

Table 2 *Ceriodaphnia reticulata* feeding experiments with radioactively labelled algae and bacteria*

Experimental time (h)	No. of <i>Ceriodaphnia</i>	Food source (cells ml ⁻¹)		Assimilated cells per individual <i>Ceriodaphnia</i> †	
		Algae	Bacteria	Algae	Bacteria
4	50	61.4 × 10 ⁴	—	2.2 × 10 ³ (0.18)	—
4	50	—	2.0 × 10 ⁷	—	1.3 × 10 ⁴ (0.033)
4	50	61.4 × 10 ⁴	2.0 × 10 ⁷	0.2 × 10 ³ (0.02)	1.5 × 10 ⁴ (0.037)
4	50	267.2 × 10 ⁴	—	0.6 × 10 ³ (0.11)	—
4	50	—	23.3 × 10 ⁷	—	3.1 × 10 ⁴ (0.007)
4	50	267.2 × 10 ⁴	23.3 × 10 ⁷	0.2 × 10 ³ (0.037)	2.1 × 10 ⁴ (0.005)
18	20	104.4 × 10 ⁴	—	31.2 × 10 ³ (0.60)	—
18	20	—	52.5 × 10 ⁷	—	85.0 × 10 ⁴ (0.32)
18	20	104.4 × 10 ⁴	52.5 × 10 ⁷	4.2 × 10 ³ (0.08)	118.0 × 10 ⁴ (0.45)
40	20	40.0 × 10 ⁴ †	—	15.0 × 10 ⁴ (7.5)	—
40	20	—	0.6 × 10 ⁶	—	0.6 × 10 ⁴ (0.20)
40	20	40.0 × 10 ⁴ †	0.6 × 10 ⁶	0.4 × 10 ⁴ (0.2)	0.8 × 10 ⁴ (0.26)
43	50	2.0 × 10 ⁴	—	15.3 × 10 ³ (38.2)	—
43	50	—	35.0 × 10 ⁷	—	8.0 × 10 ⁴ (0.11)
43	50	2.0 × 10 ⁴	35.0 × 10 ⁷	0.3 × 10 ³ (0.75)	7.2 × 10 ⁴ (0.10)

* Algae and bacteria were labelled with ¹⁴C and ³H respectively as described in the text. Algal cells were counted in a haemocytometer and bacteria by specific absorbance of bacterial chlorophyll at 715 nm or by serial dilutions in agar shake tubes. Radioactivity determinations were made with a scintillation counter using Instagel fluor (Packard). Initial activities ranged from 2 to 350 c.p.m. per 10³ algal cells, and from 100 to 6,000 c.p.m. per 10³ bacteria.

† *Chlamydomonas* (*Chlorella*) were used in all other experiments.

‡ Percentage of food source utilised in parentheses.

domonas) were incubated with ¹⁴C bicarbonate (1 μC ml⁻¹) added to a mineral growth medium (Bristol).

The results of five experiments with *Ceriodaphnia* feeding on algae, or bacteria, or both, are shown in Table 2. In each experiment twenty to fifty *Ceriodaphnia* were incubated with slow rotary agitation in 100 ml of filtered lake water, to which were added algae, or bacteria, or both. For each experimental situation, the radioactivity in three replicates of five animals was determined. The uptake of algae or bacteria is given as cells per individual *Ceriodaphnia*. These values might also be expressed in terms of fresh weight biomass (for example, 650 bacterial cells = one algal cell), carbon biomass, or calorific value. None of these parameters, however, reflect the actual dietary value of the algae and bacteria for *Ceriodaphnia*. No significant radioactivity was retained in control samples with animals poisoned by 4% formaldehyde.

In all experiments, when mixed diets were given, the *Ceriodaphnia* assimilated much less algae than when fed on algae alone. In contrast, the utilisation of bacteria was relatively unchanged when algae were also included in the diet. These experiments indicate, therefore, a preferential assimilation of bacteria by *Ceriodaphnia*. In all cases, both algae and bacteria were in excess supply, as indicated by the very low values for percentage utilisation of each food source.

In *Ceriodaphnia* the ingestion of food is a rapid process, taking less than 5 min (ref. 15). Because all the present experiments lasted 4 h or more, it is probable that the results shown in Table 2 actually represent assimilated foodstuff. Discriminatory grazing in *Ceriodaphnia* seems unlikely^{1,15} and it would thus appear that the animals could more easily digest cells of bacteria than those of algae. One reason for this may be the relative ease with which the *Chlorobium* cells are lysed (Pfennig, personal communication) as contrasted to algae with cell walls of cellulose.

The above experiments give a preliminary indication of the preferential assimilation of bacteria by *Ceriodaphnia* and imply that the photosynthetic green sulphur bacteria of Lake Kinneret may indeed be a significant dietary source for zooplankton. More importantly, we illustrate that the simple technique of labelling algae with ¹⁴C, and bacteria (or other heterotrophs) with ³H can make possible more extensive and complex experiments to elucidate the patterns of zooplankton feeding in nature.

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Feeding Posture of Modern Stalked Crinoids

Most modern crinoids (Echinodermata) are comatulids, which lack the stalk characteristic of Palaeozoic crinoids. The specialisation and adaptation to different ecological niches made possible by loss of the stalk have resulted in several different ways of spreading the arms and pinnules in an array for suspension feeding. Until the 1960s, most observations were based on specimens in aquaria. These suggested that the comatulids sit on the substratum with the mouth orientated upwards, the arms stretched out in the form of a

broad funnel or collecting bowl. The crinoid was thought to wait passively for a rain of its food material from above¹. This feeding posture is used by some deep water crinoids^{2,3}. Direct observations of the feeding behaviour of a shallow water comatulid in the Red Sea during the 1960s demonstrated that the arms are withdrawn during the day, but at night are arrayed in a vertical plane to form a filtration fan. This fan is orientated perpendicular to a prevailing weak current, filtering some 40,000 l of water at a current speed of 2 cm s⁻¹ during one period of activity⁴. These observations and a review of deep-sea photographs indicated that modern crinoids favour an environment with moderate currents and are to some degree current-seeking (rheophilic)⁵. Application of these ideas to the palaeoecology of Palaeozoic stalked crinoids suggested that most were rheophilic, using the stalk to raise the calyx above the substratum and allowing the arms to be outspread in a planar, circular filtration fan². The morphology of some ancient forms, however, was considered indicative of a rheophobic mode of life.

Direct observations of the shallow water crinoids of the West Indies using Scuba has expanded and refined knowledge of the various comatulid postures⁶. Some rheophilic comatulids which form a filtration fan are attached to elevated objects and favour habitats swept by moderate currents. In these species, as in the Red Sea comatulid, the arms are held such that the food groove faces downcurrent. Other West Indian comatulids attach the calyx within a cryptic niche but extend the arms in a fan normal to bidirectional wave surge at shallow depths. Rheophobic species may co-exist with the rheophiles, attaching within the reef infrastructure and extending the arms in several directions. The pinnules of each arm are arrayed in four directions, thus allowing effective filtration of slow, multidirectional water movements⁷. The formation of collecting bowls dependent on gravitational settling is apparently restricted to deep water species^{2,3}.

In August 1972, an extended series of dives in the submersible Nekton Gamma on the north coast of Jamaica at Discovery Bay, revealed an abundant fauna of living stalked crinoids and comatulids at depths of 200–300 m, the latter being the maximum operating depth of the submersible.

Extensive direct observation and photography by ourselves and others has demonstrated the formation of filtration fans by three species. The most prominent and largest of these is *Cenocrinus asterius* (L.), with nearly fifty arms (Fig. 1a, c). The stalk may approach 1 m in length. The arms were always seen to recurve aborally through almost 270°. In this posture the repeated branching of the arms and the pinnules form a virtually continuous parabolic filtration fan. The calyx with arms recurved in this manner was observed with the mouth orientated laterally (Fig. 1b) or upwards (Fig. 1e), appearing in the latter case like a wilted flower. The lateral tilting of the calyx (Fig. 1d) suggests current moving from left to right, but direct observations indicate that in fact the arms are recurved into the current, even in currents exceeding 0.5 knot. Thus the food grooves of the arms are directed downcurrent as in some rheophilic comatulids. The 'holding' power of the ligaments in the stalk is sufficient to keep the calyx erect even in currents, as suggested by histological studies⁶. In conditions of slack current, the calyx is horizontal, with the mouth upward. Comatulid crinoids were observed attached to the stalk of the stalked species, also forming a filtration fan (planar rather than parabolic) orientated like that of the 'host' stalked crinoid. Other comatulids attached to the substratum were also observed forming filtration fans in the same area.

Three other stalked crinoids were also present. *Endocrinus parrae* (Gervais), another large multi-armed species, arrayed the arms in a parabolic filtration fan like that of *C. asterius*. The small, five-armed *Democrinus* sp. was abundant at 240–300 m. It also forms the fan, but it is not as dense a screen as that of the former species. The calyx was observed to bend downcurrent, with the fan extended against the flow (Fig. 1g). In contrast to the three long-stalked crinoids, *Holopus rangii* d'Orbigny did not form a filtration fan. This species occurs commonly at depths of 270–300 m off Discovery Bay, cemented like barnacles to vertical rock outcrops. The ten short, massive arms were observed extended in a funnel-like arrangement which was rapidly infolded on approach of the submersible, giving the appearance of a clenched fist.

Anchorage of the two large species, *C. asterius* and *E. parrae*, is achieved solely by the cirri along the stalk. The stalk curves onto the substratum and four or five groups of cirri grasp the substratum with the terminal claws (Fig. 1f). The stalk terminates abruptly and seems not to give rise to an actual root. Some cirri along the vertical part of the stalk near the substratum seem to act as props (Fig. 1f).

Photographs obtained (by C. Neumann, personal communication) from the submersible Alvin in the Straits of Florida at 550 m demonstrate that stalked crinoids form filtration fans with the food grooves downcurrent in that location also. The genera present seem to be *Endocrinus* and *Democrinus*. Some comatulids present also form filtration fans. Sediment shadows behind sponges and sponge growth forms confirm current directions.

Several conclusions are suggested by the observations in Jamaica and the Straits of Florida. The stalked crinoids of the West Indies usually form filtration fans for suspension feeding in areas swept by moderate currents. The presence of these species in deep-sea photographs and dredge samples suggest the occurrence of moderate bottom currents. The orientation of the arms establishes current direction. The cirri are the means of anchorage in the larger species, serving also as props for the stalk. The stalk ligaments provide sufficient rigidity to hold the calyx erect even under moderate currents. It is thus highly probable that Breimer's inferences² as to the rheophilic habits of many Palaeozoic crinoids are correct. Other specialised Palaeozoic stalked crinoids may have used some of the same diverse patterns as those of modern unstalked forms.

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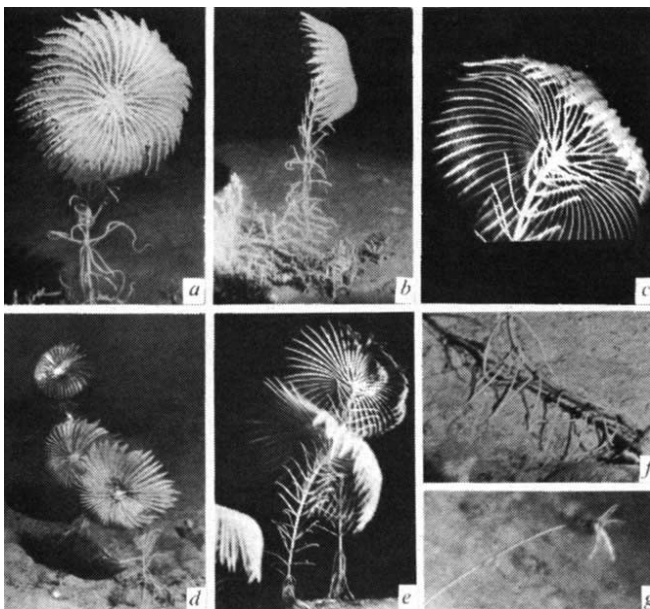


Fig. 1 *In situ* views of *Cenocrinus asterius* (L.) between 200 and 300 m depth, off Discovery Bay, Jamaica. Total vertical height of animals approximately 1 m (a–e); f, basal part of stalk with cirri, supporting animal above substrate; g, *in situ*, view of *Democrinus* sp. between 200 and 300 m depth, off Discovery Bay, Jamaica. Total vertical height of animal 0.33 m.

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Archaeocyathid-bearing Erratics from Dwyka Subgroup (Permo-Carboniferous) of South Africa, and their Importance to Continental Drift

THE Dwyka Subgroup, forming the basal division of the Karoo Group, comprises a thick sequence of glacial morainic debris and boulder shales, together with subordinate shales, varvites, and lenticular sandstones. In the southern Cape, tillitic rocks are overlain by the so-called "Upper Dwyka shales", an argillaceous sequence at the top of which are white-weathering carbonaceous shales, the "White Band". The latter is overlain by a thin but persistent chert band which forms the arbitrary boundary with the overlying Ecca Subgroup. The Upper Dwyka shales have yielded all the animal fossils of this subgroup in the southern Cape. McLachlan and Anderson¹ have recorded orthocerid nautiloids, the brachiopod *Attenuatella*, the bivalves *Phestia* and (?)*Nuculopsis*, palaeoniscoid fish, radiolarians, spiral coprolites suggestive of the presence of sharks, fossil wood, foraminifers, and miospores from the base of the succession near Kimberley. They² favoured a Sakmarian age for this marine incursion. The non-marine² White Band has yielded the aquatic reptile *Mesosaurus* and the crustaceans *Notocaris*, "Pygaspis", and *Anthrapalaemon*.

Glaciomarine beds spanning some 250 m at the base of the Dwyka succession in South West Africa³⁻⁵ have yielded the ammonite *Eoasianites* (*Glaphyrites*), an orthoconic nautiloid, possibly *Dolorthoceras*, the bivalves "Aphanaiia" and *Eurydesma*, the gasteropod *Peruvispira*, the coelenterate *Conularia*, the echinoid *Archaeocidaris*, the ectoproct *Dyscritella*, the palaeoniscoid fish *Namaichthys* and *Acrolepis*, a monasterid starfish, as well as crinoid stems, an indeterminate brachiopod, foraminifers, radiolarians, and fossil wood. *Mesosaurus*, as in the southern Cape, occurs only in white-weathering shales at the top of Dwyka succession^{3,6}.

In view of the relative scarcity of fossils within the strata of this Subgroup, it is of great interest to record the discovery of fossiliferous glacial erratics from the Prince Albert district. This find by one of us (R. O.) is all the more significant for

the fact that the fossils are Cambrian archaeocyathids (Fig. 1). They occur in grey limestone cobbles, representing transported glacial erratics, sporadically embedded in the tillites of the Dwyka Subgroup.

Archaeocyathids have a cosmopolitan distribution in Lower and Middle Cambrian marine deposits, during which period they built extensive reefs in Australia, North America, Europe, North Africa, Asia, and Antarctica. Nowhere are they known from younger deposits and the phylum is a short-lived one.

No marine rocks of Cambrian age are known from southern Africa. In South West Africa the Nama Group is of terminal Precambrian age⁷, characterised by an "Ediacaran" faunal element. Among the fossil genera recorded are *Rangea*, *Nasepia*, *Orthogonium*, *Pteridinium*, *Cyclomedusa*, *Ernietta*, and so on. Unconformably overlying the Nama Group are the "red-bed" deposits of the Fish River Formation, formerly included within the Nama Group⁸, but now considered to represent molasse deposition following the Damaran orogeny⁷. Martin⁸ considers the most

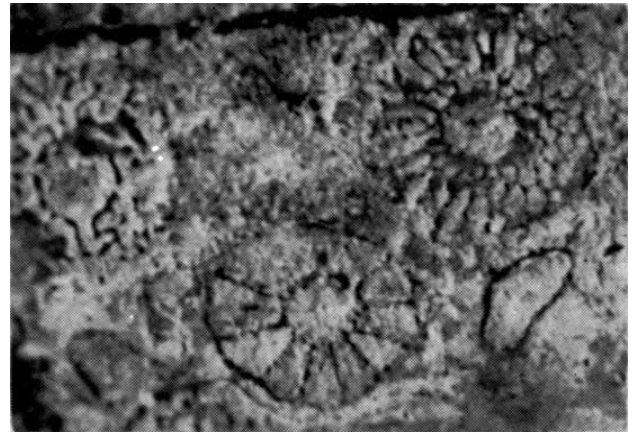


Fig. 1 Archaeocyathids from limestone cobbles embedded in the Dwyka tillite, approximately $\times 5$.

reliable age for the post-tectonic pegmatites intrusive into the Damara Group to be 510 ± 60 Myr. It seems probable, therefore, that the Fish River Formation spans at least part of the Cambrian period, a suggestion supported by Germs'⁷ record of *Phycodes pedum* Seilacher from these sediments. No undoubted marine fossils are known from these predominantly terrestrial red-beds, and they thus provide an important palaeoclimatic marker for the Cambrian period in southern Africa.

In the north-western Cape, at Vanrhynsdorp, the Table Mountain Subgroup rests unconformably upon Nama strata, while in the southern Cape it is conformably succeeded by the marine strata of the Bokkeveld Subgroup, dated at lower Devonian (early Emsian)⁹. The recent assignment of an Upper Ordovician age (Upper Ashgill)¹⁰ to a brachiopod assemblage from the Cedarberg Formation suggests that the orthoquartzites of the Nardouw Formation themselves span the entire Silurian period, as well as the base of the Devonian (Fig. 2). An Upper Cambrian age for the basal beds of the Table Mountain Subgroup thus seems likely, and is supported by the red-bed deposits of the basal Graafwater Formation, in the absence of the conglomerates of the impermanent Piekenier Formation.

The Table Mountain Subgroup is separated by a regional disconformity from the underlying Klipheuwel Formation¹¹