

# EDIACARAN-LIKE FOSSILS IN CAMBRIAN BURGESS SHALE-TYPE FAUNAS OF NORTH AMERICA

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**ABSTRACT.** A number of fossils from the Stephen Formation (Burgess Shale, Middle Cambrian, British Columbia) and Parker Slate (Lower Cambrian, Vermont) resemble Ediacaran taxa. *Thaumaptilon walcotti* gen. et sp. nov., known from three specimens, consists of a broad frond bearing a central rachis from which arise branches bearing possible zooids. The holdfast is relatively elongate and slightly swollen. *T. walcotti* approaches closely a number of Ediacaran frond-like fossils, especially *Charniodiscus*, *Vaizitsinia* and *Khatyspytia*. All these taxa appear to be pennatulacean anthozoans (Cnidaria). *Mackenzia costalis* Walcott, known from about seventy specimens, is an elongate bag-like organism. The exterior was probably thrown into longitudinal folds, and the interior may have borne septa. Attachment to the sea-bed is indicated by holdfasts of eocrinoid stems and brachiopod/sponge spicule aggregations. *M. costalis* may be compared to several Ediacaran taxa including *Inaria*, *Protechiurus* and possibly *Platypholinia*. The affinities of *M. costalis* are uncertain, but a place within the actinarian anthozoans seems possible and this animal probably had a cnidarian-grade of organization. *Emmonsaspis cambrensis* (Walcott), long interpreted as a possible chordate, is shown to be a frond-like fossil with angled branches arising from the mid-line. No trace of a holdfast exists in any of the three specimens. *E. cambrensis* resembles a number of Ediacaran frond-like fossils, but similarities to taxa such as *Pteridinium* may be superficial. The two remaining taxa are known from only single specimens. *Gelenopteron tantaculatum* gen. et sp. nov., originally described by Walcott as *Redoubtia polypodia* (pars), is tentatively interpreted as a chondrophorine, with evidence for a float and tentacular margin. A unique specimen consisting of a disc with annuli and tentacles is regarded as another type of chondrophorine. It occurs in association with *M. costalis*. The description of these animals as hold-overs from the Ediacaran assemblages casts some doubt on the general validity of Seilacher's concept of Ediacaran taxa representing a distinctive body-plan, known as the Vendobionta, separate from the metazoans.

THE identity and coherence of the Vendian (latest Proterozoic) soft-bodied Ediacaran faunas is now well-established (e.g. Glaessner 1984; Conway Morris 1985, 1990; Fedonkin 1987). With one possible exception (Hofmann *et al.* 1990), where tillites are present in the same sections (and they often are), the Ediacaran faunas lie above these glacial deposits. The age of the Ediacaran faunas remains somewhat uncertain. Glaessner (1984) proposed an approximate range of 550/570–650/660 Myr, although the apparently reliable date of  $565 \pm 3$  Myr obtained from zircons in an ash-fall that smothered an Ediacaran fauna in southeast Newfoundland (Benus 1988; see also Jenkins 1989) suggests that as a whole Ediacaran faunas may fall towards the younger end of Glaessner's (1984) spectrum of ages. Such dates are also consistent with new evidence indicating that the Precambrian–Cambrian boundary is unlikely to be older than about 540 Myr (e.g. Compston *et al.* 1992).

Ediacaran assemblages consistently underlie strata with Cambrian shelly fossils and a diversity of trace fossils that includes *Phycodes pedum* (see Narbonne and Myrow 1988). In many areas of the world the Vendian–Cambrian sections have unconformities and/or distinctive facies (e.g. fluvial or peritidal) that separate the last appearances of Ediacaran taxa and the first appearances of shelly taxa and/or Cambrian-type trace fossils. In a few sections, however, there appears to be a greater degree of continuity in rock record and facies suitable for fossil preservation. Most notable, perhaps, is a section in the Wernecke Mountains of northwest Canada where an interval above the

last appearance of Ediacaran taxa is devoid of all except millimetric trace fossils despite what appear to be facies that were appropriate for Ediacaran style preservation (see Narbonne and Hofmann 1987). What may represent a similar state of affairs was documented by Sokolov and Fedonkin (1984, 1985) in the clastic sequences of the east European platform and the carbonate sections of northern Siberia, where the Ediacaran assemblages are separated from the onset of the Cambrian faunas by a poorly fossiliferous interval. It is clear also that with certain key exceptions, many of which are discussed below, Ediacaran components are effectively absent from Cambrian assemblages.

There are broadly two explanations for the disappearance of Ediacaran faunas. The first proposes closure of a taphonomic window, thereby precluding the widespread preservation of soft-parts that typifies Ediacaran life. Most often invoked in this closure are the agents of predators, scavengers and bioturbators, whose widespread appearance was a harbinger for the Cambrian explosion. While there is little doubt that certain taphonomic factors changed between the Vendian and Cambrian, especially the onset of deeper and more extensive bioturbation, this alone seems unable to explain the absence of Ediacaran faunas in very latest Vendian sections such as those in the Wernecke Mountains and possibly elsewhere. An alternative explanation for the disappearance of Ediacaran faunas is some type of mass extinction, albeit one at present unspecified in terms of intensity, duration or cause (Seilacher 1984; Brasier 1989; Conway Morris 1989*a*; but see Jenkins 1989). There seems to be no compelling evidence for extra-terrestrial causes such as bolide impact, but some parallels might be drawn with the end Permian débâcle (see Schopf 1974, 1979; Maxwell 1989). Such factors might include withdrawal of shelf seas as part of a major regression, changes in oceanic salinity, or arguably most significant of all, a major drop in levels of atmospheric oxygen (Wignall and Hallam 1992).

A relatively neglected aspect of mass extinctions is the evolutionary and ecological behaviour of post-catastrophe taxa, be they 'Lazarus' taxa that enter unspecified refuges during time of stress or newly diversifying clades arising from surviving taxa. Here I document what appear to be hold-overs from the once-flourishing Ediacaran assemblages, present as rare specimens in soft-bodied faunas of Burgess Shale-type.

#### SUPPOSED EDIACARAN SURVIVORS: PREVIOUS REPORTS

If some Ediacaran taxa belong to the same clades as survive to the present day and are represented by Recent cnidarians or annelids, then in one sense their identification as post-Ediacaran survivors is trivial. The term 'Ediacaran-type survivors', however, is taken here to presuppose a relatively close phylogenetic relationship, perhaps at the taxonomic level of family. Moreover, while the assignments of some Ediacaran taxa to groups such as the Cnidaria now appear to be reasonably secure, in general comparisons are easier between Ediacaran and Cambrian forms than they are with extant representatives. Ideally, these relationships would be established on the basis of cladistic analysis, but these are in their infancy in terms of rigorous analysis (but see Jenkins 1985 for a preliminary attempt).

To date there are several Cambrian fossils that have been claimed to be closely related to Ediacaran taxa (see also Runnegar and Fedonkin 1992). Borovikov (1976) described a putative specimen of the flat segmented worm *Dickinsonia* (see Wade 1972*a*; Runnegar 1982), from the Lower Cambrian (Shabakty suite) of Maly Karatau, Kazakhstan. Its age is not in doubt because the specimen is associated with trilobites and brachiopods. Glaessner (1984, p. 144) remarked that the specimen might be correctly assigned, but 'some essential diagnostic characters are obscured by its preservation'. Rozanov and Zhuravlev (1992, fig. 24) re-illustrated this specimen and suggested it be better considered as a trace fossil.

Durham (1971*a*; see also Firby and Durham 1974, text-fig. 2 for the only other mention in the literature) commented in an abstract that 'poor specimens of *Dickinsonia* (?)' had been recovered from the Lower Cambrian Poleta Formation in the White Inyo Mountains, California. A single specimen (Text-fig. 1) comes from a locality on the west edge of Cedar Flat, White Inyo Mountains,



TEXT-FIG. 1. Specimen of supposed *Dickinsonia* (UCMP 37450) from the Poleta Formation (Lower Cambrian), Cedar Flat, California,  $\times 1.5$ .

eastern California (small knoll, centre of NW $\frac{1}{4}$  of SE $\frac{1}{4}$ , section 5). The outcrop also yields trilobites and the echinoderm *Helicoplacus*. The specimen, which occurs in a pale-green sandstone, is incomplete, but possesses prominent transverse markings. An attribution to *Dickinsonia* is possible, but the apparent convergence of the 'segments' on the upper side of the specimen is not a feature of *Dickinsonia*. An alternative suggestion to consider is that, as with the Borovikov (1976) ?*Dickinsonia*, this specimen represents a trace fossil, perhaps arthropod scratch marks such as *Monomorphichnus*. Typically in this ichnogenus the scratches are not as densely arrayed, form well-defined groups, and may taper in one direction (e.g. Crimes *et al.* 1977; Fritz and Crimes 1985; Peel 1990). Closely-spaced scratches in *M. multilineatus* were described by Alpert (1976, p. 234, pl. 1, figs 1–2) from the Lower Cambrian Harkless and Campito Formations (these straddle the Poleta Formation) in the White Inyo Mountains, California. In Alpert's material, however, the size of the scratches in an array varies, whereas those of the supposed *Dickinsonia* are more even. Nevertheless, a trace fossil origin is thought to be likely for this specimen. Johnson and Fox (1968) described rosette-like structures from the Silurian of Pennsylvania as being related to *Dickinsonia*, but Cloud's (1973) view that these structures are pseudofossils is accepted.

*Skania fragilis* was described by Walcott (1931) from the Burgess Shale. The specimens are typically less than 10 mm in size, and although Walcott (1931, p. 26) referred to a suite of 29

specimens, most of these are unidentifiable. Walcott's (1931) account was placed in the framework of an arthropodan anatomy, and this was accepted by some subsequent workers (e.g. Størmer 1944, pp. 34–35). Cave and Simonetta (1975), however, rejected this interpretation, and were unable to recognize either segmentation or appendages. They drew attention to an anchor-like structure, defined by what appears to be slight thickening on the leading edges of the body that links to a median strand. They interpreted these structures as intestinal caeca. As Cave and Simonetta (1975) stressed, this arrangement is similar to the Ediacaran taxon *Parvancorina minchami*. This taxon occurs in South Australia (Glaessner 1979a, 1980) and the White Sea area of Russia (Fedonkin 1985, 1987), although it appears not to have been illustrated from the latter region. Glaessner (1980) described two principal sets of elongate structures that he interpreted as appendages, this being one line of support for his tentative assignation of *Parvancorina* to the arthropods. Whether these structures genuinely represent appendages is moot. Glaessner (1980) was evidently sceptical about the relationships between *Skania* and *Parvancorina*, and Hou *et al.* (1991, fig. 5) described juvenile specimens of *Naraoia*, from the Lower Cambrian Chengjiang fauna of south China, which are similar to *Skania*. These authors noted the similarity to *Parvancorina*, but this they regarded as superficial. Their arguments, however, are largely based on the supposition that *Parvancorina* is a typical vendozoan or vendobiontan. In contrast, Gehling (1991) reiterated the case for a phylogenetic connexion between *Skania* and *Parvancorina*.

Given the diversity of medusiform elements in Ediacaran faunas, the paucity of Cambrian examples is noteworthy. Some confusion has arisen with supposed medusoids that transpire to be trace fossils (e.g. Meer Mohr 1969), while this interpretation may apply also to such examples as ?*Brooksella* from the Middle Cambrian Spence Tongue of the Lead Bell Shale, Utah (Willoughby and Robison 1979; see also Milashev 1958). In the same paper these authors identified another putative medusoid (*Cambromedusa furcula*) from the somewhat younger Wheeler Shale, and argued that it was 'most similar to the late Precambrian genus *Cyclomedusa*' (Willoughby and Robison 1979, p. 498). This interpretation is also disputed and, while the affinities of *Cambromedusa* remain problematical, an affinity to the sponges seems conceivable with the supposed thin radial canals representing spicules. Pickerill (1982) reported abundant specimens of medusiform fossils from the Upper Cambrian (Agnostus Cove Formation) of New Brunswick, but here too the author was unable to draw any convincing similarities to Ediacaran forms. In the case of the Nemakit-Daldyn horizon of north Siberia, which has received wide attention on account of its early skeletal faunas that appear at the Precambrian–Cambrian boundary, Khomentovsky (1986, p. 340) noted the presence of medusoids that survived from the Vendian, but no details of these fossils appear to have been published.

Another characteristic component of the Ediacaran assemblages is annulated discs of *Ovatoscutum*, which have been widely interpreted as the remains of the chambered floats of chondrophorine hydrozoans (e.g. Glaessner and Wade 1966; Fedonkin 1984, 1985; Gehling 1991), although proponents of the vendobiontan hypothesis (Seilacher 1989, 1992) have reinterpreted these fossils in the light of this new model.

The subsequent fossil record of Phanerozoic chondrophorines has been reviewed by Stanley (1986; but see Conway Morris *et al.* 1991). None of these purported examples appears to be significantly similar to *Ovatoscutum* (but see Runnegar and Fedonkin 1992, p. 372). In the context of Ediacaran faunas, however, attention is drawn to *Rotadiscus grandis* from the Chengjiang fauna of China (Sun and Hou 1987) and a series of related Palaeozoic fossils. The relevance of the discussion here will be apparent from a review of Ediacaran biotas by Runnegar and Fedonkin (1992, p. 372), where they write of 'The previously unemphasized but possibly significant similarities among various kinds of Vendian and Cambrian fossils such as ..... *Eldonia* Walcott, *Eomedusa* Popov, *Rotadiscus* Sun & Hou ..... *Stellostomites* Sun & Hou, *Velumbrella* Stasinska, *Yunnanomedusa* Sun & Hou'. The circular fossils of *Rotadiscus* have been interpreted as chondrophorines, with the annulated disc interpreted as the float. During my re-examination of specimens in the Nanjing collections it became clear that the chondrophorine interpretation is less likely. Important information is available in undescribed specimens presently being studied by Chen

Junyuan and Sun Weiguo, so I restrict my comments to specimens that have already been illustrated (Sun and Hou 1987, pl. 3, figs 1a, 2a–b). The cardinal observation is that the specimens are bilayered, and consist of not only the annulated disc but a separate discoidal unit that occupies the central region of the opposite side. This unit was misidentified by Sun and Hou (1987, pl. 3, fig. 1) as a superimposed specimen of the medusiform taxon *Stellostomites eunorphus* which is either very closely related or synonymous with the Middle Cambrian genus *Eldonia* (see Conway Morris and Robison 1988). This discoidal unit consists of a series of radiating plates, apparently separated by zones of softer integument, which along either side bear a distinctive series of pustules (just visible in pl. 3, fig. 1 of Sun and Hou 1987). The proposal that a trifid structure in the centre of the annulated disc represents the mouth is considered implausible, and unpublished specimens show structures that were probably involved with feeding. The trifid structures may represent a split that formed as the tough material of the disc was compacted. Adjacent to this trifid structure are two small conical structures. These were interpreted as ‘ribbon-like appendages’, possibly gonozooids by Sun and Hou (1987), but here are interpreted as probably epizoic tubes, comparable to *Cambrorhytium* (see Conway Morris and Robison 1988; Jin *et al.* 1991).

Comparisons can be drawn between *Rotadiscus* and other Palaeozoic taxa, notably the Middle Cambrian *Velumbrella* and the paropsonemids. *Velumbrella* was described by Stasinska (1960; see Bednarczyk 1970 for revision of its age to Middle Cambrian) from the Holy Cross Mountains of Poland. The large discs, which have diameters of up to 80 mm, occur in coarse sandstones. Stasinska (1960; see also Brasier 1979; Scrutton 1979) considered the fossils to represent medusoids, but Dzik (1991) considered this unlikely. Although unable to propose a systematic position for *Velumbrella*, Dzik noted (p. 50) that ‘they definitely were not scyphozoans’. Dzik (1991) also suggested that *Velumbrella* was most closely comparable to the Chengjiang genera *Yunnanomedusa* and *Stellostomites*, while ‘At the end of a morphocline of these Chinese discoidal fossils can be placed *Rotadiscus*’ (p. 50). *Yunnanomedusa* and *Stellostomites* are closely related to *Eldonia*, if not synonymous. A relationship between these taxa and *Rotadiscus* is a possibility (see below), but it seems likely that *Velumbrella* and *Rotadiscus* are even more closely related, and possibly synonymous. In this context, I propose that in *Velumbrella* the discs with prominent radial grooves are homologous with the discoidal unit composed of radiating plates in *Rotadiscus*. The fragments of a discoidal structure, that have been referred to informally as ‘Brzechowia’ (see Dzik 1991, fig. 3A) are not a related species as Dzik (1991) suggested, but are regarded here as an integral part of *Velumbrella* and correspond to the discoidal unit with concentric markings of *Rotadiscus*. Supporting evidence for this proposal comes from the holotype (Stasinska 1960, pl. 1, figs 1–2) where a portion of the concentric disc is in immediate association with the plated discoidal unit.

Specimens of *Rotadiscus* from Chengjiang may occur in close proximity (Sun and Hou 1987, pl. 3, fig. 2), and the overlap of discs of *Velumbrella* (Stasinska 1960, pl. 2, figs 1–2; see also Dzik 1991, fig. 3A) also suggests a gregarious habit. In the case of another specimen illustrated by Dzik (1991, fig. 3B), however, the superimposed discs are concordant and are interpreted here as being like the holotype, i.e. equivalent to the two discoidal units that occur in *Rotadiscus*. In his comparison of Upper Cambrian medusoids from New Brunswick, Pickerill (1982) drew comparisons to *Velumbrella*, but considered them to be slight. This may have been premature, and while these Canadian medusiforms show a number of obvious differences with *Velumbrella*, it remains possible that the supposed radial canals (Pickerill 1982, fig. 10.4) are actually comparable to the plate-like structures of the rotadiscids.

Dzik (1991) also commented on the possible relationships of these discoidal fossils to *Paropsonema*, while Rozanov and Zhuravlev (1992, fig. 25) drew attention to similarities between *Velumbrella* and paropsonemids (in the form of *Eomedusa* (Popov 1968)). This medusiform animal was described from the Devonian of New York (Clarke 1900; Ruedemann 1916), and has subsequently been noted from the Silurian of South Australia (Chapman 1926; Harrington and Moore 1956) and the Cambrian of Siberia (Popov 1967, 1968; see also Conway Morris and Robison 1982; Dzik 1991; Rozanov and Zhuravlev 1992).

The Devonian paropsonemids were described briefly by Clarke (1900, see also Ruedeman 1916,

1934). The fossils require rescrutiny, and here only a few additional remarks are made. As noted by Clarke (1900) the prominent radiating structures form two sets of intercalated rays that together extend across much of the umbrella. On occasion the two series are divided by a series of prominent nodules (NYSM 6818), but these are not invariably present. In addition, the outer series may terminate by a major bifurcation, each branch of which subdivides into two or three narrow, tapering branches. The rays may show lobate margins, and the transverse rows of pores often converge as adjacent pairs so as to impart a chevron-like appearance along each ray.

Clarke (1900) proposed that the paropsonemids were echinoderms, interpreting the rays as ambulacra. He noted the absence of calcareous spicules, let alone a skeleton, and commented that assignment to the echinoderms had not received wide support in pre-publication discussion. Thereafter, the emphasis changed with workers assigning *Paropsonema* to the chondrophores (Fuchs 1905; Ruedemann 1916, 1934; Harrington and Moore 1956; Scrutton 1979; Stanley 1986). Chapman (1926) was evidently unaware of the earlier work on paropsonemids and referred his material (as *Discophyllum mirabile*) to the scyphozoans, as did Popov (1967, 1968; as *Eomedusa datsenkoi*). Rozanov and Zhuravlev (1992, p. 258) retained this fossil (and *Velumbrella*) in the Cnidaria, but reverted to the notion of their being chondrophorines.

Pending a thorough redescription of the paropsonemids (D. Friend, pers. comm.), only preliminary remarks are necessary. Clarke's (1900) original proposal is regarded as broadly correct, and their affinities are believed to lie close to, if not within the Echinodermata. In addition, there seems reason to ally the paropsonemids with *Rotadiscus* and *Velumbrella*. This group, in turn, may be compared with *Eldonia*. In any event neither *Paropsonema* nor *Rotadiscus* are accepted as chondrophorines.

The status of *Discophyllum* in this context remains uncertain. These discs were originally described by Hall (1847, pl. 75, fig. 3) from the Middle Ordovician of New York (see also Walcott 1898, pl. 47, figs 1–2). Clarke (1900, p. 178) drew attention to similarities between *Discophyllum* and *Paropsonema*, but also noted that they were not 'identical in all structural features'. Ruedemann (1916, p. 26) restressed the similarities and considered 'that the two are closely related organisms', while Chapman (1926) placed the Australian paropsonemid in *Discophyllum*, unaware of Clarke's (1900) work. Evidence, however, for a close relationship between *Discophyllum* and *Paropsonema* remains wanting, and the arrangement of radial ridges and concentric markings in the former genus that Ruedemann (1916; see also Ruedemann 1934) emphasized as points of significant similarity are believed to be of superficial significance. Harrington and Moore (1956) reaffirmed Ruedemann's opinion that *Discophyllum* is the float of a chondrophorine.

Another characteristic component of Ediacaran faunas, that of the frond-like animals, until now seems to have been effectively unrepresented in the Cambrian. Tarlo (1967) proposed that the Lower Cambrian animal *Xenusion auerswaldae* was related to the Ediacaran taxa *Rangia* and *Charnia*, but the alternative hypothesis of a relationship with the onychophores received renewed support by Dzik and Krumbiegel (1989). A supposed specimen of *Pteridinium* from the Deep Spring Formation (Lower Cambrian) of California (Cloud and Nelson 1966; see also Cloud and Nelson 1967) transpired to be an example of the Cambrian trace fossil *Plagiogmus* (Glaessner 1968; Cloud and Bever 1973; note that Dzik and Krumbiegel (1989) proposed that one specimen might be a poorly preserved xenusionid). With the exception of new frond-like fossils described below, there appear to be no other reports from the Cambrian.

#### STRATIGRAPHY

The two occurrences described here are from Burgess Shale-type faunas (Conway Morris 1989*b*), that occur in the Lower Cambrian Parker Slate of north Vermont and the Middle Cambrian Burgess Shale (Stephen Formation) of east British Columbia.

The Noah Parker quarry (USNM locality 319m, almost certainly the same as USNM locality 319g, but not to be confused with USNM locality 25, see Shaw 1954, p. 1040) exposes the lower Parker Slate (Keith 1932; Shaw 1954; originally known as the Colchester Formation, see Keith 1923) on the south-west flank of a small hill (Parker's Cobble), 2.4 km north of Georgia Plains, Vermont. According to Shaw (1954, p. 1041) 'the Noah

Parker quarry has been entirely quarried away'. The locality is well-known on account of a rich Lower Cambrian fauna that includes trilobites (e.g. Resser and Howell 1938; Shaw 1955; Whittington 1990), other arthropods (Resser and Howell 1938; Briggs 1976, 1979; Conway Morris 1989*b*), sponges (Rigby 1987), other shelly fossils (see Shaw 1955), trace fossils (Resser and Howell 1938), and soft-bodied fossils including the putative Ediacaran survivor discussed here. It may be significant that Keith (1923, p. 111) reported boulders in the Parker Slate. A number of the other Burgess Shale-type localities around the Laurentian craton are located adjacent to the proximal edge of the outer detrital belt, in a slope zone where slumping and boulder beds often occur.

The Burgess Shale fauna has received extensive attention (e.g. Whittington 1985; Conway Morris 1989*c*, 1990). The majority of soft-bodied specimens come from an informal unit known as the Phyllopod bed, exposed in the Walcott Quarry which is located about 5 km north of Field, British Columbia. Stratigraphically this unit falls within the *Pagetia bootes* faunule of the *Bathyriscus-Elrathina* Zone of Middle Cambrian age. This unit is an integral part of the 'thick' Stephen Formation, which is composed predominantly of siltstones and mudstones. The relationship between the 'thick' Stephen Formation and the 'thick' Cathedral Formation, against which it is juxtaposed, has recently become a topic of controversy. A widely accepted interpretation has been that the carbonates (now dolomitized) of the Cathedral formation formed a reef with a precipitous escarpment against which the deep-water shales, including those of the Phyllopod bed, were deposited (McIlreath 1977; Conway Morris and Whittington 1979). This view has been challenged by Ludvigsen (1989), who argued that the abruptness of the carbonate-clastic transition is exaggerated, and that rather than a reef the original setting was a ramp with the Phyllopod bed biota owing its preservation to burial by tempestites. Evidence against this reinterpretation, in support of the existing model, is presented by the original exponents (Aitken and McIlreath 1990; Fritz 1990; see also Ludvigsen 1990).

*Institutional abbreviations.* GSC, Geological Survey of Canada, Ottawa; NYSM, New York State Museum, Geological Survey, Albany; UCMP, University of California Museum of Paleontology, Berkeley; USNM, National Museum of Natural History (formerly United States National Museum of Natural History), Smithsonian Institution, Washington, D.C.

## SYSTEMATIC PALAEOONTOLOGY

Phylum, class, family uncertain

*Emmonsaspis cambrensis* (Walcott, 1890)

Plate 1, figs 1–2

- 1886 *Diplograptus? simplex* Walcott, pp. 15, 46, 51, 92–93, pl. 11, fig. 4*a* [non fig. 4].  
 1889 *Phyllograptus? simplex*; Walcott, p. 388.  
 1890 *Phyllograptus?? cambrensis* Walcott, p. 604, pl. 59, fig. 3 [non fig. 3*a*].  
 1938 *Emmonsaspis cambrensis* [sic] (Walcott); Resser and Howell, p. 233, pl. 9, fig. 1 [non pl. 9, figs 2–4].  
 1952 *Emmonsaspis*; Termier and Termier, p. 351.  
 1954 *Emmonsaspis cambrensis* (Walcott); Shaw, p. 1040.  
 1955 *Emmonsaspis? cambrensis* (Walcott); Shaw, p. 775.  
 1955 *Emmonsaspis cambrensis* (Walcott); Shaw, pp. 785, 797.  
 1958 *Emmonsaspis cambrensis* (Walcott); Shaw, p. 531.  
 1968*a* *Emmonsaspis*; Termier and Termier, pp. 88, 91.  
 1971*b* *Emmonsaspis*; Durham, pp. 1105, 1121.  
 1972 *Emmonsaspis cambrensis* [sic] (Walcott); Firby, p. 504.  
 1979 *Emmonsaspis*; Brasier, p. 125.  
 1989*b* *Emmonsaspis cambrensis* [sic] (Walcott); Conway Morris, p. 278.  
 1990 *Emmonsaspis*; Bergström, p. 4.  
 1992 *Emmonsaspis* [sic]; Bengtson, p. 1033.

*Revised diagnosis.* Foliate body, tapering towards either end. Presumed distal termination simple; proximal termination not known. Regularly spaced branches on either side inclined proximally to impart chevron-like pattern.

*Type and locality.* The holotype (USNM 15314a) is associated on the same slab with two other specimens (USNM 15314b–c). Lower Cambrian, Parker Slate from USNM locality 319g at Parker's Quarry, Parker's Cobble, Vermont.

*History of research.* When first described, Walcott (1886) compared the material to younger graptolites that had been discussed by Emmons (1855), choosing as a name one of the junior synonyms for what Emmons (1855) referred to as *Diplograptus secalinus*. The subsequent publications by Walcott (1889, 1890) suggest that he may have become more sceptical about an assignment to the graptolites. Presumably aware that a place in this group was inappropriate, Resser and Howell (1938, p. 233) erected *Emmonsaspis*. They noted that 'The central rod, the ribbing, and the general shape of this animal argue strongly for its reference to the chordates', a proposal then echoed by subsequent workers (e.g. Termier and Termier 1952, 1968a; Durham 1971b; Brasier 1979). In contrast Shaw (1955) noted that the affinities of this animal were unknown. Further comments were precluded because the specimens appeared to have been mislaid, and the line drawings of Walcott (1886, 1890) and photographs published by Resser and Howell (1938) were inadequate for critical review. When the specimens were finally relocated, it became clear that most were arthropodan and seemingly similar to the Burgess Shale genus *Perspicaris* that had been described by Briggs (1977). What had been interpreted as the central rod (and so a chordate notochord) was a gut-filled alimentary canal, while the apparently smooth outlines revealed on closer inspection carapace and thorax, sometimes with traces of appendages. Of the illustrated specimens only one (Walcott 1886, pl. 11, fig. 4a; 1890, pl. 59, fig. 3; Resser and Howell 1938, pl. 9, fig. 1; herein Pl. 1, fig. 1) is now attributable to *Emmonsaspis*, although it occurs with two more poorly preserved specimens.

*Description.* Three specimens are on the same slab. Two are adjacent (Pl. 1, fig. 2), one of which is very poorly preserved. Both of these specimens are incomplete, although originally one of these was probably about 30 mm long. The third specimen (the holotype; Pl. 1, fig. 1) is better preserved, and although one end is incomplete owing to rock breakage, the original length is estimated to have been approximately 41 mm (maximum width is 10 mm).

Despite the vagaries of preservation and differences in size all three specimens show similar features (Pl. 1, figs 1–2). Overall the body tapers in either direction, but its orientation is conjectural and depends to some extent on comparisons made with other organisms. Assuming that *Emmonsaspis* bears some relationship to Ediacaran frond-like fossils (see below), then it is likely that the chevron-like arrangement of the branches was directed abapically. The apex, therefore, appears to have been simple and obtuse. In neither of the better-preserved specimens is the proximal region present, while in the third specimen little can be made in this region, but no evidence exists for a holdfast or stalk. The margins of the body were smooth, lacking appendages or other extensions.

Most prominent are the inclined branches of either side, that, meeting along the midline, impart the distinctive chevron shape (Pl. 1, fig. 1). So far as can be judged the branches arose opposite each other, and although a midline is defined by the convergence of the branches there is no evidence for a discrete central stem or rachis. In the holotype the branches total *c.* 14 per cm, indicating that originally this individual possessed about 55 branches on each side. The branches are simple, lack subsidiary detail, but do show slight relief indicating that in life they stood proud of the rest of the frond.

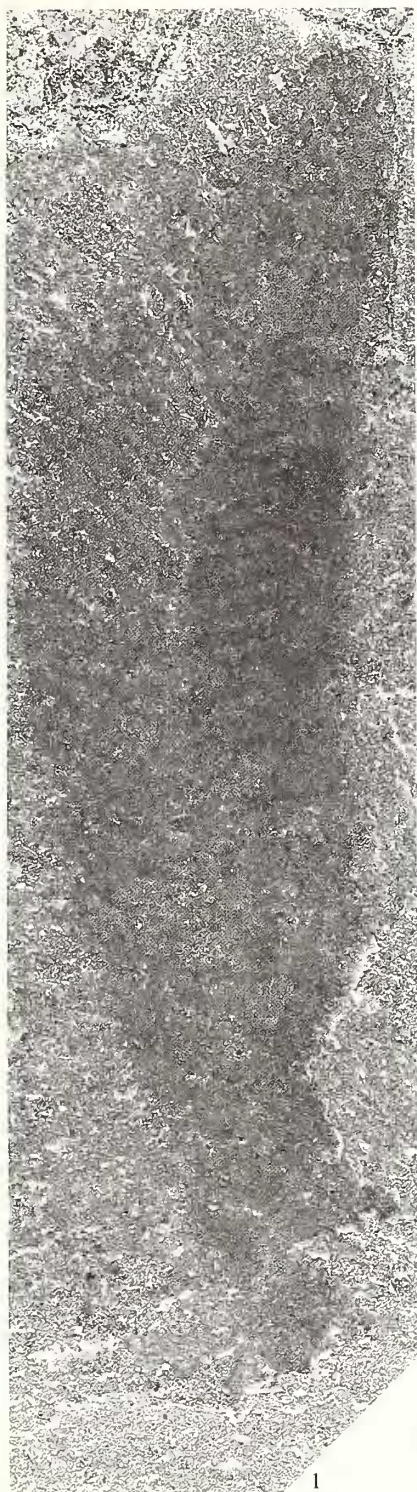
*Mode of life.* Incomplete preservation and uncertainty of taxonomic comparisons make palaeoecological pronouncement on *Emmonsaspis* difficult. The animal is tentatively interpreted as benthic, with the frond extending into the overlying water. The method of attachment is conjectural. If the branches bore zooids, for which there is no direct evidence, then suspension feeding or microcarnivory is plausible.

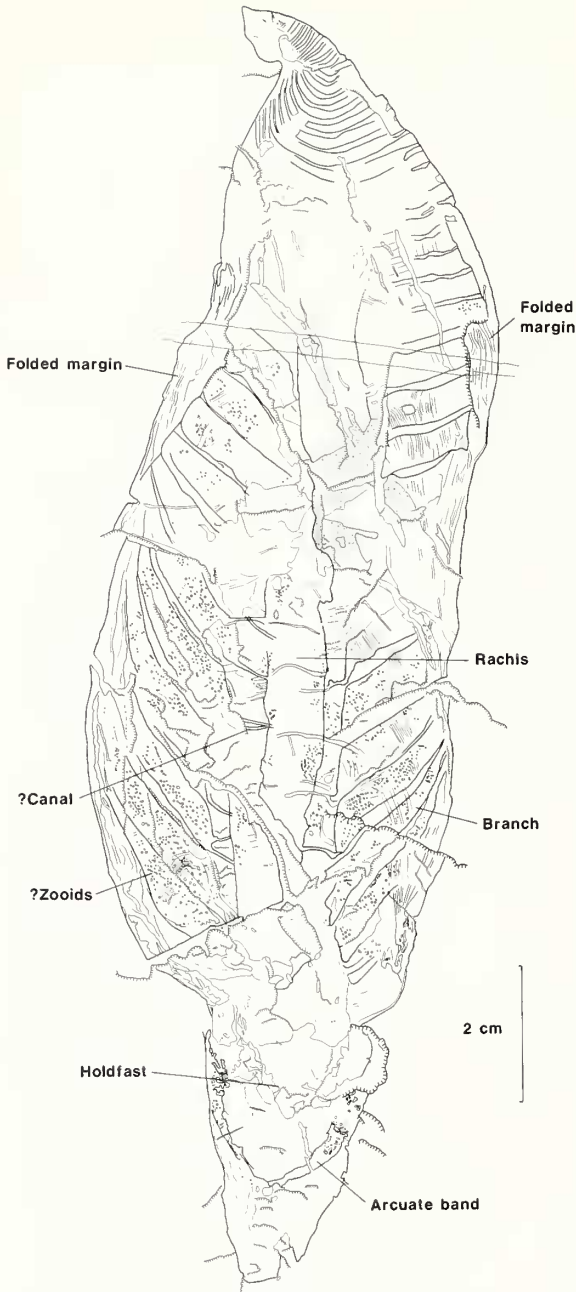
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#### EXPLANATION OF PLATE I

Figs 1–2. *Emmonsaspis cambrensis* (Walcott), Noah Parker Quarry, Georgia Plains, Vermont; Parker Slate, Lower Cambrian. 1, holotype USNM 15314a, note inclined branches that impart chevron-like appearance to the frond,  $\times 4.3$ . 2, USNM 15314b (left) and 15314c (right); the latter specimen is poorly preserved but USNM 15314b shows features similar to the holotype,  $\times 4.3$ . All three specimens co-occur on a single slab. Photographed in white light.







TEXT-FIG. 2. Camera-lucida drawing of the holotype of *Thaumaptilon walcotti* gen. et sp. nov. (USNM 468028, Walcott quarry, near Field, British Columbia; Stephen Formation (Burgess Shale), Middle Cambrian) to show interpretation of features. Drawing is of counterpart (Pl. 2, fig. 2), and some features of the part have been combined with this drawing by reversal.

EXPLANATION OF PLATE 2

Figs 1-2. *Thaumaptilon walcotti* gen. et sp. nov. Walcott quarry, near Field, British Columbia; Stephen Formation (Burgess Shale), Middle Cambrian. Holotype, USNM 468028, entire specimens. 1, part; 2, counterpart,  $\times 1$ . Photographed in white light.



*Affinities.* The graptolite affinities of *Emmonsaspis* may be rejected without further discussion. So too may the notion that this creature is a chordate. As explained above the putative notochord appears to represent the alimentary canal of *Perspicularis*-like animals filled with sediment, and their preservation is sufficient to reveal unequivocal arthropodan features (Conway Morris 1989*b*). While the chevron-like arrangement of the branches vaguely recalls the disposition of chordate myotomes, the absence of other features such as a notochord and alimentary canal render this interpretation suspect. *Emmonsaspis* appears to approach no other Cambrian animal, including those from other Burgess Shale-type faunas, and the preferred interpretation here is comparison with the Ediacaran assemblage of frond-like fossils. In the context of Ediacaran-type organisms, closest comparison of *Emmonsaspis* appears to exist with forms such as *Pteridinium*, but any similarities may be superficial (see below).

*Emmonsaspis from the Lower Cambrian of California?* In an abstract Firby (1972) drew attention to two types of Lower Cambrian fossils from the White Inyo Mountains, one lanceolate with a 'central rod or tube', the other 'with a central rod, a broadly rounded "anterior" end tapering toward a narrow "posterior" and having chevron-shaped impressions extending toward the edge of the body'. Quoted as coming from the Campito Formation (Firby 1972), subsequent mention (Firby and Durham 1974, text-fig. 2; Onken and Signor 1988, p. 142; see also Durham 1971*a*) places the finds in the overlying formation, near the top of the middle of the Poleta Formation. Firby (1972) proposed that these fossils were cephalochordates, comparable to *Emmonsaspis*. No formal description has been published, and Durham (in litt. 2 October 1978) told me that in an attempt to try a new casting technique the putative notochord of one specimen was destroyed. Thanks to the kindness of Dr Firby I was able to examine this specimen, and concluded that at least this example might be inorganic. In any event comparison of this specimen to *Emmonsaspis* or fossil cephalochordates appears to be without foundation.

?Phylum CNIDARIA Hatschek, 1888  
 ?Class ANTHOZOA Ehrenberg, 1834  
 ?Order PENNATULACEA Verrill, 1865  
 Family CHARNIIDAE Glaessner, 1979*a*  
 Genus THAUMAPTILON gen. nov.

*Type species.* *Thaumaptilon walcotti* sp. nov.

*Derivation of name.* The generic name is a construct of the Greek words *thauma* (wonderful) and *ptilon* (soft feather).

*Diagnosis.* Bilaterally symmetrical foliate animal with blunt holdfast. Leaf elongate and flattened, with central broad axis. On one side branches arise on either side of axis, connected by narrow strands, possibly canals. Proximal branches elongate, recurved adapically towards leaf margins; distal branches more quadrate. Branches and other areas adjacent to axis papillate, possibly zooids. Opposite side of leaf bears longitudinal ridges.

*Thaumaptilon walcotti* sp. nov.

Plates 2-3; Text-fig. 2

*Derivation of name.* The trivial name *walcotti* honours Charles Walcott, discoverer and first exponent of the Burgess Shale fauna.

*Diagnosis.* See genus.

*Types and locality.* Holotype USNM 468028 (part and counterpart) is the largest and best preserved of the three known specimens. Paratypes USNM 468029 and 468030 (parts only) are substantially smaller, and here are

interpreted as juveniles. Middle Cambrian, Phyllopod bed (Burgess Shale), from USNM locality 35k at Walcott Quarry near Field, British Columbia.

*History of research.* There is little doubt that Walcott had studied these specimens, especially as retouched photographs of the holotype (A. Simonetta, pers. comm.) and one of the juveniles (USNM 468030) were found with the specimens. During one of my searches through the collections the three specimens were set aside for further study. Brief allusion was made to *T. walcotti* as having 'a strong resemblance to a pennatulacean or sea pen' (Conway Morris 1979, p. 337), while the holotype was first illustrated in a recent review paper (Conway Morris 1989c, fig. 5A) where its affinities with Ediacaran taxa were made explicit (see also Conway Morris, 1990, p. 116).

*Description.* The holotype (Pl. 2, figs 1–2; Text-fig. 2) is large, assumed to be mature, and with a total length of 201 mm (straightened) and a maximum width of 55 mm. The other two specimens (Pl. 3, figs 7–9) are substantially smaller. The respective length and maximum width of USNM 468029 are 32 and 11 mm, while those of USNM 468030 are 20 and 8 mm respectively. The basic form of the animal is a foliate frond and holdfast. In USNM 468030 the frond is lanceolate (Pl. 3, fig. 9), although its proximal taper may be exaggerated by the non-preservation of the holdfast. In the holotype (Pl. 2, figs 1–2; Text-fig. 2) and USNM 468029 (Pl. 3, figs 7–8) the frond is more oblong, with the margins sub-parallel along much of their length but tapering towards the apex and also progressively narrowing especially towards the holdfast. In the two juveniles the apex is blunt, whereas in the adult it appears to be more rostrate, although this may have been accentuated by folding of the distal end. The frond is assumed to have been relatively thin, and towards its lateral margins there is evidence in the adult for overfolding (see below).

The frond consists of a central rachis and flanking areas. The rachis is most obvious in the holotype (Pl. 2, figs 1–2; Text-fig. 2). It appears not to extend into the holdfast, while its extension into the distal region is obscure. Where obvious the rachis is relatively broad (9 mm), the margins are somewhat irregular, and local deflections along the main axis occur. In USNM 468029 (Pl. 3, figs 7–8) a median zone on the frond is taken to mark the position of the rachis, but few details are evident. In USNM 468030 (Pl. 3, fig. 9) the putative axis is also marked by a dark strip, its narrowness consistent with the smaller size of the specimen. Apart from a dark central strand along the part of the midline of the rachis in the holotype, the rachis itself is devoid of specific features. On either side, however, dark strands extend from the margin of rachis adaxially to the ends of the branches. These are clearest in the mid-region of the holotype (Pl. 2, figs 1–2; Text-fig. 2), although their configuration is rather variable, perhaps due to vagaries of preservation. Their basic arrangement, however, appears to consist of two strands that arise from the proximal point of each branch and then diverge as they extend to the rachis. This divergence could indicate that on reaching the rachis the strands were inserted into upper and lower positions. There are instances, however, where instead of diverging, the strands appear to converge. Such configurations may arise by local displacement of tissues, perhaps during decay.

The branches are the most prominent feature of the frond. They arise as pairs, opposite each other on either side of the rachis. In no specimen can an exact total be counted, on account of either missing areas or incomplete preservation. In the holotype (Pl. 2, figs 1–2; Text-fig. 2) it is estimated that on each side there were about 35–40 branches, a figure close to that estimated for the much smaller USNM 468029 (Pl. 3, figs 7–8) with c. 35 branches. In USNM 468030 (Pl. 3, fig. 9), however, the total visible is lower (c. 15), but this might be an underestimate on account of incomplete preservation, especially at the proximal end. The similarity in branch totals between the holotype and USNM 468029, which is less than one-sixth of its size, indicates that branch addition was limited to restricted budding at the apex, and that growth was largely accommodated by increase in the dimensions of the individual branches. A comparison of branch width in the proximal region of the holotype and USNM 468029 is also in the order of six times.

In the holotype the smallest branches are located adapically, where they form a closely-packed zone. The branches, however, cannot be traced to the apex itself. In the proximal region the branches arise at an angle of about 45° to the rachis. Adjacent to the margins of the body the branches not only narrow, but swing to become subparallel to the edges. More distally the branches arise at a lower angle to the rachis, although the differences on either side may be due to slightly oblique burial of this region. As seen the branches have simple abrachial terminations, but this may be misleading because on both sides of the frond there appears to have been overfolding (Pl. 3, figs 4–5; Text-fig. 2), apparently truncating the branches. It may be significant that the equivalent area of branches in USNM 468029 (Pl. 3, fig. 7) shows an abrupt geniculation adjacent to the margins; this is especially pronounced on the left-hand side. In USNM 468030 (Pl. 3, fig. 9) the branches are somewhat arcuate, with a more uninterrupted swing from rachis to margin, except in the apical zone where the branches are straighter. This is also the case in USNM 468029, whereas in the holotype the apical branches are quite strongly curved.

The branches are assumed to have formed cushion-like structures on the surface of the frond. In the holotype they are connected by a series of low scarps (Pl. 3, figs 2–3), and this gives the impression that the adapical edge may have been free and was connected to the rest of the frond by a slight recess.

A notable feature of the branches are pustule-like structures (Pl. 2, figs 1–2; Pl. 3, figs 1, 4; Text-fig. 2). These structures have no precise counterpart in any other Burgess Shale fossil, but are tentatively interpreted as retracted zooids. Although visible in both paratypes (Pl. 3, figs 7, 9), they are clearest in the holotype. Locally the pustules appear to form linear arrays, but overall there is no clear evidence for a particular disposition or arrangement. As preserved the pustules form more or less homogenous blobs and in none of the specimens is there evidence for tentacles or other substructure. Although the pustules are most obvious on the branches, they also occupy quadrate areas adjacent to the rachis, most obviously in the proximal region (Pl. 1, figs 1–2; Text-fig. 2). The overlap with the rachis indicates that the latter structure may have been effectively internal.

At various points along the margin of the holotype the branches are truncated, and a change in level marked by a scarp reveals marginal areas with prominent longitudinal striations (Pl. 2, figs 1–2; Pl. 3, figs 2, 4–5; Text-fig. 2). These regions are interpreted as the overfolded edges of the opposite side of the frond, with the striations believed to represent a system of somewhat irregular longitudinal ridges. These structures appear to be also visible in USNM 468030 (Pl. 3, fig. 9), especially on the proximal region of the right-hand side where a series of prominent lineations run at a steep angle to the branches. In the holotype curving sets of lineations are faintly visible on the frond, cross-cutting the trend of the branches (Pl. 2, fig. 2; Text-fig. 2). They may represent the ridges of the opposite side being impressed by compaction.

The holdfast is only well preserved in the holotype (Pl. 2, figs 1–2; Pl. 3, fig. 6). It is attached to the frond by a fairly prominent constriction in body width, and thereafter the holdfast tapers to a blunt termination. The holdfast is devoid of anatomical detail, apart from an arcuate reflective band (Pl. 3, fig. 6) that is convex towards the proximal end.

*Mode of life.* There is little doubt that *T. walcotti* (Text-fig. 3) was benthic, with much or all of the holdfast embedded in unconsolidated sediment and the frond extending into the overlying water. Position relative to the sediment–water interface presumably was adjusted by muscular contractions of the holdfast. The mode of feeding is rather conjectural, but if the putative zooids have been identified correctly then food particles were presumably trapped by small tentacles.

?Class ANTHOZOA Ehrenberg, 1834

?Order ACTINIARIA Hertwig, 1882

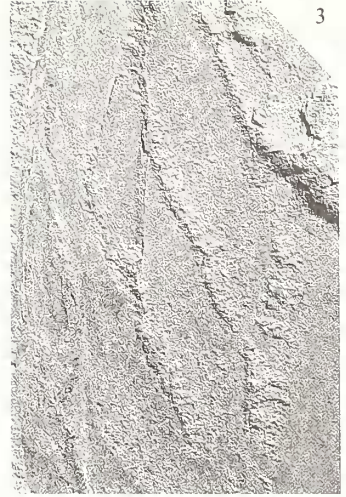
Family MACKENZIIDAE fam. nov.

*Diagnosis.* Elongate polyps, atentaculate, with longitudinally-folded exterior, internal septa lining gastric cavity.

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#### EXPLANATION OF PLATE 3

Figs 1–9. *Thaumaptilon walcotti* gen. et sp. nov. Walcott quarry, near Field, British Columbia; Stephen Formation (Burgess Shale), Middle Cambrian. 1–6, holotype, USNM 468028. 1, part, detail of branches and possible zooids,  $\times 2.5$ . 2, counterpart, detail of branches showing evidence for imbrication and folded-over edge of frond,  $\times 2.0$ . 3, counterpart, same area as in fig. 2,  $\times 2.0$ . 4, part, detail of branches and folded-over edge of frond,  $\times 1.2$ . 5, part, folded-over edge of frond and branches,  $\times 1.2$ . 6, counterpart, holdfast,  $\times 1.1$ . 7–8, USNM 468029, entire specimen, fragment in centre of specimen is a portion of eodiscid trilobite *Pagetia bootes* (note other specimen at base),  $\times 2.4$  and  $\times 2.1$  respectively. 9, USNM 468030, entire specimen,  $\times 3.3$ . All photographs taken in ultra-violet radiation; 1, 2, 4–7, 9 under high angle radiation; 3 and 8 under low angle radiation.



## Genus MACKENZIA Walcott, 1911

*Type species. Mackenzia costalis* Walcott, 1911.

*Revised diagnosis* (emended from Walcott 1911, p. 55). Bag-like animal, atentaculate, with exterior folded longitudinally in about 8–10 ridges. Probable internal septa lining extensive gastric cavity. Holdfast or other proximal modification present.

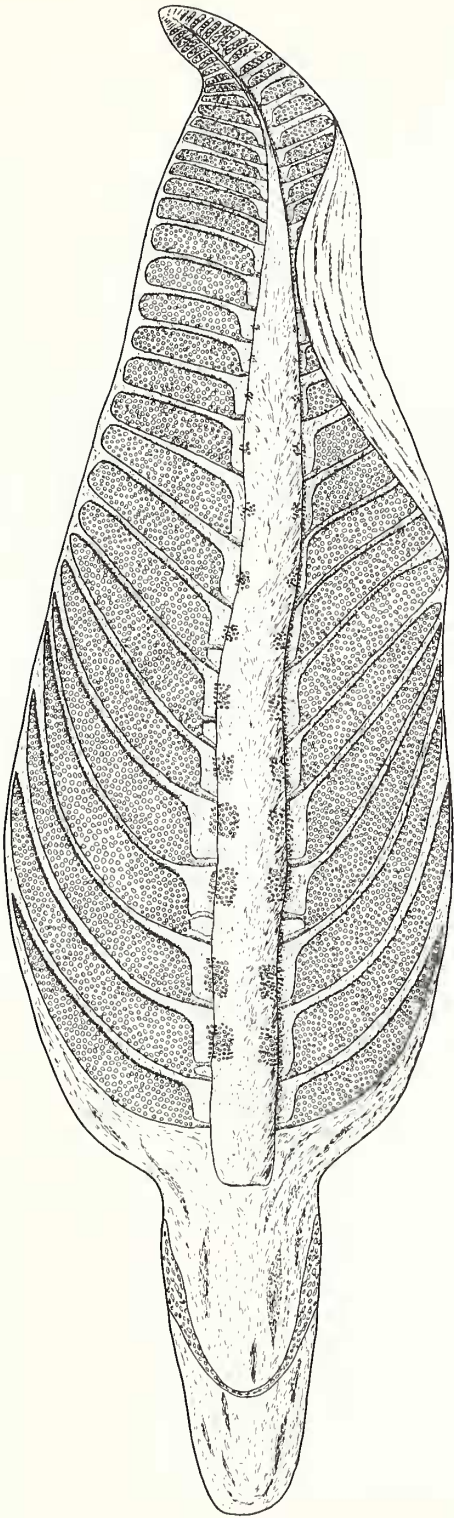
*Mackenzia costalis* Walcott, 1911

Plates 4–7

- 1911 *Mackenzia costalis* Walcott, pp. 45, 54–55, pl. 13, figs 2–3.  
 1912a *Mackenzia costalis* Walcott; Walcott, p. 153.  
 1912b *Mackenzia costalis* Walcott; Walcott, p. 190.  
 1912 *Mackenzia costalis* Walcott; H. L. Clark, pp. 276–278.  
 1913 *Mackenzia costalis* Walcott; A. H. Clark, pp. 488–489, 503–504, 507.  
 1918 *Mackenzia costalis* Walcott; Walcott, p. 10, figs 6–7.  
 1921 *Mackenzia costalis* Walcott; Raymond, pp. 343–345, fig. 3.  
 1931 *Miskoia* Walcott, p. 38, pl. 3, figs 2–3.  
 1932 *Mackenzia costalis* Walcott; Croneis and McCormack, p. 126.  
 1934 *Mackenzia costalis* Walcott; Ruedemann, p. 76.  
 1952 *Mackenzia*; Termier and Termier, p. 357.  
 1956 *Mackenzia costalis* Walcott; Wells and Hill, p. F233.  
 1957 *Mackenzia costalis* Walcott; Madsen, p. 281.  
 1960 *Mackenzia*; Termier and Termier, p. 36.  
 1968a *Mackenzia costalis* Walcott; Termier and Termier, fig. 142.  
 1968b *Mackenzia*; Termier and Termier, p. 92.  
 1968 *Mackenzia costalis* [sic] Walcott; Arai and McGugan, p. 208.  
 1969 *Mackenzia costalis* Walcott; Rolfe, p. R331.  
 1971b *Mackenzia costalis* Walcott; Durham, pp. 1106–1107.  
 1973 *Mackenzia*; Alpert, p. 919.  
 1978 *Mackenzia costalis* Walcott; Conway Morris, p. 126.  
 1979 *Mackenzia costalis* Walcott; Conway Morris, p. 337.  
 1979 *Mackenzia*; Conway Morris and Whittington, p. 126.  
 1979 *Mackenzia costalis* Walcott; Scrutton, pp. 170, 177.  
 1982 *Mackenzia*; Sepkoski, p. 23.  
 1985 *Mackenzia costalis* Walcott; Whittington, pp. 53, 124, 127, fig. 4.16A–B.  
 1989c *Mackenzia costalis* Walcott; Conway Morris, pp. 343–344, fig. 5B–C.  
 1990 *Mackenzia costalis* Walcott; Conway Morris, p. 116, fig. 4a.  
 1991 *Mackenzia*; Gehling, p. 190.  
 1992a *Mackenzia*; Sepkoski, p. 35.  
 1992b *Mackenzia*; Sepkoski, p. 1173.  
 1992 *Mackenzia costalis* Walcott; Conway Morris, p. 632.  
 1992 *Mackenzia costalis* Walcott; Bengtson *et al.*, p. 434.

*History of research.* Walcott's (1911) placement of *M. costalis* in the holothurians, with similarities being drawn with the extant *Synaptula*, was soon questioned by H. L. Clark (1912) who drew comparisons with certain actinians (Cnidaria). A. H. Clark (1913) complained about the tentativeness of H. L. Clark's (1912) discussion, and had no hesitation in regarding *M. costalis* as 'undoubtedly mud-living actinians of the family Edwardsiidae, closely related to *Edwardsia*'. Within a few years Walcott (1918) had conceded to A. H. Clark's (1913) proposal, writing that this species 'closely resembles *Edwardsia*'. This view came to be widely accepted (e.g. Croneis and McCormack 1932; Wells and Hill 1956; Madsen 1957; Termier and Termier 1960; Durham 1971b; Sepkoski 1982, 1992a, 1992b; Whittington 1985), although Scrutton (1979, p. 177) noted the need for reappraisal. An interesting parallel to this debate may be found in the discussion of *Pseudocaudina brachyura* from the Upper Jurassic Solnhofen Limestone of south Germany. The only known fossil was first described as a holothurian (Broili 1926), but subsequently Heding (1932) suggested it was an actinarian. This taxon was





TEXT-FIG. 3. Reconstruction of *Thaumaptilon walcottii* from the Middle Cambrian Stephen Formation (Burgess Shale), British Columbia. Towards the upper right the frond is depicted as being folded over to reveal opposite side. Approximately  $\times 1$ .

not mentioned by Wells and Hill (1956), and comparisons with *Mackenzia* are drawn below. In recent review papers (Conway Morris 1989c, 1990) I have introduced the notion of *M. costalis* being considered as an Ediacaran-type survivor, although this need not prejudice its relationships to the Cnidaria (see below).

*Material.* Asterisk indicates that both part and counterpart exist. Lectotype (designated herein) USNM 57556\*; other material includes USNM 57557\*, 193929\*–193937\*, 193939\*–193949\*, 193951\*–193956\*, 193959, 193961, 193964–193966, 193967\*, 193968–193969, 193971–193972, 193974–193977, 193979–193982, 193984, 193988–193990, 193994, 193997, 193999, 194001, 194652, 196174, 202304; GSC 78489–78490, 78492–78500; ROM 38643, 48471–48475.

*Stratigraphical levels in the Burgess Shale.* Although about 60 specimens reside in the USNM, most must have been collected after 1910 because at that time only two specimens had been obtained (Walcott 1911, p. 55). Walcott (1912a, p. 153) noted that within the Phyllopod bed the specimens came from the richly fossiliferous bed 10 (0.48 m above quarry floor), but apart from this information the stratigraphical range of Walcott's suite is uncertain. When the Geological Survey of Canada teams collected Burgess Shale material in 1966 and 1967 a more careful note was kept of heights of specimens within the Burgess Shale. Of the nine specimens from the Phyllopod bed, the lowest horizon at which a specimen occurred was 1' 11"–2' 4" (0.58–0.71 m) above the base of the reopened Walcott Quarry (this may not coincide exactly with the original floor) and another specimen was found at the 2' 4" (0.71 m) level. Above these three specimens came from the 2' 7"–3' 0" (0.78–0.91 m) interval, and four specimens from the 3' 0"–3' 7" (0.78–1.09 m) horizon. From a horizon substantially above the Phyllopod bed, at a level of 74–76' (22.56–23.16 m) above the base of the Walcott Quarry, two more specimens were recovered.

*Description.* Overall *M. costalis* is elongate, cylindrical, without obvious appendages or other extensions (Pl. 4, figs 1–6; Pl. 5, figs 1–2, 5, 7; Pl. 6, figs 1, 4–5; Pl. 7, figs 1–2, 4, 7). The body is more or less constant in width, with blunt terminations. *Mackenzia* shows a wide range of size: mean length ( $n = 32$ ; remaining specimens are incomplete) is 86.5 mm (SD 38.4 mm), with recorded lengths between 25 and 158 mm (Text-fig. 4). To a first order widths are directly proportional to length, although in the more elongate specimens (i.e. more than about 100 mm) greater length is achieved without noticeable increase in width (Text-fig. 4). There is, moreover, a wide variation in length to width ratios, presumably reflecting the contractability of the body.

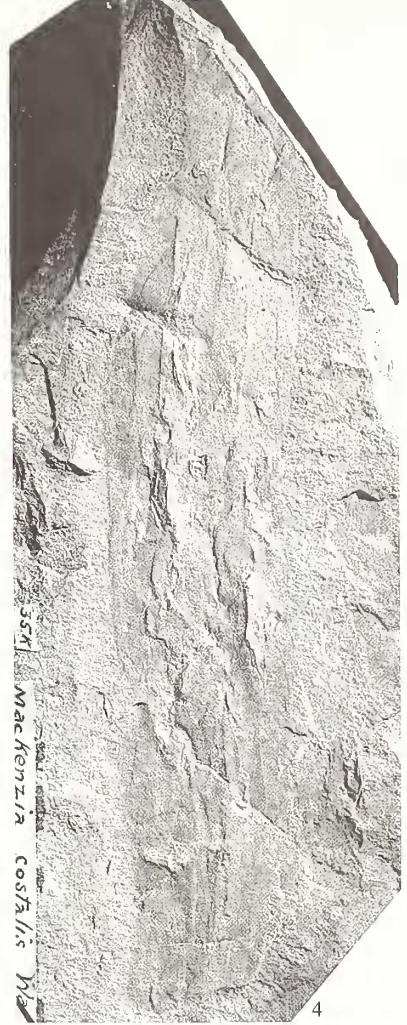
External features are few. Walcott (1911) drew attention to 'eight to ten longitudinal bands ... outlined by narrow, slightly elevated lines'. These observations are confirmed, in as much as there appears to be a direct correspondence between the relatively prominent reflective strands (Pl. 5, figs 1, 4; Pl. 6, figs 4–5) and the elongate lines that are delimited as low scarps (Pl. 4, figs 1–4; Pl. 5, figs 2–3, 5, 7; Pl. 7, figs 1–3). In a number of specimens the edges of the body are not entirely smooth, but consist of displaced margins that are also separated from one another on different levels connected by scarps (e.g. Pl. 5, figs 1–3, 7; Pl. 7, figs 1–2). It is conjectured that in life the circumference of the body was not simple but thrown into relatively deep folds and intervening ridges, the expression of which is now seen in the elevated lines and displaced margins. Further support for this comes from the distal end of some specimens which have a lobate appearance (Pl. 4, figs 1–2, 6; Pl. 5, fig. 4; Pl. 7, figs 4, 6), interpreted as arising from the convergence of the external folds and ridges.

The proximal end of the body may be attached to a holdfast, but otherwise is normally blunt. An exception to this is seen in GSC 78494, where the proximal area has an arcuate ornamentation and is connected to the rest of the body by a narrow strand (Pl. 6, figs 1–2). This unique feature is interpreted as an attachment disc, anchoring the rest of the body via a stalk.

Although many specimens are not attached to a foreign holdfast, there are exceptions. In some individuals

#### EXPLANATION OF PLATE 4

Figs 1–6. *Mackenzia costalis* Walcott. Walcott quarry, near Field, British Columbia; Stephen Formation (Burgess Shale), Middle Cambrian. 1–3, lectotype (designated herein), USNM 57556. 1–2, part, entire specimen: 1,  $\times 1.8$ ; 2,  $\times 2.0$ . 3, counterpart, entire specimen, proximal area missing owing to rock breakage,  $\times 2.4$ . 4, USNM 57557, entire specimen,  $\times 1.2$ . 5, USNM 194652, entire specimen with a holdfast of an eocrinoid stem (left),  $\times 0.9$ . 6, USNM 83927a, entire specimen, associated with the enigmatic taxon *Portalia mira*,  $\times 1$ . Figs 1–4 photographed in ultra-violet radiation (1–2 at high angle; 2, 3, 6 at low angle); fig. 5 photographed in white light.



at the proximal end there is a small cluster of skeletal debris, typically that of sponge spicules and brachiopods (Pl. 5, figs 5–6; Pl. 6, fig. 8). This debris appears to have been located in a central area of the base. In other specimens the proximal end is attached to the stem of an echinoderm (Pl. 4, fig. 5; Pl. 7, fig. 9). This association is unlikely to be due to chance both because of its multiple occurrence in *Mackenzia* and the general scarcity of echinoderm material in the Burgess Shale. The final example of a foreign holdfast is in GSC 78494 (Pl. 5, figs 1–2), where an indeterminate nodular mass is present in the basal region.

Features of internal anatomy are sparse. In his initial description Walcott (1911, p. 55) noted that at the anterior end of the two specimens then discovered there was 'a ring of what appear to be narrow plates surrounding a central opening'. The presence of this feature is somewhat enigmatic because although H. L. Clark (1912) 'was unable to make out these points satisfactorily', A. H. Clark (1913, p. 489) claimed to see this ring of plates but reported that after immersion of the specimen in acid by Walcott 'the ring seems to have disappeared'. These discrepancies are resolved, however, when it is realized that the end of the specimen in question (Pl. 4, figs 1–2) undoubtedly represents the basal termination, and a ring-like structure is present but represents the zone of attachment. In any event there is no evidence for calcareous plates or spicules in this or any other specimen.

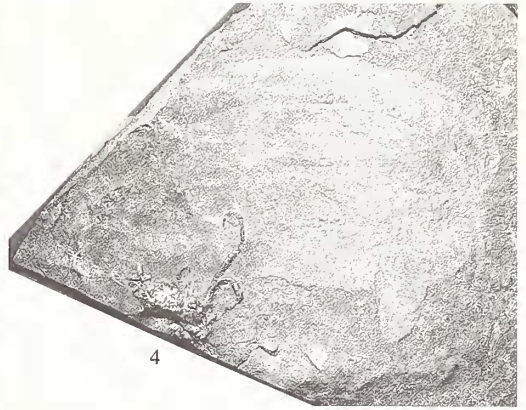
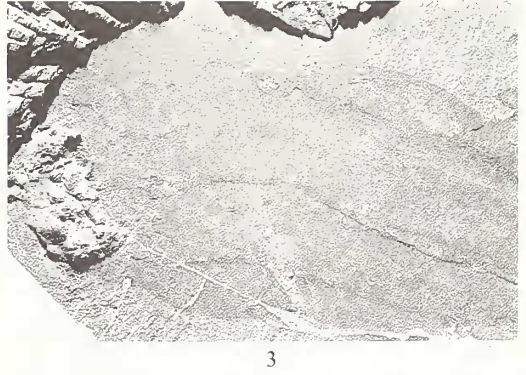
The most prominent of the unequivocal internal features are reflective strands (e.g. Pl. 5, figs 1, 4; Pl. 6, figs 4–5). They are tentatively interpreted as extensions of the body wall into an internal cavity, similar to the septa of anthozoans. Apart from longitudinal fraying seen in a few specimens (e.g. GSC 78496; Pl. 6, fig. 3), which may represent partial decay, the strands show no substructure. Possibly separate from the above-mentioned strands is a longitudinal reflective ribbon, visible in two specimens (GSC 78498, USNM 193947; Pl. 6, figs 1, 6). It has a more organized structure than the longitudinal strands, with reflective margins enclosing an area with reflective patches that range from elongate to more reticulate. The significance of this structure and its original nature are obscure. The only other internal structure is a lenticular to more elongate mass that occurs either towards the putative oral opening (Pl. 7, figs 1, 3, 4–6) or in a more mid-portion (Pl. 7, figs 7–8). They have a fibrous to granular texture, but otherwise contain no identifiable structures. These masses are tentatively identified as gastric residues.

*Mode of life.* *Mackenzia* was benthic, as inferred both from the absence of obvious floatant or swimming structures and attachment to benthic debris, including echinoderm stems. It is these latter examples that suggest that at least these specimens were not partly embedded in the sea-floor (cf. the reconstruction in Conway Morris and Whittington 1979). Otherwise the mode of life of this animal is largely enigmatic. The variation in length to width ratios (Text-fig. 4) indicates that the animal was contractile, presumably achieving this by muscular contractions. The mode of feeding is uncertain. *Mackenzia* lacks tentacles or other obvious grasping devices, and contains no identifiable food items that might indicate its dietary preferences. Its sessile mode of life makes either predatory activity or suspension feeding of particulate material more likely. In the former it could be hypothesized that abrupt suctional action could sweep macroscopic prey into the central digestive cavity. Alternatively, the ciliated tracts could induce water circulation with particles being trapped by mucous nets spun either into the surrounding water, suspended adjacent to the putative oral opening, or collected over the surface of the body.

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#### EXPLANATION OF PLATE 5

Figs 1–7. *Mackenzia costalis* Walcott. Walcott quarry, near Field, British Columbia; Stephen Formation (Burgess Shale), Middle Cambrian. 1–2, GSC 78494, entire specimen; 1,  $\times 1.2$ ; 2,  $\times 0.6$ . 3, GSC 78494, detail of proximal region and holdfast composed of nodular material,  $\times 1.3$ . 4, GSC 78490, entire specimen associated with an echinoderm and also ?chondrophorine (see Pl. 8, figs 1–2),  $\times 1.3$ . 5, USNM 193967, entire specimen,  $\times 1.3$ . 6, USNM 193967, detail of proximal region with holdfast composed of a brachiopod and sponge spicules,  $\times 6$ . 7, GSC 78497, entire specimen,  $\times 0.8$ . All specimens photographed in either high angle (1, 4) or low angle (2–3, 5–7) ultraviolet radiation.



?Class HYDROZOA Owen, 1843  
 ?Suborder CHONDROPHORINA Chamisso and Eysenhardt, 1821  
 Family uncertain  
 Genus GELENOPTON gen. nov.

*Type species. Gelenopton tentaculatum* sp. nov.

*Derivation of name.* The generic name is a construct of the Greek word *enopton* (mirror) and Latin word *gelatus* (gelatinous), an oblique reference to the strongly reflective preservation of the putative float and the inferred gelatinous composition of the animal.

*Diagnosis.* Elongate structure, possibly a float, with marginal rim of densely spaced tentacles. Separate lower unit, bearing larger, more stout tentacles with faint annulations.

*Gelenopton tentaculatum* sp. nov.

Plate 8, figs 3–4

1931 *Redoubtia polypodia* Walcott, p. 3, pl. 2, fig. 2 (non fig. 3).

1989c '*Redoubtia polypodia*' Walcott, Conway Morris, p. 343, fig. 5D.

*Derivation of name.* The trivial name *tentaculum* refers to the abundance of tentacles.

*Diagnosis.* See genus.

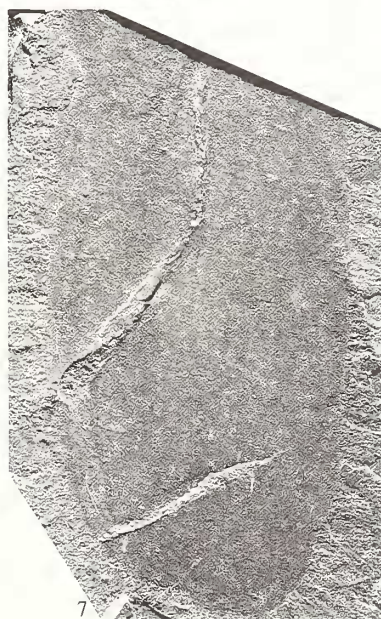
*Types and locality.* Holotype USNM 83925 (part and counterpart). Middle Cambrian, Phyllopod bed (Burgess Shale) from USNM locality 35k at Walcott Quarry near Field, British Columbia

*History of research.* In 1918 Walcott (1918, fig. 5) illustrated a lobopod-like animal as *Redoubtia polypodia*. Subsequently (Walcott 1931, pl. 2, fig. 3) this specimen was re-illustrated, with a second specimen (Pl. 8, fig. 3). Resser (*in* Walcott 1931, p. 3) noted that 'Whether the second specimen really represents the same species appears somewhat doubtful inasmuch as the tube feet [*R. polypodia* was regarded as a holothurian] are smaller and more numerous. The larger appendages above the specimen . . . are parts of another animal.' Since then *R. polypodia* has received sporadic mention, mostly concerned with its possible status as a holothurian and with evident reference to the lobopod-like specimen (e.g. Croneis and McCormack 1932; Madsen 1957) rather than the material illustrated here. Conway Morris (1989c) re-illustrated the holotype, and made passing reference to its possible status as a chondrophorine.

*Description.* Although several specimens are known, only the holotype (Pl. 8, figs 3–4) is particularly informative and even here the overall anatomy is not entirely resolved. The bulk of the specimen consists of a broad reflective area, tapering towards one end. Around the edge of this organ is a series of tentacle-like structures, densely spaced and extending outwards for about 9 mm. It appears that these tentacles formed at least two, and perhaps three, distinct layers. Each tentacle is narrow and tapers to a fine point. On the upper side of the specimen (as illustrated) a separate set of structures (Pl. 8, figs 3–4) lie at a distinctly different level

EXPLANATION OF PLATE 6

Figs 1–8. *Mackenzia costalis* Walcott. Walcott quarry, near Field, British Columbia; Stephen Formation (Burgess Shale), Middle Cambrian. 1, GSC 78498, entire specimen,  $\times 0.8$ . 2, GSC 78498, detail of proximal area and holdfast,  $\times 1.9$ . 3, GSC 78496, detail of strands of tissue, probably resulting from partial decay,  $\times 2.2$ . 4–5, USNM 193930, part and counterpart respectively, entire specimens,  $\times 1$ . 6–7, USNM 193947, counterpart and part respectively, entire specimens,  $\times 1.4$ . 8, USNM 193968, entire specimen, note holdfast with sponge spicules at proximal end,  $\times 0.9$ . Fig. 1 photographed in white light, others in ultra-violet radiation at either a high angle (2–6, 8) or low angle (7).



(lower in the part). Adjacent to the reflectively preserved organ this unit is featureless, but distally it extends into a series of stout tentacles with faint transverse annulations and pointed terminations. This structure is regarded as an integral part of the organism, rather than a chance superposition (cf. Walcott 1931).

*Discussion.* The affinities of *G. tentaculatum* are uncertain. There is no support for an affinity with the holothurians, and the recent tentative assignment to the chondrophorines (Conway Morris 1989c) is explained here. In this interpretation the broadly reflective area is interpreted as the float or pneumatophore. In contrast to known chondrophorines, however, the float shows no indication of chambers or other subdivisions. Comparing the tentacle-like structures in the fossil to the complex series of zooids in living chondrophorines is not straightforward. It could be hypothesized that the rim of tentacle-like structures is equivalent to the tentaculozooids or dactylozooids, while the larger tentacles might conceivably form part of the set of the gonozooids. This interpretation, however, is by no means secure. Attempts to compare *G. tentaculatum* with the siphonophores, another group of complex hydrozoans (Harrington and Moore 1956), are no more satisfying. The evidence for common possession of a float or pneumatophore cannot be matched by convincing comparisons between the various zooids of siphonophores and the tentacular structures of the fossil.

A number of other specimens (USNM 198613, 200621, 200607–200608, 200588 (part and counterpart)) are comparable to the holotype in having margins that are either tentacular or hirsute, but despite this similarity cannot be confidently assigned to *G. tentaculatum*. The affinities of these specimens remain obscure, except that USNM 198613 appears to be some sort of worm with a pair of prominent tentacles.

#### ?Chondrophorine

Plate 8, figs 1–2; Text-fig. 5

*Diagnosis.* Disc (?pneumatophore) with closely spaced annulations and elongate tentacles (?dactylozooids) extending beyond margin.

*Material and locality.* GSC 78491 (only known specimen, superimposed on GSC 78490, a specimen of *Mackenzia costalis* Walcott). Walcott Quarry, 5 km north of Field, British Columbia.

*Stratigraphical horizon.* About 3' 0"–3' 7" (0.91–1.09 m) (GSM 1967 collecting level 81210) above base of Phyllopod bed, 'thick' Stephen Formation, Middle Cambrian.

*Remarks.* The specimen (Pl. 8, figs 1–2; Text-fig. 5) is incomplete owing to rock breakage, and is superimposed on a specimen of *Mackenzia costalis* Walcott. Also adjacent is an unidentified echinoderm. Given the confusion that has arisen with specimens that were believed to show chance superposition but proved to be integral (Conway Morris 1978; Whittington and Briggs 1985) and continuing uncertainty about whether spinose extensions in some arthropods are in situ or chance

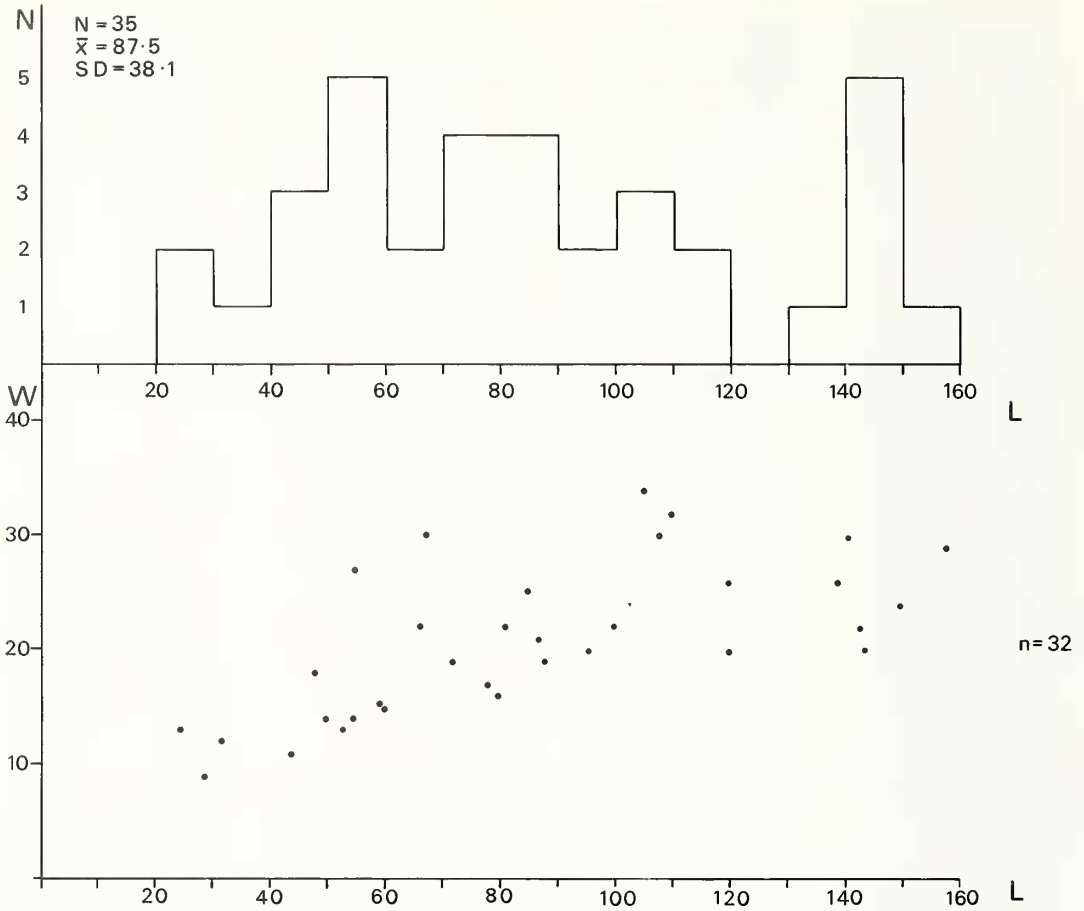
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#### EXPLANATION OF PLATE 7

Figs 1–9. *Mackenzia costalis* Walcott. Walcott quarry, near Field, British Columbia; Stephen Formation (Burgess Shale), Middle Cambrian. 1–2, USNM 193929, part and counterpart, entire specimens,  $\times 1$ . 3, USNM 193929, part, detail of possible digestive contents,  $\times 4.9$ . 4, USNM 193955, part, entire specimen,  $\times 0.7$ . 5, USNM 193955, counterpart, detail of possible digestive contents,  $\times 3.9$ . 6, USNM 193955, counterpart, detail of distal region,  $\times 1.3$ . 7, USNM 193961, entire specimen,  $\times 1.8$ . 8, USNM 193961, detail of possible digestive contents,  $\times 3.3$ . 9, USNM 196174, two individuals (proximal portions only) attached to stem of eocrinoid,  $\times 1.5$ . Specimens photographed either in white light (1–2, 4, 6–7) or low angle ultra-violet radiation (3, 5, 8–9).







TEXT-FIG. 4. Plots of size frequency (upper histogram) and bivariate scattergram of length against maximum width (lower graph) of *Mackenzia costalis* Walcott.

overlaps (Whittington 1981, p. 351; Conway Morris and Robison 1988, pp. 29–30), it is important to determine whether this unique specimen was indeed an individual or integral part of *Mackenzia*. Evidence for the former is principally the absence of anything similar in the remaining suite of *Mackenzia* from the Burgess Shale (c. 70 specimens). An alternative possibility is the discoidal fossil represents part of the life cycle of *Mackenzia*, specifically a swimming or floating stage that budded from the sessile stage for dispersal. One point against this interpretation, perhaps, is the large size of the disc relative to the specimen of *Mackenzia*.

#### EXPLANATION OF PLATE 8

Figs 1–2. Possible chondrophorine. GSC 78491, entire specimen photographed from two different angles of radiation, superimposed on an individual of *Mackenzia costalis* Walcott (see Pl. 5, fig. 4),  $\times 3.1$  and  $\times 2.6$  respectively. The branched structure on the lower side of the figures is an echinoderm.

Figs 3–4. *Gelenopteron tentaculatum* gen. et sp. nov. USNM 83925, part and counterpart respectively,  $\times 1.3$ . Walcott quarry, near Field, British Columbia; Stephen Formation (Burgess Shale), Middle Cambrian. All photographs taken in ultra-violet radiation.



*Description.* The specimen is poorly preserved, and difficult to resolve on account of its superposition with the individual of *Mackenzia*. It is most obvious from the concentric annulations, which average about 11 per 5 mm. The margins of the disc are not clear, but the original diameter is estimated to have been about 23 mm. On one side four elongate structures arise; these are interpreted as the remains of tentacular organs.

*Affinities.* This specimen is tentatively regarded as a chondrophorine hydrozoan, a group of colonial cnidarians represented today by the pelagic *Porpita* and *Veleva*. Under this interpretation the disc with concentric annulations is taken to be the chitinous pneumatophore with annular gas-filled chambers that imparted buoyancy. There is no evidence for a sail on the upper surface of the putative pneumatophore, and in this sense the specimen resembles *Porpita* which in contrast to *Veleva* lacks a sail. Pursuing the comparisons with chondrophorines would suggest that the tentacles be interpreted as some of the marginal dactylozooids. Incomplete preservation might explain why they are not visible around the remainder of the disc margin, and why the other more centrally located zooids (gonozooids and gastrozooids) are not visible.

## DISCUSSION

### *Introduction*

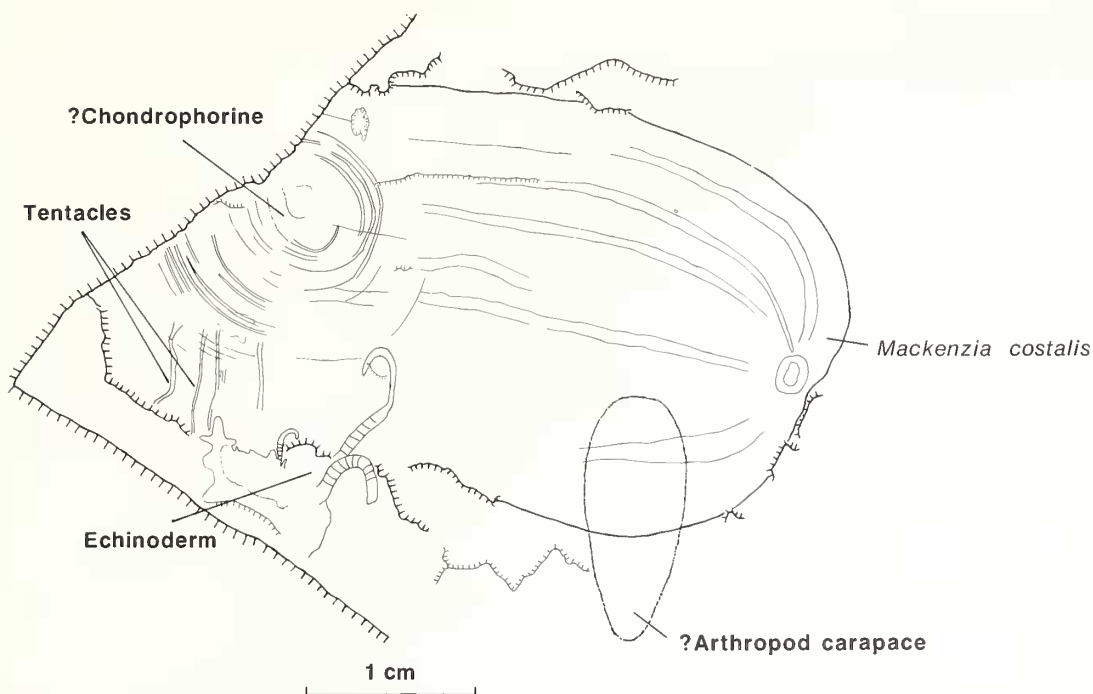
The interpretation of Ediacaran faunas is complicated considerably by the competing hypotheses of whether the various species are more or less comparable to extant taxa, notably cnidarians, annelids and arthropods (e.g. Glaessner 1984), or whether they are so distinct from known metazoans as to justify erection of a separate category of Vendozoa or Vendobionta (Seilacher 1984, 1989, 1992; see also Bergström 1989, 1990). The merits of these proposals are returned to below, but are of immediate relevance because organisms supposedly disparate according to one hypothesis are closely related if the other is correct. For example, *Spriggina* has been widely interpreted as a metamericly segmented metazoan of either annelid or arthropod grade (e.g. Birket-Smith 1981; Glaessner 1984). However, the vendobiontan interpretation (e.g. Bergström 1989; Seilacher 1989, 1992) takes the supposed head-shield as an organ for benthic attachment, and the putative segmented trunk as a frond-like body subdivided into transverse compartments.

The definition of taxonomic categories, therefore, is potentially elastic. This is especially true of the frond-like organisms abundant in many Ediacaran assemblages. Some, especially *Charniodiscus* and *Vaizitsinia*, are patently similar to *Thaumaptilon*, but other taxa differ to varying degrees. While it is possible, therefore, to provide relatively detailed comments on the likely relationships between a few Ediacaran taxa and younger forms, a comprehensive review is more difficult.

### *Possible relatives of Thaumaptilon*

Among the Ediacaran taxa are those frond-like fossils with a broad blade, usually with a median rachis, and often a stalk terminating in a more-or-less discoidal holdfast. Taxa include *Charnia* (e.g. Ford 1958; Fedonkin 1981, 1985), *Charniodiscus* (e.g. Ford 1958, 1963; Glaessner and Daily 1959; Fedonkin 1981, 1985, 1987; Jenkins *et al.* 1983; Sun 1986; Gehling 1991), *Glaessnerina* (e.g. Glaessner and Wade 1966; Germs 1973; Jenkins and Gehling 1978), *Paracharnia* (e.g. Sun 1986), *Vaizitsinia* (e.g. Fedonkin 1981, 1985), and possibly *Ramellina* (e.g. Fedonkin 1981, 1985) and *Valdania* (e.g. Fedonkin *in* Velikanov *et al.* 1983; Fedonkin 1985).

Among the Ediacaran frondose taxa, *Thaumaptilon* (Text-fig. 3) seems to approach most closely *Charniodiscus* and *Vaizitsinia*, although with the latter genus comparisons cannot be as extensive on account of more limited information. *Charniodiscus* is best known from South Australia (Jenkins and Gehling 1978; Jenkins 1984, 1992; see also Glaessner and Daily 1959; Glaessner and Wade 1966; Jenkins *et al.* 1983; Gehling 1991; Runnegar 1992), although its type occurrence is from Charnwood Forest, England (Ford 1958, 1963; Jenkins and Gehling 1978). Discoidal fossils interpreted as the basal attachment organs of *Charniodiscus* have also been reported from the White Sea, north-west Russia (Fedorin 1981, pl. 3, fig. 8), the Wernecke Mountains of Yukon (Narbonne



TEXT-FIG. 5. Camera-lucida drawing of specimen of *Mackenzia costalis* Walcott; Walcott (GSC 78490; see Pl. 5, fig. 4) with superimposed circular fossil (GSC 78491; Pl. 8, figs 1–2) tentatively interpreted as a chondrophorine. Walcott quarry, near Field, British Columbia; Stephen Formation (Burgess Shale), Middle Cambrian.

and Hofmann 1987, text-fig. 5*b–d*), and the Mackenzie Mountains of north-west Canada (Narbonne and Aitken 1990, pl. 1, fig. 7; this specimen shows an indistinct longitudinal trace to the right of the disc as illustrated, evidently representing part of the stalk). The assignment of these discs to holdfasts of frondose animals, including *Charniodiscus*, was strongly endorsed by Jenkins (1989). In particular, he (Jenkins 1989, p. 313; see also Jenkins 1992, p. 157) noted 'that *Cyclomedusa* should best be considered as a form-genus representing variable holdfasts of sea-pen-like animals', the implication being that some are probably synonymous with *Charniodiscus*. Species of *Charniodiscus* recognized on the basis of preserved fronds include *C. concentricus* (type species), *C. arboreus*, *C. longus* and *C. oppositus*. Overall similarities between the taxa include a broad lanceolate frond with central rachis, on the ventral side prominent primary branches that are fused along their bases to the frond and extend into the rachis via canal-like structures, a more or less smooth dorsal surface, and an elongate stalk and holdfast. Dimensions are also broadly comparable. Among the species of *Charniodiscus*, *Thaumaptilon* seems to approach most closely *C. oppositus* and perhaps *C. concentricus*.

There are, nevertheless, a number of differences, seemingly sufficient to denote generic separation, but still inclusion in the same family, presumably the Charniidae Glaessner, 1979*a*, if *Charnia* is accepted as being related to *Charniodiscus* and *Thaumaptilon* (see below). One difficulty in drawing objective comparisons is the different style of preservation between the compression fossils of the Burgess Shale in shale and the mouldic impressions of Ediacaran fossils in sandstones and siltstones.

The following are the most obvious differences: (a) *Thaumaptilon* appears to lack a membranous edge to the frond, and the primary branches extend close to the margin; (b) the holdfast is relatively elongate and, although showing some indication of expansion (Pl. 3, fig. 6) does not match the disc-like termination of *Charniodiscus* with its prominent radial ornamentation (?musculature; especially

in *C. oppositus*) and concentric ridges (in *C. concentricus*) (see Jenkins 1992, p. 161). It remains possible that the holdfast of *Thaumaptilon* was more contractile than present evidence would suggest, and in life could expand into a discoidal structure. It should also be noted that Jenkins (1992, p. 161) commenting on the holdfasts of *Charniodiscus* noted that 'their apparent flat shape resulted from sediment compaction and they were presumably subspherical in life'; (c) in *Thaumaptilon* the branches seem to have been more recurved at the frond margin than in *Charniodiscus*. In this latter genus, Jenkins and Gehling (1978; see also Glaessner and Daily 1959, p. 386) presented evidence that although the primary branches were fused to the frond, the zone of attachment was narrow so that overall the branches were relatively flexible. In contrast, the freedom of movement in *Thaumaptilon* appears to have been confined to the distal margin so that the branches were more cushion-like.

There are two other significant differences, but these may be effectively taphonomic. The first is the absence of spicules in *Thaumaptilon*. In *Charniodiscus* putative spicules occur (e.g. Glaessner and Daily 1959; Jenkins 1992) in the rachis. They also supposedly occur on the branches, where the clarity of demarcation between the putative anthosteles along the primary branches (so defining the secondary branches) is regarded as reflecting the presence of spicules (Jenkins and Gehling 1978). No ultrastructural information on these spicules is available, and their status as spicules remains questionable. It seems unlikely that spicules in *Thaumaptilon* were lost during diagenesis, because a wide variety of spicular structures are evident in the Burgess Shale sponges (Rigby 1986). The second difference is that the supposed anthosteles (i.e. secondary branches), in *Charniodiscus* find no exact counterpart in *Thaumaptilon*. It is true that some of the branches in the latter taxon have transverse striations, but in contrast to *Charniodiscus* these are less regular and more closely-spaced. In any event it seems unlikely that the secondary branches in *Charniodiscus* are true anthosteles, especially on account of their larger size. Jenkins (1984, p. 99) noted that if *Charniodiscus* had true polyps, then these would have been difficult to preserve. This comment accords with the size and preservation of the putative zooids (Pl. 3, fig. 1) in *Thaumaptilon*. Narbonne and Hofmann (1987, p. 655) reported 'subcircular tubercles 0.5–7.0 mm across and up to 1.0 mm relief', but considered them to be 'probably accidental'. The likelihood that these structures are zooids seems to be remote given their irregular distribution and widely variable size. Examination of the exceptionally well-preserved holotype of *Charniodiscus oppositus* with R. J. F. Jenkins (see also Jenkins 1992, p. 161) in Adelaide (July, 1992) specifically to search for zooids did reveal very slight irregularities on the sandstone surface of the branches. Nevertheless, as zooids they remained unconvincing and it remains to be established what surfaces or regions of the frond are exposed in these Ediacaran fossils.

The differences between *C. oppositus* and the other species of *Charniodiscus* also pertain to those with *Thaumaptilon*. Most notable are the alternate insertion of the primary branches in *C. arboreus* and the more elongate form of the eponymous *C. longus*. Despite being the type species relatively little is known of *C. concentricus* because of its poor preservation. It may differ from *Thaumaptilon* in having a more prominent discoidal holdfast (see Jenkins and Gehling 1978, fig. 4), but *C. concentricus* has possibly significant similarities with *Thaumaptilon* in the disposition of the primary branches, as well as possessing faint transverse striations that in spacing and arrangement resemble those of the Burgess Shale taxon.

Comparisons with other Ediacaran frond-like fossils may be kept brief. *Glaessnerina* has been illustrated on the basis of few specimens, none complete, and in the opinion of Jenkins (1992, p. 162) remains an 'enigmatic genus'. It is characterized by the primary branches meeting along the midline as a zig-zag commissure that obscures the axis. Jenkins and Gehling (1978, p. 353) indicated, however, that this juxtaposition of branches could be a post-mortem feature. Another difference with *Thaumaptilon* are the very prominent secondary branches. *Vaizitsinia*, from the White Sea region of north-west Russia, has not received extensive documentation. Existing descriptions portray a frond with a more rhomboidal outline than *Thaumaptilon*, but the slightly inflated holdfast and prominent primary branches with transverse striations (Fedonkin 1985, pl. 14, fig. 4; see also Fedonkin 1983, fig. 39) are similar to the Burgess Shale example.

There are a number of other frond-like fossils from Ediacaran faunas that either require more detailed documentation before extensive comparisons can be drawn with *Thaumaptilon* (e.g. *Khatyspytia grandis* Fedonkin 1985; note that the only description of this new taxon occurs in the plate description) or appear to differ more extensively with the Burgess Shale example. Foremost in this respect is *Charnia masoni* (e.g. Ford 1958; Fedonkin 1981, 1985), which is characterized by very well-developed secondary branches (at right angles to the primary branches) and also discernible tertiary branches (Fedonkin 1981; Jenkins 1985). Note also that Runnegar (1992, p. 76; see also Germs 1973, p. 5) proposes that *Glaessnerina* is synonymous with *Charnia*. Unpublished observations from the Mistaken Point assemblage of the Avalon peninsula, Newfoundland also demonstrate that *Charnia* possessed a circular holdfast (see also Jenkins 1984, 1985, 1992) similar to that of *Charniodiscus*. Although *Charniodiscus*, *Charnia* and *Rangea* had been linked with a number of other Ediacaran forms in a 'Hypothetical phylogeny of Precambrian frond-like octocorals' by Jenkins (1985, fig. 8; see also Jenkins 1984, p. 100, text-fig. 4), subsequently this worker (1989) emphasized differences by allying *Rangea* and *Charnia* in the Rangeomorpha, and *Charniodiscus* and *Glaessnerina* in an unspecified higher taxon. Of the Rangeomorpha Jenkins (1989, p. 313) noted 'while they were evidently of cnidarian grade, they show little direct similarity to living Cnidaria', whereas the latter genera remained within the pennatulaceans. The differences between the rangeomorphs and taxa such as *Charniodiscus* and *Thaumaptilon* are self-evident from the literature (e.g. Fedonkin 1985; Jenkins 1985), but in my opinion the case for removing the rangeomorphs from the pennatulaceans is not compelling. Apart from the general arrangement of fronds, stalk and holdfast, the differences in branch arrangement would seem to be no more remarkable than the analogous case of zooid configurations in extant scleractinians. Whether the concept of the Charniidae Glaessner, 1979a is adequate to encompass all these forms is uncertain, but with the higher taxonomy of Ediacaran fossils in a continuing state of flux this family is retained.

Among other frond-like Ediacaran taxa attention should be drawn to *Paracharnia*, but the specimens are difficult to interpret from the available photographs (Ding and Chen 1981; Sun 1986). *Paracharnia* appears to be distinct because of the numerous leaf-like extensions that arise from the main frond (see also Dorzhnamzhaa and Gibsher 1990 for a record of *Paracharnia* from Mongolia). A number of other frond-like fossils (*Archangelia valdaica*, *Vaveliksia veliknanovi* and *Zolotytsia biserialis*, e.g. Fedonkin 1985) remain rather poorly known (see also Gehling 1988, fig. 7A).

As *Thaumaptilon* (Text-fig. 3) is evidently closely related to a number of Ediacaran frond-like taxa, especially *Charniodiscus*, *Vaizitsinia* and *Charnia*, the next point to address is whether the similarity to known pennatulaceans is significant. The evidence for the *Charniodiscus*-*Thaumaptilon* complex being true pennatulaceans is based on three principal suppositions: overall shape, probable presence of autozooids, and evidence for a system of internal canals similar to extant pennatulaceans (e.g. Brafield 1969). In disputing the widely-held view that the Ediacaran fronds are pennatulaceans (e.g. Glaessner and Wade 1966; Jenkins and Gehling 1978; Runnegar 1982; Jenkins 1989, 1992), some emphasis has been given by critics of this scheme (e.g. Seilacher 1984, 1989) to the arrangement of the branches: fused to a common membrane in Ediacaran taxa, but separate in taxa such as *Pennatula*. While it remains true that no exact counterpart to extant pennatulaceans exists among the Ediacaran fronds, it is also clear that the diversity of the former is very considerable and includes forms far removed from taxa generally regarded as typical, such as *Pennatula*. In this context one could draw attention to forms such as *Renilla*, where the polyps arise from a flattened surface, and various club-like forms (e.g. *Veretillum*, *Sclerobelemon*). Whether the putative polyps in *Thaumaptilon* really are autozooids remains tentative, but their distribution and size (they are assumed to be retracted) are consistent with this interpretation. The much smaller siphonozooids are unlikely to be recognizable in fossils, but not withstanding the typical relatively coarse-grained lithology of Ediacaran preservation (see above), it is possible that putative autozooids will be identified.

The significance of the arcuate band, reflectively preserved on the holdfast of the holotype, is uncertain. There is a suggestion of a pustule-like structure, but as this region was presumably

embedded in the sediment it may be thought unlikely that the pustules represent autozooids. In the literature, however, there are reports of siphonozooids on the basal bulbous holdfast of the pennatulacean *Umbellula carpenteri* (see Hickson 1916, p. 8).

Accepting the *Charniodiscus-Thaumaptilon* complex as pennatulaceans (see also Norris 1989), it remains to be established what relationships might exist with other Ediacaran taxa as well as Phanerozoic fossils assigned to this group. Apart from the Ediacaran taxa mentioned above, the closest relations of this complex may lie with *Rangaea*. This is a distinctive form with three (or more) fused fronds arising from a common base with a bulbous holdfast (see Jenkins 1985, 1989, 1992 for further discussion).

The Phanerozoic fossil record of pennatulaceans is largely composed of isolated spicules, which may extend to the Lower Cambrian (e.g. Bengtson *et al.* 1990) and more occasional calcified axes (e.g. Kuz'micheva 1980; Malecki 1982; Kocurko 1988). While soft-bodied remains of other types of octocoral are known (e.g. Ruedemann 1916; Glinski 1956; Hamilton 1958; Sass and Rock 1975; Lindström 1978), comparable fossils of pennatulaceans seem to be exceedingly rare. Tremblay (1941) described a possible example from Quebec, apparently from the Potsdam Sandstone (Upper Cambrian). The supposed examples from the Tertiary of Trinidad and the south-eastern Moluccas (Bayer 1955) were reinterpreted as trace fossils (Häntzschel 1958, 1975). Häntzschel (1958) also discussed a number of other putative octocoral fossil remains and concluded they represented various types of trace fossil.

#### *Possible relatives of Emmonsaspis*

Concerning the comparison of *Emmonsaspis* with Ediacaran taxa, there is more uncertainty. The branching arrangement, imparting the characteristic chevron pattern, recalls approximately a number of Ediacaran fronds. Nevertheless, there is an absence of evidence for either second branches, a stalk or a holdfast. It is tentatively proposed that comparisons might be better drawn to *Pteridinium*, a widespread taxon that consists of a more or less inflated body composed of repeated transverse units (e.g. Glaessner 1963; Glaessner and Wade 1966; Pflug 1970; Fedonkin 1981, 1985; Gibson *et al.* 1984; Jenkins 1989; see also Narbonne and Aitken 1990). To my knowledge there are no other fossils which resemble *Emmonsaspis* more closely. Nevertheless, the comparisons are by no means precise. According to Pflug (1970) the body of *Pteridinium* consists of three vanes (see also Jenkins 1992), whereas so far as can be told *Emmonsaspis* had a foliate body. In addition, the ribs of *Pteridinium* are more siculate in shape and meet along a well-defined axial groove.

#### *Possible relatives of Mackenzia*

Some Ediacaran faunas contain peculiar bag-like structures, especially the erniettiids, whose systematic relationships remain uncertain. In seeking a possible relative to *Mackenzia* among the Ediacaran assemblages, one possibility is a comparison with *Platypholinia pholiata* (e.g. Fedonkin 1985, pl. 19, figs 5–6). This is a rare sac-shaped organism, only known from the White Sea region of north-east Russia. *Platypholinia* is rather featureless, but there is some evidence for an oral opening. Fedonkin's (1985) assignment of this taxon to the platyhelminths is considered unlikely. It differs from *Mackenzia* in being smaller, less elongate, and in lacking obvious external folds. Nevertheless, a relationship between the taxa is possible. Although superficially seemingly different, comparisons might also be drawn between *Mackenzia* and the putative actinian *Inaria karli*, documented by Gehling (1988) from the Pound subgroup (Rawnsley Quartzite) of the Flinders Ranges, South Australia. As reconstructed the most striking divergence is the proximal expansion of *Inaria*, most noticeably in adults, into lobate expansions that give the animal a vague resemblance to a garlic clove. From this region the polyp extends into a more cylindrical distal portion, reconstructed as having a simple opening without tentacles, although Gehling (1988) does not rule out their absence by non-preservation. In addition *Inaria* is inferred to have had internal mesenteries with muscular strands. The similarities between *Inaria* and *Mackenzia*, including simple oral opening, lobate walls, and internal mesenteries, suggest a fairly close relationship. Another



Ediacaran fossil that might be compared with *Mackenzia* is the only known specimen of *Protechiurus edmondsi* from the Kuibis Quartzite, Namibia. Glaessner (1979b) interpreted the sandstone cast, which is approximately cigar-shaped and bears seven or eight longitudinal ridges, as an early echiuroid worm. The evidence for this assignment is regarded as slender, but in shape and dimensions the fossil accords with how a *Mackenzia*-like individual would appear if its central cavity was infilled with fine sand. Mention should also be made of Ediacaran fossils such as *Beltanelliformis*, which Narbonne and Hofmann (1987) synonymize with *Nemiana* and more tentatively *Beltanelloides*. The specimens tend towards a bowl-like shape and are often found in abundance and closely spaced. They have been generally interpreted as sedentary cnidarians (e.g. Fedonkin 1985), although Narbonne and Hofmann (1987; see also Jenkins 1992) reconstructed them as globular bodies of uncertain systematic position.

In passing Jenkins (1989, p. 311) noted that some specimens of what appear to be *Eoporpita*, widely interpreted as a chondrophorine (e.g. Wade 1972b) showed structures that suggested they could 'be reasonably reconstructed as actinians'. In 1992, however, Jenkins (p. 161) returned to a comparison with chondrophorines, although not abandoning his proposed link with the actinians. This author (Jenkins 1989, fig. 2A–C) also illustrated a putative actinian (possibly *Medusinites asteroides*; see also Jenkins 1992) with evidence of tentacles, noting that further study was required. In addition, Jenkins (1989) proposed that other scyphozoan-like fossils (e.g. *Ediacaria*) had modes of life similar to actinians. All these taxa require further study (see Jenkins 1992), and while they differ from *Mackenzia* in the possession of what appear to be tentacles, they may belong to the same clade of anemone-like anthozoans.

The wider relationships of *Mackenzia* and *Inaria*, and perhaps *Platypholinia* and *Protechiurus*, are uncertain. They are regarded as being of a cnidarian grade, and may be most closely related to the anthozoan actinians (see also Gehling 1988). Concerning the apparent absence of oral tentacles a possibly significant comparison (see also Gehling 1988) might be drawn with the Recent actinians *Linnactinia nuda* and *L. laevis* (Calgren 1921, 1927). Unlike other species of *Linnactinia*, these species lack oral tentacles, but have nematocysts scattered over the exterior surface that form dense batteries in the oral region. The resemblances between *Linnactinia* and *Mackenzia* are quite striking, although in contrast to the Burgess Shale taxon, *Linnactinia* was evidently embedded in the marine muds of its cold-water habitat. In the ceriantharian anemones a number of taxa are known to lack tentacles. These include *Anactinia*, a small anemone that is interpreted as pelagic, from the Bay of Bengal (Annandale 1909), although this genus and the related *Paractinia* are probably larval forms (see Tiffon 1987). In a related context attention should also be drawn to the scleractinian coral *Leptoseris fragilis*. This species is also remarkable in lacking oral tentacles but here heterotrophic feeding is evidently facilitated by flagella (Schlichter 1991). Thus, if *Mackenzia* were to be compared with tentaculate cnidarians, then *L. fragilis* might provide some revealing similarities in terms of functional morphology. In other respects, however, this latter species differs considerably from *Mackenzia*, but as discussed below its organization might provide analogies to Ediacaran organisms.

#### *Possible relatives of Golenoptron and the ?chondrophorine*

Concerning the fossil record, the study of Phanerozoic chondrophorines has undergone a minor renaissance with a variety of fossils so assigned (see Stanley 1986 for a recent review) to complement an existing roster (see Harrington and Moore 1956). While some of these assignments appear to be reasonable, others are considerably more suspect (see Conway Morris 1989c, p. 346; Conway Morris *et al.* 1991; Landing and Narbonne 1992) and discovery of an annulated disc alone may be insufficient to place a given fossil in the chondrophorines.

In the context of this Burgess Shale fossil, however, particular interest devolves on putative chondrophorines from the Cambrian, especially Burgess Shale-type faunas, and their descent from taxa present in the Ediacaran assemblages. The status of the supposed chondrophorine *Rotadiscus grandis* (Sun and Hou, 1987) from the Chengjiang fauna is discussed above, and although its affinities are uncertain, a place within the Cnidaria, let alone the chondrophorines, seems unlikely.

Later, Chen *et al.* (1989, p. 271) mentioned another fossil which 'bears a strong resemblance to modern *Porpita*', but this is yet to be illustrated and discussed. Within the Ediacaran assemblages reasonably convincing pneumatophores are present in the form of the annulated discs of *Ovatoscutum*, known from both South Australia (Glaessner and Wade 1966; Jenkins 1984, 1989, 1992) and the White Sea area of Russia (Fedonkin 1984, 1985). Nothing is known of the soft-parts which were associated with *Ovatoscutum*. Other putative chondrophorines from Ediacaran beds are *Eoporpita* (Wade 1972b; Jenkins 1984; Narbonne and Aitken 1990, but see Jenkins 1989, 1992) and *Kullingia* (Føyn and Glaessner 1979; see also Narbonne and Hofmann 1987; Narbonne and Aitken 1990). The former is associated with structures that are interpreted as zooids (but see Norris 1989), while the latter genus has also been found in strata very close to the Precambrian–Cambrian boundary in the Burin Peninsula, southeast Newfoundland (Narbonne *et al.* 1991). *Chondroplon* was regarded by Wade (1971) as another chondrophorine, although Hofmann (1988) reinterpreted the only known specimen as an example of *Dickinsonia* (but see Jenkins 1989, p. 311; 1992, p. 161), a fossil which is widely interpreted as a putative annelid worm (Glaessner and Wade 1966; Wade 1972a; Runnegar 1982). Of all these fossils, the ?chondrophorine appears to approach most closely *Kullingia*, albeit differing in being considerably smaller (one Ediacaran specimen of ?*Kullingia* from the Wernecke Mountains, Yukon is regarded as small with a diameter of 54 mm (Narbonne and Hofmann 1987, p. 659)). *Gelenoptron tentaculatum* has no clear similarities to known Ediacaran chondrophorines, but is included here because of its possible relationships to the hydrozoans.

#### *The status of the Vendozoa*

The hypothesis that the Ediacaran fossils represent a distinctive assemblage, perhaps entirely separate from the Metazoa, whose basic body-plan has been compared to a series of chambered units (Seilacher 1984, 1989, 1992; Bergström 1989, 1990) has attracted wide attention (e.g. Gould 1984, 1989). Nevertheless, it may be fundamentally incorrect, at least so far as the entire fauna is concerned. Re-emphasis of the metazoan status of a number of the fossils has come from Gehling (1991) and Runnegar (1992), while other workers (e.g. Jenkins, 1984, 1985, 1989, 1992) have persisted with such assignments during the time of controversy.

In the context of this paper there are three items that bear on this controversy, and cast doubt on the vendobiontan hypothesis, at least in its all-embracing form promulgated by Seilacher (1992).

First, there seems reasonable evidence that *Thaumaptilon walcotti* is related to Ediacaran taxa such as *Charniodiscus*. There is also evidence that *T. walcotti* can be compared with pennatulaceans. Most significant are the putative autozooids, whose distribution and size are consistent with the pennatulaceans. In addition, although the foliate structure finds no exact parallel among extant pennatulaceans, the overall arrangement of central axis and branches with connecting canals is certainly similar. It is true that Recent pennatulaceans do not appear to have an exact counterpart to the discoidal holdfasts of some Ediacaran types, such as *Charniodiscus* (see also Jenkins 1992). However, the holdfasts of the former are quite often bulbous, and Hickson (1916) mentioned that in one form the so-called end-bulb was thin-walled and showed a spherical to oval expansion. In addition Kükenthal and Broch (1911, pl. 15, fig. 11) illustrated a specimen of *Kophobelennon heterospinosum* with its holdfast inflated to form a ball-like structure, and similar structures are depicted by Nutting (1912) in various pennatulaceans. There has, moreover, been an over-emphasis in comparing the Ediacaran fronds with genera such as *Pennatula*, *Pteroides* and *Scytalium*, and a reluctance to include the wide variety of other pennatulacean forms in the discussion. This is not to imply that other Recent taxa approach more closely in form the putative Ediacaran sea-pens, but rather to emphasize that the pennatulaceans adopt a very wide variety of shapes.

Even if *T. walcotti* and its putative Ediacaran relatives are admitted into the pennatulaceans, this leaves important questions unresolved. These include (a) the status of various other Ediacaran taxa such as *Charnia* and *Rangia* (see Germs 1973; Jenkins 1984, 1985); (b) the possible presence of Cambrian octocorals as recorded from spicular remains (e.g. Bengtson *et al.* 1990) and their connection with the soft-bodied record; and (c) the phylogenetic relationships between extant pennatulaceans and the fossil examples discussed here.

*Mackenzia costalis* Walcott is also interpreted, albeit more tentatively, as a cnidarian. The comparisons with *Limnactinia nuda* which lacks tentacles, but possesses abundant nematocysts that presumably trap prey, suggests that a comparison between *Mackenzia* and actinians is not far-fetched. Overall, the body form of *Mackenzia* with evidence for a folded transverse section, possibly reflected by internal partitions, and an attachment disc would be consistent with a cnidarian grade. Even if the phyletic status of *Mackenzia* remains uncertain, there is little doubt it is a metazoan. Paramount is the indirect evidence of a musculature, as inferred from the contractability of specimens, while the presence of possible food boluses is consistent with a digestive cavity. While placement of *Mackenzia* in the cnidarians is considered viable, there is little direct evidence to support earlier suggestions that it is an actinarian (Wells and Hill 1956), perhaps even belonging to the Edwardsiidae (Clark 1913)

In passing it is worth reviewing other putative fossil actinarians, as they are exceedingly uncommon. Three taxa are candidates. *Palaeactinia holli* is known from a single specimen in the Upper Ordovician of New York (Ruedemann 1934, pl. 10, figs 1–3). Ruedemann (1934) provided a detailed description, and I re-examined the specimen in 1991. The fossil shows an apparent holdfast and broad stalk, but it is impossible to discern details such as tentacles in the distal zone. An actinarian affinity, while reasonable, remains unproven. The status of two other claimants as fossil actinians is more suspect. *Pseudocaudina brachyura* has been variously identified as a holothurian (e.g. Broili 1926; Frizzell and Exline 1966), an actinarian (Heding 1932), or a possible ctenophore (Ziegler 1991, who proposed that this taxon is a junior synonym of *Laffonia helvetica*; see also Hess 1973, p. 650). Fossils from the Cambrian of France were described by Dollfus (1875) as an actinarian (?*Palaeactis vetula*), and this was accepted tentatively by Wells and Hill (1956). Häntzschel's (1975) reassignment of these structures to trace fossils, probably comparable to *Bergaueria*, is accepted. In the context of this paper it is worth noting that ichnotaxa such as *Bergaueria* are generally considered to have been made by semi-infaunal anemone-like cnidarians (e.g. Arai and McGugan 1968, 1969; Alpert 1973). Both *Mackenzia* and its putative relative *Inaria* were epifaunal, but Gehling (1988) depicts a hypothetical path to an effectively infaunal descendant capable of making *Bergaueria*-like traces.

#### *Vendozoans: are there modern analogues?*

Although the scleractinian *Leptoseris fragilis* is probably less relevant to a detailed understanding of *Mackenzia*, its anatomy is of particular interest because it demonstrates how a cnidarian bodyplan may be modified in a manner that would be analogous to many Ediacaran taxa. *L. fragilis* is also remarkable because although it inhabits water on the edge of the photic zone (up to 145 m) it possesses symbiotic zooxanthellae (Schlichter 1991). Various workers have speculated that Ediacaran taxa obtained nutrition from chemosymbiosis or photosymbionts. Such hypotheses are difficult to test, but one avenue of research might be the search for characteristic molecular biomarkers in adjacent sediments.

*Leptoseris fragilis*, however, does not rely exclusively on zooxanthellae, and during months of reduced sunlight it is heterotrophic, utilizing both dissolved organic matter (DOM) and capturing food particles (Schlichter 1991). The role of DOM versus abundance of particulate food in Ediacaran faunas is speculative, although one might hypothesize that in the apparent absence or rarity of advanced triploblastic suspension feeders such as brachiopods and echinoderms concentrations of suspended material were higher. The use of flagellae in *L. fragilis* to capture food particles suggests a possible parallel to how many Ediacaran species may have fed. It remains possible, of course, that true cnidarians were equipped with nematocysts, that could entangle or poison small prey.

Two other related aspects of *L. fragilis* (Schlichter 1991) may throw light on Ediacaran anatomies. First, this living coral has a series of specialized gastric ducts into which the food is channelled. This arrangement is perhaps not entirely dissimilar to the hypothesized mattress-like construction of some Ediacaran fossils where the body is composed of a series of canals. The second curious aspect of *L. fragilis* is the presence of pores (evidently also present in *Limnactinia nuda*, see Calgren 1927, p. 7) employed for exhalant flow of water from the gastric ducts.

*L. fragilis* may provide no more than a number of interesting analogies to the possible construction and functional morphology of Ediacaran bodyplans. It does, however, suggest that many of the Ediacaran species can be interpreted as diploblasts, of a grade comparable to cnidarians and ctenophores. Indeed, some Ediacaran taxa may be true cnidarians, including *Charniodiscus* and its relatives.

It is concluded that the Vendozoan hypothesis fails for many Ediacaran taxa, although this is not to deny that there are a number of enigmatic forms that could represent experiments in multicellular construction independent of the metazoans, being derived from other protistan groups. Restoring the supposed vendobiontans to the metazoans leaves unanswered the problem of the peculiar taphonomic circumstances that permitted widespread soft-part preservation in environments that in the Phanerozoic are seldom sites of Fossil-Conservation-Lagerstätten. This problem remains unsolved and understudied. However, proposals such as the role of bacterial sealing (Seilacher *et al.* 1985), possible absence of degrading enzymes such as collagenases (Runnegar 1992), absence of scavengers, and limited bioturbation are all possible. Yet another proposal could be that while mobile infaunal worms, only known from trace fossils (e.g. Glaessner 1969; Fedonkin 1981), required a thin flexible cuticle, sessile forms developed a conspicuously thick and taphonomically resistant cuticle, perhaps as a response to elevated levels of oxygen (see Derry *et al.* 1992).

*Acknowledgements.* I thank F. J. Collier (National Museum of Natural History, Smithsonian Institution, Washington D.C.) for making available specimens. In Nanjing, Chen Junyuan and Sun Weiguang generously gave access to specimens of *Rotadiscus grandis*, while E. Landing (Albany, New York) facilitated examination of the paropsonemids and possible actinian. Examination of possible specimens of *Dickinsonia* and a ?cephalochordate from California was facilitated by J. Firby, J. W. Durham and J. Lipps (Berkeley, California). The visit to China was under the auspices of a Royal Society–Academia Sinica Exchange Scheme, while work in the Smithsonian has been assisted by grants from the Royal Society and St John's College, Cambridge. Comments and assistance by R. J. F. Jenkins, J. G. Gehling, P. Cornelius and an anonymous referee are all appreciated. B. K. Harvey photographed a number of specimens, H. Alberti assisted with drafting and S. J. Last typed numerous versions of the manuscript. This is Cambridge Earth Sciences Publication 2528.

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Typescript received 26 June 1992

Revised typescript received 14 September 1992