CONCLUSIONS

On the basis of stratinomic considerations and morphological criteria, we therefore regard the interpretation of *Kirklandia texana* Caster, 1945 as a fossil medusoid as untenable. We prefer to interpret it as a trace-fossil chimaera, the 'bell' being the distal parts of a feeding burrow of *Gyrophyllites* type, while the 'arms' are fecal-pelletlined burrows of *Granularia* type. This interpretation satisfactorily explains preservational and morphological aspects of the structures described by Caster which are inconsistent with a medusoid origin.

The genus *Kirklandia* Caster, 1945 and the Family Kirklandidae Caster, 1945 should be removed from the Coelenterata; *Kirklandia* should be tentatively classed as a synonym of *Gyrophyllites* Heer, 1841 (non Wiedmann 1962, Cretaceous Ammonoidea). There is therefore no known fossil record of the medusoid hydrozoa (Order Trachylinida Haeckel, 1877).

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REFERENCES

- ADKINS, W. S. 1920. The Weno and Paw Paw formations of the Texas Comanchean. Bull. Univ. Tex. econ. Geol. Tech. 1856, 172 pp., 11 pls.
- —— 1928. Handbook of Texas Cretaceous Fossils. Ibid. 2838, 385 pp., 37 pls.
- BARTHEL, K. W. 1964. Zur Entstehung der Solnhofener Plattenkalke (unteres Untertithon). Mitt. Bayer. Staatssamml. Paläont. hist. Geol. 4, 37-69, 4 pls.
- 1970. On the deposition of the Solnhofen lithographic limestone (Lower Tithonian, Bavaria, Germany). N. Jb. Geol. Paläont. Abh. 135, 1–18.
- BATHURST, R. G. C. 1971. Carbonate sediments and their diagenesis. Developments in Sedimentology, 12, xix+620 pp. Elsevier, Amsterdam.
- CASTER, K. E. 1945. A new jellyfish (Kirklandia texana Caster) from the Lower Cretaceous of Texas. Palaeontogr. Americana, 3, 168-220, pls. 1-5.
- CLARK, D. L. 1965. Heteromorph ammonoids from the Albian and Cenomanian of Texas and adjacent areas. Mem. geol. Soc. Am. 95, 99 pp., 24 pls.
- DAMON, R. 1888. Supplement to the Geology of Weymouth, Portland and the coast of Dorset. Privately published. Weymouth.
- GLAESSNER, M. F. 1961. Pre-Cambrian animals. Scient. Am. 204, 72-78.
- 1962. Pre-Cambrian fossils. Biol. Rev. 37, 467-494, pl. 1.
- —— 1966. Pre-Cambrian Palaeontology. Earth Sci. Rev. 1, 29-50.
- and WADE, M. 1966. The late Precambrian fossils from Ediacara, South Australia. *Palaeontology*, **9**, 599-628, pls. 97-103.
- GOLDRING, R. and CURNOW, C. N. 1967. The stratigraphy and facies of the late Precambrian at Ediacara, South Australia. J. geol. Soc. Aust. 14, 195-214.
- GRUBIĆ, A. 1970. Rosetted trace fossils: a short review. Geol. J. Special Issue, 3, 185-188.
- HÄNTZSCHEL, W. 1962. Trace fossils and problematica. Pp. W.177-W.246. In MOORE, R. C. (ed.). Treatise on Invertebrate Palaeontology, W, xxv+259 pp. Geological Society of America and University of Kansas Press, Lawrence, Kansas.
- —— 1970. Star-like trace fossils. Geol. J. Special Issue, 3, 201-214.
- HARRINGTON, H. J. and MOORE, R. C. 1956. Trachylinida. Pp. F68-F76. In MOORE, R. C. (ed.). Treatise on Invertebrate Palaeontology, F, xx+498 pp. Geological Society of America and University of Kansas Press, Lawrence, Kansas.
- HERTWECK, G. 1966. Möglichkeiten des Fossilwerdens von Quallen im Experiment. Natur. Mus. 96, 456-462.
- HILL, R. T. 1901. Geography and geology of the Black and Grand Prairies, Texas. Ann. Rept. U.S. Geol. Surv. 21-27, 666 pp.
- HUENE, F. VON. 1901. Kleine paläontologische Mitteilungen. I. Medusina geryonides n. sp. N. Jb. Miner. Geol. Paläont. 1-12.
- KIDERLEN, H. 1935. Die Dogger-Medusen der Schwäbischen Alb. Jber. Mitt. oberrhein. geol. Ver. N.F. 24, 100–108.

- KOLB, A. 1951. *Hydrocraspedota mayri* n.g. n. sp., eine Hydromeduse aus den Plattenkalken von Pfalzpaint. *Geol. Bl. Nordost-Bayern.* 1, 113-116, pls. 5-6.
- KÜHN, O. 1937. Eine fossile Meduse aus dem Opalinus Ton von Franken. Zbl. Miner. Geol. Paläont. Abt. B. 1937, 334-336.
- LINCKE, O. 1956. Quallen-Spülsäume. Ökologische Voraussetzung und aktuogeologische Ausdeutung. Natur. Volk. 86, 119-127.
- LÖRCHER, E. 1931. Eine neue fossile Qualle aus den Opalinusschichten und ihre paläogeographische Bedeutung. Jber. Mitt. oberrhein. geol. Ver. N.F. 20, 44-46, pl. 1.
- MÜLLER, A. H. 1970. Aktuopaläontologische Beobachtungen an Quallen der Ostsee und des Schwarzen Meeres. Natur. Mus., Frankf. 100, 321-332.
- PIPER, D. J. W. 1972a. Turbidite origin of some laminated mudstones. Geol. Mag. 109, 115-126.
- 1972b. Sediments of the Middle Cambrian Burgess Shale, Canada. Lethaia, 5, 169-175. RÜGER, L. 1933. Medusen aus dem württembergischen unteren Dogger und Bemerkungen über die Stam-
- mesgeschichte der Medusen. Jber. Mitt. oberrhein. geol. Ver. N.F. 22, 39-43, 1 pl.
 and RÜGER-HAAS, P. 1925. Palaeosemaeostoma geryonides v. Huene sp., eine sessile Meduse aus dem Dogger von Wehingen in Württemberg und Medusina liasica nov. sp., eine Coronatenähnliche Meduse aus dem mittleren Lias von Hechingen in Württemberg. Sber. heidelb. Akad. Wiss., math. nat. Kl. Abh. 15, 22 pp., 2 pls.
- SCHÄFER, W. 1941. Fossilisations-Bedingungen von Quallen und Laichen. Senckenbergiana, 23, 189-216. - 1962. Aktuo-Paläontologie nach Studien in der Nordsee. 666 pp., 36 pls. Waldemer Kramer, Frankfurt-on-Maine
- 1972. Ecology and Palaeoecology of marine environments. Edited by CRAIG, G. Y. xii + 568 pp., Oliver & Boyd, Edinburgh.
- SEILACHER, A. 1955. Spuren und Lebensweise der Trilobiten; Spuren und Fazies im Unterkambrium. In schindewolf, o. H. and seilacher, a. Beiträge zur Kenntnis des Kambriums in der Salt Range (Pakistan). Abh. Akad. Wiss. Literatur Mainz, math. naturw. Kl. Abh. 10, 86-143, pls. 16-27.
- 1962. Palaeontological studies on turbidite sedimentation. J. Geol. 70, 227-234
- SELLARDS, E. H., ADKINS, W. S. and PLUMMER, F. B. 1966. The geology of Texas. Vol. I, Stratigraphy. Bull. Univ. Tex. econ. Geol. Tech. 3232, 1007 pp. (Fifth printing.)
- SPRIGG, R. G. 1947. Early Cambrian (?) jellyfishes from the Flinders ranges, South Australia. Trans. Roy. Soc. S. Australia, 71, 212-224, pls. 5-8.
- 1949. Early Cambrian 'jellyfishes' of Ediacara, South Australia, and Mt. John, Kimberley District, Western Australia. Ibid. 73, 72-99, pls. 9-21.
- STRAATEN, L-J. M. U. VAN. 1971. Origin of Solnhofen Limestone. Geol. Minj. 50, 3-8.
- TRUSHEIM, F. 1937. Spülsäume am Meerestrand. Natur. Museum, 61, 112-119, 187-190, 235-244
- VIALOV, O. S. 1968. On star-shaped problematica. Year-book all-unionist Palaeont. Soc. USSR, 18, 326-340. [In Russian.]
- WADE, M. 1968. Preservation of soft-bodied animals in Precambrian sandstones at Ediacara, South Australia. Lethaia, 1, 236-267.
- WAGNER, R. G. 1932. Beobachtung am Meerestrand. Aus. d. Heimat, 45, 161-173, pls. 17-48.
- WALCOTT, C. D. 1898. Fossil Medusae. Mon. U.S. Geol. Surv. 30, ix+201 pp., 47 pls.
- WALTHER, J. 1910. Die Methoden der Geologie als historische und biologische Wissenschaft. Pp. 529-658. In ABDERHALDEN, A. (ed.). Handbuch der biologischen Arbeitsmethoden, Abh. X, Methoden der Geologie, Mineralogie und Geographie. Berlin and Vienna.
- WHITTINGTON, H. B. 1971. The Burgess Shale: history of research and preservation of fossils. Proc. Palaeont.
- Convent. Chicago, 1969, 1170-1201.
 WIEDMANN, J. 1964. Unterkreide-Ammoniten von Mallorca. 2 Lieferung: Phylloceratina. Abh. Akad. Wiss. Literatur Mainz, math. naturw. Kl. (1963), 157-264, pls. 11-21.

F. T. FÜRSICH Geol. Paläontologisches Institut der Universität Sigwartstrasse 10 74 Tübingen, West Germany

W. J. KENNEDY Department of Geology and Mineralogy Parks Road, Oxford

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